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1 ARCTIC KELP FORESTS: DIVERSITY, RESILIENCE AND FUTURE.

2

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14 ABSTRACT. The Arctic is one of the most rapidly changing places on Earth and it is a sentinel
15 region for understanding the range and magnitude of planetary changes, and their impacts on
16 ecosystems. However, our understanding of arctic coastal ecosystems remains limited, and the
17 impacts of ongoing and future climate change on them are largely unexplored. Kelp forests are
18 the dominant habitat along many rocky Arctic coastlines, providing structure and food for
19 economically and ecologically important species. Here we synthesize existing information on
20 the distribution and diversity of arctic kelp forests and assess how ongoing changes in
21 environmental conditions could impact the extent, productivity, and resilience of these
22 important ecosystems. We identify regions where the range and growth of arctic kelp are likely
23 to undergo rapid short-term increase due to reduced sea ice cover, increased light, and warming.
24 However, we also describe areas where kelp could be negatively impacted by rising freshwater
25 input and coastal erosion due to receding sea ice and melting permafrost. In some regions,
26 arctic kelp forests have undergone sudden regime shifts due to altered ecological interactions
27 or changing environmental conditions. Key knowledge gaps for arctic kelp forests include
28 measures of extent and diversity of kelp communities (especially northern Canada and
29 northeastern Russia), the faunal communities supported by many of these habitats, and the role
30 of arctic kelp forests in structuring nearby pelagic and benthic food webs. Filling in these gaps
31 and strategically prioritizing research in areas of rapid environmental change will enable more
32 effective management of these important habitats, and better predictions of future changes in
33 the coastal ecosystems they support and the services that they provide.

34

35 **Keywords (6):** seaweed, climate change, polar, sea ice loss, borealization

36 1.1. INTRODUCTION

37 The effects of humans are pervasive and are transforming natural ecosystems and
38 biogeochemical cycles on global scales (Halpern et al. 2008; Waters et al. 2016). There is,
39 however, great regional variation in the nature, magnitude, and direction of these changes
40 (Burrows et al. 2011; Krumhansl et al. 2016), and it is only by understanding these
41 geographical intricacies that we can begin to grasp the full extent of our footprint on the planet.
42 Currently, the Arctic is warming 2 – 4 times faster than the global average and is now one of
43 the most rapidly changing regions in the world (IPCC 2014). Marine ecosystems along Arctic
44 coasts are experiencing increases in sea temperatures, dramatic declines in sea ice, and
45 increased input of freshwater (Wassmann and Reigstad 2011; Coupel et al. 2015; Acosta
46 Navarro et al. 2016; Ding et al. 2017). These changes are altering carbon cycling, affecting the
47 timing and magnitude of primary production, and driving shifts in the structure and function of
48 marine communities (Grebmeier et al. 2006; Nelson et al. 2014). As a result, the entire Arctic
49 region has been designated an ocean warming hotspot (Hobday and Pecl 2014). Impacts of
50 rapid environmental change on arctic ecosystems has broad significance due to both the global
51 uniqueness and large geographic extent of the region, and because it may act as a sentinel for
52 other ecosystems experiencing slower rates of change (Pecl et al. 2014; Hobday and Pecl 2014).
53 Despite this, most Arctic coasts remain relatively unexplored, and the extent and resilience of
54 coastal ecosystems are poorly understood, as are the ongoing and future impacts of climate
55 change on them. Understanding changes to arctic ecosystems is especially critical because
56 borealization (i.e., the northward shift of temperate communities) could squeeze out high arctic
57 ecosystems altogether, resulting in the planetary loss of an entire climate zone (Fossheim et al.
58 2015; Kortsch et al. 2015).

59 Kelp are large brown seaweeds that occur on rocky coasts throughout the Arctic
60 (Wernberg et al. 2018). Many (or most) kelps are important foundation species that create

61 habitat (forests) for numerous fish and invertebrates (Christie et al. 2009; Norderhaug and
62 Christie 2011; Teagle et al. 2017), provide food to marine communities through high
63 production and export of detritus and dissolved organic material (Krumhansl and Scheibling
64 2012; Renaud et al. 2015; Abdullah et al. 2017; Filbee-Dexter et al. 2018 in press), and store
65 and sequester carbon (Krause-Jensen and Duarte 2016). Currently, information on the
66 distribution, diversity, stability, and function of kelp forests is missing for large portions of the
67 Arctic (Wiencke and Clayton 2009; Krumhansl et al. 2016; Wilce 2016).

68 A recent global analysis of records of kelp abundance over the past 5 decades showed
69 that kelp forests are changing in many regions of the world (Krumhansl et al. 2016). At the
70 warmest edges of their range, sudden shifts from kelp forests to reefs dominated by low-lying
71 turf-forming algae have been increasingly documented over the last decade (Filbee-Dexter and
72 Wernberg 2018). Along other temperate coasts, native kelps are being replaced by invasive
73 kelps or other seaweeds (Wernberg et al. 2018), or are being heavily overgrazed by sea urchins
74 (Filbee-Dexter and Scheibling 2014). In many of these regions, declines in kelp abundance are
75 partly explained by the direct and indirect effects of warming sea temperatures (Ling et al.
76 2009; Catton 2016; Filbee-Dexter et al. 2016; Wernberg et al. 2016). Considering the
77 widespread changes throughout the temperate and tropical range of kelp and the ongoing
78 environmental changes occurring in the Arctic, the fate of arctic kelps in this era of rapid
79 change is a critical gap in our knowledge of arctic marine ecosystems.

80 Here we synthesize existing information on the distribution, biomass, and dominant
81 species of arctic kelp forests. We explore some of the services provided by arctic kelps and
82 identify missing baseline measures of their extent. We analyze changes in the sea ice extent
83 and temperature conditions for known locations of kelp, and explore how recent and future
84 changes in these and other conditions could impact their growth, reproduction, and survival.

85 Finally, we highlight key gaps in our understanding of these ecosystems, and suggest strategies
86 for future research.

87

88 1.2. HIDDEN BLUE FORESTS OF THE ARCTIC

89 1.2.1. Bounds of arctic marine ecosystems

90 Arctic and temperate marine ecosystems are separated by a moving boundary, generally
91 defined by latitude, sea ice cover, light variability, and the locations of the polar front and other
92 ocean currents (Piepenburg 2005). The locations of these boundaries can be seasonal,
93 unpredictable, and can shift with climate change. A precise and universally accepted
94 geographical definition of ‘Arctic marine ecosystems’ therefore does not exist, and different
95 southern limits for arctic marine ecosystems are used in the literature (Zenkevitch 1963;
96 Piepenburg 2005; Gattuso et al. 2006; Wilce 2016). For example, so called ‘Arctic conditions’
97 (ice scoured intertidal zones, ocean temperatures $< 0^{\circ}\text{C}$, and months with little to no daylight)
98 extend below the Arctic circle along the coasts of Greenland and Eastern Canada, which are
99 influenced by the cold southward moving Labrador and Greenland currents, but are restricted
100 to above the Arctic circle along the coasts of northern Norway, Iceland and in the southern
101 Bering sea, which are influenced by the warmer northward moving Gulf Stream and North
102 Pacific currents, respectively (Wilce 2016). The convergence of cool waters from the Arctic
103 Ocean and warm waters from the Atlantic and Pacific Oceans occurs around 65°N on the east
104 coast of Greenland, 80°N west of Svalbard, 76°C in the Barents Sea, in the Bering Strait, 63°N
105 in the eastern Canadian Arctic Archipelago, and then slightly north between Baffin Island and
106 the west coast of Greenland (AMAP 1998). However, other factors such as sea ice, light, and
107 glacial run-off also create Arctic conditions south of these limits (AMAP 1998). Here we define
108 ‘arctic kelps’ as kelps occurring within the boundaries defined by the Arctic Monitoring and
109 Assessment Program (AMAP). AMAP originally defined Arctic boundaries in 1991 as regions

110 north of the 10°C July isotherm. These boundaries have since been expanded to include some
111 areas that correspond to political boundaries of member nations of the Arctic Council (e.g.,
112 coastal shelf of Iceland, Norwegian northwest coast, Hudson Bay, and the Aleutian Islands)
113 (AMAP 2017). We used this definition because monitoring programs, assessments and
114 decision-making on pollution and climate change in Arctic regions often use AMAP
115 boundaries. However, despite our inclusive definition of the Arctic, much of this manuscript
116 focuses on kelp forests at higher latitudes within the AMAP region where kelps face the most
117 extreme Arctic conditions and where globally unique species compositions are found.

118

119 1.2.2. Distribution, growth forms and evolution of arctic kelps

120 Although kelps range along most Arctic coasts, sparse records of kelp in some parts of the
121 Arctic have been attributed to a lack of hard substrata (Kjellman 1883; Wilce 2016). Only about
122 35% of the Arctic basin is rocky substrate and shallow coastal areas and inner Arctic fjords are
123 often dominated by sediment due to glacial run off and river deposition (Leont'yev 2003;
124 Lantuit et al. 2012), which limits the presence of kelp. In areas with suitable substrate, dense
125 kelp forests can extend from the intertidal zone down to depths of 30 – 40 m depending on light
126 conditions, wave regime, and grazing intensity (Wernberg et al. 2018). The deepest recorded
127 kelp was observed at 60 m depth in Disko Bay, Greenland (Boertmann et al. 2013). In high
128 Arctic regions, available light and sea ice further restrict this depth range and the upper
129 sublittoral zone is a barren, low salinity environment that is constantly impacted by sea ice and
130 meltwater (Wiencke and Clayton 2011).

131 The diversity of kelp in the high Arctic tends to be lower than in temperate kelp forests
132 (Wiencke and Clayton 2011). Genetic evidence indicates that most kelps reinvaded the Arctic
133 from the Atlantic Ocean ~8,000 years ago following the last ice age, which eliminated benthic
134 flora from most current Arctic subtidal regions (Wulff et al. 2011). As a result, most arctic

135 kelps have optimal growth temperatures that exceed those experienced during the Arctic
136 summer and many of these species therefore also thrive along warmer, temperate coasts
137 (Wiencke and Amsler 2012). In the high Arctic especially, kelps tend to be morphologically
138 smaller compared to their southern range limits (e.g., Kuznetsov et al. 1994; Kuznetsov and
139 Shoshina 2003; but see Borum et al. 2002). However, kelps still form dense canopies in some
140 regions (e.g., western Alaska and northern Norway) and provide most of the algal biomass and
141 the largest three-dimensional biogenic structure on rocky coasts in Arctic regions (Wiencke
142 and Amsler 2012). In fact, these lush underwater forests are particularly striking in the Arctic,
143 where terrestrial coasts are barren and ice scoured with little three-dimensional structure.



144
145 Fig 1. Photographs of select kelps from high Arctic regions: a) *Laminaria solidungula*, b)
146 *Alaria elliptica*, c) *Saccharina longicuris*, d) *Saccharina nigripes*, and e) *Saccorhiza*
147 *dermatodea* (Guiry and Guiry 2017).

148
149 The species pool is relatively young, with only one truly arctic endemic kelp, *Laminaria*
150 *solidungula* (Kjellman 1883; Zenkevitch 1963; Wilce and Dunton 2014). All other kelp species
151 found in Arctic regions also extend into sub-arctic and northern temperate waters and include
152 *Alaria esculenta*, *Agarum clathratum*, *Eualaria fistulosa*, *Laminaria digitata*, *Laminaria*

153 *hyperborea*, *Nereocystis luetkeana*, *Saccharina latissima*, *Saccharina longicuris*, *Saccharina*
154 *nigripes*, *Saccorhiza dermatodea*, *Alaria elliptica*, and *Alaria oblonga* (the latter 2 are only
155 found in Russia) (Fig 1, Table 1). There is currently taxonomic confusion regarding some arctic
156 species; *S. nigripes*, for example, has often been misidentified as *L. digitata*, and appears to be
157 restricted to Arctic or subarctic conditions, although more information on its distribution is
158 needed (McDevit and Saunders 2010). In 2006 a new species of kelp *Aureophycus aleuticus*
159 was collected from Kagamil Island, Aleutian Islands, but its classification within the order
160 Laminariales is still unclear (Kawai et al. 2013). New DNA barcoding techniques show
161 promise for clearing up misidentifications caused by diverse growth morphologies of kelps in
162 arctic conditions (McDevit and Saunders 2010; Bringloe et al. 2017).

163

164 1.2.1. Adaptations to Arctic conditions

165 Kelps in arctic environments are challenged by extremely low water temperatures, periods of
166 low salinity, and extreme variability in light caused by large annual variations in day length,
167 light intensity, and sea ice cover. In their northernmost range, kelps live in temperatures at the
168 point of freezing sea water during polar nights (e.g., NE Greenland, Borum et al. 2002; Franz
169 Joseph Land, Shoshina et al. 2016). Day-length ranges from 24-hour sunlight in mid-summer
170 to several months of total darkness during winter (Hanelt 1998). The low angle of the sun and
171 periods of complete darkness mean that high Arctic areas only receive 30 – 40 % of the light
172 received in the tropics on an annual basis. The long period of darkness during winter is further
173 extended in areas with partial or complete sea ice cover, especially if the ice is thick or covered
174 by snow (Mundy et al. 2007). Subtidal habitats in the Arctic can therefore be without light for
175 much of the year. Studies from NE Greenland illustrates this; the annual surface irradiance
176 (PAR) in Young Sound (74° 18' N) amounts to ca. 6100 mol photons m⁻², but the ice-free

177 period is limited to August and September so that the amount of available light at 10 and 20 m
178 depth is only 234 and 40 mol photons m⁻² yr⁻¹, respectively (Borum et al. 2002).

179 The marked seasonal variation in light availability in the Arctic concentrates primary
180 production into a short period and creates strong seasonality in the growth of kelp (Chapman
181 and Lindley 1980; Dunton and Jodwalis 1988; Borum et al. 2002; Makarov et al. 2008). Arctic
182 kelps are well adapted to these long periods of darkness or low light conditions. Studies on *S.*
183 *latissima* and *L. solidungula* show that these species store most of the carbon obtained during
184 the short summer period and subsequently use these reserves to form new blades during the
185 succeeding period of almost darkness (Chapman and Lindley 1980; Dunton and Jodwalis 1988;
186 Borum et al. 2002). Remarkably, the peak growth period for Alaskan *L. solidungula* was from
187 February to April under full ice cover (Dunton 1985), and the production of new lamina in *S.*
188 *latissima* from Young Sound (NE Greenland) occurred under ice cover and in complete
189 darkness, likely based on re-allocation of C from the old lamina or stipe (Borum et al. 2002).

