

Impact of Temperature on the Rate of Bull Kelp (*Nereocystis luetkeana*) Decomposition

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Abstract

In the face of global climate change, macroalgal cultivation has emerged as a potential carbon dioxide removal (CDR) strategy. However, many key knowledge gaps exist about the true extent of macroalgal carbon sequestration, including the impacts of climate change. To assess whether elevated temperatures cause *Nereocystis luetkeana* blades to decay more rapidly, twelve 35 mm-diameter tissue disks were allowed to decay at 10-12 °C (ambient temperature treatment) and another 12 tissue disks were allowed to decay at 17-19 °C (elevated temperature treatment). After 7 days, the mean change in disk mass for the ambient temperature treatment was compared to the mean change in mass for the elevated temperature treatment. Samples at elevated temperatures were visibly flimsier and more diaphanous, which was correlated with a significantly greater decrease in mass. This finding suggests that brown algae decay more rapidly at elevated temperatures, which has important implications for how to maximize future macroalgal carbon sequestration as ocean temperatures rise.

Introduction

In 2015, the Intergovernmental Panel on Climate Change found that limiting global warming to 2 °C requires not only drastically reducing emissions, but also actively capturing CO₂ already in the atmosphere and ocean (IPCC, 2018). In the latter half of the 2010s, macroalgal cultivation—the process of planting and harvesting kelp—has emerged as a promising carbon dioxide removal (CDR) strategy (Boyd et al., 2022; Wu et al., 2023). Exceeding 1000 TgCyr⁻¹, global macroalgal net primary productivity (NPP) is comparable to that of the Amazon rainforest (Duarte et al., 2022; Krause-Jensen and Duarte, 2016; Pessarrodona et al., 2022). Following a 2016 estimate that kelp forests sequester 173 TgCyr⁻¹, seaweed aquaculture has received significant attention and funding (Krause-Jensen and Duarte, 2016; Wu et al., 2023).

However, the effectiveness and feasibility of growing kelp to remove carbon is still debated (Boyd et al., 2022; Hurd et al., 2022; Macreadie et al., 2019; Ross et al., 2022; Ricart et al., 2022). Carbon sequestration is defined as the stable storage of carbon-containing compounds for at least 100 years (Hurd et al., 2022). The primary proposed mechanism of macroalgal carbon sequestration is export to the deep sea, where kelp detritus carried out to the open ocean sinks to the deep-sea floor, locking away the carbon inside for centuries (Krause-Jensen and Duarte, 2016; Boyd et al., 2022). As of 2024, deep sea macroalgal carbon sequestration was estimated to be 4-44 TgCyr⁻¹—lower than the initial 2016 estimate, but still significant (Filbee-Dexter et al., 2024). However, recent research has also highlighted potential ecological consequences associated with kelp cultivation (Boyd et al., 2022; Ricart et al., 2022; Ross et al., 2022), suggested that the scale of macroalgal cultivation needed for significant carbon storage may be economically unfeasible (DeAngelo et al., 2022; Ross et al., 2022; Ricart et al., 2022), and underscored significant uncertainty about the net carbon sequestration potential of macroalgal cultivation ventures (Hurd et al., 2022; Ricart et al., 2022; Pessarrodona et al., 2024; Ross et al., 2022). While these considerations are extremely relevant to proposed carbon credit schemes, additional data are needed to resolve them (Boyd et al., 2022; DeAngelo et al., 2022; Hurd et al., 2022; Pessarrodona et al., 2024; Ross et al., 2022).

Climate change itself further complicates the matter of quantifying macroalgal carbon sequestration. Primary productivity in many kelp species is linked to numerous abiotic and biotic factors, including temperature, light, depth, nutrient availability, salinity, pH, competition,

grazing, and the presence of epiphytes and endophytes (Diehl et al., 2023). With global average sea surface temperatures rising and marine heat waves becoming more frequent (Gao et al., 2021; Xu et al., 2021), understanding the impact of temperature on macroalgal growth and decay is a vital question. The present study focuses on decomposition, defined here as the breakdown of macroalgal tissue—primarily by microbial respiration—into Dissolved Organic Carbon (DOC) or Dissolved Inorganic Carbon (DIC) that can reenter the carbon cycle as CO₂ (Braeckman et al., 2019; Xiong et al., 2024). Previously, decreased tissue strength and increased mortality have been reported in *Saccharina latissima*, *Laminaria digitata*, and *Agarum clathratum* at elevated temperatures (Simonson et al., 2015). Another study observed more rapid decay in *Saccharina latissima* and *Laminaria hyperborea* growing at warmer latitudes and estimated that a global temperature increase of 1.4 °C would result in 4.1% less kelp sinking to depth, and therefore a 26% decrease in macroalgal carbon sequestration (Filbee-Dexter et al., 2022). Given the direct correlation between decay and sequestration, it is important to explore whether the temperature-decomposition correlation observed in *Saccharina latissima* and *Laminaria hyperborea* is generalizable to other brown algal species.

