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Responses of shallow-water Arctic benthic communities to climate change

Anaïs Lebrun

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Anaïs Lebrun. Responses of shallow-water Arctic benthic communities to climate change. Biodiversity and Ecology. Sorbonne Université, 2023. English. NNT : 2023SORUS479 . tel-04435267

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RÉPONSES DES COMMUNAUTÉS BENTHIQUES ARCTIQUES PEU PROFONDES AU CHANGEMENT CLIMATIQUE

Thèse présentée par

Anaïs Lebrun





Sorbonne Université

École doctorale des Sciences et de l'Environnement d'Ile de France (ED 129)

Laboratoire d'Océanographie de Villefranche UMR 7093

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Thèse présentée par

Anaïs Lebrun

pour obtenir le grade de docteur de Sorbonne Université

Spécialité : Sciences du vivant et de l'environnement

Dirigée par Jean-Pierre GATTUSO (Directeur), Steeve COMEAU (Co-encadrant)

et Frédéric GAZEAU (Co-encadrant)

Présentée et soutenue publiquement le 23 octobre 2023

au Laboratoire d'Océanographie de Villefranche

Devant un jury composé de :

Dr. Catherine BOYEN	Directrice de recherche CNRS, Station Biologique de Roscoff (France)	Présidente
Pr. Kai BISCHOF	Professeur à l'Université de Brême (Allemagne)	Rapporteur
Pr. Dorte KRAUSE-JENSEN	Professeure à l'Université d'Aarhus (Danemark)	Rapporteuse
Dr. Inka BARTSCH	Directrice de recherche à l'Institut Alfred Wegener pour la recherche polaire et marine (Brême, Allemagne)	Examinatrice
Pr. Ryan KELLY	Professeur à l'Université de Washington (États-Unis)	Examineur
Dr. Jean-Pierre GATTUSO	Directeur de recherche au CNRS (France)	Directeur de thèse
Dr. Steeve COMEAU	Chargé de recherche au CNRS (France)	Co-encadrant
Dr. Frédéric GAZEAU	Chargé de recherche au CNRS (France)	Co-encadrant

À la petite fille que j'étais,



"Monaco Glacier", 12 x 22 inches, © David McEown



"Hornsund, Burgur Bay", 10 x 22 inches watercolour, © David McEown

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Acknowledgments

Ce manuscrit est l'aboutissement d'une aventure particulièrement enrichissante aussi bien d'un point de vue professionnel que personnel. Je souhaite remercier ici tous ceux qui, de près ou de loin, y ont contribué.

Je remercie tout d'abord mon directeur de thèse, Jean-Pierre, et mes encadrants, Steeve et Frédéric, pour leur expertise, leur accompagnement et leur précieux conseils tout au long de ce parcours. Je tiens à vous exprimer ma sincère gratitude pour les opportunités que vous m'avez offertes pour concrétiser des projets alignés avec mes aspirations scientifiques.

I would like to express my gratitude to all the members of the jury for accepting to evaluate my work. I would also like to thank you for coming to Villefranche-sur-Mer to allow me to defend my thesis in person, which has become a rarity since the pandemic. I am very grateful for this opportunity and I am honored to present you my work.

I thank the FACE-IT, ORCA, EC2CO, and APIL projects, as well as the Ecole Doctorale 129, for their contributions to the funding of this thesis.

Kai and Ryan, I would like to thank you both for your involvement in my thesis committee. Our discussions, your external perspective, and your encouragement have contributed to the successful completion of this thesis.

Ryan, our meeting in Seattle after more than three years of exchanges was very enriching. Thank you for inviting me.

Je remercie également la direction du LOV et l'équipe CHOC de m'avoir accueillie. Un grand merci à Isabelle et aux gestionnaires, Linda, Anne, Nadège et en particulier à toi Amandine, qui a su gérer tous ces devis, commandes, préparations et retours de missions que je t'ai envoyés (et dieu sait qu'il y en avait !).

Je souhaite également remercier les personnes avec qui j'ai pu partager de nombreux moments à la paillasse, à refaire le monde. En particulier, Samir qui a toujours été là, tel un vrai couteau suisse, à Villefranche et en Arctique. Alessandra, je te remercie pour ta bienveillance, pour l'aide immense que tu m'as apportée lors mon stage de master, et pour ton soutien depuis notre première rencontre. Cale, the days were sometimes difficult in the

cold Arctic but we were able to do a good job as a team. I wish you the best in your next adventures.

Laetitia et Chloé, je ne saurais jamais assez vous remercier pour votre soutien. Partager nos quotidiens a rendu cette aventure bien plus belle. Vous savez déjà tout mais à nouveau : merci.

Je remercie aussi tous les étudiants et membres du labo avec qui j'ai eu l'occasion de partager de nombreux repas, séminaires ou simples discussions philosophiques sur le ponton : Aurélie, Chloé T., Manon, Flo, Thelma, Kevin, Marine, Laulau, Cyril, Marc, Loïc, Arthur ...etc.

Je souhaite également remercier Rodolphe et Anne-Sophie, qui m'ont fait découvrir ce laboratoire il y a plus de 5 ans maintenant. Anne-Sophie, ce fût un grand plaisir de travailler avec toi. Je n'ai pas retrouvé la lampe torche mais je suis partante pour une nouvelle manip 24h. Rodolphe, tout cela a en partie commencé grâce à toi. Merci d'avoir souvent su trouver les mots justes (ou la blague parfaite !).

Lors de mes missions en Arctique j'ai rencontré de merveilleuses personnes que je remercie d'avoir croisé ma route. Pour ne citer qu'eux : Yohan, Matt, Christophe, Jesper, Nele, Luisa, Sarina et Nora.

Je remercie M. Baudry et M. Billi, mes professeurs de biologie au collège et au lycée. Votre engagement et votre enthousiasme ont suscité en moi une curiosité insatiable pour comprendre les processus de la vie. Votre influence a été cruciale dans la poursuite de mes études.

Mes remerciements vont également à mes amis et ma famille pour leur soutien et leur encouragement tout au long de mes études, bien qu'ils aient parfois du mal à comprendre mon travail... !

A mes amis de prépa, Joël, Marine et Nawele : le temps fait son œuvre mais nos débuts post-bacs resteront à jamais gravés dans ma mémoire. Je clôture désormais le chapitre « études » de ma vie et je ressens une immense fierté pour tout ce que nous avons accompli.

Estelle, ton soutien moral a été d'une grande aide pour surmonter les moments difficiles. Je suis particulièrement reconnaissante d'avoir une amie comme toi. *« Si t'as des soucis, j'ai les mêmes aussi, Mais je ferais n'importe quoi pour toi, [...] Parce que je suis ton ami. »*

Ma sœur, mon frère, vous avez toujours été des modèles pour moi. Merci de m'avoir donné de si merveilleux neveux et nièces et merci d'être là, même si les kilomètres nous séparent.

Papa, Maman, la base de tout cela, c'est vous. Vous avez toujours cru en moi. Papa, tu m'as toujours encouragée et pour cela tu as souvent cité Oscar Wilde : « viser la lune, car même en cas d'échec, on atterrit dans les étoiles. ». Des échecs, des déceptions, il y en a eu et il y en aura encore. Mais finalement, c'est dans la poursuite de nos aspirations que nous découvrons de nouvelles étoiles, de nouveaux horizons et de nouvelles opportunités. Maman, ton soutien inébranlable et ton empathie ont été une vraie source de réconfort pour moi. Tu as su reconnaître mes moments de doute et de découragement et tu as été là. Avec Papa vous avez illuminé mes victoires comme si c'était les vôtres, car ce sont aussi les vôtres, et vous m'avez donné une force nouvelle pour continuer. Grâce à vous deux, j'ai appris à viser haut et à poursuivre mes rêves avec ténacité.

Maxime, merci pour ta présence inestimable dans ma vie. Sans toi, tout cela n'aurait pas vraiment de sens. Tu as su me soutenir et m'encourager dans mes projets, même s'ils t'échappaient parfois. Je me réjouis de partager ta vie depuis tant d'années. Et je me réjouis d'autant plus en pensant à tout ce qui nous attend. Tu es mon pilier, mon âme sœur, mon confident, mon meilleur ami. Je t'aime.

Ces trois dernières années n'auront pas été un long fleuve tranquille et je suis profondément reconnaissante envers toutes ces personnes qui ont contribué à la réalisation de cette thèse. C'est une page qui se tourne et je n'attends que de découvrir la suite.

First-authored papers published, submitted and in preparation

- **Lebrun, A.**, Comeau, S., Gazeau, F., Gattuso, J.-P. 2022. Impact of climate change on Arctic macroalgal communities. *Global and Planetary Change* 219, 103980. 10.1016/j.gloplacha.2022.103980
- **Lebrun, A.**, Miller, C., Meynadier, M., Comeau, S., Urrutti, P., Alliouane, S., Schlegel, R., Gattuso, J.-P., Gazeau, F. Multifactorial effects of warming, low irradiance, and low salinity on Arctic kelps. Submitted in *Biogeosciences*.
- **Lebrun, A.**, Miller, C., Gazeau, F., Urrutti, P., Alliouane, S., Gattuso, J.-P., Comeau, S. Tolerance of the Arctic kelp community to ocean warming and marine heatwaves. To be submitted in *Journal of Ecology*.
- **Lebrun, A.**, Comeau, S., Gazeau, F., Gattuso, J.-P. Benthic diversity along an Arctic fjord: which are the key factors? (preprint). *bioRxiv*. 10.1101/2023.08.16.553514

Other papers published, submitted and in preparation

- Miller, C., Urrutti, P., Gattuso, J.-P., Comeau, S., **Lebrun, A.**, Alliouane, S., Schlegel, R., Gazeau, F. 2023. Technical note: an autonomous flow through salinity and temperature perturbation mesocosm system for multi-stressor experiments (preprint). *EGUsphere*. 10.5194/egusphere-2023-768
- Schlegel, R., Bartsch, I., Bischof, K., Bjørst, L.R., Dannevig, H., Diehl, N., Duarte, P., Hovelsrud, G.K., Juul-Pedersen, T., **Lebrun, A.**, Meriliet, L., Miller, C., Ren, C., Sejr, M., Søreide, J.E., Vonnahme, T.R., Gattuso, J.-P., 2023. Drivers of change in Arctic fjord socio-ecological systems: examples from the European Arctic. *Cambridge Prisms: Coastal Futures* 1, e13. 10.1017/cft.2023.1
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- Miller, C., Comeau, S., **Lebrun, A.**, Gattuso, J.-P., Alliouane, S., Urrutti, P., Gazeau, F., (in prep.). Community-scale arctic kelp response to ocean warming and marine heatwaves.
- Jungblut, S., Miller, C., **Lebrun, A.**, Dorschner, S., Hagen W., Comeau, S., Gazeau, F., Bischof K., Gattuso, J.-P. (in prep.): Part of the reason for 'winning' climate change? Biomembranes of Arctic kelps adapt to changing temperatures.

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List of abbreviations

AHDR: Arctic Human Development Report

A_T: Total Alkalinity

AWI: Alfred Wegener Institute

CCMs: CO₂ Concentrating Mechanisms

CH₄: Methane

C:N: Carbon:Nitrogen ratio

CO₂: Carbone dioxide

Chl *a*: chlorophyll *a*

CTD: Conductivity, temperature, depth

DIC: Dissolved Inorganic carbon

DW: Dry Weight

eDNA: environmental DNA

ESD: Extrem Studentized Deviation

F₀: Fluorescence measured before acidification

F_a: Fluorescence measured after acidification

FACE-IT: the Future of Arctic Coastal Ecosystem - Identifying Transitions in fjord systems and adjacent coastal areas

FPA2: Prince Albert II of Monaco Foundation

FW: Fresh Weight

GLMM: Generalized Linear Mixed Model

HCl: Hydrochloric Acid

IPCC: Intergovernmental Panel on Climate Change

IPEV: Institut polaire français Paul Emile Victor

IMEV: Institut de la Mer de Villefranche

INSU: Institut National des Sciences de l'Univers

K_d: Vertical light attenuation coefficient

LOV: Laboratoire d'Océanographie de Villefranche

MHWs: Marine Heatwaves

NO₂: Nitrite

NO₃: Nitrate

NOAA: National Oceanic and Atmospheric Administration

O₂: Oxygen

OISST: Optimum Interpolation Sea Surface Temperature

PAR: Photosynthetically Active Radiation

PCR: Polymerase Chain Reaction

pHT: pH on the total scale

PO₄: Phosphate

PCA: Principal Component Analysis

SST: Sea Surface Temperature

SSPs: Shared Socioeconomic Pathways

SiOH₄: Silicate

SRES A2: Special Report on Emissions Scenarios A2

t₀: beginning of the experiment

t_{final}: end of the experiment

Temp: Temperature

BLASTn: nucleotide-nucleotide Basic Local Alignment Search Tool

UVR: Ultraviolet radiation

This study is a contribution to the project FACE-IT (The Future of Arctic Coastal Ecosystems – Identifying Transitions in Fjord Systems and Adjacent Coastal Areas) which received funding from the European Union’s Horizon 2020 research and innovation programme under grant agreement no. 869154.

Introduction

Part 1: The Arctic Ocean and its ecosystem

1. The Arctic Ocean: unique and fragile

1.1. The Arctic: an ocean surrounded by land

The Arctic region encompasses the Arctic Ocean and surrounding lands, including Greenland (Denmark), Alaska (United States), parts of Canada, Russia, and Scandinavia (Fig. 1). Among various geographical definitions of the Arctic, we will use the one provided by the Arctic Monitoring and Assessment Programme (AMAP), which is commonly used and based on several elements such as political boundaries, vegetation limits, permafrost boundaries, and key oceanographic features.

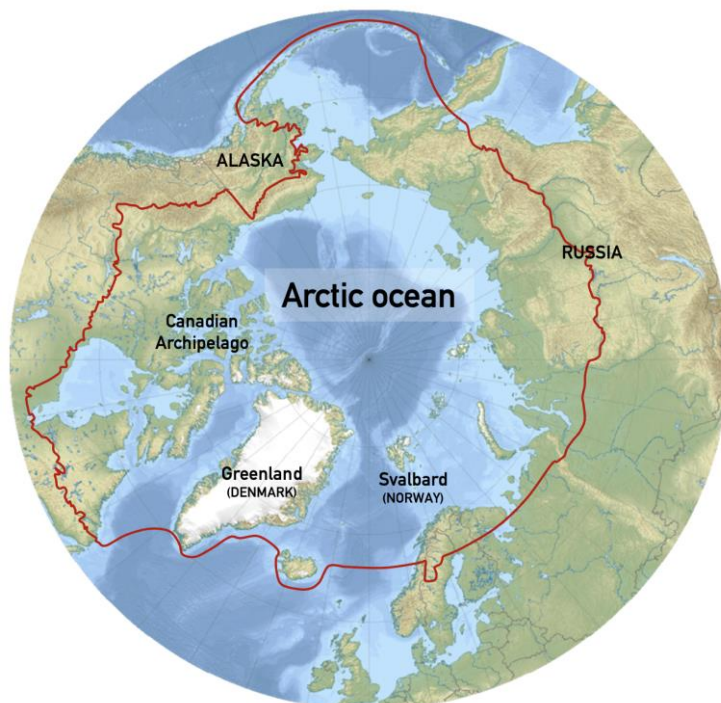


Figure 1: Map of the Arctic and its boundary (red line) as determined by the Arctic Monitoring and Assessment Programme (AMAP, amap.no).

The Arctic Ocean, surrounded by coastal plains, mountain ranges, and fjords offers diverse habitats such as sea ice, open water, and shallow coastal areas for numerous marine species (Bluhm et al., 2011). From macroalgae to marine mammals, a complex web of life has adapted to thrive in this extreme environment, bestowing the Arctic Ocean with high ecological richness and importance extending far beyond its immediate surroundings.

1.2. The importance of the Arctic Ocean

Due to its geographical isolation and extreme climate, the Arctic remains one of the least populated regions in the world (AHDR, 2015). Nevertheless, indigenous communities such as the Inuit, Sami, and Yupik people have a long history of presence in these regions for whom the Arctic Ocean holds profound cultural and subsistence value (Martello, 2008). Their cultures and way of life are closely tied to the nature and resource availability. Hunting, fishing, and gathering coastal plants are essential activities for the survival and culture of these indigenous communities.

The Arctic Ocean is globally exploited for its natural resources. By the mid-2000s, the Arctic Ocean witnessed an estimated annual fish catch of 10 200 tons, encompassing both marine and estuarine species (Zeller et al., 2011). Although the fish catch in the Arctic Ocean accounts for a relatively small portion compared to the global ocean (< 1%), the Northeast Arctic cod fishing stock is among the largest in the world (Pauly, 2008; Armstrong et al., 2014). The Arctic seafloor is also rich in oil, gas, and mineral resources (Lindholt, 2006; Henderson and Loe, 2014). Several coastal countries such as Russia, Canada, the United States, and Norway are engaged in the exploration and exploitation of these resources.

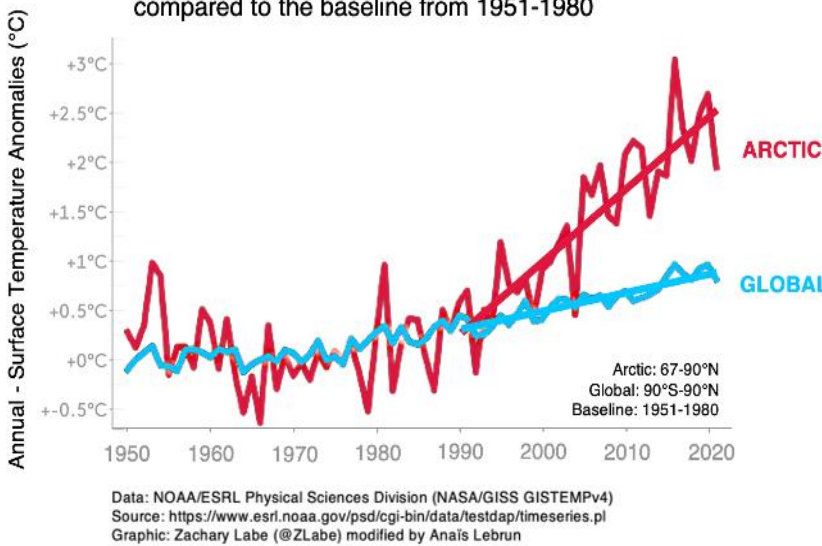
Beyond its resource potential, the Arctic Ocean plays a crucial role in regulating global climate (Olsen et al., 2011). The cryosphere, an all-encompassing term for the portions of Earth's surface where water is in solid form, including sea ice, lake ice, river ice, snow cover, glaciers, ice caps, ice sheets, and frozen ground (which includes permafrost), acts as a vast reflective surface. Snow and ice's brilliant white color reflects the incoming solar energy back into the atmosphere (the albedo effect), mitigating the Earth's warming. Additionally, the Arctic Ocean interacts with other oceans, influencing large-scale ocean circulation patterns like the thermohaline circulation, often referred to as the ocean conveyor belt (Skagseth et al., 2008).

As a recipient of heat carried by ocean currents, the Arctic helps modulate weather patterns and climate on a global scale.

This region of immense significance is currently facing the unprecedented threat of climate change.

1.3. The Arctic Ocean in a changing environment

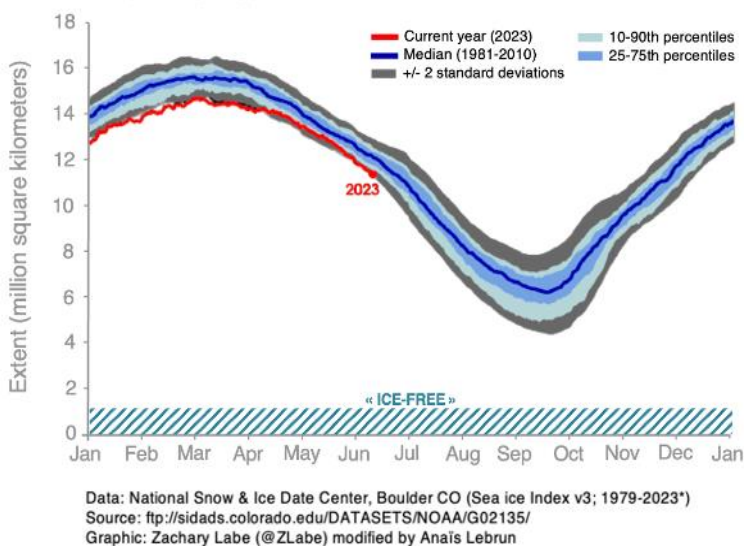
A Surface air temperature anomalies (in °C) from 1950 to 2020 at the Arctic and Global scales compared to the baseline from 1951-1980



< Figure 2: Arctic climate dynamics in (A) temperature and (B) sea ice extent.

The Arctic temperature has warmed at up to four times the rate of the global average since 1979 (Rantanen et al., 2022). Since the beginning of the 20th century, the average air temperature at the surface of the Arctic has increased by about 2 to 3 °C (NOAA data; Fig. 2A). This temperature rise is leading to a decrease in the extent of the Arctic cryosphere, year after year (Fig. 2B). From 1981 to 2010, the average ice extent reached $15.43 \cdot 10^6 \text{ km}^2$ in March and decreased down to $6.41 \cdot 10^6 \text{ km}^2$ in August (Stroeve and Notz, 2018). Niederdrenk and Notz (2018) found that for each degree of warming $1.6 \cdot 10^6 \text{ km}^2$ of sea ice is lost in March and up to 3.3 to $4 \cdot 10^6 \text{ km}^2$ in September.

B Current Arctic sea ice extent in 2023 compared to climatology and 2 standard deviations from the mean



When ice melts, it exposes the underlying seawater or land, which have lower reflectivity, to solar radiation. This leads to increased absorption of solar energy, resulting in stronger warming. Since 1982, the sea surface temperature in ice-free Arctic areas has risen by 1.3 °C

in August (Timmermans 2020). Moreover, sea ice melt releases CO₂ into the climate system, further reinforcing the warming process and accelerating cryosphere melting (Parmentier et al., 2013). It is a self-perpetuating negative feedback loop. This process contributes to what is known as the Arctic amplification, which is responsible for the intensification of warming in this region (Previdi et al., 2021).

The Shared Socioeconomic Pathways (SSPs) climate projections are based on global paths of socioeconomic development and greenhouse gas emissions. Among these pathways, SSP1-2.6 corresponds to socio-economic trajectories assuming a peak in emissions around 2020 followed by a decrease in emissions (Meinshausen et al., 2020). This scenario is now unlikely. The SSP2-4.5 scenario considers a middle-of-the-road development that does not shift markedly from historical patterns. The SSP5-8.5 depicts a more concerning scenario with an energy-intensive economy heavily reliant on fossil fuels. Projected temperature increases for the year 2100 in the Arctic Ocean exceed 2 °C under SSP1-2.6 and 5 °C under SSP5-8.5 (Kwiatkowski et al., 2020).

With warming, the reduction in ice cover, exposing more open water to the atmosphere, facilitates the exchange of gases, including CO₂ (Yamamoto-Kawai et al., 2009). Under the different scenarios, the uptake of anthropogenic carbon in the Arctic Ocean is expected to be multiplied by a factor of 3 under SSP1-2.6, 4 under SSP2-4.5, and 5.5 under SSP5-8.5 between 2000 and 2100 (Terhaar et al., 2021). This increase should amplify ocean acidification in the Arctic Ocean (Fransner et al., 2022). Projections indicate a potential decrease in pH of 0.45 units in the Arctic by the end of the 21st century under SSP5-8.5, which is the most important decline in oceanic pH globally (Terhaar et al., 2021; Fransner et al., 2022). Surface waters of the Arctic Ocean are becoming locally undersaturated with respect to aragonite, which might have serious deleterious effects on the formation of calcium carbonate shells and skeletons of various marine organisms (Yamamoto et al., 2012; Fransner et al., 2022). It is already the case in 20% of the Canadian basin (Robbins et al., 2013).

The melting of the Arctic cryosphere has created unprecedented opportunities for human activities such as shipping, fishing, mining, and resource extraction (Ng et al., 2018). However, amidst these economic prospects, climate change has direct and indirect impacts on the fragile ecosystem of the Arctic and the survival of species living in this region (Wassmann et al., 2010; Michel et al., 2012). These alterations have profound consequences for the

ecosystem that thrives in these waters. In the following sections, specific focus will be directed towards the shallow coastal regions of the Arctic, shedding light on the challenges they encounter.

1.4. The shallow coastal Arctic Ocean

The coastal fringes of the Arctic, where seawater and freshwater from rivers and ice melt converge, are of paramount importance. These regions are influenced by natural processes such as tides, ocean currents and seasonal variations. In particular, glaciers play a crucial role in these areas. Sea ice is also important, although it develops further offshore as well (Thomson et al., 2022). In winter, the absence of sunlight and low temperature lead to an expansion of ice extent. Conversely, summer is marked by longer days, rising temperature, and ice melting.

With the intensification of warming, the effects of melting cryosphere become evident. In Kongsfjorden (Svalbard), sea ice has only been present in the inner part of the fjord since 2007, except for a few exceptions such as in 2009 and 2011 when the entire fjord was frozen (Pavlova et al., 2019). Also, in this area, the retreat of all glaciers has been continuous since 1992 (Svendsen et al., 2002). In the Atlantic Arctic, glacial retreat rates increased by a factor of 3.5 between 1992-2000 and 2000-2010 (from 30.5 to 105.8 m y⁻¹, Carr et al., 2017). The disappearance of ice will lead to both positive and negative effects on the shallow coastal Arctic ecosystem. As ice melts, larger volumes of freshwater flow into the coastal ocean during spring and summer, resulting in stronger local hyposaline conditions and changing underwater light conditions (Fig. 3). On one hand, land ice melting increases water turbidity due to the accompanying sediment inputs (Melsard et al., 2018). In addition, as glaciers, icebergs, and sea ice shield the shoreline against coastal erosion, their melting leads to higher exposure to waves which consequently induces the re-suspension of sediments

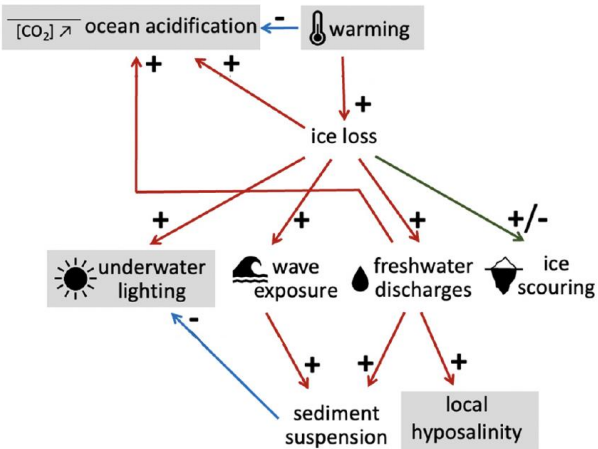


Figure 3: Cascading effects of global change in the shallow coastal Arctic. A plus (+) and a red arrow mean a positive effect, a minus (-) and a blue arrow mean a negative effect, and a (+/-) and a green arrow mean an effect that could be both positive or negative. Simplified from Lebrun et al. (2022)

(Trefry et al., 2009; Barnhart et al., 2014). On the other hand, fewer icebergs and sea ice lead to an increase in light penetration into the water column (Węslawski et al., 2010). Also, glacial retreat induces fewer ice scouring events, which are caused by the passage of icebergs in a shallow area scraping the bottom and damaging the habitat and the organisms therein (Conlan et al., 1998).

With the ongoing warming, the shallow coastal Arctic is projected to experience an increase in the frequency, intensity, and duration of marine heatwave events (MHWs). MHWs occur when the 90th percentile of the corresponding day average sea surface temperature (SST) over the past 30 years is exceeded for five consecutive days or more (Hobday et al., 2016; Golubeva et al., 2021). The shallowness of the coastal areas restricts water circulation and hampers the dissipation of heat, leading to more prolonged exposure to elevated temperature (Varela et al., 2023). Golubeva et al. (2021) revealed that the duration of MHWs extended by 10 to 12 days from 2000 to 2020 in the Kara, Laptev, and Siberian Seas. Also, in ice-free areas, the cumulative intensity of MHWs increased by 0.31 °C per year and per event between 1988 and 2017 (Hu et al., 2020).

All these changes can have profound impacts on marine ecosystems, affecting the distribution and behavior of organisms that inhabit them. In the following section, the focus will be on rocky substrates and the role of seaweed in the dynamics of the coastal Arctic ecosystem. The effects of climate change on its fragile balance will be explored.

2. The coastal Arctic ecosystem: a seaweed-centric view

2.1. Macroalgae are key components of the Arctic coastal ecosystem: focus on kelps

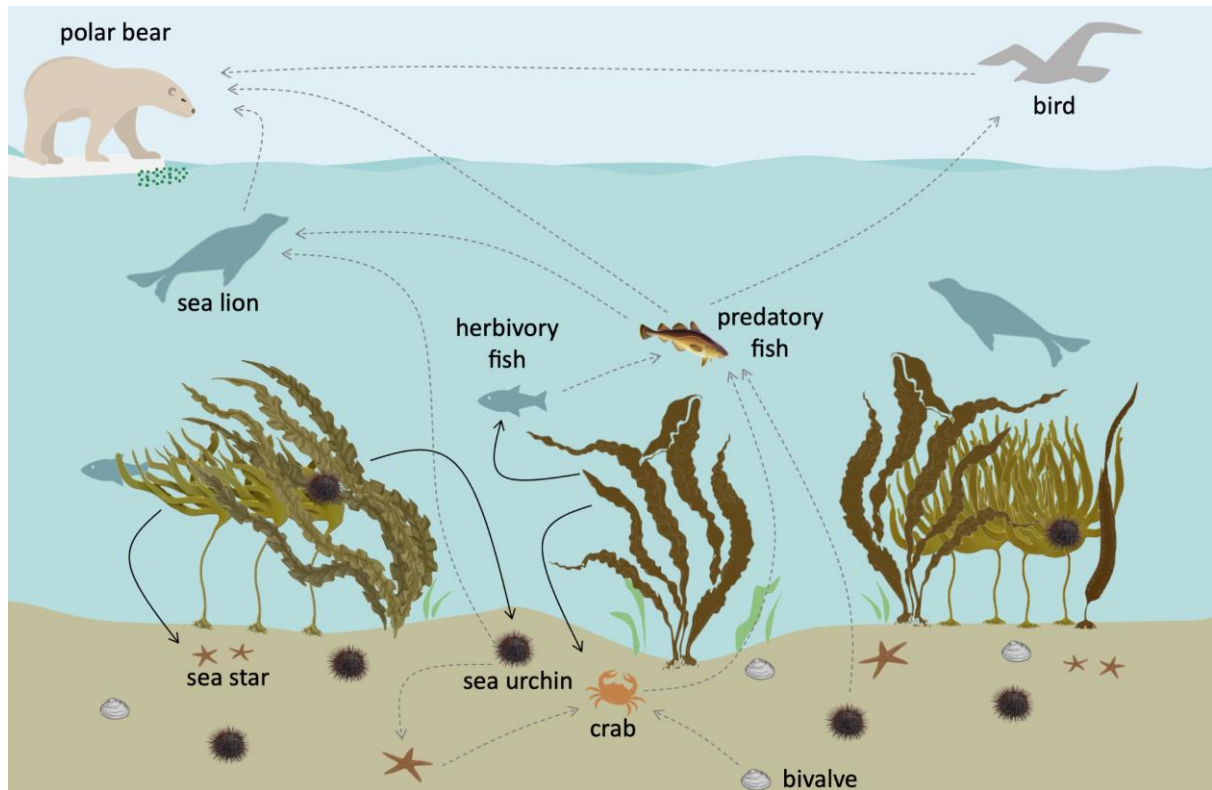


Figure 4: Seaweed-based trophic network in the Arctic.

Black arrows represent direct trophic interactions between seaweeds and other species of this network. Grey dotted arrows represent the other trophic interactions.

Design inspired by Vashon Kelp Forest (vashonkelpforest.com)

Macroalgae intertwine to create complex structures formed by fucus or kelp species that provide essential refuge and breeding grounds for many marine species including fish, crustaceans, mollusks, other macroalgal species such as coralline algae, and juveniles of many marine species (Włodarska-Kowalczyk et al., 2009; Krause-Jensen et al., 2012, Fig. 4). Fucoids are the dominant species in intertidal algal communities, while kelps thrive in the subtidal zone until they reach their low light threshold down to 60 m in some areas (Krause-Jensen et al., 2019). Coralline algae form the understory of kelp forests and can also form rhodolith beds found as deep as 77 m (Jørgensbye and Halfar, 2017). The focus will now be placed solely on kelps and their responses to environmental change. More information about coralline and fucoids can be found in chapter 1.

Kelps are large brown algae forming dense canopy structures known as kelp beds or forests. They consist of a holdfast, a stipe, and one or more blades. Microbial films, sessile colonial

filter feeders (bryozoan, hydrozoan, polychaetes), and mobile herbivores (sea urchins, polychaetes, crustaceans, mollusks) characterize their epiphytic fauna. By altering light, sedimentation, physical abrasion, and bottom currents, kelp forests provide a habitat, food, and nursery area for fish and invertebrates (Filbee-Dexter et al., 2019). Only one species is endemic from the Arctic, *Laminaria solidungula*. The other kelps found in the Arctic from the *Laminaria*, *Saccharina*, and *Alaria* genera, originate from the Atlantic and Pacific Oceans and have extended into subarctic and Arctic waters through the influence of ocean currents and thanks to their important capacity of acclimation to cold-water environments (Wulff et al., 2009). Kelps are important primary producers, contributing significantly to the global carbon cycle (Krause-Jensen and Duarte, 2016). They have a biphasic life cycle with a sporophyte and gametophyte stage.

2.2. Consequences of environmental change on Arctic kelps

Climate change is a pressing global issue that has significant implications for various ecosystems worldwide. In particular, kelp of the Arctic which play a crucial role in the region's marine ecosystems may be affected by warming, ice melting and ocean acidification. In the following section, the consequences of the main Arctic environmental changes on kelp will be addressed. However, not much emphasis will be placed on this issue as it will be thoroughly explored in chapter 1.

2.2.1. Warming

Temperature is a key physical driver in ecosystems, and warming has a profound influence on the distribution of benthic species (Drewnik et al., 2017). Many Arctic kelps are also present in more temperate regions where temperature is higher (Bischoff and Wiencke, 1993). Although they can grow in the Arctic, their temperature optima are often well above the average temperature in this region. Warming may have both positive and negative impacts on macroalgal species. While it can enhance growth, photosynthesis, germination, and fertility of, for example, *Saccharina latissima* and *Laminaria hyperborea*, excessively high temperature can negatively affect spore settlement, gametophyte growth rate, and the recruitment of certain kelp species like the endemic species *Laminaria solidungula* (Filbee-Dexter et al., 2019; Goldsmit et al., 2021).

In addition to warming, kelps may be affected by MHWs that are becoming longer, more intense, and more frequent. These extreme temperature events could further impact their photosynthetic performance and overall fitness (Golubeva et al., 2021). However, the effects of MHWs on Arctic kelps have received limited research attention (see Chapter 3).

2.2.2. Hyposalinity

Local hyposaline conditions are expected to intensify due to increased river runoff, ice melt, and precipitation. Salinity plays a vital role in the photophysiology and distribution of kelp species (Diehl et al., 2020; Li et al., 2020). When exposed to low salinity (25) combined with elevated temperature (up to 15 °C), the maximum quantum yield of photosystem II (F_v/F_m), which provides insights into the photosynthetic efficiency, of *Laminaria solidungula* significantly decreases (Diehl et al., 2020). Additionally, changing salinity conditions also contribute to reduced photosynthetic efficiency (Karsten 2007; Spurkland and Iken 2011). As a result, a local decrease in salinity could significantly affect kelp fitness by limiting their ability to photosynthesize (e.g., Traiger and Konar 2018; Filbee-Dexter et al., 2019). Overall, the influx of freshwater is expected to have an overall negative impact on Arctic kelps, leading to impaired performance.

2.2.3. Changes in underwater light

Underwater light plays a crucial role in shaping macroalgal-dominated ecosystems. It significantly influences primary production, photoperiod-dependent reproduction, and the spatial distribution of macroalgae (Bird and McLachlan, 1976; Martins et al., 2022). Climate change-related processes, such as sea ice cover reduction, increased water turbidity, and variations in cloudiness, have implications for underwater light conditions in the Arctic Ocean (Bélanger et al., 2013). Higher turbidity near glaciers and rivers can limit the vertical distribution of macroalgae, while the disappearance of the ice shadow resulting from sea-ice shrinking can promote the expansion of macroalgal species (Wiencke and Hop, 2016). Climate change is also influencing ultraviolet radiation (UVR) penetration, increasing its intensity and penetration depth. UVR can negatively impact kelp particularly during vulnerable life stages like spores and gametophytes (Roleda et al., 2007). However, kelp exhibit various photoprotection strategies and DNA damage repair mechanisms to mitigate the harmful effects of UVR (Wiencke and Hop, 2016).

2.2.4. Seabed habitat: less ice-scouring but more sedimentation

As glaciers continue to melt, the rise in ice scouring is followed by a subsequent decline as the glaciers no longer reach the sea. The reduction in ice scouring creates favorable conditions for species expansion at shallow depth, promoting species interactions and supporting a more stable and biologically regulated development of communities (Weslawski et al., 2010; Scherrer et al., 2019).

However, the reduction in sea ice cover, accompanied by rising sea level and increasing surface air and permafrost temperature, is already accelerating the erosion of Arctic coastlines (Nielsen et al., 2022). Moreover, the occurrence and severity of extreme events, including sediment slides and storms, are projected to increase, leading to more frequent and intense episodes of high sedimentation and coastal erosion (Müller et al., 2009; Kędra et al., 2010). The deposition of sediment layers on algae leads to reduced light penetration, limiting photosynthesis, and degrades the settling conditions for the algae and their associated communities (Teichert et al., 2014). These ongoing changes will inevitably influence the distribution of benthic macroalgal communities in both the short and long terms.

2.2.5. Ocean acidification

Acidification can affect kelp growth, photosynthesis, and nutrient uptake (Iñiguez et al., 2016, Wiencke and Hop, 2016). Kelp species could benefit from additional dissolved CO₂ that can enhance photosynthesis and growth but are likely to be already dissolved inorganic carbon (DIC) limited thanks to efficient CO₂ concentrating mechanisms (CCMs; Comeau and Cornwall, 2016; Iñiguez et al., 2016). Also, potential positive effects may be offset by other factors such as nutrient availability, temperature, and competition with other organisms.

The preceding sections highlighted the various factors affecting Arctic kelp, including warming, hyposalinity, changes in PAR, alterations in seabed habitat, and ocean acidification. These environmental changes have the potential to significantly impact the distribution and dynamics of kelp communities. In the following section, the objectives of this study and its different chapters will be delved into.

Part 2: Objectives of the thesis and presentation of the chapters

This thesis has been conducted within the framework of the EU Horizon 2020 project FACE-IT (the Future of Arctic Coastal Ecosystem - Identifying Transitions in fjord systems and adjacent coastal areas) which aims to enable adaptive co-management of social-ecological fjord systems in the Arctic in the face of rapid cryosphere and biodiversity changes. The objectives of this project are (1) to identify and quantify key drivers of biodiversity changes and their past and future trends, (2) to identify cascading effects of changing biodiversity associated with ongoing and projected changes in Arctic coastal food webs, (3) to assess the interdependencies between environmental changes and Arctic coastal livelihoods and (4) to support adaptive co-management at the local and national levels.

Within this broad context, the main focus of this thesis is to analyze the effects of climate change on shallow Arctic benthic communities, in particular kelp forests that host high biodiversity. This thesis focuses on the study of the effects of warming, encompassing decreasing underwater irradiance and summer hyposalinity resulting from ice melt, as well as the increase of MHWs events. While acidification influences kelp dynamics, we have considered that the aforementioned factors may have predominant impacts. Additionally, there has been limited research on the response of kelp to the intricate array of factors associated with ice melting and to MHWs.

This work includes four central research questions, each shedding light on the effects of environmental changes on coastal Arctic benthic communities.

- 1) What is the state of the current knowledge on the response of Arctic macroalgae to ongoing and projected environmental changes? (Chapter 1)
- 2) How will Arctic kelps respond to the direct effects of climate change?
 - a) How will Arctic kelps respond to the combined effects of turbid freshwater inputs from ice melting and warming? (Chapter 2)
 - b) What are the impacts of MHWs on Arctic kelp physiology and their associated species? (Chapter 3)
- 3) How do environmental factors influence the diversity patterns of Arctic coastal benthic communities? (Chapter 4)

This thesis is the fruit of a multidisciplinary approach combining *in situ* studies, mesocosm experiments, and laboratory analyses, that was supported by international collaborations with scientists from Norway, Germany, the USA, and China.

The first chapter presents a thorough review of the documented responses of Arctic macroalgal species to climate change, encompassing key habitat-forming species such as fucoids, kelps, and coralline algae. This literature review incorporates findings from both *in situ* field studies and laboratory analyses, enabling a comprehensive overview of the past and projected effects of climate change on these species. Specific attention is given to the effects of seawater warming and ice melt, which are prominent consequences of climate change in the Arctic coastal region. This chapter set the foundation and motivated the subsequent research conducted in this thesis.

The second chapter presents a mesocosm experiment conducted over a period of two months in Ny-Ålesund (Svalbard) to study the combined effects of warming, hyposalinity, and reduced irradiance on kelps. This experimental approach provided the opportunity to simulate conditions as close as possible to present and future conditions while ensuring precise control and monitoring of the key variables under investigation. We hypothesized that warming in the Arctic will enhance the growth rate of non-endemic kelp species. We also hypothesized that the combination of low salinity and low irradiance will negatively impact the physiology of kelps.

This mesocosm approach was also used in the **third chapter** for which the focus was to examine the effects of warming and MHWs on kelp and their associated community including fauna and coralline algae. We hypothesized that kelp community organisms display great acclimation to warming. Also, our hypothesis posited that kelp exhibits species-specific physiological responses to MHWs.

For the **fourth chapter**, the aim was to characterize the benthic community along the salinity and light gradient found during ice melt in summer in a glacier-surrounded fjord. Specifically, a link between biodiversity and environmental conditions was sought. Our hypothesis was that the distribution of benthic organisms is impacted by the gradient of light and salinity. In particular, we hypothesized that the distribution of macroalgae follows the light gradient and that of suspension feeders follows the salinity gradient, associated with a nutrient gradient.

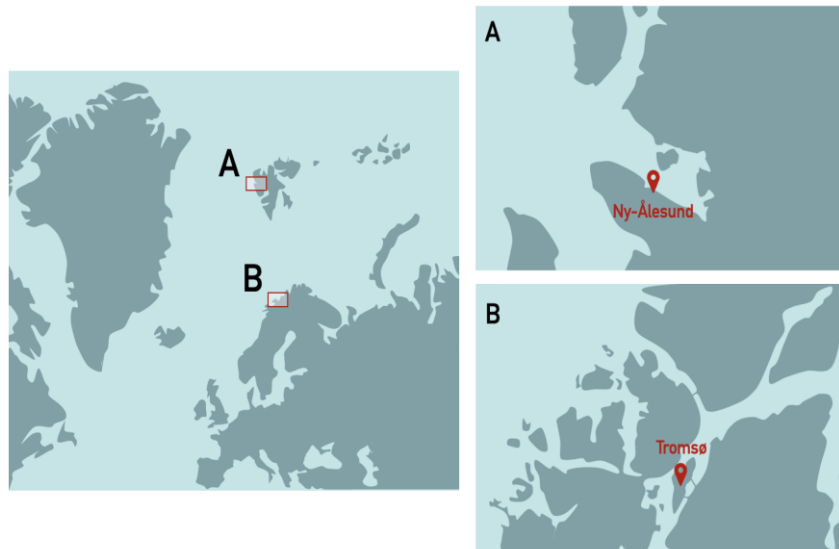
In situ investigations were conducted to examine the current environmental conditions and benthic biodiversity using environmental DNA (eDNA) (see Part 3, 3.1).

Part 3: Main methods used during this thesis

1. Study sites

Figure 5: > Field sites investigated in this thesis: (A) Kongsfjorden (Svalbard, Norway) and (B) the fjords near Tromsø (Norway).

In the context of this thesis, two field sites were investigated: Kongsfjorden and Tromsø area (Fig. 5).



Kongsfjorden (79°N, 12°E, Fig. 5A) is located on the west coast of Spitsbergen in Svalbard (Fig. 5A). Stretching approximately 26 km long, it is surrounded by towering mountains and glaciers making it an ideal location for studying warming and ice melting and its impact on Arctic marine ecosystems (Chapters 2 and 4). Some glaciers terminate in the sea, namely tidewater glaciers, such as Kronebreen and Kongsvegen. The fjord is influenced by both Arctic waters conveyed by the Spitsbergen Polar Current and Atlantic warm waters carried by the West Spitsbergen Current (De Rovere et al., 2022). However, the inflow of water is limited in the inner part of the fjord due to the presence of a sill. In the outer portion of the fjord, the maximum depth is nearly 400 m, while after the sill the depth gradually ascends to less than 100 m (Promińska et al., 2017). In winter, the fjord's surface can freeze (see previously, only in the inner part since 2007 with few exceptions). In summer, the top layer of water warms up, reaching 4 to 6 °C.

The strategic location of Ny-Ålesund, coupled with its relatively easy access, makes it an ideal site for investigating Arctic ecosystems and studying the impacts of climate change.

The second field site investigated in this thesis encompasses the surroundings of Tromsø (69.7°N, 19°E, Fig. 5B). This area benefits from the influence of the Gulf Stream that flows

along the nearby Norwegian coastline, creating relatively milder conditions compared to the high Arctic (Mörner et al., 2020). The surface temperature usually ranges from 3-4 °C in winter to 11 °C in summer (NOAA, OISST data). There are no glaciers around Tromsø terminating in the sea. However, this area is subjected to MHWs, which is the focus of chapter 3.

2. Mesocosm experiments

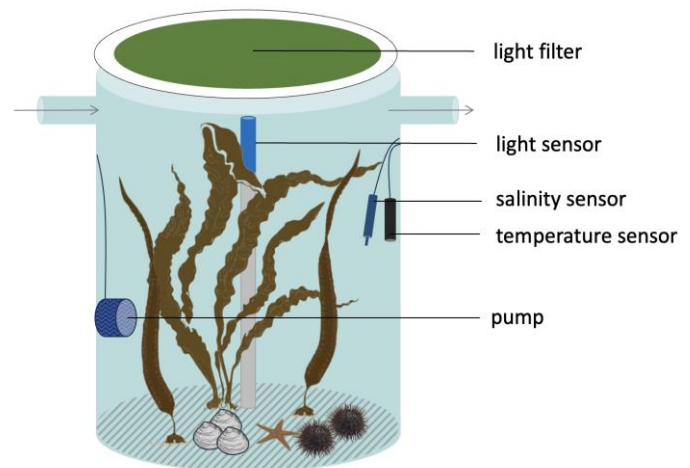
Figure 6: >

A mesocosm and its sensor system (light, salinity and temperature sensors).

Mesocosm experiments aim to recreate the intricate ecological interactions and dynamics observed in the natural environment. Within each mesocosm, a representative selection of species from the targeted community is introduced. This type of experimentation is

increasingly prominent in the ecological climate-change literature (Stewart et al., 2013). Mesocosm experiments offer an important bridge between smaller, tightly controlled microcosm experiments, which may be limited in their realism, and the intricate biological complexity found *in situ*, where identifying mechanistic relationships is challenging (Stewart et al., 2013). The responses of organisms, including changes in growth, metabolism, reproduction, behavior, and interactions, can be monitored and analyzed throughout the duration of the experiment. These experiments also provide the opportunity for observations and measurements over several months, challenging to perform *in situ*, especially in the Arctic, and often missing in the scientific literature. Considering the gaps of knowledge on Arctic marine ecosystems and their responses to climate change, this approach can provide valuable information on complex dynamics and ecological processes and has therefore been used in the present work.

We used 1 m³ tanks that were filled with kelp species commonly found in the Arctic: *Saccharina latissima*, *Alaria esculenta*, and *Laminaria digitata* together with their associated fauna. The regulated flow-through system allowed for controlling temperature and salinity. The mesocosms were equipped with a sophisticated control system that enabled precise regulation of these variables. The temperature was adjusted by mixing ambient seawater with



warmed seawater and salinity was regulated by the addition of freshwater. Each mesocosm was equipped with a wave pump to ensure proper mixing of the water. Light filters were also added on the top of the mesocosm, to reproduce and/or decrease the *in situ* light spectrum at collection depth.

In chapter 2, our objective was to explore the synergistic impacts of warming and ice melting on kelp communities. We achieved this by elevating temperature, reducing salinity, and limiting light exposure in the mesocosms. Chapter 3, on the other hand, focused on investigating the effects of warming and MHWs on kelp communities. For this purpose, we raised temperature and simulated MHWs. During both studies, we monitored key physiological parameters such as chlorophyll *a* concentration, C:N and growth. Additional details can be found in respective chapters.

3. Gradient approach

In summer, the glacier melting and increased river runoff lead to a significant local decrease in salinity and underwater light. In Kongsfjorden, glaciers and rivers are mainly situated in the inner part of the fjord. Hence, as the glaciers and snow melt, a gradient of salinity and light is established between the inner and outer parts of the fjord, where waters are more saline and less turbid. With warming, the increase in river runoff and glacier melting is expected to expand turbid and less saline waters further into the fjord, impacting kelp communities. Understanding the actual distribution of these communities along the gradient could provide important information to project future distribution patterns. Chapter 4 focuses on finding potential links between biodiversity and environmental conditions. We conducted environmental parameter measurements coupled with diversity analysis using environmental DNA. *In-situ* eDNA is an innovative approach that allows for the detection and identification of species based on the DNA left in their environment (Rees et al., 2014). This technique has revolutionized biodiversity assessment and ecological monitoring, providing a non-invasive and highly sensitive method for species detection. The concept behind *in situ* eDNA revolves around the fact that organisms shed DNA into their surroundings through various biological materials such as skin cells, feces, mucus, or even pollen. This DNA can persist in the environment, offering a trace of the species' presence even when direct observations are challenging or impossible. The first step is to collect environmental samples such as water, soil, or air from the target habitat (Fig.7, step 1). A single liter of seawater can be used to

detect species of benthic invertebrates, plankton, and mammals (Kelly et al., 2019). Water samples are filtered on a specific filter on which the DNA will settle (Fig. 7, step 2). DNA extraction is performed to isolate this genetic material, followed by the amplification and sequencing of specific DNA regions of interest (Fig. 7, steps 3 and 4). Once the DNA is sequenced (Fig. 7, step 5), bioinformatics tools are employed to compare the obtained sequences with reference databases containing the known genetic information of various species (Fig. 7, step 6). By matching the eDNA sequences to those in the database, we can identify the species present in the sampled environment (Fig. 7, step 7).

In situ, eDNA has numerous applications in ecological research and conservation. It enables the detection of cryptic species that are otherwise difficult to study directly. It can also provide valuable information about the distribution and diversity of a community within a particular habitat, not without limitations, as discussed in chapter 4.

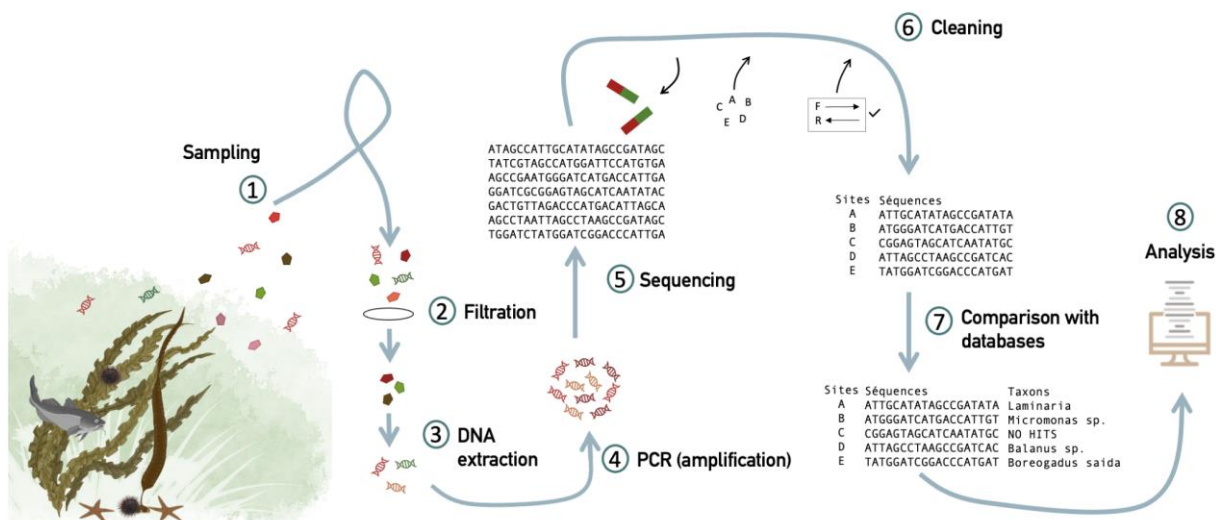


Figure 7: Key steps of eDNA analysis

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Chapter 1: Impact of climate change on Arctic macroalgal communities

Anais Lebrun¹, Steeve Comeau¹, Frédéric Gazeau¹, Jean-Pierre Gattuso^{1,2}

¹ Sorbonne Université, CNRS, Laboratoire d'Océanographie de Villefranche, 06230 Villefranche-sur-Mer, France

² Institute for Sustainable Development and International Relations, Science Po, Paris, France

This review article has been published in *Global and Planetary Change* in november 2022.

doi: 10.1016/j.gloplacha.2022.103980

Abstract

The Arctic region faces a warming rate that is more than twice the global average. Sea-ice loss, increase in precipitation and freshwater discharge, changes in underwater light, and amplification of ocean acidification modify benthic habitats and the communities they host. Here, we synthesize existing information on the impacts of climate change on the macroalgal communities of Arctic coasts. We review the short- and long-term changes in environmental characteristics of shallow hard-bottomed Arctic coasts, the floristics of Arctic macroalgae (description, distribution, life-cycle, adaptations), the responses of their biological and ecological processes to climate change, the resulting winning and losing species, and the effects on ecosystem functioning. The focus of this review is on furoid species, kelps, and coralline algae which are key ecosystem engineers in hard-bottom shallow areas of the Arctic, providing food, substrate, shelter, and nursery ground for many species. Changes in seasonality, benthic functional diversity, food-web structure, and carbon cycle are already occurring and are reshaping Arctic benthic ecosystems. Shallow communities are projected to shift from invertebrate- to algal-dominated communities. Furoid and several kelp species are expected to largely spread and dominate the area with possible extinctions of native species. A considerable amount of functional diversity could be lost impacting the processing of land-derived nutrients and organic matter and significantly altering trophic structure and energy flow up to the apex consumers. However, many factors are not well understood yet, making it difficult to appreciate the current situation and predict the future coastal Arctic ecosystem.

Efforts must be made to improve knowledge in key regions with proper seasonal coverage, taking into account interactions between stressors and across species.

1. Introduction

The Arctic Ocean and its surrounding waters contain less than 1% of the global ocean volume but comprise 25% of the world's continental shelves (Jakobsson et al., 2004). It includes the Barents and Bering Seas north of the Arctic circle, the Eurasian shelves of the Kara and Laptev seas, the Siberian coast of the Beaufort Sea, the Canadian Archipelago, Greenland, and the Chukchi Sea (Piepenburg, 2005). This ocean receives 11% of the global runoff (Shiklomanov, 1998) and is responsible for 7-10% of the global burial of organic carbon (Stein and MacDonald, 2004).

The Arctic region is warming at a rate that is more than twice that of the global average (Richter-Menge et al., 2017). From 1982 to 2017, the sea surface temperature in ice-free regions increased by 0.5 °C per decade, and it is expected to rise by 2 to 5 °C over the next 80 years, under SSP1-2.6 and SSP5-8.5 respectively (Kwiatkowski et al., 2020). With a current 10% decrease in sea ice extent per decade, the Arctic could face an ice-free summer as early as 2035 (Notz and Community, 2020). The decrease in albedo arising from the melting of sea ice and snow leads to an exacerbation of global change in this region, referred to as polar amplification (Chapman and Walsh, 1993). In addition to sea-ice loss, climate change involves increases in precipitation and freshwater discharge, changes in underwater light, and amplification of ocean acidification (pH decrease of 0.18 to 0.45 on the Arctic basin scale by 2100, vs 0.06 to 0.32 units on the global scale; Steinacher et al., 2009; Terhaar et al., 2021). All these processes modify marine habitats and the communities they host (Duarte et al., 2012; Kortsch et al., 2012). The structure and function of Arctic marine ecosystems are, thus, foreseen to change dramatically (Renaud et al., 2019). Footprints of current global change are already visible in marine Arctic ecosystems (Wassmann et al., 2011). The Arctic shelves are likely to be especially vulnerable due to their shallow depth and seasonally shifting ice cover (Piepenburg, 2005).

Macroalgal benthic communities are an essential component of hard-bottomed shallow water ecosystems in the Arctic. Furoid species and kelps are large brown seaweeds that can dominate arctic rocky intertidal and subtidal areas and exhibit a high biomass (Hop et al., 2012;

Iñiguez et al., 2016a; Ronowicz et al., 2020). Providing a food source, substrate, sheltered area, and nursery for many species (Filbee-Dexter et al., 2019), they are hotspots of Arctic marine biodiversity (Włodarska-Kowalczyk et al., 2009; Krause-Jensen et al., 2012). Furoid and kelps play an important role in the transfer of carbon (Filbee-Dexter et al., 2020; Lewis, 2020) through high production, export of dissolved organic matter and detritus, as well as carbon sequestration (Krause-Jensen and Duarte, 2016).

Coralline algae are other important ecosystem engineers in the Arctic (Teichert et al., 2014). These long-lived species (up to 1200-1600 years for individuals found in the North Pacific and the Labrador Sea; Adey et al., 2015) can form crusts or rhodolith beds that host important biodiversity (Teichert et al., 2014). Despite relatively low annual growth rates, coralline algae have a high potential for calcium carbonate accumulation (Freiwald and Henrich, 1994) providing a three-dimensional habitat dominated by vagile invertebrates (Teichert et al., 2014). Rhodolith beds are an important part of the prevailing coastal ecosystem and the biofilms on their surface represent a major food source for many grazing organisms (Steneck, 1990).

Furoid species, kelp forests, rhodolith beds and their associated flora and fauna make up the hard-substrate benthic communities of the Arctic coasts. With global change, a general expansion of both native and non-native kelp species has been documented during the last decades (Weslawski et al., 2010; Kortsch et al., 2012; Bartsch et al., 2016). Warmer waters and longer sea-ice-free periods may favour kelps growth, reproduction, and survival (Krause-Jensen and Duarte, 2016). Fucoids are also spreading in the Arctic with a coverage that has already doubled and may triple by the end of the century (Jueterbock et al., 2016; Weslawski et al., 2010). The current and projected expansion of kelp forests and Furoid species will exert cascading effects on the composition and functioning of shallow coastal Arctic ecosystems (Krause-Jensen et al., 2012). Arctic calcified algae distribution will be constrained by the upper temperature limit in the South and by calcium carbonate saturation state in the North (Steinacher et al., 2009; Chan et al., 2020). Furthermore, warming and increased advection are causing poleward migration, bringing thermally tolerant boreal-subarctic species that compete with local species adapted to cold waters (Weslawski et al., 2010). Shifts in species distribution, abundance and performance are therefore foreseen (Wiencke and Amsler, 2012; Traiger and Konar, 2018). These changes are expected to alter carbon cycling as well as the

timing and magnitude of benthic primary production (Grebmeier et al., 2006; Scherrer et al., 2019).

2. Methods

The objectives of the present study are: (1) to gather and synthesize existing information in order to provide an overview of potential impacts of climate change on the macroalgae communities of Arctic coasts and (2) to highlight knowledge gaps on species, ecological process or sub-regions of the Arctic. We explored for shallow and hard-bottomed Arctic coasts, the short- and long-term changes in environmental characteristics, species responses through biological processes, the resulting winning and losing taxa and the impacts on ecosystem functioning. Relevant articles were searched on “ISI Web of Science” and “GoogleScholar” using a Boolean search string ‘Benthos AND Arctic AND change’, ‘Benthos AND Arctic AND climate’, ‘Benthic AND Arctic AND change’, ‘Benthic AND Arctic AND climate’, ‘Kelp AND Arctic AND change’, ‘Kelp AND Arctic AND climate’, ‘Furoid AND Arctic AND change’, ‘Furoid AND Arctic AND climate’, ‘Coralline AND Arctic AND change’, ‘Coralline AND Arctic AND climate’ (database searches completed on 2022-09-24). A total of 91 papers were identified. The online tool “connectedpapers” (connectedpapers.com) was used to explore related studies; it returned 28 additional papers. An article was considered as ‘relevant’ if the study focused on the impact of climate change - using one or more environmental parameters (e.g., temperature, salinity, light) - on Arctic macroalgal communities (up to 77 m depth, which is the depth at which the deepest coralline algae are described in the studies analyzed here) - whether on a single species or a community (furoids, kelps or coralline algae). Potentially relevant articles not written in English were not considered. Each relevant article was tagged as an “*in situ*” study (i.e., conducted in the field) or “*ex situ*” study (i.e., conducted in the laboratory). Both or none of these tags could be assigned as appropriate, for example for broad review articles and modeling exercises. The references are listed in Table S1.

3. Bibliometric analysis

Until 20 years ago, only a limited number of studies have been conducted to assess how marine macroalgae communities respond to global change in the Arctic (Fig. 8). The number of *ex situ* and *in situ* studies started rising in the mid 1990s to reach a total of 53 and 54 studies respectively in 2022. Aside from studies conducted along Russian coastlines that have not

been translated into English and assessed here, *in situ* research has been carried out over the whole Arctic region (Fig. 9A). However, only a small portion of the Arctic coastlines has been studied; more than half of the papers report research conducted in Svalbard, with a particular emphasis on Kongsfjorden (Fig. 9B).

4. Shallow hard-bottomed Arctic characteristics: past, present, and future

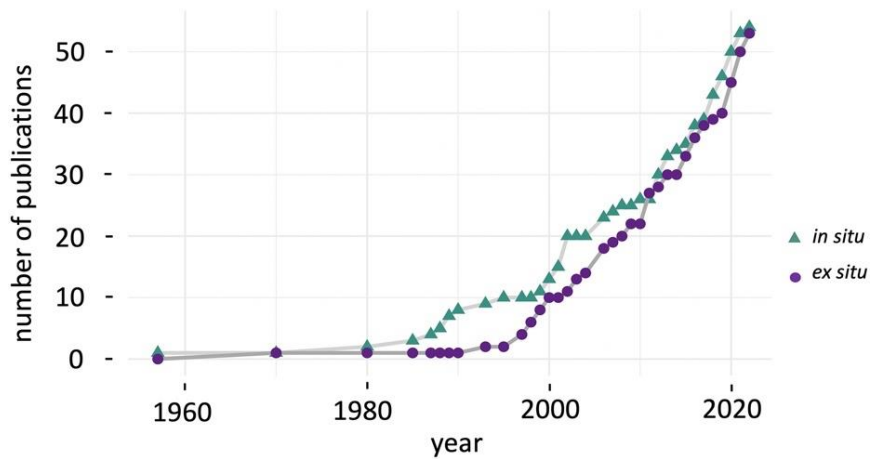


Figure 8: Cumulative number of scientific papers focusing on the impact of global change on macroalgal communities through both *ex situ* and *in situ* studies in the Arctic since 1957

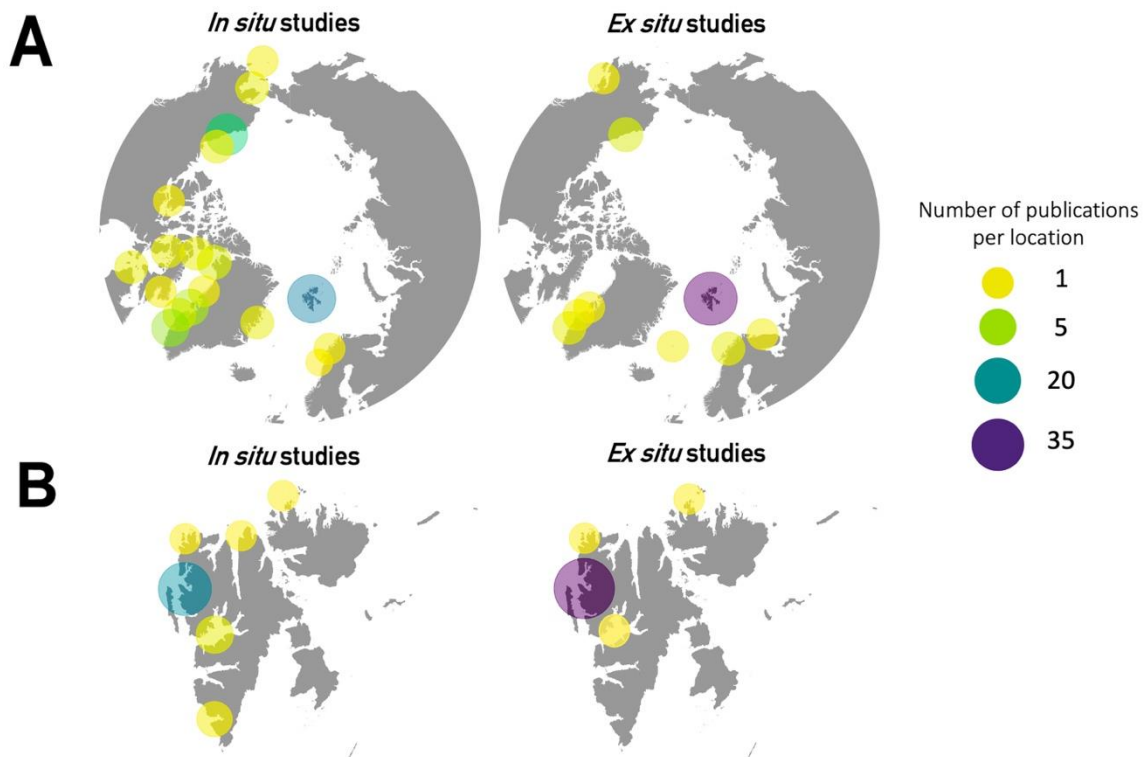


Figure 9: Number of *in situ* and *ex situ* studies per location. A) whole Arctic region, B) focus on the Svalbard coast.

