Vol. 589: 45–58, 2018
https://doi.org/10.3354/meps12496

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published February 23[§]

Mitochondrial DNA sequence data reveal the origins of postglacial marine macroalgal flora in the Northwest Atlantic

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ABSTRACT: Following the Last Glacial Maximum, the marine macroalgal flora in the Northwest (NW) Atlantic reportedly recolonized from Northeast (NE) Atlantic refugia. Genetic evidence for the few species tested, however, has indicated that some species survived glaciation in the NW Atlantic. Owing to the significant amount of data currently available, we sought to determine if COI-5P (5′ end of the cytochrome *c* oxidase subunit I gene) could distinguish between populations surviving glaciation on both sides of the Atlantic versus postglacial recolonization. COI-5P results were consistent with published findings using other markers in *Chondrus crispus*, *Mastocarpus stellatus*, *Palmaria palmata*, and *Saccharina latissima*. Having success, we then analyzed molecular data for several species of red and brown macroalgae to date isolation times between NE and NW Atlantic populations and determine what percentage of species survived in NW Atlantic refugia. We generated and gathered genetic data from COI-5P in 1560 specimens representing 20 amphi-Atlantic species, and estimated isolation times between NE and NW populations using calibrated red and brown COI-5P clocks in IMa2. Of the species surveyed, 60% had isolation time estimates between NE and NW Atlantic populations predating the Last Glacial Maximum. Recent shared ancestry was inferred in the remaining cases. Our results indicate that local refugia and/or trans-Arctic migration from the Pacific are the source populations for the majority of the NW Atlantic macroalgal flora. By shedding light on the phylogeographic history of the North Atlantic, we can better understand the nature of postglacial recolonization and forecast future changes to the NW Atlantic and Canadian Arctic.

KEY WORDS: COI-5P · Glacial refugia · Macroalgae · North Atlantic · IMa2 · Last Glacial Maximum · Seaweed

INTRODUCTION

Glaciation events undoubtedly had a major influence on present-day biota and biogeographic distributions. In the North Atlantic, glaciation events resulted in ice sheets covering most of the northern coastlines, displacing or extirpating local populations repeatedly over the past ~2.6 million years (Myr) (Miller et al. 2010a). Recent climate change, however, is accelerating warming in the Arctic and potentially allowing southerly biota to move northward, particularly marine species (Vermeij & Roopnarine 2008, Miller et al. 2010b, IPCC 2014, Renaud et al. 2015). Macroalgae act as ecosystem engineers, providing food and habitat for other species (Christie et al. 2009) and are known to raft invertebrate taxa across large oceanic distances (Fraser et al. 2011, Macaya et al. 2016). As such, macroalgae can be used to predict future changes in marine species distributions along boreal and arctic shorelines in light of diminishing perennial ice cover (Jueterbock et al. 2016). By understanding the origins of Arctic macro-

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[§]Substantial corrections were made after publication. For details see www.int-res.com/abstracts/meps/v589/c_p45-58/ This corrected version: October 26, 2018

algae, we may be able to better predict northward movement of larger-scale communities of marine species.

Understanding the origins of marine algae in the Canadian Arctic begins with understanding the origins of the Northwest (NW) Atlantic flora. Arctic species of algae are traditionally believed to be a northward range extension of cold-adapted species on the east coast of Canada (Taylor 1957, Lee 1973). Meanwhile, the prevalent understanding of the NW Atlantic marine flora was that it was extirpated during the Last Glacial Maximum (LGM), and subsequently repopulated from Northeast (NE) Atlantic populations (Vermeij 1978, Ingolfsson 1992). If true, then Arctic marine algae would have recent origins stemming from European populations. Extirpation of the NW Atlantic flora during glaciation was predicated on several factors, namely, (1) the paleoclimatic history of the NW Atlantic was much harsher as compared to the NE Atlantic (Knott & Hoskins 1968, Pflaumann et al. 2003), (2) constricted isotherms and a lack of suitable substrate south of the Laurentide Ice Sheet (Vermeij 1978, Ingolfsson 1992, Maggs et al. 2008), and (3) species lists indicated that the NW Atlantic flora appeared to be a subset of NE species, with few endemics to the NW Atlantic (Taylor 1957, South 1983, Ingolfsson 1992). The 'tabula rasa' hypothesis, the notion that all NW Atlantic flora and fauna are the result of postglacial recolonizations, has since undergone substantial scrutiny with the advent of molecular data (Brochmann et al. 2003).

A surge in genetic data and mathematical modeling is shedding new light on the phylogeographic origins of algal communities (e.g. Hu et al. 2016). This surge in data has been partly propelled by the DNA barcoding movement, which utilizes a 664 basepair (bp) fragment of the 5′ end of the cytochrome *c* oxidase subunit I (COI-5P) gene to assign specimens to previously sequenced and identified species (Saunders 2005, Le Gall & Saunders 2010). The accumulating data can be used to make inferences regarding the phylogeographic history of the North Atlantic, such as examining allelic diversity to test the 'tabula rasa' hypothesis or determine if certain populations survived in refugia. These contrasting scenarios are expected to have left distinct signatures in the genetics of amphi-Atlantic populations of marine macroalgal species. If the NE or NW Atlantic flora was reestablished by its neighboring basin within the past 10 000 yr, there should be little to no genetic divergence between amphi-Atlantic populations (Li et al. 2016a, their Fig. 12.1); directionality of recolonization may be inferred depending on the resolution of the data. In particular, recently established populations should represent a subset of the allelic diversity found in parental populations (Maggs et al. 2008). If macroalgal flora survived in refugia on both sides of the Atlantic, this should appear as divergent lineages between NE and NW Atlantic populations (Li et al. 2016a, their Fig. 12.1).

