

Assessing connectivity between MPAs: Selecting taxa and translating genetic data to inform policy

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ABSTRACT

Connectivity is frequently cited as a vital component of Marine Protected Area (MPA) networks and was formally identified as one of five key principles for marine network design in European waters. Yet, without the ability to demonstrate connectivity, it is impossible to be certain that sites designated within a MPA network do in fact constitute a network, when they may –irrespective of the diversity and rarity of the taxa within them– be in reality a set of unlinked habitats and associated species assemblages. However, the process of assessing connectivity between MPAs, and which taxa to include in assessments of connectivity, is often difficult and can be dependent on a variety of factors that can be outside the control of managers, stakeholders and policymakers. Among the many methods that have been used to assess connectivity, genetic markers are often used to infer connectivity indirectly by estimating the degree of genetic differentiation between populations of a species or by inferring the origin(s) of migrants using assignment methods. While modern molecular methods can be extremely robust and are now routinely used to address conservation issues, genetic data are, to the authors' knowledge, rarely used to inform designation of MPA networks. In this paper, several biological and methodological factors are highlighted, consideration of which may help to inform the selection of species for assessments of connectivity between MPAs in a network, and this paper suggests ways in which genetic data may be interpreted to inform MPA design and policy.

1. Introduction

Connectivity is identified as a key component in the design of European Marine Protected Area (MPA) networks [1]. However, changes to the definition of connectivity outlined in many different reports [1–3] suggest there is potential confusion or conflict amongst stakeholders and scientists concerning the exact definition and function of connectivity in the context of MPA networks. The most simplistic definition is taken from Palumbi [4] whereby “*connectivity is the extent to which populations in different parts of a species range are linked by the movement of eggs, larvae or other propagules, juveniles or adults*” [1]. In contrast, other reports have outlined a more detailed definition such that maintaining connectivity involves creating “...*ecologically connected and functional networks with ‘corridors or ‘stepping stones’ that facilitate the range shifts of populations and the movements of individuals and genes in response to ocean climate change*” [2], or that “...*the MPA network is well distributed in space and takes into account the linkages between marine ecosystems*” [3].

Connectivity is a fundamental component of population dynamics, interacting with many processes crucial to the persistence of established

populations and the (re)colonisation of new habitats [5]. The study of intra-species connectivity enables the quantification of effective larval dispersal and migration between populations, while also allowing the degree of self-recruitment within populations to be estimated [6]. This is important for optimising the location and size of MPAs to create a well-connected network (instead of individual unrelated MPAs) [7,8], and for evaluating the impacts of resource exploitation on the population dynamics of commercial marine species [9].

To assess connectivity, an ideal scenario might incorporate multiple sources of data informing on connectivity from many types of taxa within the boundaries of an MPA network; however, this is often impossible due to financial and logistical constraints. Instead, managers of MPAs have typically concentrated their efforts on species that are endangered or rare, and which may be on the brink of extirpation in parts of their range, or on so-called ‘umbrella’, ‘keystone’ or ‘flagship’ species [10,11]. The concept of an ‘umbrella’ species, a species whose protection indirectly protects many other species in an ecological community, is generally recognised as appealing for assessing connectivity. This is because the establishment of a network based on such data may extrapolate the benefits of preserving the connectivity of one focal species

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Table 1
Factors to consider before selecting a species to assess genetic connectivity between Marine Protected Areas.