3.1. Seasonality

Arctic coastal environments are characterized by strong seasonal changes in photosynthetically active radiation (PAR). In spring, daylight lengthens, temperature increases and ice begins to melt. Thawing land and sea ice decrease salinity and affect the light regime afterwards by delivering dissolved and particulate matter which increases turbidity (Fig. 10, Fig. 11). In winter, the daylight period shortens, temperature decreases, and sea and land ice form. These marked seasonal fluctuations strongly influence biological processes and marine ecosystems (Kędra et al., 2015). In particular, the vertical zonation and productivity in shallow Arctic coastal areas are controlled by fluctuating salinity, turbidity, sea-ice shading, available organic matter, ice scouring, and sedimentation rate (e.g., Conlan et al., 1998; Włodarska-Kowalczyk and Pearson, 2004).

Environmental changes impact seasonality. For all regions of the Arctic Ocean, an increase in the duration of the open water period is underway, ranging from 3.9 to 13.8 days per decade (Bliss et al., 2019). Warming induces earlier and more intense ice melt with an increase in meltwater runoff and flux of particles in spring (Fig. 11; Svendsen et al., 1996). It is projected that this will strongly affect biological diversity in Arctic fjords (e.g., Jørgensen et al., 1999; Wassmann et al., 2011). On the one hand, a shorter ice season, a smaller ice-covered area and a reduction in ice thickness reduce ice-related pressures such as ice shading or ice scouring on shallow benthic communities (Wesławski et al., 2010). On the other hand, the associated increase in turbidity will restrict the euphotic layer and will enhance local hyposalinity and coastal siltation (Węśławski et al., 2011; Bartsch et al., 2016). As a result, species expansion and primary production may be more constrained near meltwater outflows, but less further away (Hopwood et al., 2020).

3.2. Habitat and pulse disturbances

The habitat, especially the bottom structure and exposure to disturbances, are regulating factors and key elements in the structuring of benthic ecosystems (Yesson et al., 2015). Erosion, as well as river and glacial runoff, supply large amounts of sediments in coastal areas. Hard-bottom substrates only represent ca. 35% of the Arctic coasts (Lantuit et al., 2012; Filbee-Dexter et al., 2019).

As ice protects the shoreline from coastal erosion, a longer period of wave exposure is anticipated as a result of the shortening of the ice-covered season. This will lead to a considerable increase in resuspended sediments (Fig. 10a and 11; Trefry et al., 2009), a coarser sediment structure, and significant changes in community composition (Weslawski et al., 2010). Unstable substrate and fine sediment are resulting in a patchy distribution of rhodolith beds in Svalbard (Teichert et al., 2014).

During storm events, the increase in the frequency and intensity of waves leads to coastal soil erosion. In the fall and winter, seasonal storms produce detritus by detaching living seaweed from the bottom, enabling the long-term survival of benthic organisms without phytoplankton or ice algae supply in polar winter (Mincks et al., 2008; Morata et al., 2020). This accumulation of detritus due to storm events makes the Arctic food web more stable and increases its persistence over the course of the year (Kędra et al., 2012). Storms also induce the accumulation of unattached and uncemented coralline algal banks forming rhodolith beds (see section 5.3, Freiwald and Henrich, 1994).

Disturbance is an important driver of spatio-temporal biotic patterns, increasing the patchiness of benthic biomass (Gutt, 2001). Beyond coastal erosion, ice scouring and high sedimentation rate are major disturbances in glacial bays (Clark et al., 2015). Ice scouring is caused by the passage of an iceberg in a shallow area scraping the bottom and damaging the habitat and the organisms therein (Fig. 10b). High sedimentation rate is due to a huge discharge of meltwater, diluting organic matter, increasing turbidity, reducing primary production, hindering recruitment, obstructing filtering appendages and even burying bottom dwellers (Hall, 1994). Due to repeated exposure to disturbance events, the size of organisms and the complexity of the community structure both decrease when getting closer to the glacier (Włodarska-Kowalczyk and Pearson, 2004). Additionally, the faunal biomass in the macroalgal belt exhibits greater spatial and temporal variability at shallow depths revealing a fragmentation of the community by patches, such as at Hansnest (Kongsfjorden, Svalbard), down to 5 m, which indicates recurrent disturbance at various spatio-temporal scales (Paar et al., 2016).

The recolonization rate after a pulse disturbance is low in the Arctic (Al-Habahbeh et al., 2020) and the removal of a large portion of the initial biomass typically favors the establishment of early succession stages (Conlan et al., 1998). The pulse-disturbed hard bottom area is first

colonized by algae and opportunistic taxa such as hydrozoans and small chitons. Then, larger and longer-lived taxa such as barnacles, colonial sponges, or ascidians slowly overtake the area (Al-Habahbeh et al., 2020). With increasing distance to the disturbed area, trophic structure becomes more complex and biomass and diversity increase (Włodarska-Kowalczyk et al., 2005).

As glaciers thin and melt, ice scouring will become more frequent in the short-term, but less in the long-term, then promoting species interactions and leading to more stable and biologically controlled community development (Fig. 11; Weslawski et al., 2010; Bartsch et al., 2016). Reduced ice scouring will favor species expansion at shallow depths (Paar et al., 2016; Scherrer et al., 2019). However, reducing sea ice cover, sea level rise, and rising surface air and permafrost temperatures are already accelerating erosion of Arctic coastlines (Nielsen et al., 2022). Furthermore, the occurrence and severity of extreme events such as sediment slides and storms are projected to rise, increasing both the intensity and frequency of high sedimentation events and coastal erosion (Müller et al., 2009; Kędra et al., 2010). Deposit of a sediment layer on the algae and its surroundings will degrade settling conditions for the algae and its associated community (Teichert et al., 2014). The associated increase in turbidity will negatively impact growth and survival of macroalgae (see section 6.2). This will inevitably have consequences on the distribution of macroalgal benthic communities.

5. Arctic macroalgae: characteristics, distributions and ecological role

Fucoid species, kelps, and coralline algae are key species of hard-bottomed coastal ecosystems in the Arctic. Fucoids dominate intertidal algal assemblages, while kelps dominate the subtidal domain until they reach their low light threshold. The deepest kelps have been recorded at 61 m depth in the Disko Bay region (Greenland, Krause-Jensen et al., 2019). Coralline algae form the understory of kelp forests and are found down to 77 m depth (Jørgensbye and Halfar, 2017).

5.1. Fucoids

In the intertidal coasts of the Arctic, seaweed diversity is low and dominated by fucoids that can experience changes in a multitude of abiotic drivers including ice scouring, desiccation, UV radiation, and wave exposure. Fucales are an order of intertidal brown algae that inhabit a broad range of habitats from exposed rocky shores to calm bays and estuaries making this

order one of the most abundant group of organisms of intertidal rocky shores in the Northern Hemisphere (Lüning, 1991; Kucera and Saunders, 2008). Native to the North Pacific Ocean, fucoids have radiated in the North Atlantic Ocean (Coyer et al., 2006) resulting in a few common species such as *Fucus spiralis*, *F. vesiculosus*, *F. serratus*, and *F. distichus*. The latter is a homothallic cold-adapted species (Coyer et al., 2006; Jueterbock et al., 2016). They are important ecosystem engineers forming wide coastal belts in Greenland, Jan Mayen, Norway, Svalbard, Baffin Island, and Alaska (Smolina et al., 2016). They are a food source, substratum and shelter for epiphytic and epibenthic communities with high species richness (including crustacean, snails and polychaetes) preventing them from desiccation when the tide is low (Ingólfsson, 2008). Brown (*Dictyosiphon foeniculaceus*, *Stictyosiphon tortilis*, *Pylaiella littoralis*) and green algae (*Urococcus foslieanus*, *Ulothrix flacca*, *Acrosiphonia arcta* and *Prasiola crispa*) constitute the understory of fucales canopy (Wulff et al., 2009).

A fucale individual is composed of three parts: (1) a holdfast, a root-like structure that anchors the individual to the substrate, (2) a short stipe, a stem-like structure that allows the algae to sway in currents; and (3) a frond —or blade— leaf structure(s) that actively participates in photosynthesis. The frond is flattened, more or less dichotomously branched, and can contain air bladders and reproductive extremities when fertile. Fucales can reproduce both asexually by fragmentation or sexually. Once fertile, sporophytes release sperm and/or eggs from their conceptacles. Fertilization takes place and results in a zygote which settles on a hard substrate, germinates and forms a new sporophyte. The release usually happens at low tide, when there is little water motion, favouring gamete meeting but limiting dispersal (Schoenwaelder et al., 2003). Effective dispersal is however possible for homothallic fucale since only one rafting individual is enough to establish a new population by self-fertilization (Jueterbock et al., 2016). Through thalli dislodgement and receptacle release, fucoids are important contributors to carbon production as they can exhibit annual rates of production equal to that of kelps (Lewis, 2020).

5.2. Kelps

Kelps are large brown algae found in subtidal cool waters, close to the shore and forming dense canopy called kelp beds or kelp forests (Bolton, 2010). Although the term "kelp" frequently refers to large canopy-forming brown algae species (and will be used as-well in that sense in this study), in its strictest sense, the term refers to the order Laminariales (Bolton,

2010; Teagle et al., 2017). Like fucoids, they comprise three parts: a holdfast, a strong and flexible stipe and one or several blades.

Kelps have a biphasic life cycle characterized by the alternation of an asexual sporophyte and a sexual gametophyte stage (Roleda, 2016). A fertile sporophyte produces millions of spores, resulting in the germination of a gametophyte when conditions are suitable. Male and female gametophytes then produce sperm and eggs respectively. After the meeting of the gametes and a potential fertilization, the zygote settles and develops, giving a new generation of sporophyte.

Only *Laminaria solidungula* is endemic from the Arctic, other species from the common genus *Laminaria*, *Saccharina* and *Alaria* are of Atlantic and Pacific origin and extend into subarctic and cooler temperate waters (Wulff et al., 2009). These kelp species have adapted to this cold environment (Gómez et al., 2009). Metabolic strategies such as enzymes able to work at low temperature, a higher unsaturated fatty acid content and antifreeze proteins allow polar algae to survive to cold temperature (Gómez et al., 2009).

Kelps are important primary producers able to capture and store large amounts of CO₂ as biomass (Krause-Jensen and Duarte, 2016). Kelp forests substantially contribute to the global carbon cycle (Wernberg and Filbee-Dexter, 2018; Krause-Jensen and Duarte, 2016). The global seaweed productivity (including canopies of brown algae from the orders Laminariales, Fucales, Tilopteridales, and Desmarestiales) has been estimated at 536 ± 31 gC m⁻² year⁻¹ by Pessarrodona et al. (2022).

Exuded dissolved organic carbon as well as detritus resulting from detachment and fragmentation by waves and shredding by herbivores are important contributions to shallow and deep-water food webs (Krumhansl and Scheibling, 2012; Krause-Jensen et al., 2018). At the global scale, 82% of the kelp primary production is exported to adjacent communities (Krumhansl and Scheibling, 2012).

Microbial films, sessile colonial filter feeders (bryozoan, hydrozoan, polychaetes) and mobile herbivores (sea urchins, polychaetes, crustaceans, mollusks) characterize their epiphytic fauna. Kelp forests support a high biodiversity by providing habitat, food, and nursery area for fish and invertebrates (Filbee-Dexter et al., 2019). By altering light, sedimentation, physical abrasion, and bottom currents they provide optimal conditions for the development of an

understory mainly composed of red and some green and brown algae (Teagle et al., 2017; Filbee-Dexter et al., 2019). *Devaleraea ramentacea*, *Palmaria palmata*, *Phycodryis rubens*, *Ptilota gunneri* and *Chaetomorpha* and *Desmarestia* genus make up the common dense understory of kelp forest and deeper assemblages found in the Arctic (Hop et al., 2002).

5.3. Coralline algae

Coralline algae are red calcareous algae, growing as concentric laminae (i.e., crust) or radial branches or columns (i.e., nodules; Bosence, 1983). The surface of coralline algae can be smooth or matt, from reddish to deep pink with violet tinge (Jackson, 2003). They are coastal species distributed worldwide from the tropics to the Arctic areas (Foster, 2001).

Vegetative growth and division of the crust or nodules into two or more individuals is a method of propagation used by coralline algae. To propagate, coralline algae can also reproduce sexually or asexually through the formation of spores (Jackson, 2003).

Coralline algae are long-lived and precipitate calcium carbonate within their cell walls and between cells, leading some to consider them as important long-term carbon burial actors in coastal ecosystems (van der Heijden and Kamenos, 2015) although calcification is a source of CO₂.

Temperature, PAR, salinity, and seawater chemistry determine the distribution of coralline algae (Adey et al., 2015; Teichert et al., 2014). While temperature primarily determines species-specific geographical distribution, PAR limits coralline occurrence at depth even if they can be found at great depth due to highly efficient photosynthetic pigments at low light (Teichert et al., 2014).

In the Arctic, coralline thrive within extreme seasonal variations of light regime, nutrient supply, and temperature (Teichert et al., 2012). To survive the polar night, they store carbohydrates produced during the active photosynthetic season, and use them in the winter, when photosynthesis is not possible (Freiwald and Henrich, 1994). Corallines are also suspected of storing nitrogen and phosphorus during winter, when the water column is enriched, before the phytoplankton bloom depletes the water column from nutrients (Freiwald and Henrich, 1994). Thereby, despite their low growth rate (0.2 mm/month; Adey and Vassar, 1975), Arctic and subarctic coralline algae have a high standing stock that could be similar to tropical species (Freiwald and Henrich, 1994).

Rhodoliths - or maërl - are free-living structures mostly composed of crustose or branching coralline algae (>50% in volume) that settle on a particulate substrate or are detached from existing hard substrates (Teichert et al., 2014). Coralline algae are the master builders of such three-dimensional calcified frameworks, with cavities and branches, that provide shelter for a variety of organisms and support a high biodiversity (Teichert et al., 2012, Teichert et al., 2014). Rhodoliths beds support a diverse range of benthic species, including a microalgal epiphyton (comprising foraminifera and diatoms), a vagile epifauna dominated by grazers (crustaceans, gastropods and sea urchins), a sessile epifauna of filters feeders (bivalves, serpulids, spirorbids, bryozoan) and an infauna that includes boring bivalves and polychaetes living within the algal thalli and the sediment deposited around the rhodoliths (Bosence, 1983; Freiwald and Henrich, 1994). Rhodoliths act as habitat, feeding, nursery, and spawning ground for various species including fishes (Thormar, 2008).

The integrity of coralline algae requires grazers to keep them healthy by removing excessive fast growing fleshy algae and sessile invertebrates (Steneck, 1990). One conspicuous herbivore is the sea urchin *Strongylocentrotus droebachiensis* whose larvae metamorphose on the surface of living coralline algae (Pearce and Scheibling, 1990). The formation and distribution of coralline algal communities rely heavily on these interactions with herbivores (Freiwald and Henrich, 1994).

In the Arctic, rhodolith communities have been observed in Greenland (Thormar 2008, Jørgensbye and Halfar, 2017), Alaska (Konar et al., 2006), North Norway (Freiwald and Henrich, 1994), and Svalbard (Teichert et al., 2014; Sswat et al., 2015). *Phymatolithon*, *Clathromorphum*, *Lithophyllum* and *Lithothamnion*, are widespread genera in shallow shelf areas with *Lithothamnion* able to colonize a large range of the dysphotic zone (up to 90 m deep for *Lithothamnion*; Teichert et al., 2012).

6. Species responses to global change: effects on biological processes

Most studies on the response of Arctic macroalgae to climate change have been performed *ex situ*, likely due to the multiple challenges for carrying out *in situ* experiments (Table 1; Müller et al., 2009; Wilson et al., 2015). Warming, changes in underwater light regime, local hyposalinity and ocean acidification can all have large effects on biological processes including reproduction, primary production, and respiration (Müller et al., 2009; Bonsell and Dunton, 2018).

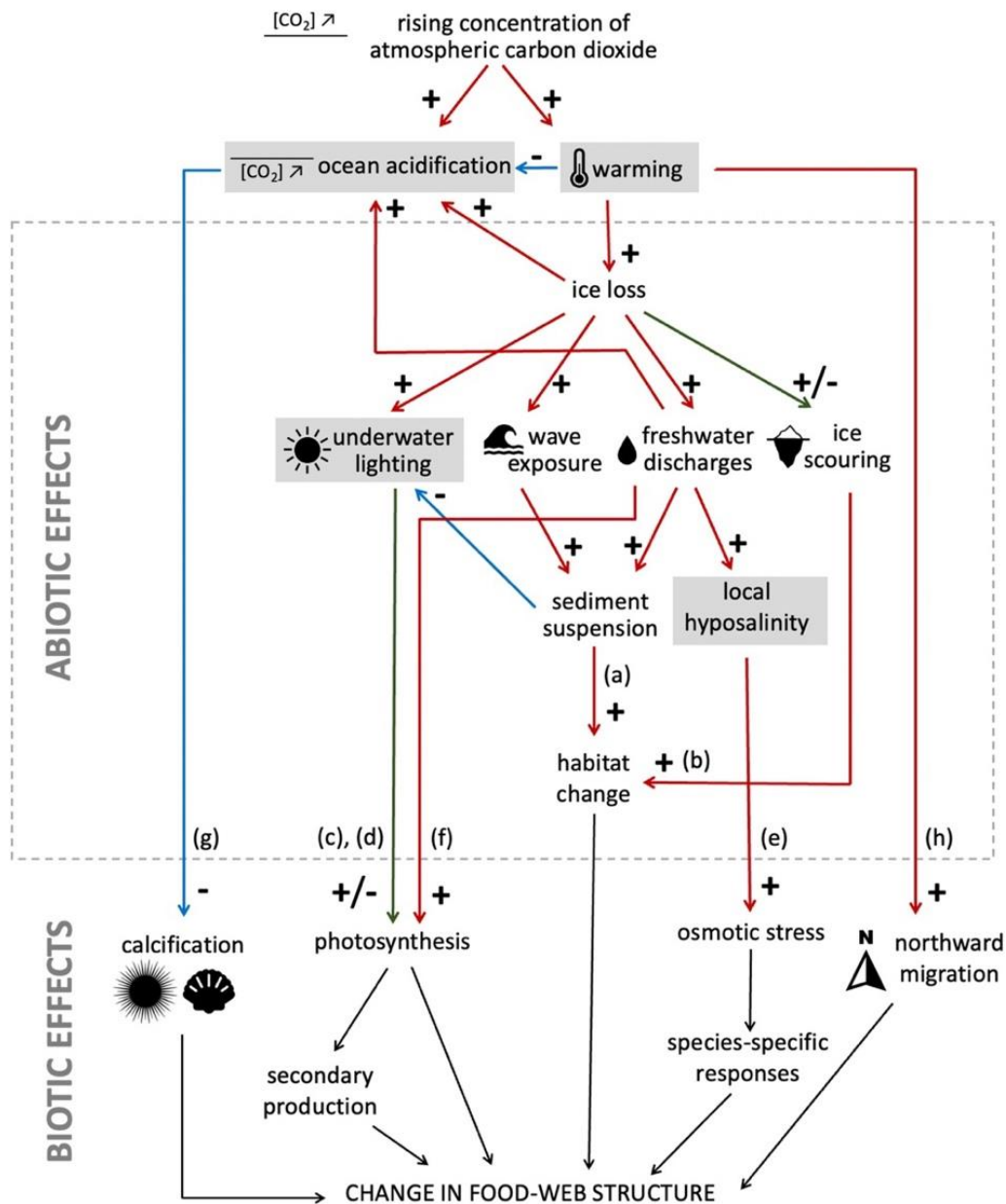


Figure 10: Cascading effects of global change in the benthic coastal Arctic environment.

The impact of processes framed in blue on benthic organisms are developed in section 5.

A plus (+) and a red arrow mean a positive effect, a minus (-) and a blue arrow mean a negative effect, and a (+/-) and a green arrow mean an effect that could be both positive or negative. Letters "a" to "h" are called in this chapter.

Table 1
Conditions of temperature, light, salinity and pCO₂ tested on major fucooid, kelp and coralline algae species found in the Arctic

Type	Species	Stages	Parameters	Conditions tested		Photosynthesis		Results		References
				Parameters	Stages	Photynthesis	Growth	Others		
Fucooid	<i>Fucus serratus</i>	sporophyte	light	light: 12:12 h L:D (PAR : 5-10 W.m-2), 24:00 h L:D			growth rate=0 in winter under 12:12 and 24:0, L:D		Makarov et al., 1999	
	<i>Fucus distichus</i>	sporophyte	light	light: 12:12 h L:D (PAR : 5-10 W.m-2), 24:00 h L:D			growth rate: increased with increasing photoperiod (from 12:12 to 24:0, L:D) and decreased with shortening the light phase (from 24 to 12 hours). growth rate: no effect of UV radiations		Makarov et al., 1999	
Kelp				light: PAR (30 µmol m-2s-1), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.7 W.m-2)		photosynthesis: no effect after 6h under UV radiations			Aguilera et al., 1999	
				light: PAR (33 µmol m-2s-1), PAR + UVA (8 W.m-2), PAR + UVA + UVB (1.2 W.m-2)			germination: 60% germinated under PAR + UVA with malformed rhizoids often and no further development. Under PAR + UVA + UVB less than 10% of zygotes germinated.		Schoenwaelder et al., 2003	
			salinity	salinity: 5, 10, 15, 20, 25, 34, 45, 55, 60		quantum yield and effect of salinity			Karsten et al., 2007	
		gametophyte	temperature, light	temp: 2, 7, 12, 18 ± 1.4°C			germination: + with temperature up to 12°C germination: - at 12°C under UVA & UVB		Müller et al., 2008	
				light: PAR (20 ± 3 µmol m-2s-1), PAR + UVA (5.8 W m-2), PAR + UVA + UVB (0.34 W m-2)					Müller et al., 2009	
				temp: 2, 7, 12, 18 ± 1.4°C		absorbance: no effect of temperature absorbance: + under UVA & UVB				
				light: PAR (20 ± 3 µmol m-2s-1), PAR + UVA (6.73 ± 0.81 W.m-2), PAR + UVA + UVB (0.35 ± 0.04 W.m-2)						Müller et al., 2012
				temp: 2, 7, 12, 18 ± 1.4°C		absorbance: + with temperature				
				light: PAR (20 µmol m-2s-1), PAR + UVA (5.5 W.m-2), PAR + UVA + UVB (0.35 W.m-2)		absorbance: + under UVA & UVB at 2°C				
			temperature	temp: 5, 9°C			germination: + at 9°C germination: no germinings at 20°C germination: close to 0%, 3, 6 and 9 days after 16h under UVA & UVB			Zacher et al., 2016 Park et al., 2017 Wienecke et al., 2004
		light	temp: 5, 10, 15, 20°C light: PAR (28.8 ± 5.05 µmol m-2s-1), PAR + UVA (8.22 ± 0.64 W.m-2), PAR + UVA + UVB (1.27 ± 0.12 W.m-2)		quantum yield: - under light exposure				Roleda et al., 2006b	
			light: PAR (21.8 µmol m-2s-1), PAR + UVA (5.65 W.m-2)						(continued on next page)	

Table 1 (continued)

Type	Species	Stages	Parameters	Conditions tested	Results		References
					Photosynthesis	Growth	
		sporophyte	temperature, light	2), PAR + UVA + UVB (0.47 W.m-2) temp: 2, 7, 12, 17°C	quantum yield: - under high PAR at 2°C and 17°C		Heinrich et al., 2012 Heinrich et al., 2015
				light: PAR (23.8 ± 3.08 μmol m-2s-1 & 107.77 ± 4.96 μmol m-2s-1), PAR + UVA (9.83 ± 1.17 W.m-2 & 9.68 ± 1.2 W.m-2), PAR + UVA + UVB (0.42 ± 0.03 W.m-2 & 0.43 ± 0.03 W.m-2) temp: 0, 4°C	quantum yield: - under high PAR and high PAR + UVA + UVB at 2, 7 & 12°C	different expression patterns under 2 and 17°C and high PAR compared to the control (12°C & low PAR); strongest effect of temperature on gene expression observed at 2°C. UVR have stronger effects on gene expression than high PAR. Higher temperatures ameliorated the negative effects of UVR.	
			temperature, pCO2	light: PAR (20 μmol m2 s-1); 18:6h light: dark), continuous dark temp: 4, 9°C CO2 conditions: 390 and 1200 ppm temp: 4, 10°C	chl _a : + at 4°C, quantum yield: no effect of temperature chl _a : + in the dark, quantum yield: no effect of light net photosynthesis: no effect of temperature & pCO2 net photosynthetic rate: + at 10°C at current pCO2 conditions	growth rate: no effect of temperature growth rate: + under light growth rate: + of about 30% at 9°C growth rate: largely unaffected by increased CO2 conditions growth rate: + at 10°C	Li et al., 2020b Iniguez et al., 2016a
			temperature, salinity	CO2 conditions: 380, 800 and 1500 ppm temp: 4, 6, 8, 10°C salinity: 25, 32/34 temp: 0, 8, 15°C salinity: 20, 30	quantum yield and chl _a : no effect of temperature quantum yield and chl _a : no effect of salinity quantum yield: - under low salinity (20) at 15°C, but not at 0 and 8°C.	lipids, proteins, and total N-content: + at 4°C. mannitol content and C/N: no effect of temperature mannitol content and C/N: no effect of salinity expression patterns: suggest interacting effects of temperature and salinity on the number of differentially expressed genes.	Olischläger et al., 2014; Olischläger et al., 2017 Diehl and Bischof, 2021 Li et al., 2020a
			light, salinity	light: 5, 20, 50 μmol m2 s-1 salinity: 10, 13, 17, 20, 31	quantum yield: no effect of light quantum yield: - at salinity=10	growth rate: - under lowest light level (5 μmol m2 s-1) growth rate: - at salinity=10	Spurkland and Iken, 2011
			light, pCO2	light: PAR (30 μmol m-2s-1), PAR + UVA (2 W.m-2) + UVB (0.2 W.m-2) CO2 condition: 380 and 1000 ppm temp: 6, 8, 10, 12°C	quantum yield: drop after 2 days under UVR and CO2 enrichment, recovery after 4 and 10 more days	growth rate: + 151% under UVR and CO2 enrichment	Gordillo et al., 2015
			temperature	light: PAR (60 μmol m-2s-1), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.7 W.m-2) light: PAR (30 μmol m-2s-1), PAR + UVA (7 W.m-2)	quantum yield: no effect of temperature quantum yield: negative correlation between recovering capacity and depth of sampling	growth rate: no effect of temperature	Diehl et al., 2021 Bischof et al., 1998
			light	light: PAR (30 μmol m-2s-1), PAR + UVA (7 W.m-2)	photosynthesis: - after 2h of exposure to UV radiations	growth rate: - under UV radiations	Aguilera et al., 1999

(continued on next page)

Table 1 (continued)

Type	Species	Stages	Parameters	Conditions tested	Photosynthesis	Results	References
						Growth	Others
				PAR + UVA + UVB (0.7 W.m-2) light: PAR (3.62 W.m-2), PAR (4.00 W.m-2) + UVA (5.01 W.m-2) + UVB (0.31 W.m-2) light: PAR PAR + UVA + UVB salinity: 5, 10, 15, 20, 25, 34, 45, 55, 60 temp: 2, 7, 12, 17°C	chl a: no effect of UV radiations quantum yield: - at salinity=5 and 10 after 2 days of treatment quantum yield: highest reduction in photosynthetic efficiency 17°C and lowest at 12°C quantum yield: exposure to PAB caused 93-98% photoinhibition	growth rate: - under UV radiations growth: gametophyte development after 16 and 48 days showed increasing size with increasing temperature	Roleda et al., 2006c Van de Poll et al., 2007 Karsten, 2007 Roleda, 2016
	<i>Laminaria solidungula</i>	gametophyte	salinity temperature, light	light: PAR (10 and 20 µmol m-2s-1) PAR + UVA (5 W.m-2) PAR + UVA + UVB (0.4 W.m-2) light: PAR (10, 20, 40 µmol m-2s-1) salinity: 10, 20, 30		gametophyte density: - under UV radiations gametophyte density: - at salinity=10 and 20 germination: under UVA & UVB, + 6 days after exposition (compared to 3 days)	Muth et al., 2021 Wiencke et al., 2004
		sporophyte	temperature, salinity	light: PAR (28.8 ±5.05 µmol m-2s-1), PAR + UVA (8.22 ± 0.64 W.m-2), PAR + UVA + UVB (1.27 ± 0.12 W.m- 2) temp: 0, 5, 10, 15°C salinity: 25, 35	quantum yield: - at 15°C after 14 days	mannitol content: + at salinity=35 at 0, 5 & 10°C C/N: + at salinity=35 at 0, 5,10 & 15°C, + at 10 & 15°C	Diehl et al., 2020
			temperature, pCO2	temp: 4, 9°C CO2 conditions: 390, 1200 ppm	net photosynthesis: + at 9°C compared to 4°C. net photosynthesis: + at increased CO2 conditions (at 4°C).	growth rate: no effect of temperature and pCO2	Inguez et al., 2016a
			light, salinity	light: PAR (10, 20, 40 µmol m-2s-1) salinity: 10, 20, 30		sporophyte density: - under UV radiations sporophyte density: - at salinity=10 and 20 Blade length: - at low light & dark exposure New blade surface area: - during dark exposure	Muth et al., 2021
			light	light: PAR (66, 18, 13, 3, 0.5, 0.2, 0 µE m-2 s-1) light: PAR (25µmol m-2s-1, 12:12h light: dark), continuous dark light: PAR (30 µmol m-2s-1), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.7 W.m-2)	photosynthesis: - after 2h of exposure to UV radiations	growth rate: no effect of UV radiations	Chapman and Lindley, 1980 Henley and Dunton, 1997 Aguilera et al., 1999
			light: PAR (3.62 W.m-2), PAR (4.00 W.m-2) +	chl a: no effect of UV radiations	growth rate: - under UV radiations		Roleda et al., 2006c

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Table 1 (continued)

Type	Species	Stages	Parameters	Conditions tested	Results		References
					Photosynthesis	Growth	
			salinity	UVA (5.01 W.m-2) + UVB (0.31 W.m-2) salinity: 5, 10, 15, 20, 25, 34, 45, 55, 60	quantum yield: - at salinity= 5, 10, 15 and 20 after 5 days of treatment		Karsten, 2007
	<i>Laminaria digitata</i>	gametophyte	temperature, light	temp: 2, 7, 12 and 18 ± 1.4°C light: PAR (20 ± 3 µmol m-2.s-1), PAR + UVA (5.8 W m-2), PAR + UVA + UVB (0.34 W m-2) temp: 2, 7, 12 and 18 ± 1.4°C light: PAR (20 ± 3 µmol m-2.s-1), PAR + UVA (6.73 ± 0.81 W.m-2), PAR + UVA + UVB (0.35 ± 0.04 W.m-2) temp: 2, 7, 12 and 18 ± 1.4°C light: PAR (20 µmol m-2s-1), PAR + UVA (5.5 W.m-2), PAR + UVA + UVB (0.35 W.m-2) temp: 2, 7 ± 1°C light: PAR (20 ± 4 W.m-2), PAR + UVA (3.8 ± 0.4 W.m-2) + UVB (0.41 ± 0.04 W.m-2) temp: 15, 20, 22.5, 25°C and dynamic heat stress: 18 to 25°C light: PAR (15 µmol m-2s-1), red light, continuous dark temp: 5, 15°C	germination: 0 to 0.1% at 18°C germination: - at 2°C and 12°C under UVA & UVB absorbance: no effect of temperature absorbance: no effect of light absorbance: increase with temperature absorbance: + under UVA and UVA & UVB at 2, 7 and 12°C absorbance: + under UVA and UVA & UVB at 2, 7 and 12°C germination: + at 9°C germination: + at 9°C gametophyte density: decreased by 48 and 40% at 0 and 23 °C, respectively germination: close to 0% 3, 6 and 9 days after 16h under UVA & UVB	Müller et al., 2008 Müller et al., 2009 Müller et al., 2012	
			temperature	temp: 5, 9°C temp: 5, 9, 15°C temp: 0, 5, 10, 15, 20, 22, 23, 24, 25 ± 0.5°C temp: 0, 3, 6, 9, 12, 15, 20, 21, 22, 23, 24, 25 ± 0.1°C light: PAR (28.8 ± 5.05 µmol m-2s-1), PAR + UVA (8.22 ± 0.64 W.m-2), PAR + UVA +	UVAB-susceptibility: increase with decreasing temperature after a high temperature stress, the recovery temperature affects the capacity to reproduce germination: + at 9°C germination: + at 9°C gametophyte density: decreased by 48 and 40% at 0 and 23 °C, respectively germination: close to 0% 3, 6 and 9 days after 16h under UVA & UVB	Olischläger and Wiencke, 2013 Martins et al., 2020 Liesner et al., 2020a Zacher et al., 2016 Zacher et al., 2019 Franke et al., 2021 Schimpf et al., 2022 Wiencke et al., 2004	

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Table 1 (continued)

Type	Species	Stages	Parameters	Conditions tested	Results		References
					Photosynthesis	Growth	
sporophyte				UVB (1.27 ± 0.12 W.m-2)	quantum yield: - under light exposure, even more under UVA & UVB	sporophyte density: + at 9°C in monospecific cultivation area growth rate: - at 5°C in July & February	Roleda et al., 2006b
				light: PAR (21.8 μmol m-2s-1), PAR + UVA (5.65 W.m-2), PAR + UVA + UVB (0.47 W.m-2)			
				temp: 4, 5, 10, 15°C			
				temp: 5, 15°C			
				temp: 15, 19, 21, 23°C			
				temp: 0, 5, 10, 15, 20, 22, 23, 24, 25 ± 0.5°C			
				temp: 0, 3, 6, 9, 12, 15 ± 0.1°C			
				light: PAR (30 μmol m-2s-1), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.7 W.m-2)			
				light: 12:12 h L:D (PAR : 5-10 W.m-2), continuous daylight			
				light			
gametophyte	<i>Alaria esculenta</i>		temperature, salinity, light	light: PAR (3.62 W.m-2), PAR (4.00 W.m-2) + UVA (5.01 W.m-2) + UVB (0.31 W.m-2)	chl.a: no effect of UV radiations	growth rate: increased with increasing photoperiod (from 12:12 to 24:0, L:D) and decreased with shortening the light phase (from 24 to 12 hours)	Roleda et al., 2006c
				salinity: 5, 10, 15, 20, 25, 34, 45, 55, 60			
				temp: 2, 7, 12, 16 ± 1°C			
				salinity: 20, 26, 28, 33, 34			
				light: PAR (20 ± 2 and 6/8 μmol m-2s-1), PAR + UVA (4.5 ± 0.5 W m-2), PAR + UVA + UVB (0.4 ± 0.04 W m-2)			
				temp: 2, 7, 12, 18 ± 1.4°C			
				light: PAR (20 ± 3 μmol m-2s-1), PAR + UVA (5.8 W m-2), PAR + UVA + UVB (0.34 W m-2)			
				temp: 2, 7, 12 and 18 ± 1.4°C			
				light: PAR (20 ± 3 μmol m-2s-1), PAR + UVA (6.73 ± 0.81 W.m-2), PAR + UVA +			
				salinity			
gametophyte	<i>Alaria esculenta</i>		temperature, salinity, light	temp: 2, 7, 12, 16 ± 1°C	absorbance: no effect of temperature	germination: no effect of UV	Fredersdorf et al., 2009
				salinity: 20, 26, 28, 33, 34			
				light: PAR (20 ± 2 and 6/8 μmol m-2s-1), PAR + UVA (4.5 ± 0.5 W m-2), PAR + UVA + UVB (0.4 ± 0.04 W m-2)			
				temp: 2, 7, 12, 18 ± 1.4°C			
				light: PAR (20 ± 3 μmol m-2s-1), PAR + UVA (5.8 W m-2), PAR + UVA + UVB (0.34 W m-2)			
				temp: 2, 7, 12 and 18 ± 1.4°C			
				light: PAR (20 ± 3 μmol m-2s-1), PAR + UVA (6.73 ± 0.81 W.m-2), PAR + UVA +			
				absorbance: + under UVA & UVB at 2°C, + under UVA and UVA & UVB at 7, 12 and 18°C			
				germination: optimal temperature range of 2-12°C			
				temperature, salinity, light			

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Table 1 (continued)

Type	Species	Stages	Parameters	Conditions tested	Results			References
					Photosynthesis	Growth	Others	
				UVB (0.35 ± 0.04 W.m-2) temp: 2, 7, 12 and 18 ± 1.4 °C light: PAR (20 µmol m-2s-1), PAR + UVA (5.5 W.m-2), PAR + UVA + UVB (0.35 W.m-2) temp: 2, 7 ± 1 °C light: PAR (20 ± 4 W.m-2), PAR + UVA (3.8 ± 0.4 W.m-2) + UVB (0.41 ± 0.04 W.m-2) temp: 5, 9 °C temp: 5, 9, 15 °C temp: 5, 10, 15, and 20 °C light: 12:12 h L:D (PAR : 5-10 W.m-2), continuous daylight light: PAR (28.8 ± 5.05 µmol m-2s-1), PAR + UVA (8.22 ± 0.64 W.m-2), PAR + UVA + UVB (1.27 ± 0.12 W.m-2) light: PAR (21.8 µmol m-2s-1), PAR + UVA (5.65 W.m-2), PAR + UVA + UVB (0.47 W.m-2) light: PAR (5.5±1.2, 20.6±3.0 µmol m-2s-1), PAR + UVA (10.9±0.4, 11.6±1.9 W.m-2), PAR + UVA + UVB (0.45 ± 0.0, 0.48±0.0 W.m-2) light: PAR (from 0.23 to 61.8 W.m-2) + UVA (from 0 to 1.9 W.m-2) + UVB (from 0 to 0.018 W.m-2) temp: 4, 8, 9, 13, 15, 17, 21 ± 1 °C salinity: 20, 28, 34 light: PAR (46 ± 8 and 80 ± 10 µmol m-2.s-1), PAR + UVA (7 ± 1 W	absorbance: increase with temperature absorbance: + under UVA and UVA & UVB at 2 °C quantum yield: - under light exposure, even more under UVA & UVB quantum yield: significant interaction between radiation and exposure time, as well as significant radiation effects photosynthesis: optimal temperature range of 13–17 °C.	germination rate: no significant effect of temperature and seasonality germination: + at 9 °C germination: + at 9 °C in co-cultivation germination: no germlings at 20 °C growth rate: increased with increasing photoperiod (from 12:12 to 24:0, L:D) and decreased with shortening the light phase (from 24 to 12 hours). germination: - 3, 6 and 9 days after 16h under UVA & UVB	Müller et al., 2012 Olischläger and Wiencke, 2013 Zacher et al., 2016 Zacher et al., 2019 Park et al., 2017 Makanov et al., 1999 Wiencke et al., 2004 Roleda et al., 2006b Steinhoff et al., 2012 Laeske et al., 2019 Fredersdorf et al., 2009	
		sporophyte	temperature, salinity, light		UVAB-susceptibility: highest at 2 °C and the beginning of July, not affected by seasonality at 7 °C no sporophyte at 15 °C			

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Table 1 (continued)

Type	Species	Stages	Parameters	Conditions tested	Results			References
					Photosynthesis	Growth	Others	
			salinity, light	m-2), PAR + UVA + UVB (0.3 ± 0.07 W m-2) salinity: 5, 15, 32 light: PAR (50 µmol m-2 s-1), PAR + UVA (6.8 and 7.5 W m-2) + UVB (0.5 and 0.8 W m-2)	quantum yield: slightly - in a low-salinity during 7 days quantum yield: slightly - under UVR	specimens previously treated with hyposalinity are significantly less susceptible to UV	Springer et al., 2017	
		light, pCO2	light, pCO2	light: PAR (30 µmol m-2s-1), PAR + UVA (2 W.m-2) + UVB (0.2 W.m-2)	quantum yield: drop after 2 days under UVR, recovery after 4 more days	growth rate: + 57% under UVR and CO2 enrichment	Gortillo et al., 2015	
		temperature	temperature	CO2 condition: 380 and 1000 ppm temp: 4, 5, 10, 15°C		sporophyte density: + at 9°C in co-cultivation	Zachler et al., 2019	
		light	light	light: PAR (60 µmol m-2s-1), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.7 W.m-2) light: PAR (20, 60, 800 µmol m-2s-1), PAR + UVA (8 W.m-2), PAR + UVA + UVB (0.8 W.m-2)	quantum yield: specimens from shallow water recover to a greater extent than those from deeper waters quantum yield: - to 25% after 4 h of exposure to low light and UV during the first 2 cycles, recovery proceeded significantly faster at the 2nd cycle		Bischof et al., 1998	
		salinity	salinity	light: PAR (46 µmol m-2s-1), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.3 W.m-2) light: 12:12h and 16:8h	quantum yield: - significantly after 1 day under PAR + UVA + UVB	growth: triggered by changing daylength from short to long days	Lätz et al., 2016	
		pCO2	pCO2	light: dark salinity: 5, 10, 15, 20, 25, 34, 45, 55, 60 CO2 conditions: 390, 1300 ppm	quantum yield: - at salinity= 5 after 2 and 5 days of treatment gross photosynthesis: no effect of CO2 conditions	reproductive success hampered under continuous light	Martins et al., 2022	
		temperature, light	temperature, light	temp: 2, 8, 11, 17°C light: PAR (4.62 ± 0.4 and 86.7 ± 19.9 µmol m-2s-1), PAR + UVA (5.31 ± 0.58 and 4.76 ± 2.9 W.m-2), PAR + UVA + UVB (0.41 ± 0.01 and 0.12 ± 0.0 W.m-2)		decreased respiration and lower accumulation of biostorage molecule under CO2 enrichment condition	Karsten et al., 2007	
	<i>Saccorhiza dermatodea</i>	gametophyte	gametophyte	light: PAR (28.8 ± 5.05 µmol m-2s-1), PAR + UVA (8.22 ± 0.64 W.m-2), PAR + UVA +	germination rate: reduced under PAR+UV-A+UV-B only at 17°C and 7°C outdoor treatment (-21.4% and 9.6% respectively)	phlorotannin content: no effect of light treatments after 8h of exposure	Iniguez et al., 2016b	
		light	light		germination: - 3 after 16h under UVA & UVB, recovery after 6 days		Steinhoff et al., 2011	
							Wiencke et al., 2004	

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Table 1 (continued)

Type	Species	Stages	Parameters	Conditions tested	Photosynthesis	Growth	Others	References
				UVB (1.27 ± 0.12 W.m-2) light: PAR (21.8 µmol m-2s-1), PAR + UVA (5.65 W.m-2), PAR + UVA + UVB (0.47 W.m-2) light: PAR (60 µmol m-2s-1), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.7 W.m-2) light: PAR (30 µmol m-2s-1), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.7 W.m-2) light: 12:12 h L:D (PAR : 5-10 W.m-2), continuous daylight	quantum yield: - with increasing total fluence quantum yield: specimens from shallow water recover to a greater extent than those from deeper waters photosynthesis: - after 6h of exposure to UV radiations	germination: strong dose-dependent inhibitory effect of UVA & UVB growth rate: - under UV radiations growth rate: increased with increasing photoperiod (from 12:12 to 24:0, L:D) and decreased with shortening the light phase (from 24 to 12 hours).		Roleida et al., 2006a, 2006b Bischof et al., 1998 Aguilera et al., 1999 Makarov et al., 1999 Karsten et al., 2007 Franke et al., 2021 Franke et al., 2021 Schoenrock et al., 2018 Biedenbender et al., 2011 Muth et al., 2020 Hofmann et al., 2018
Coralline algae	<i>Lithothamnion glaciale</i>	sporophyte	salinity temperature temperature, salinity	salinity: 5, 10, 15, 20, 25, 34, 45, 55, 60 temp: 0, 5, 10, 15, 18, 19, 21, 22 ± 0.5 °C temp: 0, 5, 10, 15, 18, 19, 21, 22 ± 0.5 °C temp: 4, 7 °C salinity: 22, 33	quantum yield: - at salinity= 5, 10 after 2 days of treatment	At 21 and 22 °C, all gametophytes died after 14 days growth rate: + at 10°C, - at 15°C calcification: reduced at low salinity and temperature treatments CO2 treatments calcification: higher at salinity=10	abundance of females decreased with increasing temperatures overtime (ratio: 0.24±0.03, day 14) metabolic processes: negatively influenced by low salinity higher pigment change at salinity=10 active calcification and no net dissolution in the dark	
	<i>Lepidophytum foecundum</i> <i>Phymatolithion tenue</i>	sporophyte sporophyte	pCO2 salinity light	CO2 conditions: 390, 815, 975 and 1570 ppm salinity: 10, 20, 30 light: PAR (100 µmol m-2 s-1), dark	calcification: reduced under high salinity			

6.1. Warming

Temperature is the main physical driver in most ecosystems and has a major influence on polar benthic species distribution (Drewnik et al., 2017). Warming will increase suitable habitat for *F. distichus*, fostering seaweed meadows in the intertidal Arctic (Coyer et al., 2011). Among cold-temperate kelp species, many have growth temperature optima well above the temperature at which they are currently growing (Bischoff and Wiencke, 1993; Müller et al., 2009; Meyer et al., 2017). Since enzymatic processes are temperature-dependent, it has a strong effect on all physiological processes (e.g., Brown et al., 2004; Gómez et al., 2009). For most kelp species, growth at 0-5 °C is typically less than one third of the rates reached at their optimal temperature ranging from 10 to 15 °C (Wiencke and Amsler, 2012; Roleda, 2016). By promoting photosynthesis, germination, gametogenesis, fertility and survival enhancement, warming is projected to increase the biomass of kelps such as *Saccharina latissima*, *Laminaria hyperborea*, *Laminaria digitata*, and *Nereocystis luetkeana* and expand their distribution to higher latitudes (Li et al., 2020a; Goldsmit et al., 2021).

Warming may also have negative impacts on some macroalgal species. Spore settlement and gametophyte growth rate can be lower at higher temperature (Filbee-Dexter et al., 2019). For *Laminaria solidungula*, the only truly Arctic endemic kelp species, the recruitment becomes limited when temperature exceeds 10 °C (Filbee-Dexter et al., 2019).

Rising temperature drives the increasing frequency of marine heatwaves (Oliver et al., 2018; Golubeva et al., 2021). Even intertidal species, adapted to extreme environmental changes, may be impacted. Photosynthetic performances of *F. distichus* and *F. serratus* decreased when exposed to temperatures higher than 24 °C and 28 °C, respectively (Jueterbock et al., 2014; Smolina et al., 2016). Except above 32 °C, these species recovered completely within a day after 60 min. of exposure to warm temperature. However, higher durations of treatment have not been tested. In the Kara, Laptev and Siberian seas, the duration of marine heatwaves increased by 10 to 12 days between 2000 and 2020 (Golubeva et al., 2021). Testing longer durations may reveal potential adaptation or, on the contrary, an increasing reduction in photosynthetic performance that may impair fucoids dispersal in the Arctic.

Arctic and subarctic coralline algae are more sensitive to warming, which is consistent with the fact that they live at greater depths and are therefore less exposed to large changes in

temperature. Present temperature appears to be warm enough for growth and cold enough to allow conceptacle production in the summer (Teichert et al., 2014). For *Lithothamnion glaciale*, the production of conceptacles, containing the spores, is limited when water temperature is above 9 °C (Hall, 1994). Warming might therefore impair its reproductive capacity. Furthermore, its primary production and calcification rates are lower at high temperature with an optimum at ca. 4 °C (Schoenrock et al., 2018). Longer duration of marine heatwaves will increase temperature deeper and may reach coralline distribution depths with significant impact on their development.

6.2. Changes in underwater light

By influencing the spatial and depth distributions of primary producers, underwater light is a driver of the composition of macroalgal dominated ecosystems. Light has a significant impact on the global carbon cycle by influencing primary production. Photoperiod also regulates the timing of reproduction of *F. distichus* (Bird and McLachlan, 1976), *L. solidungula* (Lüning, 1991) and *A. esculenta* (Martins et al., 2022). Several climate change-related processes affect light penetration in the Arctic Ocean. The underwater light conditions are influenced by sea ice cover and water turbidity which both attenuate PAR and UV-radiation (UVR; Bonsell and Dunton, 2018; Hanelt et al., 2001). In general, it can be projected that, with increasing air and water temperature, PAR will decrease during part of the summer, near glaciers and river outflows, due to a higher input of particles and coloured dissolved material (Fig. 10c). Furthermore, increased summer cloudiness with warming reduces incident PAR over most of the Arctic Ocean (Bélanger et al., 2013). However, in early spring or further away from the glaciers and rivers, PAR could increase due to the decrease in sea ice cover (Fig. 10d; Arrigo and van Dijken, 2011).

Higher turbidity near glaciers and rivers limits the vertical distribution of kelps and associated fauna, but decreased sea-ice cover promotes the expansion of kelps in new areas (Wiencke and Hop, 2016). For coralline algae, Teichert et al. (2014) found that irradiance is the most influential parameter on rhodolith CaCO₃ production rates in Svalbard. The projected decrease in PAR near glaciers and rivers will reduce the primary production of both kelps and calcareous algae with implications on the benthic fauna inhabiting this ecosystem (Hopwood et al., 2020).

The depletion of stratospheric ozone causes a significant rise in solar UVR (Wiencke and Hop, 2016) which will also be more intense over a longer period and will penetrate deeper in the water column (Laeseke et al., 2019). Down to ca. 6 m depth (Hanelt et al., 1997; Wiencke et al., 2000), UVR are intense enough to negatively affect physiological and metabolic processes such as photosynthesis, respiration, development, and reproduction (Roleda et al., 2007). For Arctic kelps, a stronger exposure to UVA and UVB leads to a decline in photosynthetic efficiency (e.g., Hanelt et al., 1997; Heinrich et al., 2015) and lowers the germination success and recruitment (Roleda et al., 2006a). Early developmental stages, such as spores, are the most vulnerable to UVA and UVB (Roleda et al., 2006a; Wiencke et al., 2007). Wiencke et al. (2000), Roleda et al. (2005) and Fredersdorf et al. (2009), identified harmful effects of increased UVR on the photosynthetic rate and motility of kelp spores.

However, photoprotection strategy and/or repair of DNA damage have been shown in several macroalgal species including at the zoospore stage (van de Poll et al., 2007; Roleda et al., 2005; Roleda et al., 2006b). Furthermore, it should be noted that most studies consider high UV intensities (Wiencke and Hop, 2016; Laeseke et al., 2019) that are not representative of *in situ* conditions even more for most Arctic kelps that are fertile in autumn-to-spring, avoiding exposure of their spores to high levels of PAR and UVR (Olischläger and Wiencke, 2013). Since ice and snow melt runoff (Hop et al., 2002), waves (Svendsen et al., 2002), and weather conditions fluctuate on short time scales and significantly decrease water clarity and light penetration, it is unlikely that spores could undergo elevated UVR exposure for time periods long enough to induce permanent photodamage (≥ 8 h; Laeseke et al., 2019). However, spores and gametophytes of kelp species fertile in summer may be limited in their vertical distribution to avoid UVR at the surface (Wiencke and Hop, 2016).

Furoid are present in the intertidal zone and therefore undergo higher levels of UVR. Schoenwaelder et al. (2003) found harmful effects of UVR on embryonic development of *F. distichus* and *F. serratus* individuals. Under high UVR, zygotes are incapable of polarization, germination and division, and finally die. Increasing UVR may restrict *F. distichus* to the lower intertidal area of Arctic coasts (Jueterbock et al., 2016).

To our knowledge, no studies on the impact of UVR on Arctic coralline algae have been conducted. Coralline algae are usually under the furoids and kelp canopy or deep enough not to be impacted by UVR.

6.3. Salinity decrease

Increase in river runoff, ice melt, and precipitation will accentuate local hyposaline conditions. Salinity is one of the drivers of the photophysiology and distribution of algal species (Hanelt et al., 2001; Li et al., 2020a; Diehl et al., 2020). Although intertidal fucoids have efficient osmoregulation mechanisms, reduced salinity leads to reduced biosynthesis of mannitol, an important source of carbon for heterotrophic bacteria (Groisillier et al., 2015). Increase in respiratory O₂ consumption at lower salinities (< ~ 21) was also found in fucoids (Munda and Kremer, 1977). Some species, such as *Fucus serratus*, have a narrower salinity spectrum, impacting their distribution (Munda and Kremer, 1977). To avoid damage in hyposaline conditions, energy is transferred from biomass production to osmoregulation, affecting the long-term growth rate (Fig. 10e; Li et al., 2020a). Hyposaline conditions can cause the loss of pigments and bleaching and in prolonged low salinity events, death of macroalgae (Li et al., 2020a). Diehl et al. (2020) found that low salinity (25) combined with elevated temperature (up to 15 °C) causes a significant decline in the maximum quantum yield of photosystem II (Fv/Fm) of the kelp *Laminaria solidungula*. Variable salinity conditions also reduce photosynthetic efficiency (Fig. 10f; Karsten, 2007; Spurkland and Iken, 2011). As a result, the projected local decrease in salinity is expected to alter kelp fitness by limiting photosynthesis (e.g., Traiger and Konar, 2018; Filbee-Dexter et al., 2019).

Rhodophyta are generally more sensitive to salinity changes than Phaeophyta and Chlorophyta (Teichert et al., 2014). Schoenrock et al. (2018) found that, when subjected to low salinity (i.e., 22), Arctic red coralline algae exhibited lower calcification and photosynthetic rates than at current salinity level (i.e., 33). However, not all rhodophytes are highly sensitive to low salinity. *Lithothamnion glaciale* can tolerate both low (< 18) and strongly fluctuating salinity, but at a cost for its photosynthetic capacities (Teichert et al., 2014; Schoenrock et al., 2018). The reduced growth associated with low salinity will have a negative impact on rhodolith beds (Teichert et al., 2014). Although certain taxa are more tolerant to a variable and low salinity, freshwater inputs are projected to hinder most Arctic macroalgae with impaired performances.

6.4. Ocean acidification

Ocean acidification is magnified in high latitude regions because cold polar waters favor the dissolution of CO₂ and low calcium carbonate saturation states (Fransner et al., 2022). Even if

warming limits CO₂ absorption, indirect effects of the increase in sea temperature such as ice loss further promote this process by enhancing air-sea gas exchange, including CO₂ (Yamamoto-Kawai et al., 2009). Also, mixing with river runoff can increase or reduce the buffering capacity of Arctic waters depending on the local geology and releases a large amount of dissolved and particulate carbon from thawing permafrost (Polukhin, 2019). With a pH decrease of up to 0.45 units projected over the 21st century (Terhaar et al., 2021), model simulations estimate that the Arctic will undergo the greatest acidification at the global scale (Fransner et al., 2022). At the current emission rate, surface waters of the Arctic Ocean will be locally undersaturated with respect to aragonite within a decade (Yamamoto et al., 2012; Fransner et al., 2022). This can be enhanced by local biological activity such as respiration inside kelp forests during periods of darkness or respiration of organic carbon from land. However, long photoperiods (>21 h) lead to a continuous increase in pH that potentially benefits calcifiers (Krause-Jensen et al., 2016).

Increased CO₂ in marine systems has consequences on biological processes such as photosynthesis, respiration, calcification, dissolved organic carbon (DOC) release and carbon accumulation in biomolecules (Fig. 10g; Iñiguez et al., 2016b, Wiencke and Hop, 2016). The decrease in pH as well as calcite saturation state may cause a rapid reduction in coralline algae cover and diversity within 10 to 30 years and could yield to their possible disappearance during this century in the Arctic (SRES A2; IPCC, 2007; Büdenbender et al., 2011). In tropical waters, coralline algae with quick generation time (6 to 8 weeks) can develop resistance to ocean acidification over multiple generations (Cornwall et al., 2020). However, it is likely that Arctic species may not have enough time or the capacity to acclimatize due to their longer generation time.

For kelps, a higher CO₂ concentration could lead to higher photosynthetic rates. However, Iñiguez et al. (2016a) found that *Saccharina latissima* and *Laminaria solidungula* were largely unaffected by elevated pCO₂ (carbon dioxide partial pressure, 1272 ± 4 µatm and 1308 ± 31 µatm respectively at 4 °C). This suggests that photosynthesis is already C-saturated at 368 ± 15 µatm for *Saccharina latissima* and 428 ± 22 µatm for *Laminaria solidungula*. In another study, Iñiguez et al. (2016b) showed a positive and a negative effect of ocean acidification on the growth rate of *Alaria esculenta* and *Desmarestia aculeata*, respectively at 1300 ± 36 µatm and 1252 ± 30 µatm. This suggests that Arctic seaweed will be affected by ocean acidification

in species-specific ways which may shift their relative biomass dominance with implications for the rest of the trophic web (Iñiguez et al., 2016b).

The impact of ocean acidification on Arctic benthic species is also determined by its interaction with other environmental constraints, such as warming, hyposalinity and PAR decrease (Olischläger et al., 2017). The combination of several environmental stressors may result in a retreat or even extinction of some populations and the expansion of others.

7. Invasive, resilient and vulnerable species: winners and losers

Global environmental change alters the spatial distribution of species by expanding or contracting suitable habitats (Lenoir and Svenning, 2015). Species invasions, declines or extinctions are projected to increase in the future (Wiencke and Hop, 2016).

Half of the benthic taxa are projected to experience significant changes in the extent of their suitable habitat (> 10% increase or decrease) including dominant and/or endemic species of Arctic shelves (Renaud et al., 2019). It could lead to a high risk of species extinction in polar and cold-temperate regions (Müller et al., 2009). Sea ice loss is thought to drive a profound regime shift in shallow polar benthos from invertebrate- to algal-dominated communities (Clark et al., 2013). For example, in Kongsfjorden (Svalbard), the abundance of the originally dominant sea anemones decreased by 80% between the 1990s and the 2000s, and were replaced by filamentous brown algae (Kortsch et al., 2012). The combination of the projected changes in sea ice and species dominance will likely induce fundamental changes in community composition with a loss of biodiversity, functions and altered ecosystem stability (Clark et al., 2013).

7.1. Fucoids

Between 1988 and 2008, Svalbard coasts experienced an increase in the cover and biomass of intertidal marine algae, including *Fucus distichus*, whose population nearly doubled (Weslawski et al., 2010). Because ice melt opens new areas for colonization, the habitat suitability of this species in the Arctic would triple by 2100 (Jueterbock et al., 2016). *F. distichus* is cold-adapted, surviving for months under ice and frequently exposed to cold temperatures during low tide, giving it an advantage over temperate species (see section 7.4; Svendsen et al., 2002). However, increases in UVR may restrict its distribution to the lower intertidal zone giving ground to other species (Fig. 11; Jueterbock et al., 2016; Schoenwaelder et al., 2003).

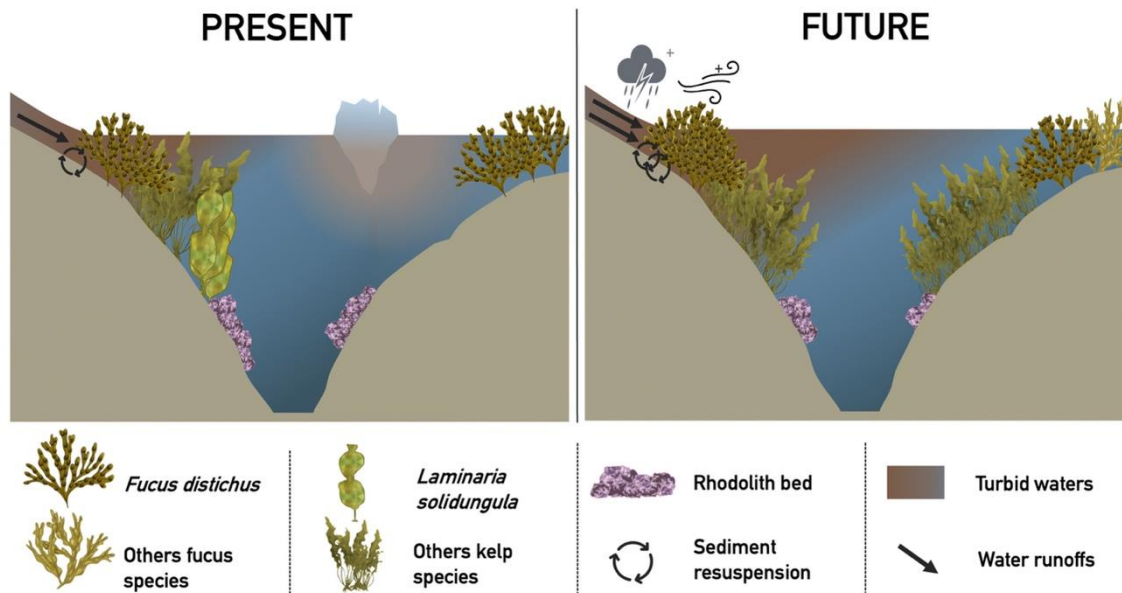


Figure 11: Schematic representation of the present and expected future Arctic coastal macroalgae communities.

Present: furoids dominate intertidal algae assemblages, while kelps dominate subtidal algae assemblages until they reach their low light threshold. *Laminaria solidungula* is present at the lower sub-littoral zone (Hop et al., 2002; Wiencke et al., 2004). Coralline algae are at the lower limit of kelp forest and deeper. Ice melt and increased river runoff increase turbidity.

Future: increase in precipitation, wind-speed, river runoff and sediment resuspension are increasing the turbidity locally. The surface cover of *F. distichus* doubled while UVR rates limit it to the lower intertidal zone giving ground to other fucoid species. Longer ice-free periods allow kelp expansion in new areas except for *L. solidungula* who retreated with warming. The coralline algae cover is reduced due to ocean acidification and competition with other macroalgae.

7.2. Kelps

Beuchel et al. (2006), Kortsch et al. (2012) and Bartsch et al. (2016) reported an increase in macroalgal biomass in Svalbard fjords since the 1980s. Between 1996 and 2014, kelp biomass, mainly *Laminaria digitata*, has increased 2-4 times most likely because of reduced sea ice cover (Hop et al., 2012; Bartsch et al., 2016).

Krause-Jensen et al. (2012) identified the duration of the open-water period, via changes in light and temperature, as the best predictor of vertical distribution and production of kelps along a latitudinal gradient. These variables explained up to 92% of the depth expansion and 80% of the variation in kelp biomass. These responses are likely to increase in the future. The loss of light-attenuating sea ice on the rocky coastlines of Russian islands, the Kola Peninsula, Spitsbergen, Greenland (Baffin Bay and Greenland Sea), and of the Canadian Archipelago, will

provide new habitats for seaweed colonization (Müller et al., 2009). Although concomitant increases in freshwater input, turbidity, and sedimentation will restrict kelp distribution and primary production in some locations, the kelp biomass could double in Arctic regions within less than 30 years (Bonsell and Dunton, 2018; Filbee-Dexter et al., 2019).

A few kelp species may gain advantage over the others by better acclimatizing to environmental stresses such as hyposalinity or increased turbidity in the summer. For example, while a poleward retreat of the endemic *Laminaria solidungula*, a stenothermic species that cannot live outside of a narrow range of cold temperature, is expected (Fig. 11; Müller et al., 2009), *Saccharina latissima* could benefit from these new conditions, especially from warming, thanks to a high degree of polymorphism, acclimatation and genetic diversity across populations (Bartsch et al., 2008; Guzinski et al., 2016). While kelp abundance and biomass may largely increase, the species composition will change, most likely impacting their associated fauna.

By gaining ground and increasing in biomass and productivity, kelps promote their associated fauna. For example, the annual growth rate of the sea urchin *Strongylocentrotus droebachiensis* is expected to increase with the increase in kelps (Blicher et al., 2007). However, distinction must be made between kelp species because the thallus morphology and species-specific interactions between macroalgae and associated epifaunal species largely affect the epifaunal composition (Lippert et al., 2001). For example, *Laminaria digitata* is not a preferred substrate for epiphytes due to its smooth surface; it therefore harbors a lower epiphytic diversity than *Alaria esculenta* (Lippert et al., 2001). By gaining ground, Kelps also decrease the abundance of taxa that are not associated with them such as sessile invertebrates and suspension feeders like ascidians, barnacles, and sea anemones (Beuchel and Gulliksen, 2008; Paar et al., 2016). By promoting only certain species while excluding others, the expansion of kelp species will most likely cause an homogenisation of Arctic coastal benthic communities (Weslawski et al., 2010; Csapó et al., 2021).

