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Genetic Fact Sheet

Common sole

Solea solea

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PANDORA

Paradigm for Novel Dynamic
Oceanic Resource Assessments

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Genetic Fact Sheets

Review of available genetic information on population structuring in exploited species

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

PANDORA aims to:

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

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

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

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

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List of abbreviations

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

North-East Atlantic ICES subareas, divisions and subdivisions

1) Subarea 1 – Barents Sea
2) Subarea 2 – Norwegian Sea, Spitzbergen and Bear Island
3) Subarea 3
   - Division 3.a, Skagerrak (subdivision 20) and Kattegat (subdivision 21)
   - Division 3.b-c, Sound (subdivision 23) and Belt Sea (subdivision 22)
   - Division 3.d, Baltic Sea (subdivisions 24-32)
4) Subarea 4 – North Sea (divisions 4.a-c)
5) Subarea 5 – Iceland (division 5.a) and Faroes Grounds (division 5.b)
6) Subarea 6 – West of Scotland (division 6.a) and Rockall (division 6.b)
7) Subarea 7
   - Irish Sea (division 7.a), West of Ireland (division 7.b), Porcupine Bank (division 7.c)
   - Eastern English Channel (division 7.d), Western English Channel (division 7.e)
   - Bristol Channel (division 7.f), Celtic Sea (divisions 7.g-h), Southwest of Ireland (divisions 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**
Lemon sole, Microstomus kitt	0	-	-	-	-	NE
Common sole, Solea solea	13	yes	no	no	yes	DD

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

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[1]

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.

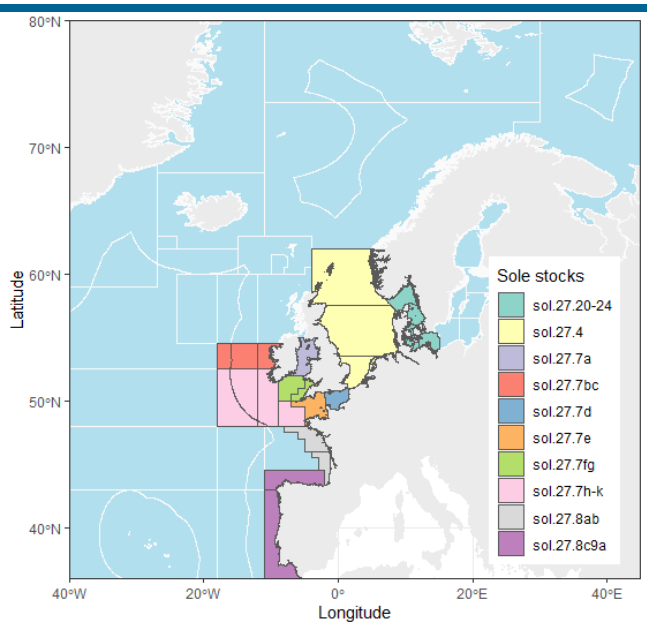

Figure 3.8. Stock assessment units (ICES) of common sole.

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-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.

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
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)

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
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	genetic unit in 8.a-c and 9.a (Diopere et al. 2018)
Sole, ***Solea* spp.**	sol.27.8c9a			- Solea spp. 8c, 8d, 8e, 9 and 10; 34.1.1[U]	