

# BENCHMARK ON SELECTED SEA BASS STOCKS—STOCK ID WORKSHOP (WKBSEABASS-ID)

VOLUME 5 | ISSUE 52

ICES SCIENTIFIC REPORTS

RAPPORTS  
SCIENTIFIQUES DU CIEM



## International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

H.C. Andersens Boulevard 44-46  
DK-1553 Copenhagen V  
Denmark  
Telephone (+45) 33 38 67 00  
Telefax (+45) 33 93 42 15  
[www.ices.dk](http://www.ices.dk)  
[info@ices.dk](mailto:info@ices.dk)

ISSN number: 2618-1371

This document has been produced under the auspices of an ICES Expert Group or Committee. The contents therein do not necessarily represent the view of the Council.

© 2023 International Council for the Exploration of the Sea

This work is licensed under the Creative Commons Attribution 4.0 International License (CC BY 4.0). For citation of datasets or conditions for use of data to be included in other databases, please refer to ICES data policy.



# ICES Scientific Reports

Volume 5 | Issue 52

## BENCHMARK ON SELECTED SEA BASS STOCKS–STOCK ID WORKSHOP (WKBSEABASS-ID)

Recommended format for purpose of citation:

ICES. 2023. Benchmark on selected sea bass stocks–stock ID workshop (WKBSEABASS-ID).  
ICES Scientific Reports. 5:52. 31 pp. <https://doi.org/10.17895/ices.pub.22794737>

### Editors

David Murray

### Reviewers

Florian Berg • Naiara Rodríguez-Ezpeleta

### Authors

Michel Bertignac • Francis Binney • Massimiliano Cardinale • Ilaria Coscia • David Curtis  
Chloé Dambrine • Françoise Daverat • Hélène de Pontual • Mickael Drogou • Kerrie-Anne Egre  
Pierre-Alexandre Gagnaire • Jolien Goossens • Jennifer Graham • Kieran Hyder • Philip Lamb  
Gwladys Lambert • David Murray • James Stewart • Anna Sturrock • Michelle Taylor • Filip Volckaert  
Joseph Watson • Ciara Wögerbauer • Mathieu Woillez • Serena Wright



**ICES**  
**CIEM**

International Council for  
the Exploration of the Sea  
Conseil International pour  
l'Exploration de la Mer

# Contents

i	Executive summary .....	ii
ii	Expert group information.....	iii
1	Introduction.....	1
1.1	Terms of reference .....	1
1.1.1	Background .....	1
1.2	Evidence presented .....	2
1.2.1	Challenges with inclusion of mixing in stock assessments (Gwladys Lambert) .....	2
1.2.2	Estimating abundance indices of juvenile fish in estuaries using geostatistics: An example of European sea bass ( <i>Dicentrarchus labrax</i> ) (Mathieu Woillez) .....	2
1.2.3	Drivers of year-class strength in European sea bass (Joseph Watson) .....	3
1.2.4	Modelling connectivity estimates of European sea bass ( <i>Dicentrarchus labrax</i> ) early life stages from spawning to nursery areas in the Northeast Atlantic using an individual based model (Chloé Dambrine).....	3
1.2.5	Pelagic connectivity estimates of European sea bass between spawning and nursery grounds (Jennifer Graham) .....	4
1.2.6	Estimating migration and mortality rates for European sea bass ( <i>Dicentrarchus labrax</i> ) off the French coast using electronic tagging (Michel Bertignac) .....	4
1.2.7	Spatio-temporal changes in behavioural strategies for European sea bass (Serena Wright).....	5
1.2.8	Seasonal migration, site fidelity and population structure of European sea bass: Shedding light from large-scale electronic tagging (Helene de Pontual).....	5
1.2.9	Chosen-mixity and safer(r) space for European sea bass: Population structure affects the degree of protection (Jolien Goossens) .....	6
1.2.10	Coupling natural and electronic tags to explore spawning site fidelity and natal homing in Northeast Atlantic European sea bass (Françoise Daverat).....	6
1.2.11	Seasonal variation in population structure of Atlantic sea bass ( <i>Dicentrarchus labrax</i> ) revealed by combining genomic variation with reconstructed trajectories (Pierre-Alexandre Gagnaire).....	6
1.2.12	Genetics of European sea bass ( <i>Dicentrarchus labrax</i> ) in the northern Atlantic using SNPs (Philip Lamb).....	7
2	Review information on stock identification of sea bass stocks bss.27.4bc7ad-h and bss.27.8ab (ToR 1) .....	8
2.1	Genetics .....	8
2.2	Otolith and scale microchemistry .....	10
2.3	Tagging.....	11
2.4	Pelagic connectivity .....	14
2.5	Summary and conclusions .....	16
3	Plausible scenarios for sea bass stocks around the UK and Bay of Biscay (ToRs 2, 3, 4).....	18
3.1	Stock delineation .....	18
3.2	Potential scenarios for the benchmark.....	20
3.3	Data call .....	21
4	Future recommendations (ToR 5) .....	22
5	References.....	23
Annex 1:	List of participants.....	26
Annex 2:	Resolutions .....	28
Annex 3:	Reviewer reports.....	30

## i Executive summary

ICES provides advice on two sea bass (*Dicentrarchus labrax*) stocks; a 'northern' stock in divisions 4.b-c, 7.a, and 7.d-h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel and Celtic Sea), and a southern stock in divisions 8.a-b (Bay of Biscay). This Workshop reviewed evidence and proposed plausible stock structure scenarios for the ICES sea bass benchmark in 2023 (WKSEABASS). In summary, evidence suggests that the current ICES stock units do not reflect the biological boundaries and connectivity of sea bass within these areas. Evidence from genetic (section 2.1), tagging (section 2.3) and larval/juvenile pelagic drift (section 2.4) studies, revealed a high degree of connectivity between the northern and southern sea bass stock units. Furthermore, genetic (section 2.3) and tagging (section 2.3) evidence revealed potential boundaries within the northern sea bass stock, particularly between the North Sea and the Celtic/Irish Sea. The group agreed that evidence suggested a single meta-population structure, meaning a group of spatially separated populations interacting at some level (i.e. migrating, reproducing, feeding). Based on evidence provided, three plausible population scenarios were identified:

- **Hypothesis 1:** Three subpopulations, Irish Sea (7.a), North Sea (4b-c), southern Bay of Biscay (8.b); with mixing among the Celtic Sea (7.f-g), Bristol Channel (7.h), English Channel (7.d-e) and Northern Bay of Biscay. Mixing is seasonally dependant with more mixing occurring during summer compared to winter.
- **Hypothesis 2:** Three subpopulations, Irish Sea (7.a), North Sea (4.b-c) and Bay Biscay (8.a-b); with mixing among the Celtic Sea (7.f-g), Bristol Channel (7.h) and English Channel (7.d-e). Mixing is seasonally dependant with more mixing occurring during summer compared to winter.
- **Hypothesis 3:** Three subpopulations, Irish Sea (7.a), North Sea/eastern English Channel (4.b-c, 7.d) and Bay Biscay (8a-b); with mixing among the Celtic Sea (7.f-g), Bristol Channel (7.h) and western English Channel (7.e). Mixing is seasonally dependant with more mixing occurring during summer compared to winter.

It was not possible to choose between these scenarios or rank them in order of likelihood. National data should be requested by ICES Division within the data call as this will allow assessment approaches to be developed at relevant scales. ICES stock assessors will need to agree on what data are necessary to consider these three scenarios before the WKSEABASS data call and benchmark in 2023. However, if the available data are insufficient to accurately assess stocks based on these hypotheses, then the group agreed on two other scenarios that could be considered:

- **Scenario A:** Continue to assess the 'southern' (ICES divisions 8a-b) and 'northern' (ICES divisions 4.b-c, 7.a and 7.d-h) stocks separately but incorporate mixing between stocks.
- **Scenario B:** Single meta-population between northern and southern stocks.

While research has provided additional information regarding biologically relevant stock boundaries for sea bass, more research is required to narrow down these scenarios and identify robust biologically relevant stock units. Additionally, similar levels of research are required to elucidate the connectivity of the sea bass populations delineated within this current workshop to West of Scotland and Ireland (ICES divisions 6.a, 7.b and 7.j) and Iberian (ICES divisions 8.c and 9.a) stocks that are not included in this benchmark process.

## ii Expert group information

<b>Expert group name</b>	Benchmark on selected sea bass stocks–stock ID workshop (WKBSEABASS-ID)
<b>Expert group cycle</b>	Annual
<b>Year cycle started</b>	2022
<b>Reporting year in cycle</b>	1/1
<b>Chair</b>	David Murray (Cefas), UK
<b>External reviewers</b>	Naiara Rodríguez-Ezpeleta (AZTI), Spain Florian Berg (IMR), Norway
<b>Meeting venue and dates</b>	29 November–31 2022, online meeting (27 participants)

# 1 Introduction

## Benchmark on selected sea bass stocks—stock ID workshop

### 1.1 Terms of reference

- 1) Review information on stock identification for bss.27.4bc7ad-h and bss.27.8ab and conduct a comparative review of Atlantic sea bass population structure, including critical evaluation of inferences from each source of information, to build up a picture of sea bass stock structure in Celtic Sea, Bay of Biscay and adjacent areas, based on the following:
- 2) Distribution and movements of different life-stages of sea bass, including changes over time, inferred from:
  - a. Tagging.
  - b. Scientific surveys.
  - c. Commercial landings.
  - d. Dispersal models (e.g. of larva/juveniles).
  - e. Genetic analyses.
  - f. Otolith microchemistry.
  - g. Morphometrics and meristics.
  - h. Life history and parasites.
  - i. Other approaches not listed above.
- 3) Based on the evidence from ToR 1, formulate scenarios for sea bass stocks in the Celtic Sea, Bay of Biscay and adjacent areas, and assess the evidence-based plausibility of each of these scenarios (including current definitions).
- 4) Consider the practical implications, for data, particularly time-series of catch data and year-class strength, and mixing rates of each of the scenarios in ToR 2, and how any difficulties might be dealt with. For example, considering spatial components with mixing in a single model has different implications for data compared to split stock units. Considerations should include how to deal with changes over time.
- 5) Make recommendations for which sea bass stock scenario(s) to take forward in the forthcoming sea bass benchmark, including in what format data should be requested and prepared.

#### 1.1.1 Background

The upcoming 2023 joint benchmark for Northern (ICES divisions 4.b-c, 7.a and 7.d-h) and Biscay (ICES divisions 8.a-b) stocks of sea bass requires information on the probable biologically relevant stock structures within the Northeast Atlantic. This workshop and its members were specifically tasked to generate potential stock scenarios for consideration at the benchmark.

Connectivity between the Northern and Biscay has long been recognized through adult movement and larval drift, but the evidence was not available at the last benchmark in 2018 to assess stock structure. However, recent studies on genomics, tagging and particle tracking has increased the evidence available for assessing the validity of current ICES sea bass advice units as well as delineating new boundaries. This report contains the evidence provided to WKSEABASS stock identification workshop as well as the group members conclusions.

## 1.2 Evidence presented

Evidence relevant to stock identification for sea bass was presented in several different areas including: pelagic connectivity, year-class strength, adult behaviour, otolith microchemistry, and genetics. These are summarized below.

### 1.2.1 Challenges with inclusion of mixing in stock assessments (Gwladys Lambert)

Currently ICES considers four sea bass assessment stock units. Two of those are assessed annually with one covering the North sea, Channel, Celtic Sea and Irish Sea and the other the Bay of Biscay. An exercise was conducted to join the two separate stock units into a single model to test the feasibility of accounting for some mixing between the two areas and to evaluate the data requirements. This was done in Stock Synthesis, which is the current modelling framework for the assessment of both these stocks, but which can also be set up to include recruitment apportionment and age-based migration rates between multiple areas. Some key challenges and aspects that would require careful considerations were identified. Those were: data inclusion and data weighting, e.g. when data in one area are more informative than in the others; time-series that cannot be disaggregated between areas; need for tagging data for model development and validation, e.g. to avoid unrealistic outputs when fitting migration rates; whether it is realistic and required to fully capture sea bass behaviour by including seasonality and more area-based disaggregation to account for feeding/spawning migrations at a smaller spatial scale; and how to forecast and predict effect of area-based management measures.

