Wave exposure influences kelp morphological and biomechanical phenotypic plasticity

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ABSTRACT: Despite global and local declines in kelp ecosystems, luxuriant kelp beds persist at the Eastern Shore Islands (ESI) in Nova Scotia, Canada. Kelp beds in other regions of Nova Scotia were defoliated as the invasive bryozoan *Membranipora membranacea* and warming temperatures weakened kelp tissues and enhanced erosion and dislodgment. We propose that the high wave exposure at the ESI causes morphological and biomechanical phenotypic plasticity of kelp tissues. We compared differences in morphology and mechanical properties of the kelps *Laminaria digitata* and *Saccharina latissima* across 3 sites with different wave exposures, and differences in mechanical properties across blade lengths. Both species showed morphological plasticity; higher wave exposure resulted in longer and thicker stipes and thicker blades with increased branching. The mechanical properties of *L. digitata* showed increased breaking stress (strength) and strain (extensibility) with higher wave exposure, whereas *S. latissima* did not show mechanical plasticity with increasing exposure. For both species, blades were weaker but more extensible at the meristem and stronger but less extensible near the distal end of the blade. Larger and stronger kelp from high-exposure areas may promote the persistence of kelp beds in the ESI despite local stressors.

KEY WORDS: Kelp · Wave exposure · Stress · Strain · Mechanical properties · Morphological plasticity · Morphology · Temperature · Persistence

1. INTRODUCTION

Kelps are ecosystem engineers which modify their physical environment, creating habitats (forests or beds) for diverse marine communities (Smale et al. 2013). Kelp ecosystems are found throughout the polar and temperate oceans, covering 36% of the world's coastlines (Jayathilake & Costello 2021). Kelps provide many ecosystem services (reviewed by UNEP 2023), such as coastal protection (Jackson 1984), moderation of pH (Krause-Jensen et al. 2016), and cultural significance for many regions (Hynes et al. 2021). Additionally, a global annual average of US $500 billion from fisheries production, nutrient cycling, and carbon removal has been attributed to these ecosystems (Eger et al. 2023). Most recently, their contribution to blue carbon through sequestration into long-term storage by export to other ecosys-tems has been receiving increased attention (Filbee-Dexter & Wernberg 2020, Eger et al. 2023).

The response of kelp ecosystems to global change over the past 50 yr has been spatially inconsistent (Krumhansl et al. 2016). Declines in kelp abundance associated with warming temperatures (Smale 2020) have been recorded in several locations, including the northwest and northeast Atlantic (Eriksson et al. 2002, Davoult et al. 2011, Moy & Christie 2012, Filbee-Dexter et al. 2016, 2020), southern and western Australia (Connell et al. 2008, Wernberg et al. 2013), and Tasmania (Johnson et al. 2011). However, some regions, such as the Arctic (Filbee-Dexter et al. 2019), South Africa (Blamey et al. 2015), southwestern UK (Smale et al. 2015), western USA (Washington: Pfister et al. 2018; Oregon: Hamilton et al. 2020), and eastern Canada (Eastern Shore of Nova Scotia: Attridge et al. 2022), harbor persistent kelp ecosystems. Local drivers play a significant

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role in kelp response to global change (Krumhansl et al. 2016), and a mechanistic understanding of such drivers can support the effective management of these essential ecosystems (Ling et al. 2009).

Wave exposure is a driver that affects kelp morphology (Coppin et al. 2020), biomechanics (Thomsen et al. 2004, Millar et al. 2021), distribution (Gorman et al. 2013), abundance (Dayton et al. 1998, Krumhansl et al. 2024), diversity (Wernberg & Goldberg 2008), growth (Millar et al. 2020), and composition (Norderhaug et al. 2012). Kelps require strong and extensible tissues to withstand wave shear and stress while surviving the harsh hydrodynamic conditions of the subtidal zone (Denny & Gaylord 2002). Moving water damages algal material if the hydrodynamic stress (force per cross-sectional area) exceeds the strength (stress to break) of the blade (Koehl 1984, Johnson & Koehl 1994). Algal material viability in wave-swept environments can be enhanced by strengthening tissues (stress to break) to withstand more force, increasing extensibility (strain to break) to prevent plastic deformation, and by increasing the amount of material in the tissue (tissue thickness) resulting in a greater cross-sectional area over which to distribute hydrodynamic forces (Martone 2007). As a result, some kelp growing in wave-exposed environments have stronger, more extensible tissues (e.g. *Laminaria digitata*: Millar et al. 2021) or better-adapted morphologies, such as thicker blades and stipes to decrease dislodgment rates (e.g. *Ecklonia maxima* and *Laminaria pallida*: Coppin et al. 2020).

Along the southwestern shore (SWS) of Nova Scotia, Canada, in the northwest Atlantic, the combination of increasing temperature and the establishment of the invasive epibiotic bryozoan *Membranipora membranacea* have contributed to the defoliation of kelp beds (Filbee-Dexter et al. 2016). Tissue lesions inflicted by the encrustation of the bryozoan compromise the strength and extensibility of affected kelp (Krumhansl & Scheibling 2011), compounding the reduction in structural integrity at increased temperatures (Simonson et al. 2015). Damage and wounds to kelp tissue such as ones from *M. membranacea* increase susceptibility to breakage by lowering the tissue failure threshold (Mach 2009, Krumhansl et al. 2011, de Bettignies et al. 2012).

Unlike at the SWS, kelp beds persist ~150 km to the northeast at the Eastern Shore Islands (ESI), an archipelago with a complex coastline (Greenlaw et al. 2013) characterized by high wave exposure and cold temperatures (Sephton et al. 2017, Attridge et al. 2022). We hypothesize that the hydrodynamic forces in the ESI influence the phenotype of kelps to allow them to better withstand breakage. To better understand the breakage dynamics of the 2 numerically dominant kelps (*Laminaria digitata* and *Saccharina latissima*), using field-based observations, we (1) described kelp morphology (blade thickness, blade length, number of branches, stipe length, stipe diameter) and mechanical properties (breaking stress and strain) of kelp blades from 3 sites of different wave exposures (Low, LE; Intermediate, IE; and High, HE) and (2) measured variation in mechanical properties across different locations on kelp blades. The exposure gradient in our study is determined by a wind- and fetch-based index, which combines island distance from the mainland and the site's orientation towards either the sheltered mainland or the exposed open ocean. *In situ* temperature was measured at each site since it also affects kelp growth (Liesner et al. 2020) and structural integrity (Simonson et al. 2015). Lastly, we compared breaking stress and strain measurements from the ESI to data from the SWS (Splitnose Point; Simonson et al. 2015) where kelp have been defoliated.

