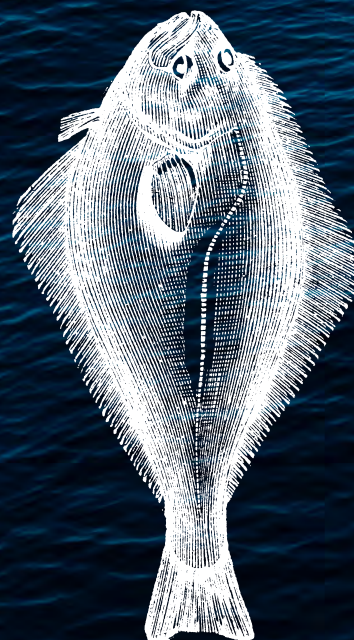


Genetic Fact Sheet

→ Greenland Halibut *Reinhardtius hippoglossoides*



2022





PANDORA

Paradigm for Novel Dynamic
Oceanic Resource Assessments

Gant agreement No: **773713**

Funded by the European Commission within the Horizon 2020 Programme

Genetic Fact Sheets

Review of available genetic information
on population structuring in exploited species

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The Blue Growth of European fisheries is at risk due to over-exploitation, unforeseen changes in stock productivity, loss of markets for capture fisheries due to aquaculture, future trade agreements opening European markets to external fleets, and fluctuations in the price of oil and other business costs. All of these risks need to be considered when providing advice needed to sustainably maximize profits for the diverse array of fisheries operating in European waters and to help safeguard the benefits this sector provides to the social coherence of local, coastal communities.

PANDORA aims to:

1. Create more realistic assessments and projections of changes in fisheries resources (30 stocks) by utilising new biological knowledge (spatial patterns, environmental drivers, food-web interactions and density-dependence) including, for the first time, proprietary data sampled by pelagic fishers.

2. Advise on how to secure long-term sustainability of EU fish stocks (maximum sustainable/"pretty good" and economic yields) and elucidate tradeoffs between profitability and number of jobs in their (mixed demersal, mixed pelagic and single species) fisheries fleets. Provide recommendations on how to stabilize the long-term profitability of European fisheries.

3. Develop a public, internet-based resource tool box (PANDORAs Box of Tools), including assessment modelling and stock projections code, economic models, and region- and species-specific decision support tools; increase ownership and contribution opportunities of the industry to the fish stock assessment process through involvement in data sampling and training in data collection, processing and ecosystem-based fisheries management.

The project will create new knowledge (via industry-led collection, laboratory and field work, and theoretical simulations), new collaborative networks (industry, scientists and advisory bodies) and new mechanisms (training courses and management tools) to ensure relevance, utility and impact.

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List of abbreviations

GFCM	General Fisheries Commission for the Mediterranean
ICES	International, Council for the Exploration of the Sea
IUCN	International Union for Conservation of Nature
IUU	Illegal, Unreported and Unregulated
MSY	Maximum sustainable yield
SAC	Scientific Advisory Committee
STECF	Scientific, Technical and Economic Committee for Fisheries
SD	Subdivision
TAC	Total Allowable Catch

North-East Atlantic ICES subareas, divisions and subdivisions

- 1) Subarea 1 – Barents Sea
- 2) Subarea 2 – Norwegian Sea, Spitzbergen and Bear Island
- 3) Subarea 3
 - Division 3.a, Skagerrak (subdivision 20) and Kattegat (subdivision 21)
 - Division 3.b-c, Sound (subdivision 23) and Belt Sea (subdivision 22)
 - Division 3.d, Baltic Sea (subdivisions 24-32)
- 4) Subarea 4 – North Sea (divisions 4.a-c)
- 5) Subarea 5 – Iceland (division 5.a) and Faroes Grounds (division 5.b)
- 6) Subarea 6 – West of Scotland (division 6.a) and Rockall (division 6.b)
- 7) Subarea 7
 - Irish Sea (division 7.a), West of Ireland (division 7.b), Porcupine Bank (division 7.c)
 - Eastern English Channel (division 7.d), Western English Channel (division 7.e)
 - Bristol Channel (division 7.f), Celtic Sea (divisions 7.g-h), Southwest of Ireland (divisions 7.i-k)
- 8) Subarea 8
 - North and Central Bay of Biscay (divisions 8.a-b)
 - South Bay of Biscay (division 8.c)
 - Offshore Bay of Biscay (division 8.d), West of Bay of Biscay (division 8.e)
- 9) Subarea 9 (Portuguese Waters)
- 10) Subarea 10
 - Azores Grounds (division 10.a) and Northeast Atlantic South (division 10.b)
- 11) Subarea 11 (incorporated in FAO Fishing Area 34)
- 12) Subarea 12 North of Azores
 - southern mid-Atlantic Ridge (division 12.a)
- 13) Subarea 13 (incorporated in FAO Fishing Area 34)
- 14) Subarea 14 East Greenland, Northeast Greenland (14.a), Southeast Greenland (14.b)

