Title: Increased clonality, decreased allele diversity and high genetic structure in tetraploid sea anemone *Aulactinia stella* populations from North Pacific to Atlantic across the Arctic Ocean

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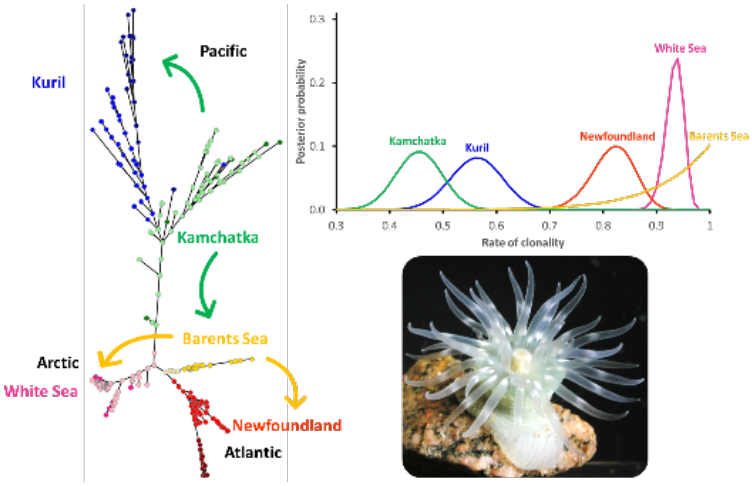

Graphical Abstract (photo: Ekaterina Bocharova)

Abstract

Reproductive modes, migration, genetic diversity and local adaptation are important evolutionary traits that limit species' ranges. Understanding the interactions between evolutionary and ecological processes at species' edges provides clues to how species adapt to rapid environmental changes. In the Arctic Ocean, melting sea ice and increasing human activity are bridging coastal populations that were once separated by extreme polar conditions. *Aulactinia stella* is a keystone tetraploid circumpolar sea anemone species that is witnessing these changes. Here, we investigated how reproduction and genetic diversity structured in *A. stella* populations and between adults and juveniles sampled across the Arctic Ocean.

Outside Kamchatka, we only found females or individuals without gonads. Genetic indices and changes in genotype frequencies confirmed that this species reproduces partially by parthenogenesis. Populations on the Atlantic side were highly clonal, while those on the Pacific side reproduced more sexually. Allelic diversity was twice as high in Kamchatka and Kuril populations, suggesting North Pacific coasts being the main last glacial refugia of *A. stella*. Patterns of genetic differentiation between site pairs revealed gene flow routes extending from Kamchatka to Atlantic populations. These routes aligned with ocean currents and reduced sea ice, and not with the past maritime exchanges between Atlantic and Pacific Oceans.

Within each population, only a subset of juvenile genetic diversity, mostly of local origin, was represented among established adults, suggesting local adaptation or kin recognition mechanisms promoting endemism. Juveniles showed less genetic differentiation across the Arctic Ocean, possibly indicating that global changes are favoring juvenile dispersal.

Introduction

The way individuals reproduce is the most influential trait in governing genetic diversity and potentially evolutionary response to environmental changes (Duminil et al., 2007; Pierre et al., 2022). Reproductive mode governs the persistence of DNA variations through generations. It has therefore major impacts on the level of genome-wide genetic diversity and its structuration within and among populations (Ellegren & Galtier 2016). Reproductive modes also profoundly affect other biological traits that play important roles for ecological processes, including population growth, dispersal, colonization of new areas and the genetic basis for neo-adaptation (Yu et al., 2016; He et al., 2024).

Clonality is a dominant reproductive mode found in populations colonizing new area, especially when enduring harsh conditions at the edge of their living range (Cadotte et al., 2006; Roiloa, 2019; Franklin et al., 2021). All groups and kingdoms of Eukaryota domain, including most of the species that are essential for ecosystem functions, reproduce using partial clonality (Avise, 2015; Schön et al., 2009; Tibayrenc et al., 2015; Orive & Krueger-Hadfield, 2021). It consists for each parent to produce at least one descendant that is genetically identical to them at all loci in its genome, with the exception of a few somatic mutations and rarer recombinations (De Meeûs et al., 2007; Stoeckel et al., 2021a). In such species, the proportion of descendants produced by clonality, i.e. the rate of clonality, is a key biological factor to understand their genetic and trait evolution (Yu et al., 2016; Becheler et al., 2017). Clonality tends to increase in populations spreading at range margins by enabling pioneers to settle and maintain without mates (Baker & Stebbins, 1965; Liu et al., 2006; Wang et al., 2019). Moreover, clonality allows genotypes that are successful locally to maintain over generations without recombining with less adapted genotypes and hasten population growth (Fouqueau & Roze, 2021; Pierre et al., 2022). It also decreases the loss of allele diversity and of heterozygosity by genetic drift,

especially in small founding populations (Navascues et al., 2010; Stoeckel & Masson, 2014; Reichel et al., 2016; Stoeckel et al., 2021b).

The Arctic Ocean has been previously considered as an insurmountable barrier for sessile and semi-sessile marine species dispersal due to limited access, harsh environmental conditions and inadequate food resources (Chan et al., 2019). Climate change is opening new routes across the Arctic Ocean, linking Pacific and Atlantic biomes (Vermeij & Roopnarine, 2008). The increasing ice melting period during summer may favor the recolonization of multiple species from their Atlantic and Pacific last glacial refugia. Understanding genetic diversity and population structure in such species provide useful insights on ecological and evolutionary processes occurring during range expansion in real and complex conditions (Sax et al., 2007; Moran & Alexender, 2014; Bridle & Hoffmann, 2022). It also provides a frame of reference to managers and decision makers to identify priorities and mechanisms to mitigate adverse effects of global changes on intraspecific diversity and to control future invasive populations (Chan et al., 2019).

Sea anemones are sessile and semi-sessile organisms reproducing using partial clonality (Bocharova & Kozevich, 2011; Bocharova, 2016). *Aulactinia stella* (Cnidaria, Anthozoa) is an intertidal and sublittoral species belonging to Actiniidae family. It was first observed and described on the eastern coast of the USA in the 19th century (Verrill, 1864), probably in the southernmost part of its distribution area. Its geographic range is rather circumpolar, along the coasts of the Arctic Ocean and of the northern parts of Atlantic and Pacific Oceans (Grebelnyi, 1980; Sanamyan & Sanamyan, 1998, 2006). *A. stella* mainly live fixed to rocky ground, even if it can occasionally be found buried in sandy or muddy soils or hidden in crevices (Bocharova, 2012). In the benthic communities, during its larval stage, *A. stella* feed predating smaller mollusks, crustaceans, fish larvae and other animals (Bocharova, 2012). First studies of *Aulactinia stella* populations in the Arctic Ocean, on the Murman Coast, were carried on about

fifty years ago (Loseva, 1974). As many circumpolar marine species, direct observations on how populations reproduce and disperse still remain unrealistic. Inferring its important biological and ecological features using genetic analyses therefore remains the best option to understand such species.

Developmental and histological evidence suggests that this species may reproduce through parthenogenesis (Bocharova, 2012). Preliminary analyses based on a limited number of mitochondrial and ribosomal sequences hypothesized that these populations are likely highly clonal and exhibit strong genetic structuring across the Arctic Ocean despite the region's increasing ice melt over recent decades (Bocharova & Mugue, 2012; Bocharova, 2015). However, while these sequences were suitable for phylogenetic analyses, they lacked the resolution necessary to confirm clonality and accurately assess the genetic structure of *A. stella* populations. The recent development of microsatellite primer pairs now makes it possible to investigate the biology of this circumpolar keystone species more precisely, using approaches based on genetic diversity and its spatial patterns (Bocharova et al., 2018).

In this study, we aimed to confirm the occurrence of clonal reproduction in *A. stella* populations in natural environments. We also sought to quantify the extent and variability of clonal reproduction across the species' range. The low and spatially structured genetic diversity previously observed from a limited number of sequences highlighted the need for a more robust assessment of current genetic structure, using neutral and high-resolution markers. This would also allow us to identify potential pathways of gene flow around the Arctic Ocean.

To investigate clonal reproduction in this species, we analyzed genotypic and genetic indices across five geographically distinct sites spanning the Arctic Ocean, including locations in the northern Atlantic and northern Pacific. A total of 315 individuals, representing two age cohorts, juveniles and adults, were sampled to estimate the contribution of clonal reproduction and its

variation across the species' range. By examining temporal changes in genotypic frequencies within each site, we aimed to infer the prevalence of clonal reproduction.

We hypothesized that clonal reproduction may facilitate the establishment and persistence of populations under harsh polar coastal conditions. Conversely, we also considered that the genetic recombination associated with sexual reproduction may promote the emergence of genotypes better adapted to local environments. Our findings on reproductive modes are interpreted in the context of the specific ecological challenges faced by species expanding into previously unfavorable habitats. In addition, we used the genotyped populations to assess genetic differentiation and coancestry between sampled sites. Sampling across the full distribution range allowed us to pinpoint regions with higher genetic diversity, which may correspond to historical refugia. By comparing genetic differentiation between juveniles and adults, we aimed to identify present-day gene flow and corresponding ongoing dispersal routes.

Although *A. stella* was first described along the North Atlantic coasts, suggesting a possible Atlantic origin, previous limited sequence data instead indicated higher genetic diversity in North Pacific populations. If confirmed, this may suggest a more recent expansion into the North Atlantic via the Arctic Ocean. This expansion could have been facilitated either by increased ice melt in recent decades or through anthropogenic means such as maritime traffic. Under the natural expansion scenario, we would expect a stepping-stone pattern of genetic structure across the Arctic. In contrast, under the anthropogenic dispersal hypothesis, we would expect low genetic differentiation between North Pacific and North Atlantic populations, especially given that the Northern Sea Route has only been regularly used for about thirty years.

Finally, we compared our results with patterns observed in other circumpolar coastal marine species and interpreted them in light of known ecological dynamics and environmental changes in these regions.

Materials and methods

Sample collection

In September 2012, we sampled at the low tide in the littoral zone 23 *Aulactinia stella* in the White Sea Biological Station of Moscow State University (WSBS), Kandalaksha Bay of the White Sea and 30 individuals at Liinkhamari, in the Varanger Fjord of the Barents Sea (see Bocharova 2015). We also sampled using SCUBA diving at 5-18 m depth in the sublittoral zone 29 individuals at the Cape Broyle in the Admirals Cove area, Newfoundland, Canada, in June 2017, 14 individuals in the Avachinsky Bay and Viluchinsky Bay of the Pacific coast of Kamchatka Peninsula in June 2010 and June 2016 and 19 individuals in the intertidal zone of the Matua Island of the Kuril Islands in August 2016.

