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Arctic kelp forests: Diversity, resilience and future

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ABSTRACT

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

1. Introduction

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

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Kortsch et al., 2015).

Kelps are large brown seaweeds that occur on rocky coasts throughout the Arctic (Wernberg et al., 2019). Many (or most) kelps are important foundation species that create habitat (forests) for numerous fish and invertebrates (Christie et al., 2009; Norderhaug and Christie, 2011; Teagle et al., 2017), provide food to marine communities through high production and export of detritus and dissolved organic material (Krumhansl and Scheibling, 2012; Renaud et al., 2015; Abdullah et al., 2017; Filbee-Dexter et al., 2018 in press), and store and sequester carbon (Krause-Jensen and Duarte, 2016). Currently, information on the distribution, diversity, stability, and function of kelp forests is missing for large portions of the Arctic (Wiencke and Clayton, 2009; Krumhansl et al., 2016; Wilce, 2016).

A recent global analysis of records of kelp abundance over the past 5 decades showed that kelp forests are changing in many regions of the world (Krumhansl et al., 2016). At the warmest edges of their range, sudden shifts from kelp forests to reefs dominated by low-lying turf-forming algae have been increasingly documented over the last decade (Filbee-Dexter and Wernberg, 2018). Along other temperate coasts, native kelps are being replaced by invasive kelps or other seaweeds (Wernberg et al., 2019), or are being heavily overgrazed by sea urchins (Filbee-Dexter and Scheibling, 2014). In many of these regions, declines in kelp abundance are partly explained by the direct and indirect effects of warming sea temperatures (Ling et al., 2009; Catton, 2016; Filbee-Dexter et al., 2016; Wernberg et al., 2016). Considering the widespread changes throughout the temperate and tropical range of kelp and the ongoing environmental changes occurring in the Arctic, the fate of arctic kelps in this era of rapid change is a critical gap in our knowledge of arctic marine ecosystems.

Here we synthesize existing information on the distribution, biomass, and dominant species of arctic kelp forests. We explore some of the services provided by arctic kelps and identify missing baseline measures of their extent. We analyze changes in the sea ice extent and temperature conditions for known locations of kelp, and explore how recent and future changes in these and other conditions could impact their growth, reproduction, and survival. Finally, we highlight key gaps in our understanding of these ecosystems, and suggest strategies for future research.

2. Hidden blue forests of the arctic

2.1. Bounds of arctic marine ecosystems

Arctic and temperate marine ecosystems are separated by a moving boundary, generally defined by latitude, sea ice cover, light variability, and the locations of the polar front and other ocean currents (Piepenburg, 2005). The locations of these boundaries can be seasonal, unpredictable, and can shift with climate change. A precise and universally accepted geographical definition of 'arctic marine ecosystems' therefore does not exist, and different southern limits for arctic marine ecosystems are used in the literature (Zenkevitch, 1963; Piepenburg, 2005; Gattuso et al., 2006; Wilce, 2016). For example, so called 'Arctic conditions' (ice scoured intertidal zones, ocean temperatures < 0 °C, and months with little to no daylight) extend below the Arctic circle along the coasts of Greenland and Eastern Canada, which are influenced by the cold southward moving Labrador and Greenland currents, but are restricted to above the Arctic circle along the coasts of northern Norway, Iceland and in the southern Bering sea, which are influenced by the warmer northward moving Gulf Stream and North Pacific currents, respectively (Wilce, 2016). The convergence of cool waters from the Arctic Ocean and warm waters from the Atlantic and Pacific Oceans occurs around 65°N on the east coast of Greenland, 80°N west of Svalbard, 76 °C in the Barents Sea, in the Bering Strait, 63°N in the eastern Canadian Arctic Archipelago, and then slightly north between Baffin Island and the west coast of Greenland (AMAP, 1998). However, other factors such as sea ice, light, and glacial run-off also create Arctic conditions south of these limits (AMAP, 1998). Here we define 'arctic kelps' as kelps occurring within the boundaries defined by the Arctic Monitoring and Assessment Program (AMAP). AMAP originally defined Arctic boundaries in 1991 as regions north of the 10 °C July isotherm. These boundaries have since been expanded to include some areas that correspond to political boundaries of member nations of the Arctic Council (e.g., coastal shelf of Iceland, Norwegian northwest coast, Hudson Bay, and the Aleutian Islands) (AMAP, 2017). We used this definition because monitoring programs, assessments and decision-making on pollution and climate change in Arctic regions often use AMAP boundaries. However, despite our inclusive definition of the Arctic, much of this manuscript focuses on kelp forests at higher latitudes within the AMAP region where kelps face the most extreme Arctic conditions and where globally unique species compositions are found.

2.2. Distribution, growth forms and evolution of arctic kelps

Although kelps range along most Arctic coasts, sparse records of kelps in some parts of the Arctic have been attributed to a lack of hard substrata (Kjellman, 1883; Wilce, 2016). Only about 35% of the Arctic basin is rocky substrate and shallow coastal areas and inner Arctic fjords are often dominated by sediment due to glacial run off and river deposition (Leont'yev, 2003; Lantuit et al., 2012), which limits the presence of macroalgae. In areas with suitable substrate, dense kelp forests can extend from the intertidal zone down to depths of 30–40 m depending on light conditions, wave regime, and grazing intensity (Wernberg et al., 2019). The deepest recorded kelp was observed at 60 m depth in Disko Bay, Greenland (Boertmann et al., 2013). In high Arctic regions, available light and sea ice further restrict this depth range and the upper sublittoral zone is a barren, low salinity environment that is constantly impacted by sea ice and meltwater (Wiencke and Clayton, 2011).

The diversity of kelp in the high Arctic tends to be lower than in temperate kelp forests (Wiencke and Clayton, 2011). Genetic evidence indicates that most kelps reinvaded the Arctic from the Atlantic Ocean ~8000 years ago following the last ice age, which eliminated benthic flora from most current Arctic subtidal regions (Wulff et al., 2011). As a result, most arctic kelps have optimal growth temperatures that exceed those experienced during the Arctic summer and many of these species therefore also thrive along warmer, temperate coasts (Wiencke and Amsler, 2012). In the high Arctic especially, kelps tend to be morphologically smaller compared to their southern range limits (e.g., Kuznetsov et al., 1994; Kuznetsov and Shoshina, 2003; but see Borum et al., 2002). However, kelps still form dense canopies in some regions (e.g., western Alaska and northern Norway) and provide most of the algal biomass and the largest three-dimensional biogenic structure on rocky coasts in Arctic regions (Wiencke and Amsler, 2012). In fact, these lush underwater forests are particularly striking in the Arctic, where terrestrial coasts are barren and ice scoured with little three-dimensional structure.

