

1 *Full paper submitted to MFR for consideration for ITRS special issue*

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3 Climate-driven shifts in species' distributions may exacerbate the impacts of  
4 storm disturbances on northeast Atlantic kelp forests

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1 **Abstract**

2 Physical disturbance through wave action is a major determinant of kelp forest structure. The  
3 North Atlantic storm season of 2013-2014 was unusually severe; the south coast of the UK  
4 was subjected to 6 of the 12 most intense storms recorded in the past 5 years. Inshore  
5 significant wave heights and periods exceeded 7 m and 13 s, respectively, with 2 storms  
6 classified as ‘1-in-30 year’ events. We examined the impacts of the storm season on kelp  
7 canopies at 3 study sites. Monospecific canopies comprising *Laminaria hyperborea* were  
8 unaffected by storm disturbance. However, at one study site a mixed canopy comprising  
9 *Laminaria ochroleuca*, *Saccharina latissima* and *L. hyperborea* was significantly altered by  
10 the storms, due to decreased abundances of the former two species. Quantification of freshly  
11 severed stipes suggested that the ‘warm water’ kelp *L. ochroleuca* was more susceptible to  
12 storm damage than *L. hyperborea*. Overall, kelp canopies were highly resistant to storm  
13 disturbance because of the low vulnerability of *L. hyperborea* to intense wave action.  
14 However, if climate-driven shifts in kelp species distributions result in more mixed canopies,  
15 as predicted, then resistance to storm disturbance may be eroded.

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18 **Additional keywords:** benthic communities, disturbance ecology Laminariales, macroalgae,  
19 physical disturbance, subtidal reefs

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21 **Running head:** storm impacts on northeast Atlantic kelp forests

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## 1 **Introduction**

2 Kelp forests dominate shallow-water rocky habitats across much of the world's temperate  
3 coastline (Steneck *et al.* 2002). As foundation species, they support high levels of primary  
4 productivity, magnified secondary productivity, and provide habitat for a highly diverse  
5 associated flora and fauna (Mann 2000; Steneck *et al.* 2002; Smale *et al.* 2013). Canopy-  
6 forming kelps influence the immediate environment by altering light availability (Wernberg  
7 *et al.* 2005), water flow (Rosman *et al.* 2007), sedimentation rates (Eckman *et al.* 1989) and  
8 physical disturbance (Connell 2003; Smale *et al.* 2011). Kelps exhibit very high levels of  
9 primary productivity and play an important role in the capture and export of energy in coastal  
10 marine food webs (Dayton 1985; Krumhansl and Scheibling 2012). In coastal waters, the  
11 primary productivity of kelp forests may be comparable to that of the phytoplankton (Leclerc  
12 *et al.* 2013; Smale *et al.* 2013).

13 The structure and extent of kelp forest habitat is influenced by a variety of physical variables,  
14 including temperature (Mabin *et al.* 2013; Wernberg *et al.* 2013), light availability (Kain  
15 1977; Luning 1979), nutrient levels (Kain 1989; Dayton *et al.* 1999) and wave disturbance  
16 (Dayton and Tegner 1984; Filbee-Dexter and Scheibling 2012). Additionally, ecological  
17 processes such as overgrazing (Hart and Scheibling 1988; Leinaas and Christie 1996),  
18 competition (Hawkins and Harkin 1985; Arkema *et al.* 2009) and facilitation (Arkema *et al.*  
19 2009; Bennett and Wernberg 2014) affect kelp forest structure and functioning. Human  
20 activities (e.g. overfishing, anthropogenic climate change and human-mediated spread of  
21 non-native species) can in turn influence the strength and direction of these ecological  
22 processes (Steneck *et al.* 2002; Russell *et al.* 2009; Johnson *et al.* 2011). As such, a range of  
23 concurrent, interacting processes operate at multiple spatial and temporal scales to exert  
24 control on kelp-dominated communities and ecosystems (Wernberg *et al.* 2011).

25 In coastal marine ecosystems, it has long been recognised that physical disturbance caused by  
26 wave action plays a key role in structuring benthic communities (Denny 1987; Gaylord  
27 1999). Exposure to wave action can have both sub-lethal and lethal effects on habitat-forming  
28 macroalgae and their associated species. For example, exposure to waves has been found to  
29 influence the morphology, size, age structure and biomass of kelp species (Sjotun and  
30 Fredriksen 1995; Pedersen *et al.* 2012; Bekkby *et al.* 2014), which in turn affects the  
31 composition and abundance of its associated assemblages (Norderhaug *et al.* 2014).  
32 Moreover, intense hydrodynamic forces generated during storms can cause high mortality of

1 habitat-forming kelp and associated species through damage and dislodgement (Cowen *et al.*  
2 1982; Krumhansl and Scheibling 2011; Filbee-Dexter and Scheibling 2012). Large waves  
3 typical of winter storms can dislodge entire kelp plants and lead to thinning or, in extreme  
4 cases, complete clearing of areas of kelp forests (e.g. *Ecklonia*, Thomsen *et al.* 2004;  
5 *Laminaria*, Saunders and Metaxas 2008; *Macrocystis*, Reed *et al.* 2011). Although occasional  
6 disturbances are thought to be vital in maintaining diversity and promoting turnover of  
7 species and nutrients (Smale *et al.* 2010; Krumhansl and Scheibling 2012), the increased  
8 frequency of high-intensity storms that is predicted for many regions may decrease kelp  
9 forest biodiversity and simplify food webs (Byrnes *et al.* 2011). The relative impact of storm  
10 disturbances will, however, vary between kelp species due to differences in morphology and  
11 phenology (Thomsen and Wernberg 2005; de Bettignies *et al.* 2014), and will also be affected  
12 by grazing damage and overgrowth by epibiota (Krumhansl *et al.* 2011). Understanding the  
13 susceptibility of habitat-forming species and entire kelp forests to intense storm disturbances  
14 is critical for predicting ecosystem structure and functioning in warmer, stormier seas.

