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# Phylogeography of the Brittle Star *Ophiura sarsii* Lütken, 1855 (Echinodermata: Ophiuroidea) from the Barents Sea and East Atlantic

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**Abstract:** *Ophiura sarsii* is a common brittle star species across the Arctic and Sub-Arctic regions of the Atlantic and the Pacific oceans. *Ophiura sarsii* is among the dominant echinoderms in the Barents Sea. We studied the genetic diversity of *O. sarsii* by sequencing the 548 bp fragment of the mitochondrial COI gene. *Ophiura sarsii* demonstrated high genetic diversity in the Barents Sea. Both major Atlantic mtDNA lineages were present in the Barents Sea and were evenly distributed between the northern waters around Svalbard archipelago and the southern part near Murmansk coast of Kola Peninsula. Both regions, and other parts of the *O. sarsii* range, were characterized by high haplotype diversity with a significant number of private haplotypes being mostly satellites to the two dominant haplotypes, each belonging to a different mtDNA clade. Demographic analyses indicated that the demographic and spatial expansion of *O. sarsii* in the Barents Sea most plausibly has started in the Bølling–Allerød interstadial during the deglaciation of the western margin of the Barents Sea.

**Keywords:** mtDNA; barcoding; echinoderms; demographic expansion



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## 1. Introduction

Marine communities of the Northern Atlantic experienced remarkable changes during the quaternary sea level oscillations when ranges of species were contracting during the advances of glaciations and expanding during warmer periods [1]. A number of taxa migrated from the Pacific to the Atlantic by trans-Arctic migrations after the first opening of the Bering Strait in the Pliocene [2]. The recent glacial cycle culminating in the last glacial maximum 21 kyr BP (thousands of years before present) lead to the southward retreat of boreal species, yet many populations survived in the northern unglaciated areas known as periglacial refugia [3–12]. Demographic expansions between the glacial cycles and after the retreat of the LGM ice sheets resulted in secondary contacts between previously isolated populations [6].

The Barents Sea is a marginal sea of the Arctic Ocean (Figure 1) and a biogeographic transition zone between East Atlantic and typical Arctic faunas. The sea is highly productive with the pronounced spatial variation in productivity of benthic communities. Southern and central parts of the Barents Sea are characterized by higher abundance and biomass of benthic species compared to the northern regions around Svalbard and Franz

Josef Land [13]. The Northern Barents Sea is often considered as the Arctic warming hotspot, where the sharp increase of water temperatures and salinity is observed since the mid-2000s [14]. Studies of the population structure of species distributed across the Barents Sea shelf are thus important for understanding the current and long-term changes in this dynamic marine ecosystem.

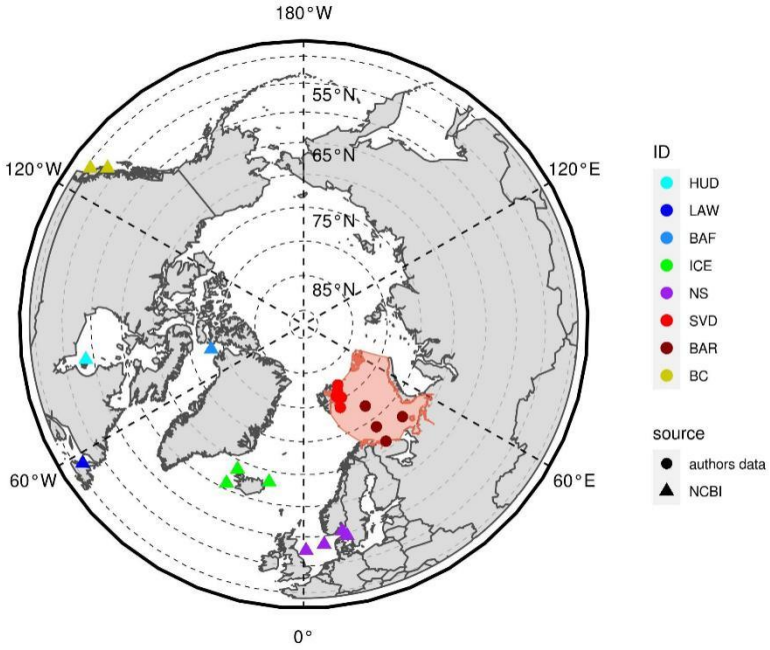


**Figure 1.** Map of *Ophiura sarsii* sampling locations. The Barents Sea is highlighted on the map. ID—locations codes: HUD—Hudson Bay, LAW—St. Lawrence Bay, BAF—Baffin Bay, ICE—Iceland, NS—the North Sea, SVD—Svalbard, BAR—Southern part of the Barents Sea, BC—British Columbia.

Ophiuroidea are important components of marine benthic communities in the Northern Hemisphere, often dominating vast areas of marine shelves [15–17]. The brittle star *Ophiura sarsii* Lütken, 1855 is a circumpolar cold-water species widely distributed throughout the North Pacific, the North Atlantic, and the Arctic oceans, where it can reach maximum depths of ca. 3000 m [18,19]. In the Barents Sea, *O. sarsii* represents up to 4% of the total echinoderm biomass, typically occurring at muddy and muddy fine sand communities at a depth range between 3 and 500 m [19]. *Ophiura sarsii* is a predator–scavenger species, and an important food item for many fish species [20]. It is also a typical marine broadcast spawner, releasing eggs and sperm in the Barents Sea in May–June [21] and then having a feeding larval stage (ophiopluteus) with planktonic existence of up to 30 days [22].

Recently, the genetic structure of *O. sarsii* was broadly evaluated across the Pacific [23]. Here we present analysis of the mitochondrial cytochrome c oxidase subunit I (COI) gene to examine the genetic diversity of *O. sarsii* in the Barents Sea and to make a pilot estimate of population structuring across the Atlantic using the previously published sequences from the barcoding studies of Echinoderms [24–26].

