





Communication

# Does Seawater Nitrogen Better Predict the Baseline Farmed Yield for Sugar Kelp (*Saccharina latissima*) Rather than the Final Yield?

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**Abstract:** Recent interest in scaling commercial kelp industries in Western cultures is juxtaposed by the apparent challenges in achieving more consistent and predictable yields. As such, site-level factors are a dominant and recurring conversation amongst stakeholders. The availability of seawater nitrogen (nitrate, ammonium, total N) can be highly variable across space and time and is often one of the top concerns for site selection and permitting. This study questions the relative importance of nitrogen availability on the yield of *Saccharina latissima* (sugar kelp) across five commercial farms on the U.S. East and West Coasts over two seasons, highlighting the relative influence of other interacting factors (i.e., farm design). We hypothesized that nitrate would strongly correlate with the harvested yield. Our results show significant spatial and annual variability in the kelp yield and ambient nutrients across and within farms, but with weak covariance. Standard linear regression suggests that seawater nitrogen is a poor explanatory factor for kelp yield, explaining 11.0% of the variation around the mean compared to the line spacing (explaining 26.1%) and the interaction between the total N and the line spacing (explaining 50.0%). Quartile regression, however, suggests that total N alone, is the strongest predictor of a lower threshold in terms of the yield (0.10 quartile,  $r^2 = 0.431$ ) relative to the median (0.50 quartile,  $r^2 0.081$ ). As such, seawater nitrogen may be a more useful metric in predicting baseline kelp yields rather than realized yields, and production above that baseline is likely more dependent on other factors that may or may not interact with seawater nitrogen.

**Keywords:** kelp; seaweed; nitrogen; aquaculture; mariculture; line spacing; biomass



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## 1. Introduction

The successful development of kelp farming involves a multifaceted approach that encompasses understanding the various challenges and opportunities within the industry. Key components include familiarity with the permit process, securing a market or buyer for the produced biomass, and choosing a suitable site that can support efficient biomass production. A critical aspect of site selection is long-term planning and sustainability, which necessitates consideration of regulatory, social, economic, and biological factors to enhance the probability of success [1–4]. This comprehensive approach includes the costs associated with farm development and operation, the potential impacts of climate change, and the interaction of cultivated crops with the surrounding environment at the chosen site [5–7].

Productivity variations in kelp farming, as well as in other seaweed farms, result from the complex interplay of both natural and anthropogenic factors. These influential factors consider a range of elements, including herbivory [8], the presence of pathogens [9], and environmental parameters, namely water temperature, salinity, water flow, light availability,

and nutrient levels [10–14]. Among these factors, nitrogen stands out as a crucial nutrient in the context of kelp growth. Nitrogen's significance arises from its central role in chlorophyll production and the formation of essential cellular components. Moreover, nitrogen serves as a vital nutrient, essential for the synthesis of amino acids, proteins, and nucleic acids, which collectively form the fundamental building blocks of kelp tissues [3,4,15–17].

Nitrogen availability in the ocean, particularly in temperate regions, follows seasonal cycles. Nitrogen levels tend to reach their maxima in winter, with concentrations ranging from 5 to 40 micromolar ( $\mu\text{M}$ ) or more, depending on the geographic location. While, in the spring, as the light and temperature increase, nitrogen becomes limited due to phytoplankton blooms at the surface [5,18–20]. Studies conducted on wild populations underscore the relevance of nitrogen in shaping the growth, distribution, and ecological interactions of kelp. For example, when nitrogen availability was limited, wild kelp exhibited reduced growth rates, smaller and thinner fronds, and reduced reproductive structures [12,17,21]. Paralleling wild kelp, it could be expected that a shortage of nitrogen (particularly nitrate, as the most energy-efficient form of nitrogen for kelp) could have detrimental consequences for farm sites. In such conditions, farmed kelp can encounter difficulties in achieving robust growth, resulting in stunted development and reduced overall productivity [2,4,18,22]. In mature seaweed industries, for example, kelp cultivation is often concentrated at the mouth of bays, where nutrient delivery is sufficient relative to other areas within the same bay [23–25].

The delivery of nutrients to the biomass, however, can be modified via interactions with the flow. The current understanding of flow dynamics within farms is mostly derived from modeling flow conditions [26–28] and limited field observations from mussel aquaculture [29,30]. These studies demonstrate that farming structures interact with local hydrodynamics to modify the flow and nutrient delivery to farmed biomass, similar to how the biogenic structure alters the flow and nutrients in wild systems [31]. As such, farm production tends to be enhanced at locations with increased nutrients and flow. When selecting sites for commercial farms, selecting for both optimal nutrient supply and optimal flow conditions may not be possible, especially when balancing the distance to the nearest port. A better understanding of the relative importance of nutrient availability versus flow in applied contexts is critical to improve site selection in emergent seaweed industries to promote optimal production and biomass quality.

We present a two-year comparison of biomass yields from five commercial kelp farm sites situated across a broad geographical range, encompassing both the East and West Coasts of the United States. Our aim is to further shed light on the relevance of nitrate only, as a predictor for the selection of suitable kelp farming sites. We compare seawater nitrogen against the line spacing, where modifying the distance between the grow lines should alter the flow conditions within farms. We hypothesize that seawater nitrogen is the dominant factor associated with increased kelp yield and that nitrate is the strongest predictor of this relationship. Our analysis includes the percentage of carbon (%C) and nitrogen (%N), the carbon-to-nitrogen ratio (C:N), and stable isotope signatures ( $\delta^{15}\text{N}$ ) in tissues collected from *Saccharina latissima* (commonly known as sugar kelp) farms. We compare these metrics to the ambient seawater nitrate ( $\text{NO}_3^-$ ) and ammonium ( $\text{NH}_4^+$ ) levels, providing evidence of the varying importance of an adequate nitrogen supply to enhance farmed kelp growth and productivity.

