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How Fish Population Genomics Can Promote Sustainable Fisheries: A Road Map

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Abstract

Maintenance of genetic diversity in marine fishes targeted by commercial fishing is a grand challenge for the future. Most of these species are abundant and therefore important for marine ecosystems and food security. Here, we present a road map of how population genomics can promote sustainable fisheries. In these species, the development of reference genomes and whole genome sequencing is key, because genetic differentiation at neutral loci is usually low due to large population sizes and gene flow. First, baseline allele frequencies representing genetically differentiated populations within species must be established. These can then be used to accurately determine the composition of mixed samples, forming the basis for population demographic analysis to inform sustainably set fish quotas. SNP-chip analysis is a cost-effective method for determining baseline allele frequencies and for population identification in mixed samples. Finally, we describe how genetic marker analysis can transform stock identification and management.

1. INTRODUCTION

With an expected world population of ~10 billion people in 2050 (1), the global demand for food is rising, and solutions for a sustainable increase in food production are still debated. Although seafood and marine proteins have a significantly lower carbon footprint and higher nutritional value than terrestrial sources (2), only 17% of human protein consumption is sourced from the oceans, including wild captures and marine aquaculture (mariculture). There is, however, potential to increase this percentage by 36–74% under various scenarios (3), including improved fisheries management. The total world fish production was 112.4 million tonnes in 2019 (4), 82% of which was wild marine captures. Ten species accounted for 21 million tonnes (**Supplemental Table 1**), 82.5% of which originated from biologically sustainable stocks (5). The high proportion of wild captures results from significant improvement in fisheries assessment and management in recent decades, leading to more productive and sustainable fisheries.

Supplemental Material >

However, at least one-third of fish stocks are currently considered overfished (5), which has in some cases led to stock collapses (6, 7). Besides overfishing, ocean ecosystems are negatively affected by habitat degradation, pollution, eutrophication, oxygen depletion, physical disturbance, and climate change (8, 9). From a fisheries perspective, the science-to-management pathway, where fisheries assessment is based on scientific knowledge, feeding into fisheries management with effective enforcement of fishing regulations and policies, improves sustainability (10). Science-based management can lead to the recovery of fish stocks when appropriate policies are implemented in time. In many cases, however, a mismatch occurs between management units and biological units, which can hamper the development and implementation of effective management.

There are two basic assumptions in fish stock assessment: first, that the stock is a closed unit (i.e., there is no immigration or emigration), and second, that the data used in stock assessments represent the entire stock (i.e., catches are not removed from certain components, and survey data are a relative measure of the entire stock throughout its geographical distribution). For this reason, fish stock identification is an essential prerequisite for fisheries stock assessment. However, a fundamental weakness in many stock assessments is the inaccurate recognition, definition, and delineation of stocks for data collection and evaluation. For management units, fisheries managers use the term stock, defined as fish with similar life-history parameters occupying a defined geographical area and being subject to a distinct fishery (11). In contrast, the biological units are populations defined as a reproductive group of individuals showing more or less reproductive isolation from other reproductive groups of the same species (12). A stock may consist of several genetically differentiated populations, and several stocks may also mix in the same geographic area at certain times of the year. Many fish stocks are separated based on simplifying assumptions, which often align with static geographical boundaries, ignoring valid biological units, life stage–specific migration patterns, or distributional changes through responses to a shifting environment. Although delineating stocks by predefined areas may be convenient for management and regulation purposes, accurately assessing the status, biomass, and sustainable exploitation rates of stocks without knowing their biological composition can result in erroneous predictions of stock dynamics and lead to overexploitation (13, 14).

We can define the appropriate level for assessment and management units by identifying the population structure of fisheries resources. However, the paradigm of static geographic management units has often been challenged, and dynamic spatial structure and boundaries have been proposed as a more appropriate framework for stock assessment and fisheries management (15). This would constitute a major paradigm shift in fisheries assessment and may be feasible mainly through case-by-case, incremental changes (15). Such real-time assessment and management have

rarely been implemented, due to the lack of appropriate tools for identifying population structure and assigning individuals in mixed survey and commercial catches to the population or assessment unit to which they belong.

Accurate definitions of populations of marine fish have been challenging due to gene flow homogenizing divergence at neutral genetic markers, but this can now be overcome through genomics (16, 17). Particularly, whole genome sequencing allows accurate estimation of population structure and identification of informative genetic markers to distinguish populations. We aim to highlight how fisheries assessment and management can benefit from modern genomic tools. **Figure 1** illustrates a road map of the steps needed to take full advantage of whole genome sequencing. At present, the implementation of this approach is far advanced for the Atlantic herring, which, therefore, is of particular focus. However, we also exemplify genomic studies in other marine fishes and propose how the outlined road map could be implemented for a broad range of commercially exploited marine organisms.

2. WHY WHOLE GENOME SEQUENCING IS NEEDED

Marine fish targeted for commercial fishing usually have huge population sizes relative to many terrestrial vertebrates. Such populations undergo limited genetic drift, resulting in low genetic differentiation at neutral markers between different populations within species, unless they are closely linked to sequence variants under selection. Therefore, small sets of neutral markers usually have low power for defining populations and managing marine species stocks. A prime example is Atlantic herring, in which an early study based on 13 polymorphic allozyme loci and population samples from the Baltic Sea, North Sea, and Northeast Atlantic Ocean failed to detect any genetic differentiation (18). Further, in a recent study, 169,394 presumed neutral single-nucleotide polymorphisms (SNPs) across the genome failed to distinguish two of the major populations, the North Sea autumn-spawning herring and the Norwegian spring-spawning herring, which can be clearly distinguished by fewer than 10 SNPs in genomic regions underlying timing of reproduction (19). The decreasing cost of whole genome sequencing makes it possible to query the entire genome in hundreds if not thousands of samples for markers that differ between genetically distinct populations, an approach that provides the greatest power for distinguishing populations. Even reduced-representation sequencing methods, such as RAD-seq (restriction site–associated DNA sequencing) (20), which can generate data on more than 100,000 SNPs, may fail to reveal genetic differentiation if the genomic regions showing differentiation are few and/or small in size.

