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Natural Selection at the Edge of Life: Allelic Polymorphism and Recruitment in High Latitude Arctic Char (*Salvelinus alpinus*) Generated and Maintained by Environmental Extremes

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Abstract: Information from extreme habitats of polymorphic populations is expected to answer questions related to evolutionary changes occurring at their niche border. Landlocked and resident/anadromous populations of the Arctic char (*Salvelinus alpinus* (L.) sp. complex), sampled during three successive years in northern Svalbard, were assessed for life-history characteristics, allele-frequency variation at the polymorphic *EST-2** locus, and tested for genotype–environment interactions. While year-class strength correlated positively with mean air temperature during the two summers preceding spawning, the *EST-2*100* allele frequency correlated positively with the air temperature in June after birth. By affecting two asynchronous and independent population variables, which are both no doubt correlated with fitness, annual temperature variation is suggested to generate and maintain polymorphism in Arctic char in the High Arctic by modifying year-class strength and selecting for variant alleles influencing cold resistance. Intra- and inter-population comparisons imply an additional selection between the two variant *EST-2** alleles to operate ontogenetically, with a fixation on the 90 allele in landlocked and resident individuals and the 100 allele in anadromous individuals. The selective mechanism behind the latter processes is unknown. Because of low substrate specificity, however, esterases may form a reserve of adaptive ability towards environmental stress during contrasting conditions.

Keywords: esterase; temperature; recruitment; population dynamics; sympatry; anadromy

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1. Introduction

Mechanisms maintaining polymorphic loci in populations are one of the main problems in population genetics, and a perpetual challenge for evolutionary and conservation ecologists. Under what circumstances does natural selection maintain rare alleles in a population? Information from extreme habitats of polymorphic populations may answer such questions. Life at the distributional edge of many species encounters severe environmental conditions, and genetic or phenotypic heterogeneity may be a prerequisite to adaptive changes and population survival under unstable circumstances.

High Arctic lakes constitute extreme habitats, in which landlocked, isolated, and ectothermic organisms may be genetically trapped, and because of colonization difficulties and/or for physiological and ecological reasons, many northern lakes are inhabited by one single taxon of salmonid fish [1–3]. On an evolutionary time scale, such surviving populations have had to demonstrate a high capacity of resilience by either adapting to major physical and biotic changes or utilizing available genetic variation; otherwise, they go extinct [4]. Exposure to contrasting environmental changes during repeated events of colonization and isolation during successive episodes of interglaciations is probably a key factor explaining the taxonomic diversity of the extreme phenotypic and ecological plasticity seen among northern salmonids, such as chars (*Salvelinus* spp.) (e.g., [5–12]).

Numerous studies have illustrated how incomplete sexual barriers and wide niche utilization may allow gene flow between sympatric populations of congeneric salmonid taxa (see ref. in [13]), while in central populations, besides adaptive changes to environmental gradients, increased interspecific competition and niche compression may cause other adaptive changes, such as character displacement (e.g., [14,15]). Until recently, few studies had demonstrated evolutionary changes occurring at the niche border (e.g., [16–18]).

Functional and kinetic differences between allelic variants have been demonstrated in numerous loci and fish taxa (e.g., [19–25]). In the Arctic char (*Salvelinus alpinus*) species complex, the highly polymorphic esterase loci offer a unique tool in testing adaptive changes at the northern species borders because of the correlation between allele frequencies and temperature, both within populations, between year classes, and among populations from different latitudes [26–28]. Similar correlations have been reported in other fish taxa as well [29–33]. Major activity changes in esterases have also been documented in individual fish experimentally exposed to increased temperature regimes [34], and a preference for hot-water effluents by individual fish with appropriate esterase genotypes has been suggested to occur [35].

In the present study, data on otolith age and allele-frequency variation within the diallelic *EST-2** locus of unexploited populations of Arctic char sampled in northern Svalbard were used to test genotype–environment interactions by analyzing the impact of air temperature on year-class strength and allele-frequency distribution.

2. Materials and Methods

2.1. The Arctic Char Species Complex

The Arctic char (*Salvelinus alpinus* (L.)) sp. complex is the northern-most freshwater fish taxon, and the circumpolar distribution of landlocked, resident, and anadromous populations include High Arctic regions, such as Svalbard, Peary Land, and Ellesmere Island. Although exploiting a variety of habitats, reproduction and over-wintering are invariably restricted to freshwater [1,36,37]. Arctic char are iteroparous, and typically spawn in autumn. While the southern border of this taxon is controlled by interspecific interactions, the northern border seems to be controlled by abiotic barriers [4,38–41]. While Low Arctic populations commonly employ anadromy to maximize energy intake during the short summer, residency in freshwater all year round seems to be more common among the extreme northern-most populations of char [1,40]. The landlocked populations of char in Svalbard commonly express a bimodal size and age distribution, with cannibalism reinforcing the numerical preponderance of large-sized individuals [42–44]. In contrast, populations with mixed resident and anadromous individuals demonstrate comparatively even polymodal size and age structures.

2.2. Sampling and Electrophoretic Analysis

A series of unexploited landlocked and mixed resident–anadromous populations of Arctic char were sampled in northern Svalbard (Figure 1) during the summers of 1979–1981 (Table 1). Test fishing, using multiple mesh size gillnets (10–75 mm) [45], was carried out to assess population structure, prey choice, parasite acquisition, and organic pollutants [40,42,43,46]. Sagittal otoliths were removed for the analysis of age and year-class identification. The age-frequency distribution of the char populations was treated as sampled by the experimental gillnets, i.e., without subsequent adjustment for possible gillnet selection effects and considered to reflect the relative strength of the various year classes represented. In addition, allele-frequency variation within the *EST-2** locus was screened with starch gel electrophoresis of serum samples [47] in order to study systematic status [26], genetic differentiation [48,49], and the possibility of a temperature-induced selection processes.

