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

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Abstract

1. Climate change is driving a redistribution of species and the reconfiguration of ecological communities at a global scale. Persistent warming in many regions has caused species to extend their geographical ranges into new habitats, with thermally tolerant species often becoming competitively dominant over species with colder affinities. Although these climate-driven changes in species abundance and diversity are well documented, their ecosystem-level implications are poorly understood, and resolving whether reconfigured communities can maintain fundamental ecosystem functions represents a pressing challenge in an increasingly warmer world.
2. Here, we investigated how climate-driven substitutions of foundation species influence processes associated with the cycling of organic matter (biomass production, detritus flow, herbivory, decomposition) by comparing two habitat-forming kelp species with contrasting thermal affinities. We examined the wider ecosystem consequences of such shifts for the observed (and predicted) emergence of novel marine forest communities in the NE Atlantic, which are expected to become more dominated by range-expanding, warm-temperate kelp species.
3. Warm-temperate kelps both accumulated and released 80% more biomass than the cold-temperate species despite being taxonomically closely related and morphologically similar. Furthermore, the warm-temperate species accumulated biomass and released detritus year-round, whereas the cold-temperate species did so during short, discrete periods. The warm-temperate kelps supported higher densities of invertebrate grazers and were a preferred food source. Finally, their detritus decomposed 6.5 times faster, despite supporting comparable numbers of detritivores. Overall, our results indicate an important shift in organic matter circulation along large sections of NE Atlantic coastline following the climate-driven expansion of a warm-affinity kelp, with novel forests supplying large amounts of temporally continuous—yet highly labile—organic matter.
4. *Synthesis*. Collectively, our results show that, like species invasions, climate-driven range expansions and consequent shifts in the identity of dominant species can modify a wide range of important ecosystem processes. However, alterations in overall ecosystem functioning may be relatively limited where foundation species share similar ecological and functional traits.

KEYWORDS
climate change, *Laminaria hyperborea*, *Laminaria ochroleuca*, Laminariales, macrophyte, novel ecosystems, range expansion, range shift, temperate reefs

1 | INTRODUCTION

Humans have increasingly impacted the natural environment over the last five millennia (Bell & Walker, 2004), to the point where very few contemporary ecosystems are free from human influence (Ellis, Goldewijk, Siebert, Lightman, & Ramankutty, 2010). Human activities have led to the reorganization of biological communities worldwide, principally by (a) introducing individuals and populations beyond species' native ranges; (b) driving species extinctions; and (c) altering key environmental factors that constrain species distributions, thereby inducing species range shifts. As a result, present-day species abundance and composition of many contemporary ecosystems does not resemble historical configurations (Hobbs, Higgs, & Harris, 2009; Hobbs et al., 2006). To date, most studies on the wider impacts of species gains or losses in ecosystems have focused on structural changes at the community level (e.g., changes in species abundance or diversity). Moving beyond describing shifts in community composition and structure and shedding light on how ecological reconfigurations alter the ecosystem functions and services on which human wellbeing depends is therefore a central challenge for ecology (Mooney et al., 2009). In the ecological literature, species' range shifts have received far less attention than species introductions or extinctions (Sorte, Williams, & Carlton, 2010), even though range shifts have been observed across a broad range of taxa and ecosystem types (Pecl et al., 2017). Given that impacts of species range shifts on ecological communities may be similar in magnitude to those of introduced nonnative species (Sorte et al., 2010), with successful range-shifting species sometimes displaying invasive properties (Engelkes et al., 2008), there is a clear and pressing need to explore the wider consequences of such shifts.

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

In temperate marine systems, large, canopy-forming seaweeds (macroalgae) function as foundation species (sensu Dayton, 1972), forming marine forests that provide biogenic habitat, alter local environmental conditions and mediate numerous ecological processes (Steneck et al., 2002; Teagle, Hawkins, Moore, & Smale, 2017). Seaweeds are especially sensitive to climatic changes, and range shifts in response to past and contemporary climate variability are well described (Li, Hu, & Duan, 2016; Neiva et al., 2016; Straub, Thomsen, & Wernberg, 2016). The majority of contemporary seaweed range shifts have been documented in temperate seas (Straub et al., 2016), where seaweed forests often dominate shallow rocky habitats. Temperate regions contain two distinct floristic elements, the cold- and warm-temperate (sensu Lüning, 1990), which differ in the temperature tolerances of the species they comprise. Climate change is driving shifts in the relative distribution of these elements, creating novel seaweed assemblages and with warmer water species replacing colder water ones, particularly in biogeographic transition zones (Fernández, 2016; Lima, Ribeiro, Queiroz, Hawkins, & Santos, 2007; Tanaka, Taino, Haraguchi, Prendergast, & Hiraoka, 2012). Although climate-driven reconfigurations of seaweed communities are documented (Harley et al., 2012), empirical evidence for their wider ecological consequences remains limited, and understanding how altered species composition affects ecosystem processes and functioning remains a persistent challenge (Pedersen, Stæhr, Wernberg, & Thomsen, 2005).

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

2 | MATERIALS AND METHODS

2.1 | Study species

The kelp *Laminaria ochroleuca* is a warm-temperate species presently distributed from Morocco to southwest England in the

United Kingdom (UK), where it was first detected in the late 1940s (Parke, 1948) (Figure 1a,b). In recent decades, *L. ochroleuca* has increased in relative abundance at the leading-edge of its distribution (Smale, Wernberg, Yunnie, & Vance, 2015; Teagle & Smale, 2018), being now common throughout the southwest coast of the UK (Brodie, Andersen, Kawachi, & Millar, 2009) and dominating forest assemblages in many wave-sheltered locations (authors' pers. obs.). The growth and performance of *L. ochroleuca* is highly sensitive to temperature (Franco et al., 2017; Hargrave, Foggo, Pessarrodona, & Smale, 2017; Izquierdo, Pérez-Ruzafa, & Gallardo, 2002), and the recent proliferation of this species at the leading edge of its distribution has been linked to recent ocean warming (Smale et al., 2015; Teagle & Smale, 2018). *Laminaria ochroleuca* is predicted to continue expanding northwards in response to climate change, occupying most of the UK and large sections of the wider NE Atlantic coastline by the end of the century (Franco et al., 2017). The prospects for *L. ochroleuca* contrast with that of the cold-temperate kelp *Laminaria hyperborea*, the current assemblage dominant along moderate to wave-exposed coastlines in the region. *L. hyperborea* does not perform well at high temperatures (tom Dieck (Bartsch), 1992; Wiencke, Bischoff, Bartsch, Peters, & Breeman, 1994), and over the past 40 years has undergone a *c.* 250-km range contraction at its warm, trailing-edge on the Iberian Peninsula (Assis, Lucas, Bárbara, & Serrão, 2016; Pereira, Engelen, Pearson, Valero, & Serrão, 2017). Continued ocean warming is expected to lead to further declines in abundance and shifts in its biogeographic distribution, with predicted extinctions of populations currently found along the coasts of Iberia, France,