## 2. Materials and Methods

### 2.1. Farm Sites and Timing

Tissue and seawater samples were collected during two consecutive kelp farming seasons (2019–2020 and 2020–2021) at five sugar kelp farms in the United States. One farm was located in Southcentral Alaska (AK) and four farms were located in Connecticut (CT1, CT2), Maine (ME), and Rhode Island (RI). All the kelp farms were positioned in the nearshore and did not include other aquaculture species. The farming methods included a series of long lines or a catenary array. The lines were suspended at 6–7 ft (1.8–2.1 m)

and were spaced between 2.5–50 ft (1.5–15.2 m). All the kelp seeds were planted on the farms between October and December for each season and remained in the water for 150–186 days until maturity and harvest.

For most North American farms, the incremental growth of juvenile sugar kelp is apparent in late January or early February and rapidly begins to accumulate biomass in early March. Harvest often occurs in late May or June. As such, operators typically increase visitations to farms around early March. Since farmers conducted all the sampling and management at each farm, following commercial practices rather than balanced experimental practices, (1) regular sampling of the seawater did not begin until March of each year and (2) the farmer harvested the final biomass when the kelp quality was the best at their site. Therefore, harvest occurred anytime in April, May, or June, depending on the preference of each farmer, for each year (see Table 1). We suggest that this disparity in timing is acceptable for this work because, based on both environmental theory and empirical research, seawater quality metrics are expected to be different across sites, even when each farming operation mirrors each other in terms of time and are within a tighter geographic location due to localized patterns in terms of depth and circulation, the water retention time within different bodies of water, and the dynamics with competing phytoplankton and nutrient drawdown. It is important to note that this work is replicated by site, where the relationship between nitrogen and kelp yield within each site serves as an independent data point that contributes to a continuous dataset, allowing the assessment of how robust seawater nitrogen is in predicting kelp yield for broader site selection purposes.

## 2.2. Seawater Nitrogen

During the active sampling window for each farm, seawater samples were collected once every four weeks using Nutrient Extraction Toolkits, NET© [32], for which the concentrations of nitrate ( $\text{NO}_3^-$ ) and ammonium ( $\text{NH}_4^+$ ) were determined. Samples were collected in triplicate (60 mL/sample) at a depth of 2 to 3 m using a water sampler, matching the depth at which the farmed kelp was deployed. The three replicates spanned the center line of each farm, each month, in relatively even intervals. The samples were immediately filtered (GF/C Whatman, 0.45  $\mu\text{m}$ , 25 mm diameter), stored in HDPE bottles, and maintained in cool, dark conditions during transportation to the shore and immediately frozen ( $-20^\circ\text{C}$ ). Within seven days of each sampling event, the samples were shipped overnight (frozen) to the Mariculture Laboratory at the University of Alaska Fairbanks (UAF) in Juneau for consolidation before being shipped, frozen, to the Nutrient Analytical Facility at UAF in Fairbanks. Samples were stored at  $-20^\circ\text{C}$ , until they were analyzed using a SEAL Analytical QuAatro39 segmented flow autoanalyzer ( $\pm 0.5\%$  measurement error). The samples were processed shortly after arrival at the analytical facility and replicates of the seawater reference materials were routinely run to ensure the accuracy of all the readings. Including the sampling period, the holding time of the seawater samples did not exceed 4.5 months.

Due to the timing of when the project started (March) and the differences in the timing of the harvest, the longest time series water sampling we can assess falls within a two-month window. Because kelp biomass and tissue physiology can reflect a time-averaged response to the ambient environment, the seawater nitrogen data were explored in two ways: seawater sampled only in the month of harvest was established as one observational variable and, then, the average of the seawater data sampled in the month of harvest and in the month prior was calculated as a second observational variable (“two-month average”).

## 2.3. Sampling Biomass

At the time of harvest, the farmers selected the grow lines at approximate, even intervals ( $n = 5$ ) across their farm, to collect biomass samples. Controlled, random selection of the lines was not utilized because preference was given to stratified sampling across the farm and the lines were approximate in interval due to missing lines or seed failure, which should not be recorded as zeros for the biomass in this study. Within the middle 10 m of

each selected grow line, one 50 cm segment was haphazardly identified, from which kelp was removed (cutting at the stipe) and transferred into large mesh bags. Holdfasts were not included. All the samples were collected from the middle of the farm to avoid edge effects, where biomass may be enhanced due to increased water flow. The mesh bags allowed for quick draining and the farmers were asked to shake the bags three times; sample weights were recorded within five minutes after collection on the boat, using a hand-held, digital crane scale to the nearest tenth of a pound. All the data were converted from imperial to metric and reported as kg/m.

