Review of the population structure of hake, megrim, white and black anglerfish, and sardine in the Northeast Atlantic waters

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1 Introduction

Understanding the stock structure of a species is an essential requirement for stock assessment and to achieve an optimal management of the resource (Cadrin, 2020). Despite this requisite is widely acknowledged, inconsistencies between the stock structure of the biological populations and the units used for assessment and management are frequent (Kerr et al. 2017).

Most stock assessment models assume that the resource is a single population and inappropriate assumptions of the stock structure, assuming more or less conservative parameters, might lead the stock to be under- or over-fished. Punt et al. (2020) indicates that novel assessment models, in which space is explicitly represented in the population dynamics, present a better representation of the spatial structure for the stocks that do not fulfill the assumption of single stock. On the other hand, the definition of the fishery management units involves other considerations such as fishery exploitation patterns and administrative and jurisdictional interests. A general recommendation is that management units should ensure the matching of biologically relevant processes and management measures (Reiss et al. 2009). Accordingly, a good definition of the stocks being exploited, their spatial distribution and biological characteristics are required.

The current stock assessment of European hake, *Merluccius merluccius*, assumes the occurrence of two stocks, the northern and southern stock, with the boundary located at the Canyon of Cape Breton (Table 1). For white and black anglerfish, *Lophius piscatorius* and *L. budegassa*, three stocks are considered: the northern and southern stocks of the Southern Shelf, which are separated by the Canyon of Cape Breton, and a third stock for both species of anglerfish combined at the Northern Shelf. Six stocks of megrims (*Lepidorhombus spp*) are assessed by ICES: megrims in ICES divisions 4a and 6a, megrims in ICES division 6b; megrim (*L. whiffiagonis*) in division's 7b-k and 8abd and in divisions 8c and 9a; and four-spot megrim (*L. boscii*) in divisions 7b-k and 8abd and in divisions 8c and 9a. Since 2017, ICES assesses sardine, *Sardina pilchardus*, as three stocks: sardine in Subarea 7 and the two stocks separated by Cape Breton Canyon, sardine in divisions 8a,b and 8d and sardine in divisions 8c and 9a.

Defining the stock structure of a species subject to exploitation is a complex task that requires an interdisciplinary approach. Genetic and non-genetic evidence are required to define the stock structure of a species. The aim of this study is to update the current knowledge about the stock structure of hake, megrim, anglerfishes, and sardine in the North East Atlantic. The results of different genetic and non-genetic stock identification studies are jointly analysed providing a synthesis of the definition of the stock structure for each species. Likewise, the uncertainties and the needs of further studies for defining the stock structure for each species are identified.

2 Methods

We reviewed the scientific articles and technical reports providing information about spatial structure and stock identification of the five species along the Northeast Atlantic (Figure 1).

Table 1. Stocks used for assessment and Management units for the species included in the study.

Species	ICES current stocks	ICES advice 2021 (t)	TAC - Management Units	TAC 2021 (t)
Lepidorhombus whiffiagonis	Lepidorhombus spp. 4a6a	7300	Lepidorhombus spp. - Subarea 4 +Div 2a	731 *
Lepidorhombus boscii	Lepidorhombus spp. 6b	? 512	Lepidorhombus spp. - Subareas 6,12,14 +Div 5b	1476 *
	L. whiffiagonis 7b-k8abd	19184	Lepidorhombus spp - Subarea 7	4683 *
	L. boscii 7b-k8abd	np	Lepidorhombus spp - Divisions 8abde	448 *
	L. whiffiagonis 8c9a	468	Lepidorhombus spp - 8c, 9 and 10; UW CECAF 34.1.1	
	L. boscii 8c9a	1690		
Lophius piscatorius	Lophius spp. 463a	17645	Lophiidae - Subarea 4 +Div 2a	3522 *
Lophius budegassa			Lophiidae- Norwegian waters Subarea 4	425 *
			Lophiidae - Subareas 6,12,14 +Div 5b	1993 *
	L. piscatorius 78abd	34579	Lophiidae - Subarea 7	15885 *
	L. budegassa 78abd	15551	Lophiidae - Divisions 8abde	2252 *
	L. piscatorius 8c9a	1872	Lophiidae - 8c, 9 and 10; UW CECAF 34.1.1	
	L. budegassa 8c9a	1800		
Merluccius merluccius	M. merluccius Sub 4,6,7 Div 3a, 8a-b, 8d	98657	M.merluccius - Subarea 4 +Div 2a	3940 *
			M.merluccius- Div 3a	3403 *
			M.merluccius - Subareas 6,7,12,14 +Div 5b	63325 *
			M.merluccius - Divisions 8abde	8206 *
	M. merluccius 8c9a	7825	M.merluccius - 8c, 9 and 10; UW CECAF 34.1.1	8517
Sardina pilchardus	S. pilchardus in Subarea 7 (southern Celtic Seas and the English Channel)	na	S. pilchardus in Subarea 7	No official TAC
	S. pilchardus in divisions 8.a–b and 8.d (Bay of Biscay)	27858	S. pilchardus in divisions 8.a–b and 8.d	No official TAC
	S. pilchardus in divisions 8.c and 9.a (Cantabrian Sea and Atlantic Iberian waters)	10871	S. pilchardus in divisions 8.c and 9.a	No official TAC

na: not available; np: not provided; * brexit pending

Figure 1. Map representing the location of stock identification studies available for hake, megrim, anglerfishes and sardine.
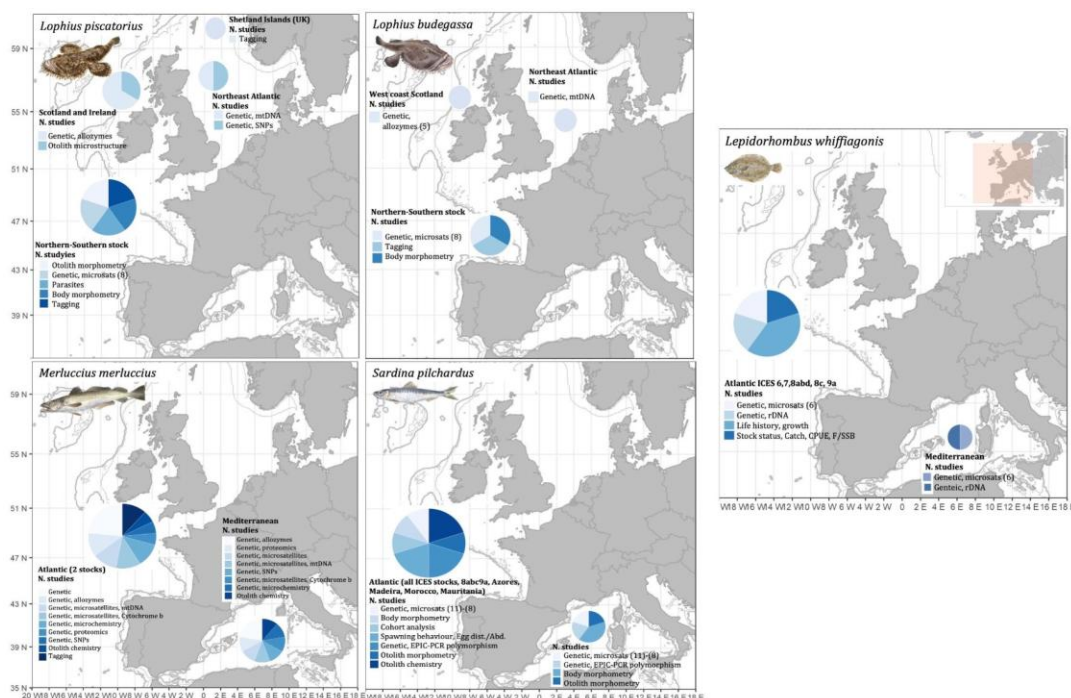