## 2. Materials and Methods

### *2.1. Samples*

Sampling was conducted in the Barents Sea during the 17th joint Barents Sea Ecosystem Survey (BESS) cruise of the Institute of Marine Research (IMR, Bergen, Norway) and the Polar branch of VNIRO (PINRO, Murmansk, Russia) [27] in September 2019 and 114th cruise of RV "Vilnyus" (Polar branch of the VNIRO) (Figure 1, Supplementary Table S1). Samples were collected using the bottom trawl from the depth range between 84 and 325 m. Individuals from the trawl were washed in seawater from sediments and preserved in 96% ethanol. Specimens of *O. sarsii* from the Barents Sea were deposited in the Zoological

Institute (ZIN RAS) in St. Petersburg with voucher numbers 964/25547–973/25556 in the collection of Echinoderms.

### *2.2. DNA Extraction, PCR, and Sequencing*

Total genomic DNA was extracted from the arm tissues using the QIAamp Fast DNA Tissue Kit (QiaGen). Newly designed forward primer OphS_COI_full_F (TTC TAC CAA CCA TAA GGA TAT AGG G) and the Folmer reverse primer HCO-2198 (TAA ACT TCA GGG TGA CCA AAA AAT CA) [28] were used to amplify a 700 bp fragment of the cytochrome c oxidase (COI) gene. PCR amplifications were carried out with a BioRad T-100 cycler. Each PCR reaction mixture (volume 25 µL) contained 3 µL template DNA, 5 µL PCR master-mix ScreenMix-HS (Evrogen), 13 µL nuclease-free water, and 2 µL each primer (10 pmol). The amplification reaction was performed with an initial denaturation step of 2 min at 94 °C, followed by 40 cycles of 94 °C denaturation for 30 s, 52 °C annealing for 60 s, 72 °C extension for 60 s, and a final 7 min extension at 72 °C during the last cycle. Amplified fragments of each individual were sequenced in both directions at Evrogen (Russia).

Following the pairwise alignments of 5′-3′ and 3′-5′ individual sequence reads, all polymorphisms were double-checked on the raw chromatograms. Sequences of this study are available in GenBank (accession numbers MW376210-MW376262).

### *2.3. Molecular Analysis*

To evaluate the patterns of O.sarsii genetic diversity across the North Atlantic, 22 *O. sarsii* cytochrome c oxidase subunit I (COI) gene sequences from the Atlantic were mined from the NCBI GenBank for the phylogeographic and demographic analyses. These sequences corresponded to the following regions: Iceland (KJ620617–KJ620623) [26], Baffin Bay (KU495754, KU495764, and KU495803) [25], Hudson Bay (KU495767, KU495777, KU495813, and KU495897) [25], St. Lawrence Bay (MG421803 and MG422945) [25], the North Sea (KX459084–KX459088) [24], and the Danish Straits (MG934897 and MG935229) [24]. Two sequences from the North Pacific (British Columbia (HM473939 and HM473940) [25]) were used as a geographical outgroup.

Sequences were aligned by Muscle 3.8.425 [29] as implemented in Geneious Prime® 2020.1.2. The mtDNA diversity was firstly illustrated with Bayesian inference phylogenetic tree reconstruction, for which the GTR+I+G model was selected by JModelTest 2.1.10 [30]. Bayesian tree reconstruction was performed in MrBayes 3.2.6 [31]. The analysis started with random trees and performed with four independent Markov Chain Monte Carlo (MCMC) chains for 100,000 generations with sampling every 100th generation, standard deviations of split frequencies were below 0.01; potential scale reduction factors were equal to 1.0; stationarity was examined in Tracer v1.7 [32]. A consensus tree was constructed based on trees sampled after 25% burn-in. Sequences of *Ophiura kinbergi* (NCBI accession No MN183291) and *Ophiura robusta* (NCBI accession No MG935300) were used as outgroups for tree reconstruction.

Descriptive genetic statistics and haplotype analysis were performed with the pegas package for R [33]. Haplotype network was built using an infinite site model (uncorrected or Hamming distance) of DNA sequences and pairwise deletion of missing data as implemented in pegas [33] (R version 3.6.3). Genetic differences between the studied *O. sarsii* samples were evaluated using the analysis of molecular variance (AMOVA) in Arlequin v3.5.2.2 [34]. The neutrality tests, Tajima' D [35] and Fu' Fs [36], were conducted for each of the major haplotype groups present in the Barents Sea.

To test departures from constant population size, three approaches were used. Firstly, the Tajima's D and Fu's Fs neutrality tests were calculated in DNAsp v6 [37] for each of the major East Atlantic mtDNA lineages occurring in the Barents Sea. The demographic history was further assessed by constructing pairwise mismatch distributions in DNAsp. For the major mitochondrial lineages, the demographic parameter tau (τ) was calculated using DNAsp software to infer the time since regional population expansion. The time

since the start of population expansion was calculated as $t = \tau/2\mu$, where t is a number of years since population expansion, $\tau$ represents a unit of mutational time and $\mu$ is the per locus per year mutation rate [38]. Finally, the coalescent-based Bayesian skyline plots (BSP) were drawn using BEAUti v 2 and BEAST v 2.6.3 [39]. For BSP, priors included the implementation of the GTR substitution model defined by jModelTest, the strict clock model, and the constant skyline model. For both mismatch and BSP analyses, a mutation rate of $2.48 \times 10^{-8}$ per lineage per year (2.48% per million years) was used for the COI, following other studies in Ophiuroidea [40,41].

## 3. Results

The total aligned COI data set consisted of 548 nucleotide positions for 77 *Ophiura sarsii* sequences, including 53 newly obtained sequences from the Barents Sea and 24 earlier published sequences deposited in GenBank [24–26] (Table 1).

