ORIGINAL RESEARCH

A future for seafood point-of-origin testing using DNA and stable isotope signatures

Marine Cusa · **Katie St John Glew** · **Clive Trueman** · **Stefano Mariani** · **Leah Buckley** · **Francis Neat** · **Catherine Longo**

Abstract Demand for seafood products is increasing worldwide, contributing to ever more complex supply chains and posing challenges to trace their origin and guarantee legal, well-managed, sustainable sources from confirmed locations. While DNA-based methods have proven to be reliable in verifying seafood authenticity at the species level, the verification of geographic origin remains inherently more complex. Both genetic and stable isotope analyses have been employed for determining point-of-origin with varying degrees of success, highlighting that their application can be effective when the right tool is selected for a given application. Developing an a priori prediction of their discrimination power for different applications can help avoid the financial cost of developing inappropriate reference datasets. Here, we reviewed the application of both techniques to seafood point-of-origin for 63 commercial finfish species certified by the Marine Stewardship Council, and showed that, even for those species where baseline data exist, real applications are scarce. To fill these gaps, we synthesised current knowledge on biological and biogeochemical mechanisms that underpin spatial variations in genetic and isotopic signatures. We describe which species' biological and distribution traits are most helpful in predicting effectiveness of each tool. Building on this, we applied a mechanistic approach to predicting the potential for successful validation of origin to three case study fisheries, using combined genetic and isotopic methodologies to distinguish

Marine Cusa and Katie St John Glew are joint first author.

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M. Cusa (✉)
School of Science, Engineering and Environment, University of Salford, Salford, UK
e-mail: M.L.Cusa@ljmu.ac.uk

M. Cusa · S. Mariani
School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, UK
e-mail: S.Mariani@ljmu.ac.uk

K. St John Glew (✉) · C. Trueman
Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, Southampton, UK
e-mail: katiestjohnglew@gmail.com

C. Trueman
e-mail: trueman@noc.soton.ac.uk

L. Buckley · C. Longo
Marine Stewardship Council, London, UK
e-mail: leah.buckley@msc.org

C. Longo
e-mail: katie.longo@msc.org

F. Neat
Sasakawa Global Ocean Institute, World Maritime University, SE-201 24, Malmö, Sweden
e-mail: fn@wmu.se

individuals from certified versus non-certified regions. Beyond ecolabelling applications, the framework we describe could be reproduced by governments and industries to select the most cost-effective techniques.

Graphic abstract
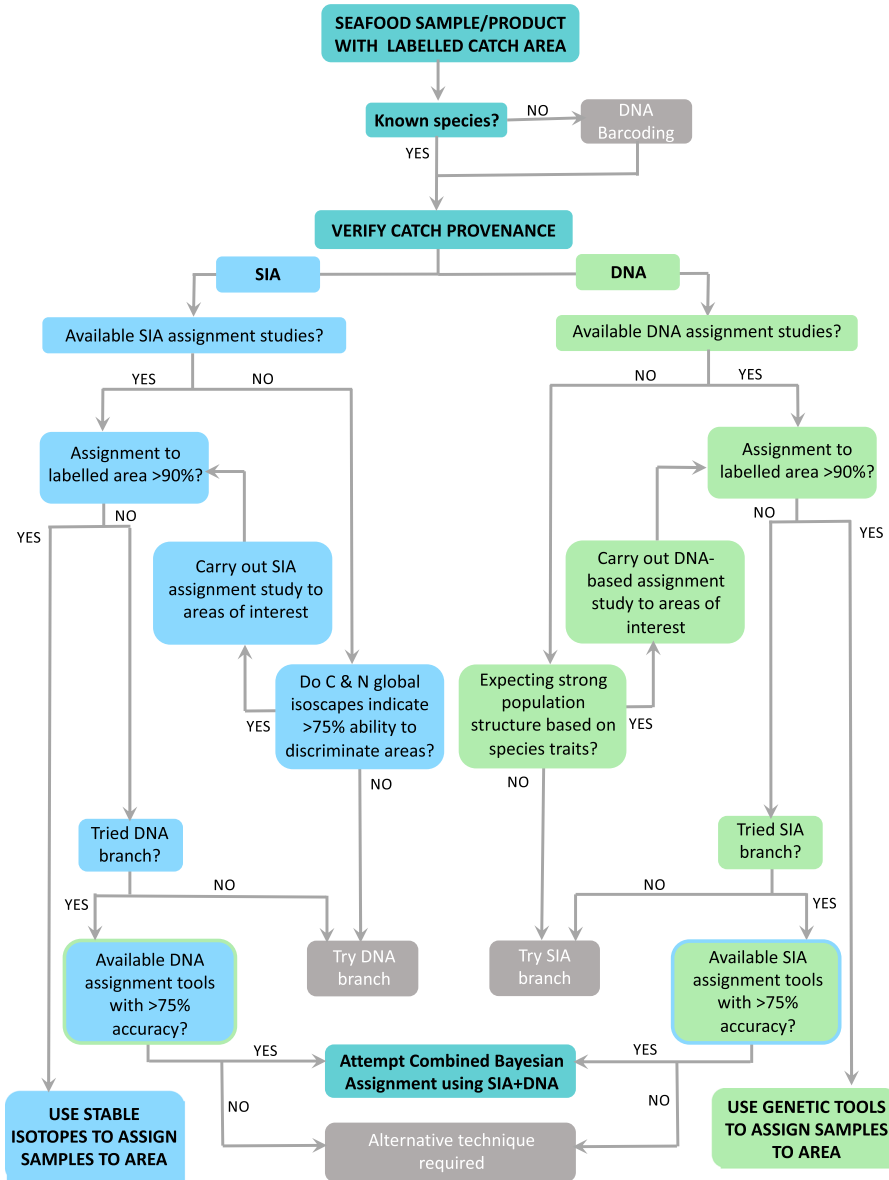
Introduction

Increasing demand for seafood from a growing global population generates concerns over sustainable exploitation and mitigation of environmental impacts of fishing activities (FAO 2020). Excluding products coming from unsustainable sources from the market is a way to support well-managed fisheries and to help remove incentive for poor or illegal practices. This is the intent, for example, of legally mandated checks at landing sites by signatory States to the FAO's Port State Measures Agreement (OECD 2018). This, however, remains the first stage in an often lengthy seafood supply chain. Once a fish is landed and starts its journey through the supply chain, it becomes increasingly difficult to track whether it originated from legal and sustainably managed fisheries as it proceeds through the far-reaching and complex global seafood trade networks (FAO 2020; Leal et al. 2015; Yasuda and Bowen 2006). To guarantee the integrity of the chain of custody, each step throughout the supply chain must be documented and fully traceable. Further checks may be needed at import border crossing, processing plants, and key points in the supply chain. Yet, traceability tools, which can be defined as the methods used to follow a product along the supply chain such as landing declarations, catch certificates, supplier self-reporting, volume reconciliation, etc., are vulnerable to manipulation. Illegally caught fish resulted in a worldwide loss of US\$ 10–23.5 billion in 2009 as estimated by Agnew et al. (2009) and of US\$ 9–17 billion in 2020 according to (Sumalia et al. 2020). Authorities checking for compliance, as well as seafood businesses interested in protecting their brand or passing denomination of origin or ecolabeling audits, require diagnostic tests to confirm provenance (i.e. the geographical point of origin) documentation.

Forensic point of origin testing is a key tool for verifying traceability information (Ogden and Linacre 2015) and it is becoming standard practice within many industries and for products such as meat, dairy, wine, and honey (Donarski and Heinrich 2015; Kelly et al. 2005; Morin and Lees 2018; RedTractor 2013). DNA profiling, stable isotope analysis, fatty acids, and elemental profiling, have all been tested to varying degrees with shellfish and finfish populations of farmed and wild caught seafood (Gopi et al. 2019). Due to the ease with which these tracers can be used in terrestrial systems, genetic and biogeochemical markers are particularly well-established as tools to verify breed and region of origin of food products in terrestrial food chains (Heaton et al. 2005, 2014; Kelly et al. 2005) but are far less frequently used in marine systems and, we argue here, deserve more attention.

Genetic and biogeochemical tracers are mechanistically and analytically different and can vary independently. This presents both difficulties and opportunities, potentially increasing the value of combined approaches. Stable isotope, fatty acid and elemental tracers for spatial origin are based on the transmission of the tracer signal from the underlying natural environment into the organism (Ramos and Gonzalez-Solis 2012). These techniques therefore directly link an organism to a physical location at a point in time, but their efficacy is dictated by underlying spatial gradients in the tracer signals. Genetic tracers are instead grounded in the fundamental processes of inheritance and are therefore based on the dynamic interplay of isolation/exchange of allelic variants existing within and among reproductive groups (Freeland et al. 2005; Wright 1931). Genetic tracers therefore reflect population spatial histories rather than recent individual movements or location at the point of capture.

Forensic provenance testing will generally require the development of a reference database of known origin samples to be collected across the regions of interest for any given species (Kelly et al. 2005) and this is often logistically and financially challenging. Provenance tests are considerably more difficult to validate across large and often poorly sampled marine environments compared to agriculture, farming, or even aquaculture, where species are often spatially constrained. In addition, since marine environments have fewer physical boundaries, individuals and populations of fish species move and migrate to varying extents and mix with other populations. The accuracy and precision associated with natural tracers used as markers of geographic origin will depend on the nature of spatial variance in the tracers in question, and on the quality of the reference dataset (Fig. 1).

