Phylogeography and molecular diversity of two highly abundant *Themisto* amphipod species in the Arctic Ocean based on the mitochondrial COI gene

Ayla Rosina Cherrington Sealey Murray

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First Examiner: Prof. Dr. Marko Rohlfs

Second Examiner: Dr. Charlotte Havermans

I Table of Contents

II List of Figures

III List of Tables

IV List of Abbreviations

WSC	West Spitsbergen Current
EGC	East Greenland Current
SCC	South Cape Current
DNA	Deoxyribose Nucleic Acid
mtCOI	Mitochondrial Cytochrome *c* Oxidase Subunit 1 gene
bp	Base Pairs
PCR	Polymerase Chain Reaction
dNTP	Deoxyribose nucleotide triphosphate
K2P	Kimura 2-parameter
NJ	Neighbour Joining
TCS	Templeton, Crandall and Sing
AMOVA	Analysis of Molecular Variance
LGM	Last Glacial Maximum

V Abstract

Rapid warming in the Arctic is drastically impacting marine ecosystems, affecting species diversity, distribution, and food web structure. Pelagic *Themisto* amphipods are a dominant component of the Arctic zooplankton community and represent a key link between secondary producers and marine vertebrates at higher trophic levels. Two co-existing species dominate in the region: *Themisto libellula*, considered a true Arctic species and *Themisto abyssorum,* a sub-Arctic, boreal species. Both have exhibited recent changes in abundance and range shifts, likely due to the Atlantification of the Arctic. Many aspects of the ecology and genetic structure of these two species are not well studied, despite their high biomass, importance in the food web and the fact that they are already being affected by rapid climate change in the Arctic. We tested both species for levels of genetic diversity, patterns of spatial genetic structure and demographic history using samples from the Greenland shelf, Fram Strait, and Svalbard. This was achieved using variation at the mitochondrial cytochrome *c* oxidase subunit 1 gene (mtCOI). These data revealed strikingly different levels of mtCOI diversity: low levels in *T. libellula* contrasted with high diversity in *T. abyssorum.* No spatial genetic structure was found, and high levels of connectivity and evidence of historic demographic expansion were exhibited by both species. These patterns of diversity and demographic signatures are likely explained by glaciation events impacting population sizes during the LGM. High population connectivity is likely due to mixing among *Themisto* populations, caused by the multi-directional currents in the region. The observed low genetic diversity, in combination with its cold adaptions, could cause *T. libellula* to be more susceptible in the Atlantification of the Arctic. In contrast, high diversity likely increases adaptive potential in *T. abyssorum* which, combined with its Atlantic affinity, could lead to it benefitting from current warming trends. This study provides new data on the phylogeography of two ecologically important species, which can contribute to predicting how zooplankton communities, species interactions and food web structure will manifest in the Arctic as a result of climate change.

1. Introduction

The Arctic is currently warming two times faster than the global mean, and many consequences of climate change have now manifested throughout the region (Pörtner et al., 2019). Ocean and air temperatures are increasing rapidly, sea ice coverage and thickness is declining, and permafrost and glaciers are melting region-wide (Stroeve et al., 2012; Wang et al., 2020). Ice-free summers are predicted to occur by the middle of the century (Notz & Stroeve, 2018; Stroeve et al., 2012; Wang & Overland, 2009). These environmental changes are already having drastic impacts on the marine ecosystem, affecting species composition, distribution and food web structure in the Arctic Ocean (Gluchowska et al., 2017; Weydmann et al., 2014).

The inflow of increasingly warmer Atlantic water into the high Arctic is a major driver of the phenomenon commonly referred to as the 'Atlantification' of the Arctic (Polyakov et al., 2017). The Fram Strait, between Greenland and the Svalbard Archipelago, is known as "the gateway to the Arctic" and is the largest source of oceanic heat into the Arctic Basin (Beszczynska-Moeller et al., 2011). The heat exchange between water masses in the Fram Strait is influenced by two opposing currents: the north-bound West Spitsbergen Current (WSC) and the south-bound East Greenland Current (EGC) (Figure 1). The WSC carries warmer and more saline Atlantic water into the Arctic Basin, travelling northwards via the west coast of Spitsbergen, the largest island in Svalbard. The ECG travels along the Greenland Shelf, carrying cold, freshwater and sea ice southwards through the Fram Strait (Wang et al., 2019).

The WSC carries increasing amounts of nutrients and sub-Arctic and boreal planktonic species into the Arctic, the consequences of which are not yet widely studied. Zooplankton community composition and functional changes have been detected and linked to this Atlantification (Gluchowska et al., 2017). Poleward range expansions of sub-arctic and boreal zooplankton species, as well as poleward contractions of Arctic species have also been observed (Basedow et al., 2018; Dalpadado et al., 2016). Environmental changes will alter the distribution of suitable habitats and are expected to have an impact on gene flow and genetic structure in a wide range of zooplankton species in the Arctic and its marginal seas (Hardy et al., 2011; Tempestini et al., 2020).

Pelagic amphipods are among the most abundant planktonic crustaceans in polar regions and are a crucial component of the Arctic food web. Hyperiidea are the dominant group of pelagic amphipods and are thought to make up approximately 4% of zooplankton biomass in the world's oceans (Longhurst, 1985). Almost all hyperiids are epipelagic, although some exceptions are mesopelagic or deep water species (Vinogradov et al., 1996). They are an important link between secondary producers (mesoplanktonic grazers) and zooplanktivorous marine vertebrates at higher trophic levels. Their role as prey in the Arctic zooplankton community has been described as on par with that of krill and copepods (Bowman, 1960; Dalpadado, 2002). The predominant hyperiids in the Arctic Ocean are of the genus *Themisto*. Two co-existing species dominate: *Themisto libellula*, considered a genuine Arctic species and *Themisto abyssorum,* considered a sub-Arctic, boreal species. Both are preyed upon by fish, seabird and marine mammal species through the Arctic and its marginal seas (Havermans et al., 2019). They are visual predators of meso- and macrozooplankton and although their geographic distributions overlap, they are thought to occupy different ecological niches (Auel et al., 2002).

T. libellula is a cold adapted species and its distributional range includes the Central Arctic Basin as well as the marginal seas (Havermans et al., 2019). It can grow up to 60mm in size and has a life cycle of up to 4 years (Auel & Werner, 2003; Kraft, 2010). An important component of its diet are ice-dependant, herbivorous copepods, indicating an indirect reliance of *T. libellula* on the cryo-pelagic pathway (Auel & Werner, 2003; Kohlbach et al., 2016). It is a key prey item for seabirds, including the Little Auk (*Alle alle*), Arctic fish species such as Polar Cod (*Boreogadus saida*) and commercially important fish species such as Atlantic Cod (*Gadus morhua*) and Salmon (Havermans et al., 2019).

T. abyssorum is largely found in waters of Atlantic origin in the marginal Arctic seas. It has also regularly been observed in Arctic waters, but in lower abundances than in warmer and deeper Atlantic waters (Dalpadado, 2002; Havermans et al., 2019). It is smaller than T. *libellula*, and while lipid content by weight is comparable, its smaller body size makes it an overall less nutritious prey (Auel et al., 2002). Previous studies indicate that the diet of *T. abyssorum* is less ice-dependent than of T. *libellula*, with a wider prey-spectrum and a higher trophic position in the Arctic food web (Auel et al., 2002; Kohlbach et al., 2016). Both species have exhibited recent changes in abundance and distribution, likely as a result of the Atlantification of the Arctic (CAFF, 2017; Havermans et al., 2019). These changes in abundance and distribution could have strong implications at higher trophic levels, with the loss of the highly nutritious *T. libellula* as a key prey item for many species (Havermans et al., 2019).

Many aspects of the current genetic diversity, population structure and phylogeography of *T. libellula* and *T. abyssorum* are not well studied, despite their importance in the Arctic food web and biogeochemical cycles (Havermans et al., 2019). Investigating patterns of genetic diversity over a spatial distribution can give insight into how historic evolutionary events have impacted genetic variation in a species, as well as ongoing processes such as gene flow (Nei, 1987; Slatkin, 1987). This can lead to better understanding of how present-day and future climate events may impact a species as well as the likelihood of adaption to these changes. This study is the first to our knowledge to focus in depth on the population genetics of *T. abyssorum*, and the first to compare the two sister species using molecular barcoding.

One of the most common genetic markers used for the analysis of inter- and intraspecific diversity for many crustaceans is the mitochondrial cytochrome *c* oxidase sub-unit 1 gene (mtCOI) (Hebert et al., 2003). It has low or no recombination, uniparental inheritance and a faster evolutionary rate compared to nucleic DNA (Moritz et al., 1987). The diversity on the mtCOI gene is less at the intra-specific level than at the inter-specific level, making it suitable tool for estimating diversity in congeneric species (Meyer & Paulay, 2005). Population bottlenecks and expansions leave signatures in the mtCOI region, making it a popular tool for inferring elements of a species demographic history (Hewitt, 2000).

This study aims to (i) assess and compare the levels of genetic diversity, (ii) determine present spatial patterns of genetic structure and connectivity as well as (iii) provide an overview of the demographic history of the two *Themisto* species, across a broad geographic gradient. This is achieved by analysing and comparing mtCOI gene variation according to the geographic location of populations from the Greenland shelf, the Fram Strait, and the Svalbard Archipelago. Considering the close phylogenetic relationship, similar life history patterns and dispersal capacities of the two species, we would expect comparative levels of genetic diversity at the mtCOI region. Both species have a holoplanktonic lifestyle, therefore, considering the multi-directional currents and the lack of major geographic barriers in the study region, we predict relatively high levels connectivity, with the potential for some genetic structure between the marginal populations.

2. Materials and methods

2.1 Study area

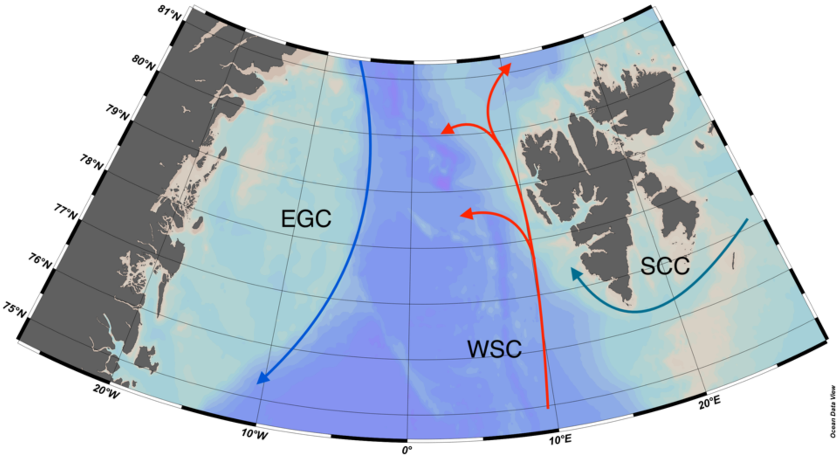

Figure 1. Map of the sampling area including the Greenland Shelf, Fram Strait and the Svalbard Archipelago and main ocean currents: Cold currents in blue and warm currents in red. *EGC* = East Greenland Current, *WSC* = West Spitsbergen Current, *SCC* = South Cape Current.