**Table 1.** Estimates of genetic diversity in *Ophiura sarsii* samples. N—sample size, Ht—total number of haplotypes, Hp—number of private haplotypes, H ± SD—haplotype diversity and its standard deviation, $\pi \pm$ SD—nucleotide diversity and its standard deviation.

| Location | Code | N | Ht | Hp | H ± SD | $\pi \pm$ SD |
|---|---|---|---|---|---|---|
| Svalbard | SVD | 34 | 14 | 8 | 0.840 ± 0.0030 | 0.0138 ± 0.00005 |
| Southern Barents Sea | BAR | 19 | 10 | 5 | 0.906 ± 0.0017 | 0.0148 ± 0.00006 |
| Iceland | ICE | 7 | 5 | 3 | 0.905 ± 0.0070 | 0.0138 ± 0.00007 |
| North Sea & Danish Straits | NS | 7 | 6 | 4 | 0.893 ± 0.0104 | 0.0097 ± 0.00004 |
| Canada | LAW, BAF, HUD | 8 | 8 | 8 | 1.000 ± 0.0020 | 0.0383 ± 0.00047 |

Across the Atlantic, the nucleotide diversity ranged from 0.0097 (North Sea) to 0.0383 (Canada) (Table 1). Among 35 identified COI *O. sarsii* haplotypes, 15 were new records in the Atlantic. *O. sarsii* mtDNA diversity in the Barents Sea consisted of 18 COI haplotypes, including 5 haplotypes shared between northern (SVD) and southern (BAR) parts of the sea. In total, 14 COI haplotypes were registered in SVD, of which 8 were private. Similarly, 5 of 10 haplotypes observed in BAR were private. Haplotype diversity (HD) was high (>0.84) among all studied regions and samples (Table 1).

Bayesian tree reconstruction revealed three major mtDNA clades in *O. sarsii* (Figure 2). Atlantic diversity of *O. sarsii* was represented by two highly supported clades that were distinguished by a 2.5% estimated sequence distance in COI (maximum composite likelihood model). Both major clades were present in the Barents Sea. Clade 1 also included four sequences from West Atlantic (Baffin Bay and St. Lawrence Bay), while Clade 2 was exclusively formed by sequences from Atlantic *O. sarsii* samples. Clade 3 consisted of *O. sarsii* from Hudson Bay and Pacific sequences from British Columbia (Figure 2) and were sister to a major group of *O. sarsii* sequences.

Haplotype diversity of *O. sarsii in the North Atlantic* mainly comprised three dominant haplotypes (A–C) and several unique satellite haplotypes (Figure 2). Clade 1 was mostly represented by a single star-shaped group of haplotypes from the Barents Sea (SVD, BAR), Iceland (ICE) and the North Sea with the central haplotype A, and was two mutation steps apart from the haplotypes from the Canadian Arctic (BAF, LAW). Clade 2 included haplotypes from the North Sea (NS), the Barents Sea (SVD, BAR), and Iceland (ICE) and was more complex with two dominant haplotypes B and C with adjacent unique satellite haplotypes, one or two mutations away from the dominant ones.Diversity of *O. sarsii* in the Hudson Bay was represented by four haplotypes that differed by four mutation steps from the Pacific haplotype. This group, equal to the Clade 3 on the phylogenetic tree, was separated from the North Atlantic haplotypes by 32 mutation steps.