15 Kelp forest habitat extends across  $>25^\circ$  of latitude in the northeast Atlantic, from Portugal to  
16 Norway and Iceland, providing critical ecosystem services along  $>30,000$  km of complex,  
17 convoluted coastline (Smale *et al.* 2013). However, kelp forests are currently subjected to  
18 multiple stressors in the region, including seawater warming, eutrophication and overgrazing  
19 (Smale *et al.* 2013), which are influencing the distribution of species and have the potential to  
20 alter entire kelp-dominated ecosystems. *Laminaria hyperborea* is the dominant species along  
21 most stretches of moderate to fully-exposed open coastline, where it often forms extensive  
22 mono-specific stands spanning depths of 1 to  $>30$  m. *L. hyperborea* is relatively long-lived  
23 (up to  $\sim 15$  years) and highly productive (Kain 1979), and can withstand the high-energy  
24 conditions characteristic of the open Atlantic coastline (Sjotun and Fredriksen 1995). Direct  
25 assessments of the susceptibility of *L. hyperborea* and other co-occurring habitat-forming  
26 kelp species to intense storm disturbances are, however, largely lacking. Understanding the  
27 resilience of coastal ecosystems to intense storms is of ever-increasing importance, given that  
28 storminess in the northeast Atlantic has probably increased in recent decades (Wolf and  
29 Woolf 2006) and is projected to increase further as a consequence of anthropogenic climate  
30 change (Wang *et al.* 2014).

31 Between November 2013 and February 2014, the coastline of northwest Europe was severely  
32 affected by an exceptional winter storm season (Slingo *et al.* 2014). Southern and western  
33 parts of the UK experienced widespread coastal damage and persistent flooding, as intensive

1 low pressure systems tracked across the Atlantic at unusually low latitudes (Slingo *et al.*  
2 2014). Record-breaking wind speeds, rainfall and wave heights were recorded (Bradbury and  
3 Mason 2014; Slingo *et al.* 2014) and the storms caused millions of pounds worth of damage  
4 to coastal infrastructure and millions more were lost in revenue (through fisheries and local  
5 commerce, for example). Based on observations of widespread coastal damage, significant  
6 changes in beach morphology and considerable deposition of kelp wrack on many shores  
7 (Fig. 1), we proposed and tested the hypothesis that the 2013-2014 winter storm season  
8 significantly impacted subtidal kelp forest structure, by causing high levels of dislodgment  
9 and mortality that led to decreased abundances of mature sporophytes.

## 10 **Materials and methods**

### 11 *Wave buoy data*

12 As part of a strategic coastal monitoring programme, continuous wave and weather data have  
13 been collected from >30 stations around the coast of England. Data are collated, stored and  
14 distributed by the Channel Coastal Observatory (CCO, National Oceanography Centre,  
15 Southampton). We examined wave data obtained from the Looe Bay monitoring station  
16 (50°20.319' N, 004°24.649' W, Fig. 1), which was deployed in June 2009. The buoy is  
17 moored at 10 m depth (below chart datum) approximately 3 km from shore. Wave parameters  
18 are obtained using a Datawell Directional WaveRider Mk III buoy and are recorded every 30  
19 minutes. We analysed the following wave parameters: significant wave height ( $H_s$ ), which is  
20 the average of the highest one-third of waves measured in the 30-minute logging event;  
21 maximum wave height ( $H_{max}$ ), which is the single highest wave height observed in the  
22 logging event; and wave period ( $T_z$ ), which is the average wave period for the logging event.  
23 Data were first quality checked before extracting and analysing the maximum value for each  
24 of the parameters for every day in the 5-year record.

### 25 *Impacts on kelp forest structure*

26 The structure of subtidal kelp forests was examined before and after the winter storm season  
27 of 2013/2014 at 3 study sites close to Plymouth, UK (Fig. 1). Sites were situated ~25 km  
28 eastwards of the Looe Bay wave buoy (Fig. 1), at a similar depth and distance from the  
29 coastline as the monitoring station (Looe Bay was the nearest wave buoy that recorded near-  
30 continuous data throughout the storm season). All sites were characterised by extensive  
31 shallow subtidal reefs, compromising both high-relief features (i.e. gullies, pinnacles) and

1 low-relief platforms, interspersed with occasional patches of sand and cobbles. The sites  
2 differed slightly in depth; Stoke Point surveys were conducted at 3 m (below chart datum),  
3 Northwest Mewstone surveys at 5 m depth and South Mewstone at 9 m depth. The South  
4 Mewstone site was fully exposed to predominant south-westerly winds and waves, Stoke  
5 Point was slightly more sheltered due to its southeast-facing aspect, and the Northwest  
6 Mewstone site was most sheltered due to its aspect and the protection offered by nearby  
7 submerged reefs and ridges (Fig. 1). Previous surveys have indicated that all sites are  
8 dominated by *Laminaria hyperborea*, while the sugar kelp *Saccharina latissima* is common  
9 at Stoke Point and Northwest Mewstone and the southerly-distributed kelp *Laminaria*  
10 *ochroleuca* is common at Northwest Mewstone (Smale *et al.* 2014). The study region is  
11 influenced by a mean spring tidal range of 4.7 m and an annual range in sea surface  
12 temperature of ~9.1 to 16.4°C (based on monthly means; see Smyth *et al.* 2010). The region  
13 experiences high seasonality in light levels, nutrient availability, wave climate and primary  
14 productivity (Woolf *et al.* 2002; Southward *et al.* 2004; Smyth *et al.* 2010).

