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1 Can ecosystem functioning be maintained despite climate-
2 driven shifts in species composition? Insights from novel
3 marine forests

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15 ABSTRACT

- 16 1. Climate change is driving a redistribution of species and reconfiguration of ecological
17 communities at a global scale. Persistent warming in many regions has caused species to
18 extend their geographical ranges into new habitats, with thermally-tolerant species often
19 becoming competitively dominant over species with colder affinities. Although these climate-
20 driven changes in species abundance and diversity are well documented, their ecosystem-
21 level implications are poorly understood, and resolving whether reconfigured communities
22 can maintain fundamental ecosystem functions represents a pressing challenge in an
23 increasingly warmer world.
- 24 2. Here, we investigated how climate-driven substitutions of foundation species influence
25 processes associated with carbon and nutrient cycling (biomass production, detritus flow,
26 herbivory, decomposition) by comparing two habitat-forming kelp species with contrasting
27 thermal affinities. We examined the wider ecosystem consequences of such shifts for the
28 observed (and predicted) emergence of novel marine forest communities in the NE Atlantic,
29 which are expected to become more dominated by range-expanding, warm-temperate kelp
30 species.
- 31 3. Warm-temperate kelps both accumulated and released 80% more biomass than the cold-
32 temperate species despite being taxonomically closely-related and morphologically similar.
33 Furthermore, the warm-temperate species accumulated biomass and released detritus year-
34 round, whereas the cold-temperate species did so during short, discrete periods. The warm-
35 temperate kelps supported higher densities of invertebrate grazers and were a preferred
36 food source. Finally, their detritus decomposed 6.5 times faster, despite supporting
37 comparable numbers of detritivores. Overall, our results indicate an important shift in the
38 cycling of organic matter along large sections of NE Atlantic coastline following the climate-
39 driven expansion of a warm-affinity kelp, with novel forests supplying large amounts of
40 temporally-continuous—yet highly labile—organic matter.

41 **4.** Synthesis. Collectively, our results show that, like species invasions, climate-driven range
42 expansions and consequent shifts in the identity of dominant species can modify a wide
43 range of important ecosystem processes. However, alterations in overall ecosystem
44 functioning may be relatively limited where foundation species share similar ecological and
45 functional traits.

46 **KEYWORDS**

47 Temperate reefs, range expansion, range shift, climate change, Laminariales, macrophyte, novel
48 ecosystems, *Laminaria ochroleuca*, *Laminaria hyperborea*

49 **INTRODUCTION**

50 Humans have increasingly impacted the natural environment over the last five millennia (Bell &
51 Walker 2004), to the point where very few contemporary ecosystems are free from human influence
52 (Ellis *et al.* 2010). Human activities have led to the reorganization of biological communities
53 worldwide, principally by (i) introducing individuals and populations beyond species' native ranges;
54 (ii) driving species extinctions; and (iii) altering key environmental factors that constrain species
55 distributions, thereby inducing species range shifts. As a result, present-day species abundance and
56 composition of many contemporary ecosystems does not resemble historical configurations (Hobbs
57 *et al.* 2006; Hobbs, Higgs & Harris 2009). To date, most studies on the wider impacts of species gains
58 or losses in ecosystems have focused on structural changes at the community level (e.g. changes in
59 species abundance or diversity). Moving beyond describing shifts in community composition and
60 structure and shedding light on how ecological reconfigurations alter the ecosystem functions and
61 services on which human wellbeing depends is therefore a central challenge for ecology (Mooney *et*
62 *al.* 2009). In the ecological literature, species' range shifts have received far less attention than
63 species introductions or extinctions (Sorte, Williams & Carlton 2010), even though range shifts have
64 been observed across a broad range of taxa and ecosystem types (Pecl & *et al* 2017). Given that

65 impacts of species range shifts on ecological communities may be similar in magnitude to those of
66 introduced non-native species (Sorte *et al.* 2010), with successful range-shifting species sometimes
67 displaying invasive properties (Engelkes *et al.* 2008), there is a clear and pressing need to explore the
68 wider consequences of such shifts.

69 Anthropogenic climate change is one of the principal drivers of the contemporary reorganization of
70 ecosystems (Pecl & *et al.* 2017). Globally, species representing a wide range of taxa have responded
71 to a changing climate by shifting their distributions to track more optimal conditions (Parmesan &
72 Yohe 2003). Differences in the magnitude and pace of species' distribution shifts results in
73 communities that are compositionally distinct from previous configurations, often called 'novel' or
74 'no-analog' communities (Williams & Jackson 2007; Hobbs *et al.* 2009). Generally, species have
75 moved upwards and polewards in response to climate warming (Parmesan & Yohe 2003;
76 Poloczanska *et al.* 2013), which has resulted in upland, temperate and austral/boreal habitats
77 receiving an influx of species with warmer affinities than indigenous biota (García Molinos *et al.*
78 2015). Given that migrating and indigenous species often belong to different thermal realms (Stuart-
79 Smith *et al.* 2015), a warming climate can result in competitive shifts, with warm-affinity species
80 displacing or replacing cool-affinity ones (Lord & Whitlatch 2015; Warren II *et al.* 2016). Although
81 such species replacements may cause no overall change in species richness, they may lead to
82 considerable changes in ecosystem functioning—particularly if they involve species which exert
83 strong control over ecosystem processes, such as dominant foundation species (Ellison *et al.* 2005).

84 In temperate marine systems, large, canopy-forming seaweeds (macroalgae) function as foundation
85 species (*sensu* Dayton 1972), forming marine forests that provide biogenic habitat, alter local
86 environmental conditions and mediate numerous ecological processes (Steneck *et al.* 2002; Teagle
87 *et al.* 2017). Seaweeds are especially sensitive to climatic changes, and range shifts in response to
88 past and contemporary climate variability are well described (Li, Hu & Duan 2016; Neiva *et al.* 2016;
89 Straub, Thomsen & Wernberg 2016). The majority of contemporary seaweed range shifts have been

90 documented in temperate seas (Straub *et al.* 2016), where seaweed forests often dominate shallow
91 rocky habitats. Temperate regions contain two distinct floristic elements, the cold- and warm-
92 temperate (*sensu* Lüning, 1990), which differ in the temperature tolerances of the species they
93 comprise. Climate change is driving shifts in the relative distribution of these elements, creating
94 novel seaweed assemblages and with warmer-water species replacing colder-water ones,
95 particularly in biogeographic transition zones (Lima *et al.* 2007; Tanaka *et al.* 2012; Fernández 2016).
96 Although climate-driven reconfigurations of seaweed communities are well-documented (Harley *et*
97 *al.* 2012), empirical evidence for their wider ecological consequences remains limited, and
98 understanding how altered species composition affects ecosystem processes and functioning
99 remains a persistent challenge (Pedersen *et al.* 2005).

100 Here, we examine whether the proliferation and predicted range expansion of a canopy-forming
101 kelp with warm affinity will compensate for the decline and predicted loss of a morphologically
102 similar—but less thermotolerant—cold-temperate species, which currently dominates across much
103 of the shallow NE Atlantic rocky coastline. To understand how climate-driven changes in species
104 composition may affect ecosystem functioning, we compared several core ecological processes
105 linked to primary producers (biomass production, detrital flow, herbivory pressure and
106 decomposition) between the two foundation species.

