






# The effect of distal-end trimming on *Saccharina latissima* morphology, composition, and productivity

Gretchen S. Grebe<sup>1,2</sup>  | Carrie J. Byron<sup>2</sup>  | Damian C. Brady<sup>1</sup>  |  
Adam T. St. Gelais<sup>2,3</sup>  | Barry A. Costa-Pierce<sup>2</sup> 

<sup>1</sup>School of Marine Sciences, University of Maine, Orono, Maine

<sup>2</sup>School of Marine & Environmental Programs, University of New England, Biddeford, Maine

<sup>3</sup>Aquaculture Research Institute, University of Maine, Walpole, Maine

## Correspondence

Gretchen S. Grebe; University of Maine; University of New England School of Marine & Environmental Programs, 11 Hills Beach Rd, Biddeford, ME, 04005.  
Email: gretchen.grebe@maine.edu

## Funding information

U.S. Department of Agriculture Northeast Sustainable Agriculture Research and Education, Grant/Award Number: GNE18-172-32231; U.S. National Science Foundation award to UMaine Office of Experimental Program to Stimulate Competitive Research, Grant/Award Number: IIA-1355457

## Abstract

As kelp cultivation increases around the world, so does the need for farm management strategies that produce specific crop characteristics, optimize yield, widen harvesting windows, and prevent biomass loss. Distal-end trimming of macroalgae has been recommended as a farm management method addressing these needs. In this study, we trimmed cultivated *Saccharina latissima* sporophytes grown in the Western Gulf of Maine (WGoM) to 60 cm above the stipe-blade interface. We characterized the effect of trimming on the morphology, tissue nutrient content, stable isotope ratio, and nitrate reductase activity of the kelp. We also evaluated the economic trade-offs of trimming using a simple production model. The results suggest that trimming the blade to 60 cm may have minimal biological consequences. Additionally, the trimming appears to benefit “short” kelp blades in proximity to the trimmed blades. Daily yield (% increase in weight day<sup>-1</sup>) after trimming was initially lower than the control, but late-season daily yields and crop-retention following storms were markedly improved. Ultimately, we conclude that growers could use trimming to acquire kelp biomass earlier in the season, retain late-season biomass, and potentially increase the total revenue

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2021 The Authors. *Journal of the World Aquaculture Society* published by Wiley Periodicals LLC on behalf of World Aquaculture Society.

gained from kelp farming if price premiums can be exacted for this biomass.

#### KEYWORDS

biomass, biometrics, ecophysiology, kelp

## 1 | INTRODUCTION

Kelp farming in the Americas and Europe is on the rise (Augyte, Yarish, Redmond, & Kim, 2017; FAO, 2020; Grebe, Byron, Gelais, Kotowicz, & Olson, 2019; Kim, Stekoll, & Yarish, 2019). Seaweed farmers in the United States produced an estimated 249–272 wet MT of farmed edible macroalgae in 2019; the majority of which was kelp (Piconi, Veidenheimer, & Chase, 2020 and references therein). This growth is a ~20-fold increase from the estimated 11–14 wet MT harvested in 2015 (MEDMR, 2019; Piconi et al., 2020 and references therein). In Europe, kelp is now permitted as a species for cultivation on at least 30 aquaculture leases across Spain, France, The Netherlands, Denmark, Ireland, The United Kingdom, Sweden, and Norway (Camia et al., 2018; EMODnet, 2021). Recently, for the budding European and American kelp farming industry to grow beyond initial proof of concept, there is a need for additional optimization of farming and engineering practices that maximize algal yields, extend the harvest season to provide a consistent supply of kelp for buyers, and increase revenue for kelp farmers (Boderskov et al., 2016; Fredriksson et al., 2020; Handå et al., 2013; Rolin, Inkster, Laing, & McEvoy, 2017).

Distal-end trimming, a crop management strategy in which a portion of the older blade is removed using a transverse cut, may be a practice that can help bring the industry closer to these necessary yields, consistency, and revenue gains. In northern China, distal-end trimming has been widely practiced on *Saccharina japonica* farms for decades, and it has been shown to improve the health of *S. japonica* blades and minimize the occurrence of diseases by increasing the light availability, water flow, and nutrients around the blades (Scoggan, Zhimeng, & Feijiu, 1989; Tseng, 1962, 1981, 1986; Wu & Zheng, 1981). Furthermore, the economic benefits of the trimming are understood to be the capture of biomass that would otherwise be lost to natural blade erosion or storms, an extended growing season, and reduced production costs (Scoggan et al., 1989; Wu, 1962; Wu & Zheng, 1981). More specifically, natural shedding can result in the loss of up to 30% of total seasonal biomass production on these *S. japonica* farms, but distal-end trimming captures this material before shedding occurs in late spring (Scoggan et al., 1989; Tseng, 1962, 1986; Wu, 1962; Wu & Zheng, 1981). In more recent studies, Gao, Endo, Yamana, Taniguchi, and Agatsuma (2013) found that distal-end trimming extended the growth phase of *Undaria pinnatifida* in Japanese waters by 1 month, and Bak, Mols-Mortensen, and Gregersen (2018) calculated that trimming could reduce that total cost per kg of wet cultivated kelp by more than two-thirds because it increased the number of harvests possible without reseeding (Bak et al., 2018).

Conversely, several studies examining the effect of trimming on other algal species suggest that distal-end trimming can result in biological disadvantages. In Laminariales, translocation brings photosynthates and nutrients from their point of production or uptake in the mature, distal blade to the growing tissue in the basal region (Davison & Stewart, 1984; Parker, 1963, 1965; Schmitz & Lobban, 1976; Tseng, 1986; Wu & Zheng, 1981). So, one potential disadvantage of distal-end trimming is the decline of translocated photosynthates and nutrients, which may potentially result in periods of decreased growth. Wu & Zheng (1981) observed a close relationship between trimming and growth in the intercalary region of *S. japonica* blades; the length and weight of *S. japonica* were not diminished if only one-third of the distal end was removed but removing any more material than this resulted in reduced growth in length. Several experiments with wild *Nereocystis luetkeana* reported reduced growth rates up to 2 weeks following blade trimming; presumably, again, because the amount of photosynthate translocated back to the growth region was reduced (Nicholson, 1970; Nicholson & Briggs, 1972; Roland, 1985; Schmitz & Lobban, 1976). In some

instances, it appears that the deficiencies resulting from the removed blade area are too great for the organism to overcome. For example, trimming *Saccharina diabolica* <30 cm from the base of the blade had a strong negative impact on its growth and total yield (Sanbonsuba, Machiguchi, & Saga, 1987). Rolin et al. (2017) trimmed *Laminaria digitata* 10 cm from the base of the blade and it did not regrow. In contrast, trimming wild *Ecklonia maxima* 10–30 cm above the base of the primary blade every 4 months has been shown to result in a four- to fivefold increase in total yields (Levitt, Anderson, Boothroyd, & Kemp, 2002).

Only a few studies have investigated the effect of distal-end trimming on *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders, despite its current status as one of the most widely cultivated macroalgal species in Europe and North America (EMODnet, 2021; Grebe et al., 2019; Grebe, Byron, Brady, Geisser, & Brennan, 2021; Yarish, Kim, Lindell, & Kite-Powell, 2017). In one study, Rolin et al. (2017) grew *S. latissima* (and *L. digitata*) off the coast of the Shetland Islands and then trimmed the kelp thalli 10 cm above the stipe–blade transition zone. The trimmed *S. latissima* regrew and did not show the same summer erosion or fouling as the control blades (Rolin et al., 2017). In another study, Bak et al. (2018) grew and trimmed *S. latissima* (and *Alaria esculenta*) near the Faroe Islands down to 5–15 cm from the stipe–blade transition zone to ensure preservation of the meristematic region. In the end, Bak et al. (2018) trimmed the same *S. latissima* thalli four times in a season and calculated that trimming could reduce that total cost per kg of wet cultivated *S. latissima* by more than two-thirds because it increased the number of harvests possible without reseeding (Bak et al., 2018). The results of these initial studies suggest that distal-end trimming has promise as an improved farming practice for *S. latissima*, but more understanding of the species-specific physiological response to this technique is needed (Bak et al., 2018; Grandfor Bak, 2019; Rolin et al., 2017).

Before incorporating distal-end trimming into existing *S. latissima* farm management, it is important to know if, and when, the practice stimulates growth or other physiological changes in the remaining sporophyte. Several studies have used changes in morphology or metabolic processes as clues. For instance, Gao, Endo, et al. (2013) removed most of the thallus (trim location 30 cm above the stipe–blade interface) of *U. pinnatifida* and observed increased gross photosynthetic rates in the remaining thallus for several months afterward. Although they were not directly studying distal-end trimming, Burnett and Koehl (2019) punched a 1 cm × 4 mm hole through the rachis of wild *Egregia menziesii* to mimic herbivore damage, and they observed that the rachis grew wider near the location of the injury. We propose that changes in thallus morphology and blade composition, and more specifically differences in blade %N, %C,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , C:N, or NRA may serve as additional indicators of trimming-induced stress. A reduced %N or %C could indicate an impact on the organism's ability to sustain itself with the remaining blade. If this N or C stress was severe, then the trimmed blades would have a lower  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  in their basal tissue when compared to control blades of the same length because when N or C is abundant, algae prefer to use lighter  $^{14}\text{N}$  and  $^{12}\text{C}$  isotopes for their metabolic processes (Peterson & Fry, 1987; Savage & Elmgren, 2004; Thornber, DiMilla, Nixon, & McKinney, 2008). If combined with other morphological or compositional observations, a shift in C:N ratio in the blade post-trim might also serve as an indicator of increased production of defense compounds (Royer, Larbat, Le Bot, Adamowicz, & Robin, 2013) and elevated nitrate reductase activity in the remaining blade might signal a shift in nitrogen metabolism of the thalli (Hurd, Berges, Osborne, & Harrison, 1995).

