

Article

Temporal and Spatial Invariance of Allometric Parameters for Predicting Leaf Biomass in *Zostera marina*: A Theoretical and Empirical Reassessment

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Abstract

Anthropogenic pressures and climate change are accelerating the degradation of seagrass ecosystems and the ecological services they provide. In temperate systems, the decline of eelgrass (*Zostera marina*) has raised noticeable concern, particularly as restoration actions (e.g., transplantation) require accurate, nondestructive estimates of leaf biomass. Allometric power-law models can provide such proxies, but their applied value depends on whether fitted parameters remain transferable across sites and sampling periods. Here, using two extensive and independently collected datasets from San Quintín Bay (SQ) and Punta Banda estuary (PB), we evaluate three formulations: M1 (biomass–length), M2 (biomass–length–width), and M3 (biomass–area surrogate). All three models produced consistent fits in both datasets, and parameter-comparison tests detected no significant between-site differences. Reciprocal cross-projections of monthly mean leaf biomass showed high concordance, supporting practical parameter stability within the SQ–PB domain. A model-selection analysis based on goodness of fit and parsimony further identified the bivariate model M2 as the best-performing proxy across sites. Taken together, these results support a practical interpretation in which eelgrass may express phenotypic plasticity through shifts in trait distributions (length and width), while the scaling relation linking morphology to biomass remains effectively stable. For applied restoration-comparison purposes, we therefore recommend using M2—preferably with site-fitted parameters, or pooled/mean parameters when supported by reproducibility tests—to estimate aerial production non-destructively and cost-effectively.

Keywords: eelgrass; nondestructive assessment; allometry; parametric invariance

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1. Introduction

Nowadays, marine ecosystems are increasingly affected by anthropogenic pressures and global climate change. In this context, changes in water attributes and other local stressors are undermining the sustainability of seagrass meadows, driving losses at unprecedented rates [1,2].

Because seagrasses offer food and shelter for many ecologically and economically important organisms [3–6], support nutrient cycling [7–9], stabilize shorelines by binding sediments with roots and rhizomes, contribute to detrital food webs [10,11], and play a key role in carbon sequestration [12,13], their decline has raised substantial scientific concern [14–16].

Eelgrass (*Zostera marina* L.) is a temperate intertidal–subtidal angiosperm [17] whose associated communities are among the richest and most diverse in coastal systems [18]. It dominates large stretches of the North Pacific and North Atlantic coasts [19]. By forming dense meadows, eelgrass can aid phytoremediation of contaminated sediments [20,21]. Eelgrass beds are also highly productive and contribute substantial organic material to shallow-water food webs [22,23] while providing habitat and shelter for fishes (including larvae), attached algae, and epifauna [24–27]. In some estuarine systems, eelgrass may account for up to 64% of total primary production [28].

Yet, like other seagrasses, eelgrass is increasingly threatened by anthropogenic impacts [29,30], motivating restoration actions such as transplantation [31–34]. A central restoration goal is to verify whether transplanted plots recover the ecological functions and values of natural meadows, which requires accurate estimates of standing stock and productivity [34–36].

Although conventional monitoring approaches can avoid long-term damage to natural populations [37], they are still invasive and may disrupt developing transplants [38]. This makes reliable, nondestructive methods essential; in this regard, allometric approaches have been widely used to support nondestructive eelgrass assessment protocols [39].

The power function setup embodied in Huxley’s theory of constant relative growth has been widely used across biology [40–47]. In functional–structural plant models, allometric relationships often serve as practical surrogates for traits that are costly or difficult to measure, using simple measurements such as length or diameter. In seagrass research, Duarte [48] compiled architectural and growth data across many species and reported consistent fits of power-law expressions like Huxley’s equation for multiple variable pairs, using them to relate module size to differences in productivity among species.

For *Zostera marina*, McRoy [24] provided an early quantitative foundation for estimating standing stocks from population traits, later extending this line of work by linking eelgrass structure to standing stock and productivity through functional relationships [49]. Penhale [50] integrated biomass and productivity in eelgrass meadows (including the macrophyte–epiphyte assemblage), reinforcing the idea that productivity can be inferred from morphological and cover measurements. Jacobs [22] likewise illustrated size–production scaling in biomass and productivity analyses, anticipating the explicit allometric formalization commonly associated with Duarte [48]. Hamburg and Homann [51] then advanced the field by proposing and applying bivariate allometric formulations for leaf biomass, establishing the joint use of length and width as descriptors in eelgrass.

In previous work, we examined how to make allometric proxies derived from Huxley’s power function model more consistent and reliable for eelgrass assessment [52]. Beyond exploring how model complexity may improve consistency, we stress-tested the projection pipeline against two major sources of inconsistency: variability in fitted parameters and data/analysis quality. Across multiple studies, we showed that fluctuations in fitted exponents/coefficients and weak quality assurance routines can bias allometric projections, and we proposed standardized checks (e.g., outlier control and sample-size sensitivity analyses) to reduce error propagation [38].

However, the usefulness of an allometric proxy is not determined solely by point-estimate accuracy. A crucial and still underexplored issue is whether allometric parameters remain stable through time—the very property that makes nondestructive projections

cost-effective. Without temporal (and contextual) invariance, parameters fitted over a restricted interval can only be expected to perform reliably within that same window; parameters calculated in the past cannot be assumed to yield accurate projections today unless their invariance has been demonstrated.

This motivates reassessing whether allometric parameters can be transferred across time and space without loss of predictive reliability. In the present work, we expand our previous assessment of eelgrass allometric parameter invariance [39] using two extensive, independently collected datasets of eelgrass leaf biomass and associated morphometrics (length, width, and derived area). The first dataset, from the Punta Banda estuary (PB), includes 1440 individual-leaf biomass measurements with corresponding length and width. The second dataset, from San Quintín Bay (SQ), comprises 7980 paired triplets of biomass, length, and width.

Importantly, in this study, we treat invariance in fitted allometric parameters as a practical criterion for transferability of biomass projections, not as direct evidence of process-level invariance in growth, allocation strategies, or biomechanical constraints. Similar parameter estimates across datasets may arise from multiple causes, including aggregation effects, compensatory trait plasticity, or relatively non-contrasting environmental conditions between sites and time periods. Because key drivers known to influence eelgrass morphology (e.g., light availability, nutrient status, hydrodynamics, sediment conditions) are not explicitly modeled here, our inference is intentionally limited to the stability and predictive performance of the allometric proxies under the observed sampling contexts.

Building on the transferability conjecture in [39] and Huxley's allometric paradigm, the objective of this study is to evaluate whether allometric parameters linking eelgrass leaf biomass to leaf morphometrics can be used across independently collected datasets from PB and SQ for non-destructive biomass estimation.

Specifically, we aim to formalize and evaluate three related allometric formulations for leaf biomass prediction: a length-based proxy (M1), a length and width proxy (M2), and an area-surrogate proxy based on length $\times$ width (M3). We then compare parameter estimates between PB and SQ for each formulation, quantify practical transferability via reciprocal cross-site projections assessed by Lin's concordance correlation coefficient (CCC) at both the leaf and monthly-mean scales, and assess whether pooled or averaged parameter values provide adequate predictive performance when supported by reproducibility tests, with emphasis on the length-width formulation.

Section 2 describes the datasets and methods, including the theoretical motivation for the three formulations. Section 3 presents the results, Section 4 discusses implications and limitations, and Section 5 concludes.

2. Methods

2.1. Theoretical Approach

A key goal of Section 2.1 is conceptual transparency rather than mathematical virtuosity. We keep the presentation self-contained so that the functional forms used in the empirical analyses can be interpreted within standard allometric theory and are not treated as purely empirical "black boxes." Readers primarily interested in applications may therefore skip the derivation details and retain only the model formulations summarized below. Throughout, $w(t)$, $l(t)$, and $h(t)$ denote, respectively, the dry weight, length, and width of an individual eelgrass leaf at time t . For clarity and consistency with the three formulations stated in the introduction, Section 2.1 is organized into three short subsections that summarize the candidate allometric surrogates and their key equations:

2.1.1. (Model M1): Scaling of Leaf Biomass $w(t)$ as a Power Law of Leaf Length $l(t)$

One example of adaptation of nondestructive estimation based on allometric methods derives from Huxley's power function representation of $w(t)$ in terms of corresponding length $l(t)$, namely,

$$w(t) = \rho l(t)^\alpha \quad (1)$$

in which the parameters α , the allometric exponent, and ρ , the normalization constant, are positive and describe how the trait $w(t)$ scales with leaf length $l(t)$ [40,41].

2.1.2. (Model M2): Bivariate Scaling of $w(t)$ as a Power Law of Leaf Length $l(t)$ and Width $h(t)$

Following [53], and also abiding by the classic hypothesis of allometry [54,55], which states that the relative growth rates of two leaf traits $l(t)$ and $h(t)$ satisfy the constant proportions rules,

$$\frac{1}{w} \frac{dw}{dt} = \frac{p}{l} \frac{dl}{dt} \quad (2)$$

$$\frac{1}{h} \frac{dh}{dt} = \frac{q}{l} \frac{dl}{dt} \quad (3)$$

where p and q are positive constants.

To offer a pertinent biological justification for the above formalization, we begin by establishing that in *Zostera marina*, the leaves exhibit a belt-shaped architecture where the longitudinal increase dominates the leaf geometry while the width adjusts in a subordinate way to the elongation. Under proportional growth and relatively homogeneous tissue composition (parenchyma with stable proportions of water and dry tissue in short time windows), it is reasonable to model that the relative rate of mass change is a constant multiple of the relative rate of change in length (parameter p) and that the relative rate of width is, in turn, a multiple of the length (parameter q). These hypotheses are consistent with the widely documented use of power rules in monocotyledonous leaves and with non-destructive biomass approaches.

By the chain rule we have the following:

$$\frac{dw}{dt} = \frac{\partial w}{\partial l} \frac{dl}{dt} + \frac{\partial w}{\partial h} \frac{dh}{dt} \quad (4)$$

Replacing (2) and (3) in (4) (and assuming $\frac{dl}{dt} \neq 0$), we get the lineal first order Partial Differential Equation (PDE):

$$l \frac{\partial w}{\partial l} + qh \frac{\partial w}{\partial h} = pw. \quad (5)$$

To find the solution to Equation (5), we can rely on the method of characteristics. For that aim, we first note that according to the existence theorem for quasi-linear equations [56], the characteristic equations satisfy the following:

$$\frac{dl}{l} = \frac{dh}{qh} = \frac{dw}{pw} \quad (6)$$

Integrating in pairs results in independent invariants (first integrals):

$$\frac{h}{l^q} \quad (7)$$

and

$$\frac{w}{l^p} \quad (8)$$

Therefore, the general integral can be written as follows:

$$F\left(\frac{h}{l^q}, \frac{w}{l^p}\right) = 0. \quad (9)$$

A useful (and biologically interpretable) family is achieved by establishing a power function-like relationship between invariants:

$$\frac{w}{l^p} = \rho \left(\frac{h}{l^q} \right)^\beta, \quad (10)$$

which implies

$$w(t) = \rho l(t)^\alpha h(t)^\beta. \quad (11)$$

provided the consistency condition

$$\alpha = p - q\beta, \quad (12)$$

is satisfied M2 is thereby justified.

2.1.3. (Model M3): Scaling of $w(t)$ Using a Leaf-Area Surrogate, $a(t) = l(t) h(t)$

Now, let us consider a particular eelgrass leaf. Then, we will have $w(t) > 0$. Denote its area by means of the symbol $a(t)$. Then by recalling that eelgrass bears an approximately belted-shape leaf architecture and also following [52] for $a(t)$, we can consider the surrogate $a_p(t)$ defined as the product of $l(t)$ and $h(t)$, namely,

$$a_p(t) = l(t)h(t). \quad (13)$$

We notice that Equation (10) can be written in the equivalent form,

$$w(t) = \rho a_p(t)^\alpha h(t)^\theta. \quad (14)$$

Then direct algebraic manipulation of Equation (14) yields

$$\frac{w(t+\Delta t)}{w(t)} = \left(\frac{a_p(t+\Delta t)}{a_p(t)} \right)^\alpha \left(1 + \frac{\Delta h}{h(t)} \right)^\theta. \quad (15)$$

Since we observed that during the chosen marking interval, eelgrass leaf architecture and growth formed, resulting in negligible values for Δh , we might expect the ratio involving $a_p(t)$ in Equation (15) to be dominant. On the other hand, if we assume that $w(t)$ can be allometrically scaled in terms of $a_p(t)$, then there will be a constant α [55], such that

$$\frac{1}{w} \frac{dw}{dt} = \frac{\alpha}{a_p} \frac{da_p}{dt}. \quad (16)$$

And from this equation, we obtain

$$\frac{w(t+\Delta t)}{w(t)} = \frac{a_p(t)^\alpha}{a_p(t)^\alpha}. \quad (17)$$

Hence the dominance of the ratio involving $a_p(t)$ in Equation (15) is consistent with the assumption of an allometric scaling of $w(t)$ in terms of the $a_p(t)$ leaf area proxy. Furthermore, if Equation (17) holds for all t values, then both sides must be equal to a constant. Let ρ be that constant. Then we will have

$$w(t) = \rho a_p(t)^\alpha. \quad (18)$$

This justifies the form for model M3 that we advanced in Section 1.

For present empirical aims, we denote by means of the symbol $w_{ki}(t)$ for $k = 1, 2, \dots, n(i)$ the dry weight of the k – th individual eelgrass leaf collected at a monthly sampling interval $i = 1, 2, \dots, m$. Correspondingly, we let $l_{ki}(t)$ stand for its length. Then, if $\bar{w}_{li}(t)$ stands for the average leaf biomass observed at the i – th sampling period, using Equation (1), $\bar{w}_i$ acquires the form

$$\bar{w}_{li}(t) = \frac{\sum_{k=1}^{n(i)} \rho l_{ki}(t)^\alpha}{n(i)}. \quad (19)$$

for $i = 1, 2, \dots, m$.

Similarly, by letting h_{ki} for $k = 1, 2, \dots, n(i)$ stand for the width of the k -th individual eelgrass leaf collected at the sampling interval $i = 1, 2, \dots, m$, Equation (11) furnishes the allometric projections $\bar{w}_{lhi}(t)$ in the form

$$\bar{w}_{lhi}(t) = \frac{\sum_{k=1}^{n(i)} \rho l_{ki}(t)^\alpha h_{ki}(t)^\beta}{n(i)} \quad (20)$$

for $i = 1, 2, \dots, m$.

Similarly, Equations (11) and (18) yield

$$\bar{w}_{ai}(t) = \frac{\sum_{k=1}^{n(i)} \rho l_{ki}(t)^\alpha h_{ki}(t)^\alpha}{n(i)} \quad (21)$$

for $i = 1, 2, \dots, m$.

Sampling sites were located at Punta Banda estuary (PB; 31°43'59" N, 116°37'59" W) and San Quintín Bay (SQ; 30°27'04" N, 115°59'00" W), Baja California, Mexico.

2.2. Statistical Methods

The analyses relied on MATLAB 2025b's default solver settings, which, for unconstrained nonlinear regression, employ the Levenberg–Marquardt algorithm. Convergence is determined internally by MATLAB 2025b, based on relative changes in parameter estimates and residual norms falling below predefined tolerance thresholds. Initial parameter values were either user-specified based on biologically reasonable values or, when not explicitly provided, automatically initialized using MATLAB 2025b's internal heuristic procedures.

To evaluate the performance of the three candidate allometric formulations (M1, M2, M3) to describe eelgrass leaf dry weight from morphological measurements, we relied on a model selection study. The comparison was based on goodness-of-fit metrics at the individual-leaf level (standard error (Se), sum of squared errors (SSE), root mean squared error (RMSE), mean squared error (MSE), the mean standard deviation (mean(e)) and standard deviation (sd(e)) of the residuals; the total sum of squares of the observed data (SST); the proportion of total variability explained by the model (R^2); information criteria that penalize model complexity (Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC)), and temporal agreement between observed and projected monthly mean dry weights (CCC) for both sites: SQ and PB.

For models M1 and M2, assuming that the two datasets SQ and PB are independent and that the estimators are approximately normally distributed, we will apply Wald-type tests for equality of parameters between SQ and PB. For a generic parameter $\theta \in \{\rho, \alpha\}$, we will test the null hypothesis $H^0: \theta_{SQ} = \theta_{PB}$ against the two-sided alternative $H^1: \theta_{SQ} \neq \theta_{PB}$. To do so we will consider the difference $\Delta_\theta = \hat{\theta}_{SQ} - \hat{\theta}_{PB}$ with standard error $SE(\Delta_\theta)$,

$$SE(\Delta_\theta) = \sqrt{SE(\hat{\theta}_{SQ})^2 + SE(\hat{\theta}_{PB})^2}, \quad (22)$$

and then compute the test statistics

$$Z_\theta = \frac{\Delta_\theta}{SE(\Delta_\theta)} \quad (23)$$

Correspondingly for model M2, for each parameter $\theta \in \{\rho, \alpha, \beta\}$, we ought to test the null hypothesis $H^0: \theta_{SQ} = \theta_{PB}$ against the two-sided alternative $H^1: \theta_{SQ} \neq \theta_{PB}$. To achieve matters, we will rely on the statement that under the usual asymptotic normality assumptions for nonlinear least-squares estimators and independence between fits at the two SQ and PB sites, the standardized difference

$$Z_{\theta} = \frac{(\hat{\theta}_{SQ} - \hat{\theta}_{PB})}{\sqrt{(SE(\hat{\theta}_{SQ}))^2 + SE(\hat{\theta}_{PB})^2}} \quad (24)$$

approximately follows a standard normal distribution under H_0 . However, since for the bivariate model M2, three parameters ρ , α , and β are being compared simultaneously, then it is more appropriate to evaluate them jointly. A global Wald statistic $W(\rho, \alpha, \beta)$ can be constructed as follows:

$$W(\rho, \alpha, \beta) = Z_{\rho}^2 + Z_{\alpha}^2 + Z_{\beta}^2. \quad (25)$$

Also, for the addressed assessment of parameter invariance, we will also rely on the triad $\bar{T} = (\bar{\rho}, \bar{\alpha}, \bar{\beta})$ given by

$$\bar{\rho} = \frac{\sum_{i=1}^{i=10} \rho_i}{10}, \quad \bar{\alpha} = \frac{\sum_{i=1}^{i=10} \alpha_i}{10}, \quad \bar{\beta} = \frac{\sum_{i=1}^{i=10} \beta_i}{10} \quad (26)$$

where ρ_i , α_i , and β_i for $i = 1, 2, \dots, 10$ are reported estimated values for the parameters ρ , α , and β composing the allometric model M2 (cf. Equation (11)).