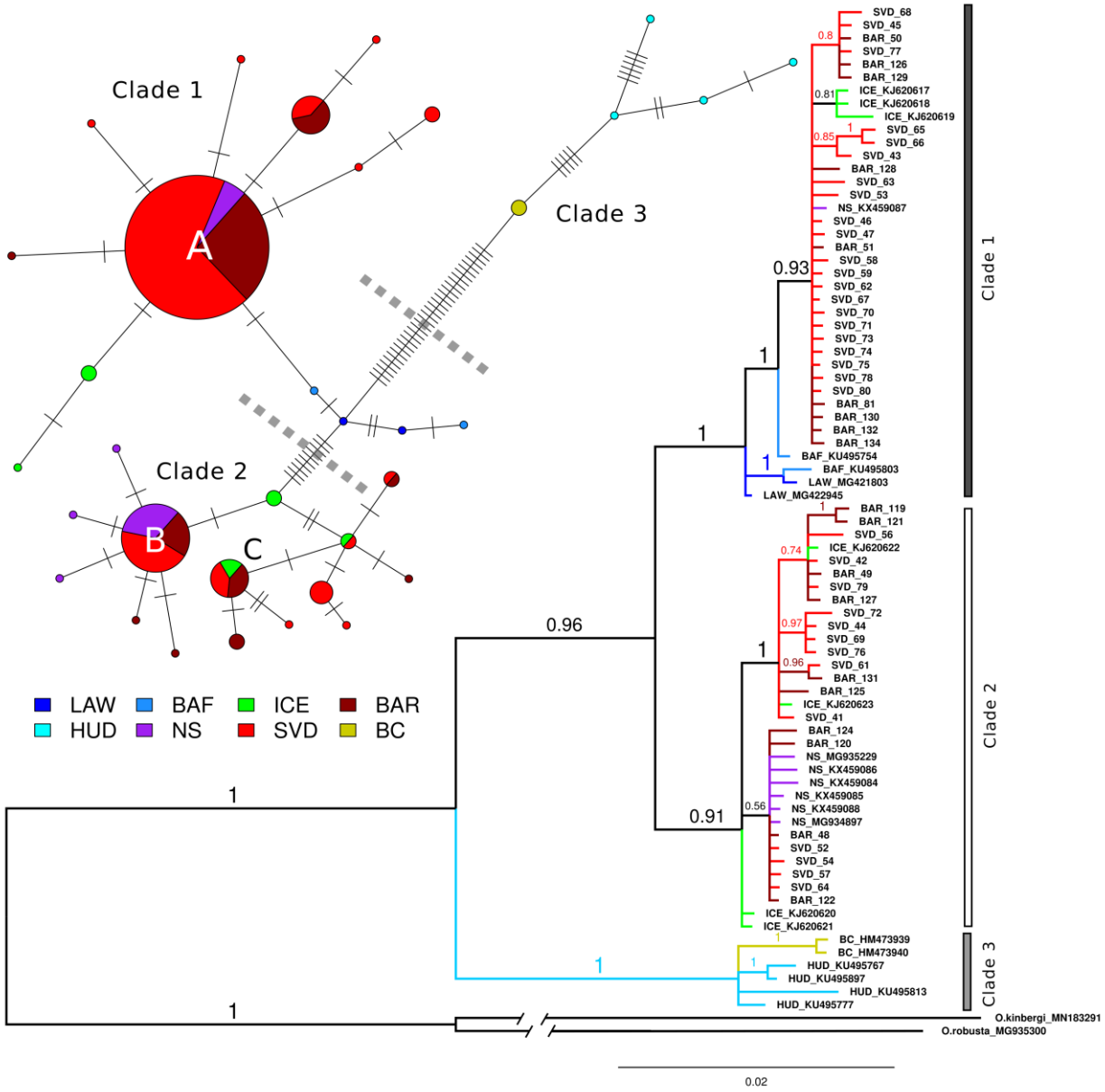


**Figure 2.** Mitochondrial diversity in *Ophiura sarsii*. Bayesian consensus tree and haplotype Hamming distance network.

To test the presence of population structure and to identify homogenous groups for the subsequent demographic analyses, a series of analyses of molecular variance (AMOVA) was implemented. We found geographical differentiation among *O. sarsii* samples either on level of complete dataset or among Atlantic samples. The group of east Atlantic samples demonstrated nearly significant differentiation, and no geographical structuring was found among the Barents Sea samples (Table 2).

As no clear population structure was confirmed among East Atlantic samples, demographic analyses were implemented for each of the two major *O. sarsii* haplotype clades. Samples from the West Atlantic, the Pacific, and Hudson Bay were excluded from the subsequent analyses. Thus, Clade 1 was represented by a star-shaped pattern formed by dominant Barents Sea haplotype, and satellite haplotypes from the Barents Sea and Iceland; Clade 2 was represented by two subdominant haplotypes shared between the Barents Sea, the North Sea, and Iceland (see Figure 2 for details).

**Table 2.** Estimates of the interpopulation component of nucleotide diversity $\Phi_{ST}$ in geographically defined population groups of *Ophiura sarsii*. Samples: HUD—Hudson Bay, LAW—St. Lawrence Bay, BAF—Baffin Bay, ICE—Iceland, NS—the North Sea, SVD—Svalbard, BAR—Southern part of the Barents Sea, BC—British Columbia. k—Sample number in analysis, N—Sequence number.

| Data Set | Samples | k | N | $\Phi_{ST}$ | *p* |
|---|---|---|---|---|---|
| Complete | BAR, SVD, ICE, NS, LAW, BAF, HUD, BC | 8 | 77 | 0.47 | <0.0001 |
| Atlantic | BAR, SVD, ICE, NS, LAW, BAF, HUD | 7 | 75 | 0.40622 | <0.0001 |
| Atlantic without Hudson Bay | BAR, SVD, ICE, NS, LAW, BAF | 6 | 71 | 0.10194 | 0.02151 |
| East Atlantic | BAR, SVD, ICE, NS | 4 | 67 | 0.07775 | 0.05181 |
| Barents Sea | BAR, SVD | 2 | 53 | 0.00215 | 0.30596 |

The neutrality Tajima' D index was not significantly different from zero for both Clade 1 (D = −1.596, $p = 0.56$) and Clade 2 (D = −0.950, $p = 0.59$). Fu's Fs was significantly negative for both Clade 1 (Fs = −6.26, $p = 0.002$) and Clade 2 (Fs = −6.58, $p = 0.001$), indicating population expansion. The mismatch distribution was unimodal for the Clade 1 and bimodal for the Clade 2 showing peaks at 1 and 4 differences (Figure 3).

