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FULL-LENGTH RESEARCH ARTICLE

Phylogeographic analysis of complete mtDNA genomes from Walleye Pollock (*Gadus chalcogrammus* Pallas, 1811) shows an ancient origin of genetic biodiversity

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Abstract
Ursvik et al. compared the complete mitochondrial DNA (mtDNA) genome sequences of Walleye Pollock (*Gadus* (= *Theragra*) *chalcogrammus*) from the Pacific Ocean with a pair of fish from an isolated population of Norwegian pollock in the Barents Sea. They concluded that the Norwegian population was recently introduced from the Pacific. We test this hypothesis within a temporal framework provided by a phylogeographic analysis of complete genomes from the pollocks' sister species, Atlantic Cod (*Gadus morhua*), and their divergence 3.5 mya. Pollock have a coalescent ancestor 189 ± 25 kya. The two Norwegian fish have a common ancestor 87 ± 7 kya, which suggests an ancient origin rather than a recent human-mediated introduction. Mitochondrial genomic biodiversity in pollock antedates the most recent glacial cycle. The clade structure of the whole-genome tree indicates that previously described single-locus mtDNA haplotypes and haplogroups are typically paraphyletic.

Keywords: Gadus chalcogrammus, Theragra, finnmarchica, *phylogeography, mitogenomics*

Introduction

Walleye or Alaska Pollock is a commercially important species on both sides of the North Pacific and the Bering Sea, and one whose population structure has been studied intensively for many years via allozymes, mitochondrial DNA (mtDNA) restriction fragment length polymorphisms (RFLPs), and microsatellites (Bailey et al. 1999; Olsen et al. 2002; O'Reilly et al. 2004; Grant et al. 2006), and most recently complete genomes (Yanagimoto et al. 2004; Ursvik et al. 2007).

Walleye Pollock was originally described in the Linnaean cod genus as *Gadus*, but was subsequently transferred to *Pollachius* (the true pollocks), and then to a new genus *Theragra* ("beast food", as the principal diet of pinnipeds), ultimately with the original species epithet as *Theragra chalcogramma* (Svetovidov, 1948). Comparison of complete mtDNA genomes shows that pollock are in fact more closely related to Atlantic Cod (*Gadus morhua* L., 1758) than is Pacific Cod (*Gadus macrocephalus* Tilesius, 1810). To keep *Gadus* monophyletic, we proposed restoration of the original nomenclature, *Gadus chalcogrammus* Pallas, 1811 (Coulson et al. 2006).

Complete mitochondrial genome sequences were obtained by Yanagimoto et al. (2004), from five pollock from the Sea of Japan and five from the Bering Sea. They did not, however, perform a formal phylogenetic analysis on these data. An isolated population of pollock, first described from a small number of specimens taken in the Barents Sea off the Finnmark region of northern Norway, was designated as a separate species, *Theragra finnmarchica* Koefoed, 1956 (Christiansen et al. 2005; Ursvik et al. 2007). Byrkjedal et al. (2008) have subsequently recommended inclusion of *T. finnmarchica* as a junior synonym of *T. chalcogramma*. Ursvik et al. (2007) obtained complete genome sequences of two specimens of this rare pollock, and together with the

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genome data from Yanagimoto et al. (2004) performed a phylogenetic analysis that showed that they formed a pair within Walleye Pollock, a pair which was most closely related to a pair of fish from the Sea of Japan. They concluded that Norwegian pollock are a recent derivative of pollock from the Sea of Japan, one that might for example have been introduced by humans within historic times. This suggestion was made, however, without reference to an explicit time frame.

We have made a phylogeographic study, based on complete mtDNA genomes, of pollock's sister species, the Atlantic Cod (*G. morhua* L., 1758) (Carr and Marshall 2008). This includes a calibration of the molecular evolutionary rate based on the observed nucleotide divergence from an eastern Pacific pollock and an assumed separation at the last opening of the Bering Strait 3.5 mya (Coulson et al. 2006). Application of this temporal framework permits a more refined insight into the biogeography of Norwegian pollock, and further illustrates the power of mitochondrial genomics for biodiversity.