Since microbial metabolism and respiration increase with temperature (Xiong et al., 2024), the present paper attempted to determine if the decomposition rate of bull kelp (*Nereocystis luetkeana*)—a major kelp species along the North American coast—is similarly influenced by temperature. Specifically, this study tested the hypothesis that *Nereocystis* tissue maintained in seawater at elevated temperatures (17-19 °C) would decompose at a greater rate than *Nereocystis* tissue maintained at ambient temperatures (10-12 °C). The results of this experiment may provide insight about strategies to maximize macroalgal carbon sequestration in warming oceans.

Materials and Methods

Field Collection

Twelve (12) *Nereocystis luetkeana* blades were collected for the present study from Beaverton Cove on May 17, 2024, (San Juan Island, Washington, USA, 48.54410 °N, 123.01737 °W; **Figure 1**). Each blade was removed from a separate individual *Nereocystis* located at a depth of 1 meter. The blade lengths ranged from 41 to 123 cm, 3 of which contained reproductive sori (**Supplemental Figure 1**). To prevent desiccation, the collected blades were transported back to the laboratory in a 5-gallon bucket filled with seawater also collected from Beaverton Cove.

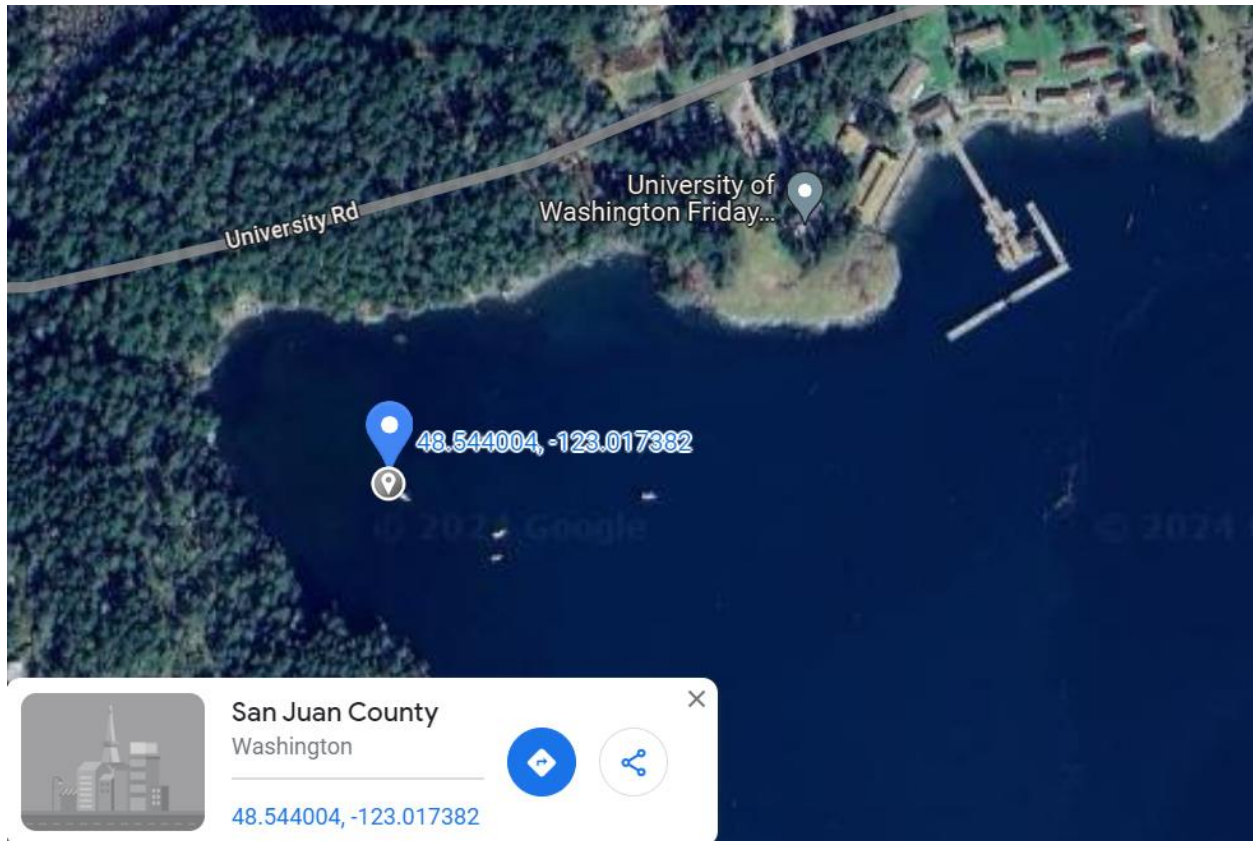


Figure 1. Sample collection location. Satellite image of Beaverton Cove, San Juan County, WA, USA, 48.54410 °N, 123.01737 °W. The pinned location in blue represents the approximate *Nereocystis luetkeana* sampling site. ©2024 Google.

Sample Processing

Immediately after arriving at the laboratory, a cork borer was used to cut out three 35 mm-diameter disks from each of the 12 collected blades, for a total of 36 disks (**Figure 2a**). To mimic natural decomposition—which primarily occurs at the end of kelp blades, furthest away from the basal meristematic region (Simonson et al., 2015)—the first disk on each blade was cut 15 cm from the distal tip of the blade. This distal portion of the blade was not sampled because these regions often visibly varied in texture and color, potentially indicating different states of decay. The second disk on each blade was cut 2 mm below the first disk, and the third blade was cut 2 mm below the second disk (**Figure 2a**).

