# In situ characterization of *Saccharina latissima* (Phaeophyceae) growth rates at varying light intensities

Heekyeong Lee[1,2], Leela Madhava[1,3], Oliver Parsons[1,3], Ariana Paulik[1, 3]

FHL 446A

MARINE BOTANY: Diversity and Ecology
Summer A 2025

[1] Friday Harbor Laboratories, University of Washington, San Juan Island, WA 98250

[2] Department of Oceanography, College of Natural Sciences, Chonnam National University, Gwangju 61186, Republic of Korea

[3] Department of Marine Biology, College of the Environment, University of Washington, Seattle, WA 98195

Contact information:
Leela Madhava
Department of Marine Biology
University of Washington
5263 University Way NE
Seattle, WA 98105
leelapm@uw.edu

Keywords: Sugar kelp, *Saccharina latissima*, growth, productivity, carbon sequestration, light attenuation

**Abstract**

Kelp species provide crucial ecosystem services in nearshore habitats, and the health of these populations and the food webs they support has arisen as a pressing concern as oceanic conditions continue to change. This study aimed to evaluate the relationship between light availability and kelp primary productivity in the model species *Saccharina latissima* (sugar kelp) by measuring in situ growth at various depths on a kelp "ladder". It determined that the kelp grown at 10 meters below the surface showed significantly less growth (change in area, $cm^2$) than the other treatments ($p = 0.01$) potentially due to the fact that the photosynthetically active radiation (PAR) (239.29 μmol photons $m^{-2}$ $s^{-1}$) that reaches to this depth is below the threshold for chlorophyll-saturated photosynthesis. Coupled with spatial kelp abundance models and carbon content ratios, these results are a potential foundation for future tools estimating large-scale kelp productivity across depth.

## 1. Introduction

In recent years, kelp and its surrounding ecosystems have become a central area of interest in global conservation efforts. Because of kelp's role as an ecosystem engineer, the health and abundance of kelp forests is critical not only to the regulation of factors such as pH, light availability, and water flow, but also to carbon and nutrient cycling in highly productive coastal ecosystems. These biogenic coastal habitats are notably sensitive to disturbance; therefore, reductions in kelp quality due to human activity can cause rapid and large-scale declines throughout the food web. These changes, in turn, drive shifts in both environmental 6structure and productivity (Berry et al., 2021; Eger et al., 2023).

While the loss of wild kelp forests due to increased oceanic temperatures and other abiotic changes has arisen as an urgent concern within marine habitats (Berry et al., 2021; Smale, 2020), commercial kelp cultivation remains a successful and important industry in many parts of the world (Forbord et al., 2020, Eger, A. et al., 2023). Due to its success, large-scale kelp cultivation has been proposed as a potential tool for carbon storage, with research showing evidence of canopy-forming macroalgae uptaking additional, potentially anthropogenic, inorganic carbon (Hepburn, C.D et al., 2011). This approach would aim to offset a portion of the effects of anthropogenic carbon dioxide emissions by growing large amounts of kelp on human-made substrates, or by supplementing existing kelp forests (Strong-Wright & Taylor, 2022).

For the purposes of this study, sugar kelp (*Saccharina latissima*) was used as a model species due to its rapid growth rates and its relatively well-studied growth patterns. Previous research has shown that this kelp – a common commercially-grown species – thrives at surface depths of 1-5 m, as opposed to deeper zones where light availability is reduced. However, *Saccharina* production has been shown not to be uniformly influenced by depth, but rather to

vary with latitude and seasonality (Forbord et al., 2020). This suggests that the intensity of light is a key factor determining new biomass production. Because of its ecological, cultural, and economic importance, a precise understanding of how environmental factors such as light availability influence kelp growth is crucial to predicting how primary productivity may shift in a changing ocean.

Kelp predominantly inhabits coastal environments with sufficient light availability, substrates suited to holdfast attachment, low temperatures, and high nutrient concentrations (e.g. Steneck et al., 2002). In coastal environments, wave or current-induced sediment resuspension and terrestrial inputs of colored dissolved organic matter (CDOM) drive variations in turbidity (Green & Coco, 2014). Tidal fluctuations lead to additional variability in environmental factors such as light availability and temperature within these habitats (Serôdio & Catarino, 1999). These changing environmental conditions impact the attenuation of light throughout the water column.

Light is a critical factor for photosynthetic organisms such as kelp. Both its intensity and spectral quality are influenced by water depth and turbidity. For instance, in clear and oligotrophic waters such as those of the Pacific Ocean, blue wavelengths are capable of reaching deeper layers in the water column. In contrast, in more turbid environments like the Baltic Sea, where CDOM concentrations are high, blue light is rapidly absorbed in shallow waters, while red light's longer wavelengths can penetrate to further depths (Stomp et al., 2007). Previous research has investigated the influence of light on the primary productivity of kelp (Graham et al., 2007; Fernández et al., 2021). However, laboratory-based experiments inherently lack the ability to replicate the complex and dynamic interplay of environmental factors such as natural light conditions, temperature, and salinity found *in situ*.

This study conducted *in situ* measurements of *S. latissima*'s primary productivity to describe its photosynthetic performance at varying light levels under realistic environmental conditions. Increasing the knowledge surrounding *Saccharina*'s *in situ* primary productivity and growth patterns was central to this study. Measurements of light intensity, primary productivity, and chlorophyll concentrations were taken from blades grown at various depths. These measurements were used to evaluate the relationship between light intensity and primary productivity in *Saccharina*. This data, combined with an extrapolated literature review, has the potential to inform future ecological models, aquaculture practices, and ecosystem health evaluations.

## 2. Methods & Materials

### *2.1. Specimen collection*

On 25 July, 2025, specimens were taken from the main dock at Friday Harbor Marine Laboratory (48.5457, -123.013), where a collection of tires lining the dock edges is designed to encourage settlement by algae. This ensured that all specimens were raised in an environment similar to one another and one similar to the experimental conditions, as the dock is approximately 150m from the experimental site. Specimens were selected to have a similar area (mean: 238.4cm$^2$, SD: 67.7cm$^2$) and to be in relatively good condition (minimal tearing, tattering, or epibionts). Specimens were attached to the experimental apparatus and installed within 3 hours of collection and kept in flow-through seawater tables whenever measurements were not being taken.


**Figure 1.** The experiment took place nearshore to Friday Harbor Labs, San Juan Island, Washington, United States of America. This location is around 15 meters deep and characterized by its mixed semidiurnal tides and constant mixing due to circulation and currents.

*2.2. Experimental design*

Specimens were suspended at four different depths (1m, 3m, 5m, and 10m from the surface), with five specimens attached at each depth. The design consisted of a "ladder" composed of polypropylene rope and PVC pipes (Fig. 2). A buoy kept the apparatus at a consistent distance from the surface, a weight was used to ensure the ropes stayed taut, and an anchor ensured it stayed in a consistent location. Specimens were attached to the rope at each "rung" (depth condition) by untwisting the fibers, inserting the holdfast and stipe through the gap, and closing the rope around the stipe with the holdfast held in place. The apparatus was then installed approximately 50 m offshore from the Friday Harbor Labs campus, in the waters of the Salish Sea adjacent to San Juan Channel (48.5456, -123.010, Fig. 1). The specimens were then

allowed to grow for two weeks with minimal disturbances, and subject to most typical *in situ* conditions (i.e. temperature, salinity, dissolved oxygen, etc.).