Materials and methods

We collated 13 previously published pollock mtDNA genome sequences from four populations (Figure 1): five fish from the Sea of Japan and five from the Bering Sea [accession numbers NCBI AB094061 and AB182300–AB182308; (Yanagimoto et al. 2004)], two Norwegian pollock from the Barents Sea [accession numbers AM489718 and AM489719; (Ursvik et al. 2007)], and a pollock from the eastern Pacific [Nanaimo, British Columbia; accession number DG356946; (Coulson et al. 2006)], with additional Control Region (CR) sequence for the last obtained by same methods described therein. Following Ursvik et al. (2007), we refer to the genomes of the Bering Sea pollock as B1–B5, those of Sea of Japan pollock as J1–J5, and those of Norwegian pollock as Tf1–Tf2. We designate the eastern Pacific pollock as Epac. The tree was initially rooted with five complete mtDNA sequences from Atlantic Cod, derived from an iterative re-sequencing microarray [GenBank accession numbers EU877731–EU877735; (Carr and Marshall 2008)]. The consensus length is 16,579 bp, in which Position 1 by our numbering is the first base of the 12S rRNA gene, which corresponds to Position 78 in Ursvik et al. (2007).

We previously calculated a divergence rate of 1.12×10^{-9} substitutions/site per year between pollock and Atlantic Cod, based on an observed 0.040 substitutions/site for two genomes, not including the CR, and the assumption that the species diverged at the time of the last opening of the Bering Strait 3.5 mya (Coulson et al. 2006; Carr and Marshall, 2008). This gave an estimated interval of 5703 years/

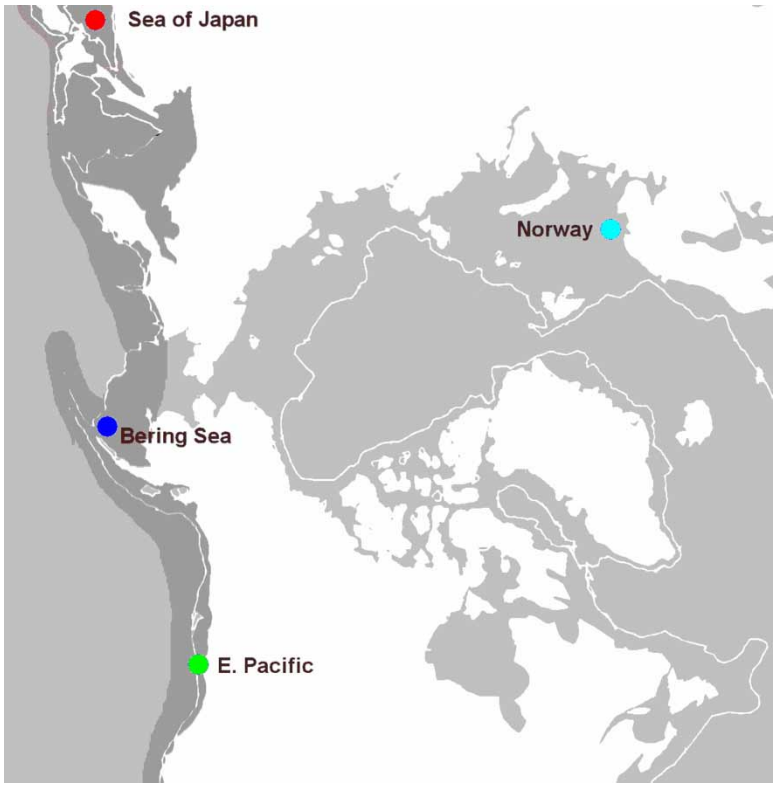

Figure 1. Distribution of pollock and origins of samples. *Note*: The Pacific distribution of Walleye Pollock is shown in dark grey. Samples sites are North Cape, Norway; Sado Island, Sea of Japan; Bogoslof Island, Aleutians, Bering Sea; Nanaimo, British Columbia, eastern Pacific. This figure is reproduced in colour in *Mitochondrial DNA* online.

substitution, somewhat slower than the equivalent interval for *Homo*, 5103 years (Achilli et al. 2004), also without the CR. Based on the mean pairwise difference among 13 pollock and five cod genomes of 666 ± 7 substitutions over 16,579 bp including the CR, the divergence rate for the present data is 1.22×10^{-9} substitutions/site per year, which gives an estimated interval of 5255 years/substitution. This adjustment reflects a slightly faster rate of substitution in the CR as compared with the genomic average. Neither the Atlantic Cod nor the pollock genome CRs are intraspecifically hypervariable in the manner of mammalian CRs [*cf.* Ingman et al. (2000)].

