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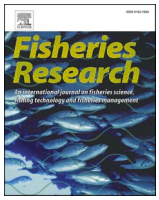

Short communication

Below and beyond the species: DNA tools for geographic traceability analysis of cod products in European markets

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ABSTRACT

DNA technology has been shown as an effective tool to monitor seafood trade and improve transparency. It has highlighted seafood species mislabelling on a global scale and has attracted the interest of policy makers, government authorities, and other stakeholders. Despite the proven success of genetic methods in seafood traceability, studies exploring the mislabelling of geographic catch location within a species remain rare. Accurately disclosing the catch location of wild-caught fish is crucial for sustainable seafood management, but verifying this information remains difficult. Tools to evaluate catch location are on the rise and offer an unprecedented opportunity to expand investigations of seafood mislabelling. Diagnostic Single Nucleotide Polymorphisms (SNPs) have been used extensively in the context of population genetics and have the potential to reveal trends in seafood fraud. In this study, we demonstrate the efficiency of a set of nine diagnostic SNPs for the identification of two heavily harvested cod populations, the Northeast Arctic cod and the North Sea cod, and conduct a market analysis of catch location mislabelling of Atlantic cod sold in four European countries. Our findings suggest that inexpensive, diagnostic molecular tools can effectively monitor mislabeling in catch locations and discuss how the method can be enhanced to minimize errors and maximize utility, towards strengthening governance, enhancing sustainability, and boosting consumer trust.

1. Introduction

Seafood substitution – i.e. the swapping of one species for another – has been reported worldwide leading to economic loss, damaging consumer trust in the industry, and threatening vulnerable species (Cawthorn et al., 2018). Though not always deliberately fraudulent, this kind of substitution can be motivated by economic gain or by high consumer demand for certain types of fish for which the supply is low (Donlan and Luque, 2019). Much less is known about the mislabelling of catch location and its impact on fisheries sustainability, due to the paucity of provenance testing market studies conducted so far (Cusa et al., 2021).

Investigating the mislabelling of a product's geographical origin is inherently complex as it depends on the level of genetic differentiation between the populations of interest (Cusa et al., 2021; Ogden and Linacre, 2015). Stock boundaries defined for management purposes add another layer of complexity as they may not match biological population boundaries (Reiss et al., 2009). Increasingly, though, the use of DNA based tools for determining geographical point-of-origin of seafood are becoming more accessible and emerging as a viable option (Bekkevold et al., 2023; Cusa et al., 2021; Ogden and Linacre, 2015). This is particularly relevant for species with somewhat isolated populations exhibiting different conservation status. The iconic Atlantic cod (*Gadus morhua,* Fig. 1.**a**) is an ideal candidate for this type of investigation as it is an extensively studied species, with several known, distinct, population boundaries, and its conservation status varies substantially between regions, with stocks being either depleted, facing declines, or displaying a healthy trend.

Atlantic cod, which is distributed throughout most of the North Atlantic and as far north as Svalbard and North Greenland, has a long history of harvest and consumption and its interplay with human societies over many centuries is possibly unparalleled (Kurlansky, 1997). Presently, Norway and Iceland are the main harvesters of Atlantic cod, and many European countries have dedicated cod fishing fleets. Despite

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what appeared to be some promising stock recoveries, the Atlantic cod stocks of the North Sea and Baltic Sea recently underwent sudden and substantial depletion, leading to severe fishing restrictions and a zero catch advised for 2020 (ICES, 2019) and though the northern shelf cod appears to have since recovered, the fishing pressure still remains above advised maximum sustainable yields (ICES, 2023). Investigating instances of catch location mislabelling can have significant implications for both fish stock management (such as when opportunistic fishing occurs in areas with lower quotas) and consumer protection, as inadequate transparency can lead to misleading information.