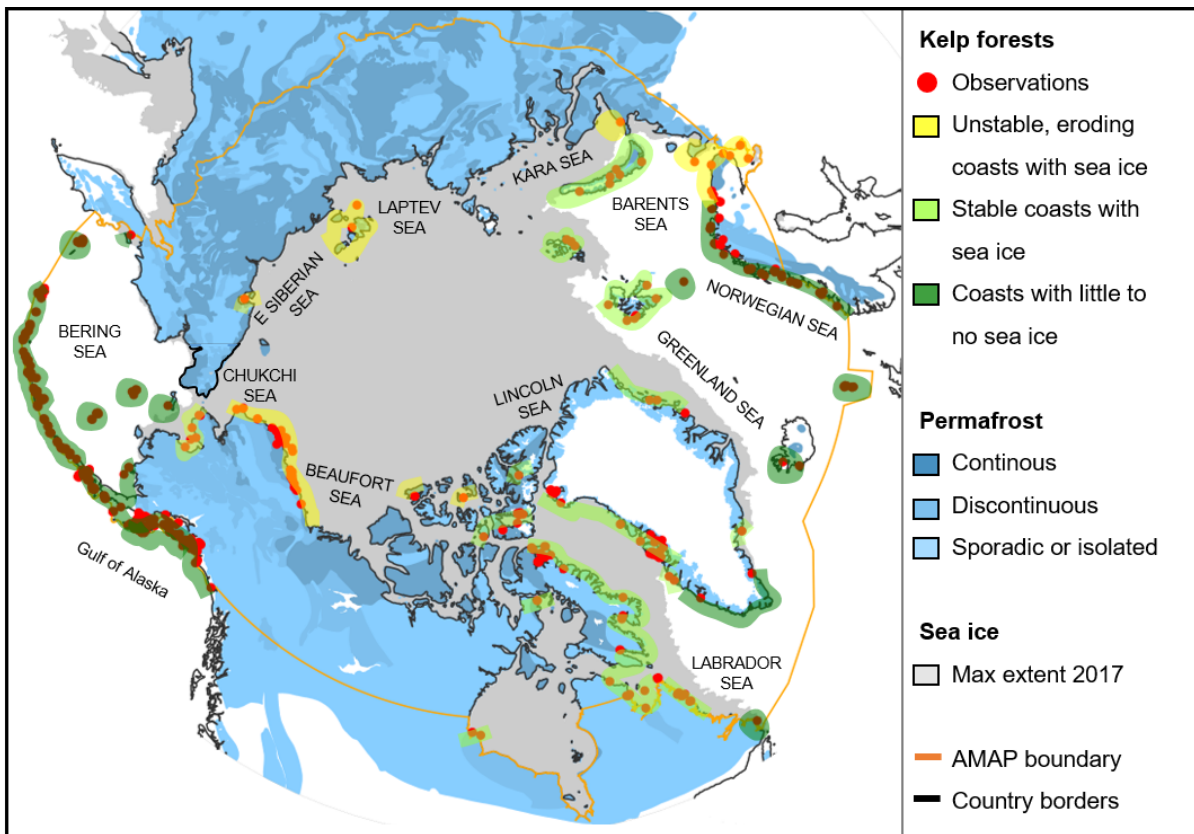
190 Many kelp species can also cope with multi-year sea ice, which can cause severe
191 mechanical damage to benthic organisms in the intertidal and upper subtidal zone (Krause-
192 Jensen et al. 2012; Dayton 2013; Shoshina et al. 2016). Most kelp forests recover from sea ice
193 damage through high reproduction and recolonization of the scoured substrate. Keats et al.
194 (1985) found, for example, that populations of *A. esculenta* recovered within a few years after
195 having been removed by ice-scour in the uppermost reaches of its range. However, Konar
196 (2013) found slow recolonization in clearing experiments on kelps in the Boulder Patch (< 10
197 % recolonization after 7 years), which is much slower than rates in many temperate kelp forests.

198

199 1.3. KNOWN LOCATIONS OF ARCTIC KELPS

200 Data on the current extent and distribution of kelps in the Arctic is not available. To overview
201 the observational data record of kelp in subarctic and Arctic seas we compiled records of kelp

202 over the last 2 centuries, within the AMAP boundaries, from primary literature, museum
203 collections, dive logs, Arctic expeditions, coastal monitoring, and local ecological knowledge
204 from Inuit and northern communities (N = 1179 records, Fig 3). The spatial extent of these
205 ecosystems ranged from 100s of km² of kelp forests to small patches of kelp within inner fjords
206 and boulder patches along sedimentary coasts. The number of kelp records decreased with
207 latitude, with the northernmost observations of kelp forests > 80° N at Svalbard, Norway and
208 Franz Joseph Land, Russia (Shoshina et al. 1997; Bartsch et al. 2016). Most records were from
209 northern Norway, western Greenland, eastern Canada, and northwestern USA. The earliest
210 records of arctic kelp were from the Canadian high Arctic during expeditions in search of the
211 Northwest passage (Lee 1980). Other early records come from Kjellman (1883), who published
212 the first comprehensive review of polar benthic algae based on expeditions from Sweden via
213 Norway to Novaya Zemlya, and into the Siberian sea, Russia, and Rosenvinge (1893, 1899),
214 who described the algal flora in Greenland a decade later. Dive research on arctic kelp forests
215 was first conducted in Greenland, Canada and USA by Wilce (1963), Chapman and Lindley
216 (1980), and Dunton et al. (1982). It is worth noting that these historical records represent a
217 baseline and may not reflect current kelp distributions.



218

219 Fig. 2. Kelp locations (red) within AMAP Arctic boundary line (orange). Gray shading shows
 220 maximum sea ice extent, blue shading shows continuous permafrost (90 - 100 % cover),
 221 discontinuous permafrost (50-90 %), and sporadic and isolated patches of permafrost (< 50 %)
 222 (2016 National Snow and Ice Data Centre,
 223 https://nsidc.org/data/docs/fgdc/ggd318_map_circumarctic/). Eroding coasts (yellow) and
 224 stable coasts (light green) in regions with sea ice were differentiated according to the Arctic
 225 coastal classification scheme developed by Lantuit et al. (2012).

226

227 Extreme variation in environmental conditions occur within the AMAP arctic
 228 boundaries. Large regional differences in coastal conditions are strongly driven by the cover of
 229 sea ice and the presence of permafrost (frozen soil, rock, or sediment) (Lantuit et al. 2012). To
 230 capture this variability in our description of arctic kelps, we grouped information from our

231 observational data into 3 general categories: (1) kelps on stable coasts with sea ice, (2) kelps
232 on unstable, eroding coasts with sea ice, and (3) kelps on coasts with little to no sea ice.



233

234 Fig 3. Photographs show examples of arctic kelp forests: (A) *Laminaria solidungula* in the
235 Beaufort Sea, Alaska, USA (Ken Dunton), (B and C) *Laminaria hyperborea* in Malangen fjord,
236 Norway (Thomas Wernberg, Karen Filbee-Dexter), (D) *Eularia fistulosa* Aleutian Islands,
237 Alaska (Pike Spector), (E) *Saccharina latissima* under sea ice in Kangiqsujuaq, Canada (PBS,
238 2017), (F) *Laminaria digitata* in Svalbard, Norway (Max Schwanitz), (G) *Saccharina*
239 *latissima*, *S. longicuris*, *Alaria esculenta*, *Laminaria solidungula* in northern Baffin Island,
240 Canada (Frithjof Küpper), and (H) *Laminaria hyperborea* along the Murmansk coast, Russia
241 (Dalnie Zelentsy).

242

243 1.3.1 Kelps on stable Arctic coasts with sea ice

244 Stable, rock bound coasts and fjord systems in Arctic areas with seasonal cover of sea ice can
245 support luxurious kelp forests, although their vertical distribution is limited by ice scour
246 (shallow) and light. These areas are expected to experience pronounced changes in
247 environmental conditions when sea ice retreats. Although this should increase overall primary
248 productivity along these coasts, the species composition of algae currently found in these Arctic

249 regions may be lost permanently if more temperate-adapted algal communities push northward
250 and outcompete kelps that are adapted to seasonal sea ice (Krause-Jensen and Duarte 2014).

251 In the northern Barents Sea, kelp forests of mixed *A. esculenta*, *L. digitata* and *S.*
252 *latissima* occur within high latitude fjords off Svalbard, the western White Sea, and Franz
253 Joseph Land (Kuznetsov et al. 1994; Cooper et al. 1998; Bartsch et al. 2016; Fig 3fh). Luxuriant
254 stands of *L. digitata*, *L. solidungula*, *S. dermatodea*, and *A. clathratum* were observed within
255 fjords in western Novaya Zemlya (Shoshina and Anisimova 2013). In the northernmost regions
256 around Svalbard and Novaya Zemlya, the arctic endemic kelp *L. solidungula* is found in inner
257 fjords and areas that receive cold polar currents (Svendsen 1959; Hop et al. 2012; Shoshina
258 and Anisimova 2013).

259 The west coast of Greenland is largely rockbound and dominated by sub-littoral kelp
260 forests from Cape Farewell in the south (59° N) to Smiths Sound in the north (>80° N,
261 Rosenvinge 1893, 1899). The western Greenland kelp forests are dominated by *S. longicuris*
262 north of 62° N and by *S. latissima* south of this latitude, while other species such as *L.*
263 *solidungula*, *A. esculenta*, *Agarum clathratum*, *S. nigripes* and *S. dermatodea* are present, but
264 less conspicuous (Rosenvinge 1899; Krause-Jensen et al. 2012). The kelp forests in western
265 Greenland are narrow and shallow in the north, but become broader, more abundant, and extend
266 deeper in the south due to less ice cover (Krause-Jensen et al. 2012). In some parts of
267 Greenland, high densities of sea urchins or a lack of hard bottom restricts the extent of the kelp
268 forests (Krause-Jensen et al. 2012). The kelp populations in eastern Greenland tend to be
269 situated deeper, have less biomass per unit area and grow more slowly than those on the west
270 coast (Borum et al. 2002; Krause-Jensen et al. 2012), which may be due to lower water
271 temperatures, longer periods with ice-cover, and more heavy scour by pack ice. *S. latissima*
272 and *A. esculenta* appear to be the dominant species along most of the east coast (recorded as

273 high as Danmarks Havn (75° N)), while *L. solidungula*, *S. nigripes*, *S. longicuris* and *A.*
274 *clathratum* are present, but less abundant (Rosenvinge 1899).

275 In Hudson Bay and Eastern Canada, sea ice extends below the Arctic circle due to the
276 influence of the cold Labrador current. *S. latissima*, *A. clathratum*, *A. esculenta*, and *L.*
277 *solidungula* have been documented between Ellesmere Island and Labrador, and along coasts
278 in Lancaster Sound, Ungava Bay, Hudson Bay, Baffin Bay, and Resolute Bay (Table 1). These
279 ecosystems can be highly productive in some areas, with luxuriant beds of 15-m long *S.*
280 *latissima* observed in Frobisher Bay, and beds containing a biomass of 19 kg wet weight m⁻²
281 of *A. esculenta* measured in Ungava Bay (Sharp et al. 2008). Kelp forests have also been
282 documented in eastern Chukchi Sea from Norton Sound to north of the Bering Strait along the
283 west coast of Alaska (70 and 71° N; Phillips and Reiss 1985).

284

285 1.3.2. Kelps on eroding, permafrost bound Arctic coasts with sea ice

286 Scattered low relief, rocky coasts in the eastern Siberian, Laptev, Beaufort, and Chukchi
287 seas, and the Canadian high Arctic have temperatures and light conditions that should support
288 kelp (Krumhansl and Scheibling 2012), but observations are rare in these regions (Zenkevitch
289 1963; Lee 1973; Wilce and Dunton 2014; Wilce 2016). These coasts are more permanently
290 icebound compared to other Arctic regions— especially in the Beaufort, eastern Siberian, and
291 Laptev seas – and the seafloor is often covered in sediment due to intense glacial run off. Low
292 salinity, high levels of sedimentation, and sparse substrate make kelps and other macroalgae
293 poorly developed (Taylor 1954; Leont'yev 2003; Dayton 2013). As a result, kelps along these
294 coasts face ‘uniquely Arctic conditions’ such as extensive sea ice scour, long periods of
295 darkness, variable salinity, turbidity, and low temperatures (Wilce 2016). The associated
296 macroalgal communities in these regions have distinct species compositions compared to other
297 regions of the Arctic, possibly because they are less connected to nearby temperate

298 communities due to outflow of polar currents from the north to south along their coasts (Wilce
299 and Dunton 2014). In the Alaskan Beaufort Sea, kelps are found in scattered rocky habitats in
300 shallow waters (5 – 10 m depth) along the mainly sedimentary coast. Research on kelps in this
301 area are from the ‘Boulder Patch’ (71° N), where *L. solidungula* forms beds intermixed with
302 *A. esculenta* and *S. latissima* on shallow cobbles and boulders (Wilce and Dunton 2014; Fig
303 3a). These isolated kelp communities contain about half of the 140 macroalgal species found
304 in the Arctic. The Boulder Patch has been studied since 1978 and revisited in 14 separate years
305 between 1978 – 2012, over which time the species composition has remained relatively static
306 (Wilce and Dunton 2014).

307 In the northwestern high Canadian Arctic, low availability of rocky substrate and a
308 harsher climate support smaller, fragmented kelp forests (Lee 1980). This region of the
309 Canadian Arctic commonly supports *L. solidungula*, which has been observed as high as 74.5°
310 N.