How to read the factsheets

Genetic structure factsheets are presented for each species. Current knowledge on genetic population structure is summarised and compared with stock units used in assessment and management. The presence of mismatches is emphasised as well as priorities for future work. At the beginning of the factsheets, a summary is presented with green-yellow-red color symbols for 'Population structure', 'Match between genetic and stock assessment units' (units for which scientific advisory bodies, as ICES and the GFCM, provide advice on stock status and fishing opportunities), 'Match between genetic and management units' (units for which TACs are set by the European Council), 'Match between stock assessment and management units'. The information in the factsheet is organized in the following sections:

Distribution: general information can be found on the distributional range of the species, with a focus on the NE Atlantic, Mediterranean and Black Sea.

Current management status: an overview is provided on the current management and assessment units present for the species in European Seas. The importance of the species for each fishery is included, reporting if the species is mainly a by-catch or if direct fishery exists for the stocks. A mismatch between stock assessment and management units already exists for certain species and it is showed in Table 2.

Genetic population structure in a nutshell: provides the key take-home messages, both in terms of current knowledge on genetic population structure and in terms of priorities for future work. In this section, an overall picture of population structure of the species is given, based on considerations on the type of markers, sampling designs and findings of the included studies. It is also discussed if genetic evidence supports the stock assessment and management units currently in use.

Mismatch: in this section the mismatch between genetic and stock assessment/management units is highlighted. Two types of mismatch can be observed. Here, we refer to 'Type I' mismatch when a genetically homogeneous population is assessed/managed in multiple stock units (oversplitting); while we refer to 'Type II' mismatch when genetically different populations are wrongly considered part of the same stock assessment/management unit (undersplitting).

Summary of genetic evidence: in this section a more detailed summary of the studies is provided in a chronological way. In general, the type of genetic markers used by different studies depends on the widely available markers at the time. Early studies used allozymes and often reported a lack of differentiation among sample locations. However, later studies using the more highly polymorphic microsatellites and SNPs showed presence of differentiation even in areas where it was not previously detected. Conversely, in other cases presence of differentiation was reported at few allozyme loci, not confirmed

subsequently with strictly neutral markers. This and other contradictions between studies were addressed if possible. Advances in sequencing technology, as well as the use of more sophisticated statistical analysis and sampling design to maximise the detection of population structure have made enormous changes in the awareness we have of genetic structure in marine fish species (Hauser and Carvalho, 2008). Most of the mismatches found in initial studies between genetic population structure and stock assessment and management units were due to a lack of differentiation reported between samples assessed/ managed in different units (referred to as 'Type I' mismatch in Table 1). However, these mismatches are often solved by more recent investigations, that applied highly polymorphic markers, as well as a sampling design that maximise the chance of detecting population structure, i.e. collecting individuals in spawning aggregations. Particular emphasis should be placed on the sampling season and individuals included in the analysis that are extremely important factors for the detection of population structure in marine fish species (Nielsen et al. 2009b). Moreover, despite in previous studies a neutral background of low differentiation was commonly detected, recently the application of markers under selection allowed the detection of high levels of differentiation and occurrence of locally adapted populations. Therefore, a summary of genetic studies found in literature is provided. For each study, sampling design, temporal and spatial analyses and markers used have been critically evaluated. Strengths and shortcomings of the available studies are reported and based on these considerations an overview is given.

Table 2.1. Summary table of available information on genetic population structure and match between genetic, assessment and management units of commercial fish species exploited in the NE Atlantic, Mediterranean and Black Sea.

Species	No. Studies	Population structure	Match genetic-Stock assessment units	Match genetic-management units	Match stock assessment-management units	IUCN status
Greenland halibut, <i>Reinhardtius</i> <i>hippoglossoides</i>	7	yes	no	no	no	NT

IUCN Abbreviations: NE= Not evaluated, DD= Data Deficient, LC= Least Concern, NT= Near Threatened, VU= Vulnerable, EN= Endangered, CR= Critically Endangered. Eu= Europe, Glo= Global, Med= Mediterranean (IUCN 2021).

