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1 **Detrital carbon production and export in high latitude kelp forests**

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20 **Running page head:** Detrital production in *Laminaria hyperborea*.

21 **ABSTRACT**

22 The production and fate of seaweed detritus is a major unknown in the global C-budget.
23 Knowing the quantity of detritus produced, the form it takes (size) and its timing of delivery
24 are key to understanding its role as a resource subsidy to secondary production and/or its
25 potential contribution to C-sequestration. We quantified the production and release of detritus
26 from 10 *Laminaria hyperborea* sites in northern Norway (69.6°N). Kelp biomass averaged
27 $770 \pm 100 \text{ g C m}^{-2}$ while net production reached $499 \pm 50 \text{ g C m}^{-2} \text{ y}^{-1}$, with most taking place
28 in spring when new blades were formed. Production of biomass was balanced by a similar
29 formation of detritus ($478 \pm 41 \text{ g C m}^{-2} \text{ y}^{-1}$), and both were unrelated to wave exposure when
30 compared across sites. Distal blade erosion accounted for 23% of the total detritus production
31 and was highest during autumn and winter, while dislodgment of whole individuals and/or
32 whole blades corresponded to 24% of the detritus production. Detachment of old blades
33 constituted the largest source of kelp detritus, accounting for >50% of the total detrital
34 production. Almost 80% of the detritus from *L. hyperborea* was thus in the form of whole
35 plants or blades and > 60% of that was delivered as a large pulse within 1-2 months in spring.
36 The discrete nature of the delivery suggests that the detritus cannot be retained and consumed
37 locally, and that some is exported to adjacent deep areas where it may subsidize secondary
38 production or become buried into deep marine sediments as blue carbon.

39

40

41 **Key words: detritus, seaweed, drift, resource subsidy, carbon sequestration**

42

43

44 INTRODUCTION

45 Flow of dead organic matter (detritus) across ecosystem boundaries connects neighboring
46 ecosystems and may fuel secondary productivity in recipient ecosystems where primary
47 productivity is low. Detrital subsidies can alter patterns of species composition and food web
48 structure in terrestrial and aquatic systems (e.g. Polis et al. 1997), but may be particularly
49 important in aquatic environments due to greater connectivity than in terrestrial systems (Carr
50 et al. 2003). The productivity of kelp-dominated ecosystems may exceed $2000 \text{ g C m}^{-2} \text{ y}^{-1}$
51 (Mann 1973, Abdullah & Fredriksen 2004) although rates in the range of $4 - 600 \text{ g C m}^{-2} \text{ y}^{-1}$
52 are more common (e.g. Krumhansl & Scheibling 2012, Pessarrodona et al. 2018, Wernberg et
53 al. 2019). Direct grazing on live kelp is often low and ranges from 10 to 15% of the annual
54 production (Krumhansl & Scheibling 2012), although grazing by sea urchins and herbivorous
55 fishes can be high in disturbed systems (Poore et al. 2012, Wernberg et al. 2013, Steneck &
56 Johnson 2013). Most kelp production is therefore channeled to the detrital pool within kelp
57 systems or in adjacent systems such as beaches (Columbini & Chelazzi 2003, Ince et al. 2007),
58 seagrass beds (Wernberg et al. 2006), distant reefs (Vanderklift & Wernberg 2008), deeper
59 sub-tidal areas (Filbee-Dexter & Scheibling 2016) and submarine canyons (Vetter & Dayton
60 1999), where it may be consumed by detritivores, decompose or accumulate and, thus,
61 contribute to C-sequestering (Cebrian 1999, Krause-Jensen & Duarte 2016).

62 Kelp detritus is generated through different processes such as continuous erosion
63 and/or pruning of the blades and dislodgement of entire plants or whole blades, including
64 phenologically determined losses of old blades in some species (Krumhansl & Scheibling
65 2012). Most studies to date have either quantified detritus formation through dislodgement or
66 through blade erosion (table 1 in Krumhansl & Scheibling 2012), while only three studies
67 have conducted concurrent measurements of erosion and dislodgment rates that allow

68 comparisons of the relative contribution of detritus formed by these different processes
69 (Gerard 1976, de Bettignies et al. 2013b, Pessarrodona et al. 2018).

70 The relative importance of the mechanisms of detritus formation may be context
71 dependent and vary as a function of species and environmental conditions. Dislodgement
72 caused by strong water movement is often considered the main driver for production of kelp
73 detritus, due to higher kelp mortality during periods of peak wave action (e.g. Ebeling et al.
74 1985, Seymour et al. 1989, Graham et al. 1997) and because large amounts of kelp detritus
75 accumulate as beach cast or in adjacent deep habitats following storms (e.g. Griffiths et al.
76 1983, Filbee-Dexter & Scheibling 2012). Other studies have shown that the formation of
77 detritus through distal erosion of blades can be significant and match annual blade production
78 (e.g. Krumhansl & Scheibling 2011a, de Bettignies et al. 2013b). Blade erosion may be
79 positively correlated to water movement, but may also be stimulated by epiphytic load (e.g.
80 bryozoans), grazing and seasonal patterns of reproduction that may weaken the blade tissue
81 and make it more susceptible to scouring (Krumhansl & Scheibling 2011b, de Bettignies et al.
82 2012, 2013b, Mohring et al. 2012). Detritus generated by these different processes varies
83 substantially in size (from small particles to whole thalli), which may affect dispersal range,
84 consumption and decomposition rate.

85 *Laminaria hyperborea* (Gunnerus) Foslie is the dominant kelp species in terms of
86 biomass along rocky shores in the NE Atlantic where it forms extensive forests that dominate
87 coastal primary production (e.g. Smale et al. 2013, Pessarrodona et al. 2018, Wernberg et al.
88 2019). *L. hyperborea* produces one annual blade that begins to form in winter and grows to
89 maximum size ($\sim 1 \text{ m}^2$) during spring and early summer, after which it erodes during fall and
90 winter. The remains of the blade are shed in spring as the new, emerging blade is formed at
91 the base of the old. A large proportion of the old blade biomass is thus discharged over a short
92 period, which may result in a significant pulse of coarse detritus (Pessarrodona et al. 2018).

93 The overall aim of this study was to quantify the spatial and seasonal variation in productivity
94 and formation of detritus through erosion, dislodgement, and the spring cast of old blades for
95 high latitude populations of *Laminaria hyperborea*. We expected that physical forcing caused
96 by waves would be an important driver for spatial and temporal variations in the formation of
97 kelp detritus through erosion and dislodgment, while the spring cast of old blades would
98 constitute a substantial pulse of coarse kelp detritus.

99

100 **METHODS**

101 **Study site.** Our study took place around the mouth of Malangen fjord in northern Norway
102 (69.6° N, 18.0° E). The area is heavily influenced by ocean swells, wind generated waves and
103 tides (± 1.5 m). The rocky subtidal is dominated by kelp *Laminaria hyperborea* to a depth of
104 ca. 20-25 m. The study area covers 126 km² of coastal ocean (Fig. 1) of which *L. hyperborea*
105 covers ca. 22 km² according to a predictive kelp forest model developed by the national
106 Norwegian mapping of marine habitats (Bekkby et al. 2013). The model uses 12 years of
107 monitoring data for the entire Norwegian coast along with wind, fetch, coastline and
108 bathymetric data to predict the presence/absence of kelp. We selected ten study sites
109 representing a range of wave exposure levels based on variations in effective fetch (Fig. 1),
110 with the most exposed site on a shoal 2.4 km offshore (site 5), and the most protected site in a
111 small bight 3.5 km in from the mouth of the fjord (site 10). The sites ranged from ‘moderately
112 exposed’ to ‘very exposed’ according to the EUNIS classification system used to classify
113 coastal habitats in Europe (Davies & Moss 2003). We quantified kelp density, biomass,
114 production, and formation of detritus through different processes at each site during autumn
115 2016, winter 2016-2017, spring 2017 and summer 2017.