2. MATERIALS AND METHODS

2.1. Study sites

We destructively sampled kelps to examine blade material properties and morphological features of *Laminaria digitata* and *Saccharina latissima* (Table 1, Fig. 1), and measured temperature at each of 3 sites of different wave exposure (Long Island, Tuffin Island, and Halibut Island: referred to as low exposure [LE], intermediate exposure [IE], and high exposure [HE], respectively) and between 6 and 9 m depth (Fig. 2). The ESI are formed by a linear coast, oriented northeast–southwest, consisting of >1000 islands with rocky substratum. Because of the orientation of the coastline, most islands are exposed to direct wave action from offshore. We estimated exposure using the relative exposure index (REI) as per Attridge et al. (2022) using 17 yr of data (2002–2019):

$$REI = \sum_{i=1}^{16} (V_i \times W_i \times F_i) \qquad (1)$$

where for 16 sections of 22.5° in the ith cardinal direction, V_i is wind speed (km h^{-1}), W_i is wind frequency, and F_i is wind fetch (Euclidean distance to the nearest land for each site, bounded to an upper limit of 2000 km). Pratt et al. (2022) measured bottom wave orbital velocity using accelerometers (u$_b$, 0.7 m s^{-1} accuracy) and confirmed the relative exposure rating of our sites based on the REI. REI does not take under-

Table 1. Measurements and associated sampling periods, wave exposure (or sampling site), species (*Laminaria digitata*, *Saccharina latissima*), and statistical analyses used in the study

| Measurement	Sampling time	Site	Species	Analysis
Blade length, blade thickness, stipe length, stipe diameter	August & November 2022	Low, Intermediate, High	*L. digitata* & *S. latissima*	Mixed effects models
Number of branches	August & November 2022	Low, Intermediate, High	*L. digitata*	Mixed effects models
Stress across wave exposure	July & August 2022	Low, Intermediate, High	*L. digitata* & *S. latissima*	Mixed effects models
Strain across wave exposure	July & August 2022	Low, Intermediate, High	*L. digitata* & *S. latissima*	Mixed beta regression
Stress along kelp blade	October 2022	The Moll	*L. digitata* & *S. latissima*	Mixed effects models
Strain along across kelp blade	October 2022	The Moll	*L. digitata* & *S. latissima*	Mixed beta regression
Stress difference between middle and outer digit	October 2022	The Moll	*L. digitata*	Paired *t*-test
Strain between middle and outer digit	October 2022	The Moll	*L. digitata*	Paired *t*-test
Stress difference in applied force	October 2022	The Moll	*L. digitata* & *S. latissima*	Paired *t*-test
Strain difference in applied force	October 2022	The Moll	*L. digitata* & *S. latissima*	Paired *t*-test
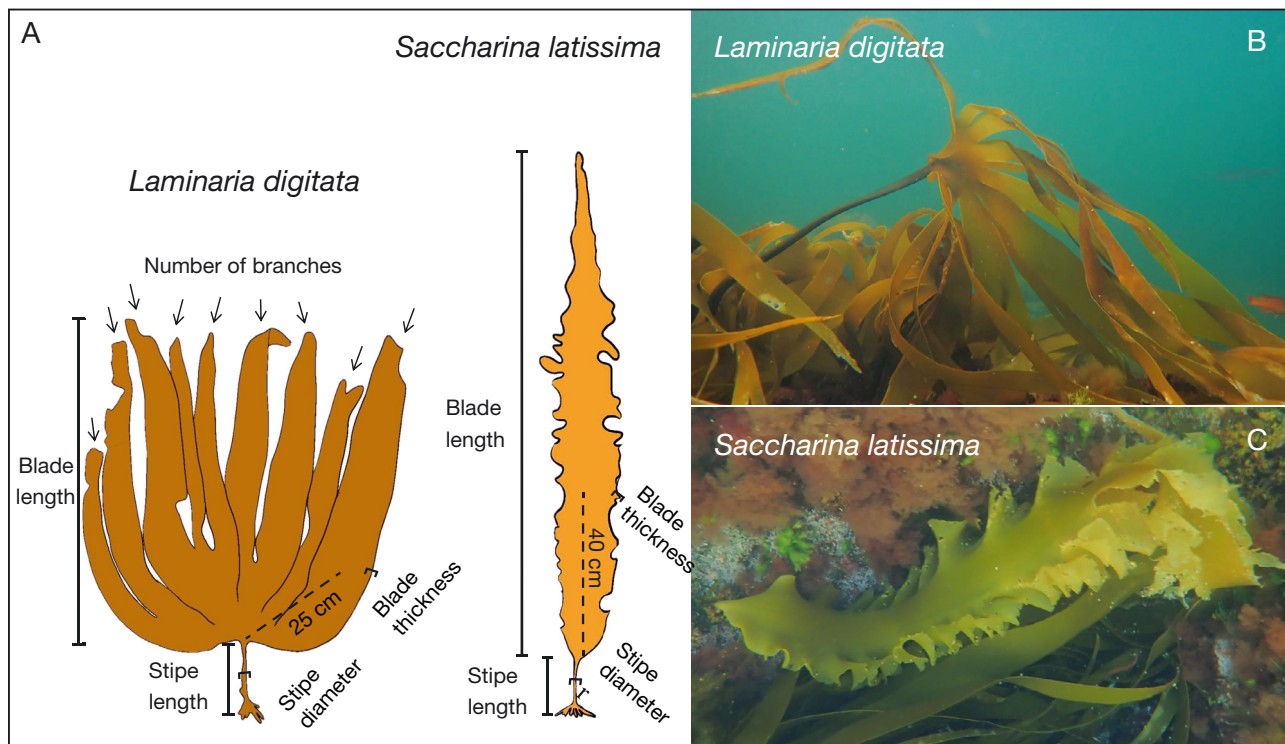
Fig. 1. (A) Conceptual methods used in morphological measurements of (B) *Laminaria digitata* and (C) *Saccharina latissima.* The blade thickness was measured in the middle of the blade at 25 and 40 cm from the stipe for *L. digitata* and *S. latissima*, respectively, represented by the dotted line
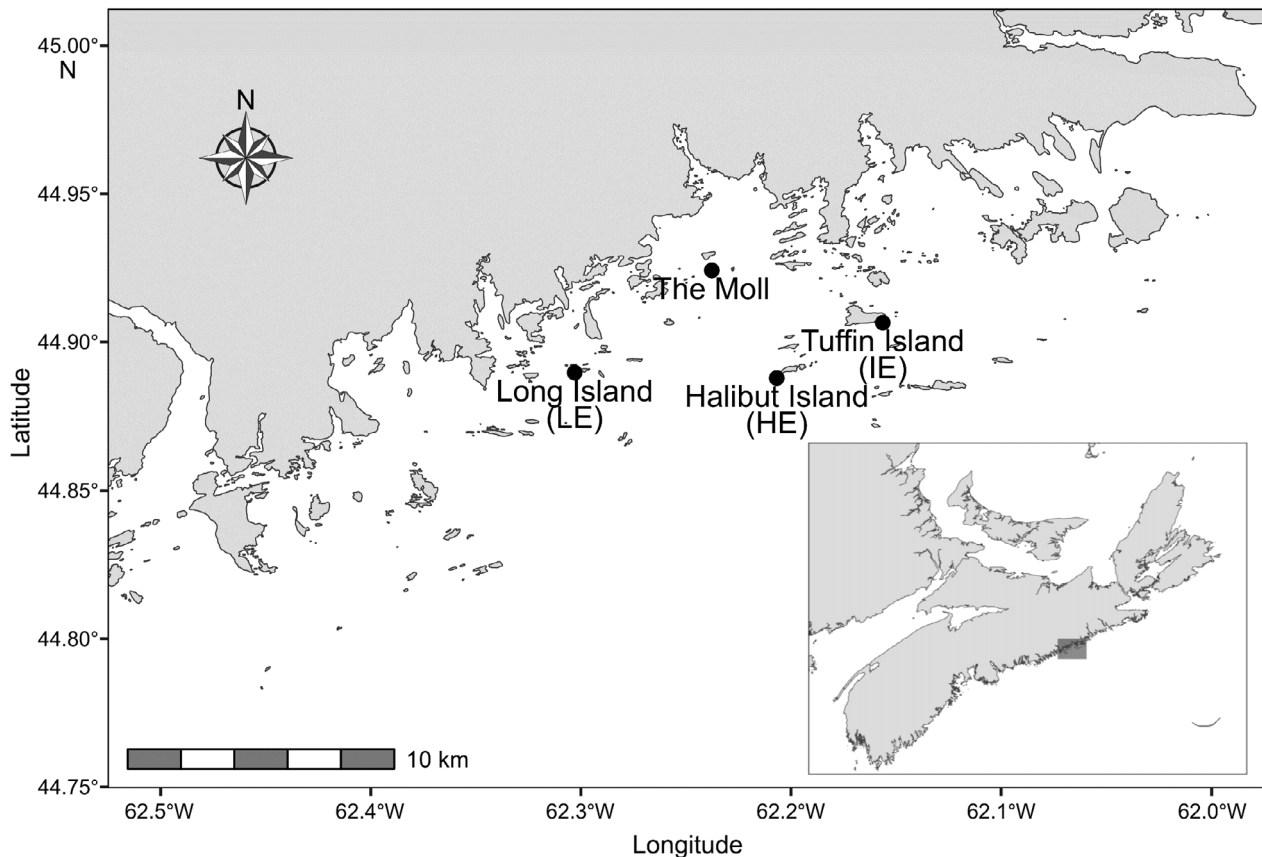
Fig. 2. Location of study sites in the Eastern Shore Islands (ESI) Area of Interest. Inset shows the location of the ESI (shaded square) within Nova Scotia, eastern Canada. The relative exposure index of each site is as follows: Long Island (low exposure, LE) = 7840, The Moll = 9340, Tuffin Island (intermediate exposure, IE) = 11 110, and Halibut Island (high exposure, HE) = 19 180. The Moll was not used to measure the effect of exposure on morphology and material properties, but instead is a secondary site where kelps were collected for data on breakage dynamics