FACT SHEET

Greenland halibut, *Reinhardtius hippoglossoides*

Number of studies	7
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗



Distribution¹

Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum, 1792), is a deep-water flatfish species widely distributed in the northern hemisphere, both in the Atlantic and the Pacific Ocean. In the North-East (NE) Atlantic it is commonly found in the Barents Sea, the Norwegian Sea and in Icelandic and Faroese waters. In the North-West (NW) Atlantic, the distribution extends from the Arctic Ocean, along Canada and Greenland, southward to the Scotian Shelf.

Current management status

ICES currently recognize two stocks of Greenland halibut in the NE Atlantic (Figure 3.1), the northeast Arctic stock in subareas 1 and 2 (ghl.27.1-2) and the West Nordic stock in subareas 5, 6, 12, and 14 (Iceland and Faroes grounds, West of Scotland, North of Azores, East of Greenland) (ghl.27.561214). The annual catches for the northeast Arctic stock in 2019 were 28832 t and exceeded the ICES advice of 23000 t (ICES 2020g). Catches from the northern North Sea (division 4a) were not included in landings of the northeast Arctic stock due to a lack of information on the origin of fish caught in this region. Further investigations are needed to understand whether Greenland halibut inhabiting the northern North Sea are part of the northeast Arctic stock, or rather represent a locally distinct population.

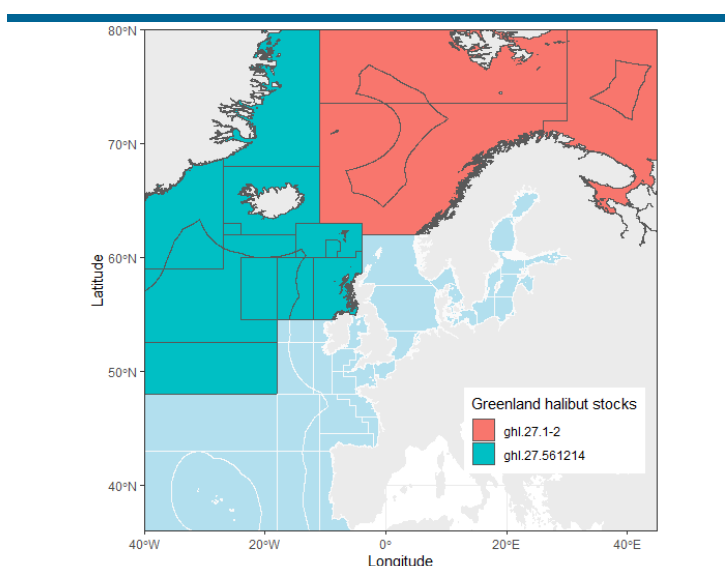


Figure 3.1 Greenland halibut ICES stock assessment units

¹ Further details on symbols and how to read the factsheet are provided on page 16

Genetic population structure in a nutshell

The available genetic information (Table 1) confirms the presence of population structure in the North Atlantic suggesting a management based on at least two separate stocks of Greenland halibut. Further studies including samples from the southern and eastern part of Iceland, the Faroe Islands and the northern North Sea would help to further investigate the population structure also in these areas with more advanced and informative techniques. Some studies (Vis et al. 1997, Igland & Nævdal 2001, Roy et al. 2014) did not find any differentiation, but a broader SNP panel and inclusion of samples collected in spawning season allowed the detection of differentiation in the North Atlantic and a potential barrier across the David Strait (Westgaard et al. 2017a).

Mismatch

Mismatch between assessment units and genetic structure was found between the Southeast Greenland and Faroe Islands (Knutsen et al. 2007), currently considered part of the same stock assessment unit (Table 2). Also the genetic structure found using SNPs (Westgaard et al. 2017a) does not match with the stock assessment units: in fact, the presence of two populations was demonstrated, one in the western part that includes the samples from Canada, Iceland, south-eastern and western Greenland and an eastern population that includes samples from the Norwegian slope, Svalbard and northern east Greenland, clearly showing a mismatch with the stock units currently in use.