3 Results

3.1. *Lepidorhombus whiffiagonis*

The genus Lepidorhombus is represented in eastern Atlantic waters by two species, megrim (*L. whiffiagonis*) and four-spot megrim (*L. boscii*). Six stocks of megrims are assessed by ICES: megrim in ICES divisions 4a and 6a, megrim in ICES division 6b, megrim in divisions 7b-k and 8abd, four-spot megrim in divisions 7b-k and 8abd, megrim in divisions 8c and 9a and four-spot megrim in divisions 8c and 9a (Figures 2, 3).

The stocks of Lepidorhombus whiffiagonis in 7b-k and 8abd and in 8c9a are analytically assessed in the ICES working group for the Bay of Biscay and the Iberian Waters Ecoregion (WGBIE). The other assessed species of Genus Lepidorhombus in these areas is *L. boscii*. There is a common TAC for both species of megrim (*L. whiffiagonis* and *L. boscii*), so the joint status of the two species should be taken into consideration when formulating management advice.

During an ICES Benchmark for *L. whiffiagonis* in 2014 (ICES, 2014a), it was suggested that 8c9a stock could be just "the tail" of the much larger stock of megrim in ICES subarea 7 and divisions 8abd and

proposed to reconsider the stock limits and the inclusion of this stock in the Northern megrim stock from ICES subarea 7 and divisions 8abd. This option was presented to the ICES Stock Identification Methods Working Group in 2015 (ICES, 2015a) and these were their findings: "SIMWG does not find biological support for combining the northern (ICES divisions VIIb-k and VIIIabd) and southern (ICES divisions VIIIc and IXa) stocks of megrim together and contends that the current stock separation stands. A key paper on population structure of megrim showed a peculiar degree and pattern of genetic separation which merits further review."

Figure 2. Current stocks of *Lepidorhombus* spp. Southern stocks-Div 8c.9a (dark green); Northern stocks – Div 7b-k.8abd (lime) and Northern shelf stock Div 6a.4a (brown).
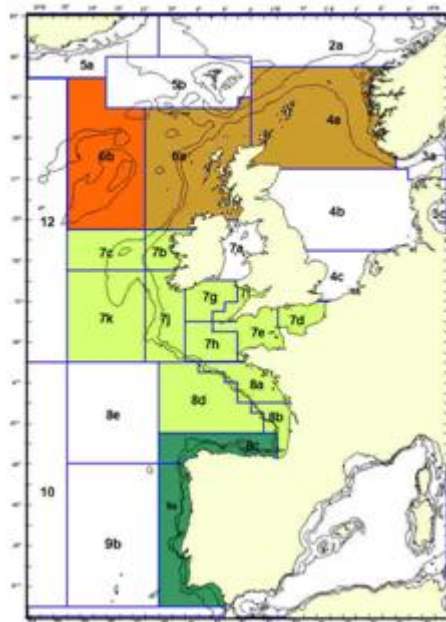
Figure 3. *L. whiffiagonis* and *L. boscii* in NE Atlantic. Stocks presently defined for assessment purposes and TAC zones. The dimension of rectangles and flow lines is proportional to catches.
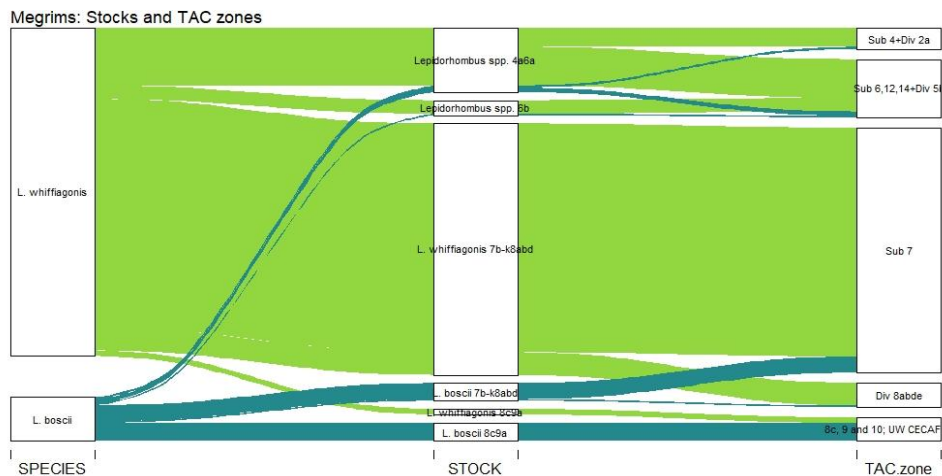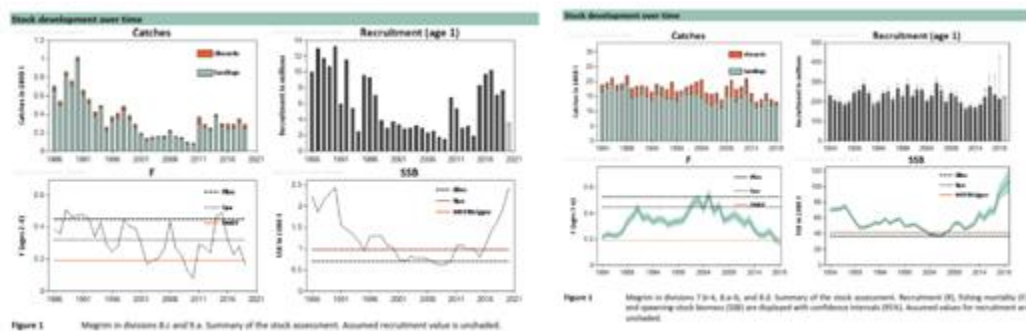
Stock identification studies

Stock status

ICES advice for both stocks in June 2020, shows the stocks development over time. For both stocks, fishing mortality shows a decreasing trend and spawning stock biomass shows an increasing trend (Figure 4).

Figure 4. *Lepidorhombus whiffiagonis*. **Stock status of meg8c9a (left) and meg78abd (right).**

Catch data

In Table 2, time series of landings and discards are shown for both stocks. Catches in megrim stock 78abd are much higher than in megrim stock 8c9a, and this is one of the reasons why it was thought that the southern stock could be part of the northern one.

In Figure 5 the time series of catches and landings of both megrims are shown in different axes and scales. Catches and landings trends in both stocks show similar patterns. Coincident rises and falls are observed but a slight time lag is observed in those trends.