Both the economic importance of this fish and the stock collapse of the Atlantic Northwest fishery have led to an important body of research being conducted on Atlantic cod, including many population genetic studies. It is now fairly well established that Atlantic cod demonstrates varied levels of population structure throughout the Atlantic with some populations being quite distinct from others (Bradbury et al., 2013). A plethora of molecular markers have long demonstrated stock subdivision within the North-east Atlantic (Hutchinson et al., 2001; Nielsen et al., 2009, 2012; O'Leary et al., 2007; Pogson and Fevolden, 2003; Poulsen et al., 2011; Skarstein et al., 2007), including fine-scale substructure along the complex Norwegian coastline (Barth et al., 2017; Jorde, Synnes, et al., 2018). The Norwegian Coastal Cod (NCC), in

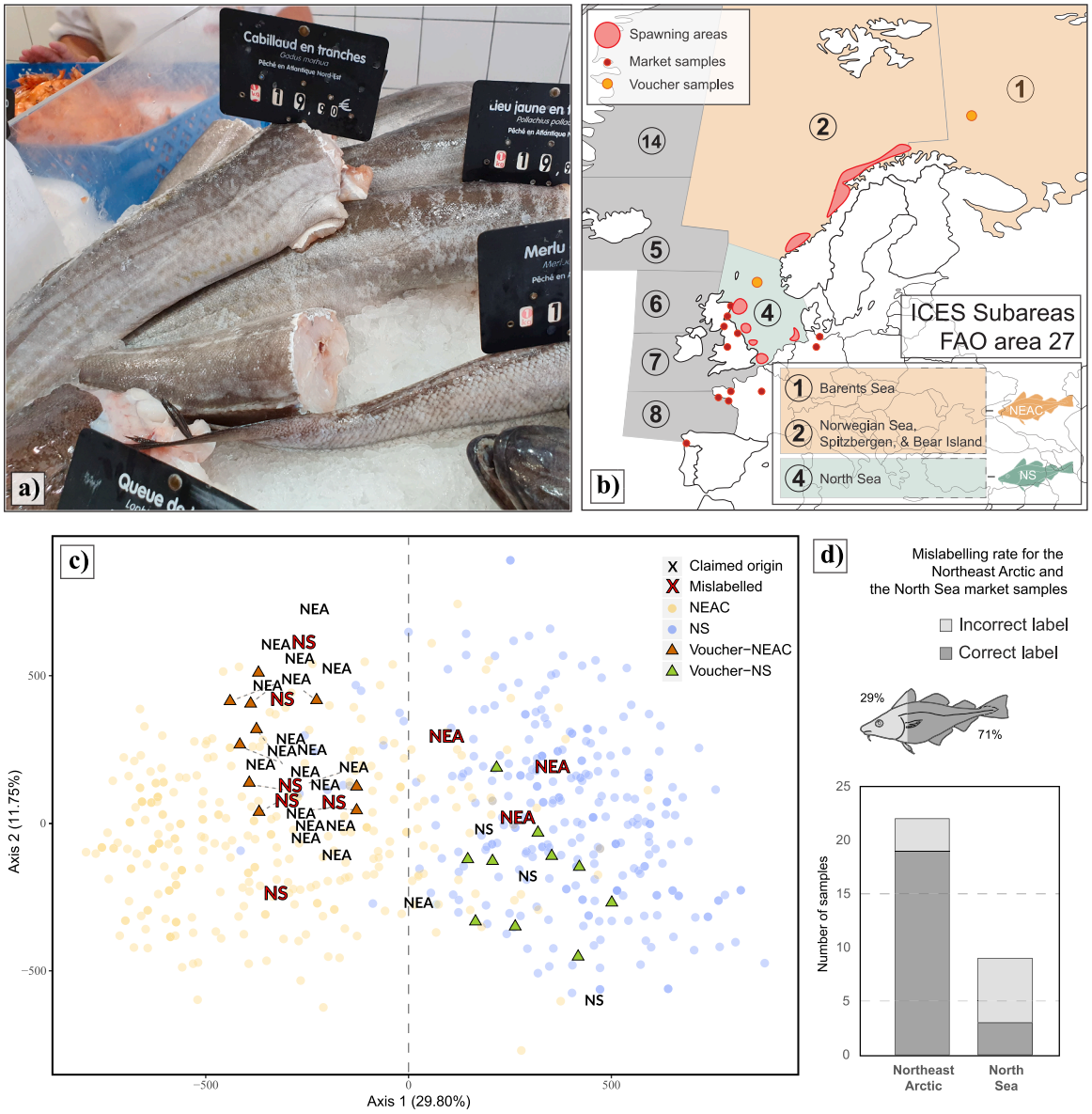

Fig. 1. **a)** Photo of fishmonger stall in France displaying Atlantic cod and vague geographical catch location ("North East Atlantic"), **b)** Map of the ICES subareas with highlights identifying the two regions and populations for which the Atlantic cod diagnostic SNPs were identified; the Northeast Arctic cod (NEA) is found in ICES subarea 27.1 and 27.2 pictured in pink, and the North Sea cod (NS) in found in ICES subarea 27.4 pictured in green. The other subareas depicted in grey are zones in which at least one marketed cod specimen was claimed to have been fished. The map also illustrates the various locations where Atlantic cod specimen were sampled for the market study (red markers), and the validation of the method (yellow markers). The spawning grounds of the two populations of interest (NEA & NS) is highlighted in red, **c)** Correspondence Analysis illustrating the distribution of Northeast Arctic (yellow) and North Sea (blue) reference samples along the two eigenvectors that explain 41.55 % of the variance. The claimed origin of the market samples is indicated by the letters NEA (samples caught in the Northeast Arctic) and NS (samples caught in the North Sea). NEA and NS in black refers to market samples that were correctly labelled, and NEA and NS in red refers to mislabelled samples. Voucher specimen (positive controls) are indicated with coloured triangles. The figure indicates that most market samples originate from the Northeast Arctic though six of them had been mislabelled as being fished in the North Sea, **d)** Apparent mislabelling rate of the claimed geographical catch location of Atlantic cod, with a total apparent mislabelling of 29 % illustrated in the cod icon, 14 % for the Northeast Arctic, and 67 % for the North Sea.

