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Article in *Aquatic Conservation Marine and Freshwater Ecosystems* · June 2021

DOI: 10.1002/aqc.3622

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RESEARCH ARTICLE

Geospatial genetics: Integrating genetics into marine protection and spatial planning

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Abstract

1. The protection of evolutionary processes and maintenance of genetic diversity is necessary for the persistence of biodiversity and ecosystem resilience. The importance of genetic diversity has been reflected in a range of marine policy mechanisms, and the genetic ‘toolbox’ has great potential to support marine protection and marine spatial planning (MSP) at multiple scales. Despite scientific advances in the application of genetics in marine protection and management, systematic integration of genetic information has been generally lacking, primarily due to a knowledge and communication disconnect between geneticists and the marine policy and management community.
2. To meet these outstanding needs, a ‘geospatial genetics’ approach to spatially map species-specific genetic data and associated information in a way that can be readily integrated by practitioners into marine protection and MSP decisions was developed. Techniques to derive geospatial genetic data layers, which can be viewed and mapped alongside other kinds of spatial data commonly used by conservation practitioners, hold promise for increasing the accessibility of genetic data to support policy decisions more fully.
3. While applicable to many mobile and sessile taxa, an initial focus was placed on marine mammals, and the approach was developed and refined through a series of international meetings and published papers, as well as the development of interactive, expert-reviewed case studies hosted on the MSP tool SeaSketch.

4. Outcomes of the work to date are currently serving in the policy arena by informing the identification of Important Marine Mammal Areas, an initiative led by the IUCN Marine Mammal Protected Areas Task Force to apply criteria to identify marine mammal habitats across the world's ocean, seas and relevant inland waters through a standardized process.
5. It has become clear that geospatial genetics has great potential to foster increased collaboration among an intersectional community of geneticists, spatial ecologists, and practitioners. This increased opportunity for dialogue and cooperation will help ensure that evolutionary processes are factored into marine protection and MSP processes, and potentially for freshwater and terrestrial systems.

KEYWORDS

genetics, habitat management, mammals, ocean

1 | INTRODUCTION

1.1 | The value of genetics in marine protection and spatial planning

The persistence of biodiversity requires the protection of evolutionary processes at the scale of individuals, populations, species, and ecosystems (Moritz, 2002; Santamaría & Mendez, 2012). The maintenance of genetic diversity is necessary to promote resilience to environmental disruption, such as habitat loss and climate change (Laikre et al., 2016; Nielsen et al., 2017); in general, the more diverse the gene pool of a species, the greater its adaptive potential under changing conditions (Laikre et al., 2016). The importance of accounting for genetic diversity and evolutionary processes has been reflected in a range of policy mechanisms. For example, reporting on the conservation of genetic resources is now required by international and regional policy processes, such as the United Nations Convention on Biological Diversity (Target 13; <https://www.cbd.int/sp/targets/default.shtm>), the European Union Biodiversity Strategy (http://ec.europa.eu/environment/nature/biodiversity/strategy/index_en.htm), the Pan-European Streamlining of European Biodiversity Indicators initiative (<https://biodiversity.europa.eu/topics/sebi-indicators>), and the Food and Agriculture Organization of the United Nations and its International Treaty for Plant Genetic Resources for Food and Agriculture (<http://www.fao.org/plant-treaty/en/>). Significant ongoing effort is required, however, to ensure that genetics is meaningfully incorporated into conservation policy (Hoban et al., 2020; Laikre et al., 2020).

A necessary precursor to protecting the marine environment is the identification of areas of high importance in relation to a specific conservation objective, such as the protection of a priority species or habitat. These priority areas may be considered within a conservation context (e.g. as a marine protected area (MPA), or an area requiring additional regulations) or within a broader marine spatial planning

(MSP) context. MSP can provide an ecosystem-based conservation approach that considers ecological, economic, and social objectives for marine areas, usually through political processes (Underwood, Taylor & Tucker, 2018; Santos et al., 2019). The identification of priority areas and the ecological aspect of MSP must rely on indicators such as habitat type, species richness, and species behaviour, as recorded in foraging locations or migration patterns (Nielsen et al., 2017). These data are usually gathered through expert opinion and from various spatial data derived from field surveys, habitat maps, and satellite telemetry studies, among others (Shucksmith et al., 2014; Dawson et al., 2017; Baker & Harris, 2020). Genetic approaches provide unique and complementary information to these commonly relied-on sources of spatial data that confer a strong rationale for integration into marine protection and MSP efforts.