The species pool is relatively young, with only one truly arctic endemic kelp, *Laminaria solidungula* (Kjellman, 1883; Zenkevitch, 1963; Wilce and Dunton, 2014). All other kelp species found in Arctic regions also extend into sub-arctic and northern temperate waters and include *Alaria esculenta*, *Agarum clathratum, Eualaria fistulosa, Laminaria digitata, Laminaria hyperborea, Nereocystis luetkeana*, *Saccharina latissima*, *Saccharina longicruris, Saccharina nigripes, Saccorhiza dermatodea, Alaria elliptica*, and *Alaria oblonga* (the latter 2 are only found in Russia) (Fig. 1, Table 1). There is currently taxonomic confusion regarding some arctic species; *S. nigripes*, for example, has often been misidentified as L. *digitata*, and appears to be restricted to Arctic or sub-arctic conditions, although more information on its distribution is needed (McDevit and Saunders, 2010). In 2006 a new species of kelp *Aureophycus aleuticus* was collected from Kagamil Island, Aleutian Islands, but its classification within the order Laminariales is still unclear (Kawai et al., 2013). New DNA barcoding techniques show promise for

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

clearing up misidentifications caused by diverse growth morphologies of kelps in arctic conditions (McDevit and Saunders, 2010; Bringloe et al., 2017).

2.3. Adaptations to arctic conditions

Kelps in arctic environments are challenged by extremely low water temperatures, periods of low salinity, and extreme variability in light caused by large annual variations in day length, light intensity, and sea ice cover. In their northernmost range, kelps live in temperatures at the point of freezing sea water during polar nights (e.g., NE Greenland, Borum et al., 2002; Franz Joseph Land, Shoshina et al., 2016). Day-length ranges from 24-h sunlight in mid-summer to several months of total darkness during winter (Hanelt, 1998). The low angle of the sun and periods of complete darkness mean that high Arctic areas only receive 30–40% of the light received in the tropics on an annual basis. The long period of darkness during winter is further extended in areas with partial or complete sea ice cover, especially if the ice is thick or covered by snow (Mundy et al., 2007). Subtidal habitats in the Arctic can therefore be without light for much of the year. Studies from NE Greenland illustrates this; the annual surface irradiance (PAR) in Young Sound (74° 18′ N) amounts to ca. 6100 mol photons m^{-2}, but the ice-free period is limited to August and September so that the amount of available light at 10 and 20 m depth is only 234 and 40 mol photons $m^{-2} yr^{-1}$, respectively (Borum et al., 2002).

The marked seasonal variation in light availability in the Arctic concentrates primary production into a short period and creates strong seasonality in the growth of kelp (Chapman and Lindley, 1980; Dunton and Jodwalis, 1988; Borum et al., 2002; Makarov et al., 2008). Arctic kelps are well adapted to these long periods of darkness or low light conditions. Studies on *S. latissima* and *L. solidungula* show that these species store most of the carbon obtained during the short summer period and subsequently use these reserves to form new blades during the succeeding period of almost darkness (Chapman and Lindley, 1980; Dunton and Jodwalis, 1988; Borum et al., 2002). Remarkably, the peak growth period for Alaskan *L. solidungula* was from February to April

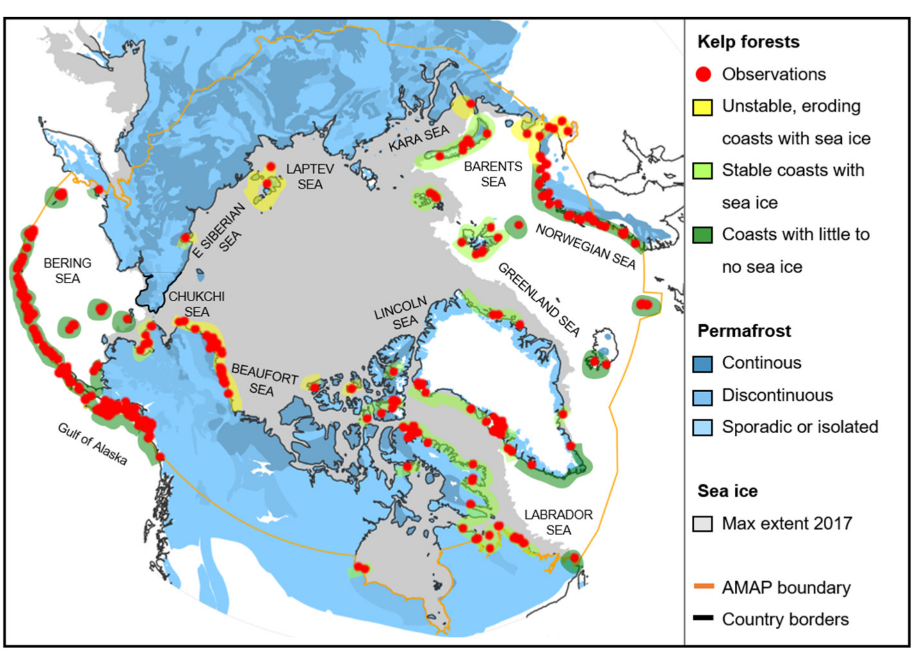

Fig. 2. Kelp locations (red) within AMAP Arctic boundary line (orange). Gray shading shows maximum sea ice extent, blue shading shows continuous permafrost (90–100% cover), discontinuous permafrost (50–90%), and sporadic and isolated patches of permafrost (< 50%) (2016 National Snow and Ice Data Centre,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

Table 1
Species composition, depth limit and biomass (wet weight per m²) of arctic kelp forests. Bolded names indicate dominant species. (−) is not reported.