Sequence assemblies were performed with Sequencher 4.7 (Gene Codes, Ann Arbor, MI, USA). Phylogenetic analyses were done with PAUP*4.0 (Swofford 2000). Maximum parsimony analysis was calculated with all sites equally weighted (i.e. unweighted), and 10,000 bootstrap replications. For pollock alone, a two-rate (HKY variant) maximum likelihood analysis was calculated with all parameters estimated from an initial analysis with 10 TBR rearrangements ($Ts/Tv = 5.56$, $\gamma = 0.86$), then with 10,000 bootstrap replicates with two TBR rearrangements each. Neighbor-joining analysis was calculated either with total pairwise differences or with the two-parameter maximum likelihood distances. The species coalescent was calculated either as the mean patristic distance from all OTUs to the root in the neighbor-joining pairwise-difference tree, or from a linearized maximum likelihood tree with the molecular clock constraint enforced [*cf.* Carr and Marshall (2008)].

Results and discussion

Phylogenetic relationships

With the five Atlantic Cod sequences as the outgroup, we obtain two maximum parsimony trees of equal length (969 events) with alternatively B1 or EPac as the outgroup to the remaining pollock. The placement of the pollock root among B1, B3, and EPac is statistically unresolved by maximum parsimony (Figure 2) or by neighbor-joining analysis with maximum likelihood distances. Similar results with respect to the placement of the root among pollock are obtained with various combinations of two and/or five Atlantic Cod sequences, with or without Epac, by parsimony, distance, and likelihood methods, and by analysis with or without the CR (results not shown).

Without Atlantic Cod, maximum parsimony analysis suggests that B1, B3, and EPac are a group or clade with respect to the remaining pollock (81% bootstrap support). Noting that this group may in fact be paraphyletic, there are then two or three major clades in these data: the basal group (B1, B3, and EPac) and two sister clades, one with four genomes (B2, J1, J2, and J5: 97% bootstrap support) and one Norway pollock-inclusive clade (B5, J3, J4, Tf1, and Tf2: 67% bootstrap support; Figure 3(a)). One fish (B4) falls as the sister to the latter two clades. The same three groups are obtained by neighbor-joining and maximum likelihood analyses, under various models, and with or without the CR (results not shown), and their topologies are substantially identical with each other and to those of Ursvik et al. (2007), based on slightly different models. Ursvik et al.

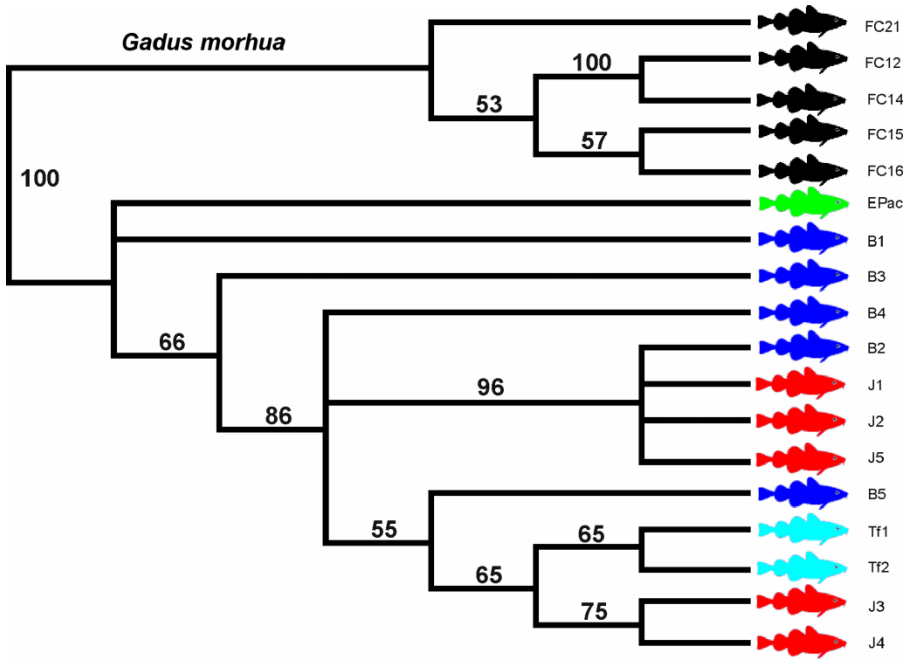

Figure 2. Phylogenetic relationships among 13 pollock mtDNA genomes with respect to an Atlantic Cod outgroup. *Note*: Numbers above the branches are the percentage support in 10,000 branch-and-bound maximum parsimony bootstrap replicates. Placement of the root with respect to B1 and Epac is unresolved. This figure is reproduced in colour in *Mitochondrial DNA* online.

