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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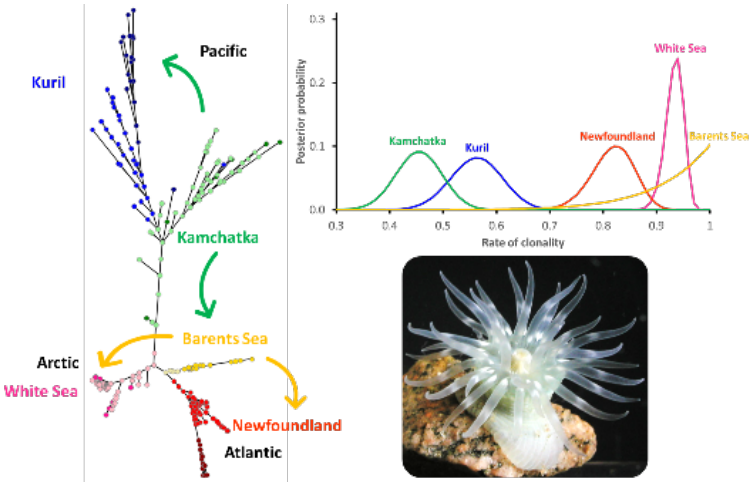

Graphical Abstract (photo: Ekaterina Bocharova)

Abstract

Reproductive mode is a key factor shaping genetic diversity, evolutionary potential, and the processes of dispersal and colonization. Clonality is particularly common in harsh environments and at the margins of species' ranges, where it supports persistence, enables rapid growth, and promotes the maintenance of locally adapted genotypes. In the rapidly changing Arctic, increasing ecological connectivity is eroding historical barriers for sessile species. Evaluating genetic diversity in this context, before global change further alters Arctic ocean, is essential for understanding evolutionary dynamics during range expansion and for informing conservation strategies.

Aulactinia stella is a circumpolar sea anemone with physiological characteristics in laboratory conditions suggesting a potential for clonal reproduction. In this study, we investigated its reproductive modes in natural populations across the Arctic ocean, from the northern Pacific to the Atlantic, and examined how genetic diversity is structured between adults and juveniles at five sampled sites.

Across all study sites, we observed only females or individuals lacking gonads, with the exception of Kamchatka, where males were also present. Genetic indices and changes in genotype frequencies between adults and juveniles confirmed that this species reproduces partially by parthenogenesis. Populations on the Atlantic side were highly clonal with clonal rates (*c*) estimated at 80-99%, whereas populations on the Pacific side reproduced more sexually (c around 50%). Allelic diversity was twice as high in Kamchatka and Kuril populations, suggesting North Pacific coasts being the main last glacial refugia of *A. stella*. We found a stepping-stone pattern of genetic structure from Kamchatka to Atlantic populations, consistent with contemporary ocean currents and melted summer sea ice. Only a subset of the juvenile genetic diversity, mostly of local origin, was found in the established adults, while juveniles exhibited lower levels of genetic differentiation across the Arctic Ocean. Our findings

underscore the need for further ecological and behavioral investigations to elucidate the mechanisms allowing the current possibilities of dispersal of this species across the Arctic Ocean.

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; Burke & Bonduriansky, 2018; Roiloa, 2019; Franklin et al., 2021) and when living further to the north in Northern hemisphere (geographic parthenogenesis; Peck et al., 1998). All groups and kingdoms of Eukaryota domain, including most of the species that are essential for ecosystem functions, have species that reproduce using partial clonality (Avise, 2015; Schön et al., 2009; Tibayrenc et al., 2015; Orive & Krueger-Hadfield, 2021). In this reproductive mode, parents can generate offspring that are genetically identical to themselves at all loci on their genomes, with the exception of rare recombination events and occasional somatic mutations (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 often increases in populations expanding at range margins, as it allows pioneers to establish and persist in the absence of mates (Baker & Stebbins, 1965; Liu et al., 2006; Wang et al., 2019). Moreover, clonality enables locally successful genotypes to persist across generations without recombining with less adapted ones, thereby accelerating 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 northern Pacific and Atlantic biomes (Vermeij & Roopnarine, 2008). The recent acceleration of summer sea-ice loss, now surpassing levels recorded since the Holocene Climatic Optimum (~8,000 years before present, estimated at +0.3 °C relative warming above pre-industrial levels; compared to +1.34 °C in the Arctic in 2024; Laakkonen et al., 2021; E.U. Copernicus Global Climate Highlights, 2024), is likely to facilitate renewed secondary contact between species and populations from the northern Atlantic and Pacific biomes (Brandt et al., 2023). Understanding genetic diversity and population structure in such species provide useful insights into the ecological and evolutionary processes that occur during range expansion under real and complex conditions (Sax et al., 2007; Moran & Alexender, 2014; Bridle & Hoffmann, 2022). It also provides a frame of reference to managers and policymakers to identify priorities and mechanisms for mitigating adverse effects of global changes on intraspecific diversity and for controlling future invasive populations (Chan et al., 2019).

Sea anemones are 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). First studies of *A. stella* populations in the Arctic Ocean, on the

Murman Coast, were carried on about fifty years ago (Loseva, 1974). Adults of *A. stella* mainly live fixed to rocky ground, even if it can occasionally be found buried in sandy or muddy soils, hidden in crevices or fixed to debris (Bocharova, 2012). It feed predating smaller mollusks, crustaceans, fish larvae and other animals (Bocharova, 2012). The population density of *A. stella* ranges from 1 to 18 individuals per square meter in the littoral zone of the White Sea, and from 1 to 14 individuals per square meter along the Barents Sea coasts (Bocharova, 2012). In laboratory conditions, adults can survive for several decades, but their natural lifespan in the wild still remains unknown.

The life cycle of *A. stella* includes a swimming larval stage, which can be brooded by the parental anemone until it develops into a polyp. The polyp stage is benthic, but it retains the ability to be transported passively by water currents until it settles as adult on a solid substrate. In response to unfavorable abiotic or biotic conditions, many sea anemone species are capable of detaching from the substrate and temporarily drifting with tidal and coastal currents, a behavior that is particularly common when winter conditions become extreme (Riemann-Zürneck, 2008). Some circum-Antarctic and Arctic sea anemones present a distinct post-metamorphic juvenile stage, following the larval phase, during which they drift within pelagic currents (Riemann-Zürneck, 2008). To date, no comparable pelagic stage has been documented or investigated for *A. stella* despite the presence of a free-living polyp stage within the benthic fauna with similar potential (Bocharova, 2012). Reproduction occurs annually from May to October, with phenological variation depending on local environmental conditions, but a peak period between June and August (Bocharova, 2012). Along the Kamchatka coasts during this time, males release gametes passively into the water column, that are later ingested by females. Females brood the developing larvae internally (Bocharova, 2012). As for many circumpolar marine species, direct observations of reproductive and dispersal processes still remain

unrealistic. Consequently, genetic analyses remain the most effective approach for inferring key biological and ecological traits of this species in natural conditions.

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). While these sequences were suitable for phylogenetic analyses, they lacked the resolution necessary required to confirm clonality and accurately characterize the genetic structure of *A. stella* populations. The recent development of microsatellite primer pairs now enables investigating the biology of this circumpolar sea anemone 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 natural populations of *A. stella*, quantify its extent and variability across the species' range, and use high-resolution, polymorphic markers to accurately assess population structure throughout 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. We leveraged previous sampling campaigns (2012–2017), which included fewer sites and greater temporal gaps in the Pacific. While this may influence some interpretations, our results still provide a robust overview of the species' reproductive variation and current biogeography, especially given its laboratory lifespan of at least more than one decade.

A total of 314 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

128 examining temporal changes in genotypic frequencies within each site, we aimed to infer the
129 prevalence of clonal reproduction. We hypothesized that the limited energetic and physiological
130 cost of clonal reproduction may facilitate the establishment and persistence of populations
131 under harsh polar coastal conditions (Peck et al., 1998; Klimeš, 2008; Wang et al., 2018).
132 Conversely, we also considered that the genetic recombination associated with sexual
133 reproduction may promote the emergence of genotypes better adapted to local environments
134 (Pierre et al., 2022). Our findings on reproductive modes are interpreted in the context of the
135 specific ecological challenges faced by species expanding into previously unfavorable habitats.
136 In addition, we used the genotyped populations to assess genetic differentiation and identity in
137 state between individuals and sampled sites. Sampling across the full distribution range allowed
138 us to pinpoint regions with higher genetic diversity, which may correspond to historical refugia.
139 By comparing genetic differentiation between juveniles and adults, we aimed to identify
140 present-day or historical corresponding dispersal routes. Although *A. stella* was first described
141 along the North Atlantic coasts, suggesting a possible Atlantic origin, previous limited sequence
142 data instead indicated higher genetic diversity in North Pacific populations. If confirmed using
143 more polymorphic and resolutive markers that are microsatellites, this may suggest a more
144 recent expansion into the North Atlantic via the Arctic Ocean. Considering the free-living polyp
145 stage which can disperse passively via marine currents, as well as the potential for semi-sessile
146 adults to be transported on drifting debris or through human-mediated movement of materials,
147 we expect a limited but ongoing level of gene flow facilitated by favorable summer sea
148 conditions. Under this scenario, we would expect to observe shared probabilities of identity in
149 state among populations and a stepping-stone pattern of genetic differentiation across the
150 Arctic, potentially with preferential dispersal routes connecting sampled populations.
151 Alternatively, considering populations evolving isolated due to current Arctic conditions for
152 ~8,000 years (Holocene Thermal Maximum) or even ~125,000 years (last interglacial Eemian

153 period), we would expect very distinct and strongly structured genetic diversity with even fixed
154 and private alleles between populations (Slatkin & Takahata, 1985), out of artefactual
155 homoplasy.
156 Ultimately, our findings will provide a baseline framework for understanding the genetic
157 structure of this species across its Arctic distribution, offering critical insights at a time of
158 profound environmental change in this region (Laakkonen et al., 2021; Brandt et al., 2023).
159

