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Title.

Distinct growth and tissue composition (CNP, natural isotopes) of the three morphotypes of holopelagic *Sargassum*

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Highlights

- *Sargassum fluitans* III growth rate is the highest.
- *Sargassum natans* I growth rate is the lowest.
- Tissue composition differs between morphotypes.

Abstract

Holopelagic *Sargassum* blooms in the tropical North Atlantic since 2011 are composed of two species, *Sargassum natans* and *S. fluitans*, and three morphotypes: *S. natans* VIII, *S. natans* I and *S. fluitans* III. The distinct morphology and the variations in space and time of the proportion of these three morphotypes suggest that they may have different physiology. For the first time, we have quantified the growth rates of these three morphotypes through *in situ* 9-day experiments on the coast of Martinique Island (French West Indies). Despite the non-optimal conditions for growth for these pelagic species, we have observed that *Sargassum fluitans* III was growing faster (approximately twice as fast) than *S. natans* VIII and *S. natans* I. *S. natans* I exhibited the slowest growth. The differences in tissue composition (CNP and CN natural isotopes) of morphotypes point to a greater benefit for *S. fluitans* III from the coastal localization of our experiment than for the two *S. natans* morphotypes, and suggest that *S. natans* I had achieved its last growth further offshore before our experiment. These contrasting growth performances are consistent with the dominance of *S. fluitans* III in recent observations in the Caribbean. This also makes this last morphotype the best candidate for cultivation. Making the distinction between the growth performances of morphotypes may improve the current predictive models.

Keywords

Holopelagic *Sargassum*, Morphotypes, Sargasso, Growth, Nutrient content, Natural isotopes

1 **1. Introduction**

2 Since 2011, the tropical North Atlantic Ocean has been the site of seasonal blooms of holopelagic
3 *Sargassum*, rooted in the North Equatorial Recirculation Region. Holopelagic *Sargassum* are currently
4 forming the Great Atlantic *Sargassum* Belt that can be observed from space (Wang et al., 2019), and
5 causes strandings westwards, along the whole of the North Atlantic coast of South America and the
6 Caribbean area, including the Gulf of Mexico, and eastwards along the West African coasts (Berline et
7 al., 2020).

8 These strandings are composed of three distinct morphotypes: *Sargassum natans* VIII Parr, *S.*
9 *natans* I Parr, and *S. fluitans* III Parr (Schell et al., 2015). Each morphotype shows a distinct
10 morphology especially blade size, number of blades and air bladders (floats) per stem, and presence
11 of thorns on the stem (García-Sánchez et al., 2020; Schell et al., 2015) suggesting that the three
12 morphotypes may have different biological characteristics.

13 Since the beginning of *Sargassum* blooms in 2011, significant variations of the abundance in
14 morphotype composition have been observed. Initially, *S. natans* VIII was dominant in the south
15 (Antilles Current, Eastern Caribbean and Western Tropical Atlantic) and *S. natans* I in the north (south
16 of the Sargasso Sea) (Schell et al. (2015) November 2014 to May 2015). In 2017, during two open
17 ocean campaigns along a latitudinal gradient from Guyana to the Sargasso Sea
18 (<https://doi.org/10.17600/17004300>) and following a longitudinal transatlantic route
19 (<https://doi.org/10.17600/17016900>) from Cabo Verde Island to Guadeloupe, *S. fluitans* III appeared
20 to be dominant north of Guadeloupe for the first cruise and everywhere for the second cruise. More
21 recently, studies have shown a quasi-permanent dominance of *S. fluitans* III in *Sargassum* strandings
22 on Mexican Caribbean shores from 2016 to 2020 (Vázquez-Delfín et al., 2021; García-Sánchez et al.,
23 2020), along the Jamaican coast (Machado et al., 2022), and on the Caribbean, Floridan and Bahaman
24 coasts (Iporac et al., 2022) as well as in the course of a 2022 transatlantic cruise
25 (<https://energieaugrandlarg.wixsite.com/website>).

26 Predictive models of *Sargassum* dynamics in the Atlantic (Brooks et al., 2018; Jouanno et al., 2021)
27 use parameters based on physiological studies that do not differentiate between morphotypes
28 (Hanisak and Samuel, 1987; Lapointe, 1995; Lapointe et al., 2014). However in macroalgae, the life
29 traits are often taxon-dependent (Vranken et al., 2022) and therefore could explain the variations in
30 dominance between morphotypes with time and across the North Atlantic. Taking into account
31 differential growth rate may improve the model's simulations.

32 Differential physiology would also impact tissue composition of *Sargassum* in CNP including C:N, N:P,
33 C:P ratios and $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ isotopes, as it integrates *Sargassum* environmental history along its drift
34 path (Lapointe et al. 2021, Vázquez-Delfín et al., 2021).

35 The aim of this work was to quantify the growth rates and tissue CNP composition of the three
36 morphotypes through *in situ* short term experiments in Martinique Island (French West Indies).