Location	Site	Year sampled	Depth limit (m)	Species	Latitude, Longitude	Kelp WW (g m^{-2}) Mean ± SE (n)	Reference
Canada							
Hudson and Ungava Bay	Kangirsuk			*L. solidungula* ***S. longicruris***	60.0373, −70.1796	11.8 ± 1.3 (25)	(Sharp et al., 2008)
Hudson and Ungava Bay	Basking I		10	*L. solidungula* ***S. longicruris***	59.9848, −69.9478	2.9 ± 0.2 (25)	(Sharp et al., 2008)
Labrador sea	E. Port Markham	2003	30	***A. clathratum*** *A. esculenta*	52.3667, −55.7333	801.8	(Adey and Hayek 2011)
Labrador sea	Tilcey I	2003	20	***A. clathratum A. esculenta*** *L. digitata S. dermatodea S. latissima*	52.2167, −55.6333	1808.8	(Adey and Hayek 2011)
Labrador sea	South Cove	2003	30	*A. clathratum A. esculenta S. dermatodea S. latissima* ***S. longicruris***	53.2167, −55.6333	4109.8	(Adey and Hayek 2011)
Baffin Bay	Walls I, Cape St. Charles	2003	12	*A. clathratum* ***A. esculenta*** *L. digitata S. dermatodea S. latissima*	52.2167, −55.6167	1903.4	(Adey and Hayek 2011)
Hudson and Ungava Bay	Tuvalik Pt.		12	*A. clathratum A. esculenta L.* ***solidungula*** *S. groenlandica* ***S. longicruris***	60.0568, −69.6745	8.4 ± 1.1 (25)	(Sharp et al., 2008)
Hudson and Ungava Bay	Pikyuluk I		12	*A. esculenta* ***L. digitata*** *L. solidungula S. longicruris*	59.9868, −69.9337	9.2 ± 2 (25)	(Sharp et al., 2008)
Greenland							
Baffin Bay	Qaanaaq	2009		*A. clathratum S. latissima S. longicruris*	77.4667, −69.2500	15.0 ± 2.6[a]	(Krause-Jensen et al., 2012)
Baffin Bay	Dundas				77.5500, −68.8667	14.9 ± 0.8[a]	(Krause-Jensen et al., 2012)
Baffin Bay	Uummannaq	2009	33	*A. clathratum S. latissima*	70.6667, −51.6000	24.1 ± 4.0[a]	(Krause-Jensen et al., 2012)
Labrador sea	Disko Bay				69.4833, −53.6333	18.8 ± 0.9[a]	(Krause-Jensen et al., 2012)
Labrador sea	uuk	2008	30	*A. clathratum A. esculenta S. longicruris*	64.1333, −51.6167	18.0 ± 1.1[a]	(Krause-Jensen et al., 2012)
Labrador sea	Eqip Sermia	2009	27	*A. clathratum S. latissima*	69.7500, −50.3500	12.6 ± 2.8[a]	(Krause-Jensen et al., 2012)
Norway							
Norwegian Sea	Finnøy-Håvær V	2012	20	*A. esculenta L.* ***hyperborea*** *S. latissima*	62.8203, 6.5472	1141.1 ± 349,1	(Christie et al., 2014)
Norwegian Sea	Finnøy-Håvær N	2012		*A. esculenta* ***L. hyperborea*** *S. latissima*	62.8252, 6.5546	1301.0 ± 360,3	(Christie et al., 2014)
Norwegian Sea	Vega-Ivarsbraken	2012	20	*A. esculenta* ***L. hyperborea*** *S. latissima*	65.6764, 11.5494	1589.7 ± 377,7	(Christie et al., 2014)
Norwegian Sea	Vega-Bubraken	2012	20	*A. esculenta* ***L. hyperborea*** *S. latissima*	65.6802, 11.5984	712.7 ± 246,2	(Christie et al., 2014)
Norwegian Sea	Vega-Igerøy	2012		*A. esculenta* ***L. hyperborea*** *S. latissima*	65.6901, 12.1310	788.3 ± 133,9	(Christie et al., 2014)
Norwegian Sea	Senja-Sjursvika	2012	20	*A. esculenta* ***L. hyperborea*** *S. latissima*	69.0956, 16.7792	818.4 ± 174,5	(Christie et al., 2014)
Norwegian Sea	Senja-Stongeland	2012	20	*A. esculenta* ***L. hyperborea*** *S. latissima*	69.0427, 16.8795	307.8 ± 69,0	(Christie et al., 2014)
Norwegian Sea	Senja-Halvardsøya	2012	20	*A. esculenta* ***L. hyperborea*** *S. latissima*	69.1599, 16.8958	864.3 ± 115,9	(Christie et al., 2014)
Norwegian Sea	Senja-Kjerringbergnes	2012	20	*A. esculenta* ***L. hyperborea*** *S. latissima*	69.3110, 16.8978	741.8 ± 135,9	(Christie et al., 2014)
Norwegian Sea	Senja-Månesodden	2012	20	*A. esculenta* ***L. hyperborea*** *S. latissima*	69.3111, 16.8978	1038.7 ± 92,3	(Christie et al., 2014)
Norwegian Sea	Senja-Lemmingsvær	2012	20	*A. esculenta* ***L. hyperborea*** *S. latissima*	69.0270, 16.9326	561.2 ± 125,3	(Christie et al., 2014)
Norwegian Sea	Hekkingen I	2016	10	*A. esculenta L. hyperborea S. latissima*	69.6167, 17.8860	21,976.0 ± 2967,0	(Filbee-Dexter et al., 2018)
Barents Sea	Kongsfjorden	2013	20	*A. esculenta* ***L. digitata*** *L. solidungula S. dermatodea S. latissima*	78.9833, 11.9632	4614.0	(Bartsch et al., 2016; Hop et al. 2016)
Barents Sea	Finnmark-Kongsfjord	2012	20	*A. esculenta* ***L. hyperborea*** *S. latissima*	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	Finnmark-Bøkefjord	2012	20	*A. esculenta* ***L. hyperborea*** *S. latissima*	69.8525, 30.1300	703.5 ± 163,9	(Christie et al., 2014)
Russia							
Barents Sea	Cape Abram		15	***S. latissima***	69.0210, 33.0226	613.3	(Shoshina et al., 2016)
Barents Sea	Cape Mishukov		6	*A. esculenta S. latissima*	69.0595, 33.0429	183.3	(Malavenda and Malavenda, 2012)
Barents Sea	Belokamenka Bay		6	***S. latissima***	69.0777, 33.1807	836.7	(Malavenda and Malavenda, 2012)
Barents Sea	Cape Retinskiy		6	*A. clathratum L. digitata S. latissima*	69.1122, 33.3793	1550.0	(Malavenda and Malavenda, 2012)
White sea	Ostrov Asafiy	1973	9	***S. latissima***	66.4210, 33.6559	1922.0	(Myagkov, 1975)
White sea	Nikolskaya Bay		8	*L. digitata* ***S. latissima***	66.2167, 33.8333	5232.0 ± 1201,0	(Plotkin et al., 2005)

(continued on next page)

Table 1 (*continued*)

Location	Site	Year sampled	Depth limit (m)	Species	Latitude, Longitude	Kelp WW (g m^{-2}) Mean ± SE (n)	Reference
USA							
Beaufort sea	Boulder patch	1980	7	*A. esculenta* ***L. solidungula*** *S. latissima*	70.3208, −147.5833	262.0	(Dunton and Schell, 1986; Dunton et al., 1982)
Gulf of Alaska	Knight Island	1998		*A. cribosum* ***E. fistulosa*** *Laminaria* spp. *S. latissima*	60.3327, −147.7644	900 ± 200 SE	(Dean et al., 2000a)
Aleutian Islands	Tanaga I, Adak I, Atka I, Chuginadak I	2016	–	*A. clathratum* ***E. fistulosa*** *Laminaria* spp. *Ondonthalia setacea Ptilota serrata Laminaria longipes*	51.5521,-178.4067; 51.6102,-177.0966; 51.8619,-175.1848; 52.3509,-170.8579	1908 ± 372 SE[b]	(Konar et al., 2017)
Aleutian Islands	Umnak I/Anangula I, Unalaska I	2016	–	*A. clathratum* ***E. fistulosa*** *Laminaria* spp. *Ondonthalia setacea Ptilota serrata Laminaria longipes*	52.7790,-169.3972; 53.2908,-167.9203	3523 ± 674 SE[b]	(Konar et al., 2017)
Aleutian Islands	Adak I	1987	30	***E. fistulosa*** *Laminaria* spp.	51.6102,-177.0966	2920 ± 1810	(Duggins et al., 1989)
Aleutian Islands	Amchitka I	1987	30	***E. fistulosa*** *Laminaria* spp.	51.5043,178.4812	2628 ± 1912	(Duggins et al., 1989)
Aleutian Islands	Kiska I	–		*A. cribosum* ***E. fistulosa Laminaria* spp.**	51.5961, −178.6748	12,645 ± 4999	(Wilmers et al., 2012)
Aleutian Islands	Ogliuga I	–		*A. cribosum*, ***E. fistulosa,Laminaria* spp.**	52.0563,177.4398	12,645 ± 4999	(Wilmers et al., 2012)