Developing an a priori prediction of the power for any given spatial marker technique to discriminate among specific fishery populations can help avoid the financial cost of developing inappropriate reference datasets. At the same time, this exercise can potentially open spatial verification methods to a wider

range of users and contexts. Here we present case studies for which two very different types of currently available tools, genetic and stable isotope tracers, can be used to establish seafood provenance at spatial scales and accuracy measures relevant to real world applications. Genetic tools are already commonly used in seafood forensics for species identification, though their use for provenance testing is less advanced. Stable isotopes are a good model biochemical tracer due to the extensive research and use within the terrestrial food traceability sector (Chesson et al. 2008, 2010; Kelly et al. 2005) and the successful use in discriminating origin in wild caught seafood products at both local and broad geographical scales (Carrera and Gallardo 2017; Gong et al. 2018; Kim et al. 2015; Pustjens et al. 2018; Trueman et al. 2017). In addition, the growing availability of varying spatial isotopic marine models resolution (Trueman and St John Glew 2019) provides an opportunity to predict where further traceability case studies are likely to succeed. We focus on commercial fisheries certified against the Marine Stewardship Council (MSC) Fishery Standard, expecting them to have good availability of biological and traceability research. In order to exhibit the ecolabel on consumer-facing products, the MSC program requires chain of custody certification for each step of the supply chain and must assure that products were harvested in the location and by the fishers covered by the certificate. The MSC example therefore represents a useful proof of concept as it combines a claim of origin from a sustainable stock and defines the unit of certification to a particular region and group of harvesters.

Through a meta-analysis we review the extent to which species biological traits can predict genetic population structure. We develop a workflow to estimate the likely efficacy of either stable isotope or genetic tools when applied to a defined spatial verification problem to enable us to investigate the capabilities of these techniques using stocks certified in specific locations by the MSC. Beyond the ecolabeling examples presented, the provenance testing protocol and methods described here can be applied to a range of provenance-testing questions for any species of both fish and shellfish within a marine environment.

Box 1: Stable isotope and genetic assignment methods

Stable isotope assignment

Isotope ratios vary spatially across terrestrial, aquatic and marine landscapes due to varying environmental conditions exerting effects on isotopic abundance (Bowen 2010), due to differences in the hydrological cycle, fluid dynamics, nutrient cycling and biological processes. To utilise this spatial isotopic variation, or determine values in unmeasured regions, isotope maps (isoscapes) are produced. In marine environments, organic isotopic composition varies across space in phytoplankton at the base of the food web due to differences in rate of photosynthesis, and the nutrients available within the water column (McMahon et al. 2013; Ramos and Gonzalez-Solis 2012). These spatial isotopic variations are then transferred up the food web, enabling isotopic ratio measured in the tissue of a fish to act as a natural tag (Ramos and Gonzalez-Solis 2012), indicating the individual's foraging location before capture.

Genetic assignment

Genetic methods can readily discriminate between most species owing to the long-standing reproductive isolation between evolving lineages, resulting in measurable DNA sequence divergence (Hebert et al. 2003). Complications arise when investigating the geographical origin of a specimen, as this requires the given species to be composed of somewhat reproductively isolated populations, and that sufficient, detectable genetic variance exists among these groups. A population can be defined as a group of individuals from a given species living in a set geographical area, interbreeding, and displaying some degree of reproductive isolation from other populations (Freeland and Petersen 2011; Waples and Gaggiotti 2006). In nature however, populations are not always fully reproductively and/or geographically isolated. The population concept can be visualized as functioning on a continuum with various degrees of connectivity, from total panmixia where individuals of reproductive age are effectively mating randomly with each other, to complete isolation where reproduction between populations is impossible (Waples and Gaggiotti 2006).

Box 2: Definition of verification and assignment

The two main uses of forensic provenance testing methods are for 'verification' or 'assignment' purposes (Nielsen 2016). Here we define 'verification' as the use of spatially varying natural markers to test the likelihood that a specific geographic claim is true, e.g., checking if the seafood actually came from the region stated on the product's label. 'Assignment' refers to the use of natural markers to infer location or origin, e.g., finding out where an unlabelled fish has come from. Assignment may be based on discrete approaches, where the sample of interest is matched against a set of reference samples chosen to characterise previously defined possible source areas, or continuous approaches where the reference data are
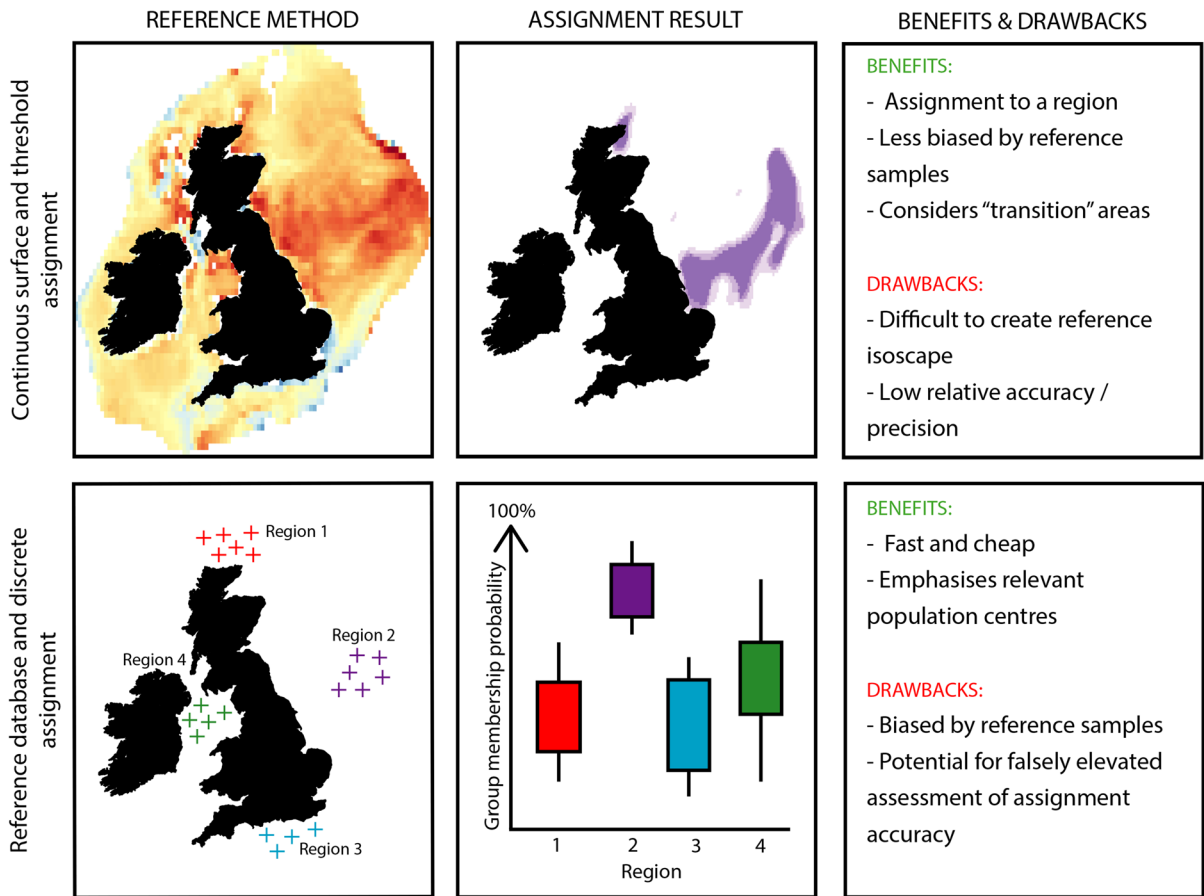
Fig. 1 Conceptual schematic depicting the differences between discrete and continuous assignment methods and associated reference materials required. Continuous assignment approaches (top row) rely on an even coverage of data over the entire study area, interpolated through a spatial model across a grid of varying resolution dependant on data availability (top left panel), and provide the highest likelihood of origin area (coloured area in the top right panel), compared to all other possible locations (ie other grid cells). Discrete assignment approaches (bottom row) require a discrete set of samples from each of the areas of interest (sample locations identified by crosses for each of four regions, lower left panel) and provide the probability of sample assignment to each of these predetermined areas (lower right panel). Benefits and drawbacks in terms of practical applicability and detection power of each approach are highlighted

transformed into a continuous probability surface or map, using a model to fill in information from areas where reference samples were not present (Fig. 1). The requirements for reference datasets increase from verification (a selection of samples from the predicted region of origin), to discrete (a broad selection of samples from the areas to be distinguished between), and continuous assignment designs (an evenly spatially gridded set of samples across the entire region of interest). Verification is overwhelmingly the most common design for natural tracer studies in food forensics and traceability applications.

Methods

Secondary source data collection

In total, we focussed on 74 marine finfish, 11 of which were in assessment and 63 of which were certified against the MSC Fishery Standard and covered under 133 different certificates (S1) as of November 2018. An MSC certified fishery is defined here as the group of vessels operating under an MSC certificate in a particular area with a particular gear and targeting a particular species (MSC 2020). For example, 17 different fisheries are certified to fish cod (*Gadus*

morhua) in the NE Atlantic. This list excludes salmon due to their anadromous life cycle which makes them akin to freshwater species in terms of reproductive isolation.

We first conducted a literature review to evaluate some of the distinct life-history traits that have previously been identified as important in influencing the outcome and interpretation of both genetic studies and stable isotope analysis (Table 1, S1). We then collected information on these traits for 70 species (four species were dropped due to a lack of information available) through another set of extensive literature review, and later gathered data on species-wide population genetic structure, in the sub-set of species for which this information was available, using a widely employed indicator of genetic dissimilarity [the F_{ST} value (Wright 1965)]. We only collected global F_{ST} or average F_{ST} values and, when possible, collected several F_{ST} values for any given species. Given that F_{ST} values for a single species may differ depending on the geographical range covered by the study, we estimated this geographical coverage for each study, and labelled it as "Entire", "Substantial", or "Regional" coverage.

For each of the 63 MSC certified species, we determined areas where a certified fishery operates to target the stock of interest (fishery area) from information found within the text and, in some cases, from the maps provided in the MSC Public Certification Reports (https://fisheries.msc.org/en/fisheries/@@search), i.e. the documents produced and published by Conformity Assessment Bodies to document when the fishery is certified, and shapefiles for each area were produced in QGIS (QGIS.org 2021). Of the 133 fisheries included, we identified fishing activities within 69 distinct fishery areas. Fishery areas ranged from whole ocean basins for highly migratory species to single bays or narrow coastal areas for more sedentary species. We also produced areal extents (in Shapefile format) for non-certified stock components,

based on species distribution data from published literature.

