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# Phylogeography of split kelp *Hedophyllum nigripes*: northern ice-age refugia and trans-Arctic dispersal

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## Abstract

Pleistocene climate cycles greatly influenced the distributions of kelps in northern seas and gated trans-Arctic dispersals between the North (N) Pacific and N Atlantic oceans. Here, we used partial sequences of the mitochondrial DNA cytochrome oxidase I-5' (*COI*) and plastid ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit-3' (*rbcL*) to resolve the phylogeography of the kelp *Hedophyllum nigripes* in the Gulf of Alaska and globally. In the Gulf of Alaska, genetic diversity was moderate (*COI*:  $h = 0.493 \pm 0.076$ ,  $n = 57$ ; *rbcL*:  $h = 0.578 \pm 0.00047$ ,  $n = 54$ ), but nucleotide diversity was small (*COI*:  $\theta_{\pi} = 0.00114 \pm 0.00100$ ,  $n = 57$ ; *rbcL*:  $\theta_{\pi} = 0.0001 \pm 0.00089$ ,  $n = 54$ ). Concatenated sequences showed strong haplotype-frequency differences among populations ( $\Phi_{ST} = 0.728$ ). The addition of previously published *COI* sequences from British Columbia showed a general absence of southern haplotypes in the Gulf of Alaska, supporting the conclusion of northern ice-age refugia. *COI* sequences in Canadian Arctic-Northwestern (NW) Atlantic populations differed by 1–2 mutation from Northeastern (NE) Pacific sequences, and unexpectedly, were marginally more closely related to populations in British Columbia than to geographically intermediate populations in the Gulf of Alaska. *COI* haplotypes from the Svalbard Archipelago in the NE Atlantic showed no variability and differed by 1–2 mutations from haplotypes in the NW Atlantic. Time-calibrated genetic divergences indicated trans-Arctic dispersal(s) from the N Pacific into the N Atlantic in the mid-Pleistocene.

**Keywords** *Hedophyllum nigripes* · Kelp · Phylogeography · Trans-arctic dispersal · Mitochondrial DNA · Chloroplast DNA · Bering strait · Pleistocene glaciation

## Introduction

Historical events and contemporary processes have shaped the genetic structures of populations of kelps at mid to high latitudes. Chief among contemporary processes is the dispersal of propagules, either as planktonic spores, or as drifting

unattached kelp (Gillespie et al. 2012), that enhances genetic connectivity between populations and seeds empty habitat patches. Metapopulation processes, involving local extinctions and colonizations, can also shape patterns of genetic variability among populations by eroding genetic diversity within and among populations (Gilpin 1991; Moy and Christie 2012). On large time scales, coastal glaciers during Pleistocene ice-ages profoundly influenced genetic variability among populations through extirpations, isolations in refugia (Maggs et al. 2008), and post-glacial colonizations.

In the North (N) Pacific and N Atlantic oceans, rocky-shore kelps, such as *Saccharina latissima*, *S. japonica*, and *Laminaria digitata* tend to show low levels of genetic variability within populations, but strong differences between populations (Zhang et al. 2015; Guzinski et al. 2016; Lutikhuizen et al. 2018; Grant et al. unpublished). These patterns of population structure have been attributed to restricted gene flow between populations because of short-lived spores and habitat discontinuities. While spores lose mobility after a few hours, non-motile spores can still be

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suspended in the water and potentially be transported in coastal currents for several days (van den Hoek 1987). However, realized spore dispersal is generally limited to only a few meters (Anderson and North 1966; Dayton 1985; Santelices 1990). Genetic differentiation between populations on spatial scales of a few meters to tens of kilometers indicates that long-distance dispersal is rare (Robuchon et al. 2014; Zhang et al. 2015; Luttikhuisen et al. 2018). Nevertheless, rare dispersals of detached kelp are possible, as evidenced by rafting of kelp across large oceanic distances (Fraser et al. 2011; Saunders 2014; Macaya et al. 2016) and the development of seaweed floras on newly formed island (van den Hoek 1987).

In addition to contemporary processes, historical events have been important influences on population structure. The margins of continental glaciers periodically covered shorelines in the Northeastern (NE) Pacific and N Atlantic oceans and displaced populations into refugia. A widely held view, based on phylogeographic patterns of terrestrial plants and animals proposes that high-latitude populations survived glacial advances in southern ice-free refugia (Hewitt 1996, 2004). Even though glaciers reached mid latitudes in North America and Europe during glacial maxima, genetic evidence and coastal climate reconstructions indicate the existence of northern refugia above the southern margins of ice sheets in the NE Pacific (Hickerson and Ross 2001; Clague and James 2002; Kaufman and Manley 2004; Carrara et al. 2007; Lindstrom 2009; Marko et al. 2010; Canino et al. 2010; Bigg 2014) and in the N Atlantic (Sarnthein et al. 2003; Provan et al. 2005; Shaw 2006; Maggs et al. 2008; Provan and Bennett 2008; Assis et al. 2018; Bringloe et al. 2020).

On a broader geographic scale, the opening and closing of the Bering Strait, in concert with glacially driven sea-level changes, repeatedly gated trans-Arctic dispersals of marine species between the N Pacific and N Atlantic oceans since the Strait first opened 7.4–4.8 million years ago (Vermeij 1991; Marinovich and Gladenkov 2001; Gladenkov et al. 2002; Marinovich et al. 2002). Genetic distances between related species or populations in the N Pacific and N Atlantic show deep and shallow divergences, indicating a range of dispersal times. Several species of fishes (Grant 1986; Grant and Ståhl 1988), invertebrates (Väinölä 2003; Marko et al. 2014; Laakkonen et al. 2015) and macroalgae (Lindstrom 2001; Rothman et al. 2017; Bringloe and Saunders 2019a) dispersed across the Arctic Ocean soon after Bering Strait opened in the late Miocene-early Pliocene Epochs. Whereas other species have only recently transited the Arctic, as evidenced by small genetic distances between N Pacific and N Atlantic populations of fishes (Laakkonen et al. 2013; Makhrov and Lajus 2018), invertebrates (Addison and Hart 2005; Albrecht et al. 2014; Laakkonen et al. 2015) and

macroalgae (van Oppen et al. 1995; Coyer et al. 2011; Neiva et al. 2018; Bringloe and Saunders 2019a).