107 MATERIALS AND METHODS

108 *Study species*

109 The kelp *Laminaria ochroleuca* is a warm-temperate species presently distributed from Morocco to
110 southwest England in the United Kingdom (UK), where it was first detected in the late 1940s (Parke
111 1948) (Figure 1a, b). In recent decades, *L. ochroleuca* has increased in relative abundance at the
112 leading-edge of its distribution (Smale *et al.* 2015; Teagle & Smale 2018), being now common
113 throughout the southwest coast of the UK (Brodie *et al.* 2009) and dominating forest assemblages in
114 many wave-sheltered locations (authors' pers. obs.). The growth and performance of *L. ochroleuca* is
115 highly sensitive to temperature (Izquierdo, Pérez-Ruzafa & Gallardo 2002; Franco *et al.* 2017;
116 Hargrave *et al.* 2017), and the recent proliferation of this species at the leading edge of its
117 distribution has been linked to recent ocean warming (Smale *et al.* 2015; Teagle & Smale 2018). *L.*
118 *ochroleuca* is predicted to continue expanding northwards in response to climate change, occupying
119 most of the UK and large sections of the wider NE Atlantic coastline by the end of the century
120 (Franco *et al.* 2017). The prospects for *L. ochroleuca* contrast with that of the cold-temperate kelp
121 *Laminaria hyperborea*, the current assemblage dominant along moderate to wave exposed
122 coastlines in the region. *L. hyperborea* does not perform well at high temperatures (tom Dieck
123 (Bartsch) 1992; Wiencke *et al.* 1994), and over the past 40 years has undergone a ~250-km range
124 contraction at its warm, trailing-edge on the Iberian Peninsula (Assis *et al.* 2016; Pereira *et al.* 2017).
125 Continued ocean warming is expected to lead to further declines in abundance and shifts in its
126 biogeographic distribution, with predicted extinctions of populations currently found along the
127 coasts of Iberia, France and southern UK (Breeman 1990; Müller *et al.* 2009).

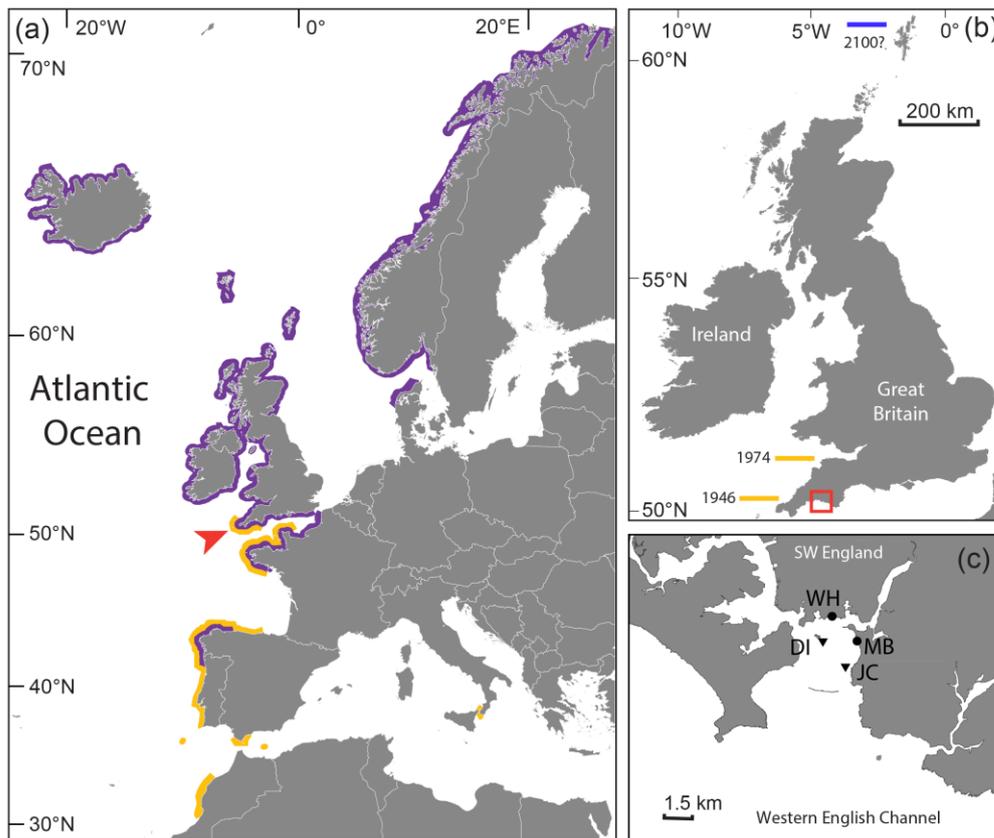
128 *Study design and location*

129 The stocks and fluxes of biomass are central to the biological, geochemical and physical processes
130 that occur within kelp forest ecosystems, as well as in spatially-disconnected habitats subsidized by
131 kelp-derived organic matter (Krumhansl & Scheibling 2012a). To investigate how future kelp forests

132 dominated by the warm-temperate kelp *Laminaria ochroleuca* might differ functionally from those
133 formerly dominated by the cold-temperate *L. hyperborea*, we compared processes related to the
134 cycling of organic matter between the two species in two mixed kelp forests. We estimated kelp
135 biomass accumulation—a widely used proxy for kelp primary production (Krumhansl & Scheibling
136 2011; de Bettignies *et al.* 2013)—and biomass loss (detrital production) over the course of an annual
137 cycle (March 2016–February 2017). Produced biomass can either (i) be directly consumed by grazers
138 *in situ* or (ii) exported as detritus and later consumed by a vast array of microbes, detritivores, and
139 suspension-feeders. To determine how biomass flows through grazing and detrital pathways in the
140 coastal food web, we quantified the abundance of grazers associated with each kelp species and
141 measured kelp detritus decomposition.

142

143 We used kelp forest ecosystems along the southwest coast of the UK—which currently represents
144 the leading range edge of *L. ochroleuca*—as model study systems as this region is expected to
145 experience major shifts in species composition and community structure in coming decades (Müller
146 *et al.* 2009; Franco *et al.* 2017). Our study sites, West Hoe (hereafter ‘WH’) and Mount Batten (‘MB’)
147 were located within Plymouth Sound (Figure 1c), and were characterised by dense kelp stands that
148 extended from the low intertidal into the shallow subtidal zone. The first individuals of *L. ochroleuca*
149 in UK waters were actually reported from that same area ~70 years ago (Parke 1948), allowing for
150 sufficient time for kelp populations and associated biota to become established within these
151 communities. The study sites are representative of moderately wave-exposed shallow rocky reefs in
152 the region and both support mixed kelp canopies primarily comprising *L. ochroleuca* and *L.*
153 *hyperborea*, the latter still being the assemblage dominant. Two additional subtidal sites were
154 chosen to study kelp decomposition using litter bag experiments (see methodology below). Subtidal
155 sites were chosen so the litter bags remained permanently submerged underwater.



156

157 **FIGURE 1.** (a) Approximate distribution of *Laminaria hyperborea* (purple line) and *L. ochroleuca*
 158 (yellow line) along the NE Atlantic coastline. The red arrow indicates the study region, which is
 159 shown in (b). *L. ochroleuca* was first detected in this region in 1946, and has since expanded its
 160 distribution northwards. The dated yellow lines denote the position of the species leading range
 161 edge. The blue line at the very top of (b) denotes the predicted range within the study region by the
 162 end of the century, according to Franco *et al.* (2017). The sampling sites within study region (red box
 163 in (b)) are shown in (c). The monthly sampling sites are denoted with a circle, the subtidal study sites
 164 are denoted with a triangle. WH = West Hoe, MB = Mt. Batten, DI = Drake's Island, JC = Jennycliff.