15 Kelp forest structure was quantified using standard survey techniques by SCUBA diving. At  
16 each site (Fig. 1) we completed multiple 10 m-long belt transects ( $n = 4$  or  $5$ ), recording the  
17 abundances of all kelp species within 0.5 m of each side of the transect tape (total sampling  
18 area per transect =  $10 \text{ m}^2$ ). Only mature canopy-forming sporophytes (stipe length  $>40$  cm,  
19 indicative of plants  $>2$  years old, see Kain 1963) were recorded because (i) juvenile  
20 *Laminaria* spp. can be difficult to distinguish from one another, and (ii) to avoid confounding  
21 the observations with seasonal differences in recruit densities. Transects were haphazardly  
22 positioned to target rocky reef habitat (as opposed to sand patches), and were positioned at  
23 least 10 m apart. Surveys were initially completed in summer 2013 (June-Sept;  $n = 4$   
24 transects per site) and were repeated in May 2014 ( $n = 5$  transects per site). The sampling  
25 area was marked by GPS in 2013 to ensure that the same reef was resurveyed (i.e. a fixed site  
26 with random transects sampling design). It was evident in the 2014 surveys that the majority  
27 of recently damaged *L. hyperborea* and *L. ochroleuca* plants had been severed at the stipe  
28 (rather than immediately above the holdfast); most frequently towards the top of the stipe,  
29 proximal to the former stipe-frond junction. Previous research on stipitate kelp species has  
30 also identified the stipe, rather than the holdfast or substratum, as a weak-point susceptible to  
31 breakage (Gaylord and Denny 1997; Duggins *et al.* 2001). As it is possible to distinguish  
32 these *Laminaria* species by stipe morphology, the number of freshly damaged individuals of  
33 each species was recorded for each transect conducted in 2014. This method did not estimate

1 'absolute' mortality rates through dislodgement, as it was not possible to quantify individuals  
2 that were lost following breakage at the holdfast. Rather, it was a comparative approach to  
3 compare the frequency of damaged stipes between the 2 *Laminaria* species.

4 Differences in the abundance of each kelp species between sites and years were examined  
5 with permutational ANOVA, using the PERMANOVA add-on for Primer v6.0 software  
6 (Anderson 2001; Clarke and Warwick 2001). We used a 2 factor design (site as random, year,  
7 as fixed) and analysed the abundance of each kelp species separately. In all cases,  
8 permutations were based on a similarity matrix constructed from Euclidean distances  
9 between untransformed data. Permutations (4999) were conducted under a reduced model  
10 and significance was accepted at  $P < 0.05$ . All mean values are presented  $\pm$  standard error  
11 (SE).

## 12 **Results**

### 13 *Wave buoy data*

14 Maximum significant wave height ( $H_s$ ), maximum recorded wave height ( $H_{max}$ ) and  
15 maximum mean wave period ( $T_z$ ) in winter 2013-2014 were 46%, 22% and 16% greater than  
16 the maximum recorded during the previous 4 years, respectively (Fig. 2). The highest-  
17 magnitude event on record occurred in mid-February 2014, when maximum  $H_s$  reached 7.32  
18 m, maximum  $H_{max}$  reached 11.2 m and maximum  $T_z$  exceeded 13 s (Fig. 2, Fig. 3). The  
19 frequency of high-magnitude wave disturbances was also high in the 2013-2014 season, as  $H_s$   
20 exceeded 5 m during 3 events (Fig. 3, Table 1). In comparison,  $H_s$  exceeded 5 m on a single  
21 occasion in the previous 4 storm seasons (in November 2009, Table 1). Indeed, a ranking of  
22 the 12 most extreme storm events in the 5-year record (as defined by  $H_s$ ) indicated that 6  
23 occurred in the 2013-2014 season (Table 1). It should be noted that these values relate to an  
24 inshore wave buoy and that wave heights of  $>20$  m and periods of  $>20$  s were recorded by  
25 offshore wave buoys (e.g. the Brittany wave buoy, data provided by the UK Met Office).  
26 Based on typical values of wave height and period recorded during the storm events (i.e.  $H_s$   
27 = 6 m,  $T_z = 10$  s) and water depth at the study sites ( $\sim 7$  m), benthic organisms would have  
28 been subjected to water velocities  $>4$  m s<sup>-1</sup> (Denny and Gaylord 2002), assuming that waves  
29 remained unbroken (the largest recorded waves would likely have broken at these depths,  
30 resulting in far greater realised water velocities, see Denny and Gaylord 2002).

### 31 *Impacts on kelp forest structure*

1 Surveys indicated that the abundance of mature, canopy-forming *Laminaria hyperborea*  
2 sporophytes was very similar in 2013 and 2014, suggesting that the winter storm season had  
3 minimal impact on subtidal populations (Fig. 4). *L. hyperborea* densities varied significantly  
4 between study sites but did not differ between years, either as an interacting or main factor  
5 (Table 2). *Laminaria ochroleuca* and *Saccharina latissima* were not recorded at either Stoke  
6 Point or South Mewstone but were common at Northwest Mewstone (Fig. 4), which is  
7 relatively more sheltered from wave action. At Northwest Mewstone, the average abundance  
8 of *L. ochroleuca* had declined by 30.7% in 2014 compared with 2013 (Fig. 4). Similarly, *S.*  
9 *latissima* was common in 2013 but was not recorded in transects in 2014 (Fig. 4), although a  
10 few individuals were observed at the study site. For both species, a significant site x year  
11 interaction was detected (Table 2), with abundances at Northwest Mewstone being  
12 significantly lower in 2014 compared with 2013 (Table 2, Fig. 4).

13 Observations of recently severed *L. hyperborea* stipes varied between sites, with the lowest  
14 density recorded at the most wave-sheltered site, Northwest Mewstone (Fig. 5). Recently  
15 damaged *L. hyperborea* individuals represented  $2.3 \pm 0.4$  (Northwest Mewstone) to  $6.9 \pm$   
16  $1.0\%$  (South Mewstone) of the adult population (Fig. 5). At Northwest Mewstone, the density  
17 of recently severed *L. ochroleuca* stipes was on average >3 times greater than that of *L.*  
18 *hyperborea* (Fig. 5; in total 3.4% of all recently damaged stipes could not be unambiguously  
19 identified to species). When expressed as a proportion of the local adult population, severed  
20 *L. ochroleuca* stipes were on average 8.7 times more prevalent than damaged *L. hyperborea*  
21 individuals (Fig 5). Statistically significant differences in the absolute and relative densities  
22 of recently severed stipes between *L. hyperborea* and *L. ochroleuca* were detected (one-way  
23 permutational ANOVA between species at Northwest Mewstone; absolute densities:  $F_{1,8}$   
24  $=10.14$ ,  $P = 0.043$ ; relative densities:  $F_{1,8} = 27.78$ ,  $P = 0.01$ ).