Summary of genetic evidence

Several studies reported the presence of a mismatch between the current stock assessment units and the genetic population structure of the species in the NE Atlantic (e.g. Knutsen et al., 2007; Westgaard et al., 2017) (Table 1), supported additionally using other methods. For instance, a recent study based on tagging (Albert & Vollen 2015) suggested that the waters off Svalbard represent a common nursery ground for two stocks. Hence, their separation into two stock assessment units is not supported. The results of that study also advocate a stock boundary shift in the NE Atlantic.

In the North Atlantic, genetic population structure of Greenland halibut has been studied by means of different genetic markers (Table 1). Initially, using sequences of the cytochrome b gene (mtDNA), Vis et al. (1997) analysed samples of Greenland halibut from 7 locations across the North Atlantic and concluded that gene flow occurs among populations in the North Atlantic and is sufficient to prevent genetic differences among putative stocks. Likewise, Igland and Nævdal (2001) using allozymes were not able to detect genetic differentiation among 6 samples from the North Atlantic. The latter study, however, did not include samples collected in spawning season, which could affect observations of proposed population homogeneity.

In contrast to earlier findings, Knutsen et al. (2007) detected a statistically significant level of genetic differentiation across the North Atlantic ($F_{ST} = 0.0018$, $p < 0.0001$), and showed the existence of one population in the East and one in the West Atlantic. Furthermore,

significant differentiation was reported between eastern Greenland and the Faroe Islands samples, that are currently part of the same stock assessment unit (Table 2). However, Roy et al. (2014) were not able to reject the hypothesis of panmixia (population similarity) and hence to support the division into separate stocks, though the study focused on the North West Atlantic represented by only one sample from eastern Greenland.

Westgaard et al. (2017) detected significant population structure and the subdivision into two stocks of the North Atlantic, an eastern and western stock with a panel of 96 SNPs. Although, the level of differentiation reported is low ($F_{ST} = 0.003$, $p < 0.001$), the overall differentiation is highly significant even when outlier loci were removed from the analysis ($F_{ST} = 0.002$, $p < 0.001$). A potential barrier between the two stocks in the Atlantic was identified by a landscape genetics technique between Iceland, south-eastern and western Greenland (that were included in the western Atlantic unit) and the northern east Greenland sample that grouped with the eastern samples.

Table 1. Summary table of genetic population structure studies of commercial marine fish species exploited in the North-East Atlantic Ocean, Mediterranean and Black Sea.

Species	Region	Sampling locations	No. Samples (Number of individuals)	Spawning	Maturity	Life stage	Genetic Marker	Differentiation	Mismatch genetic-SA	Mismatch genetic-MZ	LA, LG, MSA	Reference
Greenland halibut	North Atlantic	NWA (5), ICE (1), NOR (1)	7 (280)	na	na	na	Cyt-b (401 bp)	No	Type I	Type I		(Vis et al. 1997)
	North Atlantic	GRL (2), SJM (1), BS (1), FRO (1), SHE (1)	6 (745)	na	na	na	All (3)	No	Type I	Type I		(Igland & Nævdal 2001)
	North Atlantic	CAN (1), GRL (1), FRO (1), BS (2), NOR (1), SJM (1)	7 (639) *	y	y	Ad, juv	Msat (9)	Yes	Type II	Type II	LG	(Knutsen et al. 2007)
	North Atlantic	NWA (20), GRL (3), NOR (1)	24 (1676) *	y	y	Ad, juv	Msat (12) ^N	No	Type I	Type I	LG	(Roy et al. 2014)
	North Atlantic	GRL (2), Arctic (2), Pacific (3)	7 (323)	y	y	Ad	Msat (7)	Yes	na	na		(Orlova et al. 2017)
	North Atlantic	CAN (1), GRL (3), ICE (1), NOR (2), SJM (1)	8 (384)	y	y	Ad	SNPs (96) ^S	Yes	Type II	Type II	LG	(Westgaard et al. 2017a)
	North Atlantic	GRL (2), Arctic (2), Pacific (3)	7 (323)	y	y	Ad	Msat (8); Cyt-b (615 bp)	Yes	na	na		(Orlova et al. 2019)

