

Morphological and mechanical properties of blades of *Saccharina latissima*

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# 1 Morphological and mechanical properties 2 of blades of *Saccharina latissima*

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## 7 **Abstract**

8 Interactions between water flow and aquatic vegetation strongly depend on morphological  
9 and biomechanical characteristics of vegetation. Although any physical or numerical model  
10 that aims to replicate flow-vegetation interactions requires these characteristics, information  
11 on morphology and mechanics of vegetation living in coastal waters remains insufficient. The  
12 present study investigates the mechanical properties of blades of *Saccharina latissima*, a  
13 seaweed species spread along the shores of the UK and North East Atlantic. More than 50  
14 seaweed samples with lengths spanning from 150 mm to 650 mm were collected from Loch  
15 Fyne (Scotland) and tested. Seaweed blades had a natural ‘stretched droplet’ shape with  
16 bullations in the central fascia and ruffled edges in the area close to the stipe. Their  
17 morphological features showed high variability for samples longer than 400 mm. The blades  
18 were almost neutrally buoyant, their material was found to be very flexible and ductile, being  
19 stiffer in longer blades. The laboratory tests showed that estimates of tensile Young’s  
20 modulus appeared to be similar to bending Young’s modulus suggesting a reasonable degree  
21 of isotropy in studied seaweed tissues.

22 **Keywords:**

23 Brown alga; organism morphology; mechanical properties; elasticity; *Saccharina latissima*;  
24 Scotland

## 25 **1. Introduction**

26 In recent years, vegetation in coastal waters has been investigated for various  
27 applications. For example, it has been found to contribute to reduction of flow velocity  
28 (Fonseca and Koehl, 2006) and attenuation of waves (Möller et al., 1999; Sánchez-González  
29 et al., 2011), thus providing means for bio-inspired coastal management (e.g. Temmerman et  
30 al., 2013). Another example relates to macroalgae, also referred to as seaweeds, which are  
31 among most common vegetation in coastal waters. They were employed in the Integrated  
32 Multi-Trophic Aquaculture (IMTA) (Chan et al., 2006; Chopin and Sawhney, 2009,  
33 Lamprianidou et al., 2015) and were proposed for bioremediation purposes (Fei, 2004; Mata  
34 et al., 2010). A number of studies have also assessed the feasibility of seaweeds for the  
35 production of third generation bio-fuels (Hughes et al., 2012; Wargacki et al. 2012). In  
36 addition, seaweeds are a traditional source of food in East Asia (e.g. China, Japan, and South  
37 Korea), where they have been cultivated for centuries (Bardach et al., 1972). Nowadays  
38 seaweed farming is mainly confined to East Asia, because standard cultivation techniques  
39 necessitate a high amount of manual work and the associated costs are too high (Lucas and  
40 Southgate, 2012). The cultivation of seaweeds is expected to experience a continued  
41 expansion, prompted by the wide use of seaweed-derived components such as the  
42 hydrocolloids (Lucas and Southgate, 2012). This expansion, however, is conditioned by the  
43 development of innovative farming techniques that would make seaweed farming  
44 economically attractive (James, 2010).

45 Novel farming techniques and any of the above applications have to be supported by  
46 either numerical or physical modelling that requires a comprehensive understanding of the

47 flow-seaweed interactions at a relevant range of spatial scales. These interactions control  
48 physical, biological and ecological phenomena concerning aquatic vegetation, and depend  
49 upon their morphological and mechanical properties (Nikora, 2010). In order to describe the  
50 motion of any streamlined body in flowing water, it is sensible to start with simple geometry  
51 considering a seaweed blade as a two-dimensional beam. For any type of application, the  
52 motion of the blade can then be described by an equation of motion such as:

$$\frac{m}{l} \frac{\partial^2 z}{\partial t^2} - T \frac{\partial^2 z}{\partial x^2} + EI \frac{\partial^4 z}{\partial x^4} = F_F \quad (1)$$

53 where  $m$  is the body mass,  $l$  is the body length,  $x$  and  $z$  are the longitudinal and vertical  
54 coordinates,  $t$  is time,  $T$  is the axial tension in the body,  $E$  is Young's modulus of the material  
55 of which the body is made,  $I$  is the second moment of area of the body and  $F_F$  accounts for  
56 the forces per unit length acting on the body due to the flow action (e.g. Païdoussis, 1998;  
57 Connell and Yue, 2013). The first term in Eq. (1) represents inertia, the second term relates to  
58 the tensile force, and the third term is due to the bending force. Altogether these forces  
59 balance the forces imposed by flowing water, i.e., the total (viscous and pressure) drag force  
60  $F_F$ . Equation (1) and its variants are involved in up-scaled models describing seaweed  
61 performance at a canopy scale and larger scales relevant to seaweed management and  
62 cultivation.

63 The second and third terms in Eq. (1) contain parameters characterising mechanical  
64 properties of the body. In addition, all four terms are influenced by the body morphology. It  
65 is, therefore, clear that the knowledge of mechanical and morphological properties of aquatic  
66 vegetation is of primary importance for understanding and predicting flow-vegetation  
67 interactions and, consequently, advancing the knowledge of their multiple effects. Reliable  
68 physical and numerical models for prediction of vegetation effects on the coastal flows and of

69 vegetation performance in a variety of applications (e.g. IMTA, bioremediation, cultivation)  
70 can be developed only if relevant data on vegetation are available. In the literature,  
71 information on the mechanics and morphology of aquatic vegetation remains sparse.  
72 Mechanical data of seaweed tissues are provided by very few publications (Biedka et al.,  
73 1987; Hale, 2001; Harder et al., 2006; Boller and Carrington, 2007; Paul et al., 2014). Thus,  
74 for the development of reliable models concerning any aspect of flow-seaweed interactions,  
75 the obtaining of such data remains a priority task.

76 The present study focuses on *Saccharina latissima*, a seaweed species thriving along  
77 the shores of the North East Atlantic (Ramos et al., 2012). Studies of this species for the  
78 development of IMTA (Sanderson, 2006) and for bioethanol production (Wargacki et al.,  
79 2012) produced promising results. Therefore, the research reported in this paper aims at  
80 contributing to the knowledge of morphological and mechanical properties of coastal  
81 vegetation in relation to *S. latissima*. Section 2 is focused on methodological issues of the  
82 study, while section 3 reports and discusses the key results in relation to seaweed blade  
83 morphology and mechanical properties, keeping in mind the hydraulic conditions at the  
84 collection site.