165 *Biomass accumulation and loss*

166 Kelp biomass accumulation and loss was measured monthly using a modified hole-punch method
 167 after Krumhansl & Scheibling (2011a). This technique consists of punching a series of holes at set
 168 distances from the stipe/lamina transition zone, where the primary meristem occurs, to capture

169 growth of the lamina tissue. To obtain a growth estimate, hole-punched plants are retrieved after a
170 certain time interval and the final position of the holes are measured. During spring low tides, 10–12
171 mature kelp plants (stipe length ≥ 20 cm) of each species were randomly selected, tagged and
172 uniquely labelled at each site. Selected plants were from different areas of the forest each month.
173 Two digits of each plant lamina were punched, and their initial length measured. Since growth is not
174 uniform across the lamina (Kain 1976), a total of three holes were punched in every individual: two
175 at 15 cm and 20 cm above the stipe/lamina transition zone on the central digit respectively, and
176 another one at 20 cm above the aforementioned zone on an outer digit. The two holes punched on
177 the central digit captured the maximal growth in length, which occurs between 2.5 and 15 cm from
178 the central transition zone depending on the month (Kain 1976), while the hole on the outer digit
179 captured variability in growth across lamina digits. After approximately one month, tagged kelps
180 were harvested and returned to the laboratory for analysis. The final length of the punched digits,
181 position of the holes, and the fresh weight of the stipe and lamina were recorded to calculate
182 individual-specific lamina elongation and loss rates. The exact number of elapsed days between
183 tagging and retrieval, as well as the number of tagged kelp plants relocated and retrieved, varied
184 due to limited tidal windows and a rough sea state in some months. On average, > 8 individuals of
185 each species were recovered from each site each month (see Table S1 and Table S2 in the
186 Supporting Information for full details). In August however, bad weather hampered the retrieval of
187 tagged plants. Given the low number of replicates (Table S2), and their small size compared to the
188 plants tagged in the rest of the months (Figure S1), August data was not included in the analysis.

189 To convert elongation and loss rates of lamina tissue (cm) to gains and losses of fresh biomass (g),
190 three 5 cm-wide segments from both the basal and distal parts of the lamina of each plant were cut
191 across their width, cleaned of epiphytes, and weighed (fresh weight; FW). In order to make our
192 results more comparable with those in the literature, we converted fresh biomass to dry biomass
193 (DW). Every month and for each of the retrieved plants, we determined the relationship between
194 fresh and dry weight (FW:DW) by drying one of the basal and distal segments at 60°C for 48 hours.

195 The basal and distal parts of the laminae were examined separately as the relationship can vary
 196 between different parts of the thallus (Smale *et al.* 2016). All relationships were highly significant
 197 and had an $R^2 \geq 0.85$. We then estimated the dry weight of the rest two segments from each part
 198 (out of the three we cut) using the calculated relationship. Finally, the measured and estimated dry
 199 biomass per unit length was averaged between all three segments to give the dry biomass per unit
 200 length ($\text{g} \cdot \text{cm}^{-1}$) of the respective basal and distal parts of the lamina (B_{base} and B_{distal}). This allowed
 201 us to convert elongation and loss rates of lamina tissue (cm) to accumulations and losses of biomass.
 202 Biomass accumulation (BA) for each plant was estimated as:

$$203 \quad \text{BA} = E \times B_{\text{base}} / t$$

204 where E is the average lamina elongation from the central and outer digits (denoted by a subscripted
 205 1 and 2 respectively) obtained by subtracting the initial hole position at 15 or 20 cm from the final
 206 hole position (H_f):

$$207 \quad E = \frac{[(H_{f1,1} - 15) + (H_{f1,2} - 20)] + (H_{f2} - 20)}{2}$$

208 and t denotes the days between the initial and final measurements (Table S1). The biomass loss (BL)
 209 was calculated as:

$$210 \quad \text{BL} = M \times B_{\text{distal}} / t$$

211 where M is the average lamina loss obtained by subtracting the final length (L_f) of the central and
 212 outer digits from the sum of their initial length (L_i) and respective digit elongation (e) as follows:

$$213 \quad M = \frac{[(L_{i1} + e) - L_{f1}] + [(L_{i2} + e) - L_{f2}]}{2}$$

214 In *L. hyperborea*, we observed a marked increase in the FW:DW ratio from June to September
 215 (Figure S2, Supporting Information), which was not documented for *L. ochroleuca* (Figure S2). During
 216 this period, the average biomass of the basal lamina segments was higher than the rest of the year
 217 (Figure S3). Regrettably, we could not account for the biomass accumulation that occurred during

218 these months, since our formula was based on elongation (i.e. linear growth; E), which was
219 negligible from July to September (Figure S4). The observed biomass accumulation not related to
220 linear growth was most likely explained by (i) the accumulation of carbohydrates, increasing the
221 FW:DW ratio and (ii) increases in basal lamina thickness, which has been found to increase from July
222 to December in *L. hyperborea* (Kain 1971, 1976). Although we did not measure changes in basal
223 lamina thickness in our surveys, previous *L. hyperborea* studies have shown that there is an inverse
224 relationship between relative changes in linear growth and thickness, with thickening being greatest
225 when elongation rates are low (i.e. after June; Kain 1976). Our observations support such findings.
226 As such, to account for *L. hyperborea* lamina thickening between June–September in our biomass
227 accumulation formula, we used the minimal elongation rate recorded in the study ($0.033 \text{ cm} \cdot \text{day}^{-1}$)
228 as a surrogate of lamina thickness growth during those months.

229 *Grazer surveys*

230 To explore how produced biomass is transferred to higher trophic levels via herbivory, we quantified
231 the abundance of macroinvertebrate grazers associated with the laminae of *Laminaria hyperborea*
232 and *L. ochroleuca* at our study sites over 13 months (March 2016–March 2017). Each month, 10
233 plants with comparable lamina areas of each species were randomly selected. The entire lamina of
234 each individual was carefully placed into a large cotton bag and then cut from the stipe and the bag
235 was then sealed to retain all grazers. In the laboratory, all macroinvertebrate grazers were identified
236 and counted.

237 To examine the influence of kelp nutritional quality in determining the herbivory pressure patterns
238 observed in the field, we used a series of feeding preference assays using artificial diets (Hay *et al.*
239 1998). Fresh kelp plants were harvested in April 2016, the central and distal sections of the laminae
240 cut into strips and subsequently freeze-dried. Kelp strips were then pulverized to a fine powder
241 using an electric grinder and stored in a freezer. We prepared a seaweed solution containing 1 g of
242 kelp powder, 1 g of pulverized *Ulva sp.* and 20 ml of water. *Ulva sp.* was added to the mix as kelp