7.3. Coralline algae

Few studies have been carried out on the impacts of climate change on coralline algae. PAR decrease, as well as local hyposalinity, reduce the photosynthetic efficiency, reproduction and carbonate accumulation capacities of coralline algae (Schoenrock et al., 2018; Teichert et al.,

2014). Ocean acidification and warming may result in a fast decrease in calcification rate and percent cover which could impact the associated fauna (Fig. 11; Teichert et al., 2014; Chan et al., 2020). The distribution of Arctic calcified algae will be constrained by the upper temperature limit of the species in the South and by calcium carbonate saturation state in the North (Steinacher et al., 2009; Chan et al., 2020). Also, competition for space with kelps may hasten their demise. This will lead to ecosystem restructuring and loss of functions resulting from the possible disappearance of current subarctic coralline algae and their associated communities before the end of the century (Brodie et al., 2014).

7.4. Boreal species

The North Atlantic West Spitsbergen Current provides ca. 70% of water inputs into the Arctic Basin (Dickson et al., 1999). The Bering Sea is also an input source to the Beaufort and Chukchi Seas (Węśławski et al., 2011). In recent decades, warming combined with increased advection induced poleward migrations bringing thermal tolerant boreal-subarctic species in the Arctic Ocean (Fig. 10h; Weslawski et al., 2010). Furthermore, in response to the loss of Arctic sea ice, shipping transport along ice-free routes in the Canadian and Russian Arctic regions has increased (Lasserre and Pelletier, 2011). This will likely have a major role in the introduction of marine species in the Arctic (Jueterbock et al., 2016).

Migration may have caused the reappearance of the bivalve *Mytilus edulis* in Isfjorden (Svalbard) after more than 1,000 years of absence (Berge et al., 2005; Weslawski et al., 2010). The boreal kelp *Laminaria hyperborea* has also been recorded in the southern fjords of Spitsbergen, revealing its poleward migration progress (Peltikhina, 2002). Furthermore, over the last 20 years, at least 20 decapod species have expanded northward (Brattegard and Holthe, 1997). Migration has also been described in the Pacific Arctic (Grebmeier et al., 2006; Sirenko and Gagaev, 2007), in Kongsfjorden (Beuchel et al., 2006; Kędra et al., 2010) and in Hornsund (Węśławski et al., 2017).

New dominant species with a different ecosystem engineering role can alter local functional diversity (Zacher et al., 2019). Moreover, new species combinations and interactions modify species distributions (Pecl et al., 2017). Nevertheless, according to Renaud et al. (2019), the Arctic benthic species are unlikely to be fully replaced by boreal species because endemic species are not more vulnerable than boreal species to warming and acidification. Jueterbock

et al. (2016) predicted that habitat suitability for *Fucus serratus*, *Fucus vesiculosus*, and *Ascophyllum nodosum* would increase northward by 2100, particularly in Canada, Greenland, and Spitsbergen. They could be present at *F. distichus*' upper and lower zonation limits in the Arctic but these temperate species would not be able to compete with it because of *F. distichus* has competitive advantage such as being adapted to cold conditions and long dark periods (Jueterbock et al., 2016). Benthic taxa have restricted mobility and range changes are more likely to differ between taxon due to life-span, and dispersal capacity (Renaud et al., 2019).

As early as the 1930s, a documented warming of North Atlantic waters induced a major northward migration of boreal species (Drinkwater, 2006). Blacker's (1957) comprehensive shelf and coastal waters survey revealed changes in species distribution within the Arctic, with the northward migration of boreal echinoderms and decapods. However, only northward changes and increases in the abundance of southerly species were reported. In this early study, no new species was found in the Arctic region. Merzouk and Johnson (2011) were unable to document any significant change in dominant kelp species composition or abundance since the 1950s along the northwest Atlantic coast. Similarly, Adey and Hayek (2011) found no major changes in the distribution of subtidal algal species in Canada's eastern subarctic or boreal regions over the last 40 years. These observations suggest northward expansions are occurring slower than predicted or are being buffered by other factors (Filbee-Dexter et al., 2019). Extensive spatial gaps between suitable substrate, slow dispersal of propagules, water temperature, changes in turbidity, sea ice cover, and light penetration all influence the northward range expansion of kelps (Wernberg et al., 2019). At least in the short-term, the northern range expansions of boreal kelps across the Arctic may be overestimated (Filbee-Dexter et al., 2019).

Endemic Arctic species cope with environmental changes while also facing increasing competition pressure from invasive species, risk of infection by diseases, and predator-prey interactions with higher herbivore pressure (Weslawski et al., 2010). Borealization is expected to increase biodiversity in the short-term with coexisting inhabitants and competitors (Renaud et al., 2019). Some species may decline, other species or ecosystems may flourish to the benefit of coastal zones (Bartsch et al., 2016). New species interactions such as competition and prey-predator interactions are occurring and are yielding to new ecosystem functioning.

8. Conclusion

Coastal macroalgal communities in the Arctic are profoundly affected by increasing temperature, coastal erosion, freshwater input, coastal turbidity and sedimentation as well as decreasing ice cover and seawater pH. Changes in seasonality and food-web structure will likely result in major ecosystem restructuring (Morata et al., 2020; Bonsell and Dunton, 2021). In colder coastal Arctic regions, kelp forests may become more productive (Krause-Jensen and Duarte, 2014; Filbee-Dexter et al., 2019). Also, fucoids may largely extend in the Arctic whereas coralline algae may be more restricted under future conditions. The amount of detritus produced should rise which would affect the ecosystem functioning by damping fluctuations in seasonal carbon supply (Norkko et al., 2007). This could result in greater resilience of the benthos to variation of interannual pelagic primary production and more stable food-chains (Norkko et al., 2007; Renaud et al., 2015).

With global change, trawling and overfishing, sea urchins have become very abundant in some areas overgrazing the kelp forest (Konar et al., 2014). The disappearance of kelp forests impacts the whole ecosystem including species that feed on kelps (bristle worms, amphipods, prawns, snails, and brittle stars), species that feed on these herbivores (including species important to commercial fisheries: fishes, lobsters) - and/or species using kelp forest as a refuge area (sea lions, seals, gray whales, sea otters and even seabirds such as gulls or terns; Watson and Estes, 2011). In some areas, like around Tromsø, the ecosystem has collapsed into a bare and depauperate new state (Comeau, unpublished observations).

Many factors, including their interactions, are not yet understood, making it difficult to predict future coastal Arctic macroalgal communities and the whole ecosystem. It is likely that considerable ecological changes will occur with both positive and negative consequences on associated benthic species (Filbee-Dexter et al., 2019). Although large-scale warming, acidification and ice melting are on the way, changes at the local scale are also critical for benthic communities (Bonsell and Dunton, 2021). For example, in sheltered coastal areas, long-term ice changes could be more moderate than in exposed coastal areas (Bonsell and Dunton, 2018). The extent to which global change will affect benthic communities may differ depending on depth and regions (Weslawski et al., 2010).

Predicting the future of Arctic ecosystems is imperative to anticipate and to adapt to the coming changes (Krause-Jensen and Duarte, 2014; Filbee-Dexter et al., 2019). Nonetheless, the baseline knowledge on ecosystem structure and functioning in the Arctic is limited on both geographical and temporal scales (Wassmann et al., 2011). Long-term time series combining environmental conditions and community composition and distribution are essential but particularly scarce in the Arctic, limiting projections of future benthic communities (Piepenburg, 2005; Müller et al., 2009). Efforts must be made to improve knowledge in key regions with proper seasonal coverage to provide sound scientific advice on ecosystem management (Wassmann et al., 2011; Degen et al., 2016; Filbee-Dexter et al., 2019).

The poor knowledge about the interactions between multiple abiotic and biotic stressors, changes in climate-sensitive populations over time (including processes of acclimation and adaptation) and the general paucity of baseline species diversity and biogeographic distributions data are a significant stumbling block for understanding the current situation as well as to foresee future changes (Müller et al., 2009; Harley et al., 2012). Multifactorial studies at the community level that take into account interactions between stressors and across species are desperately lacking (Scherrer et al., 2019; Renaud et al., 2019). Only 52% of *ex situ* studies on Arctic kelps, 25% on coralline algae and 0% on fucoids focus on the impact of at least 2 parameters involved in climate change. Beyond 2 parameters, the percentages drop to 2.4 and 0% for kelps and coralline algae respectively (Table 1).

Through changes in weather and seasonal conditions and changes in biodiversity, global environmental change affects the local cultural, social, and economic life of indigenous people (Hovelsrud et al., 2011). It has also a critical impact on global markets through enhanced access to mineral resources, fisheries, and industrialization (e.g., AHDR, 2004; IPCC, 2007). Predicting and anticipating the future Arctic ecosystem is now more than ever a priority to adapt to fundamental changes in all sectors of the economy and society.

Funding

This study was conducted in the frame of the project FACE-IT (The Future of Arctic Coastal Ecosystems – Identifying Transitions in Fjord Systems and Adjacent Coastal Areas). FACE-IT has received funding from the European Union’s Horizon 2020 research and innovation programme under grant agreement No 869154.

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Supplementary data

Table S1: Articles focusing on the responses of shallow Arctic macroalgal communities to global change. The article types *in situ* and *ex situ* respectively correspond to studies conducted in the field and in the laboratory. The “none” type includes review articles and modeling exercises.

Tyoe	Location	Title	Date	Author	
none	Arctic	An Arctic Alaskan Kelp Bed	1957	Mohr	10.14430/arctic3754
<i>in situ</i>	Beaufort sea	An Arctic Alaskan Kelp Bed	1957	Mohr	10.14430/arctic3754
<i>ex situ</i>	Northern Norway	The effects of light and temperature on growth Rates in boreal-subarctic crustose corallines	1970	Adey	10.1111/j.1529-8817.1970.tb02392.x
<i>in situ</i>	Fury sound	Seasonal growth of <i>Laminaria solidungula</i> in the Canadian High Arctic in relation to irradiance and dissolved nutrient concentrations	1980	Chapman	10.1007/BF00420961
<i>in situ</i>	Stefansson Sound, Alaska	Growth of dark-exposed <i>Laminaria saccharina</i> (L.) Lamour, and <i>Laminaria solidungula</i> J. Ag. (Laminariales : phaeophyta) in the alaskan beaufort sea	1985	Dunton	10.1016/0022-0981(85)90057-7
<i>in situ</i>	Stefansson Sound, Alaska	Dependence of consumers on macroalgal (<i>Laminaria solidungula</i>) carbon in an arctic kelp community: $\delta^{13}C$ evidence	1987	Dunten & Schell	10.1007/BF00392799
<i>in situ</i>	Stefansson Sound, Alaska	Photosynthetic performance of <i>Laminaria solidungula</i> measured <i>in situ</i> in the Alaskan High Arctic	1988	Dunton	10.1007/BF00391206
<i>in situ</i>	Svalbard	The phytobenthos of the Hornsund fjord, SW Spitsbergen	1989	Florczyk & Latala	10.3402/polar.v7i1.6828
<i>in situ</i>	Hudson bay	Arctic algal communities in the region of the Nuvuk Islands, Northeastern Hudson Bay, Canada	1989	Keats	NA
<i>in situ</i>	Stefansson Sound, Alaska	Growth and production in <i>Laminaria solidungula</i> : relation to continuous underwater light levels in the Alaskan High Arctic	1990	Dunton	10.1007/BF01314813
<i>ex situ</i>	Sisimiut	Temperature requirements for growth and survival of macroalgae from Disko Island (Greenland)	1993	Bischof & Wiencke	10.1007/BF02430357
<i>in situ</i>	Stefansson Sound, Alaska	The Effects of the endicott development project on the Boulder Patch, an Arctic kelp community in Stefansson Sound, Alaska	1993	Martin & Gallaway	10.14430/arctic1271
<i>in situ</i>	Stefansson Sound, Alaska	A seasonal comparison of carbon, nitrogen, and pigment content in <i>Laminaria solidungula</i> and <i>L. saccharina</i> (Phaeophyta) in the Alaskan Arctic	1995	Henley & Dunton	10.1111/j.0022-3646.1995.00325.x

<i>ex situ</i>	Svalbard	Influence of UV radiation on the photosynthesis of arctic macroalgae in the field	1997	Hanelt	10.1016/S1011-1344(96)07415-5
<i>ex situ</i>	Stefansson Sound, Alaska	Effects of nitrogen supply and continuous darkness on growth and photosynthesis of the arctic kelp <i>Laminaria solidungula</i>	1997	Henley	10.4319/LO.1997.42.2.0209
<i>ex situ</i>	Svalbard	Acclimation of brown algal photosynthesis to ultraviolet radiation in Arctic coastal waters (Spitsbergen, Norway)	1998	Bischof	10.1007/s003000050319
<i>ex situ</i>	Svalbard	Capability of dynamic photoinhibition in Arctic macroalgae is related to their depth distribution	1998	Hanelt	10.1007/s002270050329
<i>in situ</i>	Svalbard	Effects of solar radiation on growth, photosynthesis and respiration of marine macroalgae from the Arctic	1999	Aguilera	10.3354/meps191109
<i>ex situ</i>	Svalbard	Acclimation of maximal quantum yield of photosynthesis in the brown alga <i>Alaria esculenta</i> under high light and UV radiation	1999	Bischof	10.1111/j.1438-8677.1999.tb00726.x
<i>ex situ</i>	Northern Norway	Seasonal dynamics of growth in the Barents Sea seaweeds: endogenous and exogenous regulation	1999	Marakov	10.1515/BOT.1999.007
both	Svalbard	Photosynthesis of two Arctic macroalgae under different ambient radiation levels and their sensitivity to enhanced UV radiation	2000	Brouwer	10.1007/s003000050442
none	Arctic	Life strategy, ecophysiology and ecology of seaweeds in polar waters	2000	Wiencke	10.1007/s11157-006-9106-z
both	Svalbard	Impact of UV-radiation on viability, photosynthetic characteristics and DNA of brown algal zoospores: Implications for depth zonation	2000	Wiencke	10.3354/meps197217
<i>in situ</i>	Svalbard	Light regime in an Arctic fjord: a study related to stratospheric ozone depletion as a basis for determination of UV effects on algal growth	2001	Hanelt	10.1007/s002270000481
<i>in situ</i>	Svalbard	Photosynthetic performance of Arctic macroalgae after transplantation from deep to shallow waters	2001	Karsten	10.1007/s004420000553
none	Arctic	Seasonal variation in ecophysiological patterns in macroalgae from an Arctic fjord. II. Pigment accumulation and biochemical defence systems against high light stress	2002	Aguilera	10.1007/s00227-002-0792-y
<i>in situ</i>	Svalbard	Enzymatic defences against photooxidative stress induced by ultraviolet radiation in Arctic marine macroalgae	2002	Aguilera	10.1007/s00300-002-0362-2
none	Arctic	Seasonal variation in ecophysiological patterns in macroalgae from an Arctic fjord. I. Sensitivity of photosynthesis to ultraviolet radiation	2002	Bischof	10.1007/s00227-002-0795-8
<i>in situ</i>	Svalbard	Seasonal variation in ecophysiological patterns in macroalgae from an Arctic fjord, I, Sensitivity of photosynthesis to ultraviolet radiation	2002	Bischof	10.1007/s00227-002-0795-8
<i>in situ</i>	Young Sound	Biomass, photosynthesis and growth of <i>Laminaria saccharina</i> in a high-arctic fjord, NE Greenland	2002	Borum	10.1007/s00227-002-0806-9
none	Young Sound	Biomass, photosynthesis and growth of <i>Laminaria saccharina</i> in a high-arctic fjord, NE Greenland	2002	Borum	10.1007/s00227-002-0806-9

<i>in situ</i>	Svalbard	Long-term effects of ultraviolet radiation on growth and photosynthetic performance of polar and cold-temperate macroalgae	2002	Michler	10.1007/s00227-002-0791-z
<i>in situ</i>	Young Sound	Primary production of crustose coralline red algae in a high Arctic fjord	2002	Roberts	10.1046/j.1529-8817.2002.01104.x
<i>ex situ</i>	Svalbard	Ultraviolet-B–Induced Cyclobutane-pyrimidine Dimer Formation and Repair in Arctic Marine Macrophytes	2002	Van de Poll	10.1562/0031-8655(2002)0760493UBICPD2.0.CO2
<i>ex situ</i>	Svalbard	Screening capacity of UV-absorbing compounds in spores of Arctic Laminariales	2003	Roleda	10.1016/j.jembe.2006.07.004
<i>ex situ</i>	Svalbard	The effect of elevated UV radiation on <i>Fucus</i> spp.(Fucales, Phaeophyta) zygote and embryo development	2003	Schoenwaelder	10.1055/s-2003-42716
<i>ex situ</i>	Svalbard	The Effect of Ultraviolet Radiation on Ultrastructure and Photosynthesis in the Red Macroalgae <i>Palmaria palmata</i> and <i>Odonthalia dentata</i> from Arctic Waters	2004	Holzinger	10.1055/s-2004-821003.
<i>ex situ</i>	Svalbard	Sensitivity and acclimation to UV radiation of zoospores from five species of Laminariales from the Arctic	2004	Wiencke	10.1007/s00227-004-1307-9
<i>in situ</i>	Svalbard	Long-term patterns of rocky bottom macrobenthic community structure in an Arctic fjord (Kongsfjorden, Svalbard) in relation to climate variability (1980–2003)	2006	Beuchel	10.1016/j.jmarsys.2006.05.002
<i>in situ</i>	Svalbard	The response of nutrient assimilation and biochemical composition of Arctic seaweeds to a nutrient input in summer	2006	Gordillo	10.1093/JXB/ERL029
<i>ex situ</i>	Svalbard	Exposure to ultraviolet radiation delays photosynthetic recovery in Arctic kelp zoospores	2006	Roleda	10.1007/s11120-006-9055-y
<i>ex situ</i>	Svalbard	Impact of ultraviolet radiation on cell structure, UV-absorbing compounds, photosynthesis, DNA damage, and germination in zoospores of Arctic <i>Saccorhiza dermatodea</i>	2006	Roleda	10.1093/jxb/erl154
<i>ex situ</i>	Svalbard	Thallus morphology and optical characteristics affect growth and DNA damage by UV radiation in juvenile Arctic <i>Laminaria</i> sporophytes	2006	Roleda	10.1007/s00425-005-0092-0
<i>ex situ</i>	Svalbard	Susceptibility of zoospores to UV radiation determines upper depth distribution limit of Arctic kelps: evidence through field experiments	2006	Wiencke	10.1111/j.1365-2745.2006.01102.x
<i>in situ</i>	Stefansson Sound, Alaska	Linking light attenuation and suspended sediment loading to benthic productivity within an Arctic kelp-bed community	2007	Aumack	10.1111/j.1529-8817.2007.00383.x
<i>ex situ</i>	Svalbard	Research note: Salinity tolerance of Arctic kelps from Spitsbergen	2007	Karsten	10.1111/j.1440-1835.2007.00468.x
none	Svalbard	Sensitivity of the early life stages of macroalgae from the Northern Hemisphere to ultraviolet radiation	2007	Roleda	10.1562/2006-08-17-IR-1005
<i>in situ</i>	Svalbard	Temporal patterns of benthic community development in an Arctic fjord (Kongsfjorden, Svalbard): results of a 24-year manipulation study	2008	Beuchel	10.1007/s00300-008-0429-9

<i>ex situ</i>	Svalbard	Interactive effects of UV radiation and temperature on microstages of Laminariales (Phaeophyceae) from the Arctic and North Sea	2008	Müller	10.3354/cr00762
none	Arctic	Drivers of colonization and succession in polar benthic macro- and microalgal communities	2009	Campana	10.1515/BOT.2009.076
<i>ex situ</i>	Svalbard	Interactive effects of radiation, temperature and salinity on different life history stages of the Arctic kelp <i>Alaria esculenta</i> (Phaeophyceae)	2009	Fredersdorf	10.1007/s00442-009-1326-9
none	Arctic	Light and temperature demands of marine benthic microalgae and seaweeds in polar regions	2009	Gómez	10.1515/BOT.2009.073
<i>ex situ</i>	Svalbard	Zoospores of three Arctic laminariales under different UV radiation and temperature conditions: exceptional spectral absorbance properties and lack of phlorotannin induction	2009	Muller	10.1111/j.1751-1097.2008.00515.x
<i>in situ</i>	Svalbard	Lipid content and fatty acid consumption in zoospores/ developing gametophytes of <i>Saccharina latissima</i> (Laminariales, Phaeophyceae) as potential precursors for secondary metabolites as phlorotannins	2010	Steinhoff	10.1007/s00300-011-0960-y
<i>ex situ</i>	Svalbard	Calcification of the Arctic coralline algae <i>Lithothamnion glaciale</i> in response to elevated CO ₂	2011	Büdenbender	10.3354/meps09405
<i>ex situ</i>	Svalbard	UV-radiation and elevated temperatures induce formation of reactive oxygen species in gametophytes of cold-temperate/Arctic kelps (Laminariales, Phaeophyceae)	2011	Müller	10.1111/j.1440-1835.2011.00630.x
<i>ex situ</i>	Jakalof bay	Salinity and irradiance effects on growth and maximum photosynthetic quantum yield in subarctic <i>Saccharina latissima</i> (Laminariales, Laminariaceae)	2011	Spurkland	10.1515/bot.2011.042
<i>ex situ</i>	Svalbard	Effects of water temperatures, UV radiation and low vs high PAR on phlorotannin content and germination in zoospores of <i>Saccorhiza dermatodea</i> (Tilopteridales, Phaeophyceae)	2011	Steinhoff	10.2216/09-107.1
<i>ex situ</i>	Svalbard	Phlorotannin production and lipid oxidation as a potential protective function against high photosynthetically active and UV radiation in gametophytes of <i>Alaria esculenta</i> (Alariales, Phaeophyceae)	2011	Steinhoff	10.1111/j.1751-1097.2011.01004.x
none	Arctic	Footprints of climate change in the Arctic marine ecosystem	2011	Wassmann	10.1111/j.1365-2486.2010.02311.x
<i>in situ</i>	Svalbard	The algal vegetation in the outer part of Isfjorden, Spitsbergen: revisiting Per Svendsen's sites 50 years later	2012	Fredriksen	10.3402/polar.v31i0.17538
<i>ex situ</i>	Svalbard	A comprehensive cDNA library of light- and temperature-stressed <i>Saccharina latissima</i> (Phaeophyceae)	2012	Heinrich	10.1080/09670262.2012.660639
<i>in situ</i>	Svalbard	Species composition, zonation, and biomass of marine benthic macroalgae in Kongsfjorden, Svalbard	2012	Hop	10.1515/bot-2012-0097
<i>in situ</i>	Svalbard	Climate-driven regime shifts in Arctic marine benthos	2012	Kortsch	10.1073/pnas.1207509109
<i>in situ</i>	Qaanaaq	Seasonal sea ice cover as principal driver of spatial and temporal variation in depth extension and annual production of kelp in Greenland	2012	Krause-Jensen	10.1111/j.1365-2486.2012.02765.x

none	Arctic	Seaweeds and Their Communities in Polar Regions	2012	Wiencke	10.1007/978-3-642-28451-9_13
<i>in situ</i>	Stefansson Sound, Alaska	Lack of recovery from disturbance in high-arctic boulder communities	2013	Konar	10.1007/s00300-013-1340-6
<i>ex situ</i>	Svalbard	Rapid phosphorylation of MAP kinase-like proteins in two species of Arctic kelps in response to temperature and UV radiation stress	2013	López Parages	10.1016/j.envexpbot.2013.02.005
<i>in situ</i>	Pangnirtung fjord	Food web structure of a coastal Arctic marine ecosystem and implications for stability	2013	McMeans	10.3354/MEPS10278
<i>ex situ</i>	Svalbard	Seasonal fertility and combined effects of temperature and UV-radiation on <i>Alaria esculenta</i> and <i>Laminaria digitata</i> (Phaeophyceae) from Spitsbergen	2013	Olischläger	10.1007/s00300-013-1325-5
<i>in situ</i>	Svalbard	Arctic rhodolith beds and their environmental controls (Spitsbergen, Norway)	2013	Teichert	10.1007/s10347-013-0372-2
<i>in situ</i>	Svalbard	New additions to the benthic marine flora of Kongsfjorden, western Svalbard, and comparison between 1996/1998 and 2012/2013	2014	Fredriksen	10.1515/bot-2013-0119
none	Arctic	Expansion of vegetated coastal ecosystems in the future Arctic	2014	Krause-Jensen	10.3389/fmars.2014.00077
<i>ex situ</i>	Svalbard	Ocean acidification modulates the response of two Arctic kelps to ultraviolet radiation	2015	Gordillo	10.1016/j.jplph.2014.09.008
<i>ex situ</i>	Svalbard	Increased CO ₂ modifies the carbon balance and the photosynthetic yield of two common Arctic brown seaweeds: <i>Desmarestia aculeata</i> and <i>Alaria esculenta</i>	2015	Iniguez	10.1007/s00300-015-1724-x
<i>ex situ</i>	Svalbard	The effect of ultraviolet radiation on cellular ultrastructure and photosystem II quantum yield of <i>Alaria esculenta</i> (L.) Greville from Spitsbergen (Norway)	2015	Lütz	10.1007/s00300-015-1659-2
none	Arctic	The future of Arctic benthos: Expansion, invasion, and biodiversity	2015	Renaud	10.1016/j.pocean.2015.07.007
<i>in situ</i>	Svalbard	Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient	2015	Renaud	10.3389/fmars.2015.00031
<i>in situ</i>	Svalbard	Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and 2012–2014 reflect Arctic warming	2016	Bartsch	10.1007/s00300-015-1870-1
<i>in situ</i>	Svalbard	Distribution of macroalgae in Kongsfjorden, Svalbard	2016	Hop	10.1007/s00300-016-2048-1
<i>ex situ</i>	Svalbard	Increased temperature, rather than elevated CO ₂ , modulates the carbon assimilation of the Arctic kelps <i>Saccharina latissima</i> and <i>Laminaria solidungula</i>	2016	Iñiguez	10.1007/s00227-016-3024-6
none	Arctic	The fate of the Arctic seaweed <i>Fucus distichus</i> under climate change: an ecological niche modeling approach	2016	Jueterbock	10.1002/ece3.2001
<i>in situ</i>	Qeqertarsuaq	Long photoperiods sustain high pH in Arctic kelp forests	2016	Krause-Jensen	10.1126/sciadv.1501938

<i>ex situ</i>	Svalbard	Stress physiology and reproductive phenology of Arctic endemic kelp <i>Laminaria solidungula</i> J. Agardh	2016	Roleda	10.1007/s00300-015-1813-x
<i>ex situ</i>	Svalbard	Variation in thermal stress response in two populations of the brown seaweed, <i>Fucus distichus</i> , from the Arctic and subarctic intertidal	2016	Smolina	10.1098/rsos.150429
none	Svalbard	Ecosystem Kongsfjorden: new views after more than a decade of research	2016	Wiencke	10.1007/s00300-016-2032-9
<i>in situ</i>	Sisimiut	Climate change stimulates the growth of the intertidal macroalgae <i>Ascophyllum nodosum</i> near the northern distribution limit	2017	Márba	10.1007/s13280-016-0873-7
<i>ex situ</i>	Svalbard	Implications of rising temperatures for gametophyte performance of two kelp species from Arctic waters	2017	Park	10.1515/bot-2016-0103
<i>ex situ</i>	Svalbard	Hyposaline conditions affect UV susceptibility in the Arctic kelp <i>Alaria esculenta</i> (Phaeophyceae)	2017	Springer	10.2216/16-122.1
<i>in situ</i>	Stefansson Sound, Alaska	Long-term patterns of benthic irradiance and kelp production in the central Beaufort sea reveal implications of warming for Arctic inner shelves	2018	Bonsell	10.1016/j.pocean.2018.02.016
<i>in situ</i>	Svalbard	Arctic coralline algae elevate surface pH and carbonate in the dark	2018	Hofmann	10.3389/fpls.2018.01416
<i>in situ</i>	Nuuk	Canopy-Forming Macroalgae Facilitate Recolonization of Sub-Arctic Intertidal Fauna and Reduce Temperature Extremes	2018	Ørberg	10.3389/fmars.2018.00332
none	Svalbard	Mechanistic model identifies increasing light availability due to sea ice reductions as cause for increasing macroalgae cover in the Arctic	2018	Scherrer	10.1002/lno.11043
none	Svalbard	Mechanistic model identifies increasing light availability due to sea ice reductions as cause for increasing macroalgae cover in the Arctic	2018	Scherrer	10.1002/lno.11043
<i>ex situ</i>	Nuuk	Influences of salinity on the physiology and distribution of the Arctic coralline algae, <i>Lithothamnion glaciale</i> (Corallinales, Rhodophyta)	2018	Schoenrock	10.1111/jpy.12774
<i>in situ</i>	Svalbard	The longer the better: the effect of substrate on sessile biota in Arctic kelp forests	2018	Shunatova	10.1007/s00300-018-2263-z
<i>in situ</i>	Nome, Alaska	DNA barcoding of the marine macroalgae from Nome, Alaska (Northern Bering Sea) reveals many trans-Arctic species	2019	Bringloe	10.1007/s00300-019-02478-4
none	Arctic	Arctic kelp forests: Diversity, resilience and future	2019	Filbee-Dexter	10.1016/j.gloplacha.2018.09.005
<i>in situ</i>	Qeqertarsuaq	Deep penetration of kelps offshore along the west coast of Greenland	2019	Krause-Jensen	10.3389/fmars.2019.00375
<i>in situ</i>	Svalbard	Effects of kelp canopy on underwater light climate and viability of brown algal spores in Kongsfjorden (Spitsbergen)	2019	Laeseke	10.1007/s00300-019-02537-w
none	Svalbard	Ecological drivers of and responses by Arctic benthic communities, with an emphasis on Kongsfjorden, Svalbard	2019	Molis	10.1007/978-3-319-46425-1_11

<i>ex situ</i>	Svalbard	Temperature mediates the outcome of species interactions in early life-history stages of two sympatric kelp species	2019	Zacher	10.1007/s00227-019-3600-7
<i>in situ</i>	Svalbard	Arctic coastal benthos long-term responses to perturbations under climate warming	2020	Al-Habahbeh	10.1098/rsta.2019.0355
<i>in situ</i>	Bering Sea	Population structure in Arctic marine forests is shaped by diverse recolonisation pathways and far northern glacial refugia	2020	Bringloe	10.1101/2020.03.19.999466
<i>ex situ</i>	Svalbard	Transcriptomic responses to darkness and the survival strategy of the kelp <i>Saccharina latissima</i> in the early polar night	2020	Huiru Li	10.3389/fmars.2020.592033
<i>ex situ</i>	Northern Norway	Heat stress responses and population genetics of the kelp <i>Laminaria digitata</i> (Phaeophyceae) across latitudes reveal differentiation among North Atlantic populations	2020	Liesner	10.1002/ece3.6569
<i>ex situ</i>	Svalbard	Thermal traits for reproduction and recruitment differ between Arctic and Atlantic kelp <i>Laminaria digitata</i>	2020	Martins	10.1371/journal.pone.0235388
both	Beaufort sea	Physiological responses of an Arctic crustose coralline alga (<i>Leptophytum foecundum</i>) to variations in salinity	2020	Muth	10.3389/fpls.2020.01272
<i>in situ</i>	Svalbard	Glacial and depth influence on sublittoral macroalgal standing stock in a high-Arctic fjord	2020	Ronowicz	10.1016/j.csr.2019.104045
<i>ex situ</i>	Qikiqtarjuaq	Arctic crustose coralline alga resilient to recent environmental change	2020	Williams	10.1002/Ino.11640
<i>in situ</i>	Stefansson Sound, Alaska	Slow community development enhances abiotic limitation of benthic community structure in a high Arctic kelp bed	2021	Bonsell	10.3389/fmars.2021.592295
<i>ex situ</i>	Svalbard	Coping with a changing Arctic: mechanisms of acclimation in the brown seaweed <i>Saccharina latissima</i> from Spitsbergen	2021	Diehl	10.3354/meps13532
<i>ex situ</i>	Svalbard	Summer heatwave impacts on the European kelp <i>Saccharina latissima</i> across its latitudinal distribution gradient	2021	Diehl	10.3389/fmars.2021.695821
<i>in situ</i>	Hudson/Baffin bay, Labrador sea	Sea ice and substratum shape extensive kelp forests in the Canadian Arctic	2021	Filbee-Dexter	10.32942/osf.io/t82cf
none	Hudson/Baffin bay, Labrador sea	Kelp in the Eastern Canadian Arctic: current and future predictions of habitat suitability and cover	2021	Goldsmid	10.3389/fmars.2021.742209
<i>ex situ</i>	Svalbard	Differential acclimation responses to irradiance and temperature in two co-occurring seaweed species in Arctic fjords	2021	Marambio	10.33265/polar.v40.5702
<i>ex situ</i>	White sea	On the distribution of the Arctic endemic alga <i>Laminaria solidungula</i> (Laminariales) in the White Sea	2021	Mikhaylova	10.31111/nsnr/2021.55.2.325
both	Stefansson Sound, Alaska	Inherent tolerance of extreme seasonal variability in light and salinity in an Arctic endemic kelp (<i>Laminaria solidungula</i>)	2021	Muth	10.1111/jpy.13187

<i>ex situ</i>	Svalbard	Daylength influences reproductive success and sporophyte growth in the Arctic kelp species <i>Alaria esculenta</i>	2022	Martins	10.3354/meps13950
<i>in situ</i>	Svalbard	Video survey of deep benthic macroalgae and macroalgal detritus along a glacial Arctic fjord: Kongsfjorden (Spitsbergen)	2022	Schimani	10.1007/s00300-022-03072-x
<i>ex situ</i>	Svalbard	Microscopic Stages of North Atlantic <i>Laminaria digitata</i> (Phaeophyceae) Exhibit Trait-Dependent Thermal Adaptation Along Latitudes	2022	Schimpf	10.3389/fmars.2022.870792
<i>ex situ</i>	Svalbard	Microscopic life stages of Arctic kelp differ in their resilience and reproductive output in response to Arctic seasonality	2022	Silva	10.1080/09670262.2021.2014983



In order to address the knowledge gaps identified through the literature review in the first chapter, the second chapter investigates the responses of Arctic kelp species to warming and ice melting. Multi- and uni-factorial treatments were used to study the impact of warming alone and combined with reduced salinity and underwater light through a mesocosm experiment. The experiment took place in Ny-Ålesund (Svalbard) in summer 2021.

Chapter 2: Multifactorial effects of warming, low irradiance, and low salinity on Arctic kelps

Anaïs Lebrun¹, Cale A. Miller^{1,2}, Marc Meynadier³, Steeve Comeau¹, Pierre Urrutti¹, Samir Alliouane¹, Robert Schlegel¹, Jean-Pierre Gattuso^{1,4}, Frédéric Gazeau¹

¹Laboratoire d'Océanographie de Villefranche, Sorbonne Université, CNRS, Villefranche-sur-Mer, France

²Department of Earth Sciences, Utrecht University, Utrecht, The Netherlands

³Laboratoire de Biologie du Développement de Villefranche-sur-mer, Sorbonne Université, CNRS, Villefranche-sur-Mer, France

⁴Institute for Sustainable Development and International Relations, Sciences Po, Paris, France

This article has been submitted in Biogeosciences.

Abstract

The Arctic is projected to warm by 2 to 5 °C by the end of the century. Warming causes melting of glaciers, shrinking of the areas covered by sea ice, and increased terrestrial runoff from snowfields and permafrost thawing. Warming, decreasing coastal underwater irradiance, and lower salinity are potentially threatening polar marine organisms, including kelps, that are key species of hard-bottom shallow communities. The present study investigates the physiological responses of four kelp species (*Alaria esculenta*, *Laminaria digitata*, *Saccharina latissima*, and *Hedophyllum nigripes*) to warming, low irradiance, and low salinity through a perturbation experiment conducted in *ex situ* mesocosms. Kelps were exposed during six weeks to four experimental treatments: an unmanipulated control, a warming condition mimicking future coastlines unimpacted by glacier melting under the CO₂ emission scenario SSP5-8.5, and two multifactorial conditions combining warming, low salinity, and low irradiance reproducing the future coastal Arctic exposed to terrestrial runoff following two CO₂ emission scenarios (SSP2-4.5 and SSP5-8.5). The physiological effects on *A. esculenta*, *L. digitata* and *S. latissima* were investigated and gene expression patterns of *S. latissima* and *H. nigripes* were analyzed. Specimens of *A. esculenta* increased their chlorophyll *a* content when exposed to low irradiance conditions, suggesting that they may be resilient to an increase in glacier and river runoff and become more dominant at greater depths. *S. latissima* showed a lower carbon:nitrogen (C:N) ratio at higher nitrate concentrations, suggesting coastal erosion and

permafrost thawing could benefit the organism in the future Arctic. In contrast, *L. digitata* showed no responses to the conditions tested on any of the investigated physiological parameters. The gene expressions of *H. nigripes* and *S. latissima* underscores their ability and underline temperature as a key influencing factor. Based on these results, it is expected that kelp communities will undergo changes in species composition that will vary at local scale as a function of the changes in environmental drivers. For future research, potential cascading effects on the associated fauna and the whole ecosystem are important to anticipate the ecological, cultural, and economic impacts of climate change in the Arctic.

1. Introduction

The Arctic region is warming at more than twice the global average rate (Richter-Menge et al., 2017). Over the next 80 years, sea surface temperature is projected to increase by 2 °C according to the Shared Socio-economic Pathways (SSP) 1-2.6, which foresees an increasing shift towards sustainable practices, and up to 5 °C according to the SSP5-8.5, which assumes an energy-intensive and fossil fuel-based economy (Kwiatkowski et al., 2020). Warming induces glacier and sea ice to melt at a faster rate causing an increase in terrestrial runoff from thawing snowfields and permafrost (Shiklomanov and Shiklomanov 2003; Stroeve et al., 2014). Total freshwater inflow into the Arctic Ocean rose by around 7% between 1936 and 1999 and 14% between 1980 and 2009 (Peterson et al., 2002; Ahmed et al., 2020). Combined with vertical mixing by waves and wind action, cryosphere melting results in local turbid and low-salinity waters down to 20 m (Karsten 2007). Coastal areas are therefore exposed to warming, changing light and salinity conditions (Lebrun et al., 2022).

In the coastal Arctic, kelps are key ecosystem engineers. Kelp forests provide a food source, habitat, and nursery ground for numerous fish and invertebrates as well as protect the coast from erosion (Filbee-Dexter et al., 2019). They support complex food webs and have a substantial role in storing and sequestering carbon (Krause-Jensen and Duarte 2016). *Saccharina latissima*, *Alaria esculenta*, *Laminaria digitata*, and *Hedophyllum nigripes* are four abundant kelp species that inhabit the northern hemisphere and extend to subarctic and Arctic waters (Bischof et al., 1999; Müller et al. 2009). As a result of warming, which induces more sea ice-free areas, the surface area suitable for kelps has increased by about 45% from 1940-1950 to 2000-2017 (Krause-Jensen et al., 2020). Temperature requirements and seasonal variability tolerance in irradiance and salinity for reproduction and growth determine

the geographical distribution of kelp species (Wiencke et al. 1994, Muth et al., 2021). Irradiance has a major impact on their depth distribution (e.g. Roleda et al. 2005; Krause-Jensen et al., 2012). Turbid waters alter kelp fitness by limiting photosynthesis. This has already induced a shift in the vertical distribution of kelps such as *Laminaria* and *Saccharina* genera to shallower waters (Bartsch et al., 2016; Filbee-Dexter et al., 2019). Because optimal temperature, irradiance, and salinity ranges vary between kelp species, their response to environmental changes will likely be species-specific (Eggert 2012; Karsten 2012).

We hypothesized that (1) warming will enhance the growth rate of kelps during summer, and (2) that the combined effects of high temperature, low salinity and low irradiance will negatively impact their physiology, although responses will be species-specific. To test these hypotheses and fill knowledge gaps on the multifactorial effects of climate change across species (Renaud et al., 2019; Scherrer et al., 2019), we carried out a land-based mesocosm experiment exposing four kelp species (*S. latissima*, *A. esculenta*, *L. digitata*, and *H. nigripes*) to four treatments for six weeks. The treatments consisted of a control, a warming condition mimicking the future offshore (T1), and two multifactorial conditions combining warming, low salinity, and low irradiance mimicking the future coastal Arctic (T2 and T3). In order to best represent *in situ* conditions, the different kelp species were incubated together in each mesocosm at densities mimicking natural communities. The physiological effects on *A. esculenta*, *L. digitata* and *S. latissima* were investigated and gene expression patterns of *S. latissima* and *H. nigripes* were analyzed.

2. Material and methods

2.1 Specimen collection

In June 2021, 188 sporophytes of *A. esculenta*, *L. digitata*, *S. latissima*, and *H. nigripes* shorter than 1 m were collected by research divers in Kongsfjorden (Svalbard, Norway). They were collected between 2 and 7 m depth at Hansneset and the Old Pier (Fig. 12). All samples were placed into holding tanks (> 1 m³) until their placement into final mesocosms on 2021-07-03.

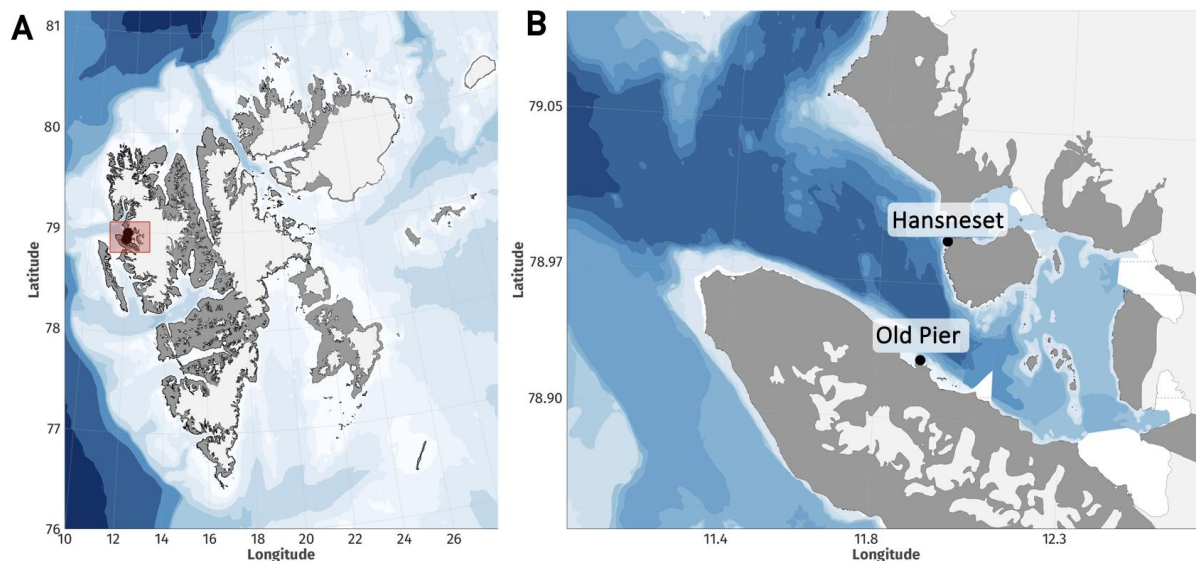


Figure 12: The study was carried out in Svalbard (A) on kelp sampled in Kongsfjorden (B) in Hansneset and the Old Pier. Maps were created using the R package ggOceanMaps (Vihtakari, 2023).

2.2 Mesocosm experiment

The experiment was carried out from 2021-07-03 (t_0) to 2021-08-28 (t_{final}), in twelve 1 m^3 mesocosms set up in Ny-Ålesund on the outdoor platform of the Kings Bay Marine Laboratory in order to expose communities to natural light cycles. Each mesocosm received 3 to 6 individuals of *A. esculenta* and *S. latissima*, 2 to 4 individuals of *L. digitata* and 0 to 2 individuals of *H. nigripes* for a total mass (wet weight) of kelp biomass per mesocosm of about 1500 g for *S. latissima* and *L. digitata* (mingled with *H. nigripes*) and 1000 g for *A. esculenta*. These biomasses are representative of those found at Hansneset down to 7 m depth (Hop et al., 2012). Since *H. nigripes* can be mistaken for *L. digitata*, each stipe of these two species was cut at t_{final} to detect individuals with mucilage, corresponding to *H. nigripes* ($n=16$, Dankworth et al., 2020).

The experimental set-up is briefly described below. More information can be found in Miller et al. (under revision). Seawater flowing through the mesocosms was pumped from 10 m depth in front of the Kings Bay Marine Laboratory (78.929°N , 11.930°E) using a submersible pump (Albatros©). The regulated flow-through system ($7 - 8 \text{ L min}^{-1}$ in each mesocosm) allowed for the automated control of temperature and salinity. Temperature was adjusted by mixing ambient seawater with warmed seawater (15°C) and salinity was regulated by addition of freshwater. Each mesocosm was equipped with one 12 W wave pump (Sunsun© JVP-132) to ensure proper mixing.

Four experimental treatments in triplicate (4x3 mesocosms) were used to study conditions representative of present and future Arctic coastal communities at proximity or not to glaciers following two different SSP scenarios (Ctrl, T1, T2, T3; Table 2). Treatments 1 and 2 (T1 and T2) mimicked the conditions expected close to glaciers and, therefore, combined warming, low irradiance, and low salinity. T1 followed the SSP 2-4.5, which describes a middle-of-the-road projection that does not shift markedly from historical patterns, while T2 followed the SSP5-8.5 that assumes an energy-intensive and fossil fuel-based economy. T3 focused on the projected change outside glacial fjords following the SSP 5-8.5, where warming acts as a single driver. Temperature was increased by 3.3 °C in T1 and 5.3 °C in T2 and T3 as an offset increase from the control condition (Ctrl) which mimicked the *in situ* temperature recorded in real-time during the whole experiment. Based on *in situ* measurements taken from week 22 to 35 in 2020 in the Kongsfjorden, salinity offsets were determined from the *in situ* relationship between temperature and salinity and extrapolated to apply to future warming. This resulted in a salinity decreased by 2.5 in T1 and 5 in T2 (Miller et al., under revision). Based on *in situ* photosynthetically active radiation (PAR) data collected in May 2021 with a LICOR, irradiance was reduced from the control by a mean of 20% for T1, corresponding to the difference between the glacier-proximal inner region and the middle of the fjord, and 30% for T2, corresponding to the difference between the inner and outer parts of the fjord. To simulate the *in situ* light spectrum (Kai Bischof, pers. com.) and reach the irradiance matching the targeted treatments, green (RL244) and neutral Lee filters[©] (RL211; RL298) were placed on top of mesocosms (Table 2). During the first week, all the mesocosms were maintained under *in situ* conditions of temperature, salinity, and irradiance. The light filters were then added to the mesocosms of T1 and T2 treatments on 2021-07-10 and all treatments gradually reached their targeted temperature and salinity conditions in six days. The experiment then lasted for six weeks.

Table 2: Temperature, salinity, and photosynthetically active radiation during the experiment. T1 and T2 treatments represent future coastline exposed to runoff conditions, whereas T3 treatment represents future conditions on shores not exposed to runoff. The quartiles and medians were calculated based on data acquired from 2021-07-10 for Photosynthetically Active Radiation (PAR) and 2021-07-16 for temperature and salinity (once the targeted treatments were reached) until the end of the experiment.

Treatment	Scenario	Temperature (°C)				Salinity				daily PAR ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)			
		Δ	1st quartile	Median	3rd quartile	Δ	1st quartile	Median	3rd quartile	Δ	1st quartile	Median	3rd quartile
Ctrl	control	<i>in situ</i>	4.8	5.3	5.8	<i>in situ</i>	33.4	33.8	34.3	<i>in situ</i>	35.1	47.8	59.5
T1	SSP2-4.5 - coastline	+3.3 °C	8.4	8.9	9.2	-2.5	30.8	31.0	31.8	-20 %	27.8	36.1	43.9
T2	SSP5-8.5 - coastline	+5.3 °C	10.3	10.8	11.2	-5	28.2	28.5	29.5	-30 %	23.8	31.4	40.7
T3	SSP5-8.5 - offshore	+5.3 °C	10.3	10.8	11.2	<i>in situ</i>	33.4	33.9	34.5	<i>in situ</i>	40.3	54.8	69.9

2.3 Tissue sampling

Tissue samples were collected in the meristem of ten individuals of *A. esculenta*, *L. digitata*, and *S. latissima* at the beginning of the experiment (t_0 , 2021-07-03) and on the healthy organisms, namely complete organisms (frond, stipe, and holdfast) that exhibit a firm brown frond without signs of disease at the end (t_{final}) pending determination of chlorophyll *a* (chl *a*, see section 2.3) and carbon:nitrogen (C:N) ratio (see section 2.4). Samples were stored in aluminum foil at -20 °C. Additional tissue samples were collected in the meristem of *S. latissima* and *H. nigripes* at t_{final} for gene expression analysis ($n=8$ for each species, see section 2.7) and immediately flash-frozen in liquid nitrogen before being stored at -80 °C.

2.4 Chl *a* content

Samples were blotted dry, weighed (wet weight), and ground with a glass pestle. Chl *a* was extracted in 90% aqueous acetone for 24 h in the dark at 4 °C. After cold-centrifugation (0 °C, 15 min, 3000 rpm), the supernatants were transferred one at a time into a glass vial and the initial fluorescence (F_0) of chl *a* and pheophytin pigment were measured using a fluorimeter (Turner Design 10-AU Fluorimeter; 667 nm). The F_a fluorescence was measured one minute after the addition of 10 μl of 0.3 N HCl to transform chl *a* into pheophytin pigment and subtract F_a from F_0 . The chl *a* content was calculated using the formula of Lorenzen (1967). Chl *a* content are expressed in μg per g of fresh weight ($\mu\text{g gFW}^{-1}$).

2.5 C:N ratio

Samples were dried at 60 °C for 48 h, weighed (dry weight), and their sizes adjusted to ensure that they did not weigh more than 10 mg, the detection limits specific to the CHN analyzer (PerkinElmer, Inc 2400). C and N contents are expressed in µg per g of dry weight (µg gDW⁻¹).

2.6 Growth rate

Growth rate was determined using the hole puncture method of Parke (1948). Sporophytes were punctured at t_0 in the meristem section of each organism, 2 cm from the base of the stipe. The distance from the base of the stipe to the hole was measured at t_{final} . The growth rate was calculated as follows:

$$Growth\ rate\ (cm.\ d^{-1}) = \frac{dist_{final} - dist_0}{t_{final} - t_0}$$

with dist: distance (in cm) from the base of the stipe to the meristem at time t (in days)

Weekly growth rates for selected individuals was also determined at different time points during the experiment for *S. latissima* (weeks 1 and 4) and *A. esculenta* (weeks 2 and 5). Results can be found in the supplementary material (Fig. S1).

2.7 Gene expression analysis

Total RNA extraction was conducted using the method described by Heinrich et al. (2012). The quantity and purity of the extracted RNA were evaluated using a Nanodrop ND-1000 Spectrophotometer (ThermoFisher), which measures RNA concentration at 260 nm and assesses purity by detecting the presence of other compounds such as DNA at 230 nm and proteins at 280 nm. The integrity of total RNA was determined by automated capillary electrophoresis using an Agilent 2100 Bioanalyzer (Agilent Technologies). The cDNA libraries were constructed by poly(A) enrichment and sequenced on a NovaSeq 6000 instrument by the Genome Quebec platform. The 100 bp paired reads were clipped using default values of the Illumina software. The quality of raw sequences was checked using FastQC v.0.11.7 (<https://www.bioinformatics.babraham.ac.uk/projects/fastqc/>). Sequences of low quality were trimmed using Trimmomatic v.0.39 (Bolger et al., 2014). For each species, a *de novo* transcriptome was constructed using the Trinity v.2.14.0 tool (Grabherr et al., 2011). The most homologous sequences were clustered using the CD-HIT-EST algorithm, part of the CD-HIT v.4.8.1 tool (Li and Godzik, 2006). To ensure the quality of the *de novo* transcriptomes, another

transcriptome per species was generated using the rnaSPAdes v.3.14.1 (Bushmanova et al., 2019). Transcriptomes generated with rnaSPAdes and Trinity were compared using BUSCO v.5.4.3, transcriptomes generated with Trinity were retained due to lower duplicated sequences (Simão et al., 2015). Transcript quantification was performed by pseudo alignment using Kallisto v0.46.0, mapping RNA sequences to an index created from *de novo* transcriptomes (Bray et al., 2016). Exploration of differentially expressed genes (DEGs) was performed with the DESeq2 v1.34.0 R package (Love et al., 2014). For each species, DEGs were obtained from the following comparisons: T1 vs. C, T2 vs. C, T3 vs. C, T2 vs. T1, T3 vs. T1, and T3 vs. T2. Transcripts with an adjusted $p < 0.05$ and \log_2 fold change (FC) > 2 or < -2 were considered significantly differentially expressed genes. Functional annotation of the genes was performed with eggNOG-mapper v2.1.10 against the eggNOG database v.5.0.2 (Huerta-Cepas et al., 2017 & 2019). To ensure they were properly annotated, annotation was also performed with TransDecoder v5.5.0 to predict coding sequences (Haas and Papanicoualo, 2015), which were aligned against a Pfam profile database v35.0 (Mistry et al., 2021) using the HMMER v3.3 alignment tool (Finn et al., 2011). Gene Ontology (Gene Ontology Consortium, 2015) terms were then retrieved from the pfam2go database (<https://pypi.org/project/pfam2go/>) and functional enrichment was performed with Ontologizer v2.1 to obtain statistically significant GOs from the DEGs of each comparison performed previously (Bauer et al., 2008). Functional enrichment results were summarized as tree plots and scatter plots using REVIGO v1.8.1 (Supek et al., 2011). Investigation of the specific functions of DEGs was carried out by manually checking the involvement of Pfam domains and EggNOG annotations on the SMART database v9.0 (Letunic et al., 2021). Some DEGs whose annotation was questionable (i.e. not referring to plant genomes such as gene collagen) were removed, as well as those whose annotation was not precise enough to be classified. DEGs were then classified into different categories: cytoskeleton, genetic transcription/translation, metabolism, signaling, transport, stress (heat stress and oxydo-reduction processes), and energy production (respiration and photorespiration). A part of DEGs (73.2% in *S. latissima* and 82.3% in *H. nigripes*) were trimmed as they lacked functional annotation. Tools and parameters are summarized in Table S2.

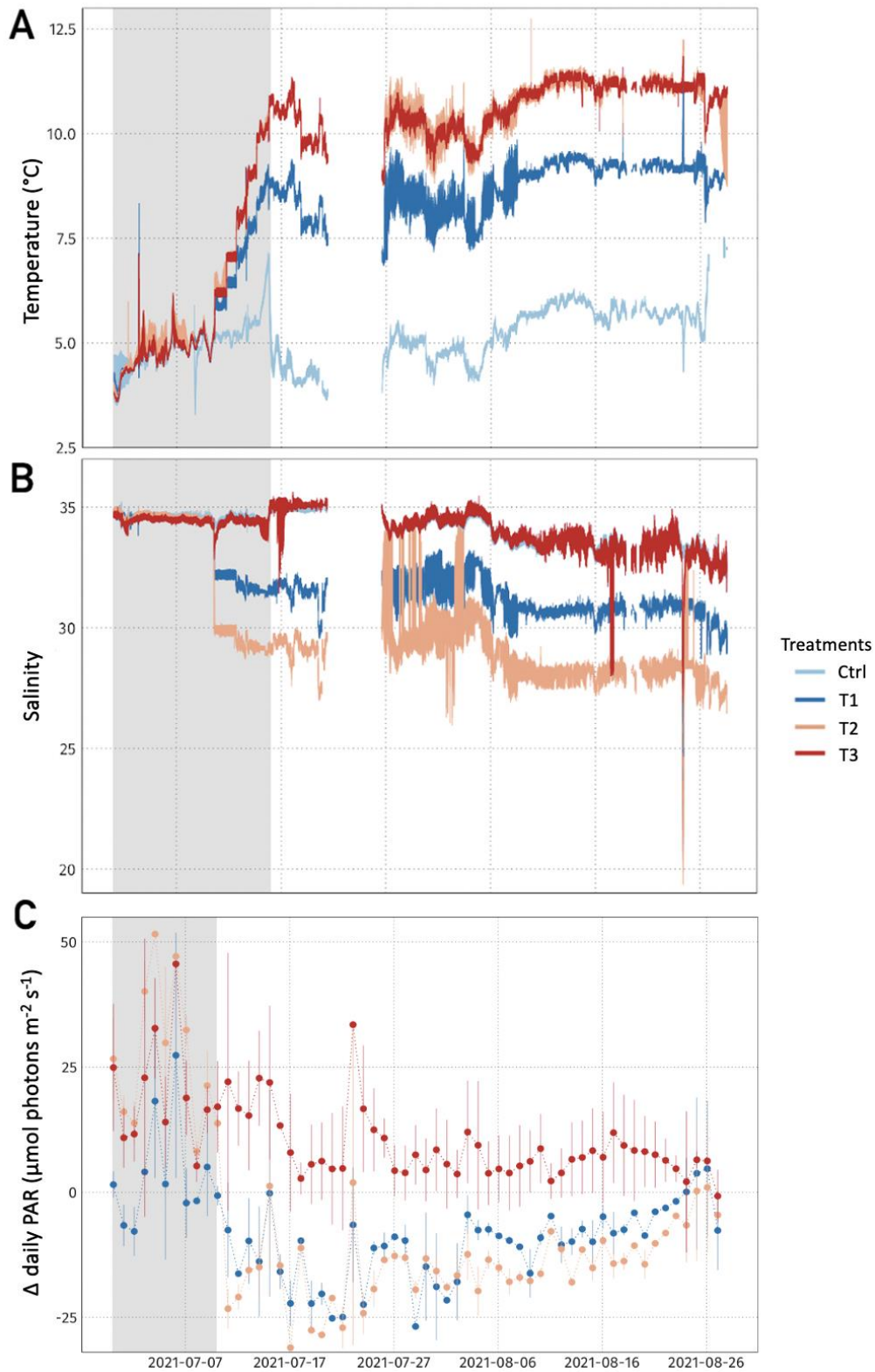


Figure 13: A) Temperature, B) salinity, and C) Δ Daily Photosynthetically Active Radiation (PAR) between the control and the treatments. Temperature, salinity, and PAR were measured every minute. PAR values were integrated over 10-minute intervals and averaged over the day. The gray-shaded region corresponds to the beginning of the experiment, before the treatment conditions of temperature, salinity and irradiance were reached. A few days of temperature and salinity data were lost (from 2021-07-21 to 2021-07-26).

2.8 Statistics

Rosner's generalized Extreme Studentized Deviation (ESD) test was used to detect the outliers using the function `rosnerTest` of the R package `EnvStats` (Millard, 2013). Out of a total of 165 individual chl *a* measurements, when combining all species and conditions, eleven were identified as outliers and removed. After the removal of the outliers, the normal distribution of the data was verified with a Shapiro-Wilk test using the function `shapiro.test` from the `stats` R package (R Core Team, 2013) ($p > 0.105$). No outliers were identified in the C:N and growth rate data and normality was verified ($p > 0.089$).

Chl *a* content and C:N were analyzed using a linear mixed model with a hierarchical structure (HLM) to evaluate treatment effects by species. The model was fitted using the function `lmer` in the R package `lme4` (Bates et al., 2015). The fixed factors for the model were treatment and species, while mesocosm was a random factor. For growth rate measurements, a generalized linear mixed model (GLMM) with a Gaussian distribution was preferred - based on an Akaike information criterion - to test for the effects of the species, treatment, and mesocosm replica.

3. Results

3.1 Experimental conditions

The median temperature value in the control treatment was 5.3 °C during the experimental period (2021-07-16 to 2021-08-28) calculated based on the mean value across replicates (Fig. 13, Table 2). The median salinity was 33.8 and the median daily PAR was 47.8 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. In treatment T1, the median temperature, salinity, and PAR were 8.9 °C, 31, and 36.1 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, respectively. For treatments T2 and T3, the median temperature was elevated to 10.8 °C. In T2, median salinity and PAR were decreased to 28.5, and 31.4 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$.

3.2 Chl *a* content

For *A. esculenta*, the concentration of chl *a* decreased significantly between t_0 and the control at t_{final} ($p < 0.01$, Fig. 14, Tables S3, S4). Values in the T2 treatment were also significantly different from the control, T1, and T3 treatments (all p were < 0.01). Values in the control, T1, and T3 treatments were not statistically different from each other ($p > 0.92$).

Similarly to *A. esculenta*, chl *a* content of *S. latissima* significantly decreased between t_0 and t_{final} ($p = 0.02$) for the control, but were not significantly impacted by the treatments ($p > 0.99$).

The chl *a* content of *L. digitata* was not significantly impacted by time and treatments ($p > 0.99$).

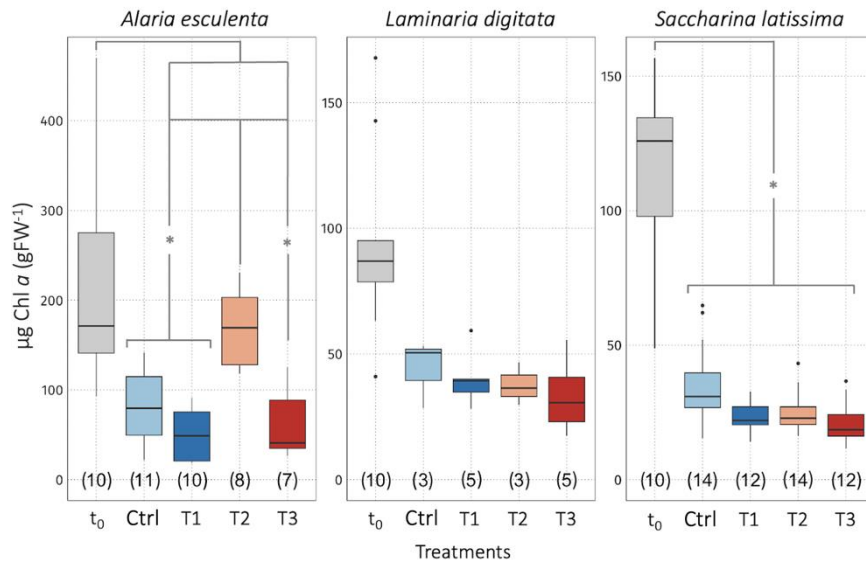


Figure 14: Chlorophyll *a* (chl *a*) content of *Alaria esculenta*, *Laminaria digitata*, and *Saccharina latissima* exposed to the four treatments, expressed per unit of fresh weight (gFW). t_0 values correspond to the chl *a* content at the start of the experiment, while Ctrl, T1, T2, and T3 correspond to the final chl *a* content of organisms maintained in the respective treatments for six weeks. The horizontal lines in each boxplot represent the median. The whiskers extend to the furthest data points within 1.5 times the interquartile range (the top and bottom of the box). Statistically significant differences are shown with an asterisk ($p < 0.05$). The number in parentheses below each boxplot corresponds to the sample size.

3.3 C:N ratio

For *S. latissima*, C:N ratios at t_0 ranged from 24.5 up to 37.1 (Fig. 15). No statistical difference was found between t_0 , the control, T1, and T3 treatment at t_{final} ($p > 0.93$, Tables S5, S6). In contrast, C:N ratios of individuals in the T2 treatment were significantly lower than at t_0 , ranging from 15.2 to 29.5 (Fig. 15A, $p = 0.045$). Although carbon content showed no significant difference across treatments and time (Fig. 15B, $p = 1$), there was a notable increase in nitrogen content in the T2 treatment compared to t_0 , but it was not statistically significant (Fig. 15C, $p = 0.06$).

The C:N ratios, carbon, and nitrogen contents of *A. esculenta* and *L. digitata* were not significantly impacted by the treatments ($p > 0.32$).

