Impact of climate change on Arctic macroalgal communities

Anais Lebrun, Steeve Comeau, Frédéric Gazeau, Jean-Pierre Gattuso

Global and Planetary Change

Impact of climate change on Arctic macroalgal communities

--Manuscript Draft--

Manuscript Number:	GLOPLACHA-D-22-00117R1
Article Type:	Review article
Keywords:	climate change; macroalgae; Arctic; fucoids; kelps; coralline algae
Corresponding Author:	Anaïs Lebrun, Ph.D. candidate Sorbonne Universite Villefranche-sur-mer, Alpes maritimes FRANCE
First Author:	Anaïs Lebrun, Ph.D. candidate
Order of Authors:	Anaïs Lebrun, Ph.D. candidate
	Steeve Comeau, Ph.D.
	Frédéric Gazeau, Ph.D.
	Jean-Pierre Gattuso, Ph.D.
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 fucoid 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. Fucoid 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.
Suggested Reviewers:	Dorte Krause-Jensen Senior scientist, Aarhus University: Aarhus Universitet dkj@bios.au.dk
	Paul Renaud Senio researcher, Akvaplan-niva AS pr@akvaplan.niva.no
	Jan Marcin Weslawski Professor, Polish Academy of Sciences Institute of Oceanology: Instytut Oceanologii Polskiej Akademii Nauk weslaw@iopan.pl
	Maria Wlodarska-Kowalczuk Polish Academy of Sciences Institute of Oceanology: Instytut Oceanologii Polskiej Akademii Nauk maria@iopan.gda.pl
Opposed Reviewers:	

Impact of climate change on Arctic macroalgal communities

Anaïs Lebrun[1], Steeve Comeau[1], Frédéric Gazeau[1], 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

Corresponding author: Anaïs Lebrun, anais.lebrun@imev-mer.fr

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 fucoid 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. Fucoid 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.

Keywords: climate change - macroalgae - Arctic - fucoids - kelps - coralline algae

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 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 SIMIP 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. Fucoid 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-Kowalczuk et al., 2009; Krause-Jensen et al., 2012). Fucoid 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).

Fucoid 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 (Węslawski 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 2016; Węsławski et al. 2010). The current and projected expansion of Fucoid species and kelp forests 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 (Węslawski 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, ‘Fucoid AND Arctic AND change’, ‘Fucoid 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 (fucoids, 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. 1). 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. 2A). 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. 2B).

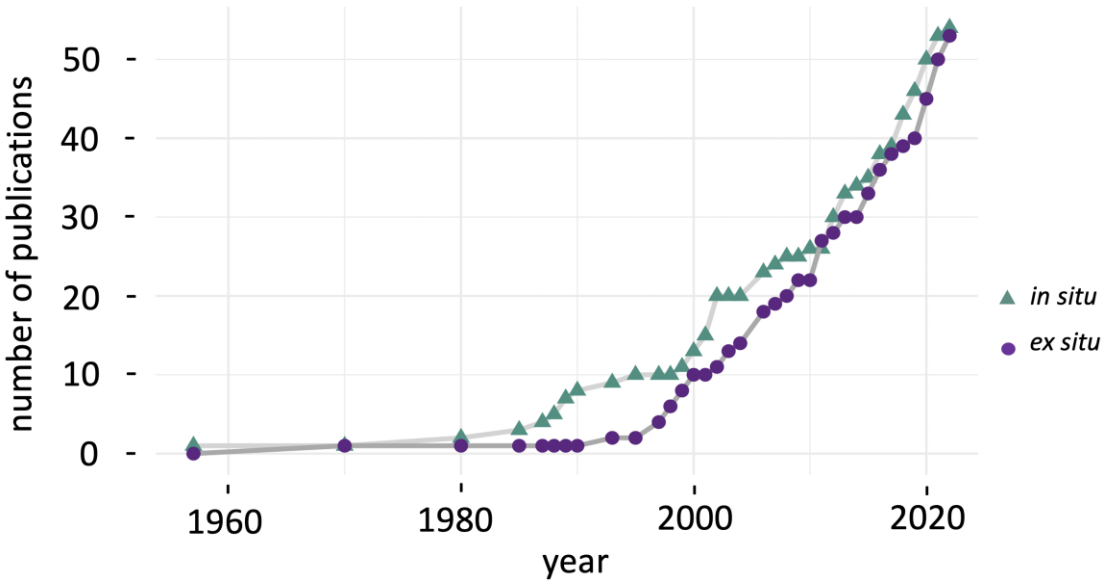


Figure 1: Cumulative number of scientific papers focusing on the impact of global change on benthic communities through both *ex situ* and *in situ* studies in the Arctic since 1957.

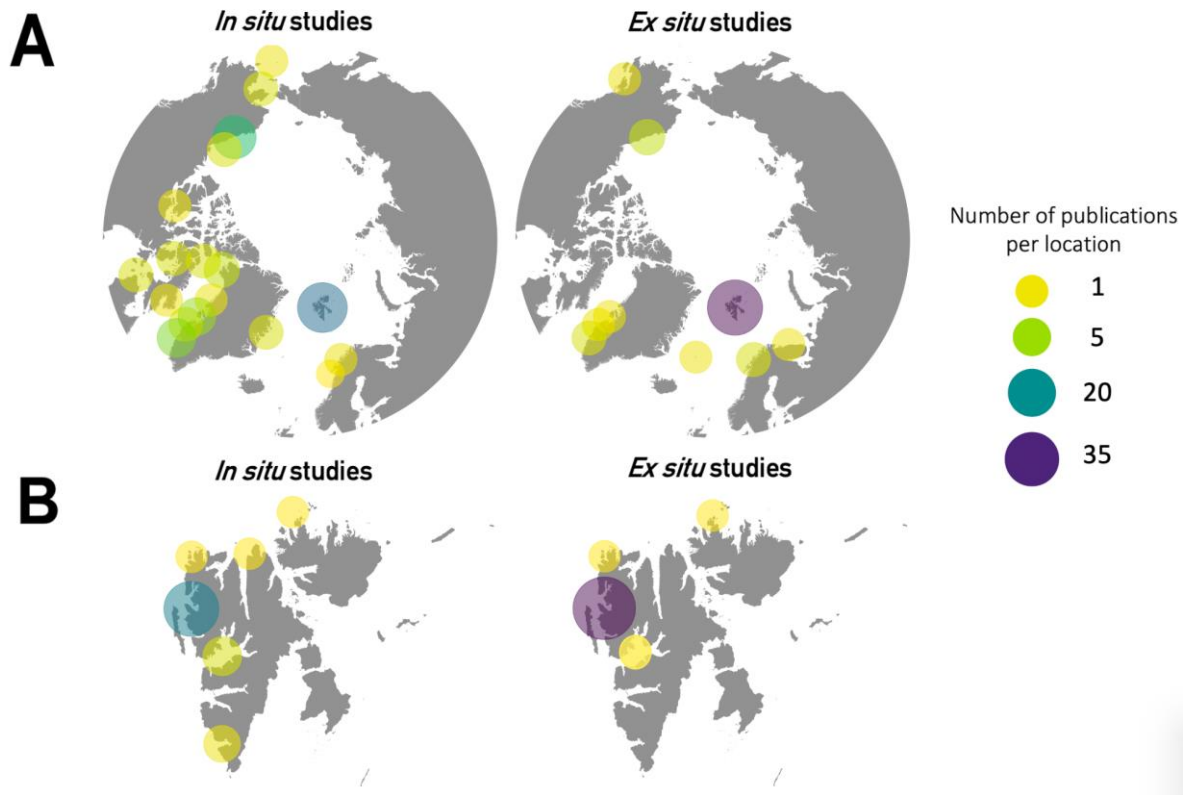


Figure 2: Number of *in situ* and *ex situ* studies per location. A) whole Arctic region, B) focus on the Svalbard coast.

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

4.1 Seasonality

Arctic coastal environments are characterized by strong seasonal changes in photosynthetically available radiation (PAR). In spring, daylight lengthens, temperature increases and ice begins to melt. Thawing land and sea ice decreases salinity and affects the light regime afterwards by delivering dissolved and particulate matter which increases turbidity (Fig. 3 and 4). In winter, the daylight period shortens, temperature decreases, and sea and land ice forms. 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; Wlodarska-Kowalczuk 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. 4; 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 due to warming reduce ice-related pressures such as ice shading or ice scouring on shallow benthic communities (Węslawski 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 (Węslawski 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).

4.2 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. 3a and 4; Trefry et al., 2009), a coarser sediment structure, and significant changes in community composition (Węslawski et al., 2010). This is called a pulse disturbance event. 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. 3b). 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 (Wlodarska-Kowalczuk 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 (Wlodarska-Kowalczuk 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. 4; Węslawski 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 or rhodolith beds and are found down to 77 m depth (Jørgensbye and Halfar, 2017).

5.1 Fucoids

In the Arctic intertidal coasts of the Arctic, seaweed diversity is low, dominated by fucoids that can experience changes in a multitude of abiotic drivers including ice scouring, desiccation, UV radiation, and wave exposure. Fucoids are an order of intertidal brown algae widely distributed along temperate and Arctic coasts (Obluchinskaya et al., 2022). They are native to the North Pacific Ocean and 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). Fucoids 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). 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 (Ingolfsoon 2008). Brown (*Dictyosiphon foeniculaceus*, *Stictyosiphon tortilis*), red (*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 et al., 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 et al., 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, and more generally polar algae, 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 them to survive to cold temperature (Gómez et al., 2009).

Kelps are important primary producers able to capture and store large amounts of CO_2 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*, *Phycodrys 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 branchs 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 CO_2.

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, 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 & 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).

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 luetkean*a 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-spencer 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. 3c). 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. 3d; 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 $CaCO_3$ 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., 2002, 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 are fertile in autumn-to-spring, avoiding exposure of their spores to high levels of PAR and UVR (Olischläger et al. 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).

Fucoid 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 fucoids and kelp canopee 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 O_2 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. 3e; 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 (F_v/F_m) of the kelp *Laminaria solidungula*. Variable salinity conditions also reduce photosynthetic efficiency (Fig. 3f; 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). However, the reduced growth associated with low salinity will have a negative impact on rhodolith beds (Teicher 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 CO_2 and low calcium carbonate saturation states (Fransner et al., 2022). Even if warming limits CO_2 absorption, indirect effects of the increase in sea temperature such as ice loss further promote this process by enhancing air-sea gas exchange, including CO_2 (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 CO_2 in marine systems has consequences on biological processes such as photosynthesis, respiration, calcification, dissolved organic carbon (DOC) release and carbon accumulation in biomolecules (Fig. 3g; 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 CO_2 concentration could lead to higher photosynthetic rates. However, Iñiguez et al. (2016a) found that *Saccharina latissima* and *Laminaria solidungula* were largely unaffected by elevated pCO_2 (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.

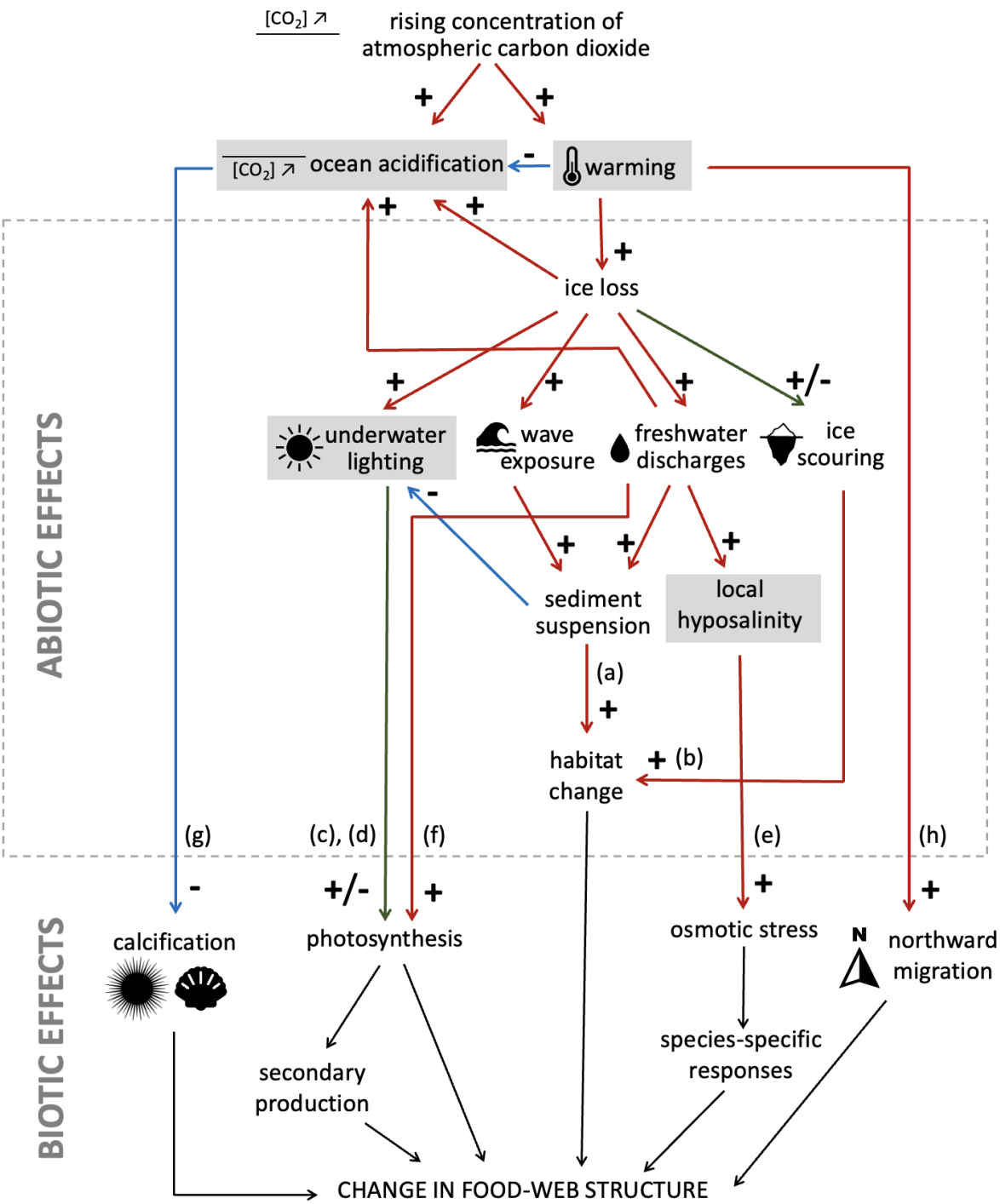


Figure 3: diagram of cascading effects of global change in the benthic coastal Arctic environment. The impact of processes framed in blue on benthic organisms are developed in section 5. A plus (+) and a red arrow mean a positive effect, a minus (-) and a blue arrow mean a negative effect, and a (+/-) and a green arrow mean an effect that could be both positive or negative.

Table 1: Conditions of temperature, light, salinity and pCO_2 tested on major fucoid, kelp and coralline algae species found in the Arctic

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 (Węsławski 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. 4; Jueterbock et al., 2016; Schoenwaelder et al. 2003).

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. 4; 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 et al., 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 (Węslawski 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. 4; 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 (Węslawski 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. 3h; Węslawski 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 and Johnsen 2005, Węslawski 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., 2009) and in Hornsund (Węslawski 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 (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 has being adaptated 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 (Węslawski 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.

