
**ENVIRONMENTAL PERMITTING (ENGLAND & WALES)
REGULATIONS 2016**

**Appeal by NNB Generation Company (HPC) Limited
Water discharge activity at Hinkley Point C, Somerset
Permit variation application relating to acoustic fish deterrent
Appeal Reference APP/EPR/573**

**REPRESENTATION BY DR JAMES STEWART
on behalf of
DEVON AND SEVERN INSHORE FISHERIES AND CONSERVATION
AUTHORITY (DEVON AND SEVERN IFCA)
08 JUNE 2021**

INTRODUCTION: Devon and Severn Inshore Fisheries and Conservation Authority

1. The Inshore Fisheries and Conservation Authorities (IFCAs), including Devon and Severn IFCA (D&S IFCA), are statutory regulators. The IFCAs are responsible for the sustainable management of sea fisheries resources in English waters from baselines out to six nautical miles.
2. D&S IFCA 's District includes waters from baselines to six nautical miles on the south and north coasts of Devon and north Somerset, and the waters of the Severn Estuary out to the median line with Wales.
3. D&S IFCA's Authority is comprised of Local Authority representatives, local stakeholders with marine and fisheries expertise, and nominees from Natural England, the Environment Agency and the MMO. There is also a team of Officers who conduct the day-to-day operations to deliver the IFCA Vision.
4. The ten regional IFCAs have a shared vision: "Inshore Fisheries and Conservation Authorities will lead, champion and manage a sustainable marine environment and inshore fisheries, by successfully securing the right balance between social, environmental and economic benefits to ensure healthy seas, sustainable fisheries and a viable industry."
5. The powers and duties of the IFCAs are provided by the Marine and Coastal Access Act (2009; the Act).
6. The IFCAs' main legal duties are described in section 153 of the Act. They must manage the exploitation of sea fisheries resources in their Districts, balancing the social and economic benefits of exploiting the resources of sea fisheries in their Districts with the need to protect the marine environment, or help it recover from past exploitation.
7. Under section 154 of the Act, IFCAs must seek to ensure the conservation objectives of any MCZs in the District are furthered.
8. IFCAs are also deemed Relevant Authorities for marine areas and EMS, under the Conservation of Habitats and Species Regulations 2017. D&S IFCA is therefore a Relevant Authority, for example, for the Severn Estuary Special Area of Conservation (SAC).
9. I am the Senior Environment Officer at D&S IFCA, and also represent D&S IFCA as the Chair of the Association of Severn Estuary Relevant Authorities.
10. Prior to joining D&S IFCA, my work has mainly been in academic and applied research, including at the University of Exeter, the Parliamentary Office of Science and Technology, and the Australian Institute of Marine Science.

INTRODUCTION: Devon and Severn IFCA's Representation

11. This representation highlights the concerns that D&S IFCA has regarding the present Appeal, specifically the potential for harm to the fish features. The estuarine fish assemblage is a qualifying feature of the Severn Estuary Ramsar site and a sub-feature of the 'Estuaries' feature of the Severn Estuary SAC. I return to this point later in this document.
12. D&S IFCA's Representation does not focus on the migratory fish species for which this Appeal is a concern, as these species fall under the remit of the EA.

13. In accordance with the precautionary nature of the Habitats Directive and European case law, for the appeal proposal to be allowed, it will be necessary for the competent authority to be certain beyond reasonable scientific doubt about the absence of adverse effects upon the integrity of European sites.
14. European Case law supports the assertion that, on the date that the decision is made by the competent authority, there must be no reasonable scientific doubt remaining as to the absence of adverse effects on the integrity of the site. The Appellant must therefore put forward an assessment that contains complete, precise and definitive findings and conclusions capable of removing all reasonable scientific doubt as to the effects of the proposed works on the protected area concerned. With regard to the HRA specifically, we agree with the EA's contention that the Appellant's/Cefas' assessment is neither suitably precautionary nor robustly evidenced enough. Detail on this can be found in the EA's Statement of Case. Additional Case law outlines that, for a breach of Article 6(2), it is sufficient "to establish the existence of a probability or risk that that operation might cause significant disturbances for that species".
15. On the balance of the considerable evidence available to date, including that highlighted by the Appellant and the EA, D&S IFCA is of the opinion that substantial evidence exists of potential harm to the integrity of European sites and that, where this potential harm cannot be clearly demonstrated, there remains a high degree of reasonable scientific doubt as to the absence of such effects.
16. It is therefore D&S IFCA's position
 - a. to support the case presented by the Environment Agency. That is, that the Water Discharge Activity permit variation should be refused on the basis that it cannot be concluded, beyond reasonable scientific doubt, that there would not be an adverse effect on the integrity of the relevant sites.
 - b. that the appeal should not be upheld, and
 - c. that the variation to the Water Discharge Activity (WDA) environmental permit should be refused.
17. D&S IFCA's support for the Agency's position is broad but in this Representation I will focus specifically on four main areas:
 1. The scale of assessment
 2. The extended approach to determining Equivalent Adult Values (EAV)
 3. The basis for considering the fish assemblage as a sub-feature of the Severn Estuary SAC's Estuaries feature
 4. The concept of adaptive management and its applicability in this case.
18. This Representation is in addition to the written representation submitted by D&S IFCA to the Planning Inspectorate in October 2020 [CD Ref. 10.1], which deals with similar and additional issues.

ISSUE 1: The Scale of Assessment

19. The Appellant's case considers impacts on fish species by comparing estimates of impingement to estimates of the size of the populations from which the impinged fish have come. For these comparisons, the Appellant relies heavily on the use of Spawning Stock Biomass (SSB) estimates for ICES stock units, or fisheries landings relating to broad ICES areas.
20. Stock-level SSBs are useful for management of commercial stocks, but are not necessarily appropriate for assessing impact to fish assemblages at a scale that relates to the Severn Estuary SAC, of which they are a feature. Similarly, whilst comparisons with landings in the absence of SSB data (e.g. for herring) may be more precautionary than using SSB, these data are typically international landings related to the commercial SSB in question, so may still underestimate impacts at the level of more local populations.
21. The suggestion in SPP106 and elsewhere that 'fish stock identities are decided after critical review of all the scientific evidence and are subject to regular peer review when new evidence becomes available' is an oversimplification of the limitations of ICES management units and the processes and procedures used to change those boundaries. In a recent paper (published in the ICES Journal of Marine Science) led by Lisa Kerr (a former Chair of the ICES Stock Identification Methods Working Group) the authors state that: "depending on the geographic location, there may be political, legal, cultural, and social pressures that prevent revision of stock boundaries or adding complexity to stock assessments. For example, in Europe, sampling units and intensities are currently fixed by regulation through the relatively inflexible data collection framework, which creates financial consequences for member states when sampling methodology is altered to accommodate a new stock area design." (Kerr et al., 2017).
22. Kerr et al. (2017) go on to discuss how, despite increased recognition of complex population structure and stock mixing, disparities between population structure and current management units have therefore not been reconciled.
23. For some commercial species (outlined in D&S IFCA's previous representation, and in greater detail in the evidence gathered by the EA) there is considerable evidence that there may be finer-scale population structuring that is extremely relevant to fish in the Bristol Channel and Severn Estuary.
24. On this basis, D&S IFCA disagrees with the size and relevance of the population sizes used by the Appellant. Our disagreement is based on the existence of good evidence from the Appellant's previous assessments (TR148 [CD Ref: 7.2]), Cefas' current population size assessments for TLP Swansea [CD Ref: 9.118], ICES stock reviews and an extensive literature review by the EA for the permit variation application to support much smaller and more relevant population sizes (TB011 [CD Ref: 8.10]).
25. The EA's technical briefs, Statement of Case and Adam Waugh's proofs of evidence summarise this evidence, and robustly support the EA's definition of the appropriate scale of assessment for each species considered.
26. Ultimately, the EA has used more appropriate scales of assessment, and thereby refined the population sizes for many species. This has led to the EA's conclusion

that it is not possible to conclude no adverse effect for four marine species – Atlantic cod, whiting, Atlantic herring and European seabass.

27. Here, D&S IFCA will also present additional evidence to support smaller and more relevant population sizes for Atlantic herring (*Clupea harengus*).

ISSUE 1.1 The Scale of Assessment for Atlantic Herring (*Clupea harengus*)

28. D&S IFCA was involved in the Marine Pioneer programme, which was run by Defra and the MMO to trial innovative, pioneering methods of delivering the Government's 25 Year Environment Plan. We sat on the Steering Group and Marine Working Group of the Marine Pioneer.
29. Through the Marine Pioneer, D&S IFCA collaborated with scientists from Swansea University on a project known as the Bristol Channel Herring Project, which investigated herring populations in the Bristol Channel.
30. The Bristol Channel Herring Project is part of a larger research collaboration between Swansea University, the Irish Marine Institute and Uppsala University (Sweden) investigating herring in the Irish and Celtic Seas.
31. The work at Swansea University was led by Dr David Clarke. Dr Clarke is a recognised fisheries science and management expert, who has worked on herring since completing his PhD on the Milford Haven herring population in the 1980s, and has worked in academic and regulatory roles including previously as Head of Fisheries at the Environment Agency.
32. The research is ongoing, but an interim report has been produced for D&S IFCA by the teams from Swansea, Ireland and Sweden. This interim report focussed on the sampling and results relevant to the Bristol Channel, and is attached as Appendix 1 to this Representation.
33. The interim report describes morphological and genetic sampling of Atlantic Herring (*C. harengus*) in the Bristol Channel and south west Wales areas. The data presented were collected in 2018 and 2019, and comprise analyses of 2876 fish from 9 locations (summarised in Figure 1, excluding Pembroke Power Station). Data collected included morphology (length, weight, spawning condition, sex, age (from scales and otoliths) and fin clips for genetic analysis.