116

117 **Temperature, light and wave exposure.** Water temperature and light intensity in the kelp

118 forests (just above the canopy) were monitored hourly at each sampling site during the entire
119 study period using HOBO data loggers (Pendant Temp-Light, Onset Computer Corporation)
120 anchored to subsurface floats. Wave exposure level was calculated for each site from August
121 2016 to August 2017 using a modified version of the method presented by Fonseca & Bell
122 (1998). Hourly wind data (mean velocity and direction) were obtained from Hekkingen
123 Lighthouse weather station (the Norwegian Metrological Institute) located in the middle of
124 the study area. Weighted effective fetch (WEF) for each sampling site was estimated by
125 placing the center of a circle on all sites and subsequently dividing each of these into 8 sectors
126 each with an angle of 45° , beginning at the N sector ($337.5^\circ - 22.5^\circ$). The fetch (F in km) was
127 measured along 5 radia (each with 11.25° spacing) within each sector and the weighted
128 effective fetch for each sector (WEF_i) was then estimated by first multiplying each fetch with
129 the cosine of the angle (γ) of departure from the major heading (of the sector) and finally
130 averaging the 5 values:

131
$$WEF_i = (\sum (F_i \times \cos \gamma_i)) / 5 \quad (\text{Eq. 1})$$

132 Relative wave exposure index (REI) was computed hour by hour for each site by multiplying
133 hourly wind speeds with the relevant effective fetch:

134
$$REI = WEF_i \times V_i \quad (\text{Eq. 2})$$

135 where i is the i^{th} compass heading (i.e. 1 to 8 [N, NE, E, etc.] in 45° increments) and V_i is the
136 wind speed from direction i . Hourly estimates of REI were finally used to estimate mean and
137 maximum REI for each site during autumn (18th Aug – 25th Oct), winter (26th Oct – 29th
138 March), spring (2nd April – 29th May) and summer (30th May – 10th Aug), respectively.

139 Maximum REI was estimated as the average of the 10% highest REI -values in a season.

140

141 **Kelp density and biomass.** The density and biomass of kelp were quantified in August and
142 October 2016 and in March, May and August 2017. SCUBA divers collected all canopy

143 plants (i.e. plants with stipes longer than ca. 0.7 m, Pedersen et al. 2012) within 4 to 6
144 quadrats (area = 0.25 m²) at each site. The quadrats were placed haphazardly in the kelp forest
145 at 5 - 7 m depth and with a minimum distance of 5 m apart. Density was quantified by
146 counting the number of canopy plants in each quadrat. The fresh weight (FW) biomass of
147 each individual stipe and blade (both old and new blades in March and May) was weighed to
148 the nearest gram and total FW biomass per quadrat was estimated as the sum of all individual
149 weights of canopy plants. Holdfasts were not collected, but they comprise ca. 13% (± 4) of the
150 FW biomass of the whole thallus (Pedersen et al. 2012, Bekkby et al. 2014).

151

152 **Blade growth and erosion.** Modified versions of the hole punch methods were used to
153 measure frond elongation (Parke 1948) and distal erosion of the blade (Tala & Edding 2005).
154 Twenty kelp individuals were tagged for growth and erosion measurements at each site and
155 field campaign and harvested during the succeeding campaign. The kelps were tagged with
156 two holes in the lower, basal part of the blade for growth measurements (5 and 10 cm above
157 the junction between the stipe and the blade, i.e. the meristem) and three holes in the distal
158 part of the blade (10, 20 and 30 cm from the distal edge of the blade) for erosion
159 measurements. Tagged individuals were marked with yellow cable ties around the top of the
160 stipe to ease identification and harvest during the following field campaign. Blade elongation
161 was quantified by measuring the distance from the lowest hole to the meristem (*bd1*) and the
162 distance between the two basal holes (*bd2*). Blade elongation (*BE*) was calculated by
163 subtraction of the sum of these two measures by 10 cm:

164
$$BE = (bd1 + bd2) - 10 \quad \text{Eq. 3}$$

165 The distance from the distal edge of the blade to each of the three terminal holes (*td1*, *td2* and
166 *td3*, respectively) was also measured and blade erosion (*ER*) was calculated by subtracting 10,

167 20 and 30 cm, respectively, from the measured distances from the edge to each of the three
168 terminal holes and averaging the results:

$$169 \quad ER = ((td1 - 10) + (td2 - 20) + (td3 - 30)) / 3 \quad \text{Eq. 4}$$

170 Each blade was finally cut in 5 cm segments that were weighed (blotted FW). The heaviest
171 segment from the basal half of the blade was used to calculate daily blade production per
172 individual (BP, g FW individual⁻¹ d⁻¹) using Eq. 5:

$$173 \quad BP = BE \times FW_B \times t^{-1} \quad \text{Eq. 5}$$

174 where BE is blade elongation (in cm), FW_B is the length specific biomass (g FW cm⁻¹) of the
175 heaviest segment from the basal half of the blade, and t is the number of days elapsed between
176 tagging the plant and its harvest. The heaviest segment from the lower half of the lamina was
177 used to calculate production because the density (g FW unit⁻¹ area) continues to increase after
178 the elongation rate has ceased. Blade production (g DW m⁻²) was finally estimated by
179 multiplying daily blade production per individual (BP) with plant density and the number of
180 days elapsed between sampling events. Stipe production was not measured in the present
181 study but was estimated from measured stipe biomass from the above quadrat collections and
182 P/B-ratios for canopy plant stipe (P/B-ratio = 0.234 ± 0.032 [mean ± sd]); Pedersen et al.
183 2012).

184 Segments from the distal half of the blade were used to calculate the biomass of
185 eroded blade material (B_E) by multiplying the erosion length (ER) with the average length
186 specific biomass (FW_D cm⁻¹) of the distal half of the blade according to Eq. 6:

$$187 \quad B_E = ER \times FW_D \times t^{-1} \quad \text{Eq. 6}$$

188 where t is the number of days elapsed between tagging the plants and its collection. Blade
189 erosion losses (g DW m⁻²) was finally estimated by multiplying daily blade erosion per
190 individual (B_E) with plant density and the number of days elapsed between sampling events.

191

192 **Dislodgement and spring cast.** Dislodgement of whole plants and blades was estimated as
193 the proportion of tagged plants that was lost between sampling events and from the number of
194 ‘fresh’ stipes without blades (i.e. with destroyed meristems) collected in the quadrats. The
195 mass of kelp detritus formed by dislodged plants (D_{DIS}) was estimated as the site-specific
196 proportion of plants lost between sampling events (P_L) multiplied by site-specific kelp density
197 (D) and individual kelp biomass (B_{IND}) to obtain daily losses in g FW m⁻² between sampling
198 events:

$$199 \quad D_{DIS} = P_L \times D \times B_{IND} \times t^{-1} \quad \text{Eq. 7}$$

200 where t is the time elapsed between two succeeding sampling events. The biomass of old
201 lamina lost during the spring cast (D_{CAST}) was estimated from site-specific changes in the
202 proportion of individuals carrying an old lamina (P_{OB}) between successive sampling events
203 (i.e. winter to spring and spring to summer) multiplied by site-specific kelp density (D) and
204 the individual biomass of old lamina (B_{LAM}) to obtain daily losses in g FW m⁻² between
205 sampling events:

$$206 \quad D_{CAST} = P_{OB} \times D \times B_{LAM} \times t^{-1} \quad \text{Eq. 7}$$

207 where t is the time elapsed between two succeeding sampling events. Units of FW were
208 finally converted to units of carbon applying a DW:FW ratio of 0.163 ± 0.047 for blades and
209 0.135 ± 0.019 for stipes, respectively, and a C-content of $33.0 \pm 3.1\%$ of DW for blades and
210 $29.7 \pm 2.6\%$ of DW for stipes (own unpublished values for this species, n = 32).

211
212 **Comparing detrital C-flux from L. kelp to that of other habitats.** We compared finally the
213 obtained values of detrital C donation by *L. hyperborea* to that of other terrestrial and coastal
214 habitats by using data obtained from the literature. Terrestrial habitats included temperate and
215 tropical forests and shrubs, temperate and tropical grass lands while coastal habitats included
216 marine phytoplankton, non-kelp seaweeds, seagrasses, mangroves and marshes. The

217 particulate detrital carbon donation included all types of litter-fall and detritus (e.g. leaves,
218 branches and twigs, reproductive structures), but in most cases not below-ground detritus
219 production. Numbers and references are in Supporting Information Table S1.

220

221 **Statistical analyses.** All values in the text are means \pm 95% CI unless otherwise stated. Mean
222 and maximum *REI* were compared across sites and seasons using two factor ANOVA.

223 Normality of the residuals was tested by Kolmogorov-Smirnoff test and homogeneity of
224 variances was tested by Levenes test. Most data (i.e. *REI*, kelp density, individual biomass,
225 biomass per unit area, blade growth, blade erosion, dislodgment of plants and loss of old
226 blades) did not meet the assumptions for parametric analysis (especially homogeneity of
227 variance) and were therefore compared across sites and seasons using non-parametric
228 repeated measures ANOVA (i.e. Friedman's test). Means were first compared across sites
229 using season as a blocking factor, then compared across seasons using site as blocking factor.
230 Multiple pair-wise comparisons were conducted using the Tukey procedure for ranked data
231 when the Friedman test provided significant results (Zar 1999). Correlations between net
232 production, blade erosion, dislodgment and relative wave exposure level (*REI*) were tested
233 using non-parametric Spearman Rank Correlation analysis. The detritus production in
234 different ecosystem types were compared using one way ANOVA. All tests were performed
235 using $\alpha = 0.05$.

