

An empirical test of 'universal' biomass scaling relationships in kelps: evidence of convergence with seed plants

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Summary

- Biomass allocation patterns have received substantial consideration, leading to the recognition of several 'universal' interspecific trends. Despite efforts to understand biomass partitioning among embryophytes, few studies have examined macroalgae that evolved independently, yet function ecologically in much the same ways as plants.
- Kelps allocate photosynthate among three organs (the blade(s), stipe(s) and holdfast) that are superficially convergent with organs of land plants, providing a unique opportunity to test the limits of 'universal' trends. In this study, we used an allometric approach to quantify interspecific biomass partitioning patterns in kelps and assess whether embryophyte-based predictions of biomass scaling can be applied to marine macrophytes that lack root-to-leaf hydraulic transport.
- Photosynthetic area and dry mass were found to scale to approximately the $\frac{3}{4}$ power and kelp biomass allocation patterns were shown to match closely to empirical measures of allometric scaling among woody plants. Larger kelp species were found to have increased relative stipe and holdfast mass than smaller species, highlighting important consequences of size for marine macroalgae.
- Our study provides insights into the evolution of size in the largest marine macrophytes and corroborates previous work suggesting that the morphology of divergent lineages of photoautotrophs may reflect similar selective pressures.

Introduction

The consequences of size for living organisms have long been a focus of studies in evolutionary biology (e.g. Huxley, 1932; Kleiber, 1932; Gould, 1966; Peters, 1983; LaBarbera, 1989; Brown *et al.*, 1993; Hanken & Wake, 1993). While many aspects of size evolution are highly variable and lineage specific (Huxley, 1932; Gould, 1966), several common patterns have emerged that may reflect convergent responses of divergent lineages to increased size (West *et al.*, 1997, 1999a,b). Perhaps the most influential and widespread consequence of size is the relationship between surface area and volume; while most organisms must inhabit three-dimensional space within their environment, they must also interact with it across a two-dimensional surface area. This 'curse of dimensionality' generally causes larger organisms to have decreased surface area to volume (SA : V) ratios relative to smaller organisms, resulting in unavoidable consequences that may drive many widespread patterns in both physiological and morphological evolution (Kleiber, 1932; Niklas, 1994, 2004; West *et al.*, 1997, 1999a,b).

In biological systems, SA : V scaling rarely matches that of traditional dimensional analysis, which predicts a scaling exponent of $\frac{2}{3}$ (Niklas, 1994, 2004; West *et al.*, 1999b). Instead,

organisms are intricate and are believed to evolve body plans that maximize exchange area with the environment, while simultaneously maintaining structural integrity and internal transport efficiency (Niklas, 1994; West *et al.*, 1997, 1999a,b). Presumably because the consequences of SA : V scaling exist for all three-dimensional organisms regardless of phyletic affiliations, several 'universal' $\frac{1}{4}$ -power scaling relationships have surfaced that may represent evolutionary 'compromises' between scaling as a plane to maximize surface area and scaling as a Euclidean solid to minimize transport distance (West *et al.*, 1997, 1999a). Although exceptions do exist (Price *et al.*, 2007), these are common scaling relationships, within a broad range of possible geometries (Price & Enquist, 2006; Price *et al.*, 2007), that are supported by large-scale data sets and can be predicted mathematically using models of fractal-like branching (West *et al.*, 1997, 1999a; Price & Enquist, 2006; Enquist *et al.*, 2007; Savage *et al.*, 2010).

Predicting 'universal' scaling

The model of West *et al.* (1997, 1999a,b; hereafter the West, Brown & Enquist (WBE) model) and extensions thereof (e.g. Price & Enquist, 2006; Price *et al.*, 2007; Savage *et al.*, 2010) rationalize some of these universal exponents and predict that the

effective exchange area (e.g. photosynthetic surface area) should scale to the $3/4$ power of volume (and therefore total mass (M_T)) across species (West *et al.*, 1997, 1999a,b). Indeed, the $3/4$ exponent has been commonly recovered in biological studies related to dimensional scaling (see Niklas & Enquist, 2001; Niklas, 2004; Savage *et al.*, 2004) and is believed to be attributed to the diverse, volume-filling branching patterns of plant and animal resource distribution networks (West *et al.*, 1997, 1999a,b). For example, across a large data set that spans several orders of magnitude of embryophytes, net photosynthetic production (NPP) has been shown to scale with the $3/4$ power of total mass (Niklas & Enquist, 2001; Niklas, 2004; Enquist *et al.*, 2007). This potential consequence of SA:V scaling has received substantial attention over the past two decades and may have far-reaching implications for the evolution and ecology of photosynthetic organisms, from single cells to entire forest communities (Enquist & Niklas 2001, 2002a; Niklas, 2004, 2006; Savage *et al.*, 2004).

The size dependence of SA:V and the $3/4$ exponent has an apparent influence on the standing organ biomass of plants, whereby increasing size of photosynthetic organs or whole organisms tends to produce 'diminishing returns' (Enquist & Niklas 2001, 2002a; Niklas & Enquist, 2002; Niklas *et al.*, 2007; Koontz *et al.*, 2009). Because plants exhibit a clear division of labor between photosynthetic and nonphotosynthetic organs, and leaf mass is generally proportional to photosynthetic area within a given species (Roderick & Cochrane, 2002), these diminishing returns drive a $3/4$ relationship between leaf biomass and total biomass in both conifers and angiosperms (Niklas & Enquist, 2001; Enquist *et al.*, 2007). Thus, larger plants have more nonphotosynthetic biomass and require increased input (carbon allocation) with disproportionately less gain in photosynthetic surface area (A). As with the predictable relationship between surface area and mass, 'universal' biomass allocation patterns are believed to represent selectively advantageous ways in which standing biomass of leaves, stems and roots should scale across seed plants to balance resource uptake and light interception across two dimensions, while maintaining internal transport and biomechanics in three dimensions.

Although substantial consideration has been given to the ways in which seed plants allocate photosynthate and how this can determine standing organ biomass, virtually no work has focused on photosynthetic area—dry mass scaling or organ biomass scaling in aquatic macrophytes. This is especially true when considering marine macroalgae, which are ecologically similar to embryophytes, yet are phylogenetically divergent and face different biophysical limitations. If we are to understand the limits of 'universal' scaling relationships and the factors driving them, then incorporation of such taxa may be critical.