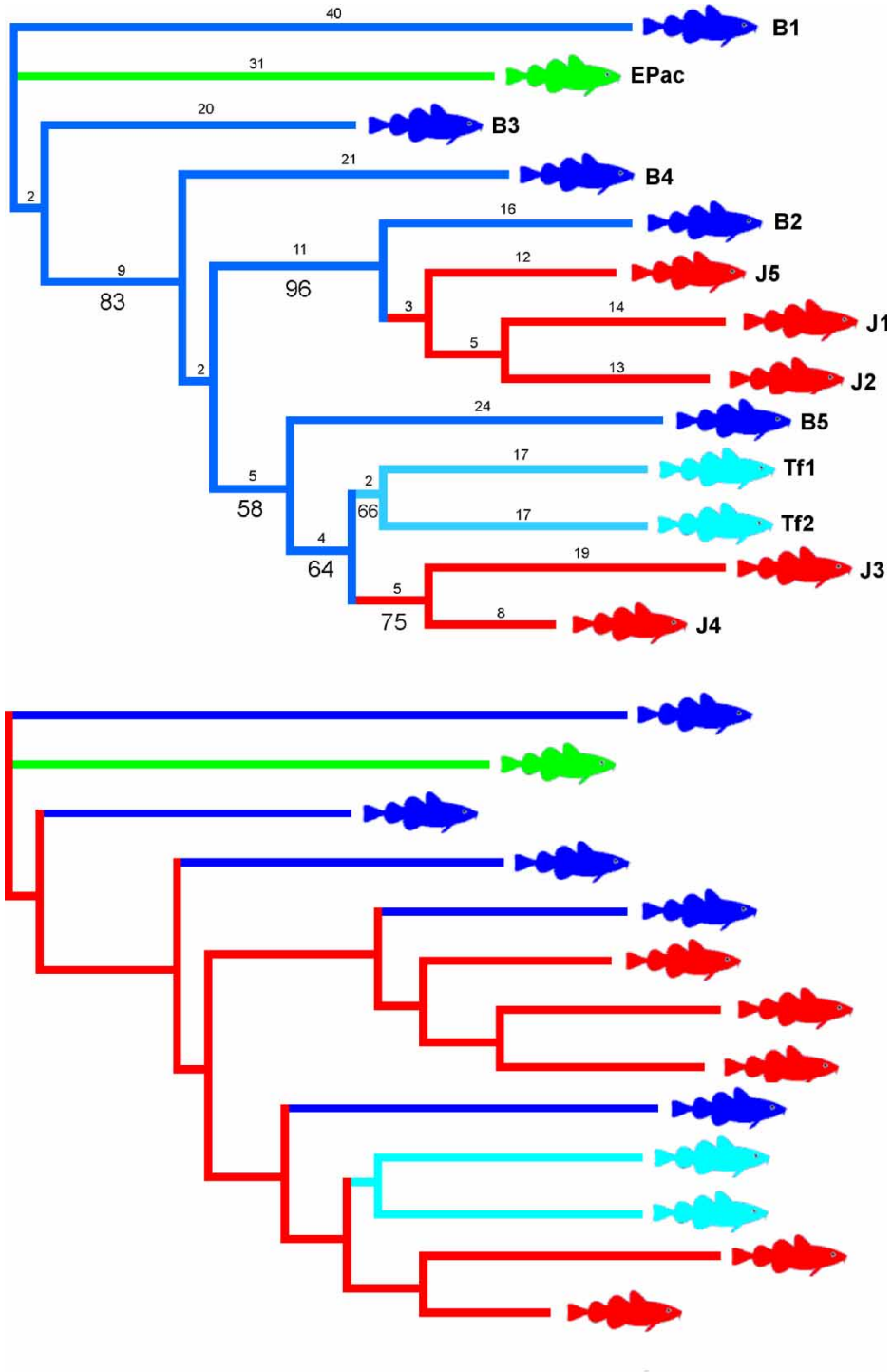

Figure 3. (a) Phylogeographic relationships among 13 pollock mtDNA genomes. (b) Alternative phylogeographic model. *Note*: (a) shows one of two maximum parsimony trees of equal minimum-length (300 events), rooted with B1 and EPac as an outgroup with respect to the remaining genomes, as in Figure 2. Branches are shaded to show a phylogeographic hypothesis of the origins of pollock mtDNA biodiversity in the Bering Sea (dark blue), and subsequent movement to the Sea of Japan (red), eastern Pacific (green), and Barents Sea, Norway (light blue) (four events) (see text). Numbers above branches are the inferred number of nucleotide substitutions on each branch; numbers below branches are bootstrap support (percentage of 10,000 replicates) for each node. Maximum-likelihood and neighbor-joining analyses give substantially identical results (not shown). (b) Branches are shaded to show a phylogeographic hypothesis of the origins of pollock mtDNA biodiversity in the Sea of Japan: color scheme as above. A total of seven events is required. This figure is reproduced in colour in *Mitochondrial DNA* online.

(2007) rooted their tree with two haddock (*Melanogrammus aeglefinus*) genome sequences, and included two Atlantic Cod sequences, which placed pollock B1 as the outgroup to all other pollock.

The maximum observed sequence divergence between any two pollock is 81/15,579 = 0.00520 substitutions/site between B1 and J1, versus a maximum intra-clade divergence of 74/15,579 = 0.00475 substitutions/site between B1 and EPac in the basal group. The minimum divergence is 27/15,579 = 0.00173 substitutions/site, observed between two pairs of Sea of Japan fish, one in either of the other two clades.

Biogeographic and temporal relationships

Ursvik et al. (2007) suggested that the occurrence of the Norwegian pollock pair as the sister group to a pair from the Sea of Japan implied an origin of the former from the latter. However, given an alternative hypothesis of a Bering Sea origin of pollock mtDNA diversity, the phylogeny presented in Figure 3(a) requires a total of four vicariance events to account for the biogeographic distribution of 13 pollock: two moves to the Sea of Japan, and one move each for eastern Pacific pollock and Norwegian pollock [*cf.* Carr and Marshall (2008), Figure 3]. Ursvik et al.'s hypothesis of a Pacific origin in the Sea of Japan (Figure 3(b)) would require seven events: one for each of the Bering Sea fish, and two again for the eastern Pacific and Norwegian fish. A two-tailed binomial test of the four versus seven event models is not statistically significant ($p > 0.05$).

