

Morphological and mechanical properties of blades of *Saccharina latissima*

Original

Morphological and mechanical properties of blades of *Saccharina latissima* / Vettori, D., Nikora, V.. - In: ESTUARINE, COASTAL AND SHELF SCIENCE. - ISSN 0272-7714. - 196:(2017), pp. 1-9. [10.1016/j.ecss.2017.06.033]

Availability:

This version is available at: 11583/2769112 since: 2019-11-22T14:42:32Z

Publisher:

Elsevier

Published

DOI:10.1016/j.ecss.2017.06.033

Terms of use:

This article is made available under terms and conditions as specified in the corresponding bibliographic description in the repository

Publisher copyright

Elsevier postprint/Author's Accepted Manuscript

© 2017. This manuscript version is made available under the CC-BY-NC-ND 4.0 license
<http://creativecommons.org/licenses/by-nc-nd/4.0/>. The final authenticated version is available online at:
<http://dx.doi.org/10.1016/j.ecss.2017.06.033>

(Article begins on next page)

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

3 Davide Vettori^{†*}, Vladimir Nikora

4 *School of Engineering, University of Aberdeen, Aberdeen, AB24 3UE, Scotland, UK*

5 [†] *Current address: Department of Geography, Loughborough University, Loughborough, LE11 3TU, UK*

6 **Corresponding author (email: d.vettori@lboro.ac.uk)*

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 10th 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.



114

115

116

117

118

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

120

121

122

123

124

125

126

127

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[®] 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.

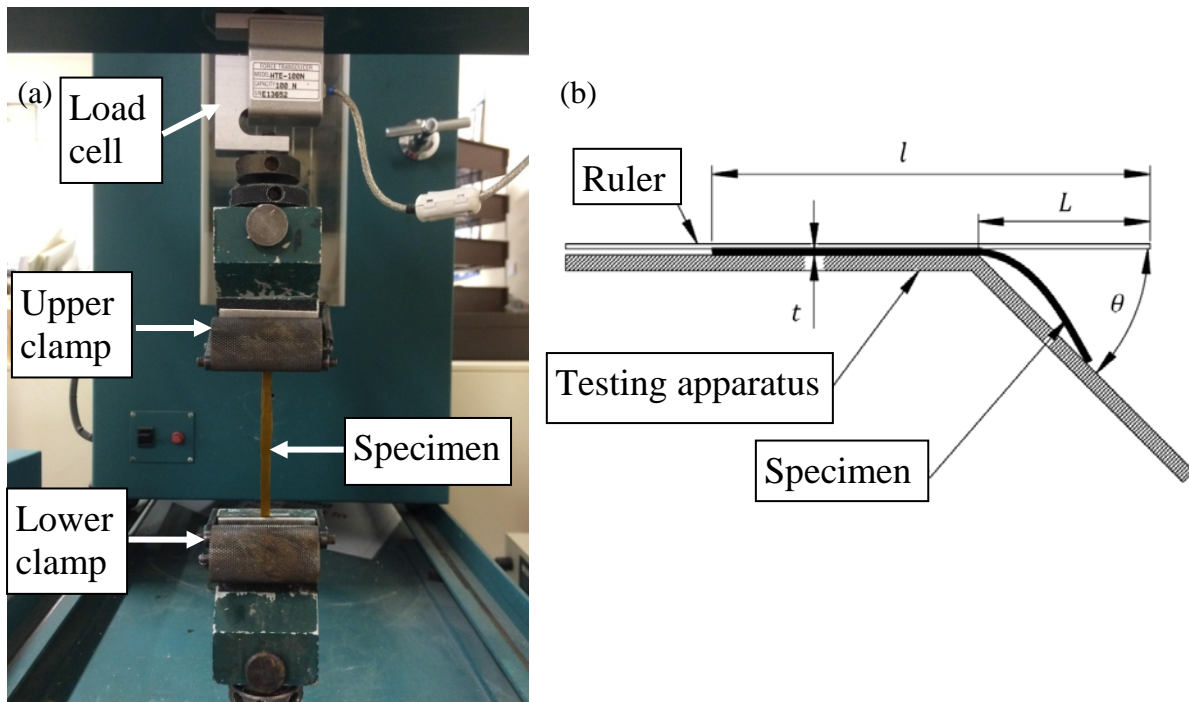
139 2.3. *Mechanical testing*

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)

