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1 **Allometric relationships for intertidal macroalgae species of commercial interest**

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8

9 **Abstract**

10 The demand for seaweeds has intensified in recent decades and will most certainly continue to
11 expand. Several methods exist to evaluate the biomass of seaweeds in the field but most of
12 them are destructive. The objectives of this study were (1) to develop and evaluate allometric
13 equations for estimating seaweed biomass in the field for some harvested species, and (2) to
14 provide uniform calculated dry/wet biomass ratios to estimate the relative water content of
15 these seaweeds. Sampling and measurements of more than 350 seaweeds individuals were
16 carried out for 8 species of commercial interest. Our models were fitted for both power and
17 linear equations and were tested for different explanatory variables. While the power equation
18 was found to be the best for predicting biomass of all species, we found that the best
19 descriptive biometric variable varies according to seaweed morphology. Species with a bushy
20 morphology were best described by the volume, while long stringy species were best
21 described by the length and flat species by the surface. This study attempts to provide
22 nondestructive tools that could be used by professional seaweed harvesters, their employers as
23 well as scientists and public regulators, to assess the harvest potential of a field of seaweed in
24 a nondestructive approach.

25 **Keywords:** biometrics, biomass, allometry, harvesting

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32 investment expenditure programme IDEALG ANR-10-BTBR-04.

33 **Introduction**

34 Seaweed diversity and community structure are highly impacted and threatened by physical
35 and/or anthropic forcing such as climatic changes (Airoldi and Beck 2007; Mangialajo et al.
36 2008). These continued stressors cause the fragmentation and loss of canopy-forming algae
37 worldwide (Connell et al. 2008; Airoldi et al. 2008), and even could lead to their extinction
38 (Estes et al. 1989). Besides producing a valuable crop to the seaweed harvesters, macroalgae
39 plays an important role in the primary production of nearshore ecosystems (Golléty et al.
40 2008; Migné et al. 2015). Within this context of increasing pressures, one can wonder about
41 the effects of the loss of canopy-forming algae on primary production and on carbon and
42 nitrogen biochemical cycles. Accurate and efficient estimation of biomass in such populations
43 is central to understand and monitor their net contribution in providing these ecosystem
44 services.

45 Ecologists, botanists and foresters estimate biomass for a wide range of purposes, such as
46 assessment of crop value, site productivity, as well as nutrient recycling. Destructive sampling
47 has generally been used to obtain an accurate measure of biomass at a particular sampling
48 point, including in seaweed populations (Mathieson and Guo 1992; Vadas, Sr. et al. 2004).
49 However, these destructive approaches can have short and long-term consequences on the
50 associated ecosystem, including decrease in invertebrate abundance and richness (Benedetti-
51 Cecchi et al. 2001; Watt and Scrosati 2013), replacement by grazers or turfs (Perkol-Finkel
52 and Airoldi 2010), or reduction in algal biomass and primary productivity (Golléty et al.
53 2008; Tait and Schiel 2011). In order to reduce these effects, nondestructive methods were
54 developed to answer specific questions in plants (Niklas and Enquist 2002; Sack et al. 2003;
55 Scrosati et al. 2005; Mccarthy and Enquist 2007; Poorter et al. 2012). Without losing their
56 scientific rigor, the use of nondestructive sampling methods permits the absence of laboratory
57 work, simplifying data processing and reducing the total monitoring costs. One of these

58 nondestructive methods is based on fitting so-called allometric equations to convert field
59 inventory data to biomass estimates (Chave et al. 2005; Jonson and Freudenberger 2011; Paul
60 et al. 2013). In seaweeds, this method was mainly applied in population dynamics of red and
61 brown algae (Åberg 1990; Lindgren et al. 1998; Engel et al. 2001) or to estimate growth
62 during two sampling events (Vaz-Pinto et al. 2014). Allometric equations are particularly
63 useful to evaluate biomass allocation pattern (i.e. the relative amount of biomass present in
64 the various organs; Niklas and Enquist 2002), to measure the temporal evolution of the
65 biomass on a specific field, or to adjust the harvesting pressure according to biomass
66 estimates at a given time. Biological ratios are often used in the literature to standardize
67 biological data. Dry/wet biomass ratios, are generally used to estimate the relative water
68 content in plants and to homogenize the parameters found in the literature (which may be
69 expressed either in dry or wet biomass). Moreover, this ratio can be used by professional
70 seaweed harvesters (or their employers) that are required, under French law, to report monthly
71 the quantities of algae they have harvested, in fresh biomass.