## 25 Discussion

26 The 2013-2014 winter storm season was the most severe in recent years, with respect to wave  
27 climate. The 5-year, high-resolution wave climate dataset examined here indicated that wave  
28 heights and periods were exceptionally high during 2 events in particular. In total, 6 discrete,  
29 high-magnitude wave disturbance events occurred during the season. Bradbury and Mason  
30 (2014) examined wave data collected from the entire southern coastline of the UK and  
31 concluded that 50% of all storms recorded in the last 10 years occurred in the 2013-2014  
32 season. They also defined 2 of the Looe Bay storms as '1 in 30 year events', although return



1 period statistics should be interpreted with caution when derived from relatively short-term  
2 datasets (Bradbury and Mason 2014). Even so, it remains unequivocal that the 2013-2014  
3 storm season was anomalously severe.

4 Wave heights and periods in excess of 6 m and 12 s would have generated substantial benthic  
5 shear stress at the depth range (3-9 m) of the study sites (Cacchione and Drake 1982; Madsen  
6 *et al.* 1993). However, contrary to our predictions, we did not record a reduction in the  
7 density of mature canopy-forming *Laminaria hyperborea* sporophytes at any of our study  
8 sites. This suggested that mortality through wave-induced dislodgement during the storms  
9 was low, and that the canopies are highly resistant to wave disturbance. Although there was  
10 some evidence of wave-induced mortality, densities of recently severed/damaged *L.*  
11 *hyperborea* stipes were low and the apparent rate of dislodgement would constitute a  
12 ‘thinning’ of the forest rather than widespread ‘clearing’. It is possible that the anomalous  
13 storm season had sub-lethal effects on *Laminaria hyperborea*, such as reduced rates of  
14 growth or zoospore production/settlement (which both peak in winter/spring, see Kain 1979),  
15 which could propagate through to the population-level over time. However, as there are no  
16 baseline data available for these subtidal populations it is not possible to examine sub-lethal  
17 effects.

18 The observed resistance of sub-surface *L. hyperborea* populations to the storm season is in  
19 stark contrast to populations of the giant kelp *Macrocystis pyrifera*, which is far more  
20 susceptible to wave disturbance (Cowen *et al.* 1982; Dayton and Tegner 1984; Ebeling *et al.*  
21 1985; Reed *et al.* 2011). High mortality rates and subsequent shifts in assemblage structure  
22 have been observed in *Macrocystis* forests following extreme storm events and, as such, the  
23 increase in storm frequency predicted for many regions is likely to alter ecosystem structure  
24 and functioning (Byrnes *et al.* 2011). Similarly, high rates of kelp loss (~45% reduction in  
25 cover) have been recorded in the Eastern Atlantic following severe hurricane activity, in  
26 habitats dominated by the prostrate kelps *Laminaria digitata* and *Saccharina latissima*  
27 (Filbee-Dexter and Scheibling 2012). However, de Bettignies *et al.* (2013b) found that year-  
28 round dislodgement rates were low for the kelp *Ecklonia radiata* in Western Australia,  
29 despite the fact that significant wave heights in excess of 5 m regularly impact the coastline  
30 (Lemm *et al.* 1999). It is clear that mortality rates associated with intense wave disturbance  
31 vary considerably between different canopy-forming kelp species, most likely due to  
32 differences in morphology and life history (Thomsen and Wernberg 2005; Krumhansl and  
33 Scheibling 2012). It is interesting to note that most of the recently damaged kelp individuals

1 were severed towards the top of the stipe, rather than at or just above the holdfast (as implied  
2 by few observations of partial or intact remnant holdfasts). This is seemingly in contrast with  
3 *Ecklonia raditata*, which tends to break at the holdfast-substratum interface (Thomsen *et al.*  
4 2004), and may be explained by (i) the longer, less flexible stipe morphology of *Laminaria*  
5 compared with *Ecklonia* (Thomsen and Wernberg 2005); (ii) possible impacts of grazing  
6 damage by gastropods, principally *Patella pellucida* (blue-rayed limpet), which may weaken  
7 the stipe and the basal blade tissue on *Laminaria* individuals (see Krumhansl *et al.* 2011 for  
8 impacts of gastropod grazing) or (iii) weaker holdfast-substratum attachment of *Ecklonia* on  
9 ‘softer’ limestone reefs (Azzarello *et al.* 2014) compared with *Laminaria* on ‘harder’  
10 slate/sandstone reefs (this study). Given that kelp populations were subjected to water  
11 velocities  $>4 \text{ m s}^{-1}$ , which is comparable to break velocities thought to dislodge other kelp  
12 species (i.e. *Ecklonia radiata*, see Thomsen *et al.* 2004), further work is needed to understand  
13 factors influencing dislodgement rates in *Laminaria* populations in the northeast Atlantic.

