Halibut mitogenomics: A study of the complete mitochondrial genome sequences of Atlantic-, Pacific- and Greenland halibut.

A master thesis in molecular biology

Master of Aquaculture

By

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Content

Summary

The complete mitochondrial DNA sequence was determined in four individuals of Atlantic halibut (*Hippoglossus hippoglossus*), Pacific halibut (*Hippoglossus stenolepis*) and Greenland halibut (*Reinhardtius hippoglossoides*) respectively. Thirteen protein-coding genes, twenty-two tRNA genes, two rRNA genes and a large non-coding control region were identified, and the conserved vertebrate gene order was confirmed. Extensive length variation of the mtDNA genome was observed, due to variations in copy number of a 61 bp heteroplasmic repeated motif in the control region.

Furthermore, 800 bp from the mtDNA genes ND2, COI and control region respectively was sequenced in 30 individuals from the Atlantic halibut broodstock at Mørkvedbukta Reseach Station. In addition, approximately 13420 bp from Common sole (*Solea vulgaris*), 15012 bp from European plaice (*Pleuronectes platessa)* and 7678 bp from Turbot (*Scophthalmus maximus)* were determined.

The overall genetic variation based on the number of nucleotide substitutions was greatest in Greenland halibut, followed by Pacific halibut and Atlantic halibut. The control region and some of the ND genes had the highest nucleotide diversity, while the rRNA genes and ATP8 (Pacific and Greenland halibut) were most conserved. Four amino acid substitutions between the three halibut species in ND5, with a negative mutation matrix score suggest that these substitutions could have an impact on functional and structional properties of the gene.

Phylogenetic investigations based on the complete mtDNA genome revealed that Atlantic halibut and Pacific halibut are closely related species, potentially separated at the sub-species level. Of all other available mtDNA genomes Greenland halibut is the closest relative to the Hippoglossus genus. Furthermore, Atlantic- and Pacific halibut was estimated to have separated 2 Ma, while divergence between Greenland halibut and the *Hippoglossus* genus took place approximately 6 million years ago.

Introduction

The Pleuronectidae family

The order of Pleuronectiformes contains 11 families and more than 700 species. Three families containing 16 species are usually represented along the Norwegian coast: Pleuronectidae, Soleidae and Scophthalmidae. The Pleuronectidae family consists of 39 genera and a total of 93 species world wide (www.fishbase.org). The three species being the main object in this thesis; Atlantic halibut (*Hippoglossus hippoglossus*), Pacific halibut (*Hippoglossus stenolepis*) and Greenland halibut (*Reinhardtius hippoglossoides*) all belong to the Pleuronectidae family.

Atlantic halibut (*Hippoglossus hippoglossus*)

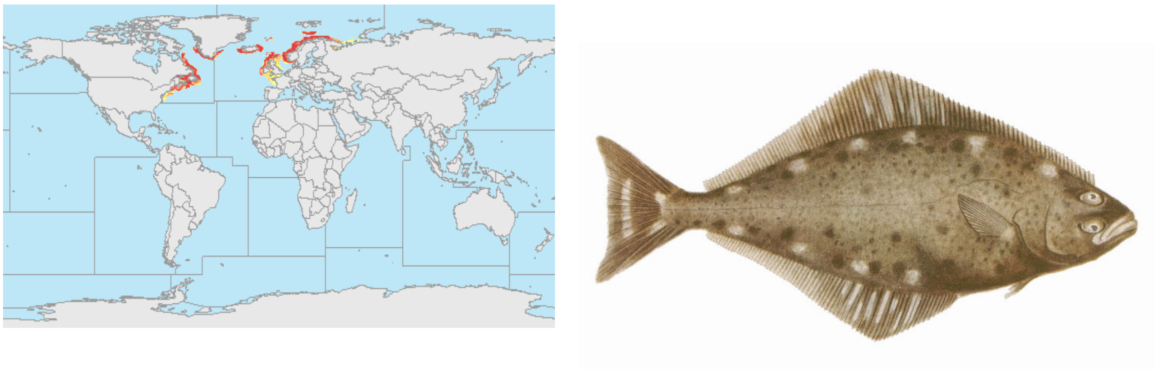


Figure 1: Distribution of the Atlantic halibut in the Atlantic ocean (left). A specimen of Atlantic halibut (right) (www.fishbase.org and www.fishlarvae.com

Physical description

The Atlantic halibut is the largest fish naturally belonging to the Northern Atlantic Ocean. The largest known specimen was captured near Iceland. It was 3,65 m long and weighed 266 kg (Bethon 2005). It has a brown-greyish eyed side and white blind side. The lateral line is arched around the pectoral fin. The caudal fin is cut straight or slightly concave. Furthermore it is a narrower fish, relatively, than most flatfishes (Fig 1, right).

Distribution

The Atlantic halibut is found in the Northern Atlantic Ocean, in the eastern Atlantic from the coast of Labrador and Newfoundland to Cape Cod and far north on the vest coast of

Greenland. Further along the coast of Iceland, from the Biscaya bay to Novaja Zemlja, including the islands of Svalbard (Bethon 2005) (Fig 1, left).

Biology

This fish prefers water at 0-10 ºC. It is found on different kind of bottom substrate, and is able to hide in the substrate, with only it`s eyes visible. The Atlantic halibut is also an excellent swimmer hunting at all depths, and able to migrate long distances. Important prey includes other fish, mollusca, arthropoda and other benthos. Both males and females mature sexually at the age of 12-13 years. Many details regarding spawning are still unknown. Along the Norwegian coast spawning has been registered at depths of 300-700 m, and as far north as Hammerfest. Other important spawning grounds are found near the Faeroe islands, at the Atlantic ridge, the Danish strait, the banks of Newfoundland and the David's strait. Spawning takes place in late winter. Eggs are dispatched and fertilized close to the bottom, but slowly rise in the water column. Eggs hatch after 9-16 days. The larvae go through metamorphosis when 3-3,5 cm long; the left eye moves over to the right side and pigmentation is increased on the right side. The fry gradually prefer deeper waters as they grow. (Bethon 2005).

Pacific halibut (*Hippoglossus stenolepis*)

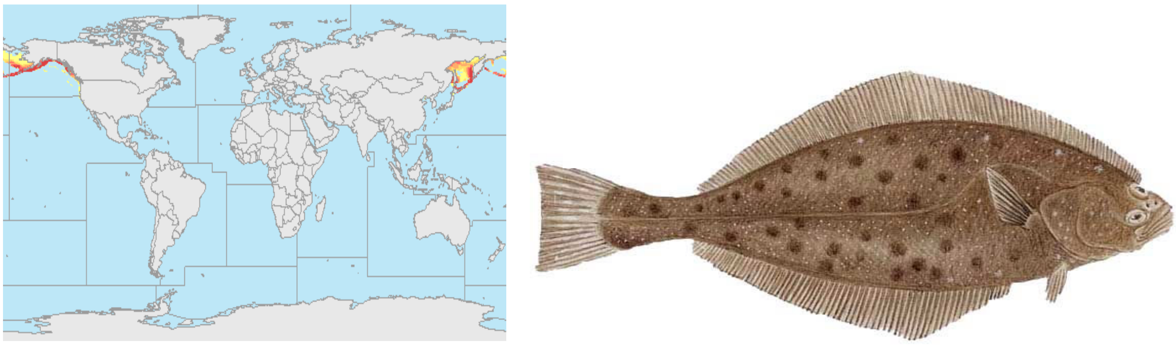


Figure 2: Distribution of Pacific halibut in the Pacific ocean (left). A specimen of Pacific halibut (right). (www.fishbase.org www.landbigfish.com)

Physical description

The pacific halibut can reach a length of 267 cm and weigh up to 363 kg. Maximum observed age is 42 years (www.fishbase.org). It is coloured only on the right (top) side. The colour varies from mottled greenish to dark brown, depending on camouflage requirements. (Fig 2, right) The underside is white. It has a concave tail, and its lateral line makes a large loop around the pectoral fin (Rodger 2005)

Distribution

Pacific halibut can be found throughout most of the marine waters of the North Pacific. It is distributed along the continental shelf of the North Pacific from Southern California to Nome, Alaska and along the coasts of Japan and Russia (www.fishbase.org).

Biology

Pacific halibut move from deep water at the edge of the continental shelf to shallower banks during the summer and return to deep water in the winter to spawn. This migration may involve hundreds of km. It is found on various types of bottoms. Young are found near shore, moving out to deeper waters as they grow older. Older individuals typically move from deeper water along the edge of the continental shelf where they spend the winter, to shallow coastal water (27-274 m) for the summer. Pacific halibut feed on fishes, crabs, clams, squids and other invertebrates (www.fishbase.org). Males mature sexually at the age of 8 years, while females mature after 12 years. Eggs are released pelagic at depths of 900-1200 m. They hatch after 16 pays. When larvae are about 2 cm long the left eye begins to travel to the right side of the head, and they become bottom dwellers (Rodger 2005).

Greenland halibut (*Reinhardtius hippoglossoides*)

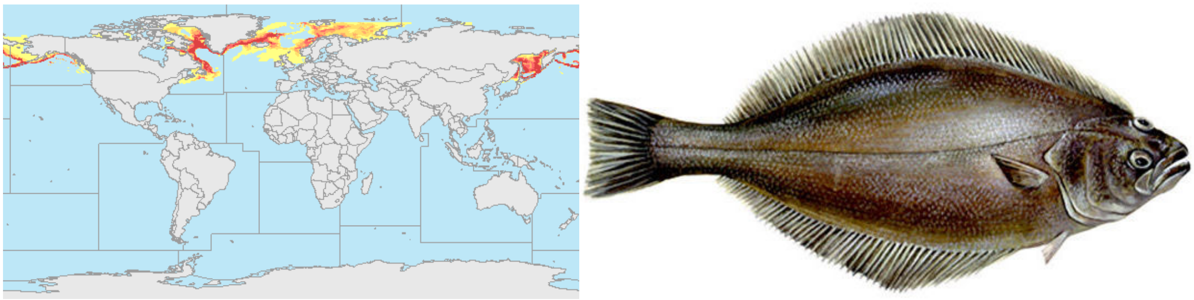


Figure 3: Distribution of Greenland halibut (left). A specimen of Greenland halibut (right). (www.fishbase.org and www.galizacig.com)

Physical description

The Greenland halibut can grow up to 1,2 m long and weigh 45 kg (Bethon 2005). Its left side is almost as dark as its right side. The lateral line does not make an arch around the pectoral fin, but is almost straight from head to caudal fin. Its left eye does not move completely over to the right side during metamorphosis (Rodger 2005). This feature makes it easy to separate Greenland halibut from Atlantic- and Pacific halibut.

Distribution

Both the Atlantic and the Pacific Ocean are home to Greenland halibut. In the Atlantic Ocean the species is found off the North American and Greenland coasts, in the Iceland / Faroes area, and in the eastern Norwegian and Barents Seas (Fig 3, left) (Andriyashev 1954). There is a subspecies in the Pacific Ocean, from the Bering Sea to northern Japan and southern California; *R.h . matsuurae*. They are separated at the subspecies level (Fairbarn 1981).

Biology

The Greenland halibut is a eurytopic species, adapted to life in a wide range of environmental conditions. It is found at a depth of 20 m to 1200 m, in temperatures between –1 and 10 °C (Fedorov 1971). It is most abundant where bottom temperatures range from –1 to 3 °C (Templeman 1973). This flatfish is benthopelagic; it spends time both close to the bottom and swimming in the pelagic. It can adopt a vertical swimming position when it moves freely in the pelagic (De Groot 1970). Sexual maturation for males and females takes place at the age of 5 and 10 years, respectively. The main spawning grounds in the Norwegian / Barents Sea are at depths between 600 and 900 m along the continental slope between 70°N and 75°N. The Davis Strait near Greenland is also an important spawning area. Eggs and larvae are pelagic. Eggs are 3,8-4,3 mm in diameter (Godø and Haug 1989). Metamorphosis is unusually slow, and takes place when the fry is 6-9 cm long. Greenland halibut in the Norwegian and Barents Sea and halibut close to Iceland and Greenland are considered to belong to different populations (Bethon 2005).

Population studies of Atlantic halibut

Joensen (1954) and Mccracken (1958) where the first who suggested that Atlantic halibut may consist of more than a single population. Mork and Haug (1983) conducted a study seeking to find genetic differentiation in halibut from three different localities along the Norwegian coast using tissue enzymes as a marker. Their study revealed no significant differences. Grant et al. (1984) also concluded with some stock differentiation. Then Haug and Fevolden (1986) screened 43 loci in halibut from Greenland and three different localities in Norwegian waters. A possible heterogenity was reported between the southernmost and the two northernmost localities. Foss et al. (1998) found halibut from Greenland, Faroes and Iceland to be similar in terms of allele frequencies. Whereas halibut from Honningsvåg (northern Norway) deviated significantly. Reid et al. (2005) investigated population structure in Atlantic halibut using 18 microsatellite markers (see "molecular markers" below). The analysis revealed no significant differentiation between samples, although uncertainties surrounding Atlantic halibut reproductive behaviour made it difficult to ascertain that only a single breeding population had been sampled at each location.

This study is by no means a population study. A population study would have to include more individuals from a wider geographic area. But mitochondrial DNA is a marker well suited for population studies, and information found in this study will be usefull in future investigation of population structure.

Organelles: Mitochondria and plastids

Organelles are structures in the cytoplasm with a specific function surrounded by a membrane. Mitochondria and plastids are two of many organelles found in the eukaryotic cell. Mitochondria are found in both plant and animal cells, whereas plastids are found in plants and algae. Plastids have the ability to differentiate and redifferentiate. The most known form is probably chloroplasts (Mathews et al. 2000).

Mitochondria are surrounded by a smooth outer membrane and a membrane on the inside that is folded into cristae. The cristae contain a set of enzymes for oxidation of fatty acids and oxidative phosphorylation of ADP into ATP. Their task is to transform energy in organic molecules from digested food items into energy in the form of ATP, the most common energy source for energy-requiring reactions in the cell (Pollard and Earnshaw 2004).

The organization of organelle genomes

Mitochondria and chloroplasts both possess DNA genomes that code for RNA species and some of the proteins involved in the functions of the organelle. Different kinds of RNA are also known to be imported into mitochondria (Entelis et al. 2001). Acceptance of the fact that mitochondria contain their own genome followed the demonstration that circular DNA was isolated from mitochondrial fractions of cells (Van Bruggen et al. 1966). Short thereafter circular DNA molecules were isolated from mitochondria from other vertebrates and some invertebrates.

In some lower eukaryotes the mitochondrial DNA (mtDNA) is linear, but more usually it is a single circular molecule of DNA. So far only a few linear mitochondrial DNA have been isolated. One of the exceptions is the mtDNA from the cnidarian *Hydra attenuata*, which consists of two unique 8-kb linear DNA molecules (Warrior and Gall 1985). Chloroplast DNA falls in the range of 120-200 kb, whereas mtDNA varies enormously in size. In animals it is relatively small, usually less than 20 kb. But in plants mtDNA can be as big as 2000 kb (Primrose and Twyman 2003).

Mitochondria are essential components of all eukaryotic cells. Despite the great diversity of genome organization, they have the same function in every organism: Cellular respiration and oxidative phosphorylation. Many of the genes for mitochondrial proteins and RNAs are found in the nucleus. The mechanisms behind the transport of proteins into mitochondria are still under debate. An enzyme called translocase is known to recognise and translocate proteins into mitochondria. There are different translocases in the outer and inner membrane. So far six different translocases have been identified (Mokranjac and Neupert 2005). Some organisms use the standard genetic code to translate nuclear mRNAs, and a different code for their mitochondrial mRNAs (Primrose and Twyman 2003).

Vertebrate mitochondrial genomes

MtDNA is a much used molecular marker because it is present in much higher copy number than nuclear DNA (Michaels et al. 1982). However, with todays Polymerase Chain Reaction (PCR) obtaining enough material for analysis is usually not a problem, even for nuclear genes. A typical somatic cell contains 500–1000 mitochondria, each with a few DNA molecules. Whereas an oocyte has a much higher concentration of mitochondria. (May-Panloup et al. 2005) measured an average of 256000 mitochondrial genomes in human oocytes. As mentioned above, mtDNA is a relatively small genome. It is mainly maternally inherited (Hutchison et al. 1974). MtDNA is generally considered to lack recombination. However, recent work in several fields has questioned the validity of this characteristic. Studies of natural populations of several animal species have provided convincing evidence for the presence of mtDNA recombination in at least some taxonomic groups (Burzynski et al. 2003; Hoarau 2002; Lunt and Hyman 1997). Although there is no doubt that certain animal mitochondrial genomes do recombine, we remain basically ignorant as to how common mtDNA recombination might be in the animal kingdom. The mitochondrial genome has a higher mutation rate than the nuclear genome, perhaps due to repair inefficiency (Parsons et al. 1997). This elevated rate of evolution is 5-10 times faster than single copy nuclear genes (Brown et al. 1979)

An mtDNA molecule is regarded as a haplotype and is treated as a single locus. Since mtDNA is maternally inherited, most copies are identical (i.e. monoclonal) in an individual. However, it is possible that more than one mtDNA type is present in an individual. This phenomenon is called heteroplasmy and it is now thought that all individuals are heteroplasmic, at least at some level. Differences can be found among single nucleotides or in the number of copies of a repeated motif. Individuals may have more than one mtDNA type in a single tissue or specific differences may be located in specific tissues. Heteroplasmy in one tissue sample and homoplasmic in another tissue sample is also a possibility. Length heteroplasmy in a homopolymeric stretch (i.e., C stretches), is more common than point heteroplasmy. See table 31 for an overview of heteroplasmy in fish.

Vertebrate mitochondrial genomes normally carry genes encoding 13 proteins: Seven NADH dehydrogenase subunits, three cytochrome oxidase subunits, ATPase 6, ATPase 8 and cytochrome B. The genome also consists of 22 transfer RNA genes (tRNAs) and two ribosomal RNA genes; 12 S and 16 S, necessary for translation of the proteins encoded by mtDNA. The proteins are involved in electron transport and ATP synthesis (Billington 2003). In addition a non-coding control region, known as displacement loop (D-loop), is present. The d-loop is only a short region of the whole control region. The non-coding control region is responsible for size variation in the mitochondrial genome due to differences in length and copy number of short repeats in various groups (Brown et al. 1996; Gissi et al. 1998; Ursing and Arnason 1998).

One strand is known as the light (L) strand and the other one as the heavy (H) strand. The two strands are called heavy and light because there is an imbalance in nucleotide composition in the two strands. The heavy strand has a higher content of purines (adenine and guanine), while the light strand is richer in pyrimidines (tymine and cytosine). Purines are heavier than pyrimidines. The majority of the genes are transcribed from the H-strand. The replication origin for the heavy-strand (O_H) is located in the control region, whereas the replication origin of the light strand (O_L) is located in the WANCY cluster between the tRNAs for aspargine and cysteine

(Fig 4). The WANCY cluster is a short region containing five tRNA genes: Trp (W),Ala (A), Asn (N), Cys (C) and Tyr (Y).

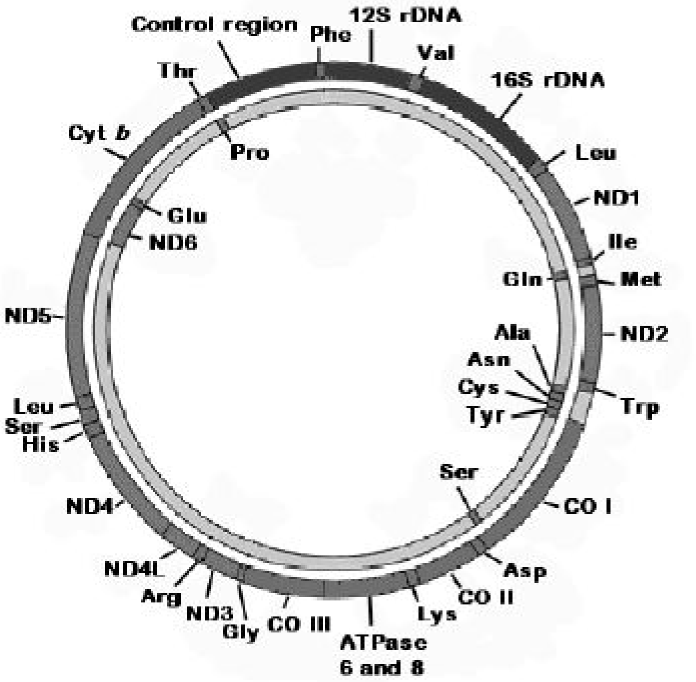


Figure 4: Schematic representation of the circular molecule of the “conserved” vertebrate mitochondrial genome organisation. Genes outside and inside the circle are transcribed from the H and L strands, respectively. Protein coding genes are presented as follows: Cyt B – cytochrome b; CO I, CO II, CO III – subunits of the cytochrome oxidase; ND1-6 – subunits 1 to 6 of the NADH reductase. tRNAs are presented by their three letter amino acid abbreviations. Figure from (Pereira 2000)

A great number of phylogenetic studies using mitochondrial gene sequences have been reported. For example, the control region is often used in population studies due to the high variability in its nucleotide sequence. While protein-coding genes, such as cytochrome b are generally used for phylogenetic analysis of taxa above the species level (Pereira 2000).

Transmembrane helices in mitochondrial proteins

Embedded within the inner membrane of mitochondria are the proton carriers, primarily cytochromes, which constitute the respiratory chain. There are totally eight of these carrier complexes. They are assembled in the form of multiprotein complexes. ND1-ND6 and ND4L are 7 of a total of 25 subunits of the NADH dehydrogenase (Complex I). NADH pumps protons into the intermembrane space of the mitochondrion, thus passing energy on to complex III. Complex II transfers energy from FADH2 to complex III. Cyt-b is one of 9-10 polypeptides in complex III. COI-COIII along with 10 other polypeptides make up cytochrome oxidase (complex IV) that pumps protons into the intermembrane region of mitochondria. ATPase6 and ATPase8 are subunits of FoH$^+$-ATPase, together with 10-12 other polypeptides (Complex V) which catalyses ATP synthesis from ADP (Mathews et al. 2000). These proteins will be further characterized by determining the number of transmembrane helices in protein coding genes in Atlantic-, Pacific- and Greenland halibut.

Organization of the fish mitochondrial DNA

Until about 1995 one believed that gene order was conserved among all fish mtDNA. The reason for this is that the first complete mitochondrial genome sequences found in vertebrate taxa had no variation in the position of the genes along the molecule. This had been observed in taxa as diverse as humans and other mammals (Anderson et al. 1981; Anderson et al. 1982; Árnason and Gullberg 1993; Gadaleta et al. 1989), *Xenopus* (Roe et al. 1985), and some fish species (Johansen et al. 1990; Tzeng et al. 1992; Zardoya et al. 1995). But in 1995 sea lamprey was reported to have a translocation of tRNA Gln – Cytb and in the location of the non coding regions (Lee and Kocher 1995). The same rearrangement was also found in river lamprey (Delarbre et al. 2000). Miya and Nishida (1999) reported an example of tRNA gene rearrangement in bony fishes between the ND6 and the control region (ND6 - Cyt *b* - tRNAGlu - tRNAPro - tRNAThr - control region). This changed the "conserved" status of mtDNA in fishes. Until this study three Pleuronectiform species were available from Gene Bank. No deviation from the "conserved vertbrate gene order" were found in these species.

As reviewed by Pereira (2000) rearrangements associated with tRNA genes have been reported in birds, lizards, crocodilians, marsupial mammals, snakes and tuatara. Tandem duplication and multiple deletion events associated with tRNA genes appear to be the most probable mechanisms for new gene rearrangements seems. Placental mammals, turtles, fishes, some lizards and the frog *Xenopus* have the most conserved mitochondrial gene order (Pereira 2000).

The genetic code for vertebrate mitochondrial DNA

As seen in Table 1 it is possible to have a change in the DNA sequence without any corresponding change in the gene product; the polypeptide. The reason for this is that all amino acids are encoded by more than one codon (Table 1). The 3rd position (synonymous position) within a codon is often a fourfold degenerate site. So a substitution in this position will have no effect on the amino acid level. A change in one of the nucleotides in the 1st codon position will in most cases change the amino acid. The exception is two tRNA genes that read different codons. tRNA$^{\mathrm{Leu(UUR)}}$ reads the codons TTA and TTG . While tRNA$^{\mathrm{Leu(CUN)}}$ reads the codons CTT, CTC, CTA and CTG. tRNA$^{\mathrm{Ser(UCN)}}$ reads TCA, TCG, TCC and TCT, and tRNA$^{\mathrm{Ser(AGY)}}$ reads AGC or AGT.

Table 1: The vertebrate mitochondrial genetic code. (https://bioinformatics.org/JaMBW/2/3/ TranslationTables.html)

Amino acid	Codon	Amino acid	Codon	Amino acid	Codon	Amino acid	Codon
Phe (F)	TTT	Ser (S)	TCT	Tyr (Y)	TAT	Cys (C)	TGT
Phe (F)	TTC	Ser (S)	TCC	Tyr (Y)	TAC	Cys (C)	TGC
Leu (L)	TTA	Ser (S)	TCA	STOP	TAA	Trp (W)	TGA
Leu (L)	TTG	Ser (S)	TCG	STOP	TAG	Trp (W)	TGG
Leu (L)	CTT	Pro (P)	CCT	His (H)	CAT	Arg (R)	CGT
Leu (L)	CTC	Pro (P)	CCC	His (H)	CAC	Arg (R)	CGC
Leu (L)	CTA	Pro (P)	CCA	Gln (Q)	CAA	Arg (R)	CGA
Leu (L)	CTG	Pro (P)	CCG	Gln (Q)	CAG	Arg (R)	CGG
Ile (I)	ATT	Thr (T)	ACT	Asn (N)	AAT	Ser (S)	AGT
Ile (I)	ATC	Thr (T)	ACC	Asn (N)	AAC	Ser (S)	AGC
Met (M)	ATA	Thr (T)	ACA	Lys (K)	AAA	STOP	AGA
Met (M)	ATG	Thr (T)	ACG	Lys (K)	AAG	STOP	AGG
Val (V)	GTT	Ala (A)	GCT	Asp (D)	GAT	Gly (G)	GGT
Val (V)	GTC	Ala (A)	GCC	Asp (D)	GAC	Gly (G)	GGC
Val (V)	GTA	Ala (A)	GCA	Glu (E)	GAA	Gly (G)	GGA
Val (V)	GTG	Ala (A)	GCG	Glu (E)	GAG	Gly (G)	GGG

There are four distinct differences between the mitochondrial genetic code and the standard genetic code (Table 2)

Table 2: Differences between the mitochondrial genetic code and the standard genetic code

	Mt genetic code	Standard genetic code
Codon	Amino acid	Amino acid
AGA	STOP	Arg (R)
AGG	STOP	Arg (R)
AUA	Met (M)	Ile (I)
UGA	Trp (W)	STOP

Codon usage bias

Synonymous codons (i.e. codons coding for the same amino acid) are often not used with equal frequency. This phenomenon is known as codon bias. There has been a debate concerning the functional role of codon bias, namely, does codon bias maximize translational efficiency (elongation rates) or translational accuracy (reducing misincorporation of incorrect amino acids). Different kind of organisms apparently have evolved unique genomic signatures (Bernardi and Bernardi 1986). It has been proposed that each species is subjected to specific genomic pressures on base composition, in turn resulting in a distinctive bias in codon choice (Grantham et al. 1980). In principle, biases in nucleotide composition and codon usage can result from natural selection and/or differential mutational pressure. In many organisms (*E. coli, D. melanogaster* and *C. elegans*) codons that use abundant tRNAs are selectively favoured (Gouy and Gautier 1982; Powell and Moriyama 1997; Stenico et al. 1994). Codon selection of this type most likely functions to optimise translational speed and/or translational accuracy, although additional factors, such as transcription efficiency and mRNA secondary structure could also exert selection pressures (Xia 1996; Zama 1990). It was found for many *E. coli* genes that the degree of bias in codon choice is directly related to the expression level of a particular gene (Klump and Maeder 1991). In mammals codon bias seems to be closely related to mutation pressure (Sharp et al. 1993). Furthermore, in a recent study in humans Kotlar and Lavner (2006) concluded that selection acts to enhance translation efficiency in highly expressed genes by preferring some codons, and acts to reduce translation rate in lowly expressed genes by preferring a different set of codons. Codon usage bias will be thoroughly investigated in the three halibut species.