72 Seaweeds are a polyphyletic group that displays a wide diversity of life cycles and
73 morphologically diverse thalli with variable growth rates. Because seaweeds species are
74 highly diverse, estimation of their biomass through allometric relationships is a challenging
75 task. The overall objective of this study was to develop and evaluate allometric equations for
76 estimating the biomass in the tree main groups of harvested seaweed (three red algal species
77 (*Chondrus crispus*, *Mastocarpus stellatus*, *Palmaria palmata*), four brown algal species
78 (*Fucus serratus*, *Fucus vesiculosus*, *Himanthalia elongata*, *Saccharina latissima*) and one
79 green algal species (*Ulva* sp.). We also provide uniform calculated dry/wet biomass ratios to
80 estimate the relative water content of seaweeds.

81

82

83 **Materials and methods**

84 Samples were collected in Brittany (Northern France) where more than 80% of macroalgae
85 are harvested in France. We pooled datasets obtained across several years (2004 to 2015), in
86 order to create sufficiently powered samples that are large enough to allow for meaningful
87 analysis. An attempt was made to obtain samples representative of the full length range of
88 each species. All datasets were obtained between March and November, the time when most
89 of the biomass is extracted due to greater harvestable biomass and legal harvest period.

90 In this study, we measured individuals, as defined by Scrosati (2005). The whole thallus
91 corresponding to all the fronds that arise from one holdfast was measured for clonal seaweeds
92 (*Chondrus crispus*, *Mastocarpus stellatus*, *Palmaria palmata*) and the whole thallus
93 corresponding to the only upright that arises from one holdfast was measured for unitary
94 seaweeds (*Fucus serratus*, *F. vesiculosus*, *Himantalia elongata* and *Ulva* sp.). For each
95 individual, the maximal length (L) and the dry biomass (DW), after drying at 60°C for 48h,
96 were recorded. For some species, the maximal circumference (C), the maximal width (w) and
97 the fresh biomass (FW) were also recorded, prior to the drying.

98 ***Length-biomass relationships***

99 Allometric length-biomass equations were obtained by regressing dry biomass on maximal
100 length (L), maximal circumference (C), volume (LC²), or surface (Lw). We wrote the models
101 using R to obtain both linear (Eq 1) and power law equation (Eq 2):

$$102 \quad DW = a \times X + b \quad \text{Eq 1}$$

$$103 \quad DW = a \times X^b \quad \text{Eq 2}$$

104 where DW = dry biomass (g), X = variable or combination of variables (L, C, LC², Lw), and a
105 and b are constants. Then we selected for each species the best model using the Akaike

106 information criterion (AIC) and the determination coefficient (R^2). The best statistical model
107 minimizes the value of AIC and maximizes the value of R^2 . It is important to note that we also
108 determined the length-biomass relationship of *C. crispus* and *M. stellatus* blended, because in
109 the field they usually form a mixed canopy that could not be harvested separately. We also
110 made a seasonal distinction for *H. elongata* by calculating the allometric equation for only
111 individuals harvested from March to June on one side (i.e. the harvestable individuals truly
112 harvested) and the allometric equation for all the individuals harvested between March and
113 October on the other side. After June or July, large individuals are no more harvested because
114 they are thick and grainy, thus less appealing for human consumption. Essentially, the first
115 equation (March-June) should be used by professional seaweed harvesters while the second
116 equation (March-October) could be better suited for scientist interest.

117 All statistical analyses were carried out with the R software package ([http://www.r-](http://www.r-project.org/)
118 [project.org/](http://www.r-project.org/)).

119 ***Mean water content***

120 The mean water content of the algae was determined by weighing before and after drying. In
121 order to quantify the relationship between fresh biomass and dry biomass, we used
122 standardized major axis (SMA) regression (also referred to as reduced major axis regression).
123 This method is more appropriate than least-squares regression for estimating the line of best
124 fit for the relationship between two variables (Warton et al. 2006). The obtained fitted line
125 does not change if the roles of “predictor” and “response” variables are switched; in contrast,
126 ordinary least squares regression yields a different fitted line if the y-axis and x-axis are
127 switched (Warton et al. 2006).

128

129 **Results and discussion**

130 *Development of allometric equations for estimating seaweed biomass*

131 Relationships between mass (expressed as dry biomass) and biometrics were established. We
132 tested linear and power models for more than 350 individuals from 8 different species. For
133 each model, we tested several explanatory variables: L, C, and LC^2 for *C. crispus*, *P. palmata*
134 *F. serratus*, and *F. vesiculosus*; L, w and Lw for *Ulva* sp.; and L for *H. elongata* and
135 *S. latissima*. The 10 selected length-biomass relationships are shown in Fig. 1 and their
136 respective parameters are given in Table 1. These inclusive relationships were all expressed as
137 a power model. The best descriptive biometric variable varied according to the seaweed
138 morphology. Species with a bushy morphology were best described by the volume (LC^2),
139 while long stringy species were best described by the length (L) and flat species by the
140 surface (Lw). All the relationships of the seaweed species analysed in this paper were highly
141 significant ($0.77 < R^2 < 0.96$) and could consequently be reliably applied (Table 1). Besides,
142 Gevaert et al. (2001) provided an allometric equation for the species *S. latissima* with a
143 scaling exponent really close ($b = 1.357$) to the one we calculated ($b = 1.358$). Allometric
144 equations ($DW = a \times X^b$) were not found for any other species studied.