The focus here is on the phylogeography of the subtidal and low-intertidal kelp, *Hedophyllum nigripes* (S. Agardh) Starko, S.C. Lindstrom and Martone. This species is distributed on wave-exposed or current-swept rocky shores from central California to Alaska and the Aleutian Archipelago in the N Pacific (Druehl 1979; Hansen 1997; Lindeberg and Lindstrom 2010; Mondragon and Mondragen 2010; Klinkenberg 2018), and in the Arctic and Northwestern (NW) Atlantic (Sears 2002; McDevit and Saunders 2010; Longtin and Saunders 2016). This kelp also occurs in the high latitude NE Atlantic, but is apparently absent along the west coast of Norway (Lien et al. 1999; Rueness et al. 2001; Lund 2014). This kelp has been observed growing under low-light conditions as deep as 20 m in SE Alaska (Ellis and Calvin 1981; Calvin and Ellis 1981) and 15 m in the Arctic (Lydon 2015; Filbee-Dexter et al. 2019).

Several authors have confused *Hedophyllum nigripes* with *Saccharina latissima*, *Laminaria digitata*, or have treated it as *Laminaria bongardiana*. In a review, Bartsch et al. (2008) listed *H. nigripes* (*Laminaria groenlandica*, Rosenvinge) as occurring only in the N Pacific Ocean, and concluded that putative populations of *L. groenlandica* in the N Atlantic belonged to a morphologically plastic *S. latissima* species complex. However, subsequent molecular and morphological analyses showed that many of the taxa in this putative species complex were distinct species, including *H. nigripes* (Lane et al. 2006; Longtin and Saunders 2015; Starko et al. 2019). McDevit and Saunders (2010) surveyed cytochrome oxidase-1 (*COI*) sequences in *H. nigripes* from the NE Pacific, Canadian Arctic, and NW Atlantic and found that populations in these areas were conspecific. However, material from the NE Atlantic was not examined where this kelp was first described from specimens collected at Spitsbergen (Agardh 1868).

In the present study, we provide new partial sequences of cytochrome *c* oxidase subunit I-5' gene (*COI*) and plastid ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit-3' (*rbcL*) from populations in the Gulf of Alaska ( $n=57$ ), and combine these sequences with available data from British Columbia and Washington ( $n=22$ ), the Canadian Arctic and the NW ( $n=26$ ) and NE ( $n=51$ ) Atlantic oceans to provide a broader phylogeographic perspective. Our first objective was to survey genetic variability among populations in the NE Pacific to assess levels of connectivity between populations and to test whether genetic signatures of northern glacial refugia were imprinted on these populations. The second objective was to infer the phylogeographic origins of Arctic and N Atlantic populations and to estimate the timing(s) of trans-Arctic dispersal(s).

## Materials and methods

Samples of sporophytes were collected at rocky intertidal sites around the Gulf of Alaska (Fig. 1). Individuals of *Hedophyllum nigripes* were misidentified as *Saccharina latissima* at some localities in the Gulf of Alaska and as *Laminaria digitata* in the Svalbard Archipelago (see Online Resource Methods; Lund 2014; Lydon 2015). The misidentifications were detected by comparing *COI* sequences with published sequences of *H. nigripes*. A 2 × 2-cm piece of frond near the basal meristem was excised, damp dried, then dried on silica beads immediately after collection. DNA was extracted with the NucleoSpin® 96 Plant II kit (Macherey–Nagel Inc. Düren, Germany).

We used mitochondrial and plastid DNA to infer phylogeographic structure, because both are generally non-recombining and uni-parentally (maternal) inherited in kelps (Motomura et al. 2010; Li et al. 2016) and hence can be used to infer historical relationships among populations (Avice 2000). Furthermore, the analyses of both mitochondria and plastids provide different perspectives of a common population history because they evolve independently of each other. Both DNAs have mutation rates that can be used to resolve the influences of environmental events in the late Pleistocene Epoch (e.g. Neiva et al. 2018).

A 658 bp segment of *COI-5'* was amplified with PCR using the forward primer *GazF2* (5' CCAACCAAYAAAG ATATWGGTAC 3') and reverse primer *GazR2* (5' GGATGACCAAARAACCAAAA 3') (Lane et al. 2007). A 735 bp segment of *rbcL-3'* was amplified with PCR using the forward primer *rbcL-543F* (5' CCWAAATTAGGTCCTTCWGGWAAAAA 3') (Bittner et al. 2008; Silberfeld et al. 2010) and reverse primer *rbcL-1381R* (5' ATATCTTTCCATARR TCTAAWGC 3') (Burrowes et al. 2003; Silberfeld et al. 2010). The PCR cocktail consisted of a 50 µL mixture of 2.0 µL template DNA in 1 × Colorless GoTaq Flexi buffer, 2.5 mM MgCl<sub>2</sub>, 0.2 mM of each dNTP, 1 µM of forward and reverse primers, and 2.5U GoTaq Flexi DNA polymerase. PCR amplifications were conducted in ABI 9700 thermocyclers with initial denaturation at 94 °C for 3 min, followed by 35 amplification cycles of 45 s at 94 °C, 1 min at primer annealing temperature 50 °C for *COI* and 52 °C for *rbcL*, and 1 min 30 s at 72 °C, and a final 5 min at 72 °C. PCR amplifications were sequenced in the forward and reverse directions by Genewiz Inc. (South Plainfield, NJ) or by the University of Arizona Genetics Core. Forward and reverse-complement sequences were aligned and edited with MEGA 7.0.20 (Kumar et al. 2016) and chromatograms viewed with Finch TV 1.4.0 (Geospiza Inc.). Kelp with unique haplotypes were selected from each of the 96-well plates for re-extraction and re-sequencing for quality control. Methods

for processing kelp samples from the Svalbard Archipelago are similar and can be found in Lydon (2015).