160 Materials and methods

161 ***Sample collection***

162 In September 2012, we sampled at the low tide in the littoral zone 23 *Aulactinia stella* in the
163 White Sea Biological Station of Moscow State University (WSBS), Kandalaksha Bay of the
164 White Sea and 30 individuals at Liinkhamari, in the Varanger Fjord of the Barents Sea (see
165 Bocharova 2015). We also sampled using SCUBA diving at 5-18 m depth in the sublittoral zone
166 29 individuals at the Cape Broyle in the Admirals Cove area, Newfoundland, Canada, in June
167 2017. Along Kamchatka coast of the Pacific Ocean, we collected 5 individuals in the
168 Avachinsky Bay in June-July 2014 and 9 individuals in the Viluchinsky Bay in June-July 2016
169 at 5-21 m depth. We used these 14 Kamchatka adult individuals for mitochondrial DNA
170 sequencing, but only 6 of them brooded juveniles. Therefore, for microsatellite analysis, we
171 additionally analysed 3 females with their brooded offspring collected in the Avachinsky Bay
172 in July 2012 (2 samples) and June 2013 (1 sample). At low tide, we sampled 20 individuals in
173 the intertidal zone of the Matua Island of the Kuril Islands in August 2016 (see map of the
174 sampled sites on Figure S1).
175 We checked that the phenotypic and biometric appearance of each individual belonged to *A.*
176 *stella* species using descriptions in Loseva (1974), Fautin Dunn et al. (1980), Sanamyan and
177 Sanamyan (2008), Sanamyan et al. (2019, 2020) and WoRMS (Rodríguez et al., 2025). In

178 addition, we used nematocyst identification from tentacles, pharynx, body wall and mesentery
179 (Manuel, 1981), and mitochondrial DNA sequence analysis to confirm the species. To analyze
180 genetic diversity in two successive generations, we purposely genotyped large females and the
181 juveniles they brooded in their gastrovascular cavity. The quantity of juveniles in such females
182 varied from 1 to 39 per female and we sequenced them all.
183
184 ***DNA extraction, mtDNA sequencing and genotyping by microsatellite loci***
185 We extracted the total DNA of each sampled adult and juvenile polyp. For each adult, we used
186 a part of the adult pedal disk measuring approximately 3x3x3 mm; And for juveniles, we
187 extracted DNA from the whole juvenile polyps which measured from 1 to 5 mm. For each
188 sample, we desiccated and grinded the sampled tissues. We then used the Wizard SV Genomic
189 DNA Purification System (Promega, USA) following the manufacturer's protocol. Extracted
190 DNA was preserved in 96% ethanol before genotyping.
191 For mitochondrial gene (12S rRNA, 16S rRNA, cytochrome oxidase III) sequencing, we only
192 used adult subsamples: 23 individuals from the White Sea, 30 from the Barents Sea, 29 from
193 Newfoundland, 14 from Kamchatka, and 20 from the Kuril Islands. We applied the primer sets
194 and methodology thoroughly described for 16S rRNA and COIII (Geller & Walton, 2001) and
195 12S rRNA mitochondrial fragments (Bocharova 2015). Sequencing was performed by 3500
196 Genetic Analyzer (Applied Biosystems, USA) using BigDye Terminator v3.1 Cycle
197 Sequencing Kit. The sequences were analyzed by Geneious Prime software. By concatenating
198 these three mtDNA sequences (12S, 16S, COIII), we grouped the samples into haplotypes that
199 were aligned and perfectly matched the five previously described haplotypes (Bocharova,
200 2015). Including these mitochondrial haplotypes (Pacific 1-5), we used geneHapR (Zhang et
201 al., 2023) package to produce the haplotype network (Figure 2). We then used the extracted
202 nuclear DNA to amplify 41 microsatellites using primer pairs previously developed in

203 Bocharova et. al. (2018) for this species and another sea anemone species of Actiniidae family,
204 *Cribrinopsis albopunctata* (Sanamyan & Sanamyan 2006, Sanamyan et al. 2019) with the
205 corresponding PCR conditions. PCR products were visualized in 3500 Genetic Analyzer
206 (Applied Biosystems, USA) using POP7 gel polymer. We analyzed the obtained
207 chromatograms using GenMapper Software (ThermoFisher Scientific, USA). Out of these 41
208 primer pairs, only ten pairs (Act007, Act011, Act028, Act067, Act173, Act177, Act235, Act238,
209 Act249, Act386,) successfully amplified and were polymorphic in our samples. We then
210 multiplexed the ten microsatellites into four PCR pools using three specific dyes (TAM, ROX,
211 FAM) for visualization: Pool 1) Act007 (FAM), Act011 (TAM); Pool 2) Act238 (FAM), Act249
212 (TAM), Act173 (ROX); Pool 3) Act067 (FAM), Act177 (ROX), Act386 (TAM); Pool 4) Act28
213 (TAM), Act235 (ROX).
214 To estimate if this marker set was powerful enough to distinguish between individuals, we
215 computed the overall observed unbiased probability of identity in state under panmixia
216 (hereafter overall pidu) and the overall observed unbiased probability of identity in state
217 between sibs (overall pids) as recommended by Waits et al. (2001). To achieve allele dosage
218 within each individual per locus, we used the dose-effect method with some modifications
219 (Rodzen & May, 2002; Drauch Schreier et al., 2011). In cases of more than 1 allele, dose-effect
220 is counted following the instruction (Figure S2): two alleles of almost the same height were
221 considered as AABB (Figure S2A); One high allele and two low alleles as AABC (Figure S2B);
222 One very high allele and one low allele as AAAB (Figure S2C); Tree alleles of the same height
223 were considered as ABC + null allele (Figure S2D); One high allele and one allele half lower
224 were considered as AAB + null allele (Figure S2E).
225
226 ***Analyses of genetic diversity within spatio-temporal samples***

227 Parents that produce descendants by clonality can result to observe multiple times the same
228 Multi-Locus Genotype (hereafter MLG) among the genotyped samples (Halkett et al., 2005;
229 Arnaud-Haond et al., 2007). However, these repeated MLGs may also come from genetic
230 marker lacking sufficient resolution to disentangle between descendants produced by sexual
231 reproduction, either under panmixia (the lower probability to observe two identical sexual
232 descendants) or between mating sibs (the higher probability to observe two identical sexual
233 descendants). To estimate the power of our marker set to distinguish different individuals and
234 assess the upper and lower bounds for the probability of observing identical MLG drawing a
235 pair of individuals sampled in a same population, we therefore computed the probabilities of
236 identity under panmixia (*pidu*) and considering only sib mating (*pids*; Jacquard, 1968, 1970;
237 Waits et al., 2001) using formula adapted for tetraploid populations implemented in
238 GenAPoPop software (Stoeckel et al., 2024).
239 To assess the level of genetic diversity within populations and compare between populations,
240 for each age cohort in one site, we reported the sample size (*N*) and computed the average
241 number of observed alleles $\bar{Na}$ and its variance Var(Na) over the ten microsatellites, the average
242 effective number of alleles $\bar{A_E}$ and its variance Var(A_E), the average gene diversity $\bar{H_E}$ and its
243 variance Var(H_E), the average observed heterozygosity $\bar{H_O}$ and its variance Var(H_O) and the
244 average value of the inbreeding coefficient $\bar{F_{IS}}$ and its variance Var(F_{IS}) over all loci.
245 We also computed genotypic indices including the number of unique genotypes (G), the
246 unbiased genotypic richness R (Dorken & Eckert, 2001), the genotypic evenness as Pareto β to
247 assess the potential uneven contribution of some clonal MLGs to the genotypic composition of
248 populations (Arnaud-Haond et al., 2007; Bailleul et al., 2016).
249 We searched for clonal signatures in genetic diversity by analyzing $\bar{F_{IS}}$ and its variance Var(F_{IS})
250 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 chose to retain 80 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 verified 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 Arctic-Atlantic and Pacific populations and between juveniles and adults, 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

276 cohorts sampled on the Atlantic side) and the probability value (p) of the hypothesis that the
277 two groups have identical distribution of their genetic indices. To compare ρST between
278 juveniles and adults among pairs of the same sites, we used Wilcoxon signed rank test. We
279 reported the median ρST value of the two groups ($median_{group1}$ versus $median_{group2}$) in the order
280 they are mentioned, the sum of the ranks of the differences above zero (W) and the probability
281 value (p) of the hypothesis that the two age cohorts have identical distribution of ρST.
282 All these tests were performed using python 3.11 and Scipy.stats 1.13 (Virtanen et al., 2020).
283

284 # Results

285 We genotyped 314 individuals of *Aulactinia stella* sampled on five sites, including a total of 75
286 adults, ranging from 9 to 21 with a median of 15 adults per site, and a total of 239 juveniles,
287 ranging from 6 to 93 with a median of 49 juveniles per site (Table 1). We found both females
288 and males in the Kamchatka population, whereas we found only females in the Kuril Islands,
289 Newfoundland, the Barents and the White Seas. For subsequent genetic analyses, we only used
290 the adult females from each site.
291 We found 15 brooding females in White Sea, 21 in Barents Sea, 14 in Newfoundland, 9 in
292 Kamchatka and 19 in Kuril Islands sampled sites. The oral disc diameter of mature females
293 varied from 10 to 45 mm while the overall size of the juveniles released from the gastrovascular
294 cavities of the adults varied from 1 to 5 mm.
295

296 **Gene, allele and genotypic diversities in nuclear microsatellites**

297 Gene, allele and genotypic diversities in nuclear microsatellites were consistent over
298 generations (Table 1). We found a maximum of four different alleles for each locus in one
299 individual over all our samples and concluded that *A. stella* must be at least an autotetraploid
300 species. Using our ten microsatellites, the mean numbers of alleles per locus per site and