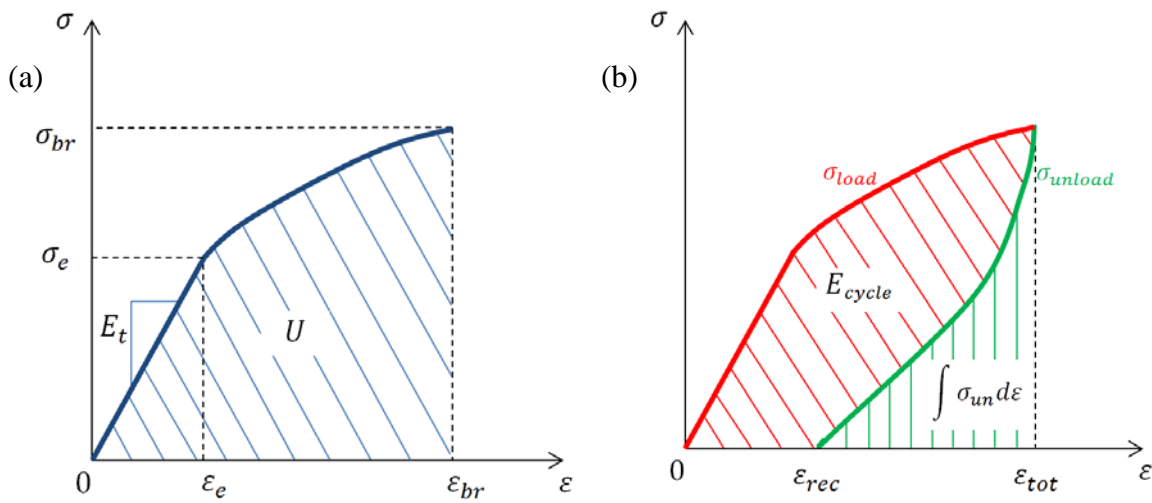
175 During the test, the upper clamp of the machine moved upwards with a constant speed
 176 that could be set via dedicated software. The tensile tests were initiated with the clamps
 177 located at a distance of 60 mm from each other. The specimens were stretched at a constant
 178 speed set to 20 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 δ were recorded with a dedicated software (Tinius Olsen, Salfords, UK). For
 184 analysis purposes, these data were converted into nominal stress σ (i.e. ratio of force to
 185 original cross-sectional area of the specimen) and nominal strain ε (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 σ to ε within a linear region of
 189 $\sigma = f(\varepsilon)$; elastic limits σ_e and ε_e ; stress σ_{br} , force F_{br} and strain ε_{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_{ε} , 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 θ of 46° . 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):

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

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 θ (46°) in Fig. 2b represents the
229 inclination of the tilted part of the apparatus (Peirce, 1930).

