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Impact of climate change on Arctic macroalgal communities

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Abstract:	<p>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 fucooid 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. Fucooid 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.</p>
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Opposed Reviewers:	

1 Impact of climate change on Arctic macroalgal communities

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8 **Abstract**

9
10 The Arctic region faces a warming rate that is more than twice the global average. Sea-ice loss,
11 increase in precipitation and freshwater discharge, changes in underwater light, and
12 amplification of ocean acidification modify benthic habitats and the communities they host. Here
13 we synthesize existing information on the impacts of climate change on the macroalgal
14 communities of Arctic coasts. We review the short- and long-term changes in environmental
15 characteristics of shallow hard-bottomed Arctic coasts, the floristics of Arctic macroalgae
16 (description, distribution, life-cycle, adaptations), the responses of their biological and ecological
17 processes to climate change, the resulting winning and losing species, and the effects on
18 ecosystem functioning. The focus of this review is on furoid species, kelps, and coralline algae
19 which are key ecosystem engineers in hard-bottom shallow areas of the Arctic, providing food,
20 substrate, shelter, and nursery ground for many species. Changes in seasonality, benthic
21 functional diversity, food-web structure, and carbon cycle are already occurring and are
22 reshaping Arctic benthic ecosystems. Shallow communities are projected to shift from
23 invertebrate- to algal-dominated communities. Furoid and several kelp species are expected to
24 largely spread and dominate the area with possible extinctions of native species. A considerable
25 amount of functional diversity could be lost impacting the processing of land-derived nutrients
26 and organic matter and significantly altering trophic structure and energy flow up to the apex
27 consumers. However, many factors are not well understood yet, making it difficult to appreciate
28 the current situation and predict the future coastal Arctic ecosystem. Efforts must be made to
29 improve knowledge in key regions with proper seasonal coverage, taking into account
30 interactions between stressors and across species.

31

32 Keywords: climate change - macroalgae - Arctic - furoids - kelps - coralline algae

33

34 **1. Introduction**

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

41 The Arctic region is warming at a rate that is more than twice that of the global average (Richter-
42 Menge et al., 2017). From 1982 to 2017, the sea surface temperature in ice-free regions
43 increased by 0.5°C per decade, and it is expected to rise by 2 to 5°C over the next 80 years,
44 under SSP1-2.6 and SSP5-8.5 respectively (Kwiatkowski et al., 2020). With a current 10%
45 decrease in sea ice extent per decade, the Arctic could face an ice-free summer as early as
46 2035 (Notz and SIMIP Community, 2020). The decrease in albedo arising from the melting of
47 sea ice and snow leads to an exacerbation of global change in this region, referred to as polar
48 amplification (Chapman and Walsh 1993). In addition to sea-ice loss, climate change involves
49 increases in precipitation and freshwater discharge, changes in underwater light, and
50 amplification of ocean acidification (pH decrease of 0.18 to 0.45 on the Arctic basin scale by
51 2100, vs 0.06 to 0.32 units on the global scale; Steinacher et al., 2009; Terhaar et al., 2021). All
52 these processes modify marine habitats and the communities they host (Duarte et al., 2012;
53 Kortsch et al., 2012). The structure and function of Arctic marine ecosystems are, thus, foreseen
54 to change dramatically (Renaud et al., 2019). Footprints of current global change are already
55 visible in marine Arctic ecosystems (Wassmann et al., 2011). The Arctic shelves are likely to be
56 especially vulnerable due to their shallow depth and seasonally shifting ice cover (Piepenburg
57 2005).

58
59 Macroalgal benthic communities are an essential component of hard-bottomed shallow water
60 ecosystems in the Arctic. Furoid species and kelps are large brown seaweeds that can dominate
61 arctic rocky intertidal and subtidal areas and exhibit a high biomass (Hop et al., 2012; Iñiguez et
62 al., 2016a; Ronowicz et al., 2020). Providing a food source, substrate, sheltered area, and
63 nursery for many species (Filbee-Dexter et al., 2019), they are hotspots of Arctic marine
64 biodiversity (Włodarska-Kowalczyk et al., 2009; Krause-Jensen et al., 2012). Furoid and kelps
65 play an important role in the transfer of carbon (Filbee-Dexter et al., 2020; Lewis, 2020) through
66 high production, export of dissolved organic matter and detritus, as well as carbon sequestration
67 (Krause-Jensen and Duarte 2016).

68 Coralline algae are other important ecosystem engineers in the Arctic (Teichert et al., 2014).
69 These long-lived species (up to 1200-1600 years for individuals found in the North Pacific and

70 the Labrador sea; Adey et al., 2015) can form crusts or rhodolith beds that host important
71 biodiversity (Teichert et al., 2014). Despite relatively low annual growth rates, coralline algae
72 have a high potential for calcium carbonate accumulation (Freiwald and Henrich 1994) providing
73 a three dimensional habitat dominated by vagile invertebrates (Teichert et al., 2014). Rhodolith
74 beds are an important part of the prevailing coastal ecosystem and the biofilms on their surface
75 represent a major food source for many grazing organisms (Steneck 1990).

76 Furoid species, kelp forests, rhodolith beds and their associated flora and fauna make up the
77 hard-substrate benthic communities of the Arctic coasts. With global change, a general
78 expansion of both native and non-native kelp species has been documented during the last
79 decades (Węslawski et al., 2010; Kortsch et al., 2012; Bartsch et al., 2016). Warmer waters and
80 longer sea-ice-free periods may favour kelps growth, reproduction, and survival (Krause-Jensen
81 and Duarte 2016). Furoids are also spreading in the Arctic with a coverage that has already
82 doubled and may triple by the end of the century (Jueterbock 2016; Węslawski et al. 2010). The
83 current and projected expansion of Furoid species and kelp forests will exert cascading effects
84 on the composition and functioning of shallow coastal Arctic ecosystems (Krause-Jensen et al.,
85 2012). Arctic calcified algae distribution will be constrained by the upper temperature limit in the
86 South and by calcium carbonate saturation state in the North (Steinacher et al., 2009; Chan et
87 al., 2020). Furthermore, warming and increased advection are causing poleward migration,
88 bringing thermally tolerant boreal-subarctic species that compete with local species adapted to
89 cold waters (Węslawski et al., 2010). Shifts in species distribution, abundance and performance
90 are therefore foreseen (Wiencke and Amsler, 2012; Traiger and Konar, 2018). These changes
91 are expected to alter carbon cycling as well as the timing and magnitude of benthic primary
92 production (Grebmeier et al., 2006; Scherrer et al., 2019).

93

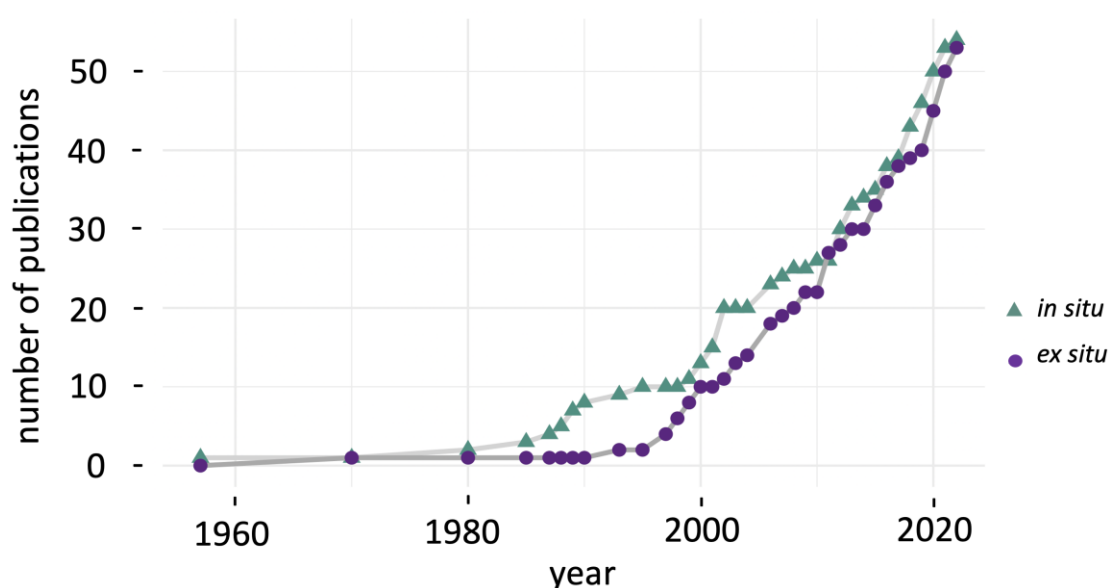
94 **2. Methods**

95 The objectives of the present study are: (1) to gather and synthesize existing information in order
96 to provide an overview of potential impacts of climate change on the macroalgae communities
97 of Arctic coasts and (2) to highlight knowledge gaps on species, ecological process or sub-
98 regions of the Arctic. We explored for shallow and hard-bottomed Arctic coasts, the short- and
99 long-term changes in environmental characteristics, species responses through biological
100 processes, the resulting winning and losing taxa and the impacts on ecosystem functioning.
101 Relevant articles were searched on "ISI Web of Science" and "GoogleScholar" using a Boolean
102 search string 'Benthos AND Arctic AND change', 'Benthos AND Arctic AND climate', 'Benthic
103 AND Arctic AND change', 'Benthic AND Arctic AND climate', 'Kelp AND Arctic AND change',
104 'Kelp AND Arctic AND climate', 'Furoid AND Arctic AND change', 'Furoid AND Arctic AND
105 climate', 'Coralline AND Arctic AND change', 'Coralline AND Arctic AND climate' (database

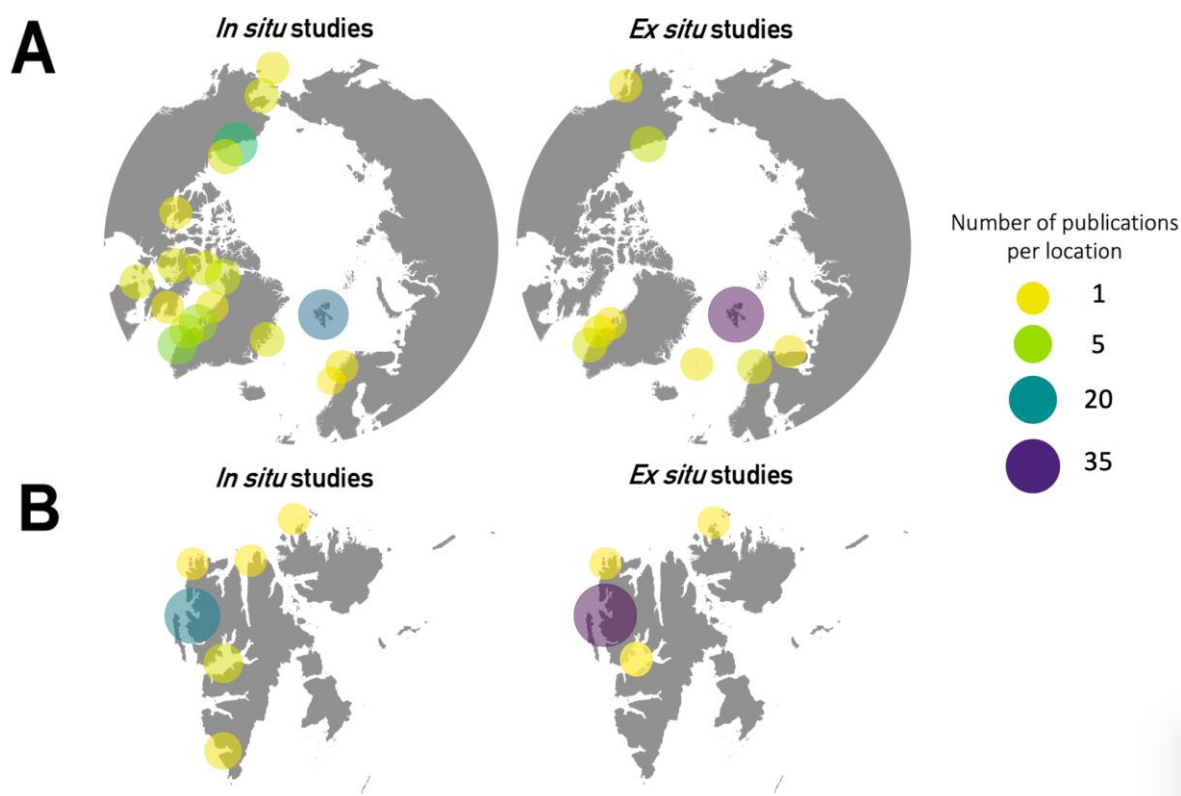
106 searches completed on 2022-09-24). A total of 91 papers were identified. The online tool
 107 “connectedpapers” (connectedpapers.com) was used to explore related studies; it returned 28
 108 additional papers. An article was considered as ‘relevant’ if the study focused on the impact of
 109 climate change - using one or more environmental parameters (e.g., temperature, salinity, light)
 110 - on Arctic macroalgal communities (up to 77 m depth, which is the depth at which the deepest
 111 coralline algae are described in the studies analyzed here) - whether on a single species or a
 112 community (fucoids, kelps or coralline algae). Potentially relevant articles not written in English
 113 were not considered. Each relevant article was tagged as an “*in situ*” study (i.e., conducted in
 114 the field) or “*ex situ*” study (i.e., conducted in the laboratory). Both or none of these tags could
 115 be assigned as appropriate, for example for broad review articles and modeling exercises. The
 116 references are listed in Table S1.
 117