301 developmental stage ranged from 1.2 to 5.7, with a median of 2.75. The mean effective numbers
302 of alleles per locus per site and developmental stage ranged from 1.19 to 2.53 with a median of
303 1.69. Over all samples, probability of identities under panmixia was 8.3×10^{-9} and probability
304 of identity between sibs was 4.5×10^{-3}. These low probabilities that two individuals generated
305 by sexual reproduction would result into similar genotypes advocated that the ten
306 microsatellites we used were powerful enough to genetically distinguish between sexual
307 descendants, even resulting from a sib mating (Waits et al. 2001). We thus considered afterward
308 that individuals with identical MLGs were clones (i.e., ramets of a same genet).
309 Over all sites and cohorts, we found 154 unique MLGs and 26 of these MLGs were found
310 repeated in more than one sampled individual, i.e. genets with more than one ramet (Table S1).
311 In Kuril Islands, we genotyped no repeated MLG. In Kamchatka, we found three individuals of
312 the same clone. In Barents Sea, we found three repeated MLGs, including respectively two,
313 five and thirteen ramets. In White Sea, we found eight repeated MLGs involving two to forty
314 ramets, for a total of 88 ramets. In Newfoundland, we found fourteen repeated MLGs involving
315 two to eleven ramets, for a total of 49 ramets. All ramets of repeated MLGs were exclusively
316 sampled on the same site. In all populations with repeated MLGs, repeated MLGs were found
317 both in adults and in juveniles. Some of these genets were even shared by adults and juveniles,
318 except in the Newfoundland samples.
319 We found higher genetic and genotypic diversity, and lower probabilities of identity on the
320 Pacific side sites (i.e., Kuril and Kamchatka) than found on the Atlantic side of the Arctic Ocean
321 (i.e., Newfoundland, Barents and White Seas), even if differences among sites within oceans
322 still remained on some indices (Table 1). The four cohorts sampled in Kuril Islands and in
323 Kamchatka showed nearly twice more average gene diversity, ranging from 0.372 to 0.460,
324 than found in the six cohorts sampled in Newfoundland, Barents and White Seas, that ranged
325 from 0.097 to 0.266 (0.427 versus 0.174, U=24, n1=4, n2=6, p=0.009), while they both showed

similar standard deviation of gene diversity over all loci (U=15, n1=4, n2=6, p=0.610; Table 1). Cohorts in the Pacific sites also showed significantly higher mean numbers of alleles per locus (4.9 versus 2.0, U=23.5, n1=4, n2=6, p=0.019) and higher effective number of alleles (2.43 versus 1.43, U=24, n1=4, n2=6, p=0.009).

Kamchatka and Kuril samples showed higher genotypic richness measured as R than populations on the Atlantic side (1.00 versus 0.37, U=24, n1=4, n2=6, p=0.009) and higher genotypic evenness measured as Pareto β values (3.64 versus 0.45, U=23.5, n1=4, n2=6, p=0.019). Over all loci, Kamchatka and Kuril samples showed lower probabilities of identity under panmixia ($<10^{-6}$ versus 0.003, U=0, n1=4, n2=6, p=0.009) and between sibs (0.008 versus 0.118, U=0, n1=4, n2=6, p=0.009) than found in samples from the Atlantic side.

Heterozygosity and deviation from the genotypic proportions expected under Hardy-Weinberg hypotheses

We found no difference in observed heterozygosity between cohorts on the Pacific and Atlantic sides (0.241 versus 0.181, U=15, n1=4, n2=6, p=0.61), though variance of observed heterozygosity between loci was nearly two times higher in cohorts on the Atlantic side (0.389 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 20 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, S1, S3). 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 S1). 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 S4). 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 star and chaplet topological 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. Some pairwise genetic distances between individuals within site, like in Kamchatka, were larger than between two individuals from different sites (Figure 5, e.g. Kamchatka's individuals linked to White and Barents seas individuals).

Discussion

We investigated reproductive modes, genetic diversity and differentiation in five populations of the autotetraploid sea anemone *Aulactinia stella*, sampled from North Pacific, Arctic, and North Atlantic coasts using three mitochondrial markers and ten nuclear microsatellites. *A. stella* is broadly distributed throughout the northern hemisphere where it is an important semi-sessile predator in shallow-water communities and prey for higher trophic levels (Ottaway, 1977). We genotyped two successive age cohorts from each of the five sites. We benefited from past sampling campaigns (from 2012 to 2017) to genotype individuals, with fewer sites and greater temporal dispersion in the Pacific Ocean: This could conceivably influence our results.

426 The ten nuclear microsatellites we used offered sufficient power to distinguish clones from
427 inbred offspring. Despite our standardized and reproducible protocol for allele dosage inference
428 (Figure S2), tetraploid microsatellite datasets remain sensitive to technical biases, particularly
429 those arising from null alleles and amplification biases, which may affect quantitative estimates
430 prior to downstream analyses.
431 Genetic differentiation in *A. stella* revealed a hierarchical structure: first separating into a
432 Pacific and an Arctic-Atlantic group, each of which was further subdivided by sampling site,
433 and then by age cohort. This type of structure closely resembles patterns seen in the intertidal
434 macroalga *Fucus distichus* and in other Arctic and peri-Arctic sessile coastal marine species
435 (Coyer et al., 2011; Bringloe et al., 2020). Environmental factors, rather than species-specific
436 biological or behavioral traits, may thus likely be the primary drivers of genetic differentiation
437 in this region. We therefore examined reproductive modes and assessed genetic diversity and
438 differentiation across these hierarchical groups.
439
440 **Reproductive modes in *Aulactinia stella* populations**
441 We found strong genetic evidence that *A. stella* reproduces clonally in natural populations,
442 consistent with the absence of males in some sites and with previous observations of embryos
443 developing parthenogenetically within parental mesenteries (Bocharova, 2012, 2015;
444 Kaliszewicz et al., 2012). In the North Pacific, repeated multilocus genotypes (MLGs) were
445 rare; however, genetic indices, including interlocus FIS variances close to 1 and low levels of
446 linkage disequilibrium, indicated intermediate levels of clonality (Navascues et al., 2010;
447 Stoeckel et al., 2021a,b, 2024). It was further supported by changes in genotype frequencies
448 between adults and juveniles, which yielded clonality estimates of 0.37 to 0.65 (Becheler et al.,
449 2017; Stoeckel et al., 2024). The high clonal evenness in these populations likely reduced the
450 probability of resampling identical MLGs (Arnaud-Haond et al., 2007, Stoeckel et al., 2021a).

451 In contrast, Arctic and North Atlantic populations, characterized by lower allelic diversity,
452 exhibited extensive clonality. Many individuals shared identical MLGs, and population-level
453 genetic indices, including negative mean FIS, large variance of FIS across loci, and significant
454 linkage disequilibrium, indicated high rates of clonal reproduction (Halkett et al., 2005; De
455 Meeûs et al., 2006; Navascues et al., 2010; Stoeckel et al., 2021a). Consistently, clonality rates
456 inferred from changes in genotype frequencies between adults and juveniles ranged from 0.74
457 to 1.0 in Arctic and North Atlantic populations, nearly twice the rates estimated for the North
458 Pacific.
459
460 **The advantages of clonal reproduction at the limits of species' ranges**
461 High levels of uniparental reproduction, including clonality, are commonly observed in species
462 expanding into new or marginal environments (Barrett, 2015; Pannel et al., 2015; Burke &
463 Bonduriansky, 2019, Pereyra et al., 2023), particularly when enduring harsh conditions (Klimeš
464 2008) and when heading towards the poles (Peck et al., 1998). The post-glacial Baltic sea
465 provides several examples, including the emblematic case of *Fucus vesiculosus* (Johannesson
466 & André 2006; Pereyra et al., 2009; 2023). In plant species, the persistence of connection
467 between ramets (mainly by roots) offers ecological advantages that may alone explain the
468 prevalence of clonality at range margins, including regeneration after injury, distribution of
469 physiological functions among ramets, translocation of resources between interconnected
470 ramets (clonal integration) and space monopolization using different strategies (including
471 phalanx versus guerrilla) to address intra- and inter-specific competitions depending on the
472 environmental context (Cadotte et al., 2006; Gonzalvez et al., 2008; Roiloa, 2019; Franklin et
473 al., 2021).
474 In contrast, dispersed clones in marine species such as *A. stella* do not benefit from such clonal
475 integration. In this context, clonality should only favor kin cooperation (e.g., through brooding

476 or cooperative behavior Bocharova, 2012; Rudin & Briffa, 2012) but more importantly it should
477 favor the persistence of local populations under harsh conditions by avoiding the energetic and
478 biological costs of sexual reproduction (Klimeš, 2008; Pierre et al., 2022).
479 Baker (1955) postulated that uniparental reproduction (including clonality) provides a critical
480 advantage for colonization: individuals arriving in new areas can reproduce clonally to establish
481 a new area. First, clonality allows a population to maintain itself locally until compatible mates
482 become available (Baker & Stebbins, 1965, Daly et al., 2023). This hypothesis is particularly
483 relevant for gonochoristic (or dioecious) sessile organisms that require close proximity for
484 successful sexual reproduction (Barrett, 2015), such as in sea anemones. Second, in new harsh
485 environments, clonal individuals that manage to survive minimize the risks of genetic
486 reassortment associated with sexual reproduction for their offspring (Peniston et al., 2021;
487 Pierre et al., 2022). Third, clonality maintains higher effective population sizes than in identical
488 more sexual populations (Reichel et al. 2016; Stoeckel et al., 2021b). Clonality limits the
489 negative effects of genetic drift during founder events, including the fixation of deleterious
490 alleles in small populations (Navascues et al., 2010; He et al., 2024).
491 Our results in *A. stella*, which indicated a twofold increase in clonality at the species' range
492 edge, suggest that clonal reproduction may play an important role in supporting population
493 persistence and maintaining higher effective population sizes under unfavorable conditions
494 during range expansion (Baker's conjecture, Pannel et al., 2015; geographic parthenogenesis,
495 Peck et al. 1998), without necessarily relying on mechanisms such as clonal integration (as
496 proposed in plants) or habitat modification (as suggested for ecological engineering species) to
497 explain clonal success.
498
499 ***Aulactinia stella* spreading across the Arctic Ocean from north Pacific?**

