Seaweed functional diversity revisited: Confronting traditional groups with quantitative traits

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Abstract
1. Macroalgal (seaweed) beds and forests fuel coastal ecosystems and are rapidly reorganizing under global change, but quantifying their functional structure still relies on binning species into coarse groups on the assumption that they adequately capture relevant underlying traits.

2. To interrogate this ‘group gambit’, we measured 12 traits relating to competitive dominance and resource economics across 95 macroalgal species collected from the UK and widespread on North-East Atlantic rocky shores. We assessed the amount of trait variation explained by commonly used traditional groups—(a) two schemes based on gross morphology and anatomy and (b) two categorizations of vertical space use—and examined species reclassification into post hoc, so-called emergent groups arising from the functional trait dataset. We then offer an alternative, emergent grouping scheme of macroalgal functional diversity.

3. (a) Morphology and anatomy-based groups explained slightly more than a third of multivariate trait expression with considerable group overlap (i.e. low precision) and extensive mismatch with underlying trait expression (i.e. low accuracy). (b) Categorizations of vertical space use accounted for about a quarter of multivariate trait expression with considerable group overlap. Nonetheless, turf species tended to display attributes of opportunistic forms. (c) A nine-group emergent scheme provided a highly explanatory and parsimonious alternative to traditional functional groupings.

4. Synthesis. Our analysis using a comprehensive dataset of directly measured functional traits revealed a general mismatch between traditional groups and underlying traits, highlighting the deficiencies of the group gambit in macroalgae. While existing grouping schemes may allow first order approximations, they risk considerable loss of information at the trait and, potentially, ecosystem levels. Instead, we call for further development of a trait-based approach to macroalgal functional ecology to capture unfolding community and ecosystem changes with greater accuracy and generality.

KEYWORDS
canopy, emergent groups, functional diversity, functional traits, Littler and Littler, seaweed, Steneck and Dethier, turfs
Macroalgae (seaweed) form extensive and productive beds in the coastal environment world-wide (Hurd, Harrison, Bischof, & Lobban, 2014). These phylogenetically and functionally diverse species fuel coastal ecosystems and provide a range of ecosystem services including food and natural products (Griffiths, Harrison, Smit, & Maharaj, 2016; McLachlan, 1985), habitat for commercially important fish (Miranda, Lopez-Alonso, & García-Vaquero, 2017) and blue carbon sequestration (Chung, Beardall, Mehta, Sahoo, & Stojkovic, 2011). Yet under accelerating anthropogenic forcing, macroalgal beds are experiencing major changes in community composition as, for instance, kelp retreat towards the poles while warmer water and non-native species expand (Harley et al., 2012; Pessarrodona, Foggo, & Smale, 2019). Such community restructuring—and its ecosystem ramifications—is mediated by species’ functional traits (Lavorel & Garnier, 2002; Suding et al., 2008; Trugman et al., 2019).

Traits hold the promise of more predictive ecology that goes beyond case studies of species or taxonomic groups (McGill, Enquist, Weiher, & Westoby, 2006). Functional traits are morphological, physiological or phenological characteristics of individuals that influence their response to the environment and/or effect on ecosystem properties and/or services (Díaz et al., 2013). Functional traits reflect adaptive strategies and underlying physiological trade-offs. In vascular plants, for example, functional trait variation largely reflects competitive dominance (plant size) and the leaf economics spectrum, which emerges from physiological trade-offs between structural integrity and growth potential (Díaz et al., 2016). As an alternative to direct use of functional trait values, so-called ‘emergent’ groups have been built through post hoc grouping of functional trait data on the premise that they represent trait variability more closely than traditional grouping approaches (Lavorel, McIntyre, Landsberg, & Forbes, 1997). In turn, functional traits or emergent groups explain species’ contributions to ecosystem functions and services. For instance, plant-specific leaf area and leaf nitrogen content have been linked to primary productivity and decomposition (Reich, 2014; Shipley, Lechowicz, Wright, & Reich, 2006). Terrestrial vascular plants have had an inordinate influence on our understanding of functional ecology of autotrophic organisms, but efforts are underway to include a variety of primary producers (de los Santos et al., 2016; Elger & Willby, 2003; Roos et al., 2019).

However, ecologists studying macroalgal beds and forests rarely directly measure functional traits and instead typically assign species to long-established form-based groups. Littler and Littler (1980) first proposed the ‘functional-form model’, categorizing species into morpho-functional groups based on gross morphology and anatomical features. Over a decade later, Steneck and Dethier (1994) proposed a less subjective grouping scheme based on branching pattern, anatomy and degree of cortication. Macroalgal ecologists have also employed broad categorizations of vertical space use, such as the binary canopy versus turf scheme, to infer ecosystem consequences of changing assemblage structure, particularly in light of the global rise of turfs over canopy-forming macroalgae (Feehan, Grace, & Narvaez, 2019; Filbee-Dexter & Wernberg, 2018). Traditional grouping methods remain highly influential; for instance, Steneck and Dethier’s paper has been cited over 1,000 times, with 60 citations in 2018 alone (Google Scholar, accessed October 2019).

