Allometric relationships for intertidal macroalgae species of commercial interest

Doriane Stagnol, Marine Macé, Christophe Destombe, Dominique Davoult

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

2   Doriane Stagnol [a,b], Marine Macé [a,b], Christophe Destombe [a,c], Dominique Davoult [a,b]

3   [a] Sorbonne Universités, UPMC Univ Paris 6, Station Biologique, Place Georges Teissier, F-29682
4   Roscoff, France
5   [b] CNRS, UMR 7144 AD2M, Place Georges Teissier, F-29682, Roscoff, France
6   c CNRS, UMI 3614 EBEA, Place Georges Teissier, F-29682, Roscoff, France
7   [*] Corresponding author: doriane.stagnol@gmail.com Tel: +33 2 98 29 23 23 Fax: +33 2 98 29 23 24
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

26   **Acknowledgements**

Introduction

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

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

Materials and methods

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

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

Length-biomass relationships

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

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

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

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

4

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-

118 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**

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 LC² 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 (LC²),

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.

182

183

184

185

186

187

188

189

190

191

192

193

194

195

196

197

198

199

200

References

Åberg P (1990) Measuring size and choosing category size for a transition matrix study of the seaweed *Ascophyllum nodosum*. Mar Ecol Prog Ser 63:281–287

Airoldi L, Balata D, Beck MW (2008) The Gray Zone: Relationships between habitat loss and marine diversity and their applications in conservation. J Exp Mar Biol Ecol 366:8–15

Airoldi L, Beck MW (2007) Loss, status and trends for coastal marine habitats of Europe. Oceanogr Mar Biol 45:345–405

Alveal K, Ponce F (1997) Determination of water content in seaweeds. Gayana Oceanol 5:1–11

Benedetti-Cecchi L, Pannacciulli F, Bulleri F, et al (2001) Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. Mar Ecol Prog Ser 214:137–150

Chave J, Andalo C, Brown S, et al (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145:87–99

Connell S, Russell B, Turner D, et al (2008) Recovering a lost baseline: missing kelp forests from a metropolitan coast. Mar Ecol Prog Ser 360:63–72

Engel C, Åberg P, Gaggiotti OE, et al (2001) Population dynamics and stage structure in a haploid-diploid red seaweed, *Gracilaria gracilis*. J Ecol 89:436–450

Estes JA, Duggins DO, Rathbun GB (1989) The Ecology of Extinctions in Kelp Forest Communities. Conserv Biol 3:252–264

Gevaert F, Davoult D, Creach A, et al (2001) Carbon and nitrogen content of *Laminaria saccharina* in the eastern English Channel: biometrics and seasonal variations. J Mar Biol Assoc UK 81:727–734

Golléty C, Migné A, Davoult D (2008) Benthic metabolism on a sheltered rocky shore: role of the canopy in the carbon budget. J Phycol 44:1146–1153

Jonson JH, Freudenberger D (2011) Restore and sequester: estimating biomass in native Australian woodland ecosystems for their carbon-funded restoration. Aust J Bot 59:640-653

Lindgren A, Bouza N, Åberg P, Sosa PA (1998) Spatial and temporal variation in distribution of *Gelidium canariensis* (Rhodophyta) from natural populations of the Canary Islands. J Appl Phycol 10:273–278

Mangialajo L, Chiantore M, Cattaneo-Vietti R (2008) Loss of fucoid algae along a gradient of urbanisation, and structure of benthic assemblages. Mar Ecol Prog Ser 358:63-74

Mathieson AC, Guo Z (1992) Patterns of fucoid reproductive biomass allocation. Br Phycol J 27:271–292

236 Mccarthy MC, Enquist BJ (2007) Consistency between an allometric approach and optimal
237   partitioning theory in global patterns of plant biomass allocation. Funct Ecol 21:713–
238   720

239 Migné A, Delebecq G, Davoult D, Spilmont N, Menu D, Gevaert F (2015) Photosynthetic
240   activity and productivity of intertidal macroalgae: in situ measurements, from thallus
241   to community scale. Aquat Bot 123:6–12

242 Niklas KJ, Enquist BJ (2002) On the Vegetative Biomass Partitioning of Seed Plant Leaves,
243   Stems, and Roots. Am Nat 159:482–497

