1 **Classification: BIOLOGICAL SCIENCES; Population biology**

2

3 **Title: Population structure in Arctic marine forests is shaped by diverse recolonisation**
4 **pathways and far northern glacial refugia**

5

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17

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Abstract

20
21 The Arctic is experiencing a rapid shift towards warmer regimes, calling for a need to understand
22 levels of biodiversity and ecosystem responses to climate cycles. This study examines marine
23 refugial locations during the Last Glacial Maximum in order to link recolonization pathways to
24 patterns of genetic diversity in Arctic marine forests. We present genetic data for 109 species of
25 seaweed to infer community-level patterns, and hindcast species distributions during the Last
26 Glacial Maximum to further pinpoint likely refugial locations. Sequence data revealed
27 contiguous populations extending from the Bering Sea to the Northwest Atlantic, with high
28 levels of genetic diversity in the East Canadian Arctic. One fifth of the species sampled appeared
29 restricted to Arctic waters. Hindcasted species distributions highlighted refugia in the Bering
30 Sea, Northwest Atlantic, South Greenland, and Europe. We hypothesize that Arctic coastal
31 systems were recolonized from many geographically disparate refugia leading to enriched
32 diversity levels in the East Canadian Arctic, with important contributions stemming from
33 northerly refugia likely centered along Southern Greenland. Moreover, we hypothesize these
34 northerly refugia likely played a key role in promoting polar endemic diversity, as reflected by
35 abundant unique population haplotypes and endemic species in the East Arctic.
36

37 **Significance Statement**
38 Our work challenges the existing paradigm that marine Arctic ecosystems are depauperate
39 extensions of southerly (temperate) communities established in the wake of recent glaciation,
40 fundamentally changing how these systems should be viewed and interpreted. We forward novel
41 hypotheses regarding the recent history of Arctic marine systems, particularly with regards to
42 endemism being an integral feature of Arctic biomes, and present a firm framework for future
43 evolutionary research in this system typically viewed as "ecologically immature."
44

45 **MAIN TEXT**
46

47 **Introduction**
48   The Arctic is characterized by a turbulent climatic history and the prospect of further
49 change. Repeated glaciations over the past 2.6 Ma had a lasting impact on biological
50 communities, forcing populations to repeatedly contract and expand with the formation and
51 retreat of ice-sheets (1). Today, warming in the Arctic is significantly exceeding the Northern
52 Hemisphere average, and boreal and temperate regimes are expected to shift northwards as a
53 result (2). A prescient need exists to understand the responses of Arctic marine communities to
54 climate change, a need that will inherently depend on understanding levels of biodiversity, the
55 recent history of Arctic ecosystems, and ultimately the potential for adaptation.
56

57   Marine forests are a model system for providing such insight on Arctic marine
58 communities. Marine forests are structurally complex seascapes created by seaweeds, are
59 ubiquitous worldwide, and provide valuable ecosystem and economic services in the forms of
60 habitat, nursery grounds, primary productivity, and harvesting resources (3). Marine forests may
61 also sequester large amounts of carbon (4), giving them a potent role in ocean-based climate
62 change mitigation (5). Arctic marine forests are broadly distributed, with circumpolar species
63 distributions extending from the Pacific through to the Atlantic with large gaps along the
64 Siberian Arctic coastline owing to unsuitable soft substrate (6) (see Fig. S1 for exemplar
65 species). Marine forests in the Arctic can also grow to incredible depths in some locations,

66 particularly off the coasts of Greenland and Svalbard where macroalgae have been recorded as
67 deep as 60 m (7). Annual ice cover is often a limiting factor in the Arctic, preventing a lush
68 intertidal community from flourishing, but nonetheless allowing annuals and hardier flora to take
69 advantage of the short growing season (6). Some species are particularly resilient to these
70 conditions. The kelp *Laminaria solidungula*, for instance, completes nearly all its growth under
71 ice, using the summer months when photosynthetic rate is high to focus exclusively on carbon
72 capture and storage (8).

74   The presence of species that are finely tuned to marine Arctic conditions raises an
75 interesting paradox, in that Arctic marine forests were historically viewed as entirely derived
76 from southerly European refugia following the Last Glacial Maximum (LGM; 9, 10). Under this
77 view, Arctic marine forests were regarded as an extension of cold-tolerant temperate species,
78 precluding the notion of Arctic endemism. While the notion of survival in refugia south of ice
79 sheets persists, alternative hypotheses regarding the recent origins of Arctic marine forests have
80 been brought forward, emphasizing contributions from the Northern Pacific (11, 12, 13). A few
81 genetic studies suggest there may have been multiple recolonization pathways for marine Arctic
82 communities, and have also revealed cryptic diversity in the Arctic, reviving the notion of Arctic
83 endemism (11, 14, 15). Being foundational to coastal ecosystems, such novel insight derived
84 from Arctic marine forests likely apply across a wide range of taxa, and have the potential to
85 dramatically shift how we view and interpret biodiversity and recent origins in Arctic marine
86 communities, along with their potential to adapt to ongoing climatic changes.