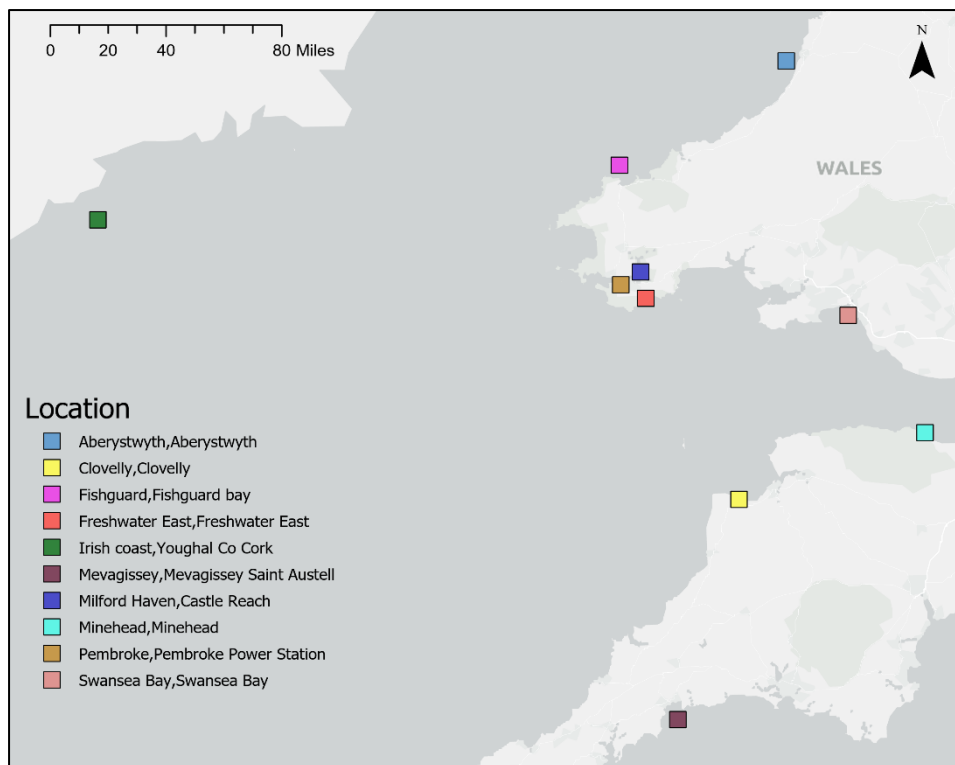


Figure 1. Sampling locations for the Bristol Channel Herring Project.

34. The report focusses on spawning distribution and stock structure. The main conclusions are:
- There are a number of spawning locations, including the North Devon Coast (Minehead to Clovelly), the south west and west Wales (around Freshwater East and Milford Haven), and in Cardigan Bay (Fishguard and Aberystwyth). These areas are those where fishing occurs and the research team have been able to obtain samples. It is possible that spawning occurs elsewhere within the Bristol Channel.
 - Morphological and genetic analysis has identified at least 3 separate spawning populations. Two of these are spring spawning – one which spawns in low salinity in Milford Haven and one which appears to spawn in fully salt water in the Freshwater East Bay area. Although these spawn in the same general area at the same time of year, they appear genetically discrete from each other and from autumn and winter spawning groups.
 - The autumn spawning samples appear to share genetic characteristics with each other and the wider Celtic sea spawners. However even within these groups there is indication of genetic structuring. Both samples from Aberystwyth and Clovelly (October 2018) show a degree of genetic distinctness and in the case of the Clovelly samples within-spawning season temporal genetic structuring.
35. The authors of the interim report conclude: “It is clear that while further work is needed to fully understand stock structures in the area, Atlantic Herring populations in the area are not a single population unit and should not be treated as such for management purposes.”

36. This draft report has not yet been through a typical peer-review process, but is currently being prepared for submission to an academic journal. The research was conducted by an international consortium of researchers with relevant expertise in population genetics, the biology of Atlantic herring, and fisheries science. The study makes good use of standard approaches to morphological and genetic analyses, based on data (including microsatellites and Single Nucleotide Polymorphisms) derived from whole genome sequencing and marker identification studies through international collaborations. The analysis uses a range of techniques to ensure that theoretical assumptions of genetic analyses (assumptions of Hardy-Weinberg and linkage equilibrium) are not violated. The results are therefore robust, and provide a clear refutation of the idea that Atlantic herring form a single panmictic population in the study area.
37. This report also supports a range of previous evidence that herring population structure is best described with the metapopulation concept, in which an array of local populations may be linked by varying degrees of gene flow (McQuinn 1997). Such local populations have been reported historically in Milford Haven (Clarke and King 1985).
38. Impacts from HPC are unlikely to be evenly distributed across the entire metapopulation and consideration of potential effects on local populations would be more appropriate. The conservation of local populations is essential for the preservation of spawning potential and for the viability of coastal fisheries which, in the Severn Estuary itself, are very small-scale. D&S IFCA is in talks to further investigate the local nature of herring populations, including their spawning grounds, and the sustainability of fishing.
39. Overall, this example provides robust evidence of recently-discovered fine-scale population structure in marine fish. This is likely to be of concern for other species which have not been so well-studied, and would lead the Appellant's assessments to underestimate the impacts to species and to Site Integrity.

ISSUE 2: Equivalent Adult Values

40. The Appellant and the EA rely on the use of Equivalent Adult Values (EAVs) to contextualise entrapment losses by converting entrapment data to an equivalent number of adult fish. This is because the mortality of a number of juvenile fish will not have the same effect on the population as the mortality of the same number of adults. However, there is more than one method for calculating EAVs (as summarised clearly in the EA's documents), and it is clear from the case documentation that the EAV method applied by the Appellant cannot be said to be precautionary because it typically underestimates the EAV.
41. To account for the weaknesses of the Appellant's approach (the 'core approach') to calculating EAVs, the EA has adopted an 'extended approach' that accounts for Spawning Production Foregone. The calculation of the EA's extended approach follows the same method and relies on the same assumptions as the Appellant's core approach, except that repeat spawners are included in the EA's calculation.
42. The use of the SPF extension contributed to the EA being unable to conclude no adverse effect on site integrity for the estuarine fish assemblage of the Severn

Estuary SAC and Ramsar, with Atlantic cod, whiting, European seabass and Atlantic herring being the species of concern.

43. The Appellant disputes the inclusion of repeat spawners in the EAV calculation. The Appellant has raised concerns that this extended approach provides values that would not be comparable with estimates of population size based on Spawning Stock Biomass. However, following a review of the evidence, D&S IFCA's position is that these concerns are misplaced, as is clearly evidenced in the documents provided by the EA (in particular TB010 [CD Ref. 8.8] and Dr Masters' Proof of Evidence [CD Ref. 6.7]).
44. The EA's extended approach provides a better comparison to measures of population size than does the Appellant's method, because the extended approach compares losses of first-time and repeat spawners to a spawning population, which is made up of first-time and repeat spawners. The extended approach counts all the adult fish that would have been present in the population had they not been impinged in previous years (Figure 2). The Appellant's method only counts some of them, ignoring fish that have spawned in previous years but that would have still been alive and part of the population (Figure 2). If not impinged, these fish that are not counted by the Appellant would still form part of the SSB against which they would seek to compare their impingement estimate.
45. Based on a review of the available methods and evidence, the Spawning Production Foregone method is considered by D&S IFCA to be the most appropriate to use to assess the entrapment losses at HPC over the operational lifetime of the station. It addresses many of the factors of relevance in the valuation of lost fish by incorporating natural mortality rates, proportional maturity rates, and repeat spawning potential, without assuming that individual fish live to their maximum lifespan. The Spawning Production Foregone method takes into account the value of repeat spawning fish, and produces numbers of equivalent adults which are directly comparable to Spawning Stock Biomass.

ISSUE 2.1: Equivalent Adult Values and Fishing Mortality

46. The Appellant states that the EA have made an error in 'the omission of fishing mortality from the SPF EAV calculation' [CD Ref. 6.3].
47. The EA have, in D&S IFCA's view, adequately countered this statement in their case documentation (e.g. section 6.4 – 6.7 of Dr Masters' Proof of Evidence [CD Ref. 6.7]).
48. D&S IFCA's position is that, by calculating EAVs without including fishing mortality, the EA is representing reasonable worst-case scenarios for Atlantic cod, whiting, European seabass, Atlantic herring, and the shad species, as required when taking the necessary precautionary approach to this assessment of an impact that will be continuous for sixty years.
49. There are substantial difficulties associated with incorporating fishing mortality in the EAV calculations, either for the core or extended approach. The principal difficulty is that fishing mortality is not constant but varies from year to year, due to a range of factors including management interventions.
50. The reason for using an EAV is to contextualise impingement losses over the whole operational life of the power station, which is expected to be around 60 years.

Applying a fixed level of fishing mortality to the EAV calculation may result in impacts being overestimated in some years and underestimated in others. In terms of Habitats Regulations Assessment (HRA), a method which underestimates impacts in some years would not be consistent with the precautionary principle.