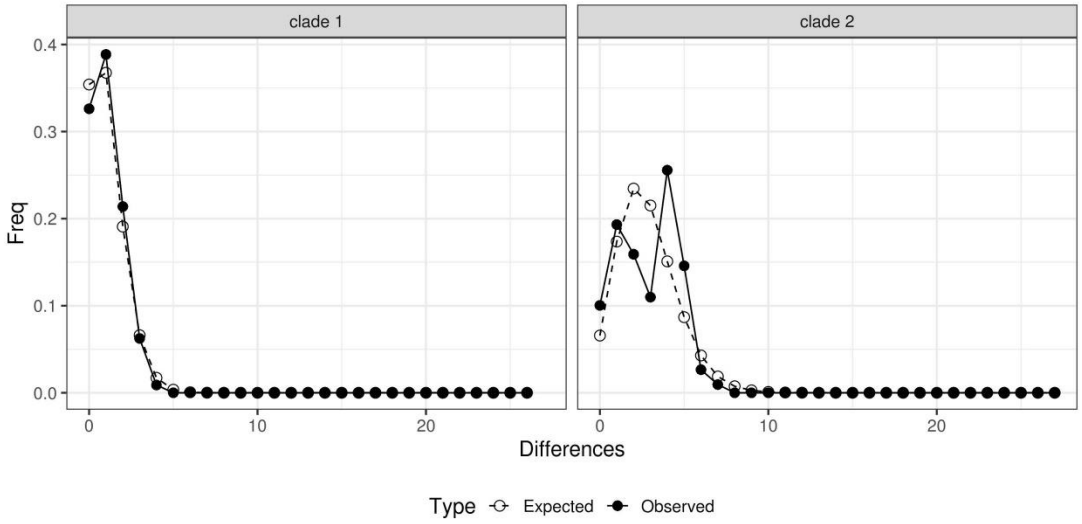


**Figure 3.** MtDNA mismatch distributions for two main haplotype clades of *Ophiura sarsii* in East Atlantic.

Star-shape of the Clade 1 with the unimodal mismatch distribution and the significantly negative values of Fu's Fs test indicated a recent expansion of this clade. Conversion of demographic parameter τ into years was performed using the 2.48% per MY divergence rate [40] and sequence length of 548 bp ($\mu = 2.8 \times 10^{-8} \times 548 = 0.0000136$). Considering $\tau = 1.039$, the expansion time for Clade 1 was calculated as 38,225 years before present (BP). Similarly, for the Clade 2 demographic parameter τ was estimated as 2.350, and time since last population expansion was calculated as 86,458 years BP. The Clade 2 itself is complex and consists of several abundant haplotypes forming star-like patterns with one dominant haplotype and several satellites differing by one or two nucleotide substitutions. We thus additionally calculated time since past population expansion for the biggest star-like pattern within the Clade 2. Mismatch analysis (not shown) yielded a demographic parameter τ equal to 0.858, and time since last population expansion was calculated as 31,566 years BP. Bayesian skyline plots further confirmed demographic expansion for both clades of *O. sarsii*, yielding younger median estimates of time since last population expansion as ca. 18,000 years BP for the Clade 1 and ca. 58,000 years for the Clade 2 (Figure 4).

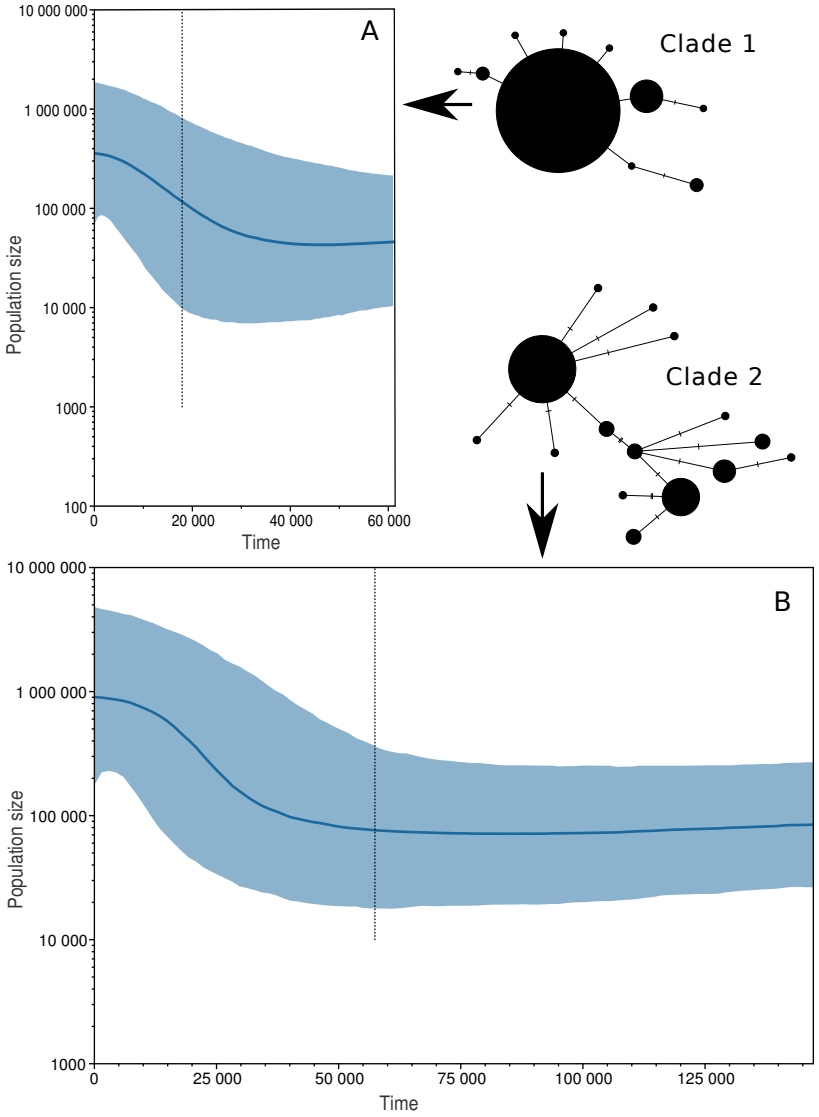


**Figure 4.** Bayesian skyline plots demographic analysis for two major Atlantic clades of *Ophiura sarsii*. (**A**) Clade 1; (**B**) Clade 2.

## 4. Discussion

Our study revealed two major mitochondrial lineages in Atlantic *O. sarsii*, while no clear population structure was found across East Atlantic. *Ophiura sarsii* sequences from Hudson Bay appeared to be closer to the Pacific than the Atlantic samples. Our findings corroborate the results of the recent study focused mostly on Pacific populations of *O. sarsii* and indicated multiple mtDNA lineages across the species range. A thorough analysis of Pacific *O. sarsii* demonstrated that the Yellow Sea lineage can be regarded as the separate subspecies, *O. sarsii vadicola,* that previously was described based on morphological features [23]. An Atlantic–Pacific lineage divergence is typical for most amphi-boreal and Sub-Aarctic marine species [2]. Bayesian tree reconstruction and haplotype network also indicated that West Atlantic *O. sarsii* sequences formed a compact cluster being sister to the East Atlantic sequences within the Clade 1, yet only four sequences were available from the region. Several intertidal and subtidal amphi-Atlantic species demonstrated pronounced divergence between West and East Atlantic haplotypes [1,12], but cases of shared haplotypes and lineages between two parts of the Atlantic are also common, e.g., the sea star *Asterias rubens* [1], the quahog *Arctica islandica* [10], and the horse mussel *Modiolus modiolus* [11].