Type	Factor	Description	Example	Significance
Biological	Ecological importance	Does the organism have a fundamental importance to a functioning ecosystem?	- Ecosystem engineers (e.g. mussel beds, mearl)	- These species may be protected under legislation.
	'Flagship' species	Is the species charismatic, well known to the public, and a poster child of conservation campaigns?	- Many large megafauna including cetaceans and sharks	- Higher potential impact.
	Economic importance	Is the species commercially exploited?	- Some threatened invertebrates	- Higher potential impact.
Taxonomy	Economic importance	Is the taxonomy not well resolved and the organism hard to identify?	- Fish and invertebrate coastal fisheries	- Opportunities for collaboration during sample collection.
	Biological knowledge	A sound knowledge of the biology and ecology of the organism.	- Sister species with very similar morphology	- Species difficult to ID morphologically demand more resources and time. In some cases, a taxonomist or DNA barcoding method may be required for validation.
	Sample collection	Collecting tissue samples from the organism for genetic analysis.	- Very small organisms	- Improve the testing of hypotheses.
Methodological	Sample sites	The number of sampling sites and the spatial separation between sites.	- Habitat / distribution	- Improve interpretation of the results.
	DNA extraction	Extracting genomic DNA for analysis.	- Larval development	- Protected species may require permits for tissue removal.
	Sample sizes	The number of individuals per sampling site.	- Dispersal	- Logistical barriers may limit sample collection in some areas (e.g. deep sea).
Choice of genetic marker	Choice of genetic marker	Choosing a genetic marker that is polymorphic enough to investigate genetic patterns.	- Feasibility / cost of collecting samples	- Adequate sampling sites in and out of MPAs could enhance hypothesis testing.
	Availability of genetic markers	Are panels of molecular markers already available for the organism?	- Consider the number of sites needed in and around MPAs	- High quantity and quality DNA can be difficult to extract from some organisms and tissue types (e.g. crustacean exoskeleton) using standard kits.
	Sample sizes	The number of individuals per sampling site.	- Consider tissue type and extraction protocol before sampling	- Experimentation with DNA extraction methods may be necessary, particularly for marine invertebrates.
Availability of genetic markers	Choice of genetic marker	Choosing a genetic marker that is polymorphic enough to investigate genetic patterns.	- Consider the number of individuals needed to draw robust conclusions	- The 'correct' number of individuals can be influenced by the choice of genetic marker.
	Availability of genetic markers	Are panels of molecular markers already available for the organism?	- Microsatellites	- During data analysis, the power of the markers and sample sizes can be tested using various software.
	Sample sizes	The number of individuals per sampling site.	- SNPs	- The choice and number of markers will depend on the power and resolution required.
Availability of genetic markers	Choice of genetic marker	Choosing a genetic marker that is polymorphic enough to investigate genetic patterns.	- Microsatellite / SNP panels	- This would avoid the need to develop markers <i>de novo</i> .
	Availability of genetic markers	Are panels of molecular markers already available for the organism?	- Microsatellite / SNP panels	
	Sample sizes	The number of individuals per sampling site.		

to other species in a community with similar life histories and dispersal traits. Hypothetically, a species associated with all three concepts ('umbrella', 'keystone' or 'flagship') would likely be the 'holy grail' species for studying connectivity between MPAs; however, identification of such species (if indeed they exist) has continued to elude those involved in marine conservation. Moreover, for a variety of reasons (Table 1), the study of species that come close to satisfying the criteria of a 'holy grail' species may not be feasible and, therefore, compromises are needed to facilitate the collection of data that are informative about connectivity in a given system.

1.1. Population genetic structure

Genetic markers are commonly used in ecology to study the spatial genetic structure of a species. Such data can facilitate exploration of patterns of genetic diversity, and can enable researchers to detect genetic differences between samples and to ascertain whether the organisms at each sampling site constitute a discrete population. However, identifying discrete populations can be challenging in marine species [12] and, while low genetic differentiation between populations may imply high gene flow (or large effective population sizes), the same pattern could also suggest that multiple samples are from a single panmictic population. Thus, when using population genetic structure to infer patterns of connectivity, it is important to collect spatially discrete samples and to be aware of the challenges of defining populations.

Three main evolutionary processes influence the population genetic structure of a species across space and time: gene flow, genetic drift and natural selection [13,14]. Low genetic differentiation between populations may be driven by high gene flow because the transfer of genetic material homogenises allele frequencies. However, large effective population sizes may also result in low genetic differentiation between populations, though, again, accurate estimation of effective population size in marine organisms can be extremely difficult [15]. In the absence of gene flow, allele frequencies can diverge over time because of the random sampling of alleles from generation to generation (genetic drift). Genetic drift is stronger in small or bottlenecked populations because sampling variance is greater when effective population size is smaller [16]. Populations can also diverge when strong natural selection favours a particular mutation that increases the fitness or survivorship of the carriers, resulting in the allele sweeping to fixation in that particular population. For studies where the primary goals are to assess inbreeding, effective population size(s) or connectivity, researchers have commonly employed neutral markers because genetic patterns at these markers are driven by the interacting processes of gene flow and genetic drift, and not selection [17]. However, hitchhiking neutral markers and markers under selection have been shown to sometimes provide more power for directly tracking migrants in assignment studies [18]; as the use of non-neutral markers in molecular ecology increases, this will likely have promising applications for inferring patterns of connectivity [19].

1.2. Genetic connectivity

Measuring dispersal and connectivity using conventional tracking methods (e.g. physical tags, satellite telemetry) is extremely difficult in many coastal marine species because of their typically large ranges and pelagic larval phases [5]. Genetic markers are naturally present in every individual in a population and this makes them ideal to infer patterns of connectivity in such species. Genetic connectivity is defined by Lowe and Allendorf [20] as the "degree to which gene flow affects evolutionary processes within subpopulations". In other words, individuals must disperse to a new population and must successfully contribute their genes to the next generation to facilitate genetic connectivity. In contrast, demographic connectivity refers to how the absolute number of exchanges (via immigration or emigration) between populations affects growth and vital rates within populations [20]. Studies of population

genetic structure can be used to infer genetic connectivity, however, they generally provide little information about demographic connectivity, unless combined with other data such as direct estimates of dispersal or abundance [20] or biophysical modelling [21].

