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The genome of a landlocked Atlantic salmon *Salmo salar* characterized through high-throughput sequencing

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A wide range of life-history tactics can be found within salmonid fish. The genetic basis for these adaptations remains largely unknown, but we have sought to investigate any large scale genetic changes associated with a non-anadromous life cycle. After the most recent ice age (approximately 9,500 years ago), some populations of Atlantic salmon *Salmo salar* L., were trapped in fresh water and developed into isolated landlocked populations that managed to complete a full life cycle without ever reaching the marine environment. To explore whether this transition was accompanied by gene-loss events, high-throughput sequencing of a non-migratory Namsblank ('småblank'), an Atlantic salmon from the river Namsen in Norway, was performed. There were no indications of loss of coding regions and a phylogenetic analysis based on the mitochondrial genome revealed a close genetic relationship between anadromous Atlantic salmon and Namsblank. Lack of large-scale genomic changes suggests that fine-scale (epi)genetic alterations and population genetics processes underlie adaptation to the landlocked life-style.

Key words: Landlocked, gene-loss, salmon, Illumina.

INTRODUCTION

Salmonidae exhibit a tremendous diversity of phenotypic traits both at the interspecific and intraspecific levels. Variation in its phenotypic traits generally relates to reproductive strategies, mobility associated with foraging tactics, habitat selection within lakes, and tendency for anadromy. Life-history variation in salmonids appears to be influenced by complex interactions involving the endocrine system, environmental parameters (temperature, photoperiod, feeding resources), individual characteristics (sex, age, or size), and their genetic background (Hendry et al., 2004; McCormick, 2009). The genetic determinants of these life-history tactics are still largely uncovered.

Most Atlantic salmon *Salmo salar* L. have an anadromous life cycle in which they hatch in fresh water, migrate to sea as juveniles, and return to fresh water to spawn and die. Migration towards the sea is triggered by light-induced hormonal burst in their first or second spring

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(Björnsson et al., 2011). Prior to, and during, this journey, they undergo smoltification. This metamorphosis represents a set of very diverse morphological, behavioral, metabolic, endocrine and physiological shifts. Many of these developmental transitions are necessary for successful acclimation to the seawater environment, including changes in osmotic regulation and induced growth rate (Björnsson et al., 2011; Dufour et al., 2012). The timing of this transition is triggered by internal information (metabolic status, age, etc.) and by environmental cues such as light and temperature. Some of these adaptations include heritable traits subject to natural selection (Hara et al., 2007; Nichols et al., 2008; Duston et al., 2011).

Entire populations of Atlantic salmon also complete their life cycle in fresh water. Such populations are found in lakes and rivers in several countries of the northern hemisphere, including USA, Canada, Finland, Sweden, Russia, and Norway (Kazakov, 1992; Garcia de Leaniz et al., 2007; King et al., 2007). Most populations represent “glaciomarine relicts” trapped by rising land and dropping sea levels following the last ice age some 10,000 years ago (Verspoor et al., 2007). Following these isolation events, non-migratory salmon populations adapted differently, depending on the environmental conditions in their freshwater habitat and developed new phenotypes. Although lakes may house larger specimens of Atlantic salmon (> 10 kg), the salmon trapped in rivers have stayed small probably due to limited space and stronger competition for food (Berg, 1985; Gibson et al., 1996). In some aquatic taxa, the loss of a marine phase has even been linked to speciation events (Waters and Wallis, 2001).

The landlocked Atlantic salmon of the Norwegian river Namsen, Namsblank, constitutes an island population that has been isolated for approximately 9,500 years (Frankham, 1997). The habitat area available for the Namsblank population includes a 75 km stretch of the upper part of the river Namsen that together with the lower reaches of a number of tributaries amounts to 12.5 km^2 of water-covered area (Sandlund et al., 2014). Effective population size estimates indicate a few thousand Namsblank fish in total, and Namsblank represents a unique cluster among Atlantic salmon populations with regard to biological and genetic characteristics. Genetic analyses suggest that Namsblank can be further divided into different subpopulations with estimated effective population sizes of a few hundred fish (Sandlund et al., 2014).

Namsblank individuals are among the smallest relict Atlantic salmon in the world and rarely grow larger than 30 cm (300 g). Fish keep the visual appearance of a young salmon parr (Berg, 1956; 1985), which may indicate that a range of developmental changes normally occurring early in life of anadromous (migrating) Atlantic salmon are not induced, along with the need to migrate, smoltify and grow to full size (Berg, 1985). The loss of such features can be linked to genetic, epigenetic or environmental differences (Garcia de Leaniz et al., 2007).

As a result of a whole-genome duplication (WGD) event 25 to 100 million years ago, salmonids have a tetraploid genome that is currently in the process of rediploidization (Allendorf et al., 1984; Macqueen and Johnston, 2014). It has been suggested that polyploids possess greater evolutionary potential than their diploid progenitors, as genetic redundancy creates opportunities for duplicated genes to be lost or to diverge and acquire new functions (Lien et al., 2016), in addition to epigenetic remodeling affecting gene expression (Comai, 2005). Thus, polyploidy may allow organisms to evolve faster or in novel directions compared to their diploid progenitors, leading to increased evolutionary success due to improved ability to diversify and adapt to new niches.

In this work, we wanted to investigate whether the Namsblank phenotype is linked to genetic changes when compared with anadromous Atlantic salmon. Given the evolutionary history of Namsblank and the nature of the salmonid genome, it is not unreasonable to expect both large-scale and small-scale genetic changes, either through genetic drift or as a result of changes in selection pressure. As an initial screen for large-scale genetic changes, we used high-throughput sequencing as an approach to identify gene-loss events in the Namsblank genome. In order to estimate the evolutionary distance between migratory Atlantic salmon and the landlocked Namsblank, a phylogenetic analysis was also performed based on the complete mitochondrial genome. This represents the first sequence data reported from a landlocked Atlantic salmon population.