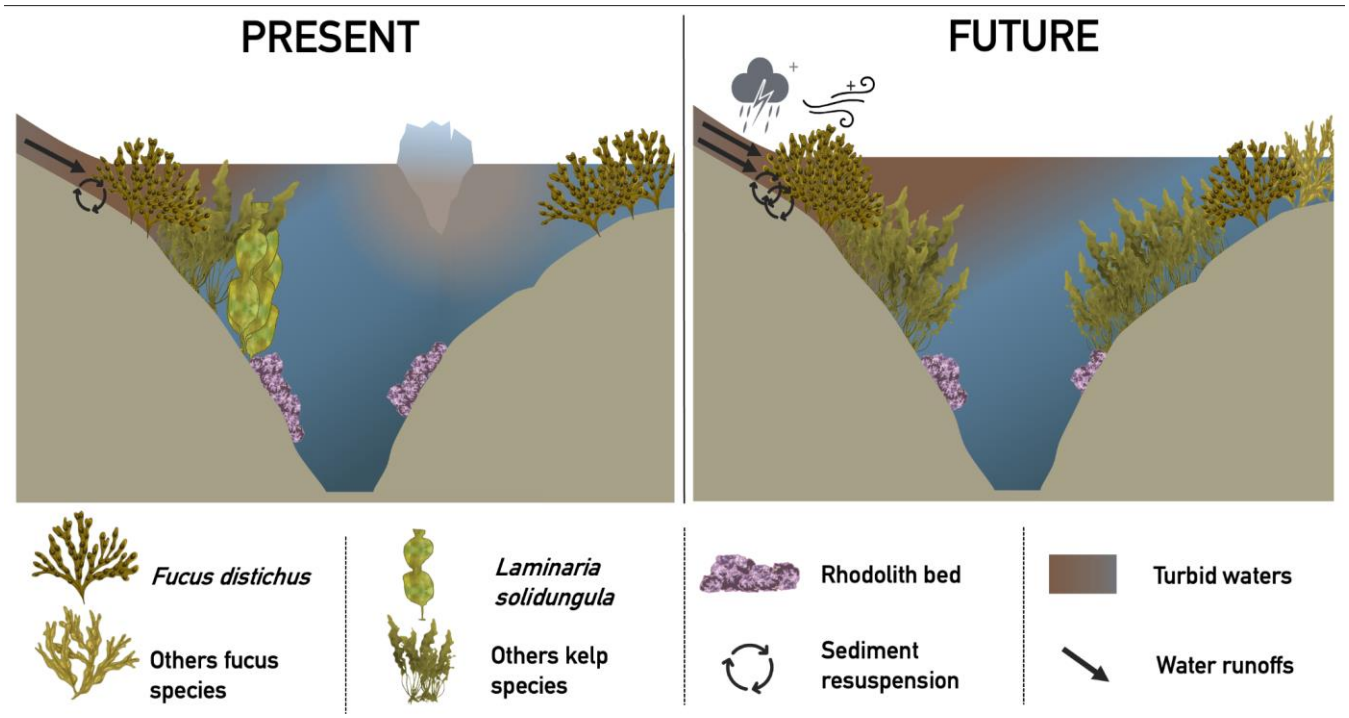


Figure 4: Schematic representation of the present and expected future Arctic coastal macroalgae communities. Present: fucoids dominate intertidal algae assemblages, while kelps dominate subtidal algae assemblages until they reach their low light threshold. *Laminaria solidungula* is present at the lower 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.

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 al., 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 (Węslawski 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 (Muth et al., 2009; Harley et al., 2012). Multifactorial studies at the community level that take into account interactions between stressors and between 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 global 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.

References

Adey, W., Halfar, J., Humphreys, A., Suskiewicz, T., Belanger, D., Gagnon, P., Fox, M., 2015. Subarctic rhodolith beds promote longevity of crustose coralline algal buildups and their climate archiving potential. PALAIOS 30, 281–293. https://doi.org/10.2110/palo.2014.075

Adey, W.H., Hayek, L.-A.C., 2011. Elucidating marine biogeography with macrophytes: quantitative analysis of the North Atlantic supports the thermogeographic model and demonstrates a distinct subarctic region in the Northwestern Atlantic. Northeast. Nat. 18, 1–128. https://doi.org/10.1656/045.018.m801

Adey, W.H., Vassar, J.M., 1975. Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales). Phycologia 14, 55–69. https://doi.org/10.2216/i0031-8884-14-2-55.1

Aguilera, J., Karsten, U., Lippert, H., Vögele, B., Philipp, E., Hanelt, D., Wiencke, C., 1999. Effects of solar radiation on growth, photosynthesis and respiration of marine macroalgae from the Arctic. Mar. Ecol. Prog. Ser. 191, 109–119. https://doi.org/10.3354/meps191109

AHDR, I., 2004. Arctic Human Development Report. red. Níels Einarsson Joan Nymand Larsen Annika Nilsson Oran R Young Stefansson Arct. Inst. Dostępne Na Stronie Internetowej Httpwww Svs Isenhome10--Lang.-Content28-Ahdr-Chapters-Engl.

Al-Habahbeh, A.K., Kortsch, S., Bluhm, B.A., Beuchel, F., Gulliksen, B., Ballantine, C., Cristini, D., Primicerio, R., 2020. Arctic coastal benthos long-term responses to perturbations under climate warming. Philos. Trans. R. Soc. Math. Phys. Eng. Sci. 378, 20190355. https://doi.org/10.1098/rsta.2019.0355

Arrigo, K.R., van Dijken, G.L., 2011. Secular trends in Arctic Ocean net primary production. J. Geophys. Res. 116, C09011. https://doi.org/10.1029/2011JC007151

Bartsch, I., Paar, M., Fredriksen, S., Schwanitz, M., Daniel, C., Hop, H., Wiencke, C., 2016. Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and 2012–2014 reflect Arctic warming. Polar Biol. 39, 2021–2036. https://doi.org/10.1007/s00300-015-1870-1

Bartsch, I., Wiencke, C., Bischof, K., Buchholz, C.M., Buck, B.H., Eggert, A., Feuerpfeil, P., Hanelt, D., Jacobsen, S., Karez, R., Karsten, U., Molis, M., Roleda, M.Y., Schubert, H., Schumann, R., Valentin, K., Weinberger, F., Wiese, J., 2008. The genus ***Laminaria sensu lato***: recent insights and developments. Eur. J. Phycol. 43, 1–86. https://doi.org/10.1080/09670260701711376

Bélanger, S., Cizmeli, S.A., Ehn, J., Matsuoka, A., Doxaran, D., Hooker, S., Babin, M., 2013. Light absorption and partitioning in Arctic Ocean surface waters: impact of multiyear ice melting. Biogeosciences 10, 6433–6452. https://doi.org/10.5194/bg-10-6433-2013

Berge, J., Johnsen, G., Nilsen, F., Gulliksen, B., Slagstad, D., 2005. Ocean temperature oscillations enable reappearance of blue mussels *Mytilus edulis* in Svalbard after a 1000-year absence. Mar. Ecol. Prog. Ser. 303, 167.

Beuchel, F., Gulliksen, B., 2008. Temporal patterns of benthic community development in an Arctic fjord (Kongsfjorden, Svalbard): results of a 24-year manipulation study. Polar Biol. 31, 913–924. https://doi.org/10.1007/s00300-008-0429-9

Beuchel, F., Gulliksen, B., Carroll, M.L., 2006. Long-term patterns of rocky bottom macrobenthic community structure in an Arctic fjord (Kongsfjorden, Svalbard) in relation to climate variability (1980–2003). J. Mar. Syst. 63, 35–48. https://doi.org/10.1016/j.jmarsys.2006.05.002

Bird, N.L., McLachlan, J., 1976. Control of formation of receptacles in *Fucus distichus* L. subsp. *distichus*(Phaeophyceae, Fucales). Phycologia 15, 79–84. https://doi.org/10.2216/i0031-8884-

15-1-79.1

Bischof, K., Hanelt, D., Tüg, H., Karsten, U., Brouwer, P.E.M., Wiencke, C., 1998. Acclimation of brown algal photosynthesis to ultraviolet radiation in Arctic coastal waters (Spitsbergen, Norway). Polar Biol. 20, 388–395. https://doi.org/10.1007/s003000050319

Bischof, K., Hanelt, D., Wiencke, C., 1999. Acclimation of maximal quantum yield of photosynthesis in the brown alga *Alaria esculenta* under high light and UV radiation. Plant Biol. 1, 435–444. https://doi.org/10.1111/j.1438-8677.1999.tb00726.x

Bischoff, B., Wiencke, C., 1993. Temperature requirements for growth and survival of macroalgae from Disko Island (Greenland). Helgoländer Meeresunters. 47, 167–191. https://doi.org/10.1007/BF02430357

Blacker, R.W., Great Britain. Ministry of Agriculture, Fisheries and Food, 1957. Benthic Animals as Indicators of Hydrographic Conditions and Climatic Change in Svalbard Waters.

Blicher, M., Rysgaard, S., Sejr, M., 2007. Growth and production of sea urchin *Strongylocentrotus droebachiensis* in a high-Arctic fjord, and growth along a climatic gradient (64 to 77°N). Mar. Ecol. Prog. Ser. 341, 89–102. https://doi.org/10.3354/meps341089

Bliss, A.C., Steele, M., Peng, G., Meier, W.N., Dickinson, S., 2019. Regional variability of Arctic sea ice seasonal change climate indicators from a passive microwave climate data record. Environ. Res. Lett. 14, 045003. https://doi.org/10.1088/1748-9326/aafb84

Bolton, J.J., 2010. The biogeography of kelps (Laminariales, Phaeophyceae): a global analysis with new insights from recent advances in molecular phylogenetics. Helgol. Mar. Res. 64, 263–279. https://doi.org/10.1007/s10152-010-0211-6

Bonsell, C., Dunton, K.H., 2021. Slow community development enhances abiotic limitation of benthic community structure in a high Arctic kelp bed. Front. Mar. Sci. 8, 592295. https://doi.org/10.3389/fmars.2021.592295

Bonsell, C., Dunton, K.H., 2018. Long-term patterns of benthic irradiance and kelp production in the central Beaufort Sea reveal implications of warming for Arctic inner shelves. Prog. Oceanogr. 162, 160–170. https://doi.org/10.1016/j.pocean.2018.02.016

Bosence, D.W.J., 1983. The occurrence and ecology of recent rhodoliths — a review, in: Peryt, T.M. (Ed.), Coated Grains. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 225–242. https://doi.org/10.1007/978-3-642-68869-0_20

Brattegard, T., Holthe, T., 1997. Distribution of marine, benthic macro-organisms in Norway: a

tabulated catalogue, Preliminary ed. ed, Utredning for DN. The Directorate for Nature Management, Trandheim.

Brodie, J., Williamson, C.J., Smale, D.A., Kamenos, N.A., Mieszkowska, N., Santos, R., Cunliffe, M., Steinke, M., Yesson, C., Anderson, K.M., Asnaghi, V., Brownlee, C., Burdett, H.L., Burrows, M.T., Collins, S., Donohue, P.J.C., Harvey, B., Foggo, A., Noisette, F., Nunes, J., Ragazzola, F., Raven, J.A., Schmidt, D.N., Suggett, D., Teichberg, M., Hall-Spencer, J.M., 2014. The future of the Northeast Atlantic benthic flora in a high CO_2 world. Ecol. Evol. 4, 2787–2798. https://doi.org/10.1002/ece3.1105

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789. https://doi.org/10.1890/03-9000

Büdenbender, J., Riebesell, U., Form, A., 2011. Calcification of the Arctic coralline red algae *Lithothamnion glaciale* in response to elevated CO_2. Mar. Ecol. Prog. Ser. 441, 79–87. https://doi.org/10.3354/meps09405

Chan, P.T.W., Halfar, J., Adey, W.H., Lebednik, P.A., Steneck, R., Norley, C.J.D., Holdsworth, D.W., 2020. Recent density decline in wild-collected subarctic crustose coralline algae reveals climate change signature. Geology 48, 226–230. https://doi.org/10.1130/G46804.1

Chapman, A.R.O., Lindley, J.E., 1980. Seasonal growth of *Laminaria solidungula* in the Canadian High Arctic in relation to irradiance and dissolved nutrient concentrations. Mar. Biol. 57, 1–5. https://doi.org/10.1007/BF00420961

Chapman, W.L., Walsh, J.E., 1993. Recent variations of sea ice and air temperature in high latitudes. Bull. Am. Meteorol. Soc. 74, 33–47. https://doi.org/10.1175/1520-0477(1993)074<0033:RVOSIA>2.0.CO;2

Clark, G.F., Marzinelli, E.M., Fogwill, C.J., Turney, C.S.M., Johnston, E.L., 2015. Effects of sea-ice cover on marine benthic communities: a natural experiment in Commonwealth Bay, East Antarctica. Polar Biol. 38, 1213–1222. https://doi.org/10.1007/s00300-015-1688-x

Clark, G.F., Stark, J.S., Johnston, E.L., Runcie, J.W., Goldsworthy, P.M., Raymond, B., Riddle, M.J., 2013. Light-driven tipping points in polar ecosystems. Glob. Change Biol. 19, 3749–3761. https://doi.org/10.1111/gcb.12337

Conlan, K., Lenihan, H., Kvitek, R., Oliver, J., 1998. Ice scour disturbance to benthic communities in the Canadian High Arctic. Mar. Ecol. Prog. Ser. 166, 1–16. https://doi.org/10.3354/meps166001

Cornwall, C.E., Comeau, S., DeCarlo, T.M., Larcombe, E., Moore, B., Giltrow, K., Puerzer, F., D'Alexis, Q., McCulloch, M.T., 2020. A coralline alga gains tolerance to ocean acidification over multiple generations of exposure. Nat. Clim. Change 10, 143–146. https://doi.org/10.1038/s41558-019-0681-8

Coyer, J.A., Hoarau, G., Oudot-Le Secq, M.-P., Stam, W.T., Olsen, J.L., 2006. A mtDNA-based phylogeny of the brown algal genus *Fucus* (Heterokontophyta; Phaeophyta). Mol. Phylogenet. Evol. 39, 209–222. https://doi.org/10.1016/j.ympev.2006.01.019

Coyer, J.A., Hoarau, G., Van Schaik, J., Luijckx, P., Olsen, J.L., 2011. Trans-Pacific and trans-Arctic pathways of the intertidal macroalga *Fucus distichus* L. reveal multiple glacial refugia and colonizations from the north Pacific to the North Atlantic: Phylogeography of *Fucus distichus* in the Northern Hemisphere. J. Biogeogr. 38, 756–771. https://doi.org/10.1111/j.1365-2699.2010.02437.x

Csapó, H.K., Grabowski, M., Węsławski, J.M., 2021. Coming home - Boreal ecosystem claims Atlantic sector of the Arctic. Sci. Total Environ. 771, 144817. https://doi.org/10.1016/j.scitotenv.2020.144817

Degen, R., Jørgensen, L., Ljubin, P., Ellingsen, I., Pehlke, H., Brey, T., 2016. Patterns and drivers of megabenthic secondary production on the Barents Sea shelf. Mar. Ecol. Prog. Ser. 546, 1–16. https://doi.org/10.3354/meps11662

Dickson, B., Meincke, J., Vassie, I., Jungclaus, J., Østerhus, S., 1999. Possible predictability in overflow from the Denmark Strait. Nature 397, 243–246. https://doi.org/10.1038/16680

Diehl, N., Bischof, K., 2021. Coping with a changing Arctic: mechanisms of acclimation in the brown seaweed *Saccharina latissima* from Spitsbergen. Mar. Ecol. Prog. Ser. 657, 43–57. https://doi.org/10.3354/meps13532

Diehl, N., Karsten, U., Bischof, K., 2020. Impacts of combined temperature and salinity stress on the endemic Arctic brown seaweed *Laminaria solidungula* J. Agardh. Polar Biol. 43, 647–656. https://doi.org/10.1007/s00300-020-02668-5

Diehl, N., Roleda, M.Y., Bartsch, I., Karsten, U., Bischof, K., 2021. Summer Heatwave Impacts on the European Kelp Saccharina latissima Across Its Latitudinal Distribution Gradient. Front. Mar. Sci. 8, 695821. https://doi.org/10.3389/fmars.2021.695821