Analysis of the secondary sourced genetic data

Using attributes in Table 1, we populated a database including, for each listed finfish species, the behaviour and life-history traits relevant to population genetics (e.g., migration mode, larval dispersal potential, etc., see Table 1), and the corresponding genetic structure information, when available. Not all these life history categories have well defined quantitative thresholds, and we therefore used the following definitions to evaluate attributes for each species: Migration (None = not migratory, Limited = displays some level of migration but too low to be considered migratory per se, Migratory = clear, well-studied migration patterns for foraging or reproduction, Highly Migratory = large intercontinental migrations); Habitat (Pelagic, Benthopelagic, Benthic—as observed and noted in the literature); Distribution (Only continental margin = only one continuous continental margin, beyond continental margin, worldwide—as observed and noted in the literature); Depth Zone (Aphotic, Euphotic, Disphotic—based on the average depth range of adults as observed and noted in the literature); Larval Dispersal Potential (A comprehensive and qualitative evaluation of larval dispersal potential which includes larval pelagic duration, larval type, larvae buoyancy, diel vertical migration behaviour, larval homing behaviour and swimming abilities, as well as observed or modelled advection patterns, based on literature evidence). We used a combination of FishBase, primary literature, and MSC public certification reports to obtain information on the life-history attributes of the species. We then applied a multivariate ordination technique to visualise these data and allow graphical representation in a two-dimensional space. Due to the categorical nature of the life-history variables and to their mutually

Table 1 Ecological attributes relevant to population genetic structure investigated for 70 marine fish species

Ecological attributes	Categories			
Migration	None	Limited	Migratory	Highly migratory
Habitat	Pelagic	Benthopelagic	Benthic	
Distribution	Only CM*	Beyond CM*	Worldwide	
Depth Zone	Aphotic	Euphotic	Disphotic	
Larval Dispersal Potential	Low	High		

*CM = Continental Margin

Table 2 Multiple regression models constructed to identify whether trait combinations affected population structure on the log transformed F_{ST} values

Coverage	Linear model	Variance explained (%)	Adjusted r^2	AIC	AICc
Substantial coverage	**LDP**	23	0.19	70.65	72.25
Substantial coverage	**LDP** + Habitat	23	0.08	74.61	79.22
Substantial coverage	**LDP** + Habitat + **Migration**	61	0.41	67.90	82.30
Substantial coverage	**LDP** + **Habitat** + **Migration** + **Depth Zone**	75	0.54	63.63	91.13
Substantial coverage	**LDP** + Habitat + **Migration** + Depth Zone + Distribution	75	0.43	67.60	119.60
Entire coverage	LDP	0.009	− 0.09	52.60	55.27
Entire coverage	LDP + Habitat	6	− 0.25	55.72	64.30
Entire coverage	LDP + Habitat + Migration	52	0.04	53.12	89.12
Entire coverage	LDP + **Habitat** + **Migration** + **Depth Zone**	94	0.82	30.15	140.15
Entire coverage	LDP + **Habitat** + **Migration** + **Depth Zone** + Distribution	94	0.76	32.03	296.03

Linear models were run separately for studies covering different geographical coverage. LDP stand for Larval Dispersal Potential. If a level was significant for a given factor, that factor is highlighted in bold. Words that are in bold had $p < 0.05$, and words that are in bold underlined had $p < 0.01$. Best fit models can be evaluated based on the maximum adjusted r^2, and on the lowest AIC and corrected AIC values

exclusive nominal levels (Eg. Distribution [Low, Medium, High], Migration level [Low, Medium, High], larval dispersal potential [Low, High]), we used a Multiple Correspondence Analysis (MCA) which is well suited to multilevel categorical, rather than continuous, variables (Abdi and Valentin 2007). For this analysis, we removed species for which life history trait information was missing to avoid missing values bias that could affect species correlations.

To evaluate the effects of life-history traits on population genetic structure, we used genetic structure estimates, i.e., F_{ST} values, as the response variable in our statistical analyses. We only retained marine fish species for which Wright's F_{ST} index values were available with the use of microsatellites or Single Nucleotide Polymorphisms (SNPs). Due to their viviparous reproduction method and to the lack of information available on their early life history, species belonging to the genus *Sebastes* were not included in this analysis. We first used an Analysis of Variance (ANOVA) to test whether the level of genetic structure was significantly different between teleost families. We log-transformed F_{ST} values to meet parametric test assumptions and approach normality, we then computed the homogeneity of variance across groups using Levene's test and the residuals normality using Shapiro–Wilk test. In order to control for some of the elements inherent to such

meta-analysis and that may bias the results, we then used a linear model to test for the effect of marker types and geographical coverage on F_{ST} values before evaluating which attributes might best predict population structure. Marker types did not significantly affect F_{ST} values, but geographical coverage did, with 'substantial coverage' displaying significantly different F_{ST} values than 'entire coverage' (S6). Based on these results and since geographical coverage is not a biological factor but rather an artefact of study methodology and quality, we conducted the rest of the analysis separately for studies that covered the entire distribution of the species and for studies that covered a substantial amount of their distribution. We removed studies that encompassed a regional coverage of a species distribution as we only had data for four of them and as they are less likely to be representative of overall species population structure. Finally, we conducted several linear models to identify whether trait combinations affected population structure on the log transformed F_{ST} values, which allowed for better approximation of normality of F_{ST} values. We then attempted to correct for the selection of over-parametrised models by accounting for the adjusted coefficient of determination and for the Akaike Information Criterion (Table 2). We ran linear models separately for studies covering different geographical coverage, as geographical coverage significantly

affected F_{ST} values whereas marker types did not (Fig. S6).

We performed the MCA analysis using R version 3.6.0 (R Core Development Team 2018) via the FactoMineR (Lê et al. 2008) and factoextra packages (Kassambara and Mundt 2017). We also performed the Linear Models and Generalized Linear Models using R version 3.6.0 (R Core Development Team 2018). We generated the figures using ggplot2 (Wickham 2016) and ggpubr (Kassambara 2020).

Analysis of the secondary sourced stable isotope data

For stable isotope markers, we drew on isotope-enabled global biogeochemical models (Magozzi et al. 2017; Somes et al. 2010) which predict spatial differences in $\delta^{13}C$ and $\delta^{15}N$ values in phytoplankton at global scales. We make an explicit assumption that on average, differences in these 'baseline' values are transferred across food chains, so that baseline model predict differences expected in common tissues of given fish species caught within different fishery areas.

For each species we extracted the model-predicted isotopic compositions of carbon and nitrogen associated for the region of each (MSC) 'fishery area' and also for 'non-certified areas' within the species range. To retain a similar number of values for each test region independent of the geographic extent, we subset these spatially referenced datapoints by taking a random draw of isotope values with the number of extracted values constrained by the number of data points available within the smallest geographical fishery area for each species. To assess the isotopic and statistical difference between possible catch locations we applied linear discriminant analysis with jack-knifed prediction of carbon and nitrogen values, between fishery areas, and between all areas (MSC and non-certified areas) for each species. We carried out all analyses using R version 3.6.0 (R Core Development Team 2018) and using MASS package (Venables and Ripley 2002) for the linear discriminant analyses.

We expressed the ability to accurately assign the extracted values back to the correct fishery area as a red/amber/green traffic light system, based on the discriminant analysis and species attribute data. If the percentage of values accurately assigned back to the correct area fell below 50%, we classified it as "No" (red). If assignment accuracy fell between 50 and 75%, we classified assignment ability as "Maybe" (amber), as assignment accuracy was found to be better than random. If the percentage of accurately assigned values was greater than 75%, but species level migration was classified as highly migratory, we also classified assignment abilities as "Maybe" (amber). On the other hand, if assignment accuracy was greater than 75% and species level migration was classed as none, limited or NA, we classified assignment ability as "Yes" (green), suggesting that there is a strong possibility that stable isotope tools may be useful in this scenario and further assignment studies are recommended. A threshold of 75% assignment accuracy indicating isotopic assignment potential, was based on the assignment results of Trueman et al. (2017), where assignment accuracy was found to be approximately 75% when assigning to precision scales equivalent to fisheries management areas in Northern Europe. If insufficient data were available to carry out discriminant analysis, e.g., only one fishery area, the area is too small, too coastal or isotope data were not modelled within this region and if only carbon or nitrogen data are available and discriminate analysis result is < 75% with only one isotope, we classified the fishery area as "NA" (black). The chosen traffic light system used to classify the relative strength of isotopic methods in verifying provenance of different species and in different areas is arbitrary. A static, simplistic system was used for ease of result presentation and comparison, but it must be recognised that this is a complex and fluid environment, and considerable variability and uncertainty has been ignored for the benefit of a simplistic approach.

Combined Bayesian assignment

We combined genetic and stable isotope assignment methods using a theoretical Bayesian assignment test, to determine the extent to which isotopic discrete assignment to all possible fishery locations could be improved with the addition of genetic assignment results as prior information. All genetic assignment accuracy results from published fisheries case studies were identified and collated (Table 3). Most of the selected studies used SNPs as genetic markers and the Bayesian approach described by Rannala and Mountain (1997) and available in the GeneClass2.0 (Piry et al. 2004) software to estimate assignment accuracy. We stress that all estimates of assignment accuracy are

Table 3 Species for which genetic population assignment studies have been performed between the listed populations, and the associated assignment accuracy to each location

Species	References	Assignment location	Genetic assignment accuracy (%)	Stable isotope assignment accuracy (%)
Atlantic herring (*Clupea harengus*)	Nielsen et al. (2012c)	Barents sea	100	93
		North sea	98	100
	Bekkevold et al. (2015)	Baltic	87	NA
		West Baltic	86	NA
		Barents Sea	98	93
		North Sea	98	100
Atlantic cod (*Gadus morhua*)	Nielsen et al. (2012c)	Barents Sea	100	93
		North Sea	100	100
		Baltic	98	NA
Common sole (*Solea solea*)	Nielsen et al. (2012c)	English Channel	94	25
		Irish & Celtic Seas	92	96
European hake (*Merluccius Merluccius*)	Nielsen et al. (2012c)	Mediterranean	98	99.1
	Milano et al. (2014)	North Sea	90	89.5
		West of UK	90	71.2
European anchovy (*Engraulis encrasicolus*)	Montes et al. (2017)	Biscay offshore	83.3	67.2
		Biscay coastal	93.3	69.2
		Mediterranean	83.3	100
		East Atlantic (UK Shelf)	94.7	11.2
Atlantic Albacore (*Thunnus alalunga*)	Montes et al. (2017)	Mediterranean	90	94.9
		Atlantic	69	67.6
		Indo-Pacific	83.9	69.6
Yellowfin tuna (*Thunnus albacares*)	Grewe et al. (2015)	Baja California	100	65.1
		Tokelau	100	93.7
		Coral Sea	100	89.4
Blue marlin (*Makaira nigricans*)	Sorenson et al. (2013)	Atlantic	94.8	72.0
		Pacific	94.8	66.9

Most of these studies used SNPs as genetic markers except for Sorenson et al. (2013) which used microsatellites and Mitochondrial DNA. Most of these studies used the Bayesian approach described by Rannala and Mountain (1997) and available in the software *GeneClass2.0* except for Milano et al. (2014) and Grewe et al. (2015) which used a combination of other software and probabilistic statistics. Stable isotope assignment accuracy for each listed location, between all listed locations for that species is also reported

vulnerable to over-estimates where samples used to define population characters are selected based on prior expectations of population differences and where the samples used to define population characteristics are drawn from the same sampling efforts as those used to test accuracy of assignment.