water features into account but has been used in multiple studies in Nova Scotia to estimate exposure, allowing for direct comparisons (e.g. Krumhansl & Scheibling 2011, O'Brien et al. 2015, Attridge et al. 2022). To examine the material properties at different positions along kelp blades and test for different force rates applied on blades (see Section 2.3), we opportunistically collected kelp from an additional site (The Moll, REI = 9340). At each site, temperature was measured with Onset HOBO pendant temperature/light 64K data loggers (model: UA-002-64) set for temperature only and programmed to record every 10 min. Data loggers were deployed at LE and HE at depths of 6 and 9 m from October 2018 to November 2022, and at IE from August 2022 to November 2022. Daily temperature measurements were averaged across depths for each site. Logger data from 2 sites in the SWS were also included in the analyses for the duration of the study period (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m748p001_supp.pdf).

2.2. Kelp morphology

At each site, we haphazardly selected 10—11 large mature thalli of each species (*L. digitata* and *S. latissima*) with no apparent tissue damage or colonies of *Membranipora membranacea* and measured stipe length, stipe diameter, blade length, and blade thickness, along with the number of blade branches (digits) for *L. digitata*, in August and November 2022. Stipe length was measured from the holdfast to the stipe blade interface and blade length from the stipe blade interface to the distal end of the blade (longest branch for *L. digitata*) using a measuring tape (mm resolution) (Fig. 1). We measured stipe diameter with digital calipers (0.01 mm resolution) at the thickest section of the stipe. We measured blade thickness at the center of the blade for *L. digitata* at 25 cm from the stipe blade interface, and for *S. latissima* at 40 cm with digital calipers (0.01 mm resolution).

2.3. Mechanical properties

To examine the effect of wave exposure on blade strength and extensibility, we collected 9—15 mature thalli of each species (*L. digitata* and *S. latissima*) from each exposure between 6 and 9 m in July and August 2022. To test material properties, we used a pull-to-break tensile test (Fig. 3), as described by Simonson et al. (2015). Other studies on blade mechanical properties have used similar approaches but with Instron testing machines (Demes et al. 2011, Krumhansl et al. 2015, Burnett & Koehl 2019). Although less accurate, our set up could be used in the field to make the measurements on site, avoiding kelp tissue degradation during transport. Moreover, our methods were identical to those of Simonson et al. (2015), allowing for direct comparisons with data from the SWS. Tissue samples were collected from individuals with no signs of tissue damage, no *M. membranacea*, no sorus tissue, and at a constant position (25 cm from the stipe blade interface for *L. digitata* and 40 cm for *S. latissima*) using a bone-shaped 'cookie cutter'. These distances were chosen because they were used by Simonson et al. (2015). Before conducting tests, we measured the thickness of each tissue sample at 3 points along the center bar of the dog-bone shape using digital calipers (0.01 mm resolution).

To conduct the pull-to-break test, we used 2 clamps lined with 5 mm neoprene and medium-grit sandpaper to hold the sample. One clamp was attached to a force meter (Pasco PS-2104, range: ±50 N, resolution: 0.1 N, 25 Hz), which was fixed by attaching it to the table (Fig. 3). The second clamp was attached to a water receptacle and suspended while a constant force rate was applied to the sample by a constant flow of water into the suspended water receptacle. Due to logistical constraints between sampling periods, the applied force rate differed between July (~18 N min^{-1}) and August (~9 N min^{-1}). However, there was no significant difference in strength between force rates and there was only a small increase in extensibility (5.6% for *L. digitata* and 9% for *S. latissima*) with the decrease in applied force (Fig. S2). Thus, we compared results directly between sampling times.

To measure blade extensibility, 2 dots were painted on the kelp tissue sample ~10 mm apart using an organic solvent-based paint. The paint did not appear to weaken the integrity of the kelp tissue as it came off when the kelp broke and did not leave any marks. To
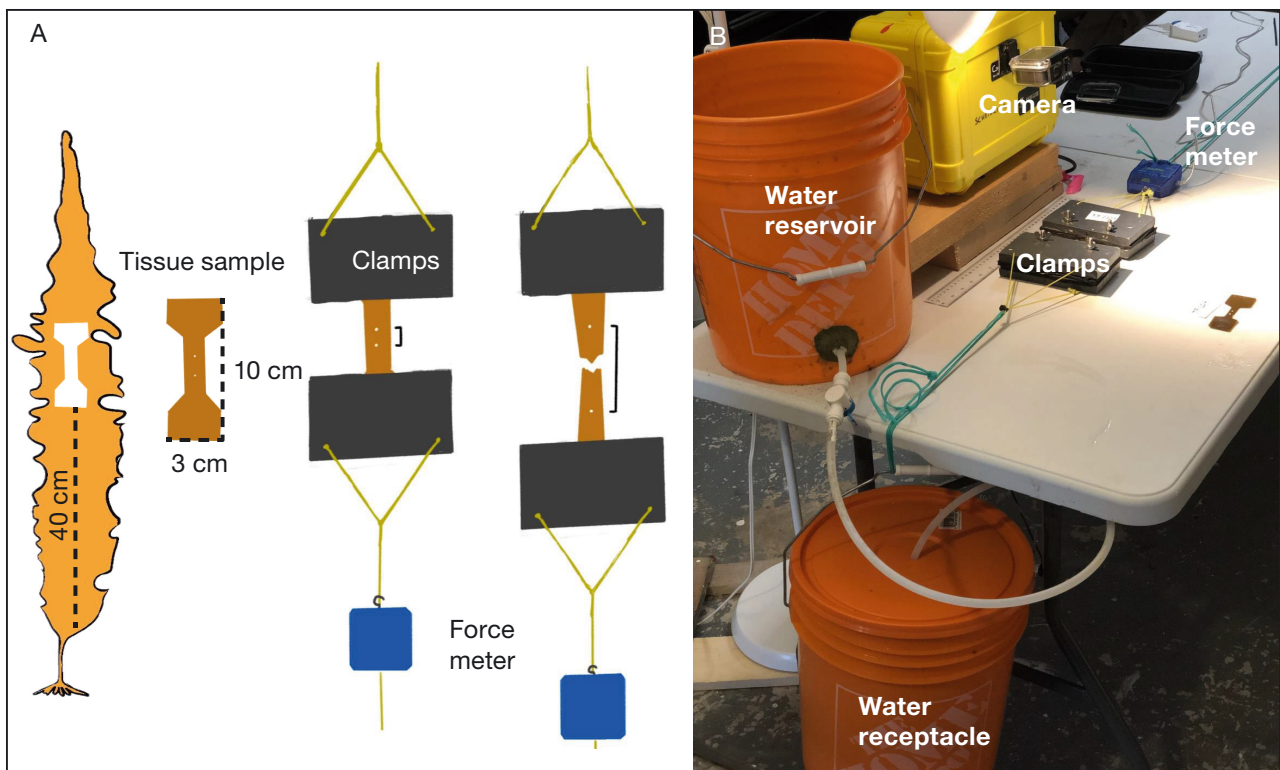