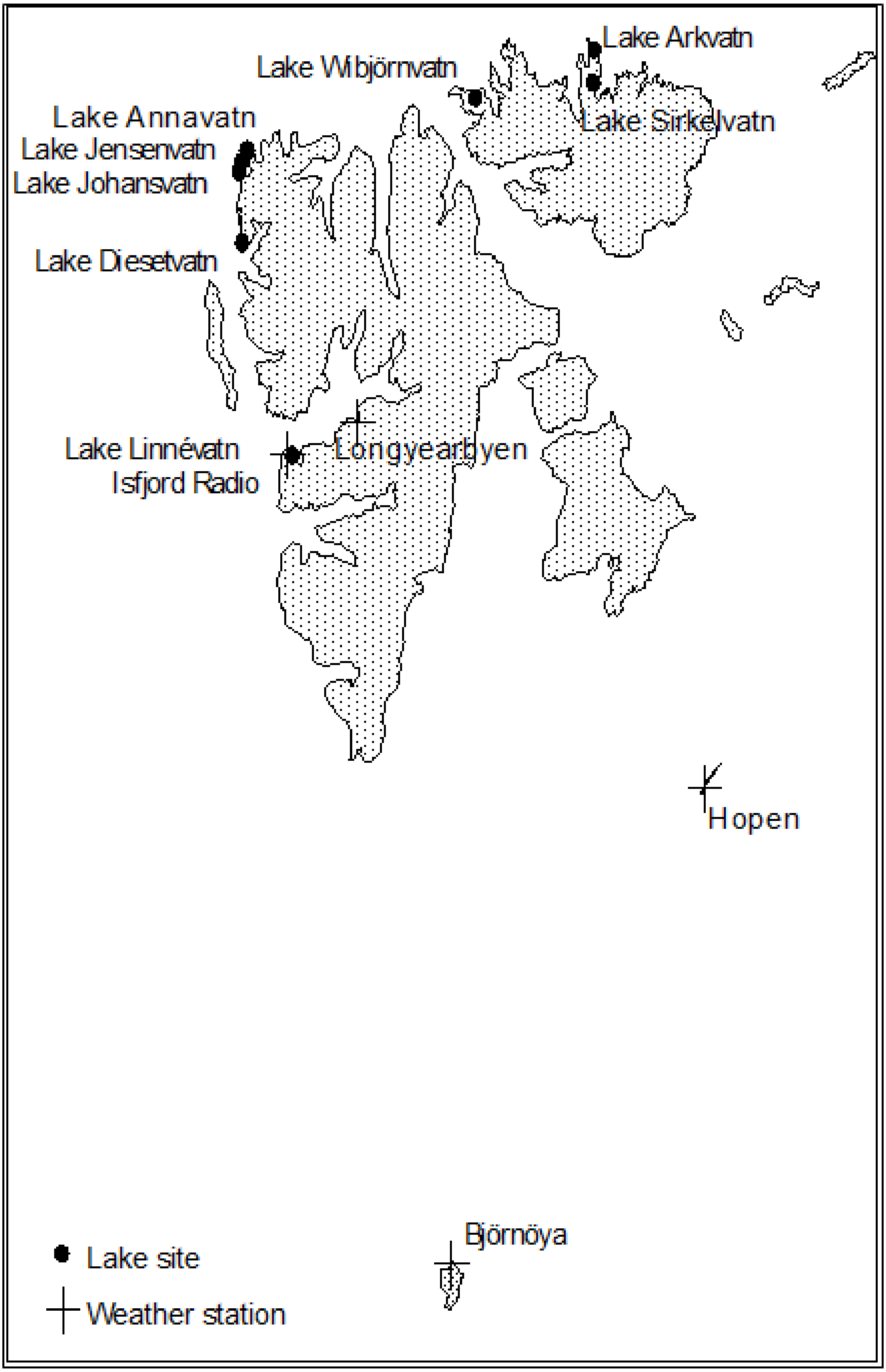

Figure 1. The geography of Svalbard at 74–81° North and 9–33° East, with sampling sites and weather stations.

Table 1. Geographic position of lakes surveyed in Svalbard, and the size and age range of the samples of Arctic char analyzed. While the char from Lakes Diesetvatn and Sirkelvatn were collected with seine and hook, respectively, the remainder were caught with multiple mesh size gillnets. The life-history abbreviations refer to anadromous (A), resident (R), and landlocked (L) populations.

Lakes	**Position of Outlet**		**Life-History**	**N**	**Length**	**Weight**	**Age**	**Date of Sampling**
	Latitude	**Longitude**	**A/R/L**		**MTL (mm)**	**(Gram)**	**(Years)**	**(y-m-d)**
Diesetvatn	79°12′ N	11°22′ E	A	5	427–578	-	8–13	1979.07.22
Linnévatn	78°04′ N	13°48′ E	A + R	17	114–262	9–137	5–12	1980.09.09
Arkvatn	80°25′ N	22°57′ E	A + R	108	101–615	7–1880	5–24	1980.08.16
Wibjørnvatn *	80°09′ N	18°28′ E	L	26	97–433	6–520	4–26	1980.08.20
Jensenvatn	79°43′ N	10°51′ E	L	7	371–590	562–1990	7–18	1979.07.29, 1981.08.24
Johansvatn *	79°40′ N	10°48′ E	L	34	100–565	7–1300	6–24	1981.08.21
Annavatn *	79°46′ N	10°53′ E	L	28	117–495	8–825	9–26	1981.08.23
Sirkelvatn	80°12′ N	22°52′ E	L	4	382–420	-	26–27	1980.07.16

* These names are unofficial working names used by the author in previous reports; thus, they may be altered in future publications.