CPUEs trend

Regarding LPUEs from commercial fleets, there are differences in trends between ports in the same area and in the same port in different areas (Figure 5). However, it must be said that they are different fleets and establishing a direct comparison may not be appropriate for this kind of study.

Three megrim abundance indices from research surveys are compared, one in subarea 7, the other in divisions 8abd and the third one in division 8c9a. Research surveys of the species show similar trends in the central and southern zones. However, to match the trend of the northern area (subarea 7) with the other two, an increasing trend is observed in recent years for the 3 abundance indices.

Table 2. *Lepidorhombus whiffiagonis*. Times series of landings and discards for both stocks.

Year	meg8c9a				meg78abd			
	Landings	Discards	Captura	TAC	Landings	Discards	Captura	TAC
1986	659	46	705		18927	2321	21248	
1987	497	40	537	13000	17114	1705	18819	16460
1988	817	42	859	13000	17577	1725	19302	18100
1989	714	47	761	13000	19233	2582	21815	18100
1990	977	45	1022	13000	14370	3284	17654	18100
1991	614	41	655	14300	15094	3282	18376	18100
1992	516	42	558	14300	15600	2988	18588	18100
1993	383	38	421	8000	14929	3108	18037	21460
1994	479	13	492	6000	13684	3284	16968	20330
1995	218	40	258	6000	15862	2652	18514	22590
1996	329	44	373	6000	15109	3026	18135	21200
1997	356	52	408	6000	14230	3066	17296	25000
1998	446	36	482	6000	14345	5371	19716	25000
1999	343	43	386	6000	13305	3297	16601	20000
2000	253	35	288	5000	15031	1870	16901	20000
2001	175	19	193	5000	15778	2262	18040	16800
2002	117	19	137	4000	15987	2813	18800	14900
2003	134	15	148	2400	15711	4008	19719	16000
2004	149	11	160	1336	14358	6243	20602	20200
2005	147	19	166	1336	12888	3275	16163	21500
2006	210	16	226	1269	12037	3751	15788	20400
2007	155	0	155	1440	13060	3033	16092	20400
2008	133	11	144	1430	11048	2860	13908	20400
2009	84	11	94	1430	15064	3278	18342	20400
2010	83	5	88	1287	15101	5343	20444	20106
2011	302	69	371	1094	13226	4187	17413	20106
2012	262	31	293	1214	14433	3704	18137	19101
2013	231	18	250	1214	16025	4885	20910	19101
2014	377	23	399	2257	13277	2569	15846	19101
2015	276	21	297	1377	11569	1507	13076	19101
2016	235	63	298	1363	11548	2445	13992	20056
2017	247	41	288	1159	13784	2173	15957	15043
2018	315	37	352	1387	12147	1738	13885	13528
2019	239	51	289	1872	12164	989	13153	19836

Figure 5. *Lepidorhombus whiffiagonis*. **Comparison of catches (top), LPUEs (medium) and survey indices (bottom) of southern and northern stocks.**
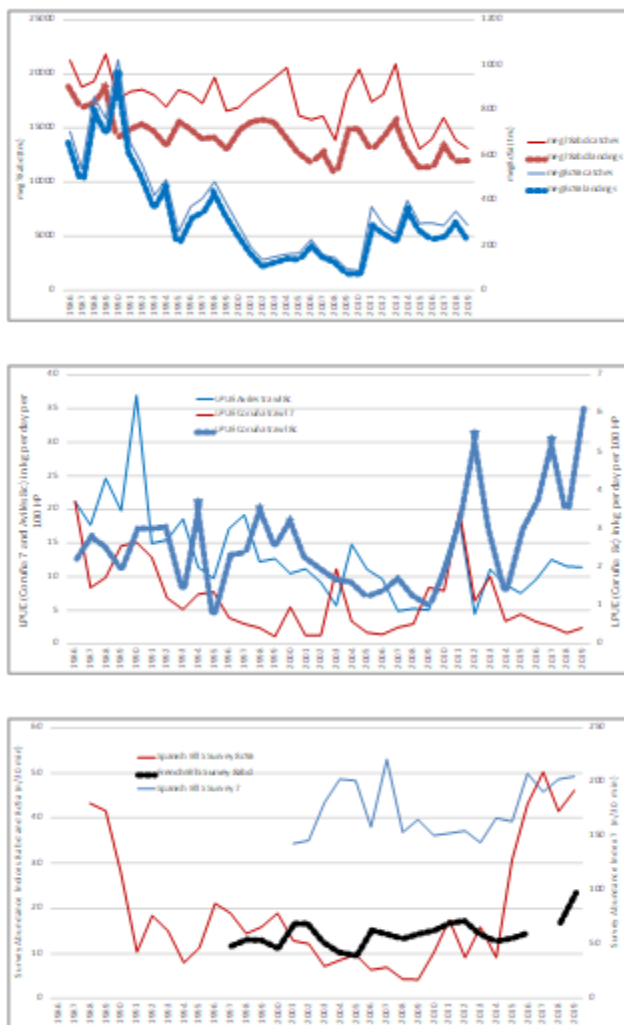
Life history parameters

The growth rate also varies in both stocks (Landa et al. 1996). Growth is quicker in the southern area but the maximum length attained is smaller than in the northern area. The maximum age for megrim also varies with latitude. In subarea 7 the maximum age of megrim is 14 years, this decreases to 12 years in divisions 8c9a (BIOSDEF, 1998; Landa and Piñeiro, 2000). This latitudinal variation in growth, with a greater age range and maximum lengths in the north (division 7chjk), intermediate in the Bay of Biscay (division 8a,b,c2), less in the north of the Galician continental shelf (division 8c1) and least in the south of the Galician continental shelf (division 9a2), where the species is very scarce (Landa and Piñeiro, 2000), can sustain the existence of several populations but does not justify the division in stocks.

Genetic studies

The results of the genetic studies in the area are not very clarifying. Danancher and García-Vázquez (2009) concluded that there are two populations of *L. whiffiagonis* in the Atlantic, fishes from division 6 corresponded to one stock and those from divisions 8c and 9 to a second one. However, the boundaries of these two stocks are not clear, 8abd was clustering with up North sample (6), whereas samples from area 7 clustered with South ones. As no further results have been found, it is difficult to determine if finally the southern stock is more like 8abd division, 7 division or both. Detailed investigations in order to describe megrim population structure and to explain the strange divergences observed in the results are needed.

Conclusion

Although it has been suggested that the southern stock may be the tail of the northern stock, there are issues that still cannot fully support this idea. Figures clearly indicate that LPUEs of megrim are different in ports and areas, suggesting that the productivity and abundance of megrim varies across subareas. It could be that the combination in a single stock will lead to the overexploitation of the less productive populations of megrim.

Furthermore, the differences in growth rates between the areas of the two stocks suggest that there is the probability of different responses to exploitation and environmental changes.

With the current information it is not possible to argue that the two stocks should be joined. In any case, it is necessary to carry out in-depth genetic studies to resolve all existing doubts on this issue in this species, as has already been done for other species that are exploited by the same fleets. The restructuring of the limits of the stocks must be done globally since the management is common to several species.