Organ biomass scaling in seed plants

Refined extensions of WBE are believed to explain patterns of standing biomass partitioning in embryophytes (Enquist & Niklas, 2002a; Niklas & Enquist, 2002) and, specifically, predict that a universal two-phase scaling relationship can approximate interspecific biomass partitioning across the embryophytes

(Niklas & Enquist, 2002; Niklas, 2006). In order to maximize both water delivery and photosynthetic area (such that $A \sim M_T^{3/4}$), across large plants with fractal-like geometries, leaf mass (M_L) should scale to the $3/4$ power of both stem (M_S) and root (M_R) mass ($M_L = \beta_1 M_S^{3/4} = \beta_2 M_R^{3/4}$, where β is the lineage-specific allometric constant of each relationship), while M_R and M_S should scale with approximate linearity ($M_R = \beta_3 M_S$) (Enquist & Niklas, 2002a; Niklas & Enquist, 2002). This scaling relationship is believed to arise as a result of the accumulation of metabolically inactive wood in the body of large plants, while leaves are periodically lost or turned over (Niklas, 2006). By producing large amounts of nonliving tissues, large trees may alleviate potential respiratory 'costs' that would otherwise be associated with size increase and allow for isometric relationships between living photosynthetic and nonphotosynthetic tissues (Sillett *et al.*, 2010, 2015). This growth strategy reduces the 'diminishing returns' associated with increased size and ensures that respiratory metabolism scales with photosynthetic production (such that metabolic rate, B , also scales with $M_T^{3/4}$; Enquist *et al.*, 2007; Mori *et al.*, 2010). In reality, scaling theory tends to underestimate allocation to stems and overestimate allocation to roots of large woody plants, and thus broad-scale interspecific scaling relationships only coarsely fit these predictions (e.g. Niklas & Enquist, 2002; Cheng *et al.*, 2007; Poorter *et al.*, 2012, 2015; Zhang *et al.*, 2015). Nonetheless, analyses of large data sets have consistently yielded large coefficients of determination (R^2), suggesting a substantial degree of invariance across taxa and convergence of distantly related species towards similar biomass partitioning patterns (Enquist & Niklas, 2002a; Niklas & Enquist, 2002).

In contrast to large plants, herbaceous and young plants (up to $c. 10^{-3}$ kg) that lack substantial secondary tissue may partition linearly (i.e. with an allometric exponent of 1) to each of their three organs (Niklas & Enquist, 2002; Poorter *et al.*, 2012). This is acceptable within the framework of WBE, as many herbaceous or young plants possess stems that are generally photosynthetic (Enquist & Niklas, 2002b), have leaves that tend to increase in thickness through development (Sack *et al.*, 2002) and are incompletely volume-filling (Enquist *et al.*, 2007; Koontz *et al.*, 2009). Additionally, gravity is less important for smaller plants that can elongate without increasing stem diameter to the same extent as larger plants (Enquist *et al.*, 2007). Together this allows for departure from the $3/4$ scaling of leaf mass with root mass while possibly maintaining $A \sim M_T^{3/4}$ on average (as in Enquist & Niklas 2001; Sack *et al.*, 2002; Niklas, 2004, 2006). Nonetheless, morphological scaling is generally believed to be less predictable in smaller plants because of the wide diversity of forms that often violate model assumptions upheld by large trees (Price & Enquist, 2006; Enquist *et al.*, 2007; Koontz *et al.*, 2009).

Like young and herbaceous plants, macroalgae are photosynthetic along their entire thalli, lack xylem and heartwood, and are not restricted in height by either gravitational or hydraulic constraints. Together, these characteristics led Niklas (2006) to hypothesize that the only predictions that are applicable to macrophytes are those drawn from the scaling of nonwoody, herbaceous plants (i.e. $M_L \sim M_S \sim M_R \sim M_A$; isometric/linear

scaling of all organs). Although a preliminary investigation provided support for these predictions (Niklas, 2006), results were equivocal because of limited sampling effort.

Testing 'universal' relationships with kelps

Brown algae (Phaeophyceae, Ochrophyta) are a clade of multicellular protists that have independently evolved a plant-like habit (Keeling, 2004). They are perhaps the most three-dimensional macroalgal taxa and form complex underwater forests that are the foundation of temperate nearshore communities (Steneck *et al.*, 2002). Kelps (Laminariales) are the largest and most anatomically complex clade of brown macroalgae (Steneck *et al.*, 2002; Graham *et al.*, 2008) with biomass partitioned between three integrated organ systems (holdfast, stipe and blades; Fig. 1) superficially similar to those of embryophytes (roots, stalk and leaves, respectively) (Niklas, 2006). Kelps therefore provide the ideal 'outgroup' with which to test hypotheses about invariance generated from data on land plants. Despite this convergence on a tripartite body plan, kelps are structurally different from land plants in several fundamental ways. First, the importance of gravity in the aquatic environment is substantially less than in the terrestrial environment, because of the high density of water compared with air. Additionally, kelps (like most, if not all algae) lack nonliving tissues and would therefore presumably experience increased respiratory costs, relative to photosynthetic production, if area and mass scale with less than unity. Finally, kelps obtain water and nutrients from the environment and therefore do not rely on root-to-leaf water transport.

In spite of these differences, there are several reasons to draw comparisons between kelps and land plants; kelps possess internal transport systems that are analogous to phloem (Lobban, 1978; Graham *et al.*, 2008; Drobnitch *et al.*, 2015) and supply sugars to nonphotosynthetic tissues, allowing some species to produce thick tissues and large nonphotosynthetic organs (i.e. holdfasts). Kelps must also be mechanically supported against water movement (i.e. drag; see Starko *et al.*, 2015; Starko & Martone, 2016)

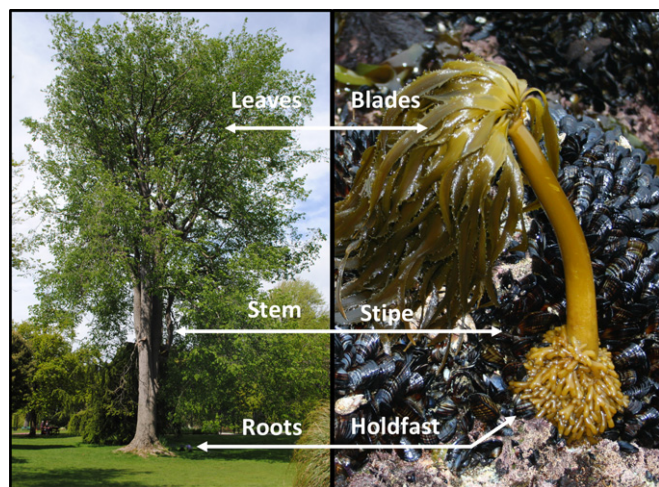


Fig. 1 A comparison of the three convergent organs of land plants and kelps (*Fraxinus* sp. and *Postelsia palmaeformis* depicted here; photos by R. B. Munger and P. T. Martone, respectively).

and therefore often thicken (Martone, 2007) and may invest increasing amounts of material into metabolically active support material as they grow larger. However, there is evidence that, despite a lack of nonliving tissue, supportive tissues (i.e. holdfasts and stipes) may have reduced metabolic demands compared to actively photosynthesizing tissues (Arnold & Manley, 1985). Thus, increasing size may be accompanied by a decrease in relative oxygen consumption, similar to respiratory scaling of large woody plants (but not herbaceous plants; Mori *et al.*, 2010). For these reasons, selection for transport distance minimization and structural support may still compete with selection for photosynthetic area maximization and converge on scaling relationships that are similar to those predicted by scaling theory.