2.3. The *EST-2** Locus

The *EST-2** locus, with its two codominant alleles 90 and 100, codes for a monomeric esterase enzyme. Nyman and Shaw [50] suggested that the esterase coded for by the *EST-2*100* allele has a higher optimal temperature than the variant (90) allele, and the frequency of the 100 allele demonstrates a positive correlation with temperature and declining frequencies in latitude (e.g., [10,26]. Temperature is known to influence enzymatic processes, including the activity of hydrolyzing enzymes, such as esterases. The functional significance of the products of the *EST-2** locus in Arctic char is, however, unknown, and a precise classification is difficult due to their overlapping substrate specificity. Using substrate and inhibitor-specificity methods, Nyman [51] classified the polymorphic serum esterase in salmonids as a carboxylic ester hydrolase with a selective affinity for alpha-naphthyl propionate. Carboxyl esterases hydrolyze various organic carboxy-ester-bonds, including lipid substrates, and in the Arctic char, the *EST-2** allozymes are present in the serum, liver, muscle, and external mucus [26].

2.4. Statistical Analysis

For genotype–temperature comparisons, air temperature data for the period 1956–1975 were available from Jan Mayen and another four weather stations in Svalbard (Figure 1). Complete sets of monthly mean air temperatures were considered variables adequately reflecting the thermic conditions in the lakes during summer. The closest weather stations were Isfjord Radio and Hopen, with Isfjord Radio being more representative of the western parts affected by the Golf Current, and Hopen being more representative of the eastern and harsher regions of Svalbard.

Linear association was tested using Pearson's coefficients for air temperature and two different sets of year-class variables. Correlations between relative year-class strength and mean annual, seasonal, and monthly temperatures were restricted to 1959–73, with the oldest year classes being disregarded because of their rare occurrence in the catches, and the youngest year classes because of the size-selective properties of the gillnets [45]. In order to identify seasonal patterns in relationships, and to avoid unwarranted conclusions because of spurious associations expected to occur in any large matrix of bivariate comparisons, year-class strength correlations were also tested with a displaced series of mean temperature representing the years before, as well as after, the actual year of birth. The probability values were adjusted for the number of tests using the sequential Bonferroni technique [52]. The correlation between the *EST-2*100* allele frequency and mean annual temperature was restricted to the middle year classes of 1960–1971, assumed to be least affected by ontogenetic changes in viability.

3. Results

The number of individuals from different year classes of the five landlocked populations examined varied greatly, suggesting variable success in recruitment across the years as a reasonable explanation. In the sample, the number of char born in 1959–63 and 1972–74 surpasses the number of char born during the colder period of 1964–71, indicating a possible covariation with temperature (Figure 2). Linear correlation tests with the pooled age structures, presented as relative year-class strengths for landlocked populations, showed positive relationships with temperature for June–September of the preceding year ($R^2 = 0.550$, n = 15, $p = 0.002$), as well as for the same period two years earlier ($R^2 = 0.493$, n = 15, $p = 0.004$). A combination of the mean temperatures during the two previous summers was found to explain 73 percent of the year-class strength of landlocked Arctic char in a given year ($p < 0.001$). When tested on the total sample of char, the correlation remained, proving that year-class-strength determination basically takes place in June–September of the previous year ($R^2 = 0.624$, n = 15, $p < 0.001$, Figure 3A) with a mean summer air temperature of below 3 °C, generating fewer recruits than the predicted average year class the next year (Mann–Whitney U-test, U = 4.0, $p < 0.01$).