Samples were collected across the Greenland Shelf, the Fram Strait, and the Svalbard Archipelago. The Greenland Shelf and western Fram Strait stations are shelf stations largely influenced by the ECG, whereas the central Fram Strait stations are deep and influenced by the WSC. The West Spitsbergen stations are under the influence of the WSC and the South Spitsbergen stations the South Cape Current (SCC). North Spitsbergen and Nordauslandet stations are colder with less influence from the WSC (Figure 1).

2.2 Sample collection

Zooplankton samples containing *Themisto* amphipods were collected from the Greenland Shelf, the Fram Strait, and the Svalbard Archipelago during oceanographic research cruises between 2016 and 2020 (Table 1 and Figure 2). Specimens from the Fram Strait and East Greenland were collected on the *R/V Polarstern* cruises PS100 in 2016 (Kanzow, 2017) and PS107 in 2017 (Schewe, 2018), with a 150µm Multinet and 300µm and 500µm Bongo nets. Multinet hauls were carried out vertically in the water column (0.5 m/s), Bongo nets were towed obliquely at 2 knots ship's speed, with a wire length varying between 20m to 450m. Additional Fram Strait and East Greenland specimens were collected on the *R/V Helmer Hanss*en cruise TUNU-VII in September 2017 with a Campelen 1800 shrimp trawl (Walsh & McCallum, 1997). Specimens from the Svalbard Archipelago were collected in 2020 on the *R/V Heincke* cruise HE560 (Knust, 2020), using 300µm and 500µm Bongo Nets and a pelagic trawl net fitted with a young fish lift (YFT) (Holst & McDonald, 2000). Samples were preserved immediately after collection and sorting procedures in 96% undenatured ethanol. Six major geographic regions were defined based on ocean bathymetry and influences of major oceanic currents (Figure 1 and Figure 2).

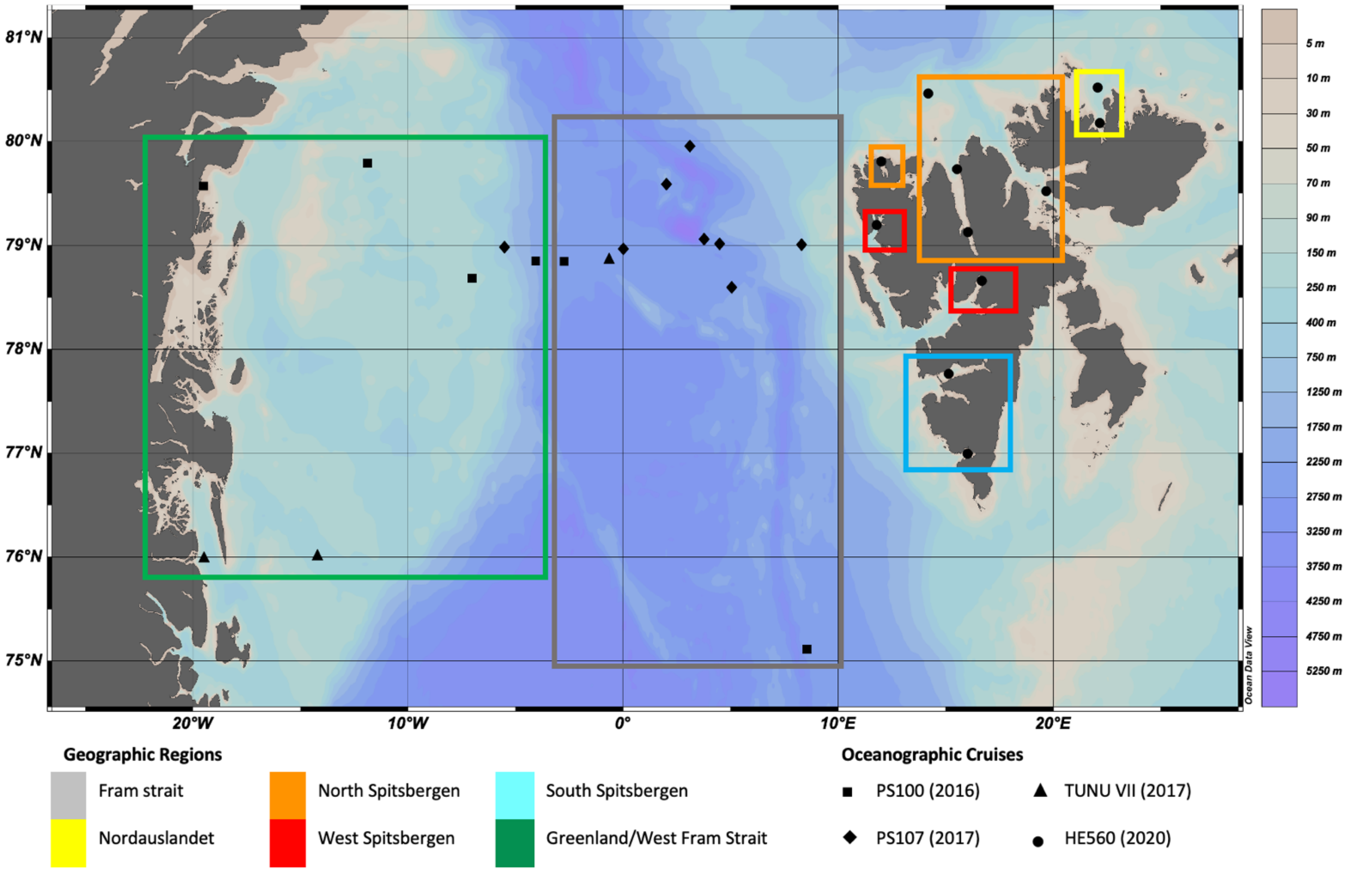

Figure 2. Sampling locations for *Themisto spp.* Colours indicate major geographic regions. Black shapes indicate stations on different oceanographic cruises between 2016 and 2020.

2.3 DNA extraction, PCR and sequence alignments

Between two and four pleopods were taken for DNA isolation from larger *Themisto* individuals, and the entire pleon including pleopods form the smaller individuals (<7mm). DNA extraction was performed using the QIAGEN DNeasy Blood & Tissue Kit, in accordance with the manufacturer's instructions. Each DNA extraction was treated with 20 µL of proteinase K and only 100 µL of AE buffer was used for sample elution to ensure a higher concentration of DNA. DNA content was measured with a Nanodrop ND-1000 (Thermo Fisher Scientific) and diluted to approximately 50ng of DNA for subsequent Polymerase Chain Reaction (PCR).

A 658 base pair (bp) fragment of the mtCOI barcoding region was amplified using the universal primers HCO 2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') and LCO 1490 (5'GGTCAACAAAT-

CTAAAGATATTGG-3’) (Folmer et al., 1994). The reaction mixture had a total volume of 25µL and consisted of: 1x PCR buffer, 0.2mM dNTP, 0.5µM of each primer, 0.2U/µL 5 PRIME HotMaster Taq DNA polymerase (QuantaBio), 1 µL (ca. 30ng) of DNA template and molecular-grade water. DNA template was substituted with molecular-grade water in negative controls. The PCR amplification was carried out using the following program: initial denaturation at 95°C for 2 minutes; followed by 36 cycles of denaturation at 94°C for 20 seconds, annealing at 42°C for 20 seconds, extension at 65°C plus a final extension at 65°C for 15 minutes. PCR products were checked for quality and length using electrophoresis on GelRed-stained, 2% agarose gel and were bidirectionally sequenced by Eurofins Genomics.

Chromatograms were manually checked for ambiguous base calls, stop codons and amino acid translations of the mtCOI sequences, using the software CondonCode Aligner 8.0.2 (Condon Code Corporation). The primers were removed, and all sequences were trimmed to a maximum 658bp length. A consensus of all forward and reverse amplicons was created, and all sequences were aligned with CLUSTAL-W (Thompson et al., 1994) in CodonCode Aligner.

2.4 Genetic diversity

The evolutionary history between individuals of each species was inferred using the Neighbour-joining method (Saitou & Nei, 1987), using Mega X software (Kumar et al., 2018). The Kimura 2-parameter (K2P) method with pair-wise deletion, was used to calculate evolutionary distances (Kimura, 1980) and 2000 bootstrap replicates (Felsenstein, 1985). A total of 416 sequences were used to construct the tree. Sequences consisting of less than 658bp were included in the Neighbour-joining tree but removed from all other analysis to avoid base-pair loss in longer sequences.

Intraspecific genetic diversity was estimated by calculating the standard diversity indices: number of haplotypes (H), number of segregating sites (S), haplotype diversity (h), nucleotide diversity (π), the number of parsimony informative sites, and average number of nucleotide differences (*K*). Haplotype diversity is the probability that two randomly sampled alleles are different and nucleotide diversity represents the average number of nucleotide differences per site in pairwise comparisons of the sequences (Nei, 1987). All diversity indices were calculated on DnaSP 6 software (Rozas et al., 2017). The relationships between identified haplotypes were explored through haplotype networks created in PopART 1.7 software (Leigh & Bryant, 2015), using the Templeton, Crandall and Sing (TCS) method (Clement et al., 2002). The TCS method is based on a maximum parsimony (MP) algorithm.

2.5 Population structure and connectivity

To test for hierarchical population genetic differentiation, an Analysis of Molecular Variance (AMOVA) was performed using the distribution of variation at the regional, sampling site and individual levels (Excoffier et al., 1992). Genetic connectivity between geographical regions was estimated by calculating pairwise F_{ST} (fixation index among populations), for which a significance level of 0.05 was determined using 10,100 permutations (Holsinger & Weir, 2009). These analyses were conducted using Arlequin 3.5.2.2.

2.6 Demographic history

The common statistical tests for neutrality; Tajima's D and Fu's F were used to infer demographic history of each species (Fu, 1997; Tajima, 1989). These tests distinguish between neutrality; sequences evolving under mutation-drift equilibrium and sequences evolving under non-neutral processes such as selection and population expansions. Tajima's D is based on the frequency of segregating nucleotide sites, whereas Fu's F is uses the distribution of haplotype frequencies and is considered to be the more sensitive test (Ramos-Onsins & Rozas, 2002). Negative values indicate an excess of rare polymorphisms when compared to the null hypothesis of population equilibrium. Due to a lack of significant population structure, all samples were pooled per species for these tests. All demographic analyses were conducted in Arlequin 3.5.2.2.

Table 1. Summary of samples sequenced: name and position of sampling stations, sampling gear and maximum depth of water column sampled, and number of sequences obtained with 658 bp on mtCOI. Numbers in parentheses () indicate sequences that were included in the Neighbour-joining tree but removed from subsequent analysis.