14 Our most sheltered study site, Northwest Mewstone, is characterised by a mixed stand of  
15 *Laminaria hyperborea*, *Laminaria ochroleuca* and *Saccharina latissima* (Smale *et al.*  
16 2014). Here, we recorded significant declines in the abundances of mature sporophytes of  
17 both *L. ochroleuca* and *S. latissima* following the 2013-2014 storm season. *S. latissima* is  
18 generally found in partially to fully sheltered habitats (Bekkby and Moy 2011; Burrows  
19 2012), where it can dominate benthic communities and form extensive low-lying canopies  
20 (Moy and Christie 2012). In more exposed habitats, it is generally found on the margins of  
21 extensive *Laminaria* forests, often attached to semi-stable substrata (i.e. cobbles) rather than  
22 bedrock (Smale pers. ob.). *S. latissima* exhibits high morphological plasticity in response to  
23 water flow (i.e. individuals in wave exposed conditions are well streamlined to reduce drag),  
24 so that the thalli of wave-adapted morphotypes can withstand wave heights in excess of 6 m  
25 (Buck and Buchholz 2005). However, the propensity of *S. latissima* to attach to semi-stable  
26 substrata means that, in large storms, the cobbles and boulders themselves are frequently  
27 displaced, thereby removing intact kelp individuals from the population (see Scheibling *et al.*  
28 2009 for study on congener *Saccharina longicuris*). We suggest that intense wave action  
29 caused displacement of cobbles and small boulders, which were attachment substrata for *S.*  
30 *latissima* individuals, resulting in a reduced abundance of *S. latissima* at the study site.

31 We also observed a significant decline in the abundance of *Laminaria ochroleuca*; a more  
32 southerly-distributed species that ranges from Morocco to southern England. *L. ochroleuca*  
33 has proliferated at its poleward range edge in recent years, perhaps in response to recent

1 seawater warming (Smale *et al.* 2014), and has seemingly declined in abundance at its  
2 equatorward range edge (Tuya *et al.* 2012). Having first been recorded in Plymouth in 1948  
3 (Parke 1948), it now persists along large stretches of fully to partially sheltered coastline in  
4 southern England, where it may co-exist with *L. hyperborea* to form mixed canopies (Smale  
5 *et al.* 2014). As a proportion of the local population, the number of recently damaged *L.*  
6 *ochroleuca* stipes far exceeded that of *L. hyperborea*, perhaps indicating its greater  
7 vulnerability to storm disturbance. Moreover, the observed decrease in *L. ochroleuca*  
8 abundance at northwest Mewstone and its affinity to sheltered or moderately exposed sites  
9 (Sheppard *et al.* 1978; Smale *et al.* 2014) would suggest it is less tolerant of wave action than  
10 *L. hyperborea*. However, the 2 species are very similar in structure and morphology (Smale  
11 *et al.* 2014) and the specific mechanisms underlying differences in susceptibility to wave  
12 action are currently unknown. Further work should examine factors of known importance,  
13 such as slight differences in stipe morphology, flexibility or physicochemical composition  
14 (Gaylord and Denny 1997), differences in drag related to blade size, morphology and  
15 phenology (de Bettignies *et al.* 2013a; de Bettignies *et al.* 2014), or differences in external  
16 factors such as grazing damage or epibiont loading (Krumhansl *et al.* 2011). Previous  
17 research has shown that encrusting epifauna such as bryozoans can weaken kelp lamina  
18 (Krumhansl *et al.* 2011), while high epiphyte loading should intuitively increase the size (and  
19 therefore drag) of kelps and increase their susceptibility to dislodgement during storms  
20 (Thomsen and Wernberg 2005). Interestingly, *L. hyperborea* is characterised by high epibiont  
21 loading on both the stipe and the blade, whereas *L. ochroleuca* is largely devoid of epibionts  
22 (Smale *et al.* 2014), yet our observations indicated that the latter species is seemingly more  
23 vulnerable to storm disturbance, suggesting that other aforementioned factors are more  
24 influential.

25 It is important to note that this opportunistic study examined mixed kelp canopies at only a  
26 single study site, and therefore the generality of the observed patterns remains unknown. The  
27 authors did, however, also observe a high occurrence of recently severed *L. ochroleuca* stipes  
28 (relative to *L. hyperborea*) within a mixed kelp canopy at an additional site within Plymouth  
29 Sound (Ramscliff Point, 4 km north of the Mewstone), following the storm season, although  
30 transect data were not collected. As such, the current study is limited by the lack of  
31 replication at the site level, and further surveys and experimental work is required to  
32 elucidate the generality of the findings.

1 Intuitively, the storm season had some impact on local kelp populations, as evidenced by  
2 anomalously high deposition of kelp-derived wrack on beaches and shorelines. Our results  
3 suggest that although some ‘thinning’ of subtidal populations would have contributed to the  
4 detritus, the majority of wrack material, which principally comprised *L. hyperborea* and *L.*  
5 *digitata* (Smale, pers ob), was probably derived from very shallow populations, (i.e. intertidal  
6 through to a depth of a few m). Indeed, anecdotal reports suggest that macroalgal populations  
7 on intertidal reefs were notably affected by the winter storms (Prof Juliet Brodie, pers comm),  
8 although no quantitative examinations are available as yet.

9 Overall, subtidal kelp forests were very resistant to the severe wave disturbance experienced  
10 during the 2013-2014 storm season. This was principally because canopies were dominated  
11 by *Laminaria hyperborea*, which is extremely tolerant of intense wave action and exhibited  
12 low rates of dislodgement and mortality (as indirectly assumed from stable abundances of  
13 mature sporophytes). However, we did record significant loss of kelp plants at our  
14 moderately exposed site, which supported a mixed kelp canopy. In the UK, the relative  
15 abundances of *L. ochroleuca* and the canopy-forming brown alga *Saccorhiza polyschides*  
16 (order Tilopteridales) are predicted to increase in response to oceanic climate change  
17 (Birchenough and Bremmer 2010; Smale *et al.* 2013), while the invasive kelp *Undaria*  
18 *pinnatifida* is now well established on natural substrata along the south coast (Heiser *et al.*  
19 2014). Recent studies in the region have confirmed the proliferation of both *L. ochroleuca*  
20 and *Undaria pinnatifida* in sheltered to moderately exposed habitats (Heiser *et al.* 2014;  
21 Smale *et al.* 2014), resulting in more mixed kelp canopies. Previous work has shown that  
22 these aforementioned species are likely to be more vulnerable to wave action than *L.*  
23 *hyperborea* (Southward and Orton 1954; Frid and Kitching 1988; Heiser *et al.* 2014), so that  
24 the predicted shift towards more mixed canopies may erode their resistance to severe wave  
25 action, particularly in moderately exposed habitats. Understanding how changes in the  
26 relative abundance of kelp species will affect the ecological functioning of kelp forests,  
27 including their resilience to physical disturbance, is critical for safeguarding the ecosystem  
28 services that they provide. In the immediate term, however, our study suggests that the  
29 continued persistence of *L. hyperborea* as the assemblage dominant (the current situation  
30 along most of the exposed coastline of northwest Europe), should instil kelp canopies with a  
31 high level of resistance to intense storm disturbance.