Molecular markers

Repeated sequences of short motifs, usually 1-13 bp long, are known as microsatellites. Such sequences are probably created when DNA helicase slips back a few bases, so that the same bases are inserted twice in the new strand. The number of copies of the repeated motif changes fast. This is the reason why microsatellites are used for population studies. They can reveal information about the history and geographical dispersal of populations. The Polymerase Chain Reaction is usually used to amplify microsatellites (Jarne and Lagoda 1996; Queller et al. 1993).

RFLPs (Restriction fragment length polymorphism) are fragments of restricted DNA (i.e. DNA cut at specific recognition sites with a restriction enzyme) and then separated according to size with gel electrophoresis. A specific DNA sequence will yield a specific pattern after gel electrophoresis. Different sequences may lack or have present different endonuclease recognition sites, thus creating different patterns (Baxevanis and Francis Ouellette 2001).

The methods mentioned above are based on differences in DNA sequence. In this method the products of the DNA sequence are used, namely proteins. Allozymes are different alleles of proteins. They are separated by electrophoresis because of differences in charge. Isozymes have been used for the same purpose. Isoenzymes have differences in the amino acid sequence, but target the same chemical reaction. Only a fraction of the genetic variation that is present can be detected by the use of allozymes. The reason being that synonymous substitutions will not cause changes in the amino acid sequence that makes up the protein. The lack of resolution is this methods main drawback (Higgs and Attwood 2005; Kephart 1990; May 1992).

Single Nucleotide Polymorphisms (SNP) are variations in one nucelotide position. This molecular marker is one of the new tools used for example in population studies. Both mitochondrial and nuclear genes are screened for SNPs (Vignal et al. 2002). Introns are DNA regions that have no known function. They are mainly found in the nuclear genome. Introns evolve faster than the rest of the gene and intron-SNPs are therefore interesting as a marker in population studies, e.g. Li et al. (2006).

Sequencing of DNA and even complete mitochondrial genomes has in the recent years become a routine, e.g. Miya et al. (2001). DNA sequences have the potential of being a powerful molecular marker. Analysis using DNA sequences often provide higher resolution and accuracy than the methods mentioned above. This is the reason why DNA sequencing was chosen in this study

Phylogenetic analysis

A phylogenetic analysis tries to explain evolutionary relationships. In molecular phylogenetics, likenesses and differences, usually in DNA or amino acid sequences, are used to create a phylogenetic tree. In such a tree a clade is a monophyletic taxon that include the most recent common ancestor and all of the descendants of that most recent ancestor. A taxon is simply a named group of organisms. It is not necessarily a clade. The length of each branch correspond to the number of changes that has occurred (Baxevanis and Francis Ouellette 2001).

An alignment were homologous nucleotides are compared is the basis from which a phylogenetic tree is created. A tree based only on observations within a single gene should be referred to as a gene tree, not a species tree. A gene tree represents the evolutionary history of the gene, but the history of the whole species might be different. To created a trustworthy species tree it is required to use data from multiple genes (Krane and Raymer 2003).

In an unrooted tree you only get information about the relationship between the nodes. While in a rooted tree evolution can be followed from the most recent common ancestor of all taxa included in the tree. Trees are usually rooted by choosing one or more uncontroversial species as an outgroup (Krane and Raymer 2003).

Molecular data can be used in two ways to generate phylogenetic trees: Character based methods and distance based methods. Distance methods summaries the differences between the sequences and use the amount of change between sequences to derive a tree. A distance method is only able to tell the true phylogenetic story if all genetic divergence events were accurately recorded in the sequence (Swofford et al. 1996). The biggest advantage is that distance methods require far less computer power (Baxevanis and Francis Ouellette 2001).

Neighbor Joining starts with a tree were all species come a single central node. Neighbors are then calculated so that the least total branch length is found. This method is far from optimal, but usually creates close to the optimal tree (Saitou and Nei 1987).

The minimum-evolution (ME) method searches for the optimal tree by finding the one with the smallest sum of branch lengths as estimated under the least-squares criterion, were negative branch lengths is not allowed (Rzhetsky and Nei 1992).

The character based methods use character data at all steps in the analysis. Maximum parsimony is based on the principle that the simplest method is the best. A MP tree is the one that requires the fewest changes to explain the inferred topology (Swofford et al. 1996). To do this, all trees are given a length, equal to the minimum number of transitions which can explain the observed distribution of character states across taxa assuming the tree. The tree with the shortest length is the maximum parsimony tree.

Long branch attraction, as reviewed by Bergsten (2005), is a problem that arises when sequences that evolve rapidly and are not closely related, cluster together. When the nucleotide substitution rate is high there is a possibility that the same nucleotide will occur at the same position, simply by chance. This is possible because there are only four different nucleotides to choose between. The problem seems to be greatest when using the MP method. By employing the maximum likelihood method this problem is reduced. It is also possible to avoid the problem by adding taxa that are related to those taxa with long branches.

Bootstrapping is a way of determining the confidence of a taxon. A part of the original sequence from each species is drawn and a new, pseudoreplicate tree is made from this data set. The process is repeated multiple times, in this study 2000 times. This is a way of testing the reliability of the tree topology (Hall 2004). The method was invented by Efron (1979). It has been suggested that a bootstrap of more than 70 % correspond to a probability of greater than 95 % that the true phylogeny has been found (Hillis and Bull 1993). Though, under less favourable conditions, a bootstrap greater than 50 % will be an overestimate of the accuracy (Hillis and Bull 1993). So conditions of the analysis must be considered.

As a general rule, if a data set yields similar trees when analysed by the fundamentally different distance matrix and parsimony methods, that tree can be considered fairly reliable (Krane and Raymer 2003).

The patterns of substitution in protein coding genes are well known. The knowledge of how mutations accumulate makes protein coding genes good candidates for phylogenetic studies in fish. Mutations in third (and rarely in first) positions of codons that do not result in amino acid substitutions occur at higher rates than substitutions causing amino acid replacements. Transitions (purine→ purine or pyrimidine → pyrimidine) in third codon position are most frequently observed, followed by transversions (purine ↔ pyrimidine) in third codon positions and silent transitions in some first codon positions (Meyer 1994). Among distantly related species, transitions in third positions will probably experience substitutional saturation, and will be unreliable for revealing evolutionary descent (Bakke and Johansen 2005). Transversions are less common and have a higher chance of being reliable indicators of descent. Second positions of codon are most conserved and contain phylogenetic information among distantly related species.

It is difficult to resolve phylogenetic relationships among the Pleuronectiformes due to their reduced morphology (Berendzen and Dimmick 2002). Traditionally eye position has been an important character in classification of flatfishes. Flounders and soles have both been divided into right- and left-hand taxa (Norman 1934). Chapleau (1993) concluded that sidedness had been derived multiple times within flatfishes and that eye position was not a good indicator of relationships within the group.

Berendzen and Dimmick (2002) used 12S and 16S mitochondrial ribosomal DNA to elucidate relationships within the Pleuronectiformes. Of the taxa included in the present thesis Soleidae and Scophthalmidae was recognized as the most basal groups, while Pleuronectidae was the most derived group. Pacific halibut was the only Pleuronectidae species from the present thesis that was also included in the study by Berendzen and Dimmick (2002). Atlantic halibut and Pacific halibut are recognized as closely related species, but this knowledge is not based on DNA sequence information (Nelson 1994).

Molecular clocks

The molecular clock hypothesis arised some four decades ago, when it was discovered that divergence in nucleotide and amino acid sequence often increase linearly as time goes by Zuckerkandl and Pauling (1962). The divergence rate vary from gene to gene, and synonomous positions evolve faster than nonsynonomous ones. Fossils records are used to estimate divergence rates and thus calibrate the molecular clock. But fossils tend to underestimate divergence times (Hedges 2002). Geological events like the rise of the Isthmus of Panama have also been used as calibration points e.g. Domingues et al. (2005). Ideally multiple calibration points should bee used. The rise of the Isthmus of Panama was chosen to calibrate the molecular clock that was used to estimate time of divergence for Atlantic-, Pacific- and Greenland halibut.

Even if homologous genes are considered, divergence rate may differ from taxa to taxa. Therefore relative rate test have been developed to detect differences in evolutionary rate among lineages, e.g. Tajima (1993). Still, divergence times are only rough estimates that depend highly on the accuracy of the calibration point and conservation of divergence rates among taxa.

Aims of the study

- Determine the complete mitochondrial DNA sequence from 4 individuals of Atlantic halibut, Pacific halibut and Greenland halibut, respectively.
- Determine part of the mtDNA sequence from Common sole, Turbot and European plaice for use as a molecular marker sequence in phylogenetic analysis.
- Investigate intraspecific and interspesific genetic variation in Atlantic halibut, Pacific halibut and Greenland halibut, both at the nucleotide- and amino acid levels.
- Contribute to phylogenetic relationship determination among Atlantic halibut, Pacific halibut, Greenland halibut, Common sole, Turbot and European plaice.
- Investigate the possibility of creating a test for easy and fast species identification based on the mtDNA molecular marker.

Materials

Table 3 displays which species were included in this study.

Table 3: English and Latin names of species from which mtDNA was completely or partially determined.

Common name	Scientific name
Atlantic halibut	*Hippoglossus hippoglossus*
Pacific halibut	*Hippoglossus stenolepis*
Greenland halibut	*Reinhardtius hippoglossoides*
Common sole	*Solea vulgaris*
Turbot	*Scophthalmus maximus*
European plaice	*Pleuronectes platessa*

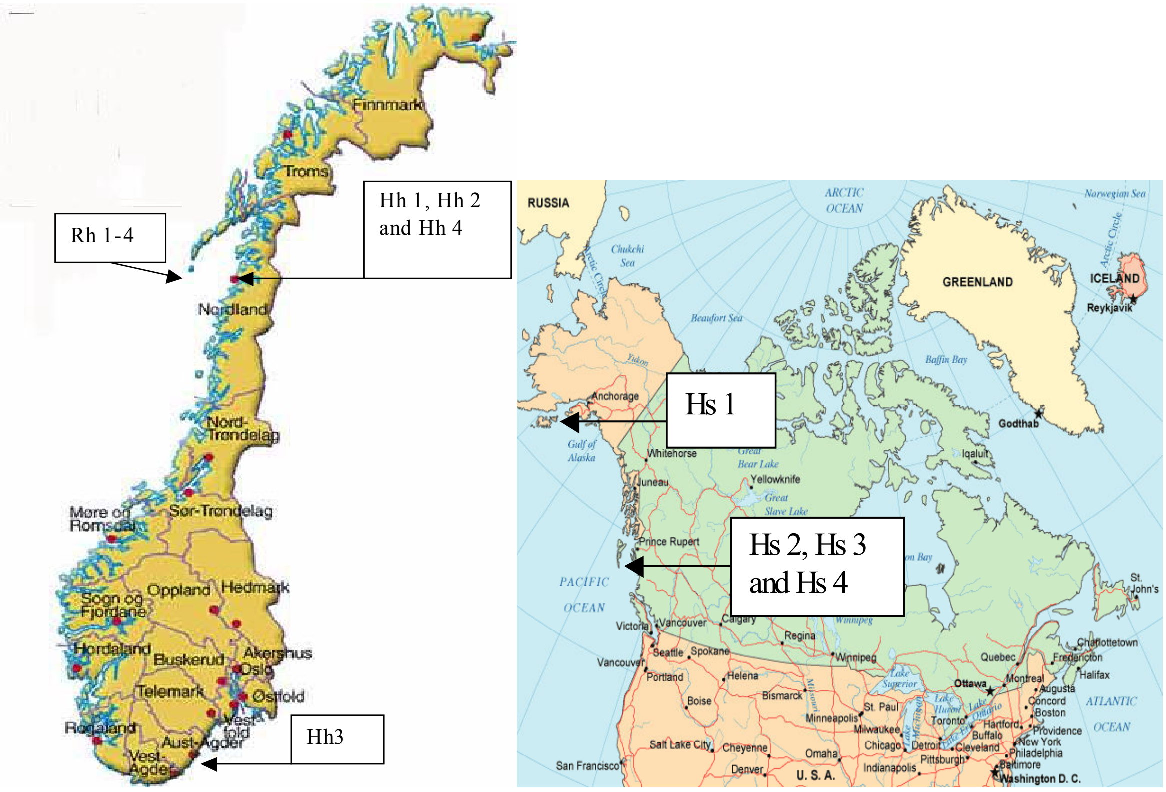


Figure 5: Location where the individuals of Atlantic halibut (Hh), Pacific halibut (Hs) and Greenland halibut (Rh) were caught. (www.tagkompaniet.se and http://encarta.msn.com/map_701511416/Canada.html)

Atlantic-, Greenland- and Pacific halibut

Figure 5 displays the location where the different individuals were caught. Atlantic halibut number one and two were born in captivity at Mørkvedbukta Research Station . Their parents were wild caught at an unknown location, but probably not very far from Bodø (N67 16 20, E14 22 04). Atlantic halibut number three was wild caught in the waters close to Bodø. A sample from Atlantic halibut number four were obtained from Risør aquarium in southern Norway (N58 42 34, E9 13 54). All four individuals of Greenland halibut were caught off the coast of the island Røst (N67 31 39, E12 06 39). Pacific halibut number one were caught outside Cook Inlet, about 37 km off Homer (N 59 35 41 W152 06 18), Alaska. Pacific halibut 2-4 were caught in Hecate Strait (N52 53 40, W130 38 10) at the west coast of Canada.

30 individuals of Atlantic halibut

Approximately 800 bp of the ND2, COI and control region respectively was sequenced in 30 individuals from the Atlantic halibut broodstock at Mørkvedbukta Reseach Station. The first eight individuals originates from Tysfjord (N68 04 11, E16 13 66). They were bought from local halibut farmers, and the relationship among them is not known. Individuals 9-23 are born at Mørkvedbukta Research Station in 2001. They are possibly siblings or half-siblings, but this information is uncertain. The last six individuals were wild-caught in 2005 at an unknown location, but probably close to Bodø (N6716201, E1422043)

Common sole, Turbot and European plaice

Samples of Common sole and Turbot were obtained from Risør aquarium (N58 42 34, E9 13 54). The European plaice was caught close to Bodø (N6716201, E1422043). Approximately 13420 bp from Common sole, 15012 bp from European plaice and 7678 bp from Turbot were determined

Table 4 presents the species, from which mtDNA sequences were used in the different alignments and in the phylogenetic studies.

Table 4: Species from which mtDNA was used in phylogenetic studies.

Common name	Latin name	Accession number
Atlantic halibut	*Hippoglossus hippoglossus 1*	This study
Atlantic halibut	*Hippoglossus hippoglossus 2*	This study
Atlantic halibut	*Hippoglossus hippoglossus 3*	This study
Atlantic halibut	*Hippoglossus hippoglossus 4*	This study
Pacific halibut	*Hippoglossus stenolepis 1*	This study
Pacific halibut	*Hippoglossus stenolepis 2*	This study
Pacific halibut	*Hippoglossus stenolepis 3*	This study
Pacific halibut	*Hippoglossus stenolepis 4*	This study
Greenland halibut	*Reinhardtius hippoglossoides 1*	This study
Greenland halibut	*Reinhardtius hippoglossoides 2*	This study
Greenland halibut	*Reinhardtius hippoglossoides 3*	This study
Greenland halibut	*Reinhardtius hippoglossoides 4*	This study
European plaice	*Pleuronectes platessa*	This study
Turbot	*Scophthalmus maximus*	This study
Common sole	*Solea vulgaris*	This study
Stone flounder	*Platichtys bicoloratus*	AP002951
Bastard halibut	*Paralichtys olivaceus*	AB028664
Spotted halibut	*Verasper variagatus*	DQ403797
Cod	*Gadus morhua*	X99772
Haddock	*Melanogrammus aeglefinus*	DQ020497
Alaska pollock	*Theragra chalcogramma*	AB094061
Atlantic salmon	*Salmo salar*	U12143
Rainbow trout	*Oncorhynchus mykiss*	L29771
Arctic charr	*Salvelinus alpinus*	AF154851
American gizzard shad	*Dorosoma cepedianum*	NC_008107
Naked shellear	*Cromeria nilotica*	NC_007881
	Lycodes toyamensis	NC_004409
Korean rockfish	*Sebastes schlegeli*	NC_005450

Methods

Various kits have been used in this study. The protocol provided by the manufacturer was followed most of the time. Any deviation from the manufacturers protocol is mentioned below. Recipes for buffers, medium and agar plates are found in the manufacturers protocol provided with each kit and also available as pdf-files from each manufacturers home page.

DNA extraction

Total DNA was extracted from red muscle with a kit from Roche (cat.# 11814770001). The manufacturer's instructions were followed. DNA was eluted in double sterilized water or TE-buffer, and stored at -20° celsius.. Concentration of DNA after elution was determined using OD_{260} readings from a Eppendorf biophotometer (cat # 952000004). DNA purity was determined using the optical density ratio between 260 and 280 nm measurements. This is based on the fact that OD at 260 nm is twice that at 280 nm if the solution contains pure DNA. Clean DNA has a OD-260/OD-280 between 1.8 and 2.0.

Polymerase chain reaction (PCR)

There are three basic steps in PCR. First, the target genetic material must be denatured-that is, the strands of its double helix must be unwound and separated-by heating to 90-96°C. The second step is hybridisation or annealing, in which the primers bind to their complementary bases on the now single-stranded DNA. The third is DNA synthesis by a polymerase. Starting from the primer, the polymerase reads the template strand in the 3`-5` direction and match it with complementary nucleotides very quickly. The result is two new double helixes in place of the first, each composed of one of the original strands plus its newly assembled complementary strand. This cycle is repeated typically 30-35 times. PCR is performed in a thermal cycler witch is programmed to change the temperature between the respective steps in each cycle.

PCR conditions used:

Component	Amount
10x PCR buffer	5 ul
DNTP	8 ul
L-primer (10 uM)	1 ul
H-primer (10 uM)	1 ul
LA-taq polymerase (Takara)	0,5 ul
Template	100-200 ng
DEPC water	X ul
Total volume	50 ul

The template was total DNA.

Cycle parameters where depending on the length of the fragment to be amplified:

Fragments of 4-5 kb

Initial denaturation	94 ºC	3 min
Denaturation	94 ºC	1 min
Annealing	48 ºC	1 min
Extension	72 ºC	4 min
Number of cycles	15	
Denaturation	94 ºC	1 min
Annealing	53 ºC	1 min
Extension	72 ºC	4 min
Number of cycles	15	
Final extension	72 ºC	10 min

The Heteroplasmic Tandem Repeat (HTR) region is located in the control region and is approximately 1 kb long.

HTR region, 1kb

Initial denaturation	94 ºC	3 min
Denaturation	94 ºC	1 min
Annealing	53 ºC	1 min
Extension	72 ºC	1 min
Number of cycles	30	
Final extension	72 ºC	10 min

PCR primer pairs

The primer combinations used to amplify mtDNA from the four halibut individuals are presented in table 5. L indicates the light strand and H the heavy strand. Specific primers where designed based on an alignment of mtDNA from *Platichtys bicoloratus* and *Paralichtys olivaceus*. These are species that belong to the Pleuronectiformes. Primer positions were based on the *Platichtys bicoloratus* and *Paralichtys olivaceus* mtDNA. The entire mitochondrial genome in Atlantic-, Pacific- and Greenland halibut was amplified in fragments of 3,5-5 kb, which partially overlapped each other.

Table 5: Primer pairs used to amplify mtDNA in Atlantic halibut, Pacific halibut and Greenland halibut.

Primer pair	Fragment	Sequence 5`-3`
L466	1	GTAGCTCTACTCATCCTGAA
H3977		AAGTGGTGTAGAGGAAGCAC
L3850	2	CGCTGGTCTCCCACCACAGCT
H7740		AGTACAAAATTCGGATGGATGG
L7104	3	ATCAATTGGTTTCAAGCCAA
H10010		GACCTCCTTGCATTCATTCG
L9615	4	TACTGATGAGGATCTTAATC
H13882		GGTAGGTTAGAGGATGCAATGG
L13125	5	CAACCCCAACTAGCATTTCTTC
H590		ATATGGAGTGTATAGTGCAA

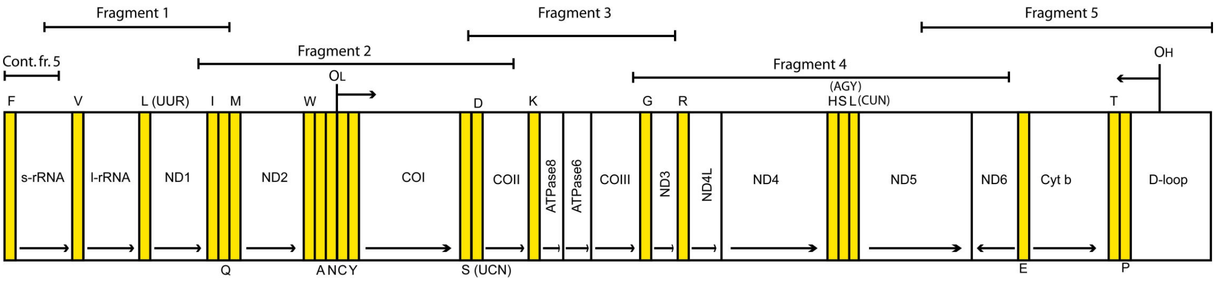


Figure 6: A schematic view of the mtDNA. Regions amplified in Atlantic halibut, Pacific halibut and Greenland halibut are presented above the mtDNA. The tRNA genes are coloured yellow and are indicated by one letter amino acid code. All tRNAs on the upper line are coded on the light strand. Arrows within genes indicates from which strand the genes are coded. Arrows pointing towards right indicated light strand, while genes encoded by heavy strand points towards left.

In some cases the primer combination presented in table 5 gave no PCR product in Common sole, Turbot and European plaice. Alternative primer combinations are presented in table 6.

Table 6: Alternative primer combinations used to amplify mtDNA from Common sole, Turbot, American plaice and European plaice, in case no PCR was produced with the primer pairs in table 3.

Primer pair	Fragment	Sequence 5`-3`
L1249	1	CGCAAGGGAAAGCTGAAA
H3058		CTACCCCTAACTCCCAAAGC
L2642	2	GTCCTACGTGATCTGAGTTC
H6200		AAAGAATCAGAATAGGTGTT
L5572	3	TCGAGCAGAGCTAAGTCAAC
H8589		CTACCCCTAACTCCCAAAGC
L8329	4	CTACCCCTAACTCCCAAAGC
H10433		CTACCCCTAACTCCCAAAGC
L9615	5	TACTGATGAGGATCTTAATC
H11931		CTAAGACCAACGGATGAGCT
L11812	6	AAACACTAGATTGTGATTCT
H13882		GGTAGGTTAGAGGATGCAATGG
L13125	7	CAACCCCAACTAGCATTTCTTC
H16200		GAGAACCCCTTACCCGCTGGAGTGAAC
L15662	8	CTACCCCTAACTCCCAAAGC
H1838		GTCCGTTCCGATTTACAC

To amplify the HTR region of Atlantic halibut and Pacific halibut primers L 16276 and H 17250 was used (Table 7). For Greenland halibut primer combination L 16604 – H 17300 was used.

Table 7: Primer pair used to amplify the HTR region in Atlantic halibut, Pacific halibut and Greenland halibut.

Primer pair	Sequence 5`-3`
L 16276	CGGAGACGTTTAAAGGGT
H 17250	CTTGAAATAATCTAAACAGTA
L 16604	ACATAAAGGATATCATGTGC
H 17300	GTTGGGATGATGCAAGAAAT

Table 8 shows sequencing primers used in this study.

Table 8: Sequencing primers used in this study

Primer	Sequence 5`-3`
H30	CCCATCTTAACATCTTCA
L466	GTAGCTCTACTCATCCTGAA
H590	ATATGGAGTGTATAGTGCAA
L1249	CGCAAGGGAAAGCTGAAA
L1630	GATCATATTCAAATAAGGACA
L2164	TAAATGAAGACCTGTATGAA
L2642	GTCCTACGTGATCTGAGTTC
L2935	TTGCTAGCCGTAGCATTCCT
H3977	AAGTGGTGTAGAGGAAGCAC
L4100	ACTGGCTCCTCGCTTGAATA
H4720	CATTGACGGTGGTCGCTTTGT
L4750	CCCTCGCCATCTCGTGAACA
L5601	AGTCTGCTTATTCGGGCAGA
H6200	AAAGAATCAGAATAGGTGTT
L7104	ATCAATTGGTTTCAAGCCAA
H7173	ACAATTCTGCCTTGACAAGG
H7740	AGTACAAAATTCGGATGGATGG
L8678	CTCATTGCAACAGCTGCCAA
L8820	AAGCCTCTACCTACAAGAAA
H8828	GGGTGTGCTTGATGGGCCAT
L9615	TACTGATGAGGATCTTAATC
H9700	GCTGTAGCTCAGGTGAACGTC
H10010	GACCTCCTTGCATTCATTCG
L10149	TAACAGGCCTGGCATTCCAC
L11350	ATTGCACACGGGCTTACTTC
H11555	CACCGGTTAATGCCAGAGTT
L11812	AAACACTAGATTGTGATTCT
H11931	CTAAGACCAACGGATGAGCT
L12716	CATGGCTTGGAATAGCAACAAAC
H12909	AGTAGGGCAGATACCGGTGTAG
L13125	CAACCCCAACTAGCATTTCTTC
H13882	GGTAGGTTAGAGGATGCAATGG
L14236	ACACCATTACCGACCAACTACC
L14331	CCACCGTTGTTATTCAACT
H14390	TTGTAGTTGAATAACAACGG
L15662	CTACCCCTAACTCCCAAAGC
H16200	GAGAACCCCTTACCCGCTGGAGTGAAC

PCR primers and nested sequencing primers used to amplify part of ND2, COI and the control region in mtDNA from 30 individuals of Atlantic halibut are presented in table 9.

Table 9: Amplified fragments and sequencing primers used in SNP analysis part of ND2, COI and the control region in 30 individuals of Atlantic halibut.

Primer	Fragment	Sequence
L4143	1	ACTGGCTCCTCGCTTGAATA
H5087		GAGAAGAAGGGTGGTTGCTG
L4287	Sequencing primer	CAAGCACTACCAACGCTTGA
L5931	2	CAATCTTCTCACTTCACCTTGC
H6601		ACTACATAGTATGTGTCATGC
H6581	Sequencing primer	CAGAACAATCTCGAGAGAGG
L15662	3	CTACCCCTAACTCCCAAAGC
H16385		GGATGACAGAAGAAATGAGC
L15711	Sequencing primer	CATAAATGTACAATGAAGG

Agarose gel electrophoresis

Gel electrophoresis is a technique for separating charged molecules with different sizes. In an agarose gel, the negatively charged DNA fragments move toward the positive electrode at a rate inversely proportional to their length. After the electric field is applied for a certain period, DNA fragments of different size will be separated. The DNA is visualised in the gel by addition of ethidium bromide. This binds strongly to DNA by intercalating between the bases and is fluorescent meaning that it absorbs invisible UV light and transmits the energy as visible light.

1. Melt 0,7% - 2,5% agarose in 0,5 x TBE electrophoresis buffer in a microwave oven and cool to 65°C.

2. Add ethidium bromide (EtBr) to a final concentration of 0,5 µg/ml and pour the gel into an appropriate mold with a slot former in place.

3. When the gel is fully set, place it in an electrophoresis chamber.

4. Add 1 µl loading buffer (Takara) to 5 µl of sample, before loading the samples. Pour electrophoresis buffer (0,5 x TBE) over the gel to cover it. 6 µl 1 kb DNA plus ladder (Invitrogen$_{\mathrm{TM}}$) is run alongside the samples for estimation of DNA size in each band and and estimation of the DNA quantity in each band.

5. Run the gel at 4-5 V/cm (measured as the distance between the cathode and the anode) until the bromophenol blue colour band has migrated 2/3 of the gel.

6. After separation, place the gel on top of a UV-transilluminator (365 nm) and photograph the gel.

10xTBE buffer stock
900 mM Tris Borate
20 mM EDTA pH 8.0

Extraction of DNA from gel

DNA bands where excised from an agarose gel and extracted from the gel using E.Z.N.A.$^{\circledR}$ Gel Extraction Kit (cat. # D2500-02). This removes primers and remaining nucleotides (dNTP). The manufacturers protocol for gel extraction was followed. DNA was eluted in 40 µl of elution buffer. Concentration and purity of DNA after elution was determined using OD$_{260}$ and OD$_{280}$ readings from a biophotometer. The PCR product was now ready for cloning or sequencing.

Cloning of the fragments into the TOPO vector

Due to heteroplasmy, PCR fragments containing the control region were cloned into a plasmid vector (pCR$^{\circledR}$4-TOPO$^{\circledR}$) using the TOPO TA Cloning kit for Sequencing from Invitrogen (cat.# K4575-01). The critical steps in the procedure are shown in figure 7 below.