2.3. Data Empirical Background and Workflow

To achieve the present exploration, we relied on two independent datasets. The first one that we distinguish by the symbol PB comes from the estuary of Punta Banda ($31^{\circ}43'59''$ N, $116^{\circ}37'59''$ W), Baja California, Mexico, and contains 1063 measurements taken from eelgrass leaves collected during 12 sampling intervals of one month duration, including dry weight (w), length (l), width (h), and leaf area (a_p) surrogates that are expressed through $a_p(t) = l(t) \cdot h(t)$. We also consider a second dataset that we differentiate by the symbol SQ comprising 10,412 similar measurements recorded during a 13-month sampling that took place during 1992–1993 at an eelgrass meadow placed at San Quintin Bay ($30^{\circ}27'04''$ N, $115^{\circ}59'00''$ W), Baja California, Mexico.

For comparison purposes, we rely on parameter estimates from different studies reported in the literature and fitted by using models M1, M2, and M3 on data collected in the Punta Banda estuary and San Quintin.

For each model M1, M2, and M3, we will perform a goodness-of-fit test to determine the extent to which they produce consistent fits to the leaf biomass data in the two independent datasets SQ and PB, which, as we have emphasized, were collected in different years. Statistical tests will also be performed to determine if there are significant differences in the parameters fitted by each model to the SQ and PB data. For each model, the parameters fitted in SQ will be used to project leaf biomasses in PB, and vice versa. The CCC value will be recorded for each comparison. We will also conduct a model selection study to determine which model is the most consistent, based on the RMSE, AIC, and BIC statistics for each model. Once the best model has been selected, two invariance verification studies of the allometric parameters associated with it will be performed. For this purpose, we will consider two surrogate models. The first will be expressed using the averages of the estimators for each parameter of the best model as reported in the literature. A second surrogate model will correspond to the parameters fitted by the best model to the combined dataset C, where $C = (SQ \cup PB)$. Then, we will corroborate the suitability of each of these surrogate models of the invariant set by analyzing the reproducibility of projections of leaf biomass values in the SQ and PB datasets that these projections produce. This statistical procedure will allow us to investigate whether the parameters of the allometric expression of eelgrass leaf biomass can be regarded as invariant. Figure 1 presents the workflow for the present exploration.

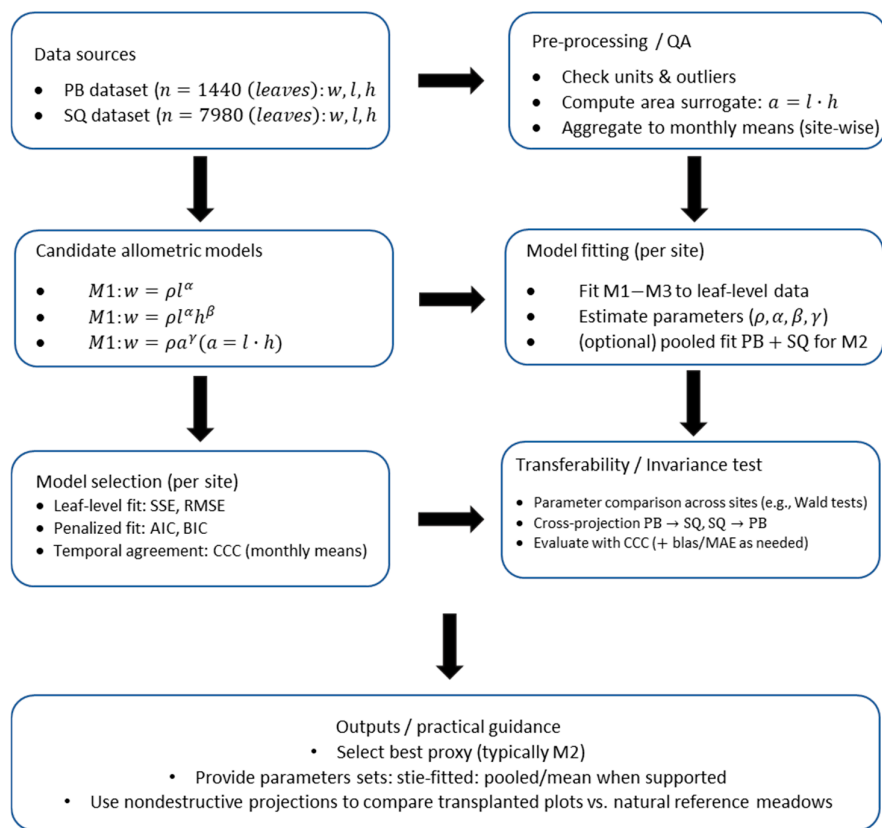


Figure 1. Flowchart of the analysis workflow used to fit and evaluate allometric models across the two independent datasets (PB and SQ). Parameters are estimated, and model performance is assessed using goodness-of-fit metrics (SSE, RMSE) and complexity-penalizing information criteria (AIC, BIC). Results are then combined through dataset comparison and reciprocal cross-projections, yielding a final integrated synthesis.

3. Results

Results are organized by model (M1–M3). For each model we report leaf-level fit/diagnostics for SQ and PB, between-site parameter comparisons, and cross-projection performance on monthly means (CCC). Comparative model selection and additional M2 robustness tests are reported in Sections 3.3.5–3.3.7.

3.1. Model M1 (Length-Based): Results for SQ and PB

This section presents the results for the length-based allometric proxy (M1) using the SQ and PB datasets, including goodness-of-fit and diagnostic checks at each site, followed by cross-site comparisons of fitted parameters and reciprocal cross-projection tests to assess transferability via CCC.

3.1.1. Goodness of Fit and Diagnostics of the Leaf Length-Based Allometric Model M1 in SQ

To begin our model suitability exploration, we rely on the SQ dataset to explore the goodness of fit of model M1, which expresses leaf dry weight as a power function of relating length (cf. Equation (1)). To achieve the ensuing tasks, we present parameter estimates and inference statistics. We also present the scatterplot of observed leaf dry weight versus length with the fitted mean response curve, residuals versus fitted values, normal Q–Q plot of the residuals, and monthly mean observed and predicted leaf dry weights;

we relied on the CCC value between the two monthly mean series, to assess reproducibility.

The nonlinear allometric model (M1) fitted to the SQ dataset shows a well-defined and highly significant length–weight relationship (Table 1). Both parameters are precisely estimated, with narrow 95% confidence intervals that do not include zero and large t statistics, confirming a strong positive allometric scaling of dry weight with leaf length. The scatter of observed dry weights around the fitted mean response curve forms a relatively narrow band over most of the length range, indicating moderate dispersion around the mean and consistency with the global fit indices in Table 2, where the model explains about 81% of the total variability in w ($R^2 = 0.81$) with an RMSE of 0.00862 g and residuals centered essentially at zero. When examined under a multiplicative lognormal error structure, the log residuals $\log(w_{\text{obs}}/\hat{w})$ display an empirical distribution and normal Q–Q plot that are broadly compatible with approximate normality, with only mild deviations in the tails, supporting the working assumption of lognormal residuals. At the temporal aggregation level, the high CCC between observed and predicted monthly mean dry weights (CCC = 0.97, Figure 2d) shows that the allometric projections based on the fitted parameters reproduce the observed monthly pattern of mean biomass with strong agreement and good reproducibility.

Table 1. Parameter estimates and inference statistics for the nonlinear model M1 fitted to the SQ dataset. We include the estimated parameter value (Estimate), its Se, the lower and upper limits of the 95% confidence interval, and the t statistics used to assess the significance of each parameter.

Parameter	Estimate	Se	Lower 95% CI	Upper 95% CI	t
ρ	1.4129×10^{-5}	6.47×10^{-7}	1.2862×10^{-5}	1.5396×10^{-5}	21.85
l	1.32368	0.00737	1.30923	1.33813	179.58

Table 2. Global fit statistics for nonlinear model M1 (cf. Equation (1)) fitted to the SQ dataset: SSE, MSE, RMSE, mean(e), sd(e), SST, R^2 , the CCC value between observed and predicted monthly mean values of $\bar{w}_{it}(t)$ (cf. Equation (19)), and BIC and AIC, which summarize model fit while penalizing model complexity.

SSE	MSE	RMSE	Mean(e)	Sd(e)	SST	R^2	CCC	AIC	BIC
0.7732	7.43×10^{-5}	0.00862	0.00000	0.00862	4.1394	0.81	0.89	−98,992.02	−98,977.52

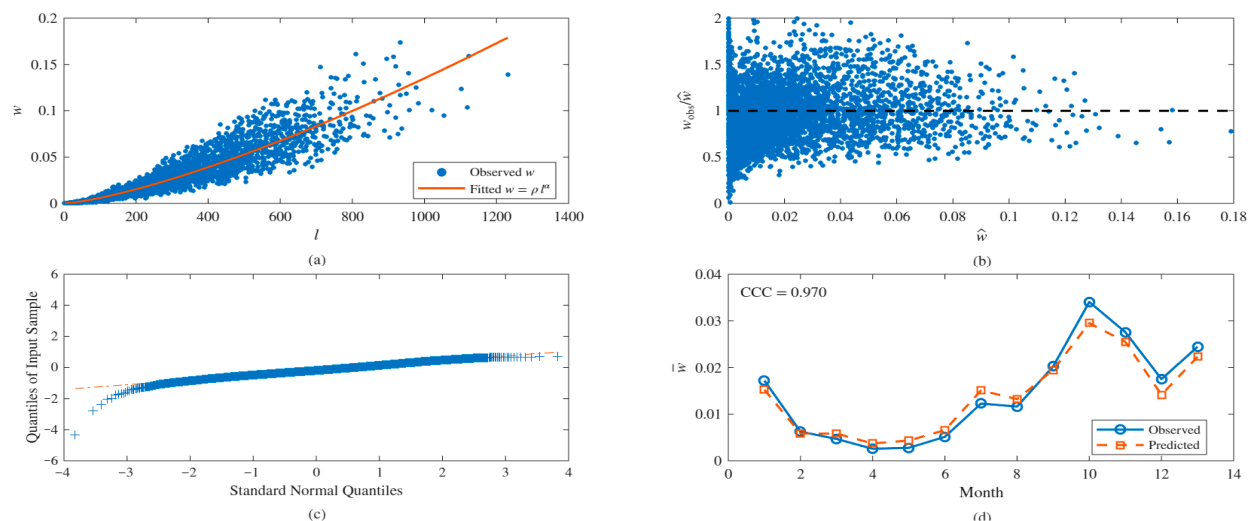


Figure 2. Diagnostic plots for the nonlinear allometric model M1 (cf. Equation (1)) fitted to eelgrass leaf dry weight data from the San Quintín dataset. Panel (a): Scatterplot of observed dry weight w_{obs}

versus leaf length l with the fitted mean response curve for M1. Panel (b): Residuals versus fitted values $\hat{w}$. Panel (c): Normal Q–Q plot of the residuals. Panel (d): Monthly mean observed and predicted leaf dry weights; Table 2 reports Lin’s CCC between the two monthly mean series.

3.1.2. Goodness of Fit and Diagnostics of the Leaf Area-Based Allometric Model M1 in PB

The nonlinear allometric model M1 (cf. Equation (1)) fitted to the PB dataset provides a well-defined mean response, with both parameters precisely estimated and highly significant (Table 3). The 95% confidence intervals for (ρ) and (α) are relatively narrow and do not overlap zero, and the t statistics confirm a strong positive allometric relationship between leaf length and dry weight. The scatter of observed dry weights around the fitted mean curve is moderate: points cluster closely to the response curve over much of the length range, but with visible dispersion that is consistent with the global fit indices in Table 4, where the model explains about 58% of the total variability in (w) ($R^2 = 0.58$) with an RMSE of 0.00682.

Table 3. Parameter estimates and inference statistics for M1 (cf. Equation (1)) fitted to the PB dataset. We include the estimated parameter value (Estimate), its Se, the lower and upper limits of the 95% confidence interval, and the t statistic used to assess the significance of each parameter.

Parameter	Estimate	Se	Lower 95% CI	Upper 95% CI	t
ρ	1.12537×10^{-5}	2.91×10^{-6}	5.5346×10^{-6}	1.6971×10^{-5}	3.86
l	1.35569	0.04711	1.26325	1.44813	28.78

Table 4. Global fit statistics of the nonlinear model M1 (cf. Equation (1)) to the PB dataset: SSE, MSE, RMSE, mean(e), sd(e), SST, R^2 , the CCC between observed and predicted monthly mean values of $\bar{w}_{li}(t)$ (cf. Equation (19)), and BIC and AIC, which summarize model fit while penalizing model complexity.

SSE	MSE	RMSE	Mean(e)	Sd(e)	SST	R^2	CCC	AIC	BIC
0.0493	4.65×10^{-5}	0.00682	−0.00000	0.00682	0.1198	0.58	0.88	−10,601.36	−10,591.42

When the error structure is examined on the logarithmic scale, the log residuals ($\log(w_{obs}/\hat{w})$) are broadly compatible with a normal distribution, and the normal Q–Q plot shows an approximately linear pattern with only mild deviations in the tails, supporting the working assumption of lognormal multiplicative errors in the regression model. At an aggregated temporal scale, the model performs even better: the CCC between observed and predicted monthly mean dry weights is moderate (CCC = 0.88, Table 4) (see Figure 3d), indicating that the allometric projections based on the fitted parameters (ρ, α) reproduce the observed monthly pattern of mean biomass with strong agreement and good reproducibility.

3.1.3. Cross-Site Evaluation of Differences Between Model M1 Parameter Estimates

To formally assess whether the allometric parameters of the model M1 (cf. Equation (1)) differ between the SQ and PB datasets, we compared the parameter estimates fitted separately to each dataset. In both cases, the fits were obtained by direct nonlinear regression in the original scale of (w) . For the SQ dataset, the performed nonlinear fit yielded $\hat{\rho}_{SQ} = 1.4129 \times 10^{-5}$ with $SE(\hat{\rho}_{SQ}) = 6.47 \times 10^{-7}$, and we correspondingly obtained $\hat{\alpha}_{SQ} = 1.3237$ with $SE(\hat{\alpha}_{SQ}) = 0.00737$. For the PB dataset, the corresponding estimates were $\hat{\rho}_{PB} = 1.1253 \times 10^{-5}$ with $SE(\hat{\rho}_{PB}) = 2.91 \times 10^{-6}$ and $\hat{\alpha}_{PB} = 1.35569$ with $SE(\hat{\alpha}_{PB}) = 0.4711$. Then, for a generic parameter $\theta \in \{\rho, \alpha\}$, we considered the difference $\Delta_\theta = \hat{\theta}_{SQ} - \hat{\theta}_{PB}$ with standard error $SE(\Delta_\theta)$ (cf. Equation (22)) and also calculated

the test statistic Z_θ as set by Equation (23), which is approximately standard normal under the null hypothesis $H_0: \theta_{SQ} = \theta_{PB}$. We then applied a Wald-type tests for equality of parameters between SQ and PB. For ρ , the difference between estimates was $\Delta_\rho = \hat{\rho}_{SQ} - \hat{\rho}_{PB} = 2.88 \times 10^{-6}$. The standard error of this difference was $SE(\Delta_\rho) \approx 2.98 \times 10^{-6}$, yielding $Z_\rho \approx 0.96$. The associated two-sided p -value was $p \approx 0.33$. The 95% confidence interval for the difference was $\Delta_\rho \in [-2.97 \times 10^{-6}, 8.72 \times 10^{-6}]$, which clearly includes zero. Thus, we do not reject the null hypothesis that ρ_{SQ} and ρ_{PB} are equal.