243 alginates made the solution too viscous, and *Ulva spp.* are less chemically defended than brown
244 algae (Duffy & Hay 1994). Agar (0.7 g) was added to a further 20 ml of water, heated to boiling point,
245 and quickly homogenized with the seaweed solution. This final mixture was then poured onto a glass
246 plate covered in microscope slides with 1×1 mm plastic mesh glued on top. Finally, another glass
247 panel was rapidly placed on top, sandwiching the mesh-covered slides and spreading the algal
248 mixture to a uniform 1-mm thickness on all slides. After 2 min, the solidified mixture had adhered to
249 the mesh slides, which were individually cut using a razor. We used the gastropod *Gibbula cineraria*
250 as a model grazer for our laboratory experiments as it was frequently observed on kelp laminae, and
251 was the largest grazer recorded in our surveys (see Results). Macroinvertebrate grazers like *Gibbula*
252 *spp.* can feed directly on kelp tissue or indirectly on the associated biofilms and epiphytic algae.
253 Kelp-derived organic matter can contribute significantly to the diet of *Gibbula spp.* (Leclerc *et al.*
254 2013), whose grazing activity leaves evident grazing marks on the kelp blades (authors' pers. obs.),
255 further suggesting that kelp organic matter is ingested. *G. cineraria* individuals were collected locally
256 and were starved for 3 days in large aerated tanks (allowing for emptying of the digestive tract),
257 before being transferred to smaller (20 × 8 × 10 cm) rectangular tanks for feeding trials. A single
258 individual was placed in the middle of the rectangular tank, which contained one slide of *L.*
259 *ochroleuca* and one slide of *L. hyperborea* agar mixture positioned at opposite ends. An air stone
260 with low air flow was also placed in the middle of the tank. We determined kelp consumption by
261 counting the number of squares that been consumed after 48h. Fourteen replicate trials were
262 conducted simultaneously.

263 *Kelp decomposability*

264 To investigate how kelp biomass is consumed and recycled once it has been cast as detritus, we
265 compared rates of detritus decomposition between the two kelp species. Lamina material from each
266 species was collected and cut into strips (ca. 5 × 15 cm). A total of 105 ± 8 grams of fresh kelp strips
267 from the same region of the laminae was then sealed within mesh bags (mesh aperture 20 mm),
268 which were uniquely labelled. The mesh size allowed mesodetritivores and microbes to access the

269 kelp detritus whilst minimizing loss of material via flushing. Four replicate bags for each species were
270 deployed at a depth of 4 m (below Chart Datum) by scuba divers at Drake's Island and Jennycliff,
271 both within Plymouth Sound (see Figure 1c) in March 2016. Litter bags were attached to a long rope
272 (positioned ~1 m apart from one another), which was secured to the seabed with anchor weights.
273 Bags were deployed on a sandy seabed adjacent to a kelp-dominated rocky reef and were retrieved
274 after 40 days. Upon retrieval, a fine mesh bag (1 μ m diameter) was placed over each litter bag to
275 retain all kelp material and detritivores, before detaching the bag from the rope. In the laboratory,
276 the contents of the bags were carefully removed and washed through a 1 mm sieve. Remaining fresh
277 kelp tissue was reweighed again to assess degradation rates ($\text{g} \cdot \text{day}^{-1}$), and the abundance of
278 detritivores associated with the kelp material was quantified.

279 *Kelp habitat structure*

280 The measurements described above were mostly collected at the scale of individual plants (i.e. per
281 capita). In order to contextualise our findings at larger spatial scales (i.e. per unit area) and increase
282 generality, we conducted ecological surveys of kelp-dominated habitats within the study area to
283 determine whether both foundation species can occur at similar densities. We surveyed a number of
284 subtidal and intertidal reefs within the study region by haphazardly placing 10 replicate 1 m²
285 quadrats and quantifying the density of mature canopy-forming plants of each species.

286 *Statistical analyses*

287 Differences in biomass accumulation and loss ($\text{g} \cdot \text{day}^{-1}$) between kelp species (2 levels, fixed factor),
288 sites (2 levels, fixed factor) and months (11 levels, fixed factor), were examined with permutational
289 ANOVA (Anderson 2001) due to observed structuring of residuals and heterogeneity of variances
290 encountered in exploratory analyses. August data were excluded from analyses as explained above
291 (see Table S2 and Figure S1). For each response variable, we generated a similarity matrix based on
292 Euclidian distances with untransformed data using PRIMER (v7.0) software (Clarke & Gorley 2015)
293 with the PERMANOVA add-on (Anderson, Gorley & Clarke 2008). Main effects and interactions were

294 then tested with 9999 permutations under a reduced model. Where significant differences were
295 recorded (usually $p < 0.05$ but see below) we conducted *post-hoc* pairwise tests between levels of
296 factors (or within levels of factors for significant interaction terms). While permutational ANOVA is
297 more robust to non-normal distributions and heterogeneity of variance than traditional ANOVA, it is
298 still influenced by differences in dispersion between treatments. To examine data dispersion, we
299 conducted PERMDISP tests to determine whether within-group variation differed between levels of
300 each factor. Where a significant difference in dispersion was recorded, the p-value of the associated
301 PERMANOVA test was reduced a more conservative $p < 0.001$.

302 To test for differences in abundance of the dominant grazers *Gibbula cineraria* and *Patella pellucida*
303 between kelp species (2 levels), sites (2 levels) and months (13 levels, March 2016–March 2017), we
304 performed the same analysis as outlined above. In the feeding preference experiments with *Gibbula*
305 *cineraria*, we used a paired Wilcoxon rank-sum test to test for differences in kelp consumption
306 between species, as pairwise differences did not follow a normal distribution.

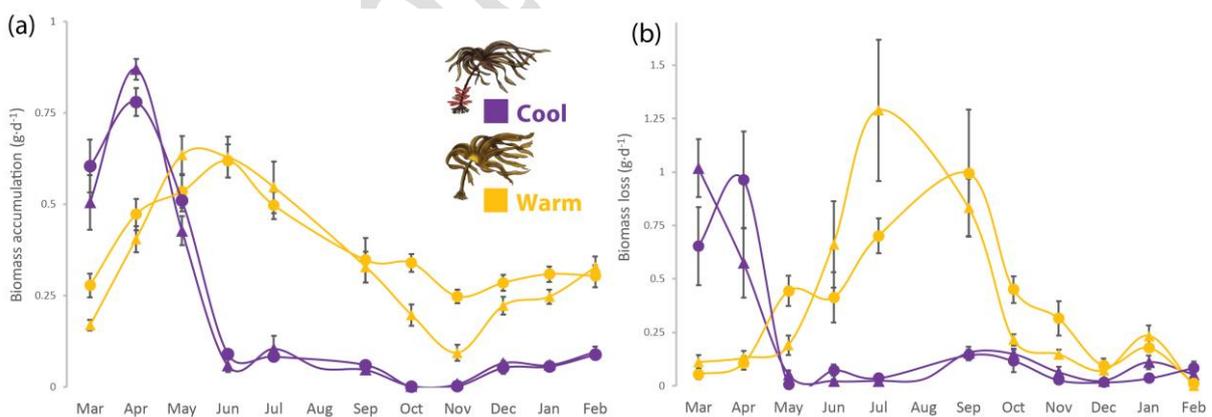
307 Finally, for the decomposition experiment, we used a univariate permutational ANOVA to test for
308 differences in kelp degradation rates ($\text{g} \cdot \text{day}^{-1}$) between species and sites (2 levels each, fixed
309 factors). We generated a similarity matrix based on Euclidian distances and examined variability
310 between factors with 9999 permutations under a reduced model.