118 3. Bibliometric analysis

119 Until 20 years ago, only a limited number of studies have been conducted to assess how marine
 120 macroalgae communities respond to global change in the Arctic (Fig. 1). The number of *ex situ*
 121 and *in situ* studies started rising in the mid 1990s to reach a total of 53 and 54 studies
 122 respectively in 2022. Aside from studies conducted along Russian coastlines that have not been
 123 translated into English and assessed here, *in situ* research has been carried out over the whole
 124 Arctic region (Fig. 2A). However, only a small portion of the Arctic coastlines has been studied;
 125 more than half of the papers report research conducted in Svalbard, with a particular emphasis
 126 on Kongsfjorden (Fig. 2B).



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



129

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

132

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

134 4.1 Seasonality

135 Arctic coastal environments are characterized by strong seasonal changes in photosynthetically
 136 available radiation (PAR). In spring, daylight lengthens, temperature increases and ice begins
 137 to melt. Thawing land and sea ice decreases salinity and affects the light regime afterwards by
 138 delivering dissolved and particulate matter which increases turbidity (Fig. 3 and 4). In winter, the
 139 daylight period shortens, temperature decreases, and sea and land ice forms. These marked
 140 seasonal fluctuations strongly influence biological processes and marine ecosystems (Kędra et
 141 al., 2015). In particular, the vertical zonation and productivity in shallow Arctic coastal areas are
 142 controlled by fluctuating salinity, turbidity, sea-ice shading, available organic matter, ice
 143 scouring, and sedimentation rate (e.g., Conlan et al., 1998; Włodarska-Kowalczyk and Pearson
 144 2004).

145

146 Environmental changes impact seasonality. For all regions of the Arctic Ocean, an increase in
147 the duration of the open water period is underway, ranging from 3.9 to 13.8 days per decade
148 (Bliss et al., 2019). Warming induces earlier and more intense ice melt with an increase in
149 meltwater runoff and flux of particles in spring (Fig. 4; Svendsen et al., 1996). It is projected that
150 this will strongly affect biological diversity in Arctic fjords (e.g., Jørgensen et al., 1999;
151 Wassmann et al., 2011). On the one hand, a shorter ice season, a smaller ice-covered area and
152 a reduction in ice thickness due to warming reduce ice-related pressures such as ice shading
153 or ice scouring on shallow benthic communities (Węslawski et al., 2010). On the other hand, the
154 associated increase in turbidity will restrict the euphotic layer and will enhance local hyposalinity
155 and coastal siltation (Węslawski et al., 2011; Bartsch et al., 2016). As a result, species expansion
156 and primary production may be more constrained near meltwater outflows, but less further away
157 (Hopwood et al., 2020).

158

159 **4.2 Habitat and pulse disturbances**

160 The habitat, especially the bottom structure and exposure to disturbances, are regulating factors
161 and key elements in the structuring of benthic ecosystems (Yesson et al., 2015). Erosion, as
162 well as river and glacial runoff, supply large amounts of sediments in coastal areas. Hard-bottom
163 substrates only represent ca. 35% of the Arctic coasts (Lantuit et al., 2012; Filbee-Dexter et al.,
164 2019).

165 As ice protects the shoreline from coastal erosion, a longer period of wave exposure is
166 anticipated as a result of the shortening of the ice-covered season. This will lead to a
167 considerable increase in resuspended sediments (Fig. 3a and 4; Trefry et al., 2009), a coarser
168 sediment structure, and significant changes in community composition (Węslawski et al., 2010).
169 This is called a pulse disturbance event. Unstable substrate and fine sediment are resulting in
170 a patchy distribution of rhodolith beds in Svalbard (Teichert et al., 2014).

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

179 Disturbance is an important driver of spatio-temporal biotic patterns, increasing the patchiness
180 of benthic biomass (Gutt 2001). Beyond coastal erosion, ice scouring and high sedimentation
181 rate are major disturbances in glacial bays (Clark et al., 2015). Ice scouring is caused by the
182 passage of an iceberg in a shallow area scraping the bottom and damaging the habitat and the

183 organisms therein (Fig. 3b). High sedimentation rate is due to a huge discharge of meltwater,
184 diluting organic matter, increasing turbidity, reducing primary production, hindering recruitment,
185 obstructing filtering appendages and even burying bottom dwellers (Hall 1994). Due to repeated
186 exposure to disturbance events, the size of organisms and the complexity of the community
187 structure both decrease when getting closer to the glacier (Włodarska-Kowalczyk and Pearson
188 2004). Additionally, the faunal biomass in the macroalgal belt exhibits greater spatial and
189 temporal variability at shallow depths revealing a fragmentation of the community by patches,
190 such as at Hansnest (Kongsfjorden, Svalbard), down to 5 m, which indicates recurrent
191 disturbance at various spatio-temporal scales. (Paar et al., 2016).

192 The recolonization rate after a pulse disturbance is low in the Arctic (Al-Habahbeh et al., 2020)
193 and the removal of a large portion of the initial biomass typically favors the establishment of
194 early succession stages (Conlan et al., 1998). The pulse-disturbed hard bottom area is first
195 colonized by algae and opportunistic taxa such as hydrozoans and small chitons. Then, larger
196 and longer-lived taxa such as barnacles, colonial sponges, or ascidians slowly overtake the area
197 (Al-Habahbeh et al., 2020). With increasing distance to the disturbed area, trophic structure
198 becomes more complex and biomass and diversity increase (Włodarska-Kowalczyk et al.,
199 2005).

200

201 As glaciers thin and melt, ice scouring will become more frequent in the short-term, but less in
202 the long-term, then promoting species interactions and leading to more stable and biologically
203 controlled community development (Fig. 4; Węslawski et al., 2010; Bartsch et al., 2016).
204 Reduced ice scouring will favor species expansion at shallow depths (Paar et al., 2016; Scherrer
205 et al., 2019). However, reducing sea ice cover, sea level rise, and rising surface air and
206 permafrost temperatures are already accelerating erosion of Arctic coastlines (Nielsen et al.,
207 2022). Furthermore, the occurrence and severity of extreme events such as sediment slides and
208 storms are projected to rise, increasing both the intensity and frequency of high sedimentation
209 events and coastal erosion (Müller et al., 2009; Kędra et al., 2010). Deposit of a sediment layer
210 on the algae and its surroundings will degrade settling conditions for the algae and its associated
211 community (Teichert et al., 2014). The associated increase in turbidity will negatively impact
212 growth and survival of macroalgae (see section 6.2). This will inevitably have consequences on
213 the distribution of macroalgal benthic communities.

214

215 **5. Arctic macroalgae: characteristics, distributions and ecological role**

216 Furoid species, kelps, and coralline algae are key species of hard-bottomed coastal ecosystems
217 in the Arctic. Fucoids dominate intertidal algal assemblages, while kelps dominate the subtidal
218 domain until they reach their low light threshold. The deepest kelps have been recorded at 61

219 m depth in the Disko Bay region (Greenland, Krause-Jensen et al., 2019). Coralline algae form
220 the understory of kelp forests or rhodolith beds and are found down to 77 m depth (Jørgensbye
221 and Halfar, 2017).

222

223 **5.1 Fucoids**

224 In the Arctic intertidal coasts of the Arctic, seaweed diversity is low, dominated by fucoids that
225 can experience changes in a multitude of abiotic drivers including ice scouring, desiccation, UV
226 radiation, and wave exposure. Fucoids are an order of intertidal brown algae widely distributed
227 along temperate and Arctic coasts (Obluchinskaya et al., 2022). They are native to the North
228 Pacific Ocean and have radiated in the North Atlantic Ocean (Coyer et al., 2006) resulting in a
229 few common species such as *Fucus spiralis*, *F. vesiculosus*, *F. serratus*, and *F. distichus*. The
230 latter is a homothallic cold-adapted species (Coyer et al., 2006; Jueterbock et al., 2016). Fucoids
231 inhabit a broad range of habitats from exposed rocky shores to calm bays and estuaries making
232 this order one of the most abundant group of organisms of intertidal rocky shores in the Northern
233 Hemisphere (Lüning 1991; Kucera and Saunders, 2008). They are important ecosystem
234 engineers forming wide coastal belts in Greenland, Jan Mayen, Norway, Svalbard, Baffin Island,
235 and Alaska (Smolina et al., 2016). They are a food source, substratum and shelter for epiphytic
236 and epibenthic communities with high species richness (including crustacean, snails and
237 polychaetes) preventing them from desiccation when the tide is low (Ingolfsoon 2008). Brown
238 (*Dictyosiphon foeniculaceus*, *Stictyosiphon tortilis*), red (*Pylaiella littoralis*) and green algae
239 (*Urococcus foslieanus*, *Ulothrix flacca*, *Acrosiphonia arcta* and *Prasiola crispa*) constitute the
240 understory of fucales canopy (Wulff et al., 2009).

241 A fucale individual is composed of three parts: (1) a holdfast, a root-like structure that anchors
242 the individual to the substrate, (2) a short stipe, a stem-like structure that allows the algae to
243 sway in currents; and (3) a frond —or blade— leaf structure(s) that actively participates in
244 photosynthesis. The frond is flattened, more or less dichotomously branched, and can contain
245 air bladders and reproductive extremities when fertile. Fucales can reproduce both asexually by
246 fragmentation or sexually. Once fertile, sporophytes release sperm and/or eggs from their
247 conceptacles. Fertilization takes place and results in a zygote which settles on a hard substrate,
248 germinates and forms a new sporophyte. The release usually happens at low tide, when there
249 is little water motion, favouring gamete meeting but limiting dispersal (Schoenwaelder et al.,
250 2003). Effective dispersal is however possible for homothallic fucale since only one rafting
251 individual is enough to establish a new population by self-fertilization (Jueterbock et al., 2016).
252 Through thalli dislodgement and receptacle release, fucoids are important contributors to carbon
253 production as they can exhibit annual rates of production equal to that of kelps (Lewis, 2020).

254

255 5.2 Kelps

256 Kelps are large brown algae found in subtidal cool waters, close to the shore and forming dense
257 canopy called kelp beds or kelp forests (Bolton et al., 2010). Although the term "kelp" frequently
258 refers to large canopy-forming brown algae species (and will be used as-well in that sense in
259 this study), in its strictest sense, the term refers to the order Laminariales (Bolton et al., 2010;
260 Teagle et al., 2017). Like fucoids, they comprise three parts: a holdfast, a strong and flexible
261 stipe and one or several blades.