#### 2.4. Carbon and Nitrogen

From each farm, one kelp frond was haphazardly selected from each of the 50 cm biomass samples during harvest to determine the C and N content in the kelp tissues ( $n = 5$ ). To collect a sample representative of the harvested biomass (entire blades), we used a corer to recover tissue discs with a diameter of 5 cm from the tip, mid-section, and base of each frond and, then, pooled the subsamples into the kelp blade mean for data analysis. The cores were taken from the midline of the blade, as well as 5–10 cm away from the basal meristem and distal tip, depending on the overall size of the kelp blade. All the discs were patted dry with absorbent paper, dried using silica beads, and shipped to the Mariculture Laboratory at the UAF in Juneau. The samples were screened upon arrival to ensure the absence of fungal development and oven dried at 40 °C for 60 min, which was sufficient to dry the tissues to a constant weight, considering the small biomass and thin blades. Once the samples were completely dry, all the tissue was ground into a homogenous, coarse powder using a BioSpec Mini-Beadbeater and prepared for analysis. Elemental C and N, and the isotopic determination for  $^{13}\text{C}$  and  $^{15}\text{N}$ , was conducted by combustion at the Alaska Stable Isotope Facility, UAF, and Auke Bay Laboratories. The carbon-to-nitrogen (C:N) molar ratios were calculated as proxies for the nutritional status and overall health of the kelp. Approximately 1.0 mg of ground tissue was weighed into tin capsules for analysis, using a Sartorius MC210S microbalance (Sartorius AG, Göttingen, Germany). The elemental composition and stable isotopic analysis were performed using a FlashSmart elemental analyzer, coupled to a Delta V continuous-flow isotope-ratio mass spectrometer (Thermo Scientific, Waltham, MA, USA). Stable isotope values are reported in delta ( $\delta$ ) notation, relative to international standards (atmospheric nitrogen for  $^{15}\text{N}$  and VPDB for  $^{13}\text{C}$ ). The instrument was calibrated for elemental analysis using purified methionine of known % C and % N elemental composition. The isotopic analyses were calibrated using certified isotopic reference materials from the International Atomic Energy Agency and the US Geological Survey. Internal laboratory standards (purified methionine and homogenized Chinook salmon muscle) were used as quality controls and yielded long-term elemental composition precision estimates (S.D.) of  $\pm 0.20\%$  for carbon and  $\pm 0.33\%$  for nitrogen, and long-term isotopic analysis precision estimates of  $\pm 0.12\%$  for carbon and  $\pm 0.13\%$  for nitrogen.

#### 2.5. Statistical Analysis

All analyses were conducted using RStudio [33]. Because the data reflected a mix of normal and non-normal distributions, as well as equal and unequal variances, we used Welch's ANOVA (non-parametric) to test for differences in the mean for seawater nitrogen ( $\text{NO}_3^-$ ,  $\text{NH}_4^+$ , and total N), harvested kelp biomass (kg/m), and tissue chemistry (%C, %N, C:N molar ratio,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$ ) across years, farms, and within farms across years. All post hoc analysis was conducted using a Bonferroni test. Linear regression analyses were conducted to assess the correlative relationship between all the variables, including line spacing, and multiple regression analysis was also used to determine how line spacing interacts with seawater nitrogen to explain the variation in harvested kelp biomass. Additionally, the relationship between seawater nitrogen and harvested biomass was analyzed using quartile regression (at 0.10, 0.25, 0.50, 0.75, and 0.90 quartiles) to assess the relationships between the variables outside of the mean of the data. Although we report

the month when the harvest occurred (see Table 1), we did not include months as interactive factors for formal analysis due to a lack of appropriate replication, it is not possible to delineate site effects from month effects. The data reflected a mix of normal and non-normal distributions, as well as equal and unequal variances; therefore, we used Welch's ANOVA (non-parametric) to explore the differences in seawater nitrogen, harvested biomass, and C and N content across sites, years, and months.

### 3. Results

#### 3.1. Seawater Nitrogen

Broadly, the concentration of seawater nitrate ( $\text{NO}_3^-$ ) was more variable across time and space than ammonium ( $\text{NH}_4^+$ ), where ammonium varied only across farms independent of time (Tables 1 and 2). Nitrate varied significantly across farms, years, and months (Tables 1 and 2), and was lower in 2020 (avg.  $0.36 \pm 0.36 \mu\text{M}$ ) than in 2021 (avg.  $1.14 \pm 1.01 \mu\text{M}$ ). Ammonium did not significantly vary across years (avg.  $1.01 \pm 0.92 \mu\text{M}$  in 2020 versus  $0.81 \pm 0.18 \mu\text{M}$  in 2021) or months (see Table 1). Total seawater nitrogen (total N;  $\text{NO}_3^- + \text{NH}_4^+$ ) was not different across years, but did vary across farms and months (Table 2). Like nitrate, the total N in ambient seawater was associated with the time of harvest for each farm, which was lower across farms in 2020 (avg.  $1.36 \pm 1.16 \mu\text{M}$  versus  $1.95 \pm 1.15 \mu\text{M}$  in 2021).