[a] Dry weight.
[b] SE of dominant species *E. fistulosa*.

under full ice cover (Dunton, 1985), and the production of new lamina in *S. latissima* from Young Sound (NE Greenland) occurred under ice cover and in complete darkness, likely based on re-allocation of carbon from the old lamina or stipe (Borum et al., 2002).

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

3. Known locations of arctic kelps

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

Extreme variation in environmental conditions occur within the AMAP arctic boundaries. Large regional differences in coastal conditions are strongly driven by the cover of sea ice and the presence of permafrost (frozen soil, rock, or sediment) (Lantuit et al., 2012). To capture this variability in our description of arctic kelps, we grouped information from our observational data into 3 general categories: (1) kelps on stable coasts with sea ice, (2) kelps on unstable, eroding coasts with sea ice, and (3) kelps on coasts with little to no sea ice.

3.1. Kelps on stable arctic coasts with sea ice

Stable, rock bound coasts and fjord systems in Arctic areas with seasonal cover of sea ice can support luxurious kelp forests, although their vertical distribution is limited by ice scour (shallow) and light (deep). These areas are expected to experience pronounced changes in environmental conditions when sea ice retreats. Although this should increase overall primary productivity along these coasts, the species composition of algae currently found in these Arctic regions may be lost permanently if more temperate-adapted algal communities push northward and outcompete kelps that are adapted to seasonal sea ice (Krause-Jensen and Duarte, 2014).

In the northern Barents Sea, kelp forests of mixed *A. esculenta*, *L. digitata* and *S. latissima* occur within high latitude fjords off Svalbard, the western White Sea, and Franz Joseph Land (Kuznetsov et al., 1994;

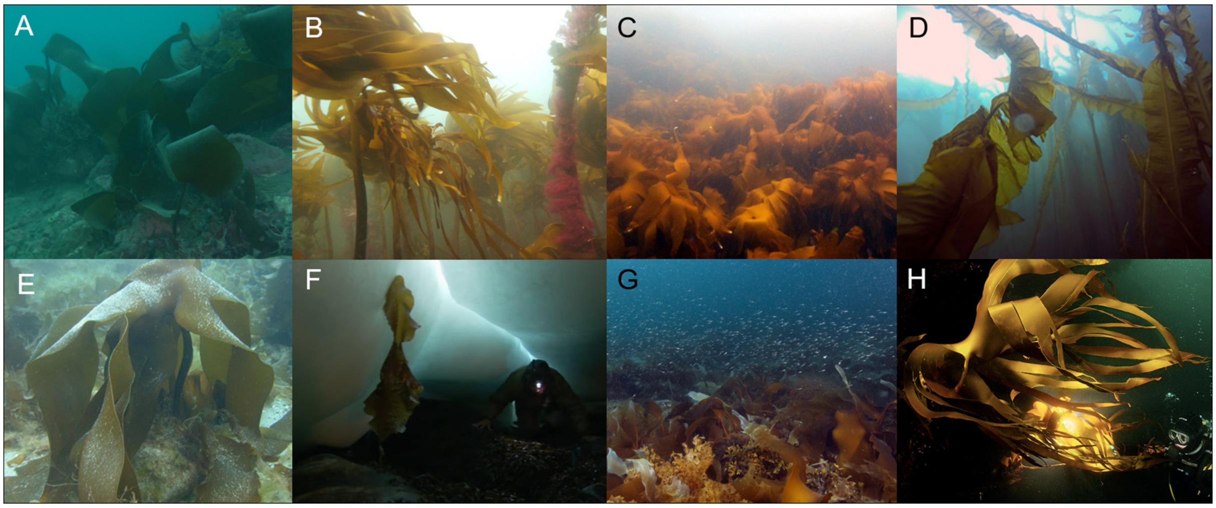

Fig. 3. Photographs show examples of arctic kelp forests: (A) *Laminaria solidungula* in the Beaufort Sea, Alaska, USA (Ken Dunton), (B and C) *Laminaria hyperborea* in Malangen fjord, Norway (Thomas Wernberg, Karen Filbee-Dexter), (D) *Eularia fistulosa* Aleutian Islands, Alaska (Pike Spector), (E)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

Cooper et al., 1998; Bartsch et al., 2016; Fig. 3F,H). Luxuriant stands of *L. digitata*, *L. solidungula*, *S. dermatodea*, and *A. clathratum* were observed within fjords in western Novaya Zemlya (Shoshina and Anisimova, 2013). In the northernmost regions around Svalbard and Novaya Zemlya, the arctic endemic kelp *L. solidungula* is found in inner fjords and areas that receive cold polar currents (Svendsen, 1959; Hop et al., 2012; Shoshina and Anisimova, 2013).

The west coast of Greenland is largely rockbound and dominated by sub-littoral kelp forests from Cape Farewell in the south (59° N) to Smiths Sound in the north (> 80° N, Rosenvinge, 1893, 1899). The western Greenland kelp forests are dominated by *S. longicruris* north of 62° N and by *S. latissima* south of this latitude, while other species such as *L. solidungula, A. esculenta, Agarum clathratum, S. nigripes* and *S. dermatodea* are present, but less conspicuous (Rosenvinge, 1899; Krause-Jensen et al., 2012). The kelp forests in western Greenland are narrow and shallow in the north, but become broader, more abundant, and extend deeper in the south due to less ice cover (Krause-Jensen et al., 2012). In some parts of Greenland, high densities of sea urchins or a lack of hard bottom restricts the extent of the kelp forests (Krause-Jensen et al., 2012). The kelp populations in eastern Greenland tend to be situated deeper, have less biomass per unit area and grow more slowly than those on the west coast (Borum et al., 2002; Krause-Jensen et al., 2012), which may be due to lower water temperatures, longer periods with ice-cover, and more heavy scour by pack ice. *S. latissima* and *A. esculenta* appear to be the dominant species along most of the east coast (recorded as high as Danmarks Havn (75° N)), while *L. solidungula, S. nigripes, S. longicruris and A. clathratum* are present, but less abundant (Rosenvinge, 1899).