Whole genome sequencing of many individuals or pools of individuals using short reads requires the existence of an annotated reference genome sequence, which is used as a backbone for aligning the short reads and calling sequence polymorphisms (**Figure 1*a*,*b***). In the last five years, the assembly of high-quality, chromosome-level reference genomes has become feasible due to improvements in genomic techniques such as (*a*) long-read sequencing (PacBio or Oxford Nanopore), (*b*) in situ HiC (21) to determine the linear order of sequences on chromosomes, and (*c*) powerful bioinformatic methods. Gene annotations can be derived from RNA sequencing. The inclusion of ultralong nanopore reads facilitates the construction of telomere-to-telomere assemblies (22). However, highly ordered assemblies are not needed to detect regions showing genetic differentiation but are crucial for interpreting patterns of differentiation across populations. In an assembly composed of thousands of unordered chromosome fragments (i.e., contigs or scaffolds), the number of independent regions showing genetic differentiation cannot be determined accurately, because such regions may be split over different chromosome fragments. This is particularly true for inversions, regions where a chromosome segment has flipped orientation.

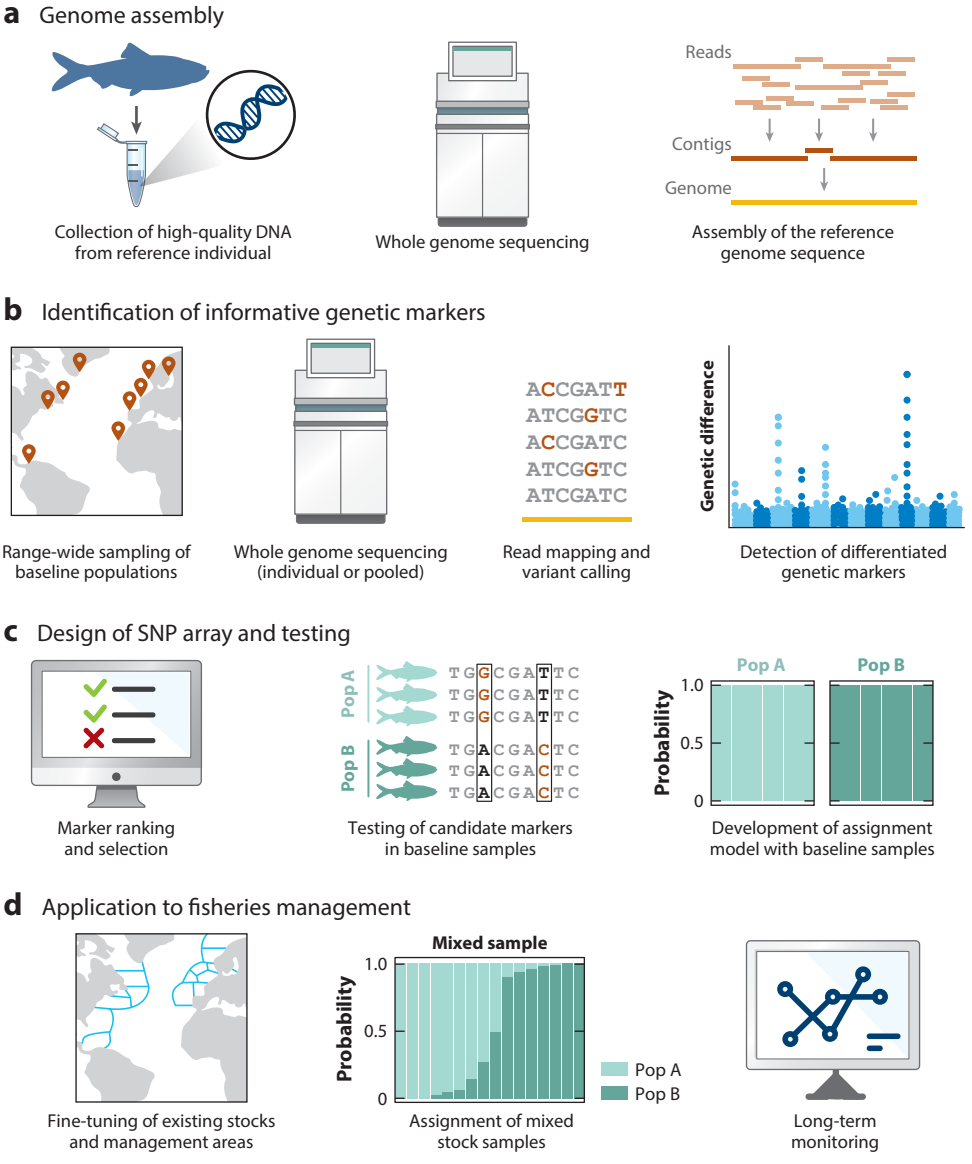

Figure 1

Road map for implementing whole genome sequencing to support stock assessment and management. This involves four phases: (*a*) establishment of a high-quality genome assembly for the target species; (*b*) collection of baseline samples (preferably from spawning fish) from the species distribution and identification of informative genetic markers by whole genome sequencing; (*c*) genetic analysis of population structure and identification of the most informative loci for population differentiation; establishment of suitable genotyping method; and (*d*) implementation of genetic marker information in stock assessment and management. Abbreviation: SNP, single-nucleotide polymorphism.

These can be several megabase pairs long and overlap hundreds of genes. Inversions suppress recombination, and recent data indicate their frequent association with ecological adaptation (19, 23, 24). The major advance with chromosome-level assemblies is illustrated by the notable improvement in our understanding of the Atlantic herring genome when the initial assembly,