### 1.2.2 Estimating abundance indices of juvenile fish in estuaries using geostatistics: An example of European sea bass (*Dicentrarchus labrax*) (Mathieu Woillez)

Estuaries play a fundamental role in the renewal of fisheries resources, as they hold nurseries for many juvenile fish species. Estimating juveniles' abundance in estuaries is therefore key to improve stock assessment models, anticipate future recruitment and prevent crises related to biomass collapse. While geostatistical methods have been widely used in fisheries science to estimate species' abundance during offshore scientific surveys, difficulties arise when using these methods in estuaries. Indeed, these ecosystems are characterized by their irregular and often non-convex morphology, their environmental gradients (salinity, depth), and their tidal dynamics which question the validity of the hypothesis of second-order stationarity, fundamental to the theory of intrinsic geostatistics. Therefore, we tested the performance of different geostatistical methods to account for the complexity of these ecosystems and quantify robust indices of abundance adapted to estuaries (Roy *et al.*, 2022). We used density data of juvenile sea bass (*Dicentrarchus labrax*) sampled with demersal trawls in the Loire River collected over three consecutive years and tested a metric space for which the distance along the estuary is considered. We considered the non-stationarity of densities with either a transitive approach or an intrinsic approach with spatio-temporal external drifts, which considers the effects of tides and environmental gradients. These geostatistical methods allowed us to produce densities distribution maps and had substantially greater predictive capabilities than the stratified random estimator (classical reference estimator). However, geostatistical methods consistently had larger CVs than the stratified random estimator because the latter ignores the spatio-temporal distribution of sampling points leading to uncertainties underestimates and hence overly optimistic confidence intervals. The use of geostatistically computed abundance indices in an assessment model

appears to be a conservative approach, whose uncertainties would allow a more robust adjustment trade-off between different indices when estimating recruitment in estuaries.

### **1.2.3 Drivers of year-class strength in European sea bass (Joseph Watson)**

The northern sea bass stock has experienced a sharp decline from 2009–2018, which has been attributed to a combination of high fishing mortality and poor year-class strength and is now showing signs of recovery. Management measures were implemented in 2015 to reduce fishing mortality, but the mechanisms behind the continued weak year classes observed are not well understood. We use generalized linear models to identify important local environmental and biological drivers of sea bass abundance/dynamics. Drivers are split into those that effect the supply of larvae to the nursery areas (the population size of possible predators of juvenile sea bass in the North Sea and English Channel, and sea bass stock size) and those that effect the abundance within the estuary (sea surface temperature, chlorophyll-a concentration, and river flow). We focus on seven estuarine areas around the British and Irish coast that are important to the northern stock of European sea bass. After analysis the main conclusion is the lack of coherence between the most important drivers across the estuaries tested. The results highlight the potential need for area specific and environmentally driven stock recruitment relationships (SRR) that could be used in ICES stock assessment models. By incorporating biophysical drivers into area specific SSRs for sea bass, it may be possible to improve the fit of assessment models and increase confidence in predictions.

### **1.2.4 Modelling connectivity estimates of European sea bass (*Dicentrarchus labrax*) early life stages from spawning to nursery areas in the Northeast Atlantic using an individual based model (Chloé Dambrine)**

Since 2013, European sea bass Northern stock has faced successive years of low recruitment. High fishing pressure and poor recruit settlement have been pointed out. To investigate the second option, and particularly the effect of the environment on sea bass early life stages, we used a coupled bioenergetics model and a particle-tracking model to simulate the growth and drift of eggs and larvae over a seven year period (2008–2014) in the Northeast Atlantic. Due to the lack of information to support our model assumptions, we tested the sensitivity of the results to spatial and temporal factors and larval vertical behaviour. Then, connectivity estimates to coastal areas from many previously identified spawning areas were investigated throughout the spawning season. To highlight recurring spawning and nursery areas among years that are likely to be key areas for the species recruitment success, we used the graph-theory approach and identified two contrasted years in terms of connectivity patterns. By comparing them, we showed that mild winters enhances the connectivity estimates and dispersion of larvae, particularly in the English Channel. We also corroborated: (i) a low percentage of connectivity estimates (< 1%) in the study area, (ii) higher settlement success in the English Channel than in the Bay of Biscay, (iii) higher success of coastal compared to offshore spawning areas, and (iv) slight differences in the supply of coastal areas in the Bay of Biscay, depending on the larval vertical behaviour. The framework developed could allow addressing how connectivity is affected by global change.

### 1.2.5 Pelagic connectivity estimates of European sea bass between spawning and nursery grounds (Jennifer Graham)

Understanding mechanisms that drive the number of young sea bass reaching nursery grounds is important for explaining observed recruitment variability, as well as the connectivity between different populations. An individual-based model (IBM) has been developed here to investigate factors affecting sea bass settlement on nursery grounds for the northern stock. Simulations considered seven years with varying environmental conditions and year-class strength, and outputs were compared to data from monitoring of nursery areas in the UK and Ireland. The model was able to reproduce some patterns of observed variability but appears to perform better in some regions than others. Nevertheless, the model provides a useful tool for understanding the factors driving sea bass year-class strength, demonstrating spawning regions that are likely to have greatest influence on recruitment in different estuaries, and how these may vary interannually. For example, sources from western Channel and Celtic Sea can supply larvae to many areas, leading to connectivity across the Channel and Celtic Sea, and into the Irish Sea. However, other regions may depend on more local spawning areas. For example, with the Solent estuary dependent on sources within the eastern and western Channel each year. Sources outside the northern stock region, in the Bay of Biscay, are likely to provide a significant source to nursery grounds in the western Channel (including Fal and Helford). With the temperature-dependence on growth, and therefore duration of the pelagic stage, results also show the potential influence of spawning timing, in relation to ocean temperatures, for connectivity between spawning and nursery grounds.

### 1.2.6 Estimating migration and mortality rates for European sea bass (*Dicentrarchus labrax*) off the French coast using electronic tagging (Michel Bertignac)

From 2010 to 2016, 1466 European sea bass, *Dicentrarchus labrax*, were tagged with archival tags and released on 11 locations along the Atlantic French coast from Dunkirk to Capbreton. By August 2021, more than 500 tags had been recovered and returned. Depths and temperatures recorded on the tags have been used to reconstruct individual trajectories using a Hidden Markov-based geolocation model (Woillez *et al.*, 2016; Heerah *et al.*, 2017; de Pontual *et al.*, 2019; de Pontual *et al.*, in revision). To analyse the reconstructed individual trajectories and estimate movement rate and fishing mortality at population scale, a spatially structured population dynamics model of the tagged fish, discrete in space and time has been developed. The spatial discretization considers two areas separated by latitude 48N and corresponding to the stocks assessed analytically by ICES. Two temporal discretisations were tested based on two different time steps (semester and trimester). Several model configurations were compared with migration rates (expressed in terms of instantaneous transfer rates  $T$  between areas) estimated by area or by area and season, fishing mortality ( $F$ ) estimated by area, by area and season or assumed constant over area and seasons. The best fits were obtained with  $F$  constant, and  $T$  estimated by area and season for the semester model and with both  $F$  and  $T$  estimated by area and season for the trimester model. On overall, seasonality on transfer rates was found to be the main factor of improvement of the fits indicating its key importance in sea bass movements between the two areas. Larger transfer rates (from 0.42 to 0.48) were estimated from north to south at the beginning of October and from south to north at the beginning of April for the semester model. For the trimester model, larger transfer rates were estimated from the north to the south at beginning of October and January (from 0.32 to 0.48) and in the other direction at the beginning of April and July with values (from 0.21 to 0.30) depending on the model configurations ( $F$  constant,  $F$  by area or  $F$  by area and season). Average fishing mortality rate estimations vary from 0.21 to 0.25 in the

semester models and from 0.28 to 0.36 in the trimester model depending on the model configuration tested (T by area or by area and season). The F estimates are in the ballpark of the ICES estimation for the northern area but are estimated higher for the southern area. A model with fishing mortality rate separated between commercial and recreational fisheries led to a ratio of about two third of total mortality allocated to the commercial fishery and one third to the recreational fishery. The tagged fish model developed for this study could be used to estimate seasonal sea bass migration rates between areas and help in the parameterization of a spatial stock assessment model.

### **1.2.7 Spatio-temporal changes in behavioural strategies for European sea bass (Serena Wright)**

This study presents the results of an extensive body of work on the movements and behaviour of mature bass in UK waters since the benchmark mark-recapture work carried out in the 1970s, 80s and 90s. The focus of this work was to 1) better understand the timing and extent of seasonal migrations by bass in UK waters, 2) provide new insights into spatial stock structure and connectivity between different regions, and 3) compare the observed results with historical mark-recapture data. Results demonstrate variability of the extent of migration at each of the release sites, between short and long distant migrators. We show that a proportion of North Sea fish remained resident within the North Sea throughout the year, however we also observed a high level of connectivity in UK waters, with movements between the Celtic Sea and the North Sea and vice versa.

### **1.2.8 Seasonal migration, site fidelity and population structure of European sea bass: Shedding light from large-scale electronic tagging (Helene de Pontual)**

The Northeast Atlantic stocks of European sea bass, *Dicentrarchus labrax*, have shown strong declines over the past decade due to poor recruitment and overfishing. The limited understanding of sea bass spatial and behavioural ecology and population structure poses severe limitations to its stock assessment and management. To fill this gap, Ifremer carried out large-scale data storage tag (DST) tagging programs in the Southern North Sea, English Channel and Bay of Biscay in 2010–2012 and 2014 - 2016. Out of 1466 deployed DSTs, 522 have been recovered by November 2022. Approximately half of the recorded depth and temperature series included at least one period of potential spawning migration. Individual trajectories were reconstructed using a geolocation model. Reconstructed tracks were used to analyse movements and migrations, which confirmed sea bass to be a partial migratory species, as individuals, exhibited either long distance migrations or residency. Most migrants exhibited seasonal movements with fidelity to summer feeding areas as well as to winter spawning areas. On a given site, different migratory strategies were observed which suggests mixing of subpopulations (and mixing stocks). In the eastern English Channel, most reproductive migration was observed within the northern stock. In the western English Channel, most reproductive migrations were observed from western English Channel (northern stock) to Bay of Biscay (eponymous stock). In the northern and central Bay of Biscay, most reproductive migration was observed within the Bay of Biscay (eponymous stock). In the southern Bay of Biscay, most reproductive migration was observed from the Bay of Biscay (eponymous stock) to Iberian Peninsula (eponymous stock). Our dataset enriches the knowledge of sea bass biological traits (temperature and depth ranges, vulnerability to predation and fishing) and opens new avenues for multidisciplinary approaches (genetic analysis – e.g. talk by P.A. Gagnaire and otolith microchemistry – e.g. talk by F. Daverat). Our results suggest a spatial structure of the Atlantic population that may differ from the stock structure currently considered

for assessment and management. The consequences need to be explored at both the European level and by regional managers involved in conservation outcomes.

### **1.2.9 Chosen-mixity and safer(r) space for European sea bass: Population structure affects the degree of protection (Jolien Goossens)**

Using acoustic telemetry, the movements of European sea bass ( $n = 63$ ) were investigated in a Belgian port area. As a result of high residency and site fidelity on a small spatial scale (3 – 15 km), sea bass in the harbour was shown to form two groups or population subunits, occupying distinct areas. The results highlighted the complexity of sea bass population structure, as well as the risks of local depletion.

### **1.2.10 Coupling natural and electronic tags to explore spawning site fidelity and natal homing in Northeast Atlantic European sea bass (Françoise Daverat)**

The structure and connectivity of European sea bass (*Dicentrarchus labrax*) populations remain poorly known and ecological evidence is missing to support the current delineation between the northern (southern North Sea, English Channel and Celtic Sea) and southern French stocks (Bay of Biscay). Adult spawning site fidelity and natal homing were analysed by coupling Data Storage Tag (DST) information and otolith microchemistry of recaptured fish to investigate, within the study area, the population structure and connectivity in European sea bass. Reconstructed trajectories, inferred from DST data, were used to assign a spawning area (English Channel or Bay of Biscay) to each spawning winter record. In addition, otolith composition (Mg, P, Mn, Zn, Sr, Ba and  $\delta^{18}\text{O}$ ) was measured in both larvae and adult otolith increments corresponding to a winter spawning event. We built a training dataset using coupled spawning area assignments and otolith elemental signatures (Mg, P, Mn, Zn, Sr and Ba) for winters with DST data. The training dataset was used to calibrate a Random Forest model and assign spawning areas based on otolith winter signatures outside the DST recording period. Results revealed that 64 % of the sea bass expressed spawning site fidelity. We also found a geographical gradient of site fidelity, with the largest proportions of spawning site fidelity found in sea bass tagged at the northern and southern limits of the studied area. Significant ontogenetic effects were observed for trace elements and  $\delta^{18}\text{O}$  with ratios significantly lower in the larval stage than in the adult stage. These biases and the variability across cohorts prevented us to use the assignment model fitted on adults to study natal homing. At the larval stage, the analysis of spatio-temporal effects on otolith trace elements did not reveal any significant difference between spawning areas. However, the patterns of difference were similar for larval and adult Zn, Sr and Ba between the two spawning areas, suggesting a homing behaviour.