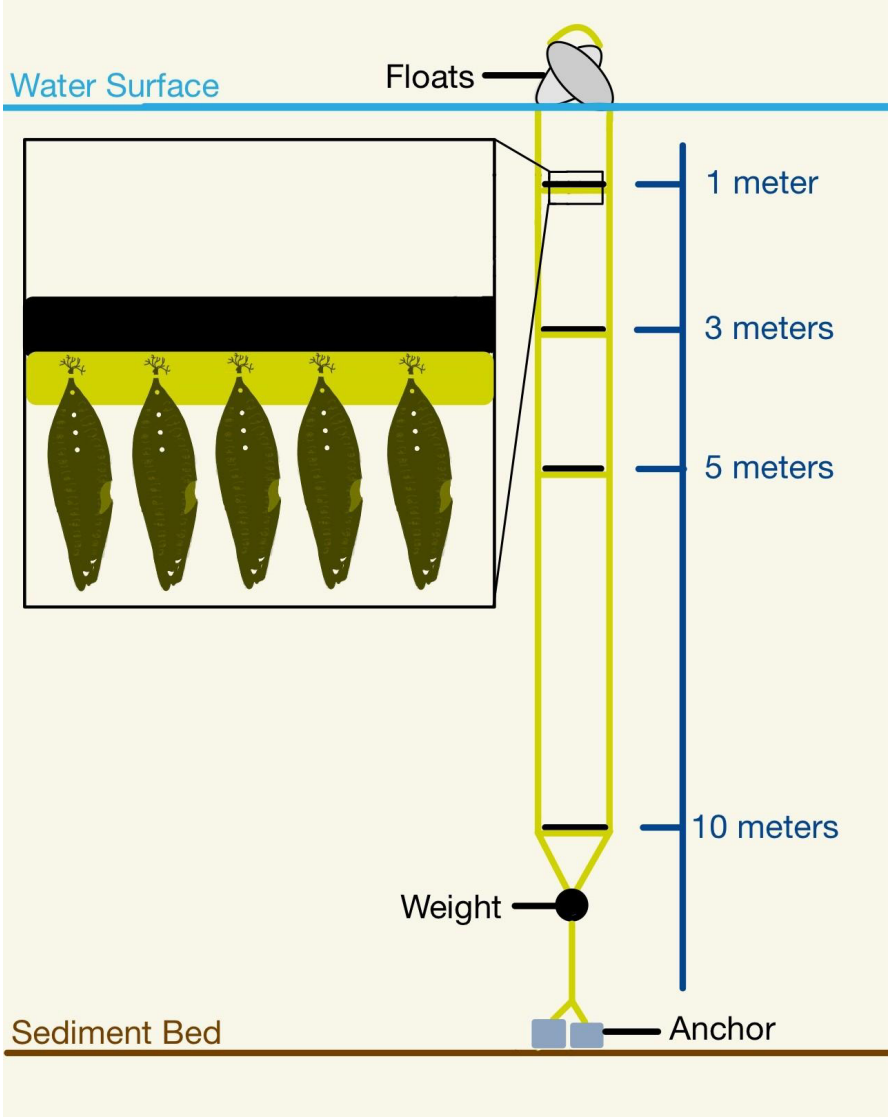



**Figure 2.** A 3-strand polypropylene line was constructed in a ladder-like structure with PVC pipes used as spreaders at each of the four depth conditions: 1, 3, 5, and 10 meters. The line was run along each PVC pipe to allow attachment of the five *Saccharina latissima* samples at each level by unravelling the line, poking the holdfast through, and closing the line back on the stipe. Enough line between the weight and anchor was provided to account for the tidal difference and ensure that the apparatus stayed upright at low tide and that the floats did not become submerged at high tide.

*2.3. Measurements taken*

A variety of measurements were taken prior to and/or after the treatment in order to estimate growth and compare for confounding factors. First, the area of each specimen was

calculated from photos using the image processing program ImageJ, and change in area was calculated by subtracting the initial area from the final.

A continuous excitation fluorescence system (Pocket PEA Chlorophyll Fluorometer, Hansatech Instruments, Norfolk, England) was used to evaluate the stress experienced by the specimens at each depth prior to and after treatment. Specimens were dark adapted for 20 minutes prior to sampling. “Yield”, the quantum yield of photosystem II as measured by chlorophyll fluorescence, gives the fraction of photons absorbed by the specimen that were utilized for photochemical reactions. This was used to assess how depth affects the efficiency of the specimen’s light-harvesting ability.

Growth rates were used as a proxy for production. This was measured by punching 4 holes at 5 cm intervals along the blade of the kelp, one of which was at the base of the stipe (below the meristem). The new distance between the other four holes and the hole at the base was then measured after treatment, yielding an estimate of elongation. This was then used to estimate productivity. Next, the “loss” rate was calculated by finding the difference between the expected final length and the actual final length (with the expected final length being calculated using the change in length of the meristem). This difference yielded an estimate of the amount of blade area that had been lost, which was then used to find a loss rate.

Photosynthetically active radiation (PAR) measurements were taken in triplicate from the experimental site in order to estimate irradiance over depth and calculate the light attenuation coefficient ($k$). Measurements were taken using the LI-192 Underwater Quantum Sensor in combination with the LI-250A Light Meter (Li-Cor, Lincoln, Nebraska).

The seaweed samples were first rinsed with fresh water to remove any symbiotic organisms, seawater residues, or debris. After removing excess surface moisture with a paper

towel, a 2 × 2 cm section of the blade was excised from the midpoint between the meristem and the tip. The collected tissue samples were then homogenized using a glass tissue homogenizer. Following homogenization, 10 mL of 100% ethanol was added, and the samples were stored in the dark at −4 °C for 24 hours. After extraction, the tissue debris was separated by centrifugation at 4000 rpm for 5 minutes, and the supernatant was filtered using a 0.45 µm syringe filter. The absorbance of each sample was measured with a spectrophotometer, and Chlorophyll-*a* concentration in the kelp was calculated using Equation 1 (Armeli Minicante et al., 2016).

$$Chl\ a\ (\mu g\ ml^{-1}) = -0.450 * A_{630} + 11.490\ 2 * A_{664} (\pm 0.011\ 54\ \mu g\ ml^{-1})$$

**Equation 1.** Ritchie algorithm for determining chlorophyll concentrations

*2.4. Statistics*

ANOVA tests were performed on each data set (fluorescence yield, growth rates, PAR, & chlorophyll concentrations) using Excel. Tukey's range test was performed as an additional step on any sets with significant results in order to determine which pairs had statistically significant differences in their means. Games and Howell's (1976) suggested error term that takes both differences in sample size and sample variance into account was used due to the high range of variances between treatments. Finally, a Growth–Irradiance (G–I) curve was fitted to the net growth rate data using the model proposed by Platt et al. (1980) in order to determine the relationship between light intensity at each depth and the corresponding average growth rate.

## 3. Results

*3.1. Blade Area*

On average, the 3m depth had the greatest change in area (371.8cm$^2$), followed by 1m (244.0cm$^2$), then 5m (194.0cm$^2$), then 10m (71.08cm$^2$). An ANOVA test showed that the average change in area (cm$^2$) was not consistent between all depth treatments ($p$=0.01). Tukey's test then demonstrated that the 10m treatment had a significantly different change in area from the 1m, 3m, and 5m treatments. None of the 1m, 3m, or 5m treatments had statistically different average change in areas from one another. However, the 3m versus 5m comparison was very close to significance ($p$=0.05).

*3.2. PEA*

| Fv/Fm | 1 m | 3 m | 5 m | 10 m |
|---|---|---|---|---|
| Day 0 | 0.68 | 0.71 | 0.69 | 0.72 |
| Day 14 | 0.75 | 0.76 | 0.78 | 0.75 |

Table 1. x

| | 1 m | 3 m | 5 m | 10 m |
|---|---|---|---|---|
| Fv/Fm Change (%) ± S.E | 7 ± 5.52 | 4.8 ± 1.88 | 8.8 ± 4.52 | 4.33 ± 5.33 |

Table 2.