37 **1 Materials and methods**

38 **1.1 Location of experimental site and *Sargassum* sampling**

39 Experiments were performed on the east coast of Martinique Island, in Baie du Robert, close to the
40 Ifremer marine station, where a meteorological station is located. It took place in May-June 2021,
41 when the Island is frequently supplied with *Sargassum* (Johns et al., 2020). This shallow bay (<30 m
42 depth) faces the Atlantic Ocean and receives *Sargassum* pushed by the northeast trade winds after
43 passing over the continental shelf, which extends for more than 15 km offshore (Fig. S1).

44 The nutrient concentrations (NO_3^- , NO_2^- , NH_4^+ , PO_4^{2-}) of surface seawater in the bay was monitored
45 once every 2 months since 2017 as part of an extension of Ifremer's REPHY network (Belin et al.,
46 2021) to the French overseas territories. The values (mean \pm SD) measured at the REPHY station,
47 situated 400 m from our experimental site (S1), were low for a coastal station, especially when
48 considering the different forms of N, $\text{NO}_3^- + \text{NO}_2^-$ ($0.3 \pm 0.3 \mu\text{mole L}^{-1}$) and NH_4^+ ($0.3 \pm 0.3 \mu\text{mole L}^{-1}$), with

49 regard to PO_4^{2-} ($0.07 \pm 0.05 \mu\text{mole L}^{-1}$). This absence of pollution is confirmed by a previous detailed
50 study of the bay (De Rock et al., 2019).

51 1.2 *Growth experiment*

52 *Sargassum* individuals were collected off the coast within the bay selecting the young clumps
53 following the criteria of Stoner and Greening (1984) to age the clumps. For each morphotype, we cut
54 fragments of 5 to 20 cm length from the apical part, free from visible epiphytes. To be consistent
55 with field observations, the three morphotypes were grown together. Approximately 20 g of wet
56 weight of each morphotype (5-10 fragments, 60 g in total) hereinafter called a batch, were placed in
57 5 L transparent plastic bottles, perforated with one hundred holes to allow good water circulation.
58 These bottles were attached to mooring cables at 2 m depth to avoid destruction of the devices by
59 wave effect. Temperature and light inside two of the four bottles was recorded with UA-002-08
60 (HOBO) data loggers.

61 The entire experiment lasted 9 days, from May 25th to June 3rd 2021. The wet weight was measured
62 every 3 days. The wet weight of each batch was measured on a BAXTRAN BR balance (0.1 g
63 readability) after dewatering using absorbent paper in a salad spinner. Inside each batch, three
64 individuals per morphotype ($n = 36$) were identified with colored beads strung on a nylon thread
65 attached to the fragment. The wet weight of each individual ($n = 12$ per morphotype) was obtained
66 as for the batch but by using a more accurate balance (PRECISA 321LT, 0.1 mg readability). In
67 addition, for each individual the number of floats was counted.

68 1.3 *Water, tissue, and data analysis*

69 At the beginning of the experiment, and before each measurement session, we sampled the water in
70 200 mL plastic bottles to measure nutrient composition. The sample was fixed with $100 \mu\text{L HgCl}_2$ per
71 bottle, and then stored in a cool place protected from light. The analyses were carried out by
72 automated colorimetry for NO_3^- , NO_2^- , NH_4^+ , PO_4^{2-} (Aminot and K erouel, 2007) and for NH_4^+ (Holmes
73 et al., 1999).

74 At the end of the experiment, eight samples of 5 g wet weight of each morphotype were analyzed for
75 C, N, P, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ tissue composition. These samples were dried in an oven at 60°C during 48 h,
76 reduced into powder, acidified to eliminate mineral sources of carbon, and analyzed by spectrometry
77 following Raimbault et al. (2008).

78 The growth rate (GR) in weight was calculated in d^{-1} following:

$$79 \quad GR_d = \frac{1}{d} \ln \left(\frac{W_d}{W_0} \right)$$

80 were d = number of days ($d = 9$ for the entire experiment) and W_d = wet weight at day d , W_0 = wet
81 weight at day 0.

82 The floats ratio (FR) was calculated (in %) with reference to the initial number of floats for the entire
83 experiment following:

$$84 \quad FR = \frac{N_9}{N_0} \cdot 100$$

85 were N_9 = number of floats at day 9 and N_0 = number of floats at day 0.

86 Non parametric Kruskal-Wallis test (KW test) followed by Dunns post-hoc test were used to test the
87 morphotype effect on *Sargassum* GR, FR and tissue composition with a significance level of 0.05.

88 **2 Results**

89 **2.1 Field conditions**

90 During the 9 days of the experiment, water temperature inside the bottles varied from 28°C at night
91 to 31°C during the day (06:00-18:00) when light inside the bottle varied from 74 to
92 740 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ with a mean value of 137 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. The nutrient concentrations
93 were high and variable compared to REPHY measurements (respectively 1.7 ± 2.0 vs 0.3 ± 0.3 μmole
94 L^{-1} for $\text{NO}_3^- + \text{NO}_2^-$, 2.1 ± 1.7 vs 0.3 ± 0.3 $\mu\text{mole L}^{-1}$ for NH_4^+ and 0.3 ± 0.3 vs 0.07 ± 0.05 $\mu\text{mole L}^{-1}$ for
95 PO_4^{2-}).

