Variation in the Morphological and Physiological Traits of a Foundational Macroalga along a 20-Degree Latitudinal Gradient

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Declarations

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed............*M.Zawadzka*..
Date...............23.09.2023..

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

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I hereby give consent for my thesis, if accepted, to be available for electronic sharing

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The University's ethical procedures have been followed and, where appropriate, that ethical approval has been granted.

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Glossary of Terms and Abbreviations

Term/Abbreviation	Meaning
STA	Specific Thallus Area
Slope of Photosynthesis (α)	(α) informing about how effectively the sunlight is converted into energy before reaching light saturation
Pmax	The maximum rate of photosynthesis under optimal conditions
ISat	The light intensity at which the rate of photosynthesis reaches its maximum
P-I Curve	Photosynthesis-Irradiance Curve

Acknowledgments

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Summary
Large brown macroalgal species are highly plastic primary producers that shape the intertidal zones of temperate regions. Their plasticity enables them to display a range of morphological traits, including variations in total length, blade thickness, and structural complexity, in response to environmental factors. Using a trait-based approach allows us to examine the effects of biotic and abiotic factors on macroalgae, offering insights into the functioning of these ecosystems. Most current studies on macroalgal traits have primarily concentrated on a limited geographical range characterized by variable environmental factors such as temperature and salinity. In this study, the variation in traits of foundation macroalgae is examined across a 20-degree latitudinal gradient, extending from Portugal, through the central region of Wales, to the cooler range in Scotland. In response to the harsher climate and increased desiccation stress in southern regions, individuals were expected to exhibit reduced size and thicker blades. Similarly, increased temperatures in the south which are known to enhance metabolic rates, were expected to increase photosynthetic performance. In each region, morphological traits of individuals sampled from two shores were collected, and their photosynthetic parameters were measured in a mesocosm study – a controlled experiment assessing photosynthetic parameters. The size, as well as blade and stipe thickness, decreased towards the south. Although a decrease in blade thickness at lower latitudes was unexpected, the study found that the more acquisitive strategy of the southern population was reflected in its blade morphology. Photosynthetic performance was higher in Wales and Portugal than in Scotland, suggesting greater photosynthetic capacity of populations inhabiting lower latitudes. In contrast to our expectations, findings indicated that Wales, rather than the southernmost location (Portugal) was characterised by individuals exhibiting the highest photosynthetic performance and the most pronounced influence of morphological traits on the rate of photosynthesis. This observation may be attributed to the mid-range morphological traits of individuals compared to other populations, resulting from the region's temperate climate.

Lay Abstract

Large brown macroalgae, such as kelps and rockweeds, are adaptable foundation species that shape the intertidal zones in temperate regions and support important environmental roles, including providing habitat for fish, and protection against coastal erosion. Their physical features (traits) in particular, total length and blade thickness, are measurable characteristics that influence how they survive, grow, and reproduce, reflecting their overall success in the environment. Using a trait-based approach to study macroalgae helps us understand how living (biotic) and non-living (abiotic) factors affect these organisms, giving us better insights into how ecosystems work. Previous research has shown that differences in traits like size and the thickness of blades are influenced by environmental factors such as water temperature, salinity, and exposure across different geographical regions. In addition, variations in physiological traits, such as photosynthesis rates, have been observed, offering insights into how the efficiency of photosynthesis influences the growth and overall performance of individual macroalgae (Figure 1). Therefore, studying both the physical features and physiological characteristics of macroalgae, as well as their relationships across different regions, could provide a deeper understanding of how these organisms adapt to their environments to enhance their performance. The following study investigates the differences in the shape and function of foundational macroalgae across a 20-degree latitudinal gradient, from the southern populations in Portugal to the central region of Wales and up to the cooler waters of Scotland. We measured the physical features of the collected samples, including total length, blade, and stipe thickness. Following this, the samples were placed in a laboratory experiment to collect data on their photosynthetic performance. Given the warmer climate and increased desiccation stress in southern regions, we anticipated that individuals from these areas would exhibit reduced sizes and thicker blades. Moreover, since higher temperatures in the south are known to enhance metabolic rates, we expected that individuals living in lower latitudes would demonstrate greater photosynthetic efficiency. Contrary to our expectations, findings showed that the size of individuals along with the thicknesses of blade and stipe decreased towards the southern region, reaching the lowest values in Portugal. This could be due to increased heat, desiccation stress, and higher grazing pressure typical of warmer regions. Additionally, both the effectiveness and the speed of photosynthesis were higher in Wales and Portugal compared to Scotland. Ultimately, the findings showed that Wales, not Portugal—the southernmost location—had the best photosynthetic performance. The physical characteristics of individuals from the central region (the mid-range compared to other populations) may be the most favourable for photosynthesis and have the greatest potential to boost their maximum ability to photosynthesize, which may be due to the moderate climate. Nevertheless, the study highlights the complexity of the relationship between physiological features and photosynthetic efficiency, suggesting that this interaction involves multiple factors and is likely influenced by region-specific environmental conditions.

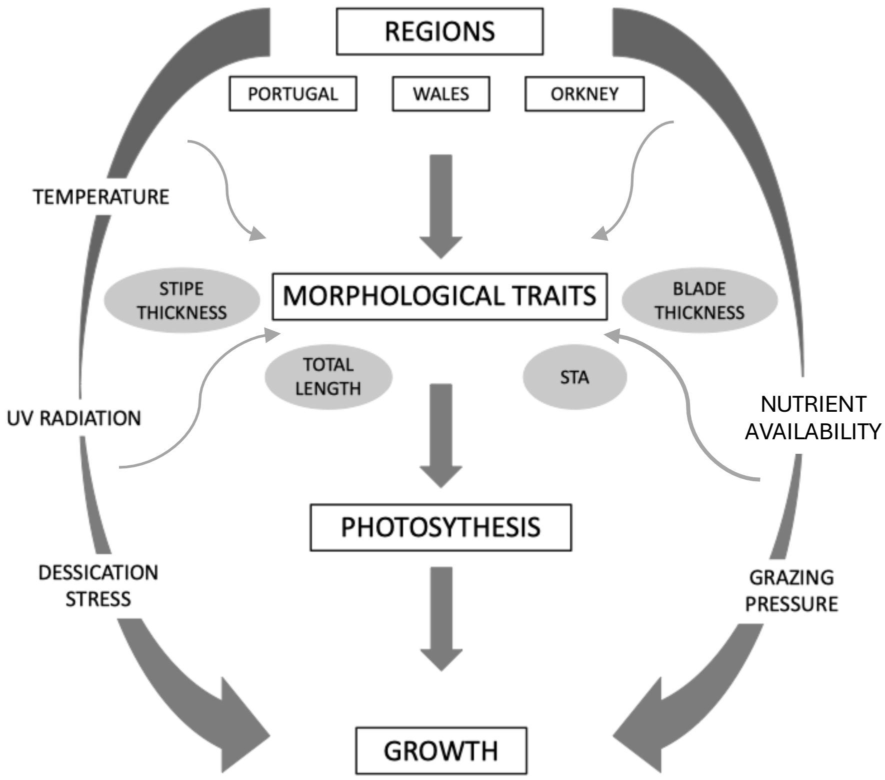

Figure 1. Schematic diagram illustrating the influence of physiological features (stipe and blade thicknesses, total length, specific thallus area (STA)) on photosynthesis and subsequent growth of *F. serratus* across three examined regions (Orkney, Wales, and Portugal). Climatic conditions specific to each region directly affect both morphological traits and growth, emphasising the complex interactions between environmental conditions, morphology, photosynthetic performance, and the growth of individuals.

1. Introduction

Examining the variation in functional traits within communities and among individuals of the same species provides essential insights into how these variations influence the ecosystem functioning by associating individual characteristics with broader ecological processes (Messier et al., 2010; Wright et al., 2005). Traits can be defined at the individual level describing the morphological and physiological characteristics that reflect how an organism responds and adapts to environmental conditions and competition, ultimately determining its fitness and survival success (Adler et al., 2014; Messier et al., 2010; Violle et al., 2007). Moreover, grouping organisms according to their traits instead of taxonomic classification could be useful in assessing ecological patterns on a larger scale by measuring the number of functional characteristics in the ecosystem and its composition rather than the abundance of species (Messier et al., 2010). The trait-based approach in ecology is usually field-specific and relies on examining the functional traits of an individual that reflects its interaction with biotic and abiotic factors, which can also impact the biodiversity-ecosystem functioning relationship (Wong et al., 2019; McGill et al., 2006).

Macroalgae are marine primary producers, characterised by the ability to adapt to a wide range of changes in environmental conditions such as variations in temperature, salinity and desiccation, which enables them to thrive in intertidal zones and contribute significantly to the biodiversity and productivity of coastal ecosystems. Their high plasticity allows them to exhibit diverse morphological traits, such as differences in total length, blade thickness, and complexity of structure, in response to distinct climatic conditions and levels of stress. Their intraspecific variation can often be found at a population level as well as within the same individual (intra-individuals) and are affected by gradients in abiotic factors at multiple spatial scales (Stelling-Wood et al., 2020; Cappelatti et al., 2019). Canopy-forming macroalgal species such as fucoids and kelps form the foundation of temperate reefs in intertidal and subtidal zones of temperate and subpolar regions (Teagle et al., 2017; Steneck et al., 2002). They are considered coastal engineers playing a key role in shaping the intertidal habitats and supporting biodiversity within these areas (Teagle et al., 2017; Bennett et al., 2016; Steneck et al., 2002). Kelps and rockweeds play an essential role in primary production, contributing to nutrient cycling and carbon fixation, creating one of the most productive coastal ecosystems on Earth (Duarte et al., 2022; Filbee-Dexter & Wernberg, 2020). Furthermore, they support food webs, create habitats crucial for commercial fish species, and protect shorelines from erosion (Duarte et al., 2022; Fragkopoulou et al., 2022; Løvås & Tørum, 2001).

Alongside broad research on the contributions of macroalgae to ecosystem functioning, recent studies have increasingly adopted a trait-based approach, primarily focusing on continuous and categorical morphological traits (Ryznar et al., 2023). Continuous morphological traits such as total length of individual, stipe, and blade thicknesses as well as categorical traits such as specific thallus area (STA) are the most frequently studied traits of macroalgae and their variation affected by abiotic factors such as salinity and wave exposure has been observed worldwide (Coppin et al., 2020; Fowler-Walker at al., 2006; Blanchette et al., 2002). Physiological traits such photosynthetic efficiency, and nutrient uptake rates provide insights into the performance of individuals, hence examining the relationship between morphological traits and physiological characteristics might indicate the possible consequences of morphological adaptations to environmental conditions for physiological processes. A connection between morphological and physiological traits has been researched previously, mostly in terrestrial plants where the shape and thickness of a leaf were demonstrated to affect the photosynthetic rates (Tholen et al., 2012; Poorter et al., 2009; Smith et al. 1997). Across large brown macroalgal species, the relationship between the thickness and area of a blade, and the photosynthetic performance within the same species has not been widely studied but it was observed in interspecific macroalgal research. Littler (1980) who researched 45 macroalgal species demonstrated that species characterised by thinner thallus or filamentous shape had higher photosynthetic rates. Similar findings were confirmed by Arnold & Murray (1980) and more recently by Johansson & Snoeijs (2002) in the study of macroalgae inhabiting the Baltic Sea, confirming that species with thinner and flatter thalli had increased photosynthetic rates and produced oxygen faster compared to species with thicker thalli. Furthermore, a study by Wing et al. (2007) on *Ecklonia radiata* inhabiting southwestern New Zealand found that thinner blades with larger surface areas had higher chlorophyll-a and fucoxanthin concentrations, which could allow more effective photosynthesis. Even though a majority of research is focused on interspecific differences, these general findings might apply to variation in thallus morphology within the same species and support the theory that thinner blades and larger surface areas enhance the photosynthetic rates.

Intraspecific variability in macroalgal species has been widely observed along various environmental gradients, including exposure, salinity, water and air temperature and nutrient availability (Coppin et al., 2020; Barboza et al., 2019; Bekkby et al. 2014). The gradient in environmental conditions along with shore exposure and nutrient availability is known to be the primary driver affecting the distribution, composition, and productivity of macroalgal ecosystems worldwide (Pedersen & Nejrup, 2012; Konar et al., 2010). The majority of current studies on macroalgal species focus on the small-scale intraspecific variability in one or a few abiotic factors such as salinity or wave exposure (Barboza et al., 2019; Thomsen 2004; Blanchette et al., 2002), while limited research has been done to assess if the variation is consistent across large-scale latitudinal gradients (Fowler-Walker et al., 2005; Wernberg et al., 2003; Cheshire & Hallam1989).

Water and air temperatures along with the sunlight availability and intensity of solar radiation increase towards the lower latitudes and are key factors affecting organism growth and metabolic rates which drive intraspecific variation (Rinde & Sjøtun, 2005; Hughes, 2000). In southern regions, individuals face a greater risk of heat and desiccation stress, which is known to limit the growth of seaweed populations at the edges of their distribution range (Eggert, 2012). As temperatures rise, the temperature-induced metabolic rates increase, leading to faster energy expenditure and higher respiration rates (Gutow et al., 2016; Eggert, 2012, Dewar et al., 1999; Ryan, 1991). Additionally, grazing pressure increases, further intensifying stress for individuals inhabiting warmer regions with a higher average temperature (Salazar et al., 2012; Hellmann et al., 2008; Rahel & Olden, 2008). These climatic factors are expected to drive variation in traits of large brown macroalgae as demonstrated in a study of three Australian species along the latitudinal gradient across the western coast by Wernberg et al. (2016) showing the better photosynthetic performance of individuals of all three species inhabiting cooler regions compared to warmer locations. Furthermore, Wernberg et al. (2016) observed variation in the morphology of *E. radiata* across the Australian coast however, consistent spatial trends have not been observed suggesting that specific characteristics of each shore might have supreme importance on changes in *E. radiata* morphology. Nevertheless, the lack of consistent trends in *E. radiata* morphology does not exclude the other species from displaying consistent trends and provides limited insight into this hypothesis. Similarly, Voerman et al. (2019) demonstrated that populations of green macroalgae - *Caulerpa filiformis* inhabiting lower latitudes had shorter and narrower blades compared to those at higher latitudes, suggesting a decrease in water temperature as a cause of variability, which along with previous findings might indicate that water temperature could be the key factor driving morphological variation across macroalgae (Mabin et al., 2013; Dudgeon et al., 1995).

The following work focuses on a fundamental canopy-forming species on European rocky shores - *Fucus serratus*, with a distribution ranging from northern Portugal, through the British Isles to Iceland. It inhabits sheltered and semi-exposed shores, extending from the average tide level down to the lower range of neap tides, reaching the kelp zone (Perry & Hill, 2015). *F. Serratus* belongs to Fucoids (class *Phaeophyceae*), which cover an estimated 2.57 million km² globally (Wernberg et al., 2024; Fragkopoulou et al. 2022) providing vital ecosystem services such as primary production, carbon sequestration, and habitat formation (Pessarrodona et al., 2023; Duare et al., 2015). *F. serratus* is considered an ecosystem engineer species with a well-studied physiology and a broad geographical distribution, which makes it a valuable model for investigating the macroalgal traits within the context of ecosystem functioning. High plasticity of morphological and physiological traits of the genus Fucus has been observed across various spatial scales. For instance, variation in total length, the complexity of form, and blade width were observed along temperature and salinity gradients in Iceland (study on *F. vesiculosis* by Kalvas, & Kautsky (1998)), and along the gradient from the North Sea to the Baltic Sea (study on *F. vesiculosis* by Barboza et al. (2019)). Furthermore, Knight and Parke (1950) observed reduced total length and thickness of fronds and stipe in populations of *F. serratus* along the latitudinal gradient from Scotland to Devon.