## 85 **2. Materials and methods**

### 86 *2.1. Seaweed collection and storage*

87 Samples of *S. latissima* were collected with the help of *Loch Fyne Oysters Limited* on  
88 the 10<sup>th</sup> of February 2015 from long-lines deployed in Loch Fyne (Scotland). The coordinates  
89 of the collection site are 56.08 N and 5.28 W (Fig. 1). Due to the loch morphology, the most  
90 important forcing factors in the loch hydrodynamics are tides. Existing current meter data sets  
91 can provide useful information to characterise the hydraulic conditions within Loch Fyne and  
92 at the collection site. The data set used in this study (available at <http://www.bodc.ac.uk>)

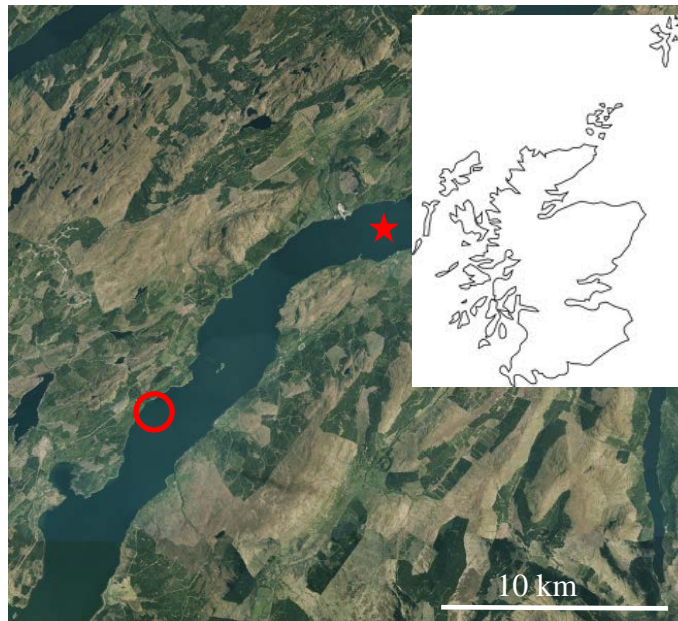
93 were recorded with an Aanderaa RCM 7/8 Recording Current Meter mounted on a subsurface  
 94 mooring approximately 10 km North East of the collection site (Fig. 1). The characteristics of  
 95 the current meter data set and the bulk statistics of the current velocity calculated by the  
 96 authors are reported in Table 1. The selected collection site on the loch can be considered to  
 97 be sheltered and thus hydraulic conditions at this site may be biased low compared to the  
 98 flowmeter deployment site (Fig. 1).

99 **Table 1** Information about the current velocity data set recorded with a current meter in Loch Fyne and current  
 100 velocity statistical parameters calculated by the authors. (2 columns)

Characteristics of current velocity data set		Current velocity parameters	
Location of current meter	56.15 N, 5.15 W	Mean (cm/s)	11.1
Number of samples	4656	Min. value (cm/s)	1.4
Start date (dd/mm/yy h:mm)	20/11/1994 12:00	Max. value (cm/s)	57.8
End date (dd/mm/yy h:mm)	25/02/1995 10:00	Stand. Dev. (cm/s)	8.4
Sampling interval (s)	1800	Skewness	1.3
Sea floor depth (m)	100	Kurtosis	-0.7
Current meter depth (m)	11		

101 Prior to collection, seaweeds were visually inspected to assess their condition. Only  
 102 seaweeds showing no signs of damage or deterioration and with no visible bryozoans on their  
 103 surface were collected, their holdfasts then were removed and they were stored in tanks filled  
 104 with seawater. Seaweeds were transported to the University of Aberdeen and placed into a  
 105 special storage container within 8 hours after collection. The storage container was a 125 l  
 106 tank filled with seawater and equipped with a custom-made aeration system. The seawater in  
 107 the container was changed every 3-4 days according to the standard practice for seaweed  
 108 storage in tanks with no recirculating flow (Frithjof Kuepper, University of Aberdeen, pers.  
 109 comm., September 2014). The tank was kept outdoor so that water temperature was as close  
 110 to the ambient temperature as possible and seaweeds were exposed to natural light conditions  
 111 (i.e. 8 h:16 h day:night cycle). Seaweeds were visually monitored on a daily basis to assess

112 their condition. The blades that showed visible signs of deterioration were discarded. All  
113 seaweeds were used within 14 days after collection.



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**Fig. 1** The collection site in Loch Fyne is located in the area identified with a circle. The star represents the location of deployment of the current meter. The inset map (top right) shows the location of Loch Fyne in Scotland (adapted from <http://digimap.edina.ac.uk/>). (1.5 column)

## 119 2.2. Morphological assessment

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At a first step, the stipe was detached from the seaweed sample. Then, the seaweed blade was carefully dried with paper towels and weighed using a digital scale (OHAUS GT 2100 or Mettler P161, Mettler Toledo, Columbus, USA). Photos of the sample were taken with a digital camera (Fujifilm Finepix S1000fd, Fujifilm, Tokyo, Japan) on a light table (Illuma System, Bencher Inc., Chicago, USA). From the photos, seaweed blade projected  $A_{proj}$  and full-one-side  $A_{real}$  surface areas were evaluated using MATLAB<sup>®</sup> image processing tools. The projected surface area of a blade was estimated as the plane surface area covered by the blade on the light table. The full-one-side surface area of a blade was estimated taking into

128 account any folded parts of the blade that resulted in an overlapping on the light table (see  
129 Vettori, 2016 for complete description of methods).

130 The following blade dimensions were measured (computed) using rulers and Vernier  
131 scales: length  $l$ , average  $w_{mean}$  and maximum  $w_{max}$  widths, and thickness  $t$ . The average  
132 width was obtained as a ratio of the projected area on the blade length. As thickness varied  
133 across and along the blade, it was measured at the centre and edges of the blade at the  
134 following distances from the juncture of stipe and blade: 2 cm,  $0.25l$ ,  $0.5l$ ,  $0.75l$ . The  
135 minimum  $t_{min}$  and maximum  $t_{max}$  thicknesses were recorded. The volume  $V$  of the seaweed  
136 blade was measured by immersing it in a measuring cylinder partially filled with unfiltered  
137 freshwater at room temperature. After these measurements were taken, the seaweed blade  
138 was stored in seawater again prior to preparation of specimens to perform mechanical tests.

### 139 2.3. *Mechanical testing*

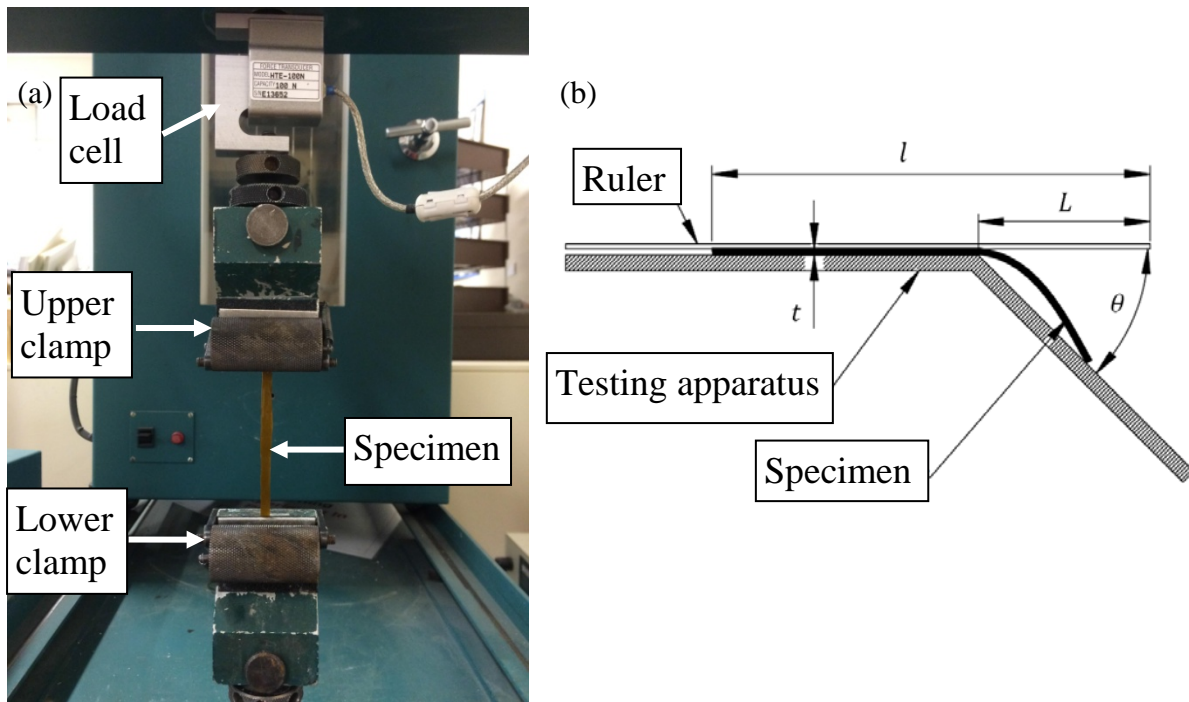
140 Mechanical tests were performed on specimens cut from 14 seaweed blades of various  
141 lengths. Two types of mechanical tests were completed: uniaxial tensile tests using a bench  
142 top testing machine (Fig. 2a); and bending tests using a Peirce's testing apparatus (Fig. 2b).  
143 Mechanical tests were conducted on specimens sliced from seaweed blades after their  
144 morphological measurements were completed (section 2.2). The specimens were cut from the  
145 central fascia of the blades to minimise the presence of undulations that could affect the  
146 mechanical tests. They were sliced along the blades in such a way that they never contained  
147 nicks or flaws, which would affect their mechanics. Furthermore, in order to prevent  
148 significant end-wall effects, the specimens were prepared with a length to width ratio equal to  
149 or higher than 10 (Niklas, 1992). Specimens were typically 100 mm long and 5-7 mm wide if  
150 used in tensile tests, and 200 mm long and 20 mm wide if used in bending tests. For bending  
151 tests to be conducted successfully, the use of longer specimens was required. This restriction



