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DEGRADATION DYNAMICS AND PROCESSES ASSOCIATED WITH THE ACCUMULATION OF KELP FRAGMENTS: AN *IN SITU* EXPERIMENTAL APPROACH

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ABSTRACT:

A high proportion of the kelp *Laminaria hyperborea* production is exported from kelp forests following seasonal storm events or natural annual old blades loss. Drift kelp is transported and can accumulate temporarily in benthic subtidal habitats. We investigated the degradation processes of *L. hyperborea* in a low subtidal (-8 m) sandy bottom ecosystem by setting up a six-month cage experiment to simulate drift kelp accumulation. During the degradation process, we compared changes in biomass, nutritional quality (C:N ratio), respiration, quantum efficiency of photosystem II (Fv/Fm) and chemical defence concentrations. We found that biomass decomposition started after 2 weeks and followed a classic negative exponential pattern. Half of the biomass had degraded after 8 weeks and only 16% of the initial biomass remained after 25 weeks. The degradation process seemed to reach a critical step after 11 weeks, with an increase in respiration rate and phlorotannin concentration. These results likely reflect an increase in bacterial activity and a weakening of the kelp cell wall. Surprisingly, the large fragments remained visually intact after 25 weeks of degradation, and photosystems were still responding correctly to light stimuli, indicating that photosynthesis appears to persist over time in fragments. Reproductive tissues appeared after 4 months of degradation, showing a capacity to maintain the reproductive function. Our results indicate that degrading kelps degrade slowly and because they maintain their major functions (photosynthesis, reproduction, etc.) and accumulate on adjacent ecosystems may play a long-term ecological role in coastal ecosystem dynamics.

KEY INDEX WORDS: Kelp, Degradation, Metabolism, Composition, Bacteria, Organic Matter

1. INTRODUCTION

Degradation is a key process in the organic matter cycle and drives biogenic ecosystems in terrestrial and marine environments. Degradation includes the decomposition (biomass breakdown) of primary producers and litter, and leads to remineralisation driven by micro- and macroorganisms that colonise the organic matter (Pandey et al., 2007; Polyakova and Billor, 2007; Rees, 2001). Litterfall amounts and dynamics are closely related to the growth and productivity of source ecosystems (Matala et al., 2008; Miller, 1984). In terrestrial ecosystems, each plant species has a specific decomposition rate depending on its lignin constituents and nitrogen content (Hendricks and Boring, 1992; Wesemael and Veer, 1992), but also depending on environmental conditions (litterfall moisture, temperature) (Krishna and Mohan, 2017). In contrast to terrestrial systems, marine environments are highly dynamic and variable in terms of water motion and environmental conditions, especially in coastal systems. Despite this major difference, accumulations of seagrass (Cardona et al., 2007; Pergent et al., 1994) and macroalgae, such as kelps, are observed on the seafloor from deep (Filbee-Dexter and Scheibling, 2014; Vetter, 1994) to subtidal (Tzetlin et al., 1997) and intertidal habitats (Bustamante et al., 1995). Macroalgal accumulations are comparable to terrestrial litterfall, modifying the recipient substratum and being influenced by associated micro- and macroorganisms and environmental conditions.

Among macroalgae, kelps are major components of marine ecosystem functioning in temperate and sub-polar regions around the globe. Kelp forests play a key role in coastal environments as habitat-forming species, wave-energy dissipaters and major actors in the carbon cycle (Christie et al., 2003; Leclerc et al., 2015; Teagle et al., 2017). As highly productive primary producers, kelps assimilate carbon dioxide to produce organic matter via photosynthetic processes (Bartsch et al., 2008). Kelps are fast growing producers that accumulate a high quantity of organic matter (>1 kg

75 C.m².yr^{-1}, Krumhansl and Scheibling, 2012a). A high proportion of this biomass is exported
76 during blade erosion, natural mortality or dislodgment related to strong hydrodynamic events (de
77 Bettignies et al., 2013; Krumhansl and Scheibling, 2012; Pessarrodona et al., 2018). Detrital
78 material can drift across habitats and, when hydrodynamic conditions are suitable, accumulates in
79 benthic habitats. Accumulation of kelp detritus can strongly influence the recipient trophic food
80 web (Krumhansl and Scheibling, 2012b; Tzetlin et al., 1997). Globally, 82% of annual kelp
81 production is exported, becoming detrital subsidies (de Bettignies et al., 2013; Krumhansl and
82 Scheibling, 2012a). Within kelp forests, detrital material contributes to the particulate organic
83 matter (POM) pool and plays an important role in trophic food webs (Leclerc et al., 2013).

84 *Laminaria hyperborea* (Laminariales) is a dominant kelp species in the North-East Atlantic,
85 distributed from Portugal to Norway (Steneck et al., 2002). In Brittany, France, this species
86 dominates subtidal rocky ecosystems from 0 to 30 m below chart datum. Growth of *L.*
87 *hyperborea* sporophytes occurs in winter and spring, ceasing in July (Lüning, 1979). In spring, *L.*
88 *hyperborea* retains the old blade from the previous year during the rapid growth of the new blade.
89 Between April and May, the old blade is shed from the fast-growing new blade. The release of
90 the previous season's growth contributes significantly to the total detritus production
91 (Pessarrodona et al., 2018). *L. hyperborea* detritus represents a trophic resource that connects
92 habitats, becoming increasingly accessible to consumers as it degrades (Norderhaug et al., 2003).
93 In some areas, within kelp forest grazers may only consume a small fraction of kelp productivity
94 (Hereward et al., 2018), whereas in other systems, grazing by sea urchins is a major process
95 structuring *L. hyperborea* forests (Ling et al., 2014). In Brittany, grazers appear to consume a
96 very small fraction of the *L. hyperborea* production, with a high proportion being exported to

97 adjacent ecosystems. Therefore, the degradation kinetics of *L. hyperborea* detritus and its impact
98 on recipient ecosystems appear to be key elements in ecosystem functioning.

