Sea ice and substratum shape extensive kelp forests in the Canadian Arctic

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26   **Abstract**

27   The coastal zone of the Canadian Arctic represents 10% of the world's coastline and is one of the most
28   rapidly changing marine regions on the planet. To predict the consequences of these environmental
29   changes, a better understanding of how environmental gradients shape coastal habitat structure in this
30   area is required. We quantified the abundance and diversity of canopy forming seaweeds throughout
31   the nearshore zone (5 - 15 m) of the Eastern Canadian Arctic using diving surveys and benthic

32 collections at 55 sites distributed over 3000 km of coastline. Kelp forests were found throughout,
33 covering on average 40.4 % (± 29.9 SD) of the seafloor across all sites and depths, despite thick sea
34 ice and scarce hard substrata in some areas. Total standing macroalgal biomass ranged from 0 to 32 kg
35 m^{-2} WW and averaged 3.7 kg m^{-2} (± 3.2 SD) across all sites and depths. Kelps were less abundant at
36 depths of 5 m compared to 10 or 15 m and distinct regional assemblages were related to sea ice cover,
37 substratum type, and nutrient availability. The most common community configuration was a mixed
38 assemblage of four species: *Agarum clathratum* (14.9% ± 12.0 SD), *Saccharina latissima* (13% cover
39 ± 14.7 SD)*, Alaria esculenta* (5.4% ± 1.2 SD), and *Laminaria solidungula* (3.7% ± 4.9 SD). *A.
40 clathratum* dominated northernmost regions and *S. latissima* and *L. solidungula* occurred at high
41 abundance in regions with more open water days. In southeastern areas along the coast of northern
42 Labrador, the coastal zone was mainly sea urchin barrens, with little vegetation. We found positive
43 relationships between open water days (e.g., without sea ice) and kelp biomass and diversity,
44 suggesting kelp forests could increase, and their species composition could shift, as sea ice diminishes
45 in some areas of the Eastern Canadian Arctic. Our findings demonstrate the high potential productivity
46 of this extensive coastal zone and highlight the need to better understand the ecology of these systems
47 and the services they provide.

48 **Introduction**

49   Kelp forests are created by canopy-forming seaweeds of the order Laminariales and dominate
50 cool-temperate and subarctic coasts (Steneck et al., 2002; Wernberg et al., 2019). These marine habitats
51 play an important role in coastal ecosystem functioning, and are declining in many regions globally
52 (Duarte et al., 2021; Krause-Jensen et al., 2018; Wernberg et al., 2019) due to a variety of drivers,
53 including increased temperatures, overgrazing by sea urchins and overharvesting (Filbee-Dexter and
54 Wernberg, 2018; Rogers-Bennett and Catton, 2019; Smale, 2020). Kelp forests in the Arctic are
55 frequently underrepresented in overviews of these ecosystems and are not always considered in
56 assessments of global change (Krause-Jensen et al., 2020; Starko et al., 2021). This is a remarkable
57 omission considering that Arctic coasts make up a third of the world's coastlines (Lantuit et al., 2012)
58 and have extensive benthic areas where light levels can sustain benthic primary production (20% of
59 the continental shelves < 20 m) (Gattuso et al., 2006). Despite sea ice, cold temperatures and long
60 periods with little to no daylight, these shallow areas can support lush marine vegetation such as kelps
61 and other seaweeds when they receive enough light and suitable substrate occurs (Filbee-Dexter et al.,
62 2019b; Wiencke and Amsler, 2012).

63   The Arctic is experiencing dramatic environmental changes, which are driving shifts in marine
64 ecosystems (Bryndum-Buchholz et al., 2020; Pecuchet et al., 2020). The entire region is an ocean
65 warming hotspot with temperatures increasing 2–4 times faster than the global average (IPCC, 2019;
66 Meredith et al., 2020). Sea ice cover is becoming thinner and starting to break up earlier, reaching
67 historic lows in the last decade (Cavalieri et al., 2020). The coastal zone is also the main recipient of
68 increasing sediment fluxes from thawing permafrost and eroding continental shelves (Fritz et al., 2017;
69 Lantuit et al., 2012), as well as increasing freshwater inputs from strong river discharge (Rood et al.,
70 2017) and glacier melt (Van Wychen et al., 2020). Overall, these environmental changes are predicted
71 to drive borealization (i.e., the northward shift of temperate species with warming), which includes
72 'Arctic greening' as plants expand northward with land ice and sea ice retreat (Krause-Jensen and
73 Duarte, 2014; Myers-Smith et al., 2020).

74   In the Arctic nearshore, sea ice cover and extreme environmental conditions can restrict both
75 the abundance and productivity of seaweeds (Filbee-Dexter et al., 2019b; Krause-Jensen et al., 2012;
76 Lee, 1980). Sea ice restricts the upper limits of seaweeds by mechanical abrasion and restricts the lower

depth limits by light shading (Filbee-Dexter et al., 2019b; Wilce, 2016). A warmer Arctic with less sea ice is thus predicted to support larger, more productive kelp forests and extend the northern distributions of many kelp species (Bartsch et al., 2016; Krause-Jensen et al., 2012; Krause-Jensen and Duarte, 2014). Ocean warming is also predicted to make Arctic coasts better suited for kelps, because many species originate from the North Atlantic or Pacific oceans, and in the Arctic occur below their thermal optimum (Wiencke and Clayton, 2011; Wulff et al., 2011). However, northern refugia do exist, and some kelp species appear to have adapted to Arctic environments (Bringloe et al., 2020). Despite these predictions, the degree to which these changes will positively affect kelps will likely vary regionally and depends on both the kelp species in question and the extent that melting sea ice, glacial melt, and permafrost erosion increase turbidity and freshening in coastal areas, all of which limit seaweeds (Bartsch et al., 2016; Bonsell and Dunton, 2018; Traiger and Konar, 2018). Currently, a pan-Arctic review of existing long-term monitoring and field studies on vegetative marine ecosystems shows a trend of increasing abundance in response to climate change, but limited direct evidence of range expansions (Krause-Jensen et al. 2020). Knowledge of the abundance and distribution of kelp forests across a range of environmental conditions found in Arctic regions can provide insights on the future of these important ecosystems.

The current knowledge of kelp forests in the Eastern Canadian Arctic is based on diving research at a few sites (e.g., Chapman and Lindley, 1980; Cross et al., 1987; Sharp et al., 2008), occurrence data (Bringloe et al. in press; Starko et al., 2021), and historical records of algal diversity (Lee, 1980). The region is biodiverse with 210 species of macroalgae reported (Archambault et al., 2010). However, most of the vast coastal zone is inaccessible because shore-based infrastructure and access (roads) are rare and use of large research vessels is limited by the shallow waters. The Canadian Arctic is also colder than most other Arctic regions, largely due to the outflow of Arctic Ocean waters along the Canadian Archipelago and eastern shelf and into the North Atlantic (Michel et al., 2015). The shallow nearshore (depths of 0 to 5 m) in the Canadian High Arctic is often described as barren, scoured heavily by sea ice with few sessile invertebrates and little to no subtidal vegetation (Renaud et al., 2021; Wilce, 2016). Early phycologists and polar explorers reported some deeper subtidal areas with lush seaweeds, which typically became smaller and more fragmented from the east to the west and did not form extensive forests due to limited rocky substrata (Lee 1971). Broader characterizations of patterns of the abundance, extent and structure of coastal vegetated habitats in this region are lacking (Filbee-Dexter et al., 2019b; Wilce, 2016).

The objective of this study was to expand substantially our knowledge of kelp distribution, abundance, and biodiversity in the Eastern Canadian Arctic. To do so, we surveyed 55 sites, distributed across 3000 km of linear coastline and 9 distinct regions throughout the Eastern Canadian Arctic between 2011 and 2020, to quantify the abundance and diversity of kelp and other seaweeds. We asked the following research questions: 1) What is the extent and species composition of kelp forests in the Eastern Canadian Arctic? 2) Do kelp forests differ across distinct ecological regions in the study area? 3) How is the abundance of kelp influenced by environmental conditions, particularly gradients in sea ice and ocean temperature?

Methods

Study area

The 55 sites fell within 9 distinct geographic regions in the Eastern Canadian Arctic (Figure 1). We defined these regional groupings *a priori* based on Spalding et al.'s (2007) ecoregions, but further divided Eclipse Sound (North Baffin Island) from Baffin Bay, and separated Hudson Bay into 4 regions

121 (Roes Welcome Sound, Hudson Strait, Foxe Basin, and Hudson Bay) using previously published
122 biogeographical and oceanographic information for the area (Adey and Hayek, 2011; Bell and Brown,
123 2018; Brown et al., 2018). We made these further subdivisions to ensure regions captured differences
124 between mid Baffin Island and northern Eclipse Sound and across the complex range of environmental
125 conditions and mixing water bodies within Hudson Bay. These known geographic and environmental
126 boundaries (e.g., range discontinuities, dominant habitats, geomorphological features, currents and sea
127 temperatures) provide a solid basis against which to explore regional trends and test the impacts of
128 targeted environmental variables known to be important for kelp species.

129 *Extent and species composition of kelp forests*

130 At all sites (Figure 1 and Table S1), we obtained kelp cover estimates from videos or
131 photographs of the seafloor and canopy. At a subset of study sites, we collected additional measures of
132 the biomass of seaweeds. Data obtained from all sites were percent cover, but sampling methods varied
133 slightly across campaigns, depending on access and equipment (Table S1). Specifically, Ellesmere
134 Island was sampled by divers and video transects from the sailboat *Vagabond* in 2020. Northern Baffin
135 Island was sampled by divers from a small fishing vessel in 2019. Southampton Island (Foxe Basin,
136 Roes Welcome Sound and Hudson Bay) was sampled by divers using an inflatable boat deployed off
137 the *R.V. William Kennedy* in 2019. Sites in Baffin Bay and northern Labrador were sampled by divers
138 using an inflatable boat deployed off the *M.S. Cape Race* in 2014. Pangnirtung (Davis Strait) was
139 sampled by researchers from a fishing vessel in 2019 (Cumberland Sound Ecosystem Survey). The
140 Steensby Inlet (Foxe Basin), Deception Bay (Hudson Strait), Iqaluit (Davis Strait), and Churchill
141 (Hudson Bay) sites were sampled by divers from small locally sourced vessels in 2011 and 2012
142 (Fisheries and Oceans Canada - DFO, Canadian Aquatic Invasive Species Network - CAISN) (Table
143 S1).

144 At the four sites in Ellesmere Island, the six sites in northern Baffin Island and the 13 sites in
145 Southampton Island, divers laid one 30 m transect along 5, 10 and (at some sites) the 15 m depth
146 contours (Table S1). Along these transects, eight 1x1 m quadrats were haphazardly placed and
147 photographed. At each of the sites in Baffin Bay, Davis Strait and northern Labrador, divers laid one
148 30 m transect along the 5, 10, and if kelp was still present below this, the 15 m depth contours. The
149 transect in these regions consisted of divers swimming ~1 m above the canopy videoing the seafloor.
150 A similar protocol was followed for the DFO-CAISN sites (in Steensby Inlet, Deception Bay, Iqaluit
151 and Churchill), except transects were 50-m long and covered a range of depths (see starting and end
152 depths in Table S1). For Pangnirtung, photographs from 10 and 15 m were taken using a drop camera
153 deployed multiple times from a small vessel at each depth. Photographs were analyzed for percent
154 cover of all kelp species and other macroalgae using ImageJ (Schindelin et al., 2012). Video transects
155 were analyzed by taking frame grabs (10 – 12 per transect) at regularly spaced intervals along the video
156 (every ~20 – 30 s depending on total video time). Only high-quality images with a clear view of the
157 canopy or substratum were used. In ImageJ, we overlaid 48-50 points over each image and identified
158 the seaweeds (or substratum) under each point and calculated percent covers (point count method).
159 Seaweeds were separated into kelp species (*Agarum clathratum, Alaria esculenta, Hedophyllum*
160 *nigripes, Laminaria digitata, Laminaria solidungula, Saccharina latissima*)*, Saccorhiza dermatodea*,
161 *Desmarestia spp.*, *Palmeria palmata*, fucoids, fleshy red algae and other non-canopy forming brown
162 fleshy and filamentous algae.