Aim of the present study

In this study, we examined interspecific biomass scaling in kelps. We used this ecologically and economically important lineage as a phylogenetic outgroup to test whether 'universal' scaling principles demonstrated in land plants can in fact be extended to independently evolved aquatic lineages. We find that kelp photosynthetic area scales to approximately the $\frac{3}{4}$ power of total dry mass, as predicted by WBE, providing support for some universal biomass partitioning patterns. Our study provides insights into the evolution of size in the largest marine macrophytes and corroborates previous work suggesting that divergent lineages of photoautotrophs may face similar morphological selective pressures.

Materials and Methods

Allometric analyses

Interspecific patterns of biomass allocation are modeled as allometric power scaling relationships, such that:

$$Y = \beta X^\alpha$$

(Y and X , the masses of two organs or parameters with coordinated growth; β , the allometric constant (absolute magnitude or intercept of the relationship); α , the scaling exponent (see Fig. 2).) Although there are many uses for allometric analyses, in the context of this study we use allometric relationships to describe scaling patterns among species of differing sizes.

Sample collection

Whole individuals ($n = 114$) of adult kelps from 23 populations spanning 19 different species were collected for interspecific allometric analyses from eight sites along the Pacific coast of British Columbia (Table 1, Supporting Information Table S1). Kelps were collected both subtidally (by a combination of SCUBA and free-diving) and intertidally at low tide. Holdfasts were carefully removed from the substratum by means of a knife or paint scraper in order to ensure complete collection of holdfast tissue. Samples that were prone to breakage (e.g. blades of *Agarum*

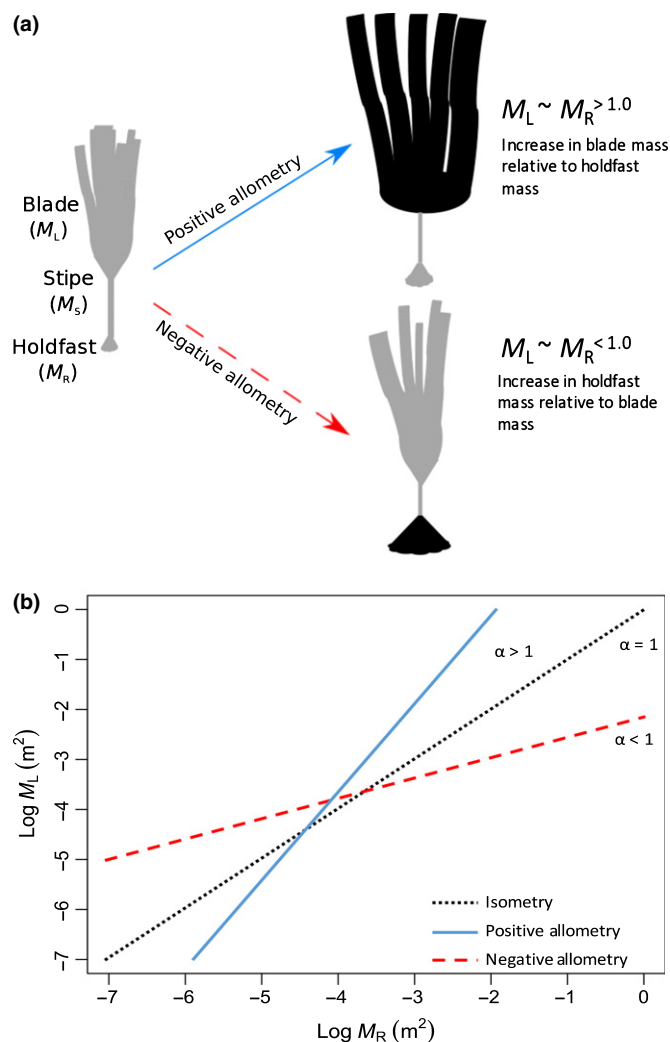


Fig. 2 (a) Pictorial and (b) graphical representations of allometry applied to kelps using the example of scaling between blade mass (analogous to leaf mass (M_L)) and holdfast mass (analogous to root mass (M_R)).

fimbriatum Harvey or holdfasts of *Egregia menziesii* (Turner) Areschoug) were kept separate so as to prevent loss of tissue before weighing.

Dry weight quantification

Kelps from Barkley Sound, Vancouver and Calvert Island were air-dried at room temperature for at least 12 h before formal drying. All but the largest of these kelps were placed in a 60°C drying oven for at least 24 h, while *E. menziesii* (Turner) Areschoug and *Macrocystis pyrifera* (Linnaeus) C. Agardh samples were dried at 37–39°C for 24 h in an industrial kelp drier (Canadian Kelp Services, Bamfield, BC, Canada). Kelps collected from Victoria were sun-dried for *c.* 20 h (over the course of 2 d), and then dried in a small room that was heated by four space heaters. The room was kept at 32°C for 48 h and then 37–39°C for 18 h. All samples were inspected before weighing to ensure complete drying of the tissue. Samples from all sites were separated into blade(s), stipe(s), and holdfast; each organ was weighed separately.

Quantification of A and regression with M_T

In order to determine how photosynthetic area and total dry mass scale across the kelps, a subsample ($n = 43$ observations, across nine kelp species; Table S2) of kelps were cut into small pieces with scissors, laid flat, and photographed with a scale from above. This ‘planform’ area measurement was then multiplied by 2 to produce an estimate of total photosynthetic surface area.

No global analysis of total leaf area–total dry weight scaling has ever been conducted on seed plants and few studies report the raw data for both parameters. However, total leaf area and dry weight were estimated as follows. First, smaller data sets on leaf area–dry weight scaling were obtained from the literature and from publicly available data sets: data on 15 species were taken from studies that directly reported both leaf area and dry mass (Table S3). Data for the two largest species, *Eucalyptus regnans* F. Muell. and *Sequoia sempervirens* (D. Don) Endl., were presented by Sillett *et al.* (2010, 2015) as aboveground mass. Root masses for these species were estimated as a proportion from the Niklas & Enquist (2004) data set (on *Eucalyptus* spp.) and Burger *et al.* (1997), respectively. Second, additional data for 23 species were used from the Niklas & Enquist (2004) data set containing both leaf mass and total mass. Assuming that leaf mass generally scales with leaf area in full-sized individuals (as does WBE; West *et al.*, 1997, 1999a), leaf mass was converted to estimates of leaf area using average leaf mass per unit area (LMA) or specific leaf area (SLA) measurements taken from Wright *et al.* (2004) and other sources (see Table S4). In studies where data were only presented graphically, data points were extracted using the software GRAPHCLICK (v.3.0; Arizona-Software, Neuchatel, Switzerland). When data were presented as one-sided surface area, values were multiplied by 2 in order to determine estimates of total (two-sided) leaf area. Interspecific allometric analysis of seed plants was conducted on species averages of A and M_T . Intraspecific area–mass scaling data for the cactus *Pachycerus pringlei* (S. Watson) Britton & Rose are also presented as adapted from Price & Enquist (2006).