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

3.2. Kelps on eroding, permafrost bound arctic coasts with sea ice

Scattered low relief, rocky coasts in the eastern Siberian, Laptev, Beaufort, and Chukchi seas, and the Canadian high Arctic have temperatures and light conditions that should support kelp (Krumhansl and Scheibling, 2012), but observations are rare in these regions (Zenkevitch, 1963; Lee, 1973; Wilce and Dunton, 2014; Wilce, 2016). These coasts are more permanently icebound compared to other Arctic regions– especially in the Beaufort, eastern Siberian, and Laptev seas – and the seafloor is often covered in sediment due to intense glacial run off. Low salinity, high levels of sedimentation, and sparse substrate make kelps and other macroalgae poorly developed (Taylor, 1954; Leont'yev, 2003; Dayton, 2013). As a result, kelps along these coasts face harsh conditions such as extensive sea ice scour, long periods of darkness, variable salinity, turbidity, and/or low temperatures (Wilce, 2016). The associated macroalgal communities in many of these regions have distinct species compositions compared to other regions of the Arctic, possibly because they are less connected to nearby temperate communities due to outflow of polar currents from the north to south along their coasts (Wilce and Dunton, 2014). In the Alaskan Beaufort Sea, kelps are found in scattered rocky habitats in shallow waters (5–10 m depth) along the mainly sedimentary coast. Research on kelps in this area are from the 'Boulder Patch' (71° N), where *L. solidungula* forms beds intermixed with *A. esculenta* and *S. latissima* on shallow cobbles and boulders (Wilce and Dunton, 2014; Fig. 3A). These isolated kelp communities contain about half of the 140 macroalgal species found in the Arctic. The Boulder Patch has been studied since 1978 and revisited in 14 separate years between 1978 and 2012, over which time the species composition has remained relatively static (Wilce and Dunton, 2014).

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

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

3.3. Kelps in arctic regions with little to no sea ice

Kelp forests in the Norwegian Sea, the Barents Sea, and the northern Pacific (Aleutian Islands and northern Gulf of Alaska) have high upper limits of biomass compared to other arctic kelp forests (Table 1; Fig. 3B,C,D). These regions have little to no sea ice and ocean temperatures that are warmer than other Arctic regions due to the influence of the Gulf Stream or the Pacific Current. Kelp forests in some of these regions (e.g., the Gulf of Alaska) are highly influenced by environmental conditions on land, namely high freshwater inputs from melting permafrost and melting glaciers that creates strong clines in salinity in coastal areas (Spurkland and Iken, 2011; Lind and Konar, 2017). Kelp in other regions with little to no sea ice appear to be more influenced by biological factors than by environmental conditions. Many kelp forests are strongly impacted by herbivorous sea urchin populations, which can increase with the loss of higher level predators (e.g., crabs, cod, otters) (Doroff et al., 2003; Filbee-Dexter and Scheibling, 2014). Importantly, kelps currently found in areas with little to no sea ice may represent future scenarios for other Arctic regions.

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

In the North Pacific Ocean, surface canopy forming kelps *E. fistulosa* and *N. luetkeana* and subsurface kelps (*A. clathratum, A. esculenta, Costaria costada, L. digitata,* and *S. latissima*) form forests along the Aleutian Island chain, the northern Gulf of Alaska coast and the northeastern coast of Russia. *E. fistulosa* dominates surface canopies in the Aleutian Islands and *E. fistulosa* and *N. leutkeana* in southeast Alaska that can grow from > 30 m depth. Subsurface kelps tend to be competitively dominant in both regions (Duggins, 1980, Dayton 1975). Kelp forests in the northern Gulf of Alaska occur within the largest freshwater discharge system in North America, and experience strong gradients of salinity due to substantial glacial inputs. The amount of glacial melt is increasing with climate change, further lowering salinity and negatively effecting kelps in these areas (Lind and Konar, 2017). In contrast, kelp forests along the shores of the Aleutian Islands are more influenced by biotic interactions. These coasts have alternated between kelp forests and urchin barrens for over a century (Estes et al., 2004). Shifts between these two ecosystem states are driven by changing abundances of sea otters, which are major predators of the sea urchin *Strongylocentrotus polyacanthus* (Estes and Duggins, 1995). Evidence from the region suggests that kelp forests established in 1911 after sea otter populations rebounded (Estes et al., 1978). The recovered kelp forests (*E. fistulos* and *Laminaria* spp.) were maintained for decades, until otter populations declined again due to predation by killer whales (Doroff et al., 2003; Estes et al., 2004), once again limiting kelp forests to exposed areas and shallow depths, which act as refuges from grazing (Konar and Estes, 2003).

4. Ecosystem services provided by arctic kelp forests

Kelps can provide extensive substrate for colonizing organisms, and their canopies create habitat for a number of marine plants, fish, and invertebrates (Teagle et al., 2017). The flora in arctic kelp forests can be diverse and has been described in detail for some high Arctic regions (e.g., Wilce and Dunton, 2014; Küpper et al., 2016). Diverse fish, invertebrate and epiphytic communities are found in kelp forests in Svalbard, Norway, the Aleutian Islands, the Gulf of Alaska, and the Boulder Patch, USA (Hamilton and Brenda, 2007; Włodarska-Kowalczuk et al., 2009; Wilce and Dunton, 2014). Kelp canopies can create favourable conditions for some understory species and were shown to provide predation refuge for juvenile cod in Newfoundland, Canada (Gotceitas et al., 1995) and rockfish and ronquils in the Gulf of Alaska (Dean et al., 2000b). Traditional knowledge from northern communities in Greenland reported higher arctic cod catches in areas near kelp forests compared to other areas (Krause-Jensen and Duarte, 2014). Despite these reports, the smaller size and patchy nature of kelps in some Arctic regions may reduce their importance as habitat forming species compared to temperate forests. Kelp also has cultural value for northern peoples and features in their traditions and stories. It is a traditional food for Inuit, who harvest it from under sea ice during low tide (Wein et al., 1996) and can be used by farmers as fertilizer or to cattle feed (Reedy and Katherine, 2016).

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

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

A comprehensive understanding of the nature and extent of kelp subsidy to other arctic benthic, pelagic, and terrestrial ecosystems is still lacking, and the magnitude and importance of kelp exported from shallow coasts to deeper habitats is a debated topic of on-going research (Renaud et al., 2015). In the subarctic and Arctic regions, most research has focused on the vertical influx of phytoplankton- or zooplankton-derived organic matter as the main source of carbon in benthic systems. In Greenland, the primary production of kelps and other benthic algae can contribute to > 20% of the total primary production in shallow coastal areas. However, at depths > 15 m this production was largely