152 reduced the number of specimens that could be tested from each seaweed blade compared to  
153 those used for tensile tests. After being prepared and prior to the mechanical tests, specimens  
154 were stored in seawater.

155 Uniaxial tensile tests were conducted with a benchtop testing machine (H10K-S UTM,  
156 Tinius Olsen, Salfords, UK) with a 100N load cell (HTE, Tinius Olsen, Salfords, UK) (Fig.  
157 2a). The machine was equipped with two friction clamps, which could hold specimen ends  
158 between a sandpaper plate and a textured sprung cylinder (a complete description can be  
159 found in Miler et al., 2012). The force values were measured with a resolution of 1 part in  
160 32000 with 200 readings per second (Hounsfield Test Equipment, 1997). The relative error of  
161 the force reading was determined, via independent calibration, as 1.5% for force below 2 N  
162 and 0.1% for force above 2 N. The relative error of the displacement readings did not exceed  
163 0.5% (Miler et al., 2012).

164 For testing seaweed blade specimens, a plate covered by sandpaper was added between  
165 the sprung cylinder and the specimen at each of its ends in order to minimise the probability  
166 of damage of specimen ends. The use of the additional sandpaper plates allowed the pressure  
167 of the cylinder to be distributed on a wider area of the specimen, rather than squeezing a  
168 narrow cross-section. Two types of tensile tests were carried out: (1) tensile tests up to the  
169 breakage point; and (2) tensile cyclic loading-unloading tests. The first type allowed the  
170 estimation of material stiffness and strength (Niklas, 1992), while the latter provided  
171 information on material resilience to periodic excitations.



172 **Fig. 2** Hounsfield S-series benchtop testing machine during the testing of a seaweed blade specimen (a). Schematic  
 173 representation of Peirce's testing apparatus during the testing of a specimen (b) with the definition of the parameters relevant  
 174 for estimating bending Young's modulus. (2 columns)

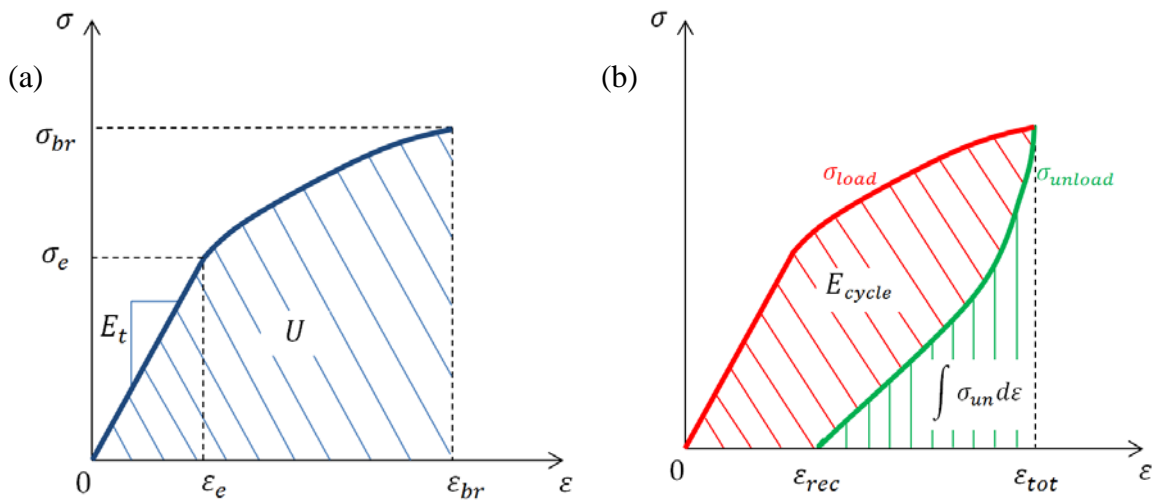
175 During the test, the upper clamp of the machine moved upwards with a constant speed  
 176 that could be set via dedicated software. The tensile tests were initiated with the clamps  
 177 located at a distance of 60 mm from each other. The specimens were stretched at a constant  
 178 speed set to 20 mm/min. The 'breakage' tests ended when the specimen failed, while cyclic  
 179 loading-unloading tests ended after three cycles were completed. During each cycle the  
 180 specimen was pulled to a displacement threshold of 20% of its original length, then the upper  
 181 clamp was returned to its initial position with the same speed (i.e. 20 mm/min).

182 During the tensile tests conducted on seaweed blade specimens the data of force  $F$  and  
 183 displacement  $\delta$  were recorded with a dedicated software (Tinius Olsen, Salfords, UK). For  
 184 analysis purposes, these data were converted into nominal stress  $\sigma$  (i.e. ratio of force to  
 185 original cross-sectional area of the specimen) and nominal strain  $\varepsilon$  (i.e. ratio of displacement  
 186 to original length of the specimen) values from which biomechanical parameters commonly