The primary aim of this study is to understand the ecological strategy (here referred to the traits that vary across species' geographic range, enabling it to adapt to and thrive in diverse environmental conditions) of *Fucus serratus* along a 20-degree latitudinal (climatic) gradient ranging from the southernmost populations in Portugal through South Wales to the cooler central range in Scotland, by examining photosynthetic parameters at three temperature stages (corresponding to average annual water temperature for each region) and variation in morphological traits of individuals. These three regions are characterised by different climatic conditions which are expected to affect the morphology and physiology of individuals.

Additionally, the study explores how these morphological variations could influence the photosynthetic parameters of individuals leading to differences across populations.

Harsher environmental conditions in the south leading to increased heat and desiccation stress as well as higher grazing pressure (Voerman et al., 2019; Mabin et al., 2013; Dudgeon et al., 1995) are expected to result in reduced sizes of individuals and in thicker stipes and blades to protect from desiccation (Dorothea & Chandler, 2018). Furthermore, we expect individuals inhabiting lower latitudes to have a higher specific thallus area (STA), based on preliminary findings of the Disturbance recovery project that showed an increase in STA towards the lower latitudes, along with the decrease in Carbon to Nitrogen ratio. Greater STA and higher nitrogen content observed among species inhabiting Portugal might implicate that these individuals have a greater surface area, that allows them to capture more sunlight enhancing the photosynthesis process and metabolic rates also indicating that individuals might have faster decomposition rates that are known to increase along with the rising temperatures (Filbee-Dexter et al., 2022). The increased rates of photosynthesis (measured under the ideal conditions) of individuals inhabiting lower latitudes are expected to result from an increased water temperature (an increase in temperature, resulting in higher enzyme activity is expected to accelerate the reaction rates and result in reaching the peak of the photosynthesis rate quicker; (Rinde and Sjøtun 2005; Hochachanka & Somero, 1984)). Moreover, the slope of photosynthesis that indicates the effectiveness of sunlight conversion into energy prior to reaching light saturation is expected to be greater for southern regions than for northern regions, as individuals living in warmer habitats are characterised by higher enzyme activity (Carr et al., 2018), which allows them to use sunlight energy more efficiently and reach the peak of the photosynthesis faster and at lower light intensity.

2. Methods and data collection

2.1 Sampling locations and sampling design

Data was collected from two shores in each of the following regions along the 20-degree latitudinal gradient during spring 2024:

- Orkney Islands, Scotland: Orphir (58.9642° N, 3.1248° W) and Guard House (58.8333° N, 3.1667° W)
- Wales: Oxwich (51.5674° N, 4.1611° W) and Mumbles (51.5732° N, 3.9946° W)
- Viana do Castelo (Portugal, 41.7006° N, 8.8442° W) and Moros (Spain, 42.3223° N, 8.7729° W) – for simplicity both locations will be further referred as 'Region Portugal' due to the similar climatic conditions

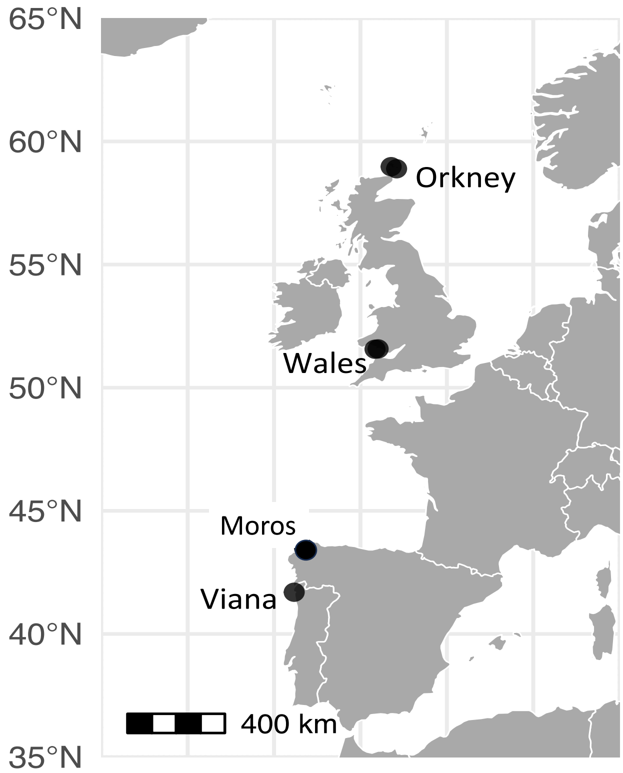

Figure 2. *F.serratus* was sampled across three regions: in the northernmost region, samples were collected in Orkney at Guard House and Ophir; the central region included Oxwich in Mumbles located in South Wales; and the southernmost locations were Moros in Spain and Viana do Castelo in Portugal.

2.2 Collection of samples in the field and trait measurements

Individuals from all three regions were collected during spring 2024 – Orkney was sampled on 12th April, Portugal on 9th May and South Wales on 20th May. Two shores were sampled in every region to ensure that the samples comprehensively represent the regional characteristics and to minimize the bias from the specific conditions of any individual location. Considering the time constraints and the limited number of tanks in the mesocosm experiment, collecting samples from two shores appeared to be an effective and sufficiently efficient approach to data collection. Selecting two sites in each region allowed us to capture the broader representation of the specific characteristics of the region and helped to exclude the potential random effects associated with factors specific to a single shore. While choosing two sites may constrain the range of variability observed, it was considered a practical compromise due to the project's logistical limitations. For each shore, eight mature and mid-sized individuals were sampled - two from the upper, four from the middle and two from the lower part of their intertidal distribution. Different numbers of individuals were sampled from each shore height to account for the distribution of *F. serratus* within the intertidal zone. The sampling effort was concentrated in the middle zone, which provides the most optimal conditions for growth, and it is characterised by the greatest abundance of individuals compared to the lower and upper shore, where environmental stress levels are higher.

In the field, each individual's total length was measured using a measuring tape (mm accuracy) and both dimensions of stipe thickness (as the stipes are ovoid in cross-section) were recorded using the digital calliper in the field (Mitutoyo 150mm, 500-196-30; with an accuracy of 0.01mm). Subsequently, frond samples of each individual were collected by cutting the side section of the individual (favourably where the thicker stipe was to minimise the time of the wound healing process; Figure 3) of a wet weight of approximately 20-40 grams to bring back to the laboratory for the photosynthesis trial. Samples collected in the field were wrapped individually in a blue roll saturated in the seawater and placed into sample bags, then kept in a cold insulated bag containing ice packs during the transport to the laboratory in Swansea. Firstly, samples were run in the mesocosm to obtain the photosynthesis parameters, then samples were processed in the laboratory to obtain measurements of additional morphological traits that could be relevant to their performance (Table 1; Mauffrey et al., 2020; Coppin et al., 2020; Blanchette et al., 2002). The blade thickness was averaged from three measurements taken across the blade (Digital Micrometers Ltd, DML3032 with an accuracy of 0.001mm); subsequently photographs of each sample were taken on a lightbox (Sony RX100 digital camera, 20.2MP) to obtain the thallus area used as the numerator for the trait specific thallus area of the whole sample (STA; Figure 4a). The whole sample included varying proportions of structural material. Therefore, to provide a more standardised STA measurement that was more specific to the photosynthetic tissue of the blade, a section of the blade approximately 3 to 5 cm in length located below the reproductive material, was also photographed on the lightbox (Figure 4b; Samples were then oven dried at 60°C until stable mass to determine dry mass). The sample area and the area of the blade section were measured using the ImageJ Software (Schneider, Rasband & Eliceiri, 2012; version 1.54g) subsequently, the STA of each sample (whole or blade) was calculated as cm^2 per gram of dry mass.

Table 1. A list of functional traits of *F. serratus* collected in this study along with their functional relevance (informing how the trait is impacting the ability of individual to perform its ecological role (Violle et al., 2007)), units of measurement and the part of individual that was used to measure the trait. References supporting each function are as follows: [1] (Hurd et al., 2014); [2] (Dudgeon & Johnson, 1992) ; [3] (Markager & Sand-Jensen, 1992); [4] (Markager & Sand-Jensen, 1996); [5] (Raven & Hurd, 2012); [6] (Nielsen &Nielsen, 2006); [7] (Binzer & Sand-Jensen, 2002).

Functional trait	Unit of measurement	Part of individual	Function
Total length	Millimeter	Whole	Structural stability; position in the water column[1]
Stipe thickness	Millimeter	Stipe	Structural support and mechanical strength attachment to the substrate; storage of carbon [2]
Blade thickness	Millimeter	Blade	Structural ; corresponds to the area available for the light absorption[3]
Specific thallus area (STA) of whole sample	Surface area/dry mass (cm^2/g)	Section of individual (might include structural material)	Potential to inform about the light absorption capacity per unit of biomass [4]
Specific thallus area (STA) of blade section	Surface area/dry mass (cm^2/g)	Section of blade measuring 3 to 5cm in length	Potential to inform about the area available for light absorption per unit of biomass [4]
Slope of photosynthesis (α)	µmol CO2 m^{2-1} s^{-1}	Side section used in mesocosm trial	How effectively the sunlight is converted into energy before reaching light saturation[5]
Maximum rate of photosynthesis (Pmax)	µmol CO2 m^{2-1} s^{-1}	Side section used in mesocosm trial	The light intensity at which photosynthesis reached its highest point [6]
Saturation irradiance (ISat)	µmol photons m^{2-1} s^{-1}	Side section used in mesocosm trial	The light intensity at which the photosynthesis reaches its plateau [7]

Figure 3. An example of side section of *F. serratus* that was cut from the whole individual for the mesocosm trial.

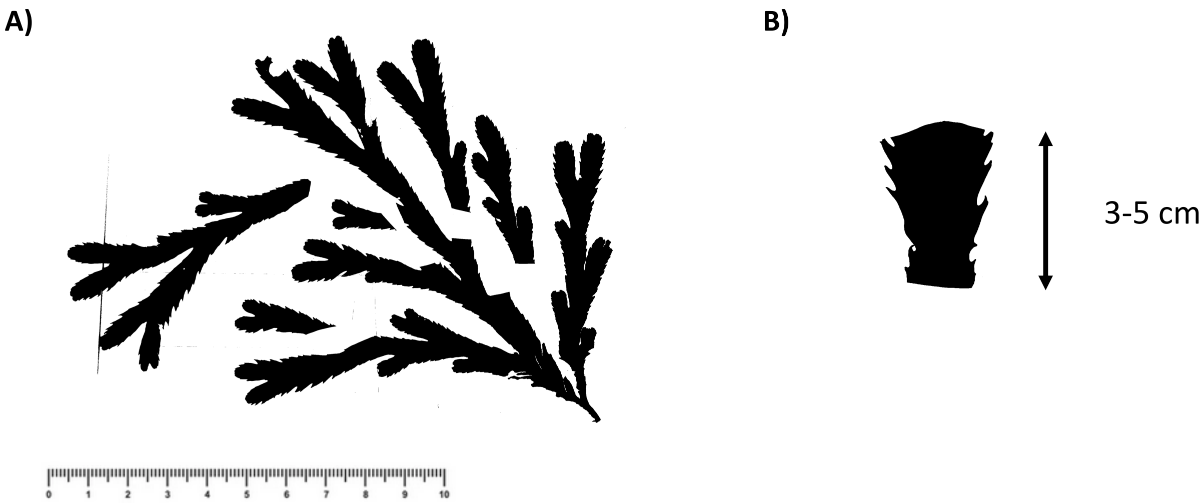

Figure 4. The example of trait screening for specific thallus area: a) the scan of whole sample that was firstly taken to obtain the specific thallus area (STA) of whole sample; b) the scan of blade section that was taken from the sample after performing the full scan to obtain the STA of the blade section.

2.3 Photosynthetic Rate Measurements in Mesocosm

The mesocosm experiment has been set up to examine the photosynthetic parameters, including the maximum photosynthetic rate (Pmax), the slope of photosynthesis that indicates the effectiveness of sunlight conversion into energy prior to reaching light saturation, and the light saturation point (Isat), which represents the light intensity at which photosynthesis reaches its maximum rate. The study aimed to explore the variations across sampled individuals and populations. During the experiment, eight chambers with a volume of 2.2 L were used, allowing for eight samples to be run simultaneously. All samples were exposed to three treatment conditions (three temperature stages) one after the other. To exclude the effect that storage time could have on photosynthetic activity, it was ensured that the time between collection from the site and the mesocosm run was the same for each of the regions.

At the start of the study, each sample was placed vertically (with the holdfast pointing downwards) in one of the eight chambers, which were immersed in a thermostatically controlled aquarium to maintain the target temperature during each temperature stage of the experiment (Figure 5). The mesocosm experiment included three temperature stages (10°C, 15°C, and 20°C), selected to closely represent the range of annual mean sea surface temperatures observed across the latitudinal gradient of the study sites, within the limits of the available equipment. This approach allowed us to replicate realistic environmental conditions and examine how populations from different regions respond to temperature variations within both their own ecologically relevant ranges and those characteristics of other populations. To account for the fact that the observations made across the three temperature treatments are not independent, 'individual' was included as a random effect in the further analysis. Each chamber was equipped with PreSens probes (Pt100 temperature sensor and oxygen dipping probe DP-PSt8; PreSens Precision Sensing GmbH) measuring the temperature and dissolved oxygen levels and was filled with artificial seawater (see below for further details) to ensure no overhead space and no oxygen bubbles, excluding the possibility of diffusion of oxygen from water to the air, which could interfere with measurements. The measurements within each chamber were taken every 20 seconds using PreSens Software (Veenhof et al., 2024; Asnes et al., 2019). In each chamber, magnetic stirrers were used to ensure sufficient water flow and prevent the build-up of a boundary layer (Binzer & Sand-Jensen 2002; Binzer & Middelboe 2005). Controlled lights were positioned directly above and on both sides of each chamber allowing for the regulation of light intensity during the trial.