Genetic diversity was nearly twice as high in North Pacific populations compared to Atlantic ones. Kamchatka and Kuril Islands harbored the greatest allelic and genotypic diversity, whereas Newfoundland, Barents Sea, and White Sea populations showed more compact identities in state. All Arctic and North Atlantic individuals carried the Pacific-3 haplotype, rare in the Pacific, while Kuril populations were fixed for Pacific-1, the dominant haplotype in Kamchatka. This distribution suggests a North Pacific origin, with Kamchatka as a likely glacial refugium (He et al., 2024). In contrast, Arctic and North Atlantic populations may be more recently established (since the last glaciation) or alternatively, may have originated from smaller, more localized glacial refugia, evolving relatively isolated since the last warmer interglacial period (Eemian, minimum ~116,000 years ago). But the DAPC results (Figure S4) and pairwise genetic distance (Figure 5) supported a stepping-stone genetic structure between sites and genetic groups rather than isolated as expected in an island model with no migration (Jombart et al., 2010). Interestingly, the path of the lowest F_{ST} genetic structure between sites align with major summer currents (e.g., Anadyr, Beaufort gyre, transpolar drift), areas of low ice cover, and coastal distances (Rudels & Carmack, 2022; Timmermans & Marshall, 2020; Constantin & Johnson, 2023) and increasing Arctic maritime traffic that may further accelerate dispersal, either through ballast water transport or passive enhancement by ship wakes (Melia et al., 2016; Boylan, 2021; PAME, 2024). Alterations in Arctic Ocean conditions, together with increasing human activities (including anthropogenic contributions to floating debris, ship-generated wake currents, and maritime transport of materials) may facilitate connectivity among *A. stella* populations, potentially via stepping-stone dispersal along coasts during the free-living polyp stage. Since at least 1993, temperatures in the upper 10 m of the water column have commonly reached 8–10 °C in coastal and sheltered bays, and 2–3 °C in the open sea, with higher temperatures in coastal and tidal currents along the Eurasian Arctic coasts, making this migration physiologically feasible (Locarnini et al. 2024; E.U. Copernicus Marine Service,

525 2024). These maritime and tidal currents are estimated to transport approximately 1 Sverdrup,
526 a volume comparable to the combined mean discharge of all the world's rivers, but substantially
527 lower than the Gulf Stream, which rather transports 60–90 Sverdrups Constantin & Johnson,
528 2023). Taken together, these factors may explain the reduced genetic differentiation observed
529 among juveniles within the established stepping-stone connectivity pattern of *A. stella*
530 populations. Similar genetic patterns along with evidence for human-mediated dispersal have
531 been reported for the coastal sea anemone *Diadumene lineata* (Glon et al., 2020), which,
532 however, is more fecund and lacks the brooding behavior observed in *A. stella*.
533 Nevertheless, the biology of *A. stella*, like that of many Arctic marine organisms, remains
534 poorly understood once individuals move beyond nearshore habitats and become inaccessible
535 to direct observation. In particular, dedicated studies are needed to determine whether this
536 Arctic sea anemone can persist while attached to debris or as free-living polyp or adult drifters
537 within coastal and tidal currents, potentially enabling effective migration across the Arctic
538 Ocean.
539
540 **Juveniles less genetically structured than adults: methodological artifacts or gene flow**
541 **with local endemism?**
542 Comparisons of genetic diversity between adults and juveniles revealed slightly lower levels of
543 genetic differentiation among juveniles (Figure S3). Several non-exclusive hypotheses could
544 explain this pattern, requiring further research to disentangle their relative contributions.
545 Methodological artefacts must first be ruled out through more geographically balanced and
546 systematically designed sampling. Using polymorphic markers with lower mutation rates could
547 also help distinguish genuine shared ancestry from homoplasy that has higher chance to occur
548 in microsatellite loci across distant populations.

549 Clarifying the life cycle of *A. stella*, particularly the dynamics of clonal interference and
550 mortality during recruitment, will be essential to assess whether reduced genetic structure in
551 juveniles and the absence of shared multilocus genotypes (MLGs) across sites reflect local
552 genetic endemism, gregarious behavior promoting shared ancestry (as found in other sea
553 anemone species: Lane et al., 2020; Ryan et al., 2021), or persistent founder effects with limited
554 gene flow. *A. stella* occupies a range of habitats, such as the Barents and White Seas, which
555 differ significantly in salinity despite their proximity (~100 km). Environmental factors,
556 including temperature, salinity, depth, tidal exposure, and substrate disturbance, are known to
557 influence reproductive modes and genetic differentiation (Eriksson & Johansson, 2005;
558 Krueger-Hadfield et al., 2013; Berković et al., 2014; Dudgeon et al., 2017; McMahon et al.,
559 2017; Ryan & Miller, 2019; Williams et al., 2024). Similar habitat-driven patterns are observed
560 in other sea anemones, such as *Actinia tenebrosa* and *Diadumene lineata*, where localized
561 clonal distributions and endemic lineages correlate with temperature, salinity, UV exposure,
562 and community composition (Sherman & Ayre, 2008; Ryan et al., 2021). It may explain the
563 higher genetic differentiation found in adults between sites.
564
565 **Restricted dispersal or local adaptation in *Aulactinia stella*?**
566 No MLGs were shared between sampling sites, even over relatively shorter distances (e.g.,
567 Barents vs. White Sea, ~360 km; Kuril Islands vs. Kamchatka, ~680 km). The presence of local,
568 site-specific clones and high levels of genetic differentiation between adult populations is
569 common in cold-water sea anemones, including *A. tenebrosa*, *Anthothoe albocincta*,
570 *Diadumene lineata*, and several North Pacific species (Veale & Lavery, 2012; Sherman et al.,
571 2007; Ryan et al., 2021; Edmands & Potts, 1997), which contrasts with tropical species that
572 often share genets across hundreds of kilometers (Russo et al., 1994; Emms et al., 2020). Such
573 patterns would suggest that Arctic conditions may constrain and challenge the dispersal of sea

anemones (Chan et al., 2019), but other passively dispersing taxa in cold-water habitats such as macroalgae, seagrasses, and bivalves, show weaker population structure (Coolen et al., 2020; Pereyra et al., 2023; Krueger-Hadfield et al., 2021). In fact, polyp stage commonly allows locally-active and passive transport by tidal flows and circumpolar maritime currents, facilitating long-distance dispersal (Riemann-Zürneck, 1998). For instance, *Urticina eques* exhibits very low differentiation over hundreds of kilometers along the British coast (Cava-Solé et al., 1994). In the case of *A. stella*, Arctic populations may have only narrow temporal windows of suitable thermal conditions for successful sexual reproduction, particularly in the intertidal and shallow sublittoral zones. These habitats are also characterized by extreme variability in salinity and desiccation at low tide. In such habitats, *A. stella* is often found hiding under *Fucus* algae, in rock crevices, or in tide pools, behaviors that indicate exposure to environmental stress. Local environmental filtering through selection and post-settlement mortality (e.g., *Fucus vesiculosus*: Johannesson & André, 2006; Pereyra et al., 2009; *Fucus distichus*: Laughinghouse et al., 2015; *Actinia tenebrosa*: Sherman et al., 2008; seagrasses: Kendrick et al., 2012; *Acropora millepora*: van Oppen et al., 2011), as well as individual habitat preferences and gregarious settlement (e.g., *Diadumene lineata*: Ryan et al., 2021), may explain the roughly twofold higher genetic differentiation observed among adults compared to juveniles in *A. stella*. These patterns highlight the need for further ecological and behavioral studies to clarify the potential mechanisms and temporal dynamics of dispersal in this species in the Arctic Ocean.

Data Availability

All data (including adults, juveniles, MLG genotypes, sampling GPS locations, and clone sizes) as well as the scripts used to reproduce the results and figures, are openly available on Zenodo https://doi.org/10.5281/zenodo.17193174

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 a map of the sample sites with the minimum spanning trees of genetic differentiation of adults, juveniles and overall among sites; Figure S2 reports how allele dosage of the microsatellites was achieved; Figure S3 reports the change of the Bayesian information criteria of the DAPC with increasing number of genetic clusters arguing for a stepping-stone genetic structure.

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Author contributions

EB and SS laid the foundation of this work while EB visited SS lab in 2018 and 2019. EB and SS conceived the study and were responsible for funding applications. EB was responsible for data acquisition. She supervised and achieved sample collection, determined the species and sexed the sampled individuals. She also conceived, developed the sequences and microsatellites, supervised and achieved sequencing and genotyping of all the samples. From sequencing 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 estimated rates of clonality using changes of genotype frequencies over one generation for each sampled site using ClonEstiMate method for autopolyploids in GenAPoPop software (Becheler et al., 2007; Stoeckel et al., 2024). Kuril Islands in blue, Kamchatka in green, Newfoundland in red, White Sea in pink and Barents Sea in gold.