Using functional groups is more practical and less time-consuming than carrying out direct trait measurements, but grouping carries implicit assumptions. Grouping approaches overlook within-group variability (Petchey & Gaston, 2006), can lead to subjective species allocation (Chapin, Bret-Harte, Hobbie, & Zhong, 1996; Diaz & Cabido, 2001; Phillips, Kendrick, & Lavery, 1997), and disregard relative influences of specific traits and intraspecific variability (Hanisak, Littler, & Littler, 1988; Padilla & Allen, 2000; Violle et al., 2012). Perhaps most importantly from the ecosystem perspective, it is assumed that macroalgal groups capture relevant suites of functional traits and, in turn, ecological processes. For instance, turf and sheet-like species are expected to possess a high relative surface area, allowing fast nutrient acquisition and high productivity (Littler & Littler, 1980; Steneck & Dethier, 1994) while canopy-forming species are expected to display high structural integrity and complexity, thereby sustaining rich epibionts (Filbee-Dexter & Wernberg, 2018; Teagle, Hawkins, Moore, & Smale, 2017). Unlike among plant functional types (Thomas et al., 2019), the assumption that traditional macroalgal functional grouping schemes capture underlying interspecific trait variation remains untested. We call this ‘the group gambit’ (following the phylogenetic hypothesis in Mazel et al., 2018).

Here we provide the first comprehensive test of the group gambit in macroalgae. Using direct measurements of traits related to two major aspects of ecological variation, competitive dominance and resource economics, we test the assumption that traditional grouping approaches accurately capture underlying trait expression across four commonly used schemes: the form- (i.e. morphology- and anatomy-) based grouping approaches of Littler and Littler (a) and Steneck and Dethier (b), as well as two categorizations of macroalgal vertical space use (i.e. stature), the binary canopy versus turf (c) and a three-level scheme adapted from Arenas, Sánchez, Hawkins, and Jenkins (2006; d). To do so, we quantify the extent of trait variation explained by each traditional grouping scheme and assess the accuracy of traditional groups by examining post hoc group reworking (i.e. species recategorization from traditional to emergent groupings).

A strong correspondence between groups and the underlying functional traits would support their continued application and bolster ecological interpretation. However, substantial mismatch between groups and traits—as well as recategorization of species into emergent groups—would indicate a loss of information and underline the potential gains offered by direct trait measurements. Our study reveals the limitations of traditional grouping schemes and provides screened trait values as well as an alternative nine-group emergent scheme as a platform for further development of trait-based macroalgal ecology.
2 | MATERIALS AND METHODS

2.1 | Sampling

We measured 11 continuous functional traits and one categorical functional trait (Table 1) at the individual level across 95 erect intertidal macroalgal species, which spanned a great variety of form and function and hence, traditional functional groups (Table S1). Samples were collected from 12 rocky shores in the UK ranging from very sheltered to very exposed (Table S2): six sites in South Wales, four sites in Orkney (Scotland) and two sites in Cornwall (England). The collected species are commonly found on North-East Atlantic rocky shores (Ar Gall et al., 2016; Araújo, Sousa-Pinto, Bárbara, & Quintino, 2006; Martínez, Viejo, Carreño, & Aranda, 2012; Martins, Hawkins, Thompson, & Jenkins, 2007), and include species restricted to the region (~25% of species), more broadly distributed across multiple temperate regions (~35%), as well as cosmopolitan and non-native species (~40%). Sampling took place from May to September 2013 and 2015–2018 (Table S3). We collected an average of six replicates per species, ranging from 1 to 45 (mode and median = 6, SD = 7.55; Table S3). Such a large difference in replication was due to the rarity of some species and to our efforts in sampling abundant species across several sites to better capture natural variability. Replicates were sampled more than 2 m apart. Whenever possible, a replicate was made up of a single individual. However, when individuals were too small for the trait measurements, a sufficient quantity was collected for each replicate by pooling several individuals or tufts (Table S3). Whenever distinguishing between individuals was not possible (e.g. for turfs), the samples were collected by isolating tufts (Table S3). Replicates within species were sampled from a variety of microhabitats to better reflect natural variability, but belonged to the same life stage (e.g. the Trailliella intricata stage of Bonnemaisonia hamifera). Samples were kept in seawater in a cooler until brought back to the laboratory. They were then either screened fresh or frozen at −18°C until processed.