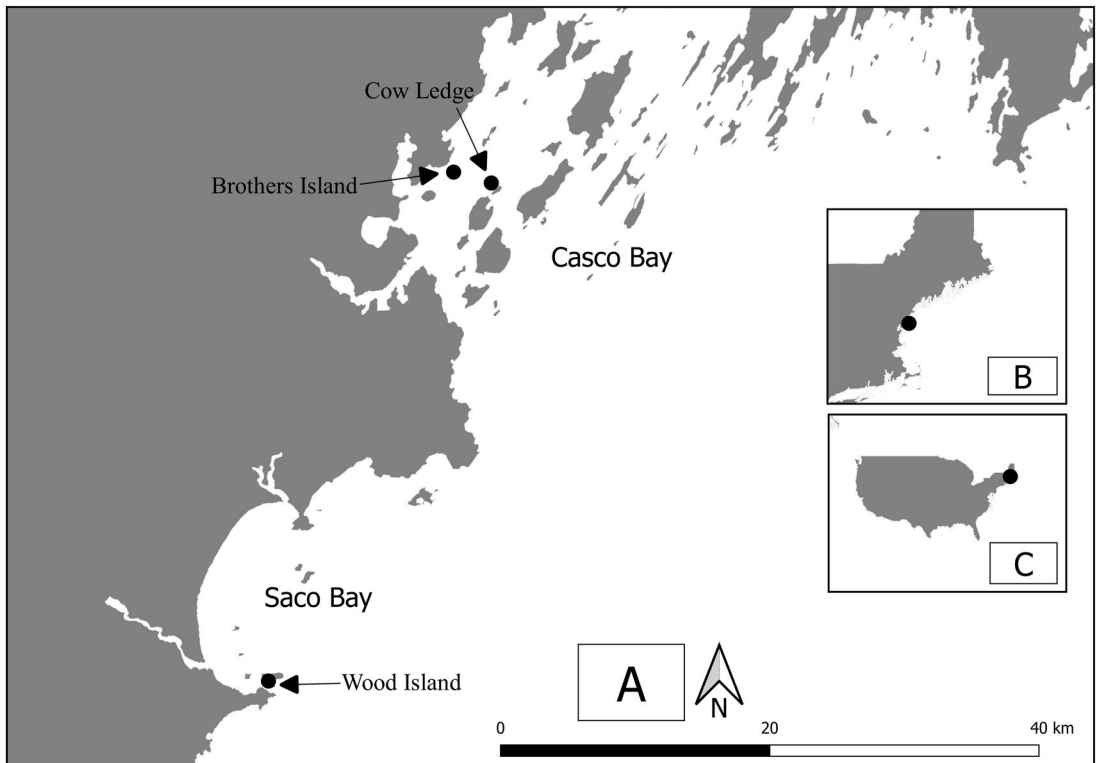
In this study, we explored the effect of distal-end trimming on the morphology, composition, and yields of cultivated *S. latissima* to help kelp farmers weigh the costs and benefits of incorporating this practice into their operations. Eager to build on the recent studies by Rolin et al. (2017) and Bak et al. (2018) and the best practices reported by Wu and Zheng (1981), we increased the length between the stipe–blade interface and the trim to 60 cm. First, we hypothesized that kelp trimmed to this length would exhibit an injury response to the trimming by growing wider near the trim. Second, we hypothesized that, even with an increased trimming length, the trimmed kelp tissue would have lower %C, %N,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$  resulting from the reduction of blade area for photosynthesis and nutrient uptake. Our third hypothesis was that nitrate reductase, one of the key enzymes for N assimilation in algae, would increase in the remaining (basal) regions of the trimmed blades as the kelp attempted to meet the nutrient demands of the growth region despite a reduced blade area. Our fourth hypothesis was that daily yield from the trimmed

sections of *S. latissima* would be lower than the control sections due to our previous hypotheses about injury response and reduction of blade area. Finally, we sought to evaluate the economic trade-offs of an expanded *S. latissima* harvest season with smaller, more frequent harvests by developing a model of biomass production from kelp aquaculture in the state of Maine, USA, with varying growth rates, total production, and sale prices.

## 2 | MATERIALS AND METHODS

### 2.1 | Site characteristics

*S. latissima* was cultivated at three sites in the Gulf of Maine, USA (Figure 1). One site, Wood Island (43.4553, -70.3367), was in Saco Bay, and two sites, Cow Ledge (43.7025, -70.1877) and Brothers Island (43.6968, -70.2095), were in Casco Bay. Site depth ranged from 8 to 17 m mean lower low water. Water temperature at each site was continuously recorded using suspended loggers (Hobo Pendant Temperature/Light Loggers; UA-002-08). Precipitation data for Saco Bay were obtained from the weather station located at the Arthur P. Girard Marine Science Center on the University of New England's Biddeford, ME campus. Regional wind and precipitation data for Casco Bay were retrieved from the National Oceanic and Atmospheric Administration's (NOAA) Climate Data Online



**FIGURE 1** *Saccharina latissima* cultivation and sampling sites in relation to: (a) Saco Bay and Casco Bay, (b) the Gulf of Maine, (c) Northeastern United States. A single, 60 m longline was deployed at Wood Island, two 120 m longlines were deployed at Brothers Island, and six 120 m longlines were deployed at Cow Ledge. Brothers Island and Cow Ledge are <3 km apart. Samples were collected from Wood Island and Cow Ledge in 2018 and from all three sites in 2019

(Station USW00014764; Portland Jetport). Surface solar radiation downwards (SSRD) was obtained from the National Aeronautics and Space Administration (NASA) Earth Observing System data collection. Current velocities at the sites were estimated using an inverted Tilt Current Meter (Lowell Instruments LLC) suspended from the longline spacer buoys.

Thirty sampling trips were completed in total: 9 during Spring 2018 and 21 during Spring 2019. Salinity, pH, and nitrate-N concentrations at each cultivation site were characterized using grab samples collected from 2 m depth during each sampling trip. Salinity was measured with a refractometer (Cole-Parmer RSA-BR90A; 0–90%). Water pH was assessed using a benchtop meter (Hach model #: PW172KB0703F01) calibrated to certified standards. Nitrate-N at the site was quantified spectrophotometrically (Hach Nitrate TNTplus Low Range Vial Tests; Hach DR3900 VIS spectrophotometer). Photosynthetically active radiation was also measured during these sampling trips using a spherical quantum sensor (LI-COR LI-193). Readings were taken above the water surface and at 2 m deep. The difference between the readings was used to determine light attenuation.

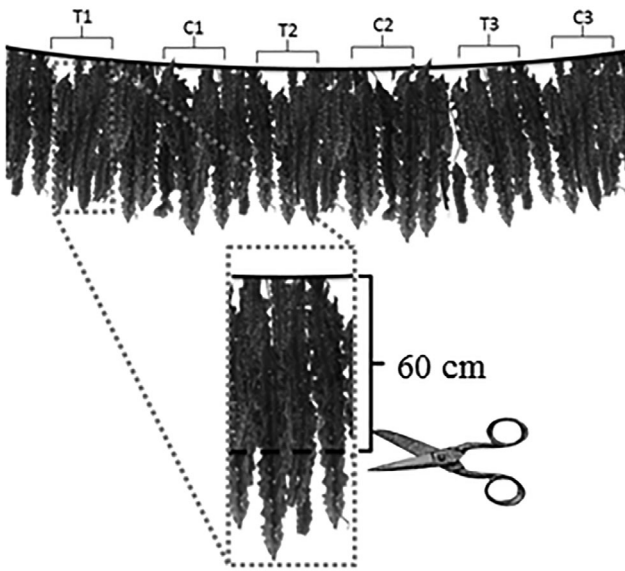
## 2.2 | Kelp cultivation

Kelp sporelings were produced using the techniques described in Redmond, Green, Yarish, Kim, and Neefus (2014). In brief, reproductive *S. latissima* tissue was collected from wild beds in Casco Bay via boat using a hand rake. In the lab, the sorus tissue was wiped dry, treated with betadine, placed between layers of paper towels, and kept cool overnight to induce spore release. Inoculation water was prepared to approximately 6,000–8,000 spores ml<sup>-1</sup>. The spores settled on thin nylon button twine (Ludlow/A&E brand). Temperature and light-controlled aquaria were used to grow the sporophytes until they were deployed at sea in November 2018 and December 2019. At deployment, the sporophyte-covered string was wound around a thicker (1.25 cm) diameter longline. A single, 60 m longline was deployed at Wood Island in 2018 and 2019. This longline was oriented parallel to the prevailing current (east–west). Fredriksson et al. (2020) provided an additional description of the hydrodynamics of this site. Two 120 m longlines were deployed at Brothers Island in 2019 and Cow Ledge in 2018. In 2019, five 120 m longlines were deployed at Cow Ledge. The longlines at Brothers Island and Cow Ledge were oriented parallel to the prevailing current (north–south) and spacing between the longlines at the same site was ≥6 m. All longlines were maintained at a depth of 2 m using buoys attached to rigid PVC spacers. After outplanting, the sporophytes were left untouched until trimming was initiated.