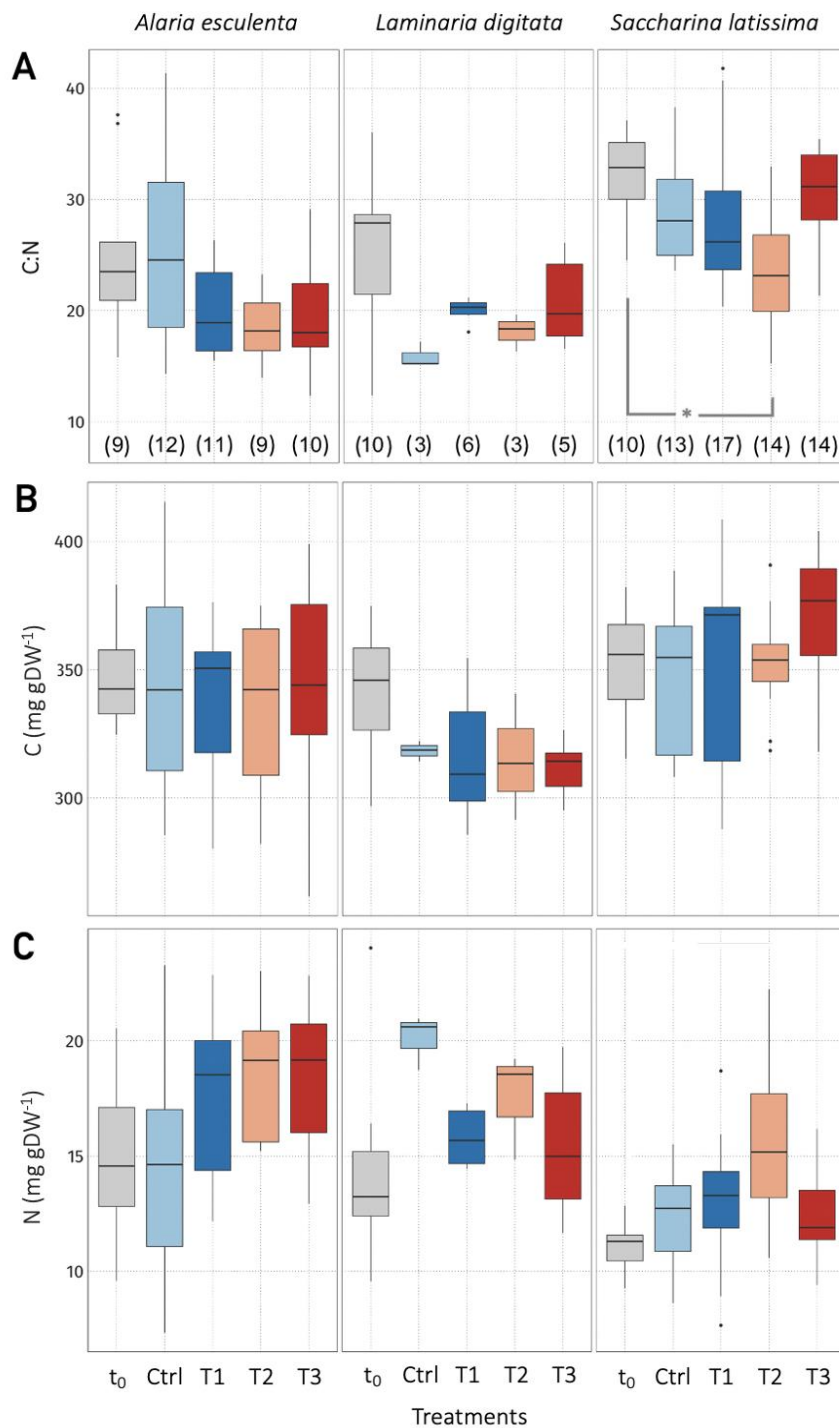


Figure 15: A) Carbon:nitrogen (C:N), B) carbon contents, and C) nitrogen contents of *Alaria esculenta*, *Laminaria digitata*, and *Saccharina latissima* exposed to the four treatments, expressed per unit of dry weight (gDW). t₀ values correspond to samples taken at the start of the experiment, while Ctrl, T1, T2, and T3 correspond to the final values from organisms maintained in the respective treatments for six weeks. The horizontal lines in each boxplot represent the median. The whiskers extend to the furthest data points within 1.5 times the interquartile range (the top and bottom of the box). Statistically significant differences are shown with an asterisk (p < 0.05). The number in parentheses below each boxplot in (A) corresponds to the sample size, respectively the same in (B) and (C).

3.4 Growth rate

The growth rates of *A. esculenta*, *L. digitata*, and *S. latissima* were not significantly impacted by the treatments (Fig. 16, $p = 1$, Tables S7, S8). They ranged from 0 to 0.037 cm d^{-1} for *A. esculenta*, 0.007 to 0.046 cm d^{-1} for *L. digitata*, and 0.040 up to 0.509 cm d^{-1} for *S. latissima*. The growth rate of *S. latissima* was significantly higher than for the two other species for each treatment ($p < 0.01$).

The growth rate of *A. esculenta* significantly decreased between week 2 and week 6 ($p < 0.01$, Fig. S1A) over time in the control. For *S. latissima*, no significant differences were found over time in the C, T1 and T2, except in the T3 treatment ($p=0.02$, Fig. S1B). No intermediate measurements of *L. digitata* growth rate were taken.

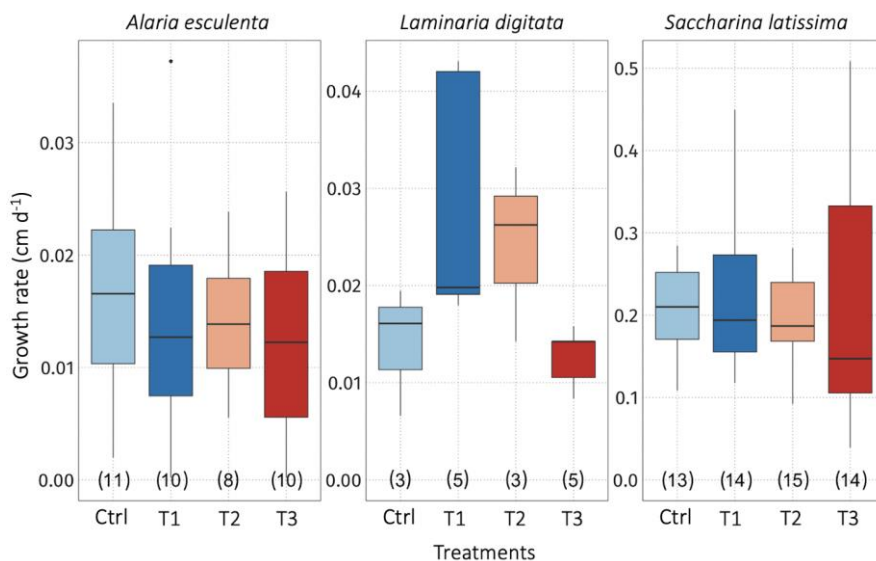


Figure 16: Growth rate of *Alaria esculenta*, *Laminaria digitata*, and *Saccharina latissima* exposed to the four treatments during six weeks. The horizontal lines in each boxplot represent the median. The whiskers extend to the furthest data points within 1.5 times the interquartile range (the top and bottom of the box). The number in parentheses below each boxplot corresponds to the sample size.

3.5 Gene expression analysis

The analysis of gene expression revealed a clear contrast between the control and the different treatments for both *S. latissima* and *H. nigripes* (Fig. S2). The number of total differentially expressed genes (DEGs, i.e. genes that are either up- or down-regulated when

comparing the different treatments to the control) were close between *S. latissima* (831 including 225 classified) and *H. nigripes* (815 including 144 classified, Fig. 17A) and mostly down-regulated for both species (84 and 65% respectively). For *H. nigripes*, the majority of overlapping DEGs were found between treatments T1 and T2 (Fig. 17A). Conversely, for *S. latissima*, the highest number of overlapping DEGs was observed between treatments T1 and T3. In both species, no overlapping genes were identified when comparing the DEGs between treatment pairs T1 vs. T2 and T2 vs. T3 (Fig. 17B).

The highest number of DEGs were exhibited in the transcription/translation and metabolism classes in *H. nigripes* (Fig. 18A) and in the transcription/translation and cytoskeleton classes for *S. latissima* (Fig. 18B). For this last species, the T3 treatments caused the highest number of down-regulated genes (607 including 152 classified) with 60% belonging to the three classes mentioned above, followed by T1 (314 including 47 classified) and T2 (247 including 56 classified; Fig. 17 and 18). For *H. nigripes*, 600 genes were observed to be regulated in T2 including 458 genes down-regulating. A substantial portion of the classified down-regulating genes belongs to the transcription/translation and metabolism class (64%), followed by an approximately equal proportion of genes associated with photorespiration (13%), stress (11%), and transport (8%) and lesser proportions of genes associated with other functions.

Genes belonging to the photorespiration/energy production class, involved either in the photosynthesis or respiration process, were found to be down-regulated in *H. nigripes* in T2 and in *S. latissima* in T2 and T3. Stress genes were down-regulated in all treatments for both species.

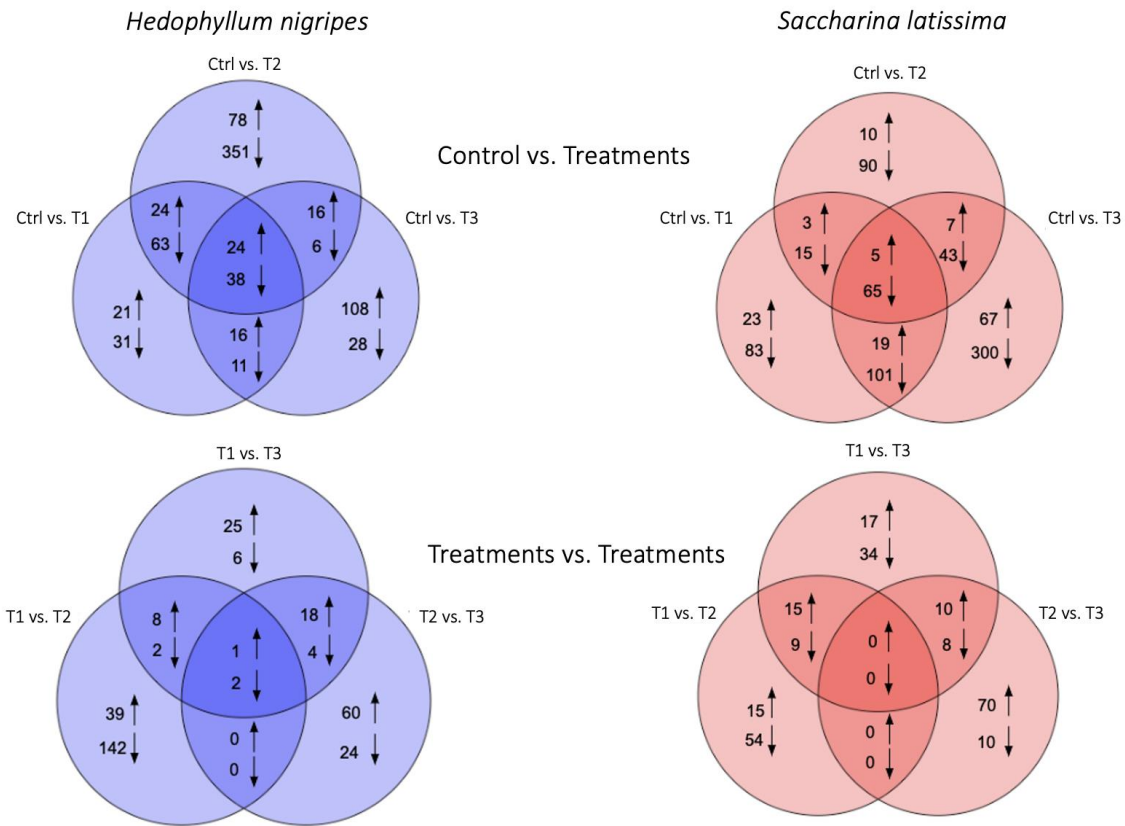


Figure 17: Venn diagrams of differentially up-regulated (↑) and down-regulated (↓) genes of *Saccharina latissima* and *Hedophyllum nigripes* between the control and the treatments (T1, T2, and T3) and between treatments.

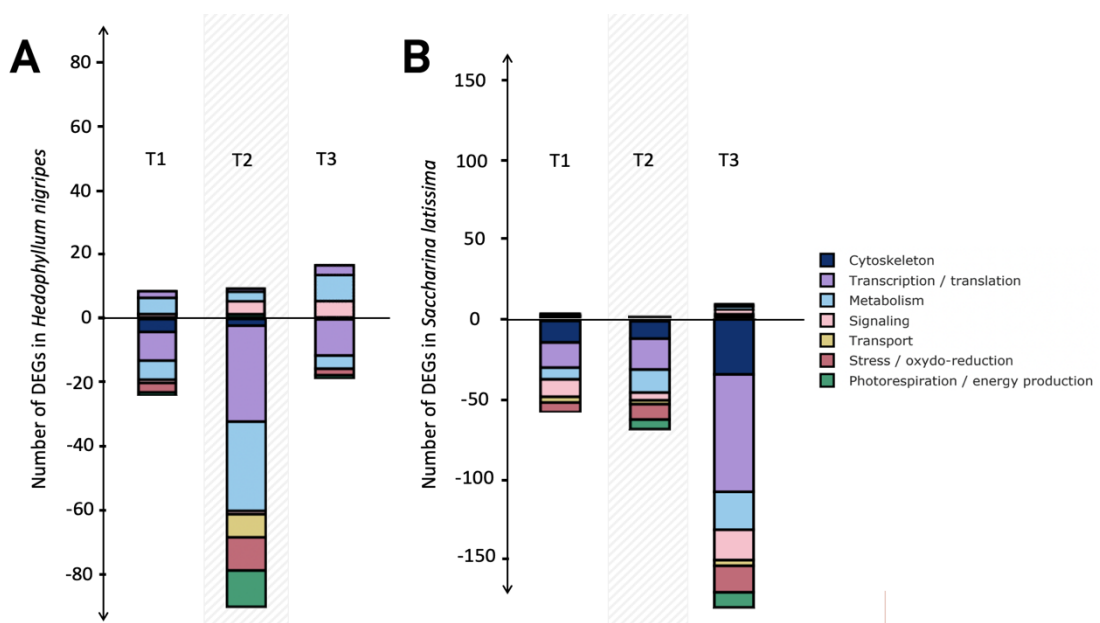


Figure 18: Number of classified differentially expressed genes (DEGs) in A) *Hedophyllum nigripes* and B) *Saccharina latissima* in response to T1, T2, and T3. The upper part of the graph displays up-regulated DEGs and the lower part down-regulated DEGs. Genes were classified with their Pfam and EggNOG annotations (see 2.7).

4. Discussion

The analysis of gene expression combined with the investigated physiological parameters show the ability of Arctic kelps to acclimate to a range of environmental conditions. Indeed, no negative impacts of the treatments was recorded, even according to the highest emissions scenario (SSP5-8.5). This observation confirms that these species, originating from lower latitudes, could thrive in a warmer Arctic. This also refutes our hypothesis that the combined effects of high temperature, low salinity, and low irradiance will necessarily have a negative impact on their physiology.

4.1 Chl *a* content

We hypothesized that different species might have different responses to a changing environment. The chl *a* content of both *A. esculenta* and *S. latissima* in the meristem part of the frond showed a significant decrease from t_0 to t_{final} in the control (-45% and -70% respectively). The same trend was observed in *L. digitata* although this is not significant due to the low number of measurements (-57%, $n=3$ at t_{final}). The high level of chl *a* measured in early summer matches the anticipation of ice melting and the following increase in turbidity (Aguilera et al., 2002). Decreasing chl *a* content between June and August has already been reported *in situ* in Kongsfjorden for *S. latissima* (Aguilera et al., 2002) with the end of the growth period (Berge et al., 2020).

In contrast to what was observed in the control as well as in the T1 and T3 treatments, for *A. esculenta*, the chl *a* content in the warm, less saline, and with lower irradiance treatment (T2) remained as high as it was at t_0 . The decrease in irradiance in this treatment may explain the persistence of elevated chl *a* levels. PAR is often negatively correlated with chl *a* content as higher chl *a* can help maintain elevated photosynthetic rates under reduced PAR (e.g. McWilliam and Naylor, 1967; Zhang et al., 2014). Bartsch et al. (2016) showed that the genus *Alaria* was more abundant than *Laminaria* and *Saccharina* between 10 and 15 m depth. Despite a decrease in irradiance caused by glacial and terrestrial runoff, *A. esculenta* is the only species that extended its maximum depth (from 15 to 18 m between 1994/96 to 2014; Bartsch et al., 2016). This shift could be explained by an effective short-term acclimation to low PAR, giving this species a competitive advantage at greater depth. Our findings shed light on the adaptive responses of *A. esculenta* to low light, and seemingly tolerance to low salinity

and warming, suggesting that this species will most likely be able to withstand future coastal environmental conditions in the Arctic.

The chl *a* content of *L. digitata* and *S. latissima* was also not affected by the treatments. This is in agreement with the study of Diehl and Bischoff (2021) where temperature (up to 10 °C), combined with low salinity (down to 25) did not affect the content of chl *a* of *S. latissima*. However, their growth rate in low light conditions remained similar to the other treatments. Other physiological processes such as photosynthetic efficiency, or resource allocation, might have been altered to maintain growth rates similar to the control.

4.2 C:N ratio

The C:N ratio of *S. latissima* was significantly lower in the T2 treatment compared to t_0 . The decrease in C:N ratio seems driven by an increase in nitrogen uptake. Benthic marine macroalgae and seagrasses from temperate and tropical regions have a mean C:N ratio of 22 (Atkinson and Smith, 1983). In northern Norway, Liesner et al. (2020) reported a C:N ratio of 21 for *L. digitata* which is consistent with our measurements for this species as well as for *A. esculenta*, all treatments and sampling times combined. However, *S. latissima* exhibited higher ratios with a mean of 29.7 ± 5.5 (t_0 and t_{final} of the control, T1 and T3 combined), which would suggest nitrogen limitation. While algae in the T2 treatment showed a higher nitrogen content, which is an essential nutrient playing a central role in photosynthesis and protein biosynthesis, the growth rate remained similar to the other treatments. Gordillo et al. (2002) showed higher nitrogen uptake at lower salinity (50% vs. 100% seawater) in *Fucus serratus* that was explained by increased N metabolism. Thus, the higher nitrogen content found here in the low saline T2 treatment (salinity down to 28) could have resulted from increased N metabolism. Indeed, the increase in nitrogen concentration in the macroalgae can induce an increase in the activity of the nitrate reductase (Korb and Gerard, 2000). This enzyme catalyzes the first step in the reduction of nitrate to organic forms and protein synthesis. In fact, nitrate concentration in water was higher in T2 ($1.68 \pm 0.8 \mu\text{M/L}$) treatment than the control ($0.87 \pm 0.9 \mu\text{M/L}$, data not shown) during the duration of the experiment. Arctic coastal waters are known to be nitrate-limited (Santos-Garcia et al., 2022). The influx of fresh and potentially more nitrate-rich waters may have induced an increase in the N metabolism of *S. latissima* which was nitrogen limited. Higher nutrient input from land through coastal erosion and

permafrost thawing may benefit this species in various processes such as photosynthesis, biosynthesis, immunity and/or molecule transport (Campbell, 1988; Meyer et al., 2005).

4.3 Growth rate

We also hypothesized that warming may enhance the growth rate of kelp. None of the growth rates of the three study species were affected by the different treatments over the total duration of the experiment. In contrast, previous studies observed an increase of the growth rate of *S. latissima* when exposed to warmer conditions (8-10 °C vs. 0-4 °C under replete irradiance; Iñiguez et al., 2016; Olischläger et al., 2017; Li et al., 2020; Diehl and Bischoff, 2021). This discrepancy with our results can be explained by the duration of the experiment (7 to 18 days in previous studies vs 6 weeks here), the study period, and the irradiance. Our study was performed at the end of the peak growth (mid-May to July) and after, while other studies were performed in early July or used sporophytes raised from gametophyte cultures. The growth rate of *A. esculenta* significantly decreased over time in the control, indicating the gradual end of the growth peak, with many of the kelp starting to senesce (Fig. S1A). For *S. latissima*, no significant differences were found over time in the C indicating that the experiment started after the growth peak (Fig. S1B; Berge et al., 2020). In the T3 treatment only, growth was stimulated only during the first four weeks of the experiment, suggesting that warming may have prolonged the growth rate of *S. latissima* after the end of the peak growth period. Further studies may focus on this aspect. The T2 treatment did not induce a growth stimulation suggesting a negative effect of salinity and/or low irradiance.

4.4 Gene expression

Both *H. nigripes* and *S. latissima* exhibited different gene expressions in the control compared to the treatments. The fact that treatments are not clustered separately from each other but are grouped together against the control suggests that the common factor among them, which is the increase in temperature, might be the key influencing factor.

Interestingly, and as we hypothesized, the response to these treatments differed between the two species. The analysis of DEGs shows that the low salinity and irradiance treatment (T2) had a higher impact on the number of genes regulated in *H. nigripes* while warming alone (T3) had a higher impact on genes regulation on *S. latissima*. Since no phenotypic response was observed for *S. latissima* in T3, this suggests that the observed down-regulation might be an

acclimation mechanism enabling the organism to maintain its main processes. Other parameters could be measured to validate this hypothesis (lipid content, photosynthesis rates, accessory pigment concentrations, etc). Li et al., (2020) found a regulation of genes involved to reduce the osmotic pressure under low-salinity stress in *S. latissima* (salinity of 20 vs. 30). We did not observe such results with this species nor with *H. nigripes*, most likely because the reduction in salinity was much smaller in our experiment (up to -5 here vs -10 in Li et al., 2020). However, for both species, T2 induced a down-regulation of photorespiratory genes. This is consistent with previous observations in *S. latissima* (Monteiro et al., 2019). Under stressful conditions like hyposalinity, kelp may prioritize acclimatization and survival strategies over photosynthesis. Photosynthesis was however not measured during the experiment to validate this hypothesis.

Finally, we noticed a down-regulation, rather than the expected up-regulation, of heat-shock proteins (HSP), despite their typical induction under abiotic stress (Sørensen et al., 2003). The regulation of HSP in response to salinity variations occurs to a lesser degree compared to its response to temperature changes (Monteiro et al., 2019). Considering that these species originate from lower latitudes, their current exposure to the low temperatures in the Arctic might induce stress, while future warmer waters may reduce it.

4.5 Future prospects of *Alaria esculenta*, *Saccharina latissima*, *Laminaria digitata*, and *Hedophyllum nigripes* in the Arctic

Our findings support the hypothesis that *A. esculenta* is more likely to be resilient to future changes in irradiance than other kelp species. In particular, our results reveal its competitive advantage at depth, through its high content in chl *a*. No discernible positive impact of its higher chl *a* content was observed on its growth rate in low light conditions. This impact may be more evident earlier in the season, during the peak growth. *A. esculenta* seems resilient to increasing glacier and river runoff, becoming more dominant in low-light environments such as greater depths (Bartsch et al., 2016). The dominance of a single kelp species in specific regions may carry ecological consequences, as reduced diversity threatens ecosystem resilience.

For *L. digitata*, our results demonstrate neither negative nor positive effects of warming, low salinity, and low irradiance. Franke et al. (2021) also found no effect of a 5 °C warming on the

growth rate of this species (control: 5 °C, warming: 10 °C). However, in our study confusion with *H. nigripes* at t_0 has split the data, making the analysis less robust. Indeed, the individuals could only be identified at the end of the experiment, after cutting the stipe. This led to the removal of 16 individuals from the analysis. The slight decrease in the content of chl *a* over time, as observed for the other two species in the study, could not be confirmed statistically. Bartsch et al. (2016) found that *L. digitata* was the only species that experienced a significant increase in biomass between 1994/1996 and 2014 on the entire transect they studied (from 0 to 15 m depth). Current and future conditions in the short term seem optimal for this species. Germination of *L. digitata* is enhanced at 9 °C compared to 5 °C and 15 °C (Zacher et al., 2016, 2019) and its growth rate is higher at 15 °C compared to 5 °C and 10 °C (Franke et al., 2021). Although warming alone may be beneficial to this species, its combined effects with other environmental factors might be detrimental once a certain threshold is reached. Muller et al., (2008) found no difference in the germination rate between 7 °C and 12 °C, but showed that germination under UV of type A and B decreased down to less than 30% at 12 °C compared to almost 80% at 7 °C.

S. latissima is widely studied throughout the northern hemisphere. In the Arctic specifically, several studies indicate that future conditions may favor the expansion of this species. This is supported by findings of enhanced germination with temperatures up to 12 °C (Muller et al., 2008) and mitigation of the negative effects of UV radiation at high temperatures (12 °C; Heinrich et al., 2015). Our results reveal that *S. latissima* may benefit from increasing N input from coastal erosion and permafrost thawing that could enhance immunity, photosynthesis, biosynthesis and/or molecule transport, although this was not measured in this study. *S. latissima* exhibits a high degree of polymorphism, acclimatation, and genetic diversity across populations (Bartsch et al., 2008; Guzinski et al., 2016). For example, its growth shows a high phenotypic plasticity that appears to be constrained within specific seasonal patterns (Spurkland and Iken, 2011). In the Canadian Arctic, Goldsmit et al., (2021) found that suitable habitat of this species may gain 64,000 km² by 2050, most of this new area being in the northernmost reaches, where temperature is rising and sea ice is receding. Bartsch et al. (2016) found a 30-time increase in its biomass between 1994/1996 in 2014 at 2.5 m depth at Hansneset (Kongsfjorden, Svalbard, Norway). *S. latissima* will most likely benefit from future

conditions although the capacity and time of dispersal, as well as competition with other species, predation, and extreme events must be considered for population projections.

So far, *A. esculenta*, *L. digitata*, and *S. latissima* have adapted successfully to the shifting Arctic environment and our results suggest that they might thrive in the conditions expected for 2100. In the short term, these species may well continue to spread in this region. Regarding *H. nigripes*, Franke et al. (2021) suggested a true Arctic affinity with a sporophyte growth optimum of 10 °C. By 2100, this species might continue to thrive in the Arctic, as evidenced by our gene expression analysis, which suggests efficient acclimatization with less stress under future scenarios.

Kelp species will, however, face more competition, grazing, and extreme events such as high sedimentation rate, ice-scouring, and marine heatwaves (Hu et al., 2020). Around Tromsø (Norway), the massive spread of sea urchins may have caused the ecosystem to collapse into a bare new state (Sivertsen et al., 1997). Moreover, with warming, the frequency and intensity of marine heatwaves will increase which could have important consequences on marine species of Arctic flora and fauna. These potential effects of climate change should be taken into account to better assess the future of Arctic kelp communities. It therefore appears essential to continue to study these communities in order to predict and anticipate future changes and impacts on fisheries, local and indigenous people, and on a global scale.

Acknowledgments

We are grateful to the staff of the Alfred Wegener Institute (AWI), Institut polaire français Paul Emile Victor (IPEV), and Kings Bay for field assistance. We thank Cátia Monteiro for her advice on RNA extraction and Erwan Corre for his expertise and guidance to process transcriptomic data. Thanks are also due to Inka Bartsch, Kai Bischof, and Simon Jungblut for their input, which improved the design and interpretation of this study, and Nathalie Leblond for her help with the CHN analysis. This study was conducted in the frame of the project FACE-IT (The Future of Arctic Coastal Ecosystems – Identifying Transitions in Fjord Systems and Adjacent Coastal Areas). FACE-IT has received funding from the European Union’s Horizon 2020 research and innovation programme under grant agreement No 869154. We also acknowledge the support of IPEV (project ARCTOS 1248) and the Prince Albert II of Monaco Foundation (project ORCA n°3051).

Author contributions

AL, CM, SC, PU, SA, RS, JPG, and FG were involved in the fieldwork. AL, CM, SC, JPG, and FG designed the study. SC, PU, and FG designed the system. The experiment was conducted by AL, CM, SC, SA, RS, JPG, and FG. AL and CM performed measurements of the chl *a* content. AL performed the C:N ratio measurement and the RNA extractions. MM processed transcriptomic data. AL analyzed the data and wrote the first draft of the manuscript, which was then finalized by all co-authors.

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Supplementary data

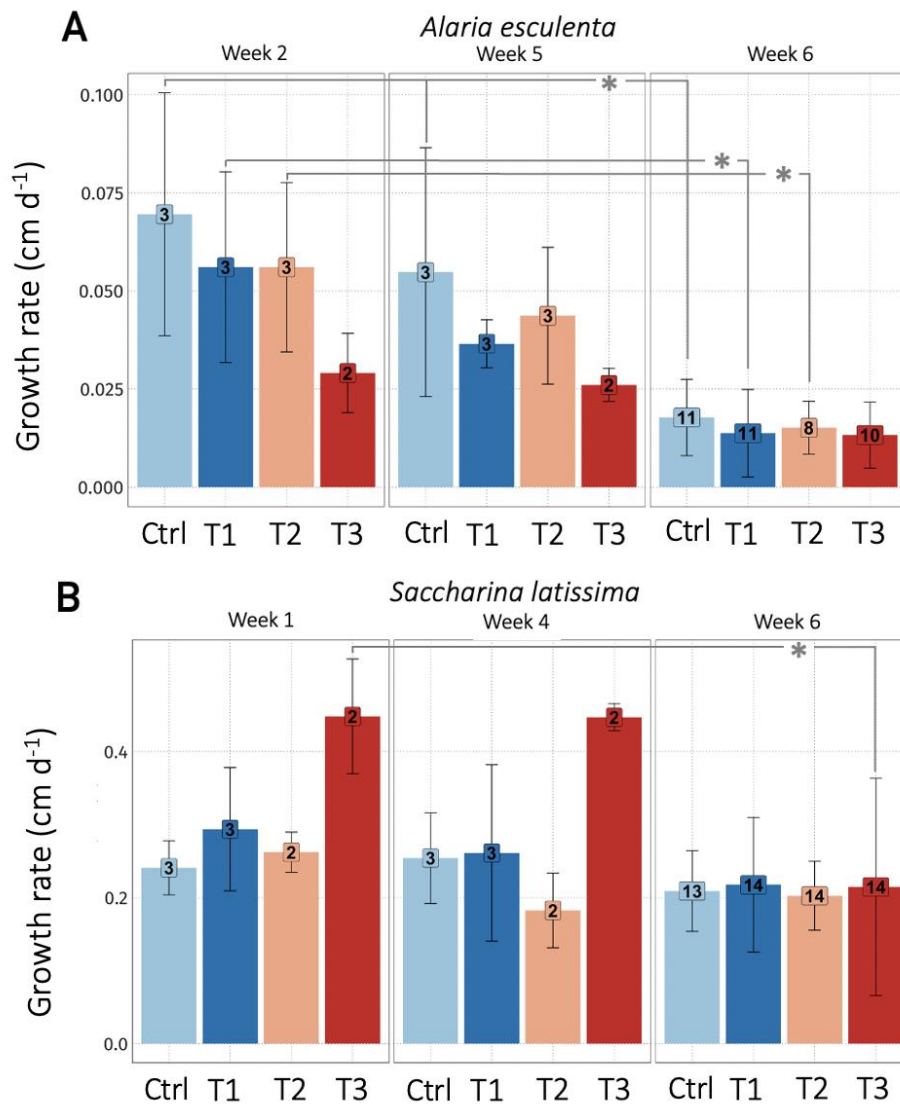


Figure S1: Growth rate calculated at different intervals during the experiment within treatments for A) *Alaria esculenta* (Week 0 to 2, 2 to 5, and 5 to 6), and B) *Saccharina latissima* (Weeks 0 to 1, 1 to 4, and 4 to 6). The number on each barplot corresponds to the sample size. *Laminaria digitata* was not represented due to its low sample size in week 3. Values from t_0 to week 6 are represented in Figure 5. A generalized linear mixed model (GLMM) with a Gaussian distribution was used to test for the effects of the species, treatment, time, and mesocosm replica. No significant differences were found between mesocosm replicas. Statistically significant differences are shown with an asterisk ($p < 0.05$).

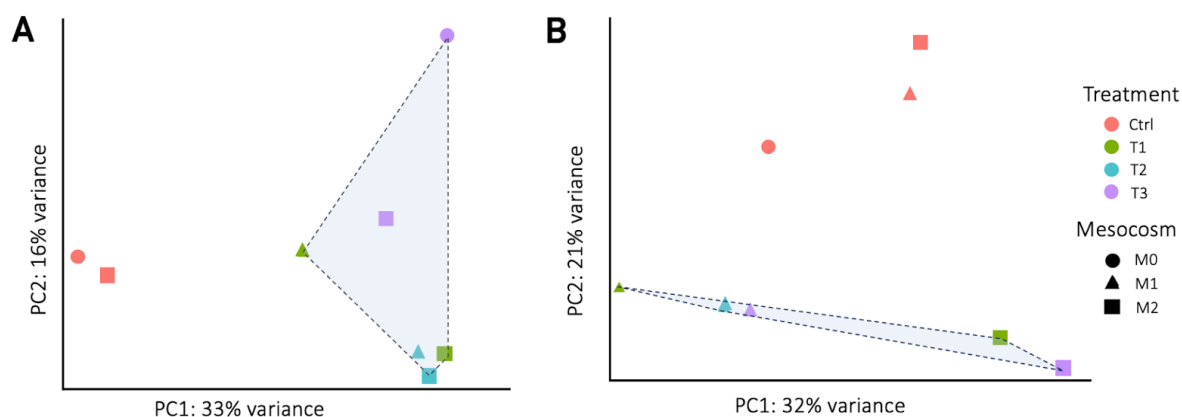


Fig. S2: Principal Component Analysis of the expressed genes in the control and treatments of A) *Hedophyllum nigripes* and B) *Saccharina latissima*. Treatments T1, T2, and T3 are grouped in the blue geometrical figures.

Table S2: Tools and parameters used for transcriptomic data processing.

Tool	Version	Arguments and parameters
FastQC	0.11.7	-o \$outputDirectory
Trimmomatic	0.39	PE -threads 10 -phred33 -trimlog LEADING:3 TRAILING:3 SLIDINGWINDOW:4:15 MINLEN:36 TruSeq3-PE.fa:2:30:10
Trinity	2.14.0	--seqType fq --max_memory 128G --samples_file \$sampleFiles --CPU 32 --output \$outputDirectory --full_cleanup
CD-HIT	4.8.1	-i \$transcriptome -o \$output -c 0.95 -n 8
rnaSPAdes	3.14.1	--pe1-1 \$seq1 --pe1-2 \$seq2 [...] --pe4-1 \$seq7 --pe4-2 \$seq8 -o \$output_directory
BUSCO	5.4.3	--in \$transcriptome --out \$output -c 24 -l /\$pathDB/eukaryota_odb10 --config \$config --mode transcriptome
Kallisto	0.46.0	quant -i \$index -o \$outputDirectory -b 100 -t 16 \$seq1 \$seq2
DESeq2	1.34.0	Counts recovery via txImport (files=DesignFile, type='Kallisto', tx2gene=tx2geneFile) Contrasts depends on biological questions with alpha=0.05
TransDecoder	5.5.0	LongOrfs : \$transcriptome Predict : \$transcriptome
HMMER	3.3	--domtblout \$output -E 1e-10 --cpu 16 \$pfamDB \$transdecoderLongestOrf
eggNOG-mapper	2.1.10	-i \$transdecoderLongestOrf -o \$eggnogAnnot
Ontologizer	2.1	-a \$associationFile -g \$goDB -s \$studySamples -p \$populationFile -c Parent-Child-Union -o \$outputDirectory -d 0.05 -r 1000

Table S3: Analysis of deviance (Type II Wald chi-square tests) in a linear mixed model with a hierarchical structure to predict the chlorophyll *a* contents.

	Chisq	Df	Pr(>Chisq)
species	91.310	2	<2.2e-16 ***
treatment	98.991	4	<2.2e-16 ***
species:treatment	39.729	8	3.599e-06 ***

Table S4: Pairwise comparisons of the chlorophyll *a* values calculated by the method of Tukey on a linear mixed model with a hierarchical structure (fixed factors: treatment and species, random factor: mesocosm). The p-values in bold (< 0.05) support the hypothesis that there is a significant difference in the pair. AE: *Alaria esculenta*, LD: *Laminaria digitata*, SL: *Saccharina latissima*

Species	Treatment vs.	Species	Treatment	estimate	SE	df	t.ratio	p.value
AE	t0	-	LD	t0	124.75	18.6	117.0	6.708 < 0.0001
AE	t0	-	SL	t0	104.37	18.6	117.0	5.612 < 0.0001
AE	t0	-	AE	Ctrl	136.06	19.0	22.9	7.146 < 0.0001
AE	t0	-	AE	T1	167.96	19.3	25.6	8.706 < 0.0001
AE	t0	-	AE	T2	48.68	20.4	30.6	2.388 0.5405
AE	t0	-	AE	T3	155.52	21.2	33.5	7.325 < 0.0001
LD	t0	-	SL	t0	-20.38	18.6	117.0	-1.096 0.9988
LD	t0	-	LD	Ctrl	49.65	27.8	69.5	1.783 0.8967
LD	t0	-	LD	T1	54.29	24.0	38.6	2.260 0.6231
LD	t0	-	LD	T2	56.08	27.8	69.5	2.014 0.7829
LD	t0	-	LD	T3	60.95	23.5	43.6	2.588 0.4048
SL	t0	-	LD	Ctrl	70.03	27.8	69.5	2.515 0.4437
SL	t0	-	SL	Ctrl	79.06	18.0	20.0	4.396 0.0158
SL	t0	-	SL	T1	90.64	18.5	22.2	4.887 0.0044
SL	t0	-	SL	T2	89.20	18.0	19.9	4.953 0.0049
SL	t0	-	SL	T3	93.45	18.6	21.9	5.019 0.0034
AE	Ctrl	-	LD	Ctrl	38.33	27.2	117.8	1.409 0.9850
AE	Ctrl	-	SL	Ctrl	47.36	17.0	118.9	2.779 0.2727
AE	Ctrl	-	AE	T1	31.89	18.4	118.7	1.733 0.9184
AE	Ctrl	-	AE	T2	-87.38	19.4	117.9	-4.497 0.0015
AE	Ctrl	-	AE	T3	19.46	20.3	118.6	0.958 0.9997
LD	Ctrl	-	SL	Ctrl	9.04	26.5	117.2	0.341 1.0000

LD	Ctrl	-	LD	T1	4.64	30.9	119.0	0.150	1.0000
LD	Ctrl	-	LD	T2	6.43	34.0	117.0	0.190	1.0000
LD	Ctrl	-	LD	T3	11.30	30.5	118.0	0.370	1.0000
SL	Ctrl	-	LD	T1	-4.40	22.6	115.7	-0.194	1.0000
SL	Ctrl	-	SL	T1	11.58	16.5	118.4	0.702	1.0000
SL	Ctrl	-	SL	T2	10.14	15.7	117.4	0.644	1.0000
SL	Ctrl	-	SL	T3	14.39	16.4	117.3	0.878	0.9999
AE	T1	-	LD	T1	11.08	23.6	117.3	0.469	1.0000
AE	T1	-	SL	T1	27.05	17.9	118.0	1.511	0.9722
AE	T1	-	AE	T2	-119.27	19.7	117.2	-6.040	<.0001
AE	T1	-	AE	T3	-12.43	20.7	118.6	-0.600	1.0000
LD	T1	-	SL	T1	15.98	22.6	119.0	0.707	1.0000
LD	T1	-	LD	T2	1.79	30.9	119.0	0.058	1.0000
LD	T1	-	LD	T3	6.66	26.4	118.0	0.252	1.0000
SL	T1	-	SL	T2	-1.44	16.6	118.8	-0.087	1.0000
SL	T1	-	SL	T3	2.81	17.2	118.9	0.163	1.0000
AE	T2	-	LD	T2	132.14	28.2	117.1	4.691	0.0007
AE	T2	-	SL	T2	144.88	18.4	117.1	7.856	<.0001
AE	T2	-	AE	T3	106.84	21.7	118.4	4.920	0.0003
LD	T2	-	SL	T2	12.74	26.5	117.3	0.481	1.0000
LD	T2	-	LD	T3	4.87	30.5	118.0	0.159	1.0000
SL	T2	-	SL	T3	4.25	16.4	117.6	0.259	1.0000
AE	T3	-	LD	T3	30.17	24.5	118.1	1.231	0.9959
AE	T3	-	SL	T3	42.29	20.2	119.0	2.091	0.7381
LD	T3	-	SL	T3	12.12	22.6	119.0	0.537	1.0000

Table S5: C:N ratios (A), carbon contents (B), and nitrogen contents as a function of the treatment were investigated with an analysis of deviance (Type II Wald chi-square tests) in a linear mixed model with a hierarchical structure.

A		Chisq	Df	Pr(>Chisq)
	species	61.003	2	5.667e-14 ***
	treatment	29.275	4	6.872e-06 ***
	species:treatment	11.285	8	0.1861

B		Chisq	Df	Pr(>Chisq)
	species	23.8694	2	6.559e-06 ***
	treatment	3.8547	4	0.4260
	species:treatment	6.0497	8	0.6417

C		Chisq	Df	Pr(>Chisq)
	species	51.647	2	6.096e-12 ***
	treatment	25.979	4	3.196e-05 ***
	species:treatment	14.373	8	0.07254

Table S6: Pairwise comparisons of A) the C:N ratios, B) the carbon contents, C) the nitrogen contents calculated by the method of Tukey on a linear mixed model with a hierarchical structure (fixed factors: treatment and species, random factor: mesocosm). The p-values in bold (< 0.05) indicates a significant difference in the pair. AE: *Alaria esculenta*, LD: *Laminaria digitata*, SL: *Saccharina latissima*.

A		Species	Treatment	vs. Species	Treatment	estimate	SE	df	t.ratio	p.value
AE	t0	-	LD	t0	-0.1152	2.63	125.0	-0.044	1.0000	
AE	t0	-	SL	t0	-6.7996	2.56	125.0	-2.654	0.3458	
AE	t0	-	AE	Ctrl	-0.4640	2.47	41.0	-0.187	1.0000	
AE	t0	-	AE	T1	5.2689	2.51	45.0	2.100	0.7276	
AE	t0	-	AE	T2	6.7233	2.83	58.0	2.378	0.5403	
AE	t0	-	AE	T3	5.8060	2.56	47.8	2.264	0.6201	
LD	t0	-	SL	t0	-6.6845	2.56	125.0	-2.609	0.3746	
LD	t0	-	LD	Ctrl	9.4646	3.72	98.2	2.546	0.4190	

LD	t0	-	LD	T1	5.3231	2.99	58.9	1.783	0.8955
LD	t0	-	LD	T2	7.2351	3.72	98.2	1.946	0.8236
LD	t0	-	LD	T3	4.4934	3.14	69.9	1.431	0.9814
SL	t0	-	SL	Ctrl	2.9358	2.36	36.1	1.246	0.9937
SL	t0	-	SL	T1	3.6898	2.22	31.4	1.659	0.9302
SL	t0	-	SL	T2	8.5439	2.32	34.5	3.686	0.0453
SL	t0	-	SL	T3	1.5997	2.36	35.2	0.677	1.0000
AE	Ctrl	-	LD	Ctrl	9.8134	3.61	125.6	2.718	0.3066
AE	Ctrl	-	SL	Ctrl	-3.3998	2.28	126.8	-1.490	0.9755
AE	Ctrl	-	AE	T1	5.7328	2.34	126.1	2.449	0.4841
AE	Ctrl	-	AE	T2	7.1873	2.67	126.2	2.694	0.3206
AE	Ctrl	-	AE	T3	6.2700	2.41	126.7	2.599	0.3810
LD	Ctrl	-	SL	Ctrl	-13.2133	3.58	125.5	-3.692	0.0247
LD	Ctrl	-	LD	T1	-4.1415	3.98	126.7	-1.041	0.9993
LD	Ctrl	-	LD	T2	-2.2295	4.55	125.0	-0.490	1.0000
LD	Ctrl	-	LD	T3	-4.9712	4.09	126.2	-1.214	0.9965
SL	Ctrl	-	SL	T1	0.7539	2.07	126.7	0.363	1.0000
SL	Ctrl	-	SL	T2	5.6081	2.17	126.8	2.581	0.3927
SL	Ctrl	-	SL	T3	-1.3361	2.21	126.6	-0.606	1.0000
AE	T1	-	LD	T1	-0.0609	2.90	126.3	-0.021	1.0000
AE	T1	-	SL	T1	-8.3787	2.16	125.5	-3.875	0.0136
AE	T1	-	AE	T2	1.4545	2.72	126.7	0.535	1.0000
AE	T1	-	AE	T3	0.5372	2.44	125.2	0.220	1.0000
LD	T1	-	SL	T1	-8.3178	2.69	126.9	-3.086	0.1367
LD	T1	-	LD	T2	1.9120	3.98	126.7	0.481	1.0000
LD	T1	-	LD	T3	-0.8297	3.38	125.1	-0.246	1.0000
SL	T1	-	SL	T2	4.8542	2.02	126.2	2.398	0.5214
SL	T1	-	SL	T3	-2.0900	2.08	127.0	-1.004	0.9995
AE	T2	-	LD	T2	0.3966	3.86	125.7	0.103	1.0000
AE	T2	-	SL	T2	-4.9791	2.61	126.9	-1.907	0.8453
AE	T2	-	AE	T3	-0.9173	2.78	126.8	-0.330	1.0000
LD	T2	-	SL	T2	-5.3757	3.55	125.4	-1.513	0.9721
LD	T2	-	LD	T3	-2.7417	4.09	126.2	-0.670	1.0000
SL	T2	-	SL	T3	-6.9442	2.15	125.7	-3.223	0.0967

AE	T3	-	LD	T3	-1.4278	3.09	126.9	-0.462	1.0000
AE	T3	-	SL	T3	-11.0059	2.36	126.1	-4.669	0.0007
LD	T3	-	SL	T3	-9.5782	3.02	125.3	-3.173	0.1101

B Species Treatment vs. Species Treatment estimate SE df t.ratio p.value

					estimate	SE	df	t.ratio	p.value
AE	t0	-	LD	t0	5.634	14.1	125.0	0.400	1.0000
AE	t0	-	SL	t0	-6.839	13.7	125.0	-0.498	1.0000
AE	t0	-	AE	Ctrl	3.002	13.3	41.0	0.226	1.0000
AE	t0	-	AE	T1	8.934	13.4	45.0	0.664	1.0000
AE	t0	-	AE	T2	10.408	15.2	58.0	0.687	1.0000
AE	t0	-	AE	T3	1.157	13.7	47.8	0.084	1.0000
LD	t0	-	SL	t0	-12.473	13.7	125.0	-0.908	0.9999
LD	t0	-	LD	Ctrl	21.981	19.9	98.2	1.103	0.9987
LD	t0	-	SL	Ctrl	-7.587	13.0	39.6	-0.583	1.0000
LD	t0	-	LD	T1	24.351	16.0	58.9	1.521	0.9679
LD	t0	-	LD	T2	25.098	19.9	98.2	1.259	0.9947
LD	t0	-	LD	T3	28.694	16.8	69.9	1.705	0.9244
SL	t0	-	SL	Ctrl	4.886	12.6	36.1	0.387	1.0000
SL	t0	-	SL	T1	0.176	11.9	31.4	0.015	1.0000
SL	t0	-	SL	T2	-0.691	12.4	34.5	-0.056	1.0000
SL	t0	-	SL	T3	-18.336	12.7	35.2	-1.447	0.9761
AE	Ctrl	-	LD	Ctrl	24.612	19.4	125.6	1.272	0.9944
AE	Ctrl	-	SL	Ctrl	-4.956	12.2	126.8	-0.405	1.0000
AE	Ctrl	-	AE	T1	5.932	12.5	126.1	0.473	1.0000
AE	Ctrl	-	AE	T2	7.406	14.3	126.2	0.518	1.0000
AE	Ctrl	-	LD	T2	27.730	19.4	125.6	1.433	0.9827
AE	Ctrl	-	AE	T3	-1.845	12.9	126.7	-0.143	1.0000
LD	Ctrl	-	SL	Ctrl	-29.568	19.2	125.5	-1.541	0.9674
LD	Ctrl	-	LD	T1	2.370	21.3	126.7	0.111	1.0000
LD	Ctrl	-	SL	T1	-34.278	18.7	125.0	-1.831	0.8810
LD	Ctrl	-	LD	T2	3.117	24.4	125.0	0.128	1.0000
LD	Ctrl	-	LD	T3	6.713	22.0	126.2	0.306	1.0000
SL	Ctrl	-	SL	T1	-4.710	11.1	126.7	-0.424	1.0000
SL	Ctrl	-	SL	T2	-5.577	11.6	126.8	-0.479	1.0000

SL	Ctrl	-	SL	T3	-23.222	11.8	126.6	-1.963	0.8153
AE	T1	-	LD	T1	21.051	15.5	126.3	1.355	0.9896
AE	T1	-	SL	T1	-15.598	11.6	125.5	-1.345	0.9903
AE	T1	-	AE	T2	1.474	14.6	126.7	0.101	1.0000
AE	T1	-	AE	T3	-7.777	13.1	125.2	-0.595	1.0000
LD	T1	-	SL	T1	-36.648	14.4	126.9	-2.537	0.4227
LD	T1	-	LD	T2	0.747	21.3	126.7	0.035	1.0000
LD	T1	-	LD	T3	4.343	18.1	125.1	0.240	1.0000
SL	T1	-	LD	T2	37.396	18.7	125.0	1.997	0.7962
SL	T1	-	SL	T2	-0.867	10.9	126.2	-0.080	1.0000
SL	T1	-	SL	T3	-18.512	11.2	127.0	-1.658	0.9414
AE	T2	-	AE	T3	-9.251	14.9	126.8	-0.621	1.0000
LD	T2	-	SL	T2	-38.262	19.1	125.4	-2.008	0.7896
LD	T2	-	LD	T3	3.596	22.0	126.2	0.164	1.0000
SL	T2	-	SL	T3	-17.645	11.6	125.7	-1.528	0.9697
AE	T3	-	LD	T3	33.171	16.6	126.9	2.001	0.7940
AE	T3	-	SL	T3	-26.332	12.6	126.1	-2.084	0.7429
LD	T3	-	SL	T3	-59.503	16.2	125.3	-3.677	0.0259

C Species Treatment vs. Species Treatment estimate SE df t.ratio p.value

					estimate	SE	df	t.ratio	p.value
AE	t0	-	LD	t0	0.2529	1.44	125.0	0.176	1.0000
AE	t0	-	SL	t0	3.5217	1.40	125.0	2.508	0.4423
AE	t0	-	AE	Ctrl	0.0322	1.36	41.0	0.024	1.0000
AE	t0	-	AE	T1	-2.8539	1.37	45.0	-2.077	0.7425
AE	t0	-	AE	T2	-3.8535	1.55	58.0	-2.487	0.4650
AE	t0	-	AE	T3	-3.8036	1.41	47.8	-2.707	0.3318
LD	t0	-	SL	t0	3.2689	1.40	125.0	2.328	0.5718
LD	t0	-	LD	Ctrl	-5.7111	2.04	98.2	-2.804	0.2626
LD	t0	-	LD	T1	-1.4098	1.64	58.9	-0.862	0.9999
LD	t0	-	LD	T2	-3.1407	2.04	98.2	-1.542	0.9665
LD	t0	-	LD	T3	-1.0560	1.72	69.9	-0.614	1.0000
SL	t0	-	SL	Ctrl	-1.1248	1.29	36.1	-0.871	0.9999
SL	t0	-	SL	T1	-1.8877	1.22	31.4	-1.550	0.9576
SL	t0	-	SL	T2	-4.5131	1.27	34.5	-3.554	0.0622

SL	t0	-	SL	T3	-1.3004	1.30	35.2	-1.004	0.9993
AE	Ctrl	-	LD	Ctrl	-5.4905	1.98	125.6	-2.776	0.2740
AE	Ctrl	-	SL	Ctrl	2.3647	1.25	126.8	1.892	0.8529
AE	Ctrl	-	AE	T1	-2.8861	1.28	126.1	-2.251	0.6282
AE	Ctrl	-	AE	T2	-3.8856	1.46	126.2	-2.659	0.3426
AE	Ctrl	-	AE	T3	-3.8358	1.32	126.7	-2.902	0.2102
LD	Ctrl	-	SL	Ctrl	7.8552	1.96	125.5	4.006	0.0087
LD	Ctrl	-	LD	T1	4.3014	2.18	126.7	1.973	0.8098
LD	Ctrl	-	LD	T2	2.5704	2.49	125.0	1.030	0.9994
LD	Ctrl	-	LD	T3	4.6552	2.24	126.2	2.075	0.7485
SL	Ctrl	-	SL	T1	-0.7629	1.14	126.7	-0.671	1.0000
SL	Ctrl	-	SL	T2	-3.3883	1.19	126.8	-2.846	0.2368
SL	Ctrl	-	SL	T3	-0.1756	1.21	126.6	-0.145	1.0000
AE	T1	-	LD	T1	1.6970	1.59	126.3	1.069	0.9991
AE	T1	-	SL	T1	4.4880	1.18	125.5	3.788	0.0181
AE	T1	-	AE	T2	-0.9995	1.49	126.7	-0.670	1.0000
AE	T1	-	AE	T3	-0.9497	1.34	125.2	-0.711	1.0000
LD	T1	-	SL	T1	2.7910	1.48	126.9	1.890	0.8536
LD	T1	-	AE	T2	-2.6966	1.72	126.8	-1.568	0.9623
LD	T1	-	LD	T2	-1.7310	2.18	126.7	-0.794	1.0000
LD	T1	-	LD	T3	0.3538	1.85	125.1	0.191	1.0000
SL	T1	-	SL	T2	-2.6254	1.11	126.2	-2.367	0.5439
SL	T1	-	SL	T3	0.5873	1.14	127.0	0.515	1.0000
AE	T2	-	LD	T2	0.9656	2.12	125.7	0.456	1.0000
AE	T2	-	SL	T2	2.8621	1.43	126.9	2.001	0.7942
AE	T2	-	AE	T3	0.0498	1.52	126.8	0.033	1.0000
LD	T2	-	SL	T2	1.8965	1.95	125.4	0.974	0.9997
LD	T2	-	LD	T3	2.0848	2.24	126.2	0.929	0.9998
SL	T2	-	SL	T3	3.2127	1.18	125.7	2.721	0.3047
AE	T3	-	LD	T3	3.0005	1.69	126.9	1.771	0.9051
AE	T3	-	SL	T3	6.0250	1.29	126.1	4.665	0.0007
LD	T3	-	SL	T3	3.0244	1.65	125.3	1.829	0.8818

Table S7: Analysis of deviance (Type II Wald chi-square tests) in a generalized linear mixed model to predict the growth rate.

	Chisq	Df	Pr(>Chisq)
species	91.310	2	<2.2e-16 ***
treatment	98.991	4	<2.2e-16 ***
species:treatment	39.729	8	3.599e-06 ***

Table S8: Pairwise comparisons of the growth rates calculated by the method of Tukey generalized linear mixed model. The p-values in bold (< 0.05) support the hypothesis that there is a significant difference in the pair. AE: *Alaria esculenta*, LD: *Laminaria digitata*, SL: *Saccharina latissima*.

Species	Treatment vs.	Species	Treatment	estimate	SE	df	t.ratio	p.value
AE	Ctrl	-	LD	Ctrl	-6.78e-03	0.0327	115	-0.207 1.0000
AE	Ctrl	-	SL	Ctrl	-1.87e-01	0.0264	115	-7.090 <.0001
AE	Ctrl	-	AE	T1	4.08e-03	0.0275	115	0.148 1.0000
AE	Ctrl	-	AE	T2	2.62e-03	0.0299	115	0.088 1.0000
AE	Ctrl	-	AE	T3	4.49e-03	0.0282	115	0.159 1.0000
LD	Ctrl	-	SL	Ctrl	-1.80e-01	0.0318	115	-5.672 <.0001
LD	Ctrl	-	LD	T1	-2.73e-03	0.0340	115	-0.080 1.0000
LD	Ctrl	-	LD	T2	3.85e-03	0.0358	115	0.107 1.0000
LD	Ctrl	-	LD	T3	9.32e-03	0.0340	115	0.275 1.0000
SL	Ctrl	-	SL	T1	-1.54e-02	0.0248	115	-0.622 1.0000
SL	Ctrl	-	SL	T2	4.00e-03	0.0244	115	0.164 1.0000
SL	Ctrl	-	SL	T3	-9.63e-03	0.0248	115	-0.388 1.0000
AE	T1	-	LD	T1	-1.36e-02	0.0290	115	-0.469 1.0000
AE	T1	-	SL	T1	-2.07e-01	0.0260	115	-7.961 <.0001
AE	T1	-	AE	T2	-1.45e-03	0.0299	115	-0.049 1.0000
AE	T1	-	AE	T3	4.14e-04	0.0282	115	0.015 1.0000
LD	T1	-	SL	T1	-1.93e-01	0.0275	115	-7.014 <.0001
LD	T1	-	LD	T2	6.57e-03	0.0325	115	0.202 1.0000
LD	T1	-	SL	T2	-1.74e-01	0.0272	115	-6.392 <.0001
LD	T1	-	LD	T3	1.20e-02	0.0304	115	0.397 1.0000
LD	T1	-	SL	T3	-1.87e-01	0.0275	115	-6.803 <.0001
SL	T1	-	SL	T2	1.94e-02	0.0239	115	0.812 0.9996

SL	T1	-	SL	T3	5.81e-03	0.0244	115	0.239	1.0000
AE	T2	-	LD	T2	-5.56e-03	0.0333	115	-0.167	1.0000
AE	T2	-	SL	T2	-1.86e-01	0.0282	115	-6.586	<.0001
AE	T2	-	AE	T3	1.87e-03	0.0306	115	0.061	1.0000
LD	T2	-	SL	T2	-1.80e-01	0.0295	115	-6.111	<.0001
LD	T2	-	LD	T3	5.48e-03	0.0325	115	0.169	1.0000
SL	T2	-	SL	T3	-1.36e-02	0.0239	115	-0.569	1.0000
AE	T3	-	LD	T3	-1.95e-03	0.0296	115	-0.066	1.0000
AE	T3	-	SL	T3	-2.01e-01	0.0267	115	-7.545	<.0001
LD	T3	-	SL	T3	-1.99e-01	0.0275	115	-7.241	<.0001



Chapter 2 uncovered the responses of Arctic kelp species to environmental stressors implicated in warming and melting ice. Keeping the same mesocosm experiment approach, the next chapter extends our investigation to warming and marine heat waves (MHWs) on Arctic kelps and their associated coralline and faunal communities. This second experiment took place in Tromsø (Norway) in summer 2022.

Chapter 3: Tolerance of Arctic kelps to ocean warming and marine heatwaves

Anaïs Lebrun¹, Cale A. Miller^{1,2}, Frédéric Gazeau¹, Pierre Urrutti¹, Samir Alliouane¹, Jean-Pierre Gattuso^{1,3}, Steeve Comeau¹

¹Laboratoire d'Océanographie de Villefranche, Sorbonne Université, CNRS, Villefranche-sur-Mer, France

²Department of Earth Sciences, Utrecht University, Utrecht, The Netherlands

³Institute for Sustainable Development and International Relations, Sciences Po, Paris, France

This article will be submitted in Journal of Ecology.

Abstract

The Arctic region is experiencing rapid warming and an increase in the frequency and intensity of marine heatwaves. Kelp communities are of great importance as they provide food and habitat for various species. It is critical to study their responses to ocean warming and associated marine heatwaves to anticipate the future of coastal Arctic ecosystems. In this study, we conducted a mesocosm experiment over one month in summer to assess the effects of warming and marine heatwaves on a kelp community in Tromsø (Norway). The response to different temperature conditions of three kelp species (*Saccharina latissima*, *Laminaria digitata*, and *Alaria esculenta*) and associated coralline algae, snails, sea urchins, and mussels was evaluated. The four conditions tested comprised a control, a high-temperature treatment (+1.8 °C), a treatment simulating a single 13-d heatwave with a maximum offset temperature of +2.8 °C compared to the control, and a treatment simulating two consecutive 5-day marine heatwaves with a maximum offset of +3.9 °C. For the three kelp species, net photosynthetic rate, maximum quantum yield, chlorophyll *a* content, carbon to nitrogen ratio, and growth rate were investigated. For the associated species, only growth rates were evaluated. None of the measured parameters or processes were affected by the treatments in *Laminaria digitata*, suggesting great tolerance to heat stress. *S. latissima* and *A. esculenta* physiology was affected by the treatment. For example, the maximum quantum yield of *S. latissima* decreased in the heatwaves treatments. Also, the observed decrease in chlorophyll *a* content and in net photosynthesis rate with time, which typically take place at the end of the summer, were enhanced by the treatments. The growth rates of coralline algae, mussels, snails, and sea

urchins were not affected by the treatments. These results suggest that the Arctic kelp community is tolerant to warming and marine heat waves although indirect effects of climate change such as predation and competition must also be considered to accurately predict the future.

1. Introduction

Temperature is one of the main drivers of marine ecosystem structure and functioning (e.g. Wernberg et al., 2013; Drewnik et al., 2017). It affects the distribution of marine organisms and influences various physiological and ecological processes such as photosynthesis, reproduction, and nutrient cycling. Generally, increased temperature significantly enhances the metabolism of marine organisms (Peck et al., 2009; Nguyen et al., 2011). Many species have the ability to regulate their physiological processes in response to temperature variations by, for example, adjusting their pigment content or utilizing storage molecules (Diehl et al., 2020; Britton et al., 2020). However, beyond a temperature threshold, detrimental physiological consequences appear and can eventually lead to death (e.g. Reed et al., 2016; Scheschonk et al., 2019).

Increasing global sea surface temperature has been linked to an increase in the frequency, intensity, and duration of marine heatwaves (MHWs; Oliver et al., 2018). MHWs are discrete, prolonged, anomalously warm-water events where the 90th percentile of the average daily sea surface temperature (SST) over the past 30 years is exceeded for five consecutive days or more (Hobday et al., 2016). MHWs can drive mass mortalities of benthic organisms including marine algae and seagrasses (e.g. Wernberg et al., 2013; Arias-Ortiz et al., 2018; Thomsen et al., 2019), as well as invertebrates (e.g. Hughes et al., 2017; Garrabou et al., 2022).

The Arctic Ocean warms at a rate that is more than twice the global average. Beyond gradual warming, in recent years, the Arctic has experienced a significant increase in MHWs duration and intensity. In the Kara, Laptev, and Siberian Seas, the duration of MHWs increased by 10 to 12 days between 2000 and 2020 (Golubeva et al., 2021). Hu et al. (2020) reported that the cumulative intensity of MHWs in ice-free areas increased by 0.31 °C per year between 1988 and 2017. As the Arctic Ocean is characterized by relatively limited seasonal changes in SST, MHWs may have important impacts on Arctic marine ecosystems (Huang et al., 2021), particularly on shallow benthic communities which are more subjected to MHWs than deeper

communities. In the Arctic, shallow benthic communities developing on rocky shores are composed of kelps, fucoids, coralline algae, and their associated fauna and flora (Lebrun et al., 2022). Kelps are key species in shallow areas because they provide habitat and food for a wide range of marine organisms, including fish, crustaceans, and sea urchins (Filbee-Dexter et al., 2019).

In Southern California, a series of MHWs from 2014 to 2016, with a peak at 5.9 °C above the average daily temperature for the period, combined with nutrient-poor waters, resulted in a dramatic decline of the kelp *Macrocystis pyrifera* and the loss of over half of the invertebrates and fish (Arafeh-Dalmau et al., 2019). In contrast, opportunistic species can benefit from the detrimental impacts of extreme events on other species. For example, the kelp *Undaria pinnatifida* invaded Pile Bay (New Zealand) after the extinction of the bull kelp (Thomsen et al., 2019). Therefore, the impact of MHWs can be positive or negative, depending on the species.

To our knowledge, no study has been conducted on the responses of Arctic or sub-Arctic kelp communities to simulated MHWs. Here we evaluated the effects of simulated heatwaves on the main organisms constituting kelp communities around Tromsø (Norway) during a 23 d mesocosm experiment designed to test the hypothesis that kelp community organisms exhibit species-specific tolerance and physiological responses to warming and MHWs. The reconstructed communities were composed of three kelp species (*Saccharina latissima*, *Laminaria digitata*, and *Alaria esculenta*), coralline algae, snails, urchins, and mussels. For the kelps, changes in net photosynthetic rate, maximum quantum yield, chlorophyll *a* content, carbon-to-nitrogen (C:N) ratio, and growth rate were evaluated. Growth rates were assessed for the other organisms.

2. Material and methods

2.1. Specimen collection

In June 2022, 163 mature sporophytes of *A. esculenta*, *L. digitata*, and *S. latissima* (shorter than 1 m), 61 coralline algae (assemblage dominated by *Lithothamnion glaciale*, about 5 cm in diameter), 40 mussels (*Modiolus modiolus*), 68 sea urchins (*Strongylocentrotus droebachiensis*) and 69 gastropods (*Neptunea despecta*) were collected by scuba diving between 1 and 7 m depth at Melhomen (69.88°N, 18.86°E), Sommarøy (69.63°N, 17.97°E) and Kvaløyvågen (69.85°N, 18.82°E). All sampling sites were located less than 50 km from Kårvik,

where the experimental system was installed. Sea urchins were put in 30 x 30 x 30 cm wire mesh cages in each mesocosm and fed with kelps that were not used for the experiment but sampled at the same locations. Coralline algae were also put in cages to facilitate sampling and measurements during the experiment. Mussels and gastropods were directly put in the mesocosms once labeled and weighed.

2.2. Mesocosm experiment

The experiment was carried out from 2022-06-30 to 2022-07-23, in twelve 1 m³ mesocosms that were installed on the outdoor platform of the Havbruksstasjonen i Tromsø (Kårvik) in order to expose communities to natural light. Each mesocosm was stocked with 5 to 8 individuals of *A. esculenta*, 3 to 6 individuals of *S. latissima*, and 2 to 3 individuals of *L. digitata*. The biomass in each mesocosm was adjusted to about 1000 g for *A. esculenta* and *L. digitata* and 500 g for *S. latissima*. Such values are representative of the biomass reported in Arctic coasts between 1.5 and 7 m depth (Hop et al., 2012).