Each session began with a dark phase lasting approximately 30 to 40 minutes, where all light sources were switched off to ensure that the oxygen levels in the tanks dropped before the first light stage (Mercado et al., 2002). This allowed us to measure the respiration rate and start the precise measurements with the linear increase in light levels starting at 50 µmol photons m^2/s (Photosynthetically Active Radiation (PAR)). There were six light levels (50 PAR, 100 PAR, 500 PAR,750 PAR, 1000 PAR, and 1450 PAR). Each light level lasted approximately 11-16 minutes, which allowed us to obtain a sufficient number of data points needed to calculate the photosynthesis rates for each light level. For each sample, measurements were repeated for all six light intensities at each temperature stage (10°C, 15°C, and 20°C). This experiment used artificial seawater that was prepared using Instant Ocean (concentration: 35g/L) and supplemented with filtered natural seawater (by adding 0.2L of natural filtered seawater to every 1L of artificial seawater) to ensure the presence of essential nutrients such as nitrate. Water in each chamber was fully replaced in each run to maintain low oxygen levels and to provide sufficient levels of nutrients**.**

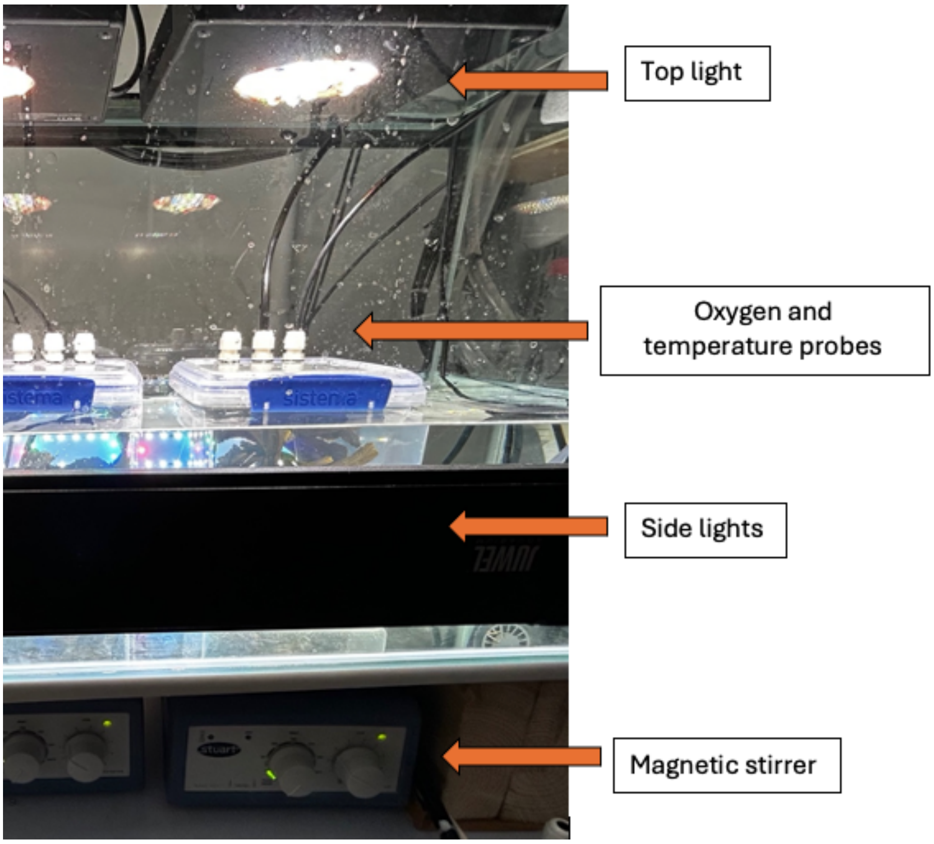

Figure 5. One of the eight chambers used in the mesocosm experiment. The sample was positioned vertically in a fully sealed transparent tank equipped with temperature and oxygen probes, as well as the magnetic stirrer to ensure adequate water circulation. The lights were positioned on both sides and top of the tank. The chamber was submerged in an aquarium equipped with a cooling system to maintain the desired temperature inside the tank.

2.4 Fitting of Photosynthesis – Irradiance Curves and Statistical Analysis

All data was analysed using R Studio (R.4.4.1 - R Core Team 2024). Firstly, mass-specific respiration rates, and rates of photosynthesis at different light levels for three separate temperature stages (10°C, 15°C, and 20°C) were calculated. Subsequently, calculated rates were used to fit the Photosynthesis – Irradiance (PI) Curves using the adjusted Michaelis-Menten model, which accounted for photoinhibition and allowed to extract the photosynthetic parameters. Three main parameters were extracted: the slope of photosynthesis (α) informing about how effectively the sunlight is converted into energy before reaching light saturation, maximum rate of photosynthesis (Pmax) representing the point where photosynthesis reached its highest point and the saturation irradiance (ISat) representing the light intensity at which the photosynthesis reaches its plateau (Figure 6).

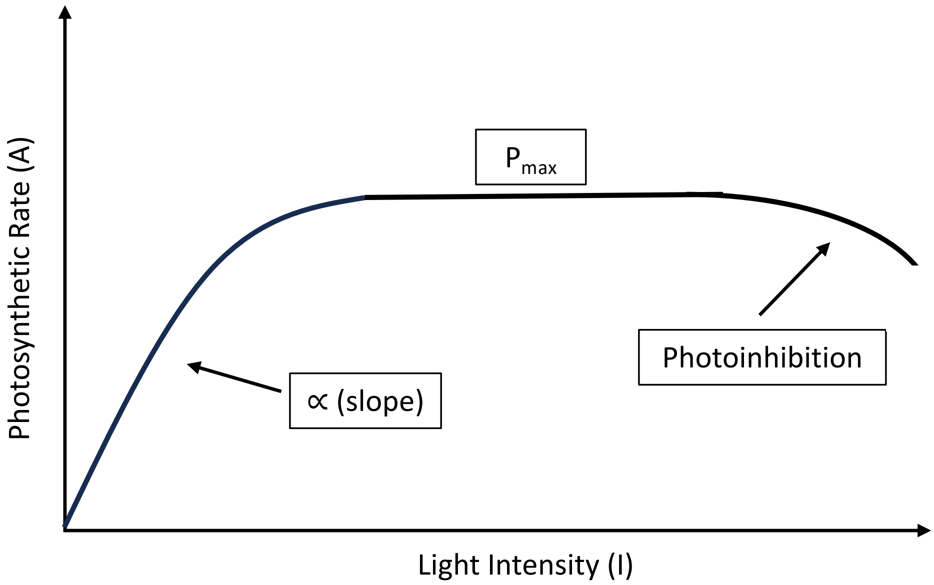

Figure 6. Schematic drawing of PI curve fitted using the adjusted Michaelis-Menten model, which accounted for photoinhibition visualising slope (α), maximum rate of photosynthesis (Pmax), and photoinhibition.

To investigate the effects of environmental factors on the parameters of photosynthesis, linear mixed models were fitted using the lme4 package (version 1.1-26; Bates et al., 2015). The model included region and temperature as well as their interaction as fixed effects, logarithmic-transformed sample mass as a covariate, and a random effect for sample identity to account for measurements of the same individual across three different temperature stages. In each model, weights as the inverse of the squared standard errors were incorporated. Subsequently, the morphological traits were added to the model as additional fixed effects to examine their impact on photosynthesis parameters. Additionally, for certain models the adjusted means (estimated marginal means) of different factor levels, accounting for other variables in the model were analysed using the emmeans package (version 1.10.4; Lenth et al., 2024). Pairwise comparisons between levels were conducted using Tukey's HSD test to account for multiple comparisons.

3. Results

A total of 48 mature, mid-sized individuals were sampled throughout the study. From each region, two individuals were collected from the upper intertidal zone, four from the middle intertidal zone, and two from the lower intertidal zone at both sites. Although logistical and time constraints limited the sample size to eight individuals per shore, the observed morphological characteristics aligned with a broader population trend previously documented in Ruby's George Disturbance-Recovery PhD Project.

3.1 Variation in morphological traits of individuals of *F. serratus*

Individuals in Orkney and Wales were longer than those in Portugal ($F_{2,124}$=30.12, p <0.001; Table 2a, Figure 7a). Both stipe and blade thickness declined with region from north to south (stipe: $F_{2, 124}$ = 72.36, p< 0.001; Table 3a, Figure 7b; blade: $F_{2, 124}$ =293.4, p< 0.001; Table 4a, Figure 8a). Additionally, Orkney had greater variability in stipe and blade thickness as well as in total length, indicating more diversity across individuals in the northern region.

There were no differences in the specific thallus area of the whole sample (whole sample STA) between the regions ($F_{2, 124}$ = 1.041, p= 0.356; Figure 8b; Table 5). In contrast, the STA of the blade section varied across regions ($F_{2, 124}$ = 7.433, p< 0.001; Figure 8c; Table 6a). Orkney had a significantly lower mean STA of the blade section than Wales (p = 0.001; Table 6b) and Portugal (p = 0.007; Table 6b) . Nevertheless, there was no significant difference in the STA of the blade section between Wales and Portugal (p = 0.812; Table 6b).

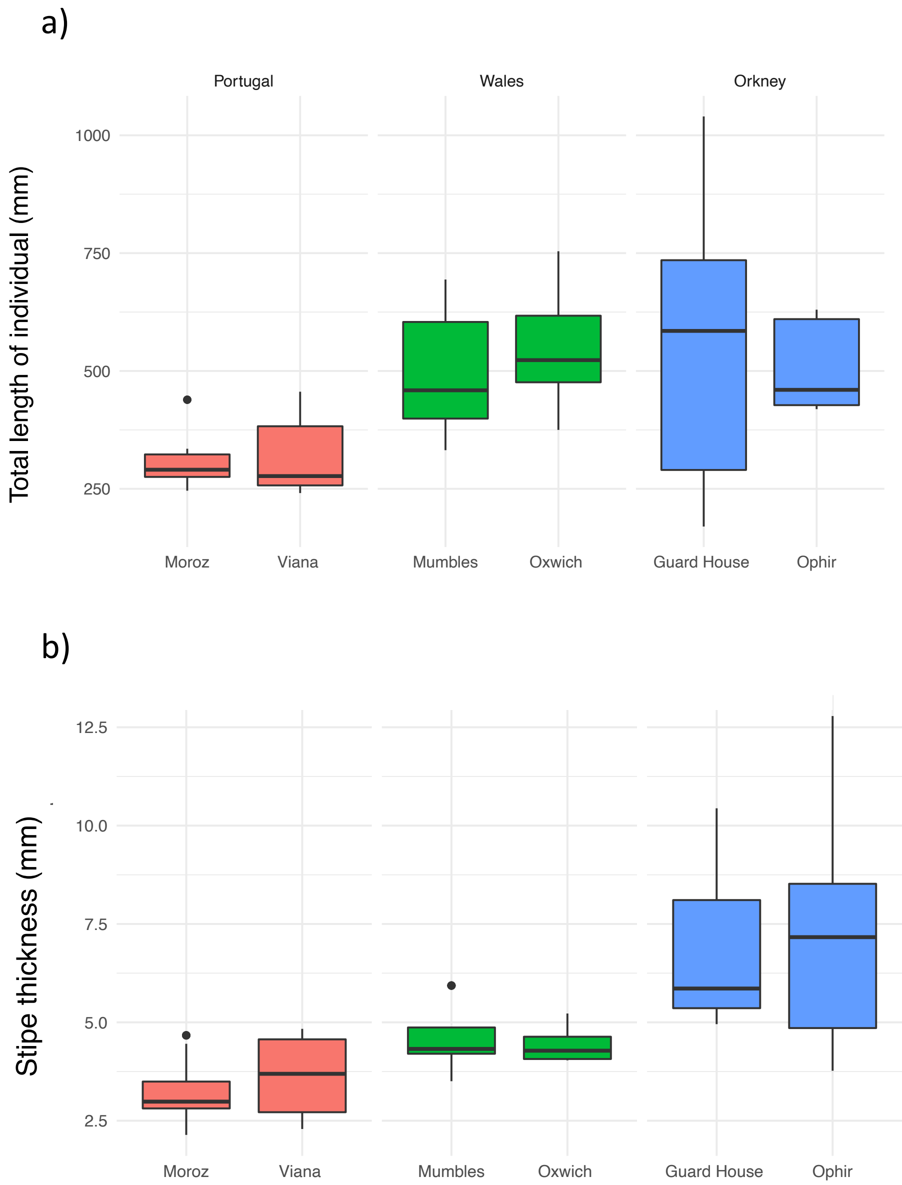

Figure 7. Variation in total length (a) and stipe thickness (b) of individuals of *F. serratus* across sites in Portugal (Moros, Viana), Wales (Mumbles, Oxwich), and Orkney (Guard House, Ophir). Horizontal black lines within each box denote median values, whiskers indicate the range of the data within the expected variability (within 1.5 interquartile range from the quartiles), while black dots represent points that fall beyond the whiskers range. Sample sizes: $n = 8$ per site, totalling $N = 48$.

Table 2. Results of one-way ANOVA and Tukey multiple comparisons of means with 95% family-wise confidence level to test for significant differences in total lengths of *F.serratus* across regions (Portugal, Wales, Orkney).

2a. One-way ANOVA Results:

	Df	Sum sq	Mean sq	F value	Pr(>F)
Regions	2	1284773	642387	30.12	2.18e-11 ***
Residuals	124	2644835	21329		

2b. TukeyHSD Results:

Comparison	Difference	Lower CI	Upper CI	Adjusted p-value
Portugal-Orkney	-211.9979	-286.52569	-137.47005	0.0000000
Wales-Orkney	-7.5500	-85.01806	69.91806	0.9709716
Wales-Portugal	204.4479	129.92005	278.97569	0.0000000

Table 3. Results of one-way ANOVA and Tukey multiple comparisons of means with 95% family-wise confidence level to test for significant differences in stipe thickness of *F.serratus* across regions (Portugal, Wales, Orkney).

3a. One-way ANOVA Results:

	Df	Sum sq	Mean sq	F value	Pr(>F)
Regions	2	323.4	161.72	72.36	<2e-16 ***
Residuals	124	277.1	2.23		

3b. TukeyHSD Results:

Comparison	Difference	Lower CI	Upper CI	Adjusted p-value
Portugal-Orkney	-3.794883	-4.557739	-3.032027	0.0000000
Wales-Orkney	-2.718375	-3.511327	-1.925423	0.0000000
Wales-Portugal	1.076508	0.313652	1.839364	0.0030801

Table 4. Results of one-way ANOVA and Tukey multiple comparisons of means with 95% family-wise confidence level to test for significant differences in blade thickness of *F.serratus* across regions (Portugal, Wales, Orkney).