To assess contemporary genetic connectivity, two types of methods are generally employed: (i) indirectly inferring genetic connectivity by examining genetic similarities or dissimilarities (genetic structure) between spatially discrete populations, or (ii) directly estimating genetic connectivity by detecting migrants through population or parentage assignment [19,22,23]. For both methods, the most widely used markers are microsatellites and single nucleotide polymorphisms (SNPs). However, SNPs are fast becoming the marker system of choice, particularly in non-model organisms [24,25], because the rapid advancement of high-throughput sequencing methodologies [26,27] can enable thousands to tens of thousands of markers to be discovered and genotyped, as opposed to tens of markers using microsatellites. Moreover, difficulties in cross-calibrating microsatellite allele sizes between sequencing platforms and laboratories [28] has limited their use in broad-scale studies, a limitation which does not affect SNPs. The use of genomic SNPs therefore provides wider coverage across the genome and potentially greater power for resolving patterns of population structure and genetic connectivity at finer spatial scales [29].

However, the general lack of genetic evidence used by marine policymakers and managers suggests much of the genetic/genomic data generated are currently not considered during the planning and designation of MPAs. In this paper, a number of biological and methodological factors are highlighted that should be considered before selecting taxa to assess genetic connectivity between MPAs. In addition, using published data from a previous study (Holland *et al.* [32]) and the MPA network in southwest Britain as an example, this paper discusses how genetic data from a typical population genetic/genomic study may be interpreted to inform managers about connectivity in a MPA network, and which areas to consider prioritising to maximise the protection of biodiversity.

2. Selecting taxa

The selection of appropriate taxa to use as surrogates for assessments of genetic connectivity between MPAs has seldom been discussed in the literature (but see Marti-Puig *et al.* [30]). Coastal benthic marine invertebrates are often good candidates because they can be relatively abundant with large ranges, and dispersal is typically defined during a pelagic phase undertaken by an early life stage (e.g. eggs or larvae), while the adults remain relatively sedentary [5]. This type of development means connectivity is mainly dependent on local hydrological conditions (as well as species-specific traits) and, therefore, better reflects natural patterns of connectivity, as opposed to studying connectivity driven by organismal behaviour in motile and migratory species. Since patterns of genetic connectivity can vary between species over similar geographical areas [31,32], it is important to consider assessing connectivity in more than one species with differing biology/ecology. This allows the exploration of species-specific genetic connectivity and patterns of connectivity common across taxa to be identified [30].

2.1. Biological factors

Some biological features of candidate species can inevitably enhance the public appeal and societal impact of a study, while other features can limit the collection of samples and the interpretation of data generated by genetic markers (Table 1). For the purpose of promoting marine conservation, charismatic megafauna such as marine mammals and sharks frequently dominate awareness campaigns ('flagship' species) because they can raise funds and change public opinions and behaviour. Although many of these species may not be the best candidates for assessing MPA connectivity, these enigmatic

animals are typically well-known by the wider public and benefit from a greater awareness and potential impact than other marine fauna. As a result, if a candidate species is poorly known to the public community, highlighting its importance for the conservation of an associated enigmatic species may have an equivalent effect (e.g. the interactions between kelp forests and sea otters [33]).

Benthic marine invertebrates are generally not ‘flagship’ species (though there are exceptions, e.g. pink sea fans). However, it is recognised that many benthic invertebrates have a crucial ecological role (e.g. mussel beds as ecosystem engineers / habitat builders) or are commercially exploited (e.g. European lobsters), meaning they are either fundamentally important to the ecosystem or the local/regional economy, or both. This may encourage relevant management bodies and/or stakeholders to collaborate, to contribute funding and/or to share equipment (depending on the organisation’s interests and capacity), all of which can serve to advance a particular project. For example, lobster fishermen have access to a potential myriad of individuals from which tissue samples can be obtained. Forming these types of collaborations can facilitate access to a virtually unlimited number of samples depending on the fishery status, thereby avoiding the need to arrange dedicated sampling trips, and the associated costs and researcher time typically required for collection. Moreover, maintaining dialogue with such a stakeholder(s) may promote more effective communication of the potential benefits of the research and, ultimately, dissemination of the results.