262 Kelps have a biphasic life cycle characterized by the alternation of an asexual sporophyte and
263 a sexual gametophyte stage (Roleda 2016). A fertile sporophyte produces millions of spores,
264 resulting in the germination of a gametophyte when conditions are suitable. Male and female
265 gametophytes then produce sperm and eggs respectively. After the meeting of the gametes and
266 a potential fertilization, the zygote settles and develops, giving a new generation of sporophyte.
267 Only *Laminaria solidungula* is endemic from the Arctic, other species from the common genus
268 *Laminaria*, *Saccharina* and *Alaria* are of Atlantic and Pacific origin and extend into subarctic and
269 cooler temperate waters (Wulff et al., 2009). These kelp species, and more generally polar
270 algae, have adapted to this cold environment (Gómez et al., 2009). Metabolic strategies such
271 as enzymes able to work at low temperature, a higher unsaturated fatty acid content and
272 antifreeze proteins allow them to survive to cold temperature (Gómez et al., 2009).

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

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

284 Microbial films, sessile colonial filter feeders (bryozoan, hydrozoan, polychaetes) and mobile
285 herbivores (sea urchins, polychaetes, crustaceans, mollusks) characterize their epiphytic fauna.
286 Kelp forests support a high biodiversity by providing habitat, food, and nursery area for fish and
287 invertebrates (Filbee-Dexter et al., 2019). By altering light, sedimentation, physical abrasion,
288 and bottom currents they provide optimal conditions for the development of an understory mainly
289 composed of red and some green and brown algae (Teagle et al., 2017; Filbee-Dexter et al.,
290 2019). *Devaleraea ramentacea*, *Palmaria palmata*, *Phycodryis rubens*, *Ptilota gunneri* and

291 *Chaetomorpha* and *Desmarestia* genus make up the common dense understory of kelp forest
292 and deeper assemblages found in the Arctic (Hop et al., 2002).

293

294 **5.3 Coralline algae**

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

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

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

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

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

319 Rhodoliths - or maërl - are free-living structures mostly composed of crustose or branching
320 coralline algae (>50% in volume) that settle on a particulate substrate or are detached from
321 existing hard substrates (Teichert et al., 2014). Coralline algae are the master builders of such
322 three-dimensional calcified frameworks, with cavities and branches, that provide shelter for a
323 variety of organisms and support a high biodiversity (Teichert et al. 2012, 2014). Rhodoliths
324 beds support a diverse range of benthic species, including a microalgal epiphyton (comprising
325 foraminifera and diatoms), a vagile epifauna dominated by grazers (crustaceans, gastropods
326 and sea urchins), a sessile epifauna of filters feeders (bivalves, serpulids, spirorbids, bryozoan)
327 and an infauna that includes boring bivalves and polychaetes living within the algal thalli and the

328 sediment deposited around the rhodoliths (Bosence, 1983; Freiwald and Henrich 1994).
 329 Rhodoliths act as habitat, feeding, nursery, and spawning ground for various species including
 330 fishes (Thormar 2008).

331 The integrity of coralline algae requires grazers to keep them healthy by removing excessive
 332 fast growing fleshy algae and sessile invertebrates (Steneck 1990). One conspicuous herbivore
 333 is the sea urchin *Strongylocentrotus droebachiensis* whose larvae metamorphose on the surface
 334 of living coralline algae (Pearce & Scheibling, 1990). The formation and distribution of coralline
 335 algal communities rely heavily on these interactions with herbivores (Freiwald and Henrich,
 336 1994).

337 In the Arctic, rhodolith communities have been observed in Greenland (Thormar 2008,
 338 Jørgensbye and Halfar 2017), Alaska (Konar et al. 2006), North Norway (Freiwald and Henrich
 339 1994), and Svalbard (Teichert et al. 2014; Sswat et al., 2015). *Phymatolithon*, *Clathromorphum*,
 340 *Lithophyllum* and *Lithothamnion*, are widespread genera in shallow shelf areas with
 341 *Lithothamnion* able to colonize a large range of the dysphotic zone (up to 90 m deep for
 342 *Lithothamnion*; Teichert et al., 2012).

343

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

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

350

351 **6.1 Warming**

352 Temperature is the main physical driver in most ecosystems and has a major influence on polar
 353 benthic species distribution (Drewnik et al., 2017). Warming will increase suitable habitat for *F.*
 354 *distichus*, fostering seaweed meadows in the intertidal Arctic (Coyer et al., 2011). Among cold-
 355 temperate kelp species, many have growth temperature optima well above the temperature at
 356 which they are currently growing (Bischoff and Wiencke 1993; Müller et al., 2009; Meyer et al.,
 357 2017). Since enzymatic processes are temperature-dependent, it has a strong effect on all
 358 physiological processes (e.g., Brown et al., 2004; Gómez et al., 2009). For most kelp species,
 359 growth at 0-5 °C is typically less than one third of the rates reached at their optimal temperature
 360 ranging from 10 to 15 °C (Wiencke and Amsler 2012; Roleda 2016). By promoting
 361 photosynthesis, germination, gametogenesis, fertility and survival enhancement, warming is
 362 projected to increase the biomass of kelps such as *Saccharina latissima*, *Laminaria hyperborea*,

363 *Laminaria digitata*, and *Nereocystis luetkeana* and expand their distribution to higher latitudes
364 (Li et al., 2020a; Goldsmit et al., 2021).

365

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

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

380 Arctic and subarctic coralline algae are more sensitive to warming, which is consistent with the
381 fact that they live at greater depths and are therefore less exposed to large changes in
382 temperature. Present temperature appears to be warm enough for growth and cold enough to
383 allow conceptacle production in the summer (Teichert et al., 2014). For *Lithothamnion glaciale*,
384 the production of conceptacles, containing the spores, is limited when water temperature is
385 above 9 °C (Hall-spencer 1994). Warming might therefore impair its reproductive capacity.
386 Furthermore, its primary production and calcification rates are lower at high temperature with an
387 optimum at ca. 4 °C (Schoenrock et al., 2018). Longer duration of marine heatwaves will
388 increase temperature deeper and may reach coralline distribution depths with significant impact
389 on their development.

390

391 **6.2 Changes in underwater light**

392 By influencing the spatial and depth distributions of primary producers, underwater light is a
393 driver of the composition of macroalgal dominated ecosystems. Light has a significant impact
394 on the global carbon cycle by influencing primary production. Photoperiod also regulates the
395 timing of reproduction of *F. distichus* (Bird and McLachlan 1976), *L. solidungula* (Lüning, 1991)
396 and *A. esculenta* (Martins et al., 2022). Several climate change-related processes affect light
397 penetration in the Arctic Ocean. The underwater light conditions are influenced by sea ice cover
398 and water turbidity which both attenuate PAR and UV-radiation (UVR; Bonsell and Dunton 2018;
399 Hanelt et al., 2001). In general, it can be projected that, with increasing air and water

400 temperature, PAR will decrease during part of the summer, near glaciers and river outflows, due
401 to a higher input of particles and coloured dissolved material (Fig. 3c). Furthermore, increased
402 summer cloudiness with warming reduces incident PAR over most of the Arctic Ocean (Bélanger
403 et al., 2013). However, in early spring or further away from the glaciers and rivers, PAR could
404 increase due to the decrease in sea ice cover (Fig. 3d; Arrigo and van Dijken 2011).
405 Higher turbidity near glaciers and rivers limits the vertical distribution of kelps and associated
406 fauna, but decreased sea-ice cover promotes the expansion of kelps in new areas (Wiencke
407 and Hop 2016). For coralline algae, Teichert et al. (2014) found that irradiance is the most
408 influential parameter on rhodolith CaCO_3 production rates in Svalbard. The projected decrease
409 in PAR near glaciers and rivers will reduce the primary production of both kelps and calcareous
410 algae with implications on the benthic fauna inhabiting this ecosystem (Hopwood et al., 2020).

411

412 The depletion of stratospheric ozone causes a significant rise in solar UVR (Wiencke and Hop
413 2016) which will also be more intense over a longer period and will penetrate deeper in the water
414 column (Laeseke et al., 2019). Down to ca. 6 m depth (Hanelt et al., 1997; Wiencke et al., 2000),
415 UVR are intense enough to negatively affect physiological and metabolic processes such as
416 photosynthesis, respiration, development, and reproduction (Roleda et al., 2007). For Arctic
417 kelps, a stronger exposure to UVA and UVB leads to a decline in photosynthetic efficiency (e.g.,
418 Hanelt et al., 1997; Heinrich et al., 2015) and lowers the germination success and recruitment
419 (Roleda et al., 2006a). Early developmental stages, such as spores, are the most vulnerable to
420 UVA and UVB (Roleda et al., 2006a; Wiencke et al., 2007). Wiencke et al. (2000), Roleda et al.
421 (2005) and Fredersdorf et al. (2009), identified harmful effects of increased UVR on the
422 photosynthetic rate and motility of kelp spores.

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

435 Furoid are present in the intertidal zone and therefore undergo higher levels of UVR.
436 Schoenwaelder et al. (2003) found harmful effects of UVR on embryonic development of *F.*

437 *distichus* and *F. serratus* individuals. Under high UVR, zygotes are incapable of polarization,
438 germination and division, and finally die. Increasing UVR may restrict *F. distichus* to the lower
439 intertidal area of Arctic coasts (Jueterbock et al., 2016).

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

443

444 **6.3 Salinity decrease**

445 Increase in river runoff, ice melt, and precipitation will accentuate local hyposaline conditions.
446 Salinity is one of the drivers of the photophysiology and distribution of algal species (Hanelt et
447 al., 2001; Li et al., 2020a; Diehl et al., 2020). Although intertidal fucoids have efficient
448 osmoregulation mechanisms, reduced salinity leads to reduced biosynthesis of mannitol, an
449 important source of carbon for heterotrophic bacteria (Groisillier et al., 2015). Increase in
450 respiratory O₂ consumption at lower salinities (< ~ 21) was also found in fucoids (Munda and
451 Kremer, 1977). Some species, such as *Fucus serratus*, have a narrower salinity spectrum,
452 impacting their distribution (Munda and Kremer, 1977). To avoid damage in hyposaline
453 conditions, energy is transferred from biomass production to osmoregulation, affecting the long-
454 term growth rate (Fig. 3e; Li et al., 2020a). Hyposaline conditions can cause the loss of pigments
455 and bleaching and in prolonged low salinity events, death of macroalgae (Li et al., 2020a). Diehl
456 et al. (2020) found that low salinity (25) combined with elevated temperature (up to 15 °C)
457 causes a significant decline in the maximum quantum yield of photosystem II (F_v/F_m) of the kelp
458 *Laminaria solidungula*. Variable salinity conditions also reduce photosynthetic efficiency (Fig. 3f;
459 Karsten 2007; Spurkland and Iken 2011). As a result, the projected local decrease in salinity is
460 expected to alter kelp fitness by limiting photosynthesis (e.g., Traiger and Konar 2018; Filbee-
461 Dexter et al., 2019).

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

471

472 **6.4 Ocean acidification**

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

488

489 Increased CO₂ in marine systems has consequences on biological processes such as
490 photosynthesis, respiration, calcification, dissolved organic carbon (DOC) release and carbon
491 accumulation in biomolecules (Fig. 3g; Iñiguez et al., 2016b, Wiencke and Hop 2016). The
492 decrease in pH as well as calcite saturation state may cause a rapid reduction in coralline algae
493 cover and diversity within 10 to 30 years and could yield to their possible disappearance during
494 this century in the Arctic (SRES A2; IPCC 2007; Büdenbender et al., 2011). In tropical waters,
495 coralline algae with quick generation time (6 to 8 weeks) can develop resistance to ocean
496 acidification over multiple generations (Cornwall et al., 2020). However, it is likely that Arctic
497 species may not have enough time or the capacity to acclimatize due to their longer generation
498 time.