MATERIALS AND METHODS

DNA was isolated from kidney tissue of an adult, male Namsblank specimen (Figure 1) using the DNeasy Blood & Tissue Kit (QIAGEN AB, Oslo, Norway) after homogenization using a glass mortar and pestle. The extracted DNA was fragmented and a 3 kb mate-pair library prepared. Sequencing (two lanes) was performed using the Illumina HiSeq 2000 platform (GATC Biotech AB, Konstanz, Germany).

Complete Atlantic salmon mitochondrial genome sequences were downloaded from GenBank (National Center for Biotechnology Information) and aligned using the Clustal W algorithm (Thompson et al., 1994). Sequence reads matching the mitochondrial genome database were identified using the Mega BLAST algorithm with default search parameters (word size 28) (Zhang et al., 2000). Matching reads were extracted from the Illumina read database and aligned with a complete reference Atlantic salmon mitochondrial genome that showed a high degree of sequence similarity with our data (GenBank accession number JQ390056) using the CLC Genomics Workbench, version 6.0.4 (CLC bio, Aarhus, Denmark), and a consensus sequence was generated.

For a comparative gene-content analysis, all Atlantic salmon mRNA sequences deposited in GenBank were downloaded (48,205). Mega BLAST was used (with the same settings as above) to align the Illumina sequence reads obtained with the downloaded salmon mRNA data. Transcript sequences for which we had matching reads were successively removed in order to identify

Figure 1. Map of Norway showing sampling location (Namsen river).

regions of possible gene-loss. Primers were designed for a set of gene-loss candidates using Primer3 (http://bioinfo.ut.ee/primer3-0.4.0/primer3/). PCR was performed according to the manufacturer's instructions using Tfi DNA polymerase (Life Technologies, Oslo, Norway). The PCR cycling conditions were 94°C for 2 min; 30 cycles of 94°C for 30 s, 55°C for 30 s, 72°C for 1 min, and a final extension step at 72°C for 10 min. Amplified products were analyzed using an Agilent 2100 Bioanalyzer using a DNA 1000 kit (Agilent Technologies). PCRs were performed using DNA from the same Namsblank specimen as was originally submitted for sequencing in addition to a small panel of anadromous Atlantic salmon specimens samples from Norwegian (wild and farmed) and Irish (farmed) locations.

RESULTS

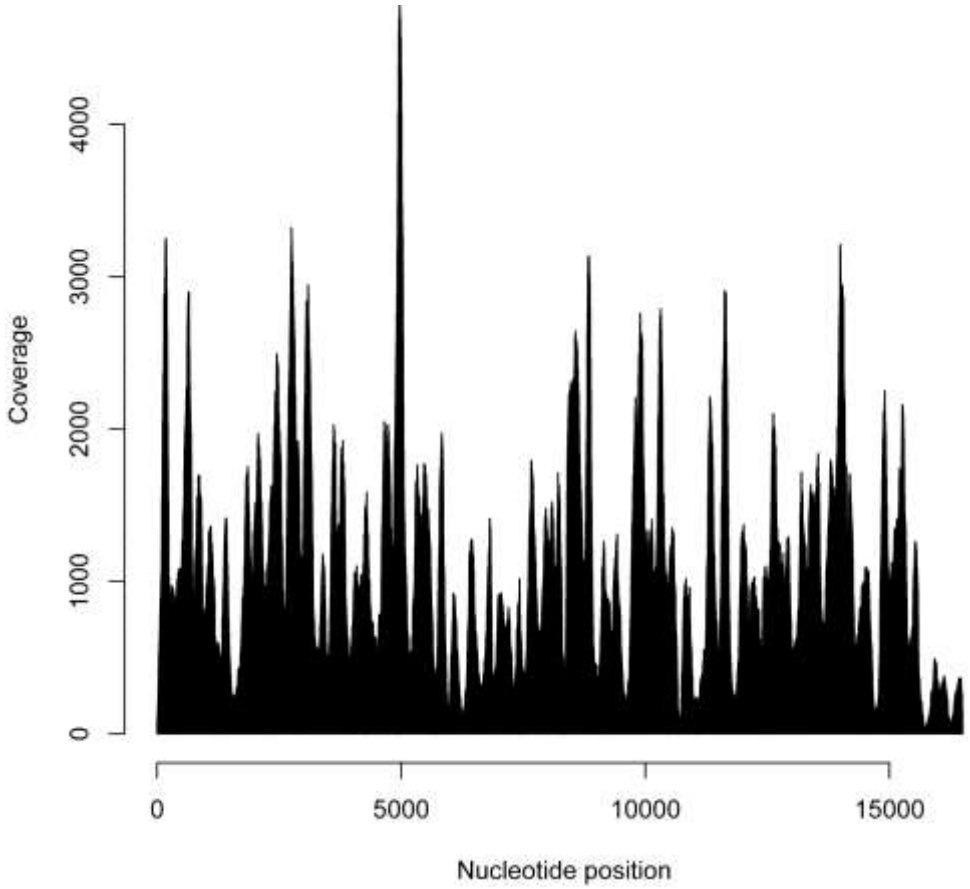
The Illumina sequencing yielded a total of 381,479,528 reads (length: 101 bases, the two sets of paired-end reads were submitted to the European Nucleotide Archive as study PRJEB15379). The haploid genome of Atlantic salmon has been reported to be approximately 2.97 gigabases (Lien et al., 2016) and the theoretical coverage of the Atlantic salmon genome should thus be approximately 12X.

When comparing our Illumina data set to our database of salmon mRNA sequences, 47,924 (99.4%) of the transcript entries had a match with one or more of our Illumina reads, leaving 281 mRNA sequences for which no matching reads were found. This number was reduced to 250 sequences by excluding identical entries (Supplementary Tables S1 and S2). Sequences were ranked according to length and primers were designed for the thirteen longest accessions having journal references (Supplementary Table S2). In order to ensure that primers were located in exonic regions, candidate mRNA sequences were mapped against available genomic sequences from Atlantic salmon or other fish species. In addition, a positive control PCR was designed using the 18S rRNA gene as target locus. PCR was performed using genomic DNA. All PCRs were negative (except the positive control).