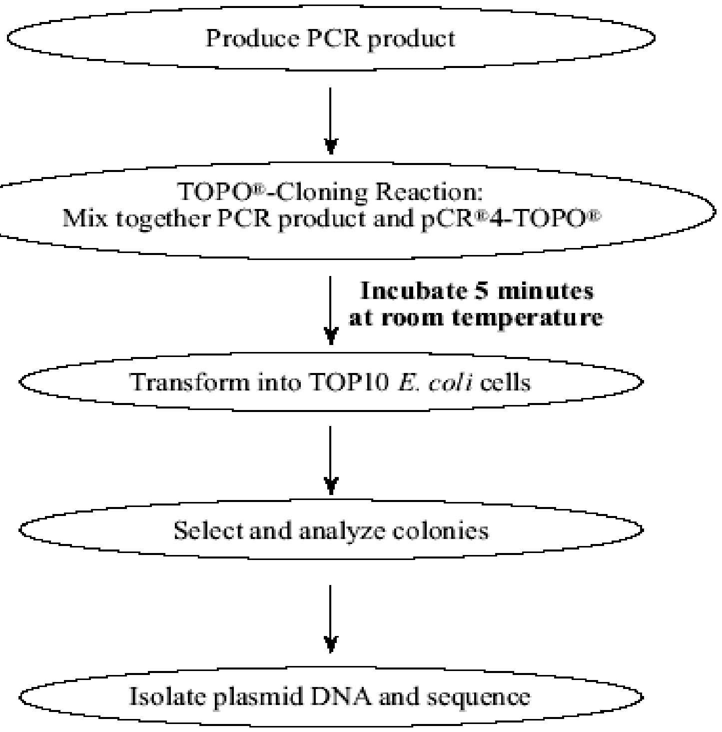


Figure 7: The flow chart above outlines the experimental steps necessary to clone PCR products. (Instruction manual TOPO TA cloning kit, Invitrogen)

The protocol for chemically competent cells was followed. LB agar plates and LB medium were made from recipies in the manufacturers protocol. Bacteria where incubated at 37ºC overnight on LB agar plates, employing kanamycin (50 µg/ml final concentration) as the selective agent and x-gal for blue-white screening (40 µl per plate, 20 mg/ml stock solution).

Assumed positive clones (white) where used to inoculate 10ml of LB medium containing 50 µg/ml kanamycin. 10 colonies from each plate where picked. The inoculated medium was incubated overnight in a shaking incubator at 37ºC.

Plasmid DNA where isolated using Wizard® Plus SV Minipreps from Promega (cat. # A1460). The centrifugation protocol was followed.

Screening for recombinants

To determine whether or not the colonies contained the insert of interest colony PCR or restriction analysis where performed.

Colony PCR

1. Pick a well isolated colony and transfer half of it to 50µl of sterile water. The other half is transferred to a 10µl disposable pipette tip and kept in a sterile 1,5 ml eppendorf tube at 4 c, awaiting the result of colony PCR.
2. Boil the 50 µl of water containing the bacteria for 10 minutes. This causes the bacteria to lyse and release the plasmid.
3. Centrifuge at 16000 x g for 5 minutes.
4. Use 5 µl of the supernatant in a 50 µl PCR with nested primers, or the same primers as in the original PCR if no suitable primers are available.
5. The product is run on a gel. A band at of expected length indicates a positive colony.

Restriction analysis

Restriction enzymes cut double stranded DNA at specific recognition sequences. The plasmid used for cloning is designed with recognition sites for several different restriction enzymes at each side of a potential DNA insert. After plasmids had been isolated they were digested with an enzyme called EcoR I for 2 hours at 37 C and the reaction was run on a gel. EcoR I cuts after the first nucleotide in the following sequence: GAATTC. A band corresponding to the length of the plasmid will always occur. The insert of interest can occur as one band or several shorter bands, that together add up to the expected length.

A digestion with EcoR I consisted of:

Plasmid approx. 100ng/ul	2 ul
EcoR I 10 U/ul	0,5 ul
Buffer 10x	2 ul
Water	15,5 ul
Total volume	20 ul

Sequencing

Sequencing was performed on PCR fragments and cloned inserts using a BigDyeTerminator Ver3.1 kit (Applied Biosystems). Primers used were the same as those used for PCR including inner primers, all presented in tables 5, 6, 7, 8 and 9.

Component	Amount
PCR product	30-300 ng
Big Dye	1 ul
Sequencing buffer 5x	2 ul
Primer 3,5 uM	1 ul
Water to adjust volume)	x ul
Total volume	10 ul

150–300 ng of plasmid or 60-80 ng of a PCR product of 4 kb was used as template for sequencing with the following cycling parameters:

Initial denaturation	96°C	1 min
Denaturation	96°C	30 sec
Annealing	50°C	15 sec
Elongation	60°C	4 min
Cycles	35	

After sequencing-reactions samples were precipitated using ethanol / EDTA and sent to UNN in Tromsø for separation analysis using the Applied Biosystems 3130xl Genetic Analyzer.

Procedure for Ethanol/EDTA precipitation:
1. 1 µl 125 mM EDTA, 1 µl 3 M Natrium acetat, pH 7.5, 27 µl 96% ethanol and 10 µl sequencing
reaction were added to a 1.5 ml eppendorf tube.
2. The mixture was gently mixed and incubated at room temperature for 15 minutes.
3. The tube was centrifugated at room temperature for 15 minutes at 13000 rpm.
4. The supernatant was removed.
5. 150 µl 70% ethanol was added.
6. The tube was centrifuged at room temperature for 5 minutes at 13000 rpm.
7. All the ethanol was removed.
8. The sample was air dried.

Bioinformatics

Computer analysis of DNA sequences, such as editing and assembling was performed using the Lasergene DNA Star package. EditSeq was used to edit the sequences. The first and last part of a sequence is often of poor quality and was therefore removed. Undetermined bases found internally in the sequence were changed into the correct bases if this could be determined by manual reading of the chromatogram files. EditSeq was also used for translation of protein coding DNA into amino acids.

After editing the sequences, they were assembled in SeqMan. When assembling the first Atlantic halibut mtDNA sequence, the entire mitochondrial sequence from stone flounder was used as a backbone to help assemble the sequences correctly. The complete mtDNA sequence from Atlantic halibut was then used as a backbone when assembling subsequent individuals of Atlantic halibut, Pacific halibut and Greenland halibut.

A variety of programs was used for further analysis: For statistical analysis of the mtDNA sequences DNASP was used (Rozas et al. 2003). The putative open reading frames (ORF) were identified Gene finder program available in NCBI using the mitochondrial genetic code. Similarity searches were done using BLAST (Altschul et al. 1990). Both programs are avilable at the NCBI web site www.ncbi.nlm.nih.gov/gorf/gorf.htm and www.ncbi.nlm.nih.gov/blast/. 21 out of 22 tRNA were identified using the computer software tRNAscan-SE 1.21 (Lowe and Eddy 1997) found at www.genetics.wustl.edu/eddy/tRNAscan-SE, with the default parameters for mitochondrial DNA. tRNA-Ser was identified by sequence homolgy with Stone flounder.

Phylogenetic analysis were performed using Clustal X (Thompson et al. 1997) and MEGA 3.1 (Kumar et al. 2004) as follows: An alignments of sequences from the species to be included was created by Clustal X A phylogenetic tree based on the alignment were produced by the use of Neighbor Joining (NJ), Minimal Evolution (ME) and maximum parsimony (MP) methods. A bootstrap with 2000 replicates was performed to determine the reliability of the different parts of the inferred trees. In trees including only Pleuronectiform species, *Lycodes toyamensis* and *Sebastes schlegeli* were used as an outgroup to root the tree. A tree including Salmonidae and Gadidae species were rooted by *Dorosoma cepedianum* and *Cromeria nilotica*. These species were chosen because they belong to the sister taxa of the least common taxonomic group of the species in quest. Two species was used as an outgroup to make sure that the outgroup really was an outgroup relative to the species in focus.

Results

Genome content

37 genes (two rRNAs, 13 proteins and 22 tRNAs) were identified in Atlantic halibut, Pacific halibut and Greenland halibut. This is the same as is found in other vertebrates, as reviewed by Boore (1999). A large non-coding control region was identified by its content of conserved sequence motifs. The majority of the genes were encoded on the H-strand, except those for ND6 and 8 tRNA genes. In some of the tRNAs and protein coding genes, base-sharing and reading frame overlaps were observed. All genes in the three species were of identical size, except for the 16S rRNA gene. Here the gene in Greenland halibut was one bp longer than the one found in Atlantic halibut and Pacific halibut. In addition to the origin of replication of the light strand (Ori L, 38 bp), a few non-coding insertion sequences were found in Atlantic-, Pacific- and Greenland halibut. The largest one was located between tRNA-Ser^{UCN} and tRNA-Asp, and was 14 bp. Extensive length variation was observed in the control region, due to variation in copy number of a 61 bp repeat motif.

Localization of protein coding genes, tRNA and rRNA, as well as other features in the mitochondrial genome from Atlantic halibut, Pacific halibut and Greenland halibut are presented in Tables 10, 11 and 12, respectively

The mtDNA genome in Atlantic halibut 1, 2, 3 and 4 was 17546 bp, 17619 bp, 17973 bp and 17729 bp.

Table 10: Localization of genes and features in the mitochondrial genome of Atlantic halibut *(Hippoglossus hippoglossus 1*). tRNA genes denoted by their three letter abbreviations

Gene	From	To	Size (bp)	Codon (Init./Term.)		Anticodon (tRNA)
Phe	1	68	68			GAA
12S rRNA	69	1017	949			
Val	1018	1091	74			TAC
16S rRNA	1092	2806	1715			
Leu^{UUR}	2807	2880	74			UUA
ND1	2881	3855	975	ATG	TAG	
Insertion	3855	3860	6			
Ile	3861	3931	71			GAU
Gln	4001	3931 (L)71				UUG
Met	4001	4069	69			CAU
ND2	4070	5115	1046	ATG	TA-	
Trp	5116	5187	72			
Insertion	5188		1			
Ala	5257	5189 (L)69				UGC
Insertion	5258		1			
Asn	5331	5259 (L)73				GUU
Ori L	5332	5369	38			
Cys	5434	5370 (L)65				GCA
Tyr	5502	5435 (L)68				GUA
Insertion	5503		1			
COI	5504	7069	1566	GTG	AGA	
Ser^{UCN}	7135	7065 (L)71				UGA
Insertion	7136	7149	14			
Asp	7150	7220	71			GUC
Insertion	7221	7226	6			
COII	7227	7917	691	ATG	T--	
Lys	7918	7990	73			UUU
Insertion	7991		1			
ATP8	7992	8159	168	ATG	TAA	
ATP6	8150	8832	683	ATG	TA-	
COIII	8833	9617	785	ATG	TA-	
Gly	9618	9689	72			UCC
ND3	9690	10038	349	ATG	T--	
Arg	10039	10107	69			UCG
ND4L	10108	10404	297	ATG	TAA	
ND4	10398	11778	1381	ATG	T--	
His	11779	11848	70			GUG
Ser^{AGY}	11849	11915	67			
Insertion	11916	11918	3			
Leu^{CUN}	11919	11991	73			UAG
ND5	11992	13830	1839	ATG	TAA	
ND6	14348	13827 (L)	522	ATG	TAG	
Glu	14417	14349 (L)	69			UUC
Insertion	14418	14421	4			
Cyt-b	14422	15562	1141	ATG	T--	
Thr	15563	15635	73			UGU
Pro	15705	15635 (L)	71			UGG
Control region	15706	17546	1841			

The mitochondrial genome of Pacific halibut 1, 2, 3 and 4 was 17841 bp, 17841 bp, 17963 bp and 17902 bp.

Table 11: Localization of genes and features in the mitochondrial genome of Pacific halibut (*Hippoglossus stenolepis 1*). tRNA genes denoted by their three letter abbreviations

Gene	From	To	Size (bp)	Codon (Init./Term.)		Anticodon (tRNA)
Phe	1	68	68			GAA
12S rRNA	69	1017	949			
Val	1018	1091	74			UAC
16S rRNA	1092	2806	1715			
Leu^{UUR}	2807	2880	74			UAA
ND1	2881	3855	975	ATG	TAG	
Insertion	3856	3860	5			
Ile	3861	3931	71			GAU
Gln	4001	3931 (L)71				UUG
Met	4001	4069	69			CAU
ND2	4070	5115	1046	ATG	TA-	
Trp	5116	5187	72			
Insertion	5188		1			
Ala	5257	5189 (L)69				UGC
Insertion	5258		1			
Asn	5331	5259 (L)73				GUU
Ori-L	5332	5369	38			
Cys	5434	5370 (L)65				GCA
Tyr	5502	5435 (L)68				GUA
Insertion	5503		1			
COI	5504	7069	1566	GTG	AGA	
Ser^{UCN}	7135	7065 (L)71				UGA
Insertion	7136	7149	14			
Asp	7150	7220	71			GUC
Insertion	7221	7226	6			
COII	7227	7917	691	ATG	T--	
Lys	7918	7990	73			UUU
Insertion	7991		1			
ATP8	7992	8159	168	ATG	TAA	
ATP6	8150	8832	683	ATG	TA-	
COIII	8833	9617	785	ATG	TA-	
Gly	9618	9689	72			UCC
ND3	9690	10038	349	ATG	T--	
Arg	10039	10107	69			UCG
ND4L	10108	10404	297	ATG	TAA	
ND4	10398	11778	1381	ATG	T--	
His	11779	11848	70			GUG
Ser^{AGY}	11849	11915	67			
Insertion	11916	11918	3			
Leu^{CUN}	11919	11991	73			UAG
Insertion	11992		1			
ND5	11993	13831	1839	ATG	TAA	
ND6	13828	14349 (L)	522	ATG	TAG	
Glu	14418	14350 (L)	69			UUC
Insertion	14419	14422	4			
Cyt-b	14423	15563	1141	ATG	T--	
Thr	15564	15636	73			UGU
Pro	15706	15636 (L)	71			UGG
Control region	15707	17841	2135			

The mitochondrial genome of Greenland halibut 1, 2, 3 and 4 was 18017 bp, 18139 bp, 17895 bp and 18078 bp.

Table 12: Localization of genes and features in the mitochondrial genome of Greenland halibut *(Reinhardtius hippoglossoides 1*). tRNA genes denoted by their three letter abbreviations

Gene	From	To	Size (bp)	Codon (Init./Term.)	Anticodon (tRNA)
Phe	1	68	68		GAA
12S rRNA	69	1017	949		
Val	1018	1091	74		UAC
16S rRNA	1092	2805	1714		
Leu^{UUR}	2806	2879	74		UAA
ND1	2880	3854	975	ATG TAA	
Insertion	3855	3859	5		
Ile	3860	3930	71		GAU
Gln	4000	3930 (L)	71		UUG
Met	4000	4068	69		CAU
ND2	4069	5114	1046	ATG TA-	
Trp	5115	5186	72		
Insertion	5187		1		
Ala	5256	5188 (L)	69		UGC
Insertion	5257		1		
Asn	5330	5258 (L)	73		GUU
Ori-L	5331	5368	38		
Cys	5433	5369 (L)	65		GCA
Tyr	5501	5434 (L)	68		GUA
Insertion	5502		1		
COI	5503	7068	1566	GTG AGA	
Ser^{UCN}	7134	7064 (L)	71		UGA
Insertion	7135	7148	14		
Asp	7149	7219	71		GUC
Insertion	7220	7225	6		
COII	7226	7916	691	ATG T--	
Lys	7917	7989	73		UUU
Insertion	7990		1		
ATP8	7991	8158	168	ATG TAA	
ATP6	8149	8831	683	ATG TA-	
COIII	8832	9616	785	ATG TA-	
Gly	9617	9688	72		UCC
ND3	9689	10037	349	ATG T--	
Arg	10038	10106	69		UCG
ND4L	10107	10403	297	ATG TAA	
ND4	10397	11777	1381	ATG T--	
His	11778	11847	70		GUG
Ser^{AGY}	11848	11915	67		
Insertion	11916	11918	3		
Leu^{CUN}	11919	11991	73		UAG
ND5	11992	13830	1839	ATG TAA	
ND6	13827	14348 (L)	522	ATG TAG	
Glu	14417	14349 (L)	69		UUC
Insertion	14418	14421	4		
Cyt-b	14422	15562	1141	ATG T--	
Thr	15563	15635	73		UGU
Pro	15705	15635 (L)	71		UGG
Control region	15706	18017	2312		

Protein coding genes

Thirteen protein coding genes were identified by sequence alignment with mtDNA from bastard halibut (*Paralichtys olivaceus*) and stone flounder (*Platichtys bicoloratus*) as well as putative open reading frames (www.ncbi.nlm.nih.gov/projects/gorf/).

Among the protein coding genes, cytochrome oxidase subunit 1 (COI) begins with the GTG codon, while the others begin with the ATG codon, the standard initiation codon. Seven of 13 protein coding genes end with a truncated termination codon, such as T or TA, judging from the 5`end of downstream tRNA genes. Complete termination codons are proposed to be created after post-transcriptional addition of adenosine at the RNA level. COI ends with AGA, and ND6 ends with TAG.

ATP8 and ATP6 share 10 bases, ND4L and ND4 share 7 bases and ND5 and ND6 share 4 bases, but ND5 and ND6 are coded on opposite strands.

Ribosomal RNA genes

The two rRNA genes are located between the tRNA^{Phe} and tRNA$^{Leu(UUR)}$, separated by tRNA^{Val}. The length of the 12S rRNA gene was 949 bp long in Atlantic halibut, Pacific halibut and Greenland halibut. 16S rRNA gene was 1714 bp long in Atlantic halibut and Pacific halibut, and 1715 bp long in Greenland halibut.

Transfer RNA genes

Twenty-two tRNA genes between 65 and 74 bp in size were identified in Atlantic halibut, Pacific halibut and Greenland halibut (figure 9). tRNA genes were derived from their gene structures and identified and located by anticodon recognition, their proposed secondary structure, and homology with already published mtDNAs within the Pleuronectiformes. The classic secondary structure of tRNAs is shown in figure 8. All but one (tRNA-Ser (AGY)) folded into the cloverleaf secondary structure with tRNAscan-SE 1.21 (Lowe and Eddy 1997). Two tRNA genes specify leucine, Leu(UUR) and Leu(CUN), and two tRNA genes specify serine, Ser(UCN) and Ser(AGY). Nucleotide substitutions between the three halibut species were found. Mostly substitutions were located in the loop structures the tRNAs. But in some cases substitutions in the stem structures were observed. Atypical (non-Watson and Crick) base pairings (G-U and G-A) and mismatches were identified in all tRNA genes. Four tRNA genes were perfectly conserved among the 12 individuals; Ser (UCN), Arg, Leu (CUN) and Glu.

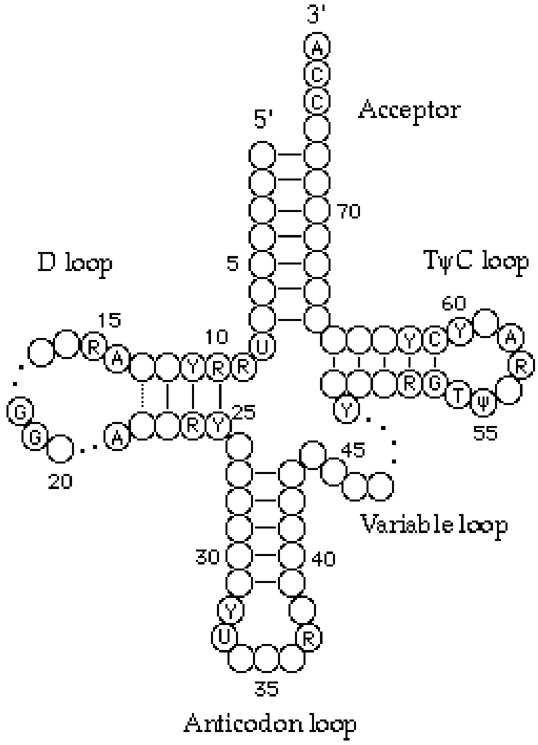
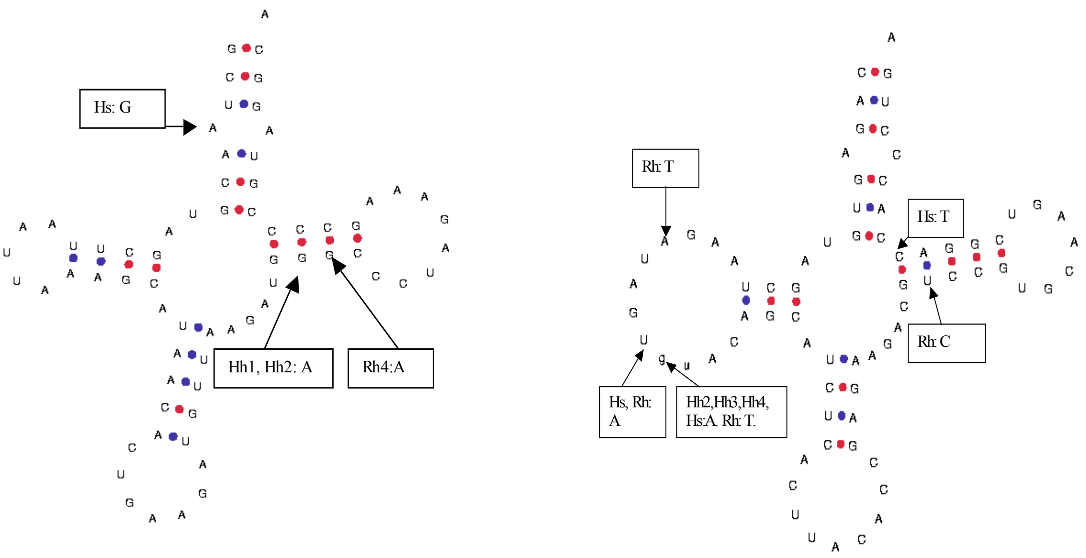


Figure 8: Secondary structure of a typical transfer RNA. Figure from www.genetics.wustl.edu/eddy/tRNAscan-SE

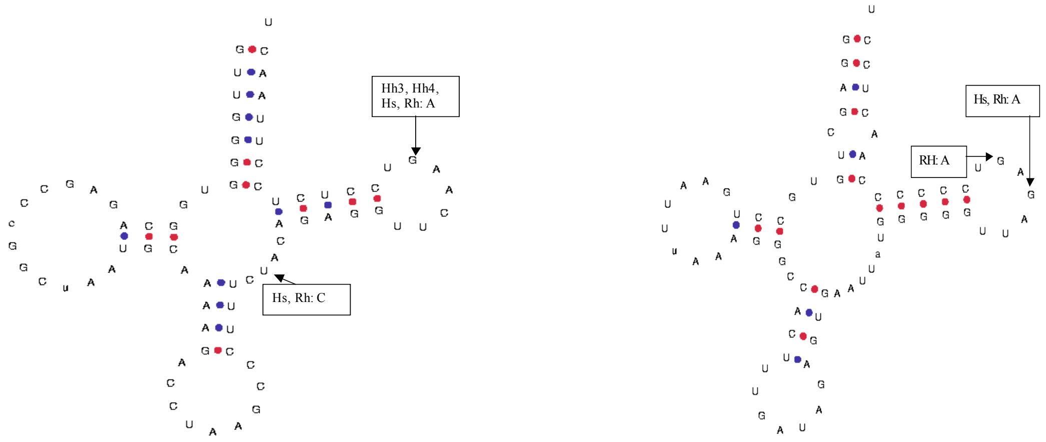
tRNA-Phe

tRNA-Val



tRNA-Leu (UUR)

tRNA-Ile



tRNA-Gln

tRNA-Met

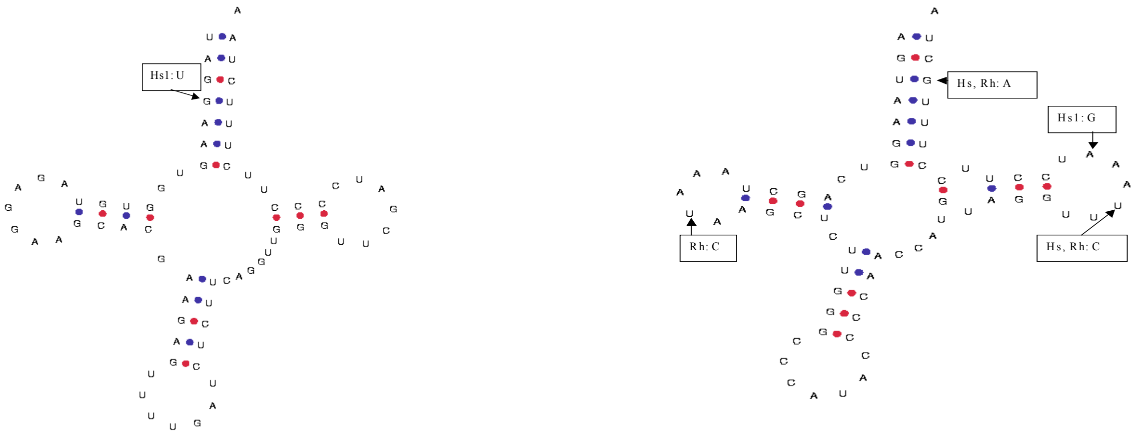
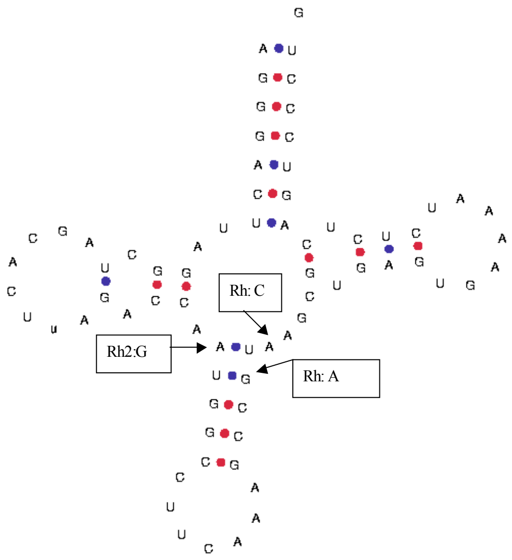
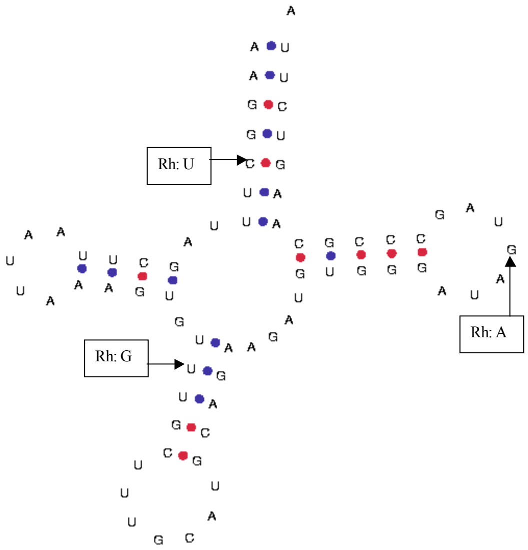


Figure 9: Proposed secondary structure of mitochondrial tRNA genes in Atlantic halibut 1, with nucleotide substitutions found in individuals of Atlantic halibut (Hh), Pacific halibut (Hs) and Greenland halibut (Rh). The amino acid recognition site in the 3` end is not shown. Figures created by tRNA-SE 2.1 (Lowe and Eddy 1997).

