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UNIVERSIDADE DO ALGARVE

Faculdade de Ciências e Tecnologia

2022

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Mestrado em Biologia Marinha

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2022

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Assessing the potential for resilience towards Marine Heatwaves and ALAN in Kelp species

Declaro ser a autora deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

Assinatura

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Assinatura

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Abstract

Identifying adaptive or mitigating solutions for climate change is especially important for high conservation value ecosystems, such as kelp forests. The effects of Marine Heatwaves (MHWs), short-term increased temperature events, on the physiology of such organisms have been greatly overlooked when addressing thermal stress impacts, with a greater attention given to ocean warming. By testing the combined effect of heatwaves and ocean acidification, it has been demonstrated that the extra Carbon source helped organisms on their resilience to the thermal stressor, yet the effect extra light sources could have has never been analysed. In this study the combined effect of MHWs (+3ºC) and Artificial Light at Night (ALAN) (24hlight-0h dark), exposure was tested on the photosynthetic parameters (Fv, Fv/Fm, ETRm and Alfa), growth and respiration (R) rates and C/N tissue ratio of the species *Laminaria digitata*. A 14-day MHW simulation was performed followed by a 10-day recovery period, in short term mesocosm experiments at the Plymouth Marine Laboratory. A "collapsed factorial design", was used with "SW Temperature" set as the main driver and "Light availability nested within SW Temperature" as the secondary one. As expected MHW alone caused significant negative impacts on growth and C/N tissue ratios, with organisms presenting the lowest rates, even in the recovery period, while it increased their fluorescence responses, with the highest's values of Fv and Fv/FM observed only during the exposure period. On the other hand, MHW combined with ALAN treatments showed the highest values of growth and C/N ratios, while presenting the lowest values of Alfa, due to down regulations of light consumption mechanisms. It was concluded that by exposing organisms to ALAN this could help them on their resilience to MHW events, by enhancing their carbon fixation rates, and hence producing the extra amount of energy necessary to withstand the thermal stressor.

Resumo

No atual contexto das mudanças ambientais observadas a nível global, compreender o seu impacto para os ecossistemas tornou-se o principal foco da comunidade científica. Identificar soluções que levem à adaptação e mitigação dos efeitos causados pelas alterações climáticas é de especial importância tendo em conta ecossistemas de alto valor de conservação. Dentro deste grupo, algas marinhas, onde florestas de "Kelps" estão incluídas, desempenham um

importante papel, sendo dos organismos marinhos fotossintéticos com maiores taxas de produção primária, atuando como "engenheiros ecossistémicos" e importantes sequestradores de carbono azul e servindo de abrigo para uma enorme diversidade de organismos marinhos, em variadas zonas costeiras. No entanto, tendo em conta a dependência direta de condições de temperatura baixas a moderadas observada para estes organismos, a maior parte dos estudos realizados neste contexto tendem a dar uma maior ênfase aos efeitos causados pelo aumento de temperatura a nível global, o aquecimento progressivo dos oceanos. Deixando assim de lado eventos locais e temporários de aquecimento das águas denominados "Ondas de Calor Marinhas" (no inglês "Marine Heatwaves"), que acabam por receber menor atenção por parte dos investigadores.

Ondas de Calor Marinhas constituem eventos locais de águas anomalamente quentes, podendo resultar de processos de escalas temporais e espaciais variadas. Os seus impactos já foram demonstrados para uma série de organismos marinhos, incluindo florestas de kelps, no entanto, maioritariamente de um ponto de vista ecológico, com abordagens a nível dos efeitos fisiológicos causados nos indivíduos ainda bastante limitadas. Com o aumento da frequência de ocorrência e intensidade das ondas de calor observadas atualmente e previstas no futuro, torna-se imprescindível compreender melhor a dinâmica destes efeitos nos organismos e a respetiva capacidade de resiliência. Embora limitados, alguns estudos já realizaram tal abordagem, simulando condições de ondas de calor em ambientes controlados, observando o seu efeito isolado e, em alguns casos, combinado com outras pressões ambientais. Em estudos simulando a exposição a ondas de calor e níveis elevados de CO_2-acidificação dos oceanos-por exemplo, foi observado que ao invés de atuar como uma fonte adicional de stress fisiológico, as condições de elevada concentração de CO_2 aumentaram a resiliência dos organismos perante o stress térmico. No entanto nenhuma abordagem foi feita até agora explorando o mesmo contexto em relação a condições de elevada disponibilidade de luz.

Desempenhando um papel igualmente importante ao do carbono inorgânico na fotossíntese, a intensidade e disponibilidade da luz, influenciam diretamente toda a atividade fotossintética dos organismos e, consequentemente, a sua sobrevivência. Embora a luz solar seja a fonte principal de luz usada por estes organismos, a luz artificial é também uma fonte opcional, e, neste contexto, o uso de Luz Artificial Noturna (em inglês "Artificial Light at Night") ganha particular atenção. Com uma crescente atenção por parte da comunidade científica, o estudo da Luz Artificial Noturna tem ganho particular ênfase tendo em conta os seus efeitos em animais

marinhos, negligenciando em parte os seus potenciais efeitos em organismos marinhos fotossintéticos, como nas macroalgas.

Neste estudo o efeito combinado de Ondas de Calor (+3°C) e Luz Artificial Noturna (24h claro-0h escuro), foi testado nos parâmetros fotossintéticos (Fv, Fv/Fm, ETRm e Alfa), taxas de crescimento e respiração (R) e razão percentual de C/N (Carbono por Azoto) nos tecidos da espécie *Laminaria digitata*. Foram simulados 14 dias de Ondas de Calor, seguidas por um período de recuperação de 10 dias, em experiências de curto prazo em mesocosmo no Plymouth Marine Laboratory ("PML", Reino Unido). A experiência foi realizada no Inverno de 2022 e o desenho experimental foi definido como um "collapsed factorial design", assim como sugerido por investigadores para diminuir o número de tratamentos e aumentar a possibilidade de replicados em estudos de múltiplos fatores. Foi definida a "Temperatura da água" como o fator principal e a "Disponibilidade de Luz aninhada dentro da Temperatura da água" como fator o secundário, tendo-se assim implementado dois tratamentos distintos: organismos expostos à onda de calor isolada e organismos expostos à onda de calor em combinação com a luz artificial noturna, além dos controlos expostos às condições ambientais de temperatura e luz.

Como esperado, a exposição à Onda de Calor isolada causou impactos negativos significativos no crescimento e na relação tecidual de C/N dos organismos. Nesses tratamentos, valores mais baixos foram observados para estes parâmetros, estendendo-se ainda durante período de recuperação. O fator também causou o aumento da fluorescência dos organismos, com maiores valores de Fv e Fv/FM observados, embora apenas durante o período de exposição ao evento. Por outro lado, os tratamentos de Onda de Calor combinada com Luz Artificial Noturna, apresentaram os maiores valores de crescimento e razão C/N, enquanto observando-se os menores valores de Alfa, devido à regulação negativa dos mecanismos de consumo de luz. Para a maior parte dos parâmetros estudados foi observado um efeito apenas do fator "Disponibilidade de Luz aninhada dentro da Temperatura da água", com a exceção do ETRm, onde não se observou efeito significativo de nenhum fator e de Fv/Fm, onde efeitos da "Temperatura da água" foram também observados.

Concluiu-se então que, ao expor organismos de Kelp à Luz Artificial Noturna, a fonte adicional de energia luminosa pode contribuir para a sua maior resiliência a eventos de Ondas de Calor, aumentando a sua atividade fotossintética e fixação de carbono, e, portanto, produzindo a quantidade de energia necessária para suportar a pressão térmica. Esta descoberta é de extrema

importância tendo em conta todos os serviços ecológicos e económicos prestados por florestas de Kelp, e outras algas marinhas. Ao identificar formas de aumentar a resiliência destes organismos às diferentes formas de pressão ambiental causados pelas alterações climáticas, contribui-se para o conhecimento de possíveis formas para melhorar a sua gestão, conservação e restauração. Em sequência, diminui-se também o impacto causado à diversidade de comunidades que estes ecossistemas abrigam e a toda sua teia trófica. Tal abordagem é também de grande interesse para indústrias de produção de florestas de Kelp. Particularmente para grandes produtores como a China, onde grandes números de eventos de ondas de calor são registados atualmente e previstos no futuro com o avanço das alterações climáticas, formas de mitigar os seus efeitos torna-se imprescindível.

Acknowledgements of the thesis

First, I would like to express my deepest gratitude to my supervisors, Catarina Vinagre and Ana Queirós, whose support has been indispensable for the accomplished of this thesis. I am extremely thankful for the opportunity you gave me to work on such an important experiment and show my capacities as a becoming scientist. I would like to say that I am very inspired by both, especially me being a young woman and seeing such powerful and successful women working on the area. I also address this recognition to Professor Francisco Arenas, from University of Porto with whom I also had the pleasure to work with and whose experience in marine plant's and seaweed's ecology and physiology played a major role on guiding me on the right path during the whole extent of the experiment.

A special thank you also to the marine institutions Centro de Ciências do Mar (CCMAR) and Plymouth Marine Laboratory (PML) for having me in your facilities and providing all the necessary support for the performance of the thesis. Particularly, to the mesocosm laboratory manager where the experiment was performed, Joana Nunes, and all the remaining PML staff, that were impeccable whenever help was needed and showed incredible support all along. Your support and advice sure made a big difference.

To all my university professors, my sincere thank you to you as well. Having completed my undergraduate and now my master's both at the University of Algarve, I ended up developing a great relationship to most my professors. I can say for certain that without your teachings along this process the development of this thesis would not be the same.

I'd like to also mention my colleagues, family, and friends for all their support, giving advice along the way and indispensable moral support.

And, lastly, my greatest thank you to my mom, my biggest inspiration and strongest supporter. I've always been and continue to be amazed by the incredible, adventuress and powerful woman you are, inspiring me to always give my best in everything and at the same time believing more than anyone in me. You are my rock.

So far, the development of this thesis was, without a doubt, my biggest challenge and allowed me to grow greatly, professionally, and personally, and I look forward to seeing what other adventures await me along this path called life.

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List of abbreviations, acronyms and symbols

IPCC- Intergovernmental Panel on Climate Change

MarLIN- Marine Life Information Network

OBIS- Ocean Biogeographic Information System

UK- United Kingdom

WEC- Western English Channel

ALAN- Artificial Light at Night

MHW(s)- Marine Heatwave(s)

NE- Northeast

IC- Inorganic Carbon

PSII- Photosystem II

ATP- Adenosine Triphosphate

NADPH- Nicotinamide adenine dinucleotide phosphate

PAR- Photosynthetic Active Radiation

Pmax- maximum photosynthetic rate

PML- Plymouth Marine Laboratory

Mt- Million tons

FAO- Food and Agriculture Organization of the United Nations

UN- United Nations

SDG's- Sustainable Development Goals

ETRm- maximum Electron Transport Rate

R- respiration

RLC- Rapid Light Curves

DW- Dry weight

FW- Fresh Weight

SWT- Seawater Temperature

LA- Light availability

THSD- Tukey's Honestly Significant Different

Chapter 1- General Introduction

1.1 Introduction

Climate change is in the current days one of the predominant causes of ecosystem changes and disruptions (Doney *et al.*, 2012; Smale *et al.*, 2019; Gissi *et al.*, 2021;). Resulting from anthropogenic greenhouse gas emissions (IPCC, 2014; IPCC, 2021), it manifests itself in different environmental parameters, affecting marine ecosystems in variable spatial and temporal scales (IPCC, 2019). Considering this, the studies performed on the topic have also been very variable, to comprehend its diversity of impacts. Two main goals have been established for the several studies done on the issue: observing the potential responses of organisms and looking for ways to counteract their effects. Nowadays, given the fast rate of environmental change (IPCC, 2014; IPCC, 2021), this second goal becomes even more important.

When identifying adaptive or mitigating solutions to these effects, high conservation value ecosystems are a particular group to consider. They represent ecosystems where restoration and conservation may have the most notable impacts, potentially contributing to the reestablishment of several other communities, hence delivering a big range of ecological, social, and economic services (Daily *et al.*, 1997; Tallis & Kareiva, 2005). And among others, seaweeds, such as kelps, represent relevant groups within these ecosystems.

1.2 Kelps Ecology

"Kelps" are defined as a non-taxonomic group (Bolton, 2010; Wernberg *et al.*, 2019) composed of large brown seaweeds, whose canopies can extend over tens of meters over the seafloor, depending on the species (Wernberg *et al.*, 2019). Despite the existing discussion over which specific orders should be included in the group (only Laminariales or also Fucales and others) (Fraser, 2012), some main characteristics are common to all of them. In general, these organisms are characterized by having a rapid growth rate, having a high longevity and producing large biomass (Mann, 1973; Krumhansl & Scheibling, 2012), forming this way so called "Kelp Forests".

Kelp forest ecology has been widely studied (Smale et al., 2013). The attention given by the scientific community to these organisms has been noted already from the XX century, with studies addressing a variety of topics around their ecology (reviewed in Dayton, 1985)). Addressing not only regular physiological topics, but also their dynamics within the ecosystem and existing pressures, these studies contributed significantly to the in-depth knowledge on the fascinating world of kelp species we possess today.

One of the topics of interest has consistently been kelp growth and productivity in different regions (e.g. Mann, 1973), along with their geographical distributions. They are multicellular organisms and their basic structure consists of a holdfast (branching root-like structure that anchors the Kelp to the substratum), a long flexible stipe and a lamina (Kelly, 2005). In the *Laminaria* genus the growth is based on the meristem (cell division area), located between the stipe and blade (Kelly, 2005). Their reproduction is composed of 2 stages, having a heteromorphic diplohaplontic life cycle, alternating between 2 generations: the microscopic haploid generation (gametophyte), producing males and females' gametes, and the diploid macroscopic one (sporophyte), resulting from the reproduction between the gametes, forming the kelp forests, that later originate the spores for the haploid generation again (Kelly, 2005; Wernberg *et al.*, 2019).