Drewnik, A., Węsławski, J.M., Włodarska-Kowalczuk, M., 2017. Benthic crustacea and mollusca distribution in Arctic fjord – case study of patterns in Hornsund, Svalbard. Oceanologia 59, 565–575. https://doi.org/10.1016/j.oceano.2017.01.005

Drinkwater, K.F., 2006. The regime shift of the 1920s and 1930s in the north Atlantic. Prog. Oceanogr. 68, 134–151. https://doi.org/10.1016/j.pocean.2006.02.011

Duarte, C.M., Agustí, S., Wassmann, P., Arrieta, J.M., Alcaraz, M., Coello, A., Marbà, N., Hendriks, I.E., Holding, J., García-Zarandona, I., Kritzberg, E., Vaqué, D., 2012. Tipping Elements in the Arctic Marine Ecosystem. AMBIO 41, 44–55. https://doi.org/10.1007/s13280-011-0224-7

Filbee-Dexter, K., Feehan, C., Smale, D., Krumhansl, K., Augustine, S., Bettignies, F. de, Burrows, M.T., Byrnes, J., Campbell, J., Davoult, D., Dunton, K., Franco, J., Garrido, I., Grace, S., Hancke, K., Johnson, L., Konar, B., Pedersen, M., Moore, P., Norderhaug, K.M., O'Dell, A., Salomon, A., Sousa-Pinto, I., Yiu, D., Wernberg, T., 2020. Ocean temperature controls kelp decomposition and carbon sink potential (preprint). In Review. https://doi.org/10.21203/rs.3.rs-38503/v1

Filbee-Dexter, K., Wernberg, T., Fredriksen, S., Norderhaug, K.M., Pedersen, M.F., 2019. Arctic kelp forests: diversity, resilience and future. Glob. Planet. Change 172, 1–14. https://doi.org/10.1016/j.gloplacha.2018.09.005

Foster, M.S., 2001. Rhodolits: between rocks and soft places. J. Phycol. 37, 659–667. https://doi.org/10.1046/j.1529-8817.2001.00195.x

Franke, K., Liesner, D., Heesch, S., Bartsch, I., 2021. Looks can be deceiving: contrasting temperature characteristics of two morphologically similar kelp species co-occurring in the Arctic. Bot. Mar. 64, 163–175. https://doi.org/10.1515/bot-2021-0014

Fransner, F., Fröb, F., Tjiputra, J., Goris, N., Lauvset, S.K., Skjelvan, I., Jeansson, E., Omar, A., Chierici, M., Jones, E., Fransson, A., Ólafsdóttir, S.R., Johannessen, T., Olsen, A., 2022. Acidification of the Nordic Seas. Biogeosciences 19, 979–1012. https://doi.org/10.5194/bg-19-979-2022

Fredersdorf, J., Müller, R., Becker, S., Wiencke, C., Bischof, K., 2009. Interactive effects of radiation, temperature and salinity on different life history stages of the Arctic kelp *Alaria esculenta* (Phaeophyceae). Oecologia 160, 483–492. https://doi.org/10.1007/s00442-009-1326-9

Freiwald, A., Henrich, R., 1994. Reefal coralline algal build-ups within the Arctic Circle: morphology and sedimentary dynamics under extreme environmental seasonality. Sedimentology 41, 963–984. https://doi.org/10.1111/j.1365-3091.1994.tb01435.x

Goldsmit, J., Schlegel, R.W., Filbee-Dexter, K., MacGregor, K.A., Johnson, L.E., Mundy, C.J., Savoie, A.M., McKindsey, C.W., Howland, K.L., Archambault, P., 2021. Kelp in the eastern

Canadian Arctic: current and future predictions of habitat suitability and cover. Front. Mar. Sci. 18, 742209. https://doi.org/10.3389/fmars.2021.742209

Golubeva, E., Kraineva, M., Platov, G., Iakshina, D., Tarkhanova, M., 2021. Marine heatwaves in siberian Arctic seas and adjacent region. Remote Sens. 13, 4436. https://doi.org/10.3390/rs13214436

Gómez, I., Wulff, A., Roleda, M.Y., Huovinen, P., Karsten, U., Quartino, M.L., Dunton, K., Wiencke, C., 2009. Light and temperature demands of marine benthic microalgae and seaweeds in polar regions. botm 52, 593–608. https://doi.org/10.1515/BOT.2009.073

Gordillo, F.J.L., Aguilera, J., Wiencke, C., Jiménez, C., 2015. Ocean acidification modulates the response of two Arctic kelps to ultraviolet radiation. J. Plant Physiol. 173, 41–50. https://doi.org/10.1016/j.jplph.2014.09.008

Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLaughlin, F.A., McNutt, S.L., 2006. A major ecosystem shift in the Northern Bering Sea. Science 311, 1461–1464. https://doi.org/10.1126/science.1121365

Groisillier, A., Labourel, A., Michel, G., Tonon, T., 2015. The mannitol utilization system of the marine bacterium *Zobellia galactanivorans*. Appl. Environ. Microbiol. 81, 1799–1812. https://doi.org/10.1128/AEM.02808-14

Gutt, J., 2001. On the direct impact of ice on marine benthic communities, a review. Polar Biol. 24, 553–564. https://doi.org/10.1007/s003000100262

Guzinski, J., Mauger, S., Cock, J.M., Valero, M., 2016. Characterization of newly developed expressed sequence tag-derived microsatellite markers revealed low genetic diversity within and low connectivity between European *Saccharina latissima* populations. J. Appl. Phycol. 28, 3057–3070. https://doi.org/10.1007/s10811-016-0806-7

Hall, S.J., 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. Oceanogr. Mar. Biol. Annu. Rev.

Hall-Spencer, J.M., 1994. Biological studies on nongeniculate Corallinaceae. University of London.

Hanelt, D., Tüg, H., Bischof, K., Groß, C., Lippert, H., Sawall, T., Wiencke, C., 2001. Light regime in an Arctic fjord: a study related to stratospheric ozone depletion as a basis for determination of UV effects on algal growth. Mar. Biol. 138, 649–658. https://doi.org/10.1007/s002270000481

Hanelt, D., Wiencke, C., Nultsch, W., 1997. Influence of UV radiation on the photosynthesis of

arctic macroalgae in the field. J. Photochem. Photobiol. B 38, 40–47. https://doi.org/10.1016/S1011-1344(96)07415-5

Harley, C.D.G., Anderson, K.M., Demes, K.W., Jorve, J.P., Kordas, R.L., Coyle, T.A., Graham, M.H., 2012. Effects of climate change on global seaweed communities. J. Phycol. 48, 1064–1078. https://doi.org/10.1111/j.1529-8817.2012.01224.x

Heinrich, S., Valentin, K., Frickenhaus, S., John, U., Wiencke, C., 2012. Transcriptomic Analysis of Acclimation to Temperature and Light Stress in *Saccharina latissima* (Phaeophyceae). PLoS ONE 7, e44342. https://doi.org/10.1371/journal.pone.0044342

Heinrich, S., Valentin, K., Frickenhaus, S., Wiencke, C., 2015. Temperature and light interactively modulate gene expression in *Saccharina latissima* (Phaeophyceae). J. Phycol. 51, 93–108. https://doi.org/10.1111/jpy.12255

Henley, W.J., Dunton, K.H., 1997. Effects of nitrogen supply and continuous darkness on growth and photosynthesis of the arctic kelp *Laminaria solidungula*. Limnol. Oceanogr. 42, 209–216. https://doi.org/10.4319/lo.1997.42.2.0209

Hofmann, L.C., Schoenrock, K., de Beer, D., 2018. Arctic coralline algae elevate surface pH and carbonate in the dark. Front. Plant Sci. 9, 1416. https://doi.org/10.3389/fpls.2018.01416

Hop, H., Pearson, T., Hegseth, E.N., Kovacs, K.M., Wiencke, C., Kwasniewski, S., Eiane, K., Mehlum, F., Gulliksen, B., Wlodarska-Kowalczuk, M., Lydersen, C., Weslawski, J.M., Cochrane, S., Gabrielsen, G.W., Leakey, R.J.G., Lønne, O.J., Zajaczkowski, M., Falk-Petersen, S., Kendall, M., Wängberg, S.-Å., Bischof, K., Voronkov, A.Y., Kovaltchouk, N.A., Wiktor, J., Poltermann, M., Prisco, G., Papucci, C., Gerland, S., 2002. The marine ecosystem of Kongsfjorden, Svalbard. Polar Res. 21, 167–208. https://doi.org/10.1111/j.1751-8369.2002.tb00073.x

Hop, H., Wiencke, C., Vögele, B., Kovaltchouk, N.A., 2012. Species composition, zonation, and biomass of marine benthic macroalgae in Kongsfjorden, Svalbard. botm 55, 399–414. https://doi.org/10.1515/bot-2012-0097

Hopwood, M.J., Carroll, D., Dunse, T., Hodson, A., Holding, J.M., Iriarte, J.L., Ribeiro, S., Achterberg, E.P., Cantoni, C., Carlson, D.F., Chierici, M., Clarke, J.S., Cozzi, S., Fransson, A., Juul-Pedersen, T., Winding, M.H.S., Meire, L., 2020. Review article: How does glacier discharge affect marine biogeochemistry and primary production in the Arctic? The Cryosphere 14, 1347–1383. https://doi.org/10.5194/tc-14-1347-2020

Hovelsrud, G.K., Poppel, B., van Oort, B., Reist, J.D., 2011. Arctic societies, cultures, and peoples

in a changing cryosphere. AMBIO 40, 100–110. https://doi.org/10.1007/s13280-011-0219-4

Ingólfsson, A., 2008. The invasion of the intertidal canopy-forming alga *Fucus serratus* L. to southwestern Iceland: Possible community effects. Estuar. Coast. Shelf Sci. 77, 484–490. https://doi.org/10.1016/j.ecss.2007.10.006

Iñiguez, C., Carmona, R., Lorenzo, M.R., Niell, F.X., Wiencke, C., Gordillo, F.J.L., 2016a. Increased CO_2modifies the carbon balance and the photosynthetic yield of two common Arctic brown seaweeds: *Desmarestia aculeata* and *Alaria esculenta*. Polar Biol. 39, 1979–1991. https://doi.org/10.1007/s00300-015-1724-x

Iñiguez, C., Carmona, R., Lorenzo, M.R., Niell, F.X., Wiencke, C., Gordillo, F.J.L., 2016b. Increased temperature, rather than elevated CO_2, modulates the carbon assimilation of the Arctic kelps *Saccharina latissima* and *Laminaria solidungula*. Mar. Biol. 163, 248. https://doi.org/10.1007/s00227-016-3024-6

IPCC (2007) Climate Change 2007: the physical science basis. Summary for policymakers. WMO and UNEF, Geneva.

Jackson, A., 2003. *Lithothamnion glaciale*. Maerl.

Jakobsson, M., Grantz, A., Kristoffersen, Y., Macnab, R., MacDonald, R. W., Sakshaug, E., Stein, R., Jokat, W., 2004. The Arctic Ocean: boundary conditions and background information, in: Stein, Ruediger, MacDonald, Robie W. (Eds.), The Organic Carbon Cycle in the Arctic Ocean. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 1–32. https://doi.org/10.1007/978-3-642-18912-8_1

Jørgensbye, H.I.Ø., Halfar, J., 2017. Overview of coralline red algal crusts and rhodolith beds (Corallinales, Rhodophyta) and their possible ecological importance in Greenland. Polar Biol. 40, 517–531. https://doi.org/10.1007/s00300-016-1975-1

Jørgensen, L.L., Pearson, T.H., Anisimova, N.A., Gulliksen, B., Dahle, S., Denisenko, S.G., Matishov, G.G., 1999. Environmental influences on benthic fauna associations of the Kara Sea (Arctic Russia). Polar Biol. 22, 395–416. https://doi.org/10.1007/s003000050435

Jueterbock, A., Kollias, S., Smolina, I., Fernandes, J.M.O., Coyer, J.A., Olsen, J.L., Hoarau, G., 2014. Thermal stress resistance of the brown alga *Fucus serratus* along the north-Atlantic coast: Acclimatization potential to climate change. Mar. Genomics 13, 27–36. https://doi.org/10.1016/j.margen.2013.12.008

Jueterbock, A., Smolina, I., Coyer, J.A., Hoarau, G., 2016. The fate of the Arctic seaweed *Fucus*

*distichus*under climate change: an ecological niche modeling approach. Ecol. Evol. 6, 1712–1724. https://doi.org/10.1002/ece3.2001

Karsten, U., 2007. Research note: Salinity tolerance of Arctic kelps from Spitsbergen. Phycol. Res. 55, 257–262. https://doi.org/10.1111/j.1440-1835.2007.00468.x

Kędra, M., Kuliński, K., Walkusz, W., Legeżyńska, J., 2012. The shallow benthic food web structure in the high Arctic does not follow seasonal changes in the surrounding environment. Estuar. Coast. Shelf Sci. 114, 183–191. https://doi.org/10.1016/j.ecss.2012.08.015

Kędra, M., Moritz, C., Choy, E.S., David, C., Degen, R., Duerksen, S., Ellingsen, I., Górska, B., Grebmeier, J.M., Kirievskaya, D., van Oevelen, D., Piwosz, K., Samuelsen, A., Węsławski, J.M., 2015. Status and trends in the structure of Arctic benthic food webs. Polar Res. 34, 23775. https://doi.org/10.3402/polar.v34.23775

Kędra, M., Włodarska-Kowalczuk, M., Węsławski, J.M., 2010. Decadal change in macrobenthic soft-bottom community structure in a high Arctic fjord (Kongsfjorden, Svalbard). Polar Biol. 33, 1–11. https://doi.org/10.1007/s00300-009-0679-1

Konar, B., Edwards, M.S., Estes, J.A., 2014. Biological interactions maintain the boundaries between kelp forests and urchin barrens in the Aleutian Archipelago. Hydrobiologia 724, 91–107. https://doi.org/10.1007/s10750-013-1727-y

Konar, B., Riosmena-Rodriguez, R., Iken, K., 2006. Rhodolith bed: a newly discovered habitat in the North Pacific Ocean. Bot. Mar. 49. https://doi.org/10.1515/BOT.2006.044

Kortsch, S., Primicerio, R., Beuchel, F., Renaud, P.E., Rodrigues, J., Lønne, O.J., Gulliksen, B., 2012. Climate-driven regime shifts in Arctic marine benthos. Proc. Natl. Acad. Sci. 109, 14052–14057. https://doi.org/10.1073/pnas.1207509109

Krause-Jensen, D., Duarte, C.M., 2016. Substantial role of macroalgae in marine carbon sequestration. Nat. Geosci. 9, 737–742. https://doi.org/10.1038/ngeo2790

Krause-Jensen, D., Duarte, C.M., 2014. Expansion of vegetated coastal ecosystems in the future Arctic. Front. Mar. Sci. 1. https://doi.org/10.3389/fmars.2014.00077

Krause-Jensen, D., Lavery, P., Serrano, O., Marbà, N., Masque, P., Duarte, C.M., 2018. Sequestration of macroalgal carbon: the elephant in the Blue Carbon room. Biol. Lett. 14, 20180236. https://doi.org/10.1098/rsbl.2018.0236

Krause- Jensen, D., Marbà, N., Olesen, B., Sejr, M.K., Christensen, P.B., Rodrigues, J., Renaud, P.E., Balsby, T.J.S., Rysgaard, S., 2012. Seasonal sea ice cover as principal driver of spatial

and temporal variation in depth extension and annual production of kelp in Greenland. Glob. Change Biol. 18, 2981–2994. https://doi.org/10.1111/j.1365-2486.2012.02765.x

Krause-Jensen, D., Marbà, N., Sanz-Martin, M., Hendriks, I.E., Thyrring, J., Carstensen, J., Sejr, M.K., Duarte, C.M., 2016. Long photoperiods sustain high pH in Arctic kelp forests. Sci. Adv. 2, e1501938. https://doi.org/10.1126/sciadv.1501938