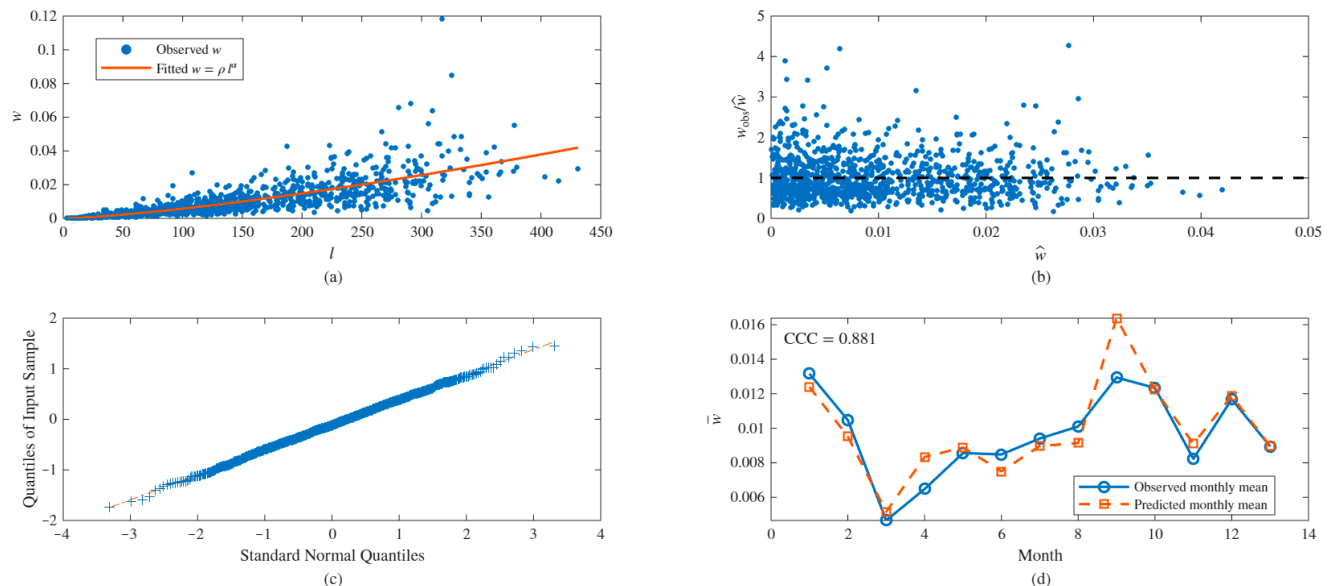


Figure 3. Diagnostic plots for the nonlinear allometric model M1 (cf. Equation (1)) fitted to eelgrass leaf dry weight data from the Punta Banda dataset. Panel (a): Scatterplot of observed dry weight w_{obs} versus leaf length l with the fitted mean response curve M1. Panel (b): Residuals versus fitted values $\hat{w}$. Panel (c): Normal Q–Q plot of the residuals. Panel (d): Monthly mean observed and predicted dry weights; the panel title reports the value of Lin’s CCC between the two monthly mean series.

For α , the difference between estimates was $\Delta_\alpha = \hat{\alpha}_{SQ} - \hat{\alpha}_{PB} = -0.03201$. The standard error of this difference was $SE(\Delta_\alpha) \approx 0.04768$, yielding $Z_\alpha \approx -0.67$. The corresponding two-sided p -value was $p \approx 0.50$. The 95% confidence interval for the difference was $\Delta_\alpha \in [-0.1255, 0.0614]$, which again includes zero. Consequently, we also do not reject the null hypothesis that α_{SQ} and α_{PB} are equal.

At the conventional significance level ($\alpha = 0.05$), both tests fail to detect statistically significant differences between the SQ and PB parameter estimates. In practical terms, the allometric parameters (ρ, α) obtained from the SQ and PB datasets are statistically indistinguishable under the model $w = \rho l^\alpha$, supporting the interpretation that a common allometric relationship between leaf length and dry weight is compatible with the data from both regions.

3.1.4. Cross-Site Evaluation of the Reproducibility Strength of the M1 Parameter Estimates

We performed a cross-validation of invariance of allometric parameters where those fitted on a site projected mean monthly values of leaf biomasses observed in another. To achieve tasks, we relied on the pairs fitted to present data and those reported [39] according to Table 5. Figure 4 provides sight assessment comparison of observed monthly leaf weight averages versus their allometrically projected surrogates. We first considered the

parameter values $\rho = 1.1253 \times 10^{-5}$, and $\alpha = 1.35$ fitted to data collected in Punta Banda during 1992 [39]. These parameter values along with model M1 and leaf length values in the present SQ data were used to allometrically project the observed monthly mean leaf dry weight values in the present SQ data. This comparison entailed an outstanding reproducibility (CCC = 0.96, Figure 4a). Then, we considered the parameter pair $\rho = 1.4129 \times 10^{-5}$ and $\alpha = 1.3237$ estimated by fitting model M1 to the present SQ data. This parameterization was then used to project the observed monthly mean leaf dry weight in the present PB dataset (Figure 4b). This comparison revealed poor agreement (CCC = 0.836) [57]. The parameter set $\rho = 7.0 \times 10^{-6}$, $\alpha = 1.43$ was obtained by the fitting of model M1 (cf. Equation (1)), to data collected at Punta Banda during 1999 as reported in [39]. These parameters were used to project the monthly mean leaf dry weight in the present SQ data. Agreement turned out to be suitable (CCC = 0.950, (Figure 4c). Finally, we considered the parameter set $\rho = 9.0 \times 10^{-6}$, $\alpha = 1.41$ corresponding to a fit of model M1 to data collected at San Quintin during a 1992 sampling, as reported by [39]. This parameterization was then used to project the monthly mean leaf dry weight in the present Punta Banda dataset. This comparison entailed poor agreement (CCC = 0.831, Figure 4d) [57].

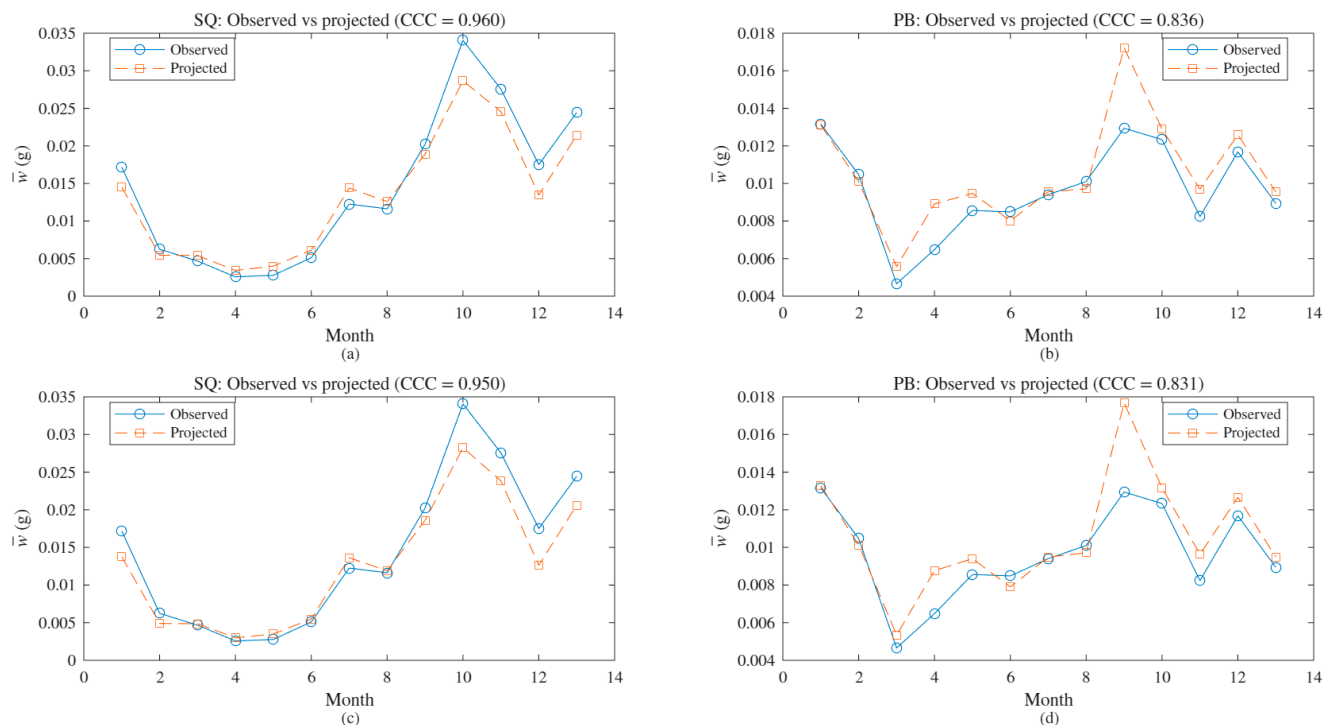


Figure 4. Monthly mean observed vs. projected eelgrass leaf dry weight under four allometric calibrations of the model M1 (cf. Equation (1)). In panel (a), observed values in present SQ data versus their projections using parameter fitted using PB data collected during 1992. In panel (b): observed values in present PB data versus their projections using parameters fitted using present SQ data. In panel (c) observed values in present SQ data versus their projections using parameters fitted using PB data collected during 1999 [39]. In panel (d): observed values in present PB data versus their projections using parameters fitted using SQ data collected during 1992 [39].

Table 5. Parametrizations to achieve the cross-site evaluation of the reproducibility strength of the parameter estimates for model M1.

Sampling	Model	Site	ρ	α	Reference
1992	M1	PB	1.1253×10^{-5}	1.3557	Present Study
2009	M1	SQ	1.4129×10^{-5}	1.3237	Present study
1999	M1	PB	7×10^{-6}	1.43	[39]
1992	M1	SQ	9×10^{-6}	1.41	[39]

In summary, we empirically assessed the invariance of the allometric parameters ρ and α in the model M1 (cf. Equation (1)) for *Zostera marina* by cross-projecting parameterizations across sites and sampling periods. Parameter sets originally fitted to Punta Banda or San Quintin data from different sampling years were used to project present-day monthly mean leaf biomass values at the opposite site, yielding very high CCC values ($\text{CCC} \approx 0.95\text{--}0.96$) in two cases and still poor agreement ($\text{CCC} \approx 0.83\text{--}0.84$) in the other two less favorable transfers [57]. These consistently high CCC values across independent datasets indicate that the length–biomass scaling relationship is remarkably stable in space and time. Moreover, CCC values around 0.83 still denote reasonably good overall agreement: model M1 captures the overall trend and level of leaf biomass, although systematic discrepancies suggest that the data-processing protocol for the presently analyzed PB dataset may warrant further revision. In practical terms, the results support the existence of empirically invariant (or at least quasi-invariant) allometric parameters for *Zostera marina* in these coastal systems, with only minor site-specific deviations superimposed on a robust, shared allometric structure.

3.2. Model M2 (Length–Width): Results for SQ and PB

This section reports results for the bivariate length–width proxy (M2) in SQ and PB, first documenting site-specific fit and diagnostics and then evaluating parameter stability and practical transferability through cross-site parameter comparisons and CCC-based reciprocal projections.

3.2.1. Goodness of Fit and Diagnostics of the Leaf Length and Width-Based Allometric Model M2 in SQ

The nonlinear allometric model M2 (cf. Equation (11)) provides a very good description of leaf dry weight in the SQ dataset. All three parameters are highly significant, with narrow 95% confidence intervals and large t-statistics (24.66 for ρ , 159.68 for α , and 65.58 for β) (see Table 6), confirming that both leaf length and width contribute importantly to explaining variation in w . The model explains about 87% of the total variability in dry weight ($R^2 = 0.87$), and the RMSE (0.00718) is small relative to the total variability ($\text{SST} = 4.1394$) (see Table 7), indicating a relatively tight dispersion of observed values around the allometric mean response. In the multiplicative scale, the residuals $w_i/\hat{w}_i$ are positive and cluster around 1, whereas their log residuals $\log(w_i/\hat{w}_i)$ display an approximately linear Q–Q plot, consistent with a lognormal error structure. At the level of monthly means, the model reproduces the temporal dynamics of dry weight very well: the high CCC value ($\text{CCC} \approx 0.98$, Figure 5d) between observed and predicted monthly means indicates excellent reproducibility of monthly mean dry weights when they are projected allometrically using the fitted parameters.

Table 6. The table reports parameter estimates and inferential statistics for the nonlinear model M2 (cf. Equation (11)) fitted to the SQ dataset: the estimated value (Estimate), its (Se), the lower and upper limits of the 95% confidence interval, and the t statistic used to assess the significance of each parameter.

Parameter	Estimate	Se	Lower 95% CI	Upper 95% CI	t
ρ	8.6889×10^{-6}	3.5233×10^{-7}	7.9983×10^{-6}	9.3796×10^{-6}	24.66
α	1.113648	0.006974	1.099977	1.127319	159.68
β	1.073154	0.016363	1.041079	1.105229	65.58

Table 7. Global fit statistics of the nonlinear model M2 (cf. Equation (11)) to the SQ dataset: SSE, MSE, RMSE, mean(e), sd(e), SST, R^2 , the value of CCC between observed and predicted monthly mean values of $\bar{w}_{lhi}(t)$ (cf. Equation (20)), and BIC and AIC, which summarize model fit while penalizing model complexity.

SSE	MSE	RMSE	Mean(e)	Sd(e)	SST	R^2	CCC	AIC	BIC
0.5368	5.15×10^{-5}	0.00718	1.294×10^{-4}	0.00718	4.1394	0.87	0.98	-73,240.89	-73,219.14

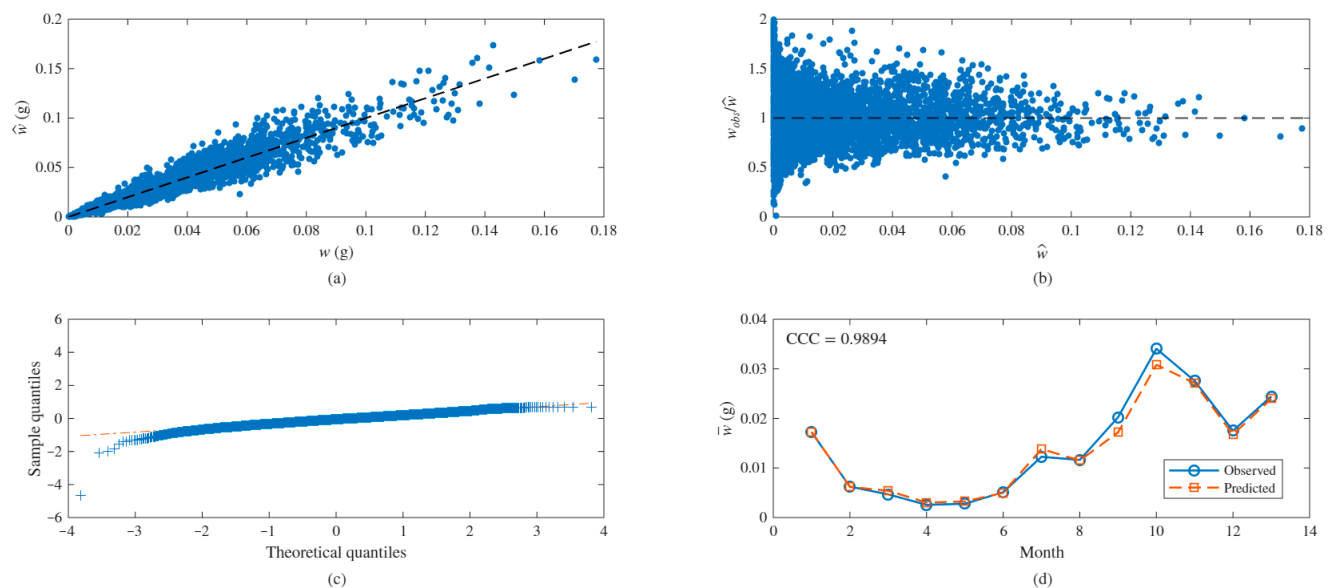


Figure 5. Diagnostic plots for the nonlinear allometric model M2 (cf. Equation (11)) fitted to eelgrass leaf dry-weight data from the San Quintín dataset. Panel (a): Scatterplot of observed dry weight w_{obs} versus predicted dry weight $\hat{w}$ with the 1:1 line as a reference. Panel (b): Residuals versus fitted values $\hat{w}$. Panel (c): Normal Q-Q plot of the residuals. Panel (d): Monthly mean observed and predicted dry weights; the panel title reports the value of Lin's CCC between the observed and predicted monthly mean series.

3.2.2. Goodness of Fit and Diagnostics of the Leaf Length and Width-Based Allometric Model M2 in PB

The nonlinear allometric model M2 (cf. Equation (11)) provides a statistically well-supported description of eelgrass leaf dry weight in the PB dataset. All parameters are clearly significant, with relatively narrow 95% confidence intervals and large t -statistics (3.89 for ρ , 22.54 for α , and 11.30 for β) (see Table 8), indicating that both leaf length and width contribute meaningfully to explaining variation in w . The model explains about 63% of the total variability in dry weight ($R^2 = 0.63$), and the RMSE (0.00643) is moderate relative to the total variability (SST = 0.1198) (see Table 9), reflecting a noticeable but not excessive dispersion of observed values around the mean allometric response. Residuals

defined as multiplicative ratios $r_i = w_i/\hat{w}_i$ fluctuate around 1, and their logarithms are approximately centered and symmetric; the corresponding normal Q–Q plot of $\log r_i$ is close to linear, with only mild deviations in the tails, which is consistent with the assumption of lognormal multiplicative errors. At the temporal scale of monthly averages, the model M2 reproduces the observed pattern of mean dry weight very well: the high CCC value between observed and predicted monthly means ($\text{CCC} \approx 0.94$, Figure 6d) indicates strong agreement and good reproducibility of the observed monthly mean dry weights when they are projected allometrically using the fitted parameters.

Table 8. The table reports parameter estimates and inferential statistics for the nonlinear model M2 (cf. Equation (11)) fitted to the PB dataset: the estimated value (Estimate), its Se, the lower and upper limits of the 95% confidence interval, and the t statistic used to assess the significance of each parameter.

Parameter	Estimate	Se	Lower 95% CI	Upper 95% CI	t
ρ	6.6773×10^{-6}	1.7186×10^{-6}	3.3050×10^{-6}	1.0050×10^{-5}	3.89
α	1.115329	0.049477	1.018245	1.212413	22.54
β	1.318956	0.116689	1.089988	1.547924	11.30

Table 9. Global fit statistics of the nonlinear model M2 (cf. Equation (11)) to the PB dataset: SSE, MSE, RMSE, mean(e), sd(e), SST, R^2 , the CCC value between observed and predicted monthly mean values of $\bar{w}_{lhi}(t)$ (cf. Equation (20)), and BIC and AIC, which summarize model fit while penalizing model complexity.