## 2.3 | Trimming technique

Trimming treatments were initiated in late March of 2018 and 2019 and continued through mid-May 2018 and 2019. During each trimming event, three 1-m sections of the line were haphazardly designated for trimming (Figure 2). We marked the start and end of these sections by attaching different-colored zip ties to the longline. In these sections, the kelp thalli were trimmed to approximately 60 cm in length using scissors. The basal end, stipe, and holdfast were left attached to the longline. The longline outside the trimming sections was left uncut to serve as a control. Overall, we conducted 12 trimming events.

Approximately 8–20 days after trimming, depending on weather, 10 cm of longline was randomly subsampled from within the trimmed section. All thalli from this subsection were harvested for analysis. A nearby section of longline was used for harvesting a subsample of the control (untrimmed) thalli. This section was at least 2 m from any previous harvesting to ensure that there was no spillover effect of prior trimming or sample harvesting on the control. The harvested thalli were transported in plastic bags in a covered cooler at 8–10°C to the laboratory where they were stored in the refrigerator at 8–10°C and processed within 24 hr of collection.



**FIGURE 2** Schematic of *Saccharina latissima* longline depicting relative positioning of trimmed (T) and control (C) sections (figure not to scale). Trimming treatments were administered to three 1-m sections of the line by trimming all thalli in the section to approximately 60 cm in length (measured from the stipe-blade transition zone). Three other sections of the longline were left untrimmed as controls. Then, 8–20 days after each trimming event, all thalli from a 10-cm section of each trimmed or control section were harvested for analysis

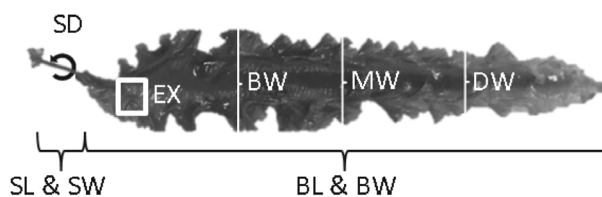
We returned to the same trimmed sections throughout the growing season to see how the characteristics of the trimmed kelp changed. We used the different-colored zip ties to quickly identify the same trimmed sections from one sampling event to the next. At each visit, we collected new, 10-cm-wide subsamples. We were able to sample the earliest trimmed sections up to nine times before the longlines were removed from the water in June. The later-trimmed sections were sampled a minimum of three times.

## 2.4 | Processing and analysis

During each sampling event, five thalli from the trimmed subsection and the control subsection were preserved for nitrate reductase analysis immediately after removing them from the water. A  $5 \times 5$  cm section of tissue was excised from the basal region of individual kelp blades, frozen in liquid N, and stored at  $-80^{\circ}\text{C}$  until processed. The individuals were haphazardly selected with one exception; the basal portion of the thalli had to be  $\geq 7$  cm wide so that the  $5 \times 5$  cm section could be removed. The nitrate reductase activity (NRA) of each tissue sample was measured using the methodology described by Young, Lavery, Van Elven, Dring, and Berges (2005) and nitrite produced during the process was measured using a Hach 3900 spectrophotometer and TNT 880 nitrite vials.

Twenty individuals from each treatment group were analyzed for changes in morphology: the five thalli selected for NRA and an additional 15 individuals haphazardly selected. Morphology measurements (Figure 3) were made by caliper, a fish measuring board, and a precision balance. Total blade length (BL), width at one-fourth of the blade (basal region) (BW), width at half of the blade (mid-region) (MW), width at three-fourth of the blade (distal region) (DW), stipe length (SL), stipe diameter (SD), stipe wet weight (SWW), and blade wet weight (BWW). A representative surface area-to-weight ratio was used to calculate the mass removed by the basal tissue sample, and this weight was added to the measured total weight to correct for the removed tissue.

Next, the samples that were analyzed for NRA were also analyzed for C and N content and stable isotope ratios. A second tissue sample was excised from the basal region of each blade, as close as possible to the original excision. This tissue was rinsed with deionized water, frozen, and then lyophilized at  $-50^{\circ}\text{C}$  for 24 hr. Each sample was ground with a mortar and pestle and encapsulated in tin (2.5–5 mg). These samples were analyzed by the UC Davis



**FIGURE 3** Location of morphological measurements for *Saccharina latissima*. The recorded characteristics included total blade length (BL), width at one-fourth of the blade (basal region) (BW), width at half of the blade (mid-region) (MW), width at three-fourth of the blade (distal region) (DW), stipe length (SL), stipe diameter (SD), stipe wet weight (SWW), and blade wet weight (BWW). The location of tissue excised for carbon and nitrogen stable isotope analysis and nitrate reductase analysis is also indicated (EX). The location of the BW measurement (0.25 BL) was intended to capture maximum blade width (Vettori & Nikora, 2017)

Stable Isotope Facility (SIF) using an elemental analyzer (PDZ Europa ANCA-GSL) interfaced with an isotope ratio mass spectrometer (PDZ Europa 20-20). Sample precision was 0.2‰ for  $^{13}\text{C}$  and 0.3‰ for  $^{15}\text{N}$  (UC Davis SIF 2020). The total C and N content measured in the samples was divided by the dry sample weight to obtain %C and %N of the dry excised tissue sample. The UC Davis SIF calculated the stable isotope ratios for each sample by comparing the difference in the  $^{15}\text{N}$  or  $^{13}\text{C}$  measured in the sample against the  $^{15}\text{N}$  or  $^{13}\text{C}$  measured in at least four different laboratory reference materials (Equation 1) (Peterson & Fry, 1987):

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} = \left( \frac{R_{\text{sample}}}{R_{\text{reference}}} - 1 \right) \times 1,000 (\text{‰}) \quad (1)$$

where R equals  $^{15}\text{N}/^{14}\text{N}$  or  $^{13}\text{C}/^{12}\text{C}$ .

## 2.5 | Statistical analysis

One-way analysis of variance (ANOVA) was used to determine the effect of sampling site on environmental characteristics, and whether the data from different sites could be combined for analysis. Determining whether samples across sites could be pooled was important because site-specific environmental conditions (i.e., temperature, water motion, light, and nutrients) and their interactions affect seasonal growth patterns, morphology, and productivity of kelp (Fortes & Lüning, 1980; Gerard, 1987; Egan & Yarish, 1990; Hurd, 2000; Hymanson, Reed, Foster & Carter, 1990). The morphological and compositional data were sorted into blades harvested from a trimming section or a control section. Distributions for each group were plotted and tested for normality (Shapiro–Wilk) and equal variance (Levene's test) (Levene, 1960; Shapiro & Wilk, 1965). When the distributions and variance were normal, Tukey's Honest Significant Difference post hoc tests were used to test the difference in the means between the trimmed treatment and the control. Nonparametric (Wilcoxon signed rank) tests were used when assumptions of normality and equal variance were not met. Significance levels of 0.05 were used for all tests unless otherwise indicated. Bivariate regression analyses were used to explore the relationship between the environmental and morphological data. Statistical analyses were conducted using JMP Pro V. 14.2 (SAS Institute) and RStudio V.1.2.1335 (RStudio, PBC).

## 2.6 | Daily yield and the production and harvesting model

We calculated biomass (wet  $\text{kg m}^{-1}$ ) and daily yield (%) for each sampling data. Biomass was calculated as wet weight (WW) per longline meter by weighing the complete 10 cm sample and linearly extrapolating to 1 m of longline. Daily yield (DY) was calculated using a Ricker relationship (Equation 2) (Ricker, 1979):

$$DY \left( \% \text{day}^{-1} \right) = (\ln(X_t) - \ln(X_0)) / t \times 100 \quad (2)$$

where  $\ln(X_t)$  is the natural logarithm of the wet biomass weight per longline meter at time  $t$  and  $\ln(X_0)$  is the natural logarithm of the initial weight. Daily yield integrates new production, erosion, and sloughing and so is not solely an indicator of growth rate. Bivariate regression analyses were used to explore the relationship between the environmental observations and daily yield.

The daily yield was used as an input in the production and harvesting model. To generate production and harvest estimates, we assumed that the observations of daily yield for trimmed and control *S. latissima* were applicable across the WGoM. Additional economic inputs were determined using a recent market analysis for U.S. seaweed production (Piconi et al., 2020). They included the following: (a) Maine's farmed edible seaweed production in 2019 was 147 t (WW), (b) presently harvesters can expect \$880–\$1,540  $\text{MT}^{-1}$  for bulk unprocessed seaweed, and (c) high-end projections suggest Maine's farmed edible seaweed production could reach up to 2,722 MT (WW) by 2,035 (Piconi et al., 2020). We set April 1 as the model start date to reflect the approximate initiation of trimming treatments in the field experiment and May 15 as the end date because the large majority of farmed *S. latissima* harvesting in the WGoM currently occurs in mid to late May. To determine the starting biomass for current scenarios, we used the highest daily yield consistently measured ( $6\% \text{ day}^{-1}$ ) in the control sections from April 1 to May 15 and back-calculated from the total production reported in 2019 (147 MT) to obtain an estimate of 133 MT on April 1. This same methodology was used for the future scenarios: back-calculating from the forecasted 2,722 MT of kelp that could be produced by 2,035 using a 6% daily yield to set a starting biomass of 2,708 MT on April 1.