	Region	**Sampling Station**	**Cruise Code**	**Latitude [N]**	**Longitude [E]**	**Year**	**Sampling Gear**	**Maximum Sampling Depth**	***T. libellula***	***T. abyssorum***
1	Fram Strait	2	PS100	75.1125	8.541	2016	Bongo Net	345 m	0	22
2		87	PS100	79.7901667	-11.886	2016	Bongo Net	250m	2 (3)	0
3		102	PS100	78.8440556	-2.7351111	2016	Bongo Net	345 m	7	3
4		2	PS107	78.5928625	5.05375	2017	Bongo Net	345 m	24	18 (2)
5		21	PS107	78.961925	0.0240025	2017	Bongo Net	191m	24	0
6		38	PS107	79.01205	4.492125	2017	Bongo Net	345 m	24	0
7		32	PS107	79.5872667	2.03102333	2017	Bongo Net	345 m	14	0
8		34	PS107	79.951375	3.1266825	2017	Bongo Net	345 m	17	0
9		45	PS107	79.0044333	8.30696667	2017	Bongo Net	345 m	0	17
10		7	PS107	79.0562333	3.77262333	2017	Bongo Net	345 m	8	0
11		1381	TUNUVII	78.863693	-0.633665	2017	Campelen Trawl	2600m	5	0
12	Greenland/West Fram Strait	95	PS100	78.6838333	-7.0228333	2016	Bongo Net/ Multinet	250m	4 (2)	1
13		98	PS100	78.85	-4.0574167	2016	Multinet	-	0	1
14		246	PS100	79.57	-19.506944	2016	Bongo Net	200m	3	3
15		241	PS100	79.5691667	-19.500167	2016	Bongo Net	300m	6 (3)	2
16		29	PS107	78.9794875	-5.5013275	2017	Bongo Net	340m	23	6
17		1306	TUNUVII	75.987477	-19.463093	2017	Campelen Trawl	480 m	7	0
18		1338	TUNUVII	76.007107	-14.189228	2017	Campelen Trawl	350 m	10 (1)	0
19	Nordauslandet	1	HE560	80.51759	22.066891	2020	Bongo Net	177 m	0	5
20		2	HE560	80.177589	22.153065	2020	Bongo Net / YFT	200 m	10	5
21	North Spitsbergen	4	HE560	79.520613	19.666993	2020	YFT	200 m	10	12
22		5	HE560	79.735243	15.537286	2020	Bongo Net	123 m	0	7
23		6	HE560	79.127639	16.0246	2020	Bongo Net / YFT	169 m	9	15 (1)
24		9	HE560	80.460108	14.187643	2020	YFT	50 m	10	0
25		10	HE560	79.805919	12.002588	2020	Bongo Net	146 m	0	12
26	West Spitsbergen	17	HE560	79.197424	11.793602	2020	Bongo Net	260 m	10	23 (2)
27		23	HE560	78.659525	16.677328	2020	YFT	170 m	10	0
28	South Spitsbergen	24	HE560	77.762499	15.139361	2020	YFT	100 m	10	0
29		25	HE560	76.993152	16.013978	2020	YFT	100 m	3	0

3. Results

The mtCOI sequence data from the two species of *Themisto* resulted in an alignment length of 658 base pairs. Specimens were sequenced from 29 sampling stations on the Greenland shelf, the Fram Strait and the Svalbard Archipelago. A total of 259 *T. libellula* specimens from 23 stations were sequenced and 157 *T. abyssorum* from 16 stations. In total

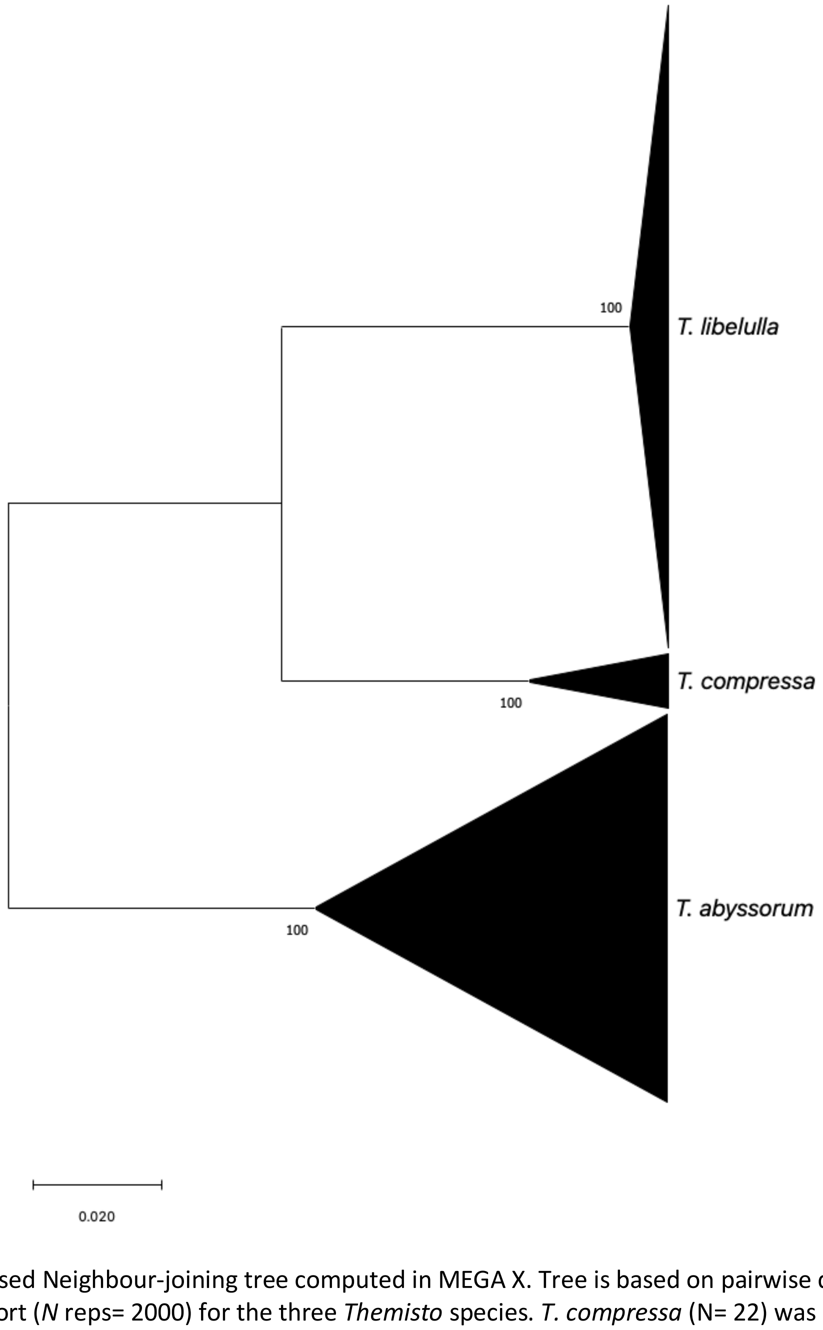

Figure 3. Collapsed Neighbour-joining tree computed in MEGA X. Tree is based on pairwise distances with bootstrap support (*N* reps= 2000) for the three *Themisto* species. *T. compressa* (N= 22) was not used in this study but is included in this tree to illustrate relationship with *T. libellula* (N= 259) and *T. abyssorum* (N= 157). The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the tree. The evolutionary distances were computed using the Kimura 2-parameter method. Depth of the nodes represents diversity and height represents sample size. All ambiguous positions were removed for each sequence pair (pairwise deletion option). There was a total of 658 positions in the final dataset.

250 and 152 of these were used in subsequent analysis (Table 1). Both species were sequenced at 10 out of the 29 stations. The mtCOI barcoding confirmed the morphological identification of all sequenced specimens (Figure 3).

3.1 Genetic diversity

T. libellula exhibited low levels of mtCOI sequence diversity. A total of 16 polymorphic sites, 4 parsimony informative sites and 16 unique haplotypes (H) were identified among 250 specimens. Genetic diversity was low with haplotype diversity, H_d= 0.360 (*SD*= 0.036); nucleotide diversity, π= 0.00064 (*SD*= 0.00008); and average number of nucleotide differences, *K*= 0.42043 (Table 2). In contrast, 136 polymorphic sites and 68 parsimony informative sites were identified for *T. abyssorum* leading to 115 unique haplotypes being assigned to 152 individuals. Genetic diversity indices were higher with H_d = 0.975 (*SD*= 0.008), π= 0.01218 (*SD*= 0.00089), and *K* = 8.01534 (Table 2). The distinctly different levels of diversity are represented by a shallow node for *T. libellula* and a deep node for *T. abyssorum* in the compressed NJ tree (Figure 3). The average intraspecific variation (K2P distance) was in *T. libellula* = 0.002% *and T. abyssorum* = 0.015%.

Table 2. Genetic diversity indices for the complete mtCOI gene sequence data sets for *T. libellula* and *T. abyssorum.* SD = Standard Deviation.

	T. libellula	*T. abyssorum*
Diversity Indices		
Sample Size (*N*)	250	152
Number of Haplotypes (H)	16	115
Polymorphic sites (S)	16	136
Parsimony informative sites	4	68
Haplotype diversity (H_d ±SD)	0.360 ± 0.036	0.975 ± 0.008
Nucleotide Diversity (π ±SD)	0.00064 ± 0.00008	0.01218 ± 0.00089
Average number of nucleotide differences (*K*)	0.42043	8.01534

TCS haplotype networks based on mtCOI illustrate contrasting diversity between the two species (Figure 4). *T. libellula* showed a low number of haplotypes (16), with two main haplotypes dominating and thirteen singletons (occurring in only one individual). These haplotypes diverge by only one or two of mutational steps, which is supported by the low nucleotide diversity value (Table 2). In contrast, *T. abyssorum* exhibited a high number of highly divergent haplotypes (115), with only one haplotype occurring in more than 10 individuals, and 107 singleton haplotypes.

