Arctic kelp forests

Diversity, resilience and future

Filbee-Dexter, Karen; Wernberg, Thomas; Fredriksen, Stein ; Norderhaug, Kjell Magnus; Pedersen, Morten Foldager

Published in:
Global and Planetary Change

DOI:
10.1016/j.gloplacha.2018.09.005

Publication date:
2019

Document Version
Peer reviewed version

Citation for published version (APA):
Filbee-Dexter, K., Wernberg, T., Fredriksen, S., Norderhaug, K. M., & Pedersen, M. F. (2019). Arctic kelp forests: Diversity, resilience and future. *Global and Planetary Change*, *172*, 1-14. https://doi.org/10.1016/j.gloplacha.2018.09.005

Karen Filbee-Dexter, Thomas Wernberg, Stein Fredriksen, Kjell Magnus Norderhaug, Morten Foldager Pedersen. Arctic kelp forests: Diversity, resilience and future. Global and Planetary Change. Volume 172, 2019, pages 1-14, ISSN 0921-8181.

The article has been published in final form by Elsevier at
http://dx.doi.org/10.1016/j.gloplacha.2018.09.005

ARCTIC KELP FORESTS: DIVERSITY, RESILIENCE AND FUTURE.

Karen Filbee-Dexter[1], Thomas Wernberg[2,5], Stein Fredriksen[3], Kjell Magnus Norderhaug[4], Morten Foldager Pedersen[5]

1. Norwegian Institute for Water Research (NIVA), Gaustadalléen 21, 0349 Oslo, Norway
2. UWA Oceans Institute and School of Biological Sciences, University of Western Australia, Crawley 6009 WA, Australia
3. University of Oslo. Department of Biosciences, PO Box 1066 Blindern, N-0316 Oslo, Norway
4. Institute of Marine Research, Nye Flødevigveien 20, NO-4817 His, Norway
5. Department of Science and Environment (DSE), Roskilde University, DK-4000 Roskilde, Denmark.

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 kelp 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.

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

1.1. 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 it 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; Kortsch et al. 2015).

Kelp are large brown seaweeds that occur on rocky coasts throughout the Arctic (Wernberg et al. 2018). 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. 2018), 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.

1.2. HIDDEN BLUE FORESTS OF THE ARCTIC

1.2.1. 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.

1.2.2. Distribution, growth forms and evolution of arctic kelps

Although kelps range along most Arctic coasts, sparse records of kelp 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 kelp. 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. 2018). 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 ~8,000 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.

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).

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

1.2.1. 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-hour 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 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 C 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.

1.3. 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 kelp in subarctic and Arctic seas we compiled records of kelp 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 100s of km^2 of kelp forests to small patches of kelp 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 kelp 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.