2.2 | Trait screening

The functional traits measured are hypothesized to capture two fundamental aspects of primary producer variability, (a) the economics spectrum and (b) competitive dominance. We consider multiple indicators (or ‘functional markers’ sensu Garnier et al., 2004) to provide a more integrated estimation of ecological strategy and

| Functional trait                          | Equation          | Unit        | Part       | Physiological and ecological significance                                                                 |
|-------------------------------------------|-------------------|-------------|------------|---------------------------------------------------------------------------------------------------------|
| Thallus dry matter content (TDMC)         | Dry mass/fresh    | None        | Whole      | Structural versus photosynthetic tissues; structural integrity (SLOW)
|                                           | mass              |             |            |                                                                                                         |
| Thickness                                 | NA                | mm          | Fronds    | Structural integrity (SLOW)                                                                                                    |
| Maximum length                            | NA                | cm          | Whole      | Competition for light (COMPETITIVE)                                                                                     |
| Aspect ratio                              | Maximum           | None        | Whole      | Competition for light versus substrate use, that is, vertical space use versus horizontal (?)^1,6        |
|                                           | length/width      |             |            |                                                                                                         |
| Specific thallus area (STA)               | SA/dry mass       | mm^2/g      | Fronds    | Photosynthetic versus structural tissues; light capture (FAST)                                                        |
| Surface area to volume (SA:V)             | SA/volume         | mm^2/ml     | Fronds    | Nutrient-absorbing versus structural tissues; nutrient capture (FAST)                                           |
| Surface area to perimeter (SA:P)          | SA/P              | None        | Whole      | Retention of resources (SLOW); structural integrity but resistance to water movement, encouraging breakage (?)^11 |
| Branching order                           | NA                | None        | Whole      | Retention of resources (SLOW); desiccation and herbivory resistance (COMPETITIVE); structural fragility but less resistance to water movement, preventing breakage (?)^9,30 |
| Pneumatocysts (yes/no)                    | NA                | None        | Whole      | Light capture (COMPETITIVE)                                                                                      |
| Carbon (C) content                        | NA                | %           | Whole      | Structural integrity (SLOW)                                                                                      |
| Nitrogen (N) content                      | NA                | %           | Whole      | Light capture (FAST)                                                                                             |
| Carbon to nitrogen (C:N)                  | C/N               | None        | Whole      | Structural versus photosynthetic tissues (SLOW)                                                                |
function. Here we briefly summarize the ecological significance of the traits with regard to photosynthesis, structural integrity, space use and complexity (Table 1; Table S4). The suite of economics-related traits indicates the relative investment in resource acquisition versus resistance to (a)biotic stress and therefore resource conservation, tying in with the r- (‘fast return’) to K- (‘slow-return’) selection continuum (Pianka, 1970). Slow-return primary producers tend to display long life spans, low maximum photosynthesis and productivity, reduced palatability and slow decomposition (Littler & Littler, 1980; Smart et al., 2017; Wright et al., 2004). Traits a–g relate to photosynthesis and/or structural integrity, and hence, position on the economics spectrum: (a) Thallus Dry Matter Content (TDMC) is the ratio between dry and wet mass and represents the proportion of structural compounds and water-filled—and therefore mainly photosynthetically active—tissues (Elger & Willby, 2003; Littler & Littler, 1981; Schonbeck & Norton, 1979). (b) Thickness also increases with the amount of structural tissue, providing resistance to physical stress and herbivore grazing (Cappelatti, Mauffrey, & Claman, & Martone, 2015). We measured both traits at the whole individual level to capture the complexity of the whole thallus, since all parts of the thallus, from holdfast to fronds, are important habitats for epibiota and nekton (Teagle et al., 2017).

Large or structurally complex individuals were subsampled, ensuring that all parts of the thallus were included at representative proportions (Table S3). We measured the surface area and perimeter of partly microscopic species on subsamples under the microscope and proportionally scaled them up to the whole sample (Table S3). The samples were cleaned of epibiota in seawater and rinsed in deionized water for elemental screening. To obtain TDMC, we recorded sample wet and oven-dried mass (g; Ohaus Scout Pro SP402, SPU602 and Pioneer Analytical PA114). Thickness (mm) was averaged from 10 measurements taken haphazardly along the fronds (Digital Micrometers Ltd, DTG03 0.005, DML3032 0.001 mm), avoiding, when applicable, the midrib. Individuals were scanned (Epson Perfection V600, V39) or displayed on a lightbox (MiniSun A1) and photographed directly (Pentax K3 digital camera, SMC DA L 18–55 mm) or via an imaging microscope (Leica S8AP0, affixed with GT Vision GXCAM-H3). We measured frond (when differentiated) or whole-individual surface area (mm²) and whole-individual perimeter (mm) using the software ImageJ (Schneider, Rasband, & Eliceiri, 2012), and calculated SA:V (mm²/ml), STA (mm²/g) and SA:P (mm). Volume (ml) was measured by water displacement. Maximum length (cm) was measured from the base of the holdfast to the tip of the longest blade. Aspect ratio was obtained by dividing maximum length by maximum width (i.e. largest width of a naturally spread out sample). Branching order was measured as the average number of divisions of the main axes of a thallus from its holdfast to the tip of the blades out of five measurements taken haphazardly within the sample. To obtain C and N content and C:N, ground samples were weighed with a microbalance (Sartorius CPA2P, 0.000001 g) and run through an elemental analyser (PDZ Europa 2020 isotope ratio mass spectrometer interfaced with an ANCA GSL elemental analyser and calibrated with acenaniile).