Genetic studies into the phylogeographic history of amphi-Atlantic marine flora and fauna suggest that both scenarios commonly occurred. Wares & Cunningham (2001) used COI data to conclude that 4 species of intertidal invertebrates in the NW Atlantic recolonized from Europe since the LGM, while 2 species appeared to have survived the most recent glaciation event. In addition, the authors pointed out several species of intertidal invertebrates endemic to the NW Atlantic with sister species in European waters, further suggesting that these species survived repeated glaciation in the NW Atlantic (Wares & Cunningham 2001). Genetic studies on amphi-Atlantic species of macroalgae are revealing a similarly mixed picture. Macroalgal species for which genetic data are consistent with recent recolonization of the NW Atlantic from the NE include *Mastocarpus stellatus* (Stackhouse) Guiry (*cox*2-3, ITS, and RLS data; Li et al. 2016b), *Porphyra umbilicalis* Kützing (ITS, 18S; Teasdale & Klein 2010), *Fucus spiralis* Linnaeus, and *F. vesiculosis* Linnaeus (microsatellite data and mtIGS, Coyer et al. 2011a). Interpretations of phylogeographic patterns in *Chondrus crispus* Stackhouse vary; Hu et al. (2010) concluded that this species recolonized the NW Atlantic postglacially, whereas Hu et al. (2011) and Provan & Maggs (2012) concluded that this species survived in NW Atlantic refugia. Recent findings in other species indicate that populations survived on both sides of the Atlantic during the LGM, including *Ascophyllum nodosum* (Linnaeus) Le Jolis (2 microsatellites and mtIGS and *trn*W; Olsen et al. 2010), *F. distichus* Linnaeus (mtIGS and COI-5P; Coyer et al. 2011b), *Palmaria palmata* (Linnaeus) F. Weber & D. Mohr (*cox*2-3 and plastid *rpl-rps* data; Li et al. 2015), and *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders (COI-5P and microsatellites; Neiva et al. 2018). In a survey of the Arctic flora in Churchill (Canada), Saunders & McDevit (2013) found that of 6 species for which limited amphi-Atlantic COI-5P data were available, 4 showed distinct haplotypes between the NW and NE Atlantic.

In light of these recent studies, the 'tabula rasa' hypothesis regarding NW Atlantic marine macroalgae can clearly be rejected in favor of a more nuanced picture, wherein some species survived

glaciation in the NW Atlantic while others did indeed migrate recently out of the NE Atlantic (to our knowledge, no macroalgal species are recorded recolonizing the NE Atlantic from the NW). Given the vast amount of DNA barcode data that has accumulated over the past decade (Saunders 2005), we decided to (1) determine if COI-5P was a suitable proxy for inferring whether or not a given species may have recolonized the NW Atlantic since the LGM or if the species survived in refugia, and (2) screen COI-5P data in 20 amphi-Atlantic species of macroalgae to quantify the percentage of species that appear to have survived glaciation in the NW Atlantic (as evidenced by divergent NE and NW Atlantic populations) versus the percentage of species that may have recent origins in the NE Atlantic (as evidenced by low divergence times estimates between NE and NW Atlantic populations). While we do not make inferences about population history beyond isolation times (e.g. estimating migration vectors and effective population sizes), we hope that our broad approach to inferring the origins of NW Atlantic flora will lead to more detailed analyses that will enhance our understanding of phylogeographic patterns in specific species, particularly in cases where NW and NE populations are closely related and the directionality of putative postglacial recolonization remains uncertain.

MATERIALS AND METHODS

Sampling and sequencing of macroalgae

In order to infer whether or not NW Atlantic populations of marine algae are the result of survival in glacial refugia, and identify cases where ancestry is recent between NE and NW Atlantic populations, macroalgae were sampled from Europe and 487–664 bp of COI-5P data were compared from European populations to existing and newly generated COI-5P records from the NW Atlantic (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m589p045_supp.pdf). We specifically sampled the area surrounding Bergen, Norway (3–14 June 2016), and various locations in the NW Atlantic (2014–2016; Table S1). Specimens were collected from the intertidal and subtidally via scuba, and occasionally via dredge in Norway. Specimens were stored in plastic bags and returned to the lab for processing, which consisted of assigning a specimen ID and storing a cm^2 portion of tissue in silica for DNA extraction with pressed material prepared as representative vouchers (Saunders & McDevit 2012). Collections were supplemented with available records from the Barcode of Life Datasystem and from publicly available data on GenBank (Table S1).

DNA extraction and amplification procedures were followed as per Saunders & McDevit (2012), using a Qiagen TissueLyser II and QIAxtractor robot for high-throughput protocols for COI-5P amplification. The red algal primers M13LF3 (5′-TGT AAA ACG ACG GCC AGT ACH AAY CAY AAR GAT ATH GG-3′) and M13Rx (5′-CAG GAA ACA GCT ATG ACA CTT CTG GRT GIC CRA ARA AYC A-3′; Saunders & Moore 2013) and the brown algal primers GazF2 (5′-CCA ACC AYA AAG ATA TWG GTA C-3′) and GazR2 (5′-GGA TGA CCA AAR AAC CAA AA-3′) were used (Lane et al. 2007). The primers GWSFn (5′-TCA ACA AAY CAY AAA GAT ATY GG-3′; Le Gall & Saunders 2010) and GWSRx (5′-ACT TCT GGR TGI CCR AAR AAY CA-3′; Saunders & McDevit 2013) were used for some specimens of the red algal genus *Coccotylus*. Our thermocycling regime consisted of an initial temperature of 94°C for 2 min; 5 cycles of 94°C for 30 s, 45°C for 30 s, and 72°C for 1 min; 35 cycles of 94°C for 30 s, 46.5°C for 30 s, and 72°C for 1 min; and a final elongation step of 72°C for 5 min (Saunders & Moore 2013). PCR products were visualized using gel electrophoresis on an 0.8% agarose gel. Successful PCR products were sent to Genome Quebec for forward and reverse sequencing using the sequencing primers M13F (5′-TGT AAA ACG ACG GCC AGT-3′) and M13R (5′-CAG GAA ACA GCT ATG AC-3′; Saunders & Moore 2013) for red algae (with the exception of *Coccotylus* specimens, which were sequenced using GWSFn and GWSRx primers) and GazF2 and GazR2 for brown algae. All genetic data were edited in Geneious version 8.0 (www.geneious.com; Kearse et al. 2012).

Haplotype networks and maps

The population structure of North Atlantic populations was visualized using COI-5P haplotype maps and networks. Species were included in the analyses if they were not listed as being introduced (e.g. moved between NE and NW Atlantic basins by human activity) and we had at least 5 sequences for a given species from both sides of the Atlantic; see Table S2 for amphi-Atlantic species not meeting these criteria and subsequently removed from the dataset). The cut-off for pooling divergent populations was a maximum pairwise distance of 2% between haplotypes except in the case of *Ceramium*

virgatum Roth given the exceptionally wide and continuous range of haplotypes sampled. We also ignored alpha taxonomy, in particular pooling data for *Dilsea carnosa* (Schmidel) Kuntze and *D. socialis* (Postels & Ruprecht) Perestenko given that they were within the 2% threshold for genetic relatedness. Haplotype networks were visualized using TCS v1.21 (Clement et al. 2000), and haplotype maps and networks were created in PowerPoint. TCS was also used to assign a putative ancestral haplotype for each species (Castelloe & Templeton 1994). The majority of the COI-5P haplotype maps and networks can be found in Figs. S1–S18 in the Supplement.