SSE	MSE	RMSE	Mean(e)	Sd(e)	SST	R^2	CCC	AIC	BIC
0.0438	4.13×10^{-5}	0.00643	6.84×10^{-5}	0.00643	0.1198	0.63	0.94	−7709.67	−7694.76

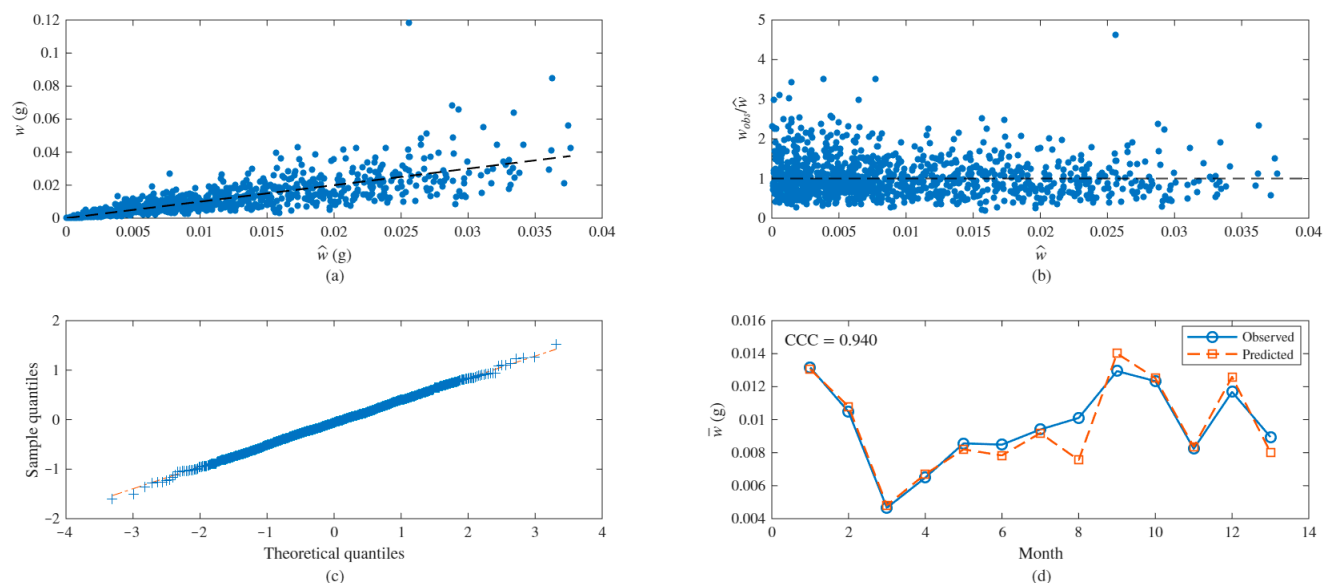


Figure 6. Diagnostic plots for the nonlinear allometric model M2 (cf. Equation (11)) fitted to eelgrass leaf dry-weight data from the Punta Banda dataset. Panel (a): Scatterplot of observed dry weight w_{obs} versus predicted dry weight $\hat{w}$ with the 1:1 line as a reference. Panel (b): Residuals versus fitted values $\hat{w}$. Panel (c): Normal Q–Q plot of the residuals. Panel (d): Monthly mean observed and predicted dry weights; the panel title reports the value of Lin's CCC between the observed and predicted monthly mean series.

3.2.3. Cross-Site Evaluation of Differences Between Parameter Estimates for Model M2

To formally assess whether the San Quintin and Punta Banda M2 allometric fits share a common parameter set, we compared the estimates of ρ , α , and β from the nonlinear model $w = \rho l^\alpha h^\beta$ using Wald-type tests based on the reported standard errors. For each parameter $\theta \in \{\rho, \alpha, \beta\}$, we tested the null hypothesis $H_0: \theta_{SQ} = \theta_{PB}$ against the two-sided alternative $H_1: \theta_{SQ} \neq \theta_{PB}$ under the usual asymptotic normality assumptions for nonlinear least-squares estimators and independence between fits at the two sites. We then considered the standardized difference Z_θ (cf. Equation (24)) that approximately follows a standard normal distribution under H_0 .

According to Equation (22), for ρ , the difference between estimates was $\Delta_\rho = \hat{\rho}_{SQ} - \hat{\rho}_{PB} = 2.01 \times 10^{-6}$, with a standard error of the difference $SE(\Delta_\rho) = 1.75 \times 10^{-6}$, yielding $Z_\rho = 1.15$ (cf. Equation (24)) and a two-sided value $p_\rho \approx 0.25$. For α , the difference was $\Delta_\alpha = \hat{\alpha}_{SQ} - \hat{\alpha}_{PB} = -0.00168$, with $SE(\Delta_\alpha) = 0.04997$, giving $Z_\alpha = -0.03$ and $p_\alpha \approx 0.97$. For β , the difference was $\Delta_\beta = \hat{\beta}_{SQ} - \hat{\beta}_{PB} = -0.246$, with $SE(\Delta_\beta) = 0.118$, yielding $Z_\beta = -2.09$ and $p_\beta \approx 0.037$. Thus, when each parameter is considered separately, the tests indicate no significant differences for ρ and α , while β shows a marginally significant difference at the conventional 0.05 level.

However, because three parameters are being compared simultaneously, it is more appropriate to evaluate them jointly. A global Wald statistic can be constructed as explained by Equation (25). Since we obtained $W(\rho, \alpha, \beta) \approx 5.67$, which, under the null hypothesis of a common parameter vector (ρ, α, β) across sites, follows approximately a χ^2 distribution with 3 degrees of freedom, the 0.05/3 corresponding p -value is $p_{global} \approx 0.13$, so the null hypothesis of equal parameters cannot be rejected at the 0.05 level. An equivalent conclusion is obtained if one controls multiple testing using a simple Bonferroni correction: with three comparisons, the adjusted significance threshold is $\alpha_{Bonf} = 0.05/3 \approx 0.017$, and the marginal difference observed for β ($p \approx 0.037$) is no longer significant under this stricter criterion. Taken together, these results indicate that there is no statistically compelling evidence that ρ, α , and β differ between the San Quintin and Punta Banda datasets; within the precision afforded by the data, the allometric model parameters can therefore be regarded as statistically invariant across the two sites.

3.2.4. Cross-Site Evaluation of the Reproducibility Strength of Parameter Estimates for Model M2

We first considered the parameterization with $\rho = 6.67729 \times 10^{-6}$, $\alpha = 1.1153$, $\beta = 1.318$. This triad resulted from the fitting of model M2 (cf. Equation (11)) to the present study's PB data (sampling 2009, Table 10). These parameters were used here to project the monthly mean leaf dry weight $\bar{w}_{lhi}(t)$ (cf. Equation (20)) in the present study's San Quintin dataset (sampling 1992–1993). This comparison resulted in a remarkable agreement between observed and projected values (CCC = 0.975, Figure 7a). Then, we picked the triad with $\rho = 8.68 \times 10^{-6}$, $\alpha = 1.113$, $\beta = 1.073$. These estimates were fitted to present SQ data (sampling 1992–1993, Table 10). When we used this triad to project (cf. Equation (20)) the monthly mean leaf dry weight in the Punta Banda dataset (sampling 2009), the resulting reproducibility was good (CCC = 0.90, Figure 7b).

Similarly, the triad $\rho = 1.00 \times 10^{-5}$, $\alpha = 1.1088$, $\beta = 1.0778$ was estimated by fitting the model M2 to data collected at San Quintin (sampling 1992–1993, Table 10) as reported by [58]. These estimates were used to project the monthly mean leaf dry weight in the presently addressed SQ data (sampling 1992–1993). Comparison of observed and projected series led to an outstanding reproducibility strength (CCC = 0.99, Figure 7c). We finally considered the triad with $\rho = 8.00 \times 10^{-6}$, $\alpha = 1.17$, $\beta = 0.922$. These parameter values associate to model M2 fitted to Punta Banda data collected from a sampling in 2000 as reported by [59], (Table 10) This triad was then used to project the monthly mean leaf

dry weight in the presently addressed Punta Banda dataset (sampling 2009), enabling cross-period comparison for the PB site. Agreement between projected and observed values was good (CCC = 0.93, Figure 7d).

Table 10. Parametrizations to achieve the cross-site evaluation of the reproducibility strength of the parameter estimates for model M2 (cf. Equation (11)).

Sampling	Site	ρ_i	α_i	β_i	Reference
1992–1993	SQ	8.68×10^{-6}	1.113	1.073	Present Study
1992–1993	SQ	1.00×10^{-5}	1.1088	1.0778	[58]
2000	PB	8.00×10^{-6}	1.17	0.922	[59]
2009	PB	6.67729×10^{-6}	1.1153	1.3189	Present Study

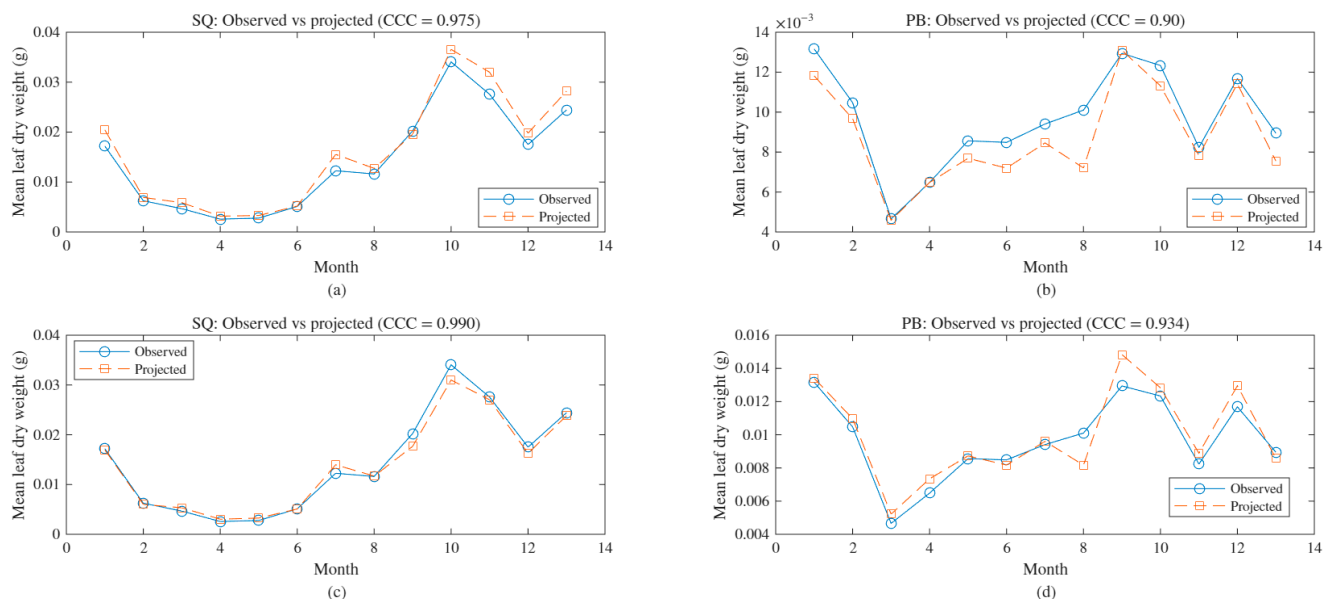


Figure 7. Monthly mean observed vs. projected eelgrass leaf dry weight under four allometric calibrations of the trivariate model M2 (cf. Equation (11)). In panel (a), observed values in present SQ data versus their projections using parameter fitted using PB data collected during 2009. In panel (b), observed values in present PB data versus their projections using parameters fitted using present SQ data collected during 1992–1993. In panel (c) observed values in present SQ data versus their projections using parameters fitted using PB data collected during 1992–1993 [58]. In panel (d): observed values in present PB data versus their projections using parameters fitted using SQ data collected during 2000 [59].

3.3. Model M3 (Area Surrogate): Results for SQ and PB

This section summarizes the results for the area-surrogate proxy (M3) across SQ and PB, including site-level fit and diagnostics, and, subsequently, cross-site tests of parameter similarity and reproducibility assessed through reciprocal projections and CCC.

3.3.1. Goodness of Fit and Diagnostics of the Leaf Area-Based Allometric Model M3 in SQ

The fit of model M3 (cf. Equation (18)) to the SQ dataset indicates a well-defined allometric relationship between leaf dry weight and leaf area. Both parameters are highly significant ($t = 24.70$ for ρ and $t = 216.48$ for α) (see Table 11), with very narrow 95% confidence intervals, indicating precise estimation of the mean response. The high coefficient of determination ($R^2 = 0.87$) and low RMSE (0.00718 g) (see Table 12) show that most

of the variability in dry weight is explained by the model and that the dispersion of observed values around the mean response curve is relatively small on the original scale. In the multiplicative scale, the residuals ($w_i/\hat{w}_i$) are positive and cluster around 1, while their log residuals $\log(w_i/\hat{w}_i)$ yield an approximately linear QQ-plot, consistent with the assumption of lognormal error and thus with a multiplicative error structure. Finally, the high CCC value between observed and projected monthly mean dry weights (CCC = 0.98, Figure 8) indicates excellent temporal reproducibility of the observed patterns when using the fitted allometric parameters.

Table 11. Parameter estimates and inferential statistics for the nonlinear model M3 (cf. Equation (18)) fitted to the SQ dataset: the estimated value (Estimate), its Se, the lower and upper limits of the 95% confidence interval, and the t statistic used to assess the significance of each parameter.

Parameter	Estimate	Se	Lower 95% CI	Upper 95% CI	t
ρ	8.7182×10^{-6}	3.53×10^{-7}	8.0263×10^{-6}	9.4101×10^{-6}	24.70
a	1.104385	0.00510	1.0944	1.1144	216.48

Table 12. Global fit statistics of the nonlinear model M3 (cf. Equation (18)) to the SQ dataset: SSE, MSE, RMSE, mean(e), sd(e), SST, R^2 , the value of CCC between observed and predicted monthly mean values of $\bar{w}_{ai}(t)$ (cf. Equation (21)), and BIC and AIC, which summarize model fit while penalizing model complexity.

SSE	MSE	RMSE	Mean(e)	Sd(e)	SST	R^2	CCC	AIC	BIC
0.5371	5.16×10^{-5}	0.00718	0.00013	0.00718	4.1394	0.87	0.98	-73,236.79	-73,215.03

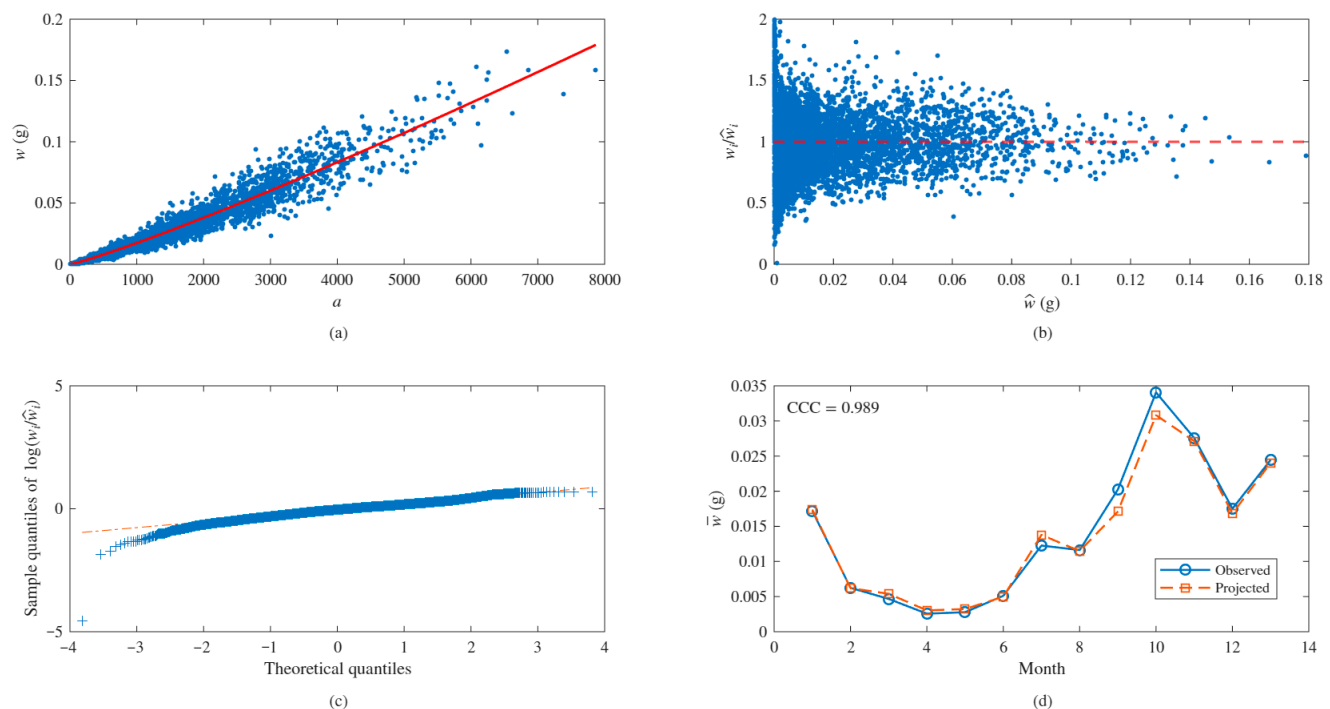


Figure 8. Diagnostic plots for the nonlinear model M3 (cf. Equation (18)) fitted to the SQ dataset (San Quintin). Panel (a): Observed leaf dry weight versus leaf area with the fitted mean response curve. Panel (b): Multiplicative residuals $w_i/\hat{w}_i$ versus projected leaf dry weight, with a horizontal reference line at 1, illustrating the lognormal multiplicative error structure. Panel (c): Normal Q-Q plot of the log residuals $\log(w_i/\hat{w}_i)$ assessing the normality assumption on the error term. Panel (d): Monthly mean observed and projected leaf dry weight, with the value of the CCC between monthly means reported in the panel title.

