
Development of a Dynamic Energy Budget Model for *Pyropia dentata* Cultivation in Korean Coastal Waters

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Abstract

We developed a Dynamic Energy Budget (DEB) model for *Pyropia dentata* cultivation in Korea, explicitly accounting for contrasting farming environments. The model integrates temperature, light, nutrients, wave exposure, and intertidal emersion to simulate reserve dynamics and structural growth, and was calibrated and validated across two sites (Imha, pole-type; Eoran, floating) and three cultivars. Performance evaluation indicates that the model reproduces observed biomass dynamics across all six site-cultivar scenarios, with R^2 values between 0.8822 and 0.9924 and RMSE values between 0.3219 and 3.2816. Sensitivity analysis using one-at-a-time perturbations shows that growth rate and thermal tolerance parameters are consistently dominant drivers, while desiccation-related parameters are particularly influential at the intertidal site. These results demonstrate that site-specific exposure processes are essential for modeling pole-type cultivation and provide a mechanistic basis for growth prediction and management under variable coastal conditions.

1 Introduction

Global seaweed aquaculture has expanded rapidly in recent decades and now contributes substantially to food supply, coastal livelihoods, and biogeochemical services such as carbon sequestration. The Food and Agriculture Organization reports continued growth in farmed seaweed production and emphasizes its role in nutrition, industrial bioproducts, and climate mitigation strategies. [FAO, 2022] These trends motivate the development of mechanistic growth models that can support sustainable cultivation planning under changing environmental conditions.

Korea is a leading producer of laver (genus *Pyropia* and *Porphyra*), and the sector has significant national economic value. Recent reports highlight both the scale of production and the need for improved management tools to stabilize yield across variable environments. [FAO, 2022, Ministry of Oceans and Fisheries, 2022] Cultivation practices in Korea include intertidal pole-type systems with periodic exposure and coastal floating systems that remain largely submerged. These contrasting settings impose distinct thermal, light, and hydrodynamic regimes that can drive site-specific growth responses.

Dynamic Energy Budget (DEB) theory provides a general framework to describe how organisms assimilate and allocate energy for maintenance, growth, and reproduction. [Kooijman, 2010a,b] DEB-based models are attractive for aquaculture because they link growth to environmental drivers through physiologically meaningful parameters. Prior macroalgal applications include DEB formulations for *Pyropia yezoensis* and other taxa such as *Saccharina latissima* and *Ulva lactuca*, as well as broader macroalgae modeling frameworks. [Tac et al., 2025, Broch and Slagstad, 2012, Lavaud, 2013, Hadley et al., 2014, Arzeno-Soltero et al., n.d.] However, existing models have focused on floating or fully submerged cultivation and do not capture the exposure dynamics of pole-type systems.

Pyropia dentata is a commercially valuable species in Korea with multiple cultivars exhibiting distinct growth traits. [Han et al., 2021] Despite its importance, no DEB model has been developed specifically for *P. dentata*, and no model has been validated across both pole-type and floating cultivation. Preprint. Under review.

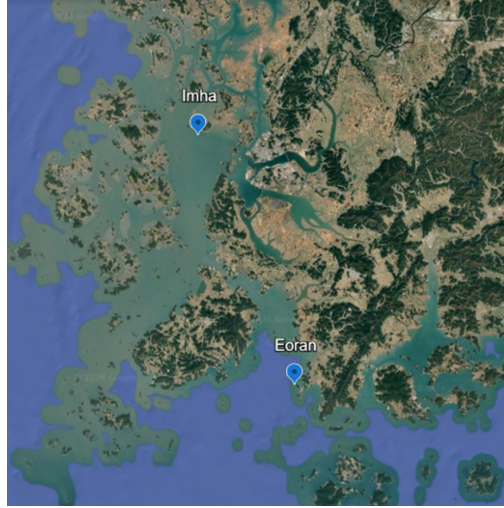


Figure 1: Location of the study sites in Haenam County, South Korea. Imha represents a tidal-flat pole-type system, and Eoran represents a coastal floating system.

tivation systems. [National Institute of Fisheries Science, 2018] The objectives of this study are to (1) develop a DEB model tailored to *P. dentata* that incorporates site-specific environmental forcing, including intertidal exposure effects, (2) calibrate and validate the model simultaneously across two sites (Imha and Eoran) and three cultivars, and (3) quantify parameter sensitivities to identify dominant drivers of biomass accumulation. By addressing these gaps, the study provides a mechanistic tool for growth prediction and management in contrasting Korean cultivation environments.