88   The notion of Arctic marine forests as a depauperate extension of temperate communities
89 is an antiquated view. Genetic signature at odds with the hypothesis of recolonization
90 predominantly out of European refugia and the presence of cryptic diversity in the Arctic
91 challenge researchers to revise our understanding of Arctic marine forests and how they persist
92 through cycles of glaciation. Our objective was to clarify the recent origin of Arctic marine
93 forests, emphasizing a community-level approach by summarizing genetic data results across
94 many species, and using species distribution models to identify likely refugial locations during
95 the LGM. We evaluated several hypotheses, employing two lines of evidence in the forms of
96 genetic surveys (DNA barcoding) and hindcasting species distributions using ecological niche
97 modelling. If Arctic marine populations were recently recolonized from southerly refugia,
98 particularly from Europe, then we should observe a decline in genetic diversity along the
99 recolonization pathway (east to west and south to north). In addition, recolonized areas should be
100 genetically closer to the source basin as compared to conspecifics in alternate basins owing to
101 vicariance during glaciation (i.e. Atlantic vs Pacific). Finally, if refugia were only available in
102 Europe, then hindcasting species distributions should reflect this, that is areas of likely species
103 occurrences lacking persistent ice cover during the LGM should be restricted to Europe. If these
104 hypotheses are rejected, our approach will otherwise yield insight on alternate locations of
105 persistence and the subsequent dynamics of recolonization following glaciation.

107 **Results**
108 *Analysis of sequence data*
109   In order to infer refugial locations and recolonization pathways in Arctic marine forest
110 assemblages, we surveyed and sequenced DNA barcode markers in specimens from several
111 areas. For analytical purposes, we pooled specimens according to the following geographic

112   distinctions: the Northeast Pacific (British Columbia, Canada, and Washington state, USA);
113   Nome, Bering Sea, Alaska (proxy for Pacific migrants into the Arctic); Beaufort, Arctic Ocean,
114   Alaska (proxy for the West North American Arctic); East Canadian Arctic (Cambridge Bay,
115   Nunavut, through to Nain, Labrador); Northwest Atlantic (Makkovik, Labrador, and southwards,
116   including the Canadian Atlantic provinces and New England States, USA); and the Northeast
117   Atlantic (Europe). In total, 4631 specimen records were amalgamated, 2018 of which were
118   collected during this study (2014-2018), representing 42 species of red algae, 49 brown algae,
119   and 18 green algae, for a total of 109 marine macroalgal species with Arctic populations. Of
120   these, 21 species (19%) were sampled exclusively within the Arctic basin, predominantly from
121   the East Arctic region (Table S1; Fig. S2). The genetic results averaged across 31 species-marker
122   combinations revealed Arctic populations that were typically distinct from conspecifics in the
123   Northeast Atlantic and Northeast Pacific. A Principal Coordinates Analysis (PCoA) of genetic
124   distances grouped populations extending from the Bering Sea through to the Northwest Atlantic,
125   within which the East Arctic fell in the middle (Table 1, Fig. 1). Northeast Pacific and Northwest
126   Atlantic populations featured greater genetic diversity, in contrast to comparable populations in
127   Europe, while genetic diversity was depleted in Nome populations and was lowest in the
128   Beaufort (Table 2). The East Arctic, on the other hand, featured levels of genetic diversity
129   comparable to the Northwest Atlantic and Northeast Pacific (Table 2). Interestingly, private
130   haplotypes were detected in all the regions, with the lowest occurrences in the Beaufort. Tajima's
131   D was negative in southerly populations (Northeast Pacific, Northwest Atlantic, and Northeast
132   Atlantic), and was 0 on average for northern populations (Nome, Beaufort, East Arctic). Of the
133   variables analysed, significant differences were detected across the regions in the number of
134   polymorphic sites, the number of haplotypes, the number of private haplotypes, and Tajima's D,
135   generally corresponding to large differences in values between the Beaufort and the Northwest
136   Atlantic. Post hoc tests, however, were unable to detect differences between specific regions
137   (Table S2).

139   The presence of private haplotypes in Arctic populations was further highlighted in the
140   haplotype distributions of some species, particularly in the East Arctic. Noteworthy examples
141   included *Alaria esculenta* (Fig. S44 and S45), *Devaleraea ramentacea* (Figs. S13 and S14),
142   *Rhodomela* sp. 1virgata (Fig. S36), and *Pylaiella washingtoniensis* (Fig. S74). Some species
143   showed signs of admixture between North Pacific and North Atlantic populations, particularly in
144   Churchill (Hudson Bay) and Northern Labrador (Northwest Atlantic); these species included
145   *Coccotylus truncatus* (Fig. S12), *Eudesme borealis* (Fig. S58), *Saccharina latissima* (Fig. S76),
146   *Scagelia pylaisaei* (Fig. S39), and possibly *Chaetopteris plumosa* (Fig. S49) and *Phycodrys*
147   *fimbriata* (Fig. S26). As well, the genetic makeup of several species populations in the Beaufort
148   was markedly different from conspecifics in Nome (Tables 1, 2; Fig. 1), including *Coccotylus*
149   *truncatus* (Fig. S11 and S12), *Odonthalia dentata* (Fig. S23), *Phycodrys fimbriata* (Fig. S26),
150   and *Rhodomela sibirica* (Figs. S34 and S35).