Seawater flowing through the mesocosms was pumped from a 30 m depth in front of the Havbruksstasjonen i Tromsø (69.9°N, 18.8°E) to a retention basin from where it was pumped to the mesocosms using a submersible pump (Albatros©, Norsk Pumpeservice AS). We estimated that water pumped from 30 meters is representative of the surface because at this time of the year, temperature in the water column is stable within the initial 50 meters (Rüggeberg et al., 2010; Walker et al., 2022). Temperature was adjusted using a modified version of the experimental set-up described in Miller et al. (2023) by mixing ambient seawater with seawater warmed by a heat pump (15 °C). The temperature-adjusted seawater was delivered to each mesocosm at 8 L min⁻¹ corresponding to a complete turnover every 2 h. Each mesocosm was equipped with a 12 W wave pump (Sunsun© JVP-132, flow rate = 8m³ h⁻¹) to ensure mixing. Mesocosms were covered with circular acrylic lids equipped with green (RL244) and neutral light filters (RL211; Lee Filters©, LA-BS) to match the *in situ* underwater irradiance and spectrum at 2 m depth.

Three experimental treatments, high temperature (HT), 1 marine heatwave (1MH) and 2 marine heatwave (2MH), and a control (Ctrl), each in triplicate (4 treatments x 3 mesocosms) were used to study the impact of increased temperature and MHWs (Fig. 19). The control treatment tracked the *in situ* temperature (Fig. 19A). The “High Temperature” treatment (HT)

consistently remained at 1.8 °C above the control, corresponding to a projection for 2100 if temperature keeps increasing in this region at the rate observed over the last forty years (+0.22 °C per decade) by the NOAA's long term climate data record (daily Optimum Interpolation Sea Surface Temperature; OISST). At the beginning of the experiment, temperature in the three treatments was increased by 1.76 °C compared to control conditions within 4 days. To consider an increase in temperature as a MHW, the offset from the mean daily historical temperature between 2022-06-30 and 2022-07-23 should be of at least 1.23 °C for 5 days or more (calculated based on the OISST-NOAA data with the R package *heatwaveR*; Schelgel and Smit, 2018). The MH1 treatment simulated a long MHW with a maximum offset of +2.8 °C compared to the control during 12 d for a total duration of 14 d. The 2MH treatment simulated two successive intense MHWs with a maximum increase in temperature of +3.9 °C compared to the control for a total duration of 6 d for each MHW that were separated by 3 d at the HT temperature. The temperature increase for MHWs simulation started on day 6. The experiment then lasted for 16 d.

2.3. Tissue sampling

Kelp tissue samples were collected in the meristem of ten individuals of each species at the beginning (t_0 , 2022-06-30), and all on the healthy organisms, namely complete organisms (frond, stipe, and holdfast) that exhibit a firm brown frond without signs of disease at the end (t_{final} , 2022-07-23) of the experiment for further analyses (see sections 2.5. and 2.6.). Samples were stored in aluminum foils at -20 °C.

2.4. Rates of net photosynthesis

Changes in the concentration of dissolved oxygen (O_2) were measured on the two kelp species *S. latissima* and *A. esculenta*. The kelps were incubated for 30 min in 24 or 30 L cylindrical perspex chambers at different times (Table 3) of the experiment, and O_2 was continuously monitored using optical oxygen sensors connected to two oxygen meters (FireSting[®]- O_2 ; PyroScience) at an acquisition rate of 1 measurement/min. Photosynthetically active radiation (PAR) was measured inside one of the four chambers for each incubation using a spherical quantum sensor (US-SQS/L, WALZ). The photosynthetic rate was calculated for each incubation using a linear model and was normalized to 1) the volume of the incubation chamber and 2) the dry weight of the individual, calculated based on a linear regression between wet and dry weight for each kelp species (data not shown). Net photosynthetic rates

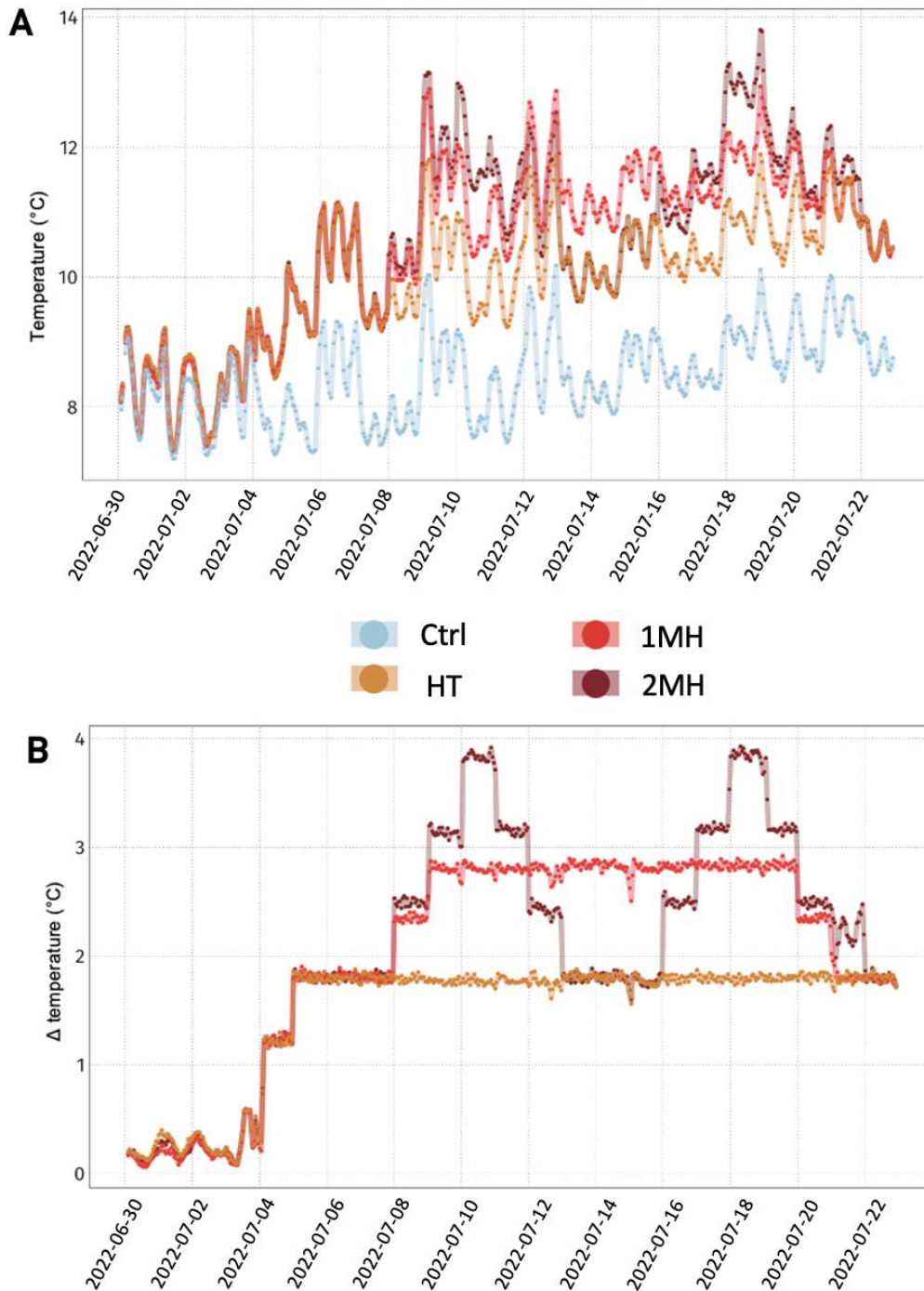


Figure 19: A) Hourly temperature measured during the experiment, B) offset of temperature between the control and each treatment. Ctrl: Control treatment, HT: High Temperature treatment, 1MH: 1 Marine Heatwave treatment, 2MH: 2 Marine Heatwaves treatment.

are expressed in $\mu\text{mol O}_2 \text{ g DW}^{-1} \text{ h}^{-1}$. To account for the variability in PAR during the different incubations, net photosynthesis was normalized with the mean PAR during the incubation which was calculated by summing the PAR measurements (1 measurement/5 min, expressed in $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and dividing by the total number of measurements.

2.5. Maximum quantum yield

The maximum quantum yield (F_v/F_m) was analyzed with a fluorometer (DIVING-PAM-II, Walz©) at different times of the experiment (Table 3). Measurements were made on the three kelp species using dark leaf clips, placed 5 min before the measurement on the meristem. For coralline algae, F_v/F_m was determined using a surface holder on organisms placed in the dark 5 min before the measurement. For kelp species, the following settings were used: gain=4, damping=3, light intensity=6, and light frequency=3. For coralline algae, the damping was increased to 9 and the other parameters remained the same as for kelps.

Table 3: Measurements timeline of net photosynthesis, maximum quantum yield, chlorophyll *a* content, C:N ratio, and growth rate of kelp, coralline algae, and fauna. AE: *Alaria esculenta*, SL: *Saccharina latissima*, LD: *Laminaria digitata*, Ctrl: Control treatment, HT: High temperature treatment, 1MH: 1 marine heatwave treatment, 2MH: 2 marine heatwaves treatment.

Date	Net photosynthesis	Maximum quantum yield	Chlorophyll <i>a</i> content	C:N ratio	Growth
2022-07-01 - t_0			AE, SL & LD: Ctrl, HT, 1MH, 2MH	AE, SL & LD: Ctrl, HT, 1MH, 2MH	<ul style="list-style-type: none"> Buoyant weight of coralline algae, mussels & snails: Ctrl, HT, 1MH, 2MH Weight of sea urchins: Ctrl, HT, 1MH, 2MH
2022-07-02- t_0	AE & SL: Ctrl, HT, 1MH, 2MH	AE & SL: Ctrl, HT, 1MH, 2MH			
2022-07-05	AE & SL: HT, 1MH, 2MH				
2022-07-07		AE & SL: Ctrl, HT, 1MH, 2MH			
2022-07-10	AE & SL: 1MH, 2MH				
2022-07-11		AE & SL: Ctrl, 1MH, 2MH			
2022-07-12	AE & SL: C	Coralline algae: Ctrl, HT, 1MH, 2MH			
2022-07-14	AE & SL: HT, 2MH	AE & SL: HT, 2MH			
2022-07-18	AE & SL: 1MH, 2MH	AE & SL: 1M, 2MH			
2022-07-20		Coralline algae: Ctrl, HT, 1MH, 2MH			
2022-07-21	AE & SL: Ctrl, HT				
2022-07-22 - t_f	AE & SL: 1MH, 2MH	AE & SL: Ctrl, HT, 1MH, 2MH			
2022-07-23 - t_f			AE, SL & LD: Ctrl, HT, 1MH, 2MH	AE, SL & LD: Ctrl, HT, 1MH, 2MH	<ul style="list-style-type: none"> Buoyant weight of coralline algae, mussels & snails: Ctrl, HT, 1MH, 2MH Distance from hole of AE, SL & LD: Ctrl, HT, 1MH, 2MH Weight of sea urchins: Ctrl, HT, 1MH, 2MH

2.6. Chlorophyll *a* content

Samples were weighed and chlorophyll *a* (chl *a*) was extracted in 90% aqueous acetone for 24 h in the dark at 4 °C. After centrifugation (0 °C, 15 min, 3000 rpm), the supernatant was transferred into glass vials, and F_0 , the initial fluorescence of chl *a* and pheophytin, was measured using a fluorimeter (Turner Design© 10-AU Fluorimeter). The F_a fluorescence was measured 1 min after the addition of 10 μ l of 0.3 N HCl to transform chl *a* into pheophytin and

subtract F_a from F_0 . The chl a content was calculated as described by Lorenzen (1967) and expressed per gram of fresh weight ($\mu\text{g chl } a \text{ (g FW)}^{-1}$).

2.7. C:N ratio

Due to logistical reasons, the t_0 samples of *A. esculenta* could not be used. The samples were dried at 60 °C for 48 h and their size was adjusted to ensure that they did not weigh more than 10 mg, in order to remain within the upper detection threshold of the CHN analyzer (PerkinElmer, Inc 2400).

2.8. Growth rate

For kelp species, growth rate was determined using the hole puncture method (Parke, 1948). Sporophytes were punctured at t_0 in the meristem section of each organism, 2 cm from the base of the stipe. The distance from the base of the stipe to the hole was measured at t_{final} . The growth rate was calculated as follows:

$$\text{Growth rate (cm d}^{-1}\text{)} = \frac{\text{dist}_{\text{final}} - \text{dist}_0}{t_{\text{final}} - t_0}$$

with dist: distance (in cm) from the base of the stipe to the hole in the meristem at time t (in days).

A log-log relationship was established between the growth rate and the total length of the organism at the beginning of the experiment. The regression equation was used to calculate the expected growth rate as a function of the kelp size and to determine its discrepancy with the measured value.

For coralline algae, snails, and mussels, growth rate was determined by subtracting their buoyant weight at t_{final} from that at t_0 , both weights were converted to dry weight using the following equation (Davies 1989).

$$\text{Dry weight (g)} = \frac{\text{wet weight}}{1 - \frac{\text{water density}}{\text{calcium carbonate density}}}$$

with wet weight in g, water density in g cm^{-3} and a calcium carbonate density of 2.93 g cm^{-3}

Water density was calculated using the Thermodynamic Equation of Seawater 2010 (TEOS 10, McDougall et al., 2009).

For sea urchins, as individual labeling was difficult, the wet weight was measured per mesocosm and not per individual.

2.9. Statistics

Rosner's generalized Extrem Studentized Deviation (ESD) test was used to detect the outliers for all parameters using the function `rosnerTest` of the R package `EnvStats` (Millard, 2013). For the net photosynthesis rate, one outlier was removed out of 72 measurements for *S. latissima*, and no outlier was detected for *A. esculenta* ($n = 79$). Regarding the maximum quantum yield, Chl *a* content and C:N, 3.5%, 4%, and 16% of measurements were considered outliers respectively, and eliminated from the analysis. No outliers were found in the growth rate of kelps while 25% of the measurements of buoyant weight of coralline algae, snails, and mussels species were removed. After the removal of the outliers, the normal distribution of the data was verified with a Shapiro-Wilk test using the function `shapiro.test` from the stats R package (R Core Team, 2013, $p > 0.156$).

A generalized linear mixed model (GLMM) with a Gaussian distribution was used to evaluate the effects of the treatment, the species, the mesocosm replica, and time when applicable on net photosynthetic rates, maximum quantum yields, chl *a* contents, C:N ratios and growth rates of kelps, and growth rates of coralline algae and faunal species.

3. Results

3.1. Experimental conditions

A MHW of 5 d was recorded around Tromsø (69.5 to 70°N; 18.5 to 19°E) in surface water between 2022-07-01 and 2022-07-05 with a mean intensity of +1.61 °C and a maximum of +2.21 °C on the 2022-07-02 reaching a temperature up to 11.1 °C (NOAA-OISST data, Fig. S3). The increase in temperature did not reach the depth (30 m) at which the water for the mesocosms was pumped as in the control treatment, notable temperature increases were only observed between 2022-07-06 and 2022-07-13, with a maximum rise to 10.2 °C recorded on 2022-07-13. The intensity of the temperature increase in the control was too low and the duration too short to classify these events as MHW. The median temperature recorded in the control treatment was 8.5 °C. In the HT, 1MH, and 2MH treatments, the medians of temperature were respectively 10.2, 10.9, and 10.8 °C. The maximum temperatures were reached on 2022-07-19 at 11.89, 12.93, and 13.8 °C respectively.

3.2. Rate of net photosynthesis

Net photosynthetic rates of *A. esculenta* were affected by both time and treatments (Fig. 20, Tables S9, S10). Net photosynthetic rates decreased between t_0 and t_{final} in all treatments ($p < 0.001$). Between t_0 and the middle of the experiment, on 2022-07-14, net photosynthetic rates significantly decreased in the HT ($p < 0.001$). A similar trend was observed in the 2MH treatment but it was not statistically significant ($p = 0.064$). Net photosynthetic rates of *S. latissima* were also significantly lower on 2022-07-14 in the HT treatment compared to the t_0 ($p = 0.045$). Although there was a declining trend of photosynthetic rates over time for *S. latissima*, it was not statistically significant ($p > 0.155$) because of an important variability between organisms.

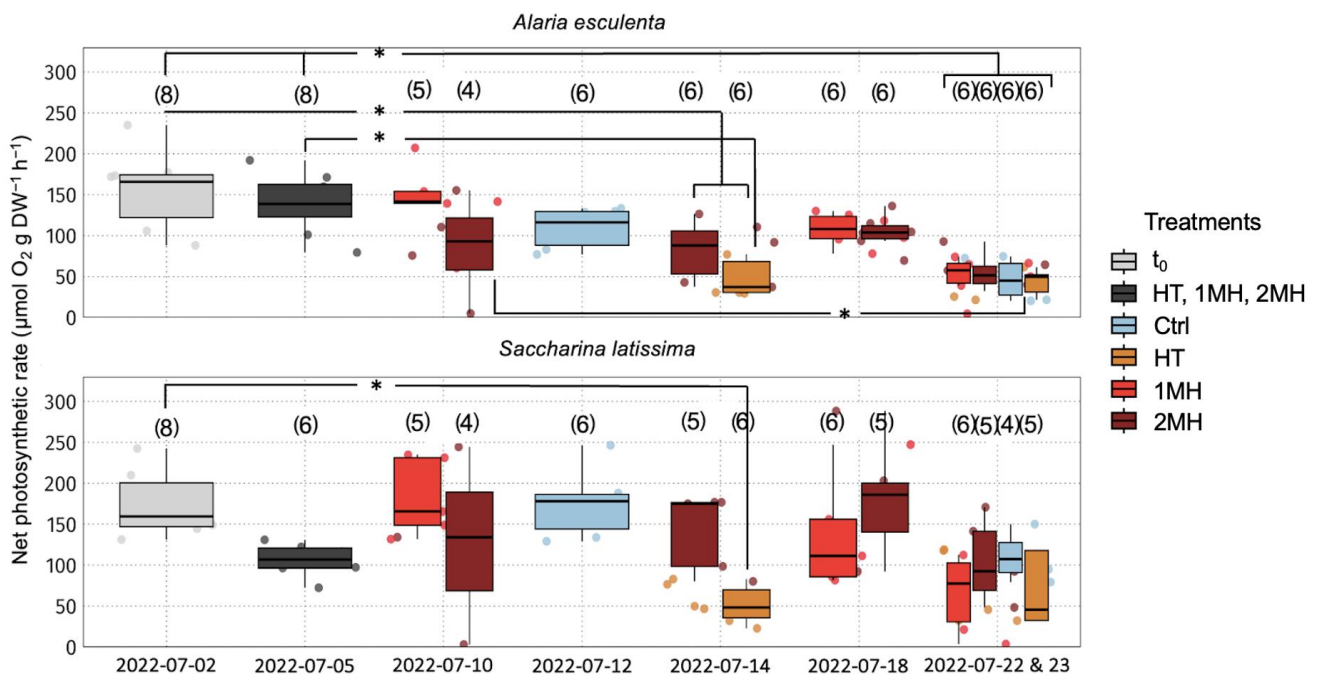


Figure 20: Net photosynthetic rates of *Alaria esculenta* and *Saccharina latissima*. The number in parentheses above each boxplot corresponds to the sample size. The horizontal lines in each boxplot represent the median. The whiskers extend to the furthest data points within 1.5 times the interquartile range (the top and bottom of the box). Statistically significant differences are shown with an asterisk ($p < 0.05$). t_0 : Beginning of the experiment, Ctrl: Control treatment, HT: High Temperature treatment, 1MH: 1 Marine Heatwave treatment, 2MH: 2 Marine Heatwaves treatment.

3.3. Maximum quantum yield

The maximum quantum yield (F_v/F_m) of *A. esculenta* and *L. digitata* was not affected by the different treatments nor by time (Fig. 21, Tables S11, S12). However, for *S. latissima*, F_v/F_m

significantly increased between t_0 and the first increase in temperature on 2022-07-07 for HT, 1MH, and 2MH treatments ($p < 0.001$). Then F_v/F_m significantly decreased in the 2MH treatment between the first and the second peak of temperature (2022-07-11, 2022-07-18), and in between (2022-07-14, $p = 0.037$ and $p < 0.001$, respectively). In the 1MH treatment, F_v/F_m also significantly decreased between 2022-07-07 and the exposition to the MHW on 2022-07-11 and 2022-07-15 ($p = 0.017$ and 0.006 , respectively). At the end of the experiment, F_v/F_m was back to the initial values in all treatments.

The maximum quantum yield of coralline algae was measured on 2022-12-07 and 2022-20-07 was not affected by time or treatment (Fig. S4; $p > 0.05$).

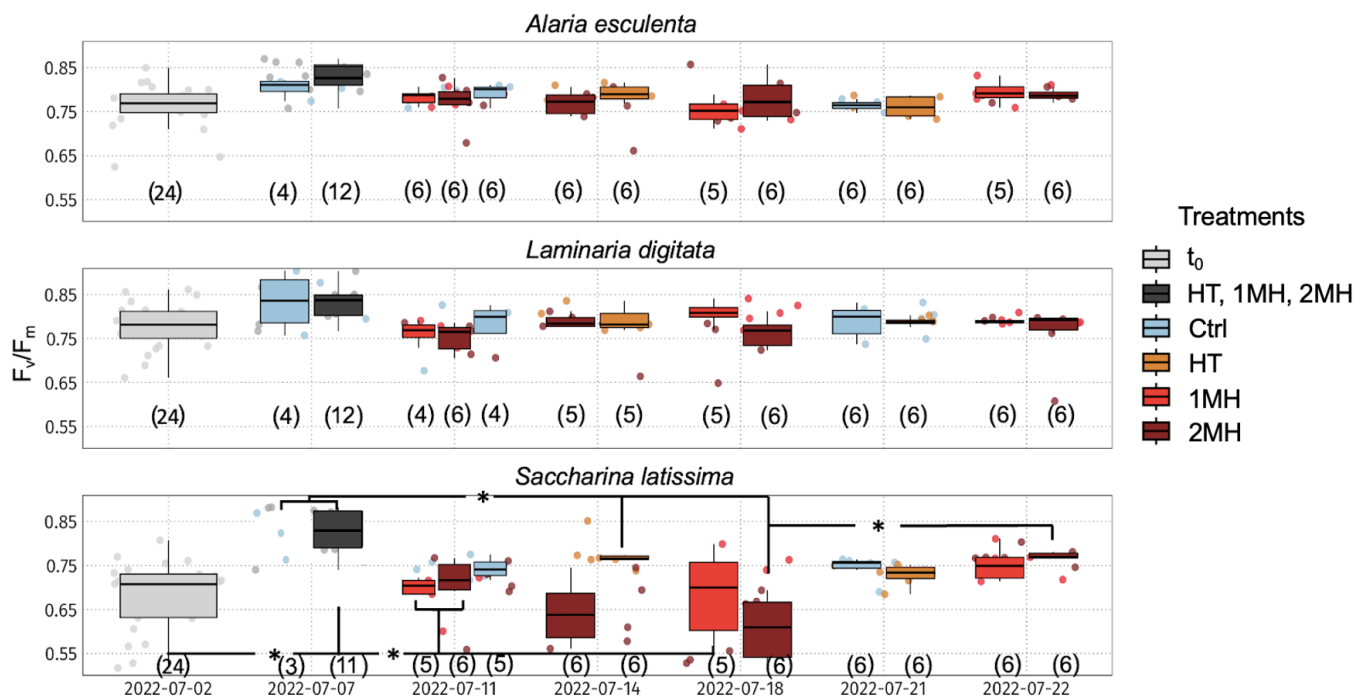


Figure 21: Maximum quantum yield (F_v/F_m) of *Alaria esculenta*, *Laminaria digitata*, and *Saccharina latissima* during the experiment. The horizontal lines in each boxplot represent the median. The whiskers extend to the furthest data points within 1.5 times the interquartile range (the top and bottom of the box). The number in parentheses below each boxplot corresponds to the sample size. Statistically significant differences are shown with an asterisk ($p < 0.05$). t_0 : Beginning of the experiment, Ctrl: Control treatment, HT: High Temperature treatment, 1MH: 1 Marine Heatwave treatment, 2MH: 2 Marine Heatwaves treatment.

3.4. Chl *a* content

For *A. esculenta* and *S. latissima*, the chl *a* content significantly decreased between t_0 and the 2MH treatment at t_{final} ($p = 0.011$ and 0.006 , Fig. 22, Tables S13, S14), while it did not vary with

time in the other treatments. The chl *a* content of *L. digitata* was not significantly impacted by time and treatments ($p = 0.167$).

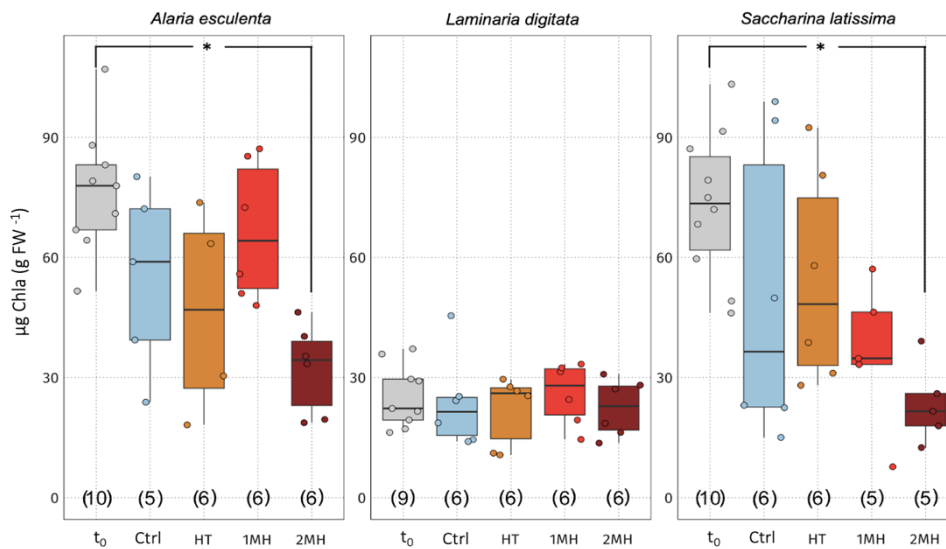


Figure 22: Chlorophyll *a* content of *Alaria esculenta*, *Laminaria digitata*, and *Saccharina latissima* exposed to the control and the three treatments. Values at t_0 correspond to the Chl *a* content at the start of the experiment, while C, HT, 1MH, and 2MH correspond to the final Chl *a* content of species maintained in the respective treatments for the whole experiment. The horizontal lines in each boxplot represent the median. The whiskers extend to the furthest data points within 1.5 times the interquartile range (the top and bottom of the box). The number in parentheses below each boxplot corresponds to the sample size. Statistically significant differences are shown with an asterisk ($p < 0.05$). t_0 : beginning of the experiment, Ctrl: Control treatment, HT: High Temperature treatment, 1MH: 1 Marine Heatwave treatment, 2MH: 2 Marine Heatwaves treatment

3.5. C:N ratios

For *S. latissima* and *L. digitata*, C:N ratios at t_0 ranged from 16.7 to 30.4 (Fig. 23). No statistical difference was found between t_0 and t_{final} for all treatments ($p > 0.167$, Tables S15, S16). C:N ratios of *A. esculenta* was statistically different between the 1MH and the 2MH treatments at t_{final} ($p = 0.007$), with lower C:N ratios in the 1MH treatment.

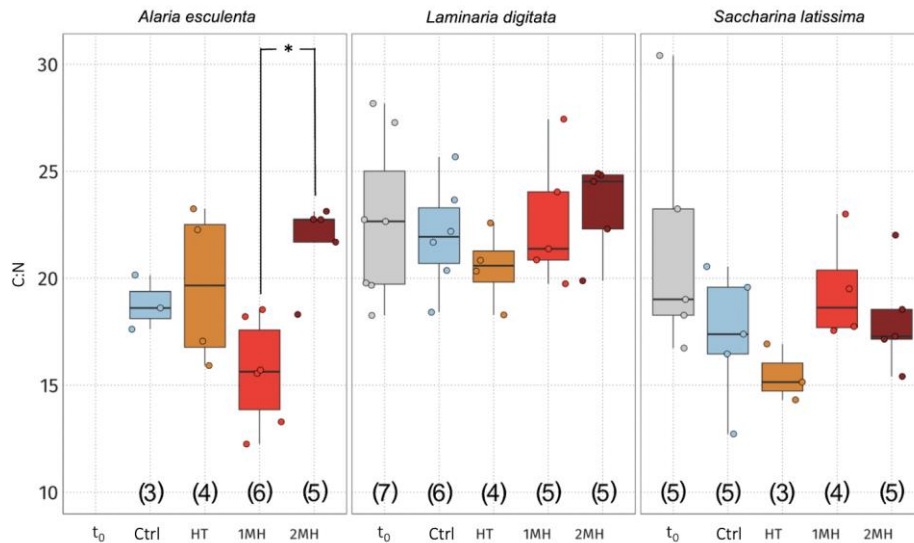


Figure 23: Carbon:nitrogen ratio of *Alaria esculenta*, *Laminaria digitata*, and *Saccharina latissima* exposed to the control and the three treatments. Values at t_0 correspond to samples taken at the start of the experiment, while C, HT, 1MH, and 2MH correspond to the final values for kelp maintained in the respective treatments during the whole experiment. The horizontal lines in each boxplot represent the median. The whiskers extend to the furthest data points within 1.5 times the interquartile range (the top and bottom of the box). The number in parentheses below each boxplot corresponds to the sample size. Statistical differences are marked by an asterisk ($p < 0.05$). t_0 : beginning of the experiment, Ctrl: Control treatment, HT: High Temperature treatment, 1MH: 1 Marine Heatwave treatment, 2MH: 2 Marine Heatwaves treatment.

3.6. Growth rate

The growth rates of *A. esculenta*, *L. digitata*, and *S. latissima* were not significantly impacted by the treatments (Fig. 24, $p = 0.149$, Tables S17, S18). Growth rates varied from 0.057 to 0.457 cm d^{-1} for *S. latissima*, 0.004 to 0.039 cm d^{-1} for *L. digitata*, and 0.004 to 0.239 cm d^{-1} for *A. esculenta*. The growth rate of *S. latissima* was significantly higher than for the two other species ($p < 0.001$).

No statistical difference was found between the different treatments for the growth rate of coralline algae, snails, mussels, and sea urchins (Fig. S5, $p > 0.476$).

4. Discussion

According to the NOAA OISST data, a MHW occurred in the Tromsø area during the course of this study in early July 2022. This event did not appear in our control mesocosms. Three non-mutually exclusive hypotheses could explain this mismatch. First, the MHW was reported over a broad area (69.5 to 70°N, 18.5 to 19°E). It may not have occurred at the study location. Second, a MHW reported at the surface may not propagate down to a depth of 30 m, the depth at which seawater was pumped in our experiment, due to stratification and heat

dissipation in the water column. Third, the temperature of the pumped water could have been altered in the transit to the control mesocosms.

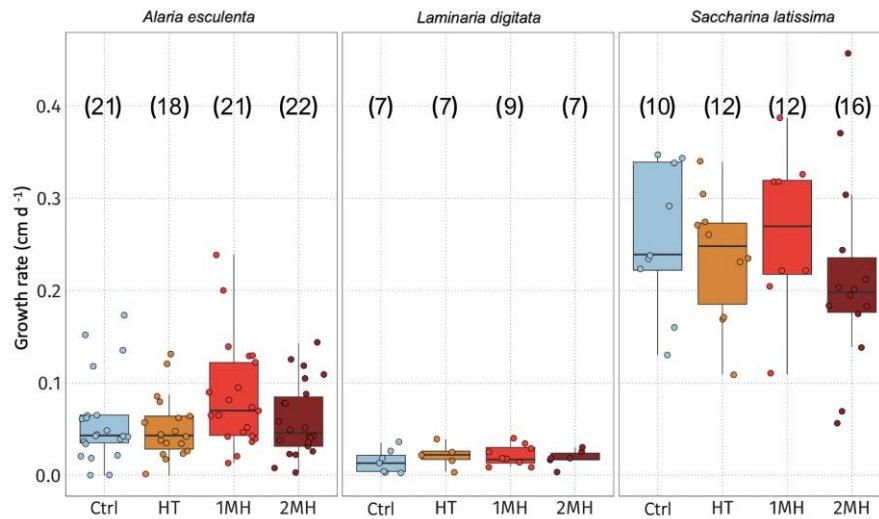


Figure 24: Growth rate of *Alaria esculenta*, *Laminaria digitata*, and *Saccharina latissima* in the control and three treatments during the whole experiment. The horizontal lines in each boxplot represent the median. The whiskers extend to the furthest data points within 1.5 times the interquartile range (the top and bottom of the box). The number in parentheses above each boxplot corresponds to the sample size. Ctrl: Control treatment, HT: High Temperature treatment, 1MH: 1 Marine Heatwave treatment, 2MH: 2 Marine Heatwaves treatment.

This study highlights distinct responses of *A. esculenta*, *L. digitata*, and *S. latissima* to the temperature treatments. While *A. esculenta* and *S. latissima* exhibit significant susceptibility to the warming treatments, *L. digitata* demonstrates greater tolerance. Our hypothesis that kelp community organisms exhibit species-specific tolerance and physiological responses to MHWs is verified for kelp species. Remarkably, MHWs had no evident detrimental impact on any of the species studied.

The decrease in net photosynthesis with time could be explained by the following hypotheses. In summer, the increase in temperature can induce an increase in the respiration rate. As a result, net oxygen production would decrease if gross photosynthesis does not increase enough (Aamot, 2011). Umanson et al. (2021) found a 150% increase in the respiration rate of the giant kelp *Macrocystis pyrifera* at 22 °C compared to 16 °C, which resulted in decreasing the gross photosynthesis:respiration ratio from 9 to 5. This hypothesis cannot be confirmed since the respiration rate was not measured during the present experiment as all incubations took place under natural light conditions and there is no darkness at this time of the year and latitude. Other hypotheses that could explain this observation are a decrease in PAR or in

nutrient concentrations over the course of the experiment. However, PAR values did not decrease during the time of the experiment, and nutrient concentrations actually increased, especially phosphate (from 0.16 ± 0.03 to 0.28 ± 0.02 between t_0 and t_{final} all treatments combined, $R^2 = 0.57$, Miller et al., unpublished). A decrease in chl *a* content could explain the observed decrease in net photosynthesis rate. Chl *a* content decreased for both *A. esculenta* and *S. latissima* in the 2MH treatment at the end of the experiment. Chl *a* content declined with time, probably due to the aging of the seaweed and the time of the year. The 2MH treatment may have accelerated this decline which started but was not yet significant in the control treatment. These observations were also noted by Nepper-Davidsen et al. (2019) who reported that chl *a* content of *S. latissima* from South Kattegat declined with time at 15 °C. Notably, when the same species was exposed to a higher temperature of 24 °C, the decline was even more pronounced, reaching 70%. Umanzor et al. (2021) also found a decrease in the chl *a* content of the giant kelp *Macrocystis pyrifera* when exposed to warmer temperatures (+6 °C) for 5 d. This finding highlights the importance of considering temporal changes in the photosynthetic pigments of seaweed species when assessing the response of their photosynthetic performance to specific treatments, such as MHWs.

The increase of the maximum quantum yield of *S. latissima* between the start of the experiment and the *in situ* temperature increase on 2022-07-07 suggests that the exposure to elevated temperature had a positive effect on the photosystem II of this species. In contrast, exposure to the MHWs treatments has a negative effect on F_v/F_m . This negative impact was however quickly reversed as F_v/F_m was back to its original values only two days after the end of the MHWs. The decrease of F_v/F_m found here is in agreement with the study of Niedzwiedz et al. (2022) where F_v/F_m of *S. latissima* from Helgoland (North Sea, Germany) decreased when exposed to MHWs lasting 9 to 13 d, with temperature increases ranging from 2 °C to 6 °C. Also, in a study conducted by Strasser et al. (2022), the maximum quantum yield of *Laminaria ochroleuca*, an Atlantic kelp species, was at its initial level during the first measurement taken 27 d after a severe MHW (+10 °C; maximum temperature of 27 °C during 5 days). Our results highlight the resilience and capacity of these species to recover and restore their photosynthetic efficiency rapidly after a heatwave.

The observed decrease and recovery in F_v/F_m do not match net photosynthetic rates for both species. It's worth highlighting that the maximum quantum yield should be compared with the

gross photosynthetic rate (not determined here) rather than the net photosynthetic rate (gross photosynthesis + respiration). However, while the measurement of the maximum quantum yield provides insights into the photosynthetic efficiency, it is important to recognize that it is not a comprehensive indicator on its own. For example, Olischläger et al. (2017) report a doubling of the photosynthetic rate of *S. latissima* at 17 °C compared to 10 °C while the maximum quantum yield was unaffected by temperature. The measure of F_v/F_m does not capture the complexity of the photosynthetic process (e.g. Skillman et al., 2008). It can however be used as a proxy for assessing cellular stress and algal vitality (Hurd et al., 2014; Niedzwiedz et al., 2022). Therefore, it cannot be used in isolation to assess the response of algae to environmental factors.

Regarding the C:N ratio and the growth rate, no significant difference was observed between the different treatments, except for *A. esculenta* which exhibited higher C:N ratios in the 2MH treatment compared to the 1MH at the end of the experiment. Benthic marine macroalgae and seagrasses from temperate and tropical regions have a mean C:N ratio of 22 (Atkinson and Smith, 1983), which is consistent with our measurements (mean ratios of 21.5 and 22.7 for *S. latissima* and *L. digitata* at t_0 and 18.8, 17.3 and 22 in the control treatment at t_{final} for *A. esculenta*, *S. latissima* and *L. digitata*, respectively). Under heat stress, organisms often prioritize resource allocation towards stress tolerance mechanisms which can affect nitrogen uptake or assimilation processes, thereby reducing nitrogen availability and increasing the C:N ratio (Diehl et al., 2020). However, for *A. esculenta*, concentrations of carbon and nitrogen as well as C:N ratio were unaffected by the treatments, which indicates that no major modification of the metabolism occurred when exposed to MHWs. Our results are consistent with Kinnby et al. (2021) who found no effect of a 5 °C warming of 7 weeks on the C:N ratio and growth rate of *Fucus vesiculosus* from Sweden.

Overall, the results suggest that the three kelp species studied here are tolerant to warming and MHWs for most parameters and resilient for the maximum quantum yield in the case of *S. latissima*. While the warming and MHWs treatments induced responses in two of the three species studied, these responses were either reversible, like the decrease of the maximum quantum yield, or enhanced such as declines in net photosynthesis rate and chl *a* content with time, which typically take place at the end of the summer. Overall, this result is not surprising since these species are also distributed at lower latitudes. These cold-temperate kelps likely

have temperature optima well above the seawater temperature of Tromsø (Bischoff and Wiencke, 1993; Müller et al., 2009). Fredersdorf et al. (2009) found that the photosynthesis optimum temperature for populations of *A. esculenta*, living in colder waters than in Tromsø (Kongsfjorden, Svalbard), was between 13 and 17 °C. This temperature was only reached for a few hours in the two MHWs treatments during our experiment. However, the three species may have different sensitivities and tolerance levels to temperature stress or might have distinct optimum temperatures for photosynthesis and respiration. *L. digitata* seems to acclimatize rapidly to MHW evidenced by the absence of effects on the parameters measured. In contrast, the physiology of *S. latissima* and *A. esculenta* exhibited treatment-induced effects. However, the observed effects, including a decline in chl *a* content and net photosynthesis rate over time, typically take place at the end of summer and were thus only enhanced by the treatments. Also, *S. latissima* displays remarkable resilience to MHWs, as evidenced by its maximum quantum yield returning to its initial level. MHWs force individuals to quickly acclimate to new conditions. In particular, individuals can adjust pigment concentration and location to maintain an elevated net photosynthetic rate, although it might not be possible over a long period of time (Niedzwiedz et al., 2022). This could elucidate the absence of impact observed from the decrease in maximum quantum yield in the MHW treatments on the photosynthesis of *S. latissima*.

With respect to coralline algae, an important component of these benthic communities, their growth rate and quantum yield did not vary significantly across the treatments, which suggests a certain tolerance to MHWs. Cornwall et al. (2020) highlighted the importance of studying coralline algae over multiple generations to characterize potential gains of tolerance to stressors. In particular, species with short generation times may be more resilient and more capable of acclimatizing to future warming (Cornwall et al., 2019). However, such acclimation might be compromised for long-lived species such as polar species. Furthermore, indirect factors are also to be considered. For example, Webster et al. (2010) showed that a microbial shift after 7 days at +5 °C is accompanied by a 50% reduction in the establishment of the coralline algae *Neogoniolithon fosliei* from Australia. The growth rate of these organisms in the Arctic and sub-Arctic is very low (0.2 mm/month; Adey and Vassar, 1975), therefore a longer experiment would be necessary to confirm our observations.

Similarly, the growth rate of snails, mussels, and sea urchins also showed no significant variations with the treatments. However, it is important to note that only growth was studied. Further investigations such as lipid content analyses or reproduction are necessary to conclude on the tolerance of these organisms to warming and MHWs. For example, Axenov-Gribanov et al. (2015) found that exposure to 20 °C (compared to 15 °C) induced a higher synthesis of HSP70, a heat-shock protein produced when the organism is exposed to a stressful environment, and caused changes in the activities of antioxidative enzymes and glycogenic metabolism of the gastropod *Lymnaea stagnalis*. Also, Hiscock et al. (2004) concluded on a negative impact of warming on the horse mussel, *Modiolus modiolus*, which may have participated in its decline since 1990 on the coast of Northern Ireland. Conversely, already in the 1980's, Hart & Scheibling (1988) alerted on the positive effect of warming and MHW on sea urchins, especially on larval growth, and the potential indirect impact on kelp forests through increased grazing. A pan-Arctic review of kelp trends also show examples of extended urchin barrens, suggesting that in some areas top-down control by sea urchins plays a larger role than climate change for kelp abundance (Krause-Jensen et al. 2020). In Tromsø, except in isolated areas with strong currents, kelp populations have been decimated by sea urchins (Sivertsen, 2006.). A more extensive study would provide deeper insights into the response of these organisms to changing environmental conditions and the impact on the whole community.

It is important to acknowledge a limitation of the present study, as in other perturbation experiments. The duration of the experiment obviously does not capture the long-term effects of warming and MHWs on kelp communities. Kelp communities are dynamic and complex, and their responses to environmental stressors can vary over different time scales. Niedzwiedz et al. (2022) found a better survival of *S. latissima* from Helgoland (North Sea, Germany) to heatwave treatments in June than in August 2018 (18 to 24 °C). A longer experimental period would provide greater insights into potential acclimation mechanisms that species could use to cope with prolonged heat stress. It would also allow for the examination of potential shifts in species composition, competitive interactions, and ecological dynamics that can occur as a result of sustained MHWs events. In any case, the duration of perturbation experiments cannot reproduce the expected future decadal changes.

The occurrence of two consecutive MHWs events within a single year highlights the urgency and relevance of understanding the impacts of prolonged heat stress on kelp populations. Finally, it appears essential to carry out *in situ* studies to observe the arrival of new opportunistic species, with affinities for warmer temperature, following the constant warming of seawater and the multiplication and intensification of MHWs (Arafeh-Dalmau et al., 2019). These newcomers will have important consequences on the benthic community and must be taken into account in the projection of the future Arctic ecosystem.

Acknowledgments

We are extremely grateful to Haakon Hop for making his boat available, his invaluable assistance for organism collection, and for the generous loan of a Diving-PAM. This work could not have been performed without his help. We also acknowledge the efforts of Havbruksstasjonen personnel and warmly thank Maxime Pistone for his invaluable assistance, Nathalie Leblond for her help with the CHN analysis, Robert Schlegel for his contribution to the experimental design, Catriona Hurd for her valuable advice, and the Alfred Wegener Institute (AWI) and Institut polaire français Paul Emile Victor (IPEV) for assisted with shipping of our equipment. This study was conducted in the frame of the FACE-IT project (The Future of Arctic Coastal Ecosystems – Identifying Transitions in Fjord Systems and Adjacent Coastal Areas) which received funding from the European Union’s Horizon 2020 research and innovation programme under grant agreement No 869154. This study was supported by the Prince Albert II of Monaco Foundation (FPA2, project ORCA n°3051).

Author contributions

AL, CM, FG, JPG, and SC designed the study. FG, PU, and SC designed the experimental system. JPG, SA, and SC collected the samples by scuba diving. AL and CM performed the experiment with the assistance of JPG, SA, and SC. AL analyzed the data and wrote the first draft of the manuscript, which was then finalized by all the co-authors.

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Supplementary data

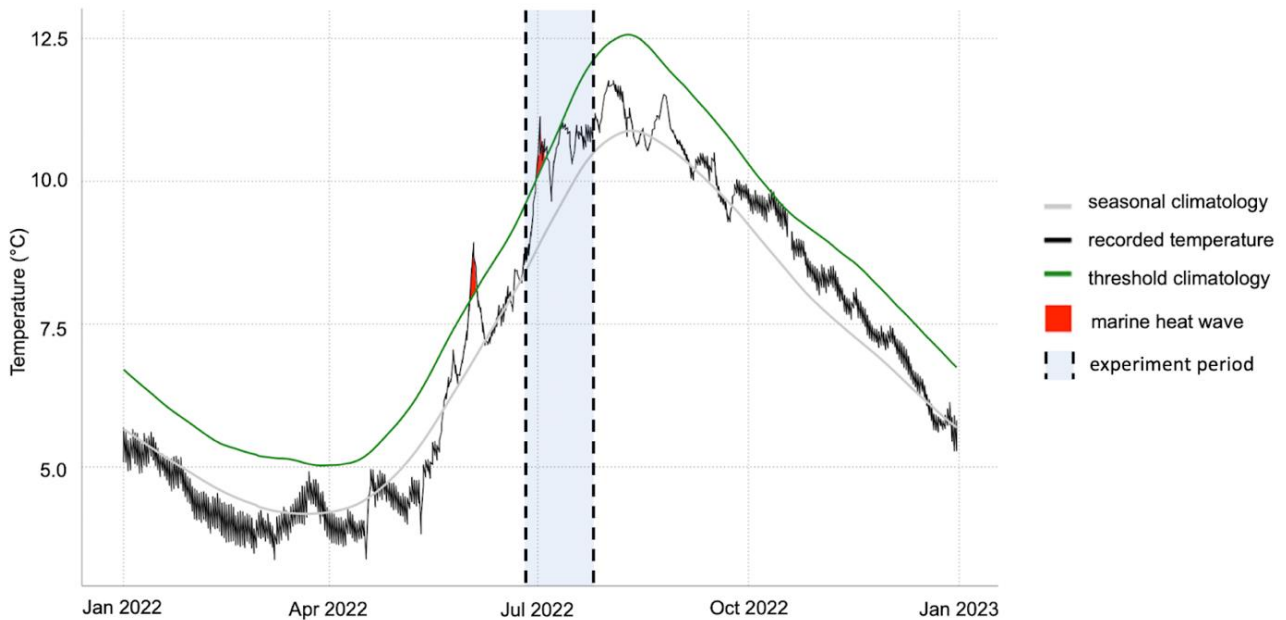


Figure S3: Sea surface water temperature around Tromsø in 2022, focusing on the latitude range of 69.5 to 70°N and longitude range of 18.5 to 19°E and based on NOAA's Long-Term Climate Data Record (OISST) which combines observations from satellites, ships, buoys, and Argo floats. The seasonal climatology, which represents the daily mean temperature from 1982 to 2022, is represented in grey. The threshold climatology, or 90th percentile, is represented in green. A heat wave is identified when the temperature exceeds this threshold for a continuous period of 5 days. Instances of marine heatwaves in 2022 are highlighted in red.

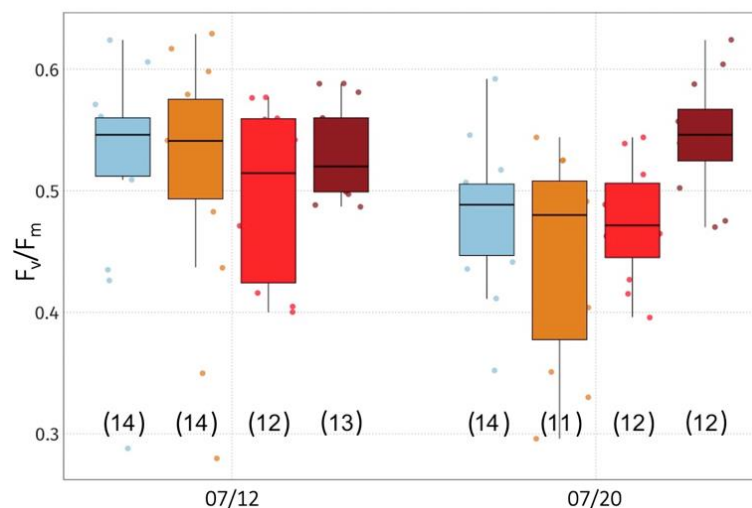


Figure S4: Maximum quantum yield (F_v/F_m) of coralline algae during the experiment. The number in parentheses below each boxplot corresponds to the sample size. The horizontal lines in each boxplot represent the median. The vertical lines start at the lowest value and end at the highest, excluding the outliers. The number in parentheses below each boxplot corresponds to the sample size.

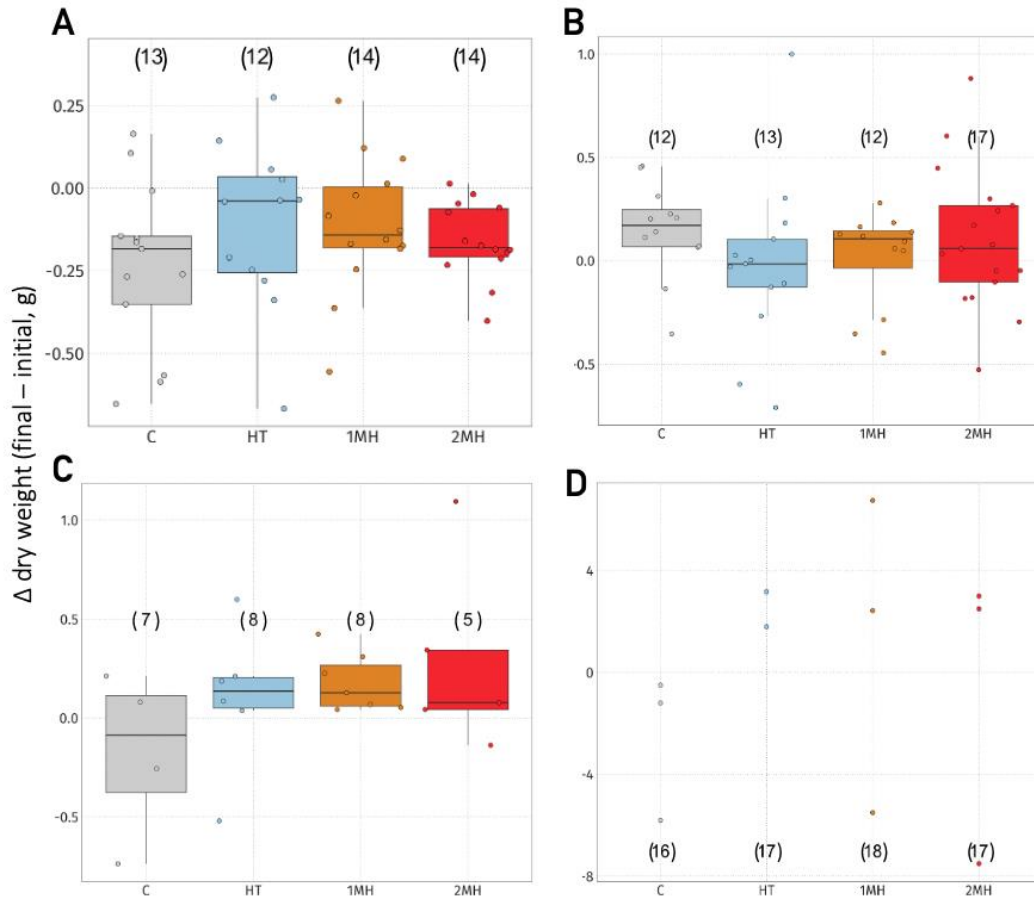


Figure S5: Difference between the initial and final dry weight of A) coralline algae, B) snails C) mussels and wet weight of D) urchins exposed to the control and the three treatments. The horizontal lines in each boxplot represent the median. The vertical lines start at the lowest value and end at the highest, excluding the outliers. The number in parentheses above or below each boxplot corresponds to the sample size.

Table S9: Analysis of deviance (Type II tests) in a generalized linear mixed model to predict the net photosynthesis rate.

	Chisq	Df	Pr(>Chisq)
time	37.343	4	1.530e-07 ***
species	10.010	1	1.294e-05 ***
treatment	7.900	3	0.048
time:species	1.025	4	0.906
time:treatment	19.005	3	0.000 ***
specie:treatment	3.527	3	0.317
time:species:treatment	3.315	3	0.346

Table S10: Pairwise comparisons of the net photosynthesis rate of A) *Alaria esculenta* and B) *Saccharina latissima* calculated with the method of Tukey generalized linear mixed model. The p-values in bold (< 0.05) support the hypothesis that there is a significant difference in the pair.

A	Date	Treatment	Date	Treatment	estimate	SE	df	t.ratio	p.value
	05/07/2022	HT. 1MH. 2MH vs.	10/07/2022	1MH	-1.646	19.096	66	-0.086	1.000
	05/07/2022	HT. 1MH. 2MH vs.	10/07/2022	2MH	52.285	20.512	66	2.549	0.856
	05/07/2022	HT. 1MH. 2MH vs.	12/07/2022	C	29.607	18.090	66	1.637	1.000
	05/07/2022	HT. 1MH. 2MH vs.	14/07/2022	2MH	56.705	18.090	66	3.135	0.453
	05/07/2022	HT. 1MH. 2MH vs.	14/07/2022	HT	90.867	18.090	66	5.023	0.003 ***
	05/07/2022	HT. 1MH. 2MH vs.	18/07/2022	1MH	31.393	18.090	66	1.735	0.999
	05/07/2022	HT. 1MH. 2MH vs.	18/07/2022	2MH	35.165	18.090	66	1.944	0.995
	05/07/2022	HT. 1MH. 2MH vs.	TF	1MH	89.047	18.090	66	4.922	0.004 ***
	05/07/2022	HT. 1MH. 2MH vs.	TF	2MH	83.452	18.090	66	4.613	0.010 **
	05/07/2022	HT. 1MH. 2MH vs.	TF	C	92.312	18.090	66	5.103	0.002 ***
	05/07/2022	HT. 1MH. 2MH vs.	TF	HT	95.496	18.090	66	5.279	0.001 ***
	10/07/2022	1MH vs.	10/07/2022	2MH	53.932	22.470	66	2.400	0.920
	10/07/2022	1MH vs.	14/07/2022	2MH	58.351	20.283	66	2.877	0.645
	10/07/2022	1MH vs.	18/07/2022	1MH	33.040	20.283	66	1.629	1.000
	10/07/2022	1MH vs.	18/07/2022	2MH	36.811	20.283	66	1.815	0.999
	10/07/2022	1MH vs.	TF	1MH	90.694	20.283	66	4.471	0.016 *
	10/07/2022	1MH vs.	TF	2MH	85.099	20.283	66	4.196	0.038 *
	10/07/2022	2MH vs.	14/07/2022	2MH	4.420	21.621	66	0.204	1.000
	10/07/2022	2MH vs.	18/07/2022	2MH	-17.121	21.621	66	-0.792	1.000
	10/07/2022	2MH vs.	TF	2MH	31.167	21.621	66	1.441	1.000
	12/07/2022	C vs.	10/07/2022	1MH	-31.253	20.283	66	-1.541	1.000
	12/07/2022	C vs.	10/07/2022	2MH	22.679	21.621	66	1.049	1.000
	12/07/2022	C vs.	14/07/2022	2MH	27.098	19.339	66	1.401	1.000
	12/07/2022	C vs.	14/07/2022	HT	61.260	19.339	66	3.168	0.430

12/07/2022	C	vs. 18/07/2022	1MH	1.786	19.339	66	0.092	1.000
12/07/2022	C	vs. 18/07/2022	2MH	5.558	19.339	66	0.287	1.000
12/07/2022	C	vs. TF	1MH	59.440	19.339	66	3.074	0.498
12/07/2022	C	vs. TF	2MH	53.846	19.339	66	2.784	0.712
12/07/2022	C	vs. TF	C	62.705	19.339	66	3.242	0.378
12/07/2022	C	vs. TF	HT	65.890	19.339	66	3.407	0.277
14/07/2022	2MH	vs. 18/07/2022	2MH	-21.540	19.339	66	-1.114	1.000
14/07/2022	2MH	vs. TF	2MH	26.747	19.339	66	1.383	1.000
14/07/2022	HT	vs. 10/07/2022	1MH	-92.513	20.283	66	-4.561	0.012 *
14/07/2022	HT	vs. 10/07/2022	2MH	-38.581	21.621	66	-1.784	0.999
14/07/2022	HT	vs. 14/07/2022	2MH	-34.162	19.339	66	-1.766	0.999
14/07/2022	HT	vs. 18/07/2022	1MH	-59.474	19.339	66	-3.075	0.497
14/07/2022	HT	vs. 18/07/2022	2MH	-55.702	19.339	66	-2.880	0.643
14/07/2022	HT	vs. TF	1MH	-1.820	19.339	66	-0.094	1.000
14/07/2022	HT	vs. TF	2MH	-7.414	19.339	66	-0.383	1.000
14/07/2022	HT	vs. TF	HT	4.630	19.339	66	0.239	1.000
18/07/2022	1MH	vs. 10/07/2022	2MH	20.892	21.621	66	0.966	1.000
18/07/2022	1MH	vs. 14/07/2022	2MH	25.312	19.339	66	1.309	1.000
18/07/2022	1MH	vs. 18/07/2022	2MH	3.772	19.339	66	0.195	1.000
18/07/2022	1MH	vs. TF	1MH	57.654	19.339	66	2.981	0.567
18/07/2022	1MH	vs. TF	2MH	52.059	19.339	66	2.692	0.774
18/07/2022	2MH	vs. TF	2MH	48.287	19.339	66	2.497	0.881
T0	T0	vs. 05/07/2022	HT. 1MH. 2MH	15.922	16.748	66	0.951	1.000
T0	T0	vs. 10/07/2022	1MH	14.276	19.096	66	0.748	1.000
T0	T0	vs. 10/07/2022	2MH	68.208	20.512	66	3.325	0.325
T0	T0	vs. 12/07/2022	C	45.529	18.090	66	2.517	0.872
T0	T0	vs. 14/07/2022	2MH	72.627	18.090	66	4.015	0.064
T0	T0	vs. 14/07/2022	HT	106.789	18.090	66	5.903	0.000 ***

T0	T0	vs. 18/07/2022	1MH	47.316	18.090	66	2.616	0.820	
T0	T0	vs. 18/07/2022	2MH	51.087	18.090	66	2.824	0.684	
T0	T0	vs. TF	1MH	104.970	18.090	66	5.803	0.000	***
T0	T0	vs. TF	2MH	99.375	18.090	66	5.493	0.000	***
T0	T0	vs. TF	C	108.234	18.090	66	5.983	0.000	***
T0	T0	vs. TF	HT	111.419	18.090	66	6.159	0.000	***
TF	1MH	vs. 10/07/2022	2MH	-36.762	21.621	66	-1.700	1.000	
TF	1MH	vs. 14/07/2022	2MH	-32.342	19.339	66	-1.672	1.000	
TF	1MH	vs. 18/07/2022	2MH	-53.882	19.339	66	-2.786	0.711	
TF	1MH	vs. TF	2MH	-5.595	19.339	66	-0.289	1.000	
TF	C	vs. 10/07/2022	1MH	-93.958	20.283	66	-4.632	0.010	**
TF	C	vs. 10/07/2022	2MH	-40.026	21.621	66	-1.851	0.998	
TF	C	vs. 14/07/2022	2MH	-35.607	19.339	66	-1.841	0.998	
TF	C	vs. 14/07/2022	HT	-1.445	19.339	66	-0.075	1.000	
TF	C	vs. 18/07/2022	1MH	-60.919	19.339	66	-3.150	0.442	
TF	C	vs. 18/07/2022	2MH	-57.147	19.339	66	-2.955	0.587	
TF	C	vs. TF	1MH	-3.265	19.339	66	-0.169	1.000	
TF	C	vs. TF	2MH	-8.859	19.339	66	-0.458	1.000	
TF	C	vs. TF	HT	3.185	19.339	66	0.165	1.000	
TF	HT	vs. 10/07/2022	1MH	-97.143	20.283	66	-4.789	0.006	**
TF	HT	vs. 10/07/2022	2MH	-43.211	21.621	66	-1.999	0.993	
TF	HT	vs. 14/07/2022	2MH	-38.791	19.339	66	-2.006	0.992	
TF	HT	vs. 18/07/2022	1MH	-64.103	19.339	66	-3.315	0.331	
TF	HT	vs. 18/07/2022	2MH	-60.331	19.339	66	-3.120	0.464	
TF	HT	vs. TF	1MH	-6.449	19.339	66	-0.333	1.000	
TF	HT	vs. TF	2MH	-12.044	19.339	66	-0.623	1.000	

B	Date	Treatment	Date	Treatment	estimate	SE	df	t.ratio	p.value
	05/07/2022	HT. 1MH. 2MH vs.	10/07/2022	1MH	-76.487	32.265	57	-2.371	0.927
	05/07/2022	HT. 1MH. 2MH vs.	10/07/2022	2MH	16.006	34.394	57	0.465	1.000
	05/07/2022	HT. 1MH. 2MH vs.	12/07/2022	C	-69.646	30.763	57	-2.264	0.957
	05/07/2022	HT. 1MH. 2MH vs.	14/07/2022	2MH	-35.488	32.265	57	-1.100	1.000
	05/07/2022	HT. 1MH. 2MH vs.	14/07/2022	HT	54.149	30.763	57	1.760	0.999
	05/07/2022	HT. 1MH. 2MH vs.	18/07/2022	1MH	-30.423	32.265	57	-0.943	1.000
	05/07/2022	HT. 1MH. 2MH vs.	18/07/2022	2MH	-74.443	30.763	57	-2.420	0.910
	05/07/2022	HT. 1MH. 2MH vs.	TF	1MH	39.799	30.763	57	1.294	1.000
	05/07/2022	HT. 1MH. 2MH vs.	TF	2MH	1.550	32.265	57	0.048	1.000
	05/07/2022	HT. 1MH. 2MH vs.	TF	C	-5.080	34.394	57	-0.148	1.000
	05/07/2022	HT. 1MH. 2MH vs.	TF	HT	36.551	32.265	57	1.133	1.000
	10/07/2022	1MH vs.	10/07/2022	2MH	92.494	35.744	57	2.588	0.833
	10/07/2022	1MH vs.	14/07/2022	2MH	41.000	33.699	57	1.217	1.000
	10/07/2022	1MH vs.	18/07/2022	1MH	46.065	33.699	57	1.367	1.000
	10/07/2022	1MH vs.	18/07/2022	2MH	2.044	32.265	57	0.063	1.000
	10/07/2022	1MH vs.	TF	1MH	116.286	32.265	57	3.604	0.187
	10/07/2022	1MH vs.	TF	2MH	78.038	33.699	57	2.316	0.944
	10/07/2022	2MH vs.	14/07/2022	2MH	-51.494	35.744	57	-1.441	1.000
	10/07/2022	2MH vs.	18/07/2022	2MH	-90.449	34.394	57	-2.630	0.809
	10/07/2022	2MH vs.	TF	2MH	-14.456	35.744	57	-0.404	1.000
	12/07/2022	C vs.	10/07/2022	1MH	-6.841	32.265	57	-0.212	1.000
	12/07/2022	C vs.	10/07/2022	2MH	85.653	34.394	57	2.490	0.881
	12/07/2022	C vs.	14/07/2022	2MH	34.159	32.265	57	1.059	1.000
	12/07/2022	C vs.	14/07/2022	HT	123.796	30.763	57	4.024	0.067
	12/07/2022	C vs.	18/07/2022	1MH	39.224	32.265	57	1.216	1.000
	12/07/2022	C vs.	18/07/2022	2MH	-4.797	30.763	57	-0.156	1.000

12/07/2022	C	vs.	TF	1MH	109.445	30.763	57	3.558	0.207
12/07/2022	C	vs.	TF	2MH	71.197	32.265	57	2.207	0.968
12/07/2022	C	vs.	TF	C	64.566	34.394	57	1.877	0.997
12/07/2022	C	vs.	TF	HT	106.198	32.265	57	3.291	0.351
14/07/2022	2MH	vs.	18/07/2022	2MH	-38.955	32.265	57	-1.207	1.000
14/07/2022	2MH	vs.	TF	2MH	37.038	33.699	57	1.099	1.000
14/07/2022	HT	vs.	10/07/2022	1MH	-130.637	32.265	57	-4.049	0.063
14/07/2022	HT	vs.	10/07/2022	2MH	-38.143	34.394	57	-1.109	1.000
14/07/2022	HT	vs.	14/07/2022	2MH	-89.637	32.265	57	-2.778	0.714
14/07/2022	HT	vs.	18/07/2022	1MH	-84.572	32.265	57	-2.621	0.814
14/07/2022	HT	vs.	18/07/2022	2MH	-128.593	30.763	57	-4.180	0.044 *
14/07/2022	HT	vs.	TF	1MH	-14.350	30.763	57	-0.466	1.000
14/07/2022	HT	vs.	TF	2MH	-52.599	32.265	57	-1.630	1.000
14/07/2022	HT	vs.	TF	HT	-17.598	32.265	57	-0.545	1.000
18/07/2022	1MH	vs.	10/07/2022	2MH	46.429	35.744	57	1.299	1.000
18/07/2022	1MH	vs.	14/07/2022	2MH	-5.065	33.699	57	-0.150	1.000
18/07/2022	1MH	vs.	18/07/2022	2MH	-44.020	32.265	57	-1.364	1.000
18/07/2022	1MH	vs.	TF	1MH	70.222	32.265	57	2.176	0.974
18/07/2022	1MH	vs.	TF	2MH	31.973	33.699	57	0.949	1.000
18/07/2022	2MH	vs.	TF	2MH	75.994	32.265	57	2.355	0.932
T0	T0	vs.	05/07/2022	HT. 1MH. 2MH	69.488	29.644	57	2.344	0.936
T0	T0	vs.	10/07/2022	1MH	-6.999	31.200	57	-0.224	1.000
T0	T0	vs.	10/07/2022	2MH	85.494	33.397	57	2.560	0.847
T0	T0	vs.	12/07/2022	C	-0.158	29.644	57	-0.005	1.000
T0	T0	vs.	14/07/2022	2MH	34.000	31.200	57	1.090	1.000
T0	T0	vs.	14/07/2022	HT	123.638	29.644	57	4.171	0.045 *
T0	T0	vs.	18/07/2022	1MH	39.065	31.200	57	1.252	1.000
T0	T0	vs.	18/07/2022	2MH	-4.955	29.644	57	-0.167	1.000

T0	T0	vs.	TF	1MH	109.287	29.644	57	3.687	0.155
T0	T0	vs.	TF	2MH	71.039	31.200	57	2.277	0.954
T0	T0	vs.	TF	C	64.408	33.397	57	1.929	0.995
T0	T0	vs.	TF	HT	106.040	31.200	57	3.399	0.287
TF	1MH	vs.	10/07/2022	2MH	-23.793	34.394	57	-0.692	1.000
TF	1MH	vs.	14/07/2022	2MH	-75.287	32.265	57	-2.333	0.939
TF	1MH	vs.	18/07/2022	2MH	-114.242	30.763	57	-3.714	0.146
TF	1MH	vs.	TF	2MH	-38.249	32.265	57	-1.185	1.000
TF	C	vs.	10/07/2022	1MH	-71.407	35.744	57	-1.998	0.992
TF	C	vs.	10/07/2022	2MH	21.086	37.677	57	0.560	1.000
TF	C	vs.	14/07/2022	2MH	-30.407	35.744	57	-0.851	1.000
TF	C	vs.	14/07/2022	HT	59.230	34.394	57	1.722	0.999
TF	C	vs.	18/07/2022	1MH	-25.343	35.744	57	-0.709	1.000
TF	C	vs.	18/07/2022	2MH	-69.363	34.394	57	-2.017	0.991
TF	C	vs.	TF	1MH	44.879	34.394	57	1.305	1.000
TF	C	vs.	TF	2MH	6.631	35.744	57	0.186	1.000
TF	C	vs.	TF	HT	41.632	35.744	57	1.165	1.000
TF	HT	vs.	10/07/2022	1MH	-113.039	33.699	57	-3.354	0.313
TF	HT	vs.	10/07/2022	2MH	-20.545	35.744	57	-0.575	1.000
TF	HT	vs.	14/07/2022	2MH	-72.039	33.699	57	-2.138	0.979
TF	HT	vs.	18/07/2022	1MH	-66.974	33.699	57	-1.987	0.993
TF	HT	vs.	18/07/2022	2MH	-110.995	32.265	57	-3.440	0.265
TF	HT	vs.	TF	1MH	3.248	32.265	57	0.101	1.000
TF	HT	vs.	TF	2MH	-35.001	33.699	57	-1.039	1.000

Table S11: Analysis of deviance (Type II tests) in a generalized linear mixed model to predict the maximum quantum yield.