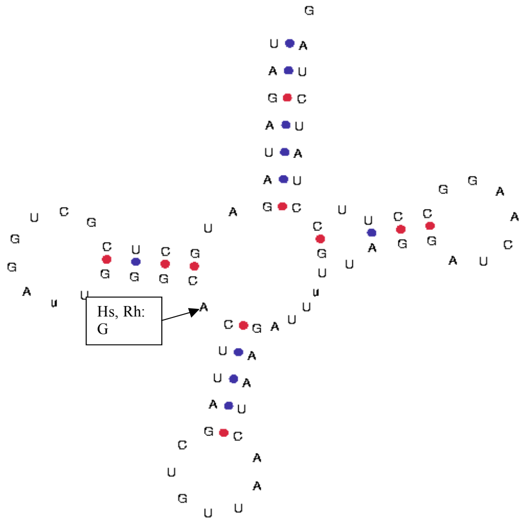
tRNA-Trp



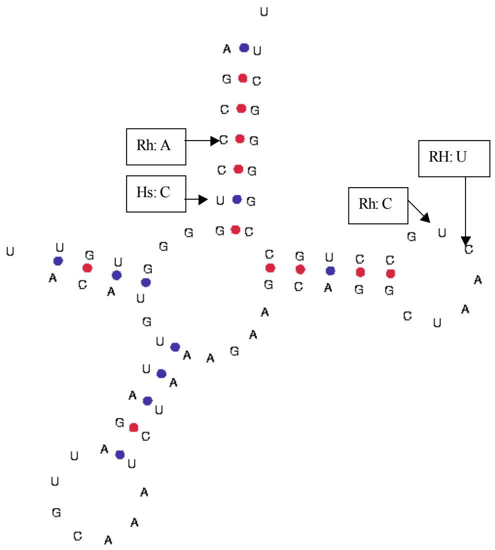
tRNA-Ala



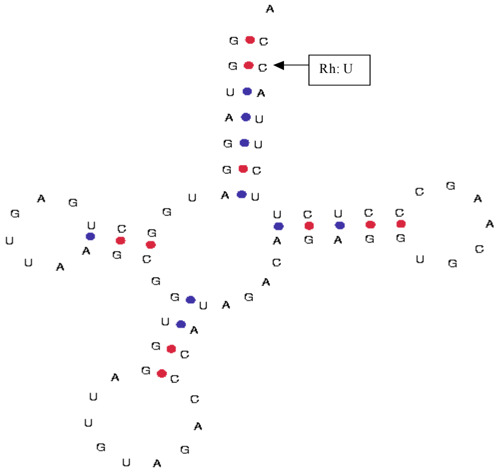
tRNA-Asn



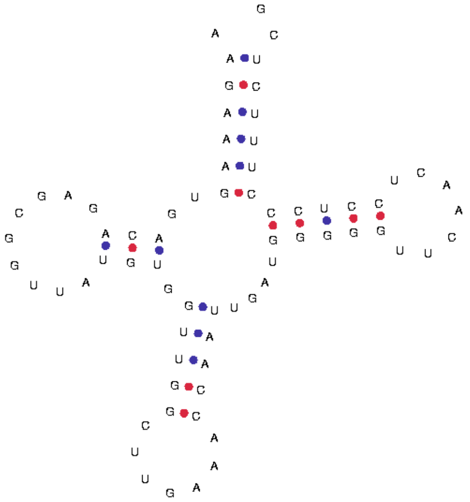
tRNA-Cys



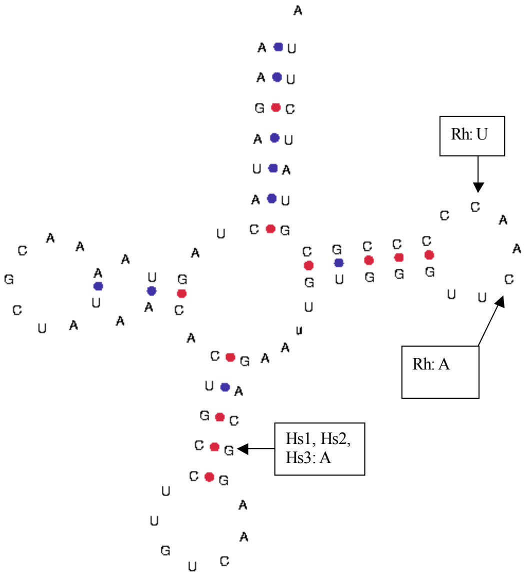
tRNA-Tyr



tRNA-Ser (UCN)



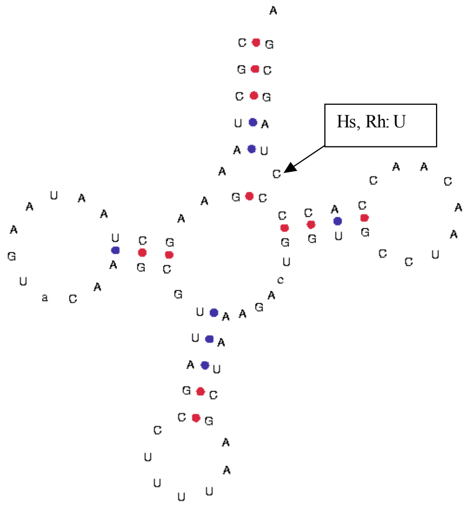
tRNA-Asp


Rh: U

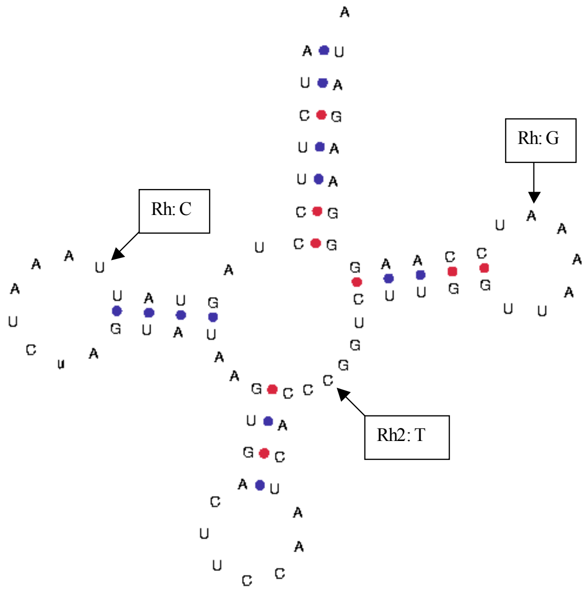
Rh: A

Hs1, Hs2,
Hs3: A

tRNA-Lys


Hs, Rh: U

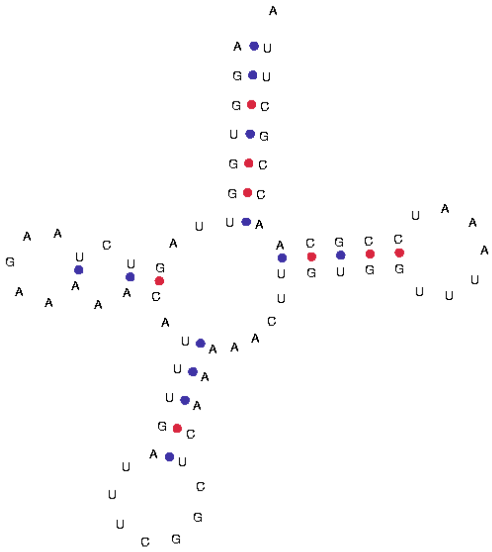
tRNA-Gly


Rh: C

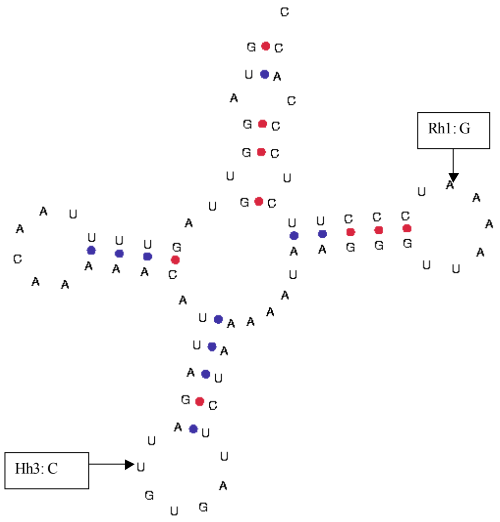
Rh: G

Rh2: T

tRNA-Arg

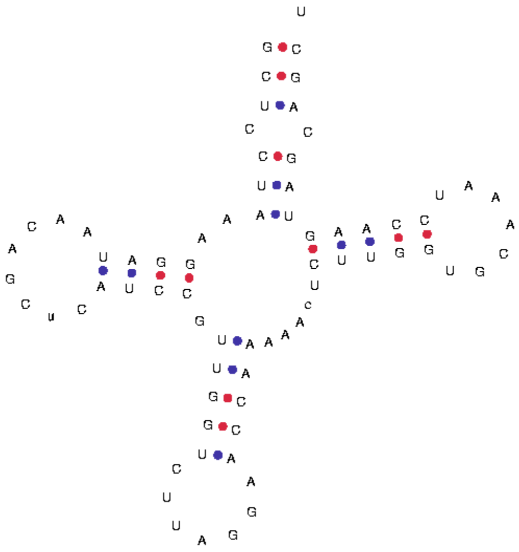


tRNA-His

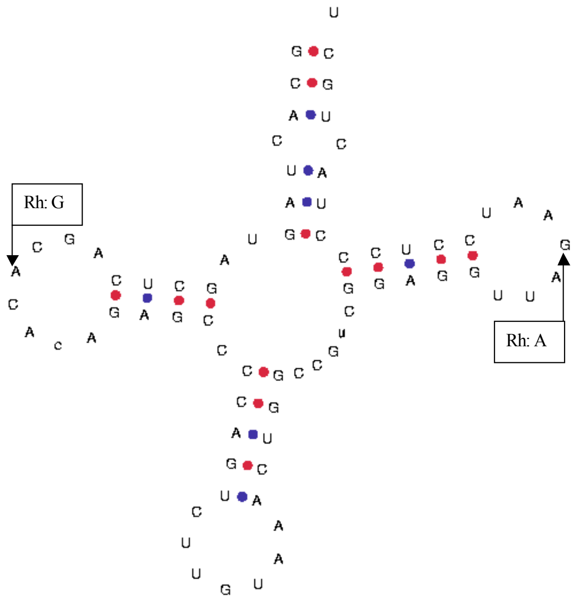

Rh1: G

Hh3: C

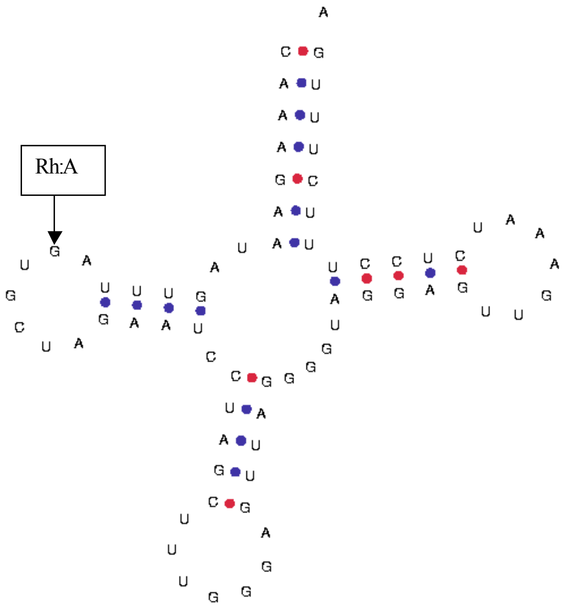
tRNA-Leu (CUN)



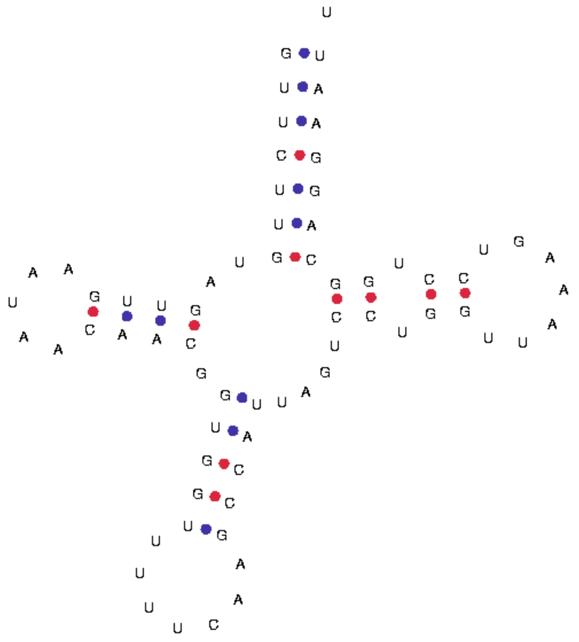
tRNA-Thr



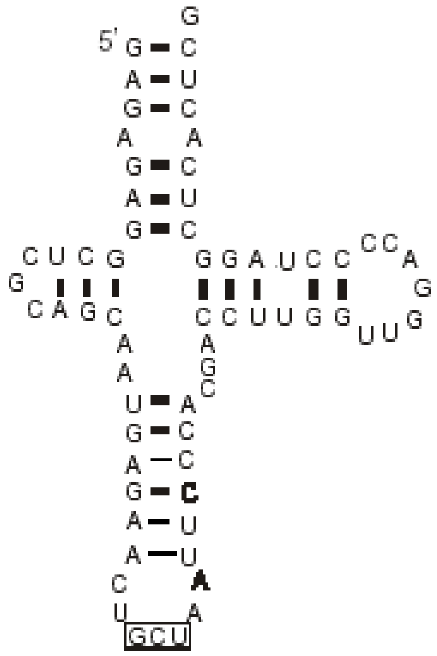
tRNA-Pro



tRNA-Glu



tRNA-Ser (AGY)



Non coding regions

Replication origin of light strand (Ori-L)

A non-coding sequence associated with the putative L-strand replication origin is 38 bp long and located between tRNA-Asn and tRNA-Cys. This region, together with a part of tRNA-Cys is able to form a stable stem-loop structure with 12 paired bases in the stem (Fig 10). The conserved motif (5`-GCCGG-3`) was found in the stem of the tRNA-Cys.

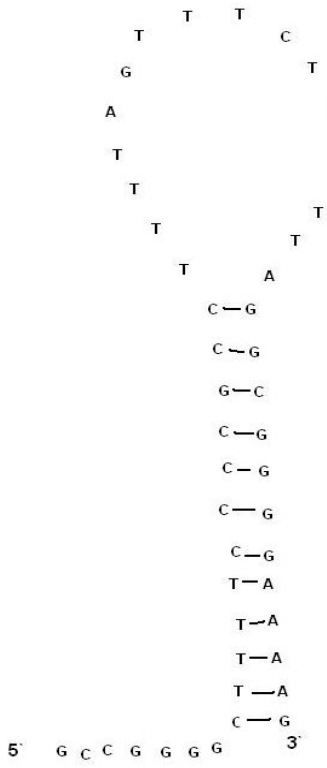


Figure 10: Proposed secondary structure of the replication origin of light strand in Atlantic halibut, with the conserved motif 5`-GCCGG-3`. Nucleotide sequence of the H-strand is shown.

Control region

The control region is the largest non coding region. It is flanked by the tRNA^{Pro} and tRNA^{Phe} -genes. Three domains are found in the control region; one hyper variable domain known as the ETAS region (Extended Termination Associated Sequences), one central conserved domain (CC region) and one conserved sequence block domain (CSB-region) (Fig 11). Several conserved motifs were identified by comparison with other fish control regions (Breines 2005; Inoue et al. 2001; Kim and Lee 2004; Lee et al. 1995; Nesbø et al. 1998; Saitoh et al. 2000) (Fig 11 and 12).

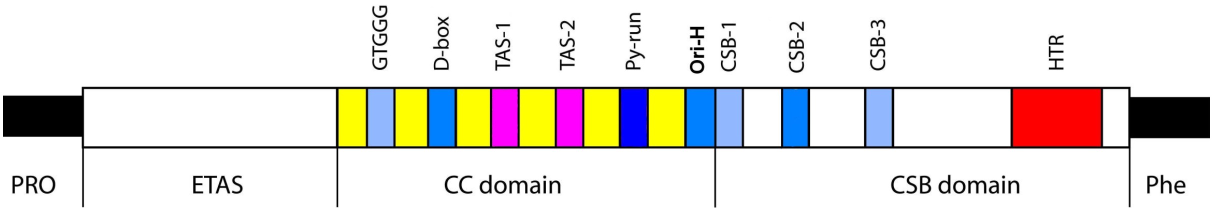


Figure 11: Schematic view of control region consisting of the three domains; ETAS, CC and CSB. The region is localized between tRNA-Pro and tRNA-Phe. A number of conserved sequence motifs were identified

```
Hippoglossus_hippoglossus_1         ---------TGGTACA-TAAATGTACAATGAAGGATTTTCA-TATACATG
Hippoglossus_stenolepis_1           ---------TGGTACA-TAAATGTACAATGAAGGATTTTCA-TATACATG
Reinhardtius_hippoglossoides_1      ---------CGGCATAATGTATGTAAAGCAAAGGATTTTTA-TATACATG
Verasper_variegatus                 TTGCATACGCAGTGTT-CATACGATACGCATGCAATTTTTA-TGTGCATA
Limanda_ferruginea                  ----------GACACAATACATGTACA--TGAAGGTTTTCA-TGTACATG
Hippoglossoides_platessoides        ----------------ATGAATGTACAATAAAGGATTTTTAATGTACATC
Paralichtys_olivaceus               -------------GGAACATATGTTTTATGAAAATT----AATATACATA
Solea_vulgaris                      ---------TTCTGTTTTATATG---TATGAAAAAT----AATA--CATA
                                                        * *            *    * *   ***

Hippoglossus_hippoglossus_1         TATGTAATAACACCATATATTTATAGTAACCATTTTATGTGATGTACTAG
Hippoglossus_stenolepis_1           TATGTAATAACACCATATATTTATAGTAACCATTTTATGTAATGTACTAG
Reinhardtius_hippoglossoides_1      TATGTATTAACACCATATATTTATAGTAACCATTTTGTGTAATGTACTAG
Verasper_variegatus                 TATGTAATAACACCATATATTTATAGTAACCATTTTATGTGATGTACTAA
Limanda_ferruginea                  TTTGTAATAACACCATATATTTATAGTAACCATTTTATATAATGAACTAG
Hippoglossoides_platessoides        TATGTAATAACACCATATATTTATAGTAACCATATTGTATAGTGTACTAG
Paralichtys_olivaceus               TATGTAATTACACCATATATTTATAGTAAACATTAAGTCCGATG-TACAA
Solea_vulgaris                      TATGTATTATCACCATTAATCTATATTAACCATTTTATATAATGCTTTCC
                                    * **** *  ******  ** **** *** ***    *    **

Hippoglossus_hippoglossus_1         GACATACATGTATAATCACCAAATCTCGTAATACAGCACTCATTCATCAA
Hippoglossus_stenolepis_1           GACATACATGTATAATCACCACATCTCGTAATAGAACACTCATTCACCAC
Reinhardtius_hippoglossoides_1      GACATACATGTATAATCACCTAACATAGTAATATAGCACTCATTCATCAC
Verasper_variegatus                 GACATTCATGTATTATAACCTAATCTAGTAATATAGCACTCATTCACCAA
Limanda_ferruginea                  GACATTCATGTATAATAACCTAATCTAGTAATTAAGCACTCATTCATCAA
Hippoglossoides_platessoides        GACATACATGTATAATAACCTAATCTAGTAAAATAGCACTCATACAACAC
Paralichtys_olivaceus               GACACAAATGGATG-TGAACAAAACATGGTGTCAAACATTCATATACCAG
Solea_vulgaris                      TACATTACTGATTAATCACCACATCTCGAAATAAACCATTCACTTATCAC
                                     ***    **  *  * * *  *    *      * ** ***   * **

Hippoglossus_hippoglossus_1         CATTTTTAACTAAGATAG-ACTAAAACC-TGAATAATCACTAATCTTAAA
Hippoglossus_stenolepis_1           CATTTTTAACTAAGACGA-ACTAAAACC-TGAGTGATCACTAATCTTAAA
Reinhardtius_hippoglossoides_1      CATTTTTAACTAAGAAATTACTAGAACCCTGACTTCACATTCACGTTACA
Verasper_variegatus                 CATTTTTAACTAAAGTAA-ACTAAAACC-TAATTAATCACTAATTTTAAA
Limanda_ferruginea                  CAATTTTACCTAAGATAG-ACTAGAACC-TAGACAAGCACTAACCTTACA
Hippoglossoides_platessoides        CA-TTTTAACTAAGAGTT-ACTAGAACC-CAACTTACTACTAATATAACA
Paralichtys_olivaceus               C-TATATAACTAAATATATACAAAAACCAA-ACCTATAA--GGTATA---
Solea_vulgaris                      T-TACTATACTAAG-ACGGACCCAAACCAATACTTGTAA--AATTCAACT
                                             ****      **   ****          *

Hippoglossus_hippoglossus_1         TATGTGA-AAGTCCAGGACCAGTCGA---AATCTAAGACCGAACACAACA
Hippoglossus_stenolepis_1           TAAGTGA-AAGTCCAGGACCAGTCGA---GATCTAAGACCGAACACAACA
Reinhardtius_hippoglossoides_1      TATGTGA-AATTCCAGGACCAGCCGA---CATTTAAGACCGAACACAACA
Verasper_variegatus                 TATGTAA-AACTCTAGGACCAATCGA---AATTTAAGACCGAACACGACA
Limanda_ferruginea                  TTAGTGA-AATTCCAGGACCAGTCGA---AACTTAAGACCGAACACAACA
Hippoglossoides_platessoides        TATGTGG-AAGTCAAGGAGTAGTCGA---AACTTAAGACCGAACACAACA
Paralichtys_olivaceus               -CAATAAAGAATTAAAGACTAGTCGA---AACTTTACACCGAACACAACC
Solea_vulgaris                      TCAATAA-GAATTCACTGCTAATCGATCCGACAAGACTCCACATAAAAAC
                                        *    * *  *     *  ***    *    *  **  * *  *
```

Figure 12: Alignment of ETAS and CC region of the control region in 8 Pleuronectiform species. Nine conserved domains were identified. CSB; conserved sequence blocks, TAS; termination associated sequence (putative position), D-box, replication origin H-strand (O_H) and Py-run; repeats of Pyrimidine bases. Nucleotide sequence of the L-strand is shown.

```
Hippoglossus_hippoglossus_1         CTCATCAGTCGAGT-TATACCAAGACTCAAAATCTCGCCGACCCCAA-AA
Hippoglossus_stenolepis_1           CTCATCAGTCGAGT-TATACCAAGACTCAAAATCTCGCCGACCTCAA-AA
Reinhardtius_hippoglossoides_1      CTCACCGGTCAAGT-TATACCAAGACTCAAAATTTCACTCACTTAAA-AA
Verasper_variegatus                 CTCATCAGTTAAGT-TATACCAAGACTCAAAATCTCGCCCATCATAA-AT
Limanda_ferruginea                  CTCATCAGTCGAGT-TATACCAAGACTCAAAATCTC-TTCACGCCAA-AA
Hippoglossoides_platessoides        CTCATCAGTCGAGT-TATACCAAGACTCAAAATCCCTTCAACATCAA-AA
Paralichtys_olivaceus               TTCATATGTCAAGT-TATACCAAGACTCAAACTTCTGTCGATCCCAA-AT
Solea_vulgaris                      TG-ACACGGTAAATATATACTTTGATCCAACATCCTATAAAATTAACTAC
                                       *   *   * * *****   **  ***  *       *    *  *

Hippoglossus_hippoglossus_1         TCCTATGTAGTAAGAGCCTACCAACC-GGTGATTCCTTAATGATAACTCT
Hippoglossus_stenolepis_1           TTCTATGTAGTAAGAGCCTACCAACC-GGTGATTCCTTAATGATAACTCT
Reinhardtius_hippoglossoides_1      ACCAACCCAATAAGAGCCTACCAACC-GGTGATCCCTTAATGATAACTCT
Verasper_variegatus                 TCCTATGTAGTAAGAGCCTACCAACC-GGTGATTTCTGAATGATAACTCT
Limanda_ferruginea                  TTCGATGTAGTAAGAGTCTACCAACC-GGTGATTTCTAAATGATAACGGC
Hippoglossoides_platessoides        CCCTATGTAGTAAGAGCCTACCAACC-GGTGATTCCTTAATGATAACGGT
Paralichtys_olivaceus               TCCCATGCAGTAAGAGCCTACCATCA-GTTGATTACTTAATGCCAACGGT
Solea_vulgaris                      AAATGCGCAGTAAGAGCCTACCAACAAGCTCATATCTTAATGATAACGGT
                                            * ****** ****** *  * * **  ** ****  ***
                                                           GTGGG-box
Hippoglossus_hippoglossus_1         TATTGAGGGTGAGGGACAAAAATTGTGGGGGTTTCACTCGGTGAATTATT
Hippoglossus_stenolepis_1           TATTGAGGGTGAGGGACAAAAATTGTGGGGGTTTCACTCGGTGAATTATT
Reinhardtius_hippoglossoides_1      TATTGAGGGTGAGGGACAAAAATTGTGGGGGTTTCACTCGGTGAATTATT
Verasper_variegatus                 TATTGATGGTCAGGGACAGAAATCGTGGGGGTTTCACTCAGTGAACTATT
Limanda_ferruginea                  TATTGAAGGTGAGGGACAAAAATTGTGGGGGTTTCACTCCGTGATTTATT
Hippoglossoides_platessoides        TATTGAAGGTGAGGGACAAAAATTGTGGGGGTTTCACTCGGTGAATTATT
Paralichtys_olivaceus               TATTGAAGGTGAGGGACAAAAATTGTGGGGGTTTCACATAGTGAACTATT
Solea_vulgaris                      TATTGATGGTCAGGGACAGATATCGTGGGGGTTTCACTTAGTGAATTATT
                                    ****** *** ******* * ** *************   ****  ****
                                        D-box
Hippoglossus_hippoglossus_1         CCTGGCATTTGGTTCC-TACTTCAGGGCCATTGATTGATGTTATCCCTCA
Hippoglossus_stenolepis_1           CCTGGCATTTGGTTCC-TACTTCAGGGCCATTGATTGATATTATCCCTCA
Reinhardtius_hippoglossoides_1      CCTGGCATTTGGTTCC-TACTTCAGGGCCATTGATTGATATTATCCCTCA
Verasper_variegatus                 CCTGGCATTTGGTTCC-TACTTCAGGGCCATTTATCGATATTATCCCTCA
Limanda_ferruginea                  CCTGGCATATGGTTCC-TACTTCAGGGTCATATACCGAT-TTATTCCCCA
Hippoglossoides_platessoides        CCTGGCATTTGGTTCC-TACTTCAGGGCCACGGATCGAT-TTATTCCCCG
Paralichtys_olivaceus               CCTGGCATTTGGTTCC-TACTTCAGGGCCATGACCTGATATTATTCCTCA
Solea_vulgaris                      CCTGGCATTTGGCTCTACATCTCAAGGCCATATTATTATCCTTTTTCTCA
                                    ******** *** **   *  *** ** **       **  * *  * *
                                                     TAS-1(both putative)TAS-2
Hippoglossus_hippoglossus_1         CACTTTCATCGACACTTACATAAGTTAATGTTGATAATACATACGACTCG
Hippoglossus_stenolepis_1           CACTTTCATCGACACTTACATAAGTTAATGTTGATAATACATACGACTCG
Reinhardtius_hippoglossoides_1      CACTTTCATCGACACTTACATAAGTTAATGTTGATAATACATACGACTCG
Verasper_variegatus                 CACTTTCATCGACGCTTGCATAAGTTAATGTTGATAATACATACGACTCG
Limanda_ferruginea                  CACTTTCATCGACACTTACATAAGTTAATGTCGATAATACATACGACTCG
Hippoglossoides_platessoides        CACTTTCACTAACACTTACATAAGTTAATGTTGATAATACATACGACTCG
Paralichtys_olivaceus               CACTTTCATCGACACTTACATAAGTTAATGTTGGTATTACATACGACTCG
Solea_vulgaris                      CAGATTTACTGGCCCTGACATTGACTGATGCTTTCGAC-TATACGACTCG
                                    **  ** *    * **  ***    * ***          **********
                                                                               Py-run
Hippoglossus_hippoglossus_1         TTACCCACCAAGCCGGGCGTTCACTCCAGCGGGTAAGGGGTTCTCTTTTT
Hippoglossus_stenolepis_1           TTACCCAGCAAGCCGGGCGTTCACTCCAGCGGGTAAGGGGTTCTCTTTTT
Reinhardtius_hippoglossoides_1      TTACCCACCAAGCCGGGCGTTCACTCCAGCGGGTAAGGGGTTCTCTTTTT
Verasper_variegatus                 TTACCCAGCAAGCCGGGCGTTCACTCCAGCGGGTAAGGGGTTCTCTTTTT
Limanda_ferruginea                  G-ACCCAGCAAGCCGGGCGTACACTCCAGCGGCTAAGGGGTTCTCTTTTT
Hippoglossoides_platessoides        TTACCCAGCAAGCCGGGCGTTCACTCCAGCGGGTAAGGGGTTCTCTTTTT
Paralichtys_olivaceus               TTACCCAGCAAGCCGGGCGTTCACTCCAGCGGGTAAGGGGTTCTCTTTTT
Solea_vulgaris                      TTACCCAGCAAGCCGGGCGTTCTCTCCAGCGAGCAAGGGGTTCTCTTTTC
                                      ***** ************ * ********   ***************


                                       Py-run             Ori-H
Hippoglossus_hippoglossus_1         -TTTTTTCCTTTCACTTGACATTTCAAAGTGCATCCAGCCAACGGAGACG
Hippoglossus_stenolepis_1           -TTTTTTCCTTTCACTTGACTTTTCAAAGTGCATCCAGCCAACAGAGACG
Reinhardtius_hippoglossoides_1      -TTTTTTCCTTTCACTTGACATTTCAGAGTGCATCCAGCCAACAGAGACG
Verasper_variegatus                 -TTTTTTCCTTTCATCTGGCATTACAGAGTGCATCCAGCCAAGAGAAACG
Limanda_ferruginea                  GTTTTTTCCTTTCACTTGGCATTACAGAGTGCATCCAGCCAACCGAAACG
Hippoglossoides_platessoides        -TTTTTTCCTTTCAATCG-CATTACAAAGGGCATCCAGCCAATAAAAACG
Paralichtys_olivaceus               -TTTTTCCTTTTCATCTGGCATTTCAGAGTGCATCTAGCCGATAGAAATA
Solea_vulgaris                      -TTTTTCCTTTTCACCTGGCATTTCAGAGTGCGCG----CGGTAATAGTT
                                     ***** * *****   * * ** ** ** **       *
```

```
Hippoglossus_hippoglossus_1         TTTAAAGGGTGAGCACTTTTCTTGCACGCGCCGTACATAGTATCCGTGT-
Hippoglossus_stenolepis_1           TTTAAAGGGGGAGCACTTTTCTTGCACGCGCCGTACATAGTATCCATGT-
Reinhardtius_hippoglossoides_1      TTTAAAGGGTGAGCACTTTTCTTGCACTCAGCGTACATAGTATCCATGT-
Verasper_variegatus                 TTTAAAGGGTGAGCATTTTTCTTGCTCGCGGCGTACATAGTATCCATGT-
Limanda_ferruginea                  TTCAAAGGGTGAGCACTTTTCTTGCACTCGTCGTACATAGTATCCATGT-
Hippoglossoides_platessoides        TTCAAAGGGGGAGCACTTTTCTTGCTCTC-TCGCACATAGTATCCATGT-
Paralichtys_olivaceus               TTCAAGGTG-GAACA-TTTCCTTGCGTGCAA-GTAAATAGTCTCAATGT-
Solea_vulgaris                      GACAAGGGG-GTACA-TTTTCTTGCTTCCAA-GGGAATAGTATGAATGTT
                                       ** * * *  ** *** *****   *   *   ***** *   ***
                                                                  CSB1
Hippoglossus_hippoglossus_1         -AATGAGTCTTTATTAGAAGGATAACATTAAGTGTTATCATGTGCATAAA
Hippoglossus_stenolepis_1           -AGGGAGTCTTTATTAAAAAAATAACATTAAGTGTTATCATGTGCATAAA
Reinhardtius_hippoglossoides_1      -TATAAGTCTTTATTAGAAGGATAACATAAAGGGATATCATGTGCATAAG
Verasper_variegatus                 -AACAAGTCTTTATTAGAAGAATAACATTAAAGGATATCATGTGCATAAA
Limanda_ferruginea                  -AATAAGACTTTTTTAGAAGAATAACATTAATGGATATCAAGTGCATAAG
Hippoglossoides_platessoides        -AATAAGACTTTATTAGAAGGATAACATTAAAGGATATCAAGTGCATAAG
Paralichtys_olivaceus               -AATTAATCTTTATCTAAAGAATAACATTAAAAGATATCAAGTGCATAAG
Solea_vulgaris                      AAAATGATATTGATA-GAAGAATTTCAT-AACTGATATCATGAGCATAAA
                                             **  *   **  **  *** **  * ***** * ******

Hippoglossus_hippoglossus_1         GATTTGCTCATTTCTTCTGTCATCC----------------CCAGGATAC
Hippoglossus_stenolepis_1           GATTTGCTCATTTCTTCTATCATCC----------------CCAGGATAC
Reinhardtius_hippoglossoides_1      AATGTGCTCCTTTCTTCTATCATCC----------------CCAGGATAC
Verasper_variegatus                 AATATGCTCATTTATCTTGTCTTCC----------------CCAGGATAC
Limanda_ferruginea                  GATGTGCTTGTTTATTCTATCTTCT----------------CCAGGATAC
Hippoglossoides_platessoides        GATGTGCTTGTTTATTCTATCTTCC----------------CCTTGATTG
Paralichtys_olivaceus               GGTGGTCTTGTTAATCCAAAGATCC---------------CTTAGATCAC
Solea_vulgaris                      TAATTATTTTTTCCCCTAAATAACCTGATATACGCCCCCTCTTAACAAAC
                                           *  **           *
                                                                     CSB-2
Hippoglossus_hippoglossus_1         CCCCTT--------TTTT-GCGCGC-AAAACCCCCC-TACCCCCCTAAAC
Hippoglossus_stenolepis_1           CCCCTT--------TTTTTGCGCGA-AAAACCCCCC-TACCCCCCTAAAC
Reinhardtius_hippoglossoides_1      CCCCTT--------TTTT--CGCGT-AAAACCCCCC-TACCCCCCTAAAC
Verasper_variegatus                 CCCCTT--------TTTC-GCGCGT-AAAACCCCCCCTACCCCCCTAAAC
Limanda_ferruginea                  CCCCTT--------TTTC-GCGCGCGAAAACCCCCCCTACCCCCCTAAAC
Hippoglossoides_platessoides        CCCCTT--------TTTT-ACGCGCGTAAAACCCCCCTACCCCCCTAAAC
Paralichtys_olivaceus               CCCC----------TTTTTGCGCGC-AAAACCCCCC-CCACCCCCCAAAC
Solea_vulgaris                      TCTCGTCAAAAAGGTTTTTTTGCGT-TAAACCCCCC-TACCCCCCTTTTC
                                     * *          ***    ***   *** *****    *****    *
                                                                  CSB-3
Hippoglossus_hippoglossus_1         CCCTGAAGTTGCTAAGACCCCTGAAAACCCCCCGGAAACAGGACAAACCT
Hippoglossus_stenolepis_1           CCCTGAAGTTGCTAAGACCCCTGAAAACCCCCCGGAAACAGGACAAACCT
Reinhardtius_hippoglossoides_1      TCCTGAAGTTGCTAAGACCCCTGAAAACCCCCCGGAAACAGGACAAACCT
Verasper_variegatus                 TCCTGAAGTTGCTAACACTCCTGAAAACCCCCCGGAAACAGGACAAACCT
Limanda_ferruginea                  CCCTGAAGTTGCTAAGAC-CCTGAAAACCCCCCGGAAACAGGACAAACCG
Hippoglossoides_platessoides        CCCTAAGGTTGTTAAGACCCCTGAAAACCCCCCGGAAACAGGACAAACCT
Paralichtys_olivaceus               TCCTAAGGTTATCTATACTCCTGAAAACCCCCCGGAAACAGGAAAACCCC
Solea_vulgaris                      TCGAAAGGTTCTTGTTACTTCTGCAAACCCCCCGGAAACAGAAAAACCCC
                                     *   *****      *   *** *****************
```