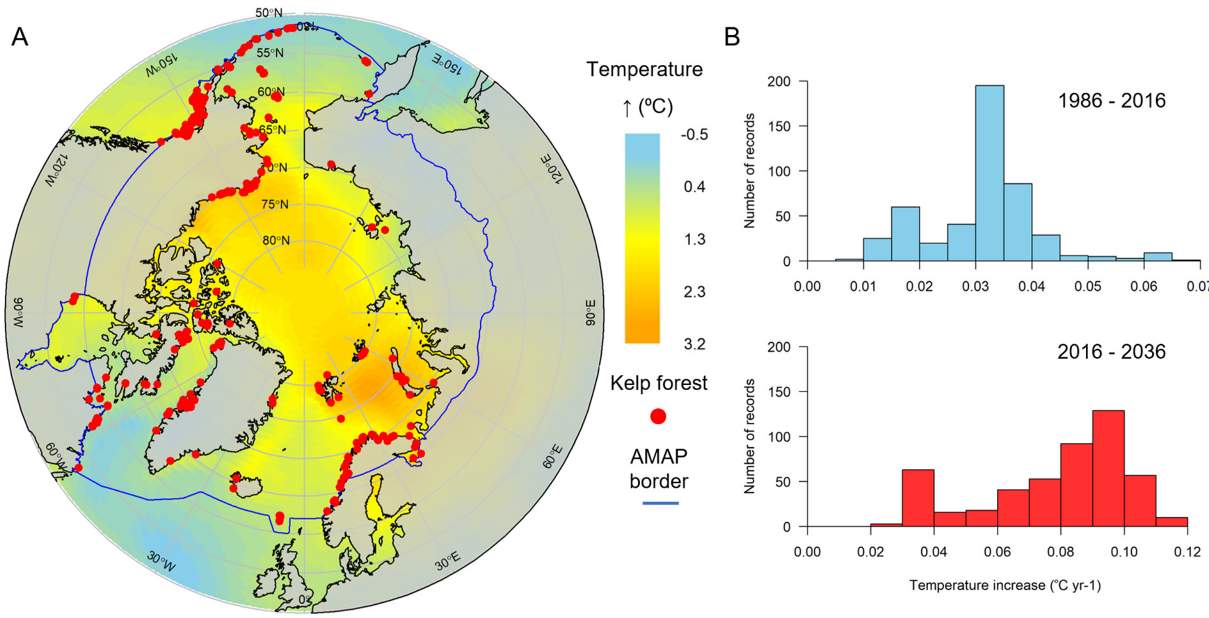

Fig. 4. (a) Global trends in predicted increase in mean summer (July 21 to Sept 21) surface temperature from 2016 to 2036 according to IPCC models. Kelp locations are shown in red within AMAP Arctic boundary line (blue). (b) Rate (y^{-1}) of historic and (c) rate of projected warming of peak summer temperature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

insignificant compared to that of phytoplankton and benthic microalgae (Krause-Jensen et al., 2007). The magnitude of, and timing by which, kelp-derived carbon enters arctic ecosystems is especially interesting because climate change is triggering earlier phytoplankton blooms in the Arctic, creating temporal mismatch between pelagic primary production and some higher trophic level species that synchronize their life cycle or behaviour to this pulsed source of energy (van Leeuwe et al., 2018). In light of this mismatch, understanding other sources of arctic primary production during food-limited periods is becoming critical.

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

5. Kelps in a sentinal region of change

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

5.1. Temperature

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

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

The mean summer temperature across all kelp locations has increased by 0.35 °C (± 0.20) per decade over the period from 1986 to 2016 (Fig. 4a) and is predicted to increase by 1.09 °C (± 0.59) per decade over the next century (Fig. 4b). Predicted temperature increases are least pronounced for kelps along the coasts of Greenland and eastern Siberia, and most pronounced in the Barents Sea, Beaufort Sea, and Canadian high Arctic, suggesting that changes to kelp forests due to warming will first occur in these regions.

Based on temperature tolerance and growth optima of most arctic kelp species, warmer temperatures should increase growth rates (Müller et al., 2009; Shoshina et al., 2016). The optimum growth temperature for most arctic and cold-temperate kelp species range from 10 to 15 °C (Wiencke and Amsler, 2012; Roleda, 2016), and growth at 0–5 °C is typically only 25–30% of growth at their optimum temperature (e.g., Bolton and Lüning, 1982). Upper temperature limits on growth of arctic kelps range from 16 to 21 °C (Assis et al., 2018), which are well above conditions found along Arctic coasts. This suggests warming could more than double kelp production in some regions the next 2–3 decades. Warming may also improve recruitment; for example, germination of spores, fertility (Golikov and Averintsev, 1977), and survival of arctic kelp gametophytes are limited by temperatures below −1 °C (Sjøtun and Schoschina, 2002; Müller et al., 2008; Assis et al., 2018). Such changes will vary across kelp species and will likely alter their competitive interactions. In the northern Gulf of Alaska, spore settlement and gametophyte growth of *E. fistulosa* were more negatively impacted by elevated temperatures and low salinity, than that of the more widely distributed *N. luetkeana* and *S. latissima* (Lind and Konar, 2017). *A. esculenta* is best adapted to low temperatures and cannot survive in waters warmer than 16 °C (Sundene, 1962). Likewise, recruitment of *L. solidungula* becomes limited when temperatures exceed 10 °C. Other, more warm adapted temperate kelps such as L. *hyperborea, L. digitata* and *Saccharina polyschides* may extend their range northward, following the trend of boreal species moving into the Arctic (Fossheim et al., 2015; Hargrave et al., 2017; Stige and Kvile, 2017). However, kelps produce short-lived zoospores that disperse slowly (current patterns of kelp diversity and structure can still be related to glacial cycles (Neiva et al., 2018), so any temperature-driven northern expansion of temperate kelp species into polar regions is likely to be slow (Konar, 2007; Wilce, 2016).

5.2. Sea ice and light

The amount of light reaching the benthos is a defining factor for benthic primary production and depends largely on the extent of sea ice cover. Sea ice is rapidly retreating in the Arctic (areal loss of 3.5–4.5% per decade, Fig. 5A). Average sea ice extent (± SD) declined by 3.7% between 2006 and 2016 (from 16.2 ± 104 to 15.6 ± 105 M km^2), and by 23% in 2016 compared to average sea ice measures from 1981 to 1989 (21.4 ± 2.4 M km^2).

To examine ongoing changes in sea ice extent at locations with records of kelp, we obtained the position of the ice edge (defined by a threshold of > 15% sea ice cover) from NASA satellite images taken weekly from 2006 to 2016 (http://nsidc.org/, NOAA, accessed 2017). We constrained our measures to this period because years prior to 2006 had lower resolution spatial measures for coastal regions. At each kelp location we calculated the nearest distance (m) to the sea ice edge each week over the 10-year period. To compare these trends over this last decade with broader patterns of sea ice loss we obtained daily measures of areal sea ice extent from NASA satellite data from 1980 to 2016 (Fig. 5).