We checked that the phenotypic and biometric appearance of each individual belonged to *Aulactinia stella* species using descriptions in Loseva (1974), Fautin Dunn et al. (1980), Sanamyan and Sanamyan (2008), Sanamyan et al. (2019, 2020) and WoRMS (Rodríguez et al., 2025). In addition, we used nematocyst identification from tentacles, pharynx, body wall and mesentery (Manuel, 1981), and mitochondrial DNA sequence analysis to confirm the species. To analyze genetic diversity in two successive generations, we purposely genotyped large females and the juveniles they brooded in their gastrovascular cavity.

DNA extraction, mtDNA sequencing and genotyping by microsatellite loci

We extracted the total DNA of each sampled adult and juvenile polyp. For each sample, we desiccated and grinded the sampled tissues. We then used the Wizard SV Genomic DNA Purification System (Promega, USA) following the manufacturer's protocol. Extracted DNA was preserved in 96% ethanol before genotyping.

For mitochondrial gene (12S rRNA, 16S rRNA, cytochrome oxidase III) sequencing, we only used adult samples: 23 individuals from the White Sea, 30 from the Barents Sea, 29 from

165 Newfoundland, 14 from Kamchatka, 19 from the Kuril Islands. We applied the primer sets and
166 methodology thoroughly described for 16S rRNA and COIII (Geller & Walton, 2001) and 12S
167 rRNA mitochondrial fragments (Bocharova 2015). Sequencing was performed by 3500 Genetic
168 Analyzer (Applied Biosystems, USA) using BigDye Terminator v3.1 Cycle Sequencing Kit.
169 The sequences were analyzed by Geneious Prime software. By concatenating these three
170 mtDNA sequences (12S, 16S, COIII), we grouped the samples into haplotypes that were aligned
171 and perfectly matched the five previously described haplotypes (Bocharova, 2015). Including
172 these mitochondrial haplotypes (Pacific 1-5), we used geneHapR (Zhang et al., 2023) package
173 to produce the haplotype network (Figure 2). We then used the extracted nuclear DNA to
174 amplify 41 microsatellites using primer pairs previously developed in Bocharova et. al. (2018)
175 for this species and another sea anemone species of Actiniidae family, *Cribrinopsis*
176 *albopunctata* (Sanamyan & Sanamyan 2006, Sanamyan et al. 2019) with the corresponding
177 PCR conditions. PCR products were visualized in 3500 Genetic Analyzer (Applied Biosystems,
178 USA) using POP7 gel polymer. We analyzed the obtained chromatograms using GenMapper
179 Software (ThermoFisher Scientific, USA). Out of these 41 primer pairs, only ten pairs (Act007,
180 Act011, Act028, Act067, Act173, Act177, Act235, Act238, Act249, Act386,) successfully
181 amplified and were polymorphic in our samples. We then multiplexed the ten microsatellites
182 into four PCR pools using three specific dyes (TAM, ROX, FAM) for visualization: Pool 1)
183 Act007 (FAM), Act011 (TAM); Pool 2) Act238 (FAM), Act249 (TAM), Act173 (ROX); Pool
184 3) Act067 (FAM), Act177 (ROX), Act386 (TAM); Pool 4) Act28 (TAM), Act235 (ROX).
185 To estimate if this marker set was powerful enough to distinguish between individuals, we
186 computed the overall observed unbiased probability of identity in state under panmixia
187 (hereafter overall pidu) and the overall observed unbiased probability of identity in state
188 between sibs (overall pids) as recommended by Waits et al. (2001). To achieve allele dosage
189 within each individual per locus, we used the dose-effect method with some modifications

(Rodzen & May, 2002; Drauch Schreier et al., 2011). In cases of more than 1 allele, dose-effect is counted following the instruction (Figure S1): two alleles of almost the same height were considered as AABB (Figure S1A); One high allele and two low alleles as AABC (Figure S1B); One very high allele and one low allele as AAAB (Figure S1C); Tree alleles of the same height were considered as ABC + null allele (Figure S1D); One high allele and one allele half lower were considered as AAB + null allele (Figure S1E).

Analyses of genetic diversity within spatio-temporal samples

Parents that produce descendants by clonality can result to observe multiple times the same Multi-Locus Genotype (hereafter MLG) among the genotyped samples (Halkett et al., 2005; Arnaud-Haond et al., 2007). However, these repeated MLGs may also come from genetic marker lacking sufficient resolution to disentangle between descendants produced by sexual reproduction, either under panmixia (the lower probability to observe two identical sexual descendants) or between mating sibs (the higher probability to observe two identical sexual descendants). To estimate the power of our marker set to distinguish different individuals and assess the upper and lower bounds for the probability of observing identical MLG drawing a pair of individuals sampled in a same population, we therefore computed the probabilities of identity under panmixia (*pidu*) and considering only sib mating (*pids*; Jacquard, 1968, 1970; Waits et al., 2001) using formula adapted for tetraploid populations implemented in GenAPoPop software (Stoeckel et al., 2024).

To assess the level of genetic diversity within populations and compare between populations, for each age cohort in one site, we reported the sample size (N) and computed the average number of observed alleles $\overline{N}a$ and its variance Var(Na) over the ten microsatellites, the average effective number of alleles $\bar{A}_E$ and its variance Var(A_E), the average gene diversity $\overline{H}_E$ and its

variance Var(H_E), the average observed heterozygosity $\overline{H_O}$ and its variance Var(H_O) and the average value of the inbreeding coefficient $\overline{F_{IS}}$ and its variance Var(F_{IS}) over all loci.

We also computed genotypic indices including the number of unique genotypes (G), the unbiased genotypic richness R (Dorken & Eckert, 2001), the genotypic evenness as Pareto β to assess the potential uneven contribution of some clonal MLGs to the genotypic composition of populations (Arnaud-Haond et al., 2007; Bailleul et al., 2016).

We searched for clonal signatures in genetic diversity by analyzing $\overline{F_{IS}}$ and its variance Var(F_{IS}) and the overall estimate of the linkage disequilibrium ($\bar{r}_d$, Agapow & Burt, 2001) as commonly interpreted using one-shoot samples (Halket et al., 2005; Arnaud-Haond et al., 2020; Stoeckel et al., 2021a). Finally, to assess rates of clonality within spatial sites, we used the Bayesian estimate of rates of clonality using genotype frequency changes between adult and juvenile at the same sample site (ClonEstiMate, Becheler et al., 2017 adapted to autpolyploids in GenAPoPop Stoeckel et al., 2024).

To assess the genetic structure between populations and generations, we computed temporal and spatial ρST (Ronfort et al., 1998) using GenAPoPop, and plotted the unrooted minimum spanning tree between individuals using their pairwise number of shared alleles (identity-in-state) using the classical equal-angle algorithm (Felsenstein, 2004) to picture the coancestry between individuals across populations at our marker set. To assess the dynamics (speed and direction) of genetic diversity along sampling sites, we compared juvenile and adult subpopulations sampled at the same sites and between sites computing the corresponding ρST.

We also used a Discriminant Analysis of Principal Components (DAPC, Jombart et al., 2010) to investigate the genetic structure of our five sites and tens cohorts. We choose to retain 200 principal component eigenvalues. We used a knee locator approach to find the minimal number of clusters best structuring the differentiation between individuals and groups. We verify this

value by increasing and decreasing the number of clusters and checking that we obtained the same groups and distribution of clusters among sites and cohorts.

Statistical analyses

To test if distribution of population genetic indices were significantly different between groups of sites and groups of generations, we used Mann-Whitney test and reported the median values of the two groups ($median_{group1}$ versus $median_{group2}$) in the order they are mentioned, the sum of the rank of the first group (U), the number of measures in each group ($n1=4$ for the cohorts sampled on the Pacific side of the Arctic Ocean and $n2=6$ for the cohorts sampled on the Atlantic side) and the probability value (p) of the hypothesis that the two groups have identical distribution of their genetic indices. To compare ρST between juveniles and adults among pairs of the same sites, we used Wilcoxon signed rank test. We reported the median ρST value of the two groups ($median_{group1}$ versus $median_{group2}$) in the order they are mentioned, the sum of the ranks of the differences above zero (W) and the probability value (p) of the hypothesis that the two age cohorts have identical distribution of ρST.

All these tests were performed using python 3.11 and Scipy.stats 1.13 (Virtanen et al., 2020).

Results

We genotyped 314 individuals of Aulactinia stella sampled on five sites, including a total of 75 adults, ranging from 6 to 21 with a median of 15 adults per site, and a total of 239 juveniles, ranging from 6 to 93 with a median of 49 juveniles per site (Table 1). We found both females and males in the Kamchatka population, but, while we found only females in the Kuril Islands, Newfoundland, the Barents and the White Seas. We then only used the adult females sampled in each site for the following genetic analysis.

262 We found 15 brooding females in White Sea, 21 in Barents Sea, 14 in Newfoundland, 6 in
263 Kamchatka and 19 in Kuril Islands sampled sites. The oral disc diameter of mature females
264 varied from 10 to 45 mm while the overall size of the juveniles released from the gastrovascular
265 cavities of the adults varied from 1 to 4 mm.
266
267 **Gene, allele and genotypic diversities in nuclear microsatellites**
268 We found a maximum of four different alleles for each locus in one individual over all our
269 samples and concluded that *A. stella* must be at least an autotetraploid species. Using our ten
270 microsatellites, the mean numbers of alleles per locus per site and developmental stage ranged
271 from 1.2 to 5.7, with a median of 2.75. The mean effective numbers of alleles per locus per site
272 and developmental stage ranged from 1.19 to 2.53 with a median of 1.69. Over all samples,
273 probability of identities under panmixia was 8.3×10^{-9} and probability of identity between sibs
274 was 4.5×10^{-3}. These low probabilities that two individuals generated by sexual reproduction
275 would result into similar genotypes advocated that the ten microsatellites we used were
276 powerful enough to genetically distinguish between sexual descendants, even resulting from a
277 sib mating (Waits et al. 2001). We thus considered afterward that individuals with identical
278 MLGs were clones (i.e., ramets of a same genet).
279 Over all sites and cohorts, we found 154 unique MLGs and 26 of these MLGs were found
280 repeated in more than one sampled individual, i.e. genets with more than one ramet (Table S1).
281 In Kuril Islands, we genotyped no repeated MLG. In Kamchatka, we found one repeated MLG
282 (genet) including three ramets. In Barents Sea, we found three repeated MLGs, including
283 respectively two, five and thirteen ramets. In White Sea, we found eight repeated MLGs
284 involving two to forty ramets, for a total of 88 ramets. In Newfoundland, we found fourteen
285 repeated MLGs involving two to eleven ramets, for a total of 49 ramets. All ramets of repeated
286 MLGs were exclusively sampled on the same site. In all populations with repeated MLGs,