Characterisation of mtDNA heteroplasmy in the control region

Heteroplasmy is the presence of a mixture of more than one type of an organelle genome within a cell or individual. Since every eukaryotic cell contains many hundreds of mitochondria with hundreds of copies of mtDNA, it is possible and indeed very common for mutations to affect only some of the copies, while the remaining ones are unaffected (Grzybowski 2000). In this case the objective was to determine whether or not there was heteroplasmy in the control region in a single individual, and determine the most common number of copies of the repeated element. The most likely mechanism behind the creation of repeated motifs is slipped-strand mispairing (Levinson and Gutman 1987)

Table 13 shows the dominating copy number of a heteroplasmic 61 bp motif found in the control region of Atlantic-, Pacific- and Greenland halibut.

Table 13: Most common copy number of a 61 bp repeat in the HTR region of the control region in Atlantic halibut (Hh), Pacific halibut (Hs) and Greenland halibut (Rh).

Individual	Most common copy number of 61 bp repeat
Hh1	13
Hh2	12
Hh3	19
Hh4	15
Hs1	17-18
Hs2	17
Hs3	Apprx. 19
Hs4	18-19
Rh1	20-21
Rh2	22-23
Rh3	18
Rh4	21

The repeated motif in the control region of Atlantic halibut, Pacific halibut and Greenland halibut was identified with the following program: http://tandem.bu.edu/trf/trf.html (Benson 1999). The motif was quite conserved among the three halibut species (Fig 13). The G + C content in the motif was lower than the average for the rest of the mtDNA: 41 % in Atlantic halibut, 41 % in Pacific halibut and 36 % in Greenland halibut.

Hh `CAACCCACAAATACCCCTGGCTTATCGTAACCCCACCAGTTGTTTTAATAATACCACTTTT`
Hs `CAACCCACAAATACCCCTGGCTTATCACAACCCCACCAGTTGTTTTAATAATACCACTTTT`
Rh `CAACCCTAAAATACCCCTGACCAAAGATAAGCCCACCAGTTATTTTAATAATGGTACTTTT`

Figure 13: Sequence of the HTR motif in the control region of Atlantic halibut (Hh), Pacific halibut (Hs) and Greenland halibut (Rh). Nucleotide sequence from L-strand is shown.

Deducing the number of copies

A common strategy to determine copy number of heteroplasmic repeated motifs is to slice out the band of interest and clone or direct sequence it. In Atlantic halibut, Pacific halibut and Greenland halibut the repeated motif is 61 bp long. Copy number is as high as 20, giving a repeated motif region of about 1200 bp. Even with a sequencing primer located perfectly outside the repeated motif region it would be very difficult to read trough this region and determine the number of repeats this way.

```
        L16276
AGCCAACGGAGACGTTTAAAGGGTGAGCACTTTTCTTGCACGCGCCGTACATAGTATCCGTGTAATGAGTCTTTATTAGAAGGATAACATTAAG
TGTTATCATGTGCATAAAGATTTGCTCATTTCTTCTGTCATCCCCAGGATACCCCCTTTTTTGCGCGCAAAACCCCCCTACCCCCCTAAACCCC
TGAAGTTGCTAAGACCCCTGAAAACCCCCCGGAAACAGGACAAACCTCTGGTAGCTCAGAAAGGG
CAATTACTTTT
CAACCACTTTT 11 bp motif
CAACCACTTTT
CAACCCACAAATACCCCTGGCTTATCATAACCCCACCAGTTGTTTTAATAATACCACTTTT 61 bp motif
CAACCCACAAATACCCCTGGCTTATCGTAACCCCACCAGTTGTTTTAATAATACCACTTTT
CAACCCACAAATACCCCTGGCTTATCGTAACCCCACCAGTTGTTTTAATAATACCACTTTT
CAACCCACAAATACCCCTGGCTTATCGTAACCCCACCAGTTGTTTTAATAATACCACTTTT
CAACCCACAAATACCCCTGGCTTATCGTAACCCCACCAGTTGTTTTAATAATACCACTTTT
CAACCCACAAATACCCCTGGCTTATCGTAACCCCACCAGTTGTTTTAATAATACCACTTTT
CAACCCACAAATACCCCTGGCTTATCGTAACCCCACCAGTTGTTTTAATAATACCACTTTT
CAACCCACAAATACCCCTGGCTTATCGTAACCCCACCAGTTGTTTTAATAATACCACTTTT
CAACCCACAAATACCCCTGGCTTATCGTAACCCCACCAGTTGTTTTAATAATACCACTTTT
CAACCCACAAATACCCCTGGCTTATCGTAACCCCACCAGTTGTTTTAATAATACCACTTTT
CAACCCACAAATACCCCTGGCTTATCGTAACCCCACCAGTTGTTTTAATAATACCACTTTT
CAACCCACAAATACCCCTGGCTTATCGTAACCCCACCAGTTGTTTTAATAATACCACTTTT
CAACCCACAAATACCCCTGGCTTATCGTAACCCCACCAGTTGTTTTAATAATACCACTTTT
CAACCCACAAATACCTAAAACCCACAAACGCCGTATCACCTTCTTCATGATCAAAAAACTACTGTTTAGATTATTTCAAGTATTCCT
                                                                          H17250
```

Figure 14: Part of the sequence of the HTR region of Atlantic halibut 1. Location of HTR primers in red and truncate copy of the 61 bp repeat in blue. Nicleotide sequence of the L-strand is shown.

To confirm a possible heteroplasmy detected in the control region during cloning, primers on each side of the heteroplasmic region were designed (Table 7). MtDNA was not fully assembled when primers were designed, so the primer numbers do not precisely correspond to the actual position in mtDNA. For Atlantic halibut the primers are located 280 bp before and 80 bp after the repeated motifs (Fig 14). This corresponds to and PCR product of 375 bp if no repeated motif is included, only a truncated motif of 15 bp. To determine the sequence of the four shortest bands in figure 13 these were carefully cut out of the gel and cloned. The shortest band contained no repeated motif, only one truncated motif. The rest of the clones contained the truncated motif and one or more copies of the 61 bp repeated motif. Thus it is possible to count the number of bands and determine which number of repeats is most common in each individual. The same approach was used for Pacific halibut. In figure 15 there are some strong, shorter bands. These could be mistaken as the most common copy number in each individual. But they are probably not, because all sequenced clones from the control region contained a larger number of repeated motifs than what is observed among the quite strong, shorter bands. A closer look at the bands for Hh2 reveals that they are slightly longer than the rest of the Atlantic halibut individuals (Fig 15). The explanation is that Hh2 has one extra copy of a 11 bp repeat (Fig 14)

For Greenland halibut primer combination L 16472 – H17300 was used to produce a PCR product that was 154 bp long when containing no repeated motifs and only a truncate motif.

The band was difficult to visualize under the 200 bp marker (Fig 15). But with proper settings of contrast and light it can be seen. There was uncertainty as how to interpret the "extra" band around 500 bp. It was chosen to regard it as a PCR artefact.

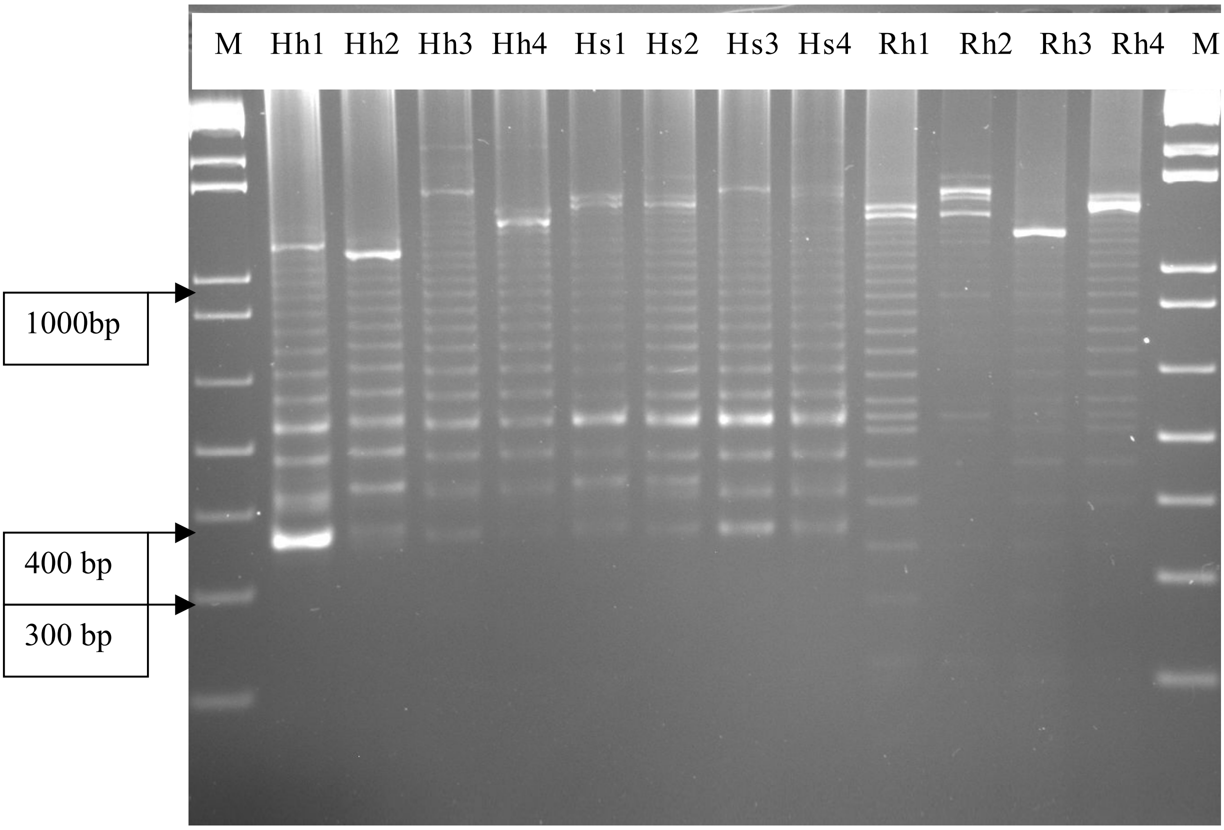


Figure 15: Gel picture of PCR containing the Heteroplasmic Tandem Repeat region in Atlantic halibut (Hh 1-4), Pacific halibut (Hs 1-4) and Greenland halibut (Rh 1-4). Most common copy number of a 61 bp repeat in each individual is seen as the strong bands above the 1000 bp marker. M: 1 kb plus DNA ladder from Invitrogen.

Secondary structure of the repeated motif

Various approaches have been devised for predicting secondary structures of RNA molecules. Many of these search to minimize the free energy of the folded macromolecule, thus searching for the most stable structure (Krane and Raymer 2003). Various number of copies of the HTR motif (Fig 14) was subjected to Zucker`s M-fold program (Zuker et al. 1999). One copy of the repeated motif in Atlantic halibut was folded with a free energy of –2,6 kcal/mol, while 13 copies had a free energy of –55 kcal/mol. The same values for Pacific halibut and Greenland halibut was –3,8 kcal/mol and –55 kcal/mol (17 copies), -3,4 kcal/mol and -155kcal/mol (20 copies) respectively (structures not shown). A lower free energy indicates a more stable secondary structure.

Base composition

The G + C content of the mtDNA in Atlantic halibut, Pacific halibut and Greenland halibut varied between 45,1 % and 46,1 % (Table 14). In protein coding genes the G + C content in the 1st codon position was 52,2 % to 53,6 %. While 2nd and 3rd codon position contained 41,5 % to 43,8 % and 43,3 % to 45,7 % G +C respectively. G + C content in tRNA was 47,2% to 47,6%. Also rRNA showed at slightly higher G + C content than total mtDNA with a variation between 47,0 % and 48,9%.

Table 14: Base composition of the H-strand of the Atlantic halibut, Pacific halibut and Greenland halibut mitochondrial genome. Numbers in parenthesis are data for ND-6

Region	G+C content Hh	G+C content Hs	G+C content Rh
Codon pos.			
1st	53,4 (49,7)	52,2 (50,9)	53,6 (51,7)
2nd	41,7 (45,7)	43,8 (45,7)	41,5 (44,8)
3rd	45,7 (39,3)	43,4 (40,4)	43,3 (43,1)
Total protein genes	47,0 (45,4)	46,8 (46,0)	46,2 (46,6)
tRNA	47,6	47,5	47,2
rRNA	47,0	48,4	48,9
Total mtDNA	46,1	45,7	45,1

Codon usage bias

Atlantic halibut

Every organism seems to prefer the use of some equivalent triplet codons over others (Krane and Raymer 2003). CUC, CUA and AUU are the most abundant codons in the protein coding genes of Atlantic halibut (Fig 16). The two codons encode the amino acid leucine, and AUU specify isoleucine. AGG, AGA, and UAA are the least common codons. This should come as no surprise as they all are termination codons.

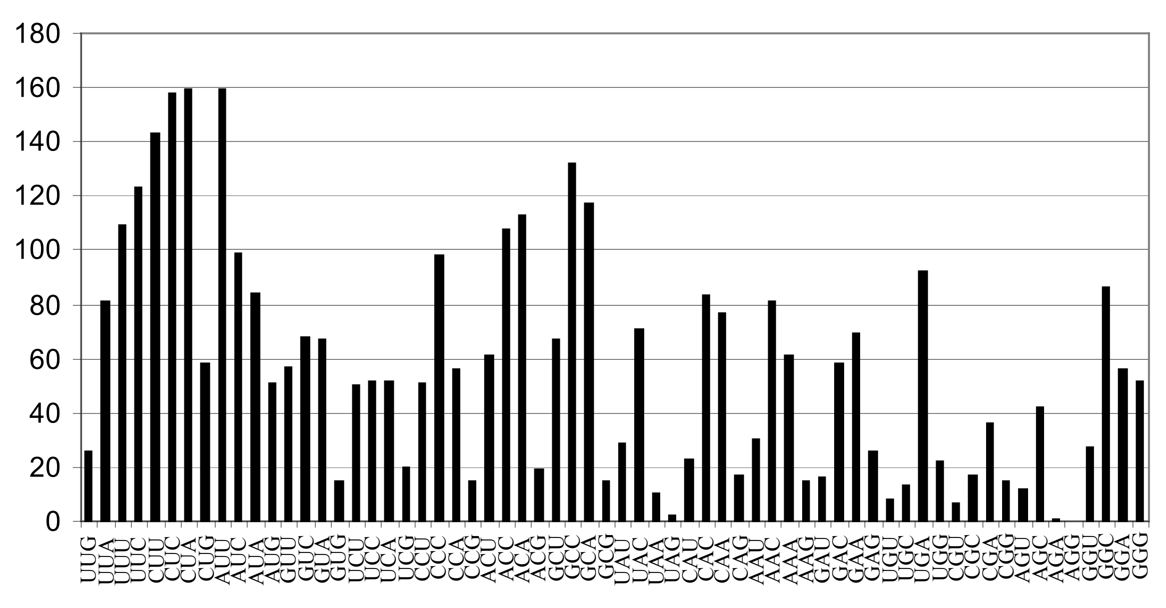


Figure 16: Codon usage in Atlantic halibut (Hh1) mtDNA. Codons along the abscissa and absolute number of each codon in mtDNA protein coding genes along the ordinate axis

In leucine, valine, serine, proline, threonine and alanine there seems to be a non-preference for codons ending with guanine (Table 15). For two-fold degenerate amino acids (tyrosine, histidine, aspargine, lysine, aspartic acid, glutamic acid, cysteine, tryptophan and serine) one codon is clearly dominating over the other. In these amino acids cytosine or adenine is the nucleotide of choice in third codon position.

Table 15: Codon preference calculated for each amino acid in mtDNA proteins of Atlantic halibut

Amino acid	Codon	%	Amino acid	Codon	%	Amino acid	Codon	%	Amino acid	Codon	%
Phe (F)	TTT	47	Ser (S)	TCT	29	Tyr (Y)	TAT	29	Cys (C)	TGT	38
Phe (F)	TTC	53	Ser (S)	TCC	29	Tyr (Y)	TAC	71	Cys (C)	TGC	62
Leu (L)	TTA	13	Ser (S)	TCA	30	STOP	TAA	83	Trp (W)	TGA	81
Leu (L)	TTG	4	Ser (S)	TCG	12	STOP	TAG	17	Trp (W)	TGG	19
Leu (L)	CTT	23	Pro (P)	CCT	23	His (H)	CAT	21	Arg (R)	CGT	9
Leu (L)	CTC	25	Pro (P)	CCC	45	His (H)	CAC	79	Arg (R)	CGC	23
Leu (L)	CTA	26	Pro (P)	CCA	25	Gln (Q)	CAA	82	Arg (R)	CGA	48
Leu (L)	CTG	9	Pro (P)	CCG	7	Gln (Q)	CAG	18	Arg (R)	CGG	20
Ile (I)	ATT	62	Thr (T)	ACT	20	Asn (N)	AAT	27	Ser (S)	AGT	22
Ile (I)	ATC	38	Thr (T)	ACC	36	Asn (N)	AAC	73	Ser (S)	AGC	78
Met (M)	ATA	62	Thr (T)	ACA	38	Lys (K)	AAA	80	STOP	AGA	100
Met (M)	ATG	38	Thr (T)	ACG	6	Lys (K)	AAG	20	STOP	AGG	0
Val (V)	GTT	28	Ala (A)	GCT	21	Asp (D)	GAT	22	Gly (G)	GGT	12
Val (V)	GTC	33	Ala (A)	GCC	40	Asp (D)	GAC	78	Gly (G)	GGC	39
Val (V)	GTA	32	Ala (A)	GCA	35	Glu (E)	GAA	72	Gly (G)	GGA	25
Val (V)	GTG	7	Ala (A)	GCG	4	Glu (E)	GAG	28	Gly (G)	GGG	24

Pacific halibut

In Pacific halibut (Fig 17) two codons encoding leucine (CUU, CUC) and one encoding isoleucine (AUU) appear with the highest frequencies. The termination codons AGG, AGA, TAG and TAA have the lowest frequencies.

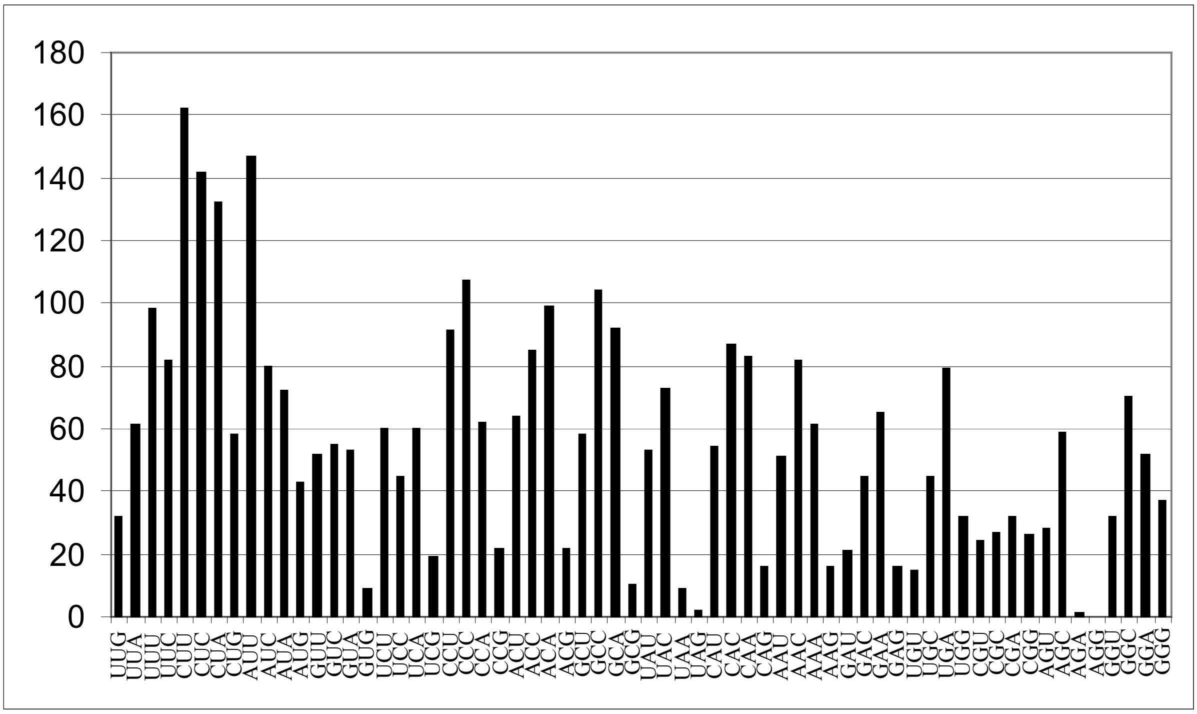


Figure 17: Codon usage in Pacific halibut (Hs1) mtDNA. Codons along the abscissa

and absolute number of each codon in mtDNA protein coding genes along the ordinate axis.

Table 16: Codon preference calculated for each amino acid in mtDNA proteins of Pacific halibut.

