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Allometric models effectively predict *Saccharina latissima* (Laminariales, Phaeophyceae) fresh weight at local scales

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Abstract

Obtaining reliable estimates of algal biomass is key to assessing the contributions of macroalgae to nearshore ecosystems and to monitoring the effects of environmental change on macroalgal-dominated reefs. Using non-destructive methods to estimate macroalgal biomass leaves algal beds intact but requires precise allometric models (e.g., length–weight relationships). In this study, we established allometric relationships for the widespread kelp, *Saccharina latissima*, in the Salish Sea. Thalli were harvested from five sites across two regions in Southern British Columbia and the abilities of four non-destructive metrics (stipe length, blade length, blade width, and total thallus length) to predict thallus fresh weight were compared. Allometric models were developed for each region for all combinations of thallus metrics to explain thallus fresh weight and models were ranked based on their *AICc* scores. Finally, using our largest sample ($n = 114$ individuals), we performed a resampling experiment to determine the appropriate sample size for constructing local models. These models can be developed from as little as 2 hours of field data collection and are inexpensive and effective methods for non-destructively estimating *S. latissima* biomass.

Keywords Phaeophyceae · Allometry · Rocky subtidal · Salish Sea · Biomass

Introduction

Kelps (Laminariales, Phaeophyceae) provide important ecosystem services to nearshore marine communities; they create habitat (Christie et al. 2003; Teagle et al. 2017), supply nutrients and detritus to food webs (Duggins et al. 1989; Krumhansl and Scheibling 2012), sequester carbon (Wilmers et al. 2012), and alter coastal hydrodynamics (Jackson and Winant 1983). Kelp forests are among the most productive habitats on the planet (Mann 1973; Brady-Campbell et al. 1984; Duggins et al. 1989) and are hotspots for coastal biodiversity (Bodkin 1988; Christie et al. 2003; Teagle et al. 2017; Miller et al. 2018; Lamy et al. 2020). Unfortunately, recent reports suggest declines in kelp abundance in many parts of the world (Filbee-Dexter et al. 2016; Krumhansl et al. 2016; Filbee-Dexter and Wernberg 2018; Christie et al. 2019; Smale 2020; Starko et al. 2019; Wernberg et al. 2019), raising concerns about the potential for losses of the ecological services kelp forests provide (Filbee-Dexter and Wernberg 2018; Smale et al. 2019; Wernberg et al. 2019). Having precise estimates of local kelp biomass is important for understanding how kelp forest ecosystems are changing and to accurately quantify the magnitude of losses (Gevaert et al. 2001; Reed et al. 2009; Kim et al. 2017).

Kelp biomass estimates are commonly used in studies for long-term ecological monitoring and to study the impacts of climate change on kelp forest ecosystems (e.g., Gevaert et al. 2001; Reed et al. 2009; Kim et al. 2017; Cavanaugh et al. 2019). For example, Gevaert et al. (2001) established a relationship between thallus length and carbon and nitrogen content in *Saccharina latissima* which they used to monitor changes in primary production over the course of a year. Similarly, the standing crop biomass and net primary productivity of *Macrocystis pyrifera* off the coast of California were determined by Reed et al. (2009) from frond and plant density metrics. This relationship was then used to distinguish between natural seasonal variation and long-term directional trends (Bell et al. 2015). Kim et al. (2017) established allometric relationships between fresh weight

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and both total length and blade number for *Ecklonia cava*, allowing non-destructive ecological monitoring of this habitat-forming, commercially valuable species.

To estimate kelp biomass, the mass of individual thalli within a predetermined area (e.g., often 1 m^2) must be measured and this biomass is then extrapolated over the study area. Such sampling, wherein the thalli within a given area are removed for weighing, is destructive and disruptive to community structure (Bodkin 1988; Clark et al. 2004; Watt and Scrosati 2013). An alternative method is to estimate biomass from non-destructive thallus measurements taken in situ (Gagne and Mann 1987; Gevaert et al. 2001; Reed et al. 2009; Kim et al. 2017). However, this requires an understanding of which thallus metrics best predict thallus fresh weight and the presence of a pre-existing model that describes the relationship(s) between the thallus metric(s) and fresh weight. Despite the wide use of biomass estimates in ecological studies, studies evaluating the use of different non-destructive in situ measurements remain scarce and restricted to only a few populations and geographical locations (e.g., Gevaert et al. 2001; Reed et al. 2009; Stagnol et al. 2016; Kim et al. 2017).

