2024

Improving growth models of cultivated sugar kelp, Saccharina latissima, by accounting for intraspecific variation in thermal tolerance

Ruby Krasnow

Sara Gonzalez

Scott Lindell

Received: 2 February 2024 | Revised: 5 May 2024 | Accepted: 16 May 2024

DOI: 10.1111/jwas.13085

Journal of the World Aquaculture Society Open Access

WORLD AQUACULTURE Society

WILEY

ORIGINAL RESEARCH

Improving growth models of cultivated sugar kelp, *Saccharina latissima*, by accounting for intraspecific variation in thermal tolerance

Ruby Krasnow[1] | **Sara Gonzalez**[2] | **Scott Lindell**[2]

[1]Department of Biology, Clark University, Worcester, Massachusetts, USA

[2]Applied Ocean Physics and Engineering Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA

Correspondence
Ruby Krasnow, Department of Biology, Clark University, Worcester, MA, USA.
Email: rkrasnow@clarku.edu

Funding information
Conscience Bay Research, the philanthropic arm of Conscience Bay Company; Bezos Earth Fund; World Wildlife Fund; U.S. Department of Energy (DOE) ARPA-E MARINER program, Grant/Award Number: DE-AR0000915

Abstract

Dynamic models of sugar kelp (*Saccharina latissima)* growth are used to estimate the production potential of seaweed aquaculture in many regions around the world. These models do not currently account for the existence of *S. latissima* ecotypes that are adapted to regional environmental conditions, particularly temperature. We tested the hypothesis that recalibrating the temperature parameters of a dynamic energy budget model using literature data for *S. latissima* from regions with a similar climate to the region of interest would result in more accurate predictions than using a general species-wide temperature response curve. Calibrating the model using data from warm regions significantly improved model accuracy for kelp cultivation at the southern end of the species range (Rhode Island, USA) in cases where the original parameters underestimated growth but resulted in drastic overestimates when heavy frond erosion occurred. In Trømso, Norway, a cold parameterization produced extremely accurate predictions: the model predicted a final frond length of 88.2 cm, compared with the observed length of 87.5 (±4.70) cm. Our results demonstrate that recalibrating temperature response curves allows one model to be applied to kelp aquaculture in different

---

regions, an important step toward the prediction of *S. latissima* productivity over large areas.

KEYWORDS
aquaculture, dynamic energy budget, ecotype, kelp, macroalgae, *Saccharina latissima*, temperature response

1 | INTRODUCTION

Seaweed aquaculture is a rapidly growing sector of the global economy, with increasing recognition of the potential for seaweed to serve as a low-carbon source of food, biofuel, animal feed, fertilizer, and other products (Araújo et al., 2021; Cai et al., 2021; C. M. Duarte et al., 2017, 2022; Kim et al., 2019). Seaweed aquaculture is also associated with numerous ecosystem services, including nutrient extraction, habitat provisioning, and protection against coastal erosion (Barrett et al., 2022; Kim et al., 2015; Theuerkauf et al., 2022; Zhu et al., 2020). The majority of the seaweed cultivated in Europe and North America is the brown algal species *Saccharina latissima*, commonly referred to as sugar kelp (Heidkamp et al., 2022; Kim et al., 2019; Sæther et al., 2024).

Predicting the potential yield of kelp grown under different environmental conditions is an essential component of site selection, and therefore a primary concern for farmers. Multiscale modeling is a key tool to support the ecological and economic sustainability of new kelp farms (Coleman et al., 2022; Sæther et al., 2024; Zollmann et al., 2021). To this end, many different mechanistic models for macroalgal growth have been developed to simulate the growth of cultivated kelp (P. Duarte & Ferreira, 1997; Frieder et al., 2022; Zhang et al., 2016; Zollmann et al., 2021), with several specifically created to represent *S. latissima* (Broch & Slagstad, 2012; Venolia et al., 2020). However, these models are generally validated for kelp in a specific area within the wide geographical and latitudinal distribution of *S. latissima*, which on the east coast of North America ranges from the Canadian high Arctic (Filbee-Dexter et al., 2019) to Long Island Sound in Southern New England (Egan & Yarish, 1988). On the west coast of North America, *S. latissima* cultivation is taking place from Washington through Alaska (Kim et al., 2019). In Europe, *S. latissima* is farmed in over a dozen countries, including Spain, Portugal, the United Kingdom, the Netherlands, Norway, Sweden, and Iceland (Araújo et al., 2021; Sæther et al., 2024). It is important to account for physiological variation between populations from such disparate regions, and to select the right model for the location of interest.

S. latissima is believed to have numerous ecotypes across its broad distribution (Bartsch et al., 2008; Gerard & Du Bois, 1988), with adaptation to environmental conditions driven by a combination of phenotypic plasticity and genetic and epigenetic changes (Diehl et al., 2023). Regional differences in growth and response to thermal stress have been observed at the physiological and biochemical levels across multiple life stages of *S. latissima* (Forbord et al., 2020; Gerard et al., 1987; Gerard & Du Bois, 1988; Müller et al., 2008; Olischläger et al., 2014, 2017). For example, in the Northeast United States, the populations of *S. latissima* from New York had higher specific growth rates and lower mortality at elevated temperatures (18 and 20°C) compared with *S. latissima* from Maine (Gerard et al., 1987).

Venolia et al. (2020) developed a model for kelp aquaculture in Rhode Island Sound (USA) based on dynamic energy budget (DEB) theory, a mechanistic framework that has become a cornerstone of ecological modeling in the over 40 years since its introduction (B. Kooijman, 2010; Lavaud et al., 2021; van der Meer et al., 2014). Venolia et al. (2020) calibrated their model using field-based growth experiments in Rhode Island, and while it was able to accurately estimate the observed blade length on the final sampling date for many growing lines, the model underestimated blade length throughout much of the growing season. This limits the potential use of DEB models for helping farmers identify optimal harvest dates to maximize yield.

Comparison of species-varying DEB parameters has yielded important insights about the comparative physiology of different species (S. A. L. M. Kooijman, 2014; Lika et al., 2022), but intraspecific genetic and phenotypic variability remains an underexplored area of DEB research (Koch & De Schamphelaere, 2020; Lavaud et al., 2021). The *S. latissima* model developed by Venolia et al. (2020) showed high sensitivity to changes in the parameters used to represent the temperature sensitivity of metabolic processes, a pattern that has also been seen for non-DEB models of kelp growth (Strong-Wright & Taylor, 2022; Zhang et al., 2016). The sensitivity of model predictions to changes in the temperature parameters and the existence of different kelp ecotypes with varying physiological responses to temperature led Venolia et al. (2020) and Strong-Wright and Taylor (2022) to urge caution in broader geographic use of their respective models and suggest that the temperature parameters may need to be regionally calibrated.

Venolia et al. (2020) originally calibrated the temperature parameters using literature data from a variety of studies conducted in Europe, farther north in the species distribution of *S. latissima* compared with Rhode Island. Here, we sought to determine whether recalibrating select DEB temperature parameters to account for intraspecific variation in thermal tolerance could improve the accuracy of growth predictions for cultivated *S. latissima* without necessitating a full model reparameterization. Our hypothesis was that because *S. latissima* from Rhode Island is likely to grow well, recalibrating the temperature response parameters based on growth data from heat-tolerant *S. latissima* strains would improve the accuracy of model predictions for kelp aquaculture in Rhode Island.

We also tested the recalibrated model on kelp grown in the middle and northern portions of the species distribution (Trondheim and Tromsø, Norway), "cold" validations to accompany the "warm" validation that used the Rhode Island data. Our hypothesis for the cold validation was that the parameters calibrated for a warm climate would perform worse than the original model when predicting the growth of *S. latissima* from Norway, but the parameter set derived from kelp acclimated to a colder climate would perform better than the original model. We hypothesized that estimating DEB temperature parameters can be a valuable tool to improve the predictive accuracy of DEB models for separate populations of the same species.

2 | METHODS

We used standardized rates of *S. latissima* growth and photosynthesis at various temperatures obtained from the literature to find new values for the Arrhenius temperature (T_A), the upper limit of temperature tolerance (T_H), and the Arrhenius temperature above the optimal range (T_{AH}) for kelp originating from warmer climates. We repeated this process using temperature response data from *S. latissima* originating from colder climates to produce two new parameterizations ("warm" and "cold") to compare against the original model. Analyses of Arrhenius temperature parameters have proven to be valuable in uncovering patterns of thermal sensitivity and identifying how organisms may respond to the impacts of climate change (Freitas et al., 2007, 2010; Teal et al., 2012).