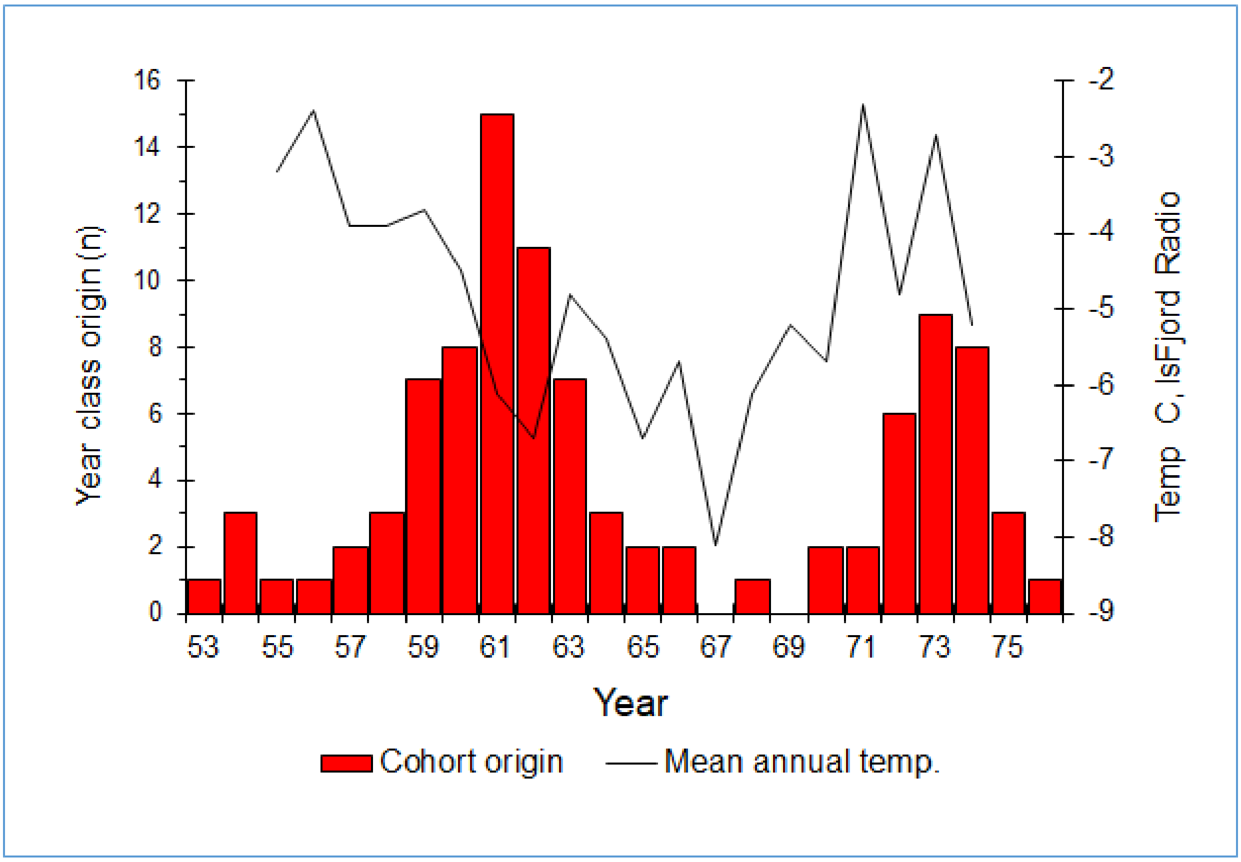

Figure 2. Year-class strength, shown as pooled numbers of all sampled landlocked char born in specific years, and the corresponding mean annual air temperature recorded at Isfjord Radio weather station.

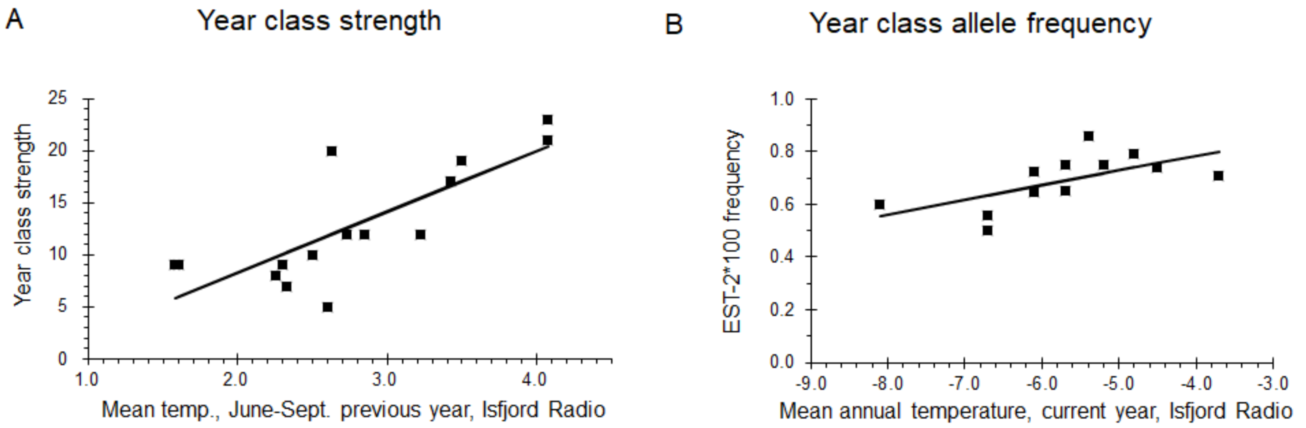

Figure 3. Correlation between air temperature recorded at Isfjord Radio. (**A**) Year-class strength, shown as pooled numbers of all sampled char born in the years 1959–73 (Mean temp., June–September, the year previous to birth), and (**B**) frequencies of the *EST-2*100* allele in the year classes 1960–71 (Mean annual temp., current year).

The *EST-2*100* allele-frequency distribution among year classes of the total sample correlated positively with mean air temperature ($R^2 = 0.390$, $p = 0.030$, n = 12, Figure 3B). More specifically, in landlocked populations, the correlation suggests selection for the 100 allele when the mean air temperature exceeds 1.5 °C in June, i.e., shortly after hatching ($R^2 = 0.842$, $p < 0.001$, n = 9).