In this study, the relationship between morphological metrics and thallus fresh weight was modeled for *S. latissima* (sugar kelp) in two regions of the Salish Sea. *Saccharina latissima* is an abundant and geographically widespread perennial kelp that provides habitat for many organisms (Bartsch et al. 2008; Christie et al. 2009). It is also cultivated for human and animal consumption, for biofuels, and for compounds used in the cosmetics, health food, and drug industries (Bartsch et al. 2008; Peteiro and Freire 2013; Peteiro et al. 2016). Additionally, *S. latissima* is used alongside fish aquaculture for bioremediation (e.g., to reduce ammonium levels; Handå et al. 2013). Allometric models of *S. latissima* could be useful for the aquaculture industry to determine crop biomass, economic yield, and product "suitability" (Peteiro and Freire 2013) as well as in monitoring or ecosystem research to determine standing crop biomass, net primary productivity, or carbon and nitrogen content (Brady-Campbell et al. 1984; Gevaert et al. 2001; Stagnol et al. 2016). However, allometric relationships have not previously been explored for this species along the Pacific coast of North America. Here, we test the ability of four non-destructive metrics to predict fresh (i.e., wet) biomass. Based on work conducted in the Northeast Atlantic on this species (Gevaert et al. 2001; Stagnol et al. 2016), we hypothesized that thallus length would serve as the single best predictor of thallus fresh weight. We therefore specifically compared the performance of models containing thallus length to more complex models that require more time to produce. We sampled from two regions to determine the generality of our results and although our intention was not to comprehensively describe morphological variation across regions and/or habitats, our comparison between regions will lend insight into the relevant spatial scale for constructing local models. Finally, using data from the site with the largest sample, we perform a resampling experiment to determine the appropriate sample size required to achieve precise local models.

Materials and methods

Study site

Saccharina latissima thalli ($n = 186$ total) were collected from five sites in two regions. The first region, Protection Island (PI), near Nanaimo, B.C. (49.1833 N, − 123.9231 W) was sampled on 16 and 31 January 2019 (Fig. 1a) resulting in the largest sample from a single site ($n = 114$). The collection area is a sheltered, shallow, sloping sandy beach. The thalli were attached to shells or small rocks or were free-floating drift. Collections were made in the evening between 0.5 and 2 m above Canadian chart datum (mean lower low water large tide), and were stored in a plastic tote and sampled the following day. The second region was the Southern Gulf Islands (SGI) of B.C., Canada which was sampled on 25 and 26 June 2018 and contained four sites: Fulford Harbour (48.7551 N, − 123.4441 W; $n = 14$), Isabella Point (48.7542 N, − 123.4427 W; $n = 12$), Russell Island (48.7502 N, − 123.4054 W; $n = 22$), and Portland Island (48.7311 N, − 123.3780 W; $n = 24$) (Fig. 1a). Each of these sites has rocky cobble substrates and limited wave action, mostly due to frequent boat and ferry traffic. Shoreline classifications conducted by ShoreZone (Howes et al. 1994) rank each of these sites as "protected" or "semi-protected". Thalli from SGI were harvested using SCUBA between 0 and 5 m depth relative to Canadian chart datum. The thalli selected for collection at each site were chosen to encompass the range of sizes present. We note that PI was sampled in the intertidal zone, while SGI collections were collected in the subtidal zone. This represents the habitat at which *S. latissima* was most abundant at each site.

Sampling methods

Four metrics of algal size (Gendron 1985; Gagne and Mann 1987; Kim et al. 2017) were measured (in cm) using a fabric tape measure: stipe length (SL), measured from the base of the holdfast to the start of the blade; blade length (BL), measured from the start of the blade to the distal tip of the blade; thallus length (TL), calculated as stipe length + blade length; and blade width (BW), measured at the widest point of the blade (Fig. 1b). Prior to weighing thalli, sand and obvious macro-organisms were removed from the thalli and excess water was shaken off to minimize its influence on fresh weight. The PI thalli fresh weights (FW, in g) were measured with Pesola brand (Kapuskasing, Ontario, Canada) spring scales (0–30 g

