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Genetic Fact Sheets

Review of available genetic information on population structuring in exploited species

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PANDORA

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Genetic Fact Sheets

Review of available genetic information on population structuring in exploited species

Sara Maggini
Alexander Papadopulous
Gary Carvalho
Einar Eg Nielsen
Ernesto Jardim
Jann Th. Martinsohn

Bangor University (UK)
School of Natural Sciences

PANDORA Project

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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1 Contents

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 27.7.j-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 (Portoguese 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
    - souther 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)

2 Executive summary

Across European waters, dramatic differences exist in the biology, ecology and status of fish stocks, as well as the amount and quality of data available for their assessment. PANDORA is designed to provide new biological knowledge on fish and their ecosystems, integrate that knowledge to build more robust tools to assess the future status of fish stocks, and improve science-based advice to fisheries management for maximizing the long-term, sustainable exploitation and Blue Growth of Europe's fisheries resources. PANDORA addresses the most urgent needs of fisheries management and its various fleets in each of five Case Study areas to provide a step change in Europe's ability to support productive fisheries, boost employment and profits in the sector and promote European food security.

The match between biological processes and management actions is essential to assure sustainable exploitation of natural resources (Reiss et al. 2009). In this report, we reviewed available information on the genetic population structure for marine fish species that are exploited in European Seas. Further, we evaluated the extent to which this information has been included in the definition of stock units used in assessment and management.

The idea that marine fish species should be managed at a subspecific level dates to the beginning of the last century, when Heincke and Hjort introduced the local self-sustaining population, rather than the species, as unit of study in fisheries (Hauser and Carvalho, 2008; and references therein). The '*stock*' was identified as the unit for the assessment and management of exploited fish species. Although *stock* is a term frequently used in fisheries, to date, there is no consensus on a universally applicable definition (Carvalho & Hauser 1994). The numerous definitions of stock present in fisheries depend mainly on who is defining it and why - for management, assessment or conservation aims and all the socio-economic and conservationist interests implied (Carvalho & Hauser 1994).

Wild-capture fisheries is the last large-scale hunting activity, targeting a natural renewable living resource. It is extremely important that a management system exists, which promotes sustainable exploitation of marine fish species in the long-term and, at the same time, conserves marine biodiversity and ecosystems. Ideally, in the framework of sustainable fisheries management, the stock units used for assessment and management should coincide with biologically defined units which can be delineated by the within species population structure estimate from genetic data (or alternative biological information). However, since assessment and management units in the North-East (NE) Atlantic are based on ICES fishing areas originally established for statistical purposes, often a mismatch between genetic units, assessment units and management units occurs (Reiss et al. 2009).

The main instrument in fisheries management is the setting of annual Total Allowable Catches (TACs), which are catch limits (expressed in tonnes) that are shared among countries as national quotas. TACs in Europe, also referred to as fishing opportunities, are set annually by the Council of Fisheries Ministers for the majority of stocks and every two years for deep-sea stocks. Scientific advice on stock status and appropriate catch levels are used as a basis for setting annual TACs by the Council (Casey et al. 2016). In Europe, fisheries management is based on scientific advice provided by several advisory bodies; the International Council for the Exploration of the Sea (ICES), the Scientific Advisory Committee (SAC) of the General Fisheries Commission for the Mediterranean (GFCM), and the Scientific, Technical and Economic Committee for Fisheries (STECF) (Casey et al. 2016). In the NE Atlantic, stock assessment is carried out by ICES for stock units that correspond to different combinations of ICES statistical subareas and divisions (Figure 2.1 and Figure 2.2), while fisheries management is based on management units for which TACs are set by the Council. Mismatches already exist between assessment and management units (unit for which TACs are set) for certain fish species (Reiss et al. 2009). According to the definition provided by ICES, a stock is "a part of a fish population usually with a particular migration pattern, specific spawning grounds and subject to a distinct fishery; in theory, a Unit Stock comprises all the individuals of fish in an area, which are part of the same reproductive process". However, the stock units underpinning assessments are also defined based on data availability and other practical considerations. This is why ICES stock assessment units do not necessarily agree with self-sustaining populations.

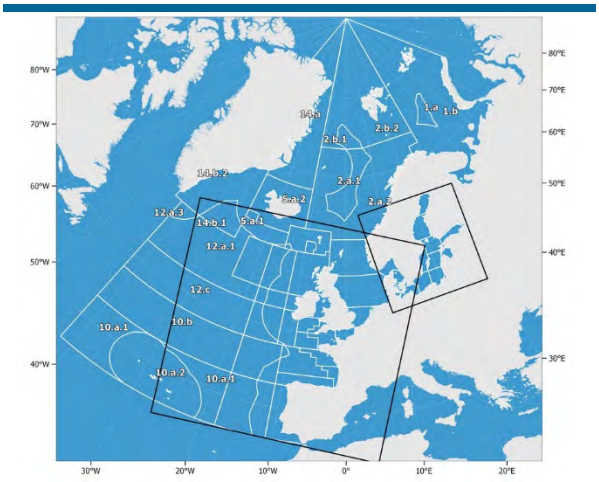


Figure 2.1 North-East Atlantic fishing area (FAO 27), subareas and divisions.

If the stock units used in assessment and management fail to acknowledge the actual population structure of the species, a mismatch between the stock assessment and management units and biological units occurs. A mismatch implies that the wrong population structure is being assumed. This can cause sub-optimal management measures, reducing productivity and, ultimately, lead to unsustainable fisheries. For instance, if more than one population is assessed and managed as a stock, the extinction of subpopulations would be possible even if the data aggregated would not indicate a population decline (Frank & Brickman 2000). The management of two different populations as one stock unit can lead to overfishing of the less productive population, and in the extreme scenario, to the depletion of the resource and the loss of genetic

diversity with it (Hutchinson et al. 2003, Reiss et al. 2009). Genetic analysis can assist in the design of appropriate stock units that reflect the genetic population structure of the species and are essential to conserve genetic diversity, thus, avoiding the loss of locally adapted populations. In natural populations, the conservation of genetic diversity is crucial to avoid the risk of local population extinction and with it the ability of the species to adapt to environmental changes and challenges. Indeed, several studies of shifts in species distributions as a result of climatic change have underscored the importance of maintaining genetic diversity and the adaptive capability of exploited fish species (e.g. Bonanomi et al., 2015).

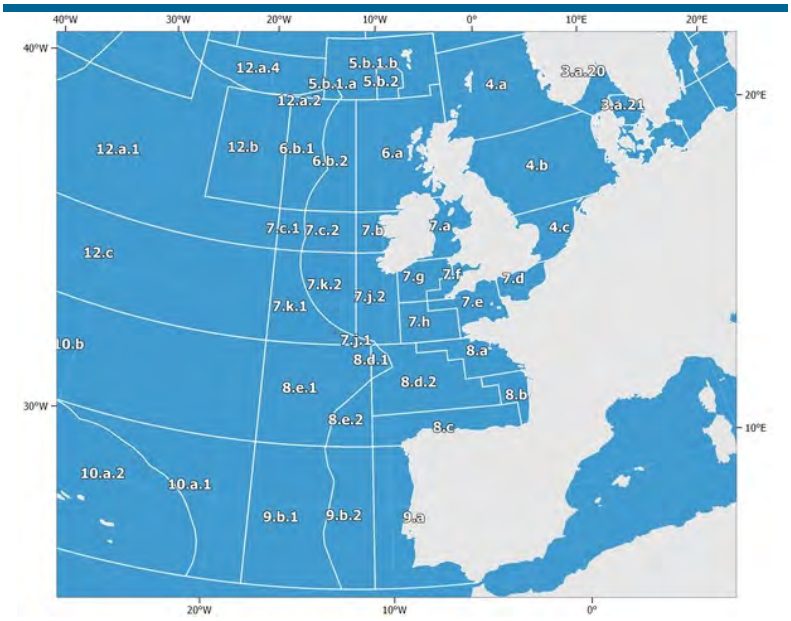


Figure 2.2. Detailed boundaries of divisions of the ICES subareas 27.4 - 27.9.

Mismatches between stock assessment, management and genetic units exist in the NE Atlantic and were reviewed in 2009 (Reiss et al. 2009). After a decade of huge technological advances in genetics, it was necessary to review genetic evidence of population structure in light of new studies that used more powerful markers and sophisticated statistical analyses. Here, we reviewed available data on genetic population structure for marine fish species exploited in the NE Atlantic, Mediterranean and Black Sea and compared it with assessment and management units. A summary of genetic population structure is given for each species. Moreover, it is evaluated whether genetic evidence supports the current stock assessment and management units or not, and mismatches are reported, if present.

Hence, the aim here is to provide an overview of the implementation of genetics into stock assessment and management and, at the same time, to identify species and areas where the implementation of genetics could be beneficial for a more sustainable management. Suggestions are provided whether it is possible to include knowledge of genetic population structure to design biologically more meaningful units in order to improve fisheries assessment and management and maximizing the long-term sustainable exploitation of marine fish stocks.

Advances in sequencing technology, as well as the use of a new generation of genetic markers, statistical analysis and sampling design to maximise the detection of population structure have considerably improved our knowledge about genetic structure

in marine fish species. 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. However, these mismatches are often resolved 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. When studying population structure in marine fish species the sampling season, life-stage of individuals included and markers used in the analysis are extremely important aspects to take into consideration (Nielsen et al. 2009b). Recently, the application of markers under selection allowed the detection of high levels of differentiation and occurrence of locally adapted populations despite the neutral background of low differentiation commonly detected in early studies.

Differences exist in available genetic information on population structure in marine fish species exploited across European waters (Table 2.1). Overall, we found that highly important commercial fish species, as Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus*), turbot (*Scophthalmus maximus*), European hake (*Merluccius merluccius*), common sole (*Solea solea*), flounder (*Platichthys* spp.) and plaice (*Pleuronectes platessa*) have more investigations than less commercially important species (Figure 2.3). Six species still lack genetic studies on population structure (Table 1). Likewise, extremely limited information exists for other species (i.e. dab, brill and pollack). For instance, this is evident in the case of pollack (*Pollachius pollachius*) for which only one exploratory study was conducted in 2006 and absence of genetic differentiation was reported. Additionally, for relatively well studied species there are regions of the distributional range that have not been analysed, yet. In general, a lack of information is particularly risky for species that are currently exploited both in directed fishery or as by-catch, and further investigations are required to address these knowledge gaps.

Evidence of genetic population structure exists for the other species (Table 2.1). However, for most of the reviewed species available information on genetic population structure has not been entirely considered in stock assessment/management resulting in mismatches (Table 2). Among the flatfish species, a lack of data is reported for lemon sole (*Microstomus kitt*) and witch (*Glyptocephalus cynoglossus*) that do not have studies on genetic population structure, and extremely limited information is available for brill and dab. Whereas, genetic information on population structure is available for Greenland halibut (*Reinhardtius hippoglossoides*), megrims (*Lepidorhombus spp*.), European and Baltic flounder (*Platichthys flesus, Platichthys solemdali*), plaice, sole and turbot. Different types of mismatches are reported for these species and genetics could be taken into account for a more sustainable assessment and management.

Among the gadoids, no studies have been found for blue ling (*Molva dypterygia*), greater forkbeard (*Phycis blennoides*) and roughsnout grenadier (*Trachyrincus scabrus*). Mismatches are reported between genetic population structure and current

assessment/management units for blue whiting (*Micromesistius poutassou*), European hake, haddock (*Melanogrammus aeglefinus*), ling (*Molva molva*), tusk (*Brosme brosme*), saithe (*Pollachius virens*), whiting (*Merlangius merlangus*), roughhead grenadier (*Macrourus berglax*) and roundnose grenadier (*Coryphaenoides rupestris*).

The existing literature exploring genetic population structure of Atlantic cod is extensive, resulting in the inclusion of 106 studies. Hence, a separate section is dedicated to Atlantic cod, the most studied marine fish species included in this review.

Among the pelagic species, genetic information on population structure is available for capelin (*Mallotus villosus*), Atlantic horse mackerel (*Trachurus trachurus*), blue jack mackerel (*Trachurus picturatus*), Atlantic mackerel (*Scomber scombrus*), European sprat (*Sprattus sprattus*) and Atlantic herring (*Clupea harengus*). Notably, European sprat is an excellent example of how genetic population structure can be integrated in fisheries assessment to define more biologically meaningful unit, in only a decade. The first genetic study was published in 2008 and in 2018 genetic evidence was used to revise the European sprat stock assessment units by ICES.

With regard to the remaining fish species, mismatches are present for the black-bellied (*Lophius budegassa*) and the white anglerfish (*L. piscatorius*), the golden redfish (*Sebastes norvegicus*), the blackspot seabream (*Pagellus bogaraveo*) and orange roughy (*Hoplostethus atlanticus*). Genetic structure is mostly considered in the definition of the Beaked redfish (*Sebastes mentella*) stock assessment units. A lack of studies focusing on the NE Atlantic was found for the striped red mullet (*Mullus surmuletus*).

Red List Categories

2.1 Approach

A review of available information on genetic population structure for marine fish species exploited in European Seas is provided. The genetic units found were compared with the stock assessment and management units to evaluate whether genetic population structure has been taken into account in their definitions. We refer to stock assessment units as the units for which scientific advisory bodies (e.g., ICES and the GFCM) provide advice on stock status and fishing opportunities. We refer to management units as the unit for which TACs are set by the European Council (EU 2020). A list of stocks assessed in the NE Atlantic can be found on the ICES website. Here, factsheets for commercial fish species are presented.

A systematic review was conducted to identify, extract and evaluate the available genetic information on population structure for marine fish species exploited in the NE Atlantic, the Mediterranean and Black Sea. Subsequently, information on genetic population structure has been compared with stock assessment and management units to appraise whether it is utilised in current stock definitions. Bibliographic databases used for searching relevant literature were Web of Science and Scopus. For each fish species, a separate search was conducted consisting of a common search string ('genetic* OR genomic*', 'population structur*', 'F-st OR F-statistics OR fixation ind*', 'local adaptation') and the common and scientific name of the species. By scrutinising the bibliography of, and studies which cited, key publications, additional studies were included. After removing the duplicates and screening the papers to include only those describing genetic population structure for the species of interest, relevant information was extracted from each study. A summary of genetic population structure studies included can be found in Table 1. From each study the following information were extracted:

- sampling design (sample locations, number of samples and temporal replicates, number of individuals analysed, spawning season or ground, maturity and life-stages);
- genetic markers, the number of loci (or base pair in case of DNA sequences), the neutrality and presence of markers under selection if tested;
- estimates of genetic differentiation;
- presence of a mismatch between the genetic populations found and the stock assessment and management units.

Genetics is a dynamic discipline and has been through profound changes in the last decade. The progess in genetics has dramatically changed our perception of the marine realm: initially, marine ecosystem were considered as open systems in which connectivity between populations was very high and barriers to gene flow mostly inexistent. Nowadays, evidence has altered this misconception and genetic population structure has been reported at very fine scales in many marine fish species (Hauser and Carvalho, 2008). Advances in DNA sequencing technology, as well as the use of more sophisticated

statistical analysis and thoughtful sampling designs have led to numerous changes in our perception of genetic population structure in marine fish species, resulting in a paradigm shift (Hauser and Carvalho, 2008). Two main changes occurred in fisheries genetics, the type of markers used and the major attention focused on sampling design. In early studies, samples were mostly collected in an opportunistic way, without taking into account the season and the life-stage of the individuals. Now, special attention is directed to sampling design to maximise the chance to detect genetic population structure.

In the past, the development of genetic markers was limiting and expensive (in terms of both time and cost), but this has changed considerably and thousands of Single Nucleotide Polymorphism (SNP) markers can be discovered in non-model species for a relatively low price. This allows the investigation of genetic population structure in species with extremely limited or no genetic resources. Furthermore, the development of techniques to detect markers under selection has allowed identification of locally adapted populations in a background of high gene flow (e.g. Nielsen et al. 2012; Diopere et al., 2018) and highlights the importance of using both neutral markers and those under selection.

Genetic tools have been shown to be valid instruments for understanding and managing fisheries, detecting meaningful biological units and locally adapted populations, for real-time management of mixed-stocks (Dahle et al. 2018a) and to avoid Illegal, Unreported and Unregulated (IUU) fishing (Nielsen et al. 2012) - as individuals can be assigned to their population of origin with high precision. Hence, the contribution of genetics is essential, and if not included already, information on genetic population structure should be incorporated into the definition of stock units for more sustainable fisheries management in the long-term.

Here, genetic structure factsheets for commercial fish species exploited in the NE Atlantic, Mediterranean and Black Sea are presented. A summary of genetic population structure is given for each species. Moreover, we evaluated whether genetic evidence supports the current stock assessment and management units or not. Mismatches are reported and discussed if present. Finally, we hope that giving an overview of genetic population structure, species and regions less studied are underlined and further studies will focus on those.

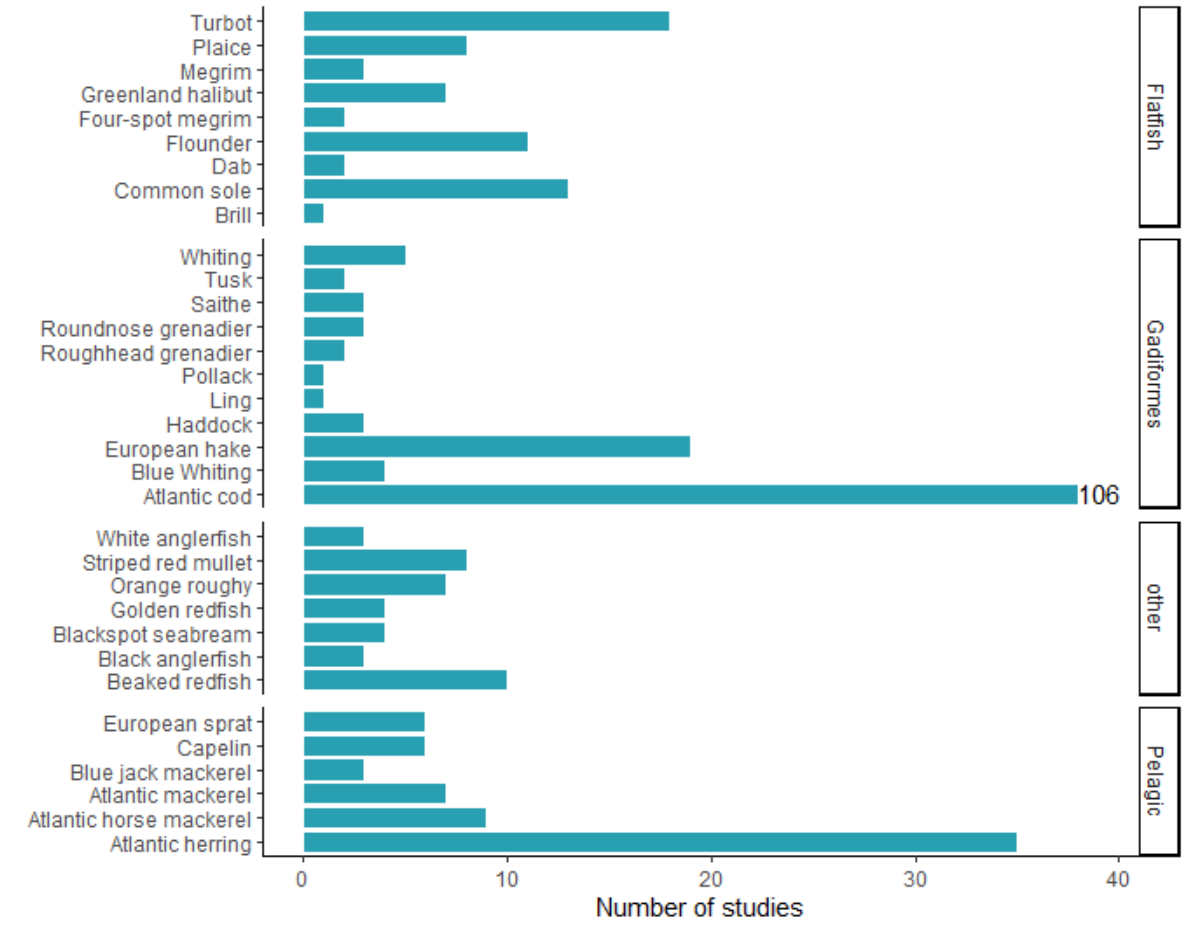


Figure 2.3 Number of genetic population structure studies included per species.

2.2 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, *Reinhardtius hippoglossoides*	7	yes	no	no	no	NT
Brill, *Scophthalmus rhombus*	2	no	no	no	no	LC
Dab, *Limanda limanda*	2	yes	yes	-	-	LC
Four-spot megrim, *Lepidorhombus boscii*	2	yes	Yes	no	no	LC
Megrim, *Lepidorhombus whiffiagonis*	3	yes	no	no	no	LC
Flounder, *Platichthys flesus*	11	yes	no	-	-	LC
Flounder, *Platichthys* spp.		yes	no	-	-	-
Baltic flounder, *Platichthys solemdali*		no	no	-	-	NE
Plaice, *Pleuronectes platessa*	8	yes	no	no	no	LC
Lemon sole, *Microstomus kitt*	0	-	-	-	-	NE
Common sole, *Solea solea*	13	yes	no	no	yes	DD
Turbot, *Scophthalmus maximus*	17	yes	no	no	no	VU
Witch, *Glyptocephalus cynoglossus*	0	-	-	-	-	NE
Blue whiting *Micromesistius poutassou*	4	yes	no	no	no	LC
Whiting, *Merlangius merlangus*	5	yes	no	no	no	LC
Greater forkbeard, *Phycis blennoides*	0	-	-	-	-	NE
Haddock, *Melanogrammus aeglefinus*	3	yes	no	no	no	LC
Ling, *Molva molva*	1	yes	no	no	no	LC $_{Eu}$, DD $_{Med}$

Blue ling, *Molva dypterygia*	0	-	-	-	-	NE
Tusk, *Brosme brosme*	2	yes	yes	no	no	LC
Saithe, *Pollachius virens*	3	yes	no	no	no	LC
Pollack, *Pollachius pollachius*	1	no	no	no	no	LC
Roughsnout grenadier, *Trachyrincus scabrus*	0	-	-	-	-	LC
Roughhead grenadier, *Macrourus berglax*	2	yes	no	no	-	LC
Roundnose grenadier, *Coryphaenoides rupestris*	3	yes	no	no	-	CR
European hake, *Merluccius merluccius*	19	yes	no	no	no	LC $_{Eu}$, VU $_{Med}$
Capelin, *Mallotus villosus*	6	yes	no	no	no	LC
Atlantic horse mackerel, *Trachurus trachurus*	9	yes	no	no	no	VU
Blue jack mackerel, *Trachurus picturatus*	3	no	no	no	no	LC
Atlantic mackerel, *Scomber scombrus*	7	yes	no	no	no	LC
Sprat, *Sprattus sprattus*	6	yes	no	no	no	LC
Atlantic herring, *Clupea harengus*	35	yes	no	no	no	LC
Anglerfish *Lophius budegassa, L. piscatorius*	4	yes	no	no	no	-
White anglerfish, *L. piscatorius*	3	yes	no	no	no	LC
Black-bellied anglerfish, *L. budegassa*	3	yes	no	no	no	DD
Beaked redfish, *Sebastes mentella*	10	yes	yes	no	no	LC
Golden Redfish, *Sebastes norvegicus*	4	yes	no	no	no	VU
Blackspot seabream, *Pagellus bogaraveo*	4	yes	no	no	yes	NT
Striped red mullet, *Mullus surmuletus*	8	yes	-	-	-	LC
Orange roughy, *Hoplostethus atlanticus*	7	yes	no	no	no	VU
Atlantic cod, *Gadus morhua*	106	yes	No	no	no	VU

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

3 Flatfish species

3.1 Greenland halibut, *Reinhardtius hippoglossoides*

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

Distribution[1]

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.

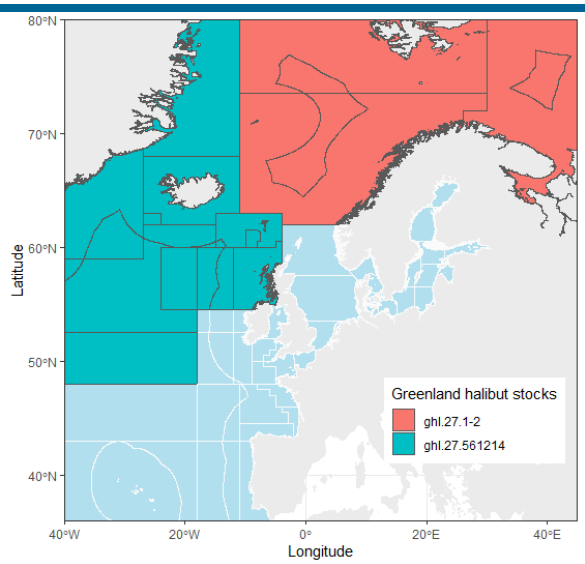


Figure 3.1 Greenland halibut ICES stock assessment units

[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.

3.2 Brill, *Scophthalmus rhombus*

Number of studies	2
Population structure	⊗
Match genetic- Stock assessment units	⊗
Match genetic- Management units	⊗
Match Stock assessment- Management units	✖

Distribution[2]

Brill, *Scophthalmus rhombus* (Linnaeus, 1758), is a widespread flatfish species in the North-East (NE) Atlantic, that occurs from Norwegian to Moroccan coasts, including the western part of the Baltic Sea, the Mediterranean and the Black Sea. It is a shallow water species. Juveniles are commonly found in inshore waters also in proximity of estuaries while mature individuals prefer offshore waters.

Current management status

ICES currently recognise two stock units in the NE Atlantic for brill (Table 2), one in the Baltic Sea and the other in the North Sea, English Channel, Skagerrak and Kattegat (Figure 3.2).

In the Baltic Sea, brill mainly occurs in the western part of the basin, where the main fishing country is Denmark that accounted for 95% of the catches in the Belt Sea (Subdivision 22) in 1985-2016 (ICES 2020b). Brill in the Baltic Sea and the North Sea is mainly a by-catch species of cod and other flatfish species directed fisheries (ICES 2018a, 2020b). For management purpose a combined TAC for brill and turbot in the North Sea (Subarea 4) and Union waters of division 2.a exists. According to ICES advice, the set of a combined TAC for these two species could lead to overexploitation (ICES 2018a). ICES currently provide separate advices on fishing opportunities and stock status for brill and turbot stocks. These two stocks have also a different geographic extension, with turbot including only the North Sea (Subarea 4), and brill extending into the English Channel, Skagerrak and Kattegat (Table 2). Furthermore, there is a mismatch between the assessment and management units for both species, in fact the TAC is set for subarea 4 and division 2.a whereas neither brill or turbot stock units include division 2.a. Therefore, ICES highlight that in order to guarantee a sustainable fisheries management and avoid overexploitation of one or the other species it is necessary to set separate TACs for brill and turbot (ICES 2018a, 2020c). Ideally, these TACs should match the assessment units, in the case of brill with the addition of the Skagerrak and Kattegat (Divisions 3.a) and the English Channel (Division 7.d and 7.e).

[2] Further details on symbols and how to read the factsheet are provided on page 16

Genetic population structure in a nutshell

Genetic studies reported a lack of population structure for brill within the NE Atlantic both with allozyme and microsatellite loci (Blanquer et al. 1992, Vandamme 2014).

Mismatch

Genetic evidence does not support the presence of stock units for brill in the NE Atlantic. Further investigations with more powerful markers are needed to examine if the geographic extension of the current assessment units is supported or not and eventually design optimal management strategies for the species, with units reflecting the real bio-logical population structure of the species, if any.

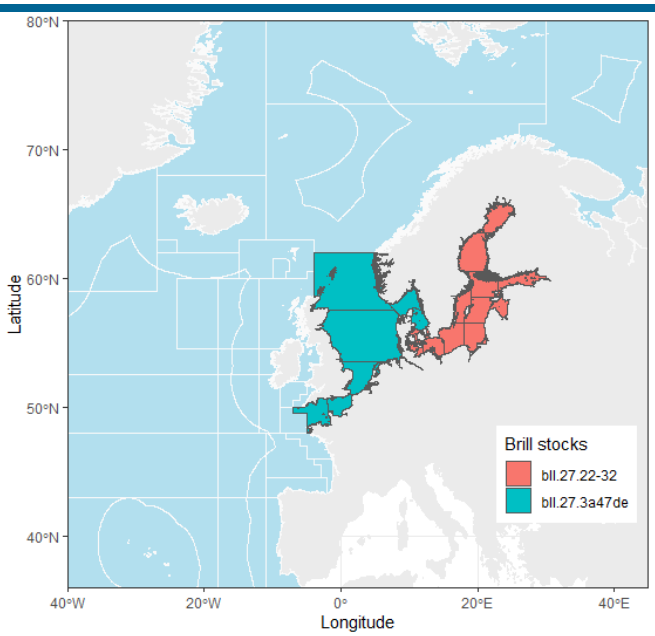


Figure 3.2. Brill ICES stock assessment units

Summary of genetic evidence

The information available on population structure for brill is extremely limited. Only one study analysed genetic variation at allozyme loci and potential geographic differences in the whole distributional range of brill (Blanquer et al. 1992) (Table 1). A lack of genetic population structure within the Atlantic and only a weak differentiation between the Atlantic and the Mediterranean samples was reported (Blanquer et al. 1992). Lack of structure was suggested also at microsatellite loci within the NE Atlantic (Vandamme 2014). Therefore, further studies are needed to test whether brill represents a panmictic population or, rather genetic differentiation exists also within the Atlantic and the Mediterranean. New and more powerful markers should be developed for brill such as SNPs, reinforced by a sampling design that maximise the possibility to detect population structure, focusing on spawning individuals.

3.3 Dab, *Limanda limanda*

Number of studies	2
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	-
Match Stock assessment- Management units	-

Distribution[3]

Dab, *Limanda limanda* (Linnaeus, 1758), is a demersal flatfish species commonly found in the North-East (NE) Atlantic shelf from the Bay of Biscay to Norway, as well as in the White Sea, Barents Sea, Baltic Sea and Iceland. Dab is a very common species in the North Sea (Daan et al. 1990).

Current management status

There are two ICES stocks in the NE Atlantic for dab (Figure 3.3): one in the North Sea, Skagerrak, Kattegat and the other in the Baltic Sea. Dab in mainly a by-catch species in the direct fishery of cod and in mixed fisheries of other flatfish (plaice and flounder) of higher commercial importance. Discard has been estimated to be close to 50% for the Baltic stock (ICES 2020b). In the Baltic Sea, it is present only in the western part of the basin (Subdivisions 22-25), in fact the majority of landings is reported from the Belt Sea (Subdivision 22), with smaller amount from subdivision 24 and 25, while the occurrence of individuals in the eastern part (Subdivisions 26-32) is rare (ICES 2020b). Total landing in the Baltic Sea for 2019 is 1102 t, mostly fished by Germany and Denmark in mixed fisheries of flatfish species (ICES 2020b). Due to a lack of studies, dab inhabiting the North Sea, the Skagerrak and Kattegat was considered as a single stock assessment unit (ICES 2016). Fish are mainly caught as by-catch in the demersal fishery for other flatfish species, mainly alongside plaice and sole (ICES 2018a). Currently, there are no TACs set for dab and ICES is not providing advices for fishing opportunities

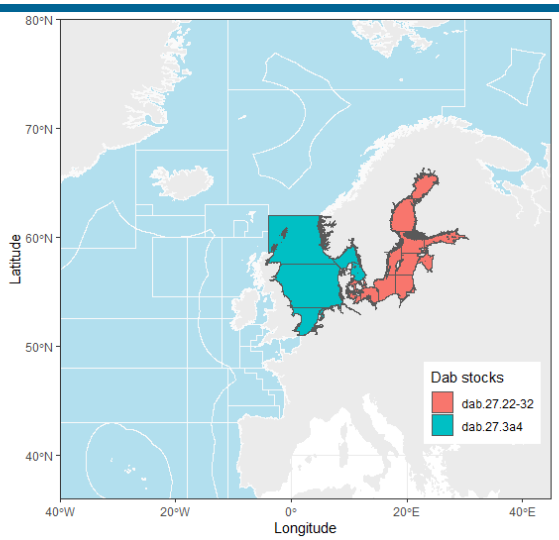


Figure 3.3. Dab ICES stock assessment units

[3] Further details on symbols and how to read the factsheet are provided on page 16

for Baltic and North Sea dab, but only information on the status of the Baltic Sea stock (ICES 2020b).

Genetic population structure in a nutshell

Microsatellites and SNPs have been used to analyse population structure of dab around the British Isles (Tysklind et al. 2013) and in the North Sea, Baltic Sea transition zone (Le Moan et al. 2019a), respectively. Genetic evidence supports the existence of separate populations of dab in the North Sea, Irish Sea and Baltic Sea. Presence of population admixture and hybridization between North Sea and Baltic Sea individuals in the transition zone was reported.

Mismatch

In contrast with the current stock assessment units for dab, the presence in the Kattegat and the transition zone of individuals of admixed origins was reported. Further investigations are needed to define the boundaries of the North Sea dab stock. Further analysis should also focus on the transition zone to unravel the extent of hybridization and population admixture of the North Sea and Baltic Sea stocks.

Summary of genetic evidence

Since Reiss's review (2009), in which an absence of genetic information on population structure for dab was reported, two studies have been published (Table 1). Tysklind et al. (2013) using microsatellites showed the presence of two temporally stable populations inhabiting the North Sea and the Irish Sea. The importance of considering population structure of species that, similar to dab, are used as bioindicators was highlighted. In fact, the biomarker responses of dab in UK waters may be population specific (Tysklind et al. 2013).

Genetic population structure of dab in the North Sea, Baltic Sea and the transition zone (the Kattegat, the Belt Sea and the Øresund) was analysed by SNP markers by Le Moan et al. (2019a). The presence of two populations and a continuum of hybridization along the transition zone, with substantial population admixture, was reported. The divergence between North Sea and Baltic Sea populations was supported (F_{ST} = 0.020) (Le Moan et al. 2019a). Genetic divergence was associated with environmental gradients of salinity, sea surface temperature and sea bottom temperature in the transition zone.

3.4 Four-spot megrim, *Lepidorhombus boscii*

Number of studies	2
Population structure	✓
Match genetic- Stock assessment units	✓
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[4]

Four-spot megrim, *Lepidorhombus boscii* (Risso, 1810), is a flatfish species distributed in the North-East (NE) Atlantic from the British Isles to the north-western African coasts, and in the Mediterranean Sea. Although adult *megrims* are demersal and fairly sedentary, larvae are pelagic and gene flow could occur at this life stage due to passive transport facilitated by ocean currents. Spawning occurs near the coast from March to June (Campo and Garcia-Vazquez, 2010; and references therein).

Current management status

There are two species of the genus *Lepidorhombus* exploited in the NE Atlantic: megrim, *L. whiffiagonis* (Walbaum 1979), and the four-spot megrim, *L. boscii*, for which fisheries management is carried out with combined TACs set for Megrims, *Lepidorhombus spp.* (Table 2).

In the NE Atlantic, two stocks of four-spot megrim are present: one including west, southwest of Ireland (Divisions 7.b-k) and Bay of Biscay (8.a, b, d) and the second one including the southern Bay of Biscay (8.c) and the Atlantic Iberian Shelf (9.a) (Figure 3.4). In southwest Ireland and Bay of Biscay catches are mainly from France, Spain, UK and Ireland (ICES 2020s). The stock of four-spot megrim in this part of the Atlantic is classified by ICES as a data-limited stock (category 5), only landings data are available and information from survey are limited. Moreover, ICES is not requested to provide information on stock status and fishing opportunities for this stock (ICES 2020s). The management is put in place with a combined TAC set from the European Council for both megrims species, preventing a sustainable fishery management and possibly leading to the overexploitation of one or both species (ICES 2020s). ICES recommend that separate TACs should be set for the two species for a better management of the fisheries. Likewise in the southern Bay of Biscay and in the Atlantic Iberian shelf, four-spot megrim is fished in mixed fisheries directed mainly to hake and anglerfish with Spain becoming the main fishing country in the Atlantic Iberian shelf (ICES 2020s). Although landings are not completely separated by species, advice on stock status and fishing opportunities are

[4] Further details on symbols and how to read the factsheet are provided on page 16

given by ICES for each species separately. However, even in this area the two species of megrim are managed under a combined TAC and ICES urges the implementation of separate TACs (ICES 2020s).

Stock units exist for Megrims species (*Lepidorhombus* ssp.) in the Rockall (Division 6.b) and in northern North Sea and west of Scotland (4.a and 6.a). However, catches of *L. boscii* are negligible in these divisions.

Genetic population structure in a nutshell

The available information on genetic population structure confirms the presence of two stocks of four-spot megrim in the NE Atlantic, reflecting the stock units used by ICES. Further studies should focus on the Mediterranean, since only one sample from this region was included to date.

Mismatch

A mismatch is revealed between genetic and management units. Four-spot megrim from Ireland and northern Bay of Biscay are genetically similar based on available data and evidence indicates currently, comprise one unit. However, TACs are set separately for Subarea 7 and Divisions 8.a-b, d, e (Table 2), hence resulting in a mismatch of the management units with genetic and also assessment units.

Summary of genetic evidence

Two studies investigated genetic population structure of four-spot megrim in the NE Atlantic and Mediterranean Sea. Danancher and Garcia-Vazquez (2009) applied a set of newly developed microsatellites to analyse samples from southwest of Ireland (7.j), the Bay of Biscay (8.a-b, d and 8.c), Portuguese waters (9.a) and the Mediterranean Sea. The presence of two distinct populations in the NE Atlantic was revealed (global F_{ST} within the Atlantic 0.145, $P < 0.001$), as well as one in the Mediterranean. The spatial genetic population structure found a match with the stock assessment units currently in use by ICES. Similar patterns of genetic differentiation were reported through a mitochondrial marker (Campo & Garcia-Vazquez 2010). Though, the level of differentiation detected by microsatellites was much higher than the one detected by the mitochondrial marker (global F_{ST} 0.177 and 0.023, respectively). Moreover, the Portuguese and the Mediterranean samples were

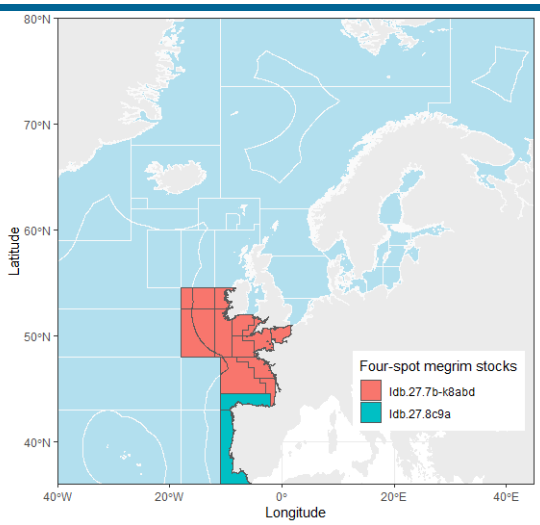


Figure 3.4. Four-spot megrim ICES stock assessment units

genetically similar at the mitochondrial marker, probably, due to past colonization events or to extensive larval drift across the Mediterranean from the Atlantic (Division 9.a). The connectivity between the NE Atlantic and the Mediterranean populations should be further explored. The only mismatch present between the genetic population structure and the assessment units is due to a lack of differentiation found between Portuguese and Mediterranean samples by a mitochondrial marker (Campo & Garcia-Vazquez 2010). However, genetic differentiation was revealed between these two basins using microsatellites, solving the mismatch.

3.5 Megrim, *Lepidorhombus whiffiagonis*

Number of studies	3
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[5]

Megrim, *Lepidorhombus whiffiagonis* (Walbaum, 1792), is a demersal flatfish species widely distributed in the North-East Atlantic, from Icelandic and Faroese waters to Cape Bojador, as well as in the Mediterranean Sea (Garcia-Vazquez et al. 2006). It is caught, together with four-spot megrim in mixed fisheries directed to other demersal species, mainly hake, anglerfish and *Nephrops*.

Current management status

Megrim is mainly a by-catch species in demersal fisheries directed to whitefish and flatfish. Two stocks of megrim are identified by ICES: one in the Celtic Seas and part of Bay of Biscay (8.a-b, d) and the other in southern Bay of Biscay and Atlantic Iberian waters (Figure 3.5). Combined TACs exist for megrim and four-spot megrim (see four-spot megrim for combined TACs), and ICES recommended the set of separate TACs to avoid overexploitation and secure a more sustainable fisheries management. Both species are part of the EU multiannual plan (MAP) for Western Waters and adjacent waters (ICES, 2020e; and references therein). Landings for megrim in 2019 were 239 t for the Iberian stock (ICES 2020j), while in the Celtic Seas and Bay of Biscay preliminary landings were 12164 t (ICES 2020i).

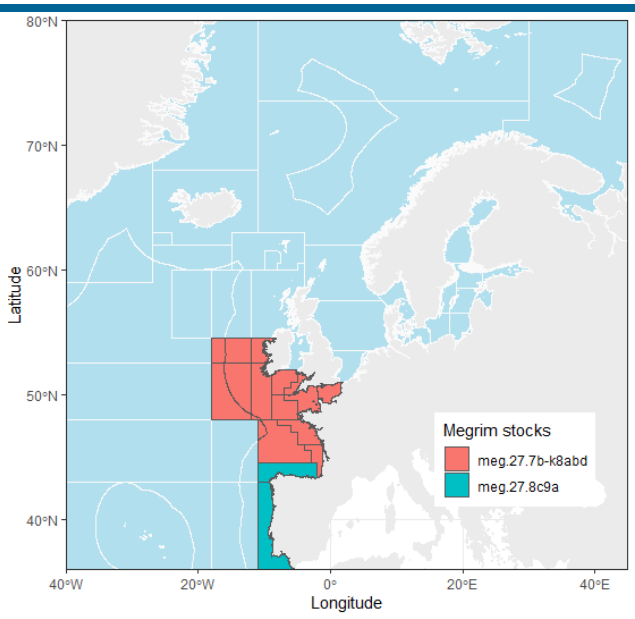


Figure 3.5. Megrim ICES stock assessment units

[5] Further details on symbols and how to read the factsheet are provided on page 16

Genetic population structure in a nutshell

In line with assessment and management units, the differentiation between the northern (division 6) and southern NE Atlantic (8.c and 9) is supported by genetic analysis, as well as the divergence between northern and southern Bay of Biscay. However, further studies are needed to understand patterns of population structure and spatial distribution of megrim in the Bay of Biscay and Celtic Sea. Genetic evidence supports the presence of different stock assessment units of megrim in the Rockall (division 6.b) and in the northern North Sea, west of Scotland (division 4.a and 6.a). Moreover, substructure was suggested in the northern North Sea and West of Scotland, currently considered part of the same stock by ICES.

Mismatch

Mismatch between stock assessment and genetic units is present for the Bay of Biscay and Celtic Sea that indicated genetically distinct units, currently part of the same stock assessment unit. Further studies are needed to elucidate genetic structure in these divisions, since the Bay of Biscay appeared more similar to northern divisions of subarea 6 while the Celtic Sea exhibits closer similarity to the southern Iberian stock.

Genetic differences were found at microsatellite loci (Macdonald & Prieto) between the northern North Sea and West of Scotland, currently considered part of the same stock by ICES. If additional analyses confirm this difference, appropriate stock units reflecting the biological populations present are recommended. Moreover, from a fisheries management perspective, a TAC is given for the Rockall and west of Scotland jointly despite that genetic differentiation of Rockall megrim was showed, resulting in a mismatch.

Summary of genetic evidence

A total of three studies investigating genetic population structure of megrim are present in the literature (Table 1). Garcia-Vazquez et al. (2006) using a combination of nuclear and mitochondrial markers detected genetic differentiation between megrim inhabiting the NE Atlantic and the Mediterranean Sea with the strait of Gibraltar acting as potential barrier to gene flow. At a finer scale, Danancher and Garcia-Vazquez (2009) developed a set of highly polymorphic markers that not only supported the differentiation between the NE Atlantic and the Mediterranean, but also indicated the presence of structure within the Ne Atlantic (global F_{ST} 0.158, $P < 0.001$). Microsatellites supported the presence of at least two populations, a northern, in division 6, and a southern including south Bay of Biscay and Portuguese waters (division 8.c and 9). Difficulties arose for samples from areas between these two stocks. Megrims from division 7 clustered with the southern stock (Division 8.c and 9) while samples from divisions 8.a-b, d clustered with the northern stock (Subarea 6). However, the sampling season is not reported and if sampling occurred outside the spawning season, there is a reduced chance of identifying genetic structuring.

Further studies are needed to better understand patterns of population structure and spatial distribution of megrim in these areas.

Furthermore, population structure of megrim in the Northern shelf was evaluated in a report from the NAFC Marine Centre (Macdonald & Prieto). Currently, ICES recognize two stocks of megrims (*Lepidorhombus* ssp.): one in the northern North Sea and west of Scotland (Division 4.a and 6.a) and the other in the Rockall (Division 6.b). The analysis through microsatellites supported the presence of these stocks and moreover detected further localised differentiation between west of Scotland (6.a) and the northern North Sea (4.a) with mixing in the northeastern part of division 6.a and the eastern part of division 4.a. Further studies are needed to confirm the differences between northern North Sea and West of Scotland and the relative patterns of mixing.

3.6 Flounder, *Platichthys flesus*

Number of studies	11
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	-
Match Stock assessment- Management units	-

Distribution[6]

The European flounder, *Platichthys flesus*, L., is a widespread flatfish species, inhabiting the North-East (NE) Atlantic, from the White Sea to the Mediterranean and the Black Sea (Whitehead et al. 1986b). It is widely distributed in the Baltic Sea, where it is among the few marine fish species that occurs also in the inner part of the basin (Florin & Höglund 2008). In fact, it is a euryhaline species, able to live and tolerate waters with a wide range of salinities, and is correspondingly commonly found in estuaries and lagoons. Adults usually feed in inshore and shallow waters while they migrate to spawn in deeper water during the spawning season. Eggs and larvae are pelagic, thus promoting population connectivity.

The presence of two ecotypes of European flounder in the Baltic Sea with different spawning strategies was known, i.e. the pelagic and demersal spawners. Genetic studies have shown the demersal spawners to represent a different species named Baltic flounder, *Platichthys solemdali* sp. nov. (Momigliano et al. 2018). Although it is not possible to distinguish between the Baltic flounder (*Platichthys solemdali*) and the European flounder by morphological or meristic characters (except for gamete physiology and morphologies), they are genetically different and the absence of hybrids show that there is strong reproductive isolation. The pelagic and demersal species coexist in the southern as well as in the eastern part of the proper Baltic Sea. These species use the same feeding grounds. However, their spawning grounds differ, with the Baltic flounder spawning demersal eggs (small and heavy) in shallow and coastal areas of the Baltic proper, while European flounder spawning occurs usually in deeper waters, where pelagic eggs are released.

Current management status

In the NE Atlantic, ICES recognize several assessment units for flounder species (Figure 3.6). A stock unit is present in the North Sea, Skagerrak and Kattegat and another in the Belt Sea and the Sound (SDs 22-23) for the European flounder (*P. flesus*). A stock unit for the Baltic flounder (*P. solemdali)* exists in the northern part of the proper Baltic Sea (SDs 27, 29–32) (Table 2). The two species (European and Baltic flounders) are assessed jointly, as *Platichthys* spp. in the remaining Baltic subdivisions (SDs 24-25, and SDs 26-28).

[6] Further details on symbols and how to read the factsheet are provided on page 16

In the North Sea stock, the European flounder is caught as by-catch species in flatfish fisheries, mainly for plaice and sole. ICES does not provide advice on fishing opportunities for the North Sea stock (ICES 2018a). European flounder is considered a non-target species and no TAC is set in the area. Previously, this stock was managed together with dab, and a common precautionary TAC for the two species was present, until its removal in 2017 (see ICES, 2018, and references therein).

European flounder in the North Sea, Belt Sea and the Sound (SDs 22 and 23) is mainly a by-catch species of direct cod fisheries or flatfish mixed-fisheries, and catches are mainly from the Belt Sea.

Both species of flounders are present in West of Bornholm, Southern Central Baltic–West subdivisions (SDs 24 and 25). Advice is given by ICES at the level of *Platichthys* spp. Correspondingly, the proportion of the two species for stock assessment are not separated (ICES 2020b). A total of 11 815 t was landed in 2019, mainly from subdivision 25 (ICES 2020b). The assessment of two different species as one stock unit is considered dangerous and could lead to the overexploitation of either species (ICES 2020b).

Likewise, both species are present in eastern Gotland and Gulf of Gdansk (SDs 26-28) and their relative proportions are not separated for assessment and management (ICES 2020b). Moreover, a decreasing trend in landings was reported from ICES for this stock, that in 2019 were 2740 t (ICES 2020b).

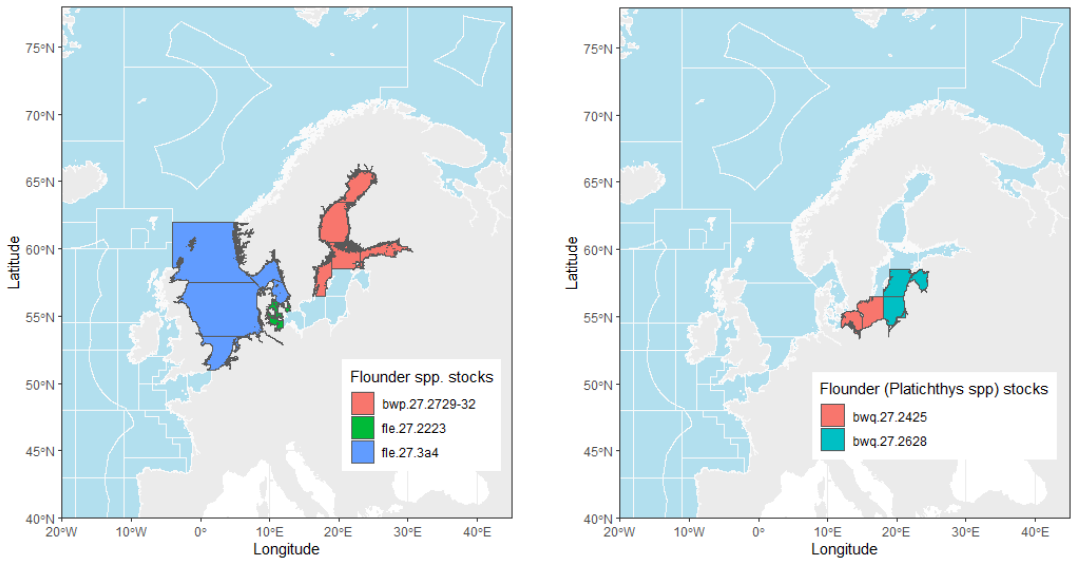


Figure 3.6. Flounder stock assessment units. Left, European flounder (fle.27.2223; fle.27.3a4) and the Baltic Flounder stocks (bwp.27.2729-32). Right, the mixed flounder species stocks.

While in the rest of the Baltic, European flounder is the most common flounder species, in the Baltic Proper (SD 27, 29-32) *P. solemdali* is the prevalent one (ICES 2020b). Hence, a stock unit for the Baltic flounder (*P. solemdali*) is present in subdivisions 27, 29-32. Since both species are present in the central Baltic (SD 28) and *P. flesus* seems to be the predominant one, subdivision 28 is not included (ICES 2020b). Although it is assumed that the Baltic flounder species is the prevalent in the proper Baltic Sea, previous analysis

showed that the two species co-occur and their proportion has changed since the 1980s. According to ICES the majority of the catch are from SD 29, however the proportion of the two species are not separated. In fact, there are not morphological or meristic characteristics that readily allow assignment of individual to either species, and currently only genetic methods and gamete physiology and morphology (eggs shape and sperm mobility) allow clear separation.

Genetic population structure in a nutshell

Genetic evidence shows European flounder is structured within the NE Atlantic, and that a cryptic species exists in the Baltic Sea (Momigliano et al. 2018). For the European flounder, the presence of separate populations in the Faroe Islands and Bay of Biscay was supported (Hemmer-Hansen et al. 2007b). Genetic differentiation was reported between *P. flesus* inhabiting the North Sea and the Baltic Sea (e.g., Momigliano et al. 2017, Le Moan et al. 2019a).

Moreover, genetic evidence supports the two flounder species in the Baltic Sea:

- Genetic homogeneity for the Baltic species (*P. solemdali*) that can be considered a genetic unit (Hemmer-Hansen et al. 2007b, Florin & Höglund 2008).
- European flounder in the Sound and western Baltic subdivisions (SDs 24,25,26) are genetically one unit (Florin & Höglund 2008, Momigliano et al. 2017).
- Presence of hybrids between North Sea and Baltic Sea pelagic flounder in the Sound (Momigliano et al. 2017) as well as in the transition zone (Le Moan et al. 2019a).
- Co-occurrence of pelagic and demersal flounder species in the central and northern Baltic Sea (SDs 27, 29,32) (Momigliano et al. 2018, 2019).
- The presence of demersal individuals in West of Bornholm and southern Central Baltic subdivisions (SDs 24, 25) (Le Moan et al. 2019a).

Mismatch

The pelagic Baltic Sea population can be considered a genetic unit, no suggestions of substructure were found despite several stock assessment units exist (Table 2), resulting in a mismatch. Likewise, the Baltic Sea flounder represent a genetically homogeneous unit. Mixing of the two species is not limited only to subdivisions 24, 25 and 26, 28, as considered by ICES. Presence of mixing between pelagic and demersal species was showed in the Baltic proper and Gulf of Finland, and it is not taken into account in fishery assessment.

Also in the inner part of the Baltic Sea the two species co-occur (Momigliano et al. 2019) and their proportion could fluctuates based on environmental variables, as currents that allow larvae and eggs dispersal of the pelagic spawners. The exploitation of two different species morphologically indistinguishable could lead to the overexploitation of the weakest stock components, hence more sustainable fisheries management practices should be implemented.

Summary of genetic evidence

Population structure of European flounder in its distributional range was studied initially by allozymes (Galleguillos & Ward 1982). Although they did not detect any differentiation within the NE Atlantic samples, differentiation between the Atlantic, the Adriatic and the Black Sea flounders was detected, confirming the presence of subspecies in the Adriatic Sea, *P. flesus italicus*, and the Black Sea, *P. flesus luscus* (Galleguillos & Ward 1982). Likewise, by including more localities within the Atlantic, a weak pattern of isolation by distance was reported by Borsa et al. (1997). The analysis supported the differentiation between flounders inhabiting the NE Atlantic and the Mediterranean Sea, and also intrabasin genetic differences were detected between the western part, the Adriatic Sea and the Aegean and Black Sea. Therefore, based on the genetic structure pattern found, the Gibraltar strait, the Siculo-Tunisian Strait and the Peloponnese Peninsula were suggested as potential barriers to gene flow (Borsa et al. 1997).

Based on microsatellite data, significant and temporally stable differentiation was found within the NE Atlantic by Hemmer-Hansen et al. (2007b), who reported the existence of several populations, namely the Faroe Islands, Bay of Biscay and the benthic spawners population in the Baltic Sea. Notably, this was the first study reporting genetic differentiation between pelagic and demersal spawners in the Baltic Sea: a genetic barrier was identified between North Sea – Bornholm (pelagic spawners) and Gotland (benthic spawners) in the eastern Baltic (Hemmer-Hansen et al. 2007b).

Hemmer-Hansen et al. (2007a) used a candidate gene (*Hsc70)* approach to study local adaptation in flounder across the NE Atlantic. The differentiation levels between flounders inhabiting the North Sea and the Baltic Sea at neutral loci was 0.02 while 0.45 at *Hsc70*, suggesting the existence of adaptive divergence despite putatively high levels of gene flow between these populations, highlighting the importance of using genetic markers under selection to determine whether locally adapted populations exist despite low levels of differentiation at neutral markers.

Florin and Höglund (2008) focussing on the North Sea, the Baltic Sea and the transition zone supported the existence of three genetically different populations, *i.e.* a demersal population in the northern Baltic Sea; a pelagic population in the western Baltic including the Sound (SD 23) and another one in the North Sea, Skagerrak and Kattegat. The genetic differences between the demersal and pelagic spawners population was confirmed and their mixing in some of the Baltic Sea subdivisions was showed.

Through SNP marker analysis Momigliano et al. (2017) provided evidence that the demersal spawners population in the Baltic Sea represent a distinct species, arising from a rapid event of ecological speciation, where the spawning behaviour is the trait under selection promoting reproductive isolation. The new species was successively described as the Baltic flounder, *Platichthys solemdali* (Momigliano et al. 2018). Moreover, the differentiation between the European flounders (*P. flesus*) inhabiting the Baltic Sea, the

North Sea and the transition zone was confirmed also by SNPs (Momigliano et al. 2017), and presence of hybrids was demonstrated especially in the transition zone.

In the Baltic proper, considered to be inhabited only by the demersal species, pelagic flounders were found, showing that the two species co-occur. The reproductive isolation was confirmed by an absence of hybrids between the two species. Hence, a multispecies fishery management should be implemented for sustainable management of flounders' fisheries in the Baltic Sea.

Since the two species cannot be distinguished morphologically, a genetic tool was designed by Momigliano et al. (2019, 2018) in order to assign individuals to the flounder species of origin in areas where the Baltic flounder and the European flounder co-occur in the Baltic Sea. This genetic tool uses 6 loci under selection that are highly discriminatory between the two species.

This tool was applied to analyse DNA from archived otolith samples in order to monitor spatio-temporal changes (1976–2011) in stock composition of flounder fisheries from the Aland Sea and Gulf of Finland (Momigliano et al. 2019). The study confirmed that both species of flounder are present in this part of the Baltic Sea and that the relative proportion of each species have showed spatio-temporal fluctuations, depending on environmental variables in the Baltic. The importance of monitoring the contribution of different component (in this case species) to mixed-stock fisheries in a spatiotemporal manner was emphasized in order to avoid the overexploitation of the less productive component and implement assessment and management measures for each species individually.

Reis-Santos et al. (2018) studied population structure of flounder across the NE Atlantic, using otoliths composition and microsatellite analyses. No information about demersal and pelagic spawners were given for the Baltic Sea samples. Microsatellites indicated genetic differentiation between the Polish and Swedish coast of the Baltic Sea and absence of differentiation between North Sea, the Polish Baltic Sea (SD 26) that are currently in two different stock assessment units. The integrated analysis indicated the presence of four groups in the NE Atlantic, i.e. (1) the Norwegian coast; (2) the Baltic Sea; (3) the southern North Sea and the Bay of Biscay; (4) the Galician shelf and Atlantic Iberian coasts (division 9.a).

Le Moan et al. (2019a) using a SNP panel reported the presence of both the demersal and pelagic species in the Baltic Sea. The strong differentiation between the two flounder species was confirmed by an absence of hybridization between them. Likewise, their mixing was confirmed, two demersal individuals were found in the South-west Baltic (SD 24) and Bornholm Sea (SD 25) that are considered habitat of the pelagic flounders. While for the European flounder, *P. flesus*, differentiation was supported between the North Sea and Baltic Sea population (F_{ST} 0.013 and highly significant), and with a continuum of hybridization through the transition zone between these basins.

3.7 Plaice, *Pleuronectes platessa*

Number of studies	8
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[7]

One of the most important commercial flatfish species in the North-East (NE) Atlantic is plaice, *Pleuronectes platessa* L., distributed on the continental shelf, from the White Sea and Barents Sea, down towards the Iberian Peninsula including Iceland, the Baltic and the western Mediterranean Sea (Nielsen 1986). Plaice is characterized by high fecundity, pelagic eggs and larvae that can be passively dispersed, feeding and spawning migrations, the existence of distinct offshore spawning grounds and coastal nursery areas in shallow waters (see references in Hoarau et al., 2002).

Current management status

Based on ICES, currently there are ten stock units for plaice in the NE Atlantic (Figure 3.7). Mismatches already exist between these stock units and management units for which TACs are set (Table 2). For instance, a separate TAC is given for the Skagerrak, that however is currently assessed by ICES together with the North Sea. ICES is aware of the existence of a local population in the basin (Ulrich et al. 2017). However, the fishery mainly occurs in the western part of the basin that receives a conspicuous number of migrants from the North Sea (Ulrich et al. 2017, ICES 2020b), hence they are assessed as part of the same stock unit.