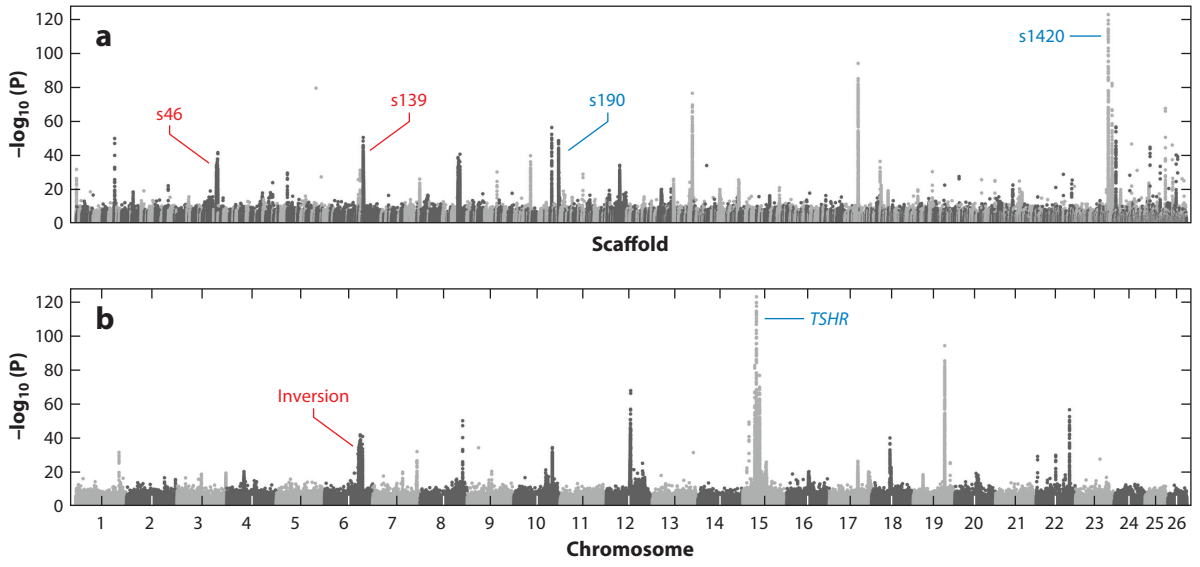

Figure 2

Allele frequency contrasts between spring- and autumn-spawning Atlantic herring. (*a*) Data plotted using assembly version 1.2 (GCA_000966335.1). The scaffolds highlighted in red (s46 and s139) harbor disjointed pieces of an inversion on chromosome 6, whereas the scaffolds highlighted in blue (s1420 and s190) harbor disjointed pieces of the *TSHR* locus [based on data from Martinez Barrio et al. (31)]. (*b*) The same data set, plotted on assembly version 2.0.2 (GCA_900700415.1). Red and blue callouts mark the two regions corresponding to the scaffolds highlighted in the same color in panel *a* [based on data from Pettersson et al. (25)].

based on short-read sequencing, was replaced with a chromosome-level assembly based on PacBio long-read and HiC sequencing (25) (**Figure 2**).

Next, a collection of baseline samples should be established, preferably representing all major spawning locations to capture the main reproductive units (**Figure 1*b***). These samples are then subjected to whole genome sequencing, obtaining information either for individual fish or for a pool of DNA from a representative number of individuals, usually 30 or more. Pooled DNA sequencing (pool-seq) is a cost-effective approach to determine allele frequencies and has been used successfully, for instance, in Atlantic herring (19). However, a drawback of pool-seq is that individual information is lost, and thus, one cannot test if a pooled sample contains a mix of genetically distinct populations. In that case, the estimated allele frequencies are not representative of any single population. An improved strategy is to carry out individual, low-coverage sequencing (for instance 1× coverage; i.e., if the genome is 1 Gbp long, 1 Gbp sequence should be generated per individual), which provides accurate population allele frequencies and can detect genetic heterogeneity but does not give confident individual genotype calls (26). To generate accurate individual genotypes, one must perform individual sequencing to medium-high coverage (10× or higher). This is more expensive but can be done on a subset of individuals representing different populations identified by pooled or low-pass sequencing. Whole genome sequencing will result in the detection of informative SNP markers that can be genotyped in a larger set of baseline samples, including temporal replicates, to distinguish all populations of interest and to develop a baseline data set for assignment modeling. Finally, the method is cross-validated, and an optimal genotyping assay that can be robustly typed and used to classify individuals of unknown population origin is established, as described below (**Figure 1*c***).

3. WHAT WE HAVE LEARNED FROM WHOLE GENOME SEQUENCING OF MARINE FISH

Supplemental Material >

In this section, we review examples of progress made toward accomplishing the steps outlined in **Figure 1**. In addition to these examples, **Supplemental Table 2** provides a more comprehensive list of population genomic studies in marine fishes of importance for food production.

3.1. The Atlantic Herring: Extensive Genetic Differentiation

The Atlantic herring (*Clupea harengus*) is restricted to the North Atlantic, Barents Sea, and Baltic Sea and plays a key ecological role as the link between plankton production and carnivorous fish, seabirds, and marine mammals feeding on different herring life stages. Atlantic herring is also crucial for human sustenance; it has been one of the top 10 most commercially harvested fish for hundreds of years, with a peak harvest of more than 4 million tonnes per year during the 1960s. Therefore, the Atlantic herring has been critical for food security in Northern Europe, likely since humans settled after the last glaciation (27). In more recent times, it has been heralded as a maker of nations, as it, e.g., provided the economic basis for Iceland to claim independence from Denmark in 1944.

More than 40 years ago, initial work to explore the genetic structure of herring populations using a small number of allozyme markers revealed no genetic differentiation, even among geographically distant populations (18, 28). As the number of markers was increased in subsequent studies, patterns of genetic differentiation emerged (29). However, only with whole genome sequencing and a reference genome (19, 30, 31) could the pattern of strong genetic differentiation between populations be identified. These data revealed that genetic differentiation in Atlantic herring is concentrated in genomic regions underlying ecological adaptation, while gene flow homogenizes allele frequencies at selectively neutral loci. Atlantic herring populations hence appear to comprise distinct ecotypes adapted to different environmental conditions and reproductive strategies.

Han et al. (19) identified seven major groups of herring based on whole genome sequencing of 53 population samples that broadly represent the entire species distribution (**Figure 3**). One major subdivision is seen between populations spawning in fully marine salinity environments [35–36 PSU (practical salinity units)] versus in brackish waters. Under the most extreme brackish conditions of the Baltic Sea's inner Gulf of Bothnia, salinity drops to 2–3 PSU yet still supports herring spawning sites. Clear genetic differentiation is also observed between populations spawning under relatively warmer versus colder water temperatures. For instance, genetic differentiation of herring spawning in the relatively warm waters surrounding Ireland and Britain and herring spawning in colder waters is concentrated in four megabase pair–long inversions on chromosomes 6, 12, 17, and 23 (19). Finally, an important genetic differentiation is related to spawning at different times of the year (19, 32).

The lack of genetic differentiation at selectively neutral loci facilitates the identification of genomic regions as well as candidate genes important for ecological adaptation. Hundreds of loci show strong genetic differentiation between herring in the Atlantic and Baltic Sea (19). Some of these are driven by adaptation to the low salinity in the Baltic Sea. Particularly strong candidate genes include *LRRC8C*, encoding an isoform of volume-regulated anion channel, and *PRLR*, encoding the prolactin receptor (19). Expansion into the Baltic Sea also required adaptation to the local red-shifted light environment, an adaptation facilitated by a missense mutation, Phe261Tyr, in *rhodopsin* (33). These results suggest that adaptation to the Baltic Sea after the last glaciation involved standing genetic variation, because many strongly differentiated genetic variants are also shared with other populations outside the Baltic, but also in some cases novel variants, such as the *rhodopsin* mutation—likely a de novo mutation that has gone through a strong selective sweep (33).