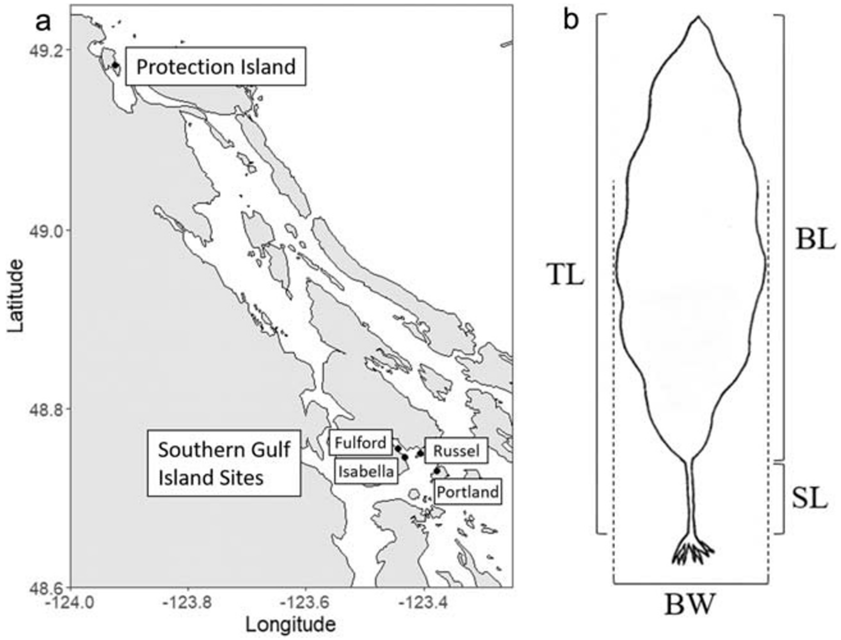

Fig. 1 Location of the five *Saccharina latissima* collection sites off of Vancouver Island, B.C (**a**). The Southern Gulf Island (SGI) sites are comprised Russell Island, Fulford Harbour, Isabella Point, and Portland Island. Only one site was sampled in the Protection Island region. Schematic of thallus metrics used to estimate thallus fresh weight: stipe length (SL), blade length (BL), thallus length (TL), and blade width (BW) (**b**)

and 0–1000 g) by hooking the thallus directly onto the spring scale. The SGI thalli fresh weights were measured using an Ohaus (USA) brand spring scale (0–20 g, 0–100 g, 0–500 g, 0–2000 g) either by placing the thallus inside a pre-weighed collection bag (for large specimens) or by hooking the thallus directly onto the spring scale and using a spring scale with appropriate resolution. All measurements were made by one researcher to reduce variability in sampling. The PI thalli were measured in the lab the morning following collection, whereas the thalli from the SGI were measured on a boat soon after being collected or on the dock at the end of the field day. Following collection and prior to measurement, thalli were kept in totes to reduce desiccation.

Data analysis

To determine the shape of relationships between fresh weight and each variable independently, we first fit both linear and power relationships to raw data and compared model fit using the corrected Akaike's information criterion (*AICc*) value. Next, in order to compare multivariable models, we log-transformed (base 10) all variables and fit uni- or multivariate linear models to these transformed data. Allometric relationships for algae are typically power relationships (Gevaert et al. 2001; Scrosati 2006; Starko and Martone 2016) and by log transforming the data, the exponent becomes the slope of the log-log plot, aiding interpretation. Moreover, because linear models are a special case of power relationships, log transformations allowed us to compare models with multiple variables that potentially have different (e.g., linear vs. power) relationships with fresh weight. Linear models were generated of thalli fresh weight as a function of each dimensional metric and combinations of them. Note that because thallus length is equal to stipe and blade length combined, thallus length was not included in any models containing these component variables. To account for potential differences in allometric relationships between the four collection sites within the SGI region, we fit models separately to each site, and then, when analyzing the pooled SGI dataset, incorporated models that allowed slopes and intercepts to vary by site. Altogether, this resulted in 9 models for the PI region, 9 models for each SGI site, and 27 models for the SGI region (pooled). The models were first checked using a series of diagnostic plots (model residuals vs. actual data, model predicted values vs. actual data, and a qqplot and histogram of model residuals) and were then ranked based on the *AICc* value. The *AICc* value was used to account for the small sample sizes (Burnham and Anderson 2002) and a difference in *AICc* of greater than 2 was used to consider whether certain models were significantly better than others. Following the comparison of region-specific models, we assessed the potential importance of incorporating regional differences in slope and intercept of models by constructing and comparing models ($n = 27$) of the full dataset ($n = 186$) including each linear measurement and allowing intercepts and slopes to vary by region. Note that due to the nested nature of "site" within only one region (SGI), we did not compare models that included both "site" and "region" but acknowledge this as a limitation of our study design.

Finally, to lend insight into the sample size required to develop an accurate local model, we performed a resampling experiment by randomly sampling (with replacement) a set number of samples from the PI dataset ($n = 114$) and fitting a linear model to fresh weight vs. thallus length (which we expected to be the best single predictor; Gevaert et al. 2001; Stagnol et al. 2016). We performed this analysis for sample sizes ranging from 10 to 100 in increments of five. For each sample size, we conducted 1000 iterations and calculated differences in slope and intercept from the model parameters generated from the full PI dataset. All analyses were conducted in R version 4.0.2 (R CORE Team 2018), using the following packages: bblme (Bolker and R Development Core Team 2020), DLMtool (Carruthers and Hordyk 2020), lme4 (Bates et al. 2015), MuMIn (Barton 2019), nls (Baty et al. 2015), Rmisc (Hope 2013), and tidyverse (Wickham et al. 2019).

Results

Modeling the allometric relationships

The thalli collected from PI and SGI had similar minimum sizes and weights, but SGI thalli reached larger maximum sizes (i.e., greater values of all metrics; Table 1). Many thalli from PI showed distinct signs of interannual growth in the form of a mid-blade width reduction, resulting in a peanut-like blade shape (Parke 1948). Of the eight univariate models fit to predict fresh weight (four for each region; Fig. 2), we found that, in seven cases, a power relationship better fits the data than linear models ($\Delta AIC > 2$). The exception was the relationship between stipe length and fresh weight for the PI sample. In this case, the linear and power curves were considered equivalent ($\Delta AICc = 0.005$). Indeed, the exponent of the power curve of this relationship was equal to 1.01, which is consistent with linearity.