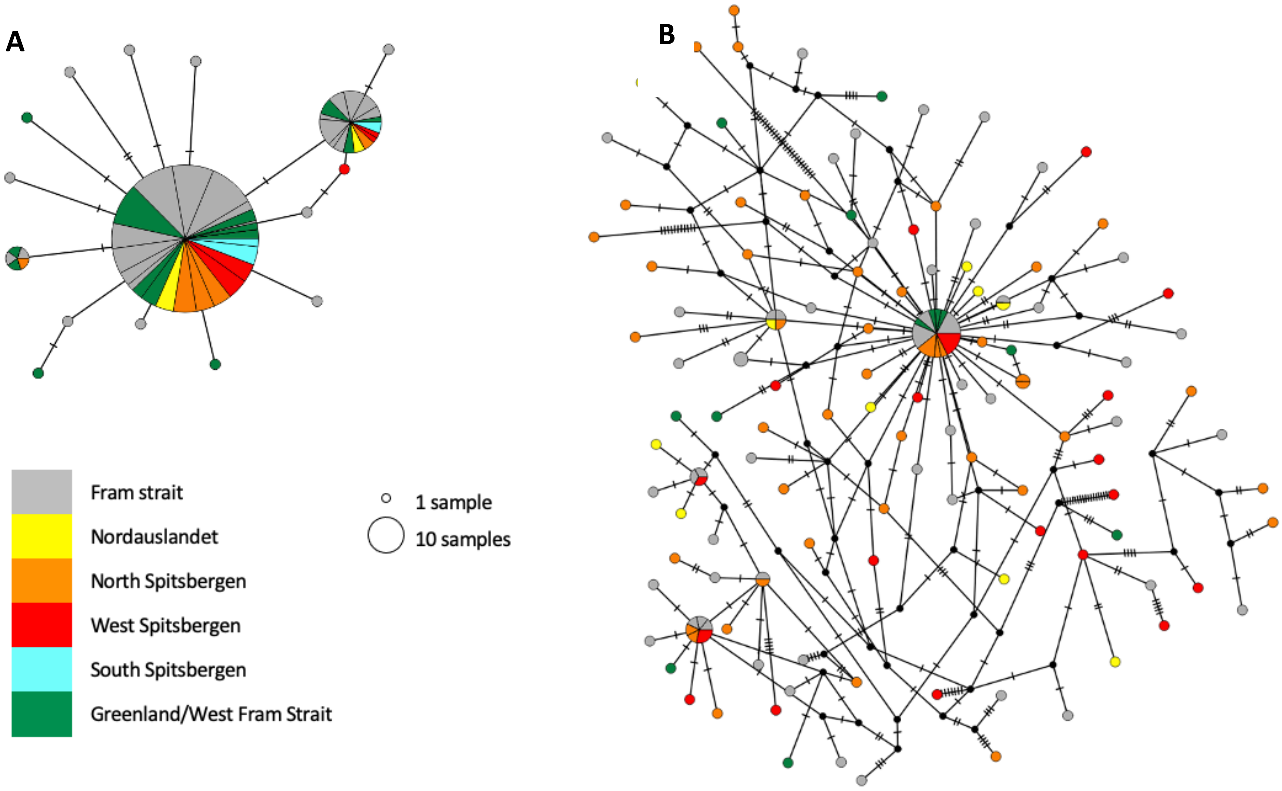

Figure 7. TCS haplotype networks for (A) *T. libellula* and (B) *T. abyssorum* based on mtCOI sequences. Each haplotype is represented by a circle and is coloured according to its geographic region. Circle size is proportionate to haplotype frequency, hypothetical haplotypes are represented by notches and mutations are represented by bars.

3.2 Population structure and connectivity

The data revealed a lack of genetic structure among all the geographic regions sampled, for both species. The TCS haplotype networks for *T. libellula* showed that the two most common haplotypes *(N*= 197 and *N*= 35) were present at all six of the main geographic regions sampled. The third most common haplotype (*N*= 5) was present at three out of the six regions (Figure

4). The haplotype network for *T. abyssorum* showed that the dominant haplotype (*N*= 23) was present at four out of five of the regions sampled (no *T. abyssorum* were sequenced from South Spitsbergen). This lack of spatial genetic structure is further illustrated in Figure 5, where haplotype frequency is shown at each sampling station. The most abundant haplotype for *T. libellula,* Haplotype 1, dominates at every station except one, where it is makes up half of the haplotypes present. In *T. abyssorum*, Haplotype 8 is present at all except the two Nordauslandet stations. Every station, except for one Fram Strait station is dominated by singletons.

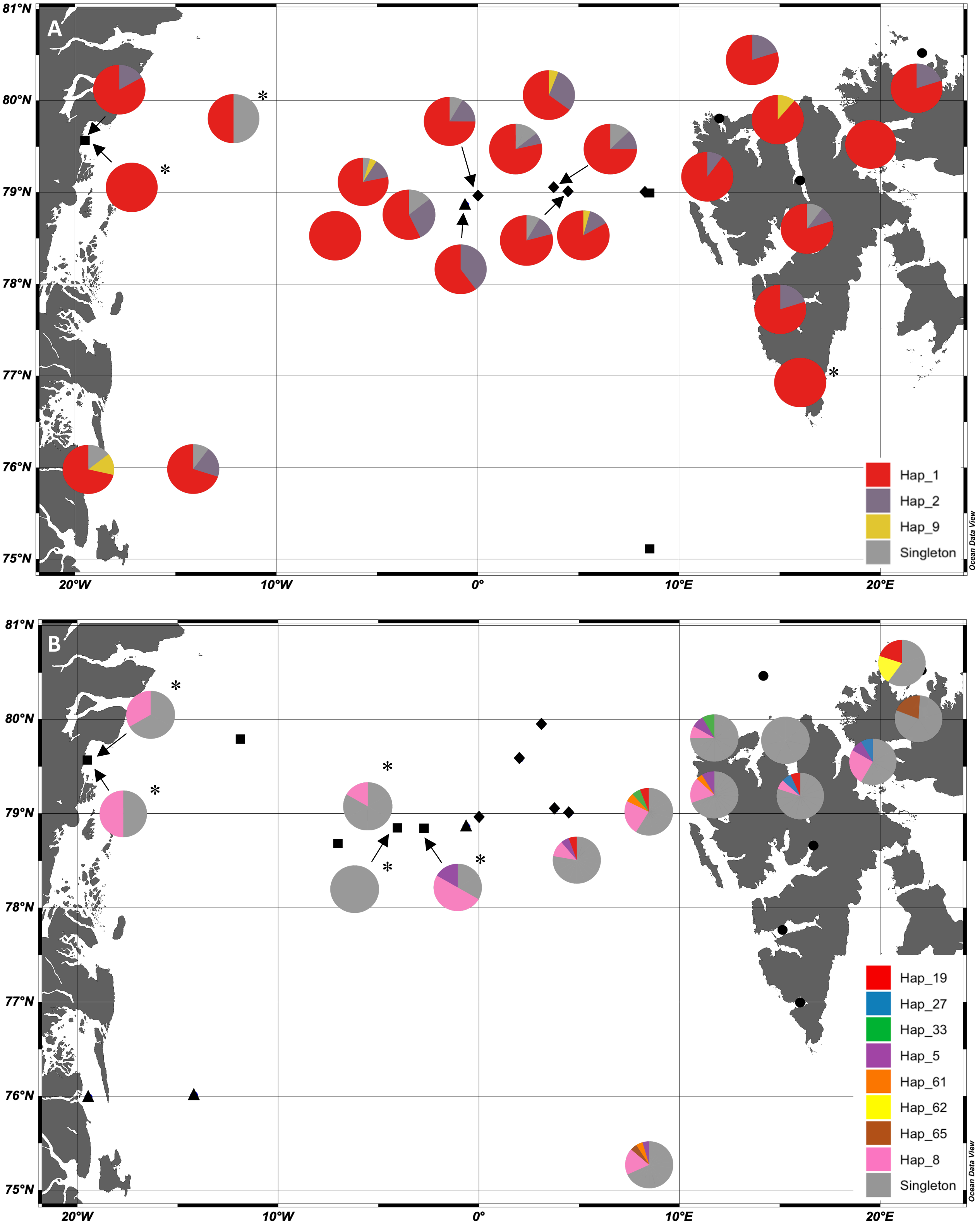

Figure 11. Relative frequency of *T. libellula* (A) and *T. abyssorum* (B) haplotypes and sampling stations. Colour indicates individual haplotypes. * indicates sites where N< 4. Small black shapes indicate stations where the species was not sequenced.

AMOVA analysis of spatial patterns of genetic variation within and among sampled populations showed no statistical significance of any of the variance components (among regions, among stations or among individuals). Based on these results, neither species exhibits significant geographic structure among the sampled populations (Table 3). Pairwise F_{ST} comparisons between the geographic regions showed no significant differences between pairs of regions. This further indicates a lack of genetic structure and high levels of connectivity between regions in both *T. libellula* and *T. abyssorum* (Table 4). All negative F_{ST} values were taken to be zero.

Table 3. The results of spatial population genetic structure using the Analysis of Molecular Variance (AMOVA) based on mtCOI. Significance tests based on 10100 permutations. Abbreviations: *df*= degrees of freedom, SS= Sums of Squares, F= fixation index.

Themisto libellula						
Source of variation	***df***	**SS**	**Variance Component**	**% variation**	**F**	***p-value***
Between regions	5	0.614	-0.00042	-0.23	-0.02596	0.55851
Between stations	17	2.374	-0.00425	-2.36	-0.02357	0.82733
Between individuals	227	41.867	0.18444	102.60	-0.00233	0.88782
Total	249	44.856		100	-	-
Themisto abyssorum						
Source of variation	***df***	**SS**	**Variance Component**	**% variation**	**F**	***p-value***
Between regions	4	1.989	0.00263	0.54	0.00540	0.09485
Between stations	11	4.904	-0.00550	-1.13	-0.01134	0.90584
Between individuals	136	66.719	0.49058	100.59	-0.00588	0.91673
Total	151	73.612	0.48771	100	-	-

Table 4. Results of pairwise F_{ST} values based on mtCOI for genetic connectivity between major geographic regions. All negative values are taken to be zero.

T. libellula

	Fram Strait	Greenland Shelf/ West Fram Strait	Nordauslandet	North Spitsbergen	West Spitsbergen	South Spitsbergen
Fram Strait	0					
Greenland Shelf/ West Fram Strait	-0.00421	0				
Nordauslandet	-0.05043	-0.04769	0			
North Spitsbergen	0.023	-0.00397	-0.00857	0		
West Spitsbergen	-0.00515	-0.02249	-0.05296	-0.0282	0	
South Spitsbergen	-0.02926	-0.03929	-0.08893	-0.03214	-0.05686	0

T. abyssorum

	Fram Strait	Greenland Shelf/ West Fram Strait	Nordauslandet	North Spitsbergen	West Spitsbergen	-
Fram Strait	0					
Greenland Shelf/ West Fram Strait	-0.01985	0				
Nordauslandet	-0.03077	-0.03182	0			
North Spitsbergen	-0.00099	-0.01505	-0.01953	0		
West Spitsbergen	-0.00808	-0.02079	-0.0403	0.00697	0	

3.3 Demographic history

The results of the Tajima's D and Fu's F tests for neutrality were significantly negative for the overall populations in both species. These results indicate an excess of rare polymorphisms are present in both species, allowing the rejection of the null hypothesis that the sampled populations are in a state of equilibrium (Table 5).

Table 5. Analysis of population history results based on the neutrality tests; Tajima's D and Fu's F. Associated p-values included and * indicates significant p-value (<0.05)

	T. libellula	*T. abyssorum*
Tajima's D test		
Sample size	250	153
Tajima's D	-2.11367	-2.18398
Tajima's D *p value*	<0.01*	<0.01*
Fu's F test		
No. of alleles	16	116
Fu's F	-19.39899	-24.51890
Fu's F *p value*	<0.01*	<0.01*

4. Discussion

Two abundant pelagic amphipod species, *T. libellula* and *T. abyssorum,* were tested for levels of genetic diversity, patterns of spatial genetic structure and connectivity and demographic history in the Fram Strait, Greenland shelf and Svalbard, using variation at the mitochondrial COI region. Overall, the levels of mtCOI diversity were low in *T. libellula* and very high in *T. abyssorum* and no evidence of spatial genetic structure was found for either species, across the sampled regions. Very high levels of connectivity and evidence of demographic expansion were exhibited by both species. These results provide new insight into the genetic diversity and phylogeography of two ecologically important zooplankton species in the Arctic ocean.