287 repeated MLGs were found both in adults and in juveniles. Some of these genets were even
288 shared by adults and juveniles, except in the Newfoundland samples.
289 Genetic and genotypic diversities showed contrasted measures between the two sites on the
290 Pacific side (i.e., Kuril and Kamchatka) and the three sites on the Atlantic side of the Arctic
291 Ocean (i.e., Newfoundland, Barents and White Seas, Table 1). The four cohorts sampled in
292 Kuril Islands and in Kamchatka showed nearly twice more average gene diversity, ranging from
293 0.372 to 0.460, than found in the six cohorts sampled in Newfoundland, Barents and White
294 Seas, that ranged from 0.097 to 0.266 (0.427 versus 0.174, U=24, n1=4, n2=6, p=0.009), while
295 they both showed similar standard deviation of gene diversity over all loci (U=15, n1=4, n2=6,
296 p=0.610). Cohorts in the Pacific sites also showed significantly higher mean numbers of alleles
297 per locus (4.9 versus 2.0, U=23.5, n1=4, n2=6, p=0.019) and higher effective number of alleles
298 (2.43 versus 1.43, U=24, n1=4, n2=6, p=0.009).
299 Kamchatka and Kuril samples showed higher genotypic richness measured as R than
300 populations on the Atlantic side (1.00 versus 0.37, U=24, n1=4, n2=6, p=0.009) and higher
301 genotypic evenness measured as Pareto β values (3.64 versus 0.45, U=23.5, n1=4, n2=6,
302 p=0.019). Over all loci, Kamchatka and Kuril samples showed lower probabilities of identity
303 under panmixia ($<10^{-6}$ versus 0.003, U=0, n1=4, n2=6, p=0.009) and between sibs (0.008 versus
304 0.118, U=0, n1=4, n2=6, p=0.009) than found in samples from the Atlantic side.
305
306 **Heterozygosity and deviation from the genotypic proportions expected under Hardy-**
307 **Weinberg hypotheses**
308 We found no difference in observed heterozygosity between cohorts on the Pacific and Atlantic
309 sides (0.241 versus 0.181, U=15, n1=4, n2=6, p=0.61), though variance of observed
310 heterozygosity between loci was nearly two times higher in cohorts on the Atlantic side (0.389
311 versus 0.701, U=1, n1=4, n2=6, p=0.019). Mean Fis over all loci were significantly lower in

Newfoundland, the Barents and the White Seas than in Kamchatka and Kurils (0.406 versus -0.066, U=24, n1=4, n2=6, p=0.009) and even negative in the juvenile cohort of Barents Sea, and in adults and juveniles of White Sea. Variances of Fis values between loci were significantly higher, three to ten times, in cohorts on the Atlantic side (1.08 versus 6.41, U=24, n1=4, n2=6, p=0.009), than found in populations on the Pacific side. Though linkage disequilibrium seemed higher in cohorts on the Atlantic side, they were not significantly different from values measured in cohorts on the Pacific side (0.051versus 0.356, U=5, n1=4, n2=6, p=0.171).

Estimated rates of clonality using temporal genotype frequencies

Credible intervals including 99% of posterior probabilities of rates of clonality estimated from temporal samples were quite sharp, spanning around their peaks on a range of 0.06 to maximum 0.25 (Figure 1). In Kuril Islands, rate of clonality was estimated between 0.47 and 0.65 with a peak at 0.56. In Kamchatka, it ranged between 0.37 to 0.53 with a peak at 0.46; In Barents Sea, between 0.75 and 1.0 with a peak at 1; In White Sea, between 0.9 and 0.96 with a peak at 0.94; In Newfoundland, between 0.74 and 0.89 with a peak at 0.82.

Genetic structure between sites using mitochondrial gene sequences

Using three gene sequences (12S, 16S, COIII), we found that all the 82 adults sampled on the Atlantic side (Newfoundland, the White and the Barents Seas) shared the same mitochondrial haplotype, Pacific-3 (classification according to Bocharova, 2015; GenBank Accession Numbers: 12S: KT310190, 16S: KT310200, COIII: KT310212). On the Pacific side, all the 19 individuals sampled in the Kuril islands belonged to another mitochondrial haplotype, Pacific-1 (GenBank Accession Numbers: 12S: KT310188, 16S: KT310198, COIII: KT310210) while Kamchatka's samples distributed among five mitochondrial haplotypes: eight individuals matching Pacific-1 haplotype; two individuals matching Pacific-2 (GenBank Accession

Numbers: 12S: KT310189, 16S: KT310199, COIII: KT310211); one individual matching Pacific-3; two individuals matching Pacific-4 (GenBank Accession Numbers: 12S: KT310191, 16S: KT310201, COIII: KT310213) and one individual matching Pacific-5 (GenBank Accession Numbers: 12S: KT310192, 16S: KT310202, COIII: KT310214). Pacific samples distributed among all the haplotypes known in this species, with Pacific-1 being the most common haplotype. In contrast, all samples on the Atlantic side matched Pacific-3 haplotype that was also found to be the rarest in Kamchatka (Figure 2).

Genetic structure between sites and cohorts using nuclear microsatellites

Among adults, genetic differentiation between sites ranged from 0.155 to 0.612 while among juveniles, genetic differentiation between sites ranged from 0.105 to 0.530 (Table S2). Within each sampled site, ρST between adults and juveniles ranged from 0.009 to 0.088, therefore between six to eleven times lower than between sites. Between sites, adults were more genetically structured than juveniles (0.366 versus 0.245, W=43, p=0.065; Figures 3, S2). Considering the adults and juveniles together by site, genetic differentiation between sites ranged from 0.096 to 0.521 (Table S2a). Globally, in juveniles, ρST between sites showed very close values and followed ranks of geographical and along-the-coast distances (Table S2b, Figure S2). In contrast, adults of White Sea appeared highly genetically isolated from the other sites, excepted from juveniles in Newfoundland. ρST genetic differentiation hierarchically structured the samples into one Pacific side group and one Atlantic side group then subdivided by sites and then by age cohorts (Table S2b, Figure 3).

This hierarchical genetic structure was congruently supported by the DAPC results (Figure 4). Interestingly, the Bayesian information criteria of the DAPC decreased continuously with the increasing number of clusters, as expected in a spatial stepping-stone model (Figure S3). The minimal number of clusters maximizing the distance between groups was 4. Whatever the

number of clusters, DAPC grouped together individuals of Barents Sea and Newfoundland into one common and compact group, while the other sites each stood for their own genetic groups with couples to handful individuals assigned to other groups. Looking at the genetic structure between cohorts and sites, juveniles from the Kuril Islands shared more genetic diversity with adults from Kamchatka than the inverse (Figure 2). Adults of Barents Sea shared more similar genetic diversity with juveniles of Newfoundland and of White Sea than the inverse. DAPC proportion of each individual assigned to one DAPC cluster also supported this dynamic tendency (Figure 4): one descendant sampled in Kuril was assigned to Kamchatka genetic cluster; Three adults sampled in Kamchatka were assigned to Barents-Newfoundland genetic cluster and one adult sampled in Barents Sea was assigned to Kamchatka genetic cluster; Four adults sampled in Barents Sea were assigned to white sea genetic cluster, and one adult and ten descendants sampled in White Sea were assigned to Barents-Newfoundland genetic cluster.

Similarly, the minimum spanning tree of pairwise genetic distances between individuals showed two main groups, one including Kurils and Kamchatka (Pacific side group), and one including Newfoundland, Barents and White Seas (Atlantic side group, Figure 5). Atlantic side group showed more compact genetic distances between individuals than found in the Pacific side group. Atlantic side group also showed more rosary and chaplet subgraphs, commonly observed in clonal lineages (Stoeckel et al., 2024). In accordance with ρST, juveniles were more centrally connected in this network and less genetically distant to the other populations than the adults within each site.

Discussion

We report here the analyses of genetic diversity, genetic differentiation and reproductive mode of five populations of the autotetraploid sea anemone, *Aulactinia stella*, living on North Pacific, Arctic and North Atlantic coasts, at three mitochondrial sequences and ten nuclear

387 microsatellites. *A. stella* is commonly distributed in the north hemisphere and play a significant
388 role in shallow-water communities as a sessile predator for smaller animals while feeding larger
389 predators such as nudibranchs, fish and crabs (Ottaway, 1977). We sampled, genotyped and
390 analyzed two successive age cohorts within the five sampled sites to assess reproductive modes
391 in these sites, and to analyze their genetic diversity and its geographical structure across the
392 Arctic Ocean. By comparing changes in genetic differentiation between adults and juveniles,
393 we also assessed the potential routes of ongoing gene flow among these sites. The ten nuclear
394 microsatellites we used provided sufficient statistical power to disentangle between individuals,
395 enabling differentiating clones of a same genet from inbred offspring.
396
397 ***Aulactinia stella* spreading across the Arctic Ocean from north Pacific?**
398 *A. stella* presented a genetic pattern typical of one main source population expanding into new
399 areas (He et al., 2024). Allelic diversity was nearly twice as high in North Pacific populations
400 compared to those on the Atlantic side of the Arctic Ocean. Pairwise genetic distances revealed
401 more recent and compact coancestry among individuals from Newfoundland, the Barents Sea,
402 and the White Sea, in contrast to the more diverse and divergent genetic profiles observed in
403 populations from the Kuril Islands and Kamchatka. Consistently, mitochondrial sequences
404 showed the highest haplotype diversity in Kamchatka. Notably, all individuals from Atlantic
405 populations belonged to the Pacific-3 haplotype, one of the least common haplotypes in Pacific
406 populations. In the Kuril Islands, only one haplotype, Pacific-1, was identified, which was also
407 the most prevalent among Kamchatka individuals. This pattern of allelic and haplotype
408 diversity suggests that *A. stella* is likely native to the North Pacific, particularly the Kamchatka
409 region, or that the Kamchatka coast served as one of its last glacial refugia. In contrast,
410 populations on the Atlantic side of the Arctic Ocean may have been established more recently
411 or may have originated from smaller, more localized glacial refugia.