We examined the sensitivity of model output as a function of price per MT of *S. latissima*. In 10 scenarios, the price per MT was constant at \$880, \$1,210, or \$1,540  $\text{MT}^{-1}$ . In two additional scenarios, we allowed the price of harvested kelp to vary as a function of harvest timing (from \$880  $\text{MT}^{-1}$  to \$1,540  $\text{MT}^{-1}$ ). These latter scenarios were developed to incorporate the possibility that the regional sale price of raw kelp may be inversely related to supply or directly related to its morphological or nutritional characteristics. Incorporating the observed daily yields, economic analysis and price variability resulted in the consideration of 12 scenarios (Table S1).

### 3 | RESULTS

#### 3.1 | Environmental conditions

Environmental conditions measured during the 2018 and 2019 cultivation periods were significantly different between the Cow Ledge, Brothers Island, and Wood Island sites. There was a significant effect of “site” on ambient temperature [ANOVA;  $F(2,584) = 12.0, p < .001$ ], salinity [ANOVA;  $F(2,709) = 40.8, p < .001$ ], pH [ANOVA;  $F(2,710) = 15.7, p < .001$ ], and nitrate [ANOVA;  $F(2,704) = 13.9, p < .001$ ]. Due to this high amount of environmental variability, the response variables (i.e., morphology, tissue composition, NRA, biomass, daily yield) were not pooled and observations from Spring 2018 and Spring 2019 were also treated as separate. Overall, Saco Bay (Wood Island) had higher ambient nitrate and minimum water temperatures, but lower salinity and maximum water temperatures than Casco Bay (Cow Ledge and Brothers). More specifically, during the growing season mean daily water temperature ranged from 1 to 14°C across sites (Figure S1). Salinity ranged from 16 to 35 psu. The lowest salinities were observed in early May 2018 and late April 2019. Salinity levels at Wood Island were generally lower than those at Cow Ledge and Brothers Island. Sunlight received, measured as SSRD, was similar between Casco and Saco Bays, although in many instances Saco Bay had slightly more SSRD than Casco Bay on the same given day. Nitrate levels in the water column ranged from 1.2 to 17  $\mu\text{M}$  and they varied by season, with the highest levels of nitrate recorded at Wood Island and the lowest levels observed at Brothers Island. A decline in ambient nitrate was observed in both



May 2018 and 2019, with an earlier and more severe decline in May 2019. The range of current velocities recorded at Wood Island and Cow Ledge were similar (5–54 cm s<sup>-1</sup> and 3–50 cm s<sup>-1</sup>, respectively). Current data are not available for Brothers Island due to logger battery failure, but the current velocities are likely similar to those at Cow Ledge because the sites are close and most of the variability in current speed within the region is driven by tidal cycles.

## 3.2 | Morphology

Distributions of the untrimmed (control) blades had high variation and they were right-skewed (Figure 4). To facilitate comparison of the trimmed and control blades, we addressed the high variation among blade lengths by dividing the morphological variation into two groups based on size classes: hereafter called (a) Long Blade Class (LBC) and (b) Short Blade Class (SBC). The trimming and control LBC had blades that were ≥60 cm. The SBC had blades that were <60 cm, and these are the thalli that were interspersed between the trimmed thalli (or long control thalli) but were too short to be trimmed themselves.

The Wood Island LBC (≥60 cm) exhibited significant differences between mean stipe length, stipe diameter, and stipe weight between the trimmed and control groups (Table S2). When compared to the control LBC, we observed a significantly higher mean stipe length (12.5%), stipe diameter (16%), and stipe weight (25%) in the trimmed LBC. There were no significant differences for the other traits. When comparing the trimmed Wood Island SBC (<60 cm) to the control SBC, we observed a significantly higher mean blade length (37%), blade basal width (75%), blade mid width (52%), blade distal width (16%), blade weight (144%), stipe length (57%), stipe diameter (63%), and stipe weight (28%) (Table S2). There were no significant differences for the other traits.

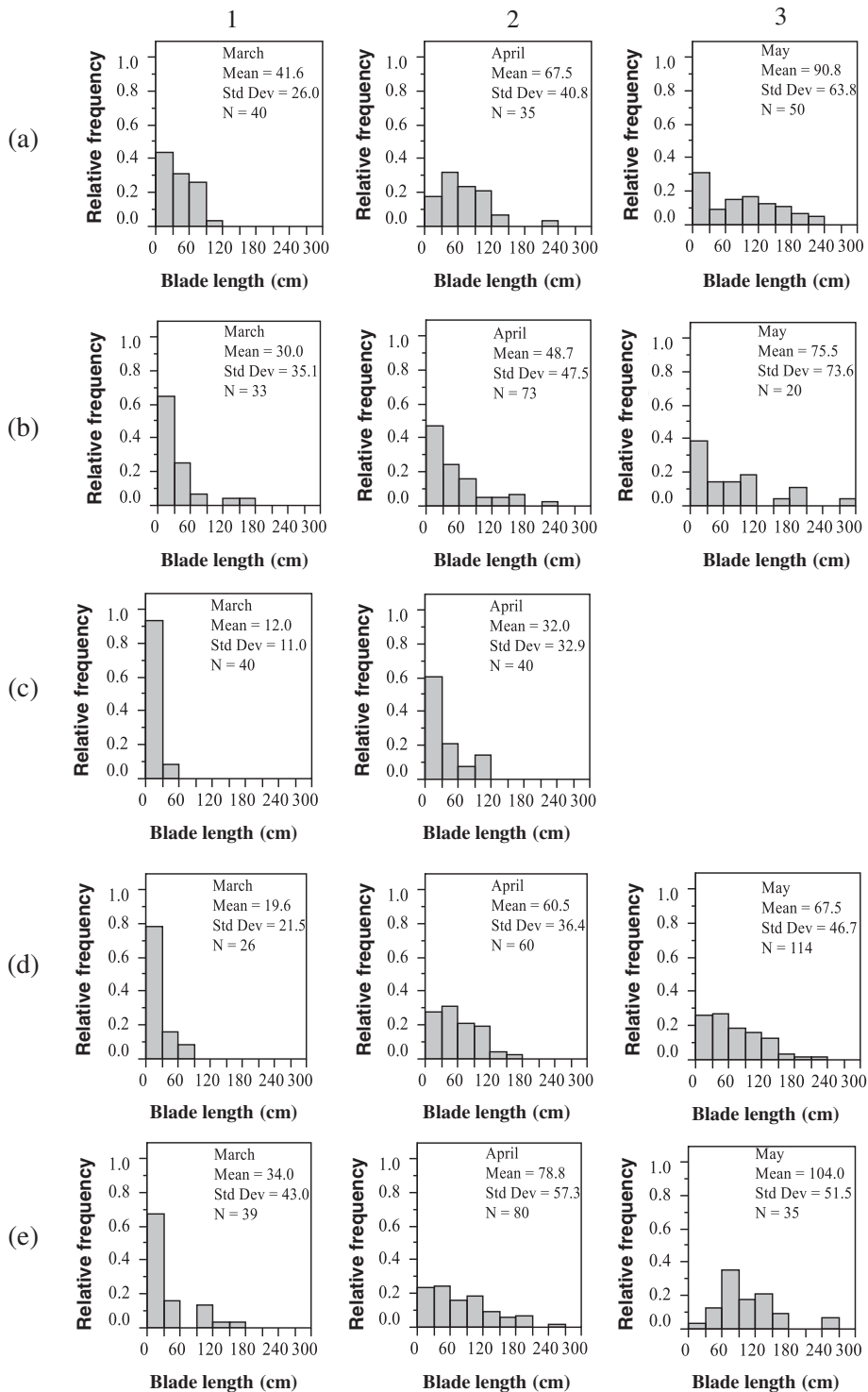
No significant morphological differences were observed between trimmed and control blades in the LBC from Brothers Island. However, most of the morphological characteristics of trimmed SBC from Brothers Island were higher than those from the control sections: mean blade length (42%), basal width (113%), mid-width (145%), blade weight (300%), stipe length (151%), stipe diameter (67%), and stipe weight (233%). The Cow Ledge site was not analyzed for specific morphological differences due to a low sample size ( $n < 20$ ) in each size class.