32

## 1 **Acknowledgements**

2 DS is supported by an Independent Research Fellowship awarded by the Natural  
3 Environment Research Council of the UK (NE/K008439/1). We thank Chris Johnson and  
4 Terri Souster for assistance with fieldwork and the University of Plymouth Marine Centre for  
5 overseeing diving operations. We acknowledge the Coastal Channel Observatory (University  
6 of Southampton/National Oceanography Centre) for data management of the Regional  
7 Coastal Monitoring Programmes and the Environment Agency for maintenance of the Looe  
8 Bay wave buoy.

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2

1 **Figure Legends**

2 **Fig. 1.** (a) High deposition of kelp-derived wrack at Wembury Beach, UK, following storm  
3 events in February 2014. (b) Map of the wider study area (boxed area) in the southwest UK  
4 and (c) map to show positions of the wave buoy and study sites.

5 **Fig. 2.** Daily maximum significant wave height (a), maximum wave height (b) and wave  
6 period (c) recorded by the Looe Bay wave buoy, from June 2009 to May 2014.

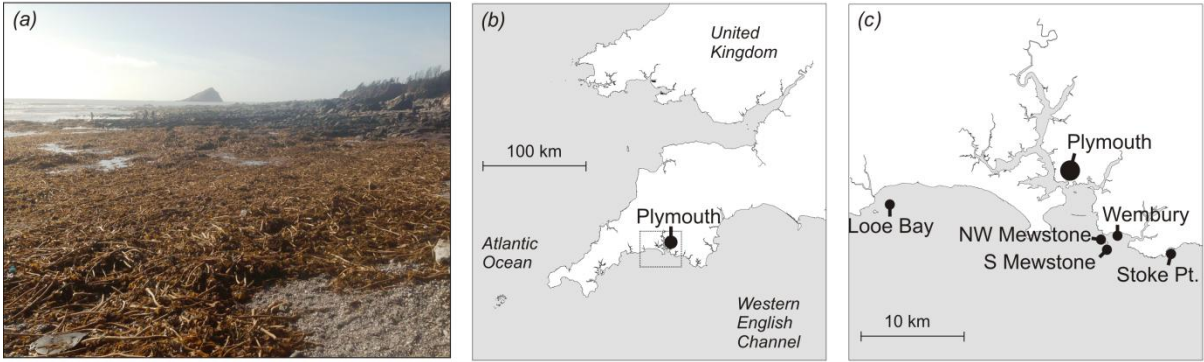
7 **Fig. 3.** Wave climate at Looe Bay during the 2013-2014 storm season.

8 **Fig. 4.** Mean abundance ( $\pm$  SE) of mature kelp sporophytes at each of the study sites ( $n = 4$  or  
9 5 transects per year). Black bars indicate abundances in 2013, grey bars represent 2014. Data  
10 are shown for (a) *Laminaria hyperborea*, (b) *Laminaria ochroleuca* and (c) *Saccharina*  
11 *latissima*. A significant difference between years is indicated by an asterisk (\*).

12 **Fig. 5.** (a) The mean density ( $\pm$  SE) of recently severed stipes recorded at each site for both  
13 *Laminaria hyperborea* (black bars) and *Laminaria ochroleuca* (light grey bars; *L. ochroleuca*  
14 not present at Stoke Point and South Mewstone, see Fig. 4) in May 2014, following the storm  
15 season, and (b) the density of damaged stipes as a proportion of the mature sporophyte  
16 population for each transect for both *L. hyperborea* and *L. ochroleuca*.



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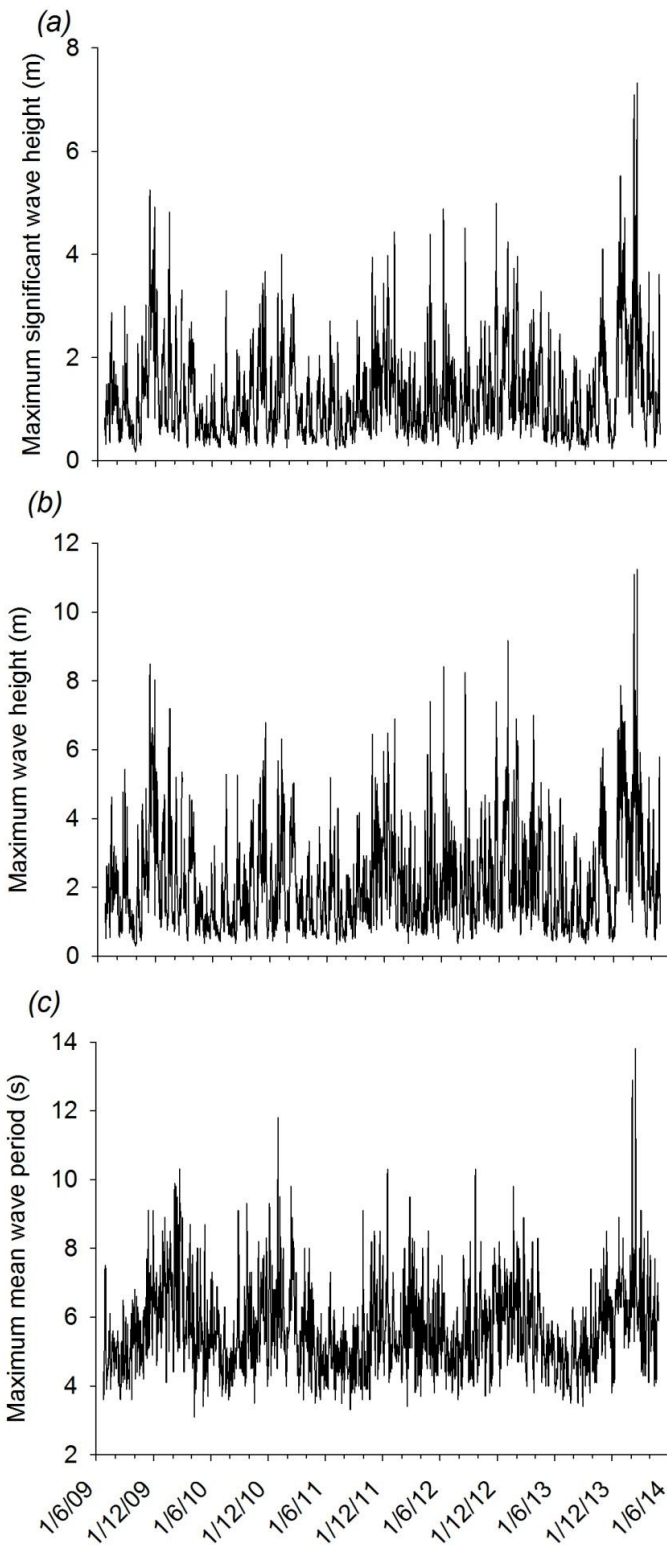