Eight new *COI* haplotypes in Gulf of Alaska populations correspond to Genbank accession numbers MT742224–MT742231, and five *rbcL* haplotypes correspond to Genbank accession numbers MT742232–MT742236 (Online Resource Table S1). Sequences of *COI* for split kelp in British Columbia, Hudson's Bay, NW and NE Atlantic were included in the study to compare with new sequences from the Gulf of Alaska (Online Resource Table S1). This larger dataset consisted of a 576 bp fragment that overlapped with *COI* sequences from the Gulf of Alaska.

ARLEQUIN 3.5.2.2 (Excoffier and Lischer 2010) was used to estimate the number of polymorphic nucleotide sites,  $N_{\text{poly}}$ , the number of observed haplotypes,  $N_{\text{H}}$ , and number of expected haplotypes under neutrality,  $N_{\text{EH}}$ . ARLEQUIN was also used to estimate gene diversity,  $h$  (standard deviation), and nucleotide diversity,  $\theta_{\pi}$  (standard deviation). Divergence between populations was estimated with  $\Phi_{\text{ST}}$  (based on haplotype frequencies and sequence divergences between haplotypes). An appropriate mutation model to estimate sequence divergence were determined with MEGA 7 (Kumar et al. 2016). Departures from neutrality were tested with Tajima's  $D$  (Tajima 1989).

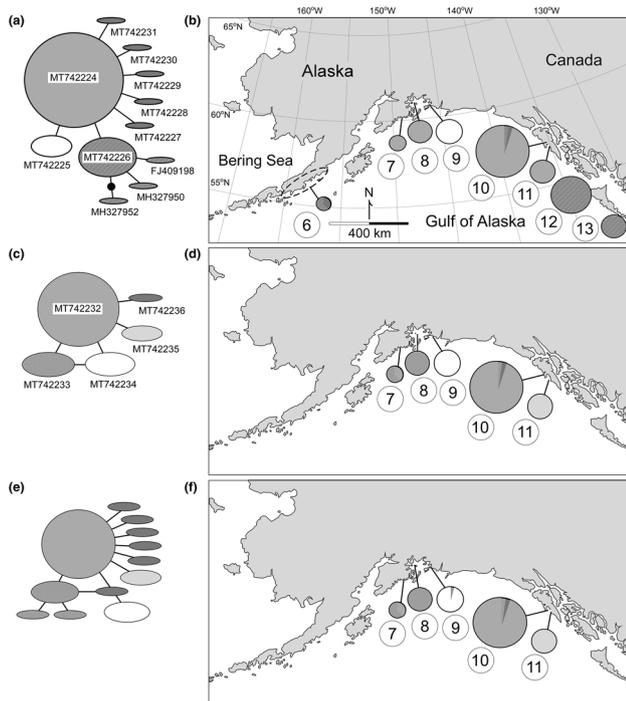
*COI* sequences were used to estimate the timing of trans-Arctic dispersal in *H. nigripes* with *H. subsessile* (Online Resource Table S2) as an outgroup. A phylogenetic tree was reconstructed with BEAST 1.8.3 (Drummond et al. 2012) with the Tamura-Nei (1993) substitution model (Online Resource Table S3), a strict clock, and a prior on the root node of the tree of 3.7 Ma with a normal distribution and a standard deviation of 2.7 to approximate the 95% HPD interval of 6.7–1.3 Ma (Starko et al. 2019). The clock rate was constrained to 0.1–0.8 Ma<sup>-1</sup> with a uniform prior distribution. The analysis was run for 10<sup>7</sup> MCMC steps and repeated three times, before combining the runs, each with a 10% burn-in.

## Results

### Gulf of Alaska

#### Cytochrome oxidase I-5' (*COI*)

*COI* sequences were available for 6 sites in Alaskan waters (Table 1). Eleven polymorphic nucleotide sites along a 658-bp fragment of *COI* defined 11 haplotypes among 57 specimens (Table 1; Fig. 1a). Nine haplotypes were unique to a particular location. Haplotype diversity ( $h$ ) ranged from 0.0 to 1.0 and was  $0.493 \pm 0.076$  ( $n = 57$ ) overall. Nucleotide diversity ( $\theta_{\pi}$ ) ranged from 0.0 to 0.0046 and was



**Fig. 1** Geographical distributions of haplotypes in the NE Pacific Ocean for *Hedophyllum nigripes*. **a** Network showing mutational relationships among *COI* haplotypes (658 bp). One connection between two haplotypes represents a single nucleotide-site change. Small solid circle represents hypothetical, unsampled haplotype. Complete list of Genbank Accession numbers appears in Supplementary Table 1. **b** Map showing frequencies of mitochondrial *COI* haplotypes among populations. Circle size is proportional to sample size. **c** Haplotype network of chloroplast *rbcL* sequences (735 bp). **d** Frequencies of chloroplast *rbcL* among samples. **e** Haplotype networks of concatenated *COI* and *rbcL* sequences (1393 bp). **f** Frequencies of concatenated *COI*+*rbcL* haplotypes among samples

$0.00149 \pm 0.0012$ ) ( $n=57$ ) overall. Tajima's test showed an overall significant departure from neutrality in a pooled sample ( $D = -1.95$ ,  $p = 0.006$ ,  $n = 57$ ) that was due to an excess of low-frequency haplotypes. Only 3.77 haplotypes were expected under neutrality, but 10 were observed.

*COI* sequences from northern and southern British Columbia were added to the collection of Alaskan samples (Table 1; Figs. 1a, b). No sequence variability was observed among kelp from northern British Columbia ( $h=0.0$ ,  $\theta_\pi=0.0$ ,  $n=15$ ) and one variant haplotype appeared among kelp from southern British Columbia and Washington ( $h=0.286 \pm 0.196$ ,  $\theta_\pi=0.00049 \pm 0.00067$ ,  $n=7$ ). In a pooled sample, haplotype ( $h=0.091 \pm 0.081$ ,  $n=22$ ) and nucleotide ( $\theta_\pi=0.00016 \pm 0.00033$ ,  $n=22$ ) diversities were small. A test for neutrality showed no significant departure ( $D = -1.162$ ,  $p = 0.146$ ,  $n = 22$ ) in the pooled sample.