163 Seaweed biomass was also sampled at 31 of the 55 sites. At these sites, we collected all
164 macroalgae in four 0.25-m^2 quadrats, haphazardly placed approximately 5 m apart, placed them in
165 mesh bags and brought them to the ship or onshore to be processed. Plants were only collected if the

166 holdfast fell within the quadrat. Small turf algae (e.g., Filbee-Dexter and Wernberg, 2018) that could
167 not be collected using a scraper and mesh bag were not collected. All collected seaweeds were
168 identified to species or coarse macroalgal groups (red fleshy, non-canopy forming brown fleshy,
169 filamentous) and weighed wet. Excess water was removed from small filamentous seaweeds with a
170 paper towel. Total biomass of each macroalgal group was recorded for each quadrat, but in addition
171 each kelp individual was weighed to the nearest gram. For sites from Cape Race, we estimated biomass
172 from species density and individual sizes, using species-specific relationships between total length and
173 biomass that we calculated from our other sites. To obtain estimates of kelp biomass at each site, we
174 calculated the average kelp biomass for all sampling depths. For regional comparisons, averages were
175 calculated by averaging across sampled depths and then across all sites within a region.

176 For species identifications, we grouped *Laminaria digitata* and *Hedophyllum nigripes* because
177 we were not confident of specific identifications determined in the field. Recent research indicates
178 these two species cannot be distinguished using morphology alone (Dankworth et al., 2020). We
179 classified *Alaria* species as *A. esculenta* in this study. However, genetic analyses on *Alaria* collected
180 from Pond Inlet during this sampling campaign revealed this species to be a unique Arctic lineage of
181 *Alaria* (Bringloe et al. unpublished data), which was also difficult to distinguish using morphology, so
182 this *A. esculenta* grouping may be two species (*A. esculenta* and *A. grandifolia*).

183 **Patterns of seaweed assemblages across regions**

184 We examined patterns of kelp diversity using community characteristics (species richness,
185 Shannon diversity, Pielou evenness) calculated for each region from biomass data, averaged for each
186 of the 31 sites. Seaweed assemblage structure for all 55 percent cover sites and 31 biomass sites was
187 also examined with multivariate analyses. First, species-level percent cover data and biomass data were
188 analyzed with a three-factor hierarchical design (region, site, depth) using permutational multivariate
189 analysis of variance (PERMANOVA; Anderson, 2001), based on a Bray–Curtis similarity matrix
190 generated from square-root transformed data. The transformation was chosen to down weight the
191 influence of the most dominant species, because we were working with abundance data. We used type
192 III sums of squares to account for unbalanced design. Depth (5, 10, and 15 m) was a fixed factor nested
193 in the site, a random factor. To examine differences in assemblages between regions (which were of
194 specific interest and therefore a fixed factor), we examined multivariate variability within and between
195 regions (estimated from the mean squares of the hierarchical PERMANOVA). A PERMDISP test was
196 performed for each factor in the model to examine heterogeneity in multivariate dispersion between
197 groups. The statistical significance of multivariate variance components was tested using a maximum
198 of 9999 permutations.

199 Metric multidimensional scaling (mMDS) ordinations, based on the Bray–Curtis similarity
200 matrix, were generated to visualize multivariate patterns in seaweed assemblage composition among
201 regions and sites (averaged across depth). Because decisions to sample transects at 5- vs. 15-m depth
202 were often based on the substratum and presence of kelp in some regions, we also analyzed regional
203 averages from only the 10-m depth, which was consistently sampled, to see whether any depth
204 sampling bias affected overall interpretations. We further examined variation in assemblages between
205 sites and regions for all data from 10-m depth using mMDS ordinations to explore effects on overall
206 structure from the different sampling resolution at the three depths. All multivariate procedures
207 reported here were performed using Primer 7 with the PERMANOVA add-on (Anderson et al., 2008).

208 **Environmental drivers of seaweed assemblages**

209   Substrata were classified into bedrock, boulders, cobbles, pebbles, shells, and sand, using a
210   simplified version of the Wentworth scale. For sites sampled with photograph quadrats (percent cover
211   data), substratum type was recorded *in situ* by divers who visually estimated the percent of total
212   substratum that was bedrock, boulders, cobbles, pebbles, shell, and sand. For sites with only video
213   measures, substratum composition was estimated using the amount of visible seafloor in each frame.
214   For frames with 100% canopy cover and no visible sea floor (7.45% all frames), substratum type was
215   estimated from nearest sections of video. This method could, however, underestimate rock cover at
216   these sites, because it would be more likely to be covered by seaweed than sand. This concern was
217   unlikely to matter in regions with sparse kelp cover where the seafloor was visible and we found high
218   kelp cover on sand and pebbles substrata. The percentage of red encrusting coralline algae on rock was
219   also quantified by either divers or from underwater videos using the point count method. All estimates
220   from sites with videos were verified using dive logs describing substratum types from each transect.
221   For site level measures of substratum types, percent cover data were pooled across depth and averaged.

222   Other environmental layers with known relationships with seaweeds (Assis et al., 2018a;
223   Wiencke and Clayton, 2011) were obtained from BioORACLEv2.1 (Assis et al., 2018b). These
224   included average sea temperature, light intensity (PAR), salinity, open water days (percent of year with
225   <10% sea ice cover), sea ice thickness, phosphate and nitrate concentrations. We used estimates for
226   the seafloor (minimum depth of the cell surrounding each study site apart from ice cover, thickness,
227   and light par) using data from the nearest neighbouring points to each study site and from present day
228   conditions (2006 – 2018).

229   Spearman's rank correlations were used to examine relationships of ordination scores for kelp
230   species percent cover and biomass with abiotic variables (BIO-ENV analyses, PRIMER). The abiotic
231   variables tested were sea ice cover, sea ice thickness, salinity, light, open water days, nitrate, % sand,
232   and % rock (summed bedrock, boulder, cobble, pebble). Variables were examined with Draftman plots
233   to check for skewness and multi-collinearity. If collinearity was present, we used one of the variables
234   in the analysis. All abiotic variables were normalized before the algorithm was run.

235   We also examined relationships between abiotic variables and seaweed communities using
236   distance-based linear models (DistLM). To define the best fitted model, we used AICc and R^2 values.
237   DistLM models were coupled to a distance-based redundancy analysis (dbRDA; 999 permutations) to
238   explore these relationships. For DistLM models we partitioned bedrock, boulders, cobble, gravel and
239   pebbles into a single set of variables ('rock). This analysis was also performed for data only from 10-
240   m depth.

241   The relationships between specific abiotic variables of importance identified in BIO-ENV and
242   DistLM analyses, and the abundance of the most dominant kelp species were further explored using
243   generalized additive models (GAM) with a Gaussian error distribution. Specifically, we examined the
244   relationships between cover of *A. clathratum* and % cover of rock substrata, cover of *S. latissima* and
245   sea ice thickness (m), and total kelp cover and salinity, which were identified as predictor variables of
246   interest by the DistLM and dbRDA analyses. We performed these statistical analyses using R 4.1.0 (R
247   Core Team 2021).

248   **Results**

249   **Widespread and abundant: extent and species composition of arctic kelp forests**

250   Kelp forests were found throughout the Eastern Canadian Arctic, covering on average 40.4 %
251   ($\pm$ 29.9 SD) of the seafloor across all sites and depths and ranging from 5 to 61.7% average cover
252   across regions (Figure 2). The most common community configuration in each region was a mixed
253   assemblage composed of four dominant kelp species: *A. clathratum* (14.9% $\pm$ 12.0 SD), *S. latissima*
254   (13% $\pm$ 14.7 SD)*, A. esculenta* (5.4% $\pm$ 1.2 SD) and *L. solidungula* (3.7% $\pm$ 4.9 SD) (Figure 2, S1).
255   The regions Hudson Strait, Roes Welcome Sound and Davis Strait had the highest average kelp cover
256   (mean across sites and depths, 57.4%, 46.0% and 44.1%, respectively). *S. latissima* in these regions
257   had upright morphologies with floating hollow stipes (identified as *S. longicruris* in Greenland
258   (Krause-Jensen et al. 2012)). Ellesmere Island and Hudson Bay had the lowest average kelp cover
259   (7.9% and 5.0%, respectively) (Figure 2).

260   Total standing macroalgal biomass ranged from 0 to 14.6 kg m^{-2} and averaged 3.7 kg m^{-2} ($\pm$
261   3.2 SD) across all 31 sites. *S. latissima* and *L. solidungula* occurred at an average biomass ($\pm$ SD) of
262   1.2 $\pm$ 1.8 kg m^{-2} and 0.99 $\pm$ 2.0 kg m^{-2}, respectively. *H. nigripes* averaged 0.18 $\pm$ 0.57 kg m^{-2} and *A.*
263   *esculenta* 0.48 $\pm$ 1.2 kg m^{-2}. *A. clathratum* occurred at a biomass averaging 0.67 $\pm$ 0.69 kg m^{-2}, reached
264   a maximum of 2.5 kg m^{-2} in the Labrador Sea, and tended to form lower-lying canopies. The highest
265   average regional kelp biomass occurred in Foxe Basin, Roes Welcome Sound, and Davis Strait, while
266   the lowest regional biomass was in the Labrador Sea and Ellesmere Island (Figure 2, S2). Sites with
267   the largest kelp biomass were dominated by *S. latissima* and *L. solidungula*, which often formed dense
268   2 to 5 m high canopies. The maximum site-level biomass for *S. latissima* was 7.8 kg m^{-2} at a site in
269   Roes Welcome Sound and the maximum site-level biomass for *L. solidungula* was 10.5 kg m^{-2} in Foxe
270   Basin. At the quadrat scale, maximum biomass was 34.4 kg m^{-2} for *S. latissima*, 23.9 kg m^{-2} for *L.*
271   *solidungula*, 13.8 kg m^{-2} for *H. nigripes*, 18.5 kg m^{-2} for *A. esculenta* and 5.6 kg m^{-2} for *A. clathratum.*

272   **Patterns of seaweed abundance and diversity across regions**

273   We found support for the hypothesis that kelps were restricted in cover at shallow depths of 5
274   m compared to 10 or 15 m, despite site-level variation in dominant species and abundance among
275   depths in some areas (Figure S2). Total kelp cover and biomass increased from 5 to 15 m, often due to
276   larger sized individual kelps at deeper depths (Table 1, Figure 3, Figure S2 – S4). The average biomass
277   per area (based on mean for each depth at each site) of *S. latissima* was 2.9X higher at 10-15 m
278   compared to 5 m and that of *L. solidungula* was 1.7X higher at 10-15 m compared to 5 m. The largest
279   *S. latissima* plants (3.2 kg ind^{-1}) were collected from 15 m in Foxe Basin and Hudson Strait. The largest
280   *A. esculenta* plants (1.0, 1.0, 2.2 kg ind^{-1}) were collected from 15 m at three sites in Roes Welcome
281   Sound and Hudson Strait and the largest *L. solidungula* plants (1.4, 1.3, 1.6 kg) were found at 15 m in
282   Roes Welcome Sound and 15 and 10 m in Foxe Basin. The largest *A. clathratum* plants (0.6, 0.6, 0.7
283   kg ind^{-1}) were collected from North Baffin Island at 10 m (the lowest depth sampled in that region).

284   Community assemblages differed significantly among regions and depths with respect to both
285   cover and biomass (Table 1). A breakdown of the variance components for percent cover in the
286   PERMANOVA indicated that variability at the smallest scales of the residual (e.g., across quadrats)
287   (34.2%) and depth level (30.0%) were the major contributors to overall variability, compared to regions
288   (24.0%). Variance components for biomass (square-root transformed) indicated that variability at the
289   smallest scales of the residual (27.3%) contributed most to overall variability, compared to regions
290   (17.5%) and depths (17.0%). Significant differences in multivariate dispersion for percent cover of
291   kelp species were observed at the scale of depth ($F_{2,823} = 4.2$, $P = 0.042$), site ($F_{51,771} = 13.87$, $P = 0.001$)
292   and region ($F_{8,814} = 97.7$, $P = 0.001$) and for biomass of kelp species at the scale of depth ($F_{2,186} = 4.6$,
293   $P = 0.026$), site ($F_{30,158} = 5.11$, $P = 0.001$) and region ($F_{7,181} = 24.2$, $P = 0.001$). This variability in
294   multivariate dispersion at various spatial scales suggests that the significant PERMANOVA tests may

295 be either due to differences in species assemblages or to variation of species abundances at each of
296 these spatial scales. Although depth significantly influenced kelp assemblages, mMDS using site-level
297 percent cover and biomass data averaged across all depths, and site level data for just 10-m depth
298 (which was consistently sampled at each site), showed similar overall patterns in cover and biomass,
299 suggesting pooling across depths was appropriate to visualize similarities in kelp assemblages across
300 the Eastern Canadian Arctic (Figure S5).