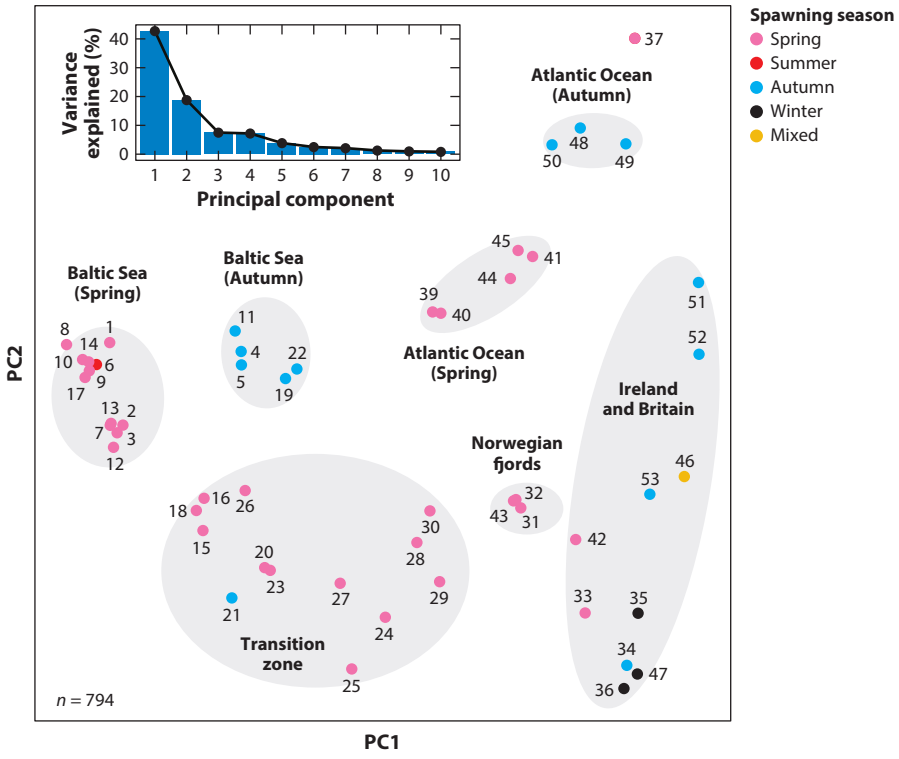

Figure 3

Population structure of Atlantic herring based on whole genome sequencing. Results of principal component (PC) analysis using 794 highly informative markers showing strong genetic differentiation among populations. The color of each population represents the spawning season, as indicated to the right. The inset bar plot indicates each principal component's explained variance percentage. n = number of SNPs used in the analysis. Figure adapted from Han et al. (19).

The number of loci showing strong genetic differentiation between spring-spawning and autumn-spawning ecotypes is considerably less than that of loci differentiating Atlantic and Baltic herring. Genes showing the most consistent association with spawning time are found on chromosomes 8, 12, 15, and 19 (19) (**Figure 2*b***). A striking feature of these associations is haplotype sharing among geographically distant populations (32). For instance, haplotypes associated with autumn spawning in the Baltic Sea are closely related to autumn-spawning haplotypes in the Northwest Atlantic Ocean. The strongest association with spawning time is observed in a 3-Mbp region on chromosome 15 that includes candidate genes with a well-established role in reproductive biology: *TSHR* (*thyroid-stimulating hormone receptor*), *SOX11B* (a transcription factor in the SOX family), *CALM1B* (*calmodulin 1B*), and *ESR2A* (*estrogen receptor 2A*) (19).

These studies suggest that Atlantic herring has a rich toolbox of gene variants, allowing it to colonize starkly different environmental conditions and evolve variation in spawning, migratory, and feeding behaviors. It is also clear that the population structure of the Atlantic herring is far more complex than is currently accounted for in stock assessment and management.

3.2. The European Sardine: Another Clupeid of Major Economic Importance

The European sardine (*Sardina pilchardus*) is subject to an important fishery in Southern Europe and North Africa, representing the world's ninth most significant commercial fishery, based on

total harvest, in 2019 (**Supplemental Table 1**). This abundant clupeid occurs from the Mediterranean Sea in the east to the Azores in the west and from the Northeast Atlantic in the north to Senegal in the south. Early population genetic studies based on microsatellites and allozymes revealed some but limited population structure (34). This was confirmed in a recent study based on whole genome sequencing of 108 individuals from 17 locations representing a large part of the species' geographic distribution, which revealed only three major populations (35). The data suggest that the European sardine does not show the same level of population differentiation as Atlantic herring (see **Figure 3**).

3.3. The Atlantic Horse Mackerel: Widely Distributed but Low Levels of Genetic Differentiation

The Atlantic horse mackerel (*Trachurus trachurus*) is a schooling fish and one of the most widely distributed species in the eastern Atlantic Ocean, occurring in coastal and offshore waters from Norway to southern Africa and in the Mediterranean Sea (36). Like herring, horse mackerel perform long-distance annual migrations between spawning, feeding, and wintering areas (37). Unlike herring, however, horse mackerel are pelagic spawners, and whether they exhibit spawning site fidelity is unknown. This species is the target of an important marine fishery, and there is therefore a strong need to characterize the population structure for assessment and management purposes. Previous studies based on mitochondrial DNA and microsatellite markers gave inconclusive results regarding population structure (38).

Recently, a whole genome pooled sequencing study addressed this knowledge gap (24) by examining the genetic variation of samples collected from the North Sea to North Africa and the western Mediterranean Sea. The study revealed low genome-wide genetic differentiation between samples distributed across this vast geographic area, compared with the structure found in Atlantic herring (19), but high differentiation at a few putatively adaptive loci. The single sample from the Mediterranean Sea was genetically differentiated from all Atlantic populations. Among the Atlantic locations, the North Sea samples were the most distinct, and a split was supported by clear genetic differentiation at multiple genomic loci. A putative 9.9-Mbp-long chromosomal inversion underlines a latitudinal pattern that distinguished samples north and south of central Portuguese waters. Interestingly, the presumed location of the genetic break coincides with an East Atlantic biogeographic transition zone also observed in other marine organisms in central Portugal, near Lisbon (~38.7–39.0°N) (39). Genome–environment associations indicated that genetic variation in the inversion is strongly associated with variation in seawater temperature/oxygen concentration or associated parameters. The study supports the existence of at least three populations of horse mackerel in the Northeast Atlantic and the Mediterranean Sea. Stock delineation and identification of potential mixing between stocks outside the reproductive season remain to be tested, but the tools to undertake these analyses are now available.