311 RESULTS

312 *Biomass accumulation and loss*

313 Across our year-long study, we retrieved a total of 197 *Laminaria ochroleuca* and 204 *L. hyperborea*
314 plants for biomass accumulation and loss determination. Biomass accumulation rates exhibited
315 marked seasonality and differed considerably between species and sites (Figure 2a, Table S3). We
316 also recorded a significant 3-way interaction between species, month and site (Table S3). Further
317 examination of variability patterns showed that seasonality in biomass accumulation differed

318 between species, but the magnitude of dissimilarity was not entirely consistent between sites
 319 (Figure 2a). Overall, we recorded a significant main effect of species and *L. ochroleuca* plants
 320 accumulated more biomass, producing an annual average of 123.8 ± 18.9 g DW yr⁻¹ and 137.1 ± 13.5
 321 g DW yr⁻¹ (means \pm standard error, SE) at WH and MB respectively, which was ~ 80 and $\sim 90\%$ more
 322 than the average 69.9 ± 6.3 g DW yr⁻¹ and 72.4 ± 4.0 g DW yr⁻¹ produced by *L. hyperborea* plants. *L.*
 323 *ochroleuca* exhibited continuous growth throughout the year, steadily increasing lamina biomass
 324 until peak production around the onset of summer (0.63 ± 0.05 g DW d⁻¹ in May at WH and $0.62 \pm$
 325 0.04 g DW d⁻¹ in June at MB). Biomass accumulation started gradually declining after June, with
 326 growth remaining relatively consistent at around 0.2–0.3 g DW d⁻¹ between September and January;
 327 the lowest biomass accumulation was recorded in November (0.09 ± 0.02 and 0.24 ± 0.02 g DW d⁻¹
 328 at WH and MB on average, respectively). Contrastingly, *L. hyperborea* biomass accumulation was
 329 markedly discontinuous; plants showed a distinct growth phase from December to June and a
 330 resting phase from July to November, during which lamina elongation was negligible (Figure S4) but
 331 increases in lamina mass and thickness occurred. Peak growth occurred in mid-spring at both sites
 332 (April: 0.87 ± 0.03 and 0.78 ± 0.04 g DW d⁻¹ at WH and MB respectively).



334 **FIGURE 2.** Annual patterns of (a) lamina biomass accumulation and (b) loss of the cool-temperate
 335 kelp *Laminaria hyperborea* (purple lines) and the warm-temperate congener *L. ochroleuca* (yellow
 336 lines) in mixed kelp forests at West Hoe (triangles) and Mount Batten (circles). Markers denote
 337 means \pm standard error (SE). Data from August was excluded from analyses due to low replication.

338

339 Loss rates of lamina biomass were consistent among sites, but varied significantly between months
340 and species (Table S3). We recorded a significant 3-way interaction between species, months and
341 sites (Table S3). Further examination of variability patterns showed that seasonality in biomass loss
342 differed between species, but the timing of peak biomass loss differed slightly between sites (Figure
343 2b). *L. ochroleuca* biomass loss occurred throughout the year, with the maximum detrital production
344 recorded between June and September ($1.29 \text{ g} \pm 0.33 \text{ DW d}^{-1}$ and $0.99 \text{ g} \pm 0.30 \text{ DW d}^{-1}$ maximum
345 loss in July at WH and in September at MB, respectively). Annual detritus production via lamina loss
346 totalled $122.4 \pm 13.4 \text{ g DW yr}^{-1}$ and $120.4 \pm 11.1 \text{ g DW yr}^{-1}$ for *L. ochroleuca* and $69.7 \pm 6.7 \text{ g DW yr}^{-1}$
347 and $66.9 \pm 9.3 \text{ g DW yr}^{-1}$ for *L. hyperborea* at WH and MB, respectively. In contrast to *L. ochroleuca*,
348 *L. hyperborea* biomass loss peaked at the beginning of spring ($1.02 \pm 0.14 \text{ g DW d}^{-1}$ in March at WH
349 and $0.96 \pm 0.22 \text{ g DW d}^{-1}$ in April at MB), when the collar of old growth produced during the previous
350 season—which had remained attached to the newly-formed meristematic lamina tissue—was cast.
351 After April, lamina biomass loss decreased to near-zero, and remained constant between 0.02–0.15
352 g DW d^{-1} for the rest of the year.

353 *Grazer surveys*

354 Only two species of macroinvertebrates, the blue-rayed limpet *Patella pellucida* and the trochid
355 gastropod *Gibbula cineraria*, were found grazing on kelp laminae. Across the 13-month-long field
356 study, we recorded a total of 4369 *Patella pellucida* individuals on *L. ochroleuca* and 2439 individuals
357 on *L. hyperborea*. Overall, *Laminaria ochroleuca* supported significantly higher abundances of *P.*
358 *pellucida* than *L. hyperborea* (Table S3, Figure 3a). *P. pellucida* occurred on kelp laminae year-round,
359 but exhibited high seasonality in abundance patterns. Both *L. ochroleuca* and *L. hyperborea*
360 supported very few *P. pellucida* individuals (between 0 and 3.5 ± 0.8 limpets per plant) until June,
361 after which abundances markedly increased (Figure 3a). The highest abundance of limpets on *L.*
362 *ochroleuca* was recorded in July and September (91.3 ± 16.5 and 54.1 ± 12.8 individuals, at MB and
363 WH, respectively), whereas limpets were most abundant on *L. hyperborea* in August and September
364 (41.6 ± 7.9 and 29.5 ± 7.9 individuals at MB and WH, respectively). We recorded a significant 3-way

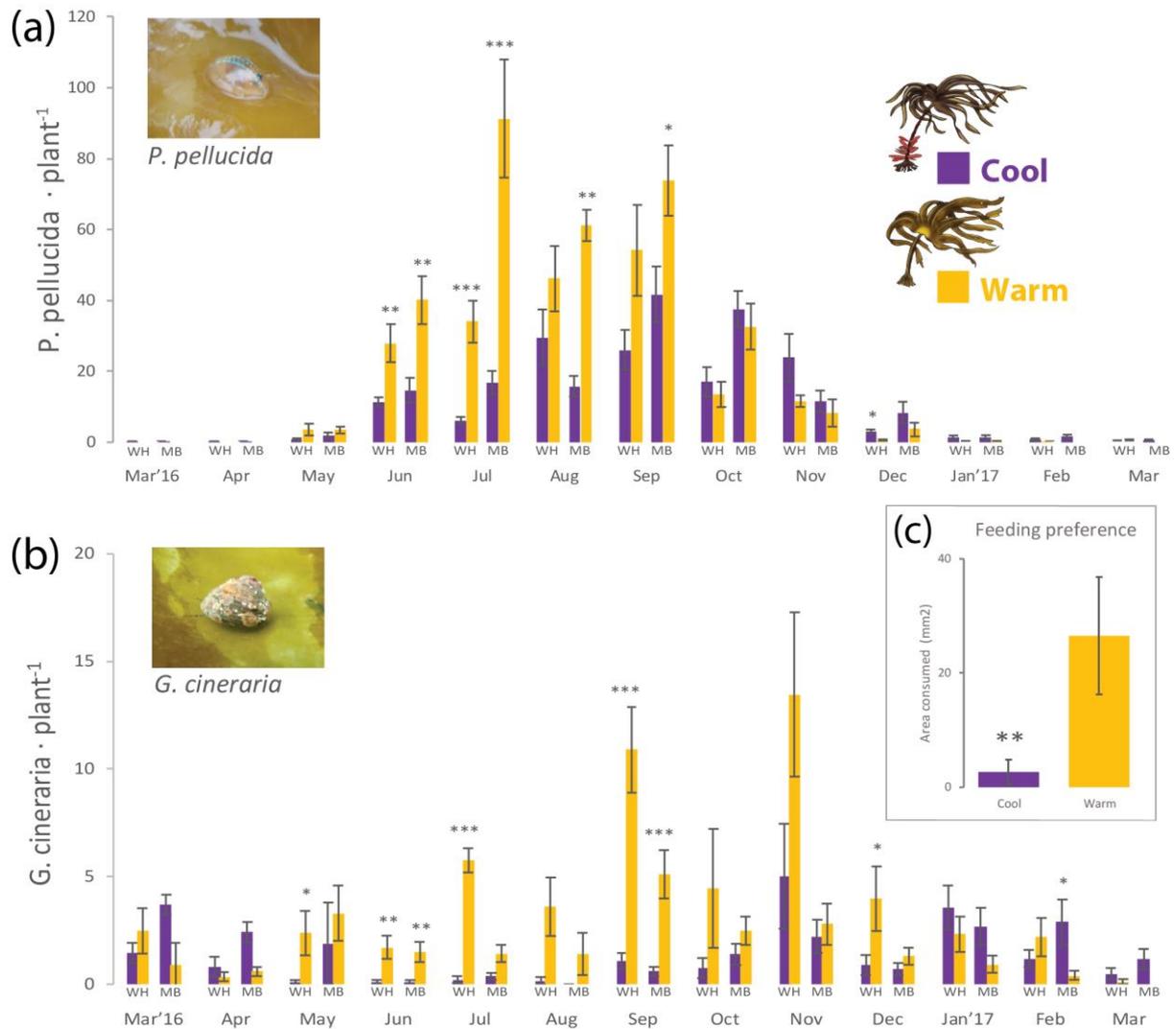
365 interaction as seasonal patterns of abundance differed between species but the magnitude of
366 dissimilarity between species was generally higher at one of our sites (MB; Figure 3a).