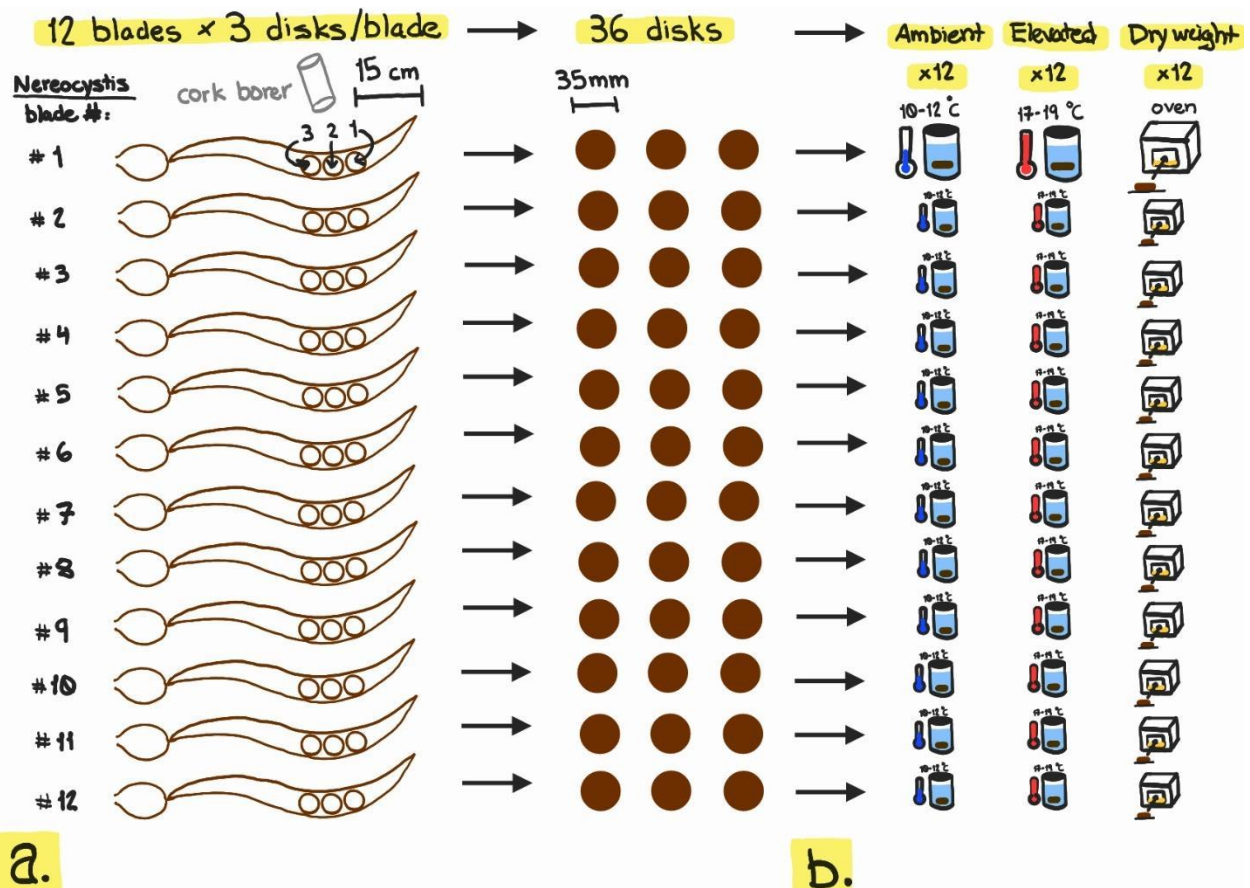


Figure 2. Process of (a) creating *Nereocystis luetkeana* disks and (b) assigning them to treatments. The 36 brown circles represent disks of tissue cut out from 12 *Nereocystis* blades using a 35-mm cork borer. Black outlined containers represent mason jars filled with 350 mL of seawater. On *Nereocystis* blade 1, the disk labeled ‘1’ was the first one cut, at a distance of 15 cm from the tip of the blade. Note that the three disks generated from each blade were assigned to the ambient treatment, elevated treatment, or dry weight group at random.

Next, each disk was gently blotted dry on a paper towel until it no longer left a visible wet mark. Disks were then individually weighed to 0.0001 g using a laboratory balance [Mettler Toledo, Columbus, Ohio]. Each disk was stored separately in a seawater-filled petri dish before and after weighing to prevent desiccation.

Experimental Premise & Weighing Methods

After weighing, 12 of the 36 *Nereocystis* disks were left to decay for one week in ambient (10-12 °C) temperature tanks, another 12 disks were left to decay for one week in elevated (17-19 °C) temperature tanks, and the remaining 12 disks were desiccated in an oven (see below) to obtain dry masses (**Figure 2b**). Decomposition of disks used in the ambient temperature treatment (ATT) and the elevated temperature treatment (ETT) was measured using change in wet mass as well as change in dry mass (disk mass on day 7 – disk mass on day 0) because both approaches have strengths and limitations. Wet weights—defined here as kelp disks weighed after being blotted dry with a paper towel—tend to be less precise than dry weights because they

are affected by the amount of evaporation that occurs prior to weighing (Wickham et al., 2019). However, with wet weights, it is possible to record the mass of a specific disk on day 0 and day 7. With dry weights, meanwhile, a single kelp disk cannot be dried out at day 0 without killing the kelp tissue. Therefore, in this study, one of the three disks from each kelp blade was dried in an oven to obtain an initial dry weight value. Based