Krause-Jensen, D., Sejr, M.K., Bruhn, A., Rasmussen, M.B., Christensen, P.B., Hansen, J.L.S., Duarte, C.M., Bruntse, G., Wegeberg, S., 2019. Deep penetration of kelps offshore along the west coast of Greenland. Front. Mar. Sci. 6, 375. https://doi.org/10.3389/fmars.2019.00375

Krumhansl, K., Scheibling, R., 2012. Production and fate of kelp detritus. Mar. Ecol. Prog. Ser. 467, 281–302. https://doi.org/10.3354/meps09940

Kucera, H., Saunders, G.W., 2008. Assigning morphological variants of *Fucus* (Fucales, Phaeophyceae) in Canadian waters to recognized species using DNA barcoding. Botany 86, 1065–1079. https://doi.org/10.1139/B08-056

Kwiatkowski, L., Torres, O., Bopp, L., Aumont, O., Chamberlain, M., Christian, J.R., Dunne, J.P., Gehlen, M., Ilyina, T., John, J.G., Lenton, A., Li, H., Lovenduski, N.S., Orr, J.C., Palmieri, J., Santana-Falcón, Y., Schwinger, J., Séférian, R., Stock, C.A., Tagliabue, A., Takano, Y., Tjiputra, J., Toyama, K., Tsujino, H., Watanabe, M., Yamamoto, A., Yool, A., Ziehn, T., 2020. Twenty-first century ocean warming, acidification, deoxygenation, and upper-ocean nutrient and primary production decline from CMIP6 model projections. Biogeosciences 17, 3439–3470. https://doi.org/10.5194/bg-17-3439-2020

Laeseke, P., Bartsch, I., Bischof, K., 2019. Effects of kelp canopy on underwater light climate and viability of brown algal spores in Kongsfjorden (Spitsbergen). Polar Biol. 42, 1511–1527. https://doi.org/10.1007/s00300-019-02537-w

Lantuit, H., Overduin, P.P., Couture, N., Wetterich, S., Aré, F., Atkinson, D., Brown, J., Cherkashov, G., Drozdov, D., Forbes, D.L., Graves-Gaylord, A., Grigoriev, M., Hubberten, H.-W., Jordan, J., Jorgenson, T., Ødegård, R.S., Ogorodov, S., Pollard, W.H., Rachold, V., Sedenko, S., Solomon, S., Steenhuisen, F., Streletskaya, I., Vasiliev, A., 2012. The Arctic coastal dynamics database: a new classification scheme and statistics on Arctic permafrost coastlines. Estuaries Coasts 35, 383–400. https://doi.org/10.1007/s12237-010-9362-6

Lasserre, F., Pelletier, S., 2011. Polar super seaways? Maritime transport in the Arctic: an analysis of shipowners' intentions. J. Transp. Geogr. 19, 1465–1473. https://doi.org/10.1016/j.jtrangeo.2011.08.006

Lenoir, J., Svenning, J.-C., 2015. Climate-related range shifts - a global multidimensional synthesis and new research directions. Ecography 38, 15–28. https://doi.org/10.1111/ecog.00967

Lewis, P., 2020. Quantifying intertidal canopy-forming macroalgal production, extent, degradation, and blue carbon potential (Ph.D.). Aberystwyth University.

Li, H., Monteiro, C., Heinrich, S., Bartsch, I., Valentin, K., Harms, L., Glöckner, G., Corre, E., Bischof, K., 2020a. Responses of the kelp *Saccharina latissima* (Phaeophyceae) to the warming Arctic: from physiology to transcriptomics. Physiol. Plant. 168, 5–26. https://doi.org/10.1111/ppl.13009

Li, H., Scheschonk, L., Heinrich, S., Valentin, K., Harms, L., Glöckner, G., Corre, E., Bischof, K., 2020b. Transcriptomic responses to darkness and the survival strategy of the kelp *Saccharina latissima* in the Early Polar Night. Front. Mar. Sci. 7, 592033. https://doi.org/10.3389/fmars.2020.592033

Liesner, D., Fouqueau, L., Valero, M., Roleda, M.Y., Pearson, G.A., Bischof, K., Valentin, K., Bartsch, I., 2020a. Heat stress responses and population genetics of the kelp *Laminaria digitata* (Phaeophyceae) across latitudes reveal differentiation among North Atlantic populations. Ecol. Evol. 10, 9144–9177. https://doi.org/10.1002/ece3.6569

Liesner, D., Shama, L.N.S., Diehl, N., Valentin, K., Bartsch, I., 2020b. Thermal plasticity of the kelp *Laminaria digitata* (Phaeophyceae) across life cycle stages reveals the importance of cold seasons for marine forests. Front. Mar. Sci. 7, 456. https://doi.org/10.3389/fmars.2020.00456

Lippert, H., Iken, K., Rachor, E., Wiencke, C., 2001. Macrofauna associated with macroalgae in the Kongsfjord (Spitsbergen). Polar Biol. 24, 512–522. https://doi.org/10.1007/s003000100250

Lüning, K., 1991. Seaweeds: their environment, biogeography, and ecophysiology. John Wiley & Sons.

Lütz, C., Di Piazza, L., Fredersdorf, J., Bischof, K., 2016. The effect of ultraviolet radiation on cellular ultrastructure and photosystem II quantum yield of *Alaria esculenta* (L.) Greville from Spitsbergen (Norway). Polar Biol. 39, 1957–1966. https://doi.org/10.1007/s00300-015-1659-2

Makarov, V.N., Makarov, M.V., Schoschina, E.V., 1999. Seasonal dynamics of growth in the Barents Sea seaweeds: endogenous and exogenous regulation. Bot. Mar. 42. https://doi.org/10.1515/BOT.1999.007

Martins, N., Barreto, L., Bartsch, I., Bernard, J., Serrão, E., Pearson, G., 2022. Daylength influences reproductive success and sporophyte growth in the Arctic kelp species *Alaria*

esculenta. Mar. Ecol. Prog. Ser. 683, 37–52. https://doi.org/10.3354/meps13950

Martins, N., Pearson, G.A., Bernard, J., Serrão, E.A., Bartsch, I., 2020. Thermal traits for reproduction and recruitment differ between Arctic and Atlantic kelp *Laminaria digitata*. PLOS ONE 15, e0235388. https://doi.org/10.1371/journal.pone.0235388

Merzouk, A., Johnson, L.E., 2011. Kelp distribution in the Northwest Atlantic Ocean under a changing climate. J. Exp. Mar. Biol. Ecol. 400, 90–98. https://doi.org/10.1016/j.jembe.2011.02.020

Meyer, K.S., Sweetman, A.K., Kuklinski, P., Leopold, P., Vogedes, D., Berge, J., Griffiths, C., Young, C.M., Renaud, P.E., 2017. Recruitment of benthic invertebrates in high Arctic fjords: Relation to temperature, depth, and season: Recruitment in Arctic fjords. Limnol. Oceanogr. 62, 2732–2744. https://doi.org/10.1002/lno.10602

Mincks, S.L., Smith, C.R., Jeffreys, R.M., Sumida, P.Y.G., 2008. Trophic structure on the West Antarctic Peninsula shelf: detritivory and benthic inertia revealed by δ13C and δ15N analysis. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 2502–2514. https://doi.org/10.1016/j.dsr2.2008.06.009

Morata, N., Michaud, E., Poullaouec, M.-A., Devesa, J., Le Goff, M., Corvaisier, R., Renaud, P.E., 2020. Climate change and diminishing seasonality in Arctic benthic processes. Philos. Trans. R. Soc. Math. Phys. Eng. Sci. 378, 20190369. https://doi.org/10.1098/rsta.2019.0369

Müller, R., Desel, C., Steinhoff, F.S., Wiencke, C., Bischof, K., 2012. UV-radiation and elevated temperatures induce formation of reactive oxygen species in gametophytes of cold-temperate/Arctic kelps (Laminariales, Phaeophyceae): ROS induction in kelp gametophytes. Phycol. Res. 60, 27–36. https://doi.org/10.1111/j.1440-1835.2011.00630.x

Müller, R., Laepple, T., Bartsch, I., Wiencke, C., 2009. Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. botm 52, 617–638. https://doi.org/10.1515/BOT.2009.080

Müller, R., Wiencke, C., Bischof, K., 2008. Interactive effects of UV radiation and temperature on microstages of Laminariales (Phaeophyceae) from the Arctic and North Sea. Clim. Res. 37, 203–213. https://doi.org/10.3354/cr00762

Munda, I.M., Kremer, B.P., 1977. Chemical composition and physiological properties of fucoids under conditions of reduced salinity. Mar. Biol. 42, 9–15. https://doi.org/10.1007/BF00392009

Muth, A.F., Bonsell, C., Dunton, K.H., 2021. Inherent tolerance of extreme seasonal variability in

light and salinity in an Arctic endemic kelp (*Laminaria solidungula*). J. Phycol. 57, 1554–1562. https://doi.org/10.1111/jpy.13187

Muth, A.F., Esbaugh, A.J., Dunton, K.H., 2020. Physiological responses of an Arctic crustose coralline alga (*Leptophytum foecundum*) to variations in salinity. Front. Plant Sci. 11, 1272. https://doi.org/10.3389/fpls.2020.01272

Nielsen, D.M., Pieper, P., Barkhordarian, A., Overduin, P., Ilyina, T., Brovkin, V., Baehr, J., Dobrynin, M., 2022. Increase in Arctic coastal erosion and its sensitivity to warming in the twenty-first century. Nat. Clim. Change 12, 263–270. https://doi.org/10.1038/s41558-022-01281-0

Norkko, A., Thrush, S.F., Cummings, V.J., Gibbs, M.M., Andrew, N.L., Norkko, J., Schwarz, A.-M., 2007. Trophic structure of coastal antarctic food webs associated with changes in sea ice and food supply. Ecology 88, 2810–2820. https://doi.org/10.1890/06-1396.1

Notz, D., Community, S., 2020. Arctic Sea Ice in CMIP6. Geophys. Res. Lett. 47. https://doi.org/10.1029/2019GL086749

Obluchinskaya, E.D., Pozharitskaya, O.N., Zakharov, D.V., Flisyuk, E.V., Terninko, I.I., Generalova, Y.E., Smekhova, I.E., Shikov, A.N., 2022. The biochemical composition and antioxidant properties of *Fucus vesiculosus* from the Arctic region. Mar. Drugs 20, 193. https://doi.org/10.3390/md20030193

Olischläger, M., Iñiguez, C., Gordillo, F.J.L., Wiencke, C., 2014. Biochemical composition of temperate and Arctic populations of *Saccharina latissima* after exposure to increased pCO_2 and temperature reveals ecotypic variation. Planta 240, 1213–1224. https://doi.org/10.1007/s00425-014-2143-x

Olischläger, M., Iñiguez, C., Koch, K., Wiencke, C., Gordillo, F.J.L., 2017. Increased pCO_2 and temperature reveal ecotypic differences in growth and photosynthetic performance of temperate and Arctic populations of *Saccharina latissima*. Planta 245, 119–136. https://doi.org/10.1007/s00425-016-2594-3

Olischläger, M., Wiencke, C., 2013. Seasonal fertility and combined effects of temperature and UV-radiation on *Alaria esculenta* and *Laminaria digitata* (Phaeophyceae) from Spitsbergen. Polar Biol. 36, 1019–1029. https://doi.org/10.1007/s00300-013-1325-5

Oliver, E.C.J., Donat, M.G., Burrows, M.T., Moore, P.J., Smale, D.A., Alexander, L.V., Benthuysen, J.A., Feng, M., Sen Gupta, A., Hobday, A.J., Holbrook, N.J., Perkins-Kirkpatrick, S.E., Scannell, H.A., Straub, S.C., Wernberg, T., 2018. Longer and more frequent marine

heatwaves over the past century. Nat. Commun. 9, 1324. https://doi.org/10.1038/s41467-018-03732-9

Paar, M., Voronkov, A., Hop, H., Brey, T., Bartsch, I., Schwanitz, M., Wiencke, C., Lebreton, B., Asmus, R., Asmus, H., 2016. Temporal shift in biomass and production of macrozoobenthos in the macroalgal belt at Hansneset, Kongsfjorden, after 15 years. Polar Biol. 39, 2065–2076. https://doi.org/10.1007/s00300-015-1760-6

Park, J., Kim, J.K., Kong, J.-A., Depuydt, S., Brown, M.T., Han, T., 2017. Implications of rising temperatures for gametophyte performance of two kelp species from Arctic waters. Bot. Mar. 60. https://doi.org/10.1515/bot-2016-0103

Pearce, C.M., Scheibling, R.E., 1990. Induction of metamorphosis of larvae of the green sea urchin, *Strongylocentrotus droebachiensis*, by coralline red algae. Biol. Bull. 179, 304–311. https://doi.org/10.2307/1542322

Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., Clark, T.D., Colwell, R.K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R.A., Griffis, R.B., Hobday, A.J., Janion-Scheepers, C., Jarzyna, M.A., Jennings, S., Lenoir, J., Linnetved, H.I., Martin, V.Y., McCormack, P.C., McDonald, J., Mitchell, N.J., Mustonen, T., Pandolfi, J.M., Pettorelli, N., Popova, E., Robinson, S.A., Scheffers, B.R., Shaw, J.D., Sorte, C.J.B., Strugnell, J.M., Sunday, J.M., Tuanmu, M.-N., Vergés, A., Villanueva, C., Wernberg, T., Wapstra, E., Williams, S.E., 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science 355, eaai9214. https://doi.org/10.1126/science.aai9214

Peltikhina, T.S., 2002. Distribution peculiarities and stocks of *Laminaria* algae in the area of Isfjord of the Spitsbergen Archipelago. Complex Investig. Spitsbergen Nat. Murm. Biol. Inst. Murm. 168–171.

Pessarrodona, A., Assis, J., Filbee-Dexter, K., Burrows, M.T., Gattuso, J.-P., Duarte, C.M., Krause-Jensen, D., Moore, P.J., Smale, D.A., Wernberg, T., 2022. Global seaweed productivity. Sci. Adv. 8, eabn2465. https://doi.org/10.1126/sciadv.abn2465

Piepenburg, D., 2005. Recent research on Arctic benthos: common notions need to be revised. Polar Biol. 28, 733–755. https://doi.org/10.1007/s00300-005-0013-5

Polukhin, A., 2019. The role of river runoff in the Kara Sea surface layer acidification and carbonate system changes. Environ. Res. Lett. 14, 105007. https://doi.org/10.1088/1748-9326/ab421e

Renaud, P.E., Sejr, M.K., Bluhm, B.A., Sirenko, B., Ellingsen, I.H., 2015. The future of Arctic benthos: Expansion, invasion, and biodiversity. Prog. Oceanogr. 139, 244–257. https://doi.org/10.1016/j.pocean.2015.07.007

Renaud, P.E., Wallhead, P., Kotta, J., Włodarska-Kowalczuk, M., Bellerby, R.G.J., Rätsep, M., Slagstad, D., Kukliński, P., 2019. Arctic Sensitivity? Suitable Habitat for Benthic Taxa Is Surprisingly Robust to Climate Change. Front. Mar. Sci. 6, 538. https://doi.org/10.3389/fmars.2019.00538

Richter-Menge, J., Overland, J.E., Mathis, J.T., Osborne, E., 2017. Arctic shows no sign of returning to reliably frozen region of recent past decades.

Roleda, M., Wiencke, C., Hanelt, D., 2005. Response of Arctic kelp zoospores to ultraviolet and photosynthetically active radiation in relation to growth depth.