2 Materials and Methods

2.1 Study sites and environmental data

The study considered two cultivation systems in Haenam County, Korea (Figure 1). The Imha site (34°49'48"N, 126°14'31"E) represents an intertidal pole-type system with periodic emersion, whereas the Eoran site (34°21'33"N, 126°27'42"E) represents a coastal floating system that remains largely submerged. Environmental forcing data were compiled for the 2018–2019 cultivation season and summarized in Table 1. Hourly meteorological variables (air temperature, wind speed, and solar radiation) were obtained from the ASOS station records, tidal height and salinity were obtained from the Korea Hydrographic and Oceanographic Agency, and water temperature data were obtained from the National Institute of Fisheries Science. [Korea Meteorological Administration, 2026, Korea Hydrographic and Oceanographic Agency, 2026, National Institute of Fisheries Science, 2026] Salinity statistics were derived from the Jindo tide station records and applied to both sites for the study period. Nutrient observations (NO₃-N and DIP as P) and growth measurements were derived from the *P. dentata* cultivar dataset. [Han et al., 2021]

All forcing series were aligned to a fixed hourly index spanning 2018-09-01 to 2019-02-28. Weather and water temperature data were resampled to hourly means and linearly interpolated; missing values were forward/back-filled to preserve continuity. Sparse nutrient observations were interpolated to hourly resolution with a hold extrapolation policy outside the sampling window. Exposure fraction for the intertidal site was computed from minute-resolution tide data by identifying low-tide times (one per half-day) on a smoothed tide series, then calculating the fraction of each hour that overlapped a ± 1 h window centered on low tide. This exposure fraction was used to reduce light- and nutrient-driven assimilation during emersion.

2.2 DEB model formulation

A hybrid DEB model was developed to describe reserve dynamics and structural growth of *Pyropia dentata*. The state variables are structural biomass proxy M_V (cm²-equivalent area), and reserve densities for carbon, nitrogen, and phosphorus (m_{EC} , m_{EN} , m_{EP}). Temperature effects are repre-

Table 1: Environmental conditions during the 2018–2019 cultivation period.

Parameter	Unit	Imha (Pole-type)		Eoran (Floating)	
		Mean±SD	Range	Mean±SD	Range
Temperature	°C	15.26±5.08	9.24–25.10	12.88±6.76	5.14–25.44
Salinity	PSU	32.26±0.60	0.20–38.20	32.26±0.60	0.20–38.20
Solar rad.	W m ⁻²	111.47±197.37	0.00–894.44	111.47±197.37	0.00–894.44
Nitrogen (NO ₃ -N)	μM	2.39±0.91	0.36–3.00	4.35±2.73	2.57–11.57
Phosphorus (DIP-P)	μM	1.38±0.54	0.32–1.74	1.24±0.24	0.74–1.39
Tidal range	m	2.33±1.24	0.00–4.56	-	-
Exposure time	h	3.25±1.47	0.00–5.03	-	-

sented with an Arrhenius function with lower and upper tolerance limits:

$$f_T(T) = \frac{\exp\left(\frac{T_A}{T_{\text{ref}}} - \frac{T_A}{T}\right)}{\left(1 + \exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right)\right) \left(1 + \exp\left(\frac{T_{AH}}{T} - \frac{T_{AH}}{T_H}\right)\right)}, \quad (1)$$

where T is water temperature in Kelvin and T_A , T_L , T_H , T_{AL} , and T_{AH} are Arrhenius parameters.

Solar radiation (MJ m⁻² per period) was converted to photosynthetically active radiation (PAR) using fixed conversion factors and the sampling period Δt (s). The carbon assimilation rate follows a saturating light response:

$$P = P_{\max} (1 - \exp(-\alpha I / P_{\max})), \quad P_{\max} = P_{\max}^{\text{ref}} f_T(T), \quad (2)$$

with a CO₂ limitation factor $f_{\text{CO}_2} = \frac{C_{\text{CO}_2}}{C_{\text{CO}_2} + K_c}$ and an emersion reduction $f_{\text{em}} = 1 - \gamma \text{exposure}$ (clamped to [0,1]). The carbon assimilation flux is

$$\dot{j}_C = \eta_C P f_{\text{CO}_2} f_{\text{em}} M_V, \quad (3)$$

where η_C is an assimilation efficiency coefficient.