96 The daily rainfall, including one day before the start of the experiment, varied from 0 to 10.6 mm,
97 with a mean of 1.52 mm which is below the average of 2.07 mm from May to June 2021 at the
98 station. The wind speed and direction were regular for the season (9.73 m.s⁻¹ oriented WNW
99 (67.27°)).

100 2.2 Patterns of change in the *Sargassum* weight and floats ratio

101 The increase in *Sargassum* weight in the course of the experiment was clearly visible when
102 considering the batches (Fig. S2). After 9 days, the initial 20 g were exceeded by all morphotypes,
103 reaching about 25 g for *S. natans* VIII and *S. natans* I and approaching 30 g for *S. fluitans* III. After 6
104 days, the weight increase slowed down for all morphotypes. In contrast, this increase was lower and
105 more variable in the individual measurements (Fig. S2). The floats ratio (FR) after 9 days was overall
106 below 100%, showing a loss of floats for all morphotypes (Fig. S3). This was especially the case for *S.*
107 *natans* I.

108 2.3 Growth rate

109 For all morphotypes, the GR over every 3-day period decreased overall over time from the beginning
110 of the experiment (Fig. 1 A). The median value of batch GR varied from 0.063 to 0.022 d⁻¹ after 3
111 days, from 0.044 to 0.018 d⁻¹ after 6 days, and from 0.019 to -0.006 d⁻¹ after 9 days.

112 *Sargassum fluitans* III had always the highest GR values and *S. natans* I the lowest. *Sargassum natans*
113 VIII GR was intermediate. After 9 days, the individual GR showed a significant variation between
114 morphotypes (KW test $\chi^2 = 16.244$, df = 2, p-value = 0.0002969). The Dunns post hoc gives two
115 significant results: *S. fluitans* III vs *S. natans* I (p=0.0000678***) and *S. fluitans* III vs *S. natans* VIII
116 (p=0.0313*). Even if the mean individual GR of *S. natans* I was negative, linked with the first signs of
117 senescence, the mean batch GR of this morphotype was positive (Fig. 1 B).

118 2.4 Tissue elemental composition (C, N, P, $\delta^{13}C$, $\delta^{15}N$) of *Sargassum*

119 The effect of morphotype was significant only for %N, $\delta^{15}N$, $\delta^{13}C$ and C:N (Table S1). For other
120 elements, the median values were %C = 23.52%, %P = 0.07%, N:P = 30.33 and C:P = 827.43.

121 The post hoc Dunn tests (Fig. 2; Table S1) showed that *S. fluitans* III was characterized by a high %N,
122 $\delta^{15}\text{N}$ and low C:N and $\delta^{13}\text{C}$. In contrast, *S. natans* VIII showed low %N, $\delta^{15}\text{N}$ and high C:N and $\delta^{13}\text{C}$ and
123 *S. natans* I was essentially characterized by a low $\delta^{15}\text{N}$.

124 **3 Discussion**

125 3.1 *Changes in growth performance during the experiment*

126 For the three morphotypes, GR (0.02-0.04 d⁻¹ for batches) were in the low range of literature growth
127 data reported by Brooks et al. (2018), *i.e.* [0.029-0.11] d⁻¹ relying on *in situ* (Lapointe 1986, Lapointe
128 et al. 2014) and laboratory experiments (Hanisak and Samuel, 1987). In addition, GR decreased with
129 time for all morphotypes. This does not align with the neritic origin of our samples, generally
130 associated with low nutrient limitation and high GR following Lapointe (1995). These results, for both
131 batches and individuals, indicate that algae were not in optimal growth conditions. This decrease of
132 GR may be due:

- 133 - to excessively high seawater temperatures [28-31°C] observed during the experiment, as
134 decrease in growth after 24°C was observed by Hanisak and Samuel (1987) for *S. natans*;
- 135 - to light limitation since our mean light measurement of 137 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in the bottle
136 corresponds to intermediate GR of 0.02 d⁻¹ (Hanisak and Samuel, 1987);
- 137 - to stress related to the confinement in the bottles despite the numerous holes made in order
138 to renew the water. Pelagic *Sargassum* are known to produce large quantities of dissolved
139 organic carbon (Powers et al., 2019) that promote, together with high nutrient level,
140 bacterial growth (Michotey et al., 2020).

141 GR did not correspond to maximum growth values, taking into account both the phenomenon of
142 growth and senescence over 9 days. Although culture conditions may be limiting, our results clearly
143 show contrasting performances among morphotypes.

144 3.2 *Differential growth between the 3 morphotypes and implications*

145 *Sargassum fluitans* III was growing faster, approximately twice as fast as *S. natans* VIII and *S. natans* I.
146 This is consistent with lab experiment results of Hanisak and Samuel (1987). Moreover, *S. natans* I
147 exhibited the slowest growth rate. This suggests that morphotypes matter. When exposed to high
148 temperature, high nutrient concentration and a slight light limitation *S. fluitans* III does better than
149 *S. natans* I.