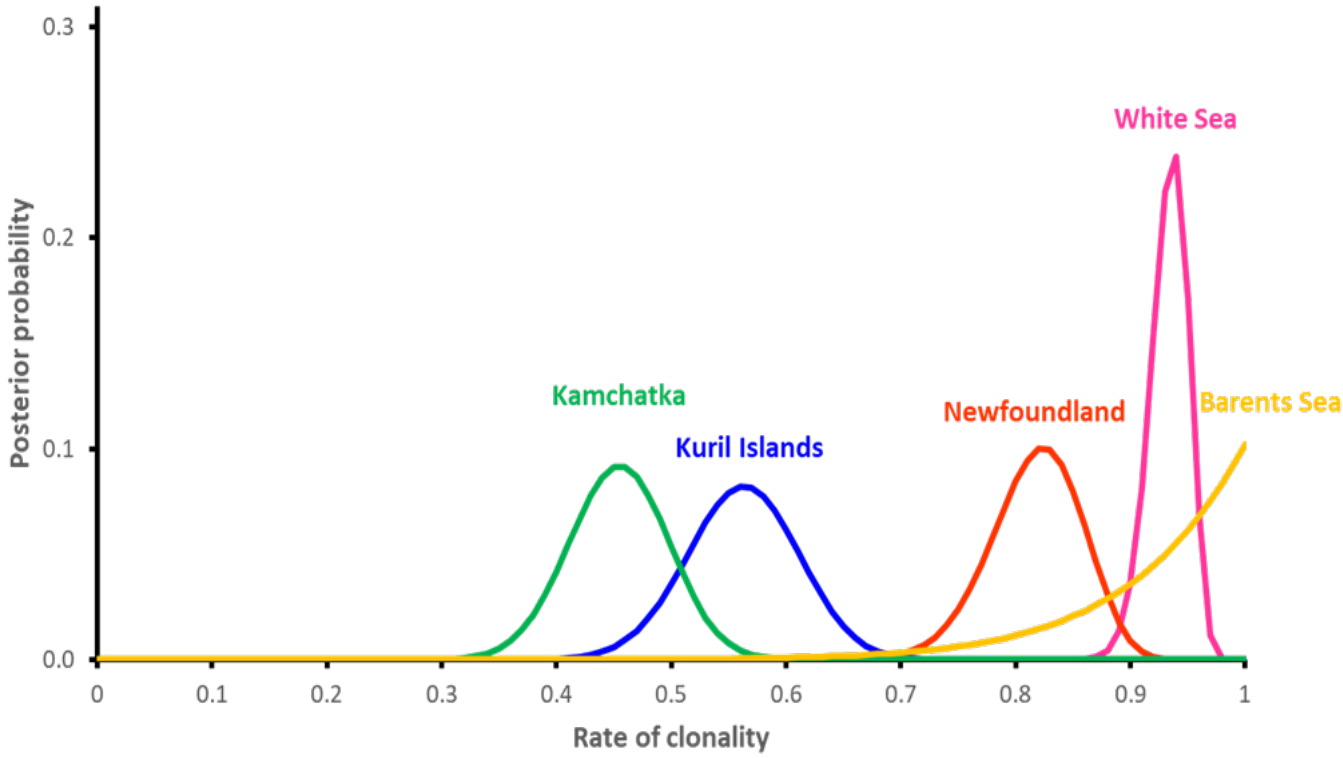


Figure 2: Haplotype network using three mitochondrial gene sequences (12S, 16S, COIII). The proportion of each sampled site per haplotype is represented in color. The circle sizes of each haplotype are proportional to their number in our dataset. We used haplotype names initially identified in Bocharova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

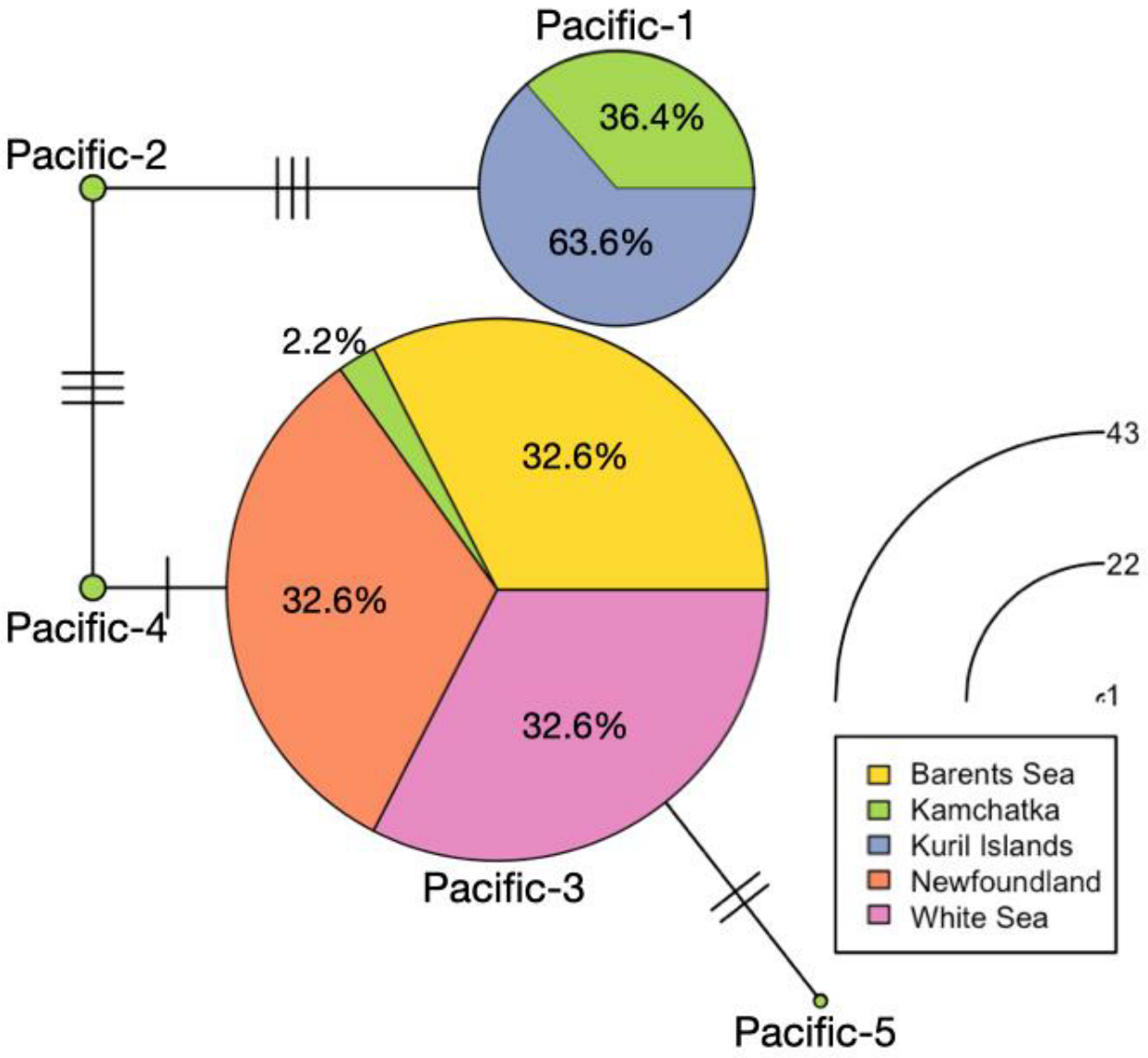


Figure 3: The oriented graph of the ρST values between sites and cohorts (vertices). Orange edges and boxes allow by comparison between pair of sites to understand the dynamics and directions of genetic spreading. Comparisons between blue boxes (adults) and green boxes (juveniles) between pairs of sites to understand the temporal genetic structure between sampled sites. Paths of decreased genetic structure can result by chance due to sampling variability from the same underlying distribution, or due to homoplasy or gene flow between populations.