236

237 **RESULTS**

238 **Temperature, light and relative wave exposure.**

239 Water temperature averaged $7.1 \pm 2.3^{\circ}\text{C}$ (\pm sd) and ranged from 4.2°C in spring (March-
240 April) to 11.5°C in late summer (August) (Fig. 2A). Daily light intensity reaching the canopy
241 averaged 765 ± 855 lux (\pm sd) and ranged from 0 lux d^{-1} in December and January to 3877 lux

242 d⁻¹ late June (Fig. 2B). Wind speed (Fig. 2C) averaged 6.5 ± 4.0 m sec⁻¹ (\pm sd) and ranged
243 from an average of 4 m sec⁻¹ in summer to 8 m sec⁻¹ in winter while maximum wind speed
244 ranged from 18 m sec⁻¹ in autumn to 26 and 32 m sec⁻¹ in winter and spring, respectively.
245 Mean and maximum wave exposure level (*REI*) varied between seasons and sites (Fig. 3A
246 and 3B). Mean *REI* varied 10 to 25-fold between sites depending on season ($\chi^2_{r,4,10} = 33.4$; p
247 < 0.001) and was significantly higher at sites 1 - 5 than at sites 6 - 10. Maximum *REI*
248 followed largely the same pattern across sites ($\chi^2_{r,4,10} = 33.8$; $p < 0.001$), but the variation was
249 larger than for mean *REI* (30 to 53-fold variation depending on season). Mean *REI* was
250 highest during winter and lowest in autumn ($\chi^2_{r,4,10} = 13.3$; $p = 0.004$), while maximum *REI*
251 was highest in winter and lowest in summer ($\chi^2_{r,4,10} = 18.8$; $p < 0.001$). Mean *REI* varied 1.6
252 to 2.8-fold between seasons (depending on site) while maximum *REI* varied 1.1 to 2.7-fold
253 between seasons. Seasonal variation in *REI* was not consistent across all sites since some sites
254 had larger seasonal variations in *REI* than others. This was likely due to seasonal variation in
255 the dominant wind direction and showed that location and, thus, weighted effective fetch,
256 played an important role for *REI*.

257

258 **Individual plant traits.** Individual kelp biomass (i.e. stipe plus lamina) averaged 48.2 ± 12.9
259 g C (\pm sd) and ranged from 24.0 to 77.0 g C depending on site and season (Fig. 4A).

260 Individual stipe biomass (mean \pm sd = 19.2 ± 6.8 g C) was larger at sites 5, 6 and 7 than at the
261 remaining sites (26.6 vs. 16.0 g C; $\chi^2_{r,10,4} = 28.0$; $p < 0.001$), but did not vary seasonally

262 ($\chi^2_{r,4,10} = 6.2$; $p = 0.188$). Individual blade biomass (mean \pm sd = 29.0 ± 8.6 g C; Fig. 4B) was
263 larger in plants from sites 1 to 6 than from sites 7 to 10 (32.8 vs. 23.3 g C kelp⁻¹; $\chi^2_{r,10,4} =$

264 24.4; $p = 0.004$). Individual blade biomass was the only morphological variable that was

265 correlated with *REI* (Spearman rank's $R = 0.745$; $p = 0.013$). Blade biomass was lowest in

266 late winter and largest in summer (22.9 vs. 33.8 g C; $\chi^2_{r,4,10} = 16.6$; $p = 0.002$). New blades

267 were initiated in early winter and increased in size during spring to reach maximum size in
268 August. Old, fully grown blades lost 35.8 ± 18.6 % of their biomass through erosion and
269 pruning between late summer and the following spring where they were cast.

270

271 **Kelp density, biomass and productivity.** Kelp density averaged 16.6 ± 1.3 (\pm sd) individuals
272 m^{-2} across sites and seasons (Figs. 5A and 5B). Density did not differ among sites ($\chi^2_{r,10,4} =$
273 13.9; $p = 0.126$), but decreased slightly over the course of the study ($\chi^2_{r,4,10} = 12.8$; $p = 0.012$;
274 density in August 2016 being higher than in March, May and August 2017; all $p < 0.015$).

275 Total kelp biomass per unit area averaged 770 ± 100 g C m^{-2} (\pm sd) across all sites
276 and sampling dates (Figs. 5C and 5D). Total biomass was higher at sites 3, 5, 6, 7 and 8 than
277 at the remaining sites (888 vs. 652 g C m^{-2} ; $\chi^2_{r,10,4} = 20.4$; $p = 0.015$). Total stipe biomass per
278 unit area averaged 313 ± 69 g C m^{-2} (\pm sd) across sites and sampling events, corresponding to
279 ca. 41% of the total biomass. Stipe biomass was higher at sites 5 to 8 than at the other sites
280 (415 vs. 245 g C m^{-2} ; $\chi^2_{r,10,4} = 28.3$; $p < 0.001$), but did not vary seasonally ($\chi^2_{r,4,10} = 6.6$; $p =$
281 0.161). Total blade biomass per unit area averaged 458 ± 64 (\pm sd) g C m^{-2} and was similar
282 across sites, except for site 3 where it was higher than at all other sites ($\chi^2_{r,10,4} = 17.4$; $p =$
283 0.043). Blade biomass varied seasonally ($\chi^2_{r,4,10} = 13.0$; $p = 0.011$), being lowest in late
284 winter (March) when the new blades were small and the old ones were heavily eroded, and
285 highest in late summer.

286 Daily blade production per unit area averaged 1.16 ± 0.11 g C m^{-2} (Fig. 5E and F)
287 and did not differ across sites ($\chi^2_{r,10,4} = 5.2$; $p = 0.813$), but was much higher in spring than in
288 other seasons (3.24 ± 0.51 vs. 0.06 ± 0.04 to 0.99 ± 0.12 $\text{g C m}^{-2} \text{d}^{-1}$; $\chi^2_{r,3,10} = 26.0$; $p < 0.001$).
289 Blade production was not correlated to *REI* ($R = -0.248$, $p = 0.489$). Annual blade production
290 (August 2016 to August 2017) amounted to 426.2 ± 39.4 g C m^{-2} , with more than 90% of that
291 taking place within 3 - 4 months in spring. The annual production of stipe biomass amounted

292 to $73.1 \pm 16.2 \text{ g C m}^{-2}$ yielding a total average productivity of $499.4 \pm 49.9 \text{ g C m}^{-2} \text{ y}^{-1}$ across
293 the ten study sites.

294

295 **Detritus production.** Erosion losses per unit area averaged $0.29 \pm 0.05 \text{ g C m}^{-2} \text{ d}^{-1}$ (Fig. 6A
296 and 6B) and did not differ across sites ($\chi^2_{r,10,4} = 3.5$; $p = 0.939$) but differed between seasons,
297 ranging from $0.05 \pm 0.05 \text{ g C m}^{-2} \text{ d}^{-1}$ in spring to $0.61 \pm 0.22 \text{ g C m}^{-2} \text{ d}^{-1}$ in late summer
298 ($\chi^2_{r,3,10} = 25.6$; $p < 0.001$).

299 Erosion losses were not correlated to *REI* ($R = 0.006$, $p = 0.987$). Annual biomass losses
300 through erosion amounted to $108.0 \pm 7.2 \text{ g C m}^{-2}$.

301 The number of kelp plants or whole blades lost through dislodgment averaged $18.6 \pm$
302 $10.8\% \text{ year}^{-1}$ (data not shown) corresponding to an average biomass loss of $0.33 \pm 0.19 \text{ g C m}^{-2}$
303 d^{-1} (Fig. 6C and D). Losses through dislodgement did not differ among sites ($\chi^2_{r,10,4} = 7.0$; p
304 $= 0.638$), were not correlated to *REI* ($R = -0.430$, $p = 0.214$) and did not vary seasonally
305 ($\chi^2_{r,3,10} = 1.4$; $p = 0.711$). Annual losses through dislodgment reached $114.5 \pm 51.9 \text{ g C m}^{-2}$ of
306 which 46% was made up by stipe material while the remaining 54% was blade material.

307 More than 99% of the plants collected during late winter (March 2017) had an old
308 blade attached to the distal end of their new blade, but this number fell to 37% in late May
309 2017. Most of the plants carrying an old blade in May lost them during our processing, so we
310 assume that these would have been lost within days in the field. None of the plants sampled in
311 August 2016 and 2017 carried an old blade. The spring cast of old blades corresponded to an
312 average biomass loss of $255.5 \pm 43.2 \text{ g C m}^{-2} \text{ y}^{-1}$ (Fig. 6E; no difference across sites: $\chi^2_{r,10,4} =$
313 5.4 ; $p = 0.803$) with the majority being lost between late March and early May (Fig. 6F).