Assessment of COI-5P as a proxy for glacial survival or postglacial recolonization

In order to determine if COI-5P was a reliable proxy for recent population history in the North Atlantic, we compared our results to detailed findings in *Chondrus crispus* (Hu et al. 2010, 2011, Provan & Maggs 2012), *Mastocarpus stellatus* (Li et al. 2016b), *Palmaria palmata* (Li et al. 2015), and *Saccharina latissima* (Neiva et al. 2018).

Dating divergence times

Isolation times were estimated in amphi-Atlantic species of red and brown algae that met our selection criteria. We began this process by calibrating separate red and brown algal COI-5P clocks, and calculating minimum, medium, and maximum rate estimates for each clock. The red algal COI-5P substitution rate was estimated using the pooled NE and NW Atlantic divergence time of 0.906 Myr in *P. palmata* (Linnaeus) F. Weber & D. Mohr, which was estimated using mitochondrial *cox*2-3 and plastid *rplrps* markers (Li et al. 2015). Owing to an error by Li et al. (2015), who confused sequence divergence with substitution rate, we had to double the isolation times reported by them. This clock was initially calibrated using divergence estimates in *Bostrychia calliptera* (Montagne) Montagne and *B. pinnata* J. Tanaka & Chihara, and a calibration point of the closing of the Isthmus of Panama 3–3.5 Myr ago (Zuccarello & West 2002). In order to estimate the COI-5P mutation rate, 20 COI-5P haplotypes (661 bp) from *P. palmata* were analyzed in BEAST 1.8.3 (Drummond et al. 2012) using the following parameters: an HKY substitution model (given this model would be used in IMa2 analyses); a strict clock; a coalescent Bayesian skyline tree prior (Drummond et al. 2005); a UPGMA starting tree; a prior for the root height of the tree set to a mean of 906000 yr with a normal distribution truncated around 696000 and 1432000 yr (as per pairwise population minimum and maximum isolation time estimates of Li et al. 2015), and a standard deviation of 100; and uninformative (e.g. uniform) priors for base frequencies, kappa, and population size parameters. A 10 million length chain was run with sampling every 1000 steps. The analysis was completed 5 times, and combined results were viewed in Tracer v1.6.0 (Rambaut et al. 2014) with a burn-in of 1 million steps for each analysis. The combined results provided a final HKY clock rate of 0.007 substitutions site^{-1} Myr^{-1} (95% highest posterior density estimates of 0.00298 and 0.01169, which acted as minimum and maximum rate estimates in our IMa2 analyses, see below). The brown algal COI-5P mutation rate was estimated based on a 10–16 Myr divergence time in *Fucus spiralis* and *Ascophyllum nodosum*. This divergence time had been previously estimated using 2 independent approaches: (1) indirectly based on a *psbA* clock calibration in diatoms (Hoarau et al. 2007), and (2) calibration using fossil record evidence (Silberfeld et al. 2010, Cánovas et al. 2011). Due to a lack of known haplotypes in these species, F84 genetic distance was calculated between a single COI-5P sequence from each species using the dnadist program in PHYLIP v.3.695 (Felsenstein 1989). The resulting F84 distance (0.063582) was divided by 2 (0.031791), and then by 10, 13, and 16 for fast, medium, and slow HKY clock rate estimates of 0.0031791, 0.002446, and 0.001987 substitutions site^{-1} Myr^{-1}. These clocks were subsequently converted to locus-wide substitution rates yr^{-1} for IMa2 analyses, which consisted of multiplying the HKY clock rate by the species-specific COI-5P bp length and dividing by 1 million.

Isolation times between NE and NW Atlantic populations were calculated in IMa2, a program that uses a Bayesian search strategy and coalescent theory to estimate population parameters (Hey 2010). With regards to our prediction, we were only interested in isolation times between populations, and ran strictly isolation models. Once the run parameters (priors, heating terms) were optimized, 3 independent 1 million length chains were run for each species using an HKY substitution model, and geometric heating (10 chains), with sampling every 100 steps, for a total of 10000 genealogies saved per run. The results from the 3 species-specific runs were combined using L mode, and the highest value of the posterior distribution after smoothing was used as the isolation time

estimate between NE and NW basins. Convergence on estimates was assessed based on consistency between first and second halves of runs, the consistency of values across the 3 independent runs, and visual inspection of the posterior probability distributions for isolation time estimates (Fig. S19). The above analysis was run for each clock estimate (minimum, medium, and maximum rates; Table S3).

A given species was considered to have divergent NE and NW Atlantic lineages if the lower 95% highest posterior density estimate for isolation times predated the LGM (20 000 yr). The population history of a given species was otherwise considered recent between NE and NW basins if estimates of isolation times postdated the LGM. Evident migrant and/or Arctic populations occurred in some species, and so isolation times between NE and NW Atlantic populations were timed with and without these populations, and the estimates without putative migrant populations were used in our final estimates as described above. Canadian Arctic populations were considered as specimens from sub-Arctic Labrador (Makkovik) and northwards. We elaborate briefly on haplotype distributions in Table 1.

RESULTS

We accumulated COI-5P records for 1560 specimens, 550 of which were generated during this study (2014–2016). These specimens represented 5 species of brown algae and 15 species of red algae, several of which represent multiple genetic groups (numbers in species names are used to indicate this; Table 1). The most COI-5P haplotypes sampled for a given species was 51 (in the case of *Ceramium virgatum*, Fig. S2), while the fewest haplotypes sampled for a given species was 2 (*Polysiphonia* sp. 2stricta, Fig. S12). On average, the number of haplotypes sampled for a given species was 10, of which 6 tended to be singletons (e.g. sampled only once).