	Chisq	Df	Pr(>Chisq)
species	60.758	2	6.405e-14 ***
time	0.342	1	0.559
treatment	10.061	3	0.018 *
species:time	1.022	2	0.600
species:treatment	7.843	6	0.250
time:treatment	2.863	3	0.413
species:time:treatment	4.337	6	0.631

Table S12: Pairwise comparisons of the maximum quantum yield of A) *Alaria esculenta*. B) *Laminaria digitata* and C) *Saccharina latissima* calculated with the method of Tukey generalized linear mixed model. The p-values in bold (< 0.05) support the hypothesis that there is a significant difference in the pair.

A	Date	Treatment	Date	Treatment	estimate	SE	df	t.ratio	p.value
	T0	T0	vs. 07/07/2022	HT. 1MH. 2MH	-0.032	0.02190	-1.543	1.000	
	T0	T0	vs. 07/07/2022	C	-0.042	0.03190	-1.326	1.000	
	T0	T0	vs. 11/07/2022	C	-0.030	0.02790	-1.117	1.000	
	T0	T0	vs. TF	C	-0.001	0.02790	-0.050	1.000	
	T0	T0	vs. 14/07/2022	HT	-0.029	0.02790	-1.098	1.000	
	T0	T0	vs. TF	HT	0.002	0.02990	0.054	1.000	
	T0	T0	vs. 11/07/2022	1MH	-0.021	0.02790	-0.784	1.000	
	T0	T0	vs. 18/07/2022	1MH	0.012	0.02990	0.424	1.000	
	T0	T0	vs. TF	1MH	-0.032	0.02790	-1.192	1.000	
	T0	T0	vs. 11/07/2022	2MH	-0.009	0.02790	-0.326	1.000	
	T0	T0	vs. 14/07/2022	2MH	0.006	0.02790	0.207	1.000	
	T0	T0	vs. 18/07/2022	2MH	-0.018	0.02790	-0.665	1.000	

T0	T0	vs.	TF	2MH	-0.025	0.027	90	-0.941	1.000
07/07/2022	HT. 1MH. 2MH	vs.	07/07/2022	C	-0.010	0.034	90	-0.295	1.000
07/07/2022	HT. 1MH. 2MH	vs.	11/07/2022	C	0.002	0.029	90	0.072	1.000
07/07/2022	HT. 1MH. 2MH	vs.	TF	C	0.030	0.029	90	1.045	1.000
07/07/2022	HT. 1MH. 2MH	vs.	14/07/2022	HT	0.003	0.029	90	0.089	1.000
07/07/2022	HT. 1MH. 2MH	vs.	TF	HT	0.033	0.031	90	1.074	1.000
07/07/2022	HT. 1MH. 2MH	vs.	11/07/2022	1MH	0.011	0.029	90	0.375	1.000
07/07/2022	HT. 1MH. 2MH	vs.	18/07/2022	1MH	0.044	0.031	90	1.417	1.000
07/07/2022	HT. 1MH. 2MH	vs.	TF	1MH	0.000	0.029	90	0.003	1.000
07/07/2022	HT. 1MH. 2MH	vs.	11/07/2022	2MH	0.023	0.029	90	0.793	1.000
07/07/2022	HT. 1MH. 2MH	vs.	14/07/2022	2MH	0.037	0.029	90	1.280	1.000
07/07/2022	HT. 1MH. 2MH	vs.	18/07/2022	2MH	0.014	0.029	90	0.484	1.000
07/07/2022	HT. 1MH. 2MH	vs.	TF	2MH	0.007	0.029	90	0.232	1.000
07/07/2022	C	vs.	11/07/2022	C	0.012	0.038	90	0.319	1.000
07/07/2022	C	vs.	TF	C	0.040	0.038	90	1.074	1.000
07/07/2022	C	vs.	14/07/2022	HT	0.013	0.038	90	0.333	1.000
07/07/2022	C	vs.	TF	HT	0.043	0.039	90	1.107	1.000
07/07/2022	C	vs.	11/07/2022	1MH	0.021	0.038	90	0.555	1.000
07/07/2022	C	vs.	18/07/2022	1MH	0.054	0.039	90	1.378	1.000
07/07/2022	C	vs.	TF	1MH	0.010	0.038	90	0.266	1.000
07/07/2022	C	vs.	11/07/2022	2MH	0.033	0.038	90	0.878	1.000
07/07/2022	C	vs.	14/07/2022	2MH	0.047	0.038	90	1.256	1.000
07/07/2022	C	vs.	18/07/2022	2MH	0.024	0.038	90	0.639	1.000
07/07/2022	C	vs.	TF	2MH	0.017	0.038	90	0.444	1.000
11/07/2022	C	vs.	TF	C	0.028	0.034	90	0.843	1.000
11/07/2022	C	vs.	14/07/2022	HT	0.001	0.034	90	0.015	1.000
11/07/2022	C	vs.	TF	HT	0.031	0.035	90	0.885	1.000
11/07/2022	C	vs.	11/07/2022	1MH	0.009	0.034	90	0.263	1.000

11/07/2022	C	vs. 18/07/2022	1MH	0.042	0.035 90	1.186	1.000
11/07/2022	C	vs. TF	1MH	-0.002	0.034 90	-0.060	1.000
11/07/2022	C	vs. 11/07/2022	2MH	0.021	0.034 90	0.625	1.000
11/07/2022	C	vs. 14/07/2022	2MH	0.035	0.034 90	1.047	1.000
11/07/2022	C	vs. 18/07/2022	2MH	0.012	0.034 90	0.357	1.000
11/07/2022	C	vs. TF	2MH	0.005	0.034 90	0.139	1.000
TF	C	vs. 14/07/2022	HT	-0.028	0.034 90	-0.828	1.000
TF	C	vs. TF	HT	0.003	0.035 90	0.081	1.000
TF	C	vs. 11/07/2022	1MH	-0.020	0.034 90	-0.580	1.000
TF	C	vs. 18/07/2022	1MH	0.013	0.035 90	0.382	1.000
TF	C	vs. TF	1MH	-0.030	0.034 90	-0.903	1.000
TF	C	vs. 11/07/2022	2MH	-0.007	0.034 90	-0.218	1.000
TF	C	vs. 14/07/2022	2MH	0.007	0.034 90	0.203	1.000
TF	C	vs. 18/07/2022	2MH	-0.016	0.034 90	-0.486	1.000
TF	C	vs. TF	2MH	-0.024	0.034 90	-0.704	1.000
14/07/2022	HT	vs. TF	HT	0.031	0.035 90	0.871	1.000
14/07/2022	HT	vs. 11/07/2022	1MH	0.008	0.034 90	0.248	1.000
14/07/2022	HT	vs. 18/07/2022	1MH	0.041	0.035 90	1.172	1.000
14/07/2022	HT	vs. TF	1MH	-0.003	0.034 90	-0.074	1.000
14/07/2022	HT	vs. 11/07/2022	2MH	0.020	0.034 90	0.610	1.000
14/07/2022	HT	vs. 14/07/2022	2MH	0.035	0.034 90	1.032	1.000
14/07/2022	HT	vs. 18/07/2022	2MH	0.012	0.034 90	0.342	1.000
14/07/2022	HT	vs. TF	2MH	0.004	0.034 90	0.124	1.000
TF	HT	vs. 11/07/2022	1MH	-0.022	0.035 90	-0.635	1.000
TF	HT	vs. 18/07/2022	1MH	0.011	0.037 90	0.288	1.000
TF	HT	vs. TF	1MH	-0.033	0.035 90	-0.942	1.000
TF	HT	vs. 11/07/2022	2MH	-0.010	0.035 90	-0.289	1.000
TF	HT	vs. 14/07/2022	2MH	0.004	0.035 90	0.113	1.000

TF	HT	vs. 18/07/2022	2MH	-0.019	0.035	90	-0.545	1.000
TF	HT	vs. TF	2MH	-0.027	0.035	90	-0.753	1.000
11/07/2022	1MH	vs. 18/07/2022	1MH	0.033	0.035	90	0.936	1.000
11/07/2022	1MH	vs. TF	1MH	-0.011	0.034	90	-0.322	1.000
11/07/2022	1MH	vs. 11/07/2022	2MH	0.012	0.034	90	0.362	1.000
11/07/2022	1MH	vs. 14/07/2022	2MH	0.026	0.034	90	0.784	1.000
11/07/2022	1MH	vs. 18/07/2022	2MH	0.003	0.034	90	0.094	1.000
11/07/2022	1MH	vs. TF	2MH	-0.004	0.034	90	-0.124	1.000
18/07/2022	1MH	vs. TF	1MH	-0.044	0.035	90	-1.243	1.000
18/07/2022	1MH	vs. 11/07/2022	2MH	-0.021	0.035	90	-0.590	1.000
18/07/2022	1MH	vs. 14/07/2022	2MH	-0.007	0.035	90	-0.188	1.000
18/07/2022	1MH	vs. 18/07/2022	2MH	-0.030	0.035	90	-0.846	1.000
18/07/2022	1MH	vs. TF	2MH	-0.037	0.035	90	-1.054	1.000
TF	1MH	vs. 11/07/2022	2MH	0.023	0.034	90	0.685	1.000
TF	1MH	vs. 14/07/2022	2MH	0.037	0.034	90	1.106	1.000
TF	1MH	vs. 18/07/2022	2MH	0.014	0.034	90	0.417	1.000
TF	1MH	vs. TF	2MH	0.007	0.034	90	0.198	1.000
11/07/2022	2MH	vs. 14/07/2022	2MH	0.014	0.034	90	0.422	1.000
11/07/2022	2MH	vs. 18/07/2022	2MH	-0.009	0.034	90	-0.268	1.000
11/07/2022	2MH	vs. TF	2MH	-0.016	0.034	90	-0.486	1.000
14/07/2022	2MH	vs. 18/07/2022	2MH	-0.023	0.034	90	-0.690	1.000
14/07/2022	2MH	vs. TF	2MH	-0.031	0.034	90	-0.908	1.000
18/07/2022	2MH	vs. TF	2MH	-0.007	0.034	90	-0.218	1.000

B	Date	Treatment	Date	Treatment	estimate	SE	df	t.ratio	p.value
	T0	T0	vs. 07/07/2022	HT. 1MH. 2MH	-0.055	0.016	86	-3.359	0.247
	T0	T0	vs. 07/07/2022	C	-0.056	0.025	86	-2.245	0.943

T0	T0	vs. 11/07/2022	C	0.002	0.025 86	0.065	1.000	
T0	T0	vs. TF	C	-0.012	0.021 86	-0.570	1.000	
T0	T0	vs. 14/07/2022	HT	-0.017	0.023 86	-0.733	1.000	
T0	T0	vs. TF	HT	-0.011	0.021 86	-0.531	1.000	
T0	T0	vs. 11/07/2022	1MH	0.013	0.025 86	0.505	1.000	
T0	T0	vs. 18/07/2022	1MH	-0.031	0.021 86	-1.462	1.000	
T0	T0	vs. TF	1MH	-0.014	0.021 86	-0.641	1.000	
T0	T0	vs. 11/07/2022	2MH	0.025	0.021 86	1.174	1.000	
T0	T0	vs. 14/07/2022	2MH	0.010	0.023 86	0.436	1.000	
T0	T0	vs. 18/07/2022	2MH	0.026	0.021 86	1.245	1.000	
T0	T0	vs. TF	2MH	0.019	0.021 86	0.897	1.000	
07/07/2022 HT. 1MH. 2MH vs. 07/07/2022				C	-0.001	0.027 86	-0.044	1.000
07/07/2022 HT. 1MH. 2MH vs. 11/07/2022				C	0.057	0.027 86	2.118	0.972
07/07/2022 HT. 1MH. 2MH vs. TF				C	0.043	0.023 86	1.855	0.996
07/07/2022 HT. 1MH. 2MH vs. 14/07/2022				HT	0.038	0.025 86	1.554	1.000
07/07/2022 HT. 1MH. 2MH vs. TF				HT	0.044	0.023 86	1.891	0.994
07/07/2022 HT. 1MH. 2MH vs. 11/07/2022				1MH	0.068	0.027 86	2.529	0.821
07/07/2022 HT. 1MH. 2MH vs. 18/07/2022				1MH	0.024	0.023 86	1.041	1.000
07/07/2022 HT. 1MH. 2MH vs. TF				1MH	0.041	0.023 86	1.790	0.998
07/07/2022 HT. 1MH. 2MH vs. 11/07/2022				2MH	0.080	0.023 86	3.446	0.203
07/07/2022 HT. 1MH. 2MH vs. 14/07/2022				2MH	0.065	0.025 86	2.634	0.755
07/07/2022 HT. 1MH. 2MH vs. 18/07/2022				2MH	0.081	0.023 86	3.511	0.175
07/07/2022 HT. 1MH. 2MH vs. TF				2MH	0.074	0.023 86	3.194	0.345
07/07/2022	C	vs. 11/07/2022	C	0.058	0.033 86	1.765	0.998	
07/07/2022	C	vs. TF	C	0.044	0.030 86	1.476	1.000	
07/07/2022	C	vs. 14/07/2022	HT	0.039	0.031 86	1.271	1.000	
07/07/2022	C	vs. TF	HT	0.045	0.030 86	1.503	1.000	
07/07/2022	C	vs. 11/07/2022	1MH	0.069	0.033 86	2.101	0.974	

07/07/2022	C	vs. 18/07/2022	1MH	0.025	0.030 86	0.845	1.000
07/07/2022	C	vs. TF	1MH	0.043	0.030 86	1.425	1.000
07/07/2022	C	vs. 11/07/2022	2MH	0.081	0.030 86	2.708	0.703
07/07/2022	C	vs. 14/07/2022	2MH	0.066	0.031 86	2.127	0.970
07/07/2022	C	vs. 18/07/2022	2MH	0.082	0.030 86	2.759	0.666
07/07/2022	C	vs. TF	2MH	0.075	0.030 86	2.513	0.830
11/07/2022	C	vs. TF	C	-0.014	0.030 86	-0.457	1.000
11/07/2022	C	vs. 14/07/2022	HT	-0.018	0.031 86	-0.589	1.000
11/07/2022	C	vs. TF	HT	-0.013	0.030 86	-0.430	1.000
11/07/2022	C	vs. 11/07/2022	1MH	0.011	0.033 86	0.336	1.000
11/07/2022	C	vs. 18/07/2022	1MH	-0.033	0.030 86	-1.088	1.000
11/07/2022	C	vs. TF	1MH	-0.015	0.030 86	-0.508	1.000
11/07/2022	C	vs. 11/07/2022	2MH	0.023	0.030 86	0.775	1.000
11/07/2022	C	vs. 14/07/2022	2MH	0.008	0.031 86	0.267	1.000
11/07/2022	C	vs. 18/07/2022	2MH	0.025	0.030 86	0.826	1.000
11/07/2022	C	vs. TF	2MH	0.017	0.030 86	0.580	1.000
TF	C	vs. 14/07/2022	HT	-0.005	0.028 86	-0.165	1.000
TF	C	vs. TF	HT	0.001	0.027 86	0.031	1.000
TF	C	vs. 11/07/2022	1MH	0.025	0.030 86	0.826	1.000
TF	C	vs. 18/07/2022	1MH	-0.019	0.027 86	-0.705	1.000
TF	C	vs. TF	1MH	-0.002	0.027 86	-0.056	1.000
TF	C	vs. 11/07/2022	2MH	0.037	0.027 86	1.378	1.000
TF	C	vs. 14/07/2022	2MH	0.022	0.028 86	0.784	1.000
TF	C	vs. 18/07/2022	2MH	0.038	0.027 86	1.435	1.000
TF	C	vs. TF	2MH	0.031	0.027 86	1.160	1.000
14/07/2022	HT	vs. TF	HT	0.005	0.028 86	0.195	1.000
14/07/2022	HT	vs. 11/07/2022	1MH	0.029	0.031 86	0.944	1.000
14/07/2022	HT	vs. 18/07/2022	1MH	-0.014	0.028 86	-0.507	1.000

14/07/2022	HT	vs. TF	1MH	0.003	0.02886	0.112	1.000
14/07/2022	HT	vs. 11/07/2022	2MH	0.041	0.02886	1.480	1.000
14/07/2022	HT	vs. 14/07/2022	2MH	0.027	0.02986	0.909	1.000
14/07/2022	HT	vs. 18/07/2022	2MH	0.043	0.02886	1.533	1.000
14/07/2022	HT	vs. TF	2MH	0.036	0.02886	1.271	1.000
TF	HT	vs. 11/07/2022	1MH	0.024	0.03086	0.798	1.000
TF	HT	vs. 18/07/2022	1MH	-0.020	0.02786	-0.736	1.000
TF	HT	vs. TF	1MH	-0.002	0.02786	-0.087	1.000
TF	HT	vs. 11/07/2022	2MH	0.036	0.02786	1.347	1.000
TF	HT	vs. 14/07/2022	2MH	0.021	0.02886	0.754	1.000
TF	HT	vs. 18/07/2022	2MH	0.038	0.02786	1.403	1.000
TF	HT	vs. TF	2MH	0.030	0.02786	1.129	1.000
11/07/2022	1MH	vs. 18/07/2022	1MH	-0.044	0.03086	-1.456	1.000
11/07/2022	1MH	vs. TF	1MH	-0.026	0.03086	-0.876	1.000
11/07/2022	1MH	vs. 11/07/2022	2MH	0.012	0.03086	0.407	1.000
11/07/2022	1MH	vs. 14/07/2022	2MH	-0.003	0.03186	-0.087	1.000
11/07/2022	1MH	vs. 18/07/2022	2MH	0.014	0.03086	0.457	1.000
11/07/2022	1MH	vs. TF	2MH	0.006	0.03086	0.212	1.000
18/07/2022	1MH	vs. TF	1MH	0.017	0.02786	0.649	1.000
18/07/2022	1MH	vs. 11/07/2022	2MH	0.056	0.02786	2.083	0.977
18/07/2022	1MH	vs. 14/07/2022	2MH	0.041	0.02886	1.456	1.000
18/07/2022	1MH	vs. 18/07/2022	2MH	0.057	0.02786	2.139	0.968
18/07/2022	1MH	vs. TF	2MH	0.050	0.02786	1.865	0.995
TF	1MH	vs. 11/07/2022	2MH	0.038	0.02786	1.435	1.000
TF	1MH	vs. 14/07/2022	2MH	0.023	0.02886	0.837	1.000
TF	1MH	vs. 18/07/2022	2MH	0.040	0.02786	1.491	1.000
TF	1MH	vs. TF	2MH	0.032	0.02786	1.216	1.000
11/07/2022	2MH	vs. 14/07/2022	2MH	-0.015	0.02886	-0.530	1.000

11/07/2022	2MH	vs. 18/07/2022	2MH	0.001	0.027 86	0.056	1.000
11/07/2022	2MH	vs. TF	2MH	-0.006	0.027 86	-0.218	1.000
14/07/2022	2MH	vs. 18/07/2022	2MH	0.016	0.028 86	0.584	1.000
14/07/2022	2MH	vs. TF	2MH	0.009	0.028 86	0.322	1.000
18/07/2022	2MH	vs. TF	2MH	-0.007	0.027 86	-0.274	1.000

C	Date	Treatment	Date	Treatment	estimate	SE	df	t.ratio	p.value
	T0	T0	vs. 07/07/2022	HT. 1MH. 2MH	-0.150	0.023 88	-6.684	0.000	***
	T0	T0	vs. 07/07/2022	C	-0.137	0.038 88	-3.630	0.130	
	T0	T0	vs. 11/07/2022	C	-0.065	0.030 88	-2.128	0.970	
	T0	T0	vs. TF	C	-0.065	0.028 88	-2.317	0.921	
	T0	T0	vs. 14/07/2022	HT	-0.097	0.028 88	-3.440	0.206	
	T0	T0	vs. TF	HT	-0.050	0.028 88	-1.756	0.998	
	T0	T0	vs. 11/07/2022	1MH	-0.007	0.030 88	-0.219	1.000	
	T0	T0	vs. 18/07/2022	1MH	-0.005	0.028 88	-0.185	1.000	
	T0	T0	vs. TF	1MH	-0.073	0.028 88	-2.577	0.792	
	T0	T0	vs. 11/07/2022	2MH	-0.023	0.028 88	-0.805	1.000	
	T0	T0	vs. 14/07/2022	2MH	0.037	0.028 88	1.298	1.000	
	T0	T0	vs. 18/07/2022	2MH	0.071	0.028 88	2.533	0.819	
	T0	T0	vs. TF	2MH	-0.093	0.028 88	-3.310	0.273	
	07/07/2022	HT. 1MH. 2MH	vs. 07/07/2022	C	0.013	0.040 88	0.324	1.000	
	07/07/2022	HT. 1MH. 2MH	vs. 11/07/2022	C	0.086	0.033 88	2.573	0.795	
	07/07/2022	HT. 1MH. 2MH	vs. TF	C	0.085	0.031 88	2.711	0.702	
	07/07/2022	HT. 1MH. 2MH	vs. 14/07/2022	HT	0.053	0.031 88	1.701	0.999	
	07/07/2022	HT. 1MH. 2MH	vs. TF	HT	0.101	0.031 88	3.216	0.331	
	07/07/2022	HT. 1MH. 2MH	vs. 11/07/2022	1MH	0.144	0.033 88	4.313	0.017	*
	07/07/2022	HT. 1MH. 2MH	vs. 18/07/2022	1MH	0.145	0.031 88	4.629	0.006	**

07/07/2022	HT. 1MH. 2MH	vs.	TF	1MH	0.078	0.031 88	2.477	0.850
07/07/2022	HT. 1MH. 2MH	vs.	11/07/2022	2MH	0.128	0.031 88	4.071	0.037 *
07/07/2022	HT. 1MH. 2MH	vs.	14/07/2022	2MH	0.187	0.031 88	5.963	0.000 ***
07/07/2022	HT. 1MH. 2MH	vs.	18/07/2022	2MH	0.222	0.031 88	7.073	0.000 ***
07/07/2022	HT. 1MH. 2MH	vs.	TF	2MH	0.057	0.031 88	1.818	0.997
07/07/2022	C	vs.	11/07/2022	C	0.073	0.045 88	1.611	1.000
07/07/2022	C	vs.	TF	C	0.072	0.044 88	1.647	0.999
07/07/2022	C	vs.	14/07/2022	HT	0.040	0.044 88	0.923	1.000
07/07/2022	C	vs.	TF	HT	0.088	0.044 88	2.010	0.986
07/07/2022	C	vs.	11/07/2022	1MH	0.131	0.045 88	2.896	0.562
07/07/2022	C	vs.	18/07/2022	1MH	0.132	0.044 88	3.024	0.464
07/07/2022	C	vs.	TF	1MH	0.065	0.044 88	1.480	1.000
07/07/2022	C	vs.	11/07/2022	2MH	0.115	0.044 88	2.624	0.762
07/07/2022	C	vs.	14/07/2022	2MH	0.174	0.044 88	3.981	0.049 *
07/07/2022	C	vs.	18/07/2022	2MH	0.209	0.044 88	4.778	0.003 **
07/07/2022	C	vs.	TF	2MH	0.044	0.044 88	1.007	1.000
11/07/2022	C	vs.	TF	C	-0.001	0.037 88	-0.020	1.000
11/07/2022	C	vs.	14/07/2022	HT	-0.032	0.037 88	-0.866	1.000
11/07/2022	C	vs.	TF	HT	0.015	0.037 88	0.403	1.000
11/07/2022	C	vs.	11/07/2022	1MH	0.058	0.039 88	1.484	1.000
11/07/2022	C	vs.	18/07/2022	1MH	0.059	0.037 88	1.588	1.000
11/07/2022	C	vs.	TF	1MH	-0.008	0.037 88	-0.216	1.000
11/07/2022	C	vs.	11/07/2022	2MH	0.042	0.037 88	1.120	1.000
11/07/2022	C	vs.	14/07/2022	2MH	0.101	0.037 88	2.706	0.705
11/07/2022	C	vs.	18/07/2022	2MH	0.136	0.037 88	3.637	0.127
11/07/2022	C	vs.	TF	2MH	-0.029	0.037 88	-0.768	1.000
TF	C	vs.	14/07/2022	HT	-0.032	0.036 88	-0.887	1.000
TF	C	vs.	TF	HT	0.016	0.036 88	0.444	1.000

TF	C	vs. 11/07/2022	1MH	0.059	0.037 88	1.569	1.000
TF	C	vs. 18/07/2022	1MH	0.060	0.036 88	1.686	0.999
TF	C	vs. TF	1MH	-0.007	0.036 88	-0.206	1.000
TF	C	vs. 11/07/2022	2MH	0.043	0.036 88	1.196	1.000
TF	C	vs. 14/07/2022	2MH	0.102	0.036 88	2.858	0.591
TF	C	vs. 18/07/2022	2MH	0.137	0.036 88	3.835	0.075
TF	C	vs. TF	2MH	-0.028	0.036 88	-0.785	1.000
14/07/2022	HT	vs. TF	HT	0.048	0.036 88	1.331	1.000
14/07/2022	HT	vs. 11/07/2022	1MH	0.090	0.037 88	2.416	0.881
14/07/2022	HT	vs. 18/07/2022	1MH	0.092	0.036 88	2.574	0.794
14/07/2022	HT	vs. TF	1MH	0.024	0.036 88	0.682	1.000
14/07/2022	HT	vs. 11/07/2022	2MH	0.074	0.036 88	2.083	0.977
14/07/2022	HT	vs. 14/07/2022	2MH	0.134	0.036 88	3.746	0.095
14/07/2022	HT	vs. 18/07/2022	2MH	0.169	0.036 88	4.722	0.004 **
14/07/2022	HT	vs. TF	2MH	0.004	0.036 88	0.103	1.000
TF	HT	vs. 11/07/2022	1MH	0.043	0.037 88	1.146	1.000
TF	HT	vs. 18/07/2022	1MH	0.044	0.036 88	1.242	1.000
TF	HT	vs. TF	1MH	-0.023	0.036 88	-0.649	1.000
TF	HT	vs. 11/07/2022	2MH	0.027	0.036 88	0.752	1.000
TF	HT	vs. 14/07/2022	2MH	0.086	0.036 88	2.415	0.881
TF	HT	vs. 18/07/2022	2MH	0.121	0.036 88	3.391	0.230
TF	HT	vs. TF	2MH	-0.044	0.036 88	-1.228	1.000
11/07/2022	1MH	vs. 18/07/2022	1MH	0.001	0.037 88	0.038	1.000
11/07/2022	1MH	vs. TF	1MH	-0.066	0.037 88	-1.765	0.998
11/07/2022	1MH	vs. 11/07/2022	2MH	-0.016	0.037 88	-0.429	1.000
11/07/2022	1MH	vs. 14/07/2022	2MH	0.043	0.037 88	1.156	1.000
11/07/2022	1MH	vs. 18/07/2022	2MH	0.078	0.037 88	2.087	0.977
11/07/2022	1MH	vs. TF	2MH	-0.087	0.037 88	-2.318	0.921

18/07/2022	1MH	vs.	TF	1MH	-0.068	0.036 88	-1.892	0.994
18/07/2022	1MH	vs.	11/07/2022	2MH	-0.018	0.036 88	-0.490	1.000
18/07/2022	1MH	vs.	14/07/2022	2MH	0.042	0.036 88	1.172	1.000
18/07/2022	1MH	vs.	18/07/2022	2MH	0.077	0.036 88	2.149	0.966
18/07/2022	1MH	vs.	TF	2MH	-0.088	0.036 88	-2.471	0.853
TF	1MH	vs.	11/07/2022	2MH	0.050	0.036 88	1.401	1.000
TF	1MH	vs.	14/07/2022	2MH	0.109	0.036 88	3.064	0.435
TF	1MH	vs.	18/07/2022	2MH	0.144	0.036 88	4.040	0.041 *
TF	1MH	vs.	TF	2MH	-0.021	0.036 88	-0.579	1.000
11/07/2022	2MH	vs.	14/07/2022	2MH	0.059	0.036 88	1.663	0.999
11/07/2022	2MH	vs.	18/07/2022	2MH	0.094	0.036 88	2.639	0.752
11/07/2022	2MH	vs.	TF	2MH	-0.071	0.036 88	-1.980	0.989
14/07/2022	2MH	vs.	18/07/2022	2MH	0.035	0.036 88	0.976	1.000
14/07/2022	2MH	vs.	TF	2MH	-0.130	0.036 88	-3.643	0.125
18/07/2022	2MH	vs.	TF	2MH	-0.165	0.036 88	-4.619	0.006 **

Table S13: Analysis of deviance (Type II tests) in a generalized linear mixed model to predict the chlorophyll a content.

	Chisq	Df	Pr(>Chisq)
species	59.883	2	9.923e-14 ***
treatment	28.542	4	9.686e-06 ***
specie:treatment	15.714	8	0.047 *

Table S14: Pairwise comparisons of the chlorophyll a content of A) *Alaria esculenta*. B) *Laminaria digitata* and C) *Saccharina latissima* calculated with the method of Tukey generalized linear mixed model. The p-values in bold (< 0.05) support the hypothesis that there is a significant difference in the pair.

A Treatment	Treatment estimate	SE	df	t.ratio	p.value
T0 vs. C	26.710	14.800	28	1.807	0.389

T0	vs.	HT	7.360	13.900	28	0.529	0.984
T0	vs.	1MH	14.970	13.900	28	1.075	0.818
T0	vs.	2MH	49.350	13.900	28	3.542	0.011 *
C	vs.	HT	-19.350	16.300	28	-1.184	0.760
C	vs.	1MH	-11.740	16.300	28	-0.718	0.951
C	vs.	2MH	22.640	16.300	28	1.386	0.642
HT	vs.	1MH	7.610	15.600	28	0.489	0.988
HT	vs.	2MH	41.980	15.600	28	2.695	0.080
1MH	vs.	2MH	34.380	15.600	28	2.207	0.207

B Treatment Treatment estimate SE df t.ratio p.value

Treatment	vs.	Treatment	estimate	SE	df	t.ratio	p.value
T0	vs.	C	1.690	4.560	28	0.370	0.996
T0	vs.	HT	3.527	4.560	28	0.773	0.936
T0	vs.	1MH	-0.557	4.560	28	-0.122	1.000
T0	vs.	2MH	2.960	4.560	28	0.649	0.965
C	vs.	HT	1.837	5.000	28	0.368	0.996
C	vs.	1MH	-2.247	5.000	28	-0.450	0.991
C	vs.	2MH	1.271	5.000	28	0.254	0.999
HT	vs.	1MH	-4.084	5.000	28	-0.817	0.923
HT	vs.	2MH	-0.566	5.000	28	-0.113	1.000
1MH	vs.	2MH	3.518	5.000	28	0.704	0.954

C Treatment Treatment estimate SE df t.ratio p.value

Treatment	vs.	Treatment	estimate	SE	df	t.ratio	p.value
T0	vs.	C	22.540	12.400	27	1.825	0.381
T0	vs.	HT	18.340	12.400	27	1.485	0.581
T0	vs.	1MH	37.300	13.100	27	2.847	0.059
T0	vs.	2MH	49.730	13.100	27	3.795	0.006 **
C	vs.	HT	-4.210	13.800	27	-0.305	0.998

C	vs.	1MH	14.760	14.50027	1.019	0.845
C	vs.	2MH	27.180	14.50027	1.877	0.353
HT	vs.	1MH	18.960	14.50027	1.309	0.688
HT	vs.	2MH	31.390	14.50027	2.167	0.223
1MH	vs.	2MH	12.430	15.10027	0.821	0.922

Table S15: Analysis of deviance (Type II tests) in a generalized linear mixed model to predict the C:N ratio.

	Chisq	Df	Pr(>Chisq)
species	20.894	2	2.904e-05 ***
treatment	8.688	4	0.070
specie:treatment	14.485	7	0.043 *

Table 16: Pairwise comparisons of the C:N ratio of A) *Alaria esculenta*. B) *Laminaria digitata* and C) *Saccharina latissima* calculated with the method of Tukey generalized linear mixed model. The p-values in bold (< 0.05) support the hypothesis that there is a significant difference in the pair.

A

Treatment	Treatment estimate	SE	df	t.ratio	p.value
C vs. HT	-0.830	1.950	14	-0.425	0.973
C vs. 1MH	3.200	1.810	14	1.771	0.327
C vs. 2MH	-2.930	1.870	14	-1.572	0.424
HT vs. 1MH	4.030	1.650	14	2.444	0.114
HT vs. 2MH	-2.100	1.710	14	-1.227	0.621
1MH vs. 2MH	-6.130	1.550	14	-3.965	0.007 **

B

Treatment	Treatment estimate	SE	df	t.ratio	p.value
T0 vs. C	0.654	1.620	22	0.403	0.994
T0 vs. HT	2.140	1.830	22	1.172	0.767

T0	vs.	1MH	-0.040	1.71022	-0.023	1.000
T0	vs.	2MH	-0.638	1.71022	-0.374	0.996
C	vs.	HT	1.486	1.88022	0.790	0.931
C	vs.	1MH	-0.694	1.76022	-0.393	0.995
C	vs.	2MH	-1.292	1.76022	-0.732	0.947
HT	vs.	1MH	-2.180	1.95022	-1.115	0.797
HT	vs.	2MH	-2.778	1.95022	-1.421	0.621
1MH	vs.	2MH	-0.598	1.84022	-0.325	0.997

C Treatment Treatment estimate SE df t.ratio p.value

Treatment	vs.	Treatment	estimate	SE	df	t.ratio	p.value
T0	vs.	C	4.200	2.200	17	1.905	0.352
T0	vs.	HT	6.070	2.540	17	2.387	0.167
T0	vs.	1MH	2.080	2.340	17	0.892	0.896
T0	vs.	2MH	3.460	2.200	17	1.569	0.535
C	vs.	HT	1.880	2.540	17	0.738	0.945
C	vs.	1MH	-2.110	2.340	17	-0.903	0.892
C	vs.	2MH	-0.740	2.200	17	-0.336	0.997
HT	vs.	1MH	-3.990	2.660	17	-1.499	0.577
HT	vs.	2MH	-2.620	2.540	17	-1.029	0.839
1MH	vs.	2MH	1.370	2.340	17	0.587	0.975

Table S17: Analysis of deviance (Type II tests) in a generalized linear mixed model to predict the growth rate.

	Chisq	Df	Pr(>Chisq)
species	314.485	2	<2e-16 ***
treatment	5.339	3	0.149

specie:treatment | 2.889 6 0.823

Table S18: Pairwise comparisons of the growth rate of A) *Alaria esculenta*. B) *Laminaria digitata* and C) *Saccharina latissima* calculated with the method of Tukey generalized linear mixed model.

A

Treatment		Treatment estimate	SE	df	t.ratio	p.value
C	vs.	HT	0.010	0.015 75	0.626	0.923
C	vs.	1MH	-0.021	0.014 75	-1.491	0.448
C	vs.	2MH	0.005	0.014 75	0.325	0.988
HT	vs.	1MH	-0.031	0.015 75	-2.088	0.167
HT	vs.	2MH	-0.005	0.015 75	-0.333	0.987
1MH	vs.	2MH	0.026	0.014 75	1.880	0.245

B

Treatment		Treatment estimate	SE	df	t.ratio	p.value
C	vs.	HT	-0.007	0.007 23	-1.037	0.730
C	vs.	1MH	-0.007	0.006 23	-1.217	0.623
C	vs.	2MH	-0.004	0.006 23	-0.600	0.931
HT	vs.	1MH	0.000	0.006 23	-0.011	1.000
HT	vs.	2MH	0.003	0.007 23	0.452	0.969
1MH	vs.	2MH	0.003	0.006 23	0.530	0.951

C

Treatment		Treatment estimate	SE	df	t.ratio	p.value
C	vs.	HT	0.020	0.041 37	0.491	0.961
C	vs.	1MH	-0.007	0.044 37	-0.150	0.999
C	vs.	2MH	0.043	0.038 37	1.114	0.684
HT	vs.	1MH	-0.027	0.043 37	-0.630	0.922
HT	vs.	2MH	0.022	0.037 37	0.604	0.930
1MH	vs.	2MH	0.049	0.040 37	1.238	0.607



After conducting two mesocosm experiment to analyze the responses of Arctic kelps and their community to climate change, this last chapter investigates the *in situ* links between environmental conditions and benthic biodiversity. This study was carried out in Ny-Ålesund during summer 2021, using the environmental DNA (eDNA) technique.

Chapter 4: Benthic diversity along an Arctic fjord: which are the key factors?

Anaïs Lebrun¹, Steeve Comeau¹, Frédéric Gazeau¹, Jean-Pierre Gattuso^{1,2}

¹Laboratoire d'Océanographie de Villefranche, Sorbonne Université, CNRS, Villefranche-sur-Mer, France

²Institute for Sustainable Development and International Relations, Sciences Po, Paris, France

This article has been submitted in bioRxiv.

Abstract

Arctic coastal ecosystems include benthic communities that hold an important role within the marine food chain. Kelps, furoid species, and coralline algae dominate rocky habitats, offering food and shelter for various species. Kelps and furoid species also aid in carbon sequestration, sediment stabilization, and erosion mitigation. In summer, the influx of freshwater from glacier and permafrost melt alters coastal waters conditions. The input of turbid freshwater influences underwater light, salinity, and substrate, impacting benthic organism distribution. This study investigates possible link between environmental conditions and benthic diversity through environmental DNA (eDNA). Six sites were monitored along Kongsfjorden (Svalbard, Norway) during the summer of 2021. Contrary to expectations, macroalgal distribution didn't correlate with light, and suspension feeders showed no clear links with chlorophyll *a* or nutrient concentrations. Glacial influence may have contributed to higher benthic diversity. Predators' presence, tied to glacier proximity, possibly explained this trend. However, further studies are needed to validate these observations and assumptions.

1. Introduction

Arctic coasts host a fragile ecosystem characterized by diverse benthic communities that play a crucial role in supporting the entire marine food web. In rocky areas, benthic communities are dominated by kelps, furoid species, and coralline algae (Lebrun et al., 2022). These species provide food and habitat for fish, crabs, and many other species. Kelps and furoid species play important roles in carbon sequestration and help stabilize sediments and reduce coastal

erosion (Løvås and Tørum, 2001; Filbee-Dexter et al., 2019). Soft-substrate communities are generally less diverse and present lower biomass but represent around 65% of the Arctic coastal areas due to the river and glacial runoffs and are dominated by polychaetes and specialized malacostracans (Lantuit et al., 2012; Filbee-Dexter et al., 2019). In both substrates, the benthic fauna such as mollusks, echinoderms, and arthropods is essential in recycling organic matter and maintaining ecosystem health (Welsh et al., 2003; März et al., 2021).

In the summer months, melting ice discharge large amounts of freshwater to Arctic coastal areas. As glaciers melt, they release sediment that has been trapped in the ice. Furthermore, as the meltwater from land-ice (snow, permafrost) flows toward the fjord, it gets enriched with sediment (Hopwood et al., 2018). As a result, when meltwater reaches the fjord, it carries a significant sediment load. The input of turbid freshwater affects the local underwater light regime, salinity, nutrients, and substrate, and, hence, the distribution and abundance of benthic organisms. From the inner to the outer part, Arctic fjords are characterized by a gradient of substrate ranging from soft to harder and gradient. Also, in summer the fjord display a distinct a gradient of underwater light and salinity with turbid and low saline waters in the inner parts to less turbid and more saline ones in the outer parts (Svendsen et al. 2002; Kedra et al., 2010). The benthic diversity is largely influenced by the substrate type and the water characteristics such as turbidity and nutrient content (Anderson et al., 2008, Saeedi et al., 2022).

With climate change, the Arctic is experiencing rapid environmental changes with temperatures rising at more than twice the global average rate (Richter-Menge et al., 2017). As temperatures rise, glacier melting is accelerating and occurs earlier in the year. Erosion of permafrost in coastal areas in the Arctic increased by 80 to 160%, in comparison to average rates from the '80s (Jones et al., 2020). This leads to an intense discharge of freshwater and sediment into the fjord (Howe et al., 2010). The increase in runoff expands the area impacted by glacier melting and therefore impacts organisms which, until now, were not affected by turbid and fresh waters (Barnhart et al., 2016).

In this study, we investigated how the benthic flora and fauna are distributed along an Arctic fjord. The main objective was to characterize potential variations in community composition related to changes in environmental conditions. We selected six sites along the Kongsfjorden (Svalbard, Norway) and monitored their environmental parameters (temperature, salinity,

photosynthetically active radiation (PAR), nutrient, chlorophyll *a* (chl *a*) concentration, pH_T, and total alkalinity) and benthic diversity during the summer of 2021. Diversity was assessed using environmental DNA (eDNA), a molecular tool allowing taxonomic identification from part of an organism's DNA, found in its environment. Our hypothesis is that the distribution of benthic organisms is impacted by the gradient of light, salinity, and substrate type. In particular, we hypothesize that the distribution of macroalgae follows the light gradient and that of suspension feeders follows the salinity gradient, associated with the chlorophyll *a* (chl *a*) gradient.

2. Material and methods

2.1. Sampling sites

Kongsfjorden is an open fjord situated on the north-western coast of Svalbard (12°E, 79°N). It hosts four tidewater glaciers (Kronebreen, Kongsbreen, Conwaybreen, and Bloomstrandbreen) on its north and east edges. We monitored the environmental parameters and diversity at six sites along the fjord from June to August 2021 (Kongsfjordneset 78.97°N, 11.48°E; Hansneset 78.99°N, 11.98°E; Bloomstrand East 78.97°N, 12.19°E; Ossian Sars 78.92°N, 12.45°E; French Bird Cliff 78.90°N, 12.20°E; and Kongsbreen South 78.91°N, 12.54°E; Fig. 25)

2.2. Environmental parameters

At the six sites, we weekly sampled seawater for nutrient concentration (NO₂, NO₃, PO₄, SiOH₄), total alkalinity, pH_T (on the total scale), and chl *a* concentration using a 12 L Niskin bottle closed 1 meter above the bottom. Salinity and temperature profiles were performed using a CTD (Seabird SBE-19). PAR profiles were conducted using a planar light sensor connected to a data logger (LICOR LI-400) to determine the vertical light attenuation coefficient (*K_d*) by linear regression between depth and the log-transformed irradiance. Three sampling times for environmental parameters (2021-06-24 & 26, 2021-07-22 & 23, and 2021-08-26 & 27) coincided with the eDNA samplings (see section 3.1.).

2.2.1. Nutrient concentration

Seawater samples for nutrient concentration measurements were filtered (porosity: 0.2 μm), transferred to acid-washed 60 mL polyethylene vials, and stored in the dark at -20 °C until analysis. All nutrient samples were analysed using a standard automated colorimetry system

(Seal Analytical continuous flow AutoAnalyser III, AA3) at the Institut de la Mer de Villefranche (IMEV, France). Nitrate (NO_3) and nitrite (NO_2) ions were analysed according to the protocol of Bendschneider and Robinson (1952) with a detection limit of 0.05 μM and 0.01 mM, respectively. The concentration of phosphate (PO_4) ions was determined following the protocol developed by Murphy and Riley (1962), with a detection limit of 0.02 μM . Silicate (SiOH_4) ions were analysed according to the protocol of Strickland and Parsons (1972) with a detection limit of 0.05 μM and 0.02 mM.

2.2.2. pH_T and total alkalinity

Seawater samples for pH_T measurements were collected directly from the Niskin in 300 mL borosilicate bottles with a stopper and were analyzed the same day. pH_T (pH on the total scale) was determined by measuring absorbances at 434, 578, and 730 nm on a Cary60 UV spectrophotometer (Agilent) before and after the addition of 50 μL of purified meta-cresol purple (R. H. Byrne, University of South. Florida) as described by Dickson et al. (2007). pH_T was calculated using formulae and constants described by Liu et al. (2011).

A volume of 500 mL of seawater was filtered on GF/F membranes for total alkalinity (A_T) measurements. A_T was determined potentiometrically using a Metrohm® titrator (Titrand 888) and a glass electrode (Metrohm®, Ecotrode Plus) calibrated using NBS buffers (pH 4.0 and pH 7.0, to check that the slope was Nernstian) and a TRIS buffer solution (salinity 35; provided by Andrew Dickson, Scripps University, USA). The accuracy of the data was validated by titrating a standard seawater provided by Andrew Dickson (Scripps University, USA). Duplicate titrations were performed on 50 mL sub-samples and A_T was calculated as described by Dickson et al. (2007).

2.2.3. Chl a concentration

A volume of 500 mL of seawater samples was filtered on GF/F membranes for chl a concentration measurements and stored at $-80\text{ }^\circ\text{C}$. Chl a was extracted in 90% aqueous acetone for 24 h in the dark at $4\text{ }^\circ\text{C}$. After cold-centrifugation ($0\text{ }^\circ\text{C}$, 15 min, 3000 rpm), the supernatant was transferred into glass vials and F_0 , the initial fluorescence of chl a and pheophytin pigment, was measured using a fluorimeter (Turner Design 10-AU Fluorimeter). The F_a fluorescence was measured one min after the addition of 10 μL of 0.3 N chlorhydric acid to transform chl a into pheophytin pigment and subtract F_a from F_0 . The concentration of chl a was calculated as described by Lorenzen (1967).

2.3. eDNA

2.3.1. Sampling and extraction

We sampled monthly (06-24 & 26, 07-22 & 23, and 08-26 & 27) 1 L of water in triplicate at each of the six sites using a 12 L Niskin bottle that was closed 1 meter above the substrate at 6 to 8 m depth. Back at the Kings Bay Marine Laboratory, samples were filtered through cellulose acetate filters (25 mm, porosity: 0.45 μ m, Sartorius) using a peristaltic pump (WATSON MARLOW) and stored at -80 °C. DNA collected on filters was extracted using 200 μ L of QuickExtract DNA extraction solution (Lucigen, Illumina) and 0.4 g of beads (glass beads 0.75A 1.0 mm, Dutscher) to dislodge the genetic material from the filter and put it in solution. After 4 min of vortex, the samples were incubated two times (6 min at 65 °C and 2 minutes at 98 °C) with 1 min of vortex between each step, before being centrifuged (8000 rpm, 30 sec). The supernatants were stored at -20 °C. DNA extracts were purified from potential PCR inhibitors using the ReliaPrep DNA Clean-up kit (Promega).

2.3.2. PCR amplification and sequencing

The DNA extracts were amplified using a PCR amplification reaction targeting 1) a 313 bp fragment encoding cytochrome c oxidase I (COI, Leray et al., 2013) and 2) the V4 SSU 18S region of 381 bp encoding 18S ribosomal DNA (18S; Stoeck et al., 2010). These gene regions allow the taxonomic identification of eukaryotes. We used the Multiplex MasterMix (Qiagen) and followed the PCR touchdown program of Leray et al. (2013) for both primers. High-throughput sequencing was performed by the G enome Quebec platform (Canada) using an Illumina MiSeq.

2.3.3. Bioinformatics

The primers were trimmed using cutadapt (version 4.2) and bash scripts written by Ramon Gallego (Kelly lab). Demultiplexing and matching of forward and reverse reads were performed using the dada2 software package (version 1.26.0) and script written by Elizabeth Andruszkiewicz Allan (Kelly lab, github.com/KellyLabUW/MiSeqPipeline). Sample replicates that did not meet the required quality standards were excluded from the study (25 out of 106 for COI primer and 21 out of 106 for 18S primer). The remaining biological and technical replicates were merged together by sites and sampling period to run the data analysis. The BLASTn (nucleotide-nucleotide Basic Local Alignment Search Tool) was performed using GenBank (NCBI) with the Octopus server from LBDV (Laboratoire de Biologie du

Développement, Villefranche-sur-Mer). The number of reads was normalized to the eDNA index (Kelly et al., 2019) to minimize amplification biases between taxa. Only benthic taxa found in two of the three sampling periods were kept for analysis to ensure reliable and consistent data as well as temporal stability.

2.4. Statistics

Multiple Hutcheson t-tests were used to test the significance of the difference between communities' Shannon diversity indexes (package `ecolTest`). Correlation tests were used to test for the link between biodiversity and environmental parameters.

3. Results

3.1. Environmental characterization of the sites

The environmental data at each site was used to establish a grouping by site and/or period (Fig. 26). Data are shown in Fig. S6. When considering all the measured parameters, the Kongsbreen South site from week 28 to 34 (early July to the end of August) and the Ossian Sars site on week 33 clearly differed from the other sites with high nutrient concentrations and a high K_d (Fig. 26, A). With a high salinity and total alkalinity, weeks 27 and 28 at French bird cliff and 32 at Kongsfjordneset also differed from the rest of the sites.

Temperature and K_d exhibited an inverse relationship because turbid waters are located in the innermost part of the fjord where temperatures are at their lowest. K_d and nutrient concentrations were positively correlated because turbid meltwaters are enriched with nutrients.

Temperature, pH, and total alkalinity were then excluded from the analyses to focus on salinity, K_d , and nutrient concentrations, which are the parameters that varied the most between sites and periods. Dimension 1 of the Principal Component Analysis (PCA) was mainly driven by nutrient concentrations and salinity and explained more than 71 % of the variances (Fig. 26B). K_d allowed to differentiate sites and periods within dimension 2. For Kongsfjordneset, the weekly measured environmental parameters did not vary much. During week 25, at the beginning of the summer, all sites were grouped together with a similar high salinity. After week 25, nutrients increased and salinity decreased at all sites, except at Kongsfjordneset (arrow, Fig. 26B). For Ossian Sars and Kongsbreen South sites, the K_d was particularly elevated on weeks 32 and 30 (early August), respectively. While K_d seemed not

correlated with salinity and nutrient concentrations, these two high values could have driven the trend and the position of the arrow representing the K_d .

3.2. eDNA

Our results show a high diversity of the faunal benthic community within the fjord with 44 taxa and Shannon indexes ranged between 2.17 to 3.18 (Fig. 25, Table S19). A number of 17 macroalgae taxa was identified with Shannon indexes for macroalgae only going from 1.11 to 2.20. The list of taxa is provided in the supplementary materials (Table S1). For both fauna and

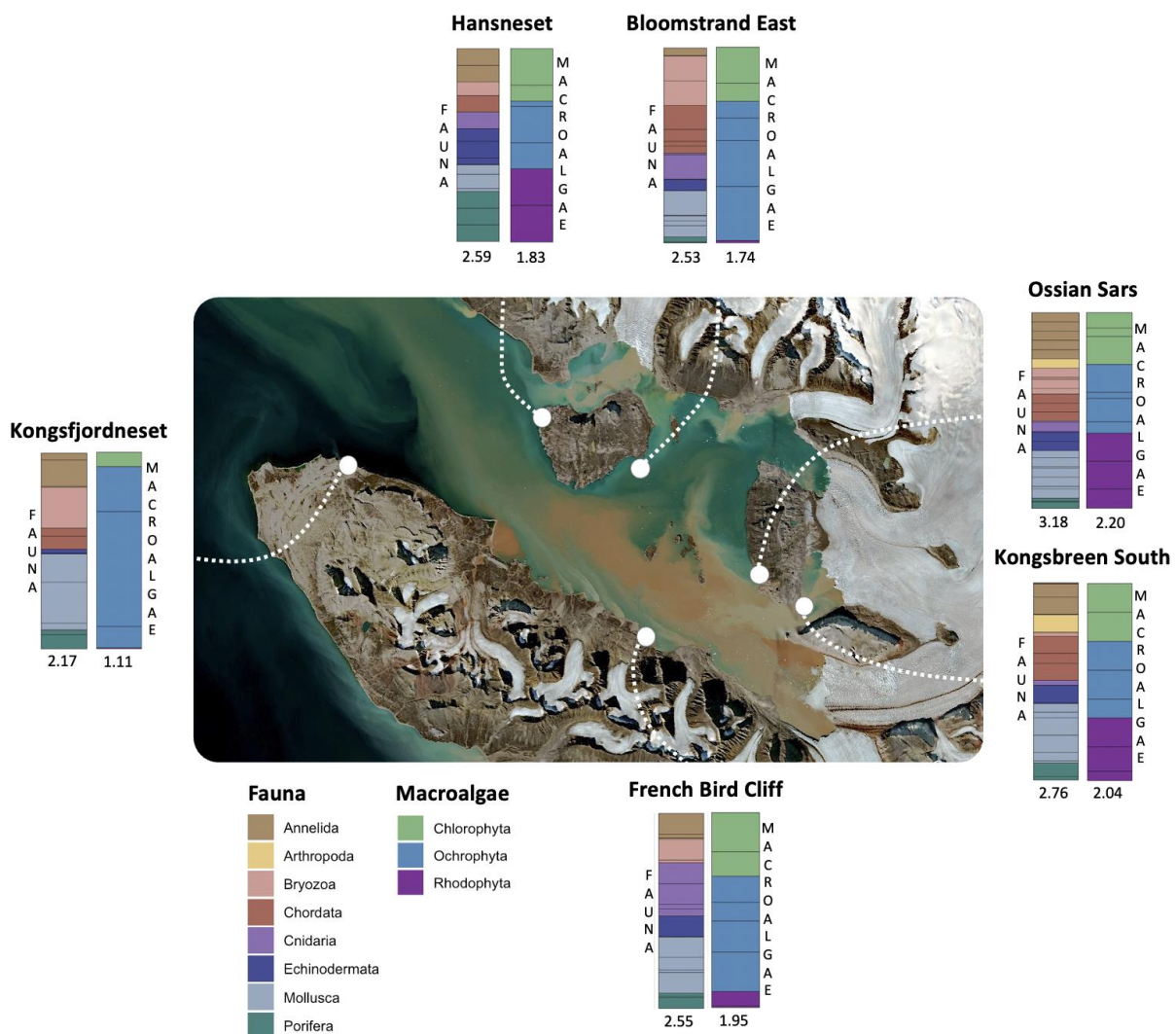


Figure 25: Satellite image of Kongsfjorden (Sentinel 2 L2A, 2020/07/27, available on sentinel-hub.com consulted on 2023/01) and the six sampling locations with stacked barplot representing eDNA faunal and macroalgal diversity at the order level. Phyla are represented by color. The size of the cells represents the proportion of the orders (separation lines) and phyla (colors) based on the eDNA indexes. The values of the Shannon diversity index are indicated below each barplot.

macroalgae, Shannon diversity indexes were significantly higher in Ossian Sars compared to the five other sites. This trend holds true when considering all periods were combined, as well as in June and July for fauna (Table S20). Ossian Sars showed both more taxa and a more balanced distribution between taxa than the other sites.

In June and July, the Kongsbreen South site, closer to the glacier, and French Bird Cliff, showed a significantly higher faunal and macroalgal diversity than Kongsfjordneset. Bloomstrand faunal diversity was also significantly higher than Kongsfjordneset both in June and July.

4. Discussion

In contrast to our initial hypotheses, we did not find a diversity gradient nor a correlation between the distribution of macroalgae and the underwater light regime nor a correlation of suspension feeders with the chl *a* or nutrient concentrations. Although we were not able to find a direct correlation between benthic diversity and environmental conditions, our results highlight some interesting observations. Apart from Kongsfjordneset, all other sites were affected by glacier melting. This was evidenced by an increase in nutrient levels observed from weeks 28 to 34 (early July to the end of August, Fig 27). In particular, during weeks 30 and 32 (early August), Ossian Sars and Kongsbreen South experienced a sharp increase in K_d , which may coincide with the melting period of the glacier. The two sites the most influenced by glaciers also exhibited the highest levels of benthic diversity. In contrast, previous studies reported a decline in species richness from the outer to the inner part of Kongsfjorden (e.g. Kedra et al., 2010; Voronkov et al., 2013; Legeżyńska et al., 2017). Also, trends of decreasing diversity when getting closer to the glaciers have been observed in other glacial-impacted regions such as Hornsund fjord (Włodarska-Kowalczyk et al., 2013) and the Canadian Arctic (Farrow et al., 1983). Previous studies have suggested that the outer and central basins of fjords may be enriched with boreal species which may coexist with arctic and sub-arctic species already inhabiting these areas (e.g. Renaud et al., 2019). In Kongsfjorden, the absence

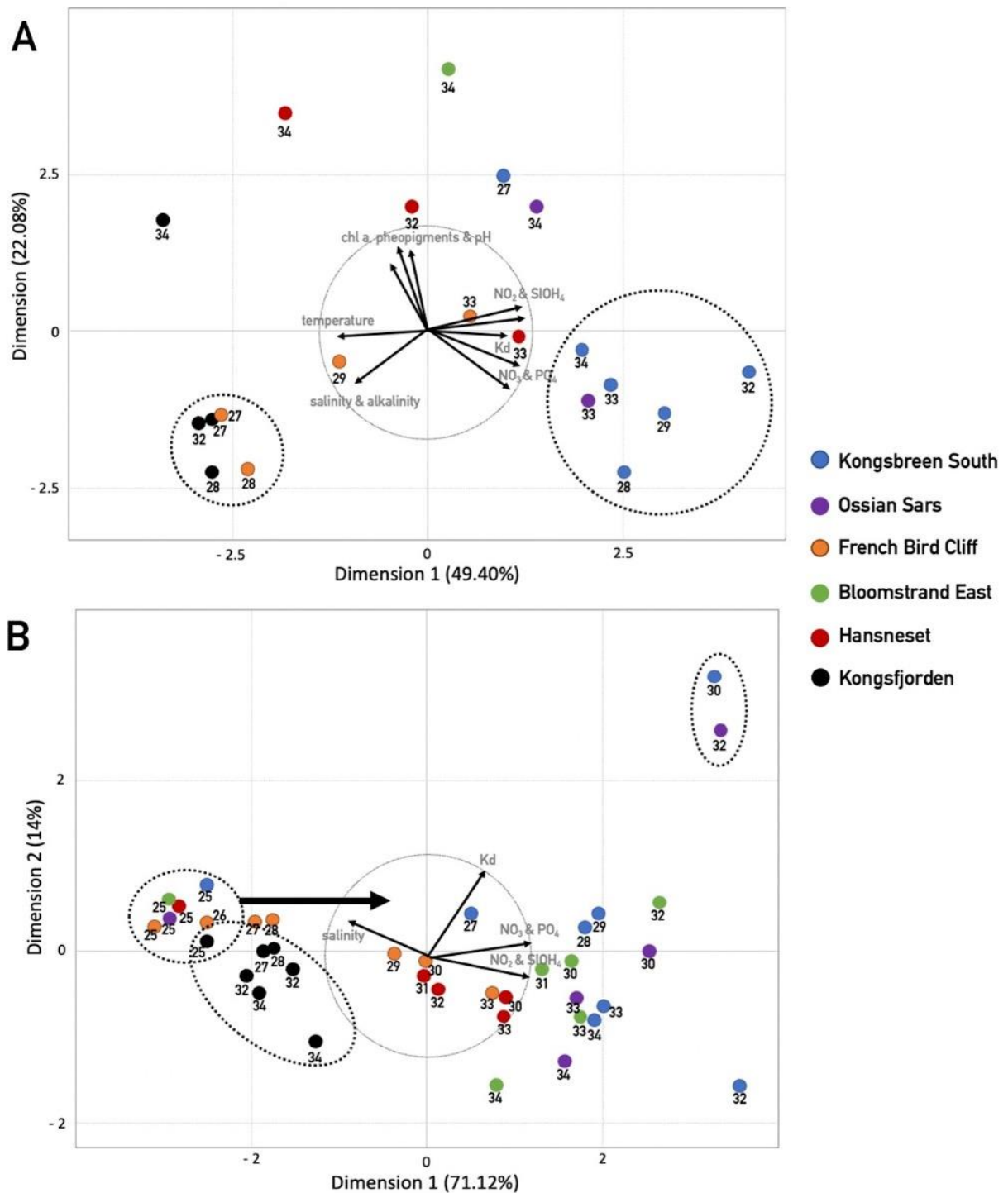


Figure 26: Principal Component Analysis (PCA) based on A) all parameters or B) salinity, K_d , and nutrient concentrations measured from week 25 to week 34 at six study sites along the Kongsfjorden. The numbers on the figure indicate the week of sampling. The bold arrow in B) represents the movement of sites from left to right of the graph after week 25.

of entrance sills allows shelf taxa to easily enter the fjord (Svendsen et al. 2002; Legezynska et al., 2017). Also, warming increases the discharge of freshwater enriched with inorganic particles into the fjord and the frequency of disturbance events such as ice scouring and

sediment slides (Wlodarska-Kowalczyk et al. 2005). Although such increased disturbance may promote opportunistic species, it has been predicted that overall benthic diversity in these areas would decrease (Wlodarska-Kowalczyk et al. 2005; Al-Habahbeh et al. 2020). Hence, we would expect a diversity increase close to the entrance of the fjord, with more boreal species, and a decrease close to the glacier where disturbances events are more frequent. However, our results do not align with these expectations.