While anadromous populations intermix genetically via strayers and thus maintain genetic variation and geographic cohesion, alleles in resident and landlocked populations tend to become fixed due to isolation, reduced population size, and perhaps less unstable environmental conditions (Figure 4). In landlocked High Arctic populations, this could lead to a fixation of the *EST-2*90* allele, as seems plausible from a comparison of the allele frequencies of the anadromous, resident, and landlocked populations (Table 2), with all the resident and landlocked populations possessing lower frequencies of the 100 allele (Mann–Whitney U-test, 10 pop., U = 0.0, $p = 0.017$). In one anadromous population (L. Arkvatn), a dramatic increase occurs in the frequency of the 100 allele at the age (>14 years) and size (>200 mm) at smoltification. Deviation from Castle–Hardy–Weinberg proportions and the change in allele frequencies, indicating a shift in the direction of selection, is also apparent (Table 3). This suggests an opposite, strong selective process to operate during a few weeks of feeding in saltwater. If the coastal water temperature is higher or lower than in fresh water, the area is not known. Differences in genotype distribution between landlocked (pooled) and anadromous (L. Arkvatn) individuals in three successive age groups, namely 4–10, 11–20, and 21–27 (Chi-square = 7.32–27.62, $p < 0.005$, d.f. 1), imply that old anadromous char tend to be homozygous for the 100 allele, whereas old landlocked char tend to be homozygous for the 90 allele (Figure 5). The present data do not yield comparisons of phenotype performance within year classes, although such an analysis would probably illustrate genetic differentiation [23,24].

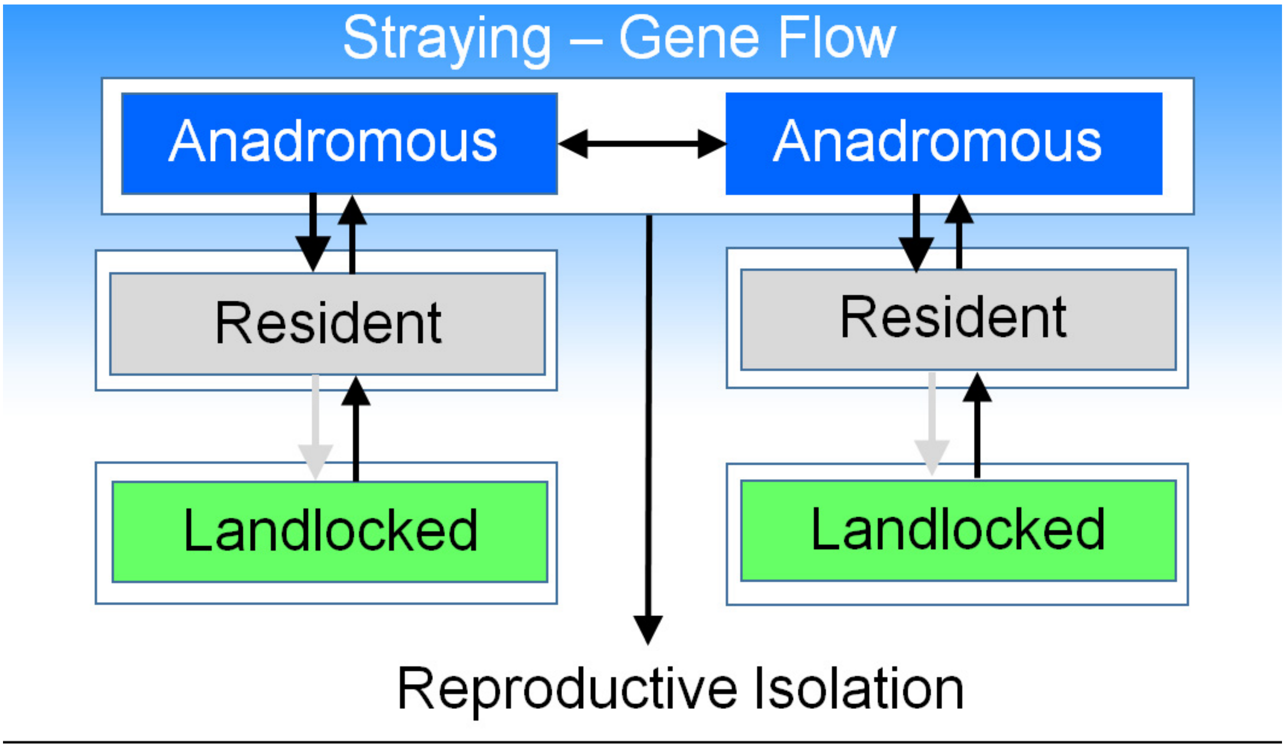

Figure 4. A model demonstrating the evolutionary processes comprising gene flow and/or reproductive isolation within two closely oriented gene pools of anadromous, resident, and eventually landlocked Arctic char.

Table 2. Observed allele and genotype frequencies, their expected genotype distribution (in parentheses), deviation from the Castle–Hardy–Weinberg proportions, and the 95% confidence interval at the *EST-2** locus in anadromous (A), resident (R), and landlocked (L) Arctic char in Svalbard.