150 These differences may have implications with regard to the relative abundance of morphotypes
151 observed at sea and in strandings. However GR cannot be simply translated into abundances. The
152 coexistence of the three morphotypes suggests that processes other than growth maintain
153 competitive success of the *S. natans* morphotypes despite lower GR. Morphotypes may have
154 differing environmental niches that were not spanned by our experimental conditions. For instance,
155 in a more oligotrophic and colder environment than ours, *S. natans* I dominated during 2014 and
156 2015 north of 24° N (Schell et al., 2015).

157 Future measurements of growth in contrasted conditions may help to explain field observations of
158 morphotype composition and the dominance of *S. fluitans* III in the Caribbean.

159 3.3 Significance of CNP and isotope composition

160 Our results showed significant differences of %N, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and C:N between morphotypes while no
161 difference has been found between *S. natans* and *S. fluitans* in the large (n = 488) and long-term
162 dataset of Lapointe et al. (2021). This discrepancy can be explained by the particular environmental
163 history of our samples.

164 Overall, %N and %P cannot explain the different GR among morphotypes. Both *S. fluitans* III and *S.*
165 *natans* I have similar %N and %P values, but different GR. It may be related to nutrient uptake that
166 occurred before the experiment.

167 The high N:P (30.33) and C:P value (827) of all morphotypes in our experiment suggests a limitation
168 in P, as pointed out by Lapointe et al. (2021) for samples collected after 2010s. This P limitation may
169 explain why %N differences do not result in growth rate variations.

170 The value of %C (23.5%) was low compared to the recent Mexican samples of Vázquez-Delfín et al.
171 (2021). Conversely, %N values were high in agreement with the Lapointe et al. (2021) data for the
172 2010s, except for *S. natans* VIII which were lower in our study. The high C:N values (36) of *S. natans*
173 VIII suggest that this morphotype was not in good growing conditions.

174 The isotopic composition showed high values in $\delta^{13}\text{C}$ which are footprints of the continental origin of
175 C as a consequence of the coastal situation of our samples. The low values of $\delta^{15}\text{N}$ of *S. natans* I may
176 be indicative of diazotrophic fixation, common in pelagic *Sargassum* (Carpenter, 1972; Philips and
177 Zeman, 1990) while higher values may indicate enrichment by NO_3^- present along the coast (Lapointe
178 et al. 2021). It is interesting to note that $\delta^{15}\text{N}$ order among morphotypes follow the GR. This suggests
179 that higher $\delta^{15}\text{N}$ indicate more recent growth fueled by coastal NO_3^- . That implies that the last
180 growth of *S. natans* I was achieved at a greater distance in time and offshore.

181 Thus, the significant variations of the elemental composition point to a greater benefit for *S. fluitans*
182 III from the coastal situation of our experiment than for the two *S. natans* morphotypes.

183 In conclusion, despite the non optimal conditions encountered in this experiment, it shows for the
184 first time contrasting growth performances between morphotypes that are consistent with their
185 abundance in the field. Current predictive models, which do not distinguish between morphotypes,
186 can be improved by taking these growth differences into account. These differences in growth are
187 probably linked to photosynthetic processes between morphotypes that will have to be specified
188 with new experiments. *Sargassum fluitans* III appears here as the best candidate for cultivation,
189 including indoors where access to light is more difficult.

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194 **5 CRediT authorship contribution statement**

195 Conceptualization, Data curation, Methodology, Software, Supervision, Validation, Visualization (TC,
196 LB), Formal analysis (TC, LB, WP), Funding acquisition, Project administration, Resources (TC, LB, TT),
197 Investigation (TC, TG), Writing (TC, LB, SC, VSP, TT).