The Fv/Fm yield measured after dark adaptation did not show any difference at a specific depth.

*3.3. Growth rates*

An ANOVA test showed that there was some variance in growth rates (cm$^2$) over treatments ($p$=0.046). Tukey's test then showed that the only pair with significantly different growth rates from one another was the 3m treatment compared with the 10m treatment.

The loss rate rate had no significant difference between treatments ($p$=0.28, $p$=0.14).

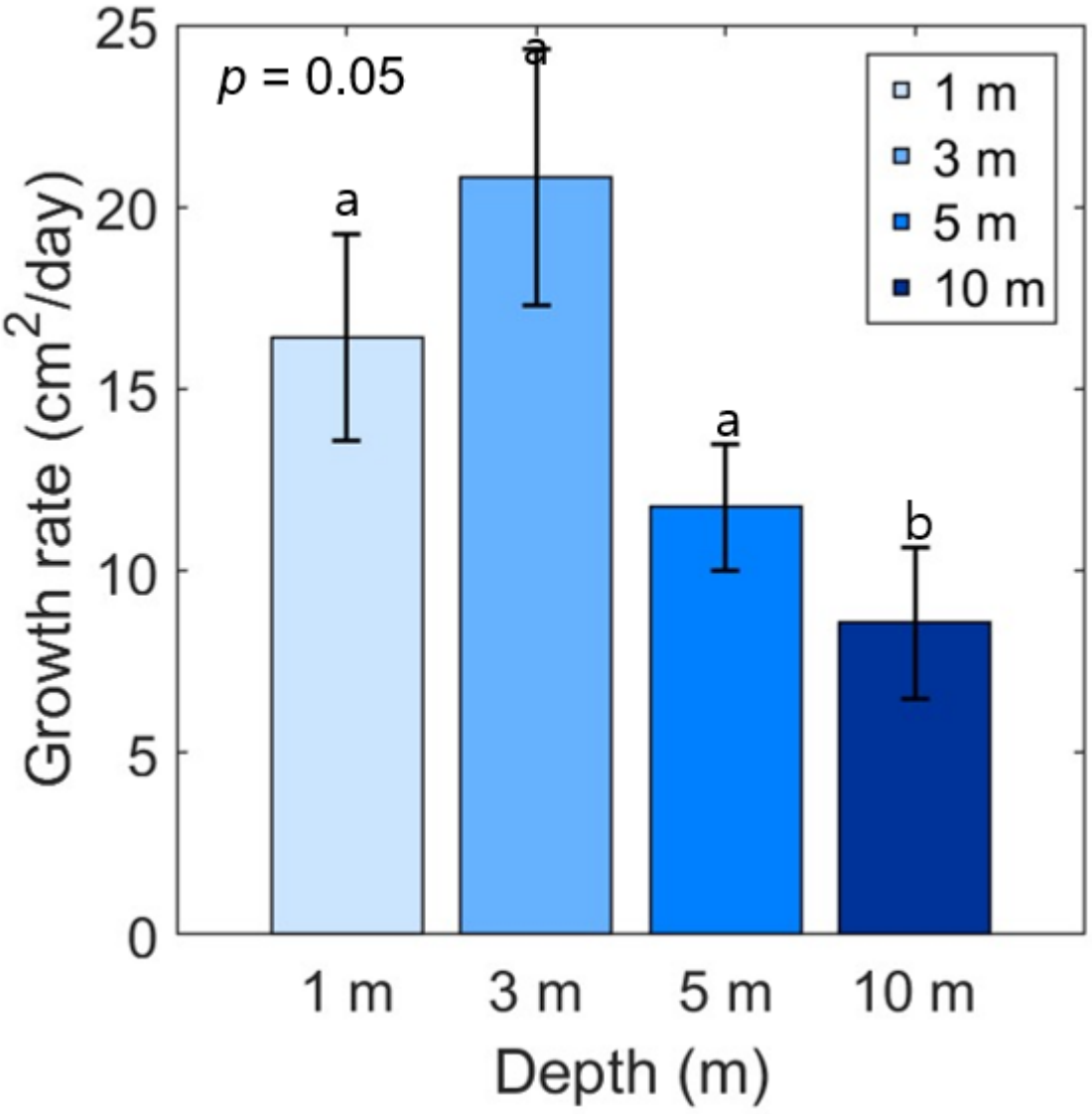



**Figure 3.** Average growth rate was calculated for the duration of the experiment, for each respective depth. Standard error bars were added to express statistical relationships. Growth rates found at 1, 3, and 5 m produced similar results, with 10 m being the only statistically different result, showing a much slower growth rate, relative to the 3 m condition.

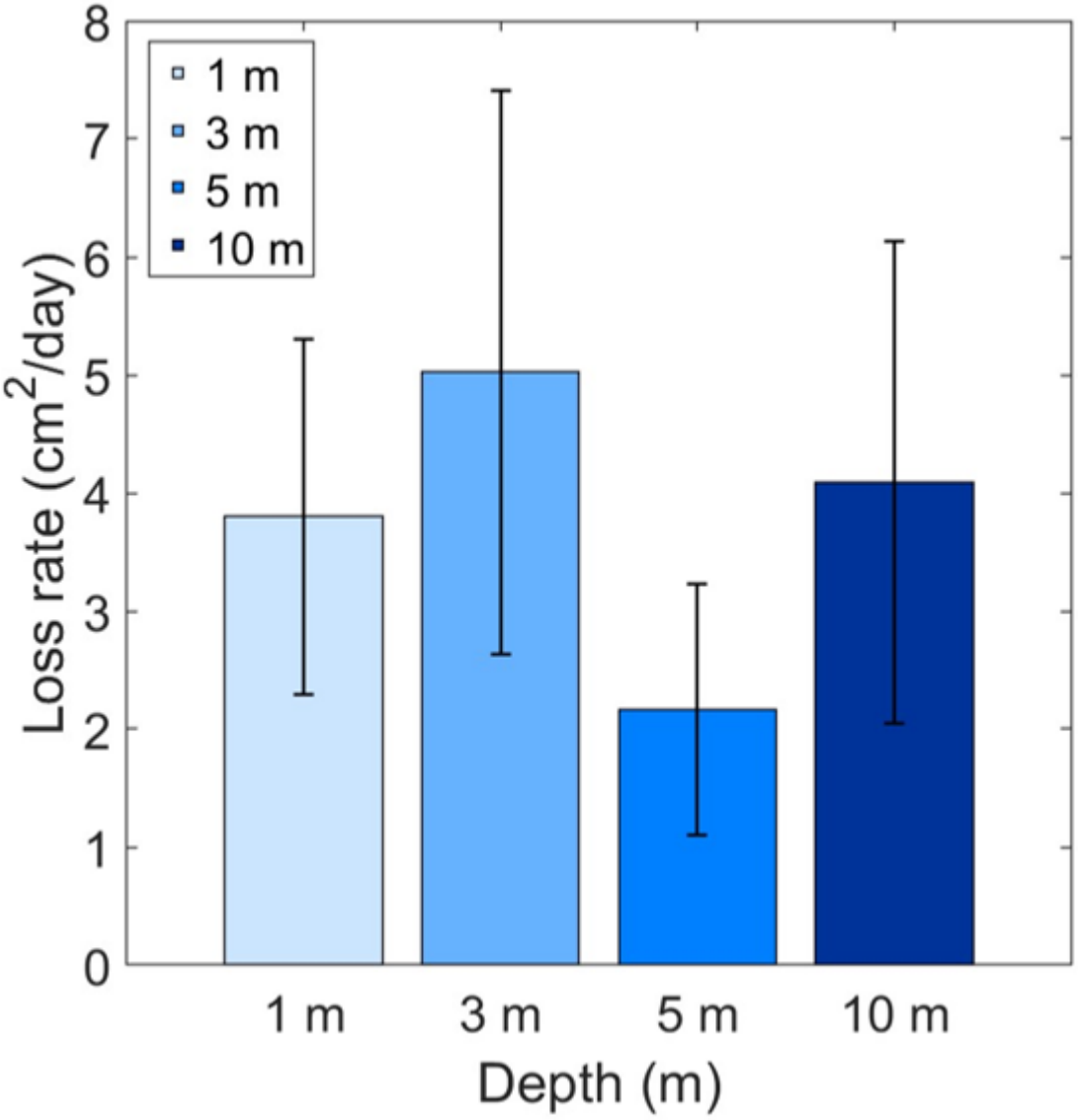



**Figure 4.** Average loss rate or erosion rate was determined through use of several calculations and represents the average area lost off of each blade at each respective condition. Standard error bars were added to express statistical relationships.