4.1 Genetic diversity

Genetic diversity of the mtCOI region was markedly different between the two species. In this study, *T. libellula* exhibited low haplotypic diversity with only 16 weakly divergent haplotypes identified in 250 specimens. Two main haplotypes dominated, and none were separated by more than two mutations. The haplotype network exhibited a star-like shape, which has also been found in its Southern Ocean congener; *Themisto gaudichaudii* (Havermans et al., unpublished data). Similarly low haplotype diversity indices were reported in a recent study by Tempestini et al. (2020), on *T. libellula* in the Canadian Arctic. They found haplotype diversity values ranging from 0.286 to 0.642 in four populations in the Chukchi and Bering Seas and the Gulf of Alaska. They identified seven weakly divergent haplotypes, two of which were dominant. These findings, combined with results in the present study suggest that *T. libellula* exhibits low genetic diversity at the mtCOI region throughout the Arctic.

The low genetic diversity found in *T. libellula* may have alternative explanations. Evolutionary bottlenecks occurred for many marine species in the Arctic when the expansion of polar ice sheets left limited glacial refugia during the last glacial maximum (LGM), approximately 10,000 years ago. This extreme habitat loss caused declines in population size and genetic diversity across many marine taxa. It was followed by rapid recolonization after deglaciation, causing founder effects in species of which few individuals were able to recolonise (Hardy et al., 2011; Shimizu et al., 2018). The subsequent impacts on present genetic diversity depend on the size and number of refugia as well as the effective population size of the survivors (Hardy et al., 2011; Hewitt, 2000). Genetic signatures of the LGM have been identified in other Arctic zooplankton taxa including the pteropod *Limacina helicina* (Shimizu et al., 2018; Sromek et al., 2015), the copepod *Pseudocalanus moultni* (Aarbakke et al., 2014) and the amphipod *Gammarus oceanicus* (Grabowski et al., 2019). However it remains unclear whether the low genetic diversity in certain Arctic species such as *T. libellula* is caused by limited former refugia, rapid colonization following deglaciation and consequent founder effects (Shimizu et al., 2018). If *T. libellula* experienced genetic bottlenecks due to the aforementioned glaciation events, insufficient time has occurred since the LGM for genetic diversity to have increased rapidly through the accumulation of mutations, especially if gene flow is high (Nei, 1987).

Another explanation for low mtCOI diversity is the occurrence of selective sweeps in a species' history. Selective sweeps occur when a neutral mitochondrial locus such as mtCOI has an association with another gene upon which positive selection acts (Hebert et al., 2003). This can leave only one or two central haplotypes, from which satellite haplotypes arise (Marko, 2004), as seen for *T. libellula* in this study. Even infrequent selective sweeps can reduce mtCOI diversity, so an occurrence could still be impacting the present-day diversity in *T. libellula*. However, with the absence of archive material for assessing changes in genetic structure over time, it is impossible to exclude that the low genetic diversity in *T. libellula* is in part caused by current selective pressures imposed by the rapid warming of the Arctic.

The high level of genetic diversity in *T. abyssorum* is strikingly different to that observed in *T. libellula*. Haplotypic diversity was two-fold higher, and the number of unique haplotypes was close to ten times that found in *T. libellula*, despite a smaller sample size. Nucleotide diversity was much higher than that of *T. libellula*, alluding to high genetic distances between haplotypes. Similarly high diversity was found in the abundant Arctic chaetognath, *Eukrohnia hamata* (DeHart et al., 2020) and the Arctic copepod *Calanus glacialis* (Weydmann et al., 2018). High genetic diversity is evident in the TCS haplotype network, which is a 'diffuse' shape with numerous mutations separating many haplotypes. This shape network has been found in other zooplankton with deep-sea distributions including the benthic shrimp *Nematocarcinus lanceopes* (Raupach et al., 2010), and the squat lobster species *Munida endeaviurae* and *Munida gracilis* (Yan et al., 2020).

Being a sub-Arctic boreal species, it is likely that larger populations of *T. abyssorum* were maintained than *T. libellula* during glaciation events in the LGM. Due to milder climate conditions, large refugia occurred along the coasts of Northern Europe during this period (Wares & Cunningham, 2001). The ability of *T. abyssorum* to thrive in deeper Atlantic waters (<50m) could have resulted in yet further, deep-sea refuges (Havermans et al., 2019). Isolation in refugia can lead to vicariant effects, where isolated populations diverge leading to an increase in local genetic diversity. When they are able to intermingle, the subsequent admixture of lineages leads to an overall increase in intraspecific diversity (Hardy et al., 2011). This mechanism may explain the high diversity, yet high levels of connectivity found in *T. abyssorum*.

Fluctuations in intra-specific genetic diversity can have strong ecological implications for population stability, resilience and adaptive potential (Bolnick et al., 2011; Des Roches et al., 2018; Thompson et al., 2019). High diversity at the mtCOI region indicates high levels of standing genetic variation in *T. abyssorum*, which can be an important source of swift adaption to selection pressures. Species with low genetic diversity are generally more susceptible to rapid environmental changes than those with high genetic diversity since the latter can result in higher adaptive potential and thus, stronger resistance to stressors such as temperature increases (Thompson et al., 2019). In a recent meta-analysis, Des Roches et al. (2018) concluded that the ecological effects of intraspecific diversity loss rival the effects of the removal or replacement of a species in an ecosystem. The decline of intraspecific diversity driven by factors such as local population extinctions is a global trend (Des Roches et al., 2018), and is especially relevant in the light of the rapid climate change in the Arctic, at its consequences for ecologically important species such as *Themisto*.

4.2 Population structure and connectivity

A lack of spatially structured genetic differentiation was observed in both species across the study area. This was clearly illustrated in the TCS haplotype networks, haplotype distribution maps and subsequent statistical analysis. The AMOVA revealed no significant genetic differentiation between major geographic regions, sampling stations or individuals. This indicates high levels of connectivity and genetic homogeneity between sampled populations. Dominant haplotypes were present across the sampling area for both species and all pairwise F_{ST} values were low and insignificant among the major geographic regions, further supporting high levels of gene flow. In contrast to the present study, Tempestini et al (2020) found Arctic populations in the Bering and Chuckchi seas to be genetically homogenous but showed a population from the Gulf of Alaska to be genetically distinct. Although their sample size was very low in comparison, this population structure was also reflected by genomic data, supporting its significance. Their results indicate that the presence of population structure on a larger geographic scale is a likelihood in *T. libellula,* but our sampling did not cover a wide enough area to detect it.

Weak or non-existent population structure is common among marine species with pelagic life stages, such as *Themisto* amphipods, due to the high potential for dispersal and gene flow through oceanic currents (Hardy et al., 2011). The absence of genetic structure in populations is often interpreted as a result of panmixia or a genetic bottleneck followed by a population expansion (Hardy et al., 2011; Yan et al., 2020). Similarly high levels of population connectivity have been demonstrated in other key Arctic zooplankton species including copepods (Weydmann et al., 2014; Weydmann et al., 2018), chaetognaths (DeHart et al., 2020) and multiple polychaete and echinoderm species with planktonic life stages (Hardy et al., 2011). The high gene flow between the studied populations is likely heavily mediated by multi-directional currents in the Fram Strait and Svalbard Archipelago. The WSC carries water northward as well as circulating it across the Fram strait, the ECG carries water southward and the SCC carries polar water around the south coast of Spitsbergen and northward again.

Site-specific genetic diversity and connectivity can be affected in part by sample size (Ryman et al., 2006), which was limited at some sampling stations in this study. Using larger sample sizes in under-sampled regions such as the Greenland shelf and Nordauslandet would improve the statistical power of these tests and allow for stronger conclusions to be drawn. The use more genetic markers, particularly nuclear DNA, would provide a more accurate picture of the population structure of these two species.

4.3 Demographic history

The results of the neutrality tests were significantly negative in both species, revealing that there is an excess of rare mutations in the sampled populations. This excess can be attributed to either a bottleneck event followed by population expansion or a selective sweep. However, both leave similar genetic signatures on the mtCOI region and distinguishing between them is difficult (Hebert et al., 2003; Tajima, 1989). Studies providing direct evidence of selective sweeps on the mtCOI region are rare and come with many caveats (Grant, 2015; Marko, 2004), while population expansion after a bottleneck has frequently been argued in

Arctic zooplankton studies (Grabowski et al., 2019; Sromek et al., 2015; Weydmann et al., 2018). Demographic expansion in the present study is supported by the lack of population structure and high levels of connectivity found in both species. In combination with significantly negative Tajima's D and Fu's F values, these results correspond to widely observed patterns of post-LGM population expansions across many marine zooplankton taxa in the Arctic. Evidence of recent demographic expansion was reported in Canadian Arctic populations of *T. libellula* (Tempestini et al., 2020), but no studies have investigated this in *T. abyssorum*. Similar patterns of demographic history have been found in other Arctic and sub-Arctic zooplankton, including *E. hamata* (DeHart et al., 2020), *L. helicina* (Sromek et al., 2015), and *C. glacialis* (Weydmann et al., 2018).

An important caveat to this study that the use of genetic markers with low levels of polymorphisms, such as the mtCOI gene, carries the risk of overlooking aspects of a species demographic history as well as the presence of weak yet significant population structure (Peijnenburg & Goetze, 2013). Demographic expansion does not necessarily reflect geographic expansion, so strong conclusions about previous range expansions and contractions cannot be drawn from this data set. The analysis of more genetic markers in combination with a wider sampling area would provide a better foundation for identifying traces of spatial expansion and attributing evidence of demographic expansions to events such as bottlenecks or selective sweeps (Grant, 2015; Madoui et al., 2017).

4.4 Future implications

Shifts in distribution linked to environmental changes have already been reported for *Themisto* species in the Arctic and its marginal seas. Overall, *T. libellula* abundance in the Barents sea and the Fram Strait has been decreasing in recent years (CAFF, 2017). Dalpadado et al. (2012) found significant decreases in *T. libellula* and other Arctic zooplankton populations over a period of 25 years, correlating with warming trends across the Barents Sea. *T. libellula* abundances have been observed to increase in cool years the southern Bering sea and disappear in warmer years (Pinchuk et al., 2013). Mass occurrences have were reported in northern parts of the Bering Sea during cooling periods, and decreased with subsequent warming (Volkov, 2012). Although these distribution changes are all not poleward, the authors identify temperature changes as the main driver.

A corresponding trend of increasing *T. abyssorum* abundance in the Fram Strait has also been observed (CAFF, 2017). In a sediment trap time series analysis in the Fram Strait, Kraft et al. (2013) found that *T. abyssorum* abundances were increasing with warming trends. Presence of the invasive boreal *T. compressa* has been reported in the Fram Strait since 2004, with proof of established reproductive events in 2011 (Kraft et al., 2013; Schröter et al., 2019). These community and abundance shifts are evidence that Atlantification of the Arctic is already impacting *Themisto* species with the smaller, boreal species coming out as the winners. Other Arctic pelagic zooplankton species have exhibited community and distribution changes as a result of Atlantification around the Svalbard Archipelago and Fram Strait. These include krill species (Buchholz et al., 2010) and *Calanus* copepods (Weydmann et al., 2014). These changes in distribution and abundance associated with the changing environmental conditions in the Arctic are evidence that zooplankton communities are already in transition to a warmer Arctic dominated by boreal species (Csapó et al., 2021).