314 The total production of detritus from *L. hyperborea* averaged $478.0 \pm 40.5 \text{ g C m}^{-2} \text{ y}^{-1}$
315 across the ten study sites. Formation of blade detritus through dislodgment and blade erosion
316 was the least important form of detritus production, accounting for 24% and 23% of the total

317 detritus production, respectively, while the spring cast of old blades represented 53% of the
318 total detritus production (Fig. 7).

319

320

321 **DISCUSSION**

322 Our study confirmed that high latitude kelp forests in Norway are very productive and deliver
323 large amounts of particulate detritus that, depending on its form and timing of delivery, may
324 support secondary production and/or contribute to Blue Carbon through permanent burial in
325 marine sediments in deeper adjacent areas. The annual production of detritus from *Laminaria*
326 *hyperborea* (478 g C m⁻²) was higher than that reported from southern England (202 g C m⁻²),
327 but comparable to that found in northern Scotland (432 g C m⁻²; Pessarrodona et al. 2018).

328 The study by Pessarrodona et al. (2018) is the only other one that reports rates of detritus
329 production for *L. hyperborea*. However, grazing on live *L. hyperborea* is usually low
330 (typically <10% of the biomass production; Norderhaug & Christie 2011) and the formation
331 of detritus can therefore be inferred from the annual production of biomass. The observed
332 production in this study (499 g C m⁻² y⁻¹) is within the range of that reported for *L.*

333 *hyperborea* along the west coast of Norway, Isle of Man (UK), Helgoland (Germany) and
334 Normandy (France) (range: 376-825 g C m⁻² y⁻¹; Lüning 1969, Jupp & Drew 1974, Sheppard
335 et al. 1978, Sjøtun et al. 1995, Pedersen et al. 2012), but higher than that reported from
336 Iceland and Finmark in northernmost Norway (ca. 250 g C m⁻² y⁻¹; Gunnarsson 1991, Sjøtun
337 et al. 1993). The production of detritus from *L. hyperborea* seems thus to range from ca. 225
338 to ca. 750 g C m⁻² y⁻¹ (assuming grazing losses ~10% of NPP) across its distributional range,
339 which is similar to the production of detritus in other kelp species (table 1 in Krumhansl &
340 Scheibling 2012). The production of detrital C from *L. hyperborea* included only particulate
341 detritus (POC), but part of the C fixed in kelp photosynthesis is released as dissolved organic

342 C (DOC), which may support pelagic microorganisms (e.g. Newell et al. 1982) or contribute
343 to C-sequestration if transported below the mixed zone of the ocean (Krause-Jensen & Duarte
344 2016). Large uncertainties remain regarding the total production and fate of DOC from kelps,
345 but the DOC released from kelps appears to range from 14 to 34% of total the production
346 (POC plus DOC) depending on species and location (e.g. Newell et al. 1980, Abdullah &
347 Fredriksen 2004, Reed et al. 2015), which would represent an important component of detrital
348 production.

349 The processes through which kelp detritus is produced have implications for its
350 transfer to other habitats and its turn-over through consumption and decomposition. More
351 than 75% of the detritus formed by *L. hyperborea* was delivered as coarse material formed
352 through dislodgement of whole plants or the spring cast of old blades, while the rest was
353 delivered as smaller particles and small blade fragments through erosion. This compares to
354 the proportions reported by Pessarrodona et al. (2018) for this species. The large proportion of
355 coarse detritus is comparable to that found in *Macrocystis pyrifera* where dislodgement
356 account for almost 80% of the annual detritus production (Gerard 1976), but contrasts the
357 pattern found in *Ecklonia radiata* where most (78%) detritus is formed through erosion (de
358 Bettignies et al. 2013b). These inter-specific variations may be due to difference in
359 morphology since the thallus of *M. pyrifera* extends 10s of meters and forms floating
360 canopies that are susceptible to wave forces (Seymour et al. 1989, Graham et al. 1997),
361 whereas *E. radiata* is much shorter with scouring canopies that may stimulate erosion rate.
362 The morphology of *L. hyperborea* is intermediate between these extremes; it has a longer
363 stipe than *E. radiata* and no floating canopy like *M. pyrifera* so scouring and drag forces may
364 be less important.

365 Water motion is often considered a major driver for the formation of kelp detritus.
366 Blade erosion may be stimulated by water motion, although weakening of the blade tissue by

367 formation of sori, grazing and encrustation by bryozoans can also play a role (Krumhansl &
368 Scheibling 2011b, de Bettignies et al. 2012, Mohring et al. 2012). Erosion is correlated to
369 water motion in some species (e.g. *Laminaria digitata*; Krumhansl & Scheibling 2011a), but
370 not in others (e.g. *Saccharina latissima*; Krumhansl & Scheibling 2011a, *E. radiata*; de
371 Bettignies et al. 2013b). Erosion rate in *L. hyperborea* was not correlated to *REI* when
372 compared across sites although maximum *REI* varied 30 – 53 fold, but varied instead
373 seasonally with fast erosion coinciding with high *REI* in autumn and winter. Winter season is
374 also the time where the blades get older and more fragile, which increases erosion rate. The
375 lack of correlation between erosion rate and *REI* when compared across sites suggests thus
376 that seasonal ageing of the blade is a more important driver of elevated erosion than water
377 motion per se. Storms may cause dislodgement of whole kelps or their blades (Ebeling et al.
378 1985, Seymour et al. 1989, Filbee-Dexter & Scheibling 2012) as may weakening of the stipe
379 by sea urchin grazing (de Bettignies et al. 2012), but dislodgement rate was neither correlated
380 to *REI* nor to sea urchin density when compared across sites or seasons. Dislodgement rates in
381 *L. hyperborea* were much lower than in *E. radiata* (18% y^{-1} versus 44 – 55% y^{-1} ; de
382 Bettignies et al. 2013b) and did not undergo any clear seasonal variation although storm
383 events were more frequent and intense in autumn and winter (Fig. 2C). de Bettignies et al.
384 (2015) found the same in a study on *E. radiata* and explained the low effect of water motion
385 by small thallus size and, thus, reduced drag, in winter when wave exposure was highest (de
386 Bettignies et al. 2013a). The blade of *L. hyperborea* is also slightly smaller in winter than in
387 other seasons (Fig. 4B), but blade size was positively correlated to *REI* when compared across
388 sites, so reduced drag in winter can hardly explain the low importance of water motion in the
389 present study.

390 Most kelp detritus was delivered as coarse fragments, but these may be transformed
391 to smaller size before reaching recipient communities outside the kelp forest. Once dislodged

392 or cast, coarse detritus can break-up mechanically due to scouring or grazers can shred it into
393 smaller pieces or consume it and deliver the remains as fecal pellets. Such transformation is
394 important for the fate of the detritus because size may affect its susceptibility to consumers,
395 its dispersal capacity and its decomposition. Sea urchins feed intensively on coarse kelp
396 detritus. The density of sea urchins (mainly the green sea urchin *Strongylocentrotus*
397 *droebachiensis*) in the study area varied from 1 to 10 m⁻² across sites and their consumption
398 of kelp detritus inside and in the vicinity of our the kelp forest sites corresponded to 60 - 65%
399 of the total detritus production (Filbee-Dexter et al. submitted). Green sea urchins fed kelp
400 defecate 50 - 70% of the consumed detritus as small undigested, but fragmented material with
401 approximately the same chemical composition as 'intact' kelp detritus (Mamalona & Pelletier
402 2005), which may support suspension and deposit feeders within and outside the kelp forest
403 (Duggins et al. 1989, Fredriksen 2003, Leclerc et al. 2013, McMeans et al. 2013, Gaillard et
404 al. 2017). However, the importance of kelp detritus as a food source has recently been
405 questioned by a review showing that trophic studies based on stable C-isotope data alone may
406 overestimate the trophic importance of kelp particles relative to that of phytoplankton (Miller
407 & Page 2012)

408 Detritus that is not mineralized by consumers within and near the kelp forests will be
409 prone to dispersal, decomposition or burial. Small kelp particles sink more slowly than larger
410 fragments, whole blades or stipes, which allow for a wider dispersal (Wernberg & Filbee-
411 Dexter 2018). Filbee-Dexter et al. (submitted) used sinking rates for different sized kelp
412 detritus and hydrodynamic modeling to simulate particle transport in the study area and found
413 that the median dispersal range of whole kelp blades was 8.5 km (maximum range = 150 km)
414 whereas it was 26 km (maximum >300 km) for small kelp particles. Beach cast of kelp is
415 often observed after storms (Griffiths et al. 1983, Seymour et al. 1989), but the coastline in the
416 study area is steep and we did not observe substantial accumulations of kelp detritus on the

417 shore. We hypothesize therefore that excess detritus is exported to the deeper parts in the area,
418 which is supported by trawl collections and video observations in the study area (Filbee-
419 Dexter et al. 2018). More than 50% of the kelp detritus was formed during the spring cast
420 between April and May, coinciding with observations of large amounts of coarse kelp detritus
421 within and around the kelp forests (Filbee-Dexter et al. 2018). Large amounts of coarse kelp
422 detritus were subsequently (late May) observed below the kelp forests at depths from 20 to 80
423 m and in the deepest portions of the study area (~ 400 m) confirming that the detritus was
424 exported several kilometers away from the source populations within days to weeks of its
425 formation. The amount of visible kelp detritus was much lower and the fragments smaller in
426 August, indicating that continuous fragmentation and transport to deeper sites in the study
427 area occurred during summer.

