



# High-density SNP panel provides little evidence for population structure in European sea bass (*Dicentrarchus labrax*) in waters surrounding the UK

Martin I. Taylor <sup>1,\*</sup>, Philip D. Lamb<sup>2</sup>, Ilaria Coscia <sup>3</sup>, David S. Murray<sup>2,4</sup>, Mary Brown<sup>2</sup>, Tom C. Cameron<sup>5</sup>, Phil I. Davison<sup>2</sup>, Howard A. Freeman<sup>5</sup>, Katerina Georgiou<sup>6</sup>, Fabio Grati <sup>7</sup>, Thron Haugen<sup>8</sup>, Paraskevi K. Karachle<sup>9</sup>, Richard Kennedy<sup>10</sup>, Thomas Lanssens<sup>11</sup>, Harriet Lincoln <sup>12</sup>, Filipe Martinho <sup>13</sup>, Ian McCarthy<sup>12</sup>, Spyros-Iasonas Petroutsos<sup>9</sup>, Pablo Pita <sup>14</sup>, João C. O. Pontes<sup>15</sup>, Marta P. Baucells<sup>16</sup>, Mafalda Rangel<sup>15</sup>, William Roche<sup>17</sup>, Valerio Sbragaglia <sup>18</sup>, Anna M. Sturrock<sup>5</sup>, Michelle L. Taylor<sup>5</sup>, Ciara Wogerbauer<sup>17</sup>, Pedro Veiga<sup>15</sup>, Sieto Verver<sup>18</sup>, Marc Simon Weltersbach <sup>19</sup>, Kieran Hyder <sup>2,4</sup>

<sup>1</sup>School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom

<sup>2</sup>Centre for Environment, Fisheries and Aquaculture Science (Cefas), Lowestoft, Suffolk NR33 0HT, United Kingdom

<sup>3</sup>Marine Institute, Rinville, Oranmore, Co., Galway H91 R673, Ireland

<sup>4</sup>School of Environmental Sciences, University of East Anglia, Norwich Norfolk NR4 7TJ, United Kingdom

<sup>5</sup>School of Life Sciences, University of Essex, Colchester, Essex CO4 3SQ, United Kingdom

<sup>6</sup>Fisheries Resources Division, Department of Fisheries and Marine Research, Ministry of Agriculture, Rural Development and the Environment, 2033 Strovolos, Nicosia, Cyprus

<sup>7</sup>Institute of Biological Resources and Marine Biotechnologies, National Research Council, 60125 Ancona, Italy

<sup>8</sup>Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, 1430 Ås, Norway

<sup>9</sup>Institute of Marine Biological Resources and Inland Waters, Hellenic Centre for Marine Research, 19013 Anavissos, Greece

<sup>10</sup>Agri-Food and Biosciences Institute, Belfast, County Antrim BT9 5PX, United Kingdom

<sup>11</sup>Flanders Research Institute for Agriculture, Fisheries and Food, 8400 Oostende, Belgium

<sup>12</sup>School of Ocean Sciences, Bangor University, LL59 5AB Wales, United Kingdom

<sup>13</sup>Centre for Functional Ecology—CFE, Department of Life Sciences, Calçada Martim de Freitas, University of Coimbra, Coimbra 3030-788, Portugal

<sup>14</sup>Department of Applied Economics, Faculty of Economic and Business Sciences, University of Santiago de Compostela, 15782 Santiago de Compostela, Spain

<sup>15</sup>Centre of Marine Sciences, University of Algarve, Campus de Gambelas, Faro 8005-139, Portugal

<sup>16</sup>Department of Marine Renewable Resources, Institute of Marine Sciences (ICM-CSIC), 08003 Barcelona, Spain

<sup>17</sup>Inland Fisheries Ireland, Dublin D24 Y265, Ireland

<sup>18</sup>Wageningen Marine Research, Passeig Marítim de la Barceloneta, NL-1970 AB IJmuiden, Netherlands

<sup>19</sup>Thünen Institute of Baltic Sea Fisheries (Thünen-OF), Rostock 18069, Germany

\*Corresponding author. School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom. E-mail: [martin.taylor@uea.ac.uk](mailto:martin.taylor@uea.ac.uk)