51. Fishing mortality is controlled by fishery managers, such that when stocks are declining, targeted fishing pressure can be reduced or even removed. For example, ICES have recommended zero catch of cod in 2020 in the western English Channel and southern Celtic Seas to allow the species to recover. When these conditions occur, HPC impacts will continue unchanged and so we need to understand the effect that the station has under conditions of zero catch for commercial species. As such, the extended method EAV calculated using natural mortality alone, is a relevant figure to refer to in assessing the potential impact of entrapment, particularly so within the context of Habitat Regulations Assessment, as low or zero fishing mortality will occur as a result of management action taken when stocks are below levels where sustainable commercial fishery exploitation could be achieved.
52. In addition to difficulties in choosing an appropriate temporal range from which to draw an estimate of fishing mortality, there are difficulties with regard to determining fishing mortality for an appropriate geographic area. Many marine fish stocks exhibit a complex, meta-population structure with species showing little population structure being the exception rather than the rule (Kerr et al., 2017) - a topic the EA explored in depth in TB010 [CD Ref. 8.8]. Fishing mortality rates used by ICES are calculated for the entire stock area and fishing effort (and thus fishing mortality) might not be uniform across the whole of this area. If fishing effort is concentrated in an area distant from the power station under consideration, then the published value of fishing mortality may not be representative of fishing mortality on the local sub-population that is being impacted by entrapment. Fishing mortality across the Bristol Channel and Celtic Sea is not uniform with fishing pressure being lower in Division 7f compared to other areas of the Celtic Sea, Irish Sea and North East Atlantic. Fishing effort in the Severn Estuary SAC in particular is very low. Fishing mortality rates used for ICES stock assessments are drawn from across the whole of the stock unit, so for example from across the Irish Sea, Celtic Sea and North Sea for European seabass. Therefore, fishing mortality rates cannot be used directly from ICES stock assessments.
53. In summary, D&S IFCA acknowledges that fishing mortality is a relevant factor for predicting the entrapment effects of nuclear new build power stations. However, the complexities of predicting fishing mortality over the operational life of the power station, the selection of a geographically relevant value for fishing mortality, and potential issues of accuracy over any fishing mortality values that may be obtained, mean that practically incorporating fishing mortality is extremely challenging. Incorporating inappropriate estimates of fishing mortality into the calculation of EAVs would add increased uncertainty to estimates.
54. Fishing mortality varies from year to year and can be controlled by fishery management, with low, or zero, fishing mortality being required when fish stocks are recognised as being fished at unsustainable rates. Consequently, EAVs calculated without including fishing mortality need to be considered when taking a precautionary approach to assessing the potential impact of a new power station over the course of its operational life.

ISSUE 2.2: Equivalent Adult Values Ecosystem Function of Non-Adult Life Stages

55. D&S IFCA has a further point to make about the use of EAVs and the ecosystem approach to the management of the marine environment, which is relevant to the precautionary nature of the approach required in this case.
56. Though EAVs can be used to estimate the equivalent adult value lost to entrapment, this does not account for what would have happened to the eggs, larvae and juveniles should they not have been taken in to the cooling water system or survived to adulthood. These individuals are not only lost to the population but are lost as a food source to those species that consume them. This interferes with the food web and with the density dependence of the population dynamics of many species.
57. In paragraph 8.50 in the Appendices of his Proof of Evidence, Dr Jennings discusses compensation in fish populations driven by density-dependent processes. Essentially, Dr Jennings makes the point that a reduction in the overall number of a certain species (as a result of entrapment by HPC) will be compensated for because the remaining individuals of those species will have fewer competitors and better access to the available food resources. However, this point is misleading.
58. Fish eggs, larvae and juveniles are key food sources for larval and juvenile fish in the Severn Estuary. However, these life stages are subject to high levels of entrapment which will remove, modify and redistribute them. These life stages will therefore be less available as food to the remaining fish that do not suffer from entrapment. This process will therefore interrupt the usual density-dependent processes and reduce the capacity for compensation.
59. This highlights another critical issue – that EAV is not the only value of an egg/larva/juvenile fish. These other ecosystem functions (e.g. as food sources) have not been given due regard through this process. This represents a key uncertainty in the impacts of HPC on the fish assemblage, and in the impact on the structure and functioning of the Estuaries feature of the SAC.

ISSUE 3: The Fish Assemblage of the Severn Estuary SAC

60. The definition of the estuarine fish assemblage as a sub-feature of the SAC Estuaries feature is consistent with section 2.1 of the Regulation 33 advice package for the Severn Estuary SAC [CD Ref12.16].
61. The fish assemblage comprises over 110 species and has specific conservation objectives. The European Commission guidance on the provisions of Article 6 of the Habitats Directive ('the guidance') confirms that when concluding an Appropriate Assessment any effects from the proposal must be assessed against the site's conservation objectives [CD Ref: 12.2] and that Site Integrity relates to these objectives [CD Ref: 12.2].
62. The guidance is also clear that if just one of the habitats or species for which the site has been designated is significantly affected, taking into account the site's conservation objectives, then Site Integrity is necessarily adversely affected [CD Ref: 12.2].
63. Furthermore, the interactions of the species in the fish assemblage and the way they interact with each other, the designated migratory fish species and designated habitats of the Severn Estuary SAC and SPA are of primary importance to the

functioning of the Severn Estuary and the consideration of Site Integrity. The guidance states that “the integrity of the site involves its constitutive characteristics and ecological functions. The decision as to whether it is adversely affected should focus on and be limited to the habitats and species for which the site has been designated and the site’s conservation objectives”. The species that form this assemblage should therefore be subject to Appropriate Assessment in their own right and are highly relevant to the conclusion of the HRA.

64. It is the view of D&S IFCA that, in the case of the Severn Estuary SAC, it would not be possible to assess the implications of the Appeal proposal for the estuary feature or Site Integrity as a whole without also understanding the impacts upon its sub-features. An assessment of these sub-features, including the estuarine fish assemblage, is therefore needed to fulfil the requirements of the Habitats Regulations. This view is consistent with Natural England’s published advice.
65. It is on this basis, and in line with Natural England’s advice, that D&S IFCA has completed Habitats Regulations Assessments for relevant fisheries activities in relation to the fish assemblage sub-feature of the Severn Estuary SAC.

ISSUE 4: Adaptive Management

66. In the Addendum to the SoCG it is stated that the Appellant does not consider it appropriate to place a limit on the mass of moribund biota (dead fish) discharged from the Fish Recovery & Return system as "in reality they cannot be controlled". Herein lies the problem – once the cooling water system is started without AFD, the fish kill cannot be controlled without shutting down the reactors and cooling system.
67. The nature of an operational power station, with a 60 year life time, does not allow the same degree of adaptive management as exercised by a fishery manager. As outlined previously, and in the proofs submitted by the EA, fishery managers can place effort and landings limits on fisheries in order to safeguard stocks, including restrictive measures such as zero Total Allowable Catch. This management is adaptive in the sense that it is able to change in response to new evidence. Power station cooling systems cannot be adaptive in this way. Therefore, a precautionary approach, as taken by the Environment Agency (and by Natural England and NRW as statutory consultees) is justifiable.

CONCLUSIONS

68. D&S IFCA considers that that the documentation provided by the EA is the product of sound scientific judgement and accounts for the best available evidence. On balance, D&S IFCA supports all of the judgments made by the EA in their Statement of Case [CD Ref. 6.2]. Therefore, having considered the available evidence, D&S IFCA finds that the EA’s conclusions regarding Site Integrity are justified and sound.
69. In summary, and in addition to the points made in D&S IFCA’s previous written representation [CD Ref. 10.1], D&S IFCA
 - a. Supports the adjusted scale of assessment applied by the EA to the fish species of concern; this approach is preferable in scientific and ecological terms to the ICES stock areas and SSBs suggested by the Appellant.

- b. Supports the EA's extended approach to determining Equivalent Adult Values. Applying the Spawning Production Foregone EAV method, without accounting for uncertain mortality due to fishing, is an appropriately precautionary assessment for this proposal.
- c. Supports the full consideration in Appropriate Assessment of the estuarine fish assemblage as a sub-feature of the Estuaries feature of the Severn Estuary SAC.
- d. Considers that the inability to apply adaptive management to the proposed activities necessitates a precautionary approach to all stages of assessment of potential effects on Site Integrity.

REFERENCES

The underlying evidence for this representation is broadly held within the Core Documents for the Inquiry, including D&S IFCA's previous written representation [CD Ref. 10.1]. Below are the few additional documents to which D&S IFCA has had to refer within this representation.

Clarke, D., and King, P. (1985). Spawning of Herring in Milford Haven. *Journal of the Marine Biological Association of the United Kingdom*, 65(3), 629-639.

Kerr, L.A., Hintzen, N.T., Cadrin, S.X., Clausen, L.W., Dickey-Collas, M., Goethel, D.R., Hatfield, E.M.C., Kritzer, J.P. and Nash, R.D.M. (2017). Lessons learned from practical approaches to reconcile mismatches between biological population structure and stock units of marine fish. *ICES Journal of Marine Science*, 74(6): 1708 – 1722.

McQuinn (1997). Metapopulations and Atlantic herring. *Reviews in Fish Biology and Fisheries*, 7: 297-329.

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08 JUNE 2021**

**Irish and Celtic Seas Herring Project: Preliminary Report for Devon
and Severn Inshore Fisheries and Conservation Authority. 2018-2020
Sampling and Morphological Data**

Swansea University

[Irish and Celtic Seas Herring Project](#)

Preliminary Report of Devon and Severn Inshore Fisheries and Conservation Authority.