Despite the forests being the presentation better known among these organisms, there are in fact 3 different morphological groups included within the kelps: the canopy kelps, the stipate and the prostrate (Dayton, 1985; Steneck et al., 2002). The canopy are the ones that form the kelp forests, characterized by flexible stipes supported by gas-filled bladders (pneumatocysts); the stipate and the prostrate constitute smaller types, and they form in this case kelp beds, having rigid stipes supporting a single blade, and blades that lie directly on the seafloor, respectively (Steneck *et al.* 2002). Irrespective of this, they all play an essential role as keystone species and "ecosystem engineers" (see Jones *et al.*, 1994) providing habitat and food for several organisms (Teagle *et al.*, 2017). Whether as part of general seaweed studies (e.g Bolton, 1994) or more specific ones (e.g. Bolton, 2010; Gorman *et al.*, 2013), researchers appear to have always understood the relevancy they could have as keystone species in the ecosystems.

Known as being highly dependent on cold temperatures (Wernberg *et al.*, 2019), the extent of brown seaweed stands has been estimated from an average of 1.68×10^6 km²- of the 6.06×10^6 km² global macroalgal area (Duarte et al., 2022)- to 2.03×10^6 km² global extend of kelp stands

specifically (Jayathilake & Costello, 2021). They dominate about 25% of subpolar and temperate coastal areas in the entire world (Krumhansl *et al.*, 2016; Teagle *et al.*, 2017; Wernberg *et al.*, 2019), deeper than 61 m in the case of artic kelps (Greenland) (Krause-Jensen et al., 2019), being also found in some deep tropical and subtropical waters (e.g Graham *et al.*, 2007a). With 112 species distributed for 33 genera, considering only the order Laminariales, they are found in 11 world regions, considering the approach taken by Bolton (2010)-adapted from the 232 ecoregions considered by Spalding *et al.* (2007)- between the North and Southern Hemisphere (Fig. 1.1) (Bolton, 2010). A higher genus diversity is found in the region of the Temperate North-East Pacific and the subregion of the Temperate North Pacific Marine Real, with 19 and 13 genera respectively, compared to the others (Artic and the Atlantic-5, Southern Hemisphere regions-2 to 4). Regarding species diversity, Japan and Korea stand out as having the highest occurrence, followed by other North Pacific regions (Bolton, 2010). They occur in the intertidal and subtidal zones (Layton *et al.*, 2020), normally up to depths of 30-40m (Wernberg *et al.*, 2019), but able to reach higher depths, depending on the conditions (Graham *et al.*, 2007a). Temperature is not the only variable affecting their distribution, as secondary ones also end up having influence, like light, waves, suitable substrates, and nutrients availability (Steneck *et al.*, 2002). These influence for example the depth we can find the organisms: in regions with less light availability and nutrients they occur in shallower depths (e.g Artic) (Wernberg *et al.*, 2019), while in places where there isn't such a limitation, they have been found reaching up to 200m depth (Žuljević et al., 2016).
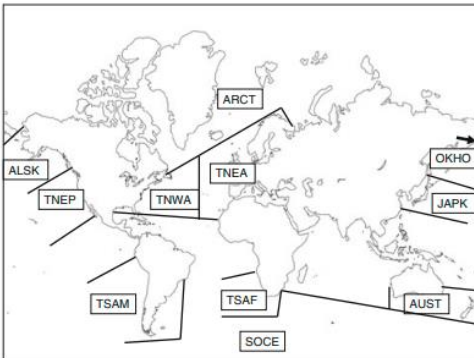
A   **B**
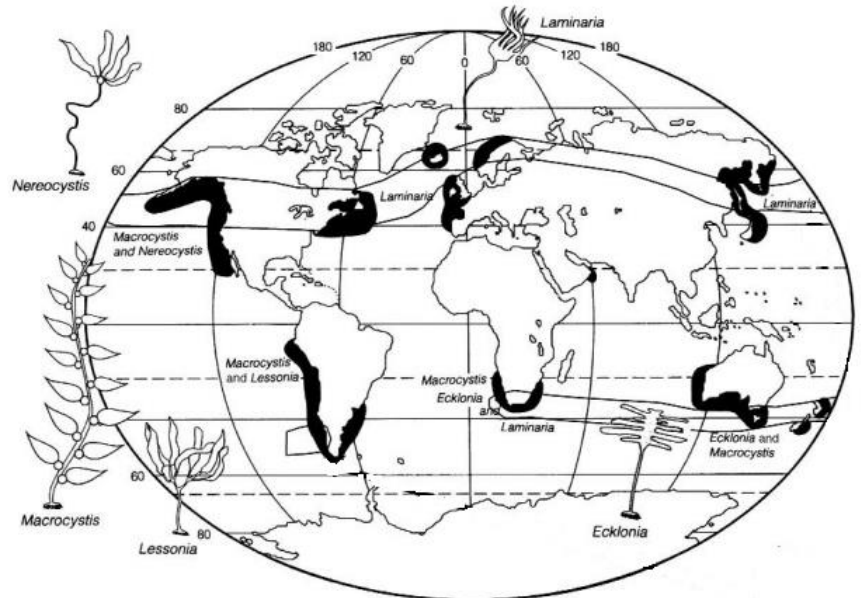
Figure 1.1- Distribution of Kelp species and dominant genera around the world ecoregions. Adapted from Steneck 2002 (b) and Bolton 2010 (a)

Considered as one of the most productive primary producers on the planet (Wernberg *et al.*, 2019), kelps exhibit production rates equivalent to those of tropical rain forests and wetlands (Mann, 1973). With an average global production of 500-900 g C m^{-2} yr^{-1} (Mann, 1973; Krumhansl & Scheibling, 2012; Duarte et al., 2022), sometimes exceeding 2000 g C m^{-2} year^{-1} (Mann 1973; Abdullah & Fredriksen, 2004; Duarte et al., 2022), they act as important food sources to marine communities, contributing substantially to the coastal productivity (Duggins *et al.*, 1989). In this way, kelps may have a direct influence on many other organisms, supporting biodiversity hotspots in widespread coastal areas (Teagle *et al.*, 2017). Their contribution is seen however also by indirect influences, such as their detritus production, with annual production rates of approximately 705 g C m-2, i.e., ~81% of their primary production. These are either consumed and decomposed within the kelp beds/forests by the local benthic invertebrates, exported to adjacent and distant ecosystems and later transferred to higher trophic levels in the food web (Krumhansl & Scheibling, 2012), or to deeper ocean depths and sediments (Queirós et al., 2019). When exported to the seabed, these detritus are sequestrated, with a macroalgal Carbon sequestration rate of 8.75 g C.m^{-2}.yr^{-1} (0.73 ± 0.82 mol.m^{-2}.yr^{-1})- of the average net sequestration rate of particulate organic carbon of 58.74 g C.m^{-2}.yr^{-1} (4.89 ± 5.50 mol.m^{-2}.yr^{-1})- with seasonal magnitude variations (Queirós et al., 2019). This way they also contribute greatly to the Blue Carbon storage, and considered within the ecosystems with potential to balance the increased C inputs in the ocean in climate change mitigation approaches (Queirós et al., 2019).

1.3 The Laminariacea group and *Laminaria digitata* in the UK

As mentioned before there is a vast diversity of species existing within the "Kelps" group, all presenting different characteristics. However, along the years, the criteria used to describe most kelp species, have always been the morphology and anatomy of their sporophytes, with no commonly accepted species typology being implemented (Wattier & Maggs, 2001). Consequently, several issues regarding previously considered species have arrived (see examples in Bolton, 2010). With the use of molecular tools, the number of species in the

dominant genera have been decreasing (Bolton, 2010). Nevertheless, some species are still considered to the date, as the one addressed in this study, part of the Laminareaceae family.

The Laminareaceae, contrary to the general tendency of kelp families, have their greatest genus diversity in the Okhotsk Sea, followed by the Northeast Pacific and Alaska, having only a few genera in Japan and Korea. Regarding the North Atlantic and Artic, their presence is only seen by the genera *Laminaria*, *Saccharina*, *Alaria* and *Agarum* (Bolton, 2010). In this study, the focus will be on the this first genus, belonging to the stipate kelps (Steneck *et al.* 2002), being the only one presenting a different pattern in species diversity, with a greater number of species at other regions of the Northern Hemisphere, compared to Japan (Bolton, 2010). More specifically, the species *Laminaria digitata* (Oarweed) will be studied.

Laminaria digitata Lamouroux, J.V.F. (1813) is distributed along the Atlantic coast, from Novaya Zemlya to the Canary Islands, including the Baltic Sea and Black sea, according to the Marine Life Information Network website (Hill, 2008) Thought as the only one of the *Laminaria* genus able to survive both the Arctic and temperate regimes (Bolton, 2010), it dominates the kelp stands present in the English Channel and The Atlantic Coast of France (Billot et al., 2003) (Fig. 1.2). With a total occurrence of 11.705 records, in the Ocean Biogeographic Information System from 1902 to 2021 (OBIS), it is mostly found in the western coast of North Atlantic (Billot *et al.*, 2003). The dependence of the species to the western part of the English Channel is believed to be due to the higher light availabilities and their influence on the ecological performance of the species, that has disappeared from several places in the eastern, more turbid, part. As with other seaweed species, this species presents a high commercial value. It is used for several industries, such as in Brittany, mainly to produce high quality alginates, gel-forming polysaccharides, that have been decreasing in market availability in the past years with the decrease of its populations (Arzel, 1989).
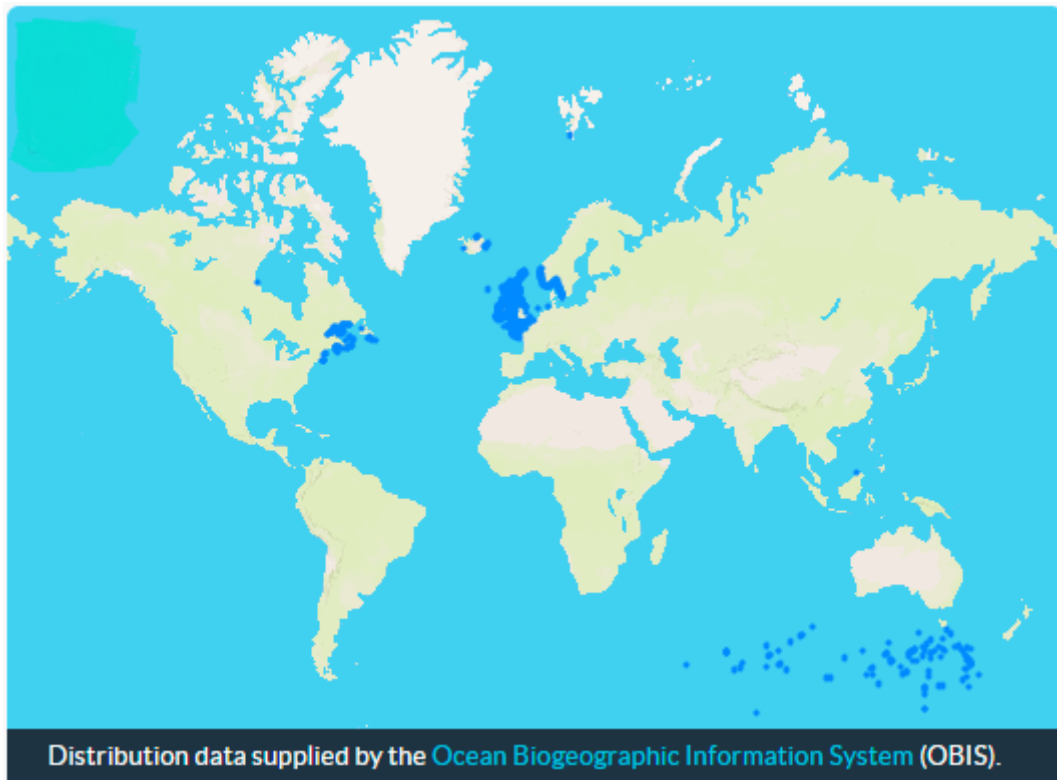
Figure 1.2- Distribution of *Laminaria digitata*, represented as blue dark dots. Extracted from MarLIN

The species is found from the lower intertidal to the uppermost part of the sublittoral fringe, up to 20m depth, according to the light and water current conditions (Gibson et al., 2001; Hill, 2008), mostly in sea surface temperatures ranging from 10-15ºC and 30-35 of salinity (OBIS). It possesses a flexible stipe, adapted for cases of extreme low water, that form a flat laying thallus for when the organisms are exposed to drought or cold conditions (Luning, 1979). Regarding its temperature and salinity optimum, these are the conditions found, for example, in the sampling area of this study, the West Hoe Bay in Plymouth (United Kingdom, UK), where it cohabitates with two other *Laminaria* species: *Laminaria hyperborea* (Tangle) and *Laminaria ochroleuca* (Golden kelp).

L.hyperborea is found mostly in the sublittoral area of the coast inhabiting generally deeper waters (Luning, 1979), up to 36m depth (Tyler-Walters, 2007), while *L.ochroleuca,* is a warm-water species, distributed along the East Atlantic and Mediterranean (Smirthwaite, 2007), noted to have increased its distribution and abundance to the southwest coast of the UK (its poleward range edge) (Smale et al., 2014). This increase is thought to be partly influenced by the increases in sea temperatures observed along the UK since the 1980s, including in the Western English Channel (WEC) (Smale *et al.*, 2014). The species has a similar vertical

distribution to *L. digitata,* from low water spring tide levels to shallow subtidal (Gibson et al., 2001; Smirthwaite, 2007; Hill, 2008), but it's able to overcome *L.hyperborea* depths in some world locations (Smirthwaite, 2007). It acts as a direct competitor of *L. hyperborea* in the WEC, although having growth strategies more akin to *L. digitata* (Luning, 1979), presenting significant productivity rates even in the summer (Smale *et al.*, 2014). As for a comparison between *L.digitata* and *L.ochroleuca*, it has been seen that this last one presents different holdfast assemblages, having relatively lower epibiont species richness compared to the first, being this explained by a possible increase in the production of antifouling chemicals[1] (Blight & Thompson, 2008).