When aligning 44,800 mitochondrial reads with a reference Atlantic salmon mitochondrial genome, a significant bias in coverage was observed (Supplementary Figure S1). This appears to have been caused by partial degradation of the template DNA (Dr. Volker Brenner, GATC Biotech AG, personal communication). A Neighbour-Joining analysis using Kimura-2-parameter distances (SeaView, version 4.2.11; Gouy et al., 2010) of the the complete Namsblank mitochondrial genome (GenBank accession number KF792729) indicated that the genetic distance between Namsblank and anadromous strains of Atlantic salmon is small (Figure 2 and Table 1) and no mutations unique for the landlocked mitochondrial DNA sequence were observed.

DISCUSSION

Assessment of single nucleotide polymorphisms (SNPs) in mitochondrial and nuclear DNA of different populations



Supplementary Figure S1. Coverage map of the Atlantic salmon mitochondrial genome when aligning 44,800 Illumina sequence reads.

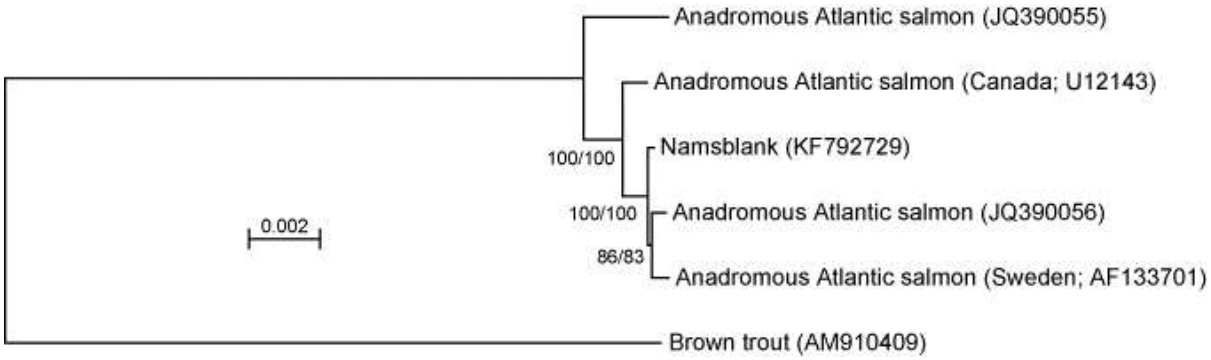


Figure 2. Neighbour-Joining tree of complete *Salmo salar* mitochondrial nucleotide sequences constructed using Kimura-2-parameter distances and brown trout *Salmo trutta* L. as outgroup. GenBank accession numbers are shown in parentheses, and, where available, eographic origin of sample has been indicated. Topology robustness was tested using bootstrapping with 100 pseudoreplicates (distance/parsimony).

of Atlantic salmon, including landlocked isolates, indicates a polyphyletic origin of these different subpopulations (Bourret et al., 2013). Still, all populations of Atlantic salmon are referred to as the same species. The mitochondrial genome has not gone through the same changes in ploidy as the nuclear salmonid genome, leading to a lower level of gene-content redundancy. Combined with the clonal mode of mitochondrial replication and the relatively short time of population separation, this might explain the close genetic

Table 1. Pairwise distances between complete Atlantic salmon mitochondrial genomes (DNADIST, version 3.5c).

Correlation	JQ390055	U12143	JQ390056	AF133701	KF792729	AM910409
JQ390055	0	0.0063	0.0070	0.0071	0.0067	0.0556
U12143		0	0.0029	0.0030	0.0023	0.0547
JQ390056			0	0.0013	0.0010	0.0554
AF133701				0	0.0011	0.0555
KF792729					0	0.0550
AM910409						0

relationship between Namsblank and anadromous Atlantic salmon populations when comparing mitochondrial genome sequences. Our dataset did not allow for a detailed comparison between the anadromous Atlantic salmon genome and our Namsblank specimen. Our strategy of discarding sequences based on a cut-off rule that requires 100% match only in a 28 basepair region may also have led to the indiscriminate filtering of paralogous genes and not just homologous alleles, so even loss of all paralogs of a given gene could be missed. When mining for salmon sequence data in the NCBI database, we found numerous examples of obvious errors and apparent contamination, for instance NM_001140589 ('Salmo salar Photosystem II 10 kDa polypeptide, chloroplast (psbr)), mRNA' and BT046286 ('Salmo salar clone ssal-evf-563-177 Photosystem II 10 kDa polypeptide, chloroplast precursor putative mRNA, complete cds'). Both of these examples are likely the result of plant material contamination of the sequenced samples, as subsequent nucleotide similarity searches revealed that both entries appeared to in fact stem from plant DNA. Our hypothesis for the lack of PCR products is thus due to either erroneously annotated GenBank accessions or mRNA sequences derived from poor quality data in our salmon transcript database. It is also possible that binding sites for some of the primers that were based on gene structure data from other fish species did not reside within the intended exonic regions. The lack of positive control material also may have introduced some false negatives due to poor primer design, but we consider this unlikely as the primers were designed using standardized software and PCRs were run using robust conditions.