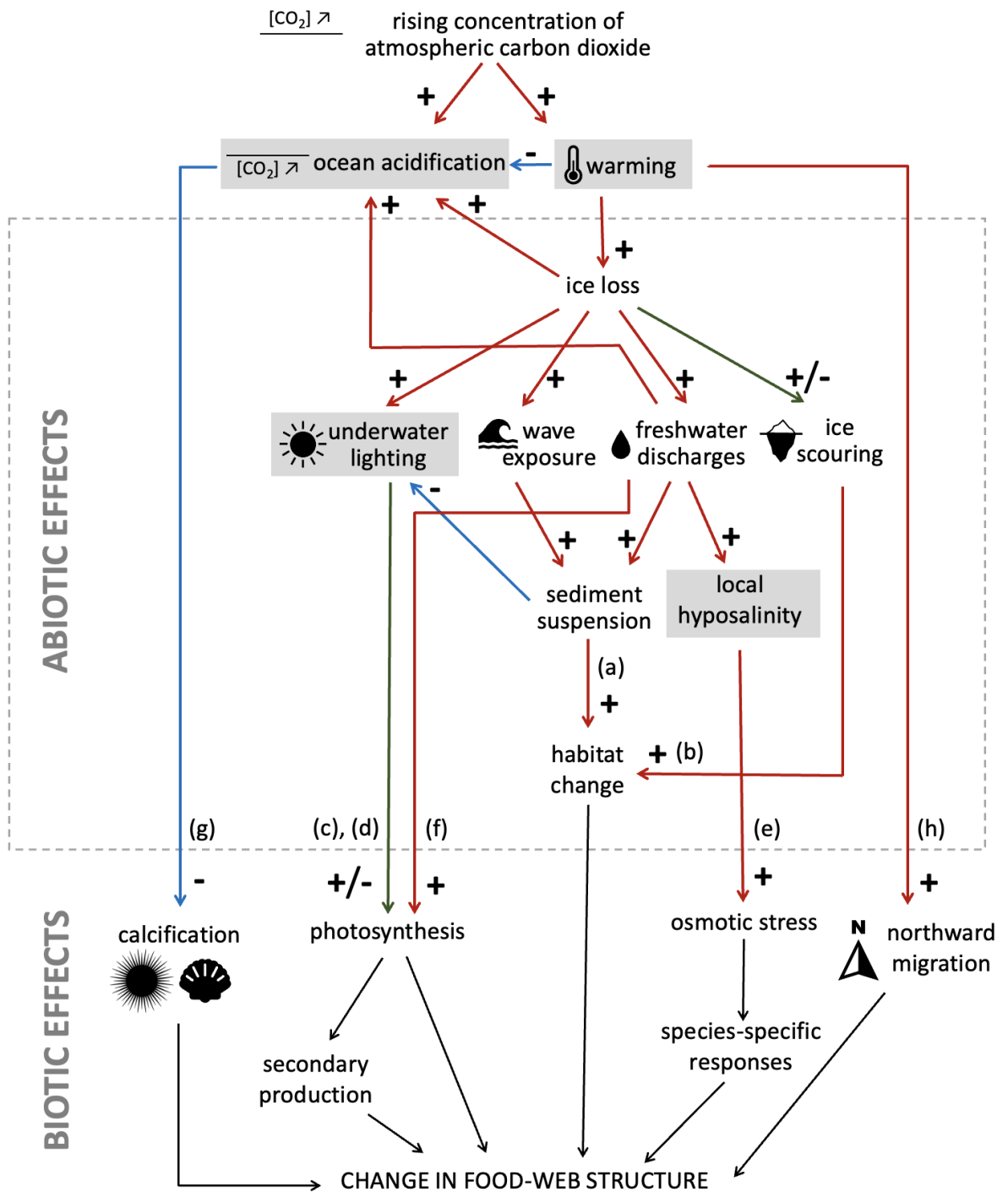
499 For kelps, a higher CO₂ concentration could lead to higher photosynthetic rates. However,
500 Iñiguez et al. (2016a) found that *Saccharina latissima* and *Laminaria solidungula* were largely
501 unaffected by elevated pCO₂ (carbon dioxide partial pressure, 1272 ± 4 µatm and 1308 ± 31
502 µatm respectively at 4°C). This suggests that photosynthesis is already C-saturated at 368 ± 15
503 µatm for *Saccharina latissima* and 428 ± 22 µatm for *Laminaria solidungula*. In another study,
504 Iñiguez et al. (2016b) showed a positive and a negative effect of ocean acidification on the
505 growth rate of *Alaria esculenta* and *Desmarestia aculeata*, respectively at 1300 ± 36 µatm and
506 1252 ± 30 µatm. This suggests that Arctic seaweed will be affected by ocean acidification in

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

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

513

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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.

523

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

526

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

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

531 Half of the benthic taxa are projected to experience significant changes in the extent of their
532 suitable habitat (> 10% increase or decrease) including dominant and/or endemic species of
533 Arctic shelves (Renaud et al., 2019). It could lead to a high risk of species extinction in polar and
534 cold-temperate regions (Müller et al., 2009). Sea ice loss is thought to drive a profound regime
535 shift in shallow polar benthos from invertebrate- to algal-dominated communities (Clark et al.,
536 2013). For example, in Kongsfjorden (Svalbard), the abundance of the originally dominant sea
537 anemones decreased by 80% between the 1990s and the 2000s, and were replaced by
538 filamentous brown algae (Kortsch et al., 2012). The combination of the projected changes in sea
539 ice and species dominance will likely induce fundamental changes in community composition
540 with a loss of biodiversity, functions and altered ecosystem stability (Clark et al., 2013).

541

542 **7.1 Furoids**

543 Between 1988 and 2008, Svalbard coasts experienced an increase in the cover and biomass of
544 intertidal marine algae, including *Fucus distichus*, whose population nearly doubled (Węśławski
545 et al. 2010). Because ice melt opens new areas for colonization, the habitat suitability of this
546 species in the Arctic would triple by 2100 (Jueterbock et al., 2016). *F. distichus* is cold-adapted,
547 surviving for months under ice and frequently exposed to cold temperatures during low tide,
548 giving it an advantage over temperate species (see section 7.4; Svendsen et al. 2002). However,
549 increases in UVR may restrict its distribution to the lower intertidal zone giving ground to other
550 species (Fig. 4; Jueterbock et al., 2016; Schoenwaelder et al. 2003).

551

552 **7.2 Kelps**

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

557

558 Krause-Jensen et al. (2012) identified the duration of the open-water period, via changes in light
559 and temperature, as the best predictor of vertical distribution and production of kelps along a
560 latitudinal gradient. These variables explained up to 92% of the depth expansion and 80% of
561 the variation in kelp biomass. These responses are likely to increase in the future. The loss of
562 light-attenuating sea ice on the rocky coastlines of Russian islands, the Kola Peninsula,
563 Spitsbergen, Greenland (Baffin Bay and Greenland Sea), and of the Canadian Archipelago, will
564 provide new habitats for seaweed colonization (Müller et al., 2009). Although concomitant
565 increases in freshwater input, turbidity, and sedimentation will restrict kelp distribution and
566 primary production in some locations, the kelp biomass could double in Arctic regions within less
567 than 30 years (Bonsell and Dunton, 2018; Filbee-Dexter et al., 2019).

568 A few kelp species may gain advantage over the others by better acclimatizing to environmental
569 stresses such as hyposalinity or increased turbidity in the summer. For example, while a
570 poleward retreat of the endemic *Laminaria solidungula*, a stenothermic species that cannot live
571 outside of a narrow range of cold temperature, is expected (Fig. 4; Müller et al. 2009),
572 *Saccharina latissima* could benefit from these new conditions, especially from warming, thanks
573 to a high degree of polymorphism, acclimatation and genetic diversity across populations
574 (Bartsch et al., 2008; Guzinski et al., 2016). While kelp abundance and biomass may largely
575 increase, the species composition will change, most likely impacting their associated fauna.

576

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

590

591 **7.3 Coralline algae**

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

595 2014). Ocean acidification and warming may result in a fast decrease in calcification rate and
596 percent cover which could impact the associated fauna (Fig. 4; Teichert et al., 2014; Chan et
597 al., 2020). The distribution of Arctic calcified algae will be constrained by the upper temperature
598 limit of the species in the South and by calcium carbonate saturation state in the North
599 (Steinacher et al., 2009; Chan et al., 2020). Also, competition for space with kelps may hasten
600 their demise. This will lead to ecosystem restructuring and loss of functions resulting from the
601 possible disappearance of current subarctic coralline algae and their associated communities
602 before the end of the century (Brodie et al., 2014).

603

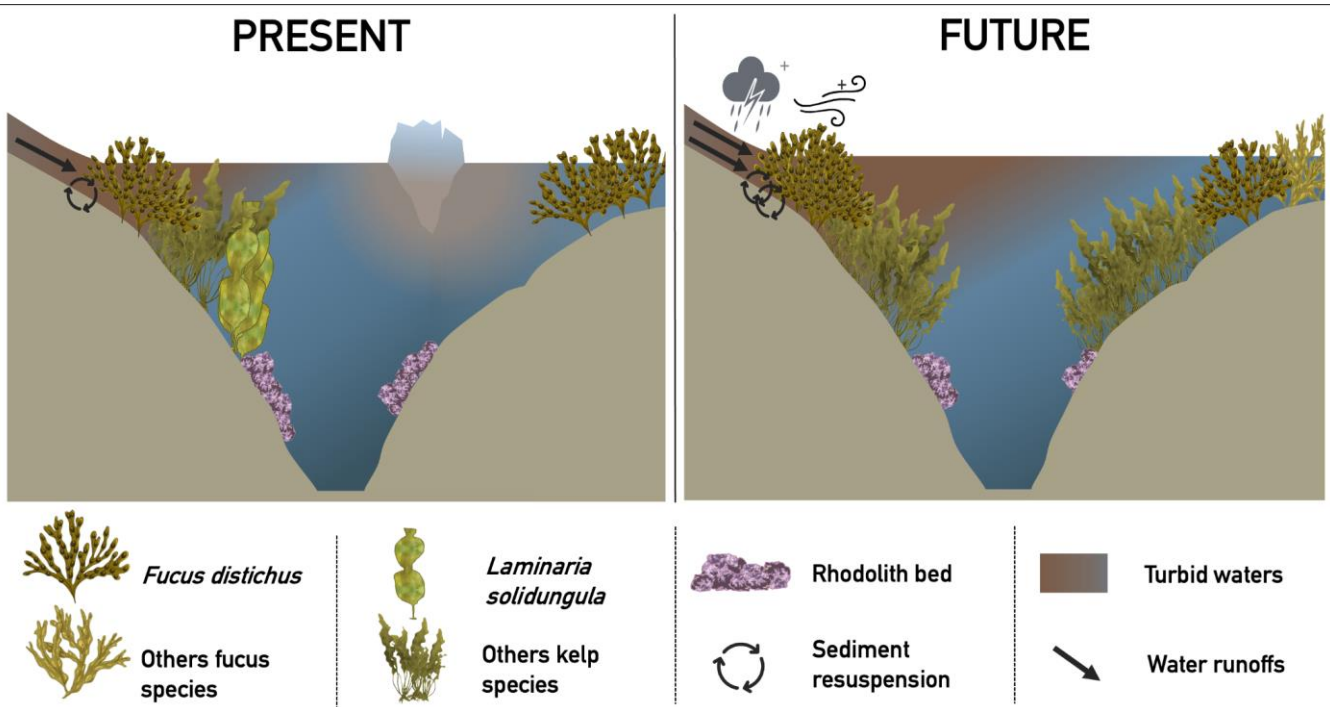
604 **7.4 Boreal species**

605 The North Atlantic West Spitsbergen Current provides ca. 70% of water inputs into the Arctic
606 Basin (Dickson et al., 1999). The Bering Sea is also an input source to the Beaufort and Chukchi
607 Seas (Węslawski et al., 2011). In recent decades, warming combined with increased advection
608 induced poleward migrations bringing thermal tolerant boreal-subarctic species in the Arctic
609 Ocean (Fig. 3h; Węslawski et al., 2010). Furthermore, in response to the loss of Arctic sea ice,
610 shipping transport along ice-free routes in the Canadian and Russian Arctic regions has
611 increased (Lasserre and Pelletier, 2011). This will likely have a major role in the introduction of
612 marine species in the Arctic (Jueterbock et al., 2016).