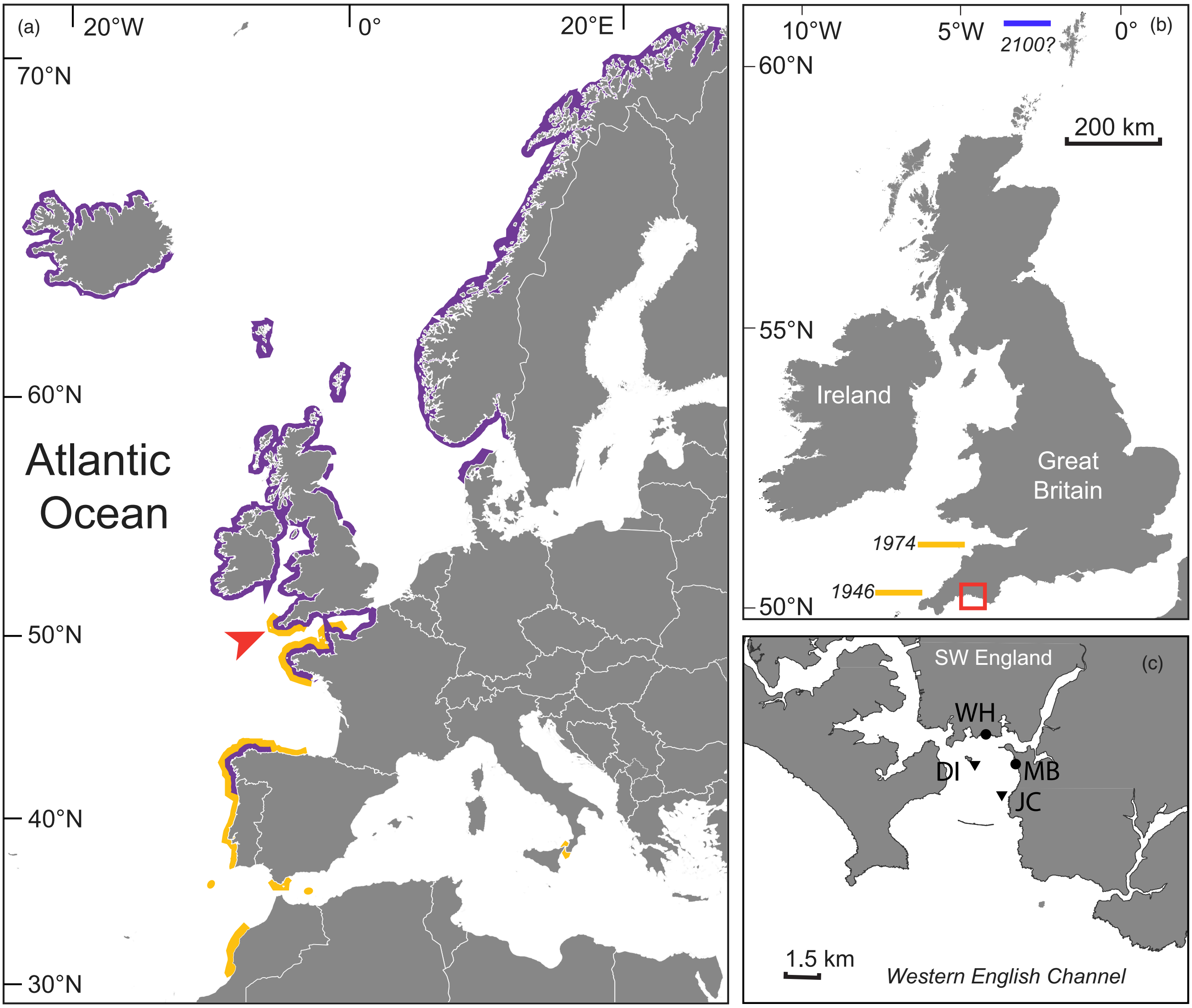

FIGURE 1 (a) Approximate distribution of *Laminaria hyperborea* (purple line) and *Laminaria ochroleuca* (yellow line) along the NE Atlantic coastline. The red arrow indicates the study region, which is shown in (b). *L. ochroleuca* was first detected in this region in 1946, and has since expanded its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

and southern UK (Breeman, 1990; Müller, Laepple, Bartsch, & Wiencke, 2009).

2.2 | Study design and location

The stocks and fluxes of organic matter are central to the biological, geochemical, and physical processes that occur within kelp forest ecosystems, as well as in spatially disconnected habitats subsidized by kelp-derived organic matter (Krumhansl & Scheibling, 2012a). To investigate how future kelp forests dominated by the warm-temperate kelp *L. ochroleuca* might differ functionally from those formerly dominated by the cold-temperate *L. hyperborea*, we compared processes related to the cycling of organic matter between the two species in two mixed kelp forests. We estimated kelp biomass accumulation—a widely used proxy for kelp primary production (de Bettignies et al., 2013; Krumhansl & Scheibling, 2011)—and biomass loss (detrital production) over the course of an annual cycle (March 2016–February 2017). Produced biomass can either (a) be directly consumed by grazers in situ or (b) be exported as detritus and later consumed by a vast array of microbes, detritivores, and suspension-feeders. To determine how biomass flows through grazing and detrital pathways in the coastal food web, we quantified the abundance of grazers associated with each kelp species and measured kelp detritus decomposition.