187 used in plant studies were estimated. The parameters estimated from the tensile tests  
 188 included: tensile Young's modulus  $E_t$ , i.e. the ratio of  $\sigma$  to  $\varepsilon$  within a linear region of  
 189  $\sigma = f(\varepsilon)$ ; elastic limits  $\sigma_e$  and  $\varepsilon_e$ ; stress  $\sigma_{br}$ , force  $F_{br}$  and strain  $\varepsilon_{br}$  at breakage; and  
 190 toughness  $U$ . Tensile Young's modulus was calculated as the slope of the initial linear part of  
 191 the stress-strain curve (i.e. where definition of  $E_t$  is applicable) (Fig. 3a) by finding the best  
 192 linear fit using the method of least squares. The elastic limits are the maximum values of  
 193 stress and strain which limit the range of  $\sigma = f(\varepsilon)$  where the material behaves as a linear  
 194 elastic material (Fig. 3a). The stress, force and strain at breakage represent the maximum  
 195 values of stress, force and strain reached during a tensile test before the specimen breaks (Fig.  
 196 3a). The toughness is the amount of energy per unit volume required for a material to  
 197 undergo breakage (Niklas and Spatz, 2012). The toughness was computed via numerical  
 198 integration using the trapezoid method and is defined as the area under the stress-strain curve  
 199 (Fig. 3a), i.e.:

$$U = \int_0^{\varepsilon_{br}} \sigma d\varepsilon \quad (2)$$

200



201 **Fig. 3** Representation of stress-strain curves for: tensile test at breakage (a) and tensile cyclic loading-unloading test (b). The  
 202 diagonal hatched area in (a) is the toughness, the diagonal hatched area in (b) is the elastic hysteresis, and the vertical  
 203 hatched area in (b) is the amount of energy recovered by the specimen during the unloading phase. (2 columns)

204 From tensile cyclic tests, three biomechanical parameters were estimated: the elastic  
 205 hysteresis  $E_{cycle}$ , the degree of elasticity  $E_{\varepsilon}$ , and the energy ratio  $E_{ratio}$ . They were  
 206 calculated using numerical integration by applying the trapezoid method. The elastic  
 207 hysteresis represents the amount of energy per unit volume used internally by the specimen  
 208 during a loading-unloading cycle (Niklas, 1992). It is highlighted by the diagonal hatched  
 209 area in Fig. 3b and is expressed as:

$$E_{cycle} = \int_0^{\varepsilon_{tot}} \sigma_{load} d\varepsilon - \int_{\varepsilon_{rec}}^{\varepsilon_{tot}} \sigma_{un} d\varepsilon \quad (3)$$

210 The degree of elasticity assesses specimen elongation due to plastic deformations (Niklas,  
 211 1992). It is the ratio of recovered (elastic) strain to the total strain in a cycle, i.e.:

$$E_{\varepsilon} = \frac{\varepsilon_{tot} - \varepsilon_{rec}}{\varepsilon_{tot}} \quad (4)$$

212 where the terms are defined in Fig. 3b. The energy ratio, also referred to as resilience (Niklas,  
 213 1992), is the ratio of the amount of energy the specimen recovered during the unloading  
 214 phase to the energy of the loading phase within the same cycle (Fig. 3b), i.e.:

$$E_{ratio} = \frac{\int_{\varepsilon_{rec}}^{\varepsilon_{tot}} \sigma_{unload} d\varepsilon}{\int_0^{\varepsilon_{tot}} \sigma_{load} d\varepsilon} \quad (5)$$

215 In addition to the tension tests, bending tests were conducted on seaweed blade  
 216 specimens using a Peirce's testing apparatus (Fig. 2b) manufactured at the University of  
 217 Aberdeen, with an inclination of the tilted plane  $\theta$  of  $46^\circ$ . This device and the theory behind it

218 are fully described in Peirce (1930) and Henry (2014). At each test, the specimen was located  
219 on the flat part of the apparatus, with one end being at its edge. A ruler was placed on the  
220 specimen, with its ‘zero’ located above the specimen edge. Then the specimen and the ruler  
221 were pushed towards the tilted part of the apparatus simultaneously. The reading of the  
222 cantilever length  $L$  (Fig. 2b) was taken as soon as the tip of the specimen touched the tilted  
223 part of the device. The test was repeated four times, on both ends of both sides of each  
224 specimen, as described by Peirce (1930) and Henry (2014), and the mean value of  $L$  was  
225 recorded. An estimate of bending Young’s modulus  $E_b$  can then be obtained from  $L$  as  
226 (Peirce, 1930):

$$E_b = \frac{3 mg L^3}{2 lw t^3} \left( \frac{\cos(\theta/2)}{\tan\theta} \right) \quad (6)$$

227 where  $m$  is the specimen mass;  $g$  is gravity acceleration;  $l$ ,  $w$ , and  $t$  are the length, width and  
228 thickness of the specimen, respectively; and the angle  $\theta$  ( $46^\circ$ ) in Fig. 2b represents the  
229 inclination of the tilted part of the apparatus (Peirce, 1930).