particular, which spreads across a wide latitudinal scale along the coast of Norway displays an isolation by distance pattern, with some level of introgression and admixture with the Northeast Arctic cod (NEA) in the north, which results in a clinal separation between Northern and Southern NCC (Dahle et al., 2018; Johansen et al., 2020; Kessel et al., 2016). This wealth of knowledge, resources and tools make Atlantic cod a strong candidate for a catch location mislabelling study.

In the European Union, the Common Organisation of the Markets (CMO) in Fishery and Aquaculture products (EU) No 1379/2013 mandates that fresh, chilled or frozen fish fillets caught in the Northeast Atlantic (FAO 27) must define the catch location by indicating the sub-area or division (ICES sub-zones) on consumer packages. At the time of sampling in 2019 and 2020, the European Union regulations still applied to the United-Kingdom. As of January 2025, the UK Fish Labelling Regulations still follow post-Brexit EU standards. We used those standards as an opportunity to conduct a pilot geographical point-of-origin market study, sampling 108 Atlantic cod products from fishmongers and grocery stores across four European countries: Spain, France, Germany and the United-Kingdom (Fig. 1**b**). We evaluated species mislabelling and the precision of label information, though our primary goal was to identify whether there were discrepancies between the catch areas indicated on the labels and the genetic origin of the product.

2. Materials and methods

2.1. Marketed cod sampling

Sampling was conducted in various cities and coastal communities around the United-Kingdom, France, Germany, and Spain (Fig. 1.**b**). In the UK, a total of 47 cod were purchased from Manchester, Liverpool, Newcastle, Fraserburgh, Peterhead, Gourdon, Arbroath, and Edinburgh. In France, a total of 28 cod were purchased from Paris, St. Malo, Guilvinec, Concarneau, and Quimper. In Germany 10 cod were sampled from Hamburg and another 10 from Kiel, and in Spain 13 cod were sampled from Vigo. Additionally, 20 samples of known origin (used as positive controls) were received from scientific surveys run by partner institutions to validate the method used for geographical assignment: 10 cod from the East Barents Sea (University of Oslo) and 10 cod from the North Sea (UK Centre for Environment, Fisheries and Aquaculture Science). Samples were all stored in a tube with silica beads or in 90 % ethanol. To avoid the bias of possibly sampling the same individual twice, only a single fish sample was obtained from individual fish mongers, and only one fish filet from a given brand was sampled from supermarkets.