367

368 We recorded a total of 685 *Gibbula cineraria* individuals on *L. ochroleuca*, compared to 363 on *L.*
369 *hyperborea*. Overall, *L. ochroleuca* supported higher abundances of *G. cineraria* (Table S3, Figure 3b).

370 The abundance of *G. cineraria* on *L. hyperborea* was generally low, with <1 individuals present
371 throughout the summer months at both sites, on average (Figure 3b). Abundance values were
372 slightly higher in winter but did not exceed 5 ± 2.4 individuals per plant and were fairly consistent
373 across months (Figure 3b). Conversely, the abundance of *G. cineraria* on *L. ochroleuca* laminae was
374 highly variable between months, often registering two-fold or three-fold differences between
375 consecutive months. Maximum abundance values were recorded in November (13.4 ± 3.8 and $5.1 \pm$
376 1.1 individuals at WH and MB, respectively). Statistically, we detected a significant interaction
377 between species and month, as the magnitude of dissimilarity between species was greater during
378 summer months (Figure 3b). In the feeding preference trials, *G. cineraria* exhibited a strong
379 preference for *L. ochroleuca* over *L. hyperborea* ($W = 179.5$, p -value <0.001), with average
380 consumption rates being an order of magnitude greater on the warm-water species (Figure 3c).

381



382

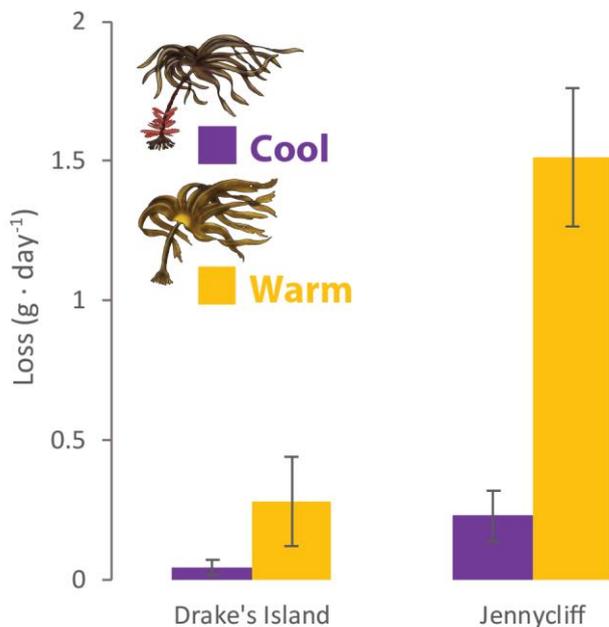
383 **FIGURE 3.** Abundance of the grazers *Patella pellucida* (a) and *Gibbula cineraria* (b) on the laminae of
 384 the cool-temperate kelp *Laminaria hyperborea* (purple bars) and the warm-temperate congener *L.*
 385 *ochroleuca* (yellow bars) in mixed kelp forests at West Hoe (WH) and Mount Batten (MB). Results
 386 from the feeding preference experiments with *G. cineraria* (n=14) are shown in (c). Bars represent
 387 mean values \pm SE.

388

389 *Kelp decomposition*

390 In the litter bag experiment, decomposition rates of *Laminaria ochroleuca* were consistently higher
 391 than *L. hyperborea* (Figure 4). We recorded a significant interaction between species and site (Table
 392 S4) as the magnitude of differences between species varied between sites, with relatively lower loss

393 rates of *L. ochroleuca* at Drake's Island compared to Jennycliff (Figure 4). After the 40-day
394 deployment, the fresh weight of *L. ochroleuca* had decreased by 56.9% and by 10.5% at Jennycliff
395 and Drake's Island respectively, whereas *L. hyperborea* biomass declined by 8.9% and just 1.6% at
396 the same sites. The structure of detritivore assemblages associated with kelp matter (which were
397 numerically dominated by amphipods and isopods) was highly variable, and did not vary significantly
398 between kelp species (Table S4).



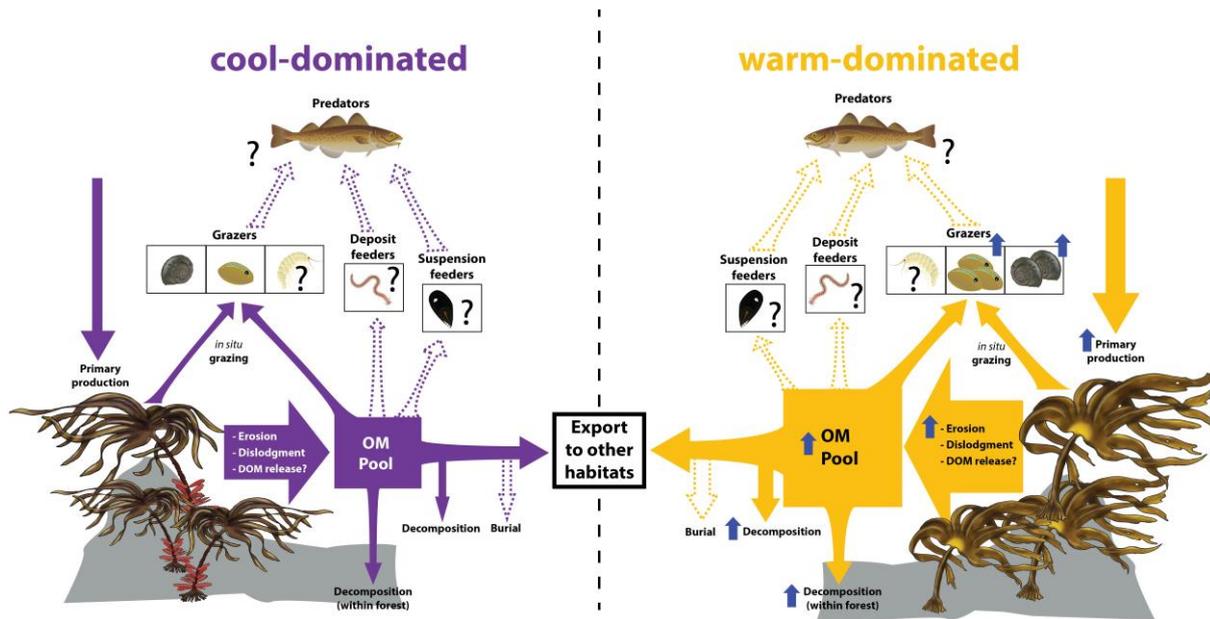
399
400 **FIGURE 4.** Kelp decomposition rates for the cool-temperate *Laminaria hyperborea* (purple bars) and
401 the warm-temperate congener *L. ochroleuca* (yellow bars) at two subtidal study sites.