The following abbreviations are used for the geographic locations: North-East Atlantic (NE Atlantic), Mediterranean Sea (Med), Northwest Atlantic (NWA), Adriatic Sea (Adr), Aegean Sea (Aeg), Africa (AFR), Alboran Sea (Alb), Atlantic (Atl), Atlantic Iberian (Atl IB), Australia (AU), Azores (Azo), Baltic Sea (BAL), Barents Sea (BS), Bay of Biscay (BOB), Black Sea (BLS), British Isles (BI), Canada (CAN), Canary (Cn), Cantabrian Sea (Cant), Celtic Sea (CS), English Channel (EC), Faraday Seamount (Far), Faroe Islands (FRO), fjord (fj), Galicia (Gal), Greece (GRC), Greenland (GRL), Gulf of Cadiz (GC), Gulf of Lion (GoL), Hebrides (Heb), Iceland (ICE), Ionian Sea (Ion), Ireland (IRE), Irish Sea (IS), Irminger Sea (Irm), Kattegat (Kat), Lake Mogilnoe (Mog), Lofoten (Lof), Madeira (Mad), Marmara Sea (MS), Mid-Atlantic Ridge (MAR), Morocco (MOR), Namibia (Nam), New Zealand (NZL), Newfoundland and Labrador (NL), North Sea (NS), North Sea-Baltic Sea Transition zone (NBTZ), Norway (NOR), Nova Scotia (Nov), Porcupine Bank (Por), Portugal (PRT), Reykjanes Ridge (Reyk), Rockall Bank (Roc), Russia (RUS), Scotian Shelf (SS), Scotland (SCO), Shetland (SHE), Sicily (SIC), Skagerrak (Ska), Spain (SPA), Svalbard and Jan Mayen (SJM), Tasman Sea (TS), Tunisia (TUN), Tyrrhenian Sea (Tyr), White Sea (WS); north (n), south (s), east (e), west (w), central (c); Norwegian Coastal Cod (NCC), North-East Arctic Cod (NEAC).

For each study the species, sampling locations (for abbreviations see below) and in brackets the number of samples are shown; the total number of samples and individuals analysed is reported, as well as the number of temporal replicates in superscript or (*) if multiple temporal replicates are included. The spawning, maturity and life-stage of samples included are summarised as follow, *Spawning*: y= if samples collected in spawning season/grounds are included, na= not available, no= samples outside spawning season/grounds. *Maturity*: y= mature individuals included; na= maturity not available; no= immature individuals. *Life-stage*: Ad= adult; juv= juveniles; lar= larvae; eg= eggs; na= not available. Genetic markers (All= allozymes; Msat= microsatellites; Minisat= minisatellites; SNPs= Single Nucleotide Polymorphisms; mtDNA= mitochondrial DNA; Cyt-b= cytochrome b; COI= Cytochrome c Oxidase subunit I; COIII= Cytochrome c Oxidase subunit III; CR= Control Region; RAPD= Random Amplified Polymorphic DNA); number of loci or base pairs analysed in brackets, in superscript S= if at least one locus is under selection, N= neutral markers (only if neutrality was tested). Differentiation, if genetic differentiation was detected (Yes, No). Mismatch genetic- SA= mismatch of the genetic units found and the stock assessment units. Mismatch genetic- MU = mismatch of genetic units with the management units. We refer to 'Type I' mismatch when a genetically homogeneous population is assessed/managed in multiple stock units (oversplitting); while we refer to 'Type II' mismatch when genetically different populations are wrongly considered part of the same stock assessment/management unit (undersplitting). LA= Local Adaptation, LG= Landscape Genetics, MSA= Mixed Stock Analysis.

Table 2. Mismatch between stock assessment (SA) units and genetic population structure (Type I and II explained) and mismatch between management

Species	Stock assessment unit	Mismatch SA unit - genetics (Type II)	Mismatch SA unit - genetics (Type I)	Management units	Mismatch management unit - genetics
Greenland halibut, <i>Reinhardtius hippoglossoides</i>	ghl.27.1-2	Genetic unit in Norwegian slope, Svalbard and northern east Greenland (Westgaard et al., 2017)	No differentiation between GRL and NOR (Roy et al. 2014)	- 2a ^U , 4; 5b, 6 ^{U, I} - 1, 2 ^N - 1, 2 ^I	No differentiation between GRL and NOR (Roy et al. 2014); FRO different from NOR (Knutsen et al. 2007);
	ghl.27.561214	Differentiation between GRL and FRO (Knutsen et al. 2007); Genetic unit in Iceland, south-eastern and western Greenland (Westgaard et al., 2017)		- 5,12,14 ^G	Northeast GRL and ICE differentiated (Westgaard et al., 2017)

and genetic units.