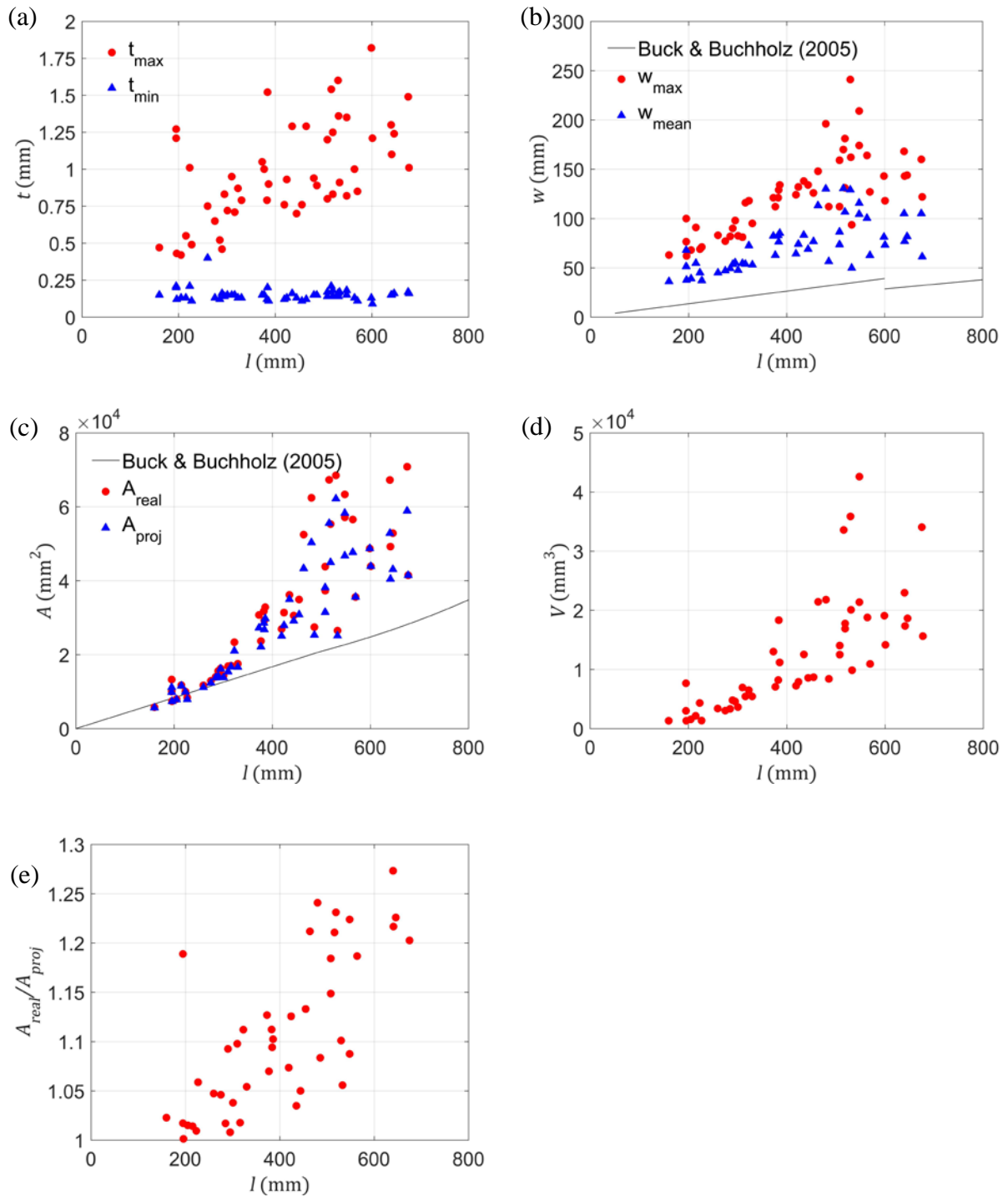
230 **3. Results and discussion**

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.

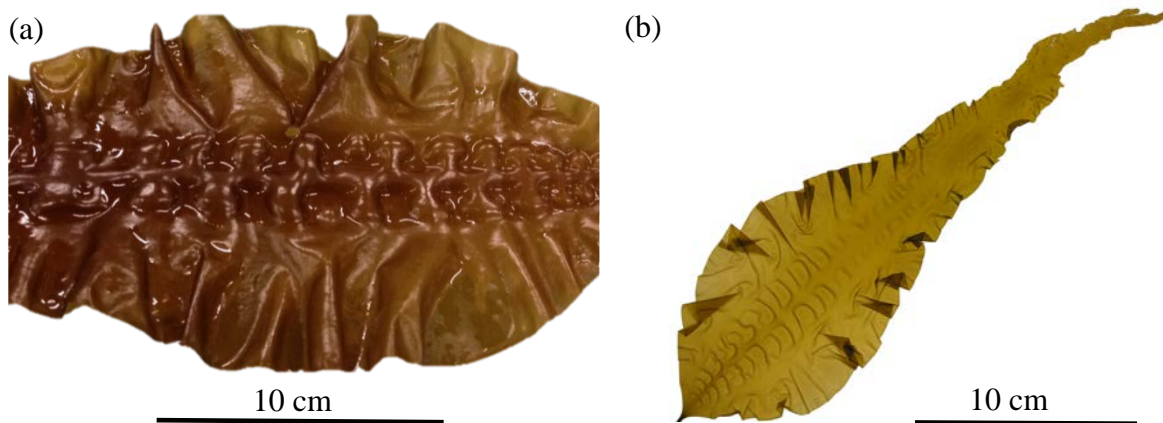


262 **Fig. 4** Relationships between the blade length l and: the maximum t_{max} and minimum t_{min} thicknesses (a); the maximum w_{max}
 263 and average w_{mean} widths (b); the full-one-side (real) A_{real} and projected A_{proj} surface areas (c); the blade volume V (d); and
 264 the level of undulation 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 kg/m³, 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 (ϵ_e

334 and σ_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).