A large majority of site or region-specific models tested explained more than 80% of the variation in fresh weight (Supplementary Table 1), suggesting that allometric models can be effectively used to predict thallus fresh weight of *S. latissima*. Of the univariate models compared, thallus length was consistently the best predictor of fresh weight. This was true for samples from four of five sites, with Fulford Harbour as the exception, where blade length explained approximately 4% more variation in thallus fresh weight than did total thallus length (Table 2). While both thallus length and blade length generally explained the most variation in fresh weight, stipe length was the worst predictor, with R^2 ranging from ~ 0.2 to 0.5 depending on site. Blade width was a much stronger predictor than stipe length, explaining more than 70% (and often > 85%) of the variation in fresh weight in all cases (Supplementary Table 1). However, blade width univariate models were always outperformed by models involving blade length and/or thallus length across all sites (Supplementary Table 1).

Table 1 Summary of *Saccharina latissima* thallus measurements taken between the two sample regions: stipe length (SL), blade length (BL), thallus length (TL), blade width (BW), and fresh weight (FW)

	Protection Island (*n* = 114)			Southern Gulf Islands (*n* = 72)		
	Min	Max	Mean ± SD	Min	Max	Mean ± SD
SL (cm)	0.5	3	1.5 ± 0.52	1	36	16.9 ± 9.13
BL (cm)	10	155	69.0 ± 33.77	8	214	62.8 ± 50.15
TL (cm)	11	157	70.4 ± 33.95	15	242	79.7 ± 54.14
BW (cm)	4	28	15.6 ± 5.37	4.5	79	28.4 ± 17.59
FW (g)	3	220	62.6 ± 43.08	2	980	171.1 ± 224.00

Among the PI models, the BL + SL + BW model was the best ranked model. However, the thallus length and blade length univariate models explained only 2.9-3.0% less variation than the best ranked multivariate model. Similarly, across all four sites in the SGI region, the top models tended to include blade length or thallus length along with blade width as predictors of fresh weight. However, the best model fit to the Fulford Harbour sample included blade length and stipe length. Across all SGI sites, the top univariate model had an R^2 that was within 0.03 of the top multivariate model. There were strong similarities between thallus length models and top-ranked multivariate models in terms of their effectiveness in making predictions about fresh weight (Fig. 3).

Identifying differences between sites and regions

To determine the effect of collection site for the SGI samples or collection region for comparisons across SGI (pooled) and PI samples, these terms were included as fixed effects in linear models. Although thallus length and blade length were the best univariate predictors across all sites, there were significant differences between allometric relationships at the site level and these were especially different when comparing across the two regions (e.g., Fig. 5). Across the entire SGI dataset, models that included "site" tended to outperform those that did not include this term. However, the difference in variation explained by each model (with or without "site" term) was small. For example, the addition of "site" into the top-ranked multivariate model containing TL and BW only resulted in an increase in R^2 of 0.006 and this model was statistically indistinguishable in terms of performance from the same model without "site" included ($\Delta AICc = 1.2$). Thus, incorporating site did not substantially improve the ability of models to predict fresh weight in the SGI region. Greater differences in allometric relationships were found between regions (i.e., PI vs. SGI). Indeed, models fit to the pooled dataset incorporating either an additive or interacting effect with "region" always outperformed similar models without these terms (Supplementary Table 1). For example, the top-ranked model of the full dataset was TL * region, suggesting differences in slope (i.e., exponent of the untransformed data)