## Abstract

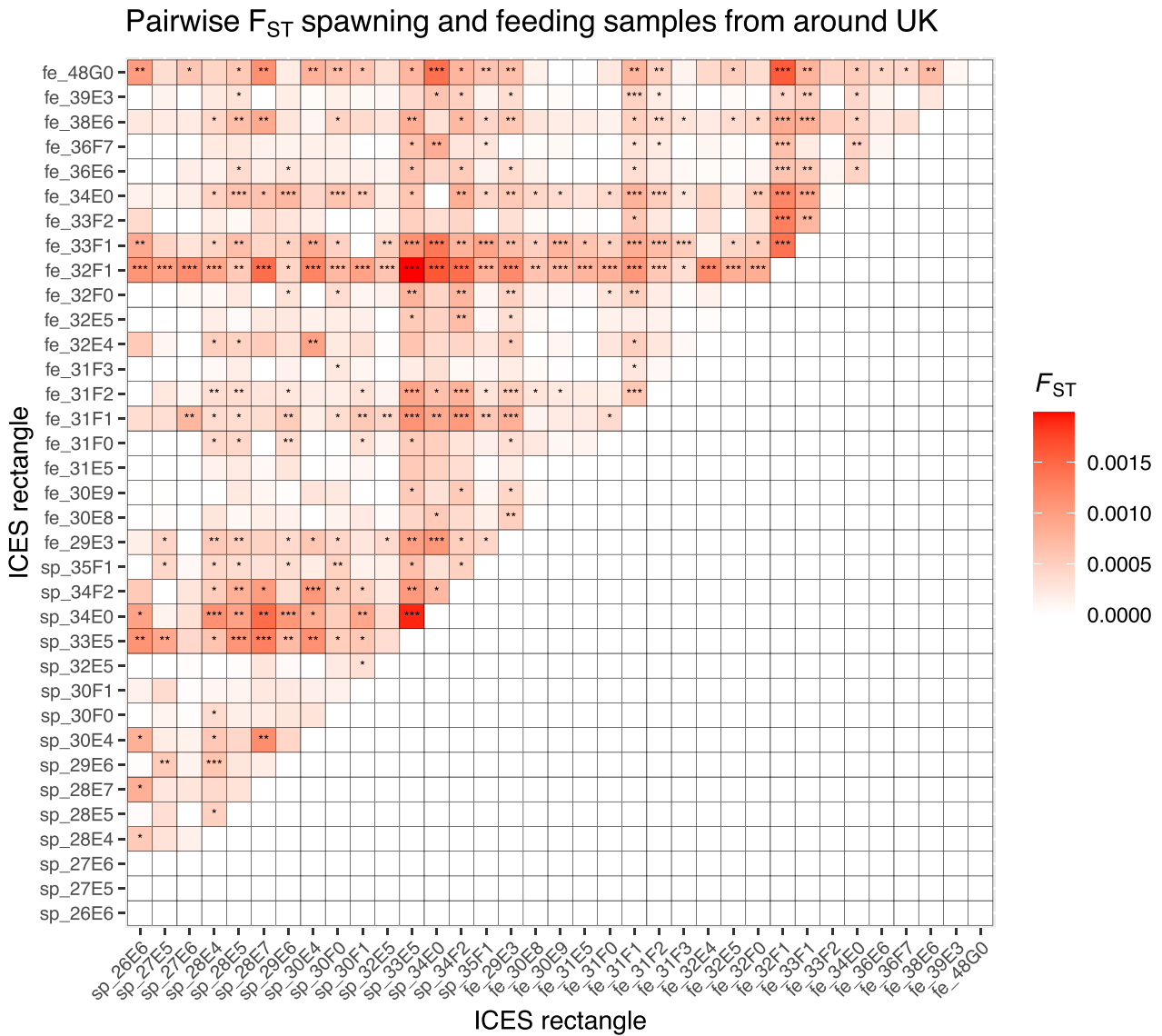
The European sea bass (*Dicentrarchus labrax*) is a commercially and recreationally important fish widely, distributed across the North-east Atlantic Ocean and Mediterranean Sea. Two distinct lineages that represent the Atlantic and Mediterranean regions have been previously identified, with a hybrid zone close to the Almería–Oran front. The presence of fine-scale population structure within the Northeast Atlantic region is less clear. Here, we investigated population structure in adult samples obtained from the northern part of the Atlantic range surrounding the UK, Ireland, Belgium, Germany, France, the Netherlands, and Norway, along with outgroups from Portugal and the Mediterranean, using a panel of 41 K single nucleotide polymorphism markers. Population structure among Northeast Atlantic Ocean samples was weak in both spawning—( $F_{ST} = 0.00022$ ) and feeding—( $F_{ST} = 0.00032$ ) season data sets, with small pairwise  $F_{ST}$  values between sample pairs. However, average  $F_{ST}$  was larger between spawning samples than between feeding samples, with a pattern of isolation-by-distance among the spawning samples, but not the feeding samples, suggesting some biologically meaningful population structure. The largest pairwise  $F_{ST}$  values at both International Council for the Exploration of the Sea (ICES) rectangle and division scales involved a sample from the west of Ireland. We found no evidence of a gradient in “Mediterranean” ancestry among samples collected around the UK in our data set or in a reanalysis of a published data set where such a pattern had been previously identified. In summary, there was no evidence that sea bass in different ICES divisions within the Northeast Atlantic Ocean represents genetically separate populations. Further work is required to reconcile evidence from tagging and modelling studies that suggest the potential for demographic independence with the genetic data.

**Keywords:** fisheries; SNPs; genetics; sea bass; population structure; connectivity









**Figure 2.** Pairwise Weir and Cockerham’s  $F_{ST}$  (theta) for feeding (fe) and spawning (sp) sea bass samples labelled by the ICES rectangle from which they were collected (see Fig 1 a, b). All samples comprise at least 10 individuals). Cells are coloured by  $F_{ST}$  value and the statistical significance after Benjamini and Hochberg (1995) correction is indicated by \*\*\* =  $P < 0.001$ , \*\*  $P = 0.01$ , \*  $P = 0.05$ . <https://www.ices.dk/data/maps/Pages/ICES-statistical-rectangles.aspx>.

**Outlier identification**

Bayescan identified no SNPs and OutFLANK identified one SNP locus potentially influenced by selection in the Atlantic + Northern Portugal dataset. Pcadapt was not run in the Atlantic only data set due to lack of structure in PCA plots. Bayescan identified 20 loci putatively under positive selection in the Atlantic Ocean vs Mediterranean Sea data set (Supplementary Fig. S1a), OutFLANK identified 1553 loci (Supplementary Fig. S1b) and pcadapt identified 1242 loci. Overall, there were 2037 loci across the three methods with 738 in common between outflank and pcadapt and 12 loci in common across the three methods.

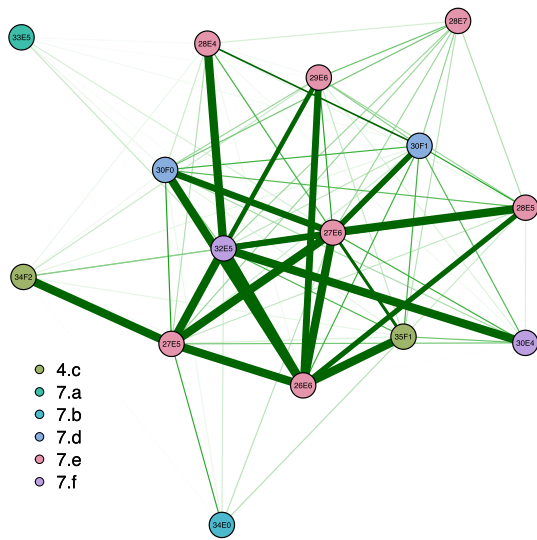
**Population structure**

Global  $F_{ST}$  among the Northeast Atlantic Ocean samples was small, with global  $F_{ST} = 0.000316$  (standard