*Ophiura sarsii* demonstrated high genetic diversity in the Barents Sea. Both major Atlantic mtDNA lineages were present in the Barents Sea and evenly distributed between the northern waters around Svalbard archipelago and the southern part near Murmansk coast of Kola Peninsula. Both regions, and other parts of the *O. sarsii* range, were characterized by high haplotype diversity with a significant number of private haplotypes, being mostly satellites to the two dominant haplotypes, each belonging to a different mtDNA clade. High mtDNA diversity has recently been recorded in Svalbard populations of intertidal North Atlantic amphipods *Gammarus* [42] and in the Barents and White Sea populations of amphi-boreal pacific herring *Clupea pallasii* [43]. On the contrary, typical boreal Atlantic intertidal species demonstrate a gradual northward decline of abundance and genetic diversity with the Barents Sea populations being largely dependent on long-distance larval dispersal from source populations of the Norwegian Sea [8].

From the demographic analyses, we estimated the time of population expansion in Clade 1 as ca. 38 kyr BP according to mismatch analysis and ca. 18 kyr BP according to the BSP analysis. Mismatch analysis also indicated similar expansion estimates (ca. 31 kyr BP) for the major star-shaped group of haplotypes in Clade 2, thus showing similar patterns of demographic expansion in both lineages present in the Barents Sea. While the estimates of different approaches vary, they both point to the Middle and Late periods of Weichselian. These estimates are based on a mutation rate conventionally used in the studies of brittle stars (2.48% per MY [40,41]), and representing average divergence between sister species pairs of family Ophiocomidae occurring on two coasts of Isthmus of Panama [40]. While the method of calibrating mutation rates by estimating the divergence rate between pairs of closely-related species on both shores of Isthmus of Panama, which emerged ca. 3.5 millions of year ago, is widely used for many taxa [44–46], in this case, it is related to species from different families within Ophiuroidea. A recent review of demographic studies of marine species [47] indicates that choosing a mutation rate to place a historical reconstruction of a population remains the main source of errors in mismatch and BSP analyses.

During the last glacial maximum, the Barents Sea was partly or nearly completely covered by ice [48]. The analysis of benthic sediments and cores indicated that signatures of glaciation can be observed down to a depth of about 200 m, and only central parts of the Barents Sea with depths more than 300 m were ice-free and connected with the Norwegian Sea [49]. The ice-sheet retreat most likely started during the Bølling–Allerød interstadial, i.e., ca. 15 kyr BP at the western margin of the Barents Sea [50], and this period thus most plausibly can indicate the beginning of eastward spread of subtidal marine species.

Until recently, the study of mtDNA diversity of *O. sarsii*, a widely distributed brittle star species in the North Atlantic, was limited to general barcoding projects being aimed on regional revisions of echinoderm faunas of Canada [25], Iceland [26], and the North Sea [24]. Our study represents an important contribution in the context of phylogeography of brittle stars in the region in line with recent studies of Atlantic-Mediterranean species [51–53]. As a result, we present the data on the northernmost European populations of *O. sarsii* from the Barents Sea, and since sampling from other parts of the Atlantic remains predominantly qualitative and not quantitative, further studies are needed to implement broader phylogeographic analysis on this brittle star species.

**Supplementary Materials:** The following are available online at https://www.mdpi.com/1424-2818/13/2/40/s1, Table S1: *Ophiura sarsii* sampling information.

**Author Contributions:** Sampling, N.Z. and N.S.; species identification and laboratory analysis, E.S.; molecular analysis, E.G.-Y., Y.L., S.N.; writing and editing, E.G.-Y. and S.N.; project administration, Q.X. and S.N. All authors have read and agreed to the published version of the manuscript.