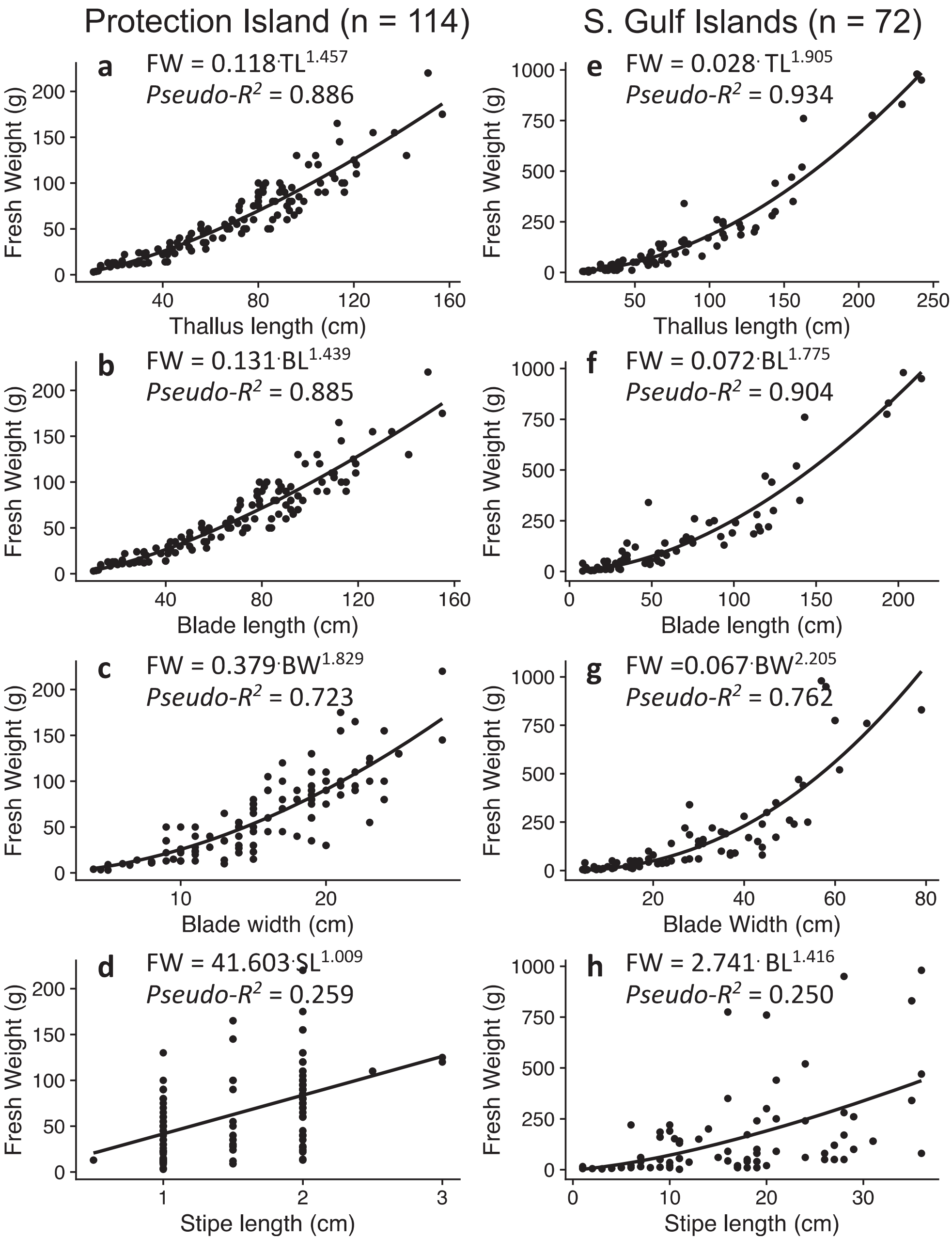

Fig. 2 Allometric relationships between thallus fresh weight and four non-destructive metrics. Thallus length (**a**, **e**), blade length (**b**, **f**), blade width (**c**, **g**), stipe length (**d**, **h**), for kelps from Protection Island (**a**–**d**) and Southern Gulf Islands (**e**–**h**). Data from sites ($n = 4$) in the Southern Gulf Islands are pooled

of allometric relationships across sites. This model explained nearly 12% more variation in fresh weight than did the top model that did not include "region" as a fixed effect (BL + SL + BW; Supplementary Table 1). Overall, models fit to the full dataset explained substantially less variation ($R^2 < 0.65$) than models fit separately to each region, strongly suggesting differences in allometric relationships between PI and SGI regions.

Evaluating the influence of sample size

To determine the appropriate sample size for developing local allometric models to predict fresh weight, we performed a resampling experiment with data collected from PI. Not surprisingly, increasing sample sizes led to greater precision in model parameters. For example, when sample sizes were as low as 15, intercepts could be off from parameter estimates of the full dataset by more than 1.5 and slopes could be off by as much as 0.8. This suggests that low sample sizes could result in large biases in allometric model construction. However, with sample sizes of approximately $n = 25$, differences from parameter estimates of the full data tended to level off and at sample sizes > 50, variation in parameter estimates was generally consistent with those of higher sample sizes. This suggests that a sample size of 25

Table 2 Top-ranked multivariate and univariate models for predicting fresh weight from non-destructive metrics as well as the thallus length univariate model, where this was not the top-ranked univariate model. Models are fit separately to each of the five sites except for the pooled sample, which includes all SGI samples. The pooled models do not include those that have site as a predictor variable. All variables are log-transformed. Variables are abbreviated as stipe length (SL), blade length (BL), thallus length (TL), blade width (BW), and fresh weight (FW)

Region	Site	Model	$\Delta AICc$	R^2
Protection Island	Protection (n = 114)	FW = 0.621*BW + 1.008*BL + 0.131*SL − 0.863	0	0.952
		FW = 1.404*TL − 0.838	51.0	0.923
Southern Gulf Islands	Fulford (n = 14)	FW = 1.975*BL − 0.356*SL − 1.149	1.9	0.944
		FW = 1.879*BL − 1.391	0	0.944
		FW = 2.282*TL − 2.367	8.2	0.900
	Isabella (n = 12)	FW = 1.082*BL + 0.755*BW − 0.931	1.0	0.869
		FW = 2.069*TL − 1.892	0	0.839
	Portland (n = 24)	FW = 0.970*BL + 1.007*BW − 1.233	0	0.929
		FW = 1.818*TL − 1.491	8.3	0.902
	Russel (n = 22)	FW = 1.641*TL + 0.213*BW − 1.318	2.4	0.900
		FW = 1.868*TL − 1.448	0	0.902
	Pooled (n = 72)	FW = 1.477*TL + 0.518*BW − 1.519	0	0.919
		FW = 1.973*TL − 1.714	8.8	0.902

may be adequate but 50 or more samples would be ideal for constructing models that effectively predict thallus fresh weight from non-destructive metrics.