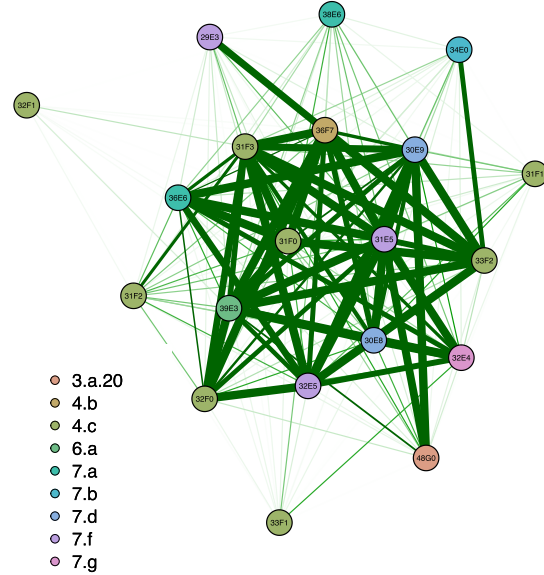
error ( $se$ ) = 0.000054) among the UK Atlantic Ocean spawning samples when partitioned at ICES rectangle level and  $F_{ST} = 0.0002235$  ( $se = 0.0000414$ ) when individuals were combined into ICES divisions. Global  $F_{ST} = 0.00022$  ( $se = 0.000032$ ) among the Atlantic feeding samples when partitioned into ICES rectangles and  $F_{ST} = 0.0001$  ( $se = 0.000026$ ) when individuals were combined into ICES divisions. When including the Mediterranean Sea and Portuguese samples, global,  $F_{ST}$  was larger, with  $F_{ST} = 0.0062$  ( $se = 0.0000796$ ) for the spawning sample data set.

Within the Atlantic samples surrounding the UK, pairwise  $F_{ST}$  was small among ICES rectangles, ranging between 0 and 0.0019 for spawning samples and between 0 and 0.0016 for feeding samples.  $P$  values for permutation tests revealed some pairwise  $F_{ST}$  values that were significantly different from zero after Benjamini and Hochberg (1995) correction (Fig. 2) with one feeding sample showing significant differences in almost

## Spawning samples similarity



## Feeding samples similarity



**Figure 3.** Forceplots of feeding and spawning pairwise similarity ( $1-F_{ST}$ ). The line colour saturation and the width of the edges show the absolute weight and scale relative to the strongest weight in the plot. Nodes represent ICES rectangles and are coloured by ICES division.

all pairwise comparisons (32F1; North Sea, ICES division 4.c). Differentiation between ICES divisions was also very low with pairwise theta ranging from 0 to 0.0019 for spawning samples, with Northern Portugal significantly different from all other ICES divisions (Fig. 1c). The Irish Sea (ICES division 7.a) and West Coast of Ireland (ICES division 7.b) showed the greatest differentiation ( $F_{ST} = 0.0019$ ). Pairwise  $F_{ST}$  between feeding samples was smaller, ranging from 0 to 0.0005 with a some statistically significant comparisons despite the small  $F_{ST}$  (Fig 1d). The West Coast of Ireland (ICES division 7.b) had somewhat larger ( $\sim$ double) pairwise  $F_{ST}$  values than other comparisons.

Pairwise  $F_{ST}$  were significantly larger between ICES rectangle spawning than between feeding samples (Permutation test,  $P = 0.015$ ; Supplementary Fig. S2). Differences between pairwise  $F_{ST}$  of the spawning and feeding assemblages is illustrated using network forceplots (Fig. 3) where similarity ( $1-F_{ST}$ ) is plotted. Thicker bars between nodes (ICES rectangles) indicate greater genetic similarity.

Mantel tests revealed a significant relationship between log geographic sea distance and genetic distance ( $F_{ST}$ ) within the Northeast Atlantic Ocean spawning date set ( $P = 0.031$ ) but not in the feeding data set ( $P > 0.05$ ) when excluding the Portuguese and Mediterranean Sea samples (Supplementary Figs S2a and b). See Supplementary Table S1a, b for samples sizes and other information for each site and season.

### Population (sample) specific $F_{ST}$

The Mediterranean Sea sample had the lowest sample specific  $F_{ST}$ . Feeding and spawning samples had similar sample specific  $F_{ST}$ , with one feeding site (32F1, North Sea, ICES division 4.c) and three spawning sites (26E6, English Channel, ICES division 7.e; 34E0, West Coast of Ireland, ICES division 7.b; and 30E4, Bristol Channel, ICES division 7.f) showing higher values (Fig. 4).

Principal components 1 and 2 accounted for 3.42% and 0.49% of the total variation in the data set, respectively in-