For those species where genetic assignment studies have been published, we extracted carbon and nitrogen isotope data from the global models (Magozzi et al. 2017; Somes et al. 2010) within the fishery areas for each species (in some cases fishery areas were divided into smaller units based on genetic population structure studies). We created "model populations" for each area, from which genetic assignment information was also available, by randomly drawing 1000 carbon and nitrogen isotope values from a normal distribution with mean and standard deviation as the mean and standard deviation values of the extracted area. We carried out discrete isotopic assignments, assigning each "individual" from the modelled populations to all the different possible fishery areas for which isotope data were available. We initially performed discrete assignments without prior information, then repeated them including the genetic

assignment probability of an individual to the selected population region as a prior. We carried out all assignment analyses using R packages mvnmle (Gross 2018) and mvtnorm (Genz and Bretz 2009) and using R version 3.6.0 (R Core Development Team 2018).

We selected three species to demonstrate the potential power of combining isotopic and genetic assignment information in a Bayesian framework. We selected these species to represent (1) species for which isotopic assignment and genetic assignment appear equally able to distinguish catch location from an alternative fishing location (Atlantic cod, *Gadus morhua*), (2) species for which genetic assignment prior information improved stable isotope assignment ability (Sole, *Solea solea*), and (3) species for which overall assignment ability improved by combining techniques (Albacore tuna, *Thunnus alalunga*).

Results

Genetic structure

The MCA grouped organisms according to the life-history features they share (Fig. 2, S5). The first two dimensions account for 31.13% of the variation observed. The MCA factor map illustrates an off-centred cluster on dimension 1 composed of several tuna species and the swordfish along with the levels indicating, as expected, highly migratory species with a worldwide distribution. As illustrated by the habitat colour pattern, most pelagic species are found on the positive side of the first dimension whereas most benthic and benthopelagic species are found on the negative side of the first dimension. These species are separated along the second dimension based on their distribution (beyond continental margin, continental margin only), and migration patterns. Thus, species like Atlantic cod (COD), saithe (POK), and Greenland halibut (GHL) are clustered on the positive side of dimension 2 describing species that are benthopelagic, migratory, and distributed beyond the continental margin; whereas several species of sole (LEM, RFE, SOL) and rockfish (RFC, SBC, SGO), are clustered on the negative side of dimension 2 and 1, describing species that display limited migration, preference for benthic habitats, and/or that only occur on the continental margin.

Population genetic structure information was collected for 32 marine fish species belonging to 15 different families. The families that contained the highest number of species were the Clupeidae with six species, the Gadidae with six species, and the Scombridae with four species. An ANOVA indicated that family is a significant factor affecting F_{ST} values (S3). Clupeidae displayed a clustered pattern with relatively and consistently low F_{ST} values (ranging from 0.002 to 0.018), this was also true for Lotidae (ranging from 0.0014 to 0.0061), and aside from one species (*Gadus morhua*, with an overall F_{ST} value of 0.051), all other Gadidae (ranging from 0.015 for Pacific cod, *Gadus macrocephalus* to 0.003 for saithe, *Pollachius virens*). On the other hand, Scombridae displayed a wider range of F_{ST} values (ranging from 0.003 to 0.1).

When focusing on the secondary sourced data from studies that covered a substantial amount of the species distribution, larval dispersal potential significantly affected population genetic structure values in all models. A linear model with larval dispersal potential as a single factor accounting for 23% of the model variance suggests a positive relationship between low larval dispersal and increasing log F_{ST} values. This phenomenon was not observed for the secondary sourced data from studies that covered the entire distribution of the species. The model that best fitted the data for both substantial coverage and entire coverage studies included larval dispersal potential, habitat, migration, and depth zone as explanatory variables but did not include distribution (Table 2). Those best fit models evaluated based on maximum adjusted r^2 and on lowest AIC values indicated that species with low larval dispersal and no-migratory behaviour are likely to exhibit highest log F_{ST} values, corresponding to higher population genetic structure. Pelagic species also had a positive relationship with log F_{ST} values. Depth zone presented some conflictual results suggesting a positive relationship between log F_{ST} values and surface-dwelling habits (disphotic and euphotic zones), for the substantial coverage studies, and negative relationship between log F_{ST} values and a euphotic zone dwelling habitat for entire coverage studies. This model was significant and explained a high proportion of the observed variance for both the substantial coverage and the entire coverage datasets (75% and 94% of the variance explained, respectively) (Table 2). Larval dispersal potential was a significant factor consistently affecting log F_{ST} values from the
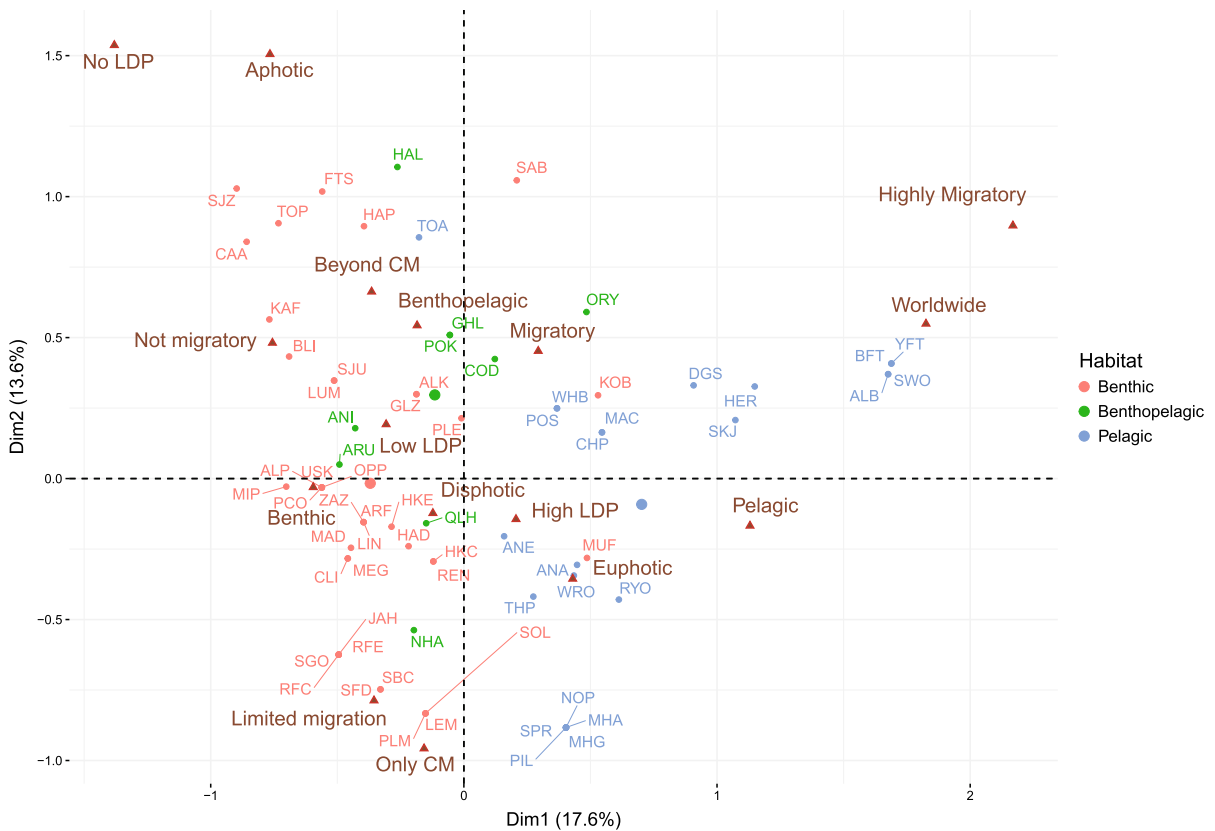
Fig. 2 Projection of the first two dimensions of a Multiple Correspondence Analysis illustrating clusters of fish species based on ecological traits. The three letter codes correspond to 70 different fish species which are listed in S5

substantial coverage dataset, but migratory habits was the variable that had the most consistent relationship with log F_{ST} values across all models and for both coverage datasets.

The interdependence of larval dispersal potential and migration pattern in affecting F_{ST} values is illustrated with Fig. S4 which highlights that some of the specimens with the lowest F_{ST} values amongst low larval dispersal species are also migratory or highly migratory species, whereas specimens with the highest F_{ST} values amongst high larval dispersal species happen to be species that display no or limited migratory behaviours.

Stable isotope approach

Discriminant analysis between MSC certified fisheries, and between MSC certified and non-certified fisheries were carried out for the 63 marine finfish species for which spatial data were available (S2).

Each fishery area (69 different fishery areas) for each species was allocated a traffic light colour categorization (S1 & S2) according to how likely the approach was to work. Where one fishery is MSC certified for the whole area of distribution of a particular species, ability to discriminate between MSC fishery areas was categorized as "NA" as there were no other regions to compare to. A summary of all stable isotope results, organised by species, are displayed in Table 4.