Genetic tools can be used to assess genetic variation pertinent to marine protection and MSP at multiple scales: between individuals (e.g. parentage-analysis), within and between populations (e.g. defining population or management units and determining effective population size, genetic diversity within a population, and degree of connectivity between populations), within and between species (e.g. taxonomic units, evolutionary potential), and within and between communities (e.g. species diversity and richness) (DeSalle & Amato, 2004). These genetic metrics can inform marine protection and spatial planning in a number of ways, including identifying priority management units (Moritz, 1994; Beger et al., 2014; von der Heyden et al., 2014), defining the appropriate boundaries of 'important' areas (Bowen, 2016; Mertens, Treml & von der Heyden, 2018), or unveiling habitats or species that may exhibit greater resilience to environmental change (Hoffmann & Sgro, 2011; Palumbi et al., 2014; Lighten et al., 2016). Research suggests that consideration of genetic data provides a better understanding of spatial patterns of biodiversity and can result in the identification of priority areas that would otherwise have been overlooked (Nielsen et al., 2017). For

example, in the development of California's network of ecologically connected MPAs, genetic sampling and analyses were conducted to determine optimal spacing and connectivity for MPAs in the network (Richards et al., 2007; Botsford et al., 2014). In the Coral Triangle, genetic data have been used to investigate species richness and barriers to dispersal, and serve to define management regions to fill a 'critical gap' in designing marine reserve systems for the region (Barber, 2009; Beger et al., 2014).

Notwithstanding the utility of genetic data and associated information in marine protection and MSP, the systematic integration of genetic information has been generally lacking (Taylor, Dussex & van Heezik, 2017; Sandström et al., 2019). One of the primary drivers of this genetics-policy implementation gap appears to be a knowledge and communication disconnect between geneticists and the policy and management community (Hoban et al., 2013b; Taylor, Dussex & van Heezik, 2017; Laikre et al., 2020). Geneticists generate a wealth of valuable data, but it is often not served in a form that can be easily used by conservation practitioners and therefore is generally overlooked in conservation planning (Hoban et al., 2013b). However, conservation practitioners have expressed a strong interest in the use of genetic information if it were more easily translated into conservation actions (Hoban et al., 2013b), and research demonstrates a need for increased public awareness of the significance of genetic information and its incorporation into management and policy decisions (von der Heyden et al., 2014; Mertens, Trembl & von der Heyden, 2018). There is, therefore, a need to develop—through partnerships between geneticists and conservation practitioners—methods that enable practitioners to understand and use genetic data; in turn, these partnerships also serve to improve geneticists' understanding of the needs of practitioners, so they can enhance communication and application of their work (Hoban et al., 2013b; Haig et al., 2016).

1.2 | Empowering scientists and decision-makers through geospatial tools

Collaboration requires that parties with disparate, complementary knowledge are able to share information and come to a common understanding of a problem or decision. To fold new science into the practice of marine protection and MSP, scientists themselves must be able to conceive of how their work contributes to spatial management. Similarly, when scientists and practitioners engage in a collaborative process, they must come to a common understanding of some set of foundational information. Datasets familiar to the scientists, and other specialized information familiar to non-scientist participants, must be shared across this diverse group. This knowledge-sharing is critical to completing the initial steps of a scientifically informed marine protection and MSP process.

Mapping has been shown to be an effective tool to promote the integration of complex sets of information. Where diverse participants are working toward solutions and agreement, geospatial tools support the development of a common language for

understanding context and conditions, and devising common solutions (Cravens, 2016). However, sharing maps and discussing individual layers is not nearly as powerful as the immersion into spatial data and the context that can be achieved with geospatial tools. Simple features—layering datasets, turning them on and off, adjusting transparency, zooming and panning across the map—allow a user to interactively explore the mapped content. The process of interrogating the map in this way allows for a deeper integration of knowledge for each individual, resulting in a stronger foundation for collaboration as a group.