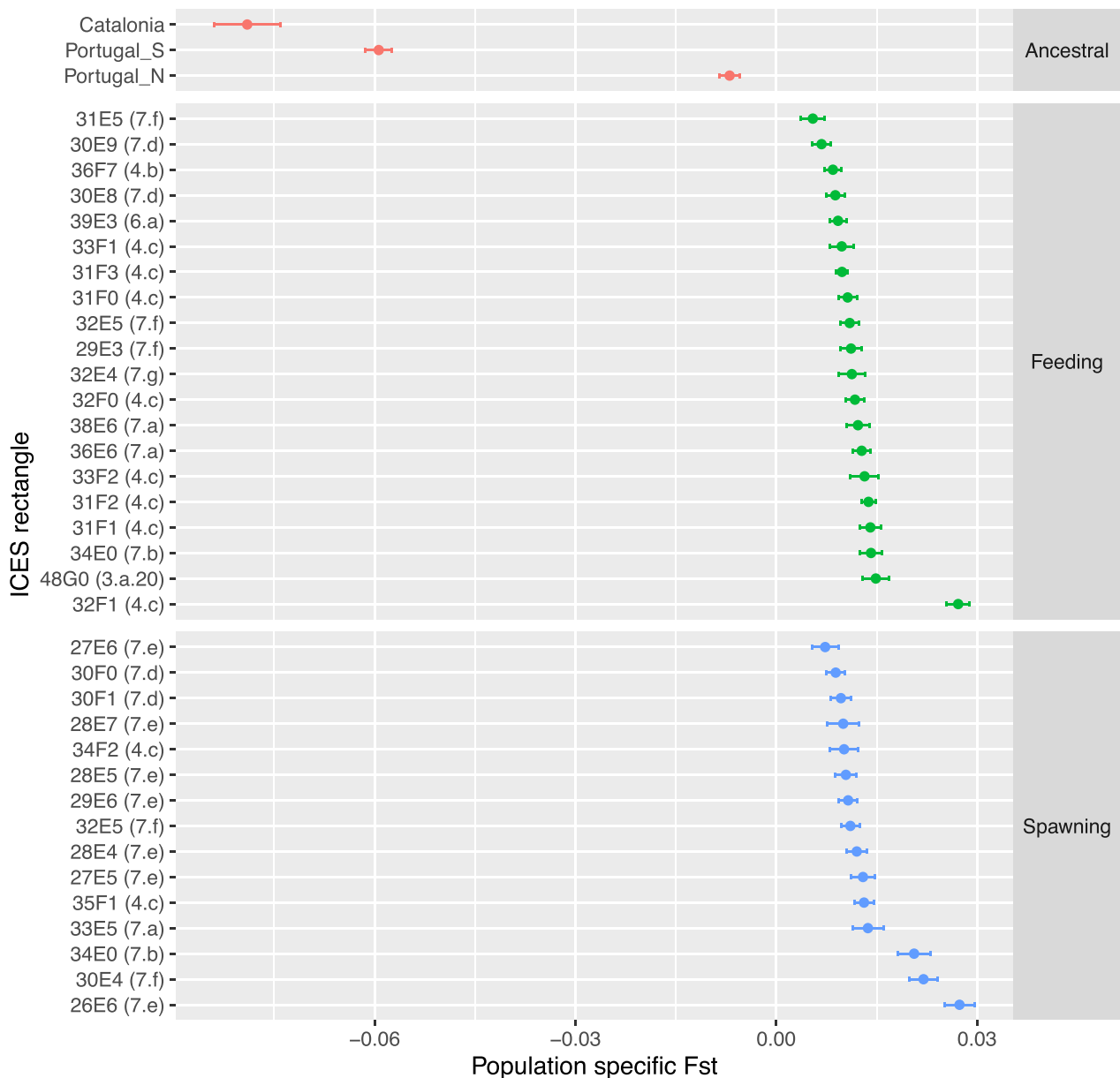
cluding the Mediterranean Sea and Portuguese samples and the PCA identified clear differentiation between the Northeast Atlantic Ocean samples, the Portuguese samples, and the Mediterranean Sea (Fig. 5a). The two Portuguese samples form a cluster with North and South Portugal samples differentiated on PC2 (Fig. 5a) with two individuals from the Southern Portuguese site intermediate with the Mediterranean Sea cluster. The Northeast Atlantic Ocean samples form a single cluster with clear differentiation from the Mediterranean Sea and Portuguese samples. Principal component analysis on solely the Northeast Atlantic Ocean samples did not reveal any site-specific clusters and there was considerable overlap between individuals across both the ICES division (Fig. 5b) and rectangle scales for both feeding and spawning data sets. The first two PCs each explained 0.43% of the total variation.

### Model-based clustering

Model-based clustering identified  $k = 2$  as the largest log-likelihood, with the Mediterranean Sea sample with strong Mediterranean ancestry and the Atlantic samples with lower Mediterranean ancestry (Fig. 6). Larger  $K$ s did not reveal additional population structure within the Northeast Atlantic Ocean (Supplementary Fig. S4). The Southern Portuguese individuals showed an average Mediterranean component of 29%, but with a wide range of Mediterranean ancestry (15%–90%). This suggested the presence of several Mediterranean migrants or admixed migrants in the sample and some individuals that had much lower Mediterranean admixture components typical of Atlantic sites. The Northern Portuguese sample showed an average of 7.8% Mediterranean ancestry, with the samples surrounding the UK showing an average of 1.2%–2.7% Mediterranean ancestry (Fig. 6).

### Mediterranean ancestry and geographic distance

There was no evidence of a relationship between the admixture proportion and distance from the Mediterranean Sea within the samples surrounding the UK and Ireland or any ev-



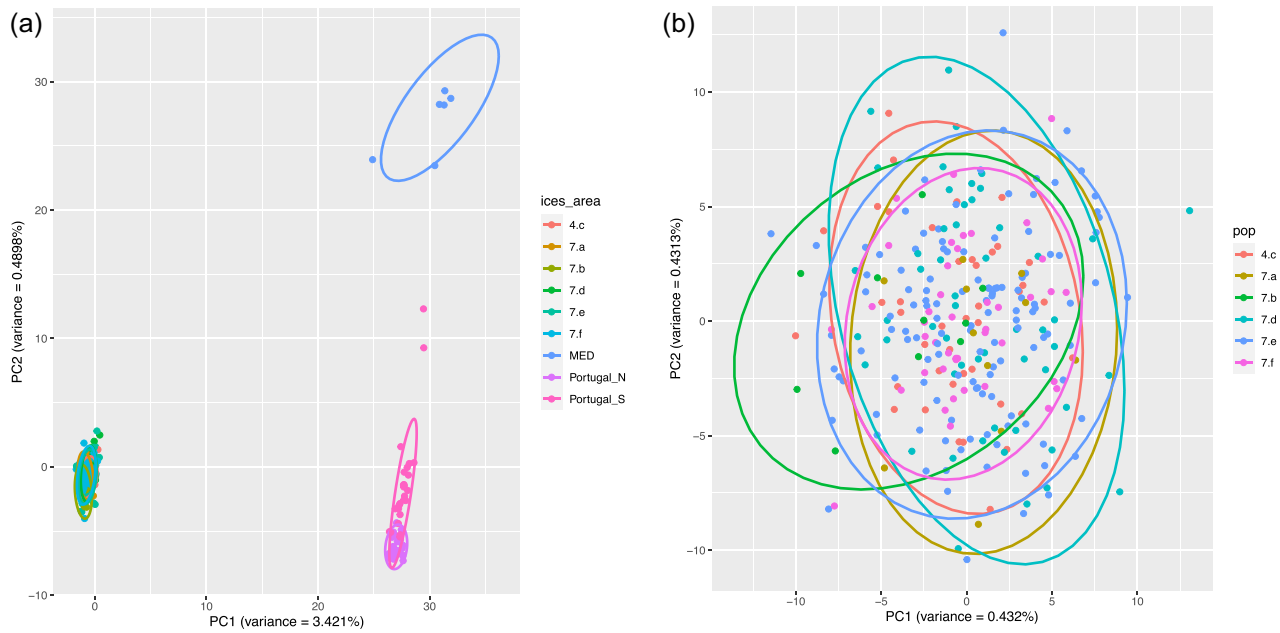
**Figure 4.** Population (sample) specific  $F_{ST}$  values for feeding and spawning sea bass samples by ICES rectangles, where the initial two-digit number indicates degrees latitude. See [Supplementary Table S1a](#). b for samples sizes and other information for each site and season.

idence of genetic breaks associated with ICES division when using solely the samples surrounding the UK and Ireland (Fig. 7). We also investigated the relationship between geographic distance and Mediterranean ancestry using the loci identified by Bayescan, OutFLANK, and pcadapt as putatively affected by selection. Similar patterns were identified as using the whole data set, but confidence intervals were larger (Fig. 8). No genetic breaks among ICES divisions in the English Channel were identified.