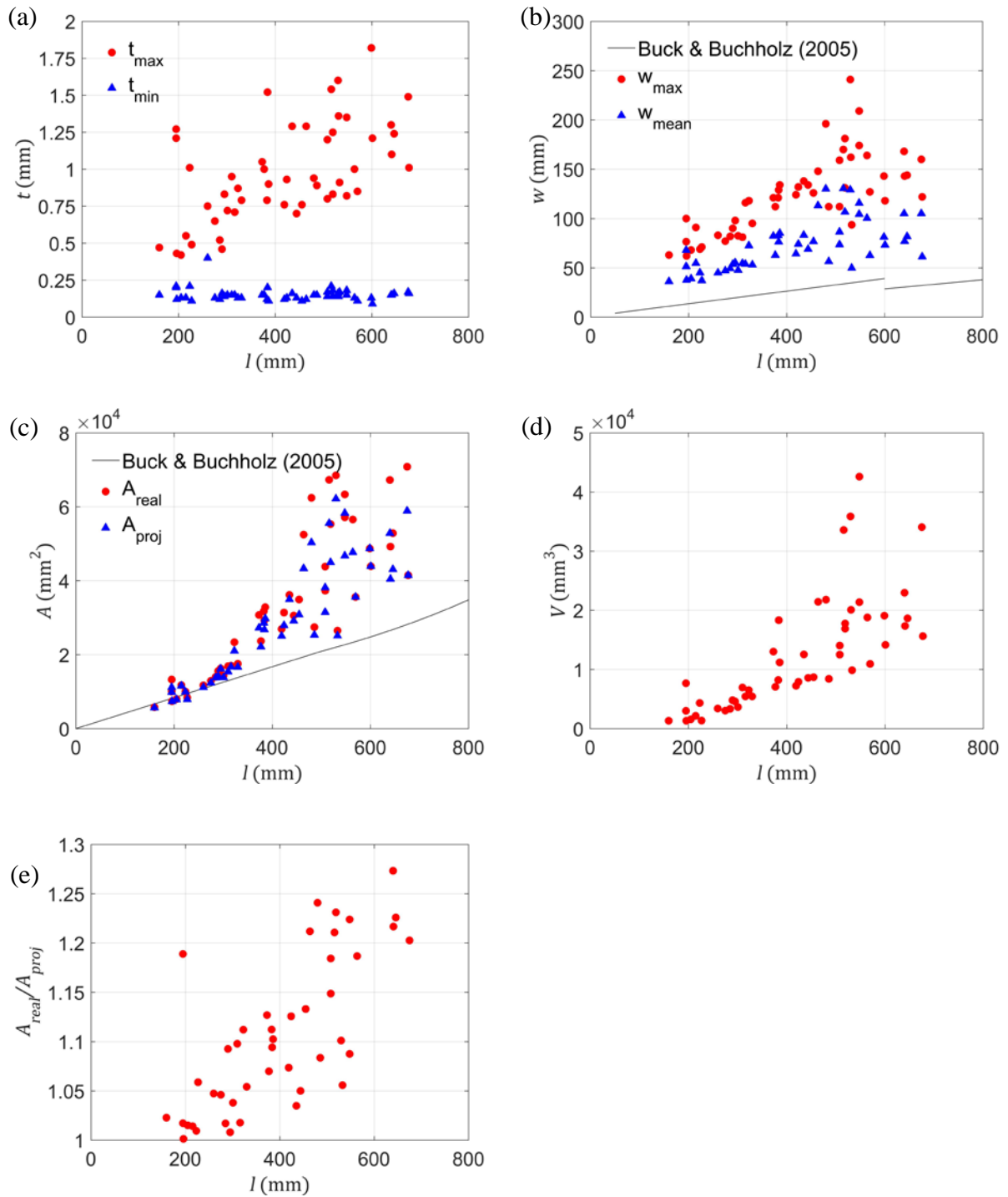
### 230 **3. Results and discussion**

#### 231 *3.1. Blade morphology*

232 The variety of morphological features in seaweed blades has been reported for a number of  
233 species. Seaweed blades are generally narrow and flat when growing in an energetic  
234 environment and wide with undulated edges when growing in a sheltered environment.  
235 Morphological variability was assessed in Gerard (1987) for *S. latissima*, in Koehl and  
236 Alberte (1988) and Koehl et al. (2008) for *Nereocystis luetkeana*, and in Hurd and Pilditch  
237 (2011) for *Macrocystis pyrifera*. The morphological adaptability in response to  
238 environmental conditions is referred to as phenotypic plasticity and is a crucial property of  
239 vegetation (Schlichting, 1986; West-Eberhard, 1989). Recalling the hydraulic conditions at

240 the collection site, samples of *S. latissima* in the present study exhibited features that are in  
241 agreement with the findings of the studies cited above. Indeed, blades of *S. latissima* from  
242 Loch Fyne were generally wide with undulated edges, as would be expected from samples  
243 collected in sheltered areas.

244 Most morphological properties of seaweed blades were found to be dependent on their  
245 length, the exception being the minimum thickness, which had an average value of 0.14 mm  
246 (Fig. 4a). Short blades were rather streamlined, while long blades had more complex  
247 morphology, with ruffles along the edges. These differences are noticeable in the  
248 relationships between the blade length and the blade maximum and average widths (Fig. 4b),  
249 the full-one-side and projected surface areas (Fig. 4c), and the blade volume (Fig. 4d).  
250 Interestingly, an apparent scale-dependent effect of phenotypic plasticity is also found within  
251 the population investigated. For blades shorter than 400 mm, the data exhibit a clear  
252 increasing trend with a narrow data collapse. However, for longer blades the data points are  
253 spread within a broader range (Fig. 4b-d). This pattern suggests that morphological variability  
254 primarily occurs in blades longer than a threshold length (i.e. 400 mm), being negligible for  
255 shorter blades. In addition, the overall trends revealed in the current study differ from the  
256 trends identified by Buck and Buchholz (2005) for blades of *S. latissima* from an exposed  
257 habitat (Fig. 4b-c). Both blade width and surface area increase at a faster rate in the samples  
258 analysed in the current study than in those reported by Buck and Buchholz (2005). These  
259 results support the idea that hydraulic conditions have a major influence on the morphology  
260 of blades of *S. latissima*, in agreement with Gerard (1987). When growing in a sheltered  
261 environment, blades grow wide and ruffled.



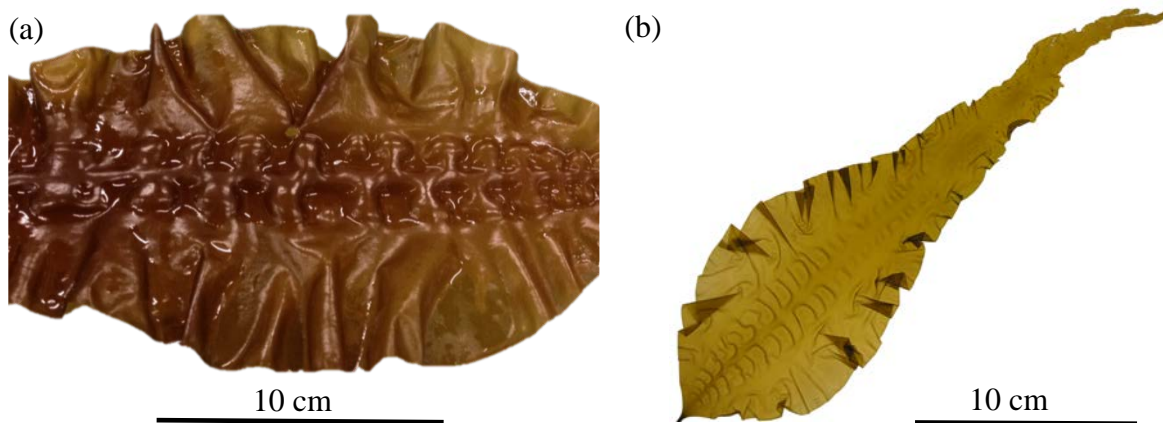
262 **Fig. 4** Relationships between the blade length  $l$  and: the maximum  $t_{max}$  and minimum  $t_{min}$  thicknesses (a); the maximum  $w_{max}$   
 263 and average  $w_{mean}$  widths (b); the full-one-side (real)  $A_{real}$  and projected  $A_{proj}$  surface areas (c); the blade volume  $V$  (d); and  
 264 the level of undulation  $A_{real}/A_{proj}$  (e). In (b) and (c) the black lines represent the regressions reported in Buck and Buchholz  
 265 (2005) to describe blade width and surface area as a function of blade length. In (b), (c), and (d) data show a narrow collapse  
 266 for blades shorter than 400 mm, while data points are distributed in a broad range for longer blades. (2 columns)

267 The ratio of the blade full-one-side  $A_{real}$  surface area to its projected  $A_{proj}$  surface  
268 area, which describes the level of undulation of the blade (Koehl and Alberte, 1988), was also  
269 calculated. The relationship between the blade length and the level of undulation  $A_{real}/A_{proj}$   
270 (Fig. 4e) is in agreement with the results from the analysis of other morphological  
271 parameters: as the blades get longer, their morphology is more complex and they become  
272 more ruffled. This trend is characteristic of sheltered environments, while seaweed blades  
273 from exposed sites exhibit values of  $A_{real}/A_{proj}$  very close to unity (Koehl and Alberte,  
274 1988).

275 Some common morphological features were identified among the seaweed blades  
276 investigated in the present study. Blade thickness varied significantly both across and along  
277 the blades. The central fascia was up to 10 times thicker than the edges (Fig. 4a). The  
278 maximum thickness was always found at the centre of the blade in proximity of the  
279 intercalary meristem. The minimum thickness was measured at the edges, typically at a  
280 distance of  $0.25l$  from the juncture of stipe and blade. Also, blade width varied along blade  
281 length, with the maximum width being usually located at  $0.25l$  from the juncture of stipe and  
282 blade. It is also noted that undulated/ruffled edges were mainly within the upstream part of  
283 the blade (i.e. close to the stipe), rather than towards the distal end. As a consequence, blades  
284 showed a ‘stretched droplet’ shape, bumped close to the stipe and streamlined towards the  
285 distal end (Fig. 5b). Seaweed blades characterised by ruffled edges also presented  
286 antisymmetric waving in their central fascia (Fig. 5a). These features are referred to as  
287 ‘bullations’ in phycology (Bold and Wynne, 1985) and have been reported for blades of *S.*  
288 *latissima* in Druehl and Kaneko (1973) and Lüning et al. (1978). Bullations started at the  
289 stipe-blade transition and spanned a good portion of the blade length. Interestingly, bullations  
290 were present only within blade parts characterised by ruffled edges, while they were not  
291 visible on streamlined parts. It is likely that bullations develop as a consequence of vertical



292 oscillations of the edges, harmonizing their waving with the flow and acting as links between  
293 the edges and the central fascia. The particular shape of the blades and the patterns in their  
294 morphology could optimize the trade-off between drag and dynamic reconfiguration (similar  
295 to freshwater plants, Siniscalchi and Nikora, 2013). In a sheltered habitat where mean flow  
296 velocity is as low as 10 cm/s (Table 1), dynamic reconfiguration is crucial to minimize light  
297 limitation, particularly within a patch.