Luning (1979), studied the photosynthetic performance and growth strategies of 3 *Laminaria* species along the year, and for *L.digitata*, it was observed higher long-persisting growth rates, compared to the two other species, *L. hyperborea* and *L. saccharina* (nowadays *Saccharina latissima*). Although there is a general concept of the existing "rapid growing periods", from December to June, and "slow growing periods", from July to December in kelps, as suggested by Parke (1948) and Kain & Jones (1963), this was not entirely observed in the study. Contrary to the other species, *L.digitata* continued its blade area increase unaffected for most of the summer, presenting a decrease (by 50%) only in September, while *L.hyperborea* had already ceased its increase completely by August and *L.saccharina* reduced it by 80%. Together with *L.saccharina*, *L.digitata* produced bigger blade areas than *L.hyperborea*. The first two presented growth rate peaks either in spring (May) or summer (June), varying with their depth distributions. Nevertheless, the 3 species were classified as "Shade-plants", presenting photosynthesis saturation responses at 150 $\mu E\, m^{-2}\, s^{-1}$ ~ 7500 lux in late spring/summer.

Other similar studies have been done in a variety of topics around the physiology of this species, along with other seaweed species, and, in all, a series of baseline parameters are typical analysed. Most of the studies observing, for example, the phenotypic plasticity of seaweeds and their performance in different environmental conditions, often tend to focus on their photosynthetic apparatus. Responsible for their carbon fixation and energy production this is, generally, the most affected body part in stress situations (Walters, 2005). Related to this some of the general studied parameters often are the photosynthetic rate of the organisms (e.g Burdett et al., 2019; McCoy et al., 2019), their oxygen production (net primary production) and consumption (respiration), growth rates (e.g Nunes et al., 2015; Burdett *et al.*, 2019), the structure and changes in the photosynthetic apparatus, such as pigments composition, the

mechanisms related to their light capture, among others. And likewise in this study some of them will be evaluated.

[1] Antifoulants are chemicals exudated by seaweeds, that prevent the growth and settlement of herbivores such as epibionts (Al-Ogily & Knight-Jones, 1977).

1.4 Climate change and anthropogenic activities effects on kelps

Despite being seen as potentially some of the most resilient marine ecosystems (Dayton *et al.*, 1992; Filbee-Dexter & Scheibling, 2014) kelp resistance to disturbances appears to be decreasing (e.g Wernberg *et al.*, 2010), and as many other ecosystems, these keystone species currently experience substantial pressures. To the extent that in some cases kelps are being used as sentinel species (Wernberg *et al.*, 2013). Most pressures of concern are climatic related, affecting kelp global abundances (Krumhansl, Okamoto, et al., 2016), and as such, are attracting the attention of the scientific community.

As a direct or indirect result of anthropogenic activities, global declines in abundances (Krumhansl, Okamoto, et al., 2016) and redistributions of several species have been recorded over the last decades (Steneck *et al.*, 2002; Filbee-Dexter & Scheibling, 2014b; Krumhansl *et al.*, 2016; Filbee-Dexter & Wernberg, 2018). They have been seen to be replaced by turf reefs (Connell *et al.*, 2008; Araújo *et al.*, 2016; Filbee-Dexter *et al.*, 2016; Wernberg *et al.*, 2016; Filbee-Dexter & Wernberg, 2018), sea-urchin barrens (Filbee-Dexter & Scheibling, 2014b), and, in some areas, invasive kelps (See references in Wernberg *et al.*, 2019). .

Many different pressures acting upon these organisms have been addressed and studied along the years, considering both the climatic changes and other direct human actions. Subjects such as marine pollution, harvesting, and deforestation by grazers (e.g sea-urchins) outbreaks, originated by the removal of large predators, have been researched in detail (reviewed in Steneck *et al.*, 2002 and Smale *et al.*, 2013). However, as the consequences of climatic pressures become more evident, a higher focus has been given to the topic.

One of the most studied issues regarding climate change is the effects of global warming, given the physiological stress high temperatures may cause on kelps (Tegner *et al.*, 1996a; Gerard, 1997). Operating at a larger temporal and spatial scale, the effects of sea water temperature increase have been addressed in several studies (Serisawa *et al.*, 2004; Harley *et al.*, 2012; see Smale *et al.*, 2013). From studies of past trends, based on previous observed events

(Krumhansl, Okamoto, et al., 2016; Krumhansl, Bergman, et al., 2016; Pessarrodona *et al.*, 2018), to simulation of possible futures both experimentally done in the laboratory and via modelling (Raybaud *et al.*, 2013; Brown *et al.*, 2014; Simonson *et al.*, 2015; Assis *et al.*, 2016; Iñiguez *et al.*, 2016; Provost *et al.*, 2016; Qiu *et al.*, 2019; Britton *et al.*, 2020; Hollarsmith *et al.*, 2020; Fernández *et al.*, 2021), in general they all appear to reach the same conclusions regarding the effects of temperature rise. Several effects have already been recorded from kelps under high temperature conditions, such as faster degradation rates (Bedford & Moore, 1984; Rothäusler et al., 2009); tissue loss or reduced strength and extensibility, and, consequently, decrease in the ability to withstand wave forces (Simonson et al., 2015); higher susceptibility to the negative impacts of kelp fisheries (Krumhansl, Bergman, et al., 2016); decreases in carbon assimilations and donations to other ecosystems (Pessarrodona et al., 2018); changes in their microbial community (Qiu et al., 2019); changes in growth rates (Fernández et al., 2021), among many others. Despite possible species-specific and regional dependent responses to different scenarios (Krumhansl, Okamoto, et al., 2016), degrees of increase or region of occurrence, the negative impacts of warming on kelp are consensual. In the study of Krumhansl, Okamoto, et al., (2016) a decline in 38% of world ecoregions of kelp forest ecosystems has been observed and this is a growing tendendy. Particularly on growth, carbon assimilation, recovery, and distribution, the changes are very obvious, hence acting as a threat to their persistence and integrity, with several range contractions, or local extinctions of varied species being observed worldwide, as reviewed by Smale (2020). Predictions for their future are equally alarming, particularly the growing possibility for changes in their geographical distributions. Potential compression and loss of species ranges, along with greater local extinctions, have been projected under different IPCC scenarios (Takao *et al.*, 2014; Assis *et al.*, 2017; Martínez *et al.*, 2018), leading also to losses of older gene pools (Assis *et al.*, 2016). And, as mentioned before, their imbalance may have broader consequences upscaling through change in food webs making the issue even more concerning.

However, regional and local factors should also be intensively studied, along with other climatic and anthropogenic related pressures, as they can be in the base of kelp forests dynamics (Krumhansl, Okamoto, et al., 2016). Some of these remain relatively understudied, as for example, the effects of ocean acidification (IPCC, 2021) beyond impacts on calcifying organisms (see Mccoy, 2013; Smale *et al.*, 2013), regime shifts (Steneck *et al.*, 2002), extreme events such as heatwaves (Wernberg *et al.*, 2013), increases in storminess (see Steneck *et al.*, 2002 and Smale *et al.*, 2013), increasing fishing pressure (Steneck *et al.*, 2002), direct

harvesting effects by whole plant removal, marine pollution (Wernberg, 2019), and light pollution effects in the marine environment (<u>Artificial Light at Night-ALAN</u>) (Bennie et al., 2016; Davies & Smyth, 2017; Grubisic et al., 2017). Multiple stressor studies have been particularly lacking (Smale *et al.*, 2013), as most of the marine climate change related studies address mainly only one single factor, resulting in knowledge gaps regarding the effects of multiple potential climate and non-climate drivers (Wernberg et al., 2012). This becomes even more challenging when the combined effect of the studied stressors can't be predicted from single stress studies (Folt et al., 1999), which is the case of this study.

1.5 Marine Heatwaves and Artificial Light at Night

As mentioned above, temperature is one of the most determining factors of kelp distribution (Luning, 1990) and this is due to its physiological effect. Sporophytes are described as the generation most vulnerable to this variable, although already from the gametogenesis effects can be noted. The uppermost limit in this phase is of 5-6ºC lower than the sporophytes upper limit itself, and so the whole reproduction cycle can be affected (e.g., Bartsch et al., 2013). However, not only long-lasting water temperature increases can be the cause of such changes, as temporary, more abrupt, and local ones can also have this impact, such as Marine Heatwaves (Hobday et al., 2016).

1.5.1   Marine Heatwaves

Hobday *et al.* (2016) broadly used definition of Marine Heatwaves (MHWs), is of discrete prolonged anomalously warm water local events and they have been shown to also affect marine organisms greatly, including kelps (Straub et al., 2019). They can result from a series of processes with different temporal and spatial scales such as air-sea heat fluxes, ocean heat advection, vertical mixing, and El-Niño events (Hobday *et al.*, 2016), having as their underlaying driver the general oceans temperature increase (Frölicher et al., 2018; Oliver et al., 2018, 2019). In turn, these abrupt localized temperature increases can trigger or be accompanied by altered environmental processes like ocean currents, wave action, solar radiation and in the intertidal zone, desiccation stress (Straub *et al.*, 2019). The indirect effects of MHW on kelps have been addressed since the 1980s (Hart & Scheibling, 1988), but as these events become more frequent, their direct effects are becoming more evident. They are thought

to cause faster biological changes in kelp systems than the increases in global average temperatures, when exceeding thermal thresholds (Thomsen *et al.*, 2019).

Several studies have demonstrated the upscaling consequences that heatwave events have caused on ecosystems worldwide (Smale *et al.*, 2019), including kelps and other seaweeds (Straub *et al.*, 2019), affecting their physiology, abundance, and ecological dynamics. The intensity and occurrence of warming events have been seen to increase greatly along the years, with records from widespread places (Coumou & Rahmstorf, 2012; Lima & Wethey, 2012; Oliver et al., 2018; Perkins et al., 2012), varying greatly in their duration and spatial extent (Smale *et al.*, 2019). Some to be cited are for example, the heatwave recorded in Russia considered as the strongest worldwide in recent decades (Russo et al., 2014); the series of MHWs that have increased greatly along the years in the North Atlantic ocean, associated also with significant declines of the Sugar kelp, *Saccharina latissima,* abundance, both on the west and east Atlantic (Filbee-Dexter et al., 2020); in the southeast Indian Ocean, particularly, in Western Australia, in 2011 (Ningaloo heatwave/ El Niño-The Blob), with anomalies up to 5ºC, causing increases in coral bleaching rates, mortalities of several organisms, algal blooms (Rose et al., 2012) and the decrease and loss in kelp (*Ecklonia radiata*) and other macroalgal coverage (Wernberg *et al.*, 2013 & 2016), that even after the stressors effect didn't manage to recover in some latitudes, due to great grazing rates that followed the MHW (Wernberg *et al.*, 2016) and the long-lasting multilayer heatwave in North Pacific, starting in 2013 and lasting until early 2016, triggered by a series of climatic events, causing several negative effects to the ecosystem (Di Lorenzo & Mantua, 2016).

This last-mentioned event has received some particular attention regarding kelps response. Significant spatial variability was observed along the California Current System, regarding the resistance and resilience of the species *Macrocystis pyrifera* to the heatwave (Arafeh-Dalmau et al., 2019; Cavanaugh et al., 2019). While in its southern range limits (in Baja California) the species presented great decline, in the northern part, a high degree of resistance and resilience was noted (Cavanaugh *et al.*, 2019; Arafeh-Dalmau *et al.*, 2019), and as shown previously for Southern California (Reed et al., 2016), no major consequences for the kelp communities were observed. Contrary to this, a much recent heatwave in New Zealand Island, 2017-2018 (Tasman Sea MHW), resulted in the loss of Bull kelp (*Durvillaea spp.)* (Thomsen et al., 2019) and Giant kelp (*Macrocystis pyrifera*) (Tait et al., 2021) coverage. In a precedent event, 2015-2016 Tasman Sea MHW, this last species had already suffered great declines, local and regional extinctions from the Tasmanians eastern coast, showing also lower resilience to other

consecutive stressors (Mathiesen, 2016). And in this second MHW, their decline was exacerbated by poor water quality, being replaced, along with the Bull kelp, by other macroalgae species, with the magnitude of the responses again varying with the latitudinal distribution of the species (Thomsen *et al.*, 2019; Tait *et al.*, 2021). In the context of these latitudinal varying responses within the kelp species, some attention must be brought also to the latitudinal expansions and contractions occurring for temperate and Artic populations because of climate change events (Bringloe et al., 2022). With a high rate of expansion predicted for cryotolerant (existing but not restricted to the Artic) and, to a certain point, cryophobic (restricted to temperate conditions) macroalgae communities, and a loss of suitable habitat for cryophilic (restricted to the Artic) species (Bringloe et al., 2020), the effect of MHW might potentially accelerate such responses. Although the successful establishment in these higher and polar latitudes and resistance to the climate related stressors is greatly dependent of their genetic diversity, other aspects are to be taken into account, as light availability and penetration in such locations, dependent on the turbidity of the water (Paar et al., 2016; Fritz et al., 2017; Gagaev et al., 2019) and the exiting light regimes reaching maximums of 24h day/night range, potentially affecting their reproductive success (e.g Martins et al., 2022).