3.4. Atlantic Cod: Adaptive Supergenes and Fisheries-Induced Evolution

In Atlantic cod (*Gadus morhua*), like in Atlantic herring, neutral genetic markers tend to reveal only weak population differentiation, whereas strong divergence is encountered at loci under selection in relation to environmental variables such as temperature, salinity, and oxygen (40–46). In particular, divergence among populations seems to be driven by four large-scale inversions in linkage groups 1, 2, 7, and 12 (23, 41–44). Initial studies using SNP-chip data combined with limited genomic data suggested the existence of such rearrangements, linking them to divergence between migratory versus stationary or coastal versus offshore ecotypes (41–44, 47, 48). A recent study confirmed the existence of these four inversions using long-read sequencing data. The study showed that the inversions originated after the split of Atlantic cod from their closest relatives and

that they have likely been important for divergence among cod ecotypes for millions of years (23, 49). These inversion polymorphisms may be favorable for the rapid adaptation of cod populations to climate change; thus, management policies could include efforts toward maintaining sufficient frequencies of these polymorphisms at levels that would allow future adaptation.

Time-series population genomic studies of Atlantic cod have been used to detect the impact of overexploitation of marine fish stocks. In the latter half of the twentieth century, several populations suffered severe decline, resulting in a reduction of age and size at maturity (50, 51). Pinsky et al. (52) used genomics to compare genetic diversity and effective population size of Atlantic cod before and after these stock crashes, revealing stable levels of both parameters. Although this apparent stability in Canadian populations had been documented using microsatellites (51), the genomic study covered Eastern and Western Atlantic populations and allowed a more confident estimation of shifts in effective population sizes. Genomic data further allowed the investigation of signatures of fisheries-induced selection on these wild populations. Contrary to expectations from captive experiments (e.g., 53), this study did not find signatures of selection that could be linked to fishing-induced phenotypic changes, such as age and size at maturation. Recent studies thus suggest that fisheries' most concerning impact is reducing population abundances rather than inducing strong selective pressures (52, 54). Some cod stocks are currently managed using genetic marker information built on whole genome sequencing (55–57). In other areas, there is clear scope for implementing the approach, e.g., cod populations mixing in the North Sea and adjacent areas (58).

3.5. The European Eel (*Anguilla anguilla*): A Single Panmictic Population

Adult European eels have a remarkable distribution spanning contrasting environmental conditions, from north of the polar circle to North Africa and from the mid-Atlantic Azores islands in the west to the Black Sea in the east. However, the species has only one common spawning ground: the Sargasso Sea (59, 60). This implies a complex life cycle, with successful reproduction only after several life stage transitions and two Atlantic crossings. The larval stages, in particular, have been a long-standing mystery that has been understood only recently (61–63).

The intriguing life history of eels, combined with a dramatic population decline over the past three decades that has rendered it Critically Endangered (64), together with its noticeable cultural and economic importance have resulted in substantial research interest, including several studies examining the population structure of this species. Several efforts using low-density markers and reduced-representation sequencing have indicated that the European eel is a single panmictic population (65, 66). However, given that low-density genome-wide screens provide limited genomic coverage, and therefore could fail to detect differentiated regions (see, e.g., Atlantic cod and Atlantic herring above), evidence for the European eel as a single, panmictic population would later be confirmed using whole genome sequencing (67). Including samples from the Baltic, Atlantic, and Mediterranean, this study corroborated lack of genetic differentiation across individuals inhabiting geographically widely separated feeding grounds. Spawning, fertilization, and early development are the most vulnerable stages of the marine fish life cycle (68), suggesting that the European eel's success, despite its low population structure, is tied to its single spawning environment, which provides stable conditions in early development. The single spawning ground then results in a lack of genetic adaptation to local environmental conditions; however, it also implies that adult eels can cope with a wide range of environmental conditions through phenotypic plasticity.

This result has several implications for fisheries management. For more than the past two decades, the scientific advice has been to keep fisheries at "the lowest possible level," and in 2021, it was extended to advise a complete fisheries moratorium (69). A full fishing stop is not implemented

currently, and the adopted management plans instead include a suite of actions aimed to increase survival to adult stage, including local fishing restrictions and restocking by transplanting juvenile glass eels across European habitats. Here, the genetic data imply that the total sum of management actions on a species level, rather than local conservation initiatives in themselves, affects local stock dynamics.

4. HOW GENOMICS CAN CONTRIBUTE TO SUSTAINABLE FISHERY

By defining the population structure of fisheries resources, we can define the appropriate level at which to aggregate or segregate data used for fisheries assessment and to define appropriate management areas. A central aim is the ability to assign population origins of individuals in mixed-stock commercial catches and scientific surveys to ensure the validity of data for inclusion in stock assessments (**Figure 1*d***). To accomplish this, one needs to collect representative samples of individual populations, establish baseline allele frequencies from such populations, and establish cost-effective genotyping methods to screen informative SNPs. Although whole genome sequencing is the method of choice for identifying the most informative genetic markers, it is still too costly to generate accurate genotype calls for many thousands of individuals.

4.1. Efficient Data Collection Strategies

The collection of fisheries data, including biological, environmental, and socioeconomic data, is complex, as national, international, and interjurisdictional collaboration and coordination are needed to ensure effective data collection and curation. Such regional coordination is essential for agreeing on standard procedures and methods for sampling, quality control, and analysis. The analysis of these data and delivery of fisheries catch advice are coordinated primarily through intergovernmental marine science organizations, e.g., the International Council for the Exploration of the Sea (ICES) in the North Atlantic region, meeting societal needs for impartial evidence on the state and sustainable use of our seas and oceans. Many factors must be considered when determining efficient and appropriate sampling strategies to implement genomic-based approaches in fisheries data collection. For instance, different sequencing, genotyping, and analytical approaches can use varying levels of sample quality. However, sampling strategies must not only consider the specific requirements of the genetic analyses but also fit within existing fisheries data collection programs to be widely adopted and implemented. Therefore, development of a standardized approach that can be incorporated easily into existing data collection programs to facilitate large-scale, population-level sampling of fisheries resources is prudent.