When scientists can come together around geospatial tools, map their data, and co-develop map data products, they are better equipped to communicate their work to planners or other decision-makers. Not only do they create a clear picture within the scientific community of how their research can inform management, but they also produce valuable resources to orient outsiders to their work.

1.3 | The need for a geospatial genetics approach

There is both a need for and value in visualizing genetic information in a geospatial manner alongside other data types commonly used as a basis for marine protection and MSP (e.g. habitat models, satellite tracking) in a way that is both ecologically meaningful and useful for practitioners. Existing tools such as Marxan (Ball, Possingham & Watts, 2009), geneGIS (Dick et al., 2014), MVMapper (Dupuis et al., 2018), SpaceMix (Bradburd, Ralph & Coop, 2016), and other geographic information system (GIS)-based approaches (Souto et al., 2015) have shown advancements in spatial mapping of genetic data, and the Conservation Genetic Resources for Species Survival or 'ConGRESS' (Hoban et al., 2013a; <http://www.congressgenetics.eu>) offers an extremely detailed resource regarding the importance of genetic information for management across species and systems. In addition, the field of landscape genetics (Manel et al., 2003), and the related seascape (Selkoe, Henzler & Gaines, 2008) and waterscape genetics (Selkoe, Scribner & Galindo, 2016), seeks to explain observed spatial genetic patterns by using environmental variables (e.g. topography, oceanography) and has established an explicitly spatial analytical framework by which to explore such relationships (e.g. McRae, 2006; Mendez et al., 2010; Peterson et al., 2019). However, tools that unify spatial genetics with conservation and enable practitioners to more easily integrate genetic data and associated information into spatial *planning* processes are lacking, and specific guidance for the policy and management community on why genetic information is important and how to accurately interpret it is needed.

1.4 | Marine mammals as a geospatial genetics study system

To date, work by the authors has focused largely on marine mammals, although the geospatial genetics approach is broadly applicable to

both mobile and sessile organisms, across a range of ecosystems (marine, terrestrial, and fresh water): essentially, any system where there is spatial genetic variation. Patterns of genetic variation within a species arise and are maintained as a result of interaction between the fundamental processes of mutation, genetic drift, natural selection, and migration. Elucidating these patterns provides important insights for management, including the identification of population units and the degree of migration and interbreeding that occurs between them, barriers that limit gene flow, population size and resulting relative vulnerability, and levels of genetic diversity that may be indicative of adaptive potential (Allendorf, Luikart & Aitken, 2012). Marine mammals represent an interesting study system from a genetics perspective as they exhibit a wide range of complex behaviours capable of influencing their genetic population structure at multiple scales. Population-level fidelity to breeding and feeding areas, as well as environmental factors, have proven to be important drivers of genetic isolation between populations for many marine mammal species (e.g. Mendez et al., 2010; Corrigan et al., 2015; Amaral et al., 2017); however, there is increasing evidence that genetic structure within populations is driven by subtle, and sometimes socially driven, differences in dispersal and migratory behaviours that form barriers to gene flow (e.g. Rendell et al., 2012; Kershaw et al., 2017). This behavioural partitioning within a population may, for example, be linked to differences in the timing of migration on the basis of age, sex, or reproductive status (e.g. Carvalho et al., 2014), habitat and foraging specializations of certain individuals (e.g. Wright et al., 2016), or different social strategies (e.g. Andrews et al., 2010). Moreover, it may be challenging to identify different species in the field without the use of genetic tools, either due to cryptic morphology (e.g. Kershaw et al., 2013) or the logistical difficulties of identifying marine mammals in the field (Taylor et al., 2017). Collectively, these factors pose challenges when developing appropriate protections for these species in the absence of genetic information.