Considering the widespread consequences of MHWs, most of the existing studies address the issue exploring past events, in an attempt to understand the dynamics behind them and the effects they have caused. Studies such as Rose *et al.* (2012), Arafeh-Dalmau *et al.* (2019), Cavanaugh *et al.* (2019), Smale *et al.* (2019), Thomsen *et al.* (2019), Filbee-Dexter *et al.* (2020), Tait *et al.* (2021), Thomsen *et al.* (2021), Wernberg (2021) and others (reviewed in Straub *et al.*, 2019), observed highly negative consequences past heatwaves had on the growth, resistance, abundance, distribution and mortality of kelps and their associated communities. Studies employing simulated heatwaves scenarios have also emerged (e.g. Nepper-Davidsen *et al.*, 2019 *Saccharina latissima*; Sánchez-Barredo *et al.*, 2020 *Macrocystis pyrifera*; Britton *et al.*, 2020 *Phyllospora comosa*; Umanzor *et al.*, 2021 *Macrosystis pyrifera*), all presenting similarly negative impacts on kelp species. Whether together with other combining stressors-e.g nutrient limitations (Umanzor et al., 2021), increased CO_2 (Britton et al., 2020) and light deprivation (Sánchez-Barredo et al., 2020)- or by their effect alone, the increased temperatures caused by these MHW simulations have shown to decrease the pigment content, the photosynthetic efficiency, photosynthetic and growth rate, increase the respiration rate, cause oxidative stress to the tissue, tissue bleaching and damage in the kelp organisms. When testing for MHW effects together with light deprivation, Sánchez-Barredo *et al.*, (2020) found

however, that this last stressor presented greater influences on the physiological traits tested for the juvenile kelp organisms than the thermal simulations them selfs. Light deprivation conditions decreased their nitrate uptake and carbohydrates contents, possibly affecting their growth and survival, although the combination of light exposition (12hr photoperiod) and thermal stress also caused specific photoacclimation responses, like the decrease in maximum quantum yield (Fv/Fm).

Regarding the target species of this study, the study of Burdett *et al.* (2019) is highlighted. Here, they tested the photosynthetic related responses of populations of *L.digitata* and *L.hyperborea,* collected from the Plymouth Sound to 3 days exposure to simulated MHW (+2ºC and +4ºC). The temperature effects were only noted in the first species, presenting greater oxygen production and more clear responses of photosynthetic characteristics, however none were seen to outcompete the natural expected responses. Until a specific threshold, increasing temperatures are known to increase the oxygen production of seaweed species, as there is a higher electron transport rate through the photosystems (Delebecq et al., 2016). And so, both species tested presented a certain degree of photophysiological resilience to the acute warming, with no significant response in photosynthetic characteristics, although it should be noted no records of net respiration rates are made, limiting the extend of such analyses. For longer term exposure of the absolute temperatures tested however, different results have been observed for *L.digitata* -whose southern range limit is located around the northern France in the NE Atlantic-causing a reduction of their ecophysiological performance (Simonson et al., 2015; Hargrave et al., 2017), increased mortality (Bartsch et al., 2013; Wilson et al., 2015), and higher taxonomic level impacts (Raybaud et al., 2013).

In studies assessing the effects of climate change on marine organisms, experiments simulating multiple conditions (i.e. factors) potentially resulting from exposure in the wild are often performed. Regarding seaweeds, a combination typically explored is the combined exposure to temperature and inorganic carbon in the form of carbon dioxide (CO_2), two of the most important variables affecting their physiology. Considering the context of ocean acidification i.e., the decrease in ocean pH, caused by the increase in the atmospheric CO_2 and consequently CO_2 ocean uptake (Doney et al., 2009), studies addressing the effects of inorganic carbon (IC), for example, are commonly performed. By looking at the increased IC, in the form of CO_2, it has been demonstrated that contrary to working as an additional obstacle to the kelps, their increase in the seawater concentration may, in turn, work as their ally, supporting resistance to warming. Some of the studies mentioned before adopted this approach and reached the results

described above, although, again, most of them focused on global warming experiences (e.g Brown *et al.*, 2014; Iñiguez *et al.*, 2016; Provost *et al.*, 2016; Qiu *et al.*, 2019; Fernández *et al.*, 2021) and less frequent approaching heatwaves (Britton *et al.*, 2020), hence remaining an important topic to address. Britton *et al.* (2020) performed a multiple stressors study, exposing the seaweed species *Phyllospora comosa* (Order Fucales), one of the most abundant in eastern Australia, to both present (15.5°C, pH 8.0) and future (18.5°C, pH 7.7) temperature and pH conditions, combined with heatwave periods. The study was performed in a collapsed factorial design and the responses were analysed during the heatwave exposure and after a 7-day recovery period. As a result, they found that heatwaves reduced the net photosynthetic rates of individuals, in current and future conditions, but did not affect their growth after the recovery period, indicative of a certain resistance of the species to the increased temperature. By their contribution to photosynthesis[2], the increase in CO_2 concentrations may promote increased photosynthetic rate and, consequently, growth (Koch et al., 2013; Kroeker et al., 2013) and increase seaweed's thermal optimum (Koch *et al.* 2013). Considering the role this inorganic carbon form may have on some seaweed species, this may on the surface seem as an expected result, and worth exploring. However, similar studies have not yet been done regarding another equally important component of photosynthesis, the light.

Whether with the objective of studying global sea water temperature increase or local anomalously warm water events (MHWs), in order to understand their real effects in the wild, considering their dynamics with other pressures, a multiple stressors approach is advised. And a combination that has not yet received great attention and should be better explored is the effect of these abrupt warm water events along with varying light conditions/availability considering the equally important effect of this second factor on the physiology of photosynthetic organisms.

1.5.2   Artificial Light at Night

Like inorganic carbon (CO_2, HCO_3 and CO_3), light is known to have an equally indispensable role in photosynthesis. Photosynthesis is the process by which organic compounds are synthetized from inorganic carbon and water, having as their energy source the light, converted into chemical energy (Lopez & Barclay, 2017). During the light-dependent reactions, in the Photosystem II (PSII), chlorophyl *a* (P680) and *b* pigments, localized in the chloroplasts of the cells, capture the light, converting it in energy that is then transferred to the electron transport chain, releasing O_2 from water molecules, to produce ATP and NADPH. These are then used

in the Calvin cycle, where the inorganic carbon is also used, ultimately leading to the production of carbohydrates (Finch et al., 2014; Casem, 2016; Lopez & Barclay, 2017). In this way, the process and amount of photosynthesis is directly dependent not only on the amount of inorganic carbon available, but also on the light availability, intensity, and duration (Finch *et al.*, 2014). For the process, a specific wavelength interval is used by the photosynthetic organisms, 400-700 nm, called the Photosynthetic Active Radiation (PAR). And, although more commonly natural sunlight is the light source used, artificial light can also act as an optional source.

From the beginning of the 20th century, the use of artificial light sources and use of outdoor artificial lighting has increased greatly around the globe, related to several different human activities, and, consequently, have started to affect the natural daily and seasonal existing light cycles (Cinzano et al., 2001). Light pollution sources are seen to influence even distant areas, as light become scattered and reflected in the atmosphere back to the Earth's surface ("skyglow") (Kyba et al., 2011; Kyba et al., 2015). Part of the globe is considered to be under a scenario of light pollution already from the yearly 2000s, with a great variability among countries (Cinzano *et al.*, 2001), seen to affect about 80% of the human population (Falchi et al., 2016) and increase at a rate of 2% annually (Kyba et al., 2017). A particular case on the subject is the use of Artificial Light at Night (ALAN), an area of growing attention by the scientific community in marine landscapes, with an existing satellite-derived atlas destined to quantify its extent and intensity on coastal and intertidal organisms at the sea surface (Falchi et al., 2016). Even so, several limitations on its exploration still exist, particularly underwater, to which some guide techniques have been developed (Tidau et al., 2021). Most studies on ALAN are done addressing its effect on marine animals (see examples in Tidau et al., 2021), however, it has been proved that it can have significant physiological effects also on higher plant organisms (Smith, 1982), although to date very few studies have addressed the topic (see review by Bennie et al., 2016; metanalysis by Sanders et al., 2021).

Bennie *et al.* (2016) call out the attention to this matter, as they point out the need for defining specific measures of artificial light in the environment that can be used to properly quantify the several physiological effects on plants and a deeper knowledge of their dose–response relationships with light-sensitive processes. They summarise a few studies done of the subject, showing that, although the detection of light in plants is complex, and partially redundant, relying sometimes on more than one physiological pathway (Song et al., 2010), the use of ALAN can in fact influence different photosynthetic systems in phototrophic organisms, and,

hence, carbon fixation. Influencing, for example, their responses to photoperiod, either by low light levels (Whitman et al., 1998) or short durations (Runkle et al., 1998), decreasing their chlorophyl *a* concentrations in the cells and Rubisco molecules in phytoplankton's (Poulin et al., 2014), changing the stomata density and opening in higher plants (Smith 1982) and species dependent inductions and suppressions of growth (Cathey & Campbell, 1975a). In the study of Sanders *et al.* (2020), it is mentioned that both negative and positive effects of the stressor on the phenology of the organisms have been observed, although with very few studies on plants being mentioned, and the great majority of studies in general being done on the field. In the study of Grubisic et al., (2017), experimentally simulating the conditions of a light polluted area on a community of benthic primary producers (periphyton), also divergent results were obtained. The effects of the exposition to the artificial light were seen to be according to the development stage of the communities. In the ones in early stages the biomass and proportion of most organisms was seen to decrease, independent of season, while for later stages of periphyton no effects of ALAN were observed. Nevertheless, studies addressing the matter on higher photosynthetic organisms are very scarce and limited, needing greater attention.

It is known that for species of the genus *Laminaria*, reductions in light availability, i.e, water clarity results in a decrease in their production rates (Aumack et al., 2007). For the species *Laminaria digitata* the effects of different environmental conditions, particularly light, have been tested by comparing 2 different populations, located in the French western (high light availability) and eastern (low light availability) parts of the English Channel (Delebecq et al., 2013). Investigating the seasonal adjustment of their photosynthetic performance, they found that populations living in the eastern part, with limiting light conditions, had a higher light-saturated maximum photosynthetic rate (Pmax), i.e., a greater light-harvesting efficiency; possessed higher total pigment and chlorophyl *a* concentration and antenna/chlorophyl *a* pigment ratios, known as one of the ways to increase light absorption and acclimation to low light conditions (Ramus et al., 1976; Sand-Jensen, 1988); and a lack of seasonal acclimation photosynthetic parameters. Despite these differences, both populations were seen to achieve similar oxygen production rates in the field, thought to be related to the different photosynthetic acclimation characteristics observed between them. However, no other studies were found testing the effects of direct light conditions change for the species, which limits the understanding of the effects it may have on the physiology of the organisms, especially to artificial lighting exposure.

1.6 Relevancy of the study and application to seaweed aquaculture

In this study, considering the high increase in magnitude and intensity (Russo *et al.*, 2014; Straub *et al.*, 2019; Filbee-Dexter *et al.*, 2020) of heatwaves, their effects will be addressed, having as a secondary pressure, the ALAN use. The combined effect of the two pressures will be analysed, in order to understand what could result from their future dynamics in kelp ecosystems. This study is intended to advance the knowledge of these two pressures acting upon kelp, taking, not only, an impact focused approach but also observing in more details the physiological responses of the seaweed. Focusing specifically on the fringe intertidal/subtidal species of kelp, the attention will be turned also to an important region for their occurrence, the NE Atlantic. More specifically focusing on the UK, a region described as poorly studied regarding kelp responses to environmental pressures in previous years (Smale *et al.*, 2013), with an increased knowledge recently rising on the theme, to which this study may help fill.

The study will be focused on the species *Laminaria digitata,* one of dominant canopy former kelp species in the UK (Smale *et al.*, 2013). By simulating conditions in short term mesocosm experiments at the Plymouth Marine Laboratory ("PML", UK), it is intended to evaluate the level of resilience individuals may exhibit, regarding their photosynthetic, growth and respiration rates, and C:N ratios. Additionally, it will be tested if and what effects increased light exposure may have on the organisms and their dynamics with the increased temperature regimes. The working hypothesis is that similar to the ocean acidification/increase CO_2 exposures effects on the kelps regarding MHW situations, the exposure to ALAN, may help the organisms to better respond to the increased temperature. By having an extra light source to increase photosynthetic activities, the organisms may be able to increase growth rates necessary to respond to energetically costly response pathways to warming. In this study, contrary to the approach taken by Britton *et al.* (2020), projections of future temperature conditions will not be additionally simulated, focusing specifically on the interactions between the MHW and ALAN exposure, using a 7-day acclimation period, 14 days MHW period and 10 days recovery period.

The results from this study may inform restoration and conservation programs regarding seaweed species within the North Devon UNESCO Biosphere Reserve, by providing parameter values for new species' distribution models for seaweeds being developed within PML in collaboration with the Biosphere, as part of the H2020 FutureMARES programme (https://www.futuremares.eu/). Additionally, as the studied species is part of one of the most economically valuable seaweed groups in aquaculture worldwide (Laminareacea, FAO, 2021), the study may contribute to an increased understanding of ways through which kelp farming may be enhanced under future climate change. This approach may be of particular interest for big producers like China (Figure 1.3), where increases in MHWs intensity and frequency have been recorded over the years (Li *et al.*, 2019; Yao *et al.*, 2020).
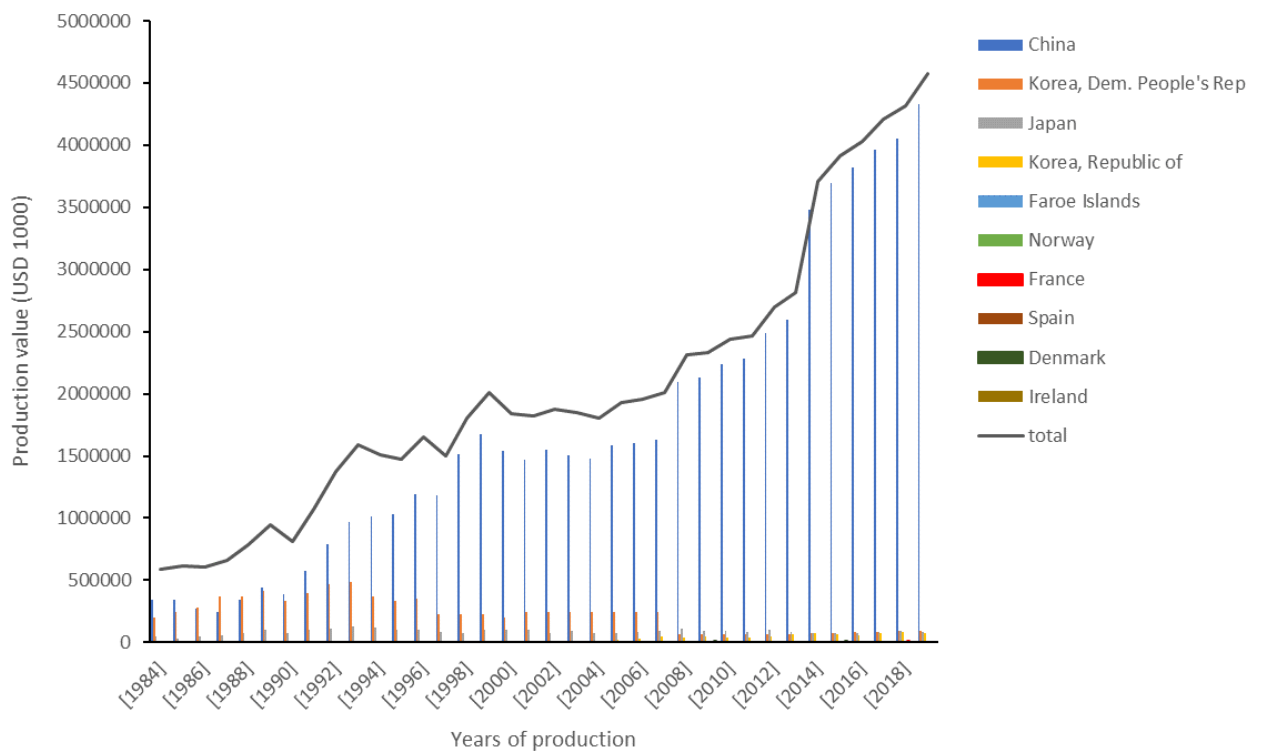
Figure 1.3- Laminariacea aquaculture production from 1984-2019. The production value is indicated as 1000 US dollars, and the producing countries are ordered in the legend from the most productive along the years to the less. The total production for the kelp family considering the sum of the countries is also represented. Source: FAO. 2021. Fishery and Aquaculture Statistics.