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

2.3 | Biomass accumulation and loss

Kelp biomass accumulation and loss was measured monthly using a modified hole-punch method after Krumhansl and Scheibling (2011). This technique consists of punching a series of holes at set distances from the stipe/lamina transition zone, where the primary meristem occurs. To obtain a growth estimate, hole-punched plants are retrieved after a certain time interval and the final position of the holes is recorded. During spring low tides, 10–12 mature kelp plants (stipe length ≥ 20 cm) of each species were randomly selected, tagged, and uniquely labelled at each site. Selected plants were from different areas of the forest each month. Two digits of each plant lamina were hole-punched and their initial length measured. Since growth is not uniform across the lamina (Kain, 1976), a total of three holes were punched in every individual: two at 15 and 20 cm above the stipe/lamina transition zone on the central digit and another one at 20 cm above the aforementioned zone on an outer digit. The two holes punched on the central digit captured the maximal growth in length, which occurs between 2.5 and 15 cm from the central transition zone depending on the month (Kain, 1976), while the hole on the outer digit captured variability in growth across lamina digits. After *c*. 1 month, tagged kelps were harvested and returned to the laboratory for analysis. The final length of the punched digits, position of the holes, and the fresh wt of the stipe and lamina were recorded to calculate individual-specific lamina elongation and loss rates. The exact number of elapsed days between tagging and retrieval, as well as the number of tagged kelp plants relocated and retrieved, varied due to limited tidal windows and a rough sea state in some months. On average, >8 individuals of each species were recovered from each site each month (see Supporting Information Table S1 and Supporting Information Table S2 for full details). In August however, bad weather hampered the retrieval of tagged plants. Given the low number of replicates (Supporting Information Table S2), and their small size compared to the plants tagged in the rest of the months (Supporting Information Figure S1), August data were not included in the analysis.

To convert elongation and loss rates of lamina tissue (cm) to gains and losses of fresh biomass (g), three 5 cm-wide segments from both the basal and distal parts of the lamina of each plant were cut across their width, cleaned of epiphytes, and weighed (fresh wt; FW). In order to make our results more comparable with those in the literature, we converted fresh biomass to dry biomass (dry wt; DW). Every month and for each of the retrieved plants, we determined the relationship between dry and fresh wt (DW:FW) by drying one of the basal and distal segments at 60°C for 48 hr. The basal and distal parts of the lamina were examined separately as the relationship can vary between different parts of the thallus (Smale et al., 2016). All relationships were highly significant and had an $R^2 \geq 0.85$. We then estimated the dry wt of the remaining two segments (out of the three we cut) from each part using the calculated relationship. Finally, the measured and estimated dry biomass per unit length was averaged between all three segments to give the dry biomass per unit length (g/cm) of the respective basal and distal parts of the lamina ($\mathrm{B}_{\mathrm{base}}$ and $\mathrm{B}_{\mathrm{distal}}$). This allowed us to convert elongation and loss rates of lamina tissue (cm) to accumulations and losses of biomass (g DW).

Biomass accumulation (BA) for each plant was estimated as:

$$\mathrm{BA} = \mathrm{E} \times \mathrm{B}_{\mathrm{base}} / t$$

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

$$E = \frac{\left[(H_{f_{1,1}} - 15) + (H_{f_{1,2}} - 20)\right] + (H_{f_2} - 20)}{2}$$

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

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

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

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

In *L. hyperborea*, we observed a marked increase in the DW:FW ratio from June to September (Supporting Information Figure S2), which was not documented for *L. ochroleuca* (Supporting Information Figure S2). During this period, the average biomass of the basal lamina segments was higher than the rest of the year (Supporting Information Figure S3). Regrettably, we could not account for the biomass accumulation that occurred during these months, since our formula was based on elongation (i.e., linear growth; E), which was negligible from July to September (Supporting Information Figure S4). The observed biomass accumulation not related to linear growth was most likely explained by (a) the accumulation of organic compounds in the cell, thus increasing the DW:FW ratio and (b) increases in basal lamina thickness, which has been found to increase from July to December in *L. hyperborea* (Kain, 1971, 1976). Although we did not measure changes in basal lamina thickness in our surveys, previous *L. hyperborea* studies have shown that there is an inverse relationship between relative changes in linear growth and thickness, with thickening being greatest when elongation rates are low (i.e., after June; Kain, 1976). Our observations support such findings. As such, to account for *L. hyperborea* lamina thickening between June–September in our biomass accumulation formula, we used the minimal elongation rate recorded in the study (0.033 cm/day) as a surrogate of lamina thickness growth during those months.

2.4 | Grazer surveys

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

To examine the influence of kelp nutritional quality in determining the herbivory pressure patterns observed in the field, we used a series of feeding preference assays using artificial diets (Hay et al., 1998). Fresh kelp plants were harvested in April 2016, the central and distal sections of the laminae cut into strips and subsequently freeze-dried. Kelp strips were then pulverized to a fine powder using an electric grinder and stored in a freezer. We prepared a seaweed solution containing 1 g of kelp powder, 1 g of pulverized *Ulva sp.* and 20 ml of water. *Ulva sp.* was added to the mix as kelp alginates made the solution too viscous, and *Ulva spp.* are less chemically defended than brown algae (Duffy & Hay, 1994). Agar (0.7 g) was added to a further 20 ml of water, heated to boiling point, and quickly homogenized with the seaweed solution. This final mixture was then poured onto a glass plate covered in microscope slides with 1 × 1 mm plastic mesh glued on top. Finally, another glass panel was rapidly placed on top, sandwiching the mesh-covered slides and spreading the algal mixture to a uniform 1-mm thickness on all slides. After 2 min, the solidified mixture had adhered to the mesh slides, which were individually cut using a razor. We used the gastropod *Gibbula cineraria* as a model grazer for our laboratory experiments as it was frequently observed on kelp laminae, and was the largest grazer recorded in our surveys (see Section 3). Macroinvertebrate grazers like *Gibbula spp.* can feed directly on kelp tissue or indirectly on the associated biofilms and epiphytic algae. Kelp-derived organic matter can contribute significantly to the diet of *Gibbula* spp. (Leclerc, Riera, Leroux, Lévêque, & Davoult, 2013), whose grazing activity leaves evident grazing marks on the kelp blades (authors' pers. obs.), further suggesting that kelp organic matter is ingested. *Gibbula cineraria* individuals were collected locally and were starved for 3 days in large aerated tanks (allowing for emptying of the digestive tract), before being transferred to smaller (20 × 8 × 10 cm) rectangular tanks for feeding trials. A single individual was placed in the middle of the rectangular tank, which contained one slide of *L. ochroleuca* and one slide of *L. hyperborea* agar mixture positioned at opposite ends. An air stone with low air flow was also placed in the middle of the tank. We determined kelp consumption by counting the number of 1 × 1 mm squares that been consumed after 48 hr. Fourteen replicate trials were conducted simultaneously.