2.3 | Categorization of species into functional groups

We allocated species to the groups defined by Littler and Littler as well as Steneck and Dethier based on a review of the literature (Table S1). The species we screened belonged to five traditional groups: ‘articulate calcareous’, ‘coarsely branched’, ‘filamentous’, ‘sheet’ and ‘thick leathery’ for Littler and Littler’s functional-form model, and ‘filamentous (S)’, ‘foliose’, ‘corticated’, ‘leathery’ and ‘articulated calcareous’, as defined by Steneck and Dethier (1994), in increasing order of cortication. Although both schemes contain groups with similar or identical names, they were originally defined using different approaches and are not assumed a priori to be analogous. We also tested Steneck and Dethier’s detailed scheme, which includes two subgroups (Supporting Information, Section 1). We used two common categorizations of vertical space use as follows: the binary canopy versus turf scheme and a three-level canopy/
subcanopy/turf scheme adapted from Arenas et al. (2006). Turfs were considered macroalgae with little to no three-dimensional structure (compared with kelp and other canopy-forming macroalgae) that form a dense layer of fine filaments, branches or plumes on the substratum (Filbee-Dexter & Wernberg, 2018). This broad definition of turf macroalgae allowed categorization of all species within our study. Vertical structure in the water column is somewhat community-dependent, so we categorized species into the three-level scheme based on what we judged was the most common scenario on the rocky shores screened.

### 2.4 Data analysis

We performed all analyses in R 3.5.3 (R Core Team, 2019) and plotted graphical results using ggplot2 (Wickham, 2016) and ggpubr (Kassambara, 2019). Prior to running analyses on species-level traits, a linear model confirmed that traits varied strongly at the species level; across continuous traits, species identity explained 82.3 ± 7.6% (M ± SD) of individual-level variance. Species trait averages were transformed to bring their distribution as close to normality as possible and to reduce differences in scale across traits (Table S4). To examine the distribution of individual traits among traditional groups, smooth density curves for each of the 11 continuous functional traits studied were drawn. To assess whether groups significantly differed from each other, we ran pairwise Wilcoxon rank sum tests on every group pair.

We imputed the 4% of average trait values that were missing from the dataset (function 'mice' in eponymous R package; van Buuren & Groothuis-Oudshoorn, 2011) to then reduce the dimensionality of the data using a Principal Coordinate Analysis (PCoA; function 'cmdscale' in built-in R package stats). We favoured a PCoA over a Principal Component Analysis because it allowed us to include presence of pneumatocyst. The PCoA was run on a weighted Gower matrix (function 'daisy' in cluster; Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2019), with equal weighting to traits associated with photosynthesis, structural integrity, space use and complexity (Table S4). To assess the strength of association between the principal coordinates and each trait, we ran linear regressions between the scores of the first two PCoA axes and the 12 traits studied.

In order to assess how precisely traditional macroalgal grouping schemes capture underlying trait variation, we tested how much trait variance they explained (PERMANOVAS; ‘adonis’ in vegan; Oksanen et al., 2019) and their parsimony (Akaike's information criterion, AIC, manually calculated). We assessed the accuracy of the groups established by Littler and Littler’s and Steneck and Dethier’s (both five-group) schemes by comparing their species composition to five-group post hoc groupings emerging from the trait dataset. Extensive species reclassification—that is, group reworking—would suggest substantial mismatch between traditional groups and underlying trait variation and hence, rather low accuracy of traditional groups. We created emergent groups from the weighted Gower matrix using k-medoids clustering (k-medoids), a top-down clustering approach whereby species are assigned to a chosen number of groups based on multivariate distance from group medoids, making it rather robust to noise and outliers (Reynolds, Richards, de la Iglesia, & Rayward-Smith, 2006; using ‘pam’ in package cluster; Maechler et al., 2019).