301   A variety of kelp assemblages were found throughout the Eastern Canadian Arctic (Figure 1,
302 S1-S3). The highest species richness and diversity were found in Roes Welcome Sound and Foxe
303 Basin. The lowest values were found in Ellesmere Island and the Labrador Sea, where only *A.
304 clathratum* was present. Roes Welcome Sound, Foxe Basin, Hudson Strait and Davis Strait had the
305 most species per site (Table 2). *A. clathratum* was dominant in the Ellesmere, North Baffin Island,
306 Baffin Bay, and Labrador Sea regions and was often the sole kelp species at a site. *S. latissima* and *L.
307 solidungula* tended to co-exist and occurred at high biomass and cover at sites in Davis Strait, Foxe
308 Basin, and Roes Welcome Sound. Prostrate morphologies were observed in North Baffin Island and
309 Labrador Sea. *A. esculenta* occurred across most regions but was rarely the dominant canopy former
310 (apart from 1 site in Pangniqtuuq, Davis Strait) and instead was usually associated with other kelp
311 species, particularly *S. latissima* (Figure 2, Figures S1, S3). *S. latissima* reached highest abundances in
312 Davis Strait, Roes Welcome Sound and Foxe Basin. Two digitated kelp species, *H. nigripes* and *L.
313 digitata*, occurred at low abundances and were often associated with *S. latissima* and *L. solidungula*,
314 but at several sites in Roes Welcome Sound and Hudson Strait these digitated species formed
315 significant biomass. These species have similar morphologies and were difficult to differentiate
316 consistently in the field by multiple researchers across the five field campaigns and without genetic
317 tools. However, based on what is known about their distribution (Bringloe et al. 2021, Savoie pers.
318 comm), *H. nigripes* was most likely present in Hudson Strait and Roes Welcome Sound, and *L. digitata*
319 in Davis Strait. *Fucus* spp. were present at minor abundances at some sites (site average 0.013 ± 0.06
320 kg m^{-2}), as were red algae (including *Palmaria palmata*; site average 0.08 ± 0.23 kg m^{-2}), both of which
321 tended to be at shallow depths (5 m). The Hudson Bay region had sites around Churchill, in a region
322 with sparse rock substrate and high cover of filamentous algae. Labrador Sea sites were rocky reefs
323 dominated by the sea urchin *Strongylocentrotus droebachiensis* with sparse *A. clathratum* except for
324 an area located just south of the Torngats (Davis Strait), where kelp cover and biomass was high. These
325 southern reefs supported similar communities to patchy *A. clathratum* kelp forests in north Baffin
326 Island and Ellesmere Island, which both had high cover of red encrusting coralline algae.

327 **Environmental associations with seaweed assemblages**

328   Coastal zones across our study area experienced a diverse range of abiotic conditions, from
329 subarctic to extreme high Arctic conditions. Average temperatures on the seafloor ranged from -1.17
330 to 1.45 °C. Sea ice cover ranged from 50 days (13.6%) to 194 days (53.2%) of the year, with average
331 sea ice thicknesses of 0.18 to 0.89 m and maximum thicknesses of 3.2 m in Ellesmere Island (Figure
332 S6). Nutrients were consistently low, ranging from 0.38 to 1.04 mol m^{-3} (phosphate) and 0.57 to 11.8
333 mol m^{-3} (nitrate). Salinity ranged from 27.2 to 34.2 and tended to increase from east to west, likely as
334 a result of salinity differences between Atlantic and Arctic water masses, as well as freshwater inputs
335 from rivers or land ice melt (Figure S7).

336   Results from BIO-ENV showed moderate correlations between the kelp assemblage similarity
337 matrix and abiotic variables. The model selected sea ice thickness for the best environmental distance
338 matrix related to the percent cover similarity matrix and salinity and % sand for the matrix best related
339 to biomass. The DistLM model showed that the presence of rock substrata best predicted cover-based

340   seaweed assemblages (explaining 25.0% of the total variation), and sea ice thickness as the second-
341   best parameter (12.6%), followed by salinity (9.8%) as the third. Using a Bonferroni-corrected
342   significance threshold of p =0.0177 to account for multiple tests, every variable but temperature (p =
343   0.364) and nitrate concentration (p = 0.019) were significantly correlated with seaweed assemblages
344   in marginal tests. The most parsimonious model consisted of sea ice thickness, salinity and rock and
345   explained 40.5% of the total variation in species assemblages. The first two axes in the dbRCA analysis
346   explained 87.8% of the fitted variation and 57.4% of the cumulative variation. The first axis was driven
347   by gradients in rock and salinity, the second by sea ice thickness. Rock was, however, likely to explain
348   more variation because it was a set of variables.

349   For sites with biomass data, seaweed assemblages were best explained by nitrate (31.6%) and
350   salinity (28.1%) in marginal DistLM tests. The most parsimonious model consisted of nitrate, % sand
351   and light, and explained 44.5% of the total variation in species assemblages. The first two axes in
352   dbRCA analyses explained 70.7% of the fitted variation and 46.4% of the cumulative variation. The
353   first axis was driven by gradients in nitrate and salinity, and the second by the cover of rock. Overall,
354   dbRCAs show that sites with the least kelp cover and biomass were found in areas of thick sea ice and
355   high nutrients. More *A. clathratum* tended to occur at sites with higher salinity and there was a weak
356   relationship between kelp cover and sea temperature for some species, with *S. latissima* occurring at
357   high biomasses at sites with higher sea temperatures compared to *A. clathratum* and to some extent *L.*
358   *solidungula* (Figure 4). *L. solidungula* showed a weak, positive relationship with low light. These
359   relationships changed slightly with kelp biomass compared to kelp cover, which was likely partially
360   due to the reduced number of study sites with biomass compared to cover data.

361   Many of the largest and most abundant kelp forests were found in areas with little sea ice. These
362   occurred at lower latitudes along the northern Labrador coast (Torngats, Davis Strait) and at higher
363   latitudes in polynya zones (Figure 1)**.** The results of the GAM analysis further supported this
364   relationship, with increasing *S. latissima* cover at sites with thinner sea ice and more open water days,
365   but a sharp decrease in areas with the least sea ice and most open water days along the coast of Labrador
366   where sea urchin barrens were abundant (Figure 5, Figure S6). The northernmost sites in Grise Fiord
367   supported little kelp and had high sea ice thicknesses (>0.8 m thick on average, BioORACLE) and
368   cover (>53%). At sites in these regions we saw evidence of scour at 5- and 10-m depths, with
369   macroalgae growing only on the sides of boulders. At some sites in north Baffin Island, we observed
370   evidence of iceberg groundings that created ~0.5-m deep furrows along the seafloor and removed all
371   upright macroalgae and appeared to bury coralline algae as well. The dbRCA also shows a negative
372   correlation between sites with thick sea ice and sites with high kelp cover (Figure 4). However, this
373   negative relationship with sea ice did not hold for sites in northern Labrador, which had the most open
374   water days and were often overgrazed by sea urchins with little to no macroalgal cover or biomass
375   except for encrusting coralline algae.

376   Interestingly, kelp forests in the Eastern Canadian Arctic did not appear to require rock
377   substratum to form high cover and biomass habitats. Sand and pebbles covered an average of 41.6%
378   (± 3.9 SE) and 6.2% (± 1.5 SE) of the seafloor across all sites and depths sampled, respectively, with
379   a smaller percentage of the substratum composed of boulders 14.4% (± 2.2 SE) and bedrock 16.4% (±
380   3.0 SE) (Figure S7). High cover of *S. latissima*, *L. solidungula* and *A. esculenta* occurred in regions
381   with sand or pebble substrata (Figure 4). These species showed a remarkable ability to attach to the
382   seafloor in areas with minimal rock cover, and it was common to see 5-10-m long plant attached by a
383   small holdfast to several ~2 cm pebbles. In contrast to Laminariaceae, *A. clathratum* occurred more
384   frequently on rock substrata, often regardless of geographic region, which is supported by the GAM
385   (Figure 5).

Discussion

Arctic kelp forests are relatively understudied compared to their temperate counterparts; yet they represent a substantial portion of the global distribution of these habitats (Filbee-Dexter et al., 2019b; Starko et al., 2021). As Arctic coastal zones continue to change rapidly with climate shifts, the consequences for benthic coastal habitats are largely unknown, with little baseline data and sparse records in many regions. Arctic kelp forests are, however, predicted to become increasingly abundant and productive in the future (Krause-Jensen et al., 2020), and this change will likely have important impacts on coastal ecosystem function and provision of services to humans (Wernberg et al., 2019). This study found that large stretches of the coastlines of the Eastern Canadian Arctic already support kelp forests, suggesting these productive seaweed habitats could currently dominate much of this extensive underwater region. Broad-scale field surveys like this, which allow the comparison of ecological conditions across different environmental conditions, can provide strong insight into how future climates might affect species and communities (Wernberg et al., 2012).

Inferring the underlying drivers of observed differences in kelp forests in the Eastern Canadian Arctic can be challenging because many potentially important factors covary in space and time. Kelp forests did not consistently decrease in biomass and extent from south to north, as expected from latitudinal patterns demonstrated in western Greenland and northern Europe (Krause-Jensen et al., 2012; Pessarrodona et al., 2018). Instead, biomass and cover varied regionally, with some sites at similar latitudes supporting either large canopies of *S. latissima* and *L. solidungula* forests, smaller canopies of *A. clathratum*, or sparse algal assemblages intermixed with bare substrate. These differences suggest that latitudinal gradients in photoperiod are not the main driver of kelp forests in the region. This variation could be a result of the convoluted coastline, differences in substrata, and the complex mixing of three water bodies in this area, originating from the Arctic Ocean, the North Atlantic, and the North Pacific (Michel et al., 2006). These three water bodies have different nutrients, temperatures and salinities, and their convergence creates gradients of environmental conditions that may drive localized patterns of kelp abundance within regions. Available rock substrata and the presence of grazers may also alter broader predictions of the poleward expansion of kelp and may limit the extent that sea ice loss and warming sea temperature will increase kelp abundance in some areas.

Kelp community composition and substratum

It is widely believed that kelp forests rely on rock substrata to thrive, yet sand-dominated substratum with little rock (e.g., gravel or scattered cobbles) was enough to support some of the largest kelp forests in the Eastern Canadian Arctic. This observation aligns with a growing recognition that macroalgae can dominate sedimentary habitats (Duarte et al. unpublished data), which has consequences for macroalgal burial and potential long-term carbon storage (Ortega et al., 2019). There was evidence of detachment in sedimentary areas, with numerous free-floating *S. latissima* observed on the sea surface in waters surrounding these forests in Roes Welcome Sound and Foxe Basin. It is possible that kelps attached to sand or pebbles could become unstable and more prone to dislodgement when they lose the protective cover of sea ice and are increasingly exposed to ocean storms and waves (Bonsell and Dunton, 2018; Filbee-Dexter and Scheibling, 2012).

The northern dominance of *A. clathratum* in the study area was unexpected. This species appears to be the proverbial 'last one standing' at the most extreme limits of the Eastern Canadian Arctic, found farther north than even the endemic arctic species *L. solidungula*. It is not clear what is driving dominance of this rather understudied species in this region. Along more temperate coasts in the north Atlantic, *A. clathratum* is typically restricted to deep waters and outcompeted by faster-

430   growing kelps such as *L. digitata*, *S. latissima*, and *A. esculenta* (Adey and Hayek, 2011; Simonson et
431   al., 2015)*.* Perhaps its slower growth rate and tolerance of low light allows *A. clathratum* to better
432   survive in regions with high cover of thick sea ice. High densities of sea urchins could also favour the
433   survival of *A. clathratum,* which has defenses against grazing (Dubois and Iken, 2012; Gagnon et al.,
434   2003), enabling it to persist while less defended kelp species are grazed.