2.5 | Kelp decomposability

To investigate how kelp biomass is consumed and recycled once it has been cast as detritus, we compared rates of detritus decomposition between the two kelp species. Lamina material from each species was collected and cut into strips (*c.* 5 × 15 cm). A total of 105 ± 8 g of fresh kelp strips from the same region of the laminae was then sealed within mesh bags (mesh aperture 20 mm), which were uniquely labelled. The mesh size allowed mesodetritivores and microbes to access the kelp detritus whilst minimizing loss of material via flushing. Four replicate bags for each species were deployed at a depth of 4 m (below Chart Datum) by SCUBA divers at Drake's Island and Jennycliff, both within Plymouth Sound (see Figure 1c) in March 2016. Litter bags were attached to a long rope (positioned *c.* 1 m apart from one another), which was secured to the seabed with anchor weights. Bags were deployed on a sandy seabed adjacent to a kelp-dominated rocky reef and were retrieved after 40 days. Upon retrieval, a fine mesh bag (1 μm diameter) was placed over each litter bag to retain all kelp material and detritivores, before detaching the bag from the rope. In the laboratory, the contents of the bags were carefully removed and washed through a 1 mm sieve. Remaining fresh kelp tissue was reweighed again to assess degradation rates (g/day), and the abundance of detritivores associated with the kelp material was quantified.

2.6 | Kelp habitat structure

The measurements described above were mostly collected at the scale of individual plants (i.e., per capita). In order to contextualize our findings at larger spatial scales (i.e., per unit area) and increase generality, we conducted ecological surveys of kelp-dominated habitats within the study area to determine whether both foundation species can occur at similar densities. We surveyed a number of subtidal and intertidal reefs within the study region by haphazardly placing 10 replicate 1 m^2 quadrats and quantifying the density of mature canopy-forming plants of each species.

2.7 | Statistical analyses

Differences in biomass accumulation and loss (g/day) between kelp species (two levels, fixed factor), sites (two levels, fixed factor) and months (11 levels, fixed factor), were examined with permutational ANOVA (Anderson, 2001) due to observed structuring of residuals and heterogeneity of variances encountered in exploratory analyses. August data were excluded from analyses as explained above (see Supporting Information Table S2 and Supporting Information Figure S1). For each response variable, we generated a similarity matrix based on Euclidian distances with untransformed data using PRIMER (v7.0) software (Clarke & Gorley, 2015) with the PERMANOVA add-on (Anderson, Gorley, & Clarke, 2008). Main effects and interactions were then tested with 9,999 permutations under a reduced model. Where significant differences were recorded (usually $p < 0.05$ but see below), we conducted post hoc pairwise tests between levels of factors (or within levels of factors for significant interaction terms). While permutational ANOVA is more robust to nonnormal distributions and heterogeneity of variance than traditional ANOVA, it is still influenced by differences in dispersion between treatments. To examine data dispersion, we conducted PERMDISP tests to determine whether within-group variation differed between levels of each factor. Where a significant difference in dispersion was recorded, the critical threshold p-value of the associated PERMANOVA test was reduced a more conservative $p < 0.001$.

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

Finally, for the decomposition experiment, we used a univariate permutational ANOVA to test for differences in kelp degradation rates (g/day) and detritivore abundance between species and sites (2 levels each, fixed factors). We generated a similarity matrix based on Euclidian distances and examined variability between factors with 9,999 permutations under a reduced model.

3 | RESULTS

3.1 | Biomass accumulation and loss

Across our year-long study, we retrieved a total of 197 *L. ochroleuca* and 204 *L. hyperborea* plants for biomass accumulation and loss determination. Biomass accumulation rates exhibited marked seasonality and differed considerably between species and sites (Figure 2a, Supporting Information Table S3). We also recorded a significant 3-way interaction between species, month and site (Supporting Information Table S3). Further examination of variability patterns showed that seasonality in biomass accumulation differed between species, but the magnitude of dissimilarity was not entirely consistent between sites (Figure 2a). Overall, we recorded a significant main effect of species and *L. ochroleuca* plants accumulated more biomass, producing an annual average of 123.8 ± 18.9 g DW/year and 137.1 ± 13.5 g DW/year (*M* ± *SE*) at WH and MB respectively—which was *c*. 80 and *c*. 90% more than the average 69.9 ± 6.3 g DW/year and 72.4 ± 4.0 g DW/year produced by *L. hyperborea* plants. *L. ochroleuca* exhibited continuous growth throughout the year, steadily increasing lamina biomass until peak production around the onset of summer (0.63 ± 0.05 g DW/day in May at WH and 0.62 ± 0.04 g DW/day in June at MB). Biomass accumulation started gradually declining after June, with growth remaining relatively consistent at around 0.2–0.3 g DW/day between September and January; the lowest biomass accumulation was recorded in November (0.09 ± 0.02 and 0.24 ± 0.02 g DW/day at WH and MB, respectively). Contrastingly, *L. hyperborea* biomass accumulation was markedly discontinuous; plants showed a distinct growth phase from December to June and a resting phase from July to November, during which lamina elongation was negligible (Supporting Information Figure S4) but increases in lamina mass and thickness occurred. Peak growth occurred in mid-spring at both sites (April: 0.87 ± 0.03 and 0.78 ± 0.04 g DW/day at WH and MB, respectively).

Loss rates of lamina biomass were consistent among sites, but varied significantly between months and species (Supporting Information Table S3). We recorded a significant 3-way interaction between species, months and sites (Supporting Information Table S3). Further examination of variability patterns showed that seasonality in biomass loss differed between species, but the timing of peak biomass loss differed slightly between sites (Figure 2b). *Laminaria ochroleuca* biomass loss occurred throughout the year, with the maximum detrital production recorded between June and September (1.29 g ± 0.33 DW/day and 0.99 g ± 0.30 DW/day maximum loss in July at WH and in September at MB, respectively). Annual detritus production via lamina loss totalled 122.4 ± 13.4 g DW/year and 120.4 ± 11.1 g DW/year for *L. ochroleuca* and 69.7 ± 6.7 g DW/year and 66.9 ± 9.3 g DW/year for *L. hyperborea* at WH and MB, respectively. In contrast to *L. ochroleuca*, *L. hyperborea* biomass loss peaked at the beginning of spring (1.02 ± 0.14 g DW/day in March at WH and 0.96 ± 0.22 g DW/day in April at MB), when the collar of old growth produced during the previous season—which had remained attached to the newly formed meristematic lamina tissue—was cast. After April, lamina biomass loss decreased to near-zero, and remained constant between 0.02 and 0.15 g DW/day for the rest of the year.