Roleda, M.Y., 2016. Stress physiology and reproductive phenology of Arctic endemic kelp *Laminaria solidungula* J. Agardh. Polar Biol. 39, 1967–1977. https://doi.org/10.1007/s00300-015-1813-x

Roleda, M.Y., Hanelt, D., Wiencke, C., 2006b. Exposure to ultraviolet radiation delays photosynthetic recovery in Arctic kelp zoospores. Photosynth. Res. 88, 311–322. https://doi.org/10.1007/s11120-006-9055-y

Roleda, M.Y., Wiencke, C., Hanelt, D., 2006c. Thallus morphology and optical characteristics affect growth and DNA damage by UV radiation in juvenile Arctic *Laminaria* sporophytes. Planta 223, 407–417. https://doi.org/10.1007/s00425-005-0092-0

Roleda, M.Y., Wiencke, C., Hanelt, D., Bischof, K., 2007. Sensitivity of the early life stages of macroalgae from the northern hemisphere to ultraviolet radiation: photochemistry and photobiology. Photochem. Photobiol. 83, 851–862. https://doi.org/10.1562/2006-08-17-IR-1005

Roleda, M.Y., Wiencke, C., Luder, U.H., 2006a. Impact of ultraviolet radiation on cell structure, UV-absorbing compounds, photosynthesis, DNA damage, and germination in zoospores of Arctic *Saccorhiza dermatodea*. J. Exp. Bot. 57, 3847–3856. https://doi.org/10.1093/jxb/erl154

Ronowicz, M., Włodarska-Kowalczuk, M., Kukliński, P., 2020. Glacial and depth influence on sublittoral macroalgal standing stock in a high-Arctic fjord. Cont. Shelf Res. 194, 104045. https://doi.org/10.1016/j.csr.2019.104045

Scherrer, K.J.N., Kortsch, S., Varpe, Ø., Weyhenmeyer, G.A., Gulliksen, B., Primicerio, R., 2019.

Mechanistic model identifies increasing light availability due to sea ice reductions as cause for increasing macroalgae cover in the Arctic: light causes arctic macroalgal increase. Limnol. Oceanogr. 64, 330–341. https://doi.org/10.1002/lno.11043

Schimpf, N.M., Liesner, D., Franke, K., Roleda, M.Y., Bartsch, I., 2022. Microscopic Stages of North Atlantic Laminaria digitata (Phaeophyceae) Exhibit Trait-Dependent Thermal Adaptation Along Latitudes. Front. Mar. Sci. 9, 870792. https://doi.org/10.3389/fmars.2022.870792

Schoenrock, K.M., Bacquet, M., Pearce, D., Rea, B.R., Schofield, J.E., Lea, J., Mair, D., Kamenos, N., 2018. Influences of salinity on the physiology and distribution of the Arctic coralline algae, *Lithothamnion glaciale* (Corallinales, Rhodophyta). J. Phycol. 54, 690–702. https://doi.org/10.1111/jpy.12774

Schoenwaelder, M.E., Wiencke, C., Clayton, M.N., Glombitza, K.W., 2003. The effect of elevated UV radiation on *Fucus* spp. (Fucales, Phaeophyta) zygote and embryo development. Plant Biol. 5, 366–377.

Shiklomanov, I.A., 1998. World water resources at the beginning of the 21st century. monograph prepared and submitted to UNESCO, Division of Water Sciences Hydrological Institute. Int. Hydrol. Programme IHP UNESCO.

Sirenko, B.I., Gagaev, S.Yu., 2007. Unusual abundance of macrobenthos and biological invasions in the Chukchi Sea. Russ. J. Mar. Biol. 33, 355–364. https://doi.org/10.1134/S1063074007060016

Smolina, I., Kollias, S., Jueterbock, A., Coyer, J.A., Hoarau, G., 2016. Variation in thermal stress response in two populations of the brown seaweed, *Fucus distichus*, from the Arctic and subarctic intertidal. R. Soc. Open Sci. 3, 150429. https://doi.org/10.1098/rsos.150429

Springer, K., Lütz, C., Lütz-Meindl, U., Wendt, A., Bischof, K., 2017. Hyposaline conditions affect UV susceptibility in the Arctic kelp *Alaria esculenta* (Phaeophyceae). Phycologia 56, 675–685. https://doi.org/10.2216/16-122.1

Spurkland, T., Iken, K., 2011. Salinity and irradiance effects on growth and maximum photosynthetic quantum yield in subarctic *Saccharina latissima* (Laminariales, Laminariaceae). Bot. Mar. 54. https://doi.org/10.1515/bot.2011.042

Sswat, M., Gulliksen, B., Menn, I., Sweetman, A.K., Piepenburg, D., 2015. Distribution and composition of the epibenthic megafauna north of Svalbard (Arctic). Polar Biol. 38, 861–877. https://doi.org/10.1007/s00300-015-1645-8

Stein, R., Macdonald, R.W., 2004. The organic carbon cycle in the Arctic Ocean.

Steinacher, M., Joos, F., Frölicher, T.L., Plattner, G.-K., Doney, S.C., 2009. Imminent ocean acidification in the Arctic projected with the NCAR global coupled carbon cycle-climate model. Biogeosciences 6, 515–533. https://doi.org/10.5194/bg-6-515-2009

Steinhoff, F.S., Graeve, M., Bartoszek, K., Bischof, K., Wiencke, C., 2012. Phlorotannin production and lipid oxidation as a potential protective function against high photosynthetically active and UV radiation in gametophytes of *Alaria esculenta* (Alariales, Phaeophyceae). Photochem. Photobiol. 88, 46–57. https://doi.org/10.1111/j.1751-1097.2011.01004.x

Steinhoff, F.S., Wiencke, C., Wuttke, S., Bischof, K., 2011. Effects of water temperatures, UV radiation and low vs high PAR on phlorotannin content and germination in zoospores of *Saccorhiza dermatodea* (Tilopteridales, Phaeophyceae). Phycologia 50, 256–263. https://doi.org/10.2216/09-107.1

Steneck, R.S., 1990. Herbivory and the Evolution of Nongeniculate Coralline Algae (Rhodophyta, Corallinales) in the North Atlantic and North Pacific, in: Garbary, D.J., South, G.R. (Eds.), Evolutionary Biogeography of the Marine Algae of the North Atlantic. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 107–129. https://doi.org/10.1007/978-3-642-75115-8_6

Svendsen, H., Beszczynska-Møller, A., Hagen, J.O., Lefauconnier, B., Tverberg, V., Gerland, S., Børre Ørbæk, J., Bischof, K., Papucci, C., Zajaczkowski, M., Azzolini, R., Bruland, O., Wiencke, C., 2002. The physical environment of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard. Polar Res. 21, 133–166. https://doi.org/10.3402/polar.v21i1.6479

Svendsen, J.I., Elverhøi, A., Mangerud, J., 1996. The retreat of the barents sea ice sheet on the western svalbard margin. Boreas 25, 244–256.

Teagle, H., Hawkins, S.J., Moore, P.J., Smale, D.A., 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. J. Exp. Mar. Biol. Ecol. 492, 81–98. https://doi.org/10.1016/j.jembe.2017.01.017

Teichert, S., Woelkerling, W., Rüggeberg, A., Wisshak, M., Piepenburg, D., Meyerhöfer, M., Form, A., Büdenbender, J., Freiwald, A., 2012. Rhodolith beds (Corallinales, Rhodophyta) and their physical and biological environment at 80°31′N in Nordkappbukta (Nordaustlandet, Svalbard Archipelago, Norway). Phycologia 51, 371–390. https://doi.org/10.2216/11-76.1

Teichert, S., Woelkerling, W., Rüggeberg, A., Wisshak, M., Piepenburg, D., Meyerhöfer, M., Form, A., Freiwald, A., 2014. Arctic rhodolith beds and their environmental controls (Spitsbergen, Norway). Facies 60, 15–37. https://doi.org/10.1007/s10347-013-0372-2

Terhaar, J., Torres, O., Bourgeois, T., Kwiatkowski, L., 2021. Arctic Ocean acidification over the 21st century co-driven by anthropogenic carbon increases and freshening in the CMIP6 model ensemble. Biogeosciences 18, 2221–2240. https://doi.org/10.5194/bg-18-2221-2021

Traiger, S.B., Konar, B., 2018. Mature and developing kelp bed community composition in a glacial estuary. J. Exp. Mar. Biol. Ecol. 501, 26–35. https://doi.org/10.1016/j.jembe.2017.12.016

Trefry, J.H., Trocine, R.P., Alkire, M.B., Semmler, C.M., Savioe, M., Rember, R.D., 2009. Sources, concentrations, composition, partitioning and dispersion pathways for suspended sediments and potential metal contaminants in the Coastal Beaufort Sea. OCS Study MMS 14.

van de Poll, W.H., Hanelt, D., Hoyer, K., Buma, A.G.J., Breeman, A.M., 2007. Ultraviolet-B-induced cyclobutane-pyrimidine dimer formation and repair in Arctic marine macrophytes. Photochem. Photobiol. 76, 493–500. https://doi.org/10.1562/0031-8655(2002)0760493UBICPD2.0.CO2

van der Heijden, L.H., Kamenos, N.A., 2015. Reviews and syntheses: Calculating the global contribution of coralline algae to total carbon burial. Biogeosciences 12, 6429–6441. https://doi.org/10.5194/bg-12-6429-2015

Wassmann, P., Duarte, C.M., Agustí, S., Sejr, M.K., 2011. Footprints of climate change in the Arctic marine ecosystem: footprints of climate change. Glob. Change Biol. 17, 1235–1249. https://doi.org/10.1111/j.1365-2486.2010.02311.x

Watson, J., Estes, J.A., 2011. Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada. Ecol. Monogr. 81, 215–239. https://doi.org/10.1890/10-0262.1

Wernberg, T., Filbee-Dexter, K., 2018. Grazers extend blue carbon transfer by slowing sinking speeds of kelp detritus. Sci. Rep. 8, 17180. https://doi.org/10.1038/s41598-018-34721-z

Wernberg, T., Krumhansl, K., Filbee-Dexter, K., Pedersen, M.F., 2019. Status and trends for the world's kelp forests, in: World Seas: An Environmental Evaluation. Elsevier, pp. 57–78. https://doi.org/10.1016/B978-0-12-805052-1.00003-6

Węsławski, J.M., Buchholz, F., Głuchowska, M., Weydmann, A., 2017. Ecosystem maturation follows the warming of the Arctic fjords. Oceanologia 59, 592–602. https://doi.org/10.1016/j.oceano.2017.02.002

Węsławski, J.M., Kendall, M.A., Włodarska-Kowalczuk, M., Iken, K., Kędra, M., Legezynska, J., Sejr, M.K., 2011. Climate change effects on Arctic fjord and coastal macrobenthic diversity—observations and predictions. Mar. Biodivers. 41, 71–85. https://doi.org/10.1007/s12526-010-

0073-9

Weslawski, J.M., Wiktor, J., Kotwicki, L., 2010. Increase in biodiversity in the arctic rocky littoral, Sorkappland, Svalbard, after 20 years of climate warming. Mar. Biodivers. 40, 123–130. https://doi.org/10.1007/s12526-010-0038-z

Wiencke, C., Amsler, C.D., 2012. Seaweeds and their communities in polar regions, in: Wiencke, C., Bischof, K. (Eds.), Seaweed Biology, Ecological Studies. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 265–291. https://doi.org/10.1007/978-3-642-28451-9_13

Wiencke, C., Clayton, M.N., Gómez, I., Iken, K., Lüder, U.H., Amsler, C.D., Karsten, U., Hanelt, D., Bischof, K., Dunton, K., 2007. Life strategy, ecophysiology and ecology of seaweeds in polar waters. Rev. Environ. Sci. Biotechnol. 6, 95–126. https://doi.org/10.1007/s11157-006-9106-z

Wiencke, C., Clayton, M.N., Schoenwaelder, M., 2004. Sensitivity and acclimation to UV radiation of zoospores from five species of Laminariales from the Arctic. Mar. Biol. 145. https://doi.org/10.1007/s00227-004-1307-9

Wiencke, C., Gómez, I., Pakker, H., Flores-Moya, A., Altamirano, M., Hanelt, D., Bischof, K., Figueroa, F., 2000. Impact of UV-radiation on viability, photosynthetic characteristics and DNA of brown algal zoospores:implications for depth zonation. Mar. Ecol. Prog. Ser. 197, 217–229. https://doi.org/10.3354/meps197217

Wiencke, C., Hop, H., 2016. Ecosystem Kongsfjorden: new views after more than a decade of research. Polar Biol. 39, 1679–1687. https://doi.org/10.1007/s00300-016-2032-9

Wilson, K.L., Kay, L.M., Schmidt, A.L., Lotze, H.K., 2015. Effects of increasing water temperatures on survival and growth of ecologically and economically important seaweeds in Atlantic Canada: implications for climate change. Mar. Biol. 162, 2431–2444. https://doi.org/10.1007/s00227-015-2769-7

Włodarska-Kowalczuk, M., Kukliński, P., Ronowicz, M., Legeżyńska, J., Gromisz, S., 2009. Assessing species richness of macrofauna associated with macroalgae in Arctic kelp forests (Hornsund, Svalbard). Polar Biol. 32, 897–905. https://doi.org/10.1007/s00300-009-0590-9

Wlodarska-Kowalczuk, M., Pearson, T., Kendall, M., 2005. Benthic response to chronic natural physical disturbance by glacial sedimentation in an Arctic fjord. Mar. Ecol. Prog. Ser. 303, 31–41. https://doi.org/10.3354/meps303031

Wlodarska-Kowalczuk, M., Pearson, T.H., 2004. Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen). Polar

Biol. 27, 155–167. https://doi.org/10.1007/s00300-003-0568-y

Wulff, A., Iken, K., Quartino, M.L., Al-Handal, A., Wiencke, C., Clayton, M.N., 2009. Biodiversity, biogeography and zonation of marine benthic micro- and macroalgae in the Arctic and Antarctic. botm 52, 491–507. https://doi.org/10.1515/BOT.2009.072

Yamamoto, A., Kawamiya, M., Ishida, A., Yamanaka, Y., Watanabe, S., 2012. Impact of rapid sea-ice reduction in the Arctic Ocean on the rate of ocean acidification. Biogeosciences 9, 2365–2375. https://doi.org/10.5194/bg-9-2365-2012

Yamamoto-Kawai, M., McLaughlin, F.A., Carmack, E.C., Nishino, S., Shimada, K., 2009. Aragonite undersaturation in the Arctic Ocean: effects of ocean acidification and sea ice melt. Science 326, 1098–1100. https://doi.org/10.1126/science.1174190

Yesson, C., Simon, P., Chemshirova, I., Gorham, T., Turner, C.J., Hammeken Arboe, N., Blicher, M.E., Kemp, K.M., 2015. Community composition of epibenthic megafauna on the West Greenland Shelf. Polar Biol. 38, 2085–2096. https://doi.org/10.1007/s00300-015-1768-y

Zacher, K., Bernard, M., Bartsch, I., Wiencke, C., 2016. Survival of early life history stages of Arctic kelps (Kongsfjorden, Svalbard) under multifactorial global change scenarios. Polar Biol. 39, 2009–2020. https://doi.org/10.1007/s00300-016-1906-1

Zacher, K., Bernard, M., Daniel Moreno, A., Bartsch, I., 2019. Temperature mediates the outcome of species interactions in early life-history stages of two sympatric kelp species. Mar. Biol. 166, 161. https://doi.org/10.1007/s00227-019-3600-7