### **1.2.11 Seasonal variation in population structure of Atlantic sea bass (*Dicentrarchus labrax*) revealed by combining genomic variation with reconstructed trajectories (Pierre-Alexandre Gagnaire)**

Assessing population connectivity in species with complex life histories involving larval dispersal and seasonal adult migrations is a challenging problem. Genetic data can provide estimates of effective gene flow, but these measures need to be contextualised in space and time to shed light on the demographic relationships between populations. However, studies of marine fish

connectivity often lack direct observations of larval and adult movements, making it difficult to integrate genetic data with spatial life history information. Here, we combined individual trajectory reconstructions from archived tag data with high-density genotyping to investigate the temporal dynamics of the spatial genetic structure of Atlantic sea bass populations throughout the feeding and breeding seasons. Our results revealed that the genetic boundary between the Bay of Biscay and Northern stocks shifts from the tip of Brittany to the central English Channel during summer. The mixing between the two stocks is therefore more pronounced in the Western Channel, especially during the feeding period. The extremely low level of genetic differentiation between the Bay of Biscay and Northern stocks limits the effectiveness of genetic stock identification methods for fisheries management in the mixture zone. Nevertheless, the identification of long genomic segments shared identical-by-descent between relatives provides a promising approach for tracing recent genetic ancestry and estimating population connectivity.

### **1.2.12 Genetics of European sea bass (*Dicentrarchus labrax*) in the northern Atlantic using SNPs (Philip Lamb)**

To test for sea bass populations in European sea bass northern range a 57k SNP chip, Axiom Dlab SNP chip (Allal *et al.*, 2020), was used to genotype 950 sea bass sampled from the waters of Ireland, the UK, Belgium, the Netherlands, Germany, and Norway. Following quality assurance and control, the SNP outliers were identified using pcadapt (Luu *et al.*, 2017). Both the outlier and neutral SNPs underwent a) sparse non-negative matrix factorization (Frichot *et al.*, 2014) (sNMF) and b) PCA to test for potential presence of populations. Neutral SNPs yielded a single population using both sNMF and PCA. Outlying SNPs had no genetic structure (*i.e.* a single population) revealed using PCA, but three clusters were revealed using sNMF. The structure of the clusters could not be explained geographically, and the cause of this structure is not yet identified. Overall, based on these results we believe a single northern population of European sea bass remains the parsimonious description of genetic structure.

## 2 Review information on stock identification of sea bass stocks bss.27.4bc7ad-h and bss.27.8ab (ToR 1)

### 2.1 Genetics

A variety of studies, utilizing a wide-ranging suite of molecular markers (e.g. allozymes, mitochondrial DNA (mtDNA), microsatellites and single nucleotide polymorphisms (SNPs)), have examined the spatial genetic structure and connectivity of sea bass stocks in the Northeast Atlantic.

The first allozyme study, which was based on five polymorphic allozyme markers, observed significantly differentiated enzymatic profiles between sea bass from the Irish Sea (ICES Division 7.a) and those from the Bristol Channel (ICES Division 7.a), English Channel (ICES divisions 7.e-d) and Thames Estuary (ICES Division 4.c) (Child, 1992). This result was the first molecular evidence of population structuring within the northern sea bass stock (ICES divisions 4.b-c, 7.a and 7.d-h). Combining allozymes and microsatellite markers, Castilho and McAndrew (1995) also observed genetic differentiation between northern and southern Portuguese populations, probably due to gene flow from the Mediterranean (Castilho and McAndrew, 1998).

Aggregating genetic evidence from several subsequent studies attempting to determine stock structure with different generations of molecular techniques does not provide a straightforward delineation of boundaries and connectivity, due to conflicting results regarding sea bass population structuring within ICES advice units. This is particularly prevalent within divisions 4.b-c, 7.a and 7.d-h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel and Celtic Sea). For example, Microsatellite data from Coscia *et al.* (2011) showed significant levels of genetic differentiation between sea bass collected from the English Channel (ICES Division 7.d) compared to the Thames Estuary (ICES Division 4.c), Belgian coast (ICES Division 4.c) and Irish Sea (ICES Division 7.a). However, within the same study and using the same samples, mtDNA failed to support equivalent levels of genetic differentiation (Coscia and Mariani, 2011; Coscia *et al.*, 2012). Likewise, Fritsch *et al.* (2007), utilizing eight microsatellites found no significant differences in the genetic profiles of sea bass collected from the Celtic Sea (ICES divisions 7.g-h), English Channel (ICES divisions 7.e d), Bay of Biscay (ICES divisions 8.a-8.b) or North Sea (ICES Division 4.c) (Fritsch *et al.*, 2007). A similar lack of genetic structuring was also reported between coastal French (ICES Division 7.e) and Belgian (ICES Division 4.c) sea bass using six microsatellite markers (Naciri *et al.*, 1999). Using 14 microsatellite and 46 SNP markers, Souche *et al.* (2015) investigated differences in the genetic profiles of sea bass between the Mediterranean Sea and Atlantic Ocean. The authors collected sea bass from coastal regions of southern and central Portugal (ICES Division 9.a), southern and western Ireland (ICES divisions 7.a, g), France (English Channel, ICES Division 7.e), Belgium (ICES Division 4.c), and Norway (ICES Division 4.a). Their results revealed that only sea bass from the southern Portuguese coast were genetically differentiated from the other sample sites, suggesting that introgression of Mediterranean genes underpins genetic differentiation in this area (Souche *et al.*, 2015). Finally, Ratcliffe *et al.* (2022) produced a spatially limited study of sea bass structure, examining samples (n=62) from the Portuguese coast (ICES Division 9.a) and Celtic shelf (ICES Division 7h). While regional replicates were limited, the authors utilized a more focused section of the genome (i.e. major histocompatibility complex related genes, 241 base pairs (bp)) to delineate populations. They found 30 unique alleles in the Celtic shelf sea bass populations which were not represented within the Portuguese population, and 22 alleles unique to the Portuguese population. The presence of regionally

specific alleles provides substantial evidence of genetic separation between Celtic Sea and Portuguese sea bass populations.

While previous investigations based on small marker datasets have provided informative perspectives on sea bass population structure, analyses using thousands or tens of thousands of SNPs are deemed desirable because they provide substantially higher resolution for delineating population structure. Increasing polymorphism data contribute to improving genetic connectivity estimates mainly by better characterizing the footprint of neutral demographic processes across the genome. However, in species with high levels of gene flow, such as sea bass, neutral marker-based methods may be ineffective for fine-scale measures of genetic connectivity when neutral genetic differentiation approaches zero. In such cases, alternative approaches based on genomic regions that are affected by different types of selection, known as outlier loci, can be used to measure connectivity depending on the context (Gagnaire *et al.*, 2015).

Robinet *et al.* (2020) used the context of admixture and introgression between Atlantic and Mediterranean sea bass lineages to assess the connectivity of sea bass populations in the Atlantic. Using a 1K SNP chip dataset of 827 individuals sampled from Portugal to the Irish and North Seas, this study detected a subtle latitudinal admixture gradient, which originated at the edge of the contact zone with the Mediterranean sea bass lineage. Using the signal of introgressed Mediterranean alleles, two significant breaks in the ancestry gradient were detected at the tip of Galicia (ICES Division 8.c) and northern Brittany (ICES Division 7.e). These were interpreted as barriers to dispersal between distinct stocks. Furthermore, a signal of northward expansion into the Irish and North Seas has been revealed by the surfing of rare Mediterranean alleles at the edge of the species range. These results suggest the existence of at least three distinct sea bass populations within the Atlantic; a southern Iberian population (ICES area 9), a central population in the Bay of Biscay (ICES areas 7-8) and a northern population (ICES areas 4-7) (Robinet *et al.*, 2020). These results also indicate regional overlaps between separate ICES sea bass stock units, specifically within northern Bay of Biscay and western English Channel indicative of possible mixture between these separately assessed and managed stocks. Additionally, identifying neutral and outlier SNPs, Robinet *et al.* (2020) used traditional population genetic distance ( $F_{st}$ ) scores to reveal that sea bass from the North Sea are genetically isolated by distance from Irish and Celtic Seas conspecifics. Future work is needed to determine the extent to which spatially restricted dispersal decouples the demography of genetically connected regions, such as the Irish Sea and North Sea.

In a recent work based on a 57K high-density SNP array, Gagnaire *et al.* (unpublished) combined individual trajectory reconstructions from archival tag data with genotyping data to investigate the temporal dynamics of the spatial genetic structure of sea bass populations along the French Atlantic and English Channel coasts. Their results revealed that the genetic boundary between the Bay of Biscay and Northern stocks moves from the tip of Brittany to the central English Channel during summer. The mixing between the two stocks appeared to be more pronounced in the Western Channel, especially during the feeding period. The extremely low level of genetic differentiation between the Bay of Biscay and Northern stocks hinders the application of genetic stock identification methods for fisheries management in the mixture zone. Nevertheless, the identification of long genomic segments shared identical-by-descent between relatives provides a promising approach for tracing recent genetic ancestry and estimating population connectivity.

Lamb *et al.* (unpublished) used 50,102 SNPs from the same high-density SNP array to examine genetic differentiation among sea bass within the Irish Sea, Celtic Sea, English Channel and North Sea. This study supplied a substantial number of spatial replicates ( $n=1,152$ ) encompassing sea bass from ICES divisions 3.a, 4.a-c, 6.a, 7.a, and 7.d-h and used outlier detection to analyse neutral and outlier SNPs separately. Analysis of neutral SNPs ( $n=49,900$ ) suggests the existence of a single panmictic population of sea bass across ICES divisions (Lamb *et al.*, unpublished). However, analysis of the outlier SNPs ( $n=202$ ) using sparse non-negative matrix factorisation

(sNMF) algorithms to estimate individual sea bass ancestry coefficients identified three clusters of genetically differentiated populations (Lamb *et al.*, unpublished). There was no clear geographical pattern linked to clusters, but additional work is ongoing to develop these analyses.

## 2.2 Otolith and scale microchemistry

Natural biogeochemical markers (trace element concentrations and stable isotope ratios) located in the hard parts of bony fishes (e.g. otoliths and scales) have great potential for studying fish stock structure and connectivity between populations (Campana, 2005). Archival structures, such as otoliths and scales, deposit new material incrementally as the fish grows, creating growth rings that can be used to assess age and growth. Different chemical markers incorporated into these layers reflect the individual's diet, the physico-chemical conditions of the surrounding water, and their physiological condition, creating a chronological record of their growth, trophic niche and habitat use, which can be used to reconstruct the geographic regions used by fish over their entire lifetime (Campana, 2005; Sturrock *et al.*, 2012; Trueman *et al.*, 2012).

Focusing on studies that have used biogeochemical tracers to infer sea bass habitat use, most to date have primarily used trophic markers (carbon and nitrogen isotopes:  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively). For example, Cambiè *et al.* (2016), collected scales from 189 adult sea bass (39–61 cm) to investigate recent connectivity and adult movement patterns around the English and Welsh coast (ICES divisions 7.a, f-g). Using scale stable isotope compositions from the last growing season and random forest classification, a machine learning algorithm used to identify and group differences within datasets, the authors tested similarities in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values between ICES divisions to estimate population boundaries (Cambiè *et al.*, 2016). Overall, the classification algorithm assigned 75% of the sea bass back to their collection region, suggesting high site fidelity, at least for the last growing season (Cambiè *et al.*, 2016). The majority of the fish classified to alternative regions had been collected from the mid- and north Welsh coastlines (within ICES 7.a), with sea bass collected from mid- Wales typically identifying as north Wales and vice versa (Cambiè *et al.*, 2016). With sea bass from ICES 7.f-g being relatively easy to identify but those from within separate regions of ICES 7.a being more difficult, the authors suggested that there was population structuring among these divisions during the last growing season. Alternatively, these results can be viewed as highlighting the high site fidelity of sea bass during the summer feeding period.