613 Migration may have caused the reappearance of the bivalve *Mytilus edulis* in Isfjorden
614 (Svalbard) after more than 1,000 years of absence (Berge and Johnsen 2005, Węslawski et al.,
615 2010). The boreal kelp *Laminaria hyperborea* has also been recorded in the southern fjords of
616 Spitsbergen, revealing its poleward migration progress (Peltikhina 2002). Furthermore, over the
617 last 20 years, at least 20 decapod species have expanded northward (Brattegard and Holthe,
618 1997). Migration has also been described in the Pacific Arctic (Grebmeier et al., 2006; Sirenko
619 and Gagaev, 2007), in Kongsfjorden (Beuchel et al., 2006; Kędra et al., 2009) and in Hornsund
620 (Węslawski et al., 2017).

621 New dominant species with a different ecosystem engineering role can alter local functional
622 diversity (Zacher et al., 2019). Moreover, new species combinations and interactions modify
623 species distributions (Pecl et al., 2017). Nevertheless, according to Renaud et al. (2019), the
624 Arctic benthic species are unlikely to be fully replaced by boreal species because endemic
625 species are not more vulnerable than boreal species to warming and acidification. Jueterbock
626 (2016) predicted that habitat suitability for *Fucus serratus*, *Fucus vesiculosus*, and *Ascophyllum*
627 *nodosum* would increase northward by 2100, particularly in Canada, Greenland, and
628 Spitsbergen. They could be present at *F. distichus*' upper and lower zonation limits in the Arctic
629 but these temperate species would not be able to compete with it because of *F. distichus* has
630 competitive advantage such as being adapted to cold conditions and long dark periods

631 (Jueterbock et al., 2016). Benthic taxa have restricted mobility and range changes are more
632 likely to differ between taxon due to life-span, and dispersal capacity (Renaud et al., 2019).
633 As early as the 1930s, a documented warming of North Atlantic waters induced a major
634 northward migration of boreal species (Drinkwater 2006). Blacker's (1957) comprehensive shelf
635 and coastal waters survey revealed changes in species distribution within the Arctic, with the
636 northward migration of boreal echinoderms and decapods. However, only northward changes
637 and increases in the abundance of southerly species were reported. In this early study, no new
638 species was found in the Arctic region. Merzouk and Johnson (2011) were unable to document
639 any significant change in dominant kelp species composition or abundance since the 1950s
640 along the northwest Atlantic coast. Similarly, Adey and Hayek (2011) found no major changes
641 in the distribution of subtidal algal species in Canada's eastern subarctic or boreal regions over
642 the last 40 years. These observations suggest northward expansions are occurring slower than
643 predicted or are being buffered by other factors (Filbee-Dexter et al., 2019). Extensive spatial
644 gaps between suitable substrate, slow dispersal of propagules, water temperature, changes in
645 turbidity, sea ice cover, and light penetration all influence the northward range expansion of
646 kelps (Wernberg et al., 2019). At least in the short-term, the northern range expansions of boreal
647 kelps across the Arctic may be overestimated (Filbee-Dexter et al., 2019).
648 Endemic Arctic species cope with environmental changes while also facing increasing
649 competition pressure from invasive species, risk of infection by diseases, and predator-prey
650 interactions with higher herbivore pressure (Węslawski et al., 2010). Borealization is expected
651 to increase biodiversity in the short-term with coexisting inhabitants and competitors (Renaud et
652 al., 2019). Some species may decline, other species or ecosystems may flourish to the benefit
653 of coastal zones (Bartsch et al., 2016). New species interactions such as competition and prey-
654 predator interactions are occurring and are yielding to new ecosystem functioning.



655

656 Figure 4: Schematic representation of the present and expected future Arctic coastal
 657 macroalgae communities. Present: fucoids dominate intertidal algae assemblages, while kelps
 658 dominate subtidal algae assemblages until they reach their low light threshold. *Laminaria*
 659 *solidungula* is present at the lower sub-littoral zone (Hop et al. 2002, Wiencke et al. 2004).
 660 Coralline algae are at the lower limit of kelp forest and deeper. Ice melt and increased river
 661 runoff increase turbidity. Future: increase in precipitation, wind-speed, river runoff and sediment
 662 resuspension are increasing the turbidity locally. The surface cover of *F. distichus* doubled while
 663 UVR rates limit it to the lower intertidal zone giving ground to other fucoid species. Longer ice-
 664 free periods allow kelp expansion in new areas except for *L. solidungula* who retreated with
 665 warming. The coralline algae cover is reduced due to ocean acidification and competition with
 666 other macroalgae.

667

668 8. Conclusion

669 Coastal macroalgal communities in the Arctic are profoundly affected by increasing temperature,
 670 coastal erosion, freshwater input, coastal turbidity and sedimentation as well as decreasing ice
 671 cover and seawater pH. Changes in seasonality and food-web structure will likely result in major
 672 ecosystem restructuring (Morata et al., 2020; Bonsell and Dunton, 2021). In colder coastal Arctic
 673 regions, kelp forests may become more productive (Krause-Jensen and Duarte al., 2014; Filbee-
 674 Dexter et al., 2019). Also, fucoids may largely extend in the Arctic whereas coralline algae may
 675 be more restricted under future conditions. The amount of detritus produced should rise which

676 would affect the ecosystem functioning by damping fluctuations in seasonal carbon supply
677 (Norkko et al., 2007). This could result in greater resilience of the benthos to variation of
678 interannual pelagic primary production and more stable food-chains (Norkko et al., 2007;
679 Renaud et al., 2015).

680 With global change, trawling and overfishing, sea urchins have become very abundant in some
681 areas overgrazing the kelp forest (Konar et al., 2014). The disappearance of kelp forests impacts
682 the whole ecosystem including species that feed on kelps (bristle worms, amphipods, prawns,
683 snails, and brittle stars), species that feed on these herbivores (including species important to
684 commercial fisheries: fishes, lobsters) - and/or species using kelp forest as a refuge area (sea
685 lions, seals, gray whales, sea otters and even seabirds such as gulls or terns; Watson and Estes,
686 2011). In some areas, like around Tromsø, the ecosystem has collapsed into a bare and
687 depauperate new state (Comeau, unpublished observations).

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

697

698 Predicting the future of Arctic ecosystems is imperative to anticipate and to adapt to the coming
699 changes (Krause-Jensen and Duarte 2014; Filbee-Dexter et al., 2019). Nonetheless, the
700 baseline knowledge on ecosystem structure and functioning in the Arctic is limited on both
701 geographical and temporal scales (Wassmann et al., 2011). Long-term time series combining
702 environmental conditions and community composition and distribution are essential but
703 particularly scarce in the Arctic, limiting projections of future benthic communities (Piepenburg
704 2005; Müller et al., 2009). Efforts must be made to improve knowledge in key regions with proper
705 seasonal coverage to provide sound scientific advice on ecosystem management (Wassmann
706 et al., 2011; Degen et al., 2016; Filbee-Dexter et al., 2019).

707 The poor knowledge about the interactions between multiple abiotic and biotic stressors,
708 changes in climate-sensitive populations over time (including processes of acclimation and
709 adaptation) and the general paucity of baseline species diversity and biogeographic distributions
710 data are a significant stumbling block for understanding the current situation as well as to foresee
711 future changes (Muth et al., 2009; Harley et al., 2012). Multifactorial studies at the community
712 level that take into account interactions between stressors and between species are desperately

713 lacking (Scherrer et al., 2019; Renaud et al., 2019). Only 52% of *ex situ* studies on Arctic kelps,
 714 25% on coralline algae and 0% on fucoids focus on the impact of at least 2 parameters involved
 715 in global change. Beyond 2 parameters, the percentages drop to 2.4 and 0% for kelps and
 716 coralline algae respectively (Table 1).