244 Paul KI, Roxburgh SH, England JR, Ritson P, Hobbs T, Brooksbank K , Raison RJ, Larmour
245   JS, Murphy S, Norris J, Neumann C, Lewis T, Jonson J, Carter JL, McArthur G,
246   Barton C, Rose B (2013) Development and testing of allometric equations for
247   estimating above-ground biomass of mixed-species environmental plantings. For Ecol
248   Manag 310:483–494

249 Perkol-Finkel S, Airoldi L (2010) Loss and Recovery Potential of Marine Habitats: An
250   Experimental Study of Factors Maintaining Resilience in Subtidal Algal Forests at the
251   Adriatic Sea. PLoS ONE 5:e10791.

252 Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P and Mommer L (2012), Biomass
253   allocation to leaves, stems and roots: meta-analyses of interspecific variation and
254   environmental control. New Phytol, 193: 30–50

255 Sack L, Grubb PJ, Marañón T (2003) The functional morphology of juvenile plants tolerant of
256   strong summer drought in shaded forest understories in southern Spain. Plant Ecol
257   168:139–163

258 Santelices B, Hormazábal M, Correa J & Flores V (2004). The fate of overgrown germlings in
259 coalescing Rhodophyta. Phycologia43:346–52.

260 Scrosati R, DeWreede RE (1997) Dynamics of the biomass-density relationship and frond
261 biomass inequality for *Mazzaella cornucopiae* (Rhodophyta, Gigartinaceae): implications for
262 the understanding of frond interactions. Phycol 36: 506-516

263 Scrosati R (2005) Review of studies on biomass-density relationships (including self-thinning
264 lines) in seaweeds: main contributions and persisting misconceptions. Phycol. Res. 53:224–33

265 Scrosati R (2006) Length–biomass allometry in primary producers: predominantly
266   bidimensional seaweeds differ from the "universal" interspecific trend defined by
267   microalgae and vascular plants. Can J Bot 84:1159–1166

268 Tait LW, Schiel DR (2011) Dynamics of productivity in naturally structured macroalgal
269   assemblages: importance of canopy structure on light-use efficiency. Mar Ecol Prog
270   Ser 421:97–107

271 Vadas, Sr. RL, Wright WA, Beal BF (2004) Biomass and Productivity of Intertidal
272   Rockweeds (*Ascophyllum nodosum* LeJolis) in Cobscook Bay. Northeast Nat 11:123–
273   142

274 Vaz-Pinto F, Martínez B, Olabarria C, Arenas F (2014) Neighbourhood competition in
275   coexisting species: The native *Cystoseira humilis* vs the invasive *Sargassum muticum*.
276   J Exp Mar Biol Ecol 454:32–41

277 Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for
278   allometry. Biol Rev 81:259–291

279 Watt CA, Scrosati RA (2013) Bioengineer effects on understory species richness, diversity,
280 and composition change along an environmental stress gradient: experimental and
281 mensurative evidence. Estuar Coast Mar Sci 123: 10-18

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	R²
Chondrus crispus & Mastocarpus stellatus	April-May-July-Oct.	66	10.02	3.5-16	LC²	0.0034	0.8259	0.93
Chondrus crispus	May	35	8.70	3.5-13	LC²	0.0006	1.0318	0.95
Mastocarpus stellatus	April-July	31	11.52	9-16	LC²	0.0067	0.7493	0.93
Fucus serratus	April-Oct.	60	36.50	8-70	LC²	0.1763	0.5996	0.92
Fucus vesiculosus	Nov.	48	41.44	13-117	LC²	0.0188	0.8028	0.87
Himanthalia elongata	March-June	65	79.58	8-232	L	0.0319	1.2878	0.77
Himanthalia elongata	March-June-Aug.-Oct.	75	98.20	8-281	L	0.0005	2.2323	0.81
Palmaria palmata	July-Oct.	40	29.73	10-65	LC²	0.0006	1.4183	0.91
Saccharina latissima	April	30	97.90	22-214	L	0.0155	1.3587	0.95
Ulva 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).