Fig. 3. (A) Conceptual methods and (B) equipment used to measure mechanical properties (stress and strain) of kelp tissue samples (see Section 2 for details)

ensure accuracy, we filmed each pull-to-break trial with a GoPro Hero 10. Breaking stress (MPa) was calculated as:

$$\text{Stress} = \frac{\text{Applied force at breaking (N)}}{\text{Cross sectional area (mm}^2)} \quad (2)$$

Cross-sectional area was calculated as the average thickness of the sample multiplied by the width of the sample before stretching. The width was measured at the center of the sample using ImageJ. Images were extracted from each trial to measure the initial length between dots and the length at breakage using ImageJ. Strain (% extension) was calculated as:

$$\text{Strain} = \frac{\text{Initial length (mm)} - \text{Length at breakage (mm)}}{\text{Initial length (mm)}} \quad (3)$$

In addition to comparisons in break stress and strain among sites of different wave exposure, we examined differences in mechanical properties: (1) along the blade for each species (meristem, middle [25cm for *L. digitata*, 40 cm for *S. latissima*], and distal end); and (2) between the middle and outer blades for *L. digitata.* For these experiments, we collected 10–11 thalli of each species from The Moll in October 2022.

2.3.1. Temperature

For each of the 3 sites in the ESI and for 2 sites from the SWS, we calculated growing degree day (GDD) as the cumulative sum of standardized temperatures (to account for freezing seawater) from 1 January to 31 December for each year averaged across depths. As temperature did not vary across sites (see Section 3), it was not included as a covariate in any analysis.

2.3.2. Kelp morphology

For each morphological characteristic (blade length, blade thickness, stipe length, stipe diameter, and number of branches), we examined the effects of exposure (fixed, 3 levels: Low, Intermediate, High) and sampling date (random, 2 levels: August 2022 and November 2022) using generalized linear mixed models (GLMMs) following a Gaussian distribution with the 'lmer' function in the 'lme4' R package (version 1.1-31). All analyses were computed with R (version 4.2.2). For all GLMMs (see also Section 2.5.3), we calculated the coefficient of determination (R^2) (Nakagawa et al. 2017) using the 'performance' function in the 'performance' package (version 0.10.2) and

standardized effect size using the 'emmeans' function in the 'emmeans' package (version 1.8.4-1). We visualized assumptions of normality and homogeneity of variance with residual plots using the 'plotResiduals' function in the 'DHARMa' package (version 0.4.6.0) (Hartig 2021). We examined model structure using p-values with a chi-squared distribution (Zuur et al. 2009), using the 'ANOVA' function in the 'car' package (version 3.1-1). If model interactions were found to be significant at $\alpha = 0.05$, we completed post hoc pairwise comparisons with grouped *t*-tests (Quinn & Keough 2002) using the 'emmeans' function in the 'emmeans' package (version 1.8.4-1) with Holm's adjustment to control increasing Type 1 errors with family size (Quinn & Keough 2002). The GLMM for blade length of *L. digitata* had a singular fit, which could be a sign of overfitting, but running a generalized linear model with the data gave similar results without overfitting. To compare the effects of wave exposure between species, we used Cohen's *d* effect size for all morphological features and material properties (Fig. S3) comparing LE and HE, averaged between sampling dates.

2.3.3. Material properties

For each kelp species, we examined the effects of exposure (fixed, 3 levels: Low, Intermediate, High), and sampling date (random, 2 levels: July 2022 and August 2022) on break stress with a GLMM following a Gaussian distribution using the 'lmer' function in the 'lme4' package (version 1.1-31); and on strain, with a GLMM following a beta distribution and a logit link using the 'glmmTMB' function in the 'glmmTMB' package (version 1.1.5).

We also examined the effects of position on the blade (fixed, 3 levels: meristem, middle, distal end) with kelp ID as random factor on break stress, using a GLMM following a Gaussian distribution using the 'lmer' function in the 'lme4' package (version 1.1-31); and on strain, using a GLMM with a beta distribution and a logit link using the 'glmmTMB' function in the 'glmmTMB' package (version 1.1.5). For all tests, strain data were transformed as per Smithson & Verkuilen (2006) to bind the data within the interval (0,1). Assumptions were tested and post hoc tests done as described above. We examined differences in break stress and strain between digits of *L. digitata* (middle, outer) using paired *t*-tests. Data fulfilled the assumptions of normality and homogeneity of variance as indicated by Shapiro and *F*-tests for homogeneity between groups.

3. RESULTS

3.1. Temperature

Average temperature was colder at ESI than at SWS in winter, with the coldest monthly averages differing across sites by 1.4−2.2°C each March between 2019 and 2022 (Fig. 4). The ESI was warmer in the summer but within less than 1°C of SWS except in 2020, when it was within 1.4°C (Fig. 4). Averaging all years, the cumulative GDD was 3377 (SE = 129) at ESI compared to 3673 (SE = 110) at SWS (Fig. 4). Temperature varied seasonally and among years, but not across sites both within the ESI and SWS (Fig. S1).

3.2. Kelp morphology

For *Laminaria digitata*, blade length did not differ across exposures, but was longest in August (GLMM: $\chi^2_1 = 6.1$, p = 0.013, $R^2 = 0.21$) (Fig. 5, Table 2). Blades thickness was thicker at HE than at LE and IE ($\chi^2_2 = 23$, p < 0.001, $R^2 = 0.14$), and thickest in November ($\chi^2_1 = 29$, p < 0.001, $R^2 = 0.51$) (Table 2, Fig. 5). The number of branches decreased from August to November ($\chi^2_1 = 16$, p < 0.001, $R^2 = 0.40$), and was marginally significantly greater at HE than at LE ($\chi^2_2 = 6.0$, p = 0.049, $R^2 = 0.05$) (Table 2, Fig. 5). For *Saccharina latissima*, blade length was longer at IE than at LE ($\chi^2_2 = 6.9$, p = 0.04, $R^2 = 0.032$) and decreased from August to November ($\chi^2_1 = 34$, p < 0.001, $R^2 = 0.61$) (Table 2, Fig. 5). Blades were thickest at HE and thinnest at LE ($\chi^2_2 = 40$, p < 0.001, $R^2 = 0.34$), and thicker in November than in August ($\chi^2_1 = 6.3$, p = 0.012, $R^2 = 0.16$) (Table 2, Fig. 5).