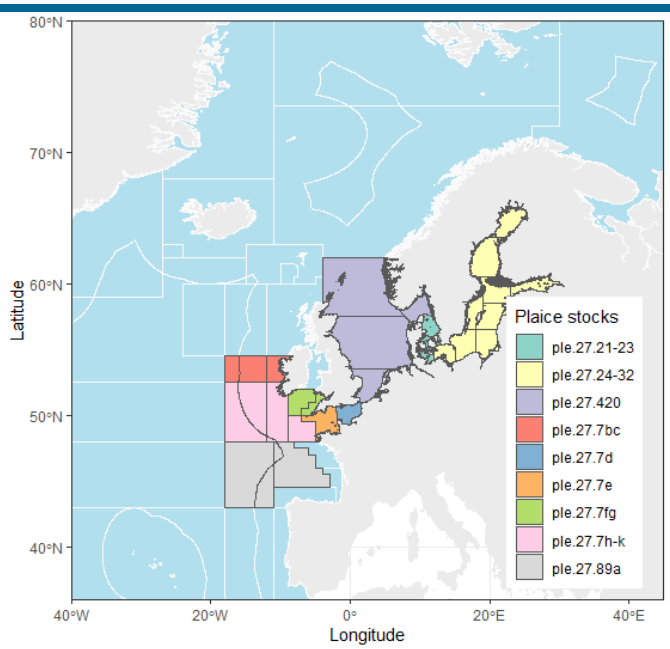


Figure 3.7. Plaice ICES stock assessment units

[7] Further details on symbols and how to read the factsheet are provided on page 16

The Kattegat (SD 21) encompasses a different stock unit, with the Belt Sea and the Sound. As showed by a multidisciplinary study (Ulrich et al. 2017), the number of migrants connecting the Skagerrak and the Kattegat is low, hence their separate assessment is supported. In this area, plaice was generally considered as a by-catch species, however its importance as a fishery resource is increasingly growing with the decline of cod (ICES 2020b).

Plaice in subarea 7 is assessed and managed as different units (Table 2). A mismatch between the assessment and management areas is evident for the English Channel where the western part (7.e) is actually managed together with the eastern (7.d), but from an assessment perspective they are considered two separate stocks. For the stocks in the rest of the divisions, (7.b, c; 7.a; 7.f, g; 7.h-k) assessment and management units agree.

The information available is limited for the stock in the Bay of Biscay and Atlantic Iberian waters (8, 9a), representing the southern boundary of plaice in the NE Atlantic. ICES considers this stock as a data limited stock and its status is therefore un-knowm (ICES 2020s).

Genetic population structure in a nutshell

Available genetic information supports the presence of population structure for plaice within the NE Atlantic. In particular:

- The differentiation between the continental shelf and the off-shelf populations (Iceland and Faroe Plateau) is supported by both microsatellites and SNPs analyses (Hoarau et al. 2002, 2004, Was et al. 2010, Le Moan et al. 2020).
- Plaice in west of Scotland is clearly differentiated from the Faroe Plateau (Hoarau et al. 2002, 2004, Was et al. 2010), hence their management in the same unit is not supported by genetic evidence.
- The existence of local populations in the Skagerrak and Kattegat was reported (Ulrich et al. 2017), as well as in the Baltic Sea. This contrast with the management of plaice in the Kattegat and the Baltic Sea in the same management unit.
- The mismatches of genetic population structure with the assessment and management units found in initial studies (Hoarau et al. 2002, 2004, Was et al. 2010) were due to the low resolution of the markers used. In fact, the use of more powerful genetic markers (Ulrich et al. 2017, Le Moan et al. 2019a, 2020), enabled the detection of differences (i.e. between the North Sea and the Baltic Sea plaice), despite the high level of gene flow experienced by the continental shelf populations and moreover indicated the presence of local adaptation (Le Moan et al. 2020).
- Genetic studies using microsatellites did not detect differentiation between the North Sea, Irish Sea and west of Scotland (Hoarau et al. 2002, 2004, Was et al. 2010), hence further investigations are required to explore population structure in these regions with more powerful markers.
- The Bay of Biscay is genetically different from the rest of the populations present in the continental shelf (Hoarau et al. 2004), however more samples also form the

southern part of the Bay of Biscay and the Atlantic Iberian waters should be analysed, since only one sample from north Bay of Biscay (division 8a) was analysed.

Mismatch

Evidence of genetic population structure and spatial distribution of plaice populations in the NE Atlantic was previously shown. Different types of mismatch are present between the genetic and stock assessment and management units, that could potentially lead to sub-optimal management of the fisheries, resulting potentially in unsustainable fisheries practises. The following mismatches are identified:

- Presence of a local population in the Skagerrak. However, plaice in the Skagerrak is assessed together with the North Sea.
- Irish Sea, North Sea assessed and managed in two different stock units, not supported by genetic evidence.
- West of Scotland differentiated from the Faroe plateau, but managed together.
- Differentiation between plaice in the Baltic Sea and the transition zone has been supported, resulting in a mismatch within the management unit.

Mismatches already exist between assessment and management units (Table 2). The implementation of management measures that reflect the stock assessment units and genetic evidence of population structure is required to promote sustainable fisheries management.

Summary of genetic evidence

Several studies have investigated genetic population structure of plaice across its distributional range, especially around the British Isles (Watts et al. 2004, 2010) and in the North Sea, Baltic Sea and their transition zone (Ulrich et al. 2017, Le Moan et al. 2019a).
Hoarau et al. (2002) using 6 microsatellite loci reported significant differentiation of plaice from Iceland and the Faroe Plateau, while no genetic differences were detected among samples in the continental shelf, from Norway to the Bay of Biscay, including the North Sea, the Irish Sea and the Belt Sea. Absence of genetic population structure was reported also from Watts et al. (2004) that analysed juveniles of plaice from nursery grounds in the Irish sea (7.a).
The importance of using different genetic markers to investigate population structure in marine fish species was illustrated by Hoarau et al. (2004), that using a combination of nuclear and mitochondrial markers, confirmed differentiation between the continental shelf and the off-shelf populations (i.e. Iceland and Faroe), and moreover showed evidence of substructure within the continental shelf. Weak but significant differentiation was reported, between the North Sea-Irish Sea (including west of Scotland) group and the Baltic Sea, Norway and the Bay of Biscay (Hoarau et al. 2004). Hence, there is a mismatch with both assessment and management units, due to absence of differentiation between the North Sea and the Irish Sea that are assessed and managed as separate units.

Additionally, another mismatch is present for plaice in west of Scotland (6.a) since this division is managed together with the Faroes grounds (5.b), however genetic investigations (Hoarau et al. 2002, 2004) have reported a differentiation between Faroe Plateau and west of Scotland, with the latter more similar to the Irish Sea, North Sea group than the Faroe Plateau.

Watts et al. (2010) analysing samples of juveniles collected along the west coast of the United Kingdom, found a pattern of isolation by distance in a background of weak population structure, contrasting with previous studies that reported no substructure. Mixing between plaice from the Irish Sea and west of Scotland was reported, questioning the panmixia within the unit, although in west of Scotland plaice is not a target species and there is not a stock unit assessed by ICES in this division.

Was et al. (2010), covering all the species range in the NE Atlantic, found significant spatial structure, with Iceland and Faroe Plateau clearly differentiated from each other and the remainder of samples. Significant differentiation was reported also between the northern samples and the Bay of Biscay. Genetic homogeneity was reported for plaice in the Baltic Sea, the Irish Sea and the North Sea, contrasting with other flatfish species that exhibit clear differentiation between these areas. Hence, mismatches are due to the lack of differentiation found between these areas that are assessed and managed as several units. However, the limited number of markers and their resolution could have affected the results of the study. Hence, these mismatches should be carefully considered in the light of the most recent studies.

In fact, using more powerful genetic markers with higher resolution as SNPs (Ulrich et al. 2017) the presence of different populations was shown in the North Sea, Baltic Sea and the transition zone. The existence of local populations in the Kattegat and Skagerrak was supported, although mixing of the local populations with individuals from the North Sea and Baltic Sea was reported.

Likewise, Le Moan et al. (2019) using a SNP panel to investigate population structure of plaice in the North Sea - Baltic Sea transition zone, found a continuum of hybridization between plaice from the North sea and Baltic Sea. Compared with other flatfish species the overall differentiation between these populations was low (F_{ST} 0.005), though two structural variants (SVs) in plaice genome were identified (Le Moan et al. 2019a).

Le Moan et al. (2020) explored the effect of these SVs on plaice population structure and investigated local adaptation, included additional samples from Iceland, the Barents Sea and Norway. The isolation of Iceland was confirmed, and a strong pattern of isolation by distance was observed at the continental shelf (Le Moan et al. 2020). In contrast with previous studies (Hoarau et al. 2002, Was et al. 2010), genome wide population structure was weak but significant at the continental shelf. Moreover, the analysis of SNPs from the two SVs suggested high divergence, correlated with environmental variables (latitude and salinity), and local adaptation in plaice populations.

3.8 Common sole, *Solea solea*

Number of studies	13
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[8]

The common sole, *Solea solea* (Linnaeus, 1758), is widely distributed in the North-East (NE) Atlantic continental shelf, from south Norway to the Mediterranean and the Black Sea (Muus & Nielsen 1999), including the western part of the Baltic Sea. It is a demersal species, with adults living in deep waters on the continental shelf, while juveniles are found in coastal and shallow waters. Nursery grounds include bays and estuaries. Sole is characterized by inshore-offshore migrations during the spawning season (winter-spring), that varies according to the latitude (Muus & Nielsen 1999).

Current management status

Sole is a commercially important flatfish species in the NE Atlantic and Mediterranean Sea. ICES consider 10 stocks for sole in the NE Atlantic (Figure 3.8). There is a general agreement between the ICES stock units and the management areas for which TACs are set (Table 2). In the Mediterranean Sea, stock assessment and management are provided for sole in the GSA 17.

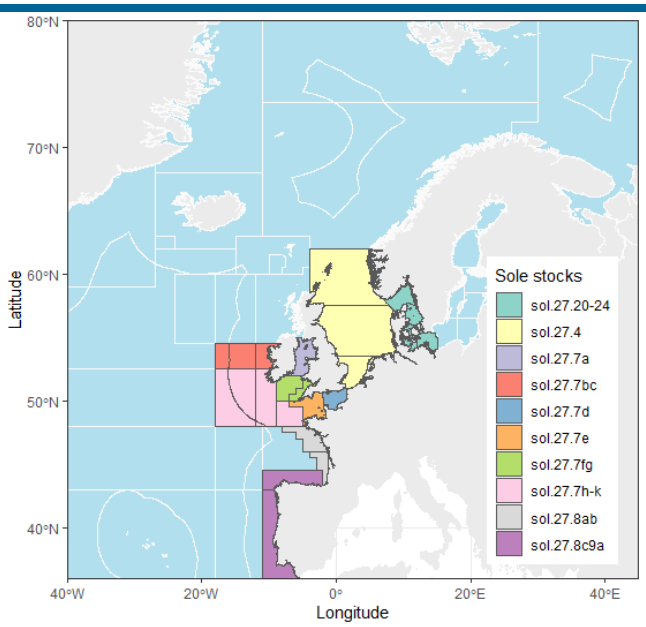


Figure 3.8. Stock assessment units (ICES) of common sole.

Sole in the Skagerrak, Kattegat, Belts and western Baltic (SDs 20-24) represent a separate stock unit from the larger North Sea stock. In the transition zone, landings are mainly from the Skagerrak and Kattegat, and presence of sole beyond the western Baltic is limited by the salinity (ICES 2020b). The sole stock in the North Sea is subject to a European multiannual plan (ICES 2020v). Fishing mainly occurs in the southern and south-

[8] Further details on symbols and how to read the factsheet are provided on page 16

eastern part of the basin, where sole is caught in mixed fisheries. In the English Channel two stock units are considered, eastern (Division 7.d) and western (Division 7.e), mostly supported by tagging studies (ICES, 2019a and reference therein). Sole in the Celtic Sea (Divisions 7.f, g) and the Irish Sea (Division 7.a) are considered two different stocks (see ICES, 2019 and references therein). The sole stock in the south Celtic Sea and southwest of Ireland (Divisions 7.h-k) is classified by ICES as a data-limited stock (ICES 2020o). Sole in the northern and central Bay of Biscay (Divisions 8.a, b) is thought to represent a distinct unit from the nearby populations (ICES 2018b). Little information is available for the stock in the southern Bay of Biscay and Atlantic Iberian waters (Divisions 8.c and 9.a). In division 9.a, sole it is fished with *Solea senegalensis* and *Pegusa lascaris* that represent the major proportion of misreported landings for *Solea solea* (ICES, 2014 and references therein).

Genetic population structure in a nutshell

Genetic investigations suggested presence of population structure for common sole within the NE Atlantic and in the Mediterranean Sea. In particular, genetic evidence supports:

- Differentiation between the NE Atlantic and Mediterranean populations (Kotoulas et al. 1995, Exadactylos et al. 1998).
- Differentiation between the North Sea (Subarea 4) and the Baltic Sea transition zone (Subdivisions 20-24) with by microsatellites (Cuveliers et al. 2012) and SNPs (Diopere et al. 2018, Le Moan et al. 2019b).
- Lack of differentiation between the Irish Sea (7.a) and Celtic Sea (7.f, g) (Cuveliers et al. 2012, Diopere et al. 2018).
- Genetic similarity for sole from the Bay of Biscay (Divisions 8.a-c) and Portuguese waters (Division 9.a) (Diopere et al. 2018) in contrast with stock assessment and management units.
- Genetic differentiation between the eastern and western English Channel supported (Cuveliers et al. 2012, Diopere et al. 2018). Eastern English Channel sole more similar to the North Sea; western English Channel more similar to Bay of Biscay.
- Differentiation between western and eastern Mediterranean (Kotoulas et al. 1995, Bahri-Sfar et al. 2011).
- Presence of a population in the Tyrrhenian and Ligurian Sea (MUs 9, 10) (Guarniero et al. 2002).
- Existence of a population in the southern part of Western Ionian Sea (MU 19) (Guarniero et al. 2002).
- Presence of two genetic units in the Adriatic Sea, one widespread (GSA 17, western part of GSA 18) and the other restricted to the eastern part of the southern Adriatic (eastern part of GSA 18) (Guarniero et al. 2002, Sabatini et al. 2018).

Mismatch

The following mismatches likely occur between the genetic population structure of common sole and the stock units used in assessment and management:

- Sole in the Irish Sea (7.a) and Celtic Sea (7.f-g) are considered two separate stock assessment units, although no evidence of genetic differentiation was reported.
- The Bay of Biscay (8.a, b) and the Atlantic Iberian coast (8.c, 9.a) are genetically homogeneous although considered two different stocks assessment and management units.
- The situation is more complex for the eastern and western English Channel stocks, that are clearly different. However, further studies are required to investigate at a finer scale their genetic connectivity with other nearby sole stocks.
- In the Adriatic Sea the western part of GSA 18 should be included in the sole stock of GSA 17 to match the assessment and management measures with the genetic unit.

Summary of genetic evidence

Population structure of common sole in its distributional range has been investigated by means of different genetic markers. Kotoulas et al. (1995) using allozymes, reported a temporally stable pattern of isolation by distance for sole. Genetic differences were detected between the English Channel, Bretagne and Bay of Biscay while in the Mediterranean between the western and eastern part the basin. However, lack of differentiation was observed between western and eastern English Channel samples, that are assessed and managed in separate units. Exadactylos et al. (1998) confirmed the differentiation between the NE Atlantic and the Mediterranean Sea, though reported near-panmixia for sole in the NE Atlantic (North Sea, Bay of Biscay, Irish Sea). While, using allozyme and Random Amplified Polymorphic DNA (RAPD) data, Exadactylos et al. (2003) reported highly significant differentiation between a continental group (Bay of Biscay and German Bright) and the British Isles (Irish Sea, North Sea) in the NE Atlantic. Rolland et al. (2007) showed genetic homogeneity for sole in the NE Atlantic (a panmictic genetic unit from Denmark to Portugal), while reported differentiation between the western and eastern part of the Mediterranean and the isolation of sole from the Adriatic Sea.

Cuveliers et al. (2011) investigation on genetic population structure of North Sea sole supported the presence of a homogeneous and temporally stable genetic unit in this basin; despite the high fishing pressure on this stock, temporally stable levels of neutral genetic diversity from 1957 to 2007 were reported. Using microsatellites and mitochondrial markers Cuveliers et al. (2012) identified several populations namely in the North Sea, the Baltic Sea transition zone (Skagerrak, Kattegat, Belt Sea), the Bay of Biscay and the Irish Sea-Celtic Sea. The situation is more uncertain for the English Channel, with the eastern English Channel sole similar to the North Sea and the western more similar to the Bay of Biscay samples, same pattern supported also with SNPs (Diopere et al. 2018).

Based on SNP markers, Diopere et al. (2018) found that population structure of sole in the NE Atlantic can be explained by an isolation by distance pattern and local adaptation along a latitudinal cline. Genetic differentiation was detected among the Baltic Sea transition zone, the North Sea and a southern group constituted by the Bay of Biscay and Portuguese samples. A separate population covering the Irish Sea and Celtic Sea was detected only by outlier loci.

A pattern of isolation by distance was reported also at a finer scale by Le Moan et al. (2019), that showed significant population structure for sole in the North Sea, Baltic Sea and the transition zone, suggesting that the divergence between North Sea and Baltic Sea sole occurred in presence of high levels of gene flow.

Within the Mediterranean, the analysis by Guarniero et al. (2002), based on a mitochondrial DNA marker, indicated the existence of several sole populations, one in the Tyrrhenian and Ligurian Sea (MUs 9, 10), two distinct populations in the Adriatic and an additional population in the southern part of the western Ionian Sea (MU 19). The existence of two genetically distinct populations in the Adriatic, one in the eastern part of the southern Adriatic (eastern part of GSA 18), and the other in the rest of the Adriatic (GSA 17 and western part of GSA 18) was confirmed by Sabatini et al. (2018). Differentiation between the western and eastern Mediterranean was reported (Kotoulas et al. 1995, Rolland et al. 2007). Bahri-Sfar et al. (2011) confirmed a west-east differentiation pattern and showed that the Siculo-Tunisian Strait is not acting as a barrier to gene flow for sole.

3.9 Turbot, *Scophthalmus maximus*

Number of studies	17
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[9]

Turbot, *Scophthalmus maximus* L., is an economically important flatfish species. It is distributed from Iceland and Norway, throughout the European coasts and down towards Morocco, including the northern Mediterranean and the Black Sea. Turbot is among the few marine fish species inhabiting the Baltic Sea. It is commonly found between 20-100 m, and spawning occurs in shallow waters between April and August. Turbot in the NE Atlantic is classified as a vulnerable species by the IUCN (IUCN 2019). Eggs and larvae are pelagic except in the Baltic sea where the eggs are demersal due to the lower salinity of the waters (Florin & Höglund 2007).

Current management status

Three stock assessment units exist for turbot in the NE Atlantic, namely 1) the Baltic Sea, 2) Skagerrak and Kattegat 3) the North Sea (Figure 3.9). The Baltic Sea stock (SDs 22-32) is mainly fished in the western subdivisions and analysis of survey data indicates that this stock is connected to the nearby turbot in the Kattegat (ICES 2020b). Turbot in Division 3.a (the Skagerrak and Kattegat) is assessed as a separate unit by ICES, it is mainly fished as a by-catch species and landings in 2019 were 204 t (ICES 2020v). ICES recognized this stock should be reviewed in light of available scientific evidence supporting the connectivity between turbot in 3.a with the North Sea and the Baltic Sea (ICES, 2020b; and reference therein). Hence, the stock of turbot in the

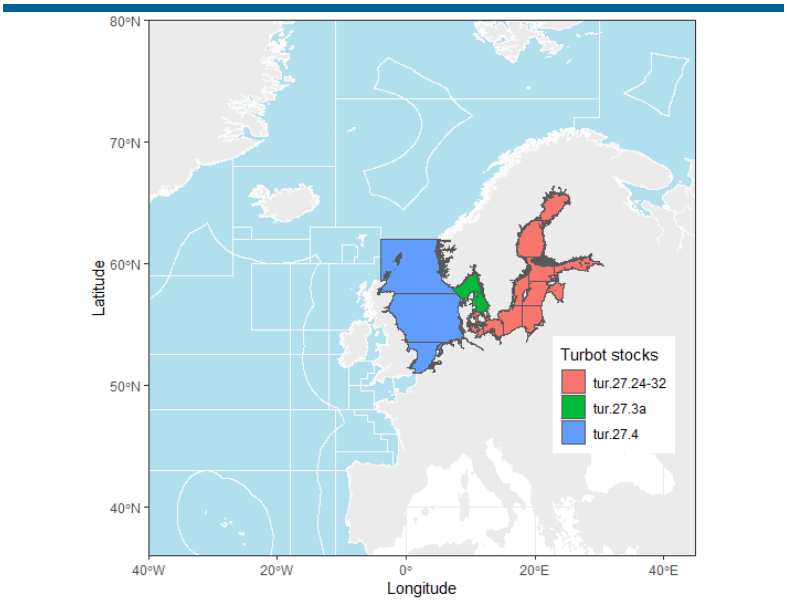


Figure 3.9 Turbot ICES stock assessment units.

[9] Further details on symbols and how to read the factsheet are provided on page 16

North Sea should include also the Skagerrak. Turbot in the North Sea is mainly fished with sole and plaice in mixed flatfish fisheries, and the Netherlands is the main fishing country. While the stocks in the Baltic Sea and Division 3.a are not managed by TACs, turbot in the North Sea is managed with brill under a combined TAC for Subarea 4 and 2.a (European waters) (Table 2). However, ICES provides separate stock assessment advice on fishing opportunities and stock status for brill and turbot. A combined TAC could lead to the overexploitation of the less valuable species (in this case brill). Additionally, this TAC does not match the stock units used for the assessment by ICES, for either of the species. Therefore, ICES highly recommended the management of these species by separate TACs that should match the spatial distribution of the stock unit used in assessment (ICES 2020v).

Genetic population structure in a nutshell

In general, population structure was observed with neutral genetic markers for turbot within the NE Atlantic. However, the presence of locally adapted populations was reported, and genetic evidence suggests the following spatial structure for turbot in its distributional range:

- Baltic Sea and North Sea are genetically different (Nielsen et al. 2004, Vilas et al. 2010, Vandamme et al. 2014), in line with assessment in two different stock units.
- The presence of a hybrid zone was reported in the Skagerrak and Kattegat, where Baltic and North Sea populations mix (Nielsen et al. 2004).
- Turbot in the Skagerrak is part of the same genetic unit inhabiting the North Sea in contrast to the existing stock units, that are separated for turbot in the North Sea (Subarea 4) and in the Skagerrak (Division 3.a) (Prado et al. 2018b).
- Kattegat is genetically part of the same unit of turbot in the Baltic Sea, however they are assessed in two different stock assessment units (Florin & Höglund 2007, Vandamme et al. 2014).
- Potential substructure was detected in the North Sea, where the southern samples were more genetically similar to the British Isles and English Channel while turbot from central and northern North Sea was more similar to the sample from Norway and Iceland (Vandamme et al. 2014).
- Turbot in the Bay of Biscay and Spanish Atlantic coast is weakly, but statistically significant, differentiated from the rest of the NE Atlantic sample (Vilas et al. 2010, Prado et al. 2018b).
- Presence of eastern and western lineages of turbot in the Mediterranean showed (Suzuki et al. 2004).
- In the Black Sea the existence of at least 3 different populations was detected (Turan et al. 2019, Firidin et al. 2020), resulting in a mismatch with the management unit since turbot is managed as one stock.
- Differentiation between turbot inhabiting the Adriatic Sea and the Black Sea was showed (Prado et al. 2018b).

Mismatch

Genetic evidence suggested presence of mismatches between stock assessment units and genetic units. The assessment of turbot in the Skagerrak and Kattegat as one stock unit (Division 3.a) is not supported by genetic studies. In fact, turbot in the Kattegat is genetically part of the same unit present in the Baltic Sea, while turbot in the Skagerrak is part of the North Sea (Subarea 4) population.

Although it is clear that turbot in the Skagerrak and North Sea belong to the same population, the status of turbot in the North Sea and adjacent waters is not. Potential substructure within the North Sea was suggested (Vandamme et al. 2014), as well as a lack of differentiation with the English Channel and British Isles samples, questioning the boundaries of the current stock assessment unit (Turbot in Subarea 4).

In the Black Sea, currently managed as one stock unit, the existence of several populations was reported (Turan et al. 2019, Firidin et al. 2020) resulting in a mismatch. Hence, for a more sustainable fisheries management of Black Sea turbot the presence of these populations should be considered.

Summary of genetic evidence

Turbot is a commercially important flatfish species in the NE Atlantic, Mediterranean and Black Sea and its population structure has been studied with several genetic markers.

Blanquer et al. (1992) using allozymes reported low levels of genetic diversity and absence of structure for turbot in the NE Atlantic (from the Kattegat to Moroccan coast) and Mediterranean Sea. The only sample differentiated was the Aegean Sea. Hence, the mismatch in this study is due to a lack of differentiation between sampling locations (the North Sea and Kattegat) that are assessed as different stocks.

A lack of genetic differentiation was reported also at a finer scale by Bouza et al. (1997) in northwest Spain. In this study samples also of farmed turbot were analysed showing lower levels of genetic diversity than wild samples. The mismatch analysis here is not applicable, since there is no stock assessment or management units proposed for turbot in this region.

In a successive investigation, Coughlan et al. (1998) analysed microsatellite variation in wild and farm samples of turbot form Ireland and Norway. Genetic differentiation was detected between the two farm samples but not between the two wild samples. This lack of differentiation could be due to high levels of gene flow at pelagic life-stages or due to the post-glacial colonization history of the species. In line with previous studies, Bouza et al. (2002) analysing domesticated turbot and wild populations in the Cantabrian Sea and Galician waters, confirmed the absence of structure at this geographic scale and loss of genetic diversity for the samples of domesticated turbot.

In contrast to previous investigations, Nielsen et al. (2004) detected genetic population structure in turbot inhabiting the NE Atlantic and Baltic Sea, despite low level of differentiation reported within the Atlantic sample (North Sea, Bay of Biscay), as well as

within the Baltic Sea. Biologically significant differentiation was observed between the Atlantic/North Sea and the Baltic Sea populations and the presence of a hybrid zone was reported in the North Sea- Baltic Sea transition zone (Skagerrak, Kattegat, Belt Sea) where individuals from both populations mix.

Florin and Höglund (2007), using microsatellites, analysed a total of 11 samples across the Baltic Sea (including temporal replicates) reporting weak genetic structure within the basin (F_{ST} 0.004). Despite the sedentary life-style of turbot, there is no indication for substructure inside the Baltic Sea. Hence, a mismatch with the stock assessment unit exists, due to absence of differentiation between turbot from the Baltic Sea and the Kattegat (Division 3a), currently considered two separate ICES stock units. Vilas et al. (2010) using a combination of neutral and outlier microsatellites confirmed the weak spatial structure of turbot in the Atlantic waters and reported the existence of 3 different populations for turbot in the North Sea, the Baltic Sea and the Atlantic Iberian waters (Cantabrian Sea and Galicia), moreover presence of adaptative divergence between the Baltic Sea- Atlantic group was shown. Therefore, no mismatches are present based on this study.

In Imsland et al. (2014) findings indicated population homogeneity for southern Norway and Icelandic turbot that were; however differentiated from the Irish Sea. The Kattegat sample was the most differentiated from the Atlantic ones, hence no mismatch was revealed with the stock assessment units.

Vandamme et al. (2014) found clear evidence of neutral population structure in the NE Atlantic, indicating the presence of at least three populations, i.e. the Baltic Sea, the NE Atlantic ground and the Irish Shelf, confirming previous studies reporting differentiation between the Baltic and the Atlantic (Nielsen et al. 2004). Including microsatellite loci under selection, substructure was detected with a break in the North Sea between northern and southern Atlantic groups. The mismatch with the stock assessment and management units is evident for the North Sea, because central and northern North Sea samples grouped with the Northern Atlantic (Norway, Iceland) while samples from southern North Sea grouped with the English Channel, British Isles and southern Atlantic. Another mismatch is present due to a lack of differentiation between the Kattegat and the Baltic Sea, assessed as two different stocks. Vilas et al. (2015) analysed, with a combination of microsatellites and SNPs, turbot collected from the Baltic Sea to the Atlantic Iberian waters, including also a sample from a farm. In line with previous studies, the divergence of turbot inhabiting the Baltic Sea and the Atlantic was confirmed. Moreover they reported the presence of candidate genes involved in local adaptation of wild turbot populations experiencing different temperature and salinity conditions. Significant differentiation was found at SNPs only when the Baltic sea or the farm samples were included in the analysis, confirming the lack of structure within the Atlantic. While, for microsatellites all the pairwise comparisons were significant, except between the Cantabrian Sea and the Atlantic Galician coast.

Prado et al. (2018) developed a genetic tool for the identification of fish with farmed origin in the wild, that can be used to evaluate the impact of escapes and restocking activities on wild populations. Significant and high genetic differentiation between farmed and wild populations was observed (mean F_{ST}= 0.059), as well as evidence for adaptation to domestication. Presence of turbot with farmed ancestry was reported especially where restocking has been carried out. Prado et al. (2018b) used SNP analysis to elucidate the genetic population structure of turbot in its distributional range. The study suggested the existence of four main regions i.e., Baltic Sea, NE Atlantic group, Adriatic Sea and Black Sea. Divergence due to local adaptation was detected between the Baltic Sea, the Atlantic and the Black Sea, and temperature and salinity were identified as likely causes. Parallel evolution was observed in the Baltic Sea and the Black Sea, with both basins exhibiting lower salinity. Substructing within the Atlantic sample was shown, with Norway and the southern Atlantic (Bay of Biscay and Atlantic coast of Spain) weakly differentiated from the rest of the Atlantic samples. Hence, a mismatch can be detected for the Skagerrak sample, which is not differentiated from the North Sea and the other Atlantic samples, clearly showing a mismatch with the assessment units (division 3a and the North Sea assessed separately). Moreover, the lack of differentiation between the North Sea and other Atlantic samples should be further investigated. For management purpose the authors suggest these four regions should be considered, as well as the differentiation of the Norway and Spanish samples, and the possible substructure within the Baltic Sea (slightly differentiated north and southern samples).

Le Moan et al. (2019) reported clear differentiation between the North Sea and Baltic Sea populations of turbot, and the presence of only 6 individuals of admixed origin in the Kattegat, the F_{ST} between North Sea and Baltic Sea was 0.044.

In the Mediterranean, Suzuki et al. (2004) analysed mitochondrial DNA variation in turbot, showing the presence of a western and eastern lineage and the existence of endemic haplotypes in the Sea of Azov. A lack of differentiation among samples from the western Black Sea was reported by Atanassov et al. (2011). In the Turan et al. (2019) study, differentiation between the Black Sea and Marmara Sea was supported by both microsatellites and mitochondrial markers. Although turbot in the Black Sea is managed with a TAC, microsatellites revealed additional substructure within the basin where all four samples were significantly differentiated from each other, hence, suggesting presence of a mismatch with the management unit. Previous findings were confirmed by Firidin et al. (2020), that by increasing the number of samples and markers, showed significant differentiation between the southern and northern (Crimea and Sea of Azov) Black Sea. Based on their analysis, the existence of 3 stocks was supported, as well as the presence of admixture between the 2 populations at the southern coasts. These units should be implemented for a more sustainable fisheries management.

4 Gadiformes

4.1 Blue Whiting, *Micromesistius poutassou*

Number of studies	4
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[10]

Blue whiting, *Micromesistius poutassou* (Risso 1826), is a pelagic fish of the Gadidae family widely distributed on the shelf edge of the North-East (NE) Atlantic, from the Canary Islands to Spitzbergen (Ryan et al. 2005). It is also present in the North-West Atlantic and in the Mediterranean. Adults migrate in early spring towards spawning grounds where the majority of the catches take place (ICES, 2020a and references therein). Spawning season varies according to latitude, starting in January in the southern areas. Spawning occurs pelagically and eggs and larvae are pelagic. Extensive spawning and feeding migrations are known for blue whiting.

Current management status

Blue whiting is a commercially important species. It is assessed as one stock unit in the Northeast Atlantic and adjacent waters (subareas 1-9, 12, and 14), however TACs are set for several management units (Table 2). The stock identity was questioned by ICES. ICES recognized that the scientific evidence supports the presence of two stocks for blue withing in the NE Atlantic. However, more information is needed for each population to generate separate advice on stock status and fishing opportunities therefore assessment is still carried out for one stock unit (Figure 4.1). It is a large fishery

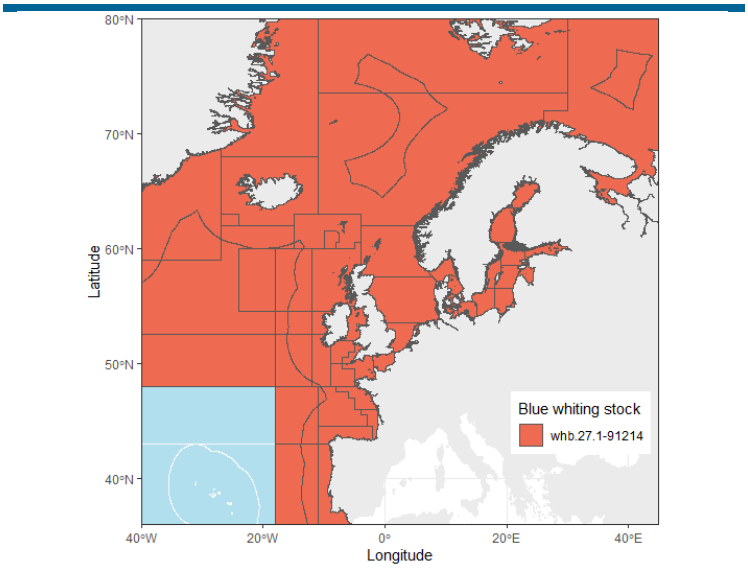


Figure 4.1. Blue whiting ICES stock assessment unit.

[10] Further details on symbols and how to read the factsheet are provided on page 16

in the NE Atlantic, with total catches in 2019 of 1 515 527 t, exceeding the recommended catch from ICES (≤ 1 143 629 t), resulting in fishing pressure above sustainable levels.
Blue whiting is mainly fished in the spawning grounds (Subarea 12; divisions 5.b, 6.a-b, 7.a-c), around the Faroes, Rockall and the western European shelf during the first and second quarter of the year (ICES 2020w). It is fished in direct fisheries by pelagic trawlers and in direct and mixed fisheries in the North Sea (Subarea 4 and division 3.a). Catches from the southern areas (subarea 8, 9; division 7.d-k) in 2019 amounted to 130 194 t, representing less than the 10% of the total catches (ICES 2020p). The main fishing countries are Norway, Iceland, the Faroes and Russia.

Genetic population structure in a nutshell

Significant genetic structure was reported for blue whiting, even though one stock unit is considered in stock assessment. Based on genetic evidence, it has been suggested:

- Presence of a local population in the Barents Sea (Giæver & Stien 1998, Ryan et al. 2005).
- Genetic homogeneity in southwest of Ireland (Mork & Giæver 1995).
- Differentiation NE Atlantic- Mediterranean Sea (Ryan et al. 2005).
- Existence of a northern (Hebrides, Rockall, Porcupine, Sulisker and Papa Banks) and southern (Celtic Sea) stock in the NE Atlantic (Was et al. 2008).
- Differentiation of southern Bay of Biscay (8.c), currently managed in a different unit but assessed in the same stock unit of the northern stock (Was et al. 2008).

Mismatch

Significant genetic structure was reported within the NE Atlantic that contrasts with the presence of one stock assessment unit. The existence of separate populations in the Barents Sea, northern and southern of Porcupine Bank (Was et al. 2008), and in south Bay of Biscay (Was et al. 2008) was reported. These findings contrast with the assessment of blue whiting in the NE Atlantic as one stock unit. These mismatches could bias stock assessment and potentially lead to the overexploitation of the weakest populations. Furthermore, a mismatch is evident also between management and genetic units. In fact, the northern and southern Porcupine Bank populations, as well as of the Barents Sea population is carried out as one management unit, despite they most likely represent genetically different units.

Summary of genetic evidence

Several studies have investigated the genetic population structure of blue whiting in the NE Atlantic. No further studies were published after the review conducted by Reiss et al. (2009). Genetic differentiation was detected for blue whiting despite pelagic life-stages and spawning and extensive feeding migrations potentially promoting gene flow. Mork and Giæver (1995) analysed genetic variation at allozyme loci in samples collected west of the British Isles (Southwest of Ireland) during the spawning season for two consecutive

years. No sign of population mixture was reported, in line with the assessment and management unit.

Giæver and Stien (1998) using allozymes studied genetic population structure of blue whiting in its distributional range, including samples from the Mediterranean Sea. The existence of a separate population of blue whiting in the Barents Sea, genetically different from the rest of the NE Atlantic was supported, despite the temporal difference observed between two of the Barents Sea samples. In fact, the population spawning at west of British Isles undertakes feeding migrations into Norwegian waters that can vary annually and explain the genetic similarity with one of the Barents Sea samples. Genetic homogeneity was reported for blue whiting in west of British Isles, the Porcupine Bank and the Norwegian Sea supporting the presence of one stock in these areas. Moreover, the presence of a genetically different populations was suggested also in a Norwegian fjord (Romsdalsfjord), even if not statistically significant. The mismatch between genetics, stock assessment and management units is due to the presence of a local population in the Barents Sea, which has not been taken into account in the current assessment and management units.

Through mini- and microsatellite analysis Ryan et al. (2005) confirmed that blue whiting in the Barents Sea and the Mediterranean are clearly differentiated from the rest of the NE Atlantic. The mismatches between genetics, assessment and management units due to the existence of a local population in the Barents Sea is confirmed. Moreover, genetic heterogeneity was reported for the Hebrides-Porcupine Bank spawning aggregations, that however was not temporally stable.

Was et al., (2008) using 5 microsatellites, reported significant genetic structure within the NE Atlantic for blue whiting, with the Celtic Sea and Bay of Biscay differentiated from the rest of the northern samples (the Hebrides, Rockall, Porcupine, Sulisker and Papa Banks) for which genetic homogeneity was shown. However, temporal variability was detected in the Rockall Bank where one of the temporal replicates differentiated from the others and the northern samples. In contrast to the existing stock unit, a northern and southern stocks was identified in the NE Atlantic, with additional substructure in the southern one. The apparent mismatch is due to the presence of local populations in the Celtic Sea and Bay of Biscay, that are, however, assessed as part of the same stock unit with the rest of the NE Atlantic. The mismatch between genetic and management units is due to the inclusion of the Celtic Sea with the rest of the NE Atlantic subareas rather than considering it as a separate unit. In contrast, the management of southern Bay of Biscay is currently carried out as a separate unit (Table 2).

Temporal variation was reported in the Barents Sea (Giæver & Stien 1998), in the Hebrides (Ryan et al. 2005) and in the Rockall Bank (Was et al. 2008) and should be further investigated. Additional studies are needed to disentangle the spatio-temporal genetic population structure of blue whiting in the NE Atlantic with more powerful markers.

4.2 Whiting, *Merlangius merlangus*

Number of studies	5
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[11]

Whiting, *Merlangius merlangus* Linnaeus 1758, is an important commercial gadoid species, widely distributed on the North-East (NE) Atlantic in inshore and shallow waters down to 200 m. whiting is present in the NE Atlantic continental shelf, form Iceland and Norway to Portugal, as well as in the western Baltic Sea, the Mediterranean and Black Sea (Hureau, 1984). Spawning season goes from early spring to mid-summer. Eggs and larvae are pelagic, allowing passive dispersion by ocean currents.

Current management status

Currently, there are 7 stock assessment units for whiting in the NE Atlantic (Figure 4.2). Mismatches already exist between assessment and management units (Table 2), for instance two different units are considered for ICES in divisions 6.a and 6.b however subarea 6 is managed together with division 5b and subareas 12, 14.

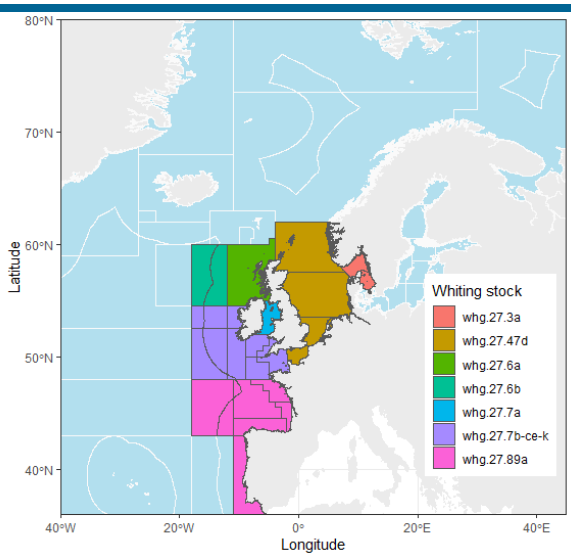


Figure 4.2 Whiting ICES stock assessment units.

The North Sea (Subarea 4) and Eastern Channel (Division 7.d) are considered part of the same stock for ICES. However, the TAC for the North Sea does not include the Eastern Channel, which is managed with the Celtic Seas divisions (7.b-k). ICES recommended the establishment of a separate TAC for the Eastern Channel for a more sustainable management of the fishery (ICES 2020v). Scientific evidence underlines a complex population structure for whiting in the North Sea (northern and southern stocks), though ICES requires more data prior to a revision of the stock (ICES 2020v).

[11] Further details on symbols and how to read the factsheet are provided on page 16

A separate stock assessment unit exist for the Skagerrak and Kattegat (Division 3.a), with limited information on population structure (ICES 2020v). The total catches in 2019 were 806 t, of which 627 t were estimated as discards, landings amounted at 179 t.
Whiting is very common in west of Scotland (Division 6.a), while less in the Rockall (Division 6.b) that are considered two separate ICES stocks. A TAC is set for whiting in subarea 6, 12 and 14 and European and international waters of Division 5.b resulting in a mismatch with the assessment units (Table 2). The stock size of whiting in west of Scotland (Division 6.a) is likely below reference points and the advice is zero catches for 2020 and 2021 (ICES 2020r).
Thought, ICES recognize that the separation of whiting inhabiting the North Sea, Irish Sea, Celtic Sea and Divisions 7.b-c is not very clear, a stock unit exist for southern Celtic Seas and Western English Channel (Divisions 7.b-c, e-k) (ICES 2019l). Here, whiting is mainly fished in mixed demersal fisheries and seine fisheries. Total catches in 2019 were 6294 t, the majority caught by otter trawlers. The stock size is below reference points despite a decrease of fishing pressure. Also the stock size of whiting in the Irish Sea (Division 7.a) is below reference points and fishing pressure was above F_{MSY} in 2018 (ICES 2019n). Total catches in 2018 were 899 t, of which 853 t were discards. Discards are high, since whiting it is fished as bycatch in *Nephrops* fishery: 98% of the discards in 2018 were from *Nephrops* fishery (ICES 2019n). Whiting in the Bay of Biscay and in Atlantic Iberian waters is at the southern limit of the distributional range in the NE Atlantic. This stock is classified as a data limited stock (category 5), since only catch data are available. It is mainly fished in mixed demersal fisheries by French and Spanish vessels (ICES 2020s).

Genetic population structure in a nutshell

Low levels of differentiation were found for whiting supporting high levels of gene flow within the NE Atlantic, likely mediated by the passive dispersion of pelagic eggs and larvae. Genetic population structure was however reported:

- Within the North Sea, where a northern and southern population have been identified in line with other methods (Charrier et al., 2007 and reference therein). Moreover, a local population in Flamborough Head was identified. The complex population structure of whiting in the North Sea does not match with the assessment and management units.
- Southern Bay of Biscay, clearly differentiated from the rest of the NE Atlantic (Charrier et al. 2007).

Mismatch

Presence of a mismatch between genetic units and assessment and management units is evident for the North Sea stock, where the complex of populations present does not match the stock assessment and management units.

Summary of genetic evidence

Genetic population structure of whiting has been investigated mainly using microsatellite markers. In line with their assessment and management in two separate units, Galvin et al. (1995) found significant differentiation between whiting from the Irish Sea and the North Sea at one minisatellite locus. This preliminary result was promising, however in general, more loci and samples are needed to study genetic population structure. Overall, low but statistically significant levels of differentiation (F_{ST} 0.006) were reported in Rico et al. (1997) analysis, with 3 microsatellite loci. Significant differentiation was detected between Norway and the North Sea whiting at one locus, as well as between the northern and the southern North Sea samples, at two loci. However, an excess of homozygosity was detected requiring a careful interpretation of the results.

Low levels of differentiation within the NE Atlantic were confirmed by Charrier et al. (2007), who reported genetic homogeneity for samples from the Celtic Sea to the western Hebrides based on microsatellites. However, the southern Bay of Biscay was clearly differentiated from the rest of the samples and complex population structure was suggested for whiting in the North Sea. Microsatellites supported differentiation between northern and southern North Sea with Dogger Bank acting as a barrier, in line with tagging, parasites and meristic analyses (Charrier et al., 2007 and reference therein). Moreover, a separate population located in Flamborough Head was identified. Despite several populations have been identified within the North Sea, this information is not taken into account in assessment and management resulting in a mismatch.

Analysis of mitochondrial DNA variations in samples from Norway, Iceland and southern North Sea (Eiríksson & Árnason 2014) supported lack of structure and high levels of gene flow in the NE Atlantic for whiting. The mitochondrial analysis was carried out with a neutral marker and confirmed low levels of differentiation in whiting over a wide geographic scale. However previous genetic studies using microsatellites found presence of population structure in whiting at a smaller geographic scale (Rico et al. 1997, Charrier et al. 2007). In both studies it was not tested the neutrality of the markers and microsatellite loci can be affected by natural selection. Hence, the population structure found at microsatellites could be due to local adaptation to different environments rather than reflect neutral divergence.

Genetic population structure was also investigated in the Black Sea, where the analysis of 8 samples from the Turkish coast, with RAPD markers did not detect any differentiation (Bektas & Belduz 2007). In line with other studies that analysed morphological and meristic characters, the presence of only one stock of whiting in the Black Sea was confirmed.

4.3 Haddock, *Melanogrammus aeglefinus*

Number of studies	3
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[12]

Haddock, *Melanogrammus aeglefinus* L., is an important commercial gadoid species in the North Atlantic. In the North-East (NE) Atlantic is distributed from Iceland and the Barents Sea in the north down to Portugal in the south. Spawning season is from January to June. Adults are demersal and live on the continental shelf and banks (40-300 m) avoiding deep-water areas. Eggs and larvae are pelagic and can be dispersed by ocean currents (Giæver and Forthun, 1999 and reference therein).

Current management status

Haddock sustains commercially important fisheries in the NE Atlantic, where 7 stock assessment units are present (Figure 4.3). There is a mismatch for several of these stock units and the management units for which TACs are set (Table 2). Haddock in the Faroese grounds (Division 5.b) is believed to be a stock unit, relatively stationary as suggested by tagging evidence (ICES 2017e). It is mainly fished at the Faroe Plateau by Faroese vessels (ICES 2017e). The Faroese and Icelandic stocks are considered separate, since they are separated by an area of deep-water which haddock is known to be reluctant to cross (ICES 2013b). It is fished in mixed demersal fisheries mostly with cod by bottom trawlers and longlines (ICES 2013b).

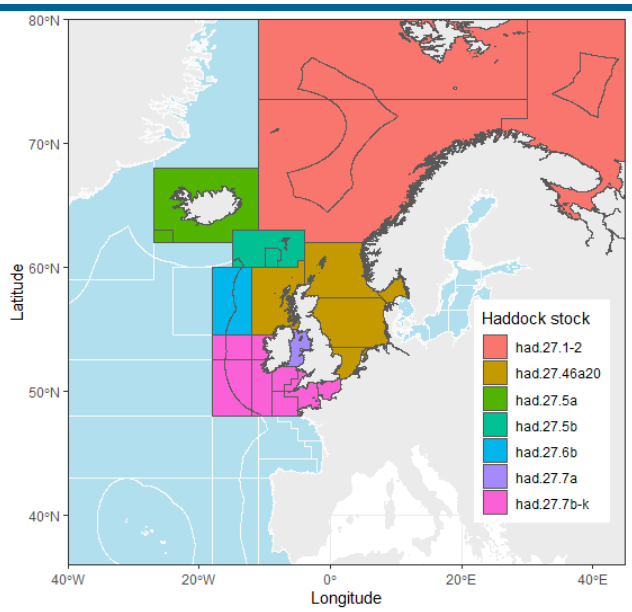


Figure 4.3. Haddock ICES stock assessment units.

[12] Further details on symbols and how to read the factsheet are provided on page 16

Haddock in the North Sea, Skagerrak and west of Scotland is assessed as a single stock unit by ICES since 2014, when west of Scotland (Division 6.a), based on multiple evidence, was included in the stock known as the 'Northern Shelf haddock' (ICES, 2020 and references therein). However, TACs are given for three different management units (Table 2) resulting in a mismatch between assessment and management measures. It is fished in direct fishery and in mixed demersal fisheries with cod, whiting and *Nephrops*. A conspicuous part of the landings are from the northern areas. Haddock in the Irish Sea is believed to represent a separate stock, distinct from neighbouring areas. Both the assessment and management units are set for the Irish Sea (Division 7.a). Part of the TAC is fished as by-catch in *Nephrops* fishery and the UK and Ireland are the main fishing countries. Southern Celtic Seas and English Channel (divisions 7.b–k) haddock is assessed as a single stock unit. Landings from 7.d (eastern English Channel) are not included in the assessment. There is a mismatch with the management unit, with the TAC is set for 7.b–k, 8, 9 and 10 only; however, the landings outside the assessment area are few. Moreover, it is not clear whether this stock (divisions 7.b-k) represent a separate population with respect to neighbouring areas (ICES 2017f).

Genetic population structure in a nutshell

Genetic population structure of haddock in the NE Atlantic has been investigated only with allozymes. Further studies are needed with more powerful markers to explore neutral and adaptive pattern of genetic differentiation. The available genetic evidence supports:

- Rockall (Division 6.b) and Faroese grounds (Division 5.b) as separate stocks in line with their assessment and management in separate units.
- Differentiation between west of Scotland (6.a) and Faroes grounds (5.b) supported (Jamieson & Birley 1989). However, a TAC is set for Division 5.b and 6.a jointly, resulting in a mismatch between genetic and management units.
- The presence of two genetically different populations in the North Sea has been reported, separated by the Greenwich meridian, a western population (east of Scotland, Shetland, west of Scotland) and an eastern population (Viking and Fisher) (Jamieson & Birley 1989). This contrasts with the assessment and management in the same unit.
- Presence of a population inhabiting west of Scotland, east of Scotland (North Sea) and the Shetland (Jamieson & Birley 1989); not taken into consideration in stock assessment and management.
- Presence of an isolation by distance pattern along the Norwegian coasts (Giæver & Forthun 1999).
- Indications of possible differentiation of haddock from Iceland and Barents Sea (Giæver & Forthun 1999), that need to be confirmed by further studies.

Mismatch

Mismatches between the genetic structure found and the assessment and management units are evident for haddock in the North Sea, where the presence of an eastern and western populations is not taken into account currently, either in assessment or management. A mismatch between genetic and management units occurs for the Faroe (5.b) and west of Scotland (6.a) stocks. They are managed with a TAC set for the two divisions jointly (Table 2) despite the existence of genetic differentiation.

Summary of genetic evidence

Information on genetic population structure of haddock in the NE Atlantic is limited.

Jamieson and Birley (1989) analysed the distribution of transferrin alleles in 1420 individuals collected between the 1976-1983 in the NE Atlantic. The presence of separate stocks for haddock in the Faroe and Rockall Bank was supported. Moreover, another unit was identified in east and west of Scotland and the Shetland. Hence, in the North Sea two different populations were detected, eastern (Fisher and Viking) and western of the Greenwich meridian. These findings clearly do not agree with the assessment and management units present in the North Sea.

Giæver and Forthun (1999) using 8 allozyme loci did not detect significant levels of genetic differentiation among samples collected off Norwegian coastal water and fjords, North Sea, Barents Sea and Iceland. However, the Icelandic sample was genetically different at one locus and haddock from the Barents Sea was identified as different unit but the low number of individuals analysed did not allow the authors to draw definitive conclusions. Moreover, a pattern of isolation by distance was described for haddock along the Norwegian coasts. In another study, Lage et al. (2001) using microsatellites investigated population structure in the North-West Atlantic and included a sample from Norway. Results indicated that Norway was differentiated from all the other western Atlantic samples. To date, studies investigating genetic population structure of haddock in the NE Atlantic using microsatellites or SNPs have not been carried out. Further investigations are needed to confirm previous findings at allozyme loci and to explore population structure of haddock with more powerful markers.

4.4 Ling, *Molva molva*

Number of studies	1
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Europe

Mediterranean

Distribution[13]

Ling, *Molva molva* L., is a commercial species widespread in the North-East (NE) Atlantic. Ling is commonly distributed in Iceland, Faroese grounds, Norway and the Barents Sea, while it is less common in western Atlantic, Atlantic Iberian waters and western Mediterranean. Despite it is considered by ICES as a deep-water species, ling does not have the particular features (i.e. low fecundity) shared by those species (Gonzalez et al. 2015). In fact, it is characterized by high fecundity. Adults are demersal and are commonly found between 100- 400 m, while eggs and larvae are pelagic and can be transported by ocean current (Gonzalez et al., 2015; and references therein). Spawning occurs in spring-early summer, and pelagic life-stages remain in the plankton for 2-5 months.

Current management status

Scientific evidence on population structure for ling in the NE Atlantic is extremely limited. Based on the observation that connectivity is unlikely, ICES proposed the existence of separate stock units, i.e. in Iceland (Division 5.a), in the Faroese grounds (Division 5.b) and in the Norwegian sea (Subarea 1 and 2) (Figure 4.4) (ICES 2020l). Though the presence of distinctive stocks is less likely in the European continental shelfs, hence the inclusion of the North Sea, the British Isles and the rest of the subareas represented as a single stock unit (ICES 2020l).

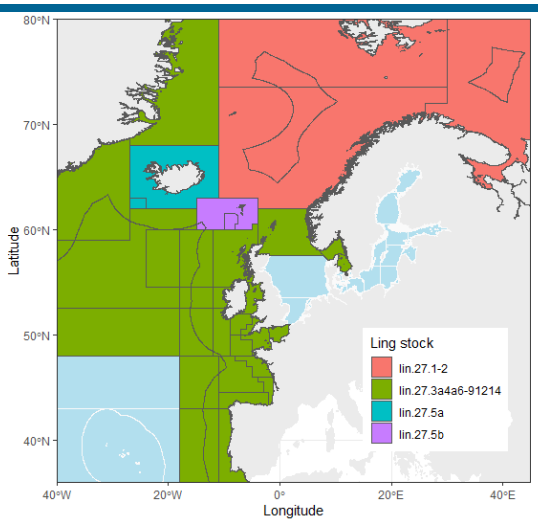


Figure 4.4. Ling ICES stock assessment units.

Ling in division 5.b is mainly caught by longline fisheries. In 2019 landings were 7 819 t, of which 67% where landed by Faroese vessels (ICES 2020l). In Iceland (Division 5.a), landings were 8 269 t in 2019, ling is mostly fished in the south,

[13] Further details on symbols and how to read the factsheet are provided on page 16

south-western and west part of the island by longline fishery (80% of the landings) (ICES 2020l). Norway is the main fishing country for the stock in Subareas 1 and 2. Compared to previous years, landings are increasing, with an estimation of 11 408 t for 2019 of which most are from Division 2.a (11 316 t) (ICES 2020l). There is a directed fishery for ling, caught mainly by longlines and gillnets but it is also a by-catch species in other fisheries. Landings for the stock of ling in the rest of the NE Atlantic (Division 3a, Subareas 4, 6-9, 12, 14) were 20 777 t in 2019, most of which were from the North Sea (11 443 t from division 4.a), subarea 6 (6 543 t from division 6.a) and 7 (ICES 2020l). In subarea 4 is caught both in directed fishery by Norwegian longline fisheries around Shetland and northern North Sea and as by-catch. In subareas 6 and 7, it is fished in direct longline fisheries and as by-catch in trawl fisheries. In the remaining subareas (8, 9, 12 and 14) ling is fished as a by-catch species.

Genetic population structure in a nutshell

Despite the commercial importance of ling in the NE Atlantic, information on genetic population structure for this species is extremely limited, but current evidence is potentially informative. The only genetic study found is by Gonzalez et al. (2015) that analysed ling at 11 microsatellites and supports:

- At a large scale, an eastern and western unit in the NE Atlantic.
- Genetic differentiation between ling in the northern North Sea (4.a) and the Rockall (division 6.b) that are however considered part of the same stock unit by ICES.
- Presence of separate units in Norway, Faroe and Iceland, in accordance with their assessment in distinct stock units.

Mismatch

In general, more studies are needed to explore genetic population structure of ling in the NE Atlantic at a finer scale. Based on available genetic evidence the inclusion of ling from the North Sea (Division 4.a) and Rockall (Division 6.b) in the same ICES stock unit is not supported. This information should be taken into account for a possible revision of the stock units in the NE Atlantic. Moreover, a TAC is set for ling in Union and international waters of subarea 5, however division 5.a (Iceland) and 5.b (Faroes grounds) are assessed as distinct stocks by ICES and genetic evidence supports their differentiation. Hence, resulting in a second mismatch.

Summary of genetic evidence

The first study investigating genetic population structure of ling in the NE Atlantic was published by Gonzalez et al. (2015) using neutral microsatellites analysing 6 samples of ling collected during the main spawning season in Iceland, in the Faroe, in the Rockall and in 3 locations along Norway. Overall differentiation was statistically significant (F_{ST} 0.002). Landscape genetics analysis supported the presence of two groups in the NE Atlantic, an

eastern (Rockall and Iceland) and western (Norway and Faroe). At a finer scale, this study supports the inclusion in different units of Iceland, Norwegian coasts and the Faroese grounds. Whereas, the presence of one unit that contains the west of British Isles and the North Sea is not supported by genetic evidence. Microsatellites confirmed a genetic break between Rockall (6.b) and the North Sea (4a), that; however, are assessed in the same stock unit by ICES. Hence, a mismatch between genetic and stock assessment units was observed.

4.5 Tusk, *Brosme brosme*

Number of studies	2
Population structure	✓
Match genetic- Stock assessment units	✓
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[14]

Tusk is a commercial fish species living in the northern part of the Atlantic. In the NE Atlantic is commonly found on the continental shelf, in east of Greenland, Iceland, in the Mid-Atlantic Ridge, around the Faroe Islands, in the Barents Sea as well as along the European shelf (Svetovidov 1986). It is commonly found between 100-400 m but can reach depths of 1000 m. Adults are demersal, while eggs and larvae are pelagic, remaining in the water column for 1-4 months. Spawning season is in spring-summer months and varies with latitude.

Current management status

Genetic evidence of populations structure for tusk in the NE Atlantic have been taken into consideration by ICES to design the stock assessment units (ICES 2020l). Currently, there are 5 distinct stock units for tusk, i.e. a stock in subdivision 5.a and 14, one in the Mid-Atlantic Ridge, one in Rockall (division 6.b) and one in subareas 1 and 2 (Figure 4.5). ICES included the remaining areas in a separate stock (Table 2) until additional evidence of population structure is available also for those regions.

Tusk in Iceland and Greenland (division 5.a and 14) is mainly fished in mixed fisheries or as a by-catch species in haddock and cod longline fisheries (ICES

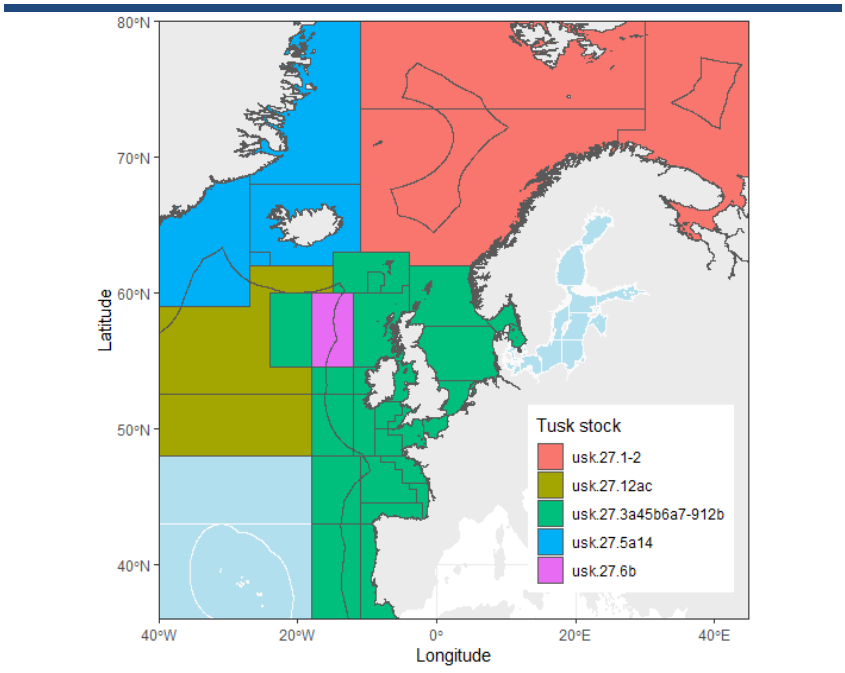


Figure 4.5. Tusk ICES stock assessment units.