**Table 1.** Mean values ( $\pm 1$  SD) for all variables observed in this study, across farms and years.

Location	Year	Month	Line Spacing (m)	Biomass (kg/m)	Nitrate ( $\mu\text{M}$ )	Ammonium ( $\mu\text{M}$ )	Total N ( $\mu\text{M}$ )	%C	%N	C:N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<b>AK</b>												
	2020	June	4.57	11.58 ( $\pm 1.50$ )	1.00 ( $\pm 0.13$ )	1.96 ( $\pm 0.68$ )	2.96 ( $\pm 0.75$ )	19.33 ( $\pm 4.99$ )	2.41 ( $\pm 0.41$ )	7.99 ( $\pm 1.70$ )	−20.05 ( $\pm 1.33$ )	6.52 ( $\pm 1.00$ )
	2021	June	4.57	12.70 ( $\pm 3.49$ )	1.57 ( $\pm 0.15$ )	0.97 ( $\pm 0.29$ )	2.54 ( $\pm 0.29$ )	23.03 ( $\pm 2.25$ )	1.52 ( $\pm 0.39$ )	16.07 ( $\pm 4.57$ )	−17.64 ( $\pm 1.67$ )	6.77 ( $\pm 1.19$ )
<b>CT1</b>												
	2020	May	15.24	17.67 ( $\pm 4.45$ )	0.28 ( $\pm 0.15$ )	0.39 ( $\pm 0.15$ )	0.68 ( $\pm 0.27$ )	24.83 ( $\pm 4.69$ )	2.46 ( $\pm 0.43$ )	10.09 ( $\pm 0.92$ )	−16.35 ( $\pm 1.39$ )	9.30 ( $\pm 0.76$ )
	2021	May	15.24	21.40 ( $\pm 5.16$ )	0.72 ( $\pm 0.08$ )	0.85 ( $\pm 0.88$ )	1.57 ( $\pm 0.95$ )	27.65 ( $\pm 3.17$ )	1.71 ( $\pm 0.42$ )	17.44 ( $\pm 6.15$ )	−21.69 ( $\pm 1.16$ )	7.10 ( $\pm 0.47$ )
<b>CT2</b>												
	2020	May	9.14	2.03 ( $\pm 4.29$ )	0.12 ( $\pm 0.01$ )	0.18 ( $\pm 0.00$ )	0.30 ( $\pm 0.01$ )	35.50 ( $\pm 1.72$ )	0.79 ( $\pm 0.41$ )	50.27 ( $\pm 13.25$ )	−24.41 ( $\pm 1.19$ )	8.74 ( $\pm 0.73$ )
	2021	June	9.14	7.66 ( $\pm 0.52$ )	0.50 ( $\pm 0.03$ )	0.57 ( $\pm 0.05$ )	1.07 ( $\pm 0.07$ )	28.58 ( $\pm 2.54$ )	1.75 ( $\pm 0.34$ )	17.18 ( $\pm 5.11$ )	−17.52 ( $\pm 0.72$ )	11.15 ( $\pm 0.61$ )
<b>ME</b>												
	2020	May	9.14	15.92 ( $\pm 2.38$ )	0.18 ( $\pm 0.02$ )	2.06 ( $\pm 0.18$ )	2.23 ( $\pm 0.18$ )	26.03 ( $\pm 3.98$ )	2.75 ( $\pm 0.33$ )	9.47 ( $\pm 0.95$ )	−16.58 ( $\pm 1.07$ )	6.06 ( $\pm 1.33$ )
	2021	June	9.14	14.04 ( $\pm 3.90$ )	2.71 ( $\pm 0.07$ )	0.96 ( $\pm 0.28$ )	3.66 ( $\pm 0.32$ )	29.31 ( $\pm 3.22$ )	2.37 ( $\pm 0.27$ )	12.45 ( $\pm 1.59$ )	−14.16 ( $\pm 2.48$ )	6.01 ( $\pm 0.78$ )
<b>RI</b>												
	2020	April	6.10	9.91 ( $\pm 2.13$ )	0.20 ( $\pm 0.05$ )	0.45 ( $\pm 0.37$ )	0.65 ( $\pm 0.39$ )	27.78 ( $\pm 2.48$ )	0.98 ( $\pm 0.29$ )	31.03 ( $\pm 11.18$ )	−20.74 ( $\pm 0.94$ )	7.16 ( $\pm 0.29$ )
	2021	April	6.10	3.08 ( $\pm 2.96$ )	0.21 ( $\pm 0.03$ )	0.68 ( $\pm 0.84$ )	0.89 ( $\pm 0.81$ )	31.71 ( $\pm 2.62$ )	0.57 ( $\pm 0.16$ )	60.23 ( $\pm 17.16$ )	−25.54 ( $\pm 1.43$ )	5.08 ( $\pm 0.61$ )