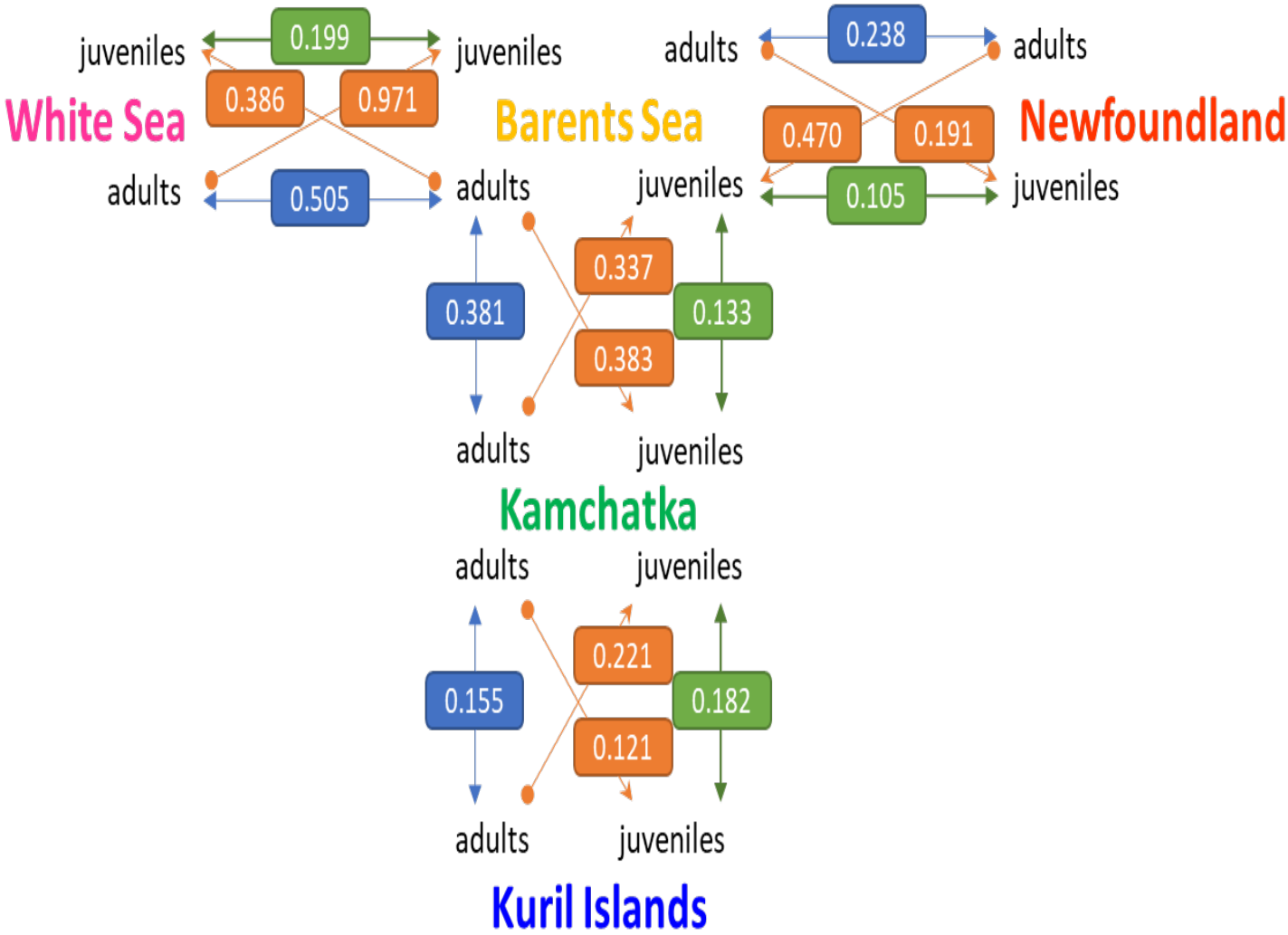


Figure 4: Discriminant Analysis of Principal Components of the genetic structure of *Aulactinia stella* across the Arctic Ocean. We found four clusters being the minimal number of clusters maximizing the distance between groups (see Figure S4). Individuals are represented as columns corresponding to the membership probability to the four supported clusters (in color). Sampled sites are represented successively, separated by a large white bar. Within each site, adults are on the left side of the dashed vertical black line and juveniles on the right.

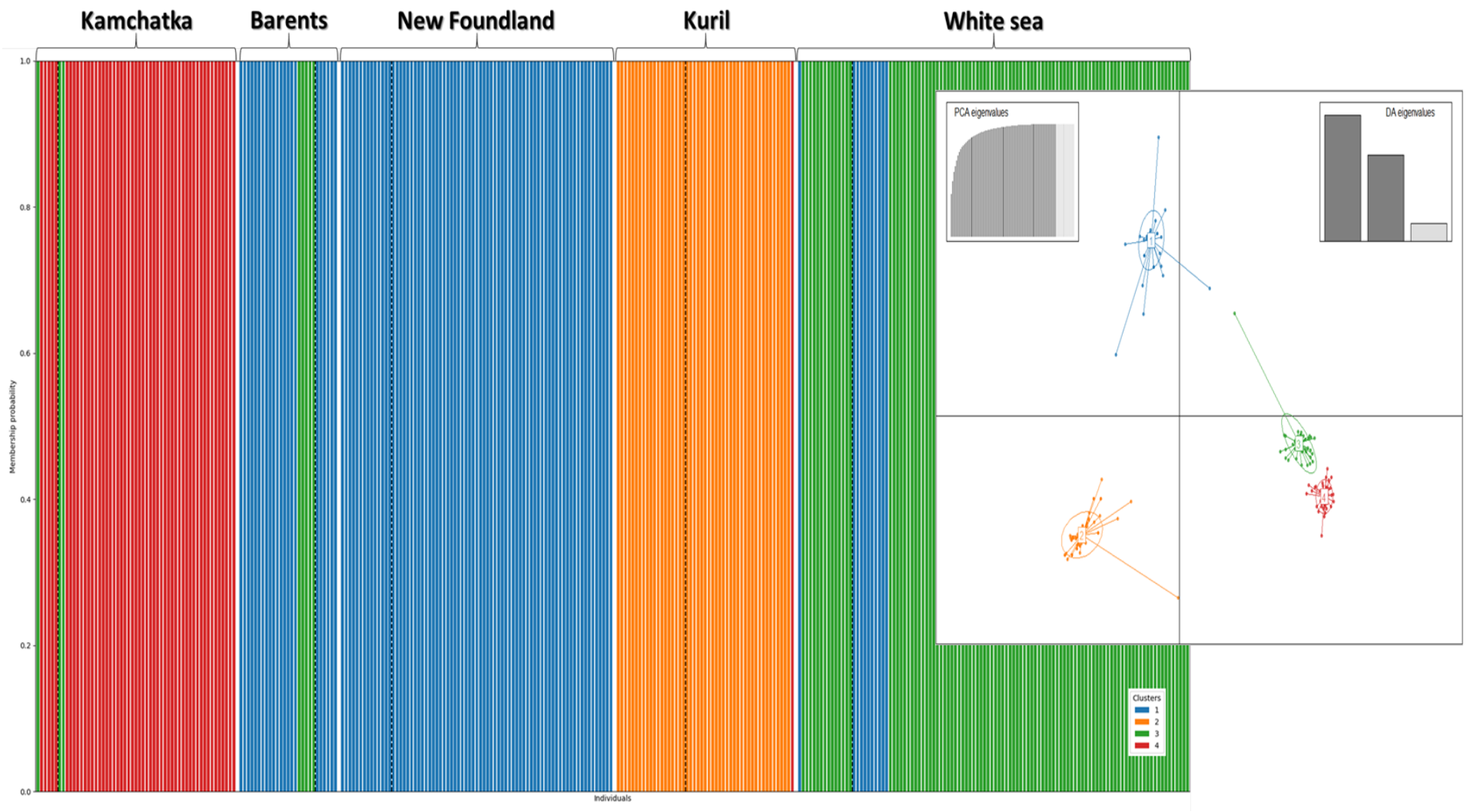
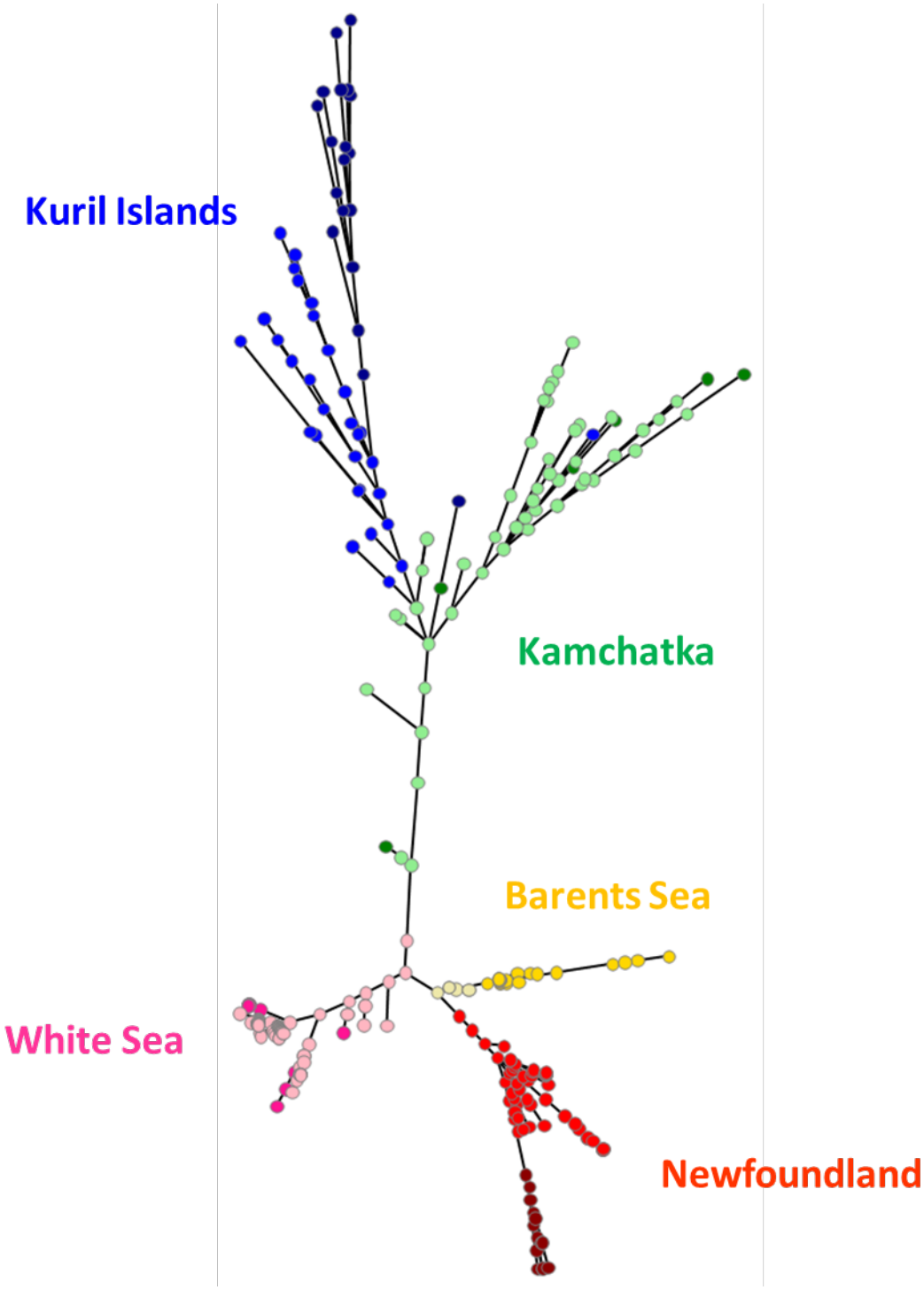