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April 2021

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Executive Summary

This report is an interim report which is part of a wider study undertaken by Swansea University as part of the SEACAMS programme. It describes morphological and genetic sampling of Atlantic Herring (*Clupea harengus*) in the Bristol Channel and south west Wales areas. The data presented was collected in 2018 and 2019, and comprises analysis of 2876 fish from 9 locations. Data collected included morphology (length, weight, spawning condition, sex, age (from scales and otoliths) and fin clips for genetic analysis.

The report focusses on spawning distribution and stock structure.

The main conclusions are:

- There are a number of spawning locations, including the North Devon Coast (Minehead to Clovelly), the south west and west Wales (around Freshwater East and Milford Haven), and in Cardigan Bay (Fishguard and Aberystwyth).
- These areas are those where fishing occurs and we have been able to obtain samples. It is possible that spawning occurs elsewhere within the Bristol Channel.
- Morphological and genetic analysis has identified at least 3 separate spawning populations. Two of these are spring spawning – one which spawns in low salinity in Milford Haven and one which appears to spawn in fully salt water in the Freshwater East Bay area. Although these spawn in the same general area at the same time of year, they appear genetically discrete for each other and from autumn and winter spawning groups.
- The autumn spawning samples appear to share genetic characteristics with each other and the wider Celtic sea spawners. However even within these groups there is indication of genetic structuring. Both samples from Aberystwyth and Clovelly (October 2018) show a degree of genetic distinctness and in the case of the Clovelly within spawning season temporal genetic structuring.

In summary it is clear that while further work is needed to fully understand stock structures across the area, Atlantic Herring populations in the area are not a single population unit and should not be treated as such for management purposes.

1 Introduction

This report is part of a wider study, primarily focussed on the status of a spring spawning herring stock which spawns within the Milford Haven waterway. The study has involved collection of samples for morphological and genetic analysis in the wider Bristol Channel and Celtic sea areas (Figure 1) as well as collaboration on genetic work with the Irish marine Institute, EDF Scientific Limited and Upsalla University. Sampling in England has been supported by the Devon and Severn Inshore Fisheries and Conservation Authority (D&S IFCA) and the Blue Marine Foundation.

This report is a preliminary report on this sampling, and focusses on the structure of Atlantic Herring (*Clupea harengus*) stocks in the Bristol Channel area.

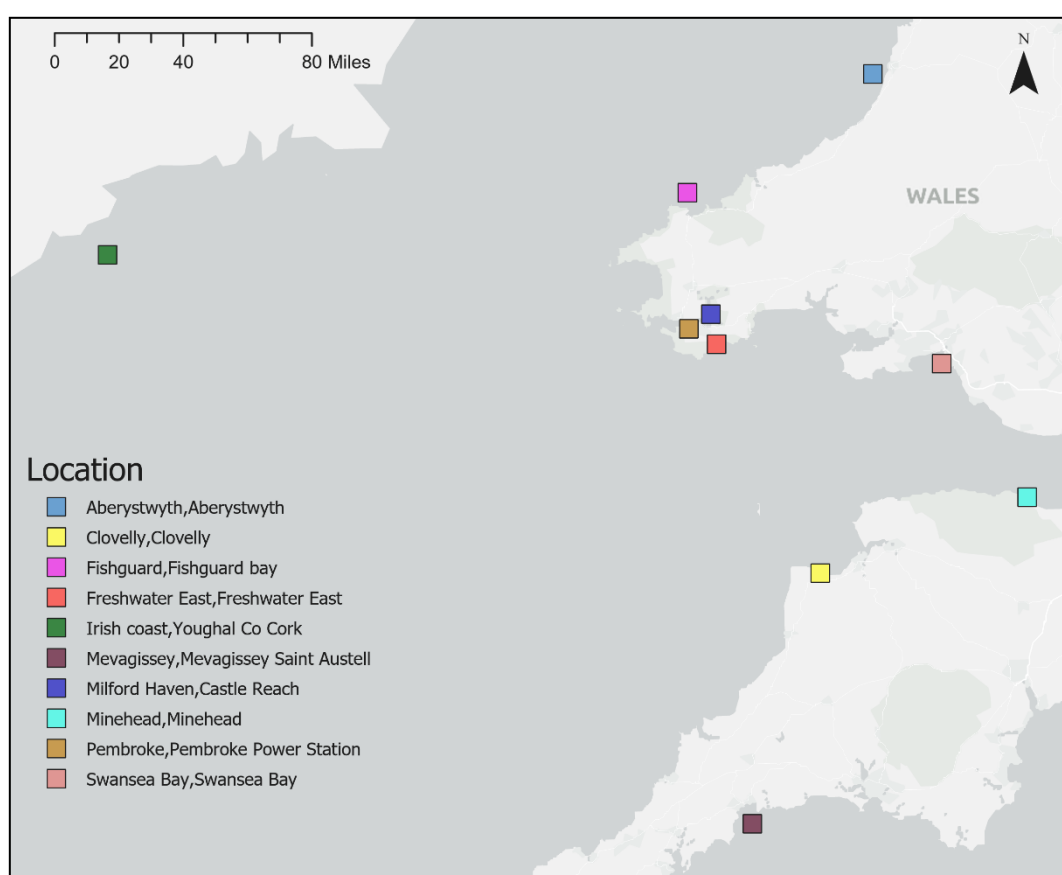


Figure 1. Sampling locations

Genetic markers have become widely used over the last three decades to study the population structure of marine fishes. Genetic markers are sections of DNA that can be used to identify individuals, populations and species. Broadly speaking there are two types of genetic markers: neutral- which can be used to establish the evolutionary history of a population inferring neutral processes such as gene flow, demographic changes and stochastic environmental events. In contrast adaptive genetic markers (i.e. genetic sequences that affect an organism's lifetime fecundity) are useful for studying genetic components driving adaptive population structuring, and have been particularly useful for stock delimitation in marine fisheries (Mariani & Bekkevold, 2014; Clucas et al., 2019). Commonly used neutral genetic markers include DNA sequences from neutral genes e.g. mitochondrial DNA and microsatellites (nuclear DNA sequences (or loci) that comprise a tandem repeated sequence of 1 – 5 bases). Whilst common adaptive markers include nuclear DNA genes under selection, Single Nucleotide Polymorphisms (SNP's) and microsatellites (if they are associated with genes under selection). Both neutral microsatellites and more recently SNPs generated through high throughput next generation sequencing (NGS) have been used to infer population structuring in Atlantic Herring.

In this study we utilise Microsatellites and Single Nucleotide Polymorphisms (SNP's) to investigate whether the Milford Haven Spring Spawning Herring Stock is genetically distinct from the Wider (autumn spawning) Herring stocks around Wales and the Bristol Channel. The SNP's and many of the microsatellite loci used in the present study are derived from a whole genome sequencing project (Han et al., 2020) carried out by our collaborators in the GENSINC (GENetic adaptations underlying population Structure IN herring, *Clupea harengus*) project, led by Uppsala University. These have then been further developed through a second project led by the Irish Marine Institute to identify practically useful markers.

2 Methods

2.1 Sample sources

All sampling nets, fishing methods and locations complied with current fishery regulations. Most samples were purchased from local inshore commercial fishermen taken and were taken using drift or fixed nets of ca 57mm mesh size. Exceptions were the Irish coast sample obtained from the Celtic Sea Herring survey undertaken by the Irish Marine Institute, Swansea bay samples which were taken with a research trawl, and the Minehead samples which were caught using a fixed beach stake net (also of 57mm mesh size).

Commercial samples were focussed on spawning periods, as the primary purpose of the work was to establish natal baseline data for genetic comparisons with the Milford Haven spring spawners. Table 1 below summarises the samples collected from all locations, which comprise the data used in this report.

Table 1. Summary of the total number of Atlantic Herring sampled for each purpose 2018-2020.

Location	Year	Total sample	Gonad State	Vertebral count	Genetic sample	SiA sample
Aberystwyth	2018	150	150	98	100	31
Clovelly	2018	312	312	312	189	86
Clovelly	2019	103	103	0	103	0
Fishguard	2018	120	119	119	120	29
Freshwater East	2019	200	200	101	100	38
Irish coast (Youghal, Co. Cork)	2018	70	62	70	70	0
Mevagissey	2019	100	100	100	100	0
Milford Haven (Castle Reach)	2018	554	310	416	294	118
Milford Haven (Castle Reach)	2019	61	0	61	61	61
Minehead	2018	333	243	242	244	83
Minehead	2019	633	197	0	313	0
Swansea Bay	2019	224	223	168	136	45
Total		2860	2019	1687	1830	491

Juvenile samples at various sites were also obtained from Pembroke Power station screen catches and from the PELTIC survey led by CEFAS. These have not been included in the present report as analysis is still being undertaken.

2.2 Sample Processing

Fish sampled were measured (total length and fork length, cm), weighed (ungutted weight, g) sex recorded where possible and scales taken. A subset of fish were bagged, frozen and processed in the laboratory. For these, fish maturity stage, gutted weight (g) and vertebral count were recorded (Bucholtz et al. 2008). Pectoral fin clips were taken from sub sample of fish and stored in absolute alcohol for genetic analysis and otoliths were also removed. Tissue samples (dorsal muscle) were removed and frozen for Stable Isotope (SIA) analysis. Fish were aged using scales and / or otoliths.