Figure1

Click here to access/download;Figure;Figure1.tiff

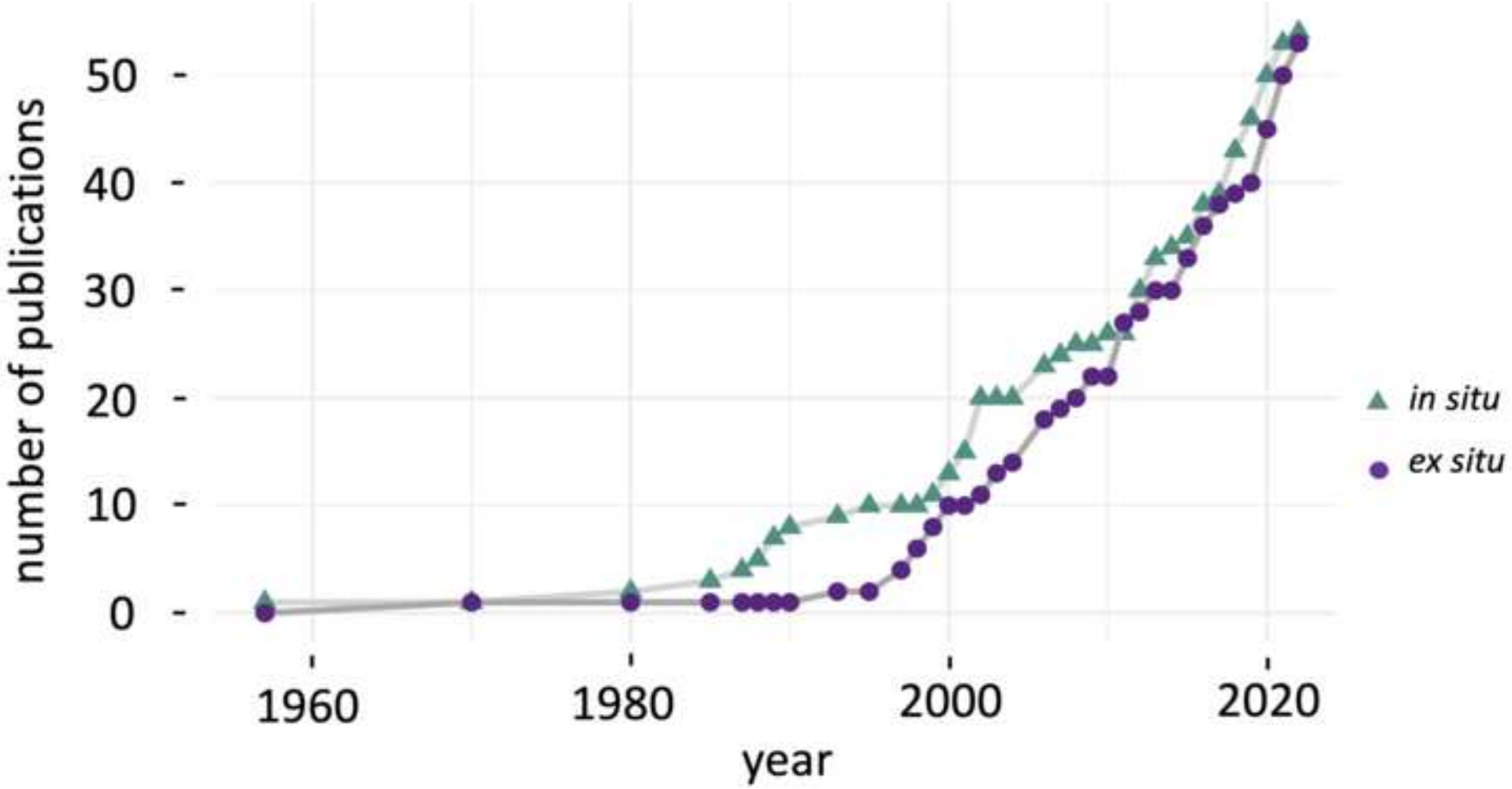
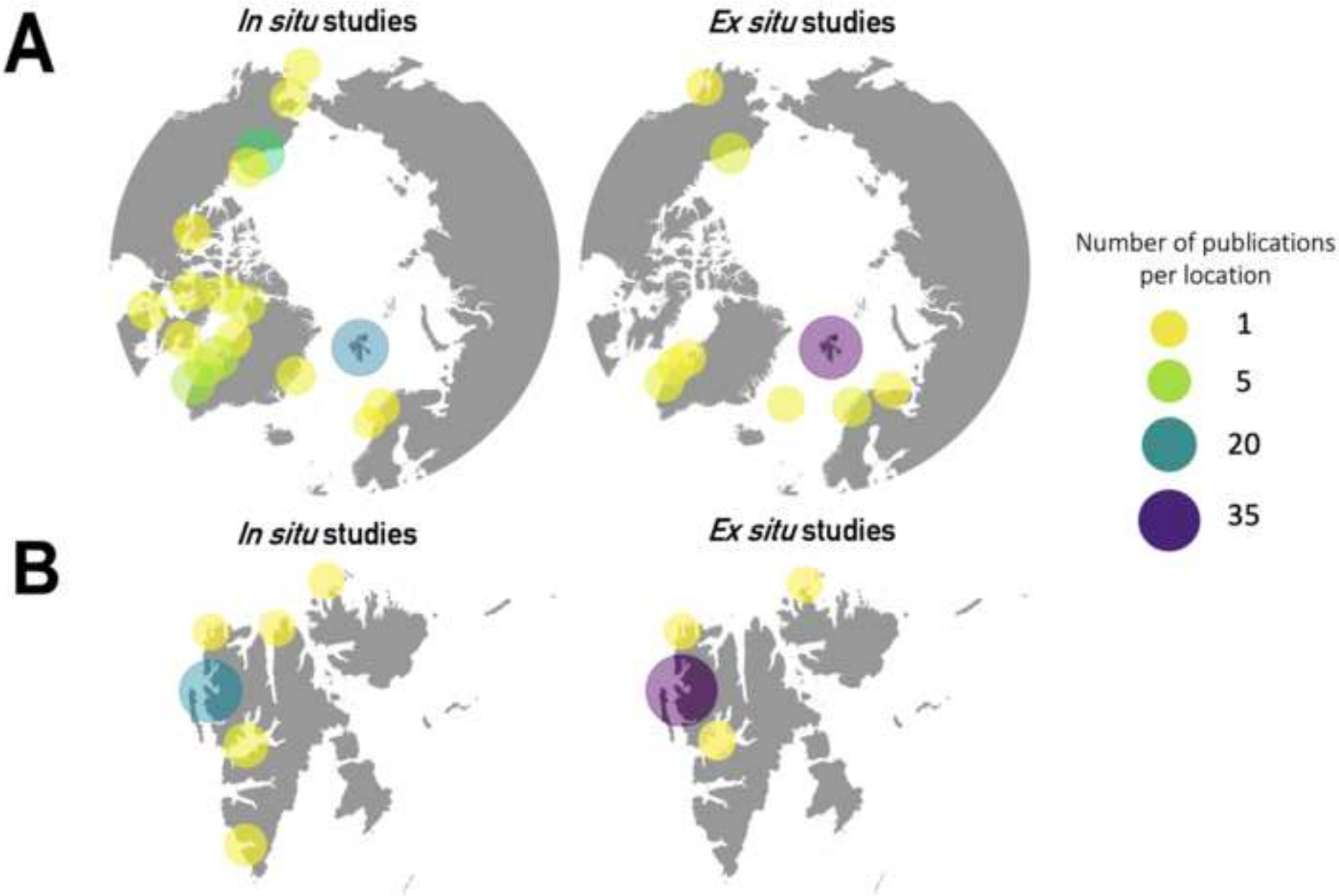


Figure2

Click here to access/download;Figure;Figure2.tif



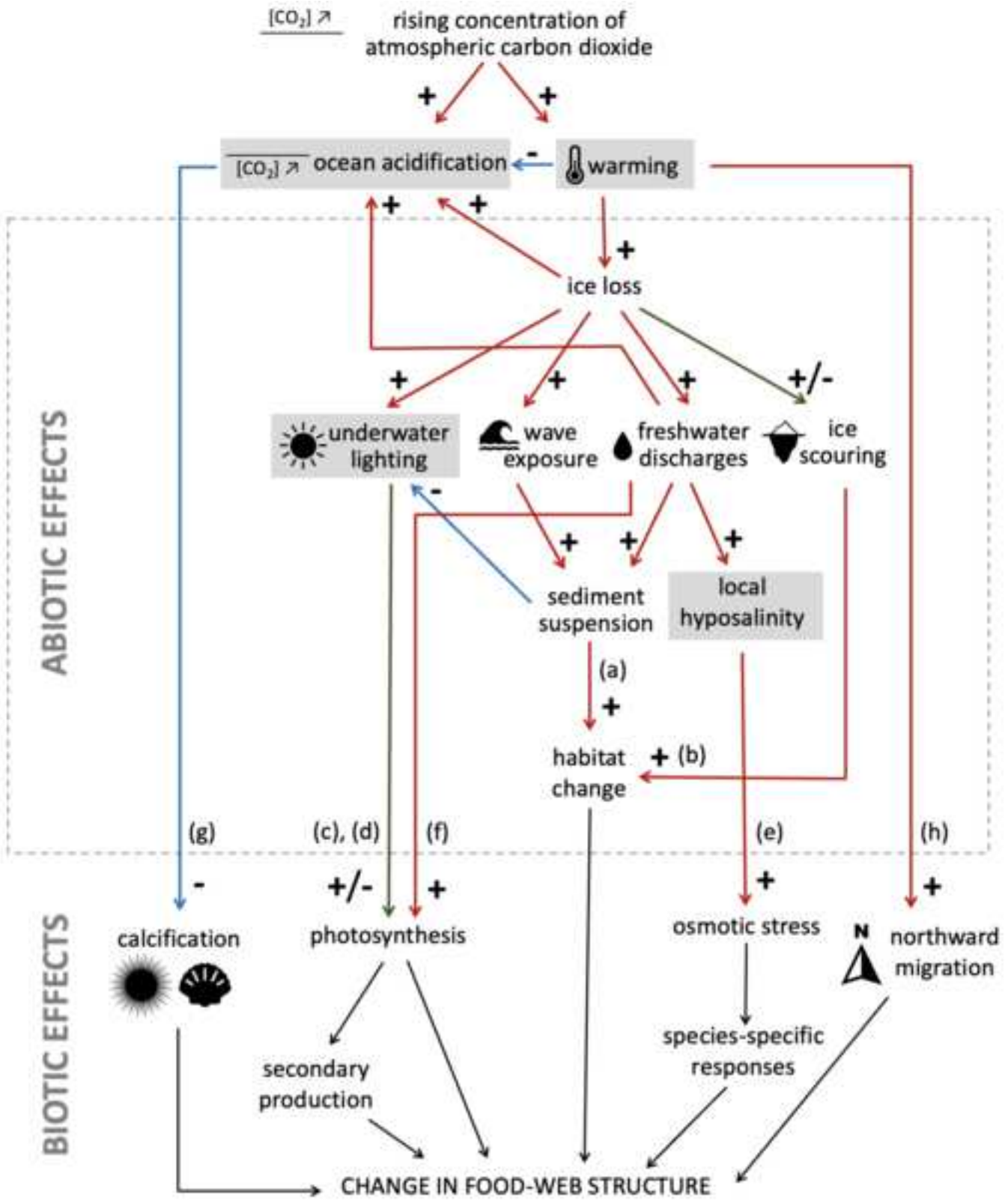

[CO2] ↗
rising concentration of atmospheric carbon dioxide
+
+
[CO2] ↗ ocean acidification
-
warming
+
+
+
ice loss
+
+
+
+/-
underwater lighting
wave exposure
freshwater discharges
ice scouring
-
+
+
+
sediment suspension
local hyposalinity
(a)
+
habitat change
+ (b)
ABIOTIC EFFECTS
(g)
(c), (d)
(f)
(e)
(h)
-
+/-
+
+
+
calcification
photosynthesis
osmotic stress
N
northward migration
BIOTIC EFFECTS
secondary production
species-specific responses
CHANGE IN FOOD-WEB STRUCTURE