*3.4. Photosynthetically active radiation*

The light attenuation coefficient and the surface irradiance were found, yielding a light intensity curve described by the relationship $l(z) = 1324.6 \times e^{-0.290z}$ with an $R^2$ of 0.99. A linear regression comparing the light received at each depth treatment to the productivity rate of that treatment found no significant relationship ($R^2$=0.47).

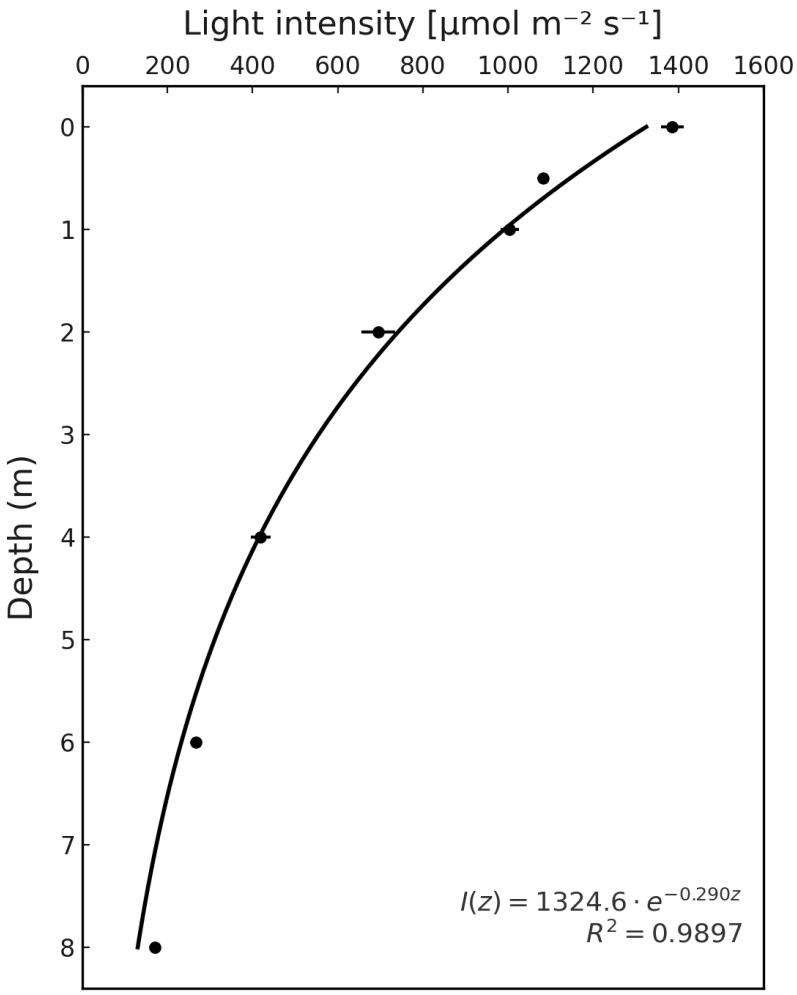



**Figure 5.** Light intensity variation with depth. Light attenuates according to the equation with a strong fit represented by the $R^2$ value. A logarithmic relationship can be observed.

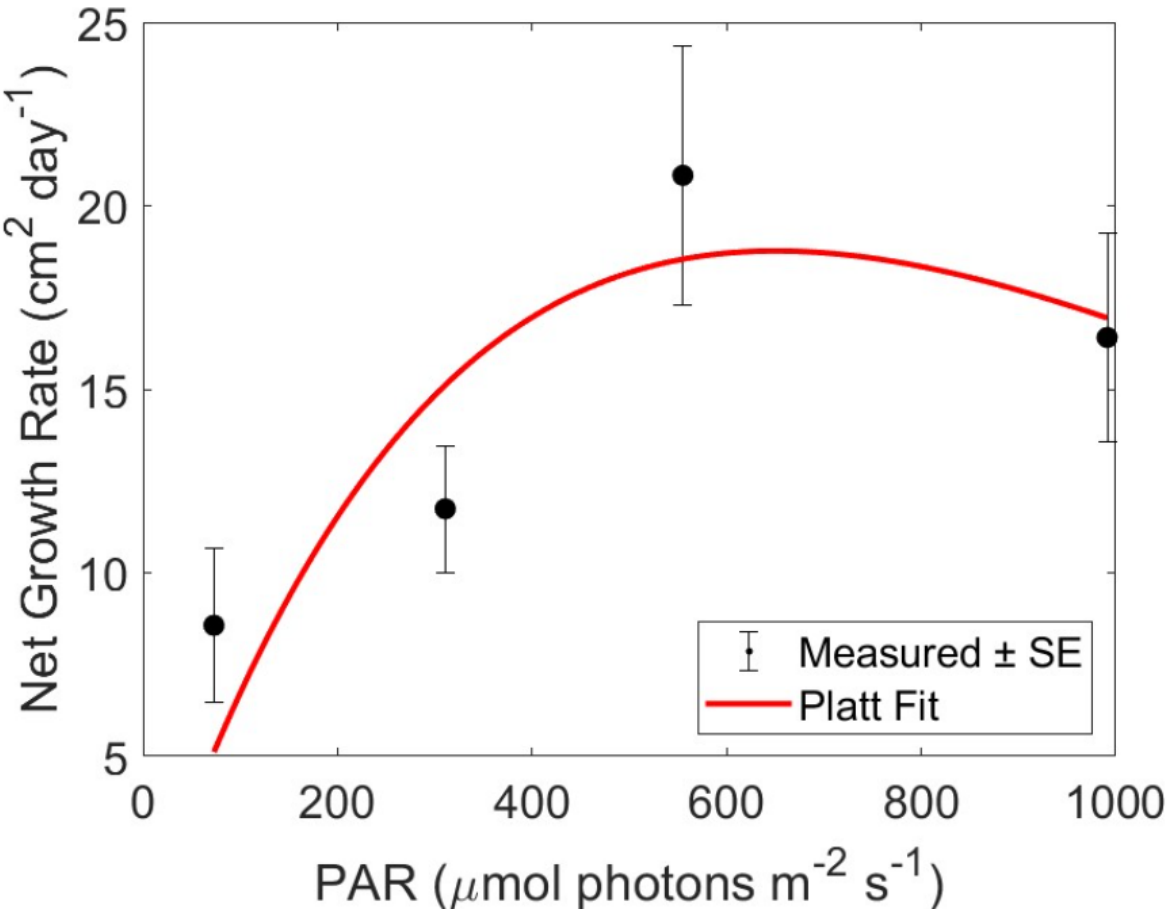



**Figure 6.** A Platt calibration was used to compare net growth rate data with PAR irradiance. Evidence of photoinhibition is present at the 1 meter condition (furthest to the right); however, PEA data (Tables 1 and 2) reveals that there was no significant evidence of photoinhibition. Maximum growth rate (Pmax) occurs at 794 µmol photons $m^{-2}$ $s^{-1}$ and the light intensity at which photosynthesis reaches saturation (Ik) occurs at 239.29 µmol photons $m^{-2}$ $s^{-1}$ (Platt, T., et al. 1980).