412 Genetic differentiation in *A. stella* revealed a hierarchical structure: first separating into a
413 Pacific and an Atlantic group, each of which was further subdivided by sampling site, and then
414 by age cohort. This type of structure closely resembles patterns seen in the intertidal macroalga
415 *Fucus distichus* and in other Arctic and peri-Arctic sessile coastal marine species (Coyer et al.,
416 2011; Bringloe et al., 2020). Environmental factors, rather than species-specific biological or
417 behavioral traits, may likely be the primary drivers of genetic differentiation in this region.
418 When comparing genetic diversity between adults and juveniles, juveniles were less genetically
419 structured, indicating ongoing gene flow across the Arctic Ocean following a stepping-stone
420 model of dispersal. Pairwise ρST between sites and age cohorts, and DAPC indicated that
421 genetic diversity from adult populations in Kamchatka seemed to flow into juvenile populations
422 in the Kuril Islands and in the Barents Sea. Then, genetic diversity found in Barents Sea adults
423 seemed to extend into juvenile populations in Newfoundland and the White Sea. These
424 dynamics may point the expansion route of *A. stella* over recent centuries from North Pacific
425 towards Atlantic coasts. Interestingly, these dispersal routes align with i). the coastal oceanic
426 currents, i.e., the Anadyr current going from the North Pacific into the Arctic Ocean, then the
427 Beaufort gyre and the transpolar drift, which split into the Baffin current to Newfoundland and
428 into the Persey current to the Barents Sea relayed by the Murman coastal current to the White
429 Sea (Rudels & Carmack, 2022; Timmermans & Marshall, 2020), ii). routes of lower ice
430 concentration along a year (Constantine & Johnson, 2023) and iii). direct and along-coasts
431 geographic distances.
432 Additionally, we may conjecture that *A. stella* may benefit from increasing maritime traffic
433 across the Arctic. This could occur either through active transport in ballast water from cargo
434 ships, fishing vessels, and tankers using the Northern Sea Route and the Northeast Passage on
435 the Asian side, or the Northwest Passage on the American side (PAME, 2024; Melia et al., 2016;
436 Boylan, 2021); or through passive dispersal, with ship wake currents enhancing the dispersal

437 of gametes and juveniles along these routes. Our results about *A. stella* foresee on the potential
438 role of increasing Arctic maritime traffic in accelerating the spread of marine organisms
439 between the North Pacific and North Atlantic, with important implications for Arctic
440 biodiversity and ecosystem dynamics.
441
442 **Reproductive modes in *Aulactinia stella* populations**
443 We found strong genetic evidence that *A. stella* reproduced clonally in natural populations.
444 These results were consistent with the absence of males in some populations despite the
445 presence of juveniles and with previous developmental observations showing that some
446 embryos can develop from unfertilized eggs within the mesenteries of parental sea anemones
447 and be released at the mid-gastrula stage (Bocharova, 2012; 2015; Kaliszewicz et al., 2012).
448 This genetic evidence, together with the absence of males in some populations despite the
449 observation of juveniles argued that clonality may commonly occur in this species, probably
450 via ameiotic parthenogenesis. We therefore assessed the quantitative significance of clonality
451 within populations.
452 In the North Pacific populations, we identified only one trio of individuals with an identical
453 MLG in Kamchatka and none in Kuril Islands. Yet, genetic indices, including interlocus F_{IS}
454 variances measured around 1 and low levels of linkage disequilibrium, indicated that these
455 populations reproduce with intermediate rates of clonality (Navascues et al., 2010; Stoeckel et
456 al., 2021a). Using changes in genotype frequencies between adults and juveniles, maximum
457 posterior probabilities and their associated 99% credible intervals estimated rates of clonality
458 between 0.37 and 0.65 in these North Pacific populations. The absence of repeated genotypes,
459 despite intermediate clonality, is common in samples from large populations or when clonal
460 offspring are spatially dispersed before settling as adults. This results in high clonal evenness

461 and reduces the likelihood of sampling identical genotypes (Arnaud-Haond et al., 2007;
462 Stoeckel et al., 2021a,b; 2024).
463 In contrast, populations from Newfoundland, the Barents Sea, and the White Sea, which are
464 likely to be more recently established due to their lower allelic diversity, showed strong signals
465 of clonal reproduction. All individuals sampled shared the same mitochondrial haplotype
466 (Pacific-3) and many shared identical nuclear MLGs, despite the low probability of such
467 identity by sexual reproduction, even between siblings, given the resolution of our
468 microsatellite markers. Mean negative F_{IS}, large variance of F_{IS} between loci and significant
469 linkage disequilibrium also indicated high rates of clonality (Halkett et al., 2005; De Meeûs et
470 al., 2006; Navascues et al., 2010; Stoeckel et al., 2021a). Estimated clonality rates in these
471 populations ranged from 0.74 to 1.0, nearly double the rates found in North Pacific populations.
472

473 **The advantages of clonal reproduction at the limits of species' ranges**

474 High levels of uniparental reproduction, including clonality, are commonly observed in species
475 expanding into new or marginal environments (Barrett, 2015; Pannel et al., 2015; Burke &
476 Bonduriansky, 2019, Pereyra et al., 2023), particularly when enduring harsh conditions (Klimeš
477 2008). The post-glacial Baltic sea provides several examples, including the emblematic case of
478 *Fucus vesiculosus* (Johannesson & André 2006; Pereyra et al., 2009; 2023). In plant species,
479 the persistence of connection between ramets (mainly by roots) offers ecological advantages
480 that may alone explain the prevalence of clonality at range margins, including regeneration after
481 injury, distribution of physiological functions among ramets, translocation of resources between
482 interconnected ramets (clonal integration) and space monopolization using different strategies
483 (including phalanx versus guerrilla) to address intra- and inter-specific competitions depending
484 on the environmental context (Cadotte et al., 2006; Gonzalvez et al., 2008; Roiloa, 2019;
485 Franklin et al., 2021).

486 In contrast, dispersed clones in marine species such as *A. stella* do not benefit from such clonal
487 integration. In this context, clonality should only favor kin cooperation (e.g., through brooding
488 or cooperative behavior Bocharova, 2012; Rudin & Briffa, 2012) but more importantly it should
489 favor the persistence of local populations under harsh conditions by avoiding the energetic and
490 biological costs of sexual reproduction (Klimeš, 2008; Pierre et al., 2022).
491 Baker (1955) postulated that uniparental reproduction (including clonality) provides a critical
492 advantage for colonization: individuals arriving in new areas can reproduce clonally to establish
493 a new area. First, clonality allows a population to maintain itself locally until compatible mates
494 become available (Baker & Stebbins, 1965, Daly et al., 2023). This hypothesis is particularly
495 relevant for gonochoristic (or dioecious) sessile organisms that require close proximity for
496 successful sexual reproduction (Barrett, 2015), such as in sea anemones. Second, in new harsh
497 environments, the more clonal individuals that manage to survive minimize the risks of genetic
498 reassortment associated with sexual reproduction for their offspring (Peniston et al., 2021;
499 Pierre et al., 2022). Third, clonality maintains higher effective population sizes than in identical
500 more sexual populations (Reichel et al. 2016; Stoeckel et al., 2021b). Clonality limits the
501 negative effects of genetic drift during founder events, including the fixation of deleterious
502 alleles in small populations (Navascues et al., 2010; He et al., 2024).
503 Our results in *A. stella*, which showed a twofold increase in clonality at the species' range edge,
504 highlight the key role of clonal reproduction in maintaining populations and higher effective
505 population size under unfavorable conditions while expanding into new areas (Baker's
506 conjecture, Pannel et al., 2015) without invoking for the benefits of clonal integration (as
507 proposed in plants) or habitat modification (as proposed in ecological engineering species) as
508 drivers of clonal success.
509
510 **Restricted dispersal or local adaptation in *Aulactinia stella*?**

Interestingly, we found no MLGs shared between sampling sites, even those in close geographic proximity, such as Barents and White Seas sampling sites (~360 kilometers), and the Kuril Islands and Kamchatka coasts (~680 kilometers). The presence of local, site-specific clones and high levels of genetic differentiation between populations appears to be a common feature of several cold-water sea anemone species. These include *Actinia tenebrosa* in New Zealand (Veale & Lavery, 2012) and on the Australia and Tasmania coasts (Sherman et al., 2007; Sherman & Ayre, 2008), *Anthothoe albocincta* on the south-eastern Australia coast (Billingham & Ayre, 1996), *Diadumene lineata* in the North Atlantic (Ryan et al., 2021), and the North Pacific species *Anthopleura elegantissima*, *Epiactis prolifera*, *Epiactis lisbethae* and *Epiactis ritteri* (Edmands & Potts, 1997) *Haliplanella lucia* (Shick & Lamb, 1977). This pattern of high genetic differentiation contrasts with tropical sea anemones, such as *Actinia bermudensis*, *Bunodosoma caissarum*, *Entacmaea quadricolor*, *Heteractis magnifica* and *Stichodactyla mertensii* which typically show much lower levels of genetic structure and often share genets across sites separated by hundreds of kilometers apart (Russo et al., 1994; Emms et al., 2020; but see Li et al., 2024 for *Paracondylactis sinensis*). These observations may support the hypothesis that the Arctic marine environments may have constrained and challenged the dispersal of sea anemones (Chan et al., 2019). However, other passively dispersing organisms in similar cold-water habitats, such as macroalgae, seagrasses, and bivalves, generally show much less population structure and often share genets between sites (Coolen et al., 2020; Pereyra et al., 2023; Krueger-Hadfield et al., 2021). In addition, juvenile sea anemones are capable of active movement in the direction of marine currents, enabling long-distance dispersal (Riemann-Zürneck, 1998). *Urticina eques*, another cold-water sea anemone, shows very low genetic differentiation beween populations distributed over hundreds of kilometers along the British coast (Cava-Solé et al., 1994).