[14] Further details on symbols and how to read the factsheet are provided on page 16

2020l). The main fishing country is Iceland, followed by the Faroes and Norway. The stock of tusk in the Mid-Atlantic Ridge (divisions 12.a,c) is fished as by-catch species, landings are low and ICES advised zero catches for this stock in 2020-24 (ICES 2020l). Tusk in Rockall (division 6.b) is exclusively caught as by-catch species (ICES 2020l). Landings in 2019 were 100 t, most of which were from Norway (70%), that is historically the main fishing country for tusk in the division (ICES 2020l). Subarea 1 and 2 are considered a distinct stock for tusk, landings are mainly from division 2.a, with Norway accounting for most of the catches (ICES 2020l). Tusk is mainly a by-catch in fisheries targeting cod and ling. A TAC is set by Europe for European vessels in Union and international waters of subarea 1, 2 and 14, while Norway does not regulate tusk fishery by TAC (ICES 2020l).
The stock of tusk present in the rest of the areas (3.a, 4.a, 5.b, 6.a, 7, 8, 9, 12b) it is mainly fished as by-catch. Landing are primarily from the Faroes grounds (division 5.b), the North Sea (subarea 4), and west of Scotland (division 6.a) (ICES 2020l). Catches in the North Sea are mostly from the northern part. In the Faroes grounds, the majority of the catches are from the Plateau by longlines.

Genetic population structure in a nutshell

Available genetic information on population structure of tusk in the NE Atlantic supports low but statistically significant levels of differentiation and the presence of distinct populations in:

- Rockall (division 6.b);
- The Mid-Atlantic Ridge.

In the rest of the NE Atlantic relatively genetic homogeneity was reported (Knutsen et al. 2009).

Mismatch

Genetic evidence supports the presence of distinct stocks in Rockall (6.b) and the Mid-Atlantic Ridge (Subarea 12.a, c) in line with their assessment in two different units by ICES. However, a TAC is set for European Union and international waters of subarea 5, 6, 7 ignoring the differentiation of the Rockall from the rest of the subareas, and resulting hence in a mismatch between genetic and management units. The scenario is less clear for the rest of the NE Atlantic locations, amongst which relatively genetic homogeneity was observed (Knutsen et al. 2009).

Summary of genetic evidence

The two studies found in literature are both investigations of population structure of tusk with the aim to detect useful information for assessment and management purposes for the species in the NE Atlantic. Two gene pools were found for tusk in the western and eastern Atlantic by Johansen and Nævdal (1995) using allozymes. The lack of differentiation observed within each area is probably due to the low resolution of the

markers, as pointed out by the authors. When haemoglobin and another locus were excluded from the analysis, no significant genetic differentiation was found.

Knutsen et al. (2009) using 7 microsatellites reported statistically significant genetic differentiation (F_{ST} 0.0014) for tusk in the NE Atlantic. Genetic differentiation between samples was explained by habitat distance, rather than geographic distance, as supported by the isolation of the Mid-Atlantic Ridge and Rockall samples, clearly differentiated from the surrounding samples both genetically and bathymetrically. Landscape genetic analysis confirmed the differentiation of Canada, the Mid-Atlantic Ridge and the Rockall. However, lack of differentiation was observed for the rest of the samples within the NE Atlantic possibly due to high levels of gene flow at both pelagic and demersal life-stages.

4.6 Saithe, *Pollachius virens*

Number of studies	3
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[15]

Saithe, *Pollachius virens* L., is a commercially important gadoid species widely distributed in the North Atlantic. In the North-East (NE) Atlantic it is found around Iceland, the Faroes, along Norway, from the Barents Sea down towards the Bay of Biscay. Adults are demersal and known to undertake extensive feeding migration (ICES, 2017; Saha et al., 2015; and references therein). Spawning is in spring and eggs and larvae are pelagic. Nursery grounds are in shallow and inshore waters, along coasts and in fjords. Juvenile feeding migrations outside nursery grounds are known. High potential for gene flow due to both oceanic drift of pelagic larvae and eggs, juvenile and adult migrations.

Current management status

ICES consider 5 stock units for saithe in the NE Atlantic (Figure 4.6). Although considered separate stocks, mixing was reported by tagging studies among the Faroes, the Northeast Arctic stock, the North Sea and west of Scotland (ICES, 2017; and references therein). In Iceland total catches reported for 2019 were 64 531 t, mainly fished by Iceland (64 295 t) with a minor contribution of Faroes (230 t) and Norway (6 t). A directed fishery is present for the stock in the Faroes grounds mainly caught around the Faroe shelf, with catches amounting at 24 119 t in 2018 (ICES 2019c).

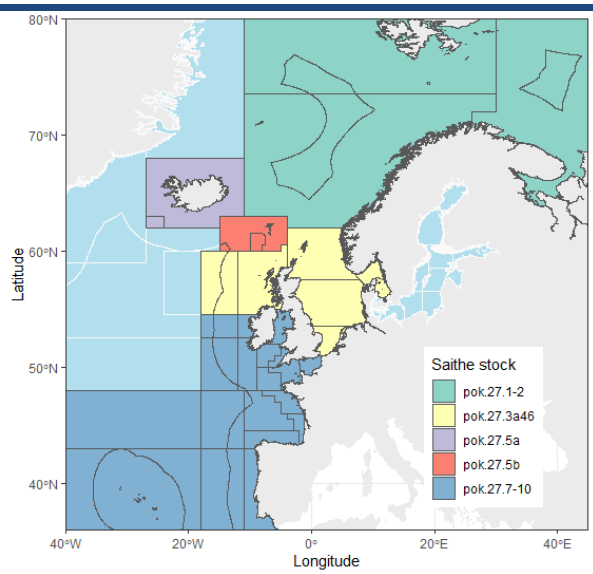


Figure 4.6. Saithe ICES stock assessment units.

For the Northeast Arctic stock of saithe (Subareas 1 and 2), the main fishing country is Norway (ICES 2020n). Total landings in 2019 were 163 180 t and Norway accounted for 144 076 t (ICES 2020a). ICES recognize

[15] Further details on symbols and how to read the factsheet are provided on page 16

the stock is not a biologically meaningful unit. Tagging showed exchange of individuals between this stock and the North Sea, Iceland and the Faroes (ICES 2020a). Saithe in the North Sea (subarea 4), west of Scotland (division 6.a) and Skagerrak (subdivision 20) is considered a stock unit. ICES is aware of genetic and tagging studies questioning the boundaries of the stock that extends further north (ICES 2019i). Saithe is mainly fished along the Norwegian Trench and the Northern Shelf edge as target species by bottom trawlers. Total catches in 2017 were estimated at 95 165 t (ICES 2019d), mainly fished in subarea 4 and division 3.a. A further stock of saithe is present in subareas 7-10; however, the stock identity is uncertain and is classified by ICES as a data-limited stock. Estimated landings in 2018 were 496 t, of which the majority (99.96%) were from Subarea 7 (mainly divisions 7.g and 7.j) (ICES 2019o).

Genetic population structure in a nutshell

Spatial population structure of saithe has been studied by means of different markers in the recent past (Behrmann et al. 2015, Eiríksson & Árnason 2015, Saha et al. 2015). The available genetic information supports:

- Sex-biased migration pattern for saithe, with males highly migratory.
- Presence of different populations in Canada, the Barents Sea, Rockall.
- High levels of gene flow and the existence of a single population in the central NE Atlantic that includes Iceland, North Sea, west of Scotland and Norway, in contrast to stock assessment and management units.

Mismatch

Several mismatches exist between genetic structure and stock assessment and management units for saithe. It was showed that the Barents Sea is a genetically separate population with respect to Norway; however, they are assessed and managed as a single stock unit (the Northeast Arctic stock). Likewise, the presence of a separate population in the Rockall is not taken into account in stock assessment and hence resulting in mismatches with the genetic units. The presence of a population in the central NE Atlantic including Iceland, Faroe, Norway, North Sea and west of Scotland is not considered neither in assessment and management.

Summary of genetic evidence

Until recently, knowledge of genetic population structure for saithe in the NE Atlantic was lacking. In a remarkably short time, population structure for saithe in the NE Atlantic was explored by means of different genetic markers. Behrmann et al. (2015) using a combination of microsatellites and RAPD loci detected statistically significant differentiation for saithe. The analysis supported the presence of two main populations overlapping in the northern North Sea, clearly in contrast with the assessment and management units present. Eiríksson and Árnason (2015) analysed mitochondrial genetic variation in saithe from Canada, Iceland, Faroe Islands and Norway, reporting a limited transatlantic differentiation. High levels of gene flow between eastern and western

Atlantic as well as within the NE Atlantic were suggested, as well as lack of differentiation between Iceland, Faroes and Norway. Moreover, sex-biased population structure was detected when female and male were analysed separately, indicating a more migratory behaviour for males.

Using neutral SNPs and applying a seascape genetic analysis, Saha et al. (2015) reported evidence of population structure for saithe in the North Atlantic with the identification of four different populations, i.e. Canada, Rockall, Barents Sea and the central NE Atlantic (including samples from Iceland, Faroe, west of Scotland, North Sea and Norway). Overall differentiation was significant even if low (F_{ST} 0.007), however, no structure was found within the central NE Atlantic. Sex-biased migration pattern for saithe was confirmed, with a more migratory behaviour for males than females.

A mismatch between genetic and stock assessment and management units is evident for saithe from Norway and the Barents Sea still considered part of the same unit though they represent two genetically different populations. Likewise, saithe in the Rockall should be considered a separate stock; however, it is included in the North Sea stock with the west of Scotland for assessment purpose (Table 2). Also, from a management perspective the presence of a separate population in the Rockall is not taken into account, resulting in a mismatch.

4.7 Pollack, *Pollachius pollachius*

Number of studies	1
Population structure	✗
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[16]

Pollack, *Pollachius pollachius* (Linnaeus, 1758), is a widespread gadoid species distributed from Portugal to Norway including the Skagerrak. Pollack is usually found between 40-100 m but is present down to 200 m (Cohen et al. 1990). Adults are demersal and live in deeper waters while juveniles live in coastal and shallow waters and move deeper gradually. Spawning takes place in winter-spring, eggs and larvae are pelagic and thus can be dispersed by ocean currents.

Current management status

Pollack is mostly a bycatch species and a recreational fish species. It is mainly exploited in the Celtic Seas, the North Sea and in the Bay of Biscay and Atlantic Iberian waters. Three stocks were designed in the ICES advisory framework based on this observation and lack of knowledge on population structure (Figure 4.7)(ICES 2019h). Since 2018, ICES does not provide advice for the stock in the North Sea, that includes also the Skagerrak and Kattegat. Pollack in the North Sea is mainly a bycatch species, specially of Norwegian vessels targeting saithe (ICES 2020v). The stock in the Celtic Seas and English Channel is classified by ICES as a data limited stock. ICES recognize that this stock could not represent a biologically meaningfull unit (ICES 2020t). TACs are set for subarea 6 and 7 separately (Table 2). Decreasing landings in 2019 from both subareas 6 and 7 were reported by ICES (ICES 2020t). All the landings from subarea 6 are from division 6.a. mainly fished during the spawning season (ICES 2020t). Likewise, the stock in the Bay of Biscay and Atlantic Iberian waters is a data-limited stock (ICES 2020s). TACs are set separately for the northern and southern divisions (Table 2).

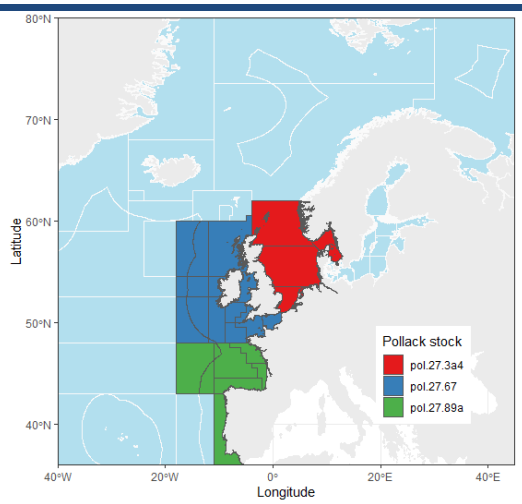


Figure 4.7. Pollack ICES stock assessment units.

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

Genetic population structure in a nutshell

Genetic population structure of pollack have been studied only at 6 microsatellite loci in the Bay of Biscay, western English Channel and a location from the North Sea off south Norway (Charrier et al. 2006b). High levels of gene flow and lack of differentiation among locations from south Bay of Biscay to the North Sea was reported, resulting in a mismatch with the assessment and management units. Further studies are needed to investigate genetic structure of pollack in the NE Atlantic.

Mismatch

Little information is available on genetic population structure for pollack. Evidence suggests a lack of differentiation between locations from the Bay of Biscay, western English Channel and North Sea, not supporting their assessment and management in different units (Table 2). However more powerful markers (e.g. genome wide SNPs) should be used to investigate genetic differentiation in pollack and to designate stock units that provide meaningful inferences on population structure for this poorly studied species.

Summary of genetic evidence

Pollack is still poorly studied. Information on genetic population structure for pollack are from an initial study conducted by Charrier et al. (2006), who explored population structure of pollack from the Atlantic coast of France (western English Channel and Bay of Biscay) and south Norway (North Sea) using 6 microsatellite loci. None the pairwise comparisons between locations were significant, and overall weak genetic structure was detected indicating high levels of gene flow for pollack from the Bay of Biscay to the North Sea. However, the authors suggested the results could be due to the low number of loci used or a combination of this and small sample sizes. Hence, more studies are needed to investigate population structure of pollack, perhaps using more high-resolution loci to increase power for the detection of genetic differentiation in this, so far, weakly structured species in the NE Atlantic.

4.8 Roughhead grenadier, *Macrourus berglax*

Number of studies	2
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	-

Distribution[17]

Roughhead grenadier, *Macrourus berglax* (Lacepède, 1801), is a deep-water fish species, distributed throughout the North Atlantic at depths between 100-1000 m but very common at 300-500 m (Cohen et al. 1990). As other deep-fish species it is extremely vulnerable to fishery activities due to life-history characteristics as low productivity, low growth rate and low fecundity (Coscia et al., 2018; and references therein). Spawning occurs in late winter-spring. It is a poorly studied species and more knowledge is needed.

Current management status

Although the unit considered by ICES for roughhead grenadier is the entire NE Atlantic (Figure 4.8), ICES is aware that such a framework is unlikely to reflect population structure fully (ICES 2020l). Roughhead grenadier is not a high valuable commercial species and landings are by-catches from other fisheries. Total landings for 2019 is 259 t (ICES 2020m). Although there is not a TAC set for roughhead grenadier, bycatches are reported under "grenadiers" quotas to avoid misreporting (ICES 2020l). Little information is available in general for this species and the state of the stock is unknown. ICES do not provide quantitative advices on fishing opportunities for this species (ICES 2020m). Based on a precautionary approach and the vulnerability of the species to fisheries, ICES advised *"there should be no directed fisheries for roughhead grenadier, and bycatch should be minimized for each of the years 2021 to 2025"* (ICES 2020m).

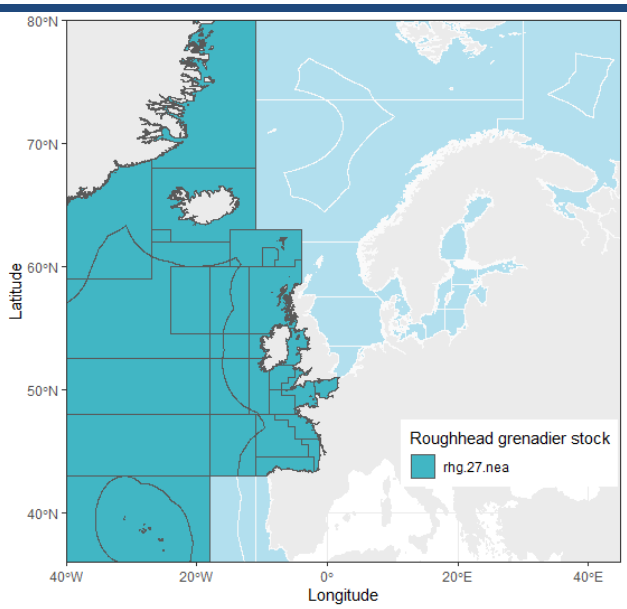


Figure 4.8. Roughhead grenadier ICES stock assessment units

[17] Further details on symbols and how to read the factsheet are provided on page 16

Genetic population structure in a nutshell

In general, roughhead grenadier is a poorly studied species. Genetic evidence supports:

- Panmixia across the North Atlantic at neutral loci.
- Presence of distinct population in west of Greenland, east of Greenland and Norwegian Sea, probably representing locally adapted populations.

Mismatch

Genetic analysis at allozyme loci detected the presence of distinct populations within the NE Atlantic in Norway and east of Greenland, resulting in a mismatch with the presence of one stock assessment unit. However, no mismatches were reported between genetic and stock assessment units using neutral loci (mitochondrial and microsatellite markers) supporting panmixia in the North Atlantic. Further investigations of genetic population structure of roughhead grenadier are needed in order to assess and confirm the presence of locally adapted populations.

Summary of genetic evidence

The first genetic population study for roughhead grenadier (Katsarou and Naevdal 2001) used allozymes and reported the presence of three populations in the North Atlantic, respectively in west of Greenland, east of Greenland and in the Norwegian Sea, contrasting with the presence of a single stock unit in the NE Atlantic.

In a successive study, Coscia et al. (2018) analysed genetic population structure of roughhead grenadier using a combination of mitochondrial and microsatellite markers. The analyses did not detect significant genetic differentiation, thus panmixia for roughhead grenadier across the North Atlantic was suggested. In contrast with the previous study (Katsarou & Naevdal 2001) no genetic differentiation was detected using strictly neutral markers by Coscia et al. (2018). However, population structure found with allozymes could be due to local adaptation at the allozyme loci investigated rather than reflecting neutral divergence among distinct populations. More studies are needed to explore population structure of roughhead grenadier also with markers under selection to investigate the presence of locally adapted populations.

4.9 Roundnose grenadier, *Coryphaenoides rupestris*

Number of studies	3
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	-

Distribution[18]

Roundnose grenadier, *Coryphaenoides rupestris*, is a deep-water fish species widely distributed in the North Atlantic (Cohen et al. 1990). In the North-East (NE) Atlantic it is present from eastern Greenland and Iceland down to North Africa. It is commonly found at 400- 1200 m depth; however, it can reach 2200 m (Cohen et al. 1990). Spawning season occurs in autumn-winter, depending on the area. Eggs and larvae are epi- and mesopelagic (Knutsen et al., 2012; and references therein). Juveniles are mesopelagic and move gradually towards deeper waters. Adults are believed to be relatively sedentary. Roundnose grenadier is listed as critically endangered due to the high vulnerability of the species to fisheries, calling for conservation actions.

Current management status

Four assessment units are considered by ICES for roundnose grenadier in the NE Atlantic, based on considerations of natural barriers for the dispersion of the species as water circulation and bathymetry by ICES (ICES 2020l) (Figure 4.9).

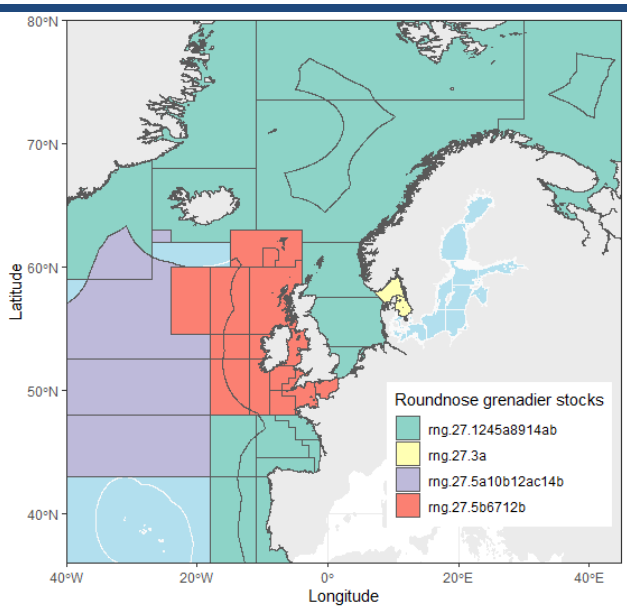


Figure 4.9. Roundnose grenadier ICES stock assessment units.

The stock of roundnose grenadier in the Skagerrak and Kattegat (Division 3.a) was target of a directed fisheries until 2006 (ICES 2020l). Currently it is fished entirely as a bycatch species and, based on a precautionary approach, ICES advised zero catches for 2020 (ICES 2020l). The stock in the Faroe-Hatton area and Celtic Seas (divisions 5.b and 12.b, subareas 6, 7) is mainly fished by bottom

[18] Further details on symbols and how to read the factsheet are provided on page 16

trawlers in multispecies fisheries (ICES 2020l). A decreasing trend in landings is reported from all the divisions and subareas included in this stock. Another stock is present in divisions 10.b, 12.c and subdivisions 5.a.1, 12.a.1, 14.b.1 (Oceanic Northeast Atlantic and northern Reykjanes Ridge). In the past it was fished mainly by the Soviet Union at the northern Mid-Atlantic Ridge (ICES 2020l). Fisheries of grenadier started again in 2010 mainly conducted by Spain but information regarding the status of the fishery extremely limited/unknown (ICES 2020l). Preliminary landings for 2019 are 215 t, all from subarea 12.a.1, catches from other divisions are scarce also in previous years (ICES 2020l).
The Northeast Atlantic and Arctic stock of roundnose grenadier includes subareas 1, 2, 4, 8, 9, divisions 14.a, and subdivisions 14.b.2 and 5.a.2 (ICES 2020l). Landings are mainly bycatch from other demersal fisheries such as Greenland halibut and redfish fisheries in Iceland and Greenland where roundnose grenadier is mainly caught as bycatch in Greenland halibut directed fisheries. Likewise, in subarea 1 and 2 it is a bycatch species in mixed deep-water fisheries mainly caught by Norway. Preliminary landings for 2019 were 192 t of which the majority originated from subdivision 14.b.2 (ICES 2020l). Catches of roundnose grenadier (only bycatch allowed) from European vessels are reported separately under the TACs of Grenadiers, *Macrourus* species. TACs are set from the EU for division 5.b, Subarea 6 and 7 and for Subareas 8, 9, 10, 12 and 14 covering three different ICES stock units (Table 2).

Genetic population structure in a nutshell

Genetic studies indicated presence of population structure within the Atlantic for roundnose grenadier. Genetic evidence supports:

- Differentiation between the north and south Mid-Atlantic Ridge, however included in the same stock unit (White et al. 2010).
- Presence of separate populations in the Skagerrak, Norway and Canada (Knutsen et al. 2012).
- Possible existence of local population in Greenland, Mid-Atlantic Ridge and in the Rockall (Knutsen et al. 2012).
- Presence of sub-populations in Norwegian fjords that should be taken into consideration for management and assessment purposes (Delaval et al. 2018).

Mismatch

A mismatch should be noted for roundnose grenadier from Norway. Although representing a separate genetic population it is included in the same stock unit of east of Greenland (Table 2).
Also, genetic differentiation between roundnose grenadier in the north and south Mid-Atlantic Ridge does not match with the current stock assessment unit.
Another mismatch between genetic and stock units can be evinced due to the existence of local populations within Norwegian fjords, possibly requiring assessment and management measures at a finer geographic scale.

Summary of genetic evidence

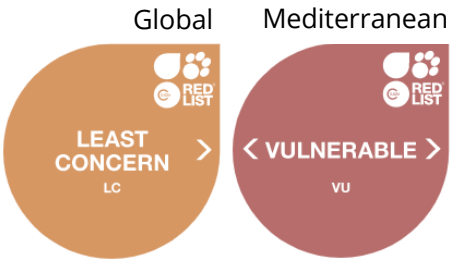
Genetic population structure of roundnose grenadier has been studied relatively recently. White et al. (2010) using neutral and under selection microsatellites detected population structure within the Atlantic (F_{ST}= 0.0043, P< 0.001). A weak pattern of isolation by distance was reported at neutral loci and the presence of local adaptation to depth was supported in the Hebrides- Bay of Biscay samples. The existence of a genetic barrier was observed at the Mid-Atlantic Ridge separating Charlie-Gibbs north and south samples, in contrast to their inclusion in the same stock assessment unit.

Knutsen et al. (2012) used neutral microsatellite loci to investigate population structure of roundnose grenadier across its distributional range. Genetic structuring was reported at different geographic scales, with the presence of clearly differentiated populations at the margin of the distributional range of the species in Canada, Norway and Skagerrak; while genetic structuring was low within the European slope, suggesting the presence of a single population off the British Isles. However, the presence of additional populations in Greenland, the Mid-Atlantic Ridge and in the Rockall cannot be excluded. The mismatch found between genetic and stock assessment units is due to the inclusion of Norway and Greenland, genetically differentiated, in the same stock unit.

Delaval et al. (2018) explored the connectivity between roundnose grenadier from 3 Norwegian fjords and 2 coastal locations along south Norway through analysis of 8 microsatellites. Significant genetic differentiation was reported (F_{ST}=0.0297, P< 0.001) at this fine geographic scale, supporting the presence of different sub-populations in Norwegian fjords. A significant correlation was reported between genetic distance and geographic distance and bottom depth. The mismatch here is due to additional genetic sub-structure within the area.

4.10 European hake, *Merluccius merluccius*

Number of studies	19
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗



Distribution[19]

European hake, *Merluccius merluccius* L. 1758*,* is a highly valuable demersal fish species exploited in both the North-East (NE) Atlantic and Mediterranean Sea. It is widespread from Norway and Iceland southward to Mauritania, including the Mediterranean and Black Sea (Cohen et al. 1990). Spawning season varies depending on latitude and it is extended in the southern locations. Adults are demersal while, larvae are pelagic as well as juveniles that lives near the coast until they reach 3 cm length and subsequently enter the nursery grounds at 100- 200 m depth (Tortonese 1970).

Current management status

Two stock assessment units exist for European hake in the NE Atlantic, a southern and northern unit separated by Cap Breton Canyon in the Bay of Biscay, proposed as natural barrier (Figure 4.10). As reported in the stock annex, these stock assessment units do not rely on biological information but rather on management considerations (ICES 2017g). The southern stock (division 8.c and 9.a) includes the southern Bay of Biscay and Atlantic Iberian waters, while the northern stock includes the central and northern Bay of Biscay (divisions 8.a, b, d), the North Sea, the Skagerrak and Kattegat and the Celtic Seas.

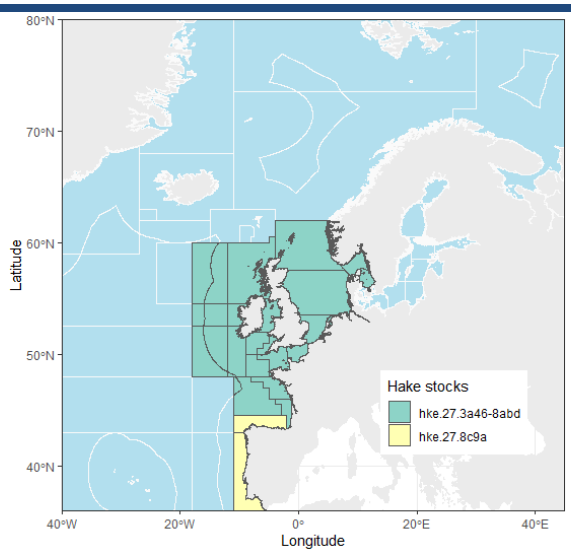


Figure 4.10. European hake ICES stock assessment units.

The southern stock is mainly fished by Spain and Portugal in mixed-species fisheries with other demersal species. This stock is managed in the European Multiannual Management Plan for Western Waters (ICES, 2020; and references therein). A TAC exists for division 8.c,

[19] Further details on symbols and how to read the factsheet are provided on page 16

subarea 9 and 10 and Union waters of 34.1.1 (Table 2). Total catches for 2019 were 12 861 t, exceeding the agreed TAC of 9 258 t and ICES catch advise (ICES 2020s). Preliminary catches for the northern stock in 2019 were 87 238 t, lower than catches advised by ICES and the agreed TAC. TACs are set for different combinations of divisions and subareas part of this stock (Table 2). Since 2001 an Emergency Plan was adopted for the recovery of the Northern hake stock that required further technical measures to decrease fishing effort (ICES, 2011; and references therein). Minimum landing size is set for 27 cm for both the northern and southern stocks.

Genetic population structure in a nutshell

Genetic studies have confirmed the differentiation between European hake in the Atlantic and Mediterranean Sea. Within the NE Atlantic a complex pattern of population structure exists for hake and genetic evidence supports:

- Differentiation between the Atlantic and Mediterranean populations.
- Presence of different populations within the northern stock, i.e. west of Scotland, Norway, Kattegat and North Sea.
- Lack of differentiation between hake sampled in the Bay of Biscay, south and north to Cape Breton Canyon, that does not represent a barrier between the two putative stocks in the NE Atlantic.
- Presence of high levels of gene flow between the northern and southern stocks (among Celtic Sea, Bay of Biscay and Galician coasts).
- Differentiation of hake from Portuguese coast and Bay of Biscay.
- It seems that the Bay of Biscay (northern, central and southern) represent a genetic unit, that is differentiated from northern populations. The genetic differentiation with the southern population in Portugal should be further investigated. Further studies need to include samples from division 9.a to understand whether hake in southern Atlantic Iberian waters belongs to the same population as the Bay of Biscay.

In the Mediterranean Sea, presence of a western central and eastern populations was demonstrated (Milano et al. 2014).

Mismatch

A lack of differentiation between northern and southern Bay of Biscay hakes was supported, in contrast with their assessment and management in separate stocks (Table 2). A mismatch between genetic and stock assessment units can be revealed for the northern stock, where the presence of local populations has been shown, i.e. in west of Scotland, Kattegat, North Sea, Norwegian coast, and however it is not taken into account.

Summary of genetic evidence

Genetic population structure of European hake in the NE Atlantic and Mediterranean Sea has been studied by means of different genetic markers. Most of the studies focused on the Bay of Biscay and Galician coasts, where the boundary between the two stocks lies. The differentiation between the NE Atlantic and Mediterranean hake is supported both with allozymes (Roldán et al. 1998, Lo Brutto et al. 2004), microsatellites (Lundy et al. 1999, Castillo et al. 2004) and SNPs analyses (Milano et al. 2014, Leone et al. 2019).

Roldán et al. (1998) analysed genetic variation at 21 polymorphic allozymes in the Mediterranean and NE Atlantic hake, supporting their differentiation. In contrast with ICES assessment of a single northern and southern stock within the NE Atlantic, genetic homogeneity was observed for the Bay of Biscay and Galician coast samples, but they were genetically different from the Ireland sample.

In the Mediterranean, Lo Brutto et al. (1998) reported genetic homogeneity for European hake from the Strait of Sicily, Adriatic Sea and Tyrrhenian Sea despite their inclusion in separate stocks.

Lundy et al. (1999), using microsatellites, confirmed the differentiation of Mediterranean and Atlantic hake. Significant differentiation was reported between Norway and Celtic Sea samples; however, both included in the same northern stock. No differentiation was detected between the southern Bay of Biscay (southern stock) and Celtic Sea (northern stock) samples. However, southern Bay of Biscay and Portuguese samples were slightly differentiated although both in the southern stock unit.

Lack of differentiation among samples collected north and south of the Cape Breton Canyon during the spawning and feeding season was reported by Lundy et al. (2000), contrasting with the stock assessment and management units.

With regards to the presence of one stock unit for hake in the Strait of Sicily, Levi et al. (2004) reported genetic homogeneity for hake sampled from both side of the strait. A more extensive study by Lo Brutto et al. (2004), using allozymes and mitochondrial markers supported genetic homogeneity throughout the Mediterranean for hake. Hence, here the mismatch is due to a lack of differentiation between samples managed and assessed in different units within the Mediterranean (Table 2).

Castillo et al. (2004), using microsatellites supported the differentiation between the Atlantic and Mediterranean Sea. Population structure was found within the NE Atlantic, where the Celtic Sea was differentiated from west of Scotland, although both included in the northern hake stock. Fine scale population structure was suggested in the Cantabrian Sea. Moreover, population structure was suggested also in the Mediterranean, where hake from the Aegean Sea clustered separately from the rest of the Mediterranean samples.

Subsequently, Castillo et al. (2005) investigated population structure of hake along the Iberian Peninsula using 5 microsatellite loci. The presence of two populations was supported in Portuguese waters and the Cantabria Sea. No genetic differentiation was

detected between samples from central-northern Bay of Biscay (divisions 8.a-b, d) and southern Bay of Biscay (division 8.c) suggesting the presence of one population in the region, resulting in a mismatch between genetic and both stock assessment and management units.
The differentiation between Atlantic and Mediterranean populations was also supported by Cimmaruta et al. (2005). However, the boundary between the two basins for hake was located in the Almeria-Oran front, as suggested by the similarity of the Malaga sample (western Mediterranean) to Atlantic locations.
Pita et al. (2010) analysed hake individuals from all across the distributional range of the species at microsatellites and mitochondrial markers and found highly significant differentiation between Atlantic and Mediterranean populatons, including the presence of haplotypes (cyt-b) private to each basin.
The connectivity between the two stocks in the NE Atlantic has been investigated in several studies. Genetic homogeneity was reported by Pita et al. (2011) among samples, thereby questioning the current assessment and management units. It was suggested that gene flow occurs between the northern stock and southern stocks specially from the northern stock at Porcupine and Great Sole bank towards the Atlantic Iberian southern stock. A pattern of high connectivity was found within the NE Atlantic and unidirectional migration from the Celtic Sea to adjacent areas was detected in a successive study (Pita et al., 2014), that reported high levels of gene flow also within the Mediterranean Sea. The differentiation between the Atlantic and Mediterranean populations was high and significant, with the Almeria–Oran Front acting as barrier to gene flow. Using microsatellites and otolith geochemistry Tanner et al. (2014) confirmed the connection between the northern and southern stock. Gene flow was detected among the Celtic Sea, Bay of Biscay and Galician coasts but in both directions rather than from northern to southern stocks as suggested by a previous study. In a successive study, Pita et al. (2016) supported bidirectional migration between northern and southern stocks within the NE Atlantic. Pita et al. (2017) analysing samples from the southern hake stock, at microsatellites and mitochondrial markers indicated presence of one gene pool and no temporal or spatial differences were reported.
The genetic population structure of hake has been investigated also with SNPs. A genetic tool to distinguish between European hake fished in the NE Atlantic and Mediterranean Sea was developed by Nielsen et al. (2012). Using highly differentiated SNP loci (13 loci) individuals can be assigned to their population of origin. The tool assures a 98% correct assignment of individuals to basin. Milano et al. (2014) investigated population structure of hake with a SNPs panel of 381 loci. Neutral markers detected the differentiation between Atlantic and Mediterranean Sea and only weak structure within these regions. However, using markers under selection populations structure at a finer scale was revealed. North Sea and Portugal samples differentiated from the other NE Atlantic samples (Celtic sea and Bay of Biscay) in contrast with the current assessment and

management units. In the Mediterranean differentiation between western, central and eastern basin was reported with outlier loci. Likewise, Westgaard et al. (2017) using a combination of neutral and outlier SNPs reported the presence of different population within the northern stock, i.e. the Kattegat, the Norwegian coast, the North Sea that were also differentiated from the Bay of Biscay even if part of the same stock assessment unit. Leone et al. (2019) used genome-wide SNPs to investigate population structure of hake. Within the NE Atlantic, genetic differentiation was found for the Norwegian sample, clearly differentiated from the Bay of Biscay and Atlantic Iberian samples. Lack of differentiation was reported among the northern and southern Bay of Biscay and the Atlantic Iberian samples that; however, belongs to different stocks. The existence of a mismatch between stocks assessment and genetic units is evident, due to a lack of genetic differentiation between samples originating from both the northern and southern stock areas. Population structure was detected with both neutral loci and outlier SNPs (Milano et al. 2014, Westgaard et al. 2017b) within the Atlantic, suggesting local adaptation in European hake populations. However, this study shows that the genetic population structure found for hake within the Atlantic generally due to pattern of migrations and gene flow rather than local adaptation as suggested from most early studies. The genetics suggests a more complex pattern of population structure for the European hake in the NE Atlantic, than reflected in the assessment and management units (Leone et al. 2019). Lack of differentiation between northern and southern Bay of Biscay was supported by genetics, as well as presence of local populations in the northern stock, i.e. west of Scotland, Kattegat, North Sea and Norwegian coast.

5 Pelagic species

5.1 Capelin, *Mallotus villosus*

Number of studies	6
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[20]

Capelin, *Mallotus villosus* (Müller, 1776) is a small pelagic fish species widely distributed in the cold waters of the northern hemisphere both in the North Atlantic and Pacific Ocean, where it sustains important commercial fisheries (Præbel et al., 2008; and references therein). Capelin has a key role in the marine ecosystem as food for marine mammals, sea birds and larger fish including commercially important species like cod. It is a shoaling fish forming large aggregations for feeding and spawning migrations. Capelin is a demersal spawner. During the spawning season in late winter-early summer, mature individuals migrate towards coastal and shallow waters where benthic eggs are released.

Current management status

ICES currently recognize two stocks of capelin in the NE Atlantic, the Barents Sea capelin in subarea 1 and 2 (excluding division 2.a west of 5°W) and Capelin in Iceland and Faroes grounds, East Greenland and Jan Mayen (Subareas 5, 14 and Division 2.a west of 5°W) (Figure 5.1).

The Barents Sea capelin fishery is regulated under the management plan of the Joint Norwegian-Russian Fishery Commission and since 1979 a minimum landing size of 11 cm has been in force (ICES 2020a). Barents Sea capelin fishery targets pre-spawning aggregations near the spawning areas during January- March, and the autumn fishery at feeding grounds is not allowed anymore (ICES 2020a). ICES advice was of zero catch for 2019, 2020 and 2021 although catches were allowed for scientific surveys (53 t and 31 t in 2019 and 2020, respectively; ICES 2020a).

ICES consider capelin around Icelandic and Faroese grounds, East Greenland and Jan Mayen area as a separate stock. Spawning grounds are located in the shallow waters southeast, south and west of Iceland (ICES 2015a). Spawning and feeding migrations are known (ICES 2015a). In Iceland, the capelin fishery is controlled and regulated with closure of areas and seasons depending on the status of the stock and the abundance of juveniles (ICES 2020k). Following the ICES advice of zero catch, no fisheries and landings of capelin were allowed in 2018/2019 and 2019/2020 fishing seasons (ICES 2020k). After two years

[20] Further details on symbols and how to read the factsheet are provided on page 16

of zero catch, ICES advised a TAC of 169 520 t for 2020/2021 fishing season based on the acoustic survey (ICES 2020k). And an initial TAC for 2021/22 of 400 000 t was adviced but will be revised after the acoustic survey in autumn 2021 (ICES 2020k).

Genetic population structure in a nutshell

Genetic differentiation between western and eastern Atlantic populations of capelin was supported by both mitochondrial (Dodson et al. 1991, Birt et al. 1995) and microsatellite data (Røed et al. 2003, Præbel et al. 2008).

Initially a lack of differentiation between the Icelandic and Barents Sea capelin was reported by mitochondrial markers (Dodson et al. 1991). Microsatellites supported genetic differentiation between two stock assessment units although no samples from Iceland were included in the study (Præbel et al. 2008). Possible substructure within the Barents Sea capelin stock was suggested:

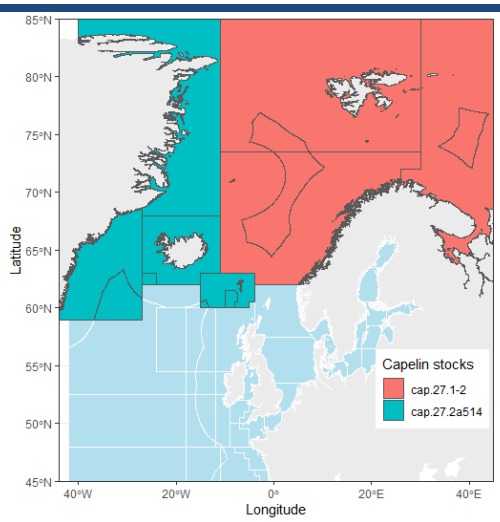


Figure 5.1. Capelin ICES stock assessment units.

- Capelin collected in a Norwegian fjord was genetically differentiated from the rest of the Barents Sea samples (Røed et al. 2003).
- The existence of a separate population of capelin was indicated in the Svalbard (Præbel et al. 2008).

Moreover, the mixing of the two stocks was suggested off Jan Mayen. Hence, further studies are needed to confirm the temporal stability of putative sub structuring found in Barents Sea capelin, as well as the extent of mixing of both stocks in Jan Mayen that is currently assessed in the East of Greenland-Iceland-Jan Mayen stock.

Mismatch

A mismatch between stock assessment and genetic structure is present in the NE Atlantic for capelin. Within the Barents Sea stock unit, genetic evidence suggested the existence of a separate population in Svalbard and in a Norwegian fjord. Moreover, mixing of the two stock stocks at Jan Mayen was supported by microsatellite data. Further studies are needed to confirm the presence of separate populations in Svalbard and Norwegian fjord as well as exploring spatio-temporal pattern of mixing as a key component of assessment and management.

Summary of genetic evidence

Genetic population structure of capelin has been investigated by means of different genetic markers. In an early study, Mork and Friis-Sørensen (1983) using allozymes reported a lack of differentiation between capelin samples from the Barents Sea stock. In a successive study, Dodson et al. (1991) analysing mitochondrial variation of capelin across the North Atlantic reported differentiation between the eastern and western Atlantic samples. Substructure was detected in the western Atlantic samples, however a lack of differentiation within the eastern Atlantic samples (Iceland and Barents Sea) was reported, resulting in a mismatch with the stock assessment units. Genetic differentiation between capelin from the western and eastern North Atlantic was successively confirmed also by Birt et al. (1995) using a combination of RFLP and sequence analysis of the cytochrome-b gene.

Microsatellite loci were characterized by Røed et al. (2003) to investigate population structure in capelin. Substructure was reported within the NE Atlantic, where capelin collected in a Norwegian fjord (Porsangerfjord) was significantly differentiated from both the Barents Sea and other fjords samples. Moreover, the genetic differentiation between eastern and western Atlantic was supported.

Using nine microsatellites Præbel et al. (2008) studied genetic population structure of capelin across its entire distributional range. The existence of four genetically different regions was reported, i.e. west Pacific, east Pacific, Newfoundland and NE Atlantic. Within the NE Atlantic, the Barents Sea and Norwegian fjords samples were genetically homogeneous. In contrast, the sample from Svalbard was identified as a separate population, due to genetic differentiation from the rest of the samples. Moreover, the two samples collected off Jan Mayen were genetically differentiated from each other possibly due to migration of individuals from the Greenlandic-Icelandic stock and the Barents Sea stock. Substructure within the NE Atlantic should be further investigated to assess the temporal stability of the spatial genetic pattern found.

5.2 Atlantic horse mackerel, *Trachurus trachurus*

Number of studies	9
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[21]

Atlantic horse mackerel, *Trachurus trachurus* (Linnaeus, 1758), is a benthopelagic species that sustains commercially important fisheries along its distributional range. It is widely distributed in the North-East (NE) Atlantic, from Norway and Iceland to West Africa (Cape Verde) and eastwards in the Mediterranean Sea and Black Sea. In the NE Atlantic three species of *Trachurus* co-occur: *T. mediterraneus*, *T. picturatus* and *T. trachurus*.

Current management status

Based on available scientific evidence ICES consider three stock assessment units for horse mackerel in the NE Atlantic: the North Sea stock (hom.27.3a4bc7d), the Western stock (hom.27.2a4a5b6a7a-ce-k8) and the Southern stock (hom.27.9a) (Figure 5.2). Atlantic horse mackerel is fished in directed trawl and purse-seine fisheries as well as in mixed fisheries.

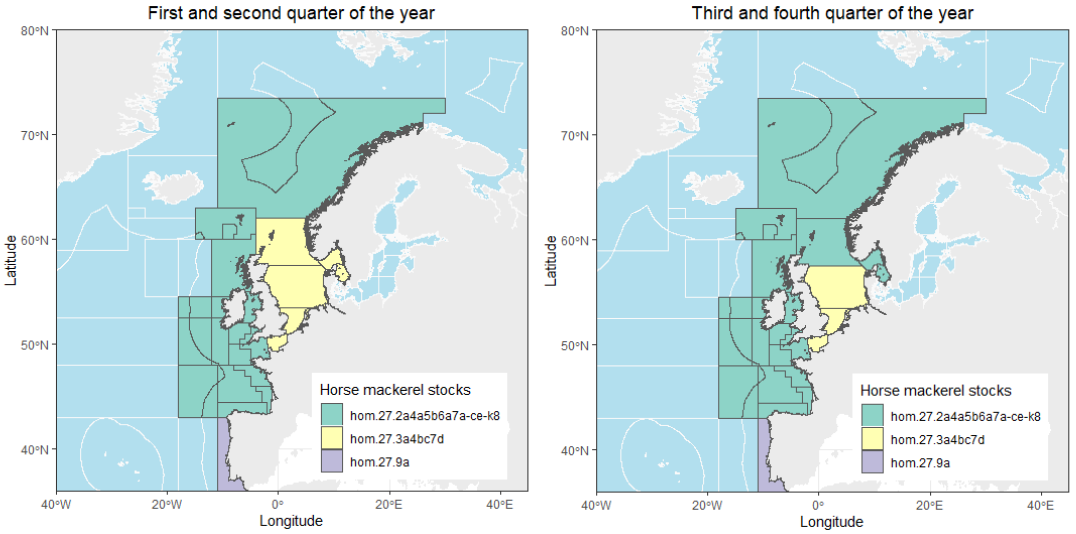


Figure 5.2. Atlantic horse mackerel ICES stock assessment units.
Left, first and second quarter of the year. Right, thrid and fourth quarter of the year.

[21] Further details on symbols and how to read the factsheet are provided on page 16

The North Sea horse mackerel stock comprises divisions 4.b-c, 7.d and divisions 3.a (Skagerrak and Kattegat) and 4.a (northern North Sea) in the first and second quarter of the year . Catches from division 3.a and 4.a are considered to be from the North Sea stock during the first and second quarter of the year, while in quarter three and four are considered originating from the Western stock (ICES 2020w). Feeding migration of horse mackerel from the Western stock into Norwegian waters and the North Sea is known, supporting this temporal dimension of the stock units and giving a significant example that fish stock delineation can be flexible and include a temporal dimension in the definition (ICES 2020w). In 2019, catches of the North Sea horse mackerel stock were 11 803 t of which around the 68% was from the eastern English Channel (division 7.d) (ICES 2020w).

The Western stock comprises Atlantic horse mackerel in division 2.a, 5.b, 6.a, 7.a-c, e-k, 8.a-e and divisions 3.a and 4.a in the third and fourth quarter of the year. The majority of the catches are from division 7.a-c, e-k (ICES 2020w). The boundaries of the Western stock were revised in light of the results of the HOMSIR project on horse mackerel stock identification research (ICES, 2020; and references therein) and horse mackerel in division 8.c is now included in the Western stock. Catches of horse mackerel from divisions 3.a (Skagerrak and Kattegat) and 4.a (northern North Sea) during the third and fourth quarter of the year are allocated to the Western stock. After the spawning season the Western stock horse mackerel undertake feeding migrations towards Norwegian feeding grounds and the northern North Sea. Mixing between these two stocks was investigated and a genetic tool was developed to assign back to the population of origin fish caught in mixing areas (e.g. English Channel, northern North Sea) (ICES 2020w). There is a mismatch between the management and assessment units. A separate TAC is given for division 8.c that is currently assessed with the Western stock by ICES (Table 2). Likewise, the North Sea management unit does not include division 4.a (Table 2).

The Southern stock include division 9.a and the TAC is set for *Trachurus* spp. while ICES advice on stock status and catches is for Atlantic horse mackerel. The stock biomass is above reference points although catches include mostly juveniles and young adults and amounted at 34 080 t in 2019 (ICES 2020u). Overall, a decline in catches of Atlantic horse mackerel has been reported by ICES although the Southern stock in showing an increase in the last years. Total catches for the North Sea and Western stock in 2019 were 136 750 t, of which more than 90% is from the Western stock, while less than 10% from North Sea stock (ICES 2020w).

In the Mediterranean Sea, a stock unit is considered for Atlantic horse mackerel in GSAs 1, 5, 6, 7. In 2016 total catches were 2442 t. Atlantic horse mackerel is fished as by-catch species and due to a lack of data, analytical stock assessment was not carried out (STECF 2017).

A different stock unit is considered in GSA 9, 10 and 11, the stock biomass showed a decline (STECF 2017), and total catches in 2016 were 3769 t. For the stock in GSAs 17-20 the advice was not provided due to the low quality of available data, here, Atlantic horse mackerel is fished as by-catch species.

Genetic population structure in a nutshell

Despite initial studies reporting a lack of differentiation for Atlantic horse mackerel, whole genome sequencing allowed the detection of significant genetic structure and presence of local populations. In particular, genetic evidence supports:

- Differentiation among NE Atlantic, Mediterranean and North African samples (Fuentes-Pardo et al. 2020).
- The existence of three different stocks within the NE Atlantic, i.e. the North Sea, Western and Southern stocks (Fuentes-Pardo et al. 2020).
- Possible presence of local population in the North Sea suggested by microsatellites (Bozano et al. 2015).

A genetic tool, consisting of 17 SNPs, was developed by Fuentes-Pardo et al. (2020) to distinguish individuals from the Western and North Sea stocks and can be used to explore mixing in the English Channel and the northern North Sea. Moreover, further analyses are needed to define the boundaries between the Western and Southern horse mackerel stocks along Portugal.

Within the Mediterranean Sea, Ionian and Aegean samples resulted genetically similar (Cimmaruta et al. 2008). Possible substructure was reported within the Black Sea, with horse mackerel in the eastern part of the basin genetically differentiated (Turan et al. 2009).

Mismatch

Initial mismatches were due to a lack of differentiation and were solved by using more powerful genetic markers. The whole genome sequencing and SNPs analysis (Fuentes-Pardo et al. 2020) showed genetic differentiation between the three stocks recognized by ICES in the NE Atlantic. However, the boundary between the Southern (division 9.a) and Western stock is not biologically meaningful resulting in a mismatch with current assessment and management units. Horse mackerel from the Spanish Atlantic coasts (northern division 9.a) should be included in the Western stock rather than in the Southern stock. Further studies are needed to define the boundaries between the two stocks in division 9.a. The mixing of North Sea and Western horse mackerel stocks in the English Channel as well as in the northern North Sea are known and can be now addressed with a genetic tool appositely developed to assign catches to the correct stocks.

Summary of genetic evidence

All the initial mismatches found between genetic, assessment and management units were due to a lack of differentiation between samples belonging to the three different stocks (i.e. Southern, Western and North Sea stock).

In a preliminary study, there was a lack of genetic evidence to support the existence of different stocks was reported by Borges et al. (1993) using the transferrin polymorphisms to analyse samples of horse mackerel from the North Sea, Celtic Sea, Bay of Biscay and Portuguese coast. A lack of differentiation within the NE Atlantic and between Atlantic and Mediterranean samples of horse mackerel was reported by Karaiskou et al. (2004) investigation throughout restriction analysis of the mitochondrial control region. Genetic differentiation was detected only between the European and African samples. Likewise, Kasapidis and Magoulas (2008) analysing 16 samples from the entire distributional range of Atlantic horse mackerel at four microsatellite loci were not able to reject the hypothesis of panmixia. However, this lack of differentiation may be ascribed to the low number of markers used, in fact to detect statistically significant levels of differentiation in pelagic species experiencing high levels of gene flow it is necessary to use more markers. The lack of genetic differentiation among samples collected in the entire distributional range of horse mackerel was confirmed by Cimmaruta et al. (2008) using allozymes. Although, subtle differentiation was reported between the Ionian and Aegean Seas and the rest of the western Mediterranean and NE Atlantic samples. In line with previous studies, no evidence of genetic structure was found by Comesaña et al. (2008) that analysed sequence variation of the mitochondrial control region in samples from the NE Atlantic and Mediterranean Sea.

At a smaller scale, Turan et al. (2009) investigated mitochondrial variation in horse mackerel from the eastern Mediterranean Sea and the Black Sea. The Black Sea sample collected from the eastern part of the basin was genetically differentiated from the rest of the samples, while the eastern Mediterranean and the Aegean samples were genetically similar.

Genetic population structure was reported by Bozano et al. (2015), that analysed samples of Atlantic horse mackerel from the North Sea and Ireland using 13 microsatellite loci. Temporal stability was indicated for the Ireland samples representing the Western stock. However, a complex spatio-temporal population structure was observed for Atlantic horse mackerel in the northern North Sea, where one of the three Norwegian samples resulted genetically similar to Ireland samples. This was due to migration of horse mackerel from the Western stock into feeding grounds in the northern North Sea. While, two other Norwegian samples were genetically different both from Ireland and the Central North Sea samples, suggesting the existence of a local population in the northern North Sea.

In line with early studies, Healey et al. (2020) using a combination of mtDNA and microsatellite analyses suggested a lack of genetic differentiation between NE Atlantic and Mediterranean horse mackerel populations.

Using a whole genome approach, Fuentes-Pardo et al. (2020) were able to support the presence of three different stocks within the NE Atlantic: the North Sea stock, the Western stock (including west of Ireland, the Galician Shelf and northern Portugal) and the Southern stock (including only samples from southern Portugal). The samples from the Spanish Atlantic shelf and northern Portugal were genetically similar to the Western stock and differentiated from the southern Portuguese samples, resulting hence in a mismatch with the current assessment and management units. However, more studies are needed to define the boundary between the southern and western stocks along Portugal. The samples from North Africa and the Alboran Sea resulted also genetically different, supporting the differentiation between Atlantic and Mediterranean basin. The lack of differentiation found in previous studies across samples from the entire distributional range of horse mackerel can be explained by the finding that only a small part of horse mackerel genome (< 1.5%) is differentiated among populations, and significant differentiation corresponds to loci under selection involved in local adaptation (Fuentes-Pardo et al. 2020).

Moreover, a SNP panel of 17 loci was developed to distinguish between the North Sea and Western stock individuals with high accuracy. The SNP panel developed is an extremely valuable tool to explore the mixing of the Western and North Sea stocks in the English Channel as well as in the northern North Sea.

5.3 Blue jack mackerel, *Trachurus picturatus*

Number of studies	3
Population structure	✗
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[22]

The blue jack mackerel, *Trachurus picturatus* (Bowdich, 1825) is a pelagic shoaling fish species distributed in the southern part of the North-East (NE) Atlantic, from the Bay of Biscay down towards Morocco including the Macaronesia, and eastward into the Mediterranean Sea. It is a neritic species found in shelves banks and seamount. The blue-jack mackerel is an important fishery resource in the Azores and Madeira representing the main pelagic species targeted by artisanal fisheries in the region.

Current management status

ICES currently recognize one stock assessment unit of blue jack mackerel in the Azores subdivision 10.a2 (Table 2). This stock is a data limited stock for which only landings and short catches history data are available (ICES 2020u). Juveniles of blue jack mackerel are commonly found in the nursery grounds on the Azores shelf while adults are found in offshore feeding grounds. The main catches of blue jack mackerel in the Azores are from artisanal fishery, that targets blue jack mackerel both for human consumption and as live bite for tuna fisheries. Catches from recreational fishery in the islands are also relevant. Catches estimated by ICES in 2019 were 1 231 t, mainly fished by artisanal purse-seines fleet (ICES 2020u). Based on the precautionary approach ICES advice a TAC of 878 t for 2021 and 2022 (ICES 2020u).

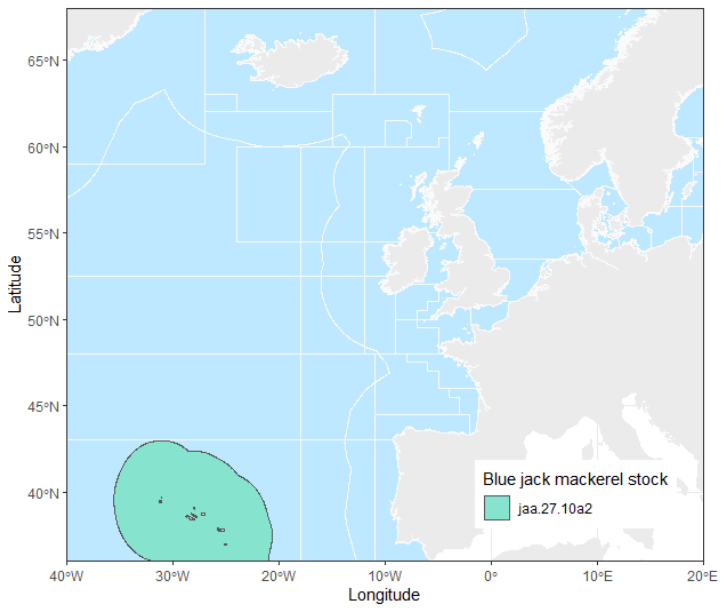


Figure 5.3. Blue jack mackerel ICES stock assessment unit.

[22] Further details on symbols and how to read the factsheet are provided on page 16

Genetic population structure in a nutshell

Genetic studies reported a lack of population structure for blue jack mackerel within the NE Atlantic both with mitochondrial and microsatellite markers. Lack of differentiation was observed also between the NE Atlantic and Mediterranean. Further studies are needed and ideally more powerful markers should be used to detect genetic structure in pelagic species for which generally low levels of genetic differentiation can be found, while highly divergence loci are restricted is small part of the genome involved in local adaptation (see for example Atlantic horse mackerel).

Mismatch

The mismatch is due to a lack of differentiation within the NE Atlantic samples that does not support the current stock assessment unit considered in the Azores (Subdivision 10.a2). However, other methods support the presence of different populations in the NE Atlantic that may be relevant for the fishery time scales (Moreira et al., 2019; and references therein).

Summary of genetic evidence

The information available on genetic population structure for blue jack mackerel is limited to three studies.

Initially, a lack of differentiation was reported by Karaiskou et al. (2004) using restriction fragment analysis of the mitochondrial control region. No evidence of differentiation was found between Atlantic and Mediterranean samples, as well as within each region. Moreira et al. (2019) supported panmixia and absence of population structure within samples from Madeira, Azores, Portuguese coast, despite previous studies using parasites, otolith microchemistry and shape analyses showed the existence of different populations in the areas. This could be due to the large connectivity between putative populations and the nature of the mitochondrial DNA used in the genetic investigation.

In line with previous investigations, Moreira et al. (2020) reported a lack of differentiation between samples collected in the NE Atlantic (Madeira, Canary, Portugal) and the Mediterranean Sea using microsatellite loci.

Large effective population size and high levels of gene flow mediated by adult dispersal capability and passive dispersion of eggs and larvae may prevent the arise of genetic differentiation at least at expected neutral markers, as the mitochondrial and microsatellite markers used. Further studies are needed and more powerful markers and loci under selection should be used to detect genetic structure and possibly local adaption in blue jack mackerel.

5.4 Atlantic mackerel, *Scomber scombrus*

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

Distribution[23]

Atlantic mackerel, *Scomber scombrus* L., is a commercially important pelagic fish species widespread in the North Atlantic, Mediterranean Sea and Black Sea. It is a shoaling fish and migrations towards spawning and feeding grounds are known. Mackerel is an extremely valuable commercial species and it has also an important role in the ecosystem. It is a forage fish for seabirds, marine mammals and larger pelagic fish commercially important as cod.

Current management status

ICES consider Atlantic mackerel in the NE Atlantic and adjacent waters as one stock assessment unit including subareas 1-8, 14 and division 9.a (Table 2). It is an internationally exploited stock and internationally agreed TACs were set until 2008. In 2014 the European Union, Norway and Faroe Islands agreed on a Management strategy to regulate the Northeast Atlantic mackerel fishery, extended until 2020 (ICES, 2020b; and references therein).