*3.5. Chlorophyll concentrations*

Each depth treatment had similar chlorophyll *a* concentrations, ranging from 12.0$\mu_{g\ ml^{-1}}$ for the 5m treatment to 15.3 $\mu_{g\ ml^{-1}}$ for the 1m treatment. An ANOVA test confirmed that there was no significant difference in average concentrations between treatment groups.

## 4. Discussion

*4.1. PEA*

The average Fv/Fm value on Day 14 was 0.76, suggesting that the experimental group was not affected by environmental stress (Huppertz et al., 1990; Franklin & Forster, 1997; Fig X.). The percentage change in Fv/Fm before and after treatment showed no significant differences among depths, indicating that environmental stress did not differ with depth. Although the 10 m samples exhibited the lowest trend in percentage change, this is likely due to their initially lower Fv/Fm values, which resulted in a smaller relative change.

*4.2. Chlorophyll*

The chlorophyll extractions completed on each blade were used to confirm the amount of chlorophyll-*a* concentrations present at varying depth conditions after 14 experimental days. No conclusive results came from the extraction process, represented by its exceptionally low $R^2$=0.05 value. This means that chlorophyll concentrations did not change significantly at the respective depth conditions over the duration of the experiment. While a very slight negative linear relationship exists between depth and chlorophyll concentrations, a definitive correlation could not be established between the two variables.

Several factors could have contributed to these inconclusive results. The reliability and accuracy of the results relied heavily on the methods used for completing the extraction, which were completed with low confidence. Additionally, it is likely that the 14 day duration of the experiment was not long enough to significantly alter the chlorophyll content in blades at varying depths. Cobos et al. (2025) found that storage of *Saccharina latissima* specimens for 16 weeks in complete darkness at 8 degrees Celsius was required for specimens to cease growth post-storage. With this, chlorophyll concentrations are unlikely to significantly change within a 1-2 week study when exposed to relatively low light irradiances, like those observed at ten meters (Cobos et al. 2025). Future studies should emphasize increased

confidence in extraction methods, a longer research window, and completing a similar project over multiple seasons in order to strengthen data quality, represent fluctuations in seasonality, and increase understanding of the most photosynthetically and ecologically productive depth and conditions for *Saccharina latissima.*

*4.3. Growth*

Although differences between productivity rates at the 1, 3, and 5 m depths were not statistically significant, the kelp plants grown 3 meters from the surface showed the greatest change in both blade length and area. Plants grown at 3 meters depth also displayed the highest average growth rate, and this rate was significantly higher in comparison with the mean growth rate at 10 meters. The plants showed markedly lower increases in blade length and area when grown at 10 meters, likely due to diminished light availability.

These results are in agreement with the findings of Forbord et al.'s 2019 study, in which researchers cultivated *Saccharina* at varying depths across a latitudinal gradient; the group found biomass and length yields to be highest at 1-2 meters depth in comparison with 8-9 meters. The intermediate depth of 5 meters also showed no significant difference in growth in comparison with the 1-2 meter treatment (Forbord et al., 2020). This data provides further support for the importance of kelps in coastal ecosystems; as productivity has been shown to decline with depth, kelps flourishing at near-surface depths are crucial primary producers, generating rich food webs and fueling secondary productivity in these habitats (Smale, 2019).

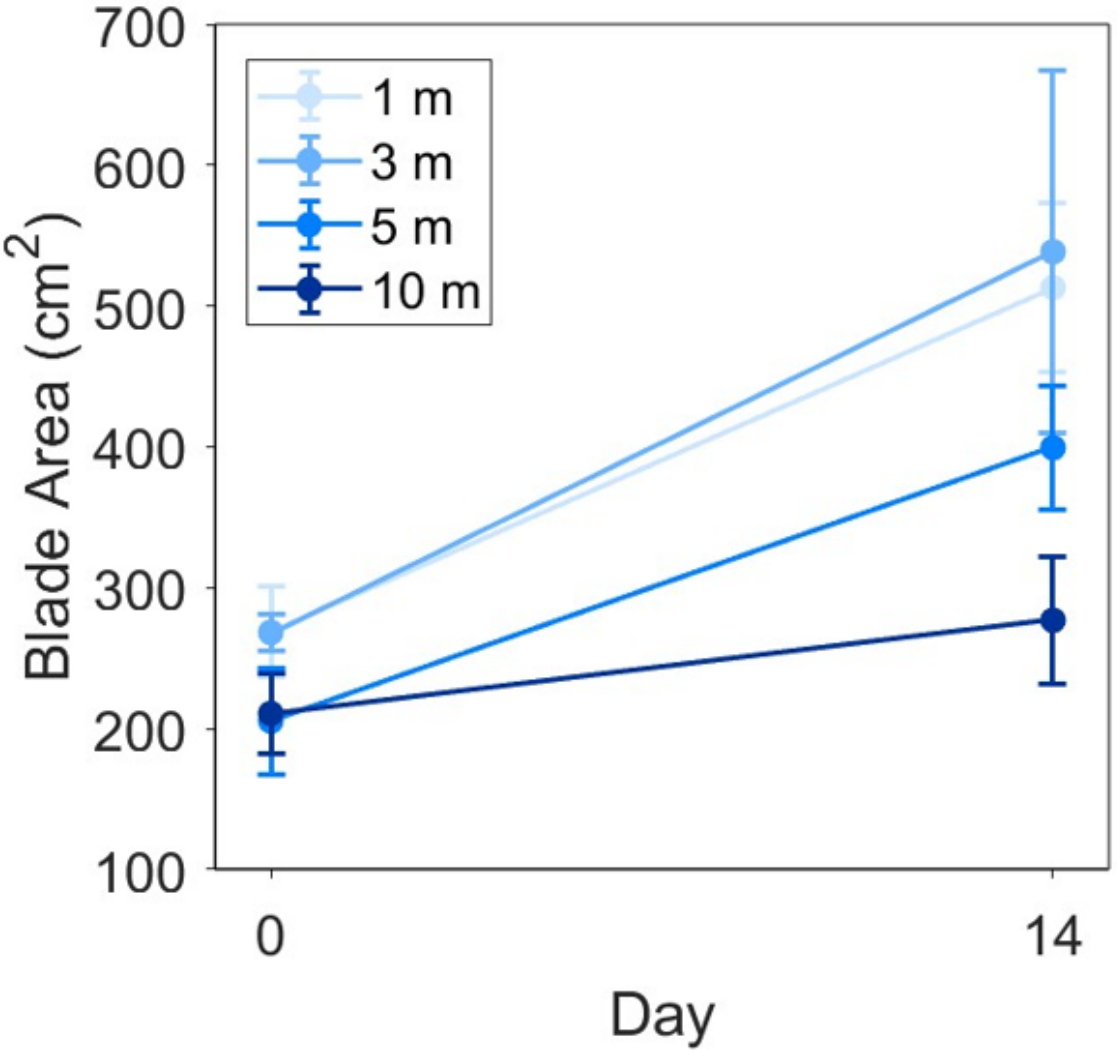



**Figure 7.** Average blade areas were calculated at the beginning (day 0) and end (day 14) by averaging area over each replicate at each respective depth. Standard error bars were added to express statistical relationships. Samples at three meters increased the greatest amount with samples at ten meters increasing in area significantly less than other conditions.