Clustering to generate emergent groups also provided a tool for generating a more functionally informative alternative to traditional functional groupings. To allow the data to inform not only the assignment of species to groups but also the number of groups, we used k-medoids (as described above) while allowing an increasing number of groups (from five upwards), searching for an emergent grouping scheme that maximized overall explanatory power and parsimony while maintaining statistically significant differences (p < 0.05) between all pairs of groups. Finally, to evaluate the robustness of the resulting grouping scheme to intraspecific trait variability, we assessed how randomly correcting the trait dataset with highest and lowest SE influenced the explanatory power of the emergent grouping scheme. To do so, we computed the explanatory power ($R^2$, based on PERMANOVA) of the emergent grouping scheme across 999 iterations while correcting randomly selected thirds of species-level trait means with +1 SE, −1 SE and no correction.

### 3 RESULTS

#### 3.1 Distributions of individual traits

For both form-based grouping approaches, species-level trait distributions were generally not unimodal and were right-skewed, suggesting that their groups captured underlying trait variation with limited accuracy (Figures 1 and 2). Under both schemes, group overlap was extensive across traits; from a possible 55 cases (11 continuous traits × 5 groups), there were only seven instances where a group was different from all others (pairwise Wilcoxon rank sum test; p < 0.05). None of the form-related groups were significantly different from all others for thickness, aspect ratio, branching order, SA:P and C:N (pairwise Wilcoxon rank sum test; p > 0.05). However, under both schemes, there were differences between roughly half of all possible group pairs (pairwise Wilcoxon rank sum test; p < 0.05), reflecting the position of groups along the continuum of trait variability (Figures 1 and 2). Overall, ‘thick’ leathery’ and ‘articulate(d) calcareous’ were the two most distinct functional groups (Figures 1 and 2).

Both categorizations of macroalgal stature (i.e. vertical structure in the water column) explained significant differences in most of the traits’ distributions (pairwise Wilcoxon rank sum test, p < 0.05; Figure 3, see Figure S1 for the three-level scheme). Specifically, in the canopy versus turf scheme, canopy species had greater thickness, maximum length, aspect ratio and C:N, while turf species had greater SA:V, STA, C and N content values. In the three-level scheme, groups differed in thickness, maximum length, SA:V and
STA (pairwise Wilcoxon rank sum test, \( p < 0.05 \); Figure S1). Canopy species also had lower values than turf for SA:P and N content, and greater values for C:N. Notwithstanding these differences, stature-based groups spanned wide ranges of trait values and, in most cases, displayed a high degree of overlap, suggesting limited precision. The prevalence of significant differences between groups, compared to the two form-based approaches, should be interpreted in light of the higher within-group sample sizes.

### 3.2 Distributions in multivariate trait space

Many of the functional traits were entrained along the first PCoA axis. Species positioned further along that axis had lower maximum length, C:N ratio and thickness and higher SA:V, STA and N content (Figures 4 and 5). Such trait values typically confer faster resource acquisition to the detriment of structural integrity and, in dense assemblages, competitive dominance (Table 1). Meanwhile, the second...
PCoA axis was clearly most strongly associated with branching order and, to a lesser extent, STA (Figures 4 and 5). This suggests that similarly to the first axis, the second captured some aspects of both resource utilization and competitive dominance. Species located further along that axis displayed lower branching order and higher STA and thus, are expected to favour light acquisition to the detriment of resistance to desiccation, herbivory and water movement (Table 1).

The first two principal coordinates accounted for 50% of inertia in the distance matrix, while the third (not shown) accounted for an additional 13%.

Both Littler and Littler’s and Steneck and Dethier’s groups explained about 37% of multivariate species-level trait expression (Figure 5; five-group PERMANOVA, $R^2 = 0.37, p < 0.001$) with a similar level of parsimony (AIC = −367.01 for Littler and Littler’s scheme;
AIC = −366.99 for Steneck and Dethier’s scheme, representing a difference of 0.02) but considerable group overlap in trait space (i.e. rather low precision). Littler and Littler’s and Steneck and Dethier’s groups were located in roughly the same locations of the trait space (Figure 5). Species categorized under ‘(thick) leathery’ displayed a wide array of trait values and were split between those characterized by high SA:P and maximum length on the one hand, and high thickness and C:N on the other (Figures 1, 2, 4 and 5). Calcareous species displayed high C content and branching order, and stood out from the rest of the species. Coarsely branched/corticated species were scattered across most of the trait space. The filamentous groups mainly gathered species with high SA:V and branching order. Finally, the ‘sheet’/‘foliose’ group principally represented species with low C:N and high STA (Figures 1, 2, 4 and 5).