McCarthy *et al.* (2021) collected and analysed 349 scale samples from sea bass located around ICES divisions 4.c, 7.a, 7.d and 7.f (North Sea, English Channel, Bristol Channel and Irish Sea) and described movement ecology using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopes. Like Cambiè *et al.* (2016), this study utilized a random forest classification model of isotope ratios to discern whether individual sea bass could be assigned back to their sampling group of origin based on scale  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Sea bass from ICES divisions 4.c, 7.a, and 7.d had a classification accuracy below 50% while samples collected from the Bristol Channel (ICES Division 7.f) were ~80% correctly identified (McCarthy *et al.*, 2021). The authors stated that the high rates of misclassification were due to migratory behaviour and that scales absorbed nutrients from a variety of ICES divisions, suggesting substantial connectivity.

Cransveld *et al.* (2017) used mercury ( $\delta^{202}\text{Hg}$  and  $\Delta^{199}\text{Hg}$ ), carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopes in the muscle tissues of juvenile sea bass to infer population structures within ICES divisions 4.c, 7.d and 9.a, as well as regions within the Mediterranean (i.e. Black Sea and Aegean Sea). Results showed that mercury isotope ratios separated sea bass from the North Sea (ICES Division 4.c) and Seine Estuary (ICES Division 7.d). As described above, juvenile sea bass remain within their settlement region until reaching adult life stages, when they beginning to migrate; so, while these authors suggest the presence of population structuring within the current sea bass ICES stock advice unit of divisions 4.b-c, 7.a and 7.d-h, these results may instead be

indicative of juvenile site fidelity and differences in local environmental conditions (Cransveld *et al.*, 2017). In a study where 0, 1, and 2-group sea bass were sampled from four Irish estuaries on the east and southwest coasts of Ireland over a four-year period, otolith element concentrations (Mg/Ca, Mn/Ca, Sr/Ca, Ba/Ca, K/Ca and Na/Ca) suggested strong site fidelity to the estuary of capture for all age classes (Ryan *et al.*, 2022)

Le Luherne *et al.* (2022) analysed adult spawning site fidelity and natal homing by coupling data storage tag (DST) information and otolith microchemistry of recaptured fish to investigate the sea bass population structure and connectivity along the French Atlantic coasts. Trajectory reconstructions inferred from DST data were used to assign a spawning area (English Channel or Bay of Biscay) to each spawning winter record. Otolith composition (Mg, P, Mn, Zn, Sr, Ba and  $\delta^{18}\text{O}$ ) was measured in both larvae and adults otolith increments corresponding to a winter spawning event (Le Luherne *et al.*, 2022). A training dataset was built using coupled spawning area assignments and otolith elemental signatures (Mg, P, Mn, Zn, Sr and Ba) for winters with DST data. The training dataset was used to calibrate a Random Forest model and assign spawning areas based on otolith winter signatures outside the DST recording period. Results revealed that 64 % of the sea bass expressed spawning site fidelity (Le Luherne *et al.*, 2022). Significant ontogenetic effects were observed for trace elements and  $\delta^{18}\text{O}$  with ratios significantly lower in the larval stage than in the adult stage (Le Luherne *et al.*, 2022). These biases and the variability across cohorts prevented us to use the assignment model fitted on adults to study natal homing (Le Luherne *et al.*, 2022). At the larval stage, the analysis of spatio-temporal effects on otolith trace elements did not reveal any significant difference between spawning areas. However, the patterns of difference were similar for larval and adult on Zn, Sr and Ba between the two spawning areas, suggesting a homing behaviour (Le Luherne *et al.*, 2022).

## 2.3 Tagging

Underpinning inferences on stock structure by all techniques, but of relevance to the interpretation of tagging data, is the natural life history and behaviour of sea bass. Tagging data has established that juvenile sea bass (<40 cm) remain sedentary for several years with limited migratory behaviour (Stamp *et al.*, 2021). As adults, sea bass undertake seasonal migrations between inshore summer feeding areas and offshore wintering and spawning areas (de Pontual *et al.*, 2019). These studies, and more (e.g. Pawson *et al.*, 2008), also reveal high migration site fidelity to summer and winter regions. During spawning, sea bass aggregate in offshore areas and release pelagic eggs, larvae hatch while drifting on currents which carry them towards coastlines around the Northeast Atlantic (Pawson *et al.*, 1987). Unlike evidence from genetic/genomic related sea bass research, observations from tagging data are relatively consistent in reporting juvenile sedentary behaviour, adult winter/summer migratory behaviour and fidelity to specific regions.

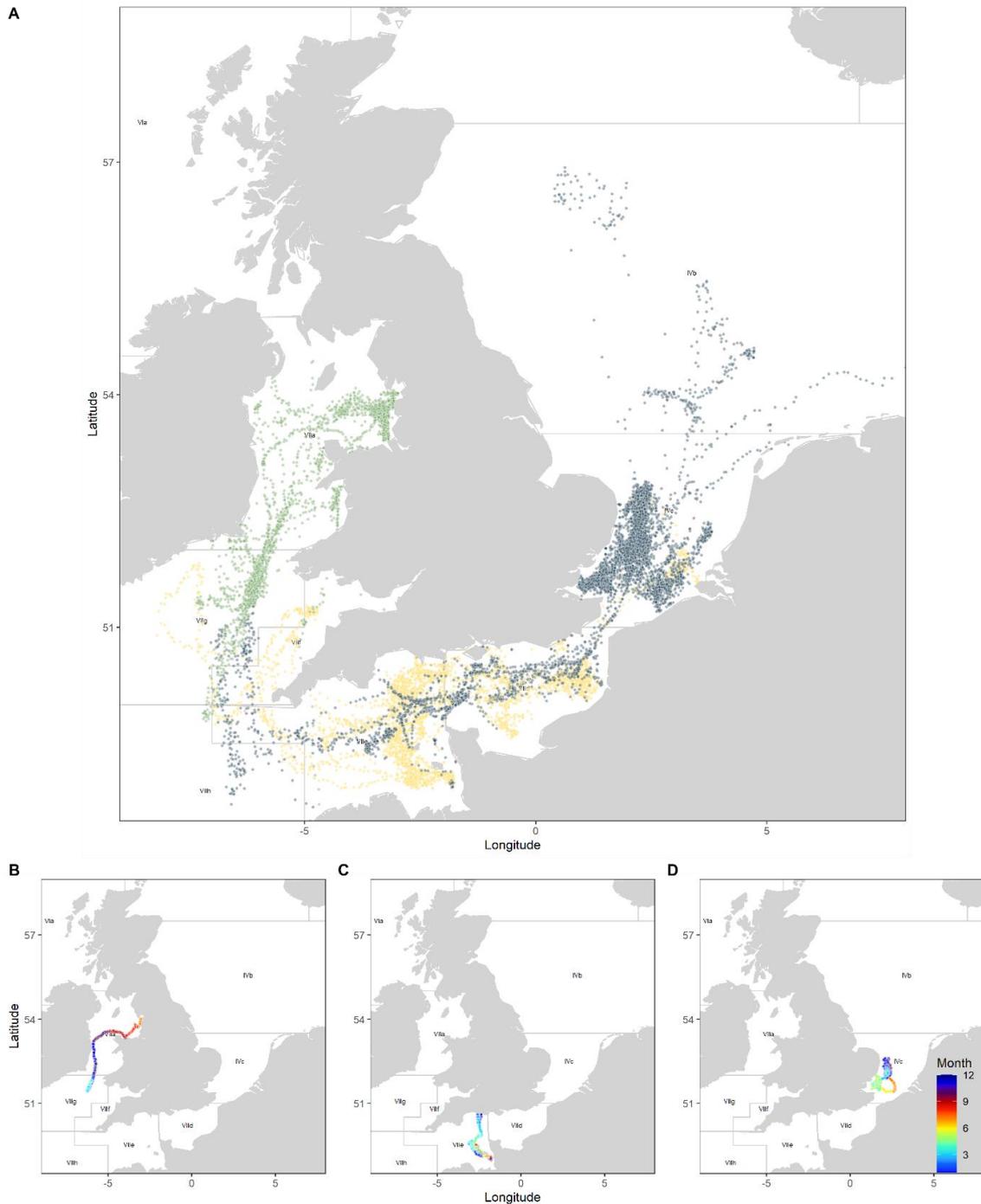
Early studies of sea bass within central and southern North Sea, Irish Sea, English Channel, Bristol Channel and Celtic Sea, utilized conventional tags to investigate the mobility of juvenile, subadult and adult sea bass (Kennedy and Fitzmaurice, 1972; Holden and Williams, 1974; Kelley, 1979; Pawson *et al.*, 1987; Fritsch *et al.*, 2007; Pawson *et al.*, 2008). Results from UK studies with conventional tags suggested two distinct populations in the English Channel; an eastern bass population (moving between the eastern English Channel and southern North Sea) and a western population (which move along the western English Channel and along the coast of Cornwall) and into the Bristol Channel and southern Celtic Sea (Pawson *et al.*, 1987; Pawson *et al.*, 2007).

In general, conventional tagging studies highlighted two behaviours: 1) most sea bass tagged within an ICES Division remained within that specific division; and 2) limited numbers of individuals were recorded travelling between ICES divisions 4.b-c, 7.a and 7.d h (Kennedy and Fitzmaurice, 1972; Holden and Williams, 1974; Pawson *et al.*, 1987; Fritsch *et al.*, 2007; Pawson *et al.*, 2007). These results must be viewed within the context of sea bass life-history behaviour

described above. However, it should be noted that summer and winter habitats can occur within the same ICES divisions or stock units. Additionally, some individuals travelled significant distances (>800 km; Pawson *et al.*, 1987) across ICES divisions, with authors concluding that high tagging site fidelity experienced by most sea bass was indicative of stock structuring within the study areas.

A growing number of studies have utilized modern data-storage tags (DST). This technology is capable of providing environmental information used to infer movement and migrations on sea bass movements for as long as the battery duration last (Quayle *et al.*, 2009; de Pontual *et al.*, 2019; Stamp *et al.*, 2021; de Pontual *et al.*, in revision; Wright *et al.*, unpublished). Between 2005–2006, 89 adult sea bass were tagged in the North Sea and English Channel (Quayle *et al.*, 2009). The author's results showed that a minority of sea bass migrated outside their tagged ICES divisions and into adjacent divisions (>100 km), but the majority remained within the division where they were tagged (Quayle *et al.*, 2009). Observations from Quayle *et al.*, (2009) again highlighted both sea bass behaviour types previously recorded by conventional tagging studies and suggested a high site fidelity within both regions was indicative of population structuring. However, these results must be considered in terms of their natural migratory behaviour.

Between 2014–2019, 244 sea bass were captured from ICES divisions 4.c, 7.a, 7.e, and 7.f and tagged with DSTs for the Cefas led C-Bass project (Wright *et al.*, unpublished). Recaptured locations and reconstructed daily positions indicated considerable mixing of adult sea bass (Wright *et al.*, unpublished; Figure 1). Fish tagged in ICES Division 4.c (southern North Sea) were found to travel to ICES divisions 4.b, and 7.d-h (northern North Sea, English Channel and Celtic Sea, while sea bass tagged in Division 7.e (eastern English Channel) migrated to ICES divisions 4.c, 7.d, and 7.f-h (southern North Sea, western English Channel and Celtic Sea; Wright *et al.*, unpublished; Fig 1). However, sea bass tagged in ICES 7.a (Irish Sea) were found to migrate only into Division 7.g (northern Celtic Sea; Wright *et al.*, unpublished; Figure 1). The authors noted that 7.e tagged sea bass where the only group that spent most of their time within the same region, while sea bass released from divisions 4.c and 7.a were predominately migratory (Wright *et al.*, unpublished). Data from this study suggest the following conclusions: 1) a high degree of biological connectivity between the English Channel (divisions 7.e and 7.d) and both the North (divisions 4.b,c) and Celtic Sea (divisions 7.f-h); and 2) limited range of sea bass migration between the Irish Sea ( Division 7.a) and northern Celtic Sea ( Division 7.g).