Tissue collection for DNA analysis from numerous samples onboard a vessel at sea can be logistically challenging and time consuming. In addition to sample quality issues, there is risk of sample cross-contamination, particularly when access to sterile sampling tools and workstations is limited (70). These issues can be mitigated by implementing simple preparatory steps, but it can be difficult to ensure consistent application through time or to change existing sampling protocols. One solution is to adopt specialized sampling tools that simplify the process and ensure consistency in tissue collection. Examples of such tools are the gene tag tool (71), the Biomark Tissue Sampling Unit (72), and the LVL Technologies Genetic Sampling Tool (73). These presterilized, single-use biopsy tools can take an internal tissue sample without surface contamination and facilitate its transfer to a prelabeled, suitable storage receptacle. These tools are commercially available and can be used to streamline sample collections at sea.

Once a standard sample collection method is established, specific protocols can be tailored to the species, stock, and sample source (e.g., survey or commercial vessels, market sampling). The species and specific stock identification issues will dictate the approach required and the level and intensity of sampling needed.

4.2. Genotyping Methods: Multispecies SNP-Chip, a Cost-Effective Diagnostic Tool for Fish Population Genomics

Several methods can be used for SNP genotyping, and the optimal method depends on the number of samples (fish) required for data collection and markers needed either for stock identification or to address specific research questions. For instance, in a recent study of Atlantic herring from the North Sea and Baltic Sea, a modest panel of 59 SNPs, carefully selected based on previous whole genome sequencing (19), was genotyped using the Fluidigm system and used successfully for mixed stock analysis (74). The reason such a relatively small number of markers may suffice is the strong genetic differentiation between populations for loci of critical importance for ecological adaptation in this species (19). However, a disadvantage with such a modest SNP panel is that it may not be optimal across the species distribution, which means that different panels must be applied in different geographic areas. Furthermore, the data on Atlantic herring have demonstrated that many adaptive loci are characterized by long haplotype blocks containing SNP markers spread over hundreds of kilobase or megabase pairs, as is the case for inversions (19). Despite appearing redundant, genotyping a cluster of SNPs within these loci enables deduction of haplotypes with great confidence and even detection of recombinant haplotypes that may be characteristic for certain populations.

At present, the most robust and cost-effective method for genotyping thousands of SNPs in thousands of samples is SNP-chip analysis. This approach has been used in huge numbers of human genetic studies, often targeting a million SNPs. SNP-chip analysis is most cost effective when the number of genotyped samples is large (>10,000), as the initial cost for designing and producing the array can be offset by running many assays. This cost trade-off has prohibited wide adoption of SNP-chip analysis in fish genomics because the sample volumes have not been large enough. However, to enable this possibility, a team led by one of the coauthors (L.A.) and in partnership with Identigen Ltd. (Dublin, Ireland) developed a MultiFishSNPChip_1.0 array containing 3,000–4,000 SNPs per species. The species included are Atlantic herring (*C. harengus*), European sprat (*Sprattus sprattus*), Atlantic horse mackerel (*T. trachurus*), brown trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*), European perch (*Perca fluviatilis*), and Atlantic cod (*G. morhua*). The SNPs included on the chip were carefully selected to include those that, based on previous data, were indicated to show genetic differentiation between populations. In addition, sets of random markers were also included. The same array is thus used across species, but only data generated for the species in question are considered in the bioinformatic analysis. For most applications in fish genomics, a few thousand carefully selected genetic markers are enough for research or stock assignment purposes, as illustrated by two recent studies using fewer than 100 SNPs for accurate stock identification directly applicable to stock assessment (74, 75).

Validation and analysis of the MultiFishSNPChip_1.0 array are ongoing. Early findings from use of the SNP-chip in Atlantic herring show that the array is scalable and has strong discriminatory power to distinguish known populations. A pilot study of only 20 samples from different locations in the North Atlantic revealed robust individual classification to their population of origin (**Figure 4*a***), and an association analysis detected several of the major loci controlling spawning time (**Figure 4*b***). Although these results are promising, further technological and methodological development are required to harness the full potential of the MultiFishSNPChip_1.0 array. Below, we discuss potential areas for advancement within the context of Atlantic herring; however, we note that similar challenges will likely emerge when developing analysis frameworks for other species.

Because whole genome sequencing technologies have only recently been more widely adopted in marine fishes, genetic resources to fully resolve and classify individual populations remain underdeveloped. SNP-chip analysis provides a means to establish baseline reference populations by