Haplotype frequencies varied strongly among locations 6–13 in the NE Pacific (Fig. 1b) with some haplotypes

widespread and other at low frequencies in only one population. Ten private haplotypes appeared at 8 locations. Some populations were fixed for a particular haplotype. Genetic distances between populations ranged from  $\Phi_{ST}=0.0$ , between locations fixed for the same haplotype, to  $\Phi_{ST}=1.0$ , between locations fixed for alternative haplotypes (Table S4). The value of  $\Phi_{ST}$  overall was 0.534 ( $p = 0.035$ ,  $n = 79$ ).

### *Ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit-3'* (*rbcL*)

Polymorphisms appeared at 4 nucleotide sites in a 735 base-pair segment of *rbcL* and defined 5 haplotypes ( $n = 54$ ) among populations 7–11 around the Gulf of Alaska (Online Resource Tables S5, S6; Figs. 2c, 2d). One nucleotide site defining haplotypes MT742232, MT742233 and MT742234 segregated for both transitions and transversions and formed a closed loop in the haplotype network. Haplotype diversity ( $h$ ) ranged from 0.0 in three locations fixed for a single haplotype to 0.667 and was  $0.578 \pm 0.047$  ( $n = 54$ ) overall. Nucleotide diversity ( $\theta_\pi$ ) ranged from 0.0 to 0.0009 and was  $0.0001 \pm 0.0009$  ( $n = 54$ ) overall (Online Resource Table S6). A test for neutrality overall was not significant ( $D = 0.343$ ,  $p = 0.677$ ,  $n = 54$ ). Pairwise genetic distances ( $\Phi_{ST}$ ) between populations ranged from 0.672 to 1.0, and all were significantly larger than 0.0 ( $p < 0.05$ ) (Online Resource Table S7). Overall in the Gulf of Alaska,  $\Phi_{ST} = 0.769$  ( $p < 0.001$ ,  $n = 54$ ).

### Concatenated *COI*-*rbcL* sequences

A total of 10 polymorphic nucleotide sites in concatenated sequences (1393 bp) produced 12 haplotypes among samples 7–11 in the Gulf of Alaska ( $n = 52$ ) (Tables 2, 3; Figs. 1e, f). Values of  $h$  ranged from 0.0 in populations fixed for a single haplotype to 0.402 among specimens from Halibut Point, SE Alaska (sample 9) that had a dominant haplotype and 6 singleton haplotypes.  $\theta_{ST}$  ranged from 0.0 to 0.00072 and was  $0.00091 \pm 0.00065$  ( $n = 52$ ) overall. Tajima's test of neutrality was not significant ( $D = -1.210$ ,  $p = 0.114$ ,  $n = 52$ ). Haplotype frequencies varied strongly among locations (Fig. 1f).  $\Phi_{ST}$  between samples ranged from 0.151 to 1.0 and were significant ( $p < 0.05$ ) for all of the pairwise comparisons after correction for multiple tests (Table 4).

### Global phylogeography of *COI*

The addition of 77 sequences of *COI* (576 bp) from 5 localities (1–5, Table 1) in the Canadian Arctic, NW and NE Atlantic provided an overview of genetic variability on a larger geographical scale. A single haplotype appeared in samples from the Svalbard Islands ( $n = 51$ ) that was one

**Table 1** Locations of samples and summary statistics for mitochondrial DNA cytochrome oxidase I-5' (COI) (576 base pairs)

Location	Lat. N	Long	N	N <sub>poly</sub>	N <sub>H</sub>	N <sub>EH</sub>	N <sub>PH</sub>	h±SD	θ <sub>π</sub> ±SD (%)	D	p
NE Atlantic											
1. Svalbard Islands	78–80	12–29E	51	0	1	1.00	0	0.0	0.0	–	–
W Arctic, NW Atlantic											
2. New Brunswick, Nova Scotia, Canada	Various		7	0	1	1.00	0	0.0	0.0	–	–
3. New Foundland, Quebec, Canada	Various		3	0	1	1.00	0	0.0	0.0	–	–
4. Labrador, Canada	Various		5	1	2	1.78	1	0.400±0.237	0.069±0.088	–0.816	0.305
5. Hudsons Bay, Manitoba, Canada	Various		11	0	1	1.00	0	0.0	0.0	–	–
Pooled											
NE Pacific, Gulf of Alaska											
6. Western Gulf of Alaska	Various		3	4	3	1.00	2	1.000±0.272	0.463±0.416	0.0	1.0
7. Resurrection Bay	60.0643	149.4427 W	4	1	2	1.90	0	0.500±0.265	0.087±0.011	–0.612	0.389
8. Northwest Bay, Prince William Sound	60.5147	147.5947 W	7	0	1	1.00	0	0.0	0.0	–	–
9. Cordova, Prince William Sound	60.5425	145.7686 W	9	1	2	1.52	1	0.222±0.166	0.039±0.057	–1.088	0.202
10. Halibut Point, Sitka	57.0796	135.3769 W	29	5	6	2.51	4	0.374±0.113	0.071±0.075	–1.868	0.009
11. Harris Island, Sitka	57.0366	135.2789 W	5	0	1	1.00	0	0.0	0.0	–	–
Pooled			57	10	10	3.77	9	0.493±0.076	0.114±0.100	–1.945	0.006
NE Pacific: British Columbia, Washington											
12. Northern British Columbia	Various		15	0	1	1.00	0	0.0	0.0	–	–
13. Southern British Columbia, Washington	Various		7	1	2	1.62	1	0.286±0.196	0.049±0.067	–1.006	0.234
Pooled			22	1	2	1.26	1	0.091±0.081	0.016±0.033	–1.162	0.146

N sample size, N<sub>poly</sub> number of polymorphic nucleotide sites, N<sub>H</sub> number of haplotypes, N<sub>EH</sub> expected number of haplotypes under neutrality, N<sub>PH</sub> number of private haplotypes, h haplotype diversity (Standard Deviation), θ<sub>π</sub> nucleotide diversity (Standard Deviation), D Tajima's test for neutrality (Probability). See Online Resource Table 1 for latitude and longitudes of sample locations in pooled collections below