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## References

1. Wares, J.P.; Cunningham, C.W. Phylogeography and historical ecology of the North Atlantic Intertidal. *Evolution* **2001**, *55*, 2455–2469. [CrossRef] [PubMed]
2. Laakkonen, H.; Hardman, M.; Strelkov, P.; Väinölä, R. Cycles of trans-Arctic dispersal and vicariance, and diversification of the amphi-boreal marine fauna. *J. Evol. Biol.* **2021**, *34*, 73–96. [CrossRef] [PubMed]
3. Colson, I.; Hughes, R.N. Contrasted patterns of genetic variation in the dogwhelk Nucella lapillus along two putative post-glacial expansion routes. *Mar. Ecol. Prog. Ser.* **2007**, *343*, 183–191. [CrossRef]
4. Rock, J.; Ironside, J.; Potter, T.; Whiteley, N.M.; Lunt, D.H. Phylogeography and environmental diversification of a highly adaptable marine amphipod, Gammarus duebeni. *Heredity* **2007**, *99*, 102–111. [CrossRef]
5. Luttikhuizen, P.C.; Campos, J.; van Bleijswijk, J.; Peijnenburg, K.T.; van der Veer, H.W. Phylogeography of the common shrimp, *Crangon crangon* (L.) across its distribution range. *Mol. Phylogenet. Evol.* **2008**, *46*, 1015–1030. [CrossRef]
6. Maggs, C.A.; Castilho, R.; Foltz, D.; Henzler, C.; Jolly, M.T.; Kelly, J.; Olsen, J.; Perez, K.E.; Stam, W.; Väinölä, R.; et al. Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. *Ecology* **2008**, *89*, S108–S122. [CrossRef]
7. Krebes, L.; Blank, M.; Bastrop, R. Phylogeography, historical demography and postglacial colonization routes of two amphi-Atlantic distributed amphipods. *Syst. Biodivers.* **2011**, *9*, 259–273. [CrossRef]
8. Genelt-Yanovskiy, E.; Nazarova, S.; Tarasov, O.; Mikhailova, N.; Strelkov, P. Phylogeography of the temperate marine bivalve Cerastoderma edule (Linnaeus, 1758)(Bivalvia: Cardiidae) in the Subarctic: Unique diversity and strong population structuring at different spatial scales. *J. Zool. Syst. Evol. Res.* **2019**, *57*, 67–79. [CrossRef]
9. Addison, J.A.; Hart, M.W. Colonization, dispersal, and hybridization influence phylogeography o North Atlantic Sea urchins (Strongylochntrotus droebachiensis). *Evolution* **2005**, *59*, 532–543. [CrossRef]
10. Dahlgren, T.G.; Weinberg, J.R.; Halanych, K.M. Phylogeography of the ocean quahog (Arctica islandica): Influences of paleoclimate on genetic diversity and species range. *Mar. Biol.* **2000**, *137*, 487–495. [CrossRef]
11. Halanych, K.M.; Vodoti, E.T.; Sundberg, P.; Dahlgren, T.G. Phylogeography of the horse mussel Modiolus modiolus. *Mar. Biol. Assoc. UK J. Mar. Biol. Assoc. UK* **2013**, *93*, 1857. [CrossRef]
12. Magnúsdóttir, H.; Pálsson, S.; Westfall, K.M.; Jónsson, Z.O.; Goodall, J.; Örnólfsdóttir, E.B. Revised phylogeography of the common whelk Buccinum undatum (Gastropoda: Buccinidae) across the North Atlantic. *Biol. J. Linn. Soc.* **2019**, *127*, 890–899. [CrossRef]
13. Cochrane, S.K.J.; Denisenko, S.G.; Renaud, P.E.; Emblow, C.S.; Ambrose, W.G.; Ellingsen, I.H.; Skarðhamar, J. Benthic macrofauna and productivity regimes in the Barents Sea—Ecological implications in a changing Arctic. *J. Sea Res.* **2009**, *61*, 222–233. [CrossRef]
14. Lind, S.; Ingvaldsen, R.B.; Furevik, T. Arctic warming hotspot in the Northern Barents Sea linked to declining sea-ice import. *Nat. Clim. Change* **2018**, *8*, 634–639. [CrossRef]
15. Piepenburg, D.; Schmid, M.K. Brittle star fauna (Echinodermata: Ophiuroidea) of the Arctic Northwestern Barents Sea: Composition, abundance, biomass and spatial distribution. *Polar Biol.* **1996**, *16*, 383–392. [CrossRef]
16. Blanchard, A.L.; Parris, C.L.; Knowlton, A.L.; Wade, N.R. Benthic ecology of the Northeastern Chukchi Sea. Part II. Spatial variation of megafaunal community structure, 2009–2010. *Cont. Shelf Res.* **2013**, *67*, 67–76. [CrossRef]
17. Ravelo, A.M.; Konar, B.; Bluhm, B.; Iken, K. Growth and production of the brittle stars *Ophiura sarsii* and *Ophiocten sericeum* (Echinodermata: Ophiuroidea). *Cont. Shelf Res.* **2017**, *139*, 9–20. [CrossRef]
18. Djakonov, A.M. Ophiuroidea of the Seas of the USSR. In *Opredeliteli po Faune SSSR [Keys to the Fauna of the USSR]*; Zoological Institute of the Academy of Sciences of the USSR: Leningrad, USSR, 1954; Volume 55, pp. 109–111. (In Russian)
19. Anisimova, N.A. Echinodermata of the Barents Sea. In *Contemporary Bentic Fauna of the Barents and Kara Seas*; KSC RAS: Apatity, Russia, 2000; pp. 228–347. (In Russian)
20. Packer, D.B.; Watling, L.; Langton, R.W. The population structure of the brittle star Ophiura sarsi lütken in the Gulf of Maine and its trophic relationship to American plaice (Hippoglossoides platessoides fabricius). *J. Exp. Mar. Biol. Ecol.* **1994**, *179*, 207–222. [CrossRef]
21. Kuznecov, V.V. Time Period and Temperature Conditions for the Reproduction of Marine Invertebrates. *Mater. Compr. Study White Sea* **1963**, *2*, 32–52. (In Russian)
22. Dautov, S.S.; Selina, M.S. Foraging conditions of planktotrophic larvae of echinoderms in the southwestern part of Peter the Great Bay of the Sea of Japan. *Russ. J. Mar. Biol.* **2009**, *35*, 25–33. [CrossRef]