428 Kelp detritus that is not consumed will ultimately decompose or become buried in
429 deeper areas. Laboratory studies show that coarse detritus from *L. hyperborea* loses more than
430 40% of its initial C-biomass within 3 - 4 weeks and decomposes completely in less than one
431 year under aerobic conditions, while decomposition under anoxic conditions (such as in
432 deeper areas) stops after 5-6 months leaving 20 - 25% of the initial biomass to decompose at
433 extremely low rates or not at all (Frisk 2017). Decomposition rate depends also on particle
434 size. Fecal pellets from sea urchins fed with kelp detritus lose almost 80% of their initial C-
435 mass in two weeks (Sauchyn & Scheibling 2009), which is much faster than for larger kelp
436 fragments. Decomposition of kelp detritus can thus be fast depending on the environmental
437 conditions and the degree of fragmentation, while burial of significant quantities of kelp C
438 requires rapid export to areas where the conditions disfavor mineralization through
439 consumption or decomposition.

440 The potential export of detrital kelp C to the non-vegetated portions of the study area
441 can be estimated from the production of kelp detritus per unit area and kelp coverage in the

442 area. Kelp covered ca. 22 km² of the 126 km² covered by ocean in the study area (Fig. 1). The
443 total production of kelp detritus in the study area amounts to 10517 T C y⁻¹ or 101 g C m⁻² y⁻¹
444 if dispersed evenly over the 104 km² of non-vegetated area and assuming no consumption and
445 decomposition. The potential input of detrital kelp C is comparable to the vertical flux of
446 POC (marine snow) from the pelagic zone, which ranges from 93 to 150 g C m⁻² y⁻¹ in the
447 outer part of Malangen Fjord (Keck & Wassmann 1996). Kelp detritus may thus contribute
448 significantly to the total input of C to the deeper portions of the study area, although the input
449 must be less than estimated above when consumption by sea urchins and rapid initial
450 decomposition are taken into account.

451 The importance of Blue C has lately received increased attention (McLeod et al.
452 2011, Duarte 2017, Raven 2017) and coastal habitats such as mangroves, marshlands and
453 seagrasses are now recognized as significant C-sinks (Chmura et al. 2003, Donato et al. 2011,
454 Fourqurean et al. 2012), while the role of kelps and other macroalgae is still being debated
455 (Howard et al. 2017, Krause Jensen et al. 2018, Smale et al. 2018). Quantifying the formation
456 of kelp detritus is a first, but important step when evaluating the potential role of kelps as
457 donors to C-sequestration. The production of detrital C by *L. hyperborea* reported here (~ 500
458 g C m⁻² y⁻¹) is well within the range of that in other kelps, seagrasses, and mangroves, but
459 significantly lower than marshes and significantly higher than marine phytoplankton, non-
460 kelp seaweeds and terrestrial habitats such as forests and grasslands (Fig. 8, one way
461 ANOVA: $F_{7,488} = 13.8$, $p < 0.001$; Suppl. information Table 1). The substantial production of
462 detrital C from kelp forests suggests that kelp systems could play an important role as Blue C-
463 donors to marine sediments. However, most of the studies on detritus production in grasslands,
464 forests, mangroves and marshes report only above-ground litter fall and do not include below-
465 ground production of detritus, which means the numbers from these systems may be under-
466 estimated.

467 Blue C is defined as the sequestration of C from marine organisms that takes place when
468 burial rates in sediments exceed long-term rates of erosion and decomposition. The
469 importance for Blue C depends therefore not only on the amount of detrital C being produced,
470 but also on re-mineralization of C through consumption by detritivores and/or through
471 decomposition, which will determine how much of the C can be buried. Kelps usually grow
472 on hard substrates and do not have below-ground tissues like seagrasses, mangrove trees and
473 marsh plants. Thus export of kelp detritus to marine sediments where the conditions disfavor
474 consumption and/or decomposition plays an important role in the final fate of kelp C. Future
475 studies should focus on the different fates of kelp detritus and explore how much is consumed,
476 how much is exported to potential Blue C sediments and how fast and under which
477 environmental conditions detrital C is re-mineralized through decomposition.

478

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676

677 **Figure legends.**

678 **Fig. 1** Map of outer Malangen fjord with study sites 1-10. Light brown is land and blue is
679 ocean surface while modeled kelp areas are shown in green. Numbers refer to the sampling
680 sites.

681 **Fig. 2** Seasonal variations (August 2016 to August 2017) in: (a) daily water temperature
682 (averaged across sites), (b) daily light intensity reaching the canopy (averaged across sites)
683 and (c) hourly measures of wind speed obtained from Hekkingen lighthouse.

684 **Fig. 3** Relative wave exposure (*REI*) at all sites and seasons: (a) mean wave exposure and (b)
685 maximum wave exposure. Sites are ranked according to increasing wave exposure along the
686 x-axis. Values are means \pm 95 CI.

687 **Fig. 4** *Laminaria hyperborea* individual plant variables: (a) individual kelp biomass at the 10
688 study sites (averaged across seasons) (b) seasonal variation in individual kelp biomass
689 (averaged across sites). Sites are ranked according to increasing wave exposure level (*REI*)
690 along the x-axis. Mean values \pm 95% CI.

691 **Fig 5** *Laminaria hyperborea* biomass and productivity: (a) kelp density at the 10 study sites
692 (averaged across seasons), (b) seasonal variation in kelp density (averaged across sites), (c)
693 kelp biomass per unit area at the 10 study sites (averaged a cross seasons), (d) seasonal
694 variation in kelp biomass (averaged across sites), (e) blade production at each site in each of
695 four seasons and, (f) seasonal variation in average blade production (averaged across sites).
696 Sites are ranked according to increasing wave exposure level (*REI*) along the x-axis. Mean
697 values \pm 95% CI.

698 **Fig. 6** *Laminaria hyperborea* detritus production: (a) seasonal erosion rate at the 10 study
699 sites, (b) seasonal variation in erosion rate (averaged across sites), (c) seasonal dislodgement
700 at the 10 study sites, (d) seasonal variation in dislodgement rate (averaged across sites), (e)

701 seasonal spring cast of old blades at the 10 study sites, and (f) seasonal variation in losses
702 through spring cast of old blades (averaged across sites). Sites are ranked according to
703 increasing wave exposure level (*REI*) along the x-axis. Mean values $\pm 95\%$ CI.

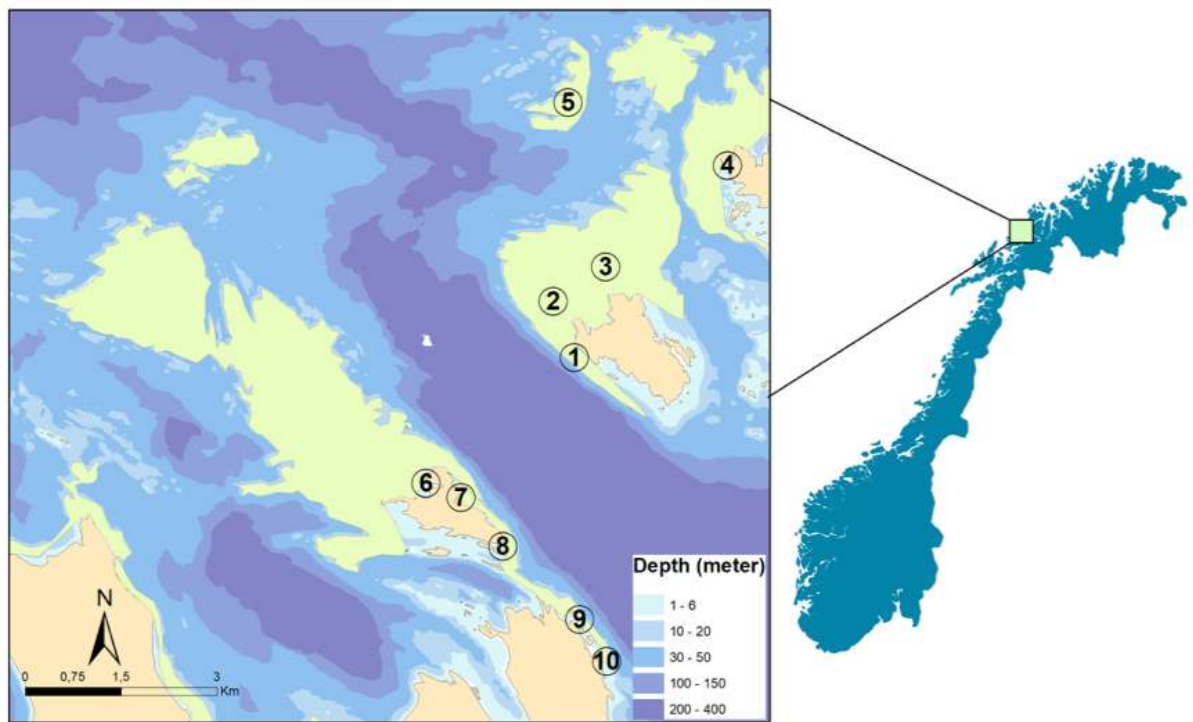
704 **Fig. 7** Cumulated production of detritus through blade erosion, dislodgement and spring cast
705 of old blades during autumn, winter, spring and summer (averaged across the 10 study sites).
706 Mean values $\pm 95\%$ CI).