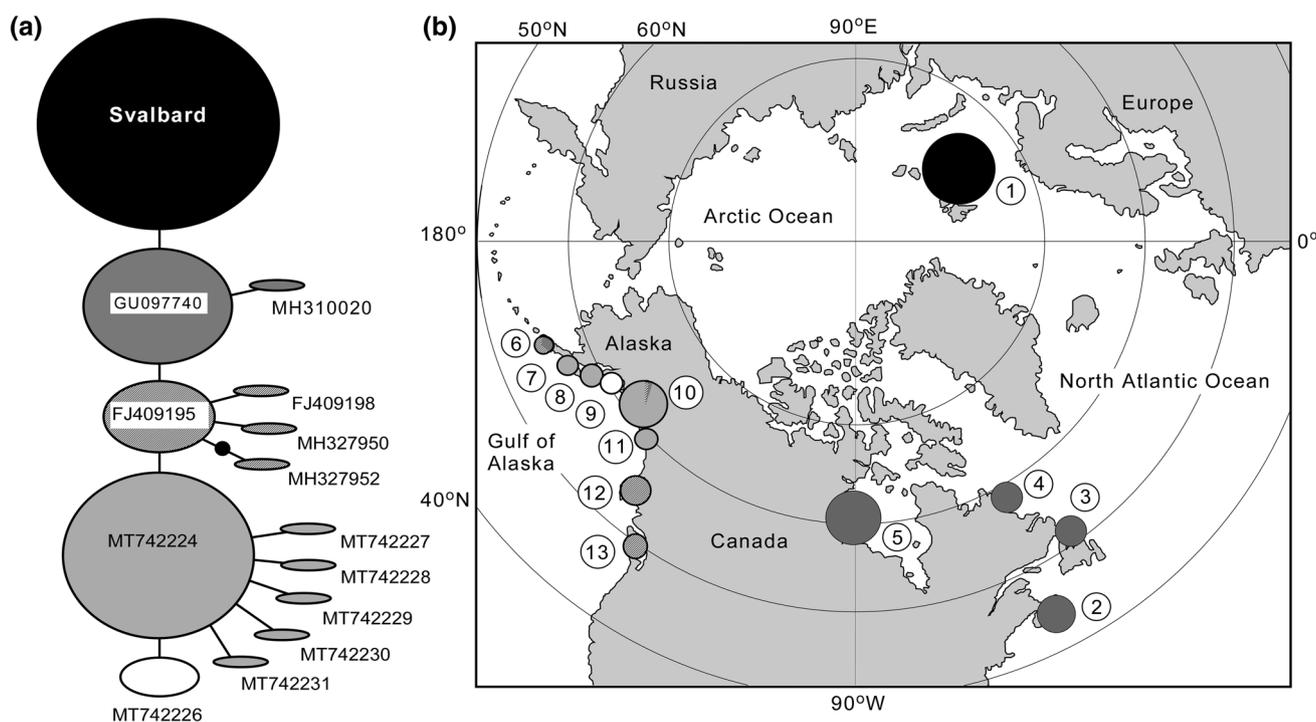
mutation removed from the dominant haplotype in the Canadian Arctic and NW Atlantic (Fig. 2). In the Canadian Arctic and NW Atlantic sequences, only a single nucleotide site was polymorphic, producing two haplotypes, one occurring in a single specimen (Location 4, Table 1, Online Resource Tables S8, S9). Overall, haplotype ( $h = 0.077 \pm 0.070$ ,  $n = 26$ ) and nucleotide ( $\theta_{\pi} = 0.00013 \pm 0.00030$ ,  $n = 26$ ) diversity were small. Tajima's test for neutrality was not significant ( $D = -1.156$ ,  $p = 0.138$ ,  $n = 26$ ).

We used *COI* divergence between *H. nigripes* and its sister taxon, *H. subsessile* and the Starko et al. (2019) estimate of 3.7 Ma for the time to the most recent common ancestor to calibrate the trans-Arctic dispersal of *H. nigripes* into the N Atlantic. The mean Tamura and Nei (1993) genetic distance between *H. nigripes* and *H. subsessile* was  $d = 0.0339$ . Distances between regional groups of *H. nigripes* were an order of magnitude smaller (Online Resource Table S3). Average genetic distance between NE Pacific and Arctic-NW Atlantic populations was  $d = 0.0046$ , and between NE Pacific and NE Atlantic (Svalbard Archipelago) was  $d = 0.0034$ . The genetic distance between populations in Arctic-NW Atlantic and the Svalbard Archipelago was  $d = 0.0026$ . The phylogenetic calibration yielded an estimate of about 0.922 Ma (posterior probability 1.0, 95% highest density

probability 1.88–0.27 Ma) for the time since populations in the NE Pacific and Arctic-NW-NE Atlantic began to diverge from one another (Fig. 3). Populations in the Gulf of Alaska and British Columbia had a common ancestor 0.568 Ma (probability 0.753, 1.186–0.155 95% HPD). The coalescence time to a common ancestor for the NW and NE Atlantic was 0.300 Ma (probability 0.718, 1.517–0.150 95% HPD), 0.324 Ma (probability 0.988, 0.732–0.077 95% HPD) for the Gulf of Alaska, and 0.384 Ma (probability 0.397, 0.858–0.074 95% HPD) for British Columbia and Washington.