**Figure 1. C-Bass daily most probable position estimates for (A) all bass tagged in the English Channel, 7.e (yellow), the Irish Sea, 7.a (green) and North Sea, 4.c (blue). Examples of releases are provided in B-C with daily positions coloured by the month for bass 15274 (B), bass 10881 (C) and bass 10932 (D). (Wright *et al.*, unpublished).**

Stamp *et al.* (2021) implanted 146 acoustic tags to juvenile and subadult sea bass (25.2–60 cm fork length) and tracked those specimens for ~370 days using an acoustic telemetry network deployed in three nursery sites in the southwest of the UK (ICES divisions 7.e-f). Most tagged juveniles remained within their ICES Division with a very limited number of tagged individuals moving up to 317 km from ICES 7.e and into 7.f (Stamp *et al.*, 2021). Previous studies have suggested that juvenile sea bass remain in nursery areas until they are ~4–5 years old but results from Stamp *et al.* (2021) suggest a limited amount of migration may take place between individual ICES divisions, but not between current ICES stocks.

Ifremer carried out large-scale data storage tag (DST) tagging programs in the Southern North Sea, English Channel and Bay of Biscay in 2010–2012 (de Pontual *et al.*, 2019) and 2014–2016 (de Pontual *et al.*, in revision). Out of 1466 deployed DSTs, 526 have been recovered by November 2022. Individual trajectories were reconstructed using a geolocation model. Reconstructed tracks were used to analyse movements and migrations, which confirmed sea bass to be a partial migratory species, as individuals, exhibited either long distance migrations or residency (de Pontual *et al.*, in revision). Most migrants exhibited seasonal movements with fidelity to summer feeding areas as well as to winter spawning areas. On a given site, different migratory strategies were observed which suggests mixing of subpopulations (and mixing stocks). In the eastern English Channel, most reproductive migration was observed within the northern stock. In the western English Channel, most reproductive migrations were observed from western English Channel (northern stock) to Bay of Biscay (eponymous stock), the Iroise Sea being likely a mixing zone for different stocks or subpopulations and may also shelter a resident population (de Pontual *et al.*, 2019). In the northern and central Bay of Biscay, most reproductive migration was observed within the Bay of Biscay (eponymous stock). In the southern Bay of Biscay, most reproductive migration was observed from the Bay of Biscay (eponymous stock) to Iberian Peninsula (eponymous stock). This dataset enriches the knowledge of sea bass biological traits (temperature and depth ranges, vulnerability to predation and fishing) and opens new avenues for multidisciplinary approaches: genetic analysis (Gagnaire *et al.*, unpublished) and otolith microchemistry (Le Luherne *et al.*, 2022). Our results suggest a spatial structure of the Atlantic population that may differ from the stock structure currently considered for assessment and management.

## 2.4 Pelagic connectivity

European sea bass migrate offshore to form spawning aggregations during winter and spring. Following spawning, the eggs and larvae are then carried by ocean currents to coastal nursery grounds. Therefore, understanding the mechanisms behind connectivity between spawning and coastal nursery grounds can help further understanding of the connectivity between the different populations. The pelagic phase is one of the most sensitive phases of the species life cycle. These early life stages encounter different environmental conditions that differ depending on the spawning location and the larval trajectory. Ocean currents and temperature (as well as other environmental factors) may lead to different durations and survival within the pelagic phase. Along with conditions at the coastal nursery grounds, understanding this pelagic phase is critical for determining the chance of survival of individuals, and therefore their chance of being recruited into the stock.

Lagrangian particle tracking provides a useful tool to assess how larval trajectories may differ both spatially and temporally. These models use physical environmental conditions from hydrodynamic models to determine the pathway of a particle released in the ocean. Combining this physical process with an individual based model (IBM) can allow for behavioural changes through pelagic larval development. For example, determining growth rates, movement, mortality, or where the larvae settle along the coast. These models can then be used to assess connectivity between spawning and settling sites, and how this may affect recruitment.

Beraud *et al.* (2018) developed an IBM to investigate the pelagic life stages of European sea bass, with focus on reproducing interannual variability for recruitment within the English Channel. This study considered 1996 and 1997, as years with significant differences in observed recruitment. This study showed the impact of temperature as well as windspeed and direction, for determining the distance and duration of larval drift. The model was shown to reproduce the difference in recruitment observed in the Solent.

Graham *et al.* (2023) builds on this earlier work to consider seven discontinuous years (1996, 1997, 2004, 2005, 2010, 2015, and 2018), with differing environmental conditions and observed

recruitment. The IBM developed by Beraud *et al.* (2018) has been further developed, to consider temperature dependent growth and mortality throughout the pelagic larval phase. Graham *et al.* (2023) also considered spawning later in the year, to allow for spawning over a wider area, including the North Sea. The results from this study have been compared with observed year-class strength for the northern stock as well as surveys conducted in estuaries in England and Ireland. Comparison between the model and ICES assessment abundance of age-class zero fish showed similar temporal variability, but with higher recruitment predicted for 2018, and a lower peak recruitment in 1997 (Graham *et al.*, 2023). The model also reproduced general patterns of inter-annual variability for the Thames estuary but performed less well for some other regions. These differences could result from either uncertainties within the model (either physical or biological processes), or limitations in the data available for comparison (Graham *et al.*, 2023). For example, comparison with recruitment derived from older year-class strength will be impacted by conditions within the nursery grounds, rather than purely pelagic life stages.

Nevertheless, the model developed here remains a useful tool for demonstrating variations in connectivity across the northern stock region. Graham *et al.* (2023) show that the Celtic Sea and western Channel can supply larvae to many areas, leading to connectivity across the Channel and Celtic Sea, and into the Irish Sea. While the model developed here did not cover the entire Biscay stock region, the model did demonstrate strong connectivity from northern Biscay (8.a) into the western Channel (7.e). The eastern Channel (7.d) is shown to depend on sources within the Channel (7.d and 7.e) each year. However, the eastern Channel also provides a significant supply for the southern North Sea. For example, variability at the Thames estuary was shown to be influenced by spawning within the eastern Channel. However, the Solent showed predominantly more local sources in the central Channel.

In terms of interannual variability, warmer temperatures did tend to provide a larger supply over the northern stock region. However, circulation patterns, and duration of the larval phase, also play a key role. Throughout the pelagic stages, growth depends on temperature within the model. When spawning occurs earlier in the year, lower temperatures lead to slower growth and longer trajectories. While longer durations may affect survival, the overall effect here was found to increase connectivity between different areas. This impact, in addition to the spawning distribution across the shelf (egg supply), can have a large influence on interannual variability seen at different nursery grounds across the stock region, with the warmest year not necessarily having the largest recruitment (Graham *et al.*, 2023).

While previous studies have assumed growth and mortality dependent on temperature (Beraud *et al.*, 2018; Graham *et al.*, 2023), factors such as food availability (for growth or starvation), as well as presence of predators, are also likely to play a significant role. These factors are often omitted due to lack of data available to constrain a model but may have a significant impact on larval growth and survival during the pelagic phase. Bioenergetics models are interesting to investigate the impact of food availability (through chlorophyll concentrations) in addition to temperature, on survival through different life stages. Dambrine *et al.* (2020) developed a bioenergetics model based on the Dynamic Energy Budget (DEB) theory for Atlantic European sea bass. This models the growth and survival of one individual through its life cycle depending on the environmental conditions (i.e. food and temperature) that it may encounter (Dambrine *et al.*, 2020). This model was then coupled with an IBM to study the pelagic phase of the species (Dambrine *et al.*, In prep). From previously identified spawning areas along the Northeast Atlantic (Dambrine *et al.*, 2021), particles were released. Temperature and food availability encountered during their drift to coastal nurseries constrained their growth and survival. Only particles that reached the coast alive with, at least, the metamorphosis size were considered to study the connectivity between spawning and nursery areas. Seven years were studied (2008–2014) and revealed a low percentage of survival (< 1%) in the study area, but with higher recruitment success in the English Channel than in the Bay of Biscay. During this period, spawning within Bay of

Biscay was found to supply the English Channel, but there was little or no supply in the other direction (from the western Channel). There was self-supply and connectivity within the English Channel, but connectivity was found to be predominantly from the western to the eastern Channel, rather than vice versa. This analysis is consistent with that shown by Beraud *et al.* (2018) and Graham *et al.* (2023), with warmer years promoting wider larval supply and more connectivity from west to east in the English Channel and into the North Sea.

## 2.5 Summary and conclusions

In general, existing evidence does not support current ICES stock advice units for sea bass in divisions 8.a-b (northern and central Bay of Biscay) and divisions 4.b-c, 7.a and 7.d-h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel and Celtic Sea).

First, there is evidence from the genetics/genomics and tagging studies of sea bass genetic structuring within divisions 4.b-c, 7.a and 7.d-h. Robinet *et al.* (2020) sea bass  $F_{st}$  scores provide evidence of differentiation between the Irish (ICES Division 7.a) and Celtic Sea (ICES division 7.f-g) compared to the southern North Sea (ICES Division 4.c) populations, which was further supported by Child *et al.* (1992) who highlighted similar genetic breaks, but also connectivity between the southern North Sea and English Channel (ICES division 7.d-e). Tagging studies have contributed substantially to helping the group delineate sea bass boundaries. For example, Wright *et al.* (unpublished) revealed little movement of sea bass tagged within the Irish or northern Celtic Sea (ICES divisions 7.f-g) beyond these regions, further strengthening this east-west break within the existing northern sea bass stock unit.

Second, there is evidence from genetic/genomic and tagging studies of connectivity between sea bass from the northern part of the Bay of Biscay (ICES division 8.a), English Channel (ICES division 7.e) and southern Celtic Sea (ICES division 7.h). The tagging data provided by both de Pontual *et al.* (2019), de Pontual *et al.* (in revision) and Wright *et al.* (unpublished), as well as the pelagic connectivity research undertaken by Beraud *et al.* (2018) and Graham *et al.* (2023) corroborated substantial areas of connectivity within the northern Bay of Biscay (ICES division 8.a), eastern English Channel (ICES division 7.d), western English Channel (ICES division 7.e) southern Celtic Sea (ICES divisions 7.h) and southern North Sea (ICES divisions 4.c). The genomics study by Lamb *et al.* (unpublished) found no significant genetic differences among sea bass within these ICES divisions, further suggesting substantial connectivity. These areas of connectivity, i.e. mixing, suggest the use of 'meta-population' terminology due to multiple biological and behavioural interaction levels, such as breeding habitats and summer feeding regions revealing, for the first time, a potential seasonal component to probable stock units (Pontual *et al.*, 2019; de Pontual *et al.*, in revision; Wright *et al.*, unpublished).

Third, from existing tagging data there is no evidence of connectivity between the southern Bay of Biscay (ICES division 8.b) sea bass and any ICES division within the current northern sea bass stock unit (de Pontual *et al.*, 2019). This information suggests a some-what isolated subpopulation within this region but with some connectivity with ICES division 8.a (northern Bay of Biscay) as highlighted by the lack of genetic differentiation between these two regions (Robinet *et al.*, 2020). However, it should be noted that research regarding the connectivity of the southern component of the Bay of Biscay to the Celtic/Irish Sea and English Channel is somewhat lacking and therefore cannot be ruled out completely.

Overall, the existing evidence supports the presence of a single metapopulation with three subpopulations, hypotheses of which are described below. While this workshop has added to the previous dearth of information regarding sea bass population structures and stock units, the group strongly believes that further research is required. Questions such as specific mixing regions, identification of regionally specific SNP's and connectivity or boundaries among non-

assessed ICES regions must be clarified. This workshop should be viewed as just the beginning of the stock identification process and not the end.

### 3 Plausible scenarios for sea bass stocks around the UK and Bay of Biscay (ToRs 2, 3, 4)

#### 3.1 Stock delineation

Using the data provided, WKSEABASS generated hypotheses related to sea bass population boundaries within divisions 4.b-c, 7.a, and 7.d-h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea), as well as in divisions 8.a-b (northern and central Bay of Biscay; see Figure 2 for current ICES stock units). Each of these scenarios are based on the idea that there is a single meta-population, defined as a group of spatially separated subpopulations interacting at some level (i.e. migrating, reproducing, feeding), with various subpopulation components:

- **Hypothesis 1:** Three subpopulations, Irish Sea (7.a), North Sea (4.b-c), southern Bay of Biscay (8.b); with mixing among the Celtic Sea (7.f-g), Bristol Channel (7.h), English Channel (7.d-e) and northern Bay of Biscay (8.a) (seasonally). More mixing in summer compared to winter.
- **Hypothesis 2:** Three subpopulations, Irish Sea (7.a), North Sea (4b-c) and Bay Biscay (8a-b); with mixing among the Celtic Sea(7f-g), Bristol Channel (7.h) and English Channel (7d-e) (seasonally). More mixing in summer compared to winter.
- **Hypothesis 3:** Three subpopulations, Irish Sea(7a), North Sea/eastern English Channel (4.b-c, 7.d) and Bay Biscay (8.a-b); with mixing among the Celtic Sea(7f-g), Bristol Channel (7.h) and western English Channel (7.e) (seasonally). More mixing in summer compared to winter.