2.3 Genetic analysis

Fin clips were removed from individual fish and stored in 95% ethanol. DNA extractions were carried out using QIAGEN Blood and tissue kits following the manufacturer's protocol. 36 microsatellite and 59 SNP loci, selected for their potential ability to discriminate between Atlantic herring populations, were amplified using several multiplex PCRs. Successful amplification was verified on a 2% agarose gel. Samples were sent for next generation sequencing (MiSeq) using FASTERIS (Switzerland).

Initial quality control and de-barcoding of the resultant sequences was carried out using FASTQC. Microsatellite allele scoring was carried out in Geneious using a genotyping by sequencing approach. Any samples with a low sequence read depth (less than 10) were excluded from analyses. SNP genotyping was carried out using Genotyping-in-Thousands by sequencing (GT-seq) Perl pipeline scripts (Campbell et al., 2015). Overall, 561 (Microsatellites)

and 576 (SNPs) individual fish were successfully amplified, sequenced, and genotyped and included in the subsequent population genetic analyses.

The fixation index (F_{ST}) is a common measurement employed to describe genetic differentiation of populations. F_{ST} values range from 0 (no population structure, genetically identical) to 1 (fully separate populations sharing no alleles). For both the microsatellite and SNP data sets the unbiased F_{ST} estimates were calculated using GenePOP.

A shortcoming of the calculation of F_{ST} are the assumptions of Hardy-Weinberg and linkage equilibrium within populations these are often violated in natural populations, which may be problematic when we are looking at loci under selection. Many of the SNP loci are located in regions of the genome controlling reproduction and may violate these assumptions. For that reason, a Discriminant Analysis of Principal Components (DAPC) analysis was also employed to identify genetic clusters (Jombart et al., 2010). This analysis makes no presumptions of the data set. DAPC was implemented in the R-package adegenet (Jombart, 2008; R Core Team, 2019). The analysis was run using priors (i.e. using the known sampling location) using the dapc() function with clusters inferred from the original sampling sites.

3 Results

3.1 Spawning and Maturity stage

Across the duration of the study 2867 adult fish were sampled overall, of which 2019 (68%) were assessed for maturity state on the ICES scale, using the method identified in Bucholtz et al. (2008). The majority of the fish were in stage 6 (active spawning state) with milt and eggs running from many fish when captured (Figures 2 and 3).

Exceptions included the Irish Coast (mainly recovering) and Swansea Bay (mainly recently spent fish).

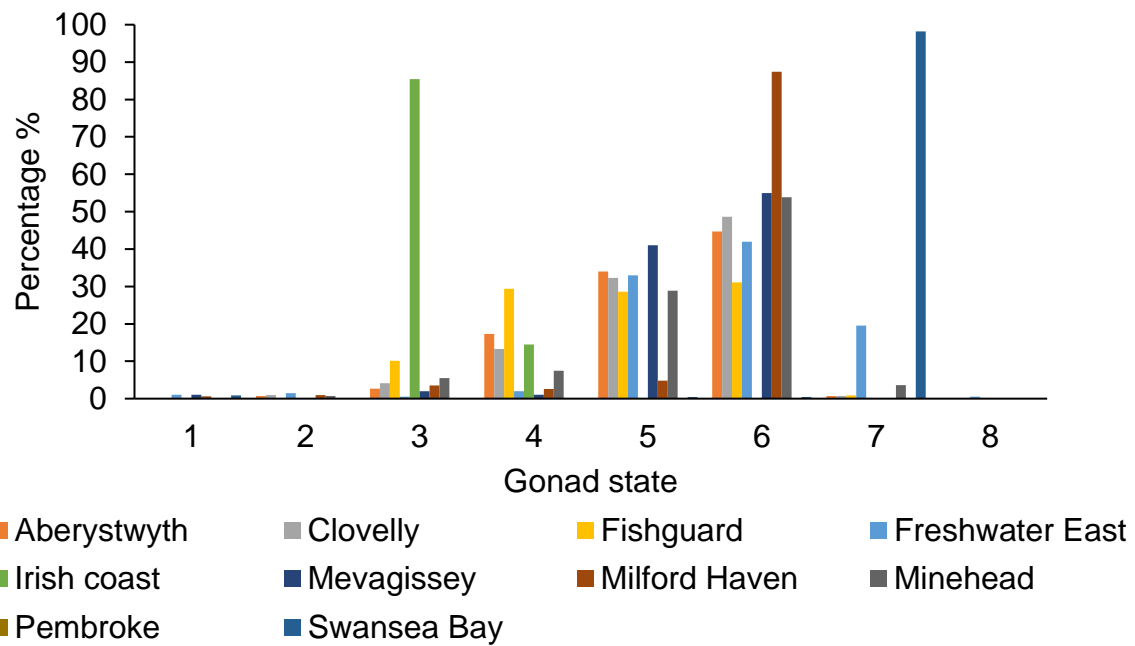


Figure 2. Maturity state (gonad state) of captured fish per location.

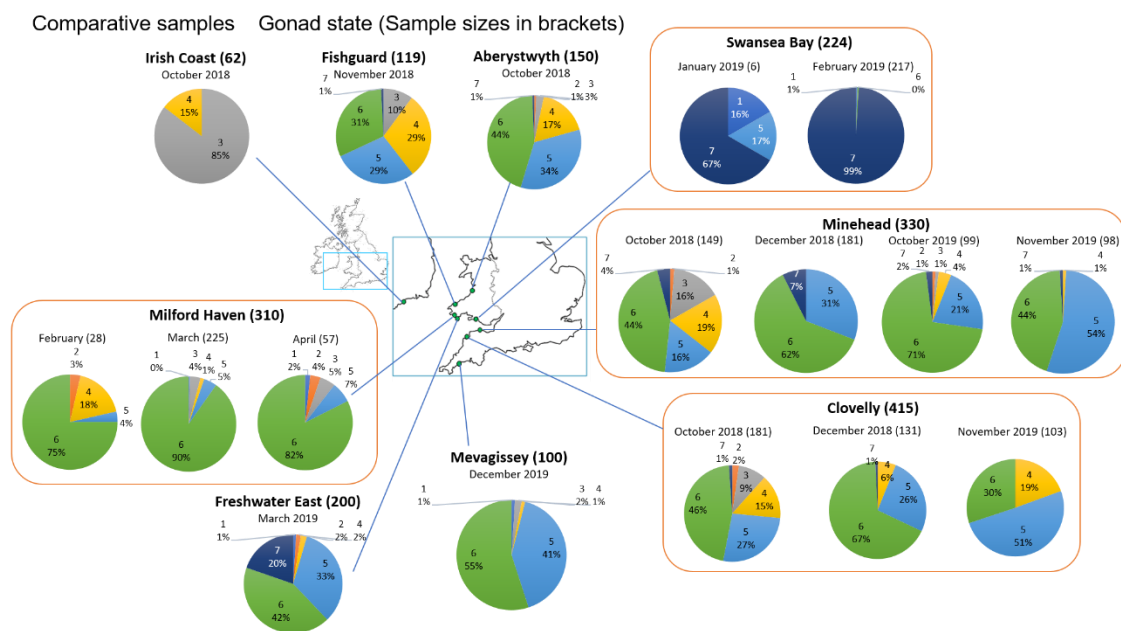


Figure 3. Maturity state (gonad state) and numbers of captured fish per location.

3.2 Age structure

The age structure of samples is shown in Figures 4a and 4b. Caution should be applied to interpretation of these data (e.g. using catch curves to calculate age structure) as the inshore netting samples are biased by net selection. Figure 4a compares samples taken with fixed or drift nets of similar mesh size; figure 4b shows trawl samples, together with the Milford Haven data as a comparator.

The data shows that the peak age class for all samples with the exception of Swansea Bay (Age 3) is age 4, with numbers declining subsequently, probably as a result of natural and fishing mortality as well as gear selection effects. Lower numbers of 2 and three year olds may reflect partial recruitment to spawning shoals, with the majority maturing at age 4 (for the avoidance of doubt, three rings on the scales /otoliths plus growth in the year prior to spawning; generally the fourth check will be being laid down around the time of sampling as they generally spawn in Autumn/winter/spring, coincident with the season of their birth).

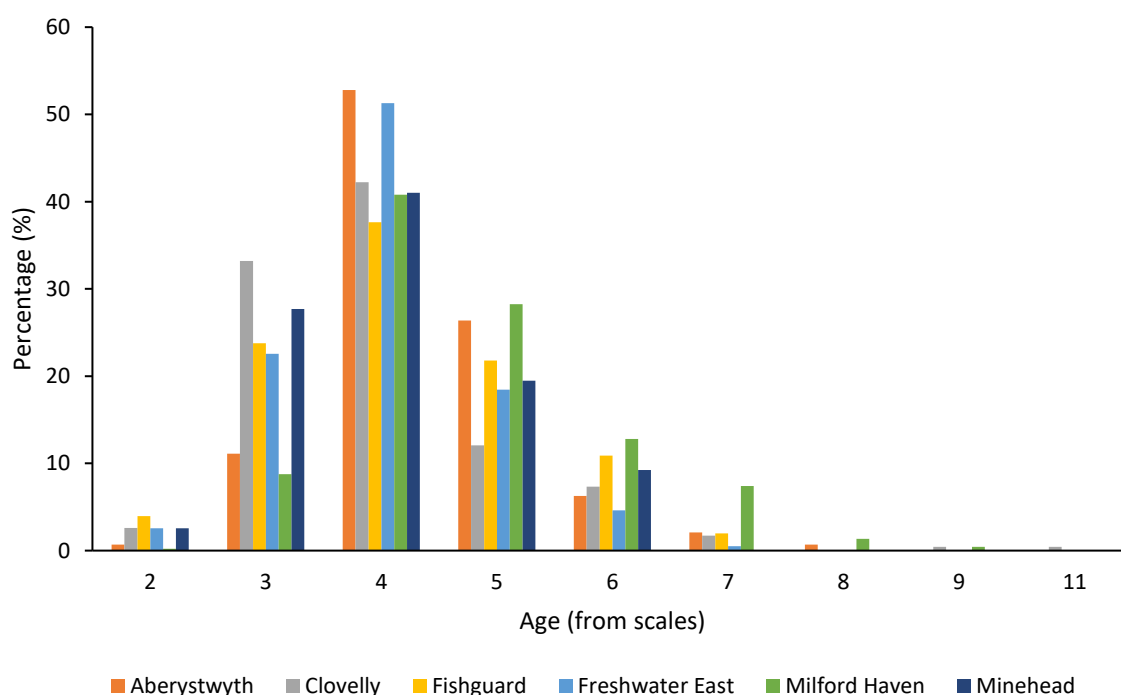


Figure 4a. Age structure of Herring samples based on samples from gill nets, mono, mixed sizes.