Figure4

Click here to access/download;Figure;Fig4.tiff

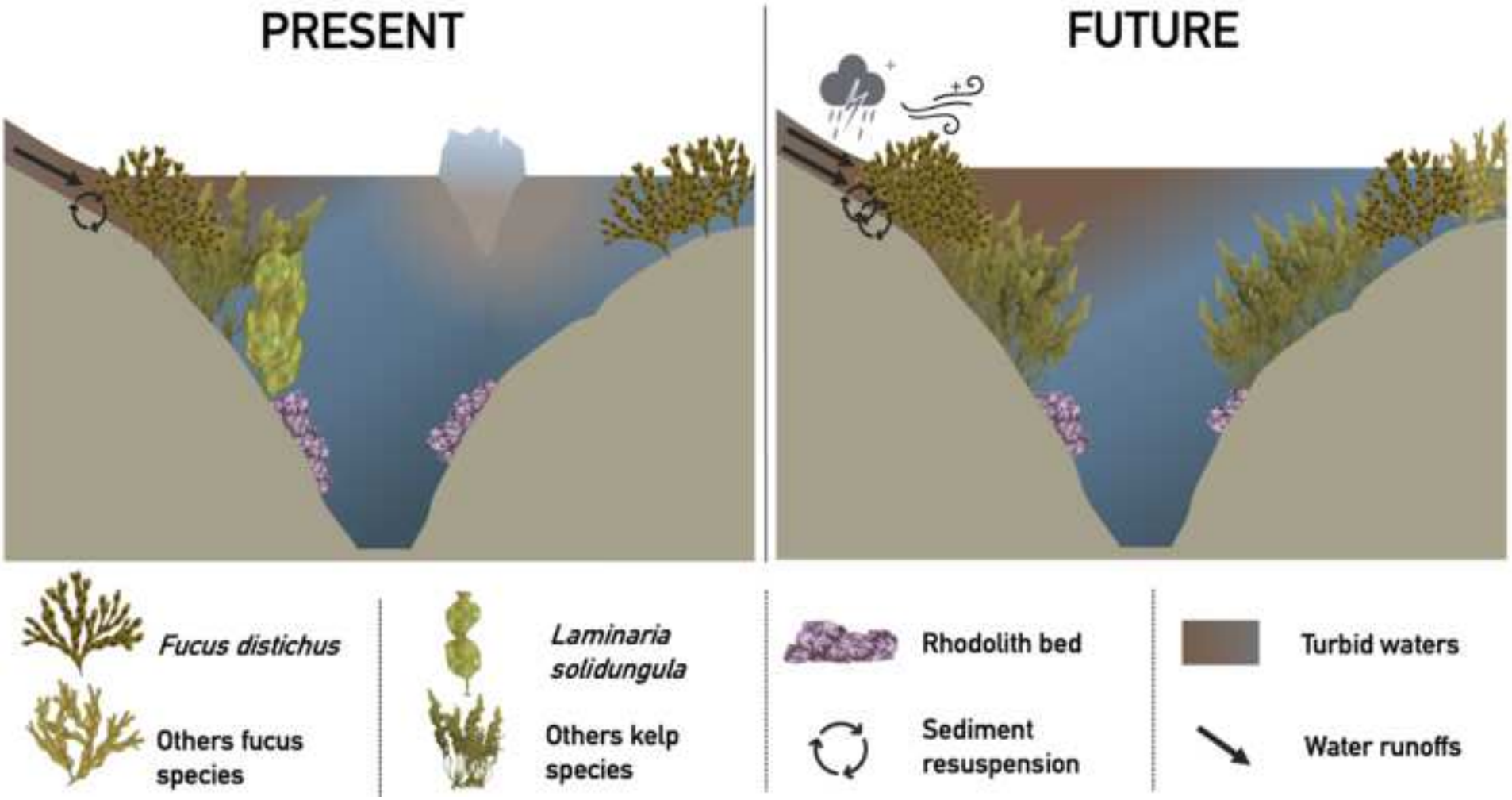


Table1

Click here to access/download;Figure;Table1.xlsx

					Key results			
Type	**Species**	**Stages**	**Parameters**	**Conditions tested**	**Photosynthesis**	**Growth**	**Others**	**References**
Fucoid	*Fucus serratus*	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		Marakov et al., 1999
	Fucus distichus	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).		Marakov et al., 1999
				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	growth rate: no effect of 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:no effect of salinity			Karsten et al., 2007
Kelp	*Saccharina latissima*	gametophyte	temperature, light	temp: 2, 7, 12, 18 ± 1.4°C		germination: + with temperature up to 12°C		Müller et al., 2008
				light: PAR (20 ± 3 µmol m–2.s–1), PAR + UVA (5.8 W m–2), PAR + UVA + UVB (0.34 W m–2)		germination:- at 12°C under UVA & UVB		
				temp: 2, 7, 12, 18 ± 1.4°C	absorbance: no effect of temperature			Müller et al., 2009
				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)	absorbance: + under UVA & UVB			
				temp: 2, 7, 12, 18 ± 1.4°C	absorbance: + with temperature			Müller et al., 2012
				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		Zacher et al., 2016
				temp: 5, 10, 15, 20°C		germination: no germlings at 20°C		Park et al., 2017
			light	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)		germination: close to 0%, 3, 6 and 9 days after 16h under UVA & UVB		Wiencke et al., 2004
				light: PAR (21.8 µmol m–2s–1), PAR + UVA (5.65 W.m-2), PAR + UVA + UVB (0.47 W.m-2)	quantum yield: - under light exposure			Roleda et al., 2006b
		sporophyte	temperature, light	temp: 2, 7, 12, 17°C	quantum yield: - under high PAR at 2°C and 17°C		different expression patterns under 2 and 17°C and high PAR compared to the control (12°C & low PAR);	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–), 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)	quantum yield: - under high PAR and high PAR + UVA + UVB at 2, 7 & 12°C		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.	
				temp: 0, 4°C	chla: + at 4°C, quantum yield: no effect of temperature	growth rate: no effect of temperature		Li et al., 2020b
				light: PAR (20 µmol m2 s−1; 18:6h light: dark), continuous dark	chla: + in the dark, quantum yield: no effect of light	growth rate: + under light		
			temperature, pCO2	temp: 4, 9°C	net photosynthesis: no effect of temperature & pCO2	growth rate: + of about 30% at 9 °C	dark respiration rate: - of 64% at 9 °C	Iñiguez et al., 2016a
				CO2 conditions: 390 and 1200 ppm		growth rate: largely unaffected by increased CO2 conditions		
				temp: 4, 10°C	net photosynthetic rate:+ at 10 °C at current pCO2 conditions	growth rate: + at 10°C		Olischläger et al., 2014; Olischläger et al., 2017
				CO2 conditions: 380, 800 and 1500 ppm			lipids, proteins, and total N-content: + at 4 °C.	
			temperature, salinity	temp: 4, 6, 8, 10°C	quantum yield and chla: no effect of temperature		mannitol content and C/N: no effect of temperature	Diehl et Bischoff, 2021
				salinity: 25, 32/34	quantum yield and chla: no effect of salinity		mannitol content and C/N: no effect of salinity	

				temp: 0, 8, 15°C	quantum yield: - under low salinity (20) at 15°C, but not at 0 and 8°C.	fresh weight: higher at 8°C and 15°C than at 0°C on day 18	expression patterns: suggest interacting effects of temperature and salinity on the number of differentially expressed genes.	Li et al., 2020a
				salinity: 20, 30		growth rate: - under low salinity (20) at day 18		
			light, salinity	light: 5, 20, 50 µmol m2 s−1	quantum yield: no effect of light	growth rate: - under lowest light level (5 µmol m2 s−1)		Spurkland et al., 2011
				salinity: 10, 13, 17, 20, 31	quantum yield: - at salinity=10	growth rate: - at salinity=10		
			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 and CO2 enrichment, recovery after 4 and 10 more days	growth rate: + 151% under UVR and CO2 enrichment		Gordillo et al., 2015
				CO2 condition: 380 and 1000 ppm				
			temperature	temp: 6, 8, 10, 12°C	quantum yield: no effect of temperature	growth rate: no effect of temperature		Diehl et al., 2021
			light	light: PAR (60 µmol m–2s–1), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.7 W.m-2)	quantum yield: negative correlation between recovering capacity and depth of sampling			Bischof et al., 1998
				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: - under UV radiations		Aguilera et al., 1999
				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)	chla: no effect of UV radiations	growth rate: - under UV radiations		Roleda et al., 2006c
				light: PAR PAR + UVA + UVB			significant light dependent repair	Van de Poll et al., 2002
			salinity	salinity: 5, 10, 15, 20, 25, 34, 45, 55, 60	quantum yield: - at salinity=5 and 10 after 2 days of treatment			Karsten et al., 2007
	Laminaria solidungula	gametophyte	temperature, light	temp: 2, 7, 12, 17°C	quatum yield: highest reduction in photosynthetic efficiency 17°C and lowest at 12°C	growth: gametophyte development after 16 and 48 days showed increasing size with increasing temperature		Roleda et al., 2016
				light: PAR (10 and 20 µmol m–2s–1) PAR + UVA (5 W.m-2) PAR + UVA + UVB (0.4 W.m-2)	quatum yield: exposure to PAB caused 93–98 % photoinhibition			
			light, salinity	light: PAR (10, 20, 40 µmol m–2s–1)		gametophyte density: - under UV radiations		Muth et al., 2021
				salinity: 10, 20, 30		gametophyte density: - at salinity=10 and 20	gametophyte unable to produce sporophyte at salinity=10	
			light	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)		germination: - under UVA & UVB, + 6 days after exposition (compared to 3 days)		Wiencke et al., 2004
		sporophyte	temperature, salinity	temp: 0, 5, 10, 15°C	quantum yield: - at 15°C after 14 days		mannitol content: + at salinity=35 at 0, 5 & 10°C	Diehl et al., 2020
				salinity: 25, 35			C/N: + at salinity=35 at 0, 5,10 & 15°C, + at 10 & 15°C	
			temperature, pCO2	temp: 4, 9°C	net photosynthesis: + at 9°C compared to 4°C.	growth rate: no effect of temperature and pCO2		Iñiguez et al., 2016a
				CO2 conditions: 390, 1200 ppm	net photosynthesis: + at increased CO2 conditions (at 4°C).			
			light, salinity	light: PAR (10, 20, 40 µmol m–2s–1)		sporophyte density: - under UV radiations		Muth et al., 2021
				salinity: 10, 20, 30		sporophyte density: - at salinity=10 and 20		
			light	light: PAR (66, 18, 13, 3, 0.5, 0.2, 0 uE m-2 s-1)		Blade lenght: - at low light & dark exposure		Chapman et al.., 1980
				light: PAR (25µmol m–2s–1, 12:12h light:dark), continuous dark		New blade surface area: - during dark exposure		Henley et al., 1997
				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		Aguilera et al., 1999
				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)	chla: no effect of UV radiations	growth rate: - under UV radiations		Roleda et al., 2006c
			salinity	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 et al., 2007
	Laminaria digitata	gametophyte	temperature, light	temp: 2, 7, 12 and 18 ± 1.4°C		germination: 0 to 0.1% at 18°C		Müller et al., 2008
				light: PAR (20 ± 3 µmol m–2.s–1), PAR + UVA (5.8 W m–2), PAR + UVA + UVB (0.34 W m–2)		germination: - at 2°C and 12°C under UVA & UVB		

				temp: 2, 7, 12 and 18 ± 1.4°C	absorbance: no effect of temperature			Müller et al., 2009
				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)	absorbance: no effect of light			
				temp: 2, 7, 12 and 18 ± 1.4°C	absorbance: increase with temperature			Müller et al., 2012
				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 and UVA & UVB at 2, 7 and 12°C			
				temp: 2, 7 ± 1°C			UVAB-susceptibility: increase with decreasing temperature	Olischläger and Wiencke, 2013
				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		growth: 3.2-fold lower at 22.5 ˚C and 25 ˚C than 15°C and 20°C	after a high temperature stress, the recovery temperature affects the capacity to reproduce	Martins et al., 2020
				light: PAR (15 µmol m–2s–1), red light, continuous dark				
			temperature	temp: 5, 15°C				Liesner et al., 2020a
				temp: 5, 9°C		germination: + at 9°C		Zacher et al., 2016
				temp: 5, 9, 15°C		germination: + at 9°C		Zacher et al., 2019
				temp: 0, 5, 10, 15, 20, 22, 23, 24, 25 ± 0.5°C		gametophyte density: decreased by 48 and 40% at 0 and 23 °C, respectively	abundance of females decreased with increasing temperatures overtime (ratio: 0.24±0.03, day 14)	Franke et al., 2021
				temp: 0, 3, 6, 9, 12, 15, 20, 21, 22, 23, 24, 25 ± 0.1°C			survival: significantly higher at 0°C (57.3% ± 8.4%) and 3°C (58.0% ± 8.6%) than at 12°C (35.3% ±2.4%) and 15°C (36.9% ± 9.7%)	Schimpf et al., 2022
			light	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)		germination: close to 0% 3, 6 and 9 days after 16h under UVA & UVB		Wiencke et al., 2004
				light: PAR (21.8 µmol m–2s–1), PAR + UVA (5.65 W.m-2), PAR + UVA + UVB (0.47 W.m-2)	quantum yield: - under light exposure, even more under UVA & UVB			Roleda et al., 2006b
		sporophyte	temperature	temp: 4, 5, 10, 15°C		sporophyte density: + at 9°C in monospecific cultivation		Zacher et al., 2019
				temp: 5, 15°C	quantum yield: - at 5°C	area growth rate: - at 5°C in July & February		Liesner et al., 2020a
				temp: 15, 19, 21, 23°C				Liesner et al., 2020b
				temp: 0, 5, 10, 15, 20, 22, 23, 24, 25 ± 0.5°C	quantum yield: maximum at 10 and 15°C	growth rate: + at 15°C		Franke et al., 2021
				temp: 0, 3, 6, 9, 12, 15 ± 0.1°C		sporophyte density: higher at 9°C and 12°C		Schimpf et al., 2022
			light	light: PAR (30 µmol m–2s–1), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.7 W.m-2)	photosynthesis: - after 6h of exposure to UV radiations	growth rate: no effect of UV radiations		Aguilera et al., 1999
				light: 12:12 h L:D (PAR : 5-10 W.m-2), continuous daylight		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).		Marakov et al., 1999
				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)	chla: no effect of UV radiations	growth rate: - under UV radiations		Roleda et al., 2006c
			salinity	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 et al., 2007
	Alaria esculenta	gametophyte	temperature, salinity, light	temp: 2, 7, 12, 16 ± 1°C		germination: optimal temperature range of 2–12°C		Fredersdorf et al., 2009
				salinity: 20, 26, 28, 33, 34				
				light: PAR (20 ± 2 and 6/8 µmol m–2.s–1), PAR + UVA (4.5 ± 0.5 W m–2), PAR + UVA + UVB (0.4 ± 0.04 W m–2)				
			temperature, light	temp: 2, 7, 12, 18 ± 1.4°C		germination: 0% at 18°C		Müller et al., 2008
				light: PAR (20 ± 3 µmol m–2.s–1), PAR + UVA (5.8 W m–2), PAR + UVA + UVB (0.34 W m–2)		germination: no effect of UV		
				temp: 2, 7, 12 and 18 ± 1.4°C	absorbance: no effect of temperature			Müller et al., 2009
				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)	absorbance: + under UVA & UVB at 2°C, + under UVA and UVA & UVB at 7, 12 and 18°C			
				temp: 2, 7, 12 and 18 ± 1.4°C	absorbance: increase with temperature			Müller et al., 2012

				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 and UVA & UVB at 2°C			
				temp: 2, 7 ± 1°C		germination rate: no significant effect of temperature and seasonality	UVAB-susceptibility: highest at 2 °C and the beginning of July, not affected by seasonality at 7 °C	Olischläger and Wiencke, 2013
				light: PAR (20 ± 4 W.m-2), PAR + UVA (3.8 ± 0.4 W.m-2) + UVB (0.41 ± 0.04 W.m-2)				
			temperature	temp: 5, 9°C		germination: + at 9°C		Zacher et al., 2016
				temp: 5, 9, 15°C		germination: + at 9°C in co-cultivation	no sporophyte at 15°C	Zacher et al., 2019
				temp: 5, 10, 15, and 20°C		germination: no germlings at 20°C		Park et al., 2017
			light	light: 12:12 h L:D (PAR : 5-10 W.m-2), continuous daylight		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).		Marakov et al., 1999
				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)		germination: - 3, 6 and 9 days after 16h under UVA & UVB		Wiencke et al., 2004
				light: PAR (21.8 µmol m–2s–1), PAR + UVA (5.65 W.m-2), PAR + UVA + UVB (0.47 W.m-2)	quantum yield: - under light exposure, even more under UVA & UVB			Roleda et al., 2006b
				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)			phlorotannin content: higher within the low PAR+UV-A treatment than under high PAR+UV-A exposure	Steinhoff et al., 2012
				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)	quantum yield: significant interaction between radiation and exposure time, as well as significant radiation effects		Germination success moderately positively correlated with initial Fv/Fm	Laeseke et al., 2019
		sporophyte	temperature, salinity, light	temp: 4, 8, 9, 13, 15, 17, 21 ± 1°C	photosynthesis: optimal temperature range of 13–17°C.		UV inhibition observed only under the lowest applied temperatures	Fredersdorf et al., 2009
				salinity: 20, 28, 34				
				light: PAR (46 ± 8 and 80 ± 10 µmol m–2.s–1), PAR + UVA (7 ± 1 W m–2), PAR + UVA + UVB (0.3 ± 0.07 W m–2)				
			salinity, light	salinity: 5, 15, 32	quantum yield: slightly - in a low-salinity during 7 days		specimens previously treated with hyposalinity are significantly less susceptible to UV	Springer et al., 2017
				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 - under UVR			
			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	quantum yield: drop after 2 days under UVR, recovery after 4 more days	growth rate: + 57% under UVR and CO2 enrichment		Gordillo et al., 2015
			temperature	temp: 4, 5, 10, 15°C		sporophyte density: + at 9°C in co-cultivation		Zacher et al., 2019
			light	light: PAR (60 µmol m–2s–1), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.7 W.m-2)	quantum yield: specimens from shallow water recover to a greater extent than those from deeper waters			Bischof et al., 1998
				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: - 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., 1999
				light: PAR (46 µmol m–2s–1), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.3 W.m-2)	quantum yield: - significantly after 1 day under PAR + UVA + UVB			Lütz et al., 2016
				light: 12:12h and 16:8h light: dark		growth: triggered by changing daylength from short to long days	reproductive success hampered under continuous light	Martins et al., 2022
			salinity	salinity: 5, 10, 15, 20, 25, 34, 45, 55, 60	quantum yield: - at salinity= 5 after 2 and 5 days of treatment			Karsten et al., 2007
			pCO2	CO2 conditions: 390, 1300 ppm	gross photosynthesis: no effect of CO2 conditions	growth rate: positively affected by CO2 enrichment	decreased respiration and lower accumulation of biostorage molecule under CO2 enrichment condition	Iñiguez et al., 2016b
	Saccorhiza dermatodea	gametophyte	temperature, light	temp: 2, 8, 11, 17°C		germination rate: reduced under PAR+UV-A+UV-B only at 17°C and 7°C outdoor treatment (- 21.4% and 9.6%	phlorotannin content: no effect of light treatments after 8h of exposure	Steinhoff et al., 2011b
				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)				

			light	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)		germination: - 3 after 16h under UVA & UVB, recovery after 6 days		Wiencke et al., 2004
				light: PAR (21.8 µmol m–2s–1), PAR + UVA (5.65 W.m-2), PAR + UVA + UVB (0.47 W.m-2)	quantum yield: - with increasing total fluence	germination: strong dose-dependent inhibitory effect of UVA & UVB		Roleda et al., 2006a,b
		sporophyte	light	light: PAR (60 µmol m–2s–1), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.7 W.m-2)	quantum yield: specimens from shallow water recover to a greater extent than those from deeper waters			Bischof et al., 1998
				light: PAR (30 µmol m–2s–1), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.7 W.m-2)	photosynthesis: - after 6h of exposure to UV radiations	growth rate: - under UV radiations		Aguilera et al., 1999
				light: 12:12 h L:D (PAR : 5-10 W.m-2), continuous daylight		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).		Marakov et al., 1999
			salinity	salinity: 5, 10, 15, 20, 25, 34, 45, 55, 60	quantum yield: - at salinity= 5, 10 after 2 days of treatment			Karsten et al., 2007
	Hedophyllum nigripes	gametophyte	temperature	temp: 0, 5, 10, 15, 18, 19, 21, 22 ± 0.5 °C		At 21 and 22 °C, all gametophytes died after 14 days	abundance of females decreased with increasing temperatures overtime (ratio: 0.24±0.03, day 14)	Franke et al., 2021
		sporophyte	temperature	temp: 0, 5, 10, 15, 18, 19, 21, 22 ± 0.5 °C		growth rate: + at 10°C, - at 15°C		Franke et al., 2021
Coralline algae	*Lithothamnion glaciale*	sporophyte	temperature, salinity	temp: 4, 7°C		calcification: reducted at low salinity and temperature treatments	metabolic processes: negatively influenced by low salinity	Schoenrock et al., 2018
				salinity: 22, 33				
			pCO2	CO2 conditions: 390, 815, 975 and 1570 ppm		calcification: reduced under high CO2 treatments		Büdenbender et al., 2011
	Leptophytum foecundum	sporophyte	salinity	salinity: 10, 20, 30		calcification: higher at salinity=10	higher pigment change at salinity=10	Muth et al., 2020
	Phymatolithon tenue	sporophyte	light	light: PAR (100 µmol m-2 s-1), dark			active calcification and no net dissolution in the dark	Hofmann et al., 2018

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.