In analyzing biogeographic data, it is important to adopt a phylogenetic perspective. Yanagimoto et al. (2004) observed the T/C polymorphism at their site 11,578 (our 11,501) as a "diagnostic" SNP for Bering Sea (11578T) versus Japan Sea (11578C) pollock. The 11578C allele is also found in Norwegian pollock (Ursvik et al. 2007). However, since the J3 + J4 pair and the J1 + J2 + J5 triplet are separate clades (Figure 2), this "diagnostic" site is in fact a homoplasy that has evolved in parallel (T > C) in each clade. As well, the 11578C allele occurs independently in the EPac pollock, for a triple play. (Alternatively, if the ancestral state is >C, five independent C > T events are required.) Use of "pattern recognition" profiles for human mtDNA CR genotyping has also confused common ancestry with homoplasious resemblance (Torroni et al. 2006).

The maximum observed mitochondrial sequence divergence of 0.00520 substitutions/site is about one-third greater than the maximum in Atlantic Cod. The minimum divergence of 0.00173 substitutions/site is four-fold greater than the minimum divergences observed in *Gadus*, and greater than the maximum difference observed in any of the six major primary clades in *Gadus* (Carr and Marshall 2008). From an estimated rate constant of 5255 years/substitutions for the divergence of pollock from Atlantic Cod 3.5 mya (see Materials and methods), the two Sea of Japan clades of are of similar age (84 ± 13 and 87 ± 7 kya). Divergence of the Norwegian pollock pair is about the same (17.5 ± 1.4 substitutions = 87 kya). These three coalescents occur well within the most recent (Weichsel/Würm) glacial period. The grand coalescent for the species estimated from the neighbor-joining tree is 35.9 ± 4.7 substitutions × 5255 years/substitution = 189 ± 25 kya. The estimate from the linearized maximum likelihood tree is 40.4 substitutions, within the bounds of the neighbor-joining estimate. Either estimate is well into the previous (Illinoian/Saale) glacial period. Standing mtDNA biodiversity in pollock is thus substantially older and of a qualitatively different pattern than in Atlantic Cod. As in Atlantic Cod, the age of the observed biogeographic patterns appears to be too old to be a direct consequence of post-Wisconsinan vicariance < 12 kya.