99 In the present study, we explored *L. hyperborea* decomposition dynamics and the degradation
100 process in an *in situ* six-month experimental approach using litterfall cages to simulate drift kelp
101 accumulation on a sandy bottom ecosystem. To investigate the kinetics of detritus biomass
102 decomposition, we monitored multiple parameters such as carbon (C) and nitrogen (N) content,
103 phlorotannin concentration, photosynthesis, respiration and abundance of cultivable alga-
104 associated bacteria. We tested whether *L. hyperborea* degradation was a quick process, with total
105 decomposition of biomass after several months. The parameters were thus expected to vary
106 accordingly, with a decrease in the C:N ratio (often related to nutritional quality and palatability),
107 a change in tissue phlorotannin concentration (related to stress and defence mechanisms) and a
108 decrease in the major functions such as production, respiration and reproduction.

109 ## 2. MATERIALS AND METHODS

110 ### 2.1. Study site

111 The present study was conducted near Roscoff, in the Bay of Morlaix, along the north-western
112 coast of Brittany, France. The bay is composed of numerous rocky reefs supporting high *L.*
113 *hyperborea* biomass stock (Gorman et al., 2013), separated by large areas of fine and soft
114 sediments that temporarily receive accumulations of drift kelp (personal observation). The
115 experimental site (Guerhéon: 48°42’33.78” N, 003°57’12.36” W) was located in a semi-enclosed
116 part of the bay, protected from the prevailing westerly winds, but exposed to north and easterly
117 winds that occasionally occur during spring and summer anticyclonic conditions. The site
118 substratum was characterised by a mixture of coarse sand and shell fragments at 4.5 m depth

below chart datum (9 m average depth) and distant by ca. 100 m from rocky reefs covered with kelp forests.

2.2. Experimental design

We set up an *in situ* cage experiment to investigate the degradation dynamics of *L. hyperborea* on a subtidal sandy ecosystem (Figure 1). The study was conducted from 18 April to 5 October 2017 (5.5 months). The experiment was deployed in April to mimic the storm events that typically occur during spring and break up and dislodge part of the kelp population and increase the amount of detrital kelp deposits. In this experiment, we chose to simulate storm damage on kelps that are losing their old frond and studied the degradation process on the physiologically active new blades.

During scuba dives, we randomly collected whole adults of *L. hyperborea* with a 80-90 cm stipe length corresponding to 5-6 year-old kelps (Sheppard et al., 1978) without visible signs of degradation from a natural population on a rocky reef close to the experimental site. Kelp samples were kept in seawater and brought back to the harbour where they were processed within 2 hours. New blades were cut once in length and once in width. This method gave different fragment sizes similar to those found in the field. Fragments from two individuals were pooled and weighed with a digital spring scale (Amiaud Durer, 40 kg, ± 10 g) for a mean ± SD wet mass of 911 ± 105 g. Batches were gently packed and randomly allocated to custom-built numbered plastic litterfall cages (30 × 25 × 10 cm, 1 cm mesh) made of hard plastic mesh used in oyster farming. The quantity of algal material in the cage corresponded a 10 cm thick accumulation of kelp fragments with a three-dimensional structure, as previously observed during prospection dives. A total of 35 litterfall cages were prepared with new blades, kept in seawater and quickly immerged on the experimental site by divers. To compare the degradation kinetics between

young and old blades, five litterfall cages were filled with old blade fragments following the same procedure. Cages were attached on four anchored chain lines arranged parallel to each other, forming a relatively continuous rectangle of accumulated fragments (Figure 1). We checked the cages throughout the experiment to ensure that they were not buried in sediment. At each sampling time (2, 4, 6, 11, 15, 20, 24 weeks), five replicates of new-blade litterfall cages were randomly collected. Additionally, one old-blade litterfall cage was randomly collected at five sampling dates (4, 6, 11, 15, 20 weeks). Cages were collected with caution using 1 mm mesh bags, for 3 of them incubated for *in-situ* respirometry measurements, brought to the surface, transported within site seawater to the laboratory for bacterial sampling before any other processing. Cages were then kept in the dark in a continuous-flow seawater tank with constant air bubbling until laboratory measurements (performed within 24 h).

2.3. Field measurements

2.3.1. Environmental parameters

An array of environmental sensors were deployed on the experimental site to measure temperature, light intensity and water motion over the six-month period. Temperature and light intensity were measured with the same sensor (HOBO Pendant Temperature/Light Weatherproof Pendant Data Logger 16K) attached on a plate fixed horizontally on a threaded rod at 20 cm from a concrete block. Relative water motion was measured with an accelerometer (HOBO Pendant G Data Logger) attached to a small dome-shaped buoy. The buoy was tethered to the seabed with a 0.75 m rope clamp on a different concrete block according to (Bennett et al., 2015) design. These sensors were deployed at 3 m from the experimental system and a replicate set was deployed to offset any sensor failure. At each sampling time, sensors were changed or cleaned to prevent too much fouling on the rope or on the sensor. All sensors were programmed to take one

measurement every five minutes. For each sampling time, the maximum, minimum and average values of the previous week were measured for temperature and relative water motion (RWM). Only the daily average was used for light. For the RWM, only two channels were used (x, y) to account for horizontal acceleration (cf. H_2O motion V2 design; Evans and Abdo (2010). The sensor was set to record acceleration ($m.s^{-2}$). The RWM was standardised and measured as the vector sum for all pairwise recordings according to (Evans and Abdo, 2010) methodology.

