Genetic Fact Sheet

→ **Plaice**

Pleuronectes platessa

2022
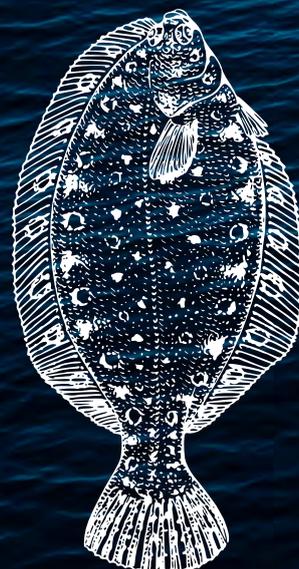
PANDORA

**Paradigm for Novel Dynamic
Oceanic Resource Assessments**

Genetic Fact Sheets

Review of available genetic information
on population structuring in exploited species

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

PANDORA aims to:

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

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

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

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

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)

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
Plaice, *Pleuronectes platessa*	8	yes	no	no	no	LC

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).

FACT SHEET

Plaice, *Pleuronectes platessa*

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

LEAST CONCERN LC — RED LIST

Distribution[1]

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
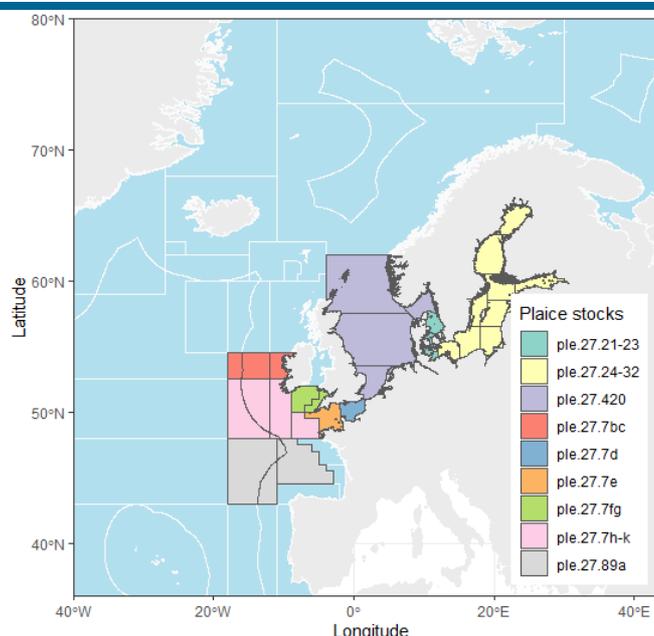
Figure 3.7. Plaice ICES stock assessment units

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

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.

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.

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
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), Kat (1), Belt (1), BAL (1)	7 (234)	y	y	Ad	SNPs (3019) [S]	Yes	no	Type II	LA, LG	(Le Moan et al. 2020)

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).

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

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

Species	Assessment unit	Mismatch SA unit - genetics (Type II)	Mismatch SA unit - genetics (Type I)	Management units	Mismatch management unit - genetics
Plaice, ***Pleuronectes platessa***	ple.27.21-23			-Kattegat (SD 21)	
	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	