435   Unlike *A. clathratum*, patterns of abundance and extent of *A. esculenta* – which was found at
436   almost all sites throughout the Arctic – were similar to those observed in temperate regions, and this
437   species never dominated the community, but rather tended to be part of mixed canopies. *A. esculenta*
438   is an opportunistic kelp species, with high dispersal ability that is often the first kelp to colonize during
439   macroalgal succession (Campana et al., 2009; Hawkins and Harkin, 1985). It can eventually be
440   outcompeted by other kelp species, such as *S. latissima* or *L. digitata*, for light or experience higher
441   rates of grazing. Although its high dispersal strategy could explain its high prevalence across the Arctic,
442   this species may represent multiple subspecies or distinct populations throughout the region (Bringloe
443   et al., 2021), suggested local adaptation.

Kelp communities and environmental conditions

445   Despite the complicated relationship of kelp cover and biomass with latitude, sea ice cover and
446   thickness did appear to shape kelp forests in the Eastern Canadian Arctic. Polynyas, where currents
447   prevent formation of sea ice and result in more open water days, or localized areas with thinner sea ice
448   create a regional mosaic of light availability that disrupts continuous latitudinal gradients (Hannah et
449   al., 2009; Melling et al., 2015). We saw this at mid-latitudes in Roes Welcome Sound, Hudson Strait
450   and Davis Strait, which supported larger and more continuous kelp forests than nearby areas with more
451   sea ice. There was also evidence of less kelp at shallower depths, which could be consistent with effects
452   of intense sea ice scour or freshwater inputs. The trend of higher kelp biomass and cover under longer
453   open-water conditions, shown by the positive relationship between abundance of high biomass *S.*
454   *latissima* forests and open-water days, is consistent with expectations that sea ice limits the abundance
455   of more temperate kelp species through shading and/or scour (Bartsch et al., 2017; Krause-Jensen and
456   Duarte, 2014; Scherrer et al., 2019). This relationship has also been confirmed by species distribution
457   models that found that sea ice thickness was one of the most important variables for predicting habitat
458   suitability and percent cover of kelp forests in the Eastern Canadian Arctic (Goldsmit et al., 2021). Yet,
459   individual kelp species appeared to be influenced more or less strongly by sea ice, suggesting that kelp
460   forests in this region could be more likely to shift in species composition and cover compared to shifting
461   in overall distribution as sea ice diminishes. Ocean temperature was not strongly correlated with
462   seaweed cover, despite being a key predictor in global models of kelp distribution (Assis et al., 2016;
463   Duarte et al., 2021; Jayathilake and Costello, 2020). This finding is again consistent with regional
464   models for the Eastern Canadian Arctic, which show the occurrence of *L. solidungula, S. latissima* and
465   *A. clathratum* has no significant relationship with temperature (Goldsmit et al., 2021). Minimum sea
466   temperatures across our study sites were highly similar, bordering on freezing (-1.8 °C) in most regions,
467   with average sea temperatures less than 1.5 °C, which could explain this pattern. Warm temperatures,
468   and in particular marine heatwaves, are important stressors for kelp forests globally, but these losses
469   frequently occur at warmer range edges (Filbee-Dexter et al., 2020; Rogers-Bennett and Catton, 2019;
470   Wernberg et al., 2016). In their more northern range limits, arctic kelps typically experience
471   temperatures well below thermal limits for mortality (Filbee-Dexter et al., 2019b). Instead, substratum
472   type and sea urchin abundances, which are variables that are not typically available for habitat
473   suitability models, seem to influence percent cover, biomass and species composition in this region.

474   Although the surface water in the Canadian Arctic are known to be nutrient poor, and seaweeds
475   thrive in nutrient-rich waters (Wernberg et al. 2019), nitrate and phosphate concentrations showed a
476   negative relationship with overall kelp abundance. This unexpected relationship could be explained by
477   the well-known nutrient storage capacity of Arctic kelp species, which may receive adequate nutrients
478   from seasonal mixing or upwelling processes that bring nutrient-rich water to the surface in some areas
479   for short periods of time (e.g., Chapman and Lindley, 1980) or seasonally (e.g., Henley and Dunton,
480   1997). The timing and intensity of such periodic nutrient inputs may not have been properly captured
481   by Bio-Oracle annual means. Alternatively, nutrient-rich areas could support greater phytoplankton
482   production and decrease light availability on the seafloor during the critical spring growth period. It is
483   also difficult to make any strong inferences regarding the relationships between nutrients and kelp
484   abundance, because nitrate and phosphate concentrations covary in space with other important
485   environmental variables. Nutrients are highest in the northern-most region around Ellesmere Island, a
486   region that receives cold Arctic surface water that flows directly out of the Arctic Basin, and that also
487   has high sea ice cover and strong seasonality in light, which both influence seaweed performance
488   (Wiencke et al., 2007). Regions with high nutrient concentrations could also reflect higher turbidity
489   (i.e., from terrestrial runoff), which leads to reduced light penetration and could contribute to the
490   negative association with seaweed abundance (Aumack et al., 2007; Fritz et al., 2017; Traiger and
491   Konar, 2018).

492   The species composition of kelp forests between regions and across smaller-scale gradients of
493   abiotic conditions within the study area also provides insights into what drives these communities and
494   how these habitats could change in the future. Kelp forests with high biomass of *S. latissima, L.*
495   *solidungula*, and *A. esculenta* at sites in polynya zones where strong turbulence slows ice formation
496   (e.g., Hudson Strait, Roes Welcome Sound and Davis Strait) (Hannah et al., 2009) could represent the
497   productive kelp habitats that could become more widespread when sea ice retreats. These high-biomass
498   forests may then develop in neighbouring regions that have similar substrata (sediment and pebbles)
499   but currently experience sea ice conditions that limit kelp growth. However, these zones are also
500   associated with high water flow and vertical mixing that likely influence the growth and abundance of
501   seaweeds, limiting how well these areas may represent future ice-free regions.

502   In contrast to regional gradients of sea ice created by polynya zones, the broader latitudinal
503   gradient of increased sea ice and sparse *A. clathratum* across the Eastern Canadian Arctic, moving
504   northwards along the rocky coast from Baffin Bay to north Baffin Island and Ellesmere Island, suggests
505   that *A. clathratum* forests could increase along this northeastern coastline as sea ice retreats. This
506   prediction is supported by models for the region under the extreme emission scenario (8.5 RCP) for
507   years 2050 and 2100 (Goldsmit et al., 2021). Moreover, the more abundant rocky substrata found to
508   the east in these regions appeared to favour *A. clathratum*, particularly at higher latitude sites, where it
509   dominated all depths. Similarly, the trend of decreasing *S. latissima* (and to some extent *L. solidungula*)
510   abundance from the relatively ice-free Davis Strait northwards into Baffin Bay, suggests that these
511   larger canopy-forming forests may be limited by high arctic conditions. Yet, despite the close
512   association of these species within our study sites, models based on their broader distributions predict
513   that *S. latissima* will encounter more suitable northern habitat under future climate change scenarios
514   than *L. solidungula*, which is expected to decrease in the region (Goldsmit et al., 2021). If conditions
515   in more northern regions converge with those currently found in subarctic locations, it is possible that
516   these species could become more dominant in northern Baffin Bay, with *S. latissima* outcompeting *A.*
517   *clathratum* at shallow depths. Replacement of *A. clathratum* with *S. latissima* would increase total kelp
518   biomass and habitat structure (i.e., canopy height) in these areas. However, although our study region
519   included southern Ellesmere Island, our sites did not capture the northern limit of kelp distribution,
520   which could be located closer to areas covered by multi-year sea ice further north. The above

521   environmentally driven predictions may differ if biological variables such as presence of grazers are
522   taken into account; for example, increases in sea urchins can favour *A. clathratum* over other kelp
523   species (Gagnon et al., 2003) as we observed in Labrador.

524   The relative importance of sea ice at the northernmost sites compared to sea urchin grazing
525   pressure at the southernmost sites in the study region along the Labrador coast, aligns with ecological
526   theory, where biological interactions become more important as you move towards the equator and
527   environmental drivers are more critical towards the poles (Moles et al., 2011; Poore et al., 2012;
528   Steneck et al., 2017). Sea urchin barrens in northern Labrador occurred at a known transition between
529   temperate and subarctic conditions (Adey and Hayek, 2011; Merzouk and Johnson, 2011). If
530   environmental conditions are creating this boundary change, sea urchins may overgraze erect
531   macroalgae northward, as they have in other regions when oceans have warmed (Christie et al., 2019;
532   Ling et al., 2009). A similar subarctic band of sea urchin barrens also occurs in Norway, Alaska and
533   eastern Russia (Filbee-Dexter and Scheibling, 2014; Konar and Estes, 2003; Norderhaug and Christie,
534   2009), but not in more high Arctic places like Greenland, Svalbard, the White Sea and the Beaufort
535   Sea (Krause-Jensen et al., 2020). This lack of extensive barrens in the northern Arctic is not because
536   sea urchins were absent in these regions (they were common around northern Baffin Island and
537   Ellesmere Island) but could instead be due to environmental conditions limiting destructive grazing
538   behaviour. For example, if cooler temperatures are suboptimal for *S. droebachiensis* urchins it may
539   lead to smaller sea urchin sizes, reduced reproductive success and slower grazing rates (Scheibling et
540   al., 2020). Alternatively, the presence of barrens in subarctic regions could reflect a legacy of high
541   fishing pressure there, which removed sea urchin predators such as large groundfish (Norderhaug et
542   al., 2020b). Accurate predictions of how this boundary could shift will require ecophysiological tests
543   of relationship between sea urchins and environmental conditions, as well as a much better knowledge
544   of predator abundance, bathymetry, dispersal ability and projections of future coastal conditions.

545   **Arctic kelp and ecosystem function**

546   Kelp forests in the Eastern Canadian Arctic are estimated to currently cover 312,000 km^2 of the
547   coastal zone, in waters 30 m or shallower (Goldsmit et al., 2021), which is 9% of the estimated global
548   distribution of kelp (1,500,000 to 2,500,000 km^2) (Assis et al., 2020; Duarte et al., 2021; Jayathilake
549   and Costello, 2020). The relatively high abundance and areal extent of these primary producers
550   compared to phytoplankton and sea ice algal production along these coasts suggests that Arctic kelp
551   forests could be an important source of primary production for marine communities (Krumhansl and
552   Scheibling, 2012; Pessarrodona et al., 2021; Vilas et al., 2020) and a standing stock of carbon. Based
553   on the average biomass per area measured in our study (3.7 kg m^2), and assuming fresh biomass to
554   carbon conversion ratios of 0.21 FW:DW and 0.3 DW:C (Pedersen et al., 2020; Pessarrodona et al.,
555   2021), we estimate a total standing stock for the Eastern Canadian Arctic of 72.7 ($\pm$ 8.4 SE) Tg C. This
556   value is 4.4× more than the standing stock of kelp forests in Australia (16.6 TgC; Filbee-Dexter and
557   Wernberg, 2020) and 10.2× than the standing stock of kelp forests in Norway (158 million tonnes WW
558   or 7.1 TgC; Frigstad et al., 2021) (using FW:C ratios for *L. hyperborea* from Pedersen et al. 2020).
559   Annual productivity rates measured for *S. latissima* and *L. solidungula* at sites around Southampton
560   Island in 2019 ranged from 23.1 - 67.8 g C m^{-2} y^{-1} (Filbee-Dexter, unpublished data) and for *L.*
561   *solidungula* from Igloolik (Foxe Basin) in 1977 were 19.6 ($\pm$ 12.1 SD) g C m^{-2} y^{-1} (Chapman and
562   Lindley, 1980). These measures of NPP are an order of magnitude lower compared to the productivity
563   of most kelp forests (global average 516 $\pm$ 30 SE g C m^{-2} y^{-1}; Pessarrodona et al 2021), yet the extensive
564   area of kelp in the Eastern Canadian Arctic suggests these habitats are still cycling large quantities of
565   carbon in the coastal zone.