Our results for COI-5P were in agreement with previous population studies in *Chondrus crispus* (Hu et al. 2010, 2011, Provan & Maggs 2012), *Mastocarpus stellatus* (Li et al. 2016b), *Palmaria palmata* (Li et al. 2015), and *Saccharina latissima* (Neiva et al. 2018). *C. crispus* generally shares haplotypes with European populations, although endemic haplotypes have been detected in the NW Atlantic (ITS and COI-5P: Hu et al. 2010; *trn*I, 2 single copy nuclear genes, 8 microsatellites: Provan & Maggs 2012). We similarly recovered 2 unique haplotypes in the NW Atlantic (Fig. S3), but estimated the divergence time between the NE and NW population to be approximately 21 000 yr (with a lower 95% highest posterior density [HPD] estimate of 2100 yr; Table 1). It is worth noting that Hu et al. (2011) also estimated divergence times between the NE and NW Atlantic based solely on COI-5P data using a slower clock rate of 0.0034 substitutions site^{-1} Myr^{-1}; they estimated the time of divergence between the NW Atlantic and Ireland to be 43 000 yr, and the divergence time between the NW Atlantic and Portugal (not sampled in our study) to be 193 000 yr. We reanalyzed our COI-5P data in *C. crispus* using the same clock rate as Hu et al. (2011) and received a divergence time estimate of 46 000 yr. *M. stellatus* is considered to have recolonized the NW Atlantic following the LGM based on ITS, *cox*2-3, and plastid RuBisCo spacer (RLS) markers; our IMa2 analyses were consistent with these findings, with an estimated divergence time of 22 000 yr (with a lower 95% HPD estimate of 1400 yr; Table 1). *P. palmata* reportedly survived multiple glaciations in the NW Atlantic, a conclusion based on *cox*2-3 and plastid *rpl-rps* data (Li et al. 2015); our COI-5P data similarly indicated a genetic break between NE and NW populations, with IMa2 analyses indicating a divergence time estimate between NE and NW Atlantic populations of 1 040 000 yr (Table 1). Finally, Neiva et al. (2018) identified several divergent lineages in *S. latissima* in the Pacific, NE and NW Atlantic, a result congruent between COI-5P and 12 microsatellite markers; our analysis of just COI-5P data yielded a divergence time estimate between NE and NW Atlantic populations of 1 416 000 yr. ITS data also suggest there is contemporary migration of Pacific and European phylogroups into the NW Atlantic (McDevit & Saunders 2010).

Regarding the 20 species we surveyed, 12 species (60%) exhibited trans-Atlantic isolation time estimates predating the LGM (Table 1). This result was consistent between slow-, medium-, and fast-evolving COI-5P clocks, with the exception of *Euthora cristata* (C. Agardh) J. Agardh, which had a lower 95% HPD estimate of 6000 yr in the fast-evolving analysis (Table S3). *Odonthalia dentata* (Linnaeus) Lyngbye is presented as an example species for the 12 cases where NE and NW Atlantic populations exhibited divergent lineages. In the case of *O. dentata*, NW and NE populations are reciprocally monophyletic, with 6 hypothesized haplotypes occurring between NE and NW clades (Fig. 1A), and an isolation time of 662 000 yr between basins. Isolation time estimates in species with divergent NE and NW Atlantic populations generally occurred within the past 800 000 yr, but

Table 1. Isolation times of trans-Atlantic species of macroalgae based on COI-5P data, and a medium COI-5P clock rate (red algae: 0.007 substitutions site^{-1} Myr^{-1}; brown algae: 0.002446 substitutions site^{-1} Myr^{-1}). Species with isolation time estimates predating the Last Glacial Maximum (LGM; 20 000 yr) are in **bold**; n (sample size) and No. of haplotypes read as western/eastern North Atlantic. Divergence times (in 10^3 yr) are given with 95% highest posterior density (HPD) intervals. See Figs. S1–S18 in the Supplement at www.int-res.com/articles/suppl/m589p045_supp.pdf for detailed biogeographic maps and haplotype networks. Divergence times in some species are tested twice, with and without certain populations (see 'Materials and methods' and 'Discussion')

Species	n	No. of haplotypes	Isolation time (95% HPD)	Comments
Rhodophyta				
Ahnfeltia plicata (Fig. S1)	120/21	6/4	24.432 (3.676, 80.216)	Shared haplotypes indicate population-level data are needed to resolve recent history. NW Atlantic endemic haplotypes indicate this species may have survived in NW refugia. Trans-Atlantic dispersal from the NE to the NW may also account for some of the patterns seen in *A. plicata* (see *C. crispus*).
***Ceramium virgatum* (Fig. S2)**	**165/5**	**50/2**	**100.540 (50.810, 154.594)**	A long history in the NW Atlantic is implied by an extensive haplotype network. Rhode Island populations could be interpreted as recent introductions from Europe.
***Ceramium virgatum* (without Rhode Island population)**	**146/5**	**49/2**	**117.838 (55.136, 243.244)**	
Chondrus crispus (Fig. S3)	53/48	6/9	21.120 (2.136, 53.868)	Shared haplotypes indicate recent shared ancestry exists between NE and NW Atlantic basins, though some haplotypes are endemic to the NW Atlantic, suggesting refugial populations existed in the NW Atlantic (see also Hu et al. 2011, Provan & Maggs 2012). Trans-Atlantic dispersal from Europe to the NW Atlantic has been inferred (Li et al. 2016a).
Coccotylus brodiei (Fig. 1B)	71/31	2/3	10.594 (0.648, 87.568)	Shared haplotypes indicate population-level data are needed to resolve recent history. The distribution of haplotypes (NW is subset of NE) suggests this species was reestablished in the NW Atlantic postglacially.
***Cystoclonium purpureum* (Fig. S4)**	**39/14**	**4/2**	**288.648 (74.594, 913.514)**	A phylogenetic break indicates a long period of isolation between NE and NW populations.
***Dilsea socialis/carnosa* (Fig. S5)**	**60/18**	**1/2**	**515.676 (83.244, 1322.162)**	A phylogenetic break indicates a long period of isolation between NE and NW populations. NW populations were recognized as *D. socialis*, NE populations were recognized as *D. carnosa* (Saunders 2008), but this taxonomic conclusion has not been robustly tested.
***Euthora cristata* (Fig. S6)**	**67/29**	**5/1**	**282.162 (44.324, 742.702)**	A phylogenetic break indicates late Pleistocene isolation occurred between NE and NW Atlantic populations.
Mastocarpus stellatus (Fig. S7)	19/26	2/3	22.00 (1.466, 168.672)	This species is listed as having recolonized the NW Atlantic from Europe postglacially (Li et al. 2016b), which is consistent with the data presented here.
***Odonthalia dentata* (Fig. 1A)**	**53/26**	**6/1**	**662.918 (125.838, 1443.892)**	A phylogenetic break indicates a long period of isolation between NE and NW populations.