A situation analogous to the isolation of Atlantic salmon populations in freshwater localities could be the Mexican tetra *Astyanax mexicanus* (Filippi). This species has given rise to several blind cave subpopulations that have lived in complete darkness and isolation for at least 10,000 years. In these populations, several loss-of-function mutations have been described (Jeffery, 2001) and mutations in genes such as *Oca2* and *Mc1r* have been linked directly to an observed reduction in pigmentation (Protas et al., 2006; Gross et al., 2009). Interestingly, there even seem to have been several constructive (gain-of-function) changes, including increased number of taste buds, extra teeth and a more robust jaw structure (Jeffery, 2001). We do not exclude the possibility that there are functionally relevant genetic differences between Namsblank and anadromous Atlantic salmon, but the transition from an anadromous life cycle to isolation in freshwater may have been accompanied by more subtle, regulatory mutations or even epigenetic changes, possibly in a combinatorial fashion where multiple genes have been affected. Experimental attempts to induce smoltification in another landlocked Norwegian population (salmon from Lake Byglandsfjord, 'Byglandsbleke') revealed reduced hormonal responses to natural spring light (plasma growth hormone and cortisol) compared to anadromous salmon. The corresponding growth hormone receptor response in gills, which is known to precede gill adaptation to seawater handling, was also reduced (Nilsen et al., 2008). In a comparison between Atlantic salmon and the less seawater-adapted Arctic char, quantitative trait loci (QTLs) linked to seawater tolerance were identified in genes encoding osmoregulatory proteins, hormonal signals of smoltification and an epithelial junction protein (Norman et al., 2012). Morphological, physiological and behavioural differences that may be linked to epigenetic adaptation have been described in teleost species such as Arctic char *Salvelinus alpinus* L. (Adams et al., 2003; Arbour et al., 2011). Such epigenetically based phenotypic plasticity may play a role in adaptation or speciation (Pfennig et al., 2010) and could also contribute to the observed differences between landlocked and anadromous Atlantic salmon. Changes in gene-expression levels have been linked with life-history variation in salmonid fish in previous studies and a gene-expression signature for future migratory behavior has been suggested for brown trout *Salmo trutta* L. (Giger et al., 2008). Another interesting finding from this study is that variance in life-history seems to be a much more important factor than genetic diversity when explaining differences in gene-expression profiles. For immune-related genes, selection sweeps have been identified using SNP data in Atlantic salmon (Kjærner-Semb et al., 2016) and it is not inconceivable that similar data might indicate that similar

Supplementary Table S1. Complete list of GenBank entries with no matching sequences in our Namsblank dataset, sorted according to length

Sequence	Length	Accession number
Salmo salar matrix metalloproteinase 13 (LOC100136348), mRNA	1714	NM_001123522.1
Salmo salar NADPH-dependent D-xylose reductase (xyl1), mRNA	1346	NM_001141348.1
Salmo salar cytotoxic granule-associated RNA binding protein 1 (tia1), mRNA	1341	NM_001141551.2
Salmo salar Actin, adductor muscle (act), mRNA	1268	NM_001141519.1
Salmo salar Fructose-bisphosphate aldolase, muscle type (alf1), mRNA	1259	NM_001141367.1
Salmo salar choline phosphotransferase 1 (chpt1), mRNA	1256	NM_001141541.1
Salmo salar clone ssal-evd-507-112 Hsp90 co-chaperone Cdc37 putative mRNA, complete cds	1203	BT125183.1
Salmo salar clone ssal-evd-513-185 Hsp90 co-chaperone Cdc37 putative mRNA, complete cds	1194	BT050306.1
Salmo salar GMP reductase (guac), mRNA	1173	NM_001140964.1
Salmo salar Digestive cysteine proteinase 2 precursor (cysp2), mRNA	1168	NM_001279029.1
Salmo salar clone ssal-evd-568-067 WD repeat-containing protein 82 putative mRNA, complete cds	1158	BT049499.1
Salmo salar clone ssal-rgb2-538-320 Nucleoporin Nup37 putative mRNA, complete cds	1126	BT046605.1
Salmo salar clone ssal-evd-549-289 Pyridoxal kinase putative mRNA, complete cds	1095	BT046481.2
Salmo salar Probable maintenance of ploidy protein mob1 (mob1), mRNA	1057	NM_001141849.1
Salmo salar clone ssal-evd-562-211 Alcohol dehydrogenase putative mRNA, complete cds	1043	BT046839.1
Salmo salar Uridine-cytidine kinase 2 (uck2), mRNA	962	NM_001140729.1
Salmo salar Probable phospholipid hydroperoxide glutathione peroxidase (gpx4), mRNA	961	NM_001146603.1
Salmo salar 60S ribosomal protein L2 (rl2), mRNA	960	NM_001141476.1
Salmo salar C30D10.14 (yb4e), mRNA	954	NM_001146536.1
Salmo salar clone ssal-evd-522-223 Mitochondrial 37S ribosomal protein S17 putative mRNA, complete cds	934	BT049440.2
Salmo salar clone ssal-evd-513-211 Survival of motor neuron-related-splicing factor 30 putative mRNA, complete cds	916	BT056643.1
Salmo salar clone ssal-evd-515-098 60S ribosomal protein L7a putative mRNA, complete cds	913	BT056574.1
Salmo salar clone ssal-rgb2-654-239 PRELI domain-containing protein 1, mitochondrial precursor putative mRNA, complete cds	909	BT049503.1
Salmo salar clone ssal-evd-543-275 60S ribosomal protein L7a putative mRNA, complete cds	902	BT057656.1
Salmo salar Acidic leucine-rich nuclear phosphoprotein 32 family member E (an32e), mRNA	882	NM_001140577.1
Salmo salar clone ssal-evd-559-166 Derlin-1 putative mRNA, complete cds	879	BT047049.1
Salmo salar Photosystem II 10 kDa polypeptide, chloroplast (psbr), mRNA	863	NM_001140589.1
Salmo salar Ras-like GTP-binding protein Rho1 (rho1), mRNA	836	NM_001140962.2
Salmo salar clone ssal-evd-538-347 AP-1 complex subunit sigma-2 putative mRNA, complete cds	822	BT057845.1
Salmo salar Heat shock protein Hsp-16.48/Hsp-16.49 (hsp17), mRNA	814	NM_001146425.1
Salmo salar survival of motor neuron protein interacting protein 1 (sip1), mRNA	799	NM_001140750.1
Salmo salar Plasma membrane proteolipid 3 (pmp3), mRNA	773	NM_001140646.1
Salmo salar clone ssal-evd-550-228 Translationally-controlled tumor protein homolog putative mRNA, complete cds	767	BT049129.2
Salmo salar clone ssal-evd-530-338 AP-2 complex subunit sigma-1 putative mRNA, complete cds	753	BT046378.1
Salmo salar clone ssal-evd-574-107 Calcyclin-binding protein putative mRNA, complete cds	749	BT057054.1
Salmo salar clone ssal-evf-567-147 DNA-directed RNA polymerase II subunit RPB11 putative mRNA, complete cds	708	BT046674.1

Supplementary Table S1. Contd.