## Discussion

Our analysis of genetic markers in split kelp provides several insights that are not possible from the analysis of morphological variability. First, populations in the NE Pacific are genetically subdivided as a result of limitations on present-day levels of gene flow between populations that maintain historical divergences during isolations in northern Pleistocene refugia. Second, the analysis confirms the relationship between NE Pacific and N Atlantic populations and indicates these populations belong to a single species that are



**Fig. 2** Geographical distributions of cytochrome oxidase I haplotypes (576 base pairs) for *Hedophyllum nigripes* globally. **a** Network showing mutational relationships among *COI* haplotypes. One step represents a single nucleotide-site change. Complete list of Genbank

Accession numbers appears in Supplementary Table 1. **b** Map showing locations of samples and haplotype frequencies within sampled populations. Size of circle is proportional to sample size

**Table 2** Summary statistics for concatenated sequences of cytochrome oxidase I-5' (*COI*) and ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit-3' (*rbcL*) (1393 base pairs) for populations in the Gulf of Alaska

Location	<i>N</i>	<i>N<sub>poly</sub></i>	<i>N<sub>H</sub></i>	<i>N<sub>EH</sub></i>	<i>N<sub>PH</sub></i>	<i>h</i> ± SD	$\theta_{\pi}$ ± SD (%)	<i>D</i>	<i>P</i>
7	4	2	3	3.04	1	0.833 ± 0.222	0.072 ± 0.071	-0.710	0.285
8	7	0	1	1.00	0	0.0	0.0	-	-
9	9	1	2	1.52	2	0.222 ± 0.166	0.016 ± 0.023	-1.088	0.203
10	27	7	7	2.63	6	0.402 ± 0.119	0.037 ± 0.036	-2.166	0.002
11	5	0	1	1.00	1	0.0	0.0	-	-
Mean	10.4	2.0	2.8	1.84	2.0	0.291	0.025	-	-
Pooled	52	10	12	8.46	10	0.770 ± 0.046	0.091 ± 0.065	-1.210	0.114

Location numbers as in Table 1

*N* sample size, *N<sub>poly</sub>* number of polymorphic nucleotide sites, *N<sub>H</sub>* number of haplotypes, *N<sub>EH</sub>* expected number of haplotypes under neutrality, *N<sub>PH</sub>* number of private haplotypes, *h* haplotype diversity (Standard Deviation),  $\theta_{\pi}$  nucleotide diversity (Standard Deviation), *D* Tajima's test for neutrality (Probability)

**Table 3** Haplotype frequencies of concatenated sequences of mitochondrial DNA cytochrome oxidase I-5' (*COI*) and chloroplast DNA ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit-3' (*rbcL*) (1393 base pairs) for populations in the Gulf of Alaska

Haplotype	Location					Total
	7	8	9	10	11	
1	1			21		22
2	2	7				9
3			8			8
4					5	5
5	1					1
6			1			1
7				1		1
8				1		1
9				1		1
10				1		1
11				1		1
12				1		1
Total	4	7	9	27	5	52

Location numbers as in Table 1

connected by trans-Arctic dispersal (McDevit and Saunders 2010).

### Mosaic population structure in the Gulf of Alaska

The combined *COI-rbcL* marker indicates that nearly all the populations sampled in the Gulf of Alaska are genetically unique. Four of the populations (7–10) were fixed, or nearly fixed for one of the four haplotype lineages. However, divergences between lineages were shallow, consisting of only 1 or 2 mutational steps and producing an overall  $\Phi_{ST}$  of only 0.0009. Populations of other NE Pacific kelps, such as *Alaria marginata* and *Saccharina latissima* also show fixed *COI* and *rbcL* frequency differences between many populations (Grant et al. unpublished). Diversities within populations were small with *h* averaging 0.291 (mean *n* = 10.4) among populations and  $\theta_{\pi}$  averaging only 0.00025 (mean *n* = 10.4).

**Table 4** Genetic distances ( $\Phi_{ST}$ ) between populations in the Gulf of Alaska based on concatenated sequences of mitochondrial DNA cytochrome oxidase I-5' (*COI*) and ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit-3' (*rbcL*) (1393 base pairs) with the Tamura and Nei (1993) model of nucleotide substitution

8	0.151			
9	<b>0.785</b>	<b>0.933</b>		
10	<b>0.467</b>	<b>0.680</b>	<b>0.794</b>	
11	<b>0.781</b>	<i>1.0</i>	<b>0.949</b>	<b>0.680</b>
	7	8	9	10

Location

Location numbers as in Table 1

Italics 0.05 > *P* > 0.01; Bold *P* < 0.01

Large frequency differences between populations and low

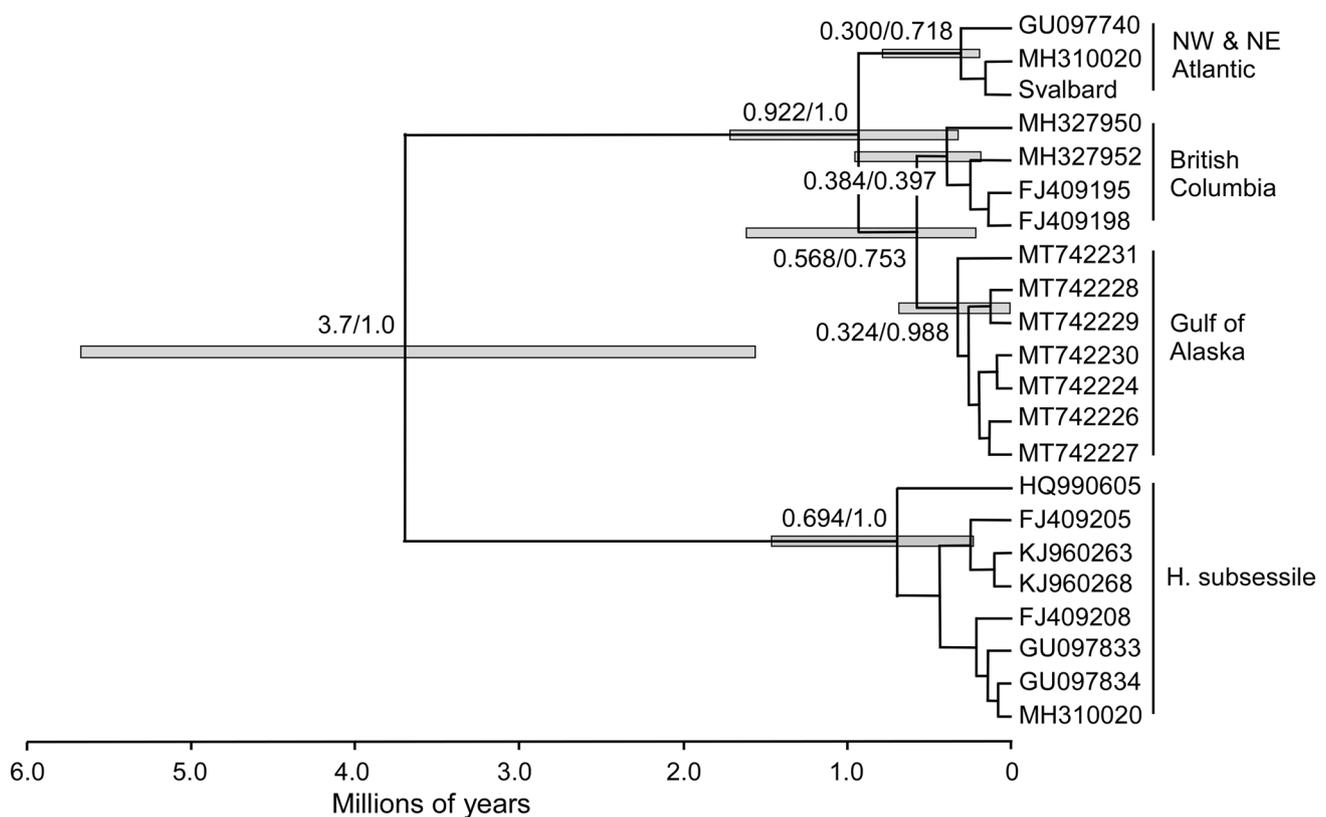
within-population diversities may reflect the effects of historical events that are maintained by ecological processes.