The combination of factors including low genetic diversity, a longer life cycle (Havermans et al., 2019), cold adaptions, and reliance on the cryo-pelagic pathway (Auel et al., 2002; Kohlbach et al., 2016) could lead to *T. libellula* becoming a loser in the Atlantification of the Arctic. These negative impacts could materialize as the loss of intraspecific diversity as well as local extinctions and further poleward distribution contractions. In contrast, high diversity and adaptive potential, a shorter life cycle, and an Atlantic affinity (Havermans et al., 2019) may result in *T. abyssorum* benefiting from a warming Arctic. The replacement of the large, nutritionally rich *T. libellula* with the smaller *T. abyssorum* and *T. compressa* is likely to negatively impact predators at the higher trophic levels. Arctic species that specialize in feeding on *T. libellula* such as the Little Auk and Polar Cod, will have to adapt to a new prey spectrum consisting of smaller and less energy-rich boreal species such as *T. abyssorum* (Dalpadado et al., 2012; Kraft et al., 2013).

In conclusion, this study shows contrasting molecular diversity for the first time between two congeneric species of pelagic amphipods that are highly abundant in the Arctic ocean. We observed an absence of genetic structure in both species, and correspondingly high levels of genetic connectivity across the studied region. The observed patterns of diversity and demographic signatures are likely caused by glaciation events impacting population sizes during the LGM. Population connectivity is likely explained by current-mediating mixing among *Themisto* populations in the region. These results contribute to the better understanding of the evolutionary processes driving molecular diversity and the adaptive potential of two ecologically important species in a changing Arctic. Further research should incorporate more genetic markers and a wider sampling range in order to detect potential population structure, provide more detailed demographic history and investigate gene flow between regions. Incorporating environmental factors such as temperature and salinity in future analysis could be useful for further understanding of the mechanisms behind potential population structure, connectivity and diversity of these two species. These results emphasize the need for further analysis of the molecular biogeography of key zooplankton species in the Arctic Ocean that are already being affected by rapid climate change. Such data are crucial to formulating accurate predictions of how future zooplankton communities, species interactions and food web structure will materialize in the Arctic and its marginal seas as a result of climate change.

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IX Appendix

1. Detailed information about individual *Themisto* specimens sequenced and used in analysis for this study.

Table 1 A1. Sample code, expedition details and sample location of all *Themisto* specimens sequenced.

Species	Sample Code	Expedition	Station	Latitude (N)	Longitude (E)
Themisto abyssorum	PS100TabN015	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabN016	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabN017	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabN018	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabN019	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabN020	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabN025	PS100	246	79.5700	19.5069
Themisto abyssorum	PS100TabN026	PS100	246	79.5700	19.5069
Themisto abyssorum	PS100TabN030	PS100	246	79.5700	19.5069
Themisto abyssorum	PS107TabN009	PS107	29	78.9795	-5.5013
Themisto abyssorum	PS107TabN010	PS107	29	78.9795	-5.5013
Themisto abyssorum	PS107TabN011	PS107	29	78.9795	-5.5013
Themisto abyssorum	PS107TabN012	PS107	29	78.9795	-5.5013
Themisto abyssorum	PS107TabN013	PS107	29	78.9795	-5.5013
Themisto abyssorum	PS107TabN014	PS107	29	78.9795	-5.5013
Themisto abyssorum	TabR035	PS107	2	78.5929	5.0538
Themisto abyssorum	TabR036	PS107	2	78.5929	5.0538
Themisto abyssorum	TabR037	PS107	2	78.5929	5.0538
Themisto abyssorum	TabR039	PS107	2	78.5929	5.0538
Themisto abyssorum	TabR044	PS107	2	78.5929	5.0538
Themisto abyssorum	TabR046	PS107	2	78.5929	5.0538
Themisto abyssorum	TabR049	PS107	2	78.5929	5.0538
Themisto abyssorum	TabR050	PS107	2	78.5929	5.0538
Themisto abyssorum	TabR089	PS100	241	79.5692	-19.5002
Themisto abyssorum	TabR090	PS100	241	79.5692	-19.5002
Themisto abyssorum	TabR096	PS100	102	78.8441	-2.7351
Themisto abyssorum	TabR097	PS100	102	78.8441	-2.7351
Themisto abyssorum	TabR098	PS100	102	78.8441	-2.7351
Themisto abyssorum	TabR119	HE560	4	79.5206	19.6670
Themisto abyssorum	TabR120	HE560	4	79.5206	19.6670
Themisto abyssorum	TabR121	HE560	4	79.5206	19.6670
Themisto abyssorum	TabR122	HE560	4	79.5206	19.6670
Themisto abyssorum	TabR123	HE560	4	79.5206	19.6670
Themisto abyssorum	TabR124	HE560	4	79.5206	19.6670
Themisto abyssorum	TabR125	HE560	4	79.5206	19.6670
Themisto abyssorum	TabR126	HE560	4	79.5206	19.6670

Themisto abyssorum	TabR127	HE560	4	79.5206	19.6670
Themisto abyssorum	TabR128	HE560	4	79.5206	19.6670
Themisto abyssorum	TabR129	HE560	4	79.5206	19.6670
Themisto abyssorum	TabR130	HE560	4	79.5206	19.6670
Themisto abyssorum	TabR131	HE560	10	79.8059	12.0026
Themisto abyssorum	TabR132	HE560	10	79.8059	12.0026
Themisto abyssorum	TabR133	HE560	10	79.8059	12.0026
Themisto abyssorum	TabR134	HE560	10	79.8059	12.0026
Themisto abyssorum	TabR135	HE560	10	79.8059	12.0026
Themisto abyssorum	TabR136	HE560	10	79.8059	12.0026
Themisto abyssorum	TabR137	HE560	10	79.8059	12.0026
Themisto abyssorum	TabR138	HE560	10	79.8059	12.0026
Themisto abyssorum	TabR139	HE560	10	79.8059	12.0026
Themisto abyssorum	TabR140	HE560	10	79.8059	12.0026
Themisto abyssorum	TabR141	HE560	10	79.8059	12.0026
Themisto abyssorum	TabR142	HE560	10	79.8059	12.0026
Themisto abyssorum	TabR143	HE560	5	79.7352	15.5373
Themisto abyssorum	TabR144	HE560	5	79.7352	15.5373
Themisto abyssorum	TabR145	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR146	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR147	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR148	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR149	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR150	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR151	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR152	HE560	5	79.7352	15.5373
Themisto abyssorum	TabR153	HE560	5	79.7352	15.5373
Themisto abyssorum	TabR154	HE560	5	79.7352	15.5373
Themisto abyssorum	TabR155	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR156	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR157	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR158	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR159	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR160	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR161	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR162	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR163	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR164	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR165	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR166	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR167	HE560	1	80.5176	22.0669
Themisto abyssorum	TabR168	HE560	1	80.5176	22.0669
Themisto abyssorum	TabR169	HE560	1	80.5176	22.0669
Themisto abyssorum	TabR170	HE560	2	80.1776	22.1531

Themisto abyssorum	TabR171	HE560	2	80.1776	22.1531
Themisto abyssorum	TabR172	HE560	2	80.1776	22.1531
Themisto abyssorum	TabR173	HE560	2	80.1776	22.1531
Themisto abyssorum	TabR174	HE560	1	80.5176	22.0669
Themisto abyssorum	TabR175	HE560	1	80.5176	22.0669
Themisto abyssorum	TabR176	HE560	2	80.1776	22.1531
Themisto abyssorum	TabR177	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR178	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR179	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR180	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR181	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR182	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR183	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR184	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR185	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR187	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR188	HE560	17	79.1974	11.7936
Themisto abyssorum	PS100TabC03	PS100	95	78.6838	-7.0228
Themisto abyssorum	PS100TabC14	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC15	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC16	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC17	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC18	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC19	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC20	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC21	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC22	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC23	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC24	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC25	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC26	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC27	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC28	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC29	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC30	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC31	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC32	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC33	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC34	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC35	PS100	2	75.1125	8.5410
Themisto abyssorum	PS100TabC46	PS100	98	78.8500	-4.0574
Themisto abyssorum	PS107TabC124	PS107	2	78.5929	5.0538
Themisto abyssorum	PS107TabC125	PS107	2	78.5929	5.0538
Themisto abyssorum	PS107TabC127	PS107	2	78.5929	5.0538

Themisto abyssorum	PS107TabC128	PS107	2	78.5929	5.0538
Themisto abyssorum	PS107TabC129	PS107	2	78.5929	5.0538
Themisto abyssorum	PS107TabC140	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC141	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC142	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC143	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC144	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC148	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC149	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC150	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC151	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC152	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC153	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC154	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC155	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC156	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC158	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC159	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC160	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC161	PS107	45	79.0044	8.3070
Themisto abyssorum	PS107TabC162	PS107	45	79.0044	8.3070
Themisto abyssorum	TabR041	PS107	2	78.5929	5.0538
Themisto abyssorum	TabR186	HE560	17	79.1974	11.7936
Themisto abyssorum	TabR268	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR269	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR270	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR271	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR272	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR273	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR275	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR277	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR278	HE560	6	79.1276	16.0246
Themisto abyssorum	TabR280	HE560	5	79.7352	15.5373
Themisto abyssorum	TabR281	HE560	5	79.7352	15.5373
Themisto libellula	PS100TliN022	PS100	102	78.8441	-2.7351
Themisto libellula	PS100TliN023	PS100	102	78.8441	-2.7351
Themisto libellula	PS100TliN024	PS100	102	78.8441	-2.7351
Themisto libellula	PS100TliN029	PS100	246	79.5700	19.5069
Themisto libellula	PS100TliN031	PS100	246	79.5700	19.5069
Themisto libellula	PS100TliN032	PS100	246	79.5700	19.5069
Themisto libellula	PrabelTliN004	TUNUVII	1381	78.5182	0.3802
Themisto libellula	PrabelTliN005	TUNUVII	1381	78.5182	0.3802
Themisto libellula	PrabelTliN006	TUNUVII	1381	78.5182	0.3802
Themisto libellula	PrabelTliN007	TUNUVII	1381	78.5182	0.3802