Salmo salar Myophilin (myph), mRNA	701	NM_001140673.1
TSA: Salmo salar isotig13250.Sasaskin mRNA sequence	698	JT826315.1
Salmo salar clone ssal-evd-552-149 Myophilin putative mRNA, complete cds	696	BT048476.1
Salmo salar clone ssal-evd-565-236 Myophilin putative mRNA, complete cds	685	BT047895.1
Salmo salar clone ssal-evd-535-219 ARMET-like protein precursor putative mRNA, complete cds	684	BT048549.2
Salmo salar clone ssal-evd-563-323 F-actin-capping protein subunit beta putative mRNA, complete cds	682	BT057498.1
Salmo salar clone ssal-evd-553-035 Myosin regulatory light chain 2, smooth muscle isoform putative mRNA, complete cds	667	BT057337.1
Salmo salar YXIE protein (yxie), mRNA	656	NM_001146576.1
Salmo salar clone ssal-eve-540-001 40S ribosomal protein S28 putative mRNA, complete cds	651	BT057248.1
Salmo salar clone ssal-evd-511-125 Succinate dehydrogenase cytochrome b560 subunit, mitochondrial precursor putative mRNA, complete cds	647	BT057268.1
Salmo salar clone ssal-evf-530-019 NADH dehydrogenase 1 beta subcomplex subunit 9 putative mRNA, complete cds	645	BT048958.1
Salmo salar clone ssal-evd-553-127 Cofilin-2 putative mRNA, complete cds	639	BT049164.1
Salmo salar clone ssal-evd-533-269 60S ribosomal protein L11 putative mRNA, complete cds	616	BT050239.1
Salmo salar clone ssal-evd-544-007 Transmembrane and coiled-coil domain-containing protein 1 putative mRNA, complete cds	616	BT057061.1
Salmo salar Ecdysteroid-regulated 16 kDa protein (es16), mRNA	587	NM_001141175.1
Salmo salar clone ssal-evd-569-295 60S ribosomal protein L24 putative mRNA, complete cds	558	BT046460.1
TSA: Salmo salar isotig16374.Sasaskin mRNA sequence	556	JT829432.1
TSA: Salmo salar isotig16459.Sasaskin mRNA sequence	555	JT829517.1
TSA: Salmo salar isotig16936.Sasaskin mRNA sequence	538	JT829994.1
Salmo salar YDR063W (yd063), mRNA	535	NM_001140783.1
Salmo salar clone ssal-evd-552-272 Histone H2B type 1-A putative mRNA, complete cds	526	BT049604.1
TSA: Salmo salar isotig17363.Sasaskin mRNA sequence	525	JT830421.1
TSA: Salmo salar contig09584.Sasaskin mRNA sequence	522	JT814582.1
TSA: Salmo salar isotig17243.Sasaskin mRNA sequence	519	JT830301.1
TSA: Salmo salar isotig17738.Sasaskin mRNA sequence	508	JT830796.1
Salmo salar clone ssal-evd-530-236 60S ribosomal protein L27 putative mRNA, complete cds	503	BT048296.1
Salmo salar clone ssal-evd-579-078 Trafficking protein particle complex subunit 2-like protein putative mRNA, complete cds	499	BT057850.1
TSA: Salmo salar isotig18347.Sasaskin mRNA sequence	495	JT831402.1
TSA: Salmo salar isotig18455.Sasaskin mRNA sequence	494	JT831510.1
TSA: Salmo salar isotig18791.Sasaskin mRNA sequence	483	JT831846.1
TSA: Salmo salar isotig18949.Sasaskin mRNA sequence	480	JT832004.1
TSA: Salmo salar isotig19362.Sasaskin mRNA sequence	475	JT832417.1
Salmo salar clone ssal-evd-569-157 Ubiquitin putative mRNA, complete cds	472	BT046483.1
Salmo salar 40S ribosomal protein S17-A (rs17a), mRNA	471	NM_001140981.1
TSA: Salmo salar isotig19846.Sasaskin mRNA sequence	465	JT832901.1
TSA: Salmo salar isotig19845.Sasaskin mRNA sequence	461	JT832900.1
TSA: Salmo salar isotig20095.Sasaskin mRNA sequence	458	JT833149.1

Supplementary Table S1. Contd.

Salmo salar clone ssal-evd-554-136 Probable prefoldin subunit 6 putative mRNA, complete cds	457	BT049827.1
TSA: Salmo salar isotig00017.Sasaskin mRNA sequence	451	JT813210.1
TSA: Salmo salar isotig20886.Sasaskin mRNA sequence	444	JT833938.1
Salmo salar Glutaredoxin-C2 (grxc2), mRNA	437	NM_001146448.1
TSA: Salmo salar isotig21309.Sasaskin mRNA sequence	435	JT834361.1
TSA: Salmo salar isotig21413.Sasaskin mRNA sequence	433	JT834465.1
TSA: Salmo salar isotig00018.Sasaskin mRNA sequence	430	JT813211.1
Salmo salar clone ssal-evd-576-162 60S ribosomal protein L31 putative mRNA, complete cds	429	BT050039.1
TSA: Salmo salar isotig21613.Sasaskin mRNA sequence	429	JT834665.1
TSA: Salmo salar isotig21498.Sasaskin mRNA sequence	427	JT834550.1
Salmo salar clone ssal-evd-526-037 60S ribosomal protein L30 putative mRNA, complete cds	426	BT049130.1
TSA: Salmo salar isotig22099.Sasaskin mRNA sequence	421	JT835150.1
TSA: Salmo salar isotig22165.Sasaskin mRNA sequence	417	JT835216.1
TSA: Salmo salar isotig22833.Sasaskin mRNA sequence	410	JT835884.1
TSA: Salmo salar isotig22811.Sasaskin mRNA sequence	408	JT835862.1
TSA: Salmo salar isotig22563.Sasaskin mRNA sequence	407	JT835614.1
TSA: Salmo salar isotig22612.Sasaskin mRNA sequence	407	JT835663.1
TSA: Salmo salar isotig23042.Sasaskin mRNA sequence	403	JT836092.1
TSA: Salmo salar isotig23403.Sasaskin mRNA sequence	397	JT836453.1
TSA: Salmo salar isotig23027.Sasaskin mRNA sequence	396	JT836077.1
TSA: Salmo salar isotig23473.Sasaskin mRNA sequence	396	JT836523.1
TSA: Salmo salar isotig23431.Sasaskin mRNA sequence	393	JT836481.1
TSA: Salmo salar isotig23135.Sasaskin mRNA sequence	389	JT836185.1
TSA: Salmo salar isotig23639.Sasaskin mRNA sequence	389	JT836689.1
TSA: Salmo salar isotig22840.Sasaskin mRNA sequence	387	JT835890.1
TSA: Salmo salar isotig23663.Sasaskin mRNA sequence	385	JT836713.1
TSA: Salmo salar isotig24087.Sasaskin mRNA sequence	385	JT837137.1
TSA: Salmo salar isotig24219.Sasaskin mRNA sequence	382	JT837269.1
TSA: Salmo salar isotig23933.Sasaskin mRNA sequence	380	JT836983.1
TSA: Salmo salar isotig24383.Sasaskin mRNA sequence	379	JT837433.1
TSA: Salmo salar isotig24395.Sasaskin mRNA sequence	377	JT837445.1
TSA: Salmo salar isotig24467.Sasaskin mRNA sequence	377	JT837516.1
TSA: Salmo salar isotig24521.Sasaskin mRNA sequence	374	JT837570.1
TSA: Salmo salar isotig24734.Sasaskin mRNA sequence	371	JT837783.1
TSA: Salmo salar isotig24635.Sasaskin mRNA sequence	370	JT837684.1
TSA: Salmo salar isotig24845.Sasaskin mRNA sequence	370	JT837893.1
TSA: Salmo salar isotig24921.Sasaskin mRNA sequence	369	JT837968.1