4a. One-way ANOVA Results:

	Df	Sum sq	Mean sq	F value	Pr(>F)
Regions	2	1.018	0.5088	293.4	<2e-16 ***
Residuals	124	0.215	0.0017		

4b. TukeyHSD Results:

Comparison	Difference	Lower CI	Upper CI	Adjusted p-value
Portugal-Orkney	-0.21670692	-0.23795711	-0.1954567	0.0000000
Wales-Orkney	-0.12728333	-0.14937189	-0.1051948	0.0000000
Wales-Portugal	0.08942358	0.06817338	0.1106738	0.0000000

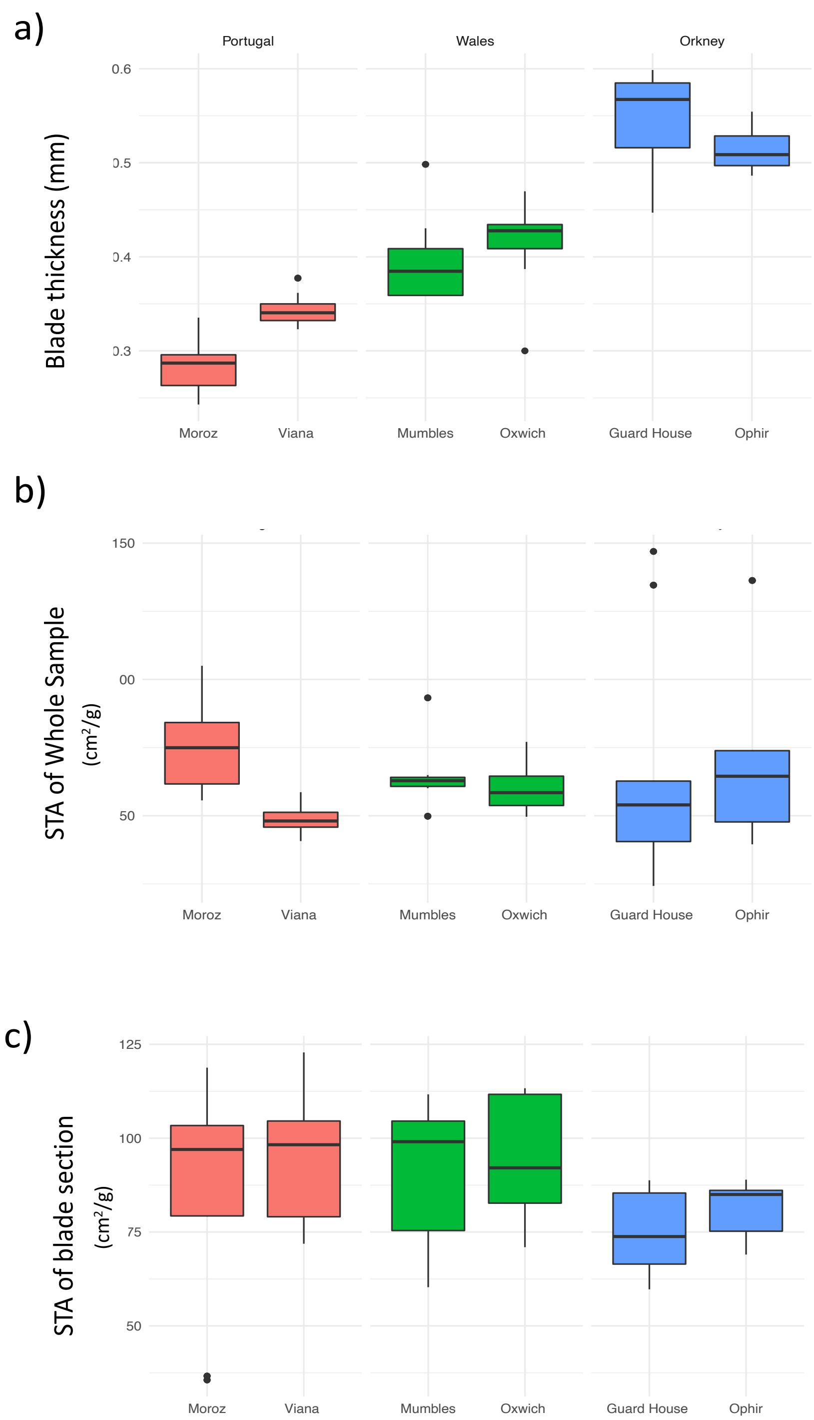

Figure 8. Variation in blade thickness (a), STA of the whole sample (b), and STA of the blade section (c) of *F. serratus,* across Portugal (Moros, Viana), Wales (Mumbles, Oxwich), and Orkney (Guard House, Ophir). Horizontal black lines within each box denote median values, whiskers indicate the range of the data within the expected variability (within 1.5 interquartile range from the quartiles), while black dots represent points that fall beyond the whiskers range. Sample sizes: n = 8 per site, totalling N = 48.

Table 5. Results of one-way ANOVA and Tukey multiple comparisons of means with 95% family-wise confidence level to test for significant differences in Whole sample STA for *F.serratus* across regions (Portugal, Wales, Orkney).

One-way ANOVA Results:

	Df	Sum sq	Mean sq	F value	Pr(>F)
Regions	2	1168	584.1	1.041	0.356
Residuals	124	69561	561.0		

Table 6. Results of one-way ANOVA and Tukey multiple comparisons of means with 95% family-wise confidence level to test for significant differences in STA of blade section of *F.serratus* across regions (Portugal, Wales, Orkney).

6a. One-way ANOVA Results:

Source	Df	Sum sq	Mean sq	F value	Pr(>F)
Regions	2	5085	2542.7	7.433	0.000894 ***
Residuals	124	42421	342.1		

6b. TukeyHSD Results:

Comparison	Difference	Lower CI	Upper CI	Adjusted p-value
Portugal-Orkney	12.325997	2.887374	21.76462	0.0067687
Wales-Orkney	14.768918	4.957926	24.57991	0.0014627
Wales-Portugal	2.442921	-6.995701	11.88154	0.8127617

3.2 Variation in parameters of photosynthesis – values of slope

Differences in slope between regions depended on temperature ($F_{4,\ 87.653}$ = 4.4087, p = 0.003; Appendix 6). At 10°C, Wales had a steeper slope compared to both Orkney (estimate: 0.0362; p<0.001, Appendix 1; Figure 9) and Portugal (estimate: 0.0229; p= 0.021, Appendix 1). At 15°C, slope did not vary between regions. At 20°C, the slope for Wales was steeper than for Orkney (estimate= 0.026, p=0.02; Appendix 1), but there were no other differences in response to temperature between regions. Moreover, shores located within the same region displayed consistent trends in response of slope to temperature levels and there were no differences found in responses between shores (Appendix 1).

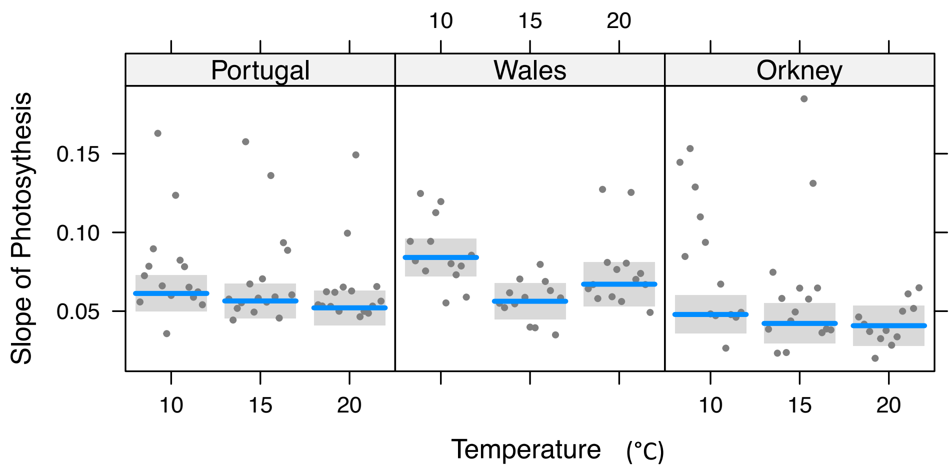

Figure 9. Predicted values of slope of photosynthesis plotted against temperature demonstrating how the effect of temperature on slope varies for *F. serratus* in Portugal, Wales and Orkney. The y-axis reflects the predicted slope of photosynthesis, which indicates the rate of change in photosynthesis with temperature, while the x-axis represents the temperature levels at which these predictions are made. For each site, the blue line indicates the predicted relationship between temperature and slope, while the shaded area represents the 95% confidence interval. The model accounts for region-specific effects and temperature, while also including log-transformed mass as covariate, which is controlled for in the predictions but not shown directly in the graph. Sample sizes: *n*= 16 per region, totalling *N* =48.

3.3 Variation in parameters of photosynthesis – the maximum rate of photosynthesis under optimal conditions (Pmax)

The differences in Pmax between regions also depended on temperature (Figure 10). There was no clear increase in Pmax with temperature in Orkney. In contrast, in Wales Pmax increased when temperatures rose from 10°C to 15°C (estimate=1.958, p-value<0.001; Appendix 2) and from 10°C to 20°C (estimate=3.365, p-value=0.006; Appendix 2). A similar pattern was observed in Portugal, where Pmax increased when temperatures rose from 10°C to 15°C (estimate= 0.8619, p=0.016; Appendix 2), and from 10°C to 20°C (estimate = 1.8767, p= 0.006; Appendix 2). Furthermore, sites located within the same region displayed consistent trends in response of Pmax to temperature levels and there were no significant differences between shores within the same region (Appendix 2).

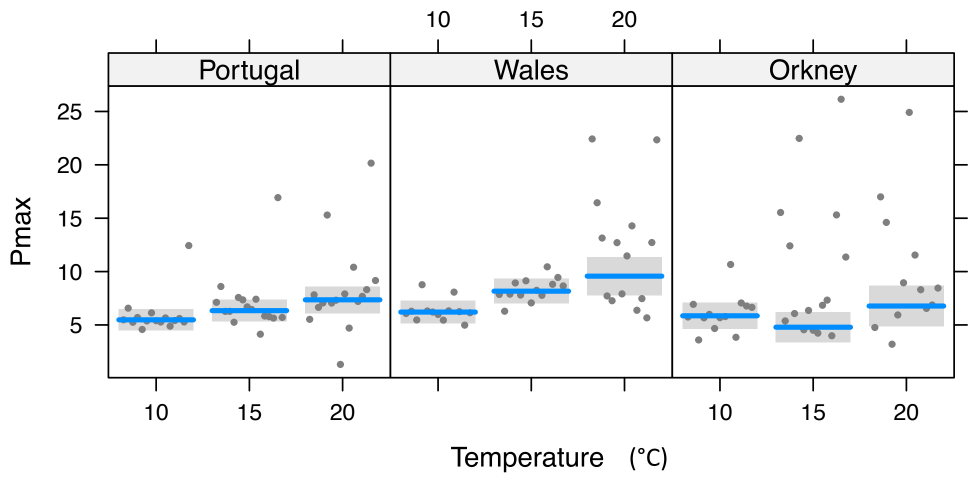

Figure 10. Predicted values of Pmax of photosynthesis plotted against temperature demonstrating how the effect of temperature on the Pmax varies for *F. serratus* in Portugal, Wales and Orkney. The y-axis reflects the predicted Pmax of photosynthesis, which indicates the rate of change in photosynthesis with temperature, while the x-axis represents the temperature levels at which these predictions are made. For each site, the blue line indicates the predicted relationship between temperature and Pmax, while the shaded area represents the 95% confidence interval. The model accounts for region-specific effects and temperature, while also including log mass as covariate, which is controlled for in the predictions but not shown directly in the graph. Sample sizes: n = 16 per region, totalling N = 48.

3.4 Variation in parameters of photosynthesis - the light intensity at which the rate of photosynthesis reaches its maximum (ISat)

The response of ISat to temperature also varied among regions ($F_{4,100.9}$=7.21, p<0.001p; Figure 11; Appendix 3). In Orkney ISat did not differ significantly with temperature and data for this region was characterised by very high variability. In Wales and Portugal, ISat tended to decrease with temperature (Wales: 10°C vs 20°C, estimate: -22214.66, p< 0.001; 15°C vs 20°C, estimate:-1324.86, p <0.001; Portugal 15°C vs 20°C, estimate= -880.28, p= 0.002; Appendix 3). Furthermore, Orkney consistently showed higher ISat values compared to both Wales and in Portugal, however these observations were only significant at 20°C (Orkney compared to Wales: estimate = 2946.88, p= 0.004; Appendix 3; and to Portugal: estimate= 2059.46, p= 0.037; Appendix 3).

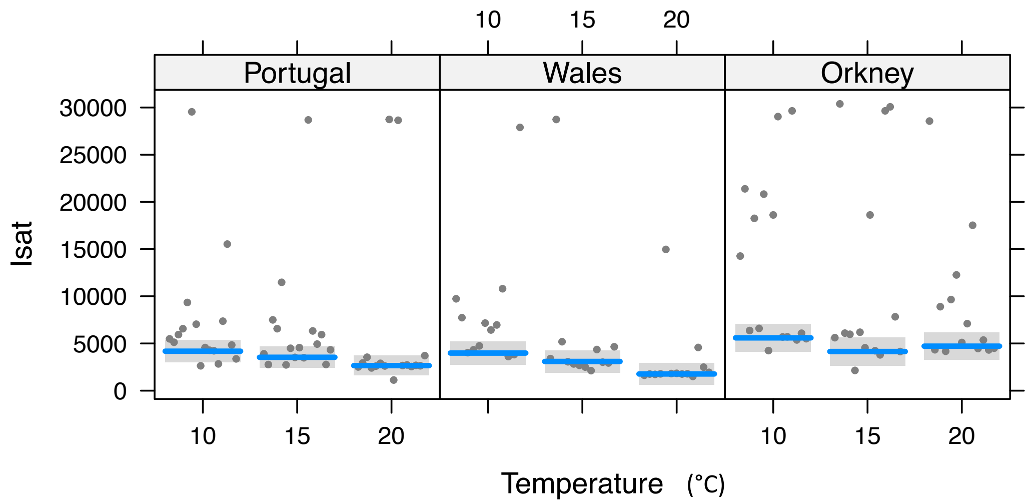

Figure 11. Predicted values of ISat of photosynthesis plotted against temperature demonstrating how the effect of temperature on the ISat varies for *F. serratus* across sites in Portugal, Wales and Orkney. The y-axis reflects the predicted ISat, which indicates the rate of change in photosynthesis with temperature, while the x-axis represents the temperature levels at which these predictions are made. Each line indicates how the ISat changes with temperature for that specific site within the region, while the shaded area represents the 95% confidence interval. The model accounts for region-specific effects and temperature, while also including log mass as covariate, which is controlled for in the predictions but not shown directly in the graph. Sample sizes: *n*= 16 per region, totalling *N* = 48.

3.5 The effect of the blade thickness and STA on Pmax of photosynthesis

Blade thickness had no clear effect on Pmax across regions ($F_{1,51.238}$=1.04, p=0.312; Figure 12a; Appendix 5). Additional exploratory analysis of the separate models for each region showed that blade thickness had a significant positive effect for Portugal (p =0.014; Appendix 7), while for Wales it was close to the significance level (p=0.079; Appendix 8) and was not significant for Orkney (p=0.741; Appendix 6).

The STA of the whole sample had no distinct effect on Pmax ($F_{1,49.449}$=2.40, p=0.128, Appendix 7; Figure 12b). Separate models exploring the effect in each region showed that there was a positive effect observed for Wales (p<0.001; Appendix 6), while there was no clear effect in Portugal and Orkney (p=0.717 and p=0.2933 respectively; Appendix 6). Notably, there appeared to be a clear effect within the Portugal site of Moroz, but no effect within the sites of Viana, where there was also very little variability (all samples had rather low STA values). This observation might suggest that the effect of STA of whole sample is likely to vary depending on the region and the variability of samples within each site. Furthermore, the STA of blade section had no clear effect on Pmax and was characterised by very high variability of predicted values of Pmax within regions ($F_{1,39.005}$=0.8895, p=0.351; Appendix 6; Figure 12c).