198 **6 Declaration of Competing Interest**

199 None

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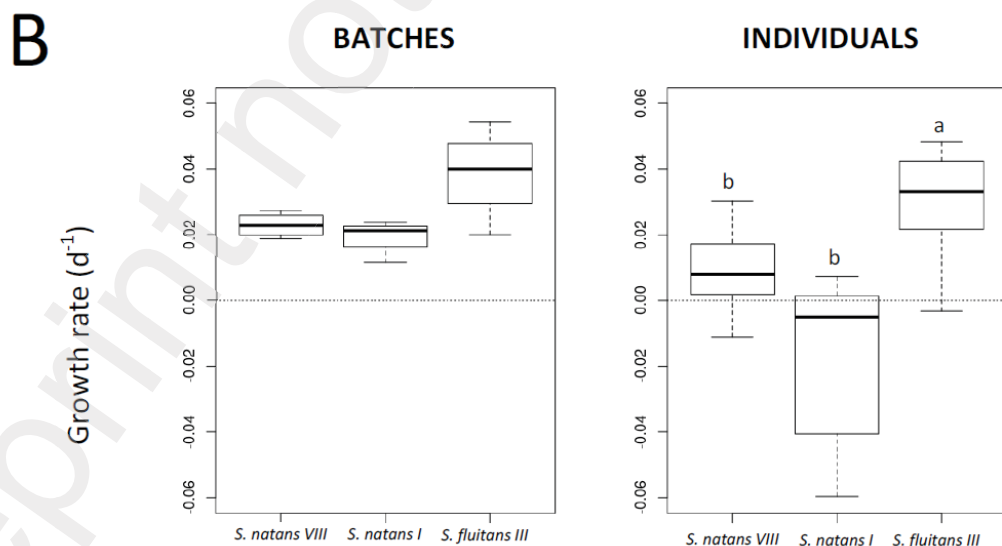
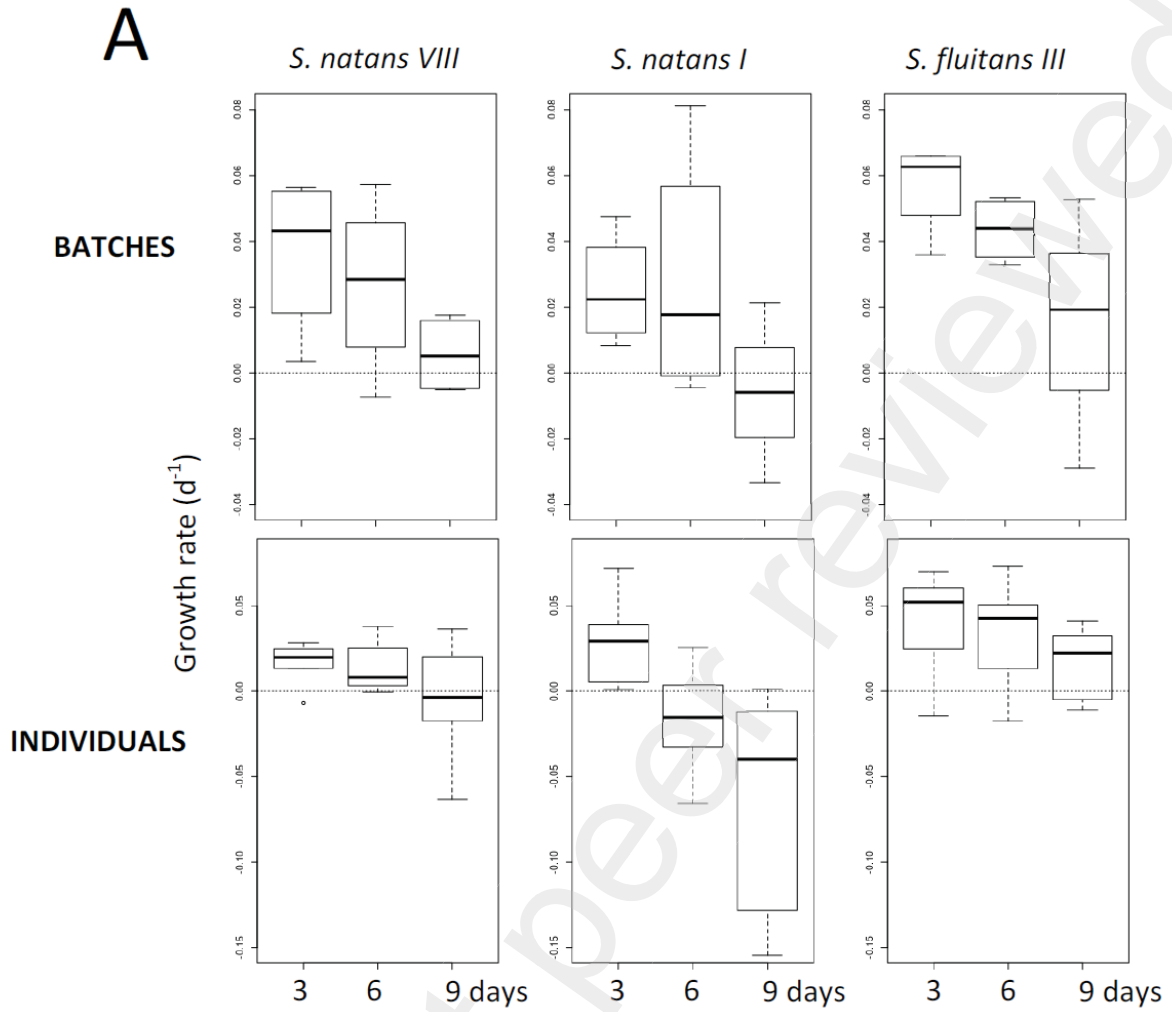
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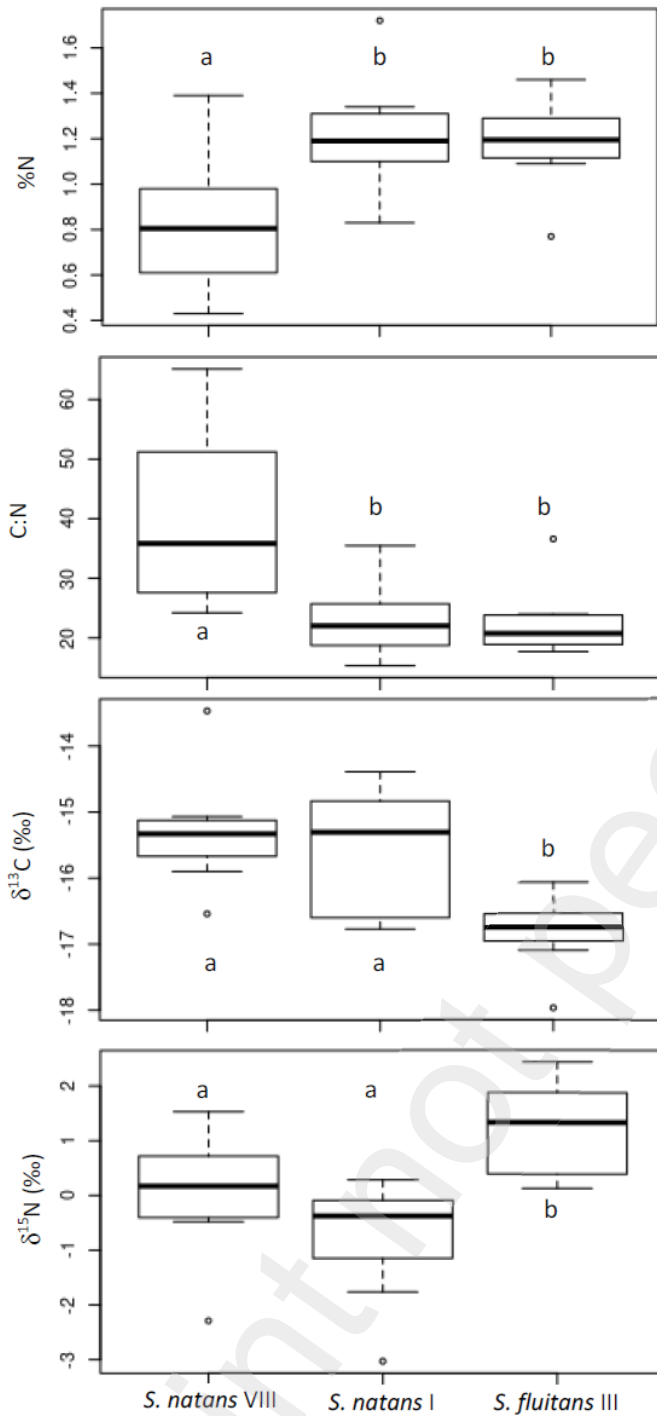
300 Fig. 1: Holopelagic *Sargassum* growth rate (d⁻¹) for each morphotype measured on batches (n=4) and
 301 individuals (n=12 per morphotype) every 3 days (A.) and over the 9 days of the experiment (B.). Box
 302 shows the sample median and the first and third quartiles. Whiskers extend to the last data point