311 In northeastern Russia, observations of kelp are limited to a handful of records along
312 these sedimentary coasts, namely, *S. latissima* off Amderma, mainland Russia, Kotel Nyy
313 Island (Cooper et al. 1998), and along the Russian coast of Chukchi Sea (Zenkevitch 1963); *L.*
314 *solidungula* on islands in the Laptev Sea and within bays in the Siberian Sea (Cooper et al.
315 1998), and *S. latissima*, *L. solidungula*, *S. nigripes*, *A. elliptica* and *A. oblonga* in the Kara sea
316 (Zenkevitch 1963; Guiry and Guiry 2017).

317

318 1.3.3. Kelps in Arctic regions with little to no sea ice

319 Kelp forests in the Norwegian Sea, the Barents Sea, and the northern Pacific (Aleutian
320 Islands and northern Gulf of Alaska) have high upper limits of biomass compared to other
321 arctic kelp forests (Table 1; Fig 3bcd). These regions have little to no sea ice and ocean
322 temperatures that are warmer than other Arctic regions due to the influence of the Gulf Stream

323 or the Pacific Current. Kelp forests in some of these regions (e.g., the Gulf of Alaska) are highly
324 influenced by environmental conditions on land, namely high freshwater inputs from melting
325 permafrost and melting glaciers that creates strong clines in salinity in coastal areas (Spurkland
326 and Iken 2011; Lind and Konar 2017). Kelp in other regions with little to no sea ice appear to
327 be more influenced by biological factors than by environmental conditions. Many kelp forests
328 are strongly influenced by the density of herbivorous sea urchins, which increase with the loss
329 of higher level predators (e.g., crabs, cod, otters) (Doroff et al. 2003; Filbee-Dexter and
330 Scheibling 2014). Importantly, kelps currently found in areas with little to no sea ice may
331 represent future scenarios for other Arctic regions.

332 Along the western and northern coast of Norway, and along low-lying, rock-bounded
333 coasts within the Murmansk region of Russia, *Laminaria hyperborea* dominates the exposed
334 coasts (Fig 3bc, Table 1) and kelp forests can obtain biomasses up to 21 kg fresh weight m⁻²
335 (Fig S1). In the mid-1970s, high densities of the green sea urchin *Strongylocentrotus*
336 *droebachiensis* destructively grazed kelp forests and created extensive urchin barrens,
337 restricting the distribution of kelp to exposed regions or shallow surf zones (Leinaas and
338 Christie 1996). Currently, regional recovery of kelp forests is occurring following decreases in
339 sea urchin populations due to reduced urchin recruitment in the south (Fagerli et al. 2013) and
340 increased crab predation in the north (Fagerli et al. 2015).

341 In the North Pacific Ocean, surface canopy forming kelps *Eularia fistulosa* and
342 *Nereocystis luetkeana* and subsurface kelps (*Agarum clathratum*, *Alaria esculenta*, *Costaria*
343 *costada*, *Laminaria digitata*, and *Saccharina latissima*) form forests along the Aleutian Island
344 chain, the northern Gulf of Alaska coast and the northeastern coast of Russia. *Eularia fistulosa*
345 dominates surface canopies in the Aleutian Islands and *E. fistulosa* and *N. luetkeana* in
346 southeast Alaska that can grow from > 30 m depth. Subsurface kelps tend to be competitively
347 dominant in both regions (Duggins 1980, Dayton 1975). Kelp forests in the northern Gulf of

348 Alaska occur within the largest freshwater discharge system in North America, and experience
349 strong gradients of salinity due to substantial glacial inputs. The amount of glacial melt is
350 increasing with climate change, further lowering salinity and negatively effecting kelps in these
351 areas (Lind and Konar 2017). In contrast, kelp forests along the shores of the Aleutian Islands
352 are more influenced by biotic interactions. These coasts have alternated between kelp forests
353 and urchin barrens for over a century (Estes et al. 2004). Shifts between these two ecosystem
354 states are driven by changing abundances of sea otters, which are major predators of the sea
355 urchin *Strongylocentrotus polyacanthus* (Estes and Duggins 1995). Evidence from the region
356 suggests that kelp forests established in 1911 after protection of sea otters enabled their
357 populations to rebound (Estes et al. 1978). The recovered kelp forests (*Eualaria fistulos* and
358 *Laminaria* spp.) were maintained for decades, until otter populations declined again due to
359 predation by killer whales in the 1990s (Doroff et al. 2003; Estes et al. 2004), once again
360 limiting kelp forests to exposed areas and shallow depths, which serves as refuges from grazing
361 (Konar and Estes 2003).

362

363 1.4. ECOSYSTEM SERVICES PROVIDED BY ARCTIC KELP

364 Kelps can provide extensive substrate for colonizing organisms, and their canopies create
365 habitat for a number of marine plants, fish, and invertebrates (Teagle et al. 2017). The flora in
366 arctic kelp forests can be diverse and has been described in detail for some high Arctic regions
367 (e.g., Wilce and Dunton 2014; Küpper et al. 2016). Diverse fish, invertebrate and epiphytic
368 communities are found in kelp forests in Svalbard, Norway, the Aleutian Islands, the Gulf of
369 Alaska, and the Boulder Patch, USA (Hamilton and Brenda 2007; Włodarska-Kowalczyk et al.
370 2009; Wilce and Dunton 2014). Kelp canopies can create favourable conditions for some
371 understory species and were shown to provide predation refuge for juvenile cod in
372 Newfoundland, Canada (Gotceitas et al. 1995) and rockfish and ronquils in the Gulf of Alaska

373 (Dean et al. 2000b). Traditional knowledge from northern communities in Greenland reported
374 higher arctic cod catches in areas near kelp forests compared to other areas (Krause-Jensen and
375 Duarte 2014). Despite these reports, the smaller size and patchy nature of kelps in some Arctic
376 regions may reduce their importance as habitat forming species compared to temperate forests.
377 Kelp also has cultural value for northern peoples and features in their traditions and stories. It
378 is a traditional food for Inuit, who harvest it from under sea ice during low tide (Wein et al.
379 1996) and can be used by farmers as fertilizer or to cattle feed (Reedy and Katherine 2016).

380 Kelp-derived organic material constitutes a significant component of coastal primary
381 production, often forming the base of benthic food webs in nearby habitats (Dunton and Schell
382 1987; Fredriksen 2003; Krumhansl and Scheibling 2012). Direct consumption rates on most
383 high arctic kelps are unknown, but are likely lower than those along temperate and subarctic
384 coasts, as herbivores tend to be less abundant and the digestion of algae hypothesized to be less
385 energy efficient in colder ecosystems compared to warmer ecosystems (Floeter et al. 2005;
386 Konar 2013; Wilce 2016). Konar (2007) deployed grazer exclusion cages in experimental
387 clearings in kelp forests in the Beaufort Sea, Alaska, and found that the overall increase in algal
388 recruitment due to grazing was < 1% of the total area cleared. Similarly, the sea urchin
389 *Strongylocentrotus droebachiensis*, a key grazer of kelps along temperate coasts in the North
390 Atlantic (Filbee-Dexter and Scheibling 2014), is confined to shallow waters in the south
391 western Barents Sea (Murman coast), localized patches in Jan Mayen (Gulliksen et al. 1980),
392 Novaya Zemlya (Nordenskiöld 1880) and southern parts of Svalbard (Gulliksen and Sandnes
393 1980), and is rare or absent around Franz Josefs Land and the Laptev and Kara Sea (Levin et
394 al. 1998). Clear exceptions to this pattern of low grazing pressure at higher latitudes include
395 kelp forests in the Aleutian islands and northern Norway, where high consumption rates by sea
396 urchins have been recorded (Estes and Duggins 1995; Leinaas and Christie 1996).

397 Kelp carbon contributions to marine organisms in coastal environments can be
398 substantial. On average, around 80% of the kelp production globally (91% for the Boulder
399 Patch in the Beaufort Sea) enters coastal food webs as detritus, through detachment or
400 exudation of dissolved organic carbon, which is exported to adjacent ecosystems on beaches
401 and deeper offshore areas (Krumhansl and Scheibling 2012). Macroalgal-derived carbon can
402 be used by benthic herbivores and predators, while upper trophic level fishes and marine
403 mammals generally use phytoplankton-derived carbon (McMeans et al. 2013). Stable isotope
404 analyses show kelp carbon contributed 57% to nearshore fish populations in the Gulf of Alaska
405 (von Biela et al. 2016), 15 to 75% to rock greenling, predatory sea stars, and cormorants in the
406 Aleutian Islands (Duggin et al. 1989), 0 to 42% for diverse marine predators in Baffin Island,
407 Canada (McMeans et al. 2013), and 50% to mysid crustaceans in the Beaufort Sea (Dunton and
408 Schell 1987). The latter predatory snails are a critical food source for higher trophic levels such
409 as fish, whales, and birds, indicating the high importance of kelp as a primary producer (Dunton
410 and Schell 1987).

411 A comprehensive understanding of the nature and extent of kelp subsidy to other arctic
412 benthic, pelagic, and terrestrial ecosystems is still lacking, and the magnitude and importance
413 of kelp exported from shallow coasts to deeper habitats is a debated topic of on-going research
414 (Renaud et al. 2015). In the subarctic and Arctic regions, most research has focused on the
415 vertical influx of phytoplankton- or zooplankton-derived organic matter as the main source of
416 carbon in benthic systems. In Greenland, Krause-Jensen et al. (2007) showed that primary
417 production of kelps and other benthic algae can contribute to > 20% of the total primary
418 production in shallow coastal areas. However, at depths > 15 m this production was largely
419 insignificant compared to that of phytoplankton and benthic microalgae (Krause-Jensen et al.
420 2007). The magnitude of, and timing by which, kelp-derived carbon enters arctic ecosystems
421 is especially interesting because climate change is triggering earlier phytoplankton blooms in

422 the Arctic, creating temporal mismatch between pelagic primary production and some higher
423 trophic level species that synchronize their life cycle or behaviour to this pulsed source of
424 energy (van Leeuwe et al. 2018). In light of this mismatch, understanding other sources of
425 arctic primary production during food-limited periods is becoming critical.

426 Knowing the residence time of kelp detritus in Arctic environments is important in light
427 of increased interest in blue carbon sequestration worldwide (Krause-Jensen and Duarte 2016).
428 In the Canadian High Arctic, large amounts of macroalgal detritus have been observed on the
429 seafloor in sheltered fjords (Küpper et al. 2016). In northern Norway (70°N), pulses of whole
430 kelp blades rapidly reached deep-fjord communities (> 400 m depth) during the spring
431 shedding of old *L. hyperborea* lamina (Filbee-Dexter et al. 2018). If kelp material degrades
432 slower and remains intact longer in colder arctic environments, it may be more likely to be
433 sequestered in ocean sediments than kelp carbon produced at lower latitudes.

434

435 1.5. KELPS IN A SENTINAL REGION OF CHANGE

436 Key changes that will influence kelps in the Arctic include elevated temperatures (Najafi et al.
437 2015; Wang et al. 2017), decreased cover and thickness of sea ice (Arctic Monitoring and
438 Assessment Programme. 2011; Parkinson and Comiso 2013; Ding et al. 2017), reduced
439 salinity, and increased turbidity (IPCC 2014; Günther et al. 2015). Other environmental
440 changes that could impact kelps are altered nutrients levels and increased UV radiation.
441 Reduced sea ice and warming could also bring in invasive species by increasing shipping traffic
442 or warm water species migration (Miller and Ruiz 2014), which could impact kelp
443 communities. The cumulative impact of these stressors will likely affect kelp growth rates and
444 periods severely, but ultimately depends on their nature and strength, the interactions between
445 them, and the ways in which different kelp species acclimate and/or adapt to new conditions
446 (Harley et al. 2012).

447

448 1.5.1. Temperature

449 Temperatures in the Arctic are projected to increase by 3 – 4°C by the end of the 21st Century
450 under realistic warming scenarios (IPCC 2014; Huang et al. 2017). Currently, kelps in Arctic
451 waters experience low temperatures with little seasonal variation. Water temperatures rarely
452 exceed 5°C in summer in the high Arctic, but may reach 10°C during summer in the southern-
453 most parts of Arctic or where warm ocean currents affect local climate. Average temperatures
454 may be below 0° C with a variation as small as $\pm 1^\circ$ C in high latitude places affected by cold
455 currents (e.g., Igloolik, Northwest Territories, Canada (Bolton and Lüning 1982); Young
456 Sound, eastern Greenland (Borum et al. 2002); Franz Joseph Land, Russia (Shoshina et al.
457 2016)).