The evidence provided indicates that ‘northern’ and ‘southern’ sea bass are not separate populations but exist as a meta-population with potentially distinct subpopulation components with connectivity between current ICES advice units (Figure 3). However, it was not possible to select a most probable scenario between the three hypotheses, as the data available could be used to support all hypotheses.

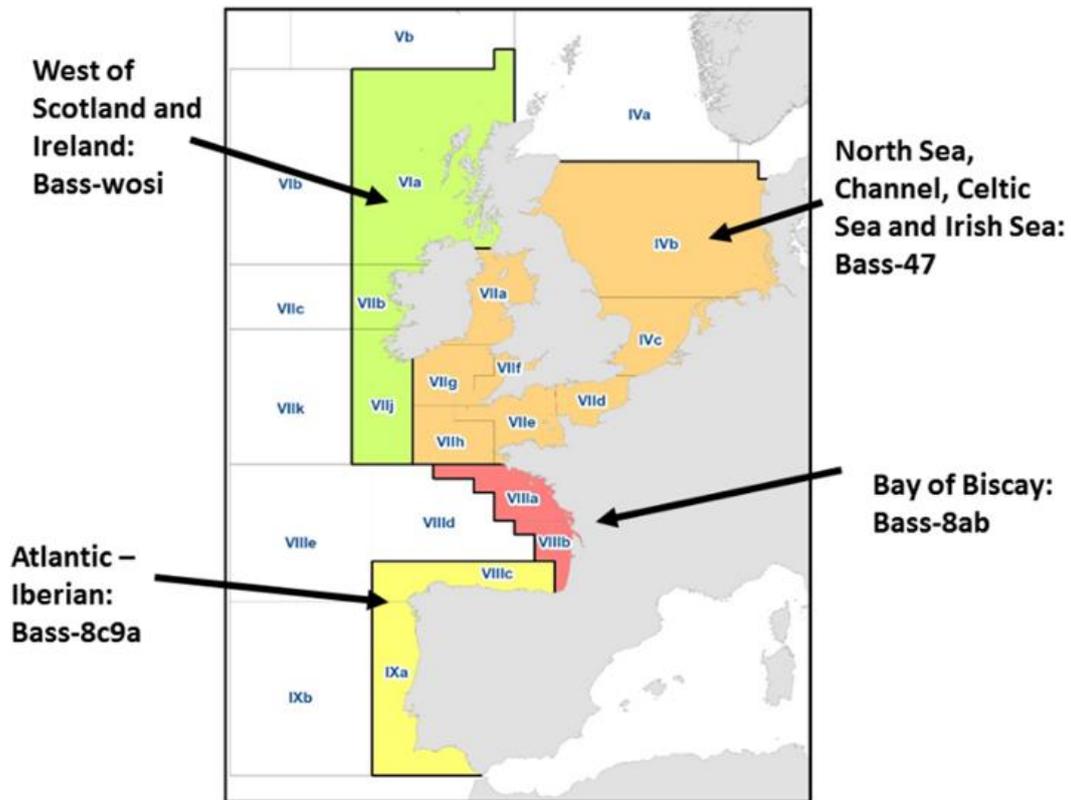
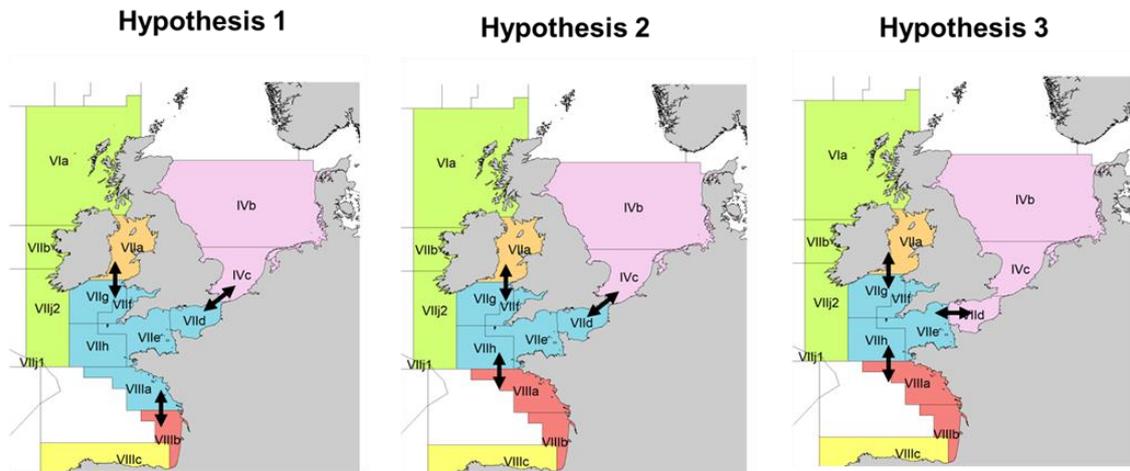


Figure 2. Currently recognized sea bass stock structures (adapted from de Pontual *et al.*, 2019).

Tagging, genetic, particle tracking, and isotope data highlighted substantial biological exchange between current ICES stock units. Tagging data revealed mixing among Celtic Sea (divisions 7.f-h), English Channel (7.d-e) and Bay of Biscay (8a) sea bass. Results from recent tagging studies also indicated that there was a seasonal component regarding the level of connectivity among these areas with sea bass mixing more during summer feeding compared to winter spawning. However, according to tagging and genetic data there was less evidence of connectivity among Irish Sea (7.a) North Sea (4.b-c) and southern Bay of Biscay (8.b) sea bass.



**Figure 3.** Sea bass stock unit scenario's generated by this working group (graphics courtesy of Zach Radford and Kieran Hyder, Cefas). Black arrows indicate areas of mixing which is considered seasonally dependant.

Due to their migratory behaviour, exact sea bass subpopulation boundaries are difficult to extrapolate, as such workshop attendees attempted to encapsulated delineated boundaries in each of the hypotheses described above and based on the best available evidence.

### 3.2 Potential scenarios for the benchmark

The stock delineation hypotheses identified create several challenges for stock assessments and management advice (e.g. splitting stocks, incorporating mixing rates). These relate to the resolution and robustness of the data available and the modelling approach. Specific challenges are outlined in this section alongside alternative scenarios that could be considered if none of the hypotheses can be implemented.

The current approach is to assess the Northern and Biscay stocks independently. The main abundance index survey that informs both these assessments is a time-series of French commercial LPUE. It is unclear what tuning index could be used for the North Sea and Irish Sea if the model required to define them as their own areas with their own data sources. In addition, each area in a spatial model will have a different level of information, for example, currently recruitment for the Northern is represented by a single time from the Solent, which is in ICES Subdivision 7d. The recreational data are collected at the national level with the objective of providing yearly removal estimates at the country/stock interaction level. The nature of the sampling design may not allow for disaggregating the data at the required granularity. It is unclear how the different levels and robustness of data between areas would be accounted for, and the impact of alternate weighting approaches on the set up of and outcomes from the model particularly if using a Stock Synthesis approach.

There is a possibility that changing the stock units may lead to downgrading ICES stock assessment category due to data issues, or model convergence issues for example. Adding complexity to the current assessments by making them spatially explicit may be reflected in the uncertainty outputs. Equally, the model may not reflect the true uncertainty of this more complex set up. In addition, temporal differences in mixing rates due to sea bass spawning and feeding migrations would require inclusion of seasonality in the model. The seasonality required/possible would need to be determined (e.g. quarter, semester), and will add additional complexity to the model. However, adding complexity to the model may not be possible with the data available, characterizing uncertainty will be challenging, and could lead the spurious dynamics or unstable outcomes.

Stock Synthesis (SS) is the current framework within which the sea bass stocks are assessed. SS will allow the implementation of a spatially explicit model with mixing (age-based movement) and recruitment apportionment. However, obtaining these parameters at the right granularity may be difficult and could generate variability/uncertainty that is difficult to characterize. SS also has a growth pattern feature, which allows definition of cohorts of fish that have different biological characteristics, and which are independently tracked as they move among areas but is difficult to implement.

In the end, the choice of approach will be a balance between stock identification, the data that is available to parameterize the model, and the robustness of the modelling approach. As there are concerns about the ability to overcome the challenges of assessing the stock using the stock delineation hypotheses outlined in Section 3.1, two additional fallback scenarios were identified that should be tested during the benchmark. These still include mixing, but would be simpler to implement in models, and were:

- **Scenario A:** Continue to assess the ‘southern’ (ICES divisions 8a-b) and ‘northern’ (ICES divisions 4.b-c, 7.a and 7.d-h) stocks separately but incorporate mixing between stocks.
- **Scenario B:** Single meta-population between northern and southern stocks.

Selection of the best approach should be done during the benchmark based on the data and modelling approaches that generate robust outcomes. However, the data call should be developed at the ICES division level to allow all the approaches to be tested.

### 3.3 Data call

The ICES data call should be structured in a way that allows implementation of any of the scenarios. Hence, data should be requested at the highest spatial resolution of the scenarios (i.e. ICES division), as it is always possible to aggregate data if needed.

All data listed below should be provided for the period 1985–2022 by ICES division groups as follows: Irish Sea (7a), Celtic Sea (7fgh), Western Channel (7e), Eastern Channel (7d), southern North Sea (4b-c), north Biscay (8a), south Biscay (8b). If not possible, data submitters (of either commercial data, recreational, or survey) should provide the reason and aggregate the data to the closest grouping level possible.

- Commercial data should be provided by quarter and at the métier level for each country. This includes landings weight- and numbers-at-length and -at-age, discards weight- and numbers-at-length and -at-age, and effort (kW days).
- Recreational data providers should consider how/if data can be formatted to match the hypothesis tested and provide removal estimates by ICES Subdivision group, season (quarter) and gear type.
- Commercial tuning data include the French LPUE should be requested by gear type and season.
- Survey data including the French Channel survey (CGFS), the Solent survey and any additional time-series of recruitment within the assessment area provided.
- Migration rates-at-age and larval connectivity rates between the different ICES Subdivision groups should be provided, matching the hypotheses to be tested, i.e.:
  - Hypothesis 1: three areas 7a, 4bc, 8b mixing with 7defgh8a, seasonally.
  - Hypothesis 2: three areas 7a, 4bc, 8ab mixing with 7defgh, seasonally.
  - Hypothesis 3: three areas 7a, 4bc7d, 8ab mixing with 7efgh, seasonally.

## 4 Future recommendations (ToR 5)

Recent research on sea bass population structures and movement patterns has produced a substantial amount of genomic and behavioural data via multiple individual studies. During this meeting there was a consensus and willingness to eventually combine these significant resources to produce more robust research on sea bass stock units. ICES Stock Identification and Methods Working Group (SIMWG) is aware of collaborative genomic research partnerships which are building repositories of regionally specific SNPs. These agreements can take many forms including but not limited to formal/informal data sharing, sample collection assistance and collaborative peer reviewed literature. Collectively, international fisheries institutes along with fishing industry and academic partners are working together and using these technologies to provide comprehensive population structures for species such as hake, monkfish, herring, mackerel, and sprat. Similar collaborative partnerships also exist for returning fish tags to host research institutes. This group agrees that implementing collaborative data sharing networks would greatly benefit future efforts to, if necessary, update sea bass stock boundaries.

Although this meeting exclusively examined the northern and southern sea bass stock units, future studies must extend this effort to investigate evidence of boundaries and/or connectivity with other areas. ICES advice is currently provided for divisions 8.a-b (northern and central Bay of Biscay), as well as divisions 4.b-c, 7.a and 7.d-h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel and Celtic Sea (de Pontual *et al.*, 2019) (Figure 2). Additionally, two stocks are recognized but no advice is provided by ICES: divisions 8.c-9.a (Iberian), and divisions 6.a, 7.b, 7.j (West of Scotland and Ireland) (de Pontual *et al.*, 2019) (Figure 2). Due to the high degree of connectivity revealed by this report, it is highly unlikely that the Iberian and West of Scotland/Ireland sea bass are isolated components. Therefore, additional genomics, tagging, pelagic connectivity and microchemistry will need to be undertaken to reveal how sea bass within these regions link to the scenarios suggested within this workshop.