Nitrogen and phosphorus assimilation were modeled with Michaelis–Menten uptake modulated by temperature and emersion:

$$\dot{j}_N = V_{\max, N} f_T(T) \frac{N}{N + K_N} \cdot \phi_N \cdot M_V \cdot (1 - \text{exposure})^{p_e}, \quad (4)$$

$$\dot{j}_P = V_{\max, P} f_T(T) \frac{P}{P + K_P} \cdot \phi_P \cdot M_V \cdot (1 - \text{exposure})^{p_e}, \quad (5)$$

where N and P are dissolved nutrient concentrations (converted to model units), ϕ_N and ϕ_P are cultivar-specific scaling factors, and p_e is the emersion nutrient power.

Reserve dynamics are expressed per unit structural mass:

$$\frac{dm_{EC}}{dt} = \frac{\dot{j}_C - \dot{j}_{ECM}}{M_V}, \quad \frac{dm_{EN}}{dt} = \frac{\dot{j}_N - \dot{j}_{ENM}}{M_V}, \quad \frac{dm_{EP}}{dt} = \frac{\dot{j}_P - \dot{j}_{EPM}}{M_V}, \quad (6)$$

where maintenance fluxes \dot{j}_{ECM} , \dot{j}_{ENM} , and \dot{j}_{EPM} are proportional to M_V . A quota limitation factor was defined as the minimum of normalized C, N, and P reserves:

$$q = \min\left(\frac{m_{EC} - C_{\min}}{C_{\max} - C_{\min}}, \frac{m_{EN} - N_{\min}}{N_{\max} - N_{\min}}, \frac{m_{EP} - P_{\min}}{P_{\max} - P_{\min}}\right), \quad (7)$$

clamped to the interval [0,1].

Structural growth was modeled as

$$\frac{dM_V}{dt} = v_{\text{eff}} q M_V - L_{\text{shade}} - L_{\text{wave}} - L_{\text{des}}, \quad (8)$$

where $v_{\text{eff}} = v_{\text{effective}} f_T(T) \exp(-k_v \text{exposure})$. Shading loss is $L_{\text{shade}} = k_{\text{shade}} \max(0, M_V - K)$, with carrying capacity K . Wave loss is proportional to significant wave height H_s computed

from wind speed and local fetch/depth, $L_{\text{wave}} = k_{\text{wave}} w_{\text{exp}} H_s M_V$. Desiccation loss was applied only to the intertidal site and scaled with exposure and weather forcing:

$$L_{\text{des}} = r_{\text{des}} \text{exposure}^{p_{\text{des}}} M_V (1 + s_w(0.1I + 0.05U)), \quad (9)$$

where I is solar radiation (MJ m^{-2} per period) and U is wind speed (m s^{-1}).

Biomass output was computed as $B = k_A M_V$, and thallus length and width were derived from the modeled area assuming a fixed shape factor and width-to-length ratio. Initial conditions (L_0 , W_0) were set from the first observation in each site-cultivar series.

2.3 Numerical integration

The model was integrated with a fourth-order Runge–Kutta scheme at hourly time steps ($\Delta t = 1$ h), matching the temporal resolution of the forcing series. This ensured consistent coupling between environmental inputs and physiological responses.

2.4 Parameter calibration and validation

Calibration used the growth observations for three cultivars (Supoom 1, Supoom 2, and Yuldo) at Imha and Eoran. [Han et al., 2021] For each cultivar, the parameter set was tuned jointly across the two sites. Observed biomass was estimated from measured length and width using a constant areal density (0.004 g cm^{-2}) and a shape factor (0.65). The objective function minimized the root mean square error (RMSE) between observed and simulated biomass aggregated across both sites:

$$J(\theta) = \sum_{s \in \{\text{Imha}, \text{Eoran}\}} \text{RMSE}(B_s^{\text{obs}}(t), B_s^{\text{sim}}(t; \theta)). \quad (10)$$

A site-specific scaling coefficient k_A was estimated by least squares from predicted M_V and observed biomass for each site, and was constrained to $[0.05, 10]$.