2.3.2. In situ *litterfall cage respiration rate*

Litterfall cage respiration rates were measured underwater at the experimental site during each collection time on three of the five randomly collected new-blade litterfall cages. Three benthic chambers were set up *in situ* by scuba divers. The custom-built incubation chambers (Ouisse et al., 2014) were composed of a base to isolate the measured sample from the sediment, a Plexiglas cylinder and dome sealed by a clamp system enclosing a total volume of 26.2 L of seawater. Chambers were assembled ensuring no air bubbles remained inside and seawater was mixed within the chambers with an autonomous stirrer. The three selected cages harvested in their mesh bags were allocated to one benthic chamber each. Cages were incubated in the benthic chambers covered by black tarpaulins to ensure darkness for 30 min. A sample of seawater was collected from each chamber by using 100 mL syringes at the beginning and at the end of the incubation (two-point method) and directly brought to the surface after sampling. Dissolved oxygen concentration was immediately measured on the boat using a portable multi-meter (HQ40d, Hach®, Loveland, CO, USA) coupled with a luminescent/optical dissolved oxygen probe (Intellical™ LDO101, Hach®, accuracy ± 0.2 $mg.L^{-1}$). Litterfall cage respiration rate was estimated from the difference between initial and final oxygen (O_2) concentrations after being corrected for temperature change. Respiration was expressed as O_2 consumption in mg $O_2.cage^{-}$

188 $^{1}.h^{-1}$, to allow comparisons between litterfall cages over time. Although continuous O_2
189 measurement is recommended, measurement only at the beginning and at the end of the
190 incubation is considered acceptable to obtain a correct measurement of community metabolism
191 for short incubations (Ouisse et al., 2014).

192 2.4. Laboratory measurements

193 In the laboratory, the contents of each cage were placed in the corresponding 1 mm mesh bag,
194 and kept in the dark in a large tank with running seawater. For each sample and measurement,
195 bags were opened in the laboratory and directly brought back to the seawater tank after
196 processing.

197 *2.4.1. Cultivable bacteria counts*

198 For each litterfall cage, 10 pieces of algal tissue were collected using a stainless steel punch (13
199 mm diameter) sterilised by flaming with 70% ethanol. Algal pieces were transferred to 20 mL of
200 sterile saline solution (for 1 L: 24.7 g NaCl, 6.3 g $MgSO_4 \cdot 7H_2O$, 4.6 g $MgCl_2 \cdot H_2O$, 0.7 g KCl),
201 stored on ice and returned within 1 h to the laboratory for further processing. The 10 algal pieces
202 from one cage were rinsed twice in 20 mL sterile saline solution and homogenised in a single
203 batch for 1 min at 8000 rpm in 20 mL sterile saline solution using a T25 Ultra-Turrax blender,
204 followed by 1 min of vortex agitation at maximum speed. Serial dilutions (from 10^{-1} to 10^{-4}) of
205 homogenates were prepared in sterile saline solution. Then, 100 µL of the dilutions were spread-
206 plated in duplicate and incubated at 20°C for 7 days. Four media were used to screen cultivable
207 bacteria presenting different functions. The Zobell agar medium (for 1 L: 5 g tryptone, 1 g yeast
208 extract, 15 g agar in natural seawater), a highly nutritive medium, was used as a proxy of the total
209 community of cultivable bacteria. Bacteria resisting high concentrations of iodine, one of the

defence compounds released by kelps (Verhaeghe et al., 2008), were screened on a Zobell agar medium supplemented with 100 mM KI. Bacteria were also grown on a minimum medium solidified with Phytagel (for 1 L: 24.7 g NaCl, 6.3 g $MgSO_4 \cdot 7H_2O$, 4.6 g $MgCl_2 \cdot H_2O$, 2 g NH_4Cl, 0.7 g KCl, 0.6 g $CaCl_2$, 200 mg $NaHCO_3$, 100 mg K_2HPO_4, 1X vitamin mix, 20 mg $FeSO_4 \cdot 7 H_2O$, 20 g Phytagel) (Thomas et al., 2011) and supplemented with 4 $g.L^{-1}$ alginate, a polysaccharide accounting for 10-45% of the dry mass of brown algal cell wall (Kloareg and Quatrano, 1988) or 4 $g.L^{-1}$ mannitol, one of the main carbon storage forms in brown algae (Iwamoto and Shiraiwa, 2005). (Technical) duplicate measurements were averaged and results were expressed as the number of colony-forming units per unit area of algal tissue ($cfu.cm^{-2}$). The detection limit was 75 $cfu.cm^{-2}$. The proportion of iodine-resistant cultivable bacteria was estimated as the ratio of counts obtained on KI-supplemented Zobell agar compared to counts obtained on Zobell agar.

2.4.2. Phlorotannin assay

For each cage, 10 disks of 28 mm diameter were randomly cored on kelp fragments and stored at -20°C before processing. Phlorotannin extraction was performed using an method adapted from Li et al. (2017) and Koivikko et al. (2007). Frozen samples were stored overnight at -80°C and freeze-dried for 24 h. First, 100 mg of freeze-dried tissue were ground into a fine homogeneous powder under liquid nitrogen with a mortar and pestle and stored at -20°C until analyses. The extraction buffer consisted of a 30:70 ethanol:water mixture acidified with hydrochloric acid (pH = 2.6) to prevent oxidation. Extraction was performed at 25°C for 30 min with 0.5 mL of extraction buffer under constant agitation. The extract was centrifuged and the supernatant was retrieved and stored at -20°C. Total soluble phlorotannin quantification in the extracts was determined using a modified Folin-Ciocalteu method (Van Alstyne et al., 1999; Zhang et al.,

2006). Phloroglucinol (Sigma) was used as a standard. Extracts were diluted 2 to 10 times with extraction buffer for absorbance to be in the range of the standard curve. Absorbance measurements were performed using multiwall plates (Nunc UV-Star 96 wells) containing 10 µL of extract, 50 µL of Folin-Ciocalteu reagent (Sigma) and 40 µL of Na_2CO_3 7.5 % (m/v). Plates were incubated in the dark at room temperature for 2 h. Absorbance was measured at $\lambda = 750$ nm on a spectrophotometric microplate reader (Safire²Tecan Multi-detection Microplate reader). For each sampling time, the cage was used as biological replicate (n = 5) and each sample was measured in two technical replicates. Technical (measurement) replicate values were averaged prior to statistical analyses. Each standard solution was run in triplicate. The concentration of soluble phlorotannins within kelp fragments was calculated according to the phloroglucinol standard curve and expressed in phloroglucinol equivalent in $mg.g_{DM}^{-1}$ (where DM is kelp dry mass).