For five (European sprat, sardine, Pacific cod, arrow tooth flounder, sablefish) of the 63 species investigated, all MSC certified fishery areas were distinguishable from all other MSC certified fishery areas with greater than 75% accuracy. For 11 species all MSC certified fishery areas either could or maybe could (> 50% assignment accuracy) be distinguished from all other MSC certified fishery areas (Table 4) (for example, herring, Atlantic cod, and Patagonian toothfish). Looking beyond those fishery areas certified by the MSC, for 18 listed species (for example,

Table 4 Summary of stable isotope discriminant analysis results of 63 MSC certified fish species

Species	Species Common Name	Number of different MSC certified fishery activity areas	Number of fishery areas distinguishable from all other MSC areas				Number of MSC fishery areas distinguishable from all other possible fishery areas			
			Yes	Maybe	No	NA	Yes	Maybe	No	NA
Ammodytes marinus	Lesser sand-eel	2		1 50%	1 50%			1 50%	1 50%	
Anarhichas lupus	Wolffish (Atlantic)	1				1 100%			1 100%	
Anoplopoma fimbria	Sablefish	2	2 100%				1 50%	1 50%		
Argentina silus	Smelt (silver)	1				1 100%		1 100%		
Atheresthes evermanni	Flounder (Kamchatka)	1				1 100%		1 100%		
Atheresthes stomias	Flounder (arrow-tooth)	2	2 100%							2 100%
Brosme brosme	Tusk (=Cusk)	3	1 33%	1 33%	1 33%		1 33%	1 33%	1 33%	
Champsocephalus gunnari	Mackerel icefish	2				2 100%		2 100%		
Clupea harengus	Herring	10	3 30%	2 20%		5 50%	1 10%	1 10%	3 30%	5 50%
Cyclopterus lumpus	Lumpfish (=Lumpsucker)	2	1 50%	1 50%			1 50%	1 50%		
Dissostichus eleginoides	Toothfish (Patagonian)	5	4 80%	1 20%						5 100%
Dissostichus mawsoni	Toothfish (Antarctic)	1				1 100%		1 100%		
Engraulis anchoita	Anchovy (Argentine)	1				1 100%	1 100%			
Engraulis encrasicolus	Anchovy (European)	1				1 100%	1 100%			
Eopsetta jordani	Sole (petrale)	1				1 100%	1 100%			
Gadus chalcogrammus Theragra chalcogramma	Pollock (walleye)	2		2 100%						2 100%
Gadus macrocephalus	Cod (Pacific)	2	2 100%					2 100%		
Gadus morhua	Cod (Atlantic)	3	2 66%	1 33%			1 33%	1 33%	1 33%	
Genypterus blacodes	Ling (Genypterus blacodes)	1				1 100%		1 100%		
Glyptocephalus zachirus	Sole (rex)	1				1 100%		1 100%		
Hippoglossoides elassodon	Sole (flathead)	1				1 100%		1 100%		
Hippoglossus hippoglossus	Halibut (Atlantic)	1				1 100%		1 100%		
Hippoglossus stenolepis	Halibut (Pacific)	1				1 100%	1 100%			
Hoplostethus atlanticus	Orange roughy	1				1 100%			1 100%	
Katsuwonus pelamis	Skipjack Tuna	3		1 33%	2 66%			1 33%	2 66%	
Lepidopsetta bilineata	Sole (Southern rock)	1				1 100%		1 100%		
Lepidopsetta polyxystra	Sole (Northern rock)	1				1 100%		1 100%		
Melanogrammus aeglefinus	Haddock	6	2 33%	1 16%	3 50%		1 16%	1 16%	4 66%	
Merluccius merluccius	Hake (European)	1				1 100%	1 100%			
Merluccius productus	Hake (North Pacific)	1				1 100%	1 100%			
Micromesistius australis	Whiting (southern blue)	1				1 100%		1 100%		
Micromesistius poutassou	Blue Whiting	1				1 100%		1 100%		
Microstomus kitt	Lemon Sole	1				1 100%			1 100%	
Microstomus pacificus	Dover Sole	1				1 100%	1 100%			
Molva dypterygia	Blue Ling	1				1 100%			1 100%	
Molva molva	Ling	4	3 75%		1 25%		1 25%		3 75%	
Mugil cephalus	Mullet (flathead grey)	1				1 100%				1 100%

Table 4 continued

Species	Common name	N								
Ophiodon elongatus	Lingcod	1				1 100%	1 100%			
Opisthonema libertate	Pacific thread herring	1				1 100%	1 100%			
Pleuronectes platessa	European Plaice	3	1 33%	1 33%		1 33%		1 33%	1 33%	1 33%
Pleuronectes quadrituberculatus	Alaskan Plaice	1				1 100%		1 100%		
Pleuronectes vetulus	English Sole	1				1 100%	1 100%			
Pollachius virens	Saithe	10	3 30%	1 10%	3 30%	3 30%	1 10%	3 30%	3 30%	3 30%
Raja rhina	Longnose Skate	1				1 100%	1 100%			
Reinhardtius hippoglossoides	Greenland Halibut	3		1 33%	2 66%				3 100%	
Sardina pilchardus	European Pilchard (Sardine)	1				1 100%		1 100%		
Sardinops sagax	Sardine	2	2 100%					1 50%	1 50%	
Scomber scombrus	Mackerel	1				1 100%		1 100%		
Sebastes diploproa	Splitnose rockfish	1				1 100%	1 100%			
Sebastes entomelas	Widow rockfish	1				1 100%	1 100%			
Sebastes fasciatus	Acadian redfish	2	1 50%	1 50%				1 50%	1 50%	
Sebastes flavidus	Yellowtail rockfish	1				1 100%	1 100%			
Sebastes goodei	Chillipepper rockfish	1				1 100%	1 100%			
Sebastes marinus / Sebastes norvegicus	Golden redfish	1				1 100%			1 100%	
Sebastolobus alascanus	Shortspine Thornyhead	1				1 100%	1 100%			
Sebastolobus altivelis	Longspine Thornyhead	1				1 100%	1 100%			
Solea solea	Sole	3		2 66%	1 33%			2 66%	1 33%	
Sprattus sprattus	European Sprat	2	2 100%				1 50%	1 50%		
Squalus acanthias	Spiny Dogfish	1				1 100%	1 100%			
Thunnus alalunga	Albacore Tuna	2			2 100%				2 100%	
Thunnus albacares	Yellowfin Tuna	3		2 66%	1 33%			2 66%	1 33%	
Trisopterus esmarkii	Norway Pout	1				1 100%		1 100%		
Xiphias gladius	Swordfish	2			2 100%				2 100%	

The number of different MSC certified fishery areas are listed for each species and the number of these regions which could be discriminated from all other possible certified or non-certified stock areas. Ability to discriminate each fishery area is categized into four groups: Yes = > 75% assignment accuracy, Maybe = 50–75% assignment accuracy, No = < 50% assignment accuracy and NA. Those areas listed as NA are where either no isotope data were available or where there was only one MSC certified fishery area or all possible fishery areas fell within MSC certified fishery areas (highlighted in grey), and therefore there were no other regions to discriminate between
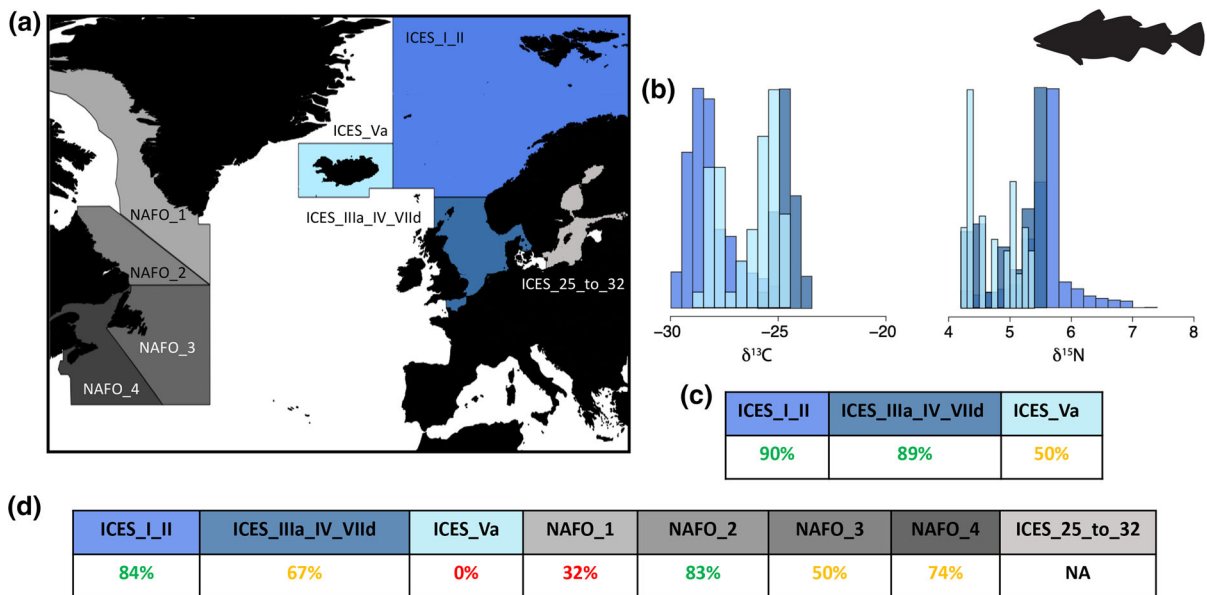
Fig. 3 Fishing activity locations (**a**) for both non MSC certified (grey) and MSC certified (blue) Atlantic cod fisheries, and the associated carbon and nitrogen isotope values (**b**) of the MSC certified fishery areas, extracted from the global carbon and nitrogen mechanistic models (Magozzi et al, 2017; Somes et al 2010). Discriminant analysis was carried out between MSC certified fishery areas (**c**) and between all Atlantic cod fishery areas (**d**) using a subsample of carbon and nitrogen isotope data extracted from each fishery area. Ability to discriminate each fishery area from all other areas is colour coded in a traffic light system where green indicates greater than 75% ability to discriminate the fishery, yellow indicates 50–75% ability to discriminate the fishery location and red indicates less then 50%. No isotope data were available for fishery areas assigned "NA"

European hake, Dover sole, and Pacific halibut), all listed fishery areas were distinguishable (> 75% assignment accuracy) from all other possible stock areas and 35 listed species either could or maybe could (> 50% assignment accuracy) be distinguished from all other possible fishery areas (Table 4). For only 8 listed species (Atlantic wolffish, orange roughy, lemon sole, blue ling, Greenland halibut, Golden redfish, Albacore tun, and swordfish), all listed fishery areas were not distinguishable (< 50% assignment accuracy) from all other fishery areas (Table 4).