## Discussion

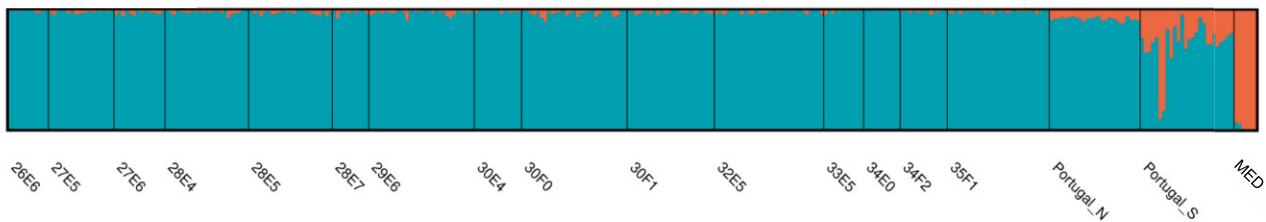
This study utilized dense sampling of European sea bass from across the Northeast Atlantic Ocean, in waters surrounding the UK, and more than 41 000 SNP markers suggests extremely low levels of population structure. Global and pair-

wise levels of  $F_{ST}$  are smaller than those previously identified in other commercially important marine fishes at similar geographic scales (see below). Measures of population differentiation, as measured by  $F_{ST}$ , were small across almost all sample pairs with statistically significant differences identified mainly in comparisons involving a few specific sites. The West of Ireland (ICES division 7.b) spawning sample was the most differentiated of the samples with a higher pairwise  $F_{ST}$  value and was statistically significantly differentiated from the Irish Sea (ICES division 7.a) with lower pairwise  $F_{ST}$  values compared to other divisions. While pairwise  $F_{ST}$ s were small, spawning samples had significantly larger pairwise  $F_{ST}$  values than feeding samples, suggesting some biologically meaningful structure within the data set. There was evidence of isolation-by-distance among spawning samples surrounding the UK and Ireland, but not within the feeding data set. Principal com-

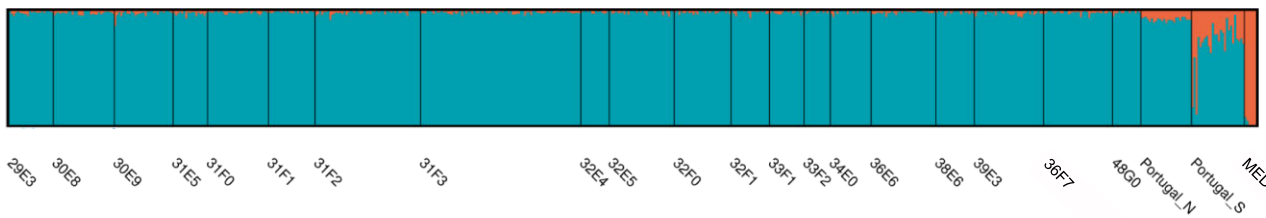


**Figure 5.** Principal component analysis of spawning sea bass samples by ICES division, including (a) and excluding (b) samples from the Mediterranean Sea and Portugal.

### (a) Spawning (K=2)



### (b) Feeding (K=2)



**Figure 6.** Output of model-based clustering for spawning (a) and feeding (b) sea bass samples arranged by ICES rectangle [for  $K = 2$  (greatest log likelihood clustering)]. Portuguese and MED outgroups are included in both plots.

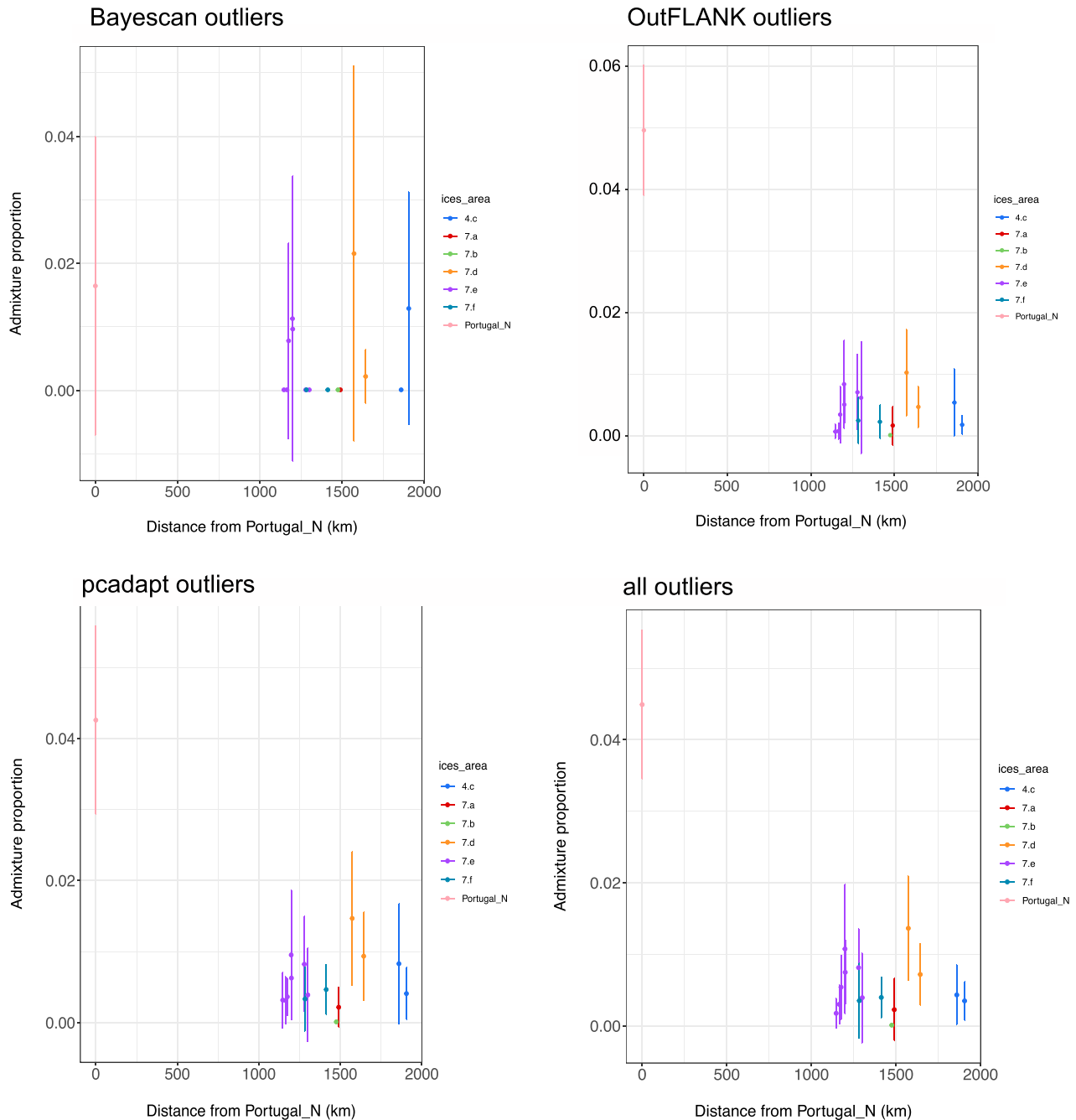
ponent analysis and model-based clustering failed to identify any evidence of population structure within the Northeast Atlantic Ocean samples. We identified an expected steep decline in Mediterranean ancestry between the Mediterranean Sea and the Northeast Atlantic Ocean, but there was no evidence of a decrease in Mediterranean ancestry in relation to geographic distance within the Northeast Atlantic Ocean samples (when excluding Portugal).