707 **Fig. 8.** Annual per area production of detrital C in different habitats. The flow of C via
708 detritus includes various kinds of litterfall and detritus production. One-way ANOVA
709 revealed significant differences between habitats ($F_{7,488} = 13.8$, $p < 0.001$) and Dunnett's test
710 was subsequently used to compare the detrital production of each habitat to that of kelps.
711 Asterix indicate significant differences when compared to kelps (*: $p < 0.05$, **: $p < 0.01$, ns:
712 non-significant). Details and references are provided in Supporting Information Table S1.
713 Values are means $\pm 95\%$ CI.

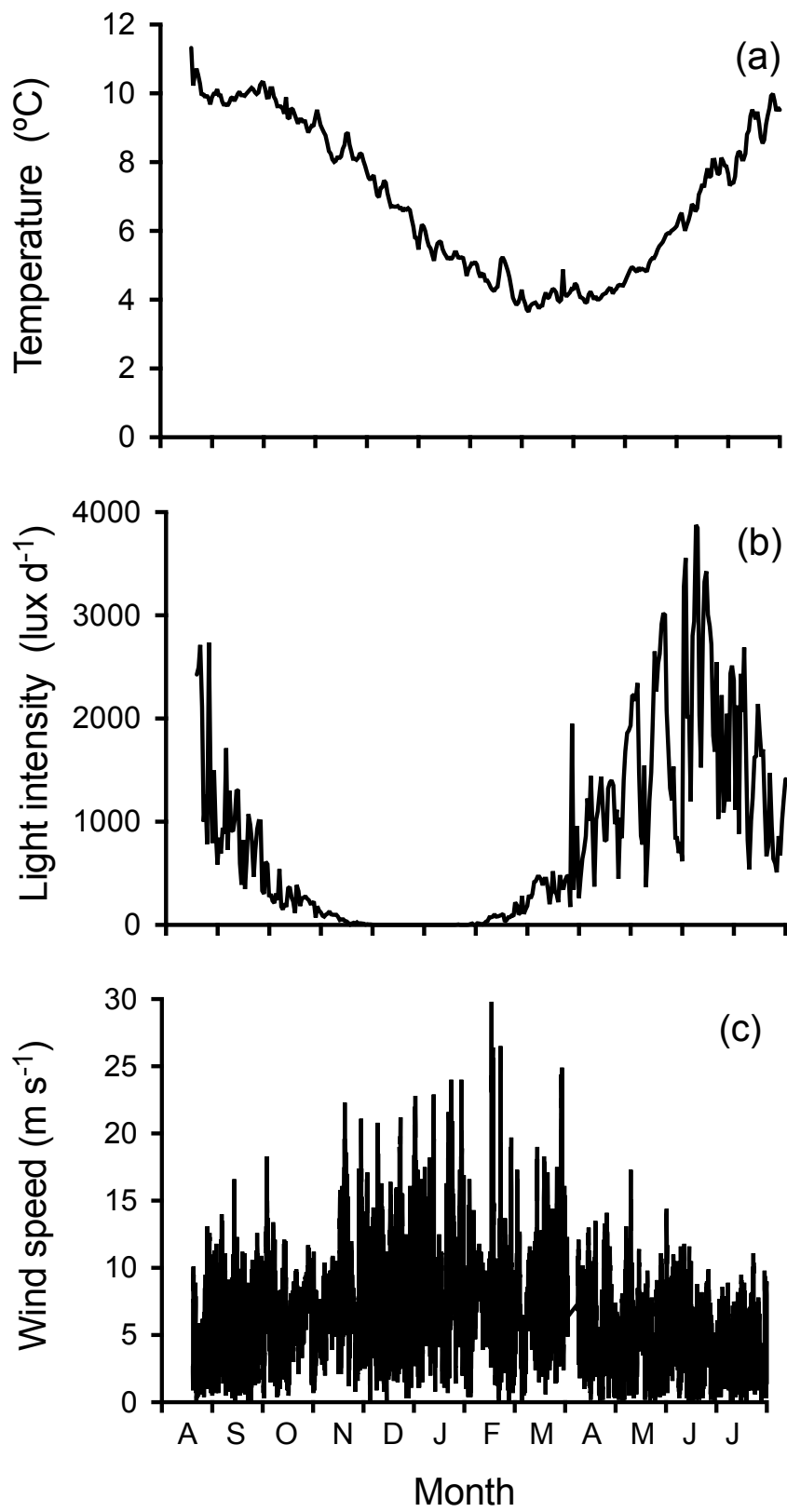
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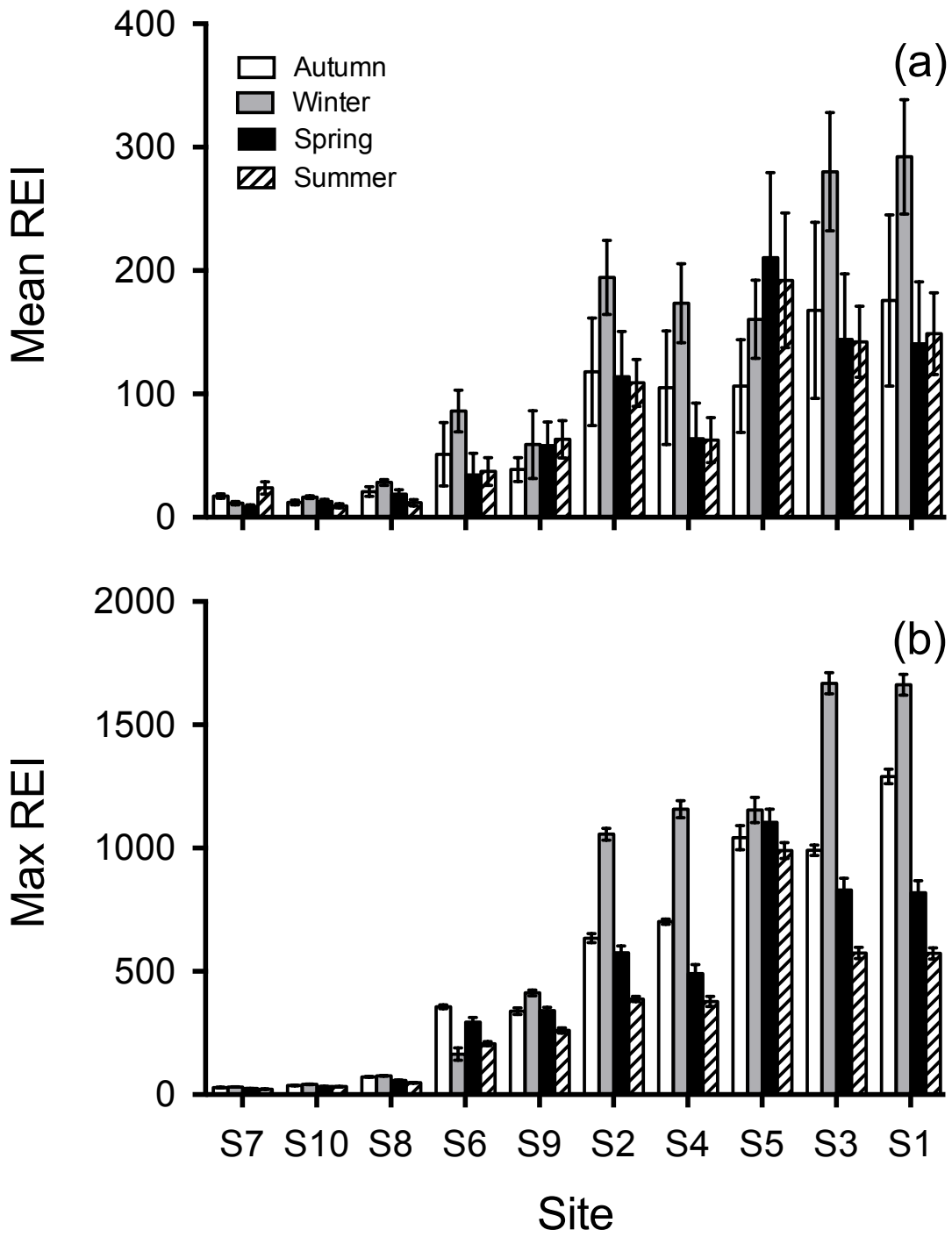
Figure 1