152   *Hindcasting species distributions during the Last Glacial Maximum*
153   In order to further pinpoint marine refugial locations, we used species distribution models
154   to hindcast the availability of suitable habitat during the LGM. Hindcasting results differed
155   between Arctic endemic marine forest species (as proxied by the kelp *Laminaria solidungula*)
156   and cold-temperate species ranging into the Arctic (as proxied by the red alga *Odonthalia*
157   *dentata*). Cold-temperate species featured a present-day circumpolar distribution with large areas

158   of probable occurrence in the North Pacific and North Atlantic. Projections during the LGM
159   similarly indicated areas of probable occurrence throughout the Pacific and Atlantic basins,
160   though highly reduced in total area compared to the present-day projection and particularly
161   limited in South Greenland and the Northwest Atlantic (Fig. 2). Areas of probable occurrence for
162   Arctic endemics for both time projections were more northernly as compared to cold-temperate
163   species, with clear areas of probable occurrence projected in Southern Greenland during the
164   LGM.
165
166   **Discussion**
167   *Recolonization of the Arctic via multiple refugial nuclei*
168   Our understanding of biodiversity patterns in Arctic marine forests has lagged compared
169   to marine animals. The reported similarity of Arctic marine floral assemblages to Atlantic
170   communities was an observation historically at odds with the Pacific origins inferred in Arctic
171   marine fauna, particularly in the Western Arctic (10). Besides noting the "paradox of marine
172   benthic fauna and flora," Dunton (10) also predicted the importance of molecular data in
173   resolving such disjunct perspectives. Today, with over 4500 sequence records for more than 100
174   species, the increased fidelity to resolve historical events in populations of Arctic marine forests
175   can shed light on not just recent origins, but also the potential for evolution and northern
176   adaptation in Arctic marine communities.
177
178   The results presented here reject the hypothesis that Arctic marine forests are entirely or
179   predominantly derived from European conspecifics (9, 10). This was first evident in the genetic
180   distances, which indicated a series of populations extending from the Northwest Atlantic through
181   to the Northern Bering Sea distinct from the Northeast Atlantic and Northeast Pacific (Fig. 1,
182   Table 1). Furthermore, a decline in diversity from the Atlantic into the Arctic was not evident,
183   which ought to occur in the wake of recolonization (Table 2). In fact, levels of diversity were
184   typically highest in the Northwest Atlantic and maintained in the East Arctic, and Tajima's D test
185   suggested at a general trend towards population expansion in the Northwest Atlantic, consistent
186   with the presence of refugia (Table 2, Table S3). Hindcasting also showcased areas of probable
187   occurrence during the LGM in the Bering Sea, Southern Greenland, Northwest Atlantic (though
188   highly limited), in addition to Europe (Fig. 2). Finally, haplotype patterns in several species
189   presented here strongly imply the presence of multiple refugia in the Northwest Atlantic (e.g.
190   *Ceramium virgatum*; Fig. S6).
191
192   Clearly the European recolonization hypothesis, stemming from a legacy of
193   morphological identifications and the persistent perception of inhospitable glacial conditions in
194   the Northwest Atlantic (9, 10), can be put to rest. For one, refugia in the Northwest Atlantic have
195   been increasingly recognized, downplaying the importance of postglacial recolonization from
196   European refugia (2, 16, 17). Trans-Atlantic populations of marine flora also typically exhibit
197   genetic divergence, corresponding to isolation events during the Pleistocene, further supporting
198   the notion that an abundant marine flora was available to recolonize the Artic out of the
199   Northwest Atlantic (18). Assis *et al.* (2) also used ecological niche modelling to hindcast kelp
200   distributions during the LGM, which suggested several species likely survived glaciation in the
201   Northwest Atlantic, a result further supported in the hindcasting results presented here (Fig. 2).
202   Other modelling work indicated Arctic and sub-Arctic Atlantic marine forests have evolutionary
203   origins in the North Pacific owing to Pleistocene climate and geography, suggesting recurring

204 recolonization occurred out of the Pacific (though not necessarily clarifying origins since the
205 LGM; 13).
206
207   Rather, the emerging story of Arctic marine recolonization is more nuanced than
208 anticipated, even in more recent studies. Pacific origins to Arctic flora since the LGM have been
209 speculated in the past (6, 9), interpreted in more recent reviews of floristic surveys (19), and
210 increasingly inferred by molecular data (11; 12). Molecular work has been slow to recognize the
211 significance of unique Arctic lineages that are difficult to reconcile with the emphasis on
212 recolonization hypotheses stemming from refugia south of continental ice-sheets. For instance,
213 Neiva *et al.* (12) attribute an Arctic phylogroup of *Saccharina latissima* restricted to the
214 Canadian Arctic and Western Greenland to unsampled Bering Sea populations, and consistently
215 reveal northern or "cold" phylogroups across the species range. The hesitation to consider
216 northern refugia as a possible explanation (e.g. Southern Greenland) likely stems from several
217 sources, including a lack of comprehensive geographic coverage in genetic sampling, limited
218 insight from single species, and confusion regarding the extent of seasonal ice cover during the
219 LGM. Here, the position of East Arctic genetic distances between populations sampled in the
220 Bering Sea and Northwest Atlantic (Fig. 1) and sustained levels of genetic diversity in East
221 Arctic populations (Table 2) can be attributed to a combination of admixture between Pacific and
222 Atlantic populations and vicariance, the latter of which invoke the presence of high northern
223 refugia. Hindcasting identified the most likely area of occurrence for these refugia along the
224 coastlines of Southern Greenland where ice cover was seasonal during the LGM (Fig. 2; 20),
225 particularly in species specifically outfitted to thrive in Arctic conditions (e.g. *Laminaria
226 solidungula*). It is worth noting hindcasting results are consistent with the work of Assis *et al.*
227 (2), though these authors also inferred high Arctic refugia in areas we identified as having
228 persistent ice cover (namely Baffin Island and Northern Labrador). In sum, the origin of Arctic
229 marine forests, as revealed by our community level analysis, forwards the West Arctic as likely
230 derived from Bering Sea refugia, while the East Canadian Arctic exhibits a "melting pot"
231 character, with input from the Pacific, the Atlantic (predominantly the Northwest), and Arctic
232 refugia.
233
234 *High northern refugia drive Arctic endemism*
235   The conclusion that refugia were abundant and occurred far north offers an explanation
236 for marine Arctic endemism, which is generally assumed to be rare or impossible given the
237 perception of intolerable ice conditions during the LGM. Lee (9) suggested less than 7% of the
238 Arctic flora was confined to the Arctic and perceived low levels of adaptation, characterizing the
239 flora as "ecologically immature." More recent estimates bump up the level of Arctic endemism
240 to 13.5% (21). Molecular taxonomic work reflects the trend towards recognizing Arctic
241 affinities, for example, in the recently described species *Ahnfeltia borealis*, *Chorda borealis*, and
242 *Eudesme borealis* (22). Here, 21 species (19%) of the sampled flora appeared to be confined to
243 the Arctic, not to mention the cryptic lineages reported by Laughinghouse *et al.* (14), Küpper *et
244 al.* (15), and species with distinct Arctic populations reported here (e.g. *Alaria esculenta*; Fig.
245 S45 and S46). Altogether, these results suggest that a large portion of the Arctic flora has
246 persisted far north through cycles of glaciation, raising the possibility that Arctic marine forests
247 do not simply tolerate but rather are adapted to polar conditions.
248