For *L. digitata*, stipes were longest at HE, and shortest at LE ($\chi^2_2 = 45$, p < 0.001, $R^2 = 0.42$) (Table 3, Fig. 6), and their diameter was greater at HE than at LE ($\chi^2_2 = 8.9$, p = 0.012, $R^2 = 0.12$) (Table 3, Fig. 6). For *S. latissima*, stipes were longest at HE and shortest at LE ($\chi^2_2 = 40$, p < 0.001, $R^2 = 0.40$), and their diameter was longer at HE compared to other exposures ($\chi^2_2 = 22$, p < 0.001, $R^2 = 0.26$) (Table 3, Fig. 6). Neither stipe length nor diameter varied between August and November for either species (Table 3, Fig. 6). Overall, variation in blade characteristics was explained more by sampling date than exposure level, while that of stipe characteristics was mostly explained by exposure, as indicated by the coefficient of determination (R^2).
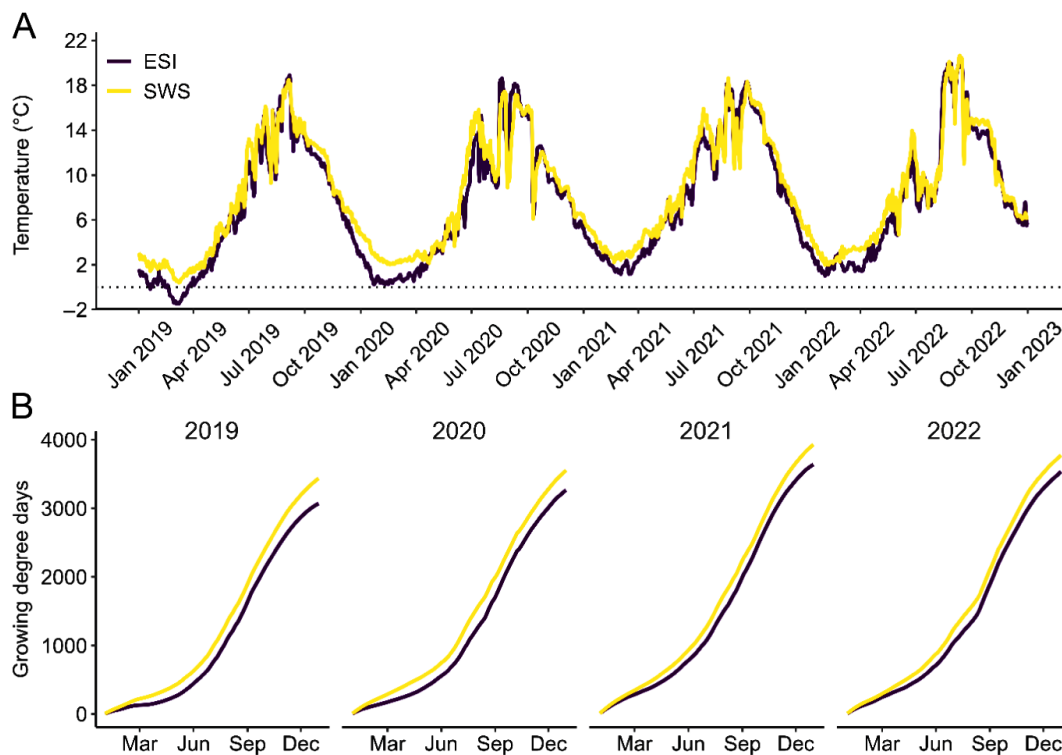

Fig. 4. (A) Temperature at the Eastern Shore Islands (ESI) (averaged between 6 and 9 m depth, 3 sites at ESI) and the Southwestern Shore (SWS, 2 sites averaged), and (B) growing degree days (GDD) from January 2019 to December 2022. Fig. S1 shows results from individual sites. Dotted line indicates 0°C
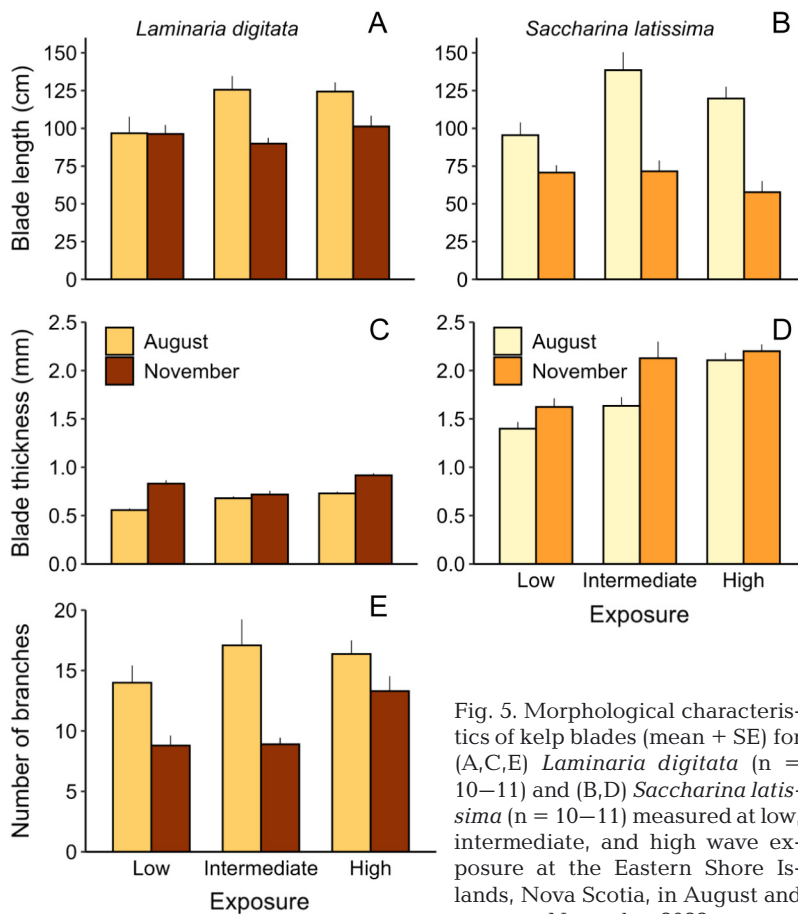
Fig. 5. Morphological characteristics of kelp blades (mean + SE) for (A,C,E) *Laminaria digitata* (n = 10–11) and (B,D) *Saccharina latissima* (n = 10–11) measured at low, intermediate, and high wave exposure at the Eastern Shore Islands, Nova Scotia, in August and November 2022

3.3. Mechanical properties

For *L. digitata*, stress was higher for thalli from HE than LE (χ^2_2 = 13, p = 0.01, R^2 = 0.04) and strain was lower for thalli from LE than both IE and HE (χ^2_2 = 28, p < 0.001, R^2 = 0.55) (Table 4, Fig. 7). Both mechanical properties varied among months (stress: χ^2_1 = 58, p < 0.001, R^2 = 0.75; strain: χ^2_1 = 11, p = 0.001, R^2 = 0.34) (Table 4). For *S. latissima,* neither stress nor strain differed among exposures (Table 4, Fig. 7), but strain varied among months (χ^2_1 = 6.7, p = 0.010, R^2 = 0.87).