Supplementary Table S1. Contd.

TSA: Salmo salar isotig25014.Sasaskin mRNA sequence	365	JT838061.1
TSA: Salmo salar isotig25133.Sasaskin mRNA sequence	362	JT838180.1
TSA: Salmo salar isotig25132.Sasaskin mRNA sequence	357	JT838179.1
TSA: Salmo salar isotig25535.Sasaskin mRNA sequence	356	JT838581.1
TSA: Salmo salar isotig25569.Sasaskin mRNA sequence	356	JT838615.1
TSA: Salmo salar isotig08632.Sasaskin mRNA sequence	355	JT821762.1
TSA: Salmo salar isotig25179.Sasaskin mRNA sequence	355	JT838226.1
TSA: Salmo salar isotig25676.Sasaskin mRNA sequence	353	JT838722.1
TSA: Salmo salar isotig25618.Sasaskin mRNA sequence	352	JT838664.1
TSA: Salmo salar isotig25650.Sasaskin mRNA sequence	352	JT838696.1
TSA: Salmo salar isotig25809.Sasaskin mRNA sequence	352	JT838855.1
TSA: Salmo salar isotig25713.Sasaskin mRNA sequence	350	JT838759.1
TSA: Salmo salar isotig25845.Sasaskin mRNA sequence	348	JT838891.1
TSA: Salmo salar isotig25502.Sasaskin mRNA sequence	347	JT838548.1
TSA: Salmo salar isotig26157.Sasaskin mRNA sequence	343	JT839201.1
TSA: Salmo salar isotig26190.Sasaskin mRNA sequence	343	JT839234.1
TSA: Salmo salar isotig26136.Sasaskin mRNA sequence	342	JT839180.1
TSA: Salmo salar isotig26296.Sasaskin mRNA sequence	341	JT839340.1
TSA: Salmo salar isotig26499.Sasaskin mRNA sequence	338	JT839543.1
TSA: Salmo salar isotig26441.Sasaskin mRNA sequence	337	JT839485.1
TSA: Salmo salar isotig27010.Sasaskin mRNA sequence	328	JT840053.1
TSA: Salmo salar isotig26911.Sasaskin mRNA sequence	327	JT839954.1
TSA: Salmo salar isotig08056.Sasaskin mRNA sequence	318	JT821189.1
TSA: Salmo salar isotig27279.Sasaskin mRNA sequence	317	JT840322.1
TSA: Salmo salar isotig27409.Sasaskin mRNA sequence	317	JT840452.1
TSA: Salmo salar isotig27023.Sasaskin mRNA sequence	316	JT840066.1
TSA: Salmo salar isotig27297.Sasaskin mRNA sequence	316	JT840340.1
TSA: Salmo salar isotig27384.Sasaskin mRNA sequence	316	JT840427.1
TSA: Salmo salar isotig27492.Sasaskin mRNA sequence	314	JT840535.1
TSA: Salmo salar isotig27483.Sasaskin mRNA sequence	313	JT840526.1
TSA: Salmo salar isotig27612.Sasaskin mRNA sequence	312	JT840655.1
TSA: Salmo salar isotig27754.Sasaskin mRNA sequence	310	JT840797.1
TSA: Salmo salar isotig27645.Sasaskin mRNA sequence	308	JT840688.1
TSA: Salmo salar isotig27683.Sasaskin mRNA sequence	307	JT840726.1
TSA: Salmo salar isotig27733.Sasaskin mRNA sequence	307	JT840776.1
TSA: Salmo salar isotig27941.Sasaskin mRNA sequence	304	JT840984.1
TSA: Salmo salar isotig27524.Sasaskin mRNA sequence	303	JT840567.1

Supplementary Table S1. Contd.