*4.4. Light Attenuation and Growth Rates*

Establishing an estimate of productivity among the samples exposed to varying concentrations of light was important in understanding the relationship between growth and irradiance, which could be useful for future model development. Using net growth rates averaged over each depth level, a fit modeled after Platt et al. (1980) was used to estimate growth rates

given a certain photosynthetically active radiation (PAR) value. While the growth rate data gained from this experiment fit this model poorly, there were several nodes of interest within these results. Surface conditions were found to be near photoinhibition, but narrowly missed this growth-inhibiting cutoff, as seen in the PEA data (Tables 1 and 2). Additionally, the condition just below the surface at 3 meters was seen to almost overlap with the PAR value corresponding to the maximum growth rate, indicating high efficiency in PAR usage. In contrast, conditions deeper in the water column, like those at 10 meters, saw a substantial decrease in net growth rate when exposed to PAR levels that were less than those necessary for photosynthetic saturation. Given the rough fit of this experiment's data with the model, future studies are necessary in further investigating this relationship; however, an idea of the PAR levels needed to yield certain growth rates in *S. latissima* was revealed, and may be used to estimate productivity given similar conditions in alternate locations/environments.

### *4.5. Limitations*

The two-week period may be relatively short for observing physiological changes in kelp (Cobos et al., 2025). This suggests that species grown for longer time periods within the environment may exhibit different physiological response patterns, although none were observed in this study. Additionally, physiological differences might appear in kelps that naturally occur at varying depths, as this study used kelp collected at similar depth conditions.

Since the data in this study reflects only the summer growth rates of *S. latissima*, analyzing seasonal variations in growth could also deepen our understanding of productivity differences on a broader scale.

This study focused on light attenuation at various fixed depths, and was conducted in an intertidal setting. Because this experimental design excluded the influence of Puget Sound's semidiurnal tides, which cause fluctuations in depth for kelp species, conducting experiments that reflect the actual variation in subtidal environments may serve as an important direction for future research.

What other factors might influence growth and productivity? What did you do with your CTD data? And nitrogen levels from Bailey?

What differences in light might you expect from a system that was attached to the bottom as opposed to being suspended from the surface?

*4.6. Implications*

Kelp forests are increasingly threatened by the effects of climate change and ocean warming, having declined as much as 38% according to a 2016 review (Krumhansl et al., 2016). Kelps' status as ecosystem engineers means that variation in environmental factors– such as temperature, light and nutrient availability, and substrate quality– can have widespread effects across trophic levels.

Evaluating the relationship between light attenuation and growth at depth can help predict how kelp forest health is impacted by changing light availability, and this methodology may also enhance the efficacy of models which estimate ecosystem productivity. Any dataset that includes spatial estimates of kelp density throughout the upper zones of the water column could be coupled with this methodology to create a large-scale model of productivity throughout an area. For example, the Washington Department of Natural Resources' kelp monitoring program

collects a wide range of datasets which estimate kelp abundance throughout Puget Sound (*Kelp Monitoring | Department of Natural Resources*, 2023). This data could be used in conjunction with these methods to estimate primary productivity on large scales.

As conditions continue to change in coastal habitats, kelp populations will respond to these shifts, causing broader alterations to food web structures and carbon export (Smale, 2019). It is urgent, therefore, to study the response of these key species to changing environmental drivers.

**Acknowledgements & Attribution**

Thank you to T. Mumford, D.W. Freshwater, & D. Claar for guidance and support throughout the experimental process, and to E. Carrington for the use of her equipment. Thank you to Friday Harbor Laboratories and the broader University of Washington for funding and resources. Thank you to M. Mallone and I. Robinson for contributions in the form of synonyms and morale.

**References**

Armeli Minicante, S., Ambrosi, E., Back, M., Barichello, J., Cattaruzza, E., Gonella, F., Scantamburlo, E., & Trave, E. (2016). Development of an eco-protocol for seaweed chlorophylls extraction and possible applications in dye sensitized solar cells. *Journal of Physics D: Applied Physics*, 49(29), 295601. https://doi.org/10.1088/0022-3727/49/29/295601

Berry, H. D., Mumford, T. F., Christiaen, B., Dowty, P., Calloway, M., Ferrier, L., Grossman, E. E., & VanArendonk, N. R. (2021). Long-term changes in kelp forests in an inner basin of the Salish Sea. *PLOS ONE, 16*(2), e0229703.

Cobos, P., Gordillo, F. J. L., Roza, P., Wulff, A., Smerdou, C. (2025). Short-term response to light after the polar night in the Arctic kelps Alaria esculenta and Saccharina latissima. Marine Environmental Research, 210. https://doi.org/10.1016/j.marenvres.2025.107298

Diehl, N., Li, H., Scheschonk, L., Burgunter-Delamare, B., Niedzwiedz, S., Forbord, S., Sæther, M., Bischof, K., & Monteiro, C. (2024). The sugar kelp *Saccharina latissima* I: Recent advances in a changing climate. *Annals of Botany, 133*(1), 183–212. doi:10.1093/aob/mcad173

Eger, A.M., Marzinelli, E.M., Beas-Luna, R. *et al.* The value of ecosystem services in global marine kelp forests. *Nat Commun* 14, 1894 (2023). https://doi.org/10.1038/s41467-023-37385-0

Fernández, P. A., Navarro, J. M., Camus, C., Torres, R., & Buschmann, A. H. (2021). Effect of environmental history on the habitat-forming kelp *Macrocystis pyrifera* responses to ocean acidification and warming: A physiological and molecular approach. *Scientific Reports*, 11, Article 2510. https://doi.org/10.1038/s41598-021-82094-7

Forbord, S., Matsson, S., Brodahl, G. E., Bluhm, B. A., Broch, O. J., Handå, A., Metaxas, A., Skjermo, J., Steinhovden, K. B., & Olsen, Y. (2020). Latitudinal, seasonal and depth-dependent variation in growth, chemical composition and biofouling of cultivated *Saccharina latissima* (Phaeophyceae) along the Norwegian Coast. *Journal of Applied Phycology, 32*(4), 2215–2232. doi:10.1007/s10811-020-02038-y

Franklin, L. A., & Forster, R. M. (1997). The changing irradiance environment: consequences for marine macrophyte physiology, productivity and ecology. *European Journal of Phycology*, 32(3), 207–232. https://doi.org/10.1080/09670269710001737815

Games, P.A. and Howell, J.F. (1976) Pairwise Multiple Comparison Procedures with Unequal N's and/or Variances: A Monte Carlo Study. *Journal of Educational and Behavioural Statistics*, 1, 113-125. https://doi.org/10.3102/10769986001002113

Graham, M. H., Vásquez, J. A., & Buschmann, A. H. (2007). Global ecology of the giant kelp *Macrocystis*: From ecotypes to ecosystems. In R. N. Gibson, R. J. A. Atkinson, & J. D. M. Gordon (Eds.), *Oceanography and Marine Biology: An Annual Review* (Vol. 45, pp. 39–88). CRC Press.