717

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

724

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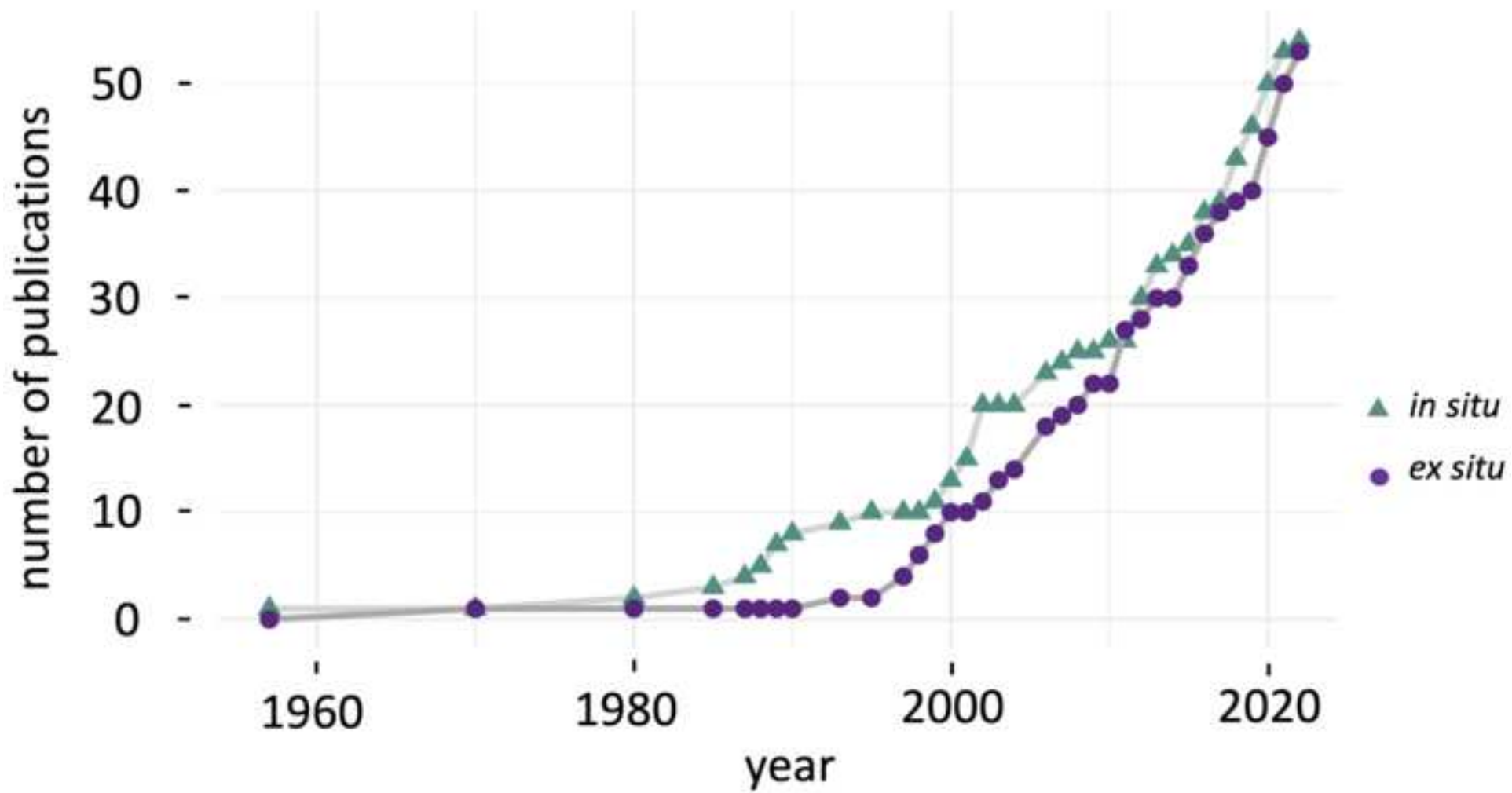
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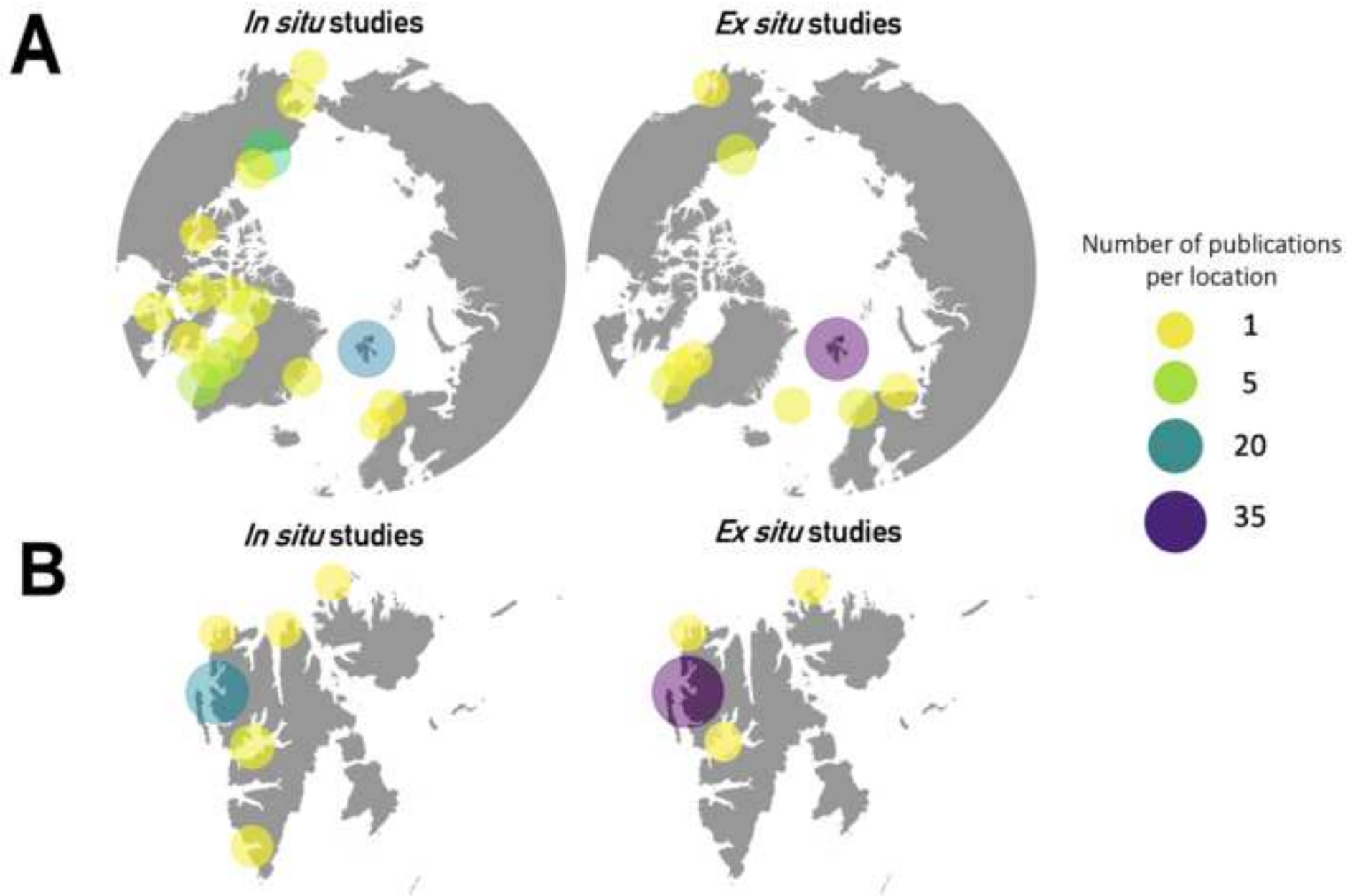
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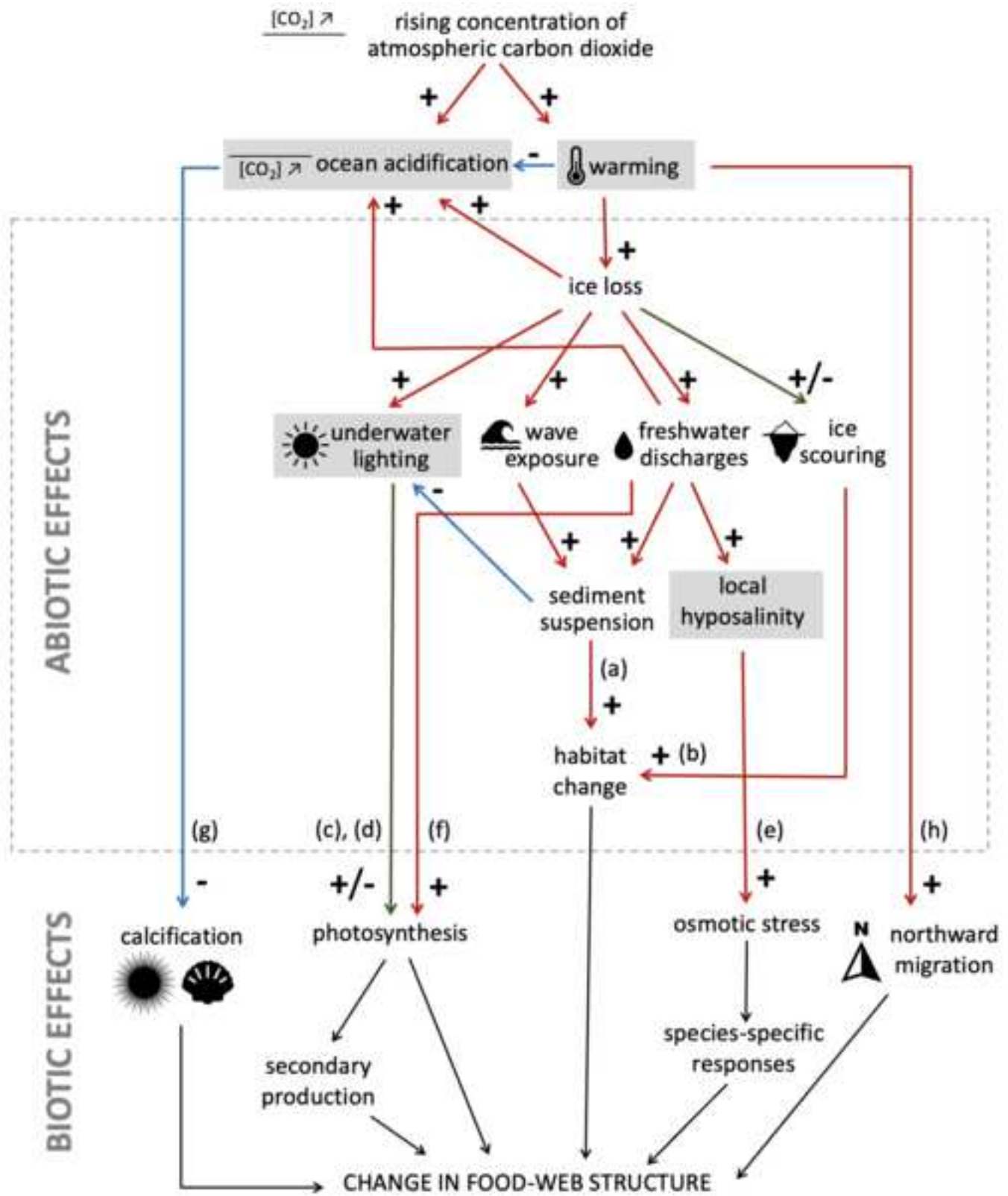
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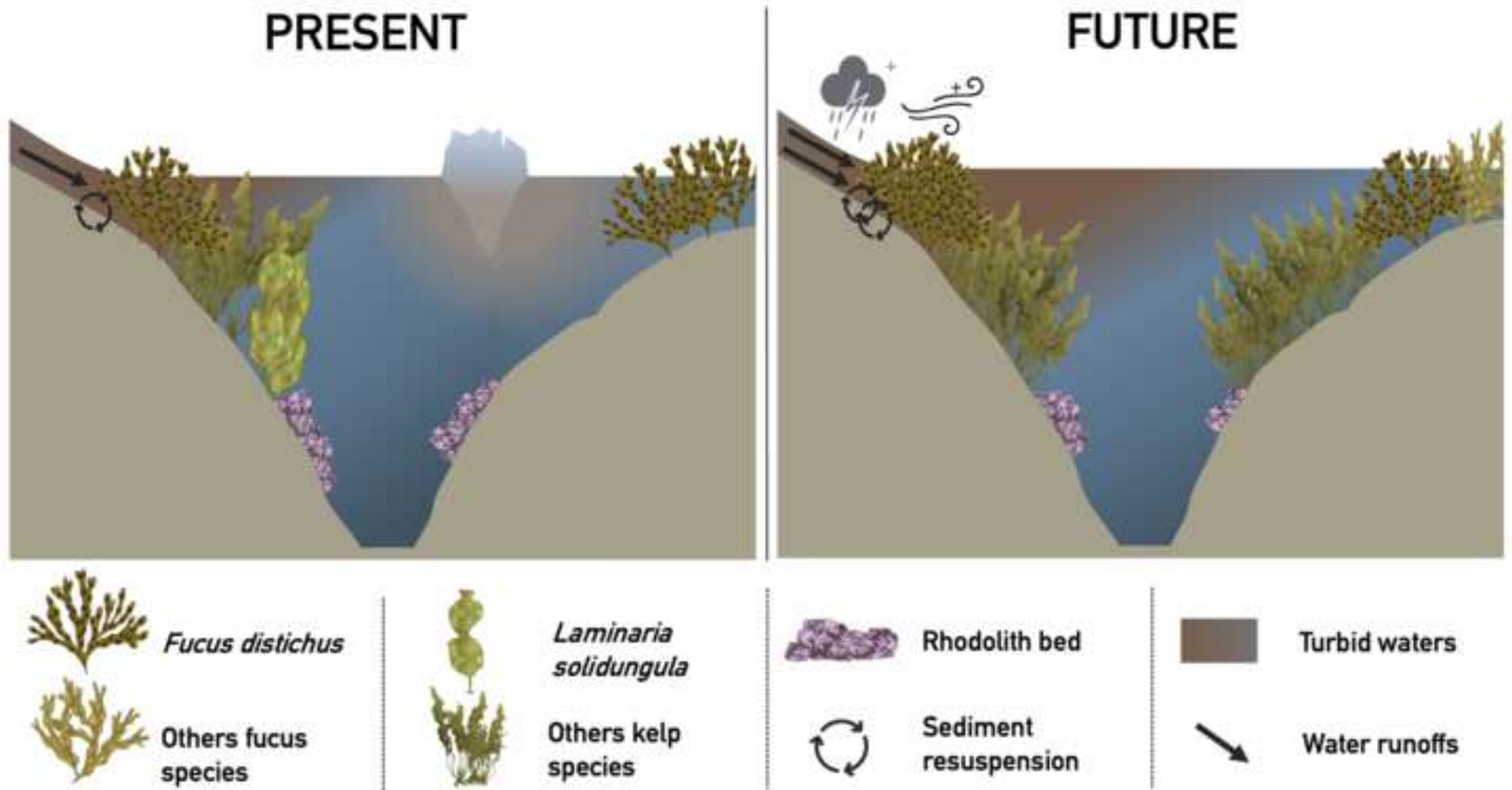
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Type	Species	Stages	Parameters	Conditions tested	Key results			References
					Photosynthesis	Growth	Others	
Furoid	<i>Fucus serratus</i>	sporophyte	light	light: 12:12 h L:D (PAR : 5-10 W.m-2), 24:00 h L:D		growth rate=0 in winter under 12:12 and 24:0, L:D		Marakov et al., 1999
		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 $\mu\text{mol m}^{-2}\text{s}^{-1}$), 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 $\mu\text{mol m}^{-2}\text{s}^{-1}$), 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	<i>Saccharina latissima</i>	gametophyte	temperature, light	temp: 2, 7, 12, 18 \pm 1.4°C		germination: + with temperature up to 12°C		Müller et al., 2008
				light: PAR (20 \pm 3 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (5.8 W m-2), PAR + UVA + UVB (0.34 W m-2)		germination: - at 12°C under UVA & UVB		
			temperature	temp: 2, 7, 12, 18 \pm 1.4°C	absorbance: no effect of temperature			Müller et al., 2009
				light: PAR (20 \pm 3 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (6.73 \pm 0.81 W.m-2), PAR + UVA + UVB (0.35 \pm 0.04 W.m-2)	absorbance: + under UVA & UVB			
			temperature	temp: 2, 7, 12, 18 \pm 1.4°C	absorbance: + with temperature			Müller et al., 2012
				light: PAR (20 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (5.5 W.m-2), PAR + UVA + UVB (0.35 W.m-2)	absorbance: + under UVA & UVB at 2°C			
		light	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	
		sporophyte	temperature, light	light: PAR (28.8 \pm 5.05 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (8.22 \pm 0.64 W.m-2), PAR + UVA + UVB (1.27 \pm 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 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (5.65 W.m-2), PAR + UVA + UVB (0.47 W.m-2)	quantum yield: - under light exposure			Roleda et al., 2006b
		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 \pm 3.08 $\mu\text{mol m}^{-2}\text{s}^{-1}$ & 107.77 \pm 4.96 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (9.83 \pm 1.17 W.m-2 & 9.68 \pm 1.2 W.m-2), PAR + UVA + UVB (0.42 \pm 0.03 W.m-2 & 0.43 \pm 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.	
		temperature, pCO2	temp: 0, 4°C	chl a: + at 4°C, quantum yield: no effect of temperature chl a: + in the dark, quantum yield: no effect of light	growth rate: no effect of temperature growth rate: + under light			Li et al., 2020b
			light: PAR (20 $\mu\text{mol m}^{-2}\text{s}^{-1}$), 18:6h light: dark, continuous dark	net photosynthesis: no effect of temperature & pCO2	growth rate: + of about 30% at 9 °C growth rate: largely unaffected by increased CO2 conditions		dark respiration rate: - of 64% at 9 °C	Íñiguez et al., 2016a
temperature, salinity	temp: 4, 9°C	CO2 conditions: 390 and 1200 ppm	net photosynthetic rate: + at 10 °C at current pCO2 conditions	growth rate: + at 10°C		Olischläger et al., 2014; Olischläger et al., 2017		
	temp: 4, 10°C	CO2 conditions: 380, 800 and 1500 ppm			lipids, proteins, and total N-content: + at 4 °C. mannitol content and C/N: no effect of temperature mannitol content and C/N: no effect of salinity	Diehl et Bischoff, 2021		