249   The implications of these findings extend beyond marine forests. Patterns in
250 accompanying hard-bottom marine fauna, some of which thrive in the habitat provided by
251 macroalgae, are readily resolved by invoking northern refugia. A phylogeographic review of
252 Arctic marine fauna highlighted substantial geographical subdivision in the COI-5P complex of
253 the polychaete *Harmothoe imbricata*, with lineages that appeared to be restricted to the East
254 Canadian Arctic (23). The presence of cryptic Arctic lineages was further revealed in
255 polychaetes (24), molluscs (25) and amphipods (26). In concert with the results for Arctic
256 forests, these studies demonstrate the resilience of Arctic marine communities to cycles of
257 glaciation and the potential for adaptation to extreme-cold environments. Given the relative
258 scarcity of genetic surveys in the Arctic, these results also suggest levels of Arctic marine
259 endemism remain underestimated, a disparity that is likely further exacerbated at the population
260 level.
261
262   On a final note, it is possible northern refugia are not confined to the Southern coast of
263 Greenland. Though the Western Arctic was locked in multi-year sea ice, portions of the Siberian
264 coastline as far east as the Laptev Sea appear to have remained seasonally ice-free at least as
265 early as 16 ka (27). This was due to warm Atlantic water entering the Arctic through the Fram
266 Strait, which may have provided Arctic refuge for marine forests. The role of katabatic winds
267 and the formation of polynyas, recurrent areas of ice-free water, also may have played a role
268 maintaining a seasonally ice-free shoreline (27). The modern day Arctic features numerous
269 polynyas, particularly along the margins of the Arctic basin, enhancing early spring productivity
270 and creating biodiversity hotspots (28). Lee (9) even describes seaweed communities in a
271 polynya near Brock island (78ºN), including *Laminaria solidungula*, *Desmarestia viridis*, and
272 *Turnerella pennyi*. Hypotheses regarding the role of polynyas maintaining Arctic refugial
273 locations during the LGM may need to be invoked to explain the population structure of the
274 Beaufort, which is oddly more genetically distant from Atlantic conspecifics than Nome
275 populations (which are geographically further away, Fig. 1). We do caution in interpreting this
276 pattern, however, given the limited sampling of the West Arctic/Bering Sea, lack of sampling
277 from Russia, and "founder-takes-all" effects, which can result in sharp demarcations in
278 macroalgal population structure, even at small spatial scales (29). Even so, if history is an
279 indication, we need to temper our assumptions regarding the inability for marine forests to
280 flourish in areas with "harsh" ice conditions.
281
282 *Conclusions*
283   Over the decades, our understanding of Arctic marine forests has gradually evolved from
284 a one-vector ecosystem stemming from European refugia to many melding pathways, and from a
285 biologically depauperate expanse into a complex genetic landscape. Ultimately, our goal was to
286 provide a checkpoint in our understanding of Arctic marine diversity, particularly by sampling
287 Arctic locations where DNA barcode surveys are rare or absent (i.e. Bering Sea, East Arctic,
288 Northern Europe) and by summarizing genetic patterns across macroalgal species with sequence
289 data from the Arctic. We emphasize the significance of summarizing insight across species, with
290 over 100 examined through this work spanning three phyla and two kingdoms of life, and
291 extensively so in 26 (Table S1; Fig. S1). Single-species studies have struggled to reconcile post-
292 glacial dynamics, particularly where findings do not align with prevailing views (e.g. 12, 14). As
293 well, a population genetic approach to resolving these patterns in Arctic marine communities
294 oftentimes falls short of conclusive owing the inherent difficulty in sampling any individual