566   The presence of kelp forests is likely significant for coastal productivity in the Eastern Canadian
567   Arctic, as kelps provide food for coastal food webs through direct consumption by grazers (Filbee-
568   Dexter et al., 2019a; Franco et al., 2015; O'Brien and Scheibling, 2016; Wernberg et al., 2016) or
569   through detrital pathways (Duggins et al., 1989; Vanderklift and Wernberg, 2008; Vilas et al., 2020).
570   Kelp forests also act as important nutrient filters, focal points for high biodiversity and carbon sinks
571   (Filbee-Dexter, 2020; Krause-Jensen and Duarte, 2016; Teagle et al., 2017; Wernberg et al., 2019). In
572   fact, the slower decomposition of kelp carbon at high latitudes could mean that kelp detritus in these
573   regions has a greater chance to reach long-term sinks and be sequestered (i.e., long-term storage in the
574   deep ocean) (Filbee-Dexter et al., 2021)

575   The spatial gradients in kelp biomass, cover and dominant species shown in this study likely
576   have follow-on consequences for coastal ecosystem functioning in these regions. Benthic primary
577   production is most likely higher in areas with higher kelp cover and biomass, as there is generally a
578   positive relationship between total standing biomass and areal net primary production (NPP) for many
579   kelp species (Pedersen et al., 2019; Pessarrodona et al., 2018). In regions characterized by a higher
580   biomass and cover, more kelp carbon should be available for uptake by coastal food webs or carbon
581   sequestration (Pessarrodona et al., 2018). The canopy coverage and height of kelp forests will also
582   affect how these species 'engineer' the local environment, altering the overall habitat structure. Kelp
583   forests with high cover and biomass ('marine forests') (Wernberg and Filbee-Dexter, 2019), often have
584   more three-dimensional space for associated species to use for shelter and habitat and can support
585   distinct understory communities through shading (Norderhaug et al., 2020a; Teagle et al., 2017). Thus,
586   the sparse *A. clathratum* kelps in high latitude regions that do not form continuous canopies likely
587   provide limited vertical habitat structure compared to larger *S. latissima* and *L. solidungula* forests
588   farther south (although *A. clathratum* holdfasts do provide habitat for numerous species (Kimberly
589   Howland, pers. comm.)). Shifts in dominant kelp species in the Eastern Canadian Arctic, as well as
590   overall increases in kelp abundance and geographic extent, could therefore alter coastal carbon cycles,
591   coastal biodiversity and overall primary and secondary productivity of this extensive coastal zone.

Conclusions

593   Our results suggest that kelp forests are prevalent throughout the Eastern Canadian Arctic and
594   form one of the dominant coastal ecosystems along this extensive coastline. Both the small-scale
595   environmental gradients within regions of the Eastern Canadian Arctic and the broad range of abiotic
596   and biotic conditions across the entire study area provide an initial yet nuanced understanding of what
597   drives kelp community structure in this relatively unexplored region of the planet, highlighting the
598   importance of sea ice, substratum type, and herbivory in shaping kelp assemblages. As sea ice becomes
599   less prominent in some regions, arctic kelp forests could experience a shift from abiotic drivers to more
600   biotic drivers of community structure, such as herbivory and competition with other seaweeds that
601   characterize more temperate kelp forests. Our findings are consistent with the hypothesis that kelp
602   forests will expand in the Arctic under climate change but suggest that this expansion will largely be
603   due to a change in dominant species or shifts in overall cover and biomass within existing ranges. This
604   could represent a negative feedback mechanism on climate change, whereby less sea ice means more
605   subsurface carbon capture from underwater seaweeds. Our findings also demonstrate the high potential
606   productivity of this extensive coastal zone and highlight the need to better understand the ecology of
607   these systems and the services they provide, particularly in the context of global change.

608

609

610   **Figures**
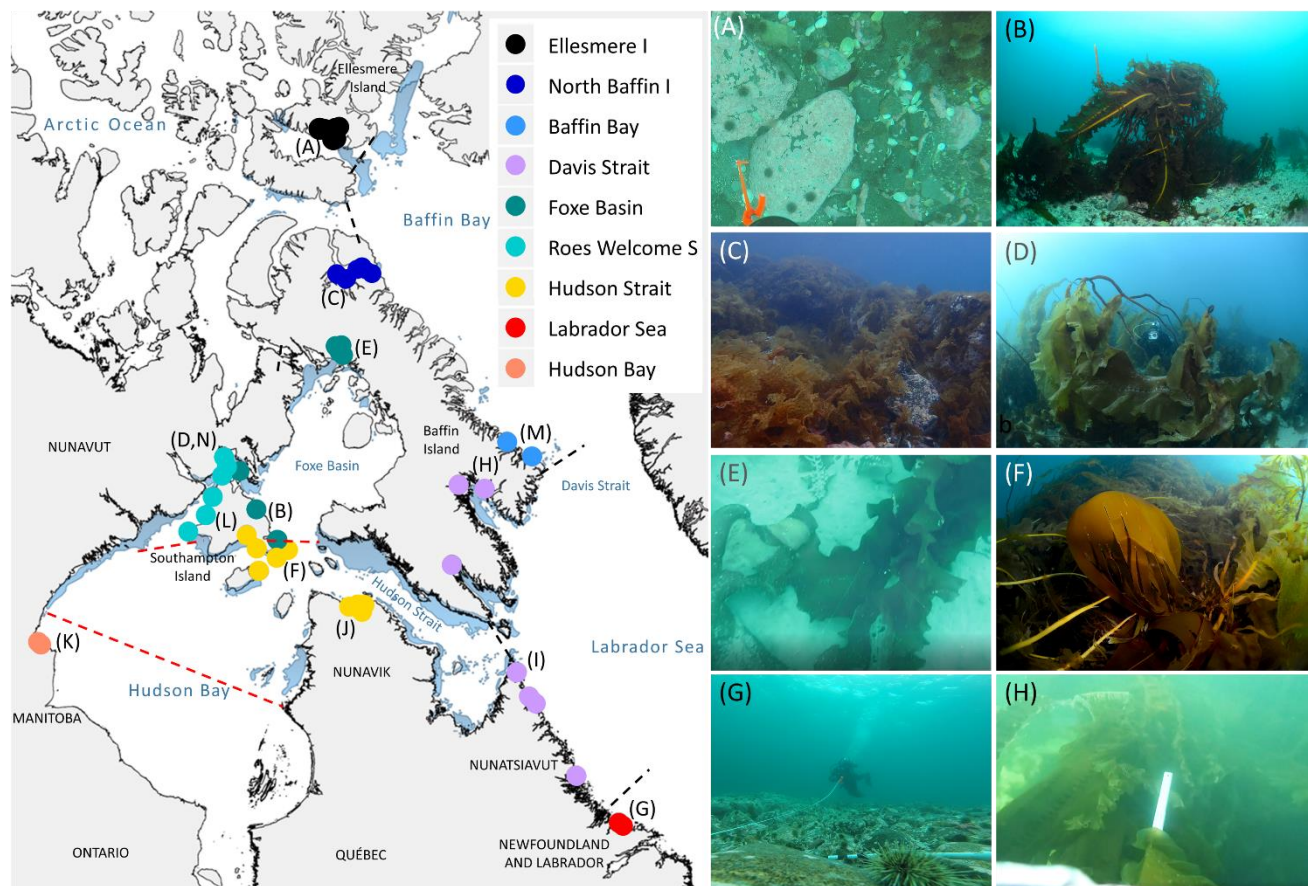
611

612   **Figure 1**. Location of study sites within the Eastern Canadian Arctic. Colours show distinct regions
613   divided by Spalding et al. (2007) classification (dashed black lines) and known oceanographic features
614   (Adey and Hayek, 2011; Brown et al., 2018) (red lines). Light blue shading shows polynya zones
615   (WWF Global Arctic Program). Study site names and coordinates provided in Table S1. Note some
616   points are overlapping. Letters correspond to photographs showing diverse configurations of
617   assemblages across regions. a) Coralline algae with sea urchins and sparse *Agarum clathratum* 10 m
618   depth in Ellesmere Island (Starnes Fiord; credit Eric Brossier), b) *Alaria esculenta* on sand and pebbles
619   in Foxe Basin (Southampton Island, credit Ignacio Garrido); c) *A. clathratum*-dominated bedrock in
620   north Baffin Island (Mittimatalik; credit Karen Filbee-Dexter); d) 'floating' *S. latissima* forest rising
621   over diver in Rose Welcome Sound (Southampton Island; credit Ignacio Garrido); e) sand with
622   *Laminaria solidungula* and prostrate *Saccharina latissima* in Igloolik (Foxe Basin; credit: CAISN); f)
623   *Hedophyllum nigripes* and *A. esculenta* in Hudson Strait (Southampton Island; credit Ignacio Garrido);
624   g) sea urchin barren devoid of erect algae at 10 m depth in Labrador (Makkovik; credit Kathleen
625   MacGregor); and h) *S. latissima* and *A. esculenta* forests in Davis Strait (Pangnirtung; Jonathan Fisher)
626   and i-n in Figure S1.
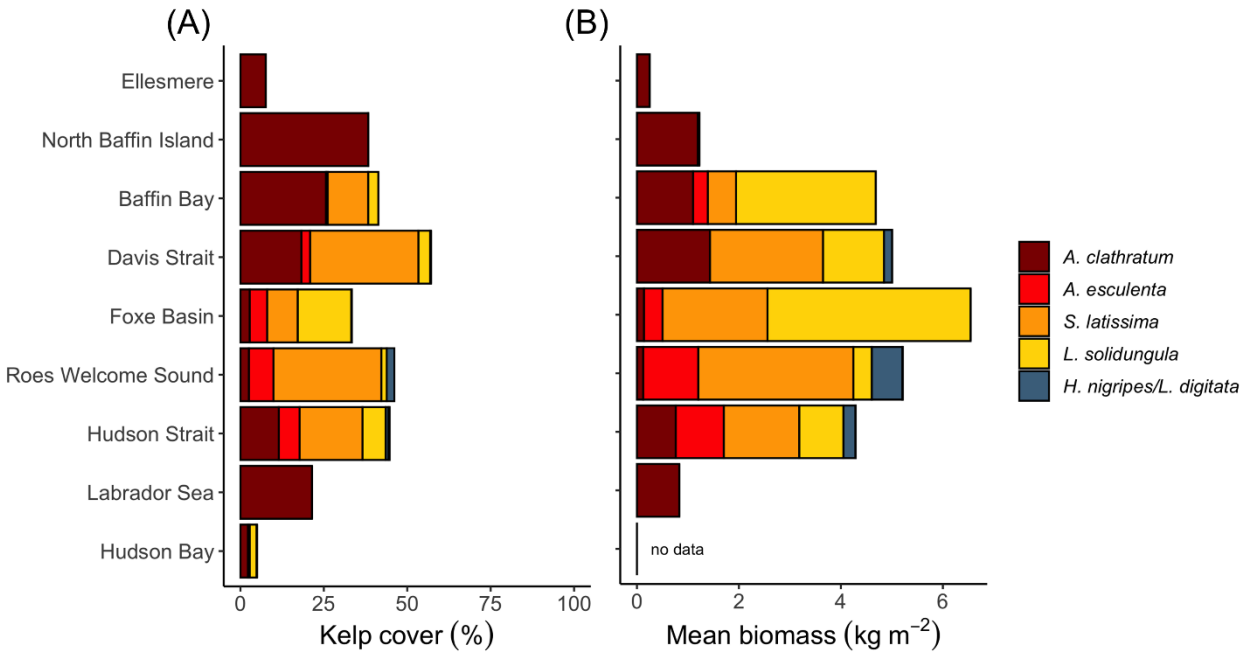
Figure 2. Average percent canopy cover and biomass of kelp species in different regions, averaged across depth and then site. Total bar length is total kelp cover or total biomass. Note biomass was only sampled at a subset of sites with percent cover data.
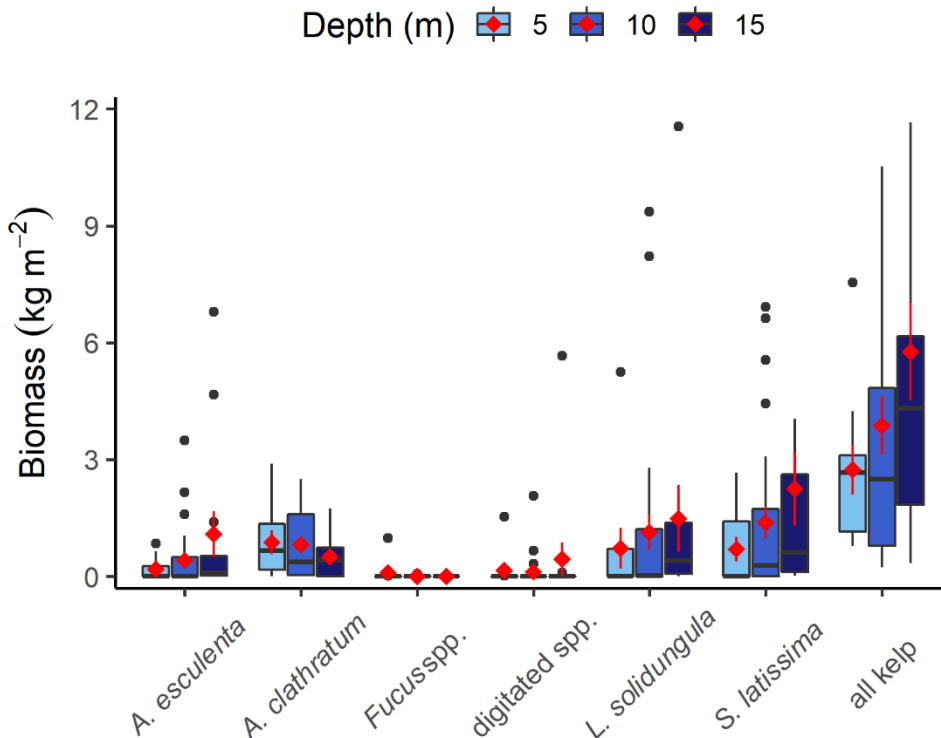