298 **Fig. 5** Detail of seaweed blade showing ruffled edges and bullations in the central fascia (a). A seaweed blade showing the  
299 'stretched droplet' shape (b). (2 columns)

### 300 3.2. *Mechanical properties of blade tissues*

301 As described in section 2.3, a number of biomechanical parameters were calculated for  
302 seaweed blade tissues. The density of algal material was estimated from weight (obtained  
303 using a weighing scale) and volume (measured as the volume of water displaced by an  
304 immersed blade) of 50 seaweed blades. Its mean value is equal to  $1092 \text{ kg/m}^3$ , with a  
305 coefficient of variation of 8.3%. In other words, seaweeds are slightly heavier than seawater.  
306 The mean density is consistent with the values reported in the previous studies (Table 2),  
307 while the standard deviation cannot be compared due to lack of information in the literature.

308 Tensile  $E_t$  and bending  $E_b$  Young's moduli were estimated from data collected during  
309 tensile and bending tests. The former was evaluated using force-displacement data from

310 about 40 tensile tests. Due to the appropriate length of specimen required for Peirce's test to  
311 be successfully conducted (see section 2.3), the estimate of bending Young's modulus was  
312 obtained from 14 specimens only. As a result, the coefficient of variation associated with the  
313 estimate of  $E_b$  (73%) is higher than that associated with the estimate of  $E_t$  (38%). The mean  
314 values of Young's moduli are close to each other, with  $E_t$  being estimated to be 4.7 MPa and  
315  $E_b$  to be 3.7 MPa (Table 2). This suggests a reasonable degree of internal isotropy in seaweed  
316 blade tissues.

317 The estimate of bending Young's modulus calculated in the present study is compatible  
318 with the results for blades of *L. digitata* (Henry, 2014) obtained using Peirce's tests. The  
319 authors are not aware of any data on bending Young's modulus of *S. latissima* available in  
320 the literature. Tensile Young's modulus of *S. latissima* was estimated by Boller and  
321 Carrington (2007) using a small number of samples. The estimates of  $E_t$  in the present study  
322 are lower than those reported by Boller and Carrington (2007). This does not appear to be due  
323 to a mechanical adaptation to environmental conditions (Harder et al., 2006; Hurd et al.  
324 2014), but is believed to be related to other factors. The specimens tested by Boller and  
325 Carrington (2007) had a small length to width ratio (i.e. 3), making the results susceptible to  
326 end-wall effects. In addition, the different strain rates (20 mm/min vs 50 mm/min) of tensile  
327 tests may also account for the lower  $E_t$  reported in the present study compared to the results  
328 in Boller and Carrington (2007). In fact, there is evidence that the use of a higher strain rate  
329 produces a higher  $E_t$  in parenchymous tissues (Niklas, 1992). In general, it is visible from the  
330 data in Table 2 that the mean value of  $E_t$  estimated in the present study is consistent with the  
331 findings for several other seaweed species (see references in Table 2).

332 Tensile Young's modulus  $E_t$  describes the response of material to tensile stress within  
333 the elastic region of a stress-strain curve only (Fig. 6a). The upper limits of this region ( $\epsilon_e$

334 and  $\sigma_e$ ) were estimated and are shown in Table 2. On average, the response of seaweed blade  
 335 material can be considered to be elastic up to 15% strain and 0.67 MPa, indicating that  $E_t$  is a  
 336 good descriptor of material behaviour in a broad range of conditions (i.e. up to  $0.8\sigma_{br}$  and  
 337  $0.6\varepsilon_{br}$ ). Differently from Harder et al. (2006), who identified two tensile Young's moduli in  
 338 specimens from seaweed stipe, in the present study a linear elastic region is found only within  
 339 the initial part of the stress-strain curves (see Fig. 6a).

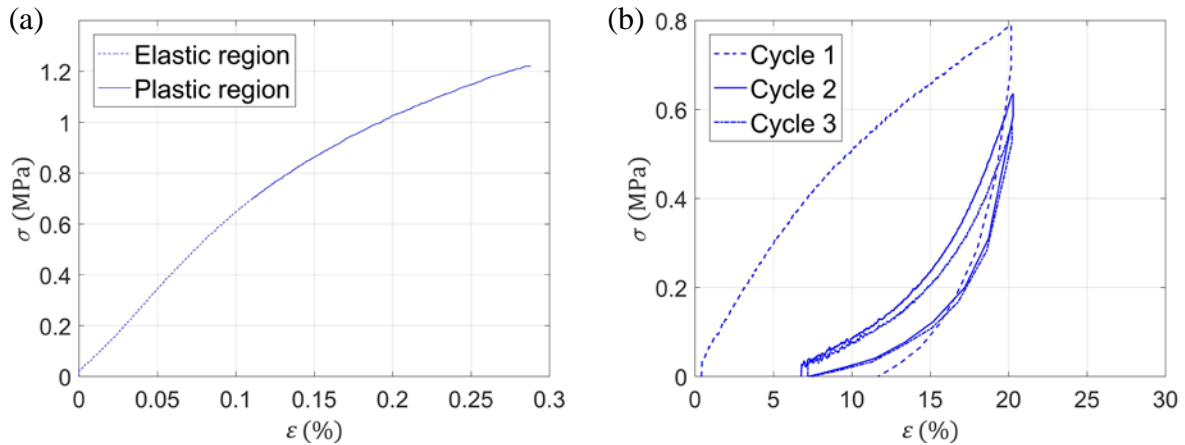
340 **Table 2** Summary of estimates of the mechanical properties (density, elastic strain limit, elastic stress limit, tensile Young's  
 341 modulus, bending Young's modulus, breaking force, breaking strain, breaking stress, toughness) of algal material obtained  
 342 in the present study compared with the data available in the literature for a number of seaweed species. Estimates from the  
 343 present study are shown as mean value  $\pm$  standard deviation. (2 columns)