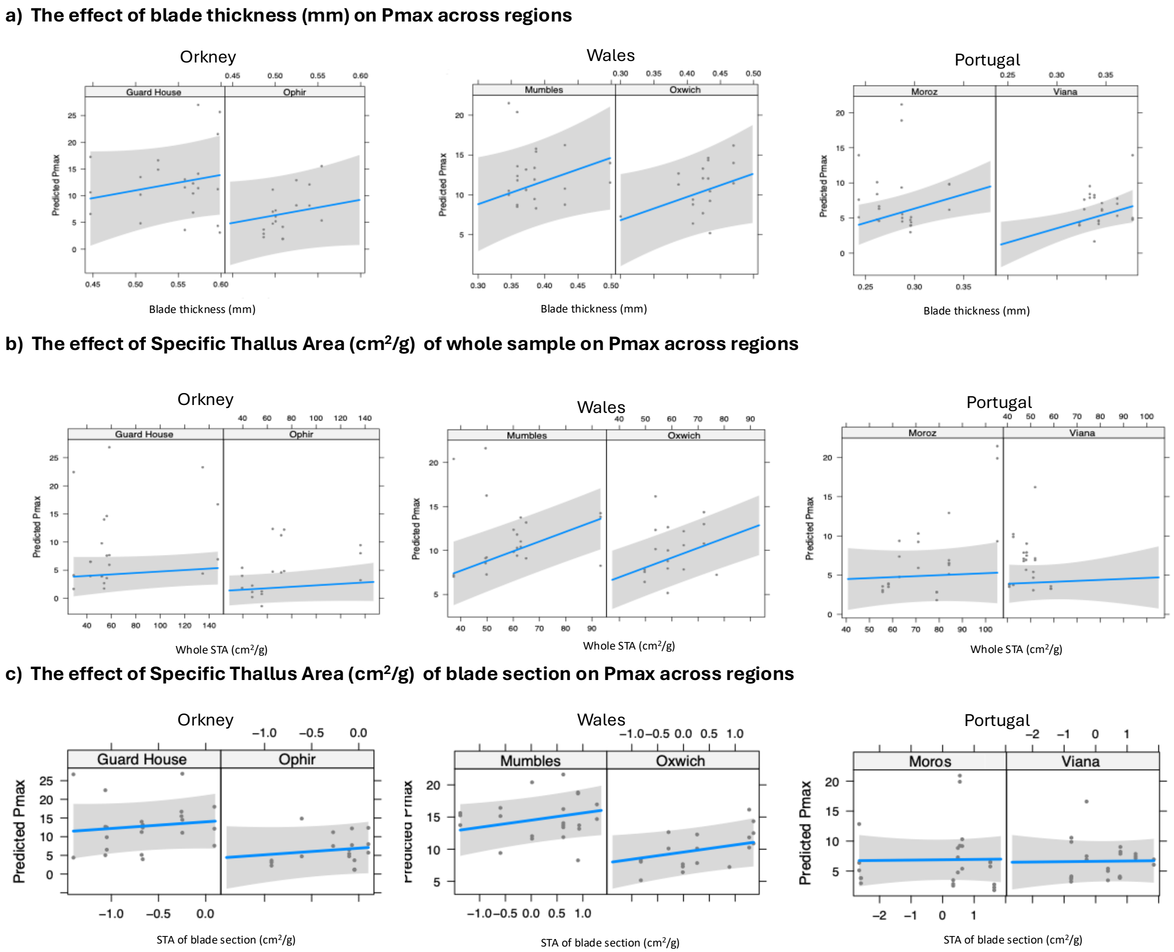

Figure 12. The effect of blade thickness (a), specific thallus area of the whole sample (b), and specific thallus area of the blade section (c) on *Pmax* of *F. serratus* across sites in Portugal (Moros, Viana), Wales (Mumbles, Oxwich), and Orkney (Guard House, Ophir), as predicted by a linear mixed-effects model. The model includes Region and Temperature as fixed effects, along with their interaction. Plots show *Pmax* (y-axis) against morphological parameters (x-axis), with model predictions overlaid. Log-transformed mass is included as a covariate, and random intercepts are specified for sample. Blue lines indicate predicted relationships, with shaded areas representing 95% confidence intervals. Sample sizes: $n = 8$ per site, total $N = 48$.

3.6 A conceptual PI curves for each region, created for comparable temperature stages

The conceptual PI curves were drawn based on photosynthetic parameters obtained for each region. Comparisons were made at a temperature stage of 15°C, which was an intermediate temperature level for all three regions, followed by comparisons at temperatures corresponding to the annual average of water temperature at each region (10°C for Orkney, 15°C for Wales, and 20°C for Portugal), and for temperature levels at which individuals reached their highest potential values of these photosynthetic parameters (Figure 14). The estimated slope of photosynthesis at 15°C did not vary between Portugal and Wales, while Orkney had the lowest estimated slope across all comparable levels (Appendix 4a). Similarly, at both local temperatures and the temperatures where the highest potential was achieved, the slope for Wales and Portugal was steeper than for Orkney. Estimated values of Pmax were consistently the highest for Wales across all compared temperature stages, while the lowest for Orkney (Appendix 4b). Additionally, the light intensity at which the rate of photosynthesis reaches its maximum (ISat) was consistently higher for Orkney than for other regions.

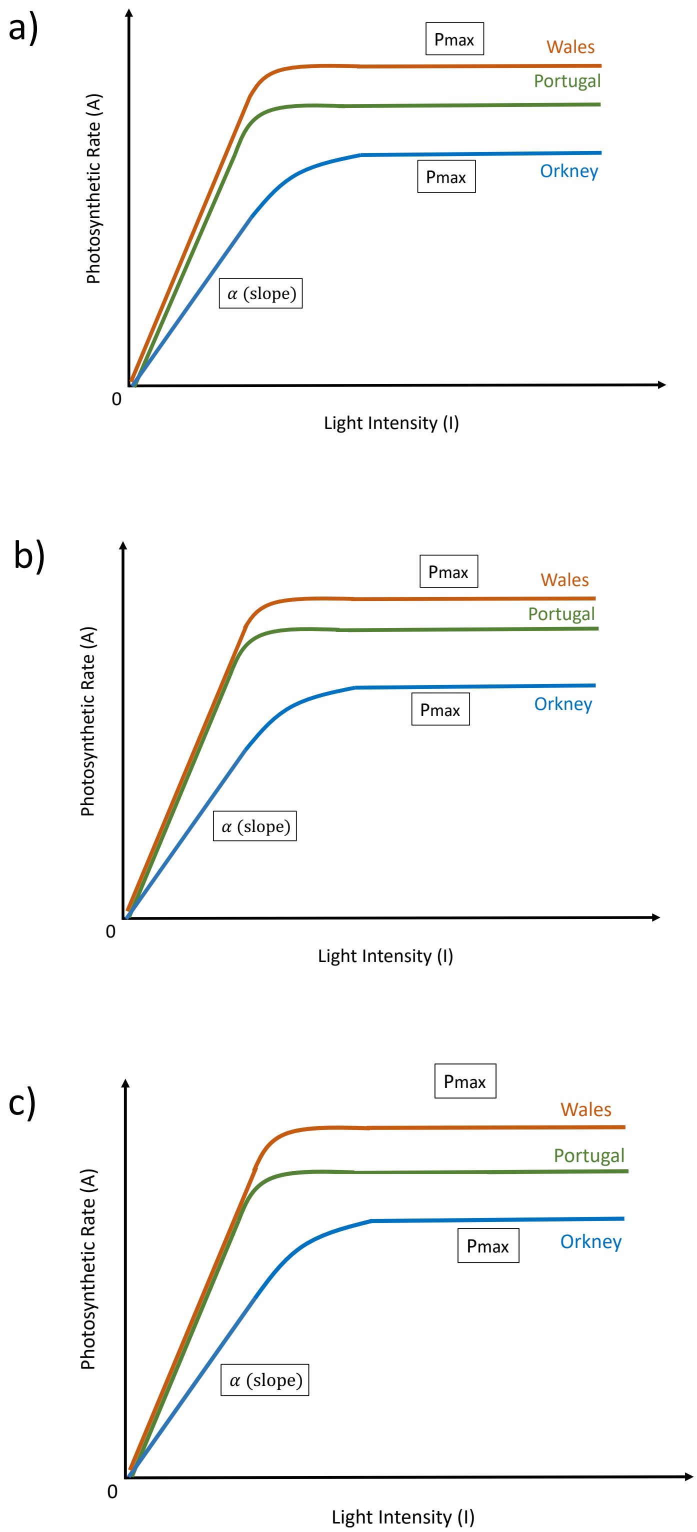

Figure 14. The predicted PI curves for each region based on estimated values of Pmax and slope for *F. serratus* at: a) temperature stage of 15°C; b) temperature stage corresponding to the regional annual means of water temperatures within the region (20°C for Portugal, 15°C for Wales, and 10°C for Orkney); c) temperature at which individuals reached the highest photosynthetic performance. Sample sizes: $n = 16$ per region, totalling $N = 48$.

4.Discussion

This study examined the geographical variation in the morphological and physiological traits of *Fucus serratus* across a 20-degree latitudinal gradient. By comparing populations of this foundational macroalga from three distinct regions—Scotland, Wales, and Portugal—we identified notable differences in both morphology and physiology. Furthermore, we investigated the relationship between the morphological features of individuals and their photosynthetic performance, which was measured in the mesocosm experiment at three temperature stages. These variations suggest that local climatic conditions influence the species' morphological traits and physiological performance, ultimately affecting its resilience and success along the latitudinal gradient.

Findings of the study indicate that individuals from northern locations tend to be larger with thicker stipes and blades, and exhibit signs of less efficient photosynthesis, which aligns with a longevity-oriented living strategy. Yet, the smaller individuals of the more southern regions that are characterised by more acquisitive traits (thinner blades and higher specific thallus area) exhibited signs of more efficient photosynthesis. Both the response of photosynthesis to increasing light intensity (slope) and the maximum rate of photosynthesis (Pmax) were higher in Wales and Portugal compared to Orkney, although these differences depended on incubation temperature to some extent. Orkney was also characterised by the highest ISat values across all regions, further suggesting lower photosynthetic efficiency of populations inhabiting more northern locations. Ultimately, findings identified Wales as a region with the best photosynthetic performance and the most pronounced impact of morphological traits on Pmax of photosynthesis, which is possibly attributed to mild climatic conditions and intermediate ranges of morphological traits among individuals.

4.1 Variation in morphological traits across regions

The total length, stipe and blade thickness displayed a clear gradient, from south to north, with an increase from Portugal to Orkney. Individuals in Orkney were twice as large as in Portugal with the thickest stipes and were characterised by high variability, particularly at Ophir, which might suggest that the environment in that region is more heterogeneous and allows more diverse morphologies to develop. Knight and Parke (1950) proposed the length of individuals as one of the indicators of the age of fucoids, hence longer individuals with thicker stipes could be older. The more stable climatic conditions in the north may tend to favour slower and steady growth (Boyer 1982; Bliss 1971; Bliss, 1956) inclining more towards a longevity living strategy compared to individuals inhabiting southern regions where climatic conditions are harsher. Additionally, reduced grazing pressure, as well as lower heat stress, might allow them to successfully reach greater body sizes over longer periods and invest more in structural resilience than individuals inhabiting southern regions, which is likely reflected in thicker stipes and blades.

There were no notable differences observed in the specific thallus area (STA) of the whole sample across regions however, a large variation in its values especially between sites in Portugal has been observed. This high variation in STA of the whole sample in Portugal could result from variations in the quantity of the structural material and the extent of disturbance to a blade surface resulting from intensified grazing in this region. The increase in temperature in the southern regions is known to lead to higher enzyme activity increasing the metabolic rates of organisms (Carr et al., 2018; Hawkins et al., 2009; Clarke & Fraser, 2004). Respiration rates in animals increase with temperatures more rapidly than in plants, leading to elevated grazing pressure (O'Connor, 2009). The most southern-located populations of *F. serratus* in Europe, inhabiting Viana do Castelo (Portugal) had numerous grazing marks, that often significantly affected the overall health of individuals reducing the area available for sunlight absorbance for photosynthesis. In addition to increased heat stress and grazing from invertebrates, this population also faces grazing pressure from herbivorous fish – *Sarpa salpa* which is specific to the region and not found at higher latitudes (Paiva et al., 2018; Gianni, 2016). This species migrated from North Africa as a result of the topicalization of fish fauna driven by ocean warming, which along with 50 other fish species extending their latitudinal range observed since 1945 poses a threat to marine ecosystems of the West Iberian Peninsula (Bañón et al., 2024). Numerous fish bite marks on this population have been identified during sampling, confirming that this additional grazing force increased the stress of individuals within the area, which may be adversely impacting local communities resulting in loss of canopy, reduced STA, and reduced biomass of *F. serratus.* In contrast, in more northern regions where water temperatures are lower, the grazing pressure is reduced diminishing stress on individuals (Coleman et al., 2006). The STA of the blade section, a more sensitive parameter unaffected by the size of the individual or the amount of structural material within the sample – unlike the STA of the whole sample - showed higher values for Portugal and Wales, reflecting thinner blades with larger surface area within these regions. A higher STA of the blade section, hence a larger surface area of photosynthetic cells that allows greater light absorption, resulted in a steeper initial slope and enhanced rates of photosynthesis. This observation corroborates previous findings on terrestrial plants, where individuals with lower leaf mass per area had higher photosynthetic rates and were characterised by faster resource acquisition and faster growth rates (Wright et al., 2004). Thus, it can be concluded that individuals inhabiting lower latitudes are characterised by faster resource acquisition likely related to higher temperatures (Yang et al., 2020). In contrast, a significant decrease in STA of the blade section was observed in Orkney, where blades were the thickest across all regions, which along with the lower photosynthetic rate suggests slower resource acquisition rates.

4.2 Differences in photosynthetic characteristics across regions

Estimated Pmax for comparable temperature stages consistently showed the lowest values in Orkney, while the highest in Wales suggesting that the central population had overall the best photosynthetic performance. It could be linked to the milder, more favourable climate and reduced environmental stress compared to more northern and southern edge populations of *F. serratus* distribution. Furthermore, the maximum photosynthetic rate (Pmax) was increasing along with an increase in temperature in Portugal and Wales nonetheless, no such trend was evident for Orkney. It might suggest that populations in Portugal and Wales are better adapted to higher temperatures and can adjust their photosynthetic rates accordingly, while populations in Orkney are less responsive to temperature changes. The lack of increase in Pmax in Orkney could be linked to lower water temperatures, which exhibit less annual fluctuation compared to more southern regions. Acclimation to higher temperatures requires high energy expenditure and the allocation of nitrogen for the synthesis of photopigments (Davison, 1991), this might reduce the potential of individuals to quickly adapt to temperature changes and consequently, to enhance their maximum photosynthetic rate.