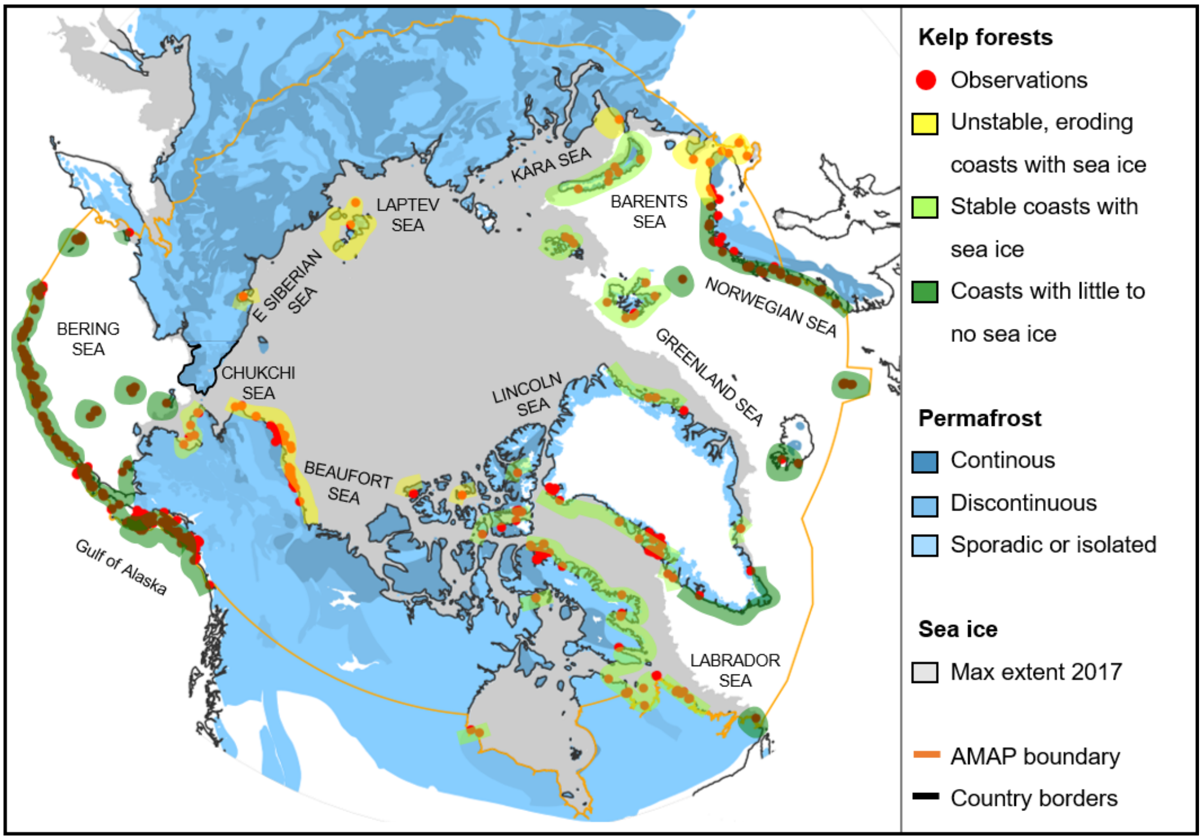


Fig. 2. Kelp locations (red) within AMAP Arctic boundary line (orange). Gray shading shows maximum sea ice extent, blue shading shows continuous permafrost (90 - 100 % cover), discontinuous permafrost (50-90 %), and sporadic and isolated patches of permafrost (< 50 %) (2016 National Snow and Ice Data 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).

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.

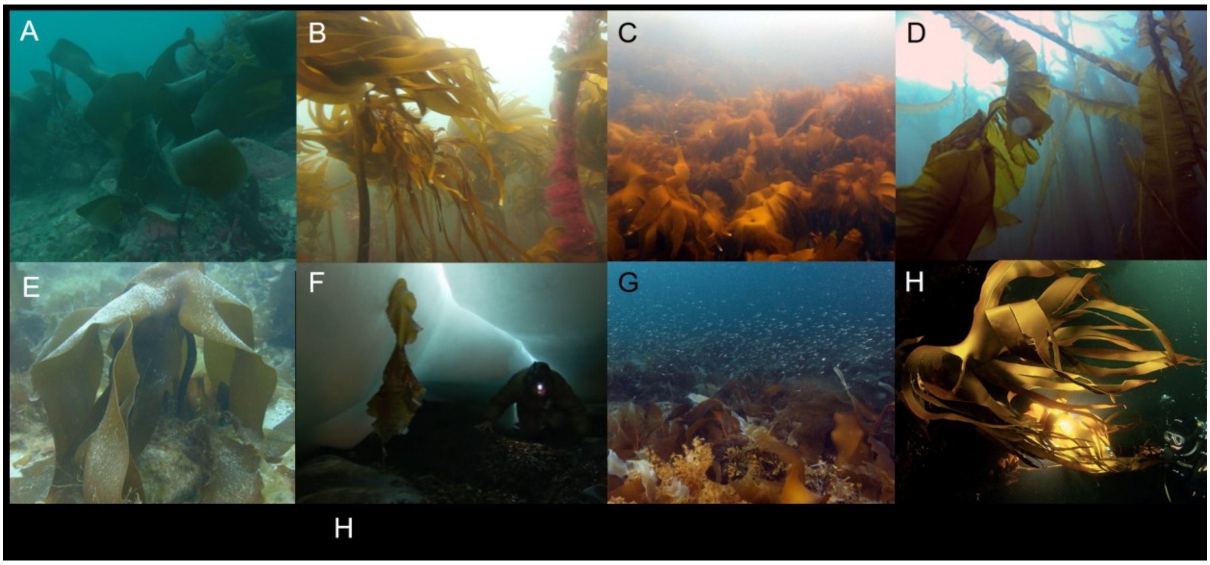


Fig 3. Photographs show examples of arctic kelp forests: (A) *Laminaria solidungula* in the Beaufort Sea, Alaska, USA (Ken Dunton), (B and C) *Laminaria hyperborea* in Malangen fjord, Norway (Thomas Wernberg, Karen Filbee-Dexter), (D) *Eularia fistulosa* Aleutian Islands, Alaska (Pike Spector), (E) *Saccharina 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* along the Murmansk coast, Russia (Dalnie Zelentsy).