The mechanical properties of kelp blades varied depending on the location along the blade from where the tissue was extracted (p < 0.001, R^2 > 0.4 for all, Table 5). For both species, stress was lower (p < 0.001) and strain higher (p < 0.001) at the meristem than the at tip and middle (except p = 0.028 for *S. latissima* strain between meristem and middle) (Table 5, Fig. 8). For *L. digitata*, neither mechanical property varied between samples taken from the center and outer blade (stress: t_8 = 0.64, p = 0.54, and strain: t_8 = 1.09, p = 0.31) (Fig. 8).

Table 2. Summary of results from mixed effects models and likelihood ratio tests examining the effects of wave exposure (Low, Intermediate, High; fixed effect) and sampling date (August, November; random effect) on blade morphology of *Laminaria digitata* and *Saccharina latissima* (blade length, blade thickness, number of branches). R^2 is the coefficient of determination for each effect; estimates are given for each significant pairwise contrast; p-values are adjusted using Holm's p-value adjustment: significant p-values (α = 0.05) are **bolded**

	Term	*Laminaria digitata*				*Saccharina latissima*			
		df	χ^2	p	R^2	df	χ^2	p	R^2
Blade length	Exposure	2	4.7	0.098	0.06	2	6.9	**0.032**	0.04
	Sampling date	1	6.1	**0.013**	0.21	1	34	**<0.001**	0.61
Blade thickness	Exposure	2	23	**<0.001**	0.14	2	40	**<0.001**	0.34
	Sampling date	1	29	**<0.001**	0.51	1	6.3	**0.012**	0.16
Number of branches	Exposure	2	6.0	**0.049**	0.05	2	—	—	—
	Sampling date	1	16	**<0.001**	0.40	1	—	—	—
	Exposure contrasts	Estimate	*t*-ratio	p	Direction	Estimate	*t*-ratio	p	Direction
Blade length	High − Low	—	—	—	—	5.93	0.7	0.768	
	Intermediate − Low	—	—	—	—	22.0	2.5	**0.036**	>
	High − Intermediate	—	—	—	—	−16.0	−1.9	0.155	
Blade thickness	High − Low	0.13	4.2	**0.001**	>	0.65	6.3	**<0.001**	>
	Intermediate − Low	0.01	0.2	0.969		0.37	3.6	**0.002**	>
	High − Intermediate	0.12	4.1	**0.001**	>	0.28	2.7	**0.024**	>
Number of branches	High − Low	3.38	2.5	**0.045**	>	—	—	—	—
	Intermediate − Low	1.67	1.2	0.45		—	—	—	—
	High − Intermediate	1.71	1.3	0.423		—	—	—	—

Table 3. Summary of mixed effects model (stipe length), beta regression (stipe diameter), and corresponding likelihood ratio tests examining the effects of wave exposure (Low, Intermediate, High; fixed effect) with sampling date as a random effect (July, August) on stipe morphology of *Laminaria digitata* and *Saccharina latissima* (stipe length, stipe diameter). R^2 is the coefficient of determination for each effect; estimates are given for each significant pairwise contrast; p-values are adjusted using Holm's p-value adjustment: significant p-values (α = 0.05) are **bolded**

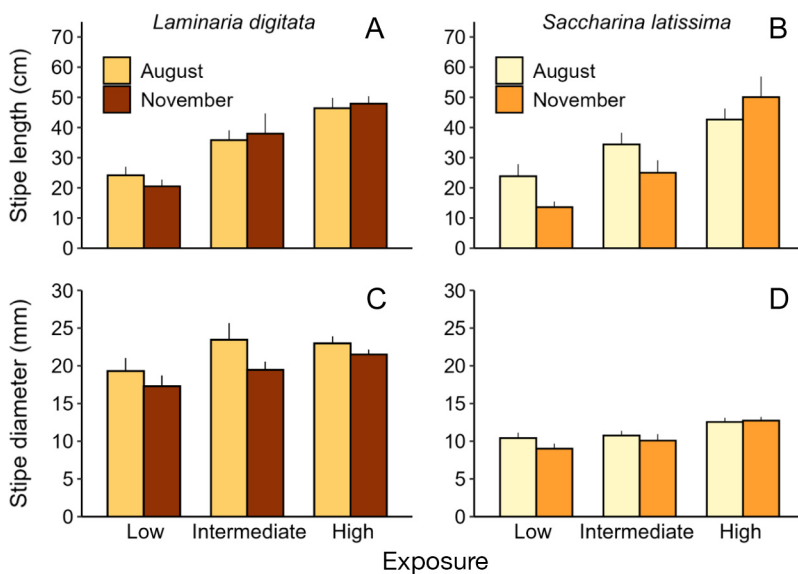|	Term	*Laminaria digitata*				*Saccharina latissima*			
		df	χ^2	p	R^2	df	χ^2	p	R^2
Stipe length	Exposure	2	45	**<0.001**	0.42	2	40	**<0.001**	0.40
	Sampling date	1	0.0001	1.000	—	1	0.01	0.915	0.01
Stipe diameter	Exposure	2	8.9	**0.012**	0.12	2	22	**<0.001**	0.26
	Sampling date	1	2.2	0.141	0.10	1	0.04	0.838	0.01
	Exposure contrasts	Estimate	*t*-ratio	p	Direction	Estimate	*t*-ratio	p	Direction
Stipe length	High − Low	24.8	6.7	**<0.001**	>	27.4	6.2	**<0.001**	>
	Intermediate − Low	14.5	3.9	**0.001**	>	11.0	2.5	**0.044**	>
	High − Intermediate	10.3	2.8	**0.019**	>	16.5	3.7	**0.001**	>
Stipe diameter	High − Low	3.94	2.8	**0.017**	>	2.92	4.5	**<0.001**	>
	Intermediate − Low	3.11	2.4	0.073		0.70	1.1	0.541	
	High − Intermediate	0.84	0.6	0.815		2.22	3.4	**0.004**	>

Fig. 6. Stipe length and diameter (mean + SE) for (A,C) *Laminaria digitata* (n = 10−11) and (B,D) *Saccharina latissima* (n = 10−11) measured at low, intermediate, and high wave exposure at the Eastern Shore Islands, Nova Scotia, in August and November 2022

4. DISCUSSION

Kelp beds have persisted at the ESI despite significant declines in other parts of Nova Scotia, such as the SWS (Attridge et al. 2022 and references therein). We found a high degree of plasticity in kelp morphology and mechanical properties induced by high wave exposure. *Laminaria digitata* had stronger and more extensible tissues with thicker blades and stipes at high exposures, and while the mechanical properties of

Saccharina latissima did not vary with wave exposure, blade tissue thickness increased significantly. *L. digitata* and *S. latissima* may have different strategies for resisting hydrodynamic forces. Although we did not replicate sites within each level of wave exposure and thus cannot generalize our results, we believe that the observed patterns are sound based on the strength of the statistical tests and support from the literature.