### 3.2. *Lophius piscatorius* and *L. budegassa*

Two species of anglerfish (the white *Lophius piscatorius* and the black *L. budegassa*) are found in the Northeast Atlantic; however *L. budegassa* has a more southerly distribution than *L. piscatorius.* Both species can be distinguished primarily by the colour of the peritoneum (white or black, from here on the common names, white anglerfish, *L. piscatorius*, and black anglerfish, *L. budegassa* will be used) (Caruso 1986). However, genetic studies show that this method can lead to misidentification of the species due to the lack of colour in the peritoneum in the *L. budegassa* (Aguirre-Sarabia et al. 2021). So, alternative characteristics for species identification such us dorsal and anal fin ray counts or length of the cephalic dorsal fin spines could be also important to consider distinguishing both species (Caruso, 1986). In

addition, genetic studies also showed that some hybrids of both species can be found in the Northeast Atlantic (Aguirre-Sarabia et al. 2021).

Both species are managed by a common TAC and quota system as it is not possible to distinguish species in landings (Table 1; Figure 6).The combined landings are split into species at national level, based on the species composition in the sampling data. Some countries use annual proportions of the two species, others estimate proportions by fleet, port and/or quarter.

Figure 6. *Lophius piscatorius* and *L. budegassa* **in NE Atlantic. Stocks presently defined for assessments purposes and TAC zones. The dimension of rectangles and flow lines is proportional to catches.**
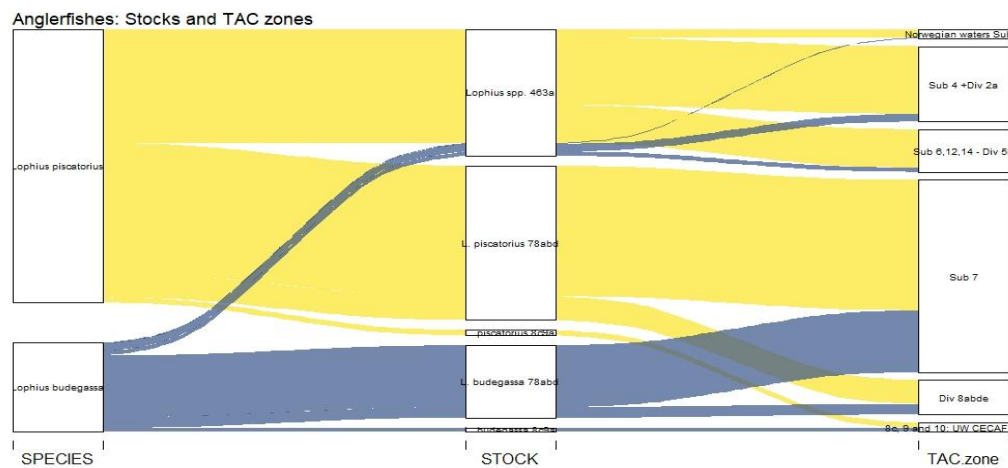
Lophius piscatorius

In the Atlantic northeast, ICES delimits three areas for assessment of white anglerfish: Northern Shelf stock, as combined stock together with black anglerfish (ICES subareas 4 and 6 and division 3a), northern stock (of Southern Shelf) (ICES subarea 7 and divisions 8abd), and southern stock (of Southern Shelf) (ICES divisions 8c and 9a) (Figure 6) (ICES, 2020, 2021). These stocks are considered to be distinct to facilitate the management of the fishery of the species.

In the past two decades, the stock structure of white anglerfish has been studied following different genetic and non genetic approaches (Figure 1). Since 1995, various programs of mark-recapture were carried to characterize the movements and spatial structure of northern and southern white anglerfish stocks (Fariña et al. 2002; Landa et al. 2008; Pereda and Landa, 1997). The displacements observed point to some degree of migratory behaviour of this species and movements of juveniles and adults between the northern and southern stocks. These findings put into question that Canyon of Cape Breton is a geographical barrier for these two stocks. The large-scale movements of adults recorded between Shetland Islands and Faroe and Iceland raised the idea of stock mix (Laurenson et al. 2005).

The morphological study of the otoliths revealed that they were not sufficient evidence to sustain the separation between northern and southern stocks (Cañás et al. 2012). However, this study showed indications of the existence of subpopulations in this area, so a totally panmictic population is not expected. In addition, the meta-analysis of the abundance and prevalence of parasites populations, pointed that there was certain variability between the northern and southern stocks but differences were not enough to discriminate between two stocks (Cañás, 2012). Although morphometric analysis provided reasonable discrimination among populations from western and southern European waters (Duarte et al. 2004), the number samples analysed was considered low to produce robust conclusions. The study of the microstructure of the otoliths suggested that for early life stages the exchange between areas is very limited (Swan, 2004).

The molecular approaches for studying the stock structure of white anglerfish made use of various marker types. Using allozymes, low genetic variation has been detected off the west coast of Scotland (Crozier, 1988) and between populations from the Irish Sea and the west of Scotland (Crozier, 1987). The mitochondrial DNA study of Charrier et al. (2006) revealed a limited genetic structure and lack of isolation by distance. A genetic analysis using polymorphic microsatellite markers (Blanco et al. 2008) strongly concluded that the boundary between northern and southern stocks was not genetically supported. The proportion of total genetic variation between stocks was relatively small (0.35%) and more than 98% of the total genetic variation was attributed to differences within populations, which suggest high gene flow among populations (Blanco et al. 2008). O'Sullivan et al. (2006) means screening adults for nine DNA microsatellites, revealed that there was no evidence of spatial or temporal differences in ICES divisions 4a, 6ab and 7b, deriving from a single panmictic population. Finally, the most recent genetic analysis following a genome-wide approach to identify Single Nucleotide Polymorphisms markers, also pointed at white anglerfish is composed by a single panmictic population throughout the Northeast Atlantic (Aguirre-Sarabia et al. 2021).

Conclusion

Based on the results of genetic and non-genetic studies, it can be concluded that there is no biological evidence, neither genetic nor phenotypic, that supports the separation between stocks presently established. However, phenotypic studies as otolith morphometry and parasites composition, point that the Atlantic population of *Lophius piscatorius* is probably made up of subpopulations.

The spawning mode of white anglerfish, where eggs are enclosed in a gelatinous ribbon that drifts passively on the sea surface, could have a strong effect on dispersal distance and population connectivity (Fariña et al. 2008). Also, the long pelagic larval phase, which is extended during four months, is considered as indicative of the high dispersal potential of the species (Hislop et al. 2001). The eggs and larvae dispersal capacities and the displacements of adults and juveniles support the conclusion of the

existence of a panmictic population, and also confirm that Cape Breton Canyon is not a geographical barrier between northern and southern stocks.

The mismatch between the population structure, the stock structure defined for the assessment and the management units defined for white anglerfish must be led to question the appropriateness of these assessment/management units. One of the main assumptions to establish the northern and southern stocks was that the Canyon of Cape Breton constituted a geographical barrier for population interchanges. The results of the main stock identification studies refute this hypothesis, holding up the presence of a unique panmictic population in the Atlantic Ocean. The management units are usually defined by managers as a group of fish exploited in a specific area or by a specific method, and also taking in consideration administrative and political reasons. As for many other species, the management units of white anglerfish do not reflect the real spatial structure of the species. The impact of this divergence in an efficient management of the resource should be explored and, also, it should be tried to find a balanced definition of stock that includes biological, environmental, and political factors.