on the assumption that the three disks from a single *Nereocystis* blade had similar masses, the dry weight value for the oven-heated disk was used as a proxy for the initial dry weight value of the other two disks from that blade. Measuring decay in terms of both wet and dry masses provided greater confidence that any observed results were not due to the limitations of one weighing method.

Ambient and Elevated Temperature Treatments

The ATT consisted of two 5-gallon aquarium tanks filled halfway with seawater (**Figure 3a,b**). The two aquarium tanks were placed side-by-side in a sea table with a constant inflow of seawater directly from the Puget Sound. Each aquarium tank contained 6 sealed, submerged mason jars filled with 350 mL of water (**Figure 3a,b**). The ETT consisted of the same setup as above, except the tanks were placed in an empty sea table and each heated to 18 °C with a 25 W aquarium heater (**Figure 3c,d**). *Nereocystis* disks were randomly assigned to the 3 treatment groups so that one of the three disks from each blade was assigned to the ATT, one was assigned to the ETT, and one was desiccated to obtain a dry mass (**Figure 2b**). For the disks in the ambient and elevated temperature treatments, a single disk was placed in each sealed mason jar (**Figure 2b**). In total, 12 disks were placed in the ambient temperature treatment and 12 disks were placed in the elevated temperature treatment (**Figure 2b**).



Figure 3. Ambient (a,b) and elevated (c,d) temperature treatment setups. **a)** Overhead view of two ambient temperature aquarium tanks in a sea table with flowing seawater from the Puget Sound. **b)** Side view of an ambient temperature aquarium tank. Note that one kelp disc is present in each of the 6 mason jars in the tank and that the water level of the sea table is equal to that inside the aquarium tank. **c)** Overhead view of two elevated temperature aquarium tanks in an empty sea table. **d)** Side view of an elevated temperature aquarium tank. Note that one kelp disc is present in each of the 6 mason jars in the tank and an aquarium heater is present to heat the tank to 18 °C.