Green, L. A., & Coco, G. (2014). Review of the influence of hydrodynamics on algal morphology, with a focus on macroalgae. *Journal of Phycology, 50*(5), 1005–1020. doi:10.1111/jpy.12236

HEPBURN, C.D., PRITCHARD, D.W., CORNWALL, C.E., McLEOD, R.J., BEARDALL, J., RAVEN, J.A. and HURD, C.L. (2011), Diversity of carbon use strategies in a kelp forest community: implications for a high CO2 ocean. Global Change Biology, 17: 2488-2497. https://doi.org/10.1111/j.1365-2486.2011.02411.x

Howell, D. C. (2018). Multiple Comparisons With Unequal Sample Sizes. *University of Vermont Website*. https://www.uvm.edu/~statdhtx/StatPages/MultipleComparisons/unequal_ns_and_mult_comp.html

Huppertz, K., Hanelt, D., & Nultsch, W. (1990). Photoinhibition of photosynthesis in the marine brown alga *Fucus serratus* as studied in field experiments. *Marine Ecology Progress Series*, 66(1/2), 175–182. https://doi.org/10.3354/meps066175

*Kelp Monitoring | Department of Natural Resources*. (2023). WA.gov. https://dnr.wa.gov/aquatics/aquatic-science/nearshore-habitat-program/kelp-monitoring

Krumhansl, K. A., Okamoto, D. K., Rassweiler, A., Novak, M., Bolton, J. J., Cavanaugh, K. C., Connell, S. D., Johnson, C. R., Konar, B., Ling, S. D., Micheli, F., Norderhaug, K. M., Pérez-Matus, A., Sousa-Pinto, I., Reed, D. C., Salomon, A. K., Shears, N. T., Wernberg,

T., Anderson, R. J., … Byrnes, J. E. (2016). Global patterns of Kelp Forest change over the past half-century. *Proceedings of the National Academy of Sciences*, *113*(48), 13785–13790. https://doi.org/10.1073/pnas.1606102113

Meng, C., & Mumford, T. (2020). Patterns of growth and erosion of blades of the kelp *Saccharina latissima*. Remote Internship Report. University of Washington Friday Harbor Labs. https://digital.lib.washington.edu/server/api/core/bitstreams/b453e954-762d-4d4a-bfea-d3e8e634bc43/content

Minicante, S. A. et al. (2016) . Development of an eco-protocol for seaweed chlorophylls extraction and possible applications in dye sensitized solar cells . Journal of Physics D: Applied Physics 49 295601. doi:10.1088/0022-3727/49/29/295601

Pfister, C. A., Berry, H. D., & Mumford, T. (2017). The dynamics of kelp forests in the Northeast Pacific Ocean and the relationship with environmental drivers. *Journal of Ecology, 106*(4), 1520–1533. doi:10.1111/1365-2745.12908

Platt, T., C. L. Gallegos, and W. G. Harrison. 1980. "Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton." *Journal of Marine Research* 38, (4). https://elischolar.library.yale.edu/journal_of_marine_research/1525

Robin, F. J. (2023). Climate change impacts on kelp: Physiological responses across habitats, species, and populations. Doctoral dissertation, University of Washington. http://hdl.handle.net/1773/50707

Roy, S., et al. (2024) Subarctic sugar kelp (*saccharina latissima*, Phaeophyceae) summer productivity and contribution to carbon budgets. *Journal of Phycology*, 60(6), 1585–1600, https://doi.org/10.1111/jpy.13525.

Serôdio, J., & Catarino, F. (1999). Fortnightly light and temperature variability in estuarine intertidal sediments and implications for microphytobenthos primary productivity. *Aquatic Ecology, 33*(3), 235–241. doi:10.1023/A:1009907003562

Smale, D.A. (2020), Impacts of ocean warming on kelp forest ecosystems. New Phytol, 225: 1447-1454. https://doi.org/10.1111/nph.16107

Steneck, R. S., Graham, M. H., Bourque, B. J., Corbett, D., Erlandson, J. M., Estes, J. A., & Tegner, M. J. (2002). Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environmental Conservation, 29*(4), 436–459. doi:10.1017/S0376892902000322

Stomp, M., Huisman, J., Stal, L. J., & Matthijs, H. C. P. (2007). Colorful niches of phototrophic microorganisms shaped by vibrations of the water molecule. *The ISME Journal, 1*, 271–282. doi:10.1038/ismej.2007.59

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

Tallis, H. (2009). Kelp and rivers subsidize rocky intertidal communities in the Pacific Northwest (USA). *Marine Ecology Progress Series, 389*, 85–96. doi:10.3354/meps08138