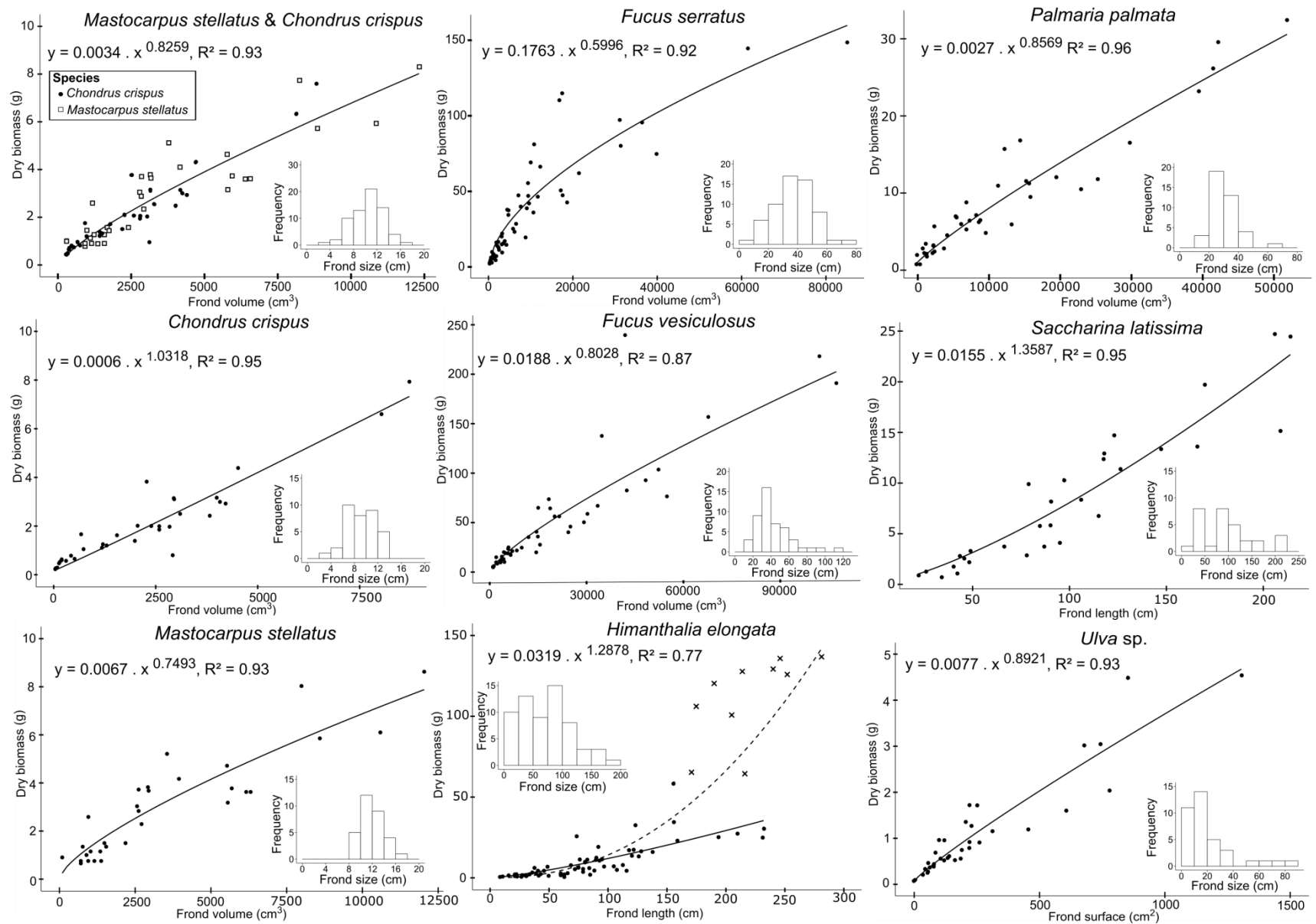| *Species*	n	Mean water content	a	b	R²
Chondrus crispus & Mastocarpus stellatus	66	74.4%	0.257	-0.034	0.96
Chondrus crispus	35	77.4%	0.226	0.048	0.99
Mastocarpus stellatus	31	71.7%	0.284	-0.139	0.96
Fucus serratus	30	78.4%	0.216	0.694	0.99
Himanthalia elongata	37	83.3%	0.167	-1.365	0.90
Palmaria palmata	40	87.3%	0.127	0.777	0.95
Saccharina latissima	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.

13