When not provided in tabular form, literature data were extracted from paper figures using the online software program WebPlotDigitizer (Rohatgi, 2022). All modeling and data analysis were conducted in the statistical computing language R (version 4.3.2; R Core Team, 2023). The differential equations in the DEB model were solved using the ode() function from the deSolve package (version 1.38; Soetaert et al., 2010) and nonlinear least-squares regression was performed using the nlsLM() function from the minpack.lm package (version 1.2.4; Elzhov et al., 2023). Other packages used included the tidyverse collection (Wickham et al., 2019) and rstatix (version 0.7.2; Kassambara, 2023).

2.1 | Model calibration

The Arrhenius temperature response curve (Equation 1 in Table S2) is a temperature correction function applied to almost all of the fluxes in the DEB model, with the exception of the photon binding rate (Lorena et al., 2010). The shape of the Arrhenius function is dictated by five parameters: T_L, T_{AL}, T_H, T_A, and T_{AH}, as well as a reference temperature (T_0) that is typically taken to be 293.15 K, equivalent to 20°C. T_A is the Arrhenius temperature, representing the sensitivity of the physiological rates to changes in temperature (Gillooly et al., 2006), which is functionally similar to the Q10 parameter often used to model thermal sensitivity (B. Kooijman, 2010). T_L and T_H represent the lower and upper bounds of the temperature tolerance range, while T_{AL} and T_{AH} represent the Arrhenius temperatures for the rates of decrease in performance at their respective extremes (Freitas et al., 2007). The formulation for the reduction in rate beyond an optimal range, derived by Sharpe and DeMichele (1977) and Schoolfield et al. (1981), is based on the idea that the enzymes mediating biological reactions are inactivated at high or low temperatures.

As a relatively cold-adapted species, high temperatures induce greater stress responses in *S. latissima* than low temperatures (Heinrich et al., 2012), so we chose to focus on the parameters controlling temperature response at the upper end of the curve, keeping the values for T_L, T_{AL}, and T_0 the same as those used by Venolia et al. (2020). We used starting values of 6000 for T_A, 18,000 for T_{AH}, and 286 for T_H. We also constrained the parameter space to ensure biological realism: lower and upper limits for T_A were set at 6000 and 12,500 (B. Kooijman, 2010), limits for T_H were set at 282.15 and 292.15 based on expectations about the upper temperature tolerance of *S. latissima*, and limits for T_{AH} were set at 12,000 and 25,000, as T_{AH} is generally much higher than T_A (B. Kooijman, 2010).

We first performed the Arrhenius parameter estimation using only the literature used by Venolia et al. (2020) (Bolton & Lüning, 1982; Davison, 1987; Davison & Davison, 1987; Fortes & Lüning, 1980; additional details in Table S3). This ensured our technique of extracting the data from published figures and method of nonlinear regression could replicate the process used for the original parameterization and would confirm that any differences in T_A, T_{AH}, and T_H could be attributed to the inclusion of additional data points, not a difference in methodology.

We searched online databases (including Google Scholar and Web of Science, using the keywords "Saccharina" OR "latissima" AND "temperature") to find papers documenting *S. latissima* growth or photosynthetic rates under different temperatures. Suitable studies were limited to those that included 20°C as one of the experimental temperatures, as Arrhenius calibration is typically done using rates standardized by dividing by the rate at 20°C (Freitas et al., 2007). While we followed this approach for consistency with Venolia et al. (2020), scaling literature by the maximum rate observed in each experiment instead of the rate at 20°C would greatly expand the collection of data sets that could be used for Arrhenius calibration (Agüera et al., 2015; Freitas et al., 2007).

The new calibration studies (Table 1) were grouped as either "cold" or "warm" based on mean summer sea surface temperatures: "cold" locations did not exceed 20°C, while the "warm" locations regularly reached 20°C. We then performed nonlinear regression on the original standardized rates in combination with the standardized rates from either the warm or cold locations (1–4 in Table 1) to find "warm" and "cold" estimates of T_A, T_{AH}, and T_H.

TABLE 1 Sources of new data used for model calibration or validation.

	Study	Location of origin for kelp	Climate
Used for calibration			
1	Andersen et al., 2013	Bergen, Norway	Cold
2	Gerard, 1997	Walpole, ME, USA	Cold
3	Gerard, 1997	Long Island Sound, NY, USA	Warm
4	Pedersen, 2015	Limfjorden, Denmark	Warm
Used for validation			
5	Venolia et al., 2020	Narragansett Bay, RI, USA	Warm
6	Matsson et al., 2021	Trømso, Norway	Cold
7	Jevne et al., 2020	Trondheim, Norway	Cold

Note: Locations where kelp samples originated were designated as "cold" if mean summer sea surface temperatures did not exceed 20°C in years near the period of sample collection and "warm" if summer temperatures consistently exceeded 20°C.

2.2 | Model validation

Model predictions using the new parameter sets were tested against the environmental and growth data from Rhode Island, United States, that were used to validate the original DEB model (Venolia et al., 2020). Improvements in model accuracy using the new parameters were quantified based on increases or decreases in the root mean square error (RMSE) between model predictions and the observations. Normality was tested using the Shapiro–Wilk test and homogeneity of variance was tested using Levene's test. If these assumptions were violated, a Wilcoxon rank-sum test was used in place of a *t*-test and a Friedman test (with parameters as groups and location or treatment as blocks) was used instead of a standard repeated-measures analysis of variance. If the Friedman test showed statistically significant ($p < 0.05$) differences between parameter groups, Nemenyi's test (function "frdAllPairsNemenyiTest" from the R package PMCMRplus, version 1.9.8) was used for post hoc analysis (Nemenyi, 1963; Pohlert, 2023).

We also sought to determine how the "warm" and "cold" parameterizations would perform when applied to kelp aquaculture farther north in the species distribution. To this end, we forced the model with environmental data associated with kelp cultivation studies in Trondheim (Jevne et al., 2020) and Trømso, Norway (Matsson et al., 2021). The Trondheim study (Jevne et al., 2020) used a land-based tank cultivation system with four different combinations of light and nutrient levels. Each tank contained water pumped from either the surface (1 m) or 100-m depth of the fjord adjacent to the tank setup, containing low- and high-nutrient concentrations, respectively. Tanks were covered with one or four layers of plant cover filter (high and low-light intensity, respectively). *S. latissima* in the Trømso study was outplanted on horizontal long lines. PAR (photosynthetically active radiation), temperature, and dissolved inorganic nitrate data were provided in Jevne et al. (2020) and Matsson et al. (2021) and are compiled in Figures S1 and S2. DIC in Trømso at the time of cultivation was estimated from Table 12 in Jones et al. (2019), while DIC in Trondheim was estimated from Possenti et al. (2021).

3 | RESULTS

3.1 | Model calibration

The recalibrated parameters ("literature") were essentially identical to those provided by Venolia et al. (2020), indicating relatively high inter-user consistency with this methodology for parameter estimation (Table 2). T_A and T_{AH} were much higher for the warm kelp than for the cold kelp; the cold T_A was approximately the same as the original T_A and the cold T_{AH} was lower than the original value, but both warm T_A and warm T_{AH} were higher than the original estimates (Table 2). The warm temperature response curve had a higher maximum standardized rate than the low temperature response curve, which never exceeded the maximum rate of the original curve (Figure 3).

TABLE 2 Original and new values for Arrhenius temperature parameters used in the dynamic energy budget model.

	T_A (K)	T_H (°C)	T_{AH} (K)
Warm	8454	10.37	19,266
Cold	6403	11.65	16,328
Original	6314	13.39	18,702
Literature	6372	13.20	18,515

Note: "Original" refers to the values of T_A, T_{AH}, and T_H from Venolia et al. (2020), while the other values were obtained from nonlinear regression to the same data as used by Venolia et al. ("literature") and from nonlinear regression to the original data in combination with new data from either warm or cold climates.

3.2 | Model validation: Rhode Island

Both the warm and cold parameter sets predicted higher growth than the original calibration, with warm model runs predicting higher growth than model runs using the cold parameters (Figures 1 and 2).

Within the Rhode Island validation, changes in RMSE varied dramatically depending on the year and location (Table S1). In some cases, the new parameters had a strong positive impact on model accuracy: for example, the warm curve resulted in a decrease in RMSE by around 6 for both Point Judith Pond North Line 1 in Year 2 and Narragansett Bay South Line 2 in Year 1. In contrast, using the warm parameters for the two lines planted earlier in the season in Year 1 at Point Judith Pond increased the RMSE by over 25 (Table S1). These extreme outliers resulted in a negative mean change in RMSE for warm parameters in Year 1 but a positive median change (Table 3).

A Friedman test where parameter results were matched by site/year showed statistically significant differences between the RMSE of the warm, cold, original, and recalibrated literature parameters (Friedman rank-sum test, $\chi^2 = 13.714$, df $= 3$, $p < 0.01$). Post hoc pairwise comparisons using Nemenyi test with a Bonferroni correction revealed that the significant difference was between the warm and original parameters ($p = 0.0025$; Table S6).