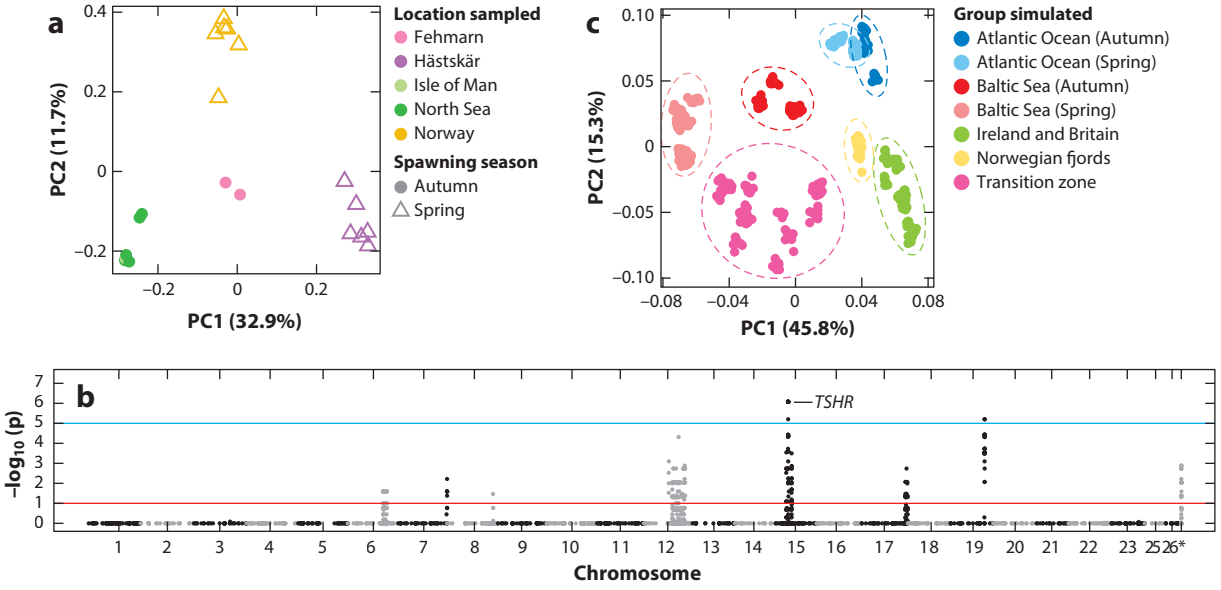

Figure 4

Summary of pilot analysis using the MultiFishSNPChip_1.0 array in Atlantic herring. (*a*) Principal component (PC) analysis of 20 individuals sampled from the North Atlantic and Baltic Sea, using 4,355 single-nucleotide polymorphisms (SNPs). (*b*) Manhattan plot highlighting significant SNPs in a comparison of spring and autumn spawners, from the same 20 individuals. Associations are detected across multiple chromosomes previously associated with the control of spawning time including chromosomes 12, 15, and 19, with the *TSHR* region displaying the strongest association. Asterisks indicate unplaced scaffolds. Chromosome 24 is missing due to lack of informative SNPs. (*c*) PC analysis of all MultiFishSNPChip_1.0 array-specific loci, simulated from pooled DNA sequencing allele frequency data for 53 North Atlantic and Baltic Sea sites. Groups simulated correspond to the seven primary population clusters described by Han et al. (19).

enhancing the comparability of findings among institutions and facilitating the merger of data from different studies. However, the capacity to discriminate between populations showing genetic differentiation depends on the size of the initial reference population, with larger sample sizes improving discrimination capacity because allele frequencies are determined more accurately. When sample sizes are limited, such data can be simulated from existing whole genome–derived population data and used as references to assign individuals to their population of origin. For example, simulation of individual genotypes at all array-specific loci using pool-seq allele frequency data (19) recovered all seven described primary population clusters (J. Goodall et al., unpublished data) (**Figure 4*c***). When used as baseline reference samples (53 sites across the North Atlantic and the Baltic Sea), simulated data showed high assignment confidence (greater than 90%) using both simulated and non-simulated samples (J. Goodall et al., unpublished data). Although simulated data can expand the sources of temporal and geographic data, they are ultimately supplemental, with the comprehensive sampling of wild populations remaining the preferred approach. Moreover, ensuring data accessibility and standardization across genetic and analytical techniques is crucial for the development of universal population assignment models.

As genomic data become available for an increasing number of fish species, SNP-chips that can serve more species can be developed, making the analysis even more cost effective. A major advantage of this approach is that the same SNP markers can be used across geographic areas and data sets can be compared and combined, which lends itself to the national, international, and interjurisdictional nature of fisheries data collection and curation.

4.3. Stock Assignments and Establishment of Baseline Allele Frequencies

Most fished stocks include mixed population assemblages that are exploited in complex spatial and temporal patterns (76). The need to know which populations are fished, and where and when they are fished, has driven the development of a plethora of methods for assigning the population origin of individuals within a statistical framework. Assignment analysis methods were first developed for morphological traits, but increased genomic resources and decreasing costs of molecular work have promoted genetic data as the tool of choice. In genetic assignment analyses, reference baselines are constructed using comprehensive population information, where care is taken to include all biological units potentially contributing to mixed-origin samples. This is done by genotyping mature individuals across representative local spawning habitats and age classes to incorporate temporal variation. Based on genome-wide analyses, sets of genetic markers exhibiting strong differentiation among populations can be selected to allow accurate population classification (30, 77). Cross-validation analysis estimates the accuracy (assignment success) with which samples of unknown origin can be correctly assigned to their natal population (e.g., 78, 79). Assignment success depends on the levels of population divergence observable with the applied markers, which was often a severely limiting factor prior to genome-wide sequencing studies.

Moreover, limited access to markers and sampling error causing inaccurate allele frequency estimates lead to a risk of overestimating assignment accuracy through high-grading bias (80). Even with whole genome sequencing data, correct assignment hinges on accurately determining population allele frequency differences. Moving from neutral markers to SNPs associated with adaptation may pose a challenge to genetic stock identification, as signals from adaptive SNPs and co-segregating loci can vary over relatively short timescales (81). Indeed, adaptive SNP variants are shown to track local habitat heterogeneity and may be under balancing selection (e.g., 49), which must be considered in genetic assignment applications.

For example, climatic projections indicate impeding changes in salinity levels and amplitude in brackish water bodies, many of which are essential spawning and larval habitats. Gene ontology studies have repeatedly indicated salinity adaptation as a driver of genomic differentiation across taxa (31, 82). If altered selection pressures lead to directional selective responses in local populations, reference samples could become gradually less relevant as populations evolve, with negative impact on assignment accuracy.

Nonetheless, evidence also points to strong effects of stabilizing selection acting on highly divergent supergenes maintaining stable gene frequencies over decadal and longer timescales (52, 81, 83). For example, adaptive loci in Irish and UK Atlantic herring populations have shown temporal stability for up to 18 spawning seasons (75). Still, even if SNPs used for population assignment are expected to remain diagnostic, stock resampling should be pursued during continuous baseline data set development. If significant temporal shifts in allele frequencies are observed in reference samples (for instance, in response to climate change), time limits on the relevancy of baseline samples could be implemented (e.g., ~15 years, mirroring species longevity). The high cost of field campaigns to resample populations may complicate the need for baseline updates. Here it can be assessed synthetically by simulating incrementally altered genotypes and testing their assignment success under a suite of potential future mixing scenarios (e.g., 84), although practical applications remain scarce.

4.4. Case Study: SNP-Based Stock Identification of Atlantic Herring in the Northeast Atlantic and Western Baltic Sea

Herring is fished for consumption in large parts of the Northeast Atlantic and the Baltic Sea. Individual trawling hauls typically represent mixtures of multiple populations, with individual fish potentially originating from spawning areas >1,000 km from capture sites. Specific populations