Seaweed aquaculture, constitutes an important part of the world's global marine aquaculture, accounting for approximately 27% of its total production in 2014, when it reached the production of 27.3 Mt (million tons) (FAO, 2016), and progressing to 51.3% in 2018, with a production of 31.8 Mt and a commercial value of 11.3 billion US$ (FAO, 2020). For kelp farming specifically, the industry is dominated by the order Laminariales, with a commercial

value of 5.2 9 109 US$, that developed a particular importance considering the great decline in resources observed along the years globally (FAO 2017b). Having the largest scale kelp cultivation industry in the world, about half of the global seaweed production (FAO, 2020), the registered productions in China are recorded already from the 1940's (Fang & Zhang 1982), although large scale cultivations were mainly implemented in the 90's (Fei, 2004), with a great contribution also seen from Indonesia (FAO, 2020). Along with them, other countries are highlighted when addressing the subject of kelp farming, like Korea and Japan, as about 99% of the production is seen coming from Asia (FAO, 2020). But an increasing trend is also observed towards American and European countries, presenting a total production in 2014, for example, of approximately 54,000 tonnes valued at US $51 million, accounting for 1.5% of the global gross production (FAO, 2016) and African countries (FAO, 2020).

The activity is seen to help balance the negative environmental impacts of human related activities (Fei, 2004), providing a series of environmental and ecosystem goods and services (Zheng et al., 2019), and contributing to meeting several United Nation's Sustainable Development Goals (SDGs 2, 3, 7, 13 and 14, directly and 1, 4, 5, 8–12 and 15 indirectly, https://sdgs.un.org/) (Duarte et al., 2022). Some examples to be cited are: its intensive food supply, with 90% of seaweeds production directed to human consumption; its use as food source for other aquaculture productions; its role in diminishing the soil impacts caused by agriculture, improving plant growths; its high biomass use in the production of "clean" and affordable forms of energy (e.g bio-oil, biogas, etc) and other industries, such as cosmetics (Duarte et al., 2021) and, finally the possibility to use it on mitigating the impacts of climate related changes (Duarte et al., 2017, 2021)(Duarte et al., 2017, 2021). As mentioned before, seaweed forests, in which produced cultures are included, provide an important source of CO_2 removal from the atmosphere, by their very high production rates (Mann, 1973; Krumhansl & Scheibling, 2012; Duarte et al., 2022), and other organisms from low oxygen levels (Duarte et al., 2017), and as Blue Carbon sequestrators by their detritus exportations to higher depths and sediments (Duarte et al., 2017; Queirós et al., 2019).

Despite of this, with the increasing pressures they became exposed to, kelp and seaweed aquaculture in general, currently experience several challenges. Long lasting ocean warming, marine heatwaves, acidification, among others, have been causing large decreases in the aquaculture production rates or generating less healthy cultivations (see Hu *et al.*, 2021), with the industry becoming relatively static in 2015, particularly in Indonesia (Kambey et al., 2020). Additionally to these, other local pressures also act as potential treats, such as decreased

nutrient availability and increased storminess (Callaway et al., 2012), invasives species introduction impacts (McLaughlan et al., 2014) etc. Considering this and other obstacles, some recommendations are made to enhance the resilience and resistance of the activity and produce more sustainable cultivations, whether for Asian productions (Hu et al., 2021) or American and European (Grebe et al., 2019). One of the suggestions made passes by developing climate change resiliency within the kelp aquaculture industry to help ensure that farmed kelps can continue to contribute to food supplies and other services even in a scenario of changing climate (Grebe *et al.*, 2019; Hu *et al.*, 2021). By increasing the area of production of such forests, and maybe locating more resilient productions in areas under higher climate change impacts, it might be possible to improve their benefits in the context of global change (Duarte et al., 2017), and in this context, the results of the current study may be of a great contribution to potential possibilities to this approach.

1.7 References

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Chapter 2- Manuscript

Assessing the potential for resilience towards Marine Heatwaves and Artificial Light at Night in Kelp species

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Keywords

Climate change; Marine Heatwaves; ALAN; Kelps; *Laminaria digitata*; Resilience

Abstract

Identifying adaptive or mitigating solutions for climate change is especially important for high conservation value ecosystems, such as kelp forests. The effects of Marine Heatwaves (MHWs), short-term increased temperature events, on the physiology of such organisms have been greatly overlooked when addressing thermal stress impacts, with a greater attention given to ocean warming. By testing the combined effect of heatwaves and ocean acidification, it has been demonstrated that the extra Carbon source helped organisms on their resilience to the thermal stressor, yet none has analyzed the effect extra light sources could have. In this study the combined effect of MHWs (+3ºC) and Artificial Light at Night (ALAN) (24hlight-0h dark), exposure was tested on the photosynthetic parameters (Fv, Fv/Fm, ETRm and Alfa), growth and respiration (R) rates and C/N tissue ratio of the species *Laminaria digitata*. A 14-day MHW simulation was performed, followed by a 10-day recovery period, in short term mesocosm experiments at the Plymouth Marine Laboratory ("PML", UK). A "collapsed factorial design", was used with "Sea Water Temperature (SW Temperature)" set as the main driver and "Light availability nested within SW Temperature" as the secondary one. As expected MHW alone caused significant negative impacts on growth and C/N tissue ratios, with organisms presenting the lowest rates, even in the recovery period, while it increased their fluorescence responses, with the highest's values of Fv and Fv/FM observed only during the exposure period. On the other hand, MHW combined with ALAN treatments showed the highest values of growth and C/N ratios, while presenting the lowest values of Alfa, due to down regulations of light consumption mechanisms. It was concluded that by exposing organisms to ALAN this could help them on their resilience to MHW events, by enhancing their carbon fixation rates, and hence producing the extra amount of energy necessary to withstand the thermal stressor.

2.1 Introduction

Since the rise in greenhouse emissions, triggered by human activities, several climatic changes have been registered worldwide (IPCC, 2014;IPCC, 2021), marking the era of the

Anthropocene. Acting in combination with other more direct human stressors, these have led and continue to cause great consequences for ecosystems across the globe (Doney *et al.*, 2012; Smale *et al.*, 2019; Gissi *et al.*, 2021), in different temporal and spatial scales, including marine ecosystems (IPCC, 2019).

One of the most concerning changes is the fast rate of sea surface warming, of ~0.11ºC per decade since 1880 (IPCC, 2014; IPCC 2021) and increasing to an excess of ~1.5ºC by 2100 (RCP 6.0, IPCC 2014). As a consequence of ocean warming, changes in marine ecosystem interactions, declines of populations abundances, loss of biodiversity and redistributions of several species have been recorded along the years (reviewed in Doney et al., 2012; Gissi et al., 2021).

In addition to progressive long term ocean's temperature increase, localized more intense warming events have also been recorded, Marine Heatwaves (MHWs) (Frölicher et al., 2018; Oliver et al., 2018, 2019). Marine Heatwaves are described as discrete prolonged anomalously warm water local events, resulting from different temporal and spatial scale processes, such as air-sea heat fluxes, ocean heat advection, vertical mixing, and El-Niño events (Hobday et al., 2016). With an increase in occurrence, frequency and intensity (Russo *et al.*, 2014; Straub *et al.*, 2019; Filbee-Dexter *et al.*, 2020), such events have also caused great impacts on several marine communities, such as local extinctions, mortality, range contractions and loss of biodiversity, along with general decreases in ecosystems resilience (Smale et al., 2019). As such, studies addressing their potential consequences and mitigating solutions to their effects have become indispensable, specifically considering high conservation value ecosystems (Daily *et al.*, 1997; Tallis & Kareiva, 2005), such as kelps.

Kelps are a non-taxonomic group of large brown seaweeds, producing very long canopies (Bolton, 2010; Wernberg *et al.*, 2019) and large biomass (Mann, 1973; Krumhansl & Scheibling, 2012), forming the known "Kelp Forests". They are highly productive organisms (Wernberg *et al.*, 2019) and act as keystone species, providing habitat and food for several different communities directly dependent on them (Teagle *et al.*, 2017). Dominating about 25% of subpolar and temperate coastal areas worldwide (Krumhansl, Okamoto, et al., 2016; Teagle et al., 2017), in the intertidal and subtidal regions (Layton *et al.*, 2020), they are directly dependent on cold temperatures (Wernberg *et al.*, 2019) and, consequently, greatly impacted by temperature increases beyond their thermal limits (Tegner *et al.*, 1996a; Gerard, 1997). As a consequence of such increases, several effects of MHWs have already been recorded on these

organisms, from physiological levels, such as faster degradation rates (Bedford & Moore, 1984; Rothäusler et al., 2009); tissue loss, reduced strength and extensibility (Simonson et al., 2015); decreases in carbon assimilation (Pessarrodona et al., 2018) and changes in growth rates (Fernández et al., 2021); to greater scale changes local extinctions and range contractions (reviewed in Smale, 2020) and widespread declines in their abundance, with a 38% decline in the world ecoregions registered in (Krumhansl, Okamoto, et al., 2016).

It is believed, that MHWs, may be the main driver of the observed disturbances and declines of kelps, fundamental to local population dynamics (Krumhansl, Okamoto, et al., 2016). Decreases in abundances and loss of several species have been recorded along the years, as a consequence of MHWs all over the world ocean's basins, observed in the North Atlantic, with declines of the Sugar kelp, *Saccharina latissima* (K. Filbee-Dexter et al., 2020); in the southeast Indian Ocean, decrease in the *Ecklonia radiata* (Wernberg et al., 2013; Wernberg, et al., 2016); in the North Pacific, with the great decline of *Macrocystis pyrifera* in its southern distribution range (Arafeh-Dalmau et al., 2019; Cavanaugh et al., 2019), and the loss of the Bull kelp *Durvillaea spp.* in the Tasman Sea (Thomsen et al., 2019). Several studies have explored past MHWs events and their negative consequences for kelp communities, on growth, resistance, abundance, distribution and even mortality of organisms (Rose *et al.*, 2012; Arafeh-Dalmau *et al.*, 2019; Cavanaugh *et al.,* 2019; Smale *et al.*, 2019; Straub *et al.*, 2019; Thomsen *et al.*, 2019; Filbee-Dexter *et al.*, 2020; Tait *et al.*, 2021; Thomsen *et al.*, 2021). Studies using simulated heatwave scenarios have also been conducted (e.g. Nepper-Davidsen *et al.*, 2019 *Saccharina latissima*; Sánchez-Barredo *et al.*, 2020 *Macrocystis pyrifera*; Britton *et al.*, 2020 *Phyllospora comosa*; Umanzor *et al.*, 2021 *Macrosystis pyrifera*), equally negative effects on photosynthetic efficiency, photosynthetic, growth and respiration rates, whether addressing the stressor alone or by their combined effect with other pressures.

Besides temperature, the physiology, and consequently the distribution of these organisms is also dependent on other environmental factor. Some to be cited are for example wave action, substrate type and the , inorganic carbon avalilability, and light intensity in different locations (Steneck et al., 2002). Considering their role in photosynthesis, these two last variables are highlighted, as their magnitude and intensity can directly influence the amount and efficiency of the photosynthetic activity on phototrophic organisms and hence their ability to sustain other stressors (Giordano et al., 2005; Koch et al., 2013; Kroeker et al., 2013; Kübler & Dudgeon, 2015). The combined effect of temperature and inorganic carbon, in the form of CO_2, has been widely addressed, in studies of ocean warming and ocean acidification (Brown *et al.*, 2014;

Iñiguez *et al.*, 2016; Provost *et al.*, 2016; Qiu *et al.*, 2019; Fernández *et al.*, 2021), though less frequently assessing MHWs scenarios (Britton et al., 2020). For all cases it has been observed, that, instead of working as an additional negative pressure, the increase of dissolved CO_2 helped to increase the resistance of the organisms to the thermal stress. An important approach that has been constantly lacking however is the study of light effects combined with the thermal stressors.