Classifications of vertical space use explained the least multivariate trait expression and were the least parsimonious of all traditional schemes (AIC = −357.94 for canopy vs. turf; AIC = −356.84 for canopy/subcanopy/turf, representing a difference of 9.07 and

FIGURE 3 Distribution of species-level traits among a common binary categorization of vertical space use. Values of the 11 continuous functional traits are transformed species-level means across the 95 macroalgal species screened (Table S4). Groups that are significantly different from all others are marked by asterisks (pairwise Wilcoxon rank sum test; **: p < 0.05, ***: p < 0.01, ****: p < 0.001; lowest common p is shown) [Colour figure can be viewed at wileyonlinelibrary.com]
Proportion of inertia accounted for by each axis is given in 'leathery' and 'articulate calcareous' to 'articulated calcareous'. All of 'sheet' to 'foliose', 'coarsely branched' to 'corticated', 'thick leathery' to corresponded to 'filamentous (S)' in Steneck and Dethier's scheme, between groups—the 'filamentous' group of Littler and Littler's model earlier scheme (Tables S1 and S5). Correspondences were evident species remained grouped together compared to Littler and Littler's objective basis of Steneck and Dethier's scheme, largely the same sets of including emergent groups), the group membership of individual species reclassification across grouping approaches

3.3 Reclassification across grouping approaches

To evaluate how species are classified under different approaches (including emergent groups), the group membership of individual species can be traced across grouping schemes (Figure 6). Despite the less subjective basis of Steneck and Dethier's scheme, largely the same sets of species remained grouped together compared to Littler and Littler's earlier scheme (Tables S1 and S5). Correspondences were evident between groups—the 'filamentous' group of Littler and Littler's model corresponded to 'filamentous (S)' in Steneck and Dethier's scheme, 'sheet' to 'foliose', 'coarsely branched' to 'corticated', 'thick leathery' to 'leathery' and 'articulate calcareous' to 'articulated calcareous'. All of the mismatches in species allocation between the two schemes were due to Littler and Littler's groups 'coarsely branched' and 'thick leathery' being reclassified by Steneck and Dethier's approach (Figure 6). The addition of an extra category to the canopy versus turf scheme, to form canopy/subcanopy/turf, led to the reclassification of larger turf species into the subcanopy group (11% of all species reclassified; Tables S1 and S5). These reclassified species were primarily coarsely branched under Littler and Littler's scheme.

To assess whether traditional grouping schemes accurately capture underlying trait expression, we examined species reclassification—that is, group reworking—from five-group traditional to emergent groupings. Most species were vastly reworked in their group allocation, with only a few tight nuclei of species left unchanged. Notably, (thick) leathery species became split into two different groups (Figures 5 and 6; Tables S1 and S5). The first group, emergent group 2, corresponded to species typically displaying high maximum length and SA:P. The second group, emergent group 3, mostly represented species with high C:N and thickness. Most species belonging to the much spread out 'coarsely branched' and the corresponding 'corticated' groups were re-allocated across all emergent groups, leaving a tight nucleus of species unchanged (emergent group 1; Figures 5 and 6; Tables S1 and S5). Filamentous species tended to be grouped together regardless of the grouping scheme (emergent group 4), corresponding mainly to high-SA:V species. The low degree of overlap between traditional and trait-based, emergent functional groups reveals substantial mismatch between traditional groups and macroalgal trait values and underlines the low functional accuracy of traditional schemes. This suggests that current grouping approaches are far from optimal solutions to capture species’ dispersion in trait space, while trait-based, post hoc emergent groupings have the potential to better capture macroalgal functional expression.

3.4 A proposed nine-group emergent scheme

In order to identify an alternative, trait-based grouping scheme emerging from our dataset, we ran k-medoids with an increasing number of groups. While we observed a monotonic increase in the extent of trait variation explained as well as parsimony, a nine-group emergent scheme maximized explanatory power and parsimony while maintaining significant differences between all groups. This scheme explained about two-thirds of multivariate trait expression (PERMANOVA, $R^2 = 0.69$, $p < 0.001$), and all emergent groups were significantly different from each other (pairwise PERMANOVA, $p < 0.05$; Table S6). The scheme’s explanatory power remained substantial even when we conducted resampling to allow for intraspecific variability in species’ traits [PERMANOVA, $R^2 = 0.57 \pm 0.02$ (M \(\pm\) SD)]. The species composition of the groups emerging from our trait data is largely uncoupled from macroalgal general appearance (i.e. gross morphology, anatomy, and stature; Figure 7; Table S1). Emergent groups 2 and 3 (thick leathery), 4 (coarsely branched) and 6 (articulate calcareous) gather species belonging to a single morpho-functional group; still, all traditional groups but articulate(d) calcareous were broken down into more fine-tuned functional units [e.g. (thick) leathery species are