3.2 | Grazer surveys

Only two species of macroinvertabrates, the blue-rayed limpet *P. pellucida* and the trochid gastropod *G. cineraria*, were found grazing on kelp laminae. Across the 13-month-long field study, we recorded a total of 4,369 *P. pellucida* individuals on *L. ochroleuca* and 2,439 individuals on *L. hyperborea*. Overall, *L. ochroleuca* supported significantly higher abundances of *P. pellucida* than *L. hyperborea* (Supporting Information Table S3, Figure 3a). *Patella pellucida* occurred on kelp laminae year-round, but exhibited high seasonality in abundance patterns. Both *L. ochroleuca* and *L. hyperborea* supported very few *P. pellucida* individuals (between 0 and 3.5 ± 0.8 limpets per plant) until June, after which abundances markedly increased (Figure 3a). The highest abundance of limpets on *L. ochroleuca* was recorded in July and September (91.3 ± 16.5 and 54.1 ± 12.8 individuals, at MB and WH, respectively), whereas limpets were most abundant on *L. hyperborea* in August and September (41.6 ± 7.9 and 29.5 ± 7.9 individuals at MB and WH, respectively). We recorded a significant 3-way interaction as seasonal patterns of abundance differed between species but the magnitude of dissimilarity between species was generally higher at one of our sites (MB; Figure 3a).

We recorded a total of 685 *G. cineraria* individuals on *L. ochroleuca*, compared to 363 on *L. hyperborea*. Overall, *L. ochroleuca* supported higher abundances of *G. cineraria* (Supporting Information Table S3, Figure 3b). The abundance of *G. cineraria* on *L. hyperborea* was generally low, with <1 individuals present throughout the summer months at both sites, on average (Figure 3b). Abundance values were slightly higher in winter but did not exceed 5 ± 2.4 individuals per plant and were fairly consistent across months (Figure 3b). Conversely, the abundance of *G. cineraria* on *L. ochroleuca* laminae was highly variable between months, often registering two-fold or three-fold differences between consecutive months. Maximum abundance values were recorded in November (13.4 ± 3.8 and 5.1 ± 1.1 individuals at WH and MB, respectively). Statistically, we detected a significant interaction between species and month, as the magnitude of dissimilarity between species was greater during summer months (Figure 3b). In the feeding preference trials, *G. cineraria* exhibited a strong preference for *L. ochroleuca* over *L. hyperborea* ($W = 179.5$, $p < 0.001$), with average consumption rates being an order of magnitude greater on the warm-water species (Figure 3c).

3.3 | Kelp decomposition

In the litter bag experiment, decomposition rates of *L. ochroleuca* were consistently higher than *L. hyperborea* (Figure 4). We recorded a significant interaction between species and site (Supporting Information Table S4) as the magnitude of differences between species varied between sites, with relatively lower loss rates of *L. ochroleuca* at Drake's Island compared to Jennycliff (Figure 4). After the 40-day deployment, the average fresh wt of *L. ochroleuca* had decreased by 56.9% and by 10.5% at Jennycliff and Drake's Island respectively, whereas *L. hyperborea* biomass declined by 8.9% and just 1.6% at the same sites. The detritivore assemblages associated with kelp matter (which were numerically

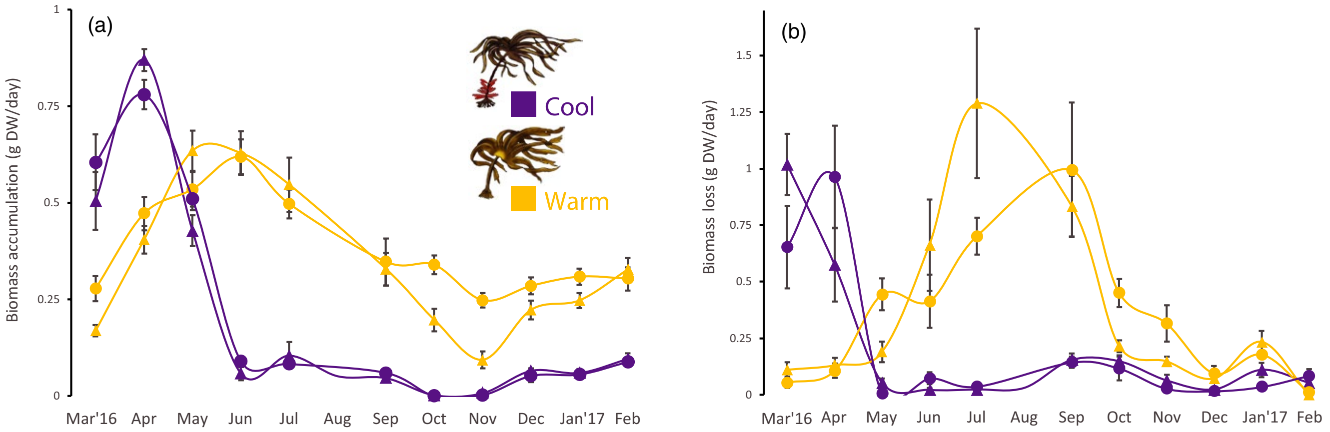

FIGURE 2 Annual patterns of (a) lamina biomass accumulation and (b) loss of the cool-temperate kelp *Laminaria hyperborea* (purple lines) and the warm-temperate congener *Laminaria ochroleuca* (yellow lines) in mixed kelp forests at West Hoe (triangles) and Mount Batten (circles). Markers denote *M* ± *SE*. Data from August were excluded from analyses due to low replication [Colour figure can be viewed at wileyonlinelibrary.com]