				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
		light, salinity		salinity: 20, 30 light: 5, 20, 50 µmol m ⁻² s ⁻¹	quantum yield: no effect of light	growth rate: - under low salinity (20) at day 18 growth rate: - under lowest light level (5 µmol m ⁻² s ⁻¹)		Spurkland et al., 2011
		light, pCO ₂		salinity: 10, 13, 17, 20, 31 light: PAR (30 µmol m ⁻² s ⁻¹), PAR + UVA (2 W.m-2) + UVB (0.2 W.m-2) CO ₂ condition: 380 and 1000 ppm	quantum yield: - at salinity=10 quantum yield: drop after 2 days under UVR and CO ₂ enrichment, recovery after 4 and 10 more days	growth rate: + 151% under UVR and CO ₂ enrichment		Gordillo et al., 2015
		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 ⁻² s ⁻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 ⁻² s ⁻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)	chl _a : no effect of UV radiations	growth rate: - under UV radiations		Roleda et al., 2006c
		salinity		light: PAR PAR + UVA + UVB salinity: 5, 10, 15, 20, 25, 34, 45, 55, 60	quantum yield: - at salinity=5 and 10 after 2 days of treatment	significant light dependent repair		Van de Poll et al., 2002
				temp: 2, 7, 12, 17°C	quatum yield: highest reduction in photosynthetic efficiency 17°C and lowest at 12°C			Roleda et al., 2016
	<i>Laminaria solidungula</i>	gametophyte	temperature, light	light: PAR (10 and 20 µmol m ⁻² s ⁻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 ⁻² s ⁻¹) salinity: 10, 20, 30		gametophyte density: - under UV radiations gametophyte density: - at salinity=10 and 20	gametophyte unable to produce sporophyte at salinity=10	Muth et al., 2021
			light	light: PAR (28.8 ± 5.05 µmol m ⁻² s ⁻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 salinity: 25, 35	quantum yield: - at 15°C after 14 days		mannitol content: + at salinity=35 at 0, 5 & 10°C C/N: + at salinity=35 at 0, 5, 10 & 15°C, + at 10 & 15°C	Diehl et al., 2020
			temperature, pCO ₂	temp: 4, 9°C CO ₂ conditions: 390, 1200 ppm	net photosynthesis: + at 9°C compared to 4°C. net photosynthesis: + at increased CO ₂ conditions (at 4°C).	growth rate: no effect of temperature and pCO ₂		Iñiguez et al., 2016a
			light, salinity	light: PAR (10, 20, 40 µmol m ⁻² s ⁻¹) salinity: 10, 20, 30		sporophyte density: - under UV radiations sporophyte density: - at salinity=10 and 20		Muth et al., 2021
			light	light: PAR (66, 18, 13, 3, 0.5, 0.2, 0 uE m-2 s-1) light: PAR (25µmol m ⁻² s ⁻¹ , 12:12h light:dark), continuous dark light: PAR (30 µmol m ⁻² s ⁻¹), PAR + UVA (7 W.m-2), PAR + UVA + UVB (0.7 W.m-2) light: PAR (3.62 W.m-2), PAR (4.00 W.m-2) + UVA (5.01 W.m-2) + UVB (0.31 W.m-2)	photosynthesis: - after 2h of exposure to UV radiations chl _a : no effect of UV radiations	Blade length: - at low light & dark exposure New blade surface area: - during dark exposure growth rate: no effect of UV radiations		Chapman et al., 1980 Henley et al., 1997 Aguilera et al., 1999
			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	growth rate: - under UV radiations		Roleda et al., 2006c Karsten et al., 2007
	<i>Laminaria digitata</i>	gametophyte	temperature, light	temp: 2, 7, 12 and 18 ± 1.4°C light: PAR (20 ± 3 µmol m ⁻² s ⁻¹), PAR + UVA (5.8 W m ⁻²), PAR + UVA + UVB (0.34 W m ⁻²)		germination: 0 to 0.1% at 18°C germination: - at 2°C and 12°C under UVA & UVB		Müller et al., 2008

			temp: 2, 7, 12 and 18 ± 1.4°C light: PAR (20 ± 3 μmol m ⁻² s ⁻¹), PAR + UVA (6.73 ± 0.81 W.m ⁻²), PAR + UVA + UVB (0.35 ± 0.04 W.m ⁻²)	absorbance: no effect of temperature		Müller et al., 2009
			temp: 2, 7, 12 and 18 ± 1.4°C light: PAR (20 μmol m ⁻² s ⁻¹), PAR + UVA (5.5 W.m ⁻²), PAR + UVA + UVB (0.35 W.m ⁻²)	absorbance: no effect of light		Müller et al., 2012
			temp: 2, 7 ± 1°C light: PAR (20 ± 4 W.m ⁻²), PAR + UVA (3.8 ± 0.4 W.m ⁻²) + UVB (0.41 ± 0.04 W.m ⁻²)	absorbance: increase with temperature		Olischläger and Wiencke, 2013
			temp: 15, 20, 22.5, 25°C and dynamic heat stress : 18 to 25°C light: PAR (15 μmol m ⁻² s ⁻¹), red light, continuous dark	absorbance: + under UVA and UVA & UVB at 2, 7 and 12°C	UVAB-susceptibility: increase with decreasing temperature	Martins et al., 2020
			temp: 5, 15°C temp: 5, 9°C temp: 5, 9, 15°C	germination: + at 9°C germination: + at 9°C	after a high temperature stress, the recovery temperature affects the capacity to reproduce	Liesner et al., 2020a Zacher et al., 2016 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 light: PAR (28.8 ± 5.05 μmol m ⁻² s ⁻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	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 Wiencke et al., 2004
			light: PAR (21.8 μmol m ⁻² s ⁻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 temp: 5, 15°C temp: 15, 19, 21, 23°C temp: 0, 5, 10, 15, 20, 22, 23, 24, 25 ± 0.5°C	sporophyte density: + at 9°C in monospecific cultivation quantum yield: - at 5°C quantum yield: maximum at 10 and 15°C	area growth rate: - at 5°C in July & February growth rate: + at 15°C	Zacher et al., 2019 Liesner et al., 2020a Liesner et al., 2020b Franke et al., 2021
		light	temp: 0, 3, 6, 9, 12, 15 ± 0.1°C light: PAR (30 μmol m ⁻² s ⁻¹), PAR + UVA (7 W.m ⁻²), PAR + UVA + UVB (0.7 W.m ⁻²)	photosynthesis: - after 6h of exposure to UV radiations	sporophyte density: higher at 9°C and 12°C growth rate: no effect of UV radiations	Schimpf et al., 2022 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	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) salinity: 5, 10, 15, 20, 25, 34, 45, 55, 60	chia: no effect of UV radiations quantum yield: - at salinity= 5, 10, 15 and 20 after 5 days of treatment	growth rate: - under UV radiations	Roleda et al., 2006c Karsten et al., 2007
	<i>Alaria esculenta</i>	gametophyte	temp: 2, 7, 12, 16 ± 1°C 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)		germination: optimal temperature range of 2–12°C	Fredersdorf et al., 2009
		temperature, light	temp: 2, 7, 12, 18 ± 1.4°C light: PAR (20 ± 3 μmol m ⁻² s ⁻¹), PAR + UVA (5.8 W m ⁻²), PAR + UVA + UVB (0.34 W m ⁻²)		germination: 0% at 18°C germination: no effect of UV	Müller et al., 2008
			temp: 2, 7, 12 and 18 ± 1.4°C light: PAR (20 ± 3 μmol m ⁻² s ⁻¹), PAR + UVA (6.73 ± 0.81 W.m ⁻²), PAR + UVA + UVB (0.35 ± 0.04 W.m ⁻²)	absorbance: no effect of temperature absorbance: + under UVA & UVB at 2°C, + under UVA and UVA & UVB at 7, 12 and 18°C		Müller et al., 2009
			temp: 2, 7, 12 and 18 ± 1.4°C	absorbance: increase with temperature		Müller et al., 2012