***Palmaria palmata* (Fig. S8)**	**58/19**	**11/9**	**1039.488 (259.002, 1736.354)**	A phylogenetic break indicates a long period of isolation between NE and NW populations, a result consistent with other markers (Li et al. 2015).
Phycodrys sp. 1NB (Fig. S9)	17/22	2/4	44.432 (4.864, 305.838)	Shared haplotypes indicate population-level data are needed to resolve recent history. This is a rare member of the NW Atlantic flora.
***Phycodrys rubens* (Fig. S10)**	**9/45**	**2/5**	**583.870 (121.506, 1284.946)**	A phylogenetic break indicates a long period of isolation between NE and NW populations. This is a rare member of the NW Atlantic flora.
Polyides rotundus (Fig. S11)	29/10	4/3	25.964 (6.244, 76.578)	Low genetic diversity and a single widespread haplotype indicate population-level data are needed to resolve recent history.
Polysiphonia sp. 2stricta (Fig. S12)	23/10	1/2	6.966 (0, 165.880)	Low genetic diversity and a single widespread haplotype indicate population-level data are needed to resolve recent history.
Rhodomela lycopodioides (Fig. S13)	97/12	11/1	24.204 (4.840, 346.924)	A putative migrant population from Europe occurs in the Canadian Arctic. NE and NW populations otherwise exhibit a phylogenetic break.
***Rhodomela lycopodioides* (without Arctic sequence)**	**96/12**	**10/1**	**463.640 (143.072, 1393.072)**	
Phaeophyceae				
Alaria esculenta (Fig. S14)	33/21	4/2	164.698 (15.538, 1190.180)	A putative migrant population from Europe occurs in sub-Arctic Northern Labrador. Otherwise the NE, NW, and Arctic basins all appear to be evolving independently. Possible Pacific origins in Arctic collections.
***Alaria esculenta* (without Arctic populations)**	**23/21**	**2/2**	**706.650 (124.922, 2183.344)**	
***Ectocarpus fasciculatus* (Fig. S15)**	**16/35**	**4/14**	**328.776 (92.604, 634.566)**	High haplotype diversity in southern Europe suggests this species has origins in the NE Atlantic, having moved into the NW Atlantic sometime before the LGM.
Laminaria digitata (Fig. S16)	52/13	3/1	19.266 (0, 113.736)	Low genetic diversity and a single widespread haplotype indicates population-level data are needed to resolve recent history.
***Pylaiella* sp. 2littoralis (Fig. S17)**	**8/14**	**13/6**	**654.688 (248.438, 1257.812)**	A phylogenetic break indicates a long period of isolation between NE and NW populations. Possible incomplete lineage sorting or trans-Atlantic introductions combined with sampling artifacts may explain haplotypes from each lineage occurring on either side of the Atlantic. This amphi-Atlantic genetic group corresponds to MtA in Geoffroy et al. (2015).
***Saccharina latissima* (Fig. S18)**	**132/21**	**11/2**	**1575.092 (442.890, 3486.514)**	A phylogenetic break indicates a long period of isolation between NE and NW Atlantic, and Arctic/Pacific populations (McDevit & Saunders 2010).
***Saccharina latissima* (without Arctic populations)**	**97/21**	**8/2**	**1415.252 (449.550, 3439.894)**	

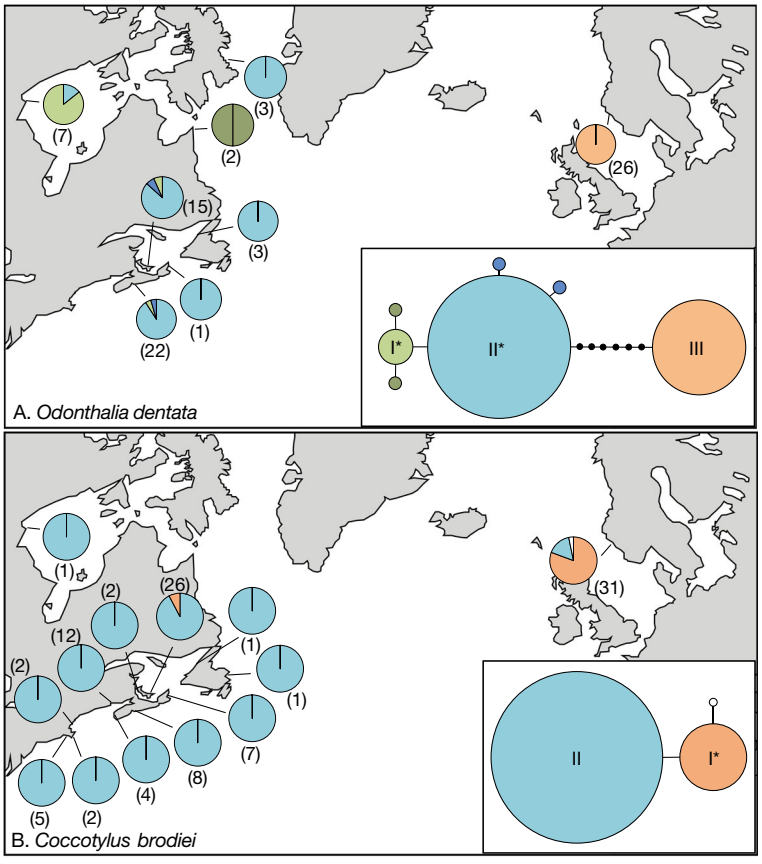

Fig. 1. Haplotype networks and maps based on COI-5P data for 2 trans-Atlantic macroalgae. In the maps, numbers in parentheses refer to sample sizes from given locations. In the haplotype network, roman numerals refer to repeatedly sampled haplotypes. An asterisk indicates putative ancestral haplotypes based on TCS analyses. Black dots indicate hypothesized haplotypes between clades. The size of the circles is proportional to sampling frequency. Shown are haplotype distributions for (A) *Odonthalia dentata*, an example consistent with allopatric fragmentation (e.g. NW Atlantic populations are not derived from the NE Atlantic), and (B) *Coccotylus brodiei*, an example wherein recent population history cannot be resolved with COI-5P data, but shared haplotypes suggest a recent connectivity between populations

extended as far back as 1416000 yr (in the case of *S. latissima*; Table 1, Fig. 2).