### Population structure

Overall, we identified low levels of population structure among sea bass in the Northeast Atlantic Ocean. Global  $F_{ST}$  was small in both spawning and feeding data sets. Global

$F_{ST}$  ranged between 0.0001 and 0.000316 depending on the scale (ICES rectangles vs divisions), and between spawning and feeding collection periods. This is comparable to the  $F_{ST} = 0.0002$  estimated in the SNP-based sea bass study of Robinet et al. (2020), which included a wider sampling area, but fewer SNPs ( $n = 1012$ ). However, it is smaller than the value of  $F_{ST} = 0.009$  found by Coscia and Mariani (2011) using microsatellite markers.  $F_{ST}$  values in marine fish are typically considered to be small, with Ward et al. (1994) identifying an average  $F_{ST}$  of 0.062 across 57 marine species. This value was estimated using mainly allozyme based studies, but more recent analyses using SNP markers have found comparable values. For example, Wright et al. (2021) found a global





**Figure 8.** Proportion of Mediterranean ancestry in spawning samples in relation to geographic sea distance from the Portugal North sample using outlier loci. Error bars are 2x standard error. Populations are coloured by ICES division. (a) Bayescan outliers (20 loci), (b) OutFLANK outliers (1553 loci), (c) pcadapt outliers (1242 loci), and (d) all outliers (2037 loci).

levels of individual missing data. Thus, we refiltered the Robinet et al. (2020) data to exclude individuals with  $>5\%$  missing data (Supplementary Fig. S5a and S5b) and replotted the Robinet et al. (2020) MED ancestry figure (Robinet et al. Fig. 4a and c), which no longer showed an increase in MED ancestry in the northeast Atlantic along with smaller error bars across the whole data set as a result of outlying individuals being removed (Supplementary Fig. S6a and S6b). The finding of increasing Mediterranean ancestry in the samples around the UK, appears to have been driven by a single sample from the North East UK (NEUK), which had a small sample size ( $n = 8$ ) and large  $F_{IS}$ . Two individuals had very high levels of missing

data and large MED ancestry (Supplementary Fig. S5a). Thus, a combination of small sample size and missing data in some individuals appears to have led to an artefactual increase in MED ancestry in the northeastern Atlantic from the English Channel northwards in the Robinet et al. (2020) paper. After filtering the Robinet et al.'s (2020) data, the results for the northeastern Atlantic are similar to those found in our study.

### Management implications

This study identified weak structure within the Northeast Atlantic Ocean sea bass stock, but identified some structure

between the West of Ireland and Irish Sea/English Channel, indicating the potential for differentiation between the "West Coast of Ireland and Scotland" and "North Sea, English Channel, Celtic and Irish Sea" stocks. Some previous studies have indicated population structuring across similar geographic areas, (e.g. Fritsch et al. 2007), but the results were not consistent (e.g. Child 1992, Coscia and Mariani 2011). Large scale studies have not found distinct population structure within the northern stock (e.g. Souche et al. 2015, Robinet et al. 2020) making the identification of stocks based on genetic structure difficult (ICES 2023). However, high levels of fidelity to feeding and spawning areas as adults (de Pontual et al. 2023) would suggest that smaller management units are needed than are currently in place to effectively manage the stock and ensure sustainability. As a result, it is important to consider connectivity between areas in terms of pelagic drift of eggs and larvae, and adult movements to define subpopulations that could be included within a single metapopulation management unit that could be used to drive future ICES assessments (ICES 2023).

Bringing together all existing data on genetics, pelagic drift, and migration suggest that "Northern" and "Biscay" sea bass are not separate populations but exist as a metapopulation with potentially distinct subpopulation components with connectivity between current ICES advice units (ICES 2023). However, there was insufficient evidence to identify the subpopulations or zones of mixing as the evidence was contradictory (ICES 2023). In addition, it is likely that connectivity exists between all four of the existing stock units (i.e. Northern, Biscay, Atlantic-Iberian, and West of Scotland and Ireland), so further genomics, tagging, biophysical modelling, and otolith microchemistry studies, are needed to understand exactly how sea bass within the Northeast Atlantic Ocean are connected, the subpopulations that should be considered, in order to define the relevant management units. Utilizing additional analytical methods may also be informative, including novel population-specific genotype by phenotype associations to identify introgressed individuals and migrants (Leitwein et al. 2024), species essential habitat modelling to identify suitable spawning habitat and environmental barriers (Dambrine et al. 2021), and dynamic energy budget modelling to predict size and season specific distributions based on physiological parameters (Teal et al. 2012).

## Acknowledgements

Thanks to Carole Confolent, Pauline Izorche, and Benjamin Tyssandier at GENTYANE INRAE who ran the SNP chip. P.K.K. and S.I.P. would like to thank the president (Mr Margaritis Mproumpis) and the members of the "Xanthi Spearfishing Club," in Xanthi, Greece for their assistance in acquiring samples.