				Observed (Expected) Distribution					
Lake	**Life-Hist.**	**n**	**f(100)**	**90/90**	**90/100**	**100/100**	**$\chi 2$**	***p***	**95% c.i.**
Diesetvatn	A	5	0.900	0 (0.1)	1 (0.9)	4 (4.1)	0.062	0.97	0.190
Linnévatn	A	4	0.875	0 (0.1)	1 (0.9)	3 (3.1)	0.082	0.96	0.234
	R	13	0.692	1 (1.2)	6 (5.5)	6 (6.2)	0.090	0.96	0.181
	Total	17	0.735	1 (1.2)	7 (6.6)	9 (9.2)	0.057	0.97	0.151
Arkvatn	A	58	0.819	4 (1.9)	13 (17.2)	41 (38.9)	3.456	0.18	0.072
	R	50	0.610	7 (7.6)	25 (23.8)	18 (18.6)	0.129	0.94	0.098
	Total	108	0.722	11 (8.3)	38 (43.3)	59 (56.3)	1.636	0.44	0.061
Wibjørnvatn	L	26	0.788	1 (1.2)	9 (8.7)	16 (16.2)	0.037	0.98	0.113
Jensenvatn	L	7	0.714	0 (0.6)	4 (2.9)	3 (3.6)	1.120	1.12	0.241
Johansvatn	L#1	17	0.735	1 (1.2)	7 (6.6)	9 (9.2)	0.057	0.57	0.151
Johansvatn	L#2	16	0.344	6 (6.9)	9 (7.2)	1 (1.9)	0.974	0.97	0.168
Johansvatn	Total	33	0.545	7 (6.8)	16 (16.4)	10 (9.8)	0.016	0.99	0.123
Annavatn	L	28	0.446	9 (8.6)	13 (13.8)	6 (5.6)	0.103	0.95	0.133
Sirkelvatn	L	3	0.000	3 (3.0)	0 (0)	0 (0)	-	-	-

Table 3. Observed allele and genotype frequencies, their expected genotype distribution (in parentheses), deviation from the Castle–Hardy–Weinberg proportions, and the 95% confidence interval at the *EST-2** locus in different sex and age groups of anadromous/resident Arctic char from Lake Arkvatn, Svalbard.

Age and Sex Groups	**Observed (Expected) Distribution**							
Age Groups, Total	**n**	**f(100)**	**90/90**	**90/100**	**100/100**	**$\chi 2$**	***p***	**95% c.i.**
9–5	35	0.600	5 (5.6)	18 (16.8)	12 (12.6)	0.179	0.91	0.117
10–14	29	0.655	4 (3.5)	12 (13.1)	13 (12.5)	0.206	0.90	0.125
15–19	28	0.893	1 (0.3)	4 (5.4)	23 (22.3)	1.797	0.41	0.083
20–24	15	0.833	1 (0.4)	3 (4.2)	11 (10.4)	1.176	0.56	0.136
Age groups, males								
9–5	26	0.596	5 (4.2)	11 (12.5)	10 (9.2)	0.383	0.83	0.136
10–14	17	0.676	1 (1.8)	9 (7.4)	7 (7.8)	0.746	0.69	0.160
15–19	15	0.933	1 (0.1)	0 (1.9)	14 (13.1)	15.00	<0.001	0.091
20–24	12	0.833	1 (0.3)	2 (3.3)	9 (8.3)	1.920	0.38	0.152
Age groups, females								
9–5	9	0.611	0 (1.4)	7 (4.3)	2 (3.4)	3.645	0.16	0.230
10–14	12	0.625	3 (1.7)	3 (5.6)	6 (4.7)	2.613	0.27	0.198
15–19	13	0.846	0 (0.3)	4 (3.4)	9 (9.3)	0.430	0.81	0.142
20–24	2	0.750	0 (0.1)	1 (0.8)	1 (1.1)	0.222	0.89	0.433

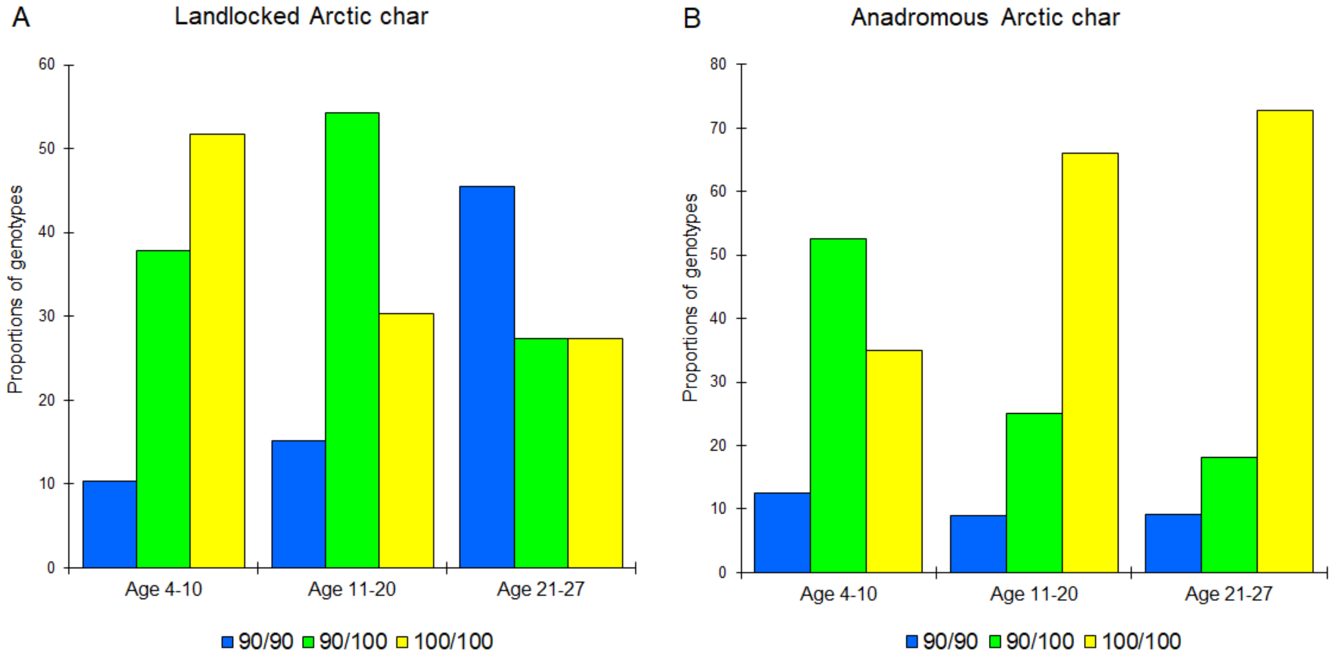

Figure 5. Ontogenetic shifts in the *EST-2** genotype dominance in (**A**) landlocked (pooled populations, n = 97) and (**B**) anadromous (Lake Arkvatn, n = 107) Arctic char sampled in Svalbard, 1979–81.