295 location and subsequent limited geographical coverage for analysis. Ecological niche modelling
296 can close these gaps in our knowledge by highlighting likely locations of persistence during
297 glaciation and aiding in the interpretation of genetic patterns.
298
299   We forward the view that the marine Arctic environment was recolonized from numerous
300 and globally distributed source populations, including unrecognized far northern refugia that
301 additionally contribute to endemism in polar waters. This work raises the possibility of
302 investigating complex evolutionary processes born out of the Arctic environment, particularly
303 the interplay between incipient speciation and secondary contact, and adaptation to the marine
304 Arctic environment. Ecosystem management will need to acknowledge diversity endemic to the
305 Arctic and the potential impacts of climate change on these populations. Future work should
306 emphasize sampling in Russia where DNA barcodes are virtually absent, and Southern
307 Greenland as a putative refugial location. A consensus must also be reached regarding the extent
308 of persistent sea ice cover during the LGM, and what role, if any, continental ice-sheets had in
309 extirpating marine populations. As well, given the range of challenges and limited opportunity to
310 sample the marine Arctic environment, future collectors should consider sampling protocols
311 amendable to downstream genomic analyses, whatever the primary purpose for Arctic fieldwork.
312 The DNA barcode surveys presented here are a checkpoint towards the genomic era of Arctic
313 investigations, a realm that will certainly reveal novel and exciting insight into levels of
314 biodiversity in the Arctic, and potential for further adaptation and evolution in a changing
315 climate.
316
317 **Materials and Methods**
318
319 *Genetic data and analyses*
320   Marine macroalgae were sampled in several key locations across the Arctic over the
321 course of five years, including Japan; Kamchatka (Russia); Haida Gwaii, British Columbia,
322 Canada; Nome, Alaska (Northern Bering Sea); the Beaufort Sea, Northern Alaska; Cambridge
323 Bay (Nunavut, Canada); Hudson Bay, Manitoba, Canada; Baffin Island, through Northern
324 Labrador to Makkovik, Canada; and Bergen, Norway. Specimen records, including pictures,
325 collection information, sequence data, and GenBank accessions can be accessed via the Barcode
326 of Life Data System (BOLD; doi: dx.doi.org/10.5883/DS-TAMMA) and FigShare:
327 (https://doi.org/10.6084/m9.figshare.11301929.v1). Marine macroalgae were generally collected
328 from the intertidal and via scuba, but occasionally via dredge. A portion of each specimen
329 (approx. 1 cm^2) was preserved in silica gel for DNA extraction, while several representatives of
330 putative species were preserved as pressed vouchers. Specimens were brought back to the
331 University of New Brunswick (where specimens are stored) for DNA extraction. Several genes
332 were amplified, including the 5' end of the cytochrome *c* oxidase subunit I gene (COI-5P) in red
333 and brown algae, *tufA* in green algae, and partial reads of the ribulose-1, 5-biphosphate
334 carboxylase large subunit (*rbc*L-3P; Table S4) in red and brown algae. Secondary markers were
335 acquired in select species, including the full length nuclear internal transcribed spacer region
336 (ITS) and plastid *ycf35*, in order to further clarify or support COI-5P patterns (Table S4).
337 Successful PCR products were sent to Genome Quebec for forward and reverse sequencing. All
338 genetic data were edited in Geneious v.8.0 (30), and any relevant previously published DNA
339 barcodes were added to the dataset.
340

341   Populations were pooled for analysis according to broad geographic regions: Northeast
342 Pacific (British Columbia, Canada, and Washington state, USA); Nome, Alaska (proxy for
343 Pacific migrants into the Arctic); Beaufort, Alaska (proxy for the West North American Arctic);
344 East Canadian Arctic with the southern distribution delimited using the 10°C air temperature
345 isotherm for July (Cambridge Bay, Nunavut, through to Nain, Labrador); Northwest Atlantic
346 (Makkovik, Labrador, and southwards, including the Canadian Atlantic provinces and New
347 England States, USA); Northeast Atlantic (Europe; Fig. 2). The Northwest Pacific was excluded
348 given the paucity of data. Species generally corresponded to Barcode Index Numbers (BINs), a
349 binning system provided through BOLD which utilizes a fluid threshold to proxy species units
350 based on levels of intra- and inter-specific genetic variation (31). Species were included in
351 genetic analyses provided they featured in at least one Arctic region for which $\geq$10 individuals
352 were sampled. Out of 109 species sampled with Artic populations, we analysed 26 (Fig. S1), five
353 of which had sequence data from multiple markers, for a total of 31 species-marker
354 combinations. All 109 species were considered in additional analyses evaluating total diversity
355 levels in the Arctic, which were used to quantify the number of Arctic endemic species. These
356 analyses are presented as supplementary material, and include accumulation curves of all
357 genotypes sampled (32; Fig. S2), a table interpreting haplotype patterns in all 109 species
358 sampled (Table S1), and haplotype maps and networks (Figs. S3-S95).
359
360   Various populations statistics were calculated for each region, including measures of
361 genetic diversity, genetic differentiation, and Tajima's D test for neutrality. Sequences were
362 truncated to the shortest length sequence within each species prior to all genetic analyses.
363 GenAlEx 6.51 (33) was used to run an Analysis of Molecular Variance (AMOVA) and derive
364 values of PhiST (Φ_{ST}), an analogue to Fst that incorporates nucleotide diversity in distance
365 calculations (i.e. haplotypes are not assumed to be equidistant from each other). Calculations for
366 Φ_{ST} followed that of Miermans (34). Pairwise tests for significant Φ_{ST} values were conducted
367 using 9999 permutations of the dataset. Null values for Φ_{ST} occurred wherein two populations
368 were monotypic for the same haplotype and were changed to 0 (no genetic differentiation).
369 Species specific analyses are presented in Table S5. Φ_{ST} values were averaged for each region
370 across all species, and a Principal Coordinates Analysis (PCoA) was conducted on the pairwise
371 distance matrix using the covariance-standardized method in GenAlEx. Given notably few
372 measurements were available between the Northeast Pacific and the Beaufort (only two species
373 with 2-7 records from the Beaufort, and no genetic differentiation), we "normalized" this
374 pairwise distance by taking the average of genetic distances between the Northeast Pacific and
375 Nome, and the Northeast Pacific and the East Arctic. The unaltered PCoA figure is presented in
376 Figure S96. We also conducted the same analysis with low sample size populations removed
377 (<10 individuals; Fig. S97). Alternate PCoAs revealed the same pattern, except the Beaufort
378 grouped closer to the Northeast Pacific when not "normalized."
379
380   Frequency based parameters were also calculated for each region within each species,
381 including the number of haplotypes (Na), the number of effective alleles (Ne), the number of
382 private haplotypes within populations (N$_{PH}$), and haplotype diversity (h). Ambiguous sites were
383 removed for these calculations. DnaSP v6 (35) was also used to calculate the number of
384 polymorphic sites, nucleotide diversity (θ_{π}), and Tajima's D statistic with accompanying p-
385 values. These results were again averaged across all species-marker combinations, and
386 differences in measures between populations were assessed using Kruskal-Wallis H tests (36).