## 5 References

- Allal Francois, Griot Ronan, Phocas Florence, Brard-Fudulea Sophie, Morvezen Romain, Bestin Anastasia, Haffray Pierrick, François Yoannah, Morin Thierry, Poncet Charles, Vergnet Alain, Cariou Sophie, Brunier Joseph, Bruant Jean-Sébastien, Peyrou Bruno, La, V. M. (2020). 2020. Axiom DlabCHIP, a 57K SNPs genotyping array for European sea bass (*Dicentrarchus labrax*): array design and genetic map. SEANOE.
- Beraud, C., van der Molen, J., Armstrong, M., Hunter, E., Fonseca, L., and Hyder, K. 2018. The influence of oceanographic conditions and larval behaviour on settlement success—the European sea bass *Dicentrarchus labrax* (L.). *ICES Journal of Marine Science*, 75: 455–470. <https://doi.org/10.1093/icesjms/fsx195>
- Cambiè, G., MJ, K., AL, M., Fox, J., Lambert, G., JG, H., Overy, T., *et al.* 2016. Stable isotope signatures reveal small-scale spatial separation in populations of European sea bass. *Marine Ecology Progress Series*, 546: 213–223. <https://www.int-res.com/abstracts/meps/v546/p213-223/>
- Campana, S. E. 2005. Chapter 12 - Otolith Elemental Composition as a Natural Marker of Fish Stocks. *In pp.* 227–245. Ed. by S. X. Cadrin, K. D. Friedland, and J. R. B. T.-S. I. M. Waldman. Academic Press, Burlington. <https://www.sciencedirect.com/science/article/pii/B9780121543518500137>
- Castilho, R., and McAndrew, B. J. 1998. Population structure of seabass in Portugal: evidence from allozymes. *Journal of Fish Biology*, 53: 1038–1049. John Wiley & Sons, Ltd. <https://doi.org/10.1111/j.1095-8649.1998.tb00461.x>
- Child, A. R. 1992. Biochemical polymorphism in bass, *Dicentrarchus labrax*, in the waters around the British Isles. *Journal of the Marine Biological Association of the United Kingdom*, 72: 357–364. Cambridge University Press. <https://www.cambridge.org/core/article/biochemical-polymorphism-in-bass-dicentrarchus-labrax-in-the-waters-around-the-british-isles/BC1EBDA9750B3EAD4254BDB0570BE1D9>
- Coscia, I., and Mariani, S. 2011. Phylogeography and population structure of European sea bass in the north-east Atlantic. *Biological Journal of the Linnean Society*, 104: 364–377. John Wiley & Sons, Ltd. <https://doi.org/10.1111/j.1095-8312.2011.01712.x>
- Coscia, I., Desmarais, E., Guinand, B., and Mariani, S. 2012. Phylogeography of European sea bass in the north-east Atlantic: a correction and reanalysis of the mitochondrial DNA data from Coscia & Mariani (2011). *Biological Journal of the Linnean Society*, 106: 455–458. <https://doi.org/10.1111/j.1095-8312.2012.01875.x>
- Cransveld, A., Amouroux, D., Tessier, E., Koutrakis, E., Ozturk, A. A., Bettoso, N., Mieiro, C. L., *et al.* 2017. Mercury Stable Isotopes Discriminate Different Populations of European Seabass and Trace Potential Hg Sources around Europe. *Environmental Science & Technology*, 51: 12219–12228. American Chemical Society. <https://doi.org/10.1021/acs.est.7b01307>
- Dambrine, C., Huret, M., Woillez, M., Pecquerie, L., Allal, F., Servili, A., and de Pontual, H. 2020. Contribution of a bioenergetics model to investigate the growth and survival of European seabass in the Bay of Biscay – English Channel area. *Ecological Modelling*, 423: 109007. <https://www.sciencedirect.com/science/article/pii/S030438002030079X>
- Dambrine, C., Woillez, M., Huret, M., and de Pontual, H. 2021. Characterising Essential Fish Habitat using spatio-temporal analysis of fishery data: A case study of the European seabass spawning areas. *Fisheries Oceanography*, 30: 413–428. John Wiley & Sons, Ltd. <https://doi.org/10.1111/fog.12527>
- Dambrine C., Huret M., de Pontual H., Drouineau H. & Woillez M. (In Prep.) Modeling connectivity estimates of European seabass (*Dicentrarchus labrax*) early-life stages from spawning to nursery areas in the Northeast Atlantic using an Individual Based Model.
- de Pontual, H., Lalire, M., Fablet, R., Laspougeas, C., Garren, F., Martin, S., Drogou, M., *et al.* 2019. New insights into behavioural ecology of European seabass off the West Coast of France: implications at

- local and population scales. *ICES Journal of Marine Science*, 76: 501–515. <https://doi.org/10.1093/icesjms/fsy086>
- Frichot, E., Mathieu, F., Trouillon, T., Bouchard, G., and François, O. 2014. Fast and efficient estimation of individual ancestry coefficients. *Genetics*, 196: 973–983. Oxford University Press.
- Fritsch, M., Morizur, Y., Lambert, E., Bonhomme, F., and Guinand, B. 2007. Assessment of sea bass (*Dicentrarchus labrax*, L.) stock delimitation in the Bay of Biscay and the English Channel based on mark-recapture and genetic data. *Fisheries Research*, 83: 123–132. <https://www.sciencedirect.com/science/article/pii/S0165783606003134>
- Graham, J. A., Watson, J. W., García García, L. M., Bradley, K., Bradley, R., Brown, M., Ciotti, B. J., *et al.* 2023. Pelagic connectivity of European sea bass between spawning and nursery grounds. <https://www.frontiersin.org/articles/10.3389/fmars.2022.1046585>
- Heerah, K., Woillez, M., Fablet, R., Garren, F., Martin, S., and De Pontual, H. 2017. Coupling spectral analysis and hidden Markov models for the segmentation of behavioural patterns. *Movement Ecology*, 5: 20. <https://doi.org/10.1186/s40462-017-0111-3>
- Holden, M. J., and Williams, T. 1974. The Biology, Movements and Population Dynamics of Bass, *Dicentrarchus labrax*, in English Waters. *Journal of the Marine Biological Association of the United Kingdom*, 54: 91–107. Cambridge University Press. <https://www.cambridge.org/core/article/biology-movements-and-population-dynamics-of-bass-dicentrarchus-labrax-in-english-waters/05B3A64A5F0DB6985B311602F353EC68>
- Kelley, D. 1979. Bass populations and movements on the west coast of the U.K. *Journal of the Marine Biological Association of the United Kingdom*, 59: 889–936. Cambridge University Press. <https://www.cambridge.org/core/article/bass-populations-and-movements-on-the-west-coast-of-the-uk/F8DC9D599D4A68887DF3FD2204A001CF>
- Kennedy, M., and Fitzmaurice, P. 1972. The Biology of the Bass, *Dicentrarchus labrax*, in Irish Waters. *Journal of the Marine Biological Association of the United Kingdom*, 52: 557–597. Cambridge University Press. <https://www.cambridge.org/core/article/biology-of-the-bass-dicentrarchus-labrax-in-irish-waters/44DD8A5F21A24372805F1A0578534C0D>
- Le Luherne, E., Daverat, F., Woillez, M., Pécheyran, C., and de Pontual, H. 2022. Coupling natural and electronic tags to explore spawning site fidelity and natal homing in northeast Atlantic European seabass. *Estuarine, Coastal and Shelf Science*, 278: 108118. <https://www.sciencedirect.com/science/article/pii/S0272771422003766>
- Luu, K., Bazin, E., and Blum, M. G. B. 2017. pcadapt: an R package to perform genome scans for selection based on principal component analysis. *Molecular Ecology Resources*, 17: 67–77. John Wiley & Sons, Ltd. <https://doi.org/10.1111/1755-0998.12592>
- Naciri, M., Lemaire, C., Borsa, P., and Bonhomme, F. 1999. Genetic study of the Atlantic/Mediterranean transition in sea bass (*Dicentrarchus labrax*). *Journal of Heredity*, 90: 591–596. Oxford University Press.
- Pawson, M. G., Pickett, G. D., and Kelley, D. F. 1987. The distribution and migrations of bass, *Dicentrarchus labrax* L., in waters around England and Wales as shown by tagging. *Journal of the Marine Biological Association of the United Kingdom*, 67: 183–217. Cambridge University Press. <https://www.cambridge.org/core/article/distribution-and-migrations-of-bass-dicentrarchus-labrax-l-in-waters-around-england-and-wales-as-shown-by-tagging/16A68911764ECC13D2CC92AB626B92B3>
- Pawson, M. G., Brown, M., Leballeur, J., and Pickett, G. D. 2008. Will philopatry in sea bass, *Dicentrarchus labrax*, facilitate the use of catch-restricted areas for management of recreational fisheries? *Fisheries Research*, 93: 240–243. <https://www.sciencedirect.com/science/article/pii/S016578360800088X>
- Quayle, V. A., Righton, D., Hetherington, S., and Pickett, G. 2009. Observations of the Behaviour of European Sea Bass (*Dicentrarchus labrax*) in the North Sea. *In* pp. 103–119. [http://link.springer.com/10.1007/978-1-4020-9640-2\\_7](http://link.springer.com/10.1007/978-1-4020-9640-2_7)
- Robinet, T., Roussel, V., Cheze, K., and Gagnaire, P.-A. 2020. Spatial gradients of introgressed ancestry reveal cryptic connectivity patterns in a high gene flow marine fish. *Molecular Ecology*, 29: 3857–3871. John Wiley & Sons, Ltd. <https://doi.org/10.1111/mec.15611>

- Roy, A., Lebigre, C., Drogou, M., and Woillez, M. 2022. Estimating abundance indices of juvenile fish in estuaries using Geostatistics: An example of European sea bass (*Dicentrarchus labrax*). *Estuarine, Coastal and Shelf Science*, 269: 107799. <https://www.sciencedirect.com/science/article/pii/S0272771422000580>
- Ryan, D., and Wogerbauer, C. 2022. Otolith microchemistry to investigate nursery site fidelity and connectivity of juvenile European sea bass in Ireland. *Marine Ecology Progress Series*, MFC: MFCav2. [https://www.int-res.com/abstracts/meps/MFC/p\\_av2/](https://www.int-res.com/abstracts/meps/MFC/p_av2/)
- Souche, E. L., Hellemans, B., Babbucci, M., MacAoidh, E., Guinand, B., Bargelloni, L., Chistiakov, D. A., *et al.* 2015. Range-wide population structure of European sea bass *Dicentrarchus labrax*. *Biological Journal of the Linnean Society*, 116: 86–105. John Wiley & Sons, Ltd. <https://doi.org/10.1111/bij.12572>
- Stamp, T., Clarke, D., Plenty, S., Robbins, T., Stewart, J. E., West, E., and Sheehan, E. 2021. Identifying juvenile and sub-adult movements to inform recovery strategies for a high value fishery—European bass (*Dicentrarchus labrax*). *ICES Journal of Marine Science*, 78: 3121–3134. <https://doi.org/10.1093/icesjms/fsab180>
- Sturrock, A. M., Trueman, C. N., Darnaude, A. M., and Hunter, E. 2012. Can otolith elemental chemistry retrospectively track migrations in fully marine fishes? *Journal of Fish Biology*, 81: 766–795. John Wiley & Sons, Ltd. <https://doi.org/10.1111/j.1095-8649.2012.03372.x>
- Trueman, C. N., MacKenzie, K. M., and Palmer, M. R. 2012. Identifying migrations in marine fishes through stable-isotope analysis. *Journal of Fish Biology*, 81: 826–847. John Wiley & Sons, Ltd. <https://doi.org/10.1111/j.1095-8649.2012.03361.x>
- Woillez, M., Fablet, R., Ngo, T.-T., Lalire, M., Lazure, P., and de Pontual, H. 2016. A HMM-based model to geolocate pelagic fish from high-resolution individual temperature and depth histories: European sea bass as a case study. *Ecological Modelling*, 321: 10–22. <https://www.sciencedirect.com/science/article/pii/S0304380015005098>