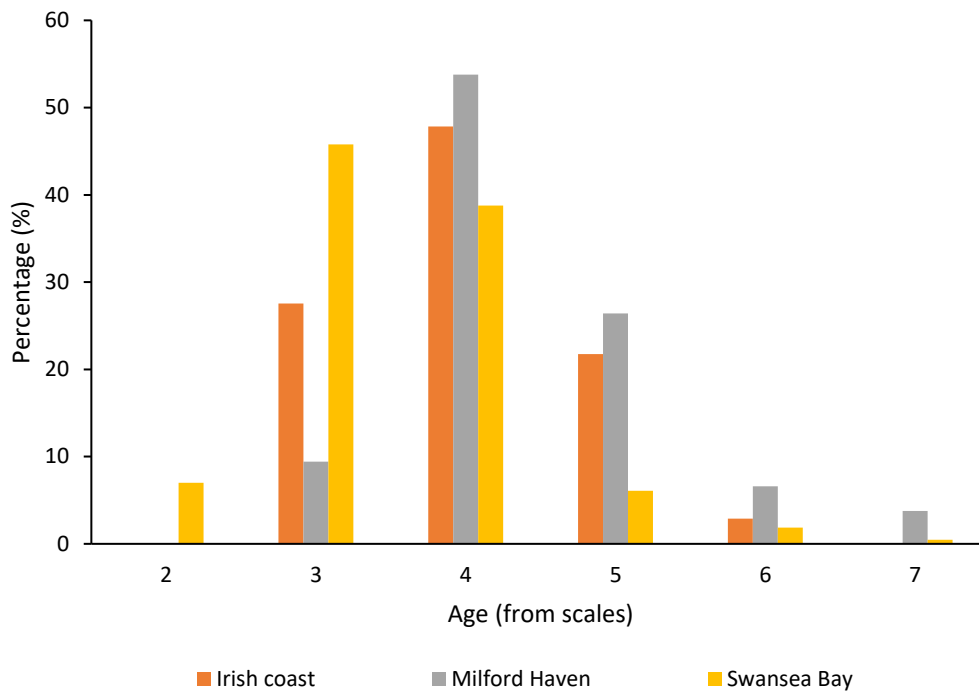


Figure 4b. Age structure of trawl samples; Milford Haven fixed net samples also included as a comparator

3.3 Growth rates and condition

The average total length at age for fish were compared for all Herring at all locations between 2018 and 2020. Most samples show broadly similar growth rates but the Freshwater East spring spawners are larger at age compared to other locations.

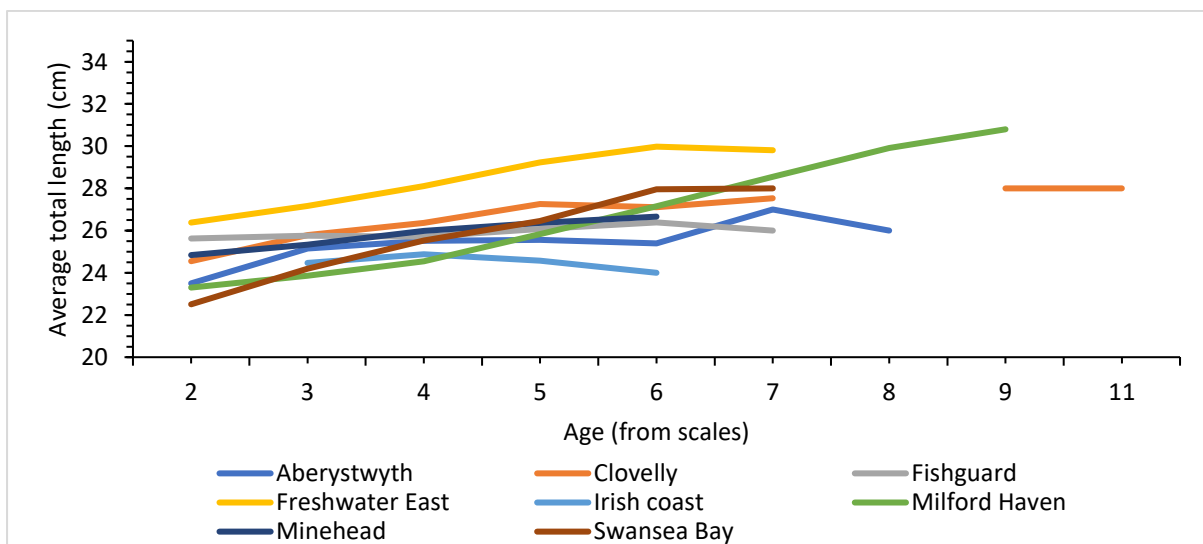


Figure 5. Comparison of average length at age (total length) of Herring from sampling locations 2018-2020.

3.4 Vertebral counts

Vertebral counts are often used as part of stock identification studies of Atlantic Herring (Berg et al. 2017). Vertebral count (VS) is lower overall in the spring spawning samples of Milford Haven and Freshwater East (Fig. 6, Table 3).

Comparison with samples taken from other locations show that all the spring samples, both past and present, have a significantly lower VS than the Autumn and winter spawners. While VS cannot be used to determine spawning time for individuals, it is distinctive at the sample level for spring and Autumn/Winter samples.

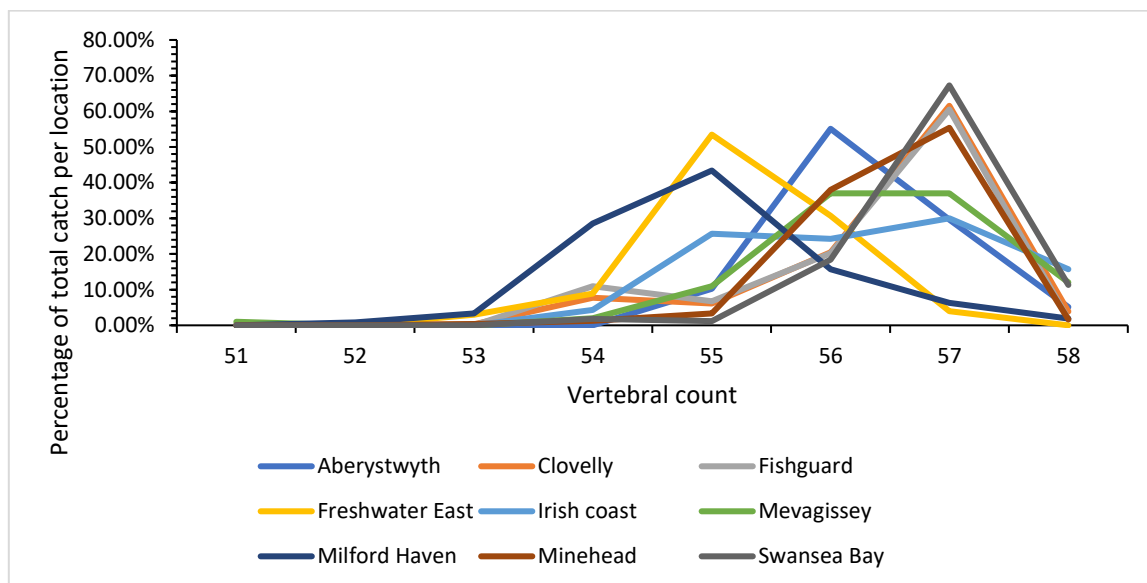


Figure 6. Comparison of vertebral counts between locations

Table 2. Mean vertebral counts from all locations plus some other reported data.

