Length–biomass allometry in primary producers: predominantly bidimensional seaweeds differ from the “universal” interspecific trend defined by microalgae and vascular plants

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Abstract: This study tests whether the value (0.25, or 1/4) of the interspecific allometric exponent currently thought to be universal for the length–biomass relationship for primary producers (based on data for vascular plants and unicellular microalgae) also applies to macroalgae. Length and dry biomass were measured for four phylogenetically distinct seaweed species, *Chondrus crispus* Stackhouse, *Pterocladia capillacea* (Gmelin) Santelices & Hommersand, *Fucus vesiculosus* Linnaeus, and *Laminaria saccharina* (Linnaeus) J.V. Lamouroux, which are representatives of four different orders: Gigartiniales and Gelidiales (Rhodophyta) and Fucales and Laminariales (Phaeophyceae). The interspecific exponent found for these seaweeds (0.47) differs significantly from the interspecific “universal” value stated above. The 95% confidence interval for the interspecific exponent for these seaweeds includes 0.5 (or 1/2), a value that is related to an idealized form of bidimensional growth. While vascular plants and unicellular microalgae can be viewed as clearly growing in three dimensions, the studied seaweeds are predominantly flat, which thus seems to explain their divergent allometry. The present study indicates that the comprehensive understanding of allometric trends for primary producers should be based on studies covering the morphological diversity that different groups of primary producers display.

Key words: length–biomass allometry, seaweed.

Introduction

Biological variables are often related allometrically to one another through power functions (Brown and West 2000; Niklas 1994, 2004). This is especially true for the relation-

ship between the length and biomass of an organism, as biomass increases faster than length as larger organisms are considered. Recently, an interspecific allometric exponent ($\alpha$) of 0.25 (1/4) has been proposed as universal for primary producers for the

$$L = \beta M^\alpha$$

relationship, where $L$ is body length, $M$ is dry biomass, and $\beta$ is the allometric constant (Niklas and Enquist 2001). The above value for the scaling exponent was originally pro-
posed for trees (considering tree height; West et al. 1999), but Niklas and Enquist (2001) later found a statistical fit when adding data for several unicellular microalgae and one macroalgal species (*Macrocystis*, Laminariales). The theoretical basis for such an exponent results from an extension of a broader model, proposed for plants and animals in general, that claims that metabolic rate scales with the organism’s biomass at the 3/4 power (West et al. 1997).

Universal scaling relationships are, in theory, useful because they would simplify the understanding of pattern and process at a variety of biological scales. Before a model becomes widely accepted as universal, however, rigorous tests must be conducted. Testing can be done through empirical analyses on previously unstudied taxa or through the critical examination of the theoretical consistency of the model (van der Meer 2006). The present study aims to test for the apparent generality of the interspecific length–biomass exponent among primary producers using the first approach. In this sense, it is important to note that seaweeds, or marine macroalgae, were almost neglected when determining the interspecific length–biomass exponent for primary producers, as only one macroalgal species (*Macrocystis*) was considered among the many species of unicellular microalgae and vascular plants used by Niklas and Enquist (2001). Therefore, it is not known whether the “universal” interspecific exponent would apply to seaweeds as a group.

There is reason to hypothesize that a number of seaweed groups would depart from the length–biomass allometric exponent proposed as universal for primary producers. In particular, many seaweed species have relatively flat forms. For such species, morphological diversity goes from an un-branched, laminar blade to a highly branched frond, but the common property for them all is the predominantly bidimensional nature of their bodies. The present study tests whether the interspecific length–biomass exponent for such seaweeds differs from the universal interspecific value proposed for primary producers in general (Niklas and Enquist 2001). For this objective, a sample of four predominantly flat macroalgal species representing two orders of the Rhodophyta (red algae) and two orders of the Phaeophyceae (brown algae) was used. Phylogenetically divergent measurements are needed when the possible existence of general trends is to be tested because focusing the study exclusively or disproportionately on some taxonomic groups may bias the conclusions (Harvey 2000).

Materials and methods

Length and dry biomass were measured for the following species: *Chondrus crispus* Stackhouse (Gigartinales, Rhodophyta), *Pterocladiella capillacea* (Gmelin) Santelices & Hommersand (Gelidiales, Rhodophyta), *Fucus vesiculosus* Linnaeus (Fucales, Phaeophyceae), and *Laminaria saccharina* (Linnaeus) J.V. Lamouroux (Laminariales, Phaeophyceae).