ICES is aware of the existence of different spawning components within the stock (ICES 2020q). However, biologically meaningful differences between mackerel from these components has not been detected although extensive mixing and homing behaviour were reported. After the revision in 2017, the working group concluded that the NE Atlantic mackerel should be considered as one stock (ICES 2020q) until new evidence will be

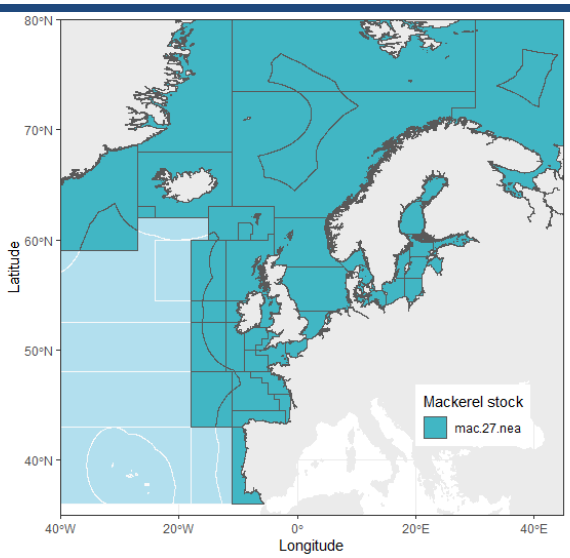


Figure 5.4. Atlantic mackerel ICES stock assessment unit.

[23] Further details on symbols and how to read the factsheet are provided on page 16

available. Catches are assigned to each component based on the subarea and division in which are taken:

- Western spawning component in subarea 5-7, 8.a, b, d and e
- Southern spawning component in subdivisions 8.c and 9.a
- North Sea spawning component in subarea 4 and division 3.a

The Western component is estimated to account for the 75% of the entire stock, while the Southern component for the 22% and the North Sea component only for the 3% (ICES 2020q). Measures are in place to protect the North Sea spawning component and to promote its recovery, i.e. seasonal closure and minimum landing size (ICES 2020q). The North Sea is closed to mackerel fishery in the first half of the year based on the observation that mackerel from the Western component enter the North Sea in summer (July-August) and leave in winter (ICES 2020q). Hence, part of the Western component quota can be fished also in division 4.a between 1 September and 15 February (ICES 2020w). The minimum landing size is 30 cm for the North Sea mackerel component and 20 cm for the Western component (ICES 2020w). In the last decade, feeding migrations of Atlantic mackerel in the NE Atlantic are expanding their extension northwards and westwards. However, in 2020 the feeding stock was less widely distributed and Atlantic mackerel was not reported in Greenland and a lower concentration was observed in Iceland. Since 2016 fishing mortality has declined below F_{MSY} and the spawning stock biomass is estimated to be above 3.7 million t in 2019 (ICES 2020w). Total catches were 840 021 t in 2019, mostly caught is subareas 1, 2, 5 and 14 and subareas 3 and 4 (ICES 2020w). Several mackerel TACs exist for European countries (Table 2) with special conditions and limits for quantities that may be fished in certain zones and seasons.

Genetic population structure in a nutshell

Genetic population structure in mackerel have been investigated by the means of different markers and on a wider scale differentiation between mackerel from the western Atlantic, eastern Atlantic and the Mediterranean Sea was showed. In the NE Atlantic, genetic evidence supports:

- Differentiation between western and eastern Atlantic mackerel, indicated by mitochondrial DNA (Scoles et al. 1998, Nesbø et al. 2000), microsatellite (Gíslason et al. 2020) and SNP (Rodríguez-Ezpeleta et al. 2016) analyses.
- Within the NE Atlantic, genetic differentiation between spawning stocks i.e. the northern (North Sea), western and southern stocks (Nesbø et al. 2000).
- The lack of differentiation reported by Gíslason et al. (2020) between the Bay of Biscay and Irish shelf, could be due to the inclusion of samples exclusively belonging to the Western spawning component. The samples were collected from the northern and central part of the Bay of Biscay (division 8.a and 8.b) currently considered part of the western component.

Samples from the southern, western and northern spawning stocks should be analysed in further studies to confirm the differentiation found at mtDNA markers (Nesbø et al. 2000).
Within the Mediterranean genetic population structuring of mackerel was supported by mitochondrial, microsatellite and SNP markers. Genetic structure was detected within the Adriatic basin with mackerel in the norther-central part of the basin (GSA 17) genetically differentiated from the southern Adriatic (GSA 18) (Papetti et al. 2013). The southern Adriatic resulted genetically similar to the Greek sample (Zardoya et al. 2004). Differentiation between eastern and western Mediterranean was supported by SNPs, that suggested also genetic homogeneity for the western Mediterranean samples and the Tyrrhenian Sea (Rodríguez-Ezpeleta et al. 2016).

Mismatch

The Northeast Atlantic mackerel is considered as a stock assessment unit although catches are assigned to each spawning component by ICES and particular measures are implemented to protect the North Sea component. The mismatch is due to the presence of genetically differentiated spawning units within the stock unit, i.e. the western, southern and northern units. Further investigations with more powerful markers and the inclusion of samples collected from spawning aggregations should be carried out in order to confirm the differentiation and design more appropriate unit and eventually evaluate the contribution of each spawning components to mixing feeding aggregations.

Summary of genetic evidence

The first study investigating genetic population structure of mackerel in the NE Atlantic was conducted by Jamieson et al. (1987), that analysed variation at two allozyme loci in 1164 individuals sampled across the European continental shelf. No significant differentiation was reported between samples collected in the northern North Sea, west of British Islands and the Bay of Biscay.
On a larger geographic scale, Scoles et al. (1998) detected genetic differentiation between mackerel in the north-western and NE Atlantic waters, confirmed also by Nesbø et al. (2000). Moreover, Nesbø et al. (2000) reported genetic structure within the NE Atlantic samples and suggested the existence of three genetically different spawning stocks, i.e. the North Sea, the western and southern stocks. In this study was also showed mixing of individuals from the three stocks in samples collected during the feeding season, highlighting the importance of sampling strategy in investigating genetic population structure of marine fish species.
Genetic structure was detected also within the Mediterranean Sea by Zardoya et al. (2004) analysis of the mitochondrial control region sequences of samples collected off Greece, Italy, Spain and Portugal. The eastern samples from Greece and Italy clearly differentiated from the Spanish sample (western Mediterranean), that was more similar to mackerel

from the Atlantic Portuguese coast. Substructure within the Mediterranean should be taken into account in management and assessment.

Using a combination of different methods, including fisheries data, otolith microchemistry and microsatellite analyses, Papetti et al. (2013) examined samples of mackerel from the Adriatic Sea. The presence of a panmictic population of mackerel in the northern-central Adriatic Sea was supported by genetic and otolith microchemistry analyses. However, genetic differentiation was detected between the northern-central population (GSA 17) and the southern Adriatic (GSA 18). This result is in line with a previous investigation indicating the southern Adriatic sample being genetically similar to the Greek sample, referred as eastern Mediterranean unit in Zardoya et al. (2004).

Rodríguez-Ezpeleta et al. (2016) investigated genetic population structure in Atlantic mackerel using RAD-sequencing data and supported the existence of genetic differentiation among the Northwest Atlantic (Canada), Northeast Atlantic (Bay of Biscay) and the Mediterranean regions. Within the Mediterranean samples, significant genetic structure was reported. The western Mediterranean and Tyrrhenian Sea resulted genetically similar and significantly differentiated from the Adriatic Sea. In contrast with previous analysis, here the genetic differentiation between mackerel inhabiting the western Mediterranean and the Atlantic is showed.

Gíslason et al. (2020) using microsatellite markers confirmed the differentiation between mackerel in the north western and NE Atlantic. Moreover, individuals collected in feeding aggregations in Greenland, Iceland and Faroese were analysed and resulted genetically similar to the NE Atlantic spawning samples, showing that feeding aggregations are composed of individuals from the NE Atlantic mackerel stock.

5.5 European sprat, *Sprattus sprattus*

Number of studies	6
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[24]

European sprat, *Sprattus sprattus* L., is a small pelagic species widely distributed in the North-East (NE) Atlantic from Norway to Morocco, and in the Baltic Sea, the Mediterranean and the Black Sea. It is a short-lived commercially important clupeid. Sprat is a forage fish for seabirds, marine mammals and important gadoids.

Current management status

In the NE Atlantic, ICES currently recognize four stock assessment units for sprat (Table 2): sprat in the Baltic Sea (Subdivisions 22-32), sprat in the North Sea, Skagerrak and Kattegat (Subarea 4 and division 3.a), sprat in Subarea 6 and southern Celtic Seas (divisions 7.a-c, f-k) and a separate stock unit in the English Channel (spr.27.7de).

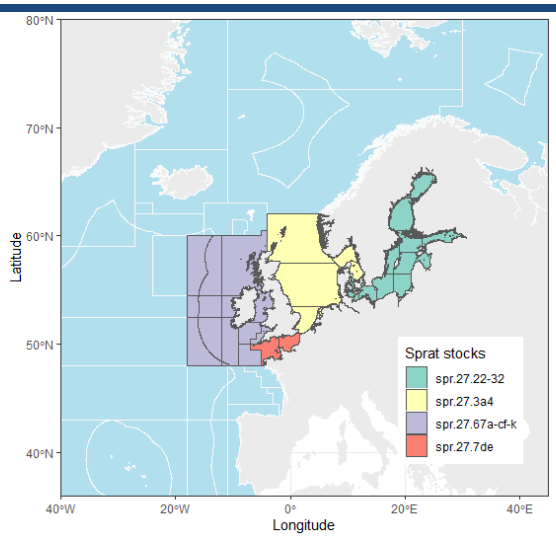


Figure 5.5. European sprat ICES stock assessment units.

Since 1992, sprat in the Baltic Sea has been considered a separate stock assessment unit (ICES 2020b). In the Baltic Sea, the natural mortality of sprat is subject to cod biomass. The stock is managed under an European multiannual plan (ICES 2020b). Mixed shoal of juvenile herring and sprat are commonly found in the Baltic Sea. Most of sprat catches are from the fish meal fishery, in which sprat is caught in a mixed fishery with herring and uncertainties in reported landings exist for both species. Thanks to the strong year class of 2014 the spawning stock biomass is increasing and is estimated to be above 1 million t in 2022 if the stock will be exploited at

[24] Further details on symbols and how to read the factsheet are provided on page 16

F_{MSY} (ICES 2020b). The total catches in 2019 were 314 147 t, mainly taken in subdivision 26 (37%), followed by subdivisions 25 (21%) and 28 (20%).

Sprat in the North Sea, Skagerrak and Kattegat (spr.27.3a4) is assessed as a stock unit since 2018, when based on genetic evidence, otolith shape analysis and cohort dynamics, sprat in division 3.a was merged to the North Sea stock (ICES 2020h). The stock is defined as sprat in 3.a and 4 with the exclusion of the Norwegian fjords. Although the two stocks were merged in 2018 in one stock assessment unit, TACs are still set for division 3.a and subarea 4 separately. ICES recognize that different stocks may be included within the main one and their conservation should be an issue (ICES 2020h). ICES is also aware of potential isolation of sprat populations in northeastern and eastern of Scotland that may be not connected with the southern North Sea, where the main stock resides (ICES 2019k). Total catches were 147 793 t in 2019, mainly from division 4.b (90%) and the main fishing country was Denmark, accounting for the 83% of the catches (ICES 2020h). Most of the catches are fished in the third and fourth quarter of the year. Sprat in the North Sea is mainly targeted from industrial fishery and bycatch of herring is inevitable. Hence, a by-catch quota for juvenile herring is set for sprat industrial fisheries. The spawning stock biomass is increasing and ICES advice a TAC of 207 807 t for sprat (increasing of 50% respect to the previous year) (ICES 2020h).

Sprat in the English Channel (division 7.d-e) is a target fish and is mainly caught for human consumption (ICES 2020h). Catches are mostly from division 7.e. (western English Channel) and fishery takes place from August to February-March of the following year (ICES 2020h). Historically, the UK is the main fishing country accounting for 99% of the catches in the last decade (ICES 2020h). Landing in 2019 were 1573 t. There is limited information whether this is a biologically meaningful unit or not and until new evidence will be available ICES advice are based on these divisions (7.d and 7.e) as a unit. A TAC exists for sprat in the English Channel.

The stock structure of sprat in the Celtic seas (subarea 6 and 7), is not very clear and further investigations are needed (ICES 2020h). ICES reported lack of information to assess if there is one or multiple units and to evaluate the status of the stock. It is not managed with a TAC, although the fishery is limited by the herring bycatch quotas (ICES 2020h). Total landings from the Celtic Seas in 2019 were 14 350 t (incl. division 7.d-e).

A stock assessment unit exists for sprat in the Black Sea (GSA 29), it is declining due to a combination of fishing pressure and environmental conditions (İlhan et al. 2018). Total catches in 2017 were 52 530 t and the main fishing country was Turkey. A TAC is set for European waters to Bulgaria and Romania.

Genetic population structure in a nutshell

In a remarkably short time, population structure of sprat in the NE Atlantic and the Mediterranean Sea was explored by means of different genetic markers. Sprat is an excellent example of how genetic population structure can be studied and implemented

in fisheries assessment to define more biologically meaningful unit in only a decade. The first genetic study was published in 2008 and a broad panel of genetic markers have been applied in the following investigations (mtDNA, microsatellites, SNPs). In 2018, genetic evidence (supported also by other methods) were used to merge the North Sea (subarea 4) and the Skagerrak-Kattegat (division 3.a) in one stock assessment unit by ICES. Showing how genetics can be implemented in stock definition of commercially important fish species to redraw the stock unit in line with the best available scientific evidence.
In summary, genetic evidence supported:

- Genetic differentiation among sprat in the NE Atlantic, Mediterranean and Black Sea.
- Significant differentiation was confirmed by microsatellites and mtDNA sequence analyses as well as by SNPs between the North Sea and Baltic Sea, and a transition zone was identified in the Belt Sea.
- Mixing, both admixture and mix of individuals form the two stocks, was reported in the Belt sea and in the transition zone between the Kattegat and the Baltic Sea. Further studies are needed to explore potential spatio-temporal pattern of this mixing. A genetic tool to distinguish between North Sea and Baltic Sea sprat populations was developed and can be used to explore spatio-temporal pattern of mixing in the transition zone.
- A lack of differentiation was reported in the North Sea, English Channel, Celtic Sea and Bay of Biscay, further studies covering the whole area are needed as well as the use of multidisciplinary approach to reveal population structure relevant to a fisheries management time scale. In fact, the lack of differentiation may be due to historical gene flow rather than actual. Further studies will shed light on sprat population structure.

Mismatch

A mismatch is reported between genetic and management units due to the existence of separate management units in division 3.a (Skagerrak and Kattegat) and the North Sea (Subarea 4). Moreover, despite no genetic differentiation was found among sprat from the North Sea, Celtic Seas and English Channel, sprat in these regions in assessed and managed in different units, resulting hence in mismatches between genetic, stock assessment and management units. However, further analyses are needed to explore population structure in this highly mobile pelagic fish species, with a combination of different approaches and methods to detected differentiation relevant at a fishery-time scale.

Summary of genetic evidence

Until recently, knowledge of genetic population structure in sprat in its distributional range was lacking. In a remarkably short time, population structure for sprat in the NE Atlantic and the Mediterranean Sea was explored by means of different genetic markers.

Debes et al. (2008) using the mtDNA sequence variation of the control region detected significant differentiation between sprat sampled in the NE Atlantic and the Mediterranean Sea. Differentiation was reported also between sprat sampled in the Gulf of Lyon, in the Adriatic Sea and in the Black Sea.

The differentiation of the Adriatic sample was confirmed by Limborg et al. (2009) using microsatellites. In this study genetic differentiation between the North Sea and Baltic Sea samples was showed, with the Belt Sea representing a transition zone. Moreover, the existence of weak structure was observed in the North Sea and the Celtic Seas suggesting that sprat may be not a panmictic population in this region.

Glover et al. (2011) supported the differentiation between the North Sea and Baltic sea sprat and furthermore showed also the presence of a genetically different population inhabiting the Norwegian fjords. However, no significant substructure was reported between the North Sea and Celtic Sea samples.

The study of Limborg et al. (2012) confirmed the overall population structure of sprat detected by previous studies supporting the presence of at least five reproductively isolated populations of sprat in the Baltic Sea, NE Atlantic, western Mediterranean, Adriatic and Black Sea, respectively.

The existence of three genetically distinct groups was confirmed also by Quintela et al. (2020) using 91 SNPs analysed in 2500 individuals, i.e. the Norwegian fjords, the North Sea, Kattegat-Skagerrak (including the English Channel, Bay of Biscay and Celtic Sea samples) and the Baltic Sea. Results from this study were used by ICES to redraw sprat stock assessment units. The North Sea (Subarea 4) and the Skagerrak and Kattegat (division 3.a) were merged in a stock unit, showing how genetics can be implemented in stock definition of commercially important fish species to design biologically meaningful unit in a reasonable time. However, further studies are needed to explore population structure of sprat around the British Isles, i.e. in the North Sea, English Channel, Celtic Seas and Bay of Biscay, as well as to estimate the spatio-temporal pattern of mixture between the North Sea and Baltic Sea sprat in the transition zone.

A similar pattern was found by McKeown et al. (2020) that used a wider SNP panel (4131 loci). Genetically different groups were identified in the NE Atlantic i.e. the North Sea (including the Kattegat, English Channel and Celtic Sea), the Baltic Sea and Norwegian fjords. Lack of differentiation at both neutral and outlier loci was observed among the North Sea, English Channel and Celtic Sea samples. However, the authors highlighted that a lack of genetic differentiation cannot rule out the isolation of the stocks on a fishery relevant time scale, suggesting the need to use a multidisciplinary approach for sprat stock identification in the NE Atlantic.

5.6 Atlantic herring, *Clupea harengus*

Number of studies	35
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[25]

Atlantic herring, *Clupea harengus* L., is amongst the most important commercial fish species in the North Atlantic. It is a pelagic and shoaling marine fish species widely distributed in the North-East Atlantic, from south Greenland and Iceland to the Barents Sea and northern bay of Biscay, including the Baltic Sea (Whitehead 1985). Feeding and spawning migrations of large herring shoals exist. Spawning occurs in coastal waters, but during the feeding season herring are commonly found in offshore waters, often forming identifiably distinct assemblages. Several such distinct populations have been identified across the North Atlantic, mostly identified by spawning time (spring, or summer-autumn), spawning location and ecological and morphological characteristics. Herring is a demersal spawner and releases benthic eggs on the bottom whereas larvae are pelagic and can be transported by ocean currents (Whitehead 1985).

Current management status

ICES consider 10 stock assessment units for herring in the NE Atlantic and mismatches already exist with management units (Table 2). Details for each stock are provided below:

The Norwegian Spring Spawning Herring (NSSH) stock includes herring in subareas 1, 2 and 5 and divisions 4.a and 14.a (her.27.1-24a514a) and is one of the largest herring stocks worldwide. Herring from this stock spawns along the Norwegian coasts during spring and migrate into the open Norwegian Sea during the feeding season (ICES 2020w). ICES is aware of the possible mixing with nearby herring stocks, as the North Sea, the Icelandic summer spawning herring, the Norwegian fjords autumn spawning herring and the Faroese autumn spawning herring (ICES 2020w). The development of methods to distinguish between the Norwegian spring spawning herring and the surrounding stocks may be appropriate to investigate potential mixing. The stock is declining, however the spawning stock biomass is above sustainable reference points (ICES 2020w). Since 2019, it is managed under an international management plan (ICES, 2020; and references therein). In 2019 the 64% of the catches were caught in the fourth quarter of the year, mostly in international waters of the Norwegian Sea (ICES 2020w). Total catches in 2019

[25] Further details on symbols and how to read the factsheet are provided on page 16

were 777 165 t and exceeded the 50% the ICES advice on catches for the year (ICES 2020w).

The Icelandic summer spawning herring stock is a local Icelandic stock (division 5.a), managed by the Icelandic Ministry of Fisheries. In Icelandic waters two local stocks of herring are present with different spawning seasons: the Icelandic summer and the spring spawning stocks (ICES 2019b). Due to overfishing both stocks collapsed in the late 1960s, and the Icelandic spring spawning stock has not recovered, yet (ICES 2019b). Hereafter, only one assessment unit for herring is considered in Icelandic waters. However, proportions of the herring spring spawning stock in catches are estimated annually (ICES 2019b). Moreover, herrings belonging to the Norwegian spring spawning stock can be found in east of Iceland feeding areas during summer, mixing with the local stock (ICES 2019b). Catches from the two stocks are estimated based on the maturity stage of the individuals. Directed fishery occurs in the fourth quarter of the year mainly in offshore areas in West of Iceland (ICES 2019b). However, herring is also fished as by-catch in mackerel fishery and that of the Norwegian spring spawning herring in Icelandic feeding grounds in summer (ICES 2019b). ICES did not provide advice for the Icelandic stock in 2020 due to Covid-19 disruption. Total landings in 2018/2019 fishing season were 40 683t (ICES 2019b). Icelandic spring spawning herring contributed to 1.3% of the autumn catches in the west coast (ICES 2019b). As reported by ICES, although fishing mortality is below reference points, since the 2000s the size of the stock is declining due to high natural mortality resulting from parasite outbreaks and below average recruitment (ICES 2019b).

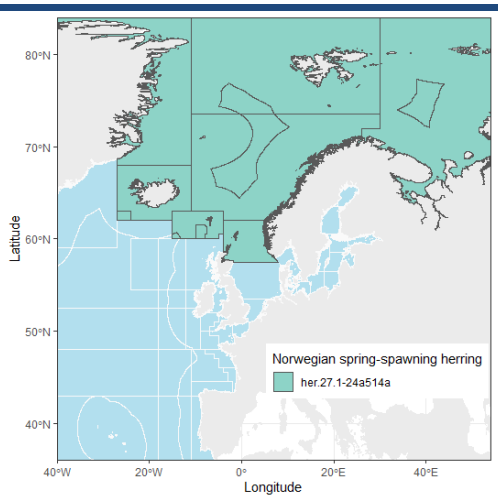


Figure 5.6.1. Norwegian spring spawning herring ICES stock assessment unit.

Four stock assessment units exist for herring in the Baltic Sea and an equal number of management units are in place (Table 2) (Figure 5.6.3). Herring is targeted by pelagic trawlers in a mixed fishery with sprat, and as reported by ICES misreporting of catches adds some uncertainty (ICES 2020b). Uncertainties arise also due to mixing in subdivisions 24-

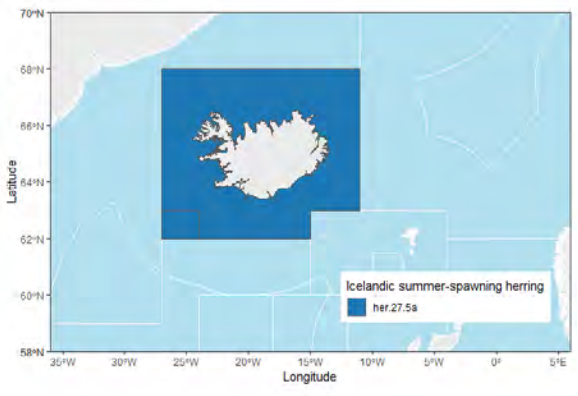


Figure 5.6.2. Icelandic summer spawning herring ICES stock assessment unit.

26 of the Central Baltic herring and Western Baltic herring stocks, that will be further investigated by ICES (ICES 2020b). The following stock assessment units are found in the Baltic Sea:

- Central Baltic herring (Spring spawning herring in subdivisions 25-27, 28.2, 29 and 32). Preliminary catches of this stock estimated by ICES in 2019 were 204 438 t (including the Gulf of Riga) (ICES 2020b). The mixing of Central Baltic and Western Baltic herring stocks in subdivisions 24-26 adds some uncertainty and will be further investigated by ICES (ICES 2020b).
- Herring in the Gulf of Riga (Subdivision 28.1) is a separate stock, as supported by specific characteristics of Riga herring, i.e., slow growth and otolith structure (ICES 2020b). The stock is resident in the Gulf of Riga (Subdivision 28.2) although older individuals may leave the Gulf after the spawning season in summer-autumn (ICES 2020b). Assessment and management of herring take into account that Riga herring may be fished also in subdivision 28.2 and *vice versa* the Central Baltic herring may be caught in the Gulf of Riga (subdivision 28.1), and otolith structure is used to assign catches to the correct herring stock (ICES 2020b). Catches of Riga herring in the Gulf amounted at 27 721 t and 1 200 t of Riga herring were fished outside the Gulf, resulting in a total of 28 922 t of Riga herring caught in 2019 (ICES 2020b). Catches of Central Baltic herring in the Gulf of Riga were 3 560 t (ICES 2020b).
- Herring in the Gulf of Bothnia (subdivisions 30-31). Herring in the Gulf of Bothnia is assessed as a stock by ICES since 2017 when subdivisions 30 and 31 were merged (ICES 2020b). Catches of herring are mainly from subdivision 30 (ICES 2020b).
- The Western Baltic Spring Spawners herring stock in division 3.a and subdivisions 22-24 is a complex stock (ICES 2020b). In the Skagerrak and Kattegat (division 3.a) herring is caught in a mixed stock fishery exploiting the North Sea Autumn Spawners and Western Baltic Spring Spawners herring stocks (ICES 2020b). Feeding and spawning migrations of Western Baltic herring are known, individuals migrate to feed in the Skagerrak and the eastern part of the North Sea while in winter they migrate back to Rugen (subdivision 24) and other spawning areas in the western Baltic Sea (ICES 2020b). Recent evidence suggested also migration of the Central Baltic herring into subdivision 24 (ICES, 2020b; and references therein). Moreover, the Western Baltic herring stock includes different populations: the dominant is the Spring Spawning but there are also local autumn and winter spawning components. The existence of these components, and the Central Baltic herring migration in subdivisions 22-24, add some uncertainties to the assessment (ICES 2020b). The Western Baltic herring is exploited in different divisions, comprising the eastern North Sea. The stock is declining and was at an historical minimum in 2019 due to poor recruitment and no appropriate levels of fishing mortality for a stock rebuilding (ICES 2020b). Catches in 2019 decreased

and were 25 420 t, 8 832t caught in division 3.a (Kattegat and Skagerrak), 8 832 t in subdivisions 22-24, and 6 757 t in the North Sea, respectively (ICES 2020b). ICES,

- based on the MSY approach advice zero catch in 2021 for the Western Baltic spring spawning herring in subdivisions 20-24 and eastern part of the North Sea.

The North Sea autumn spawning stock includes herring in subarea 4 (North Sea), divisions 3.a (Skagerrak-Kattegat) and 7.d (eastern English Channel) (Figure 5.6.4). Four different spawning components contributes equally to the stock and their conservation is crucial for successfully manage this fishery (ICES 2020h). ICES is aware of potential mixing with neighbour stocks particularly in division 3.a with herring from the Western Baltic spring spawning stock. Furthermore, the existence of local fjord spring spawning herring and Norwegian spring spawning herring near the Norwegian coast in the eastern part of the northern North Sea (division 4.a) is address by the set of a separate TAC (ICES 2020h). Similarly, herring from the Thames estuary, known as blackwater herring is managed with a separate quota. Based on ICES advice, the North Sea herring stock is harvested sustainably and fishing pressure is below sustainable reference points, although recruitment has been low since 2014 (ICES 2020h). Total landings of North Sea herring in 2019 were 444 001t (ICES 2020h). Catches from the local fjord herring amounted at 5t in 2019 (ICES 2020h). The main fishing country is Norway, followed by Denmark, the Netherlands and the United Kingdom. Herring in divisions 6.a, 7.b and 7.c is assessed as a stock unit by ICES since 2016 (ICES 2020h). However, ICES is aware this stock contains different populations and effort is made to assure that the more vulnerable ones are not overexploited. Moreover, ICES reports of ongoing projects to define stock boundaries for herring

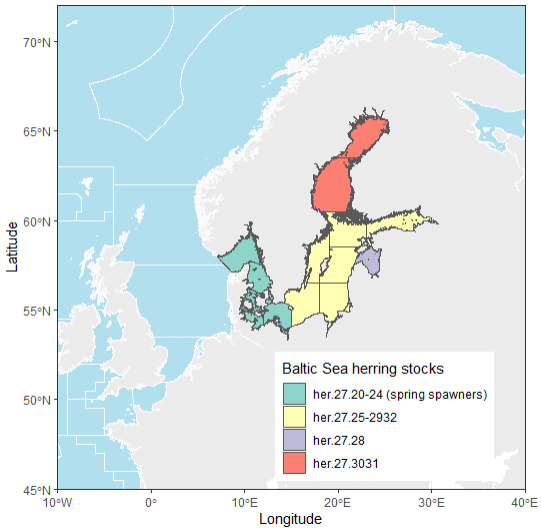


Figure 5.6.3. Atlantic herring ICES stock assessment units in the Baltic Sea.

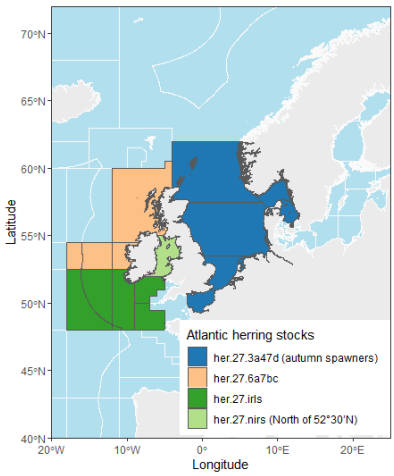


Figure 5.6.4. Atlantic herring ICES stock assessment units in the North Sea and adjacent waters.

populations in these divisions. Since 2016, ICES advice is of zero catches. However, a monitoring TAC is set to allow scientific survey and sample collection to assess the stock status (ICES 2020h). Although there is a mismatch with the management units (Table 2), the ICES working group recommended to maintain those management units (ICES 2020h). When new evidence will be available the stock will be benchmarked and biologically meaningful stock unit defined (ICES 2020h).

A separate stock unit exists for herring in division 7.a North (Irish Sea). Based on ICES assessment the stock is harvested sustainably and fishing mortality is below F_{MSY} (ICES 2020h). It is mostly caught from the UK (ICES 2020h). Herring in division 7.a South of 52°30' and 7.g, h, j is considered as a separate stock assessment unit. The spawning stock biomass is declining and fishing mortality is above F_{MSY} (ICES 2020h), hence only a monitoring catch is allowed for scientific surveys.

Three other stocks of herring are present in the NE Atlantic for which extremely limited information is available, Clyde herring (part of division 6.aN), herring in divisions 7.e.f and herring in the Bay of Biscay (ICES 2020h).

Genetic population structure in a nutshell

Using a variety of markers genetic population structure has been detected in herring in the NE Atlantic. Although high levels of gene flow are suggested by neutral markers, coincident with the highly migratory habit of the species, the existence of locally adapted populations was reported through loci under selection. Genetic differentiation was confirmed also between autumn and spring spawning herring. A genetic tool is available to distinguish between these two ecotypes. In general, genetic evidence suggests:

- Significant differentiation between herring in the northwest and northeast Atlantic (McPherson et al. 2004).
- Parallel evolution in herring populations, six SNP loci associated with reproductive time across populations in the western and eastern Atlantic as well as in the Baltic were found (Lamichhaney et al. 2017).
- The existence of local populations in Norwegian fjords was supported by allozymes (Jørstad et al. 1991, Turan et al. 1998), microsatellites (Shaw et al. 1999, Pampoulie et al. 2015b) and SNPs (Han et al. 2020).
- Differentiation among local Norwegian fjord population, Norwegian spring spawning herring, Icelandic summer spawning herring was detected (Shaw et al. 1999) in line with stock assessment units, as well as among Icelandic herring, Baltic Sea and Celtic Sea herring (Hauser et al. 2001, McPherson et al. 2004).
- A pattern of isolation by distance was reported for herring in the North Sea and adjacent waters (Mariani et al. 2005). Herring from the English Channel and the Norwegian coast were genetically different and the existence of a different unit was suggested also in Northern Scotland. However, a lack of structure within the North Sea- British Isles was reported successively by Limborg et al. (2012). Further studies are needed to explore herring population structure around the British Isles.

In the Baltic Sea, genetic studies indicated:

- Genetically different spawning waves in Rügen (subdivision 24) (Jørgensen et al. 2005b a) and Aland (Jørgensen et al. 2008).
- Significant differentiation was showed among the western Baltic, Central Baltic, Gulf of Riga and northeast Baltic basin (Jørgensen et al. 2005a, 2008).
- Substructure was detected within the Central Baltic herring unit, genetic differentiation was reported between herring in subdivision 29 and 28.2, in contrast to current stock assessment and management unit (Corander et al. 2013). Samples along the Swedish coasts in subdivisions 25, 27, 29 were genetically similar and differentiated from Rügen (subdivision 24), Kattegat, Skagerrak and a coastal sample from subdivision 28.2, that were genetically homogeneous (Teacher et al. 2013).
- A genetically distinct population was identified in the Gulf of Finland (subdivision 32) (Guo et al. 2016).

In the Baltic Sea- North Sea transition zone:

- Genetic differentiation between North Sea, Skagerrak and Baltic Sea was confirmed with both neutral and outlier markers (André et al. 2010). Outlier showed higher levels of divergence also confirmed by SNPs (e.g. Lamichhaney et al., 2012).
- Mixing in feeding aggregations of the North Sea herring, local Skagerrak and Western Baltic herring in the transition zone was reported by microsatellite and SNP analyses (Ruzzante et al. 2006, Bekkevold et al. 2011, 2015).
- The genetic differentiation between North Sea and Baltic Sea herring is associated with salinity differences (Bekkevold et al. 2005, Jørgensen et al. 2008, Gaggiotti et al. 2009)
- Temporally stable groups were identified, namely herring in the Baltic Sea, transition zone, North Sea-British Isles and North Atlantic (Limborg et al. 2012b).

Differentiation between autumn and spring spawning populations:

- The genetic differentiation between autumn and spring spawning herring ecotypes was supported by SNP analyses in the Gulf of Riga (Bekkevold et al. 2016), and in the Baltic Sea (Barrio et al. 2016).
- Parallel evolution in herring populations from the western and eastern North Atlantic Ocean and loci associated with reproductive time across populations in the North Atlantic and Baltic Sea was reported (Lamichhaney et al. 2017).
- Whole-genome sequencing analysis (Han et al. 2020) and SNP analyses (Barrio et al. 2016, Bekkevold et al. 2016) supported the existence of genetic differentiation among herring populations restricted to small portions of the genome involved in local adaptation (genomic islands of divergence). Evolution of these locally adapted loci is maintained despite current gene flow through chromosomal inversions (Han et al. 2020).

- A genetic tool was developed to distinguish between spring and autumn spawning herring (Lamichhaney et al. 2017). It was tested in a Norwegian fjordic area showing high spawning fidelity of herring populations to the correct spawning season (spring and autumn). However, individuals spawning in the opposite season were observed supporting gene flow between the two populations (Berg et al. 2020).

Mismatch

In general, population structure in the NE Atlantic is taken into account in assessment and management with separate assessment and management units for the Icelandic herring stock, the Norwegian spring spawning stock and Norwegian local fjord herring. However, further studies are needed to investigate genetic population structure of herring around the British Isles, in the North Sea and adjacent areas.

Genetic population structure found in the Baltic Sea challenges the current stock assessment and management units of herring. Local populations are present in the transition zone, although the assessment unit is for Western Baltic Spring Spawners herring in division 3.a and subdivision 22-24. Mixing of different populations in the North Sea- Baltic Sea transition zone was reported and ICES is aware of the complexity this mix can add to the assessment of the Western spring spawning herring stock. Genetic tools could be implemented to explore the spatio temporal pattern of mixing and take it into consideration in assessment and management.

Mismatches with stock assessment and management units in the Central Baltic (SD 25-29, 32) are suggested, due to differentiation of herring collected along the Swedish coast and the southern coastal samples. Likewise, herring in the Gulf of Finland (subdivision 32) was genetically differentiated, resulting in a mismatch with the assessment unit.

Another mismatch exists for Gulf of Riga herring (subdivision 28.1). The existence of two genetically different populations, namely the spring and autumn spawning herring in the Gulf of Riga was observed although the assessment consider herring in the Gulf of Riga as a stock assessment unit, hence ulterior substructure is not taken into account. In order to protect and conserve the unique genetic diversity harboured in each population, the presence of the two populations should be considered in assessment and management.

Summary of genetic evidence

Herring in a well-studied species in the NE Atlantic. Genetic population structure has been studied by means of different genetic markers, and most of the studies focused on the Baltic Sea and the North Sea-Baltic Sea transition zone.

Early investigations were based on allozymes and mitochondrial DNA markers and have failed to detect genetic structure in herring distributional range in the NE Atlantic. A lack of differentiation was reported by Ryman et al. (1984) that used allozyme to analyse samples from the North Sea, Norway and the Baltic Sea. Likewise, King et al. (1987) found no genetic differentiation among mature herring samples collected in spawning grounds

around the British Isles and in the Baltic Sea. The lack of differentiation was confirmed also by Dahle and Eriksen (1990) mitochondrial DNA restriction analysis in samples of spring and autumn spawner herring collected at several spawning locations in the North Sea, Skagerrak and Kattegat.

Jørstad et al. (1991) reported also a lack of differentiation among samples from the British Isles, the Baltic and Norwegian Seas, though significant differentiation was found between oceanic and Norwegian fjord samples, and the existence of local population in Norwegian fjords was supported.

Using a combination of allozyme loci and mtDNA analyses, Jørstad et al. (1994) observed significant differentiation between herring in Balsfjord and the Norwegian spring spawning herring. In line with previous study, Turan et al. (1998) reported the co-occurrence of local fjordic herring and Norwegian spring spawning herring within Norwegian fjords. The microsatellite analysis conducted by Shaw et al. (1999) showed significant differentiation among Icelandic summer spawning herring, the Norwegian spring spawning and local Norwegian fjord populations (F_{ST} = 0.024, p <0.001), supporting current assessment and management units. Hauser et al. (2001) using RFLP analysis of two mitochondrial genes detected significant differentiation between Icelandic herring and the rest of the NE Atlantic samples, as well as between the Baltic Sea and Celtic Sea herring samples. However, in contrast with previous studies no differentiation was found between the Norwegian spring spawning herring and local fjord populations.

Successively, McPherson et al. (2004) microsatellite analysis revealed significant differentiation between the northwest and northeast Atlantic herring. Moreover, within the NE Atlantic the three samples of herring from Iceland, the Celtic Sea and the Baltic Sea were genetically different, in line with existing stock assessment units. At a finer scale, Mariani et al. (2005) investigated genetic population structure of herring in the North Sea throughout microsatellite loci. A pattern of isolation by distance driven by the differentiation of herring in the English Channel and the Norwegian coast was detected as well as the existence of a genetically different unit in Northern Scotland.

Within the Baltic Sea, Jørgensen et al. (2005b) reported genetic differentiation between temporal replicates of spawning aggregations sampled in Rugen (subdivision 24), but not in Gdansk Bay (subdivision 26). Using a landscape genetics approach, Jørgensen et al. (2005a) confirmed, as supported by other methods, the presence of three main groups of herring in the Baltic Sea, i.e. the Western Baltic herring, the Baltic Proper herring and the Gulf of Riga herring. The presence of genetically different spawning waves was confirmed in Rugen and in Aland.

Significant differentiation was found also by Bekkevold et al. (2005) that used neutral microsatellites to analyse 11 herring samples collected across the North Sea and the western Baltic Sea. Remarkably, population differentiation was associated with differences in salinity. Successively, Ruzzante et al. (2006) carried out a mixed stock analysis in the Baltic Sea-North Sea transition zone, using microsatellites and otolith

morphology. Presence of mixing of North Sea, local Skagerrak and Western Baltic herring was reported. The contribution of each populations to these aggregations varied seasonally, spatially and with the life-stage.

In the Baltic Sea, Jørgensen et al. (2008) using a combination of genetic, meristic and morphometric analyses found significant spatial and temporal differentiation in samples collected during the spawning season. The western Baltic Sea, the Gulf of Riga and the northeast group (Bothnia and Aland) were clearly differentiated. Significant differentiation was found also between temporal replicates collected in Aland, suggesting the existence of genetically different spawning waves.

In previous microsatellite investigations, the microsatellite loci used were assumed to be neutral although the neutrality was not routinely tested. Watts et al. (2008) showed how the chosen markers can affect the levels of genetic structure found in herring; when loci were under selection were included in the analysis, higher levels of differentiation were observed. The power of using a combination of neutral and under selection markers was highlighted and their potential in improving herring mixed stock analysis suggested. Jørgensen et al. (2008) through a combination of neutral and under selection markers showed natural selection and feeding migrations as two main forces shaping population structure in the North and Baltic Sea herring. The genetic differentiation found among spawning aggregations was explained by differences in salinity among sites. In line with this study, Gaggiotti et al. (2009) observed similar correlation between genetic differentiation and salinity differences, and reported salinity as selective pressure shaping herring population structure and associated allele frequencies at an outlier locus. Within the Baltic Sea, Larsson et al. (2010) found significant differentiation among samples of herring collected along the Swedish coasts. The Skagerrak and Central Baltic Sea samples were differentiated and populations were demographically independent. André et al. (2010) using both neutral and under selection microsatellites confirmed the differentiation among herring populations in the North Sea, Skagerrak and the Baltic Sea. The level of divergence between the Baltic Sea and the other samples was higher at the outlier locus, indicating that the utilization of markers under selection may be extremely valuable for stock identification and mixed stock analysis in species experiencing low levels of differentiation at neutral loci.

The existence of local Skagerrak and Kattegat populations was confirmed by Bekkevold et al. (2011). A mixed stock analysis was performed to explore the contribution of the four genetically different herring populations, namely North Sae, local Skagerrak, Kattegat and Rügen herring in transition zone. Higher proportions of herring form the North Sea were found in the western samples while higher proportion of Rügen herring in the eastern. Hence, population structure at a finer scale should be implemented in assessment and management.

Lamichhaney et al. (2012), through SNPs confirmed local adaptation in herring populations. Despite low levels of differentiation were detected in neutral region of the

genome, highly divergent loci were observed in restricted regions involved in local adaptation. The study supported the differentiation between Atlantic and Baltic Sea herring, and samples from the southern Baltic Sea resulted more similar to the Atlantic herring (Skagerrak and Kattegat) than Baltic herring.

Teacher et al. (2012) analysed the whole mitochondrial genome, showing that mitochondrial variation is not useful to investigate population structure in herring, although genes in the NADH complex showed sign of selection and may be used.

Limborg et al. (2012) used a transcriptome derived panel of 281 SNP loci to analyse herring samples collected at 18 spawning sites. Temporally stable genetic structure was reported and four genetically different groups were detected, namely the Baltic Sea, transition zone, North Sea-British Isles and the North Atlantic. When only neutral loci were used, the North Atlantic clustered with the North Sea and British Isles samples, showing once again the valuable information added by outlier loci. At a finer scale genetic differentiation was supported also for two eastern North Sea fjord samples and between Rugen and the Baltic populations. Loci under selection were reported, of these, nine were correlated with temperature and salinity reflecting local adaptation in herring populations.

Population structure at a finer scale was detected by Teacher et al. (2013) in the Baltic Sea (F_{ST}= 0.008) using 60 transcriptome-derived microsatellite loci. The pattern found was explained by oceanographic and environmental variables shaping genetic structure of herring in the Baltic Sea. The samples collected along the Swedish coasts in subdivisions 25, 27, 29 were genetically homogeneous and differentiated from the other populations. Likewise, another genetic unit included samples from Rügen (subdivision 24), Kattegat, Skagerrak and a coastal sample from subdivision 28.2, that were genetically homogeneous. Genetically distinct populations were reported also in the northern part of the basin. The population structure found is not taken into account in herring management, suggesting a possible revision of the units. The authors suggested the inclusion of subdivision 28.2 with the Western Baltic herring stock (subdivisions 20-24), and the splitting of the Central Baltic stock in Swedish and southern coastal samples.

Using a RAD-sequencing approach Corander et al. (2013) identified 5 985 novel SNPs in herring and 79% of the loci showed high divergence between two Baltic sea populations currently assessed in the same Central Baltic stock unit (SD 29 and 28.2) supporting existence of genetic differentiation and challenging the current stock assessment and management units.

Bekkevold et al. (2015) using gene associated markers, developed a tool to assign herring individuals to the region of origin in the NE Atlantic: feeding aggregations from the Skagerrak and the western Baltic Sea were analysed through 156 SNP loci. Western Baltic feeding aggregations represented a mix of local western Baltic herring and eastern Baltic herring; moreover, a low contribution of individuals with NE Atlantic origin was observed.

The Skagerrak mixed samples were mainly constituted of fish of North Sea and Transition zone origin in different proportions and a low contribution from Baltic Sea herring.
Genetic population structure of herring in the Norwegian Sea and adjacent waters was investigated with a combination of neutral and outlier microsatellites. A lack of genetic differentiation was reported by Pampoulie et al. (2015) among herring stocks in the NE Atlantic. However, one fjord sample was genetically different from the remaining samples supporting existence of substructure for herring within Norwegian waters. The lack of differentiation found between the Icelandic summer spawning herring and Norwegian spring spawners and other NE Atlantic samples need further investigation. Guo et al. (2016) used SNPs for analysing herring collected at 20 localities in the Baltic Sea, North Sea and Atlantic Ocean. The differentiation between Atlantic and Baltic Sea herring was confirmed. However, populations in the transition zone, although differentiated resulted more similar to the North Sea herring. In line with other studies, levels of differentiation among Baltic Sea samples were low at neutral loci, the existence of highly divergent genomic regions among Baltic Sea populations was showed and local adaptation to temperature and salinity was supported. Substructure was suggested within the Baltic Sea for herring, mismatching with the Central Baltic stock unit (25-29, 32) that includes genetically different populations i.e. Gulf of Finland is genetically divergent from the other populations. The study supported the need to managed Baltic Sea herring at a finer scale, taking into account the adaptive divergence between populations.
Bekkevold et al. (2016) detected genetic differentiation between two ecotypes of herring occurring in the Gulf of Riga, namely the autumn spawning and the spring spawning herring ecotypes. The divergence was restricted to certain region of the genome (islands of divergence) and using 15 outlier SNPs was possible to distinguish between the two ecotypes. The analysis of neutral loci showed that Baltic autumn spawning herring was closely related to the Baltic spring spawning herring. However, at SNPs under selection the Gulf of Riga autumn spawning herring was more similar to the North Sea autumn spawning herring supporting convergent evolution and adaptation to the same selective pressure. Despite the occurrence of two divergent populations of herring in the Gulf of Riga (autumn and spring spawners), herring in this subdivision is considered as one stock. As Bekkevold et al. (2016) reported, the contribution of autumn spawners to herring catches in the Gulf of Riga was higher in the past while currently it is less than 1% of the landings. Hence, measures to protect the autumn spawning herring in the Gulf of Riga mixed stock fishery should be implemented to avoid overexploitation and potential loss of unique genetic diversity.
The genetic basis of ecological adaptation in herring was investigated by Barrio et al. (2016) through genome assembly and the development of a SNP chip. Outlier loci involved in adaptive divergence between spring and autumn spawners were reported as well as between oceanic and Baltic Sea populations. In line with previous studies, low levels of genetic differentiation among populations were observed and the existence of

confined regions of the genome with highly differentiated SNPs (large haplotype blocks) was reported. Hence, genetic differentiation between autumn and spring spawners in the Baltic Sea was confirmed, as well as the need to implement measures to protect and conserve the genetic diversity harboured by these populations that underlies ecological adaptation. The study supports high gene flow between herring populations and natural selection acting to promote local adaptation.

Lamichhaney et al. (2017) found parallel evolution in herring populations in the western and eastern North Atlantic Ocean and reported six loci associated with reproductive time across populations in the western and eastern Atlantic as well as in the Baltic Sea. Moreover, this study provides genetic markers than can identified autumn and spring spawning populations.

In line with previous findings, the whole-genome sequencing analysis conducted by Han et al. (2020) supported the existence of genetic differentiation among herring populations restricted to small portions of the genome involved in local adaptation. The existence in herring genome of a tool box of highly associated loci involved in adaptation to local climatic condition (temperature, salinity, light) and spawning season was supported. The evolution of these locally co-adapted loci is maintained despite current gene flow thanks to chromosomal inversions that suppress recombination. Hence, loci associated with ecological adaptation are the best suitable markers to study population structure in herring while neutral loci are less powerful as previous studies showed.

The genetic tool developed to distinguish between spring and autumn spawning herring (Lamichhaney et al. 2017) was used by Berg et al. (2020) to assign individuals caught in a Norwegian fjordic area to the correct spawning herring ecotype. Spawning phenotypes, otolith microstructure analysis and the genetic tool were used in combination to distinguish between autumn and spring spawning herring populations in samples collected during both spawning seasons (spring and autumn). High fidelity to the spawning season was observed, however the presence of individuals having otolith structure and genotype of autumn spawners in spring spawning season and vice versa was reported. These results are consistent with the low levels of genetic differentiation found at neutral loci supporting gene flow between autumn and spring spawning herring. Moreover, it was showed that using the genetic tool improves the assignment to the correct population (spring or autumn spawner herring).

6 Other species

6.1 Anglerfish, *Lophius piscatorius* and *L. budegassa*

		L. piscatorius	*L. budegassa*
Number of studies	4		
Population structure	✓		
Match genetic- Stock assessment units	✗		
Match genetic- Management units	✗		
Match Stock assessment- Management units	✗		

Distribution[26]

Two species of the genus *Lophius* are exploited in the NE Atlantic and western Mediterranean Sea: the white anglerfish *Lophius piscatorius,* Linnaeus 1758, and the black-bellied anglerfish *L. budegassa*, Spinola 1807. In the NE Atlantic, the white anglerfish is distributed at more northern latitudes than *L. budegassa*: from the Barents Sea and Iceland down towards the Mauritian coasts (Caruso 1986). The black anglerfish has a more southern distribution and can be found from the Celtic Seas, across the Bay of Biscay and down towards Senegal (Caruso 1986). Both species can be found in the Mediterranean Sea, though the black anglerfish is more common. They are caught in mixed fisheries in most of the European Seas where their distribution overlap. A species-specific distribution pattern in bathymetry is known with the black anglerfish common at depths ranging between 100 and 500 m, and the white anglerfish between 20-1000 m (Caruso 1986). Adults are demersal and eggs are characterized by a long larval pelagic phase, varying between 2-4 months, conferring to the species high ability for dispersion. The two species are morphologically similar, but the colour of the peritoneum, which gives the name to the white and black bellied anglerfish, is considered a diagnostic character for species identification (Caruso 1986).

Current management status

Management is carried out for *L. piscatorius* and *L. budegassa* through combined TACs set for anglerfish *Lophiidae* (Table 2). ICES distinguishes several stocks in the NE Atlantic (ICES 2020a) and advice are given for the two species combined in subarea 1 and 2 (anf.27.1-2) and in the North Sea, west of Scotland and the Skagerrak and Kattegat (anf.27.3a46). Though assessment is provided for each species separately in the Celtic Seas, Bay of Biscay and Atlantic Iberian waters (Table 2).

ICES is aware of scientific evidence from tagging, genetics and otolith analyses not supporting the current stock assessment units and indicating exchanges between anglerfish in subareas 1-2 (anf.27.1-2) and the nearby subareas 4 and 6 (ICES 2020a). Anglerfish in subarea 1 and 2 may represent an influx of juveniles from subareas 4 and 6

[26] Further details on symbols and how to read the factsheet are provided on page 16

(ICES, 2020a; and references therein). However, results are inconclusive and ICES recommended further studies for stock delineation and until new information will be available anglerfish in subarea 1 and 2 will be treated as a separate stock. In subareas 1 and 2 Norway is the main fishing country accounting for 96-99% of anglerfish catches (ICES 2020a). The Norwegian fishery is regulated although a TAC does not exist (ICES 2020a). Catches are increasing and in 2019 were 2 809 t (ICES 2020a).

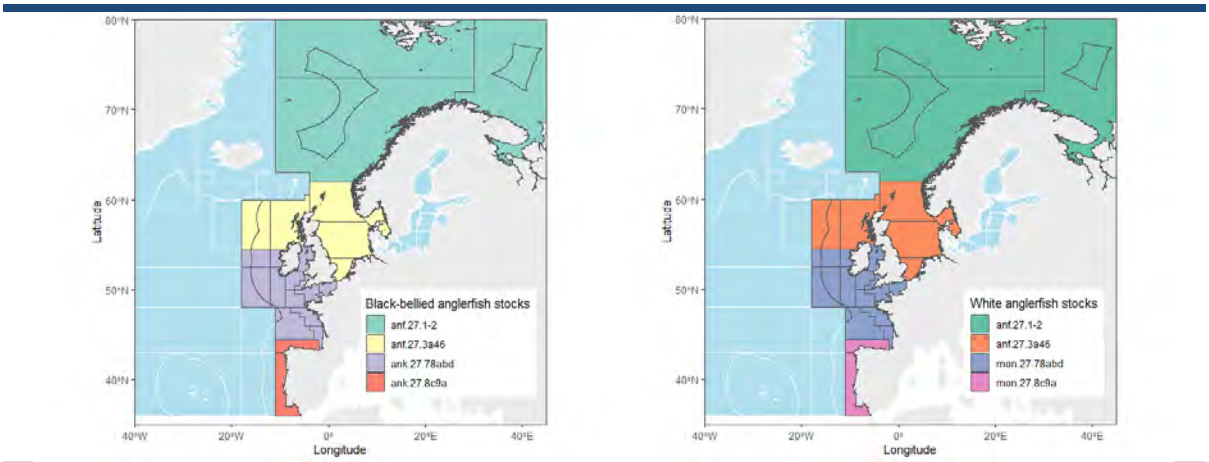


Figure 6.1. Anglerfish ICES stock assessment units; *Lophius* spp. stocks in subarea 1-2 (anf.27.1-2) and division 3.a, subareas 4 and 6 (anf.27.3a46). Left, black-bellied anglerfish stocks. Right, white anglerfish stocks.

Anglerfish in subareas 4 (North Sea), 6 (west of Scotland) and division 3.a (Skagerrak and Kattegat) are considered as a stock unit by ICES (ICES 2020t). This stock is included in the North Sea management plan (ICES 2020t). Landings in 2019 were 20 152 t of which 12 498 t were landed in subarea 4 and 7654 t in subarea 6 (ICES 2020t). Anglerfish is mainly fished as by-catch by demersal trawlers targeting white fish or *Nephrops*. The stock advice is given for the two species combined (ICES 2020t) and ICES estimates black anglerfish represents the 10% of the estimated stock biomass in this region. However, in west of Scotland (division 6.a) the proportion of black anglerfish is estimated to be the 28% and ICES is going to consider a possible split of the stock in a future benchmark (ICES 2020t). A mismatch between stock assessment and management units exists, TACs are set separately for anglerfish in the North Sea and west of Scotland. Moreover, no TAC or quota exist for the Skagerrak and Kattegat (division 3.a) although catches of anglerfish from this division are increasing. Due to these mismatch, catches may exceed the ICES advice (ICES 2020t).

In subarea 7 and divisions 8.a, b, d both white and black anglerfish are present and landings are often not separated by species (ICES 2020s). Anglerfish are caught in mixed fisheries with whitefish, flatfish and *Nephrops*. Landings of both species in 2019 amounted at 30 946 t, with white anglerfish accounting for the 69% of the landings (ICES 2020s). The main fishing country is France and the 80% of the catches is from subarea 7 (ICES 2020s). The two anglerfish species are assessed in separate stock assessment units

by ICES, however, a common TAC is set for their management (Table.2). The management - through a combined TAC for the two species - may lead to overexploitation of the weakest stock and the implementation of single-species management is recommended by ICES (ICES 2020s). ICES reported an increase in biomass for both anglerfish species due to good recruitments and fishing mortality below F_{MSY}, hence the risk of overexploitation is low (ICES 2020s).

The white and black anglerfish in the southern Bay of Biscay (divisions 8.c) and Atlantic Iberian waters (division 9.a) are fished in mixed fisheries and artisanal fisheries. Most of the catches are taken in division 8.c by Spanish vessels. Despite stock assessment units are separated for the two species, they are managed under a common TAC. Landings are at an historical minimum in the time series and reached 1 577 t in 2019. The proportions of the two species in landings have been fluctuating.

A stock assessment unit exists for *L. budegassa* in the Mediterranean, in southern Sicily and Malta (GSA 15, 16) although no information was available, based on hydrogeographic considerations and fishery distribution, the stock was considered to be restricted in these subareas in 2012.

Genetic population structure in a nutshell

For the black anglerfish (*L. budegassa*), the available information on genetic stock structure supports:

- Differentiation between Atlantic and Mediterranean basin (Charrier et al. 2006a, Blanco et al. 2008).
- Substructure was suggested by microsatellite data along the Atlantic Iberian coasts (Blanco et al. 2008). The Spanish Atlantic and the Portuguese samples were genetically different, not supporting their inclusion in the same stock assessment and management unit.

For the white anglerfish (*L. piscatorius*), genetic evidence supports:

- Differentiation between the NE Atlantic and Mediterranean populations showed by SNPs (Aguirre-Sarabia et al. 2021).
- Although, microsatellite data (Blanco et al. 2008) supported the differentiation of white anglerfish from the Atlantic French coast (northern Bay of Biscay), the SNP analysis reported the presence of a homogeneous population of white anglerfish in the NE Atlantic (Aguirre-Sarabia et al. 2021).
- The existence of hybrids between the two anglerfish species was indicated, especially in the northern Bay of Biscay (Aguirre-Sarabia et al. 2021).
- Misidentification of individuals based on morphological characters in use for species identification. It was observed particularly in the southern NE Atlantic divisions and in the Mediterranean Sea (Aguirre-Sarabia et al. 2021). Other diagnostic characters for species identification are needed.

Mismatch

Mismatches between stock assessment and management units are already present for anglerfish in the NE Atlantic, as previously discussed. Based on genetic evidence, the existence of separate populations of *L. budegassa* along the Atlantic Iberian waters was reported (Blanco et al. 2008), northern and southern samples in division 9.a were genetically differentiated suggesting a mismatch. However, more studies are needed to confirm this finding indicating population structure in division 9.a. Moreover, a lack of differentiation within the NE Atlantic was reported for the white anglerfish challenging the stock assessment units currently in use. Moreover, further studies are required to address the effects on assessment and management of both species of hybridization (especially in the northern Bay of Biscay) and misidentifications. In particular, misidentification of individuals through diagnostic characters commonly in use demands the development of new methods.

Summary of genetic evidence

Genetic population structure of *L. budegassa* and *L. piscatorius* has been investigated by means of different genetic markers. Using allozymes, Crozier (1987) in an initial study reported limited differentiation between the Irish Sea and west of Scotland samples of white anglerfish.

(Charrier et al. 2006a) investigated sequence variation of the mitochondrial control region. A lack of genetic differentiation was reported for the white anglerfish between the Mediterranean and the NE Atlantic (Northern Ireland and Norway down to southern Bay of Biscay), as well as within each region. However, significant genetic differentiation was found between Atlantic and Mediterranean samples for the black anglerfish. Blanco et al. (2008), using microsatellites, confirmed the differentiation between Atlantic and Mediterranean populations of black anglerfish. However, microsatellite data did not support the current assessment and management units in the NE Atlantic for both species. Genetic differentiation was reported between samples of black *L. budegassa* from the Spanish Atlantic coasts of division 9.a and the Portuguese samples collected in the southern part of division 9.a. Likewise, substructure was indicated in *L. piscatorius*. The white anglerfish from the Atlantic French coast of the Bay of Biscay was genetically differentiated from the rest of the samples. No pattern of isolation by distance was detected in either species.

Aguirre-Sarabia et al. (2021) through SNP loci confirmed the genetic differentiation between *L. piscatorius* populations in the Mediterranean and Atlantic. The SNP analysis indicated the presence of a homogeneous population of white anglerfish within the NE Atlantic, hence not supporting assessment and management in different stock units. The study also arises caution due to misidentification through diagnostic characters commonly in use for species identification especially in the southern divisions and the Mediterranean Sea. Moreover, hybridization between the white and black anglerfish was

reported occurring particularly in the northern Bay of Biscay and Celtic Seas where the two species overlap and a hybrid zone may exist. Interestingly, the Northern Shelf stock was not affected neither by misidentification or hybridization.

6.2 Beaked redfish, *Sebastes mentella*

Number of studies	10
Population structure	✓
Match genetic- Stock assessment units	✓
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[27]

The beaked redfish, *Sebastes mentella* (Travin, 1951) is a commercially valuable rockfish species in the family Scorpaenidae. Three different redfish species are exploited in the NE Atlantic, namely the beaked redfish (*Sebastes mentella*), the golden redfish (*Sebastes norvegicus,* historic name *S. marinus*) and the Acadian redfish (*Sebastes fasciatus*). ICES provides scientific advice for the first two species. The beaked redfish is widely distributed across the North Atlantic Ocean, from Norway and the Barents Sea throughout the Faroe Islands, Iceland, the Irminger Sea and westward towards Greenland and North America. The beaked redfish is a deep-water fish species exhibiting typical life-history characteristics as low grow rath and late maturation that makes it extremely vulnerable to fishery activities. It is ovoviviparous and mature females release pelagic larvae in spring, a few months after autumn copulation.