Parameter search used Optuna with a TPE sampler (60 trials, seed 42) when available; otherwise, a two-stage adaptive search (uniform random sampling followed by local perturbation) was applied. Tuned parameters included the common growth rate $v_{\text{effective}}$, cultivar-specific nutrient assimilation factors (ϕ_N , ϕ_P), emersion and desiccation parameters (k_v , r_{des} , p_{des} , p_e , and weather scaling), and site-specific wave exposure coefficients. The search bounds followed the ranges defined in the model code. Model performance was evaluated with RMSE and R^2 for each of the six site-cultivar scenarios.

2.5 Sensitivity analysis

One-at-a-time (OAT) sensitivity analysis was conducted using the calibrated parameter sets for each cultivar and site. Non-temperature parameters were perturbed by $\pm 10\%$, while temperature parameters (T_A , T_L , T_H , T_{AL} , T_{AH}) were perturbed by ± 1 K. Sensitivity was quantified using the normalized change in final biomass:

$$S = \frac{B_+ - B_-}{0.2 B_0}, \quad (11)$$

where B_0 is baseline final biomass and B_+ and B_- are the perturbed outputs. Results were summarized by the top-ranked parameters for each site and cultivar.

3 Results

3.1 Model performance

Model performance metrics are summarized in Table 2. Across the six site–cultivar scenarios, RMSE ranged from 0.3219 to 3.2816 and R^2 ranged from 0.8822 to 0.9924. For all three cultivars, the floating Eoran site showed lower RMSE (0.3219–0.7450) than the intertidal Imha site (0.8228–3.2816). The fitted site-specific biomass scaling coefficient k_A varied from 0.0611 (Supoom1, Imha) to 0.9347 (Supoom2, Eoran), reflecting differences in biomass conversion between cultivation systems. The validation periods were 2018-10-19 to 2018-11-07 for Eoran and 2018-11-21 to 2019-01-06 for Imha, matching the observation windows used for calibration.

Table 2: Best-model performance after parameter tuning.

Cultivar	Location	Mode	n	RMSE	R^2	k_A	Period
Supoom1	Eoran	floating	3	0.5263	0.9924	0.4443	2018-10-19–2018-11-07
Supoom1	Imha	fixed	4	3.1239	0.9696	0.0611	2018-11-21–2019-01-06
Supoom2	Eoran	floating	3	0.7450	0.8849	0.9347	2018-10-19–2018-11-07
Supoom2	Imha	fixed	4	3.2816	0.8822	0.3223	2018-11-21–2019-01-06
Yuldo	Eoran	floating	3	0.3219	0.9885	0.6709	2018-10-19–2018-11-07
Yuldo	Imha	fixed	4	0.8228	0.8889	0.3507	2018-11-21–2019-01-06