TSA: Salmo salar isotig27698.Sasaskin mRNA sequence	303	JT840741.1
TSA: Salmo salar isotig27944.Sasaskin mRNA sequence	303	JT840987.1
TSA: Salmo salar isotig27999.Sasaskin mRNA sequence	301	JT841042.1
TSA: Salmo salar isotig28049.Sasaskin mRNA sequence	298	JT841092.1
TSA: Salmo salar isotig28105.Sasaskin mRNA sequence	298	JT841148.1
TSA: Salmo salar isotig28212.Sasaskin mRNA sequence	297	JT841255.1
TSA: Salmo salar isotig28246.Sasaskin mRNA sequence	297	JT841289.1
TSA: Salmo salar isotig28254.Sasaskin mRNA sequence	297	JT841297.1
TSA: Salmo salar isotig28154.Sasaskin mRNA sequence	295	JT841197.1
TSA: Salmo salar isotig28367.Sasaskin mRNA sequence	293	JT841410.1
TSA: Salmo salar isotig28394.Sasaskin mRNA sequence	292	JT841437.1
TSA: Salmo salar isotig28467.Sasaskin mRNA sequence	292	JT841510.1
TSA: Salmo salar isotig28525.Sasaskin mRNA sequence	291	JT841568.1
TSA: Salmo salar isotig28326.Sasaskin mRNA sequence	290	JT841369.1
TSA: Salmo salar isotig28546.Sasaskin mRNA sequence	285	JT841589.1
TSA: Salmo salar isotig28644.Sasaskin mRNA sequence	285	JT841686.1
TSA: Salmo salar isotig28680.Sasaskin mRNA sequence	285	JT841722.1
TSA: Salmo salar isotig28759.Sasaskin mRNA sequence	283	JT841801.1
TSA: Salmo salar isotig28553.Sasaskin mRNA sequence	282	JT841596.1
TSA: Salmo salar isotig28747.Sasaskin mRNA sequence	282	JT841789.1
TSA: Salmo salar isotig28841.Sasaskin mRNA sequence	282	JT841883.1
TSA: Salmo salar isotig28894.Sasaskin mRNA sequence	280	JT841936.1
TSA: Salmo salar isotig28974.Sasaskin mRNA sequence	278	JT842016.1
TSA: Salmo salar isotig28983.Sasaskin mRNA sequence	278	JT842025.1
TSA: Salmo salar isotig28994.Sasaskin mRNA sequence	278	JT842036.1
TSA: Salmo salar isotig28881.Sasaskin mRNA sequence	276	JT841923.1
TSA: Salmo salar isotig29087.Sasaskin mRNA sequence	275	JT842129.1
TSA: Salmo salar isotig29080.Sasaskin mRNA sequence	274	JT842122.1
TSA: Salmo salar isotig28926.Sasaskin mRNA sequence	272	JT841968.1
TSA: Salmo salar isotig29122.Sasaskin mRNA sequence	271	JT842163.1
TSA: Salmo salar isotig29147.Sasaskin mRNA sequence	271	JT842188.1
TSA: Salmo salar isotig08613.Sasaskin mRNA sequence	270	JT821743.1
TSA: Salmo salar isotig29168.Sasaskin mRNA sequence	269	JT842209.1
TSA: Salmo salar isotig29234.Sasaskin mRNA sequence	269	JT842275.1
TSA: Salmo salar isotig29241.Sasaskin mRNA sequence	269	JT842282.1
TSA: Salmo salar isotig29329.Sasaskin mRNA sequence	268	JT842368.1
TSA: Salmo salar isotig29389.Sasaskin mRNA sequence	267	JT842428.1

Supplementary Table S1. Contd.

TSA: Salmo salar isotig29323.Sasaskin mRNA sequence	265	JT842362.1
TSA: Salmo salar isotig29364.Sasaskin mRNA sequence	265	JT842403.1
TSA: Salmo salar isotig29399.Sasaskin mRNA sequence	265	JT842438.1
TSA: Salmo salar isotig29404.Sasaskin mRNA sequence	265	JT842443.1
TSA: Salmo salar isotig29498.Sasaskin mRNA sequence	263	JT842537.1
TSA: Salmo salar isotig00019.Sasaskin mRNA sequence	262	JT813212.1
TSA: Salmo salar isotig29541.Sasaskin mRNA sequence	262	JT842580.1
TSA: Salmo salar isotig29223.Sasaskin mRNA sequence	258	JT842264.1
TSA: Salmo salar isotig29612.Sasaskin mRNA sequence	258	JT842651.1
TSA: Salmo salar isotig29652.Sasaskin mRNA sequence	258	JT842691.1
TSA: Salmo salar isotig29688.Sasaskin mRNA sequence	257	JT842727.1
TSA: Salmo salar isotig29539.Sasaskin mRNA sequence	256	JT842578.1
TSA: Salmo salar isotig29631.Sasaskin mRNA sequence	255	JT842670.1
TSA: Salmo salar isotig29713.Sasaskin mRNA sequence	255	JT842752.1
TSA: Salmo salar isotig29813.Sasaskin mRNA sequence	252	JT842851.1
TSA: Salmo salar isotig29943.Sasaskin mRNA sequence	248	JT842979.1
TSA: Salmo salar isotig29986.Sasaskin mRNA sequence	245	JT843021.1
TSA: Salmo salar isotig01054.Sasaskin mRNA sequence	244	JT814249.1
TSA: Salmo salar isotig29783.Sasaskin mRNA sequence	243	JT842821.1
TSA: Salmo salar isotig30022.Sasaskin mRNA sequence	243	JT843057.1
TSA: Salmo salar isotig30089.Sasaskin mRNA sequence	243	JT843123.1
TSA: Salmo salar isotig30157.Sasaskin mRNA sequence	243	JT843191.1
TSA: Salmo salar isotig30096.Sasaskin mRNA sequence	242	JT843130.1
TSA: Salmo salar isotig08633.Sasaskin mRNA sequence	241	JT821763.1
TSA: Salmo salar isotig30188.Sasaskin mRNA sequence	239	JT843222.1
TSA: Salmo salar isotig30292.Sasaskin mRNA sequence	239	JT843326.1
TSA: Salmo salar isotig30194.Sasaskin mRNA sequence	238	JT843228.1
TSA: Salmo salar isotig30231.Sasaskin mRNA sequence	238	JT843265.1
TSA: Salmo salar isotig30268.Sasaskin mRNA sequence	236	JT843302.1
TSA: Salmo salar isotig30230.Sasaskin mRNA sequence	235	JT843264.1
TSA: Salmo salar isotig30304.Sasaskin mRNA sequence	235	JT843338.1
TSA: Salmo salar isotig30404.Sasaskin mRNA sequence	232	JT843438.1
TSA: Salmo salar isotig30435.Sasaskin mRNA sequence	231	JT843469.1
TSA: Salmo salar isotig30147.Sasaskin mRNA sequence	228	JT843181.1
TSA: Salmo salar isotig30544.Sasaskin mRNA sequence	227	JT843578.1
TSA: Salmo salar isotig30600.Sasaskin mRNA sequence	226	JT843634.1
TSA: Salmo salar isotig30569.Sasaskin mRNA sequence	224	JT843603.1

Supplementary Table S1. Contd.