3.3.2. Goodness of Fit and Diagnostics of the Leaf Area-Based Allometric Model M3 in PB

The fit of the model M3 (cf. Equation (18)) to the PB dataset reveals a well-defined allometric relationship between leaf dry weight and leaf area. Both parameters are highly significant ($t = 12.41$ for ρ and $t = 82.13$ for α) (see Table 13), with narrow confidence intervals, indicating precise estimation of the mean response. The coefficient of determination $R^2 = 0.62$ and the RMSE of 0.00658 (see Table 14) show that the model explains an important, though not complete, proportion of the variability in dry weight, so that observed values display a moderate dispersion around the mean response curve on the arithmetic scale.

On the multiplicative scale, the residuals $w_i/\hat{w}_i$ are positive and cluster around 1, and their log residuals $\log(w_i/\hat{w}_i)$ yield an approximately linear QQ-plot, consistent with the assumption of lognormal error and, therefore, with a strictly multiplicative error model. Finally, the value of the CCC between observed and projected monthly mean dry weights (CCC = 0.86) (see Figure 9d) indicates good temporal reproducibility of the observed patterns when dry weights are projected allometrically using the fitted parameters.

Table 13. Parameter estimates and inferential statistics for the nonlinear model M3 (cf. Equation (18)) fitted to the PB dataset: the estimated value (Estimate), its Se, the lower and upper limits of the 95% confidence interval, and the t statistic used to assess the significance of each parameter.

Parameter	Estimate	Se	Lower 95% CI	Upper 95% CI	t
ρ	8.3314×10^{-6}	6.71×10^{-7}	7.1141×10^{-6}	9.7570×10^{-6}	12.41
α	1.109250	0.01351	1.0828	1.1357	82.13

Table 14. Global fit statistics of the nonlinear model M3 (cf. Equation (18)) to the PB dataset: SSE, MSE, RMSE, mean(e), sd(e), SST, R^2 , the CCC value between observed and predicted monthly mean values of $\bar{w}_{ai}(t)$ (cf. Equation (21), and BIC and AIC, which summarize model fit while penalizing model complexity.

SSE	MSE	RMSE	Mean(e)	Sd(e)	SST	R^2	CCC	AIC	BIC
0.0460	4.33×10^{-5}	0.00658	0.00098	0.00651	0.1198	0.62	0.86	1326.17	1341.08

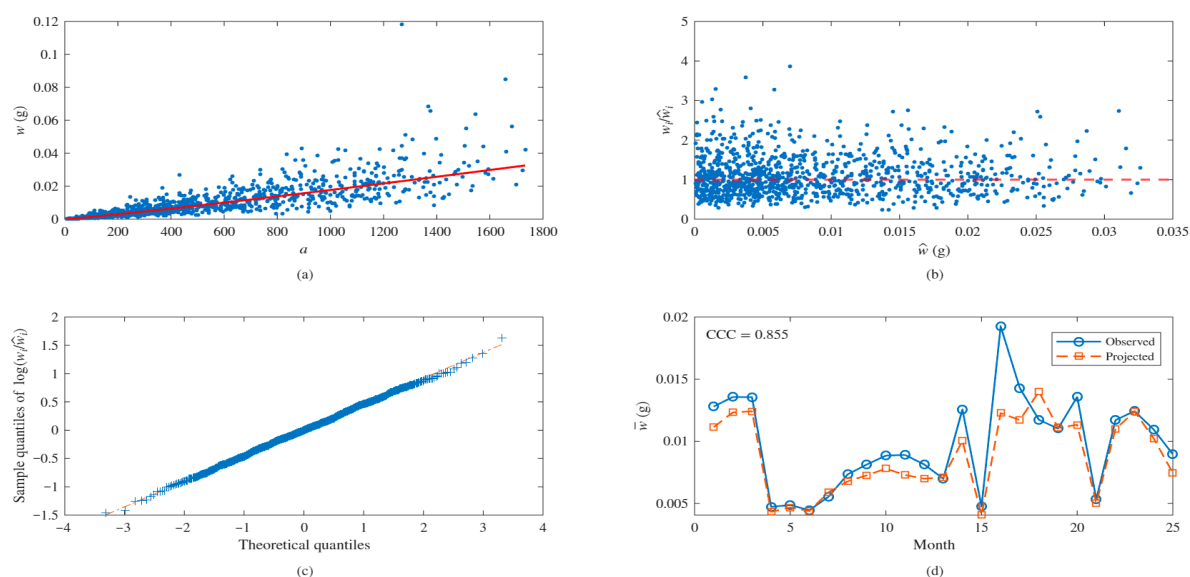


Figure 9. Diagnostic plots for the nonlinear model M3 (cf. Equation (18)) fitted to the PB dataset (Punta Banda). Panel (a): Observed leaf dry weight versus leaf area with the fitted mean response curve. Panel (b): Multiplicative residuals $w_i/\hat{w}_i$ versus projected leaf dry weight, with a horizontal

reference line at 1, illustrating the assumed lognormal multiplicative error structure. Panel (c): Normal Q–Q plot of the logresiduals $\log(w_i/\hat{w}_i)$, assessing the adequacy of the normality assumption for the error term. Panel (d): Mean observed and projected leaf dry weight by sampling time (“month”), with the value of the CCC between mean observed and projected values reported in the panel title.

We have stressed the relevance of data quality in assuring robustness on allometric fits [60]. In this respect, we add that while various operators carried away the sampling and processing of the extensive SQ data—thereby introducing potential sources of variability—for the PB site, these duties were achieved solely by Cecilia Leal Ramirez. Therefore, the Q–Q plots behavior for PB data-based fits is consistent with a data-collection protocol that enforced standardized sampling and measurement procedures and thus minimized uncontrolled sources of noise. Under these conditions, the remaining biological and measurement variability is expected to be approximately symmetric on the log scale, yielding nearly linear Q–Q plots.

A related (and tentative) explanation may also help interpret the residual patterns observed in the SQ diagnostics: if measurement uncertainty has a size-dependent component, then when predicted dry weights are small, limitations in analytical-scale precision and operator-dependent reading/recording effects could translate into comparatively larger relative deviations; conversely, for larger leaves (and thus larger predicted values), these sources of error would be relatively less influential, so multiplicative residuals would tend to concentrate closer to 1 as $\hat{w}$ increases. This hypothesis is consistent with prior observations that errors in leaf dry-weight (and area) assessments can vary with leaf size, with small leaves being particularly prone to measurement and recording issues.

3.3.3. Cross-Site Evaluation of Differences Between Parameter Estimates for Model M3

To formally assess whether the fitted allometric parameters for model M3 (cf. Equation (18)) differ between sites, we compared the estimates of ρ and α obtained from the SQ and the PB dataset using Wald-type tests based on their asymptotic standard errors, assuming independence between datasets.

For SQ, the nonlinear fit of M3 yielded $\hat{\rho}_{SQ} = 8.7182 \times 10^{-6}$ ($SE = 3.53 \times 10^{-7}$) and $\hat{\alpha}_{SQ} = 1.104385$ ($SE = 0.00510$). For PB, the corresponding estimates under the same model were $\hat{\rho}_{PB} = 8.3314 \times 10^{-6}$ ($SE = 6.71 \times 10^{-7}$) and $\hat{\alpha}_{PB} = 1.109250$ ($SE = 0.01351$). The estimated difference in the scale parameter was $\widehat{\Delta\rho} = \hat{\rho}_{SQ} - \hat{\rho}_{PB} = 3.87 \times 10^{-7}$ with $SE(\widehat{\Delta\rho}) = 7.58 \times 10^{-7}$, giving a Wald statistic $Z_\rho = 0.51$ and a two-sided p -value of approximately 0.61. The corresponding 95% confidence interval for $\rho_{SQ} - \rho_{PB}$ ranged from -1.10×10^{-6} to 1.87×10^{-6} , clearly including zero. Likewise, the estimated difference in the allometric exponent was $\widehat{\Delta\alpha} = \hat{\alpha}_{SQ} - \hat{\alpha}_{PB} = -0.0049$ with $SE(\widehat{\Delta\alpha}) = 0.0144$ (cf. Equation (22)), yielding $Z_\alpha = -0.34$ (cf. Equation (23)) and a two-sided p -value of approximately 0.74. The 95% confidence interval for $\alpha_{SQ} - \alpha_{PB}$ was $[-0.0332, 0.0234]$, which again includes zero.

Taking together, these results provide no statistically significant evidence that either ρ or α differs between SQ and PB at conventional significance levels. Thus, within the precision afforded by the data, the allometric parameters of the model $w = \rho a^\alpha$ can be regarded as statistically indistinguishable between the two sites, supporting the use of a common allometric relationship for both datasets.

3.3.4. Cross-Site Evaluation of the Reproducibility Strength of M3 Parameter Estimates

The parameter pair $\rho = 8.3314 \times 10^{-6}$ and $\alpha = 1.109250$ (see Table 15), estimated in the present study using the PB dataset (sampling 2009) for model M3 (cf. Equation (18)), was used here to project monthly mean leaf dry weight in the SQ dataset (sampling 1992), yielding a remarkably high reproducibility (CCC = 0.98, Figure 10a).

The parameterization for model M3, with $\rho = 8.7182 \times 10^{-6}$ and $\alpha = 1.104385$ (see Table 15), was estimated in the present study for San Quintín (SQ, sampling 1992). These SQ parameters were then applied to project monthly mean leaf dry weight in the Punta Banda dataset (sampling 2009). This produced a significant agreement between observed and projected series (CCC = 0.90, Figure 10b). Similarly, the parameterization for model M3 with $\rho = 3.0 \times 10^{-6}$ and $\alpha = 1.25$ (see Table 15), estimated using the PB dataset (sampling 1998) as reported by [52], was used here to project monthly mean leaf dry weight in the San Quintín dataset (sampling 1992) allowing comparison with present-study calibrations. Resultant reproducibility was remarkable (CCC = 0.96, Figure 10c). Finally, we selected the parameterization for model M3, with $\rho = 2.5 \times 10^{-6}$ and $\alpha = 1.30$, also reported by [52] for eelgrass at Punta Banda (sampling 1998, Table 15). For these PB parameters applied to project monthly mean leaf dry weight in the Punta Banda dataset (sampling 2009), we recorded a significant reproducibility (CCC = 0.90, Figure 10d).

Table 15. Parametrizations to achieve the cross-site evaluation of the reproducibility strength of the parameter estimates for model M3.

Sampling	Model	Site	ρ	α	Reference
2009	M3	PB	8.3314×10^{-6}	1.109250	Present Study
1992	M3	SQ	8.7182×10^{-6}	1.104385	Present Study
1998	M3	PB	0.000003	1.25	[52]
1998	M3	PB	0.0000025	1.3	[52]

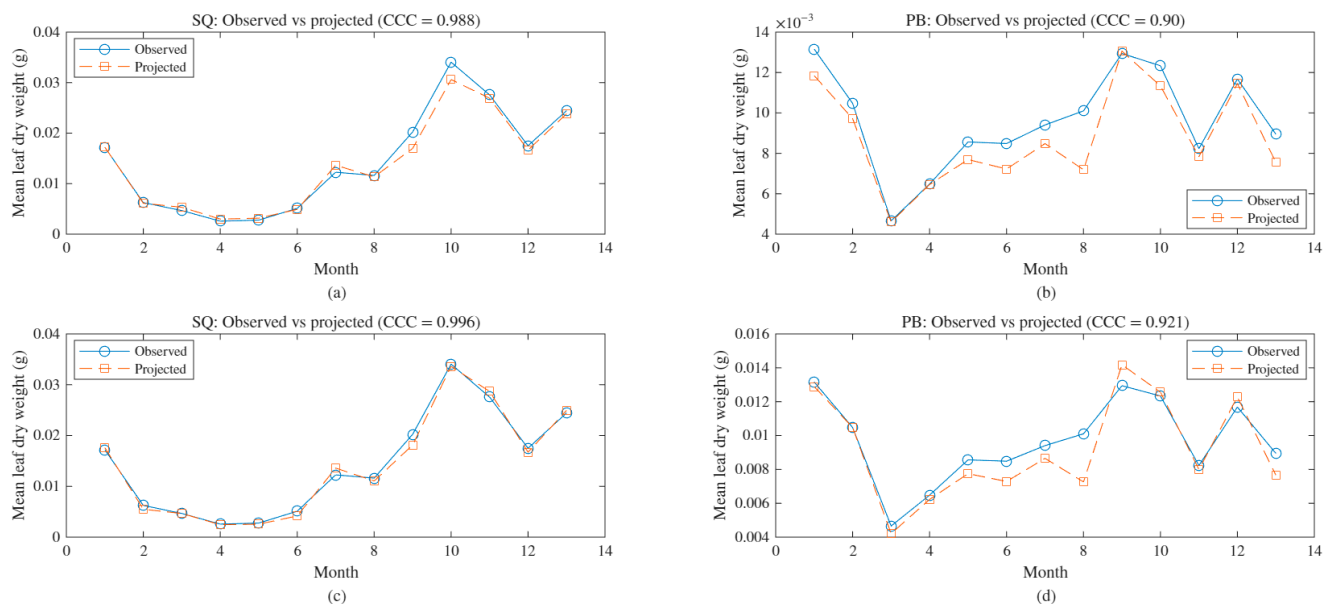


Figure 10. Monthly mean observed vs. projected eelgrass leaf dry weight under four calibrations of the area-based allometric model M3 (cf. Equation (18)). In panel (a), observed values in present SQ data versus their projections using parameter fitted using PB data collected during 2009. In panel (b), observed values in present PB data versus their projections using parameters fitted using present SQ data collected during 1992. In panel (c) observed values in present SQ data versus their projections using parameters fitted using PB data collected during 1998 [52]. In panel (d): observed

values in present PB data versus their projections using parameters fitted using PB data collected during 1998 [52].

Table 16 displays the values of Lin's CCC obtained in the cross-projection exercises (across sites and/or sampling periods) for models M1–M3, using monthly mean leaf dry weight. For the single-covariate baseline model M1, CCC values were high (≈ 0.95 – 0.96) in two transfers but decreased to ≈ 0.83 – 0.84 in the two less favorable transfers. Values in this range fall below 0.90 and are often classified as having poor agreement [57]. In monitoring contexts, discrepancies of this magnitude may be ecologically consequential depending on (i) the minimum change a program aims to detect and (ii) the presence of systematic bias (over- or underestimation). Accordingly, CCC should be interpreted together with error magnitudes in biomass units (e.g., mean absolute error or percent error) and bias, relative to the expected effect size (e.g., transplanted plots versus natural reference meadows). Importantly, these lower CCC values arise for M1, which is not favored by our model-selection analysis; therefore, they are not the basis for our monitoring guidance. For restoration-comparison purposes, our relevant recommendation is to use the bivariate model M2, with site-fitted parameters (or pooled/mean parameters when supported by the reproducibility tests), to estimate aerial production non-destructively and cost-effectively.

Table 16. This table compiles the CCC values reported for the cross-validation (cross-projection) exercises for Models M1, M2, and M3, using monthly mean leaf biomass.

Model	Figure	Panel	Calibration (Parameters)	Target Series Projected	CCC
M1	3	a	PB (reported in [39])	SQ (present data)	0.96
M1	3	b	SQ (present fit)	PB (present data)	0.836
M1	3	c	PB (reported in [39])	SQ (present data)	0.950
M1	3	d	SQ (reported in [39])	PB (present data)	0.831
M2	6	a	PB (present fit; 2009 sampling)	SQ (present data; 1992–1993 sampling)	0.975
M2	6	b	SQ (present fit; 1992–1993 sampling)	PB (present data; 2009 sampling)	0.90
M2	6	c	SQ (reported in [57]; 1992–1993 sampling)	SQ (present data; 1992–1993 sampling)	0.99
M2	6	d	PB (reported in [58]; 2000 sampling)	PB (present data; 2009 sampling)	0.93
M3	9	a	PB (present fit; 2009 sampling)	SQ (1992 sampling)	0.98
M3	9	b	SQ (present fit; 1992 sampling)	PB (2009 sampling)	0.90
M3	9	c	PB (reported in [52]; 1998 sampling)	SQ (1992 sampling)	0.96
M3	9	d	PB (reported in [52]; 1998 sampling)	PB (2009 sampling)	0.90

3.3.5. Model Selection Study for M1, M2, and M3 Across PB and SQ

In San Quintin, model M1 showed a clearly poorer fit than the two-dimensional formulations: its RMSE (0.00862) is larger than that of M2 (0.00718) and M3 (0.00718), indicating a wider dispersion of data around the mean response. M2 and M3 have practically identical RMSE and explain a similar fraction of the total variability, so the discrimination between them relies mainly on the information criteria. In this regard, M2 attains slightly lower (more favorable) AIC ($-73,240.89$, Table 7) and BIC ($-73,219.14$, Table 7) values than M3 (AIC $\approx -73,236.79$, BIC $\approx -73,215.03$, Table 12), which is usually interpreted as positive but moderate evidence in favor of M2, despite having one additional parameter (β).

In Punta Banda, differences among models are more pronounced. M2 has the smallest RMSE (0.00643), improving both the univariate model M1 (RMSE = 0.00682) and the area-based model M3 (RMSE = 0.00658). This superiority in fit is strongly reinforced by AIC and BIC: for the two-dimensional models, M2 shows much lower AIC (-7709.7) and BIC (-7694.8) values than M3 (AIC ≈ 1326.2 ; BIC ≈ 1341.1), which constitutes overwhelming evidence in favor of M2 as the best two-dimensional formulation. Although M3

slightly improves M1 in terms of RMSE and R^2 , its temporal performance (CCC) is lower, and, more importantly, its information criteria are extremely unfavorable compared to M2.