303 which is no more than 1.5 times the interquartile range. Outliers are shown as dots. The letter

304 identifies the significant differences ($p\text{-value} < 0.05$).

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307 Fig. 2: Tissue composition (%N, C:N, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$) between *Sargassum* morphotypes. Box, whiskers and

308 letters are shown as in Fig. 1.

Supplementary material of Growth and tissue composition (CNP, isotopes) of the three morphotypes of pelagic sargassum

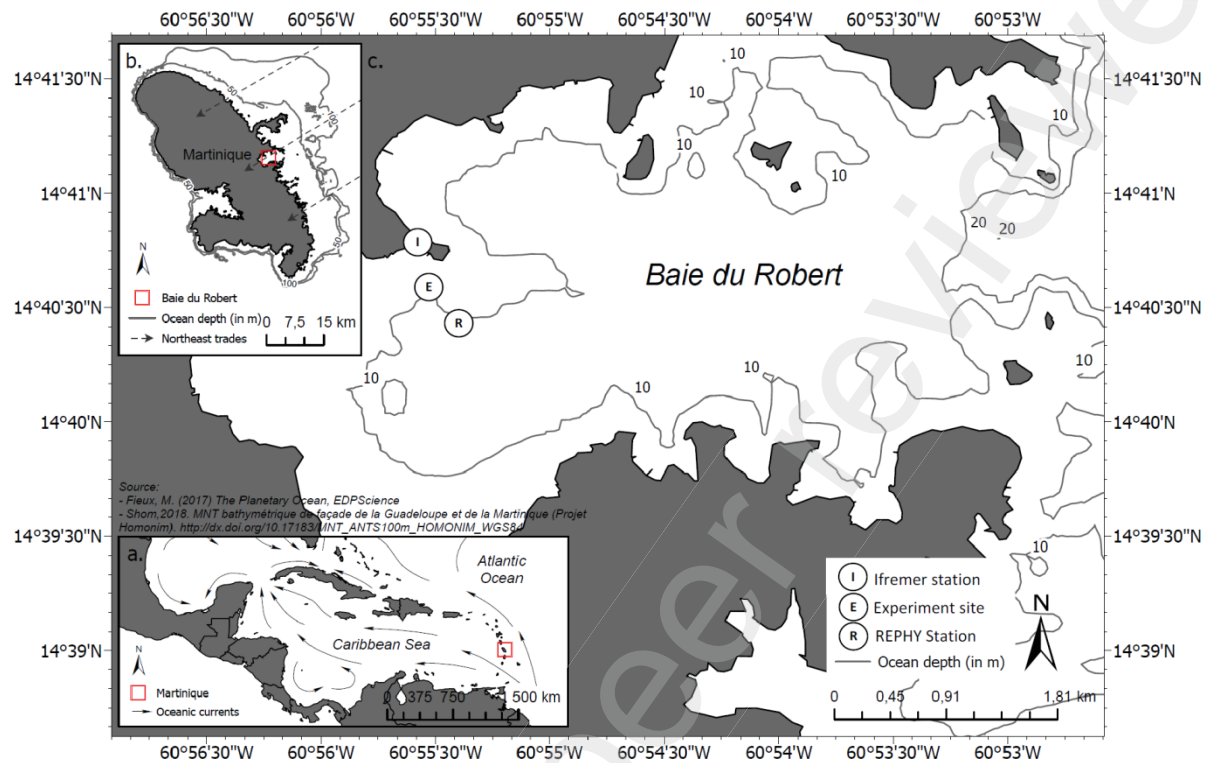


Fig. S1: Location of Ifremer station (I), experimental site (E) and REPHY monitoring station (R) with bathymetry. (a.) Regional position of Martinique Island, framed in red, with the main oceanic currents. (b.) Martinique Island with the orientation of the trade winds and location of Baie du Robert framed in red.

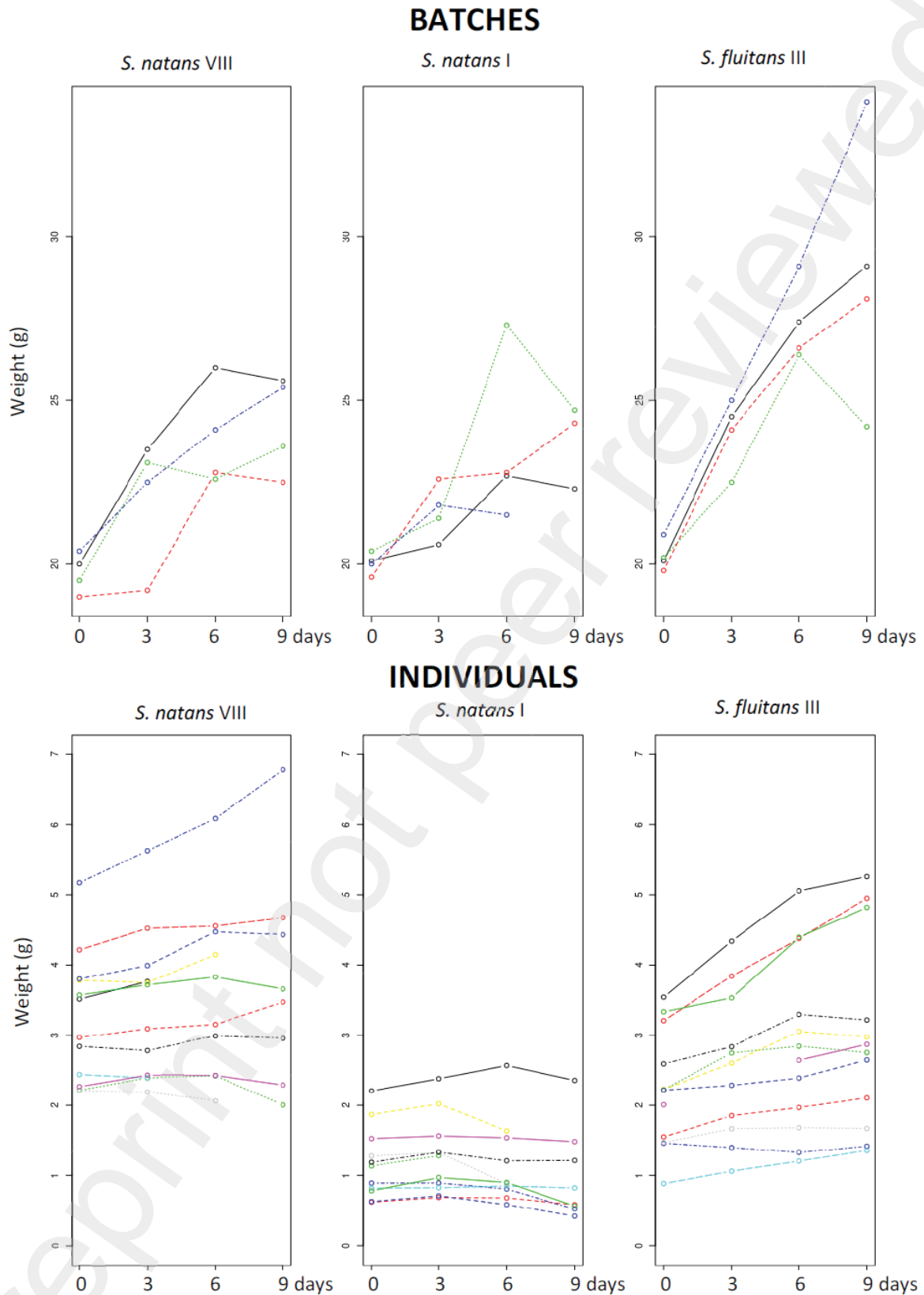


Fig. S2: *Sargassum* wet weight patterns of change over time for measurements of batches ($n = 4$) and individuals considering the different morphotypes (*S. natans VII* ($n = 12$), *S. natans I* ($n = 12$), and *S. fluitans III* ($n = 12$)). Each line is a batch or an individual. It can be interrupted when a mark was lost or an apex dead or an individual broken in two parts.