## Author contributions

M.I.T., P.D.L., I.C., D.M., and K.H. conceived the study, developed the approach, completed the analysis, and drafted the manuscript. M.B., T.C.C., H.A.F., K.G., F.G., T.H., P.K.K., R.K., T.L., H.L., F.M., I.M., P.P., J.C.O.P., M.P.B., M.R., W.R., V.S., A.S., M.L.T., C.W., P.V., S.V., and M.S.W. provided samples for analysis. All authors gave critical comments on each draft of the manuscript, as well as guidance on interpretation of the results.

## Supplementary material

Supplementary material is available at the *ICESJMS Journal* online version of the manuscript.

*Conflict of interest:* None declared.

## Funding

This research was supported by the UK Department for Environment, Food, and Rural Affairs (Defra Grants FRD009 and FRD052) and UKRI [MR/V023578/1]. F. M. was supported by Fundação para a Ciência e Tecnologia, I.P. (FCT) in the scope of Decree-Law 57/2016, CFE-UC by project reference UIDB/04004/2020 and DOI identifier 10.54499/UIDB/04004/2020 (<https://doi.org/10.54499/UIDB/04004/2020>), and Associate Laboratory TERRA by project reference LA/P/0092/2020 and DOI identifier 10.54499/LA/P/0092/2020 (<https://doi.org/10.54499/LA/P/0092/2020>).

## Data availability

Data files underpinning the analyses contained in this study have been archived on Zenodo (doi: 10.5281/zenodo.15025594). R Scripts for analyses and plots are available from Github ([https://github.com/martiniantaylor/ICES\\_sea\\_bass](https://github.com/martiniantaylor/ICES_sea_bass)).

## References

- Affymetrix. *Axiom Analysis Suite*. 2011 Available from: <https://www.thermofisher.com/uk/en/home/life-science/microarray-analysis/microarray-analysis-instruments-software-services/microarray-analysis-software/axiom-analysis-suite.html> [Accessed January 2024].
- Allal F, Griot R, Phocas F et al. Axiom DlabCHIP, a 57 K SNPs genotyping array for European sea bass (*Dicentrarchus labrax*): array design and genetic map. *SEANOE* 2020. <https://doi.org/10.17882/75680>
- Andersson L, Bekkevold D, Berg F et al. How fish population genomics can promote sustainable fisheries: a road map. *Annu Rev Anim Biosci* 2024;12:1–20. <https://doi.org/10.1146/annurev-animal-0212-102933>
- Assis J, Castilho Coelho N, Alberto F et al. High and distinct range-edge genetic diversity despite local bottlenecks. *PLoS One* 2013;8:e68646. <https://doi.org/10.1371/journal.pone.0068646>
- Behr AA, Liu KZ, Liu-Fang G et al. pong: fast analysis and visualization of latent clusters in population genetic data. *Bioinformatics* 2016;32:2817–23. <https://doi.org/10.1093/bioinformatics/btw327>
- Bekkevold D, Berg F, Polte P et al. Mixed-stock analysis of Atlantic herring (*Clupea harengus*): a tool for identifying management units and complex migration dynamics. *ICES J Mar Sci* 2023;80:173–84. <https://doi.org/10.1093/icesjms/fsac223>
- Benjamini Y, Hochberg Y. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *J R Stat Soc Ser B Stat Method*, 1995;57:289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>
- Beraud C, Van Der Molen J, Armstrong M et al. The influence of oceanographic conditions and larval behaviour on settlement success—the European sea bass *Dicentrarchus labrax* (L.). *ICES J Mar Sci* 2018;75:455–70. <https://doi.org/10.1093/icesjms/fsx195>
- Britton JR, Harrison A, Andreou D et al. *Review and Synthesis of Current Evidence on the Biology, Ecology and Fisheries for Sea Bass and Assessment of Evidence Gaps*. BU Global Environmental Solutions (BUG) Report (BUG2931a) to Cefas; 2023, 95.