One example of the results from the discriminant analysis for Atlantic cod is displayed in Fig. 3. Atlantic cod was chosen as an example species as it has previously been shown to be a successful target species in both genetic (Nielsen et al. 2012b) and stable isotope (Wilson et al., unpublished data demonstrates strong isotopic differences between different biological stocks of Atlantic cod) forensic provenance testing studies, and using the approach discussed here, demonstrates a range of assignment results for different fishery areas. In 2018, at the time the data were obtained, MSC certification was awarded to fisheries

based within the North Sea, Barents Sea and Icelandic waters (Fig. 3a). The average carbon and nitrogen baseline isotopic composition of each of these areas differed with the most notable differences apparent between the North Sea and the Barents Sea (Fig. 3b). Both the North Sea and the Barents Sea were distinguishable from all other MSC certified areas with 89–90% accuracy (Fig. 3c). However Icelandic waters could only be discriminated from the Barents Sea and North Sea 50% of the time (Fig. 3b). When comparing between all Atlantic cod fishery areas on both the eastern and western Atlantic (Fig. 3a), discrimination ability for each certified area decreased (Fig. 3d). Ability to distinguish the Barents Sea and North Sea from all other Atlantic cod fishery areas remained high (84% and 67%, respectively), however ability to distinguish Icelandic fisheries decreased to 0% (Fig. 3d).

Combined approach

Independent genetic population assignment and isotope discrete assignment, for the areas and species

where genetic population assignment studies have previously been carried out are listed in Table 3. For all species listed, genetic provenance tools enabled successful assignment back to true origin with accuracies of 69–100% for all assignment areas. On the whole, assignment accuracies using stable isotope analysis tools were comparable but slightly lower than genetic assignments, with assignment accuracies ranging from greater than 90% accuracy for all fishery areas for herring and Atlantic cod but only 25% assignment accuracy of sole to the English Channel and 11% assignment accuracy of anchovy to the whole UK shelf sea area (Table 3).

For Atlantic cod, stable isotope data could be extracted from three fishery locations (North Sea, Barents Sea and Icelandic waters) whereas genetic population assignment studies had not been carried out with Icelandic stocks but had included populations located within the Baltic (Fig. 4a). When assigning individuals from the North Sea and the Barents Sea, ability to assign to the correct region was relatively high for both stable isotope (93% accuracy to Barents Sea, 100% accuracy to North Sea) and genetic methods independently (100% accuracy to both Barents and North Seas). When combining techniques by adding in a genetic assignment prior probability of 100% to both the North Sea and Barents Sea, absolute assignment ability remained identical, however relative assignment ability to each location improved (Fig. 4a.ii).

For sole, carbon and nitrogen isotope data could be extracted from five fishery locations (North Sea, Bay of Biscay, Northwest Scotland, English Channel and Irish and Celtic Seas), however genetic population assignment studies had only previously been performed between the English Channel and Irish and Celtic Sea populations (Fig. 4b). Initial stable isotope discriminant analysis indicated that populations with Northwest Scotland were likely (> 75% assignment accuracy) to be isotopically distinguishable from all other populations, and populations within the North Sea and Bay of Biscay were "maybe" (> 50% assignment accuracy) distinguishable from all other fishery areas (Fig. 4b). However, populations within the Irish and Celtic Seas, and the English Channel were less likely (< 50% assignment ablity) to be distinguished using a discriminant analysis approach (Fig. 4b). In contrast, genetic population studies between Irish and Celtic, and English Channel sole

Fig. 4 Maps displaying the different fishing activity locations ▶ for Atlantic Cod (*Gadus morhua*) (Ai), Sole (*Solea solea*) (Bi) and Albacore tuna (*Thunnus alalunga*) (Ci) and the ability to accurately assign individuals to each fishery area using only stable isotope analysis and both stable isotope analysis and genetic techniques combined (Aii, Bii, Cii). Fishery areas for which only isotope data are available are coloured in blue, areas for which only genetic assignment results are available are coloured in orange, and areas for which both genetic and isotope information are available, and for which combined Bayesian assignments were carried out, are coloured in green. Genetic and stable isotope assignment results are displayed for each fishery area (Ai,Bi,Ci). For those fishery areas where both isotope and genetic assignment data are available (green), discrete isotopic assignments of 1000 model individuals from these known locations to all locations, were subsequently performed with only stable isotope data (light grey) and both stable isotope and genetic assignment ability (black). The percentage of individuals accurately assigned and misassigned to each fishery area are displayed

populations demonstrated high assignment ability (92% and 94% respectively (Fig. 4b.ii). Discrete isotopic assignment of individuals from the English Channel to all other fishery areas, was relatively poor, with an assignment accuracy of 9.4% (Fig. 4b), with the majority of individuals (76.4%) incorrectly assigned to the Bay of Biscay. When genetic assignment probability was included as prior information, although the absolute assignment probability remained at 9.4%, the relative assignment improved with likelihood of assignment to all other areas decreasing (Fig. 4b) resulting in the highest overall assignment to the English Channel. Discrete assignment ability of individuals from the Irish and Celtic seas including or excluding prior knowledge were found to vary little, with relative assignment ability only slightly increasing when the genetic prior was included (Fig. 4b).

For albacore tuna, isotopic and genetic assignment data were available for three oceanic regions (Atlantic, Pacific and Mediterranean) to distinguish between broad ranging populations (Fig. 4c). Carbon and nitrogen isotope data indicated both the Mediterranean and Pacific populations were distinguishable from all other areas, whereas the Atlantic population had a lower assignment accuracy of 67% (Fig. 4c). Likewise, genetic population assignment accuracy was high for both the Mediterranean (90%) and Pacific (83.9%), but lower for Atlantic populations (69%). Inclusion of genetic prior information into the isotope
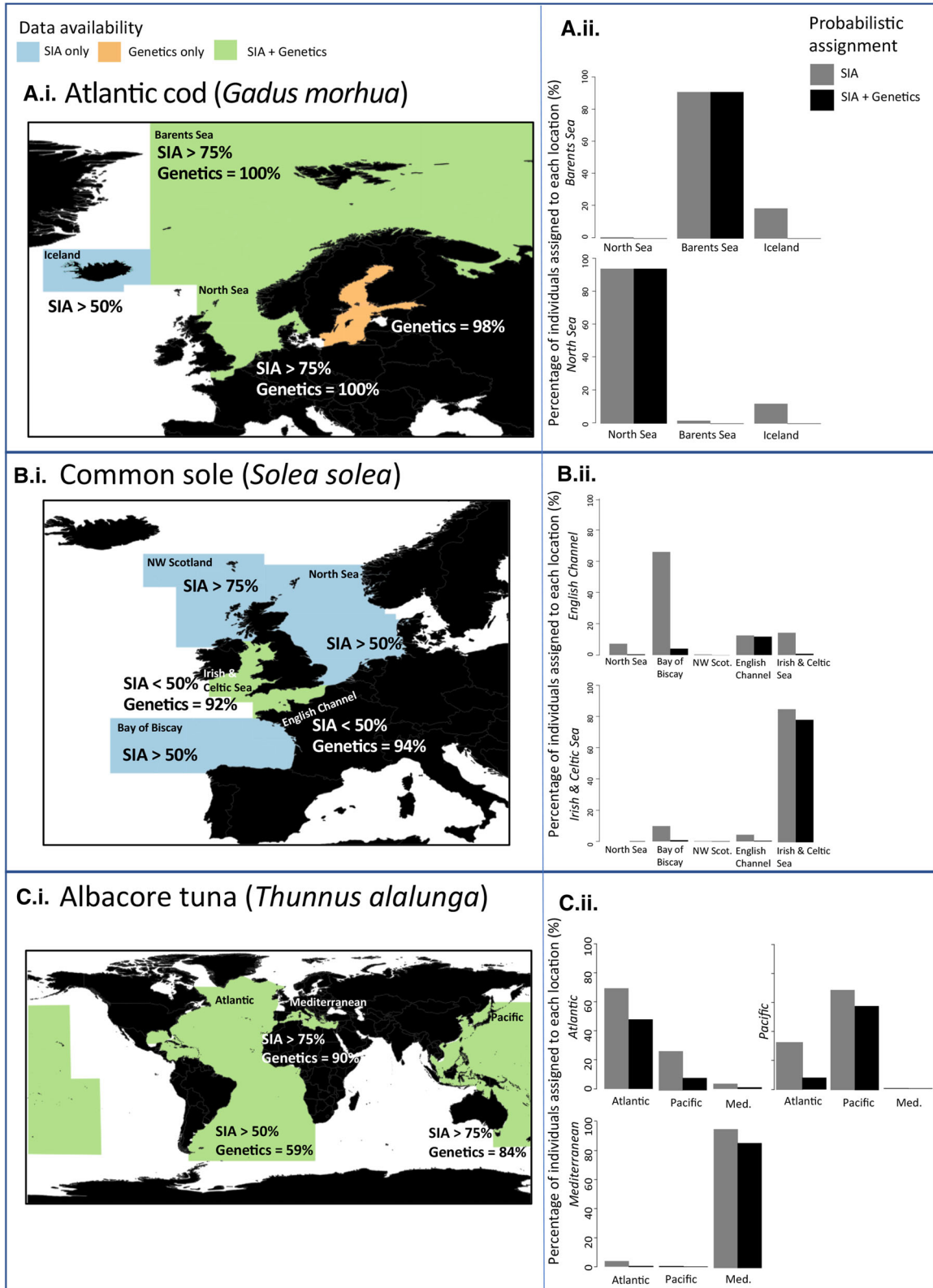
assignment, improved the relative assignment ability of individuals from both the Pacific and Atlantic populations, by decreasing the percentage of incorrect assignments (Fig. 4c). Assignment accuracy to the Mediterranean remained high irrespective of whether genetic prior information was included (Fig. 4c.ii).