Light energy is used during the light-dependent reactions of photosynthesis. The light is converted into chemical energy, necessary photosynthetic reactions (Finch et al., 2014; Casem, 2016; Lopez & Barclay, 2017) hence, influencing photosynthetic activity by its availability, intensity and duration. At the time of this study, the only study found addressing the combined influence of temperature and light stressors was the study of Sánchez-Barredo et al. (2020)Sánchez-Barredo et al. (2020). Testing for the effect of light-deprivation together with MHWs simulations on *Macrosystis pyrifera* organisms, it was observed that the factor presenting greater influence on the physiology of the organisms was in fact light-deprivation, decreasing their nitrate uptake and carbohydrates contents. Nevertheless, other variations of this stressor have not yet been tested for kelp communities, as for example, checking the effects of increased light conditions or the effects of artificial light sources (see review by Bennie et al., 2016; and metanalysis by Sanders et al., 2021). However, from the beginning of the 20th century, the use of artificial light sources and use of outdoor artificial lighting has increased greatly around the globe, related to several different human activities. Consequently, light pollution has started to affect the natural daily and seasonal existing light cycles (Cinzano et al., 2001). The use of Artificial Light at Night (ALAN), for example, has been seen to greatly influence physiological traits on plant organisms (Smith, 1982). Bennie *et al.* (2016) synthetised few studies done on the subject, showing that the use of ALAN can in fact influence different photosynthetic systems in phototrophic organisms, and, hence, carbon fixation. And yet no study was found addressing this subject for higher marine photosynthetic organisms, such as kelps.

In this study, considering the high increase in magnitude and intensity of heatwaves (Russo *et al.*, 2014; Straub *et al.*, 2019; Filbee-Dexter *et al.*, 2020), their effects will be addressed, having as a secondary pressure, ALAN use. The combined effect of the two pressures will be analysed, in order to understand what could result from their future dynamics in kelp ecosystems. Focusing specifically on the fringe intertidal/subtidal species of kelp, the attention will be turned to an important region for their occurrence, the NE Atlantic, more specifically the UK,

in West Hoe Bay, in Plymouth. The study will be focused on the species *Laminaria digitata,* one of dominant canopy former kelp species in the UK (Smale et al., 2013). Thought the only one of the *Laminaria* genus able to survive both the Arctic and temperate regimes (Bolton, 2010), the species is distributed along the Atlantic coast, from Novaya Zemlya to the Canary Islands, including the Baltic Sea and Black sea (Hill, 2008). The effects of MHW period will be tested for a ~14 day simulated event, followed by a recovery period of ~10 days, simulating conditions in short term mesocosm experiments at the Plymouth Marine Laboratory ("PML", UK). The effects of MHW alone and combined with ALAN will be tested, extending the experiment beyond the increased temperature exposure period, to cover also the recovery period. This study was designed to I) evaluate the level of resilience individuals may exhibit, regarding their photosynthetic, growth respiration rates and C:N ratios under MHW, and II) test what effects increased light exposure may have on the organisms and their dynamics under MHW. It is hypothesized that, similar to the ocean acidification, that is, increased CO_2 exposures effects on the kelps regarding MHW situations, the exposure to ALAN, may help the organisms to better respond to the increased temperature. By providing an extended available light period that can perhaps increase the photosynthetic performance of the organisms, their energy production can also be enhanced, and this way increase resistance to the thermal stress,

2.2 Material and methods

2.2.1) Sampling and laboratory conditions.

Individuals of *Laminaria digitata* were collected from the Plymouth Hoe coastal area (50.36400922009365 N, 4.14598110630881 W), during a low spring tide in the beginning of March 2022, with permission from Natural England. In total, 36 either mature or juvenile organisms (stipe length 9-36 cm) were sampled, carefully removing them from the substratum by their holdfast. Each individual was identified using the morphological characteristics described for *L. digitata* identification in Hill (2008), based on their stipe flexibility, smooth texture and oval cross section and the absence of epiphytes. After sampling, they were immediately transferred to PML's mesocosm laboratory, to be measured, weighted and, lastly, placed in $1m^3$ mesocosm tanks in groups of 3. Individuals were kept at the bottom of tanks by attachment to rocks by their holdfast, with the use of rubber bands.

In the mesocosm laboratory, the room temperature was controlled according to the average monthly sea surface temperature of the Western Channel Observatory L4 station, (https://www.westernchannelobservatory.org.uk/), and the tanks filled with filtered 1 and 100 micron filtered 700L seawater from the station. Each tank was maintained in a closed recirculating system, with mean salinity value of 35,24± 0,452 and maximum of 36. Salinity values were controlled by the addition of dechlorinated freshwater when necessary, and the control temperature tanks were maintained at a mean value of 13,27± 1,124, varying between 12-14 ºC along the experiment course. Tanks were not covered to avoid light filtration processes and hence decrease the amount of available light reaching the organisms. In addition to the mesocosm room light (Biolumen, Tropical Marine Centre) (set for a 12h photoperiod), covering the whole extent of the laboratory, LED lights (Aquabeam 2000HD Ultima RW Reef White) were also used in each tank for an increasing light availability. These were set according to the environmental photoperiod variation (± 12 hours) with an intensity of 10,000-14,000 lux (mean 11,45 klux ± 2,325) reaching the water surface, along with individual pumps and ambient air oxygenation systems placed in each tank. All organisms were kept in these conditions for a 6-7days acclimation period before the beginning of the experimental treatments.

2.2.2) Experimental setup

The experimental design was set in accordance with what proposed by Boyd et al (2018), for multiple drivers experiments, using a "collapsed factorial design". A two-way design was created, setting SW Temperature as the main driver, testing its effects as one treatment alone, while Light availability, set as a secondary driver, was nested within SW Temperature, being this the second treatment. This way the interactive effect of the two drivers was collapsed into a single second factor, not testing the effect of ALAN alone, hence preventing the use of a full factorial design and allowing for a greater number of replicates to be used (Boyd et al., 2018).

In total, 12 tanks were used, providing 4 replicates for each of 3 experimental treatments. As illustrated in Figure 2.1, the control group consisted of ambient temperature, salinity and light availability conditions. In the MHW group, a 3ºC temperature increase over the control conditions was implemented, maintaining the environmental light photoperiod (± 12h). And, finally, in the MHW+ALAN group, in addition to the 3ºC temperature increase, a 24h light- 0h dark photoperiod was implemented, simultaneously from the start of the heatwave simulation. The ALAN exposure lasted until the end of the experiment, covering the recovery period as well. In both cases, the heatwave period was set for an average of 14 days.

The experimental course was divided in 3 periods, according to the temperature variations implemented. In the acclimation period, control temperatures were established for all tanks (T1); during the marine heatwave period, increase in temperature was set for the all but control tanks (T3); and during the final 10 days recovery period, water tanks were returned to control values, simulating the end of the heatwave (T4).

2.2.3) Response variables measured

At the end of each experimental period specific variables were measured for all organisms to observe any physiological differences caused by the treatments implemented. In T1, measurements were focused only on Photosynthetic parameters (quantum efficiency, photosynthetic rate, maximum and variable fluorescence). Whereas in T3 and T4, besides these, Growth and Respiration (R) rates were measured, along with Carbon (C%)/Nitrogen (N%) tissue contents sampled in T4. Additionally, water temperature and salinity were measured daily, using a multiprobe (Multi 3420 WTW) and light intensity and nutrients concentrations measured weekly, to account for their variation within the established values along the experiment. These were measured using Spectrosense 2+ meter (number SKUW 310/sc7 51401, Skye Instruments Ltd) and based on the analytical methods described in (Woodward & Rees, 2001), respectively. Briefly, the concentrations of dissolved nutrients Nitrate, Nitrite, Silicate, Phosphate and Ammonium were measured using stored frozen samples, weekly sampled, and a 5-channel segmented flow colorimetric nutrient autoanalyzer (Seal Analytical AA3). The samples were analysed along with nutrient reference materials (KANSO Technos, Japan), to confirm data quality and analytical confidence. Limits of detection for the nutrients were 0.02 µmol/L for Nitrate and Silicate with an analytical uncertainty of 3-4%.

- Photosynthetic parameters

Photosynthetic variables were estimated *via* non-invasive techniques, using the Junior PAM (Pulse Amplitude Modulated) device (WALZ). Using a gain of 3, Rapid Light Curves (RLC), with 12 levels of actinic light intensity (18, 32, 46, 63, 88, 133, 200, 294, 438, 574, 805, 1050), at a 20 second interval were fitted to each organism. These were performed directly on the tanks after acclimating the organisms to 20 minutes in the dark. Measurements were taken at the meristem of the organisms, observing the values of variable fluorescence (Fv-as the difference between Fm- maximum fluorescence and F0- basal fluorescence), Maximum photochemical quantum yield of PSII (photosystem II)

(Fv/Fm), Alfa, as an estimator of quantum efficiency, and ETRm (maximum Electron Transport Rate), as an estimator of photosynthetic rate (Walz, 2013; McCoy et al., 2019).

- Growth rates

To measure growth rates, we used the hole-punching method (Parke 1948; Nunes et al., 2015). Nine (9) mm of diameter circular holes were made on the meristem of all organisms at T1, and their migration and perforation area (equation 1 and 2) measured during the course of experiments (T3 and T4). Checking the distance from the base of meristem and their circular area variation (πr^2) at the different periods, the following were measured:

$$Equ.\,\mathbf{1}\ \ Perforation\ migration\ (cm) = hole\ distance\ Tn + 1 - hole\ distance\ Tn$$

$$Equ.\,\mathbf{2}\ \ Area\ variation\ (cm2) = hole\ area\ Tn + 1 - hole\ area\ Tn$$

- Respiration (R) rates

Incubations for R were performed outside of the mesocosm tanks, in incubation chambers, maintaining the same experimental conditions by using the corresponded water tank for each organism. Being the species known for its high productivity, each incubation was performed for an average of 30 minutes, in the dark, after acclimating the organisms to 15 minutes in opened incubation chambers. Dissolved oxygen variations were measured using an optic oxygen sensor (OxyMini) (World Precision Instruments), with the rates being calculated as the difference in the final oxygen concentrations per the initial ones. Calculations accounted for the volume of the tanks and organisms, time of incubation and Dry weight (DW) biomass of each organism (equation 3). Before performing the measurements, calibrations of the instrument were made, using a two-point calibration in oxygen-free water (cal 0) and air-satured water (cal 100). Details of the calibration procedure are described in the manual of the instrument as "Calibration of Oxygen-Sensitive Fiber-Optic Minisensors. For each tank, a blank incubation was also performed, with only water being incubated, to account for the planktonic contribution to the oxygen variations, that was later subtracted from the individual rates obtained. Water temperature measures of the chambers were simultaneously done along with the O_2 measures, by an attached probe belonging to the instrument, to automatically account for the temperature compensation in the dissolved oxygen values obtained.

$$Equ.\,\mathbf{3}\ \ \ R\ rates\ = \frac{(O2Tn + 1 - O2Tn)\cdot V}{t\ incubation \cdot B}$$

R rates (μmol.min^{-1}.g^{-1})

V= Volume of the chamber-Volume of the organism (L)

t incubation= Time of incubation in minutes

B =Biomass of the organism (g)

- Carbon and Nitrogen tissue content

As the last part of the experiment, 0.3-0.5g of Fresh weight (FW) of meristem samples of each organism were collected to measure their Carbon and Nitrogen content. The samples were dried at 60°C for a minimum of 48hours in a muffle furnace, after which they were weighted to determine their DW and sequentially manually grained to fine powder. Each sample was placed in individual capsules with a minimum of 0,030g sample content and sent to an external laboratory (OEA Laboratories, UK), where their C% and N% were determined. With the results, the C/N were determined and analysed.

2.2.4) Statistical Analysis

All statistical testes were done using the statistical software R, version 4.0.3 and RStudio (2022.02.3, 492). One-way Anova tests (p-value < 0.05) were applied to test for potential significant differences existing from the salinity and light variations along the experimental course, across treatments and sampling times. To identify the significance of the independent variables tested (Sea water Temperature and Artificial Light availability), nested Linear Models (LM) and PERMANOVA analyses were performed.

Using the function "*lm*", two fixed factors were used as the predictors for the response variables tested, "SW-Temperature" (2 levels: ambient and high) and "Light availability", nested within SW-Temperature (2 levels: 12 h, 24h). The influence of the fixed factors was analysed along the experimental course, in the 3 determined sampling times (T1, T3, T4). All models were inspected according to linear models' assumptions, of normality and homoscedasticity of residuals and related diagnostic plots performed. When normality and/or homoscedasticity were not found, even with logarithmic transformations of the response variables, Permutational multivariate anova (PERMANOVA) tests (p-value < 0.05) were performed, using the function "*adonis2*" in the package "*vegan*", maintaining the defaults of the R program (999 permutations and "Bray-Curtis" method). The light availability treatment was still maintained as being nested within the SW Temperature treatment, as in the Linear Models, and

homogeneity of variances was confirmed for the response variables, using the function "*betadisper*", to check for possible dispersion effects.

When significant effects of the tested factors were observed (p-value < 0.05), Tukey's Honestly Significant Different (THSD) post hoc tests were performed to identify any significant groupings within the tested treatment levels (C, MHW, MHW+ALAN), applying the "*emmeans*" (package "*emmeans*") and "*pairwise.adonis*" function, to the LM and PERMANOVA tests, respectively.

Figure 2.4- Experimental setup design, illustrating the 12 tanks randomly assigned to the 3 experimental treatments, with 4 replicates, containing 3 individuals each. The experimental treatments are as follows: Control, here mentioned as the "C" group, with baseline temperatures and ambient photoperiod/ normal light regime; Marine Heatwave, as "MWH", with a +3ºC heat spike exposure, and normal light regime; and the Marine Heatwave + ALAN, "MHW+ALAN", with a +3ºC heat spike exposure and 24hrs light artificial light exposure. The 3 different periods set along the experimental course are illustrated to the left, with their respective duration in days.

2.3) Results

Tank conditions were maintained according to the corresponding treatments and experimental times. The temperature variations, light and salinity conditions are described below (Table 2.1). No statistical differences were found for neither the light intensity (One-way Anova p-value =

0.901) or salinity (One-way Anova p-value= 0.300) variations observed along the experiment, both across treatments and sampling times.

Table 2.1- Mean temperature (ºC), salinity and artificial light intensity (klux) variations along the experimental course, for the 3 corresponding treatments.