Species	$\rho_s$ (kg/m <sup>3</sup> )	$\varepsilon_e$ (%)	$\sigma_e$ (MPa)	$E_t$ (MPa)	$E_b$ (MPa)	$F_{br}$ (N)	$\varepsilon_{br}$ (%)	$\sigma_{br}$ (MPa)	$U$ (MPa)	Reference
<i>S. latissima</i>	1092 $\pm$ 91	15 $\pm$ 6	<u>0.67 <math>\pm</math></u> <u>0.23</u>	<u>4.71 <math>\pm</math></u> <u>1.81</u>	<u>3.73 <math>\pm</math></u> <u>2.71</u>	<u>3.83 <math>\pm</math></u> <u>2.14</u>	<u>25 <math>\pm</math> 12</u>	<u>0.84 <math>\pm</math></u> <u>0.31</u>	<u>0.14 <math>\pm</math></u> <u>0.1</u>	Present study
n/a.	1050	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	Gaylord and Denny, 1997
n/a	1025	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	Gaylord et al., 2001
<i>A. esculenta</i>	n/a	n/a	n/a	1.2	n/a	8.9	51	1.4	0.3	Hale, 2001
<i>A. esculenta</i>	862	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	Paul et al., 2014
<i>A. marginata</i>	n/a	n/a	n/a	n/a	n/a	n/a	30	2.9	n/a	Krumhansl et al., 2015
<i>E. arborea</i>	n/a	n/a	n/a	6.4	n/a	11.9	42	2.1	0.6	Hale, 2001
<i>F. serratus</i>	1486	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	Paul et al., 2014
<i>F. vesiculosus</i>	840	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	Paul et al., 2014
<i>L. complanata</i>	n/a	n/a	n/a	n/a	n/a	n/a	27	1.3	n/a	Krumhansl et al., 2015
<i>L. digitata</i>	n/a	n/a	n/a	n/a	0.8	n/a	n/a	n/a	n/a	Henry, 2014
<i>L. digitata</i>	1001	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	Paul et al., 2014
<i>L. setchellii</i>	n/a	n/a	n/a	9.0	n/a	22.3	33	2.3	0.3	Hale, 2001
<i>L. setchellii</i>	n/a	n/a	n/a	n/a	n/a	n/a	43	3.0	n/a	Krumhansl et al., 2015
<i>L. sinclairii</i>	n/a	n/a	n/a	n/a	n/a	n/a	30	2.9	n/a	Krumhansl et al., 2015
<i>M. pyrifera</i>	n/a	n/a	n/a	5.4	n/a	7.0	18	0.8	0.1	Hale, 2001
<i>M. pyrifera</i>	n/a	n/a	n/a	n/a	n/a	n/a	18	0.9	n/a	Krumhansl et al., 2015
<i>P. fascia</i>	n/a	n/a	n/a	7.3	n/a	n/a	n/a	n/a	n/a	Boller and Carrington, 2007
<i>S. latissima</i>	n/a	n/a	n/a	9.9	n/a	n/a	n/a	n/a	n/a	Boller and Carrington, 2007
<i>S. sessilis</i>	n/a	n/a	n/a	n/a	n/a	n/a	52	1.9	n/a	Krumhansl et al., 2015

344

345 A summary of the results of tensile tests up to the breakage point is shown in Table 2.  
346 The breaking strain, breaking stress, and toughness are within the range of values reported in  
347 the previous studies for a number of seaweed species. They are among the lowest values  
348 reported for seaweeds, suggesting that blades of *S. latissima* are relatively flexible, and  
349 cannot sustain high axial loads (i.e. they are weak in this respect). We should note here that  
350 the force at breakage is not a useful parameter for comparison of different studies because it  
351 is specimen size-dependent.

352 When a specimen was tested, the following phases typically occurred (Fig. 6a): (a)  
353 there was a linear elastic response of the material with no visible variation in the cross-  
354 sectional area of the specimen (up to elastic limits); (b) a localised reduction in the cross-  
355 sectional area close to the centre of the specimen occurred, a phenomenon referred to as  
356 ‘necking’ (Niklas, 1992), and the response of the material was plastic; and (c) the specimen  
357 soon broke. The material of which *S. latissima* is made is ductile, as it shows plastic  
358 deformations after the elastic region, and exhibits a strain hardening behaviour, which is  
359 visible on the stress-strain curve plotted in Fig. 6a. This behaviour is common to many  
360 biomaterials, such as silk and plant tissues (Niklas and Spatz, 2012). It implies that the  
361 material can sustain further loading as the strain increases over the linear elastic region and is  
362 linked to the re-alignment of tissues in the direction parallel to the uniaxial force. The shape  
363 of the stress-strain curve (so called ‘r-shape’) also indicates that high values of stress, rather  
364 than high strains, are critical for breakage of seaweed tissues.



365 **Fig. 6** Examples of stress-strain curves from a tensile test up to the breakage point (a) and a tensile cyclic loading-unloading  
 366 test (3 cycles showed) (b). In (a) linear elastic region and plastic region are shown; (b) shows the changes in the stress-strain  
 367 curve after the first loading. (2 columns)

368 Effects of tensile loading-unloading cycles on the properties of seaweed tissues are  
 369 visible in the stress-strain curves in Fig. 6b. The curvature varies after the 1<sup>st</sup> loading (Cycle  
 370 1), the curve changing from concave downward to concave upward, and the stress required to  
 371 reach the same level of deformation decreases. A similar behaviour was reported by Hale  
 372 (2001) for algal materials from several seaweed species. In other words, the material loses  
 373 stiffness at small strains, while it becomes stiffer for values of strain close to the maximum  
 374 previously experienced, resembling the trend shown by the previous unloading curve. The  
 375 material does not recover completely from the applied strain and experiences permanent  
 376 deformations. However, a part of these deformations is recovered between the end of the  
 377 unloading phase and the beginning of the 2<sup>nd</sup> loading cycle, which are separated by a time lag  
 378 of a few seconds (time required to set up the testing machine), suggesting a viscoelastic  
 379 behaviour of the material. After the 2<sup>nd</sup> loading cycle, the stress-strain curves do not appear to  
 380 change significantly.

381 Variations between loading-unloading cycles can be assessed quantitatively comparing  
 382 the values of the elastic hysteresis, degree of elasticity, and energy ratio of each cycle (Table

383 3). The elastic hysteresis  $E_{cycle}$  decreases significantly between the 1<sup>st</sup> and 2<sup>nd</sup> cycles, result  
384 that is apparent in Fig. 6b. A decrease in elastic hysteresis indicates that the specimen  
385 dissipates a lower amount of energy after the 1<sup>st</sup> cycle. The degree of elasticity  $E_\epsilon$  does not  
386 vary significantly between the 1<sup>st</sup> and 2<sup>nd</sup> cycles (ANOVA,  $P=0.087$ ; variances homogenous:  
387 Levene's test,  $P=0.79$ ). This result is somewhat unexpected, as most plastic deformations  
388 occur during the 1<sup>st</sup> cycle. However, the values of  $E_\epsilon$  are biased as, by definition, the original  
389 length of the specimen is taken into account for the calculation of  $E_\epsilon$  in every cycle (i.e. any  
390 extension from the original length of the specimen accounts as a deformation). A more  
391 appropriate approach is to consider only the deformations that extend the specimen beyond  
392 its length at the beginning of each cycle (i.e. sum of its original length and plastic  
393 deformations caused by the previous cycle). This way,  $E_\epsilon$  is very close to unity both in the 2<sup>nd</sup>  
394 and 3<sup>rd</sup> cycles, meaning that no plastic deformations occur after the 1<sup>st</sup> cycle. The energy ratio  
395  $E_{ratio}$  increases significantly between the 1<sup>st</sup> and 2<sup>nd</sup> cycles (ANOVA,  $P \ll 0.0001$ ; variances  
396 homogenous: Levene's test,  $P=0.92$ ), indicating that the material enhances its ability to  
397 release strain energy applied by external forces (i.e. it becomes more resilient). This variation  
398 in resilience is linked to the fact the plastic deformations occur mainly during the 1<sup>st</sup> cycle.  
399 None of these parameters show significant variation between the 2<sup>nd</sup> and 3<sup>rd</sup> cycles, in  
400 agreement with visual observation of the stress-strain curves. These results suggest that once  
401 the material has experienced a certain level of strain it becomes more resilient, lowering the  
402 chances of damages associated with that strain level. A higher resilience comes at the price of  
403 the material experiencing plastic deformations that are not recoverable in the short term.  
404 Nevertheless, permanent deformations that may occur due to extreme events or biotic factors  
405 in a natural environment can be important to enhance organism growth (Niklas and Spatz,  
406 2012).