When we excluded the final measurement date in Year 1 (April 17, 21, or 22, depending on the site), the potential improvement in model performance using the warm parameters became much more apparent (Table 3). Improvements in RMSE (ΔRMSE, $n = 14$ for each parameter set) were significantly greater for warm than cold parameters (one-tailed Wilcoxon rank-sum test, $W = 55$, $p = 0.0249$) when we did not consider the final measurement but were nonsignificant when it was included (one-tailed Wilcoxon rank-sum test, $W = 71$, $p = 0.114$).

In Year 2, where the original model substantially underestimated growth, the warm parameterization decreased RMSE for all eight cultivation lines, but final predictions were still around 25–50 cm below observed frond lengths for most lines (Figures 1 and 2). In Year 1, the warm parameters improved model accuracy earlier in the season (before the fronds experienced heavy erosion) but ended up overestimating final yields, especially at the Point Judith Pond site where losses resulting from blade erosion were high.

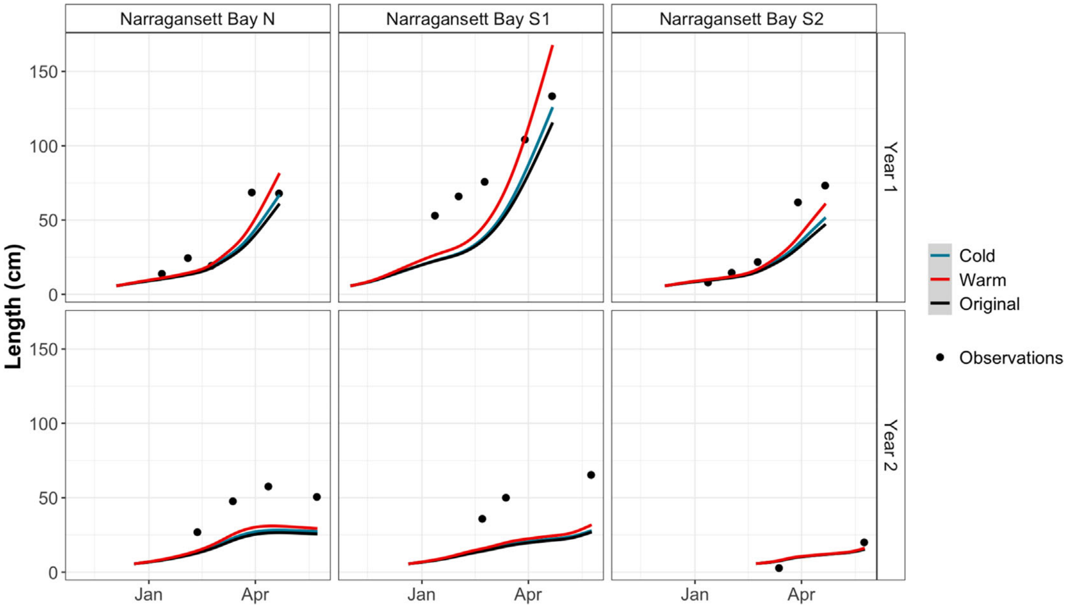

FIGURE 1 Model predictions for each parameterization versus observed frond length for Year 1 (2017–2018) and Year 2 (2018–2019) of *S. latissima* cultivated on three different lines (N, S1, and S2) in Narragansett Bay, Rhode Island.

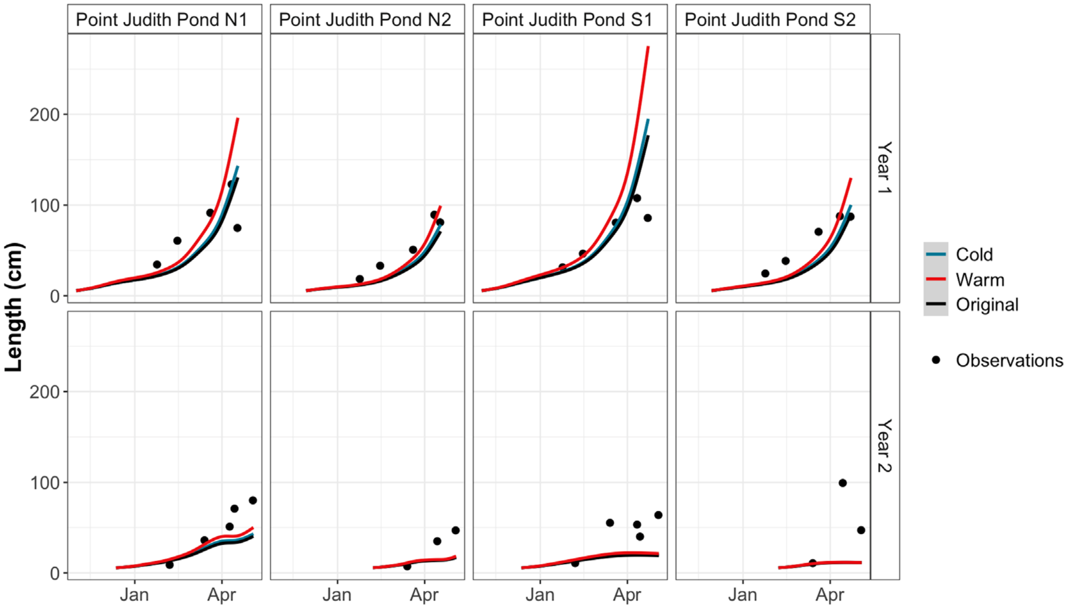

FIGURE 2 Model predictions for each parameterization versus observed frond length for Year 1 (2017–2018) and Year 2 (2018–2019) of *S. latissima* cultivated on four different lines (N1, N2, S1, and S2) at Point Judith Pond, Rhode Island.

3.3 | Model validation: Trømso

Model RMSE using the cold parameters (7.43) was lower than model RMSE using the original parameters (10.98) (Table 4). RMSE for the warm parameters (17.71) was much higher than either of the other two parameter sets (Table 4). The high maximum standardized rate of the warm curve meant that the warm parameters severely overestimated frond length later in the growing season.

The fact that the cold temperature curve is slightly higher than the original curve between ~5 and 10°C (Figure 3) meant that the cold parameterization predicted slightly higher growth than the original parameters, resulting in extremely accurate estimates of frond length in the later portion of the season in Trømso (Figure 4). With the cold parameterization, the model predicted a final frond length of 88.2 cm, which was within one standard deviation of the observed length of 87.5 cm (SD ±4.70 cm). Similar accuracy was seen for the cold parameterization over the last 2 months of the growing season, but all parameter sets underestimated frond length compared with the observed length on the earliest sampling date (June 2018).

3.4 | Model validation: Trondheim

All parameterizations of the model generally overestimated growth rates in low-light tanks and for the high-light, low-nutrient tanks (Figure 5). However, model predictions were within the range of experimental error for the high-light, high-nutrient tanks, which represented the high-nutrient situation in deeper waters off the Norwegian coast (Jevne et al., 2020). For each treatment, the lowest RMSE was obtained using the cold parameters (Table 5). Post hoc pairwise comparisons following a statistically significant Friedman test ($\chi^2 = 10.8$, df $= 3$, $p = 0.0129$) showed the cold parameterization was significantly more accurate than the warm parameterization (Nemenyi test with a Bonferroni correction; $p = 0.0025$; Table S7).

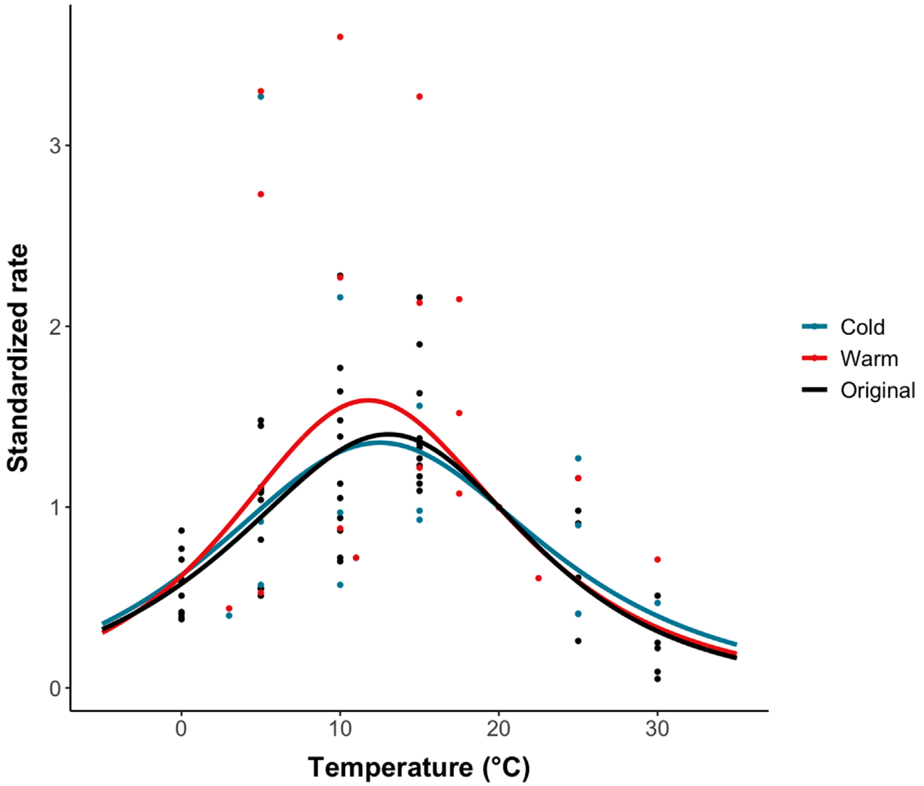

FIGURE 3 Arrhenius curves corresponding to the original temperature parameters (black line), the warm parameters (red line), and the cold parameters (blue line). Curves shown resulted from nonlinear least-squares regression to the original data (black points) added to either the warm data (red points) or the cold data (blue points).