Current management status

Five different stock assessment units exist for *S. mentella* in the NE Atlantic and adjacent waters (Table 2). The stock structure of the beaked redfish was reviewed by ICES in 2009 (ICES, 2020; and references therein) and based on scientific evidence three stocks are now considered for *S. mentella* in the Irminger Sea and adjacent waters: the Deep pelagic (reb.2127.dp), the Shallow pelagic (reb.2127.sp) and the demersal Icelandic slope (reb.27.5a14) stocks. A separate stock is considered for *S. mentella* on the Greenlandic slope (reb.27.14b) although further investigations are needed to confirm it. However, the

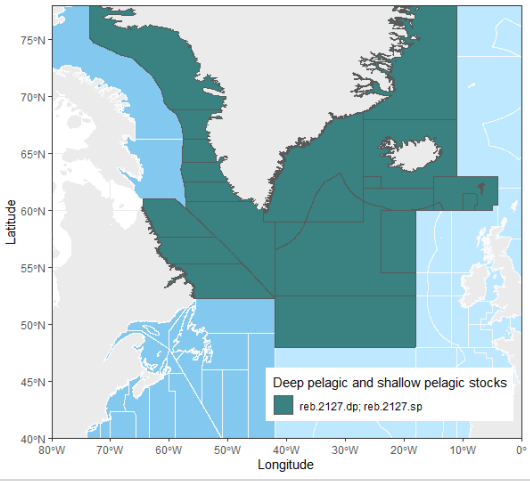


Figure 6.2.1. ICES stock units of the deep pelagic (reb.2127.dp) and shallow pelagic (reb.2127.sp) *S. mentella* in division 5.a, subarea 12 and 14 and eastern part of NAFO divisions 1F, 2H and 2J.

[27] Further details on symbols and how to read the factsheet are provided on page 16

Russian Federation does not agree on these stock units for *S. mentella* and contemplate only one stock for the beaked redfish in the Irminger Sea and adjacent waters.

The Icelandic slope stock includes demersal *S. mentella* on the Icelandic shelf and slope (division 5.a and subarea 14 within the Icelandic EEZ). Adult fish (> 30 cm) are found in the Icelandic ecoregion although juveniles share a nursery area in the East of Greenland shelf with other *S. mentella* stocks (ICES 2019b). The beaked redfish in Iceland is mainly fished in a bottom trawl directed fishery at depths between 500 and 800 m (ICES 2020k). This is a data limited stock and ICES reported is on a low level (ICES 2019b).
The shallow pelagic stock includes *S. mentella* at depth shallower than 500 m in the Irminger Sea and adjacent areas (division 5.a, subarea 12 and 14, eastern part of NAFO divisions 1F, 2H and 2J). ICES reported uncertainties due to a lack of data disaggregated by depth, precluding ICES to carry out analytical assessment for the stock in the Irminger Sea (ICES 2020k). Catches in 2019 were 3 184 t, fished by Russian vessels in subarea 12 and NAFO 1F (ICES 2020k). Despite the ICES advice was of zero catch for the shallow pelagic stock and NEAFC TAC was set to zero for 2015-2018, the Russian Federation has its own annual quota that is fished from both the Shallow and Deep pelagic *S. mentella* stocks (not recognized as stock units) (ICES 2020k). Based on the precautionary approach, the ICES advice is of zero catch also for 2020 and 2021 (ICES 2020k).
The Deep pelagic *S. mentella* stock in the Irminger Sea and adjacent areas includes division 5, subareas 12 and 14 and NAFO 1-2 at depths below 500 m and demersal habitats of western Faroe Islands. The ICES working group requires more reliable data and catches disaggregated by depth since not all the fishing countries provide them (ICES 2020k).

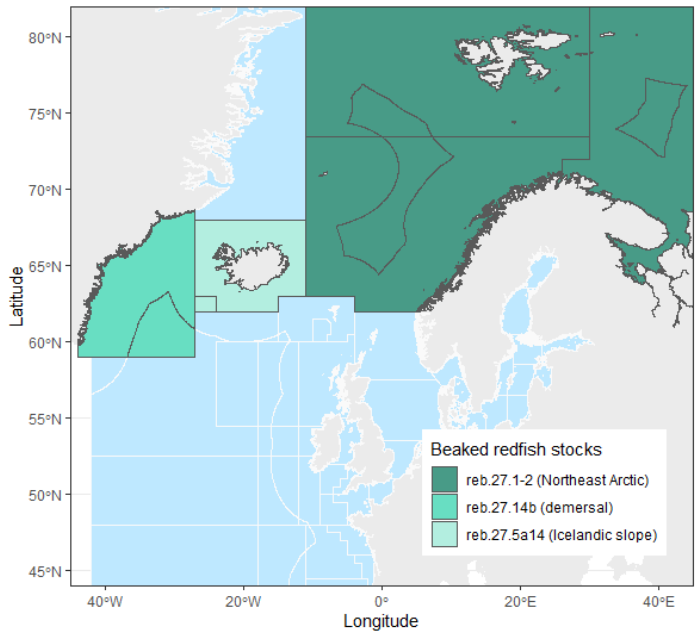


Figure 6.2.2. Beaked redfish ICES stock assessment units.

Following the ICES advice, the NEAFC set a TAC of 6 500 t for this stock in 2018 (ICES 2020k). However, the Russian Federation set an annual TAC of 24 900 t for both pelagic and deep *S. mentella* stocks (ICES 2020k). Hence, total catches in 2018 were 21 453 t and exceeded the ICES advice (ICES 2020k). Most of the catches were from Russia (20 113 t). The

Spawning stock biomass is below reference point, and fishing pressure is above F_{MSY} (ICES 2020k). ICES advice is of zero catches for 2020 and 2021.
The Greenlandic slope stock includes *S. mentella* in division 14.b (Southeast Greenland). It is a demersal stock and fisheries on the Greenlandic slope exploit *S. norvegicus* and *S. mentella* in different proportions (ICES 2020k). The species splits rely on assignment of individuals to the correct species through morphological differences, adding some uncertainties. Total catches in 2019 were split as 3 998 t of *S. mentella* and 2 665 t of *S. norvegicus* (ICES 2020k). A mixed TAC is set for both species. ICES is concerned by a lack of juveniles in East of Greenland (ICES 2020k). The fishery is concentrated in an area and directed towards larger fish and may be detrimental, exploiting a local population (ICES 2020k). Further studies are needed in these areas to design more biologically meaningful stock units for *S. mentella*.
The Norwegian Barents Sea stock (Northeast Arctic stock) includes ICES subarea 1 and 2 (ICES 2020a), where the beaked redfish is commonly found along the continental slope. Directed trawl fishery exists although *S. mentella* is caught as well as by-catch in cod fishery. After a declining in catches, ICES recommended no directed fishery and reduction of by-catches for 1997-2012 (ICES 2020a). Minimum size is in force and measures as closure areas are adopted to protect juveniles of both *S. norvegicus* and *S. mentella* redfish stocks (ICES 2020a). Since 2014 the directed demersal and pelagic fisheries have reopened. Total landings in 2019 were 45 955 t (ICES 2020a). Although *S. mentella* caught in the North Sea is part of the Northeast Arctic stock, catches are not considered in the assessment.

Genetic population structure in a nutshell

Most of the studies investigating genetic population structure are focused on the Irminger Sea and adjacent areas. Genetic evidence shows beaked redfish is structured within the NE Atlantic. In particular:

- Differentiation between deep and shallow water *S. mentella* in the Irminger Sea and adjacent waters was supported by allozymes (Johansen et al. 2000a, Daníelsdóttir et al. 2008), microsatellites (Stefánsson et al. 2009b a, Saha et al. 2017b), mitochondrial DNA and rhodopsin variation (Shum et al. 2014, 2015).
- Significant genetic structure was found within the deep-pelagic group, with *S. mentella* in the Irminger Sea and west of Faroe significantly differentiated at the mitochondrial control region (Shum et al. 2015).

Based on microsatellite data (Saha et al. 2017b):

- A separate group of *S. mentella* 'slope' is found on the Icelandic slope and east of Greenland continental shelf.
- The shallow water *S. mentella* comprises three genetically different populations, namely the Northeast Arctic, Irminger Sea-Greenland and the Northwest Atlantic.
- The deep-waters *S. mentella* group is found in the Irminger Sea and Greenlandic waters.

Genetic divergence among the three groups was observed despite ongoing gene flow. An area of mixing was found in east of Greenland where individuals of slope, deep and shallow waters co-occur. Hybrids were found in high proportion and genetic introgression was supported. Despite hybridization and introgression the shallow, deep and slope *S. mentella* are genetically distinct and maintain their genetic integrity (Saha et al. 2017b).

Mismatch

Genetic population structure is taken into consideration in designing the stock assessment units by ICES. However, the presence of mixing within the east of Greenland waters needs further investigations to explore potential pattern and explore the relative proportions of the Icelandic slope, shallow and deep pelagic *S. mentella*. Sustainable fisheries cannot be assured in mixed fisheries exploiting genetically different populations not taken into consideration in assessment and management, without risking overexploitation of the weakest components. Based on the precautionary approach, the ICES advice is of zero catch for 2020 and 2021 for the shallow and deep pelagic *S. mentella* stocks. Furthermore, complexity in the management of *S. mentella* is added by the Russian Federation not considering *S. mentella* deep and shallow pelagic stocks as separate units. The Russian Federation has its own self-allocated quota. In 2019, catches exceeded ICES advice and fishing pressure was above sustainable reference points for both stocks.

Summary of genetic evidence

The depth at which samples are collected is an extremely important factor in investigating population structure of the beaked redfish *S. mentella*. In most of the studies sample depth is reported alongside geographic coordinates.

Initially, Johansen et al. (2000) through allozymic and haemoglobin markers reported genetic differentiation between the Irminger Sea oceanic and deep-water samples, collected at depths below 400 m. The Irminger Sea samples resulted genetically differentiated from the Norwegian and Canadian ones. However, no genetic differentiation was found with beaked redfish immature samples collected in Greenlandic waters. Results of this study are in line with assessment and management units present for the oceanic and deep-water *S. mentella* in the Irminger Sea.

Roques et al. (2002) using 8 microsatellites reported the presence of three genetically different units of *S. mentella*, namely the eastern (in Norway and Barents Sea), the Panoceanic and the Western Atlantic one. The lack of differentiation found within samples in the Panoceanic unit (including *S. mentella* from Grand Bank to the Faroe Islands) results in a mismatch with current assessment and management units.

However, based on allozymes, Daníelsdóttir et al. (2008) rejected the panmixia hypothesis for *S. mentella* in the Irminger Sea and the Icelandic slope. The existence of two genetically

different populations the deep-sea and oceanic beaked redfish was supported, as well as possible hybridization or mixing. The differentiation between Icelandic slope and deep-water Irminger Sea was also supported.

Depth as factor promoting population structure in beaked redfish was confirmed also by Stefánsson et al. (2009a). Through microsatellite data, Stefánsson et al. (2009a) supported the existence of three genetically different and temporally stable populations of *S. mentella*: one in the Icelandic Shelf, another including deep-water samples from the Irminger Sea and western Faroese ground and a third one including shallow-water samples collected in the Irminger Sea shallow southeast area, Faroe east, Norwegian shelf and the Barents Sea. Hence, the differentiation between shallow, deep waters Irminger Sea and Icelandic shelf was supported. This finding explains also the result of panmixia previously found by Daníelsdóttir et al. (2008), since samples analysed were collected within 500 m. Hence, this study confirms depths has to be considered in designing stock units for the beaked redfish.

Stroganov et al. (2009) investigating morphological characters and genetic variation at 3 allozyme loci reported similarity between *S. mentella* sampled in the Norwegian and Irminger Seas. However, samples from the Irminger Sae were collected at depths between 275-350 m, hence only individuals from the shallow pelagic *S. mentella* stock were potentially included in the analysis.

The existence of two populations segregating by depths (below and above 550 m) in the Irminger Sea was supported also by Stefánsson et al. (2009), through microsatellite loci. Although their geographical distribution overlap, the two populations clearly segregate by depths. Incipient speciation between the deep and shallow pelagic *S. mentella* was suggested.

However, Zelenina et al. (2011), using 10 microsatellite loci, reported the presence of one pelagic population of beaked redfish in the Irminger Sea and Norway, contrasting with previous studies and the current assessment units, although samples were collected above and below 500 m.

In line with previous studies, Shum et al. (2014) analysis of the mitochondrial control region supported the differentiation between the deep and shallow beaked redfish in the Irminger Sea, suggesting also incipient speciation. Moreover, variation at the rhodopsin gene was analysed and possible adaptation to depth was reported.

On a wider scale, Shum et al. (2015), analysing variation of the mitochondrial control region gene, confirmed the existence of two divergent haplogroups, namely the shallow (group A, including *S. mentella* above 500 m in southwest and west of Irminger Sea, east of Faroe and Norway) and the deep pelagic *S. mentella* (group B, including *S. mentella* found below 500 m northeast of the Irminger Sea and west of Faroe). The split between the two lineages occurred in the late Pleistocene and divergence is ongoing. Depth explains the population structure found, as supported also by rhodopsin gene variation and microsatellite analyses. Moreover, significant genetic structure was found within the

deep-pelagic group, with the Irminger Sea and west of Faroe significantly differentiated (F_{ST} = 0.176, P>0.001).

The genetic divergence between shallow and deep-water groups was further supported by Saha et al. (2017) that analysed population structure of *S. mentella* across the North Atlantic using 13 microsatellites. A third group, *S. mentella* 'slope', was found on the Icelandic slope and east of Greenland continental shelf. The genetic differentiation between western and eastern Atlantic was confirmed. Substructure was found within the shallow group, comprising three populations of *S. mentella*, namely the Northeast Arctic, Irminger Sea-Greenland and the Northwest Atlantic. The deep-waters *S. mentella* group was found in the Irminger Sea and Greenlandic waters. The 'slope' *S. mentella* was found in the Icelandic slope and east of Greenland shelf. Genetic divergence among the three groups was observed despite ongoing gene flow. In the area of mixing in east of Greenland where individuals of 'slope', deep and shallow water co-occur, hybrids were found in high proportion. The existence of genetic introgression was found in the shallow, deep and slope groups. However, these three groups are genetically distinct and maintain their genetic integrity.

6.3 Golden redfish, *Sebastes norvegicus*

Number of studies	4
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[28]

The golden redfish, *Sebastes norvegicus* (Ascanius, 1772) (Syn: *S. marinus*) is a commercially valuable redfish species. The golden redfish is widely distributed across the North Atlantic. It is a long-lived species, characterized by slow growth rate and late maturation. It is ovoviviparous, females release larvae few months after the copulation in autumn. The golden and beaked redfish species *S. norvegicus* and *S. mentella* contribute to mixed fisheries. As with other deep-sea fish species it is vulnerable to fishery activities.

Current management status

ICES considers two stock assessment units for the golden redfish in the NE Atlantic, the Northeast Arctic stock (subarea 1 and 2) and the stock in subareas 5, 6, 12 and 14.

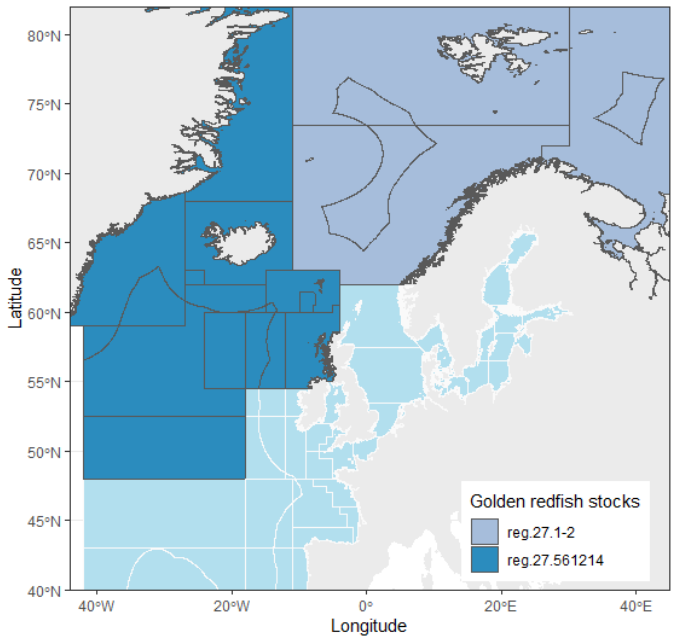


Figure 6.3. Golden redfish ICES stock assessment units.

The golden redfish in subarea 1 and 2 (reg.27.1-2) is fished in a mixed fishery with *S. mentella* (ICES 2020a). Total landings in 2019 were 8 248 t and most of the catches are taken by Norway and Russia in division 2.a (ICES 2020a). The species is considered threatened and is included in the Norwegian Red list (ICES 2020a). Despite directed fishery is not allowed, *S. norvegicus* is caught as by-catch and fishing pressure is above F_{MSY} (ICES 2020a). ICES advice zero catch in 2021 and 2022, and recommended that by-catch should set as low as possible to allow rebuilding the stock (ICES 2020a).

[28] Further details on symbols and how to read the factsheet are provided on page 16

Based on scientific evidence ICES consider the golden redfish on the East Greenlandic, Icelandic and Faroese shelves (subareas 5 and 14) as one stock unit (ICES 2019g), however, catches from subarea 6 are included in this unit. In the Greenlandic EEZ, it is managed by Greenland through a TAC set for both *S. mentella* and *S. norvegicus* exploited in a mixed fishery. In Iceland, the Icelandic Ministry is responsible for the management of the golden redfish fishery. Total landings in 2019 were 48 464 t and decreased since the beginning of the fishery (ICES 2020k). The 92% of the catches were taken by bottom trawlers in directed fishery in Iceland (division 5.a). Landings from subarea 14 have been decreasing and in 2019 were 2 665 t, while landings from division 5.b and 6 were 1 053 t and 101 t, respectively. Despite low fishing mortality, the stock is not fished sustainably and total biomass is decreasing. There is no agreement among Iceland, Greenland and Faroe and the catch levels exceed ICES advised TACs (ICES 2020k).

Genetic population structure in a nutshell

Genetic investigations show presence of population structure within the Atlantic for the golden redfish *S. norvegicus*. In particular, genetic evidence supports:

- Significant differentiation between Greenland and Iceland at allozymes
- Differentiation between the 'giant' (Reykjanes Ridge and Greenland) and *S. norvegicus* in Iceland and Norway.
- *S. norvegicus* in Greenland is a genetically distinct population.

Microsatellite data support the existence of three genetically isolated group (cryptic species) of *S. norvegicus* in the North Atlantic, overlapping their distributions in Greenlandic waters:

1. *S. norvegicus* A in the NE Atlantic
2. *S. norvegicus* B in Greenland, Norway and in the Northwest Atlantic
3. The giant *S. norvegicus* found around the Irminger Sae and Greenland.

Mismatch

The genetic structure found in *S. norvegicus* is not taken into account in assessment and management. Genetic data support the presence of three genetically isolated groups of *S. norvegicus* that can be considered cryptic species in the North Atlantic, overlapping their distributions in Greenland waters. The ICES stock unit include *S. norvegicus* in (subareas 5 and 14) Iceland and Greenland. Mixed fishery in Greenlandic waters targeting *S. norvegicus* from different populations (cryptic species) may not assure sustainable exploitation and potentially lead to the overexploitation of the weakest component. Hence, assessment and management measures at a finer scale are required.

Summary of genetic evidence

Genetic population structure of the Golden redfish in the NE Atlantic has been initially investigated by Nedreaas et al. (1994) that using allozymes reported significant differentiation between Greenlandic and Icelandic samples. Johansen et al. (2000)

analysed redfish samples from the Reykjanes Ridge, where 'giant' redfish morphologically similar to *S. norvegicus,* but with an average length greater than 60 cm can be found. Allozymes and haemoglobin were used in the analysis. Complex genetic structure was found, the Giant redfish caught in Reykjanes Ridge and Greenland were genetically different from samples collected in Iceland and Norway. Moreover, substructure was reported within the 'giants' from Reykjanes Ridge and Greenlandic waters that are genetically different.

In a preliminary landscape genetic study, Pampoulie et al. (2009) used 9 microsatellite loci to analyse 376 individuals of *S. norvegicus*. The existence of two gene pools (F_{ST} 0.012 $p < 0.05$) was suggested, one including samples from Norway, the Flemish Cap and Iceland while the other samples from east and west Greenland and some individuals from southeast Iceland. Hence, *S. norvegicus* in Greenlandic waters is a genetically distinct population. This study does not support the existence of one stock unit in Icelandic and Greenlandic waters for *S. norvegicus* as is currently assessed by ICES, resulting in a mismatch. However, the temporal stability of the pattern found should be investigated as well as connectivity between putative populations.

Saha et al. (2017) through microsatellite data reported the existence of three genetically isolated groups that can be considered cryptic species of *S. norvegicus* in the North Atlantic, overlapping their distributions in Greenlandic waters:

- *S. norvegicus* A, restricted to the NE Atlantic
- *S. norvegicus* B, present in Greenland, Norway and in the Northwest Atlantic
- The giants *S. norvegicus*, found in the Irminger Sae and Greenland, mostly in the west.

Despite a lack of morphological characters to distinguish between two of the species, the 'giant' *S. norvegicus* has specific phenotypic characteristics allowing adult identification. The genetic structure found in *S. norvegicus* and the potential three cryptic species are not taken into account in assessment and management. As highlighted by the authors, these populations/cryptic species could have different size and sustainable fisheries cannot be ensure if they are not considered as separate units. Particularly, mixed fishery in Greenland exploiting these different populations may not assure a sustainable exploitation of the giant *S. norvegicus*.

6.4 Blackspot seabream, *Pagellus bogaraveo*

Number of studies	4
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✓

Distribution[29]

The blackspot seabream, *Pagellus bogaraveo* (Brünnich, 1768), is a commercially valuable species commonly found in the NE Atlantic and Mediterranean Sea. In the NE Atlantic is distributed from southern Norway towards the Mauritania coasts, including the Azores, Madeira and the Canary Islands. The blackspot seabream is a long-lived and late maturing species. It is a protandrous hermaphrodite species. Spawning season is in spring, larvae are pelagic. Juveniles are found in coastal waters while adults on the continental slope (Stockley et al., 2005; and references therein).

Current management status

ICES consider three different stocks in the NE Atlantic (Table 2): one in the Celtic Seas and Bay of Biscay (Subareas 6, 7 and 8); one in the Atlantic Iberian waters (Subarea 9); one in the Azores (Subarea 10). ICES is aware of evidence suggesting connectivity between these stocks (ICES 2020l).

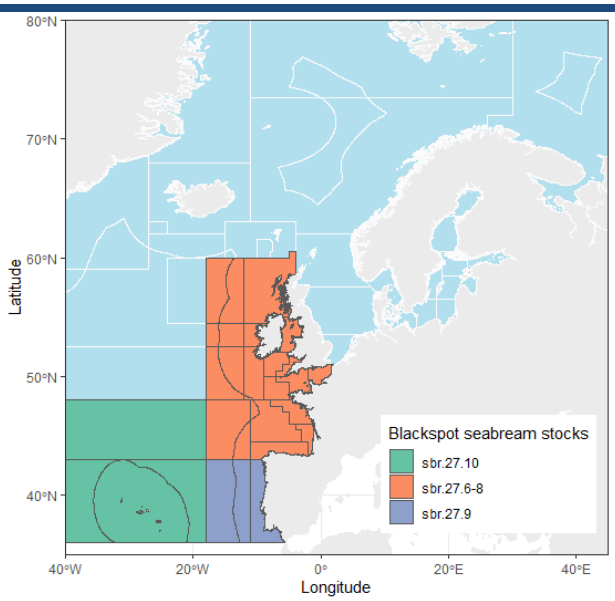


Figure 6.4. Blackspot seabream ICES stock assessment units.

The blackspot seabream stock in subareas 6, 7 and 8 was mainly exploited in the eastern Bay of Biscay and in the Cantabrian Sea (Subarea 8). The stock is depleted and ICES recommends the establishment of a recovery plan (ICES 2020l). Currently, directed fishery is not allowed and ICES advise by-catches should be minimized (ICES 2020l). Total landings in 2019 were 98 t mainly from subarea 8 (63 t), representing exclusively by-catches (ICES 2020l). Juvenile nursery areas are near the coast and high fishing morality is due to recreational fishing (ICES 2020l). ICES emphasised that the protection of juveniles is crucial for a stock

[29] Further details on symbols and how to read the factsheet are provided on page 16

rebuilding and urges the implementation of measures to regulate recreational fishery. The blackspot seabream stock in subarea 9 (Atlantic Iberian waters) is fished mainly by Spain and Portugal. ICES reports the stock extends outside subarea 9 and a management plan to cover the entire stock is needed (ICES 2020l). Catches in 2019 were at an historical minimum amounting at 60 t (ICES 2020l). ICES advice is to reduce catches and implement measures to protect juveniles.

P. bogaraveo is a target species of the Azorean demersal fishery, the stock in division 10.a.2 (Azores Grounds) is caught mainly in directed artisanal and long-line fisheries (ICES 2020l). Landings have been decreasing and in 2019 were 474 t (ICES 2020l). The blackspot seabream fishery in the Azores is extremely tightly regulated through coastal and offshore protected areas, and minimum landing size (ICES 2020l).

The blackspot seabream in a highly commercially important species in the Strait of Gibraltar, exploited by Spanish and Moroccan fleets. In the Strait of Gibraltar GSA 01 and 03, it was assessed by the Scientific Advisory Committee on Fisheries (SAC) in 2019 (SAC 2019). A Spanish directed fishery in which *P. bogaraveo* is the target species exists in the subareas. While the Morocco fishery targets the blackspot seabream through longlines as well as in an artisanal multispecies fishery. Based on the 2019 assessment, the stock is overexploited and the biomass is at low levels (SAC 2019).

Genetic population structure in a nutshell

Genetic population structure of the blackspot seabream has been studied by the means of mitochondrial and microsatellite markers. Genetic evidence supports:

- Genetic differentiation of *P. bogaraveo* in the Azores (Stockley et al. 2005, Robalo et al. 2021), supporting its assessment and management in a separate unit;
- Lack of differentiation between the NE Atlantic and western Mediterranean is supported by mitochondrial, allozymes and microsatellite markers (Bargelloni et al. 2003, Stockley et al. 2005, Robalo et al. 2021).;
- Microsatellite data support genetic differentiation between the NE Atlantic and eastern Mediterranean samples (Lemos et al. 2006).

A new study was published in 2021 (Robalo et al. 2021), confirming the differentiation of the Azores samples and a lack of structure within the NE Atlantic and across the Strait of Gibraltar. Further studies are needed to investigate genetic population structure in the blackspot seabream and samples from the northern subareas should be included. The use of genetic markers with high resolution and possibly under selection may be extremely valuable to explore population structure in this species.

Mismatch

The assessment and management of *P. bogaraveo* in the Azores as a separate stock is supported by genetic evidence showing differentiation between the Azores and the rest of the NE Atlantic. However, a mismatch is present due to lack of differentiation among

samples collected within the NE Atlantic, from the Bay of Biscay to southern Portugal, that are assessed and managed in two stock units. Moreover, a lack of differentiation between the NE Atlantic and the western Mediterranean was reported, mismatching with the current assessment units. Further studies are required and a possible joint management of the Atlantic Iberian stock and the Mediterranean (GSA 01 and 03) stock should be explored.

Summary of genetic evidence

Initially, a lack of genetic differentiation between NE Atlantic and Mediterranean samples of *P. bogaraveo* via mitochondrial and allozymic markers was reported (Bargelloni et al. 2003). Population structure was detected by Stockley et al. (2005) within the NE Atlantic using mitochondrial DNA and microsatellite markers: genetic structure at a regional scale was reported, with the Azores samples significantly differentiated from the European shelf samples collected off Portugal and Madeira.

Lemos et al. (2006) used a combination of mitochondrial and nuclear markers to study population structure in *P. bogaraveo*. Although the cytochrome-b analysis suggested a lack of differentiation between NE Atlantic and Mediterranean samples (eastern Mediterranean), microsatellite data detected a significant differentiation between the two basins.

Piñera et al. (2007) investigated genetic diversity of *P. bogaraveo* samples from the Atlantic and Mediterranean Spanish coasts through microsatellites. No significant genetic structure was detected, the genetic homogeneity among samples suggested a lack of barriers between the Atlantic and Mediterranean basins for the blackspot seabream. The lack of differentiation found among the European continental slope and western Mediterranean could be due to current gene flow or may be due to recent divergence of the Mediterranean and Atlantic *P. bogaraveo* populations.

Recently, a new study was published in 2021 and findings from previous studies were confirmed: a separate population of *P. bogaraveo* exists in the Azores while a lack of genetic differentiation was reported in the rest of the NE Atlantic (northern Bay of Biscay to southern Portugal) and western Mediterranean Sea. Further studies using more powerful genetic markers are needed to investigate population structure of the blackspot seabream.

6.5 Striped red mullet, *Mullus surmuletus*

Number of studies	8
Population structure	✓
Match genetic- Stock assessment units	✓
Match genetic- Management units	-
Match Stock assessment- Management units	-

Distribution[30]

The striped red mullet, *Mullus surmuletus* Linnaeus, 1758 is a commercially important demersal fish species in European Seas. It is widely distributed in the NE Atlantic from South Norway, including the Baltic Sea, North Sea, Celtic Seas and the Bay of Biscay down towards the Northern coasts of Africa, as well as in the Mediterranean and Black Sea (Whitehead et al. 1986a). Adults are found offshore while juveniles have a more coastal distribution. Spawning season is in spring- early summer (May to June). Eggs and larvae are pelagic, as well as juveniles while adults are benthic.

Current management status

Two stock assessment units are present in the North-East Atlantic for the striped red mullet: the western unit and the Northern unit (Subarea 4 and divisions 7.d and 3.a). The stocks are not managed by TACs. The striped red mullet is fished in demersal mixed stock fisheries both as target and by-catch species. ICES is aware of scientific evidence suggesting a separate population in the Skagerrak and Kattegat and mixing in the southern North Sea with individuals from the Western English Channel (division 7.e). The striped red mullet in the North Sea (subarea 4), eastern English Channel (division 7.d) and in the Skagerrak and Kattegat (division 3.a) is considered a stock unit by ICES (ICES 2020v). Landings, after a decreasing trend, increased due to a strong recruitment in 2018 (ICES 2020v). However, catches represent mainly juveniles individuals and ICES suggests the implementation of

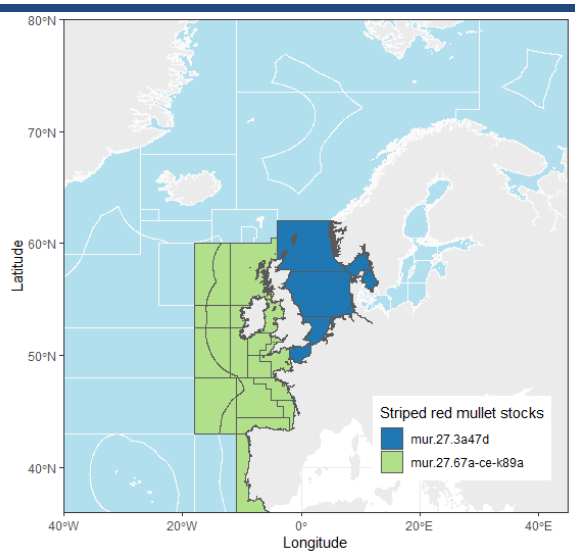


Figure 6.5. Striped red mullet ICES stock assessment units.

[30] Further details on symbols and how to read the factsheet are provided on page 16

measures to protect juveniles, as area and season closures (ICES 2020v). Fishing pressure is above sustainable reference points (ICES 2020v). In 2019, landings were 4 043 t mostly fished in southern North Sea and eastern English Channel and exceeded the ICES advice of 465 t (ICES 2020v). Landings are mainly from the Netherlands, France and the UK (ICES 2020v) .

The Western stock unit includes striped red mullet in subareas 6 and 8 and divisions 7.a-c, e-k and 9.a (ICES 2020w). This stock is a data limited stock of category 5.2 and there is no assessment, hence no information on the stock status and exploitation levels is available. Total landings in 2019 were 1 855 t mainly caught in the Bay of Biscay (Subarea 8), in the western English Channel (Division 7.e) and division 9.a (ICES 2020w). ICES is aware of scientific evidence indicating different populations within the Western stock unit: landing distribution, morphological and otolith analyses support differences between striped red mullet in the Western Channel-Celtic Seas and the Bay of Biscay (ICES 2020w). While, based on catch and survey evidence, the striped red mullet in division 9.a represents a distinct unit (ICES 2020w).

In the western Mediterranean Sea, a stock assessment unit is present in GSA 05 (Balearic Islands) where the striped red mullet is targeted by commercial trawlers in the shallow shelf. The striped red mullet is also an important resource for the artisanal fisheries. Fishing mortality is low and based on the 2020 assessment the stock is not overfished (STECF 2020).

In the eastern Mediterranean Sea, stock assessment was carried out in 2018 for the striped red mullet in GSA 25 (Cyprus) (Charilaou & Thasitis 2017). The striped red mullet is fished with other demersal species in a mixed fishery. Several management measures are applied and area and seasonal closures are present. However, based on the assessment in 2018, the striped red mullet stock in GSA 25 was overfished. A different stock is considered in GSA 26 (South Levant Sea). Based on the assessment carried out in 2018 the striped red mullet in GSA 26 is in overfishing and fishing mortality is higher than reference point (Mahmoud et al. 2018).

Genetic population structure in a nutshell

There is a lack of studies investigating genetic population structure in striped red mullet in the NE Atlantic. The available studies are focused on the Mediterranean Sea. Genetic investigations suggested presence of population structure for the striped red mullet in the Mediterranean Sea. In particular, genetic evidence supports:

- Differentiation between the NE Atlantic and the Mediterranean Sea (Matić-Skoko et al. 2018).
- A pattern of isolation by distance within the Mediterranean Sea was supported by allozymes and RAPDs (Mamuris et al. 1999), mitochondrial marker (Mamuris et al. 2001), microsatellite (Matić-Skoko et al. 2018) and SNPs (Dalongeville et al. 2018a).

- Genetically differentiated populations in the Ionian Sea, Aegean Sea and Gulf of Lion (Mamuris et al. 1999), in the Balearic Islands and Greece (Galarza et al. 2009).
- Significant substructure was found in the Adriatic Sea with the south-eastern samples genetically differentiated (Matić-Skoko et al. 2018).
- A lack of genetic differentiation within the Northwest Mediterranean Sea (Galarza et al. 2009).
- Substructure along the Spanish Mediterranean coasts (Félix-Hackradt et al. 2013).
- Candidate genes involved in local adaptation to salinity in striped red mullet populations across the Mediterranean Sea were identified (Dalongeville et al. 2018b).
- Genetically differentiated populations in Gibraltar and the Alboran Sea (Dalongeville et al. 2018b).

Mismatch

Genetic population structure studies of the striped red mullet were mostly focused on the Mediterranean Sea, only in two out of eight studies NE Atlantic samples have been included. Hence, a lack of investigations on population structure is evident for the NE Atlantic. However, ICES reported scientific evidence suggesting presence of different populations within the current stock assessment units. Hence, genetic markers could be used to further investigate whether the current units are biologically meaningful or rather need to be revisited.

Within the Mediterranean Sea, a pattern of isolation by distance was confirmed for the striped red mullet and genetically different populations were found. The Balearic Islands stock assessment unit was supported by microsatellite data indicating presence of a genetically differentiated population of striped red mullet.

Summary of genetic evidence

Genetic investigations on population structure for the striped red mullet are focused particularly in the Mediterranean Sea. A lack of studies investigating population structure in the NE Atlantic is evident (Table 1). A pattern of isolation by distance was supported by Mamuris et al. (1999) through allozymes and RAPDs analyses for the striped red mullet in the Mediterranean Sea. Significant differentiation was reported among the Gulf of Lion, the Aegean and the Ionian samples. The same pattern was confirmed in a successive study by Mamuris et al. (2001) investigating mitochondrial variation in the same samples. At a finer scale, Apostolidis et al. (2009) showed evidence of genetic differentiation between samples of striped red mullet collected in and outside Pagasitikos Gulf (Aegean Sea) using a combination of nuclear and mitochondrial markers. Galarza et al. (2009) reported genetic differentiation at 10 microsatellite loci between Atlantic and Mediterranean samples of striped red mullet. Within the Mediterranean Sea the populations from the Balearic Islands and Greece were genetically differentiated while a lack of genetic differentiation was observed for the striped red mullet within the

Northwest Mediterranean Sea. Genetic structure was found by Félix-Hackradt et al. (2013) along the Spanish Mediterranean coasts; the northern samples were clearly differentiated and substructure was suggested also for the remaining samples despite admixture and gene flow. Significant, but weak, genetic structure across the Mediterranean was reported also by Matić-Skoko et al. (2018) (F_{ST}=0.011 P<0.001), supporting a pattern of isolation by distance. Samples from the Atlantic and Mediterranean Sea were differentiated although ongoing gene flow between basins was suggested. Within the Adriatic Sea, differentiation of the south-eastern samples was reported due to hydrodynamic characteristics favouring high larval retention.

Genetic population structure in the Mediterranean Sea was confirmed using SNPs. Dalongeville et al. (2018a) found that genetic differentiation among samples is explained by geographic distances and adult migrations at a larger spatial scale. Though, at a finer scale gene flow mediated by larval dispersion among nearby localities is an important factor shaping population structure of the striped red mullet. Using the same samples, Dalongeville et al. (2018b) identified candidate genes involved in local adaptation to salinity in striped red mullet collected all across the Mediterranean Sea. Isolation by distance was confirmed with SNPs. Local adaptation to salinity was supported and genetic distances were correlated to salinity differences suggesting salinity has a role in population structuring for striped red mullet in the Mediterranean. The samples from Gibraltar and the Alboran Sea were the most differentiated.

6.6 Orange roughy, *Hoplostethus atlanticus*

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

Distribution[31]

Orange roughy, *Hoplostethus atlanticus*, is a worldwide widespread deep-water fish species, present in the Atlantic, Indian and Pacific Oceans at depth ranging between 450-1800 m (Branch 2001). In the NE Atlantic is found along the continental slopes and seamounts west of the British Isles, around the Faroe Islands, Iceland and in the Mid-Atlantic Ridge. During the spawning season, orange roughy forms large aggregations on seamounts, and spawning migrations are known. The orange roughy is characterized by low fecundity and a short planktonic larval phase (on average 10 days) (White et al., 2009; and references therein). As other deep-water fish species, the orange roughy is a long-lived species characterized by slow growth rate, late maturation and low fecundity, hence it is particularly vulnerable to fishing. Commercially important fisheries targeting orange roughy are known in the Tasman Sea in the South-West Pacific Ocean and around New Zealand. The orange roughy was believed to be uncommon in the NE Atlantic (Smith 1986), however with fishing activities exploring deeper waters resulted abundant also in this ocean. In the 70s and 80s it was already known the species could not support commercial fisheries in the NE Atlantic (Smith 1986).

Current management status

ICES reported a lack of scientific evidence to define population of orange roughy in the North Atlantic. ICES recommended *'when the precautionary approach is applied, there should be zero catch in each of the years 2021– 2024'* (ICES 2020l). Based on fishery activities, ICES currently consider three components (ICES 2020l). In subarea 6, a spawning aggregation was targeted by French vessels however, since 2017 no catches have been reported due to the implementation of a fishery ban for deep-water trawling (< 800 m) in European waters and for European vessels in international waters (ICES, 2020; and references therein). A TAC is present for orange roughy in subarea 6 and since 2010 is set to 0 t (ICES 2020l). Likewise, in subarea 7 orange roughy fishery has stopped due to a combination of zero catch advice and the trawling ban in waters deeper than 800 m (ICES 2020l). As a result of this ban, by-catches of orange roughy are minimal as it is not found in waters above 800 m. Since 2010 there have been no landings of orange roughy from

[31] Further details on symbols and how to read the factsheet are provided on page 16

subarea 7. The TAC is set to 0 also for orange roughy in the rest of the NE Atlantic (subareas 1, 2, 4, 5, 8-10, 12 and 14 and division 3.a). As ICES reported orange roughy fisheries occur mainly in subareas 10 and 12, and in 2019 landings were 31.07 t and 28.96 t, respectively (ICES 2020l). Based on the precautionary approach, ICES advice was of zero catch in 2017-2020 as well as in 2021-2024 (ICES 2020l). The TAC set by EU was of 0 t and management measures are in place to avoid by-catches and directed fishery is not allowed. An Orange roughy fishery in the NE Atlantic is not sustainable.

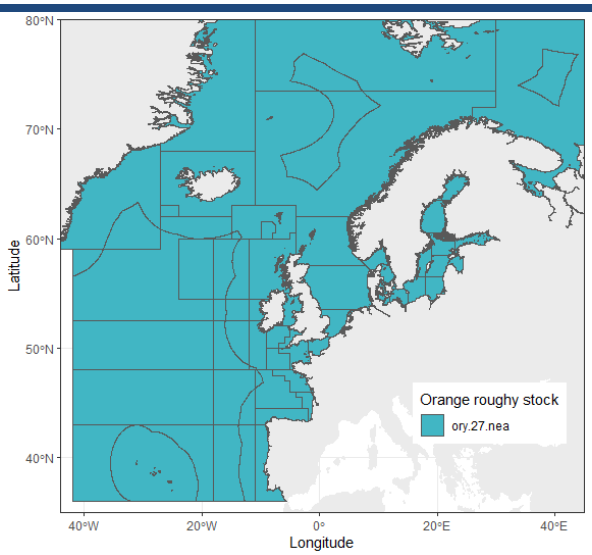


Figure 6.6. Orange roughy ICES stock unit.

Genetic population structure in a nutshell

Despite results from initial studies indicating a lack of genetic structure, successive studies have shown orange roughy within the NE Atlantic does not represent a panmictic population. Worldwide, genetic investigations indicated the differentiation of orange roughy inhabiting the NE Atlantic from the South Atlantic, Indian and Pacific Oceans populations (Elliott et al. 1994, White et al. 2009, Varela et al. 2013). In particular, genetic evidence supports:

- Genetic differentiation between North and South Atlantic.
- Fine-scale population structure within the Porcupine Bank (Carlsson et al. 2011).
- Substructure within the NE Atlantic at both neutral and outlier SNP loci (Gonçalves da Silva et al. 2020). A genetically distinct population was found in the Faraday Seamount and a pattern of isolation by distance was supported for the orange roughy along the slope supporting adult migration promoting gene flow.

Mismatch

In line with the assessment and management units, the SNP data supports distinct stock units in Rockall-Hebrides (Subarea 6) and in Porcupine Bank (subarea 7). However, a locally adapted population of orange roughy was reported on the Faraday Seamount and it is not considered in assessment and management. Ulterior measures to assess and managed this locally adapted population, separately from the rest of the NE Atlantic, are required.

Summary of genetic evidence

Initially, Smith (1986) found significant genetic differentiation between Tasman-Pacific and Atlantic samples of orange roughy at 3 allozyme loci. The genetic differentiation

between Australia and NE Atlantic was confirmed also in a successive study that supported differentiation at allozyme and mitochondrial markers (Elliott et al. 1994). However, the little levels of differentiation found suggested ongoing gene flow mediated by connectivity among adjacent populations in a stepping-stone model.

Genetic differentiation between North and South Atlantic (Namibia) orange roughy samples was reported by White et al. (2009) through 14 microsatellite loci. However, within the NE Atlantic no evidence of genetic structure was found supporting panmixia for orange roughy from the Bay of Biscay, the Porcupine Bank, the Hebrides, Faraday and Sedlo Bank. In contrast with the previous studies, Carlsson et al. (2011) using eight neutral microsatellites and otolith analysis found evidence of weak population structure (F_{ST} = 0.0031, P<0.0001) for orange roughy in the Porcupine Bank. The importance of the sampling season was highlighted, in fact samples were spawning adults and juveniles collected during the spawning season peak. The genetic structure reported, was largely due to the genetic differentiation between the flat and mounds samples, supported also by otolith analysis. Though, genetic differences were reported also among mounds, supporting fine-scale population structure for orange roughy in the Porcupine Bank.

Analysing variation at two mitochondrial genes, Varela et al. (2012) reported a lack of differentiation for orange roughy from New Zealand, Australia, Namibia and Chile. However, significant differentiation was found between these sites and the NE Atlantic samples. Further, through microsatellite analysis, Varela et al. (2013) found substructure also within the Southern hemisphere and the differentiation of the NE Atlantic was confirmed. A pattern of isolation by distance was supported. A population genomic study was conducted by Gonçalves da Silva et al. (2020) that used SNPs to investigate population structure of orange roughy in the Atlantic. Significant differentiation was reported between the South and North Atlantic samples both at neutral (F_{ST} = 0.0103) and outlier loci (F_{ST} = 0.077). Substructure was detected also within the NE Atlantic samples; at both neutral and outlier loci the Faraday Seamount samples were differentiated and a pattern of isolation by distance was supported along the slope (path between 500 and 2500 m). The SNP data supported orange roughy in Subarea 6 (Rockall and Hebrides) and 7 (Porcupine Bank) in two separate units, and a distinct population on the Faraday Seamount.

7 Atlantic cod, *Gadus morhua*

Number of studies	106
Population structure	✓
Match genetic- Stock assessment units	✗
Match genetic- Management units	✗
Match Stock assessment- Management units	✗

Distribution[32]

The Atlantic cod, *Gadus morhua* Linnaeus, 1758, is one of the most important of all commercial marine fish species in the North Atlantic. It is widely distributed in the North Atlantic, from the North American coasts throughout Greenland, Iceland, the Faroese Islands, in the Barents Sea, along Norway, around the British Isles and down towards the Bay of Biscay (Cohen et al. 1990).

It inhabits also the Baltic Sea, where locally adapted populations can be found. Atlantic cod is found within the continental shelf, and is widely distributed both in offshore and coastal areas, including fjords (Cohen et al. 1990). Stationary and migratory ecotypes have been shown occurring in most of cod distributional range, both in western and eastern Atlantic (Berg et al. 2017); e.g. in Norway (NE Arctic cod and coastal cod), in the Skagerrak and around Iceland.

The migratory ecotypes undertake spawning migration towards coastal and shallow waters in early winter to spawn and then migrate back to offshore areas for feeding. Whereas coastal cod ecotypes are more sedentary and remain in coastal and fjordic areas all year around. Adults are demersal, while eggs and larvae are pelagic and spawning is in late winter and spring (Cohen et al. 1990). Nursery areas can be found in coastal waters (Cohen et al. 1990). Oceanic circulations favouring connectivity between adjacent stocks are known, as well as clockwise currents preventing the drift of pelagic life stages.

Genetic population structure of Atlantic cod has been investigated using various methods, making it one of the most studied commercial marine fish species. The existing literature exploring population structure of Atlantic cod is extensive, with more than 100 studies available for the NE Atlantic. Mechanisms maintaining genetic divergence between cod ecotypes spawning in the same locations and season have been unravelled thanks to advances in genomics (e.g., Berg et al., 2017). Genetic tools are available to distinguish among most of cod stocks within the NE Atlantic. Hence, the incredible scientific effort comprising the work of several generations of researchers exploring

[32] Further details on symbols and how to read the factsheet are provided on page 16

population structure of cod in the NE Atlantic is reviewed here. This is an attempt to summarize the existing literature gathering together more than three decades of research which offers the opportunity to understand the evolution of the contribution genetic markers have made to investigate population structure in marine fish species.

7.1 Cod in Greenlandic waters

Current management status

ICES recognize three stock assessment units for cod around Greenland according to genetics and spawning areas (ICES 2020k): inshore west of Greenland (cod.21.1, in NAFO subarea 1), offshore west of Greenland (cod.21.1a-e, in NAFO divisions 1.A-E) and offshore south and east of Greenland (cod.2127.1f14, in NAFO 1F and ICES subarea 14). There is a management unit for the European Union in NAFO 1F and Greenlandic waters of 5, 12 and 14. While, the East and West Greenland cod units are managed by Greenland. The government of Greenland regulates Greenlandic fisheries and set annual TACs based on advice provided by ICES and the Greenland Institute of Natural Resources. For the West of Greenland stock, no fishery is allowed and a TAC of 0 t was set for 2020. The East of Greenland cod is managed under a management plan covering offshore NAFO subarea 1F and ICES subarea 14 (Ministry of Fisheries Hunting and Agriculture, 2019), with the aim to guarantee a sustainable exploitation of the stock. The management plan is based on the assumption that the East of Greenland cod is a component of the East Greenland-Icelandic cod stock, hence migration between Greenland and Iceland is considered. Migration of cod from Greenlandic waters towards Iceland is known during the spawning season. Cod fishing in Greenland is a mixed stock fishery exploiting local cod that remains in Greenland and cod that migrates to Iceland once maturity is reached. The local cod stock is protected and the main spawning area (Kleine Banke) is closed to fishing during the spawning period. Furthermore, cod fishery is also regulated by technical conservation measures and regulations to avoid bycatches.

The Inshore West of Greenland stock includes cod in NAFO subarea 1 within the inshore baseline and is assessed as a separate stock by ICES since 2012. It is caught in directed fishery and as by-catch in Greenland halibut fishery (ICES 2020k). Total catches in 2019 were 19 753 t, higher than ICES advice, resulting in a fishing effort above sustainable reference points (ICES 2020d). ICES is aware of genetic investigations supporting mixing of three cod stocks, namely, the offshore West of Greenland, inshore West of Greenland and the East of Greenland-Icelandic offshore stock in inshore waters of West of Greenland (ICES 2020k). As ICES reported, the inshore and offshore West of Greenland stocks will be benchmarked in 2022.

The offshore West and the offshore East of Greenland cod stocks are assessed as different units since 2015. The offshore West of Greenland stock includes cod in offshore waters of NAFO Subdivision 1A-E (Table 2). ICES advice is of zero catches in 2020 and 2021 (ICES 2020k). The stock collapsed in the 1990s due to a combination of overfishing and adverse environmental conditions (ICES 2020k). ICES is aware that west of Greenland grounds represent a common nursery area for the three cod stocks. When fish belonging to the East and South Greenland stock reach maturity, they migrate back to spawning grounds in East of Greenland and Iceland. Hence, the cod fishery in west of Greenland is

a mixed stock including West of Greenland, East of Greenland and Icelandic cod. However, the contribution of the different stocks is not considered in the assessment. As previously reported, mixing of the inshore and offshore stocks in inshore West of Greenland, was indicated by genetic investigation, and in inshore Greenlandic waters the 30% of individuals were estimated to be from the West Greenland offshore stock (ICES 2020k). In order to explore spatio-temporal migration patterns of cod around Greenland, further tagging and genetic analyses are needed as recommended by ICES.

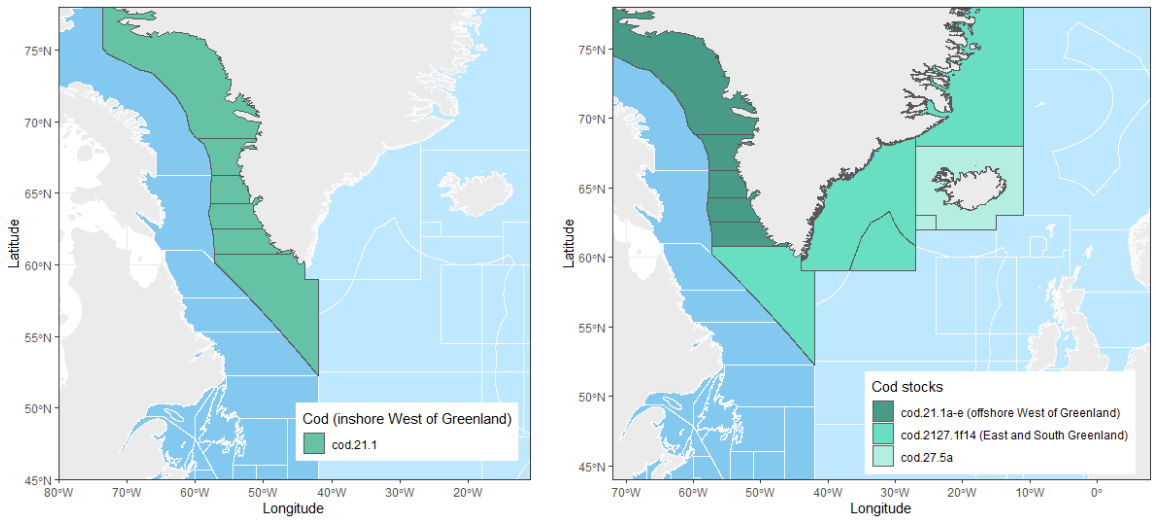


Figure 7.1. ICES stock assessment units for cod around Greenland. Left, the inshore West of Greenland stock in NAFO subarea 1. Right, offshore West of Greenland cod (cod.21.1-a-e); East and south Greenland cod (cod.2127.1f14) and Icelandic cod (cod.27.5a).

The South and East of Greenland stock includes cod in offshore waters of south and east of Greenland (NAFO 1F and ICES subarea 14). ICES is aware of the presence of individuals of Icelandic origin in these grounds due to an influx of larvae and eggs from Iceland. This is indicated also by the observation of migration of mature cod from Greenlandic grounds towards Iceland (natal homing), as previously reported. The migration of cod individuals from the East of Greenland stock to Iceland, as supported also by tagging studies, is considered in the assessment and management. A management plan entered in force in 2019. In order to protect local spawning individuals, the main spawning area is closed to fishery. Total catches for 2019 were 18 074 t the majority of which from ICES division 14.b (17 158 t) and the remaining from NAFO 1F (ICES 2020k). Fishing pressure in 2019 was above sustainable reference points, with higher catches than the ICES advice (≤ 5 363 t) (ICES 2020k).

Genetic population structure in a nutshell

Genetic evidence suggests the presence of four genetically differentiated cod populations in Greenland and adjacent regions:

- Offshore West of Greenland
- Inshore West of Greenland

- East of Greenland-Iceland offshore
- Iceland inshore

Local adaptation was supported by the existence of regions of the genome highly differentiated between populations. The genetic divergence is maintained through natal homing for spawning. Restricted gene flow and natural selection shape genetic population structure in cod around Greenland. This information was used by ICES to revise the stocks. Notably, these stocks share nursery and feeding grounds in Greenland and can be exploited in mixed stock fisheries.

Mismatch

Overall, the genetic units are taken into account in assessment and management, ICES used genetic evidence (Therkildsen et al. 2013) to revise the stock units. Moreover, the influx of Icelandic cod is estimated each year and taken into account for advice on catch levels for the South and East of Greenland cod stock. A genetic tool, consisting of 81 informative SNPs, is available to assign samples to their population of origin (West of Greenland inshore, West of Greenland offshore, Iceland offshore and Iceland inshore) (Bonanomi et al. 2015). This genetic tool was used to explore the spatiotemporal proportions of cod populations in West of Greenland fishery (Bonanomi et al. 2015).
Moreover, mixing in inshore waters of West of Greenland of local inshore cod, offshore West of Greenland, and East of Greenland-Icelandic offshore stocks was shown (ICES, 2020a; and references therein). As ICES reported, the inshore and offshore West of Greenland stocks will be benchmarked in 2022.

Summary of genetic evidence

Initially, Árnason et al. (2000) reported a lack of differentiation between Icelandic and Greenlandic samples of cod at the mitochondrial cytochrome b. Hence, this study does not support their separation into distinct assessment and management units. O'Leary et al. (2007), using microsatellites to investigate population structure of cod in its distributional range, confirmed the lack of differentiation between Greenlandic and Icelandic cod samples. Overall, cod was structured in the North Atlantic, but a lack of differentiation between east of Greenland sample and the Barents Sea, as well as between Greenland and Faroese and Icelandic samples was reported at six microsatellite loci.
The first population genetic study focused on Atlantic cod in Greenlandic waters was conducted by Pampoulie et al. (2011), that using a combination of neutral and outlier microsatellite loci and Pan I, reported genetic divergence between inshore and offshore populations. Restricted gene flow between these units was supported as well as natural selection promoting genetic divergence and local adaptation. The valuable contribution gained by using a combination of neutral and under selection markers in studying population structure was shown. The pattern found was temporally stable. Therkildsen

et al. (2013), through a population genomic approach and an extensive spatio-temporal sampling, detected four genetically different cod units in Greenlandic waters:

- inshore west of Greenland
- offshore West of Greenland
- offshore east of Greenland/Iceland offshore
- inflow from Iceland

Mixing of individuals from different populations was observed supporting previous tagging studies. Moreover, the existence of highly differentiated regions of the genome between populations was reported, supporting adaptive divergence. These four units represent locally adapted populations that harbour unique genetic diversity and may have different evolutionary responses to environmental and climate change. Results of this study were used to revise the cod stock units around Greenland. This highlights the importance of using genomics to detect biocomplexity and gather extremely valuable information that can be used in management and conservation of marine fish resources. Bonanomi et al. (2015) using archived otoliths described 80 years of cod population dynamics in West of Greenland. Individuals were assigned back to their population of origin throughout SNPs, and the contribution of different populations to the West of Greenland commercial fisheries was explored. Catches were mainly from the local offshore west of Greenland stock during the 1930s. Subsequently, the contribution of the local, offshore, west of Greenland population decreased and, during the peak of fishing, disappeared from the southwest catches. Local, offshore, west of Greenland cod is still present in catches from the northern regions. At the same time, the proportion of the Icelandic offshore cod increased in west of Greenland fishing grounds and represented the major proportion of fish caught during and after the fishery collapsed. The offshore west of Greenland stock collapsed due to overfishing, while, the Icelandic offshore cod did not migrate in these fishing grounds due to colder water conditions, resulting in the West of Greenland cod fishery's collapse. Hence, via a genetic tool and archived samples, spatiotemporal changes in the proportion of genetically different populations in West of Greenland fisheries was described. ICES reported genetic investigation exploring mixing in inshore waters of West of Greenland of the three cod stocks, namely the offshore West of Greenland, inshore West of Greenland and the East of Greenland-Icelandic offshore stock (ICES, 2020a; and references therein). Results suggested that 50% of fish examined were individuals from the local inshore stock, 30% were individuals from the offshore West of Greenland stock, and the remaining 20% were cod from the East of Greenland-Icelandic offshore stock.

7.2 Icelandic cod

Current management status

Icelandic cod includes cod in division 5.a (Iceland grounds) and is considered a homogeneous unit by ICES (ICES 2015b). The main spawning grounds are localized in the southwest coasts and other minor areas are found all around Iceland (ICES 2015b). A clockwise current drifting around the island retains pelagic cod eggs and larvae in Icelandic nursery grounds (ICES 2015b). Though, larval drift towards Greenland is known, as well as migration of mature cod from Greenland towards Icelandic spawning grounds (ICES 2015b). ICES is aware of genetic similarity between Icelandic offshore cod and East and South of Greenland cod and also of investigations supporting genetic differentiation between northern and southern spawning aggregations and the existence of genetically different ecotypes (shallow and deep waters) spawning in the same areas (ICES, 2015; and references therein). Therefore, this stock definition may not be biologically meaningful and mechanisms to take the biocomplexity of cod around Iceland into consideration in stock assessment are currently under investigations. In 2018, total catches were 264 992 t, the majority of which fished by bottom trawlers (51%) and long-lines (30%) (ICES 2019b). Icelandic cod is managed under a management plan (ICES 2019b). Fishing effort is declining and the spawning stock biomass is above reference points (ICES 2019b).

Genetic population structure in a nutshell

Genetic population structure of cod around Iceland have been studied through different genetic markers and in combination with tagging methods. Genetic evidence suggests:

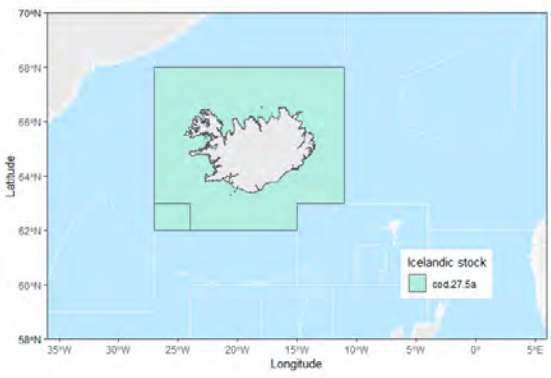


Figure 7.2. Icelandic cod ICES stock assessment unit.