1.3.1 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. 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; Cooper et al. 1998; Bartsch et al. 2016; Fig 3fh). 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).

1.3.2. 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 'uniquely Arctic conditions' such as extensive sea ice scour, long periods of darkness, variable salinity, turbidity, and low temperatures (Wilce 2016). The associated macroalgal communities in 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 – 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.

In northeastern Russia, observations of kelp are limited to a handful of records along these sedimentary coasts, 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).

1.3.3. 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 3bcd). 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 influenced by the density of herbivorous sea urchins, which 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, *Laminaria hyperborea* dominates the exposed coasts (Fig 3bc, 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 the distribution of kelp 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 *Eualaria fistulosa* and *Nereocystis luetkeana* and subsurface kelps (*Agarum clathratum, Alaria esculenta, Costaria costada, Laminaria digitata,* and *Saccharina latissima*) form forests along the Aleutian Island chain, the northern Gulf of Alaska coast and the northeastern coast of Russia. *Eularia 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 protection of sea otters enabled their populations to rebound (Estes et al. 1978). The recovered kelp forests (*Eualaria fistulos* and *Laminaria* spp.) were maintained for decades, until otter populations declined again due to predation by killer whales in the 1990s (Doroff et al. 2003; Estes et al. 2004), once again limiting kelp forests to exposed areas and shallow depths, which serves as refuges from grazing (Konar and Estes 2003).

1.4. ECOSYSTEM SERVICES PROVIDED BY ARCTIC KELP

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 *Strongylocentrotus 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). Clear 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 to 75% to rock greenling, predatory sea stars, and cormorants in the Aleutian Islands (Duggin et al. 1989), 0 to 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, Krause-Jensen et al. (2007) showed that 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 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 sequestered in ocean sediments than kelp carbon produced at lower latitudes.

1.5. 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).

1.5.1. Temperature

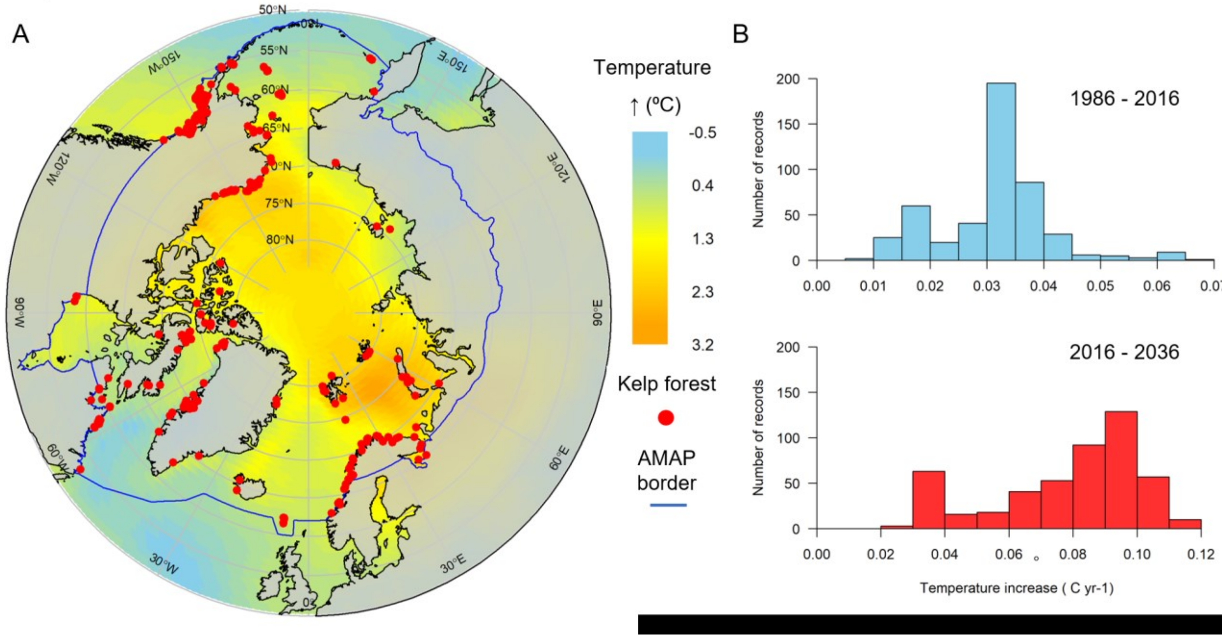
Temperatures in the Arctic are projected to increase by 3 – 4°C by the end of the 21st Century under realistic warming scenarios (IPCC 2014; Huang et al. 2017). Currently, kelps in Arctic waters experience low temperatures with little seasonal variation. Water temperatures rarely exceed 5°C in summer 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 to 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 to 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 ranges from 16°C 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) (Table 2). 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 *Eualaria 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).