Wales showed consistently a steeper slope of photosynthesis compared to Orkney. At 10°C slope for Wales was greater than for both Orkney and Portugal, while there were no differences in slope between Wales and Portugal at 20°C. Portugal, rather than Wales, was expected to exhibit the steepest slope, given that individuals in southern regions are exposed to higher temperatures known to enhance the enzyme activity, accelerating the reaction rates (Carr et al., 2018), allowing individuals to utilize sunlight more efficiently and reach peak photosynthesis quicker and at lower light intensities. Yet, the slope being not as steep as expected might result from the increased risk of photoinhibition within the region, thus individuals may be adapted or acclimated to be less sensitive to light in Portugal. The steeper initial slope of photosynthesis could allow individuals in Wales to achieve a maximum photosynthetic rate at lower temperatures without the increased risk of photoinhibition, which would be higher in warmer, southern regions (Powles, 1984; Hirata et al., 1983). A shallower slope could also be a result of regional differences across individuals on a molecular level. The spatial arrangements of proteins and photopigments in photosystem II could facilitate the release of the excess light energy as an adaptation preventing photoinhibition (Horton et al., 1996), which could be reflected in a more gradual slope allowing avoid the damage under harsher conditions, representing more conservative photosynthetic strategy.

Furthermore, the relationship between slope and temperature varied across regions, suggesting that regional conditions might play a significant role in these responses. In Wales the slope decreased while temperature rose from 10°C to 15°C, while the slope for Portugal and Orkney did not vary significantly with temperature, pointing to a more stable response to changes in water temperature within these areas. It might indicate that populations living closer to the end of their distribution have broader physiological thermotolerance than populations inside the range as a result of regional adaptations (Kawecki, 2008). Enhanced thermal tolerance of edge populations compared to central populations has been previously observed in both kelps (King et al., 2019) and fucoids (Saada et al., 2016; Pearson et al., 2009), emphasizing the greater resilience of their edge populations.

The values of the slope were consistently the lowest for Orkney, where the light intensity at which the rate of photosynthesis reaches its maximum before plateauing (ISat) was the highest across all regions. As individuals from this population have the thickest blades, a higher light intensity might be needed to penetrate through thicker layers of tissue to reach photopigment and reach the Pmax of photosynthesis as suggested in research on terrestrial plants (Karabourniotis et al., 2021; Kong et al., 2016), resulting in more gradual slope.

4.3 The potential impact of morphological traits on Pmax of photosynthesis

Additionally, the effect of morphological traits (blade thickness, STA of the whole sample and STA of the blade) on Pmax of photosynthesis has been analysed to test for the regional differences. The whole sample STA did not have a distinct overall effect on the maximum photosynthetic rate, as the relationship was only significant for Wales, where the slope of this relationship was the steepest. In Portugal and Orkney, the slope of this relationship was very gradual suggesting the reduced importance of whole STA on Pmax within these regions, potentially due to high variability in sizes and the amount of structural material across individuals, which were highly variable, especially in Viana, Portugal. The lack of a strong effect might also indicate that other region-specific factors could outweigh the importance of the STA of the whole sample on the Pmax of photosynthesis. The STA of the blade section showed no clear effect on Pmax and again was characterised by high variability within regions, especially across individuals in Viana, which could lower the potential for this trait to affect the Pmax. Nevertheless, there was a positive trend observed for Wales, which was again characterised by the steepest slope, fostering the potential for a concept that thinner blades with larger surfaces enhance the Pmax of photosynthesis as studied before across other macroalgal species (Litter, 1980; Arnold & Murray, 1980; Johanson & Snoeijs, 2002). Another examined trait – blade thickness, showed no clear effect on Pmax across regions. Additional analysis revealed that the significant trend was solely observed in Portugal and the near-significant effect was detected in Wales, suggesting the possible correlation between blade thickness and Pmax nevertheless, this relationship had low statistical reliability.

Overall, this analysis suggested the potential increase in Pmax along with an increase in STA however, there were strong regional differences in the strength of this relationship, with individuals from Portugal and Wales being the most responsive to this parameter, while individuals from Orkney showed reduced responsiveness. Furthermore, Wales was characterised by the most pronounced response to all three parameters, suggesting that these traits could be particularly advantageous in this region, which along with the best photosynthetic performance in Wales might suggest that mid-range morphological traits of these individuals, especially STA have a positive impact on Pmax of photosynthesis. In contrast, these factors had limited impact on individuals from Portugal and almost no effect on individuals from Orkney, suggesting that climatic differences or individual-specific features of these populations might outweigh the importance of these traits and interfere with an interaction diminishing its impact.

4.4 Conclusions

Individuals inhabiting more northern regions are larger and have thicker stipes and blades, however the efficiency of their photosynthesis is lower. They are most likely to display slow and steady growth, leaning towards the longevity strategy and being more resource-conservative. In contrast, individuals inhabiting lower latitudes are smaller and have thinner blades, while the efficiency and pace of photosynthesis are higher. They are likely to be short-lived, taking on a fast-growing strategy that allows them to acquire recourses quickly, but constrains their investment in structural parts. Furthermore, findings indicate that the more central range of the population of *F. serratus* across the examined latitudinal gradient had a better photosynthetic performance compared to more northern and southern edge populations. Temperatures in Wales are moderately higher than in the north, which allows the optimal pace of metabolic rates, while there is a significantly reduced heat and desiccation stress together with grazing pressure compared to the southern region, which could benefit these populations. Beyond that, environmental conditions in Wales appear to favour middle-sized individuals, with average blade thickness demonstrating moderate investment in structural parts and resilience.

Moreover, the morphology of individuals from the central region might be the most favourable for the photosynthesis process and the morphological traits of these individuals might have the highest potential to enhance the Pmax of photosynthesis. Nevertheless, results emphasize the complexity of the relationship between morphological traits and photosynthetic efficiency, suggesting that is likely influenced by region-specific environmental factors. Additionally, findings suggest that populations of *F. serratus* in Portugal and Wales might have higher plasticity and can be better adapted to temperature fluctuations as they can adjust their photosynthetic rates (Pmax) to temperature, while populations from Orkney have limited Pmax adaptability.

4.5 Study limitations and potential future research

This study provides valuable insights into the variation in morphological and physiological traits of foundational macroalgal species – *F. serratus*, yet the study has several limitations that could be addressed in further research. Firstly, increasing the number of individuals sampled at each shore, as well as the number of shores per region, would allow for a more reliable and representative assessment of variation in macroalgal traits. Future research could also assess the long-term resilience of various populations of *F. serratus* to climate change stressors, such as heatwaves, storms, and ocean acidification, to gain a deeper understanding of their adaptability. Additionally, transplant experiments could be performed to confirm that the observed differences are due to the ability to adjust to the environment rather than genetic adaptation. Future samples could also be analysed using molecular techniques to help understand the genetic differences between populations of *F. serratus* and enhance our understanding of how this species adapts to varying environmental conditions. Finally, this research could be expanded to include other foundational macroalgal species within this 20-degree latitude gradient, which could help to determine whether the observed patterns are consistent across taxa, providing insights into how environmental factors shape traits across diverse macroalgal communities. Addressing these aspects in future macroalgal research could provide a more comprehensive understanding of variation in morphological and physiological traits of macroalgae across climatic gradients.

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Supplementary materials

1.1 Regional differences in abiotic factors

Numerous differences in environmental data are observed across regions, illustrating how abiotic factors change across the latitudinal gradient. The annual average air temperatures are the lowest in Orkney (Guard House and Orphir) and the highest in Portugal (Moros and Viana do Castelo), highlighting the differences between the warmest and the cooler ends of distribution range. Furthermore, Orkney has the lowest water temperature at an average of 10°C, followed by Wales with a yearly average of 12°C, and Portugal with an average of 15°C. There are no strong differences in water pH levels or salinity across regions that could affect these populations. Northern region (Orkney: Guard House and Orphir) has on average fewer hours of sunlight per year than Portugal however, during the summertime northern areas are characterised by more hours of sunlight per day (up to 18 hours, Table 7). Furthermore, the ultraviolet radiation does not exceed a value of 3 in the UVI Index in summer months in Orkney compared to 6 in Wales and 10 in Portugal.

The limiting concentration thresholds in seawater are 0.1 mmol m^{-3} for NO_3 and 0.003 mmol m^{-3} for PO_4. Based on the average yearly concentrations of Phosphorus and Nitrogen across all examined sites (Table 7), and its yearly fluctuations through seasons (Appendices 8 and 9), there appears to be no deficiency of these nutrients that could potentially affect the growth of seaweed. Furthermore, the chlorophyll-a concentrations remain at a similar level across regions except for sites within Wales with a significantly higher Chlorophyll a concentration that remains stable throughout the year (Appendix 9). Increased Chlorophyll a concentration in this region could result from proximity to the large estuary of the River Severn.

Table 7. The comparison of abiotic factors across regions (based on data sourced from EU Copernicus Marine Service Information (https://marine.copernicus.eu) and from the Met Office (Weather and Climate Data (https://www.metoffice.gov.uk).; the average values for parameters were obtained based on observations made from June 2022 to July 2024).

Site name	Highest UV Index in summer months	Maximum number of hours of sunlight during summer months	Water pH	Annual average minimum air temperature (°C)	Annual average maximum air temperature (°C)	Average yearly water temperature (°C)	Water salinity ((so) $1e^{-3}$)	Sea surface wave significant height (m)	Concentration of nitrate in sea water ((NO_3) mmol m^{-3})	Concentration of phosphate in sea water ((PO_4) mmol m^{-3})	Concentration of chlorophyll a in sea water (mg m^{-3})
Guard House	3	19	8.084	5.8	11.2	10.2	34.67	1.469	6.389	0.445	0.456
Orphir	3	19	8.093	5.8	11.2	10.5	34.61	0.857	0.434	0.427	0.719
Mumbles	6	16	8.079	8.81	13.72	11.4	32.60	0.990	n/a	n/a	n/a
Oxwich	6	16	8.110	8.81	13.72	13.4	32.87	1.098	2.158	0.220	1.820
Viana do Castelo	10	15	8.064	10.2	20.3	15.9	33.60	1.462	1.944	0.144	0.450
Moros	10	15	8.065	10.2	20.3	15.7	34.78	1.067	1.865	0.127	0.434

Appendices

Appendix 1. The summary outcome for the mixed linear model examining the effect of temperature, region, and log mass on slope of photosynthesis.

Scaled residuals

Min	1Q	Median	3Q	Max
-1.4367	-0.3875	0.1805	0.7334	3.2790

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	0.0976179	0.0159333	41.6823065	6.127	2.69e-07***
RegionPortugal	0.0133406	0.0083440	56.3867438	1.599	0.115447
RegionWales	0.0362003	0.0088666	54.3331525	4.083	0.000147***
Temperature15	-0.0056990	0.0047624	86.0427401	-1.197	0.234727
Temperature20	-0.0071398	0.0055555	95.0061705	-1.285	0.201860
Log_mass	-0.0334012	0.0089322	37.3735968	-3.739	0.000617***
RegionPortugal:Temperature15	0.0009301	0.0066078	87.2067998	0.141	0.888388
RegionWales:Temperature15	-0.0221258	0.0064768	85.0642266	-3.416	0.000976**
RegionPortugal:Temperature20	-0.0019881	0.0071204	90.8088210	-0.279	0.780715
RegionWales:Temperature20	-0.0098484	0.0084195	90.0385740	-1.170	0.245202

The summary outcome for Type III Analysis of Variance Table with Satterthwaite's method

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
Region	8.9248	4.4624	2	38.664	5.0665	0.0111118 *
Temperature	22.8357	11.4179	2	87.788	12.9637	1.167e-05 ***
log_mass	12.3158	12.3158	1	37.374	13.9831	0.0006167 ***
Region:Temperature	15.5320	3.8830	4	87.653	4.4087	0.0027047 **

The output of pairwise comparisons using estimated marginal means (EMMs) to assess differences in the slopes of the model across different levels of Region and Temperature levels. The Tukey-adjusted p-values were used to account for multiple comparisons:

contrast	**Region**	**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Temperature10 - Temperature15	Orkney	0.005698	0.00476242374624782	2478441749.22456	1.1966	0.45514
Temperature10 - Temperature20	Orkney	0.007139	0.00555557549884591	1787645665.96223	1.2851	0.40354
Temperature15 - Temperature20	Orkney	0.00144	0.00595596222521468	1205940492.44677	0.24190	0.96825
Temperature10 - Temperature15	Portugal	0.0047	0.00457845356374031	2488237539.48871	1.04159	0.5505
Temperature10 - Temperature20	Portugal	0.0091	0.00444382306512239	2784061295.49551	2.0540	0.0996
Temperature15 - Temperature20	Portugal	0.0043	0.00425204899675745	3044187657.74638	1.0251	0.5609
Temperature10 - Temperature15	Wales	-0.0278	0.00439482091900585	4156052511.16084	6.331	7.29409E-10
Temperature10 - Temperature20	Wales	-0.0169	0.00634336877362596	788305652.118802	2.6781	0.02024

Temperature15 - Temperature20	Wales	0.01083	0.00609305320186744	836615649.961694	-1.7785	0.17680

Pairwise Comparisons using estimated marginal means (EMMs) Between Regions at Each Temperature Level

contrast	Temp	estimate	SE	df	t.ratio	p.value
Orkney - Portugal	10	-0.01334058	0.00834	40612308.0	-1.59875139131443	0.24614
Orkney - Wales	10	-0.036200	0.0088	39592416.3	-4.08256325898001	0.00013
Portugal - Wales	10	-0.02285	0.008	39107013.5	-2.65887396983023	0.021391
Orkney - Portugal	15	-0.0142706	0.0084	39801277.01	-1.68914917862737	0.209313
Orkney - Wales	15	-0.014074	0.00896	38211551.82	-1.57064595628139	0.258407
Portugal - Wales	15	0.0001962	0.0083	37518675.4	0.0236281042752645	0.99969
Orkney - Portugal	20	-0.011352	0.0084	46109785.1	-1.33971595425268	0.37311
Orkney - Wales	20	-0.02635	0.0098	46387944.64	-2.68062719280494	0.020098
Portugal - Wales	20	-0.014999	0.00928	40201479.02	-1.61533503538325	0.239090

Pairwise Comparisons using estimated marginal means (EMMs) Between shores within each region at each temperature level

contrast	Shore	estimate	SE	df	t.ratio	p.value
Temperature10 - Temperature15	Mumbles	0.025260	0.012691	33.0000	1.99032474652159	0.130458201487257
Temperature10 - Temperature20	Mumbles	0.008864	0.013137	33	0.67474066516565	0.779681953772683
Temperature15 - Temperature20	Mumbles	-0.01639	0.01272	33	-1.28811968606622	0.411746624412742
Temperature10 - Temperature15	Oxwich	0.03064	0.0148	32.999	2.06311851272295	0.113283908901596
Temperature10 - Temperature20	Oxwich	0.01176	0.013651	33	0.861473189678759	0.667958849782891
Temperature15 - Temperature20	Oxwich	-0.01888	0.01438	32.999	-1.31263191414905	0.398361187401239
Temperature10 - Temperature15	Moroz	-0.00313	0.020131	39.999	-0.155608104232821	0.986744001684928
Temperature10 - Temperature20	Moroz	0.006521	0.0201	39.999	0.323942353323591	0.943877571484533
Temperature15 - Temperature20	Moroz	0.00965	0.02013	40.000	0.479550457556412	0.881328829999066
Temperature10 - Temperature15	Viana	0.01392	0.020842	39.999	0.668248859778408	0.783127425937492
Temperature10 - Temperature20	Viana	0.0192	0.02084	39.999	0.921516291077556	0.630050337225133
Temperature15 - Temperature20	Viana	0.00527	0.02013	40	0.262205276408376	0.962844727882255
Temperature10 - Temperature15	Guard House	0.02504	0.01920	32.9999	1.3041577075288	0.402963789601565
Temperature10 - Temperature20	Guard House	0.04743	0.019873	32.99	2.38699367788605	0.0578963117939996

Temperature15 - Temperature20	Guard House	0.02238	0.019179	32.99	1.16739726610562	0.480612804617605
Temperature10 - Temperature15	Ophir	0.010057	0.02061	33	0.4879269388401	0.877508771152313
Temperature10 - Temperature20	Ophir	0.029258	0.022464	33	1.30243101891096	0.403904862779328
Temperature15 - Temperature20	Ophir	0.01920	0.02175	32.999	0.882621708909513	0.654883989056794

Appendix 2. The summary outcome for the mixed linear model examining the effect of temperature, region, and log mass on Pmax of photosynthesis for *F.serratus*.