*Chondrus crispus* is a clonal seaweed. A clonal seaweed is one in which the holdfast produces a number of fronds (= ramets) vegetatively, each frond having the potential capacity for autonomous life if it becomes physically isolated from the rest of the thallus while remaining attached to the substrate by an original portion of the holdfast. Considering that the frond is a potentially independent individual, length...
and biomass were measured for *C. crispus* fronds. Fronds of this species are attached to the holdfast by a thin stipe and undergo a number of dichotomous divisions in one plane as they grow. Large fronds may appear curved when viewed in a natural stand (Fig. 1), but they are basically flat when pressed on a surface. On 31 July 2004, 56 fronds were collected during low tide (cutting at the holdfast–stipe junction) from the low intertidal zone at Tor Bay Provincial Park on the Atlantic coast of Nova Scotia, Canada. In the laboratory, length was measured to the nearest 1 mm and wet biomass to the nearest 1 mg, previously eliminating surface water with paper towels. Tissue desiccation occurs to some extent during low tides, so a state of full hydration was ensured before measuring wet biomass by submerging the fronds in seawater in the laboratory until constant (fully hydrated) wet biomass was achieved. Frond dry biomass was then calculated by multiplying each frond’s value of wet biomass by 0.239 because the mean water content of fronds was found to be 70% for this species (Scrosati 2000).

*Laminaria saccharina* is also a unitary seaweed, which means that the holdfast only produces one frond or axis. Thalli of this species are also relatively flat. The unique frond is composed of a number of relatively flat branches that result from repeated dichotomous divisions from the unique stipe (Fig. 3). On 16 August 2004, 35 nonreproductive (without receptacles) thalli of *F. vesiculosus* were collected during low tide from the mid- to low intertidal zone at Tor Bay Provincial Park on the Atlantic coast of Nova Scotia, Canada. In the laboratory, thallus length was measured to the nearest 1 mm and (fully hydrated) wet biomass to the nearest 1 dg. Dry biomass was calculated by multiplying each thallus’ value of wet biomass by 0.207 because the mean water content was found to be 79.3 ± 0.7% (mean ± SE) for this species. This value was determined by completely desiccating a separate set of six fully hydrated thalli (range = 0.3–10.5 g of wet biomass) and quantifying the percent difference between fully hydrated biomass and fully desiccated biomass.

*Fucus vesiculosus* is a unitary seaweed, which means that the holdfast only produces one stipe and gives rise to a flat, unbranched blade (Fig. 4). On 17 April 2003, 50 thalli of *L. saccharina* were collected from the low intertidal zone at one of the rocky ends of Kitsilano Beach on the coast of Vancouver, British Columbia, Canada. In the laboratory, thallus length was measured to the nearest 1 mm and (fully hydrated) wet biomass to the nearest 1 cg. Dry biomass was calculated by multiplying each thallus’ value of wet biomass by 0.124 because the mean water content was found to be 87.6 ± 1.6% (mean ± SE) for this species. This value was determined by completely desiccating a separate set of four fully hydrated thalli (range = 0.3–10.5 g of wet biomass) and quantifying the percent difference between fully hydrated biomass and fully desiccated biomass.

Focus on macroalgal length–biomass allometry is at the interspecific level in the present study. Thus, data for the species described above were analyzed together. The similar sample sizes used for these species ensure that the interspecific nature of the calculated functional relationship is unbiased.

Power functions can be linearized when both variables are
transformed logarithmically, which facilitates data handling and comparisons (Niklas 2004). Then, the length–biomass relationship as shown above can be restated as

\[
\log L = \log \beta + \alpha \log M
\]

where \(\alpha\) is now the slope of a straight line and \(\log \beta\) is the intercept. Both length and biomass are random variables, subject to measurement error, so model parameterization cannot be done through the commonly used technique of least squares (model I) linear regression. Instead, techniques such as reduced major axis regression, which is a model II regression procedure, may be used (Sokal and Rohlf 1995). For the present study, all length and biomass values were log_{10}-transformed and model parameters were calculated using the reduced major axis technique. A 95\% confidence interval was then calculated for the slope (\(\alpha\), the exponent in the power version of the relationship) according to Sokal and Rohlf (1995). Using the standard error of the intercept (\(\log \beta\)), a 95\% confidence interval was also calculated for the allometric constant (\(\beta\)) using the correction factor described in Niklas (1994) because of the biased nature of antilog estimations. The strength of the linear association between log-transformed variables was assessed with Pearson’s correlation coefficient, \(r\) (Sokal and Rohlf 1995). Calculations were done with SYSTAT 5.2 for Macintosh (Wilkinson et al. 1992).

**Results and discussion**

The interspecific length–biomass relationship was highly significant (\(r = 0.90, p < 0.001\)) for the seaweed species analyzed in the present study (Fig. 5). The measurement units used for model parameterization (m for length and kg for dry biomass) were selected to facilitate comparisons with values published for unicellular microalgae and vascular plants (Niklas and Enquist 2001).
Based on a 95% confidence interval (0.442–0.502), the interspecific length–biomass exponent ($\alpha = 0.472$) for these predominantly flat seaweeds was significantly higher than the value (0.25, or 1/4) proposed as universal for primary producers (Niklas and Enquist 2001). Species-specific length–biomass exponents were also significantly higher than the “universal” value (Table 1).

Based on form, which may be used to predict functional traits, seaweed diversity can be reduced to a few main categories (Littler et al. 1983; Steneck and Dethier 1994). The species used in the present study are representatives of the “coarsely branched group” and the “thick, leathery group” (sensu Littler et al. 1983) and of “corticated macrophytes” and “leathery macrophytes” (sensu Steneck and Dethier 1994). These functional-form groups comprise many species, which depict a morphological diversity similar to that displayed by the species used for the present study. Therefore, it can reasonably be predicted that a large number of seaweeds will differ from the universal length–biomass exponent as described by unicellular microalgae and vascular plants.