Figure 3. Biomass for kelp species at 5, 10, and 15 m depths, at all sites. Final column shows total kelp biomass. Red diamonds are average over all sites ± se, black line is median. Upper and lower bars of boxplot show first and third quartiles, upper whiskers show 1.5 IQR. Digitated category includes *Laminaria digitata* and *Hedophyllum nigripes*.

636
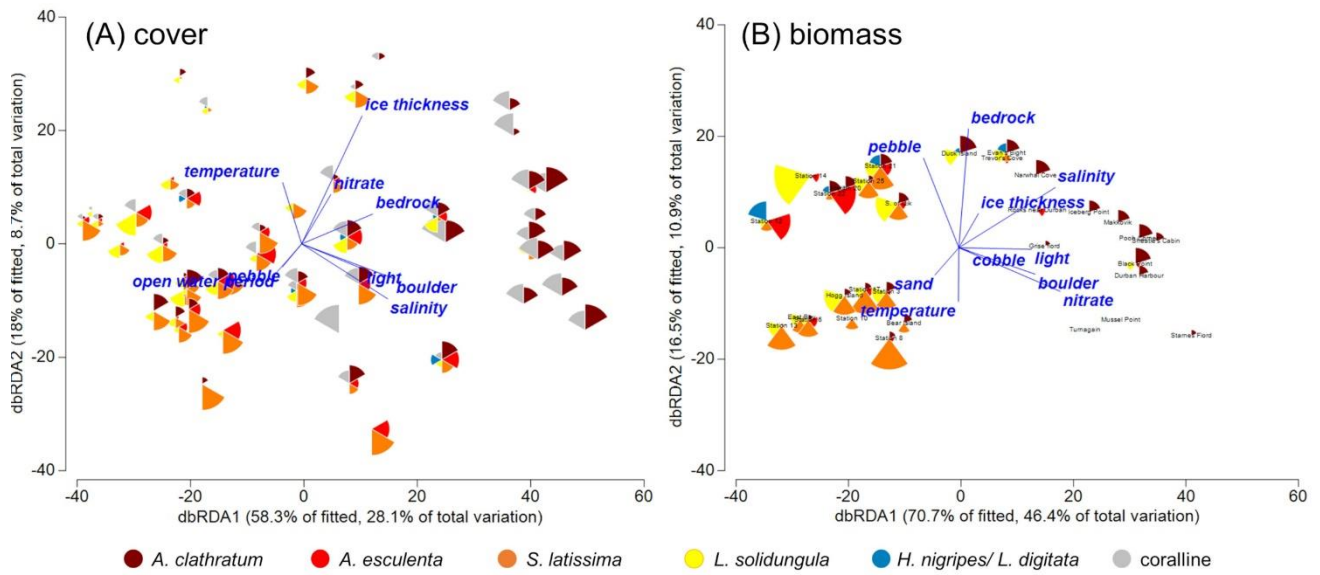
637
638 **Figure 4.** Seaweed assemblage relationship with abiotic variables across the Eastern Canadian Arctic.
639 Data are presented for cover (a) and biomass (b), pooled over 5, 10 and 15 m depths. Points are based
640 on dbRDA using Bray Curtis dissimilarity matrix of square-root transformed data. Vectors (blue) show
641 correlations between ordinations for macroalgal assemblages and average environmental conditions
642 and substrata at each site. Colour and size of the pie sections shows the relative abundance of the 5
643 most dominant kelp species. The size of each piece indicates the percent cover of different species,
644 from 0 to 100% or 0 to 10 kg m^{-2}. Note 'sand' substrata is not shown for clarity in (a) because it occurs
645 directly under 'open water days'. For site key see Table S1.
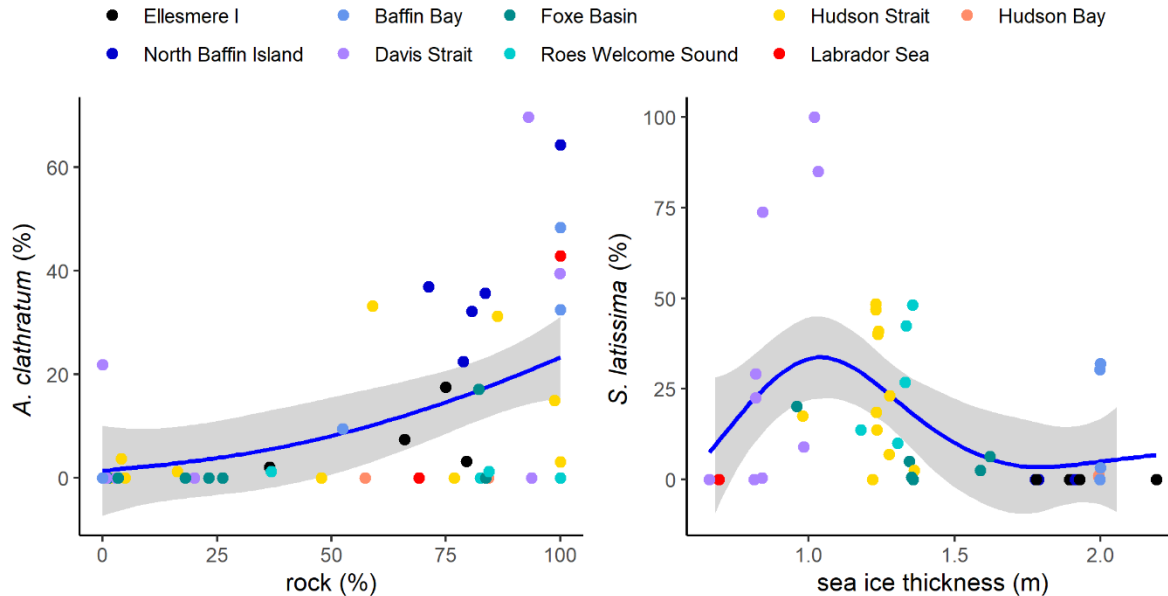
646

647 **Figure 5**. Relationships between a) percent cover of *Agarum clathratum* and substrate (% rock), for
648 each site, and b) percent cover of *Saccharina latissima* and sea ice thickness. Colours of bubbles show
649 regions. Blue lines are single predictor Generalized Additive Models (GAMs) with 95% CI in gray
650 shading.

17

651 **Tables**

652 **Table 1**. Permutational multivariate analyses of variance, based on Bray–Curtis similarity matrices of
653 square-root transformed percent cover and average biomass (WW) data, at depth level and sites in
654 each region. All tests used 9999 permutations under the reduced model.

Source	Percent cover				Biomass			
	df	MS	Pseudo-F	P(perm)	df	MS	Pseudo-F	P(perm)
Region	8	59649	4.39	0.001	7	8043	3.50	0.001
Site (Region)	43	14339	12.3	0.001		2614	3.50	0.001
Depth (Site)	45	8661	7.40	0.001		1585	2.12	0.001
Residual	726	1170				746		

655

656 **Table 2**. Mean (SE) diversity indices - species number, richness, evenness and Shannon diversity for
657 regions from biomass collections (site measures are averaged across depths).

Region	No. species	Richness	Evenness	Shannon diversity
Ellesmere Island	1.00	-	-	-
North Baffin Island	1.33	0.73	0.04	0.07
Baffin Bay	2.33	2.09	0.48	0.58
Davis Strait	3.33	1.21	0.89	0.63
Foxe Basin	3.67	8.76	0.73	1.57
Roes Welcome Sound	5.40	7.51	0.81	1.12
Hudson Strait	3.83	2.14	0.87	0.71
Labrador Sea	0.33	-	-	-

658

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

KFD led the writing, data analysis, and conceived the study. KFD, KAM, IG, LCG, KM, LEJ, CWM, CJM, TS collected the data. CL, JG, RS, PA, KAM analysed the data. PA, KFD, LEJ, KH, CJM, CWM, KH acquired funding. CL, KAM, KFD created the graphics. All authors contributed to writing and editing the manuscript.

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697 We also recognize the Traditional Inhabitants of both ceded and unceded territory on which this
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699

700 **Reference styles**

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

705 Anderson, M., Clark, M. R., and Gorley, R. (2008). *PERMANOVA+ for primer: Guide to software
706   and statistical methods*.

707 Archambault, P., Snelgrove, P. V. R., Fisher, J. A. D., Gagnon, J. M., Garbary, D. J., Harvey, M., et
708   al. (2010). From sea to sea: Canada's three oceans of biodiversity. *PLoS One* 5, e12182.
709   doi:10.1371/journal.pone.0012182.

710 Assis, J., Araújo, M. B., and Serrão, E. A. (2018a). Projected climate changes threaten ancient
711   refugia of kelp forests in the North Atlantic. *Glob. Chang. Biol.* 24, e55–e66.
712   doi:10.1111/gcb.13818.

713 Assis, J., Fragkopoulou, E., Frade, D., Neiva, J., Oliveira, A., Abecasis, D., et al. (2020). A fine-
714   tuned global distribution dataset of marine forests. *Sci. Data* 7, 1–9. doi:10.1038/s41597-020-
715   0459-x.

716 Assis, J., Lucas, A. V., Bárbara, I., and Serrão, E. Á. (2016). Future climate change is predicted to
717   shift long-term persistence zones in the cold-temperate kelp Laminaria hyperborea. *Mar.
718   Environ. Res.* 113, 174–182. doi:10.1016/j.marenvres.2015.11.005.

719 Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., and De Clerck, O. (2018b). Bio-
720   ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Glob. Ecol. Biogeogr.*
721   27, 277–284. doi:10.1111/geb.12693.

722 Aumack, C. F., Dunton, K. H., Burd, A. B., Funk, D. W., and Maffione, R. A. (2007). Linking light
723   attenuation and suspended sediment loading to benthic productivity within an arctic kelp-bed
724   community. *J. Phycol.* 43, 853–863. doi:10.1111/j.1529-8817.2007.00383.x.

725 Bartsch, I., Paar, M., Fredriksen, S., Hop, H., Asmus, R., Asmus, H., et al. (2017). Arctic warming
726   affects kelp forest with associated fauna in Kongsfjorden, Svalbard. *Epic. Froniers, White Sp. -
727   Blue Futur. Tromsö, 2017-01-22-2017-01-27*. Available at: http://epic.awi.de/43693/ [Accessed
728   February 5, 2018].