Forty percent of the species surveyed had estimated isolation times postdating the LGM (Fig. 2). Of these species, 1 is previously confirmed as having recolonized the NW Atlantic out of the NE (*M. stellatus*; Li. et al. 2016b). *Coccotylus brodiei* (Turner) Kützing is used as our representative species for this scenario (Fig. 1B). *C. brodiei* has a putative ancestral allele that is common in Norway, while NW Atlantic populations are a subset of NE Atlantic haplotypes and are dominated by a sister haplotype to the putative ancestral allele (Fig. 1B). Three species wherein isolation estimates were recent (e.g. postglacial) had extremely low haplotype diversity (a single haplotype dominating both sides of the Atlantic; *Laminaria digitata* [Hudson] J.V. Lamouroux [Fig. S16], *Polyides rotundus* [Hudson] Gaillon [Fig. S11], and *P.* sp. 2stricta [Fig. S12]).

Four species appeared to have migrant populations from Europe into the NW Atlantic or Canadian Arctic (*Alaria esculenta* [Linnaeus] Greville [Fig. S14], *Ceramium virgatum* [Fig. S2], *Rhodomela lycopodioides* (Linnaeus) C. Agardh [Fig. S13]), and/or had distinct Arctic populations not matching NW or NE Atlantic populations (*A. esculenta* [Fig. S14], *S. latissima* [Fig. S18]). Isolation times in these species were timed with and without these putative migrant/Arctic populations. Results were generally the same, except in the case of *R. lycopodioides*, wherein the isolation time was much greater when an Arctic sequence was removed from the NW Atlantic population (24000 yr with putative migrant population, 464000 yr without).

DISCUSSION

The hypothesis that the NW Atlantic marine flora was mostly recolonized from the NE Atlantic following the LGM (Vermeij 1978, Ingolfsson 1992) is no longer tenable in light of repeated DNA-based studies, including the trans-Atlantic survey presented herein. Given that a variety of population scenarios likely occurred, we sought to quantify the number of species with genetic patterns consistent with survival in refugia in the NW Atlantic (namely divergence between NE and NW Atlantic populations) using COI-5P data; species with low divergence times between populations (e.g. <20000 yr) would likely indicate recent shared ancestry between basins, although details such as the directionality of recolonization will require more in-depth population genetic analyses. By studying 20 species in tandem, we hope to comment on broad-scale patterns across species and improve on current understanding of postglacial recolonization in the North Atlantic and its impact on biodiversity distributions.

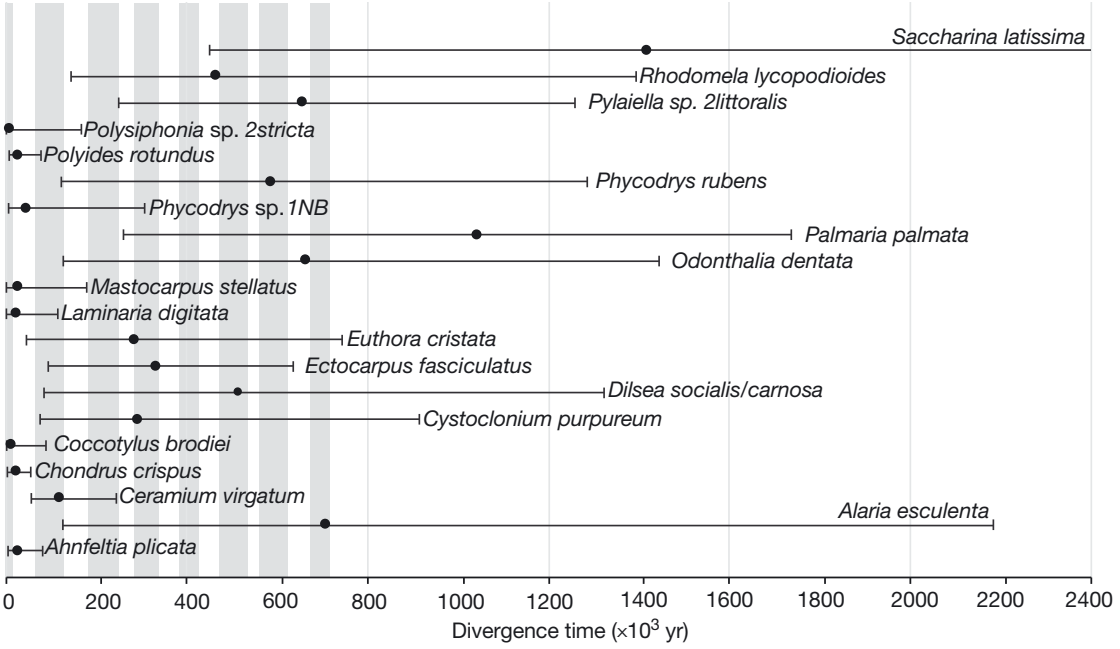

Fig. 2. Divergence times in trans-Atlantic red and brown macroalgae in conjunction with glaciation events over the past 800 000 yr (as proxied from globally distributed $\delta^{18}O$ records; Lisiecki & Raymo 2005). Non-shaded intervals approximate glacial maxima. The error bars are 95% highest posterior density intervals; note that sampling densities across the range of divergence times are normally distributed around the means, and the upper bound of the highest posterior density for *Saccharina latissima* is 3 438 000 yr

COI-5P as a proxy for glacial survival or postglacial recolonization

We began by examining whether or not COI-5P was a suitable proxy for distinguishing between the 2 contrasting population histories under question (i.e. postglacial shared ancestry between NE and NW Atlantic populations, and survival on both sides of the Atlantic in glacial refugia). COI-5P patterns were consistent with other genetic markers used in more detailed population genetic studies in 4 of our target species (*Chondrus crispus, Mastocarpus stellatus, Palmaria palmata,* and *Saccharina latissima*). Indeed, the consistent genetic break between NE and NW Atlantic populations in *P. palmata* detected in *cox*2-3, *rpl-rps* (Li et al. 2015), and our own COI-5P data were the basis for the calibration of our red algal molecular clock. COI-5P was also able to correctly assign the correct population scenario of recent shared ancestry between NE and NW Atlantic populations in *M. stellatus* (Li et al. 2016b). Interestingly, molecular data show consistent patterns across genomes in *C. crispus* (Hu et al. 2010, 2011, Provan & Maggs 2012), but conclusions as to whether or not this species recolonized the NW Atlantic following the LGM varied across studies. Our analysis indicated that ancestry is recent between NE and NW Atlantic basins, despite a small number of rare endemic haplotypes to the NW Atlantic that may point to NW refugial populations (Hu et al. 2011, Provan & Maggs 2012). Li et al. (2016a) estimated migration vectors in *C. crispus* and found that trans-Atlantic dispersal likely occurred between Ireland and the NW Atlantic. It therefore seems reasonable to expect that both scenarios contributed to postglacial NW Atlantic populations of *C. crispus* (Table 1). Genomic-level datasets may be needed to confidently resolve whether or not *C. crispus* survived in glacial refugia in the NW Atlantic and where these refugia occurred. It is worth reemphasizing that the COI-5P data were consistent overall with the results from microsatellite data, and nuclear (ITS, single copy nuclear regions), plastid (RLS, *rpl-rps*), and other mitochondrial genes (*cox*2-3, *trn*I) for these 4 species in all studies published to date.