Type	Location	Title	Date	Author	DOI
none	Arctic	An Arctic Alaskan Kelp Bed	1957	Mohr	10.14430/arctic3754
in situ	Beaufort sea	An Arctic Alaskan Kelp Bed	1957	Mohr	10.14430/arctic3754
ex situ	Northen 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
in situ	Fury sound	Seasonal growth of *Laminaria solidungula* in the Canadian High Arctic in relation to irradiance and dissolved nutrient concentrations	1980	Chapman	10.1007/BF00420961
in situ	Stefansson Sound, Alaska	Growth of dark-exposed *Laminaria saccharina* (L,) Lamour, and *Laminaria solidungula* J. Ag. (laminariales : phaeophyta) in the alaskan beaufort sea	1985	Dunton	10.1016/0022-0981(85)90057-7
in situ	Stefansson Sound, Alaska	Dependence of consumers on macroalgal (*Laminaria solidungula*) carbon in an arctic kelp community: δ13C evidence	1987	Dunten & Schell	10.1007/BF00392799
in situ	Stefansson Sound, Alaska	Photosynthetic performance of *Laminaria solidungula* measured in situ in the Alaskan High Arctic	1988	Dunton	10.1007/BF00391206
in situ	Svalbard	The phytobenthos of the Hornsund fjord, SW Spitsbergen	1989	Florczyk & Latala	10.3402/polar.v7i1.6828
in situ	Hudson bay	Arctic algal communities in the region of the Nuvuk Islands, Northeastern Hudson Bay, Canada	1989	Keats	NA
in situ	Stefansson Sound, Alaska	Growth and production in *Laminaria solidungula*: relation to continuous underwater light levels in the Alaskan High Arctic	1990	Dunton	10.1007/BF01314813
ex situ	Sisimiut	Temperature requirements for growth and survival of macroalgae from Disko Island (Greenland)	1993	Bischof & Wiencke	10.1007/BF02430357
in situ	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
in situ	Stefansson Sound, Alaska	A seasonal comparison of carbon, nitrogen, and pigment content in *Laminaria solidungula* and *L. saccharina* (Phaeophyta) in the Alaskan Arctic	1995	Henley & Dunton	10.1111/j.0022-3646.1995.00325.x
ex situ	Svalbard	Influence of UV radiation on the photosynthesis of arctic macroalgae in the field	1997	Hanelt	10.1016/S1011-1344(96)07415-5
ex situ	Stefansson Sound, Alaska	Effects of nitrogen supply and continuous darkness on growth and photosynthesis of the arctic kelp *Laminaria solidungula*	1997	Henley	10.4319/LO.1997.42.2.0209
ex situ	Svalbard	Acclimation of brown algal photosynthesis to ultraviolet radiation in Arctic coastal waters (Spitsbergen, Norway)	1998	Bischof	10.1007/s003000050319
ex situ	Svalbard	Capability of dynamic photoinhibition in Arctic macroalgae is related to their depth distribution	1998	Hanelt	10.1007/s002270050329
in situ	Svalbard	Effects of solar radiation on growth, photosynthesis and respiration of marine macroalgae from the Arctic	1999	Aguilera	10.3354/meps191109
ex situ	Svalbard	Acclimation of maximal quantum yield of photosynthesis in the brown alga *Alaria esculenta* under high light and UV radiation	1999	Bischof	10.1111/j.1438-8677.1999.tb00726.x
ex situ	Northen Norway	Seasonal dynamics of growth in the Barents Sea eeaweeds: 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
in situ	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
in situ	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
in situ	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
in situ	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
in situ	Young Sound	Biomass, photosynthesis and growth of *Laminaria saccharina* in a high-arctic fjord, NE Greenland	2002	Borum	10.1007/s00227-002-0806-9
none	Young Sound	Biomass, photosynthesis and growth of *Laminaria saccharina* in a high-arctic fjord, NE Greenland	2002	Borum	10.1007/s00227-002-0806-9
in situ	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
in situ	Young Sound	Primary production of crustose coralline red algae in a high Arctic fjord	2002	Roberts	10.1046/j.1529-8817.2002.01104.x
ex situ	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
ex situ	Svalbard	Screening capacity of UV-absorbing compounds in spores of Arctic Laminariales	2003	Roleda	10.1016/j.jembe.2006.07.004
ex situ	Svalbard	The effect of elevated UV radiation on *Fucus* spp.(Fucales, Phaeophyta) zygote and embryo development	2003	Schoenwaelder	10.1055/s-2003-42716
ex situ	Svalbard	The Effect of Ultraviolet Radiation on Ultrastructure and Photosynthesis in the Red Macroalgae Palmaria palmata and Odonthalia dentata from Arctic Waters	2004	Holzinger	10.1055/s-2004-821003.
ex situ	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
in situ	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
in situ	Svalbard	The response of nutrient assimilation and biochemical composition of Arctic seaweeds to a nutrient input in summer	2006	Gordillo	10.1093/JXB/ERL029
ex situ	Svalbard	Exposure to ultraviolet radiation delays photosynthetic recovery in Arctic kelp zoospores	2006	Roleda	10.1007/s11120-006-9055-y
ex situ	Svalbard	Impact of ultraviolet radiation on cell structure, UV-absorbing compounds, photosynthesis, DNA damage, and germination in zoospores of Arctic *Saccorhiza dermatodea*	2006	Roleda	10.1093/jxb/erl154
ex situ	Svalbard	Thallus morphology and optical characteristics affect growth and DNA damage by UV radiation in juvenile Arctic Laminaria sporophytes	2006	Roleda	10.1007/s00425-005-0092-0
ex situ	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
in situ	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
ex situ	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 cife stages of macroalgae from the Northern Hemisphere to ultraviolet radiation	2007	Roleda	10.1562/2006-08-17-IR-1005
in situ	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
ex situ	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
ex situ	Svalbard	Interactive effects of radiation, temperature and salinity on different life history stages of the Arctic kelp Alaria esculenta (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
ex situ	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
in situ	Svalbard	Lipid content and fatty acid consumption in zoospores/ developing gametophytes of *Saccharina latissima* (Laminariales, Phaeophyceae) as potential precursors for secondary metabolites as phlorotannins	2010	Steinhoff	10.1007/s00300-011-0960-y
ex situ	Svalbard	Calcification of the Arctic coralline algae *Lithothamnion glaciale* in response to elevated CO2	2011	Büdenbender	10.3354/meps09405
ex situ	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
ex situ	Jakalof bay	Salinity and irradiance effects on growth and maximum photosynthetic quantum yield in subarctic *Saccharina latissima* (Laminariales, Laminariaceae)	2011	Spurkland	10.1515/bot.2011.042
ex situ	Svalbard	Effects of water temperatures, UV radiation and low vs high PAR on phlorotannin content and germination in zoospores of *Saccorhiza dermatodea* (Tilopteridales, Phaeophyceae)	2011	Steinhoff	10.2216/09-107.1
ex situ	Svalbard	Phlorotannin production and lipid oxidation as a potential protective function against high photosynthetically active and UV radiation in gametophytes of *Alaria esculenta* (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
in situ	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
ex situ	Svalbard	A comprehensive cDNA library of light- and temperature-stressed *Saccharina latissima* (Phaeophyceae)	2012	Heinrich	10.1080/09670262.2012.660639
in situ	Svalbard	Species composition, zonation, and biomass of marine benthic macroalgae in Kongsfjorden, Svalbard	2012	Hop	10.1515/bot-2012-0097
in situ	Svalbard	Climate-driven regime shifts in Arctic marine benthos	2012	Kortsch	10.1073/pnas.1207509109
in situ	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
in situ	Stefansson Sound, Alaska	Lack of recovery from disturbance in high-arctic boulder communities	2013	Konar	10.1007/s00300-013-1340-6
ex situ	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
in situ	Pangnirtung fjord	Food web structure of a coastal Arctic marine ecosystem and implications for stability	2013	McMeans	10.3354/MEPS10278
ex situ	Svalbard	Seasonal fertility and combined effects of temperature and UV-radiation on *Alaria esculenta* and *Laminaria digitata* (Phaeophyceae) from Spitsbergen	2013	Olischläger	10.1007/s00300-013-1325-5
in situ	Svalbard	Arctic rhodolith beds and their environmental controls (Spitsbergen, Norway)	2013	Teichert	10.1007/s10347-013-0372-2
in situ	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

ex situ	Svalbard	Ocean acidification modulates the response of two Arctic kelps to ultraviolet radiation	2015	Gordillo	10.1016/j.jplph.2014.09.008
ex situ	Svalbard	Increased CO2 modifies the carbon balance and the photosynthetic yield of two common Arctic brown seaweeds: Desmarestia aculeata and Alaria esculenta	2015	Iniguez	10.1007/s00300-015-1724-x
ex situ	Svalbard	The effect of ultraviolet radiation on cellular ultrastructure and photosystem II quantum yield of *Alaria esculenta* (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
in situ	Svalbard	Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient	2015	Renaud	10.3389/fmars.2015.00031
in situ	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
in situ	Svalbard	Distribution of macroalgae in Kongsfjorden, Svalbard	2016	Hop	10.1007/s00300-016-2048-1
ex situ	Svalbard	Increased temperature, rather than elevated CO2, modulates the carbon assimilation of the Arctic kelps *Saccharina latissima* and *Laminaria solidungula*	2016	Iñiguez	10.1007/s00227-016-3024-6
none	Arctic	The fate of the Arctic seaweed *Fucus distichus* under climate change: an ecological niche modeling approach	2016	Jueterbock	10.1002/ece3.2001
in situ	Qeqertarsuaq	Long photoperiods sustain high pH in Arctic kelp forests	2016	Krause-Jensen	10.1126/sciadv.1501938
ex situ	Svalbard	Stress physiology and reproductive phenology of Arctic endemic kelp *Laminaria solidungula* J. Agardh	2016	Roleda	10.1007/s00300-015-1813-x
ex situ	Svalbard	Variation in thermal stress response in two populations of the brown seaweed, *Fucus distichus* , 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
in situ	Sisimiut	Climate change stimulates the growth of the intertidal macroalgae *Ascophyllum nodosum* near the northern distribution limit	2017	Márba	10.1007/s13280-016-0873-7
ex situ	Svalbard	Implications of rising temperatures for gametophyte performance of two kelp species from Arctic waters	2017	Park	10.1515/bot-2016-0103
ex situ	Svalbard	Hyposaline conditions affect UV susceptibility in the Arctic kelp *Alaria esculenta* (Phaeophyceae)	2017	Springer	10.2216/16-122.1
in situ	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
in situ	Svalbard	Arctic coralline algae elevate surface pH and carbonate in the dark	2018	Hofmann	10.3389/fpls.2018.01416
in situ	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
ex situ	Nuuk	Influences of salinity on the physiology and distribution of the Arctic coralline algae, *Lithothamnion glaciale* (Corallinales, Rhodophyta)	2018	Schoenrock	10.1111/jpy.12774
in situ	Svalbard	The longer the better: the effect of substrate on sessile biota in Arctic kelp forests	2018	Shunatova	10.1007/s00300-018-2263-z
in situ	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
in situ	Qeqertarsuaq	Deep penetration of kelps offshore along the west coast of Greenland	2019	Krause-Jensen	10.3389/fmars.2019.00375

in situ	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
ex situ	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
in situ	Svalbard	Arctic coastal benthos long-term responses to perturbations under climate warming	2020	Al-Habahbeh	10.1098/rsta.2019.0355
in situ	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
ex situ	Svalbard	Transcriptomic responses to darkness and the survival strategy of the kelp *Saccharina latissima* in the early polar night	2020	Huiru Li	10.3389/fmars.2020.592033
ex situ	Northen Norway	Heat stress responses and population genetics of the kelp *Laminaria digitata* (Phaeophyceae) across latitudes reveal differentiation among North Atlantic populations	2020	Liesner	10.1002/ece3.6569
ex situ	Svalbard	Thermal traits for reproduction and recruitment differ between Arctic and Atlantic kelp *Laminaria digitata*	2020	Martins	10.1371/journal.pone.0235388
both	Beaufort sea	Physiological responses of an Arctic crustose coralline alga (*Leptophytum foecundum*) to variations in salinity	2020	Muth	10.3389/fpls.2020.01272
in situ	Svalbard	Glacial and depth influence on sublittoral macroalgal standing stock in a high-Arctic fjord	2020	Ronowicz	10.1016/j.csr.2019.104045
ex situ	Qikiqtarjuaq	Arctic crustose coralline alga resilient to recent environmental change	2020	Williams	10.1002/lno.11640
in situ	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
ex situ	Svalbard	Coping with a changing Arctic: mechanisms of acclimation in the brown seaweed *Saccharina latissima* from Spitsbergen	2021	Diehl	10.3354/meps13532
ex situ	Svalbard	Summer heatwave impacts on the european kelp *Saccharina latissima* across its latitudinal distribution gradient	2021	Diehl	10.3389/fmars.2021.695821
in situ	Hudson/Baffin bay, Labrador se	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 se	Kelp in the Eastern Canadian Arctic: current and future predictions of habitat suitability and co	2021	Goldsmit	10.3389/fmars.2021.742209
ex situ	Svalbard	Differential acclimation responses to irradiance and temperature in two co-occurring seaweed species in Arctic fjords	2021	Marambio	10.33265/polar.v40.5702
ex situ	White sea	On the distribution of the Arctic endemic alga *Laminaria solidungula* (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 (*Laminaria solidungula*)	2021	Muth	10.1111/jpy.13187
ex situ	Svalbard	Daylength influences reproductive success and sporophyte growth in the Arctic kelp species *Alaria esculenta*	2022	Martins	10.3354/meps13950
in situ	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
ex situ	Svalbard	Microscopic Stages of North Atlantic *Laminaria digitata* (Phaeophyceae) Exhibit Trait-Dependent Thermal Adaptation Along Latitudes	2022	Schimpf	10.3389/fmars.2022.870792
ex situ	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