Kedra et al., (2010) have shown, using a sediment sampling method, that the diversity of the macrobenthic soft-bottom community in the middle and outer part of the Kongsfjorden decreased between 1997 and 2006. In contrast, the inner glacial bay, well-separated from the outer fjord by a chain of islands and a shallow sill (20 to 50 m; Svendsen et al. 2002) that acted as a barrier, remained as diverse, although it was still less than outer sites in this study. There was no major change in substrate type during this period, which therefore cannot explain this change. Kedra et al. (2010) put forward the hypothesis that the decline in diversity in the outer part of the fjord could be attributed to the decreasing influence of the Blomstrandbreen glacier which retreats quickly (Burton et al., 2016). With its retreat, its melting would no longer benefit the most distant sites. Indeed, glacier melting provides nutrients that support the growth of phytoplankton communities which form the basis of the food web (Piquet et al., 2014), and macroalgae, which are key habitat species in the ecosystem (Lebrun et al., 2022). Also, the presence of top predators in the Arctic coastal marine ecosystem is closely tied to the glacier front (Lydersen et al., 2014; Bouchard Marmen et al., 2017). In fact, top predators such as seabirds and sea lions migrate to the Arctic during the summer to live near glacier fronts, which underscores the importance of the nutritional richness these areas provide (Hop et al., 2002; Lydersen et al., 2014). Predators play a crucial role in regulating the ecosystem through top-down control, which may in turn further increase its diversity (Wessels et al., 2006; Bouchard Marmen et al., 2017). Hence, glaciers harbor key species and regulate the diversity of the benthic communities (Gutt et al., 2001).

The presence of top predators at the inner sites could explain our results. Seabirds are present in Ossian Sars, Kongsbreen South, Bloomstrand East, and French Bird Cliff (Varpe and Gabrielsen, 2022; pers. obs.). Sea Lions have been observed at Ossian Sars, Kongsbreen South, and Hansneset (Everett et al., 2018; pers. obs.). By identifying the presence of these top predators and their interactions with the benthic community, we established a trophic

network diagram at each of the six sites (Fig. 27). Not surprisingly, the most diverse site also exhibited the most complex ecosystem with numerous trophic links and an homogenous repartition of taxa within and between the different trophic levels. Kongsbreen South, the site very close to the glacier, also presents a very complex ecosystem but with more heterogeneity between the first and the second levels. The presence of the bird colony at Ossian Sars could explain a better top-down regulation at that site than at Kongsbreen South. Conversely, Kongsfjordneset, the furthest site from the glaciers, only exhibits two heterogenous trophic levels. The presence of these top predators could therefore explain a greater diversity at Ossian Sars and Kongsbreen South, near the glaciers, in comparison with Kongsfjordneset, which no longer seems influenced by their melting.

The type of substrate (rocky vs. sediment) can also hold substantial importance in shaping the community composition (Lantuit et al., 2012; Filbee-Dexter et al., 2019). Hansneset and Kongsfjordneset feature rocky substrates, while the other sites predominantly consist of sediment accompanied with rocks. According to our findings, the rocky-substrate communities do not exhibit higher diversity. This align with the idea of predators being the key factor.

With warming, the retreat of glaciers could have a significant impact on the ecosystem. Specifically, the disappearance of the glacier front may lead to substantial changes in phytoplankton blooms and the properties of water masses in the fjord (Ardyna and Arrigo, 2020). These changes could, in turn, cause modifications in top predators' presence and, hence, in ecosystem diversity. However, predicting these changes is very challenging.

It is important to note that like any other analysis method, eDNA sampling also has biases (Yates et al., 2019). During our exploration of Kongsfjordneset, the outermost site of the fjord, we observed a strong abundance of coralline algae while diving and using a drone, compared to other sites (Steeve Comeau pers. obs.). However, despite being present in the collected seawater samples from this site, the coralline algae exhibited a low eDNA index. Similarly, we observed a high presence of sea urchins while diving at Kongsfjordneset, but the eDNA index rather indicated a high abundance of mollusks, ochrophytes, and bryozoans. These differences in abundance determined by eDNA are difficult to interpret because although the eDNA index makes it possible to establish a value based on the number of sequences between 0 and 1, the number of sequences is not only linked to the abundance of a taxon. The eDNA index does

not only reflect the abundance or biomass of a species or genus, but also the ability of its sequence to be amplified (Kelly et al., 2019). Additionally, the sequences can come from a dead organism or from the eggs or sperm, which can further bias the results. Therefore, while our results provide insights into the diversity of the studied sites, caution should be taken when interpreting them.

Furthermore, part of our replicates (40%) did not meet the quality standards required to be included in our study. These replicates were randomly of poor quality, i.e., not targeted on a specific date, site, or primer. This suggests that the quality issue was not due to a problem during sampling or extractions, which were done following the same protocols for all samples. Also, the PCR amplification was realized on all samples at the same time, with the same products. The poor per-base sequence quality obtained could have arisen from various sources, including errors during the sequencing process, which may lead to inaccuracies in base calling and subsequent data analysis. Also, DNA degradation before or during the sequencing procedure can significantly impact the quality of the obtained sequences, as damaged DNA molecules may result in incomplete or unreliable data. This limitation forced us to merge the remaining filtration and PCR replicates, thus reducing the robustness of our results.

The trend of decreasing diversity when approaching the interior of the fjord described previously could be reversed now as suggested by our results but further studies must validate it. Additional sampling of seawater for eDNA analysis throughout the fjord could determine the consistency of our results. Also, other biodiversity assessment methods like community sampling or photography of quadrats could validate our findings. Combined with stable isotope analysis to look into the trophic food web, the hypothesis of predator regulation could be tested. Overall, while our study provides some insight into the benthic diversity of Kongsfjorden, caution should be exercised when interpreting the results due to the limitations of our sampling method and the need for additional research.

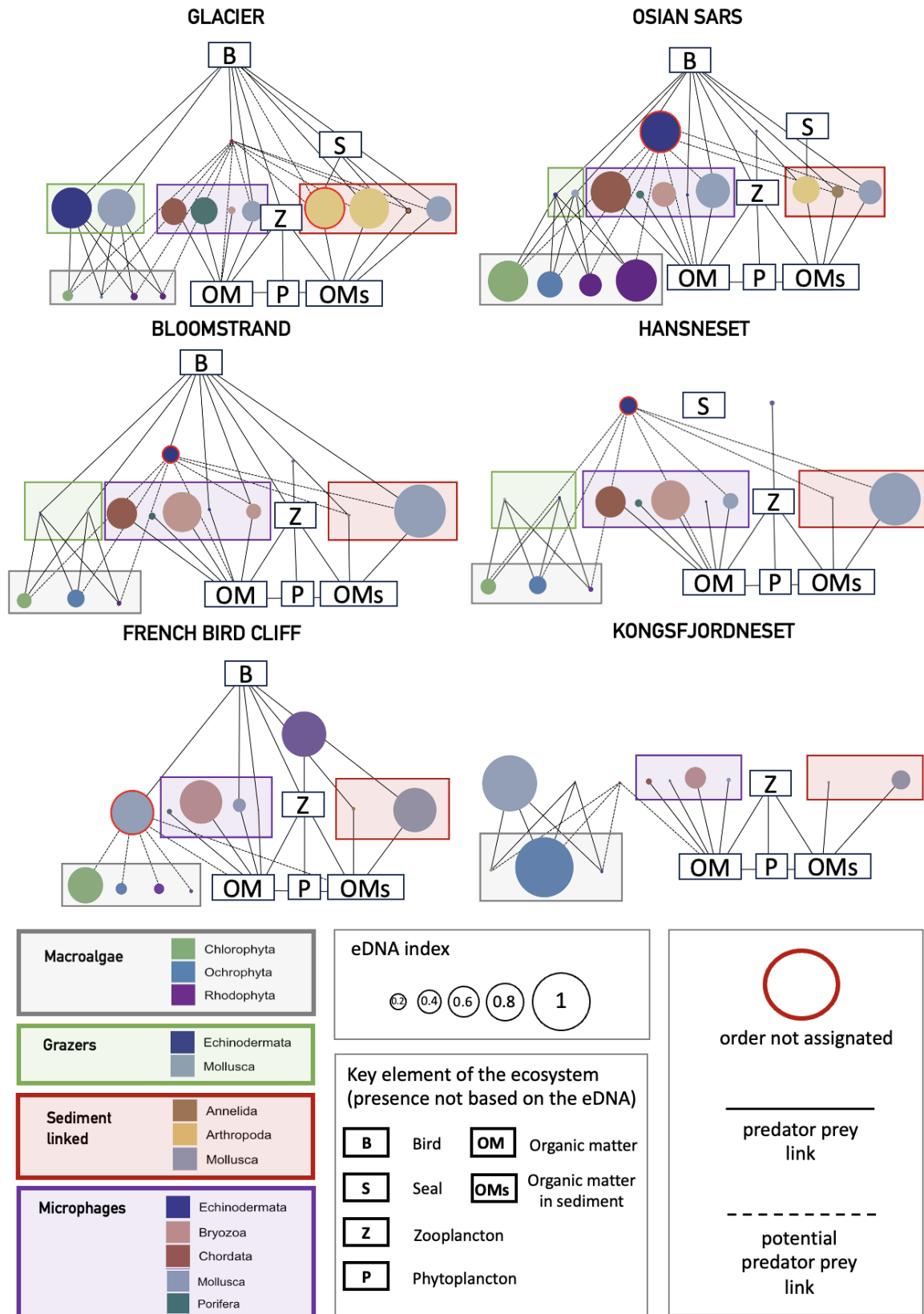


Figure 27: Trophic network diagram of each site based on the known predator-prey links between phyla, presence of predators, and the eDNA index.

Acknowledgments

We are extremely grateful to Ryan Kelly for his contribution to experiment design and his invaluable assistance throughout the bioinformatics cleaning steps. Additionally, we express our sincere appreciation to Guri Gledis and Elizabeth Andruszkiewicz Allan for their help in the bioinformatic process. We thank Samir Alliouane and Cale Miller for their assistance during the data collection process. Cale Miller also contributed in helping to measure pH, alkalinity, and chl *a* concentrations. We thank the Molecular Biology Platform of Institut de la Mer de Villefranche (IMEV) that is supported by IR EMBRC-France, whose fundings are managed by the ANR within the Investments for Future Program under reference ANR-10-INBS-02. This study was supported by the EC2CO program of the Institut National des Sciences de l'Univers (INSU, CNRS).

Author contributions

All authors designed the study and were involved in the fieldwork. AL, SC, FG, and JPG measured pH and alkalinity. AL performed the nutrient analysis. AL measured chl *a* concentrations. AL and SC performed the filtration of eDNA seawater samples. AL performed the extraction, PCR, and purification steps. AL performed the bioinformatics cleaning steps. AL analyzed the data and wrote the first draft of the manuscript which was accepted by all co-authors.

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Supplementary data

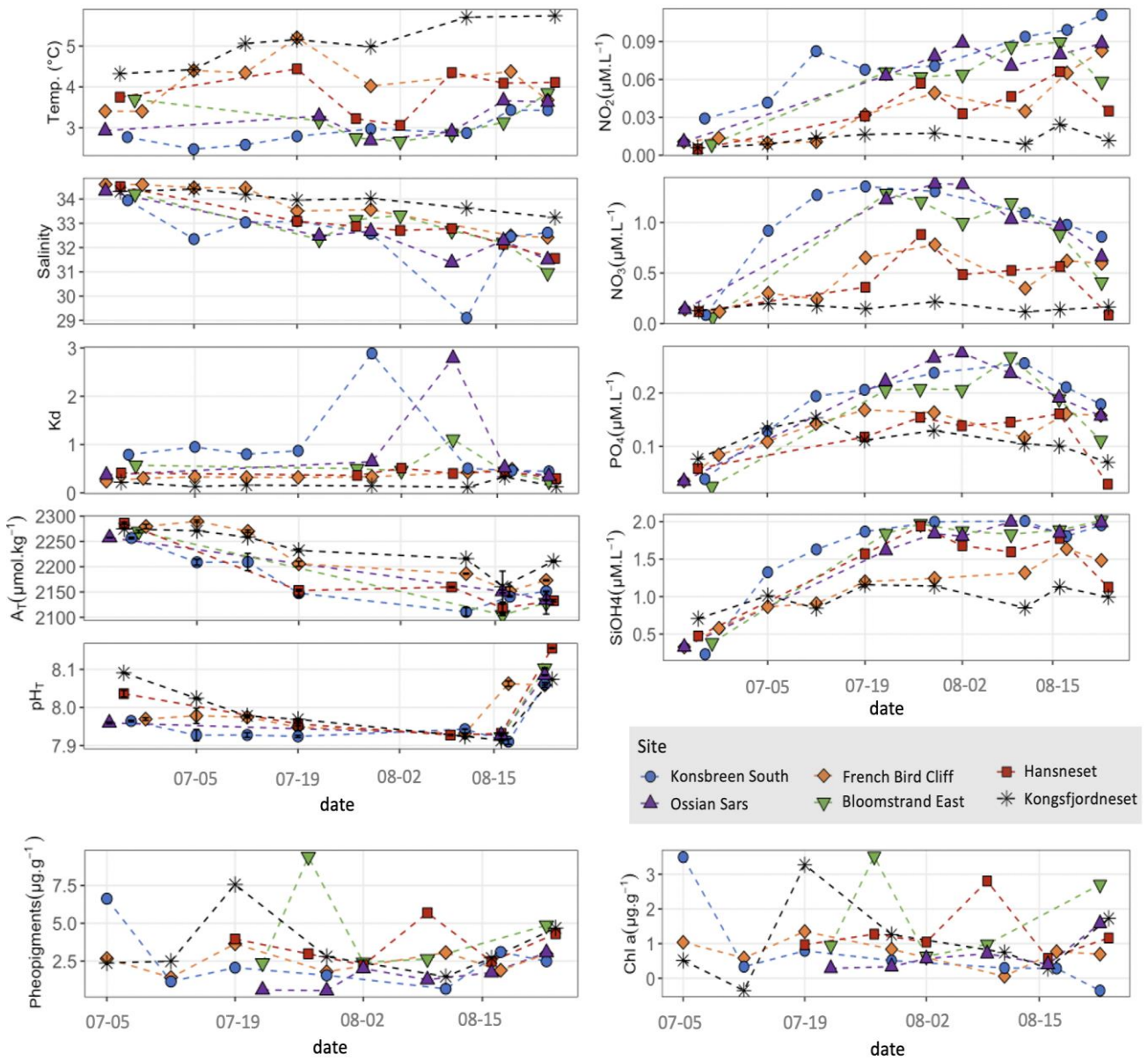


Figure S6: Environmental parameters measurements at each site within the summer 2021 in Kongsfjorden

Table S19: eDNA-based records of phylum, order, and species across sites and sampling periods. The eDNA index was calculated using species-scale reads counts or, if not available (NA) the order or phylum scales.

Month	Site	Phylum	Order	Species	nReads	eDNA index
June	Bloomstrand Est	Amnielida	Sabellida	<i>Sabellidae</i> sp. CMC02	4	1
June	Bloomstrand Est	Amnielida	Phyllocladida	NA	7	0.551
June	Bloomstrand Est	Bryozoa	Cyclostomatida	<i>Crisia eburnea</i>	7	1
June	Bloomstrand Est	Bryozoa	Cyclostomatida	NA	33	1
June	Bloomstrand Est	Chlorophyta	Ulotrichales	NA	31	0.638
June	Bloomstrand Est	Chordata	Stolidobranchia	NA	5	1
June	Bloomstrand Est	Chordata	Stolidobranchia	<i>Peloniaia corrugata</i>	13	2
June	Bloomstrand Est	Chordata	Phlebobranchia	NA	2	0.571
June	Bloomstrand Est	Echinodermata	Ophiuroidea sp. EAC01	NA	2	1
June	Bloomstrand Est	Echinodermata	Echinoida	<i>Strongylocentrotus pallidus</i>	2	1
June	Bloomstrand Est	Echinodermata	Littorinimorpha	<i>Lacuna vincta</i>	3	0.034
June	Bloomstrand Est	Mollusca	Adapedonta	<i>Hiattella sp. K HML-2015</i>	23	1
June	Bloomstrand Est	Mollusca	Myioida	<i>Choradria flagelliformis</i>	61	0.103
June	Bloomstrand Est	Ochrophyta	Ectocarpales	<i>Microsporangium alariae</i>	34	0.446
June	Bloomstrand Est	Ochrophyta	Ectocarpales	NA	3	1
June	Bloomstrand Est	Ochrophyta	Ectocarpales	NA	10	1
June	Bloomstrand Est	Ochrophyta	Ectocarpales	<i>Pylorella littoralis</i>	16	1
June	Bloomstrand Est	Ochrophyta	Ectocarpales	NA	26	1
June	Bloomstrand Est	Ochrophyta	Laminariales	NA	198	0.296
June	Bloomstrand Est	Porifera	Suberitida	NA	9	1
June	Bloomstrand Est	Porifera	Bubarida	NA	235	0.486
June	French Bird Cliff	Amnielida	Capitellida	<i>Arenicola marina</i>	5	1
June	French Bird Cliff	Amnielida	Phyllocladida	NA	23	1
June	French Bird Cliff	Arthropoda	Decapoda	<i>Hyas araneus</i>	119	1
June	French Bird Cliff	Bryozoa	Ctenostomatida	<i>Vesicularia spinosa</i>	2	1
June	French Bird Cliff	Chlorophyta	Ulotrichales	NA	88	1
June	French Bird Cliff	Cnidaria	Siphonophorae	<i>Apolemia sp. BO-2009</i>	143	1
June	French Bird Cliff	Cnidaria	Leptothecata	<i>Calycella syringa</i>	3	1
June	French Bird Cliff	Cnidaria	Anthoathecata	<i>Sarsia princeps</i>	45	1
June	French Bird Cliff	Cnidaria	Anthoathecata	<i>Eudendrium racemosum</i>	2	0.075
June	French Bird Cliff	Echinodermata	Amphilepida	NA	13	1
June	French Bird Cliff	Echinodermata	Ophiurida	<i>Ophiopholis aculeata</i>	59	0.097
June	French Bird Cliff	Mollusca	Hydrobia	<i>Blomphalaria oligosa</i>	101	1
June	French Bird Cliff	Mollusca	Veneroida	<i>Macoma calcareo</i>	51	1
June	French Bird Cliff	Mollusca	Cardida	NA	9	1
June	French Bird Cliff	Mollusca	Myioida	NA	21	1
June	French Bird Cliff	Mollusca	Adapedonta	<i>Hiattella arctica</i>	96	0.089
June	French Bird Cliff	Mollusca	Ectocarpales	<i>Hiattella sp. K HML-2015</i>	47	0.340
June	French Bird Cliff	Mollusca	Ectocarpales	<i>Scinetosporaceae</i> sp. 2 AP-2014	7	1
June	French Bird Cliff	Ochrophyta	Laminariales	<i>Chorda filum</i>	7	1
June	French Bird Cliff	Ochrophyta	Ectocarpales	<i>Cladophoron zosterae</i>	25	1
June	French Bird Cliff	Ochrophyta	Laminariales	NA	19	0.015
June	French Bird Cliff	Ochrophyta	Ectocarpales	<i>Choradria flagelliformis</i>	4	0.735
June	French Bird Cliff	Porifera	Suberitida	<i>Hiattella sp. BO-2009</i>	22	0.300
June	French Bird Cliff	Porifera	Bubarida	<i>Halichondria panicea</i>	364	0.415
June	French Bird Cliff	Rhodophyta	Laminariales	NA	4	1
June	French Bird Cliff	Rhodophyta	Bangiales	<i>Devaleraea ramentacea</i>	4	1
June	French Bird Cliff	Rhodophyta	Laminariales	<i>Pyropia halatanensis</i>	6	1
June	French Bird Cliff	Rhodophyta	Laminariales	NA	8	0.227
June	French Bird Cliff	Rhodophyta	Phyllocladida	NA	15	0.253
June	Glacier	Amnielida	Spionida	<i>Girettulus cirratus</i>	31	1
June	Glacier	Amnielida	Phyllocladida	<i>Glyceria capitata</i>	2	1
June	Glacier	Amnielida	Spionida	<i>Polydora onagawaensis</i>	2	0.000
June	Glacier	Amnielida	Terebellida	<i>Amphitrite cirrata</i>	9	0.074
June	Glacier	Arthropoda	Cyclopoida	<i>Silicosomatoida</i> sp. OS9PROBE-08	10	1
June	Glacier	Bryozoa	Cheliostomatida	<i>Caularnaphis magnus</i>	4	0.974
June	Glacier	Chordata	Stolidobranchia	<i>Halocynthia pyriformis</i>	2	0.028
June	Glacier	Cnidaria	Siphonophorae	<i>Apolemia sp. BO-2009</i>	18	0.034
June	Glacier	Echinodermata	Camarodonta	NA	2	0.053
June	Glacier	Echinodermata	Echinoida	<i>Strongylocentrotus pallidus</i>	264	0.454
June	Glacier	Mollusca	Lepidopleurida	NA	7	1
June	Glacier	Mollusca	Nudibranchia	<i>Zelentia willowsi</i>	4	1
June	Glacier	Mollusca	Hydrophila	<i>Blomphalaria</i> sp. GC-2010	3	0.012

Month	Site	Phylum	Order	Species	nReads	eDNA index
June	Bloomstrand Est	Mollusca	Myioida	<i>Hiattella sp. K HML-2015</i>	94	0.185
June	Bloomstrand Est	Mollusca	Chitonida	<i>Tonicella undocaelulea</i>	698	0.377
June	Bloomstrand Est	Mollusca	Littorinimorpha	<i>Lacuna vincta</i>	68	0.445
June	Bloomstrand Est	Mollusca	Adapedonta	<i>Hiattella arctica</i>	2916	0.743
June	Bloomstrand Est	Ochrophyta	Ectocarpales	<i>Choradria sp. 4nov</i>	6	1
June	Bloomstrand Est	Ochrophyta	Ectocarpales	<i>Pylorella washingtoniensis</i>	6	1
June	Bloomstrand Est	Ochrophyta	Laminariales	NA	25	0.005
June	Bloomstrand Est	Ochrophyta	Ectocarpales	<i>Microsporangium alariae</i>	6	0.090
June	Bloomstrand Est	Ochrophyta	Ectocarpales	<i>Choradria flagelliformis</i>	6	0.301
June	Bloomstrand Est	Porifera	Suberitida	<i>Halichondria panicea</i>	27	0.100
June	Bloomstrand Est	Porifera	Bubarida	NA	502	0.156
June	Bloomstrand Est	Rhodophyta	NA	NA	16	1
June	Bloomstrand Est	Rhodophyta	Palmariales	NA	5	0.043
June	Bloomstrand Est	Rhodophyta	Palmariales	<i>Rhodophysema kielimani</i>	4	0.123
June	Bloomstrand Est	Rhodophyta	Palmariales	<i>Devaleraea ramentacea</i>	8	0.290
June	Bloomstrand Est	Rhodophyta	polychaeta sp. OS9PROBE-0831:	NA	6	1
June	Bloomstrand Est	Amnielida	Spionida	<i>Polydora onagawaensis</i>	264	1
June	Bloomstrand Est	Amnielida	Veneroida	<i>Tridacna squamosa</i>	2	1
June	Bloomstrand Est	Amnielida	Myioida	<i>Hiattella sp. K HML-2015</i>	4	0.090
June	Bloomstrand Est	Mollusca	Littorinimorpha	<i>Lacuna vincta</i>	3	0.224
June	Bloomstrand Est	Ochrophyta	Ectocarpales	<i>Dictyosiphon foeniculaceus</i>	2	0.492
June	Bloomstrand Est	Porifera	Bubarida	NA	138	1
June	Bloomstrand Est	Amnielida	Phyllocladida	NA	13	1
June	Bloomstrand Est	Amnielida	NA	<i>Arenicola marina</i>	3	0.041
June	Bloomstrand Est	Amnielida	NA	NA	2	0.366
June	Bloomstrand Est	Bryozoa	Cyclostomatida	<i>Crisia eburnea</i>	7	0.357
June	Bloomstrand Est	Chlorophyta	Ulotrichales	<i>Ulvela leptochaete</i>	4	1
June	Bloomstrand Est	Chlorophyta	Ulotrichales	NA	26	0.191
June	Bloomstrand Est	Chordata	Stolidobranchia	<i>Dendrodoa grossularia</i>	2	0.195
June	Bloomstrand Est	Mollusca	Chitonida	<i>Tonicella undocaelulea</i>	12	0.015
June	Bloomstrand Est	Mollusca	Adapedonta	<i>Hiattella arctica</i>	965	0.584
June	Bloomstrand Est	Ochrophyta	Desmarrestiales	NA	19	1
June	Bloomstrand Est	Ochrophyta	Laminariales	NA	925	0.495
June	Bloomstrand Est	Ochrophyta	Laminariales	<i>Halosiphon tomentosus</i>	35	0.631
June	Bloomstrand Est	Porifera	Dendroceratida	<i>Haliscara dujardini</i>	6	1
June	Bloomstrand Est	Amnielida	NA	<i>Arenicola marina</i>	4	1
June	Bloomstrand Est	Amnielida	Spionida	<i>Chaetozoa setosa</i>	35	1
June	Bloomstrand Est	Amnielida	NA	NA	94	1
June	Bloomstrand Est	Amnielida	Sabellida	<i>Simplaria potswaidi</i>	4	1
June	Bloomstrand Est	Amnielida	Terebellida	<i>Spinisphaera hutchingsae</i>	4	1
June	Bloomstrand Est	Amnielida	Sabellida	NA	33	0.245
June	Bloomstrand Est	Amnielida	Phyllocladida	NA	17	0.682
June	Bloomstrand Est	Bryozoa	Cyclostomatida	<i>Annectocyma tubulosa</i>	2	1
June	Bloomstrand Est	Bryozoa	Cheliostomatida	NA	5	0.027
June	Bloomstrand Est	Bryozoa	Cyclostomatida	<i>Crisia eburnea</i>	2	0.052
June	Bloomstrand Est	Ossian Sars	Ulotrichales	NA	124	0.467
June	Bloomstrand Est	Ossian Sars	Stolidobranchia	<i>Dendrodoa grossularia</i>	20	1
June	Bloomstrand Est	Ossian Sars	Stolidobranchia	NA	7	0.140
June	Bloomstrand Est	Ossian Sars	Stolidobranchia	<i>Peloniaia corrugata</i>	10	0.256
June	Bloomstrand Est	Ossian Sars	Leptothecata	<i>Obelia longissima</i>	5	1
June	Bloomstrand Est	Ossian Sars	Camarodonta	NA	31	1
June	Bloomstrand Est	Ossian Sars	Echinodermata	NA	2	0.051
June	Bloomstrand Est	Ossian Sars	Amphilepida	NA	11	1
June	Bloomstrand Est	Ossian Sars	Trichida	<i>Margarites helacinus</i>	39	1
June	Bloomstrand Est	Ossian Sars	Littorinimorpha	NA	9	0.021
June	Bloomstrand Est	Ossian Sars	Myioida	<i>Hiattella sp. K HML-2015</i>	39	0.025
June	Bloomstrand Est	Ossian Sars	Chitonida	<i>Tonicella undocaelulea</i>	644	0.199
June	Bloomstrand Est	Ossian Sars	Adapedonta	<i>Hiattella arctica</i>	17	0.268
June	Bloomstrand Est	Ossian Sars	Myioida	NA	26	0.958
June	Bloomstrand Est	Ossian Sars	Cardida	NA	18	0.205
June	Bloomstrand Est	Ossian Sars	Ectocarpales	NA	20	0.538
June	Bloomstrand Est	Ossian Sars	Desmarrestiales	NA	20	0.538

Month	Site	Phylum	Order	Species	nReads	eDNA Index
July	Ossian Sars	Porifera	Leucosolenida	<i>Sycon abyssale</i>	11	1
July	Ossian Sars	Porifera	Suberitida	<i>Halichondria panicea</i>	10	0.033
July	Ossian Sars	Porifera	Bubarida	NA	60	0.178
July	Ossian Sars	Rhodophyta	Palmariales	<i>Devaleraca ramentacea</i>	72	1
July	Ossian Sars	Rhodophyta	Palmariales	NA	129	1
July	Ossian Sars	Rhodophyta	Ceramiales	<i>Savoiea arctica</i>	3	0.067
July	Ossian Sars	Rhodophyta	NA	NA	21	0.737
August	Bloomstrand Est	Chordata	NA	NA	12	0.074
August	Bloomstrand Est	Chordata	NA	NA	3	0.064
August	Bloomstrand Est	Cnidaria	Siphonophorae	<i>Apolemia sp. BO-2009</i>	44	0.059
August	Bloomstrand Est	Cnidaria	Anthoathecata	<i>Eudendrium racemosum</i>	18	0.132
August	Bloomstrand Est	Echinodermata	Echinoidea	<i>Strongylocentrotus pallidus</i>	6	0.007
August	Bloomstrand Est	Echinodermata	Ophiurida	<i>Ophiopholis aculeata</i>	31	0.009
August	Bloomstrand Est	Mollusca	Chitonida	<i>Tonicella undocaculea</i>	54	0.020
August	Bloomstrand Est	Mollusca	Veneroidea	<i>Macoma calcarata</i>	8	0.030
August	Bloomstrand Est	Mollusca	Myioida	<i>Hiatella sp. K HML-2015</i>	52	0.073
August	Bloomstrand Est	Mollusca	Hygrophila	<i>Biomphalaria oligoza</i>	46	0.088
August	Bloomstrand Est	Mollusca	Myiida	NA	65	0.601
August	Bloomstrand Est	Mollusca	Adapedonta	<i>Hiatella arctica</i>	5481	0.995
August	Bloomstrand Est	Ochrophyta	Laminariales	<i>Halosiphon tomentosus</i>	185	1
August	Bloomstrand Est	Ochrophyta	Ectocarpales	<i>Claosiphon zosterae</i>	4	0.031
August	Bloomstrand Est	Ochrophyta	Laminariales	NA	223	0.035
August	Bloomstrand Est	Ochrophyta	Ectocarpales	NA	29	0.115
August	Bloomstrand Est	Ochrophyta	Ectocarpales	<i>Pyraliella littoralis</i>	28	0.194
August	Bloomstrand Est	Porifera	Bubarida	NA	447	0.099
August	French Bird Cliff	Annelida	NA	NA	58	0.280
August	French Bird Cliff	Bryozoa	Phyllocladida	<i>Eucratea loricata</i>	42	0.285
August	French Bird Cliff	Bryozoa	Chelostomatida	NA	64	1
August	French Bird Cliff	Bryozoa	Ulotrichales	NA	14	0.505
August	French Bird Cliff	Bryozoa	Anthoathecata	<i>Eudendrium racemosum</i>	172	0.967
August	French Bird Cliff	Mollusca	Adapedonta	<i>Hiatella arctica</i>	6745	1
August	French Bird Cliff	Ochrophyta	Ectocarpales	<i>Pyraliella littoralis</i>	95	0.084
August	French Bird Cliff	Ochrophyta	Laminariales	NA	1173	0.148
August	French Bird Cliff	Ochrophyta	Desmarestiales	NA	14	0.174
August	French Bird Cliff	Ochrophyta	Ectocarpales	NA	16	0.309
August	French Bird Cliff	Rhodophyta	Palmariales	NA	23	0.111
August	Glacier	Annelida	NA	NA	3	0.095
August	Glacier	Arthropoda	Euphausiacea	NA	211	1
August	Glacier	Chlorophyta	Ulotrichales	NA	30	0.339
August	Glacier	Cnidaria	Siphonophorae	<i>Apolemia sp. BO-2009</i>	107	0.745
August	Glacier	Mollusca	Hygrophila	<i>Biomphalaria sp. GC-2010</i>	67	1
August	Glacier	Mollusca	Adapedonta	<i>Hiatella arctica</i>	37	0.034
August	Glacier	Mollusca	Chitonida	<i>Tonicella undocaculea</i>	33	0.065
August	Glacier	Mollusca	Myioida	<i>Hiatella sp. K HML-2015</i>	16	0.115
August	Glacier	Ochrophyta	Laminariales	NA	48	0.039
August	Glacier	Porifera	Bubarida	NA	750	0.854
August	Glacier	Rhodophyta	Ceramiales	<i>Rhodomela confervoides</i>	2	1
August	Glacier	Rhodophyta	Palmariales	NA	8	0.252
August	Hansneset	Annelida	Phyllocladida	<i>Pholoe baltica</i>	8	1
August	Hansneset	Annelida	Polychaeta	<i>Polydora onagawaensis</i>	21	0.009
August	Hansneset	Annelida	Spionida	<i>Amphitrite cirrata</i>	33	0.372
August	Hansneset	Annelida	Terebellida	<i>Sabellidae sp. CMC02</i>	17	0.875
August	Hansneset	Arthropoda	Decapoda	<i>Hyas araneus</i>	14	0.043
August	Hansneset	Bryozoa	Chelostomatida	<i>Cauloramphus magnus</i>	3	1
August	Hansneset	Bryozoa	Chelostomatida	<i>Dendrobaemia murrayana</i>	3	1
August	Hansneset	Bryozoa	Chelostomatida	<i>Tricellaria ternata</i>	7	1
August	Hansneset	Chordata	Stolidobranchia	NA	21	0.089
August	Hansneset	Cnidaria	Stolidobranchia	<i>Halocynthia pyriformis</i>	18	0.353
August	Hansneset	Cnidaria	Siphonophorae	<i>Apolemia sp. BO-2009</i>	264	0.688
August	Hansneset	Echinodermata	Ophiurida	<i>Ophiopholis aculeata</i>	1618	1
August	Hansneset	Echinodermata	Echinoidea	<i>Strongylocentrotus pallidus</i>	183	0.430
August	Hansneset	Echinodermata	Echinoidea	NA	1	0.688
August	Hansneset	Mollusca	Adapedonta	<i>Hiatella arctica</i>	110	0.038
August	Hansneset	Mollusca	Adapedonta	<i>Hiatella sp. K HML-2015</i>	21	0.056
August	Hansneset	Mollusca	Myioida	<i>Chordaria chordaeformis</i>	2	1
August	Hansneset	Ochrophyta	Ectocarpales	NA	311	0.095
August	Hansneset	Ochrophyta	Ectocarpales	<i>Microspangium alariae</i>	17	0.350
August	Hansneset	Porifera	Pocilloclerida	<i>Ceella elegans</i>	12	1
August	Hansneset	Porifera	Suberitida	<i>Halichondria panicea</i>	196	1
August	Hansneset	Porifera	Bubarida	NA	535	0.228
August	Hansneset	Rhodophyta	Acrochaetiales	<i>Acrochaetium secundatum</i>	2	1
August	Hansneset	Rhodophyta	Ceramiales	<i>Savoiea arctica</i>	29	1
August	Hansneset	Rhodophyta	Palmariales	NA	19	0.224
August	Hansneset	Rhodophyta	Palmariales	<i>Devaleraca ramentacea</i>	17	0.360
August	Hansneset	Rhodophyta	Palmariales	<i>Arenicola marina</i>	3	1
August	Hansneset	Rhodophyta	Sabellida	<i>Chitonopoma serrula</i>	3	0.054
August	Hansneset	Annellida	Spionida	<i>Cirratulus cirratus</i>	40	0.107
August	Hansneset	Annellida	Phyllocladida	NA	19	0.200
August	Hansneset	Annellida	NA	NA	13	0.613
August	Hansneset	Bryozoa	Ctenostomatida	<i>Amathia gracilis</i>	61	1
August	Hansneset	Bryozoa	Chelostomatida	<i>Eucratea loricata</i>	3	0.039
August	Hansneset	Bryozoa	NA	NA	2	0.007
August	Hansneset	Chlorophyta	Stolidobranchia	NA	4	0.057
August	Hansneset	Chordata	Stolidobranchia	<i>Halocynthia pyriformis</i>	10	0.068
August	Hansneset	Cnidaria	Anthoathecata	<i>Sarsia princeps</i>	4	0.011
August	Hansneset	Echinodermata	Echinoidea	<i>Strongylocentrotus pallidus</i>	3	0.002
August	Hansneset	Echinodermata	Camarodonta	NA	7	0.088
August	Hansneset	Mollusca	Chitonida	<i>Tonicella undocaculea</i>	3882	1
August	Hansneset	Mollusca	Littorinimorpha	<i>Lucina vincla</i>	5	0.015
August	Hansneset	Mollusca	Myioida	<i>Hiatella sp. K HML-2015</i>	71	0.066
August	Hansneset	Mollusca	Adapedonta	<i>Hiatella arctica</i>	5485	0.665
August	Hansneset	Ochrophyta	Laminariales	NA	119	0.012
August	Hansneset	Ochrophyta	Desmarestiales	NA	71	0.748
August	Hansneset	Porifera	Bubarida	NA	263	0.038
August	Hansneset	Porifera	Haploclerida	NA	4	0.521
August	Hansneset	Rhodophyta	Haploclerida	<i>Leptophyllum laeve</i>	7	1
August	Hansneset	Rhodophyta	Palmariales	NA	3	0.012
August	Hansneset	Annellida	NA	<i>Polydora onagawaensis</i>	16	1
August	Hansneset	Annellida	Sabellida	<i>Paradeixiospira vitrea</i>	5	0.275
August	Hansneset	Annellida	Phyllocladida	NA	23	0.566
August	Hansneset	Bryozoa	Cyclotomatida	<i>Crisia eburnea</i>	12	0.260
August	Hansneset	Bryozoa	Chelostomatida	<i>Tricellaria circumternata</i>	14	0.787
August	Hansneset	Chlorophyta	Ulotrichales	NA	61	0.190
August	Hansneset	Chordata	Stolidobranchia	<i>Pelonaia corrugata</i>	13	0.151
August	Hansneset	Chordata	Stolidobranchia	<i>Dendroba grossularia</i>	4	0.165
August	Hansneset	Cnidaria	Siphonophorae	<i>Apolemia sp. BO-2009</i>	11	0.021
August	Hansneset	Echinodermata	Apodida	NA	89	1
August	Hansneset	Mollusca	Adapedonta	<i>Hiatella arctica</i>	3886	1
August	Hansneset	Mollusca	Chitonida	<i>Tonicella undocaculea</i>	35	0.019
August	Hansneset	Mollusca	Cardida	NA	32	0.978
August	Hansneset	Ochrophyta	Ectocarpales	NA	11	0.052
August	Hansneset	Ochrophyta	Laminariales	NA	414	0.094
August	Hansneset	Ochrophyta	Ectocarpales	<i>Pyraliella littoralis</i>	9	0.104
August	Hansneset	Ochrophyta	Desmarestiales	NA	18	0.402
August	Hansneset	Porifera	Bubarida	NA	61	0.019
August	Hansneset	Porifera	Suberitida	NA	5	0.084
August	Hansneset	Rhodophyta	Haploclerida	NA	2	0.079
August	Hansneset	Rhodophyta	Palmariales	NA	29	0.252

Month	Site	Phylum	Order	Species	nReads	eDNA Index	Month	Site	Phylum	Order	Species	nReads	eDNA Index
June	Ossian Sars	Ochrophyta	Laminariales	NA	2295	0.628	July	Glacier	Mollusca	Hydrophilia	<i>Biomphalaria oligoza</i>	6	0.094
June	Ossian Sars	Ochrophyta	Laminariales	<i>Halosiphon tomentosus</i>	95	0.877	July	Glacier	Mollusca	Veneroida	<i>Macoma calcareo</i>	4	0.124
June	Ossian Sars	Porifera	Haplosclerida	NA	3	1	July	Glacier	Mollusca	Myioida	<i>Hiatella sp. K HML-2015</i>	20	0.229
June	Ossian Sars	Porifera	Suberitida	<i>Halichondria panicea</i>	2	0.009	July	Glacier	Mollusca	Littorinimorpha	<i>Lacuna vineta</i>	9	0.342
June	Ossian Sars	Porifera	Bubaria	NA	187	0.070	July	Glacier	Ochrophyta	Ecocarpaceae	<i>Actinospiraceae sp. 1 AP-2016</i>	2	1
June	Ossian Sars	Porifera	Suberitida	NA	14	0.284	July	Glacier	Ochrophyta	Laminariales	NA	122	0.159
June	Ossian Sars	Rhodophyta	Hapalidiales	NA	21	1	July	Glacier	Ochrophyta	Ecocarpaceae	<i>Pyraliella littoralis</i>	17	0.572
June	Ossian Sars	Rhodophyta	Palmariales	<i>Rhodomela confervoides</i>	90	0.243	July	Glacier	Porifera	Suberitida	<i>Halichondria panicea</i>	18	0.390
June	Ossian Sars	Rhodophyta	Ceramiales	NA	11	0.665	July	Glacier	Porifera	Suberitida	NA	8	0.777
July	Ossian Sars	Rhodophyta	NA	NA	49	0.945	July	Glacier	Porifera	Bubaria	NA	450	0.815
July	Bloomstrand Est	Amnelliida	Phyllocladida	<i>Tricellaria circumternata</i>	5	0.196	July	Glacier	Rhodophyta	Corallinales	NA	5	1
July	Bloomstrand Est	Bryozoa	Cheilostomatida	<i>Crisia eburnea</i>	26	0.395	July	Hansneset	Amnelliida	Spionida	<i>Polydora onagawaensis</i>	99	0.118
July	Bloomstrand Est	Bryozoa	Cyclostomatida	NA	45	0.098	July	Hansneset	Chlorophyta	Ultrichales	NA	60	0.067
July	Bloomstrand Est	Chlorophyta	Ultrichales	NA	5	0.145	July	Hansneset	Cnidaria	Siphonophorae	<i>Apoletmia sp. BO-2009</i>	6	0.413
July	Bloomstrand Est	Chordata	Stolidobranchia	<i>Dendrodoa grossularia</i>	18	0.147	July	Hansneset	Echinodermata	Ophiurida	<i>Ophiopholis aculeata</i>	7	0.011
July	Bloomstrand Est	Chordata	Stolidobranchia	<i>Peloniaia corrugata</i>	6	0.112	July	Hansneset	Echinodermata	Echinoidea	<i>Strongylocentrotus pallidus</i>	19	0.118
July	Bloomstrand Est	Echinodermata	Camarodonta	NA	29	0.228	July	Hansneset	Mollusca	Myioida	<i>Hiatella sp. K HML-2015</i>	140	1
July	Bloomstrand Est	Echinodermata	Apodida	NA	6	0.002	July	Hansneset	Mollusca	Adapedonta	<i>Hiatella arctica</i>	30	0.027
July	Bloomstrand Est	Mollusca	Chitonida	<i>Toniceila undacaerulea</i>	4389	0.791	July	Hansneset	Mollusca	Hydrophilia	<i>Biomphalaria oligoza</i>	51	0.497
July	Bloomstrand Est	Mollusca	Adapedonta	<i>Hiatella arctica</i>	18	0.057	July	Hansneset	Mollusca	Myioida	NA	11	0.516
July	Bloomstrand Est	Ochrophyta	Ecocarpaceae	NA	22	0.118	July	Hansneset	Mollusca	Myioida	NA	12	0.652
July	Bloomstrand Est	Ochrophyta	Laminariales	<i>Halosiphon tomentosus</i>	14	0.119	July	Hansneset	Porifera	Ecocarpaceae	<i>Microspongium alariiae</i>	888	1
July	Bloomstrand Est	Ochrophyta	Ecocarpaceae	<i>Pyraliella littoralis</i>	13	0.203	July	Hansneset	Porifera	Bubaria	NA	4	0.053
July	Bloomstrand Est	Ochrophyta	Desmarrestiales	NA	2066	0.328	July	Kongsfjordneset	Porifera	Suberitida	<i>Halichondria panicea</i>	7	1
July	Bloomstrand Est	Ochrophyta	Laminariales	NA	58	0.012	July	Kongsfjordneset	Amnelliida	NA	<i>Scalibregma inflatum</i>	209	0.000
July	Bloomstrand Est	Porifera	Bubaria	NA	10	0.118	July	Kongsfjordneset	Amnelliida	NA	<i>Polydora onagawaensis</i>	6	0.478
July	Bloomstrand Est	Porifera	Suberitida	NA	9	0.249	July	Kongsfjordneset	Amnelliida	NA	NA	7	1
July	Bloomstrand Est	Rhodophyta	Hapalidiales	NA	4	0.043	July	Kongsfjordneset	Arthropoda	NA	NA	7	1
July	French Bird Cliff	Amnelliida	Phyllocladida	NA	2	0.061	July	Kongsfjordneset	Chlorophyta	NA	NA	484	1
July	French Bird Cliff	Amnelliida	NA	NA	3	0.118	July	Kongsfjordneset	Mollusca	Adapedonta	<i>Hiatella arctica</i>	499	0.033
July	French Bird Cliff	Bryozoa	Terebellida	<i>Amphitrite cirrata</i>	6	0.321	July	Kongsfjordneset	Ochrophyta	Laminariales	NA	16949	1
July	French Bird Cliff	Bryozoa	Cyclostomatida	<i>Crisia eburnea</i>	5	0.345	July	Kongsfjordneset	Ochrophyta	Ecocarpaceae	NA	23	0.056
July	French Bird Cliff	Chlorophyta	Cheilostomatida	<i>Euratea loricata</i>	82	0.058	July	Kongsfjordneset	Porifera	Bubaria	NA	129	0.010
July	French Bird Cliff	Chlorophyta	Ultrichales	NA	3	0.632	July	Ossian Sars	Amnelliida	NA	<i>Arenicola marina</i>	5	1
July	French Bird Cliff	Chordata	Stolidobranchia	<i>Peloniaia corrugata</i>	8	0.230	July	Ossian Sars	Amnelliida	Terebellida	<i>Spinosphaera hutchingsae</i>	4	0.379
July	French Bird Cliff	Chordata	Stauroumedusae	<i>Lucernaria quadricornis</i>	2	1	July	Ossian Sars	Amnelliida	Sabellida	NA	17	0.549
July	French Bird Cliff	Echinodermata	Amphipleurida	NA	19	0.992	July	Ossian Sars	Amnelliida	Phyllocladida	NA	92	0.629
July	French Bird Cliff	Mollusca	Chitonida	<i>Toniceila undacaerulea</i>	12	0.016	July	Ossian Sars	Amnelliida	NA	NA	70	0.737
July	French Bird Cliff	Mollusca	Myioida	NA	7	0.226	July	Ossian Sars	Arthropoda	Terebellida	<i>Amphitrite cirrata</i>	135	0.978
July	French Bird Cliff	Mollusca	Adapedonta	<i>Hiatella arctica</i>	1179	0.748	July	Ossian Sars	Arthropoda	Decapoda	<i>Hyas araneus</i>	3	0.006
July	French Bird Cliff	Ochrophyta	Ecocarpaceae	NA	12	0.100	July	Ossian Sars	Arthropoda	Euphausiacea	NA	281	0.326
July	French Bird Cliff	Ochrophyta	Laminariales	<i>Pyraliella littoralis</i>	383	0.214	July	Ossian Sars	Bryozoa	Cheilostomatida	<i>Tricellaria circumternata</i>	20	1
July	French Bird Cliff	Ochrophyta	Ecocarpaceae	<i>Halosiphon tomentosus</i>	7	0.281	July	Ossian Sars	Chlorophyta	Ultrichales	<i>Ulvelia leptochaete</i>	4	0.154
July	French Bird Cliff	Porifera	Poecilosclerida	<i>Myxilla incrustans</i>	9	0.415	July	Ossian Sars	Chlorophyta	Ultrichales	NA	77	0.214
July	French Bird Cliff	Porifera	Bubaria	NA	130	0.100	July	Ossian Sars	Chordata	Urochordata	<i>Dendrodoa grossularia</i>	23	0.848
July	French Bird Cliff	Porifera	Suberitida	NA	3	0.124	July	Ossian Sars	Cnidaria	Leptothecata	<i>Orthopyxis integra</i>	2	1
July	French Bird Cliff	Porifera	Dendroceratida	<i>Halissarca dulardinii</i>	3	0.523	July	Ossian Sars	Cnidaria	Anthoathecata	<i>Zanicia implexa</i>	2	1
July	French Bird Cliff	Rhodophyta	Palmariales	NA	26	0.559	July	Ossian Sars	Cnidaria	Anthoathecata	<i>Sarsia princeps</i>	3	0.016
July	Glacier	Amnelliida	Spionida	<i>Polydora onagawaensis</i>	16	0.030	July	Ossian Sars	Cnidaria	Siphonophorae	<i>Apoletmia sp. BO-2009</i>	24	0.041
July	Glacier	Amnelliida	Phyllocladida	NA	2	0.137	July	Ossian Sars	Echinodermata	Ophiurida	<i>Ophiopholis aculeata</i>	7	0.002
July	Glacier	Amnelliida	Terebellida	<i>Amphitrite cirrata</i>	9	0.432	July	Ossian Sars	Echinodermata	Echinoidea	<i>Strongylocentrotus pallidus</i>	10	0.015
July	Glacier	Amnelliida	Capitellida	<i>Arenicola marina</i>	2	0.634	July	Ossian Sars	Echinodermata	Camarodonta	NA	19	0.452
July	Glacier	Arthropoda	Balanomorpha	<i>Chthamalus fragilis</i>	2	1	July	Ossian Sars	Mollusca	Chitonida	<i>Toniceila undacaerulea</i>	224	0.108
July	Glacier	Bryozoa	Cyclostomatida	<i>Crisia eburnea</i>	4	0.500	July	Ossian Sars	Mollusca	Adapedonta	<i>Hiatella arctica</i>	899	0.205
July	Glacier	Chlorophyta	Ulvelae	NA	4	1	July	Ossian Sars	Mollusca	Myioida	NA	23	0.267
July	Glacier	Chordata	Stolidobranchia	<i>Halocynthia pyramis</i>	12	1	July	Ossian Sars	Mollusca	Trochida	<i>Margarites helacinus</i>	8	0.536
July	Glacier	Chordata	Phlebobranchia	NA	4	1	July	Ossian Sars	Mollusca	Myioida	<i>Hiatella sp. K HML-2015</i>	319	0.565
July	Glacier	Chordata	Stolidobranchia	<i>Peloniaia corrugata</i>	6	0.403	July	Ossian Sars	Mollusca	Cardida	NA	26	0.706
July	Glacier	Echinodermata	Dendrochirotrida	<i>Cucumaria frondosa</i>	3	1	July	Ossian Sars	Ochrophyta	Ecocarpaceae	NA	43	0.362
July	Glacier	Echinodermata	Echinoidea	<i>Strongylocentrotus pallidus</i>	100	1	July	Ossian Sars	Ochrophyta	Laminariales	NA	2015	0.407
July							July	Ossian Sars	Ochrophyta	Laminariales	<i>Halosiphon tomentosus</i>	68	0.463
July							July	Ossian Sars	Ochrophyta	Desmarrestiales	NA	34	0.675

Table S20: Paired Hutchinson tests' p-values for testing the significance of the difference between Shannon diversity of macroalgae and fauna for different periods (i.e., all periods combined, June, July, and August). Statistical significances are highlighted in gray (p-value < 0.5). Shannon diversity indexes are also indicated (H').

Macroalgae

All periods	H'	Kongsbreen South	Ossian Sars	Bloomstrand East	Hansneset	French Bird Cliff	Kongsfjordneset
Kongsbreen South	2.04	NA					
Ossian Sars	2.2	0.002	NA				
Bloomstrand East	1.74	0.001	0.000	NA			
Hansneset	1.83	0.001	0.000	0.178	NA		
French Bird Cliff	1.93	0.050	0.000	0.038	0.118	NA	
Kongsfjordneset	1.11	0.000	0.000	0.003	0.001	0.000	NA
June	H'	Kongsbreen South	Ossian Sars	Bloomstrand East	Hansneset	French Bird Cliff	Kongsfjordneset
Kongsbreen South	1.5	NA					
Ossian Sars	1.8	0.079	NA				
Bloomstrand East	1.2	0.096	0.011	NA			
Hansneset	NA	NA	NA	NA	NA		
French Bird Cliff	1.58	0.340	0.182	0.065	NA	NA	
Kongsfjordneset	1.1	0.005	0.000	0.278	NA	0.007	NA
July	H'	Kongsbreen South	Ossian Sars	Bloomstrand East	Hansneset	French Bird Cliff	Kongsfjordneset
Kongsbreen South	1.59	NA					
Ossian Sars	2.17	0.000	NA				
Bloomstrand East	1.63	0.458	0.081	NA			
Hansneset	0.69	0.000	0.000	0.018	NA		
French Bird Cliff	1.63	0.436	0.020	0.499	0.002	NA	
Kongsfjordneset	0.69	0.000	0.000	0.018	NA	0.002	NA
August	H'	Kongsbreen South	Ossian Sars	Bloomstrand East	Hansneset	French Bird Cliff	Kongsfjordneset
Kongsbreen South	1.3	NA					
Ossian Sars	1.76	0.057	NA				
Bloomstrand East	1.36	0.388	0.050	NA			
Hansneset	1.72	0.057	0.441	0.041	NA		
French Bird Cliff	1.43	0.344	0.179	0.402	0.196	NA	
Kongsfjordneset	1.08	0.165	0.007	0.042	0.003	0.133	NA

Fauna

All periods	H'	Kongsbreen South	Ossian Sars	Bloomstrand East	Hansneset	French Bird Cliff	Kongsfjordneset
Kongsbreen South	2.76	NA					
Ossian Sars	3.18	0.023	NA				
Bloomstrand East	2.53	0.229	0.016	NA			
Hansneset	2.59	0.209	0.000	0.408	NA		
French Bird Cliff	2.55	0.230	0.008	0.467	0.437	NA	
Kongsfjordneset	2.17	0.090	0.018	0.216	0.150	0.189	NA
June	H'	Kongsbreen South	Ossian Sars	Bloomstrand East	Hansneset	French Bird Cliff	Kongsfjordneset
Kongsbreen South	2.38	NA					
Ossian Sars	2.95	0.011	NA				
Bloomstrand East	2.53	0.263	0.002	NA			
Hansneset	1.3	0.007	0.001	0.005	NA		
French Bird Cliff	2.61	0.153	0.007	0.237	0.004	NA	
Kongsfjordneset	1.62	0.005	0.000	0.001	0.191	0.001	NA
July	H'	Kongsbreen South	Ossian Sars	Bloomstrand East	Hansneset	French Bird Cliff	Kongsfjordneset
Kongsbreen South	2.66	NA					
Ossian Sars	2.95	0.011	NA				
Bloomstrand East	1.88	0.002	0.000	NA			
Hansneset	2.05	0.001	0.000	0.247	NA		
French Bird Cliff	2.29	0.014	0.000	0.049	0.093	NA	
Kongsfjordneset	1	0.001	0.001	0.009	0.004	0.002	NA
August	H'	Kongsbreen South	Ossian Sars	Bloomstrand East	Hansneset	French Bird Cliff	Kongsfjordneset
Kongsbreen South	1.69	NA					
Ossian Sars	2.35	0.006	NA				
Bloomstrand East	1.87	0.343	0.139	NA			
Hansneset	2.44	0.003	0.282	0.103	NA		
French Bird Cliff	1.59	0.325	0.000	0.258	0.000	NA	
Kongsfjordneset	2.12	0.105	0.225	0.300	0.148	0.050	NA

Conclusion

1. Main findings and limits

Arctic benthic communities are experiencing rapid changes. Warming, hyposalinity, underwater light changes, high sedimentation, coastal turbidity, and other environmental changes are modifying the water column and ocean bottom characteristics, reshaping ecosystems. Given the importance of macroalgal communities for the rest of the Arctic ecosystem as well as for local communities and fisheries, there is an urgent need to evaluate their response to climate change and their capacity to maintain their key ecological functions such as habitat, food source, and nursing ground for various species. This thesis aimed to enhance our knowledge and understanding of the response of these communities to climate change. In this final section, we will discuss the main findings and potential avenues for improving our projection before concluding and proposing future research directions.

Macroalgal communities are already profoundly affected by climate change in the Arctic. The first chapter aimed at synthesizing the current knowledge and assessing knowledge gaps. In particular, we found that multi-factorial studies on macroalgal communities are still scarce in the Arctic while crucial. This thesis work was built upon these gaps to enhance our understanding of the responses of these communities to climate change and project their future in the Arctic.

1.1. How will Arctic kelps respond to the direct effects of climate change?

1.1.1. Main results

In light of the pressing concerns about climate change's impacts, chapters 2 and 3 aimed at investigating the response of Arctic kelp communities to warming, marine heat waves, and ice melting. The kelp species we studied are also known to inhabit regions at lower latitudes. Given the higher temperature found in these lower latitude regions such as Brittany where seawater temperature can exceed 18°C, the mild response of kelps to the warming treatments in our two studies is not really surprising (Chevallier et al., 2014). The addition of hyposalinity

and reduced underwater light conditions did not induce an overall negative impact on these species (chapter 2). Warming appears to be the key factor impacting these organisms, effectively outweighing potential negative effects caused by ice melting, at least over a two-month period and on the measured parameters. However, our results do not demonstrate a beneficial effect of warming alone.

In addition to warming, short and intense thermal stress caused by marine heat waves (MHWs) could have negative effects on kelp species. Kelps are known to have species-specific responses to such stressful events (Arafeh-Dalmau et al., 2019; Thomsen et al., 2019). Our results highlight the tolerance of both kelp and fauna species to MHWs.

All three species demonstrated a remarkable ability to acclimate to the conditions anticipated for 2100, endorsing the hypothesis that their expansion in the Arctic will continue with warming and the emergence of new habitats resulting from ice melting. However, it is important to acknowledge that variations exist between the acclimation abilities of the kelp species studied leading to differing dominance patterns in various areas. For instance, *Alaria esculenta*, which exhibits a higher chl *a* content in low light environments, is the only species who extends in depth in Kongsfjorden (down to 18 m depth, Bartsch et al., 2016; Inka Bartsch and Luisa Düsedau pers. com.) Also, due to its lack of response to MHW treatments, *Laminaria digitata* may thrive in areas subjected to those events such as very shallow areas. The tolerance of this species to MHWs could allow it to outcompete other macroalgae that may be more vulnerable to extreme temperature events. For *Saccharina latissima*, we did not observe any physiological benefit from the condition tested in contrast to the other two species. However, this species has already shown significant expansion in the Arctic (Krause-Jensen and Duarte, 2014), and our study highlights its high tolerance to climate change. Our results show growth rates 3 to 10 times higher for *Saccharina latissima* than for the two other species. Its rapid growth could lead to increased competition for resources with other kelps, potentially leading to shifts in local kelp community composition.

The substantial dominance of one kelp species over others in certain areas could have significant ecological implications for the ecosystem. A decrease in diversity poses a risk, making the ecosystem less resilient. In a more diverse ecosystem, when a species is adversely impacted by a disturbance or disease, other species can step in and fulfill comparable ecological roles, ensuring the overall functioning of the ecosystem is sustained (Mori et al.,

2013). However, this is not the case in a less diverse ecosystem. Furthermore, herbivores, such as urchins or gastropods actively select a combination of various food sources that not only promote their growth but also support successful reproduction (Watanabe, 1984; Lyons and Scheibling, 2008). This tendency towards a varied diet allows them to efficiently meet their nutritional requirements, leading to their overall well-being and flourishing within the ecosystem. Thus, a pronounced dominance of a single kelp species could have negative consequences. Further experimental studies need to be undertaken to investigate this.

1.1.2. Constraints and limits of the two perturbation experiments

Some limits and constraints must be considered to analyze our results. During the two perturbation experiments in mesocosms, we encountered several issues that are worth mentioning here to suggest possible improvements.

It is important to acknowledge that, in Kongsfjorden, we have not been able to sample the only endemic kelp species, *Laminaria solidungula*. This species seems to not be able to acclimate to climate change (e.g. Müller et al., 2009; Diehl et al., 2020). Investigating this species during our multifactorial experiment (chapter 2) would have been interesting to compare it with non-endemic species. Over time, *L. solidungula* has become more and more difficult to find in the fjord (Kai Bischof, pers. comm.). It is difficult to conclude on an effect of climate change without strong environmental and biological data to support it, but several studies suggest a possible decline of this species with warming (e.g. Müller et al., 2009; Diehl et al., 2020).

For the second mesocosm experiment, the original idea was to conduct the same multifactorial experiment as in Kongsfjorden but in Porsanger (70.5°N, 25.5°E), a low Arctic fjord, to compare the responses of high vs. low Arctic communities. Porsanger fjord is one of the sites selected by the FACE-IT project. It has several interesting characteristics, particularly because it experiences low anthropogenic impacts and it is a boreal fjord without glaciers where sea ice forms during winter (Cieszyńska and Stramska, 2018). This fjord could therefore offer a glimpse into what could be Kongsfjorden following the disappearance of its sea-terminating glaciers. However, the research station in Porsanger was finally not able to accommodate our experiment due to technical reasons. We reconsidered the design and chose to focus on the Tromsø area. This archipelago does not experience significant local decreases in salinity and light due to currents (Białogrodzka et al., 2018). Therefore, the goal

was no longer to make a direct comparison between locations but rather to explore a new factor related to warming, which is the occurrence of MHWs. Upon our arrival in Tromsø in June 2022, a MHW occurred, further validating our interest in studying MHWs and their impact on benthic shallow communities that are directly impacted by these events.

The kelps present in the waters of Tromsø have been decimated by sea urchins (Sivertsen, 2006; pers. obs.). It was challenging to find a sufficient number of individuals to fill the mesocosms. The only kelp individuals we found were located in isolated areas with strong currents out of the reach of sea urchins. Divers had to explore a large area to locate kelp populations unaffected by sea urchins. Most of the individuals of *Saccharina latissima* and *Alaria esculenta* were very young (about 30 cm long) and were not sampled. Because we did not find individuals at the desired depth of 7-8 m, the individuals were collected shallower (up to 2 m). These individuals are influenced by tides and are already adapted to more variable temperature conditions. The general conclusion of this experiment is that the kelps we studied are tolerant to MHWs. However, their responses were species-specific, suggesting different acclimation capacities.

For both studies, we conducted the experiment in summer, while spring is the actual optimal growth period of kelp species. Hence, our findings may not fully capture the responses of these species. Conducting the same experiments in spring could have led to higher growth rate and possibly to significant variations between the control and the treatments. The same observations may also be done with the photosynthesis rate or chl *a* content. However, conducting such experiments in the Arctic during spring is logistically more complicated due to the harsh climate and effects of ice melting, the focus of our experiment, are heightened during the summer months.

In Kongsfjorden, challenges related to the handling of *Alaria esculenta* were encountered. It exhibited increased fragility during the final two weeks of the experiment (mid to late August). This fragility was exacerbated by the onset of senescence, typically observed towards the end of summer in this high Arctic area (Inka Bartsch, pers. comm.), making measurements particularly difficult. During fall and winter, this species experiences a significant loss of tissue until the next growth period. In Tromsø, by conducting the experiment in July only, we avoided the period of heightened fragility of this species observed in the previous study.

In these two mesocosm experiments, the aim was to measure a large number of parameters to ensure a comprehensive understanding of the response of kelps to different environmental conditions. We incorporated molecular tools such as gene expression analysis and the assessment of epiphytic kelp microbiome diversity for the study conducted in Ny-Ålesund. However, the complexity of the extraction processes and logistical challenges resulted in a delay, preventing the integration of microbiome analysis results into this manuscript. This collaboration with Rui Zhang and Yunlan Yang (members of the FACE-IT project, Xiamen University, China) is on-going. The results will be published in a subsequent article.

Additionally, we conducted individual incubations to assess the net photosynthesis of the three kelp species. Unfortunately, the O₂ sensor malfunctioned for a significant number of incubations during the first experiment in Ny-Ålesund, failing to detect linear trends and instead displaying erratic spikes without any discernible patterns. After excluding abnormal profiles, the number of replicates became insufficient (down to only one per species and treatment) and the inter-individual variability too high to work with such a limited number of replicates. As a result, the photosynthesis data could not be used. It would have been valuable to compare our results for the warming treatment with those of Olischläger et al. (2017) which reported an increase in photosynthetic rate with temperature for *Saccharina latissima*. Furthermore, the combined effects of decreased light and salinity might have influenced the response of photosynthesis to warming. The quantum yield of *Laminaria solidungula* sporophytes significantly decreases when exposed to a temperature of 15°C combined with low salinity (25), as compared to the effects of warming alone (Diehl et al., 2020). During the MHWs experiment, photosynthetic rates were successfully measured. We acquired a new measurement system and reduced the number of species (from 3 to 2) to increase the number of replicates for the selected species. However, we encountered high variability between replicates, making it challenging, if not impossible, to detect treatment effects. As discussed previously, conducting this experiment in summer might have reduced the magnitude of the response, further limiting our ability to detect any treatment effects.

In both experiments, we focused on various parameters related to kelp growth and photosynthesis. While these parameters provided valuable insights, additional measurements of other pigments and storage molecules concentration like phlorotannin or mannitol which play essential roles in stress responses and defense mechanisms (Diehl et al., 2020) would

have further enhanced our understanding of the observed tolerance mechanisms. Investigating the reproductive mechanisms of kelps, which occur in summer or in autumn, would also help predict future kelp communities. Indeed, understanding the effects of future conditions on reproduction could shed light on their adaptive potential and long-term sustainability.

Regarding the faunal-associated communities, we were unable to sample a large portion of the associated fauna in Kongsfjorden which led us to shift our focus solely to kelps. The only taxa that we had in significant quantities in our mesocosms were sea urchins. Lipid content analysis of sea urchins and kelps will be the topic of another article led by Simon Jungblut (Bremen University). In Tromsø, we were able to sample several species associated with kelps (sea urchins, snails, mussels, and coralline algae). Unfortunately, time constraints limited us to only measuring their growth rate which was not significantly affected by the experimental treatments. Further measurements such as lipid content, gene expression analyses, or reproduction would enable to conclude on the tolerance of these organisms to warming and MHWs.