**Table 2.** Statistical parameters for all variables observed in this study, across farms and years.

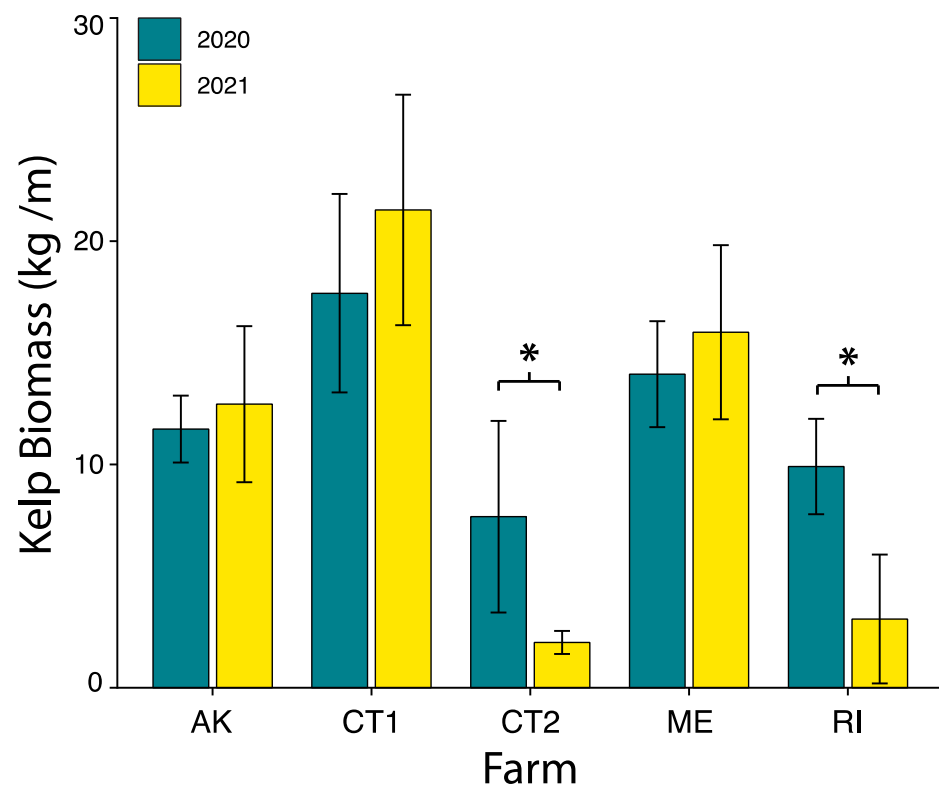
	DF	Denom DF	F	p-Value
<b>Biomass (kg/m)</b>				
Year	1	37.359	0.368	0.548
Farm	4	22.166	17.810	<0.001
Farm × Year	9	15.395	42.108	<0.001
<b>Seawater nitrate (μM)</b>				
Year	1	17.741	9.214	0.007
Farm	4	10.313	15.363	<0.001
Farm × Year	9	7.837	345.50	<0.001
<b>Seawater ammonium (μM)</b>				
Year	1	20.192	0.882	0.359
Farm	4	11.519	5.238	0.012
Farm × Year	6	5.623	1.717	0.271
<b>Seawater total N (μM)</b>				
Year	1	26.977	1.398	0.247
Farm	4	11.954	16.085	<0.001
Farm × Year	9	7.408	75.672	<0.001
<b>Tissue %C</b>				
Year	1	27.916	2.447	0.129
Farm	4	12.441	7.189	0.003
Farm × Year	9	7.978	23.559	<0.001
<b>Tissue %N</b>				
Year	1	26.419	3.994	0.056
Farm	4	12.091	33.775	<0.001
Farm × Year	9	7.923	39.039	<0.001
<b>Tissue C:N</b>				
Year	1	18.151	5.889	0.026
Farm	4	11.065	6.385	0.006
Farm × Year	9	7.829	539.22	<0.001
<b>Tissue δ<sup>13</sup>C</b>				
Year	1	24.73	8.308	0.008
Farm	4	12.123	10.36	<0.001
Farm × Year	9	7.986	74.467	<0.001
<b>Tissue δ<sup>15</sup>N</b>				
Year	1	25.387	3.768	0.063
Farm	4	12.412	9.029	0.001
Farm × Year	9	7.842	20.118	<0.001

### 3.2. Harvested Biomass and Correlative Relationships

The collective harvested biomass (kg/m) in 2020 (avg.  $11.42 \pm 6.12$  kg/m) did not significantly differ compared to 2021 (avg.  $11.78 \pm 6.91$  kg/m) but did vary across farms and within farms across years (Table 2). Farms CT2 and RI yielded a statistically different



biomass across years, whereas the other farms were similar (see Figure 1). Farms CT2 and RI were also the farms with the lowest biomass production and the lowest seawater nutrients.



**Figure 1.** Mean harvested biomass (kg/m) for *S. latissima* in 2020 and 2021 across farms in Alaska and New England. Biomass varied within farms across years only for farms CT2 and RI. Error bars represent  $SD \pm 1$ . The asterisks highlight statistically significant differences across years.

When considering the timing of seawater nutrient data, the harvested kelp biomass correlated better with the seawater nitrogen concentrations collected in the same month as the harvest (nitrate:  $p = 0.036$ ,  $r^2 = 0.088$ ; ammonium:  $p = 0.011$ ,  $r^2 = 0.043$ ; total N:  $p = 0.019$ ,  $r^2 = 0.110$ ) than with the two-month average of seawater nitrogen (nitrate:  $p = 0.227$ ,  $r^2 = 0.044$ ; ammonium:  $p = 0.151$ ,  $r^2 = 0.062$ ; total N:  $p = 0.189$ ,  $r^2 = 0.052$ ). Similarly, when considering the seawater nutrient species (nitrate vs. ammonium vs. total N), the kelp biomass (kg/m) correlated strongest with the total N than it did with nitrate; there was no relationship between biomass and ammonium (see correlative values in Table 3). Therefore, we elected to use the total N ( $\mu\text{M}$ ) in the majority of the remaining analysis, unless nitrate or ammonium were explicitly notable.

Standard linear regression suggests that the total N of ambient seawater is a weak explanatory factor for harvested biomass ( $p = 0.019$ , Figure 2a). Quartile regression, however, showed a stronger relationship at the 10th percentile (0.10 quartile:  $p < 0.001$ ,  $r^2 = 0.431$ ) relative to the median (0.50 quartile:  $p = 0.045$ ,  $r^2 = 0.081$ ), indicating a potential threshold effect (Figure 3). The relationship between biomass and line spacing (m) was also assessed. The line spacing in the farms in this study ranged from 4.57 to 15.25 m (or 15 to 50 ft, imperial units are commonly used by farmers). Standard linear regression suggests that line spacing explains 26.1% ( $p < 0.001$ ) of the variation observed in harvested biomass (Figure 2b). Incorporating both the total N ( $\mu\text{M}$ ) and line spacing (m) into a multiple regression analysis explains 50.0% ( $F = 75.6$ ,  $p < 0.001$ ) of the variation in harvested biomass (see Figure 2c). This relationship is plotted as a two-dimensional heatmap in Figure 2d.