## 3.3 | Composition

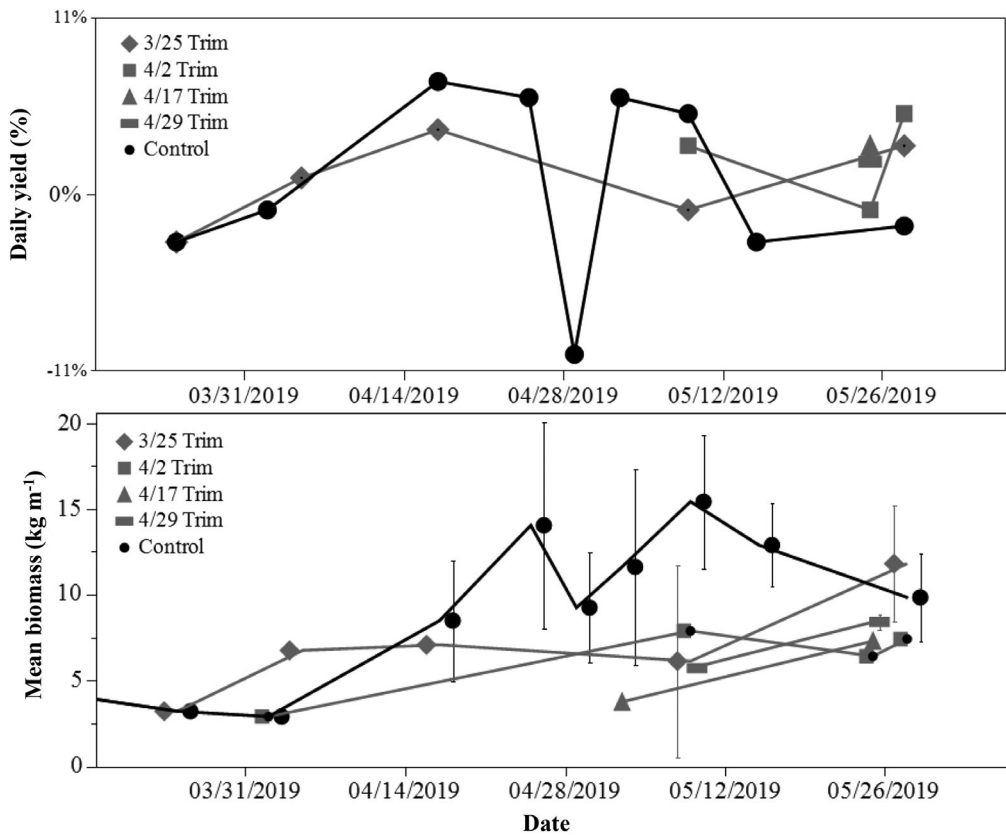
No significant differences were observed in the %C, %N, δ<sup>13</sup>C, or δ<sup>15</sup>N of the trimmed LBC from Wood Island (Table S2). Trimmed thalli in the LBC at Brothers Island had significantly lower %C and δ<sup>13</sup>C in their blades. The SBC in the trimmed sections at Wood Island had a 9% higher %C, a 19% higher C:N (16%), and 35% higher δ<sup>15</sup>N in their blades than the SBC blades from the control sections. The %C of the trimmed SBC at Brothers Island was also 9% higher than the control. No significant differences in NRA were observed between individuals in the treatment or control group, regardless of length class or site.

## 3.4 | Biomass and daily yield

We analyzed mean biomass and daily yield for the control and trimmed sections at Wood Island in 2019 because this site-year combination had the most consistent biomass measurements (winter-early spring conditions in Maine precluded consistent visits to other sites Figure 5; Table S3). We were able to measure biomass 12 times at this site in 2019: sampling approximately every 4–15 days from March to June 2019. The highest observed daily yield of the control group (6–7% day<sup>-1</sup>) was observed between mid-April and early May. After this point, daily yield of the control group was negative (–2 to –3% day<sup>-1</sup>). The trimmed sections, in contrast, exhibited a mostly



**FIGURE 4** Un-trimmed *Saccharina latissima* blade lengths (cm) at the study sites in 2018 and 2019. Rows are ordered by year and site: A) Brothers Island in 2019, B) Cow Ledge in 2018, C) Cow Ledge in 2019, D) Wood Island in 2018, and E) Wood Island in 2019. Columns are in ordered by month: 1) March, 2) April, and 3) May. Means and standard deviations are rounded to the nearest tenth

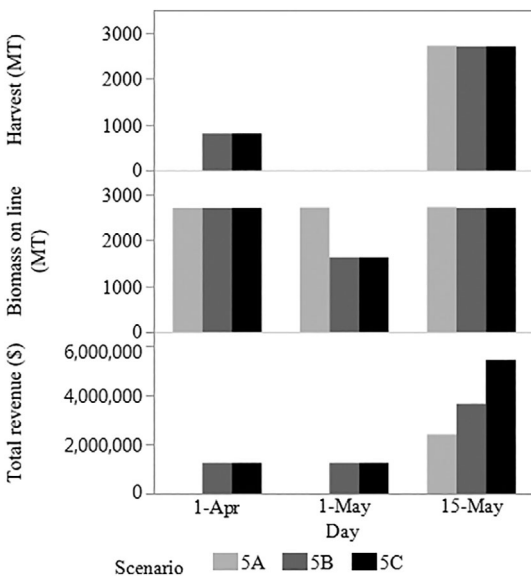


**FIGURE 5** Measured *Saccharina latissima* biomass ( $\text{kg m}^{-1}$ ) and daily yield for control and trimmed groups at Wood Island, Spring 2019. The lines represent different trimming treatments, and the points indicate sampling events. The steep drop in daily yield of the control group in late April 2019 was a storm that dislodged kelp off the longline. Error bars are standard deviation

positive daily yield through the end of the season ( $-1-5\% \text{ day}^{-1}$ ). The mean daily yield of all the trimmed sections throughout the season was  $2.25\% \text{ day}^{-1}$ , and the mean daily yield resulting from a trim administered on April 17th was 3% (Table S3).

### 3.5 | Biomass production and harvesting model

Using Maine's forecasted 2,035 production of 2,722 MT of seaweed (Piconi et al., 2020), the model predicts that trimming could result in an additional \$3 million in revenue for the industry if the maximum price per tonne (\$1,540) is assigned to the early season and late season harvests (Scenario 5C; Figure 6). Using the 2019 production reported for Maine ( $147 \text{ WW MT year}^{-1}$ ), the model estimates that late-season erosion and sloughing result in approximately \$4,700 of lost revenue when kelp is sold at the lowest reported price (\$880; Table S4, Scenario 3A). If 30% of the kelp is harvested via trimming on April 1, and no price premium is associated with the sale of early-season kelp, then the subsequently reduced growth rate from trimming (3%) results in approximately \$4,300 of lost revenue (Scenario 4A). When the highest price per MT (\$1,540) is assigned to the early season kelp, then the model predicts that early-season trimming would result in an additional \$17,293 of revenue, even if the final harvest is still assigned the lowest price per MT (Scenario 4B). If all the kelp produced were assigned the highest price, the model predicts that an additional \$40,000 in revenue would be captured by trimming that maintained a 3% daily yield until May 15.



**FIGURE 6** Forecasted harvest, biomass, and total revenue for Scenario 5A – 5C of *Saccharina latissima* biomass production model. Scenario 5A shows increased production in 2035 (2722 MT total) and a harvest on May 15 with - 3% daily yield (DY) May 1 -15. Scenario 5B shows increased production in 2035, removal of 30% biomass on April 1 with 3% DY after trim, a high sale price (\$1540 WW t<sup>-1</sup>) for April 1 harvest and low sale price (\$880 WW t<sup>-1</sup>) for May 15 harvest. Scenario 5C shows increased production in 2035, removal of 30% biomass on April 1 with 3% DY after trim, and a high sale price (\$1540 WW t<sup>-1</sup>) for April 1 and May 15 harvest

## 4 | DISCUSSION

### 4.1 | Morphology

Our hypothesis that trimmed kelp blades would grow wider than the control kelp blades in response to the injury from trimming was not supported. No significant differences in basal or mid-region blade width were observed between the trimmed and control blades in the LBC. We did, however, observe a significant difference in the stipe morphology between the trimmed and control thalli in the LBC at Wood Island. The stipes of the trimmed blades were significantly longer, thicker, and heavier than the stipes of the control blades.

There are several possible explanations for the longer, thicker, and heavier stipes. One reason might be that the removal of the distal end of the blade altered the hydrodynamic forces on the blade and the stipe. Johnson and Koehl (1994) observed that drag coefficients on wild *N. luetkeana* varied with blade shape and that kelp compensated for higher drag coefficients with stipe elongation and thickening to maintain elastic strain similarity. Wernberg and Vanderklift (2010) showed that elongation and thickening of stipes can even occur in response to short-term fluctuations in wave exposure. It is also possible that trimming triggered a shift in the allocation of photosynthate and nutrients between blade and stipe, in which a greater quantity than normal was sent to the stipe. Under normal circumstances, *Nereocystis* sp. stipes receive a minimal amount of photosynthate and are not dependent on translocated materials (Nicholson, 1970; Nicholson & Briggs, 1972). However, two-way translocation of organic material has been observed between mature *Macrocystis* blades and stipes (Parker, 1963, 1965; Sargent & Lantrip, 1952). Increased delivery of photosynthate or nutrients to the stipe following distal-end trimming cannot be determined with the results of this study, but it could be further explored by quantifying the %C, %N in the stipes before and after trimming, or with the use of <sup>14</sup>C-labeled products as demonstrated by Parker (1965). Genetics are an additional factor influencing kelp blade and stipe morphology, so incorporating genotype investigations into future studies may also shed additional light on this observed response to trimming. From the perspective of the kelp farmer, substantially longer, thicker, and heavier stipes can lead to issues of entanglement and floating stipes on the farm, so additional characterization of the potential relationship between distal-end trimming and stipe growth is important.

Several studies have promoted staggered harvesting to mitigate light or nutrient shading (Bak et al., 2018; Gao, Endo, et al., 2013; Grandforf Bak, 2019; Sanderson, Dring, Davidson, & Kelly, 2012; Scoggan et al., 1989; van den Burg, van Duijn, Bartelings, van Krimpen, & Poelman, 2016), which is also common practice in parts of Asia. We

observed evidence that distal-end trimming affected adjacent blades in the SBC. The SBC individuals in the trimmed sections had longer, wider, and heavier blades than those in the control sections. Their stipes were also longer, thicker, and heavier. The starting density of sporophytes on the lines was relatively high, so before trimming, we suspect that the SBC may have been receiving insufficient light or nutrients. When trimming removed biomass, this might have allowed increased light and nutrients to reach the shorter sporophytes, enabling them to grow longer and wider than the SBC sporophytes in the control sections. We did not directly measure the change in light or nutrient availability after trimming, but this effect has been previously documented by Tseng (1962, 1981, 1986), Wu and Zheng (1981), and Scoggan et al. (1989).