Other factors to consider include whether the biology and ecology of the candidate species are well known. This process starts –perhaps obviously– by accurate identification of the candidate species and avoiding the erroneous inclusion of closely related or cryptic species, which can drastically influence the results of population genetic structure analyses [34]. The difficulty of accurate taxonomic identification can be further exacerbated when the organism is very small; in some cases, a second opinion from a dedicated taxonomist or molecular verification (e.g. DNA barcoding) may be required. In addition, a thorough understanding of the dispersal, life history and habitat of the candidate species will usually help to explain some of the genetic patterns observed, thereby improving interpretation of the genetic data.

2.2. Methodological factors

The sampling design of a study should be carefully considered prior to sample collection to ensure that the resulting genetic data are robust and applicable for assessments of genetic connectivity. This typically includes assessing whether the desired sampling strategy is feasible and that sufficient tissue samples from a broad enough range of sites can be taken for meaningful genetic analysis. For example, as suggested previously, if an organism is commercially fished, it may be possible to have tissue samples collected *in situ* by fishery personnel. Moreover, ensuring that samples of a species of interest are collected from both within the boundaries of a MPA network and from sites outside ensures that hypotheses about connectivity beyond MPA boundaries can be tested. This approach has provided useful data in several previous studies [32,35,36], allowing the performance of a MPA network to be evaluated for the species being studied.

Other factors to consider include the type(s) of tissue to sample and which genetic markers to use in assessments of population genetic structure. This is of critical importance because the type of tissue can profoundly influence the quantity and quality of DNA obtained post-extraction. For example, crustacean exoskeletal tissues, such as pleopods, are advantageous because they are easily obtained and constitute a non-destructive tissue sample; however, extracting sufficient amounts of pure (contaminant-free) DNA from these tissue types can be extremely difficult using both conventional and kit-based protocols [37]. Moreover, obtaining high molecular weight, non-degraded DNA can be important for methods that utilise next-generation sequencing technology, for example, whole-genome sequencing and SNP discovery

from restriction-site associated DNA sequencing (RADseq) [38–40]. In these cases, optimising the preservation and extraction of DNA will need to be considered prior to sampling and DNA extraction. Choosing appropriate genetic markers and the method of isolation for studies of population genetic structure is also a non-trivial task. Discussion of which genetic markers to employ for a particular study is outside the scope of this paper; however, a number of comprehensive review papers have been published to address this question [13,41–44]. In addition, tools exist that can help practitioners choose the appropriate number of samples and genetic markers (e.g. SPOTG [45]). Prior to commencing development work, the literature should be screened thoroughly to determine whether genetic markers of a suitable resolution are already available for a candidate species – this can avoid the costs and time typically required for the development of novel markers. For example, SNP panels are now available for a wide range of marine species (e.g. salmonids [46], crustaceans [47] and molluscs [48]), and are likely to be useful for the analysis of genetic structure, population assignment and connectivity.

3. Translating genetic data to inform policy

Translating primary research into the language and terminology required by policymakers and conservation managers to allow them to make decisions is not a trivial task. Often, it may be more beneficial to present a few points that represent the key findings of a study, while trying to avoid unnecessary technical jargon, which could lead to misinterpretation or confusion. Several papers have discussed the challenges of translating genetic data to inform management and have asserted the importance of strong collaboration and communication between scientists and practitioners [49–55]. Some of the reasons put forward for the avoidance of genetic data in fisheries management include a lack of understanding of the potential value of genetic data, the assumption that genetic studies are expensive, and the suggestion that other data types are significantly more important than genetic information in management decisions [9]. One feature of genetic data is that they cannot be seen or measured without the use of specialist molecular techniques, meaning it can sometimes be difficult to articulate the level of variation and the importance of genetic diversity to non-scientists [49]. Moreover, in cases where research is carried out by non-academic bodies, these institutions often have little incentive to publish, or have internal deadlines or political/legal constraints that may delay scientific publication, so the findings may not be widely-disseminated [52].

However, while some barriers to the dissemination of genetic research exist, there are examples across various taxa and systems where genetic data have successfully informed policy and conservation, and have led to improved management decisions. This suggests that some barriers to the application of genetic data are starting to be overcome. Some examples include the genetic restoration of Florida panthers [56], the selective reintroduction of endangered Burmese roof turtles [57], the genetic management of salmonids [58,59], the identification of stock/management units for commercial species in the Mediterranean [60], the authenticity and monitoring of seafood in sushi bars [61], and the traceability of fisheries resources (e.g. FishPopTrace, [62]). In the latter case, the FishPopTrace Consortium was an international project funded by the European Union with the aim of developing genetic marker panels capable of pinpointing the stock/population origin of a particular individual from a species [18,62]. Monitoring the origin of a fishery product is seen as a strategy to potentially increase transparency in the food supply chain and reduce illegal, unreported and unregulated fishing (IUU) and product mislabelling [62]. The project focused on four commercially important fish species: cod (*Gadus morhua*), hake (*Merluccius merluccius*), herring (*Clupea harengus*) and common sole (*Solea solea*), and the results indicated that gene-associated SNP markers could assign individual fish to their population of origin at 93–100% accuracy across a range of spatial scales [18]. The study