2.4.3. Carbon-nitrogen content

For each cage, 10 disks of 28 mm diameter were randomly cored on kelp fragments and stored at -20°C until preparation and analysis. Algal samples were rinsed with freshwater to remove possible epiphytes and dried at 60°C during 48 h. Dried material was ground with a mortar and a pestle and powder samples were put in tin capsules before C:N analyses. Carbon and nitrogen content were measured using a Flash EA 1112 CHN analyser (ThermoFinningan) coupled with a Finningan Delta Plus mass spectrometer, via a Finnigan Con-Flo III interface. C:N data were expressed as a mass ratio.

2.4.4. Chlorophyll fluorescence measurements

Fluorescence was measured to evaluate the conservation of photosynthetic capacity of algal tissues. Blades were transported from the seawater tank to the laboratory inside a dark box filled with seawater. All measurements were carried out 24 h after collection between 4:00 pm and 6:00 pm to avoid differences in physiology related to daily cycles (Edwards and Kim, 2010; Gevaert et al., 2002). Visually, the degradation state of blade fragments varied with size. Fragments were therefore separated in two groups according to their surface area: small (area < 25 cm²) and large (area > 50 cm²) fragments. The fluorescence signals were taken from the middle of the fragments for three small and three large fragments randomly selected from each cage. At each sampling time, measurements were taken for the five new-blade cages collected. Fragments were dark-adapted for an additional 15 min using the Dark Leaf Clip Diving-LC (Walz) to which the optical fibre of the fluorometer was applied to perform the measurements. *In vivo* Chl. a fluorescence of photosystem II (PSII) was measured from each fragment using an underwater pulse amplitude modulated fluorometer (Diving-PAM; Heinz Walz, Effeltrich, Germany). The maximum quantum yield (Fv/Fm) of PSII, here used as a proxy of physiological capacity, was measured using a 0.8 s saturating light pulse of white light (2500 µmol photons.m^{-2} s^{-1}). F_v represents the variable fluorescence and corresponds to the difference between the minimum fluorescence yield (F_0) measured under weak red modulated light and the maximal fluorescence (F_m) measured following the short saturating light pulse.

2.4.5. Remaining biomass

The remaining fragments from each litterfall cage were air-dried for 1 minute and wet-weighed (wet mass, WM). Samples were then dried at 60°C for at least 48 h until reaching a constant mass before being reweighed (dry mass, DM). The remaining biomass was estimated by dividing the final WM by the initial WM measured at the beginning of the experiment and expressed in

277 percentage of remaining biomass (%RB). To estimate the decomposition kinetics, we calculated a
278 decomposition rate with a single exponential decay model commonly used in the literature
279 (Enríquez et al., 1993; Olson, 1963). The decomposition rate (k, in day^{-1}) was calculated from the
280 change of biomass (M) over time (t, in days) since the beginning of the experiment following the
281 equation:

282 $$M_t = M_0\, e^{-kt}$$

283 From this equation, the half-life of fragment detritus was measured ($T_{1/2} = k^{-1}.\mathrm{Ln}(2)$, days). It
284 gives a more intuitive description of detritus turnover times (Enríquez et al., 1993). In our case,
285 M_0 corresponds to the initial percentage of remaining biomass that is equal to 100. Additionally,
286 before drying algae, frond surface was checked for reproductive tissue presence.

287 2.5. Data analysis

288 Phlorotannin concentrations and C:N contents were compared with a one-way ANOVA using
289 degradation time as fixed factor. Post-hoc comparisons were applied using Tukey's honestly
290 significant difference (HSD) tests when significant ANOVA results were found ($p < 0.05$).
291 Phlorotannin concentration data were square-root transformed prior to analysis to meet the
292 assumptions of normality (Shapiro Wilk's test, $\alpha = 0.05$) and homogeneity of variance (Levene's
293 test, $\alpha = 0.05$). Remaining biomass, litterfall cage respiration and bacterial count values were
294 compared using a non-parametric one-way analysis of variance Kruskal-Wallis H-test with
295 degradation time as fixed factor. This procedure was used for biomass data because assumptions
296 of normality and homoscedasticity were not met even after log(x) and square-root
297 transformations. For litterfall cage respiration and bacterial counts, the low number of replicates
298 ($n = 3$) at each sampling time were not amenable to parametric analyses. Bonferroni adjustment

and the low number of replicates precluded the detection of differences by post-hoc Dunn pairwise tests. Fv/Fm data within the same litterfall cage were averaged for small and large fragments prior to analysis, due to data dependency. Fv/Fm values were compared using a two-way ANOVA with degradation time and fragment size as fixed factors. Given that the response of the fragment size depended on degradation time, we chose a nested design. The assumption of homoscedasticity was met. Although the data did not meet the assumption of normal distribution of residuals (Shapiro Wilk's test, $\alpha = 0.05$), we nonetheless selected this parametric analysis because the distribution of residuals was nearly normal in the histograms and the ANOVA is robust to small deviations from normality (Schmider et al., 2010).

All statistical analyses and graphics were carried out using the freeware R statistical environment (R Core Team 2019).

3. RESULTS

3.1. Environmental parameters

During the experiment, temperature ranged from 11.7 to 17.8 °C reflecting seasonal fluctuation typically observed in the Bay of Morlaix. No lengthy strong storms were experienced during the experiment, indicating that there were no long periods of low light and high RWM between experimental times (Table 1).

3.2. Decomposition of biomass and tissue content

The biomass of new *L. hyperborea* blades decreased with degradation time (Kruskal-Wallis, $H = 34.2$, $df = 7$, $p < 0.001$). Biomass decomposition started after 2 weeks and showed negative exponential dynamics with rapid loss during the first 11 weeks and then slowing after 15 weeks (Figure 2a). After 24 weeks (5.5 months), the remaining biomass represented 16.5% and 3.8% of

initial mass for new blades and old blades, respectively. The decomposition rate calculated with the non-linear regression model was three times higher for old blades ($k = 0.0366$ day^{-1}, $p < 0.001$, $R_{raw}^2 = 0.9682$) compared with new blades ($k = 0.0107$ day^{-1}, $p < 0.001$, $R^2_{raw} = 0.949$), corresponding to a fragment degradation half-life ($T_{1/2}$) of 18.9 and 65.0 days, respectively (Figure 2b). Furthermore, after 20 and 24 weeks of degradation, reproductive tissues were observed on the surface of degrading new blades.