Discussion

In this study we used allometric models to estimate the fresh weight of *S. latissima* thalli in two regions of the Salish Sea. Similar to past work conducted in Europe and Asia (e.g., Gevaert et al. 2001; Stagnol et al. 2016; Kim et al. 2017), we found that allometric models (particularly those involving thallus or blade length) explained a substantial portion of the variation in total thallus fresh weight. Models were evaluated based on their $AICc$ and R^2 values and many of the models compared showed the potential to effectively predict thallus fresh weight. The best multivariate models and the univariate thallus length model for *S. latissima* accounted for high levels of thallus biomass variability for samples from both PI (R^2 = 0.952, R^2 = 0.923 respectively) and SGI (R^2 = 0.919, R^2 =

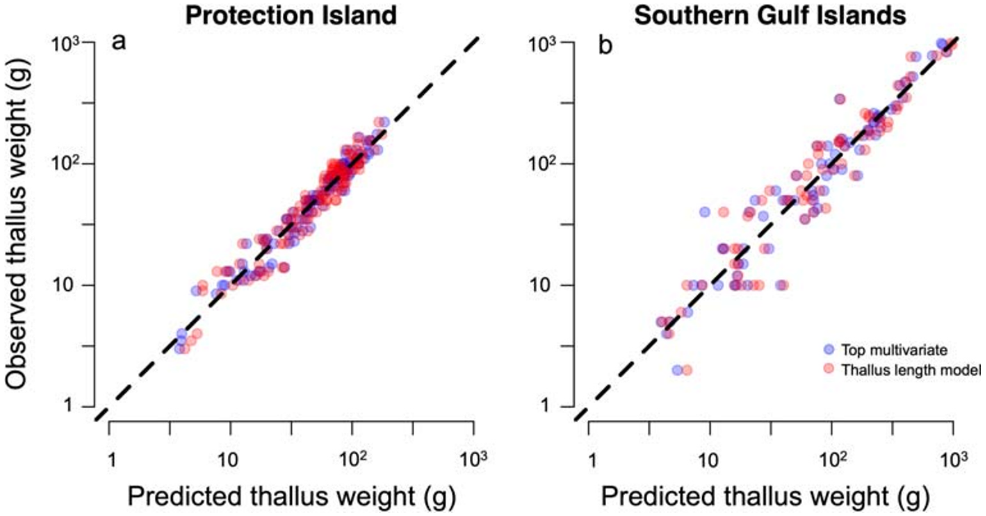

Fig. 3 Top multivariate (see Table 2) and thallus length models from the Protection Island sample (**a**) collected January 2019 (n = 114) and Southern Gulf Islands sample (**b**) collected June 2018 (n = 72). Dotted line represents a 1:1 relationship between observed and predicted thallus weight. All models are significant: Protection Island (top multivariate: BL + SL + BW, F = 745.1, df = 3, 110, P < 0.0001, R^2 = 0.952; thallus length: F = 1358.0, df = 1, 112, P < 0.0001, R^2 = 0.923), Southern Gulf Islands (top multivariate: TL + BW + Site, F = 372.2, df = 2, 69, P < 0.0001, R^2 = 0.913; thallus length: F = 656.3, df = 1,70, P < 0.0001, R^2 = 0.902)

0.902, respectively; Table 2) and offer effective tools to estimate biomass in those areas. Although the univariate thallus length model accounted for less of the variation than the multivariate models (2.9% less from PI and 1.7% less in the SGI), the univariate model may be preferred for field work. Reducing the number of measurements needed per thallus increases the sampling speed and could allow researchers or aquaculturists to increase their sample size or reduce their time spent sampling. Upon testing for differences in model parameters across sites and regions, we have shown that the model scope should be limited to local areas or areas with similar environmental conditions for precise results. While our methods do not comprehensively address the importance of spatial scale in driving allometric relationships, they do suggest that across some sites with similar environmental conditions (i.e., SGI), site-level variation may be small enough to ignore when constructing models. However, in other cases, populations at different locations may differ substantially in their allometric equations, requiring the construction of site or region-specific models to allow for precise estimation of thallus fresh weight (i.e., PI vs. SGI).