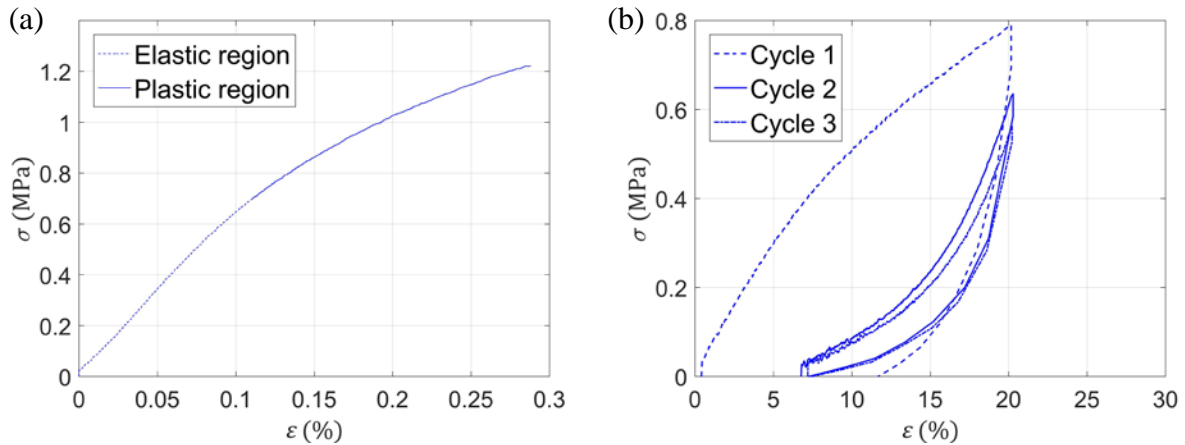
340 **Table 2** Summary of estimates of the mechanical properties (density, elastic strain limit, elastic stress limit, tensile Young's
 341 modulus, bending Young's modulus, breaking force, breaking strain, breaking stress, toughness) of algal material obtained
 342 in the present study compared with 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	ρ_s (kg/m ³)	ε_e (%)	σ_e (MPa)	E_t (MPa)	E_b (MPa)	F_{br} (N)	ε_{br} (%)	σ_{br} (MPa)	U (MPa)	Reference
<i>S. latissima</i>	1092 \pm 91	15 \pm 6	<u>0.67 \pm</u> <u>0.23</u>	<u>4.71 \pm</u> <u>1.81</u>	<u>3.73 \pm</u> <u>2.71</u>	<u>3.83 \pm</u> <u>2.14</u>	<u>25 \pm 12</u>	<u>0.84 \pm</u> <u>0.31</u>	<u>0.14 \pm</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 1st 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 2nd 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 2nd 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 1st and 2nd 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 1st cycle. The degree of elasticity E_{ϵ} does not
386 vary significantly between the 1st and 2nd 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 1st cycle. However, the values of E_{ϵ} are biased as, by definition, the original
389 length of the specimen is taken into account for the calculation of E_{ϵ} 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_{ϵ} is very close to unity both in the 2nd
394 and 3rd cycles, meaning that no plastic deformations occur after the 1st cycle. The energy ratio
395 E_{ratio} increases significantly between the 1st and 2nd 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 1st cycle.
399 None of these parameters show significant variation between the 2nd and 3rd 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 1st 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)