23. Li, Y.; Dong, Y.; Xu, Q.; Fan, S.; Lin, H.; Wang, M.; Zhang, X. Genetic differentiation and evolutionary history of the circumpolar species *Ophiura sarsii* and subspecies *Ophiura sarsii vadicola* (Ophiurida: Ophiuridae). *Cont. Shelf Res.* **2020**, *197*, 104085. [CrossRef]
24. Laakmann, S.; Boos, K.; Knebelsberger, T.; Raupach, M.J.; Neumann, H. Species identification of echinoderms from the North Sea by combining morphology and molecular data. *Helgol. Mar. Res.* **2016**, *70*, 1–18. [CrossRef]
25. Layton, K.K.; Corstorphine, E.A.; Hebert, P.D. Exploring Canadian echinoderm diversity through DNA barcodes. *PLoS ONE* **2016**, *11*, e0166118. [CrossRef] [PubMed]
26. Khodami, S.; Arbizu, P.M.; Stöhr, S.; Laakmann, S. Molecular species delimitation of Icelandic brittle stars (Ophiuroidea). *Pol. Polar Res.* **2014**, *35*, 243–260. [CrossRef]
27. Michalsen, K.; Dalpadado, P.; Eriksen, E.; Gjøsæter, H.; Ingvaldsen, R.B.; Johannesen, E.; Jørgensen, L.L.; Knutsen, T.; Prozorkevich, D.; Skern-Mauritzen, M. Marine living resources of the Barents Sea—Ecosystem understanding and monitoring in a climate change perspective. *Mar. Biol. Res.* **2013**, *9*, 932–947. [CrossRef]
28. Folmer, O.; Black, M.; Hoeh, W.; Lutz, R.; Vrijenhoek, R. DNA Primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol.* **1994**, *3*, 294–299.
29. Edgar, R.C. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* **2004**, *32*, 1792–1797. [CrossRef]
30. Darriba, D.; Taboada, G.L.; Doallo, R.; Posada, D. JModelTest 2: More models, new heuristics and parallel computing. *Nat. Methods* **2012**, *9*, 772. [CrossRef]
31. Ronquist, F.; Teslenko, M.; Van Der Mark, P.; Ayres, D.L.; Darling, A.; Höhna, S.; Larget, B.; Liu, L.; Suchard, M.A.; Huelsenbeck, J.P. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* **2012**, *61*, 539–542. [CrossRef]
32. Rambaut, A.; Drummond, A.J.; Xie, D.; Baele, G.; Suchard, M.A. Posterior summarization in Bayesian phylogenetics using tracer 1.7. *Syst. Biol.* **2018**, *67*, 901. [CrossRef]
33. Paradis, E. Pegas: An R package for population genetics with an integrated-modular approach. *Bioinformatics* **2010**, *26*, 419–420. [CrossRef] [PubMed]
34. Excoffier, L.; Lischer, H.E. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Resour.* **2010**, *10*, 564–567. [CrossRef] [PubMed]
35. Tajima, F. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* **1989**, *123*, 585–595. [CrossRef] [PubMed]
36. Fu, Y. New statistical tests of neutrality for DNA samples from a population. *Genetics* **1996**, *143*, 557–570. [CrossRef]
37. Rozas, J.; Ferrer-Mata, A.; Sánchez-DelBarrio, J.C.; Guirao-Rico, S.; Librado, P.; Ramos-Onsins, S.E.; Sánchez-Gracia, A. DnaSP 6: DNA sequence polymorphism analysis of large data sets. *Mol. Biol. Evol.* **2017**, *34*, 3299–3302. [CrossRef]
38. Rogers, A.R.; Harpending, H. Population growth makes waves in the distribution of pairwise genetic differences. *Mol. Biol. Evol.* **1992**, *9*, 552–569.
39. Bouckaert, R.; Heled, J.; Kühnert, D.; Vaughan, T.; Wu, C.-H.; Xie, D.; Suchard, M.A.; Rambaut, A.; Drummond, A.J. BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Comput. Biol.* **2014**, *10*, e1003537. [CrossRef]
40. Naughton, K.M.; O'Hara, T.D.; Appleton, B.; Cisternas, P.A. Antitropical distributions and species delimitation in a group of Ophiocomid brittle stars (Echinodermata: Ophiuroidea: Ophiocomidae). *Mol. Phylogenet. Evol.* **2014**, *78*, 232–244. [CrossRef]
41. Sands, C.J.; O'Hara, T.; Barnes, D.K.; Martín-Ledo, R. Against the flow: Evidence of multiple recent invasions of warmer continental shelf waters by a Southern Ocean brittle star. *Front. Ecol. Evol.* **2015**, *3*, 63. [CrossRef]
42. Grabowski, M.; Jabłońska, A.; Weydmann-Zwolicka, A.; Gantsevich, M.; Strelkov, P.; Skazina, M.; Węslawski, J.M. Contrasting molecular diversity and demography patterns in two intertidal amphipod crustaceans reflect Atlantification of High Arctic. *Mar. Biol.* **2019**, *166*, 155. [CrossRef]
43. Laakkonen, H.M.; Lajus, D.L.; Strelkov, P.; Väinölä, R. Phylogeography of amphi-Boreal fish: Tracing the history of the Pacific herring Clupea pallasii in North-East European Seas. *BMC Evol. Biol.* **2013**, *13*, 67. [CrossRef] [PubMed]
44. Kolman, C.J.; Bermingham, E. Mitochondrial and nuclear DNA diversity in the Choco and Chibcha Amerinds of Panama. *Genetics* **1997**, *147*, 1289–1302. [CrossRef] [PubMed]
45. Lessios, H.A. The Great American Schism: Divergence of marine organisms after the rise of the Central American Isthmus. *Annu. Rev. Ecol. Evol. Syst.* **2008**, *39*, 63–91. [CrossRef]
46. Donaldson, K.A.; Wilson, R.R.J. Amphi-Panamic geminates of snook (Percoidei: Centropomidae) provide a calibration of the divergence rate in the mitochondrial DNA control region of fishes. *Mol. Phylogenet. Evol.* **1999**, *13*, 208–213. [CrossRef]
47. Grant, W.S. Problems and cautions with sequence mismatch analysis and Bayesian skyline plots to infer historical demography. *J. Hered.* **2015**, *106*, 333–346. [CrossRef]
48. Ingólfsson, Ó.; Landvik, J.Y. The Svalbard-Barents Sea ice-sheet—Historical, current and future perspectives. *Quat. Sci. Rev.* **2013**, *64*, 33–60. [CrossRef]
49. Biryukov, V.Y.; Faustova, M.A.; Kaplin, P.A.; Pavlidis, Y.A.; Romanova, E.A.; Velichko, A.A. The paleogeography of Arctic Shelf and Coastal Zone of Eurasia at the time of the Last Glaciation (18,000 Yr BP). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **1988**, *68*, 117–125. [CrossRef]
50. Polyak, B.; Lehman, S.J.; Gataullin, V.; Timothy Jull, A.J. Two-step deglaciation of the Southeastern Barents Sea. *Geology* **1995**, *23*, 567–571. [CrossRef]

51. Pérez-Portela, R.; Almada, V.; Turon, X. Cryptic speciation and genetic structure of widely distributed brittle stars (Ophiuroidea) in Europe. *Zool. Scr.* **2013**, *42*, 151–169. [CrossRef]
52. Weber, A.A.-T.; Stöhr, S.; Chenuil, A. Genetic data, reproduction season and reproductive strategy data support the existence of biological species in *Ophioderma longicauda*. *C. R. Biol.* **2014**, *337*, 553–560. [CrossRef]
53. Taboada, S.; Pérez-Portela, R. Contrasted phylogeographic patterns on mitochondrial DNA of shallow and deep brittle stars across the Atlantic-Mediterranean Area. *Sci. Rep.* **2016**, *6*, 1–13. [CrossRef]