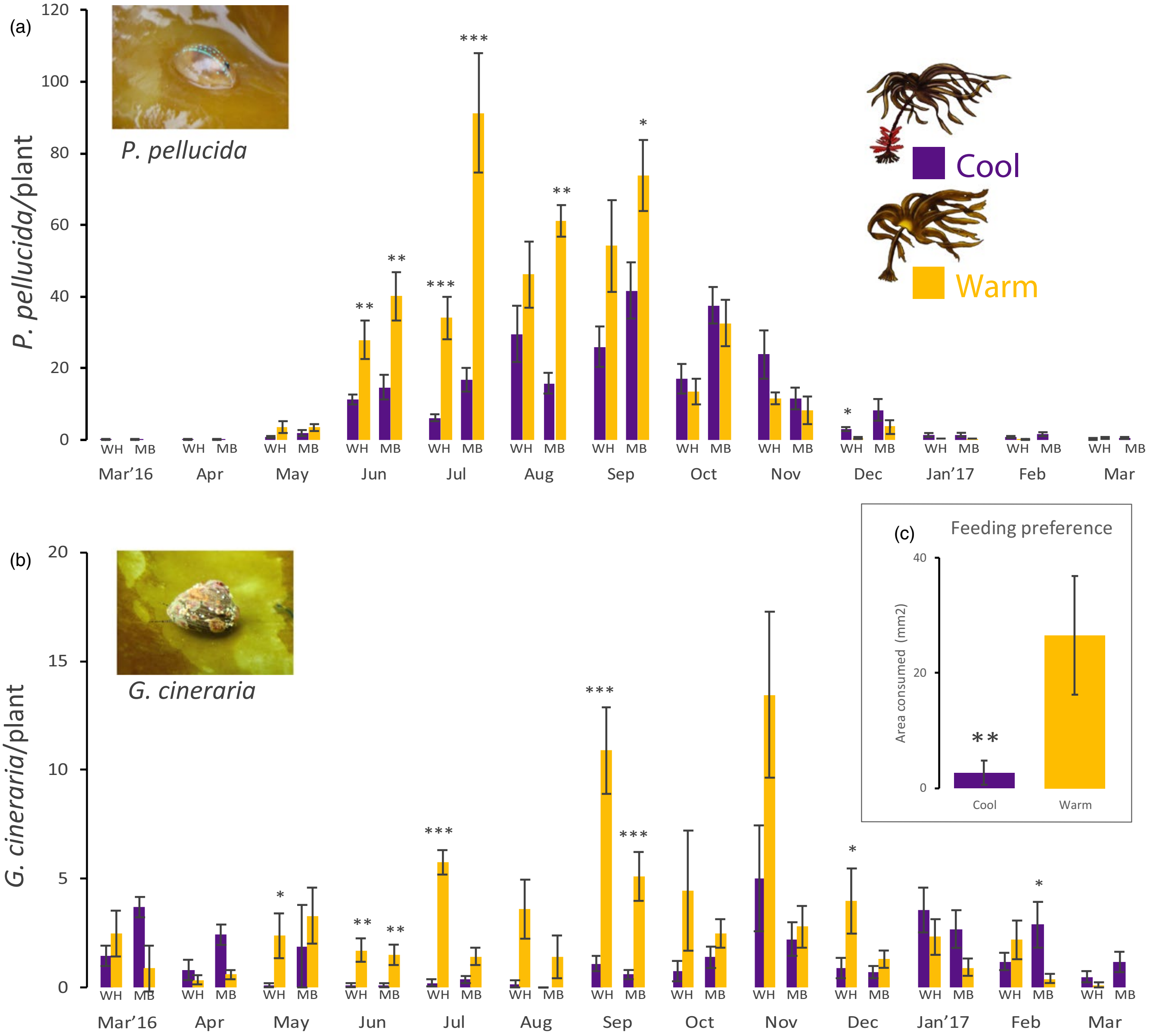

FIGURE 3 Abundance of the grazers *Patella pellucida* (a) and *Gibbula cineraria* (b) on the laminae of the cool-temperate kelp *Laminaria hyperborea* (purple bars) and the warm-temperate congener *Laminaria ochroleuca* (yellow bars) in mixed kelp forests at West Hoe (WH) and Mount Batten (MB). Results from the feeding preference experiments with *G. cineraria* ($n = 14$) are shown in (c). Bars represent $M \pm SE$. Asterisks denote probability values from pairwise tests between species within a location, with significance at $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$ [Colour figure can be viewed at wileyonlinelibrary.com]

dominated by amphipods and isopods) was highly variable, and detritivore abundance did not vary significantly between kelp species (Supporting Information Table S4).

3.4 | Kelp habitat structure

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

4 | DISCUSSION

Our results reveal fundamental differences in several processes central to ecosystem functioning (biomass production, detrital flow, herbivory, and decomposition) between two foundation species with contrasting thermal affinities. These findings suggest a substantial shift in the cycling of organic matter within the forests of the study region following the replacement of a cold-temperate

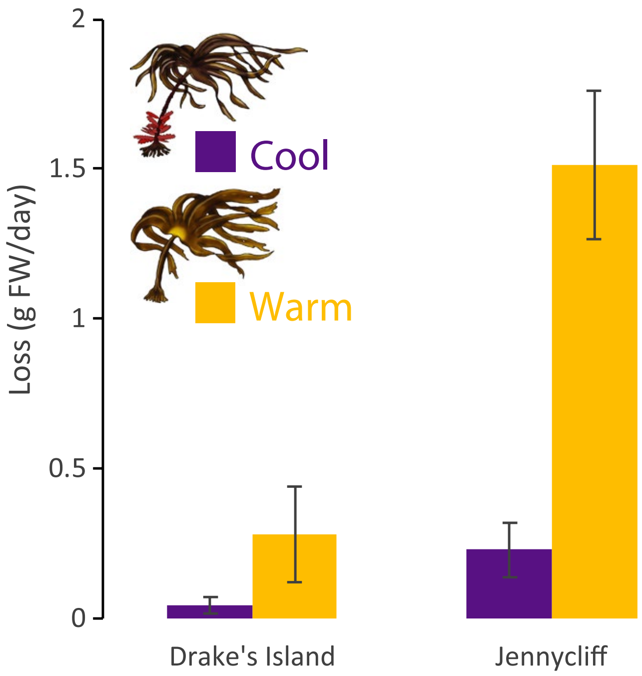

FIGURE 4 Kelp decomposition rates for the cool-temperate *Laminaria hyperborea* (purple bars) and the warm-temperate congener *Laminaria ochroleuca* (yellow bars) at two subtidal study sites. Bars represent *M* ± *SE* [Colour figure can be viewed at wileyonlinelibrary.com]

species by a warm-temperate one, and provide rare evidence of how range shifts and species substitutions can affect ecosystem functioning in marine ecosystems. Despite being taxonomically related and morphologically similar to the cool-temperate *L. hyperborea*, the warm-temperate kelp *L. ochroleuca* was *c*. 1.8 times more productive and generated *c*. 1.8 times more detritus via lamina erosion, resulting in a larger pool of organic matter entering detrital food webs (Figure 5). Given that the warm-temperate species supported greater numbers of grazers and was a preferred food source, the proliferation of this kelp into cool-temperate communities will also likely alter trophic pathways within kelp forests (and potentially beyond) by increasing the amount of production that enters higher trophic levels via herbivory (Figure 5). It is yet unclear how other consumers of kelp-derived organic matter (e.g., suspension feeders and deposit feeders) might be affected, and whether the changes we document here will extend to secondary consumers (Figure 5, dashed arrows). However, given the magnitude of the changes we report, it seems unlikely that effects will be negligible. Finally, the higher detritus decomposability of warm-temperate plants will increase nutrient turnover and decrease the residence time of kelp detrital exports, potentially affecting trophic connectivity between kelp forests and other habitats (Figure 5).