When assessing the relationship between harvested biomass and tissue chemistry, standard linear regression revealed that biomass is positively correlated with %N and negatively correlated with the C:N molar ratio within sampled tissues (Figure 4). There

was no relationship between biomass and %C ( $p = 0.100$ ),  $\delta^{13}\text{C}$  signatures ( $p = 0.079$ ), or  $\delta^{15}\text{N}$  signatures ( $p = 0.804$ ). Figure 4 suggests that %N and the C:N molar ratio interacts with seawater nitrogen (further explored below).

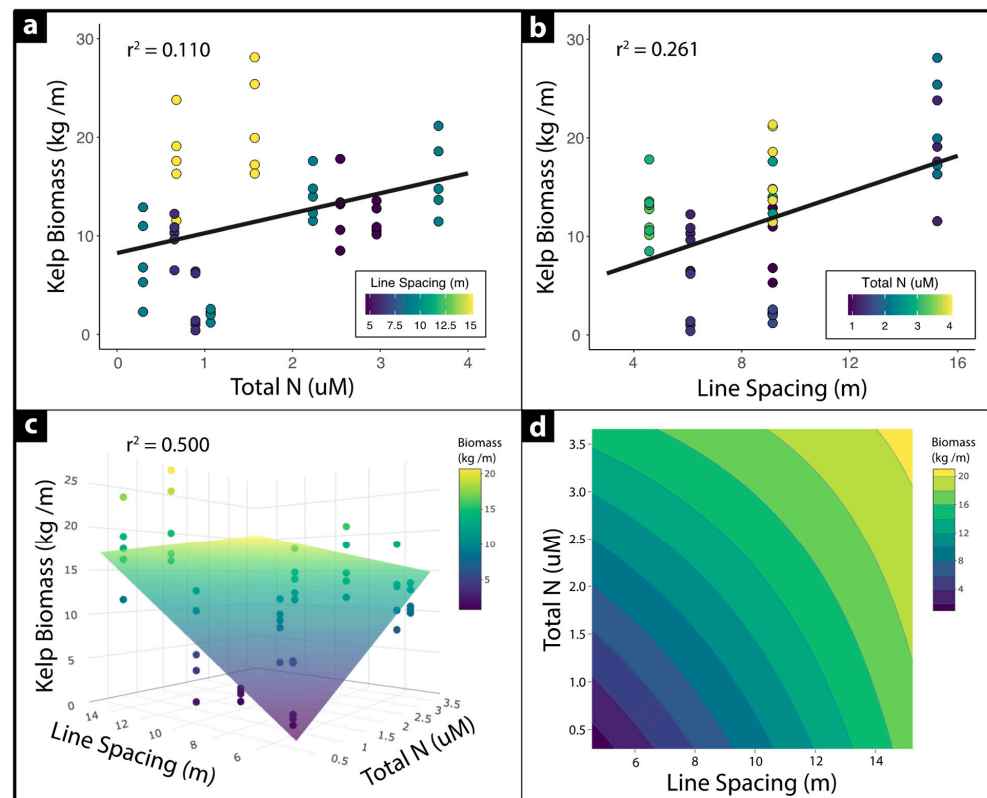
**Table 3.** Correlative values assessing the linear relationship between tissue metrics (%C, %N, C:N,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) and seawater nitrogen values (nitrate, ammonium, total N) observed during the month of harvest and for the two-month average.

	Harvest		2-Month Average	
	<i>p</i> -Value	$r^2$ Value	<i>p</i> -Value	$r^2$ Value
<b>Biomass (kg/m)</b>				
Nitrate	0.036	0.088	0.227	0.044
Ammonium	0.233	0.043	0.151	0.062
Total N	0.019	0.110	0.192	0.052
<b>Tissue %C</b>				
Nitrate	0.004	0.146	<0.001	0.364
Ammonium	0.005	0.137	0.010	0.158
Total N	<0.001	0.249	<0.001	0.341
<b>Tissue %N</b>				
Nitrate	0.001	0.181	0.024	0.119
Ammonium	<0.001	0.197	<0.001	0.387
Total N	<0.001	0.326	<0.001	0.183
<b>Tissue C</b>				
Nitrate	0.007	0.126	0.002	0.224
Ammonium	0.007	0.123	0.002	0.230
Total N	<0.001	0.220	0.001	0.247
<b>Tissue <math>\delta^{13}\text{C}</math></b>				
Nitrate	0.093	0.038	<0.001	0.319
Ammonium	0.029	0.076	<0.001	0.321
Total N	0.014	0.102	<0.001	0.349
<b>Tissue <math>\delta^{15}\text{N}</math></b>				
Nitrate	0.012	0.105	0.151	0.033
Ammonium	<0.001	0.337	0.042	0.093
Total N	<0.001	0.323	0.102	0.051