By contrast, the AIC and BIC values reported for M1 at both sites lie on a very different numerical scale and are not consistent with the ranking based on RMSE and R^2 , which consistently places M1 below M2 and M3. This inconsistency suggests that AIC/BIC for M1 were computed under a different likelihood scaling or parametrization and are therefore not directly comparable to those for M2 and M3. Consequently, M1 is rejected primarily on the basis of its higher RMSE and lower explanatory power, and the information criteria are used more reliably to discriminate between M2 and M3.

Taken together, the combined evidence from RMSE (leaf-level fit) and AIC/BIC (likelihood-based model comparison with complexity penalty) is consistent: (a) M1 is systematically inferior to the two-dimensional formulations and is discarded as a working model; (b) in SQ, M2 and M3 are practically equivalent in RMSE, but M2 has slightly more favorable AIC and BIC; (c) in PB, M2 clearly dominates M3 in RMSE, AIC, and BIC, with a very strong advantage in the information criteria.

The above model-selection procedure provides additional foundation required before one can legitimately claim that fitted parameters are invariant across sites. Invariance of parameters presupposes that the same structural model offers the best description of the data in all settings being compared. The statements above collectively support this prerequisite in three keyways: (a) They identify a single allometric formulation (M2) as the superior model in both PB and SQ. The assertions show that at each site model, M1 consistently underperforms according to RMSE, and its AIC/BIC are not directly comparable due to a scaling inconsistency. The statements above also sustain the conclusion that M2 and M3 outperform M1, thereby establishing that eelgrass leaf dry weight demands a two-dimensional (bivariate) description. M2 provides equal or better fit than M3 in SQ and decisively better fit in PB, particularly through AIC/BIC. Because invariance can only be discussed if the same allometric structure is appropriate for both datasets, the identification of M2 as the cross-site best model strengthens a conclusion of parameter invariance based in a maximum reproducibility criterion. (b) The worked model selection study shows that model M2 performance is consistent across sites, reinforcing the stability of the underlying allometric relationship. Moreover, the model contrast demonstrates that the relative ranking of the models is preserved across sites: M1 is worst in both PB and SQ; M2 and M3 are better than M1 in both PB and SQ; and M2 is the best-performing formulation in both PB and SQ. Unraveled consistency implies that the functional form governing leaf biomass scaling does not change with location, which is a conceptual requirement for concluding parameter invariance. If the preferred model changed from one site to another, one would expect changes in the underlying scaling exponents as well. The stability in model preference therefore supports the hypothesis that the same parameters govern the two systems. (c) The model selection findings also help by discarding models that would corrupt or bias the comparison of parameters. The discussion about AIC/BIC values for M1 (specifically the recognition that they are on a different numerical scale and cannot be compared) removes a source of methodological noise. This is better explained by noticing that the performed model contrast helps by establishing that M1 is not a valid competitor and that M2 and M3 are the only models with comparable likelihood-based metrics. Besides, the output of the model selection procedure ensures that the parameter comparison across sites is not affected by a technically flawed likelihood parametrization. This methodological clarity is crucial: parameter invariance must be evaluated within a self-consistent likelihood framework, and the yield of the model comparison task explicitly ensures that.

All this leads to parameter invariance. Once the passage has shown that M2 is superior at both sites, demonstrated coherence in model ranking across environments, and ensured comparability and technical soundness of the likelihood-based measures, it becomes reasonable to treat M2 as the common structural model for PB and SQ. Only under this shared structural formulation does it make sense to interrogate whether $(\rho_{SQ}, \alpha_{SQ}, \beta_{SQ})$ and $(\rho_{PB}, \alpha_{PB}, \beta_{PB})$ are statistically indistinguishable. Thus, the results of the performed model selection study serve as the key justification supporting the premises of an important inference. These read as follows: M2 is the most appropriate model for both datasets, and M2 provides a consistent, high-quality description of leaf biomass at both sites. Then, comparing M2 parameters across PB and SQ is meaningful, and any observed lack of statistical difference among those parameters can be interpreted as evidence of statistical parameter stability (i.e., transferability) for the purposes of prediction within the analyzed domain. The performed Wald difference test offers preliminary support for this statistical stability. We stress, however, that statistical similarity of fitted parameters does not necessarily imply invariance in underlying biological processes, particularly because environmental covariates (e.g., light, nutrients, hydrodynamics, sediments) were not included. Moreover, considering leaf-level fit, temporal reproducibility, and information criteria simultaneously, model M2 can be selected as the best allometric formulation among the three candidates and could be adopted as the reference model for subsequent analyses. Accordingly, because M1 underperforms the two-dimensional formulations in the leaf-level fit and exhibits weaker cross-site temporal concordance in the less favorable transfers (Section 3.1.4), we retain M1 only as a baseline and confirm M2 as the reference formulation for the subsequent transferability analyses and practical guidance.

3.3.6. Evaluation of the Reproducibility Strength of the Averages of Reported Fitted Parameters for Model M2

For present aims for $i = 1, 2, \dots, 10$, we arranged triads $T_i = (\rho_i, \alpha_i, \beta_i)$ of parameter estimates, identifying a suitable form of model M2 (cf. Equation (11)) given a dataset collected at different sampling dates at the Punta Banda estuary BC Mexico (PB) or San Quintin Bay BC México (SQ) study sites. In Table 17, triad $T_1 = (\rho_1, \alpha_1, \beta_1)$ of ρ , α , and β estimates were identified by [61] using measurements of leaf dry weight (w) and the corresponding length (l) and width (h) composing a dataset collected during July 1990 in a first transect located in San Quintin BC Mexico (SQ). The second row in Table 16 shows the $T_2 = (\rho_2, \alpha_2, \beta_2)$ triad fitted to data collected from a second transect at SQ bay also in July 1990 and both reported in Solana Arellano et al. (1992) [61]. Likewise, the parameter estimates in $T_3 = (\rho_3, \alpha_3, \beta_3)$ were fitted to the present study dataset corresponding to a sampling of an extensive dataset collected at SQ during 1992–1993 as explained in [58]. Correspondingly, $T_4 = (\rho_4, \alpha_4, \beta_4)$ was reported by [58], who fitted the bivariate model of Equation (1) to data collected from a first transect placing in SQ bay and during 1992–1993. In turn, the $T_5 = (\rho_5, \alpha_5, \beta_5)$ triplet was also obtained by fitting M2 to data collected in a second transect in SQ bay during 1992–1993, as explained in [58]. Similarly, the $T_6 = (\rho_6, \alpha_6, \beta_6)$ was fitted to the present study dataset collected during 1992–1993 at San Quintin Bay as reported in [52]. Correspondingly $T_7 = (\rho_7, \alpha_7, \beta_7)$ links to data collected in Punta Banda estuary during 1998–1999 and reported in [52]. A triad $T_8 = (\rho_8, \alpha_8, \beta_8)$ was produced by fitting model M2 to data collected from a source area plot in Punta Banda during 2000–2001 as described by [59]. Correspondingly, $T_9 = (\rho_9, \alpha_9, \beta_9)$ links to data collected from a transplanted bank also in Punta Banda during 2000–2001 and reported in [59]. Finally, $T_{10} = (\rho_{10}, \alpha_{10}, \beta_{10})$ was obtained by fitting M2 to the present study dataset collected in Punta Banda estuary during 2009.

Table 17. Triads $T_i = (\rho_i, \alpha_i, \beta_i)$; $i = 1, 2, \dots, 10$ of estimated values of the allometric parameters ρ , α , and β composing model M2 (cf. Equation (11)) reported in the given references.

Sampling	Site	ρ_i	α_i	β_i	Reference
1990	SQ	6.31×10^{-6}	1.12628	1.3353	[39]
1990	SQ	5.50×10^{-6}	1.5268	0.2625	[39]
1992–1993	SQ	8.68×10^{-6}	1.113	1.073	Present Study
1992–1993	SQ	1.00×10^{-5}	1.1088	1.0778	[57]
1992–1993	SQ	5.00×10^{-6}	1.22294	0.98405	[57]
1992–1993	SQ	6.00×10^{-6}	1.24	0.8	[52]
1998	PB	4.00×10^{-6}	1.36	0.75	[52]
2000	PB	8.00×10^{-6}	1.17	0.922	[58]
2000	PB	1.00×10^{-5}	1.187	0.751	[58]
2009	PB	6.67729×10^{-6}	1.1153	1.3189	Present Study

Next, we consider $\bar{T}$ as given by Equation (26), with values reported in Table 18. These values were used to project through the model M2 (cf. Equation (11)) the observed values of average monthly individual-leaf biomass $\bar{w}_{lhi}(t)$ (cf. Equation (20)) in the present SQ data; the agreement was remarkable (CCC = 0.97, Figure 11a). Analogously, the corresponding comparison for the presently addressed PB dataset entailed good reproducibility (CCC = 0.91, Figure 11b). Then, our exploration here demonstrates that the triad of averages $\bar{T} = (\bar{\rho}, \bar{\alpha}, \bar{\beta})$ of fitted parameters projects observed values of the response in the presently addressed SQ and PB datasets in a highly significant way.

Table 18. Triad $\bar{T} = (\bar{\rho}, \bar{\alpha}, \bar{\beta})$ of averages (cf. Equation (26)) of the values of the parameter estimates ρ_i , α_i , and β_i composing the triads $T_i = (\rho_i, \alpha_i, \beta_i)$ appearing in Table 17.

$\bar{\rho}$	$\bar{\alpha}$	$\bar{\beta}$
7.016729×10^{-6}	1.2170	0.9275

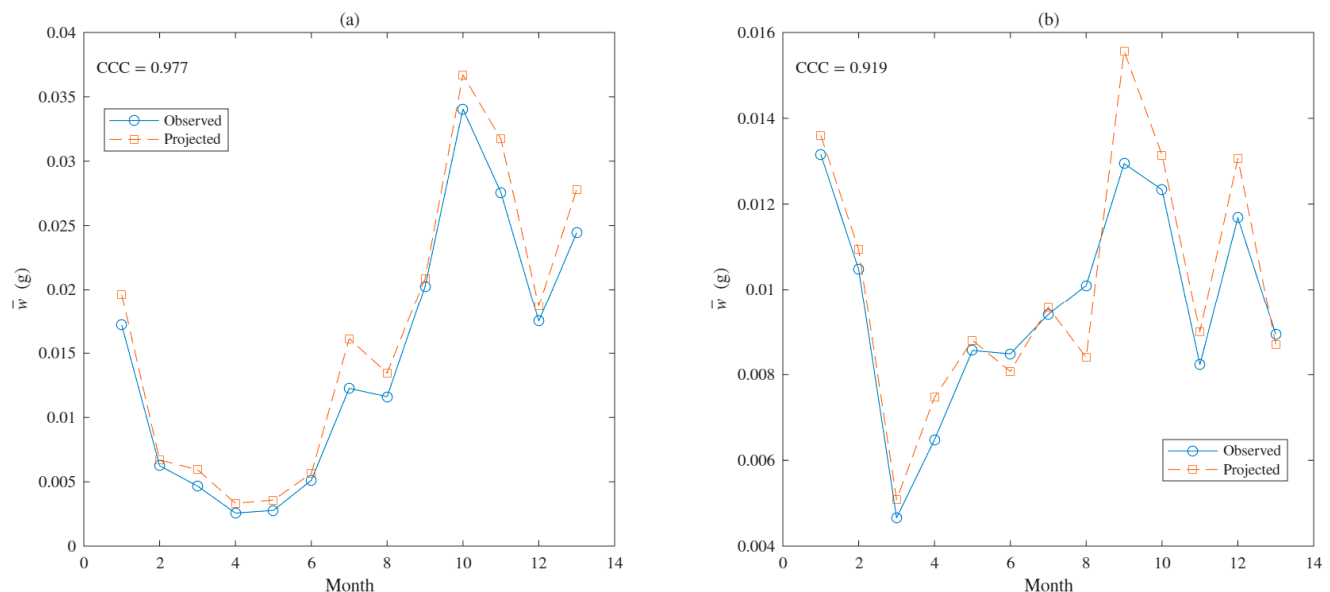


Figure 11. Monthly mean observed vs. projected eelgrass leaf dry weight under two alternative parameterizations of the bivariate allometric model M2 (cf. Equation (11)). Panel (a): Observed monthly averages of leaf dry weight values in the presently addressed SQ data compared to their allometric projections obtained using model M2 and the triad of averages $\bar{T} = (\bar{\rho}, \bar{\alpha}, \bar{\beta})$ of fitted parameters ρ , α , and β combined with leaf length and width in the presently arranged SQ dataset. Panel (b): Comparison of observed values of monthly averages of leaf dry weight in the present

study PB dataset with their allometric projections obtained using model M2 and the average parameter triad $\bar{T} = (\bar{\rho}, \bar{\alpha}, \bar{\beta})$ (cf. Equation (26)).

3.3.7. Evaluation of the Reproducibility Strength of the Parameter Estimates Achieved by Fitting Model M2 to the Composite Set $D_c = (PB \cup SQ)$

Similarly, in assessing invariance of allometric parameters tied to model M2, we also rely in a triad $T_c = (\rho_c, \alpha_c, \beta_c)$ where ρ_c, α_c , and β_c are estimates of the parameters ρ, α , and β produced by fitting the model M2 to the combined dataset $C = (SQ \cup PB)$ (Table 19).

Table 19. Triad $T_c = (\rho_c, \alpha_c, \beta_c)$ of parameter estimates deriving by fitting the model M2 (cf. Equation (11)) to the combined dataset $C = (SQ \cup PB)$.

ρ_c	α_c	β_c
9.1390×10^{-6}	1.10849	1.06386

It turned out that when the $T_c = (\rho_c, \alpha_c, \beta_c)$ triad of allometric parameters derived by fitting model M2 to the combined dataset $D_c = (PB \cup SQ)$ was used to project the observed values of average monthly individual-leaf biomass w in the present SQ data, the agreement was outstanding (CCC = 0.99, Figure 12a). In turn, a comparison of observed monthly averages of leaf dry weight values in the presently addressed PB data to their allometric ally-based $(\rho_c, \alpha_c, \beta_c)$ projections bear good agreement (CCC = 0.90, Figure 12b).

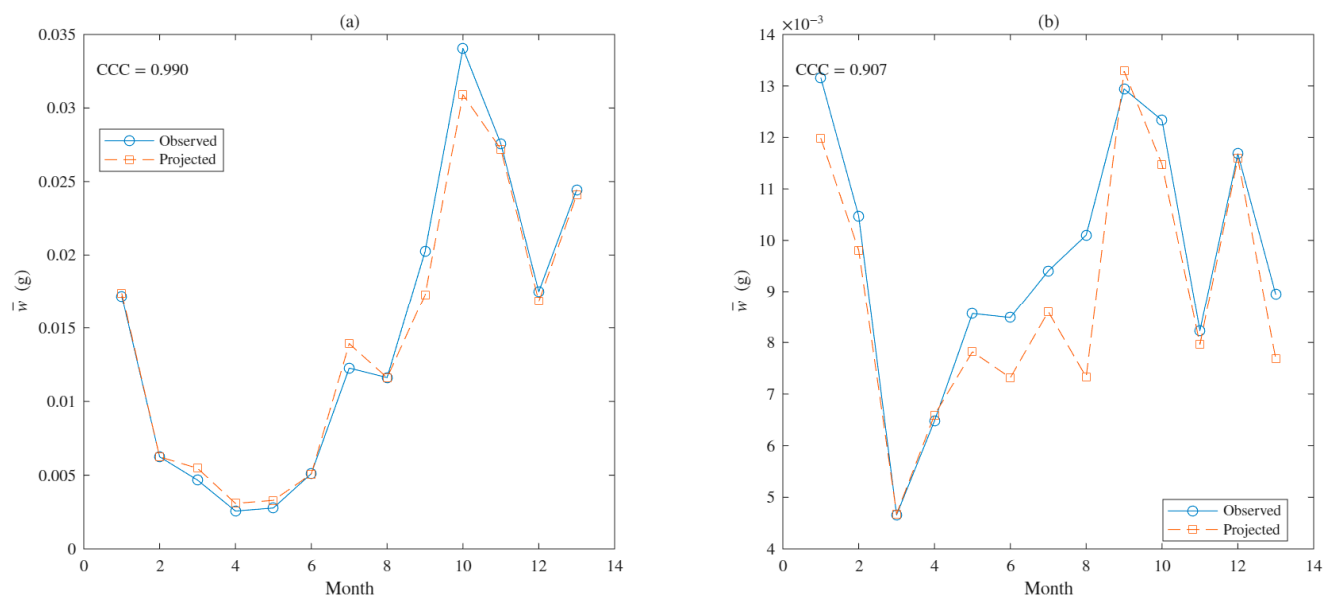


Figure 12. Observed monthly mean eelgrass leaf dry weight vs. their projected values under the $T_c = (\rho_c, \alpha_c, \beta_c)$ parameterization of the bivariate allometric model M2 (cf. Equation (11)) estimated using the D_c dataset obtained as explained above (Table 19). Panel (a): Comparison of observed monthly averages of leaf dry weight values in the presently addressed SQ data to their allometric projections obtained using the $T_c = (\rho_c, \alpha_c, \beta_c)$ triad. Panel (b): Comparison of observed monthly averages of leaf dry weight values in the presently addressed PB data, to their allometric projections obtained using the $T_c = (\rho_c, \alpha_c, \beta_c)$ triad.