The warm- and cold-temperate kelps exhibited markedly different growth strategies, which can explain the differences in total annual biomass accumulation to some extent. The warm-temperate species showed continuous growth and erosion of the lamina throughout the year, providing a steady supply of particulate organic matter and essentially acting as a "conveyor belt" of biomass accumulation and detritus production. Conversely, the growth strategy of the cool-temperate species was characterized by discrete phases, with a distinct growing phase and an intense period of detrital production during the casting of the old lamina growth, which remains attached to the newly growing lamina until March–May (Kain, 1971). The cool-water species is considered a "season anticipator" (sensu Kain, 1989) as its growth is controlled by a strategic circannual rhythm (Schaffelke & Lüning, 1994), and shows little response to environmental conditions. In contrast, the growth strategy of the warm-temperate species is characteristic of a "season responder", with growth rates closely correlated with irradiance levels (Kain, 1989).

Such fundamental differences in growth strategies—and the consequent temporal alterations to the production and release of organic matter—are likely to translate into wider changes in the way energy and nutrients flow through grazing and detrital pathways in the coastal food web. A greater amount of kelp production will enter the food web via direct grazing, as evidenced by the warm-water kelp supporting greater densities of the grazer *G. cineraria* and being a preferred food source. A similar pattern was found for the tiny limpet *P. pellucida*, which feeds almost exclusively on kelp (Hereward, Foggo, Hinckley, Greenwood, & Smale, 2018; Leclerc et al., 2013). The contrasting grazer preference between kelp species could relate to differences in their biochemical composition, which influences food palatability and nutritional quality. As variability in grazer preferences can influence the ecological performance and population structure of seaweed species (Duffy & Hay, 2000), the interspecific variability we recorded here may have implications for the population dynamics of these habitat-forming kelps. Grazers can exert considerable influence upon macroalgal assemblages (Hay, 1991) especially at early stages of algal development (Korpinen, Jormalainen, & Honkanen, 2007), and relationships between grazers and their host algae are pivotal in characterizing community organization (Duffy & Hay, 2000) and ecosystem functioning (Bruno, Boyer, Duffy, & Lee, 2008). However, compared with other algal groups, herbivores generally consume a relatively low proportion of kelp primary production (Krumhansl & Scheibling, 2012b), particularly when the primary grazers are small in size—as is the case with the studied region (Hereward et al., 2018; Smale, Burrows, Moore, O'Connor, & Hawkins, 2013; Smale et al., 2016).

Indeed, more than 90% of the biomass accumulated in the laminae of tagged plants was lost as eroded fragments in both kelp species, providing further evidence that the vast majority of kelp primary production enters the detrital food web (Krumhansl & Scheibling, 2012b). The continuous and considerably larger supply of detritus generated by the warm-temperate kelp will provide a larger pool of organic matter available to consumers such as deposit- and suspension-feeders. This pool is an important food source for consumers both within the kelp forest but also within spatially disconnected habitats such as seagrass meadows or sedimentary substrates, where kelp organic matter constitutes an important trophic subsidy (Abdullah, Fredriksen, & Christie, 2017; Vanderklift & Wernberg,