[redacted]



[redacted]

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.

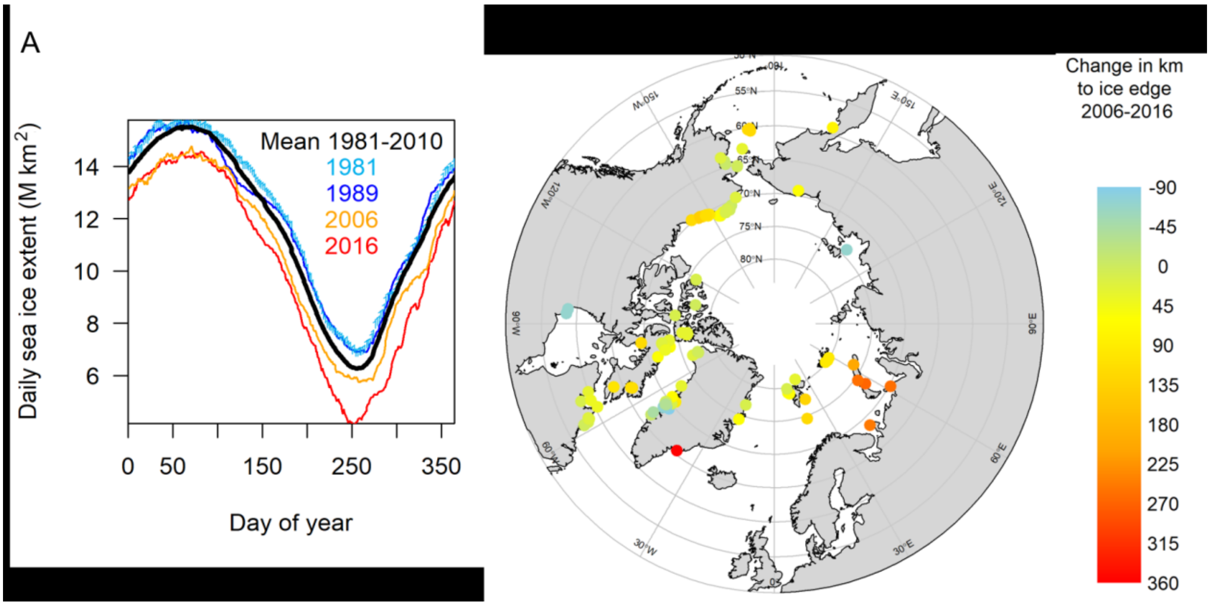
1.5.2. Sea ice and light

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 *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).