Dry Weights

The 12 disks not used in the decomposition treatments were desiccated in a heated oven and their dried masses were used as a proxy for the initial dry weights of the ambient temperature disks as well as for the elevated temperature disks. First, twelve 4x4 cm squares of aluminum foil were weighed, and one kelp disc was set on top of each square of foil. Then, the

12 disks were placed in a convection oven preheated to 60 °C and weighed to 0.0001 g after 8 hours and 16 hours. To confirm that the samples were completely dry, it was confirmed that no disk changed in mass by more than 0.0005 between the first and second weighing.

Sample Decomposition

Kelp disks in the decomposition treatments were left to decay for seven days. Throughout the duration of the experiment, tank seawater temperatures were measured three times per day with a handheld Fluke-62 MAX Infrared Thermometer to monitor temperature (**Supplemental Figure 2**). While each tank was originally intended to contain an aquarium air pump to facilitate water mixing, pumps were not used due to their propensity to raise water temperatures by several degrees. Therefore, to control for the possibility of unequal heating or cooling within a single tank due to a lack of circulation, all 6 mason jars in each tank were rotated clockwise every 24 hours.

After 7 days, all kelp disks from the ATT and ETT were weighed. First, to obtain wet weights, each disk was blotted dry until it no longer left a visible wet mark on a paper towel and then weighed to 0.0001 g. Then, following the procedure outlined in “dry weights,” a dry weight value was also obtained for all 24 disks.

Data Analysis

The mean change in disk mass for the ATT was compared to the mean change in disk mass for the ETT using the Analysis ToolPak add-in in Microsoft Excel. Two Welch’s *t*-tests were conducted, one for wet weights and one for dry weights. Welch’s *t*-tests were selected over Student’s *t*-tests to account for unequal standard deviations between treatments (West, 2021). All charts and figures were generated in Excel.

Results

Qualitatively, *Nereocystis* samples in the ETT (17-19 °C) showed signs of greater decay than samples in the ATT (10-12 °C). Prior to being removed from the seawater, all samples retained their circular shape. However, 8 out of the 12 ETT disks appeared visibly thinner, flimsier, and diaphanous than their ATT counterparts. Indeed, upon removal from the water, these 8 samples collapsed inwards on themselves, losing their circular shape (**Figure 4**). With the exception of one disk, all of the ATT samples mostly retained their initial circular shape after removal from the water (**Figure 4**).



Figure 4. Photographs of *Nereocystis luetkeana* blade samples after decaying for 7 days at 10-12 °C (amb/ambient) vs. 17-19 °C (elev/elevated) temperatures. Samples with the same numerical label (ex. amb 1 and elev 1) were cut from the same *Nereocystis* blade and had similar masses initially. Note that of ambient treatment samples, only disk 9 lost its initial circular shape, while of the elevated treatment samples, disks 1, 3, 6, 7, 8, 9, 10, and 12 all lost their initial circular shapes.

Quantitative analyses of both wet and dry weights confirmed that differences between the ATT and ETT were significant. The 12 samples in the ETT (wet weight: *Mean [M]* = 0.1286 g, *Standard Error [SE]* = 0.0295; dry weight: *M* = 0.0137 g, *SE* = 0.0025) lost more mass than the 12 samples in the ATT (wet weight: *M* = 0.0164 g, *SE* = 0.0061; dry weight: *M* = 0.0040 g, *SE* = 0.0012; **Figure 5, Tables 1, 2**). Welch's *t*-tests confirmed that these differences were statistically significant (wet weights: $t_{11} = 3.7271$, $p = 0.0033$; dry weights: $t_{16} = 3.5148$, $p = 0.0029$; **Table 3**).

Table 1. Wet and dry weights (g) of *Nereocystis luetkeana* samples placed in ambient temperature (10-12 °C) seawater for 7 days.