Themisto libellula	PrabelTliN008	TUNUVII	1381	78.5182	0.3802
Themisto libellula	TliR027	PS107	32	79.5873	2.0310
Themisto libellula	TliR028	PS107	32	79.5873	2.0310
Themisto libellula	TliR029	PS107	32	79.5873	2.0310
Themisto libellula	TliR030	PS107	32	79.5873	2.0310
Themisto libellula	TliR032	PS107	32	79.5873	2.0310
Themisto libellula	TliR033	PS107	32	79.5873	2.0310
Themisto libellula	TliR061	PS100	95	78.6838	-7.0228
Themisto libellula	TliR062	PS100	95	78.6838	-7.0228
Themisto libellula	TliR063	PS100	95	78.6838	-7.0228
Themisto libellula	TliR065	PS100	95	78.6838	-7.0228
Themisto libellula	TliR066	PS100	87	79.7902	-11.8860
Themisto libellula	TliR070	PS100	87	79.7902	-11.8860
Themisto libellula	TliR071	PS100	241	79.5692	-19.5002
Themisto libellula	TliR072	PS100	241	79.5692	-19.5002
Themisto libellula	TliR074	PS100	241	79.5692	-19.5002
Themisto libellula	TliR076	PS100	241	79.5692	-19.5002
Themisto libellula	TliR077	PS100	241	79.5692	-19.5002
Themisto libellula	TliR078	PS100	241	79.5692	-19.5002
Themisto libellula	TliR091	PS100	102	78.8441	-2.7351
Themisto libellula	TliR092	PS100	102	78.8441	-2.7351
Themisto libellula	TliR093	PS100	102	78.8441	-2.7351
Themisto libellula	TliR094	PS100	102	78.8441	-2.7351
Themisto libellula	TliR001	PS107	7	79.0562	3.7726
Themisto libellula	TliR002	PS107	7	79.0562	3.7726
Themisto libellula	TliR003	PS107	7	79.0562	3.7726
Themisto libellula	TliR004	PS107	7	79.0562	3.7726
Themisto libellula	TliR005	PS107	7	79.0562	3.7726
Themisto libellula	TliR006	PS107	7	79.0562	3.7726
Themisto libellula	TliR007	PS107	7	79.0562	3.7726
Themisto libellula	TliR008	PS107	7	79.0562	3.7726
Themisto libellula	TliR009	TUNUVII	1306	75.9875	-19.4631
Themisto libellula	TliR010	TUNUVII	1306	75.9875	-19.4631
Themisto libellula	TliR011	TUNUVII	1306	75.9875	-19.4631
Themisto libellula	TliR012	TUNUVII	1306	75.9875	-19.4631
Themisto libellula	TliR013	TUNUVII	1338	76.0071	-14.1892
Themisto libellula	TliR014	TUNUVII	1338	76.0071	-14.1892
Themisto libellula	TliR015	TUNUVII	1338	76.0071	-14.1892
Themisto libellula	TliR016	TUNUVII	1338	76.0071	-14.1892
Themisto libellula	TliR017	TUNUVII	1306	75.9875	-19.4631
Themisto libellula	TliR018	TUNUVII	1306	75.9875	-19.4631
Themisto libellula	TliR019	TUNUVII	1306	75.9875	-19.4631
Themisto libellula	TliR020	TUNUVII	1338	76.0071	-14.1892
Themisto libellula	TliR021	TUNUVII	1338	76.0071	-14.1892

Themisto libellula	TliR022	TUNUVII	1338	76.0071	-14.1892
Themisto libellula	TliR023	TUNUVII	1338	76.0071	-14.1892
Themisto libellula	TliR024	TUNUVII	1338	76.0071	-14.1892
Themisto libellula	TliR025	TUNUVII	1338	76.0071	-14.1892
Themisto libellula	TliR099	HE560	2	80.1776	22.1531
Themisto libellula	TliR100	HE560	2	80.1776	22.1531
Themisto libellula	TliR101	HE560	2	80.1776	22.1531
Themisto libellula	TliR102	HE560	2	80.1776	22.1531
Themisto libellula	TliR103	HE560	2	80.1776	22.1531
Themisto libellula	TliR104	HE560	2	80.1776	22.1531
Themisto libellula	TliR105	HE560	2	80.1776	22.1531
Themisto libellula	TliR106	HE560	2	80.1776	22.1531
Themisto libellula	TliR107	HE560	2	80.1776	22.1531
Themisto libellula	TliR108	HE560	2	80.1776	22.1531
Themisto libellula	TliR109	HE560	4	79.5206	19.6670
Themisto libellula	TliR110	HE560	4	79.5206	19.6670
Themisto libellula	TliR111	HE560	4	79.5206	19.6670
Themisto libellula	TliR112	HE560	4	79.5206	19.6670
Themisto libellula	TliR113	HE560	4	79.5206	19.6670
Themisto libellula	TliR114	HE560	4	79.5206	19.6670
Themisto libellula	TliR115	HE560	4	79.5206	19.6670
Themisto libellula	TliR116	HE560	4	79.5206	19.6670
Themisto libellula	TliR117	HE560	4	79.5206	19.6670
Themisto libellula	TliR118	HE560	4	79.5206	19.6670
Themisto libellula	PS107TliC002	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC003	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC004	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC005	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC006	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC007	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC008	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC009	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC010	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC011	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC012	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC013	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC014	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC015	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC016	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC017	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC018	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC019	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC020	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC021	PS107	2	78.5929	5.0538

Themisto libellula	PS107TliC022	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC023	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC024	PS107	2	78.5929	5.0538
Themisto libellula	PS107TliC025	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC026	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC027	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC028	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC029	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC030	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC031	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC032	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC033	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC034	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC035	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC036	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC037	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC038	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC039	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC040	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC041	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC042	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC043	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC044	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC045	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC046	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC047	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC048	PS107	21	78.9619	0.0240
Themisto libellula	PS107TliC049	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC050	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC051	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC052	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC053	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC054	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC055	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC056	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC057	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC058	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC059	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC060	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC061	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC062	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC063	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC064	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC065	PS107	38	79.0121	4.4921

Themisto libellula	PS107TliC066	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC067	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC068	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC069	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC070	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC071	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC072	PS107	38	79.0121	4.4921
Themisto libellula	PS107TliC073	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC074	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC075	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC076	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC077	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC078	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC079	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC080	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC081	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC082	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC083	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC084	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC085	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC086	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC087	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC088	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC089	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC090	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC091	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC092	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC093	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC094	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC095	PS107	29	78.9795	-5.5013
Themisto libellula	PS107TliC098	PS107	32	79.5873	2.0310
Themisto libellula	PS107TliC099	PS107	32	79.5873	2.0310
Themisto libellula	PS107TliC100	PS107	32	79.5873	2.0310
Themisto libellula	PS107TliC101	PS107	32	79.5873	2.0310
Themisto libellula	PS107TliC103	PS107	32	79.5873	2.0310
Themisto libellula	PS107TliC104	PS107	32	79.5873	2.0310
Themisto libellula	PS107TliC105	PS107	32	79.5873	2.0310
Themisto libellula	PS107TliC106	PS107	32	79.5873	2.0310
Themisto libellula	PS107TliC107	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC108	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC109	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC110	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC111	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC112	PS107	34	79.9514	3.1267

Themisto libellula	PS107TliC113	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC114	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC115	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC116	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC117	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC118	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC119	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC120	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC145	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC146	PS107	34	79.9514	3.1267
Themisto libellula	PS107TliC147	PS107	34	79.9514	3.1267
Themisto libellula	PS107TspC121	PS107	2	78.5929	5.0538
Themisto libellula	TliR060	PS100	95	78.6838	-7.0228
Themisto libellula	TliR064	PS100	95	78.6838	-7.0228
Themisto libellula	TliR067	PS100	87	79.7902	-11.8860
Themisto libellula	TliR068	PS100	87	79.7902	-11.8860
Themisto libellula	TliR069	PS100	87	79.7902	-11.8860
Themisto libellula	TliR073	PS100	241	79.5692	-19.5002
Themisto libellula	TliR075	PS100	241	79.5692	-19.5002
Themisto libellula	TliR080	PS100	241	79.5692	-19.5002
Themisto libellula	TliR026	TUNUVII	1338	76.0071	-14.1892
Themisto libellula	TliR216	HE560	6	79.1276	16.0246
Themisto libellula	TliR217	HE560	6	79.1276	16.0246
Themisto libellula	TliR218	HE560	6	79.1276	16.0246
Themisto libellula	TliR219	HE560	6	79.1276	16.0246
Themisto libellula	TliR220	HE560	6	79.1276	16.0246
Themisto libellula	TliR221	HE560	6	79.1276	16.0246
Themisto libellula	TliR222	HE560	6	79.1276	16.0246
Themisto libellula	TliR223	HE560	6	79.1276	16.0246
Themisto libellula	TliR224	HE560	6	79.1276	16.0246
Themisto libellula	TliR225	HE560	17	79.1974	11.7936
Themisto libellula	TliR226	HE560	17	79.1974	11.7936
Themisto libellula	TliR227	HE560	17	79.1974	11.7936
Themisto libellula	TliR228	HE560	17	79.1974	11.7936
Themisto libellula	TliR229	HE560	17	79.1974	11.7936
Themisto libellula	TliR230	HE560	17	79.1974	11.7936
Themisto libellula	TliR231	HE560	17	79.1974	11.7936
Themisto libellula	TliR232	HE560	17	79.1974	11.7936
Themisto libellula	TliR233	HE560	17	79.1974	11.7936
Themisto libellula	TliR234	HE560	17	79.1974	11.7936
Themisto libellula	TliR235	HE560	23	78.6595	16.6773
Themisto libellula	TliR236	HE560	23	78.6595	16.6773
Themisto libellula	TliR237	HE560	23	78.6595	16.6773
Themisto libellula	TliR238	HE560	23	78.6595	16.6773

Themisto libellula	TliR239	HE560	23	78.6595	16.6773
Themisto libellula	TliR240	HE560	23	78.6595	16.6773
Themisto libellula	TliR241	HE560	23	78.6595	16.6773
Themisto libellula	TliR242	HE560	23	78.6595	16.6773
Themisto libellula	TliR243	HE560	23	78.6595	16.6773
Themisto libellula	TliR244	HE560	23	78.6595	16.6773
Themisto libellula	TliR245	HE560	24	80.4601	14.1876
Themisto libellula	TliR246	HE560	24	80.4601	14.1876
Themisto libellula	TliR247	HE560	24	80.4601	14.1876
Themisto libellula	TliR248	HE560	24	80.4601	14.1876
Themisto libellula	TliR249	HE560	24	80.4601	14.1876
Themisto libellula	TliR250	HE560	24	80.4601	14.1876
Themisto libellula	TliR251	HE560	24	80.4601	14.1876
Themisto libellula	TliR252	HE560	24	80.4601	14.1876
Themisto libellula	TliR253	HE560	24	80.4601	14.1876
Themisto libellula	TliR254	HE560	24	80.4601	14.1876
Themisto libellula	TliR255	HE560	9	80.4601	14.1876
Themisto libellula	TliR256	HE560	9	80.4601	14.1876
Themisto libellula	TliR257	HE560	9	80.4601	14.1876
Themisto libellula	TliR258	HE560	9	80.4601	14.1876
Themisto libellula	TliR259	HE560	9	80.4601	14.1876
Themisto libellula	TliR260	HE560	9	80.4601	14.1876
Themisto libellula	TliR261	HE560	9	80.4601	14.1876
Themisto libellula	TliR262	HE560	9	80.4601	14.1876
Themisto libellula	TliR263	HE560	9	80.4601	14.1876
Themisto libellula	TliR264	HE560	9	80.4601	14.1876
Themisto libellula	TliR265	HE560	25	76.9932	16.0140
Themisto libellula	TliR266	HE560	25	76.9932	16.0140
Themisto libellula	TliR267	HE560	25	76.9932	16.0140