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

Available evidence indicates that the loss of sea ice currently occurring in the Arctic will lead to the northward expansion of kelps (Müller et al., 2009), and an increase in the depth range and productivity of these habitats due to increased light and reduced scour in the surf zone, which narrows the vertical distribution of kelp (Krause-Jensen et al., 2012; Krause-Jensen and Duarte, 2014). Kelps cannot exist in areas with permanent sea ice (Shoshina et al., 2016), so ice loss may open new habitats in the high Arctic. The effect of sea ice loss on kelps may even be stronger than anticipated because day length increases rapidly during the period of ice break-up (Clark et al., 2013), implying a slight reduction in ice cover will result in a disproportionately large increase in the amount of light reaching kelp. These expectations are supported by correlative studies from along the west coast of Greenland showing that the extent of sea ice cover explained 92% of the variation in maximum depth distribution and 80% of the variation in kelp growth (Krause-Jensen et al., 2012). Hop et al. (2012) monitored the biomass and depth range of kelps in Svalbard, Norway between 1996 and 2014 and found that kelp biomass (mainly

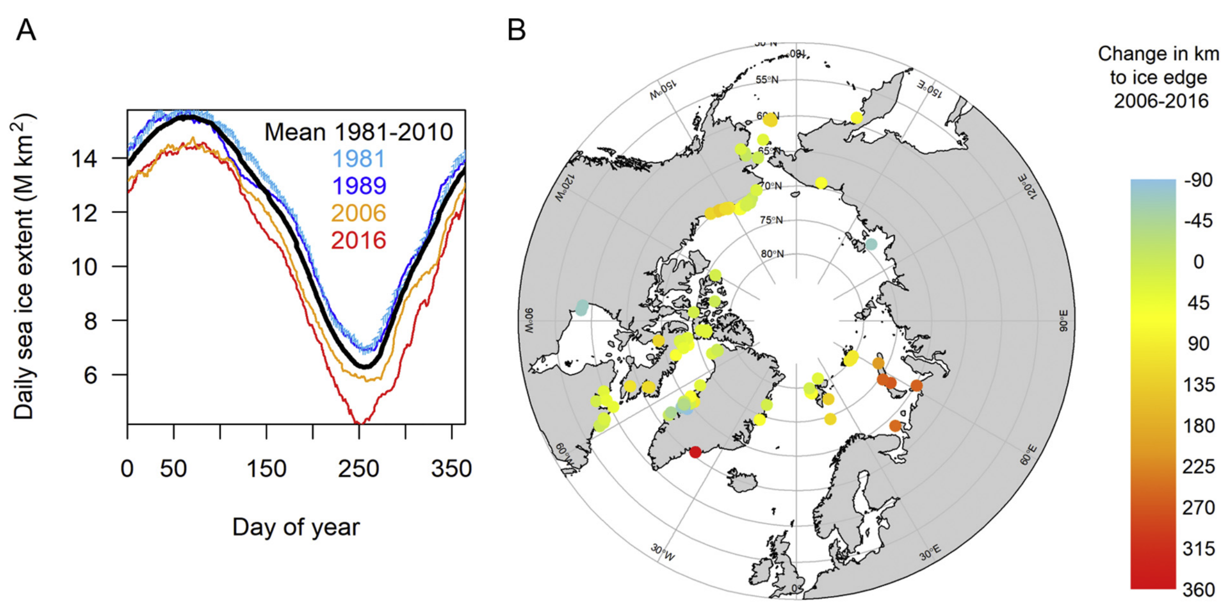

Fig. 5. (A) Daily sea ice extent in millions of km for entire Arctic region between 1981 and 2010. (B) Change in mean distance to sea ice edge (km) between 2006 and 2016, for locations of kelp that occurred under ice for at least 1 week over this period.

L. *digitata*) recently increased 2–4 fold in the shallow zone (2.5 m depth). They ascribed these changes to reductions in sea ice cover (Bartsch et al., 2016).

5.3. Salinity and turbidity

As a consequence of reduced sea ice and melting permafrost, many Arctic coastlines are breaking apart and eroding into the sea. These traditionally icebound coasts can be fragile because ice provides protection from storms and waves, and its loss can expose the ground to the elements and make it unstable (Lantuit et al., 2012). Coastal environments near these eroding regions are receiving higher amounts of sediment loading and freshwater inputs, resulting in longer and more extreme periods of low salinity and intense turbidity and sedimentation (Lantuit et al., 2012; McClelland et al., 2012; Fritz et al., 2017). Since 2000, average erosion rate of permafrost-bound coasts was 0.5 m yr^{-1}, and reached 10 m per yr^{-1} along some segments. Inputs of sediment and particulate organic carbon (POC) from coastal erosion are currently entering the Arctic ocean at rates ~430 Tg yr^{-1} sediment and 4.9–14 Tg yr^{-1} POC (Fritz et al., 2017). Coastal erosion is most severe along the shallow coasts of the Laptev, East Siberian and Beaufort Seas (Lantuit et al., 2012), but increased turbidity from melting ice can also be pronounced near the heads of Arctic fjords (Bartsch et al., 2016) and in areas receiving glacial discharge (Traiger and Konar, 2018).

Increased turbidity and reduced salinity is expected to reduce the performance and lower depth limit of kelp by reducing light penetration and restricting photosynthesis (Aumack et al., 2007; Fredersdorf et al., 2009; Spurkland and Iken, 2011; Wiencke and Amsler, 2012; Traiger and Konar, 2018) (Fig. 6). Variable salinity reduced photosynthetic efficiency of *L. solidungula, S. dermatodea*, *L. digitata*, *A. esculenta* and *S. latissima* (Karsten, 2007). Laboratory experiments on kelps collected from Svalbard, Norway found that sediment from melting ice negatively impacted their recruitment (Zacher et al., 2016). Manipulative field experiments on kelp forests in Alaska showed that glacier run-off reduced kelp settlement and recruitment by increasing sedimentation in the coastal zone (Traiger and Konar, 2018). Research from Kola bay and anecdotal reports from areas along the Siberian shelf in Russia describe declines in the lower depth limit of kelp forests due to low transparency of water (< 3 m visibility) caused by domestic pollution, sediment plumes and agricultural run-off (Malavenda and Malavenda, 2012). These negative impacts may offset the possible positive effects of warming and increased light on kelp growth in some Arctic regions. This was evident in the Beaufort Sea, where long-term records of annual growth of *L. solidungula* showed no change in productivity since 1979, despite earlier sea ice break-up and a longer ice-free period in recent years (Bonsell and Dunton, 2018). This pattern was explained by increasing resuspension of sediment and larger coastal erosion following sea ice break-up, which counter balanced the positive effect of longer ice-free periods.