Statistical analysis

Interspecific scaling relationships were determined for three pairwise comparisons, blade (M_L) and holdfast (M_R), stipe (M_S) and holdfast (M_R), and blade (M_L) and stipe (M_S), as well as frond (stipe + blade; analogous to aboveground mass (M_A)) and holdfast (analogous to belowground mass (M_B)). All regression analyses were performed using reduced major axis (RMA) slopes of log–log data. This is the standard statistical technique used in allometric analyses as it aims to minimize residual size across both axis, rather than just the y -axis as with ordinary least squares (OLS) regression (see Niklas, 1994). All scaling analyses were performed in R v.3.1.3 (R Development Core Team, 2008) using the ‘LMODEL2’ package. Differences from unity ($\alpha = 1$) were evaluated by calculating confidence intervals of allometric exponents (α) to determine whether parameter estimates differed significantly from 1. Data for *Saccharina sessilis* (C. Agardh) Kuntze were excluded from allometric analyses that included M_S because adult individuals of this species do not have stipes.

Table 1 Collection information for biomass partitioning analyses; all sites are located in British Columbia, Canada

Habitat	Site	Location	Species	Sample size
Intertidal (<i>n</i> = 70)	Brady's Blowhole	Barkley Sound	<i>Alaria nana</i>	<i>n</i> = 5
	Brady's Blowhole	Barkley Sound	<i>Costaria costata</i>	<i>n</i> = 5
	Brady's Blowhole	Barkley Sound	<i>Lessoniopsis littoralis</i>	<i>n</i> = 5
	Brady's Blowhole	Barkley Sound	<i>Saccharina sessilis</i>	<i>n</i> = 5
	Cape Beale	Barkley Sound	<i>Postelsia palmaeformis</i>	<i>n</i> = 5
	Eagle Bay	Barkley Sound	<i>Alaria marginata</i>	<i>n</i> = 5
	Eagle Bay	Barkley Sound	<i>Egregia menziesii</i>	<i>n</i> = 5
	Eagle Bay	Barkley Sound	<i>Laminaria setchellii</i>	<i>n</i> = 5
	Eagle Bay	Barkley Sound	<i>Macrocystis pyrifera</i>	<i>n</i> = 5
	Eagle Bay	Barkley Sound	<i>Saccharina groenlandica</i>	<i>n</i> = 5
	Edward King Island	Barkley Sound	<i>Laminaria ephemera</i>	<i>n</i> = 5
	Kitsilano Beach	Vancouver	<i>Saccharina latissima</i>	<i>n</i> = 5
	West Beach	Calvert Island	<i>Laminaria yezoensis</i>	<i>n</i> = 5
	West Beach	Calvert Island	<i>Saccharina groenlandica</i>	<i>n</i> = 5
Subtidal (<i>n</i> = 44)	Bamfield Inlet	Barkley Sound	<i>Agarum fimbriatum</i>	<i>n</i> = 5
	Bamfield Inlet	Barkley Sound	<i>Ecklonia arborea</i>	<i>n</i> = 5
	Bamfield Inlet	Barkley Sound	<i>Saccharina latissima</i>	<i>n</i> = 4
	Ogden Point	Victoria	<i>Alaria tenuifolia</i>	<i>n</i> = 5
	Ogden Point	Victoria	<i>Costaria costata</i>	<i>n</i> = 5
	Ogden Point	Victoria	<i>Nereocystis luetkeana</i>	<i>n</i> = 5
	Ogden Point	Victoria	<i>Pleurophycus gardneri</i>	<i>n</i> = 5
	Ogden Point	Victoria	<i>Pterygophora californica</i>	<i>n</i> = 5
	Ogden Point	Victoria	<i>Saccharina groenlandica</i>	<i>n</i> = 5

In order to determine whether scaling relationships differed between subtidal and intertidal kelps, we compared the slopes and intercepts of each scaling relationship using the 'SMATR' package (Warton *et al.*, 2012) in R. Data from *Laminaria ephemera* (the smallest species) were excluded from analyses such that data were compared across the same range of values. This, however, had no effect on the interpretation of any of our results.

Results and Discussion

Scaling of *A* and *M_T*

Despite the phyletic and ecological dissimilarity of land plants and brown algae, the relationship posed by WBE, $A \sim M_T^{3/4}$, appears to hold approximately true even among these distantly related taxa (Fig. 3). Across more than three orders of magnitude in both area and mass, photosynthetic area of kelps scales to the 0.78 power of total dry weight (RMA regression: $A = 2.38M_T^{0.78 \pm 0.09}$; $P < 0.001$; $df = 47$; Table 2; Fig. 3), similar to the $3/4$ relationship predicted by WBE. The $3/4$ scaling of *A* and *M_T* has been previously demonstrated not only in herbaceous and woody plants (as number of leaves; see Niklas, 2004), but also among some unicellular algae (as number of chloroplasts or pigment content; Niklas, 1994; Niklas & Enquist, 2001) and succulent plants (Price & Enquist, 2006; Fig. 3) that lack substantial branching or an external fractal-like morphology, suggesting that this relationship may be common throughout Chlorophyta. Indeed, interspecific scaling data presented here (Fig. 3) suggest that area tends to scale to the $c. 3/4$ power of total biomass in seed plants. On average, kelps tend to have greater photosynthetic area per unit dry mass than land plants (as

indicated by the higher *y*-intercept; Fig. 3; Table S5), but they share similar scaling exponents. Thus, our results further corroborate the findings of Price & Enquist (2006) and the predictions of WBE (West *et al.*, 1999b) by demonstrating that a near $3/4$ scaling relationship has evolved independently in a lineage of aquatic macroalgae. Interestingly, the *y*-intercept and slope of the kelp data set are similar to intraspecific data for *Arabidopsis thaliana*, clearly demonstrating that kelp area–biomass scaling