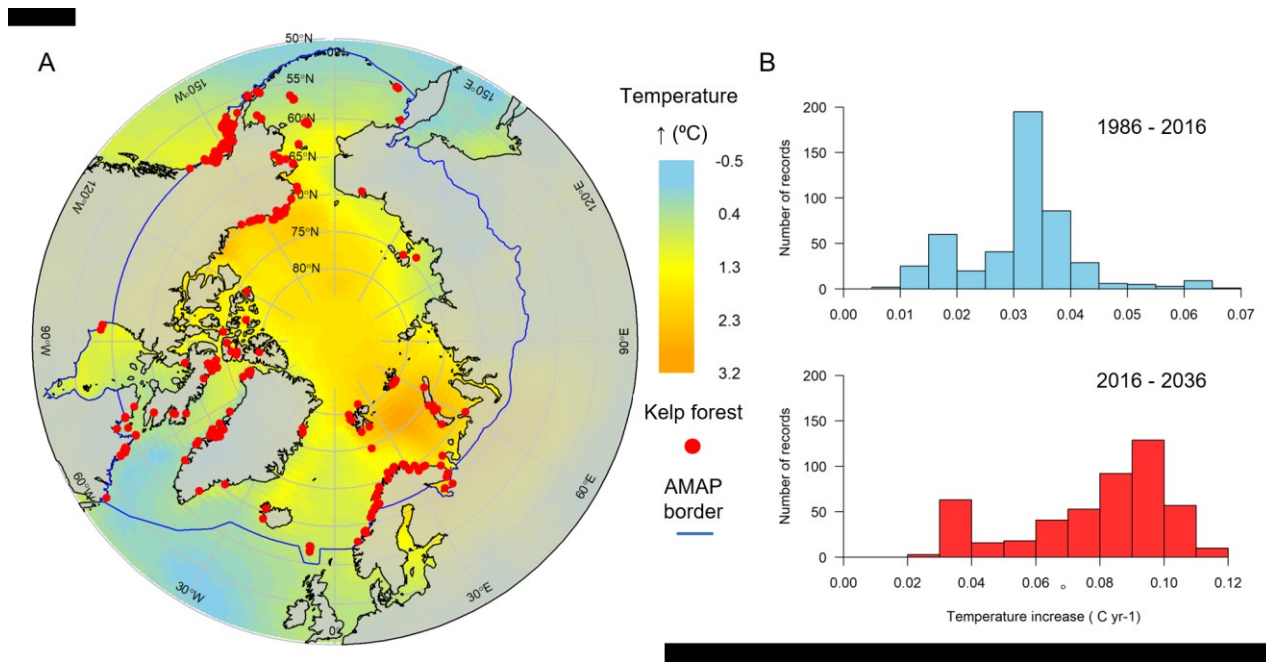
458 To explore prior and ongoing temperature changes in the vicinity of documented
459 locations of arctic kelp, we related these to maps of surface temperature for the region. We
460 calculated average temperature measures from 1986 and 2016 at each of our kelp locations
461 using historical IPCC temperature maps (IPCC 2014, accessed through
462 gisclimatechange.ucar.edu). Around each kelp location we averaged the mean summer (July to
463 September) temperature over this 20-year period within a buffer radius of 1° latitude, which
464 corresponded to the spatial error associated with locations of early records. We also calculated
465 the magnitude and rate of the predicted increase in mean summer temperature at each location
466 using climate model forecasts for 2016 to 2036 (IPCC 2014). We used the model based on the
467 conservative greenhouse gas emission scenario B1, which predicted a conservative increase of
468 1.1 to 2.9 °C by 2090-2099 relative to 1980-1999 (SRES 2000).

469 The mean summer temperature across all kelp locations has increased by 0.35° C (\pm
470 0.20) per decade over the period from 1986 to 2016 (Fig. 4a) and is predicted to increase by
471 1.09° C (± 0.59) per decade over the next century (Fig 4b). Predicted temperature increases are

472 least pronounced for kelps along the coasts of Greenland and eastern Siberia, and most
473 pronounced in the Barents Sea, Beaufort Sea, and Canadian High Arctic, suggesting that
474 changes to kelp forests due to warming will first occur in these regions.

475 Based on temperature tolerance and growth optima of most arctic kelp species, warmer
476 temperatures should increase growth rates (Müller et al. 2009; Shoshina et al. 2016). The
477 optimum growth temperature for most arctic and cold-temperate kelp species range from 10 to
478 15°C (Wiencke and Amsler 2012; Roleda 2016), and growth at 0 to 5°C is typically only 25 –
479 30% of growth at their optimum temperature (e.g., Bolton and Lüning 1982). Upper
480 temperature limits on growth of arctic kelps ranges from 16°C to 21°C (Assis et al. 2018),
481 which are well above conditions found along Arctic coasts. This suggests warming could more
482 than double kelp production in some regions the next 2 – 3 decades. Warming may also
483 improve recruitment; for example, germination of spores, fertility (Golikov and Averintsev
484 1977), and survival of arctic kelp gametophytes are limited by temperatures below -1° C
485 (Sjötun and Schoschina 2002; Müller et al. 2008; Assis et al. 2018) (Table 2). Such changes
486 will vary across kelp species and will likely alter their competitive interactions. In the northern
487 Gulf of Alaska, spore settlement and gametophyte growth of *Eualaria fistulosa* were more
488 negatively impacted by elevated temperatures and low salinity, than that of the more widely
489 distributed *N. luetkeana* and *S. latissima* (Lind and Konar 2017). *A. esculenta* is best adapted
490 to low temperatures and cannot survive in waters warmer than 16°C (Sundene 1962).
491 Likewise, recruitment of *L. solidungula* becomes limited when temperatures exceed 10° C.
492 Other, more warm adapted temperate kelps such as *L. hyperborea*, *L. digitata* and *Saccharina*
493 *polyschides* may extend their range northward, following the trend of boreal species moving
494 into the Arctic (Fossheim et al. 2015; Hargrave et al. 2017; Stige and Kvile 2017). However,
495 kelps produce short-lived zoospores that disperse slowly (current patterns of kelp diversity and
496 structure can still be related to glacial cycles (Neiva et al. 2018), so any temperature-driven

497 northern expansion of temperate kelp species into polar regions is likely to be slow (Konar
 498 2007; Wilce 2016).



499
 500 Fig. 4. a) Global trends in predicted increase in mean summer (July 21 to Sept 21) surface
 501 temperature from 2016 to 2036 according to IPCC models. Kelp locations are shown in red
 502 within AMAP Arctic boundary line (blue). b) Rate (y^{-1}) of historic and c) rate of projected
 503 warming of peak summer temperature (Aug to Sept) calculated on basis on linear trend analysis
 504 for all for all 1° latitude radius buffers around each kelp forest record.

505
 506 1.5.2. Sea ice and light

507 The amount of light reaching the benthos is a defining factor for benthic primary production
 508 and depends largely on the extent of sea ice cover. Sea ice is rapidly retreating in the Arctic
 509 (areal loss of 3.5 – 4.5% per decade, Fig 5a). Average sea ice extent (\pm SD) declined by 3.7%
 510 between 2006 and 2016 (from 16.2 ± 104 to 15.6 ± 105 M km²), and by 23% in 2016 compared
 511 to average sea ice measures from 1981 to 1989 (21.4 ± 2.4 M km²).

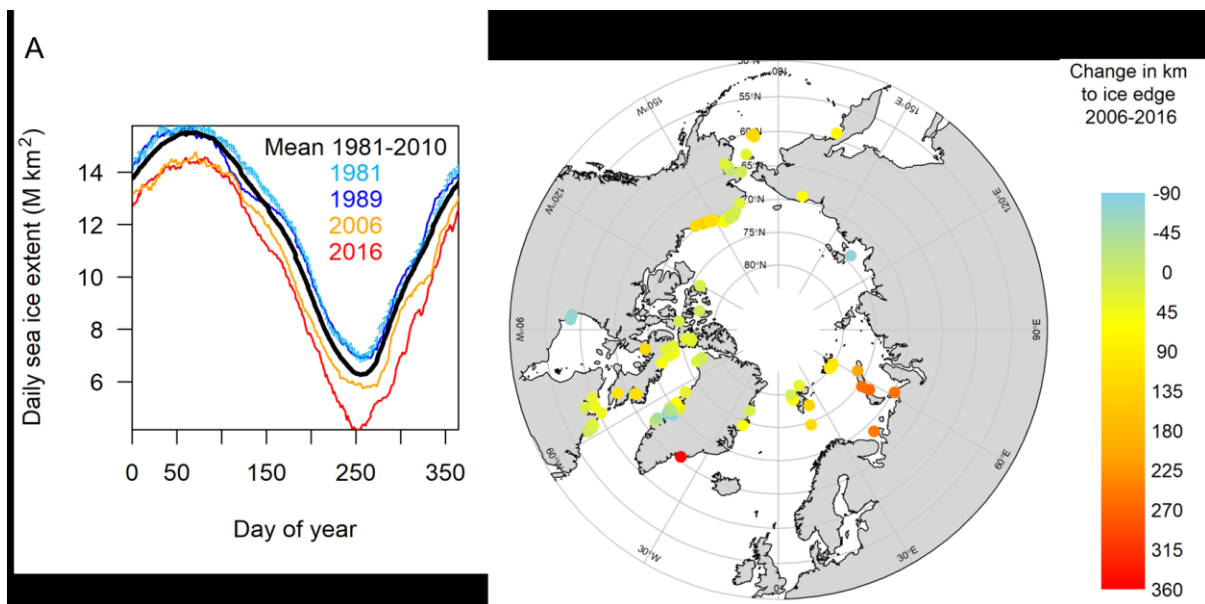
512 To examine ongoing changes in sea ice extent at locations with records of kelp, we
 513 obtained the position of the ice edge (defined by a threshold of >15% sea ice cover) from NASA

514 satellite images taken weekly from 2006 to 2016 (<http://nsidc.org/>, NOAA, accessed 2017).
515 We constrained our measures to this period because years prior to 2006 had lower resolution
516 spatial measures for coastal regions. At each kelp location we calculated the nearest distance
517 (m) to the sea ice edge each week over the 10-year period. To compare these trends over this
518 last decade with broader patterns of sea ice loss we obtained daily measures of areal sea ice
519 extent from NASA satellite data from 1980 to 2016 (Fig 5).

520 Of the total 1179 records of kelp, 2.6% occurred in locations where the ice-free period
521 was < 1 week in 2006 and 0.12% occurred where the ice-free period was < 1 week in 2016
522 (mean 0.55 ± 0.99 SD), supporting evidence of survival and growth under extremely low light
523 conditions (Wilce 2016). On average, the annual mean and minimum distance (km) to sea ice
524 (mean \pm SD) were highly variable at kelp locations (mean 221 ± 156 km and minimum $30 \pm$
525 62 km in 2006, and mean 274 ± 341 km and minimum 49 ± 138 km in 2016; Fig. S2). For
526 records that were under sea ice for at least 1 week during this period, the mean distance to the
527 sea ice edge increased from 45 ± 24 km to 88 ± 72 km and the minimum distance to sea ice
528 edge increased from 0.53 ± 1.52 km to 0.59 ± 1.88 km from 2006 to 2016. Increases in distance
529 to sea ice were largest in the White Sea and Novaya Zemlya, Russia and southeastern
530 Greenland, and lowest in northern Canada and northeastern Russia (Fig. 5b).

531 Available evidence indicates that the loss of sea ice currently occurring in the Arctic
532 will lead to the northward expansion of kelps (Müller et al. 2009), and an increase in the depth
533 range and productivity of these habitats due to increased light and reduced scour in the surf
534 zone, which narrows the vertical distribution of kelp (Krause-Jensen et al. 2012; Krause-Jensen
535 and Duarte 2014). Kelps cannot exist in areas with permanent sea ice (Shoshina et al. 2016),
536 so ice loss may open new habitats in the high Arctic. The effect of sea ice loss on kelps may
537 even be stronger than anticipated because day length increases rapidly during the period of ice
538 break-up (Clark et al. 2013), implying a slight reduction in ice cover will result in a

539 disproportionately large increase in the amount of light reaching kelp. These expectations are
 540 supported by correlative studies from along the west coast of Greenland showing that the extent
 541 of sea ice cover explained 92% of the variation in maximum depth distribution and 80% of the
 542 variation in kelp growth (Krause-Jensen et al. 2012). Hop et al. (2012) monitored the biomass
 543 and depth range of kelps in Svalbard, Norway between 1996 and 2014 and found that kelp
 544 biomass (mainly *L. digitata*) recently increased 2 – 4 fold in the shallow zone (2.5 m depth).
 545 They ascribed these changes to reductions in sea ice cover (Bartsch et al. 2016).
 546
 547



548
 549 Fig 5. A) Daily sea ice extent in millions of km for entire Arctic region between 1981 and 2010.
 550 B) Change in mean distance to sea ice edge (km) between 2006 and 2016, for locations of kelp
 551 that occurred under ice for at least 1 week over this period.




552
 553 1.5.3. Salinity and turbidity

554 As a consequence of reduced sea ice and melting permafrost, many Arctic coastlines are
 555 breaking apart and eroding into the sea. These traditionally icebound coasts can be fragile
 556 because ice provides protection from storms and waves, and its loss can expose the ground to

557 the elements and make it unstable (Lantuit et al. 2012). Coastal environments near these
558 eroding regions are receiving higher amounts of sediment loading and freshwater inputs,
559 resulting in longer and more extreme periods of low salinity and intense turbidity and
560 sedimentation (Lantuit et al. 2012; McClelland et al. 2012; Fritz et al. 2017). Since 2000,
561 average erosion rate of permafrost-bound coasts was 0.5 m yr^{-1} , and reached 10 m per yr^{-1} along
562 some segments. Inputs of sediment and particulate organic carbon (POC) from coastal erosion
563 are currently entering the Arctic ocean at rates $\sim 430 \text{ Tg yr}^{-1}$ sediment and $4.9 - 14 \text{ Tg yr}^{-1}$ POC
564 (Fritz et al. 2017). Coastal erosion is most severe along the shallow coasts of the Laptev, East
565 Siberian and Beaufort Seas (Lantuit et al. 2012), but increased turbidity from melting ice can
566 also be pronounced near the heads of Arctic fjords (Bartsch et al. 2016) and in areas receiving
567 glacial discharge (Traiger and Konar 2018).

568 Increased turbidity and reduced salinity is expected to reduce the performance and
569 lower depth limit of kelp by reducing light penetration and restricting photosynthesis (Aumack
570 et al. 2007; Fredersdorf et al. 2009; Spurkland and Iken 2011; Wiencke and Amsler 2012;
571 Traiger and Konar 2018) (Fig 6). Variable salinity reduced photosynthetic efficiency of *L.*
572 *solidungula*, *S. dermatodea*, *L. digitata*, *A. esculenta* and *S. latissima* (Karsten 2007).
573 Laboratory experiments on kelps collected from Svalbard, Norway found that sediment from
574 melting ice negatively impacted their recruitment (Zacher et al. 2016). Manipulative field
575 experiments on kelp forests in Alaska and found that glacier run-off reduced kelp settlement
576 and recruitment by increasing sedimentation in the coastal zone (Traiger and Konar 2018).
577 Research from Kola bay and anecdotal reports from areas along the Siberian shelf in Russia
578 describe declines in the lower depth limit of kelp forests due to low transparency of water (< 3
579 m visibility) caused by domestic pollution, sediment plumes and agricultural run-off
580 (Malavenda and Malavenda 2012). These negative impacts may offset the possible positive
581 effects of warming and increased light on kelp growth in some Arctic regions. This was evident

582 in the Beaufort Sea, where long-term records of annual growth of *L. solidungula* kelps showed
 583 no change in productivity since 1979, despite earlier sea ice break-up and a longer ice-free
 584 period in recent years (Bonsell and Dunton 2018). This pattern was explained by increasing
 585 resuspension of sediment and larger coastal erosion following sea ice break-up, which counter
 586 balanced the positive effect of longer ice-free periods.