Sample ID	Initial Wet	Final Wet	Change Wet	% Change Wet	Initial Dry	Final Dry	Change Dry	% Change Dry
Amb 1	0.3183	0.2873	-0.0310	-9.7392	0.0277	0.0224	-0.0053	-19.1336
Amb 2	0.3370	0.3434	0.0064	1.8991	0.0268	0.0281	0.0013	4.8507
Amb 3	0.3866	0.3526	-0.0340	-8.7946	0.0360	0.0284	-0.0076	-21.1111
Amb 4	0.3268	0.3168	-0.0100	-3.0600	0.0318	0.0270	-0.0048	-15.0943
Amb 5	0.2532	0.2576	0.0044	1.7378	0.0235	0.0226	-0.0009	-3.8298
Amb 6	0.2861	0.2960	0.0099	3.4603	0.0238	0.0242	0.0004	1.6807
Amb 7	0.3049	0.2823	-0.0226	-7.4123	0.0232	0.0207	-0.0025	-10.7759
Amb 8	0.4300	0.4153	-0.0147	-3.4186	0.0394	0.0360	-0.0034	-8.6294
Amb 9	0.3096	0.2453	-0.0643	-20.7687	0.0279	0.0130	-0.0149	-53.4050
Amb 10	0.4276	0.3985	-0.0291	-6.8054	0.0390	0.0333	-0.0057	-14.6154
Amb 11	0.3392	0.3373	-0.0019	-0.5601	0.0322	0.0291	-0.0031	-9.6273
Amb 12	0.2975	0.2881	-0.0094	-3.1597	0.0256	0.0238	-0.0018	-7.0312
Avg	0.3347	0.3184	-0.0164	-4.7185	0.0297	0.0257	-0.0040	-13.0601
SD	0.0545	0.0528	0.0212	6.6577	0.0059	0.0061	0.0043	14.8699
SE	0.0157	0.0152	0.0061	1.9219	0.0017	0.0017	0.0012	4.2926

Table 2. Wet and dry weights (g) of *Nereocystis luetkeana* samples placed in elevated temperature (17-19 °C) seawater for 7 days.

Sample ID	Initial Wet	Final Wet	Change Wet	% Change Wet	Initial Dry	Final Dry	Change Dry	% Change Dry
Elev 1	0.3205	0.1045	-0.2160	-67.3947	0.0277	0.0114	-0.0163	-58.8448
Elev 2	0.3258	0.2992	-0.0266	-8.1645	0.0268	0.0243	-0.0025	-9.3284
Elev 3	0.4087	0.1190	-0.2897	-70.8833	0.0360	0.0106	-0.0254	-70.5556
Elev 4	0.3401	0.3143	-0.0258	-7.5860	0.0318	0.0273	-0.0045	-14.1509
Elev 5	0.2312	0.2366	0.0054	2.3356	0.0235	0.0215	-0.0020	-8.5106
Elev 6	0.2739	0.1402	-0.1337	-48.8134	0.0238	0.0100	-0.0138	-57.9832
Elev 7	0.2932	0.0475	-0.2457	-83.7995	0.0232	0.0050	-0.0182	-78.4483
Elev 8	0.4276	0.1769	-0.2507	-58.6296	0.0394	0.0172	-0.0222	-56.3452
Elev 9	0.2933	0.1991	-0.0942	-32.1173	0.0279	0.0093	-0.0186	-66.6667
Elev 10	0.4293	0.2705	-0.1588	-36.9904	0.0390	0.0143	-0.0247	-63.3333
Elev 11	0.3354	0.2918	-0.0436	-12.9994	0.0322	0.0271	-0.0051	-15.8385
Elev 12	0.3088	0.2452	-0.0636	-20.5959	0.0256	0.0140	-0.0116	-45.3125
Avg	0.3323	0.2037	-0.1286	-37.1365	0.0297	0.0160	-0.0137	-45.4432
SD	0.0617	0.0866	0.1021	28.5756	0.0059	0.0075	0.0086	26.0596
SE	0.0178	0.0250	0.0295	8.2491	0.0017	0.0022	0.0025	7.5228