On shorter, ecological time scales, the small within-population genetic diversity and large haplotype differences between populations may be explained in part by habitat patch extinctions and mode of colonizations. Fecundity and reproductive skew act synergistically with patch extinctions and colonizations so that habitat patches are colonized by propagules from only a few parents (Sargsyan and Wakeley 2008; Castorani et al. 2017). Little is known about the population dynamics of *H. nigripes* along NE Pacific shores, but populations of *H. nigripes* in the NW Atlantic Bay of Fundy are ephemeral on decadal time scales (Longtin and Saunders 2016), as are populations of *Saccharina latissima* in Europe (Moy and Christie 2012; Christie et al. 2019) and *Macrocystis pyrifera* in California (Reed et al. 2006).

The addition of *COI* sequences from British Columbia and Washington shows a phylogeographic break between SE Alaska and northern British Columbia that roughly coincides with a marine biogeographic boundary between the North American Pacific Fjordland and the Gulf of Alaska ecoregion (Spalding et al. 2007), areas that differ in average sea

surface temperatures (Payne et al. 2012). A similar genetic discontinuity has also been observed for marine fishes in this area (Withler et al. 2001). These phylogeographic breaks may reflect adaptive responses to environmental differences between regions, or may represent contact between groups previously isolated by Pleistocene glaciations.

On longer time scales, the chaotic genetic structure of populations in the Gulf of Alaska likely reflects historical isolations between lobes of the Cordilleran ice sheet during ice-age maxima (Mann and Hamilton 1995; Carrara et al. 2007). The greater genetic diversity in the Gulf of Alaska relative to neighboring southern populations in British Columbia points to northern glacial refugia. During glaciations, the eastward flowing North Pacific Drift and the transition zone were pushed to the south from their present position along central British Columbia (Sabin and Pisias 1996). However, average sea surface temperatures in the Gulf of Alaska dropped to only 5–6 °C during the last glacial maximum (Moore et al. 1980). These temperatures would have been within physiological tolerances of *H. nigripes*, as it presently occurs at high latitudes in subtidal waters that experience freezing temperatures in winter (Lydon 2015;



**Fig. 3** Phylogenetic reconstruction of *COI* lineages in *Hedophyllum nigripes* with rooting by *Hedophyllum subsessile* and with the Tamura and Nei (1993) model of substitution. Time scale based on divergence between *H. nigripes* and *H. sessile* in a kelp phylogeny reconstructed

by Starko et al. (2019). Numbers at nodes represent Ma of divergence and 95% Bayesian support for the node. Grey bars represent 95% highest probability density

Filbree-Dexter et al. 2019). The well-studied kelp assemblage on 'boulder patches' off Alaska's Arctic coast and off Greenland can be considered contemporary analogues of a glacial refugial community. Kelps in the Arctic persist despite several months of darkness under snow-covered sea ice (Dunton 1985; Wilce and Dunton 2014; Küpper et al. 2016; Bringloe and Saunders 2019b; Filbree-Dexter et al. 2019).

The chief genetic evidence for the existence of northern refugia in NE Pacific *H. nigripes* is a mosaic population structure and greater *COI* genetic diversity ( $h=0.652$ ,  $\theta_{\pi}=0.0015$ ,  $n=57$ ) relative to diversity in southern populations ( $h=0.100$ ,  $\theta_{\pi}=0.0002$ ,  $n=20$ ) (Table 1). The general lack of shared haplotypes between the Gulf of Alaska and British Columbia is also consistent with northern glacial refugia (Fig. 2b). The lack of samples from western Alaska and the northern reaches of the Bering Sea limits our ability to determine whether these northern refugia were located in the central and eastern Gulf of Alaska, along unglaciated shorelines of the Bering Land Bridge, or possibly in the NW Pacific, where this kelp may be listed as *S. bongardiana* (Selivanova et al. 2007).

Northern refugia are further supported by the discovery of coastal ice-age refugia for large mammals and terrestrial plants in the NE Pacific (Peteet and Mann 1994; Heaton et al. 1996; Byun et al. 1997; Holder et al. 1999). These terrestrial refugia may have been associated with stretches of ice-free shorelines. The time-calibrated phylogenetic tree places the initial divergences between lineages in the Gulf of Alaska at 0.300–0.200 Ma, indicating that populations survived two or three Croll-Milankovitch climate cycles in local refugia. Divergence between populations is maintained by contemporary limits on gene flow between populations. Low levels of genetic diversities within populations may reflect population bottlenecks, or local extinction and colonizations.