			light: PAR (20 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (5.5 W.m^{-2}), PAR + UVA + UVB (0.35 W.m^{-2})	absorbance: + under UVA and UVA & UVB at 2°C			
		temperature	temp: 2, 7 \pm 1°C light: PAR (20 \pm 4 W.m^{-2}), PAR + UVA (3.8 \pm 0.4 W.m^{-2}) + UVB (0.41 \pm 0.04 W.m^{-2}) temp: 5, 9°C temp: 5, 9, 15°C temp: 5, 10, 15, and 20°C		germination rate: no significant effect of temperature and seasonality germination: + at 9°C germination: + at 9°C in co-cultivation germination: no germlings at 20°C	UVAB-susceptibility: highest at 2 °C and the beginning of July, not affected by seasonality at 7 °C no sporophyte at 15°C	Olischläger and Wiencke, 2013 Zacher et al., 2016 Zacher et al., 2019 Park et al., 2017
		light	light: 12:12 h L:D (PAR : 5-10 W.m^{-2}), continuous daylight light: PAR (28.8 \pm 5.05 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (8.22 \pm 0.64 W.m^{-2}), PAR + UVA + UVB (1.27 \pm 0.12 W.m^{-2}) light: PAR (21.8 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (5.65 W.m^{-2}), PAR + UVA + UVB (0.47 W.m^{-2}) light: PAR (5.5 \pm 1.2, 20.6 \pm 3.0 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (10.9 \pm 0.4, 11.6 \pm 1.9 W.m^{-2}), PAR + UVA + UVB (0.45 \pm 0.0, 0.48 \pm 0.0 W.m^{-2}) light: PAR (from 0.23 to 61.8 W.m^{-2}) + UVA (from 0 to 1.9 W.m^{-2}) + UVB (from 0 to 0.018 W.m^{-2})	quantum yield: - under light exposure, even more under UVA & UVB quantum yield: significant interaction between radiation and exposure time, as well as significant radiation effects	growth rate: increased with increasing photoperiod (from 12:12 to 24:0, L:D) and decreased with shortening the light phase (from 24 to 12 hours). germination: - 3, 6 and 9 days after 16h under UVA & UVB		Marakov et al., 1999 Wiencke et al., 2004 Roleda et al., 2006b Steinhoff et al., 2012 Laeseke et al., 2019
	sporophyte	temperature, salinity, light	temp: 4, 8, 9, 13, 15, 17, 21 \pm 1°C salinity: 20, 28, 34 light: PAR (46 \pm 8 and 80 \pm 10 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (7 \pm 1 W m^{-2}), PAR + UVA + UVB (0.3 \pm 0.07 W m^{-2})	photosynthesis: optimal temperature range of 13–17°C.		UV inhibition observed only under the lowest applied temperatures	Fredersdorf et al., 2009
		salinity, light	salinity: 5, 15, 32 light: PAR (50 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (6.8 and 7.5 W m^{-2}) + UVB (0.5 and 0.8 W m^{-2})	quantum yield: slightly - in a low-salinity during 7 days quantum yield: slightly - under UVR		specimens previously treated with hyposalinity are significantly less susceptible to UV	Springer et al., 2017
		light, pCO2	light: PAR (30 $\mu\text{mol m}^{-2}\text{s}^{-1}$), 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 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (7 W.m^{-2}), PAR + UVA + UVB (0.7 W.m^{-2}) light: PAR (20, 60, 800 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (8 W.m^{-2}), PAR + UVA + UVB (0.8 W.m^{-2}) light: PAR (46 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (7 W.m^{-2}), PAR + UVA + UVB (0.3 W.m^{-2}) light: 12:12h and 16:8h light: dark	quantum yield: specimens from shallow water recover to a greater extent than those from deeper waters quantum yield: - to 25% after 4 h of exposure to low light and UV during the first 2 cycles, recovery proceeded significantly faster at the 2nd cycle quantum yield: - significantly after 1 day under PAR + UVA + UVB			Bischof et al., 1998 Bischof et al., 1999 Lütz et al., 2016
		salinity	salinity: 5, 10, 15, 20, 25, 34, 45, 55, 60	quantum yield: - at salinity= 5 after 2 and 5 days of treatment	growth: triggered by changing daylength from short to long days	reproductive success hampered under continuous light	Martins et al., 2022 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
<i>Saccorhiza dermatodea</i>	gametophyte	temperature, light	temp: 2, 8, 11, 17°C light: PAR (4.62 \pm 0.4 and 86.7 \pm 19.9 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PAR + UVA (5.31 \pm 0.58 and 4.76 \pm 2.9 W.m^{-2}), PAR + UVA + UVB (0.41 \pm 0.01 and 0.12 \pm 0.0 W.m^{-2})		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

		sporophyte	light	light: PAR (28.8 ± 0.05 μmol m ⁻² s ⁻¹), PAR + UVA (8.22 ± 0.64 W.m ⁻²), PAR + UVA + UVB (1.27 ± 0.12 W.m ⁻²)	quantum yield: - with increasing total fluence quantum yield: specimens from shallow water recover to a greater extent than those from deeper waters photosynthesis: - after 6h of exposure to UV radiations	germination: - 3 after 16h under UVA & UVB, recovery after 6 days		Wiencke et al., 2004	
			light	light: PAR (21.8 μmol m ⁻² s ⁻¹), PAR + UVA (5.65 W.m ⁻²), PAR + UVA + UVB (0.47 W.m ⁻²)		germination: strong dose-dependent inhibitory effect of UVA & UVB		Roleda et al., 2006a,b	
			light	light: PAR (60 μmol m ⁻² s ⁻¹), PAR + UVA (7 W.m ⁻²), PAR + UVA + UVB (0.7 W.m ⁻²)				Bischof et al., 1998	
			light	light: PAR (30 μmol m ⁻² s ⁻¹), PAR + UVA (7 W.m ⁻²), PAR + UVA + UVB (0.7 W.m ⁻²)			growth rate: - under UV radiations	Aguilera et al., 1999	
			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	
			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	
			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
			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
			temperature, salinity	temp: 4, 7°C			calcification: reduced at low salinity and temperature treatments	metabolic processes: negatively influenced by low salinity	Schoenrock et al., 2018
			salinity	salinity: 22, 33					
Coralline algae	<i>Lithothamnion glaciale</i>	sporophyte	pCO2	CO2 conditions: 390, 815, 975 and 1570 ppm	calcification: reduced under high CO2 treatments		Büdenbender et al., 2011		
			salinity	salinity: 10, 20, 30	calcification: higher at salinity=10	higher pigment change at salinity=10	Muth et al., 2020		
	<i>Leptophytum foecundum</i>	sporophyte	light	light: PAR (100 μmol m ⁻² s ⁻¹), dark		active calcification and no net dissolution in the dark	Hofmann et al., 2018		
	<i>Phymatolithon tenue</i>	sporophyte							

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 <i>Laminaria solidungula</i> 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 <i>Laminaria saccharina</i> (L.) Lamour, and <i>Laminaria solidungula</i> J. Ag. (laminariales : phaeophyta) in the alaskan beaufort sea	1985	Dunton	10.1016/0022-0981(85)90057-7
in situ	Stefansson Sound, Alaska	Dependence of consumers on macroalgal (<i>Laminaria solidungula</i>) carbon in an arctic kelp community: $\delta^{13}\text{C}$ evidence	1987	Dunten & Schell	10.1007/BF00392799
in situ	Stefansson Sound, Alaska	Photosynthetic performance of <i>Laminaria solidungula</i> 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 <i>Laminaria solidungula</i> : 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 <i>Laminaria solidungula</i> and <i>L. saccharina</i> (Phaeophyta) in the Alaskan Arctic	1995	Henley & Dunton	10.1111/j.0022-3646.1995.00325.x
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 <i>Laminaria solidungula</i>	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 <i>Alaria esculenta</i> 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 <i>Laminaria saccharina</i> in a high-arctic fjord, NE Greenland	2002	Borum	10.1007/s00227-002-0806-9
none	Young Sound	Biomass, photosynthesis and growth of <i>Laminaria saccharina</i> in a high-arctic fjord, NE Greenland	2002	Borum	10.1007/s00227-002-0806-9
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)0760493UBIC PD2.0.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 <i>Fucus</i> 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 <i>Palmaria palmata</i> and <i>Odonothalia dentata</i> 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 <i>Saccorhiza dermatodea</i>	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 <i>Laminaria</i> 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 life 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 <i>Alaria esculenta</i> (Phaeophyceae)	2009	Fredersdorf	10.1007/s00442-009-1326-9
none	Arctic	Light and temperature demands of marine benthic microalgae and seaweeds in polar regions	2009	Gómez	10.1515/BOT.2009.073
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 <i>Saccharina latissima</i> (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 <i>Lithothamnion glaciale</i> 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 <i>Saccharina latissima</i> (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 <i>Saccorhiza dermatodea</i> (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 <i>Alaria esculenta</i> (Alariales, Phaeophyceae)	2011	Steinhoff	10.1111/j.1751-1097.2011.01004.x
none	Arctic	Footprints of climate change in the Arctic marine ecosystem	2011	Wassmann	10.1111/j.1365-2486.2010.02311.x
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 <i>Saccharina latissima</i> (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 <i>Alaria esculenta</i> and <i>Laminaria digitata</i> (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: <i>Desmarestia aculeata</i> and <i>Alaria esculenta</i>	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 <i>Alaria esculenta</i> (L.) Greville from Spitsbergen (Norway)	2015	Lütz	10.1007/s00300-015-1659-2
none	Arctic	The future of Arctic benthos: Expansion, invasion, and biodiversity	2015	Renaud	10.1016/j.pocean.2015.07.007
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 <i>Saccharina latissima</i> and <i>Laminaria solidungula</i>	2016	Iñiguez	10.1007/s00227-016-3024-6
none	Arctic	The fate of the Arctic seaweed <i>Fucus distichus</i> under climate change: an ecological niche modeling approach	2016	Jueterbock	10.1002/ece3.2001
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 <i>Laminaria solidungula</i> 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, <i>Fucus distichus</i> , from the Arctic and subarctic intertidal	2016	Smolina	10.1098/rsos.150429
none	Svalbard	Ecosystem Kongsfjorden: new views after more than a decade of research	2016	Wiencke	10.1007/s00300-016-2032-9
in situ	Sisimiut	Climate change stimulates the growth of the intertidal macroalgae <i>Ascophyllum nodosum</i> near the northern distribution limit	2017	Márba	10.1007/s13280-016-0873-7
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 <i>Alaria esculenta</i> (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/Ino.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/Ino.11043
ex situ	Nuuk	Influences of salinity on the physiology and distribution of the Arctic coralline algae, <i>Lithothamnion glaciale</i> (Corallinales, Rhodophyta)	2018	Schoenrock	10.1111/jpy.12774
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 <i>Saccharina latissima</i> in the early polar night	2020	Huiru Li	10.3389/fmars.2020.592033
ex situ	Northern Norway	Heat stress responses and population genetics of the kelp <i>Laminaria digitata</i> (Phaeophyceae) across latitudes reveal differentiation among North Atlantic populations	2020	Liesner	10.1002/ece3.6569
ex situ	Svalbard	Thermal traits for reproduction and recruitment differ between Arctic and Atlantic kelp <i>Laminaria digitata</i>	2020	Martins	10.1371/journal.pone.0235388
both	Beaufort sea	Physiological responses of an Arctic crustose coralline alga (<i>Leptophytum foecundum</i>) to variations in salinity	2020	Muth	10.3389/fpls.2020.01272
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/Ino.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 <i>Saccharina latissima</i> from Spitsbergen	2021	Diehl	10.3354/meps13532
ex situ	Svalbard	Summer heatwave impacts on the European kelp <i>Saccharina latissima</i> 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 cover	2021	Goldsmid	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 <i>Laminaria solidungula</i> (Laminariales) in the White Sea	2021	Mikhaylova	10.31111/nsnr/2021.55.2.325
both	Stefansson Sound, Alaska	Inherent tolerance of extreme seasonal variability in light and salinity in an Arctic endemic kelp (<i>Laminaria solidungula</i>)	2021	Muth	10.1111/jpy.13187
ex situ	Svalbard	Daylength influences reproductive success and sporophyte growth in the Arctic kelp species <i>Alaria esculenta</i>	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 <i>Laminaria digitata</i> (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