4.1. Wave exposure affects kelp morphology

We found that at higher exposures, both species had longer and thicker stipes and thicker blades, and *L. digitata* had increased branching. Since the forces a material can withstand depend on its thickness, thicker kelp blades should resist stronger hydrodynamic forces (Martone 2007). *S. latissima* showed a higher degree of morphological plasticity for blade thickness than *L. digitata*. Kelps from exposed areas generally have thicker and narrower blades and longer, thicker stipes to better resist dislodgment from increased hydrodynamic forces (Hurd 2000, Koehl et al. 2008, Demes et al. 2011, Bekkby et al. 2014, Coppin et al. 2020). Stipe size (volume) can be used as a proxy for age (as in *Ecklonia radiata*; Lees 2001), suggesting that both *L. digi-*

Table 4. Summary of mixed effects model (stress), beta regression (strain), and corresponding likelihood ratio tests examining the effects of wave exposure (Low, Intermediate, High; fixed effect) with sampling date as a random effect (July, August) on stress and strain for *Laminaria digitata* and *Saccharina latissima*. R^2 is the coefficient of determination for each effect; estimates are given for each significant pairwise contrast; p-values are adjusted using Holm's p-value adjustment: significant p-values ($\alpha = 0.05$) are **bolded**

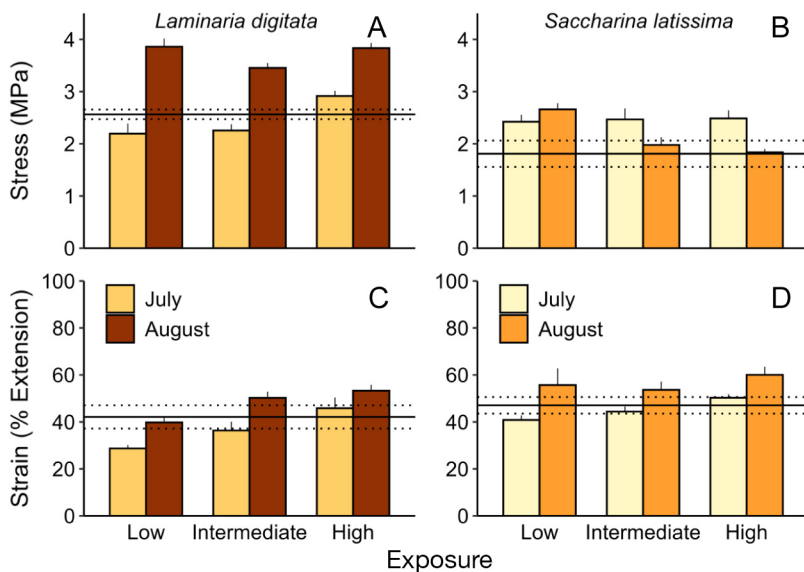|	Term	*Laminaria digitata*				*Saccharina latissima*			
		df	χ^2	p	R^2	df	χ^2	p	R^2
Stress	Exposure	2	13	**0.001**	0.04	2	4.8	0.091	0.06
	Sampling date	1	58	**<0.001**	0.75	1	1.8	0.182	0.09
Strain	Exposure	2	28	**<0.001**	0.55	2	1.7	0.433	0.13
	Sampling date	1	11	**0.001**	0.34	1	6.7	**0.010**	0.87
	Exposure contrasts	Estimate	*t*-ratio	p	Direction	Estimate	*t*-ratio	p	Direction
Stress	High − Low	0.37	2.5	**0.036**	>	—	—	—	—
	Intermediate − Low	−0.16	−1.1	0.538		—	—	—	—
	High − Intermediate	0.52	3.5	**0.003**	>	—	—	—	—
Strain	High − Low	0.63	5.3	**<0.001**	>	—	—	—	—
	Intermediate − Low	0.38	−3.1	**0.008**	>	—	—	—	—
	High − Intermediate	0.25	2.1	0.11		—	—	—	—

Fig. 7. Stress and strain (mean + SE) measured for kelp thalli of (A,C) *Laminaria digitata* (n = 9−12) and (B,D) *Saccharina latissima* (n = 10−15) measured at low, intermediate, and high wave exposure at the Eastern Shore Islands, Nova Scotia, in July and August 2022. Dotted line represents the break stress and strain (mean ± SE, n = 3) measured for both kelp species from Splitnose Point, Nova Scotia (data from Simonson et al. 2015)

viduals (Gerard 1997). Although many environmental factors such as temperature affect the kelp life cycle, wave exposure was shown to be the main driver for morphological differences among *E. maxima* and *L. pallida* in South Africa (Coppin et al. 2020). Moreover, transplant experiments have confirmed that differences in morphology are to the result of morphological plasticity rather than genetic variation (Fowler-Walker et al. 2006), with plasticity directly linked to mechanical stress from waves and currents (Koehl et al. 2008).

4.2. Wave exposure affects material properties of kelp blades

Our tensile tests confirmed a difference in material properties among exposures, but the relationships varied between *L. digitata* and *S. latissima*. Kelp blades of *L. digitata* were stronger and more extensible at higher wave exposures, while the strength and extensibility of *S. latissima* were not affected by wave exposure. For *L. digitata*, wave exposure explained 55% of the variance in extensibility, but only 4% of the variance in strength. For both species, we found highly extensible tissue with generally low break stress, similarly to previous studies (Carrington et al. 2001, Denny & Gaylord 2002). The effects of

itata and *S. latissima* survive longer in areas of high wave exposure. The increased branching morphology of *L. digitata* at high wave exposure generates more drag and requires a stronger attachment to the substratum, while the slim and tapered shape of *S. latissima* minimizes drag (Starko et al. 2015). Branched morphologies may also provide increased nutrient uptake (Hurd & Pilditch 2011, Starko et al. 2015), which can influence the thermal tolerance of indi-

Table 5. Summary of mixed effect model (stress) and beta regression (strain) and corresponding likelihood ratio tests examining the effects of tissue sampling position along kelp blade (meristem, middle, tip) with kelp replicates as a random effect on stress and strain of *Laminaria digitata* and *Saccharina latissima*. R^2 is the coefficient of determination for each effect; estimates are given for each significant pairwise contrast; p-values are adjusted using Holm's p-value adjustment: significant p-values ($\alpha = 0.05$) are **bolded**

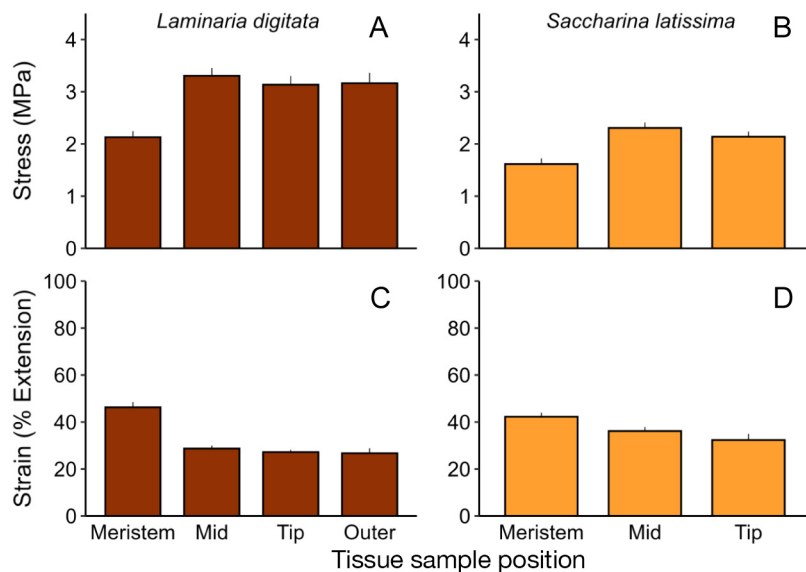|	Term	*Laminaria digitata*				*Saccharina latissima*			
		df	χ^2	p	R^2	df	χ^2	p	R^2
Stress	Position	2	56	**<0.001**	0.57	2	85	**<0.001**	0.45
	Kelp ID	9	2.8	0.096	0.15	10	15	**<0.001**	0.39
Strain	Position	2	150	**<0.001**	0.86	2	21	**<0.001**	0.49
	Kelp ID	9	3.7	0.06	0.10	10	3.7	0.055	0.40
	Position contrasts	Estimate	*t*-ratio	p	Direction	Estimate	*t*-ratio	p	Direction
Stress	Meristem — Tip	−1.01	−6.2	**<0.001**	<	−0.56	−6.79	**<0.001**	<
	Meristem — Middle	−1.16	−6.8	**<0.001**	<	−0.69	−8.76	**<0.001**	<
	Middle — Tip	0.16	0.9	0.642		0.14	1.66	0.244	
Strain	Meristem — Tip	0.84	11	**<0.001**	>	0.44	4.49	**<0.001**	>
	Meristem — Middle	0.75	9.7	**<0.001**	>	0.26	2.73	**0.028**	>
	Middle — Tip	0.09	1.1	0.552		0.18	1.85	0.174	