It is interesting to speculate on possible explanations for the differing trends among these groups of primary producers. The most striking difference between the seaweeds analyzed in this study and the unicellular microalgae and vascular plants used in Niklas and Enquist’s (2001) study is that these seaweeds are relatively flat. They may reconfigure with water flow (Denny and Gaylord 2002), but they are essentially flat when pressed on a surface. On the contrary, vascular plants and unicellular microalgae are better viewed as organisms clearly growing in three dimensions. In this sense, it is interesting to note that, based on its confidence interval, the allometric length–biomass exponent found for these seaweeds is statistically indistinguishable from 0.5 (1/2), a value that is in accordance with an idealized form of bidimensional growth. For a quadrat, side length scales to the 1/2 power of area. For an extremely flat object resembling a quadrat, side length will scale closely to the 1/2 power of that object’s mass. The seaweeds studied here are obviously far from being a quadrat, but their bodies certainly grow mostly across two dimensions.

The original models by West et al. (1997, 1999) were not developed having seaweeds with flat forms in mind. Rather, one of the main assumptions on which the models by West et al. (1997, 1999) were based is that organisms have fractal-like distribution networks for the internal transport of metabolites that branch three-dimensionally throughout the entire body. Species of the Fucales and Laminariales do...
have cells adapted for long-distance transport of metabolites throughout the thallus (Buggeln 1983; Moss 1983; Schmitz 1990), but studies on the spatial arrangement of these systems in the Laminariales (Nicholson 1976; Schmitz 1984; Scrosati 1993) showed important differences from vascular plants. Sieve filaments (the translocation structures) in kelps commonly run in parallel along the medulla, from the blade tip to the holdfast, showing transverse interconnections between neighboring filaments. In the blade, sieve filaments branch from the medulla sideways towards the blade surface in a more or less continuous manner throughout the length of the blade, producing an intricate lateral network because of the abundant branching in the filaments. For generally single-bladed genera, such as Laminaria, such an internal architecture does not resemble the fractal-like three-dimensional pattern of iterative branching typically shown by transport systems in vascular plants (West et al. 1999), although the pattern may be more complex in kelps that produce several blades through iterative branching, such as Macrocystis (Lobban 1978; North 1994). Species of the Gigartinales and Gelidiales, on the other hand, lack a specialized network of cells for long-distance transport (Graham and Wilcox 2000). These seaweeds do not need a specialized distribution network for metabolites because they are generally thinner and smaller than kelps and, as all seaweeds do, take up nutrients from the seawater and perform photosynthesis throughout the entire thallus surface (Lobban and Harrison 1994). Therefore, on theoretical grounds, the value of 0.25 (1/4) predicted for the interspecific length–biomass exponent for plants (West et al. 1999) would not be expected to apply to seaweeds with flat bodies. The empirical findings of the present study confirm such an expectation.

It is worth noting that even some of the plant groups used by Niklas and Enquist (2001) to test the universality of the length–biomass relationship among primary producers do not conform to the predicted trend when analyzed separately. For example, the length–biomass exponent found for trees (0.35) is significantly higher than the universal value of 0.25 (Niklas and Enquist 2001). In fact, Niklas and Spatz (2004) recently found that no single scaling rule applies across the entire size range for vascular plants with self-supporting stems. They found that scaling relationships vary across species owing to the variability in biomass partitioning patterns and ecological responses to habitat conditions. The conclusions of Niklas and Spatz’s (2004) study and the results of the present study suggest that the taxonomic reach of the biomass–length predictions made by the model developed by West et al. (1999) should be further investigated.

At the beginning of the present report, it was mentioned that another approach to testing the universality of a model is to critically examine its theoretical basis. This was not within the objectives of the present study, but it is important to note that the theory behind the models developed by West et al. (1997, 1999) is being currently debated. Criticisms on model assumptions and data analyses used for model validation are frequently being provided (Dodds et al. 2001; Darveau et al. 2002; Weibel 2002; Borrego and Konarzewski 2004, 2005; Li et al. 2005; Reich et al. 2006; White et al. 2006), although clarifications and refutations to such arguments are also appearing as a result (Savage et al. 2004; West et al. 2004; Brown et al. 2004a, 2004b, 2005; West and Brown 2005). A particularly relevant criticism is that even vascular plants do not display an ideal fractal-like pattern in their vascular system (McCulloh et al. 2003; Kołowski and Konarzewski 2005), as originally assumed by West et al. (1997, 1999) to build their models for primary producers. The current intensity of the discussion suggests that the theoretical basis of the models by West et al. (1997, 1999) may have room for improvement (Harte 2004;
It is now clear that future theoretical developments for primary producers should be based on a greater diversity of organisms than previously considered, including groups, like predominantly bidimensional seaweeds, that display patterns of length–biomass allometry different from the proposed universal trend.

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References