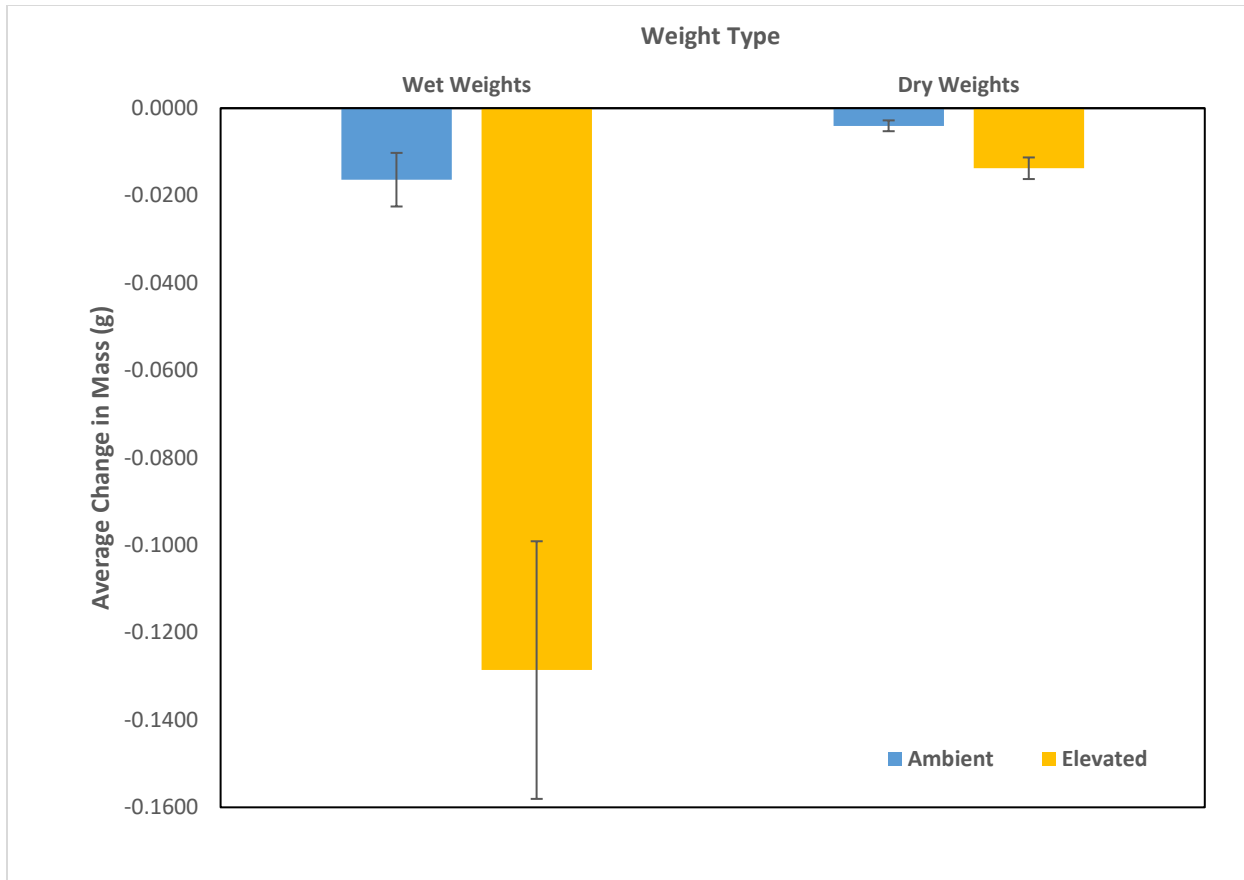


Figure 5. Average change in wet and dry weights for *Nereocystis luetkeana* disks placed in ambient (10-12 °C) and elevated (17-19 °C) temperature treatments for 7 days. Blue bars represent the ambient temperature treatment, and yellow bars represent the elevated temperature treatment. Negative values represent a decrease in mass. Error bars represent the standard error, the variability in the estimate of each mean.

Table 3. Results of two Welch's *t*-tests for the change in wet weight and the change in dry weight of *Nereocystis luetkeana* samples that decayed at ambient temperatures vs. elevated temperatures.

	Wet Weights		Dry Weights	
	Ambient	Elevated	Ambient	Elevated
Mean	-0.0164	-0.1286	-0.0040	-0.0137
Variance	0.0005	0.0104	0.0000	0.0001
Observations	12	12	12	12
df	11		16	
t Stat	3.7271		3.5148	
P(T<=t) two-tail	0.0033		0.0029	
t Critical two-tail	2.2010		2.1199	

Discussion

Because kelp can be grown for a variety of purposes—including carbon sequestration, direct consumption, biofuel creation, fertilizer production, and the harvest of compounds for cosmetic and pharmaceutical products—macroalgal cultivation is primed for rapid expansion in the upcoming decades (Barbier et al., 2020; Naylor et al., 2021; Spillias et al., 2024). As such, it is important that future macroalgal cultivation projects maximize social, economic, and environmental outcomes (Spillias et al., 2024). From the perspective of growing kelp to mitigate climate change, estimates of macroalgal carbon sequestration are limited by a lack of knowledge about the impacts of warming oceans on kelp growth and decomposition. While more rapid decay at higher temperatures has been observed in two brown algal species in Atlantic, the present study tested whether this relationship also occurs in blades of *Nereocystis luetkeana*, a widespread foundational species along the North American coast. In one week, kelp disks in the ETT (17-19 °C) lost significantly more mass than kelp disks in the ATT (10-12 °C), supporting the hypothesis that *Nereocystis* blades decompose more rapidly at elevated temperatures due to increased microbial respiration (Xiong et al., 2024). This finding suggests that the temperature-decomposition observed in *Saccharina latissima* and *Laminaria hyperborea* (Filbee-Dexter et al., 2022) may be generalizable to other brown algal species. Additionally, the results of the present study have important implications for the timing of macroalgal harvests and the selection of optimal sites to grow macroalgae for carbon sequestration.