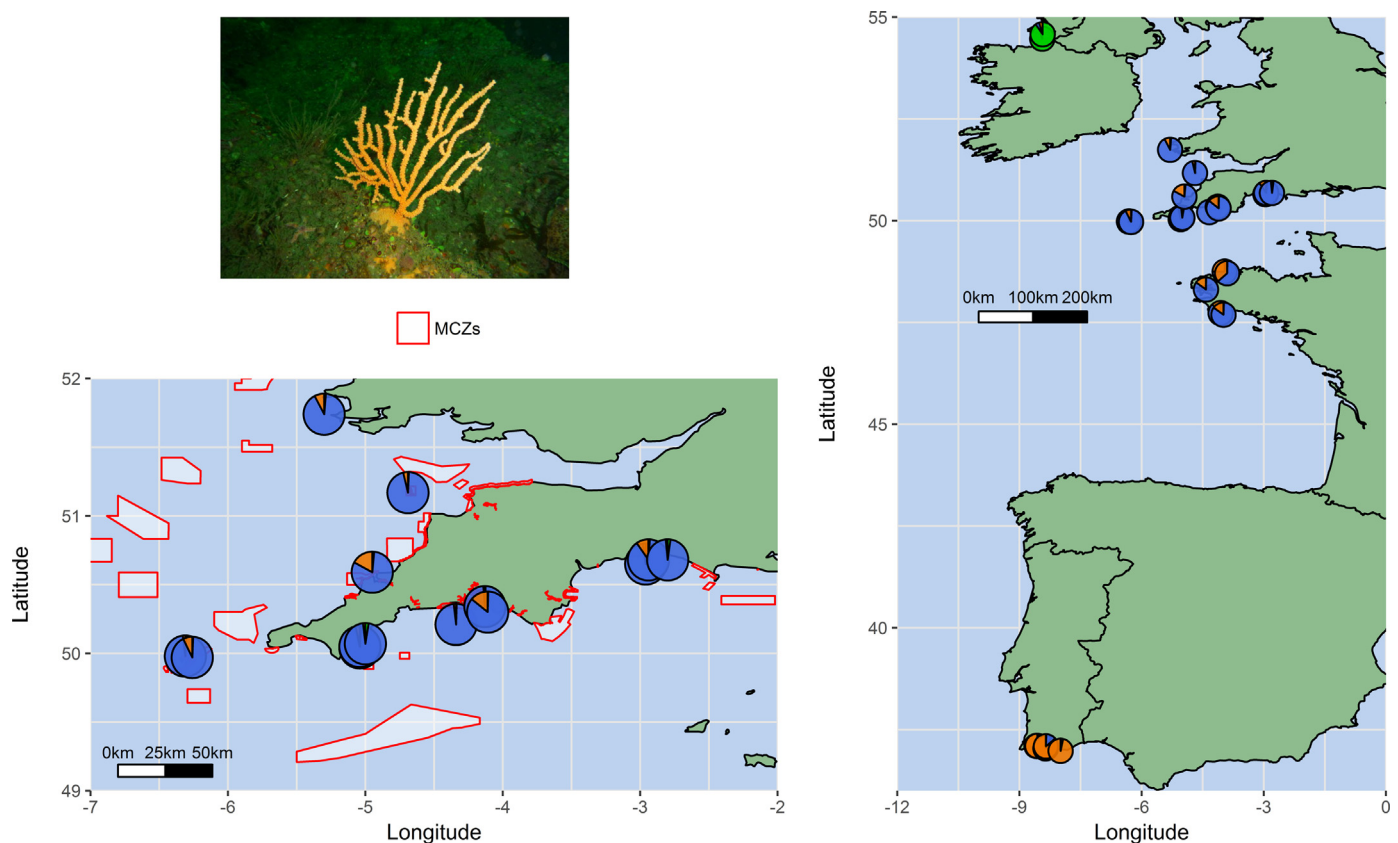


Fig. 1. Pink sea fan (*Eunicella verrucosa*) (top left) average cluster memberships derived from STRUCTURE analysis of 13 microsatellite markers – re-drawn from Holland et al. [32]. The right map shows the average membership coefficients for each genetic cluster for each population studied in the original paper. The bottom left map zooms in on southwest Britain and includes overlays (red outlines) of the Marine Conservation Zones designated in English and Welsh waters to-date.

illustrates the remarkable potential of genetic data to help enforce fisheries regulations and conservation measures across different species and geographical areas.