Whole-genome versus single-locus mtDNA data for biogeography

The whole-genome data also provide a more highly-resolved structure within which to reconsider the biogeographic implications of previous single-locus mtDNA data, as has been done in Atlantic Cod (Carr and Marshall 2008). Grant et al. (2006) recently reviewed the mtDNA haplogroup structure of pollock. They identified three major haplogroups designated A, B, and C across their northern Pacific range, based on RFLP haplotypes from various restriction endonucleases for complete (Olsen et al. 2002) or partial (Mulligan et al. 1992; Kim et al. 2000; Brykov et al. 2004) mtDNA molecules. Homotopies among groups across studies were identified by "their positions in haplotype networks and by frequencies in geographically overlapping samples . . . ". Equivalencies between mtDNA genome sequences and RFLP haplotypes based on band sharing are difficult to make out from the data as published [*cf.* Olsen et al. (2002), Figure 2]. However, Grant et al. (2006) also describe 15 different 479-bp COI haplotypes from 50 fish, from Puget Sound, Washington, and these are readily placed in genomic context. Five of these haplotypes can be associated with one or another of the 13 genomes sequence lineages by a shared substitution (Table I): haplotypes 2 and 6 with EPac, haplotype 5 with Tf1, haplotype 7 with J1 + J2, and haplotype 12 with B1. However, genome Tf1 is also associated with haplotypes 4, 14, and 15; genome B1 is also associated with 15. The phylogenetic relationships of haplotypes 2, 4, 12, 14, and 15 are thus ambiguous due to homoplasy. Similarly, genomes B2, B4, and B5 share a SNP at position 5409A not seen in the single-locus data, which indicates homoplasy at this site with respect to their relationships in the genome tree. Of the remaining pollock haplotypes, six have one or more unique SNPs not seen in any of the available

Table I. Correspondence of mtDNA COI haplotypes and whole-genome sequences.

Position	SNP	Haplotype	Genome
5409	T > A	–	B2 B4 B5
5439	A > G	13	–
5422	C > T	–	EPac
5460	C > T	13	–
5472	C > T	10	–
5487	*A > C*	***12***	***B1***
5538	T < > A	5, 15	–
5538	T < > C	–	B4
5574	A > C	–	EPac
5601	*A > G*	***15***	***EPac***
5625	C > T	1, 4, 11	–
5640	A > G	11	–
5673	*A > G*	*7*	***J1, J2***
5679	T > C	6	–
5694	*G > A*	***2, 6***	***EPac***
5727	G > A	15	–
5748	C > T	9	–
5775	T > C	3, 11	–
5799	*C > T*	***4, 5, 14, 15***	***Tf1***

Note: Position refers to the genome sequence position in the COI locus as numbered in Carr and Marshall (2008): add 77 for equivalent positions in Ursvik et al. (2007). SNP refers to the inferred direction and nature of change observed at each position. Directions of interchanges at position 5538 are indeterminate. Haplotypes refer to the 15 numbered COI mtDNA haplotypes in Grant et al. (2006). Genomes refer to the 12 mtDNA genome sequence designations from Ursvik et al. (2007) Table I, plus Epac. Rows in *italics* associate one or more single-locus haplotypes with one or more genome sequences. Haplotype 8 (not listed) shows the plesiomorphic (left-hand) character state at all positions, and thus is symplesiopmorphically identical with the seven genomes without COI SNPs in this region (B2–B3, B5, J3–J5, and Tf2).

genome sequences (haplotypes 1, 3, 9, 10, 11, and 13), and in several cases their interrelationships are ambiguous, again due to homoplasy.