Amino acid	Codon	%	Amino acid	Codon	%	Amino acid	Codon	%	Amino acid	Codon	%
Phe (F)	TTT	54	Ser (S)	TCT	33	Tyr (Y)	TAT	42	Cys (C)	TGT	25
Phe (F)	TTC	46	Ser (S)	TCC	24	Tyr (Y)	TAC	58	Cys (C)	TGC	75
Leu (L)	TTA	10	Ser (S)	TCA	33	STOP	TAA	81	Trp (W)	TGA	71
Leu (L)	TTG	5	Ser (S)	TCG	10	STOP	TAG	19	Trp (W)	TGG	29
Leu (L)	CTT	28	Pro (P)	CCT	33	His (H)	CAT	62	Arg (R)	CGT	22
Leu (L)	CTC	24	Pro (P)	CCC	37	His (H)	CAC	38	Arg (R)	CGC	25
Leu (L)	CTA	23	Pro (P)	CCA	22	Gln (Q)	CAA	84	Arg (R)	CGA	29
Leu (L)	CTG	10	Pro (P)	CCG	8	Gln (Q)	CAG	16	Arg (R)	CGG	24
Ile (I)	ATT	65	Thr (T)	ACT	24	Asn (N)	AAT	38	Ser (S)	AGT	32
Ile (I)	ATC	35	Thr (T)	ACC	31	Asn (N)	AAC	62	Ser (S)	AGC	68
Met (M)	ATA	63	Thr (T)	ACA	37	Lys (K)	AAA	79	STOP	AGA	100
Met (M)	ATG	37	Thr (T)	ACG	8	Lys (K)	AAG	21	STOP	AGG	0
Val (V)	GTT	31	Ala (A)	GCT	22	Asp (D)	GAT	32	Gly (G)	GGT	17
Val (V)	GTC	33	Ala (A)	GCC	39	Asp (D)	GAC	68	Gly (G)	GGC	37
Val (V)	GTA	31	Ala (A)	GCA	35	Glu (E)	GAA	80	Gly (G)	GGA	27
Val (V)	GTG	5	Ala (A)	GCG	4	Glu (E)	GAG	20	Gly (G)	GGG	19

In third codon position of leucine, valine, serine, proline, threonine and alanine there is a strong preference for tymine, cytosine or adenine over guanine (Table 16). For arginine and glycine there is a relatively even distribution of the respective four possible triplet codons in the protein coding genes.

Greenland halibut

Three codons encoding leucine; CUC, CUA and CUU are most abundant in Greenland halibut (Fig 18). Termination codons AGG, AGA and UAA are the least common codons.

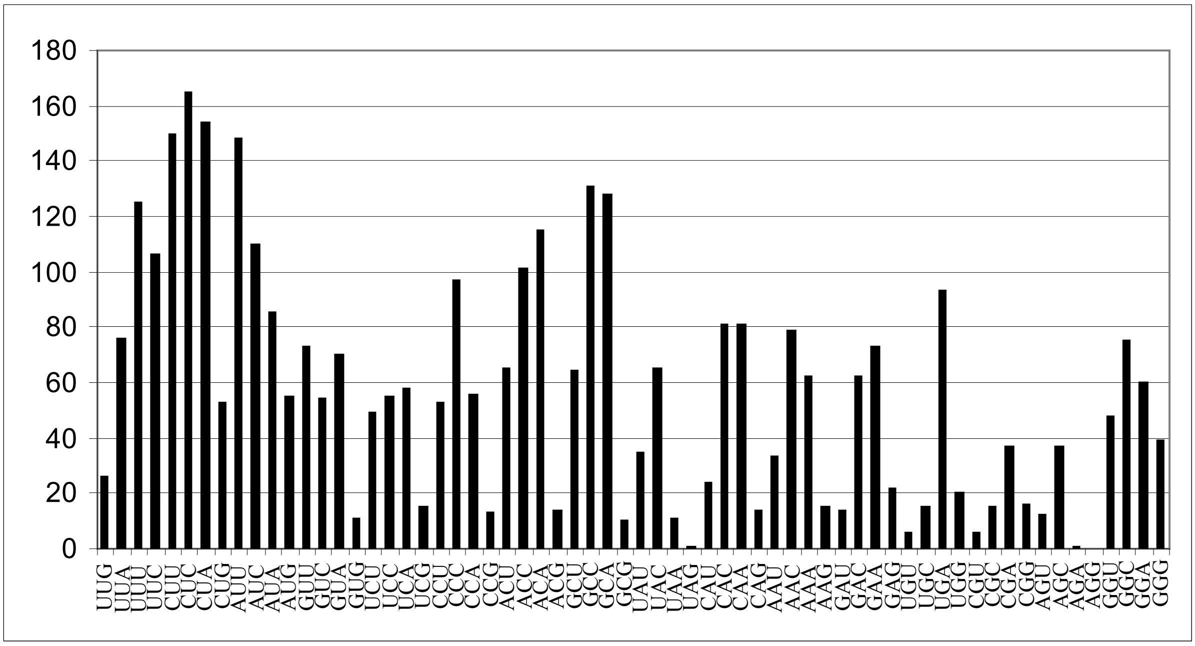


Figure 18: Codon usage in Greenland halibut (Rh1) mtDNA. Codons along the abscissa and absolute number of each codon in mtDNA protein coding genes along the ordinate axis.

Some amino acids show a relatively even distribution of triplet codons, though there seems to be a non-preference for any triplet codons ending with guanine (Table 17). In other amino acids the distribution is skewed. For example, the amino acid arginine is specified by CGA 50 % of the time. Especially amino acids with only two alternative codons have a very uneven distribution of codons, for example aspartic acid, histindine and glutamine.

Table 17: Codon preference calculated for each amino acid in mtDNA proteins of Greenland halibut.

Amino acid	Codon	%	Amino acid	Codon	%	Amino acid	Codon		Amino acid	Codon	
Phe (F)	TTT	54	Ser (S)	TCT	28	Tyr (Y)	TAT	35	Cys (C)	TGT	28
Phe (F)	TTC	46	Ser (S)	TCC	31	Tyr (Y)	TAC	65	Cys (C)	TGC	72
Leu (L)	TTA	12	Ser (S)	TCA	33	STOP	TAA	40	Trp (W)	TGA	69
Leu (L)	TTG	4	Ser (S)	TCG	8	STOP	TAG	60	Trp (W)	TGG	16
Leu (L)	CTT	24	Pro (P)	CCT	24	His (H)	CAT	30	Arg (R)	CGT	8
Leu (L)	CTC	26	Pro (P)	CCC	44	His (H)	CAC	70	Arg (R)	CGC	20
Leu (L)	CTA	25	Pro (P)	CCA	26	Gln (Q)	CAA	85	Arg (R)	CGA	50
Leu (L)	CTG	9	Pro (P)	CCG	6	Gln (Q)	CAG	15	Arg (R)	CGG	22
Ile (I)	ATT	57	Thr (T)	ACT	22	Asn (N)	AAT	29	Ser (S)	AGT	24
Ile (I)	ATC	43	Thr (T)	ACC	34	Asn (N)	AAC	71	Ser (S)	AGC	76
Met (M)	ATA	60	Thr (T)	ACA	39	Lys (K)	AAA	81	STOP	AGA	100
Met (M)	ATG	40	Thr (T)	ACG	5	Lys (K)	AAG	19	STOP	AGG	0
Val (V)	GTT	24	Ala (A)	GCT	19	Asp (D)	GAT	18	Gly (G)	GGT	22
Val (V)	GTC	36	Ala (A)	GCC	39	Asp (D)	GAC	82	Gly (G)	GGC	34
Val (V)	GTA	39	Ala (A)	GCA	38	Glu (E)	GAA	77	Gly (G)	GGA	27
Val (V)	GTG	6	Ala (A)	GCG	4	Glu (E)	GAG	23	Gly (G)	GGG	17

In figure 19 the frequency of every codon is compared in Atlantic halibut, Pacific halibut and Greenland halibut. The over-all codon frequencey patterns are highly conserved among the halibut species. However, for some codons Pacific halibut appears to differ from Atlantic halibut and Greenland halibut. Compared to Atlantic halibut and Greenland halibut codons UUU, UUC (both phenylalanine), CUA (leucine), AUG (methionine), ACA (threonine) and GCC (alanine) have lower frequencies in Pacific halibut. CGU and CGG (both arginine) have higher frequencies.

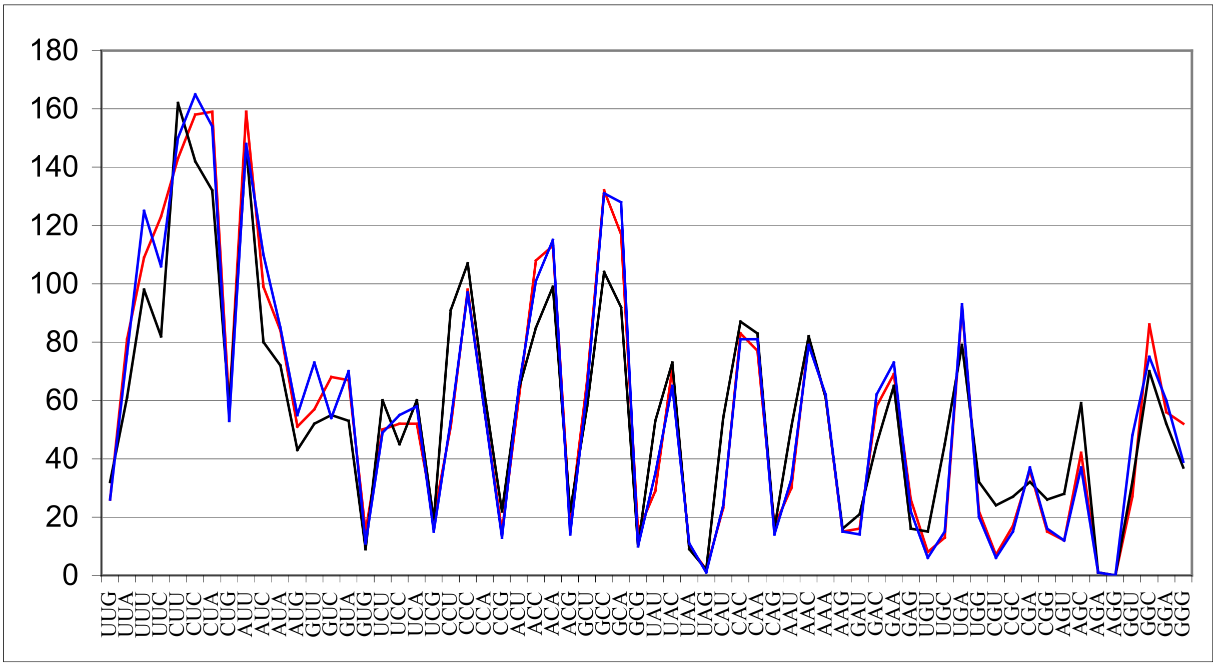


Figure 19: Comparison of codon preference in mtDNA proteins of Atlantic halibut (Hh1, red), Pacific halibut (Hs1, black) and Greenland halibut (Rh1, blue). Absolute abundance of codons along the ordinate-axis.

Intraspecific variation in nucleotide sequences

Atlantic halibut

A comparison of the complete mtDNA from four individuals of Atlantic halibut revealed 91 variable nucleotide positions, also known as single nucleotide polymorphisms (SNP) (Table 18). There were 79 singleton variable positions and 12 parsimony informative sites. In protein coding genes 83 % of the variability was in the 3rd codon position, 3 % in 2nd position and 14 % in 1st codon position. The transition to transversion ratio was 3,8. One insertion was observed in the control region of Hh2.

Table 18: Single nucleotide polymorphisms in mtDNA from four individuals of Atlantic halibut, except for HTR region. Nucleotide positions are based on Hh1.

Region	Phe	12S rRNA			Val	16S rRNA			Leu	ND1		
Position	46	312	340	734	1038	1372	1909	1999	2866	3117	3237	3315
Codon pos										3	3	3
Hh1	G	C	A	A	G	A	A	G	G	G	A	G
Hh2	G	A	A	C	A	G	G	G	G	G	G	A
Hh3	A	C	G	C	A	A	A	A	A	A	A	A
Hh4	A	C	A	C	A	A	A	G	A	A	A	A

Region	ND1					ND2						
Position	3507	3585	3669	3720	3849	4318	4384	4462	4501	4507	4522	4642
Codon pos	3	3	3	3	3	3	3	3	3	3	3	3
Hh1	A	A	T	G	G	G	G	A	G	G	G	G
Hh2	G	A	C	A	A	A	A	G	A	A	C	G
Hh3	A	A	C	A	G	G	A	A	A	A	G	C
Hh4	A	G	C	A	G	G	A	A	A	A	G	C

Region	CO1							CO2		ATP8		ATP6
Position	5633	5971	6220	6244	6337	6379	6442	7444	7616	8046	8072	8234
Codon pos	1	3	3	3	3	3	3	2	3	1	3	1
Hh1	C	A	C	C	G	A	G	T	C	A	A	A
Hh2	C	A	C	T	A	G	G	T	T	A	A	G
Hh3	T	C	T	C	G	A	A	C	C	G	G	A
Hh4	C	C	T	C	G	A	A	T	C	A	A	A

Region	ATP6				CO3		ND3		ND4L		ND4		
Position	8290	8662	8680	8815	9405	9418	9821	9992	10175	10313	10599	10748	11129
Codon pos	3	3	3	3	3	1	3	3	3	2	1	3	3
Hh1	G	T	A	C	A	A	G	C	G	G	G	G	A
Hh2	A	C	G	T	A	A	G	C	A	G	G	G	A
Hh3	G	T	A	C	G	G	A	T	G	G	C	A	G
Hh4	G	T	A	C	G	A	A	T	G	C	G	G	G

Region	His		ND5							ND6		
Position	11778	11809	12079	12363	12654	12984	13206	13642	13684	13893	13914	14061
Codon pos			1	3	3	3	3	1	1	3	3	3
Hh1	T	T	A	G	A	A	A	C	T	T	T	G
Hh2	T	T	G	A	G	G	G	T	C	C	T	A
Hh3	C	C	A	A	A	A	G	C	T	T	C	G
Hh4	T	T	A	A	A	A	G	C	T	T	C	G

Region	ND6		Cyt-b						Control region			
Position	14115	14283	14538	14901	14910	15051	15453	15492	15801	15828	15867	15879
Codon pos	3	3	3	3	3	3	3	3				
Hh1	C	T	C	A	A	G	A	C	C	C	A	T
Hh2	T	C	A	G	G	A	G	T	T	A	G	C
Hh3	C	T	C	A	A	G	A	T	C	C	A	T
Hh4	C	T	C	A	A	G	A	T	C	C	A	T

Region	Control region											
Position	15981	16260	16277	16327	16352	16400	16402	16404	16405	16408	16410	16411
Hh1	C	A	G	C	G	G	-	A	T	C	A	G
Hh2	A	G	A	T	A	A	A	C	A	T	T	A
Hh3	C	G	A	T	A	G	-	A	T	C	A	G
Hh4	C	G	A	T	A	G	-	A	T	C	A	G

Region	Control region					
Position	16510	16515	17363	17436	17540	17557
Hh1	T	C	G	A	G	C
Hh2	G	G	A	G	T	G
Hh3	T	C	G	A	G	C
Hh4	T	C	G	A	G	C

Nucleotide diversity is a concept in molecular genetics that is used to measure the degree of polymorphism within a population. It was first introduced by Nei and Li (1979). It is defined as the average number of nucleotide differences per site between any two DNA sequences chosen randomly from the sample population. The highest nucleotide diversity was found in the control region at 1,05%, followed by ATP8 0,60% and ND6 0,51. The lowest nucleotide diversity was found in 16S rRNA with 00,087%. Both COII and COIII had a nucleotide diversity of 0,15% (Table 19).

Table 19: Nucleotide diversity in mtDNA from 4 individuals of Atlantic halibut

Region	Variable sites	Variable sites / sites in gene (%)	Nucleotide diversity (%)
12S rRNA	3	0,32	0,16
16S rRNA	3	0,17	0,087
ND1	8	0,82	0,43
ND2	7	0,67	0,35
COI	7	0,44	0,26
COII	2	0,29	0,15
ATP8	2	1,2	0,60
ATP6	5	0,73	0,37
COIII	2	0,25	0,15
ND3	2	0,57	0,38
ND4L	2	0,67	0,33
ND4	4	0,29	0,16
ND5	7	0,38	0,19
ND6	5	1,0	0,51
Cyt-b	6	0,52	0,26
Control region	22	2,0	1,1

Pacific halibut

The four individuals of Pacific halibut had a total of 99 variable nucleotide positions (Table 20). In protein coding genes 94 % of the variability was found in the 3rd codon position. 3 % of variability was found in both 1st and 2nd codon position. The transition to transversion ratio was 4,7.

Table 20: Single nucleotide polymorphisms in mtDNA except for HTR region in four individuals of Pacific halibut. Nucleotide positions are based on Hs 1.

Region	12SrRNA	16SrRNA			ND1				Gln	Met	ND2	
Position	953	1408	1518	1529	3330	3516	3564	3735	3998	4055	4150	4342
Codon pos					3	3	3	3			3	3
Hs1	A	G	A	A	C	A	G	A	A	G	T	C
Hs2	G	A	A	G	T	G	A	G	C	A	C	T
Hs3	A	A	G	A	T	A	G	A	C	A	C	T
Hs4	A	A	G	A	T	A	G	A	C	A	C	T

Region	ND2				COI							
Position	4507	4849	4957	5074	5800	5923	6133	6199	6331	6403	6475	6541
Codon pos	3	3	3	3	3	3	3	3	3	3	3	3
Hs1	G	A	A	C	C	G	G	G	C	T	C	T
Hs2	A	G	G	T	T	A	A	G	T	T	T	C
Hs3	A	A	G	T	T	A	A	A	T	C	C	C
Hs4	A	A	G	T	T	A	A	G	T	C	C	C

Region	COI		Asp		COII	ATP6						
Position	6571	6763	7188	7223	7616	8212	8251	8284	8404	8617	8656	8662
Codon pos	3	3			3	3	3	3	3	3	3	3
Hs1	C	A	G	C	C	T	G	G	A	T	C	T
Hs2	T	A	A	C	T	A	A	A	G	T	C	C
Hs3	T	G	A	C	T	A	G	A	G	T	C	T
Hs4	T	A	A	A	T	A	G	A	G	C	T	T

Region	ATP6	COIII					ND3	ND4				ND4L
Position	8668	8853	9078	9165	9468	9594	9836	9926	10254	10263	10271	10935
Codon pos	3	3	3	3	3	3	3	3	3	3	2	1
Hs1	A	A	A	A	G	C	G	T	A	C	A	C
Hs2	G	C	T	G	G	C	A	A	C	T	G	G
Hs3	A	C	T	G	G	C	A	A	C	T	G	C
Hs4	A	A	T	G	A	T	A	A	C	T	G	C

Region	ND4L							ND5				
Position	10943	11033	11441	11474	11655	11681	11711	11997	12157	12310	12586	12595
Codon pos	3	3	3	3	1	3	3	2	3	3	3	3
Hs1	T	G	A	G	A	A	T	A	T	G	T	A
Hs2	C	A	G	A	C	G	T	A	T	A	A	A
Hs3	C	A	A	A	C	G	T	A	C	G	A	G
Hs4	C	A	A	A	C	G	C	G	C	G	A	A

Region	ND5									ND6		Cyt-b
Position	13015	13018	13066	13114	13378	13453	13459	13573	13654	13975	14041	14653
Codon pos	3	3	3	3	3	3	3	3	3	3	3	3
Hs1	T	A	T	C	G	C	T	C	T	T	T	A
Hs2	C	G	C	C	A	T	G	T	C	T	T	A
Hs3	C	G	T	C	A	T	T	C	C	C	C	G
Hs4	C	G	T	T	A	T	T	C	C	T	T	G

Region	Cyt-b						Control region					
Position	14719	14839	14971	15217	15274	15475	15876	15878	15900	15989	16255	16264
Codon pos	3	3	3	3	3	3						
Hs1	C	G	T	C	C	G	G	G	A	T	T	T
Hs2	T	A	C	C	T	A	A	A	G	C	T	T
Hs3	T	A	C	T	T	A	A	A	G	C	A	G
Hs4	T	A	C	C	T	A	A	A	G	C	T	T

Region	Control region											
Position	16279	16281	16314	16336	16349	16352	16383	16410	16432	16472	16518	17599
Hs1	G	G	G	G	A	A	G	A	G	G	G	G
Hs2	G	G	G	G	A	A	G	A	G	G	G	C
Hs3	A	A	A	T	A	A	A	C	A	C	A	C
Hs4	G	G	G	T	G	G	G	A	G	G	G	C

Region	Control region		
Position	17689	17758	17807
Hs1	G	A	A
Hs2	G	G	G
Hs3	G	G	G
Hs4	A	G	G

The three regions with the highest nucleotide diversity was the control region 0,97%, ATP6 0,58% and ND4L 0,51. ATP8, 12S rRNA and COII had the lowest nucleotide diversity with 0%, 0,053 % and 0,072% respectively 8 (Table 21).

Table 21: Nucleotide diversity in mtDNA from 4 individuals of Pacific halibut

Region	Variable sites	Variable sites / sites in gene (%)	Nucleotide diversity (%)
12S rRNA	1	0,11	0,053
16S rRNA	3	0,18	0,097
ND1	4	0,41	0,21
ND2	6	0,57	0,29
COI	10	0,64	0,33
COII	1	0,15	0,072
ATP8	0	0	0
ATP6	8	1,2	0,59
COIII	5	0,64	0,34
ND3	2	0,57	0,28
ND4L	3	1,0	0,51
ND4	8	0,58	0,29
ND5	14	0,76	0,39
ND6	2	0,38	0,19
Cyt-b	7	0,60	0,31
Control region	21	1,9	0,97

Greenland halibut

The number of single nucleotide polymorphisms found in four individuals of Greenland halibut was 110 (Table 22). Of the nucleotide variability found in protein coding genes 89 % was in 3rd codon position, 10 % was in 1st codon position and 1 % was in 2nd codon position. The ratio transitions to transversions were 5,5.

Table 22: Single nucleotide polymorphisms (SNP) in mtDNA except for HTR region in four individuals of Greenland halibut. Nucleotide positions are based on Rh1.

Region	Phe	16S rRNA				ND1										
Position	47	1262	1540	1815	2261	2937	2972	3146	3161	3197	3296	3299	3398	3503	3551	3605
Codon pos.						1	3	3	3	3	3	3	3	3	3	3
Rh1	A	A	A	A	A	C	G	A	G	G	A	A	A	A	A	C
Rh2	G	A	A	A	A	T	A	G	G	G	G	G	G	G	G	T
Rh3	G	A	A	T	G	T	G	A	G	C	G	G	G	G	G	C
Rh4	G	G	T	A	A	T	A	G	C	G	G	G	G	G	G	T

Region	ND2												Trp	Asn
Position	4089	4194	4422	4440	4452	4539	4542	4560	4602	4792	4872	4884	5141	5336
Codon pos.	3	3	3	3	3	3	3	3	3	1	3	3		
Rh1	T	G	A	T	A	T	A	G	G	C	G	G	A	T
Rh2	C	A	G	C	T	C	G	A	C	C	A	A	G	C
Rh3	C	A	G	C	T	C	G	A	C	T	G	A	A	T
Rh4	C	A	G	C	T	C	G	A	C	C	A	A	A	T

Region	COI				COII					ATP6	COIII	Gly	ND4L	
Position	6510	6555	6774	6849	7597	7615	7618	7669	7831	8295	9461	9660	10218	10247
Codon pos.	3	3	3	3	3	3	3	3	3	3	3		1	3
Hh1	A	C	G	A	C	T	G	C	A	A	C	C	T	G
Hh2	G	G	A	T	T	T	A	T	G	G	T	T	C	A
Hh3	G	G	A	T	T	C	A	T	G	G	T	C	C	A
Hh4	G	G	A	T	T	T	A	T	G	G	T	C	C	A

Region	ND4										HIS	ND5
Position	10436	10612	10876	10928	11032	11119	11200	11287	11313	11650	11833	12174
Codon pos.	1	3	3	1	3	3	3	3	2	3		3
Hh1	A	A	T	T	G	A	A	G	C	G	G	C
Hh2	A	G	C	C	A	A	G	A	C	A	A	T
Hh3	A	A	C	C	A	A	G	A	C	A	A	T
Hh4	T	G	C	C	A	G	G	A	T	A	A	T

Region	ND5											
Position	12342	12348	12528	12534	12585	12960	13023	13107	13156	13191	13308	13347
Codon pos	3	3	3	3	3	3	3	3	1	3	3	3
Hh1	G	G	C	G	G	T	G	A	A	T	T	C
Hh2	A	A	T	A	A	C	A	G	G	T	T	T
Hh3	A	A	T	A	A	C	A	G	A	T	C	T
Hh4	A	A	T	A	A	C	A	G	A	C	T	T

Region	ND5			ND6					Cyt-b			
Position	13425	13543	13794	13908	13947	13959	14067	14166	14586	14724	14838	14893
Codon pos.	3	1	3	3	3	3	3	3	3	3	3	1
Hh1	C	T	A	C	T	G	C	C	C	G	C	G
Hh2	T	T	G	T	C	G	T	T	T	A	G	A
Hh3	T	T	G	T	T	A	T	T	T	A	G	A
Hh4	T	C	G	T	C	G	T	T	T	A	G	A

Region	Cyt-b						Control region					
Position	15006	15159	15372	15435	15510	15516	15724	15842	15859	16257	16263	16266
Codon pos	3	3	3	3	3	3						
Hh1	C	T	T	T	A	A	G	T	G	A	G	T
Hh2	T	A	C	T	G	G	A	C	A	A	A	G
Hh3	T	A	C	C	A	G	A	C	G	T	A	G
Hh4	T	A	C	T	G	G	A	C	A	A	A	T

Region	Control region											
Position	16281	16283	16286	16289	16296	16314	16316	16351	16354	16355	16377	16384
Codon pos.												
Hh1	G	G	G	T	T	T	A	G	G	G	T	G
Hh2	A	A	G	C	G	G	G	A	A	A	G	A
Hh3	A	A	T	C	G	G	G	A	G	G	T	A
Hh4	A	A	G	C	G	G	G	A	G	G	T	A

Region	Control region					
Position	16472	16518	17888	17912	17915	17942
Codon pos.						
Hh1	G	G	A	T	G	G
Hh2	A	A	G	C	A	A
Hh3	A	G	G	C	A	A
Hh4	A	A	G	C	A	A

The highest nucleotide diversity in Greenland halibut was found in the control region with 1,1%, ND1 0,62% and ND2 0,59%. Three genes showed no nucleotide diversity: 12S rRNA, ATP8 and ND3 (Table 23).

Table 23: Nucleotide diversity in mtDNA from 4 individuals of Greenland halibut

Region	Variable sites	Variable sites / sites in gene (%)	Nucleotide diversity (%)
12S rRNA	0	0	0
16S rRNA	4	0,23	0,12
ND1	11	1,1	0,62
ND2	12	1,1	0,59
COI	4	0,26	0,13
COII	5	0,72	0,36
ATP8	0	0	0
ATP6	1	0,15	0,073
COIII	1	0,13	0,064
ND3	0	0	0
ND4L	2	0,67	0,34
ND4	10	0,72	0,37
ND5	16	0,87	0,44
ND6	5	0,96	0,51
Cyt-b	10	0,88	0,45
Control region	24	2,2	1,1

Nucleotide diversity compared in Atlantic-, Pacific- and Greenland halibut

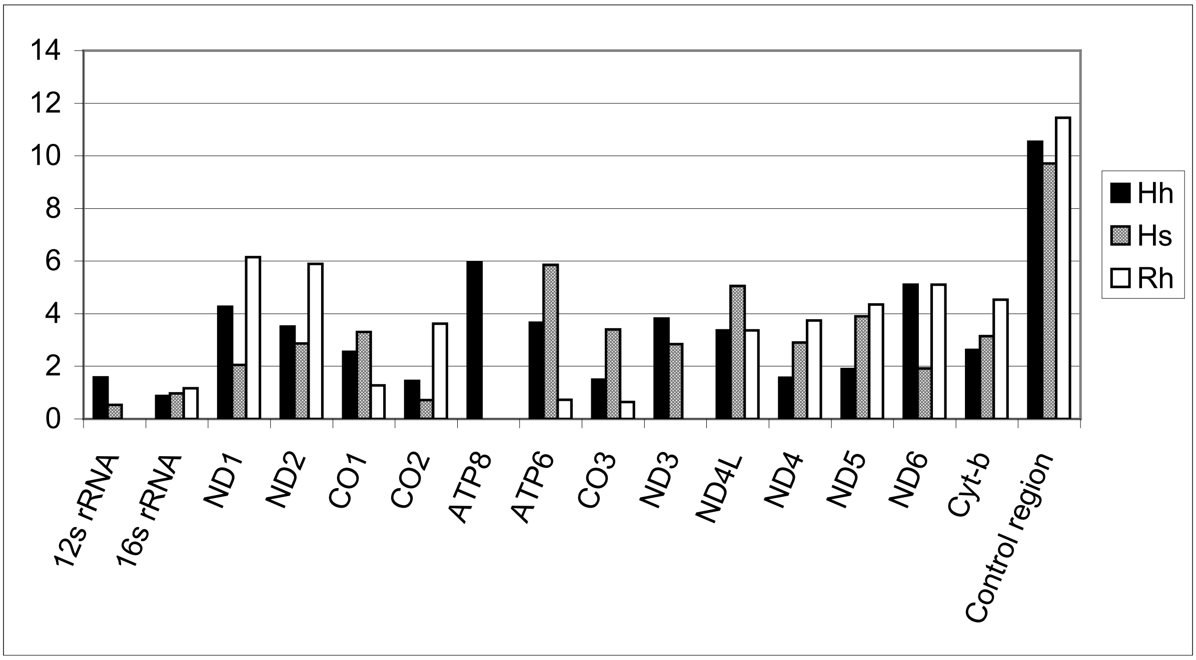


Figure 20: Comparison of nucleotide diversity in different regions of mtDNA in Atlantic halibut (blue), Pacific halibut (pink) and Greenland halibut (yellow). Respective regions along the abscissa and nucleotide diversity along the ordinate axis per thousand.