Yet, while there are a myriad of studies documenting the spatial genetic structure and genetic connectivity of benthic marine species, very few of these studies, to our knowledge, have been directly used as evidence to inform or support MPA designations and/or network connectivity. This may be a consequence of ineffective dissemination of the key findings of research projects to managers and policymakers, but also likely relates to the availability of data at the time when large-scale MPA projects were commissioned and candidate lists were first drawn-up. Nevertheless, as these data are becoming more available to practitioners, it is crucial that gaps between primary research (i.e. academic researchers) and applied science (i.e. policymakers) are overcome in order to realise the potential of genetic data to inform MPA design and conservation planning [50,52].

3.1. UK MPA network

Across the UK, as of December 2017, approximately 23% of marine/estuarine environments are within MPAs (see: <http://jncc.defra.gov.uk/page-4549>). At the time of writing, the network comprised 298 MPAs including: Special Areas of Conservation (SACs; 105) and Special Protected Areas (SPAs; 106) with marine components, Nature Conservation Marine Protected Areas (NCMPAs; 30 in Scotland), Ramsar sites (Isle of Man), and Marine Conservation Zones (MCZs; 56 in England, Wales and Northern Ireland). This network of MPAs has been created to satisfy the UK's commitments to the Convention on Biological Diversity, EU habitat and marine strategy regulations, and the Oslo/Paris (OSPAR) Convention to protect the marine environment of the northeast Atlantic.

In England and Wales, the MCZ project began in 2008 with the aim of filling gaps in the MPA network and potentially addressing any deficits in connectivity; following the EU Marine Strategy Framework Directive (2008), the UK Marine and Coastal Access Act (2009) enshrined the designation of MCZs into UK Law. After identification of 127 candidate MCZs in 2011 by four regional stakeholder groups, 50 MCZs in England (27 in tranche one, November 2013; 23 in tranche two, January 2016) and one in Wales (Skomer Island, Pembrokeshire, 2014) have been designated, with a final tranche for England to be announced in 2018. This has, in the view of some commentators, coincided with a shift from a bottom-up to a top-down approach, with stakeholder engagement now limited to bilateral consultations [63]. The MCZ project has also steered away from its initial focus on broad-scale networks and instead has concentrated efforts on single-feature conservation [63], such as protecting vulnerable species (e.g. pink sea fans) and key habitats (e.g. intertidal boulder communities).

One of the main ambitions of the UK MPA project was to create an ecologically coherent network of MPAs, for which connectivity was seen as one of five key planning principles, alongside representativity, adequacy, replication, and ecologically and biologically significant areas [64]. Assessing connectivity of the English and Welsh MPA network has primarily focused on linking discrete habitats (e.g. littoral rock and hard substrata, sublittoral sediment, etc.), such that each habitat is represented by a MPA every 80 km or less [3,65], the spacing recommended by Roberts et al. [66] to maintain ecological connectivity. Connectivity for a discrete habitat is deemed sufficient when 40 km buffers drawn around two adjacent MPAs converge [3,65]. For many benthic marine species, defining a network in this way may be sufficient to maintain connectivity between nearby populations. However, it is important to note that it may not suit all species because connectivity can be influenced by a number of biological (e.g. larval

Table 2
Summary of the promises and pitfalls of genetic data for informing Marine Protected Area design.

Genetic data	Description	Promises	Pitfalls
Genetic diversity	The amount of genetic variation contained within a population or species. Statistic is a combination of the number of allelic variants and their frequency in a sample.	<ul style="list-style-type: none"> • Populations with unique/high genetic diversity may have more resilience to environmental change. • Can inform the location and boundaries of MPAs. • Could prioritise placement of MPAs to safeguard this diversity. 	<ul style="list-style-type: none"> • Patterns and magnitude of genetic diversity measures may differ depending on the molecular marker used. • Mutations in primer sites can lead to null alleles which can lead to inaccurate estimates of genetic diversity.
Population genetic structure	The spatial distribution of genetic variation among populations in a species, allowing genetic similarities or dissimilarities between sample groups to be explored.	<ul style="list-style-type: none"> • Infer gene flow between populations. • Identify potentially genetically isolated and source/sink populations. • Indirectly infer dispersal distances and genetic connectivity. • Can inform the location and boundaries of MPAs. • Infer connectivity between MPAs, providing information about ecological coherency. 	<ul style="list-style-type: none"> • Large effective population size, not gene flow, can be responsible for low genetic differentiation. • It is difficult to infer gene flow from marine species with overlapping or long-life spans. • Genetic markers only provide information on the number of effective migrants. Genetic data cannot reliably estimate demographic connectivity without additional data. • A single effective migrant per generation can homogenise populations; thus, genetically similar populations may have only very limited larval exchange.
Population assignment (Individual assignment)	Assign an individual to a population or cluster in which their genotype has the highest probability of occurring.	<ul style="list-style-type: none"> • Infer the origin of an individual and track migrants. • Infer dispersal distances and genetic connectivity. • Infer connectivity between MPAs, providing information about ecological coherency. 	<ul style="list-style-type: none"> • Requires sound knowledge of the species distribution. • Accuracy reduces with decreasing genetic differentiation. Therefore, markers with high power to distinguish differences are necessary for species with low overall levels of genetic differentiation.
Parentage assignment	Assign an individual to their biological parents based on their genotypes.	<ul style="list-style-type: none"> • Infer the origin of an individual and track migrants. • Infer dispersal distances and genetic connectivity. • Infer connectivity between MPAs, providing information about ecological coherency. 	<ul style="list-style-type: none"> • Requires sound knowledge of the species distribution. • Requires a significant proportion of potential parents to be sampled. Can be logistically difficult to sample a sufficient proportion of contributing parents to make assignment accurate.