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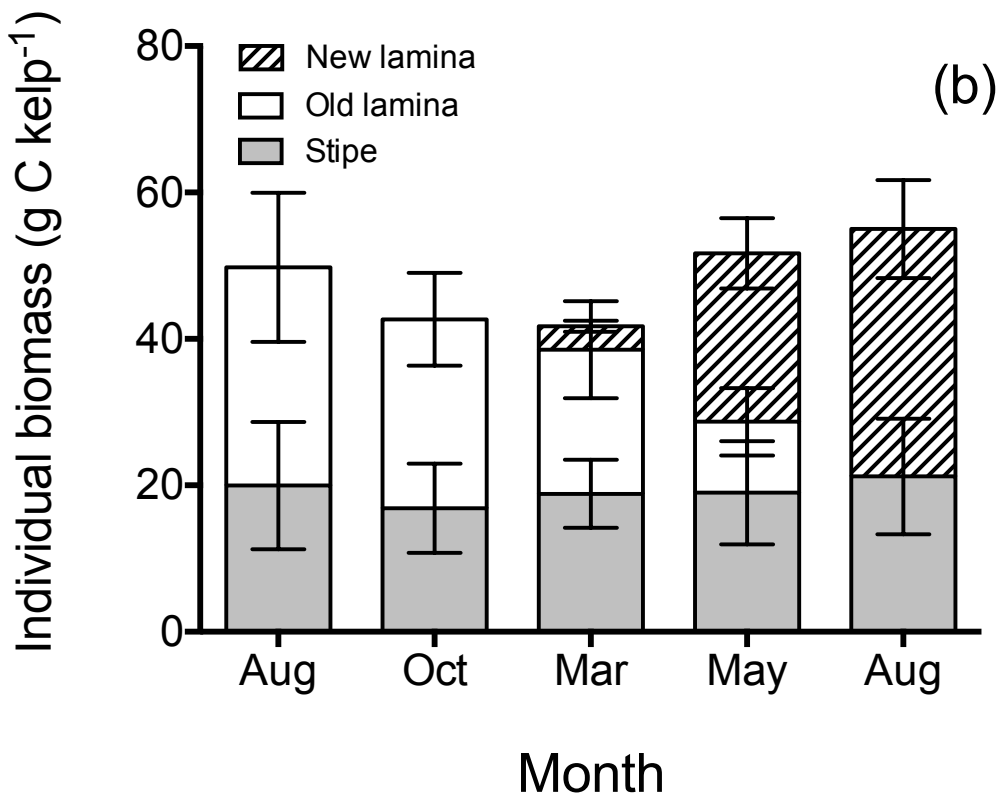
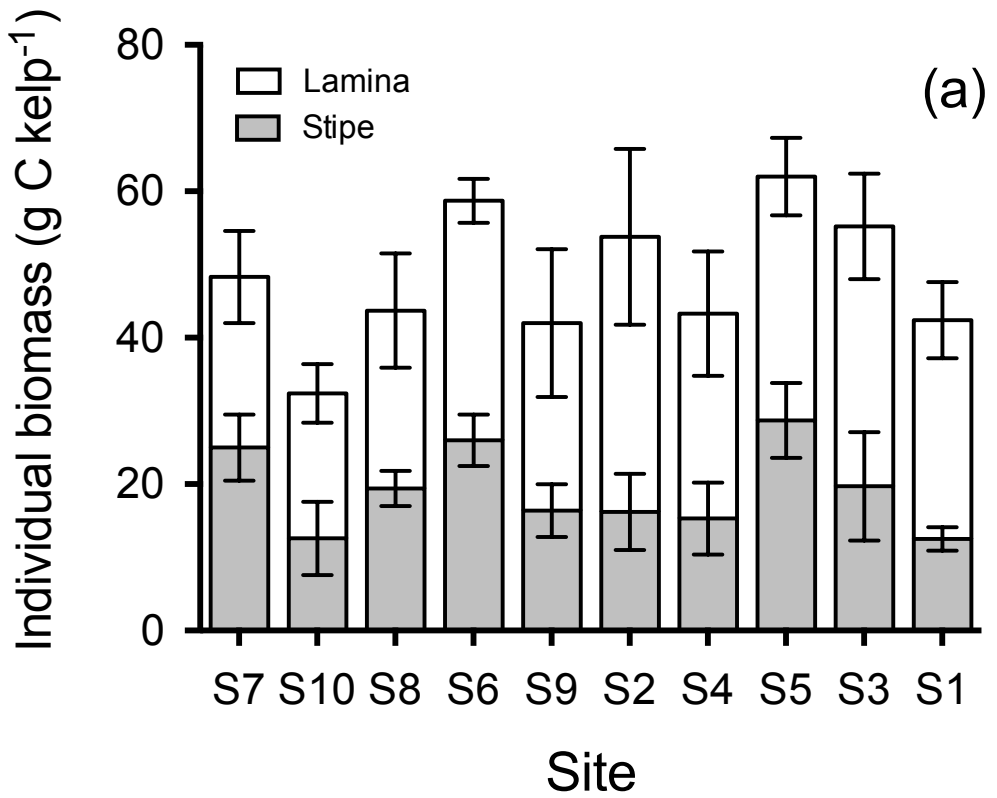