387 Dunn's post hoc tests with Bonferroni corrections were performed for variables yielding
388 significant Kruskal-Wallis H tests. The analyses for individual species are presented in Table S3,
389 and the post hoc tests are presented in Table S2.
390
391 *Hindcasting species distributions*
392   The distribution of marine forests during the Last Glacial Maximum was inferred using
393 ecological niche modelling. Modern and paleo marine environmental data layers were
394 downloaded from MARSPEC (37, 38), in particular, bathymetry, mean annual sea surface
395 temperatures (SST) and SST of the coldest ice-free month. Seaweed distributions are highly
396 tuned to marine isotherms, and ecological niche modelling consistently indicate SST is the most
397 important variable in modelling macroalgal species distributions (2). Paleo environmental data
398 layers represent average values as derived from six coupled ocean atmosphere general circulation
399 climatic models, including salinity-adjusted CCSM3. Occurrence records were gathered for
400 *Odonthalia dentata* and *Laminaria solidungula*. These species were selected to proxy
401 distributions in boreal to temperate species with Arctic populations (i.e. the classical view of
402 Arctic marine forests; *O. dentata*), and putative Arctic endemic species (*L. solidungula*). These
403 species were also selected given they are reliably distinguished morphologically, and as such,
404 historical records would not be conflated by cryptic species. Occurrence records were derived
405 from Lüning (6). Distribution maps were scanned and georeferenced, and GPS locations for
406 occurrences were subsequently derived. For continuous distributions, GPS coordinates were
407 haphazardly recorded at approximately 250 km intervals. Historical occurrence records were
408 then pooled with locations from DNA barcode records (BOLD), and the Macroalgal Herbarium
409 Portal (https://macroalgae.org/portal/index.php). To correct for sampling bias during training of
410 the ecological niche models, occurrence records in close proximity to each other were randomly
411 removed using the R package spThin (39), with a thinning parameter of 100 kms. The resulting
412 datasets kept 111/260 occurrence records for *Odonthalia dentata*, and 87/164 for *Laminaria*
413 *solidungula* (FigShare: https://doi.org/10.6084/m9.figshare.11301929.v1). The thinned
414 occurrence records and environmental layers were then trained using Maxent (40) and projected
415 onto conditions during the LGM. Models were built using threshold features in order to better
416 reflect lethal temperature limits in macroalgae, and model performance was assessed using cross
417 validation. A regularization multiplier of 1 was used, as was a default prevalence of 0.5 (the
418 probability of presence at average presence locations). Clamping was used to restrict variables
419 outside the training range. Multivariate Environmental Similarity Surfaces (MESS) were also
420 used to evaluate the distribution of environmental values outside the training data range
421 projected during the LGM, which functioned to indirectly map persistent ice cover and restrict
422 inferences of refugial locations to seasonally ice-free waters. Output asc files were converted to
423 figures in R using ggmap and ggplot2 packages (39).
424

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528

529   **Acknowledgments**

546   **Figures Legends**
547   **Fig. 1**. **Principal Coordinates Analysis results for genetic distances between the sampled
548   regions.** Genetic distances are inferred from 31 species-marker combinations. Positive and
549   negative symbols represent the distributions of coordinates with ±SE.
550
551   **Fig. 2. Present day and Last Glacial Maximum distributions of Arctic marine forest
552   species.** Endemic species are proxied by the kelp *Laminaria solidungula*, and cold-temperate
553   species ranging into the Arctic are proxied by the red alga *Odonthalia dentata*. The heatmap
554   represents relative probability of occurrence amongst global marine locations as proxied by mean
555   annual sea surface temperatures and temperatures of the coldest ice-free month. Light grey areas
556   represent persistent ice cover during the LGM.
557