TSA: Salmo salar isotig30608.Sasaskin mRNA sequence	224	JT843642.1
TSA: Salmo salar isotig30553.Sasaskin mRNA sequence	223	JT843587.1
TSA: Salmo salar isotig30565.Sasaskin mRNA sequence	223	JT843599.1
TSA: Salmo salar isotig30664.Sasaskin mRNA sequence	222	JT843698.1
TSA: Salmo salar isotig30753.Sasaskin mRNA sequence	220	JT843787.1
TSA: Salmo salar isotig30741.Sasaskin mRNA sequence	219	JT843775.1
TSA: Salmo salar isotig30757.Sasaskin mRNA sequence	218	JT843791.1
TSA: Salmo salar isotig08637.Sasaskin mRNA sequence	217	JT821767.1
TSA: Salmo salar isotig30834.Sasaskin mRNA sequence	216	JT843868.1
TSA: Salmo salar isotig30920.Sasaskin mRNA sequence	213	JT843951.1
TSA: Salmo salar isotig30832.Sasaskin mRNA sequence	210	JT843866.1
TSA: Salmo salar isotig30985.Sasaskin mRNA sequence	210	JT844016.1
TSA: Salmo salar isotig30871.Sasaskin mRNA sequence	209	JT843904.1
TSA: Salmo salar isotig31011.Sasaskin mRNA sequence	209	JT844040.1
TSA: Salmo salar isotig31013.Sasaskin mRNA sequence	208	JT844042.1
TSA: Salmo salar isotig30978.Sasaskin mRNA sequence	206	JT844009.1
TSA: Salmo salar isotig31008.Sasaskin mRNA sequence	206	JT844038.1
TSA: Salmo salar isotig30971.Sasaskin mRNA sequence	204	JT844002.1
TSA: Salmo salar isotig31085.Sasaskin mRNA sequence	204	JT844110.1
TSA: Salmo salar isotig31101.Sasaskin mRNA sequence	204	JT844123.1
TSA: Salmo salar isotig08669.Sasaskin mRNA sequence	202	JT821795.1
TSA: Salmo salar isotig31080.Sasaskin mRNA sequence	201	JT844105.1
TSA: Salmo salar isotig31180.Sasaskin mRNA sequence	201	JT844175.1
TSA: Salmo salar isotig31167.Sasaskin mRNA sequence	200	JT844170.1
Salmo salar hect domain and RLD 4 (herc4), mRNA	119	NM_001141198.1
Salmo salar clone ssal-rgb2-622-380 BMP and activin membrane-bound inhibitor homolog precursor putative mRNA, complete cds	115	BT049459.1
Salmo salar Serine/threonine-protein kinase ppk13 (ppk13), mRNA	109	NM_001141573.1
Sequence 9 from Patent EP1626055	30	CS259514.1
Salmo salar phosphatase 1 regulatory subunit 3D (ppr3d), mRNA	11	NM_001140754.1

adaptational processes have taken place in the transition from a migratory to a residential life-history.

Until a fully annotated reference genome as well as information on genetic (expression) variability on a population level is available for a large number of Atlantic salmon isolates, it will be very challenging to pinpoint the exact genetic differences that enable subpopulations to spend their entire life cycle in freshwater. However, a more detailed understanding of the underlying mechanisms should give insight into Atlantic salmon adaptive processes in general and could prove very useful when optimizing the smoltification process for Atlantic salmon reared in aquaculture, as well as for any future attempts to keep adult salmon in land-based freshwater facilities.

Supplementary Table S2. Primers designed for PCR amplification of gene-loss candidates.

Gene	Accession No.	Forward/reverse primers
xyl1	NM_001141348.1	ATGGCTCCTTCTATTGAGC* TCGACTTTCCACAAGCCG
tia1	NM_001141551.2	ATGGTGGGCCGATTTATTC ACATTCTCATCTACAGCACT
act	NM_001141519.1	ATGGTTGGAATGGGTCAGA TCACAATCCCGTGGTCGA
alf1	NM_001141367.1	GTCTACCTCGAAGGAACA AAACGGTTGCCATGGCAAT
chpt1	NM_001141541.1	ATGTTGAAATTGACCACACT TCCAAAATCTCCCCAAATAC
hsp90 co-chaperone cdc37	BT125183.1	ATGGTAGACTACAGCAGAT GGTGACGCCAACGAAACA
guac	NM_001140964.1	ATGCGCATTGAATCCGAAAT TTCTCTCGAGAGACACATC
cysp2	NM_001279029.1	ATGAATGCCAATGCTGCTTT TGTGTTCACTCCATTGACC
prot82	BT049499.1	ATGAAACTGGACGAAGAGC GTTTTCCTTCATAGTGAAAGT
nup37	BT046605.1	CTAATGGTTGCAGAGAAGAA CTGACATTAATGGCACTTGT
pyridoxal kinase	BT046481.2	ATGTCTAAAGGAAAGGTGTT CATCGTAGCCATTAGTCTC
mob1	NM_001141849.1	CGTCCTCGCGTGGGCA GCAGCTTCACCACCTTTC
alcohol dehydrogenase	BT046839.1	ATGTTGCCAATATTTAGGACT ACAGCATCCTTCACAAGATTA
18S rRNA	-	GCGGTGACGTCTCATTCGAA ATCGAACCCTGATTCCCCGT

* For genes with fish genome BLAST hits, primers were designed to anneal within a predicted exon sequence and amplify a short (~100 bp) fragment. Otherwise, primers were designed to amplify a short region starting from the ATG start codon (in bold). 18S was included as a positive control. Tm=54-56°C.

Conflict of Interests

The authors have not declared any conflict of interests.

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