![FIGURE 4 Associations between functional traits and principal coordinate axes. Associations were assessed by a series of linear regressions based on the sample size of 95 species. The strength and direction of trait–axis association are indicated, respectively, by the coefficients of determination ($R^2$) and colour of the bars. Proportion of inertia accounted for by each axis is given in parenthesis [Colour figure can be viewed at wileyonlinelibrary.com]](image-url)
**FIGURE 5** Distribution of functional grouping schemes in macroalgal trait space. Group distribution in macroalgal functional trait space as yielded by the first two axes of a Principal Coordinate Analysis (PCoA) is given for: (a) Littler and Littler’s ‘functional-form’ model (ordered alphabetically), (b) Steneck and Dethier’s scheme (ordered by degree of cortication), (c) canopy versus turf, (d) canopy/subcanopy/turf, and (e) emergent groups yielded by post hoc grouping of the species using divisive k-medoids clustering. Confidence ellipses (50%) are represented, assuming a multivariate normal distribution. Arrows indicate most strongly related functional traits to each PCoA axis (trait-axis relationships are given in Figure 4) [Colour figure can be viewed at wileyonlinelibrary.com]

**FIGURE 6** Species reclassification across grouping schemes. Species allocation to groups is given for (a) Littler and Littler’s functional-form model (species are ordered alphabetically within group), (b) Steneck and Dethier’s scheme, (c) the binary canopy versus turf and (d) the three-level canopy/subcanopy/turf categorizations of vertical space use, and (e) emergent groups yielded by post hoc grouping of the species using divisive k-medoids clustering. Within each grouping scheme, stacked horizontal bars correspond to individual species. The order of individual species remains consistent across columns and is initially ordered according to Littler and Littler’s groups. Tracking individual species from left to right shows reclassification across grouping schemes. Exact species attribution to the groups of all grouping approaches can be found in Table S1 [Colour figure can be viewed at wileyonlinelibrary.com]
spread over groups 1, 2, 3 and 5]. Group composition appeared to be partly driven by taxonomic identity and underlying phylogenetic relationships: group 1 gathered all—but not exclusively—kelps (i.e. orders Laminariales and Tilopteridales), group 4 consisted entirely of the two unusually thick, low-TDMC Codium fragile subspecies, and group 6 gathered all calcified species. Presence of pneumatocysts emerged as an important predictor of group composition, as all pneumatocyst-bearing species were allocated to group 3. This nine-group emergent scheme provides a more functionally informative alternative compared to traditional seaweed groups.

4 | DISCUSSION

As rapid global change dramatically alters community composition, it is imperative that functional schemes—across all major producer groups—are fit-for-purpose. We assessed whether common categorizations of form and stature explained trait differences across macroalgae collected from rocky shores with, to our knowledge, the largest set of macroalgal traits assembled to date. Despite their convenience and prevalence in macroalgal ecology, the traditional grouping schemes all left substantial amounts of interspecific trait variation unexplained. These results highlight the need for a re-evaluation of macroalgal grouping approaches and an increased focus on underlying functional trait variation.

4.1 | Traditional groups are incomplete representatives of underlying physiological and ecological variation

Groups established by Littler and Littler (1980) and Steneck and Dethier (1994) were built on the premise that morphology and anatomy capture interspecific differences in physiology and function.
4.2 | Common categorizations of vertical space use provide coarse assessments of the ecological impacts of fast-paced changes in macroalgal assemblages

Categorizations of vertical space use are widely used because of their convenience in accounting for changes in macroalgal community composition (Filbee-Dexter & Wernberg, 2018). These were the least parsimonious of traditional approaches that accounted for the least multivariate trait expression, and showed a high degree of overlap for individual traits. Accordingly, species turnover within these groups—besides canopy to turf transitions—will have different ecological consequences depending on species traits. Recently focused comparative work on two kelp (canopy) species supports this point—along the southern coast of Britain under ocean warming, replacement of Laminaria hyperborea with L. ochroleuca results in ecologically significant changes in supported biodiversity and ecosystem processes (Pessarrodona et al., 2019; Smale, Wernberg, Yunnie, & Vance, 2015). Moreover, various definitions of turfs have been employed, resulting in a lack of generality across ecosystems (Connell, Foster, & Airoldi, 2014). Our findings imply that coarse categorizations of macroalgal stature will hinder explanatory power and the generality of global synthesis when assessing the ecological impacts of environment-mediated changes in macroalgal assemblages.