Besides the individual haplotypes, both of the two major haplogroups identified in Coulson et al. (2006) are subject to homoplasy. The more common (A) is a star phylogeny centered around the abundant haplotype 8 (49% of fish examined at Puget Sound). This haplotype is identical with the symplesiomorphic sequence for this 479-bp segment of the genome, which is found in seven of 13 genomes in all three clades across all seas and oceans (B2–B3, B5, J3–J5, and Tf2). The less common group (B) is defined by the synapomorphy at position 5799T (Table I), which is also found in Tf1, an evident homoplasy. Finally, haplotypes 6 and 12 versus haplotype 7 mark pollock genomes in two distinct clades, but both are included in group A, which further confirms the poor fit of the haplotype data to the genomic tree.

Conclusions

Phylogenomic analysis within a more highly-resolved temporal framework extends previous biogeographic and population studies. The current genome data set is limited, but we sketch preliminary conclusions and suggest directions for future research.

Given the genetic relationships established in Ursvik et al. (2007) and here, we support the recommendation of Byrkjedal et al. (2008) that *T. finnmarchica* be considered a junior synonym of *T. chalcogramma*, and in so doing reiterate our recommendation that *Theragra* be included within *Gadus* (Coulson et al. 2006). Norway pollock might then be a separate subspecies of pollock, *G. chalcogrammus finnmarchica* (Koefoed 1956).

Ursvik et al. (2007) suggested that Norwegian pollock are recently derived from pollock in the Sea of Japan, either by a problematic northward movement through the Bering Strait and via the Arctic Ocean, or perhaps by human transplantation in historic times. The molecular clock shows instead that this pair is part of an ancient, independent lineage. Given the alternative biogeographic hypotheses of an origin of this lineage either from fish in the Bering Sea (Figure 3(a)) or in the western North Pacific (Figure 3(b)), independent derivation from the former is more direct and part of a scenario that requires fewer total vicariant events.

The 13 available genomes are a very limited sample of the extensive range of the species. It remains possible that the Norwegian fish are part of lineages from elsewhere in the species' range that are as yet unidentified. Were they found to be closely related to or identical with such fish, the Norwegian fish could then be explained as a paraphyletic assemblage of recent origin. Alternatively, the two fish might be closely related and yet have distinct mtDNA genotypes as a retained ancestral polymorphism. Kuch et al. (2007) report such a case in humans, where the only two representatives of an extinct First Nations group, the Newfoundland Beothuks, are a husband and wife who have distinct mtDNA HVS-1 haplotypes. However, the Beothuk nation was continuous with the Algonquin group of northeastern North America, which along with other New World First Nations peoples share four major mtDNA lineages as ancestral polymorphisms derived from ancestral populations in northeastern Asia (Malhi et al. 2001). The Beothuk HVS-1 haplotypes are very similar (but not identical) to two of these lineages as seen in other Algonquin peoples (Pope et al. 2009). In contrast, the Norwegian pollock genome lineages occur in geographic isolation, are not known to exist elsewhere, and are more closely related to each other than to any other known lineages.

Single-locus COI haplotypes that appear genetically uniform turn out to be paraphyletic or polyphyletic assemblages when analyzed genomically, and include lineages that go back to the base of the species tree. Biogeographic analyses and hypotheses that assume common, widely-distributed haplotypes are identical throughout the species, range need to be reconsidered (Grant et al. 2006). Inferred phylogenetic relationships among these haplotypes do not correspond well to lineages indicated by genomic analysis. This same

phenomenon occurs in Atlantic Cod, where the most common single-locus Cytb mtDNA haplotype, which occurs at the center of a star phylogeny and in one-half of all fish examined (Árnason, 2004), turns out to be a paraphyletic assemblage of distantly-related genome sequences (Carr and Marshall 2008). Unlike pollock, in Atlantic Cod all three of the major secondary genomic clades are recognizable on the basis of single-locus mtDNA haplotypes. More extensive biogeographic coverage of both species is required to place previous genetic work in a highly-resolved phylogenomic context.

Similar genetic and temporal assumptions underlying the analysis of the many single-gene "star phylogenies" observed in other species (Avise 2000) may also need to be re-examined in light of whole-genome analysis. Iterative DNA re-sequencing microarrays provide a practical means of providing such coverage (Carr et al. 2008). A common "DNA chip" design may be practical for iterative sequencing of species groups whose interspecies genome differences are $<4\%$ (Flynn and Carr 2007), as for example the present species pair.

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