dispersal [36], spawning periodicity [67]) and hydrological (e.g. ocean currents and fronts [68]) factors, which further complicate the positioning of MPAs within a network.

3.2. Genetic data as evidence: pink sea fan case study

Genetic data are currently not (to the authors' knowledge) used by managers as evidence to inform MPA designation or network connectivity in England and Wales. Discussions with national agencies suggest that the personnel and infrastructure are not in place to process, grade and assess the usefulness of spatially relevant genetic data. This may explain the lack of genetic data currently used as evidence to support existing MPA designations or to inform new designations around southwest Britain. However, genetic data from single-species studies can provide an empirical estimate of connectivity within evolutionary timescales [20]. This, therefore, gives an approximation of genetic connectivity over the last few generations in the species studied [50], which would likely supplement the present assessments of connectivity discussed in Section 3.1. Moreover, genetic data can reveal distinct localised genetic diversity –otherwise undetectable using only presence/absence data or biophysical modelling– which can be of major importance for identifying populations or areas that should be prioritised for protection.

In Fig. 1, STRUCTURE [69] results taken from a recent study [32] are presented; the study analysed patterns of variation at 13 micro-satellite loci and explored the population structure and genetic connectivity of a 'flagship' species in English and Wales, *Eunicella verrucosa* (the pink sea fan). *Eunicella verrucosa* is listed as 'Vulnerable' by the IUCN Red List and is a Biodiversity Action Plan priority species in English and Welsh waters; accordingly, several MCZs specifically identify *E. verrucosa* as a protected feature in their designations (e.g.

The Manacles, The Isles of Scilly, Chesil Beach and Stennis Ledges). Moreover, colonies are sessile, dispersal is achieved by broadcast spawning, and 60% of colonies recorded by diver surveys fall within MPAs [70]; therefore, *E. verrucosa* fulfils several criteria associated with the ideal surrogate species to assess connectivity between MPAs. In Fig. 1, each pie chart represents a sampling site and the colours represent genetic cluster memberships for each population, averaged across all individuals in that population. In effect, when two pie charts are primarily composed of the same colour, this implies that these two populations are genetically similar, suggesting high genetic connectivity (or large effective population sizes). In southwest Britain, the composition of the pie charts are relatively similar, indicating genetic similarity; as the original authors report, this suggests that the current MPA network is likely sufficient to maintain genetic connectivity in this species across southwest England and Wales. In comparison, Portuguese and Irish colonies are genetically different. As reported in the original study, the genetic differences observed in Portugal likely represent a stepping-stone model of genetic connectivity, driven by isolation-by-distance, whereby gene flow occurs more frequently between populations that are closer together than further apart and over time populations diverge due to genetic drift. In contrast, the authors suggested the genetic differences observed in northwest Ireland could be the result of a barrier to gene flow and subsequent genetic drift, or possibly a result of local adaptation driven by natural selection at this northerly location, though it was unclear which process was primarily responsible [32].

The pink sea fan study discussed above was indirectly commissioned and funded by the UK Government with the aim of assessing connectivity of *E. verrucosa* using genetic techniques, and with the potential to inform and support the designations of MPAs that included *E. verrucosa*. The key finding of this study which might constitute evidence

for MPA managers is that, as it stands, the MPA network in southwest Britain appears to be sufficient to maintain genetic connectivity in this protected species [32]. The integration of these data in future reviews or monitoring reports would likely serve as another piece of evidence to support the designation of these MPAs and to help demonstrate the ecological coherency of the network in southwest Britain. To facilitate more efficient translation and transparency going forward, researchers aiming to inform MPA designation using population genetic data are encouraged to create a visual representation similar to Fig. 1 to better simplify and standardise interpretation for managers and policymakers.