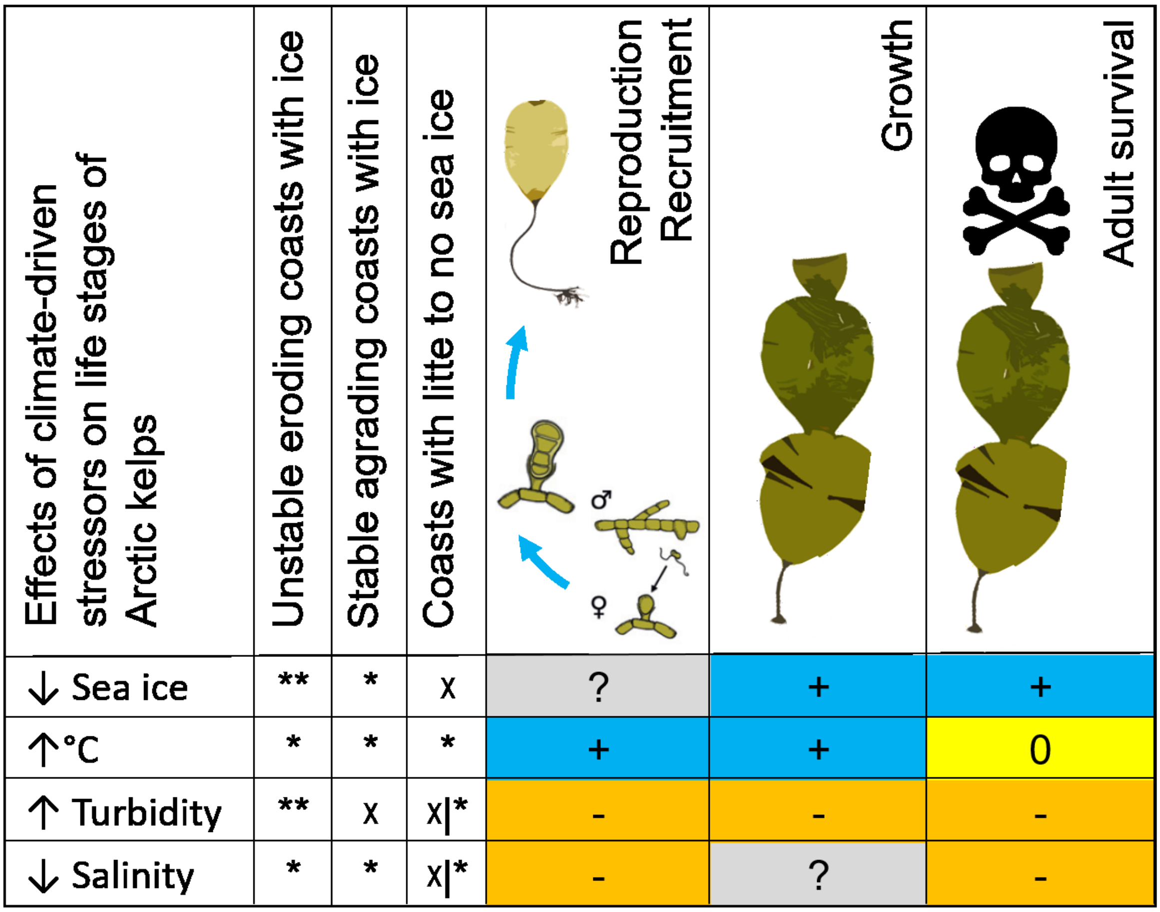
[redacted]

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.

1.5.3. 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 and found 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* kelps 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.



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

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.

1.5.4. 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 therefore 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*, decreases significantly in early spring as nutrient concentrations drop (Chapman and Lindley 1980; Dunton et al. 1982). This suggests that some kelp species and/or kelps in certain extremely nutrient poor areas can be limited by low nutrient availability, and therefore would be 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.

1.5.5. 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 Svaldbard 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 *A. esculenta* could tolerate a range of UV conditions.

1.6. 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 *Alaria 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 & 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. 2018). 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.

1.7. 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. 2017; 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.

Acknowledgements. This work was funded by the Norwegian Research Council through the KELPEX project (NRC grant no. 255085/E40). In addition, TW received funding from The Australian Research Council (DP170100023). We are grateful for comments from Eva Ramirez Llodra.