TABLE 3 Performance of dynamic energy budget (DEB) model with new temperature parameters compared with original DEB model for Rhode Island environmental and growth data.

	Year	% lines with improved RMSE	Median improvement in RMSE	Mean improvement in RMSE
Cold	1	71.4	1.80	−0.06
Warm	1	57.1	3.10	−8.45
Cold	1—truncated	85.7	1.80	1.33
Warm	1—truncated	85.7	4.66	0.88
Cold	2	85.7	0.66	0.73
Warm	2	100	2.19	2.39

Note: Truncated results do not include the final measurement date (April 17, 21, or 22, depending on the line) when calculating root mean squared error (RMSE).

4 | DISCUSSION

4.1 | Temperature response curves

The higher estimates for T_A and T_{AH} for warm populations compared with cold populations are consistent with a reduction in Q10 values observed for kelp grown at low temperatures compared with kelp grown at high

TABLE 4 Root mean squared error (RMSE) and final frond length (cm) resulting from dynamic energy budget model forced with environmental data from Trømso, Norway, compared with the mean final frond length observed in Trømso.

	RMSE	Final length (cm)
Warm	17.71	119.1
Original	10.98	81.2
Cold	7.43	88.2
Observed	-	87.5 (±4.70)

Note: Observed value is mean (±SD).

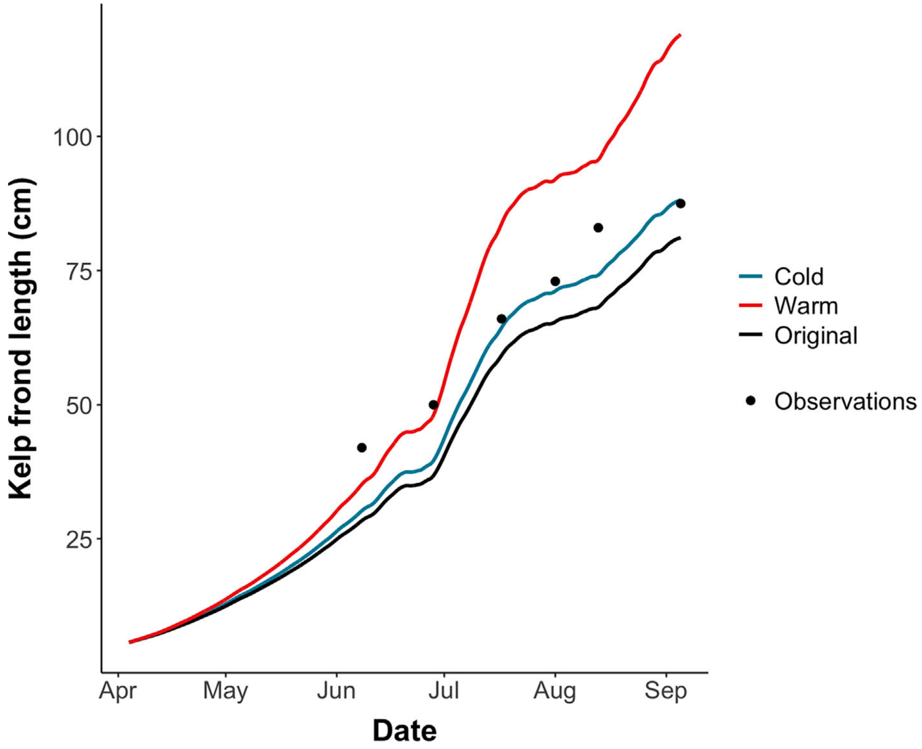

FIGURE 4 Model predictions for each parameterization versus observed frond length for *S. latissima* grown in 2018 in Trømso, Norway.

temperatures, which enables the cold-acclimated kelp to maintain a higher percentage of maximum photosynthetic rates at low temperatures (Davison, 1987).

However, the lower T_H value for *S. latissima* from warm locations compared with the cold *S. latissima* (Table 2) is inconsistent with the literature documenting lower upper limits of thermal tolerance for *S. latissima* populations in colder climates (Gerard & Du Bois, 1988; Lüning et al., 1978). With T_L set at 273.15°C, such low T_H values would suggest an optimal thermal tolerance range of less than 12°C. It is possible that setting a higher lower bound on T_H when performing the nonlinear regression could yield a local optimization with a broader and more realistic range of optimal temperatures. Differences between study methodologies (e.g., duration of pre-acclimation period) could also have significantly impacted our estimated parameters (Diehl et al., 2021; Terblanche et al., 2007).

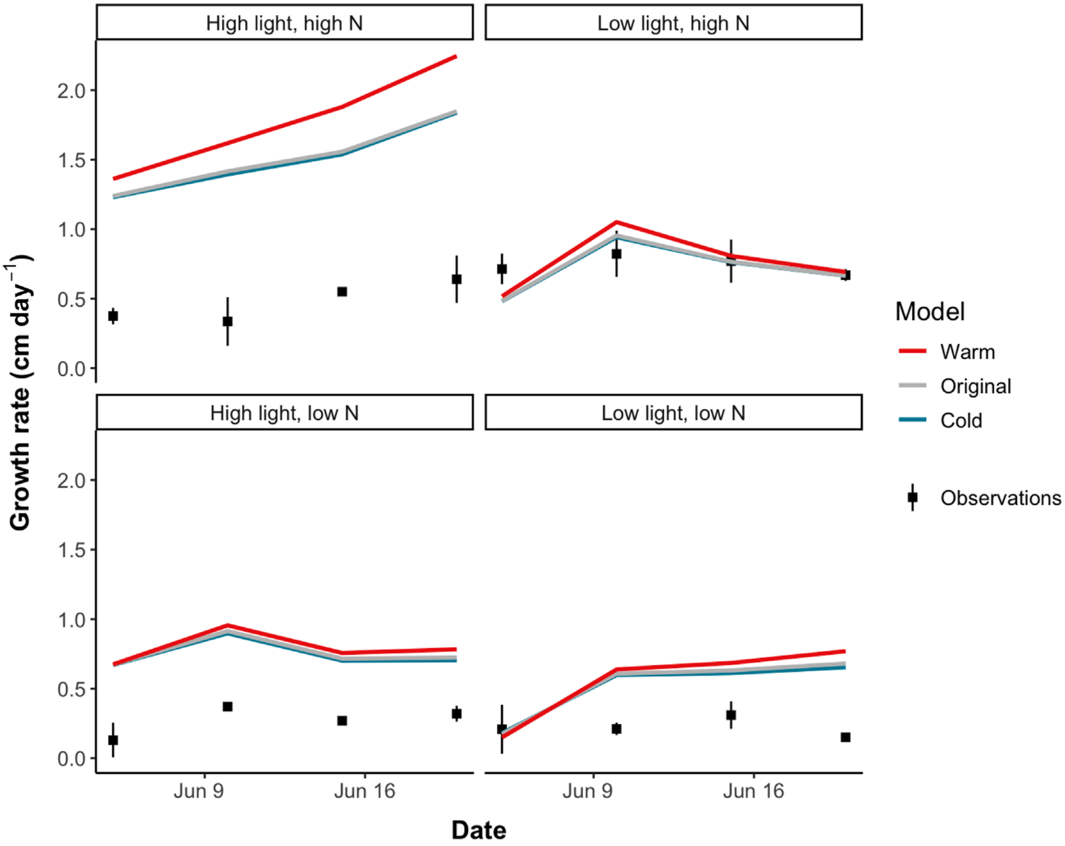

FIGURE 5 Model predictions for each parameterization versus observed frond length for *S. latissima* from Trondheim, Norway, grown in 2014 in experimental tanks under two different light and nutrient regimes.