402 *Kelp habitat structure*

403 The densities and relative abundances of canopy-forming *Laminaria hyperborea* and *L. ochroleuca*
404 plants varied between sites (Table S5). Crucially, however, the total density of kelp plants was
405 broadly similar across sites, regardless of the proportional representation of each species. Indeed,
406 plant densities at sites dominated by *L. hyperborea* were similar, albeit slightly higher, to those at
407 sites dominated by *L. ochroleuca* (Table S5).

408 DISCUSSION

409 Our results reveal fundamental differences in several processes central to ecosystem functioning
410 (biomass production, detrital flow, herbivory and decomposition) between two foundation species
411 with contrasting thermal affinities. These findings suggest a substantial shift in the cycling of organic
412 matter within the forests of the study region following the replacement of a cold-temperate species
413 by a warm-temperate one, and provide rare evidence of how range shifts and species substitutions
414 can affect ecosystem functioning in marine ecosystems. Despite being taxonomically related and
415 morphologically similar to the cool-temperate *Laminaria hyperborea*, the warm-temperate kelp *L.*
416 *ochroleuca* was ~1.8 times more productive and generated ~1.8 times more detritus via lamina
417 erosion, resulting in a larger pool of organic matter entering detrital food webs (Figure 5). Given that
418 the warm-temperate species supported greater numbers of grazers and was a preferred food
419 source, the proliferation of this kelp into cool-temperate communities will also likely alter trophic
420 pathways within kelp forests (and potentially beyond) by increasing the amount of production that
421 enters higher trophic levels via herbivory (Figure 5). It is yet unclear how other consumers of kelp-
422 derived organic matter (e.g. suspension feeders and deposit feeders) might be affected, and
423 whether the changes we document here will extend to secondary consumers (Figure 5, dashed
424 arrows). However, given the magnitude of the changes we report, it seems unlikely that effects will
425 be negligible. Finally, the higher detritus decomposability of warm-temperate plants will increase
426 nutrient turnover and decrease the residence time of kelp detrital exports, potentially affecting
427 trophic connectivity between kelp forests and other habitats (Figure 5).



429

430 **FIGURE 5.** Schematic representation of the expected fluxes of kelp organic matter as some kelp
 431 forests within the study region transition from being dominated by cool- to warm-temperate
 432 foundation species. Blue arrows indicate changes in the processes measured; question marks and
 433 dashed, empty arrows denote mechanisms and pathways that were not evaluated in this study.
 434 Results suggest that, in forests dominated by the warm-temperate species, a larger fraction of kelp-
 435 derived matter may be consumed by grazers (principally snails, limpets and amphipods), which can
 436 feed directly on the standing or dislodged plants. Warm-temperate plants produced larger amounts
 437 of detritus, thus creating a large pool of organic matter (OM). That pool is either (i) consumed by
 438 suspension and/or deposit feeders, (ii) decomposed by microbes or (iii) exported to other habitats,
 439 where it may be consumed/decomposed or eventually buried. Detritus from warm-temperate plants
 440 decomposed much faster, which may affect the fate of the OM pool and/or its export. The kelp
 441 organic matter assimilated by primary consumers may flow to higher trophic levels via predation.

442

443 The warm- and cold-temperate kelps exhibited markedly different growth strategies, which can
 444 explain the differences in total annual biomass accumulation to some extent. The warm-temperate
 445 species showed continuous growth and erosion of the lamina throughout the year, providing a
 446 steady supply of particulate organic matter and essentially acting as a “conveyor belt” of biomass

447 accumulation and detritus production. Conversely, the growth strategy of the cool-temperate
448 species was characterized by discrete phases, with a distinct growing phase and an intense period of
449 detrital production during the casting of the old lamina growth, which remains attached to the newly
450 growing lamina until March–May (Kain 1971). The cool-water species is considered a “season
451 anticipator” (sensu Kain 1989) as its growth is controlled by a strategic annual rhythm (Schaffelke &
452 Lüning 1994), and shows little response to environmental conditions. In contrast, the growth
453 strategy of the warm-temperate species is characteristic of a “season responder”, with growth rates
454 closely correlated with irradiance levels (Kain 1989).

455

456 Such fundamental differences in growth strategies—and the consequent temporal alterations to the
457 production and release of organic matter—are likely to translate into wider changes in the way
458 energy and nutrients flow through grazing and detrital pathways in the coastal food web. A greater
459 amount of kelp production will enter the food web via direct grazing, as evidenced by the warm-
460 water kelp supporting greater densities of the grazer *Gibbula cineraria* and being a preferred food
461 source. A similar pattern was found for the tiny limpet *Patella pellucida*, which feeds almost
462 exclusively on kelp (Leclerc *et al.* 2013; Hereward *et al.* 2018). The contrasting grazer preference
463 between kelp species could relate to differences in their biochemical composition, which influences
464 food palatability and nutritional quality. As variability in grazer preferences can influence the
465 ecological performance and population structure of seaweed species (Duffy & Hay 2000), the
466 interspecific variability we recorded here may have implications for the population dynamics of
467 these habitat-forming kelps. Grazers can exert considerable influence upon macroalgal assemblages
468 (Hay 1991) especially at early stages of algal development (Korpinen *et al.* 2007), and relationships
469 between grazers and their host algae are pivotal in characterising community organization (Duffy &
470 Hay 2000) and ecosystem functioning (Bruno *et al.* 2008). However, compared with many other algal
471 groups, herbivores generally consume a relatively low proportion of kelp primary production

472 (Krumhansl & Scheibling 2012b), particularly when the primary grazers are small in size—as is the
473 case with the current study region (Smale *et al.* 2013, 2016; Hereward *et al.* 2018).