- Carvalho GR, Hauser L. Molecular genetics and the stock concept in fisheries. *Rev Fish Biol Fish* 1994;4:326–50. <https://doi.org/10.1007/BF00042908>
- Cheung WWL, Pinnegar J, Merino G et al. Review of climate change impacts on marine fisheries in the UK and Ireland. *Aquat Conserv Mar Freshw Ecosyst* 2012;22:368–88. <https://doi.org/10.1002/aqc.2248>
- Child AR. Biochemical polymorphism in bass, *Dicentrarchus labrax*, in the waters around the British Isles. *J Mar Biol Assoc UK* 1992;72:357–64. <https://doi.org/10.1017/S0025315400037759>
- Coscia I, Mariani S. Phylogeography and population structure of European sea bass in the north-east Atlantic. *Biol J Linn Soc* 2011;104:364–77. <https://doi.org/10.1111/j.1095-8312.2011.01712.x>
- Dambrine C, Woillez M, Huret M et al. Characterising Essential Fish Habitat using spatio-temporal analysis of fishery data: a case study of the European seabass spawning areas. *Fish Oceanogr* 2021;30:413–28. <https://doi.org/10.1111/fog.12527>
- Darnaude AM, Tanner SE, Hunter E et al. Advancing research in marine functional connectivity for improved policy and management. *Mar Ecol Prog Ser* 2024;731:1–8. <https://doi.org/10.3354/meps14550>
- de Pontual H, Heerah K, Goossens J et al. Seasonal migration, site fidelity, and population structure of European seabass (*Dicentrarchus labrax*). *ICES J Mar Sci* 2023;80:1606–18. <https://doi.org/10.1093/icesjms/fsad087>
- Dray S, Dufour A. The ade4 package: implementing the duality diagram for ecologists. *J Stat Softw* 2007;22:1–20. <https://doi.org/10.18637/jss.v022.i04>
- Epskamp S, Cramer AO, Waldorp LJ et al. qgraph: network visualizations of relationships in psychometric data. *J Stat Softw* 2012;48:1–18. <https://doi.org/10.18637/jss.v048.i04>
- European Commission. Regulation (EU) No 1380/2013 of the European Parliament and of the Council of 11 December 2013 on the Common Fisheries Policy, amending Council Regulations (EC) No 1954/2003 and (EC) No 1224/2009 and repealing Council Regulations (EC) No 2371/2002. <https://eur-lex.europa.eu/eli/reg/2013/1380/oj/eng> *Off J Eur Union* 2013;L354.
- Fisheries Act. 2020. Retrieved June 13, 2022, from <https://www.legislation.gov.uk/ukpga/2020/22/contents/enacted>
- Foll M, Gaggiotti OE. A genome scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. *Genetics* 2008;180:977–93. <https://doi.org/10.1534/genetics.108.092221>
- Frichot E, François O. LEA: an R package for landscape and ecological association studies. *Methods Ecol Evol* 2015;6:925–9. <https://doi.org/10.1111/2041-210X.12382>
- Fritsch M, Morizur Y, Lambert E et al. 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. *Fish Res* 2007;83:123–32. <https://doi.org/10.1016/j.fishres.2006.09.002>
- Graham JA, Watson JW, García García LM et al. Pelagic connectivity of European sea bass between spawning and nursery grounds. *Front Mar Sci* 2023;9:1–18. <https://doi.org/10.3389/fmars.2022.1046585>
- Gruber B, Unmack PJ, Berry OF et al. DART: an R package to facilitate analysis of SNP data generated from reduced representation genome sequencing. *Mol Ecol Resour* 2018;18:691–9. <https://doi.org/10.1111/1755-0998.12745>
- Helyar SJ, Hemmer-Hansen J, Bekkevold D et al. Application of SNPs for population genetics of nonmodel organisms: new opportunities and challenges. *Mol Ecol Resour* 2011;11:123–36. <https://doi.org/10.1111/j.1755-0998.2010.02943.x>
- ICES. Benchmark on selected sea bass stocks—stock ID workshop (WKBSEABASS-ID). *ICES Sci Rep* 2023;5:52. <https://doi.org/10.17895/ices.pub.22794737>
- Jennings S, Ellis JR. Bass (Moronidae). In: HJL Heessen, N Daan, JR Ellis (eds). *Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea*. Wageningen Academic Publishers/KNNV Publishing, Wageningen, 2015, 324–7.
- Johansen T, Besnier F, Quintela M et al. Genomic analysis reveals neutral and adaptive patterns that challenge the current management regime for East Atlantic cod *Gadus morhua* L. *Evol Appl* 2020;13:2673–88. <https://doi.org/10.1111/eva.13070>
- Jombart T. ADEGENET: an R package for the multivariate analysis of genetic markers. *Bioinformatics* 2008;24:1403–5. <https://doi.org/10.1093/bioinformatics/btn129>
- Kitada S, Nakamichi R, Kishino H. Understanding population structure in an evolutionary context: population-specific FST and pairwise FST. *G3* 2021;11:jkab316. <https://doi.org/10.1093/g3journal/jkab316>
- Leitwein M, Durif G, Delpuech E et al. The fate of a polygenic phenotype within the genomic landscapes of introgression in the European seabass hybrid zone. *Mol Biol Evol* 2024;41:msae194. <https://doi.org/10.1093/molbev/msae194>
- Lemaire C, Versini JJ, Bonhomme F. Maintenance of genetic differentiation across a transition zone in the sea: discordance between nuclear and cytoplasmic markers. *J Evol Biol* 2005;18:70–80. <https://doi.org/10.1111/j.1420-9101.2004.00828.x>
- Limborg MT, Helyar SJ, De Bruyn M et al. Environmental selection on transcriptome-derived SNPs in a high gene flow marine fish, the Atlantic herring (*Clupea harengus*). *Mol Ecol* 2012;21:3686–703. <https://doi.org/10.1111/j.1365-294X.2012.05639.x>
- Luu K, Bazin E, Blum MGB. pcadapt: an R package to perform genome scans for selection based on principal component analysis. *Mol Ecol Resour* 2017;17:67–77. <https://doi.org/10.1111/1755-0998.12592>
- Mayer I, Shackley E, Witthames PR. Aspects of the reproductive biology of the bass, *Dicentrarchus labrax* L. II. Fecundity and pattern of oocyte development. *J Fish Biol* 1990;36:141–8. <https://doi.org/10.1111/j.1095-8649.1990.tb05590.x>
- Nielsen E, Cariani A, Aoidh E et al. Gene-associated markers provide tools for tackling illegal fishing and false eco-certification. *Nat Commun* 2012;3:851. <https://doi.org/10.1038/ncomms1845>
- Ovenden JR, Berry O, Welch DJ et al. Ocean's eleven: a critical evaluation of the role of population, evolutionary and molecular genetics in the management of wild fisheries. *Fish Fish* 2015;16:125–59. <https://doi.org/10.1111/faf.12052>
- Pawson MG, Pickett GD, Leballeur J et al. Migrations, fishery interactions, and management units of sea bass (*Dicentrarchus labrax*) in Northwest Europe. *ICES J Mar Sci* 2007;64:332–45. <https://doi.org/10.1093/ICESjms/fsl035>
- Pickett GD, Pawson MG. Sea bass: biology, exploitation and conservation. *Am Fish Soc Symp* 1994;124:643. <https://doi.org/10.1577/1548-8659-124.4.643>
- Purcell S, Neale B, Todd-Brown K et al. PLINK: a tool set for whole-genome association and population-based linkage analyses. *Am J Hum Genet* 2007;81:559–75. <https://doi.org/10.1086/519795>
- R Core Team. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing, 2023. <https://www.R-project.org/>
- Ratcliffe FC, Garcia de Leaniz C, Consuegra S. MHC class I- $\alpha$  population differentiation in a commercial fish, the European sea bass (*Dicentrarchus labrax*). *Anim Genet* 2022;53:340–51. <https://doi.org/10.1111/age.13184>
- Robinet T, Roussel V, Cheze K et al. Spatial gradients of introgressed ancestry reveal cryptic connectivity patterns in a high gene flow marine fish. *Mol Ecol* 2020;29:3857–71. <https://doi.org/10.1111/mec.15611>
- Rodríguez-Ezpeleta N, Díaz-Arce N, Walter JF et al. Improved Atlantic bluefin tuna management through genetic assignment of natal origin. *Front Ecol Environ* 2019;17:439–44. <https://doi.org/10.1002/fee.2090>
- Souche EL, Hellems B, Babbucci M et al. Range-wide population structure of European sea bass *Dicentrarchus labrax*. *Biol J Linn Soc* 2015;116:86–105. <https://doi.org/10.1111/bij.12572>