729 Bartsch, I., Paar, M., Fredriksen, S., Schwanitz, M., Daniel, C., Hop, H., et al. (2016). Changes in
730   kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and
731   2012–2014 reflect Arctic warming. *Polar Biol.* 39, 2021–2036. doi:10.1007/s00300-015-1870-
732   1.

733 Bell, T., and Brown, T. (2018). From science to policy in the Eastern Canadian Arctic: An Integrated

734   Regional Impact Study (IRIS) of climate change and modernization. Quebec City.

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

738 Bringloe, T. T., Zaparenkov, D., Starko, S., Vieira, C., Kawai, H., Hanyuda, T., et al. (2021). Whole
739   genome sequencing reveals forgotten lineages and recurrent hybridizations within the kelp
740   genus Alaria (Phaeophyceae) whole genome sequencing reveals forgotten lineages and (
741   Phaeophyceae). *J. Phycol.*, in press.

742 Bringloe, T., Verbruggen, H., and Saunders, G. (2020). Population structure in Arctic marine forests
743   is shaped by diverse recolonisation pathways and far northern glacial refugia. *bioRxiv*,
744   2020.03.19.999466. doi:10.1101/2020.03.19.999466.

745 Brown, T., Bell, T., and Forbes, D. (2018). "Regional geography of the Eastern Canadian Arctic," in
746   *An integrated regional impact study (IRIS) of climate change and modernization: from science*
747   *to policy in the eastern Canadian Arctic*, eds. T. Bell and T. Brown (ArcticNet), 27–51.

748 Bryndum-Buchholz, A., Prentice, F., Tittensor, D. P., Blanchard, J. L., Cheung, W. W. L.,
749   Christensen, V., et al. (2020). Differing marine animal biomass shifts under 21st century climate
750   change between Canada's three oceans. *FACETS* 5, 105–122. doi:10.1139/facets-2019-0035.

751 Campana, G. L., Zacher, K., Fricke, A., Molis, M., Wulff, A., Liliana Quartino, M., et al. (2009).
752   Drivers of colonization and succession in polar benthic macro- and microalgal communities.
753   *Bot. Mar.* 52, 655–667. doi:10.1515/BOT.2009.076.

754 Cavalieri, D. J., Parkinson, C. L., Gloersen, P., and Zwally, H. J. (2020). Sea ice concentrations from
755   Nimbus-7 SMMR and DMSP SSM/ISSMIS passive microwave data. *NASA Natl. Snow Ice Data*
756   *Cent. Distrib. Act. Arch. Cent.*, updated yearly. Available at:
757   https://doi.org/10.5067/8GQ8LZQVL0VL.

758 Chapman, A. R. O., and Lindley, J. E. (1980). Seasonal growth of *Laminaria solidungula* in the
759   Canadian High Arctic in relation to irradiance and dissolved nutrient concentrations. *Mar. Biol.*
760   57, 1–5. doi:10.1007/BF00420961.

761 Christie, H., Gundersen, H., Rinde, E., Filbee-Dexter, K., Norderhaug, K. M., Pedersen, T., et al.
762   (2019). Can multitrophic interactions and ocean warming influence large-scale kelp recovery?
763   *Ecol. Evol.* 9, 2847–2862. doi:10.1002/ece3.4963.

764 Cross, W. E., Wilce, R. T., and Fabijan, M. F. (1987). Effects of experimental releases of oil and
765   dispersed oil on Arctic nearshore macrobenthos. III. Macroalgae. *Arctic* 40, 211–219. Available
766   at:
767   https://www.jstor.org/stable/pdf/40510552.pdf?refreqid=excelsior%3A9438a68d47dc36079038f
768   501825d6619 [Accessed October 14, 2019].

769 Dankworth, M., Heinrich, S., Fredriksen, S., and Bartsch, I. (2020). DNA barcoding and mucilage
770   ducts in the stipe reveal the presence of Hedophyllum nigripes (Laminariales, Phaeophyceae) in
771   Kongsfjorden (Spitsbergen). *J. Phycol.* 56, 1245–1254. doi:10.1111/JPY.13012.

772 Duarte, C. M., Gattuso, J., Hancke, K., Gundersen, H., and Filbee-Dexter, K. (2021). Global
773   estimates of the extent and production of algal forests. *Global Biogeochem. Cycles* In review.
774   doi:10.1093/biosci/bix147.2.

775 Dubois, A., and Iken, K. (2012). Seasonal variation in kelp phlorotannins in relation to grazer
776   abundance and environmental variables in the Alaskan sublittoral zone. *ALGAE* 27, 9–19.
777   doi:10.4490/ALGAE.2012.27.1.009.

778 Duggins, D. O., Simenstad, C. A., and Estes, J. A. (1989). Magnification of secondary production by
779   kelp detritus in coastal marine ecosystems. *Science (80-.).* 245, 170–173.
780   doi:10.1126/SCIENCE.245.4914.170.

781 Filbee-Dexter, K. (2020). Ocean forests hold unique solutions to our current environmental crisis.
782   *One Earth* 2, 398/401. doi:10.1016/j.oneear.2020.05.004.

783 Filbee-Dexter, K., Feehan, C., Smale, D., Krumhansl, K., Augustine, S., De Bettignies, F., et al.
784   (2021). Ocean temperature controls kelp decomposition and carbon sink potential. *PNAS* in
785   review. doi:10.21203/rs.3.rs-38503/v1.

786 Filbee-Dexter, K., Pedersen, M., Fredriksen, S., Norderhaug, K., Rinde, E., Kristiansen, T., et al.
787   (2019a). CARBON EXPORT IS FACILITATED BY SEA URCHINS TRANSFORMING
788   KELP DETRITUS. *Oecologia* in revisio.

789 Filbee-Dexter, K., and Scheibling, R. E. (2012). Hurricane-mediated defoliation of kelp beds and
790   pulsed delivery of kelp detritus to offshore sedimentary habitats. *Mar. Ecol. Prog. Ser.* 455, 51–
791   64. doi:10.3354/meps09667.

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

794 Filbee-Dexter, K., and Wernberg, T. (2018). Rise of Turfs : A new battlefront for globally declining
795   kelp forests. *Bioscience* 68, 64–76. doi:10.1093/biosci/bix147.

796 Filbee-Dexter, K., and Wernberg, T. (2020). Substantial blue carbon in overlooked Australian kelp
797   forests. *Sci. Reports 2020 101* 10, 1–6. doi:10.1038/s41598-020-69258-7.

798 Filbee-Dexter, K., Wernberg, T., Fredriksen, S., Norderhaug, K. M., and Pedersen, M. F. (2019b).
799   Arctic kelp forests: Diversity, resilience and future. *Glob. Planet. Change* 172, 1–14.
800   doi:10.1016/j.gloplacha.2018.09.005.

801 Filbee-Dexter, K., Wernberg, T., Grace, S. P., Thormar, J., Fredriksen, S., Narvaez, C. N., et al.
802   (2020). Marine heatwaves and the collapse of marginal North Atlantic kelp forests. *Sci. Rep.* 10,
803   13388. doi:10.1038/s41598-020-70273-x.

804 Franco, J., Wernberg, T., Bertocci, I., Duarte, P., Jacinto, D., Vasco-Rodrigues, N., et al. (2015).
805   Herbivory drives kelp recruits into 'hiding' in a warm ocean climate. *Mar. Ecol. Prog. Ser.* 536,
806   1–9. doi:10.3354/meps11445.

807 Frigstad, H., Gundersen, H., Andersen, G. S., Borgersen, G., Kvile, K. O., Krause-Jensen, D., et al.
808   (2021). Blue Carbon – climate adaptation, CO2 uptake and sequestration of carbon in Nordic

809   blue forests. NMR TemaNord doi:http://dx.doi.org/10.6027/temanord2020-541.

810   Fritz, M., Vonk, J. E., and Lantuit, H. (2017). Collapsing Arctic coastlines. *Nat. Clim. Chang.* 7, 6–7.
811   doi:10.1038/nclimate3188.

812   Gagnon, P., Himmelman, J. H., and Johnson, L. E. (2003). Algal colonization in urchin barrens:
813   defense by association during recruitment of the brown alga Agarum cribrosum. *J. Exp. Mar.*
814   *Bio. Ecol.* 290, 179–196. doi:10.1016/S0022-0981(03)00077-7.

815   Gattuso, J.-P., Gentili, B., Duarte, C. M., Kleypas, J. A., Middelburg, J. J., and Antoine, D. (2006).
816   Light availability in the coastal ocean: impact on the distribution of benthic photosynthetic
817   organisms and contribution to primary production. *Biogeosciences* 3, 489–513. doi:10.5194/bg-
818   3-489-2006.

819   Goldsmit, J., Schlegel, R., Filbee-Dexter, K., and Al, E. (2021). Kelp in the Eastern Canadian Arctic:
820   current and future predictions of habitat suitability and cover. *Front. Mar. Sci.* in review.

821   Hannah, C. ., Dupont, F., and Dunphy, M. (2009). Polynyas and tidal currents in the Canadian Arctic
822   Archipelago. *Arctic* 62, 83–95. Available at:
823   https://www.jstor.org/stable/40513267?casa_token=tE_BhnRzVuoAAAAA%3A3xh_fgKGy67c
824   wwC8oYEVbFHBiqSoLSyjHoeCVGCPBR-
825   3dS0opqcm2sWszzrySZ9kI_tN6Bt609WtoMFRIQNOV0cu6kWLyL-
826   HR9Z_cWErcnumcIMIgD-tIw&seq=1#metadata_info_tab_contents [Accessed July 24, 2021].

827   Hawkins, S. J., and Harkin, E. (1985). Preliminary canopy removal experiments in algal dominated
828   communities low on the shore and in the shallow subtidal on the Isle of Man. *Bot. Mar.* 28, 223–
829   230. doi:10.1515/botm.1985.28.6.223.

830   Henley, W. J., and Dunton, K. H. (1997). Effects of nitrogen supply and continuous darkness on
831   growth and photosynthesis of the arctic kelp *Laminaria solidungula*. *Limnol. Oceanogr.* 42,
832   209–216. doi:10.4319/lo.1997.42.2.0209.

833   IPCC (2019). Summary for policymakers. In: IPCC special report on the ocean and cryosphere in a
834   changing climate [H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E.
835   Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, . Hamish
836   Pritchard.

837   Jayathilake, D. R. M., and Costello, M. J. (2020). A modelled global distribution of the kelp biome.
838   *Biol. Conserv.* 252, 108815. doi:10.1016/J.BIOCON.2020.108815.

839   Konar, B., and Estes, J. A. (2003). The stability of boundary regions between kelp forests and
840   deforested areas. *Ecology* 84, 174–185. doi:10.1890/0012-
841   9658(2003)084[0174:TSOBRB]2.0.CO;2.

842   Krause-Jensen, D., Archambault, P., Assis, J., Bartsch, I., Bischof, K., Filbee-Dexter, K., et al.
843   (2020). Imprint of Climate Change on Pan-Arctic Marine Vegetation. *Front. Mar. Sci.* 7,
844   617324. doi:10.3389/fmars.2020.617324.

845   Krause-Jensen, D., and Duarte, C. M. (2014). Expansion of vegetated coastal ecosystems in the
846   future Arctic. *Front. Mar. Sci.* 1, 77. doi:10.3389/fmars.2014.00077.

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

849 Krause-Jensen, D., Lavery, P., Serrano, O., Marbà, N., Masque, P., and Duarte, C. M. (2018).
850   Sequestration of macroalgal carbon: the elephant in the Blue Carbon room. *Biol. Lett.* 14,
851   20180236. doi:10.1098/rsbl.2018.0236.

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

856 Krumhansl, K., and Scheibling, R. (2012). Production and fate of kelp detritus. *Mar. Ecol. Prog. Ser.*
857   467, 281–302. doi:10.3354/meps09940.

858 Lantuit, H., Overduin, P. P., Couture, N., Wetterich, S., Aré, F., Atkinson, D., et al. (2012). The
859   Arctic coastal dynamics database: A new classification scheme and statistics on arctic
860   permafrost coastlines. *Estuaries and Coasts* 35, 383–400. doi:10.1007/s12237-010-9362-6.

861 Lee, R. K. S. (1980). *A catalogue of the marine algae of the Canadian Arctic*. Ottawa: National
862   Museums of Canada Available at:
863   https://trove.nla.gov.au/work/23122580?q&versionId=28031871 [Accessed February 6, 2018].