535 In the case of *A. stella*, we found lower genetic differentiation between sites in juveniles and
536 pairwise genetic distances were more compact in juveniles than in adults. The DAPC results
537 supported a stepping-stone genetic structure. These results suggest that the lack of shared MLGs
538 between sites and the observed genetic structure may be better explained by local genetic
539 endemism or gregarious reproductive behavior promoting shared ancestry, rather than by
540 persistent founder effects or a complete lack of gene flow (Lane et al., 2020; Ryan et al., 2021).
541 We rather observed *A. stella* occupying diverse habitats across sampling sites. For example,
542 although the Barents and White Seas are separated by only about 100 km, the White Sea is
543 characterized by significantly lower salinity. In marine environments, factors such as water
544 temperature, depth, tidal exposure, and substrate disturbance are known to influence both
545 reproductive strategies and levels of genetic differentiation (Eriksson and Johansson 2005;
546 Krueger-Hadfield et al., 2013; Berković et al., 2014; Dudgeon et al., 2016; McMahon et al.,
547 2017; Ryan & Miller, 2019; Ryan et al., 2021; Williams et al., 2024). Similar to *A. stella*, *Actinia*
548 *tenebrosa*, a partially clonal brooding sea anemone, localized clonal distributions and endemic
549 genetic lineages have been linked to specific habitat characteristics, such as atmospheric
550 exposure, temperature, salinity, UV radiation, and local community composition, despite its
551 potential for wider dispersal (Sherman & Ayre, 2008). *Diadumene lineata* also reproduces with
552 various different rates of clonality depending on water temperature and shows similar
553 geographic genetic differentiation, particularly between northern and southern Atlantic
554 populations (Ryan et al., 2021).
555 In the case of *A. stella*, Arctic populations may have only narrow temporal windows of suitable
556 thermal conditions for successful sexual reproduction, particularly in the intertidal and shallow
557 sublittoral zones. These habitats are also characterized by extreme variability in salinity and
558 desiccation at low tide. In such habitats, *A. stella* is often found hiding under *Fucus* algae, in
559 rock crevices, or in tide pools, behaviors that indicate exposure to environmental stress. Our

results, showing approximately twice the level of genetic differentiation among adults compared to juveniles, highlight the need for further ecological and behavioral studies. *A. stella* presents a paradoxical tension between its current ability to disperse into new diverse areas and an interesting tendency towards endemism, commonly observed in several other sea anemone species. The spread of *A. stella* to the North Atlantic sites may provide an interesting opportunity to study how endemism can arise in populations colonizing new areas from a common genetic background. Experiments using common gardens and reciprocal transplantations between sites could help to assess the role of local adaptation versus migration in shaping the genetic endemism of *A. stella* and to identify which environmental conditions are most influential for this species. If local adaptation is confirmed, an important question remains: how has *A. stella* successfully colonized such a wide and environmentally diverse range across the Arctic? Experimental studies that expose both clones and sexually-derived offspring to novel habitats over multiple generations may reveal the pace and mechanisms of adaptation in this species as it makes its odyssey through the Arctic Ocean.

Data Availability

MLG genotypes, sample GPS locations and clone sizes are openly available on Zenodo https://doi.org/10.5281/zenodo.15102245

Supplementary Material

Supplementary material provides two tables and three figures. Table S1 reports distributions of repeated MLGs within sites and MLGs shared between adults and juveniles; Table S2 reports pairwise ρST between sites and between age cohorts; Figure S1 reports how allele dosage of the microsatellites was achieved; Figure S2 reports the minimum spanning trees of genetic differentiation of adults, juveniles and overall among sites; Figure S3 reports the change of the

585 Bayesian information criteria of the DAPC with increasing number of genetic clusters arguing
586 for a stepping-stone structure of demes.
587

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601

602 ## Author contributions

603 EB and SS laid the foundation of this work while EB visited SS lab in 2018 and 2019, conceived
604 the study and were responsible for funding applications. EB was responsible for data
605 acquisition. She supervised and achieved sample collection, determined the species and sexed
606 the sampled individuals. She also conceived, developed the sequences and microsatellites,
607 supervised and achieved sequencing and genotyping of all the samples. From sequencing
608 machines, she genotyped the samples. AV contributed to methodology, supervision and

administration of data acquisition. EB performed data analyses and produced figure on mitochondrial sequences. SS performed data analyses and produced tables and figures on microsatellites. SS and EB tracked and managed the bibliography, interpreted results, wrote the manuscript and managed its edition. All authors read and approved this manuscript.

Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

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Tables and Figures

Figure 1: Posterior density probabilities of estimates of rates of clonality using changes of genotype frequencies over one generation for each sampled site using ClonEstiMate method for autopolyploids in GenAPoPop software. Kuril Islands in blue, Kamchatka in green, Newfoundland in red, White Sea in pink and Barents Sea in gold.

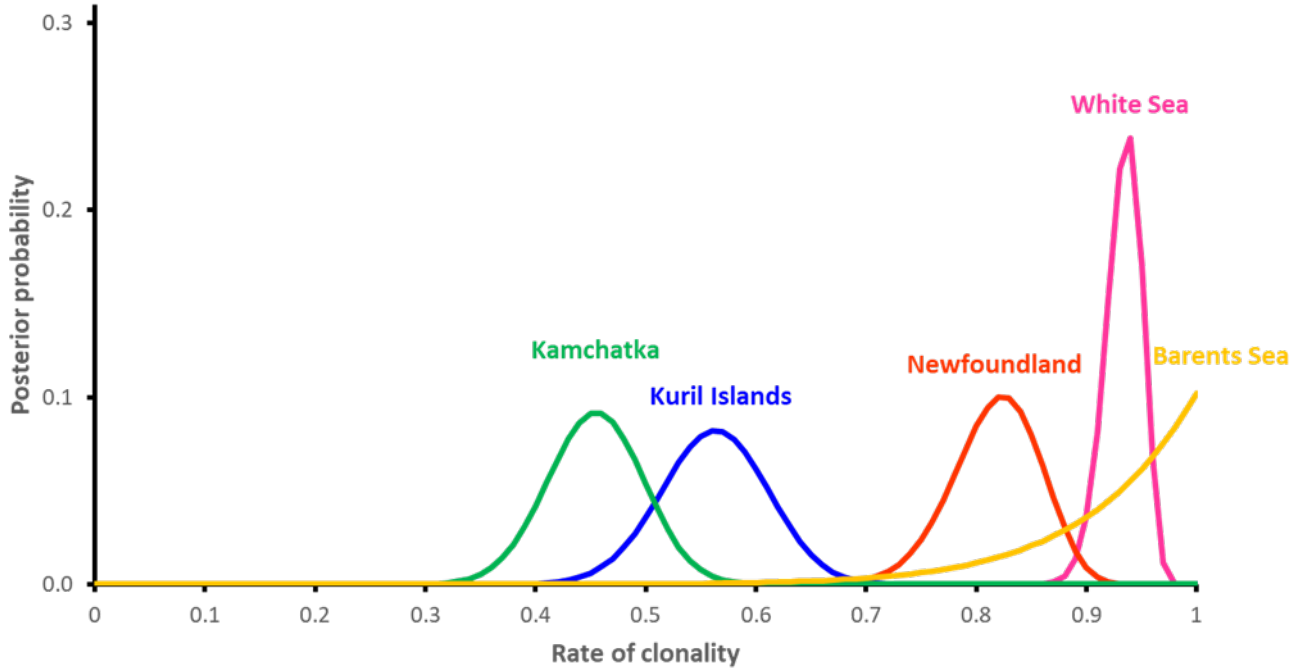


Figure 2: Haplotype network using three gene sequences (12S, 16S, COIII). The proportion of each sampled site per haplotype is represented in color. The circle sizes of each haplotype are proportional to their number in our dataset. We used haplotype names initially identified in Bocharova (2015), thus Pacific 1 to 5. We found no new haplotypes.

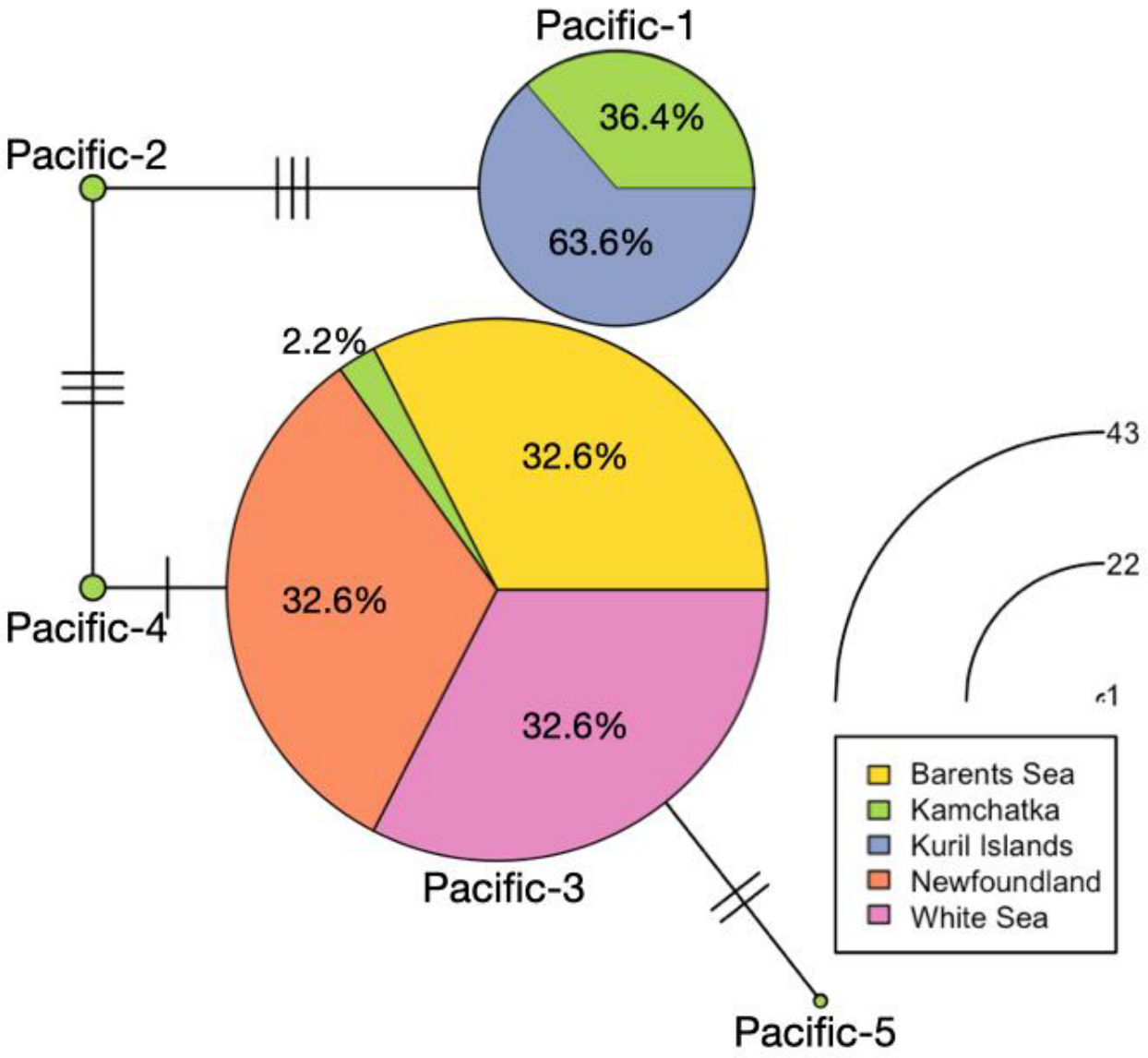


Figure 3: The oriented graph of the ρST values between sites and cohorts (vertices). Orange edges and boxes allow by comparison between pair of sites to understand the dynamics and directions of genetic spreading. Comparisons between blue boxes (adults) and green boxes (juveniles) between pairs of sites to understand the temporal genetic structure between sampled sites.