		Temperature (°C)	Salinity	Light intensity (klux)
	C	12,17	35,38	11,30
T1	MHW	12,33	35,51	11,63
	MHW+ALAN	12,38	35,55	11,42
	C	14,44	34,85	11,30
T3	MHW	16,96	35,24	11,63
	MHW+ALAN	16,74	35,29	11,42
	C	12,61	35,30	11,30
T4	MHW	12,43	35,50	11,63
	MHW+ALAN	12,51	35,44	11,42

- Photosynthetic parameters

After acclimation (T1) and recovery (T4) no differences were observed among the experimental tanks and related treatments for any of the photosynthetic parameters. On the other hand, at the end of the MHW period (T3), it was possible to identify significant differences among treatments and the corresponding different groups. A significant effect of the Light availability was detected for most parameters in this experimental point, except ETRm, while SW Temperature only presented significant influences for the Fv/Fm ratio. For Fv and Fv/Fm, the MHW was found as the significantly different group, from controls and MHW+ALAN, presenting the highest values of all; while for Alfa it was found the lowest value corresponding to the MHW+ALAN group, being significantly different from controls and MHW groups (Figure 2.2 A & B). The obtained values for each in the 3 experimental times are described in Table 2.2, along with the statistical models and related parameters, while p-values and statistically different groups can be found in Table 2.3.

Table 2.2- Mean values and standard error of mean for the different photosynthetic parameters, and respective R squared (R_2) and F/pseudo F statistic values of the statistical models applied

C	MHW+ALAN	MHW	Models used and respective parameters

Fv (T1)	292.818 ± 8.6390	283.846 ± 16.6506	290.0 ± 7.3328	two-way PERMANOVA, SW Temperature R_2=0.00786 pseudo F=0.2740; Light availability R_2=0.01682 pseudo F=0.5864
Fv/Fm (T1)	0.638 ± 0.0090	0.640 ± 0.0071	0.656 ± 0.0051	nested LM, R_2= 0.06056, $F_{2,34}$= 2.16
Alfa (T1)	0.112 ± 0.0108	0.116 ± 0.0155	0.100 ± 0.0137	nested LM, R2= -0.03685, $F_{2,34}$=0.3603
ETRm (T1)	17.472 ± 1.6562	22.653 ± 4.5389	20.212 ± 2.2257	nested LM, R2= -0.03416, $F_{2,30}$=0.4715
Fv (T3)	734.083 ± 94.1892	953.692 ± 15.5631	686.846 ± 89.1011	two-way PERMANOVA, SW Temperature R_2 0.01897 pseudo F =0.7727, Light availability R_2 0.12191 pseudo F=4.9665
Fv/Fm (T3)	0.641 ± 0.0166	0.688 ± 0.0039	0.651 ± 0.0092	two-way PERMANOVA, SW Temperature R_2=0.09361 pseudo F= 4.1448, Light availability R_2=0.11588 pseudo F= 5.1305
Alfa (T3)	0.124 ± 0.0180	0.0691 ± 0.0049	0.1212 ± 0.0120	nested LM, R_2= 0.2525, $F_{2,34}$=7.248
ETRm (T3)	15.675 ± 3.5057	13.594 ± 1.0718	13.670 ± 1.0718	nested LM, R_2= -0.05551, $F_{2,30}$=0.05343
Fv (T4)	912.4167 ± 37.16353	980.7692 ± 24.74256	909.0 ± 12.1834	two-way PERMANOVA, SW Temperature R_2=0.03365 pseudo F= 1.3322, Light availability R_2=0.08243 pseudo F=3.2637
Fv/Fm (T4)	0.662 ± 0.0063	0.659 ± 0.0058	0.672 ± 0.0048	nested LM, R_2= 0.02499, $F_{2,35}$=1.474
Alfa (T4)	0.072 ± 0.0122	0.073 ± 0.0055	0.093 ± 0.0092	nested LM, R_2= 0.06635, $F_{2,34}$=2.279
ETRm (T4)	12.426 ± 3.5289	8.532 ± 0.8217	8.737 ± 0.9730	nested LM R2= -0.01681, $F_{2,30}$=0.7355

Table 2.3- P-values of Water Temperature (SWT) and Light availability (LA) on kelp photosynthetic parameters tested (Alfa, ETRm, Fv, Fv/Fm) for each experimental period. Significant p-values are highlighted in bolt and respective different groups are described, with "M" corresponding to the MHW treatments and "M+A" corresponding to the MHW+ALAN ones.

	T1		T3			T4	
	SWT p-value	Nested LA p-value	SWT p-value	Nested LA p-value	Sig.groups	SWT p-value	Nested LA p-value
Alfa	0.8046	0.4228	0.100745	**0.001634**	M+A	0.1304	0.1512
ETRm	0.3483	0.8526	0.8532	0.7899	~	0.2412	0.8400
Fv	0.676	0.467	0.404	**0.026**	M	0.265	0.073
Fv/Fm	0.26714	0.08986	**0.049**	**0.013**	M	0.6692	0.1054

- Growth rates

For the growth rate measures, the parameters were tested in different sampling times to check for potential differences along the experiment course. As seen in Table 2.3, both for area increase rates and perforation migration rates, statistically significant effects were found only for the Light availability factor, with no influence being found for the SW Temperature variable alone. For the area increase rates, along the whole experimental course (T1-T4), the heatwave period (T1-T3) and the recovery period (T3-T4), significant effects of the factor were found. For the perforation migration rates however, this was not observed in the recovery period, where there is no longer an exposition to the increased temperature stressor. Nevertheless, for all cases where statistically significant results were found, both MHW and MHW+ALAN treatments stood out as significantly different groups from controls groups, with MHW presenting the lowest values of increase and MHW+ALAN the highest's (Table 2.4) (Figure 2.2 C & D).

Table 2.3- P-values of Sea Water Temperature (SWT) and Light availability (LA) factors, with significant ones highlighted in bolt, for the different growth rate parameters, and respective different groups in cases of significancy.

	SWT p-value	Nested LA p-value	Sig.groups
Area increase rate (T1-T3)	0.5062	**0.00007314**	M+A & M
Area increase rate (T3-T4)	0.532265	**0.005892**	M+A & M
Area increase rate (T1-T4)	0.8824640	**0.0001459**	M+A & M
Perforation migration rate(T1-T3)	0.786062	**0.004979**	M+A & M
Perforation migration rate (T3-T4)	0.5480	0.0531	~
Perforation migration rate (T1-T4)	0.805715	**0.004468**	M+A & M

Table 2.4- Mean values and standard error of mean for the different growth rate parameters, and respective R squared (R_2) and F statistic values of the statistical models applied.

	C	M	M+A	R_2	F value
Area increase rate (T1-T3)	0.070 ± 0.0053	0.049 ± 0.0040	0.087 ± 0.0084	0.3351	$F_{2,35}=10.32$
Area increase rate (T3-T4)	0.182 ± 0.0469	0.089 ± 0.0235	0.224 ± 0.0257	0.1591	$F_{2,35}=4.499$
Area increase rate (T1-T4)	0.109 ± 0.0181	0.067 ± 0.0081	0.145 ± 0.0143	0.3042	$F_{2,35}=9.088$
Perforation migration rate (T1-T3)	0.083 ± 0.0170	0.051 ± 0.0087	0.105 ± 0.0122	0.1602	$F_{2,35}=4.53$
Perforation migration rate (T3-T4)	0.157 ± 0.0256	0.136 ± 0.0164	0.196 ± 0.0222	0.06033	$F_{2,35}=2.188$
Perforation migration rate (T1-T4)	0.110 ± 0.0165	0.084 ± 0.0010	0.144 ± 0.0155	0.1647	$F_{2,35}=4.649$

- Respiration rates

A high degree of variability was observed among oxygen consumption values estimated. As observed in Table 2.5, no significant differences were found among the experimental treatments for the R rates, neither during the MHW (T3) or the recovery period (T4). In T3, values of -0.2309828 $\mu mol.min^{-1}.g^{-1}$, -0.2419261 $\mu mol.min^{-1}.g^{-1}$ and -0.203423 $\mu mol.min^{-1}.g^{-1}$ were found for C, MHW and MHW+ALAN groups, respectively; while in T4, -0.1127823 $\mu mol.min^{-1}.g^{-1}$, ⁻0.2742449 $\mu mol.min^{-1}.g^{-1}$ and   -0.2181354 $\mu mol.min^{-1}.g^{-1}$ for the same mentioned groups (Figure 2.2 E).

Table 2.5- P-values of Sea Water Temperature (SWT) and Light availability (LA) factors for the respiration rates during MHW (T3) and recovery (T4), and respective R squared (R_2) and F statistic values of the statistical models applied

	SWT p-value	Nested LA p-value	R_2	F value
T3	0.8828	0.5891	-0.06899	$F_{2,24}=0.161$
T4	0.0631	0.4323	0.08934	$F_{2,23}=2.226$

- Carbon and Nitrogen contents

For the Carbon/Nitrogen ratio, only measured at the end of the experiment (T4), the same pattern as in most of the other parameters was observed, with significant influences found only for the Light availability factor, with a p-value of **0.0006795** and none observed for the SW Temperature alone, p-value= 0.8317803. Same as in the above cases, both MHW and MHW+ALAN were found as significantly different groups from controls, with MHW+ALAN presenting the greatest C/R ratio value= 16.745 ± 0.4707, M the smallest C/N ratio = 14.617 ± 0.2189, and the C group the intermediate C/N ratio = 15.582 ± 0.5220 (R_2= 0.2441, $F_{2,35}=$ 6.974) (Figure 2.2 F).
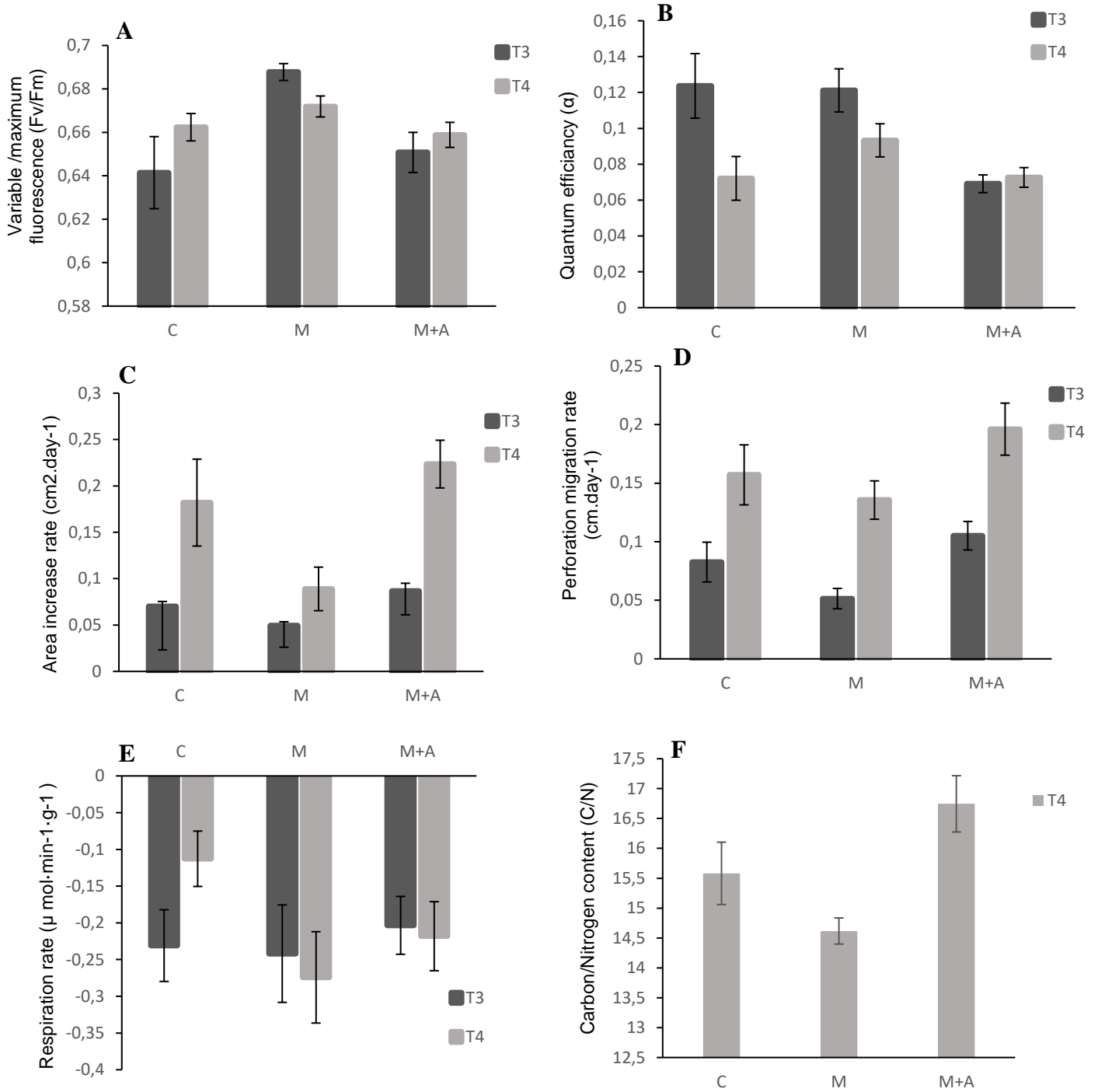
Figure 2.5- Mean values and SE (standard error) of mean of (A) Fv/Fm ratio; (B) quantum efficiency; (C) area increase rate ($cm^2.day^{-1}$); (D) perforation migration rate ($cm.day^{-1}$); (E) respiration rate ($\mu mol.min^{-1}.g^{-1}$) and (F) C/N ratio content, after the heatwave (T3) and recovery period (T4)

2.4) Discussion

This study describes the first experiment testing for the combined effect of MHWs and the use of ALAN on the physiology of the species *L.digitata*. As hypothesized, it was found that increased light availability seemed to help organisms better respond to the MHW than those exposed to MHW alone. Organisms exposed to MHW alone appeared generally negatively affected by the increased temperature exposure, when compared to the responses observed in organisms in control conditions. Whereas the combined effect of MHW and ALAN appeared to result in generally positive responses, compared to the other tested conditions, with the ALAN effect outcompeting the negative effects caused by increased temperature. For most of the tested parameters, a significant effect was found only for the Light availability factor, whereas for SW Temperature its influence was observed only for a single parameter.