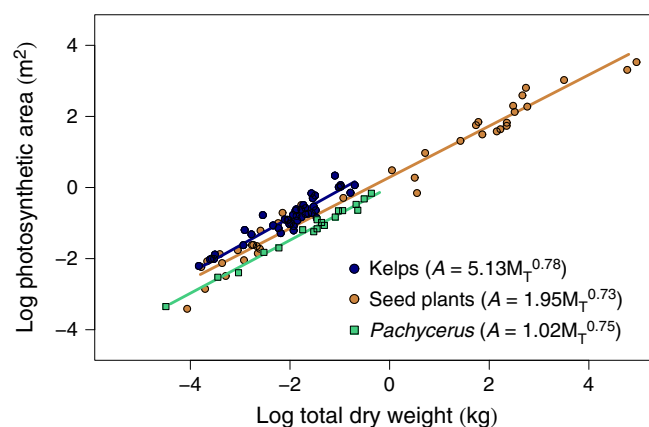


Fig. 3 Interspecific scaling relationships for photosynthetic area (*A*) and total mass (*M_T*) reveal similar scaling relationships, but different absolute values (*y*-intercepts). Reduced major axis (RMA) regression analysis of kelps indicated that $A \sim M_T^{0.78}$ ($n = 43$), similar to the interspecific scaling exponent of 0.73 in land plants and the 0.75 intraspecific scaling exponent of the cactus *Pachycerus pringlei* (from Price & Enquist, 2006). Data shown represent total thallus area of kelps (see Table 1) and *P. pringlei*, but represent the total leaf area of land plants (see Supporting Information Tables S3, S4).

Table 2 Parameter estimates ($\pm 95\%$ confidence intervals) of the reduced major axis regression analyses for each interspecific comparison among kelp species

Regression	Samples	Allometric exponent (α)*	Allometric constant ($\log \beta$)	R^2
A vs M_T	Subsample ($n = 43$)	0.78 (0.69–0.86)	0.71 (0.54–0.90)	0.89
M_L vs M_R	All ($n = 114$)	0.85 (0.74–0.96)	0.60 (0.32–0.90)	0.67
	Subtidal ($n = 44$)	0.87 (0.64–1.15)	0.82 (0.24–1.54)	0.54
	Intertidal ($n = 70$)	0.79 (0.68–0.92)	0.35 (0.06–0.68)	0.73
M_S vs M_R	All ($n = 109$)	1.14 (1.02–1.26)	0.24 (–0.06–0.58)	0.76
	Subtidal ($n = 44$)	1.58 (1.28–1.95)	1.38 (0.62–2.33)	0.72
	Intertidal ($n = 65$)	1.01 (0.90–1.14)	–1.00 (–0.40–0.25)	0.80
M_L vs M_S	All ($n = 109$)	0.71 (0.58–0.86)	0.32 (–0.04–0.74)	0.48
	Subtidal ($n = 44$)	0.51 (0.30–0.79)	–0.06 (–0.60–0.65)	0.35
	Intertidal ($n = 65$)	0.77 (0.61–0.96)	0.42 (–0.04–0.96)	0.53
M_{A+L+S} vs M_R	All ($n = 114$)	0.85 (0.77–0.95)	0.68 (0.46–0.93)	0.75
	Subtidal ($n = 44$)	0.89 (0.69–1.12)	0.92 (0.43–1.51)	0.63
	Intertidal ($n = 70$)	0.81 (0.72–0.91)	0.46 (0.22–0.73)	0.81

*Bold values significantly exclude null hypotheses for organ scaling ($\alpha = 1$). A = photosynthetic area; MT = total dry mass; ML = blade mass; MS = stipe mass; MR = holdfast mass.

relationships are not greater than those of all plants, just the average trends (Fig. S1). Weedier species, like *A. thaliana*, may closely match kelps in terms of the intercept of area–dry mass scaling, probably contributing to their fast growth and competitive ability. The convergence of seed plants and kelps on a near- $3/4$ relationship may suggest that the form and function of plants with divergent phyletic affiliations are influenced by similar selective pressures despite the many phylogenetic, ecological and biophysical differences between these lineages.

Biomass partitioning across kelp taxa

In spite of near- $3/4$ scaling of A and M_T , kelps differ substantially from herbaceous embryophytes in all of the organ biomass scaling relationships examined in this study and partition considerably more biomass to blades than predicted from embryophytes across all sizes (as indicated by $\log \beta > 0$ in M_L vs M_R and M_L vs M_S ; Tables 2, 3; Fig. 4). On average, the biomass of kelps is 78.6% blade, 11.1% stipe, and 10.8% holdfast, which are notably different proportions from biomass allocation in land plants (8%, 67% and 25% for leaf, stipe and root, respectively; Niklas & Enquist, 2002). Additionally, none of the organ biomass scaling relationships examined in this study follow clear $1/4$ power scaling relationships, and demonstrate scaling exponents that are not easily interpreted as the outcome of dimensional scaling rules (e.g. $2/3$,

$3/4$ or 1). Organ biomass scaling exponents of kelps do, however, match quite closely to the actual (observed) values of biomass allometry for large vascularized plants (and not herbaceous plants; Tables 2, 4). Specifically, blade mass scales with negative allometry towards both stipe and holdfast biomasses (RMA regression: $M_L \propto M_R^{0.85}$; $P < 0.001$; $df = 114$; see Table 2; Fig. 4a; RMA regression: $M_L \propto M_R^{0.71}$; $P < 0.001$; $df = 109$; see Table 2; Fig. 4b) with confidence intervals that exclude unity (95% CI 0.69–0.97), but not $3/4$ (the prediction from woody species). In general, larger kelps, like large embryophytes, have increased relative M_R and M_S compared with species of smaller biomass. By contrast, however, stipe mass and holdfast mass scale with significant positive allometry (RMA regression: $M_S \propto M_R^{1.15}$; $P < 0.001$; $df = 109$; see Table 2; Fig. 4c; 95% CI 1.02–1.26) that excludes the linear predictions from both herbaceous and woody taxa but not the observed M_S – M_R scaling ($c. 1.10$) of woody taxa. Together, these results suggest that biomass scaling exponents in kelps do in fact match up well with observed interspecific allometric exponents from woody plants, but not herbaceous plants. Moreover, woody plants and kelps deviate from the model of Niklas and Enquist in similar ways.