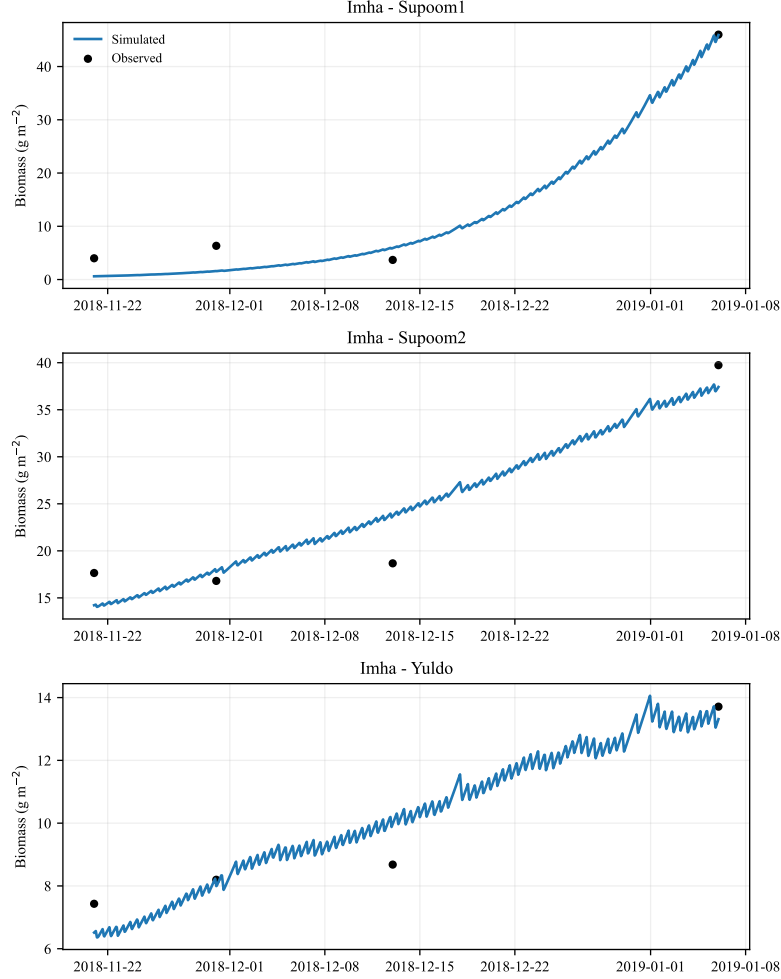


Figure 2: Observed (symbols) and simulated (lines) biomass for three cultivars at the Imha site.

3.2 Growth predictions

Figures 2 and 3 compare observed and simulated biomass for the three cultivars at each site. The model reproduced the overall temporal trajectories for all cultivars, capturing the timing and magnitude of the observed growth increases within the sampling windows. Site-specific differences were evident: growth at the floating Eoran site exhibited smoother trajectories and consistently lower error metrics, whereas the intertidal Imha site showed larger deviations at some observation points. Figure 4 highlights the contrast between cultivation systems, with differences in growth rates and final biomass linked to the distinct exposure regimes.

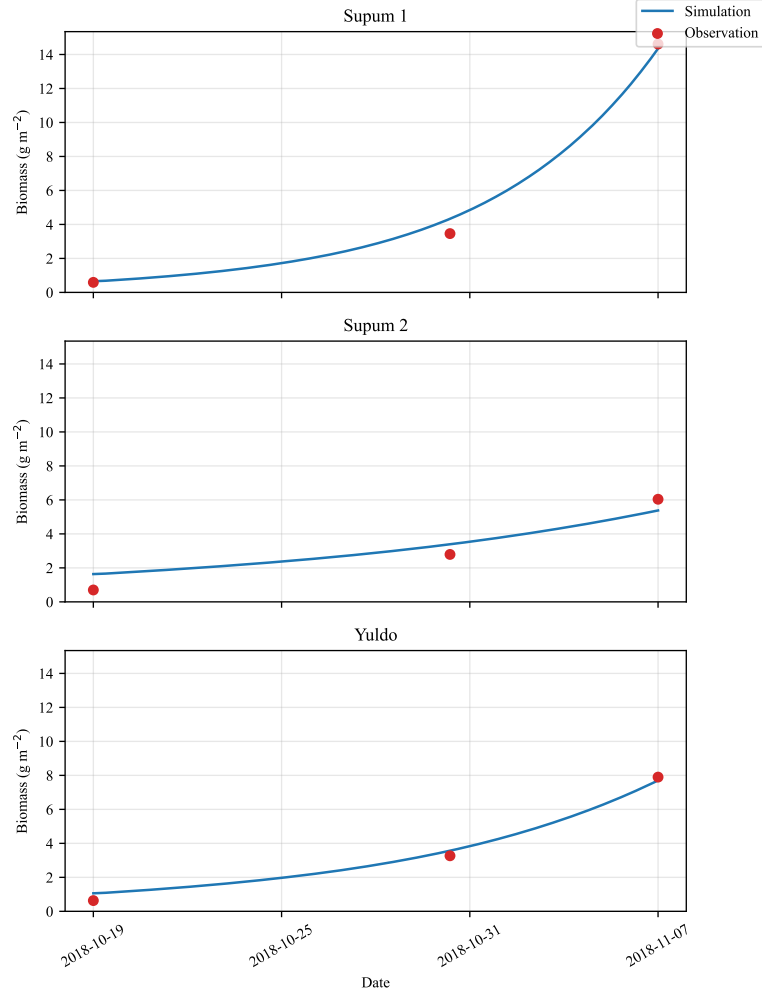


Figure 3: Observed (symbols) and simulated (lines) biomass for three cultivars at the Eoran site.