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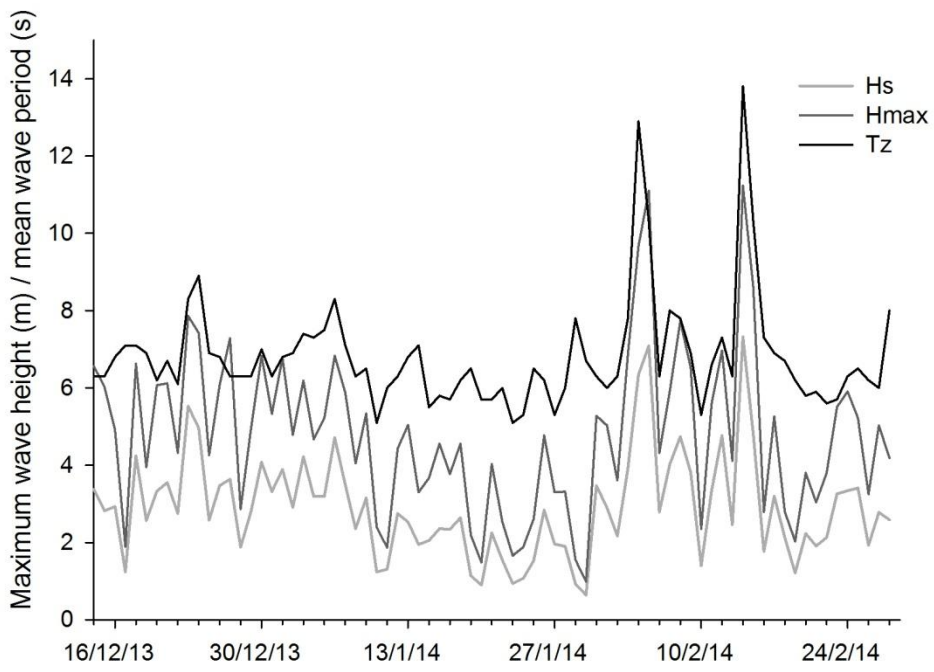
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5 Fig. 1.