The predictive model of Niklas & Enquist (2002) is founded on several assumptions that have been more or less supported empirically in seed plants (Niklas, 2003), at least for large individuals (Price *et al.*, 2009), but are believed to be a result of hydraulic rather than mechanical (i.e. gravitational) constraints (Niklas & Enquist, 2001; Niklas, 2003; Niklas & Spatz, 2004). Intuitively, any assumption that is based on hydraulic requirements cannot be assumed to apply to marine algae, which obtain water and nutrients along their entire thallus by means of simple diffusion (Graham *et al.*, 2008). Because macroalgae are not restricted in structure by the internal transport of water, most kelps are largely blade ($c. 78\%$ by mass; note the strongly positive allometric constants in Table 2). However, the scaling exponents of all biomass partitioning patterns were statistically indistinguishable from those observed for woody land plants (see Table 2). How kelps closely match the scaling exponents of large

Table 3 Log-transformed standing biomass scaling constants ($\log \beta$) for land plants (data from the literature) and kelps

Regression	Herbaceous plants ¹	Woody conifers ²	Woody angiosperms ²	Kelps
M_L vs M_R	–0.03	–0.12	–0.89	0.60
M_L vs M_S	–0.19	–0.47	–0.52	0.32
M_S vs M_R	0.10	0.44	0.42	0.24

¹From Niklas (2006); ²from Enquist & Niklas (2002a). ML = leaf/blade mass; MR = root/holdfast mass; MS = stem/stipe mass.

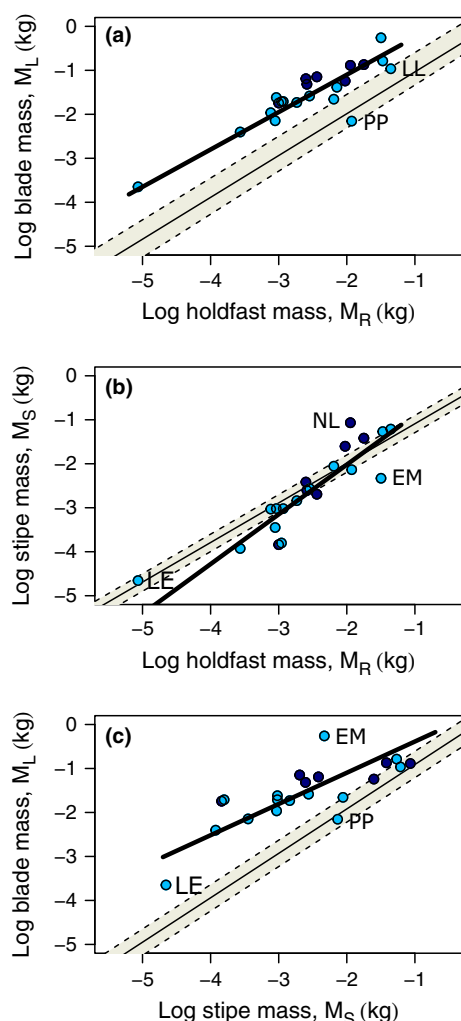


Fig. 4 (a) Blade mass (M_L) plotted as a function of holdfast mass (M_R). (b) Stipe mass (M_S) plotted as a function of M_R . (c) M_L as a function of M_S . Shaded polygons represent the 95% confidence intervals of scaling relations in herbaceous land plants (from Niklas, 2006). Solid black lines are fitted to all kelp (see Table 1) data (a, $n = 114$; b, c, $n = 109$), while data points represent population averages. Dark-blue data points represent populations collected from subtidal sites, while light-blue points represent intertidal populations. Outliers from general trends are labeled (LL, *Lessoniopsis littoralis* (Tilden) Reinke; PP, *Postelsia palmaeformis*; LE, *Laminaria ephemera*; EM, *Egregia menziesii*; NL, *Nereocystis luetkeana*).

trees, which are highly vascularized and must transport water great distances, remains an open question. However, one possible explanation is that both holdfasts and roots interact with their environment across two-dimensional exchange areas (holdfast attachment area and root exchange area). Therefore, if holdfast attachment area in kelps scales somewhat proportionally with blade area to resist drag caused by waves, then this would be analogous to embryophyte root exchange area and leaf area scaling proportionally to provide water for photosynthesis. Thus, although differences in the actual magnitude of organs (i.e. allometric constant) may reflect functional differences between roots and holdfasts, similar allometric exponents may result from shared consequences of dimensional scaling.

Table 4 Standing biomass scaling exponents (α) for land plants (data from the literature) and kelps

Regression	Herbaceous plants ¹	Woody conifers ²	Woody angiosperms ²	Kelps
M_L vs M_R	0.93	0.86	0.76	0.85
M_L vs M_S	0.90	0.78	0.73	0.71
M_S vs M_R	1.01	1.10	1.10	1.14

¹From Niklas (2006); ²from Enquist & Niklas (2002a). M_L = leaf/blade mass; M_R = root/holdfast mass; M_S = stem/stipe mass.

Larger kelps also tended to have disproportionately massive stipes, which is similar to patterns seen in land plants. For example, two of the largest species, *Nereocystis luetkeana* (bull kelp) and *Macrocystis pyrifera* (giant kelp), form underwater canopies with stipes that can grow tens of meters long. While larger holdfasts are probably associated with resisting hydrodynamic forces, larger relative stipe biomass may provide kelps with the competitive advantage required to grow to a larger total body mass. Stipes lift kelps up off the substratum, and thus large stipes could both improve light capture and minimize space requirements along the substratum. This parallels closely the selection for uprightness among land plants, which must also compete for light in a forest canopy (Falster & Westoby, 2003). However, stipes also play an important role in resistance to mechanical forces (e.g. Koehl & Wainwright, 1977; Johnson & Koehl, 1994; Utter & Denny, 1996; Denny *et al.*, 1997). As mechanical forces on the stipe are generally related to tension (see Utter & Denny, 1996), increases in blade size may require concurrent increases in stipe diameter or length in order to resist breakage (see Johnson & Koehl, 1994; Denny *et al.*, 1997; Martone, 2007; Starko & Martone, 2016 for discussions of stipe diameter allometry).

Influence of habitat on biomass allocation

Habitat had a strong effect on organ biomass scaling relationships. Subtidal and intertidal kelps differed in the allometric constant (i.e. intercept) of blade–holdfast, blade–stipe and frond (‘above-ground’)–holdfast scaling regressions but not the exponents of these relationships (Fig. 5; Table S6). Across almost three orders of magnitude in holdfast (M_R) and stipe (M_S) mass, subtidal kelps had significantly more blade mass (M_L) and frond mass ($M_L + M_S$) than intertidal kelps. Additionally, there was a significant effect of habitat on the slope of stipe–holdfast scaling, such that more biomass was allocated to stipes in larger subtidal kelps (Table S6). This is probably a response to selection for increased light interception in deep, subtidal species (e.g. *Nereocystis luetkeana*, *Pterygophora californica* and *Ecklonia arborea*).