145 Nondestructive methods of seaweed biomass estimation have successfully been applied in the
146 past. For example Scrosati and DeWreede (1997) have successfully applied nondestructive
147 methods to estimate stand biomass in a biomass-density study that was based on the fronds
148 and not on the individuals of one species (*Mazzaella cornucopiae*).

149 The two allometric equations obtained for *H. elongata* showed different allometric parameter
150 values, with the scaling exponent (b) of harvestable individuals (March-June) being lower (-
151 57%) than the one calculated with all individuals (March-October). This difference reveals an
152 ontogenetic shift, partly because in late summer and autumn, individuals of *H. elongata* get

153 thicker which increases their biomass, become not consumable and so are no more harvested
154 after June-July.

155 With the exception of *H. elongata*, seasonal variations were not completely taken into account
156 (no sampling in winter), which may potentially cause a difference between the predicted DW
157 and the observed DW at the individual scale, due to differences in tissue density (Åberg
158 1990). However, as stated above, most of the seaweed harvesting occurs between March and
159 November, which corresponds to the period when we made our samples. Also, we do believe
160 than any potential biases should be reduced at the scale of the quadrat or seaweed field.
161 Therefore, these tools can be applied to large populations and are relevant to provide accurate
162 estimates of the standing biomass of a seaweed field, in a rapid and nondestructive way.

163

164 *Development of ratios for estimating water content*

165 Relationships between DW and FW were expressed as a linear relation and were also highly
166 significant ($R^2 > 0.90$). They showed that mean water content ranged from 71.7% (*M.*
167 *stellatus*) to 88.5% (*S. latissima*) (Table 2). While DW:FW ratios may vary depending on the
168 season, our results are quite consistent with those found in the literature: Scrosati (2006)
169 described a mean water content of 76.1% for *C. crispus*, 79.3% for *F. vesiculosus* and 87.6%
170 for *S. latissima*; Gevaert et al. (2001) found a mean water content of 89% for *S. latissima*; and
171 Alveal and Ponce (1997) estimated a mean water content of 72% for *M. stellatus*. Due to
172 technical, commercial and infrastructural reasons, harvesters dry some harvested algae prior
173 to weighing them, and then convert the dry biomass into fresh biomass with a ratio that is
174 specific to each harvester or employer. These ratios are often confidential and may lead to
175 over- or underestimate the quantities of algae that are actually harvested. Here we attempt to

176 provide uniform and rigorously calculated ratios that could be used by all the professional
177 seaweed harvesters and their employers.

178 Global environment change coupled to the increased demand for seaweeds are likely to exert
179 some significant pressure on the standing seaweed biomass. The relationships established in
180 the study will provide a basis for future studies to estimate more easily and by a
181 nondestructive way the biomass of seaweed populations.

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Table 1 Length-biomass relationships of macroalgal species collected in Brittany (NW France). Power equation: $DW = a \times X^b$.

Species	Date of sampling	n	Mean total length (cm)	Total length range (cm)	Explanatory variable			
						a	b	R ²
<i>Chondrus crispus</i> & <i>Mastocarpus stellatus</i>	April-May-July-Oct.	66	10.02	3.5-16	LC ²	0.0034	0.8259	0.93
<i>Chondrus crispus</i>	May	35	8.70	3.5-13	LC ²	0.0006	1.0318	0.95
<i>Mastocarpus stellatus</i>	April-July	31	11.52	9-16	LC ²	0.0067	0.7493	0.93
<i>Fucus serratus</i>	April-Oct.	60	36.50	8-70	LC ²	0.1763	0.5996	0.92
<i>Fucus vesiculosus</i>	Nov.	48	41.44	13-117	LC ²	0.0188	0.8028	0.87
<i>Himantalia elongata</i>	March-June	65	79.58	8-232	L	0.0319	1.2878	0.77
<i>Himantalia elongata</i>	March-June-Aug.-Oct.	75	98.20	8-281	L	0.0005	2.2323	0.81
<i>Palmaria palmata</i>	July-Oct.	40	29.73	10-65	LC ²	0.0006	1.4183	0.91
<i>Saccharina latissima</i>	April	30	97.90	22-214	L	0.0155	1.3587	0.95
<i>Ulva</i> sp.	Oct.	37	21.10	2-87	Lw	0.0077	0.8921	0.93

Table 2 Mean water content of macroalgal species collected in Brittany (NW France).