3.3. Promises and pitfalls of genetic data

Genetic data have much promise in informing the planning stages of MPA network design and in supporting previously designated MPAs. Accordingly, it is important that managers and policymakers are aware of the opportunities provided by genetic studies but are also aware of some of the pitfalls that are linked to the methods and interpretations before action is undertaken (Table 2).

Genetic data have the potential to inform managers in two main ways: single feature designations and network connectivity. For priority species that cover a relatively large spatial area within and across political boundaries (e.g. pink sea fans), designating a MPA has to be strategic and knowing where to place a MPA can be extremely difficult. By studying the population genetic structure, data of suitable resolution may allow managers to identify key populations or areas that harbour unique or high genetic diversity, as shown in the case study above, thereby providing additional ecological evidence to support a designation. This information may also be useful for determining the boundaries of MPAs that are designated to safeguard protected species. The appropriate authorities should be encouraged to consider protecting these rare genetic variants, particularly in ecologically or economically important species, even if the exact cause of the unique diversity is not known. This is because if these individuals/populations are wiped out due to anthropogenic causes, this diversity will be permanently lost to the species before these genetic variants have an opportunity (potentially) to benefit the species in a constantly dynamic environment. Such studies can also allow a species' effective population size to be inferred which can reveal the genetic health of a population; however, estimating effective population size in marine species can be notoriously difficult [15]. For MPA networks, information about dispersal distances, potentially isolated populations, and connectivity between populations or habitat patches can be inferred through the analysis of intraspecific genetic data [5]. Additionally, by using appropriate genetic software, the direction of gene flow can be estimated – this can be particularly important for identifying source populations that export potential recruits to nearby populations [71]. The protection of source populations is extremely important for marine conservation because it can facilitate replenishment or recolonisation of populations that have suffered from local declines and/or are not self-sustaining (i.e. sites relying on immigrants to maintain healthy population sizes) [5]. However, while genetic data can provide some understanding into source and sink dynamics on evolutionary timescales, these analyses would likely benefit from incorporating biophysical modelling data into their conclusions to evaluate whether contemporary hydrological conditions (e.g. ocean currents) are the potential driver behind any asymmetrical connectivity found. Such integrative studies have typically been referred to as 'seascape genetics/genomics' [72,73] and have been shown to enhance studies of marine connectivity by providing insights into both demographic and genetic connectivity [21,74].

Limitations associated with the inference of genetic data are usually reported in the original published studies; nonetheless, some general limitations are discussed here. Firstly, managers are typically interested in the absolute number of migrants (demographic connectivity), but genetic markers can only provide information on the number of

effective migrants (e.g. individuals/larvae that successfully disperse to a new population and reproduce/survive to the next generation). Moreover, a single effective migrant per generation can be sufficient to homogenise populations [20], meaning, despite being genetically similar, some populations may have minimal larval exchange [23]. Parentage assignment can circumvent this issue to some degree by attempting to track migrants; however, to be useful, these methods require a significant proportion of potential parents to be sampled/characterised [19]. Secondly, inferring patterns of connectivity from marine species with overlapping generations or long-life spans (e.g. corals) can be difficult because genetic profiles can remain essentially unchanged for many decades, even after barriers to gene flow have been introduced [23]. Therefore, interpretations of population differentiation and genetic structure can, in some cases, represent historical and not contemporary gene flow [75]. This difference in timescales is critical to consider in assessments of connectivity because MPA networks are generally established to protect and maintain present-day and future patterns of diversity and connectivity, or to facilitate recovery/restoration to a previous level of abundance and diversity. However, as with genetic data, most methods of assessing connectivity have their own assumptions and limitations, so consideration of all of the best available scientific knowledge will be crucial to create well-connected networks that maximise the protection of marine biodiversity.

4. Conclusion

Over 11,000 MPAs have been designated globally (~3.7% of global oceans) to protect the world's oceans (<http://www.mpatlas.org/explore/>). There are also numerous published studies of population genetic structure for a variety of marine organisms across small (i.e. within seas) and large (i.e. across seas and oceans) geographic scales. Therefore, the potential for genetic data to provide evidence to support the designation of existing or new MPAs is profound. In this paper, a number of factors are presented that could help practitioners select appropriate taxa to assess connectivity between MPAs. In addition, this paper has discussed how genetic data from a typical population genetics/genomics study may be interpreted to inform MPA designation and network connectivity. These two sections are anticipated to be useful for managers involved in MPA designation processes, and particularly for those tasked with the designation, monitoring, review and enforcement of the current UK MPA network.

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Data accessibility

R code and data files required to produce Fig. 1 are available as Supplementary material.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.marpol.2018.04.022>.

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