864 Ling, S. D., Johnson, C. R., Ridgeway, K., Hobday, A. J., and Haddon, M. (2009). Climate-driven
865   range extension of a sea urchin: inferring future trends by analysis of recent population
866   dynamics. *Glob. Chang. Biol.* 15, 719–731. doi:10.1111/j.1365-2486.2008.01734.x.

867 Melling, H., Haas, C., and Brossier, E. (2015). Invisible polynyas: Modulation of fast ice thickness
868   by ocean heat flux on the Canadian polar shelf. *J. Geophys. Res. Ocean.* 120, 777–795.
869   doi:10.1002/2014JC010404.

870 Meredith, M., Sommerkorn, M., Cassotta, S., Derksen, C., Ekaykin, A., Hollowed, G., et al. (2020).
871   Polar Regions. In: IPCC special report on the ocean and cryosphere in a changing climate e [H.-
872   O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K.
873   Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weye.

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

876 Michel, C., Hamilton, J., Hansen, E., Barber, D., Reigstad, M., Iacozza, J., et al. (2015). Arctic Ocean
877   outflow shelves in the changing Arctic: A review and perspectives. *Prog. Oceanogr.* 139, 66–
878   88. doi:10.1016/j.pocean.2015.08.007.

879 Michel, C., Ingram, R. G., and Harris, L. R. (2006). Variability in oceanographic and ecological
880   processes in the Canadian Arctic Archipelago. *Prog. Oceanogr.* 71, 379–401.
881   doi:10.1016/j.pocean.2006.09.006.

882 Moles, A. T., Bonser, S. P., Poore, A. G. B., Wallis, I. R., and Foley, W. J. (2011). Assessing the
883   evidence for latitudinal gradients in plant defence and herbivory. *Funct. Ecol.* 25, 380–388.
884   doi:10.1111/j.1365-2435.2010.01814.x.

Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J., et al. (2020). Complexity revealed in the greening of the Arctic. *Nat. Clim. Chang.* 10, 106–117. doi:10.1038/s41558-019-0688-1.

Norderhaug, Filbee-Dexter, K., Freitas, C., Birkely, S.-R., Christensen, L., Mellerud, I., et al. (2020a). Ecosystem-level effects of large-scale disturbance in kelp forests. *Mar. Ecol. Prog. Ser.* 656, 163–180. doi:10.3354/MEPS13426.

Norderhaug, K. M., and Christie, H. C. (2009). Sea urchin grazing and kelp re-vegetation in the NE Atlantic. *Mar. Biol. Res.* 5, 515–528. doi:10.1080/17451000902932985.

Norderhaug, K. M., Nedreaas, K., Huserbråten, M., and Moland, E. (2020b). Depletion of coastal predatory fish sub-stocks coincided with the largest sea urchin grazing event observed in the NE Atlantic. *Ambio 2020 501* 50, 163–173. doi:10.1007/S13280-020-01362-4.

O'Brien, J. M., and Scheibling, R. E. (2016). Nipped in the bud: mesograzer feeding preference contributes to kelp decline. *Ecology* 97, 1873–1886. doi:10.1890/15-1728.1.

Ortega, A., Geraldi, N. R., Alam, I., Kamau, A. A., Acinas, S. G., Logares, R., et al. (2019). Important contribution of macroalgae to oceanic carbon sequestration. *Nat. Geosci.* 12, 748–754. doi:10.1038/s41561-019-0421-8.

Pecuchet, L., Blanchet, M. A., Frainer, A., Husson, B., Jørgensen, L. L., Kortsch, S., et al. (2020). Novel feeding interactions amplify the impact of species redistribution on an Arctic food web. *Glob. Chang. Biol.* 26, 4894–4906. doi:10.1111/gcb.15196.

Pedersen, M. F., Filbee-Dexter, K., Fagerli, C. W., Fredriksen, S., Norderhaug, K., and Wernberg, T. (2019). Detrital carbon production and export in high latitude kelp forests. *Oecologia*, 1–33. doi:https://doi.org/10.1007/s00442-019-04573-z.

Pedersen, M. F., Filbee-Dexter, K., Norderhaug, K. M., Fredriksen, S., Frisk, N. L., Fagerli, C. W., et al. (2020). Detrital carbon production and export in high latitude kelp forests. *Oecologia* 192, 227–239. doi:10.1007/s00442-019-04573-z.

Pessarrodona, A., Filbee-Dexter, K., Krumhansl, K. A., Moore, P. J., and Wernberg, T. (2021). A global dataset of seaweed net primary productivity. *bioRxiv*, 2021.07.12.452112. doi:10.1101/2021.07.12.452112.

Pessarrodona, A., Moore, P. J., Sayer, M. D. J., and Smale, D. A. (2018). Carbon assimilation and transfer through kelp forests in the NE Atlantic is diminished under a warmer ocean climate. *Glob. Chang. Biol.* 24, 4386–4398. doi:10.1111/gcb.14303.

Poore, A. G. B., Campbell, A. H., Coleman, R. A., Edgar, G. J., Jormalainen, V., Reynolds, P. L., et al. (2012). Global patterns in the impact of marine herbivores on benthic primary producers. *Ecol. Lett.* 15, 912–922. doi:10.1111/j.1461-0248.2012.01804.x.

Renaud, P. E., Węsławski, J. M., and Conlan, K. (2021). "Ecology of Arctic shallow subtidal and intertidal benthos," in *Arctic Ecology* (Wiley), 289–324. doi:10.1002/9781118846582.ch11.

Rogers-Bennett, L., and Catton, C. A. (2019). Marine heat wave and multiple stressors tip bull kelp

922   forest to sea urchin barrens. *Sci. Rep.* 9, 1–9. doi:10.1038/s41598-019-51114-y.

923   Rood, S. B., Kaluthota, S., Philipsen, L. J., Rood, N. J., and Zanewich, K. P. (2017). Increasing
924   discharge from the Mackenzie River system to the Arctic Ocean. *Hydrol. Process.* 31, 150–160.
925   doi:10.1002/hyp.10986.

926   Scheibling, R. E., Feehan, C. J., and Hatcher, B. G. (2020). *Strongylocentrotus droebachiensis*. *Dev.*
927   *Aquac. Fish. Sci.* 43, 553–591. doi:10.1016/B978-0-12-819570-3.00031-7.

928   Scherrer, K. J. N., Kortsch, S., Varpe, Ø., Weyhenmeyer, G. A., Gulliksen, B., and Primicerio, R.
929   (2019). Mechanistic model identifies increasing light availability due to sea ice reductions as
930   cause for increasing macroalgae cover in the Arctic. *Limnol. Oceanogr.* 64, 330–341.
931   doi:10.1002/lno.11043.

932   Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., et al. (2012).
933   Fiji: An open-source platform for biological-image analysis. *Nat. Methods* 9, 676–682.
934   doi:10.1038/nmeth.2019.

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

938   Simonson, E., Scheibling, R., and Metaxas, A. (2015). Kelp in hot water: I. Warming seawater
939   temperature induces weakening and loss of kelp tissue. *Mar. Ecol. Prog. Ser.* 537, 89–104.
940   doi:10.3354/meps11438.

941   Smale, D. A. (2020). Impacts of ocean warming on kelp forest ecosystems. *New Phytol.* 225, 1447–
942   1454. doi:10.1111/nph.16107.

943   Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., et al. (2007).
944   Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *Bioscience* 57,
945   573–583. doi:10.1641/B570707.

946   Starko, S., Wilkinson, D. P., and Bringloe, T. T. (2021). Recent global model underestimates the true
947   extent of Arctic kelp habitat. *Biol. Conserv.* 257. doi:10.1016/J.BIOCON.2021.109082.

948   Steneck, R. S., Bellwood, D. R., and Hay, M. E. (2017). Herbivory in the marine realm. *Curr. Biol.*
949   27, R484–R489. doi:10.1016/j.cub.2017.04.021.

950   Steneck, R. S., Graham, M. H., Bourque, B. J., Corbett, D., Erlandson, J. M., Estes, J. A., et al.
951   (2002). Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.*
952   29, 436–459. doi:10.1017/S0376892902000322.

953   Teagle, H. A., Hawkins, S. J., Moore, P. ., and Smale, D. A. (2017). The role of kelp species as
954   biogenic habitat formers in coastal marine ecosystems. *J. Exp. Mar. Bio. Ecol.* 492, 81–98.
955   doi:10.1016/J.JEMBE.2017.01.017.

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

958   Van Wychen, W., Copland, L., and Burgess, D. (2020). "Ice masses of the Eastern Canadian Arctic
959   Archipelago," in *World Geomorphological Landscapes* (Springer), 297–314. doi:10.1007/978-
960   3-030-35137-3_13.

961   Vanderklift, M. A., and Wernberg, T. (2008). Detached kelps from distant sources are a food subsidy
962   for sea urchins. *Oecologia* 157, 327–335. doi:10.1007/s00442-008-1061-7.

963   Vilas, D., Coll, M., Pedersen, T., Corrales, X., Filbee-Dexter, K., Pedersen, M. F., et al. (2020).
964   Kelp-carbon uptake by Arctic deep-sea food webs plays a noticeable role in maintaining
965   ecosystem structural and functional traits. *J. Mar. Syst.* 203. doi:10.1016/j.jmarsys.2019.103268.

966   Wernberg, T., Bennett, S., Babcock, R. C., de Bettignies, T., Cure, K., Depczynski, M., et al. (2016).
967   Climate-driven regime shift of a temperate marine ecosystem. *Science (80-.).* 353, 169–72.
968   doi:10.1126/science.aad8745.

969   Wernberg, T., and Filbee-Dexter, K. (2019). Missing the marine forest for the trees. *Mar. Ecol. Prog.*
970   *Ser.* 612, 209–215. doi:10.3354/meps12867.

971   Wernberg, T., Krumhansl, K. A., Filbee-Dexter, K., and Pedersen, M. F. (2019). "Status and trends
972   for the world's kelp forests," in *World Seas: An Environmental Evaluation, Vol III: Ecological*
973   *Issues and Environmental Impacts*, ed. C. Sheppard (Academic Press), 57–78.

974   Wernberg, T., Smale, D. A., and Thomsen, M. S. (2012). A decade of climate change experiments on
975   marine organisms: procedures, patterns and problems. *Glob. Chang. Biol.* 18, 1491–1498.
976   doi:10.1111/j.1365-2486.2012.02656.x.

977   Wiencke, C., and Amsler, C. D. (2012). *Seaweeds and their communities in polar regions*. Berlin,
978   Heidelberg: Springer doi:10.1007/978-3-642-28451-9_13.

979   Wiencke, C., and Clayton, M. N. (2011). "Introduction: Biology of polar benthic algae," in *Biology*
980   *of polar benthic algae*, ed. C. Wiencke (Berlin: De Gruyter), 337. Available at:
981   https://books.google.no/books?hl=en&lr=&id=7LMmABMEhdwC&oi=fnd&pg=PR1&dq=Wie
982   ncke+algae&ots=q4PeCqikp4&sig=by5MWjJ0yiR0KGe3nYh1U_qqY7Q&redir_esc=y#v=one
983   page&q=Wiencke algae&f=false [Accessed February 5, 2018].

984   Wiencke, C., Clayton, M. N., Gómez, I., Iken, K., Lüder, U. H., Amsler, C. D., et al. (2007). Life
985   strategy, ecophysiology and ecology of seaweeds in polar waters. *Life Extrem. Environ.* 6, 213–
986   244. doi:10.1007/978-1-4020-6285-8-13.

987   Wilce, R. T. (2016). The "Arctic Stamp", its imprint on an endangered marine flora. *Perspect.*
988   *Phycol.* 3, 155–180. doi:10.1127/pip/2016/0046.

989   Wulff, A., Iken, K., Quartino, M. L., Al-Handal, A., Wiencke, C., and Clayton, M. N. (2011).
990   "Biodiversity, biogeography and zonation of marine benthic micro- and macroalgae in the
991   Arctic and Antarctic," in *Biology of Polar Benthic Algae*, ed. C. Wiencke (Berlin, New York:
992   De Gruyter), 337. doi:10.1515/BOT.2009.072.

993