REFERENCES

Abdullah MI, Fredriksen S, Christie H (2017) The impact of the kelp (Laminaria hyperborea) forest on the organic matter content in sediment of the west coast of Norway. Mar Biol Res 0:1–10 . doi: 10.1080/17451000.2016.1240369

Acosta Navarro JC, Varma V, Riipinen I, et al (2016) Amplification of Arctic warming by past air pollution reductions in Europe. Nat Geosci 9:277–281 . doi: 10.1038/ngeo2673

Adey WH, Hayek L-AC (2011) Elucidating marine biogeography with macrophytes: quantitative analysis of the North Atlantic supports the thermogeographic model and demonstrates a distinct subarctic Region in the Northwestern Atlantic. Northeast Nat 18:1–128 . doi: 10.1656/045.018.m801

AMAP (1998) Physical/Geographical Characteristics of the Arctic. In: AMAP assessment report: Arctic pollution issues. Arctic Monitoring and Assessment Programme (AMAP), Oslo, pp 9–24

AMAP (2017) Snow, Water, Ice and Permafrost in the Arctic (SWIPA) 2017. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway. Oslo

Arctic Monitoring and Assessment Programme. (2011) Snow, water, ice and permafrost in the arctic (SWIPA) : climate change and the cryosphere. AMAP

Assis J, Araújo MB, Serrão EA (2018) Projected climate changes threaten ancient refugia of kelp forests in the North Atlantic. Glob Chang Biol 24:e55–e66 . doi: 10.1111/gcb.13818

Aumack CF, Dunton KH, Burd AB, et al (2007) Linking light attenuation and suspended sediment loading to benthic productivity within an arctic kelp-bed community. J Phycol 43:853–863 . doi: 10.1111/j.1529-8817.2007.00383.x

Bartsch I, Paar M, Fredriksen S, et al (2016) Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996-1998 and 2012-2014 reflect Arctic warming. Polar Biol 39:2021–2036 . doi: 10.1007/s00300-015-1870-1

Boertmann D, Mosbech A, Schiedek D, Dünweber M (2013) Disko West : a strategic environmental impact assessment of hydrocarbon activities. Aarhus University, DCE - Danish Centre for Environment and Energy

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

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

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

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

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

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

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

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

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

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

Coupel P, Ruiz-Pino D, Sicre MA, et al (2015) The impact of freshening on phytoplankton production in the Pacific Arctic Ocean. Prog Oceanogr 131:113–125 . doi: 10.1016/J.POCEAN.2014.12.003

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Nordenskiøld A (1880) Vegas fård kring Asien och Europa jemte en historisk å terblick på føregående resor længs Gamla Verldens nordkust. F & G Beijers Førlag, Stockholm

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

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

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

014-9355-9

Phillips RL, Reiss TE (1985) Nearshore marine geologic investigations, Point Barrow to Skull Cliff, northeast Chukchi Sea. Menlo Park

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

Plotkin AS, Railkin AI, Gerasimova EI, et al (2005) Subtidal underwater rock communities of the White Sea: Structure and interaction with bottom flow. Russ J Mar Biol 31:335–343 . doi: 10.1007/s11179-006-0001-9

Pueschel CM, Korb RE (2001) Storage of nitrogen in the form of protein bodies in the kelp *Laminaria solidungula*. Mar Ecol Prog Ser 218:107–114 . doi: 10.3354/meps218107

Reedy K, Katherine (2016) Kelp-Fed Beef, Swimming Caribou, Feral Reindeer, and Their Hunters: Island Mammals in a Marine Economy. Sustainability 8:113 . doi: 10.3390/su8020113

Renaud PE, Løkken TS, Jørgensen LL, et al (2015) Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. Front Mar Sci 2:31 . doi: 10.3389/fmars.2015.00031

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

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

Rosenvinge LK (1893) Grønland havalger. Meddr. Grønland 3:763–981

Rosenvinge LK (1899) Deuxième mémoire sur les algues marines du groenland. Reitzel, København

Rysgaard S, Glud RN (2007) Carbon cycling and climate change: Predictions for a High Arctic marine ecosystem (Young Sound, NE Greenland). In: Rysgaard S, Glud RN (eds) Carbon cycling in Arctic marine ecosystems: Case study Young Sound. Bioscience, Meddr, pp 206–214

Sharp G, Allard M, Lewis A, et al (2008) The potential for seaweed resource development in subarctic Canada; Nunavik, Ungava Bay. J Appl Phycol 20:491–498 . doi: 10.1007/s10811-008-9323-7

Shoshina E, Makarov V, Makarov M (1997) Biological features of laminarians of Frantz Josef Land.

Biol morya 5:286–292.