When comparing the nucleotide diversity in the same gene of Atlantic halibut, Pacific halibut and Greenland halibut similarities were discovered in some genes, while other genes had quite different nucleotide diversities (Fig 20). The two ribosomal RNA genes showed a very low nucleotide diversity in all species. ATP8 had no nucleotide substitutions in Pacific halibut and Greenland halibut, but a relatively large (0,6%) nucleotide diversity in Atlantic halibut. In ND3 Greenland had no nucleotide polymorphisms and both Atlantic halibut and Pacific halibut had a relatively equal higher nucleotide diversity. ND4l, ND4, ND5-6, Cytb and control region had relatively similar nucleotide diversities, when compared to the large differences in some of the other genes.

SNPs in 30 individuals of Atlantic halibut

When the complete mtDNA sequence from four individuals of Atlantic halibut had been determined, regions with high concentration of single nucleotide polymorphisms and interesting substitutions (i.e. transversions) were identified. 800 bp from ND2, COI and the control region respectively from 30 individuals of the Atlantic halibut brood stock population at Mørkvedbukta Research Station was determined. For primers and fragments see table 9.

Half of the individuals had genoype f (table 24). This observation and additional information available suggest that they probably have the same mother.

Table 24: Single nucleotide polymorphisms (SNPs) in selected regions within the genes ND2, COI and the control region of 30 individuals of Atlantic halibut

Region	ND2							COI			Control region			Genotype
Pos	4450	4501	4507	4718	4828	4849	4882	5971	6280	6442	15867	15921	16114	
Codon pos	3	3	3	1	3	3	3	3	3	3				
Hh1	A	A	A	G	T	G	A	A	A	G	A	T	A	a
Hh2	A	A	A	G	T	G	A	A	A	G	A	C	A	b
Hh3	G	A	A	G	T	G	A	A	C	G	A	T	A	c
Hh4	G	G	G	G	T	G	A	A	A	G	A	C	A	d
Hh5	G	G	G	G	T	G	A	A	A	G	A	C	A	d
Hh6	G	A	A	G	T	G	A	A	C	G	A	C	A	c
Hh7	G	A	A	G	T	G	A	A	C	G	A	C	A	c
Hh8	G	A	A	A	T	G	A	A	A	G	G	C	A	e
Hh9	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh10	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh11	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh12	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh13	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh14	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh15	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh16	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh17	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh18	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh19	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh20	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh21	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh22	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh23	G	G	G	G	T	G	A	A	A	G	A	C	A	f
Hh24	G	A	A	G	T	A	G	C	A	A	G	C	A	g
Hh25	G	A	A	A	T	G	A	A	A	G	G	C	A	e
Hh26	G	A	A	G	C	G	A	C	A	A	G	C	A	h
Hh27	A	A	A	G	T	G	A	A	A	G	A	C	A	b
Hh28	G	A	A	G	C	G	A	C	A	A	A	C	C	i
Hh29	G	A	A	G	T	G	A	A	A	G	A	C	A	j
Hh30	G	A	A	G	T	G	A	C	A	A	A	C	A	k

Intraspecific variation in amino acid sequences

A table of physiochemical distances, based on properties of the amino acid like polarity, molecular volume and chemical composition, was used to investigate amino acid substitutions (Grantham 1974). The smallest distance is 5, while 215 is the highest possible distance.

Atlantic halibut

A total of ten amino acid substitutions were observed between four individuals of Atlantic halibut (Table 25). The Pro→Ser substitution in COI is a change from a non-polar to a polar amino acid, both being neutral. The same is true for the Thr → Val substitution in COIII. In ND4L the Arg → Gln represents a change from a basic to a neutral, non-polar amino acid. The ND4 Cys → Arg substitution is a change from a neutral, polar to a basic amino acid. In ND5 the neutral, polar Thr is exchanged with the neutral, but non-polar Ala. The other amino acid substitutions were relatively innocent.

Table 25: Substitutions of amino acids in mtDNA in four individuals of Atlantic halibut

Region	COI	COII	ATP8	ATP6	COIII	ND4L	ND4L	ND4	ND4	ND5
Dist.[A]	74	98	29	29	69	43	112	32	180	58
Hh1	Pro	Leu	Ile	Ile	Thr	Arg	Cys	Val	Cys	Thr
Hh2	Pro	Leu	Ile	Val	Thr	Gln	Cys	Val	Cys	Ala
Hh3	Ser	Pro	Val	Ile	Val	Arg	Cys	Leu	Arg	Thr
Hh4	Pro	Leu	Ile	Ile	Thr	Arg	Ser	Val	Cys	Thr

A: Physiochemical distance (Grantham 1974)

Pacific halibut

The four amino acid substitutions in four individuals of Pacific halibut (Table 26) appeared to be relatively non-dramatic, as all changes involved amino acids belonging to the same group. The substitution in ND5 have a very high distance value, even though they are both polar, hydrophilic amino acids.

Table 26: Substitutions of amino acids in mtDNA in four individuals of Pacific halibut

Region	ND4L	ND4	ND4	ND5
Dist.[A]	46	32	5	194
Hs1	Asn	Leu	Ile	Tyr
Hs2	Ser	Val	Leu	Tyr
Hs3	Ser	Val	Leu	Tyr
Hs4	Ser	Val	Leu	Cys

A: Physiochemical distance (Grantham 1974)

Greenland halibut

Five substitutions in amino acids were registered in four individuals of Greenland halibut (Table 27). Of these both the Ser → Leu substitution in ND4 and the Thr → Ala substitution in ND5 is a change from a neutral and from a polar to a neutral, non-polar amino acid. In ND5 the neutral, polar Tyr is also exchanged with the basic His. Finally, in Cyt-b the neutral, polar Asn is replacing the acidic Asp.

Table 27: Substitutions of amino acids in mtDNA in four individuals of Greenland halibut

Region	ND4	ND4	ND5	ND5	Cyt-b
Dist.[A]	58	145	58	83	23
Rh1	Thr	Ser	Thr	Tyr	Asp
Rh2	Thr	Ser	Ala	Tyr	Asn
Rh3	Thr	Ser	Thr	Tyr	Asn
Rh4	Ser	Leu	Thr	His	Asn

A: Physiochemical distance (Grantham 1974)

Interspecific variation in amino acid sequences

A comparison of the amino acid sequence form Atlantic halibut 1, Pacific halibut 1 and Greenland halibut 1 revealed 70 substitutions, but no indels of amino acids (Table 28). COI, ATP8 and ND4L were perfectly conserved. ND5, ND4, ND2 and Cyt-b showed the greatest amount of variability, with 29, 10, 9 and 8 substitutions, respectively. Each end of a polypeptide seemed to be more prone to accumulating substitutions. Specially the first and last hundred amino acids of ND5 were regions with a very high concentration of amino acid substitutions.

Table 28: Amino acid substitutions between Atlantic halibut 1 (Hh1), Pacific halibut 1 (Hs1) and Greenland halibut (Rh1)

	ND1		ND2									COII			ATP6		COIII			ND3	ND4									
Hh1	I	V	L	V	T	L	T	I	V	V	T	I	I	F	S	S	I	K	H	L	V	S	V	S	L	S	A	L	T	V
Hs1	I	L	L	V	T	V	T	I	V	V	T	I	I	F	S	S	I	K	H	L	V	N	V	S	L	S	A	I	T	V
Rh1	V	L	M	I	A	L	A	V	M	M	A	L	M	Y	V	T	V	M	V	I	I	S	I	N	S	G	T	I	A	I

	ND5																													ND6		
Hh1	Y	I	I	R	D	T	N	V	S	S	H	L	A	T	S	I	E	P	N	M	A	V	I	T	A	A	V	L	T	L	G	T
Hs1	Y	I	I	R	G	T	N	I	N	S	H	I	A	T	S	I	E	P	G	M	A	V	I	T	S	A	V	M	T	L	G	T
Rh1	H	V	M	Q	E	S	D	I	N	L	N	L	V	S	N	L	K	S	D	V	T	K	V	I	S	S	I	L	A	M	A	I

	Cyt-b							
Hh1	I	L	V	I	N	L	S	W
Hs1	I	L	V	I	N	L	S	W
Rh1	V	I	I	V	D	V	A	L

Non-conservative amino acid substitutions

All amino acid substitutions have a mutation score. A negative score denotes a non-conservative replacement for transmembrane proteins. Scores were determined by the amino acid mutation matrix for transmembrane proteins (Jones et al. 1994). Nine of the 70 substitutions between Atlantic halibut, Pacific halibut and Greenland halibut had a negative score (Table 29). Four were in ND5, two in COIII and one in ATP6, ND4 and Cyt-b respectively. In all mutations that had a negative score Atlantic halibut and Pacific halibut had the same amino acid, and Greenland halibut had a different one. The exception was one substitution in ND5 were all species had a different amino acid. The mutation between Atlantic halibut and Pacific halibut (N/G) had a score of –2. Amino acid substitutions with a negative mutation score were also observed between four individual of Atlantic halibut and four individuals of Greenland halibut

Table 29: Amino acid substitutions showing a negative mutation matrix score

	ATP6	COIII		ND4	ND5				Cyt-b		COII	ND4		ND4
Hh1	S	K	H	L	S	P	V	N*	W	Hh1	L	C	Rh1	S
Hs1	S	K	H	L	S	P	V	G	W	Hh2	L	C	Rh2	S
Rh1	V	M	V	S	L	S	K	D	L	Hh3	P	R	Rh3	S
										Hh4	L	C	Rh4	L
Score	-1	-1	-4	-2	-2	-1	-4	-2	-2		-3	-4		-3

*Score for mutation N-G is -2

Transmembrane helices

The number of helices was predicted by the help of the TMHMM 2.0 program (http://www.cbs.dtu.dk/services/TMHMM/). Results are presented in table 30. The same number of transmembrane helices was predicted in all individuals of Atlantic halibut, Pacific halibut and Greenland halibut. So the amino acid substitutions observed in some individuals did not have any effect on transmembrane helices.

Table 30: Number of predicted transmembrane helices in 13 mitochondrial proteins of Atlantic halibut (Hh), Pacific halibut (Hs) and Greenland halibut (Rh).

	No of transmembrane helices		
	Hh	Hs	Rh
ND1	8	8	8
ND2	9	9	9
COI	11	11	11
COII	2	2	2
ATP8	1	1	1
ATP6	6	6	6
COIII	6	6	6
ND3	3	3	3
ND4L	3	3	3
ND4	12	12	12
ND5	16	16	16
ND6	5	5	5
Cyt-b	9	9	9

Phylogenetic investigation of mtDNA sequences from Pleuronectiform species.

Three different trees were created, each by the help of the methods Neighbor Joining, Minimum Evolution and Maximum Parsimony. NJ and ME trees based on nucleotide sequence were inferred with the Kimura 2 Parameter distance model. This model take into consideration that transitions occur more often than transversion, which were the case here. The K2P model gives better distance estimates than the often used Jukes-Cantor method, because the JK method does not correct for a higher rate of transitional substitutions as compared to transversional substitutions (Higgs and Attwood 2005). P-distances were used in analysis of amino acid sequences. MP analysis were performed with the branch and bound method. The MP method works best when the amount of variation among sequences is similar. Distance methods like NJ and ME are less stringent about sequence similarity, while

Maximum Likelihood methods do not require a clear reqognizeable sequence similarity (Mount 2001).

When considering which model to chose one have to remember that the single most important step in tree construction is the sequence alingment. No amount of care, tweaking of parameters or choise of model can infer a correct tree if the alignment is poorly done. The key to determining evolutionary distances between sequences lies in the degree of divergence between sequences. All alignments were manually inspected and adjusted if necessary. Ambiguously aligned regions and gaps were excluded from the analyses. The number of bootstrap replicates was 2000. When using the complete mtDNA genome the highest possible resolution is achieved, but there is a posibility that 3^{rd} codon position will experience substitutional saturation between taxa that diverged a long time ago. These positions will not be informative and only create "noise" in the analysis. To avoid this problem when inferring deep branch phylogenies one can use 1^{st} and 2^{nd} position of codons and stem regions of tRNA genes e.g. Miya et al. (2001)

The tree in figure 21 is based on the complete mtDNA sequence from all available Pleuronectiform species. By using the complete mitochondrial genome a high resolution and accuracy is acchieved.

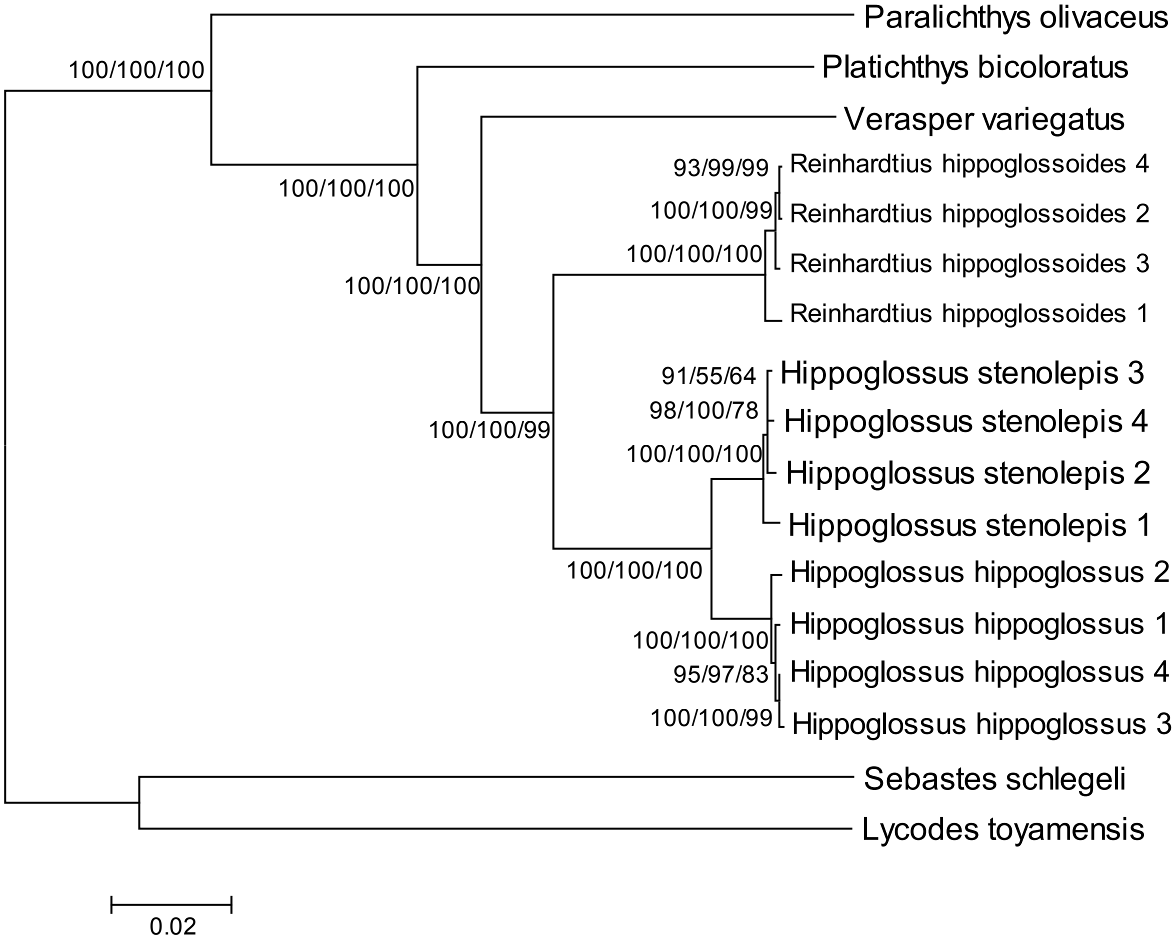


Figure 21: Minimum evolution tree based on complete mtDNA sequences, except control region. The numbers beside the nodes denote bootstrap percentages for 2000 replicates for the tree models Neighbor Joining, Minimum Evolution and Maximum Parsimony. Outgroup: *Sebastes schlegeli* and *Lycodes toyamensis.*

The complete mtDNA sequence was not obtained from Common sole (*Solea vulgaris*), European plaice (*Pleuronectes platessa*) and Turbot (*Scophthalmus maximus*). The available mtDNA sequences from these species were aligned together with the sequences used in figure 21. Regions that lacked sequence in one or more species were excluded. Then one was left with approximately 5000 homologous base pairs between position 30 and 9890, from which the tree presented in figure 22 was made. This includes ND1, COII, ATP8, ATP6, partial sequence from ND2 and ND3 and sequence from multiple tRNAs in this region. These protein coding genes and tRNAs were identified in the same way as in the halibut species, to make sure all sequences were homologous.

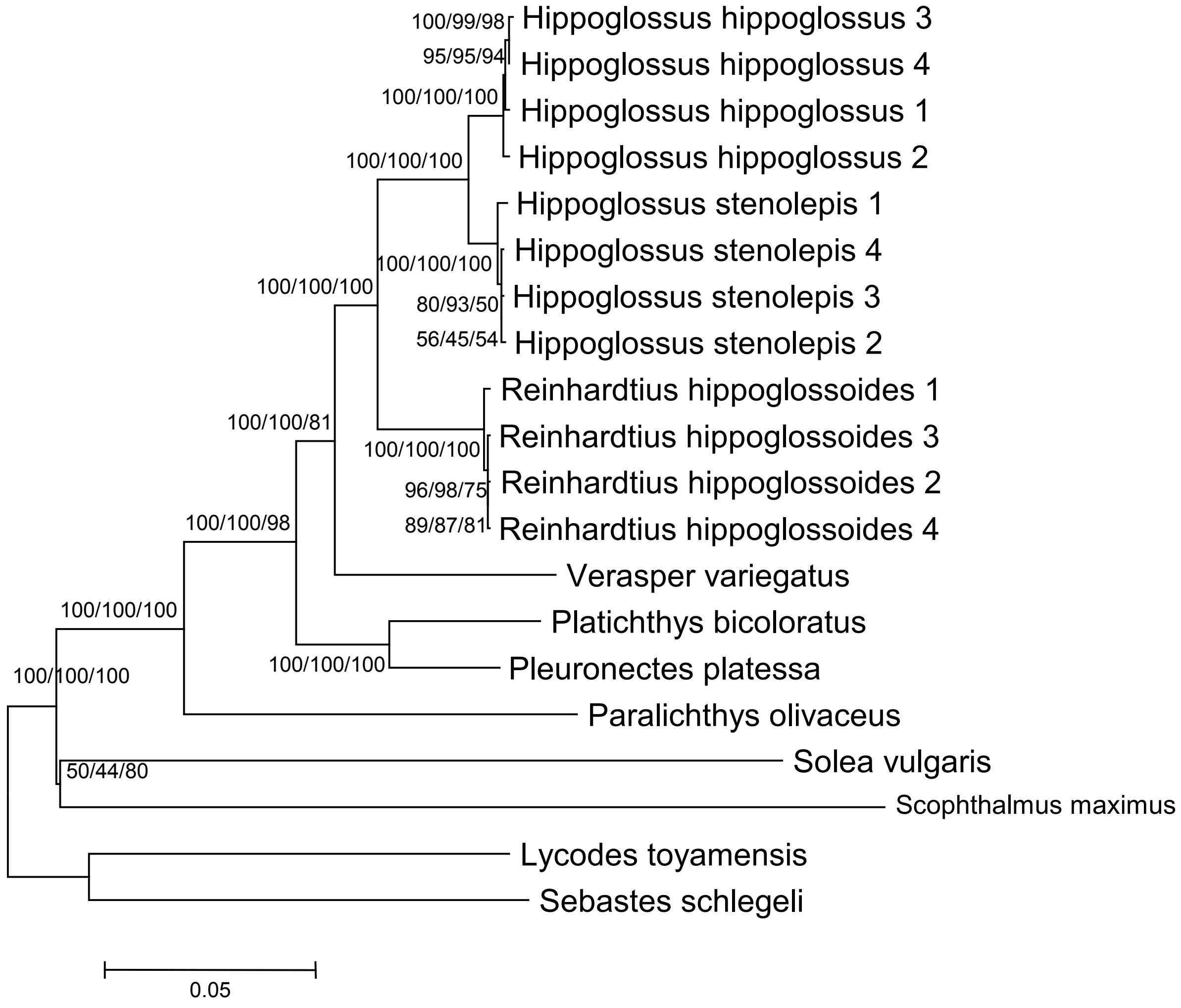


Figure 22: Minimum evolution tree based on alignments of approximately 5000 bp of 9 pleuronectiform species. The numbers beside the nodes denote bootstrap percentages for 2000 replicates for the tree models Neighbor Joining, Minimum Evolution and Maximum Parsimony. A dash instead of a bootstrap value indicates that the method did not support the clade in question. Outgroup: *Sebastes schlegeli* and *Lycodes toyamens.*

The phylogenetic information in figure 21 and figure 22 can be summarized as follows: Soleidae (*Solea vulgaris*) and Scophthalmidae (*Scophthalmus maximus*) appeared to be sister taxa and also the most basal taxa. Paralichthyidae formed a sister taxa to Pleuronectidae. Within the Pleuronectidae, *Platichtys bicoloratus* and *Pleuronectes platessa* clustered into one group and was most basal. *Verasper variegatus* appeared to be the closest taxon to the three halibut species. Furthermore, the Reinhardtius genus formed a sister taxa to the Hippoglossus genus. The Hippoglossus genus was the most derived clade. Finally, the interspesific genetic variation between *Hippoglossus hippoglossus* and *Hippoglossus stenolepis* was greater than the intraspecific variation within each species, meaning that they are probably separate species, but speciation took place relatively recently. Bootstrap support was generally high in all trees when considering phylogenetic relationship above species level. The tree based on

5000 bp did not separate all individuals well enough with all methods (Fig 22). Bootstrap values as low as 55 % and 64 % were observed between individuals of *Hippoglossus stenolepis* in the tree produced with the help of complete mtDNA sequences (Fig 21).

To investigate the phylogenetic relationship between Pleuronectiformes and the “well-known” taxa Gadidae and Salmonidae a concatamer of amino acid sequences from the thirteen mtDNA protein-coding genes were used to create the tree in figure 23. Amino acid sequences were choosen because the problems with saturation in third codon position is, to a high degree, excluded, as many amino acids are two- or four-fold degenerated (i.e. substitution can occur in third codon position without changing the amino acid). Phylogenetic investigation of Pleuronectiformes, Gadidae and Salmonidae based on amino acid sequences revealed that Salmonidae is the most basal taxon, while Gadidae is closer related to the Pleuronectiformes (Fig 23).

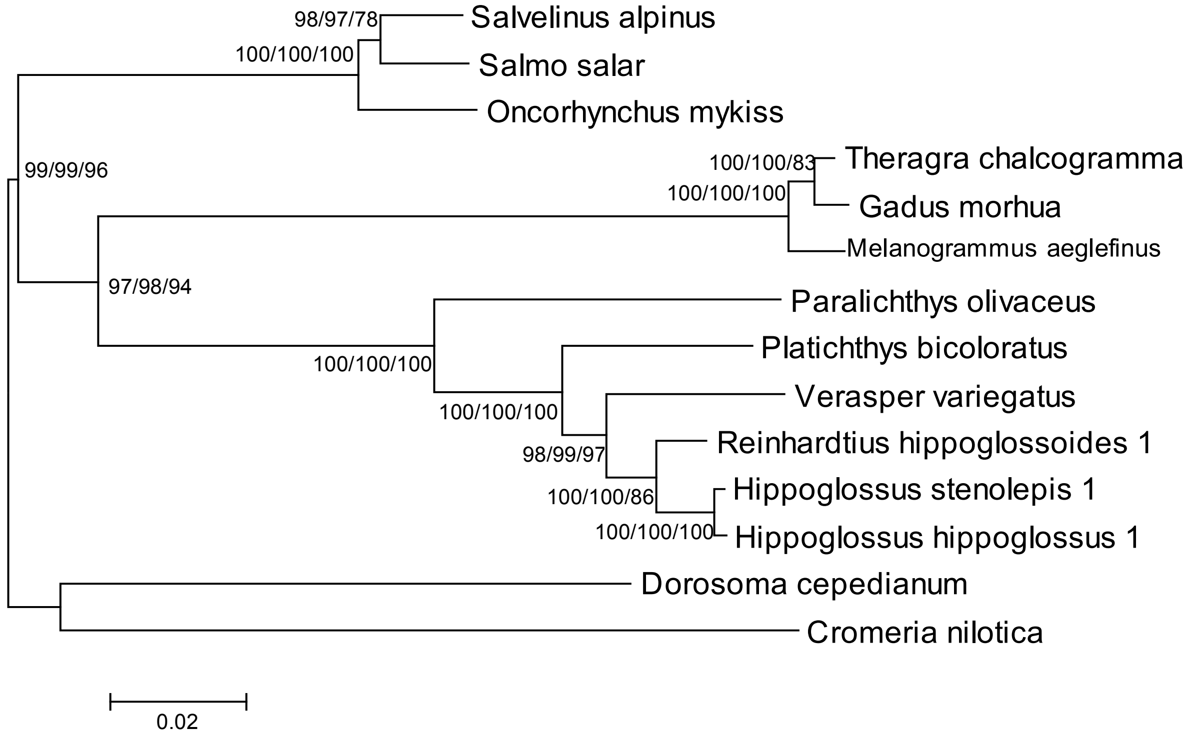


Figure 23: Minimum evolution tree of 6 pleuronectiform species, 3 Gadidae species and 3 Salmonidae species tree based on amino acid sequences from 13 mitochondrial protein coding genes. The numbers beside the nodes denote bootstrap percentages for 2000 replicates for the tree models Neighbour Joining, Minimum Evolution and Maximum Parsimony. Outgroup: *Dorosoma cerpedianum* and *Cromeria nilotica.*

Estimation of divergence times

Sequence divergence in COI between Atlantic halibut 1 and Pacific halibut 1 was 2,3% . Divergence between Atlantic halibut 1 and Greenland halibut 1 was 7,0%, while divergence between Pacific halibut 1 and Greenland halibut 1 was 7,3%. According to Bermingham et al. (1997) sequence divergence in COI of recently separated teleost taxa is roughly 1,2% per million years. Based on these numbers the divergence time between Atlantic- and Pacific halibut was estimated to 2 million years, while divergence between Greenland halibut and the *Hippoglossus* genus took place approximately 6 million years ago (Ma). Tajimas test of relative rate was used to evaluate rate constancy among lineages (Tajima 1993).

Authenticity of the Mitochondrial Sequences

Nuclear mitochondrial pseudogenes (numt) are parts of the mtDNA molecule that have been copied and incorporated into the nuclear genome. As reviewed by Bensasson et al. (2001) numts have contaminated PCR-based mitochondrial studies of over 64 different animal species. When numt sequences are present, the nuclear and mitochondrial products are often co amplified by PCR, and sequences from these products may exhibit double peaks and ambiguities at some positions (Sorenson and Fleischer 1996). In this study PCR products were mostly rather large, 3kb - 4,5 kb, and all PCR products appeared as clean single bands of the expected molecular weight when controlled using agarose gel electrophoresis. Data files from sequencing reactions that exhibited multiple peaks were discarded. Unspecific primer binding is also a possible explanation for multiple peaks. Thus, it did not appear that co-amplification of both nuclear and mitochondrial copies of genes were a problem.