During the acclimation period, where there wasn't yet an exposure to the stressors, no significant differences were found for any of the parameters analysed, i.e., no initial differences existing among the organisms, despite the variation in their individual characteristics such as on their stipe length and biomass. With the assumption of the same happening along the whole experimental period, it is suggested that the following differences found among the experimental treatments were caused mainly by the exposure of the organisms to the tested treatments, being this way possible to evaluate their influence.

After the MHW, two different patterns were observed among the photosynthetic and growth rate parameters. For two distinct photosynthetic parameter indicators, either the MHW+ALAN or the MHW treatments were found as belonging to different groups at a time, from the control group and remaining treatment. For quantum efficiency (α), MHW+ALAN was found as the significantly different one, presenting the smallest values observed, while for fluorescence (Fv & Fv/Fm), MHW was highlighted as the significantly different, with the highest values observed. Quantum efficiency characterizes the percentage of light absorbed during photosynthesis by photosynthetic organisms (Walz, 2013; McCoy et al., 2019), and it is regulated according to the available light existing at a certain environment. By being exposed to increased light conditions, a down regulation of the light consumed by the organisms can take place, by adjustments to their photosynthetic pigments (Frost-Christensen & Sand-Jensen, 1992), working as a photoacclimation mechanism. This way less energy is spent on the absorption of light when this is seen to be greatly available, that can later be spent in other necessary mechanisms, including to stimulate greater light absorptions when light is poorly available. Such responses have been previously described in the literature for studies on kelp

species, where as a consequence of increased light exposure, decreased photosynthetic efficiency (α) responses or photoinhibition mechanisms have been observed (Cabello-Pasini et al., 2000; Colombo-Pallotta et al., 2006). In the same context, studies mentioning the opposite response, i.e, increased quantum efficiency, when testing for decreased light conditions have also emerged (Sanchéz-Barredo et al. 2020).

As for the fluorescence responses, in the present study, it was observed an up regulation of their emissions, i.e, increases as a consequence of increased temperature exposure. There are 3 different possible pathways for the excitation energy derived from the light energy absorbed during photosynthesis: the main percentage (about 90%) is used in the photochemical reactions, where the energy conversion takes place (primary photochemistry), while the smaller non used energy, is either emitted in the form of fluorescence, to deactivate the excited pigments, or is dissipated in the form of heat (Krause & Weis, 1991). Most fluorescent energy is emitted by chlorophyll *a* pigments, and the more reaction centres remain in an active state during the light capture process, the less energy is emitted in the form of fluorescence, on the contrary, the maximum fluorescence yield is obtained (Krause & Weis, 1991). It is affirmed that as PSII is affected by environmental stresses, the Fv/Fm tends to decrease (Krause & Weis, 1991), as a result from the impairment of the photosystem to the photosynthetic and metabolic process or by an increased dissipation of the energy as heat (Davison, 1987; Sharkey, 2005; Pereira et al., 2015; Mabin et al., 2019). Such response has already been registered regarding thermal stress in previous studies (Davison and Davison 1987; Sharkey 2005; Pereira et al. 2015; Mabin et al. 2019; Nepper-Davidsen et al., 2019), enhancing even more the effects of higher light availability in α (Bruhn & Gerard, 1996; Sánchez-Barredo et al., 2020). As such responses were not observed in this study, it can hence be thought that the thermal stress implied may not have negatively affected the photosystem of the studied species. Contrarily, it stimulated the photosynthetic activities, as seen by the increased fluorescence emissions in organisms exposed to MHW alone, compared to control conditions and MHW+ALAN treatments. It has been previously seen that *L. digitata* organisms may present higher capacities for photoprotection, driven by an elevated and more light-responsive non-photochemical quenching response (Burdett et al., 2019). This may help organisms to better dissipate the excessive energy absorbed during increased temperature exposures, and hence not affect their photosynthetic efficiency. Nevertheless, for a deeper understanding of such mechanisms analysing specifically the responses of the photosynthetic pigments is also necessary. Regarding the recovery period, where the exposure to the heat spike is interrupted, differences among treatments are no longer

observed, showing a recovery ability both for the organisms exposed to ALAN and those with normal photo-period regimes. In this case neither photoinhibition mechanisms or variations in fluorescence emissions are longer observed, demonstrating a capacity to return to the ground state in organisms previously exposed to the anomalous environmental conditions, presenting similar responses as control organisms.

For growth rate and C/N ratio, both the MHW and MHW+ALAN treatments were found as significantly different from control groups, presenting the lowest and highest's values, respectively. Increased temperature exposures were seen to cause a significant reduction on the growth rate of the organisms, which was also translated to their C/N tissue relation. Being affected even during the recovery, organisms exposed to MHW alone were seen to grow generally less than in remaining treatments, despite the higher photosynthetic activity observed (by higher Fv/Fm) in this treatment. Even with the enhanced photosynthetic activities and the greater level of photoprotection observed, while being exposed to increased temperature conditions, the carbon fixation mechanisms of *L.digitata* seemed to be affected. This might result from an energetic trade off, where energy normally directed to photosynthesis is in turn used in thermal protection mechanisms (Hurd et al., 2014; Britton et al., 2020). Observed both on the growth levels and on the reduced Carbon percentage presented in the tissue, compared to Nitrogen levels, it appears that a general lower C acquisition takes place as a result of the exposure (Gerard & Du Bois, 1988; Nepper-Davidsen et al., 2019). Such responses have already been reported for other seaweed species, although in these cases accompanied also by a reduction in the photosynthetic parameters (alfa and Fv/Fm) (Nepper-Davidsen et al., 2019; Britton et al., 2020; Umanzor et al.; 2021) and net photosynthetic rates -O_2 production fluxes- (Britton et al., 2020), that were not explored in the present study. Decreased growth rates appear to trigger the accumulation of Nitrogen percentages in the tissues of macroalgae species (Umanzor et al., 2021). The increase in the % of N can be related to the increased microbial colonization and transformation activities that occur as the kelp tissues start to degrade (Duggins & Eckman, 1997; Norderhaug et al., 2003; Krumhansl & Scheibling, 2012), and their phlorotannins concentrations decrease (Duggins & Eckman 1997). Here the decomposition rates of MHW exposed organisms were also seen to be increased along the whole experiment, with intermediate levels of degradation observed for MHW+ALAN and smaller ones for control organisms.

As for the effect of increased light exposure on growth and C/N, it seems to have counteracted the negative effects caused by high temperature. Organisms exposed to ALAN, presented the

highest's growth rate values of all, both for area increase and blade migration rates, even during exposure to the MHW event. As mentioned before, light plays an indispensable role in the photosynthetic process, serving as the energy source that supports the activity (Finch *et al.*, 2014; Casem, 2016; Lopez & Barclay, 2017). By being exposed to extra available light, the organisms seemed to have increased their photosynthetic metabolic rates, and hence, their carbohydrates production (carbon fixation). Resulting this way in higher growth and producing the increased amount of energy necessary to address the temperature stress and/or increase their thermal optimum (Koch et al. 2013). Such responses are observed even during the recovery period, with organisms previously exposed only to MHW still presenting smaller growth values and C/N and MHW+ALAN the highest's, compared to controls. However, in this sampling point, these parameters appear to have generally lower values compared to the ones obtained right after the exposure to abrupt thermal stress. This suggests that, although alone increased sea water temperatures may downregulate the carbon fixation rates of the organisms, the combined effect of high temperature and increased light exposures, is the factor leading to the highest's growth values observed and not the increased light exposure alone. Increased short-term temperature exposures have been seen to result in increased kelp production rates, in other studies simulating shorter MHWs (Burdett et al., 2019). For temperature values up to a certain threshold such responses can be expected, as it causes an increase in the electron transport rate through the photosystems (Delebecq et al., 2016). By stimulating organism's mechanistic photosynthetic activities, as observed in the photosynthetic parameters, the exposure to the temperature levels implemented simultaneously to the increased light, seem to provide organisms the necessary light to sustain their higher production.

Being able to utilize the increased available light in their favour, as previously observed for increased CO_2 concentration (Koch et al., 2013; Kroeker et al., 2013; Britton et al., 2020), kelp organisms decrease greatly the potential for physiological impacts caused by warming events. Such ability can play a relevant role, particularly considering that kelp organisms, provide habitat for variable communities, only possible by their fast and big biomass productions, and considering their role as active Blue Carbon sequestrators. If affected by temperature increases, the decrease in such abilities can have major consequences, upscaling throughout entire food webs, especially considering the predictions for increased frequencies and intensities of MHW events in the future (Li et al., 2019; Yao et al., 2020). This is also translated in lower levels of carbon sequestration and sink, and hence less Blue Carbon sequestration contributions. If

identified ways such impacts can be diminished or avoided, these mechanisms can be implied in conservation and kelp restoration programs, and even be utilized in aquaculture kelp productions. However, other issues should also be considered and better explored before a full application of the method, considering other potential effects expositions to ALAN can have on seaweed species. For example, effects on their reproductive success should be analysed, taking as an example the impacts caused by 24h daylight exposure for seaweeds in polar latitudes, considering their photoperiod regulated reproductive strategies (Martins et al., 2022). Such prolongated light exposures have resulted also in changes in the photoperiod responses of terrestrial plants (Runkle et al., 1998; Whitman et al., 1998), decreased chlorophyl *a* concentrations in the cells and Rubisco molecules in phytoplankton's (Poulin et al., 2014) and inductions and suppressions of growth (Cathey & Campbell, 1975).

Regarding the respiration rates, contrary to what was hypothesized, no effects of either factor were observed, although these results should be carefully considered. While in the MHW period no visible differences were seen among the obtained values of respiration, the treatment groups presented a considerable variation among them during recovery. Generally lower respiration, that is, less oxygen consumption values were found in the control groups and slightly higher in the MHW compared to the MHW+ALAN, though this result was not statistically significant. It should be noted, however, that since net primary production (NPP) rates (i.e., oxygen production in the light) were not measured in this study due to experimental difficulties, the evaluation of the complete oxygen dynamic cycle was not possible. *L.digitata*, among other kelps, is known to be highly affected by increased long term temperature exposures, decreasing their ecophysiological performance (Simonson et al., 2015; Hargrave et al., 2017), increase mortality (Bartsch et al., 2013; Wilson et al., 2015) and affect their oxygen fluxes (Burdett et al., 2019). As a consequence of increased temperature exposures, generally, higher respiration rates are found for seaweed organisms, as their oxygen production rates are seen to decrease (e.g. Nepper-Davidsen et al., 2019; Britton et al., 2020; Umanzor et al., 2021). This is related to the negative effects of the stressor to the carbon fixation mechanisms (Cabello-Pasini et al., 2000; Fernández et al., 2021) and the increased metabolic energy required to better respond to it (Koch et al., 2013; Wernberg et al. 2016). However, in the current study such responses are not found, with no variations in the Respiration values among treatments observed, neither at the MHW exposure nor the recovery period. One explanation for such observed response might pass by the increased photoprotective ability of *L.digitata* organisms to thermal stress, as mentioned above. However, if resilience in the Respiration rates

had in fact been related to such ability, it is believed that the same response would be observed for the growth of the organisms, not being the case. Hence another possible explanation for such anomalous results could be the high degree of variation found for the data related to this parameter, not being possible to statistically detect significant differences. Considering the variations observed in the recovery period, where higher respiration rates were found for controls, compared to MHW and MHW+ALAN groups, this can be seen as an acceptable hypothesis. If the increased respiration rates caused by increased temperature are considered, the lack of differences between MHW and MHW+ALAN group may indicate that even when exposed to increased light conditions, organisms may not be able to counteract the effects of high temperature on respiration the same way done for growth. Nevertheless, for a deeper understanding of such mechanisms studies exploring also the effects caused on net photosynthetic rates should be performed, evaluating the different possible outcomes.

In general, very small R_2 fits were found for the statistical tests applied to the variables (LM & PERMANOVA), with smaller, or even negative, values observed, as expected, in cases where no significant effect was found for neither tested factors. This may have been caused by the high degree of variability found within the data, influencing also their normality. Nevertheless, the p-values of each test applied resulted in very clear results, with no doubts remaining about the influences of the stressors tested to the parameters analysed.

In conclusion, it is observed that as initially thought, increased light availability may in fact be used to decrease the negative effects caused by high temperature exposures on kelp species. We observed a positive trend regarding the factor in several different parameters analysed for the species *L.digitata* that seem to counteract the negative effects caused by the thermal stress. Such thermal effects were also observed here, as in other studies, affecting positively some of their photosynthetic mechanisms (namely the fluorescence), to their general growth and tissue contents (Carbon and Nitrogen) negatively, when testing for the stressor alone. From an ecological point of view, such finding may represent an important step in the context of ecosystems restoration and conservation, where increased artificial light availability may be used as a mitigating strategy for managed kelp communities in the presence of MHW events. This approach may also be of great interest to the kelp farming industry, contributing also to economical purposes, where great producers like China, suffering from increasing MHW events may use it to enhance its production and resilience in the context of future climate change. Kelps constitute essential ecosystems, acting as keystone species, food sources and habitat to several other communities. As such finding ways to help them maintain or increase

their resilience to environmental stressors that threaten their survival becomes an indispensable goal. In this way, future studies with similar approaches such as in the current study are greatly advised, and, the use of ALAN should be further explored, testing the response in other kelp species and seaweed organisms, in additional physiological parameters. Something to consider also is the fact that the current study is performed at the end of Winter, hence lower intensities of MHW are simulated. Studies on later Spring and Summer should also be performed, as MHWs can outcome the annual Temperature maximums experienced by kelp and other seaweed species, hence resulting in greater stress levels. For the summer, the smaller levels of growth rate these organisms may present can also be a determining factor. This can be especially important for seaweeds located at lower latitudes, already exposed to their thermal maximum ranges, and where exposures to MHWs can be even higher, and taking into account potential latitudinal variable responses, as observed for other stressors before.

2.5) Acknowledgements

2.6) References

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