558
559 **Fig. 1**
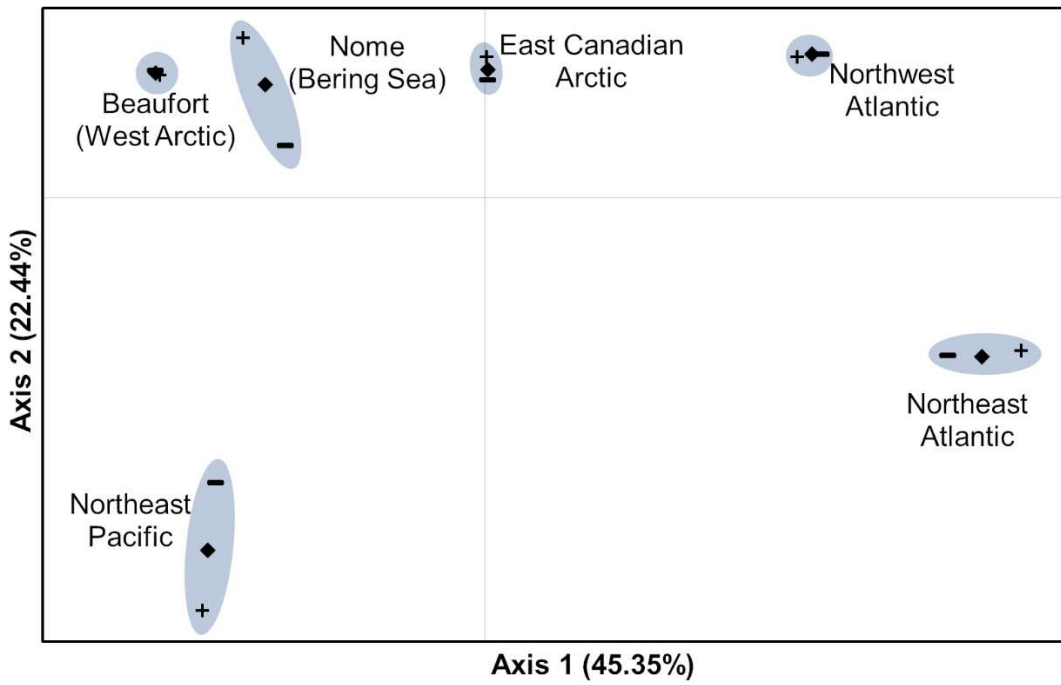
560
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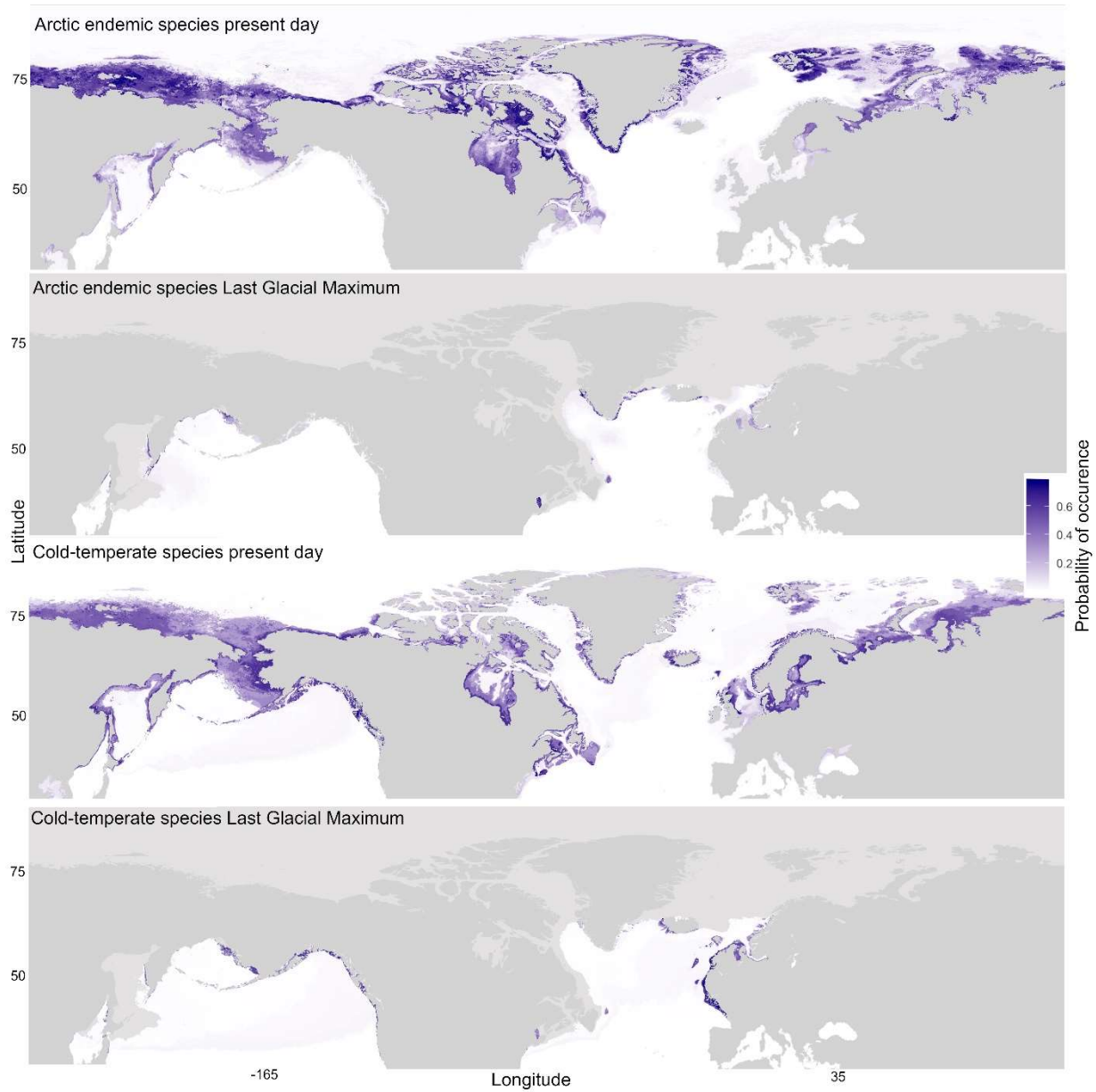
562 **Table 1. Genetic distances (Φ_{ST}) between pairwise populations in 26 species of marine**
563 **macroalgae with Arctic populations**. Genetic distances were evaluated based on four genetic
564 markers (COI-5P, *tufA*, ITS, *ycf35*). Note, the pairwise value between Beaufort and the Northeast
565 Pacific was "normalized" by taking the average of genetic distances between Nome and the NE
566 Pacific, and the East Arctic and NE Pacific. Sample sizes for pairwise distances are in the top
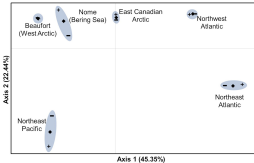567 right corner of the table. SE for genetic distances are indicated in brackets.