Tissue composition was significantly affected by degradation time (Figure 2c, 2d). Phlorotannin concentration in degrading *L. hyperborea* fragments increased significantly with time ($F_{7, 32} = 30.492$, $p < 0.001$). The concentration was two times higher after 11 weeks of degradation compared with any time point the first 6 weeks. This increase was significant (Tukey's HSD test, $p < 0.05$) except for the comparison between week 4 and 15 ($p = 0.116$, Figure 2c). The content in C:N (mass ratio) was significantly affected by degradation time ($F_{7, 32} = 6$, $p < 0.001$), with the ratio increasing slightly from 4.6 after 2 weeks to a maximum of 7.3 after 15 weeks of degradation. The Post-hoc Tukey's HSD test showed only some differences between times within the first 6 weeks and after 11 weeks. No significant differences in C:N ratio were observed among sampling times after 11 weeks (Figure 2d).

3.3. Detritus metabolism

The litterfall cage respiration rate was significantly influenced by degradation time (Kruskal-Wallis, $H = 15.406$, $df = 7$, $p < 0.05$, Figure 2e). Respiration dramatically decreased by a factor of 3 after 2 weeks of degradation; thereafter the rate did not vary from 2 to 6 weeks. A gradual increase was measured starting from 11 weeks with a maximum rate after 20 and 24 weeks of degradation. At the end of the experiment, the respiration rate doubled relative to the rate observed between 2 and 6 weeks (Figure 2e).

344 The photosynthetic capacity (Fv/Fm) of degrading algae varied significantly across degradation
345 time ($F_{7, 60} = 6.858$, $p < 0.001$) and according to fragment size ($F_{7, 60} = 11.821$, $p < 0.001$) (Figure
346 2f). Under optimal conditions, Fv/Fm values range from 0.7 to 0.8 for brown algae (Bischof et
347 al., 1999) and a reduction reflects a stress response in algae (Pearson et al., 2009). In large
348 fragments, Fv/Fm remained stable (Tukey's HSD, $p > 0.05$) and high (between 0.70 and 0.76),
349 reflecting satisfactory photosynthetic capacity, whereas the Fv/Fm of small fragments was
350 affected over time. Especially after 15 weeks, Fv/Fm values decreased and were highly variable
351 (mean ± SD; 0.43 ± 0.24, 0.32 ± 0.15, 0.59 ± 0.16 after 15, 20, 24 weeks, respectively, Figure 2f).

352 3.4. Fluctuations of cultivable bacteria during the degradation of L. hyperborea

353 Bacterial counts on Zobell agar, alginate-Phytagel and mannitol-Phytagel plates increased by 1-2
354 orders of magnitude in the first two weeks of the experiment (Figure 3), and thereafter remained
355 stable until the end of the experiment. This variation over time was found to be statistically
356 significant for counts on alginate-Phytagel (Kruskal-Wallis chi-squared = 11.697, df = 5, P =
357 0.039) and mannitol-Phytagel (Kruskal-Wallis chi-squared = 11.655, df = 5, P = 0.040) plates.
358 Furthermore, the proportion of iodine-resistant bacteria decreased with time (Kruskal-Wallis chi-
359 squared = 10.5, df = 4, P = 0.033, Fig. 3b), from 75% at the beginning of the experiment to 5%
360 after 24 weeks.

361 4. DISCUSSION

362 Understanding the kinetic and the processes of kelp fragments degradation is essential regarding
363 the quantity of organic matter exported within adjacent habitats by kelps forests. During our
364 experiment, the degradation of kelp biomass followed a classic pattern of organic matter
365 decomposition according to a simple negative exponential model, with high heterogeneity

366 between young and old *L. hyperborea* blades. Old blades showed degradation kinetics that were
367 three times faster than those of young blades. An additional study showed that stipes degrade
368 slightly faster than old blades and four times faster (data not shown) than young blades (k =
369 0.0425 d^{-1}, compared to k = 0.0366 d^{-1} and k = 0.0107 d^{-1} for respectively old and young blades).
370 This shows that, depending on the export process (detachment of old blades, erosion or
371 dislodgment during storms), fragments may have different residence times in coastal ecosystems.
372 The degradation of kelp organic matter thus follows two different types of patterns. The classic
373 export due to the natural kelp life cycle results in a pulse of organic matter during spring and
374 summer, and this tissue degrades relatively quickly. By contrast, material exported during storms
375 is more variable, producing slowly degrading material. Considering these accumulations or
376 drifting fragments as a transient habitat and resource for adjacent ecosystems, their influence in
377 benthic systems can be significant for several months. Surprisingly, the *L. hyperborea*
378 degradation rate appeared slow compared with other macroalgae that dominate coastal
379 ecosystems. The measured degradation rate for young *L. hyperborea* blades is 10 to 20 times
380 slower than fast growing ephemeral algal species such as *Ulva* sp. (k = 0.34 -0.51 d^{-1}) or
381 *Gracilaria* sp. (k = 0.5 d^{-1}) (Conover et al., 2016), more than 5 times slower than intertidal
382 canopy-forming species such as *Fucus vesiculosus* (k = 0.09 d^{-1}) (Conover et al., 2016), about 3
383 times slower than other kelp species such as *Macrocystis integrifolia* for young blades (k = 0.032
384 d^{-1}) (Albright et al., 1980) and similar to seagrass species (k ≈ 0.01 d^{-1}) (Harrison, 1989;
385 Hemminga and Nieuwenhuize, 1991) and mangrove leaves (k= 0.011 d^{-1}) (Gladstone-Gallagher
386 et al., 2014). In addition, degradation dynamics may be strongly affected by seasonal patterns and
387 environmental conditions including changes in local hydrodynamics and temperature
388 fluctuations. For example, physical mechanisms certainly fragment detritus more than that
389 observed within our cages. Furthermore, our study covered the spring-summer period that

corresponds to late spring storms. The lower temperatures during winter likely slow down the degradation process, but the high water motion during winter may speed up the process. For these reasons, winter and autumn degradation kinetics are not readily predictable. Further research is also needed to understand change of degradation dynamics depending on the type of recipient habitat.