Discussion

Both stable isotope and genetic methods effectively determine provenance in at least some species and in some areas (Carrera and Gallardo 2017; FishPopTrace 2013; Kim et al. 2015; Martinsohn et al. 2019; Nielsen et al. 2012a; Rampazzo et al. 2020; Trueman et al. 2017) yet, for both methods, only a limited number of applied verification studies have been carried out, often with some degree of dependency between samples used to define population characteristics and those used to estimate assignment accuracy. Here, we introduce an operational framework to evaluate the species and areas for which it is reasonable to expect that genetic or stable isotope tools will prove useful. Biological traits proved relevant when evaluating species' population genetic structure and could therefore be used to inform when genetic provenance testing tools may be useful. Use of global mechanistic isoscape models appear beneficial in distinguishing which fishery areas are likely to be isotopically distinct, and therefore where isotopic provenance testing tools may be used. In addition, combining genetic and stable isotope tools can, in some cases, increase provenance verification power and decrease misassignment errors. The guidance provided here can also serve the important role of identifying those species or stocks where neither genetic nor isotopic approaches are expected to resolve provenance so that effort is spent on alternative solutions to provenance verification.

Genetic tools

Though it was not possible to estimate the number of species for which genetic analysis would be expected to confidently determine point-of-origin, we identified some traits which seem to affect population genetic structure and should be accounted for in provenance testing. Larval dispersal potential and migration mode could be used to guide expectation to find population genetic structure. Family might be a good predictor of population genetic structure, with some families exhibiting little range in structure levels and others exhibiting a larger range making structure potentially more difficult to predict. These results corroborate some of the observations reported by Bradbury et al. (2008) who noted that genetic differentiation calculated using F_{ST} values varied significantly across a range of higher-order taxa (e.g. polychaetes, crustaceans, echinoderms, teleosts, etc.). Irrespective of family however, identifying clusters of species based on the traits they share (Fig. 2) might help decide whether genetic tools should be further investigated or not for any given species.

Larval dispersal potential was an important factor in determining population genetic structure which contrasts with a number of studies examining pelagic larval duration as a factor (Galarza et al. 2009; Riginos et al. 2011; Weersing and Toonen 2009). This discrepancy might be due to methodological differences in our assessment of larval dispersal potential compared to pelagic larval duration. Based on the assumption that larvae are planktonic and easily advected (Bohonak 1999; Doherty et al. 1995; Waples 1987) larval dispersal potential has previously been defined as the pelagic larval duration of a marine species (Weersing and Toonen 2009). In an attempt to use a more comprehensive early life history trait however, we here not only accounted for larval pelagic duration information when available, but also used a thorough literature review to identify a variety of additional, non-exclusive set of variables such as larval type, larvae buoyancy and diel vertical migration behaviour, larval homing behaviour and swimming abilities, as well as observed or modelled advection patterns. Consequently, while our assessment of larval dispersal potential is a multidimensional, qualitative factor, it accounts for a more comprehensive description of early life-history.

When exploring whether methodological procedures could affect F_{ST} values and add to the variance observed within models we did not find any effect of marker type on F_{ST} values, which has previously been reported (Bradbury et al. 2008; Kinlan and Gaines 2003) though none of the these studies included SNPs in their analysis. Although surprising, given the increasing use of outlying SNP loci for maximising genetic differences, the findings may simply reflect the general tendency to report and publish studies showing

significant population structure, far more frequently than those showing no spatial differentiation. On the other hand, geographical coverage of a given study did affect F_{ST} values, and similar metrics such as biogeography and study distance have also revealed such patterns (Riginos et al. 2011).

The meta-analysis for the DNA-based methods may suffer from biases and inaccuracy resulting from combining over 50 studies to draw inferences on population genetic structure. In the context of population genetic structure, we assume comparability of results between studies, but despite only selecting for studies using microsatellites or SNPs, the number of screened and selected loci as well as the genome coverage varied widely between studies thereby influencing robustness and comparability. Sampling design, overall methodological approaches, and even species type will affect the precision and accuracy of the results and introduce important variances among studies, and we attempted to reduce some of the variance by accounting for marker type and geographical coverage.

When using life-history traits to predict the ability to detect geographical point-of-origin via population genetic structure, no one trait is sufficiently reliable (Bradbury et al. 2008; Galarza et al. 2009; Riginos et al. 2011). Reproductive isolation in marine organisms is not only dictated by a set of diverse species-specific ecological and life-history traits (Chopelet et al. 2009), but also by complex bathymetric and oceanographic conditions that differ between sites, seasons, and years (Selkoe et al. 2008). Despite these complexities, we were able to demonstrate that some traits, particularly larval dispersal potential and migratory habits, have the potential to affect population genetic structure and should be accounted for in studies attempting to use ecological traits to predict point-of-origin. Specifically, species with demonstrably low larval dispersal potential and limited migratory behaviour appear to exhibit the geographic structuring that would make an investment in genetic characterisation worthwhile. It should be noted however that the low F_{ST} values collected for our meta-analysis are not always synonymous with indiscernible population genetic structure and should not necessarily lead to an exclusion of genetics as an effective provenance testing tool. Rapidly developing genomic technologies will likely allow for detection of population genetic sub-structure in most scenarios

(Barth et al. 2019; Bernatchez et al. 2017), as has been documented multiple times with commercially important species such as Atlantic cod (Barth et al. 2019; Johansen et al. 2020; Willette et al. 2014) and with the advent of genome wide assembly, the development of SNP arrays and increasingly performant computational methods. The financial and technical investment for this level of scrutiny however—and its practical application—will likely be outside the scope of routine traceability testing for the majority of commercial species. For the purpose of this study, however, and considering the number of studies accounted for in the analyses presented here, F_{ST} does offer a good estimate of population genetic structure and can provide guidance for the development of operational tools in time- and budget-limited contexts.

Stable isotope tools

For 42% of species investigated within this study, stable isotope analysis tools were predicted to be beneficial for verifying provenance in at least one or more fishery areas. Stable isotope tools worked particularly well for species with limited range size (basin scale), geographically distant, and correspondingly isotopically distant, fishery areas such as Patagonian toothfish, Atlantic cod and Atlantic herring. In this study, we also estimated the performance of stable isotope tools to discrete stock areas of a variety of species. For Atlantic cod and Atlantic herring, assignment accuracies to the Barents and North Sea regions were 93% and 100% respectively. Hake, blue marlin, albacore and yellowfin tuna were also correctly assigned to basin and ocean wide populations with estimated accuracies of greater than 65%. On the whole, isotopic tools deemed less useful for species with ocean scale fishery areas such as the different species of tuna and swordfish, due to the broad range of isotope values from which to distinguish between. Isotope tools are expected to be less effective tools for establishing provenance for those species with numerous potential fishery areas, in comparison to fewer possible catch locations, due to the increased likelihood of similar isotopic ranges.

In the stable isotope approach, we made an explicit simplifying assumption that the isotopic spacing between particulate organic matter and the target species' diet is consistent between regions, and

thereby presumed that any isotopic variability subsequently measured in fish populations originating from these regions was solely due to geographical differences. If individuals are feeding on different prey items but still forage at the same broad trophic level (Cabral 2000), the isotopic spacing will remain relatively consistent across different areas. This assumption may not hold however where species have different diet compositions between fishery areas, where differences in baseline isotopic compositions could be enhanced, reduced or overwhelmed by dietary differences (Goni et al. 2011; Lee and Khan 2000; Ramos and Gonzalez-Solis 2012). Diet is also known to vary within species between juvenile and mature life stages (Cabral 2000; Link and Garrison 2002), however as validation techniques are only designed to distinguish between commercial landings originating from different fishery areas, we argue that all individuals should be bigger than minimum landing size thereby reducing diet variability introduced by small juveniles. The strength of differences between isotopic values of particulate organic matter used to model the global scale isoscapes, between regions may also not be equivalent higher up the food web. Small scale fluctuations in isotopic ratio are dampened with each stage up the food web (MacKenzie et al. 2014; Trueman et al. 2017), meaning strong isotopic differences between fishery areas presented here may not be as clear in higher trophic level fish foraging in these areas. Rapid developments in the use of compound-specific stable isotope methods, targeting essential amino acids that are not influenced by diet are likely to greatly increase confidence in isotope-based geographic assignment (McMahon and Newsome 2019), but at present such methods are too analytically complex and costly to provide viable routine assignment tools. The approach outlined here goes as far as indicating for which fishery areas spatial isotopic differences are likely, providing one piece of the isotopic spacing puzzle. To fully determine isotopic differences among populations originating from different fishery areas, a species-specific assignment study is proposed, as outlined in Fig. 5.

For many of the fishery areas investigated there were insufficient isotope data available using the global isoscape models, as the regions were too coastal or too small, to determine whether they could be distinguished from other fishery areas. In addition, the global isoscapes are modelled at relatively coarse resolutions, ignoring local scale isotopic differences which may be useful in distinguishing between smaller scale neighbouring fisheries. Targeted isotope studies of these regions could reveal additional isotopic differentiation. It must also be noted that the discriminant analysis approach used to classify the isotopic distinctness between regions is highly dependent on the random draw of isotope values selected from the range of isotope values found within the baseline fishery area and is therefore subject to change on each analysis replication.

Using the stable isotope methodology through global scale isoscape models enables comparisons of isotopic differences between all possible fishery areas, and individuals to be assigned to all likely regions of origin. Ability to assign to or discriminate between all possible catch location areas is extremely important because the most likely application will require provenance to be tested against all potential catch locations. Isotopic methods are inherently based on spatial data, enabling the tool to adapt to the specific scale or resolution required for the provenance test, as demonstrated by the ability to use this technique over local or ocean scale areas. However, their utility will still depend on whether areas distantly separated in space are isotopically distinct.