Northern refugia in the NE Pacific have been postulated for fishes (Canino et al. 2010; Bigg 2014), intertidal whelks (Marko et al. 2010), and other kelps (Lindstrom 2009; Grant et al. unpublished). Northern glacial refugia have also been postulated for numerous species in the N Atlantic that show high levels of genetic diversity at high latitudes (Maggs et al. 2008) and by ecological niche models that identify suitable high-latitude habitats during glacial maxima (Bigg et al. 2008; Assis et al. 2014, 2018; Bringloe et al. 2020).

### Canadian Arctic, NW Atlantic and NE Atlantic

Unlike the mosaic population structure in the Gulf of Alaska, a single dominant *COI* haplotype occurred among populations in the Canadian Arctic and NW Atlantic oceans. This dominant haplotype was one mutation removed from the dominant haplotype in British Columbia, but two mutations from the dominant haplotype in the Gulf of Alaska, a pattern

that is difficult to explain with the available data. Two haplotypes (MH327950 and MH327952) from the 'southern' lineage in British Columbia appeared in two kelp from the western Gulf of Alaska (Fig. 1a, b) and may indicate that southern-lineage haplotypes occur farther to the west. Hence, one possibility is that the NW Atlantic haplotype is present along the Aleutian Islands, in the Bering Sea, or in the NW Pacific and was carried by migrants across the Arctic Ocean.

The low levels of genetic variability within and homogeneity among Canadian Arctic-NW Atlantic populations contrast with the greater genetic heterogeneity among NE Pacific populations of *H. nigripes*. Only a single sequence variant was recovered in northern Labrador (location 3; Fig. 2). Although samples from the Canadian Arctic-NW Atlantic populations were small ( $n=26$  in total), they extended from Hudsons Bay to New Brunswick, Canada, so that a conclusion of genetic homogeneity is unlikely to change with further sampling. A single dominant haplotype in these samples invokes three non-exclusive and plausible scenarios: (1) gene flow is much greater in the NW Atlantic than in the NE Pacific, (2) population structure exists, but is not detectable because of low levels of *COI* sequence variability, or (3) populations have expanded recently from a single refugium and insufficient time has elapsed for genetic differences among populations to emerge in the *COI-5'* gene segment.

Levels of contemporary gene flow between Canadian-Arctic and NW Atlantic populations, as in scenario 1, are unlikely to be greater than those in the NE Pacific. Short-lived spores are unlikely to contribute to dispersals over long distances (Santelices 1990), and bidirectional long-distance dispersals of mature plants are also unlikely. In scenario 2, the lack of *COI* polymorphisms may limit the ability to detect population structure, if it exists. The use of microsatellites or other nuclear markers may provide greater resolution of populations structure than mitochondrial or plastid DNA, as has been the case for other kelps (*Saccharina latissima*, Luttikhuisen et al. 2018; Neiva et al. 2018). Further sampling and analysis with additional molecular markers and genomic methods will provide insights, not only into gene-flow patterns, but also into the kelp's adaptive seascape.

In scenario 3, low levels of genetic diversity and genetic homogeneity among Canadian Arctic-NW Atlantic populations may reflect repeated contractions into a glacial refugium and subsequent expansions. The classic southern refugium hypothesis would place a refugium along mid-latitudes of North America during glacial maxima. However, northern refugia have been postulated for several species of marine invertebrates (Maggs et al. 2008). Distributional modelling during the last glacial maximum of other N Atlantic kelps indicates that northern refugia were possible, particularly

along the southern shorelines of Greenland (Assis et al. 2018; Bringloe et al. 2020).

The genetic affinity between Arctic-NW and NE Atlantic and NE Pacific populations and the reduced levels of genetic diversity in the Arctic-NW and NE Atlantic populations, typical of populations founded by a small number of individuals (Nei et al. 1975), support a model of trans-Arctic dispersal of migrants from the N Pacific. Dispersal has periodically been possible after Bering Strait first opened 7.4–4.8 Ma (Marincovich and Gladenkov 2001), not only during warm interglacial periods in the 0.100 Ma Croll-Milankovich climate cycle, but also during warm interstadials when rising sea levels breached the Bering Land Bridge (Jouzel et al. 2007). The Bering Sea Strait has been open whenever global sea levels rose above –60 m below present-day sea level (Hopkins 1959) and has provided trans-Arctic dispersal opportunities for about 20% of the Pleistocene (Waelbroeck et al. 2002; Spratt and Lisiecki 2016).

The temporal estimate of trans-Arctic dispersal of *H. nigripes* provides insight into whether Arctic-NW Atlantic populations have only recently been established, or whether they have endured one or more ice-age cycles in the NW Atlantic. A divergence time between *H. nigripes* and its sister taxon *H. subsessile* of 3.7 Ma (Starko et al. 2019) places trans-Arctic dispersal of *H. nigripes* into the N Atlantic at about 0.900 Ma (Fig. 3, probability 1.0, 95% HPD: 1.880–0.280 Ma) in the mid-Pleistocene Epoch. The mutational progression of haplotypes (Fig. 2a) indicates that Svalbard kelps were seeded by kelps in the Arctic NW Atlantic.

In conclusion, *Hedophyllum nigripes* populations in the NE Pacific show low levels of within-population genetic diversity, but strong differences among populations that may have arisen from isolation in multiple northern glacial refugia and maintained by contemporary ecological dynamics. The greater amount of genetic diversity among populations in the Gulf of Alaska than among southern populations indicates persistence in northern refugia during multiple ice-age cycles. This conclusion further challenges the traditional view that shallow-water, marine species in northern seas were displaced into southern refugia (Hewitt 1996, 2004). Arctic-NW Atlantic populations are genetically distinctive from NE Pacific populations, have low levels of *COI* diversity, and are genetically homogeneous. It is uncertain from this genetic profile whether N Atlantic populations survived in northern glacial refugia or expanded from southern refugia. Together these results again show the profound influence Pleistocene climate shifts had in shaping the genetic population structures of northern marine species.

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## Compliance with ethical standards

**Conflict of interest** All authors declare that they have no conflict of interest.

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