Nevertheless, categorizations of macroalgal stature can remain insightful when applied to ecosystem functioning. Perhaps aided by greater within-group sample sizes, both categorizations of vertical space use explained significant differences for most individual functional traits. The trait differences entailed in canopy-to-turf shifts, such as reduced C:N and higher STA, correspond to contrasts between ‘slower’, longer-lived species, and ‘faster’ opportunistic forms (Airoldi, 1998; Littler & Littler, 1980, 1981). These differences may partially explain the global rise of turfs with altered environmental conditions (Feehan et al., 2019; Filbee-Dexter & Wernberg, 2018) as well as the consequences of canopy-to-turf shifts for carbon flow and habitat provisioning (Copertino, Connell, & Cheshire, 2005; Filbee-Dexter & Wernberg, 2018). Therefore, despite risking substantial loss of information and lack of generality, broad categorizations of macroalgal stature may offer quick first-order assessments of the ecological impacts of fast-paced changes in macroalgal assemblages.

4.3 | Functional traits and emergent groups offer more ecologically informative alternatives to traditional macroalgal groups

Although traditional functional groups can allow practical and rapid assessments of macroalgal assemblages, functional trait values—as the closest proxies of primary producer functional variation and ecological roles (Diaz et al., 2016; Vile, Shipley, & Garnier, 2006)—provide a more ecologically informative alternative. Our study
provides a fresh perspective on the functional differentiation and diversity of seaweed species, and the accompanying trait data provides a platform for researchers to more accurately capture functional identity and diversity (Boye et al., 2019; Villéger, Mason, & Mouillot, 2008) and therefore more strongly connect changes in community structure to ecosystem processes (Cadotte, 2017; Gagic et al., 2015). As an alternative to direct use of trait values, we also provide a nine-group emergent scheme, potentially simplifying field and analytical methods, while still allowing meaningful measurements of functional diversity (Chapin et al., 1996; Chen et al., 2017; Díaz & Cabido, 2001). Although intraspecific variation was relatively small in our dataset—and in a previous study where large brown seaweeds were sampled across sites of contrasting wave exposure (Cappelatti et al., 2019)—care should be taken when applying the trait data at sites with unusual conditions (e.g. very sheltered sea loughs) or in regions distant from the UK (e.g. other regions of the NE Atlantic). There are additional considerations before applying emergent groups; they make the simplifying assumption that species are equivalent within groups, can force outlying species into groups and can be somewhat sensitive to the clustering method. Therefore, while emergent groups have the potential to more accurately capture macroalgal functional diversity compared to traditional groups, we recommend the direct use of functional traits wherever possible.

Our study on UK rocky shores highlights the continuous nature of macroalgal trait expression and underlines the usefulness of functional traits as direct, continuous measures of macroalgal functional variation. Yet, more broadly unleashing the potential of trait-based approaches to macroalgal ecology will require trait data covering other regions and a much greater proportion of the world’s seaweed taxa. This could be achieved by geographically distributed research groups undertaking trait-screening using standardized methods and curating data within open-access databases. Because trait screening demands substantial resources, a key challenge is to identify a manageable set of ideally orthogonal, ecologically relevant traits before embarking on globally coordinated efforts. Here maximum length, branching order and surface area to volume ratio emerge as contenders because, collectively, these traits are highly associated with orthogonal axes of variation and relate to both competitive dominance and resource economics. Prioritizing abundant or otherwise functionally important (e.g. habitat-forming) species would further reduce the burden of trait screening.

5 | CONCLUSIONS

Our analysis using a comprehensive dataset of directly measured functional traits revealed substantial limitations to the group gambit of macroalgae. Despite accounting for up to more than a third of trait expression, traditional groups appeared to inadequately capture macroalgal functional variation; we found substantial group overlap (i.e. low precision) and mismatch between traditional groups and underlying traits values (i.e. low accuracy). Therefore, gross morphology and anatomy as well as vertical position in the community are incomplete representatives of macroalgal functional identity. Conversely, post hoc emergent grouping schemes such as that proposed herein have the potential to more accurately capture macroalgal trait expression than traditional groups while retaining the convenience of species grouping. Ultimately, functional traits are the closest proxies of macroalgal functional variation and hence, should provide the strongest assessments of macroalgal roles under global change. Studies like ours, which emphasize the potential of direct use of functional traits in capturing macroalgal form and function, can act as an incentive to build large, coordinated datasets spanning all main aspects of macroalgal eco-physiology.

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AUTHORS’ CONTRIBUTIONS

A.R.L.M., L.C. and J.N.G. conceived the ideas and designed methodology; A.R.L.M. and L.C. collected the data and created the figures and tables; A.R.L.M. and L.C. analysed the data with the help of J.N.G.; A.R.L.M. and J.N.G. led the writing of the manuscript with input from L.C. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

We have archived our data on Dryad Digital Repository: https://doi.org/10.5061/dryad.nvx0k6dpn (Mauffrey, Cappelatti, & Griffin, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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