In addition to the slow degradation dynamics, photosynthetic capacity was maintained for 5.5 months for large fragments and for 3.5 months for small fragments. However, this capacity appears to be highly variable depending on the degree of fragmentation and time of degradation. Here, small fragments tended to lose their photosynthetic ability. These results have wide implications for coastal ecosystem functioning, because exported detritus may continue to carry out primary production and retain the energy and capacity to renew their tissues, potentially explaining their partial recalcitrance to degradation. In highly hydrodynamic systems such as the English Channel, this recalcitrance may increase the area of kelp forest influence and magnify the impact of kelp forests on coastal and deep-sea ecosystems. Furthermore, reproductive tissues were observed on degrading fragments during this six-month experiment (data not shown). The persistence of reproductive tissue in drift kelp may increase the dispersal capacity of *L. hyperborea*, partly compensating for the naturally short dispersal ranges of spores (5-200 m) (Fredriksen et al., 1995).

Respiration showed a rapid decline at the beginning of the experiment. This early change can be attributed to the capacity of kelps to modulate their metabolism depending on environmental conditions (Kregting et al., 2016). Respiration increased after 11 weeks, likely reflecting the metabolism of the holobiont complex formed by the degrading kelp and its associated microorganisms. Degrading kelp is rapidly colonised by bacteria such as those growing on

alginate or mannitol, reaching an apparent maximum abundance as early as 2 weeks after fragmentation.

Kelps possess a unique defence metabolism, associated in particular with the production of toxic iodine compounds and phlorotannins (Potin et al., 2002). Iodine is highly concentrated in the peripheral cell layers, creating specific niches for associated bacteria during iodovolatilisation (Küpper et al., 2008; Verhaeghe et al., 2008). Our preliminary results on iodine-tolerant bacteria suggest some changes in bacterial community composition. As *L. hyperborea* tissue is degrading, iodine from the alga may be released in the environment, making the associated specific niches disappear. Interestingly, the detected concentration of phlorotannins in degrading tissues doubled after 11 weeks. This result is counterintuitive and refutes the claim that kelps quickly initiate defence responses to minimise grazing pressure and stress soon after dislodgement (Norderhaug et al., 2006). Instead, this apparent increase in phlorotannins may reflect the early degradation stage of kelp tissue after 11 weeks. The degradation of cell walls by colonising bacteria may make phlorotannins more accessible and increase the extraction efficiency during phlorotannin concentration assays.

The C:N ratio also followed a counterintuitive trend and remained stable for 5.5 months. Previous studies have shown a decrease in the C:N ratio related to the degradation of kelps, reflecting an enrichment in nitrogen (Norderhaug et al., 2006; Sosik and Simenstad, 2013). Our results show the opposite trend, with no change or a slight increase in C:N as previously observed by Dethier et al. (2014). We suggest that, in the present experiment, kelp tissues did not degrade enough to observe a decrease in C:N.

Our study allows a better understanding of *in situ* kelp degradation dynamics over the spring/summer period. We showed that drifting *Laminaria hyperborea* have a high capacity to

436 resist degradation, maintaining photosynthesis function for 5.5 months depending on the degree
437 of fragmentation. Confirming this pattern of degradation dynamics requires testing different
438 environmental conditions (hydrodynamism, depth) and seasons in future studies. In natural
439 conditions, accumulations or marine litterfall vary over time and fragments can drift between
440 different habitats after being exported. Although these changes in environmental conditions
441 during the degradation process complicate the understanding of the impact of kelp fragments on
442 coastal ecosystems, there is no doubt that this pulse of organic matter can be used by recipient
443 ecosystem food webs.

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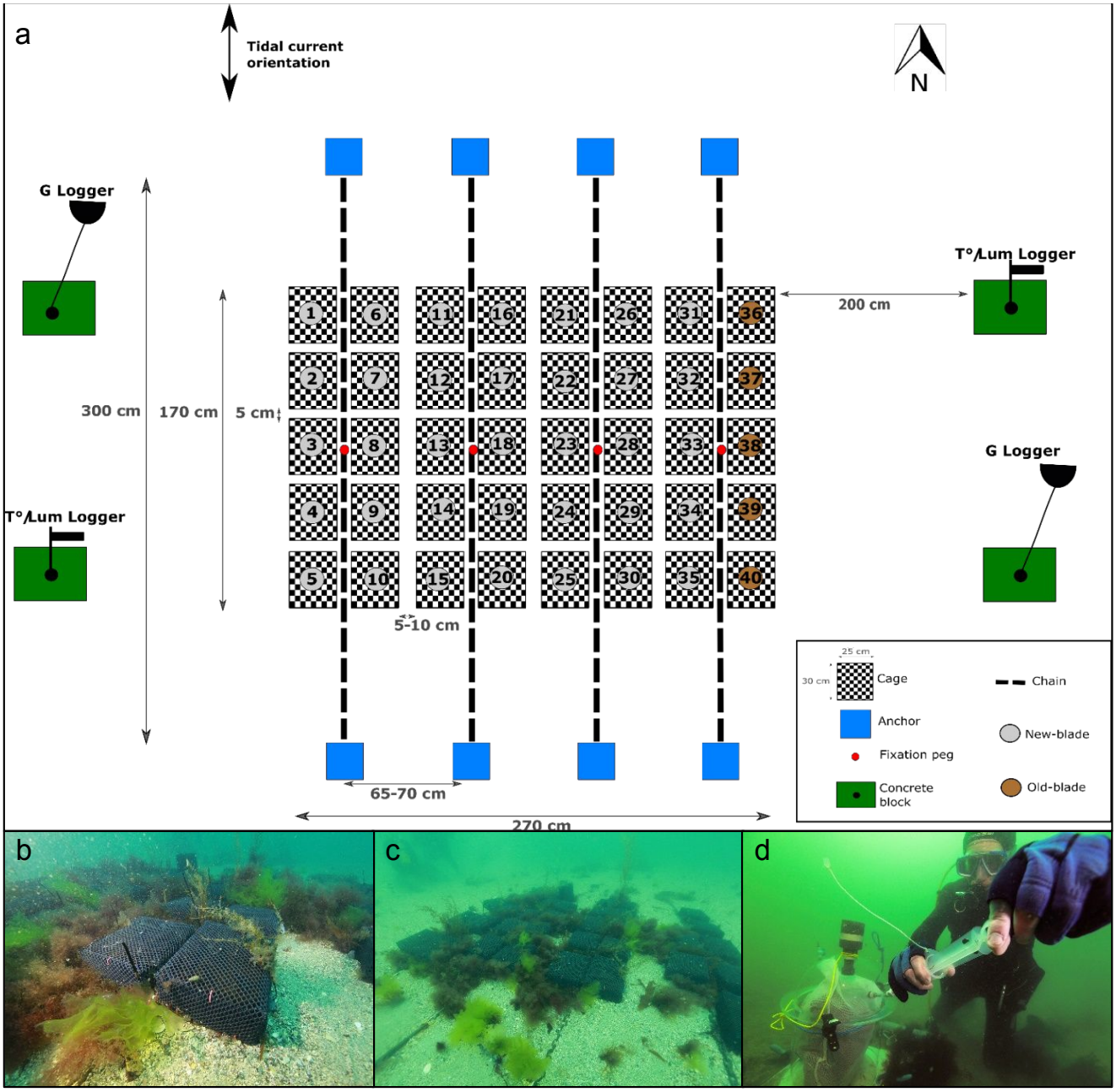