4. Discussion

In addition to cannibalism and parasites [43], temperature is also found to affect the magnitude of year-class strength and thus the demography of High Arctic populations of Arctic char; therefore, it may thus explain the exaggerated bimodal population structure recorded in 1979–81 in Svalbard. The present results demonstrate a climatic impact on year-class strength both one and two years before birth, thus pointing at the significance of parental traits affecting reproduction, such as the sexual maturity process, frequency of spawners, and number and quality of eggs.

As in most northern animals, any factor reducing the accumulation of energy of juveniles during their first summer is likely to reduce their survival during the first critical winter. This has long been a principle suggested to govern year-class strength among temperate fishes and has been especially emphasized among such species at their northernmost distributional limits (e.g., [53]). A latitudinal reduction in the growth period, used in the past as an evolutionary argument for autumn spawning and early spring hatching among northern salmonids [54], may thus be a serious constraint to somatic, as well as gonadal, growth. Anadromous char may stay for an entire year in freshwater in order to fully develop their gonads and may need at least another year to recover after spawning [55]. Energy resources built up by early spring may influence whether energy is allocated to gonads or continued somatic growth [56,57]. In Svalbard, individual landlocked char seem to spawn at least every third year until well above 20 years of age [43]. The present results suggest that the maturity process is influenced by the temperature in the summer preceding spawning, with a mean temperature for June–September of less than ca 3 °C, generating fewer recruits than average in the next year. A series of warmer summers provide the potential for higher numbers of recruits in High Arctic char which, during the actual year of hatching, face selection among variant *EST-2** genotypes. Three successive "warm" summers may thus generate a large year class of individuals with a reduced ability to cope with extreme cold. The temporally displaced selection processes influencing year-class strength and allele frequency are proposed to grant the maintenance of both alleles, and thus also polymorphism, in isolated populations living in the far north.

This model may perhaps explain the genetic divergence of sympatric Arctic char in Lake Johansvatn, Danskøya [42]. Almost contrasting distributions of genotypes shift from one modal group to another in less than 10 years (Figure 6). However, differential mortality is unlikely to cause a dramatic change in *EST-2*100* frequencies between two modal gene pools of adult fish. One alternative explanation is that the lower modal group with a high allele frequency (0.74 ± 0.15) was born during a series of warmer years or is the offspring of a rich year class of parents born during a series of such years, while the low frequency group (0.34 ± 0.17) has the opposite origin. The two groups thus seem to be genetically isolated by their year of recruitment. Another explanation is simply that the Arctic char in Lake Johansvatn is yet another example of coexisting, reproductively isolated populations of either pre- or post-glacial origin, or both (e.g., [8,48,49,58–60]).

The findings in Svalbard raise the question of the exact mechanisms involved in the selection, and thus the functional significance of the allozymes produced by the *EST-2** locus in Arctic char. As shown by the latitudinal gradients and year class–temperature correlations, esterases seem primarily to be involved in a temperature-dependent process affecting juvenile survival. Koehn [30] provided elegant molecular evidence of temperature-related differences in the direct activity of different allozymes, fitting with his observations of a latitudinal cline of allele frequencies. The present study adds a selective process connected with differential survival during repeated transformations to a life in the sea. The striking decline of homozygotes and heterozygotes for the *EST-2*90* allele among older and larger individuals in Lake Arkvatn strongly suggests a selective loss of individuals from the system (Table 3). Selection favoring the *EST-2*90* allele in freshwater and the *EST-2*100* allele in saltwater suggests a disruptive selection, although the mechanism of such a selective process is not known. Anadromy manifests a major change in physiology, growth, and diet, as well as in dramatic exposure to the marine environment. Additionally, in comparison to other salmonids, Arctic char seem to be less capable of acclimating to the marine habitat. Besides the stress, the metamorphosis of smoltifying fish induces a number of extraordinary physiological changes, and the exact mechanism of selection may be found among changes in the activity of various enzymes and hormones, increased lipid utilization, etc. Individuals which have not yet acquired the ability to osmoregulate die if they are transferred to sea water, and smolts which are prevented from migrating to sea may also die (e.g., [61]). The fact that esterases are active in external mucus may indicate a defense function towards various environmental toxicants. Smith [32] indicated that the selection agent may be an associated parameter, such as salinity, pH, or even food, because esterases are known to act on externally derived substrates. Carboxyl esterases have been suggested to form a reserve of adaptive ability towards certain toxicants and pollutants, and the fact that they have a low substrate specificity makes them more efficient in destroying a variety of foreign agents [62]. Another parameter combining temperature with differential survival and smoltification is the photoperiod. Temperature, and thus latitudinal gradients and ice cover duration, are likely to affect the photoperiod perception of fish, and this has been pointed out as a major synchronizing cue for year-class strength and seasonal cycles of growth, as well as smolting in juvenile salmonids [63,64].