Effects of climate-driven stressors on life stages of Arctic kelps	Coastal regions			Reproduction Recruitment	Growth	Adult survival
	Unstable eroding coasts with ice	Stable aggrading coasts with ice	Coasts with little to no sea ice			
↓ Sea ice	**	*	x	?	+	+
↑ °C	*	*	*	+	+	0
↑ Turbidity	**	x	x *	-	-	-
↓ Salinity	*	*	x *	-	?	-

587
 588 Fig 6. Effects of environmental changes on arctic kelps from laboratory and field experiments.
 589 + is positive, - negative, 0 is no measurable effect, and ? is unknown. Relative importance of
 590 stressors for 3 different coastal regions (see Fig 2): ** = strong impact, * = moderate impact,
 591 and 'x' little to no impact. Note increased turbidity and decreased salinity can also occur along
 592 coasts with no sea ice that receive glacial melt or other freshwater inputs.

593
 594 1.5.4. Nutrients

595 Nutrient concentrations are predicted to increase and change their seasonal timing along Arctic
596 coasts with increased (and earlier) spring melts, but the impacts of elevated nutrient richness
597 on arctic kelps are unclear. Nutrient availability is typically low in most Arctic waters, and
598 nutrient concentrations tend to increase during winter when primary production is low, but
599 decrease to extremely low levels during the short Arctic summer. Therefore, pelagic primary
600 production is therefore often limited by low nutrient availability in late summer.

601 This may not be the case for kelps. In a study of twenty-one different species of arctic
602 macroalgae (including *Laminaria* spp.), none of them were significantly nitrogen-limited in
603 July (Gordillo et al. 2006). Kelps may be able to acquire and accumulate nutrients in winter
604 when nutrient availability is relatively high. Nutrients can be translocated from the blade
605 towards the meristem (Davison and Stewart 1983) and nutrient reserves can subsequently be
606 used to support photosynthesis and, thus, prolong blade growth during summer when insolation
607 is high and nutrient availability is low (Gagne et al. 1982; Henley and Dunton 1997; Pueschel
608 and Korb 2001). Most kelp species should therefore remain rather unaffected by increasing
609 nutrient availability, but studies have shown that the growth of at least some species, here *L.*
610 *solidungula*, decreases significantly in early spring as nutrient concentrations drop (Chapman
611 and Lindley 1980; Dunton et al. 1982). This suggests that some kelp species and/or kelps in
612 certain extremely nutrient poor areas can be limited by low nutrient availability, and therefore
613 would be stimulated by increased nutrient levels.

614 It is important to note that pelagic phytoplankton are more stimulated by increasing
615 nutrient and light levels compared to benthic algae. Estimates predict thus that the pelagic
616 production by phytoplankton in some Arctic waters will increase 3-fold within this century due
617 to longer ice-free periods and increased run-off from land (e.g., Rysgaard and Glud 2007). This
618 significant increase in phytoplankton biomass and productivity will decrease light penetration

619 in the water column, which will negatively affect kelp biomass and depth limit, possibly
620 offsetting any benefits that higher nutrient levels could have on some kelp species.

621

622 1.5.5. UV radiation

623 Other changes in environmental conditions that could impact kelps include increased
624 UV radiation, which is especially pronounced at high latitudes (Garcia-Corral et al. 2014).
625 Increases in UV radiation negatively impacts photosynthesis of arctic kelps (Roleda et al. 2006;
626 Müller et al. 2008; Roleda 2016) and reduces their performance (Heinrich et al. 2015).
627 However, research to date indicates that UV damage will have a minor impact on arctic kelps
628 compared other environmental changes, and will mainly affect early life stages (Roleda et al.
629 2006; Wiencke et al. 2006). In laboratory experiments on *L. solidungula* collected from
630 Svalbard by Roleda (2016), high UV radiation disrupted the life cycle of meiospores and
631 gametophytes. UV exposure also caused significant declines in photosynthetic efficiency, and
632 increased transcription of DNA repair genes, but these effects were less pronounced in kelps
633 collected from the field compared to cultured plants (Heinrich et al. 2015). Fredersdorf et al.
634 (2009) examined combined effects of different temperatures, salinity, and UV radiation levels
635 on photosynthesis of *A. esculenta* collected from Svalbard. They found that *A. esculenta*
636 zoospores were sensitive to synergistic effects of temperature and salinity changes (Fredersdorf
637 et al. 2009), but that adults *A. esculenta* could tolerate a range of UV conditions.

638

639 1.6. PREDICTING CHANGES TO DISTRIBUTION OF ARCTIC KELPS

640 Predicting changes to arctic kelps under rapidly changing environmental conditions remains
641 challenging. Assis et al. (2018) developed models that described the current distributions of
642 *Alaria esculenta*, *L. solidungula*, *L. digitata*, *L. hyperborea*, *S. latissima*, and *S. dermatoda* in
643 the northern Atlantic according to environmental parameters (mainly sea temperature, sea ice,

644 salinity, upwelling), and used these relationships to predict the impacts of climate change on
645 their future distribution. These models predicted large northward expansions of these species,
646 including the expansion of *L. hyperborea* to Svalbard, Norway, and further into the White Sea,
647 the spread of *S. dermatoadae* and *L. digitata* (or *S. nigripes* depending on source, S. Fredriksen
648 personal communication) along the northeastern coast of Greenland, and the expansion of *A.*
649 *esculenta* into the Canadian high Arctic. The models also predicted *L. solidungula* and *S.*
650 *latissima* would extend northward to cover the northernmost coasts of Greenland, Russia and
651 Canada, suggesting that all Arctic coasts would have environmental conditions suitable for kelp
652 forests in the future. Similar range expansions have been predicted for *L. solidungula* and *S.*
653 *latissima* with models by Müller et al (2009) and for a number of furoid species by Jueterbock
654 et al. (2013, 2016). However, there is a discrepancy between these predictive models and long-
655 term field observations of changes to arctic kelps. In Canada, Adey and Hayek (2011) were
656 unable to identify significant shifts in the distributions of subtidal algal species in the eastern
657 subarctic or boreal regions over the past 40 years. Likewise, Merzouk & Johnson (2011)
658 reviewed the distribution of kelp along the northwest Atlantic shores from records dating back
659 to the 1950s and were unable to document any significant change in dominant kelp species
660 composition or abundance over that period, despite increasing sea temperature, although, the
661 lack of sufficient spatially and temporally extensive datasets for this region prevented them
662 from concluding that no change had occurred. Northward range expansions of kelps may be
663 limited by extensive gaps between suitable substrate (e.g., from northern Norway to Svalbard)
664 and low dispersal potential of kelps (Wernberg et al. 2018). It is also possible that the spread
665 and performance of kelps may be more influenced by changes in turbidity, sea ice cover, and
666 light penetration compared to relatively small changes in sea temperatures. This suggests that
667 model predictions may overestimate northern range expansions of kelps, at least in the short-
668 term.

669

670 1.7. CONCLUSIONS

671 The Arctic is at the epicenter of the global climate crisis, and emerging opportunities and
672 developments have increased international attention on changes to ecosystems in this area.
673 Long-term research from Greenland and Norway suggests a warmer Arctic with less sea ice
674 may support higher kelp productivity and biomass and expand the northern range and lower
675 depth limit of these species. However, the degree to which these changes will positively affect
676 kelps will vary regionally and depend on the extent that melting sea ice and permafrost
677 increases turbidity in coastal areas, as well as the available substrate in the lower depth range
678 (Bartsch et al. 2017; Bonsell and Dunton 2018). Predictive models and laboratory experiments
679 suggest the ‘borealization’ of arctic kelp forests will occur as temperatures warm, altering the
680 species composition of existing cold and ice-adapted kelp communities in high Arctic regions.
681 Although current predictions are highly uncertain, the possible expansion of kelp forests should
682 provide new habitats for fish and other marine organisms, and a suite of valuable ecosystem
683 services along Arctic coastlines. Interestingly, where data are available, kelp abundance
684 appears relatively stable, suggesting these changes are occurring slower than predicted or are
685 being buffered by other factors. Either way, anticipating these changes, and understanding
686 these new ecosystems will be a key priority for northern communities.

687 Our understanding of kelp forests is rapidly expanding in many regions of the Arctic.
688 However, baseline measures of the extent of kelp communities are missing in northern and
689 eastern Canadian Arctic, Siberia, the east Greenland Shelf, and Russia. This lack of data is not
690 unique to kelp ecosystems. Despite the fact that over 28% of the world’s coastlines are found
691 in the Arctic (Lantuit et al. 2012), they remain largely unstudied, which jeopardizes current
692 strategies to protect or conserve arctic environments and will have consequences for northern
693 communities that rely on them. Lack of data has already greatly hindered our ability to detect

694 and understand the impacts of climate change on these and other ecosystems (e.g., Merzouk
695 and Johnson 2011). Exploring effects of ongoing and future climate changes will provide
696 important insight on the stability of these ecosystems. Maintaining and augmenting current
697 monitoring initiatives and time series data sets should be a priority. For kelp forests,
698 understanding how these ecosystems influence the structure and function of coastal arctic food
699 webs is an important focus for ongoing research. There is also a critical lack of knowledge on
700 the contribution of kelp forests to carbon cycling in the Arctic. Filling in these gaps and
701 strategically prioritizing research in areas of rapid environmental variation will enable us to
702 more effectively understand and conserve these ecosystems.

703 Arctic coasts are in line to become one of the most impacted environments in the world
704 under changing climate. For this region to act as a sentinel for climate change it is critical to
705 monitor and understand the impacts of environmental stressors on arctic ecosystems. Kelp
706 forests provide a key example of the regional diversity of responses to climate change, and
707 demonstrate the need for a mechanistic understanding of how multiple stressors and diverse
708 ecological processes influence ecosystem structure and function. Although it is tempting to
709 make generalized statements about broad-scale climate-driven impacts, the reality is much
710 more nuanced, regionally specific, and highly uncertain. What is clear is that extensive
711 ecological changes are likely to occur in these rapidly changing environments, with both
712 ‘positive’ or ‘negative’ consequences for a range of species.

713

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718

719 REFERENCES

- 720 Abdullah MI, Fredriksen S, Christie H (2017) The impact of the kelp (*Laminaria hyperborea*) forest
721 on the organic matter content in sediment of the west coast of Norway. *Mar Biol Res* 0:1–10 .
722 doi: 10.1080/17451000.2016.1240369
- 723 Acosta Navarro JC, Varma V, Riipinen I, et al (2016) Amplification of Arctic warming by past air
724 pollution reductions in Europe. *Nat Geosci* 9:277–281 . doi: 10.1038/ngeo2673
- 725 Adey WH, Hayek L-AC (2011) Elucidating marine biogeography with macrophytes: quantitative
726 analysis of the North Atlantic supports the thermogeographic model and demonstrates a distinct
727 subarctic Region in the Northwestern Atlantic. *Northeast Nat* 18:1–128 . doi:
728 10.1656/045.018.m801
- 729 AMAP (1998) Physical/Geographical Characteristics of the Arctic. In: AMAP assessment report:
730 Arctic pollution issues. Arctic Monitoring and Assessment Programme (AMAP), Oslo, pp 9–24
- 731 AMAP (2017) Snow, Water, Ice and Permafrost in the Arctic (SWIPA) 2017. Arctic Monitoring and
732 Assessment Programme (AMAP), Oslo, Norway. Oslo
- 733 Arctic Monitoring and Assessment Programme. (2011) Snow, water, ice and permafrost in the arctic
734 (SWIPA) : climate change and the cryosphere. AMAP
- 735 Assis J, Araújo MB, Serrão EA (2018) Projected climate changes threaten ancient refugia of kelp
736 forests in the North Atlantic. *Glob Chang Biol* 24:e55–e66 . doi: 10.1111/gcb.13818
- 737 Aumack CF, Dunton KH, Burd AB, et al (2007) Linking light attenuation and suspended sediment
738 loading to benthic productivity within an arctic kelp-bed community. *J Phycol* 43:853–863 . doi:
739 10.1111/j.1529-8817.2007.00383.x
- 740 Bartsch I, Paar M, Fredriksen S, et al (2016) Changes in kelp forest biomass and depth distribution in
741 Kongsfjorden, Svalbard, between 1996-1998 and 2012-2014 reflect Arctic warming. *Polar Biol*
742 39:2021–2036 . doi: 10.1007/s00300-015-1870-1
- 743 Boertmann D, Mosbech A, Schiedek D, Dünweber M (2013) Disko West : a strategic environmental
744 impact assessment of hydrocarbon activities. Aarhus University, DCE - Danish Centre for
745 Environment and Energy

746 Bolton JJ, Lüning K (1982) Optimal growth and maximal survival temperatures of Atlantic *Laminaria*
747 species (Phaeophyta) in culture. *Mar Biol* 66:89–94 . doi: 10.1007/BF00397259

748 Bonsell C, Dunton KH (2018) Long-term patterns of benthic irradiance and kelp production in the
749 central Beaufort Sea reveal implications of warming for Arctic inner shelves. *Prog Oceanogr.*
750 doi: 10.1016/j.pocean.2018.02.016

751 Borum K, Pedersen MF, Krause-Jensen D, Christensen N (2002) Biomass, photosynthesis and growth
752 of *Laminaria saccharina* in a high-arctic fjord, NE Greenland. *Mar Biol* 141:11–19 . doi:
753 10.1007/s00227-002-0806-9

754 Bringloe T, Dunton KH, Saunders GW (2017) Updates to the marine algal flora of the Boulder Patch
755 in the Beaufort Sea off northern Alaska as revealed by DNA barcoding. *Arctic* 70:343–348 . doi:
756 10.14430/arctic4679

757 Burrows MT, Schoeman DS, Buckley Lauren B., et al (2011) The pace of shifting climate in marine
758 and terrestrial ecosystems. *Science* 334:652–655 . doi: DOI: 10.1126/science.1210288