Figure 1: (a) *In situ* experimental set-up on the seabed in the Bay of Morlaix (Guerhéon: 48°42'33.78" N, 003°57'12.36" W) at 9 m depth (on average). Panel (b) shows 40 custom-built plastic cages filled with 1 kg of fresh *Laminaria hyperborea* blades arranged to form an artificial accumulation of kelp fragments (c). (d) Benthic chamber incubations to estimate the holobiont respiration rates. Photographs: Wilfried Thomas, experimental schematic: Florian de Bettignies.

Table 1: Environmental parameters for each sampling time. Data provided are those measured the week before retrieval. Relative water motion data for week 20 are missing due to sensor failure.

	Temperature (°C)			Light (lux)	Relative Water Motion ($m.s^{-2}$)		
Time (weeks)	**Mean**	**MinT°**	**Max T°**	**Mean**	**Mean**	**Min**	**Max**
0	12.7	12.2	13.3	2284	0.38	0.00	1.98
2	12.3	11.7	13.7	650	0.30	0.00	2.63
4	13.4	12.6	14.5	1154	0.13	0.00	1.08
6	14.5	13.5	16.5	2260	0.25	0.00	2.02
11	15.9	15.2	17.1	956	0.33	0.00	3.08
15	16.5	15.9	17.1	272	0.22	0.00	2.27
20	17.2	16.4	17.8	199	--	--	--
24	16.1	15.9	16.4	515	0.15	0.00	1.86