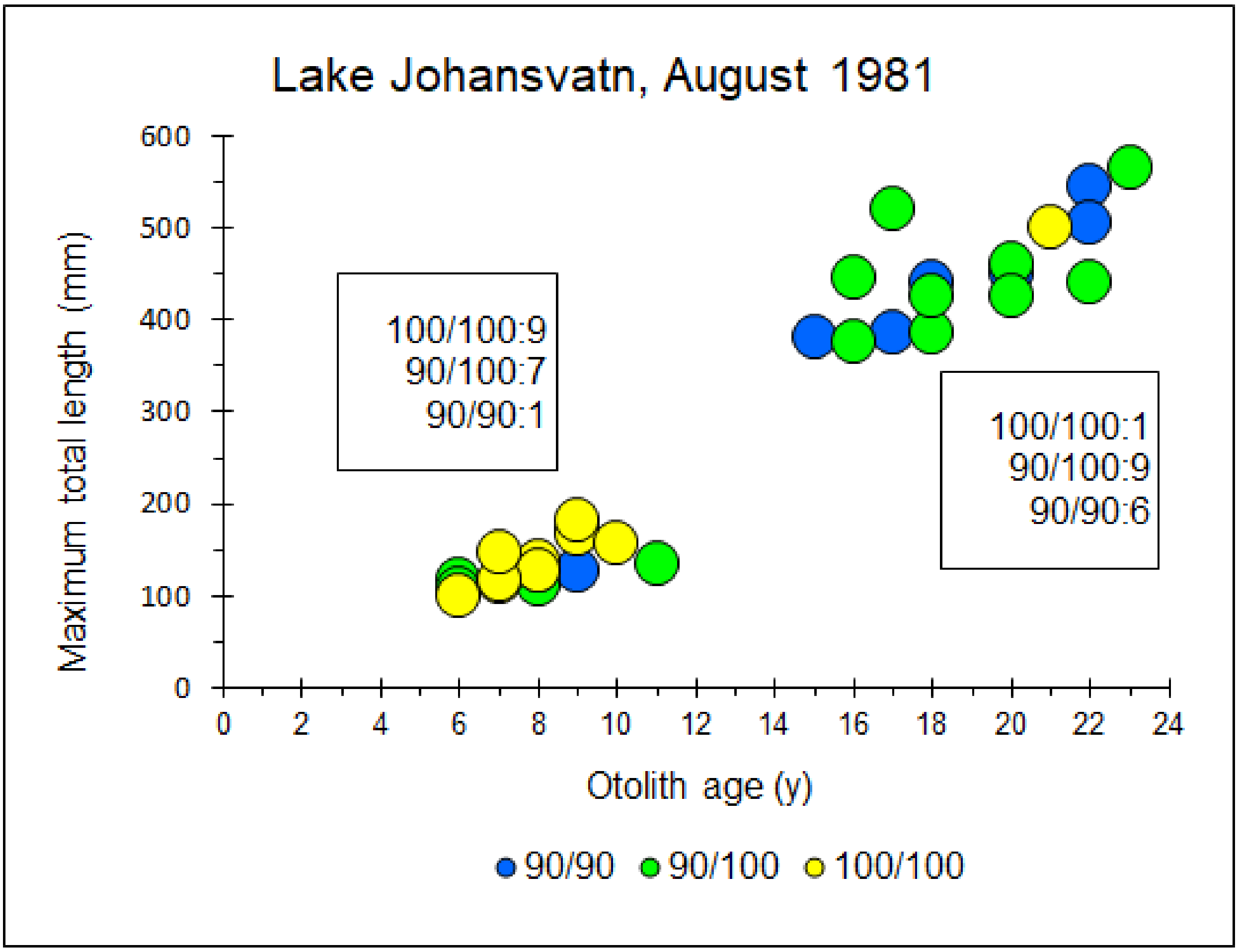

Figure 6. *EST-2** genotype designation and length by otolith age correlations in two modal groups of landlocked Arctic char sampled in Lake Johansvatn, Danskøya, Svalbard, 20–21 August 1981.

Other enzyme loci isozymes, particularly the products of the *LDH-B** locus [24], are also differentially selected in different thermal environments. This suggests the possibility of polygenic correlations, including the combined effects of several genes, and in an important study of vendace (*Coregonus albula*) transplanted 92 years earlier into a new and colder environment, significant changes in eight of ten polymorphic loci were detected [65].

5. Conclusions

The relative strength of year classes and their frequency in the *EST-2*100* allele has been found to correlate positively with summer temperature in high latitude Arctic char. The climatic impact on these two fitness-correlated population variables seem to vary asynchronically, with relative year-class strength being correlated with temperature during one or two summers preceding spawning, and year-class allele frequency being correlated with temperature after hatching. The results suggest temperature affects parental traits, thus affecting reproductive success, as well as selection of a variant allele influencing cold resistance. As a complication, an additional ontogenetic option between the two variant *EST-2** alleles, generated by selection in coastal habitats, may also evolve. Varying selection processes during warm and cold summers, and because of contrasting habitat conditions for resident and anadromous char, may thus generate and maintain allelic polymorphism in these marginal populations. My results also imply that landlocked populations in the High Arctic may have adapted to cold freshwater conditions and, in the process, lost capability to adopt an anadromous life history. With the ongoing dramatic increase in environmental temperature in the Arctic [66,67], these conclusions may already be historical.

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Conflicts of Interest: The authors declare no conflict of interest.

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