Lophius budegassa

ICES delimits three areas for assessment of black anglerfish, the same areas defined previously for white anglerfish (ICES, 2020, 2021) (Table 1).

The studies on the population structure of black anglerfish in the NE Atlantic included genetic studies using allozymes, mitochondrial DNA and microsatellites as markers, tagging experiences and morphometric analysis (Figure 1). Tagging studies detected movements of the black anglerfish between northern and southern populations (Landa et al. 2008). Charrier et al. (2006) found that black anglerfish in the NE Atlantic presented a limited genetic structure and lack of significant relationship between genetic distance and geographic distance (lack of isolation by distance), that are suggesting a high larval dispersal capacity. A low genetic variation of black anglerfish off the west coast of Scotland was also confirmed (Crozier, 1988). Besides, the microsatellite study suggested the existence of differences between populations of different areas, even though the genetic variability is very low (0.21%) and does not support the current separation between northern and southern stock (Blanco et al. 2008). In contrast with previous results, the morphometric analysis showed a high segregation of the Portuguese coast (division 9a) and a north-south gradient, pointing to a more complex population structure than the current one.

Conclusion

Except for morphometric analysis, the stock identification studies support that there is no biological reason for the separation between northern and southern stocks of black anglerfish. However, more studies with samples from the Northern shelf stock are needed to confirm that black anglerfish in NE

Atlantic is a panmictic population. As it happens for white anglerfish, the high dispersal capacity of the larval pelagic phase, that are passively transported by the currents (Hislop et al. 2001; Leslie and Grant, 1990), would support the presence of a panmictic population in the NE Atlantic.

The impact of the current mismatch between the northern and southern stocks established for assessment, management purposes, and the population structure supported by the stock identification studies should be analysed.

3.3. *Sardina pilchardus*

Three stocks of sardine (*Sardina pilchardus*) are assessed by ICES: Sardine in Subarea 7 (southern Celtic Seas and the English Channel), Sardine in divisions 8.a–b and 8.d (Bay of Biscay) and Sardine in divisions 8.c and 9.a (Cantabrian Sea and Atlantic Iberian waters) (Table 1; Figure 7).

Figure 7. *Sardina pilchardus* in NE Atlantic. Stocks presently defined for assessments purposes. The dimension of rectangles and flow lines is proportional to catches.
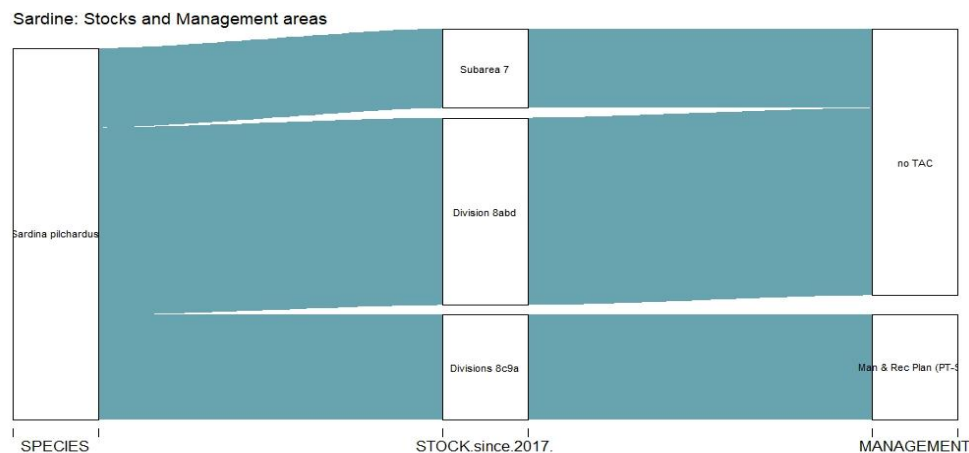

The stock of the Iberian Peninsula (8c, 9a) has always been evaluated separately, but in the case of the northern stocks, they were evaluated jointly until 2017, when the last benchmark takes place. This workshop concluded (Duhamel et al. 2017) that in the absence of evidence of connectivity between the Bay of Biscay and Subarea 7 sardine populations, and taking into account the indications of shelf sustained populations in each area it would be preferable to deal with the Bay of Biscay and Subarea 7 separately.

Stock identification studies

Stock status

In the case of sardine in the southern Celtic Seas and the English Channel (Figure 8), the lack of reliable data makes it impossible to provide advice on fishing opportunities for 2020 and 2021 for this stock. For the other two stocks, ICES advice published in 2020 shows the stocks development over time.

Figure 8. Official landings (1000 t) of sardine in subarea 7 from 1970 to 2018 (ICES, 2019).
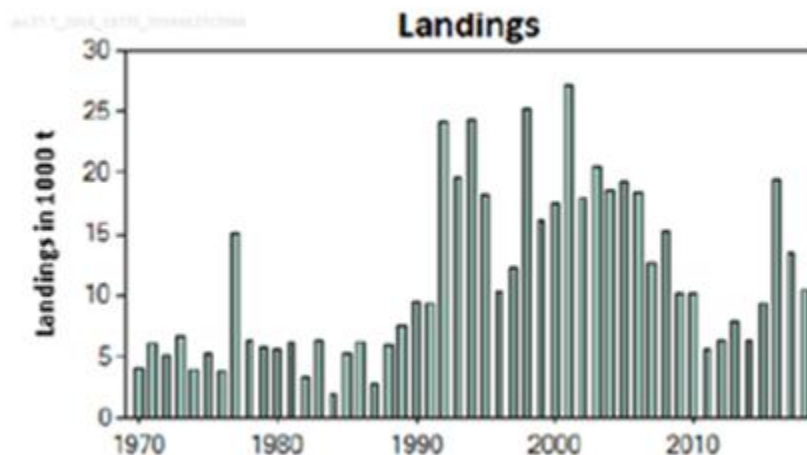
The population of Iberian sardine (sardine in 8c and 9a subdivisions), after a period of crisis, shows signs of recovery. The biomass of age 1 and older fish (biomass 1+ or B1+) is above MSY Btrigger for the first time since 2009. Recruitment in 2019 is the highest since 2004 and above the long-term geometric mean. Fishing mortality has been declining since 2012 and is the lowest in the time-series, but still above F_{MSY} (Figure 9).

The spawning–stock biomass (SSB) of sardine in the Bay of Biscay (Sardine in divisions 8.a–b and 8.d) is above MSY Btrigger. SSB has decreased from 2010 to 2012 to the lower value of the series and has been since then stable. Fishing mortality is now estimated to be below FMSY and recruitment in 2019 is around the time-series average (Figure 10).