759 Catton C (2016) “Perfect Storm” Decimates Northern California Kelp Forests | CDFW Marine
760 Management News. In: Calif. Dep. Fish Wildl. Mar. Manag. News.
761 <https://cdfwmarine.wordpress.com/2016/03/30/perfect-storm-decimates-kelp/>. Accessed 25 Feb
762 2018

763 Chapman ARO, Lindley JE (1980) Seasonal growth of *Laminaria solidungula* in the Canadian High
764 Arctic in relation to irradiance and dissolved nutrient concentrations. *Mar Biol* 57:1–5 . doi:
765 10.1007/BF00420961

766 Christie H, Norderhaug KM, Fredriksen S (2009) Macrophytes as habitat for fauna. *Mar. Ecol. Prog.*
767 *Ser.* 396:221–234

768 Clark GF, Stark JS, Johnston EL, et al (2013) Light-driven tipping points in polar ecosystems. *Glob*
769 *Chang Biol* 19:3749–3761 . doi: 10.1111/gcb.12337

770 Cooper LW, Beasley TM, Zhao X-L, et al (1998) Iodine-129 and plutonium isotopes in Arctic kelp as
771 historical indicators of transport of nuclear fuel-reprocessing wastes from mid-to-high latitudes
772 in the Atlantic Ocean. *Mar Biol* 131:391–399 . doi: 10.1007/s002270050332

773 Coupel P, Ruiz-Pino D, Sicre MA, et al (2015) The impact of freshening on phytoplankton production

774 in the Pacific Arctic Ocean. Prog Oceanogr 131:113–125 . doi:
775 10.1016/J.POCEAN.2014.12.003

776 Davison IR, Stewart WDP (1983) Occurrence and significance of nitrogen transport in the brown alga
777 *Laminaria digitata*. Mar Biol 77:107–112 . doi: 10.1007/BF00396307

778 Dayton PK (2013) Polar benthos. In: Smith WO (ed) Polar Oceanography: Chemistry, Biology, and
779 Geology. Academic Press, p 614

780 Dean TA, Bodkin JL, Jewett SC, et al (2000a) Changes in sea urchins and kelp following a reduction
781 in sea otter density as a result of the Exxon Valdez oil spill. Mar Ecol Prog Ser 199:281–291

782 Dean TA, Haldorson L, Laur DR, et al (2000b) The Distribution of Nearshore Fishes in Kelp and
783 Eelgrass Communities in Prince William Sound, Alaska: Associations with Vegetation and
784 Physical Habitat Characteristics. Environ Biol Fishes 57:271–287 . doi:
785 10.1023/A:1007652730085

786 Ding Q, Schweiger A, L’Heureux M, et al (2017) Influence of high-latitude atmospheric circulation
787 changes on summertime Arctic sea ice. Nat Clim Chang 7:289–295 . doi: 10.1038/nclimate3241

788 Doroff AM, Estes JA, Tinker MT, et al (2003) Sea otter population declines in the aleutian
789 archipelago. J Mammal 84:55–64 . doi: 10.1644/1545-1542(2003)084<0055:SOPDIT>2.0.CO;2

790 Duggins DO, Simenstad CA, Estes JA (1989) Magnification of secondary production by kelp detritus
791 in coastal marine ecosystems. Science (80-) 245:170–173

792 Dunton KH (1985) Growth of dark-exposed *Laminaria saccharina* (L.) Lamour. and *Laminaria*
793 *solidungula* J. Ag. (laminariales : phaeophyta) in the Alaskan Beaufort Sea. J Exp Mar Bio Ecol
794 94:181–189 . doi: 10.1016/0022-0981(85)90057-7

795 Dunton KH, Jodwalis CM (1988) Photosynthetic performance of *Laminaria solidungula* measured in
796 situ in the Alaskan High Arctic. Mar Biol 98:277–285 . doi: 10.1007/BF00391206

797 Dunton KH, Reimnitz E, Schonberg S (1982) An Arctic Kelp Community in the Alaskan Beaufort
798 Sea. Arctic 35:465–484

799 Dunton KH, Schell DM (1987) Dependence of consumers on macroalgal (*Laminaria solidungula*)
800 carbon in an arctic kelp community: 13C evidence. Mar Biol 93:615–625 . doi:
801 10.1007/BF00392799

802 Estes JE, Smith NS, Palmisano JF (1978) Sea otter predation and community organization in the
803 Western Aleutian Islands, Alaska. *Ecology* 59:822–833 . doi: 10.2307/1938786

804 Estes JA, Danner EM, Doak DF, et al (2004) Complex trophic interactions in kelp forest ecosystems.
805 *Bull Mar Sci* 74:621–638

806 Estes JA, Duggins DO (1995) Sea otters and kelp forests in Alaska: generality and variation in a
807 community ecological paradigm. *Ecol Monogr* 65:75–100 . doi: 10.2307/2937159

808 Fagerli C, Norderhaug K, Christie H (2013) Lack of sea urchin settlement may explain kelp forest
809 recovery in overgrazed areas in Norway. *Mar Ecol Prog Ser* 488:119–132 . doi:
810 10.3354/meps10413

811 Fagerli CW, Stadniczeňko SG, Pedersen MF, et al (2015) Population dynamics of *Strongylocentrotus*
812 *droebachiensis* in kelp forests and barren grounds in Norway. *Mar Biol* 162:1215–1226 . doi:
813 10.1007/s00227-015-2663-3

814 Filbee-Dexter K, Feehan CJ, Scheibling RE (2016) Large-scale degradation of a kelp ecosystem in an
815 ocean warming hotspot. *Mar Ecol Prog Ser* 543:141–152 . doi: 10.3354/meps11554

816 Filbee-Dexter K, Scheibling RE (2014) Sea urchin barrens as alternative stable states of collapsed
817 kelp ecosystems. *Mar Ecol Prog Ser* 495:1–25 . doi: 10.3354/meps10573

818 Filbee-Dexter K, Wernberg T (2018) Rise of Turfs : A new battlefield for globally declining kelp
819 forests. *Bioscience* 68: . doi: 10.1093/biosci/bix147

820 Filbee-Dexter K, Wernberg T, Ramirez-Llodra E, et al (2018) Movement of pulsed resource subsidies
821 from shallow kelp forests to deep fjords. *Oecologia* 187:291-304

822 Floeter SR, Behrens MD, Ferreira CEL, et al (2005) Geographical gradients of marine herbivorous
823 fishes: patterns and processes. *Mar Biol* 147:1435–1447 . doi: 10.1007/s00227-005-0027-0

824 Fossheim M, Primicerio R, Johannesen E, et al (2015) Recent warming leads to a rapid borealization
825 of fish communities in the Arctic. *Nat Clim Chang* 5:673–677 . doi: 10.1038/nclimate2647

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

829 Fredriksen S (2003) Food web studies in a Norwegian kelp forest based on stable isotope analysis.

830 Mar Ecol Prog Ser 260:71–81 . doi: 10.3354/meps260071

831 Fritz M, Vonk JE, Lantuit H (2017) Collapsing Arctic coastlines. Nat Clim Chang 7:6–7 . doi:
832 10.1038/nclimate3188

833 Gagne JA, Mann KH, Chapman ARO (1982) Seasonal patterns of growth and storage in *Laminaria*
834 *longicurris* in relation to differing patterns of availability of nitrogen in the water. Mar Biol
835 69:91–101 . doi: 10.1007/BF00396965

836 Garcia-Corral LS, Agustí S, Regaudie-de-Gioux A, et al (2014) Ultraviolet radiation enhances Arctic
837 net plankton community production. Geophys Res Lett 41:5960–5967 . doi:
838 10.1002/2014GL060553

839 Gattuso J-P, Gentili B, Duarte CM, et al (2006) Light availability in the coastal ocean: impact on the
840 distribution of benthic photosynthetic organisms and contribution to primary production.
841 Biogeosciences 3:489–513 . doi: 10.5194/bg-3-489-2006

842 Golikov AN, Averintsev V. (1977) Biotsenozy verhnih otdelov shelfa arhipelaga Zemlya Frantsa
843 Iosifa [Biocenosis of the high part of archipelago Franz Josef land shelf]. Issled fauny morey
844 14:5–54

845 Gordillo FJL, Aguilera J, Jiménez C (2006) The response of nutrient assimilation and biochemical
846 composition of Arctic seaweeds to a nutrient input in summer. J Exp Bot 57:2661–2671 . doi:
847 10.1093/jxb/erl029

848 Gotceitas V, Fraser S, Brown JA (1995) Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the
849 presence of an actively foraging and non-foraging predator. Mar Biol 123:421–430 . doi:
850 10.1007/BF00349220

851 Grebmeier JM, Overland JE, Moore SE, et al (2006) A major ecosystem shift in the northern Bering
852 Sea. Science 311:1461–4 . doi: 10.1126/science.1121365

853 Guiry M, Guiry G (2017) Algaebase. In: Natl. Univ. Ireland, Galw.

854 Gulliksen B, Haug T, Sandnes O (1980) Benthic macrofauna on new and old lava grounds at Jan
855 Mayen. Sarsia 65:13745

856 Gulliksen B, Sandnes O (1980) Marine bunndyrsamfunn, nøkkelarter og felteksperimenter på
857 hardbunn. Fauna 33:19

858 Günther F, Overduin PP, Yakshina IA, et al (2015) Observing Muostakh disappear: permafrost thaw
859 subsidence and erosion of a ground-ice-rich island in response to arctic summer warming and
860 sea ice reduction. *Cryosph* 9:151–178 . doi: 10.5194/tc-9-151-2015

861 Halpern BS, Walbridge S, Selkoe KA, et al (2008) A global map of human impact on marine
862 ecosystems. *Science* 319:948–52 . doi: 10.1126/science.1149345

863 Hamilton J, Brenda K (2007) Implications of substrate complexity and kelp variability for south-
864 central Alaskan nearshore fish communities. *Fish Bull* 105:189–196

865 Hanelt D (1998) Capability of dynamic photoinhibition in Arctic macroalgae is related to their depth
866 distribution. *Mar Biol* 131:361–369 . doi: 10.1007/s002270050329

867 Hargrave MS, Foggo A, Pessarrodona A, Smale DA (2017) The effects of warming on the
868 ecophysiology of two co-existing kelp species with contrasting distributions. *Oecologia*
869 183:531–543 . doi: 10.1007/s00442-016-3776-1

870 Harley CDG, Anderson KM, Demes KW, et al (2012) Effect of climate change on global seaweed
871 communities. *J Phycol* 48:1064–1078 . doi: 10.1111/j.1529-8817.2012.01224.x

872 Heinrich S, Valentin K, Frickenhaus S, Wiencke C (2015) Temperature and light interactively
873 modulate gene expression in *Saccharina latissima* (Phaeophyceae). *J Phycol* 51:93–108 . doi:
874 10.1111/jpy.12255

875 Henley WJ, Dunton KH (1997) Effects of nitrogen supply and continuous darkness on growth and
876 photosynthesis of the arctic kelp *Laminaria solidungula*. *Limnol Oceanogr* 42:209–216 . doi:
877 10.4319/lo.1997.42.2.0209

878 Hobday AJ, Pecl GT (2014) Identification of global marine hotspots: sentinels for change and
879 vanguards for adaptation action. *Rev Fish Biol Fish* 24:415–425 . doi: 10.1007/s11160-013-
880 9326-6

881 Hop H, Wiencke C, Vögele B, Kovaltchouk NA (2012) Species composition, zonation, and biomass
882 of marine benthic macroalgae in Kongsfjorden, Svalbard. *Bot Mar* 55:399–414 . doi:
883 10.1515/bot-2012-0097

884 Huang J, Zhang X, Zhang Q, et al (2017) Recently amplified arctic warming has contributed to a
885 continual global warming trend. *Nat Clim Chang* 7:875–879 . doi: 10.1038/s41558-017-0009-5

886 IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to
887 the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing
888 Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva

889 Jueterbock A, Smolina I, Coyer JA, Hoarau G (2016) The fate of the Arctic seaweed *Fucus distichus*
890 under climate change: an ecological niche modeling approach. *Ecol Evol* 6:1712–1724 . doi:
891 10.1002/ece3.2001

892 Jueterbock A, Tyberghein L, Verbruggen H, et al (2013) Climate change impact on seaweed meadow
893 distribution in the North Atlantic rocky intertidal. *Ecol Evol* 3:1356–1373 . doi:
894 10.1002/ece3.541

895 Karsten U (2007) Research note: Salinity tolerance of Arctic kelps from Spitsbergen. *Phycol Res*
896 55:257–262 . doi: 10.1111/j.1440-1835.2007.00468.x

897 Kawai H, Hanyuda T, Ridgway LM, Holser K (2013) Ancestral reproductive structure in basal kelp
898 *Aureophycus aleuticus*. *Sci Rep* 3:2491 . doi: 10.1038/srep02491

899 Keats DW, South GR, Steele DH (1985) Algal biomass and diversity in the upper subtidal at a pack-
900 ice disturbed site in eastern Newfoundland. *Mar. Ecol. Prog. Ser.* 25:151–158

901 Kjellman F (1883) The algae of the Arctic Sea: a survey of the species, together with an exposition of
902 the general characters and the development of the flora. Norstedt

903 Konar B (2013) Lack of recovery from disturbance in high-arctic boulder communities. *Polar Biol*
904 36:1205–1214 . doi: 10.1007/s00300-013-1340-6

905 Konar B (2007) Recolonization of a high latitude hard-bottom nearshore community. *Polar Biol*
906 30:663–667 . doi: 10.1007/s00300-007-0261-7

907 Konar B, Edwards MS, Bland A, et al (2017) A swath across the great divide: Kelp forests across the
908 Samalga Pass biogeographic break. *Cont Shelf Res* 143:78–88 . doi: 10.1016/j.csr.2017.06.007

909 Konar B, Estes JA (2003) The stability of boundary regions between kelp forests and deforested areas.
910 *Ecology* 84:174–185 . doi: 10.1890/0012-9658(2003)084[0174:TSOBRB]2.0.CO;2

911 Kortsch S, Primicerio R, Fossheim M, et al (2015) Climate change alters the structure of arctic marine
912 food webs due to poleward shifts of boreal generalists. *Proceedings Biol Sci* 282:20151546 . doi:
913 10.1098/rspb.2015.1546

914 Krause-Jensen D, Duarte CM (2016) Substantial role of macroalgae in marine carbon sequestration.
915 Nat Geosci 9:737–742 . doi: 10.1038/ngeo2790

916 Krause-Jensen D, Duarte CM (2014) Expansion of vegetated coastal ecosystems in the future Arctic.
917 Front Mar Sci 1: . doi: 10.3389/fmars.2014.00077

918 Krause-Jensen D, Kühl M, Christensen P, Borum J (2007) Benthic primary production in Young
919 Sound, Northeast Greenland. In: Ryssguard S, Glud RN (eds) Benthic primary production in
920 Young Sound, Northeast Greenland. Grønland, Bioscience, Meddr, pp 160–173

921 Krause-Jensen D, Marbà N, Olesen B, et al (2012) Seasonal sea ice cover as principal driver of spatial
922 and temporal variation in depth extension and annual production of kelp in Greenland. Glob
923 Chang Biol 18:2981–2994 . doi: 10.1111/j.1365-2486.2012.02765.x

924 Krumhansl K, Scheibling R (2012) Production and fate of kelp detritus. Mar Ecol Prog Ser 467:281–
925 302 . doi: 10.3354/meps09940

926 Krumhansl KA, Okamoto DK, Rassweiler A, et al (2016) Global patterns of kelp forest change over
927 the past half-century. Proc Natl Acad Sci 113:13785–13790 . doi: 10.1073/pnas.1606102113

928 Kuznetsov L, Makarevich P, Makarov M (1994) Structural-condition-indicators of marine
929 phytocenoses // habitat and ecosystems of Franz Josef Land (Archipelago and shelf). Apatity
930 89–94.