3.4. Summary of Parameter-Invariance Results

The performed goodness-of-fit tests for each model M1, M2, and M3 determined that one by one, they produce consistent fits to the leaf biomass data in the two independent datasets SQ and PB, which, as we have emphasized, were collected at different sites and

in different years. The statistical tests also determined that there are no significant differences in the parameters fitted by each model to the SQ and PB data. It is worth stating that such a property provides a first indication of parameter invariance. We also corroborated that cross-reproducibility features can be asserted: for each model M1, M2, and M3, the corresponding allometric parameters fitted in SQ projected, with high CCC values, the observed leaf biomasses in PB, and vice versa.

A model selection study based on contrasting RMSD, AIC, and BIC statistics for each model determined that M2 was the one exhibiting the highest consistency. Moreover, when M2 was supplied with the triad of averages $\bar{T} = (\bar{\rho}, \bar{\alpha}, \bar{\beta})$ (Table 18), the reproducibility of monthly averages of leaf biomass values observed in SQ and PB through their allometrically projected proxies was remarkable.

Results also demonstrate that if we form a dataset $D_c = (PB \cup SQ)$ by combining the SQ and PB datasets, the model M2 also yields a highly consistent fit. In addition, the $T_c = (\rho_c, \alpha_c, \beta_c)$ of M2 parameters fitted on D_c indeed projects, with high reproducibility, the individual-leaf biomass values of the allometric response (w) in both SQ and PB datasets. Consequently, in this context, it could be argued that the parameters of the M2 model exhibit a high robustness or practical invariance with respect to the structure of the data. This statement is, at first sight, supported by the consistent fits it produces.

Moreover, the fact that M2 produces highly consistent independent fits to SQ, PB, and D_c (the combination of both) suggests that the underlying structure that M2 is modeling is the same in both SQ and PB datasets and that combining them does not introduce new complexities or biases that the model cannot handle. The key point here is the highly consistent agreement between the response values when using the parameters estimated by D_c to project the values in SQ and PB. This implies that the optimal parameters obtained from D_c are very similar to those that would have been obtained by fitting M2 separately to SQ or PB.

The strong reproducibility of predicted values achieved by M2 when using $\bar{T} = (\bar{\rho}, \bar{\alpha}, \bar{\beta})$, that is, the averages of reported values of its estimated parameters across independent datasets, provides a first strong clue of empirical evidence suggesting a degree of underlying parameter invariance across the conditions represented by those datasets.

Additionally, the triad $T_c = (\rho_c, \alpha_c, \beta_c)$ captures a fundamental relationship that does not depend on the particularities of the sample (whether SQ, PB or D_c). Indeed, if the parameters of M2 are effective in predicting responses in SQ and PB using parameter values fitted in D_c , it could be said that M2 provides strong evidence of parameter invariance to the extent that these parameters are generalizable and stable across the different subpopulations or conditions represented by SQ and PB data. In essence, high reproducibility implies low variability in the parameters across different observations, which is a key characteristic of invariance.

Across the two independent datasets (SQ and PB, collected at different sites and years), goodness-of-fit analyses indicate that each of the three formulations (M1, M2, and M3) provides internally consistent fits to leaf biomass. For each model, parameter-comparison tests detected no statistically significant differences between estimates obtained from SQ and PB, offering an initial indication of cross-site stability of the fitted allometric parameters. Cross-site validation through M2 further supported transferability: parameters fitted on SQ reproduced PB observations (and vice versa) with high CCC values for monthly mean biomass projections.

4. Discussion

4.1. Applied Context and Motivation

This work brings together two applied science themes. First, it builds on the use of allometric methods as practical tools for seagrass conservation and restoration. Duarte [48] provided a widely cited allometric framework linking size and architecture to seagrass dynamics and productivity; Marbà [62] extended allometric reasoning to clonal resource translocation and productivity; and Cebrián [63] examined leaf size–growth relationships across species, helping to embed scaling ideas into growth analyses. Second, it relates to safeguarding the ecological functions and services that seagrass meadows provide to society. A global valuation study [64] highlights the magnitude of these benefits and supports the view that seagrass restoration can yield substantial societal returns when integrated into broader coastal conservation programs.

Anthropogenic pressures threaten eelgrass, a key macrophyte that supports nursery habitat for fish and waterfowl, shoreline stabilization, nutrient cycling, and carbon sequestration. Restoration commonly relies on transplanted plots, and evaluating success requires noninvasive estimates of standing stock and productivity. Allometric scaling can provide cost-effective proxies for these assessments, but true cost-effectiveness depends on (i) accurate parameter estimation, because parameter uncertainty propagates into biomass projections, and (ii) demonstrating parameter invariance (transferability) over the relevant spatial and temporal domain when proxies are applied nondestructively.

4.2. Parameter Invariance: Definition and Scope of Transferability

In traditional allometry, we use “parameter invariance” in an operational/statistical sense: the scaling exponent α and proportionality constant q are considered stable when their fitted estimates remain statistically similar across valid datasets (e.g., across the analyzed sites, years, or samples). If an allometric parameter is statistically invariant in this sense, its estimated value remains (statistically) similar regardless of which valid dataset is used for fitting. We emphasize that statistical invariance should not be equated with invariance of the underlying biological processes, because environmental drivers can alter morphology and allocation even when fitted parameters appear stable, and environmental covariates were not explicitly modeled here.

Because environmental covariates (e.g., light availability, nutrient status, hydrodynamics, sediment conditions, temperature, turbidity, or disturbance history) were not explicitly modeled, broader transferability across strongly contrasting environments cannot be asserted from the two sites analyzed here. We therefore scope our conclusions to the spatial–temporal and environmental domain represented by the SQ and PB datasets. Importantly, our aim is not to develop an environmental-response model but to test the practical transferability of fitted allometric parameters for nondestructive biomass estimation. This is evaluated directly through between-site parameter-comparison tests and reciprocal cross-projections assessed by concordance on monthly means. Within this domain—especially for the preferred bivariate model M2—the parameter estimates behave as practically stable and transferable for prediction. Future work that co-measures environmental forcing across stronger gradients can apply the same statistical pipeline to quantify when (and how) the parameter triad departs from this practical invariance.

4.3. Relation to Prior Work and Expectations for α and ρ

In the context of Equation (1), the allometric exponent α has long been studied because it often appears to take a relationship-specific constant value [65–70], although variability has also been documented [71–76]. Likewise, the normalization constant ρ is commonly viewed as characteristic of a species or population [77] and may vary with

environmental conditions [65,66,78–81]. Some authors have therefore proposed interpreting ρ as environmentally responsive, especially when it is treated as a theoretically constrained parameter rather than a purely empirical regression estimate. In the present study, however, such added complexity is not required: across sites and sampling times, the estimated allometric parameters remain practically invariant within the analyzed domain.

Solana-Arellano [39] fitted the model in Equation (1), relating eelgrass leaf dry weight to length, and estimated α and ρ using data from two natural East Pacific populations (México) and three West Pacific populations (two natural sites in Korea and one mesocosm in Japan). By comparing observed leaf growth rates with allometric projections (Equation (19)) obtained from site-specific parameter estimates, they found that consistent results were achieved only when parameters were transferred within the same geographic region. They therefore conjectured that, under this regional constraint, previously fitted parameters could be used for reliable non-destructive assessments of eelgrass leaf growth rates, suggesting statistical similarity of α and ρ within a region. However, they emphasized that demonstrating time invariance of α and ρ would require a larger pool of datasets. A further question left open by Solana-Arellano [39] concerns how model complexity affects the assessment of parameter invariance—an issue that directly motivates the present work.

4.4. Empirical Evidence for Transferability Across PB and SQ

In the present reassessment of parameter invariance for allometric projection of *Zostera marina* leaf biomass, we considered three models: M1 (leaf biomass as a function of length), M2 (leaf biomass as a function of length and width), and M3 (leaf biomass as a function of an area surrogate). Goodness-of-fit analyses for M1, M2, and M3 showed that each formulation yields consistent fits to eelgrass leaf biomass in both independent datasets (SQ and PB), collected at different sites and in different years. Formal statistical tests further indicated no significant differences between the parameter sets fitted by each model to SQ and PB. Together with the high CCC values obtained in reciprocal cross-projections (using parameters estimated at one site to project the other, and vice versa), these results indicate that the observed differences between estimators are compatible with sampling variation rather than with systematic changes in allometric structure within the analyzed domain.

4.5. Model Performance and the Role of Complexity (Why M2 Is Preferred)

A model-selection study based on RMSD, AIC, and BIC identified M2 as both the most complex and the most consistent formulation addressed here. Projections of individual leaf biomass derived from M2 showed the highest reproducibility across sites and sampling dates. Moreover, when M2 was supplied with the averaged parameter triad $\bar{T} = (\bar{\rho}, \bar{\alpha}, \bar{\beta})$ (cf. Equation (26)), derived from independent fits to SQ and PB, it yielded stronger reproducibility of monthly mean leaf biomass at both sites than M1 or M3. The predictive strength of $\bar{T}$ when used with M2 implies that the site-specific parameter estimates must be tightly clustered around their average; if parameters varied widely across datasets, averaged values would be poor predictors, and cross-projections would not remain stable. Thus, the strong reproducibility based on $\bar{T}$ provides empirical support for practical invariance of the M2 parameter triad across the range of conditions represented by the independent datasets. Consistent results are also obtained when M2 is fitted to the composite dataset $D_c = (SQ \cup PB)$. The pooled-fit parameter triad $T_c = (\rho_c, \alpha_c, \beta_c)$ (Table 19) yields a model that fits D_c closely while providing accurate predictions for each individual dataset. This indicates that the allometric relationship captured by M2 is shared by both groups of observations and does not require site-specific parameterizations within

the analyzed domain. We caution, however, that this statistical stability does not rule out site differences in growth processes or environmental responses, because similar fitted parameters can result from compensatory plasticity or aggregation effects, and environmental covariates were not explicitly modeled.

4.6. Ecological Interpretation and Implications for Restoration Monitoring

In summary, we find (i) no significant between-site differences in the M2 parameter estimates and (ii) strong robustness of both the averaged triad $\bar{T}$ and the pooled-fit triad T_c for projecting observed leaf biomass at SQ and PB. Together, these lines of evidence support practical statistical parameter stability for the M2 formulation within the domain of conditions represented by our datasets. This directly addresses the research gap stated in the Introduction: the practical value of nondestructive allometric proxies depends on demonstrating that fitted parameters are transferable across time and space, rather than assuming that past calibrations remain valid.

A plausible (and testable) interpretation is that eelgrass morphology may be plastic while the scaling relation linking morphology to biomass remains effectively stable in aggregate: environmental variation may shift the distributions of leaf length and width, while plants move along an approximately stable allometric curve. This interpretation also carries broader ecological implications. If eelgrass exhibits strong phenotypic plasticity in leaf dimensions while remaining close to a stable biomass–morphometrics scaling relation, then environmental variability may primarily reallocate individuals along a common allometric “manifold,” rather than altering the underlying conversion between morphology and biomass. Ecologically, this would imply that (i) morphological adjustment can act as a buffering mechanism, allowing plants to track changes in light availability and hydrodynamic exposure by adjusting length and width while maintaining a predictable biomass yield for a given morphometric state; (ii) apparent scaling stability may reflect shared biomechanical and hydraulic constraints (e.g., drag, support costs, tissue density) that remain similar across the domain considered, even as trait distributions shift; and (iii) because canopy structure influences habitat complexity, epifaunal load, and trophic support, plastic shifts in leaf shape may affect community interactions and ecosystem functioning mainly through changes in the distribution of leaf sizes and canopy architecture, while still permitting robust biomass estimation from simple morphometrics.

Because environmental covariates were not explicitly modeled in this reassessment, we cannot disentangle whether the observed stability reflects compensatory trait plasticity, aggregation effects, or limited environmental contrast between sites, and we do not interpret it as evidence for universal scaling laws. In applied terms, these results support using M2—preferably with site-fitted parameters, or pooled/mean parameters when supported by reproducibility tests—to estimate aerial production non-destructively and cost-effectively when comparing transplanted plots against natural reference meadows.

5. Conclusions

This study tests whether simple, non-destructive allometric proxies can estimate *Zostera marina* leaf biomass reliably across two independently collected datasets from San Quintín and Punta Banda, sampled in different years. In practical terms, our results show that eelgrass leaf biomass can be estimated cost-effectively from simple leaf measurements and that using both leaf length and width provides the most reliable and transferable estimates across the two bays examined. Across the range of conditions represented by these datasets, the same allometric relationships provide adequate descriptions of the data, and parameter estimates are statistically similar between sites. Reciprocal cross-projections—using parameters calibrated at one site to predict the other—show high concordance on monthly mean leaf biomass, indicating that the observed differences between fitted

parameters are consistent with sampling variation rather than systematic changes in the scaling relationship. We stress that this conclusion is scoped to the spatial–temporal and environmental domain represented by SQ and PB and does not imply invariance of the underlying biological processes.

Among the candidate proxies evaluated—M1 (length-only), M2 (length–width), and M3 (area surrogate based on length $\times$ width)—M2 performed best. Model performance was assessed using RMSE at the leaf level and by AIC and BIC, which penalize unnecessary complexity. Under these criteria, M2 provided the most consistent description across both sites and also produced the strongest cross-projection agreement. Importantly, M2 remained highly reproducible when (i) it was supplied with averaged parameter values obtained from independent site fits and (ii) it was fitted to the pooled dataset (SQ $\cup$ PB). Together, these results support practical statistical stability (transferability) of the M2 parameters for prediction within the analyzed domain. Accordingly, when site-specific calibration is available it should be preferred, but when it is not, a single pooled or averaged parameter set can still provide reliable biomass estimates under comparable conditions.

Finally, cross-validation based on the length-only baseline proxy (M1) yielded CCC values around 0.83–0.85, indicating relatively weak agreement between projected and observed monthly mean leaf biomass under commonly used CCC interpretation criteria (e.g., [57]). In monitoring or restoration applications, deviations of this magnitude may be ecologically consequential depending on the minimum detectable change and on any systematic bias of the proxy. Consequently, CCC should be interpreted alongside error magnitudes expressed in biomass units (e.g., mean absolute error or percent error) and bias and relative to the expected effect size (e.g., transplanted plots versus natural reference meadows). Because these weaker CCC values pertain to the baseline proxy that is not favored by our model-selection results, they do not support applied guidance. For the restoration-comparison use case considered here, we recommend using the length–width proxy (M2)—with site-fitted parameters when available, or pooled/mean parameters when supported by reproducibility tests—to estimate aerial production non-destructively and to compare transplanted plots against natural reference meadows. More generally, the recommended workflow is to (i) measure leaf length and width, (ii) apply the best-supported length–width proxy to estimate biomass, and (iii) interpret changes in estimated biomass in light of expected effect sizes and error/bias, recalibrating the proxy if conditions shift outside the domain represented here.