TABLE 5 Root mean squared error values resulting from comparing growth predictions from dynamic energy budget model forced with environmental data from four different light/nutrient combinations used in a kelp cultivation experiment conducted in Trondheim, Norway, to observed growth rates of *Saccharina latissima* under each treatment.

	Parameter set		
	Cold	**Original**	**Warm**
High light, high *N*	1.032	1.047	1.319
Low light, high *N*	0.131	0.133	0.152
High light, low *N*	0.476	0.488	0.522
Low light, low *N*	0.352	0.368	0.421

Some morphological differences, such as the hydrodynamic streamlining of kelp fronds resulting from exposure to high current velocities, can be safely attributed to phenotypic plasticity (Buck & Buchholz, 2005; Gerard & Mann, 1979). On the other hand, the increasing application of modern genetic and genomic tools to *S. latissima* has resulted in mounting evidence for a genetic and/or epigenetic basis for physiological and biochemical differences between *S. latissima* ecotypes (Augyte et al., 2017; Diehl et al., 2023; Evankow et al., 2019; Heinrich et al., 2012, 2015; Mao et al., 2020; Monteiro et al., 2019; Scheschonk et al., 2023). Substantial progress has been made toward understanding the mechanisms (e.g., changes in pigment concentrations and ratios) underlying adaptation and acclimation of *S. latissima* to different thermal and light regimes, as well as exposure to elevated CO_2 concentrations and extreme salinities (Andersen et al., 2013; Bischof et al., 1998; Diehl & Bischof, 2021; Machalek et al., 1996; Monteiro et al., 2021; Olischläger et al., 2014, 2017).

The Arrhenius temperature response curve used in DEB models is based on the concept of enzyme activation energy (B. Kooijman, 2010; Schoolfield et al., 1981; Sharpe & DeMichele, 1977). In addition to changes in photosystem quantity, size, and thermal stability, alterations in the kinetic characteristics of Calvin Cycle enzymes (particularly Rubisco) have been implicated in observed differences in photosynthetic efficiency between Arctic and temperate ecotypes of *S. latissima* (Andersen et al., 2013; Davison, 1987; Machalek et al., 1996; Olischläger et al., 2017). However, actual differences in *S. latissima* photosynthesis are opposite to what would be predicted by the temperature response curves developed in this study: Arctic kelps produce more oxygen but have lower Rubisco concentrations compared with temperate kelps at 10°C, demonstrating increased photosynthetic efficiency in the Arctic ecotype (Machalek et al., 1996; Olischläger et al., 2017).

Somewhat counterintuitively, this increased photosynthetic performance does not result in increased growth, for example, Olischläger et al. (2017) found that Artic *S. latissima* grew significantly slower than a temperate ecotype when both were kept at 10°C and that raising temperatures to 17°C had no effect on the growth rate of the temperate *S. latissima*. One possible explanation is increased storage of carbohydrates and lipids by the Arctic *S. latissima* to endure the long polar night (Olischläger et al., 2014, 2017; Scheschonk et al., 2019). Arctic and Antarctic seaweeds must store large quantities of polysaccharides like laminarin and mannitol to survive the months of darkness that occur at extreme latitudes, which may decrease their growth rate compared with temperate kelps that do not have to build up such reserves (Bartsch et al., 2008; Scheschonk et al., 2019).

In general, the disconnect between the thermal responses of photosynthesis and growth (Davison, 1991; Kuebler et al., 1991) means that although our “warm” and “cold” Arrhenius parameters may be inconsistent with physiological changes that allow different ecotypes to have similar short-term photosynthetic responses to temperature stress (Andersen et al., 2013), our new Arrhenius relationships effectively captured the organism-level response of different ecotypes to temperature fluctuations.

4.2 | Comparisons with observed growth

The new temperature parameters decreased RMSE for model predictions of most of the 14 model runs in Rhode Island (7 lines × 2 years), with warm parameters improving model accuracy more frequently than cold parameters and demonstrating greater median improvements in RMSE. While recalibrating the temperature response based on data from warm regions did improve model performance enough to be statistically significant, the overall magnitude of improvements were low. This may limit the practical implications of the new parameterization for this location, especially for sites that experience heavy erosion. In years/sites where high erosion resulted in net negative changes in frond length between sampling days, the rapid growth predicted by the warm parameters resulted in major overestimates of final blade length.

Overall, applying the new parameters to Rhode Island partially remediated the underestimation noted by Venolia et al. (2020) and demonstrates the potential of our approach, but underscores the need for an erosion mechanism to be incorporated into the DEB model. To our knowledge, the Norway validations are the first application of a kelp DEB model to a cultivation scenario outside the United States. The cold parameterization was shockingly accurate for Trømso (Figure 4): if values are rounded to the nearest centimeter, the DEB model perfectly predicted the mean final observed frond length (Table 4). Such precision is especially remarkable given the many assumptions (e.g., estimates of initial conditions of the model state variables) and relatively coarse resolution of the nutrient forcing data that went into the model.

In Trondheim, the model was highly accurate for the kelp grown under low-light and high-nutrient conditions, representing the environment found in deeper waters (Jevne et al., 2020). The discrepancy between model predictions and observed growth rates in the high-light treatments might be explained by photoinhibition, which is not accounted for by the model. Light levels reached 250 μmol m^{-2} s^{-1} in some of the tanks in the high-light treatments, which is high enough to suppress the growth of *S. latissima* (Fortes & Lüning, 1980).

The results of the cold validations strongly supported our hypothesis that cold parameters would perform better than the original parameterization, while warm parameters would perform worse than the original. The accuracy of the cold parameterization suggests that calibrating the Arrhenius temperature response curve using ecotype-specific data can enable applications of the kelp DEB model developed by Venolia et al. (2020) outside of the geographical region for which it was initially developed.

Dynamical models of kelp growth are being used to predict farm yields and ecosystem services from kelp aquaculture in China, Denmark, Australia, Norway, the United Kingdom, and both the Atlantic and Pacific coasts of the United States, encompassing a wide range of farm scales as well as temperature, light, salinity, and nutrient levels (Broch & Slagstad, 2012; Hadley et al., 2015; Jiang et al., 2022; Zhang et al., 2016). Increasing the accuracy of algal growth models is an important component of expanding the kelp aquaculture industry (Araújo et al., 2021; Zollmann et al., 2021), and accounting for the tremendous plasticity of *S. latissima* across its wide distribution will be an important component of realizing this goal. Incorporating spatial heterogeneity in environmental conditions and biological parameters is crucial when upscaling dynamic growth models to estimate the global potential of seaweed farming, such as for carbon dioxide removal (Arzeno-Soltero et al., 2023). Additionally, incorporating the possibility of regional adaptation into species distribution models (SDMs) has been proposed as a method of resolving discrepancies between model predictions and observed changes in the distribution of *S. latissima* because of climate change (Diehl et al., 2023). Our results demonstrate a tangible way to improve the accuracy of large-scale kelp growth models by introducing regional specificity in modeled temperature response.

4.3 | Future work and implications

B. Kooijman (2010) mentions the complexity of modeling the effects of temperature on photosynthesis and the increase in carbohydrate storage at low temperatures, acknowledging that optimum temperatures for photosynthesis are highly plastic and that multiple reserves are needed to allow for process-specific temperature responses. The DEB assumptions that all physiological processes have the same response to temperature and there is a single reserve for both short- and long-term resource storage are clearly inapplicable for plant and macroalgae growth models (Russo et al., 2022). Partitioning the frond biomass into different structures and/or creating within-reserve compartments with different temporal dynamics would be an important step toward addressing this shortcoming (Russo et al., 2022; Schouten et al., 2020).

However, given the already strong performance of the kelp DEB model, introducing additional complexity with a more mechanistically accurate representation of photosynthesis may not be necessary for applied purposes. Exploring differences in the allometric relationships used to convert model state variables into measurable quantities could be an alternative approach that, as with temperature parameter calibration, accounts for genetic and phenotypic diversity to improve predictive accuracy without sacrificing model parsimony.

For example, the *S. latissima* DEB model uses a defined power relationship to convert whole blade dry weight into blade length (Venolia et al., 2020, taken from Gévaert et al., 2001). These allometric relationships can be significantly different even between *S. latissima* individuals from sites with similar environmental conditions (Campbell & Starko, 2021). Allometric relationships can also vary temporally—in the Arctic kelp study used for model validation, length-to-width ratio varied throughout the growing season and was significantly higher for kelp outplanted in February compared with April or May (Matsson et al., 2021).

Applications of the kelp DEB model for estimating the production potential of coupled seaweed–shellfish aquaculture additionally assumed a dry weight to wet weight ratio of 0.1 for *S. latissima* (Lavaud et al., 2023). However, this value can range from below 0.06 to over 0.37 depending on the location and timing of cultivation (Bruhn et al., 2016; Nielsen et al., 2016). As the economic value of kelp harvested in the United States is typically measured in dollars per unit wet weight (Coleman et al., 2022; St. Gelais et al., 2022), under- or overestimates of wet weight yield resulting from inaccurate conversion factors could have major implications for the model-based conclusions about the potential economic viability of a kelp farm.