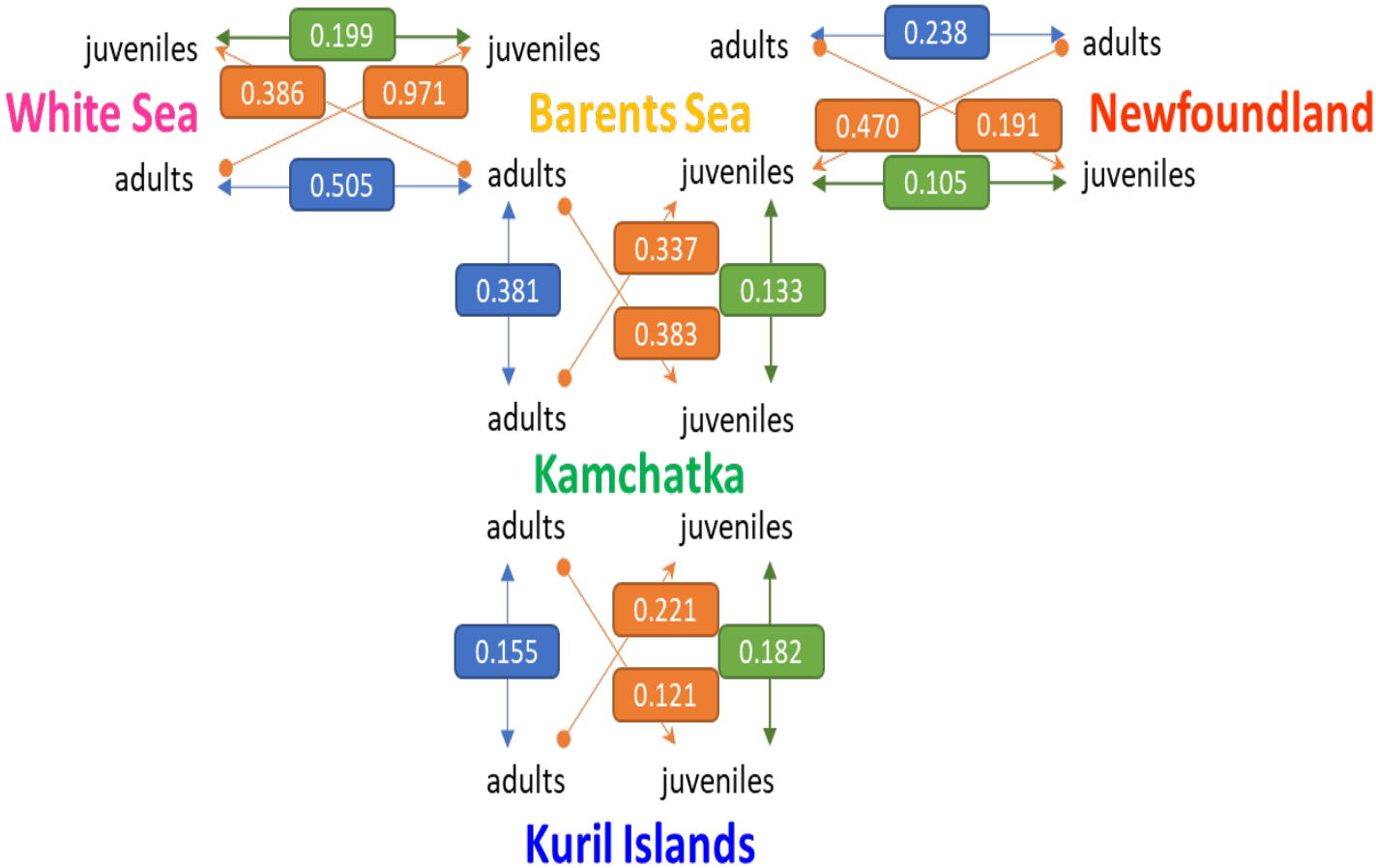


Figure 4: Discriminant Analysis of Principal Components of the genetic structure of *Aulactinia stella* across the Arctic Ocean. We found four clusters being the minimal number of clusters maximizing the distance between groups.

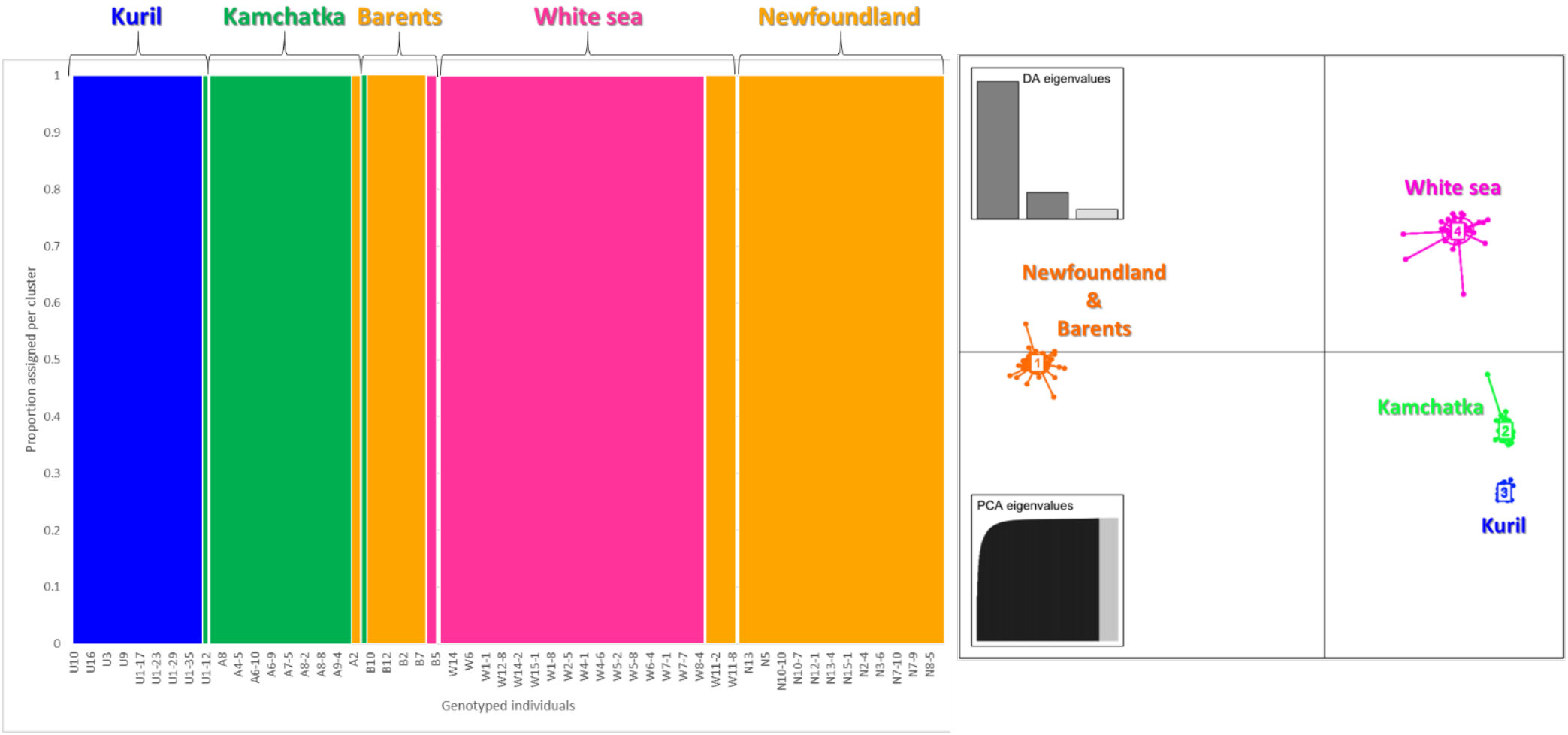
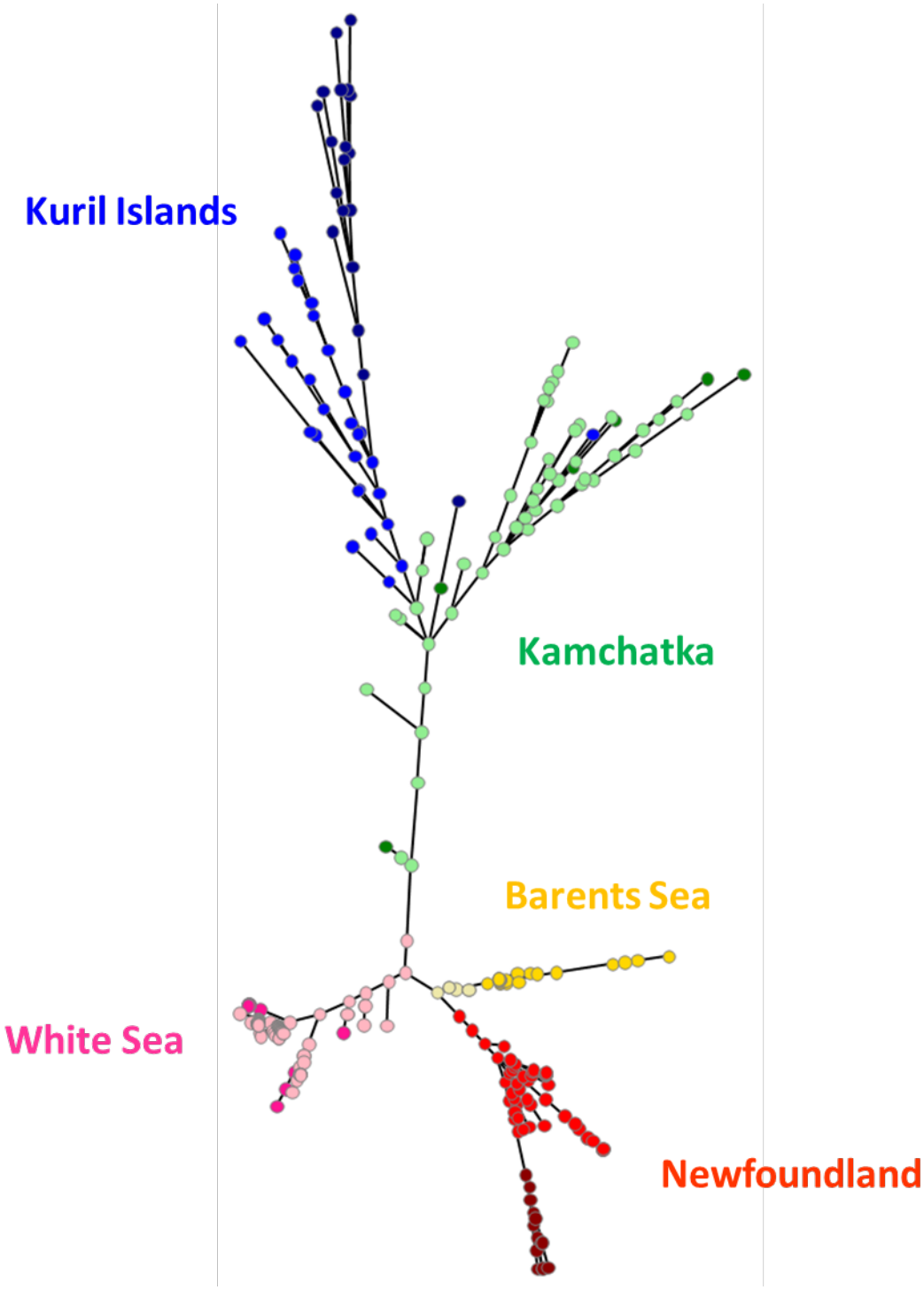


Figure 5: Minimum spanning tree of the genetic differentiation between sampled sites and cohorts of *A.stella* using pairwise ρ_{ST}. Kamchatka adults and juveniles respectively in green and pale green; Kuril adults and juveniles respectively in dark blue and blue; Barents sea adults and juveniles respectively in gold and pale gold colors; White sea adults and juveniles respectively in pink and pale pink; Newfoundland adults and juveniles respectively in dark red and red.