5.4. Nutrients

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

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

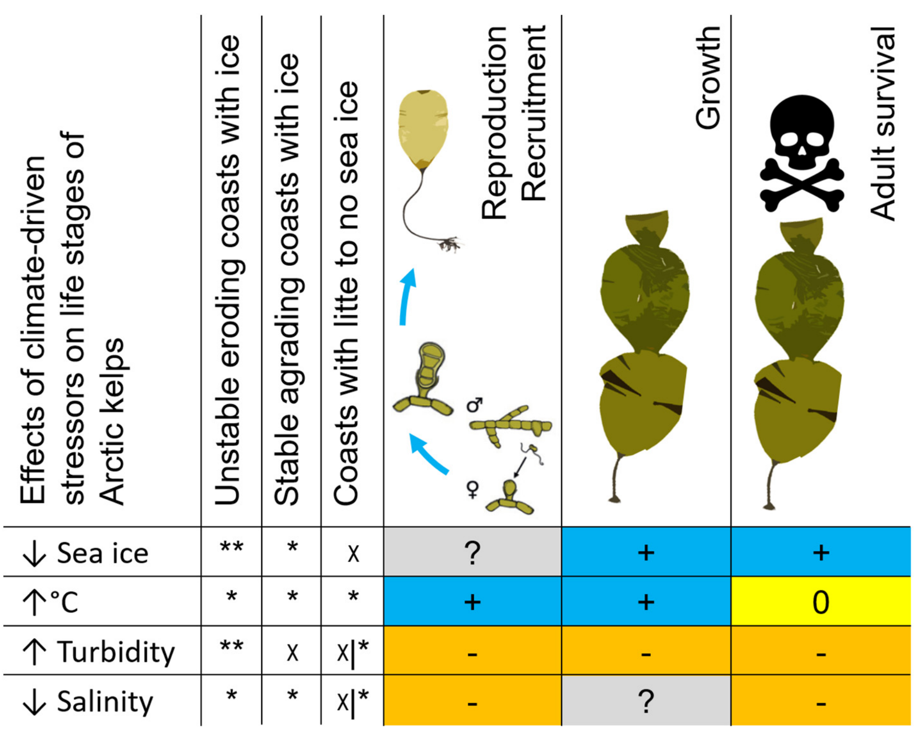

Fig. 6. Effects of environmental changes on arctic kelps from laboratory and field experiments. + is positive, − negative, 0 is no measurable effect, and? is unknown. Relative importance of stressors for 3 different coastal regions (see Fig. 2): ** = strong impact, * = moderate impact, and 'x' little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

stimulated by increased nutrient levels.

It is important to note that pelagic phytoplankton are more stimulated by increasing nutrient and light levels compared to benthic algae. Estimates predict thus that the pelagic production by phytoplankton in some Arctic waters will increase 3-fold within this century due to longer ice-free periods and increased run-off from land (e.g., Rysgaard and Glud, 2007). This significant increase in phytoplankton biomass and productivity will decrease light penetration in the water column, which will negatively affect kelp biomass and depth limit, possibly offsetting any benefits that higher nutrient levels could have on some kelp species.

5.5. UV radiation

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

6. Predicting changes to distribution of arctic kelps

Predicting changes to arctic kelps under rapidly changing environmental conditions remains challenging. Assis et al. (2018) developed models that described the current distributions of *A. esculenta, L. solidungula, L. digitata, L. hyperborea, S. latissima,* and *S. dermatoada* in the northern Atlantic according to environmental parameters (mainly sea temperature, sea ice, salinity, upwelling), and used these relationships to predict the impacts of climate change on their future distribution. These models predicted large northward expansions of these species, including the expansion of *L. hyperborea* to Svalbard, Norway, and further into the White Sea, the spread of *S. dermatoada* and *L. digitata* (or *S. nigripes* depending on source, S. Fredriksen personal communication) along the northeastern coast of Greenland, and the expansion of *A. esculenta* into the Canadian high Arctic. The models also predicted *L. solidungula* and *S. latissima* would extend northward to cover the northernmost coasts of Greenland, Russia and Canada, suggesting that all Arctic coasts would have environmental conditions suitable for kelp forests in the future. Similar range expansions have been predicted for *L. solidungula* and *S. latissima* with models by Müller et al. (2009) and for a number of fucoid species by Jueterbock et al. (2013, 2016). However, there is a discrepancy between these predictive models and long-term field observations of changes to arctic kelps. In Canada, Adey and Hayek (2011) were unable to identify significant shifts in the distributions of subtidal algal species in the eastern subarctic or boreal regions over the past 40 years. Likewise, Merzouk and Johnson (2011) reviewed the distribution of kelp along the northwest Atlantic shores from records dating back to the 1950s and were unable to document any significant change in dominant kelp species composition or abundance over that period, despite increasing sea temperature, although, the lack of sufficient spatially and temporally extensive datasets for this region prevented them from concluding that no change had occurred. Northward range expansions of kelps may be limited by extensive gaps between suitable substrate (e.g., from northern Norway to Svalbard) and low dispersal potential of kelps (Wernberg et al., 2019). It is also possible that the spread and performance of kelps may be more influenced by changes in turbidity, sea ice cover, and light penetration compared to relatively small changes in sea temperatures. This suggests that model predictions may overestimate northern range expansions of kelps, at least in the short-term.

7. Conclusions

The Arctic is at the epicenter of the global climate crisis, and emerging opportunities and developments have increased international attention on changes to ecosystems in this area. Long-term research from Greenland and Norway suggests a warmer Arctic with less sea ice may support higher kelp productivity and biomass and expand the northern range and lower depth limit of these species. However, the degree to which these changes will positively affect kelps will vary regionally and depend on the extent that melting sea ice and permafrost increases turbidity in coastal areas, as well as the available substrate in the lower depth range (Bartsch et al. 2016; Bonsell and Dunton, 2018). Predictive models and laboratory experiments suggest the 'borealization' of arctic kelp forests will occur as temperatures warm, altering the species composition of existing cold and ice-adapted kelp communities in high Arctic regions. Although current predictions are highly uncertain, the possible expansion of kelp forests should provide new habitats for fish and other marine organisms, and a suite of valuable ecosystem services along Arctic coastlines. Interestingly, where data are available, kelp abundance appears relatively stable, suggesting these changes are occurring slower than predicted or are being buffered by other factors. Either way, anticipating these changes, and understanding these new ecosystems will be a key priority for northern communities.

Our understanding of kelp forests is rapidly expanding in many regions of the Arctic. However, baseline measures of the extent of kelp communities are missing in northern and eastern Canadian Arctic, Siberia, the east Greenland Shelf, and Russia. This lack of data is not unique to kelp ecosystems. Despite the fact that over 28% of the world's coastlines are found in the Arctic (Lantuit et al., 2012), they remain largely unstudied, which jeopardizes current strategies to protect or conserve arctic environments and will have consequences for northern communities that rely on them. Lack of data has already greatly hindered our ability to detect and understand the impacts of climate change on these and other ecosystems (e.g., Merzouk and Johnson, 2011). Exploring effects of ongoing and future climate changes will provide important insight on the stability of these ecosystems. Maintaining and augmenting current monitoring initiatives and time series data sets should be a priority. For kelp forests, understanding how these ecosystems influence the structure and function of coastal arctic food webs is an important focus for ongoing research. There is also a critical lack of knowledge on the contribution of kelp forests to carbon cycling in the Arctic. Filling in these gaps and strategically prioritizing research in areas of rapid environmental variation will enable us to more effectively understand and conserve these ecosystems.

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

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Appendix A. Supplementary data

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