We also note the critical importance of a reliably calibrated molecular clock for estimations of population divergence times. This is evidenced by the discrepancy in isolation time estimates between our present study and that of Hu et al. (2011) for *C. crispus*. Hu et al. (2011) calibrated their COI-5P clock using an isolation time between *C. crispus* and congeners in the North Pacific, and a calibration time of 3.5 Myr. The resulting clock rate (0.34% Myr^{-1}, 2×

slower than our clock estimate of 0.7% Myr^{-1}), yielded an estimated divergence time between Irish and NW Atlantic populations of 43 000 yr (Hu et al. 2011), a result we replicated in our IMa2 analyses using the same clock rate. Differing clock rates were therefore the crux between determining if NW Atlantic populations survived the LGM or otherwise had very recent shared ancestry with European populations. We believe our red algal COI-5P clock rates are more accurate for several reasons. For one, our red algal clock was indirectly calibrated from markers calibrated using the closing of the Isthmus of Panama (Zuccarello & West 2002); the estimated closing time of the Isthmus is likely more accurate than estimations of the opening time of the Bering Strait (Gladenkov et al. 2002, Coates & Stallard 2013), and the cessation of gene flow likely coincides closer to the closing of the Isthmus of Panama than the congruency between the opening of the Bering Strait and the initiation of gene flow (e.g. species may not have speciated out of the Pacific into the Atlantic immediately after the Bering Strait opened). In addition, the rate of mitochondrial evolution in red algae appears to be greater than the rate in Ochrophyta (the Phylum containing brown algae; Smith 2015), a finding in agreement with our rate estimations.

We also tested a range of clock rates in both red and brown algal lineages, which yielded mostly consistent results (Table S3). The notable exception was *Euthora cristata*, which had a shallow phylogenetic break between NE and NW Atlantic populations (Table 1, Fig. 2). While the break suggests that these populations are indeed isolated, a fast clock scenario (>1% change Myr^{-1}) could not exclude more recent divergence dates between populations (<20 000 yr). Given the uncertainty surrounding the rate estimates for COI-5P evolution, a transition period is expected wherein the range of divergence time estimates cannot definitively exclude one scenario over another (recent shared ancestry between the NW and NE Atlantic, or glacial survival in the NW Atlantic). While our estimates of divergence dates certainly side with glacial survival of *E. cristata* in the NW Atlantic, additional markers will be needed to further resolve its population history.

Glacial survival in the NW Atlantic: the rule, not the exception

Having established COI-5P as a reasonable proxy for our 2 population scenarios, we went on to consider broad-scale patterns regarding the phylogeographic history of the North Atlantic by amalgamating general patterns in 20 trans-Atlantic species. While it is generally accepted that some species of macroalgae survived glaciation in the NW Atlantic while others likely recolonized from the NE Atlantic, it is not clear if one scenario is more common than the other. Premolecular hypotheses favored a postglacial migration hypothesis (Vermeij 1978, Ingolfsson 1992); however, emerging molecular studies have challenged this paradigm (Li et al. 2016a). Our results indicate that possibly 60% of the NW Atlantic marine flora survived the LGM, as evidenced by isolation times between NE and NW Atlantic populations predating 20 000 yr (Fig. 1, Table 1). Such a scenario was exemplified in *Odonthalia dentata* (Fig. 1A). In this case, a putative ancestor likely migrated into the Atlantic from the North Pacific, where several species of *Odonthalia* occur, sometime since the Bering Strait opened (Lindstrom 1987, 2001, Wynne & Heine 1992). This ancestor subsequently became established along NE and NW Atlantic coasts and has possibly undergone incipient speciation, as evidenced by the deep COI-5P divergence among NE and NW Atlantic populations (Figs. 1A & 2). Phylogeographic analyses are needed to fully resolve the origins of this species and its current taxonomic status in the North Atlantic, but prior to this study, there was no reason to question the assumption that this species represented a single population/species in the North Atlantic.

The deep lineage splits in several of the species studied here, particularly in *O. dentata* (Fig. 1A), *P. palmata* (Fig. S8), *Phycodrys rubens* (Linnaeus) Batters (Fig. S10), *Pylaiella* sp. 2littoralis (Fig. S17), *Rhodomela lycopodioides* (Fig. S13), and *S. latissima* (Fig. S18), warrant taxonomic investigation. Presumably the NE and NW Atlantic populations are on their way to speciation. Most of these species have isolation times greater than *Dilsea carnosa* and *D. socialis*, which have haplotype variation similar to the above-mentioned species, and yet they are recognized as 2 separate species (Saunders 2008; Fig. 2). Note, however, that COI-5P divergence alone does not indicate that populations of the above species have reached reproductive isolation on either side of the Atlantic. Additional markers and detailed molecular analyses are needed to determine if these populations are separate species, or if previously recognized amphi-Atlantic sister species are simply divergent populations (e.g. *D. socialis*/*carnosa*). Either way, this discussion further highlights that endemism, either at the population or species level, is far greater in the NW Atlantic than previously realized (Fig. 2).

Our results highlight important questions regarding the origins of NW Atlantic macroalgal species. Firstly, our results suggest that marine refugia were more readily available in the NW Atlantic than previously thought. Reconstructions of past sea-surface conditions suggest that the Grand Banks off Newfoundland remained unglaciated (Pflaumann et al. 2003, Maggs et al. 2008), while genetic evidence in several marine and terrestrial species indicates the presence of a refugium near Nova Scotia (Coyer et al. 2011b and references therein; Einfeldt et al. 2017). Indeed, COI-5P variation in *Ceramium virgatum* indicates that refugia likely existed in these locations (Fig. S2). Given the constricted isotherms and lack of suitable substrate south of the Laurentide Ice Sheet (Vermeij 1978, Ingolfsson 1992, Maggs et al. 2008), it is likely that the species studied here survived in the above locations, or in yet unidentified refugia. Genomic-level analyses could be carried out in the species identified here as having survived the LGM in the NW Atlantic to identify refugial locations. Secondly, it is worth considering whether some of these 'survivor' species are the result of recent trans-Arctic migrations from the North Pacific. Some North Pacific species of algae have colonized the Canadian Arctic and subsequently extended into the NW Atlantic (Saunders & McDevit 2013). Indeed, some of the species analyzed here have unique Arctic haplotypes that appear to have migrated from the Pacific, in addition to having migrants out of the NE Atlantic (*Alaria esculenta,* Fig. S14) or NW Atlantic populations (*S. latissima*, Fig. S18; also see McDevit & Saunders 2010), while other species (e.g. *E. cristata* and *O. dentata*) are also reported as having conspecifics in the North Pacific (Wynne & Heine 1992). An analysis of population genetic structure in trans-Arctic species would help resolve this question.