Shoshina E, Anisimova N (2013) Makrovodorosli iz rayona buhty Ledyanaya Gavan (Novaya Zemlya, o. Severnyi, Karskoe more) [Seaweeds from Ledjanaya Haven Inlet (Novaya Zemlja, Northern Island, Kara Sea)]. Vestn MGTU 16:530–535

Shoshina E V, Kapkov VI, Belenikina OA (2016) Ecological factors regulating growth of seaweeds in Arctic communities. Вестник МГТУ 19:334–344

Sjøtun K, Schoschina E V. (2002) Gametophytic development of Laminaria spp. (Laminariales, Phaeophyta) at low temperature. Phycologia 41:147–152 . doi: 10.2216/i0031-8884-41-2-147.1

Spurkland T, Iken K (2011) Kelp bed dynamics in estuarine environments in subarctic alaska. J Coast Res 275:133–143 . doi: 10.2112/JCOASTRES-D-10-00194.1

SRES (2000) IPCC special report: Summary for policymakers emissions scenarios

Stige LC, Kvile KØ (2017) Climate warming drives large-scale changes in ecosystem function. Proc Natl Acad Sci U S A 114:12100–12102 . doi: 10.1073/pnas.1717090114

Sundene o (1962) The implications of transplant and culture experiments on the growth and distribution of Alaria esculenta. Nytt Mag Bot 9:155–174.

Svendsen P (1959) The algal vegetation of Spitsbergen a survey of the marine algal flora of the outer part of isfjorden. Nor Polarinst Skr 116:1–49

Taylor WR (1954) Algae: Non-Planktonic. Bot. Rev. 20:363–399

Teagle HA, Hawkins SJ, Moore P., Smale DA (2017) The role of kelp species as biogenic habitat formers in coastal marine ecosystems. J Exp Mar Bio Ecol 492:81–98 . doi: 10.1016/J.JEMBE.2017.01.017

Traiger SB, Konar B (2018) Mature and developing kelp bed community composition in a glacial estuary. J Exp Mar Bio Ecol 501:26–35 . doi: 10.1016/J.JEMBE.2017.12.016

van Leeuwe MA, Tedesco L, Arrigo KR, et al (2018) Microalgal community structure and primary production in Arctic and Antarctic sea ice: A synthesis. Elem Sci Anth 6: . doi: 10.1525/elementa.267

von Biela VR, Newsome SD, Bodkin JL, et al (2016) Widespread kelp-derived carbon in pelagic and benthic nearshore fishes suggested by stable isotope analysis. Estuar Coast Shelf Sci 181:364–

374 . doi: 10.1016/J.ECSS.2016.08.039

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

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

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

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

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

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

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

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

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

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

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

Wilce RT (2016) The "Arctic Stamp", its imprint on an endangered marine flora. Perspect Phycol

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

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

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

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

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

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

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

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

Table 1/S1. Species composition, depth limit and biomass (wet weight per m^2) of Arctic kelp forests. Bolded names indicate dominant species. (-) is not reported.

Location	**Site**	**Year Sampled**	**Depth limit (m)**	**Species**	**Latitude, Long**	**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 2013)
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 2013)
Labrador sea	South Cove	2003	30	*A. clathratum A. esculenta S. dermatodeaS. latissima* ***S. longicruris***	53.2167, -55.6333	4109.8	(Adey and Hayek 2013)
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 2013)
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[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	Uummannaq	2009	33	*A. clathratum S. latissima*	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	*A. clathratum A. esculenta S. longicruris*	64.1333, -51.6167	18.0 ± 1.1[1]	(Krause-Jensen et al. 2012)
Labrador sea	Eqip Sermia	2009	27	*A. clathratum S. latissima*	69.7500, -50.3500	12.6 ± 2.8[1]	(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 (NIVA report))
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	21976.0 ± 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)
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*** *L.* 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*** *L.* 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[2]	(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[2]	(Konar et al. 2017)
Aleutian Islands	Adak I	1987	30	***E. fistulosa*** *Laminaria* spp.	51.6102,-177.0966	2920 ± 1810	(Duggins et al. 1989)
	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	12645 ± 4999	(Wilmers et al. 2012)

Aleutian Islands	Ogliuga I	-	*A. cribosum*, ***E. fistulosa***, ***Laminaria*** **spp.**	52.0563,177.4398	12645 ± 4999	(Wilmers et al. 2012)

[1] Dry weight. [2] SE of dominant species *E. fistulosa*