## 4.2 | Composition

We hypothesized that trimmed blades would have a lower %C and  $\delta^{13}\text{C}$  resulting from the loss in blade photosynthetic area. The trimmed LBC from Brothers Island did indeed have a significantly lower mean %C and  $\delta^{13}\text{C}$  than the control LBC in the control sections. In contrast, the mean %C and  $\delta^{13}\text{C}$  of trimmed blades were not significantly different from the control at Woods Island. We also observed evidence that biomass removal via trimming affected the composition of the adjacent SBC. At both sites, the SBC in the trimmed sections had a significantly higher %C than the control sections, which would support the notion that more light and nutrients were available to these sporophytes after trimming the LBC. Interestingly, the site variability in carbon content of the trimmed LBC matched the difference in stipe morphology between the two sites. However, linear regression analyses showed little relationship between LBC stipe morphology, %C, and  $\delta^{13}\text{C}$  at either site. Another possibility is that trimming changed the floating angle of the kelp and its access to light. Wu and Zheng (1981) observed that distal-end trimming changed the floating angle of the *S. japonica* blades (from  $8^\circ$  to  $27^\circ$  in  $5\text{ cm s}^{-1}$  current), which resulted in better lighting of the blade and higher photosynthetic activity. We did not attempt to measure a potential change in floating angle, but future studies could build on the results presented here by incorporating this measurement. A final explanation for the incongruency of %C and  $\delta^{13}\text{C}$  in the trimmed LBC between sites could be disparate environmental conditions between the sites.

Our hypothesis that blades in the trimmed LBC would have lower %N and  $\delta^{15}\text{N}$  than the control resulting from the loss of available tissue for nutrient uptake was not supported. Additionally, we hypothesized that NRA in the remaining thallus would be elevated as the kelp compensated for the loss of nutrient-acquiring blade area, but this was not supported either. The lack of different %N,  $\delta^{15}\text{N}$ , and NRA in the trimmed LBC suggests that trimming the blade down to 60 cm may not result in physiologically induced nutrient stress on the remaining *S. latissima* thallus. However, we recommend further assessment of this trimming length in regions with dissimilar environmental conditions because NRA, %N, and  $\delta^{15}\text{N}$  in algae are highly influenced by ambient nutrient levels, irradiance, and temperature (Chapman, 1978; Davison & Stewart, 1984; Peterson & Fry, 1987).

## 4.3 | Daily yield

Our hypothesis that distal-end trimming would result in reduced daily yields from the trimmed sections was not supported. Rather, the late-season negative daily yield we observed in the control group ( $-2$  to  $-3\%$   $\text{day}^{-1}$ ) and mostly positive daily yield observed in the trimmed groups ( $-1$  to  $5\%$   $\text{day}^{-1}$ ) suggest that trimming facilitates the capture kelp distal biomass that would otherwise be fouled or lost to the environment. Routine and substantial loss of cultivated seaweed biomass has been shown to occur through dislodgement, thalli breakage, and seasonal erosion of distal tissue (Buck & Buchholz, 2005; Peteiro, Salinas, Freire, & Fuertes, 2006; Zhang et al., 2012). At our sites, it appears that the distal-end trimming helped to prevent biomass loss from both dislodgement and erosion of the LBC.

The case for retaining thalli that would otherwise be dislodged or broken during a storm is most compelling at Wood Island in April 2019. On April 25, 2019, a mean biomass of 14.0 ( $\pm 6.0$ ) WW kg m<sup>-1</sup> was calculated for the Wood Island site. Then on the night of April 26, a powerful Nor'easter moved through the region which produced wind gusts up to 17.4 m s<sup>-1</sup> (62.6 km hr<sup>-1</sup>) within a 5-min period at the closest weather station (Portland Jetport). Approximately 53 mm of precipitation in 24 hr was recorded at the Portland Jetport. At the UNE weather station near Wood Island, approximately 33 mm of precipitation was recorded in a 12-hr period and 44 mm in 24 hr. These conditions, likely in combination with large waves, resulted in the considerable loss of kelp from the Wood Island site. On April 29, just 4 days after the previous biomass measurement, the mean biomass was only two-thirds (9.3 [ $\pm 3.2$ ] WW kg m<sup>-1</sup>) of the prior measurement. The sampling interval of the trimmed section biomass for Wood Island is, unfortunately, not conducive to direct comparison for that short window. However, the mean biomass for kelp trimmed earlier in the spring during a 3-week window including the storm only declined by 13% (7.08–6.13 [ $\pm 5.6$ ] WW kg m<sup>-1</sup>) and the daily yield ranged from -1 to 4% day<sup>-1</sup>. This is an indication that the distal-end trimming can significantly reduce risk for kelp farmers as it allows farmers to reap biomass that would otherwise be lost during extreme weather events.

In addition to severe weather that results in biomass loss, blade erosion can also lead to reduced daily yields in the late spring. Wild Laminariales commonly shed up to 25% of their mass from the distal blade in the late spring or summer, and this, combined with a decline in new growth, results in a “seasonally determined negative length growth” for many kelp species (Boderskov et al., 2016; Tseng, 1986). We posit that this erosion contributes to the decline in daily yield observed in the control sections at Wood Island in mid- and late May 2019, although some additional dislodgement or breakage of the LBC may have also occurred during this time. Encouragingly, the daily yield of the trimmed sections during this period was higher than the control and the rates are generally positive. Based on the increased SBC blade and stipe weight in the trimmed sections, we venture that these positive daily yields may be associated with reduced erosion of the LBC and growth of the SBC without erosion. Additional parsing of the relative contributions of each of these factors was beyond the scope of this study, but our results concur with previous studies promoting the use of distal-end trimming to extend the kelp growout season (Bak et al., 2018; Gao, Endo, et al., 2013; Sanderson et al., 2012; Scoggan et al., 1989; van den Burg et al., 2016).

Furthermore, the comparison of the daily yield associated with specific trimming time suggests that there may be an optimal window for distal-end trimming based on the ambient water temperature at the farm. Scoggan et al. (1989), who examined trimming practiced on *S. japonica* farms in China, also concluded that timing the trimming with water temperature may be important. They observed that the yields of *S. japonica* were highest if blade tip cutting occurred when seawater temperatures were 5–6°C; ostensibly, because nutrients had accumulated in the distal end, and the remaining blades received more light, which supported growth (Scoggan et al., 1989). Trimming blade tips when the water was <5°C was ineffective because there was insufficient nutrient content in the tips and trimming once the water temperature surpassed 6°C was ineffective because thalli overcrowding on the line resulted in insufficient light, photosynthesis, and accumulation of photosynthates (Scoggan et al., 1989). We suspect that the observation from Scoggan et al. (1989) may hold for *S. latissima* farms in the WGoM. For instance, at Wood Island, when trimming was conducted in late March, the calculated daily yield 4 weeks later in mid-April was 4% day<sup>-1</sup> for the trimmed group and 7% day<sup>-1</sup> for the control group. However, when trimming occurred in early to late April, the calculated daily yield was -1 to 3% day<sup>-1</sup> for the trimmed groups and -2 to -3% day<sup>-1</sup> for the control group. The highest daily yields observed from the trimmed kelp in the present study were measured following trims made before the end of April 2018 and 2019, when the water temperature was between 5 and 6°C. More observations linking water temperature, daily yield, and the timing of distal-end trimming can help to confirm this relationship for the WGoM.

#### 4.4 | Production and harvesting model

We sought to evaluate the trade-offs of an expanded *S. latissima* harvest season with smaller, more frequent harvests with a relatively simple biomass and harvesting model. The results of this modeling effort indicate that the

potential economic gains from distal-end trimming depend on a price premium for the trimmed kelp. Scenario 4A in our model showed that at current U.S. production rates, distal-end trimming in early April results in a loss of approximately \$4,300 if all the kelp is sold at the lowest price per tonne (\$880 MT<sup>-1</sup> WW). In this scenario, the combination of the short-term reduction in daily yield following trimming and a flat price for the *S. latissima* biomass does not support the incorporation of distal-end trimming into current farming practices if the purpose of trimming is simply to reduce the risk of losing product during storms. Moreover, the real financial loss is likely greater because the biomass and production model do not consider the additional, and potentially considerable (Scoggan et al., 1989), labor costs of trimming.

Conversely, if a price premium can be obtained for trimmed kelp, then the model predicts financial gains from the trimming practice. We considered two obvious ways that the price premium could emerge. In a supply-limited market or seasonally limited market, kelp biomass harvested in April could demand a higher price per tonne before the mid-May harvest significantly increases market supply. Scenario 4B demonstrates that an early-season price premium (\$1,540 MT<sup>-1</sup> WW) could result in an additional \$17,000 in revenue at current U.S. production rates and \$1.2 million at forecasted production for 2035. Although this forecast is encouraging, the current U.S. market for raw seaweed has relatively high price elasticity (i.e., demand for seaweed, measured in \$ kg<sup>-1</sup>, does not change much with supply) so a large shift in this market would be required to obtain these financial gains from distal-end trimming. A second possibility is that price premiums emerge for *S. latissima* that is more tender and flavorful (Fossberg et al., 2018). Tenderness and blade morphology is already a central factor driving price in the more established Asian seaweed markets (Gao, Agatsuma, & Taniguchi, 2013; Kawashima, 1984, 1993; Mairh, Ohno, & Matsuoka, 1991; Peteiro & Freire, 2011). In Japan, *U. pinnatifida* thalli harvested during their growth phase typically sell for five times more than the regular-priced adult thalli (Gao, Endo, et al., 2013); and thalli tenderness presumably factors into this consumer preference. The results of our field experiments with *S. latissima* illustrate the potential of distal-end trimming to promote the growth of the SBC, and because the SBC is likely more tender than the LBC at final harvest, it could also exact a price premium in a market that favors tender thalli. Ultimately, if all kelp biomass harvested from U.S. farms employing distal-end trimming were sold at the highest market price considered in the biomass and production model (\$1,540 MT<sup>-1</sup> WW), then this would result in an additional \$40,000–\$3 million in revenue.