Figure 9. Summary of the stock assessment for sardine in divisions 8c and 9a. Assumed recruitment is unshaded. Recruitment, fishing mortality and biomass are indicated with 95% confidence intervals (ICES, 2020a).
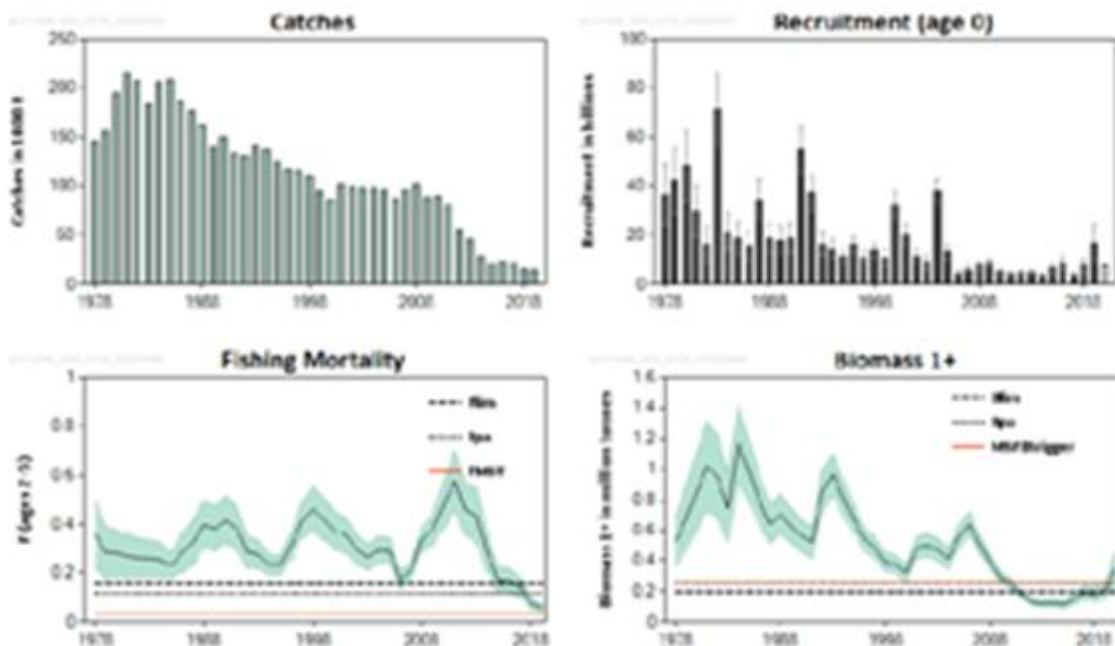

Figure 10. Summary of the stock assessment for sardine in divisions 8a-b and 8d. Recruitment and SSB are estimated at the beginning of the year. The lighter blue 2020 bar in the recruitment graph represents the geometric mean 2000-2019 (ICES, 2020b).

Figure 1   Sardine in divisions 8.a–b and 8.d. Summary of the stock assessment. Recruitment and SSB are estimated at the beginning of the year. The lighter blue 2020 bar in the recruitment graph represents the geometric mean (2000–2019).

Catch data

Catches in the Iberian sardine stock have experienced a drastic reduction from the beginning of the historical series to the present, as a consequence of the significant reduction in biomass and the management measures applied in recent years. In the case of Bay of Biscay stock, catches have been stable since 2000, with a slight rebound since 2012. By contrast, landings in the Celtic Sea have experienced significant fluctuations since 1970, with the highest values recorded in the years 90-2000.

Spawning behaviour and egg and larval dispersion

Several studies on ichthyoplankton phases and sardine reproduction (Bernal et al. 2007; Stratoudakis et al. 2007) have demonstrated overlap in spawning period and continuous egg distribution of sardine along the Atlantic Iberian and French coast with only a persistent gap at the north-western corner of the Iberian Peninsula.

Simulation of egg and larval dispersion (Santos et al. 2018) have shown a high level of larval retention of individuals on local spawning areas, with low transportation between neighbour regions, but with some level of connectivity, especially between western Iberian area and Cantabrian Sea. This study also showed that the existing connectivity between Iberian stock and Mediterranean and Morocco areas was low.

Morphometry

Morphometric studies (Silva 2003; Silva et al. 2008) support the eastern limit of the Atlanto-Iberian stock in the Strait of Gibraltar. For conclusive results, especially in the limits of the stocks (Celtic Channel and Cadiz), more samples are needed.

Otolith shape and microchemistry

Otolith shape differences, due to changes in environmental conditions affecting growth, failed to detect significant structuring between Atlantic and Mediterranean sardine samples (Jemaa et al. 2015). This study found three different groups among the analysed samples: Mediterranean and Gulf of Gabes (Tunisia), Northern Atlantic Morocco to South Alboran, and European Atlantic Coast.

Data on otolith microchemistry (Castro 2007; Correia et al. 2014) support the hypothesis of a metapopulation around the Iberian Peninsula, where sardine stray from western Iberian to North Galicia and the Cantabrian Sea during their first 2–3 years of life.

Cohort track analysis

The analysis of survey data by sub-area inside Iberian area shows recruitment is localized in a few areas and generally asynchronous among areas, although some recruitment peaks are noticeable across wide regions (Silva et al. 2009). A recent modelling study, using number-at-age data of acoustic surveys between 2000 and 2016 from Bay of Biscay to Cadiz, shows that movement was relatively low between three recruitment areas (Bay of Biscay, northern Spain and Portuguese waters). This connectivity pattern does not invalidate the limit between Bay of Biscay and Iberian stock but suggest that the Gulf of Cadiz population should be treated as a separate stock (Silva et al. 2019).

Other studies have demonstrated that migration directions may change over time. These movements seem however to be rather limited and do not indicate any large-scale migration but rather a connectivity between sub-populations (Carrera and Porteiro, 2003; Silva et al. 2009).

Genetic studies

This species has been the subject of numerous genetic studies, using different molecular markers, both in the Iberian stock and in adjacent areas to the North, in Morocco or in the Mediterranean (Atarhouch et al. 2007; Gonzalez & Zardoya 2007; Kasapidis et al. 2012). In general, results question the northern (Cantabrian Sea-southern France) and southern stock limits (Gulf of Cadiz-northern Morocco) because they do not appreciate evident genetic structure (see Kasapidis, 2014 for a review).

Conclusion

Most of the studies have focused on the limits of the Atlantoiberian area. With the multidisciplinary results obtained so far, there is no sufficient evidence to modify the current boundaries of the stock, although there are signs of regional structuring, especially in the area of Gulf of Cadiz, despite no genetic differences have been found.

Dynamics of the Southern stock is not significantly affected by the dynamics of the Northern stock.

3.4. *Merluccius merluccius*

European hake, *Merluccius merluccius,* is widely distributed along the North East Atlantic, from Mauritanian in the North to Norway in the North, and the Mediterranean. ICES identifies two stocks of *M. merluccius* in the Atlantic area: the northern stock distributed in ICES subareas 4, 6, and 7, and in divisions 3.a, 8.a–b, and 8.d, and the Southern stock in ICES Divisions 8c and 9a. The definition of the two Atlantic stocks (Northern and Southern) separated by the 8c-8abd boundary, was decided in 1979 (ICES, 1979). Previously their population was split in 3 parts, in 1979 the ICES working group that assessed the stocks had a ToR asking if the two stocks in the Bay of Biscay in the French and Spanish coast were a common stock. However, it was decided to join the two areas in the North corresponding to

the fish caught in Community waters and leaving as a separate stock the Southern stock, those caught outside community waters (at that time) in the coast of Spain and Portugal. The reason was based on:

1.   Lack of biological basis for existence of sub-stocks

2.   Imprecise allocation of catches in ICES sub-areas and divisions

3.   No evidence of juveniles in 4a and 6a, assuming that catches there were derived from nursery grounds further south.

4.   Evidences from Spain and Portugal of recruitment failure, not apparent in the Northern stock

There are some contradictory reasons here since the imprecise allocation of catches mainly referred to Spain whose statistics were based on the port were the catches were landed instead of origin of catches. Then, catches in Sub area 8 were reported jointly without considering the division they belonged to, and catches in 9a included catch from the North of Africa, a quite important hake fishery at that time. However, the conclusion on the recruitment failure in the Southern stock was based on this imprecise catches and their length structure that included catches in all the Bay of Biscay and also in the North of Africa.