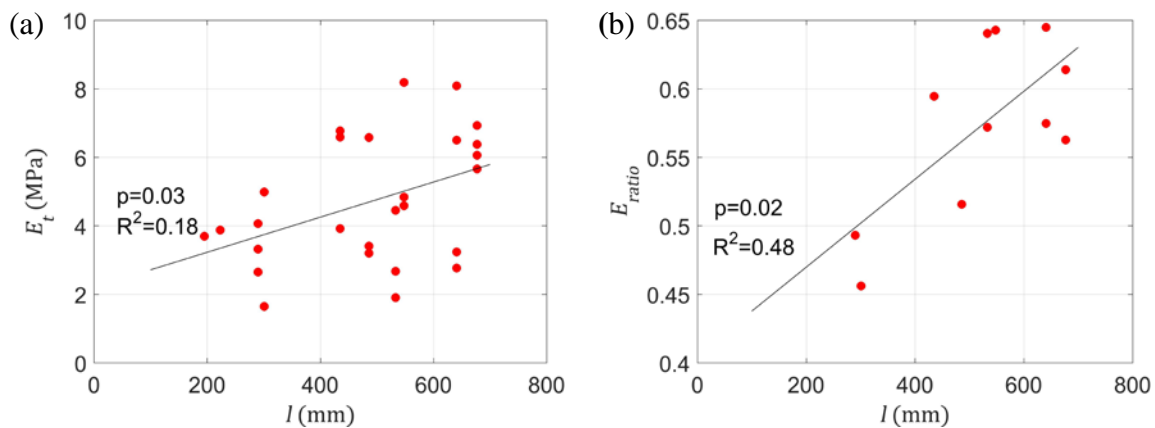
	E_{cycle} (MJ/m ³)	E_{ϵ} (-)	E_{ratio} (-)
Cycle 1	0.069 \pm 0.028	0.497 \pm 0.067	0.208 \pm 0.031
Cycle 2	0.015 \pm 0.006	0.562 \pm 0.094	0.527 \pm 0.030
Cycle 3	0.012 \pm 0.004	0.620 \pm 0.062	0.574 \pm 0.060

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 2nd and 3rd
 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.

469 **Acknowledgements**

470 The work described in this publication was conducted during the Ph.D. study of D. Vettori,
471 funded by the Northern Research Partnership. The authors thank Olivia McCabe for her
472 contribution to conducting morphological and mechanical tests, David Attwood and Hamish
473 Biggs for their assistance during seaweed collection and transport to the University of
474 Aberdeen.

475 **References**

- 476 Bardach, J. E., Ryther, J. H., McLarney, W. O., 1972. Aquaculture - The Farming and
477 Husbandry of Freshwater and Marine Organisms. John Wiley and Sons, Inc., New York,
478 868 pp.
- 479 Biedka, R. F., Gosline, J. M., and DeWreede, R. E., 1987. Biomechanical analysis of wave-
480 induced mortality in the marine alga *Pterygophora californica*. Marine Ecology Progress
481 Series, 36, 163-170.
- 482 Bold, H. C., and Wynne, M. J., 1985. Introduction to the Algae. Prentice-Hall, Inc.,
483 Englewood Cliffs, New Jersey, 720 pp.
- 484 Boller, M. L., and Carrington, E., 2007. Interspecific comparison of hydrodynamic
485 performance and structural properties among intertidal macroalgae. The Journal of
486 Experimental Biology, 210(11), 1874-1884.
- 487 Buck, B. H., and Buchholz, C. M., 2005. Response of offshore cultivated *Laminaria*
488 *saccharina* to hydrodynamic forcing in the North Sea. Aquaculture, 250(3), 674-691.
- 489 Chan, C. X., Ho, C. L., and Phang, S. M., 2006. Trends in seaweed research. Trends in Plant
490 Science, 11(4), 165-166.

491 Chopin, T., and Sawhney, M., 2009. Seaweeds and their mariculture. The Encyclopedia of
492 Ocean Sciences, 4477-4487.

493 Connell, B. S., and Yue, D. K., 2007. Flapping dynamics of a flag in a uniform stream.
494 Journal of fluid mechanics, 581, 33-67.

495 Druehl, L. D., and Kaneko, T., 1973. On *Laminaria saccharina* from Hokkaido. Journal of
496 Plant Research, 86(4), 323-327.

497 Fei, X., 2004. Solving the coastal eutrophication problem by large scale seaweed cultivation.
498 Hydrobiologia, 512(1-3), 145-151.