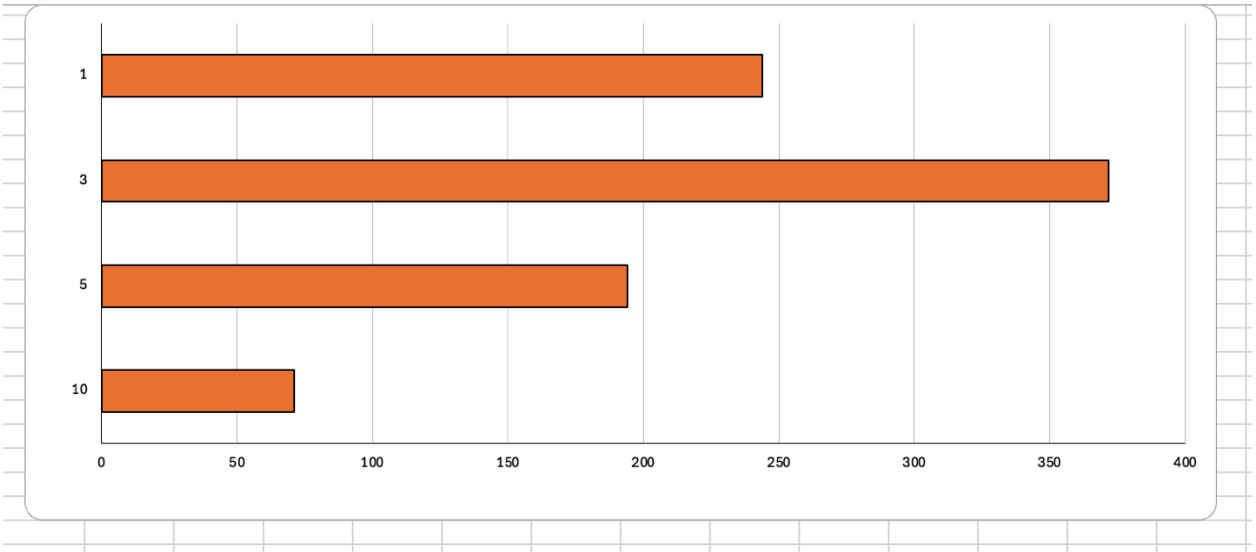
# Appendices

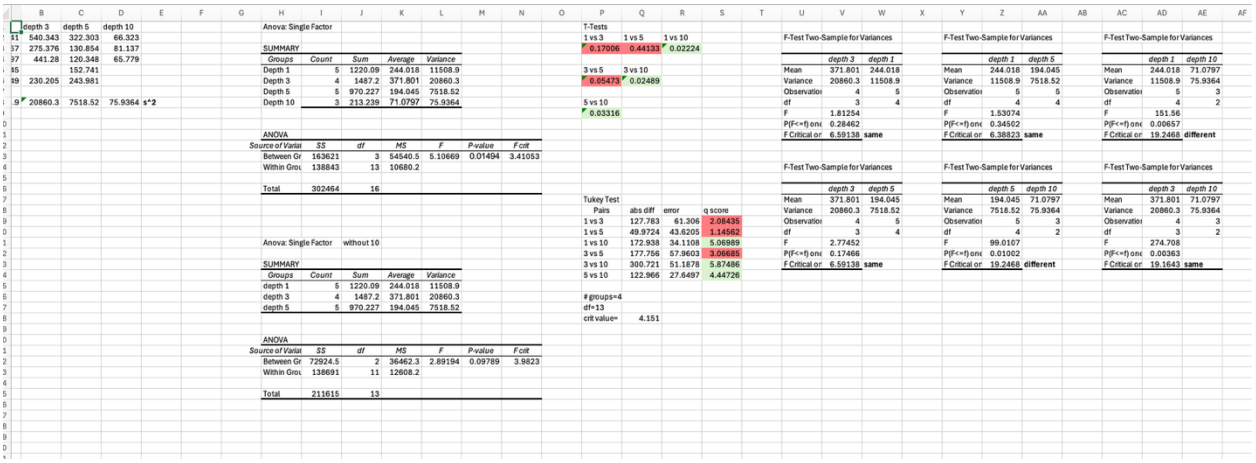
| Sample # | 0 (cm2) | 8 (cm2) | 14 (cm2) | in Area |
|---|---|---|---|---|
| 1 | 348.996 | 370.909 | 453.237 | 104.241 |
| 2 | 309.114 | 285.225 | 667.071 | 357.957 |
| 3 | 207.481 | 251.58 | 433.878 | 226.397 |
| 4 | 298.557 | 371.915 | 642.602 | 344.045 |
| 5 | 181.373 | 257.599 | 368.822 | 187.449 |
| 6 | 290.825 | 464.683 | 831.168 | 540.343 |
| 7 | 277.283 | 390.87 | 552.659 | 275.376 |
| 8 | 290.825 | 499.238 | 732.105 | 441.28 |
| 9 | 221.436 | 364.967 | 86.077 | |
| 10 | 260.596 | 301.967 | 490.801 | 230.205 |
| 11 | 177.599 | 333.954 | 499.902 | 322.303 |
| 12 | 232.811 | 253.07 | 363.665 | 130.854 |
| 13 | 144.35 | 180.567 | 264.698 | 120.348 |
| 14 | 340.163 | 326.057 | 492.904 | 152.741 |
| 15 | 132.267 | 157.367 | 376.248 | 243.981 |
| 16 | 297.033 | 293.98 | 363.356 | 66.323 |
| 17 | 173.882 | 161.458 | 255.019 | 81.137 |
| 18 | 146.865 | 175.554 | 212.644 | 65.779 |
| 19 | 177.158 | 220.141 | | |
| 20 | 259.305 | 246.361 | | |

| Condition | Day 0 | Day 8 | Day 14 |
|---|---|---|---|
| 1 | 269.104 | 307.446 | 513.122 |
| 3 | 268.193 | 404.345 | 538.562 |
| 5 | 205.438 | 250.203 | 399.483 |
| 10 | 210.849 | 219.499 | 277.006 |

| Condition | in Area | SE |
|---|---|---|
| 1 | 244.018 | 47.9769 |
| 3 | 371.801 | 72.2155 |
| 5 | 194.045 | 38.7776 |
| 10 | 71.0797 | 5.03112 |







| | A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|---|
| 1 | **Specimen** | **Depth** | **Replicates** | **Day 13 Yield** | **Day 0 Yield** | **Yield change (%)** | **Yield change Average(%)** | **Yield change STD(%)** | |
| 2 | 1 | | 1 | 0.76 | 0.66 | 10 | 7 | 12.34908904 | |
| 3 | 2 | | 2 | 0.77 | 0.5 | 27 | | | |
| 4 | 3 | 1 | 3 | 0.73 | 0.77 | -4 | | | |
| 5 | 4 | | 4 | 0.74 | 0.71 | 3 | | | |
| 6 | 5 | | 5 | 0.75 | 0.76 | -1 | | | |
| 7 | 6 | | 1 | 0.76 | 0.72 | 4 | 4.8 | 4.207136794 | |
| 8 | 7 | | 2 | 0.76 | 0.72 | 4 | | | |
| 9 | 8 | 3 | 3 | 0.78 | 0.75 | 3 | | | |
| 10 | 9 | | 4 | 0.74 | 0.73 | 1 | | | |
| 11 | 10 | | 5 | 0.74 | 0.62 | 12 | | | |
| 12 | 11 | | 1 | 0.8 | 0.59 | 21 | 8.8 | 10.10940156 | |
| 13 | 12 | | 2 | 0.76 | 0.81 | -5 | | | |
| 14 | 13 | 5 | 3 | 0.78 | 0.71 | 7 | | | |
| 15 | 14 | | 4 | 0.78 | 0.62 | 16 | | | |
| 16 | 15 | | 5 | 0.77 | 0.72 | 5 | | | |
| 17 | 16 | | 1 | 0.75 | 0.76 | -1 | 4.333333333 | 9.237604307 | |
| 18 | 17 | | 2 | 0.76 | 0.61 | 15 | | | |
| 19 | 18 | 10 | 3 | 0.75 | 0.76 | -1 | | | |
| 20 | 19 | | 4 | | 0.73 | | | | |
| 21 | 20 | | 5 | | 0.75 | | | | |
| 22 | | | | | | | | | |

*Figure 1. PEA Raw Data*

| | A | B | C | D | E | F |
|---|---|---|---|---|---|---|
| 1 | **Specimen** | **Depth** | **Replicates** | **Yield** | **PI** | |
| 2 | 1 | | 1 | 0.66 | 0.54 | |
| 3 | 2 | | 2 | 0.5 | 0.1 | |
| 4 | 3 | 1 | 3 | 0.77 | 1.47 | |
| 5 | 4 | | 4 | 0.71 | 0.65 | |
| 6 | 5 | | 5 | 0.76 | 4.42 | |
| 7 | 6 | | 1 | 0.72 | 0.83 | |
| 8 | 7 | | 2 | 0.72 | 1.27 | |
| 9 | 8 | 3 | 3 | 0.75 | 1.05 | |
| 10 | 9 | | 4 | 0.73 | 0.78 | |
| 11 | 10 | | 5 | 0.62 | 0.36 | |
| 12 | 11 | | 1 | 0.59 | 0.16 | |
| 13 | 12 | | 2 | 0.81 | 2.12 | |
| 14 | 13 | 5 | 3 | 0.71 | 1.04 | |
| 15 | 14 | | 4 | 0.62 | 0.6 | |
| 16 | 15 | | 5 | 0.72 | 1.09 | |
| 17 | 16 | | 1 | 0.76 | 0.86 | |
| 18 | 17 | | 2 | 0.61 | 0.5 | |
| 19 | 18 | 10 | 3 | 0.76 | 3.5 | |
| 20 | 19 | | 4 | 0.73 | 0.82 | |
| 21 | 20 | | 5 | 0.75 | 1.59 | |
| 22 | | | | | | |

*Figure 2. PEA 250625 data*

| | A | B | C | D | E |
|---|---|---|---|---|---|
| 1 | **Specimen** | **Depth** | **Replicates** | **Yield** | **PI** |
| 2 | 1 | | 1 | 0.76 | 1.77 |
| 3 | 2 | | 2 | 0.77 | 1.54 |
| 4 | 3 | 1 | 3 | 0.73 | 0.93 |
| 5 | 4 | | 4 | 0.74 | 1.64 |
| 6 | 5 | | 5 | 0.75 | 1.29 |
| 7 | 6 | | 1 | 0.76 | 2.12 |
| 8 | 7 | | 2 | 0.76 | 1.71 |
| 9 | 8 | 3 | 3 | 0.78 | 2.49 |
| 10 | 9 | | 4 | 0.74 | 0.77 |
| 11 | 10 | | 5 | 0.74 | 1.58 |
| 12 | 11 | | 1 | 0.8 | 2.17 |
| 13 | 12 | | 2 | 0.76 | 1.86 |
| 14 | 13 | 5 | 3 | 0.78 | 2.12 |
| 15 | 14 | | 4 | 0.78 | 2.74 |
| 16 | 15 | | 5 | 0.77 | 1.69 |
| 17 | 16 | | 1 | 0.75 | 2.03 |
| 18 | 17 | | 2 | 0.76 | 4.27 |
| 19 | 18 | 10 | 3 | 0.75 | 1.35 |
| 20 | 19 | | 4 | | |
| 21 | 20 | | 5 | | |
| 22 | | | | | |

*Figure 3. PEA 250709 Data*