Finally, the inability of the DEB model to capture the severe blade-tip erosion that can plague kelp farmers (Fieler et al., 2021; Zhang et al., 2012) represents a major impediment to the large-scale use of this model. Explicitly incorporating mechanisms of erosion and dislodgement will be necessary if this model is to be used for predicting *S. latissima* production potential on regional, national, or global scales.

With the continuing development of morphologically distinct *S. latissima* strains, it will be increasingly important that models can account for intraspecific variation when predicting farm yields. Although this study demonstrates a promising approach to representing thermal acclimation, the truly global scale of seaweed aquaculture necessitates the development of additional methods to incorporate regional adaptation, distinct genotypes, and phenotypic plasticity into both DEB and non-DEB mechanistic growth models.

ACKNOWLEDGMENTS

We would like to thank the faculty and staff affiliated with the Semester in Environmental Science program at the Marine Biological Laboratory, during which this research was conducted.

FUNDING INFORMATION

Funding was provided by the U.S. Department of Energy's (DOE) ARPA-E MARINER program contract No. DE-AR0000915, the World Wildlife Fund with support from the Bezos Earth Fund, and the Conscience Bay Research, the philanthropic arm of Conscience Bay Company.

CONFLICT OF INTEREST STATEMENT

The authors have no competing interests to declare.

DATA AVAILABILITY STATEMENT

The data and R code that support the findings of this study are openly available in Zenodo at http://doi.org/10.5281/zenodo.10607130.

ORCID

Ruby Krasnow https://orcid.org/0009-0007-0531-8420

REFERENCES

Agüera, A., Collard, M., Jossart, Q., Moreau, C., & Danis, B. (2015). Parameter estimations of dynamic energy budget (DEB) model over the life history of a key Antarctic species: The Antarctic Sea Star Odontaster validus Koehler, 1906. *PLoS One*, *10*, e0140078.

Andersen, G. S., Pedersen, M. F., & Nielsen, S. L. (2013). Temperature acclimation and heat tolerance of photosynthesis in Norwegian *Saccharina latissima* (Laminariales, Phaeophyceae). *Journal of Phycology*, *49*, 689–700.

Araújo, R., Vázquez Calderón, F., Sánchez López, J., Azevedo, I. C., Bruhn, A., Fluch, S., Garcia Tasende, M., Ghaderiardakani, F., Ilmjärv, T., Laurans, M., Mac Monagail, M., Mangini, S., Peteiro, C., Rebours, C., Stefansson, T., & Ullmann, J. (2021). Current status of the algae production industry in Europe: An emerging sector of the blue bioeconomy. *Frontiers in Marine Science*, *7*, 626389. https://doi.org/10.3389/fmars.2020.626389

Arzeno-Soltero, I. B., Saenz, B. T., Frieder, C. A., Long, M. C., DeAngelo, J., Davis, S. J., & Davis, K. A. (2023). Large global variations in the carbon dioxide removal potential of seaweed farming due to biophysical constraints. *Communications Earth & Environment*, *4*, 1–12.

Augyte, S., Yarish, C., Redmond, S., & Kim, J. K. (2017). Cultivation of a morphologically distinct strain of the sugar kelp, *Saccharina latissima* forma angustissima, from coastal Maine, USA, with implications for ecosystem services. *Journal of Applied Phycology*, *29*, 1967–1976.

Barrett, L. T., Theuerkauf, S. J., Rose, J. M., Alleway, H. K., Bricker, S. B., Parker, M., Petrolia, D. R., & Jones, R. C. (2022). Sustainable growth of non-fed aquaculture can generate valuable ecosystem benefits. *Ecosystem Services*, *53*, 101396.

Bartsch, I., Wiencke, C., Bischof, K., Buchholz, C. M., Buck, B. H., Eggert, A., Feuerpfeil, P., Hanelt, D., Jacobsen, S., Karez, R., Karsten, U., Molis, M., Roleda, M. Y., Schubert, H., Schumann, R., Valentin, K., Weinberger, F., & Wiese, J. (2008). The genus *Laminaria sensu lato*: Recent insights and developments. *European Journal of Phycology*, *43*, 1–86.

Bischof, K., Hanelt, D., Tüg, H., Karsten, U., Brouwer, P. E. M., & Wiencke, C. (1998). Acclimation of brown algal photosynthesis to ultraviolet radiation in Arctic coastal waters (Spitsbergen, Norway). *Polar Biology*, *20*, 388–395.

Bolton, J. J., & Lüning, K. (1982). Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. *Marine Biology*, *66*, 89–94.

Broch, O. J., & Slagstad, D. (2012). Modelling seasonal growth and composition of the kelp *Saccharina latissima*. *Journal of Applied Phycology*, *24*, 759–776.

Bruhn, A., Tørring, D., Thomsen, M., Canal-Vergés, P., Nielsen, M., Rasmussen, M., Eybye, K., Larsen, M. M., Balsby, T. J. S., & Petersen, J. K. (2016). Impact of environmental conditions on biomass yield, quality, and bio-mitigation capacity of *Saccharina latissima*. *Aquaculture Environment Interactions*, *8*, 619–636.

Buck, B. H., & Buchholz, C. M. (2005). Response of offshore cultivated *Laminaria saccharina* to hydrodynamic forcing in the North Sea. *Aquaculture*, *250*, 674–691.

Cai, J., Lovatelli, A., Aguilar-Manjarrez, J., Cornish, L., Dabbadie, L., Desrochers, A., Diffey, S., Garrido Gamarro, E., Geehan, J., Hurtado, A., Lucente, D., Mair, G., Miao, W., Potin, P., Przybyla, C., Reantaso, M., Roubach, R., Tauati, M., & Yuan, X. (2021). *Seaweeds and microalgae: An overview for unlocking their potential in global aquaculture development Food and Agriculture Organization of the United States (FAO) fisheries and aquaculture circular* (Vol. 1229). FAO.

Campbell, J., & Starko, S. (2021). Allometric models effectively predict *Saccharina latissima* (Laminariales, Phaeophyceae) fresh weight at local scales. *Journal of Applied Phycology*, *33*, 491–500.

Coleman, S., St. Gelais, A. T., Fredriksson, D. W., Dewhurst, T., & Brady, D. C. (2022). Identifying scaling pathways and research priorities for kelp aquaculture nurseries using a techno-economic modeling approach. *Frontiers in Marine Science*, *9*, 894461. https://doi.org/10.3389/fmars.2017.00100

Davison, I. R. (1987). Adaptation of photosynthesis in *Laminaria saccharina* (phaeophyta) to changes in growth temperature. *Journal of Phycology*, *23*, 273–283.

Davison, I. R. (1991). Environmental effects on algal photosynthesis: Temperature. *Journal of Phycology*, *27*, 2–8.

Davison, I. R., & Davison, J. O. (1987). The effect of growth temperature on enzyme activities in the brown alga *Laminaria saccharina*. *British Phycological Journal*, *22*, 77–87.

Diehl, N., & Bischof, K. (2021). Coping with a changing Arctic: Mechanisms of acclimation in the brown seaweed *Saccharina latissima* from Spitsbergen. *Marine Ecology Progress Series*, *657*, 43–57.

Diehl, N., Li, H., Scheschonk, L., Burgunter-Delamare, B., Niedzwiedz, S., Forbord, S., Sæther, M., Bischof, K., & Monteiro, C. (2023). The sugar kelp *Saccharina latissima* I: Recent advances in a changing climate. *Annals of Botany*, *133*(1), 183–212.

Diehl, N., Roleda, M. Y., Bartsch, I., Karsten, U., & Bischof, K. (2021). Summer heatwave impacts on the European kelp *Saccharina latissima* across its latitudinal distribution gradient. *Frontiers in Marine Science*, *8*, 695821. https://doi.org/10.3389/fmars.2021.695821

Duarte, C. M., Bruhn, A., & Krause-Jensen, D. (2022). A seaweed aquaculture imperative to meet global sustainability targets. *Nature Sustainability*, *5*, 185–193.

Duarte, C. M., Wu, J., Xiao, X., Bruhn, A., & Krause-Jensen, D. (2017). Can seaweed farming play a role in climate change mitigation and adaptation? *Frontiers in Marine Science*, *4*, 100. https://doi.org/10.3389/fmars.2017.00100

Duarte, P., & Ferreira, J. G. (1997). A model for the simulation of macroalgal population dynamics and productivity. *Ecological Modelling*, *98*, 199–214.