Location	Source	Mean
Milford Haven	2018 - This study	55.05
Milford Haven	2019 - This study	54.39
Freshwater East	2019 – This study	55.24
Aberystwyth	2018 - This study	56.30
Clovelly	2018 - This study	56.47
Fishguard	2018 - This study	56.35
Irish coast	2018 - This study	56.27
Mevagissey	2019 - This study	56.41
Minehead	2018 - This study	56.52
Swansea Bay	2019 - This study	56.85
Oxwich	1981-1982 (Clarke 1984)	55.2-55.6
Tenby	1981 (Clarke 1984)	55.6
Celtic Sea and Dunmore	Parrish & Saville (1965), Molloy (1968), Molloy & Corten (1975)	56.7-57.1
Mourne	Molloy & Corten (1975) ⁸	56.7
Plymouth	Ford (1928)	56.7-56.8
Isle of Man	Bowers (1980)	56.1-56.6
Minch	Baxter (1958)	56.4-56.52
Clyde	Wood (1960), Molloy & Corten (1975)	56.9-57.2
Thames Estuary/Blackwater	Wood (1981)	54.6-55.8

3.5 Genetics

All the analytical approaches identified a clear genetic split (Msats F_{ST} = 0.018- 0.031; SNP F_{ST} = 0.540-0.679) between the spring spawning (Milford Haven and Freshwater East) and autumn spawning (all other samples). Further genetic sub structuring is identified within both the Autumn Spawning and Spring Spawning groups. Within the Autumn Spawning group both Clovelly October 2018 and Aberystwyth 2018 samples show significant F_{ST} values from the other Autumn spawning samples; in the case of Clovelly this sample is also genetically distinct from the December 2018 Clovelly sample (Table 4). Discriminant Analysis of Principal Components (DAPC) using both microsatellites and SNP data showed clear differences between autumn and spring spawning Herring. DAPC also identifies the separation of the Milford and Freshwater East samples and the Clovelly October 2018 (Figure 7).

Table 3. Pairwise F_{ST} values between samples based upon the 36 microsatellite loci (below the diagonal) and 59 SNPs (above the diagonal). Bold indicates statistically significant F_{ST} values.

	MH '18	MH '19	FWE	FIS	SWA	ABE	CLO- Oct	CLO- Dec	MIN- Oct	MIN- Dec
MH '18	-	0.032	0.076	0.579	0.569	0.555	0.540	0.595	0.558	0.580
MH '19	0.002	-	0.158	0.660	0.650	0.638	0.619	0.679	0.634	0.665
FWE	0.016	0.021	-	0.437	0.428	0.409	0.367	0.453	0.414	0.433
FIS	0.018	0.018	0.018	-	-0.002	0.037	0.141	0.007	0.005	0.010
SWA	0.031	0.029	0.024	0.002	-	0.027	0.121	0.000	0.001	0.003
ABE	0.031	0.045	0.031	0.015	0.023	-	0.085	0.040	0.023	0.020
CLO- Oct	0.020	0.028	0.007	0.009	0.016	0.020	-	0.143	0.086	0.105
CLO- Dec	0.020	0.017	0.016	0.002	0.002	0.016	0.012	-	0.011	0.009
MIN- Oct	0.019	0.018	0.015	0.000	0.000	0.021	0.010	0.000	-	0.002
MIN- Dec	0.023	0.027	0.017	0.002	0.004	0.014	0.007	0.003	0.001	-

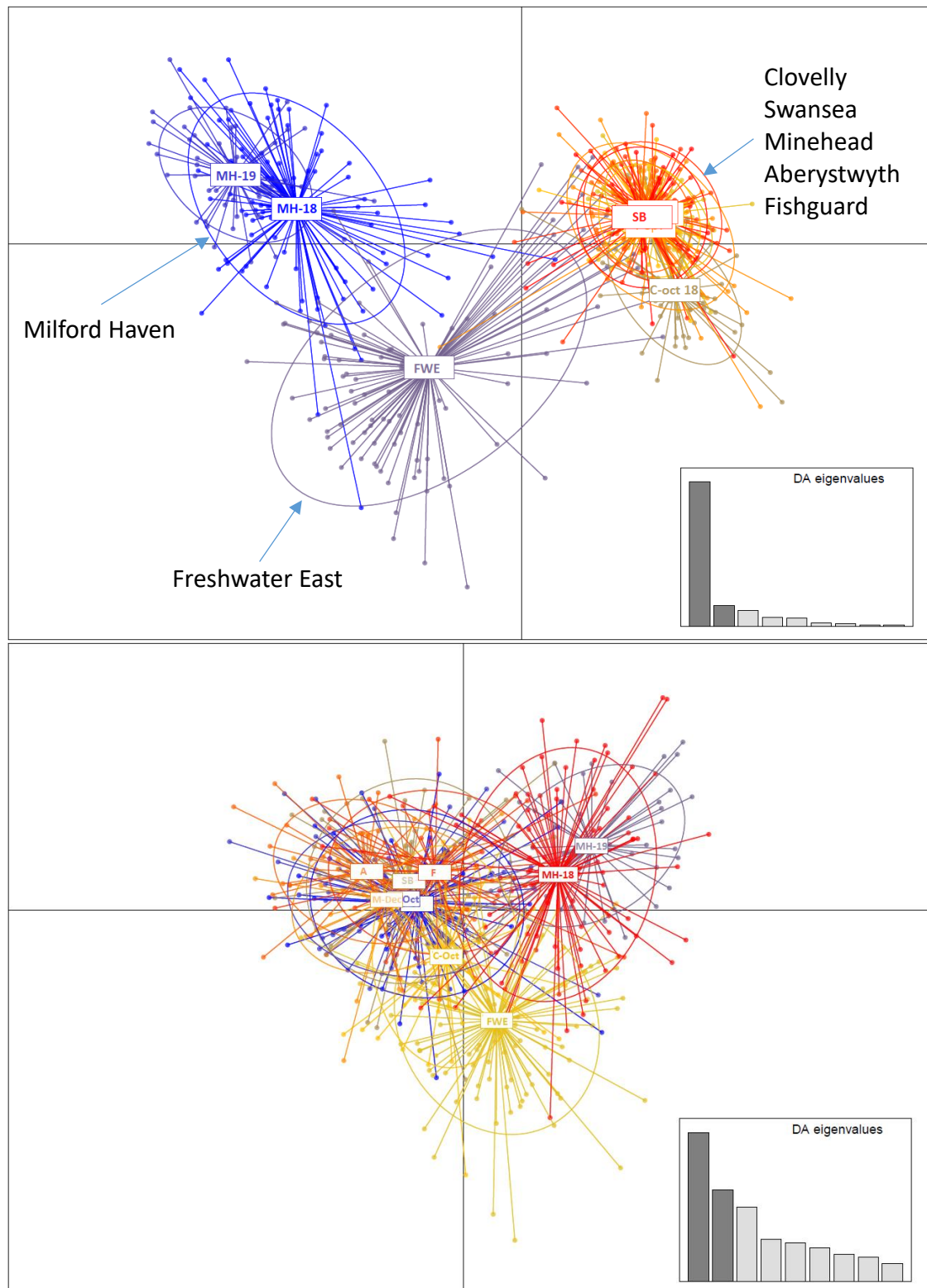


Figure 7. scatter plot of individual herring on the first two principal components of the DAPC with groups defined *a priori* as per sample site. TOP= the microsatellite data set and BOTTOM= the SNP data. The graph represents individuals as dots and the groups as inertia ellipses. Eigenvalues of the analysis are displayed in inset.

4 Discussion

Morphological data show that age structure is broadly similar across all samples with number declining sharply from the fourth year, consistent with a high fishing mortality rate in the area as advised by ICES. Growth rate is also broadly similar for all samples, with the exception of the Freshwater East sample which showed a much faster growth rate than other samples.

Vertebral count data showed that the spring samples had a significantly lower count (means of 54.39 to 55.24); this is consistent with expectation for spring fish (see for example the Thames Estuary/Blackwater data in table 2, which is also a spring spawning sample). The Milford Haven data are also comparable to, though slightly lower than the values described for the same stock between 1980-1982 (Clarke, 1984). In contrast other samples collected in this study (mainly autumn winter spawners) show mean values > 56. This can be used at sample level to discriminate the groups.

Microsatellite studies have previously identified large scale geographical structuring of Herring for example: North West Atlantic; (McPherson et al., 2001), Norwegian vs Barents Sea- (Shaw et al., 1999) the North Sea (Mariani et al., 2005) and more recently using SNPs the wider North East Atlantic (Bekkevold et al., 2015). SNPs in particular have allowed more fine scale structuring to be identified in Atlantic Herring (Kerr et al., 2018;). This study has also found that SNP's are more informative than the microsatellite markers with SNP's consistently demonstrating far higher F_{ST} values (Table 3) and greater discriminating power in the DAPC (Figure 7).

Genetic analyses indicate several distinct stocks around Wales and the Bristol Channel. The most obvious split of the genetic data is between the autumn and winter spawning samples, shown in the SNP results (F_{ST} Table 4). Additional further genetic sub structuring is identified within the autumn and spring spawning samples. Milford Haven, Freshwater East, Clovelly (October 2018) and Aberystwyth form distinct genetic stocks whilst the remaining samples appear to be part of a larger more connected population (Figure 7 and Table 3). It is clear from these results that the population of Atlantic Herring in the Bristol Channel and around Wales is not a single panmictic stock.

Genetic separation of spring spawning and autumn spawning herring is typical of Atlantic Herring (Kornfield 1982; Bekkevold et al. 2015 & 2016), although this is the first confirmation in the UK. Whilst there is further genetic structuring within the autumn groups this is at a reduced level when comparing such genetic splits between the autumn and spring spawning samples reflecting the 'unique' status of the comparatively rare (in UK waters) spring spawning populations. Unexpectedly, we also identified a second genetically distinct spring spawning stock in the Pembrokeshire area represented here in the FWE sample. The FWE population does appear to be clearly distinct in both genetic marker sets and is identified as such in all the population genetic analyses; it also shows a much higher growth rate than other samples including the Milford Haven spring spawners which spawn in geographically close proximity at the same time of year.