The next ICES WG on Hake (ICES, 1980) supported the new stock distribution with the following arguments: "This arrangement has been based primarily on the distribution of nursery grounds and apparent differences in recruitment trends between the two areas. In addition, the narrow continental shelf along the northern coast of Spain and the Cap Breton depression also serve as a geographical barrier. … noting that different arrangements may be more appropriate when additional data become available".

Figure 11. *Merluccius merluccius* in NE Atlantic. Stocks presently defined for assessments purposes and TAC zones. The dimension of rectangles and flow lines is proportional to catches.
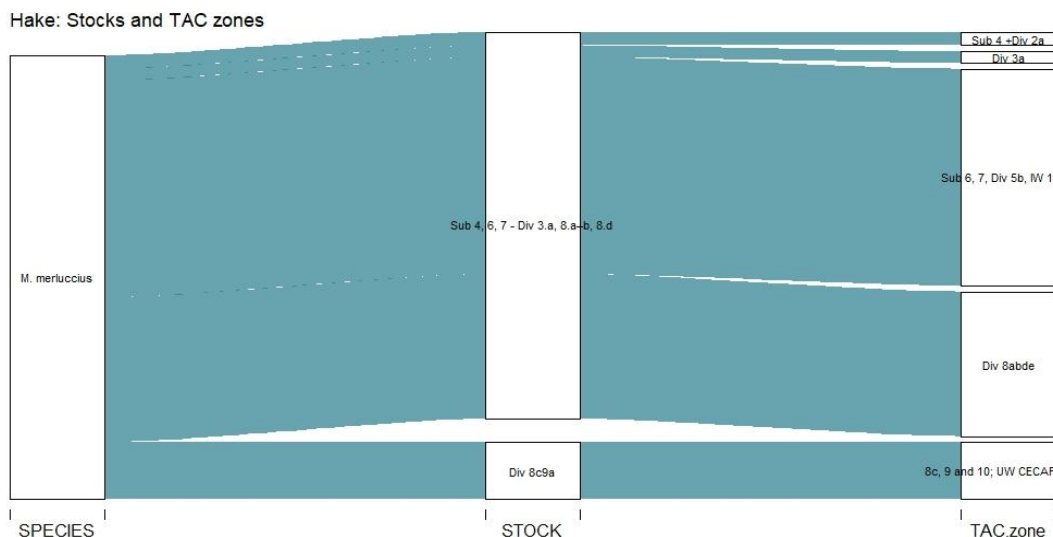
Stock identification studies

Stock status

In the last part of the 20th century and the beginning of the current one, the biomass level of both stocks followed similar trends. At the beginning of 2000s' the depletion of both stocks was high which led to the implementation of two of the first recovery plans in the CFP (COM 2003, 2004). Both stocks showed signals of good recruitments around 2005-10 and eventually increased the SSB. However, the fishing mortality in the Northern stock decreased meanwhile that in the Southern stock remained high which led to a different stock status. Around 2010 both stocks were considered to be recovered, although the increase in the biomass in the northern stocks was considerably higher which led the stock to a better state. The high increase in the biomass of Northern stock produced a north east expansion of the stock (ICES, 2017). The expansion has been a matter of concern for the fishing fleets in the North Sea because the high abundance together with the landing obligation and the low catch quotas produced a choke effect for the mixed fisheries (Baudron and Fernandes, 2015). The big retrospective pattern in the assessment of the Southern stock of hake motivated the rejection of the assessment ICES (2020). Thus, the current biological state in relation to reference points is unknown.

Surveys trend

The correlation between survey estimates of recruitment and total biomass in the Bay of Biscay and Iberian peninsula was analysed using the time series available to the group and considering as recruits individuals below 20 cm. The obtained correlations are shown in Figure 12, the order of the surveys in the figure follows their spatial distribution from north to south. The correlations were stronger at biomass level probably motivated by the differences in length frequency distributions at spatio-temporal level. For instance, there is an strong positive correlation between nhke_EVHOE and nhke_GFS surveys at biomass level but for recruitment the correlation is negative. In the recruitment surveys in the south, there was a correlation between adjacent surveys. Surprisingly, there was a positive correlation between the survey further south (shke_cdAutGFS) and that further north (nhke_PORCUPINE). The nhke_PORCUPINE surveys also had a positive correlation between the Irish survey (nhke_IGFS). At biomass level, nhke_PORCUPINE index did not have any correlation with the other two surveys that correspond with the northern stock. However, there was a strong correlation with those in the South. The population segment sampled by nhke_PORCUPINE and the other two northern hake surveys are very different, with the nhke_IGFS and nhke_EVHOE more focused in younger individuals.

Figure 12. *Merluccius merluccius* **in NE Atlantic. Correlation between abundance estimated from scientific surveys in Bay of Biscay. The left hand plot corresponds with the correlation of number of individuals smaller than 20 cm over time and the right hand side with total biomass.**
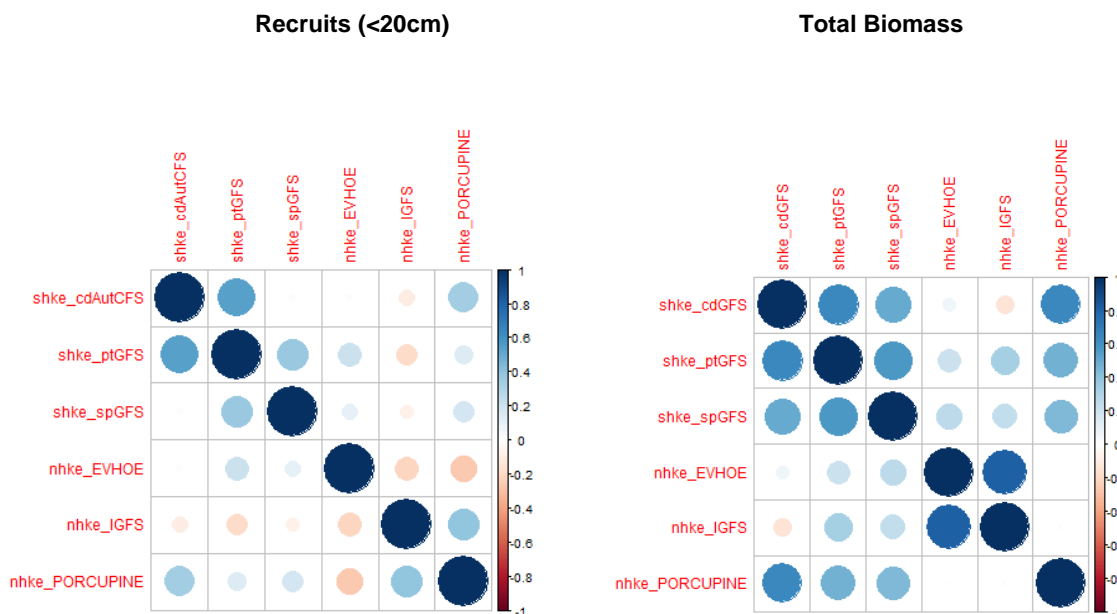
Life history parameters