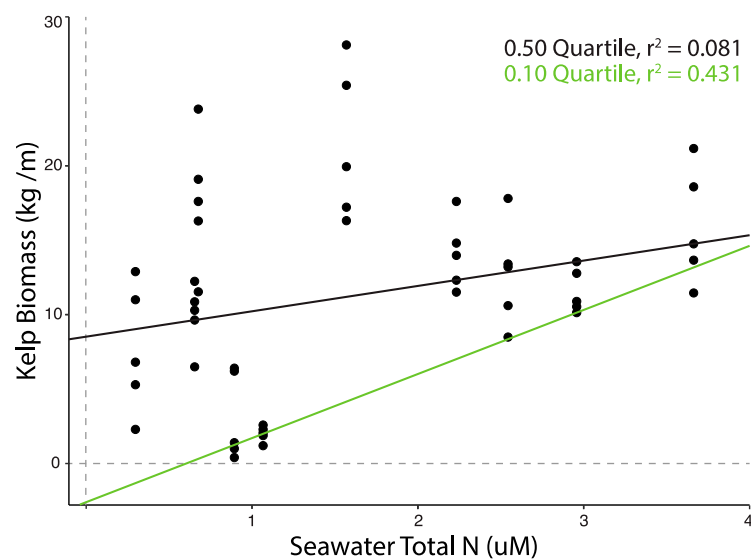
### 3.3. Tissue Carbon and Nitrogen

The %C and %N within harvested tissues did not vary across years (marginally, for %N), but did across farms (Table 2); %C ranged from 19.33–35.50% and %N ranged from 0.57–2.75% (see Table 1). The C:N molar ratio, however, varied significantly across both years and farms (Table 2). The C:N molar ratio was lower in 2020 and the notably higher C:N molar ratios (50.27 for farm CT2 in 2020 and 60.23 for farm RI in 2021) correspond with the lowest harvested biomass (see Table 1, Figure 4). Moreover,  $\delta^{13}\text{C}$  differed across years and farms, while  $\delta^{15}\text{N}$  varied only across farms (Table 2). Linear regression was used to assess the relationship between tissue chemistry and seawater nitrogen. The variation in %N and  $\delta^{15}\text{N}$  was better explained by seawater nitrogen sampled in the same month as the harvest, while the variation in %C, C:N, and  $\delta^{13}\text{C}$  was better explained by the two-month average of the seawater nutrients (Table 3).

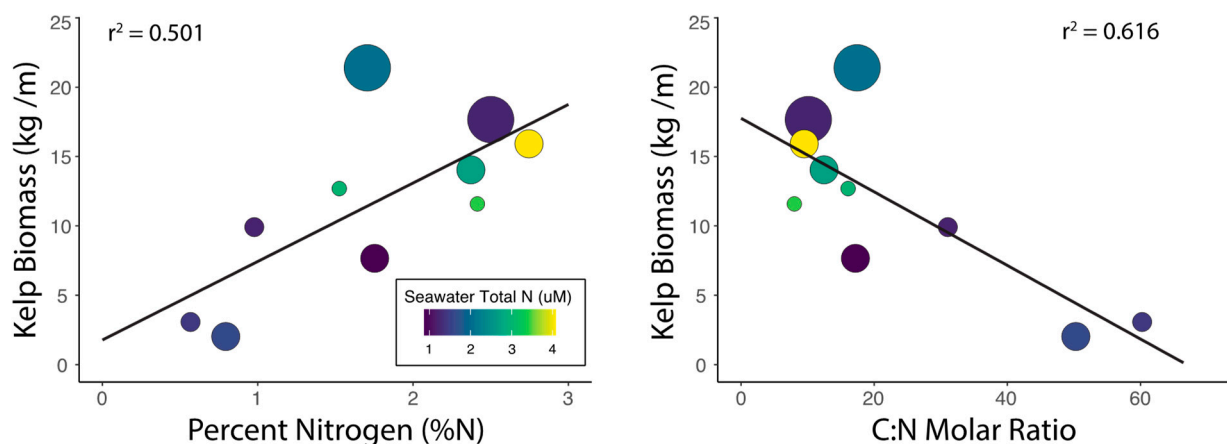




**Figure 2.** (a) Linear regression between harvested biomass (kg/m) and seawater total N (μM); the point color varies as a function of line spacing (m). (b) Linear regression between harvested biomass and line spacing; where the point color varies as a function of seawater total N. (c) A 3-D plot of multiple regression that combines harvested biomass (kg/m), seawater total N, and line spacing into one model; the surface color varies as a function of biomass. (d) The surface in 2c is converted into a 2-D heatmap to better explore how biomass responds to the interaction between seawater total N and line spacing in this study.



**Figure 3.** Kelp biomass (kg/m) plotted against seawater total N (μM). The black line represents the quantile regression for the median (50th percentile), where total N explains 8.1% of the variation in the biomass. The green line represents the quantile regression for the lowest 10th percentile, where N explains 43.1% of the variation for this lower threshold.



**Figure 4.** Linear regression comparing kelp biomass (kg/m) to the %N in kelp tissues (**left**) and the C:N molar ratio (**right**). The circle color varies as a function of seawater total N (µM). The size of the circles varies as a function of line spacing (m), where larger circles equate to larger spacing between kelp lines.

#### 4. Discussion

We assessed the dominance of ambient nitrogen as a predictor of farmed kelp yield to offer support for ongoing considerations about the interplay and weighting of site-level factors in variable coastal environments. We predicted that seawater nitrogen (specifically nitrate) would best explain variation in farmed biomass, but our hypothesis was not supported by the data. In this study, the amount of nitrogen in seawater had a weak role in explaining farmed kelp biomass, accounting for 11% of the variation around the mean. Seawater nitrogen, however, may better explain the lower threshold of this interaction, where a higher total nitrogen in seawater increases the baseline of the lowest 10th percentile for the expected yield (predicting 43% of the variation), regardless of other factors that contribute to variation in biomass above that threshold. Given the equation of the line for the 10th percentile regression ( $y = 4.31x - 2.59$ ), it is estimated that at least  $0.60 \mu\text{M}$  of seawater N is necessary to support the production of *Saccharina latissima* in the observed farms, notably lower than the  $1 \mu\text{M}$  threshold suggested for wild *Macrocystis pyrifera* to sustain metabolic function (values below  $1 \mu\text{M}$  can lead to N depletion, while N concentrations between  $1\text{--}2 \mu\text{M}$  is the range for limitation; see [34]). Although  $0.60 \mu\text{M}$  is not an unreasonable value, we do not mean to suggest it is a robust threshold for informing site selection for all *S. latissima* farms; more data collected across space and time are needed to verify the relevance for site selection. Instead, we mean to emphasize that seawater nitrogen may be a more useful metric in predicting baseline kelp yields rather than realized yields, and that production above that baseline is likely more dependent on other factors that may or may not interact with seawater nitrogen.