Sympatric (i.e. co-occurring) genetic sub structuring within the spring spawning herring ecotype has been identified previously (Bekkevold et al., 2016). A similar spawning situation occurs in Norwegian waters with two separate spring spawning stocks- an oceanic stock and a coastal stock (spawning largely in the Fjords). This has been attributed to local adaptation to abiotic factors such as salinity and temperature (Bekkevold et al., 2016; Kerr et al., 2019; Fuentes-Pardo et al., 2019). Salinity in particular is reduced in the Haven compared to the FWE site where the Herring were actively spawning generating the potential for local adaptation in the Milford population. Further analyses and studies are needed to establish the relationship between Milford and the FWE population, ideally with temporal samples being taken over a number of spawning seasons.

Both the Clovelly and Aberystwyth October 2018 samples are genetically distinct from the other Autumn spawning samples- this is supported by both SNP and microsatellite data sets (Table 3). Geographical genetic population structuring in autumn spawning Atlantic Herring has been identified numerous times (e.g. Bekkevold et al, 2007; Lamichhaney et al., 2017). Of particular interest is that the Clovelly sample is also genetically distinct from the sample taken from the same site later that year in December- indicating temporal genetic separation within a spawning season. Such genetic stock delimitations within seasonal spawning have been identified in Atlantic Herring before in before (e.g. McPherson et al 2003; Jørgensen et al, 2005) but again this is the first time it has been characterised in UK waters. Timing of spawning in Herring is thought to be one of the major factors driving stock delimitations over both short temporal scales (weeks) and seasons (Barrio et al., 2016; Petrou et al., 2021). Such discrete spawning waves are believed to ensure reproduction and larval emergence are synchronized to cycles of marine productivity (Cushing, 1990). Future studies on assessing herring stock structures around the Bristol Channel and Wales (and the rest of the UK) will need to ensure that such fine scale temporal structuring is considered when designing sampling regimes.

Finally, given the complexity of the stock structure of Herring revealed by the present study it is possible, if not likely, that there are more discrete Herring populations in the Bristol Channel and around Wales.

5 References

Baxter, I.G. (1958). The composition of the Minch Herring stocks. ICES, Rapports et proces verbaux des reunions 143; 2; pp. 81-94.

Barrio, A.M., Lamichhaney, S., Fan, G., Rafati, N., Pettersson, M., Zhang, H.E., Dainat, J., Ekman, D., Höppner, M., Jern, P. and Martin, M., 2016. The genetic basis for ecological adaptation of the Atlantic herring revealed by genome sequencing. *elife*, 5, p.e12081.

Bekkevold, D., Clausen, L.A., Mariani, S., André, C., Christensen, T.B. and Mosegaard, H., 2007. Divergent origins of sympatric herring population components determined using genetic mixture analysis. *Marine Ecology Progress Series*, 337, pp.187-196.

Bekkevold, D., Gross, R., Arula, T., Helyar, S.J. and Ojaveer, H., 2016. Outlier loci detect intraspecific biodiversity amongst spring and autumn spawning herring across local scales. *PloS one*, 11(4).

Bekkevold, D., Helyar, S.J., Limborg, M.T., Nielsen, E.E., Hemmer-Hansen, J., Clausen, L.A. and Carvalho, G.R., 2015. Gene-associated markers can assign origin in a weakly structured fish, Atlantic herring. *ICES Journal of Marine Science*, 72(6), pp.1790-1801.

Bowers, A. (1980) The Manx herring stock, 1948-1976. ICES, rapports et proces des reunions 177; pp. 166-174.

Bucholtz, R.H., Tomkiewicz, J. & Dalskov, J. (2008). Manual to determine gonadal maturity of herring (*Clupea harengus* L.). DTU Aqua-report 197-08, Charlottenlund: National Institute of Aquatic Resources. 45 p.

Campbell, N.R., Harmon, S.A. and Narum, S.R., 2015. Genotyping-in-Thousands by sequencing (GT-seq): A cost effective SNP genotyping method based on custom amplicon sequencing. *Molecular ecology resources*, 15(4), pp.855-867.

Clarke, D.R.K & King, P.E (1985). Spawning of Herring (*Clupea harengus* L.) in Milford Haven. Journal of the Marine Biological Association of the UK 65(03): 629 – 639.

Clarke, D.R.K & King, P.E. (1986) The estimation of gillnet selection curves for Atlantic herring (*Clupea harengus* L.) using length/girth relations. *ICES Journal of Marine Science* 43(1): 77–82.

Clarke, D.R.K. (1984). The Milford Haven Herring Stock. PhD Thesis, University College, Swansea.

Clucas, G.V., Kerr, L.A., Cadrin, S.X., Zemeckis, D.R., Sherwood, G.D., Goethel, D., Whitener, Z. and Kovach, A.I., 2019. Adaptive genetic variation underlies biocomplexity of Atlantic Cod in the Gulf of Maine and on Georges Bank. *PloS one*, 14(5).

Cushing, D. H. 1990 Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. In *Advances in marine biology*, vol. 26 (eds Blaxter JHS, Southward AJ), pp. 249-293. New York, NY: Academic Press.

Ford, E. (1928). Herring Investigations at Plymouth II. The average number of vertebrae for herrings from the English Channel and South East of Ireland. *J.M.B.A. U.K.* 15; pp.267-278.

Fuentes-Pardo, A.P., Bourne, C., Singh, R., Emond, K., Pinkham, L., McDermid, J.L., Andersson, L. and Ruzzante, D.E., 2019. Adaptation to seasonal reproduction and thermal minima-related factors drives fine-scale divergence despite gene flow in Atlantic herring populations. *bioRxiv*, p.578484.

Han, F., Jamsandekar, M., Pettersson, M.E., Su, L., Fuentes-Pardo, A.P., Davis, B.W., Bekkevold, D., Berg, F., Casini, M., Dahle, G., Farrell, E.D., Folkvord, A., and Andersson, L. 2020. Ecological adaptation in Atlantic herring is associated with large shifts in allele frequencies at hundreds of loci. *Elife*, 9, p.e61076.

Jombart, T., 2008. adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics*, 24(11), pp.1403-1405.

Jombart, T., Devillard, S. and Balloux, F., 2010. Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC genetics*, 11(1), p.94.

Jørgensen, H.B., Hansen, M.M., Bekkevold, D., Ruzzante, D.E. and Loeschcke, V., 2005. Marine landscapes and population genetic structure of herring (*Clupea harengus* L.) in the Baltic Sea. *Molecular Ecology*, 14(10), pp.3219-3234.

Kerr, Q., Fuentes-Pardo, A.P., Kho, J., McDermid, J.L. and Ruzzante, D.E., 2019. Temporal stability and assignment power of adaptively divergent genomic regions between herring (*Clupea harengus*) seasonal spawning aggregations. *Ecology and evolution*, 9(1), pp.500-510.

Kornfield, I., Sidell, B.D. and Gagnon, P.S., 1982. Stock definition in Atlantic herring (*Clupea harengus harengus*): genetic evidence for discrete fall and spring spawning populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 39(12), pp.1610-1621.

Lamichhaney, S., Fuentes-Pardo, A.P., Rafati, N., Ryman, N., McCracken, G.R., Bourne, C., Singh, R., Ruzzante, D.E. and Andersson, L., 2017. Parallel adaptive evolution of geographically distant herring populations on both sides of the North Atlantic Ocean. *Proceedings of the National Academy of Sciences*, 114(17), pp.E3452-E3461.

Mariani, S. and Bekkevold, D., 2014. The nuclear genome: neutral and adaptive markers in fisheries science. In *Stock identification methods* (pp. 297-327). Academic Press.

Mariani, S., Hutchinson, W.F., Hatfield, E.M., Ruzzante, D.E., Simmonds, E.J., Dahlgren, T.G., Andre, C., Brigham, J., Torstensen, E. and Carvalho, G.R., 2005. North Sea herring population structure revealed by microsatellite analysis. *Marine Ecology Progress Series*, 303, pp.245-257.

McPherson, A.A., Stephenson, R.L., O'reilly, P.T., Jones, M.W. and Taggart, C.T., 2001. Genetic diversity of coastal Northwest Atlantic herring populations: implications for management. *Journal of Fish Biology*, 59, pp.356-370.

Molloy, J. and Corten, A. (1975). Young herring surveys in the Irish Sea. ICES pelagic fish (Northern) Committee CM 1975/H:11.

Molloy, J., 1968. Herring investigations on the southwest coast of Ireland 1967. *ICES CM*, 68.

Parrish, B.B. and Saville, A (1965). The biology of the North East Atlantic herring populations. *Oceanographic and Marine Biology Annual Reviews* 3; pp. 323-373.

Petrou, E.L., Fuentes-Pardo, A.P., Rogers, L.A., Orobko, M., Tarpey, C., Jiménez-Hidalgo, I., Moss, M.L., Yang, D., Pitcher, T.J., Sandell, T. and Lowry, D., 2021. Functional genetic diversity in an exploited marine species and its relevance to fisheries management. *Proceedings of the Royal Society B*, 288

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

Shaw, P.W., Turan, C., Wright, J.M., O'connell, M. and Carvalho, G.R., 1999. Microsatellite DNA analysis of population structure in Atlantic herring (*Clupea harengus*), with direct comparison to allozyme and mtDNA RFLP analyses. *Heredity*, 83(4), pp.490-499.

Wood, H. (1960) The herring of the Clyde Estuary. *Mar. Res. Scot.*,1; pp. 24.

Wood, R.J. (1981). The Thames estuary herring stock. Ministry of Agriculture, Fisheries and Food, U.K. Fisheries research technical report, 64.