474

475 Indeed, more than 90% of the biomass accumulated in the laminae of tagged plants was lost as
476 eroded fragments in both kelp species, providing further evidence that the vast majority of kelp
477 primary production enters the detrital food web (Krumhansl & Scheibling 2012b). The continuous
478 and considerably larger supply of detritus generated by the warm-temperate kelp will provide a
479 larger pool of organic matter available to consumers such as deposit- and suspension-feeders. This
480 pool is an important food source for consumers both within the kelp forest but also within spatially-
481 disconnected habitats such as seagrass meadows or sedimentary substrates, where kelp organic
482 matter constitutes an important trophic subsidy (Vanderklift & Wernberg 2008; Abdullah, Fredriksen
483 & Christie 2017; Figure 5). Interestingly however, we found that detritus from the warm-temperate
484 species decomposed an average of 6.5 times faster than that of the cool-temperate one; this may
485 decrease detritus residence time and its availability for long-range transport, thus affecting trophic
486 connectivity between kelp forests and other habitats. Changes in the magnitude and identity of
487 detrital subsidies can also alter the structure of kelp detritivore communities (Bishop, Coleman &
488 Kelaher 2010), as documented after the arrival of invasive species (Taylor *et al.* 2010). Although we
489 did not find significant differences in the abundance of detritivores between our mesh bags, further
490 work is required to examine how the composition of detritivore assemblages will be influenced by
491 the continuous—but ephemeral—supply of *L. ochroleuca* detritus. Determining whether changes in
492 the abundance of detritivores and grazers—which are important prey items for fish and crustacean
493 predators (Muntz, Ebling & Kitching 1965; Norderhaug *et al.* 2005)—will impact higher trophic levels
494 should also be a priority for future research.

495

496 Despite the observed contrasting biomass dynamics between the kelp species, some of the key
497 ecosystem functions and services delivered by kelps in the NE Atlantic will likely persist in the future,

498 as several ecological processes were maintained or even enhanced. For instance, kelp forests
499 dominated by the warm-temperate species will still exhibit high rates of carbon capture, as plant
500 primary production—and therefore carbon assimilation—was higher than that of the cool-water
501 kelp. Both species are also morphologically similar and form canopies of similar heights and plant
502 densities (Smale *et al.* 2015; Table S5) and, as such, kelp forests dominated by the range-expanding
503 species are likely to continue to provide habitat for wide range of fish, invertebrate and algal species
504 (O'Brien *et al.* 2018; Teagle *et al.* 2018). That said, recent work has shown that the epibiotic
505 assemblages associated with kelp stipes, which are typically dominated by red seaweeds and sessile
506 invertebrates, are less diverse in the warm-temperate species (Teagle & Smale 2018). The future of
507 NE Atlantic kelp forests contrasts with that in other marine temperate regions where, in many cases,
508 ecological functions provided by kelps have not been replaced following their decline, as they have
509 been superseded by structurally-dissimilar algae (Terazono *et al.* 2012; Dijkstra *et al.* 2017) and even
510 completely different foundation species such as corals (Vergés *et al.* 2014). For example, gradual
511 ocean warming and discrete marine heatwaves have resulted in structurally-complex kelp forests
512 being replaced by low-lying, architecturally-poor habitats dominated by turf-forming algal species in
513 several regions across the globe (Filbee-Dexter & Wernberg 2018). Since the ecological
514 characteristics of algal turfs differ markedly from those of larger canopy-forming seaweeds, such
515 replacements can lead to substantial reductions in associated biodiversity (Smale & Wernberg 2013;
516 Cheminée *et al.* 2017) and alterations to key functions such as net primary productivity (Copertino,
517 Connell & Cheshire 2005). Similarly, the introduction of non-native seaweeds with traits differing
518 from those of kelps modified the trophic dynamics and the circulation of organic matter within
519 recipient marine ecosystems (Pedersen *et al.* 2005; Dijkstra *et al.* 2017). Such shifts in the structure
520 and functioning of marine forests have major implications for human societies. For instance, the
521 climate-driven loss of kelp forests from the temperate coasts of Japan culminated in a dramatic
522 decline in kelp-associated abalones and, ultimately, the crash of one the most important fisheries in
523 the region (Serisawa *et al.* 2004; Kiyomoto *et al.* 2013).

524

525 The magnitude of change in NE Atlantic kelp forests as waters continue to warm will partly depend
526 on whether the warm-temperate kelp can entirely replace its cold-affinity congener as it retracts
527 polewards. While the warm-temperate kelp attained similar densities to those of the cold-water
528 species and even dominated kelp forest assemblages in the surveyed sites within moderate to low
529 wave exposure, it was less abundant in wave exposed locations (Table S5). This is likely because *L.*
530 *ochroleuca* is more susceptible to being dislodged by wave action (Smale & Vance 2015).
531 Interestingly however, within recent decades this species has extended its distribution from
532 sheltered to moderately wave-exposed locations (Smale *et al.* 2015). The broadly comparable
533 densities we found at our survey sites thus suggest that the plant-level differences we report here
534 will broadly scale up to larger spatial scales at the ecosystem level, at least in sheltered moderately
535 wave-exposed coasts. Further, the central NE Atlantic contains a rich diversity of canopy-forming
536 seaweeds, and it remains to be seen whether other kelp species with warmer affinities than *L.*
537 *hyperborea* (e.g. *Saccorhiza polyschides*) may play a more influential role within kelp forest habitats
538 in the future. Contrastingly, kelp forests in regions with fewer foundation species and with lower
539 functional redundancy may be more vulnerable to ecosystem shifts. For instance, an extreme
540 warming event led to the loss of extensive areas of kelp forests in Australia—which are dominated
541 by a single species of kelp—fundamentally altering ecosystem dynamics and forcing a regime shift to
542 algal turfs (Wernberg *et al.* 2016). It is also likely that kelp-dominated habitats located towards the
543 warm-water limit of the kelp species' distributions are more vulnerable to ocean warming, and are
544 more susceptible to radical shifts in canopy structure and consequent loss of core ecosystem
545 functions (Raybaud *et al.* 2013; Wernberg *et al.* 2016).

546

547 Climate change has resulted in an upward and poleward migration of warm-affinity species, which
548 often displace and replace cold-affinity ones (Peñuelas & Boada 2003; Beck *et al.* 2011; Warren II *et*
549 *al.* 2016). *Laminaria hyperborea* forests are currently the dominant vegetation type along much of

550 the NE Atlantic coastline, with an estimated spatial extent of $\sim 18,000 \text{ km}^2$ (Pessarrodona *et al.*
551 2018). As a consequence of ocean warming, this species is predicted to lose between 8.41% and
552 39.44% of its entire suitable habitat by the end of the century, as moderate expansions at its
553 northern poleward range edge will not compensate for extensive losses further south (Assis *et al.*
554 2016). Our findings suggest that the predicted expansion (Franco *et al.* 2017) of a warm-temperate
555 congener into habitat formerly dominated by *L. hyperborea* will likely result in noticeable shifts in
556 the magnitude and flow of organic matter in NE Atlantic kelp forest ecosystems and interconnected
557 nearshore habitats. Even so, these novel forest communities could potentially preserve some of the
558 key ecosystem functions and services delivered by current kelp-dominated habitats. Our work
559 demonstrates that, like species invasions (Mascaro, Hughes & Schnitzer 2012), climate-driven shifts
560 in species composition can maintain or even enhance ecosystem processes to some extent, and
561 suggests that the impact of species replacements will depend, to some degree, on the similarity in
562 functional traits between climate change ‘winners’ and ‘losers’. Overall, our findings point to the
563 need to consider functional traits over species identity when examining the wider impacts of human-
564 mediated shifts in species composition on ecosystem processes, functions and services.

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571 AUTHOR CONTRIBUTIONS

572 All authors contributed to the development of ideas, interpretation of results, and writing of the
573 manuscript. AP led fieldwork, sample collection and processing, and data analysis. AF orchestrated

574 the feeding preference assays and provided valuable advice. DS originally conceived the study and
575 co-wrote the first draft of the manuscript with AP.

576 DATA ACCESSIBILITY

577 Data is deposited in the Dryad Digital Repository (doi:10.5061/dryad.1d9p080)

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