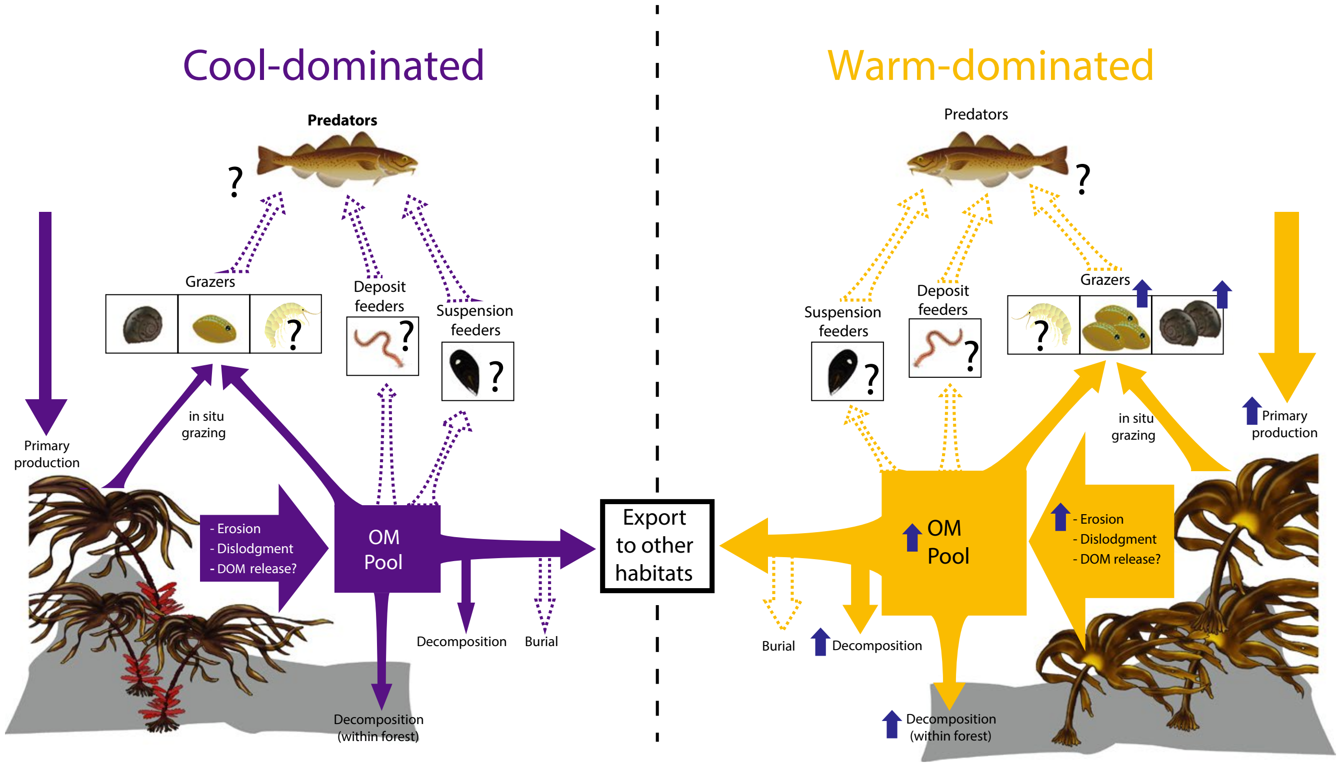

FIGURE 5 Schematic representation of the expected fluxes of kelp organic matter as some kelp forests within the study region transition from being dominated by cool- to warm-temperate foundation species. Blue arrows indicate changes in the processes measured; question marks and dashed, empty arrows denote mechanisms and pathways that were not evaluated in this study. Results suggest that, in forests dominated by the warm-temperate species, a larger fraction of kelp-derived matter may be consumed by grazers (e.g., snails, limpets, and amphipods), which can feed directly on the standing or dislodged plants. Warm-temperate kelps produced larger amounts of detritus, thus creating a large pool of organic matter (OM). That pool is either (a) consumed by suspension and/or deposit feeders, (b) decomposed by microbes or (c) exported to other habitats, where it may be consumed/decomposed or eventually buried. Detritus from warm-temperate plants decomposed much faster, which may affect the fate of the OM pool and its export. The kelp organic matter assimilated by primary consumers may flow to higher trophic levels via predation [Colour figure can be viewed at wileyonlinelibrary.com]

2008; Figure 5). Interestingly however, we found that detritus from the warm-temperate species decomposed an average of 6.5 times faster than that of the cool-temperate one; this may decrease detritus residence time and its availability for long-range transport, thus affecting trophic connectivity between kelp forests and other habitats. Changes in the magnitude and identity of detrital subsidies can also alter the structure of kelp detritivore communities (Bishop, Coleman, & Kelaher, 2010), as documented after the arrival of invasive species (Taylor, Bishop, Kelaher, & Glasby, 2010). Although we did not find significant differences in the abundance of detritivores between our mesh bags, further work is required to examine how the composition of detritivore assemblages will be influenced by the continuous—but ephemeral—supply of *L. ochroleuca* detritus. Determining whether changes in the abundance of detritivores and grazers—which are important prey items for fish and crustacean predators (Muntz, Ebling, & Kitching, 1965; Norderhaug et al., 2005)—will impact higher trophic levels should also be a priority for future research.

Despite the observed contrasting biomass dynamics between the kelp species, some of the key ecosystem functions and services delivered by kelps in the NE Atlantic will likely persist in the future, as several ecological processes were maintained or even enhanced. For instance, kelp forests dominated by the warm-temperate species will still exhibit high rates of carbon capture, as plant primary production—and therefore carbon assimilation—was higher than that of the cool-water kelp. Both species are also morphologically similar and form canopies of similar heights and plant densities (Smale et al., 2015; Supporting Information Table S5) and, as such, kelp forests dominated by the range-expanding species are likely to continue to provide habitat for fish, invertebrate, and algal species (O'Brien, Mello, Litterer, & Dijkstra, 2018; Teagle, Moore, Jenkins, & Smale, 2018). That said, recent work has shown that the epibiotic assemblages associated with kelp stipes, which are typically dominated by red seaweeds and sessile invertebrates, are less diverse in the warm-temperate species (Teagle & Smale, 2018).

The future of NE Atlantic kelp forests contrasts with that in other marine temperate regions where, in many cases, ecological functions provided by kelps have not been replaced following their decline, as they have been superseded by structurally dissimilar algae (Dijkstra et al., 2017; Terazono, Nakamura, Imoto, & Hiraoka, 2012) and even completely different foundation species such as corals (Vergés et al., 2014). For example, gradual ocean warming and discrete marine heatwaves have resulted in structurally complex kelp forests being replaced by low-lying, architecturally poor habitats dominated by turf-forming algal species in several regions across the globe (Filbee-Dexter & Wernberg, 2018). Since the ecological characteristics of algal turfs differ markedly from those of larger canopy-forming seaweeds, such replacements can lead to substantial reductions in associated biodiversity (Cheminée et al., 2017; Smale & Wernberg, 2013) and alterations to key functions such as net primary productivity (Copertino, Connell, & Cheshire, 2005). Similarly, the introduction of nonnative seaweeds with traits differing from those of kelps modified the trophic dynamics and the circulation of organic matter within recipient marine ecosystems (Dijkstra et al., 2017; Pedersen et al., 2005). Such shifts in the structure and functioning of marine forests have major implications for human societies. For instance, the climate-driven loss of kelp forests from the temperate coasts of Japan culminated in a dramatic decline in kelp-associated abalones and, ultimately, the crash of one of the most important fisheries in the region (Kiyomoto et al., 2013; Serisawa, Imoto, Ishikawa, & Ohno, 2004).

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

Climate change has resulted in an upward and poleward migration of warm-affinity species, which often displace and replace cold-affinity ones (Beck et al., 2011; Peñuelas & Boada, 2003; Warren II et al., 2016). *Laminaria hyperborea* forests are currently the dominant vegetation type along much of the NE Atlantic coastline, with an estimated spatial extent of *c.* 18,000 km^2 (Pessarrodona, Moore, Sayer, & Smale, 2018). As a consequence of ocean warming, this species is predicted to lose between 8.41% and 39.44% of its entire suitable habitat by the end of the century, as moderate expansions at its northern poleward range edge will not compensate for extensive losses further south (Assis et al., 2016). Our findings suggest that the predicted expansion (Franco et al., 2017) of a warm-temperate congener into habitat formerly dominated by *L. hyperborea* will likely result in noticeable shifts in the magnitude and flow of organic matter in NE Atlantic kelp forest ecosystems and interconnected nearshore habitats. Even so, these novel forest communities could potentially preserve some of the key ecosystem functions and services delivered by current kelp-dominated habitats. Our work demonstrates that, like species invasions (Mascaro, Hughes, & Schnitzer, 2012), climate-driven shifts in species composition can maintain or even enhance ecosystem processes to some extent, and suggests that the impact of species replacements will depend, to some degree, on the similarity in functional traits between climate change "winners" and "losers". Overall, our findings point to the need to consider functional traits over species identity when examining the wider impacts of human-mediated shifts in species composition on ecosystem processes, functions, and services.

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AUTHORS' CONTRIBUTIONS

All authors contributed to the development of ideas, interpretation of results, and writing of the manuscript. A.P. led fieldwork, sample collection and processing, and data analysis. A.F. orchestrated the feeding preference assays and provided valuable advice. D.A.S. originally conceived the study and cowrote the first draft of the manuscript with A.P.

DATA ACCESSIBILITY

Data are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.1d9p080 (Pessarrodona, Foggo, & Smale, 2018).

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