Scaled residuals

Min	1Q	Median	3Q	Max
-2.0704	-0.2950	0.0751	0.5831	3.4421

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	9.8641	1.5344	42.9914	6.429	8.71e-08 ***
RegionPortugal	-0.3786	0.7875	56.4212	-0.481	0.632556
RegionWales	0.3490	0.8408	53.9211	0.415	0.679706
Temperature15	-1.0685	0.6352	99.8109	-1.682	0.095650
Temperature20	0.9155	0.9731	97.4557	0.941	0.349129
Log_mass	-2.6922	0.8576	37.0595	-3.139	0.003319 **
RegionPortugal:Temperature15	1.9305	0.7077	97.3160	2.728	0.007567 **
RegionWales:Temperature15	3.0269	0.7610	96.7955	3.978	0.000134 ***
RegionPortugal:Temperature20	0.9612	1.0951	95.1214	0.878	0.382293
RegionWales:Temperature20	2.4498	1.2948	94.5968	1.892	0.061549

Type III Analysis of Variance Table with Satterthwaite's method for the mixed linear model examining the effect of temperature, region, and log mass on Pmax of photosynthesis for *F.serratus*

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
Region	40.479	20.240	2	49.122	3.7795	0.029734 *
Temperature	112.556	56.278	2	94.414	10.5092	7.572e-05 ***
log_mass	52.770	52.770	1	37.060	9.8541	0.003319 **
Region:Temperature	94.151	23.538	4	92.874	4.3954	0.002676 **

The pairwise comparisons of different temperature stages (10°C, 15°C, and 20°C) across each region. The comparisons were performed using Tukey's adjustment for multiple comparisons.

contrast	Region	estimate	SE	df	t.ratio	p.value
Temperature10 - Temperature15	Orkney	1.06852	0.6386	265.83	1.67299	0.21749
Temperature10 - Temperature20	Orkney	-0.9154	0.96675	55.251	-0.94695	0.61318
Temperature15 - Temperature20	Orkney	-1.9839	1.02793	44.6940	-1.930070	0.1420
Temperature10 - Temperature15	Portugal	-0.86194	0.312848	4029.28	-2.75513	0.016239

Temperature10 - Temperature20	Portugal	-1.8767	0.50349	465.3156	-3.727323	0.00635
Temperature15 - Temperature20	Portugal	-1.0147	0.49743	459.74342	-2.0399	0.1039129
Temperature10 - Temperature15	Wales	-1.9583	0.42179	1702.7547	-4.64287	1.1033637E-05
Temperature10 - Temperature20	Wales	-3.3653	0.8545	63.01755	-3.93804	0.00060244
Temperature15 - Temperature20	Wales	-1.4069	0.88535	62.1500	-1.589169	0.2578788

The pairwise comparisons of different regions as different temperature stages (10°C, 15°C, and 20°C) The comparisons were performed using Tukey's adjustment for multiple comparisons.

contrast	**Temp**	**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Orkney - Portugal	10	0.378569	0.7900	111.792657128997	0.479166	0.881279890
Orkney - Wales	10	-0.3490	0.8428	119.516181912938	-0.414080	0.90989796
Portugal - Wales	10	-0.7275	0.7617	103.915181098188	-0.95520	0.60673781
Orkney - Portugal	15	-1.551	0.8768	95.7837123335526	-1.769875	0.18522908
Orkney - Wales	15	-3.3758	0.9457	107.198066923658	-3.56965	0.0015445
Portugal - Wales	15	-1.8239	0.8142	104.103772259506	-2.2400	0.0692352
Orkney - Portugal	20	-0.5826	1.15791	69.2722534792016	-0.50319	0.870015
Orkney - Wales	20	-2.7988	1.34148	56.1629495680895	-2.086404	0.10181
Portugal - Wales	20	-2.216	1.1323	69.2696079074585	-1.9571	0.130671

Model output for subset Region Orkney to test if there are significant differences between shores within this region

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	7.027e+00	7.398e+00	1.924e-06	0.950	1.000
Temperature15	-2.832e-01	1.396e+00	3.200e+01	-0.203	0.841
Temperature20	-3.812e-02	1.498e+00	3.200e+01	-0.025	0.980
ShoreOphir	-2.355e+00	3.087e+00	1.459e-08	-0.763	1.000
Log_mass	5.797e-01	1.884e+00	3.200e+01	0.308	0.760
Temperature15:ShoreOphir	-1.644e+00	1.625e+00	3.200e+01	-1.012	0.319
Temperature20:ShoreOphir	2.504e+00	2.129e+00	3.200e+01	1.176	0.248

Model output for subset Region Portugal to test if there are significant differences between shores within this region

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	-2.704e+00	5.077e+00	8.786e-07	-0.533	1.000
Temperature15	2.104e+00	1.023e+00	3.900e+01	2.057	0.0464*
Temperature20	3.054e+00	1.464e+00	3.900e+01	2.086	0.0435*
ShoreViana	-1.612e+00	1.576e+00	2.037e-09	-1.023	1.000
Log_mass	-3.260e+00	6.542e-01	3.900e+01	-4.983	1.32e-05 ***

Temperature15: ShoreViana	-1.199e+00	1.258e+00	3.900e+01	-0.953	0.3465
Temperature20: ShoreViana	-1.290e+00	1.885e+00	3.900e+01	-0.684	0.4980

Model output for subset Region Wales to test if there are significant differences between shores within this region

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	-4.985e+00	7.340e+00	3.946e-07	-0.679	1.000
Temperature15	2.012e+00	7.827e-01	3.200e+01	2.571	0.0150 *
Temperature20	4.706e+00	2.154e+00	3.200e+01	2.185	0.0363 *
ShoreOxwich	-1.389e+00	2.699e+00	1.803e-09	-0.515	1.000
Log_mass	2.759e-01	1.404e+00	3.200e+01	0.197	0.8455
Temperature15: ShoreOxwich	-1.765e+00	1.556e+00	3.200e+01	-1.134	0.2652
Temperature20: ShoreOxwich	-6.095e-01	2.991e+00	3.200e+01	-0.204	0.8398

Appendix 3. The summary outcome for the mixed linear model examining the effect of temperature, region, and log mass on ISat of photosynthesis.

Scaled residuals

Min	1Q	Median	3Q	Max
-2.1499	-0.1492	0.0713	0.3539	4.0497

Groups	Variance	Std. Dev.
Region(Shore:sample)	3.501e+06	1871.184
Shore:sample	2.692e+04	164.070
Sample	6.373e+05	798.312
Residual	1.842e+00	1.357

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	9173.73	1911.19	39.95	4.800	2.24e-05***
RegionPortugal	-819.48	1272.69	97.95	-0.644	0.5211
RegionWales	-205.86	1301.17	84.53	-0.158	0.8747
Temperature	-110.37	49.01	88.03	-2.252	0.0268*
Log_mass	-1731.21	995.94	26.39	-1.738	0.0938
RegionPortugal:Temperature	-47.37	56.75	86.00	-0.835	0.4062
RegionWales:Temperature	-122.62	55.17	86.21	-2.223	0.0288*

Type III Analysis of Variance Table with Satterthwaite's method for the mixed linear model examining the effect of temperature, region, and log mass on ISat of photosynthesis

	Sum sq	Mean sq	NumDF	DenDF	F value	Pr(>F)
Region	0.000145	0.000073	2	42.653	0.1030	0.9024
Temperature	0.069394	0.034697	2	101.750	49.1475	1.157e-15 ***

Log_mass	0.000213	0.000213	1	36.656	0.3018	0.5861
Region:Temperature	0.020358	0.005089	4	100.901	7.2090	3.795e-05 ***

The pairwise comparisons using estimated marginal means (EMMs) to assess differences in the Iasat values of the model across different levels of temperature within region. The Tukey-adjusted p-values were used to account for multiple comparisons.

contrast	**Region**	**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Temperature10 - Temperature15	Orkney	619.001	2659.1635	25.0	0.233	0.9707
Temperature10 - Temperature20	Orkney	3090.173	2885.578	25.7	1.071	0.5401
Temperature15 - Temperature20	Orkney	2471.827	2885.578	25.7	0.857	0.6718
Temperature10 - Temperature15	Portugal	644.6075	177.4782	5.2290	3.632036	0.0314457348429903
Temperature10 - Temperature20	Portugal	1524.883	204.2882	8.1343	7.464370	0.000170988576420172
Temperature15 - Temperature20	Portugal	880.2757	219.333	17.4091	4.013409	0.00236299034994591
Temperature10 - Temperature15	Wales	891.02374	255.0231	29.087916	3.493893	0.00427697446073427
Temperature10 - Temperature20	Wales	2214.66	248.7608	30.85064	8.902771	1.47931644711718E-09
Temperature15 - Temperature20	Wales	1323.637	186.22070	150.8898	7.1078961	1.31415656134948E-10

The pairwise comparisons using estimated marginal means (EMMs) to assess differences in the Iasat values of the model across different regions and temperature levels. The Tukey-adjusted p-values were used to account for multiple comparisons.

contrast	**Temp**	**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Orkney - Portugal	10	1418.7517	854.28174	148.397999348605	1.66075387925291	0.22381721
Orkney - Wales	10	1616.389	933.77269	329.283133598847	1.73103095628313	0.19517082
Portugal - Wales	10	197.6377	856.69316	396.213541319686	0.23069837705305	0.97108896
Orkney - Portugal	15	616.3577	844.8604	138.681417562935	0.729537892872161	0.74640834
Orkney - Wales	15	1060.4116	911.05554	216.018887022121	1.16393741966176	0.47604159
Portugal - Wales	15	444.05389	842.13344	3508.61565807936	0.52729636110261	0.85796172
Orkney - Portugal	20	2059.461	834.757773	442.327326470051	2.46713643270418	0.03718745
Orkney - Wales	20	2946.8769	908.553763	669.282417016315	3.24348110911534	0.0035452
Portugal - Wales	20	887.41565	820.856306	255017.106637437	1.08108525934698	0.5258208

Appendix 4a. Estimated values of slope for compromised temperature stage of 15 °C, the temperatures corresponding to annual average of water temperatures at each region (10°C for Orkney, 15°C for Wales, and 20°C for Portugal), and for temperatures at which individuals reached the highest potential values of slope. Values represents the average (predicted) slope, adjusted for the other variables in the model (region, log mass) and weighted by the inverse of the squared standard error.

Region	At 15°C	Local temperatures	Temperature at which the highest potential was reached
Portugal	0.0552	0.0511	0.0552 (for 15°C)

Wales	0.0549	0.0549	0.066 (for 20°C)
Orkney	0.041	0.0466	0.0466 (for 10°C)

Appendix 4b. Estimated values of Pmax for compromised temperature stage of 15 °C, the temperatures corresponding to annual average of water temperatures at each region (10°C for Orkney, 15°C for Wales, and 20°C for Portugal), and for temperatures at which individuals reached the highest potential values of Pmax. Values represents the average (predicted) slope, adjusted for the other variables in the model (region, log mass) and weighted by the inverse of the squared standard error.

Region	At 15°C	Local temperatures	Temperature at which the highest potential was reached
Portugal	6.25	7.27	7.27 (at 20°C)
Wales	8.08	8.08	9.48 (at 20°C)
Orkney	4.7	5.77	6.68 (at 20°C)

Appendix 5. The summary outcome for the mixed linear model examining the effect of blade thickness on Pmax of photosynthesis.

Scaled residuals

Min	1Q	Median	3Q	Max
-2.0858	-0.3234	0.0677	0.5688	3.4683

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	5.2512	4.7679	52.4506	1.101	0.275769
Temperature15	-1.0546	0.6344	99.4593	-1.662	0.099598
Temperature20	1.0321	0.9779	96.0933	1.055	0.293873
RegionPortugal	1.4450	1.9510	55.3324	0.741	0.462020
RegionWales	1.5535	1.4492	57.1300	1.072	0.288234
Blade.thickness	8.1275	1.4492	51.2363	1.021	0.311887
Log_mass	-2.5349	0.8742	37.4092	-2.900	0.006218 **
Temperature15:RegionPortugal	1.9050	0.7070	96.9032	2.695	0.008310 **
Temperature20:RegionPortugal	0.8334	1.1001	93.7139	0.758	0.450609
Temperature15:RegionWales	3.0206	0.7599	96.5214	3.975	0.000136 ***
Temperature20:RegionWales	2.3765	1.2946	94.0291	1.836	0.069563

Type III Analysis of Variance Table with Satterthwaite's method for the mixed linear model examining the effect of blade thickness on Pmax of photosynthesis.