Egan, B., & Yarish, C. (1988). The distribution of the genus *Laminaria* (Phaeophyta) at its southern limit in the Western Atlantic Ocean. *Botanica Marina*, *31*, 155–162.

Elzhov, T. V., Mullen, K. M., Spiess, A.-N., & Bolker, B. (2023). *minpack.lm: R Interface to the Levenberg–Marquardt nonlinear least-squares algorithm found in MINPACK, plus support for bounds*. 1.2-4.

Evankow, A., Christie, H., Hancke, K., Brysting, A. K., Junge, C., Fredriksen, S., & Thaulow, J. (2019). Genetic heterogeneity of two bioeconomically important kelp species along the Norwegian coast. *Conservation Genetics*, *20*, 615–628.

Fieler, R., Greenacre, M., Matsson, S., Neves, L., Forbord, S., & Hancke, K. (2021). Erosion dynamics of cultivated kelp, *Saccharina latissima*, and implications for environmental management and carbon sequestration. *Frontiers in Marine Science*, *8*, 632725. https://doi.org/10.3389/fmars.2021.632725

Filbee-Dexter, K., Wernberg, T., Fredriksen, S., Norderhaug, K. M., & Pedersen, M. F. (2019). Arctic kelp forests: Diversity, resilience and future. *Global and Planetary Change*, *172*, 1–14.

Forbord, S., Matsson, S., Brodahl, G. E., Bluhm, B. A., Broch, O. J., Handå, A., Metaxas, A., Skjermo, J., Steinhovden, K. B., & Olsen, Y. (2020). Latitudinal, seasonal and depth-dependent variation in growth, chemical composition and biofouling of cultivated *Saccharina latissima* (Phaeophyceae) along the Norwegian coast. *Journal of Applied Phycology*, *32*, 2215–2232.

Fortes, M. D., & Lüning, K. (1980). Growth rates of North Sea macroalgae in relation to temperature, irradiance and photoperiod. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, *34*, 15–29.

Freitas, V., Campos, J., Fonds, M., & Van der Veer, H. W. (2007). Potential impact of temperature change on epibenthic predator–bivalve prey interactions in temperate estuaries. *Journal of Thermal Biology*, *32*, 328–340.

Freitas, V., Cardoso, J. F. M. F., Lika, K., Peck, M. A., Campos, J., Kooijman, S. A. L. M., & van der Veer, H. W. (2010). Temperature tolerance and energetics: A dynamic energy budget-based comparison of North Atlantic marine species. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *365*, 3553–3565.

Frieder, C. A., Yan, C., Chamecki, M., Dauhajre, D., McWilliams, J. C., Infante, J., McPherson, M. L., Kudela, R. M., Kessouri, F., Sutula, M., Arzeno-Soltero, I. B., & Davis, K. A. (2022). A macroalgal cultivation modeling system (MACMODS): Evaluating the role of physical-biological coupling on nutrients and farm yield. *Frontiers in Marine Science*, *9*, 752951. https://doi.org/10.3389/fmars.2022.752951

Gerard, V. A. (1997). The role of nitrogen nutrition in high-temperature tolerance of the kelp, *Laminaria saccharina* (Chromophyta). *Journal of Phycology*, *33*(5), 800–810. https://doi.org/10.1111/j.0022-3646.1997.00800.x

Gerard, V. A., & Du Bois, K. R. (1988). Temperature ecotypes near the southern boundary of the kelp *Laminaria saccharina*. *Marine Biology*, *97*, 575–580.

Gerard, V. A., DuBois, K., & Greene, R. (1987). Growth responses of two *Laminaria saccharina* populations to environmental variation. *Hydrobiologia*, *151*, 229–232.

Gerard, V. A., & Mann, K. H. (1979). Growth and production of *Laminaria longicruris* (Phaeophyta) populations exposed to different intensities of water movement. *Journal of Phycology*, *15*, 33–41.

Gévaert, F., Davoult, D., Creach, A., Kling, R., Janquin, M.-A., Seuront, L., & Lemoine, Y. (2001). Carbon and nitrogen content of *Laminaria saccharina* in the eastern English Channel: Biometrics and seasonal variations. *Journal of the Marine Biological Association of the United Kingdom*, *81*, 727–734.

Gillooly, J. F., Allen, A. P., Savage, V. M., Charnov, E. L., West, G. B., & Brown, J. H. (2006). Response to Clarke and Fraser: Effects of temperature on metabolic rate. *Functional Ecology*, *20*, 400–404.

Hadley, S., Wild-Allen, K., Johnson, C., & Macleod, C. (2015). Modeling macroalgae growth and nutrient dynamics for integrated multi-trophic aquaculture. *Journal of Applied Phycology*, *27*, 901–916.

Heidkamp, C. P., Krak, L. V., Kelly, M. M. R., & Yarish, C. (2022). Geographical considerations for capturing value in the U.S. sugar kelp (*Saccharina latissima*) industry. *Marine Policy*, *144*, 105221.

Heinrich, S., Valentin, K., Frickenhaus, S., John, U., & Wiencke, C. (2012). Transcriptomic analysis of acclimation to temperature and light stress in *Saccharina latissima* (Phaeophyceae). *PLoS One*, *7*, e44342.

Heinrich, S., Valentin, K., Frickenhaus, S., & Wiencke, C. (2015). Temperature and light interactively modulate gene expression in *Saccharina latissima* (Phaeophyceae). *Journal of Phycology*, *51*, 93–108.

Jevne, L. S., Forbord, S., & Olsen, Y. (2020). The effect of nutrient availability and light conditions on the growth and intracellular nitrogen components of land-based cultivated *Saccharina latissima* (Phaeophyta). *Frontiers in Marine Science*, *7*, 557460.

Jiang, L., Blommaert, L., Jansen, H. M., Broch, O. J., Timmermans, K. R., & Soetaert, K. (2022). Carrying capacity of *Saccharina latissima* cultivation in a Dutch coastal bay: A modelling assessment. *ICES Journal of Marine Science*, *79*, 709–721.

Jones, E., Chierici, M., Skjelvan, I., Norli, M., Børsheim, K. Y., Lødemel, H. H., Kutti, T., Sørensen, K., King, A. L., Lauvset, S., Jackson, K., de Lange, T., Johannsessen, T., & Mourgues, C. (2019). Monitoring ocean acidification in Norwegian seas in 2018. Monitoring report No. M–1417.

Kassambara, A. (2023). *rstatix: Pipe-friendly framework for basic statistical tests*. 0.7.2.

Kim, J. K., Kraemer, G. P., & Yarish, C. (2015). Use of sugar kelp aquaculture in Long Island sound and the Bronx River Estuary for nutrient extraction. *Marine Ecology Progress Series*, *531*, 155–166.

Kim, J. K., Stekoll, M., & Yarish, C. (2019). Opportunities, challenges and future directions of open-water seaweed aquaculture in the United States. *Phycologia*, *58*, 446–461.

Koch, J., & De Schamphelaere, K. A. C. (2020). Estimating inter-individual variability of dynamic energy budget model parameters for the copepod Nitocra spinipes from existing life-history data. *Ecological Modelling*, *431*, 109091.

Kooijman, B. (2010). *Dynamic energy budget theory for metabolic organisation* (3rd ed.). Cambridge University Press.

Kooijman, S. A. L. M. (2014). Metabolic acceleration in animal ontogeny: An evolutionary perspective. *Journal of Sea Research*, *94*, 128–137.

Kuebler, J. E., Davison, I. R., & Yarish, C. (1991). Photosynthetic adaptation to temperature in the red algae *Lomentaria baileyana* and *Lomentaria orcadensis*. *British Phycological Journal*, *26*, 9–19.

Lavaud, R., Filgueira, R., & Augustine, S. (2021). The role of Dynamic Energy Budgets in conservation physiology. *Conservation Physiology*, *9*, coab083.

Lavaud, R., Ullman, D. S., Venolia, C., Thornber, C., Green-Gavrielidis, L., & Humphries, A. (2023). Production potential of seaweed and shellfish integrated aquaculture in Narragansett Bay (Rhode Island, U.S.) using an ecosystem model. *Ecological Modelling*, *481*, 110370.

Lika, K., Augustine, S., & Kooijman, S. A. L. M. (2022). The comparative energetics of the ray-finned fish in an evolutionary context. *Conservation Physiology*, *10*, coac039.

Lorena, A., Marques, G. M., Kooijman, S. A. L. M., & Sousa, T. (2010). Stylized facts in microalgal growth: interpretation in a dynamic energy budget context. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1557), 3509–3521. https://doi.org/10.1098/rstb.2010.0101

Lüning, K., Chapman, A. R. O., & Mann, K. H. (1978). Crossing experiments in the non-digitate complex of *Laminaria* from both sides of the Atlantic. *Phycologia*, *17*, 293–298.