Wave-induced forces are probably also a strong source of natural selection, have imposed mechanical limitations on the structure and function of kelps (Wernberg, 2005; de Bettignies *et al.*, 2013; Starko *et al.*, 2015; Starko & Martone, 2016), and play an important role in size limitation of marine macroalgae (e.g. Martone & Denny, 2008). Subtidal kelps generally do not experience forces applied by breaking waves, but instead experience

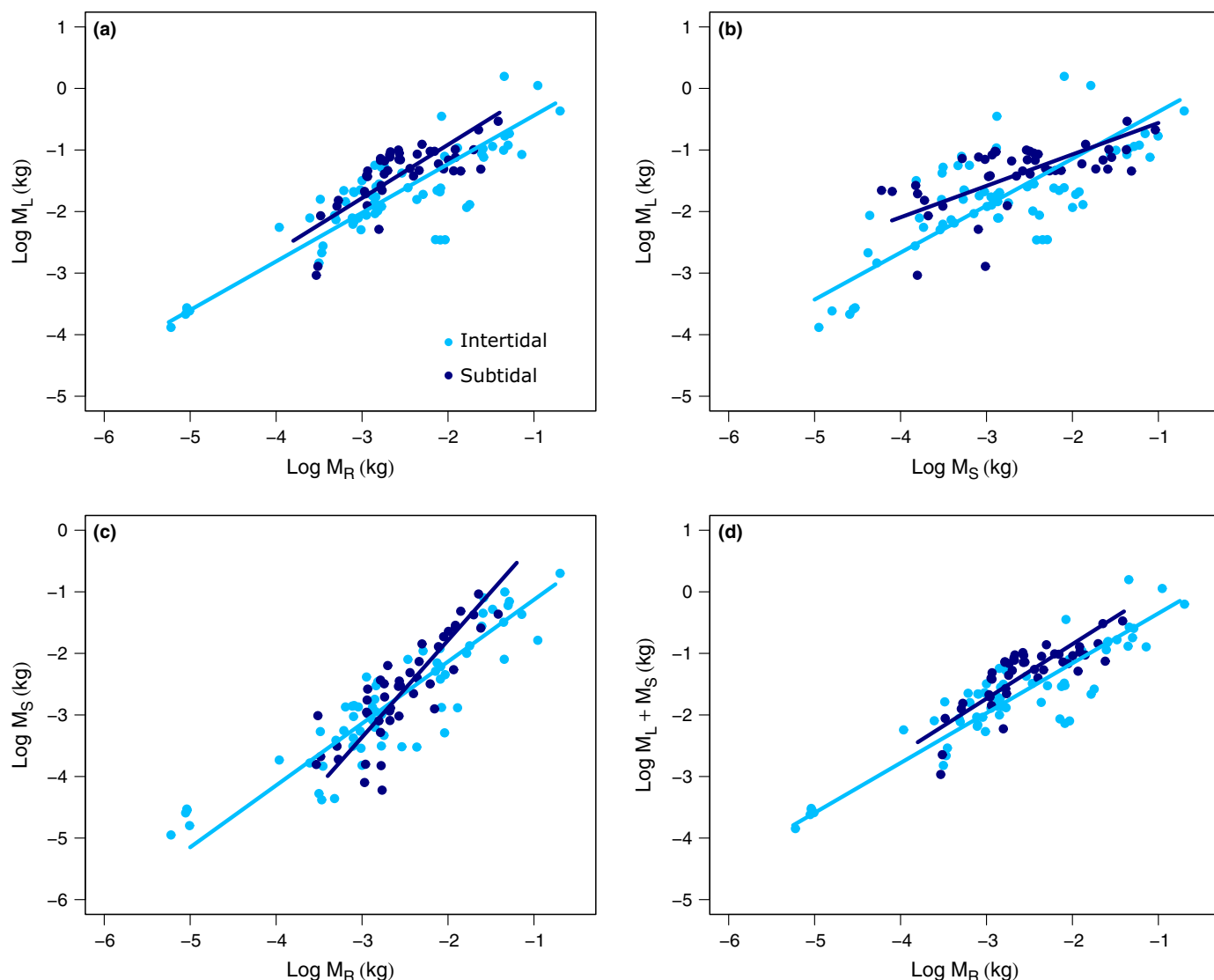


Fig. 5 Biomass scaling relationships for blade mass (M_L), stipe mass (M_S), holdfast mass (M_R) and frond mass ($M_L + M_S$) of kelps (Table 1). Reduced major axis (RMA) regressions are fitted separately to subtidal and intertidal kelps.

slower and more predictable currents (Gaylord *et al.*, 2008). Our results demonstrate that kelps growing at subtidal sites develop larger blades relative to their holdfasts (Fig. 5; Tables 2, S3). However, blade–stipe and blade–holdfast scaling exponents (α) remain constant across environments (Fig. 5). Additionally, two species that are obligate to highly wave-swept coastlines, *Postelsia palmaeformis* (the sea palm) and *Lessoniopsis littoralis* (the pom pom kelp), had the highest relative M_R of any species evaluated here (47% and 27% of dry mass, respectively), and closely matched seed plants in terms of absolute organ mass (see Fig. 4). Larger blades in subtidal or less wave-exposed kelps could result from differences in allometric growth patterns, whereby certain species have evolved larger or smaller holdfasts in response to their environment, or it could be a result of increased blade breakage in the intertidal zone as a result of wave stress. Nevertheless, differences among subtidal and intertidal species highlight the importance of hydrodynamic forces in influencing biomass allocation patterns among kelps.

‘Diminishing returns’ with increasing biomass

In this study, we provide multiple lines of evidence for diminishing returns of net productivity with increased body size as seen in higher plants (Niklas & Enquist, 2002; Niklas & Cobb, 2008; Niklas *et al.*, 2009). Larger kelps have larger stipes and holdfasts and thus probably face increased relative metabolic costs compared with smaller kelps. Additionally, total photosynthetic area scaled with approximately the $3/4$ power of total dry mass, suggesting that increases in size are associated with reductions in the relative proportion of photosynthetic biomass. Organ biomass scaling relationships in this study suggest that larger kelps have greater proportions of less productive organs, similar to trends seen in large land plants.

Changes in relative blade mass alone cannot explain the $3/4$ scaling relationship between photosynthetic area and dry mass. Instead, this relationship must also be influenced by changes in blade thickness. For example, at reproductive size the smallest

kelp in this study, *L. ephemera*, is generally 0.7 mm or less in thickness. Even in subtidal environments, larger bladed species (*Agarum fimbriatum* and *Saccharina latissima*) tend to have central portions that are twice as thick (1.25–1.45 mm) (S. Starko, unpublished). Despite this size dependence of blade thickness, kelps and other macroalgae may grow more in length than either thickness or width (Scrosati, 2006), and thus the $\frac{3}{4}$ scaling exponent of A vs M_T probably reflects an intermediate between Euclidean scaling (equal growth in all dimensions: A vs $V^{2/3}$) and growth in only two dimensions (no change in thickness or relative holdfast contribution: A vs V^1) that is accomplished without fractal-like external branching.