Site	Age cohort	N	G	R	Paretoβ	$\bar{r}_d$	Na	Var(Na)	$\bar{A}_E$	Var(A_E)	$\bar{H}_O$	Var(H_O)	$\bar{H}_E$	Var(H_E)	$\overline{F_{IS}}$	Var(F_{IS})	pidu	pids
	Adults	6	6	1.000	1.807	3.0	30.0	2.2	17.3	17.27	0.294	0.488	0.416	0.590	0.292	1.635	1.4E-06	0.010
Kamchatka	**Juveniles**	49	48	0.979	4.615	5.2	151.6	2.4	24.3	24.25	0.314	0.397	0.460	0.534	0.318	1.156	0.0E+00	0.006
	Both	55	53	0.963	2.648	5.4	180.4	2.4	29.1	29.06	0.312	0.397	0.459	0.544	0.321	1.140	0.0E+00	0.006
	Adults	19	19	1.000	3.322	4.6	84.4	2.5	46.9	46.90	0.176	0.121	0.438	0.640	0.598	1.016	0.0E+00	0.006
Kuril Islands	**Juveniles**	30	30	1.000	3.954	5.7	234.1	2.5	53.1	53.09	0.188	0.301	0.372	0.891	0.494	0.948	0.0E+00	0.013
	Both	49	49	1.000	4.644	7.8	315.6	2.7	69.7	69.69	0.184	0.131	0.454	0.580	0.595	0.722	0.0E+00	0.005
	Adults	21	10	0.450	0.302	2.5	14.5	1.4	1.0	0.98	0.197	0.425	0.223	0.287	0.115	3.124	1.8E-03	0.096
Barents Sea	**Juveniles**	6	2	0.200	0.591	1.2	1.6	1.2	1.4	1.42	0.125	0.628	0.097	0.376	-0.290	13.323	1.3E-01	0.364
	Both	27	10	0.346	0.265	2.5	14.5	1.3	1.0	1.00	0.181	0.448	0.198	0.275	0.088	3.357	4.6E-03	0.126
	Adults	14	12	0.846	1.807	2.1	18.9	1.4	6.5	6.47	0.165	0.656	0.170	0.512	0.024	4.971	3.8E-03	0.151
Newfoundland	**Juveniles**	61	28	0.450	0.716	1.8	9.6	1.4	6.6	6.63	0.158	0.747	0.178	0.596	0.112	4.875	5.6E-03	0.140
	Both	75	40	0.527	0.799	2.2	17.6	1.5	6.3	6.35	0.160	0.694	0.210	0.551	0.241	3.604	2.0E-03	0.100
	Adults	15	5	0.286	0.129	1.9	18.9	1.6	7.8	7.81	0.314	1.526	0.238	0.886	-0.322	10.807	8.8E-04	0.069
White Sea	**Juveniles**	93	28	0.293	0.261	3.0	48.0	1.7	8.5	8.53	0.308	1.447	0.266	0.912	-0.157	7.841	1.9E-04	0.048
	Both	108	28	0.252	0.224	3.0	48.0	1.7	8.5	8.47	0.309	1.457	0.264	0.912	-0.171	8.048	2.2E-04	0.049
Over All	**Both**	314	180	0.572	0.482	11.1	468.9	2.1	6.2	6.24	0.243	0.387	0.440	0.454	0.448	0.870	2.0E-07	0.007

Table1: Summary of population genetic indices in ten spatio-temporal populations of *Aulactinia stella*. For each age cohort at one site, are reported the sample size *N*, number of genotypes *G*, genotypic richness *R*, genotypic evenness *Paretoβ*, overall estimate of linkage disequilibrium $\bar{r}_d$, average number of observed alleles *Na* and its variance *Var(Na)* over the ten microsatellites, average effective number of alleles $\bar{A}_E$ and its variance Var(A_E), average observed heterozygosity $\overline{H}_O$ and its variance Var(H_O), average gene diversity $\overline{H}_E$ and its variance Var(H_E), average value of the inbreeding coefficient $\overline{F_{IS}}$ and its variance Var(F_{IS}) over all loci, unbiased probability of identity under panmixia *pidu* and between sibs *pids*.

Supplementary information

Table S1: Distribution of repeated MLGs within sites and MLGs shared between adults and juveniles. Genet ID, the number of ramets within the genet and if the considered genet has been found in adults, juveniles or both are reported. No repeated MLG was found in Kuril islands sampled genotypes.

Site	Genet ID	Number of ramet	In the two cohorts?
Kamchatka	MLG123	3	Both
Barents	MLG32	2	Adults
Barents	MLG54	5	Both
Barents	MLG26	13	Both
Newfoundland	MLG12	2	Adults
Newfoundland	MLG7	2	Juveniles
Newfoundland	MLG37	2	Juveniles
Newfoundland	MLG67	2	Juveniles
Newfoundland	MLG11	2	Adults
Newfoundland	MLG5	2	Juveniles
Newfoundland	MLG19	2	Juveniles
Newfoundland	MLG6	3	Juveniles
Newfoundland	MLG62	3	Juveniles
Newfoundland	MLG52	3	Juveniles
Newfoundland	MLG63	4	Juveniles
Newfoundland	MLG68	4	Juveniles
Newfoundland	MLG53	7	Juveniles
Newfoundland	MLG57	11	Juveniles
White Sea	MLG47	2	Juveniles
White Sea	MLG15	3	Juveniles
White Sea	MLG66	3	Both
White Sea	MLG44	4	Both
White Sea	MLG22	4	Both
White Sea	MLG38	8	Both
White Sea	MLG16	24	Juveniles
White Sea	MLG46	40	Both

Table S2: Pairwise ρST between sites (A) and between age cohorts within sites and among sites (B).

A).

	Barents	Kamchatka	Kuril	Newfoundland	White sea
Barents	#				
Kamchatka	0.411	#			
Kuril	0.364	0.168	#		
Newfoundland	0.096	0.352	0.315	#	
White sea	0.442	0.348	0.521	0.167	#

B).

		Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
		Barents		**Kamchatka**		**Kuril**		**Newfoundland**		**White sea**	
Barents	**Adults**	#									
	Juveniles	0.088	#								
Kamchatka	**Adults**	0.381	0.337	#							
	Juveniles	0.383	0.133	0.014	#						
Kuril	**Adults**	0.361	0.482	0.155	0.221	#					
	Juveniles	0.422	0.290	0.122	0.183	0.103	#				
Newfoundland	**Adults**	0.238	0.470	0.489	0.285	0.312	0.465	#			
	Juveniles	0.191	0.105	0.224	0.290	0.278	0.432	0.054	#		
White sea	**Adults**	0.505	0.971	0.359	0.279	0.371	0.387	0.612	0.058	#	
	Juveniles	0.386	0.199	0.155	0.352	0.459	0.530	0.372	0.118	0.009	#

Figure S1: Counting of allele dosage of the microsatellite locus 249TAM (as an example) in *Aulactinia stella* (within each individual per locus): A). 129, 129, 133, 133 (AABB), B). 129, 129, 137, 141 (AABC), C). 137, 137, 137, 141 (AAAB), D). 129, 133, 137 (ABC+null allele), E). 133, 133, 137 (AAB+null allele).