Machalek, K. M., Davison, I. R., & Falkowski, P. G. (1996). Thermal acclimation and photoacclimation of photosynthesis in the brown alga *Laminaria saccharina*. *Plant, Cell & Environment*, *19*, 1005–1016.

Mao, X., Augyte, S., Huang, M., Hare, M. P., Bailey, D., Umanzor, S., Marty-Rivera, M., Robbins, K. R., Yarish, C., Lindell, S., & Jannink, J. L. (2020). Population genetics of sugar kelp throughout the northeastern United States using genome-wide markers. *Frontiers in Marine Science*, *7*, 694. https://doi.org/10.3389/fmars.2020.00694

Matsson, S., Metaxas, A., Forbord, S., Kristiansen, S., Handå, A., & Bluhm, B. A. (2021). Effects of outplanting time on growth, shedding and quality of *Saccharina latissima* (Phaeophyceae) in its northern distribution range. *Journal of Applied Phycology*, *33*, 2415–2431.

Monteiro, C., Li, H., Bischof, K., Bartsch, I., Valentin, K. U., Corre, E., Collén, J., Harms, L., Glöckner, G., & Heinrich, S. (2019). Is geographical variation driving the transcriptomic responses to multiple stressors in the kelp *Saccharina latissima*? *BMC Plant Biology*, *19*, 513.

Monteiro, C., Li, H., Diehl, N., Collén, J., Heinrich, S., Bischof, K., & Bartsch, I. (2021). Modulation of physiological performance by temperature and salinity in the sugar kelp *Saccharina latissima*. *Phycological Research*, *69*, 48–57.

Müller, R., Wiencke, C., & Bischof, K. (2008). Interactive effects of UV radiation and temperature on microstages of Laminariales (Phaeophyceae) from the Arctic and North Sea. *Climate Research*, *37*(2–3), 203–213. https://doi.org/10.3354/cr00762

Nemenyi, P. (1963). *Distribution-free multiple comparisons*. [PhD Thesis]. Princeton University.

Nielsen, M. M., Manns, D., D'Este, M., Krause-Jensen, D., Rasmussen, M. B., Larsen, M. M., Alvarado-Morales, M., Angelidaki, I., & Bruhn, A. (2016). Variation in biochemical composition of *Saccharina latissima* and Laminaria digitata along an estuarine salinity gradient in inner Danish waters. *Algal Research*, *13*, 235–245.

Olischläger, M., Iñiguez, C., Gordillo, F. J. L., & Wiencke, C. (2014). Biochemical composition of temperate and Arctic populations of *Saccharina latissima* after exposure to increased pCO_2 and temperature reveals ecotypic variation. *Planta*, *240*, 1213–1224.

Olischläger, M., Iñiguez, C., Koch, K., Wiencke, C., & Gordillo, F. J. L. (2017). Increased pCO_2 and temperature reveal ecotypic differences in growth and photosynthetic performance of temperate and Arctic populations of *Saccharina latissima*. *Planta*, *245*, 119–136.

Pedersen, M. (2015). *Temperature effects on the kelp Saccharina latissima*. Grenada.

Pohlert, T. (2023). *PMCMRplus: Calculate pairwise multiple comparisons of mean rank sums extended*. 1.9.10.

Possenti, L., Skjelvan, I., Atamanchuk, D., Tengberg, A., Humphreys, M. P., Loucaides, S., Fernand, L., & Kaiser, J. (2021). Norwegian Sea net community production estimated from O_2 and prototype CO_2 optode measurements on a Seaglider. *Ocean Science*, *17*, 593–614.

R Core Team. (2023). *R: A language and environment for statistical computing*. 4.3.2. R Foundation for Statistical Computing.

Rohatgi, A. (2022). *WebPlotDigitizer*. 4.6. Pacifica.

Russo, S. E., Ledder, G., Muller, E. B., & Nisbet, R. M. (2022). Dynamic energy budget models: Fertile ground for understanding resource allocation in plants in a changing world. *Conservation Physiology*, *10*, coac061.

Sæther, M., Diehl, N., Monteiro, C., Li, H., Niedzwiedz, S., Burgunter-Delamare, B., Scheschonk, L., Bischof, K., & Forbord, S. (2024). The sugar kelp *Saccharina latissima* II: Recent advances in farming and applications. *Journal of Applied Phycology*. https://doi.org/10.1007/s10811-024-03213-1

Scheschonk, L., Becker, S., Hehemann, J.-H., Diehl, N., Karsten, U., & Bischof, K. (2019). Arctic kelp eco-physiology during the polar night in the face of global warming: A crucial role for laminarin. *Marine Ecology Progress Series*, *611*, 59–74.

Scheschonk, L., Bischof, K., Kopp, M. E. L., & Jueterbock, A. (2023). Differences by origin in methylome suggest ecophenotypes in the kelp *Saccharina latissima*. *Evolutionary Applications*, *16*, 262–278.

Schoolfield, R. M., Sharpe, P. J. H., & Magnuson, C. E. (1981). Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. *Journal of Theoretical Biology*, *88*, 719–731.

Schouten, R., Vesk, P. A., & Kearney, M. R. (2020). Integrating dynamic plant growth models and microclimates for species distribution modelling. *Ecological Modelling*, *435*, 109262.

Sharpe, P. J. H., & DeMichele, D. W. (1977). Reaction kinetics of poikilotherm development. *Journal of Theoretical Biology*, *64*, 649–670.

Soetaert, K., Petzoldt, T., & Setzer, R. W. (2010). Solving differential equations in R: Package deSolve. *Journal of Statistical Software*, *33*, 1–25. https://doi.org/10.18637/jss.v033.i09

St. Gelais, A. T., Fredriksson, D. W., Dewhurst, T., Miller-Hope, Z. S., Costa-Pierce, B. A., & Johndrow, K. (2022). Engineering a low-cost kelp aquaculture system for community-scale seaweed farming at nearshore exposed sites via user-focused design process. *Frontiers in Sustainable Food Systems*, *6*, 848035. https://doi.org/10.3389/fsufs.2022.848035

Strong-Wright, J., & Taylor, J. R. (2022). Modeling the growth potential of the kelp *Saccharina Latissima* in the North Atlantic. *Frontiers in Marine Science*, *8*, 793977. https://doi.org/10.3389/fmars.2021.793977

Teal, L. R., van Hal, R., van Kooten, T., Ruardij, P., & Rijnsdorp, A. D. (2012). Bio-energetics underpins the spatial response of North Sea plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) to climate change. *Global Change Biology*, *18*, 3291–3305.

Terblanche, J. S., Deere, J. A., Clusella-Trullas, S., Janion, C., & Chown, S. L. (2007). Critical thermal limits depend on methodological context. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1628), 2935–2943. https://doi.org/10.1098/rspb.2007.0985

Theuerkauf, S. J., Barrett, L. T., Alleway, H. K., Costa-Pierce, B. A., St. Gelais, A., & Jones, R. C. (2022). Habitat value of bivalve shellfish and seaweed aquaculture for fish and invertebrates: Pathways, synthesis and next steps. *Reviews in Aquaculture*, *14*, 54–72.

van der Meer, J., Klok, C., Kearney, M. R., Wijsman, J. W. M., & Kooijman, S. A. L. M. (2014). 35 years of DEB research. *Journal of Sea Research*, *94*, 1–4.

Venolia, C. T., Lavaud, R., Green-Gavrielidis, L. A., Thornber, C., & Humphries, A. T. (2020). Modeling the growth of sugar kelp (*Saccharina latissima*) in aquaculture systems using dynamic energy budget theory. *Ecological Modelling*, *430*, 109151.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., … Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, *4*, 1686.

Zhang, J., Fang, J., Wang, W., Du, M., Gao, Y., & Zhang, M. (2012). Growth and loss of mariculture kelp Saccharina japonica in Sungo Bay, China. *Journal of Applied Phycology*, *24*, 1209–1216.

Zhang, J., Wu, W., Ren, J., & Lin, F. (2016). A model for the growth of mariculture kelp Saccharina japonica in Sanggou Bay, China. *Aquaculture Environment Interactions*, *8*, 273–283.

Zhu, L., Huguenard, K., Zou, Q.-P., Fredriksson, D. W., & Xie, D. (2020). Aquaculture farms as nature-based coastal protection: Random wave attenuation by suspended and submerged canopies. *Coastal Engineering*, *160*, 103737.

Zollmann, M., Rubinsky, B., Liberzon, A., & Golberg, A. (2021). Multi-scale modeling of intensive macroalgae cultivation and marine nitrogen sequestration. *Communications Biology*, *4*, 1–11.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Krasnow, R., Gonzalez, S., & Lindell, S. (2024). Improving growth models of cultivated sugar kelp, *Saccharina latissima*, by accounting for intraspecific variation in thermal tolerance. *Journal of the World Aquaculture Society*, e13085. https://doi.org/10.1111/jwas.13085