Water motion, for example, is known to influence kelp biology and biomass. Kelp farms provide a three-dimensional structure that can modulate a site's flow environment, where more structure disrupts more flow (see [35]), often leading to increases in the thickness of boundary layers associated with the farm. Thicker boundary layers slow the transfer of dissolved matter (e.g., dissolved nutrients and gases) to and from kelp tissues, but water motion can disrupt their formation to increase mass transfer, including at localized spatial scales [12,13,31,36]. In addition, flow can mechanically stimulate kelp, where drag forces can result in elevated growth rates and the thickening of kelp tissues [37,38]. In addition to selecting sites with inherently more flow (see [39,40]), farmers can alter the flow environment within their farm by adjusting the number and spacing of kelp grow lines [35]. In this study, we found a positive relationship between harvested kelp biomass and line spacing, where line spacing explained 26% of the variation in biomass (compared to the 11% explained by total N in seawater), and line spacing combined with total N in seawater

explained 50% of the variation. It is important to note, however, that we opportunistically included line spacing in our analysis. Although the spacing between kelp grow lines is highlighted as an important consideration for farm design [41], we were not able to identify any existing literature that empirically tests the relationship between line spacing and kelp yield.

Temperature and light are other factors known to strongly influence yields. The project for which these data were collected prioritized efforts towards nutrient sampling. Efforts to record the temperature resulted in an incomplete dataset, which restricted proper inclusion in the analysis. It is known, however, that temperature affects seaweed physiology through basal metabolic activity, enzyme activity, and physical controls on nutrient uptake and assimilation at the cellular level, where warmer temperatures increase the rates of these processes [42]. Light data were not collected, but it is known that increased light levels (without reaching photoinhibition) allow for higher rates of carbon fixation to fuel biomass production, as well as increase the uptake and assimilation of nitrogen [4,43,44]. Adjusting the design of farm infrastructure can provide some control over these factors. Deeper grow lines are more likely to be exposed to cooler waters, but they may also receive less light (see [45]), depending on the attenuation of light through the water column. Increased line spacing may reduce self-shading; measuring light at strategic points throughout an array will be critical to tease apart light vs. nutrient effects.

Finally, kelp growth in response to its environment can also be influenced by the genetics of the parental stock accessed by each farm. For example, a common garden experiment comparing two morphotypes of *S. latissima* identified trait stability across strains for blade length and width, while blade ruffles and thickness varied with the environment [46]; notably, *S. latissima* forma *angustissima* has consistently yielded a higher farmed biomass per effort compared to *S. latissima* [47]. As such, the selection of strains via controlled breeding is a powerful tool for increasing yields or other traits, sometimes to overcome the response to undesired environmental conditions and/or farm locations [48,49]. In some areas, like Alaska (USA), however, the strain selection of seaweed is prohibited in commercial operations, and site selection that carefully considers nutrients, water motion, temperature, and light is especially important.

Currently, much discussion and effort are aimed at supporting aquaculture efforts, with site-level descriptions for site selection and management. For example, (1) the Alaska Ocean Observing System (AOOS) actively maintains a Mariculture Map for aquaculture stakeholders, a web-based tool for planning and the granting of permits for marine aquaculture projects in Alaska and (2) the National Atmospheric and Oceanic Administration (NOAA) leads efforts in identifying Aquaculture Opportunity Areas to support coordinated aquaculture. During these endeavors, site-level seawater nitrogen data are frequently requested. Still, the importance of such data as a predictor of expected kelp yield is poorly understood in practice. Although the notion that higher seawater nitrogen supports a higher biomass is not controversial, the study here suggests that ambient nitrogen may play a more nuanced role in determining farmed kelp yield than currently leveraged by the industry at large. This emphasizes that physical characteristics like infrastructure design and local water flow are crucial to consider in parallel with nutrient availability, which we identify as a knowledge gap for refined decision-making around optimizing farmed yields.

## 5. Conclusions

Overall, this study outlines practical considerations for sugar kelp farmers to optimize biomass production through informed site selection and farm design, addressing the strength of seawater nitrogen as a criterion for site suitability. Generalized recommendations based on the work presented here include: (1) selecting sites where the total seawater nitrogen does not dip below 0.6–1.0  $\mu\text{M}$  during the farming season and (2) when farming in a site that experiences seasonal nitrogen limitation, increase the spacing between the grow lines to maximize the flow and nutrient transfer. We could not identify empirical research that better addresses line spacing with relevance to measured kelp yields, but based on

the limited data available here and the personal observations/communications by the authors, spacing of at least 5 ft (1.52 m) in sites with moderate flow and at least 10 ft (3.05 m) in sites with low flow are not unreasonable minimum distances to implement. Optimal spacing between the lines will vary based on the ambient flow environment; resolving the within-farm flow and the influence on nutrient delivery is key to better controlling and predicting farm production.

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