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References

- Unsworth, R.K.F.; van Keulen, M.; Coles, R.G. Seagrass meadows in a globally changing environment. *Mar. Pollut. Bull.* **2014**, *83*, 383–386. <https://doi.org/10.1016/j.marpolbul.2014.02.026>.
- Jiménez-Casero, J.; Belando, M.D.; Bernardeau-Esteller, J.; Marín-Guirao, L.; García-Muñoz, R.; Sánchez-Lizaso, J.L.; Ruiz, J.M. A Critical Gap in Seagrass Protection: Impact of Anthropogenic Off-Shore Nutrient Discharges on Deep Posidonia oceanica Meadows. *Plants* **2023**, *12*, 457. <https://doi.org/10.3390/plants12030457>.
- Holmquist, J.; Powell, G.; Sogard, S. Decapod and stomatopod assemblages on a system of seagrass-covered mud banks in Florida Bay. *Mar. Biol.* **1989**, *100*, 473–483.
- Montague, C.L.; Ley, J.A. A possible effect of salinity fluctuation on abundance of benthic vegetation and associated fauna in Northeastern Florida Bay. *Estuaries* **1993**, *16*, 703–717. <https://doi.org/10.2307/1352429>.
- Plummer, M.L.; Harvey, C.J.; Anderson, L.E.; Guerry, A.D.; Ruckelshaus, M.H. The role of eelgrass in marine community interactions and ecosystem services: Results from ecosystem-scale food web models. *Ecosystems* **2013**, *16*, 237–251.
- Douglas, J.; Niner, H.; Garrard, S. Impacts of Marine Plastic Pollution on Seagrass Meadows and Ecosystem Services in South-east Asia. *J. Mar. Sci. Eng.* **2024**, *12*, 2314. <https://doi.org/10.3390/jmse12122314>.
- Blackburn, T.; Nedwell, D.; Wiebe, W. Active mineral cycling in a Jamaican seagrass sediment. *Mar. Ecol. Prog. Ser.* **1994**, *110*, 233–239.
- Park, S.-R.; Li, W.-T.; Kim, S.-H.; Kim, J.-W.; Lee, K.-S. A comparison of methods for estimating the productivity of *Zostera marina*. *J. Ecol. Environ.* **2010**, *33*, 59–65. <https://doi.org/10.5141/JEFB.2010.33.1.059>.
- Bass, A.V.; Wang, Z.; Chung, N.M.; So, M.W.K.; Falkenberg, L.J.; Thibodeau, B. Altered nutrient cycling functionality in seagrass meadows under a simulated future marine heatwave event. *New Phytol.* **2025**, *247*, 2616–2629. <https://doi.org/10.1111/nph.70382>.
- Liu, X.; Zhou, Y.; Yang, H.; Ru, S. Eelgrass detritus as a food source for the sea cucumber *Apostichopus japonicus* Selenka (Echinodermata: Holothuroidea) in coastal waters of North China: An experimental study in flow-through systems. *PLoS ONE* **2013**, *8*, e58293. <https://doi.org/10.1371/journal.pone.0058293>.
- Infantes, E.; Hoeks, S.; Adams, M.P.; van der Heide, T.; van Katwijk, M.M.; Bouma, T.J. Seagrass roots strongly reduce cliff erosion rates in sandy sediments. *Mar. Ecol. Prog. Ser.* **2022**, *700*, 1–12. <https://doi.org/10.3354/meps14196>.
- Kennedy, H.; Beggins, J.; Duarte, C.M.; Fourqurean, J.W.; Holmer, M.; Marbà, N.; Middelburg, J.J. Seagrass sediments as a global carbon sink: Isotopic constraints. *Glob. Biogeochem. Cycles* **2010**, *24*, GB4026. <https://doi.org/10.1029/2010GB003848>.
- Fu, C.; Frappi, S.; Havlik, M.N.; Howe, W.; Harris, S.D.; Laiolo, E.; Gallagher, A.J.; Masqué, P.; Duarte, C.M. Substantial blue carbon sequestration in the world's largest seagrass meadow. *Commun. Earth Environ.* **2023**, *4*, 474. <https://doi.org/10.1038/s43247-023-01154-0>.
- Short, F.T.; Neckles, H.A. The effects of global climate change on seagrasses. *Aquat. Bot.* **1999**, *63*, 169–196. [https://doi.org/10.1016/S0304-3770\(98\)00117-X](https://doi.org/10.1016/S0304-3770(98)00117-X).
- Grech, A.; Chartrand-Miller, K.; Erftemeijer, P.; Fonseca, M.; McKenzie, L.; Rasheed, M.; Taylor, H.; Coles, R. A comparison of threats, vulnerabilities and management approaches in global seagrass bioregions. *Environ. Res. Lett.* **2012**, *7*, 024006. <https://doi.org/10.1088/1748-9326/7/2/024006>.
- Vargas-Fonseca, O.A.; Frazier, M.; Lombard, A.T.; Halpern, B.S. Knowns and Unknowns in Future Human Pressures on the Ocean. *Earth's Future* **2024**, *12*, e2024EF004559. <https://doi.org/10.1029/2024EF004559>.
- Oakley, B.A.; Watling, E.; Musco, N.; Bradley, M.; Desbonnet, A.; August, P.V.; Cole, D.T. Changes in Eelgrass (*Zostera marina*) in the Little Narragansett Bay Estuary Between 2019 and 2022. *Coasts* **2025**, *5*, 35. <https://doi.org/10.3390/coasts5030035>.
- Phillips, R.C. Temperate grass flats. In *Coastal Ecological Systems of the U.S.*; Odum, H.T., Copeland, B.J., McMahan, E.A., Eds.; The Conservation Foundation: Washington, DC, USA, 1974; Volume 2, pp. 244–299.
- Short, F.T.; Coles, R.G.; Pergent-Martini, C. Global seagrass distribution. In *Global Seagrass Research Methods*; Short, F.T., Coles, R.G., Eds.; Elsevier Science B.V.: Amsterdam, The Netherlands, 2001; pp. 5–30.
- Williams, T.P.; Bubb, J.M.; Lester, J.N. Metal accumulation within salt marsh environments: A review. *Mar. Pollut. Bull.* **1994**, *28*, 277–290.
- Wang, W.; Wu, S.; Sui, X.; Cheng, S. Phytoremediation of contaminated sediments: Mechanisms, plant–microbe interactions, and ecological applications. *J. Hazard. Mater.* **2023**, *465*, 133135. <https://doi.org/10.1016/j.jhazmat.2023.133135>.
- Jacobs, R.P.W.M. Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. *Aquat. Bot.* **1979**, *7*, 151–172. [https://doi.org/10.1016/0304-3770\(79\)90019-6](https://doi.org/10.1016/0304-3770(79)90019-6).

23. Kindeberg, T.; Attard, K.M.; Hüller, J.; Müller, J.; Quintana, C.O.; Infantes, E. Structural complexity and benthic metabolism: Resolving the links between carbon cycling and biodiversity in restored seagrass meadows. *Biogeosciences* **2024**, *21*, 1685–1705. <https://doi.org/10.5194/bg-21-1685-2024>.
24. McRoy, C.P. The Standing Stock and Ecology of Eelgrass (*Zostera marina* L.) in Izembek Lagoon, Alaska. Master's Thesis, University of Washington, Seattle, WA, USA, 1966; p. 138.
25. Thayer, G.W.; Kenworthy, W.J.; Fonseca, M.S. *The Ecology of Eelgrass Meadows of the Atlantic Coast: A Community Profile*; U.S. Fish and Wildlife Service, Division of Biological Services: Washington, DC, USA, 1984; FWS/OBS-84/02.
26. Heck, K.L.; Able, K.W.; Roman, C.T.; Fahay, M.P. Composition, abundance, biomass, and production of macrofauna in a New England estuary: Comparisons among eelgrass meadows and other nursery habitats. *Estuaries* **1995**, *18*, 379–389.
27. Koehler, K.S.; Hovel, K.A. Eelgrass habitat structure affects epifaunal biodiversity and community composition but not the distribution of functional traits among taxa. *Mar. Ecol. Prog. Ser.* **2024**, *751*, 37–52. <https://doi.org/10.3354/meps14745>.
28. Williams, R. Nutrient level and phytoplankton productive in the estuary. In *Proceedings of the Coastal Marsh and Estuary Management Symposium*; Chabreck, R., Ed.; Louisiana State University: Baton Rouge, LA, USA, 1973; Volume 59.
29. Novak, A.B.; Plaisted, H.K.; Hughes, Z.J.; Mittermayr, A.; Molden, E. Eelgrass (*Zostera marina* L.) populations are threatened by high sea-surface temperatures and impaired waters on Nantucket Island, USA. *Mar. Pollut. Bull.* **2023**, *197*, 115689.
30. Montesinos-López, A.; Villa-Diharce, E.; Echavarría-Heras, H.; Leal-Ramírez, C. Improved allometric proxies for eelgrass conservation. *J. Coast. Conserv.* **2019**, *23*, 71–91. <https://doi.org/10.1007/s11852-018-0647-4>.
31. Orth, R.J.; Harwell, M.C.; Fishman, J.R. A rapid and simple method for transplanting eelgrass using single, unanchored shoots. *Aquat. Bot.* **1999**, *64*, 77–85.
32. Campbell, M.L.; Paling, E.I. Evaluating vegetative transplant success in *Posidonia australis*: A field trial with habitat enhancement. *Mar. Pollut. Bull.* **2003**, *46*, 828–834.
33. Fishman, J.R.; Orth, R.J.; Marion, S.; Bieri, J. A comparative test of mechanized and manual transplanting of eelgrass, *Zostera marina*, in Chesapeake Bay. *Restor. Ecol.* **2004**, *12*, 214–219.
34. Ward, M.; Beheshti, K. Lessons learned from over thirty years of eelgrass restoration on the US West Coast. *Ecosphere* **2023**, *14*, e4642.
35. Boardman, F.C.; Ruesink, J.L. Eelgrass (*Zostera marina*) recovery affected by disturbance timing on mechanically harvested oyster culture beds. *Estuaries Coasts* **2025**, *48*, 32. <https://doi.org/10.1007/s12237-024-01454-4>.
36. Sanders, R.D.; Obaza, A.K.; Ginsburg, D.W.; Carmack, O.C.; Grime, B.C.; Burdick, H.; Ford, T.K.; Leichter, J.J. Open-coast eelgrass (*Zostera marina*) transplant catalyzes rapid mirroring of structure and function of extant eelgrasses. *Estuaries Coasts* **2025**, *49*, 2.
37. Echavarría-Heras, H.; Solana-Arellano, E.; Lee, K.S.; Hosokawa, S.; Franco-Vizcaino, E. An evaluation of leaf biomass: Length ratio as a tool for nondestructive assessment in eelgrass (*Zostera marina* L.). *Sci. World J.* **2012**, *2012*, 543730. <https://doi.org/10.1100/2012/543730>.
38. Cronau, R.J.T.; de Fouw, J.; van Katwijk, M.M.; Bouma, T.J.; Heusinkveld, J.H.T.; Hoeijmakers, D.; Lamers, L.P.M.; van der Heide, T. Seed- versus transplant-based eelgrass (*Zostera marina* L.) restoration success in a temperate marine lake. *Restor. Ecol.* **2023**, *31*, e13786. <https://doi.org/10.1111/rec.13786>.
39. Solana-Arellano, E.; Echavarría-Heras, H.; Leal-Ramírez, C.; Lee, K.S. The effect of parameter variability in the allometric projection of leaf growth rates for eelgrass (*Zostera marina* L.). *Lat. Am. J. Aquat. Res.* **2014**, *42*, 1099–1108. <https://doi.org/10.3856/vol42-issue5-fulltext-14>.
40. Huxley, J.S. Constant differential growth-ratios and their significance. *Nature* **1924**, *114*, 895–896.
41. Huxley, J.S. *Problems of Relative Growth*; Methuen & Co., Ltd.: London, UK, 1932.
42. Savage, V.M.; Gillooly, J.F.; Woodruff, W.H.; West, G.B.; Allen, A.P. The predominance of quarter-power scaling in biology. *Funct. Ecol.* **2004**, *18*, 257–282.
43. Marquet, P.A.; Quiñones, R.A.; Abades, S.; Labra, F.; Tognelli, M. Scaling and power-laws in ecological systems. *J. Exp. Biol.* **2005**, *208*, 1749–1769.
44. West, G.B.; Brown, J.H. The origin of allometric scaling laws in biology from genomes to ecosystems: Towards a quantitative unifying theory of biological structure and organization. *J. Exp. Biol.* **2005**, *208*, 1575–1592.
45. Harris, L.A.; Duarte, C.M.; Nixon, S.W. Allometric laws and prediction in estuarine and coastal ecology. *Estuaries Coasts* **2006**, *29*, 343–347.
46. Filgueira, R.; Labarta, U.; Fernández-Reiriz, M.J. Effect of condition index on allometric relationships of clearance rate in *Mytilus galloprovincialis* Lamarck, 1819. *Rev. Biol. Mar. Oceanogr.* **2008**, *43*, 391–398.

47. Kaitaniemi, P. How to derive biological information from the value of the normalization constant in allometric equations. *PLoS ONE* **2008**, *3*, e1932.
48. Duarte, C.M. Allometric scaling of seagrass form and productivity. *Mar. Ecol. Prog. Ser.* **1991**, *77*, 289–300.
49. McRoy, C.P. Standing stock and other features of eelgrass (*Zostera marina*) populations on the coast of Alaska. *J. Fish. Res. Board Can.* **1970**, *27*, 1811–1821.
50. Penhale, P.A. Macrophyte-epiphyte biomass and productivity in an eelgrass (*Zostera marina* L.) community. *J. Exp. Mar. Biol. Ecol.* **1977**, *26*, 211–224. [https://doi.org/10.1016/0022-0981\(77\)90109-5](https://doi.org/10.1016/0022-0981(77)90109-5).
51. Hamburg, S.P.; Homann, P.S. Utilization of growth parameters of eelgrass, *Zostera marina*, for productivity estimation under laboratory and in situ conditions. *Mar. Biol.* **1986**, *93*, 299–303. <https://doi.org/10.1007/BF00508267>.
52. Echavarría-Heras, H.; Solana-Arellano, E.; Franco-Vizcaíno, E. An allometric method for the projection of eelgrass leaf biomass production rates. *Math. Biosci.* **2010**, *223*, 58–65.
53. Echavarría-Heras, H.A.; Lee, K.S.; Solana-Arellano, M.E.; Franco-Vizcaíno, E. Formal analysis and evaluation of allometric methods for estimating above-ground biomass of eelgrass. *Ann. Appl. Biol.* **2011**, *159*, 503–515. <https://doi.org/10.1111/j.1744-7348.2011.00511.x>.
54. Gayon, J. History of the concept of allometry. *Am. Zool.* **2000**, *40*, 748–758.
55. Batschelet, E. *Introduction to Mathematics for Life Scientists*; Springer: New York, NY, USA, 2012.
56. Zachmanoglou, E.C.; Thoe, D.W. *Introduction to Partial Differential Equations with Applications*; Williams & Wilkins: Baltimore, MD, USA, 1976.
57. McBride, G.B. *A Proposal for Strength-of-Agreement Criteria for Lin's Concordance Correlation Coefficient*; NIWA Client Report: HAM2005-062; National Institute of Water & Atmospheric Research Ltd.: Hamilton, New Zealand, 2005.
58. Borbón González, D.J. Estimación de Biomasa Aérea de *Zostera marina* Linneo en Bahía San Quintín, B.C., Mediante Modelos Matemáticos. Master's Thesis, Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, México, 1997.
59. Solana-Arellano, E.; Echavarría-Heras, H.A.; Flores-Uzeta, O.; Nieto-García, E. Experimental transplant of *Zostera marina* L. shoots in Punta Banda Estuary B.C., México: Production parameters and associated benthic fauna. In *Oceanography of the Eastern Pacific II*; Farber Lorda, J., Ed.; Centro de Investigación Científica y de Educación Superior de Ensenada: Ensenada, México, 2002; pp. 99–105.
60. Echavarría-Heras, H.; Leal-Ramírez, C.; Villa-Diharce, E.; Cazarez-Castro, N. On the suitability of an allometric proxy for non-destructive estimation of average leaf dry weight in eelgrass shoots I: Sensitivity analysis and examination of the influences of data quality, analysis method, and sample size on precision. *Theor. Biol. Med. Model.* **2018**, *15*, 4. <http://doi.org/10.1186/s12976-018-0076-y>.
61. Solana-Arellano, M.E.; Ibarra-Obando, S.E.; Echavarría-Heras, H. Calibración de un modelo alométrico para evaluar la producción foliar de *Zostera marina* L. *Hidrobiológica* **1992**, *1*, 41–44.
62. Marbà, N.; Hemminga, M.A.; Duarte, C.M. Resource translocation within seagrass clones: Allometric scaling to plant size and productivity. *Oecologia* **2006**, *150*, 362–372. <https://doi.org/10.1007/s00442-006-0524-y>.
63. Cebrián, J.; Duarte, C.M.; Marbà, N. Leaf growth response to simulated herbivory in *Zostera marina*. *J. Exp. Mar. Biol. Ecol.* **1998**, *220*, 67–90.
64. Costanza, R.; d'Arge, R.; de Groot, R.; Farber, S.; Grasso, M.; Hannon, B.; Limburg, K.; Naeem, S.; O'Neill, R.V.; Paruelo, J.; et al. The value of the world's ecosystem services and natural capital. *Nature* **1997**, *387*, 253–260.
65. Winter, J.E. A critical review on some aspects of filter feeding in lamellibranchiate bivalves. *Halictis* **1976**, *7*, 71–87.
66. Bernard, F.R. *Physiology and the Mariculture of Some Northeastern Pacific Bivalve Molluscs*; Canadian Special Publication of Fisheries and Aquatic Sciences; Government of Canada, Fisheries and Oceans, Scientific Information and Publications Branch: Ottawa, ON, Canada, 1983; Volume 63, 24p.
67. Jones, H.D.; Richards, O.G.; Southern, T.A. Gill dimensions, water pumping rate and body size in the mussel *Mytilus edulis* L. *J. Exp. Mar. Biol. Ecol.* **1992**, *155*, 213–237.
68. Enquist, B.J.; Brown, J.H.; West, G.B. Allometric scaling of plant energetic and population density. *Nature* **1998**, *395*, 163–165.
69. Niklas, K.J.; Enquist, B.J. Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proc. Natl. Acad. Sci. USA* **2001**, *98*, 2922–2927.
70. West, G.B.; Woodruff, W.H.; Brown, J.H. Allometric scaling of metabolic rate from molecules and mitochondria to cells and mammals. *Proc. Natl. Acad. Sci. USA* **2002**, *99*, 2473–2478.
71. Riisgård, H.U. No foundation of a '3/4 power scaling law' for respiration in biology. *Ecol. Lett.* **1998**, *1*, 71–73.

72. Atanasov, A.T.; Dimitrov, D.B. Changes of the power coefficient in the ‘metabolism-mass’ relationship in the evolutionary process of animals. *BioSystems* **2002**, *66*, 65–71.
73. Bokma, F. Evidence against universal metabolic allometry. *Funct. Ecol.* **2004**, *18*, 184–187.
74. Muller-Landau, H.C.; Condit, R.S.; Chave, J.; Thomas, S.C.; Bohlman, S.A.; Bunyavejchewin, S.; Davies, S.; Foster, R.; Gunatilleke, S.; Harms, K.E.; et al. Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecol. Lett.* **2006**, *9*, 575–588.
75. Reich, P.B.; Tjoelker, M.G.; Machado, J.-L.; Oleksyn, J. Universal scaling of respiratory metabolism, size and nitrogen in plants. *Nature* **2006**, *439*, 457–461.
76. White, C.R.; Phillips, N.F.; Seymour, R.S. The scaling and temperature of vertebrate metabolism. *Biol. Lett.* **2006**, *2*, 125–127.
77. Niklas, K.J. *Plant Allometry: The Scaling of Form and Process*; University of Chicago Press: Chicago, IL, USA, 1994; pp. 412.
78. West, G.B.; Brown, J.H.; Enquist, B.J. A general model for the origin of allometric scaling laws in biology. *Science* **1997**, *276*, 122–126.
79. Gillooly, J.F.; Brown, J.H.; West, G.B.; Savage, V.M.; Charnov, E.L. Effects of size and temperature on metabolic rate. *Science* **2001**, *293*, 2248–2251.
80. Brown, J.H.; Gupta, V.K.; Li, B.-L.; Milne, B.T.; Restrepo, C.; West, G.B. The fractal nature of nature: Power laws, ecological complexity and biodiversity. *Philos. Trans. R. Soc. London. Ser. B Biol. Sci.* **2002**, *357*, 619–626.
81. Kaitaniemi, P.; Lintunen, A. Precision of allometric scaling equations for trees can be improved by including the effect of ecological interactions. *Trees* **2008**, *22*, 579–584.

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