	Sum sq	Mean sq	NumDF	DenDF	F value	Pr(>F)
Region	44.236	22.118	2	48.371	4.1471	0.021761 *
Temperature	116.396	55.198	2	93.947	10.9121	5.479e-05 ***
Log_mass	44.848	0.44.848	1	37.410	8.4089	0.006217 **
Blade thickness	5.564	5.564	1	51.238	1.0432	0.311885
Region:Temperature	93.907	0.005089	4	92.383	4.4019	0.002657 **

Summary output for subset data Orkney

Scaled residuals

Min	1Q	Median	3Q	Max
-1.4382	-0.3350	0.4608	0.8833	2.1202

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	7.027e+00	7.398e+00	1.924e-06	0.950	1.000
Temperature15	-2.832e-01	1.396e+00	3.200e+01	-0.203	0.841
Temperature20	-3.812e-02	1.498e+00	3.200e+01	-0.025	0.980
ShoreOphir	-2.355e+00	3.087e+00	1.459e-08	-0.763	1.000
Blade thickness	-4.224e+00	1.265e+01	3.200e+01	-0.334	0.741
Log_mass	5.797e-01	1.884e+00	3.200e+01	0.308	0.760
Temperature15:ShoreOphir	-1.644e+00	1.625e+00	3.200e+01	-1.012	0.319
Temperature20:ShoreOphir	2.504e+00	2.129e+00	3.200e+01	1.176	0.248

Summary output for subset data Portugal

Scaled residuals

Min	1Q	Median	3Q	Max
-2.2358	-0.3114	0.1158	0.7076	2.4135

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	-2.704e+00	5.077e+00	8.786e-07	-0.533	1.000
Temperature15	2.104e+00	1.023e+00	3.900e+01	2.057	0.0464*
Temperature20	3.054e+00	1.464e+00	3.900e+01	2.086	0.0435*
ShoreViana	-1.612e+00	1.576e+00	2.037e-09	-1.023	1.000
Blade thickness	4.059e+01	1.576e+00	3.900e+01	2.575	0.0139*
Log_mass	-3.260e+00	6.542e-01	3.900e+01	-4.983	1.32e-05 ***
Temperature15: ShoreViana	-1.199e+00	1.258e+00	3.900e+01	-0.953	0.3465
Temperature20: ShoreViana	-1.290e+00	1.885e+00	3.900e+01	-0.684	0.4980

Summary output for subset data Wales

Scaled residuals

Min	1Q	Median	3Q	Max
-1.8673	-0.4414	0.1345	0.8291	1.8943

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	-4.985e+00	7.340e+00	3.946e-07	-0.679	1.000
Temperature15	2.012e+00	7.827e-01	3.200e+01	2.571	0.0150 *
Temperature20	4.706e+00	2.154e+00	3.200e+01	2.185	0.0363 *

ShoreOxwich	-1.389e+00	2.699e+00	1.803e-09	-0.515	1.000
Blade thickness	2.915e+01	1.606e+01	3.200e+01	1.815	0.0789 .
Log_mass	2.759e-01	1.404e+00	3.200e+01	0.197	0.8455
Temperature15: ShoreOxwich	-1.765e+00	1.556e+00	3.200e+01	-1.134	0.2652
Temperature20: ShoreOxwich	-6.095e-01	2.991e+00	3.200e+01	-0.204	0.8398

Appendix 6a. The summary outcome for the mixed linear model examining the effect of Whole Sample STA on Pmax of photosynthesis including the effect of temperature and region as well as their interaction in the model.

Scaled residuals

Min	1Q	Median	3Q	Max
-2.1614	-0.3136	0.0969	0.5360	3.4086

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	3.61114	1.12445	51.23134	3.211	0.002283 **
RegionPortugal	-0.15988	0.83858	56.64356	-0.191	0.849482
RegionWales	1.25676	0.86812	55.87401	1.448	0.153293
Temperature15	-1.03248	0.63869	97.58717	-1.617	0.109205
Temperature20	1.09304	0.97392	97.45204	1.122	0.264492
Whole.STA	0.02733	0.01362	51.20801	2.006	0.050105 .
RegionPortugal:Temperature15	1.89941	0.71107	95.21090	2.671	0.008890 **
RegionWales:Temperature15	3.04392	0.76387	94.97128	3.985	0.000132 ***
RegionPortugal:Temperature20	0.77228	1.09488	95.27677	0.705	0.482308
RegionWales:Temperature20	2.29671	1.29588	94.73332	1.772	0.079556 .

Type III Analysis of Variance Table with Satterthwaite's method

	Sum sq	Mean sq	NumDF	DenDF	F value	Pr(>F)
Region	49.348	24.674	2	48.327	4.6067	0.014750 *
Temperature	109.080	54.540	2	94.776	10.1828	9.865e-05 ***
Log_mass	41.723	41.723	1	36.733	7.7898	0.008285 **
Whole STA	12.848	12.848	1	49.449	2.3987	0.127812
Region:Temperature	98.504	24.626	4	93.020	4.5977	0.001969 **

Summary output for subset data Orkney

Scaled residuals

Min	1Q	Median	3Q	Max
-1.4764	-0.1936	0.4687	0.9364	2.2081

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	5.00287	1.39921	33	3.576	0.0011 **

Temperature15	-1.53447	1.20205	33	-1.277	0.2107
Temperature20	-0.03350	1.34418	33	-0.025	0.9803
ShoreOphir	-2.09649	1.85360	33	-1.131	0.2662
Whole.STA	0.01293	0.01211	33	1.068	0.2933
Temperature15:ShoreOphir	-0.36578	1.47502	33	-0.248	0.8057
Temperature20:ShoreOphir	2.15112	2.04556	33	1.052	0.3006

Summary output for subset data Wales

Scaled residuals

Min	1Q	Median	3Q	Max
-2.1732	-0.3676	0.2236	0.5682	2.1954

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	0.12970	1.36538	33	0.095	0.924897
Temperature15	1.95184	0.52521	33	3.716	0.000747 ***
Temperature20	3.13791	1.55946	33	2.012	0.052423
ShoreOxwich	-0.43847	1.37622	33	-0.319	0.752036
Whole.STA	0.11077	0.01846	33	6.002	9.59e-07 ***
Temperature15: ShoreOxwich	-1.33109	1.10299	33	-1.207	0.236087
Temperature20: ShoreOxwich	-0.29855	2.11464	33	-0.141	0.888586

Summary output for subset data Portugal

Scaled residuals

Min	1Q	Median	3Q	Max
-1.5882	-0.1533	0.2051	0.5557	3.5005

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	2.92646	2.68128	40	1.091	0.282
Temperature15	1.07466	1.46398	40	0.734	0.467
Temperature20	2.75230	2.13123	40	1.291	0.204
ShoreViana	-0.43041	1.85679	40	-0.232	0.818
Whole.STA	0.01244	0.03411	40	0.365	0.717
Temperature15: ShoreViana	-0.16978	1.79147	40	-0.095	0.925
Temperature20: ShoreViana	-1.10436	2.74211	40	-0.403	0.689

Type III Analysis of Variance for Portugal subset Moroz

	Sum sq	Mean sq	NumDF	DenDF	F value	Pr(>F)
Temperature	82.755	41.378	2	14.9072	7.5312	0.005488 **
Whole STA	12.008	12.008	1	6.5594	2.1855	0.185655

Type III Analysis of Variance for Portugal subset Viana

	Sum sq	Mean sq	NumDF	DenDF	F value	Pr(>F)
Temperature	26.4185	13.2093	2	13.7089	4.3798	0.03382 *
Whole STA	2.7209	2.7209	1	5.3592	0.9022	0.38304

The pairwise comparisons using estimated marginal means (EMMs) to assess differences in the model across different regions and temperature levels

contrast	Temp	estimate	SE	df	t.ratio	p.value
Orkney - Portugal	10	0.2806481	0.7811147	110.800610510392	0.3592	0.9313
Orkney - Wales	10	-0.57452755	0.8429125	114.762988414352	-0.6815980	0.7746
Portugal - Wales	10	-0.85517571	0.75273915	104.363733448613	-1.136085	0.49416
Orkney - Portugal	15	-1.7586563	0.87491732	94.219180173936	-2.01008	0.1153
Orkney - Wales	15	-3.693141	0.954904480	103.388444458573	-3.867550	0.0005
Portugal - Wales	15	-1.934484	0.805085022	104.514371500524	-2.40283	0.0470
Orkney - Portugal	20	-0.7559681	1.154252282	67.3976091066587	-0.654941	0.7902
Orkney - Wales	20	-3.0310875	1.340729784	55.1515773130772	-2.26077	0.0700
Portugal - Wales	20	-2.2751193	1.124308525	68.472557492117	-2.0235	0.1142

The pairwise comparisons using estimated marginal means (EMMs) to assess differences in the model across different temperature levels within the region.

contrast	Region	estimate	SE	df	t.ratio	p.value
Temperature10 - Temperature15	Orkney	1.1597122	0.639233	265.9833	1.814224	0.1668735
Temperature10 - Temperature20	Orkney	-0.861785	0.965360	55.59776	-0.8927088	0.64713
Temperature15 - Temperature20	Orkney	-2.021498	1.02621	45.048226	-1.96985	0.131440
Temperature10 - Temperature15	Portugal	-0.879592	0.31281	4028.5433	-2.811859	0.01371
Temperature10 - Temperature20	Portugal	-1.89840	0.503371	465.58510	-3.771375	0.000536
Temperature15 - Temperature20	Portugal	-1.01880	0.497167	460.689881	-2.04922	0.10182
Temperature10 - Temperature15	Wales	-1.958	0.421434	1708.07181	-4.64467	1.07523
Temperature10 - Temperature20	Wales	-3.318	0.8542696	62.822711	-3.8844	0.00072
Temperature15 - Temperature20	Wales	-1.359	0.8850274	62.050743	-1.536047	0.28130

Appendix 6b. The summary outcome for the mixed linear model examining the effect of blade section STA on Pmax of photosynthesis including the effect of temperature and region as well as their interaction in the model.

Scaled residuals

Min	1Q	Median	3Q	Max
-2.0900	-0.2970	0.0550	0.5783	3.4328

	Estimate	Std. Error	df	t-value	p-value
(Intercept)	4.58603	0.6908	66.1462	8.089	1.81e-11 ***

RegionPortugal	-0.4728	0.9114	57.4630	-0.519	0.60590
RegionWales	0.8814	0.9312	54.0242	0.946	0.34814
Temperature15	-0.8993	0.6391	97.3608	-1.407	0.16257
Temperature20	1.1916	0.9759	96.6581	1.221	0.22505
STA	0.01152	0.3525	42.1665	0.634	0.52925
RegionPortugal:Temperature15	1.75829	0.7105	95.3306	2.475	0.01510 *
RegionWales:Temperature15	2.9176	0.7641	94.5789	3.818	0.00024 ***
RegionPortugal:Temperature20	0.6586	1.0962	94.5386	0.601	0.54939
RegionWales:Temperature20	2.2355	1.2986	94.125	1.721	0.08846

Type III Analysis of Variance Table with Satterthwaite's method for the mixed linear model examining the effect of blade section STA on Pmax of photosynthesis including the effect of temperature and region as well as their interaction in the model

	Sum sq	Mean sq	NumDF	DenDF	F value	Pr(>F)
Region	32.166	16.083	2	47.977	3.0177	0.058285
Temperature	112.020	56.010	2	94.447	10.5093	7.57e-05 ***
Log_mass	54.142	54.142	1	37.049	10.1587	0.002915 **
STA	4.741	4.741	1	39.005	0.8895	0.351423
Region:Temperature	92.258	23.065	4	92.881	4.3276	0.002965 **

Appendix 7. The summary outcome for two-way ANOVA examining the effect of temperature and region on respiration rates of *F. serratus*.

	Df	Sum sq	Mean sq	F value	Pr(>F)
Temperature	2	0.2218	0.11088	11.483	2.8e-05 ***
Region	2	0.0185	0.00927	0.960	0.3859
Temperature:Region	4	0.0854	0.01236	2.212	0.0718
Residuals	117	1.1297	0.00996		

Tukey multiple comparisons of means 95% family-wise confidence level for three temperature stages (10°C, 15°C, 20°C).

	diff	lwr	upr	P adj
15-10	0.06457558	0.01266862	0.11648254	0.0105122
20-10	0.10310335	0.05061118	0.15559553	0.0000240
20-15	0.03852777	-0.01272774	0.08978327	0.1794377

Appendix 8. The concentration of Nitrate ((NO_3) mmol m^{-3}) in the sea water calculated for each season based on daily observations made from January 2023 to end of December 2023 sourced from EU Copernicus Marine Service.

	Spring	Summer	Autumn	Winter
Viana do Castelo	1.64731224	1.66214269	0.5862722	1.90765268
Muroz	1.99093866	1.17089886	1.23705079	1.79085755
Oxwich	1.87848386	0.50083404	0.67006522	3.40730824
Mumbles	n/a	n/a	n/a	n/a
Guard House	6.53118388	6.11858522	6.31095888	6.57279384
Ophir	0.49120788	0.41960777	0.32072075	0.47633489

Appendix 9. The concentration of Phosphate ((NO3) mmol m^{-3}) in the sea water calculated for each season based on daily observations made from January 2023 to end of December 2023 sourced from EU Copernicus Marine Service.

	Spring	Summer	Autumn	Winter
Viana do Castelo	0.12892661	0.12169225	0.04820446	0.14132359
Muroz	0.11933483	0.07117115	0.02910318	0.13146131
Oxwich	0.2452921	0.14470626	0.15830654	0.3005584
Mumbles	n/a	n/a	n/a	n/a
Guard House	0.49231701	0.43632747	0.32847602	0.48386326
Ophir	0.49135303	0.41952809	0.32163911	0.48014583

Appendix 10. The concentration of Chlorophyll a (mg m^{-3}) in the sea water calculated for each season based on daily observations made from January 2023 to end of December 2023 sourced from EU Copernicus Marine Service.

	Spring	Summer	Autumn	Winter
Viana do Castelo	0.69214267	0.50858328	0.3661548	0.4590844
Muroz	0.71623486	0.30601997	0.28245576	0.48084269
Oxwich	2.39281394	2.01056486	2.17862001	1.60479526
Mumbles	n/a	n/a	n/a	n/a
Guard House	0.48501331	0.29091635	0.3268122	0.49178138
Ophir	1.04547181	0.68724125	0.38560225	0.51280214

Appendix 11. A copy of the ethical approval confirmation letter.

Approval Date: 16/06/2024

Research Ethics Approval Number: 2 2024 9507 9087

Thank you for completing a research ethics application for ethical approval and submitting the required documentation via the online platform.

Project Title	Ethics form for MRes
Applicant name	MISS MARTYNA EWA ZAWADZKA
Submitted by	MISS MARTYNA EWA ZAWADZKA /
Full application form link	https://swansea.forms.ethicalreviewmanager.com/Project/Index/11545

The Science and Engineering ethics committee has approved the ethics application, subject to the conditions outlined below:

Approval conditions

1. The approval is based on the information given within the application and the work will be conducted in line with this. It is the responsibility of the applicant to ensure all relevant external and internal regulations, policies, and legislations are met.
2. This project may be subject to periodic review by the committee. The approval may be suspended or revoked at any time if there has been a breach of conditions.
3. Any substantial amendments to the approved proposal will be submitted to the ethics committee prior to implementing any such changes.

Specific conditions in respect of this application:

The application has been classified as Low Risk to the University.

No additional conditions.

Statement of compliance

The Committee is constituted in accordance with the Governance Arrangements for Research Ethics Committees. It complies with the guidelines of UKRI and the concordat to support Research Integrity.

Science and Engineering Research and Ethics Chair

Swansea University.

Appendix 12. A confirmation of completed and signed risk assessment form**.**

Risk Assessment Outcome:

Risk Rating: Negligible/Low risk **Submitted Date:** 14 Jun 2024
Approved Date: 14 Jun 2024 **Approved by:** John Griffin

Student Details

Student Number: 1906932 **Project Supervisor:** Dr John Griffin
Course: Biosciences Masters by Research Full-time **Level:** 7

Appendix 13. Statement of Contributions.

Contributor Role	**Persons involved**
Conceptualization	MZ, JG
Data Curation	MZ
Formal Analysis	MZ
Investigation	MZ
Methodology	MZ, JG
Project Administration	MZ,JG
Resources	JG
Supervision	JG
Visualization	MZ
Writing – Original Draft Preparation	MZ
Writing – Review & Editing	JG, MZ

Appendix 14. Statement of Expenditures related to the project.

Category	**Item**	**Description**	**Cost**
Travel	Train	Train from Swansea to Bristol	£21.39
Travel	Train	Train from Bristol to Swansea	£24.49
Travel	Flight	Return flight to Porto	£116.56
Accommodation	Accommodation in Porto		£355.76
Total:			**£518.2**