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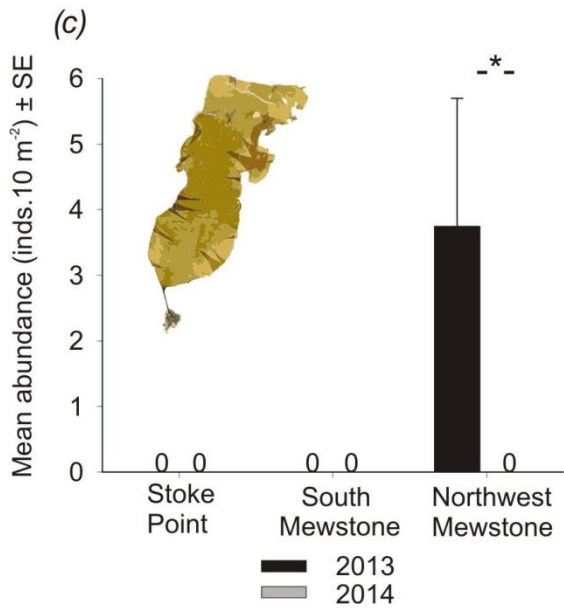
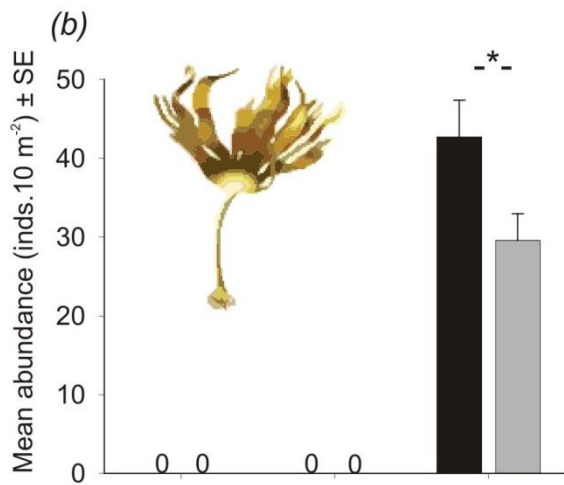
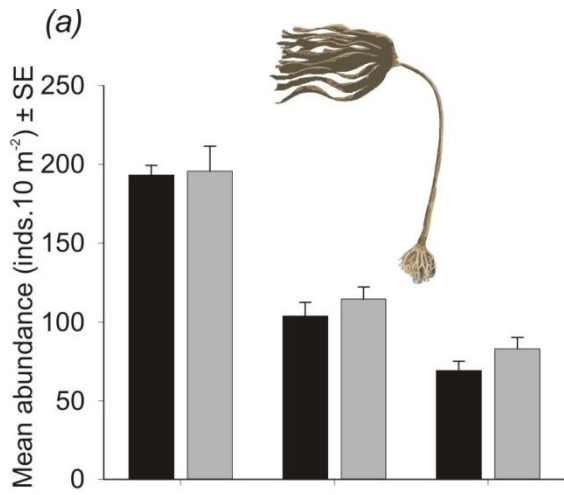
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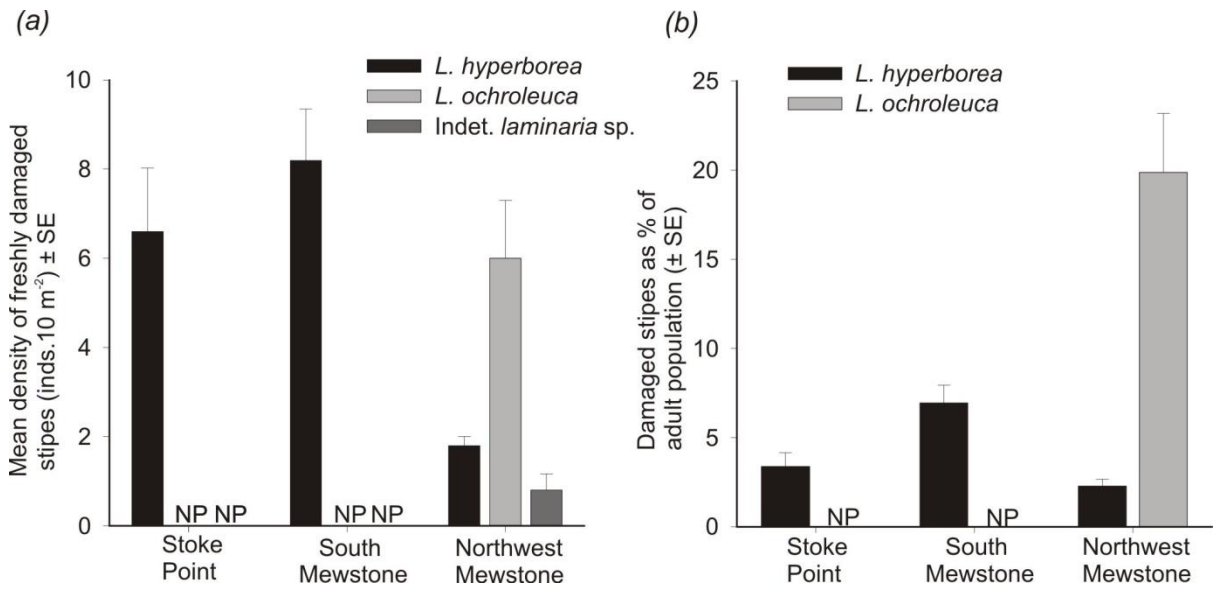
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1 Table 1. Rank of the 12 most severe storm events (as determined by significant wave height)  
2 recorded in Looe Bay from June 2009 to May 2014.

3	<b>Rank</b>	<b>Date</b>	<b>Max H<sub>s</sub></b>	<b>2013/2014?</b>
4	1	14/02/2014	7.32	y
5	2	05/02/2014	7.09	y
6	3	23/12/2013	5.53	y
7	4	14/11/2009	5.14	n
8	5	22/11/2012	4.99	n
9	6	29/11/2009	4.92	n
10	7	07/06/2012	4.88	n
11	8	16/01/2010	4.82	n
12	9	12/02/2014	4.77	y
13	10	08/02/2014	4.74	y
14	11	06/01/2014	4.71	y
15	12	15/08/2012	4.51	n

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17

1 Table 2. PERMANOVA tests to examine differences between years and sites in the  
 2 abundance of (a) *Laminaria hyperborea*, (b) *Laminaria ochroleuca* and (c) *Saccharina*  
 3 *latissima*. Where a significant interaction was detected, post-hoc pairwise tests within each  
 4 level of ‘site’ were conducted to examine differences between years (Northwest Mewstone  
 5 being the only relevant site for *L. ochroleuca* and *S. latissima*). Significant P values (at  
 6 <0.05) are indicated with an asterisk (\*).

7

8 (a) *Laminaria hyperborea*

9 Source	df	SS	MS	F	P
10 Site	2	66447	33223	75.63	0.001*
11 Year	1	538	538	7.36	0.122
12 Site x Year	2	146	73	0.16	0.858
13 Residual	21	9225	439		
14 Total	26	76488			

15

16 (b) *Laminaria ochroleuca*

17 Source	df	SS	MS	F	P(perm)
18 Site	2	7754	3877	148.60	0.001*
19 Year	1	128	128	1.00	0.410
20 Site x Year	2	256	128	4.90	0.016*
21 Residual	21	547	26.1		
22 Total	26	8470			

23

24 *Post-hoc* test for ‘Year’ within Northwest Mewstone level of ‘Site’:  $t = 3.02$ ,  $P = 0.033^*$

25

26

27 (c) *Saccharina latissima*

28

29 Source	df	SS	MS	F	P
30 Site	2	20.8	10.4	3.85	0.010*
31 Year	1	10.4	10.4	1.00	0.441
32 Site x Year	2	20.8	10.4	3.85	0.002*
33 Residual	21	56.7	2.7		
34 Total	26	104			

35

36 *Post-hoc* test for ‘Year’ within Northwest Mewstone level of ‘Site’:  $t = 2.23$ ,  $P = 0.014^*$

37