Multi-tool approach

We found potential benefits of including genetic assignment results into discrete isotope assignments in a combined approach across tools. For the three species presented here, Atlantic cod, common sole and albacore tuna, the addition of prior genetic assignment probabilities improved the relative assignment to the correct fishery area in all examples. Although absolute assignment accuracy to the correct fishery area did not improve, the chance of misassignment to the incorrect area decreased. Similar results were observed when combining genetic and chemical markers to assign Atlantic bluefin tuna back to their spawning population of origin (Brophy et al. 2020). The combined technique we describe could therefore prove quite useful for situations where misassignment is likely, due to isotopically similar fishery areas or genetically similar populations of potential origin stocks. In addition, for high value fish species, this combined approach can increase confidence in assignment to the 'true' catch location which was also noted by studies

Fig. 5 Decision tree depicting the recommended steps for selecting the most appropriate testing tool in verifying the provenance of a sample of fish or fish product, and providing considerations to help decide when DNA, stable isotope, or both markers combined are likely to be most effective
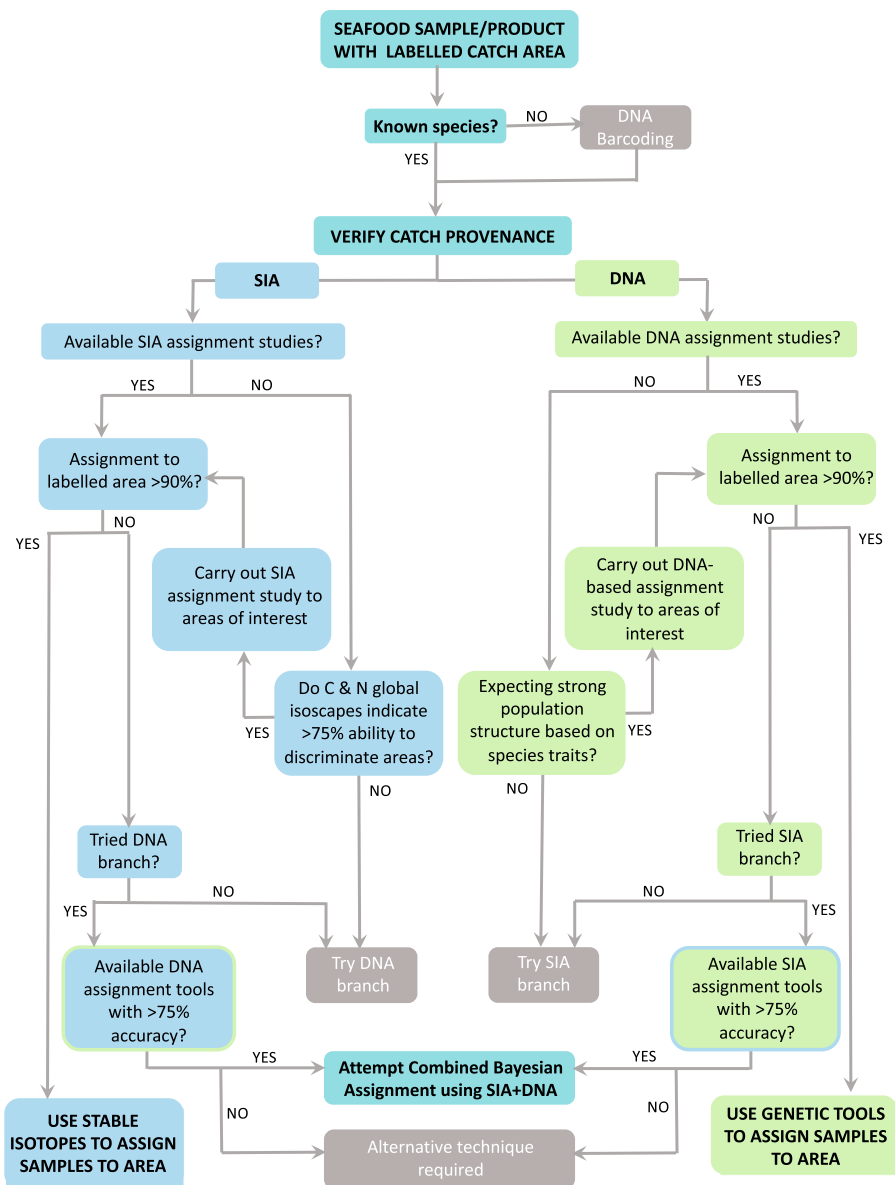
assessing the value of combining genetic and chemical markers on model organisms such as Atlantic bluefin tuna (Brophy et al. 2020), black scabbardfish (Longmore et al. 2014), as well as Hermit Thrush and Wilson's Warbler (Rundel et al. 2013).

Both stable isotope and genetic tools are shown to be effective for provenance testing in some cases. Although, it must also be noted that the lack of reference data, where both isotope and genetic samples have been collected on the same populations in the same areas, prevents direct comparison between the two techniques. Lower assignment accuracies are expected when using continuous (stable isotope) compared to discrete (genetic) approaches as the continuous approach considers the composition of markers in all possible regions whereas discrete assignment compares among a restricted number of a priori identified population centres. Furthermore, the fishery regions presented are commonly defined in terms of presumed fish stocks, which can be expected to favour genetic assignment methods.

Both methods are also subject to temporal fluctuations, with baseline isotope values likely to change over time (St. John Glew and Espinasse, unpublished demonstrates strong seasonal influence on spatial isotope values in the Southern Ocean) which will propagate up the food web, and different population behaviours and movement patterns possibly influencing the genetic structure of a species over time, especially in a context of increased climate-driven changes (Lo Brutto et al. 2011). The accuracy measure of each provenance verification tool is also not sufficiently standardised across studies to be interpreted consistently. As theoretical methods have been explored, in situ data measurements are currently unavailable to calculate true accuracies of assignment to different areas for either techniques or for the combined approach. Therefore, a suggestion that either or both methods may work for a particular species or area, should be taken as a first result for further work. It should also be recognised that for some species and/or between some fishery areas, neither method will work, alone or combined, and for these species, efforts should be focussed on alternative provenance testing techniques. This might be the case for highly migratory species or in the case of genetic techniques, for species with strong larval advection and dispersal.

Roadmap for method selection

Based on the results, we developed a decision tree approach to help guide users in deciding what tool to use when, and whether to invest in further baseline and validation efforts (Fig. 5). For each new sample requiring provenance testing, we propose initially verifying the species using genetic barcoding to ensure species substitution has not occurred. The second critical step is to identify the labelled fishery location, and all other areas or interest or possible locations in which the fish could have been caught. If genetic or isotopic assignment studies have been carried out for the species of interest, covering all likely fishery areas, the genetic profile or stable isotopic ratio of the sample can be compared to existing forensic databases for that species and stated provenance can be either confirmed or disputed. However, to date, assignment studies have not been carried out for many species, and, of those, all likely fishery areas have not yet been compared. Therefore, the next stage of the process would be to

determine if the species is listed within those presented here (S1) and to determine whether the labelled fishery area is isotopically distinct from all other possible fishery areas based on global mechanistic isoscapes, and/or whether the species is likely to have strong population structure.

If the labelled fishery area can be distinguished from all other fishery areas with greater than 75% accuracy, a targeted stable isotope study is proposed where known origin samples of the species of interest are collected and measured across the species range. A threshold of 75% accuracy was determined based on the discrete assignment results of herring fishery areas, with three regions displaying assignment accuracy results of greater than 74% (S2), compared with successful unpublished results from a targeted stable isotope study of herring in the same regions. If a strong population structure is predicted, a targeted genetic assignment study is proposed, where known origin samples are collected from all possible populations. For both methods, known origin test samples should then be measured for their isotopic ratio or genetic profile and assigned to each discrete area or population to measure assignment accuracy. If assignment accuracy to the labelled region is greater than 90%, a full provenance test is proposed. If assignment accuracy is less than 90% for any one method, and the alternative method has also been explored, either a combined genetic and isotopic assignment method or an alternative method is proposed. For application of these techniques into real world scenarios, we recommend that the threshold values be adapted to suit the accuracy requirements of the specific question.

Conclusions

A stark conclusion from this study is the fact that there are very few genetic or isotopic assignment studies available. Exploring the level of population genetic structure between putative populations and determining the range and variation in isotopic ratios between individuals caught within different fishery areas are necessary steps towards evaluating the point-of-origin of a product. However very few studies progress toward estimating the probability with which specimens can be assigned back to their population of origin (Bekkevold et al. 2015; Drinan et al. 2018; Fish-PopTrace 2013; Nielsen et al. 2012a; Trueman et al.

2017; Zhang et al. 2019). Yet certainty around assignment is ultimately what stakeholders and management agencies are seeking. Whereas F_{ST} values can appear vague and variable, and the resolution of global predictive isoscapes can be too coarse, assignment probabilities to reference data on known origin can offer concrete evidence for supply chain provenance verification, especially when these might be associated with court cases and loss of accreditation.

Future users of provenance verification tools, including seafood processors, retailers, government enforcement agencies, and certification bodies will need to invest in bringing these tools to operational readiness and the framework developed here is a first step towards prioritising these efforts. The framework helps to discern whether genetic or isotope tools might be successful in the application at hand, and the option to use a combined approach is also available. However, the increase in verification assurance needs to outweigh the costs involved with carrying out analyses for both genetic and stable isotope markers. Such cost will vary substantially, depending on the organisations faced with them; thus, future multi-stakeholder engagement would be desirable to identify the best strategies to meet such investments, which, in a majority of cases, offer a hardly replaceable step to achieve stock traceability.

While sustainability and ocean conservation concerns rise on international agendas (UN 2019), even with the advancement of digital traceability tools, such as blockchain, independent verification via forensic tools will remain a crucial asset to provide assurance of provenance in global seafood supply chains. To ensure this goal can be realised at the scale needed to support global efforts for sustainable fisheries, advancing the issues presented here could help operationalize provenance testing, so that it will become more widespread, technically feasible and financially accessible.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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