## 5 | CONCLUSION

Given the recent boom in the cultivation of *S. latissima*, additional knowledge about the costs and benefits of distal-end trimming on this species is especially timely and important. Previous studies have shown that removing the distal-end of long blades can offer biological benefits like increased sunlight and nutrients for the remaining thalli. Our study confirms these biological benefits for *S. latissima*. When compared to the control group, the thalli in proximity to the trimmed blades had wider, longer, and heavier blades and stipes, and greater %C in their blade tissue. The potentially negative impacts of distal-end trimming on kelps can vary with species, season, the location of the trim relative to the growth region, and the ambient environmental conditions at the cultivation site. However, at *S. latissima* farms in the WGoM, trimming blades to 60 cm in late March or April does not appear to cause stress to the remaining blade. We did not observe differences in the %N, NRA, C:N ratio,  $\delta^{15}\text{N}$ , or width of the trimmed blades that would suggest trimming-induced nutrient limitation or an injury-related growth response. Furthermore, trimming the distal ends of *S. latissima* shows promise as a tool to help farmers in the WGoM maintain positive daily yields into late spring and capture biomass that would otherwise be naturally lost or dislodged during storms. Our biomass and production model illustrate that the potential economic benefits of this practice are highly dependent on production scale and price premiums for early season kelp, both of which are largely speculative for the present-day European and North American cultivated kelp markets.

## ACKNOWLEDGMENTS

Field support was provided by the University of New England Marine Science Center Staff (Addie Waters, Tim Arenti, Adam St. Gelais, and Liz Johndrow) and Tollef Olson. We thank the Byron Lab students who assisted with sample processing and analysis, especially Mary Hollandbeck, Alex Geisser, Kyle Brennan, Emma Jones, and Everett Pierce. We also thank Wei Lu for his help processing the SSRD data. We are grateful to Charlie Yarish, Simona Augyte, Susan Brawley, and two anonymous reviewers for their thorough editing suggestions. This activity was supported by National Science Foundation award #IA-1355457 to Maine EPSCoR at the University of Maine and USDA NESARE Graduate Student Award # GNE18-172-32231.

## ORCID

Gretchen S. Grebe  <https://orcid.org/0000-0003-4793-0312>

Carrie J. Byron  <https://orcid.org/0000-0003-3820-7392>

Damian C. Brady  <https://orcid.org/0000-0001-9640-2968>

Adam T. St. Gelais  <https://orcid.org/0000-0002-9007-0007>

Barry A. Costa-Pierce  <https://orcid.org/0000-0003-3059-1828>

## REFERENCES

- 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.
- Bak, U. G., Mols-Mortensen, A., & Gregersen, O. (2018). Production method and cost of commercial-scale offshore cultivation of kelp in The Faroe Islands using multiple partial harvesting. *Algal Research*, 33, 36–47.
- Borderskov, T., Schmedes, P., Bruhn, A., Rasmussen, M., Nielsen, M., & Pedersen, M. (2016). The effect of light and nutrient availability on growth, nitrogen, and pigment contents of *Saccharina latissima* (Phaeophyceae) grown in outdoor tanks, under natural variation of sunlight and temperature, during autumn and early winter in Denmark. *Journal of Applied Phycology*, 28, 1153–1165.
- Buck, B. H., & Buchholz, C. M. (2005). Response of offshore cultivated *Laminaria saccharina* to hydrodynamic forcing in the North Sea. *Aquaculture*, 250, 674–691.
- Burnett, N. P., & Koehl, M. A. R. (2019). Mechanical properties of the wave-swept kelp *Egregia menziesii* change with season, growth rate and herbivore wounds. *Journal of Experimental Biology*, 222, jeb190595.
- Camia, A., Robert, N., Jonsson, R., Pilli, R., García-Condado, S., López-Lozano, R., van der Velde M., Ronzon T., Gurria P., M'Barek R., Tamosiunas S., Fiore G., Araujo R., Hoepffner N., Marelli L., & Giuntoli, J. (2018). Biomass production, supply, uses and flows in the European Union. First results from an integrated assessment, EUR 28993 EN, Publications Office of the European Union, Luxembourg, 2018. JRC109869. doi: <https://doi.org/10.2760/539520>.
- Chapman, A. R. O. (1978). Effects of nitrate concentration on the growth and physiology of *Laminaria saccharina* (Phaeophyta) in culture. *Journal of Phycology*, 14, 195–198.
- Davison, I. R., & Stewart, W. D. P. (1984). Studies on nitrate reductase activity in *Laminaria digitata* (Huds.) Lamour. II: The rôle of nitrate availability in the regulation of enzyme activity. *Journal of Experimental Marine Biology and Ecology*, 79(1), 65–78.
- Egan, B., & Yarish, C. (1990). Productivity and life history of *Laminaria longicuris* at its southern limit in the Western Atlantic Ocean. *Marine Ecology Progress Series*, 1990, 263–273.
- EMODnet (The European Marine Observation and Data Network). (2021). Retrieved Jan 10, 2021 from <https://www.emodnet-humanactivities.eu/view-data.php>.
- FAO. (2020). The state of world fisheries and aquaculture 2020. Sustainability in action. Rome: FAO. <https://doi.org/10.4060/ca9229en>
- Fortes, M. D., & Lüning, K. (1980). Growth rates of North Sea macroalgae in relation to temperature, irradiance and photoperiod. *Helgoländer Meeresuntersuchungen*, 34, 15–29.
- Fossberg, J., Forbord, S., Broch, O. J., Malzahn, A. M., Jansen, H., Handå, A., ... Olsen, Y. (2018). The potential for upscaling kelp (*Saccharina latissima*) cultivation in salmon-driven integrated multi-trophic aquaculture (IMTA). *Frontiers in Marine Science*, 5, 418.
- Fredriksson, D. W., Dewhurst, T., Drach, A., Beaver, W., Gelais, A. T. S., Johndrow, K., & Costa-Pierce, B. A. (2020). Hydrodynamic characteristics of a full-scale kelp model for aquaculture applications. *Aquacultural Engineering*, 90, 102086.
- Gao, X., Agatsuma, Y., & Taniguchi, K. (2013). Effect of nitrate fertilization of gametophytes of the kelp *Undaria pinnatifida* on growth and maturation of the sporophytes cultivated in Matsushima Bay, northern Honshu, Japan. *Aquaculture International*, 21, 53–64.