Kamchatka
Barents
New Foundland
Kuril
White sea
Membership probability
1.0
0.8
0.6
0.4
0.2
0.0
Individuals
PCA eigenvalues
DA eigenvalues
Clusters
1
2
3
4

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)	$\bar{F}_{IS}$	Var(F_{IS})	pidu	pids
Kamchatka	**Adults**	6	6	1.000	1.807	0.011	2.2	30	2.2	17.27	0.294	0.488	0.416	0.590	0.292	1.635	1.1E-8	0.0043
	Juveniles	49	48	0.979	4.615	0.122	2.4	151.6	2.4	24.25	0.314	0.397	0.460	0.534	0.318	1.156	1.6E-7	0.0093
Kuril Islands	**Adults**	19	19	1.000	3.322	0.026	2.5	84.4	2.5	46.90	0.176	0.121	0.438	0.640	0.598	1.016	9.9E-9	0.0040
	Juveniles	30	30	1.000	3.954	0.077	2.5	234.1	2.5	53.09	0.188	0.301	0.372	0.891	0.494	0.948	1.9E-9	0.0026
Barents Sea	**Adults**	21	10	0.450	0.302	0.444	1.4	14.5	1.4	0.98	0.197	0.425	0.223	0.287	0.115	3.124	3.8E-4	0.1901
	Juveniles	6	2	0.200	0.591	1.000	1.2	1.6	1.2	1.42	0.125	0.628	0.097	0.376	-0.290	13.323	0.0776	0.5125
Newfoundland	**Adults**	14	12	0.846	1.807	0.025	1.4	18.9	1.4	6.47	0.165	0.656	0.170	0.512	0.024	4.971	0.0011	0.1556
	Juveniles	61	28	0.450	0.716	0.076	1.4	9.6	1.4	6.63	0.158	0.747	0.178	0.596	0.112	4.875	0.0019	0.1606
White Sea	**Adults**	15	5	0.286	0.129	0.619	1.6	18.9	1.6	7.81	0.314	1.526	0.238	0.886	-0.322	10.807	2.3 E-4	0.0635
	Juveniles	93	28	0.293	0.261	0.268	1.7	48	1.7	8.53	0.308	1.447	0.266	0.912	-0.157	7.841	3.9E-5	0.0358
Over All	**Both**	314	180	0.572	0.482	0.293	2.1	468.9	2.1	6.24	0.243	0.387	0.440	0.454	0.448	0.870	8.3E-9	0.0045

Table 1: 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 $\bar{H}_O$ and its variance Var(H_O), average gene diversity $\bar{H}_E$ and its variance Var(H_E), average value of the inbreeding coefficient $\bar{F}_{IS}$ and its variance Var(F_{IS}) over all loci, unbiased probability of identity under panmixia *pidu* and between sibs *pids*.

Supplementary information

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 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.

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	#

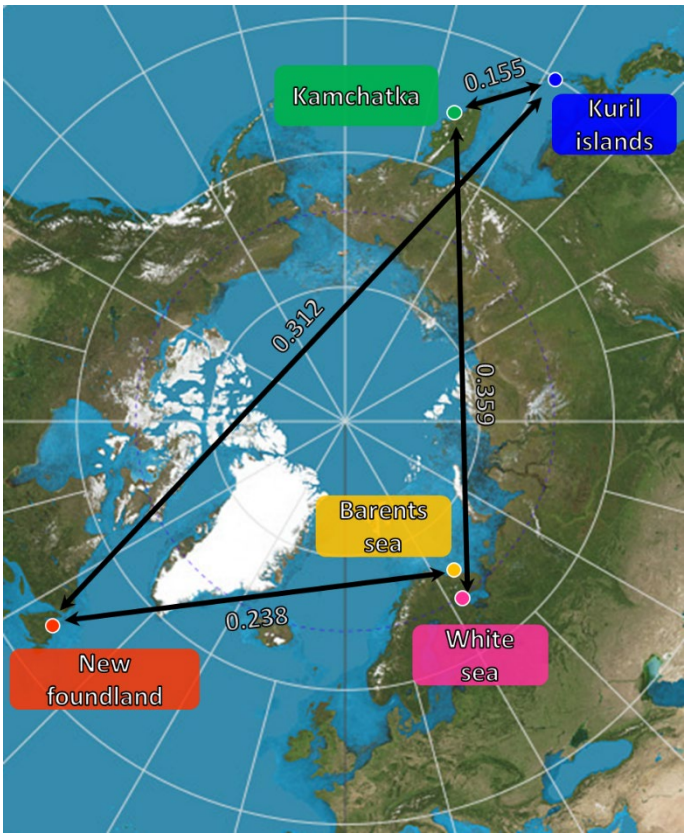
B).

		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	#

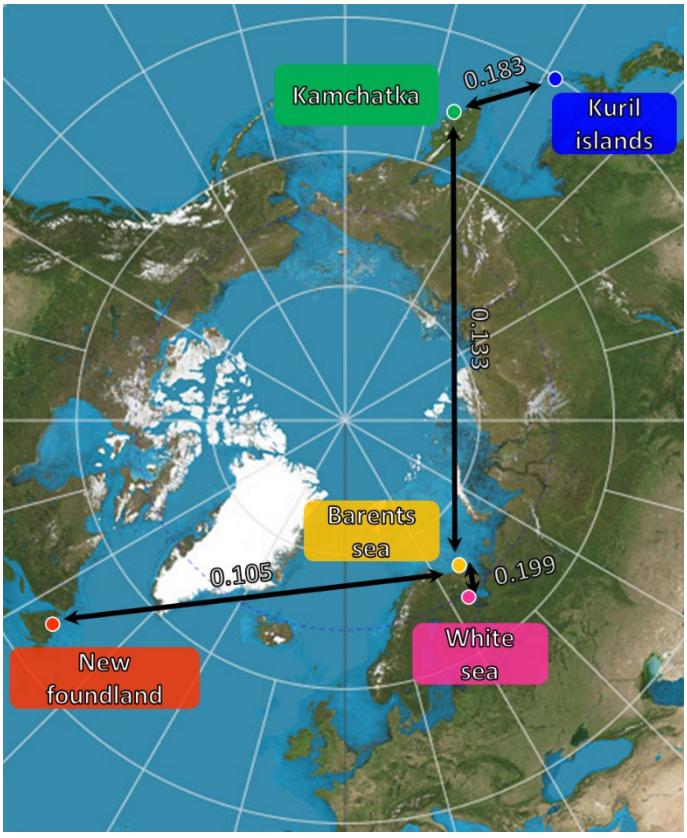
Table S2: Pairwise ρST between sites (A) and between age cohorts within sites and among sites (B).

Figure S1: 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).

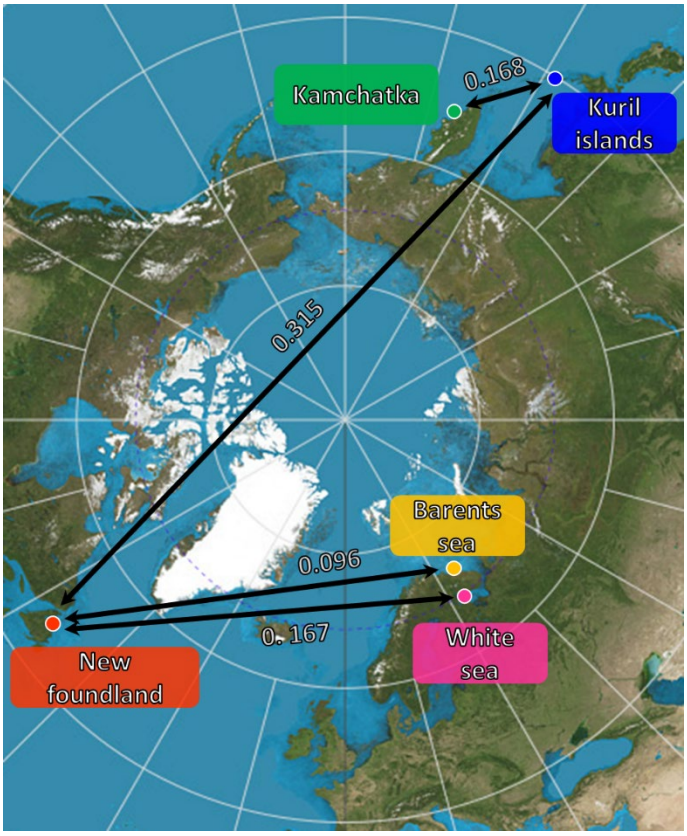

Kamchatka
0.168
Kuril
islands
0.315
Barents
sea
0.096
0. 167
White
sea
New
foundland

Figure S2: 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).