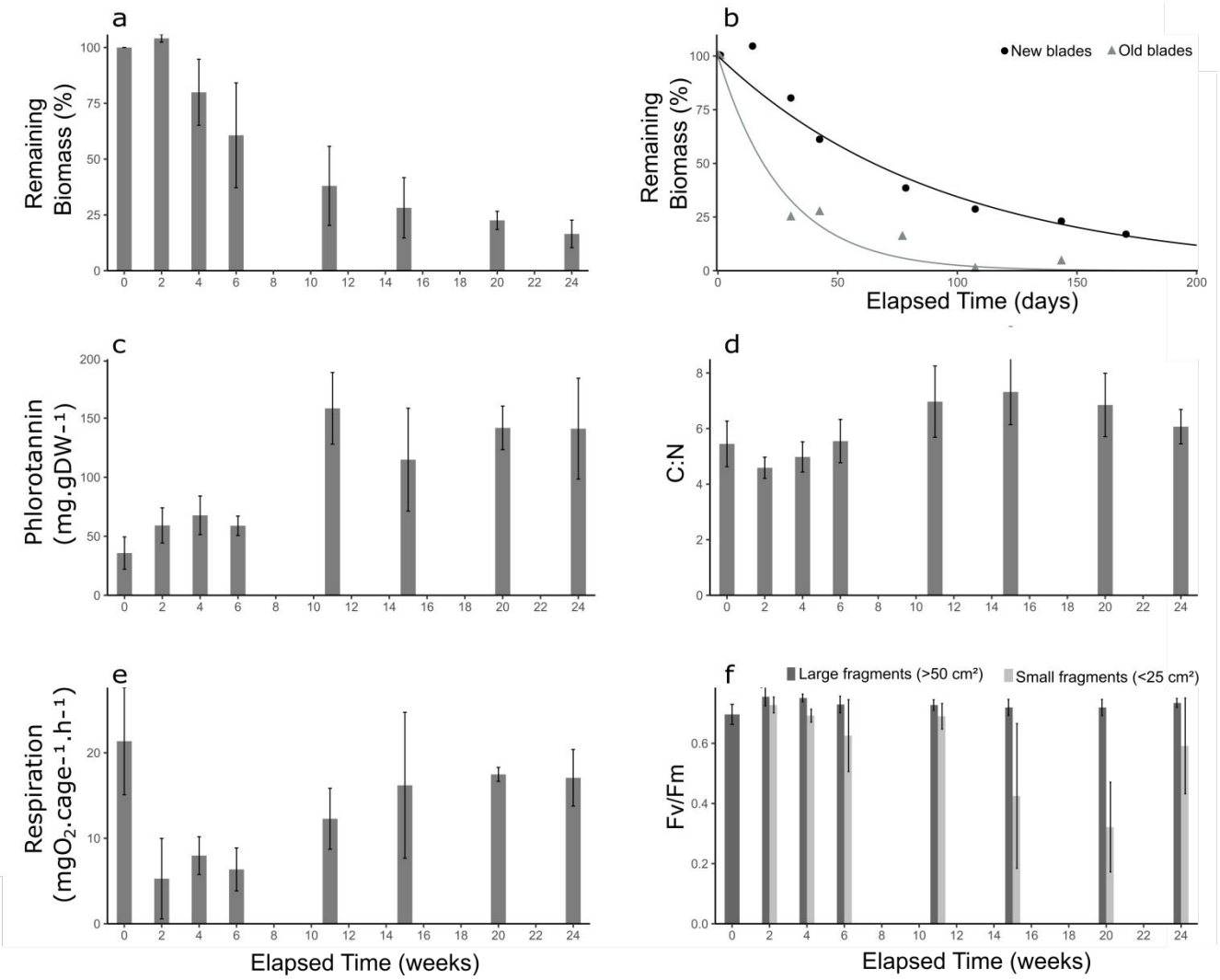

Figure 2: Parameters of degradation dynamics showing the change in (a) remaining biomass, (b) biomass decomposition models for new-blades (black circles) and old-blades (grey triangles) cages, (c) phlorotannin content, (d) C:N composition, (e) holobiont respiration rate and (f) Fv/Fm values for large (dark grey) and small (light grey) fragments. Bars give means with standard deviations (n = 5, except for respiration n = 3). Measures were taken at seven sampling times (0, 2, 4, 6, 11, 15, 20, 24 weeks). All measures are for new blades, except in panel b.

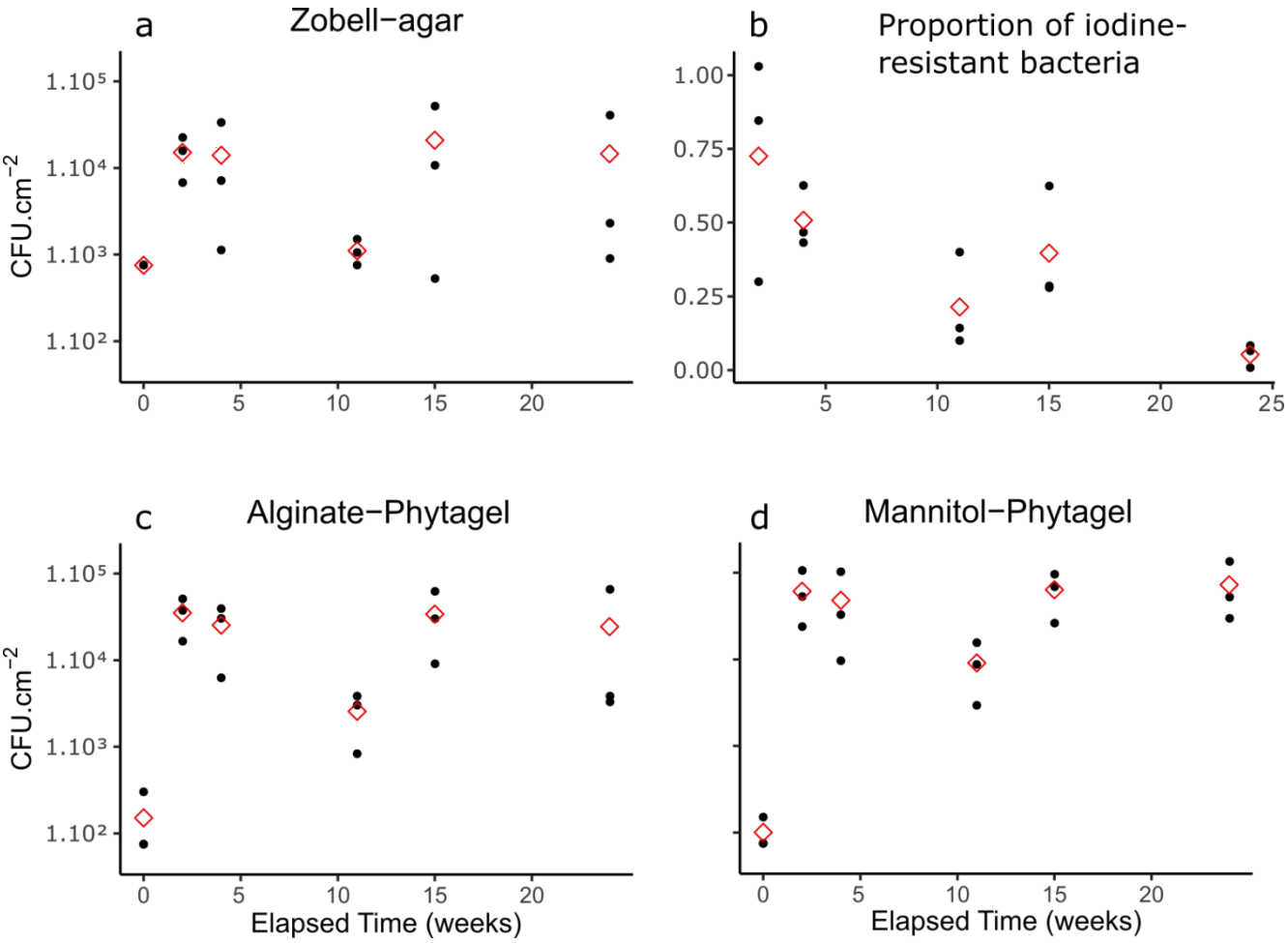

Figure 3: Cultivable bacterial counts (in number of colony-forming units per unit area of algal tissue: cfu.cm^{-2}) on different growth media: (a) Zobell-agar, (b) KI-supplemented Zobell-agar, (c) alginate-Phytagel, (d) mannitol-Phytagel. Proportion of iodine-resistant bacteria was estimated as the ratio of counts obtained on KI-supplemented Zobell agar relative to the counts obtained on Zobell agar. Dots represent the raw data points from each cage replicate and the open diamonds represent the mean values.