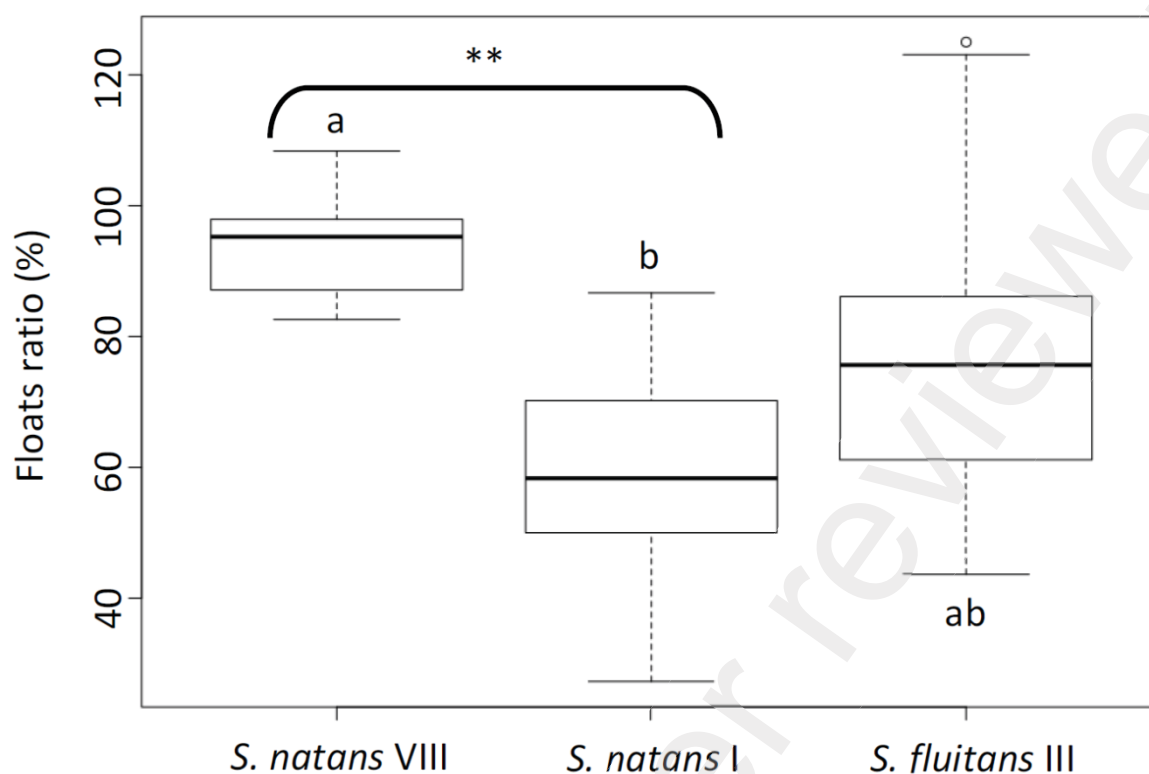


Fig. S3: Floats ratio after 9 days for the 3 morphotypes. Box shows the sample median and the first and third quartiles. Whiskers extend to the last data point which is no more than 1.5 times the interquartile range. Outliers are shown as dots. The KW test $\chi^2 = 10.76$, $df = 2$, $p\text{-value} = 0.004608$. The only significant Dunns post hoc test is between *S. natans* VIII vs *S. natans* I ($p = 0.00104^{**}$). Note that some individuals *S. fluitans* III and *S. natans* VII show values over 100% since they have more floats at the end of the experiment than at the beginning.

Table S1: Synthesis of Kruskal-Wallis and Dunns post hoc test results for the morphotype effect on *Sargassum* composition in %C, %N, %P, C:N, N:P, C:P, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$.

	%C	%N	%P	C:N	N:P	C:P	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Kruskal Wallis Chi2	3,62	6,635	5,235	10,955	1,28	0,335	11,115	11,185
df	2	2	2	2	2	2	2	2
p-value	0,164	0,036	0,073	0,004	0,527	0,846	0,004	0,004
Dunns p-value <i>S. natans</i> VIII vs <i>S. natans</i> I		0,022		0,005			0,671	0,179
Dunns p-value <i>S. natans</i> VIII vs <i>S. fluitans</i> III		0,031		0,003			0,002	0,048
Dunns p-value <i>S. natans</i> I vs <i>S. fluitans</i> III		0,888		0,888			0,008	0,001
Median	23,52%	1,14%	0,07%	23,85	30,33	827,43	-15,99	0,16
Median <i>S. natans</i> VIII		0,80%		35,86			-15,33	0,17
Median <i>S. natans</i> I		1,19%		22,03			-15,31	-0,38
Median <i>S. fluitans</i> III		1,20%		20,76			-16,75	1,33