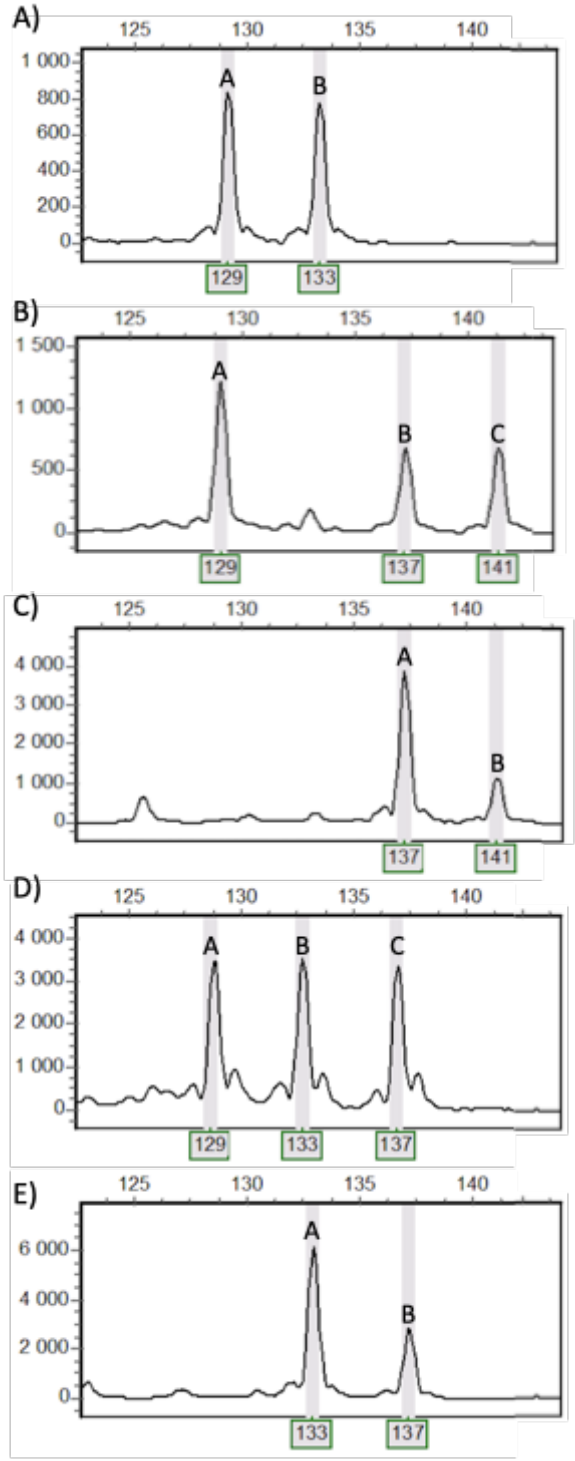
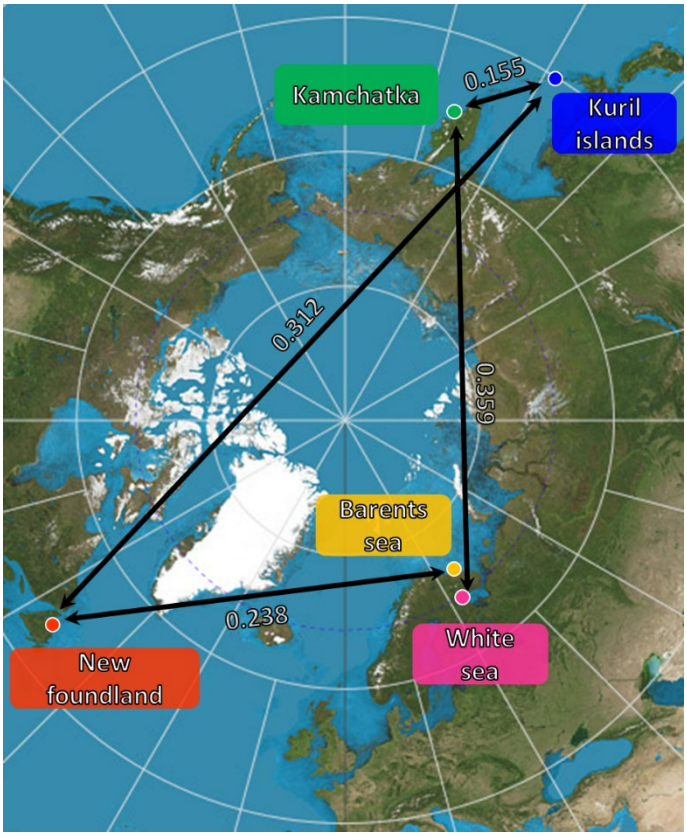
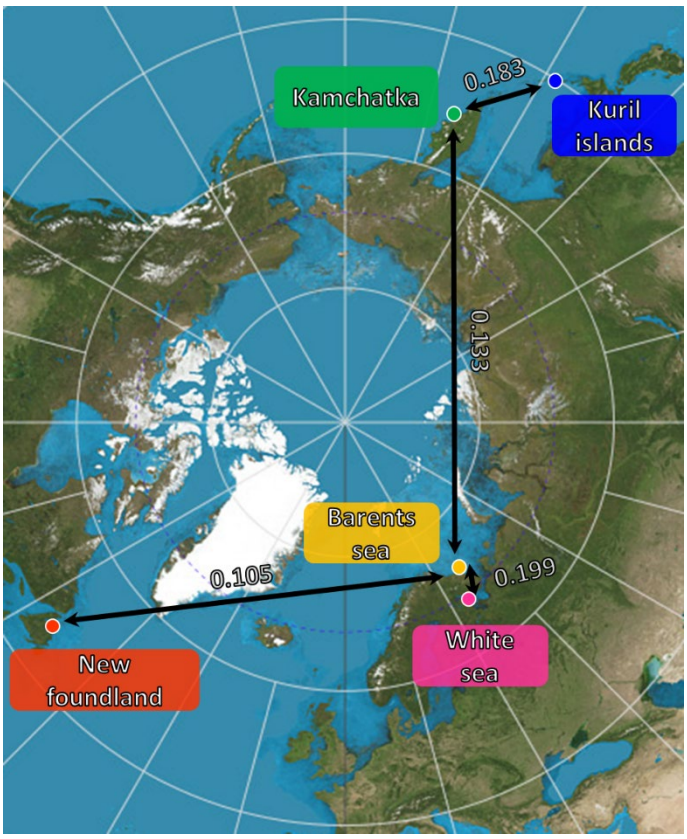


Figure S2: Minimum spanning tree of A). the ρST of adults, B). the ρST of juveniles and C). the ρST of all age cohorts over all loci between sampled sites.

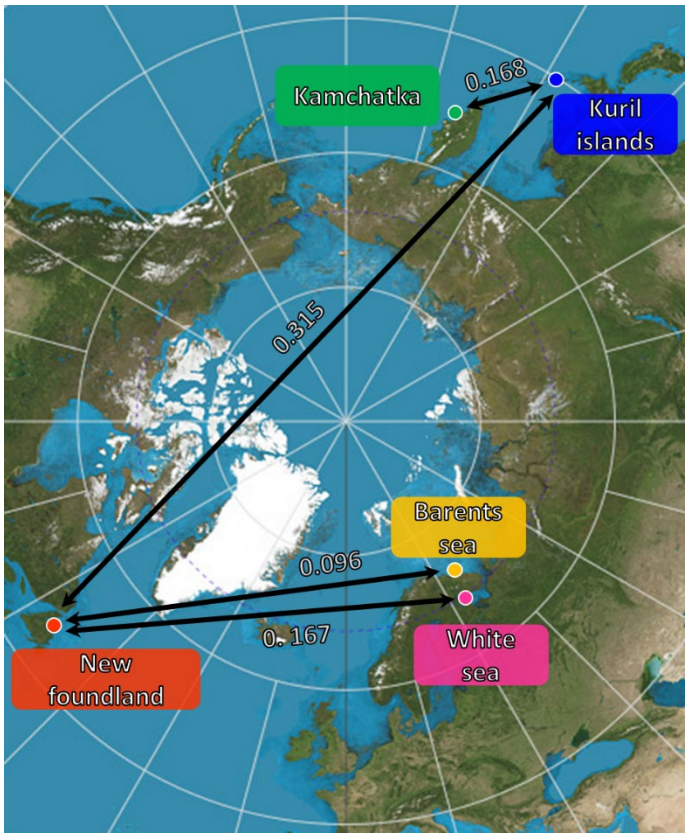
A).



B).



C).


Kamchatka
0.168
Kuril islands
0.315
Barents sea
0.096
0.167
White sea
New foundland

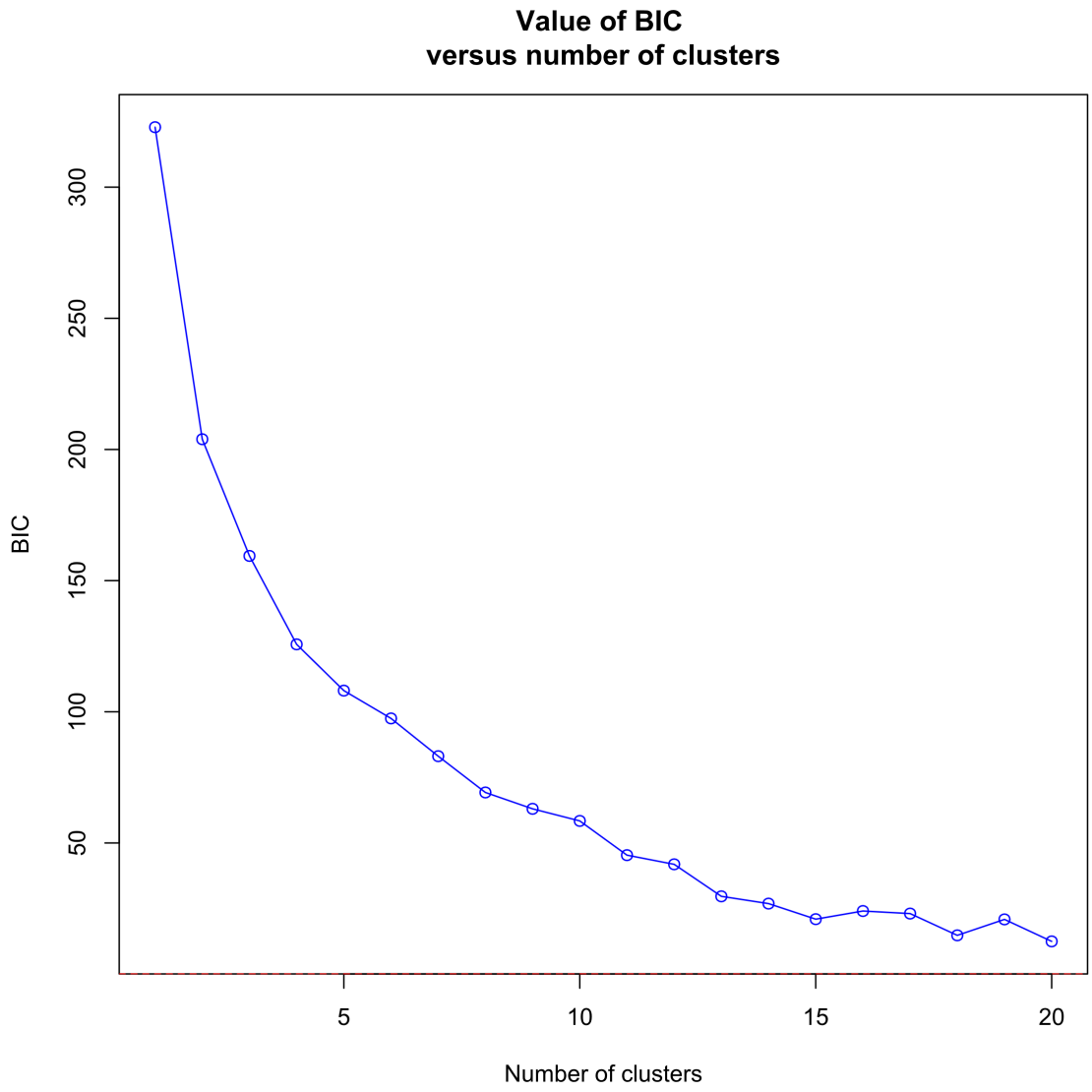



Figure S3: Change of the Bayesian information criteria (BIC) with increasing number of genetic clusters used in the Discriminant Analysis of Principal Components to investigate the genetic differentiation between individuals and among sampled sites and cohorts. The continuously decreasing pattern observed is typical of a stepping-stone structure of the studied demes.