3.3 Sensitivity analysis

Sensitivity results for the Imha and Eoran sites are shown in Figures 5 and 6. The dominant drivers were consistent across cultivars: the effective growth rate $v_{\text{effective}}$ and temperature tolerance parameters (particularly T_H , and to a lesser extent T_L) produced the largest absolute sensitivities. At the intertidal Imha site, desiccation rate (r_{des}) was among the top three parameters for all cultivars, indicating strong dependence on exposure-related losses. At the floating Eoran site, desiccation effects were comparatively small, and temperature-related parameters ranked highest. These patterns indicate that exposure-driven losses dominated sensitivity in the pole-type system, whereas thermal response controlled sensitivity in the floating system.

4 Discussion and Conclusions

4.1 Model contributions and performance

This study presents the first DEB model tailored to *Pyropia dentata* and the first to explicitly incorporate intertidal emersion dynamics for pole-type cultivation in Korea. The model was calibrated and evaluated across two sites and three cultivars, demonstrating robust performance in six scenarios. The consistently high R^2 values (0.8822–0.9924) indicate that the model captures observed biomass variability, while the larger RMSE values at the Imha site highlight the greater complexity of intertidal conditions.

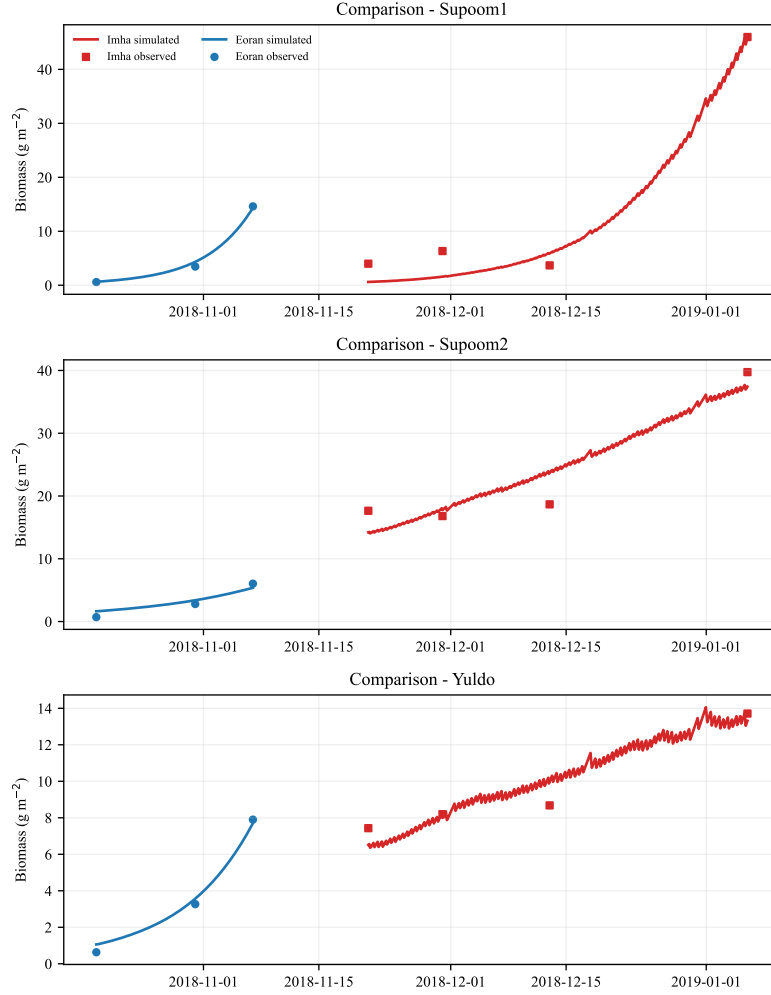


Figure 4: Comparison of growth patterns between Imha (pole-type) and Eoran (floating) cultivation systems.