407 Due to the relative complexity of performing the tests and the difficult interpretation of  
 408 the results, very few data sets are available in the literature regarding tensile cyclic loading-  
 409 unloading tests on algal material. According to the results in Hale (2001), the energy ratio for  
 410 algal materials ranges from 0.15 to 0.43 for the 1<sup>st</sup> cycle and from 0.62 to 0.89 for successive  
 411 cycles. These values are compatible with the results from the present study (Table 3).

412 **Table 3** Summary of estimates of mechanical properties (elastic hysteresis, degree of elasticity,  
 413 energy ratio) of algal material from tensile cyclic loading-unloading tests. Estimates are shown  
 414 for each loading-unloading cycle as mean value  $\pm$  standard deviation. (1 column)

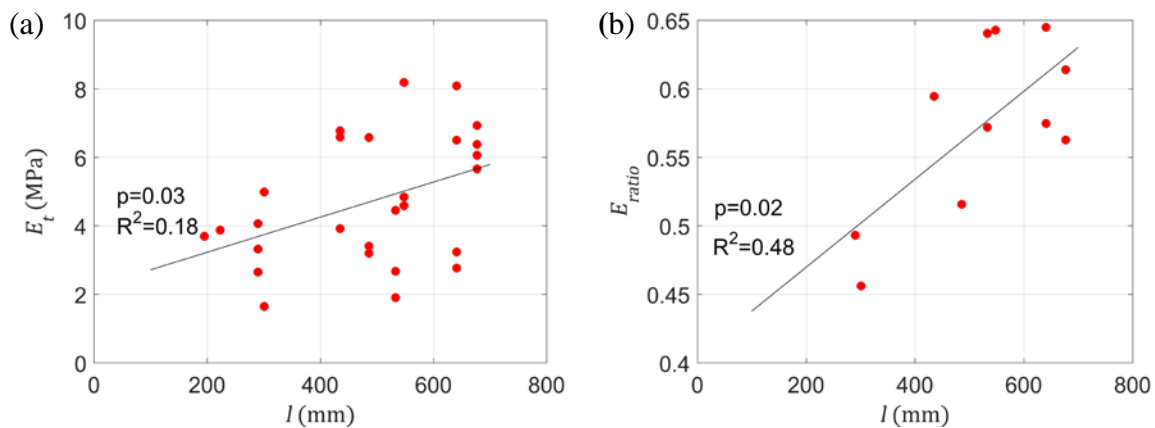
	$E_{cycle} (MJ/m^3)$	$E_{\epsilon} (-)$	$E_{ratio} (-)$
<b>Cycle 1</b>	0.069 $\pm$ 0.028	0.497 $\pm$ 0.067	0.208 $\pm$ 0.031
<b>Cycle 2</b>	0.015 $\pm$ 0.006	0.562 $\pm$ 0.094	0.527 $\pm$ 0.030
<b>Cycle 3</b>	0.012 $\pm$ 0.004	0.620 $\pm$ 0.062	0.574 $\pm$ 0.060

### 415 3.3. *Effects of blade length on its mechanical properties*

416 The mechanical properties of algal material were also analysed as a function of the blade  
 417 length, by checking potential correlations between the blade length and the biomechanical  
 418 parameters introduced in section 2.3. Almost all biomechanical parameters were found to be  
 419 independent of the blade length, including material density, stress at breakage, and toughness.  
 420 On the other hand, tensile Young's modulus  $E_t$  (Fig. 7a) and resilience for the 2<sup>nd</sup> and 3<sup>rd</sup>  
 421 (Fig. 7b) cycles increase significantly with blade length. The regression lines, however, do  
 422 not appear to be able to fully describe the broad variance shown by the data, particularly for  
 423  $E_t$  ( $R^2=0.18$ ). The lack of correlation between the blade length and biomechanical parameters  
 424 can be explained by considering the way in which specimens were prepared in the present  
 425 study and findings reported in Krumhansl et al. (2015).

426 Growth in *S. latissima* occurs in the intercalary meristem, located in the transition  
 427 region between the stipe and the blade (Bold and Wynne, 1985). Consequently, the newest  
 428 material is close to the transition region and it gets older towards the distal end of the blade.

429 Krumhansl et al. (2015) reported that mechanical properties of seaweed material vary  
 430 depending on its position along the blade and, as a consequence, on its age: tensile Young's  
 431 modulus and breaking stress increase with age, while breaking strain reduces. In the present  
 432 study, however, specimens were cut haphazardly from the central part of the blades, without  
 433 measuring the distance from the intercalary meristem. Biomechanical parameters of material  
 434 from long seaweed blades were characterised by high variance, which affected the  
 435 identification of correlations between the blade length and most of these parameters. The  
 436 natural tendency of aging materials to affect their mechanics (e.g. Niklas, 1992) is a plausible  
 437 explanation for this lack of correlation. However, this does not appear to be the case for  
 438 material density, which showed a homogenous variance across the range of blade lengths.



439 **Fig. 7** Relationships between the blade length and tensile Young's modulus (a) and energy ratio for Cycle 3 (b). Both  
 440 regression lines are significant (i.e.  $p<0.05$ ), however they do not describe most of the variance shown by the data. (2  
 441 columns)

#### 442 **4. Conclusions**

443 The present study addresses the existing lack of knowledge on biomechanics and  
 444 morphology of vegetation living in coastal waters. In particular, the mechanical and  
 445 morphological properties of *S. latissima*, a seaweed species widely distributed along the  
 446 coasts of the North East Atlantic, were investigated. The morphology of seaweed blades is



447 strongly influenced by the hydraulic conditions (i.e. phenotypic plasticity), showing a  
448 particularly high variability among blades longer than 400 mm. A common ‘stretched  
449 droplet’ shape is reported for most blades, and may play a role in reducing the drag force  
450 experienced by the seaweeds.

451         The density of algal material and a number of mechanical parameters that can improve  
452 understanding of seaweed interactions with the water flow were successfully estimated.  
453 Samples of *S. latissima* are slightly heavier than seawater and their tissues are flexible,  
454 allowing them to go with the flow passively. Algal material is ductile but weak, has a good  
455 ability to recover from cyclic excitations and its tensile and bending Young’s moduli have  
456 similar values. The estimated values of the elastic limits indicate that tensile Young’s  
457 modulus is an adequate descriptor of the mechanics of algal material in tension in a wide  
458 range of stresses and deformations that a blade may experience before breaking. On average,  
459 tissues from long seaweed blades are stiffer and more resilient than those from short blades.  
460 However, in future studies the effect of blade length on mechanical properties should be  
461 assessed taking into account the different ages of tissues along the blade.

462         The results from the current study can be used for designing physical models of  
463 seaweeds to be tested for a number of applications (for example, to investigate the drag force  
464 experienced by a seaweed patch, either artificial or natural). This study is also helpful for the  
465 development of numerical models involving flow-vegetation interactions, providing  
466 information (i.e. Young’s modulus and density of seaweed material) required for predicting  
467 seaweed motion. The other biomechanical parameters estimated can contribute to the  
468 understanding of seaweed mechanical response to physical stresses.

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