often show divergent demographics regarding population sizes and growth rates, as well as divergent phenology and functional traits. Individual stock sizes and their development are estimated and predicted in annual stock assessments, which are used to produce fisheries management advice on sustainable catch limits per stock and area. In the Northeast Atlantic, herring stock assessments are based on fisheries data delivered by individual states to ICES. The assessed stock units are defined largely based on simplifying assumptions about the geographical distributions of individual populations, which in several cases were classified based on morphological characteristics. Genetic analyses have proven these assumptions to be inaccurate, which likely has impacted the assessment and management of some populations (e.g., 74, 75). Genetic methods have allowed higher classification precision at the geographically defined stock level and, perhaps more importantly, at a population level (74, 75). This has significantly expanded knowledge regarding population distributions in time and space and has demonstrated gaps in our understanding of the relative importance of local populations to fisheries. Importantly, these new opportunities have created increased scope for developing stock assessment models that simultaneously incorporate multiple populations underlying varying demographics and exploitation rates. Full incorporation of spatial structure has been heralded as a paradigm shift in fisheries management (15). Although such developments have considerable value to fisheries science, they are perhaps especially important for pelagic species like herring, given their highly dynamic populations. This applies not least in a context of a changing climate that alters the dynamics and relative strengths of individual populations, some of which are predicted to be under more severe pressure than others (85). Here, time series data with information about population-specific distributions in time and space will be crucial to understanding and predicting biological changes that may impact ecosystems and economics. Nonetheless, the delivery of reliable stock assessment data for herring is complicated by a lack of aggregated biological data sets for individual herring. For example, in Europe, some member states still provide aggregated stock-separated fisheries data based on a suite of different methods, each associated with different degrees of accuracy and precision, which complicates the reliability of stock modeling (86). ICES has paved the way for improving fisheries data collation and curation with an initiative (87) envisaged to become a central international fisheries data hub. It is important that such systems can incorporate genetic data, which is becoming increasingly important for improving the basis of fisheries stock assessment. Here, work is still urgently required to fully explore genomic tools to optimize their use in stock assessment, and not least to safeguard that internationally agreed and implemented methods are simultaneously cost efficient and fully transferrable across users.

5. HOW MARINE FISHERIES CAN BE MORE SUSTAINABLE IN THE FUTURE

5.1. Future Possibility to Perform Stock Identification in Real Time During Fishing

It would be a major advantage if stock identification could be made in real time during fishing to direct fishing efforts to specific biological units and control the catch of individual populations. The management of the Norwegian North East Arctic cod (NEAC) and Norwegian Coastal cod (NCC) fisheries presents a good example of this (55). These two stocks comprise genetically distinct populations with markedly different demographics and abundances. The NEAC stock is the larger of the two and undertakes long-distance migrations to feeding grounds in the Barents Sea but spawns in coastal regions of Norway. In contrast, the NCC displays limited migratory behavior, remaining in coastal areas throughout its life, and has significantly declined in recent years. The two stocks spawn in the same areas and are targeted by a mixed-stock fishery. To reduce the

catch of NCC, it would be necessary to also reduce the catch of NEAC, which would have significant socioeconomic impacts on the Norwegian fishing industry. To avoid this, a genetic stock identification method was developed based on a single locus in the *Pantophysin* gene that enabled rapid identification of the proportions of individual stocks within the mixed fishery (55). Samples were collected and analyzed weekly during the fishery, and when the proportion of NCC reached a predetermined threshold, the fishery was closed or moved away from a particular area with a high proportion of NCC to protect the NCC spawning stock. The program proved highly effective and remains one of the few examples of real-time genetic assignment and management of marine fish species. Further development of genetic screening methods should make it possible to take this a step further and perform population identification in real time during trawling. This would make it possible to transform a fishery where quotas are set per geographic region to one where quotas are set per population.

There are no scientific or technological limitations on introducing improved management regimes for marine fish stocks targeted in mixed-stock or mixed-population fisheries. The difficulty arises primarily in science's ability to influence management regimes and coordinate management between multiple countries and jurisdictions. As genetic stock identification gains credibility as a valuable input into the stock assessment process, it may be possible to pursue this further.

5.2. How Genomic Forecasting Can Contribute to Fisheries Management

Rapid environmental change will pose major adaptive challenges to natural systems, with marine ecosystems impacted specifically by increasing seawater temperature, acidification, and deoxygenation (8, 9). Mitigating the potential impact of climate change in fisheries would thus require incorporating information on the genetics of climate change adaptation into management.

New evolutionary and population genomics methods aim to predict the impact of climate change on local adaptation by integrating spatial distribution modeling with intraspecific adaptive variation (88, 89). These approaches rely on identifying adaptive loci, either by explicitly testing the association of alleles with adaptive phenotypes or by pinpointing genomic regions whose allelic variants show strong correlation with particular environmental gradients. Once adaptive genotypes have been identified and mapped across the landscape, the relationship between genotype and the current environment is generalized in a model that can project genotype–environment associations in a future climate (88, 90). The difference in allele frequencies between current and forecasted climates can be used to estimate the risk of maladaptation in the future, referred to by some authors as a risk of nonadaptedness (91) or genomic offset (90). Furthermore, by determining which genomic regions will be adaptive under future environments, simulation approaches that incorporate life history and demography parameters can be used to determine baseline allele-frequency levels at adaptive loci that can seed future adaptation (92, 93).

These approaches can be used in two ways for fisheries management. First, they could be used to predict which populations might be more vulnerable (maladapted) under future climates (90, 94–98). For instance, a study of the genetic offset of Arctic charr (*Salvelinus alpinus*) populations across Newfoundland and Labrador in northeastern Canada indicated that the southernmost populations are the most vulnerable to the predicted rapid rise in Arctic temperatures (99). The loss of these populations could impact ecosystem function and food security of local human communities; therefore, preventive measures could be taken to protect stocks that will be more vulnerable to climate change. Second, markers that are identified as important for future climate change adaptation could be incorporated into monitoring programs to maintain frequencies of adaptive alleles at sufficient levels to allow future adaptation (92, 100).

5.3. Major Hurdles to Implementing Population Genomics in Fisheries Management

Fisheries stock assessment and management are two distinct processes, with the latter depending on the former. To implement appropriate management measures, the management process must assimilate the scientific assessment outputs with socioeconomic and political considerations. So, although sustainable management should be based on robust science, socioeconomic and political considerations often make applying the best science difficult. For example, the existing management areas for stocks in the Northeast Atlantic region are inflexible and hard to change even with robust scientific evidence supporting a change. Another hurdle is that stock assessment relies on long time series of fisheries-dependent and -independent data that inform models used to predict sustainable catch limits. These time series are established mostly without considering varying levels of population mixing within predefined stock areas, or by making simplifying assumptions. Thus, implementing stock identification methods is not straightforward, as the payoff for improved assessment of the biological units is not realized until solid time series have been obtained. These major hurdles must be overcome before the full potential for how population genomics can contribute to sustainable marine fisheries is realized.

DISCLOSURE STATEMENT

E.D.F. declares a conflict of interest as regards the LVL Technologies Genetic Sampling Tool, as he and the Killybegs Fishermen's Organisation were involved in the design, development, and production of the tool. The authors are not aware of any other affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Errata

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