4.2 Cultivation system differences

Growth dynamics differed between the floating and pole-type systems. The floating Eoran site showed smoother trajectories and lower prediction errors, consistent with more stable submergence and reduced exposure stress. In contrast, the intertidal Imha site required explicit loss terms for wave action and desiccation, reflecting the combined effects of emersion and weather forcing. These results emphasize that site-specific processes, particularly exposure and desiccation, are critical for modeling pole-type cultivation and cannot be inferred directly from floating-system models. [National Institute of Fisheries Science, 2018]

Sensitivity analysis further supports these system-level differences. At Imha, desiccation parameters ranked among the most influential drivers across cultivars, whereas at Eoran, temperature-related parameters dominated. This indicates that management strategies for pole-type systems should prioritize mitigating exposure-related stress, while floating systems are more sensitive to thermal variability. The consistent importance of the effective growth rate and thermal tolerance parameters across sites underscores the central role of temperature response in *P. dentata* growth.

4.3 Limitations

Several limitations should be acknowledged. First, the model does not include explicit competition with phytoplankton for dissolved nutrients, which can affect nutrient availability in coastal waters. [Hein et al., 1995] Second, nutrient observations were sparse and required interpolation and extrapo-

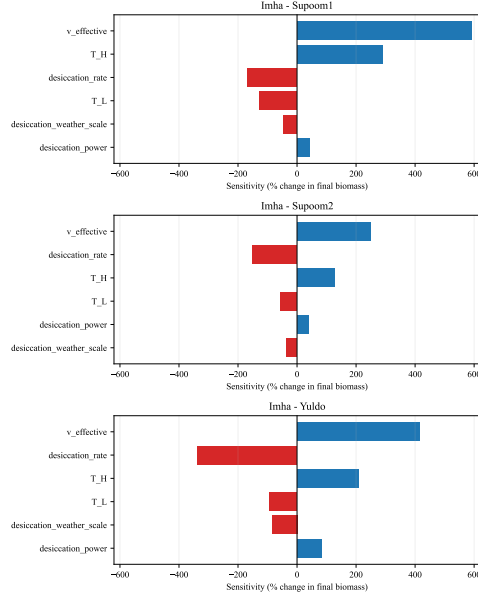


Figure 5: Sensitivity analysis for the Imha site. Bars show the effect of parameter perturbations on final biomass.

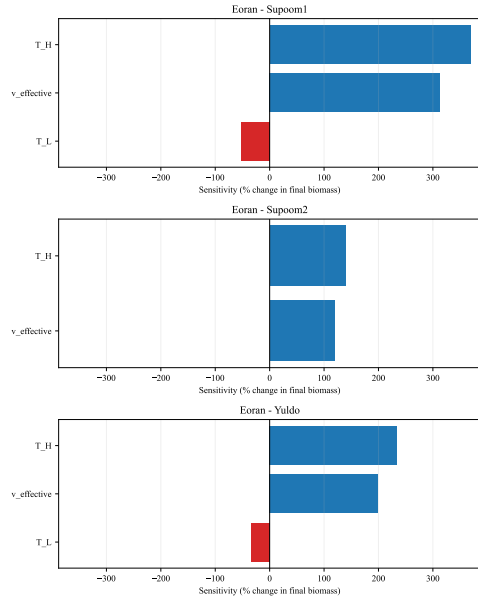


Figure 6: Sensitivity analysis for the Eoran site. Bars show the effect of parameter perturbations on final biomass.

lation, which may introduce uncertainty in the forcing inputs. Third, calibration and validation were limited to a single growing season, so interannual variability and extreme events are not captured. Finally, the model focuses on biomass dynamics and does not explicitly represent reproductive allocation or tissue composition changes.

4.4 Future directions

Future work should incorporate multi-species competition and improved nutrient dynamics, including phytoplankton interactions and higher-frequency nutrient monitoring. Extending the model to climate change scenarios would enable assessment of cultivation resilience under warming and altered hydrodynamic regimes. Additional datasets across years and sites would allow stronger validation and enable refinement of cultivar-specific parameters. Integration of the model with farm

management decision tools could further enhance its practical value for optimizing cultivation timing and site selection.

4.5 Conclusions

The proposed DEB model provides a mechanistic framework for predicting *P. dentata* biomass across contrasting Korean cultivation systems. By calibrating and validating across two sites and three cultivars, the model demonstrates robust performance beyond single-site or single-cultivar studies. Sensitivity analysis reveals site-dependent dominant drivers, highlighting the importance of exposure-related losses in intertidal systems and thermal response in floating systems. These findings support the model's utility for aquaculture planning and provide a foundation for future extensions to climate and management applications.

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