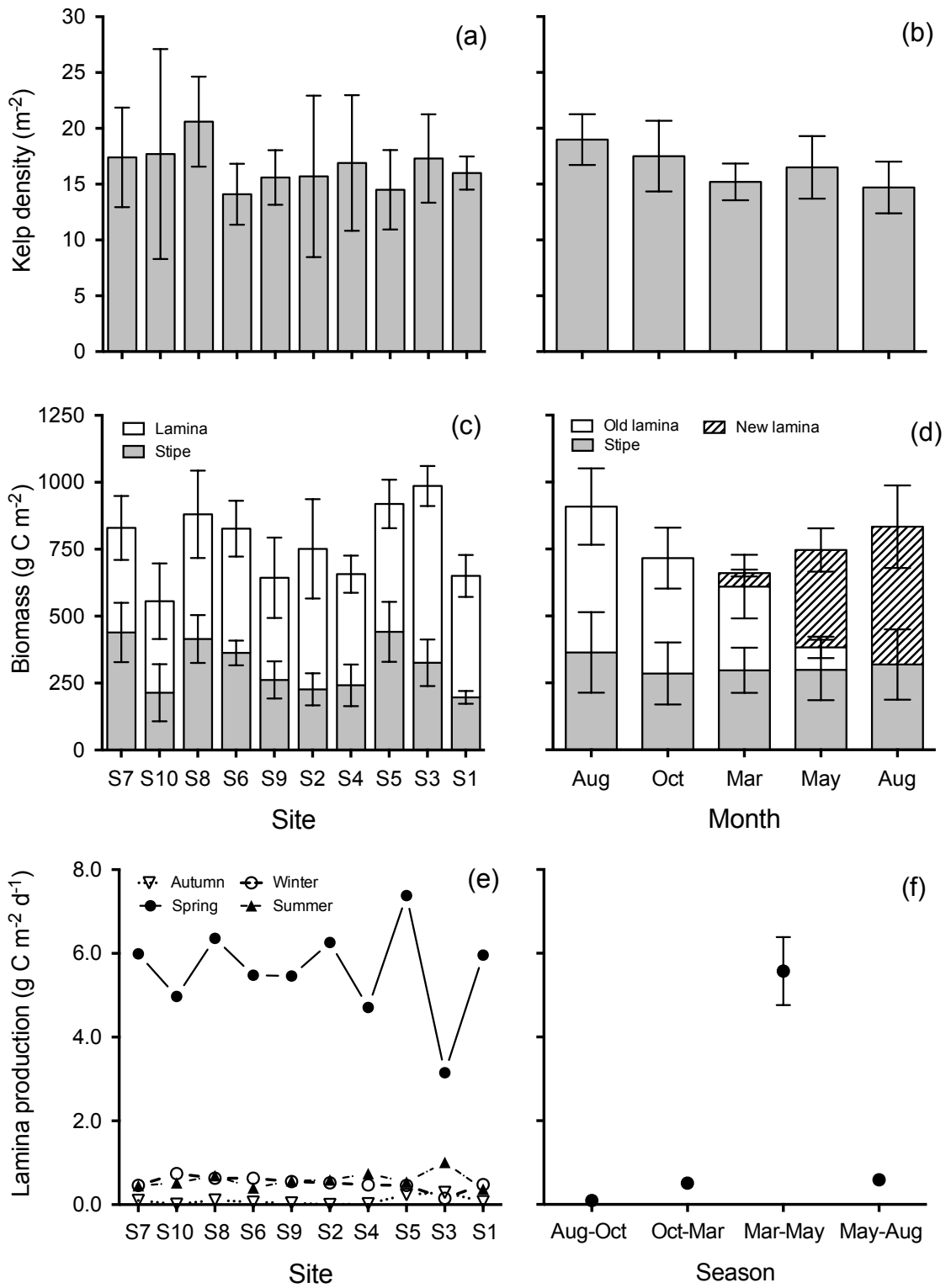
719 **Figure 3**



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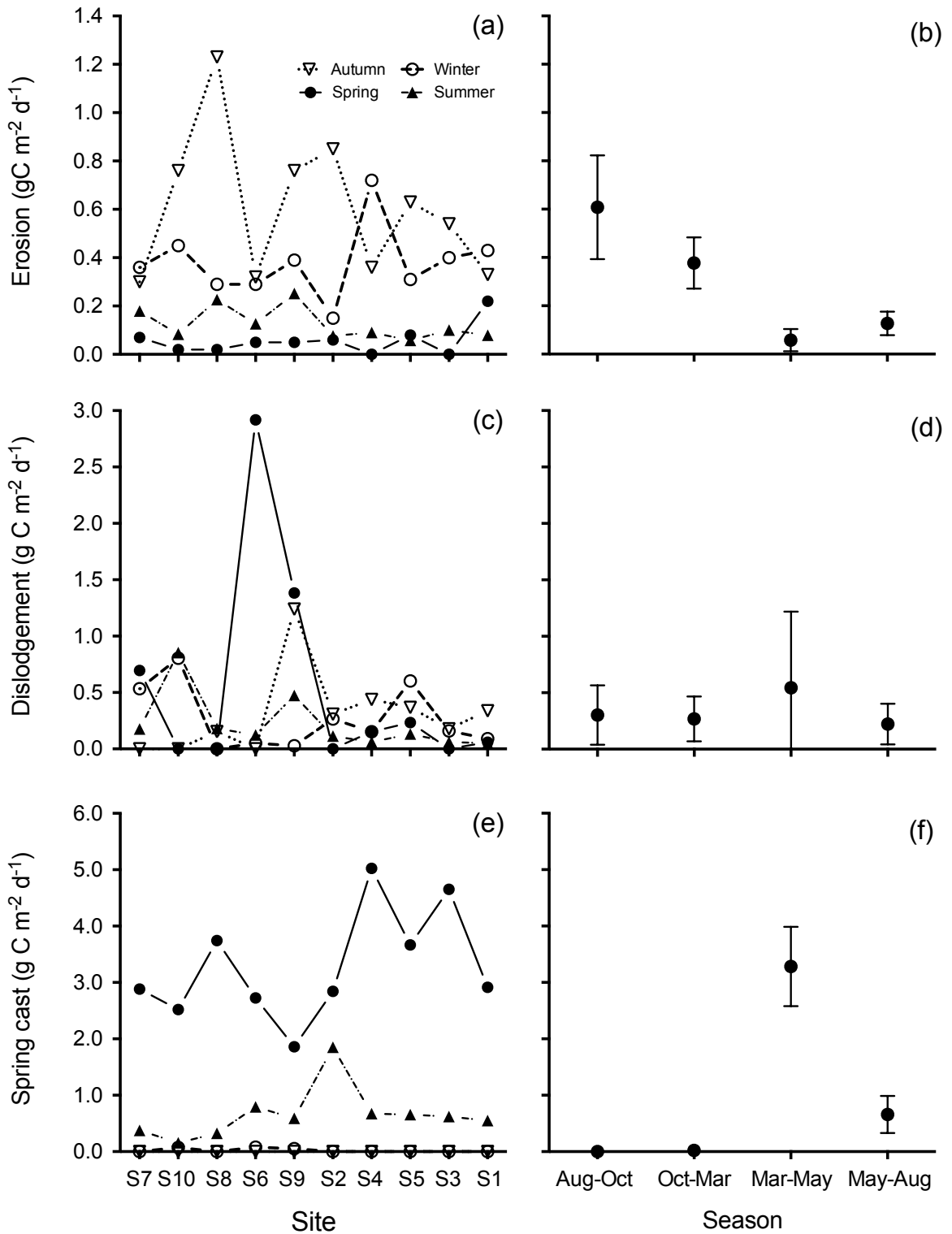
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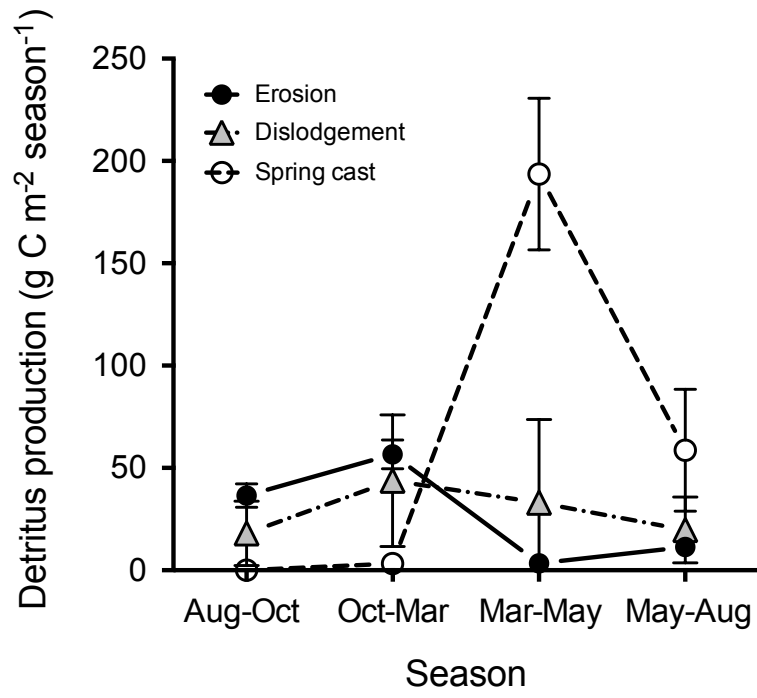


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731 **Figure 7**

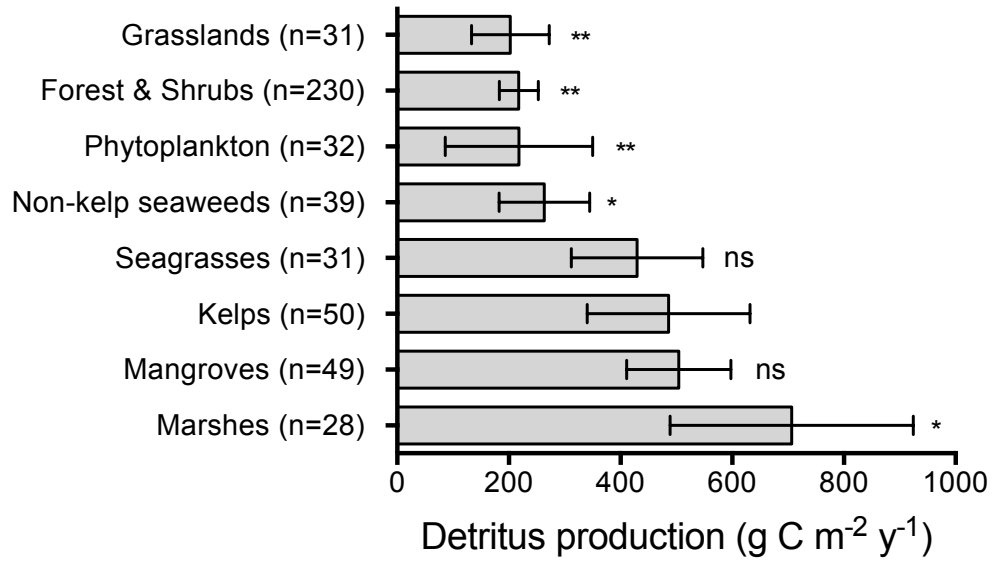


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735 **Figure 8**



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