The top *S. latissima* models from each region (PI and SGI) were compared to determine if allometric models could be feasibly developed for the broader Salish Sea region. Results suggested the model's ability to predict thallus fresh weight was restricted to the location for which the model was derived. The top-ranked model from the full data set predicted 27.3–30.6% less of the variation in thalli fresh weight than the top-ranked region-specific models. Use of a "global" model would, for example, substantially overestimate the fresh weight of samples collected from PI when using thallus length as a predictor, especially as thalli increased in length (Fig. 4). Lower fresh weight per unit thallus length from the PI site (relative to SGI sites) may be due to narrower blades found at PI or may suggest that kelps from the PI site have thinner blades or lighter, smaller holdfasts, two metrics that were not accounted for in the models.

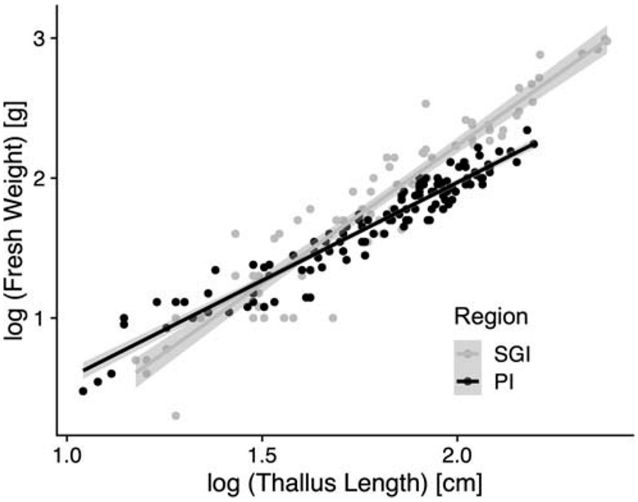

Fig. 4 Thallus fresh weight as a function of total thallus length for samples from the Southern Gulf Islands (pooled; $n = 72$) and Protection Island ($n = 114$). Linear models and 95% confidence intervals of those models are also shown. The relationship between fresh weight and thallus length significantly differs between regions (ANCOVA: thallus length: $F = 1838.38$, $P < 0.001$; region: $F = 41.64$, $P < 0.001$; thallus length * region: $F = 52.79$, $P < 0.001$)

Multiple environmental variables could explain differences in allometric models between PI and SGI. In particular, PI samples were collected intertidally during the winter, while SGI samples were collected from the subtidal zone during the summer. Kelps are a morphologically diverse group and exhibit a high degree of morphological variability (Dayton 1985; Koehl 2008). Previous studies have linked factors such as time-of-year (Gevaert et al. 2001 in *S. latissima*), wave exposure (Krumhansl and Scheibling 2012; Starko et al. 2020 in multiple kelp species including *S. latissima*), age of thalli (Nielsen et al. 2014 in *S. latissima*), light levels (Peteiro and Freire 2013 in *S. latissima*), and tidal height (Starko and Martone 2016 in multiple kelp species including *S. latissima*) to morphological variation such as blade thickness and holdfast size. Although the current study did not take environmental factors or kelp age into account, such parameters are likely important and may explain differences between populations from these two regions. Measuring seasonal differences in wave exposure, water temperature, nutrients, light levels, and tidal forces among locations might help determine what processes in the Salish Sea act as drivers for *S. latissima* allometry. PI and SGI are separated by approximately 80 km, which may be enough to result in genetic isolation of these regions. If this is true, then it is feasible that differences in allometric models could be the result of local adaptation and genetic differences between populations, perhaps in response to variation in the environment—intertidal sandy beach vs. subtidal cobble slope (e.g., Augyte et al. 2019; Starko et al. 2020). Alternatively, phenotypic plasticity may explain this variation in allometric relationships. While phenotypic plasticity is well known from kelps (including *S. latissima*) (Koehl et al. 2008), plasticity in allometric relationships per se has not previously been demonstrated, to our knowledge. Regardless of the drivers behind variation in allometric equations across regions, our results suggest that the seasonal or habitat variability may be too great to develop a model that is applicable to the entire Salish Sea, but models derived for local populations are effective for predicting thallus fresh weight.

When the models developed here are compared to models developed in the eastern English Channel by Gevaert et al. (2001), there are notable differences in parameters of the thallus length models, indicative of morphological differences between European and Salish Sea populations. The models developed for *S. latissima* in the Salish Sea had similar exponents to that developed for specimens in France (1.457 to 1.905 here vs. 1.782 in France; Gevaert et al. 2001) but allometric constants (i.e., intercept) were larger in Salish Sea