2. List of identified Haplotypes: *T. libellula,* where Hap = Haplotype and number indicates the unique haplotype.

Hap_1
TACTCTTTATTTTTTTTTAGGTCTTTGAAGAGGTTTAGTAGGTACGTCTATAAGTACTATTATTCGTATAGAATTAAGAACTA
AAGGTTCTTTATTAGGAGATGATCAGATTTATAATGTTATAGTGACAGGGCACGCTTTTATTATAATTTTTTTTATAGTTAT
ACCTATTATAATTGGGGGGTTTGGTAATTGACTTGTTCCTTTAATGTTAGGGAGTGTAGATATAGCTTTTCCTCGTATAAAT
AACATAAGGTTTTGATTATTAGTTCCTTCTTTTATACTATTAGCTTTAAGTAGAATAGTGGAGAGAGGCGTAGGGGCTGGT
TGGACTTTATACCCTCCTCTATCTTCTTCTATAGGCCACAGAGGTTCTGCTGTTGATGTTGCTATTTTTTCTTTACATTTAGCA
GGTGTTTCTTCTATTTTAGGAGCTATTAATTTTATAACTACTATTTTAAATATACGAAGAAGAGGGTTTAAAATATTTTATAT
AAGTCTATTTGTTTGAGCTGTTTTTATCACAGCTATTTTGTTACTATTATCGTTACCTGTATTAGCAGGGGGGATTACTATAC
TTTTATTAGATCGGAATTTAAACACTTCTTTTTTTAACCCTATGGGAGGAGGGGATCCTGTTTTATACCAACATTTGTTT

Hap_2
TACTCTTTATTTTTTTTTAGGCCTTTGAAGAGGTTTAGTAGGTACGTCTATAAGTACTATTATTCGTATAGAATTAAGAACTA
AAGGTTCTTTATTAGGAGATGATCAGATTTATAATGTTATAGTGACAGGGCACGCTTTTATTATAATTTTTTTTATAGTTAT
ACCTATTATAATTGGGGGGTTTGGTAATTGACTTGTTCCTTTAATGTTAGGGAGTGTAGATATAGCTTTTCCTCGTATAAAT
AACATAAGGTTTTGATTATTAGTTCCTTCTTTTATACTATTAGCTTTAAGTAGAATAGTGGAGAGAGGCGTAGGGGCTGGT
TGGACTTTATACCCTCCTCTATCTTCTTCTATAGGCCACAGAGGTTCTGCTGTTGATGTTGCTATTTTTTCTTTACATTTAGCA
GGTGTTTCTTCTATTTTAGGAGCTATTAATTTTATAACTACTATTTTAAATATACGAAGAAGAGGGTTTAAAATATTTTATAT
AAGTCTATTTGTTTGAGCTGTTTTTATCACAGCTATTTTGTTACTATTATCGTTACCTGTATTAGCAGGGGGGATTACTATAC
TTTTATTAGATCGGAATTTAAACACTTCTTTTTTTAACCCTATGGGAGGAGGGGATCCTGTTTTATACCAACATTTGTTT

Hap_3
TACTCTTTATTTTTTTTTAGGTCTTTGAAGAGGTTTAGTAGGTACTTCTATAAGTACTATTATTCGTATAGAATTAAGAACTA
AAGGTTCTTTATTAGGAGATGATCAGATTTATAATGTTATAGTGACAGGGCACGCTTTTATTATAATTTTTTTTATAGTTAT
ACCTATTATAATTGGGGGGTTTGGTAATTGACTTGTTCCTTTAATGTTAGGGAGTGTAGATATAGCTTTTCCTCGTATAAAT
AACATAAGGTTTTGATTATTAGTTCCTTCTTTTATACTATTAGCTTTAAGTAGAATAGTGGAGAGAGGCGTAGGGGCTGGT
TGGACTTTATACCCTCCTCTATCTTCTTCTATAGGCCACAGAGGTTCTGCTGTTGATGTTGCTATTTTTTCTTTACATTTAGCA
GGTGTTTCTTCTATTTTAGGAGCTATTAATTTTATAACTACTATTTTAAATATACGAAGAAGAGGGTTTAAAATATTTTATAT
AAGTCTATTTGTTTGAGCTGTTTTTATCACAGCTATTTTGTTACTATTATCGTTACCTGTATTAGCAGGGGGGATTACTATAC
TTTTATTAGATCGGAATTTAAACACTTCTTTTTTTAACCCTATGGGAGGAGGGGATCCTGTTTTATACCAACATTTGTTT

Hap_4
TACTCTTTATTTTTTTTTAGGTCTTTGAAGAGGTTTAGTAGGTACGTCTATAAGTACTATTATTCGTATAGAATTAAGAACTA
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ACCTATTATAATTGGGGGGTTTGGTAATTGACTTGTTCCTTTAATGTTAGGGAGTGTAGATATAGCTTTTCCTCGTATAAAT
AACATAAGGTTTTGATTATTAGTTCCTTCTTTTATACTATTAGCTTTAAGTAGAATAGTGGAGAGAGGCGTAGGAGCTGGT
TGGACTTTATACCCTCCTCTATCTTCTTCTATAGGCCACAGAGGTTCTGCTGTTGATGTTGCTATTTTTTCTTTACATTTAGCA
GGTGTTTCTTCTATTTTAGGAGCTATTAATTTTATAACTACTATTTTAAATATACGAAGAAGAGGGTTTAAAATATTTTATAT
AAGTCTATTTGTTTGAGCTGTTTTTATCACAGCTATTTTGTTACTATTATCGTTACCTGTATTAGCAGGGGGGATTACTATAC
TTTTATTAGATCGGAATTTAAACACTTCTTTTTTTAACCCTATGGGAGGAGGGGATCCTGTTTTATACCAACATTTGTTT

Hap_5
TACTCTTTATTTTTTTTTAGGTCTTTGAAGAGGTTTAGTAGGTACGTCTATAAGTACTATTATTCGTATAGAATTAAGAACTA
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ACCTATTATAATTGGGGGGTTTGGTAATTGACTTGTTCCTTTAATGTTAGGGAGGGTAGATATAGCTTTTCCTCGTATAAAT
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TGGACTTTATACCCTCCTCTATCTTCTTCTATAGGCCACAGAGGTTCTGCTGTTGATGTTGCTATTTTTTCTTTACATTTAGCA
GGTGTTTCTTCTATTTTAGGAGCTATTAATTTTATAACTACTATTTTAAATATACGAAGAAGAGGGTTTAAAATATTTTATAT
AAGTCTATTTGTTTGAGCTGTTTTTATCACAGCTATTTTGTTACTATTATCGTTACCTGTATTAGCAGGGGGGATTACTATAC
TTTTATTAGATCGGAATTTAAACACTTCTTTTTTTAACCCTATGGGAGGAGGGGATCCTGTTTTATACCAACATTTGTTT

Hap_6
TACTCTTTATTTTTTTTTAGGTCTTTGAAGAGGTTTAGTAGGTACGTCTATAAGTACTATTATTCGTATAGAATTAAGAACTA
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ACCTATTATAATTGGGGGGTTTGGTAATTGACTTGTTCCTTTAATGTTAGGGAGTGTAGATATAGCTTTTCCTCGTATAAAT
AACATAAGGTTTTGATTATTAGTTCCTTCTTTTATACTATTAGCTTTAAGTAGAATAGTGGAGAGAGGCGTAGGGGCTGGT
TGGACTTTATACCCTCCTCTATCTTCTTCTATAGGCCATAGAGGTTCTGCTGTTGATGTTGCTATTTTTTCTTTACATTTAGCA
GGTGTTTCTTCTATTTTAGGAGCTATTAATTTTATAACTACTATTTTAAATATACGAAGAAGAGGGTTTAAAATATTTTATAT

AAGTCTATTTGTTTGAGCTGTTTTTATCACAGCTATTTTGTTACTATTATCGTTACCTGTATTAGCAGGGGGGATTACTATAC
TTTTATTAGATCGGAATTTAAACACTTCTTTTTTTAACCCTATGGGAGGAGGGGATCCTGTTTTATACCAACATTTGTTT

Hap_7

TACTCTTTATTTTTTTTTAGGTCTTTGAAGAGGTTTAGTAGGTACGTCTATAAGTACTATTATTCGTATAGAATTAAGAACTA
AAGGTTCTTTATTAGGAGATGATCAGATTTATAATGTTATAGTGACAGGGCACGCTTTTATTATAATTTTTTTTATAGTTAT
ACCTATTATAATTGGGGGGTTTGGTAATTGACTTGTTCCTTTAATGTTAGGGAGTGTAGATATAGCTTTTCCTCGTATAAAT
AACATAAGGTTTTGATTATTATTTCCTTCTTTTATACTATTAGCTTTAAGTAGAATAGTGGAGAGAGGCGTAGGGGCTGGT
TGGACTTTATACCCTCCTCTATCTTCTTCTATAGGCCACAGAGGTTCTGCTGTTGATGTTGCTATTTTTTCTTTACATTTAGCA
GGTGTTTCTTCTATTTTAGGAGCTATTAATTTTATAACTACTATTTTAAATATACGAAGAAGAGGGTTTAAAATATTTTATAT
AAGTCTATTTGTTTGAGCTGTTTTTATCACAGCTATTTTGTTACTATTATCGTTACCTGTATTAGCAGGGGGGATTACTATAC
TTTTATTAGATCGGAATTTAAACACTTCTTTTTTTAACCCTATGGGAGGAGGGGATCCTGTTTTATACCAACATTTGTTT

Hap_8

TACTCTTTATTTTTTTTTAGGTCTTTGAAGAGGTTTAGTAGGTACTTCTATAAGTACTATTATTCGTATAGAATTAAGAACTA
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Hap_9

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Hap_10

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Hap_11

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Hap_12

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Hap_13
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Hap_14
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Hap_15
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Hap_16
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3. List of identified Haplotypes: *T. abyssorum*, where Hap = Haplotype and number indicates the unique haplotype

Hap_1
TACTCTTTATTTTTTTTTAGGGGTATGGAGGGGGTTAGTGGGTACGTCTATAAGCACTATTATCCGTATGGAGTTGAGGAC
TAAGGGTTCTTTATTAGGAGATGATCAGGTCTATAATGTCATAGTGACAGGTCACGCTTTTATTATAATTTTTTTTATAGTA
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Hap_2
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Hap_3
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Hap_4
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Hap_5
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Hap_6
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Hap_7

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TTT

Hap_8

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Hap_9

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Hap_10

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Hap_11

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Hap_12
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Hap_13
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Hap_14
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Hap_15
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Hap_16
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Hap_17
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Hap_18

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Hap_22

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Hap_23

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Hap_41

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Hap_42

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Hap_43

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Hap_44

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Hap_45

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Hap_46
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Hap_47
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Hap_48
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Hap_49
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Hap_50
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Hap_52
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Hap_53
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Hap_54
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Hap_55
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Hap_56
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Hap_57
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Hap_58
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Hap_59
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Hap_60
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Hap_61
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Hap_62
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Hap_63
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Hap_64
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Hap_65
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Hap_86

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Hap_87

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Hap_88

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Hap_89

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Hap_90

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Hap_91

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Hap_92

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Hap_93

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Hap_94

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Hap_95

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Hap_96

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Hap_97
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Hap_98
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Hap_103

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Hap_104

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Hap_105

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Hap_106

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Hap_107

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Hap_108

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Hap_110
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Hap_111
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Hap_113
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Hap_114
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T

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TACCCTTTATTTTTTTTTAGGGGTATGGAGGGGGTTAGTGGGTACGTCTATAAGCACTATTATCCGTATGGAGTTGAGGAC
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TTT