- Gao, X., Endo, H., Yamana, M., Taniguchi, K., & Agatsuma, Y. (2013). Compensation of the brown alga *Undaria pinnatifida* (Laminariales; Phaeophyta) after thallus excision under cultivation in Matsushima Bay, northern Japan. *Journal of Applied Phycology*, 25, 1171–1178.
- Gerard, V. A. (1987). Hydrodynamic streamlining of *Laminaria saccharina* Lamour. In response to mechanical stress. *Journal of Experimental Marine Biology and Ecology*, 107, 237–244.
- Grandforf Bak, U. G. (2019). Seaweed cultivation in the Faroe Islands: An investigation of the biochemical composition of selected macroalgal species, optimised seeding technics, and open-ocean cultivation methods from a commercial perspective [Doctoral dissertation, Technical University of Denmark]. Retrieved from <https://core.ac.uk/reader/200211710>.
- Grebe G. S., Byron C. J., Brady D. C., Geisser A. H., Brennan K. D. (2021). The nitrogen bioextraction potential of nearshore *Saccharina latisima* cultivation and harvest in the Western Gulf of Maine. *Journal of Applied Phycology*, <https://doi.org/10.1007/s10811-021-02367-6>.
- Grebe, G. S., Byron, C. J., Gelais, A. S., Kotowicz, D. M., & Olson, T. K. (2019). An ecosystem approach to kelp aquaculture in the Americas and Europe. *Aquaculture Reports*, 15, 100215.
- Handå, A., Forbord, S., Wang, X., Broch, O. J., Dahle, S. W., Størseth, T. R., ... Skjermo, J. (2013). Seasonal- and depth-dependent growth of cultivated kelp (*Saccharina latisima*) in close proximity to salmon (*Salmo salar*) aquaculture in Norway. *Aquaculture*, 414–415, 191–201.
- Hurd, C. L. (2000). Water motion, marine macroalgal physiology, and production. *Journal of Phycology*, 36, 453–472.
- Hurd, C. L., Berges, J. A., Osborne, J., & Harrison, P. J. (1995). An in vitro nitrate reductase assay for marine macroalgae: Optimization and characterization of the enzyme for *Fucus gardneri* (Phaeophyta). *Journal of Phycology*, 31(5), 835–843.
- Hymanson, Z. P., Reed, D. C., Foster, M. S., & Carter, J. W. (1990). The validity of using morphological characteristics as predictors of age in the kelp *Pterygophora californica* (Laminariales, Phaeophyta). *Marine Ecology Progress Series*, 59, 295–304.
- Johnson, A. S., & Koehl, M. (1994). Maintenance of dynamic strain similarity and environmental stress factor in different flow habitats: Thallus allometry and material properties of a giant kelp. *Journal of Experimental Biology*, 195, 381–410.
- Kawashima, S. (1984). Kombu cultivations in Japan for human foodstuff. *Japanese Journal of Phycology*, 32, 379–394.
- Kawashima, S. (1993). Cultivation of the brown alga, *Laminaria* “kombu”. In M. Ohno & A. T. Critchley (Eds.), *Seaweed cultivation and marine ranching* (pp. 25–40). Yokosuka, Kanagawa, Japan: Japan International Cooperation Agency (JICA).
- Kim, J., Stekoll, M., & Yarish, C. (2019). Opportunities, challenges and future directions of open-water seaweed aquaculture in the United States. *Phycologia*, 58(5), 446–461.
- Levene, H. (1960). Robust tests for equality of variances. In I. Olkin, S. G. Ghurye, W. Hoeffding, W. G. Madow, & H. B. Mann (Eds.), *Contributions to probability and statistics* (pp. 278–292). Stanford, California: Stanford University Press.
- Levitt, G. J., Anderson, R. J., Boothroyd, C. J. T., & Kemp, F. A. (2002). The effects of kelp harvesting on its regrowth and the understorey benthic community at danger point, South Africa, and a new method of harvesting kelp fronds. *South African Journal of Marine Science*, 24(1), 71–85.
- Mairh, O. P., Ohno, M., & Matsuoka, M. (1991). Culture of brown alga *Laminaria japonica* (Phaeophyta, Laminariales) in warm waters of Shikoku, Japan. *Indian Journal of Marine Sciences*, 20, 55–60.
- MEDMR (Maine Department of Marine Resources) (2019). *Maine aquaculture harvest data: marine algae (2015 - 2019)*, <https://www.maine.gov/dmr/aquaculture/harvestdata/index.html/> (Accessed 1 May 2020).
- Nicholson, N. L. (1970). Field studies on the giant kelp *Nereocystis*. *Journal of Phycology*, 6, 177–182.
- Nicholson, N. L., & Briggs, W. R. (1972). Translocation of photosynthate in the brown alga *Nereocystis*. *American Journal of Botany*, 59, 97–106.
- Parker, B. C. (1963). Translocation in the giant kelp *Macrocystis*. *Science*, 140, 891–892.
- Parker, B. C. (1965). Translocation in the giant kelp *Macrocystis* I. rates, direction, quantity of  $C^{14}$ -labeled products and fluorescein. *Journal of Phycology*, 1, 41–46.
- Peteiro, C., & Freire, Ó. (2011). Offshore cultivation methods affect blade features of the edible seaweed *Saccharina latisima* in a bay of Galicia, Northwest Spain. *Russian Journal of Marine Biology*, 37, 319–323.
- Peteiro, C., Salinas, J. M., Freire, Ó., & Fuentetaja, C. (2006). Cultivation of the autochthonous seaweed *Laminaria saccharina* off the Galician coast (NW Spain): Production and features of the sporophytes for an annual and biennial harvest. *Thalassas*, 22, 45–52.
- Peterson, B. J., & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual Review of Ecological Systems*, 18, 293–320.
- Piconi, P., Veidenheimer, R., & Chase, B. (2020). *Edible seaweed market analysis*. Rockland: Island Institute. Retrieved from <http://www.islandinstitute.org/edible-seaweed-market-analysis-2020>
- Redmond, S., Green, L., Yarish, C., Kim, J., & Neefus, C. (2014). New England seaweed culture handbook. Retrieved from [https://opencommons.uconn.edu/seagrant\\_weedcult/1/](https://opencommons.uconn.edu/seagrant_weedcult/1/).
- Ricker, W. E. (1979). Growth rates and models. In W. S. Hoar, D. J. Randall, & J. R. Brett (Eds.), *Fish physiology*, Vol. VIII. *Bioenergetics and growth* (pp. 673–743). New York, NY: Academic Press.

- Roland, W. G. (1985). Effects of lamina harvest on the bull kelp, *Nereocystis luetkeana*. *Canadian Journal of Botany*, 63, 333–336.
- Rolin, C., Inkster, R., Laing, J., & McEvoy, L. (2017). Regrowth and biofouling in two species of cultivated kelp in the Shetland Islands, UK. *Journal of Applied Phycology*, 29(5), 2351–2361.
- Royer, M., Larbat, R., Le Bot, J., Adamowicz, S., & Robin, C. (2013). Is the C: N ratio a reliable indicator of C allocation to primary and defence-related metabolisms in tomato? *Phytochemistry*, 88, 25–33.
- Sanbonsuba, Y., Machiguchi, Y., & Saga, N. (1987). Productivity estimation and evaluation of the cultivation factors in bio-mass production of *Laminaria*. *Bulletin of the Hokkaido Regional Fisheries Research Laboratory (Japan)*, 51, 45–50.
- Sanderson, J. C., Dring, M. J., Davidson, K., & Kelly, M. S. (2012). Culture, yield, and bioremediation potential of *Palmaria palmata* (Linnaeus) Weber & Mohr and *Saccharina latissima* (Linnaeus) CE lane, C. Mayes, Druehl & GW Saunders adjacent to fish farm cages in Northwest Scotland. *Aquaculture*, 354, 128–135.
- Sargent, M. C., & Lantrip, L. W. (1952). Photosynthesis, growth, and translocation in giant kelp. *American Journal of Botany*, 39, 99–107.
- Savage, C., & Elmgren, R. (2004). Macroalgal (*Fucus vesiculosus*)  $\delta^{15}\text{N}$  values trace decrease in sewage influence. *Ecological Applications*, 14, 517–526.
- Schmitz, K., & Lobban, C. S. (1976). A survey of translocation in Laminariales (Phaeophyceae). *Marine Biology*, 36, 207–216.
- Scoggan, J., Zhimeng, Z., & Feijiu, W. (Eds.) (1989). Culture of kelp (*Laminaria japonica*) in China. In *Food and agriculture organization training manual 89/5 (RAS/86/024)*. Qingdao: China. Retrieved from <http://www.fao.org/3/AB724E/AB724E00.htm>
- Shapiro, S. S., & Wilk, M. B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, 52(3/4), 591–611.
- Thornber, C. S., DiMilla, P., Nixon, S. W., & McKinney, R. A. (2008). Natural and anthropogenic nitrogen uptake by bloom-forming macroalgae. *Marine Pollution Bulletin*, 56, 261–269.
- Tseng, C. K. (1962). Cultivation of *Laminaria japonica* in China. In C. K. Tseng & C. Y. Wu (Eds.), *Manual of haidai (Laminaria japonica Aresch.) cultivation* (pp. 99–112). Beijing, China: Science Press.
- Tseng, C. K. (1981). Commercial cultivation. In C. S. Lobban & M. J. Wynne (Eds.), *The biology of seaweeds*, 17 (pp. 680–725). Berkeley and Los Angeles: University of California Press.
- Tseng, C. K. (1986). *Laminaria* mariculture in China. In M. S. Doty, J. F. Caddy, & B. Santelices (Eds.), *Case studies of seven commercial seaweed resources*. Rome: FAO Fisheries Technical Papers (281). Retrieved from <http://www.fao.org/3/X5819E/x5819e09.htm#3.5%20the%20tip%20cutting%20practice>
- van den Burg, S. W., van Duijn, A. P., Bartelings, H., van Krimpen, M. M., & Poelman, M. (2016). The economic feasibility of seaweed production in the North Sea. *Aquaculture Economics & Management*, 20, 235–252.
- Vettori, D., & Nikora, V. (2017). Morphological and mechanical properties of blades of *Saccharina latissima*. *Estuarine, Coastal and Shelf Science*, 196, 1–9.
- Wernberg, T., & Vanderklift, M. A. (2010). Contribution of temporal and spatial components to morphological variation in the kelp *Ecklonia* (Laminariales). *Journal of Phycology*, 46, 153–161.
- Wu, C. Y. (1962). Growth and development of the sporophyte (of *Laminaria japonica*) in relation to the environmental factors. In C. K. Tseng & C. Y. Wu (Eds.), *Manual of cultivation of haidai (Laminaria japonica)* (pp. 34–71). Beijing, China: Science Press.
- Wu, C. Y., & Zheng, S. Q. (1981). Tip-cutting of fronds as a means of increasing production in *Laminaria* aquaculture. In T. Levring (Ed.), *Proceedings of the Xth International Seaweed Symposium* (pp. 637–642). Berlin: Walter de Gruyter. & Co.
- Yarish, C., Kim, J. K., Lindell, S., & Kite-Powell, H. (2017). Developing an environmentally and economically sustainable sugar kelp aquaculture industry in southern New England: from seed to market. Retrieved from [https://opencommons.uconn.edu/eeb\\_articles/38](https://opencommons.uconn.edu/eeb_articles/38).
- Young, E. B., Lavery, P. S., Van Elven, B., Dring, M. J., & Berges, J. A. (2005). Nitrate reductase activity in macroalgae and its vertical distribution in macroalgal epiphytes of seagrasses. *Marine Ecology Progress Series*, 288, 103–114.
- 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.

## SUPPORTING INFORMATION

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

**How to cite this article:** Grebe, G. S., Byron, C. J., Brady, D. C., St. Gelais, A. T., & Costa-Pierce, B. A. (2021). The effect of distal-end trimming on *Saccharina latissima* morphology, composition, and productivity. *Journal of the World Aquaculture Society*, 52(5), 1081–1098. <https://doi.org/10.1111/jwas.12814>