2.2. Compliance with EU labelling rules on ICES subareas

We evaluated compliance with the EU regulation on seafood labels by recording the number of ICES subareas indicated for each product.

2.3. DNA extractions and species identification

The DNA extraction was conducted using the E.Z.N.A. tissue DNA Kit from omega bio-tek, Inc and a Mu-DNA extraction protocol (Sellers et al., 2018). Identification and validation of species were conducted in-house using the FASTFISH-ID™ protocol and reagents (Naaum et al., 2021). The results were imported onto the FASTFISH-ID™ online software for species authentication.

2.4. Massive parallel sequencing

We used a targeted approach (Nielsen et al., 2012) based on a set of nine previously identified Single Nucleotide Polymorphisms (SNPs) (Ogden and Murray-Dickson, 2014) selected to be diagnostic between the NEA and the North Sea (NS) stocks among 1290 SNPs from a total of 942 reference genotypes.

The sequences containing the nine diagnostic SNPs identified by Ogden and Murray-Dickson (2014) and following the method described by Nielsen et al. (2012) are about 120 nucleotide long and the primers were designed using an online primer design software (Primer3). Meyer and Kircher's (2010) protocol – and associated python script (https://bioinf.eva.mpg.de/multiplex/) – was used to design the indexed barcodes that allow to multiplex each sample. Both tailed and non-tailed forward and reverse primers were then commercially synthesized as 5' - 3' DNA oligos for all nine amplicons (Table S1).

The optimization of the adequate PCR profile and parallel sequencing protocol was performed using a subset of 28 samples. Once the best primer runs were selected for each sample, all nine SNP amplicons were combined into a single solution for each sample with a unique combination of P5 and P7 barcodes (i.e. indices). A second PCR was then run for each sample in duplicate to permit the annealing of the unique barcodes to each sample amplicons. Samples were multiplexed and the library was sequenced at a final concentration of 12.5 pM on an Illumina MiSeq using v3 chemistry cartridge (with 2 ×150 cycles).

We used the FASTQC package (Andrews, 2010) to check the quality of the sequences using a QC analysis. Subsequently, reads were trimmed to 199 bp using OBICUT (Boyer et al., 2016). The package FLASH (Fast Length Adjustment of Short Reads) (Magoč and Salzberg, 2011) was then used to align and merge the reverse and forward sequences. We then used the GTseq pipeline (Campbell et al., 2015) to genotype each individual cod.

2.5. Data analysis and assignment of market samples

To visually evaluate the position of our market and voucher samples relative to the reference samples, we first performed a Correspondence Analysis (CA) using the GENETIX 4.05.4 software (Belkhir et al., 2004). Genetic assignment analyses were then conducted using the GENECLASS 2.0 software (Piry et al., 2004). We used the partial Bayesian approach developed by Rannala and Mountain (1997) to evaluate population allele frequencies based on the cod reference samples and assign market samples to those populations. The voucher specimens from known locations collected in 2020 (Barents Sea and North Sea) were also included among the 'unknown location' samples to verify whether they would be attributed correctly back to their known population of origin.

For samples showing potential mislabelling (i.e. the most likely location of origin was not the same as the one on the label), we first calculated the exclusion probability, using Monte-Carlo resampling with a simulated number of 10 000 individuals and a type one error set to 0.01, to check that the genotype of the sample was not excluded from originating from the most likely location. As assignment tests will always provide a most-likely location of origin from a given set of options, it is important to verify that this most likely location is also a genetically credible (non-excluded) result.

Next, in the case of samples claimed to have been caught in the North Sea or the Northeast Arctic, the log-likelihood ratio (logLR) for the claimed location and identified location were calculated to assess the strength of the evidence for the sample originating from the most likely location, rather than the claimed location, given the genotype of the sample. Probabilities of correct assignment were calculated from the two logLR distributions by evaluating the region of overlap (misassignment) between the two distributions following Ogden and Linacre (2015).