931 Kuznetsov L, Shoshina E (2003) Barents Sea Phytocenoses (physiological and structural
932 characteristics) 308 p. Apatity Publ house KSC RAS

933 Küpper FC, Peters AF, Shewring DM, et al (2016) Arctic marine phytobenthos of northern Baffin
934 Island. J Phycol 52:532–549 . doi: 10.1111/jpy.12417

935 Lantuit H, Overduin PP, Couture N, et al (2012) The Arctic coastal dynamics database: A new
936 classification scheme and statistics on arctic permafrost coastlines. Estuaries and Coasts 35:383–
937 400 . doi: 10.1007/s12237-010-9362-6

938 Lee RKS (1980) A catalogue of the marine algae of the Canadian Arctic. National Museums of
939 Canada

940 Lee RKS (1973) General ecology of the Canadian Arctic benthic marine algae. Arctic 26:32–43

941 Leinaas HP, Christie H (1996) Effects of removing sea urchins (*Strongylocentrotus droebachiensis*):

942 Stability of the barren state and succession of kelp forest recovery in the east Atlantic. *Oecologia*
943 105:524–536 . doi: 10.1007/BF00330016

944 Leont'yev IO (2003) Modeling erosion of sedimentary coasts in the western Russian Arctic. *Coast*
945 *Eng* 47:413–429 . doi: 10.1016/S0378-3839(02)00145-X

946 Levin V, Muller O, Anisimova N (1998) Part II Bottom invertebrates. In: *Harvesting and prospective*
947 *algae and invertebrates for uses of the Barents and White seas*. Kola Science Centre Apatity,
948 Murmansk, pp 394–440

949 Lind AC, Konar B (2017) Effects of abiotic stressors on kelp early life-history stages. *ALGAE*
950 32:223–233 . doi: 10.4490/algae.2017.32.8.7

951 Ling SD, Johnson CR, Ridgeway K, et al (2009) Climate-driven range extension of a sea urchin:
952 inferring future trends by analysis of recent population dynamics. *Glob Chang Biol* 15:719–731 .
953 doi: 10.1111/j.1365-2486.2008.01734.x

954 Makarov M, Ryizhik I, Voskoboynikov G (2008) *Mehanizmy suschestvovaniya buryh vodorosley v*
955 *period polyarnoy nochi: funktsionalnaya differentsiatsiya i geterotrofiya* [Mechanisms of
956 existence of brown seaweeds during polar night: Functional differentiation and heterotrophy].
957 *Sovrem Probl Algol* 225–227

958 McClelland JW, Holmes RM, Dunton KH, Macdonald RW (2012) The Arctic ocean estuary.
959 *Estuaries and Coasts* 35:353–368 . doi: 10.1007/s12237-010-9357-3

960 McDevit DC, Saunders GW (2010) A DNA barcode examination of the Laminariaceae
961 (Phaeophyceae) in Canada reveals novel biogeographical and evolutionary insights. *Phycologia*
962 49:235–248 . doi: 10.2216/PH09-36.1

963 McMeans B, Rooney N, Arts M, Fisk A (2013) Food web structure of a coastal Arctic marine
964 ecosystem and implications for stability. *Mar Ecol Prog Ser* 482:17–28 . doi:
965 10.3354/meps10278

966 Merzouk A, Johnson LE (2011) Kelp distribution in the northwest Atlantic Ocean under a changing
967 climate. *J Exp Mar Bio Ecol* 400:90–98 . doi: 10.1016/j.jembe.2011.02.020

968 Miller AW, Ruiz GM (2014) Arctic shipping and marine invaders. *Nat Clim Chang* 4:413–416 . doi:
969 10.1038/nclimate2244

970 Mundy CJ, Ehn JK, Barber DG, Michel C (2007) Influence of snow cover and algae on the spectral
971 dependence of transmitted irradiance through Arctic landfast first-year sea ice. *J Geophys Res*
972 112:C03007 . doi: 10.1029/2006JC003683

973 Myagkov GM (1975) Composition, distribution and the seasonal dynamics of algal biomass in the
974 *Laminaria* biocenosis of the bay of the White Sea USSR based on diving data. *Bull Leningr*
975 *State Univ, Ser Biol* 3:48–53

976 Müller R, Laepple T, Bartsch I, Wiencke C (2009) Impact of oceanic warming on the distribution of
977 seaweeds in polar and cold-temperate waters. *Bot Mar* 52: . doi: 10.1515/BOT.2009.080

978 Müller R, Wiencke C, Bischof K (2008) Interactive effects of UV radiation and temperature on
979 microstages of Laminariales (Phaeophyceae) from the Arctic and North Sea. *Clim. Res.* 37:203–
980 213

981 Najafi MR, Zwiers FW, Gillett NP (2015) Attribution of Arctic temperature change to greenhouse-gas
982 and aerosol influences. *Nat Clim Chang* 5:246–249 . doi: 10.1038/nclimate2524

983 Neiva J, Paulino C, Nielsen MM, et al (2018) Glacial vicariance drives phylogeographic
984 diversification in the amphi-boreal kelp *Saccharina latissima*. *Sci Rep* 8:1112 . doi:
985 10.1038/s41598-018-19620-7

986 Nelson RJ, Ashjian CJ, Bluhm BA, et al (2014) Biodiversity and biogeography of the lower trophic
987 taxa of the pacific Arctic region: sensitivities to climate change. In: *The Pacific Arctic Region*.
988 Springer Netherlands, Dordrecht, pp 269–336

989 Nordenskiöld A (1880) *Vegas färd kring Asien och Europa jemte en historisk å terblick på föregående*
990 *resor längs Gamla Verldens nordkust*. F & G Beijers Förlag, Stockholm

991 Norderhaug KM, Christie H (2011) Secondary production in a *Laminaria hyperborea* kelp forest and
992 variation according to wave exposure. *Estuar Coast Shelf Sci* 95:135–144 . doi:
993 10.1016/J.ECSS.2011.08.028

994 Parkinson CL, Comiso JC (2013) On the 2012 record low Arctic sea ice cover: Combined impact of
995 preconditioning and an August storm. *Geophys Res Lett* 40:1356–1361 . doi: 10.1002/grl.50349

996 Pecl GT, Hobday AJ, Frusher S, et al (2014) Ocean warming hotspots provide early warning
997 laboratories for climate change impacts. *Rev Fish Biol Fish* 24:409–413 . doi: 10.1007/s11160-

- 998 014-9355-9
- 999 Phillips RL, Reiss TE (1985) Nearshore marine geologic investigations, Point Barrow to Skull Cliff,
1000 northeast Chukchi Sea. Menlo Park
- 1001 Piepenburg D (2005) Recent research on Arctic benthos: Common notions need to be revised. *Polar*
1002 *Biol* 28:733–755 . doi: 10.1007/s00300-005-0013-5
- 1003 Plotkin AS, Railkin AI, Gerasimova EI, et al (2005) Subtidal underwater rock communities of the
1004 White Sea: Structure and interaction with bottom flow. *Russ J Mar Biol* 31:335–343 . doi:
1005 10.1007/s11179-006-0001-9
- 1006 Pueschel CM, Korb RE (2001) Storage of nitrogen in the form of protein bodies in the kelp *Laminaria*
1007 *solidungula*. *Mar Ecol Prog Ser* 218:107–114 . doi: 10.3354/meps218107
- 1008 Reedy K, Katherine (2016) Kelp-Fed Beef, Swimming Caribou, Feral Reindeer, and Their Hunters:
1009 Island Mammals in a Marine Economy. *Sustainability* 8:113 . doi: 10.3390/su8020113
- 1010 Renaud PE, Løkken TS, Jørgensen LL, et al (2015) Macroalgal detritus and food-web subsidies along
1011 an Arctic fjord depth-gradient. *Front Mar Sci* 2:31 . doi: 10.3389/fmars.2015.00031
- 1012 Roleda MY (2016) Stress physiology and reproductive phenology of Arctic endemic kelp *Laminaria*
1013 *solidungula* J. Agardh. *Polar Biol* 39:1967–1977 . doi: 10.1007/s00300-015-1813-x
- 1014 Roleda MY, Hanelt D, Wiencke C (2006) Exposure to ultraviolet radiation delays photosynthetic
1015 recovery in Arctic kelp zoospores. *Photosynth Res* 88:311–322 . doi: 10.1007/s11120-006-9055-
1016 y
- 1017 Rosenvinge LK (1893) Grønland havalger. *Meddr. Grønland* 3:763–981
- 1018 Rosenvinge LK (1899) Deuxième mémoire sur les algues marines du groenland. Reitzel, København
- 1019 Rysgaard S, Glud RN (2007) Carbon cycling and climate change: Predictions for a High Arctic
1020 marine ecosystem (Young Sound, NE Greenland). In: Rysgaard S, Glud RN (eds) *Carbon*
1021 *cycling in Arctic marine ecosystems: Case study Young Sound*. Bioscience, Meddr, pp 206–214
- 1022 Sharp G, Allard M, Lewis A, et al (2008) The potential for seaweed resource development in
1023 subarctic Canada; Nunavik, Ungava Bay. *J Appl Phycol* 20:491–498 . doi: 10.1007/s10811-008-
1024 9323-7
- 1025 Shoshina E, Makarov V, Makarov M (1997) Biological features of laminarians of Frantz Josef Land.

- 1026 Biol morya 5:286–292.
- 1027 Shoshina E, Anisimova N (2013) Makrovodorosli iz rayona buhty Ledyanaya Gavan (Novaya
 1028 Zemlya, o. Severnyi, Karskoe more) [Seaweeds from Ledjanaya Haven Inlet (Novaya Zemlja,
 1029 Northern Island, Kara Sea)]. Vestn MGTU 16:530–535
- 1030 Shoshina E V, Kapkov VI, Belenikina OA (2016) Ecological factors regulating growth of seaweeds in
 1031 Arctic communities. Вестник МГТУ 19:334–344
- 1032 Sjøtun K, Schoschina E V. (2002) Gametophytic development of *Laminaria* spp. (Laminariales,
 1033 Phaeophyta) at low temperature. Phycologia 41:147–152 . doi: 10.2216/i0031-8884-41-2-147.1
- 1034 Spurkland T, Iken K (2011) Kelp bed dynamics in estuarine environments in subarctic alaska. J Coast
 1035 Res 275:133–143 . doi: 10.2112/JCOASTRES-D-10-00194.1
- 1036 SRES (2000) IPCC special report: Summary for policymakers emissions scenarios
- 1037 Stige LC, Kvile KØ (2017) Climate warming drives large-scale changes in ecosystem function. Proc
 1038 Natl Acad Sci U S A 114:12100–12102 . doi: 10.1073/pnas.1717090114
- 1039 Sundene o (1962) The implications of transplant and culture experiments on the growth and
 1040 distribution of *Alaria esculenta*. Nytt Mag Bot 9:155–174.
- 1041 Svendsen P (1959) The algal vegetation of Spitsbergen a survey of the marine algal flora of the outer
 1042 part of isfjorden. Nor Polarinst Skr 116:1–49
- 1043 Taylor WR (1954) Algae: Non-Planktonic. Bot. Rev. 20:363–399
- 1044 Teagle HA, Hawkins SJ, Moore P., Smale DA (2017) The role of kelp species as biogenic habitat
 1045 formers in coastal marine ecosystems. J Exp Mar Bio Ecol 492:81–98 . doi:
 1046 10.1016/J.JEMBE.2017.01.017
- 1047 Traiger SB, Konar B (2018) Mature and developing kelp bed community composition in a glacial
 1048 estuary. J Exp Mar Bio Ecol 501:26–35 . doi: 10.1016/J.JEMBE.2017.12.016
- 1049 van Leeuwe MA, Tedesco L, Arrigo KR, et al (2018) Microalgal community structure and primary
 1050 production in Arctic and Antarctic sea ice: A synthesis. Elem Sci Anth 6: . doi:
 1051 10.1525/elementa.267
- 1052 von Biela VR, Newsome SD, Bodkin JL, et al (2016) Widespread kelp-derived carbon in pelagic and
 1053 benthic nearshore fishes suggested by stable isotope analysis. Estuar Coast Shelf Sci 181:364–

1054 374 . doi: 10.1016/J.ECSS.2016.08.039

1055 Wang K, Zhang T, Zhang X, et al (2017) Continuously amplified warming in the Alaskan Arctic:
1056 Implications for estimating global warming hiatus. *Geophys Res Lett* 44:9029–9038 . doi:
1057 10.1002/2017GL074232