Uncertain origins

Low isolation time estimates postdating the LGM occurred in 8 out of 20 of the species surveyed. Of these species, *M. stellatus* was identified as having postglacial origins stemming out of the NE Atlantic, as was reported in a more detailed study (Li et al. 2016a,b); *C. crispus* possibly survived in NW Atlantic refugia, but European migrants also likely contributed to the present-day population (Table 1, Fig. 2; Hu et al. 2010, 2011, Provan & Maggs 2012, Li et al. 2016a). The remaining 6 species require more extensive population-level work to resolve details about their recent history, particularly whether or not they originated out of the NE Atlantic. Shared haplotypes between NW and NE Atlantic basins in these species suggest a recent shared ancestry and possible contemporary migration pathways across the Atlantic. *Coccotylus brodiei*, in particular, appeared to have haplotype distributions suggesting that a recent recolonization event occurred in the NW Atlantic from European populations (Fig. 2B), namely a single widespread haplotype in the NW Atlantic that occurs in the NE, and seemingly greater haplotype diversity in the NE Atlantic (Wares & Cunningham 2001). Again, while the patterns here are suggestive, more detailed population work is needed. Indeed, we may find that some of these species survived very recent glaciation events in the NW Atlantic, further bolstering the 60% figure reported here.

The generally low haplotype diversity in nearly all of the species studied indicates that genetic drift is playing an important role in North Atlantic populations of marine algae. Given that these populations are undergoing repeated bottlenecking due to glaciation events, the low amounts of genetic variation within species is not surprising. Genetic drift may lead to spurious results by masking genetic patterns, causing populations to randomly appear more or less related and impacting isolation time estimates. In our case, all but one of the species with isolation times predating the LGM had unique NE and NW Atlantic lineages, often separated by several mutational steps (e.g. *Ectocarpus fasciculatus* Harvey shared haplotypes between basins but had an estimated isolation time of 328000 yr; Table 1). As such, genetic drift is generally a concern with interpreting patterns in the species for which NW Atlantic populations appear to have a recent shared history with European populations. Detailed population-level or genomic datasets (e.g. *C. crispus*) will be needed to confirm the nature of recent ancestry between the NE and NW Atlantic in these species (Table 1).

Conclusions

We attempted to address assumptions regarding molecular clocks and single-marker use in our study, but some additional limitations must be addressed regarding sampling effort. Our data may be biased where we have not sampled the full biogeographic range in some species, and where sample sizes are small in several populations. Southern Europe ought to be better sampled considering this

is where many refugia are hypothesized to have occurred (Maggs et al. 2008). Because we may have missed the southern European distribution in some species, it is entirely possible the putative scenarios presented here will change in light of more data; however, we note that several of the sampled species likely have their southern limit close to the sampling locations in Norway (e.g. *R. lycopodioides*, *Phycodrys* spp., *O. dentata*, *E. cristata*, *C. brodiei*). Sampling sufficient numbers of specimens for species with ambiguous field identifications also proved difficult. For instance, *Phycodrys* occurs as 3 species in the North Atlantic: the abundant *P. fimbriata* (Kuntze) Kylin is found at high densities only on the western coast of the North Atlantic, and *P. rubens* and *Phycodrys* sp. 1NB occur concurrently with *P. fimbriata* in very specific and patchy locations, or at low densities across a much wider area in the NW, but dominate in the NE Atlantic. Until methods to discriminate these species in the field are developed, detailed population studies will be challenging because it will be difficult to obtain sufficient specimen numbers for the rare cryptic species. Lastly, many amphi-Atlantic species were not included in our analysis due to insufficient sampling numbers, but could be targeted in the future (Table S2). Sampling more species will yield a more complete picture of the phylogeographic history of the North Atlantic.

To conclude, we have shown that COI-5P is in agreement with other markers used in more detailed studies to resolve the population history of several species in the North Atlantic. Surveying COI-5P data in 20 species also revealed that 60% of the NW Atlantic marine flora appears to have survived the LGM. This finding was consistent across the 2 phyla studied here (Rhodophyta and Ochrophyta), suggesting that our results may be broadly applicable to marine coastal species. In addition, it would be worth investigating what physiological or life history differences, if any, may have allowed these species to survive glaciation in the NW Atlantic as compared to species that were extirpated during the last glaciation. Macroalgal species with recent shared ancestry between NE and NW Atlantic populations can be further investigated using other markers or genomic datasets to resolve details like migration rates and location(s) of origin. The proportion of NW Atlantic refugial species is likely to increase as we resolve recent population histories in several of the species studied here (e.g. *Ahnfeltia plicata*, *C. crispus*; Table 1) and include known NW Atlantic endemic species. On a final note, detailed floristic comparisons between the NW Atlantic and North Pacific will be the next step to further elucidating past and contemporary origins of marine flora in the North Atlantic and Canadian Arctic.

Acknowledgements. We thank the many researchers who participated in the large number of collecting episodes associated with our dataset. In particular, we thank Dr. Kjersti Sjøtun at the University of Bergen for facilitating our sampling in Norway. We also thank everyone who generated the COI-5P data, particularly Tanya Moore, and the following researchers for providing sequence data and trace files: Alex Geoffroy, Line Le Gall, Akira F. Peters, and Hu Zi-Min. We also thank Jason Addison for helpful comments on the manuscript. This project was funded by the Natural Sciences & Engineering Research Council of Canada through an NSERC Post-Graduate Scholarship to T.T.B. and a Discovery Grant (170151-2013) to G.W.S., the New Brunswick Innovation Foundation, and the Northern Scientific Training Program.

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Editorial responsibility: Per Palsbøll, Groningen, The Netherlands

Submitted: September 22, 2017; Accepted: January 23, 2018
Proofs received from author(s): February 16, 2018