Fig. 8. Stress and strain (mean + SE) measured across tissue sample positions on kelp blades (center digit: meristem, middle, tip; and middle of outer digit) of (A,C) *Laminaria digitata* (n = 9−10) and (B,D) *Saccharina latissima* (n = 9−10, single blade) from The Moll in the Eastern Shore Islands, Nova Scotia

tential, as the reproductive tissue for both species is located on the mid- to distal portions of blades. In our study, mechanical differences between summer and autumn may be the result of strong and larger kelp surviving longer into autumn. Interestingly, not every kelp species benefits from having the strongest tissues; for example, breakage of the weaker fronds before winter storms in *Egregia menziesii* reduces drag forces and increases survivorship (Demes et al. 2013, Burnett & Koehl 2019).

For both species, the meristem had greater extensibility and lower strength than both the middle and the tip of the blades, while it was similar for the middle and tip. Moreover, strength and extensibility did not differ between branches of *L. digitata*. Observed patterns in mechanical properties along the blades suggest that stronger yet less extensible tissues may be related to tissue aging and accumulation of cortex cells (Krumhansl et al. 2015, Millar et al. 2021). Tissue damage also propagates differently across tissues depending on the location on algal blades (Mach et al. 2007) and therefore on location-specific material properties (Burnett & Koehl 2022). Both species have the same pattern in the distribution of mechanical properties along the blade, which is expected, since kelp blades typically erode from the distal end. Although never experimentally

wave exposure on material properties of kelp tissues are becoming well established (Koehl & Wainwright 1977, Armstrong 1989, Johnson & Koehl 1994, Demes et al. 2013, Millar et al. 2021). More robust kelps are more likely to retain a greater proportion of their thallus in winter (Demes et al. 2013). The onset of storms and consequent kelp defoliation in autumn (Attridge et al. 2022) coincide with peak reproduction for both species (Chapman 1984). Thus, mechanically more robust kelp may have increased reproductive po-

tested on algal material, erosion depends on material properties, as the destruction of a material happens when the stress occurring on a body surpasses its strength (Bitter 1963). Kelp would therefore benefit from stronger tissue at distal ends in areas with strong hydrodynamic forces.

4.3. Ecological implications of phenotypic plasticity in kelp

The strength of kelp tissue has a positive relationship with the force required to break wounded tissue, with stronger kelp tissue being able to withstand a greater break force when damaged (Burnett & Koehl 2018). We found that the strength and extensibility of *L. digitata* and the tissue thickness of *S. latissima* increased at high wave exposures. This plasticity could play a role in the resilience of kelps in the ESI. Similar patterns have been measured in British Columbia, Canada, where kelp forests in areas of high wave exposure were more resistant to heat waves, while those in sheltered areas experienced major losses of kelp diversity between 1993 and 2018 (Starko et al. 2019). In our system, the invasive bryozoan *Membranipora membranacea* creates fractures in kelp blades, compromising their structural integrity and making them more vulnerable to breakage (Krumhansl et al. 2011). Stronger blades may reduce the impact of *M. membranacea* and increase the probability of survival and thus lead to the higher kelp density observed at exposed sites (Attridge et al. 2022). However, other factors can also modulate the impact of wave exposure on kelp dynamics. For example, the sweeping action of kelp blades at high exposure may clear sediments from the substrate and allow kelp to outcompete other algae (Russell 2007), and wave action can affect the transport of nutrients across the blade boundary layer (Hurd 2000).

The ecological implications of morphology combined with mechanical properties of macroalgae are complex and not fully resolved. Therefore, it is difficult to determine whether, for example, morphology has a greater effect on population dynamics than strength or extensibility. However, the combination of all of these properties likely contributes to stronger kelp and thus lower vulnerability to defoliation in wave-exposed areas (Denny et al. 1989). The stronger and more extensible tissues of *L. digitata* most likely contribute to its higher abundance in more wave-exposed environments (Attridge et al. 2022). Greater tissue thickness (which disperses hydrodynamic stress over a greater area) exhibited by *S. latissima* also al-

lows it to better withstand hydrodynamic forces, but the species is most abundant at intermediate exposures (Attridge et al. 2022), suggesting that other drivers are influencing its distribution in the ESI. Interestingly, Krumhansl et al. (2011) found *S. latissima* to be less resistant than *L. digitata* to strength reductions caused by *M. membranacea.*

4.4. Comparisons between ESI and SWS

Kelps from the SWS (site at ~3000 REI, calculated by Krumhansl & Scheibling 2011), were weaker and less extensible (Simonson et al. 2015) than at the ESI, possibly making them more vulnerable to lesions by *M. membranacea.* Sheltered embayments dominate the SWS, whereas the ESI is composed of islands exposed to prevailing southwest winds (DFO 2019), and winter temperatures are lower in the ESI than in the SWS. Colder temperatures can benefit growth and the carbon and nitrogen content of juvenile *L. digitata* (Liesner et al. 2020, Gauci et al. 2022), leading to increased recruitment (Martins et al. 2017). However, there was no variation in temperature among sites at the ESI; thus, temperature is most likely not the main driver for kelp dynamics within the archipelago. A recent assessment (Krumhansl et al. 2024) showed that *L. digitata* and *S. latissima* in Nova Scotia may be more resilient than previously thought by comparing their respective canopy cover between 2000 and 2022 in an embayment on the SWS. The complex evidence from studies on kelp dynamics highlight the need for long time series to assess long-term ecosystem persistence (Connell & Sousa 1983). Continued monitoring is required to fully understand the future trajectory of and patterns influencing kelp beds in the ESI.

4.5. Conclusion and implications

Overall, we showed that wave exposure induces mechanical and morphological plasticity in kelps, with larger and stronger kelp found in more wave-exposed areas, providing a potential mechanism for the continued high abundance of kelp beds at wave-exposed sites in the ESI. The reduction in strength and extensibility in kelps caused by *M. membranacea* could be dampened by the plastic response of kelp to wave exposure. With increasing temperatures and storm intensity in the Northwest Atlantic, erosion and dislodgment could increase the vulnerability of kelp beds throughout Nova Scotia, including at the ESI. Long-term monitoring of kelp abundance is needed

to better understand the trajectory of these ecosystems and their potential persistence in the future, particularly under climate change. Our study underscores the importance of exploring potential mechanisms that can lead to persistence. Understanding the mechanisms that drive the long-term survival of foundational species, such as kelp, can help ensure the effectiveness of conservation tools to preserve marine ecosystems (Jackson et al. 2014, Arafeh-Dalmau et al. 2021).

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