There are many life history studies published on growth, reproduction or natural mortality for European hake in Atlantic water. A good summary can be found in Korta et al. (2015). Growth studies are not conclusive regarding stock structure because problems identifying otolith rings and lack of other kind of data. Extensive tagging experiences were only developed in French Brittany waters. Natural mortality studies are not conclusive for similar reasons. Reproductive studies show that length at maturity increases with latitude and also that the reproductive season is more extended in the South than in the North (Korta et al. 2015). Significance differences between Galician coast and French coast reproductive parameters were found by Korta et al. (2010) although the authors explain that these can be caused by phenotypic plasticity driven by environmental or fishing differences. Domínguez et al. (2008) also found reproductive differences between areas (Galician and French desks) getting similar conclusions and suggesting that there is no reason to split both stocks although some kind of substock structure may be in play.

Tagging experiences

Two tagging experiences were performed in Northern stock (de Puntual et al. 2003 and 2013) and the Southern stock (Piñeiro et al. 2007). 27 690 were tagged in French Brittany waters between 2002 and 2007 and 1199 (4.3%) have been recovered (de Puntual et al. 2013) with a maximum time before

recovery of 1555 days. Data did not reveal seasonal movements of hake and none of these tagged hake in Northern stock area was recovered in the Southern stock one. Most fish were recovered near their release locations although a few of them travelled long distances (around 150 miles), suggesting that some exchange at a population level would be possible. However none was recovered outside their original stock area.

A similar tagging experience was developed in the Northwest of Spain following the procedure designed by de Puntual et al. (2003) although the amount of tagged and recovered fish was lower. 527 live tagged individuals were release and fifteen months after tagging, seven individuals (1.3%) had been recaptured with times at liberty ranging from 29 to 466 days. None of them was recovered far away from the release area. The maximum distance recorded was around 15 miles from release location after 347 days.

Results from both analyses revealed homing behaviour and/or inshore residency. None of the hake tagged in Northern or Southern waters was recaptured out of their original stock area.

Genetic studies

We have made an extensive analysis of all genetic data of European hake published up to date. The approach of the genetic studies has been different regarding the genetic markers, spatial coverage, time series, sampling procedure or statistical tests used. In general, all the genetic information shows a pattern of connectivity among Atlantic populations of hake regardless of the subdivision in stocks by the ICES, although the level of connectivity is different depending on the type of data.

The genetic structure of the Atlantic population has been addressed in the last decades using different genetic markers such as allozymes (Roldán et al 1998; Cimmaruta et al. 2005), mtDNA (Lundy et al. 1999; Pita et al. 2010, 2017) or microsatellites (Lundy et al. 1999; Castillo et al. 2004; Pita et al. 2014; 2016; 2017). In all cases, the results suggested that this two stocks model does not reflect the actual population dynamic between these areas, which seems to be more complex than that established by ICES.

The data obtained from North and South stocks shows higher genetic homogeneity than those expected for two independent populations. A heterozygote deficit was observed for genetic markers in most areas (Lundy et al. 1999; Castillo et al. 2004) and recent spatiotemporal studies suggest the wide genetic connectivity within the North-eastern Atlantic metapopulation (Pita et al. 2011, 2014, 2016). The migration hypothesis proposed by Pita et al. 2011 suggests that no barriers to migration seem to exist between the main Atlantic hake stocks, and there is a migrant flow of adult hakes from Porcupine Bank and Great Sole to the Bay of Biscay, the Cantabrian Sea and the Iberian Atlantic waters. These results are congruent with the observations on the dynamics of egg and larvae in the Bay of Biscay (Álvarez et al. 2004) as well as with a migration between "stocks" mediated by the passive drift of larvae and pre-recruits (Bartsch et

al. 1996). However, other studies suggested the existence of a more complex population structure within each ICES stock in the North-eastern Atlantic than just a single panmictic population. For instance, significant genetic differences were reported in the Northern stock between Norwegian and Celtic samples using six microsatellites (Lundy et al. 1999; Castillo et al. 2004), or between Irish and French samples using 21 allozymes (Roldán et al. 1998). Recent analyses of SNP Outlier loci showed differentiation between the Bay of Biscay and the North Sea and the Norwegian Sea samples (Milano et al. 2014; Westgaard et al. 2017). According to Leone et al. (2019) additional analyses are needed to consider the Norwegian Sea and possibly the North Sea as a separate stock. In addition, proteomics surveys showed two different cluster when samples from the Bay of Biscay and the Cies Island were compared (González et al. 2010), and the genetic differentiation increases progressively as the samples are taken from southern waters off the Portugal coast (Lundy et al. 1999). In the Gulf of Cádiz (SW of Iberian Peninsula), the genetic structure seems to be more related with the Mediterranean population rather than the North-East Atlantic stocks (Tanner et al. 2014). Pita et al. (2017) using microsatellites conclude that the Southern Stock is formed by a single gene pool provided its wide Atlantic connectivity.

Combination of markers and methods

The combination of genetic markers and other methodological approaches, such otolith chemistry, improves the overall accuracy in the determination of the fishery units (Tanner et al. 2014), and represents a useful tool to establish the exploitation and biological status of the stock. However, the choice of one genetic parameter to integrate this information is not a simple question, due to the high variability in time and space scales among the sampling procedures.

In general, all genetic data show a pattern of connectivity among Atlantic populations of hake regardless of the subdivision in stocks by the ICES. The Bayesian inference made on multilocus genotypic data (microsatellites) of *Merluccius merluccius* populations provides evidence that a large genetic connectivity exists among Atlantic grounds and is mediated by significant migration rates stepping up from the Celtic Sea towards its adjacent Atlantic grounds. SNPs analysis shows similar results.

Conclusion

The original ICES scientific support for splitting both stocks in 1977 were not consistent. Imprecise catch data and flaw scientific evidence were the basis to take this decision that remains since then.

Genetic studies show a pattern of connectivity among Atlantic populations of hake regardless of the division of the population in two stocks by the ICES. Genetic differences between 8c (Southern stock) and 8abd (Northern stock) are lower than those between 8c and 9a (both in the Southern stock).

Tagging studies show that hake migrations are not large. However there is a continuity in the hake distribution along the coast of both stocks without any clear barrier impeding movements along.

Life history studies show differences between reproductive traits in both stocks. However there are environmental and fishing pressure differences that can explain these phenotypic differences.

Current ICES stock structure with two stocks is not supported by any of the studies reviewed.

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