- Significant differentiation between southwest and south and east Icelandic samples at *Pan* I (Jónsdóttir et al. 1999).
- Lack of differentiation at microsatellites between Greenland and Iceland and Iceland and Faroe cod (O'Leary et al. 2007).
- Two temporally stable populations in southwestern and northeast Icelandic waters are supported by tagging evidence, microsatellites and *Pan* I (Pampoulie et al. 2006b).
- Significant genetic differentiation between south Iceland and east Iceland-Faroese cod was supported by microsatellites and *Pan I*, hence genetic similarity between

samples from east of Iceland and the Faroe Plateau was supported (Pampoulie et al. 2008c).

- Mixed-stock analysis was carried out to unravel the contribution of individuals from the southwestern and northeastern spawning aggregation in northeast and northwest feeding aggregations (Pampoulie et al. 2012).
- Two divergent ecotypes, the shallow and deep-waters (migratory) cod co-occur in Icelandic waters. Genomic island of divergence (linkage group 1) and weak differentiation across the genome, suggested current gene flow between ecotypes and natural selection promoting adaptive differentiation (Hemmer-Hansen et al. 2013).
- Low levels of genetic differentiation are reported in neutral regions of the genome (F_{ST} = 0.0002) while adaptative divergence is present between the two ecotypes mainly at SNPs in linkage groups 1, 2 and 7 (F_{ST} = 0.0547) (Berg et al. 2017). Most of the divergence between the two ecotypes is due to SNPs in linkage group 1, of which *Pan* I and the rhodopsin gene are part.

Based on data storage tags evidence (Pampoulie et al. 2008a) two cod ecotypes are found in Icelandic waters with different feeding behaviours: the coastal cod, that remains stationary in coastal and shallow waters also during the feeding season, and the migratory cod, that after spawning in shallow waters migrates to deeper areas during the feeding season. Although these ecotypes share the same spawning grounds in coastal waters, genetic divergence between coastal and migratory Icelandic cod ecotypes was reported (Pampoulie et al. 2008a, Hemmer-Hansen et al. 2013, Berg et al. 2017). The pattern of genetic divergence found between the two ecotypes, with neutral region of the genome weakly differentiated and non-neutral region highly divergent, can be explained by interbreeding (current gene flow) and selection forces promoting adaptation to divergent environments (Berg et al. 2017).

Mismatch

Genetic evidence supports substructure for cod within Iceland. The existence of two genetically divergent ecotypes within Icelandic waters was supported, however, this is not taken into account in stock assessment and management. Moreover, genetic differentiation was reported between southwest and eastern Icelandic spawning grounds, although they are not considered as separate stock. A mixed stock analysis was performed to explore contribution of the genetically differentiated southwest and northeast cod spawning aggregations to mixed feeding aggregations in northern Iceland feeding grounds. Hence, the complex spatial structure of cod around Iceland in not reflected in stock assessment and management, resulting in mismatches between genetic, assessment and management units. Furthermore, connectivity between Icelandic offshore cod and East of Greenland was reported, which is taken into account in Greenlandic cod assessment and management.

Summary of genetic evidence

Genetic population structure of cod in Icelandic grounds has been investigated throughout different markers. Initially, Árnason et al. (1992) using restriction analysis of mitochondrial DNA reported high levels of gene flow and lack of differentiation among samples collected around Iceland suggesting a panmictic population. Jónsdóttir et al. (1999) supported the presence of two genetically distinct groups of cod in Icelandic waters. Analysing spawning and feeding aggregations at the nuclear synaptophysin (*Syp* I) and haemoglobin (*Hb I)* loci, significant differentiation was reported between the southwest samples and the samples collected in south and east Iceland at the *Syp I* locus (F_{ST}=0.25, p<0.001). Genetic divergence was higher between spawning samples, supporting the presence of genetically differentiated cod populations in Iceland. However, results of this study were based on one locus. On a larger scale, O'Leary et al. (2007) using microsatellites reported a lack of differentiation between Greenlandic and Icelandic samples, as well as between cod sampled in the Faroe and Iceland.

Successively, Pampoulie et al. (2006b) using a combination of microsatellites, the Pantophysin (*Pan* I, previously known as synaptophysin) locus and tagging data reported the existence of two temporally stable populations in southwestern and northeast Icelandic waters. Tagging data showed low connectivity between the two regions, supporting limited exchange. Higher levels of differentiation were found at the locus under selection *Pan I* (F_{ST} = 0.261) than at microsatellites (F_{ST} = 0.003), suggesting local adaptation for cod in Icelandic waters.

In line with previous studies, Pampoulie et al. (2008c) found significant genetic differentiation between South and East of Iceland cod. Though, genetic similarity was reported between East of Iceland and the Faroe Plateau both at microsatellites and *Pan* I locus. This is probably due to passive drift of pelagic larvae and eggs toward the Faroese Plateau rather than active migration of adult cod as suggested by tagging evidence reporting rare migrations between the areas. Moreover, using a landscape genetic approach a barrier to gene flow was identified between the South Iceland and the East Iceland-Faroese groups, mismatching with the current stock assessment units. On a larger scale, Pampoulie et al. (2008b) unravelled genetic population structure of Atlantic cod, reporting the presence of temporally stable and genetically differentiated population in southwest Iceland, in the Faroe Islands, in the Celtic Sea and Baltic Sea, respectively.

On a finer scale, Pampoulie et al. (2008a) investigated genetic divergence between two cod ecotypes in Icelandic waters. Based on Data Storage Tags (DSTs) evidence, able to register movement of individuals, two feeding behaviour are known for cod in Icelandic waters: the coastal cod that is more stationary staying for feeding in shallow waters throughout the year, experimenting seasonal changes in water temperature and the migratory cod that after spawning in shallow waters, migrates for feeding in deeper and colder waters. (Pampoulie et al. 2008a) analysed individuals from the DST experiment at the Pantophysin locus and reported different genotypes for coastal (*Pan* I^{AA}) and

migratory cod (*Pan* I^{BB}) ecotypes. While heterozygous individuals (*Pan* I^{AB}) were both among coastal and migratory cod. Jakobsdóttir et al. (2011) reported temporal changes in *Pan* I allele frequencies in Icelandic cod samples concomitant with higher fishing pressure on older individuals.

Pampoulie et al. (2012) employed a mixed-stock analysis to investigate composition of adult and juvenile feeding aggregations of cod collected around Iceland in three successive years. Based on previous studies, two genetically different populations are present in Iceland, the northeast and southwest cod populations. Using a combination of neutral microsatellites and *Pan* I locus, individuals were assigned to their population of origin. Results showed in juvenile and adult feeding aggregations the majority of individuals was of Southwest origin. The proportion of fish of Northeast origin was temporally variable, depending mainly on oceanic currents. Thought, the contribution of juveniles of Northeast origin was important (22%-39% in 2002 and 2003 respectively) in northeast Iceland. The existence of mixing in feeding aggregations is not taken into account in assessment and management of cod. Fishery that exploit cod in these areas is a mixed-stock fishery and contribution of each populations should be considered in order to have more sustainable fisheries. Notably, combining the neutral microsatellites and the *Pan* I locus, the assignment power improved showing once again the importance of using genetic marker under selection.

Successively, Kristjánsson (2013) showed low but statistically significant genetic differentiation at 16 microsatellites among samples collected in northern and southern Icelandic locations suggesting high levels of gene flow. Though, no quantitative differences in growth rate, maturation and length were reported for cod from these locations reared under common conditions.

Hemmer-Hansen et al. (2013) showed the presence of two divergent cod ecotypes in Icelandic waters, the coastal and the deep-water (migratory) ecotypes. Although weakly differentiated across the genome the two ecotypes are highly differentiated in certain regions of the genome, referred as genomic islands of divergence. The overall weak differentiation suggests current gene flow between ecotypes, while the highly differentiated SNPs in linkage group 1 suggest natural selection promoting adaptive divergence.

Therkildsen et al. (2013) using SNPs supported previous tagging studies suggesting presence of Icelandic cod in Greenlandic waters. The contribution of Icelandic offshore and inshore cod populations in west of Greenland fishery was monitored using a panel of gene-associated SNPs to analyse archived otoliths by Bonanomi et al. (2015).

Pampoulie et al. (2015) supported genetic divergence between coastal and migratory Icelandic cod at two SNP loci within the rhodopsin gene suggesting the visual system may be involved in local adaptation of these ecotypes. As previous studies suggested (e.g. Pampoulie et al., 2008a), the migratory and the coastal ecotypes have different feeding behaviour: coastal cod is more stationary and remains in shallow and coastal waters also in the feeding season, while the migratory cod spawns in shallow waters and migrates to

deeper waters to feed, hence experimenting different environmental conditions and selective pressure.

Berg et al. (2017) detected highly differentiated genomic islands of divergence in Icelandic cod ecotypes. Low levels of genetic differentiation are observed at neutral regions of the genome between the two ecotypes (F_{ST} = 0.0002) while adaptative divergence is mainly at SNPs in linkage groups 1, 2 and 7 (F_{ST} = 0.0547). Remarkably, most of the divergence is due to SNPs in linkage group 1, of which *Pan* I and the rhodopsin gene are part. These ecotypes share the same spawning grounds in Icelandic coastal waters and these patterns of genetic variation with neutral region of the genome weakly differentiated and non-neutral region highly divergent can be explained by current gene flow and natural selection promoting adaptation to divergent environments.

7.3 Faroese cod

Current management status

In the Faroese grounds (Division 5.b) two ICES stock assessment units exist for cod, one in the Faroese Bank (Subdivision 5.b.2) and the other in the Faroese Plateau (Subdivision 5.b.1). Cod in the Faroese Bank is found in shallow waters mainly at depths above 200 m (ICES 2013a). Tagging evidence supports little exchange between the two stocks that have different growth rates, as ICES reported cod in the Faroese Bank has a higher growth rate than cod from the Plateau stock (ICES 2013a). Cod in the Faroese Bank spawns in spring in the shallow part of the Bank and pelagic eggs and larvae are retained by oceanic currents (ICES 2013a). As informed by ICES, landings are not reported separately for cod caught in the Plateau and the Bank during the same fishing trip, adding some issues in landing estimations for both stocks (ICES 2019b). The Faroese Bank stock is depleted and fishery is closed until the stock will recover (ICES 2019b). Based on the precautionary approach, ICES advise zero catches in 2020-22 (ICES 2019a). Landings in 2018 were 31 t and cod was exclusively caught as by-catch (ICES 2019b).

The Faroe Plateau stock is treated as an isolated cod stock as supported by tagging studies (ICES, 2017 and references therein). Spawning occurs in February-March and eggs and larvae are retained in the Faroe Plateau by clockwise water circulations. After a collapse of cod fishery in the early 1990s the stock recovered due to environmentally favourable conditions. Landings in 2018 have been estimated to be 12 214 t and Faroese Islands is the main fishing country. ICES recommended to avoid depletion of the stock in future, however in 2018 and 2019 catches exceeded the ICES catch advice (ICES 2020f). As ICES highlighted, genetic and tagging evidence suggests the presence of three different stocks around the Faroe Islands, i.e. the Faroe Bank, the Faroe Plateau and the Faroe-Icelandic Ridge (ICES 2019b). The Faroe-Icelandic Ridge cod is considered a component of the Icelandic stock, hence, catches from this area are excluded from the catch-at-age calculations of the Faroe Plateau stock by ICES (ICES 2019b).

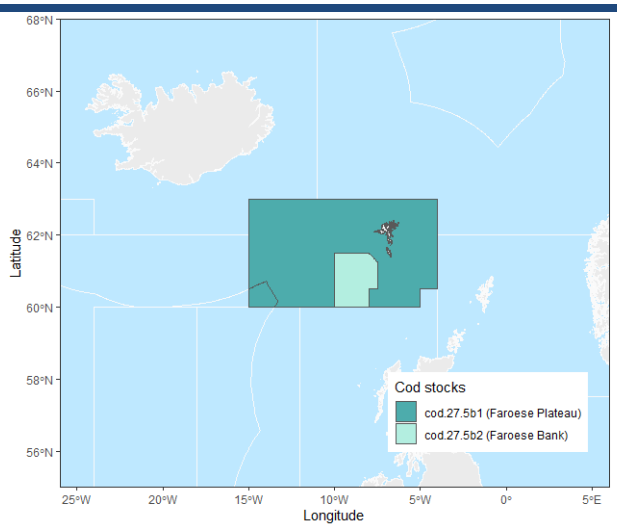


Figure 7.3. Faroese Plateau and Faroese Bank cod stock assessment units.

Genetic population structure in a nutshell

Genetic evidence supports:

- Faroe Plateau is genetically homogeneous at mitochon-drial DNA (Sigurgíslason & Árnason 2003).
- Initially a lack of differentia-tion between east of Green-land, Iceland, Faroese Ridge at microsatellites was supported by O'Leary et al. (2007).
- Temporal stability for cod populations in the Faroese Plateau and Bank and possible migrations of individuals from the Icelandic Ridge (Nielsen et al. 2007).
- Genetic similarity between cod in East Iceland and the Faroe Plateau at microsatellite loci and *Pan* I (Pampoulie et al. 2008c).
- The presence of two genetically distinct cod populations the Faroe Plateau and the Faroe Bank was supported by Nielsen et al. (2009), that are also differentiated from the rest of the NE Atlantic cod populations.
- The Faroese cod is genetically different from surrounding stocks (Norwegian, Ireland, the North Sea and the NE Arctic cod stocks) (Johansen et al. 2020).
- The Faroe Plateau and Bank samples were weakly differentiated through SNP analysis supporting panmixia in the Faroese grounds (Johansen et al. 2020). However, chromosomal inversions in linkage groups 7 and 12 were found, suggesting ulterior differentiation and further investigations are needed to explore it.

A lack of differentiation was found between cod in east of Iceland and the Faroe Plateau at microsatellite loci, with gene flow probably mediated by larval and eggs drift from Iceland towards the Faroe Plateau. However, in successive studies in which SNPs were used, no samples from East or southeast Iceland were included hence further analysis are needed to explore the connectivity between East of Iceland and the Faroe Plateau.

Mismatch

Based on life-history differences, tagging evidence and genetic studies, the stocks on the Faroe Plateau and Faroe Bank are supported. Genetic differentiation was reported between cod sampled in the Faroese Plateau and Bank through microsatellites supporting their assessment in two different units, as supported also by tagging evidence and life-history differences. Although, a weak differentiation was reported by SNPs, chromosomal inversions in linkage group 7 and 12 were found suggesting adaptive divergence. Further studies are needed to explore in more detail. Moreover, connectivity between cod in south and east Iceland and the Faroese Plateau stock needs further investigation.

Summary of genetic evidence

Sigurgíslason and Árnason (2003), investigating mitochondrial DNA variation of cod on the Faroe Plateau, reported genetic similarity among samples. On a larger scale, O'Leary et al. (2007) used microsatellites to analyse population structure of cod in the North

Atlantic and a lack of differentiation between east of Greenland, Iceland and the Faroese Ridge samples was reported.

Using microsatellites and *Pan* I, Nielsen et al. (2007) analysed archived and contemporary cod samples and no significant temporal changes were found in these areas. The Faroe Plateau and the Faroe Bank samples were polymorphic for *Pan* I; although the *Pan* I^A allele is more frequent. As the authors suggested, cod with the *Pan* I^B allele found in the contemporary sample could represent migrants from the Icelandic-Faroese Ridge stock showing higher frequency of *Pan* I^B.

Pampoulie et al. (2008c) reported genetic similarity between cod in East Iceland and the Faroe Plateau at microsatellite loci and *Pan* I. This lack of genetic differentiation is probably due to passive larvae and eggs drift rather than active migration of adult cod, that as tagging evidence suggested is rare. Significant genetic differentiation was found between South Iceland and East Iceland-Faroese cod and a barrier to gene flow was identified throughout a landscape genetic approach.

The presence of two genetically distinct populations of cod in the Faroese waters was supported by Nielsen et al. (2009). Genetic differentiation was reported between the Faroe Plateau and the Faroe Bank samples, differentiated also from the rest of the NE Atlantic. Andersen et al. (2011) using SNP analysis reported no differentiation at the transferrin gene (Tf1) allele frequencies between Faroe Bank and Plateau populations. However, this is a functional genetic marker under strong positive selection. Hence, this marker is not useful in studying population structure in cod in this part of its distributional range.

Johansen et al. (2020) using a panel of 8 174 SNPs, confirmed the differentiation of the Faroese samples from the rest of the NE Atlantic populations. However, the Faroe Plateau and Bank samples were weakly differentiated, supporting possible panmixia for cod in the Faroese grounds (subdivision 5.b). This is in contrast with previous genetic studies, life history divergences and tagging evidence supporting two different stocks in these areas. However, chromosomal inversions in linkage groups 7 and 12 were reported, suggesting genetic differentiation between the samples that requires alternative analyses (Johansen et al. 2020).

A lack of studies investigating population structure and connectivity between east (south east) Iceland and the Faroese Plateau through SNPs is evident. Hence, further investigations exploring genetic population structure in east of Iceland and Faroese grounds are needed.

7.4 North-East Arctic cod and Norwegian coastal cod

Current management status

In ICES subareas 1 and 2, two stocks of cod were traditionally recognized: the Norwegian coastal cod inhabiting the fjords and coastal regions of Norway and the North-East (NE) Arctic cod widely distributed in the Barents Sea and adjacent areas. The Norwegian coastal cod was split into two stocks south and north of 67°N at the WKBarFar 2021 benchmark (ICES, 2021; and references therein).

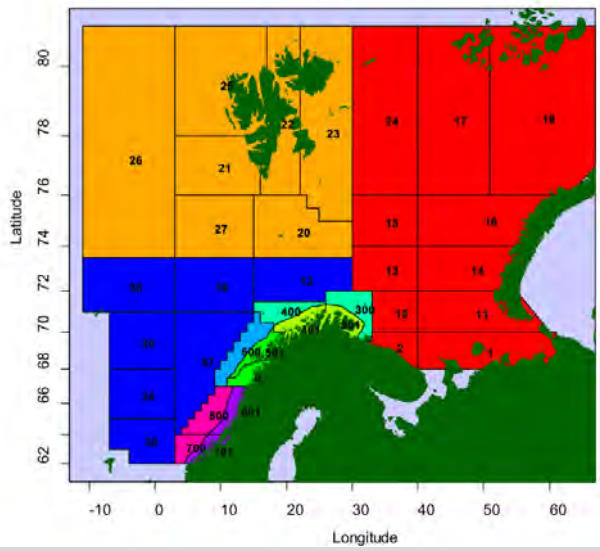


Figure 7.4.1. Norwegian statistical rectangles, the rectangles 3-7 are split along the 12 nautical mile in 300-301, 400-401, 500-501, 600-601 and 700-701. The figure is taken from the ICES Stock Annex (ICES 2015c).

This is supported by genetic evidence suggesting substructure within the former Norwegian coastal cod stock (Dahle et al. 2018b, Johansen et al. 2020). Alongside, nearly 75% of the Norwegian coastal cod biomass is estimated to be north of 67°N, where the majority of the catches (80%) are from, as reported by ICES (ICES 2021a). Moreover, available data for stock assessment are of a higher quality north of 67°N (ICES 2021a). The remaining 20% of Norwegian coastal cod catches are from the Norwegian coastal cod between and 67°N and 62°N. Based on the quality of the available data, ICES designated this as a data limited stock (ICES 2021b).
Assessment areas of the Norwegian Coastal cod north of 67°N comprise the Norwegian statistical rectangles 0, 3, 4, 5 (ICES 2015c) (figure). While, the Norwegian coastal cod stock between 67°N and 62°N, includes cod in statistical rectangles 6 and 7 (figure). ICES is aware of ulterior substructure and genetic divergence within both coastal cod stocks (Johansen et al. 2020) and reported that the Norwegian coastal cod *'can therefore be viewed as a stock complex, with several more or less resident stocks inhabiting different fjords and shelf areas along the coast'* (ICES 2021a).

The following information refers to the Norwegian coastal cod (including both stocks) as assessed prior to 2021. The coastal and Arctic cod stocks share the same spawning grounds along the Norwegian coasts between 67°30' N and 70° N (ICES 2017b). The Norwegian coastal cod is mainly fished as by-catch in the North-East Arctic cod fishery. Most of the catches are from the first half of the year, when the NE Arctic cod comes to spawn in coastal waters (ICES 2015c). As reported in the stock annex, the Coastal and Arctic cod share the same spawning grounds during the spawning season, that goes from

March to June, with a peak in early April (ICES 2015c). The NE Arctic cod can be found both in inshore and offshore areas throughout the year (ICES 2021a). Fish are not assigned to the stock of origin at landings. However, at the end of the fishing year proportions of coastal cod in catches are estimated throughout otolith analyses of commercial samples (ICES 2015c). This separation method, although applicable only to individual of ages 2+, is highly accurate and was also compared with genetic methods. Various issues are present for the Norwegian coastal cod stock due to uncertainty of commercial catches (ICES 2020a). Special regulations (e.g. restriction to vessels of certain size and fishing gears, closed areas and seasons) have been implemented to protect the Norwegian coastal cod, reducing catches and promoting fishing outside fjords and in areas where the proportion of the NE Arctic cod is higher (ICES 2020a). Moreover, the limited information available on recreational fisheries represents an issue for catch estimates (ICES 2020a). The ICES advice for the former Norwegian coastal cod was based on the Norwegian rebuilding plan and recreational catches are fixed since 2009 at 12 700 t (ICES 2020a). Based on otolith analyses from commercial samples, ICES estimated that 40 100 t were caught in 2019 (ICES 2020a). Adding the fixed catches from recreational fishery, total catches in 2019 were 52 807 t.

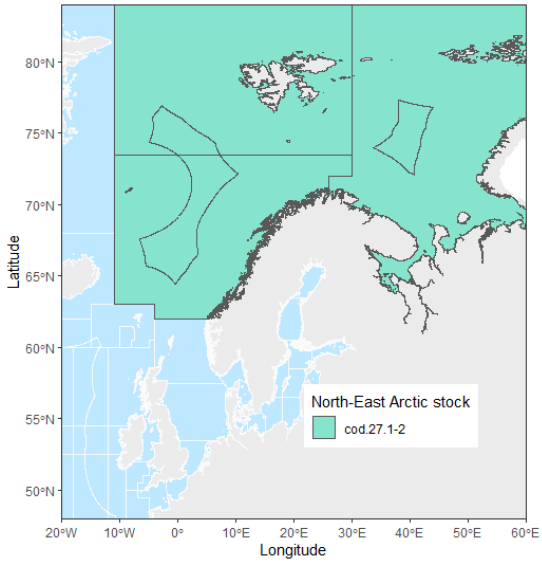


Figure 7.4.2. North-East Arctic cod stock unit.

The North-East Arctic cod stock (ICES Subareas 1-2) is the largest remaining stock of Atlantic cod. The NE Arctic cod is widely distributed in the Barents Sea and adjacent areas (Figure 7.4.2). During the spawning season, mature individual migration towards the main spawning grounds along the Norwegian coasts (between 67°30' and 70°N) is known as well as the following drift of juveniles eastwards and northwards (ICES 2017b). The fishery of the NE Arctic cod is highly regulated - e.g., with quotas, minimum size (44 cm), restriction to certain fishing grounds and seasons and protection of nursery areas (ICES 2017b). It is fished in both offshore and inshore areas, mostly in the first half of the year. ICES advice is based on the Joint Norwegian–Russian Fisheries Commission management plan (ICES 2020a). Catches have fluctuated and in the last years are declining from a peak reached in 2014 of 986 449 t (ICES 2020e). Total catches in 2019 were 692 609 t, the main fishing countries, Russia (316 813 t) and Norway (282 120 t), accounted for almost the 90% of the catches.

Moreover, an experimental cod fishery started in 2019 (total catches 638 t) in Jan Mayen (Division 2.a). Based on otoliths and genetic analyses, cod in this area is a mix of NE Arctic cod and Icelandic cod (ICES 2020a). These catches were not considered in assessment of NE Arctic cod by ICES (ICES 2020a).
Although a separate management unit does not exist for the Norwegian coastal cod, a quota is considered for the Norwegian coastal cod within the TAC set for the NE Arctic cod. Hence, we do not treat evidence suggesting differentiation between Arctic and Norwegian coastal cod as a mismatch between genetic and management unit.

Genetic population structure in a nutshell

The existing literature exploring population structure of Atlantic cod in the Norwegian Sea and Barents Sea is extensive and focuses particularly on the NE Arctic and Norwegian coastal cod populations.
Genetic studies confirmed the differentiation between NE Arctic and Norwegian coastal cod populations. Substructure along Norway was supported suggesting a complex pattern of population structure for cod along the Norwegian coast that was not taken into account in assessment and management until 2021, when the stock was benchmarked by ICES. Two Norwegian coastal cod stock units are considered by ICES, more in line with genetic population structure of coastal cod along Norway. In particular, genetic evidence supports:

- Genetic differentiation within and between Norwegian fjords was reported.
- Genetic divergence between NE Arctic cod and Norwegian coastal cod is supported by the means of several genetic markers as haemoglobin and blood proteins (Dahle, 1991; Jørstad and Nævdal, 1989; and references therein), nuclear RFLP loci (Pogson et al. 1995), *Pan* I (Fevolden & Pogson 1997, Pogson & Fevolden 2003, Sarvas & Fevolden 2005b), microsatellites (e.g. Skarstein et al., 2007), genome-wide investigation (Karlsen et al. 2013) and SNPs analysis (Berg et al. 2016, 2017, Kirubakaran et al. 2016, Johansen et al. 2020).
- A lack of differentiation was found between Arctic and Norwegian coastal cod through mitochondrial markers (Árnason & Pálsson 1996, Karlsen et al. 2014, Jørgensen et al. 2018). The genetic divergence found at the nuclear genome between Arctic and Norwegian coastal cod was not observed in cod mitogenome, suggesting these genomes have been evolving under different evolutionary constraints.
- Haemoglobin can be effectively use as a reliable marker to distinguish between Norwegian costal cod and Arctic cod (Dahle & Jørstad 1993).
- The spatial distribution of Arctic cod and Norwegian coastal cod was described (Nordeide 1998) as well as their co-occurrence within the same fjord (Sarvas & Fevolden 2005b, Westgaard & Fevolden 2007).
- The *Pan* I locus (previously known as *Syp* I), was identified as useful marker to distinguish between Arctic and coastal cod. Arctic cod shows higher frequencies

of the *Pan* I^B allele than Norwegian coastal cod (Fevolden & Pogson 1997, Pogson & Fevolden 2003, Sarvas & Fevolden 2005a).

- Fevolden et al. (2012) confirmed co-occurrence in northern Norway of Arctic and coastal cod. The spatial distribution of cod settlers was described, with deep-water settlers (*Pan* I^{BB}) belonging to the Arctic cod population, shallow-water settlers to the coastal population (*Pan* I^{AA}), and non-settled individuals of mixed origin.
- Genetic divergence between ecotypes at *Pan* I is strong and related to depths. Andersen et al. (2015) reported linkage disequilibrium between *Pan* I and rhodopsin gene in the Norwegian coastal and NE Arctic cod: shallow settlers (Norwegian coastal cod) showed higher frequencies of *Pan* I^A and rho^A alleles while the deep-water settlers (Arctic cod) higher frequencies of *Pan* I^B and rho^B alleles.
- Genomic divergence between coastal and Arctic cod was confirmed by Karlsen et al. (2013) genome-wide investigation. Highly differentiated SNPs were identified in genomic islands of divergence, in linkage group 1, 2 and 7 of cod genome.
- In linkage group 1, two inversions were found to be responsible of the divergence between Arctic and Norwegian coastal cod populations (Kirubakaran et al. 2016).
- The genetic divergence between stationary and migratory ecotypes is due to genomic islands of divergence maintained by chromosomal inversions (Berg et al. 2016, 2017). Chromosomal inversions prevent recombination during the meiosis, thus allowing genes within the inversions to co-adapt and co-evolve despite current gene flow.
- Significant population structure was reported for cod along Norway following an isolation by distance pattern. The division at 62°N (boundary between divisions 4.a and 2.a) does not reflect the complex population structure of cod along the Norwegian coasts (Dahle et al. 2018b).
- Johansen et al. (2020), through SNPs, supported complex population structure for Norwegian coastal cod that is structured at a finer scale. Overall, the differentiation between Norwegian coastal cod and NE Arctic cod was confirmed, as well as the differentiation with cod from the Faroe Islands, Irish Sea and White Sea.

Substructure along the coast of Norway was supported suggesting a complex pattern of population structure for cod that was not taken into account in assessment and management (Dahle et al. 2018b, Johansen et al. 2020). Genetic evidence was used in conjunction with other methods to split the Norwegian coastal cod into two stocks during the WKBarFar 2021 benchmark: the Norwegian coastal cod north of 67°N and the Norwegian coastal cod stock between 62 and 67°N (ICES, 2021; and references therein). These stock units are more in line with genetic population structure of cod. Although substructure exists within both Norwegian coastal cod stock units. As ICES reported Norwegian coastal cod can be considered a stock complex including several stocks in Norwegian fjords and coasts (ICES 2021a).

Mismatch

Genetic divergence between NE Arctic cod and Norwegian coastal cod was supported and the co-occurrence of these genetically divergent populations is already considered in stock assessment and management. Genetic tools have been shown to be able to assign individuals to the correct stock with high accuracy and can be used for a real-time fisheries monitoring (Dahle et al. 2018a). Moreover, a genetically different cod population is supported inhabiting the White Sea by allozyme, microsatellite and mitochondrial markers.

Substructure within the historical Norwegian coastal cod stock was confirmed by both microsatellite and SNPs data. Hence, mismatch between genetic and assessment units existed. Genetic information on population structure was considered by ICES to split the stock assessment unit into two separate stock units: the Norwegian coastal cod north of 67°N and the Norwegian coastal cod between 62 and 67°N (ICES, 2021), that are more in line with genetic structure of cod. Although, genetic evidence suggests substructure at a finer scale within both Norwegian coastal cod stocks. As ICES reported, Norwegian coastal cod can be considered a stock complex including several stocks in Norwegian fjords and coasts (ICES 2021a). The revision of the Norwegian coastal cod stock unit was an extraordinary example of how genetics can inform to design more accurate stock assessment units. Genetic tools have shown to be a valuable instrument also for a real-time monitoring of the mixed stock fishery exploiting the largest remaining stock of Atlantic cod (NE Arctic cod) and the Norwegian coastal cod.

Summary of genetic evidence

Historically, two different cod stocks were known in subareas 1 and 2: the stationary Norwegian coastal cod, distributed in inshore coastal waters and fjords along Norway, and the migratory NE Arctic cod, whose spawning migration towards Norwegian coasts in spring is well known as well as the following eggs and larvae drifts into the Barents Sea where nursery and feeding areas are found. The Norwegian coastal cod stock unit was revised in 2021 (ICES 2021a), and two stocks are now considered by ICES: the Norwegian coastal cod north of 67°N and the Norwegian coastal cod stock between 62 and 67°N.

Earlier studies based on haemoglobin and blood proteins supported genetic differentiation between the Arctic and the Norwegian coastal cod, and indicated also substructure along the Norwegian coast (Dahle, 1991; Jørstad and Nævdal, 1989; and references therein). Jørstad and Nævdal (1989) using allozymes indicated a complex spatio-temporal population structure for cod in northern Norway; genetic differentiation within and between fjords was reported, as well as among temporal replicates. Dahle (1991) using restriction fragment analysis of mitochondrial DNA reported genetic differentiation between Norwegian coastal cod and Arctic cod populations. This finding was also supported by haemoglobin and otolith shape analyses by Dahle and Jørstad (1993). Dahle and Jørstad (1993) through the analysis of more than 5000 cod individuals

collected during 5 years in Troms area (northern Norway), Lofoten and the Barents Sea showed that haemoglobin can be effectively use as a reliable marker to distinguish between Norwegian costal cod and NE Arctic cod. A detailed sampling design allowed to observe the arrive of the Arctic cod in the spawning areas of Lofoten and along the Norwegian coasts: where only few weeks earlier the analysis indicated the presence of coastal cod, few weeks later presence of Arctic cod within the spawning site was registered by a change in haemoglobin allele frequencies. Hence, genetic evidence made it possible to monitor the arrival of the Arctic cod in coastal spawning areas, movements of offspring in the nursery areas, and the migration of Arctic cod adults into the Barents Sea.

However, a lack of differentiation was found among Arctic and Norwegian coastal cod samples by Árnason and Pálsson (1996) through the analysis of mitochondrial cytochrome b sequences. In line with previous studies, highly significant genetic differentiation was reported between the Arctic and the Norwegian coastal cod by Pogson et al. (1995) that used nuclear RFLP loci and suggested GM798, (nowadays known as pantophysin and previously called synaptophysin), could be used as possible marker to distinguish between Arctic and coastal cod.

Fevolden and Pogson (1997) analysed Atlantic cod samples at the synaptophysin (*Syp* I) locus, reporting significant differentiation between Arctic and Norwegian coastal cod populations. Genetic heterogeneity was detected also within the coastal and fjordic samples suggesting the presence of substructure. The *Syp* I locus was identified as useful marker to distinguish between Arctic and coastal cod, with Arctic cod showing higher frequencies of the *Syp* I^B allele (mean frequency= 0.902) than the coastal cod (*Syp* I^B mean frequency= 0.194). Results from this study contrast with a lack of differentiation found between coastal and Arctic cod at a mitochondrial marker by Árnason and Pálsson (1996) that was perhaps due to the recent origin of the Arctic and coastal cod populations and current gene flow. Nordeide (1998) using haemoglobin variation investigated spatial distribution of Arctic and Norwegian coastal cod individuals in the Lofoten spawning grounds. Individuals from both stocks were found in the same area, although Arctic cod was more frequent in deeper waters. Mork and Giæver (1999) showed that using neutral allozymes was not possible to distinguish the NE Arctic and the Norwegian coastal cod. However, the inclusion of a locus under selection (LDH-3*) showed existence of genetic heterogeneity along Norway, and genetic differentiation between northern Norway and the mid-Norway samples. No significant genetic differentiation was detected within northern Norway samples that had previously been classified as Arctic and costal cod by otolith analysis.

Pogson and Fevolden (2003) reported genetic differentiation at the pantophysin *Pan* I locus (previously called synaptophysin) between Arctic and Norwegian coastal cod populations, as well as within coastal samples. The divergence is due to diversifying selection. The value of using markers under selection in studying population structure in

marine fish species was highlighted, providing important information on local adaptation and divergence undetectable through neutral markers (e.g. mitochondrial markers). Husebø et al. (2004) analysed haemoglobin variation in 1209 individuals collected during spawning season along Norway. A north-south cline was detected and genetic differentiation was significant between northern Norway and southern Norway and Danish samples. The presence of both Norwegian and Arctic cod was reported by Sarvas and Fevolden (2005a) that investigated genetic population structure of Atlantic cod within a fjord in northern Norway (Ullsfjord) using *Pan* I locus. Norwegian coastal cod individuals were found in the inner part of the fjord while immature Arctic cod individuals occurred in the outer part of the fjord in juvenile feeding grounds. Temporal variation was reported in the outer part of the fjord where both Arctic and coastal cod were observed. Sarvas and Fevolden (2005b) confirmed the differentiation at *Pan* I between Arctic and coastal cod, with allele frequencies showing a latitudinal cline for post-juvenile individuals and correlation to depth in post-juvenile and young of the year samples: genetic differentiation was significant in inshore-offshore comparisons.

Skarstein et al. (2007), through microsatellites and *Pan* I, reported three genetically distinct populations, the NE Arctic cod, Norwegian coastal cod and the North Sea cod, respectively. Although levels of genetic divergence among populations were higher at *Pan* I, microsatellite loci allowed the detection of ulterior substructure. Westgaard and Fevolden (2007) analysing samples from inner and outer coastal locations along Norway showed that the highly migratory NE Arctic cod in early life stages shares the coastal areas with the Norwegian coastal cod all year around. The presence of two non-neutral microsatellite loci, Gmo 34 and Gmo 132, was reported. Similar to *Pan* I, these loci can be used to distinguish between coastal and Arctic cod individuals. Hence, Atlantic cod in the inner and outer coastal areas have divergent genetic signature at loci under selection, supporting their assessment and management in two different units. Wennevik et al. (2008) tested different genetic markers, namely allozymes, microsatellites, *Pan* I and haemoglobin to distinguish between Arctic and coastal cod. Genetic techniques were compared with the conventional otolith classification, showing that molecular markers perform well in mixed stock analysis similarly to otoliths.

Fevolden et al. (2012) confirmed genetic differentiation between Arctic and coastal cod at microsatellite loci and showed their co-occurrence in northern Norway. The spatial distribution of cod settlers was described, with deep-water settlers, homozygous *Pan* I^{BB}, belonging to the Arctic cod population, shallow-water settlers to the coastal population (*Pan* I^{AA}), while non-settled individuals were of mixed origin. The correlation between depth and *Pan* I allele frequencies was confirmed.

Genomic divergence between Norwegian coastal and Arctic cod was confirmed by Karlsen et al. (2013) genome-wide investigation. The existence of three genomic regions highly divergent between the migratory Arctic cod and stationary Norwegian coastal cod ecotypes was supported. Highly differentiated SNPs were identified in genomic island of divergence, namely in linkage group 1, 2 and 7. However, the divergence found at the

nuclear genome was not observed in the mitogenome (16.7 kb) by Karlsen et al. (2014) that analysed the same samples. Weak differentiation between the two ecotypes was reported only at two genes (ND1 and ND2). Hence, the mitochondrial and nuclear genome evolve under different evolutionary constraints.

The role of *Pan* I polymorphism in genetic differentiation between the stationary and migratory ecotypes of Atlantic cod was investigated by Andersen et al. (2015). Genetic divergence between ecotypes at *Pan* I is strong and related to depths as previous studies reported. Linkage disequilibrium was found between *Pan* I and the rhodopsin (*rho*) gene in the stationary (Norwegian coastal) and migratory (NE Arctic) cod: shallow water settlers showed higher frequencies of *Pan* I^A and rho^A alleles while deep-water settlers showed higher frequencies of *Pan* I^B and rho^B alleles.

Berg et al. (2016) using more than 8000 SNPs suggested chromosomal rearrangements promoting genomic divergence between migratory and stationary ecotypes of Atlantic cod. Highly divergent loci were identified in three regions covering the 4% of cod genome, contrasting with low levels of differentiation found in neutral regions of the genome between migratory and non-migratory ecotypes. The authors suggested these regions represent genomic inversions promoting local adaptation in cod ecotypes. Similarly, Sodeland et al. (2016) supported the presence of genomic islands of divergence across cod genome representing chromosomal rearrangements (inversions) in the North Sea-Skagerrak areas.

Kirubakaran et al. (2016) reported two chromosomal inversions within a region of 17.4 Mb in cod genome (linkage group 1) repressing recombination between Arctic cod and Norwegian coastal cod. A specific haplotype represented by 186 SNPs was observed in the Arctic cod individuals. Kirubakaran et al. (2016) indicated this genomic region includes 763 genes, potentially involved in adaptation to migratory behaviour and vertical movement into deeper waters typical of the Arctic cod population. Despite gene flow between the Arctic and Norwegian coastal cod, chromosomal inversions maintain genetic divergence between the two ecotypes restricted in certain regions of the genome. The existence of multiple co-adapted and co-evolving genes that can be considered supergenes in the NE Arctic cod population was supported. Hence, biological mechanism promoting adaptive divergence between migratory and stationary cod ecotypes sharing the same spawning grounds and season were found out.

Berg et al. (2017) confirmed genetic divergence between stationary and migratory cod ecotypes is due to genomic islands of divergence maintained by chromosomal inversions on both side of the North Atlantic. Chromosomal inversions prevent recombination during the meiosis, thus allowing genes within the inversions to co-adapt and co-evolve despite current gene flow between the two ecotypes.

Jørgensen et al. (2018) analysed cod mitogenomes from samples collected across the Atlantic. Genetic differentiation was reported between western and eastern populations, following an isolation by distance pattern. Mitochondrial DNA evolution is shaped by gene

flow and genetic drift, in line with previous studies (e.g. Árnason, 2004) no differentiation was reported between the migratory and stationary ecotypes in Norway.

Dahle et al. (2018b) explored population structure of Norwegian coastal cod, analysing samples from 55 spawning locations using a combination of neutral and under selection microsatellites. Significant population structure was reported for cod along Norway following an isolation by distance pattern. Also, a gradient of introgression was showed between the NE Arctic cod and Norwegian coastal cod. The authors observed that the division at 62°N (the boundary between divisions 4.a and 2.a) does not reflect the complex population structure of cod along Norwegian coasts resulting in a mismatch.

The division of Norwegian coastal cod into two assessment units, south and north of 62°N, was not supported either by Johansen et al. (2020). Using a SNP array of more than 8 000 loci, Johansen et al. (2020) supported complex population structure for cod along Norwegian coasts that was not reflected in the former Norwegian coastal cod assessment unit. Although the boundary at 62°N could be used as a boundary between northern and southern Norwegian coastal cod units, this study showed that cod is structured at a finer scale, both norther and southern. Overall, the differentiation between Norwegian coastal and NE Arctic cod was confirmed, as well as the differentiation with cod samples from the Faroe Islands, the Irish Sea and the White Sea.

Genetic evidence from these studies suggesting substructure within Norwegian coastal cod northern than 62°N was considered to split the Norwegian coastal cod stock into two stock assessment unit in, the Norwegian coastal cod north of 67°N and the Norwegian coastal cod stock between 62 and 67°N during the WKBarFar 2021 benchmark (ICES, 2021; and references therein).

There is a body of literature focusing on Atlantic cod in the White Sea. Stroganov et al. (2013) using a combination of allozymes and microsatellites reported temporally stable genetic differentiation between cod in the Barents Sea and White Sea, indicating the existence of a reproductively isolated cod population in the latter. Zelenina et al. (2016) analysing mitochondrial cytochrome b gene sequences supported the isolation of Atlantic cod in the White Sea.

A small population of Atlantic cod, known as Kildin cod, is found in the Mogilnoe Lake in Kildin Island, a Russian island in the Barents Sea. Kildin cod has specific morphological and life-history traits (Andreev et al. 2015, Zhivotovsky et al. 2016). It is characterized by a small effective population size and it is reproductively isolated from the marine Atlantic cod populations as genetic evidence supported (Andreev et al. 2015, Zhivotovsky et al. 2016). A loss of genetic variation in Kildin cod was reported at mitochondrial DNA and microsatellites due to genetic drift by Zhivotovsky et al. (2016) and conservation measures are in place to protect this unique cod population. Stroganov et al. (2017) confirmed the loss of genetic diversity in Kildin cod and the genetic and morphological differences from marine Atlantic cod populations, promoting the adaptation of Kildin cod to particular environmental conditions of Lake Mogilnoe.

7.5 North Sea cod

Current management status

The North Sea cod stock assessment unit covers the North Sea (Subarea 4), the eastern English Channel (Division 7.d) and the Skagerrak (Subdivision 20). ICES is aware of substructure within the current stock that comprises different populations and hence it is not biologically meaningful. Mismatches already exist between assessment and management units for which TACs are set. Separate TACs exist for the Skagerrak, the eastern English Channel, the North Sea and Norwegian waters south of 62°N (Table 2). In the North Sea cod is caught in mixed stock demersal fisheries by all demersal gears. Cod is both a target species and a by-catch species, e.g. in beam trawling directed to flatfish species (ICES 2020v). In order to assure sustainable fishery of this commercial important shared resource in the North Sea, several management plans were adopted (ICES, 2020; and references therein). In 2018 a multiannual management plan was adopted by the European Union but not from Norway; hence it is not used by ICES for advice that are based on the MSY approach since 2015 (ICES 2020v). The stock in 2019 was fished outside biological safe limits: fishing mortality was above precautionary reference points while the spawning biomass below reference points (ICES 2020v). Historically, fishing mortality was high until 2000 when started declining and reached the lowest level in 2013, followed by a successive increase in 2016-18. Total catches in 2019 were 35 684 t, the majrity landed in Subarea 4 (North Sea) (ICES 2020v).

Differences in recruitment indices and changes in biomass at regional scale are reported by ICES, e.g. the increase in recruitment observed in the northern North Sea was not followed by cod in the rest of the areas. Moreover, as suggested by ICES the decreases in landings in the eastern English Channel (36 t were landed in 2019) and data from the scientific annual survey may indicate a collapse of cod in this division (ICES 2020v). Landings were low also in the southern North Sea (divisions 4.c) amounting at 90 t. The existence of different populations should be considered for more reliable stock assessment and management of cod in the North Sea.

In 2020, available information on population structure for North Sea cod inferred by the means of different methods (genetics, tagging, otolith microchemistry and shape etc.) was reviewed during the ICES Workshop on Stock Identification of North Sea Cod (WKNSCodID) in order to design biologically meaningful units which might be used in assessment and management. The workshop concluded that two reproductively isolated populations, namely the Viking and the Dogger cod are present within the North Sea, mixing in some areas after spawning. The two units were described as follow:

- Based on genetic evidence (supported also by other methods), Viking cod is distributed in the Viking Bank (Division 4.a.), in the northeast North Sea, westwards to the Shetlands and southward to the Fischer and Jutland Banks (northern

Division 4.b); Viking cod uses as nursery area the Skagerrak (Division 20) and juveniles can be found also in the Kattegat (Division 21).

- The Dogger cod is found in the southern and central part of the North Sea around the Dogger Bank (Division 4.b), along the Scottish coast towards north of Scotland (northern 6.a), and in the eastern English Channel (Division 7.d) and is partially connected with the western English Channel (Division 7.e). Although genetic differentiation was not detected within the Dogger cod population, phenotypic traits suggest the presence of two different units with a possible boundary in division 4.b, with one subpopulation in the north (4.a and part of 4.b) and the other in the southern (portion of division 4.b and division 4.c) part of the region.

The WKNSCodID concluded that the stock assessment unit currently in use is not biologically meaningful and does not reflect the real structure of cod in the North Sea. It was highly recommended that ICES take into account the Dogger and Viking cod populations and possibly also considers the sub-populations within the Dogger units for a more reliable stock assessment.

Genetic population structure in a nutshell

The available information on genetic population structure confirms on a broader scale North Sea cod is differentiated from the rest of the NE Atlantic cod populations, namely the Baltic Sea, the Faroese Bank and Plateau, Norwegian coastal cod and NE Arctic cod populations. In particular, genetic evidence supports:

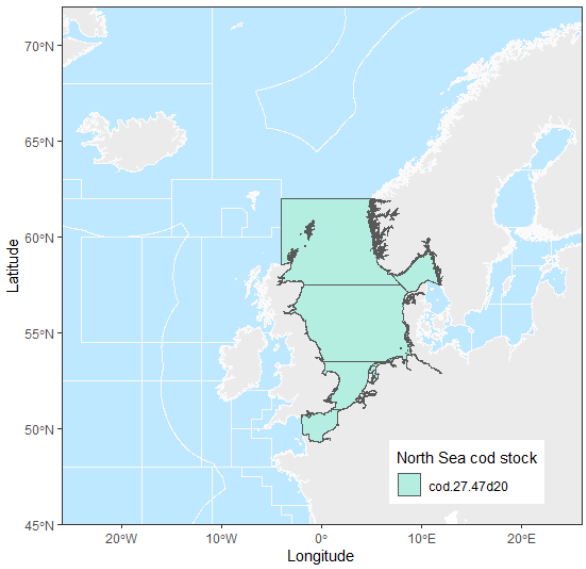


Figure 7.5. North Sea cod ICES stock assessment unit.

- Isolation by distance within the North Sea for cod (Pogson et al. 1995, 2001).
- Hutchinson et al. (2001) using microsatellites supported the existence of four genetically distinct populations within the North Sea, namely in Bergen, Moray Firth, Flamborough Head and in Southern Bight.
- North Sea and Baltic Sea cod genetically differentiated (e.g. Hemmer-Hansen et al., 2013; Nielsen et al., 2003)
- Genetic differentiation between North Sea cod and adult cod from the Skagerrak. Juveniles of North Sea origin presence in the Skagerrak depended on the strength of the North Sea water inflow into the Skagerrak, transporting cod early life stage (pelagic eggs and larvae).

- Genetic divergence between Skagerrak and western North Sea (Dogger Bank) (Pampoulie et al. 2008b)
- Viking Bank cod clearly differentiated when the microsatellite locus Gmo 132 was included in the analysis. Genetic differentiation between the Scottish samples (west of Scotland, Moray Firth and Shetland) and the central North Sea and Viking Bank cod samples was supported (Nielsen et al. 2009b)
- A genetic tool, constituted of 8 highly differentiated SNPs, was developed to assign cod individuals back to their population of origin the Northeast Arctic, North Sea and Baltic Sea (Nielsen et al. 2012)
- Three genetically different populations were found through SNPs around the British Isles, namely the Viking cod (restricted to the northern North Sea), the Dogger cod (widely distributed across the basin) and another population in the Celtic Sea, extending from the western English Channel, through the Celtic Sea, the Irish Sea and the southern part of division 6.a (west of Scotland) (Heath et al. 2014).
- Genetic differentiation between eastern and western northern North Sea (division 4.a) and the connectivity between Moray Firth and Kattegat was supported by SNPs (Wenne et al. 2020).
- Fine and temporally stable genetic structure was confirmed within the North Sea, where the presence of a reproductively isolated cod population in Viking Bank (eastern Division 4.a) and in waters shallower than 100 m east of Shetland, and extending as far as 1°W was reported (Wright et al. 2021).

Mismatch

Substructure is present within the North Sea stock assessment unit that does not reflect the real structure of cod in the North Sea. Most of the studies reviewed support the hypothesis that the stock units used in assessment and management for North Sea cod are not biologically meaningful. Hence, a revision is required to take into consideration population structure of cod in the North Sea and adjacent waters. As the WKNSCodID highly recommended the Dogger and Viking cod populations and possibly also the sub-populations within the Dogger units should be taken into account for a more reliable stock assessment. The existence of mixing between the Dogger unit and the Celtic unit as suggested by Heath et al. (2014) requires further studies to explore the spatio-temporal pattern of this mixing. A separate section is dedicated to cod in the Skagerrak, where substructure and local populations were found mismatching with the current stock assessment and management units.

Summary of genetic evidence

A large and growing body of literature has investigated North Sea cod. On a broader scale, these studies support cod in the North Sea is differentiated from the other NE Atlantic populations, namely the Baltic Sea, Faroese, Norwegian coastal and Arctic cod populations (e.g. Nielsen et al., 2005) Hemmer-Hansen et al. (2013). Available genetic

studies exploring genetic divergence between North Sea and Baltic Sea cod populations are described in the Baltic Sea cod section. Initially, Pogson et al. (1995) reported significant genetic differentiation among six cod populations sampled across the North Atlantic, including the North Sea. Furthermore, a pattern of isolation by distance was supported by nuclear restriction fragment length polymorphism analyses both at a small and larger geographic scale (Pogson et al. 1995, 2001). Hutchinson et al. (2001) investigated population structure of Atlantic cod using microsatellite markers. Notably, samples included were mature cod collected at spawning grounds. The existence of four genetically distinct populations within the North Sea was reported, respectively in Bergen, Moray Firth, Flamborough Head and in the Southern Bight, mismatching with the stock assessment and management units currently in use. Presence of gene flow was indicated between the southern North Sea and eastern English Channel. The western English Channel was genetically differentiated from the rest of the samples, and no ulterior substructure was found within the Celtic Sea- Irish Sea samples, that however were genetically differentiated from cod sampled in the Outer Hebrides.

The first of numerous studies investigating genetic population structure in the Skagerrak was published by Knutsen et al. (2004). Significant genetic differentiation was found between adult cod from the North Sea and the Skagerrak, as well as substructure within the Skagerrak, through microsatellites. Significant research effort has been put to study population structure of cod within the Skagerrak, especially along the Norwegian coast where evidence of local fjordic populations is available, alongside mixing with North Sea cod and cod from the adjacent Kattegat and Baltic Sea stocks. Microsatellites, SNPs, landscape genetics analyses, population genomics approach have been applied to explore genetic structure of cod in the Skagerrak in conjunction with tagging analysis for almost two decades unrevealing the existence of a local cod population. Genetic and behavioural mechanisms maintaining adaptive divergence between the North Sea and the local fjord ecotypes have been revealed. Hence, a separate section is dedicated to the incredible research effort and the results achieved for Atlantic cod into the Skagerrak. Poulsen et al. (2006) analysing historical (archived otoliths) and contemporary cod samples from the North Sea and Baltic Sea, reported temporally stable genetic differentiation between the two regions, and no evidence of loss of genetic diversity although the stocks have been severely depleted. Skarstein et al. (2007) reported a lack of differentiation within the North Sea at the *Pan* I locus for cod. Despite the geographic distance between samples (700 km), North Sea cod was monomorphic for the *Pan* I^A allele. In line with previous studies suggesting substructure within the North Sea, Pampoulie et al. (2008) reported genetic divergence between samples collected in the eastern North Sea (within the Skagerrak) and western North Sea (nearby the Dogger Bank). In 2009, the first population genomic study focusing on cod in the NE Atlantic was published by Nielsen et al. (2009a). Genomic signature of local adaptation and presence of loci under selection associated with spawning grounds and temperature were reported for cod in

the NE Atlantic also at a fine scale between the North Sea and the Baltic Sea cod populations. Moreover, Nielsen et al. (2009b) using microsatellites showed that including in the analysis a locus under selection (Gmo 132) allowed the detection of population structure at a microgeographical scale for cod in the North Sea. When this locus was included, samples from Viking Bank were clearly differentiated, supporting genetic differentiation between Scottish samples (west of Scotland, Moray Firth and Shetland) and the central North Sea and Viking Bank cod samples. The pattern of weak population structure detected by neutral loci and significant differentiation detected by loci under selection at a microgeographical scale was supported also through SNPs. Poulsen et al. (2011) using neutral SNP loci reported weak population structuring for cod in the North Sea. However, when loci under selection were included in the analysis, significant population structure even at a small scale was detected within the North Sea, supporting the existence of a locally adapted population in the northeastern North Sea. Nielsen et al. (2012) using gene-associated SNPs developed a genetic tool to assign cod individuals back to their population of origin, namely the Northeast Arctic, North Sea and Baltic Sea. The tool, consisting of eight highly differentiated SNP loci, was tested and all individuals were correctly assigned to their population of origin with the exception of one individual from the Baltic Sea assigned to the North Sea, hence considered a migrant. This tool ensures a correct assignment of individuals to the NE Arctic cod and North Sea population. Hemmer-Hansen et al. (2013) confirmed the genetic differentiation and reproductive isolation of the North Sea cod population. Moreover, the existence of highly differentiated loci across several linkage groups between the North Sea and the Baltic Sea populations, as well as among the North Sea, the Norwegian coastal cod and western Atlantic cod was reported.

Heath et al. (2014) using a SNP panel of 96 loci identified three cod populations around the British Isles, namely the Viking cod (restricted to the northern North Sea), the Dogger cod (widely distributed across the basin) and another population in the Celtic Sea, extending from the western English Channel, through the Celtic Sea, the Irish Sea and the southern part of division 6.a (west of Scotland). The spatial distribution of these three populations does not match with the stock assessment and management units currently in use. In west of Scotland (Division 6.a) individuals belonging to the Dogger unit were found in the northern part while individuals belonging to the Celtic units in the southern part (Firth of Clyde). The lack of differentiation between cod in the western English Channel, Celtic Sea, Irish Sea and southern part of West of Scotland (division 6.a) does not support their assessment and management in separate units. A mismatch exists also for the North Sea where two genetically different populations, namely Viking and Dogger cod are assessed and managed in the same stock unit.

Berg et al. (2015) supported adaptive genetic divergence between the North Sea, Baltic Sea, the Kattegat and the Sound cod populations. Discrete regions of cod genome were highly differentiated in these populations, supporting presence of islands of divergence

in cod genome. Fairweather et al. (2018) supported genetic differentiation of cod in the North Sea and divergence with the Baltic Sea population mainly due to adaptation to salinity and temperature, in line with earlier studies.

Wenne et al. (2020) using SNPs reported genetic differentiation between eastern and western northern North Sea (division 4.a). Cod sampled at the Moray Firth (western division 4.a) was genetically differentiated from the sample collected in a Norwegian fjord (Egersund) in the eastern part of the northern North Sea. Cod in Egersund fjord may represents a local cod population showing genomic signatures of adaptation similar to the Kattegat sample. In line with previous studies, the connectivity between North Sea cod in Moray Firth and the Kattegat was supported also by SNPs.

Fine and temporally stable genetic structure was confirmed within the northern North Sea by Wright et al. (2021) using SNPs and phenotypic traits to analyse samples from both spawning and feeding season. A pattern of isolation by distance was reported along the west-east gradient of samples collected in west of Scotland and in the northern North Sea. In line with previous investigations, this study supports the presence of a reproductively isolated cod population in Viking Bank (eastern Division 4.a) extending as well in waters shallower than 100 m east of the Shetlands. The population structure found does not support the current assessment units and advocates a stock boundary shift at 1°W, instead of the boundary currently in use between division 4.a and division 6.a for the North Sea cod stock unit. Moreover, the existence of region of the genome highly divergent in a background of weak differentiation was reported. Outlier loci were localized in linkage group 12, previously identified as an inverted region in cod genome and associated with temperature differences (Sodeland et al. 2016, Barth et al. 2019).

7.6 Cod in the Skagerrak

Genetic population structure in a nutshell

An extensive literature has investigated population structure of cod within the Skagerrak, especially along the Norwegian coast where evidence of local fjordic populations is available, alongside mixing with the North Sea and adjacent cod stocks. In particular, genetic evidence supports:

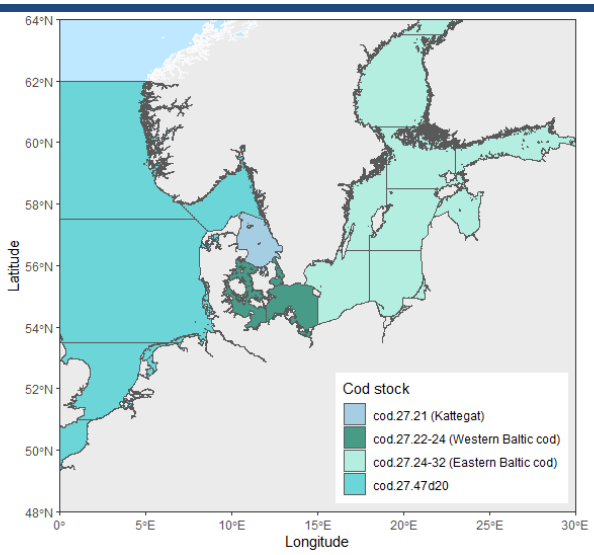


Figure 7.6. Atlantic cod ICES stock assessment units in the North Sea (including the Skagerrak), Baltic Sea and in the transition zone.

- Genetic differentiation between North Sea cod and local Norwegian Skagerrak populations supported by microsatellites Knutsen et al. (2003) Knutsen et al. (2004) and SNPs
- Temporal analyses confirm proportions of cod juveniles of North Sea origin into the Norwegian Skagerrak coast depends on the strength of the water influx from the North Sea favouring the drift of pelagic eggs and larvae Knutsen et al. (2004).
- (Jorde et al. 2007) confirmed presence of coastal cod populations along the Norwegian Skagerrak coast.
- Knutsen et al. (2011) found out that substructure between inner and outer Skagerrak fjord is biologically meaningful as supported by a combination of genetics, tagging and temporal analysis.
- Sodeland et al. (2016) supported through a population genomic approach adaptive divergence between inner and outer cod populations into the Skagerrak. Three chromosomal inversions maintain genetic divergence restricted in genomic islands of divergence in cod genome, involved in adaptation.
- Barth et al. (2017) supported chromosomal rearrangements promote and maintain adaptive divergence among cod populations despite gene flow within the Skagerrak. The existence of locally adapted population within the western Skagerrak coast was supported as well as mixing with North Sea and Kattegat cod. While in the eastern Skagerrak (along the Swedish coast) absence of local populations was reported.
- Local adaptation of cod allowed by genome architecture (inversions) despite high levels of gene flow between North Sea and local fjord Skagerrak cod (Barth et al. 2017).

- Knutsen et al. (2018) developed a genetic tool consisting of 26 SNPs to explore mixing of the two genetically divergent cod ecotypes (fjord-type and North Sea-type) into the Skagerrak.
- Svedäng et al. (2019) suggested a possible recovery of the depleted local cod population along the Swedish Skagerrak coast
- Barth et al. (2019) reported mixing in a Norwegian Skagerrak fjord of cod belonging to three different populations, the North Sea, the western Baltic and a local population. Alongside chromosomal inversions maintaining adaptive divergence, tagging data suggested local cod and North Sea cod occupied different depths. Hence, behavioural barriers to gene flow alongside chromosomal inversion were suggested maintaining genetic divergence between North Sea cod and local fjordic cod in the Skagerrak.