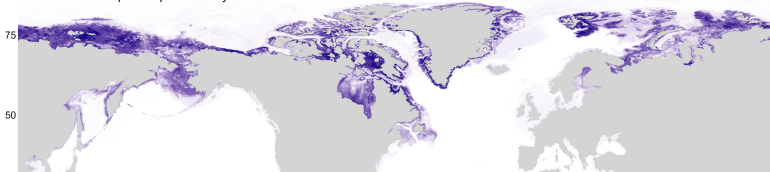|	Northeast Pacific	Nome, Alaska	Beaufort, Alaska	East Arctic	Northwest Atlantic	Northeast Atlantic
Northeast Pacific	-	6	-	8	8	4
Nome, Alaska	0.438(0.158)	-	11	20	17	5
Beaufort, Alaska	0.471(0.141)	0.251(0.089)	-	15	12	5
East Arctic	0.503(0.124)	0.300(0.059)	0.338(0.090)	-	27	11
Northwest Atlantic	0.751(0.101)	0.518(0.085)	0.675(0.089)	0.347(0.063)	-	11
Northeast Atlantic	0.822(0.141)	0.741(0.149)	0.867(0.086)	0.539(0.109)	0.437(0.131)	-

568

Table 2. Summary statistics for populations of Arctic marine macroalgae with Arctic populations. n = sample size (number of species), bp = number of basepairs, N_{poly} = number of polymorphic nucleotide sites, Na = number of haplotypes, Ne = number of effective alleles, N_{PH} = number of private haplotypes, h = haplotype diversity, θ_π = nucleotide diversity, D = Tajima's test for neutralilty, p= Kruskal-Wallis tests for independent distributions of values (Dunn's post hoc tests with Bonferroni correstion did not detect disgnificant pairwise differences); NE=Northeast, NW=Northwest. Note sample sizes from NE Pacific to NE Atlantic in N_{PH} are 10, 20, 16, 31, 29, 13, and from NE Pacific to Overall in D, 6, 15, 5, 23, 19, 5, 31. Values for 1 SE are presented below values for each variable.
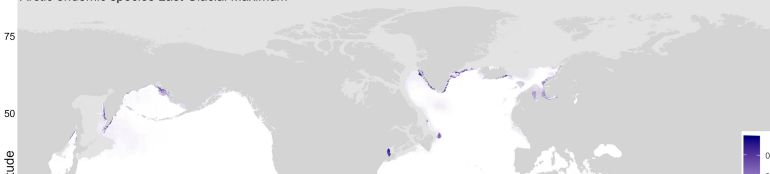
Location	NE Pacific	Nome	Beaufort	East Arctic	NW Atlantic	NE Atlantic	Overall	p
n	8	20	15	31	27	11	31	
bp	649	639	625	631	632	593	631	
N_{poly}	5.375	1.600	1.000	4.387	4.444	1.727	9.516	**0.021**
	2.187	0.461	0.390	0.931	0.894	0.740	1.433	
Na	4.000	2.300	1.933	2.935	4.148	2.273	8.097	**0.041**
	1.102	0.242	0.330	0.321	0.574	0.702	0.995	
Ne	1.782	1.542	1.312	1.753	1.821	1.474	2.834	0.157
	0.334	0.115	0.136	0.141	0.192	0.248	0.265	
N_{PH}	2.500	1.000	0.625	1.323	2.655	1.538	-	**0.035**
	0.806	0.218	0.202	0.287	0.526	0.656		
h	0.32325	0.29515	0.14760	0.32958	0.32674	0.20782	0.53132	0.143
	0.09617	0.04919	0.05954	0.04680	0.05140	0.07419	0.04820	
θ_π	0.001544	0.000744	0.000399	0.001873	0.001383	0.000852	0.002605	0.093
	0.000794	0.000268	0.000181	0.000407	0.000569	0.000345	0.000395	
D	-1.19122	-0.02702	0.01276	-0.00114	-1.06532	-0.60136	-0.25835	**0.012**
	0.35562	0.29170	0.44359	0.28512	0.21389	0.53250	0.21314	

Axis 2 (22.44%) — vertical axis

Axis 1 (45.35%) — horizontal axis

Beaufort (West Arctic)

Nome (Bering Sea)

East Canadian Arctic

Northwest Atlantic

Northeast Atlantic

Northeast Pacific