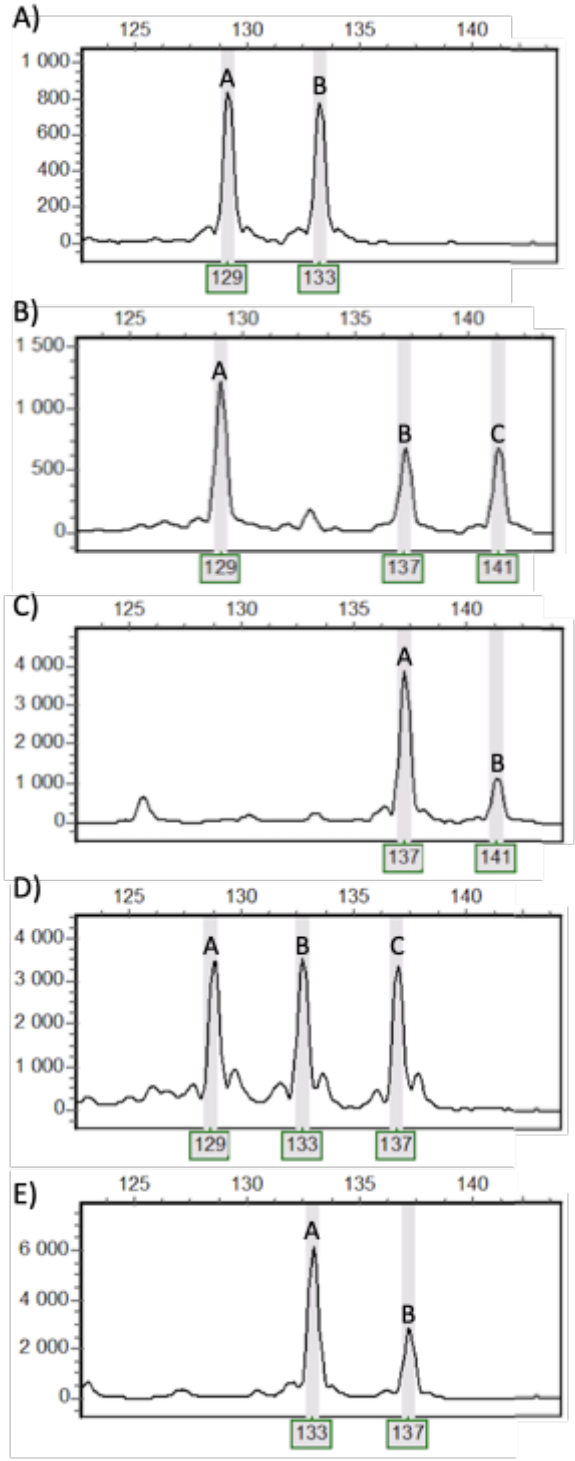


Figure S3: Distributions of Fst between pairs of sites among juveniles and adults (light blue violin plots). We reported the probability that difference of Fst between juveniles and adults would be due to a random (sampling, locus) effects as a Wilcoxon test (significance bar), the Fst values in each age cohort (Black dots), the extremum and mean values (dark blue bars).

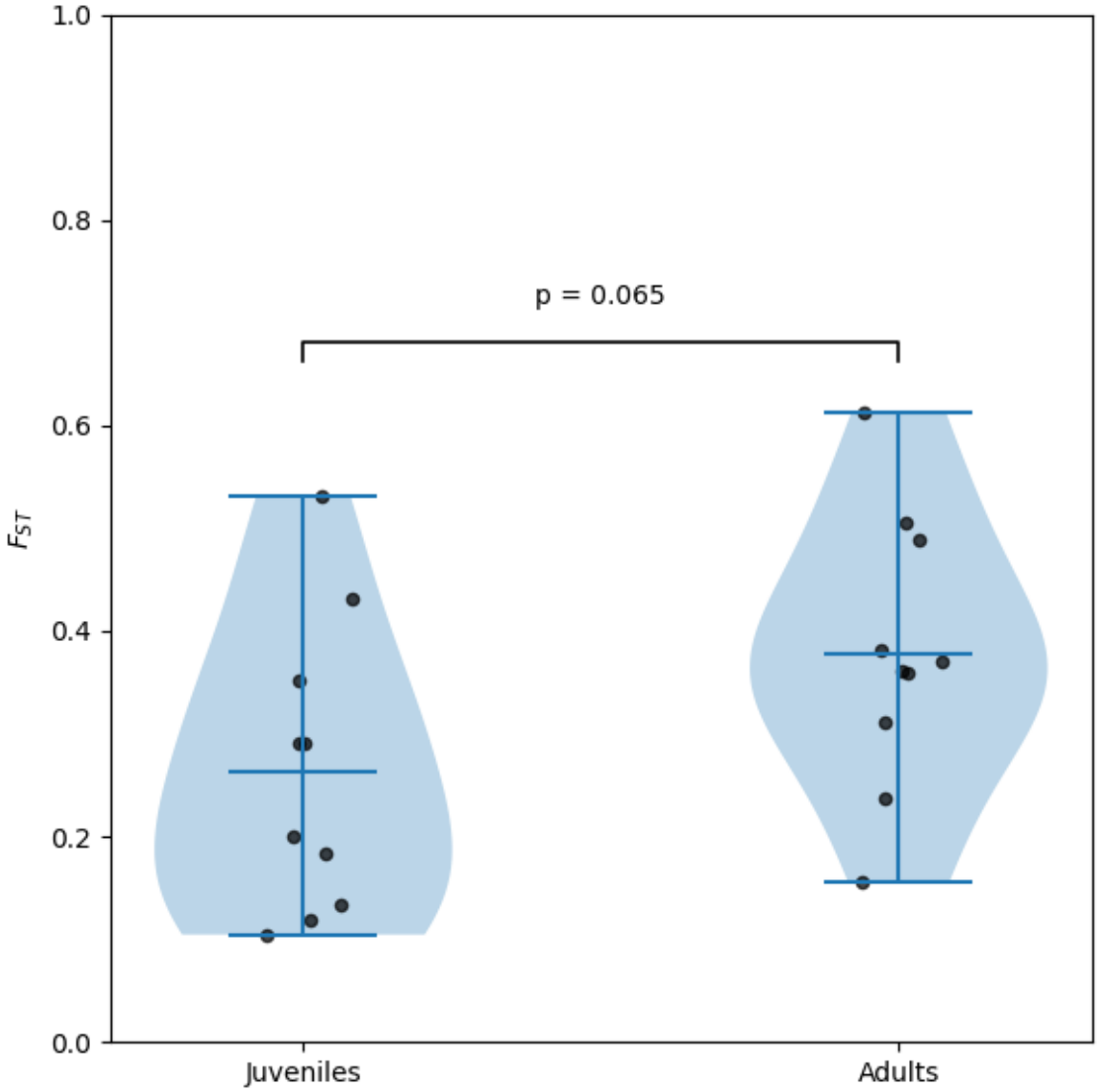
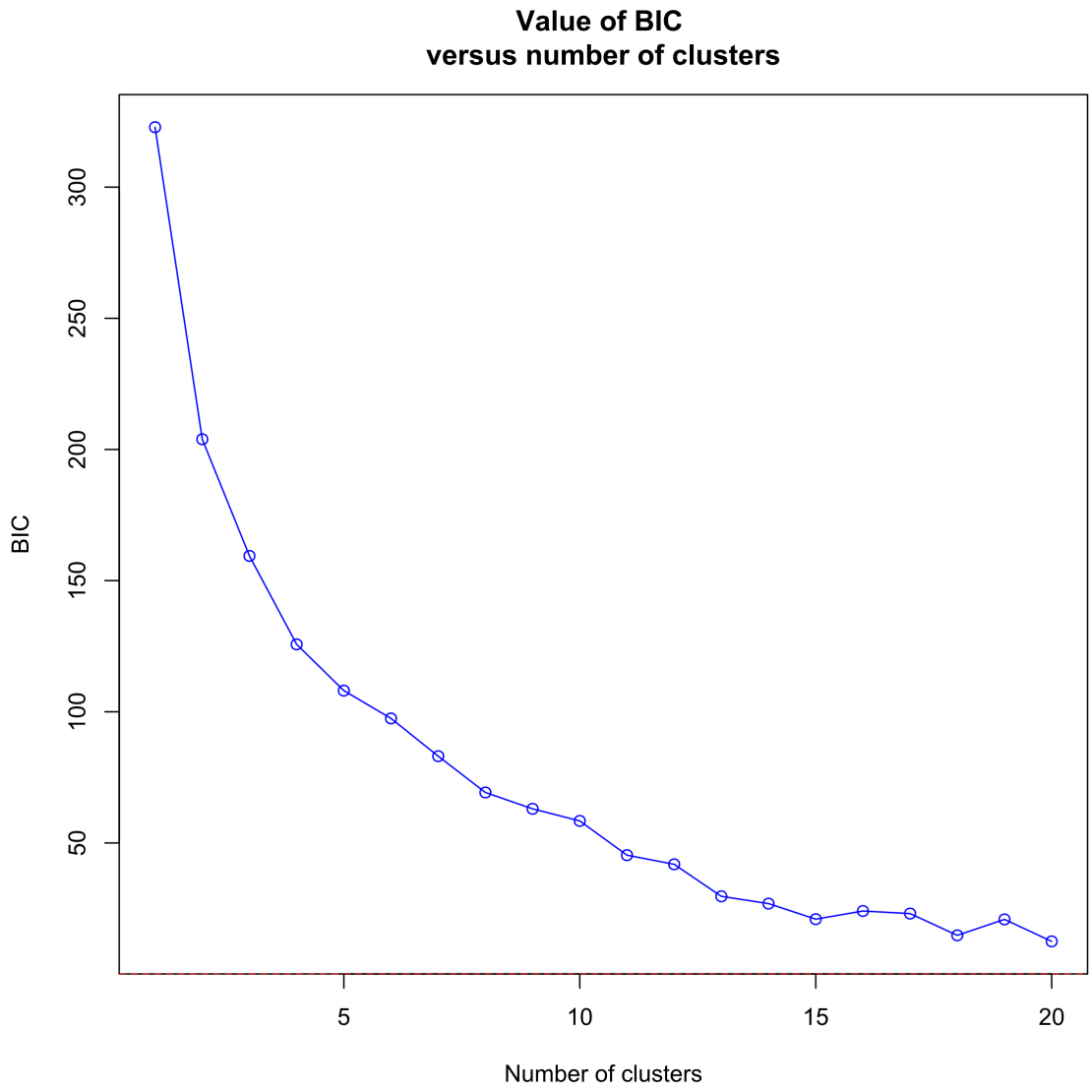



Figure S4: Change of the Bayesian information criteria (BIC) with increasing number of genetic clusters used in the Discriminant Analysis of Principal Components to investigate the genetic differentiation between individuals and among sampled sites and cohorts. The continuously decreasing pattern observed is typical of a stepping-stone structure of the studied demes.