Mismatch

The cod fishery in the Skagerrak is a mixed stock exploiting cod from genetically differentiated populations. The existence of local populations along the Norwegian Skagerrak coast and mixing of North Sea cod, Kattegat and local fjordic populations is supported by genetic evidence. In almost two decades of genetic investigations, spatio-temporal genetic studies suggested coexistence of two ecotypes (North Sea and fjordic ecotypes) within the Skagerrak, that urge assessment and management to take this information into account implementing mixed stock fishery measures. Management and assessment do not consider the presence of two genetically divergent cod ecotypes within the Skagerrak. Genetic (adaptive divergence) and phenotypic differences in growth and size were reported between these ecotypes, that may have different productivity and population size leading to the potential depletion of the weakest stock and possibly affecting population recovery. Hence, the necessity to take into account the two ecotypes to guarantee sustainable fisheries is reported. Moreover, the Skagerrak is well known as nursery areas for North Sea cod and during the last 20 years of genetic investigations, evidence showed mixing of North Sea cod and local fjord populations.

Summary of genetic evidence

Initially, Gjøsæter et al. (1992) found no differentiation at allozyme loci among samples collected in four fjords along the Norwegian Skagerrak coast.

Population structure at a fine scale was reported by Knutsen et al. (2003), that using 10 microsatellite loci detected significant differentiation among samples of Atlantic cod collected in the Norwegian Skagerrak coast. The presence of local coastal cod populations was suggested alongside the need of measures to protect spawning and nursery grounds at a finer scale.

The influence of North Sea cod larval drift into the Skagerrak mediated by ocean currents was investigated by Knutsen et al. (2004). Significant genetic differentiation was confirmed between adult cod from the North Sea and the Skagerrak and substructure was supported, indicating presence of local populations within the Skagerrak. Notably,

based on the strength of the North Sea water inflow into the Skagerrak, the proportion of North Sea cod juveniles changed. Juvenile samples collected in 2001 were mainly of North Sea origin while in 2000 were mostly of local Skagerrak origin and the inflow of North Sea waters was higher in 2001 than 2000, endorsing the drift of North Sea cod pelagic eggs and larvae into the Skagerrak. In line with previous studies, Jorde et al. (2007) using microsatellites found genetically differentiated populations along the Skagerrak coast. Moreover, it was shown that the geographic extension of these local populations is limited at 30 km or less and that Atlantic cod may be sedentary. Hence, in case of depletion of local coastal populations, migration of spawners from other fjords/coastal areas may be not sufficient for rebuilding stock. Therefore, the author suggested conservations and management measures should be implemented at a finer scale to protect local populations of Atlantic cod in coastal areas.

Combining genetic and capture-mark-recapture data, Knutsen et al. (2011) reported temporally stable population structure for Atlantic cod in the Norwegian Skagerrak. A total of 1287 individuals were analysed at 13 neutral microsatellite loci and highly significant genetic differentiation was detected between inner fjord and outer skerries samples (F_{ST}= 0.0037, P< 0.0001) and temporal analyses (over 10 years) supported the pattern found. In addition, capture-mark-recapture data confirmed inner fjord adults remain stationary within the fjord. The outer population in the skerries may represent a distinct local cod population receiving an influx of larvae and eggs from the North Sea cod or rather a segment of the North Sea cod population. Hence, despite the low level of differentiation found, population structure is biologically significant as confirmed by temporal analysis and tagging data. Management measures at a finer scale are required. These findings were confirmed also by SNP analysis. Sodeland et al. (2016) investigated cod population structure in the Skagerrak and North Sea using 9 187 SNP loci. Spatial genetic structure was reported with inner Skagerrak coast samples similar to each other and genetically differentiated from the outer coast and oceanic samples. Genomic regions of elevated differentiation were observed in linkage group 12 (between inner and oceanic samples and between outer and oceanic samples), in linkage group 2 (85 SNPs spanning 5 Mb) and in linkage group 7 (193 SNPs spanning 9.5 Mb). These regions of elevated differentiation are the results of chromosomal inversions that repressing recombination limit the exchanges between divergent alleles. Hence, these chromosomal inversions allow adaptive divergence to arise and persist despite gene flow. In Atlantic cod genetic differentiation between populations and ecotypes is limited to distinct regions of the genome, so called genomic islands of divergence (Bradbury et al. 2010; Hemmer-Hansen et al. 2013; Karlsen et al. 2013; Berg et al 2015). In previous studies, allelic clines for loci within linkage groups 2, 7 and 12 correlated with latitudinal and climatic gradients were observed on both sides of the Atlantic (Bradbury et al. 2010, 2013). Sodeland et al. (2016) showed three of these regions are maintained by chromosomal inversions. These chromosomal rearrangements involve a large number of

SNPs showing high divergence between inverted and non-inverted chromosomes. Hence, the pattern of population structure found by Sodeland et al. (2016) is due to natural selection on loci within these inversions.

André et al. (2016) through neutral microsatellites supported drift of eggs and larvae from the North Sea population into coastal Skagerrak and Kattegat. Juveniles collected along the Skagerrak coasts were genetically similar to the North Sea adult reference sample and differentiated from the local Skagerrak adults. It was also supported a drift of North Sea early life stages into the Kattegat. Notably, in this study the North Sea reference samples are from the central North Sea, presumably representing the Dogger cod unit.

Barth et al. (2017) using a population genomic approach (12K SNPs) confirmed local adaptation of cod in the Skagerrak is promoted by chromosomal inversions. Overall, genetic differentiation was reported between North Sea-English Channel-Skagerrak and the Kattegat-Western Baltic samples. Mixing of North Sea and Kattegat individuals was observed in eastern Skagerrak fjords receiving an influx of eggs and larvae from both regions. No local population was found in the eastern Skagerrak suggesting the loss of resident cod populations along the Skagerrak Swedish coast. Though, the presence of local fjord cod populations was supported in the western Skagerrak, genetically differentiated from both the North Sea and Baltic Sea cod. The North Sea and local fjord populations share the same environments and despite gene flow, local adaptation in fjordic cod is maintained through chromosomal inversions. Hence, Barth et al. (2017) findings supported presence of local populations of cod in western Skagerrak fjords and mechanical mixing of individuals from the North Sea and Kattegat-western Baltic in eastern Skagerrak fjords. The authors suggested the reported populations likely correspond to the coastal and oceanic ecotypes previously found along the Norwegian Skagerrak coast.

Knutsen et al. (2018) developed a genetic tool consisting of 26 highly differentiated SNPs to assign individuals back to the North Sea and local Skagerrak fjord ecotypes. This tool was used to assign 6483 individuals sampled across 15 regions along the Norwegian Skagerrak coast for over 14 years. The two divergent ecotypes were observed in similar proportions, although the fjord ecotype was found mainly in the inner part of the fjords and the North Sea ecotype mainly in offshore areas. Genetics and phenotypic differences in growth and size were reported between these two ecotypes. Management does not consider the presence of two genetically divergent cod ecotypes within the Skagerrak leading potentially to unstainable mixed stock fishery. Cod along the Norwegian Skagerrak coast is managed with cod along the Norwegian coast up to 62°N. Ignoring substructure precludes sustainable fisheries. These ecotypes may have different productivity and population size leading to potential depletion of the weakest stock and potentially affecting population recovery. Similarly, assessment does not take into account the existence of fjord populations along the Skagerrak.

Using a SNP panel Svedäng et al. (2019) suggested a possible recovery of the depleted local cod population along the Swedish Skagerrak coast. In fact, the presence of cod eggs that were genetically similar to the local adult cod population and differentiated from North Sea cod was reported. Though, genetic similarity was indicated between the local Swedish Skagerrak cod population and the Kattegat and the Sound supporting connectivity between these regions in the transition area.

In a Norwegian Skagerrak fjord Barth et al. (2019) reported mixing of cod belonging to three different populations, namely the North Sea, the western Baltic and a local cod population. Although, the overall genetic differentiation among populations was weak, highly differentiated genomic regions were identified involving three chromosomal inversions. Tagging evidence (behavioural tracking) indicated temporally stable presence of these populations within the fjord. The authors reported individuals from the local population and North Sea cod are distributed at different depths representing a possible behavioural barrier to gene flow. Hence, alongside chromosomal inversions maintaining adaptive divergence between North Sea and local cod populations, segregation by depth may play a role representing a prezygotic barrier to gene flow.

7.7 Cod in the Baltic Sea and Kattegat

Current management status

Cod in the Baltic Sea is evaluated as two stock assessment units by ICES since 2003: western Baltic cod in subdivisions 22-24 and eastern Baltic cod in subdivisions 24-32 and a separate unit exists for cod in the Kattegat (ICES, 2020). Genetics, tagging and phenotypic evidence supports these stocks (ICES, 2019 and references therein). Furthermore, tagging evidence showed mixing of western and eastern cod in the Arkona Basin (Subdivision 24), confirmed also by genetics and otolith shape analysis. Therefore, since 2015 in subdivision 24 stock assessment is carried out for both stocks and the proportion of landings is assigned to the correct stock according to genetic and otolith shape analyses. In the Baltic Sea, there is a minimum conservation reference size of 35 cm and fish below minimum size (BMS) cannot be sold for human consumption (ICES 2020b).

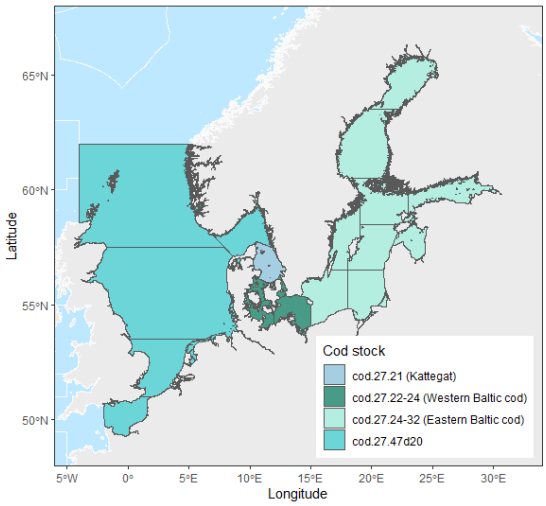


Figure 7.7. Atlantic cod ICES stock assessment units in the Baltic Sea, Kattegat and North Sea.

The main spawning season of Western Baltic cod goes from January to March. Eggs are pelagic and are transported by currents. Though, egg exchange between the western and eastern basin is limited by water salinity for neutral buoyancy: the water salinity range in the eastern Baltic Sea is not favourable for western Baltic cod eggs. Western Baltic cod landings in 2019 were 7 701 t (ICES 2020b). Catches of Western Baltic cod are mainly from the Belt Sea (subdivision 22) and the Arkona Basin (subdivision 24) (ICES 2020b). Landings from recreational fishery accounted for the 28% of the total catches and are included in stock assessment (ICES 2020b). The 36% of the total landings were from subdivision 24, although ICES reported usually landings from this subdivision amount at the half of the catches. This decrease is due to the temporary closure of the subdivision to direct cod fishery in quarter three and four of 2019 in order to protect the more vulnerable eastern Baltic cod stock.

Cod in the eastern Baltic Sea is adapted to the low salinity of the basin - e.g., egg buoyancy is reached at lower salinities (ICES, 2019b; and references therein). Spawning is restricted to deeper waters and spawning season extends from February-March to October with a peak in April-May (ICES, 2019b; and references therein). In the eastern Baltic, directed cod fishery in the early 1980s landed 350-400 000 t (ICES 2020b). However, as reported by ICES the stock declined due to a combination of poor environmental conditions, intense

fishing effort, reduced growth and high natural mortality. A decreasing in size at maturation is reported by ICES and the biomass of cod ≥35 cm is at the lowest historical level (ICES 2020b). The Eastern Baltic cod is found mainly in the Southern central Baltic (subdivisions 25 and 26) and in the eastern part of the Arkona Basin, subdivision shared with the western Baltic cod (ICES 2020b). Mixing is reported also in subdivision 25 in quarter four when large aggregations of western Baltic cod juveniles are found. The 16% of the landings in 2019 were from subdivision 24 (ICES 2020b). Total catches in 2019 were 11 938 t, almost the 50% of landings in 2018 (ICES 2020b). In order to reduce fishing pressure on this stock, the European Commission closed direct cod fishery in quarter three and four in 2019 (ICES 2020b). Overall, the spawning stock biomass is declining, fishing mortality is at the lowest level and the size at maturation is decreasing. ICES advise was of zero catches in 2020 and 2021 in all the eastern Baltic Sea subdivisions including subdivision 24 (ICES 2020b).

In the Kattegat, considered a separate stock both in assessment and management, cod is mainly fished as bycatch in the *Nephrops* fishery (ICES 2020b). Landings were 84 t in 2019 and Denmark is the main fishing country. Fishing pressure on this stock is highly dependent on fishing effort directed to *Nephrops.* ICES highly recommended the use of measures and devices to reduce bycatches of cod and allow the recovery of the cod stock in the Kattegat (ICES 2020b). The spawning stock biomass was at an historical low level in 2020 and fishing mortality is increasing. ICES advised zero catches for 2021. Moreover, ICES is aware of genetic investigations indicating the occurrence of North Sea cod in the Kattegat and that local Kattegat cod may be present in the Skagerrak (ICES 2017c).

Genetic population structure in a nutshell

Several studies investigated genetic population structure of cod within the Baltic Sea and adjacent waters through different genetic markers. Cod is structuring in the Baltic Sea and information on genetic structure are considered in the designation of the stock units. Moreover, an area of mixing exists, the Arkona Basin, and genetics has been used in conjunction with otolith shape analysis to estimate the proportion of individuals form the Western and Eastern Baltic cod stocks (Hüssy et al. 2016). A genetic tool to distinguish between fish of North Sea origin and Kattegat local cod (Hemmer-Hansen et al. 2020) also exists. In particular, genetic evidence supports:

- Divergence of the Baltic Sea cod from the other NE Atlantic cod populations (e.g. Mork et al., 1985; Nielsen et al., 2003; O'Leary et al., 2007)
- A hybrid zone in the Baltic Sea-North Sea transition zone (Nielsen et al. 2003)
- Presence of juveniles of local origin was reported in the transition zone (Nielsen et al. 2005)
- Divergence between the North Sea and Baltic Sea cod (e.g. Nielsen et al., 2009b, 2005, 2003; Pampoulie et al., 2008; Poulsen et al., 2006)
- Adaptive divergence between North Sea and Baltic Sea cod was supported by SNPs (Nielsen et al. 2009a),

- Differentiation eastern and western Baltic cod (Kijewska et al. 2011)
- Gene expression analysis suggested local adaptation to salinity in Baltic Sea cod (Larsen et al. 2012) and genomic signatures of local adaptation were found also through a population genomic approach (Berg et al. 2015)
- Through a population genomic approach the existence of four genetically differentiated cod populations, the North Sea, Baltic Sea (eastern Baltic), Kattegat and the Sound (western Baltic) was detected (Berg et al. 2015)
- Using SNP-arrays, Poćwierz-Kotus et al. (2014) confirmed substructure within the Baltic Sea, supporting the existence of two genetically divergent populations the western and eastern Baltic cod.
- Transcriptome analysis of gill tissue of Baltic Sea cod confirmed significant differences with Atlantic cod transcriptome
- Mixing between the eastern and western Baltic Sea cod stocks was supported in Arkona Basin (Hüssy et al. 2016), otolith shape analysis and SNPs are valuable tools for the assignment of individuals in mixed stock fishery to the correct cod stock within the Baltic Sea.
- Mechanical mixing between the eastern and western Baltic cod populations was supported and a genetic tool consisting of 39 SNPs was developed to investigate spatio-temporal trends in their mixing (Hemmer-Hansen et al. 2019).
- A genetic tool was developed to study mixing of North Sea and local Kattegat cod within the Kattegat (Hemmer-Hansen et al. 2020); a greater contribution of North Sea individuals was observed among younger fish, while adult spawning individuals were of local Kattegat cod origin; the contribution of North Sea cod individuals was larger in the northern part of the Kattegat and lower in the southern.
- Weist et al. (2019) identified and validated a SNP panel of 20 highly discriminatory loci to assign back individuals to the western and eastern Baltic Sea cod stocks and a second panel of 38 loci to investigate local adaptation of cod in the Baltic Sea.
- Wenne et al. (2020) confirmed divergence between western and eastern Baltic cod stocks, though, substructure within the eastern Baltic cod stock was reported and further studies are needed to confirm it.

Mismatch

The genetic structure of cod in the Baltic Sea is taken into account in assessment and management. Mixing between the eastern and western population have been shown in the central Baltic subdivisions (mainly in the Arkona Basin) and a genetic tool is used alongside otolith shape analysis to estimate the proportions in landings of eastern and western Baltic Sea cod. This information is taken into account in stock assessment: catches from subdivision 24 are split between Eastern and Western Baltic cod stocks based on that tool. In the Kattegat, a local population is present and separate stock assessment and management units exist for Kattegat cod. Though, the basin represents also a nursery area for North Sea cod.

Summary of genetic evidence

The genetic differentiation of cod in the Baltic Sea from the other NE Atlantic populations is supported by the mean of different genetic methods, comprising microsatellites (e.g. O'Leary et al., 2007) Pampoulie et al. (2008), SNPs and gene expression investigations.

Initially, Mork et al. (1985) using allozymes, reported low levels of differentiation for cod across the Atlantic, though the Baltic Sea sample was the most genetically divergent, suggesting geographic or environmental barriers promoting genetic isolation of cod in the Baltic Sea.

In 2001, Nielsen et al. published the first study in which using microsatellites individuals of a marine fish species, Atlantic cod, were assigned back to their population of origin, namely the North Sea, the Baltic Sea and the North-east Arctic cod populations.

Nielsen et al. (2003) reported genetic divergence between the North Sea and the Baltic Sea cod and the presence of a hybrid zone in the transition area: divergence between North Sea and Baltic Sea samples increased along a transect, towards the Baltic proper.

Successively, genetic population structure of juveniles of Atlantic cod in the North Sea-Baltic Sea transition zone was analysed throughout microsatellite loci by Nielsen et al. (2005). Weak, but statistically significant, genetic differentiation among samples was reported (F_{ST}= 0.003), and juvenile samples clustered with adult samples from the same location. Moreover, the existence of juveniles of local origin in the transition zone was reported.

Poulsen et al. (2006) analysing archived and contemporary samples confirmed genetic differentiation between the two regions. Despite the levels of exploitation of the North Sea and the Baltic Sea cod stocks, no evidence of loss of genetic diversity was observed.

Nielsen et al. (2006) pointed out the presence of a microsatellite locus (Gmo 132), often used in Atlantic cod population genetic studies, subject to hitch-hiking selection and possibly inflating estimates of genetic differentiation. O'Leary et al. (2007) using microsatellites confirmed the genetic differentiation of the Baltic Sea cod respect to other cod populations in the NE and western Atlantic.

The genetic differentiation between North Sea and Baltic Sea cod was supported also by Pampoulie et al. (2008), that ascribed it to the diverse environmental conditions possibly acting as barrier to gene flow between the two populations.

Nielsen et al. (2009b) confirmed the genetic divergence of Baltic Sea cod, that both with neutral and under selection microsatellite loci, was clearly differentiated from the North Sea and the rest of the NE Atlantic cod samples. The first study using SNPs to investigate population structure of cod within the NE Atlantic was published by Nielsen et al. in 2009. Genomic signatures of local adaptation and loci under selection correlated with spawning grounds and spawning season temperatures were reported. Four loci under selection were detected in the North Sea and Baltic Sea cod populations, supporting local adaptation to these environmentally different basins.

Possible substructure within the Baltic Sea was indicated by Kijewska et al. (2011), that found strong differentiation between the eastern and western Baltic cod samples, and confirmed influences of North Sea cod individuals within the transition zone.
However, Stroganov et al. (2013) did not detect significant differentiation between eastern and western Baltic Sea cod at six allozymes. This lack of differentiation can be ascribed to the low resolution of allozymic markers.
Likewise, the gene expression analysis conducted by Larsen et al. (2012) suggested local adaptation to salinity in Baltic Sea cod. Larsen et al. (2012) through a common garden experiment showed that the Baltic Sea and North Sea cod individuals have differences in salinity tolerance as well as in gene expression responses to salinity stress.
In line with previous studies, Berg et al. (2015) using a population genomic approach confirmed adaptation to salinity promoting genetic divergence in cod populations. Using only neutral SNPs three genetically divergent groups were identified, namely the North Sea, the eastern Baltic Sea and the transition zone (including the Kattegat and the Sound samples). However, outlier loci allowed the detection of genetic differentiation also between the Kattegat and the Sound in line with current assessment and management units. Genomic signatures of local adaptation were found in cod genomes. Allele frequencies of outlier loci correlated to environmental differences in salinity, oxygen and temperature. Moreover, discrete regions of cod genome were highly differentiated indicating the presence of genomic islands of divergence. Notably, most of the loci under selection were in genes involved in egg buoyancy and osmoregulation responses, extremely important traits in adaptation to the low salinity of the Baltic Sea. The existence of two genetically divergent populations the western and eastern Baltic cod was confirmed also by Poćwierz-Kotus et al. (2014) that using a SNP-arrays, supported substructure within the Baltic Sea.
The transcriptome analysis of gill tissue of Baltic Sea cod conducted by Małachowicz et al. (2015) confirmed differences with Atlantic cod gill tissue transcriptome. Moreover, the stress responses of eastern and western Baltic cod to different salinities was studied by Kijewska et al. (2016) through gene expression analyses that supported the adaptation of eastern and western cod to lower and higher salinity, respectively. In line with previous studies, salinity was identified as a factor shaping and maintaining population structure of cod within the Baltic Sea.
The occurrence of mixing between the two Baltic Sea stocks in Arkona Basin was supported by Hüssy et al. (2016) that investigated the applicability of otolith shape analysis and SNPs for assignment of individuals from mixed stock fishery in the Baltic Sea to the correct Eastern or Western Baltic cod stock. Hence, the eastern and western Baltic cod stocks are fished in a mixed-stock fishery in certain Baltic Sea subdivisions.
Hemmer-Hansen et al. (2019) supported mechanical mixing between the two genetically different eastern and western Baltic cod populations. A genetic tool consisting of 39 SNPs was developed to investigate spatio-temporal trends in their mixing. Their distribution relatively matches with the current stock assessment units in use, that account for mixing

in the Arkona Basin (subdivision 24), confirming the valuable contribution of genetics (genetic as a tool for complex fisheries management) genetically assisted fisheries monitoring.

The interaction of different cod populations within the Kattegat was explored by Hemmer-Hansen et al. (2020) that developed a genetic tool to study mixing in this region. Genetic analyses supported the presence of local Kattegat and North Sea cod individuals within the basin. In fact, early life stages, eggs and larvae, of North Sea cod are transported towards the Kattegat throughout water inflow of North Sea origin. Hence, also the Kattegat represents a nursey area for North Sea cod individuals that once reached maturity migrate back to the North Sea. As genetic evidence supports, local spawning individuals collected in the southern Kattegat are fish of local origin. Moreover, a gradient, with a higher contribution of North Sea cod in the northern Kattegat and lower in the southern was reported, as well as higher proportion of North Sea cod individuals among younger fish.

Weist et al. (2019) identified and validated two SNP panels to explore populations structure of cod within the Baltic Sea. A SNP panel of 20 highly discriminatory loci was developed to assign back individuals to the western and eastern Baltic Sea cod stocks. While a second panel of SNPs (38 loci) was developed to investigate local adaptation of cod in the Baltic Sea. Genetic divergence at loci involved in candidate genes was found, confirming local adaptation even at a small scale within the Baltic Sea. The genetic divergence between eastern and western Baltic cod was confirmed, in line with previous studies and assessment and management units, as well as the mixing of the two populations in subdivision 24.

Wenne et al. (2020) confirmed the genetic differentiation between western and eastern Baltic cod stocks. Though, substructure within the eastern Baltic cod stock was reported, explained by possible environmental barriers to gene flow between two spawning areas within subdivision 26, the Gdansk Deep and Gotland Basin. Further studies are needed to confirm these findings, including temporal analysis to explore if the differentiation found is temporally stable and significant.

7.8 Cod in west of Scotland, Rockall, Irish Sea and Celtic Seas

Current management status

Cod in west of Scotland (Division 6.a) is assessed as a stock unit by ICES, however includes multiple subunits. ICES is aware of the presence of substructure within the area (ICES 2020t), as well as of the connectivity between the southern population and the Irish Sea, and of the lack of genetic differentiation between cod in the north West of Scotland and in the Shetlands (Division 4.a) (ICES 2020t). Cod in west of Scotland is fished as a bycatch species. Catches are mainly from the northern part of the division and landings in 2019 were 1 286 t, the majority from UK vessels (ICES 2020t). The TAC is set for division 6.a and Union and International waters of 5.b east of 12°00' W, and does not match with the assessment unit. No directed fisheries for cod are allowed under this quota. The TAC in 2020 was set to 1 279 t and cod can be fished exclusively as bycatch species (ICES 2020t). The existence of multiple populations within this ICES stock unit and the connectivity between west of Scotland and northern North Sea will be addressed in a future benchmark, when ICES will evaluate the merging of northern North Sea and West of Scotland divisions and the possible split of division 6.a in a northern and southern cod stock (ICES 2020t).

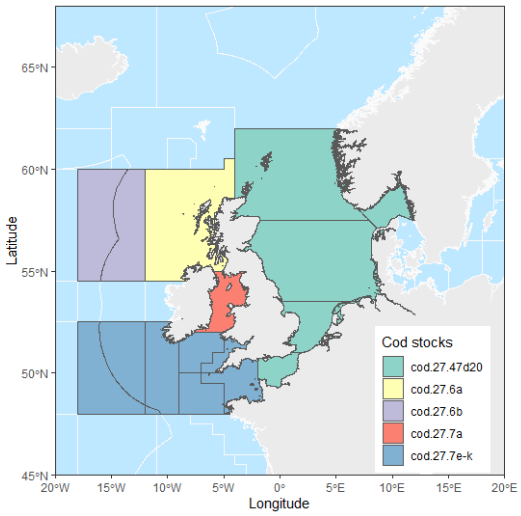


Figure 7.8. Atlantic cod ICES stock assessment units in West of Scotland (division 6.a), Rockall (6.b), Irish Sea (7.a) and Celtic Seas (divisions 7.e-k).

Cod in the Rockall (Division 6.b) is assessed in a separate stock unit. In the Rockall cod is mainly fished as a bycatch species in fisheries targeting other demersal species as haddock and anglerfish (ICES 2020t). Total landing in 2019 were 66.4 t (ICES 2020t). It is a data limited stock and following a precautionary approach ICES advises no more than 14 t for 2021-23 (ICES 2020t). Data from catches and survey are extremely limited and insufficient to be used in stock assessment (ICES 2020t). The TAC is set for a management unit that does not match the stock unit used in assessment, including division 6.b, Union and International waters of 5.b west of 12°00' W and subareas 12 and 14.

Cod in the Irish Sea (Division 7.a) is assessed as a separate stock unit, in line with the management unit set for cod in the Irish Sea (Division 7.a). Landings in 2019 were 334.4 t (ICES 2020t). After the establishment of the cod recovery plan in 2002, the successive closure of all fisheries targeting cod in 2003 and the ICES advice of zero catch for 2004-12, ICES advice in 2018-19 was based on the MSY approach (ICES 2020t). A precautionary

TAC of 257 t was set for 2020, however no directed fisheries are allowed under this quota and cod can only be taken as bycatch (ICES 2020t). ICES is aware of a lack of evidence supporting the presence of different populations in the Irish Sea and adjacent waters. As highlighted in the stock annex further studies are needed to unravel stock structure of cod in the Irish Sea and explore potential mixing with neighbour areas. Recent tagging evidence suggests migrations of mature cod towards the Celtic Sea, but more investigations are required for evaluating impacts on assessment and management (ICES 2017a).

Cod in the Celtic Sea (Divisions 7.e-k) is assessed as a stock unit. The mixing of cod from 7.e-k and adjacent areas is minimal although migration of mature individuals from the Irish Sea (Division 7.a) in divisions 7.e-g was showed by a recent tagging investigation (ICES, 2020; and references therein). In the Celtic Sea cod is a bycatch in mixed demersal fisheries and fisheries targeting haddock, whiting and *Nephrops* (ICES 2020t). Reported catches for 2019 were 1 351 t, and the main fishing country is Ireland. Catches are mainly from subdivision 7.g, 7.h, 7.e, 7.j (ICES 2020t). Based on the MSY approach ICES advise zero catch in 2020 (ICES 2020t). Although the management unit for which the TAC is set includes division 7.b-c, and subareas 8, 9 and 10 and Union waters of CECAF 34.1.1, catches outside divisions 7.e-k are minimal (ICES 2020t). No directed fisheries are permitted and cod can be fished only as bycatch species in the Celtic Seas.

Genetic population structure in a nutshell

The available information on genetic population structure confirms cod populations in this area are genetically differentiated from the adjacent Faroese, Icelandic, Baltic and Norwegian coastal and NE Arctic stocks. In particular, genetic evidence supports:

- Irish sea differentiated from north Norway (Galvin et al. 1995b).
- Gene flow between southern North Sea and eastern English Channel. Though the western English Channel is genetically differentiated, a lack of differentiation was reported for cod in the Celtic Sea-Irish Sea that were however differentiated from the Outer Hebrides (Hutchinson et al. 2001).
- The divergence of the Celtic Sea and the North Sea was confirmed by Jónsdóttir et al. (2003)
- O'Leary et al. (2007) supported cod in the Celtic Sea is genetically differentiated from the rest of the NE Atlantic samples.
- The existence of a temporally stable population in the Celtic Sea was confirmed, differentiated from the North Sea and the rest of the NE Atlantic samples (Pampoulie et al. 2008b).
- Mixing in the Irish Sea of cod from adjacent stocks was reported (Pampoulie et al. 2008b).
- Genetic differentiation between the Scottish samples (Moray Firth, Shetland and west of Scotland) and the central North Sea with Viking Bank samples was supported by microsatellites (Nielsen et al. 2009b).

- Bradbury et al. (2010) using a genome-scan approach reported the presence of loci showing parallel clines in NE and western Atlantic and transition in allele frequencies between Iceland and Ireland.
- The central North Sea and the eastern English Channel samples part of the same genetic unit (Hemmer-Hansen et al. 2014)
- The presence of a cod population in the Celtic Sea extending from the western English Channel, throughout the Celtic Sea, the Irish Sea and the southern part of division 6.a (west of Scotland) was reported by SNPs (Heath et al. 2014) .
- Mixing in West of Scotland (division 6.a) of individuals belonging to the Dogger unit and the Celtic unit, found in the northern and southern part of the division, respectively.
- No significant genetic differentiation was found between the English Channel and the North Sea samples based on SNPs outside rearranged regions of cod genome (Barth et al. 2017). However, different distribution of allele frequencies at SNPs within linkage group 12 was reported.
- Lack of mitochondrial genetic divergence within the NE Atlantic (Jørgensen et al. 2018).
- The existence of reproductively isolated cod populations in the Viking Bank (eastern division 4.a) and northwest North Sea and west of Scotland was supported (Wright et al. 2021).

Mismatch

Mismatches exist between genetic, assessment and management units for cod in these divisions.

Cod from southern West of Scotland (division 6.a), the Irish Sea, Celtic Sea and western English Channel is part of the same genetic unit based on SNPs. However, separate assessment and management units exist for the Irish Sea, west of Scotland and Celtic Seas, mismatching with the presence of one population in these divisions. Moreover, the west of Scotland unit is not biologically meaningful due to the observation of cod from the Celtic Sea population in the southern part of the division and cod from the North Sea (Dogger unit) in the northern part. This information should be taken into account to design more realistic stock units.

Summary of genetic evidence

In a preliminary study using minisatellite analysis to investigate population structure in Atlantic cod, Galvin et al. (1995) reported genetic divergence between eastern and western Atlantic samples and between the Irish Sea and northern Norway at a minisatellite locus. Hutchinson et al. (2001) using microsatellites to analyse mature samples collected at spawning grounds indicated the presence of different cod populations around the British Isles. The western English Channel was genetically differentiated from the North Sea populations, Celtic Sea and Outer Hebrides. No substructure was found within the Celtic Sea-Irish Sea samples that were genetically

differentiated from the Outer Hebrides. Jónsdóttir et al. (2003) using restriction fragment length polymorphism analysis of nuclear DNA reported genetic differentiation between eastern and western Atlantic cod populations, and divergence of the Celtic Sea from other samples, including the North Sea. O'Leary et al. (2007) using microsatellites to investigate population structure of cod in its distributional range, supported a pattern of isolation by distance. Moreover, cod in the Celtic Sea was genetically differentiated from the rest of the NE Atlantic samples.

In line with earlier findings, Pampoulie et al. (2008) reported a temporally stable population in the Celtic Sea, differentiated from the North Sea and the rest of the NE Atlantic samples (Iceland, Faroe Islands, Baltic Sea). While, a complex population structure was suggested for cod in the Irish Sea, exposed to migration with cod from adjacent stocks.

Interestingly, Nielsen et al. (2009b) detected microgeographical population structure for cod with the inclusion of a microsatellite locus under selection (Gmo 132), supporting the genetic differentiation between the Scottish samples (Moray Firth, Shetland and west of Scotland) and the central North Sea and Viking Bank samples.

Successively, Bradbury et al. (2010) using a genome-scan approach reported the presence of loci showing parallel clines in NE and western Atlantic with a clear transition in allele frequencies between Iceland and Ireland, associated with average annual bottom temperature.

Hemmer-Hansen et al. (2014) using a combination of neutral SNPs and loci associated with life-history trait candidate genes described adaptive variation in Atlantic cod populations in the NE Atlantic. The use of outlier markers allowed detection of population structure at a finer scale: a genetic unit was identified comprising the central North Sea and the eastern English Channel samples.

Heath et al. (2014) using a SNP panel of 96 loci identified three populations around the British Isles, two in the North Sea (namely, the Viking cod restricted to the northern North Sea and the Dogger cod widely distributed in the basin) and one in the Celtic Sea extending from the western English Channel, throughout the Celtic Sea, the Irish Sea and the southern part of division 6.a (west of Scotland). The lack of differentiation between the western Channel, the Celtic Sea, the Irish Sea and the southern part of West of Scotland division (Firth of Clyde) does not support their assessment/management in separate units. Moreover, in division 6.a (West of Scotland) individuals belonging to the Dogger and the Celtic units were found in the northern and southern part of the division, respectively.

Local adaptation of cod allowed by genome architecture (chromosomal inversions) despite high levels of gene flow was reported by Barth et al. (2017). No significant genetic differentiation was found between the English Channel and the North Sea samples based on SNPs outside rearranged regions of cod genome. However, different distribution of allele frequencies at SNPs within linkage group 12 was reported. Genes under selection involved in adaptation to local environmental conditions reside in rearranged regions of cod genome. These findings suggest that despite high levels of gene flow, as shown by

neutral loci, adaptive divergence is maintained in locally adapted cod populations by chromosomal inversions preventing recombination.

Jørgensen et al. (2018) analysed mitogenome sequence variation of cod from both sides of the North Atlantic, including samples from the British Isles and the Irish Sea. Genetic differentiation was reported between eastern and western Atlantic, though a lack of divergence within the NE and western Atlantic samples, suggesting high levels of gene flow despite the known genetic divergence between cod ecotypes (coastal and migratory) at rearranged chromosomal regions.

Fine and temporally stable population structure was reported by Wright et al. (2021), that used a combination of SNPs and phenotypic traits and an exhaustive sampling design, including samples of cod from both spawning and feeding season. The existence of reproductively isolated populations in Viking bank (eastern division 4.a) and north-western North Sea and west of Scotland was supported. Wright et al. (2021) reported also a lack of differentiation among samples collected in the western part of the northern North Sea (western division 4.a) and west of Scotland (division 6.a). Moreover, a pattern of isolation by distance with a west-east gradient of differentiation was described. Based on these findings, the authors suggested that a shift at 1°W of the current stock boundary would be more biologically meaningful and reflect population structure of cod in this part of its range.

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)
Brill	NE Atlantic, Med	Kat (1), NS (1), EC (1), PRT (1), Med (2)	6 (117)	na	na	na	All (10)	No	Type I	Type I		(Blanquer et al. 1992)
	NE Atlantic	NS (3), NBTZ (3), EC (2), BI (5), BOB (1), w SPN (1)	23 (879)^{8}	na	na	na	Msat (14)	No	Type I	Type I	LG	(Vandamme 2014)

Dab	NE Atlantic	NS (4), EC (2), IS (7), Atlantic (2)	39 (3006) *	y	y	Ad	Msat (14) [N]	Yes	no	na		(Tysklind et al. 2013)
	NE Atlantic	NS (1), NBTZ (3), BAL (2)	6 (148)	y	na	na	SNPs (3468) [S]	Yes	Type II	na	LG, LA	(Le Moan et al. 2019a)
Four-spot megrim	NE Atlantic, Med	IRE (1), BOB (3), PRT (1), Med (1)	6 (198)	na	na	Ad	Msat (7)	Yes	no	Type II	LG	(Danancher & Garcia-Vazquez 2009)
	NE Atlantic, Med	IRE (1), BOB (2), PRT (1), Med (1)	5 (163)	na	na	Ad	CR (438 bp)	Yes	Type I	Type II	LG	(Campo & Garcia-Vazquez 2010)
Megrim	NE Atlantic, Med	w SCO (1), EC (1), BOB (2), PRT (1), Med (1)	6 (303)	na	na	Ad	mtDNA (16S); nDNA (5S)	Yes	Type I	Type I		(Garcia-Vazquez et al. 2006)
	NE Atlantic, Med	w SCO (1), CS (2), BOB (2), PRT (1), Med (1)	7 (191)	na	na	Ad	Msat (6)	Yes	Type II	Type II	LG	(Danancher & Garcia-Vazquez 2009)
	NE Atlantic	Roc (3), NS (3), w SCO (3)	9 (270)	y	na	Ad	Msat (6); mtDNA (1)	Yes	Type II	Type II	LG	(Macdonald & Prieto)
Flounder	NE Atlantic, Med	UK (3), Belt (1), ADR (2), BLS (2)	7 (270)	na	na	Ad, juv	All (38)	Yes	Type I	na		(Galleguillos & Ward 1982)
	NE Atlantic, Med	NS (4), BAL (2), Kat (1), BOB (2), PRT (5), Med (4)	18 (796)	y	na	Ad	All (8), mtDNA (RFLP)	Yes	Type I	na	LG	(Borsa et al. 1997)
	NE Atlantic	FRO (1), NOR (2), NS (4), IS (1), BAL (5), BOB (1)	22 (1062) [9]	y	y	Ad, juv	Msat (9)	Yes	Type I	na	LG	(Hemmer-Hansen et al. 2007b)
	NE Atlantic	FRO (1), NOR (2), NS (3), IS (1), BAL(4), BOB (1)	20 (809) [8]	y	y	Ad, juv	Msat (9)[N]; *Hsc70* [S]	Yes	Type I [N]	na	LA, LG	(Hemmer-Hansen et al. 2007a)
	NE Atlantic	NS (1), Ska (1), Kat (1), NBTZ (1), BAL (16)	20 (960)	y	y	Ad	Msat (7)	Yes	Type I	na	LG	(Florin & Höglund 2008)

	NE Atlantic	ENG (1), FRA (3), PRT (1)	5 (250)	no	na	Ad, juv	Msat (8); COI (689 bp); candidate gene [S]	Yes	na	na	LG	(Calvès et al. 2013)
	NE Atlantic	NS (2), NBTZ (1), BAL (10)	13 (282)	Y	y	Ad	SNPs (2051) [S]	Yes	Type I	na	LA, LG	(Momigliano et al. 2017)
	NE Atlantic	BAL (4)	4 (69)	y	y	Ad	SNPs (5861) [S]	Yes	Type I	na	LA, MSA	(Momigliano et al. 2018)
	NE Atlantic	NOR (1), BAL (2), NS (1), BOB (1), Gal (1), PRT (1)	7 (318)	na	na	Ad	Msat (12)	Yes	Type I	na	LG	(Reis-Santos et al. 2018)
	NE Atlantic	BAL (2)	21 (444) [19 H]	na	na	Ad	SNPs (5) [S]	Yes	Type II	na	LA, MSA	(Momigliano et al. 2019)
	NE Atlantic	NS (1), NBTZ (3), BAL (4)	8 (214)	y	na	na	SNPs (5472) [S]	Yes	na	na	LA, LG	(Le Moan et al. 2019a)
Plaice	NE Atlantic	NS (4), ICE (1), FRO (1), NOR (2), BOB (1), IS (1), Belt (1)	11 (480)	Y	Y	Ad, juv	Msat (6)	Yes	Type I	Type I, II	LG	(Hoarau et al. 2002)
	NE Atlantic	IS (6), NS (2)	8 (109)	na	no	juv	Msat (8)	No	na	na		(Watts et al. 2004)
	NE Atlantic	NS (3), IS (1), FRO (1), ICE (1), NOR (2), Belt (1), B0B (1), w SCO (1)	11 (480)	Y	y	Ad, juv	CR (150 bp)	Yes	Type I	Type I, II	LG	(Hoarau et al. 2004)
	NE Atlantic	IS (4), BAL (1), ICE (1)	7 (348) [1]	y	y	Ad	Msat (8)	Yes	Type I	Type I, II	LG	(Was et al. 2010)
	NE Atlantic	SCO (12), IS (14)	38 (864) [12]	no	no	Juv	Msat (9)	Yes	na	Type I	LG	(Watts et al. 2010)
	NE Atlantic	NS (1), Ska (2), Kat (1), Baltic (2)	6 (118)	y	y	Ad	SNPs (5605)	Yes	Type II	no		(Ulrich et al. 2017)
	NE Atlantic	NS (1), Ska (1), NBTZ (3), BAL (2)	7 (180)	y	y	Ad	SNPs (6685) [S]	Yes	na	na	LA, LG	(Le Moan et al. 2019a)
	NE Atlantic	ICE (1), BS (1), NOR (1), NS (1),	7 (234)	y	y	Ad	SNPs (3019) [S]	Yes	no	Type II	LA, LG	(Le Moan et al. 2020)

		Kat (1), Belt (1), BAL (1)										
Sole	NE Atlantic, Med	EC (2), BOB (4), w Med (6), e Med (2)	26 (1251) [12]	y	y	Ad, juv	All (8)	Yes	Type I	Type I	LG	(Kotoulas et al. 1995)
	NE Atlantic, Med	IS (3), NS (2), BOB (1), Med (1)	7 (303)	no	no	Ad, juv	All (27)	Yes	Type I	Type I	LG	(Exadactylos et al. 1998)
	Med	Adr (5), Ion (2), Thy (2)	9 (209)	no	no	Ad	CR (283 bp)	Yes	Type II	Type II		(Guarniero et al. 2002)
	NE Atlantic	IS (3), NS (2), BOB (1)	6 (96)	no	no	Ad, juv	RAPD (37)	Yes	Type I, II	Type I, II	LG	(Exadactylos et al. 2003)
	NE Atlantic, Med	Kat (1), EC (1), BOB (8), PRT (1), Adr (1), Aeg (1), w Med (1)	24 (749) [10]	na	na	Juv	EPIC (3)	Yes	Type I	Type I	LG	(Rolland et al. 2007)
	Med	Adr (2), Thy (1), e Med (1)	4 (172)	n	n	n	Msat (15) [N], AFLP [N]	Yes	no	no	LG	(Garoia et al. 2007)
	NE Atlantic	BOB (4)	11 (330) [7]	n	n	Ad	EPIC (3)	No	no	no	LA	(Guinand et al. 2008)
	NE Atlantic	NS (6)	25 (1159) [19,H]	y	y	Ad, juv	Msat (11)	No	no	no		(Cuveliers et al. 2011)
	Med	w Med (2), TUN (7), e Med (2)	11 (374)	na	na	na	All (7)	Yes	na	na	LG	(Bahri-Sfar et al. 2011)
	NE Atlantic	NS (5), Ska (1), Kat (2), Belt (1), CS (1), IS (1), EC (2), BOB (3)	28 (1579) [12]	y	y	Ad, juv	Msat (10)[N], cyt-b (590 bp) [N]	Yes	Type I	Type I	LG	(Cuveliers et al. 2012)
	NE Atlantic	NS (5), IS (1), CS (1), NBTZ (3), EC (2), BOB (3), PRT (2)	17 (539)	y	y	Ad, juv	SNPs (539) [S]	Yes	Type I	Type I	LA, LG	(Diopere et al. 2018)
	Med	Adr (6)	6 (184)	no	no	Ad, juv	cyt b (624bp)	Yes	Type II	Type II		(Sabatini et al. 2018)

	NE Atlantic	NS (2), NBTZ (3), BAL (1)	6 (131)	y	y	Ad	SNPs (3714) [S]	Yes	no	no	LG	(Le Moan et al. 2019b)
Turbot	NE Atlantic, Med	NS (2), EC (1), Kat (1), BOB (1), PRT (1), MOR (1), Med (3)	10 (179)	na	na	na	All (6)	Yes	Type I	Type I		(Blanquer et al. 1992)
	NE Atlantic	Gal (3), farm (8)	11 (366)	na	na	na	All (14)	No	na	na		(Bouza et al. 1997)
	NE Atlantic	NOR (1), IRE (1), farm (2)	4 (195)	na	na	na	Msat (3)	Yes	na	na		(Coughlan et al. 1998)
	NE Atlantic	Gal (2), farm (1)	3 (149)	na	na	na	All (17), Msat (12)	No	na	na		(Bouza et al. 2002)
	NE Atlantic	NS (1), NBTZ (4), BAL (2), BOB (1)	16 (706)[8]	y	y	Ad	Msat (8)	Yes	Type I, II	Type I	LG	(Nielsen et al. 2004)
	NE Atlantic, Med	ATL (1), w Med (1), e Med (2), BLS (2)	6 (66)	n	n	n	CR (435 bp)	Yes	na	na		(Suzuki et al. 2004)
	NE Atlantic	Kat (1), BAL (8)	11 (489)[2]	y	y	Ad	Msat (8)	No	Type I	na	LG	(Florin & Höglund 2007)
	NE Atlantic	BAL (1), NS (1), w SPA (2)	4 (190)	n	n	n	Msat (60) [S]	Yes	no	no	LA	(Vilas et al. 2010)
	Black Sea	BLS (4)	4 (76)	y	n	n	CR (432 bp)	No	no	no		(Atanassov et al. 2011)
	NE Atlantic	s NOR (1), IS (1), Kat (1), ICE (1)	4 (201)	na	na	na	Msat (12)	Yes	no	no	LA	(Imsland et al. 2014)
	NE Atlantic	BAL (3), NBTZ (3), ICE (1), w NOR (1), NS (3), EC (2), BI (4), BOB (2), PRT (1)	29 (999)[9]	na	na	na	Msat (17) [S]	Yes	Type I, II[S]	Type I, II[S]	LG, LA	(Vandamme et al. 2014)
	NE Atlantic	NS (1), BAL (1), EC (1), BOB (2), farm (1)	6 (286)	na	na	na	Msat (120) [S], SNPs (136) [S]	Yes	Type I	Type I	LA	(Vilas et al. 2015)

	NE Atlantic, Med	BAL (2), Ska (1), NOR (1), NS (3), ICE (1), BI (4), EC (1), BOB (3), w SPA (1), ADR (1) BLS (2)	20 (672) *	y	na	na	SNPs (755) [S]	Yes	Type I	Type I	LG, LA	(Prado et al. 2018b)
	NE Atlantic	BAL (2), Ska (1), NOR (1), NS (3), ICE (1), BI (4), EC (1), BOB (3), w SPA (1), farm (4)	21 (908)	y	na	na	SNPs (755) [S]	Yes	na	na	LA	(Prado et al. 2018a)
	Black Sea	BLS (4), MS (1)	5 (50)	n	n	n	Msat (5), COIII (bp) [N]	Yes	Type II	Type II	LG	(Turan et al. 2019)
	Black Sea	BLS (12)	12 (414)	y	y	Ad	Msat (6), COIII (bp), cyt-b ()	Yes	Type II	Type II	LA, LG	(Firidin et al. 2020)
	NE Atlantic	NS (4), EC (1), NBTZ (3), BAL (4)	12 (275) **	y	n	n	SNPs (3348) [S]	Yes	Type I	Type I	LG	(Le Moan et al. 2019a)
Blue whiting	NE Atlantic	BI (1)	2 (130) [1]	y	n	Ad	All (3)	No	no	no		(Mork & Giæver 1995)
	NE Atlantic, Med	Heb (1), SHE (1), FRO (1), BS (5), NOR (35), ICE (1), w IRE (3), CS (1), BOB (1), Med (2)	65 (5025) [10]	y	y	Ad	All (2)	Yes	Type II	Type II		(Giæver & Stien 1998)
	NE Atlantic, Med	ICE (1), Heb (1), Por (1), CS (2), NOR (1), BS (1), PRT (1), Med (1)	11 (850) [2]	y	y	Ad, juv	Minisat (1), Msat (5)	Yes	Type II	Type II		(Ryan et al. 2005)
	NE Atlantic	BI (2), Heb (1), Roc (1), Por (1), CS (1), BOB (1)	16 (755) [9]	Y	Y	Ad	Msat (5)	Yes	Type II	Type II	LG	(Was et al. 2008)

Whiting	NE Atlantic	IS (1), BAL (1), NOR (1), NS (2)	5 (350)	na	na	na	Minisat (1) [N]	Yes	no	no		(Galvin et al. 1995a)
	NE Atlantic	NS (2), IS (1), BAL (1), NOR (1)	5 (367)	y	na	na	Msat (3)	No	na	na		(Rico et al. 1997)
	NE Atlantic	NS (4), Heb (1), IS (1), CS (1), IRE (1), BOB (2)	10 (488)	y	y	Ad, juv	Msat (7)	Yes	Type II	Type II	LG	(Charrier et al. 2007)
	Black Sea	BLS (8)	8 (270)	y	na	na	RAPD	No	no	no		(Bektas & Belduz 2007)
	NE Atlantic	ICE (1), NOR (1), NS (1)	3 (139)	no	na	na	COI (621 bp) [N]	No	Type I	Type I		(Eiríksson & Árnason 2014)
Haddock	NE Atlantic	NS (35), SCO (4), FRO (12), Roc (12)	63 (1420) *	yes	na	Ad, juv	All (1)	Yes	Type II	Type II		(Jamieson & Birley 1989)
	NE Atlantic	ICE (1), NS (3), Ska (1), NOR (32), BS (1)	38 (3459) *	y	no	Ad, juv	All (8) [N]	No	Type I	Type I	LG	(Giæver & Forthun 1999)
	North Atlantic	NWA (5), NOR (1)	16 (1556) [10]	y	y	Ad	Msat (4)	Yes	na	na		(Lage et al. 2001)
Ling	NE Atlantic	ICE (1), Roc (1), NS (1), NOR (2), FRO (1)	8 (647) *	y	na	Ad	Msat (11) [N]	Yes	Type II	Type II	LG	(Gonzalez et al. 2015)
Tusk	North Atlantic	w SCO (1), FRO (1), Roc (1), GRL (2), Ska (1), NOR (2)	8 (963)	y	y	Ad	All (9) [Hb]	Yes	na	na		(Johansen & Nævdal 1995)
	North Atlantic	CAN (1), Roc (1), MAR (1), GRL (1), ICE (1), FRO (1), NOR (2)	10 (764) [2]	y	y	Ad, juv	Msat (7)	Yes	no	Type II	LG	(Knutsen et al. 2009)
Saithe	North Atlantic	BS (1), NOR (1), ICE (1), NS (3), w SCO (1), Roc (1), FRO (2), CAN (1)	11 (524)	y	y	Ad, juv	SNPs (131) [N]	Yes	Type II	Type II	LG	(Saha et al. 2015)

	NE Atlantic	GRL (2), ICE (1), NOR (1), NS (2)	6 (155)	na	na	Ad	Msat (3), RAPD (9)	Yes	Type II	Type II		(Behrmann et al. 2015)
	North Atlantic	CAN (2), ICE (3), FRO (2), NOR (8)	17 (1163) [2]	y	n	Ad	COI (460 bp) [N]	No	Type I	Type I	LG	(Eiríksson & Árnason 2015)
Pollack	NE Atlantic	NS (1), w EC (2), BOB (2)	6 (268)	y	y	Ad	Msat (6)	No	Type I	Type I	LG	(Charrier et al. 2006b)
Roughhead grenadier	North Atlantic	GRL (5), NOR (2)	7 (651) *	y	na	na	All (7)	Yes	Type II	na		(Katsarou & Naevdal 2001)
	North Atlantic	NWA (3), GRL (2), Hatton Bank (1), NOR (1), SJM (1)	8 (638)	na	na	Ad, juv	Msat (7) [N], CR (1100 bp) [N]	No	no	na		(Coscia et al. 2018)
Roundnose grenadier	NE Atlantic	BOB (1), Heb (5), MAR (3)	9 (417)	na	na	na	Msat (16) [S]	Yes	Type II	na	LG, LA	(White et al. 2010)
	North Atlantic	CAN (1), MAR (1), GRL (1), Ska (1), Roc (1), BI (2), NOR (1)	10 (917) [2]	y	y	Ad	Msat (6) [N]	Yes	Type II	na	LG	(Knutsen et al. 2012)
	NE Atlantic	NOR (4), Ska (1)	8 (440) *	y	y	Ad, juv	Msat (8) [S]	Yes	Type II	na	LG	(Delaval et al. 2018)
European hake	NE Atlantic, Med	Tyr (1), w Med (3), Atl (1), IRE (1), BOB (2), Gal (2)	10 (910)	na	na	na	All (21)	Yes	Type II	Type I		(Roldán et al. 1998)
	Med	SIC (7), Adr (1), Tyr (2)	10 (420)	na	na	juv	All (4)	No	Type I	Type I		(Lo Brutto et al. 1998)
	NE Atlantic, Med	NOR (1), CS (1), s BOB (1), PRT (1), Adr (1), TUN (1)	6 (483)	y	n	Ad	Msat (6)	Yes	Type II	no		(Lundy et al. 1999)

	NE Atlantic, Med	NOR (1), BOB (2), TUN (1)	8 (600) [4]	y	n	Ad	Msat (5), CR (900 bp)	Yes	Type I	Type I		(Lundy et al. 2000)
	NE Atlantic, Med	NOR (1), w Med (1), c Med (5), Adr (1), e Med (1)	9 (418)	na	na	Ad, juv	All (5); mtDNA (RFLP)	Yes	Type I	Type I		(Lo Brutto et al. 2004)
	Med	SIC (5)	5 (270)	y	na	Ad, juv	All (5)	No	no	no		(Levi et al. 2004)
	NE Atlantic, Med	w SCO (1), IRE (1), BOB (3), PRT (1), w Med (1), Aeg (1), Ion (1)	11 (504) [2]	no	na	Ad, juv	Msat (5)	Yes	Type II	Type II		(Castillo et al. 2004)
	NE Atlantic, Med	BOB (4), PRT (3), Med (1)	8 (328)	y	n	n	Msat (5)	Yes	Type II	Type II	LG	(Castillo et al. 2005)
	NE Atlantic, Med	e Med (3), c Med (1), Adr (1), w Med (6), MOR (1), Gal (1), BOB (1), IRE (1)	23 (1306) [8]	na	na	na	All (21)	Yes	Type I	Type I	LG	(Cimmaruta et al. 2005)
	NE Atlantic, Med	BI (4), BOB (10), Atl IB (5), Med (8)	27 (712)	na	na	na	Msat (5), cyt-b (465 bp)	Yes	na	na		(Pita et al. 2010)
	NE Atlantic	Atl (7), BOB (2), Cant (3), Atl IB (3)	52 (1123) [37]	na	y	Ad	Msat (5)	Yes	Type I	Type I		(Pita et al. 2011)
	NE Atlantic, Med	Atl (5), Med (14)	19 (766)	y	y	Ad	SNPs (395) [S]	Yes	na	na		(Nielsen et al. 2012)
	NE Atlantic, Med	CS (1), BOB (1), Gal (1), PRT (1), GC (1), w Med (2)	7 (339)	no	no	juv	Msat (5)	Yes	Type I	Type I		(Tanner et al. 2014)
	NE Atlantic, Med	Atl North (6), Cant (6), Atl IB (6), Cn (1) w Med (7), c Med (1)	27 (712)	na	na	Ad	Msat (5), cyt-b (465 bp) [N]	Yes	na	na	LG	(Pita et al. 2014)

	NE Atlantic, Med	NS (1), w SCO (1), CS (1), Gal (1), PRT (1), w Med (3), c Med (3), SIC (2), Adr (2), e Med (3)	19 (850)	y	na	na	SNPs (395) [S]	Yes	Type II	Type II	LG	(Milano et al. 2014)
	NE Atlantic	NOR (2), NS (1), Kat (2), BOB (1)	6	y	y	Ad, juv	SNPs (53) [S]	Yes	Type II	Type II		(Westgaard et al. 2017b)
	NE Atlantic	n Atl (1), s BOB (1)	22 (755) [20]	y	na	na	Msat (5)	No	Type I	Type I	LG	(Pita et al. 2016)
	NE Atlantic	Cant (2), Atl IB (1)	82 (1833) [79]	y	y	Ad	Msat (5), cyt-b (465 bp)	No	no	no		(Pita et al. 2017)
	NE Atlantic, Med	BOB (1), Atl IB (1), NOR (1), Med (1)	5 (111) [1]	y	y	Ad, juv	SNPs (14120) [S]	Yes	Type I	Type I		(Leone et al. 2019)
Capelin	NE Atlantic	NOR fj (1), BS (1)	2 (180)	no	na	na	All (4)	No	no	na		(Mork & Friis-Sørensen 1983)
	North Atlantic	NWA (7), ICE (1), BS (1)	9 (226)	y	y	Ad	mtDNA (RFLP)	Yes	Type II	na		(Dodson et al. 1991)
	North Atlantic	NL (1), NOR (1)	3 (54)*	y	y	Ad	mtDNA (RFLP), cyt-b (253 bp)	Yes	no	no		(Birt et al. 1995)
	North Atlantic	NOR (2), BS (1), NL (2)	7 (301) [2]	y	na	na	msat (11)	Yes	Type II	no		(Røed et al. 2003)
	Atlantic, Pacific	Pacific (2), NWA (2), GRL (2), SJM (1), BS (4), NOR fj (1)	12 (1155)*	y	y	Ad	msat (9)	Yes	Type II	na	LG	(Præbel et al. 2008)
	North Atlantic	NWA (9), Arctic (2), GRL (2)	13 (273)	y	y	Ad	AFLP (214)[S], cyt-b (572 bp)	Yes	na	na	LA	(Colbeck et al. 2011)
Atlantic horse mackerel	North-East Atlantic	NS (1), BOB (1), CS (1), PRT (1)	4 (710)	y	na	na	All (1)	No	Type I	Type I		(Borges et al. 1993)

	NE Atlantic, Mediterranean	NS (2), EC (1), PRT (1), BOB (2), Med (4), AFR (2)	12 (344)	y	na	na	CR (RFLP)	No	Type I	Type I	LG	(Karaiskou et al. 2004)
	NE Atlantic, Mediterranean	NS (1), IRE (1), BOB (1), Gal (1), PRT (1), Med (5), AFR (1)	16 (1504)[5]	y	na	na	Msat (4)	No	Type I	Type I		(Kasapidis & Magoulas 2008)
	NE Atlantic, Med	NS (2), IRE (2), BOB (3), PRT (3), Med (9)	33 (2241)[14]	na	na	na	All (12)	No	Type I	Type I	LG	(Cimmaruta et al. 2008)
	NE Atlantic, Med	BOB (2), PRT (3), Med (4)	9 (359)	y	na	na	CR (363 bp)	No	Type I	Type I		(Comesaña et al. 2008)
	Med, Black Sea	Med (4), MS (2), BLS (2)	26 (307)	na	na	Juv	mtDNA (RFLP)	Yes	na	na	LG	(Turan et al. 2009)
	NE Atlantic	IRE (1), NOR (1), NS (1)	7 (339)[4]	no	na	na	Msat (13)	Yes	Type II	Type II		(Bozano et al. 2015)
	North Atlantic	w Med (1), PRT (1), MOR (2), w AFR (2), s AFR (1)	7 (189)	na	na	Ad	Msat (10), COI (605 bp)[N], CR (450 bp)[N]	No	na	na		(Healey et al. 2020)
	NE Atlantic, Med	IRE (4), NS (4), PRT (5), n AFR (10), w SPA (5), w Med (5)	33 (716) [4]	y	y	Ad	Whole genome sequencing, SNPs (63)[S]	Yes	Type II	Type II	LA, MSA	(Fuentes-Pardo et al. 2020)
Blue jack mackerel	NE Atlantic, Mediterranean	PRT (1), Med (4)	5 (140)	na	na	na	CR (RFLP)	No	na	na	LG	(Karaiskou et al. 2004)
	NE Atlantic, Mediterranean	Azo (1), Mad (1), Cn (1), PRT (1), Med (1)	5 (195)	na	na	Ad	cyt-b (678 bp), COI (455 bp), CR (647 bp)	No	Type I	na		(Moreira et al. 2019)
	NE Atlantic, Mediterranean	Azo (1), Mad (1), Cn (1), PRT (3), Med (1)	12 (306)[5]	y	y	Ad	Msat (12)	No	Type I	na		(Moreira et al. 2020)