2.6. Interpretation of the data

We excluded from the analysis all the samples that displayed imprecise label catch location (i.e. more than two geographical location), and those whose claimed geographical origin could not be verified with this SNP panel, specifically any location falling outside of the North Sea and Northeast Arctic range. In order to make scrupulous inference on the mislabelling rate, we took the conservative approach of removing

samples with an assignment certainity lower than 80 % or for which less than 8 SNPs had amplified. Fifty-one samples remained, 31 of which were market samples, and 20 of which were recent voucher specimens from known locations, screened to further verify the robustness of the SNP panel, which was originally validated using samples collected nearly two decades ago (Nielsen et al., 2012; Ogden and Murray-Dickson, 2014).

3. Results

Only two amongst the 108 Atlantic cod product samples were identified as different species (both were haddock, *Melanogrammus aeglefinus*), documenting a species mislabelling rate of < 2 %. From the 64 packages we collected in supermarkets, we noted that about 34 % ($N = 22$) of them displayed imprecise labelling on geographical catch locations, listing more than two ICES fishing sub-areas or division or offering vague information such as "fished in Iceland, may come from other zones" or "fished in the North-East and North-West Atlantic", which in this case covers the entire distribution of the species. Country of retail played an important role in labelling precision with 54 %, 44 %, and 22 % of French, UK, and Spanish products respectively displaying imprecise labels, and with German products all containing precise catch location information (defined here as two or less ICES subareas).

All ten Barents Sea voucher specimens could be assigned with high certainty to the Northeast Arctic region, and nine out of the ten North Sea voucher specimens were assigned to their catch area, the remaining one was assigned to the wrong location, but with extremely low assignment certainty. This further corroborated the effectiveness of the chosen SNP panel. Out of the 22 cod claimed to have originated from the Northeast Arctic, three of them were assigned to the NS with over 80 % certainty, while out of the nine samples claimed to have originated in the North Sea, 6 of them were assigned to the NEA source samples with over 88 % certainty (Fig. 1**.c**). This brings the total rate of possibly erroneous claims to 29 % (Fig. 1**.d** – but see "Interpretation of the assignment results" in the Supplementary Material for more detail). For all the nine mislabelled samples, a likelihood ratio indicated that the assignment probabilities were very high, over 98 %. All but one Northeast Arctic-labelled samples were purchased in supermarkets, while all but one NS samples were purchased at fish mongers.

4. Discussion

The low species mislabelling rate we observed may find its root in the public's demand for increased transparency and traceability following a plethora of articles and associated media release exposing widespread species mislabelling in the seafood industry (Mariani et al., 2014). This notably low rate of species mislabelling is similar to what other studies have reported for Atlantic cod products in Europe (Feldmann et al., 2021; Helgoe et al., 2020; Mariani et al., 2015), which seems to confirm stipulations over improving traceability trends, at least for this staple species.

According to Regulation (EU) No 1379/2013 and Regulation (EU) 1169/2011, it is mandatory for any EU prepacked and non-prepacked fresh or frozen seafood product to not only state the scientific name of the species sold, but also to display detailed information on the catch area for fish caught at sea. For any fish that was caught in the Northeast Atlantic, the ICES subarea or division must be indicated and defined clearly so that consumers can understand the provenance of the seafood. The ICES Northeast Atlantic subareas relevant for this study within FAO area 27 are unambiguously defined on the FAO resource website (Fig. 1**.b**). Notwithstanding EU incentives to increase transparency via more detailed labels through the CMO (EU) No 1379/2013, the industry might currently struggle to keep this level of information accurate throughout the supply chain, and additional steps may be needed to provide consumers with both precise and reliable information on the provenance of the seafood products they wish to purchase.

Despite a low apparent mislabelling rate at species level, the geographical catch location seems to be often misrepresented. Lower mislabelling in Northeast Arctic-labelled samples and in supermarkets likely reflects the main volumes and logistics of trade, with the NEA cod production being over 35 times greater than the North Sea (ICES, 2021) and sustaining the bulk of cod product provision to European consumers.

The underlying reasons for mislabelling products are numerous (Donlan and Luque, 2019), and though we did not formally assessed why we observed such mislabelling, field observations led us to believe that, in some cases, it might have been deliberate. A possible reason for the passing of NEA cod for fish belonging to the less sustainable NS stock became apparent during the sampling process. In line with evidence that consumers prefer to purchase local fish (European Commission, 2018; C. Feldmann and Hamm, 2015), we noted that some fishmongers erroneously described their cod products as local rather than coming from the distant Arctic regions where it had originated from. Another plausible explanation for the mislabelling observed is simply a lack of adequate traceability, leading to loss of information. The stage of the supply chain at which such loss of information might occur remains difficult to evaluate.