Discussion

Genetic variation

Complete mitochondrial genome

The number of single nucleotide polymorphisms (SNP) observed among Atlantic halibut individuals was 91. The same numbers for Pacific halibut and Greenland halibut was 99 and 110 respectively. Thus, no significant difference in genetic variation within the three halibut species could be observed. Very few population studies based on complete mtDNA sequences have been performed. In a study of complete mtDNA sequences from 10 individuals of Walley pollock Yanagimoto et al. (2004) observed 179 SNPs. The number of nucleotide substitutions found between Norwegian Coastal stock and Norwegian Shelf stock of cod was 75. Between Norwegian Coastal stock and Arcto-Norwegian stock of cod, 83 nucleotide substitutions were identified, while the number of nucleotide substitutions between Norwegian Shelf stock and Arcto-Norwegian stock was 68 (Breines 2005). These are comparisons between two individuals only, and more variable sites are expected if more individuals are analysed and compared. Brown et al. (2006) detected 156 nucleotide substitutions between five individuals of Rainbow trout. However, this number could be lower, because they questioned the accuracy of the sequencing work in one individual done by Zardoya et al. (1995)

Ribosomal RNA genes

The overall rRNA substitutions rates are about half of those compared to protein coding genes (Brown and Simpson 1982; Hixson and Brown 1986). The same appears true for Atlantic halibut, Pacific halibut and Greenland halibut. In a study of mtDNA from ten individuals of Walleye pollock (*Theragra chalcogramma)* Yanagimoto et al. (2004) found relatively low substitution rates in rRNA genes. Similar findings were discovered in cod *(Gadus morhua)* by Breines (2005) and in a comparison between saithe (*Pollachius virens*) and pollack (*Pollachius pollachius*) by Nymark (2006).

Protein coding genes

The patterns of substitution in protein coding genes are well known. The knowledge of how mutations accumulate makes protein coding genes good candidates for phylogenetic studies in fish.

The genes coding for the cytochrome oxidase subunits and cytochrome b are the most conserved genes (Meyer 1994). This appears to be true also for Atlantic halibut, Pacific halibut and Greenland halibut (Fig 20). These genes were found to be very conserved in saithe and pollack by Nymark (2006), but only relatively well conserved in cod (Breines 2005) and Walley pollock (Yanagimoto et al. 2004). A study that compared mtDNA from Arctic charr and Brook charr found 4.8 %, 3.5 % and 5.9 % sequence divergence COI, COII and COIII respectively (Doiron et al. 2002). The most variable are the ND and ATPase genes (Billington 2003). The ND genes have a nucleotide diversity of 0.2-0.6 % in Atlantic halibut 1-4, Pacific halibut 1-4 and Greenland halibut 1-4, respectively. Though ND3 in Greenland halibut 1-4 had no nucleotide substitutions. ATP8 had a high nucleotide diversity (0.6%) in Atlantic halibut 1-4, and ATP6 had the same nucleotide diversity in Pacific halibut 1-4 and 0.3% in Atlantic halibut 1-4. Otherwise the ATP genes had no or little nucleotide diversity. Brown et al. (2006) found the highest nucleotide variability in ND4 and ND5 in a study of intraspecific variability in five individuals of Rainbow trout. Saithe and pollack had a very low nucleotide variability in the ATP genes (Nymark 2006). While Walley pollock and cod had a moderately substitution rate in these genes (Breines 2005; Yanagimoto et al. 2004). Sequence divergence was high between Arctic charr and Brook charr in all ND genes, except ND4L. Sequence divergence in ATP6 was also high (Doiron et al. 2002). The total number of nucleotide substitutions in protein coding genes of Atlantic halibut, Pacific halibut and Greenland halibut was 59, 71 and 79 respectively. The same number in five individuals of Rainbow trout was 47 (Brown et al. 2006)

Some suggestions as to why some genes are well conserved, while others show a higher variability, are given below. Substitution rates are influenced by the rate of mutation and the probability of fixation of a mutation. Fixation depends on whether the mutation provides an advantage, is neutral or deleterious. Substitution rates in regions that are likely to affect the function of the gene product will be lower (Graur and Li 1999). Apparently, mitochondrial genes have different mutation rates and some genes evolve faster than others. The rate of evolution of a gene or mutation that is under selection will be very different from one that is not. Selection resists substitutions at some sites, while allowing substitutions at other sites to become fixed. Different genes with different functions, or different parts of a gene with different functions will have different rates of evolution. Thus, different regions of DNA with different functional constraints will evolve at different rates. This is true for both nuclear and mitochondrial genes (Higgs and Attwood 2005). Genes evolve at different rates because, although mutations are usually random events, some proteins are much more tolerant to changes in their amino acid sequence than are other proteins. For this reason, the genes that encode these more tolerant, less constrained proteins evolve faster (Nei 1987). Furthermore, structure, function and expression level affect the rate of evolution. So does the position of a gene in a pathway or network. Genes more central to a network have a greater number of pleiotropic effects on other genes and biological processes. These genes evolve slower, because they are very constrained: a mutation that has a beneficial effect on one process is very likely to have deleterious effects on the other processes, and would be negatively selected (Graur and Li 1999).

The rate of mutations might not always be similar along the mitochondrial genome. Sites in the mtDNA control region of humans known to be hyper variable have been identified as mutational hotspots. Though, it is not known what features of these hyper variable sites and/or the mtDNA replication machinery cause them to be mutational hotspots (Stoneking 2000). Some of the mechanisms discussed here are likely to be the cause of the differentiated evolutionary rate observed in mtDNA genes in Atlantic halibut, Pacific halibut and Greenland halibut.

Variability in protein complexes

Eight protein complexes mediate the processes carried out by the electron transport chain. Each of these complexes plays a vital role in the health of the cell and any slight mutation in any one of the proteins that make up these complexes can lead to cell death or stress, which can both in turn lead to a number of diseases. As an example a mutation in complex I genes been associated with Parkinsons disease and aging (Smigrodzki et al. 2004).

Proteins with more interactors are known to evolve more slowly not because they are more important to the organism, but because a greater proportion of the protein is directly involved in its function (Fraser et al. 2002). The faster evolving ND genes belong to multiprotein complex I, consisting of 25 polypeptides. It seems that the ND genes do not have a central role in the network of polypeptides in complex I. Otherwise the high occurrence of mutations in the ND genes would make it difficult to cooperate properly with the rest of the polypeptides in the complex. Apparently, there is no strong negative selection acting on mutations in ND genes.

On the other hand, the more conserved CO genes belonging to complex IV could hold a central position among the 13 polypeptides in this complex. It is also possible that there is a regional heterogenity along the mtDNA molecule, when it comes to occurrence of mutations. Maybe the CO genes, along with ATP8 and ATP6 are located at a part of the molecule that is somehow more protected against mutations. ATP8 was very conserved in Pacific halibut and Greenland halibut, but ATP8 and ATP6 were very variable in Atlantic halibut and Greenland halibut respectively. This hypothesis seems unlikely as Cyt-b, a relatively conserved gene, is located in a different part of the mtDNA molecule, close to the control region, which has a elevated evolutionary rate. Regions that are frequently exposed as a single strand during transcription or replication (O_H and O_L) have also been reported to have a higher rate of mutations (Ramiro et al. 2003).

Control region

The control region is partially constrained in primary sequence and secondary structure in order to regulate replication and transcription of the mtDNA molecule (Clayton 1991). The control region is characterized by the displacement loop (d-loop), a stretch of DNA that is complementary to the light strand; the d-loop displaces the heavy strand. Of all mitochondrial defined regions and genes the control region has the highest substitution rate, at least when considering the two peripheral domains, while the central domain is remarkably conserved (Pesole et al. 1999). Nucleotide diversity was not calculated for the three domains in the control region separately. But one gets an impression of variability in the different domains by viewing the alignment in figure 12. The nucleotide diversity for the control region as a whole, except heteroplasmic tandem repeats, was approximately 1%, about 3 times higher than the average nucleotide diversity in protein coding genes. The intraspecific substitution rate in the control region of cod was found to be slightly higher than that of the rest of the protein coding genes (Breines 2005). Interspecific substitution rate in 10 individuals of Walley pollock was not found to be significantly higher than the protein coding genes (Yanagimoto et al. 2004). The same observation was done regarding the interspesific substitution rate in the control region of saithe and pollack (Nymark 2006).

Functional consequences of amino acid substitutions

Substitutions at the amino acid level will change the properties of the polypeptide. Some changes are small and would probably not have any adaptive value. Others that, for instance, could improve the function of an enzyme at certain temperatures would be of great adaptive value if the organism preferred this temperature (Doiron et al. 2002). A negative score suggests that this substitution serve a vital function in the structure and function of a polypeptide. Doiron et al. (2002) found a high concentration of substitutions with a negative score in the ND genes. They suggested that the transmembrane multiprotein complex I, which ND genes are a part of, could be a target where selection acted on the char's mitochondrial genome for specific environmental factors. For example temperature niches. Five out of nine amino acid substitutions with a negative mutation score between Atlantic halibut, Pacific halibut and Greenland halibut were located in the ND genes. This could be an adaptation to temperature niches. Greenland halibut prefer lower temperatures than both Atlantic halibut and Pacific halibut (see introduction), and the observed mutation was, with one exception, always observed between Atlantic halibut / Pacific halibut and Greenland halibut.

Transmembrane helices

The number of transmembrane helices in the three halibut species is compared to similar data from Saithe (*Pollachius virens*) and Pollack (*Pollachius pollachius*) in a study by Nymark (2006) in table 31. Saithe and Pollack have one more helic in ND1, COI and ND4. Saithe has to helices in ND4L, while all other species have 3.

Table 31: Comparison of transmembrane helices in mtDNA proteins in Atlantic halibut (Hh), Pacific halibut (Hs), Grenland halibut (Rh), Saithe (Pv) and Pollack (Pp)

	No of transmembrane helices	
	Hh/Hs/Rh	Pv/Pp
ND1	8	9
ND2	9	9
COI	11	12
COII	2	2
ATP8	1	1
ATP6	6	6
COIII	6	6
ND3	3	3
ND4L	3	2/3
ND4	12	13
ND5	16	16
ND6	5	5
Cyt-b	9	9

Heteroplasmic tandem repeats in the control region

The control region is responsible for tremendously length variation in mtDNA due to tandem duplications (Brown 1985). Such heteroplasmic tandem repeats (HTR) have been reported in several teleost species (Table 32).

Table 32: Selected teleost species with HTR reported in the control region.

Organism	Repeat size (bp)	No. of repeats	Heteroplasmy	Reference
Atlantic halibut (*Hippoglossus hippoglossus*)	61	12-19	Yes	This study
Pacific halibut (*Hippoglossus stenolepis*)	61	17-19	Yes	This study
Greenland halibut (*Reinhardtius hippoglossoides*)	61	18-23	Yes	This study
Amercan Plaice (*Hippoglossoides platessoides*)	61	2	Not determined	(Lee et al. 1995)
Winter flounder (*Pseudopleuronectes americanus*)	62	6-8	Not determined	(Lee et al. 1995)
Yellowtail flounder (*Limanda ferruginea*)	62	6-8	Not determined	(Lee et al. 1995)
European flounder (*Platichtys flesus*)	19	1-10	Yes	(Hoarau 2002)
Sea bass (*Dicentrarchus labrax*)	17 48	1-19 6-19	Yes Yes	(Cesaroni et al. 1997)
Cod (*Gadus morhua*)	40	2-6	Yes	(Árnason and Rand 1992)
Sturgeon (*Acipenser transmontanus*)	82	1-6	Yes	(Brown et al. 1992)

Atlantic halibut, Pacific halibut and Greenland halibut are all heteroplasmic with respect to a 61 bp motif in the CSB domain of the control region. There were large differences in the sequence of the motif in the three species. It was possible to fold both one copy and the most common copy number of the motif into secondary structures. The G + C content was low in all motifs. This could be a way of resisting the formation of a stable secondary structure. The function of these repeated elements is not known. The most likely mechanism behind the creation of repeated motifs is slipped-strand mispairing (Levinson and Gutman 1987)

A number of conserved sequence motifs were identified in the control region of several pleuronectiform species (Fig 11 and 12). Some sequence blocks were more conserved than others, suggesting that these are vital in mitochondrial metabolism. Different approaches have been tried (Mignotte et al. 1987; Saccone et al. 1987), but the function of the central conserved region is not well understood. Studies of the control region in mammals (Hoelzel et al. 1991) and in X*enopus* (Wong et al. 1983) have revealed that secondary structure of sequences found in the control region are not conserved among vertebrates. This could suggest that secondary structure of RNA does not play a major role in the function of these sequences.

Codon usage bias

In this study it was observed that Atlantic halibut, Pacific halibut and Greenland halibut in four-fold degenerate codons have a non-preference for codons with guanine in third codon position. For two-fold degenerate codons there was a clear preference for one codon over the other. Here adenine or cytosine was the preferred nucleotide in third codon position. Johansen et al. (1990) also found a clear tendency to exclude guanine in third codon position. This phenomenon is observed in many other species of teleosts, from which codon usage tables are available (http://www.kazusa.or.jp/codon/Mitochondrion.html). It seems likely that some of the mechanisms mentioned in the introduction, translational efficiency and / or translational accuracy, are the cause of the observed codon bias in the three halibut species. The pattern seems too clear to be random.

Nucleotide composition

G+C content was compared between pleuronectiform species (*Hippoglossus hippoglossus, Hippoglossus stenolepis, Reinhardtius hippoglossoides, Platichtys bicoloratus* and *Paralichtys olivaceus*), Gadidae species (*Theragra chalcogramma, Boreogadus saida* and *Gadus macrocephalus*) and Salmonidae species (*Salmo salar* and *Salmo trutta*) (http://www.kazusa.or.jp/codon/Mitochondrion.html). Pleuronectiform species had a G+C content in protein coding genes of approximately 46%, Gadidae 42% and Salmonidae 46%. G +C content in 1st position in pleuronectiform species was around 53%, Gadidae 52% and Salmonidae 55%. 2nd position had a G+C content of 42% in pleuronectiform, 39% in Gadidae and 42% in Salmonidae. Pleuronectiform species had a G+C content of 45% in 3rd codon position, Gadidae 35% and Salmonidae 41%. So there seems to be a selection against a high

G+C content in protein coding genes of Gadidae species, compared to pleuronectiform and Salmonidae species. The specific reason is not known, but it seems to be less beneficial for Gadidae species to have guanine in third codon position. A possible explanation could be related to transcriptional and translational efficiency and accuracy, as mentioned above.

Lin et al. (2006) reported a G+C content in mtDNA from Asian seabass (*Lates calcarifer*) of 46,1% as high compared to many other teleosts. They suggest that a high G+C content is associated with higher temperatures in tropical waters. However, non-tropical fishes like Atlantic salmon (*Salmo salar*) (Hurst et al. 1998), Arctic charr (*Salvelinus alpinus*) (Doiron et al. 2002), Atlantic halibut, Pacific halibut and especially Greenland halibut have G+C contents in the range of 45,1% - 46,2%. A possible explanation could be that these species once originated in warmer waters and then changed their temperature niches faster than the evolution of mtDNA, given that the assumptions by Lin et al. (2006) are correct.

SNP analysis of 30 Atlantic halibut individuals

Part of ND2, COI and the control region were target for an SNP analysis in 30 Atlantic halibut individuals from the broodstock in Mørkvedbukta Research Station (Table 24). The relationship between these indviduals was not fully known beforehand. Eleven different genotypes were observed. What is interesting is that one genotype (f) appear 15 times. A possible explaination is that they are siblings or half-siblings, sharing the same mother. Aditional information about the breeding of their possible parents suggests that this is true. By also using nuclear microsatellites it would be possible to finally determine the genetic relationships. Normally one would seek to have a wide variety of genetic material in a broodstock. The use of closely related indviduals in a broodstock will eventually lead to inbreeding, i.e. inceased homozygosity, which leads to reduced larval and juvenile survival and performance (Beaumont and Hoare 2003). For this reason it is important to know the history of each individual in a breedning programme, and preferably genotype every individual to avoid inbreeding.

Phylogenetic investigation of mtDNA sequences

The focus on the three halibut species through this study will continue in the phylogenetic investigation. Their position among other known complete Pleuronectiform mtDNA genomes will be considered. The Norwegian waters normally host three different families of

Pleuronectiform species: Soleidae, Scophthalmidae and Pleuronectidae (Bethon 2005). Partial mtDNA sequence from *Solea vulgaris* (Soleidae) and *Scophthalmus maximus* (Scophthalmidae) was also determined, and the relationship between these three families will be discussed.

Results from this study suggest that Soleidae and Scophthalmidae are the most basal families. (Berendzen and Dimmick 2002) were not able to fully determine the position of Scophthalmidae, though it appears to be more basal than Soleidae. Chapleau (1993) resolved Scophthalmidae as a polytomy containing Bothidae, Paralictyidae and Pleuronectidae. So the position of these two families remain uncertain.

Paralichthyidae has been recognized as polyphyletic (Chapleau 1993; Hensley and Ahlstrom 1984). One clade was determined to be closely related to Pleuronectidae (Berendzen and Dimmick 2002). Paralichthyidae represented by *Paralictys olivaceus* was recognized as the family closest to Pleuronectidae in this study.

Within the Pleuronectidae *Platichtys bicoloratus* and *Pleuronectes platessa* formed a group. This group is recognized as Pleuronectini (Haaramo 2004), a sister group to Hippoglossini. Hippoglossini includes *Verasper variegatus*, *Reinhardtius hippoglossoides, Hippoglossus stenolepis* and *Hippoglossus hippoglossus*. The last two species appear to be very close related. They could even be separated at the sub-species level. There are 358 SNPs between Hh1 and Hs1. 1100 SNPs was found between HH1 and Rh1 (control region was excluded due to gaps). Nymark (2006) detected 877 nucleotide substitutions between Saithe (*Pollachius virens)* and Pollack (*Pollachius pollachius).* The number of nucleotide substitutions between Arctic char (*Salvelinus alpinus*) and Brook trout (*Salvelinus fontalis*) was approximately 760 (Doiron et al. 2002).

Species divergence times

Atlantic- and Pacific halibut was estimated to have separated 2 Ma, while divergence between Greenland halibut and the *Hippoglossus* genus took place approximately 6 million years ago.

One should be very careful with drawing conclusions based on estimated divergence times, but some cautious suggestions as to what caused this speciation can be made. Important geological events in the area were these species live or their ancestors might have lived include the generally warmer periods Miocene 23-5.3 Ma (Billups 2002) and Pliocene 5.3-1.8 Ma (Crowley 1991), the submergence of the Bering Strait 3.5 Ma (Vermeij 1991) and the rise of the Isthmus of Panama 3.1-3.5 Ma (Coates and Obando 1996). These events might have influenced speciation that led to the three halibut species.

Miocene was warm until 14 Ma when temperatures dropped. This happened again 8 Ma (Billups 2002). The first speciation was the separation of Greenland halibut from the ancestor of the *Hippoglossus* genus. It is difficult to tell why this happened. So possible explanations suggested here would only be speculations. One have to bear in mind that other species not included in this study could be involved in this process.

One possible mechanism behind the separation of the *Hippoglossus* genus is that the ancestor of this genus might have been able to move freely between the Atlantic- and the Pacific Ocean via the Arctic basin during the warm period of Pliocene. Speciation might have occurred when temperatures in the Arctic waters dropped too low during late Pliocene for the ancestor to inhabitat these high latitudes.

Species identification based on molecular markers

Illegal fishing could potentially be a threat to many species, specially those with a slow growth rate and long generation time, such as Atlantic halibut, Pacific halibut and Greenland halibut. Therefore, accurate species identification is a necessary part of each fishery management program as well as any conservation approach (Ludwig 2005). Morphological species identification is very difficult and unreliable when the fish has been processed into filet and other products. PCR based restriction fragment length polymorphism (RFLP) has many advantages. After establishing the species-specific restriction patterns, this approach was used to differentiate 17 Acipenseriform species by Ludwig et al. (2002). Wolf et al. (1999) were able to distinguish between several species of game fish and even closely related deer species with PCR-RFLP. The same approach was used by Graves (2001) to separate several popular fish species. He digested amplification products from ND4 and 12S/16S rRNA region in mtDNA with restriction enzymes and identified species-specific patterns. This approach should prove useful in separating between the three halibut species in this study. The regions of choice should be the control region or one of the ND genes, due to the high degree of nucleotide variability found here.

An alignment of the complete mtDNA sequence from the four individuals of Atlantic halibut, Pacific halibut and Greenland halibut revealed 27 SNPs where each species had a different nucleotide (i.e. species specific SNP). Some regions had a higher concentration of these SNPs than others. Six SNPs were found between position 3090 and 3696. By sequencing this stretch, or a part of it, one can easily determine which species the mtDNA sample belongs to.

Real time PCR (RT-PCR) is a innovative technique in molecular genetics that makes it possible to quantitative measure polymorphic DNA regions and identify SNPs at the same time. After PCR amplification, SNPs can be detected by analysing a melting-curve: The temperature is raised from somewhere between 40°C and 75°C to a the temperature were a hybridisation probe melts off the DNA. No SNP means a perfect match between DNA and probe and is indicated by a higher melting temperature. If a mutation is present the melting temperature will be lower (Reuter et al. 2005). Then one would have to identify an SNP were species 1 have a specific nucleotide (e.g. C) and species 2 and 3 have a different nucleotide from species 1 (but both the same, e.g. G). Now you have excluded or confirmed species 1. If species 1 was excluded, the process is repeated, but now with a SNP were species 1 and 2 have the same nucleotide and species 3 have a different one. Then species 2 or 3 is also ruled out, and the correct species has been identified. Two sensor probes would have to be designed according to SNP 1 and 2 to separate between three species. More possible species requires more SNPs and probes. Multiple sets of SNPs can be added depending on the degree of certainty that is required in species identification. To make sure that the SNP really is diagnostic and no intraspecific variation is found at this position, a large number of samples from each species might be needed when establishing the test.

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Appendix

A. Complete L-strand nucleotide sequence of the mitochondrial genome from Atlantic halibut 1-4, Pacific halibut 1-4 and Greenland halibut 1-4. The sequences do not yet have an accession number, but they will be submitted to Gene bank.

B. Concatamer of all available mtDNA sequence from European plaice, Turbot and Common sole. L-strand.

C. Part of the results from this thesis was used in a poster presentation:
Kenneth A. Mjelle, Tor E. Jørgensen, Bård O. Karlsen, Steinar D. Johansen and Truls Moum 2006. Genetic markers in Atlantic halibut: Tools for breeding success.

The poster was presented at the 2006 Winter Meeting of the Norwegian Biochemical Society

Hippoglossus_hippoglossus_1 17546 bp

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   1 GCTAACGTAG CTTAATTAAA GCATAACACT GAAGATGTTA AGATGGGCCC TAGAAAGCCC
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 121 AGTATCCGCC CCCCTGTGAG AATGCCCACA ACTCCCTGCT TGGGAACTAG GAGCCGGTAT
 181 CAGGCACAAG CCCAGCTAGC CCACGACGCC TTGCTTAGCC ACACCCTCAA GGGAACTCAG
 241 CAGTGATAAA TATTAAGCCA TAAGTGAAAA CTTGACTTAG TTAAGGTTAA GAGGGCCGGT
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 361 AGAGTGGTTA GGGGATTTAC TAAACTAGAG CCGAACGCTT TCAAAGCTGT TATACGCACC
 421 CGAAAGTATG AAACCCAATT ACGAAAGTAG CTCTACTCAT CCTGAACCCA CGAAAGCTAA
 481 GAAACAAACT GGGATTAGAT ACCCCACTAT GCTTAGCCCT AAACATCGAT TGCACTATAC
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 661 TCTTGTTTTA TCCGCCTATA TACCACCGTC GTCAGCTTAC CCTGTGAAGG CTTTACAGTA
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Hippoglossus stenolepis 1 17841 bp

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Hippoglossus stenolepis 2 17841 bp

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Hippoglossus stenolepis 3 17963 bp

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Hippoglossus stenolepis 4 17902 bp

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Reinhardtius hippoglossoides 2 18139 bp

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Reinhardtius hippoglossoides 3 17895 bp

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Genetic Markers in Atlantic Halibut: Tools for Breeding Success

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The Background

Animal mitochondrial DNA (mtDNA) is maternally inherited and supposedly lacks recombination. It is a useful genetic marker for intraspecific studies, due to its small size and conserved gene content, yet high nucleotide substitution rate.

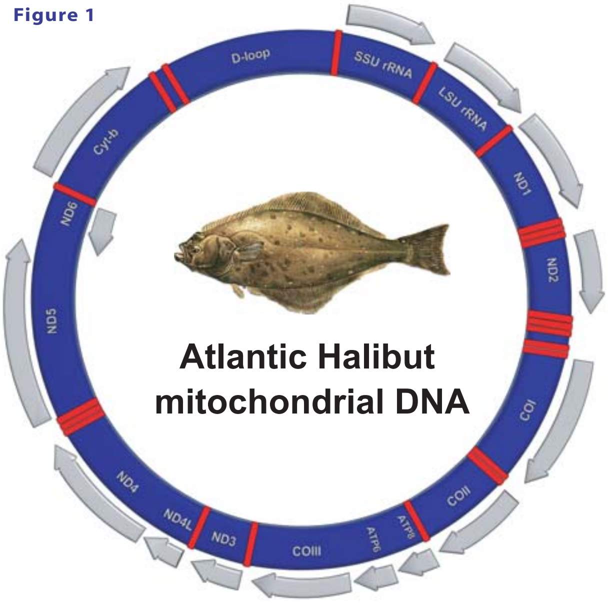
The aim of the project is to identify single nucleotide polymorphisms (SNPs) among Atlantic halibut (*Hippoglossus hippoglossus*) mitochondrial genomes. We screen for SNPs by determining the complete primary DNA sequence of the mitochondrial genome in four Norwegian halibut individuals.

The Results

The Genome

The mitochondrial genome of Atlantic halibut has a typical vertebrate gene content and organization. It contains the usual 13 protein coding genes, 22 tRNA genes, two rRNA genes, a noncoding control region, and short intergenic spacers (Fig. 1). The genome size is approximately 17400 bp and varies slightly due to a variable number of tandem repeats in the control region.

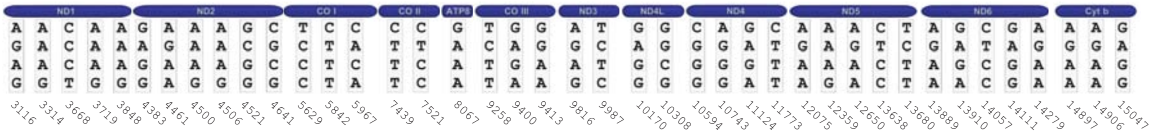
Figure 1



The SNPs

The sequence analyses revealed SNPs in all of the 13 protein coding genes except ATPase 6. Fig. 2 shows the distribution of 42 SNPs found among the four halibut individuals. The ND1 and ND2 genes seem to contain clusters of SNPs that may provide a target for further analyses. A larger sample of halibuts will be screened for SNPs along the complete mitochondrial genome.

Figure 2



	ND1					ND2						CO I			CO II		ATP8
Halibut 1	A	A	C	A	A	G	A	A	A	G	C	T	C	C	C	C	G
Halibut 2	G	A	C	A	A	A	G	A	A	C	G	C	T	A	T	T	A
Halibut 3	A	A	C	A	A	G	A	A	A	G	C	C	T	C	T	C	A
Halibut 4	G	G	T	G	G	G	A	G	G	G	G	C	T	A	T	C	A
Position	3116	3314	3668	3719	3848	4383	4461	4500	4506	4521	4641	5629	5842	5967	7439	7521	8067

	CO III			ND3		ND4L		ND4				ND5					ND6					Cyt b		
Halibut 1	T	G	G	A	T	G	G	C	A	G	C	A	A	A	C	T	A	G	C	G	A	A	A	G
Halibut 2	C	A	G	G	C	A	G	G	G	A	T	G	A	G	T	C	G	A	T	A	G	G	G	A
Halibut 3	T	G	A	A	T	G	C	G	G	G	T	A	A	A	C	T	A	G	C	G	A	A	A	G
Halibut 4	T	A	A	G	C	G	G	G	G	A	T	A	G	A	C	T	A	A	C	G	A	A	A	G
Position	9258	9400	9413	9816	9987	10170	10308	10594	10743	11124	11773	12075	12359	12650	13638	13680	13889	13910	14057	14111	14279	14897	14906	15047

The Conclusion

The mitogenomics approach is used to investigate the molecular evolution of the mitochondrial genomes and develop genetic markers to be applied in marine ecology, i.e. to investigate population relatedness, introgression events and dispersal histories. Also, assessments of inter- and intraspecific genetic variations of Atlantic halibut and related species are important for halibut breeding. Mitochondrial SNPs should prove useful as a fast screening and diagnostic tool in breeding programs.

Aknowledgement

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