Atlantic mackerel	North-East Atlantic	NS (11), w BI (18), BOB (5)	34 (1164)*			All (2)	No	no	Type I		(Jamieson et al. 1987)
	North Atlantic	NW (1), BI (1)	2 (40)			RFLP (mtDNA), cyt-b (294 bp)	Yes	no	no		(Scoles et al. 1998)
	North Atlantic	NW (1), NS (1), w IRE (1), BOB (1), Med (1)	7 (205)[2]	y	y	Ad	cyt-b (398 bp) [N], CR (272 bp) [N]	Yes	Type II	no	LG	(Nesbø et al. 2000)
	North Atlantic	PRT (1), SPA (1), e Med (2)	4 (196)	y	y	Ad	CR (414 bp) [N]	Yes	na	na		(Zardoya et al. 2004)
	Mediterranean	Adr (4)	4 (222)	no	na	Ad	Msat (8)	Yes	na	na		(Papetti et al. 2013)
	North Atlantic	NW (1), BOB (1), Adr (1), w Med (2)	5 (122)	na	na	Ad	SNPs (29394) [S]	Yes	na	na		(Rodríguez-Ezpeleta et al. 2016)
	North Atlantic	NW (2), IRE (1), BOB (3), GRL (1), ICE (2), FRO (1)	10 (1231)[2]	y	y	Ad	Msat (14) [N]	Yes	no	no		(Gíslason et al. 2020)
Sprat	NE Atl, Med, Black Sea	BAL (1), NS (1), BOB (1), w Med (1), Adr (1), BLS (2)	7 (210)	na	na	na	CR (530 bp)	Yes	Type I	Type I	LG	(Debes et al. 2008)
	NE Atl, Med	BAL (4), Belt (1), Kat (1), NS (1), CS (1), Adr (1)	11 (931)[2]	y	y	Ad	Msat (9)	Yes	no	Type II	LG	(Limborg et al. 2009)
	NE Atl	NOR fj (11), NS (1), CS (1), BAL (1)	14 (1025)	y	na	Ad, juv	Msat (8) [S]	Yes	Type I	Type I, Type II		(Glover et al. 2011)
	NE Atl, Med, Black Sea	BAL (5), NBTZ (3), Atl (5), Med (2), BLS (2)	17 (1467)[2]	y	y	Ad	Msat (8) [S], CR (530 bp)	Yes	Type I	Type I, Type II	LG	(Limborg et al. 2012a)
	NE Atlantic	BAL (1), Kat (1), NS (4), EC (3), CS (2)	11 (228)	no	y	Ad, juv	SNPs (4131)[S]	Yes	Type I	Type I, Type II	LA, MSA	(McKeown et al. 2020)

	NE Atlantic, Med	NOR fj (15), BAL (8), Ska-Kat (6), NS (7), IRE (1), BOB (1), Adr (1), BLS (1)	40 (2500)*	y	y	Ad	SNPs (91)[S]	Yes	Type I	Type I, Type II	LA	(Quintela et al. 2020)
Herring	North-East Atlantic	Ska (1), Kat (1), BAL (1)	3 (160)	no	na	Ad	All (25)	Yes	na	na		(Andersson et al. 1981)
	North-East Atlantic	NOR (1), NS (1), Ska (4), Kat (3), BAL (8)	17 (1415)	y	na	Ad	All (13)	No	Type I	Type I		(Ryman et al. 1984)
	North-East Atlantic	SCO (1), IRE (9), NS (1), BAL (1)	27 (2428)[15]	y	y	Ad, juv	All (5)	No	Type I	Type I		(King et al. 1987)
	North-East Atlantic	NS (4), Ska (1), Kat (2)	7 (193)	y	y	Ad	RFLP (mtDNA)	No	Type I	Type I		(Dahle & Eriksen 1990)
	North-East Atlantic	NWA (3), IRE (5), CS (1), NS (3), NOR (8), Ska (1), Kat (2), BAL (5)	28 (2519)	y	y	Ad	All (6)	Yes	Type I	Type I		(Jørstad et al. 1991)
	North-East Atlantic	Pacific (1), NOR (2)	3 (198)	no	na	na	All (6), mtDNA (RFLP)	Yes	no	no		(Jørstad et al. 1994)
	North-East Atlantic	ICE (1), NOR (3)	4 (196)	no	na	Ad	mtDNA (RFLP)	Yes	Type I	Type I		(Turan et al. 1998)
	North-East Atlantic	ICE (1), NOR (2), BS (1)	4 (194)	na	n	Ad	Msat (4)	Yes	no	no		(Shaw et al. 1999)
	North-East Atlantic	ICE (1), BS (1), NOR (3), NS (2), CS (1), BAL (1)	10 (447)[1]	y	na	Ad	mtDNA (2)	Yes	Type I	Type I		(Hauser et al. 2001)
	North Atlantic	NWA (10), ICE (1), CS (1), BAL (1)	17 (1501) [4]	y	y	Ad	Msat (9)	Yes	no	no	LG	(McPherson et al. 2004)
	North-East Atlantic	BAL (2)	12 (1189)[10]	y	y	Ad	Msat (9)	Yes	Type II	Type II		(Jørgensen et al. 2005b)

	North Atlantic	CAN (1), EC (1), NS (9)	16 (1660)[5]	y	y	Ad	Msat (8)	Yes	Type II	no	LG	(Mariani et al. 2005)
	North-East Atlantic	BAL (11)	24 (2440)[13]	y	y	Ad	Msat (9)	Yes	no	no	LG	(Jørgensen et al. 2005a)
	North-East Atlantic	NWA (1), NS (2), Ska (3), Kat (4), BAL (1)	20 (1951)[9]	y	y	Ad	Msat (9)	Yes	no	no	LG	(Bekkevold et al. 2005)
	North-East Atlantic	NS (6), SHE (1) SCO (2), EC (1), Kat (3), Ska (4), w BAL (1)	44 (5841)[26]	y	y	Ad, juv	Msat (9)	Yes	no	no	MSA	(Ruzzante et al. 2006)
	North-East Atlantic	EC (1), NS (3), Ska (1), Kat (1), w BAL (2)	11 (1039)[3]	y	y	Ad	Msat (9)	Yes	Type II	Type II	MSA	(Bekkevold et al. 2007)
	North-East Atlantic	BAL (4)	7 (754)[3]	y	y	Ad	Msat (9)	Yes	na	na	LG	(Jørgensen et al. 2008)
	North-East Atlantic	NWA (1), NOR (2), BI (6), BAL (1)	10 (na)	y	y	Ad	Msat (12)[S]	Yes	na	na		(Watts et al. 2008)
	North-East Atlantic	NS (4), Ska (2), Kat (3), BAL (10)	19 (1859)	y	y	Ad	Msat (8)[S]	Yes	na	na	LA, LG	(Gaggiotti et al. 2009)
	North-East Atlantic	Ska (2), BAL (2)	15 (1517)[10]	y	y	Ad	All (11), Msat (9)[S]	Yes	no	no	LA	(Larsson et al. 2010)
	North-East Atlantic	NS (2), Ska (1), BAL (1)	8 (743)[4]	y	y	Ad	All (11), mtDNA (1), Msat (8)[S]	Yes	no	no	LA	(André et al. 2010)
	North-East Atlantic	NS (10), Ska (3), Kat (4), w BAL (1), Ska (11)	47 (1900)[20]	y	y	Ad, juv	Msat (9)[S]	Yes	Type II	Type II	MSA	(Bekkevold et al. 2011)
	North-East Atlantic	NS (1), NOR (1), Ska (1), Kat (1), BAL (4)	8 (400)	y	na	na	SNPs (2827)[S]	Yes	no	no	LA	(Lamichhaney et al. 2012)
	North-East Atlantic	Ska (1), Kat (1), BAL (14)	16 (98)	y	na	na	whole mtDNA (16700 bp)[S]	Yes	Type I	Type I	LA, LG	(Teacher et al. 2012)

	North-East Atlantic	ICE (1), IRE (1), IS (1), CS (1), NS (5), NOR (1), Ska (1), Kat (1), BAL (6)	21 (607)[3]	y	y	Ad	SNPs (281)[S]	Yes	na	na	LG, LA	(Limborg et al. 2012b)
	North-East Atlantic	BAL (15)	15 (705)	y	na	na	Msat (68)[S]	Yes	Type I, II	Type II	LA, LG	(Teacher et al. 2013)
	North-East Atlantic	BAL (2)	2 (12)	y	y	Ad	SNPs (5985)[S]	Yes	Type II	Type II	LA	(Corander et al. 2013)
	North-East Atlantic	NOR (1), ICE (1), FRO (1), NS (3), IRE (1), CS (1), IS (1), EC (1), Ska (3), NBTZ (6), BAL (6)	30 (1039)[5]	y	y	Ad	SNPs (156)[S]	Yes	Type II	Type II	MSA	(Bekkevold et al. 2015)
	North-East Atlantic	ICE (4), FRO (2), NOR (3), SCO (1), NOR fj (4)	14 (1258) *	y	y	Ad	Msat (24)[S]	Yes	Type I, II	Type I, II		(Pampoulie et al. 2015b)
	North-East Atlantic	BS (1), Ns (1), Ska (1), BAL (17)	20 (878)	y	y	Ad	SNPs (68182)[S]	Yes	Type II	Type II	LA, LG	(Guo et al. 2016)
	North-East Atlantic	NS (2), BAL (5)	10 (400)[3]	y	y	Ad	msat (18), SNPs (95)[S]	Yes	Type II	Type II	LA	(Bekkevold et al. 2016)
	North-East Atlantic	ICE (1), NOR (1), NS (2), Ska (2), Kat (2), BAL (12)	21 (1501)	y	na	na	SNPs (70 000)[S]	Yes	Type II	Type II	LA	(Barrio et al. 2016)
	North Atlantic	NWA (6), ICE (1), NOR (2), NS (1), Ska (2), Kat (2), BAL (12)	26 (1788)	y	y	Ad	WGS [S]	Yes	Type II	Type II	LA	(Lamichhaney et al. 2017)
	North Atlantic	NWA (6), GRL (1), ICE (1), NOR (6), BI (7), IRE (2), BAL (22), NBTZ (8)	53 (3369)	y	y	Ad	WGS [S]	Yes	Type II	Type II	LA	(Han et al. 2020)

	North-East Atlantic	NOR (1)	5 (213) 4	y	y	Ad	SNPs (2)[S]	Yes	na	na	MSA	(Berg et al. 2020)
White Anglerfish	NE Atlantic	IS (4), SCO (1)	5 (181)	no	na	Ad, juv	All (11)	Yes	No	No		(Crozier 1987)
	NE Atlantic, Med	NOR (1), SCO (3), IS (1), Por (1), CS (2), EC (1), BOB (4), Med (2)	16 (382)[1]	na	na	na	CR (488 bp)[N]	No	Type I	Type I	LG	(Charrier et al. 2006b)
	NE Atlantic	IRE (1), CS (1), BOB (2), Atl SPA (1), PRT (1)	6 (255)	na	na	Ad	Msat (8)	Yes	Type II	Type II	LG	(Blanco et al. 2008)
Black anglerfish	NE Atlantic, Med	IRE (1), CS (1), Cant (1), PRT (1), Med (2)	7 (134)[1]	na	na	na	CR (487 bp)[N]	Yes	Type I	Type I	LG	(Charrier et al. 2006b)
	NE Atlantic, Med	IRE (1), CS (1), BOB (3), Atl Spa (1), PRT (1), Med (1)	8 (367)	na	na	Ad	Msat (8)	Yes	Type II	Type II	LG	(Blanco et al. 2008)
	NE Atlantic, Med	NS (1), w SCO (1), IRE (3), CS (1), BOB (1), Atl SPA (1), PRT (1), Med (2)	11 (693)	na	y	Ad	SNPs (23 126)	Yes	Type I	Type I		(Aguirre-Sarabia et al. 2021)
Beaked redfish	North Atlantic	Irm (6), CAN (2), ICE (2), NOR (2)	41 (1946) [29]	y	y	Ad	All (5), Hb	Yes	no	no		(Johansen et al. 2000a)
	North Atlantic	NWA (9), GRL (2), ICE (1), Irm (1), FRO (1), BS (1), NOR (1)	21 (973)[5]	y	y	Ad	Msat (8)	Yes	Type I	Type I	LG	(Roques et al. 2002)
	NE Atlantic	Irm (10), ICE (4)	26 (1763)[12]	y	na	Ad	All (8)	Yes	no	no	LG	(Daníelsdóttir et al. 2008)

	NE Atlantic	Irm (2), ICE (1), FRO (2), NOR (2), BS (1)	23 (1240)[15]	y	na	Ad	Msat (12)	Yes	Type I	Type I	LG	(Stefánsson et al. 2009a)
	NE Atlantic	NOR (6), Irm (6)	12 (502)	y	y	Ad	All (3)	No	Type I	Type I		(Stroganov et al. 2009)
	NE Atlantic	Irm (23)	27 (1901)[4]	no	na	Ad	Msat (9)[N]	Yes	no	no	LG	(Stefánsson et al. 2009b)
	NE Atlantic	Irm (18), NOR (3)	24 (509)[3]	no	na	na	Msat (10)	No	Type I	Type I		(Zelenina et al. 2011)
	North Atlantic	Irm (2)	2 (50)	y	y	Ad	CR, rho (744 bp)[S]	Yes	no	no	LA	(Shum et al. 2014)
	North Atlantic	Irm (7), FRO (4), NOR (3)	16 (261)[2]	na	na	na	CR (444 bp)[N], rho (722 bp)[S]	Yes	Type II	Type II	LG	(Shum et al. 2015)
	North Atlantic	NE Arctic (4), Irm (2), ICE (1), GRL (19), NWA (1)	35 (2562)*	y	y	Ad, juv	Msat (13)	Yes	no	no		(Saha et al. 2017b)
Golden redfish	NE Atlantic	ICE (6), GRL (6)	12 (599)	no	na	Ad	All (3), Hb[S]	Yes	Type II	Type II		(Nedreaas et al. 1994)
	NE Atlantic	ICE (5), GRL (2)	16 (560) 9**	y	y	Ad	All (3), Hb[S]	Yes	na	na		(Johansen et al. 2000b)
	North Atlantic	NWA (1), GRL (3), ICE (2), NOR (1)	7 (376)	na	na	na	Msat (9)	Yes	Type II	Type II	LG	(Pampoulie et al. 2009)
	NE Atlantic	GRL (2), Reyk (1), NOR (1)	7 (411)[3]	y	y	Ad, juv	Msat (13)	Yes	Type II	Type II		(Saha et al. 2017a)
Blackspot seabream	NE Atlantic, Med	PRT (1), SPA (1), ITA (1), Aeg (1)	4 (131)	na	na	na	All (17), D-loop (190 bp)[N]	No	Type I	Type I		(Bargelloni et al. 2003)
	NE Atlantic	Azo (4), Mad (1), PRT (1)	6 (370)	no	na	Ad	Msat (7), CR (306 bp), Cyt-b (379 bp)	Yes	no	no		(Stockley et al. 2005)
	NE Atlantic, Med	Azo (1), Mad (1), Atl IB (1), PRT (1), Med (2)	6 (96)	na	na	na	Msat (7), Cyt-b (370 bp)	Yes	Type I	Type I	LG	(Lemos et al. 2006)

	NE Atlantic, Med	Med (1), Gal (1), Cant (2)	4 (123)	na	na	na	Msat (12)	No	Type I	Type I	LG	(Piñera et al. 2007)
Striped red mullet	Mediterranean	GoL (1), Ion (2), Aeg (3)	6 (342)[2]	y	na	na	All (9), RAPDs	Yes	na	na	LG	(Mamuris et al. 1999)
	Mediterranean	GoL (1), Ion (2), Aeg (3)	6 (110)	na	y	Ad	RFLP (mtDNA)	Yes	na	na	LG	(Mamuris et al. 2001)
	Mediterranean	GRC (5)	5 (150)	na	na	na	All (20), RFLP (mtDNA), RAPDs	Yes	na	na		(Apostolidis et al. 2009)
	NE Atlantic, Med	Atl (2), SPA Med (4), ITA (1), GRC (1)	8 (290)	na	na	Ad	Msat (10)	Yes	no	no		(Galarza et al. 2009)
	Mediterranean	SPA (7)	7 (230)	na	y	Ad	Msat (10)[S]	Yes	na	na	LG	(Félix-Hackradt et al. 2013)
	Mediterranean	Alb (3), w Med (16), Adr (2), Aeg (12), Ion (5), c Med (2), e Med (6)	47 (727)	y	na	Ad	SNPs (1153)[S]	Yes	na	na	LA, LG	(Dalongeville et al. 2018b)
	NE Atlantic, Med	PRT (1), w Med (1), c Med (2), Adr (5), e Med (4)	13 (599)	na	na	Ad	Msat (11)	Yes	na	na	LG	(Matić-Skoko et al. 2018)
	Mediterranean	Alb (3), w Med (16), Adr (2), Aeg (12), Ion (5), c Med (2), e Med (6)	47 (727)	y	na	Ad	SNPs (1123)[S]	Yes	na	na	LG	(Dalongeville et al. 2018a)
Orange roughy	NE Atlantic, Pacific	Por (2), Pacific (3), TS (2)	7 (482)[4]	na	na	Ad	All (22)	Yes	no	no		(Smith 1986)
	NE Atlantic, Pacific	Roc (1), AU (6)	2 (814)	na	na	Ad	All (11), mtDNA (RFLP)	Yes	no	no		(Elliott et al. 1994)

	Atlantic	BOB (1), w SCO (1), Por (1), Far (1), Sedlo (1), Nam (1)	6 (294)	y	y	na	Msat (14)	No	no	no	(White et al. 2009)
	NE Atlantic	Por (9)	11 (388)[2]	y	y	Ad, juv	Msat (8)[N]	Yes	Type II	Type II	LG	(Carlsson et al. 2011)
	Global	NZL (7), AU (2), Nam (1), Chile (1), NE Atl (2)	13 (546)	na	na	na	COI (630 bp)[N], Cyt-b (416 bp)[N]	Yes	no	no	LG	(Varela et al. 2012)
	Global	NZL (16), AU (2), Nam (1), Chile (1), NE Atl (2)	30 (812)[8]	y	na	na	Msat (9)[N]	Yes	no	no	LG	(Varela et al. 2013)
ory.Gon20	Atlantic	BOB (1), Far (1), Roc (1), Heb (1), Nam (1), Por (1), Sedlo (1), AFR (1)	7 (365)	y	na	Ad	SNPs (4179)[S]	Yes	Type II	Type II	LG, LA	(Gonçalves da Silva et al. 2020)

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.

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 Zeland (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).

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

Species	Stock assessment unit	Mismatch SA unit - genetics (Type II)	Mismatch SA unit - genetics (Type I)	Management units	Mismatch management unit - genetics
Greenland halibut, ***Reinhardtius hippoglossoides***	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)
Brill, ***Scophthalmus rhombus***	bll.27.22-32				
	bll.27.3a47de		No differentiation within NE Atlantic (Blanquer et al. 1992, Vandamme 2014)	- 4, 2a [U] (combined TAC with turbot)	No differentiation within NE Atlantic (Blanquer et al. 1992, Vandamme 2014)
Dab, ***Limanda limanda***	dab.27.22-32		Hybridization and population admixture in the NS-BS transition zone (Le Moan et al., 2019)		
	dab.27.3a4				
Four-spot megrim, ***Lepidorhombus boscii***	ldb.27.7b-k8abd			- 7 (Combined TAC with megrim) - 8.a-b, d, e (Combined TAC with megrim)	Genetic unit in Ireland and northern Bay of Biscay
	ldb.27.8c9a			- 8.c, 9, 10; 34.1.1 [U] (Combined TAC with megrim)	
	lez.27.4a6a	Differentiation between 4.a and 6.a, likely for megrim (Macdonald & Prieto)			

Megrim spp., ***Lepidorhombus spp.***	lez.27.6b			- 5b [U, I]; 6; 12, 14 [I]	Megrim in 6.a and 6.b, genetically different, managed in one TAC (Macdonald & Prieto)
Megrim, ***Lepidorhombus whiffiagonis***	meg.27.7b-k8abd	Differentiation between 7.j and 8.a-b, d (Danancher & Garcia-Vazquez 2009)		- 7 (Combined TAC with four-spot megrim) - 8.a-b, d, e (Combined TAC with four-spot megrim)	
	meg.27.8c9a			- 8.c, 9, 10; 34.1.1 [U] Combined TAC with four-spot megrim	
Flounder, ***Platichthys flesus***	fle.27.3a4	Hybrids of NS and BS pelagic flounders in the transition zone (Le Moan et al. 2019a)		-	
	fle.27.2223	The Sound (23), southern Baltic (24,25,26) genetically one unit (Florin & Höglund 2008) presence of NS and Baltic Sea pelagic flounders in SD 23 (Momigliano et al. 2017)		-	
Flounder, ***Platichthys* spp.**	bwq.27.2425	no differentiation between pelagic flounder in SD 25,26,28 (Momigliano et al. 2017)		-	
	bwq.27.2628			-	
Baltic flounder, ***Platichthys solemdali***	bwp.27.2729-32	SD 26,27,28,29,32 demersal and one unit (Florin & Höglund 2008) presence of pelagic flounders in SD27, 29, 32 (Momigliano et al. 2018)	No differentiation between SD 28 (benthic) and SD 29 (benthic) (Hemmer-Hansen et al. 2007b)	-	
Plaice,	ple.27.21-23			-Kattegat (SD 21)	

Pleuronectes platessa	ple.27.24-32			-Baltic (SDs 22-32)	Possible genetic unit in Kat (SD 21) and Belt Sea (SD 22) (Le Moan et al. 2020)
	-			-6, 5b [U, I], 12[I],14[I]	Differentiation between w SCO (6a) and FRO(5b), in one TAC (Hoarau et al. 2002, 2004, Was et al. 2010)
	ple.27.420	Local population in Skagerrak (Ulrich et al. 2017)	Lack of differentiation between NS (4), IS (7a) (Hoarau et al. 2002, 2004, Was et al. 2010) Lack of differentiation IS, NS, Baltic (Was et al. 2010)	-Skagerrak (SD 20) -4, 2a[U], 3a[P]	
	ple.27.7a			- 7.a	Lack of differentiation between NS (4), IS (7a) (Hoarau et al. 2002, 2004, Was et al. 2010) Similarity IS, west of SCO (Hoarau et al. 2002, 2004, Was et al. 2010)
	ple.27.7bc			- 7.b, c	
	ple.27.7d			- 7.d, e	
	ple.27.7e				
	ple.27.7fg			- 7.f, g	
	ple.27.7h-k			- 7.h, j, k	
	ple.27.89a			- 8, 9, 10, 34.1.1[U]	
Sole, ***Solea solea***	sol.27.20-24			- 3.a (SDs 20, 21), SDs 22-24	
	sol.27.4			- 4, 2a[U]	
	-			- 6, 5b [U, I], 12[I],14[I]	
	sol.27.7a		Genetic unit in IS (7a), CS (7.f, g) (Cuveliers et al. 2012, Diopere et al. 2018)	- 7.a	Genetic unit in IS (7a), CS (7.f, g) (Cuveliers et al. 2012, Diopere et al. 2018)
	sol.27.7bc			- 7.b, c	
	sol.27.7d			- 7.d	
	sol.27.7e			- 7.e	
	sol.27.7fg		See 7.a	- 7.f, g	See 7.a
	sol.27.7h-k			- 7.h-k	

	sol.27.8ab		genetic unit in 8.a-c and 9.a (Diopere et al. 2018)	- 8.a, b - *Solea* spp. 8c, 8d, 8e, 9 and 10; 34.1.1 [U]	genetic unit in 8.a-c and 9.a (Diopere et al. 2018)
Sole, ***Solea* spp.**	sol.27.8c9a				
Turbot, ***Scophthalmus maximus***	tur.27.22-32		Lack of differentiation Kattegat- Baltic Sea (Florin & Höglund 2007) (Vandamme et al. 2014)		
	tur.27.3a	Hybrid zone in SKA, Kat between Baltic and NS (Nielsen et al. 2004)			
	tur.27.4	Substructure within North Sea (Vandamme et al. 2014)	Lack of structure NS, BOB (Nielsen et al. 2004) Lack of structure NS and adjacent waters (Prado et al. 2018b) Lack of differentiation Skagerrak and North Sea (Prado et al. 2018b)	- 4, 2a [U] Combined turbot and brill	
Blue whiting ***Micromesistius poutassou***	whb.27.1-91214	Barents Sea local population (Giæver & Stien 1998, Ryan et al. 2005) northern and southern populations (Was et al. 2008); Bay of Biscay (8.c) differentiated (Was et al. 2008)		- 2, 4 [N] - (1, 2, 3, 4, 5, 6, 7, 8a, 8b, 8d, 8e, 12, 14) [U, I] - 8c, 9, 10; CECAF 34.1.1 [U] - 2, 4a, 5, 6 [U] - Faroese waters	Barents Sea local population (Giæver & Stien 1998, Ryan et al. 2005) Northern and southern populations (Was et al. 2008)
Whiting, ***Merlangius merlangus***	whg.27.3a			-3a	
	whg.27.47d	Southern and northern populations in NS, local population in Flamborough Head (Charrier et al. 2007)		-4; 2a [U] - Norwegian waters south of 62° N (combined TAC with pollack)	Southern and northern populations in NS, local population in Flamborough Head (Charrier et al. 2007)
	whg.27.6a			-6; 5b [UI]; 12, 14 [I]	
	whg.27.6b				
	whg.27.7a			-7a	
	whg.27.7b-ce-k			-7b, 7c, 7d, 7e, 7f, 7g, 7h, 7j and 7k	
	whg.27.89a			8	

Haddock, ***Melanogrammus aeglefinus***	had.27.1-2		- 1, 2 [N]	
	had.27.46a20	Eastern and western population in the NS (Jamieson & Birley 1989)	- 3a - 4; 2a[U] - Norwegian waters south of 62° N	Eastern and western population in the NS (Jamieson & Birley 1989)
	had.27.5a			
	had.27.5b		- 5b, 6a [U, I] - 5b [Faroese Waters] (cod, haddock)	Differentiation Faroe (5.b) and west of SCO (6.a) (Jamieson & Birley 1989)
	had.27.6b		- 6b, 12, 14 [U, I]	
	had.27.7a		- 7a	
	had.27.7b-k		- 7b-k, 8, 9, 10; 34.1.1[U]	
Ling, ***Molva molva***	lin.27.1-2		- 1, 2 [U, I]	
	lin.27.3a4a6-91214	Differentiation between NS and Rockall (Gonzalez et al. 2015)	- 4 [N] - 3a[U] - 4 [U] -6, 7, 8, 9, 10, 12, 14 [U, I]	
	lin.27.5a		- 5 [U, I] - 5b [F] combined TAC with blue ling	Differentiation between Faroe (5.b) and Iceland (5.a) (Gonzalez et al. 2015)
	lin.27.5b			
Tusk, ***Brosme brosme***	usk.27.1-2		- 1, 2, 14 [U, I]	
	usk.27.12ac			
	usk.27.3a45b6a7-912b		-3a -4 [U] -4 [N] -5, 6, 7 [U, I]	
	usk.27.5a14			
	usk.27.6b			Differentiation of Rockall (6.b) (Knutsen et al. 2009)
Saithe, ***Pollachius virens***	pok.27.1-2	Norway and Barents Sea two different populations (Saha et al. 2015)	-1, 2 [N] - 1, 2 [I]	Norway and Barents Sea are two different populations (Saha et al. 2015)
	pok.27.3a46	Overlap in the northern NS of two populations	- south of 62°N [N]	Presence of a separate population in the Rockall (Saha et al. 2015)

		Separate population in the Rockall (Saha et al. 2015)	Norway, NS, w SCO, Faroe, Iceland same genetic unit (Saha et al. 2015)	- 3a, 4; 2a [U] -6; 5b, 12, 14 [U, I]	Norway, NS, w SCO, Faroe, Iceland same genetic unit (Saha et al. 2015)
	pok.27.5a				
	pok.27.5b			- 5b [F]	
	pok.27.7-10			-7, 8, 9, 10; 34.1.1 [U]	
Pollack, ***Pollachius pollachius***	pol.27.3a4		lack of differentiation BOB, w English Channel and NS	- south of 62°N [N] combined with whiting	lack of differentiation BOB, w English Channel and NS
	pol.27.67			- 6; 5b[U, I]; 12, 14 [I] - 7	
	pol.27.89a			- 8a, 8b, 8d and 8e - 8c - 9, 10; CECAF 34.1.1 [U]	
Roughhead grenadier, ***Macrourus berglax***	rhg.27.nea	Possibly two different populations in east of Greenland and Norwegian Sea (Katsarou & Naevdal 2001)		- 5 and 14 [G, Macrourus spp.] - NAFO 1 [G, Macrourus spp.]	
Roundnose grenadier, ***Coryphaenoides rupestris***	rng.27.1245a8914ab	Presence of local populations in south NOR fjords (Delaval et al. 2018) NOR sample differentiated from Greenland (Knutsen et al. 2012)		- 8, 9, 10, 12 and 14 [U,I] - 8, 9, 10, 12 and 14 [U,I] - 5 and 14 [G, Macrourus spp.] - NAFO 1 [G, Macrourus spp.]	
	rng.27.3a			- 3 [U, I]	
	rng.27.5a10b12ac14b	Two populations north and south Mid-Atlantic Ridge (White et al. 2010)			
	rng.27.5b6712b			- 5b, 6 and 7 [U,I]	
European hake,	hke.27.3a46-8abd	West of Scotland and Celtic Sea differentiated (Castillo et al. 2004)	CS and s BOB same genetic unit (Lundy et al. 1999)	- 3a - 2a, 4 [U] - 6, 7; 5b [U, I]; 12, 14 [I] - 8a, b, d, e	West of Scotland and Celtic Sea differentiated (Castillo et al. 2004)

Merluccius merluccius			Bay of Biscay and Atlantic Iberian same genetic unit differentiated from Ireland (Roldán et al. 1998) No differentiation northern and southern Cape Breton (Lundy et al. 2000) Lack of differentiation with northern BOB (Leone et al. 2019)		Same genetic unit for BOB and Galician coast (Roldán et al. 1998)
	hke.27.8c9a	Possible substructure in 8.c (Cantabric sea) (Castillo et al. 2004) Differentiation PRT and s BOB (Lundy et al. 1999)		- 8c, 9, 10; 34.1.1 [U]	Differentiation PRT and s BOB (Lundy et al. 1999) Substructure in 8.c (Cantabria sea) (Castillo et al. 2004) No differentiation northern and southern Cape Breton (Lundy et al. 2000) Lack of differentiation with northern BOB (Leone et al. 2019)
Capelin, ***Mallotus villosus***	cap.27.1-2	Possible substructure in Norwegian fjords (Røed et al. 2003); Svalbard genetically differentiated (Præbel et al. 2008)		- 2b	
	cap.27.2a514		Possible mixing of the two stocks in Jan Mayen (Præbel et al. 2008)	- 5 and 14[G]	
Horse mackerel, ***Trachurus trachurus***	hom.27.2a4a5b6a7a-ce-k8	Local population in 4.a (Bozano et al. 2015)		- 2a, 4a [U]; 6, 7a-c,7e-k, 8a, 8b, 8d and 8e; 5b [U,I]; 12 and 14 [I] (JAX/2A-14) - 8c	Local population in 4.a (Bozano et al. 2015)
	hom.27.3a4bc7d		Mixed stock fishery in the English Channel	- 4b, 4c and 7d [U](JAX/4BC7D) (horse mackerel and associated by-catches *Trachurus* spp.)	
	hom.27.9a	Northern part of the division genetically similar to Western stock (Fuentes-Pardo et al. 2020)		- 9 -10, 34.1.1 [U] - Union waters of CECAF (adjacent to Madeira)	Northern part of the division genetically similar to Western stock (Fuentes-Pardo et al. 2020)

				- Union waters of CECAF (adjacent to the Canary Islands)	
Blue jack mackerel, ***Trachurus picturatus***	jaa.27.10a2		Lack of differentiation with Portugal and Mediterranean (Karaiskou et al. 2004, Moreira et al. 2019, 2020)	TACs for *Trachurus* spp. - 8.c - 9 -10, 34.1.1 U (adjacent Azores) - 34.1.1 U (adjacent to Madeira) - 34.1.1 U (adjacent to Canary)	
Atlantic mackerel, ***Scomber scombrus***	mac.27.nea	At leaste three stocks within the NE Atlantic (NS, western, southern) (Nesbø et al. 2000)		- 3a and 4; 2a, 3b, 3c and subdivisions 22-32 U (MAC/2A34.) - 2a and 4a N (MAC/2A4A-N) - 6, 7, 8a, 8b, 8d and 8e; 5b U,I ; 2a, 12 and 14 I (MAC/2CX14-) - 8c, 9, 10; 34.1.1 U	
Sprat, ***Sprattus sprattus***	spr.27.22-32	NS-BS mixing in the transition zone		- SDs 22-32	
	spr.27.3a4		Lack of differentiation NS, EC, CS, BoB (Debes et al. 2008, Limborg et al. 2009, 2012a, Glover et al. 2011, McKeown et al. 2020, Quintela et al. 2020)	- 3a - 2a and 4 U	Genetic unit in NS, Ska- Kat (Limborg et al. 2009, 2012a, McKeown et al. 2020, Quintela et al. 2020) Lack of differentiation NS, EC, CS, BoB (Debes et al. 2008, Limborg et al. 2009, 2012a, Glover et al. 2011, McKeown et al. 2020, Quintela et al. 2020)
	spr.27.67a-cf-k			-	

	spr.27.7de			- 7d, 7e	
Atlantic herring, ***Clupea harengus***	her.27.1-24a514a Norwegian spring-spawning herring	ss		- 1, 2 [U, F, N, I] - south of 62° N [N] - 4 north of 53° 30' N [U,N]	
	her.27.20-24	Spring spawning herring	Within Rugen genetically different spring spawning waves Substructure within Skagerrak, Kattegat, western Baltic and Central Baltic	- SDs 22-24 (Western herring)	
	her.27.25-2932	Substructure within central Baltic. Gulf of Finland (SD 32) genetically different (Guo et al. 2016) Herring in 28.2 and 29 genetically different (Corander et al. 2013)		- SDs 25-27, 28.2, 29, 32 (Central herring)	Substructure within central Baltic. Gulf of Finland (SD 32) genetically different (Guo et al. 2016); Herring in 28.2 and 29 genetically different (Corander et al. 2013)
	her.27.28 summer-autumn spawners		Gulf of Riga (spring and autumn sapwners genetically different. Autumn spawner population urges to be protected)	- SD 28.1 (Riga herring)	Gulf of Riga (spring and autumn sapwners genetically different. Autumn spawner population urges to be protected)
	her.27.3031			- SDs 30-31 (Bothnian herring)	
	her.27.3a47d Autumn spawning herring			- 3a (direct) - 3a (by-catch) - 4, 7d; 2a[U] (by-catch) - 4c, 7d	
	her.27.5a Summer spawning herring			- Icelandic management	

	her.27.6a7bc			- 5b, 6b, 6aN [U,I] - 6aS, 7b, 7c - 6 Clyde	
	her.27.irls Division 7.a South of 52°30'N, 7.g-h, and 7.j-k			- 7a - 7g, 7h, 7j, 7k	
	her.27.nirs Division 7.a North of 52°30'N				
				- 7e and 7f	
Anglerfish *Lophius budegassa, L. piscatorius*	anf.27.1-2			- 2a and 4 [U]	
	anf.27.3a46			- 4 [N] - 6; 5b [U,I]; 12 and 14 [I]	
White anglerfish, ***L. piscatorius***	mon.27.78abd		Lack of differentiation within the NE Atlantic (Aguirre-Sarabia et al. 2021)	- 7 - 8a, 8b, 8d and 8e - 8c, 9 and 10; 34.1.1 [U]	White anglerfish, lack of differentiation within the NE Atlantic (Aguirre-Sarabia et al. 2021)
	mon.27.8c9a				
Black-bellied anglerfish, ***L. budegassa***	ank.27.78abd				Black anglerfish in southern and northern division 9.a genetically differentiated (Blanco et al. 2008)
	ank.27.8c9a	Southern and northern division 9.a genetically differentiated (Blanco et al. 2008)			
Beaked redfish,	reb.2127.dp deep pelagic stock > 500 m	in subareas 5, 12, and 14 (Iceland and Faroe grounds, North of		- 5 [U, I]; 12 and 14 [I] Deep pelagic	

Sebastes mentella		Azores, East of Greenland) and NAFO subareas 1, 2		
	reb.2127.sp shallow pelagic stock < 500 m	in subareas 5, 12, and 14 (Iceland and Faroe grounds, North of Azores, East of Greenland) and NAFO subareas 1, 2		- 5 [U, I]; 12 and 14 [I] Shallow pelagic - NAFO 1F [G]; 5, 12 and 14 [G] pelagic
	reb.27.1-2			- 1 and 2 [N] (S. mentella) all the other TAC for Redfish spp. - 1 and 2 [I]
	reb.27.14b demersal (Southeast Greenland)		Mixing in Greelandic waters of Icelandic slope, shallow and deep pelagic *S. mentella* (Saha et al. 2017b)	- NAFO 1F [G]; 5 and 14 [G] demersal - NAFO 3LN - NAFO 3M - NAFO 3O - NAFO Subarea 2, Divisions 1F and 3K
	reb.27.5a14 Icelandic slope stock			- 5b [F]
Golden Redfish, ***Sebastes norvegicus***	reg.27.1-2			- 1 and 2 [I]
	reg.27.561214	Three cryptic species in Greenlandic waters and North Atlantic (Saha et al. 2017a). Differentiation between the giant in Reykjanes Ridge and Greenland. Greenlandic waters genetically distinct (Pampoulie et al. 2009).		- 5b [F] - 5 [U, I]; 12 and 14 [I] Shallow pelagic (Redfish spp.) - 5 [U, I]; 12 and 14 [I] Deep pelagic (Redfish spp.) - NAFO 1F [G]; 5, 12 and 14 [G] pelagic - NAFO 1F [G]; 5 and 14 [G] demersal

				- NAFO 1F [G]; 5 and 14 [G] - NAFO 3LN - NAFO 3M - NAFO 3O - NAFO Subarea 2, Divisions 1F and 3K	
Blackspot seabream, ***Pagellus bogaraveo***	sbr.27.10			- 10 [U, I]	
	sbr.27.6-8		Lack of differentiation between subareas 8 and 9	- 6, 7 and 8 [U, I]	Lack of differentiation between subareas 8 and 9
	sbr.27.9			- 9 [U, I]	
Striped red mullet, ***Mullus surmuletus***	mur.27.3a47d			-	
	mur.27.67a-ce-k89a			-	
Orange roughy, ***Hoplostethus atlanticus***	ory.27.nea	Locally adapted population reported on the Faraday Seamount (Gonçalves da Silva et al. 2020)		-	

For the management units: [U] Union waters; [I] International waters; [N] Norwegian waters; [G] Greenland waters; [P] part not covered by Skagerrak and Kattegat.
For the geographic location abbreviations see Table 1.

Table 3. Summary table of Atlantic cod genetic population structure studies.

Species	Region	Sampling locations	No. Samples (Number of individuals)	Spawning	Maturity	Life stage	Genetic Marker	Differentiation	Mismatch genetic-SA	Mismatch genetic- MZ	LAS, LG, MSA	Reference
Atlantic cod	North Atlantic	NWA (1), GRL (1), ICE (1), BS (1), NOR (2), NS (1), Ska (1), BAL (1)	9 (880)	y	na	Ad, juv	All (13)	Yes	Type I	Type I	LG	(Mork et al. 1985)
	North Atlantic	NS (1), NL (1)	2 (35)	y	y	Ad	mtDNA (RFLP)	No	Type I	Type I		(Smith et al. 1989)
	NE Atlantic	NOR (28)	28 (1903) *	y	na	na	All (5); Hb	Yes	Type I	Type I		(Jørstad & Nævdal 1989)
	NE Atlantic	BS (3), NOR (6)	9 (101)	y	na	na	mtDNA (RFLP); Hb	Yes	no	no		(Dahle 1991)
	NE Atlantic	ICE (12)	12 (56) *	y	y	Ad	mtDNA (RFLP)	No	no	no		(Árnason et al. 1992)
	NE Atlantic	Ska (4)	12 (1201) [8]	y	na	Ad, juv	All (5); Hb	No	na	na		(Gjøsæter et al. 1992)
	NE Atlantic	NOR (7), BS (2)	9 (100)	no	na	Ad	mtDNA (Cyt-b) [N]	No	Type I	Type I		(Árnason & Pálsson 1996)
	NE Atlantic	BS (1), NOR (5)	18 (5290) [12]	y	y	Ad, juv	Hb (1)	Yes	no	no		(Dahle & Jørstad 1993)
	North Atlantic	SS (1), NL (1), IS (1), n NOR (1)	4 (119)	na	na	na	Minisat (1)	Yes	no	no		(Galvin et al. 1995b)
	North Atlantic	ICE (1), NS (1), BS (1), NOR fj (1), Nov (1), NL (1)	6 (603)	na	na	na	RFLP (17)	Yes	na	na	LG	(Pogson et al. 1995)
	North Atlantic	NL (6), Nov (1), BS (1)	12 (702) [4]	y	y	Ad, larv	Msat (6)	Yes	no	no		(Bentzen et al. 1996)

	NE Atlantic	BS (2), NOR (20)	22 (965) *	y	y	Ad, juv	Pan I (1)	Yes	Type II	Type II		(Fevolden & Pogson 1997)
	NE Atlantic	NOR (8)	24 (1586) [16]	y	y	Ad	Hb (1)	Yes	no	no		(Nordeide 1998)
	NE Atlantic	ICE (6)	6 (344)	y	y	Ad	Pan I, Hb	Yes	Type II	Type II		(Jónsdóttir et al. 1999)
	NE Atlantic	NOR (8)	8 (521)	y	na	Ad	All (6)[S]	No	Type I	Type I		(Mork & Giæver 1999)
	North Atlantic	ICE (49), GRL (9)	2 (597) *	no	no	Ad, juv	Cyt-b (250 bp)	No	Type I	Type I		(Árnason et al. 2000)
	North Atlantic	Nov (4), NL (4), ICE (1), NS (1), NOR fj (1), BS (1)	6 (1174)	na	na	na	RFLP (10), Pan I	Yes	no	no	LG	(Pogson et al. 2001)
	North Atlantic	NS (6), CS (2), IS (1), EC (2), w SCO (1), BS (1), SS (1)	14 (700)	y	y	Ad	Msat (5)	Yes	Type I, II	Type I, II	LG	(Hutchinson et al. 2001)
	NE Atlantic	NS (2), BAL (2), BS (1)	5 (381) *	y/n	na	na	Msat (9)	Yes	no	no		(Nielsen et al. 2001)
	NE Atlantic	ICE (2)	8 (749) *	y	n	Ad	Pan I, Hb	Yes	Type II	Type II		(Jónsdóttir 2001)
	North Atlantic	SS (1), CS (1), NS (1), NOR (1), BS (1), ICE (1)	6 (551) *	no	no	Ad	RFLP (5), Pan I	Yes	Type I	Type I		(Jónsdóttir et al. 2003)
	NE Atlantic	NOR Ska coast (6)	6 (611)	y	y	Ad	Msat (6)	Yes	Type II	Type II	LG	(Knutsen et al. 2003)
	NE Atlantic	BAL (6), NS (2), NBTZ (6)	14 (870) *	y	y	Ad	Msat (9)	Yes	Type I	Type I		(Nielsen et al. 2003)
	NE Atlantic	FRO (5)	5 (74)	y	na	na	Cyt-b (566 bp)	No	no	no		(Sigurgíslason & Árnason 2003)
	NE Atlantic	n NOR (8)	8 (846)	na	na	Ad, juv	Pan I	Yes	no	no	LG	(Pogson & Fevolden 2003)
	NE Atlantic	ICE (5)	5 (404)	y	na	Ad	RFLP (5)	Yes	Type II	Type II		(Imsland et al. 2004)
	NE Atlantic	NOR (7), Belt (2)	9 (1209)[6]	y	na	Ad	All (1), Hb	Yes	na	na		(Husebø et al. 2004)

	NE Atlantic	NS (1), Ska (9), Kat (1), BAL (1)	12 (1801) [6]	y	y	Ad, juv, lar	Msat (8)	Yes	Type II	Type II		(Knutsen et al. 2004)
	NE Atlantic	NS (6), ICE (7), FRO (2), IRE (2), CS (1), BAL (1), BS (2), NOR (2)	23 (1699) *	y	na	Ad, juv	Pan I	Yes	na	na	LG	(Case et al. 2005)
	NE Atlantic	NOR (7)	43 (2597) *	y	y	Ad, juv	Pan I	Yes	no	No		(Sarvas & Fevolden 2005b)
	NE Atlantic	NOR (35), BS (5), SJM (5), NS (1)	119 (6356) *	y	no	juv	All (1), Pan I	Yes	no	no		(Sarvas & Fevolden 2005a)
	NE Atlantic	NS (3), NBTZ (6), BAL (4)	13 (766) *	y	y	Ad, juv	Msat (9)	Yes	Type II	Type II		(Nielsen et al. 2005)
	NE Atlantic	NS (1), BAL (1)	4 (233) *	y	y	Ad	Msat (9)	Yes	no	no		(Poulsen et al. 2006)
	NE Atlantic	ICE (22)	28 (2534)[6]	y	y	Ad	Msat (9)	Yes	Type II	Type II		(Pampoulie et al. 2006b)
	NE Atlantic	NOR (4)	4 (270)	y	y	Ad	Msat (10), All (5), Pan I, Hb	Yes	Type II	Type II		(Dahle et al. 2006)
	NE Atlantic	SJM (1), BS (1), NOR (10), NS (2)	14 (777)	no	na	Ad	Msat (7)[S]	Yes	Type II	Type II	LG	(Skarstein et al. 2007)
	NE Atlantic	ICE (3), farm (3), NOR (1)	7 ()	y	na	Ad	Msat (8), Pan I	Yes	na	na		(Pampoulie et al. 2006a)
	North Atlantic	BAL (1), NS (1), BS (1), NL (1)	4 (274)	na	na	na	Msat (11)[S]	Yes	no	no		(Nielsen et al. 2006)
	NE Atlantic	NOR Ska coast (5)	5 (493)	y	y	Ad	Msat (13)	Yes	Type II	Type II	LG	(Jorde et al. 2007)
	North Atlantic	SS (1), GRL (2), ICE (2), FRO (1), CS (1), BS (1), BAL (1)	9 (431)	na	y	Ad	Msat (6)	Yes	Type I	Type I	LG	(O'Leary et al. 2007)
	NE Atlantic	BAL (2), NS (2), FRO (5)	9 (442)[5]	y	y	Ad, juv	Msat (9), Pan I	Yes	na	na		(Nielsen et al. 2007)
	NE Atlantic	SJM (1), BS (2), RUS (1), NOR (11)	15 (1107) *	y	na	Ad, juv	Msat (10)[S], Pan I	Yes	no	No		(Westgaard & Fevolden 2007)

	NE Atlantic	NOR (12)	12 (910) *	y	y	Ad	Msat (6), All (5), Pan I, Hb	Yes	no	No	MSA	(Wennevik et al. 2008)
	NE Atlantic	ICE (6), FRO (2)	9 (771) *	y	na	Ad	Msat (9), Pan I	Yes	Type I, II	Type I, II	LG	(Pampoulie et al. 2008c)
	North Atlantic	BAL (2), NS (2), CS (2), IS (2), ICE (2), NOR (2), FRO (2), CAN (1)	15 (954) *	y	y	Ad	Msat (8), Pan I	Yes	Type II	Type II	LG	(Pampoulie et al. 2008b)
	North Atlantic	CAN (1), GRL (1), ICE (2), FRO (2), Lof (2), NS (3), EC (1), Kat (1), BAL (4)	18 (708) [1]	na	na	Ad	SNPs (98)[S]	Yes	na	na	LG, LA	(Nielsen et al. 2009a)
	NE Atlantic	SCO (2), n NS (4), FRO (2), NS (2), BAL NBTZ (3), NEAC (1)	21 (1256)[7]	y	y	Ad, juv	Msat (10)[S]	Yes	Type II	Type II	LG	(Nielsen et al. 2009b)
	NE Atlantic	NS (1), BS (1), BAL (1), ICE (1)	4 (120)	y	y	Ad	mtDNA (CR, Cyt-b)	Yes	na	na		(Kijewska et al. 2009)
	NE Atlantic	NOR (3), BS (1), NS (1), Kat (1), BAL (2)	8 (363)	na	na	Ad	SNPs (2)[S]	Yes	na	na	LA	(Andersen et al. 2009)
	North Atlantic	NWA (8), ICE (1), IRE (1), BS (1), BAL (1)	14 (300) *	y	y	Ad	SNPs (1641) [S]	Yes	no	no	LG, LA	(Bradbury et al. 2010)
	NE Atlantic	BAL (4), NS (1), BS (1)	6 (230)	no	na	Ad	Msat (6)	Yes	Type II	Type II		(Kijewska et al. 2011)
	NE Atlantic	NS (5), EC (1), Kat (1), FRO (2), w SCO (1)	15 (585) *	no	na	Ad	SNPs (92)[S]	Yes	Type II	Type II	LA	(Poulsen et al. 2011)
	North Atlantic	BAL (2), Kat (1), NS (1), NOR (2), FRO (2), BS (1), GRL (2), NL (2), Nov (1)	14 (375)	no	na	Ad	SNPs (6)[S]	Yes	na	na	LA	(Andersen et al. 2011)

	NE Atlantic	NOR fjords -Ska (11), NS (2)	13 (1287) *	y	y	Ad, Juv	Msat (13)[N]	Yes	Type II	Type II		(Knutsen et al. 2011)
	North Atlantic	NWA (10), ICE (1), BS (1), IRE (1)	13 (279)	na	na	Na	SNPs (1641) [S]	Yes	na	na		(Bradbury et al. 2011)
	NE Atlantic	GRL (16)	19 (1581) *	no	no	Ad, juv	Msat (18)[S], Pan I	Yes	Type I	Type I		(Pampoulie et al. 2011)
	NE Atlantic	ICE (3)	16 (1286)[13]	y	y	Ad	Msat (6)[N], Pan I	Yes	no	no	LA	(Jakobsdóttir et al. 2011)
	NE Atlantic	NS (1), BAL (1)	2 (40)	na	na	Ad	Gene expression	Yes	no	no	LA	(Larsen et al. 2012)
	North Atlantic	BAL (2), NBTZ (2), Kat (1), NS (4), EC (1), IS (1), CS (1), FRO (2), NOR (2), BS (1), WS (1), ICE (3), GRL (1), CAN (1)	21 (980) *	y	y	Ad	SNPs (69)[S]	Yes	na	na	LA	(Nielsen et al. 2012)
	NE Atlantic	NOR fjords (7)	7 (521) *	no	no	Juv	Msat (16)[S], Pan I	Yes	no	no	LA	(Fevolden et al. 2012)
	NE Atlantic	ICE (2)	8 (2361)	no	no	Ad, juv	Msat (9)[N], Pan I	Yes	Type II	Type II	MSA	(Pampoulie et al. 2012)
	North Atlantic	NWA (1), BAL (1), NS (1), NOR (3), ICE (2)	12 (295) [4]	y	na	Ad	SNPs (1199) [S]	Yes	Type II	Type II	LA	(Hemmer-Hansen et al. 2013)
	NE Atlantic	WS (4), BS (4)	8 (491) [6]	y	na	Ad	All (6), Msat (14)	Yes	Type II	Type II		(Stroganov et al. 2013b)
	NE Atlantic	ICE (5)	5 ()	y	y	Ad	Msat (16)	No	no	no		(Kristjánsson 2013)
	NE Atlantic	BS (1), NOR (1)	2 (88)	y	na	na	SNPs (961619) [S]	Yes	no	no		(Karlsen et al. 2013)
	North Atlantic	NWA (15), ICE (1), BS (1), IRE (1), BAL (1)	23 (466) *	y	y	Ad	SNPs (1405) [S]	Yes	na	na	LA	(Bradbury et al. 2013)
	NE Atlantic	BAL (3)	6 (181)[3]	y	y	Ad	All (6)	No	Type I	Type I	LG	(Stroganov et al. 2013a)

	NE Atlantic	ICE (2)	2 (845) *	y	y	Ad	Msat (6) [S]	No	no	no		(Eiríksson & Árnason 2013)
	North Atlantic	GRL (16), ICE (3), CAN (1)	29 (847) [8]	y	y	Ad	SNPs (935) [S]	Yes	no	Type II	LG, LA	(Therkildsen et al. 2013)
	NE Atlantic	BI (20)	28 (1338) [11]	y	y	Ad, eggs, lar	SNPs (96)	Yes	Type I, II	Type I, II	LA	(Heath et al. 2014)
	NE Atlantic	GRL (1), ICE (1), NEAC (1), NCC (1), NS (1), EC (1), BAL (2)	8 (304)	y	y	Ad	SNPs (103) [S]	Yes	no	no	LG, LA	(Hemmer-Hansen et al. 2014)
	NE Atlantic	BS (1), SJM (1), Lof (1)	5 (1097) *	no	na	Ad	Msat (6) [S]	Yes	no	no	MSA	(Michalsen et al. 2014)
	NE Atlantic	BS (1), NOR (1)	2 (88)	y	na	na	SNPs (mtDNA)	No	na	na		(Karlsen et al. 2014)
	NE Atlantic	NS (1), NBTZ (2), BAL (4)	8 (194) [1]	y	y	Ad	SNPs (8809) [S]	Yes	no	no	LG, LA	(Berg et al. 2015)
	North Atlantic	GRL (6)	6 (872)*	no	na	na	SNPs (81)	Yes	Type II	Type II	LA, MSA	(Bonanomi et al. 2015)
	NE Atlantic	BAL (3)	3 (95)	no	na	na	SNPs (7944) [S]	Yes	no	no	LG	(Poćwierz-Kotus et al. 2014)
	NE Atlantic	BS (2), Mog (1)	2 (97)	no	na	Ad	Msat (17), All (20)[S]	Yes	no	no		(Andreev et al. 2015)
	NE Atlantic	ICE (DST)	148	no	na	Ad	Msat (26)[N]; rho SNPs (20); Pan I [S]	Yes	Type II	Type II	LA	(Pampoulie et al. 2015a)
	NE Atlantic	BAL (2)	2 (36)	no	na	Ad	Transcriptome analysis	Yes	na	na	LA	(Małachowicz et al. 2015)
	NE Atlantic	NOR (1)	3 (144)	no	no	Juv	SNPs (rho, Pan I) [S]	Yes	no	no	LA	(Andersen et al. 2015)
	NE Atlantic	NS (2), Ska fj (6)	8 (378) *	y	y	Ad, juv	SNPs (9187) [S]	Yes	Type II	Type II	LA	(Sodeland et al. 2016)
	NE Atlantic	NS (2), Ska (2), Kat (1), NBTZ (1)	15 (1330) *	y	y	Ad, juv	Msat (12) [N]	Yes	Type II	Type II		(André et al. 2016)

	NE Atlantic	NEAC (1), NCC (1), NS (1)	3 (141)	y	y	Ad	SNPs (8168) [S]	Yes	no	no	LA	(Berg et al. 2016)
	NE Atlantic	BAL (2)	2 (131)	no	na	Ad	Gene expression	Yes	no	no	LA	(Kijewska et al. 2016)
	NE Atlantic	Mog (1), BS (2), WS (1)	7 (190) [3]	no	na	Ad	Msat (15)[S], cyt-b (879 bp), ND2 (631 bp)	Yes	Type II	Type II		(Zhivotovsky et al. 2016)
	NE Atlantic	BAL (3)	6 (971) *	y	y	Ad	SNPs (39) [S]	Yes	no	no	MSA	(Hüssy et al. 2016)
	North Atlantic	GRL (1), BS (2), NOR (1), NEAC (1), WS (1), Mog (1), NWA (1)	8 (274)	no	na	na	cyt-b (970 bp) [N]	Yes	Type II	Type II		(Zelenina et al. 2016)
	NE Atlantic	BS (1), NOR (5), Ska (3), NS (1), BAL (1), CS (1), IS (1), WS (1)	14 (959)	na	na	Ad	SNPs (10913) [S]	Yes	no	no	LA	(Kirubakaran et al. 2016)
	NE Atlantic	EC (1), NS (1), Ska-Kat (10), BAL (2)	14 (527)	y	y	Ad, juv	SNPs (7973) [S]	Yes	Type II	Type II	LG, LA	(Barth et al. 2017)
	NE Atlantic	Mog (1), BS (1)	3 (97)	na	na	Ad	All (6); Msat (8)	Yes	na	na	LA	(Stroganov et al. 2017)
	North Atlantic	CAN (5), ICE (2), NOR (2)	9 (316)	y	y	Ad, juv	SNPs (8165) [S]	Yes	Type II	Type II	LA	(Berg et al. 2017)
	NE Atlantic	NOR Ska coast (2)	11 (409) *	y	y	Ad, juv, eggs	SNPs (25) [S]	Yes	Type II	Type II	MSA	(Jorde et al. 2018)
	North Atlantic	NWA (), GRL (13), ICE (4), FRO (2), IRE (1), BI (5), NS (2), NOR (3), BAL (1), WS (1), BS (1)	54 (1494)	y	y	Ad	SNPs (796) [S]	Yes	na	na	LG	(Fairweather et al. 2018)
	North Atlantic	NWA (1), NEAC (1), NCC (1), BAL (1), NS (1), IS (1)	6 (156)	na	na	na	mtDNA (15592 bp)	Yes	na	na		(Jørgensen et al. 2018)

	NE Atlantic	NOR Ska coast (15)	15 (6383) *	no	no	Juv	SNPs (26) [S]	Yes	Type II	Type II	MSA	(Knutsen et al. 2018)
	NE Atlantic	NOR coasts (55)	66 (4346) *	y	y	Ad	Msat (6) [S]	Yes	Type II	Type II	LG, LA, MSA	(Dahle et al. 2018b)
	NE Atlantic	BS (1), NOR (1), BAL (3)	10 (598) [5]	y	y	Ad	Msat (8) [S]	Yes	no	no	MSA	(Stroganov et al. 2018)
	North Atlantic	NWA (12) NOR (1), BAL (1)	14 (153)	n	na	na	SNPs (mtDNA)	Yes	na	na	LG	(Lait et al. 2018)
	NE Atlantic	BAL (14)	14 (2302) *	y	y	Ad, juv	SNPs (499) [S]	Yes	no	no	MSA	(Hemmer-Hansen et al. 2019)
	North Atlantic	NOR (3), BS (3), GRL (2), NWA (1)	13 (671) *	y	na	na	All (5); Msat (8)	Yes	na	na	LG	(Stroganov et al. 2019)
	NE Atlantic	NS (2), Ska (8), Kat (1), BAL (1)	17 (673) *	y	y	Ad, eggs	SNPs (25) [S]	Yes	Type II	Type II		(Svedäng et al. 2019)
	NE Atlantic	NOR (1), NS (2), Ska fj (1), BAL (3)	7 (204) *	y	na	Ad	SNPs (781038) [S]	Yes	Type II	Type II	LG, LA, MSA	(Barth et al. 2019)
	NE Atlantic	BAL (16)	16 (603) *	y	y	Ad, juv	SNPs (38)	Yes	no	no	LA, MSA	(Weist et al. 2019)
	NE Atlantic	NS (2), Kat (1), w BAL (2), e BAL (4)	9 (240)	y	na	Ad	SNPs (8076) [S]	Yes	Type II	Type II	LG, LA	(Wenne et al. 2020)
	NE Atlantic	WS (1), BS (1), NOR (6), FRO (2), IS (2)	12 (486)	y	y	Ad	SNPs (8174) [S]	Yes	Type II	Type II	LG, LA	(Johansen et al. 2020)
	NE Atlantic	NS (4), SCO (2)	24 (1044)[18]	y	y	Ad, juv	SNPs (90) [S]	Yes	Type II	Type II	LG, LA	(Wright et al. 2021)

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