Species	n	Mean water content	a	b	R ²
<i>Chondrus crispus</i> & <i>Mastocarpus stellatus</i>	66	74.4%	0.257	-0.034	0.96
<i>Chondrus crispus</i>	35	77.4%	0.226	0.048	0.99
<i>Mastocarpus stellatus</i>	31	71.7%	0.284	-0.139	0.96
<i>Fucus serratus</i>	30	78.4%	0.216	0.694	0.99
<i>Himantalia elongata</i>	37	83.3%	0.167	-1.365	0.90
<i>Palmaria palmata</i>	40	87.3%	0.127	0.777	0.95
<i>Saccharina latissima</i>	30	88.5%	0.116	0.107	0.99

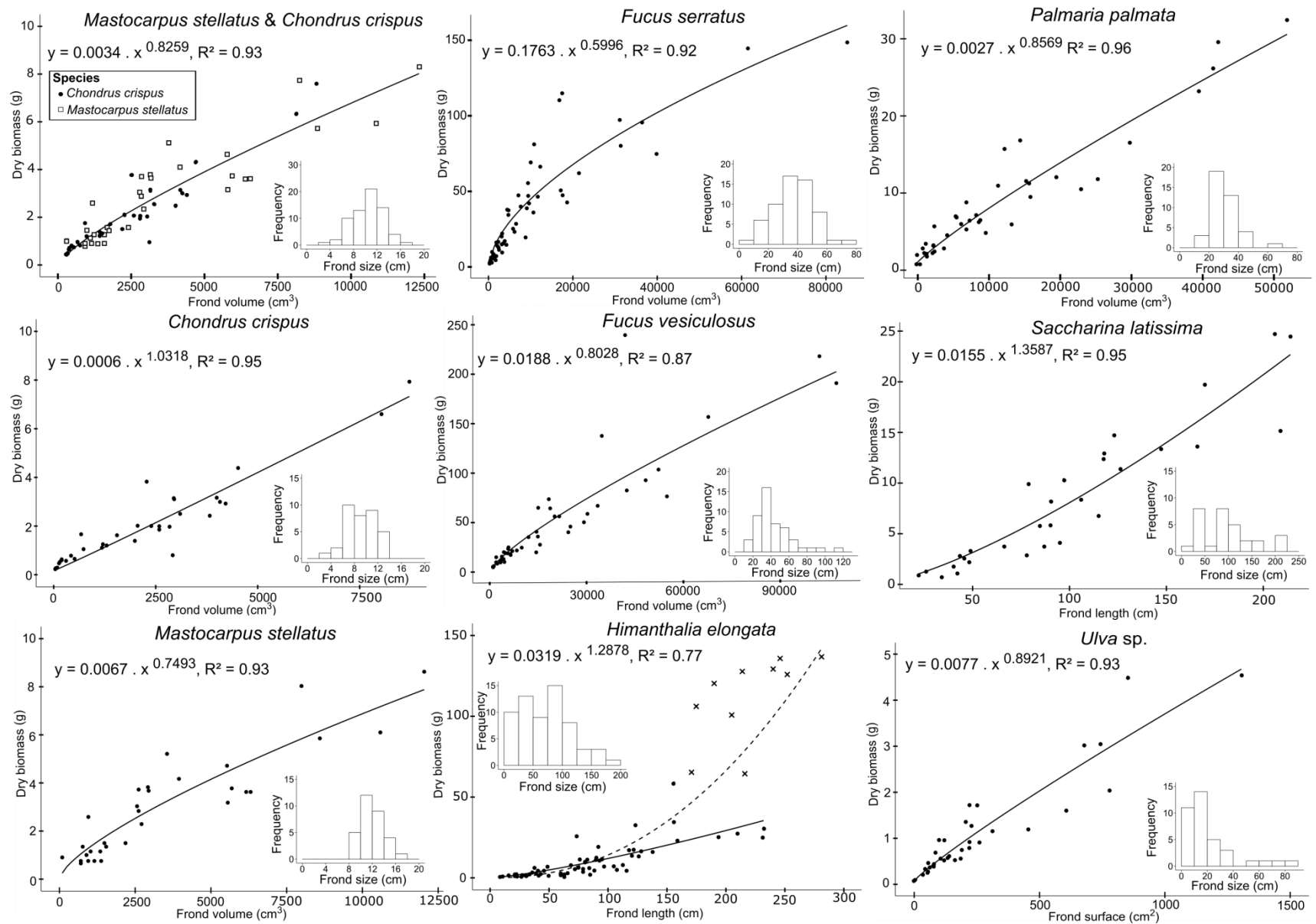


Fig. 1 Relationships between dry biomass (g) and biometric variables (in cm, cm², or cm³). For *Himanthalia elongata*, the plain line represents individuals harvested between March and June (i.e. the harvestable individuals truly harvested; round data points), while the dotted line also includes the older large individuals (cross-shaped data points) harvested in October.