1058 Wassmann P, Reigstad M (2011) Future arctic ocean seasonal ice zones and implications for pelagic-
1059 benthic coupling. *Oceanography* 24:220–231 . doi: 10.5670/oceanog.2011.74

1060 Waters CN, Zalasiewicz J, Summerhayes C, et al (2016) The Anthropocene is functionally and
1061 stratigraphically distinct from the Holocene. *Science* (80-) 351:137–148 . doi:
1062 10.1126/science.aad2622

1063 Wein EE, Freeman MMR, Makus JC (1996) Use of and preference for traditional foods among the
1064 Belcher Island Inuit. *Arctic* 49:256–264

1065 Wernberg T, Bennett S, Babcock RC, et al (2016) Climate-driven regime shift of a temperate marine
1066 ecosystem. *Science* (80-) 353:169–72 . doi: 10.1126/science.aad8745

1067 Wernberg T, Krumhansl KA, Filbee-Dexter K, Pedersen MF (2018) Status and trends for the world’s
1068 kelp forests. In: Sheppard C (ed) *World Seas: An Environmental Evaluation, Vol III: Ecological*
1069 *Issues and Environmental Impacts*. Elsevier

1070 Wiencke C, Clayton MN (2011) Introduction: Biology of polar benthic algae. In: Wiencke C (ed)
1071 *Biology of polar benthic algae*. De Gruyter, Berlin, p 337

1072 Wiencke C, Clayton MN (2009) Biology of polar benthic algae. *Bot Mar* 52: . doi:
1073 10.1515/BOT.2009.083

1074 Wiencke C, Roleda michael y., Gruber A, et al (2006) Susceptibility of zoospores to UV radiation
1075 determines upper depth distribution limit of Arctic kelps: evidence through field experiments. *J*
1076 *Ecol* 94:455–463 . doi: 10.1111/j.1365-2745.2006.01102.x

1077 Wiencke C, Amsler CD (2012) *Seaweeds and their communities in polar regions*. Springer, Berlin,
1078 Heidelberg, pp 265–291

1079 Wilce R (1963) Studies on benthic marine algae in north-west Greenland. In: *Proc Int Seaweed Symp.*
1080 pp 280–287

1081 Wilce RT (2016) The “Arctic Stamp”, its imprint on an endangered marine flora. *Perspect Phycol*

1082 3:155–180 . doi: 10.1127/pip/2016/0046

1083 Wilce RT, Dunton KH (2014) The Boulder Patch (North Alaska, Beaufort Sea) and its Benthic Algal
1084 Flora. *Arct. Inst. North Am.* 67:43–56

1085 Wilmers CC, Estes JA, Edwards M, et al (2012) Do trophic cascades affect the storage and flux of
1086 atmospheric carbon? An analysis of sea otters and kelp forests. *Front Ecol Environ* 10:409–415 .
1087 doi: 10.1890/110176

1088 Włodarska-Kowalczyk M, Kukliński P, Ronowicz M, et al (2009) Assessing species richness of
1089 macrofauna associated with macroalgae in Arctic kelp forests (hornsund, svalbard). *Polar Biol*
1090 32:897–905 . doi: 10.1007/s00300-009-0590-9

1091 Wulff A, Iken K, Quartino ML, et al (2011) Biodiversity, biogeography and zonation of marine
1092 benthic micro- and macroalgae in the Arctic and Antarctic. In: Wiencke C (ed) *Biology of polar*
1093 *benthic algae*. De Gruyter, p 337

1094 Zacher K, Bernard M, Bartsch I, Wiencke C (2016) Survival of early life history stages of Arctic
1095 kelps (Kongsfjorden, Svalbard) under multifactorial global change scenarios. *Polar Biol*
1096 39:2009–2020 . doi: 10.1007/s00300-016-1906-1

1097 Zenkevitch L (1963) *Biology of the Seas of the U.S.S.R.* J Chem Inf Model 1–955 . doi:
1098 10.1017/CBO9781107415324.004

1099 Malavenda C, Malavenda C (2012) Черты деградации в фитоценозах южного и среднего колен
1100 Кольского залива Баренцева моря. *Bull Moscow State Tech Univ* 15:794–802

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1102 Table 1/S1. Species composition, depth limit and biomass (wet weight per m²) of Arctic kelp forests. Bolded names indicate dominant species. (-
 1103) is not reported.

Location	Site	Year	Depth Sam pled limit (m)	Species	Latitude, Long	Kelp WW (g m ⁻²) Mean ± SE (n)	Reference
Canada							
Hudson and Ungava Bay	Kangirsuk			<i>L. solidungula</i> <i>S. longicuris</i>	60.0373, -70.1796	11.8 ± 1.3 (25)	(Sharp et al. 2008)
Hudson and Ungava Bay	Basking I		10	<i>L. solidungula</i> <i>S. longicuris</i>	59.9848, -69.9478	2.9 ± 0.2 (25)	(Sharp et al. 2008)
Labrador sea	E. Port Markham	2003	30	<i>A. clathratum</i> <i>A. esculenta</i>	52.3667, -55.7333	801.8	(Adey and Hayek 2013)
Labrador sea	Tilcey I	2003	20	<i>A. clathratum</i> <i>A. esculenta</i> <i>L. digitata</i> <i>S. dermatodea</i> <i>S. latissima</i>	52.2167, -55.6333	1808.8	(Adey and Hayek 2013)
Labrador sea	South Cove	2003	30	<i>A. clathratum</i> <i>A. esculenta</i> <i>S. dermatodea</i> <i>S. latissima</i> <i>S. longicuris</i>	53.2167, -55.6333	4109.8	(Adey and Hayek 2013)
Baffin Bay	Walls I, Cape St. Charles	2003	12	<i>A. clathratum</i> <i>A. esculenta</i> <i>L. digitata</i> <i>S. dermatodea</i> <i>S. latissima</i>	52.2167, -55.6167	1903.4	(Adey and Hayek 2013)
Hudson and Ungava Bay	Tuvalik Pt.		12	<i>A. clathratum</i> <i>A. esculenta</i> <i>L. solidungula</i> <i>S. groenlandica</i> <i>S. longicuris</i>	60.0568, -69.6745	8.4 ± 1.1 (25)	(Sharp et al. 2008)

Hudson and Ungava Bay	Pikyuluk I		12	<i>A. esculenta</i> L. digitata , <i>L. solidungula</i> , <i>S. longicruris</i>	59.9868, -69.9337	9.2 ± 2 (25)	(Sharp et al. 2008)
Greenland							
Baffin Bay	Qaanaaq		2009	<i>A. clathratum</i> <i>S. latissima</i> <i>S. longicruris</i>	77.4667, -69.2500	15.0 ± 2.6 ¹	(Krause-Jensen et al. 2012)
Baffin Bay	Dundas				77.5500, -68.8667	14.9 ± 0.8 ¹	(Krause-Jensen et al. 2012)
Baffin Bay	Ummannaq		2009 33	<i>A. clathratum</i> <i>S. latissima</i>	70.6667, -51.6000	24.1 ± 4.0 ¹	(Krause-Jensen et al. 2012)
Labrador sea	Disko Bay				69.4833, -53.6333	18.8 ± 0.9 ¹	(Krause-Jensen et al. 2012)
Labrador sea	uuk		2008 30	<i>A. clathratum</i> <i>A. esculenta</i> <i>S. longicruris</i>	64.1333, -51.6167	18.0 ± 1.1 ¹	(Krause-Jensen et al. 2012)
Labrador sea	Eqip Sermia		2009 27	<i>A. clathratum</i> <i>S. latissima</i>	69.7500, -50.3500	12.6 ± 2.8 ¹	(Krause-Jensen et al. 2012)
Norway							
Norwegian Sea	Finnøy-Håvær V		2012 20	<i>A. esculenta</i> L. hyperborea <i>S. latissima</i>	62.8203, 6.5472	1141.1 ± 349,1	(Christie et al. 2014 (NIVA report))
Norwegian Sea	Finnøy-Håvær N		2012	<i>A. esculenta</i> L. hyperborea <i>S. latissima</i>	62.8252, 6.5546	1301.0 ± 360,3	(Christie et al. 2014)
Norwegian Sea	Vega-Ivarsbraken		2012 20	<i>A. esculenta</i> L. hyperborea <i>S. latissima</i>	65.6764, 11.5494	1589.7 ± 377,7	(Christie et al. 2014)
Norwegian Sea	Vega-Bubraken		2012 20	<i>A. esculenta</i> L. hyperborea <i>S. latissima</i>	65.6802, 11.5984	712.7 ± 246,2	(Christie et al. 2014)
Norwegian Sea	Vega-Igerøy		2012	<i>A. esculenta</i> L. hyperborea <i>S. latissima</i>	65.6901, 12.1310	788.3 ± 133,9	(Christie et al. 2014)
Norwegian Sea	Senja-Sjursvika		2012 20	<i>A. esculenta</i> L. hyperborea <i>S. latissima</i>	69.0956, 16.7792	818.4 ± 174,5	(Christie et al. 2014)
Norwegian Sea	Senja-Stongeland		2012 20	<i>A. esculenta</i> L. hyperborea <i>S. latissima</i>	69.0427, 16.8795	307.8 ± 69,0	(Christie et al. 2014)

Norwegian Sea	Senja-Halvardsoya	2012	20	<i>A. esculenta</i> <i>L. hyperborea</i> <i>S. latissima</i>	69.1599, 16.8958	864.3 ± 115,9	(Christie et al. 2014)
Norwegian Sea	Senja- Kjerringbergnes	2012	20	<i>A. esculenta</i> <i>L. hyperborea</i> <i>S. latissima</i>	69.3110, 16.8978	741.8 ± 135,9	(Christie et al. 2014)
Norwegian Sea	Senja-Månesodden	2012	20	<i>A. esculenta</i> <i>L. hyperborea</i> <i>S. latissima</i>	69.3111, 16.8978	1038.7 ± 92,3	(Christie et al. 2014)
Norwegian Sea	Senja-Lemmingsvær	2012	20	<i>A. esculenta</i> <i>L. hyperborea</i> <i>S. latissima</i>	69.0270, 16.9326	561.2 ± 125,3	(Christie et al. 2014)
Norwegian Sea	Hekkingen I	2016	10	<i>A. esculenta</i> <i>L. hyperborea</i> <i>S. latissima</i>	69.6167, 17.8860	21976.0 ± 2967,0	(Filbee-Dexter et al. 2018)
Barents Sea	Kongsfjorden	2013	20	<i>A. esculenta</i> <i>L. digitata</i> <i>L. solidungula</i> <i>S. dermatodea</i> <i>S. latissima</i>	78.9833, 11.9632	4614.0	(Bartsch et al. 2016; Hop et al. 2016)
Barents Sea	Finmark- Kongsfjord	2012	20	<i>A. esculenta</i> <i>L. hyperborea</i> <i>S. latissima</i>	70.6991, 29.4393	691.7 ± 110,7	(Christie et al. 2014)
Barents Sea	Posangerfjord	-	-			4.1 ± 1.8	(Christie et al. 2014)
Barents Sea	Finmark-Bøkefjord	2012	20	<i>A. esculenta</i> <i>L. hyperborea</i> <i>S. latissima</i>	69.8525, 30.1300	703.5 ± 163,9	(Christie et al. 2014)
Russia							
Barents Sea	Cape Abram		15	<i>S. latissima</i>	69.0210, 33.0226	613.3	(Shoshina et al. 2016)
Barents Sea	Cape Mishukov		6	<i>A. esculenta</i> <i>S. latissima</i>	69.0595, 33.0429	183.3	(Malavenda and Malavenda 2012)
Barents Sea	Belokamenka Bay		6	<i>S. latissima</i>	69.0777, 33.1807	836.7	(Malavenda and Malavenda 2012)

Barents Sea	Cape Retinskiy		6	<i>A. clathratum L. digitata S. latissima</i>	69.1122, 33.3793	1550.0	(Malavenda and Malavenda 2012)
White sea	Ostrov Asafiy	1973	9	<i>S. latissima</i>	66.4210, 33.6559	1922.0	(Myagkov 1975)
White sea	Nikolskaya Bay		8	<i>L. digitata S. latissima</i>	66.2167, 33.8333	5232.0 ± 1201,0	(Plotkin et al. 2005)
USA							
Beaufort sea	Boulder patch	1980	7	<i>A. esculenta L. solidungula S. latissima</i>	70.3208, -147.5833	262.0	(Dunton and Schell 1986; Dunton et al. 1982)
Gulf of Alaska	Knight Island	1998		<i>A. cribosum E. fistulosa L. spp. S. latissima</i>	60.3327, -147.7644	900 ± 200 SE	(Dean et al. 2000a)
Aleutian Islands	Tanaga I, Adak I, Atka I, Chuginadak I	2016	-	<i>A. clathratum E. fistulosa L. spp. Ondonthalia setacea Ptilota serrata Laminaria longipes</i>	51.5521,-178.4067; 51.6102,-177.0966; 51.8619,-175.1848; 52.3509,-170.8579	1908 ± 372 SE ²	(Konar et al. 2017)
Aleutian Islands	Umnak I/Anangula I, Unalaska I	2016	-	<i>A. clathratum E. fistulosa Laminaria spp. Ondonthalia setacea Ptilota serrata Laminaria longipes</i>	52.7790,-169.3972; 53.2908,-167.9203	3523 ± 674 SE ²	(Konar et al. 2017)
Aleutian Islands	Adak I	1987	30	<i>E. fistulosa Laminaria spp.</i>	51.6102,-177.0966	2920 ± 1810	(Duggins et al. 1989)
	Amchitka I	1987	30	<i>E. fistulosa Laminaria spp.</i>	51.5043,178.4812	2628 ± 1912	(Duggins et al. 1989)
Aleutian Islands	Kiska I		-	<i>A. cribosum E. fistulosa Laminaria spp.</i>	51.5961, -178.6748	12645 ± 4999	(Wilmers et al. 2012)

Aleutian Islands	Ogliuga I	-	<i>A. cribosum, E. fistulosa, Laminaria spp.</i>	52.0563,177.4398	12645 ± 4999	(Wilmers et al. 2012)
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1104 ¹Dry weight. ²SE of dominant species *E. fistulosa*

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