499 Fonseca, M. S., and Koehl, M. A. R., 2006. Flow in seagrass canopies: the influence of patch
500 width. Estuarine, Coastal and Shelf Science, 67(1), 1-9.

501 Gaylord, B., and Denny, M., 1997. Flow and flexibility. I. Effects of size, shape and stiffness
502 in determining wave forces on the stipitate kelps *Eisenia arborea* and *Pterygophora*
503 *californica*. Journal of Experimental Biology, 200(24), 3141-3164.

504 Gaylord, B., Hale, B. B., and Denny, M. W., 2001. Consequences of transient fluid forces for
505 compliant benthic organisms. Journal of Experimental Biology, 204(7), 1347-1360.

506 Gerard, V. A., 1987. Hydrodynamic streamlining of *Laminaria saccharina* Lamour in
507 response to mechanical stress. Journal of Experimental Marine Biology and Ecology,
508 107(3), 237-244.

509 Hale, B. B., 2001. Macroalgal materials: foiling fracture and fatigue from fluid forces. Ph.D.
510 thesis, Stanford University, California.

511 Harder, D. L., Hurd, C. L., and Speck, T., 2006. Comparison of mechanical properties of four
512 large, wave-exposed seaweeds. American Journal of Botany, 93(10), 1426-1432.

513 Henry, P. Y. T., 2014. Bending properties of a macroalga: Adaptation of Peirce's cantilever
514 test for in situ measurements of *Laminaria digitata* (Laminariaceae). American Journal
515 of Botany, 101(6), 1050-1055.

516 Hounsfield Test Equipment, 1997. S-Series operating instructions. UK.

517 Hughes, A. D., Kelly, M. S., Black, K. D., and Stanley, M. S., 2012. Biogas from
518 macroalgae: is it time to revisit the idea. Biotechnology for Biofuels, 5(86), 1-7.

519 Hurd, C. L., and Pilditch, C. A., 2011. Flow-induced morphological variations affect
520 diffusion boundary-layer thickness of *Macrocystis pyrifera* (Heterokontophyta,
521 laminariales). Journal of Phycology, 47(2), 341-351.

522 Hurd, C. L., Harrison, P. J., Bischof, K., and Lobban, C. S., 2014. Seaweed ecology and
523 physiology. Cambridge University Press, New York, 551 pp.

524 James, M.A., 2010. A review of initiatives and related R&D being undertaken in the UK and
525 internationally regarding the use of macroalgae as a basis for biofuel production and
526 other non-food uses relevant to Scotland. Report commissioned by the Marine Scotland,
527 79pp [online] Available at: <http://www.gov.scot/Resource/Doc/295194/0115064.pdf>
528 [accessed 17/04/2015]

529 Koehl, M. A. R., and Alberte, R. S., 1988. Flow, flapping, and photosynthesis of *Nereocystis*
530 *leutkeana*: a functional comparison of undulate and flat blade morphologies. Marine
531 Biology, 99(3), 435-444.

532 Koehl, M. A. R., Silk, W. K., Liang, H., and Mahadevan, L., 2008. How kelp produce blade
533 shapes suited to different flow regimes: a new wrinkle. Integrative and Comparative
534 Biology, 48(6), 834-851.

535 Krumhansl, K. A., Demes, K. W., Carrington, E., and Harley, C. D., 2015. Divergent growth
536 strategies between red algae and kelps influence biomechanical properties. *American Journal*
537 *of Botany*, 102(11), 1938-1944.

538 Lamprianidou, F., Telfer, T., and Ross, L. G., 2015. A model for optimization of the
539 productivity and bioremediation efficiency of marine integrated multitrophic
540 aquaculture. *Estuarine, Coastal and Shelf Science*, 164, 253-264.

541 Lucas, J. S., and Southgate, P. C., 2012. *Aquaculture: Farming aquatic animals and plants.*
542 *Wiley-Blackwell, Hoboken, New Jersey, 648 pp.*

543 Lüning, K., Chapman, A. R., and Mann, K. H., 1978. Crossing experiments in the non-
544 digitate complex of *Laminaria* from both sides of the Atlantic. *Phycologia*, 17(3), 293-
545 298.