## Annex 1: List of participants

Name	Institute	Country (of institute)	E-mail
Anna Sturrock	University of Essex	UK	anna.sturrock@essex.ac.uk
Chloé Dambrine	INRAE	France	chloe.dambrine@orange.fr
Ciara Wögerbauer	Inland Fisheries Ireland	Ireland	cwoerbauer@fisheriesireland.ie
David Curtis	Bass Anglers' Sportfishing Society	UK	david1curtis@yahoo.co.uk
David Murray (chair)	Cefas	UK	david.murray@cefas.gov.uk
Filip Volckaert	University of Leuven	Belgium	filip.volckaert@kuleuven.be
Florian Berg (reviewer)	IMR	Norway	florian.berg@hi.no
Francis Binney	Government of Jersey	UK	f.binney@gov.je
Françoise Daverat	INRAE	France	francoise.daverat@inrae.fr
Gwladys Lambert	Cefas	UK	gwladys.lambert@cefas.gov.uk
Hélène de Pontual	Ifremer	France	helene.de.pontual@ifremer.fr
Iliaria Coscia	Marine Institute Ireland	Ireland	ilaria.coscia@marine.ie
James Stewart	Devon & Severn Inshore Fisheries & Conservation Authority	UK	j.stewart@devonandsevernifca.gov.uk
Jennifer Graham	Cefas	UK	jennifer.graham@cefas.gov.uk
Jolien Goossens	Ghent University	Belgium	jolien.goossens@ugent.be
Joseph Watson	Cefas	UK	joseph.watson@cefas.gov.uk
Kerrie-Anne Egge	Government of Jersey	UK	k.egge@gov.je
Kieran Hyder	Cefas	UK	kieran.hyder@cefas.gov.uk
Massimiliano Cardinale	SLU	Sweden	massimiliano.cardinale@slu.se
Mathieu Woillez	Ifremer	France	mathieu.woillez@ifremer.fr
Michel Bertignac	Ifremer	France	michel.bertignac@ifremer.fr
Michelle Taylor	University of Essex	UK	michelle.taylor@essex.ac.uk
Mickael Drogou	Ifremer	France	mickael.drogou@ifremer.fr
Naiara Rodríguez-Ezpeleta (reviewer)	AZTI	Spain	nrodriguez@azti.es
Philip Lamb	Cefas	UK	philip.lamb@cefas.gov.uk

Name	Institute	Country (of institute)	E-mail
Pierre-Alexandre Gagnaire	University of Montpellier	France	pierre-alexandre.gagnaire@umontpellier.fr
Serena Wright	Cefas	UK	serena.wright@cefas.gov.uk

## Annex 2: Resolutions

2022/2/FRSG49 The benchmark on selected sea bass stocks<sup>1,2</sup> (WKBSEABASS) is **composed of three meetings**; a stock ID workshop, a data workshop, and benchmark workshop.

The stock ID workshop will be chaired by David Murray, UK, and will be attended by two invited experts Naiara Rodríguez-Ezpeleta, Spain and Florian Berg, Norway. The ID workshop will meet online for a three-day meeting 29 November to 1 December 2022.

The data and benchmark workshops will be chaired by Pia Schuchert, UK, and Massimiliano Cardinale, Sweden, and attended by three invited external experts TBD. The data workshop will meet in Copenhagen, Denmark 25–29 September 2023, and the final assessment benchmark workshop will take place 22–26 January 2024 in Copenhagen, Denmark, to:

*As part of the stock ID workshop*

- a) Review information on stock identification for bss.27.4bc7ad-h and bss.27.8ab and conduct a comparative review of Atlantic seabass population structure, including critical evaluation of inferences from each source of information, to build up a picture of seabass stock structure in Celtic Sea, Bay of Biscay and adjacent areas, based on the following:
  - i) Distribution and movements of different life-stages of seabass, including changes over time, inferred from:
    - 1) Tagging;
    - 2) Scientific Surveys;
    - 3) Commercial landings;
    - 4) Dispersal models (e.g. of larva/juveniles);
  - ii) Genetic analyses;
  - iii) Otolith microchemistry;
  - iv) Morphometrics and meristics;
  - v) Life-history and parasites;
  - vi) Other approaches not listed above.
- b) Based on the evidence from ToR 1, formulate scenarios for seabass stocks in the Celtic Sea, Bay of Biscay and adjacent areas, and assess the evidence-based plausibility of each of these scenarios (including current definitions).
- c) Consider the practical implications, for data, particularly time-series of catch data and year class strength, and mixing rates of each of the scenarios in ToR 2, and how any difficulties might be dealt with. For example, considering spatial components with mixing in a single model has different implications for data compared to split stock units. Considerations should include how to deal with changes over time.
- d) Make recommendations for which seabass stock scenario(s) to take forward in the forthcoming seabass benchmark, including in what format data should be requested and prepared.

*As part of the data workshop*

- e) Conduct a 4-day data workshop. Stakeholders are invited to contribute data (including data from non-traditional sources) and to contribute to data preparation and evaluation

---

<sup>1</sup> bss.27.4bc7ad-h – Sea bass (*Dicentrarchus labrax*) in divisions 4.b-c, 7.a, and 7.d-h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea)

<sup>2</sup> bss.27.8ab – Sea bass (*Dicentrarchus labrax*) in divisions 8.a-b (northern and central Bay of Biscay)

of data quality. Data, particularly catch information, should be collated as far back in time as possible. As part of the data compilation workshop consider the quality of data including discard and estimates.

- f) Make a proposal to the benchmark on the use and treatment of data for each assessment, including discards, surveys, life history, recreational fisheries etc.
- g) Following the DEWK, produce working documents to be reviewed during the Benchmark workshop at least one month prior to the workshop.

*As part of the benchmark workshop*

- h) Evaluate the appropriateness of data and methods to determine stock status and investigate methods for short term forecast taking agreed or proposed management plans into account for the stocks listed in the text table below. The evaluation shall include consideration of:
  - i) Life-history data;
  - ii) Fishery-dependent and fishery-independent data;
  - iii) Further consideration of environmental drivers, multispecies information, and ecosystem impacts for stock dynamics in the assessments and outlook.
- i) Agree and document the most appropriate method for evaluating stock status and (where applicable) short-term forecast and update the stock annex as appropriate. Knowledge about environmental drivers, including multispecies interactions, and ecosystem impacts should be integrated in the methodology.
- j) A full suite of diagnostics (regarding data, retrospective behaviour, model fit etc.) should be examined as a whole to evaluate the appropriateness of any model developed and proposed for use in generating advice. If no analytical assessment method can be agreed, then an alternative method for providing advice (ideally one of the WKLIFE X<sup>3</sup> methods should be put forward.
- k) Re-examine and update (if necessary) MSY and PA reference points according to ICES guidelines (see Technical document on reference points)).
- l) Draft stock annexes for each of the stocks part of the benchmark outcomes.
- m) Develop recommendations for future improvements of the assessment methodology and data collection.
- n) Provide detailed guidance on the mechanics of the sea bass allocation tool.

---

<sup>3</sup> <https://doi.org/10.17895/ices.pub.5985>

## Annex 3: Reviewer reports

### **Review of the WKSEABASS stock identification workshop and report by Florian Berg**

The workshop was conducted in November 2022 and all ToRs were dealt with as summarized in the report. The main aim of this workshop was to provide evidence of potential stock mixing of the two sea bass stocks; a ‘northern’ stock in divisions 4.b-c, 7.a, and 7.d-h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel and Celtic Sea), and a southern stock in divisions 8.a-b (Bay of Biscay). The final conclusions of the workshop and report are three potential hypothesis, each accounting for mixing of the two stocks, but the mixing occurs in different areas. The presented evidences and historical literature is not very conclusive and not precise either. In most cases data from specific areas were missing and thus the full extent of mixing could not be evaluated in the single case studies. However, the overall results and hypothesis are solid. Considering the provided case studies combined, it has been clearly demonstrated that mixing occurs. The participants of the workshop also concluded that three main/stationary components of sea bass exist, 1) Irish Sea, 2) North Sea, and 3) Bay of Biscay. From the presented studies, the conclusion of a North Sea and Bay of Biscay component is clearly supported. The Irish Sea component is not as conclusive as the other two as most presented studies did not account for this region. Only one tagging study included sea bass from the Irish Sea that were also recaptured in the defined mixing area. Genetic studies demonstrate differentiation between the North Sea component and sea bass in the Irish Sea and Celtic Sea, but no differentiation between the Irish and Celtic Sea directly. Thus, clear evidence that this is a single population is still missing, even though it is most likely. Furthermore, the presented mixing occurred during the feeding period. Study using otolith chemistry to investigate natal homing was again only conducted on a limited distribution area. Personally, I would favour the option with most mixing areas (Hypothesis 1), because there is evidence that mixing exists in all of these areas based on several case studies. Different studies provide evidence of mixing in different areas, but none of the other studies can reject mixing. Thus, the most plausible stock structure is described by Hypothesis 1.

Despite the presented mixing of component, precise and accurate stock identification methods are lacking. Thus, an individual assignment to one of the three main components is not possible. Even though from a biological point of view the current stock structure does not reflect biological units, there are several shortcomings that need to be considered for the stock assessment. Results from tagging studies might be valid to estimate mixing rates, but the interannual variation might be challenging to consider. The presented studies included several years of data sampling, but it is questionable if such tagging studies can be conducted to estimate annual mixing rates. The report highlights the potential shortcomings regarding the assessment of these three biological components, and have therefore presented potential scenarios for the benchmark. How realistic these benchmark scenarios are, must be evaluated after the data call at the benchmark. Based in the workshop and present workshop, this would be out of the scope for this review.

### **Review of the WKSEABASS stock identification workshop and report by Naiara Rodriguez-Ezpeleta**

The stock structure of the seabass (*Dicentriscus labrax*) is reviewed based on evidence derived from alternate sources, with the final aim of informing the WKSEABASS benchmark and data call in 2023. In this report, I will review the evidence, the hypothesis formulated from them and the potential assessment scenarios proposed.

The **evidence** presented in the workshop and summarized in the report consist on pelagic connectivity, tagging, otolith microchemistry and genetic studies.

Pelagic connectivity studies suggest higher settlement in the English Channel, which is seen as a supplier of larvae to many other areas.

Tagging studies suggest seasonal differences in movements, with larger transfer rates from north to south in around October and from south to north around April. They also reveal movements between Celtic Sea and the North Sea with some individuals being North Sea residents. There seems to be seasonal fidelity to feeding (summer) and spawning (winter) areas. Within the English Channel most reproductive migrations are from western EC to the Bay of Biscay and within Northern and Central BOB, most reproductive migrations are from BOB to the Iberian Peninsula.

Otolith microchemistry studies suggest spawning fidelity (64%), which is higher in areas at the northern and southern limits of the study.

Genetic studies suggest very low levels of differentiation within the Atlantic ( $F_{ST}$  near 0) and differentiation (with contemporary gene flow) between Atlantic and Mediterranean. The gene flow from the Mediterranean to the Atlantic can be used to determine connectivity within the Atlantic, being the Mediterranean ancestry higher in the coast of Portugal, intermediate in the Bay of Biscay and lower in the North and Celtic Seas. Thus, although genetic data reveal that a full mixing does not exist, genetic stock ID (GSI) is not possible.

Thus, what is clear from the evidence presented is that **there is no support for the current stock division**. However, they are not conclusive for any other potential scenario. Although in the report the scenario of a three metapopulations is advanced, I think the data is still too inconclusive even for that, as in some studies some areas are missing and there is strong seasonality which challenges the conclusions raised from studies not taking seasonality into account.

Three **hypotheses**, assuming the three metapopulations with a mixing area, are proposed. The only difference between them is the areas considered mixing zone and the areas considered part of the “pure” metapopulations: North Sea (4b-c), the Irish Sea (7a) and the Southern Bay of Biscay (8b) in hypothesis 1, North Sea (4b-c)/English Channel (7d), the Irish Sea (7a) and the Bay of Biscay (8a-b) in hypothesis 2 and North Sea (4b-c), the Irish Sea (7a) and the Bay of Biscay (8a-b) in hypothesis 3. Although the three hypotheses are supported by at least (or partially) some of the data presented, no clear support for any globally is provided. Thus, perhaps the safest option would be to assume mixing in areas where at least one of the studies has shown mixing.

Thus, in the absence of an alternative stock delimitation proposal that considers the potential metapopulations and mixing within, only two alternative **scenarios** can be proposed: the stocks keep separated as they are; they are assessed as one. I agree with this proposal as I find it too risky to come up with a new scenario with the data and evidence currently available. Thus, I also agree with the conclusion of needing more studies and data to further understand connectivity of seabass and that in those studies, not only the two assessed stocks should be included, but also the Iberian Peninsula and the West Ireland/Scotland stocks.