The presented panel of nine SNPs were developed for the differentiation of NEA and NS cod, and therefore market control for catch location was only tested on cod being clearly labelled as coming from these regions. Including a larger diagnostic SNP panel could help differentiate between more populations. Due to the probabilistic nature of geographical assignments of individuals belonging to the same species, it is difficult to achieve 100 % certainty when examining potential instances of mislabelling; however, the addition of affordable complementary techniques, such as Stable Isotopes (Cusa et al., 2021), can lead to stronger assignment. Beyond Atlantic cod, which is a species that has been extensively studied due to its economic and cultural importance in the European industry, hundreds of species worldwide are composed of a range of population structure patterns (Cusa et al., 2021; Mariani and Bekkevold, 2014; Reiss et al., 2009), whose relative representation in the markets remains largely unchecked and unmonitored. Given the rate of species mislabelling worldwide (Luque and Donlan, 2019), and the present results on one of the most studied and traded species on the planet, it is evident that these now widely available and increasingly nimble DNA tools should be developed for population assignment and become a centrepiece of supply chain traceability monitoring, towards more sustainable seafood industry operations.

It should also be noted that, unlike biochemical tracers such as stable isotopes, which vary spatially and indicate specific habitat use locations, genetic based methods reflect the reproductive population of origin of an individual organism (Cusa et al., 2021; Ogden and Linacre, 2015). Therefore, and despite marked genetic differences among several well-characterised cod populations (Hutchinson et al., 2001; Jorde, Kleiven, et al., 2018; Nielsen et al., 2001, 2009; Poulsen et al., 2011; Skarstein et al., 2007), migration between populations or climate-driven distribution shifts could be a problem when ascertaining the exact catch location of a specimen using DNA-based methods. This is particularly problematic in the many species where stock management boundaries do not match true biological boundaries (Ogden and Linacre, 2015; Reiss et al., 2009). In the specific case of Atlantic cod from the NS and NEA, the barriers to population interbreeding, due to their diverging habitat range and preferences, migratory patterns, and reproductive locations (Hemmer-Hansen et al., 2013, 2014) are strong, as are a number of other high-profile geographic delineations in other important commercial species. This means that the present study can serve as a robust showcase of the effectiveness of currently available genetic tools for monitoring geographic provenance; but much remains to be done with marker development, optimisation, and validation, in the case of numerous other commercial species and stocks before this philosophy can be widely applied.

5. Conclusion

Against the backdrop of substantial research and applications aimed at monitoring species substitution in the seafood trade, the analysis of seafood point-of-origin lags noticeably behind. This study suggests mislabelling of cod stock provenance, which may come as a surprise given the low level of species mislabelling recently noted for Atlantic cod in Western European countries. The reasons for geographical mislabelling are unclear and could span from genuine errors across a complex supply chain, to more blatant fraudulent behaviour motivated by economic gain. Despite a relatively low sample size, this study highlights the need to further investigate fish catch location mislabelling. Including additional cod populations and geographical areas to such an investigation might increase the complexity of the work but would offer finer resolution and a better understanding of the scale of the issue. Using a small panel of diagnostic SNPs such as here has the added benefit of being quick and reliable but limits the scope of the investigation in terms of geographical range and precision. This study highlights that catch location mislabeling is likely prevalent and calls for further work to evaluate its magnitude and scale. Given the poor state of certain fish stocks, authorities and retailers should be able to verify seafood provenance, and customers should be given the ability to choose where their seafood originates from using reliable labels.

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CRediT authorship contribution statement

Cusa Marine: Writing – original draft, Visualization, Project administration, Investigation, Formal analysis, Conceptualization. **Mariani Stefano:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **Shum Peter:** Writing – review & editing, Methodology, Formal analysis. **Ogden Rob:** Writing – review & editing, Resources, Methodology. **Baillie Charles:** Software, Methodology, Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2025.107302.

Data Availability

Data will be made available on request.

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