546 Mata, L., Schuenhoff, A., and Santos, R., 2010. A direct comparison of the performance of
547 the seaweed biofilters, *Asparagopsis armata* and *Ulva rigida*. *Journal of Applied*
548 *Phycology*, 22(5), 639-644.

549 Miler, O., Albayrak, I., Nikora, V., and O'Hare, M., 2012. Biomechanical properties of
550 aquatic plants and their effects on plant–flow interactions in streams and rivers. *Aquatic*
551 *Sciences*, 74(1), 31-44.

552 Möller, I., Spencer, T., French, J. R., Leggett, D. J., and Dixon, M., 1999. Wave
553 transformation over salt marshes: a field and numerical modelling study from North
554 Norfolk, England. *Estuarine, Coastal and Shelf Science*, 49(3), 411-426.

555 Niklas, K. J., 1992. *Plant biomechanics: an engineering approach to plant form and function.*
556 *University of Chicago press, Chicago, Illinois, 622 pp.*

557 Niklas, K. J., and Spatz, H. C., 2012. Plant physics. University of Chicago Press, Chicago,
558 Illinois, 448 pp.

559 Nikora, V., 2010. Hydrodynamics of aquatic ecosystems: an interface between ecology,
560 biomechanics and environmental fluid mechanics. River Research and Applications,
561 26(4), 367-384.

562 Païdoussis, M. P., 1998. Fluid-Structure Interactions: Slender Structures and Axial Flow.
563 Elsevier, Amsterdam, The Netherlands, 1585 pp.

564 Paul, M., Henry, P. Y., and Thomas, R. E., 2014. Geometrical and mechanical properties of
565 four species of northern European brown macroalgae. Coastal engineering, 84, 73-80.

566 Peirce, F. T., 1930. The “handle” of cloth as a measurable quantity. Journal of the Textile
567 Institute Transactions, 21, T377-T416.

568 Ramos, E., Juanes, J.A., Galván, C., Neto, J.M., Melo, R., Pedersen, A., Scanlan, C., Wilkes,
569 R., van den Bergh, E., Blomqvist, M., Karup, H.P., Heiber, W., Reitsma, J.M., Ximenes,
570 M.C., Silió, A., Méndez, F., González, B., 2012. Coastal waters classification based on
571 physical attributes along the NE Atlantic region. An approach for rocky macroalgae
572 potential distribution. Estuarine, Coastal and Shelf Science, 112, 105-114.

573 Sánchez-González, J. F., Sánchez-Rojas, V., and Memos, C. D., 2011. Wave attenuation due
574 to *Posidonia oceanica* meadows. Journal of Hydraulic Research, 49(4), 503-514.

575 Sanderson, J. C., 2006. Reducing the environmental impact of seaweed fish farming through
576 cultivation of seaweed. Ph.D. thesis, The Open University, UK and UHI Millenium
577 Institute.

- 578 Schlichting, C. D., 1986. The evolution of phenotypic plasticity in plants. Annual review of
579 Ecology and Systematics, 17(1), 667-693.
- 580 Siniscalchi, F., and Nikora, V., 2013. Dynamic reconfiguration of aquatic plants and its
581 interrelations with upstream turbulence and drag forces. Journal of Hydraulic Research,
582 51(1), 46–55.
- 583 Temmerman, S., Meire, P., Bouma, T.J. et al. 2013. Ecosystem-based coastal defence in the
584 face of global change. Nature, 504(7478), 79–83.
- 585 Vettori, D., 2016. Hydrodynamic performance of seaweed farms: an experimental study at
586 seaweed blade scale. Ph.D. thesis, University of Aberdeen, UK.
- 587 Wargacki, A. J., Leonard, E., Win, M. N., Regitsky, D. D., Santos, C. N. S., Kim, P. B.,
588 Cooper, S. R., Raisner, R. M., Herman, A., Sivitz, A. B., Lakshmanaswamy, A.,
589 Kashiya, Y., Baker, D., and Yoshikuni, Y., 2012. An engineered microbial platform
590 for direct biofuel production from brown macroalgae. Science, 335(6066), 308-313.
- 591 West-Eberhard, M. J., 1989. Phenotypic plasticity and the origins of diversity. Annual review
592 of Ecology and Systematics, 20(1), 249-278.