Unlike embryophytes, kelps do not produce nonliving tissues, analogous to the ‘hoarding of wood’ observed in large trees. Because kelps lack dead structural tissue, size-dependent effects of $SA : V$ probably reduce the relationship between living photosynthetic and living nonphotosynthetic tissues with increased size. Perhaps larger kelps are able to offset some of these diminishing returns by reducing the metabolic requirement of some structural tissues (Arnold & Manley, 1985). Indeed, holdfast and stipe tissues from *Macrocystis* have substantially reduced respiratory demands (as little as 1/5 of the O_2 consumption, by weight) than actively photosynthesizing blade tissues (Arnold & Manley, 1985). Moreover, thicker parts of the blade may have reduced respiratory rate compared with thinner tissues (Arnold & Manley, 1985). Thus, despite the apparent lack of nonliving tissues within kelp thalli, larger species may accumulate metabolically less demanding tissues, similar to the inner sapwood and heartwood of trees. Future work should address the scaling of respiration and photosynthesis with body size in kelps, in order to determine the extent to which diminishing returns exist, physiologically, and how these scaling parameters compare to those of seed plants.

Despite these diminishing returns, the large size of kelps may still be favorable for many reasons. Smaller or deeper kelps may be more light-limited than larger kelps, as a consequence of competition and light attenuation, and may be poorer competitors for space, making them likely to be overgrown by larger species. Thus, large size may allow increased photosynthetic production by allowing kelps to reach the surface, improving light interception (see Colombo-Pallotta *et al.*, 2006). Kelps are also highly productive (Mann, 1973; Steneck *et al.*, 2002), and the y -intercept of interspecific area–mass scaling across the kelp lineage is higher than the interspecific scaling of plants (Fig. 3). This suggests that, even at large sizes, $SA : V$ may still be relatively high compared with seed plants. Reductions in $SA : V$ with increasing size may therefore not be particularly disadvantageous if the initially high area : mass ratio allows a substantial surplus of carbon production, despite the increase in respiratory metabolism. In addition to this, reproduction requires little extra cost for the kelps. With the exception of *Alaria* spp., which produce metabolically demanding reproductive blades (Pfister, 1992), most kelps reproduce by forming soral patches on pre-existing blades, rather than on separate structures (Graham *et al.*, 2008). Thus, where seed plants must reserve energy for the production of specialized reproductive structures, kelps probably require little additional

energy, beyond blade elongation, in order to reproduce. In this way, larger size may be selectively advantageous, despite increased metabolic demands, as reproductive output probably depends on available blade area for soral production.

Thicker tissues together with increased investment in stipe and holdfast may explain why A and M_T scale with negative allometry, but why $\frac{3}{4}$? According to the WBE model, fractal-like structures can reach a maximum A – M_T scaling relationship of $\frac{3}{4}$; however, many of these kelps do not have volume-filling, fractal-like body plans, but instead often possess only one of each organ. Price & Enquist (2006) argue that, despite the simple (and not fractal-like) external morphologies of succulent plants, for example, volume-filling internal transport systems are still required in order to deliver photosynthate and water throughout the plant. With simple adjustments to WBE, these authors were able to rationalize why $A \sim M_T^{3/4}$ in succulents despite their lack of a fractal-like external morphology and selection for branch minimization. Similar to succulents, many kelps are unbranched or minimally branched, perhaps as a result of negative hydrodynamic consequences associated with proliferation of branching (Starko *et al.*, 2015). Despite this, our results provide phylogenetically independent evidence for the universality of the $\frac{3}{4}$ scaling relationship between A and M_T (see Fig. 3). Kelps possess phloem-like internal transport systems that are ‘optimized’ in certain species, from the perspective of conduit diameter and packing scaling relationships (Drobnitch *et al.*, 2015). Thus, although kelps may possess morphologies that reduce mechanical stress, internal transport systems must still work as complex supply networks within the thallus, in order to maintain physiological function or improve growth. For this reason, a $\frac{3}{4}$ scaling relationship may still be predicted. Alternatively, this relationship may have arisen as a result of mechanical selection: larger species must resist greater drag forces than smaller kelps from the same water velocities and probably require thicker tissues that can resist these increased mechanical forces (see Demes *et al.*, 2011; Starko & Martone, 2016). Future work on red algae or other brown algal orders that lack vasculature could help to tease apart the effects of vasculature and mechanics.

Regardless of the mechanism, our findings suggest that the relationship that probably has the greatest influence on plant productivity (i.e. A vs M_T) may be remarkably similar (and nearly invariant) among decidedly divergent photosynthetic lineages. All plants and macroalgae, with the exception of some crusts and biofilms, photosynthesize and exchange nutrients across a two-dimensional surface area while necessarily occupying three dimensions in their environment. Because of this dimensional constraint associated with surface area to volume scaling, diminishing returns may be an important consequence of size evolution across all plants and macroalgae regardless of evolutionary history. Given this predictable effect of size on surface area to volume scaling, accumulation of metabolically less active structural tissue (as in Arnold & Manley, 1985), similar to heartwood and inner sapwood of seed plants, may partially explain why kelps (but not other macroalgae), are capable of growing so large.

Conclusion

In our study, we tested current hypotheses about biomass partitioning in an independently evolved lineage of photosynthetic macrophytes. We provide support for the general prediction of the WBE model that photosynthetic area scales with the $\frac{3}{4}$ power of dry mass, and establish that interspecific organ biomass scaling patterns match closely to those of woody plants despite substantial differences in the absolute magnitude of these organs. Larger kelps were found to have increased relative holdfast and stipe biomass similar to leaf–stem–root scaling in land plants. The results of this study improve our interpretations of previous models and highlight important consequences of size in a group of organisms that, to date, has been understudied.

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Author contributions

This work represents part of S.S.'s PhD dissertation. S.S. collected algae in the field, analyzed the data and wrote the manuscript. P.T.M. contributed ideas and guidance, helped to refine the manuscript and provided laboratory equipment and funding.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Total thallus or leaf surface area of kelps (data from this study) and *Arabidopsis thaliana* (data from Weradewage *et al.*, 2015) plotted against total dry weight.

Table S1 Kelp collection site locations

Table S2 Populations and sample sizes used in photosynthetic area vs total mass scaling analysis

Table S3 Sources for data from which leaf area and dry weight were reported together in the same study

Table S4 Sources for LMA or SLA data that were used to estimate leaf area from the Niklas & Enquist (2004) data set

Table S5 RMA regression coefficients and confidence intervals for area–dry weight scaling in kelps, seed plants and *Pachyceris pringlei*

Table S6 Results of statistical comparisons of intertidal and subtidal scaling relationships (performed using SMATR)

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