Implications for Macroalgal Cultivation and Carbon Sequestration

While macroalgae uptake carbon as they grow, previous research has demonstrated that kelp can also become sources of CO₂ as they age and decompose (Xiong et al., 2024). As warmer seawater temperatures are projected to occur earlier in the year due to climate change (Xu et al., 2021), the finding that *Saccharina* (Filbee-Dexter et al., 2022), *Laminaria* (Filbee-Dexter et al., 2022), and *Nereocystis* (present study) decompose more rapidly at higher temperatures suggests that harvesting macroalgae earlier in the season may maximize carbon removal. Furthermore, for ventures that propose to sequester carbon by growing macroalgae and then sinking them to the seafloor (Krause et al., *In Press*; Troell et al., 2022), the results of the present study suggest that cooler, higher latitude sites and earlier times of year may be optimal.

Beyond macroalgal cultivation, the positive correlation between temperature and decay has significant implications for carbon sequestration by naturally-occurring kelp forests: as global sea temperatures rise, wild forests may sequester less carbon due to increased decomposition, further amplifying climate change. This may represent a positive feedback loop not accounted for in climate models (Ripple et al., 2023). Additional research is needed to quantify changes in macroalgal sequestration in warming oceans and ultimately increase the accuracy of climate models.

Limitations and Future Research

While the present study identified a significant correlation between temperature and decay, the magnitude of this relationship remains to be explored. The present study compared decay in disks maintained in treatments that differed by roughly 7 °C; however, sea surface temperatures are projected to increase by 0-3 °C (Ruela et al., 2020). With a larger sample size, future studies could assess the extent to which subtler increases in temperature impact decomposition. Additional research is also needed to explicitly quantify the relationship between decomposition and carbon sequestration. A future study might address this knowledge gap by

monitoring the pH of seawater in treatments containing kelp fragments allowed to decay for different amounts of time.

Supplementary Materials

Table 1. Maximum length and presence/absence of reproductive sori for 12 sampled *Nereocystis* blades. Each blade was removed from a separate individual *Nereocystis* located at a depth of 1 meter in Beaverton Cove on May 17, 2024.

Blade	Length (cm)	Sori Present/Absent
1	73	Absent
2	61	Absent
3	76	Present
4	80	Absent
5	60	Absent
6	83	Absent
7	41	Absent
8	123	Present
9	95	Absent
10	117	Present
11	100	Absent
12	65	Absent

Table 2. Seawater temperature values of ambient temperature treatment (ATT) and elevated temperature treatment (ETT) tanks at 9AM, 1PM, and 8PM from May 17-24, 2024. Each temperature value is the average of two readings taken at opposite ends of the tank. Readings were taken with a handheld Fluke-62 MAX Infrared Thermometer.

Time of Day	Date	ATT Tank 1	ATT Tank 2	ETT Tank 1	ETT Tank 2
5PM	5/17/2024	10.8	11.0	19.1	17.7
9AM	5/18/2024	10.7	10.8	18.6	17.6
8PM	5/18/2024	10.7	10.7	17.4	20.4
1PM	5/19/2024	11.6	11.8	17.1	19.3
8PM	5/19/2024	11.2	11.2	18.4	17.7
9AM	5/20/2024	11.5	11.7	18.1	18.4
8PM	5/20/2024	11.0	11.0	22.8	18.3
9AM	5/21/2024	10.7	10.8	19.0	21.5
1PM	5/21/2024	11.1	11.1	17.7	17.6
8PM	5/21/2024	10.6	10.8	17.7	17.3
9AM	5/22/2024	11.3	11.3	17.7	22.0
1PM	5/22/2024	11.8	11.9	16.9	18.5
8PM	5/22/2024	11.8	11.9	19.9	17.7
9AM	5/23/2024	11.1	11.3	20.6	18.2
1PM	5/23/2024	11.4	11.2	19.0	20.0
8PM	5/23/2024	11.0	11.1	18.5	17.4
1PM	5/24/2024	11.4	11.3	17.8	18.2
5PM	5/24/2024	11.2	11.2	17.6	19.2
Average		11.2	11.2	18.6	18.7

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