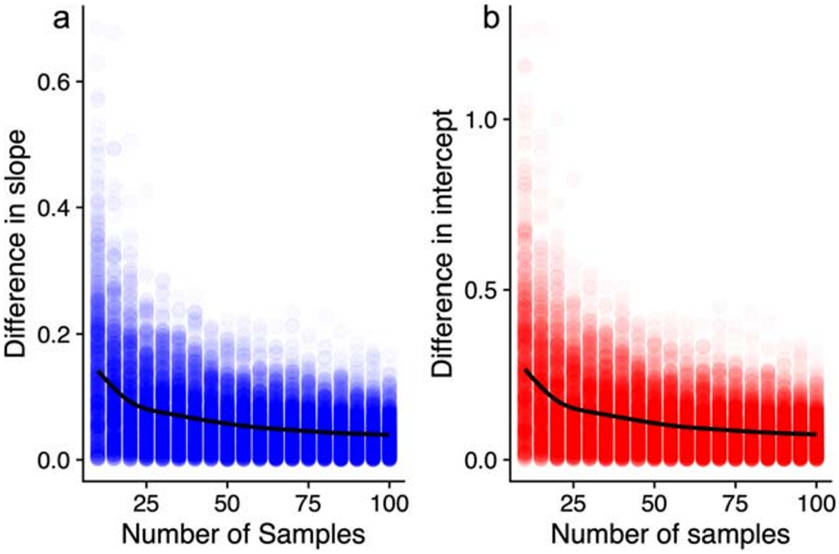

Fig. 5 Influence of sample size on allometric model precision. Difference in slope (**a**) and intercept (**b**) from the full Protection Island dataset ($n = 114$ kelps) for fresh weight vs. thallus weight models constructed from random samples of increasing size. Each point represents one of 1000 random samples drawn from the full dataset with replacement for sample sizes ranging from 10 to 100 (by increments of five)

populations (0.028 to 0.118 here vs. 0.00949 in France). Our results therefore indicate that thalli sampled by Gevaert et al. in France were lighter for a given length than Salish Sea populations from either region (PI or SGI) investigated in our study. This strongly supports the notion that models should be created at a regional level as opposed to using a "global" model.

To produce a field-efficient, non-destructive univariate model, a region-specific model is required to account for the morphological variability among *S. latissima* thalli collected from different habitats and in different seasons. Based on our resampling experiment, a minimum of 25–50 specimens should be used to construct these models. We measured the amount of time it took to construct models and the time required to sample 50 thalli is approximately 2 h. The breakdown of time required is: 30 min to collect specimens; 7 min to measure thallus lengths when using the univariate thallus length model, or 24 min to measure all four metrics when using a multivariate model; 20 min to lay out specimens for measurement and weigh them; and 60 min to complete data entry and model creation in software such as R. Creating region-specific allometric models allows for more accurate predictions of biomass and therefore should lead to more robust, precise studies.

While the results of this study strongly suggest that even univariate allometric models are effective at estimating thallus fresh weight, there are caveats to our results. In particular, that PI samples were collected intertidally in the winter and SGI samples were collected subtidally during the summer makes it impossible for us to tease apart the effects of season, habitat, collection depth, and region. While our goal was not to comprehensively investigate the drivers of variation in allometric models, this could offer an enlightening avenue for future research. Moreover, regardless of which factor(s) drive variation in allometric models, univariate models of thallus length were effective at predicting fresh weight at all sites. Another caveat of our study is that although we detected only minimal differences in allometric models across individual SGI sites, each site had relatively low sample sizes ($n = 12$ to 24). Our resampling experiment suggests that a sample size of 50 or greater is ideal for constructing allometric models and thus it is possible that our sample sizes for individual SGI sites were too low to effectively determine the extent of allometric variation across SGI sites. Nonetheless, variation in thallus fresh weight was strongly predicted from allometric models regardless of whether SGI sites were pooled or kept separate (Table 2, Supplementary Table 1).

There were also several sources of error in this study that, if controlled for, could potentially improve the predictive power of allometric models. Differences in methodology between the two regions may have contributed to some of the perceived variation. The thalli from the SGI were measured on a boat soon after being collected or on the dock at the end of the field day, whereas the PI thalli were collected in the evening and measured in the lab the morning following collection. When thalli were not measured immediately after collecting, they were kept in totes to reduce desiccation; however, partial desiccation between collection and weighing may have impacted model parameters. Undulations in the thallus also make measuring thallus length challenging at times. However, the fact that thallus length models still tended to predict 90% or more of the variation in fresh weight suggests that error introduced by undulations may have little effect on the effectiveness of allometric models.

Ecological studies often require estimates of kelp biomass, which usually require destructive sampling that can disrupt community structure. As a non-destructive sampling alternative, we developed predictive allometric models to estimate thallus fresh weight in the sugar kelp, *S. latissima* in the Salish Sea, B.C., Canada. Although some multivariate models explained slightly more of the variability in sugar kelp thalli fresh weight, the univariate model based on thallus length alone explained almost as much variation but was more time-efficient because only one metric was needed. Although the allometric models were not robust enough to capture the allometric variation across the two regions investigated, local models were quickly and easily generated and provide accurate results. This approach offers a non-destructive yet efficient in situ method for estimating the local biomass of this and likely other ecologically or commercially important kelp species. This approach could be of use both to field ecologists and to aquaculturalists interested in estimating the standing biomass of kelp forests or kelp farm crops without destructive sampling.

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