Mesocosm experiments provide a controlled set-up to replicate environmental conditions and manipulate specific variables to study their effects on kelp communities. Moreover, mesocosms offer the advantage of replication, increasing statistical robustness and facilitating the establishment of cause-and-effect relationships. Also, the environmental variability can be considered through the utilization of differentials (e.g., in temperature, in salinity) with *in situ* conditions. However, mesocosm experiments do have certain limitations. Simulated conditions may not fully capture the complexity and biological variability of Arctic kelp ecosystems. Not all interacting factors, such as species interactions and the presence of predators, were accounted for. Additionally, the volume of mesocosms is limited, which may restrict the ability to capture the entirety of large-scale ecological processes that shape kelp communities.

While ongoing warming may increase the area with suitable environmental conditions for kelps, further *in situ* research is needed to investigate the long-term effects of climate change at the community level, and how it may influence the distribution and abundance of kelp and associated faunal species in the future. To address this issue, we conducted an *in situ* study in Kongsfjorden to explore the links between environmental factors and benthic diversity.

Complementarily to mesocosm experiments, *in situ* studies allow for direct observation of Arctic kelps communities in their natural environment, providing a more comprehensive and ecologically realistic view of the communities. *In situ* monitoring considers the intricacies of biotic and abiotic interactions. Furthermore, large-scale observations enable the study of spatial and temporal variations in kelp communities, which are crucial for understanding diversity patterns and responses to long-term environmental changes.

1.2. How do environmental factors influence the diversity patterns of Arctic coastal benthic communities?

The purpose of the last chapter was to characterize potential variations in community composition associated with a natural gradient of environmental conditions. We found no direct correlation between benthic diversity and environmental conditions. However, in contrast to many studies, biodiversity was higher in the inner part than in the outer of the fjord, which could be explained by the presence of predators such as seabirds and sea lions near the glaciers. These predators play a crucial role in regulating the ecosystem through top-down control, which may in turn further increase its diversity.

As mentioned previously, we encountered several obstacles when conducting this study. The issues related to poor sequencing quality of part of the replicates have already been extensively discussed in the chapter and will, therefore, not be addressed again here.

In addition to eDNA, we deployed Autonomous Reef Monitoring Structures (ARMS) in triplicates at four out of the six selected sites along the fjord. These PVC-plates recruitment structures would have allowed us to assess diversity and recruitment rates over a year (June 2021 to September 2022). However, we only recovered fragments from two out of the 12 structures. Consequently, the original plan had to be abandoned. The recovered ARMS were partially buried in sediment and damaged by icebergs. We suspect that the structures which were not found experienced a similar fate. For future research, an alternative method would be to secure the ARMS to rocks in iceberg-protected areas along the coastline such as deeper areas or coves.

Therefore, this *in situ* study would benefit from being repeated. Molecular tools, including eDNA or transcriptomics, as used in chapter 2, provide an overview of biodiversity and adaptation mechanisms by identifying species and acclimation through changes in metabolic

pathways, respectively. This enables a better understanding of spatial and temporal variations in kelp communities with changes in environmental conditions. In particular, in addition to being non-invasive, eDNA offers increased sensitivity and enables the detection of rare or cryptic species that would be difficult to observe during conventional surveys. Despite its many advantages, eDNA also has some disadvantages. These include the costs and the challenges of translating data into quantitative results. However, integrating other methods with molecular approaches can help overcome some challenges. For example, simultaneous monitoring through direct observation alongside eDNA analysis can allow to establish equations to link the number of sequences (reads) to the number of individuals (Ushio et al., 2017). Nevertheless, this process is time-consuming and requires a specific protocol for each taxa.

To improve our study and confirm or refute our hypothesis that trophic networks near glaciers are more complex and thus more diverse, it would be interesting to use isotopic measurements such as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ taken from particulate organic matter and animal tissue along the fjord, for tracking the food web structure. This would enable us to gain valuable insights into the trophic interactions among different organisms in the ecosystem.

2. General discussion

Although the two mesocosm experiments we conducted concluded on non-negative effects of climate change on kelp species, the *in situ* analysis provided a more nuanced perspective by considering the influence of predators and the cascading effect on the ecosystem. In addition to the direct effects of climate change, such as temperature increases, changes in light regimes, decreasing salinity, and increasing MHWs intensity and frequency as discussed in the first three chapters, it is crucial to expand our focus to a broader temporal and spatial scale. This entails examining the entire ecosystem over an extended period of time.

Warming is accompanied by the melting of sea and terrestrial ice. In the short term, the increased water turbidity triggers local community reshaping by limiting the expansion of some species but giving others such as *Alaria esculenta* a competitive advantage, as previously discussed in Kongsfjorden (Bartsch et al., 2016; Niedzwiedz and Bischof, 2023). Over the longer term, the melting of glaciers and sea ice will expand the potential habitat range for kelps (Wiencke and Hop, 2016), which, as suggested by this thesis work, are projected to be

able to withstand increasing temperatures, MHWs, decreasing salinity and underwater light. However, the disappearance of ice, especially glaciers, which serve as habitats for apex predators, may also lead to the decline of these crucial species responsible for ecosystem regulation (Blundell et al., 2011; Womble and Gende; 2013). This will consequently have implications for macroalgal communities in the Arctic. As mentioned earlier, in Tromsø but also in other Norwegian fjords or in southwest Alaska, the overabundance of sea urchins caused a significant reduction in kelp populations (Hagen, 1983; Sivertsen, 2006; Estes et al., 2009). In Vestfjorden (Norway), the kelp beds underwent complete destruction within a year following the invasion of the urchin *Strongylocentrotus droebachiensis* (Hagen, 1983). Predators of sea urchins such as sea otters, are insufficient in the area to counterbalance the situation (Estes et al., 1998). The shift from kelp forests to barren areas, dominated by sea urchins, has been extensively examined over many years in more temperate areas such as in Australia, Canada, and the USA (Filbee-Dexter and Scheibling, 2014; Rogers-Bennett and Catton, 2019; Carnell and Keough, 2020). Kelp regeneration can occur in areas that are exposed to waves and characterized by warmer temperatures and higher salinity where sea urchins are at a disadvantage (Rinde et al., 2014). In Porsanger, the invasion of the red king crab, after its introduction in the 1960s, has led to a significant increase in predation pressure, particularly on sea urchins (Jørgensen, 2005). This invasion proved advantageous for kelp forests, but disrupted the entire ecosystem, notably leading to the decline of the Norwegian coastal cod (Christie et al., 2019).

Predicting the future Arctic ecosystem is not easy and must be done on a case-by-case basis, considering both the species present and the particularities of the study area. Fucus could experience a similar fate to kelps with the expansion of their habitat and local increases in predation pressures by gastropods and sea urchins (Jueterbock et al., 2016). Regarding coralline algae, the expected decrease in pH and warming might cause their decline in the Arctic (Steinacher et al., 2009; Chan et al., 2020). Moreover, the competition for space with kelps could accelerate the decline of coralline algae and their associated communities, potentially leading to ecosystem restructuring and the loss of vital functions by the end of this century (Brodie et al., 2014).

In addition to the direct and indirect effects of climate change on these ecosystems, it is important to consider their global implications. As mentioned earlier, the Arctic holds

significant importance in various aspects such as in supporting important fishing stocks and contributing to global climate patterns. In recent years, the melting of ice has created new opportunities for sea bed mining, shipping, and fisheries with the emergence of new ice-free areas (Tai et al., 2019; Li and Lynch, 2023). According to Lam et al. (2014), projections indicate a potential 39% increase in total fisheries revenue in the Arctic region by 2050 compared to the baseline year of 2000. However, several important fish species, including haddock, herring, cod, walleye pollock, rockfish, salmon, and flatfish, depend on kelp forests for their adult or juvenile stages (Johnson, 2003; Mueter, 2022). These species are potentially at risk due to the potential loss of their critical habitat in areas such as urchin barrens (Johnson, 2003; Mueter, 2022). Moreover, the intrusion of competitive or predatory species into these habitats could further exacerbate their decline. The highest species turnover in the world, including both invading and locally extinct species, among fishes and invertebrates, would occur in the Arctic region by 2050 (Cheung et al., 2009). According to Mueter et al. (2021), we are likely to observe the development of new fisheries, accompanied by new difficulties in the management of transboundary fish stocks, which could result in conflicts among those who rely on these resources. The shift in fish populations is leading to substantial disruption in local communities, such as the Inuit, who are additionally experiencing a reduced fishing season due to the rapid melting of sea ice and the delayed formation of new ice (Galappaththi et al., 2019). These circumstances can have detrimental effects on the economy and well-being of these communities. It is worth noting that kelps are an important seasonal resource holding significance for the health, culture, and overall well-being of local human communities.

The impact of climate change such as melting ice and circulation changes could undermine the role of the Arctic in mitigating global warming (Tomas et al., 2016; Huang et al., 2017; Timmermans and Marshall, 2020). The potential of kelps for carbon sequestration is hotly debated among scientists (Filbee-Dexter and Wernberg, 2020; Hurd et al., 2022). In recent years, various companies engaged in kelp farming, as well as scientists, have highlighted the potentially significant role of kelps in blue carbon, which refers to the carbon stored in coastal and marine ecosystems (Filbee-Dexter and Wernberg, 2020; Eger et al., 2021). Carbon sequestration involves securely storing carbon-containing molecules for over 100 years. However, determining whether the CO₂ absorbed by kelp through photosynthesis leads to actual carbon sequestration in the marine environment is extremely complex compared to

terrestrial systems (Hurd et al., 2022). This complexity arises from the need to consider multiple factors simultaneously, such as the rapid turnover of seaweed biomass, tracking the fate of carbon through particulate and dissolved organic carbon pathways in dynamic coastal waters, and the crucial role of atmosphere-ocean CO₂ exchange (Hurd et al., 2022). Regardless, even if kelp productivity were to double in the Arctic due to climate change, remember that, in parallel, the melting cryosphere diminishes the Arctic's ability to mitigate global warming. Climate change in the Arctic brings numerous repercussions on ecosystems, local communities, and the planet as a whole.

The primary aim of this thesis was to examine the impacts of climate change on shallow Arctic macroalgal communities, particularly focusing on kelp forests, in order to enhance our understanding and future predictions of these ecosystems. Within the context of the FACE-IT project, we have partially addressed the first two objectives, which involve identifying key factors driving biodiversity changes and investigating the cascading effects of changing biodiversity on Arctic coastal food webs. However, as with any research field, there is still a need for further investigations into the responses of Arctic coastal communities in order to refine our predictions and provide robust scientific recommendations for ecosystem management (Wassmann et al., 2011; Filbee-Dexter et al., 2019).

3. Perspectives

It is evident that conducting laboratory experiments combined with *in situ* studies is crucial for understanding the ecosystem's functioning. To investigate the long-term effects of climate change on kelp communities, both *ex situ* experiments spanning several months and *in situ* monitoring programs within multiple locations in the Arctic would be very relevant. During these prolonged experiments, measurements such as lipid content, gene expression analyses, or reproduction would shed light on the adaptive potential of kelp species and their associated community and their long-term sustainability. Moreover, monitoring surveys of species' presence within fjords would help to understand the link with environmental conditions but also with other species' presence. As discussed previously, isotopic measurements from particulate organic matter and animal tissue along the fjord would help to understand the food web dynamic and variations along the fjord.

An intriguing avenue for further investigation would be to examine the influence of environmental change during the polar night, in winter. Indeed, kelp species exhibit different behaviors during this period. The endemic species *Laminaria solidungula* experiences a period of growth during the polar night through organic reserves, whereas *Saccharina latissima* and *Alaria esculenta* await the arrival of spring (Chapman and Lindley, 1980; Berge et al., 2020). Krause-Jensen et al. (2016) demonstrated that photosynthesis during the long photoperiod of summer leads to pH more elevated in kelp forests than in the surrounding seawater. In contrast during the polar night, pH declines due to ocean acidification and respiration. Additionally, the colder temperatures during this time increase the solubility of CO₂, further intensifying the effects of ocean acidification (Fransner et al., 2022). Investigating the repercussions of ocean acidification with combined factors like warming on kelp communities, including calcifiers, during the polar night is an important area for future research. It will allow us to identify advantaged or disadvantaged species, thereby further refining our predictions. An experiment conducted by Comeau et al. (in prep.), in which I have been involved, has taken the initial steps to address this topic. The study investigated the effects of ocean acidification combined with warming on *Saccharina latissima* and coralline algae through a tank experiment conducted at the start of the polar night in the Arctic.

Another interesting research topic involves harmful algal blooms (HABs), which are substantial threats to marine ecosystems globally, including the Arctic (Anderson et al., 2022). Since these occurrences predominantly happen in coastal regions, the release of toxins may have consequences for kelp and, more specifically, for its associated communities (shellfish and crustaceans). In an experiment conducted by Sylvers and Gobler (2021) in New York, *Saccharina latissima* mitigated the HAB caused by *Alexandrium catenella* inducing a reduction in the toxin accumulation in associated bivalves. Understanding the triggers, ecological consequences, and potential mitigation processes related to HABs in Arctic waters would be crucial for protecting these vulnerable ecosystems and preserving human health.

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Résumé en français

Les références utilisées ici sont documentés dans leurs sections respectives.

Introduction

La région arctique englobe l'océan Arctique et les terres environnantes telles que le Groenland (Danemark), l'Alaska (États-Unis), certaines parties du Canada, la Russie et la Scandinavie (Fig. 1). L'océan Arctique, entouré de plaines côtières, de chaînes de montagnes et de fjords, offre divers habitats tels que la glace de mer, les eaux libres et les zones côtières peu profondes à de nombreuses espèces marines (Bluhm et al., 2011). Des macroalgues aux mammifères marins, un réseau complexe prospère dans cet environnement extrême, conférant à l'océan Arctique une grande richesse écologique et une importance qui s'étend bien au-delà de son environnement immédiat.

L'écosystème côtier de l'Arctique est soumis à d'importantes variations saisonnières qui influencent fortement les processus biologiques (Kędra et al., 2015). En hiver, l'absence de lumière solaire et les basses températures entraînent une expansion de l'étendue de la glace. À l'inverse, l'été est marqué par des journées plus longues, une hausse des températures et la fonte des glaces.

Les forêts de macroalgues, formées par des espèces de fucus ou de laminaires constituent des refuges et des lieux de reproduction essentiels pour de nombreuses espèces marines notamment des poissons, des crustacés, des mollusques, d'autres espèces de macroalgues telles que les algues corallines, et des juvéniles de nombreuses espèces marines (Włodarska-Kowalczyk et al., 2009 ; Krause-Jensen et al., 2012). Les fucoïdes sont les espèces dominantes des communautés d'algues intertidales, tandis que les laminaires prospèrent dans la zone subtidale jusqu'à ce qu'elles atteignent leur seuil de faible luminosité, jusqu'à 60 m dans certaines régions (Krause-Jensen et al., 2019). Les algues corallines forment le sous-étage des forêts de laminaires et peuvent également former des lits de rhodolithes que l'on trouve jusqu'à 77 m de profondeur (Jørgensbye et Halfar, 2017). Dans ce manuscrit, l'accent sera mis

sur les laminaires et leurs réponses aux changements environnementaux. De plus amples informations sur les corallines et les fucoïdes sont disponibles dans le chapitre 1.

Les laminaires sont de grandes algues brunes formant des structures de canopée denses connues sous le nom de lits ou de forêts de laminaires. Elles se composent d'un crampon, d'un stipe et d'une ou plusieurs lames. Les films microbiens, les filtreurs coloniaux sessiles (bryozoaires, hydrozoaires, polychètes) et les herbivores mobiles (oursins, polychètes, crustacés, mollusques) caractérisent leur faune épiphytique. En modifiant la lumière, la sédimentation, l'abrasion physique et les courants de fond, les forêts de laminaires constituent un habitat, une nourriture et une zone de reproduction pour les poissons et les invertébrés (Filbee-Dexter et al., 2019). Une seule espèce est endémique de l'Arctique, *Laminaria solidungula*. Les autres laminaires présentes dans l'Arctique, appartenant aux genres *Laminaria*, *Saccharina* et *Alaria*, sont originaires des océans Atlantique et Pacifique et se sont répandues dans les eaux subarctiques et arctiques sous l'influence des courants océaniques et grâce à leur importante capacité d'acclimatation aux environnements d'eau froide (Wulff et al., 2009).

Depuis le début du 20^e siècle, la température moyenne de l'air à la surface de l'Arctique a augmenté d'environ 2 à 3 °C (données NOAA ; Fig. 2A). Cette augmentation rapide de la température entraîne une diminution constante de l'étendue de la cryosphère arctique d'année en année (Fig. 2B). La fonte des glaces induit une augmentation de la turbidité et une diminution de la salinité des eaux côtières et entraîne la modification des habitats naturels (Irrgang et al., 2022). De plus, avec le réchauffement en cours, l'Arctique côtier peu profond connaît une augmentation de la fréquence, de l'intensité et de la durée des vagues de chaleur marine. Les vagues de chaleur marine surviennent lorsque le 90^e centile de la température moyenne de surface de la mer du jour correspondant au cours des 30 dernières années est dépassé pendant cinq jours consécutifs ou plus (Hobday et al., 2016 ; Golubeva et al., 2021). La faible profondeur des zones côtières limite la circulation de l'eau et entrave la dissipation de la chaleur, ce qui entraîne une exposition plus prolongée à des températures élevées (Varela et al., 2023).

Tous ces changements peuvent avoir de profondes répercussions sur l'écosystème marin arctique, en affectant la distribution et le comportement des organismes qui y vivent. L'objectif principal de cette thèse est d'analyser les effets du changement climatique sur les

communautés benthiques de l'Arctique peu profond, en particulier les forêts de laminaires qui abritent une grande biodiversité.

Ce travail comprend quatre questions, chacune mettant en lumière les effets des changements environnementaux sur les communautés benthiques côtières de l'Arctique.

- 1) Quel est l'état des connaissances actuelles sur la réponse des macroalgues arctiques aux changements environnementaux en cours et prévus ? (Chapitre 1)
- 2) Comment les laminaires arctiques réagiront-elles aux effets directs du changement climatique ?
 - a) Comment les laminaires arctiques répondront-elles aux effets combinés des apports d'eau douce turbide provenant de la fonte des glaces et du réchauffement (chapitre 2) ?
 - b) Quels sont les impacts des courants marins sur la physiologie des laminaires arctiques et sur les espèces qui leur sont associées ? (Chapitre 3)
- 3) Comment les facteurs environnementaux influencent-ils la diversité des communautés benthiques côtières de l'Arctique ? (Chapitre 4)

Cette thèse est le fruit d'une approche multidisciplinaire combinant des études *in situ*, des expériences en mésocosmes et des analyses en laboratoire, qui ont été soutenues par des collaborations internationales avec des scientifiques de Norvège, d'Allemagne, des États-Unis et de Chine.

Chapitre 1 : Impact du changement climatique sur les communautés de macroalgues de l'Arctique

Les objectifs de la présente étude sont les suivants : (1) rassembler et synthétiser les informations existantes afin de fournir une vue d'ensemble des impacts potentiels du changement climatique sur les communautés de macroalgues des côtes arctiques et (2) mettre en évidence les lacunes dans les connaissances sur les espèces, les processus écologiques ou les sous-régions de l'Arctique. Nous avons étudié, pour les côtes arctiques à substrat dur et peu profond, les changements à court et à long terme des caractéristiques environnementales, les réponses des macroalgues, les taxons gagnants et perdants, ainsi que les impacts sur le fonctionnement de l'écosystème.

La moitié des taxons benthiques devraient subir des changements importants dans l'étendue de leur habitat (augmentation ou diminution de plus de 10 %), y compris les espèces dominantes et/ou endémiques des plateaux arctiques (Renaud et al., 2019). Cela pourrait entraîner un risque élevé d'extinction d'espèces (Müller et al., 2009). La disparition de la glace de mer pourrait entraîner un profond changement dans le benthos polaire peu profond, qui passera d'une communauté dominée par les invertébrés à une communauté dominée par les macroalgues (Clark et al., 2013). Par exemple, dans le Kongsfjorden (Svalbard), les anémones de mer initialement dominantes ont diminué de 80 % entre les années 1990 et 2000 et ont été remplacées par des algues brunes filamenteuses (Kortsch et al., 2012). Entre 1988 et 2008, les côtes du Svalbard ont connu une augmentation de la couverture et de la biomasse des algues marines intertidales, notamment *Fucus distichus*, dont la population a presque doublé (Weslawski et al., 2010). La fonte des glaces ouvrant de nouvelles zones, l'habitat de cette espèce dans l'Arctique devrait tripler d'ici 2100 (Jueterbock et al., 2016). Concernant les laminaires, quelques espèces pourraient prendre l'avantage sur les autres en s'acclimatant plus efficacement aux stress environnementaux. Par exemple, alors que l'on s'attend à un recul vers le nord de l'espèce endémique *Laminaria solidungula*, une espèce sténotherme (i.e qui ne peut pas vivre en dehors d'une plage étroite de températures, Fig. 11 ; Müller et al., 2009), *Saccharina latissima* pourrait bénéficier de ces nouvelles conditions, en particulier du réchauffement, grâce à un degré élevé de polymorphisme, d'acclimatation et de diversité génétique parmi les populations (Bartsch et al., 2008 ; Guzinski et al., 2016). Si l'abondance et la biomasse des laminaires peuvent largement augmenter, la composition des espèces changera, ce qui aura très probablement un impact sur la faune associée. Enfin, la répartition des algues corallines de l'Arctique sera limitée par la limite supérieure de température de l'espèce dans le sud et par l'état de saturation du carbonate de calcium dans le nord (Steinacher et al., 2009 ; Chan et al., 2020). En effet, l'acidification et le réchauffement des océans entraîneront une diminution rapide du taux de calcification (Fig. 11 ; Teichert et al., 2014 ; Chan et al., 2020). De plus, la compétition pour l'espace avec les laminaires pourrait accélérer leur disparition.

Les espèces arctiques font face aux changements environnementaux tout en étant confrontées à une pression concurrentielle croissante des espèces invasives, au risque d'infection par des maladies et aux interactions prédateur-proie avec une augmentation de la

pression herbivore (Weslawski et al., 2010). La boréalisation accroît la biodiversité à court terme avec la coexistence de nouvelles espèces (Renaud et al., 2019). Toutefois, de nouvelles interactions entre espèces, telles que la compétition et les interactions entre proies et prédateurs, apparaissent déjà et donnent lieu à un nouveau fonctionnement des écosystèmes.

Le manque de connaissances sur les interactions entre les multiples facteurs de stress abiotiques et biotiques, les réponses des populations face aux changements environnementaux et la pénurie générale de données de base sur la diversité des espèces et leur répartition biogéographique constituent un obstacle majeur pour comprendre la situation actuelle et prévoir les changements futurs (Müller et al., 2009 ; Harley et al., 2012). Les études multifactorielles à l'échelle des communautés qui prennent en compte les interactions entre les facteurs de stress et entre les espèces font cruellement défaut (Scherrer et al., 2019 ; Renaud et al., 2019).

Afin de combler les lacunes de connaissances identifiées par l'analyse de la littérature dans le premier chapitre, le deuxième chapitre étudie les réponses des espèces de laminaires arctiques au réchauffement et à la fonte des glaces. Des traitements uni- et multifactoriels ont été utilisés pour étudier l'impact du réchauffement seul et combiné à une réduction de la salinité et de la lumière sous-marine dans le cadre d'une expérience en mésocosme. L'expérience a eu lieu à Ny-Ålesund (Svalbard) pendant l'été 2021.

Chapitre 2 : Effets multifactoriels du réchauffement, de la faible lumière sous-marine et de la faible salinité sur les laminaires arctiques

Nous avons émis l'hypothèse que (1) le réchauffement augmentera le taux de croissance des laminaires pendant l'été, et (2) les effets combinés d'une température élevée, d'une faible salinité et d'une faible lumière sous-marine auront un impact négatif sur leur physiologie, bien que les réponses soient spécifiques à chaque espèce. Pour tester ces hypothèses nous avons réalisé une expérience en mésocosme exposant quatre espèces de laminaires (*S. latissima*, *A. esculenta*, *L. digitata* et *H. nigripes*) à quatre traitements pendant six semaines. Les traitements consistaient en un contrôle, une condition de réchauffement projetant le futur arctique au large (T1), et deux conditions multifactorielles combinant le réchauffement, une faible salinité et une faible irradiance projetant le futur arctique côtier selon deux scénarios

d'émissions (SSP2-4.5 pour T2 et SSP5-8.5 pour T3). Afin de représenter au mieux les conditions *in situ*, les différentes espèces de laminaires ont été incubées ensemble dans chaque mésocosme à des densités reproduisant les communautés naturelles. Les effets physiologiques sur *A. esculenta*, *L. digitata* et *S. latissima* ont été étudiés et les profils d'expression génique de *S. latissima* et *H. nigripes* ont été analysés.

L'analyse de l'expression des gènes combinée aux paramètres physiologiques étudiés montre la capacité des laminaires arctiques à s'acclimater à une gamme de conditions environnementales. En effet, aucun impact négatif des traitements n'a été observé, même selon le scénario d'émissions le plus élevé (SSP5-8.5). Cette observation confirme que ces espèces, originaires de latitudes plus basses, pourraient prospérer dans un Arctique plus chaud. Elle réfute également notre hypothèse selon laquelle les effets combinés d'une température élevée, d'une faible salinité et d'une faible irradiance auront un impact négatif sur leur physiologie.

Nos résultats soutiennent l'hypothèse selon laquelle *A. esculenta* est plus susceptible d'être résiliente aux futurs changements de lumière que les autres espèces de laminaires. En particulier, nos résultats révèlent son avantage compétitif en profondeur, grâce à sa teneur élevée en chl *a*. Toutefois, aucun impact positif discernable de sa teneur plus élevée en chl *a* n'a été observé sur son taux de croissance dans des conditions de faible luminosité. Cet impact pourrait être plus évident plus tôt dans la saison, pendant le pic de croissance. *A. esculenta* semble résister à l'augmentation du ruissellement des glaciers et des rivières, seule espèce à étendre sa distribution dans des zones à faible luminosité telles que les grandes profondeurs (Bartsch et al., 2016). La dominance d'une seule espèce de laminaire dans des régions spécifiques peut avoir des conséquences écologiques, car une diversité réduite menace la résilience de l'écosystème.

Pour *L. digitata*, nos résultats ne démontrent aucun effet négatif ou positif du réchauffement, de la faible salinité et de la faible irradiance. Franke et al. (2021) n'ont pas non plus constaté d'effet d'un réchauffement de 5 °C sur le taux de croissance de cette espèce (contrôle : 5 °C, réchauffement : 10 °C). Bartsch et al. (2016) ont constaté que *L. digitata* était la seule espèce à avoir connu une augmentation significative de sa biomasse entre 1994/1996 et 2014 sur l'ensemble du transect étudié (de 0 à 15 m de profondeur). Les conditions actuelles et futures à court terme semblent optimales pour cette espèce. La germination de *L. digitata* est plus

rapide à 9 °C qu'à 5 °C et 15 °C (Zacher et al., 2016, 2019) et son taux de croissance est plus élevé à 15 °C qu'à 5 °C et 10 °C (Franke et al., 2021). Bien que le réchauffement seul puisse être bénéfique pour cette espèce, ses effets combinés avec d'autres facteurs environnementaux pourraient être préjudiciables une fois qu'un certain seuil est atteint. Muller et al. (2008) n'ont pas trouvé de différence dans le taux de germination entre 7 °C et 12 °C, mais ont montré que la germination sous UV de type A et B diminuait jusqu'à moins de 30 % à 12 °C contre près de 80 % à 7 °C.

S. latissima est largement étudiée dans tout l'hémisphère nord. Dans l'Arctique en particulier, plusieurs études indiquent que les conditions futures pourraient favoriser l'expansion de cette espèce. Cette hypothèse est étayée par les résultats d'une germination plus importante à des températures allant jusqu'à 12 °C (Muller et al., 2008) et d'une atténuation des effets négatifs du rayonnement UV à des températures élevées (12 °C ; Heinrich et al., 2015). Nos résultats révèlent que *S. latissima* peut bénéficier d'un apport croissant d'azote provenant de l'érosion côtière et du dégel du pergélisol, qui pourrait renforcer l'immunité, la photosynthèse, la biosynthèse et/ou le transport de molécules, bien que cela n'ait pas été mesuré dans le cadre de cette étude. *S. latissima* présente un degré élevé de polymorphisme, d'acclimatation et de diversité génétique entre les populations (Bartsch et al., 2008 ; Guzinski et al., 2016). Par exemple, sa croissance présente une grande plasticité phénotypique qui semble être limitée par des schémas saisonniers spécifiques (Spurkland et Iken, 2011). Dans l'Arctique canadien, Goldsmit et al. (2021) ont constaté que l'habitat approprié de cette espèce pourrait gagner 64 000 km² d'ici à 2050, la majeure partie de cette nouvelle zone se trouvant dans les parties les plus septentrionales, où la température augmente et où la glace de mer recule. Bartsch et al. (2016) ont constaté une augmentation de biomasse d'un facteur 30 entre 1994/1996 et 2014 à 2,5 m de profondeur à Hansneset (Kongsfjorden, Svalbard, Norvège). *S. latissima* bénéficiera très probablement des conditions futures, bien que la capacité et le temps de dispersion, ainsi que la compétition avec d'autres espèces, la prédation et les événements extrêmes doivent être pris en compte pour les projections de population.

Jusqu'à présent, *A. esculenta*, *L. digitata* et *S. latissima* se sont adaptées avec succès à l'environnement arctique et nos résultats suggèrent qu'elles pourraient prospérer dans les conditions attendues pour 2100. À court terme, ces espèces pourraient bien continuer à se répandre dans cette région. En ce qui concerne *H. nigripes*, Franke et al. (2021) ont suggéré

une véritable affinité arctique avec un optimum de croissance des sporophytes à 10 °C. D'ici 2100, cette espèce pourrait continuer à prospérer dans l'Arctique, comme le montre notre analyse de l'expression des gènes, qui suggère une acclimatation efficace avec moins de stress dans les scénarios futurs. Les espèces de laminaires seront toutefois confrontées à une concurrence accrue, au broutage et à des événements extrêmes tels qu'un taux de sédimentation élevé, l'affouillement de la glace et les vagues de chaleur marines (Hu et al., 2020). Autour de Tromsø (Norvège), la propagation massive des oursins pourrait avoir provoqué la disparition des laminaires (Sivertsen et al., 1997). En outre, avec le réchauffement, la fréquence et l'intensité des vagues de chaleur marine augmenteront, ce qui pourrait avoir des conséquences importantes sur les espèces marines de la flore et de la faune arctiques. Ces effets potentiels du changement climatique doivent être pris en compte pour mieux évaluer l'avenir des communautés de laminaires arctiques.

Le chapitre 2 met en évidence les réponses des espèces de laminaires arctiques aux facteurs de stress environnementaux liés au réchauffement et à la fonte des glaces. En conservant la même approche expérimentale en mésocosme, le chapitre suivant élargit notre étude au réchauffement et aux vagues de chaleur marines sur les laminaires arctiques et leurs communautés corallines et faunistiques associées. Cette deuxième expérience a eu lieu à Tromsø (Norvège) au cours de l'été 2022.

Chapitre 3 : Tolérance des laminaires arctiques au réchauffement de l'océan et aux vagues de chaleur marine

L'augmentation de la température de surface de la mer à l'échelle mondiale a été liée à une augmentation de la fréquence, de l'intensité et de la durée des vagues de chaleur marine (Oliver et al., 2018). Les vagues de chaleur marine sont des événements discrets, prolongés et anormalement chauds où le 90^e centile de la température moyenne quotidienne de la surface de la mer (SST) au cours des 30 dernières années est dépassé pendant cinq jours consécutifs ou plus (Hobday et al., 2016). Les vagues de chaleur marine peuvent entraîner des mortalités massives d'organismes benthiques, notamment d'algues marines et d'herbiers (par exemple, Wernberg et al., 2013 ; Arias-Ortiz et al., 2018 ; Thomsen et al., 2019), ainsi que d'invertébrés (par exemple, Hughes et al., 2017 ; Garrabou et al., 2022). L'Arctique a connu ces dernières années une augmentation significative de la durée et de l'intensité de ces événements. Dans les mers de Kara, de Laptev et de Sibérie, leur durée a augmenté de 10 à 12 jours entre 2000

et 2020 (Golubeva et al., 2021). Hu et al. (2020) ont rapporté que l'intensité cumulée des vagues de chaleur marines dans les zones libres de glace a augmenté de 0,31 °C par an entre 1988 et 2017.

À notre connaissance, aucune étude n'a été menée sur les réponses des communautés de laminaires arctiques ou subarctiques aux vagues de chaleur intense simulées. Ici, nous avons évalué les effets de vagues de chaleur simulées sur les principaux organismes constituant les communautés de laminaires autour de Tromsø (Norvège) au cours d'une expérience en mésocosme de 23 jours conçue pour tester l'hypothèse selon laquelle les organismes des communautés de laminaires présentent une tolérance et des réponses physiologiques spécifiques aux espèces face au réchauffement et aux vagues de chaleur. Les communautés reconstituées étaient composées de trois espèces de laminaires (*Saccharina latissima*, *Laminaria digitata* et *Alaria esculenta*), d'algues corallines, d'escargots, d'oursins et de moules. Pour les laminaires, les changements dans le taux net de photosynthèse, le rendement quantique maximal, la teneur en chlorophylle *a* (chl *a*), le rapport carbone/azote (C:N) et le taux de croissance ont été évalués. Les taux de croissance ont été évalués pour les autres organismes.

Cette étude met en évidence des réponses distinctes d'*A. esculenta*, de *L. digitata* et de *S. latissima* aux traitements de température. Alors que *A. esculenta* et *S. latissima* montrent une sensibilité significative aux traitements, *L. digitata* démontre une plus grande tolérance. Notre hypothèse selon laquelle les organismes de la communauté des laminaires présentent une tolérance et des réponses physiologiques spécifiques à chaque espèce à l'égard des eaux moyennes de surface est vérifiée pour les espèces de laminaires. Il est remarquable que les vagues de chaleurs simulées n'aient pas eu d'impact négatif évident sur les espèces étudiées.

Dans l'ensemble, les résultats suggèrent que les trois espèces de laminaires étudiées ici sont tolérantes au réchauffement et aux vagues de chaleurs pour la plupart des paramètres et résilientes pour le rendement quantique maximum dans le cas de *S. latissima*. Alors que les traitements de réchauffement et de vagues de chaleur marines ont induit des réponses chez deux des trois espèces étudiées, ces réponses étaient soit réversibles, comme la diminution du rendement quantique maximal, soit renforcées, comme les diminutions du taux de photosynthèse net et de la teneur en chl *a* avec le temps, qui se produisent généralement à la fin de l'été.

En ce qui concerne les algues corallines, une composante importante de ces communautés benthiques, leur taux de croissance et leur rendement quantique n'ont pas varié de manière significative entre les traitements, ce qui suggère une certaine tolérance aux eaux de surface. Cornwall et al. (2020) ont souligné l'importance d'étudier les algues corallines sur plusieurs générations afin de caractériser les gains potentiels de tolérance aux facteurs de stress. En particulier, les espèces ayant des temps de génération courts peuvent être plus résilientes et plus capables de s'acclimater au réchauffement futur (Cornwall et al., 2019). Toutefois, cette acclimatation pourrait être compromise pour les espèces à longue durée de vie telles que les espèces polaires. En outre, des facteurs indirects doivent également être pris en compte. Par exemple, Webster et al. (2010) ont montré un changement microbien après 7 jours à +5 °C qui s'accompagne d'une réduction de 50 % de l'établissement de l'algue coralline *Neogoniolithon fosliei* d'Australie. Le taux de croissance de ces organismes dans l'Arctique et le subarctique est très faible (0,2 mm/mois ; Adey et Vassar, 1975), une expérience plus longue serait donc nécessaire pour confirmer nos observations.

De même, le taux de croissance des escargots, des moules et des oursins n'a pas montré de variations significatives en fonction des traitements. Cependant, il est important de noter que seule la croissance a été étudiée. D'autres études telles que l'analyse du contenu en lipides ou la reproduction sont nécessaires pour conclure sur la tolérance de ces organismes au réchauffement et aux vagues de chaleur marines.

Après avoir mené deux expériences en mésocosme pour analyser les réponses des laminaires arctiques et de leur communauté au changement climatique, le dernier chapitre étudie les liens *in situ* entre les conditions environnementales et la biodiversité benthique. Cette étude a été réalisée à Ny-Ålesund pendant l'été 2021, en utilisant la technique de l'ADN environnemental (ADNe).

Chapitre 4 : Diversité benthique le long d'un fjord arctique : quels sont les facteurs clés ?

Pendant les mois d'été, la fonte de la glace déverse de grandes quantités d'eau douce dans les zones côtières de l'Arctique. La fonte des glaciers libère les sédiments qui étaient emprisonnés dans la glace. En outre, lorsque l'eau de fonte du pergélisol et de la neige s'écoule vers le fjord, elle s'enrichit de sédiments (Hopwood et al., 2018). L'apport d'eau douce turbide affecte le régime lumineux sous-marin local, la salinité, les nutriments et le substrat et, par conséquent,

la distribution et l'abondance des organismes benthiques. De l'intérieur à l'extérieur, les fjords arctiques sont caractérisés par un gradient de substrat allant de mou à plus dur et un gradient en été de lumière sous-marine et de salinité avec des eaux turbides et faiblement salées dans les parties intérieures et des eaux moins turbides et plus salées dans les parties extérieures (Svendsen et al. 2002 ; Kedra et al., 2010). La diversité benthique est largement influencée par le type de substrat et les caractéristiques de l'eau telles que la turbidité et la teneur en nutriments (Anderson et al., 2008, Saeedi et al., 2022). Avec le changement climatique, l'Arctique connaît des changements environnementaux rapides, les températures augmentant plus de deux fois plus vite que la moyenne mondiale (Richter-Menge et al., 2017). Avec la hausse des températures, la fonte des glaciers s'accélère et se produit plus tôt dans l'année.

Dans cette étude, nous avons étudié la répartition de la flore et de la faune benthiques le long d'un fjord arctique. L'objectif principal était de caractériser les variations potentielles de la composition de la communauté liées aux changements des conditions environnementales. Nous avons sélectionné six sites le long du Kongsfjorden (Svalbard, Norvège) et surveillé leurs paramètres environnementaux (température, salinité, rayonnement photosynthétiquement actif (PAR), nutriments, concentration de chl a , pH et alcalinité totale) et la diversité benthique au cours de l'été 2021. La diversité a été évaluée à l'aide de l'ADN environnemental (ADNe), un outil moléculaire permettant l'identification taxonomique à partir d'une partie de l'ADN d'un organisme, trouvé dans son environnement. Notre hypothèse est que la distribution des organismes benthiques est influencée par le gradient de lumière, de salinité et de type de substrat. En particulier, nous supposons que la distribution des macroalgues suit le gradient de lumière et que celle des suspensivores suit le gradient de salinité, associé au gradient de chl a .

Contrairement à nos hypothèses initiales, nous n'avons pas trouvé de gradient de diversité, ni de corrélation entre la distribution des macroalgues et le régime lumineux sous-marin, ni de corrélation des suspensivores avec la chl a ou les concentrations en nutriments. Bien que nous n'ayons pas pu établir de corrélation directe entre la diversité benthique et les conditions environnementales, nos résultats mettent en évidence certaines observations intéressantes.

À l'exception de Kongsfjordneset, tous les autres sites ont été affectés par la fonte des glaciers. Ceci a été mis en évidence par une augmentation des niveaux de nutriments observée entre

les semaines 28 et 34 (début juillet et fin août, Fig 2). En particulier, au cours des semaines 30 et 32 (début août), Ossian Sars et Kongsbreen South ont connu une forte augmentation de K_d , qui pourrait coïncider avec la période de fonte du glacier. Les deux sites les plus influencés par les glaciers présentaient également les niveaux les plus élevés de diversité benthique. Pourtant, des études antérieures ont fait état d'une diminution de la richesse en espèces de la partie extérieure à la partie intérieure du Kongsfjorden (par exemple, Kedra et al., 2010 ; Voronkov et al., 2013 ; Legeżyńska et al., 2017). En outre, des tendances à la diminution de la diversité en se rapprochant des glaciers ont été observées dans d'autres régions influencées par les glaciers, comme le fjord de Hornsund (Włodarska-Kowalczyk et al., 2013) et l'Arctique canadien (Farrow et al., 1983). Des études antérieures ont suggéré que les bassins extérieurs et centraux des fjords peuvent être enrichis d'espèces boréales qui peuvent coexister avec les espèces arctiques et subarctiques qui habitent déjà ces zones (par exemple Renaud et al., 2019). Dans le Kongsfjorden, l'absence de seuils permet aux taxons du plateau continental de pénétrer facilement dans le fjord (Svendsen et al. 2002 ; Legezynska et al., 2017). En outre, le réchauffement augmente le débit d'eau douce enrichie en particules inorganiques dans le fjord et la fréquence des perturbations telles que l'affouillement de la glace et les glissements de sédiments (Wlodarska-Kowalczyk et al. 2005). Bien que ces perturbations accrues puissent favoriser les espèces opportunistes, il a été prédit que la diversité benthique globale dans ces zones diminuerait (Wlodarska-Kowalczyk et al. 2005 ; Al-Habahbeh et al. 2020). On pourrait donc s'attendre à une augmentation de la diversité près de l'entrée du fjord, avec plus d'espèces boréales, et à une diminution près du glacier, où les perturbations sont plus fréquentes. Cependant, nos résultats ne correspondent pas à ces attentes.

Kedra et al. (2010) ont montré, en utilisant une méthode d'échantillonnage des sédiments, que la diversité de la communauté macrobenthique des fonds mous dans les parties centrale et extérieure du Kongsfjorden a diminué entre 1997 et 2006. En revanche, la baie glaciaire intérieure, bien séparée du fjord extérieur par une chaîne d'îles et un seuil peu profond (20 à 50 m ; Svendsen et al. 2002) qui fait office de barrière, est restée aussi diversifiée, bien que cette diversité soit toujours inférieure aux sites extérieurs dans cette étude. Il n'y a pas eu de changement majeur dans le type de substrat au cours de cette période, ce qui ne peut donc pas expliquer ce changement. Kedra et al. (2010) ont émis l'hypothèse que le déclin de la diversité dans la partie extérieure du fjord pourrait être attribué à l'influence décroissante du

glacier Blomstrandbreen qui recule rapidement (Burton et al., 2016). Avec son recul, sa fonte ne profiterait plus aux sites les plus éloignés. En effet, la fonte du glacier fournit des nutriments pour soutenir la croissance des communautés de phytoplancton qui forment la base du réseau trophique (Piquet et al., 2014), et pour fournir des nutriments essentiels aux macroalgues, qui sont des espèces clés de l'habitat dans l'écosystème (Lebrun et al., 2022). De plus, la présence de prédateurs supérieurs dans l'écosystème marin côtier de l'Arctique est étroitement liée au front glaciaire (Lydersen et al., 2014 ; Bouchard Marmen et al., 2017). En effet, les prédateurs supérieurs tels que les oiseaux de mer et les lions de mer migrent vers l'Arctique pendant l'été pour vivre près des fronts glaciaires, ce qui souligne l'importance de la richesse nutritionnelle que ces zones fournissent (Hop et al., 2002 ; Lydersen et al., 2014). Les prédateurs jouent un rôle crucial dans la régulation de l'écosystème par un contrôle descendant, qui peut à son tour accroître sa diversité (Wessels et al., 2006 ; Bouchard Marmen et al., 2017). Ainsi, les glaciers abritent des espèces clés et régulent la diversité des communautés benthiques (Gutt et al., 2001).

La présence de prédateurs supérieurs sur les sites intérieurs pourrait expliquer nos résultats. Des oiseaux de mer sont présents à Ossian Sars, Kongsbreen South, Bloomstrand East et French Bird Cliff (Varpe et Gabrielsen, 2022 ; observations personnelles). Des lions de mer ont été observés à Ossian Sars, Kongsbreen South et Hansneset (Everett et al., 2018 ; observations personnelles). En identifiant la présence de ces prédateurs supérieurs et leurs interactions avec la communauté benthique, nous avons établi un diagramme de réseau trophique sur chacun des six sites (Fig. 27). Sans surprise, le site le plus diversifié présente également l'écosystème le plus complexe avec de nombreux liens trophiques et une répartition homogène des taxons au sein et entre les différents niveaux trophiques. Kongsbreen South, le site le plus proche du glacier, présente également un écosystème très complexe, mais avec une plus grande hétérogénéité entre le premier et le deuxième niveau. La présence d'une colonie d'oiseaux à Ossian Sars pourrait expliquer une meilleure régulation descendante sur ce site que sur Kongsbreen South. A l'inverse, Kongsfjordneset, le site le plus éloigné des glaciers, ne présente que deux niveaux trophiques hétérogènes. La présence de ces prédateurs supérieurs pourrait donc expliquer une plus grande diversité à Ossian Sars et Kongsbreen South, proches des glaciers, par rapport à Kongsfjordneset, qui ne semble plus influencé par leur fonte.

Avec le réchauffement, le recul des glaciers pourrait avoir un impact important sur l'écosystème. En particulier, la disparition du front glaciaire peut entraîner des changements substantiels dans la prolifération du phytoplancton et les propriétés des masses d'eau dans le fjord (Ardyna et Arrigo, 2020). Ces changements pourraient, à leur tour, entraîner des modifications de la présence des prédateurs supérieurs et, par conséquent, de la diversité de l'écosystème. Cependant, il est très difficile de prédire ces changements.

Il est important de noter que comme toute autre méthode d'analyse, l'échantillonnage de l'ADN électronique comporte aussi des biais (Yates et al., 2019). Lors de notre exploration de Kongsfjordneset, le site le plus externe du fjord, nous avons observé une forte abondance d'algues corallines en plongée et à l'aide d'un drone, comparativement aux autres sites (Steeve Comeau pers. obs.). Cependant, malgré leur présence dans les échantillons d'eau de mer prélevés sur ce site, les algues corallines présentaient un faible indice (eDNA index). même, nous avons observé une forte présence d'oursins lors de la plongée à Kongsfjordneset, mais l'indice d'ADNe indiquait plutôt une forte abondance de mollusques, d'ochrophytes et de bryozoaires sur le site échantillonné. Ces différences d'abondance déterminées par l'ADNe sont difficiles à interpréter car si l'indice ADNe permet d'établir une valeur basée sur le nombre de séquences entre 0 et 1, le nombre de séquences n'est pas uniquement lié à l'abondance d'un taxon. L'indice d'ADNe ne reflète donc pas seulement l'abondance ou la biomasse d'une espèce ou d'un genre, mais aussi la capacité de sa séquence à être amplifiée (Kelly et al., 2019). En outre, les séquences peuvent provenir d'un organisme mort, d'œufs ou de sperme, ce qui peut biaiser davantage les résultats. Par conséquent, bien que nos résultats donnent un aperçu de la diversité des sites étudiés, il convient d'être prudent lors de l'interprétation des résultats de l'étude.

En outre, une partie de nos répliques (40 %) n'avait pas la qualité requise pour être inclus dans notre étude. Ces répliques étaient aléatoirement de mauvaise qualité, c'est-à-dire qu'ils n'étaient pas ciblés sur une date, un site ou une amorce spécifique. Ceci suggère que le problème de qualité n'était pas dû à un problème lors de l'échantillonnage ou des extractions, qui ont été effectuées selon les mêmes protocoles pour tous les échantillons. Également, l'amplification PCR a été réalisée sur tous les échantillons en même temps, avec les mêmes produits. La mauvaise qualité de la séquence par base obtenue pourrait provenir de diverses sources, notamment d'erreurs au cours du processus de séquençage, qui peuvent entraîner

des inexactitudes dans l'appel de base et l'analyse ultérieure des données. En outre, la dégradation de l'ADN avant ou pendant la procédure de séquençage peut avoir un impact significatif sur la qualité des séquences obtenues, car les molécules d'ADN endommagées peuvent donner lieu à des données incomplètes ou peu fiables. Cette limitation nous a contraints à fusionner les répliques de filtration et de PCR restants, ce qui a réduit la robustesse de nos résultats.

La tendance à la diminution de la diversité lorsque l'on s'approche de l'intérieur du fjord, décrite précédemment, pourrait être inversée, comme le suggèrent nos résultats, mais d'autres études doivent valider cette observation. Un échantillonnage supplémentaire de l'eau de mer pour l'analyse de l'ADN environnemental dans l'ensemble du fjord pourrait déterminer la cohérence de nos résultats. D'autres méthodes d'évaluation de la biodiversité, telles que l'échantillonnage des communautés ou la photographie de quadrats, pourraient également valider nos résultats. L'hypothèse d'une régulation par les prédateurs pourrait être testée en combinaison avec l'analyse des isotopes stables pour étudier le réseau trophique. Dans l'ensemble, bien que notre étude donne un aperçu de la diversité benthique de Kongsfjorden, il convient d'être prudent dans l'interprétation des résultats en raison des limites de notre méthode d'échantillonnage et de la nécessité d'effectuer des recherches supplémentaires.

Conclusion

Bien que les deux expériences en mésocosme que nous avons menées aient conclu à des effets non négatifs du changement climatique sur les espèces de laminaires, l'analyse *in situ* a fourni une perspective plus nuancée en considérant l'influence des prédateurs et l'effet de cascade potentiel sur le reste de l'écosystème. Outre les effets directs du changement climatique, tels que l'augmentation de la température, les changements dans des régimes lumineux marins, la diminution de la salinité et l'augmentation de l'intensité et de la fréquence des vagues de chaleurs marines, comme indiqué dans les trois premiers chapitres, il est essentiel d'élargir notre champ d'action à une échelle spatiale et temporelle plus large. Cela implique d'examiner l'ensemble de l'écosystème sur une longue période.

Le réchauffement s'accompagne de la fonte de la glace. À court terme, l'augmentation de la turbidité de l'eau induite par la fonte des neiges et de la glace terrestre déclenche un

remodelage locale des communautés en limitant l'expansion de certaines espèces mais en donnant à d'autres, comme *Alaria esculenta*, un avantage concurrentiel, comme cela a déjà été évoqué dans le Kongsfjorden (Bartsch et al., 2016 ; Niedzwiedz et Bischof, 2023). À plus long terme, la fonte des glaciers et de la glace de mer élargira l'aire d'habitat potentielle des laminaires (Wiencke et Hop, 2016), qui, comme le suggère ce travail de thèse, devraient être capables de résister à l'augmentation des températures, aux vagues de chaleurs marines, et à la diminution de la salinité et de la lumière sous-marine. Cependant, la disparition de la glace, en particulier des glaciers, qui servent d'habitats aux prédateurs du sommet de la chaîne trophique, peut également entraîner le déclin de ces espèces cruciales responsables de la régulation de l'écosystème (Blundell et al., 2011 ; Womble et Gende ; 2013). Cela aura donc des répercussions sur les communautés de macroalgues dans l'Arctique. Comme mentionné précédemment, à Tromsø mais aussi dans d'autres fjords norvégiens ou dans le sud-ouest de l'Alaska, la surabondance d'oursins a provoqué une réduction significative des populations de laminaires (Hagen, 1983 ; Sivertsen, 2006 ; Estes et al., 2009). Dans le Vestfjorden (Norvège), les forêts de laminaires ont subi une destruction complète en l'espace d'un an à la suite de l'invasion de l'oursin *Strongylocentrotus droebachiensis* (Hagen, 1983). Les prédateurs des oursins, tels que les loutres de mer, sont insuffisants dans la région pour contrebalancer la situation (Estes et al., 1998). Il est important de souligner que le passage des forêts de laminaires aux zones stériles, dominées par les oursins, a fait l'objet d'une étude approfondie ces dernières années dans des zones plus tempérées telles qu'en Australie, au Canada et aux États-Unis (Filbee-Dexter et Scheibling, 2014 ; Rogers-Bennett et Catton, 2019 ; Carnell et Keough, 2020). La régénération des laminaires peut se produire dans des zones exposées aux vagues et caractérisées par des températures plus chaudes et une salinité plus élevée, où les oursins sont désavantagés (Rinde et al., 2014). À Porsanger, l'invasion du crabe royal rouge, après son introduction dans les années 1960, a entraîné une augmentation significative de la pression de prédation, notamment sur les oursins (Jørgensen, 2005). Cette invasion s'est avérée avantageuse pour les forêts de laminaires, mais a perturbé l'ensemble de l'écosystème, entraînant notamment le déclin de la morue côtière norvégienne (Christie et al., 2019).

Prédire le futur écosystème arctique n'est pas aisé et doit se faire au cas par cas, en considérant à la fois les espèces présentes et les particularités de la zone d'étude. Les fucus

pourraient connaître un sort similaire à celui des laminaires avec l'expansion de leur habitat et l'augmentation locale des pressions de prédation par les gastéropodes et les oursins (Jueterbock et al., 2016). En ce qui concerne les algues corallines, comme nous l'avons vu au chapitre 1, la diminution attendue du pH et le réchauffement pourraient entraîner leur déclin dans l'Arctique (Steinacher et al., 2009 ; Chan et al., 2020). En outre, la compétition pour l'espace avec les laminaires pourrait accélérer le déclin des algues coralliennes et de leurs communautés associées, ce qui pourrait entraîner une restructuration de l'écosystème et la perte de fonctions vitales d'ici la fin du siècle (Brodie et al., 2014).

Au-delà des effets directs et indirects du changement climatique sur ces écosystèmes, il est important de prendre en compte leurs implications globales. Comme nous l'avons déjà mentionné, l'Arctique revêt une importance considérable à divers égards : il abrite d'importants stocks de poissons et contribue au climat mondial. Ces dernières années, la fonte des glaces a créé de nouvelles opportunités pour l'exploitation des fonds marins, la navigation et la pêche, avec l'émergence de nouvelles zones libres de glace (Tai et al., 2019 ; Li et Lynch, 2023). Selon Lam et al. (2014), les projections indiquent une augmentation potentielle de 39 % des recettes totales de la pêche dans la région arctique d'ici 2050 par rapport à l'année 2000. Cependant, plusieurs espèces de poissons importantes, notamment l'aiglefin, le hareng, le cabillaud, le doré jaune, le sébaste, le saumon et les poissons plats, dépendent des forêts de laminaires pour leurs stades adultes ou juvéniles. Ces espèces sont potentiellement menacées en raison de la perte potentielle de leur habitat essentiel dans des zones telles que rencontrées à Tromsø i.e. dominées par les oursins (Johnson, 2003 ; Mueter, 2022). En outre, l'invasion d'espèces compétitives ou prédatrices dans ces habitats pourrait encore aggraver leur déclin. Cheung et al. (2009) ont prédit que le taux de renouvellement des espèces le plus élevé au monde, comprenant à la fois des espèces envahissantes et des espèces localement éteintes, parmi les poissons et les invertébrés, se produirait dans la région arctique d'ici à 2050. Il est probable que nous observions le développement de nouvelles pêcheries, accompagné de nouvelles difficultés dans la gestion des stocks de poissons transfrontaliers, ce qui pourrait entraîner des conflits entre ceux qui dépendent de ces ressources (Mueter et al., 2021). Le déplacement des populations de poissons entraîne des perturbations importantes dans les communautés locales, telles que les Inuits, qui connaissent déjà une saison de pêche réduite en raison de la fonte rapide de la glace de mer et de la formation

tardive de la nouvelle glace (Galappaththi et al., 2019). Ces circonstances peuvent avoir des effets néfastes sur l'économie et le bien-être de ces communautés. Il convient de noter que les laminaires sont une ressource saisonnière importante qui revêt une grande importance pour la santé, la culture et le bien-être général des communautés humaines locales.

L'impact du changement climatique, tel que la fonte des glaces et les modifications de la circulation, pourrait compromettre le rôle de l'Arctique dans l'atténuation du réchauffement climatique (Tomas et al., 2016 ; Huang et al., 2017 ; Timmermans et Marshall, 2020). Le potentiel de piégeage du carbone par les laminaires fait l'objet d'un vif débat parmi les scientifiques (Filbee-Dexter et Wernberg, 2020 ; Hurd et al., 2022). Ces dernières années, plusieurs entreprises actives dans la culture des laminaires, ainsi que des scientifiques, ont souligné le rôle potentiellement important des laminaires dans le carbone bleu, qui désigne le carbone stocké dans les écosystèmes côtiers et marins (Filbee-Dexter et Wernberg, 2020 ; Eger et al., 2021). La séquestration du carbone consiste à stocker des molécules contenant du carbone pendant plus de 100 ans. Cependant, il est extrêmement complexe de déterminer si le CO₂ absorbé par les laminaires par le biais de la photosynthèse conduit à une réelle séquestration du carbone dans le milieu marin par rapport aux systèmes terrestres (Hurd et al., 2022). Cette complexité résulte de la nécessité de prendre en compte simultanément de multiples facteurs, tels que le renouvellement rapide de la biomasse des algues, le suivi du devenir du carbone par les voies du carbone organique particulaire et dissous dans les eaux côtières dynamiques, et le rôle crucial des échanges de CO₂ entre l'atmosphère et l'océan (Hurd et al., 2022). Quoiqu'il en soit, même si la productivité des laminaires devait doubler dans l'Arctique en raison du changement climatique, il ne faut pas oublier que, parallèlement, la fonte de la cryosphère diminue la capacité de l'Arctique à atténuer le réchauffement de la planète. Le changement climatique dans l'Arctique induit de nombreux impacts sur les écosystèmes, les communautés locales et la planète dans son ensemble.

L'objectif principal de cette thèse était d'examiner les impacts du changement climatique sur les communautés de macroalgues de l'Arctique peu profond, en se concentrant particulièrement sur les forêts de laminaires, afin d'améliorer notre compréhension et les prévisions futures de ces écosystèmes. Dans le cadre du projet FACE-IT, nous avons partiellement atteint les deux premiers objectifs, qui impliquent l'identification des facteurs clés à l'origine des changements de biodiversité et l'étude des effets en cascade des

changements de biodiversité sur les réseaux alimentaires des côtes arctiques. Cependant, comme dans tout domaine de recherche, il est encore nécessaire d'approfondir les recherches sur les réponses des communautés côtières de l'Arctique afin d'affiner nos prédictions et de fournir des recommandations scientifiques solides pour la gestion des écosystèmes (Wassmann et al., 2011 ; Filbee-Dexter et al., 2019).

Il est évident que la réalisation d'expériences en laboratoire combinée à des études *in situ* est cruciale pour comprendre le fonctionnement de l'écosystème. Pour étudier les effets à long terme du changement climatique, des expériences *ex situ* s'étendant sur plusieurs mois et des programmes de surveillance *in situ* dans plusieurs endroits de l'Arctique seraient très utiles. Au cours de ces expériences prolongées, des mesures telles que la teneur en lipides, les analyses de l'expression génétique ou la reproduction permettraient de mettre en lumière le potentiel d'adaptation des espèces de laminaires et leur viabilité à long terme. En outre, des études de suivi de la présence des espèces dans les fjords permettraient de comprendre le lien avec les conditions environnementales, mais aussi avec la présence d'autres espèces. Comme indiqué précédemment, les mesures isotopiques de la matière organique particulaire et des tissus animaux le long du fjord permettraient de comprendre la dynamique et les variations du réseau trophique le long du fjord.

Une piste à approfondir serait d'examiner l'influence des changements environnementaux pendant la nuit polaire, en hiver. En effet, les espèces de laminaires présentent des comportements différents pendant cette période. L'espèce endémique *Laminaria solidungula* connaît une période de croissance pendant la nuit polaire grâce à ses réserves organiques, tandis que *Saccharina latissima* et *Alaria esculenta* attendent l'arrivée du printemps (Chapman et Lindley, 1980 ; Berge et al., 2020). Krause-Jensen et al. (2016) ont démontré que la photosynthèse pendant la longue photopériode de l'été conduit à un pH plus élevé dans les forêts de laminaires que dans l'eau de mer environnante. En revanche, pendant la nuit polaire, le pH diminue en raison de la respiration. En outre, les températures plus froides pendant cette période augmentent la solubilité du CO₂, ce qui intensifie les effets de l'acidification des océans (Fransner et al., 2022).

Un autre sujet de recherche intéressant concerne les efflorescences algales nuisibles (HAB), qui constituent une menace importante pour les écosystèmes marins du monde entier, y compris l'Arctique (Anderson et al., 2022). Comme ces phénomènes se produisent

principalement dans les régions côtières, la libération de toxines peut avoir des conséquences pour les laminaires et, plus particulièrement, pour les communautés qui leur sont associées (mollusques et crustacés). Dans une expérience menée par Sylvers et Gobler (2021) à New York, *Saccharina latissima* a atténué l'HAB causé par *Alexandrium catenella* en induisant une réduction de l'accumulation de toxines dans les bivalves associés. Il serait intéressant de comprendre les déclencheurs, les conséquences écologiques et les processus d'atténuation potentiels liés aux HAB dans les eaux arctiques pour protéger ces écosystèmes vulnérables et préserver la santé humaine.

Résumé

Depuis le début du 20^e siècle, la température moyenne de l'air à la surface de l'Arctique a augmenté de 2 à 3 °C. Cette augmentation rapide de la température entraîne une diminution de l'étendue de la cryosphère arctique d'année en année. La fonte des glaces induit une augmentation de la turbidité et une diminution de la salinité des eaux côtières entraînant la modification des habitats naturels. De plus, avec le réchauffement en cours, l'Arctique côtier peu profond connaît une augmentation de la fréquence, de l'intensité et de la durée des vagues de chaleur marine. Tous ces changements ont de profondes répercussions sur l'écosystème marin arctique, en affectant la distribution et le comportement des organismes qui y vivent. L'objectif principal de cette thèse est d'analyser les effets du changement climatique sur les communautés benthiques de l'Arctique peu profond, en particulier les forêts de laminaires qui abritent une grande biodiversité. En modifiant la lumière, la sédimentation, l'abrasion physique et les courants de fond, les forêts de laminaires constituent un habitat, une source de nourriture et une zone de reproduction pour de nombreuses espèces de l'écosystème côtier Arctique. À court terme, l'augmentation de la turbidité de l'eau induite par la fonte des neiges et de la glace terrestre déclenchera un remodelage local de ces communautés en limitant l'expansion de certaines espèces mais en donnant à d'autres, un avantage concurrentiel, comme à *Alaria esculenta* dans les zones à faible lumière. À plus long terme, la fonte des glaciers et de la glace de mer élargira l'aire d'habitat des laminaires qui, comme le suggère ce travail de thèse, devraient être capables de résister à l'augmentation des températures, aux vagues de chaleurs marines et à la diminution de la salinité et de la lumière sous-marine. Cependant, la disparition des glaciers pourrait entraîner le déclin des prédateurs au sommet de la chaîne trophique tels que les lions de mer et les oiseaux marins, espèces essentielles pour réguler la diversité de l'écosystème. La surabondance de leurs proies, notamment des herbivores tels que les oursins, pourrait induire une réduction significative des populations de laminaires. Il est nécessaire d'approfondir les recherches sur les réponses des communautés côtières de l'Arctique afin d'affiner nos prédictions et de fournir des recommandations scientifiques solides pour la gestion des écosystèmes. Pour étudier les effets à long terme du changement climatique, des expériences *ex situ* s'étendant sur plusieurs mois et des programmes de *surveillance in situ* dans plusieurs endroits de l'Arctique apparaissent essentiels.

Abstract

Since the beginning of the 20th century, the average surface air temperature in the Arctic has risen by around 2 to 3°C. This rapid rise in temperature is leading to a year-on-year reduction in the extent of the Arctic cryosphere. Melting ice leads to increased turbidity and reduced salinity in coastal waters, resulting in changes of natural habitats. In addition, with ongoing warming, the shallow coastal Arctic is experiencing an increase in the frequency, intensity and duration of marine heat waves. All these changes can have profound repercussions on the Arctic marine ecosystem, affecting the distribution and behavior of the organisms that live there. The main aim of this thesis is to analyze the effects of climate change on benthic communities in the shallow Arctic, in particular kelp forests, which are home to a high level of biodiversity. By modifying light, sedimentation, physical abrasion and bottom currents, kelp forests provide a habitat, food source and breeding ground for fish and invertebrates. In the short term, the increase in water turbidity induced by melting snow and land ice will trigger a local remodeling of communities, limiting the expansion of some species but giving others a competitive advantage, such as *Alaria esculenta* in low-light areas. In the longer term, the melting of glaciers and sea ice will expand the potential habitat range of kelp which, as this thesis suggests, should be able to withstand rising temperatures, marine heat waves, and decreasing salinity and underwater light. However, the disappearance of ice, particularly glaciers, which serve as habitats for top predators, could lead to the decline of these crucial species regulating ecosystem diversity and induce, as in Tromsø but also in other Norwegian fjords or in south-west Alaska, a significant reduction in kelp populations due to an overabundance of herbivores, particularly sea urchins. Further research into the responses of Arctic coastal communities is needed to refine our predictions and provide sound scientific recommendations for ecosystem management. To study the long-term effects of climate change, *ex situ* experiments spanning several months and *in situ* monitoring programs in several Arctic locations appear essential.