In addition to their genetic complexity, marine mammals are a global conservation priority. Important habitats for marine mammal species occur throughout the ocean, from the tropics to the poles, across shallow estuarine and riverine areas, along coastal shoreline and rocks (i.e. rookeries and haul-outs), and to the deep ocean and marine areas beyond the limits of national jurisdiction. Despite this wide range of habitats, the threats to the vital activities of marine mammal species are often similar: fishing; shipping; anthropogenic noise; oil and gas exploration and development; and habitat degradation (Avila, Kaschner & Dormann, 2018). The resulting impacts on marine mammals include habitat loss and displacement, food scarcity, impaired reproduction and health, injury, and direct mortality. Marine mammals are also viewed as sentinel species, alerting us to changes in ocean environments that may be in some cases associated with anthropogenic activities (e.g. shifts in prey distribution or availability, habitat deterioration or loss) that we have not yet detected by other means; this makes them a valuable resource as we try to understand the impact of climate change on the ocean (Bossart, 2011). In a broader context, the protection of important

habitat for marine mammals, which is often on a sizable spatial scale, may serve as an 'umbrella' of protection for other vulnerable species (Roberge & Angelstam, 2004; Caro, 2010; Hoyt, 2011). Area-based protection and management, as informed by marine mammal habitat delineation, also provides a framework for assessing cumulative impacts by enabling the analysis of multiple sectors or impacts operating within a defined area.

While these factors have led us to focus initial efforts on developing geospatial genetic tools for marine mammal protection, the values and spatial mapping techniques described herein are broadly applicable to any species group or ecosystem. That said, our approach is necessarily dependent on species-specific data, and therefore is limited in scope when contrasted to some existing generic tools and guidance (e.g. ConGRESS; Hoban et al., 2013a).

1.5 | Case study: Identifying Important Marine Mammal Areas

1.5.1 | Brief Introduction to the Important Marine Mammal Area process

In 2016, after 3 years of preparatory work, the Marine Mammal Protected Areas Task Force rolled out a new tool, Important Marine Mammal Areas (IMMAs), to apply criteria to identify marine mammal habitats across the world's ocean, seas and relevant inland waters through a standardized process (Notarbartolo di Sciara et al., 2016). IMMAs are defined as *discrete portions of habitat important to marine mammal species, that have the potential to be delineated and managed for conservation*. They consist of areas that may merit space-based protection of some kind, or at least periodic monitoring, and can be seen as a potential 'marine mammal layer' for consideration by governments, inter-governmental organizations, conservation groups, industry, and the public. Methods for identifying IMMAs were developed and reviewed by experts and distributed for wide public consultation in 2015. There are eight criteria and sub-criteria, divided into four main categories: (i) species or population vulnerability (based on the IUCN Red List status); (ii) distribution and abundance, including small and resident populations and aggregations; (iii) key life cycle activities, including reproductive areas, feeding areas and migration routes; and (iv) special attributes, including distinctiveness and diversity (IUCN Marine Mammal Protected Areas Task Force, 2018).

IMMAs are not prescriptive, and as an evidence-driven, purely biocentric process, they have no inherent legislative or intended management result. Still, by highlighting areas of regional or global importance for cetaceans, pinnipeds, and other marine mammals, they can serve as powerful tools to inform MSP and the selection of MPAs and MPA networks, especially where nations have specific commitments to marine mammal protection. For example, at the 12th Conference (Manila, October 2017), the Parties to the Convention on Migratory Species of Wild Animals (CMS) adopted Resolution 12.13 ("Important Marine Mammal Areas – IMMAs"). The endorsement of

IMMAs by the CMS Parties effectively links science-based evidence of the presence and whereabouts of marine mammal habitat to the decision-making process. The resolution also highlighted how IMMAs complement and contribute to other spatial assessment tools such as the Convention on Biological Diversity's ecologically or biologically significant areas, the International Maritime Organization's particularly sensitive sea areas, and IUCN's key biodiversity areas standard (Notarbartolo di Sciara et al., 2016).

To identify IMMAs, the world's ocean and seas were subdivided into various regions. Up to early 2020, 127 IMMAs had been identified in six regions: the Mediterranean (2016); Pacific Islands (2017); North-East Indian Ocean and South-East Asian Seas (2018); Extended Southern Ocean (2018); Western Indian Ocean and Arabian Seas (2019); and Australia, New Zealand, and South-East Indian Ocean (2020). IMMA identification work will continue to complete coverage of the southern hemisphere, before moving to the remainder of the northern hemisphere. The identification of IMMAs in each region is based on a four-stage process: (i) submissions of Areas of Interest (Aols) by the scientific community and the collation of an inventory of the available knowledge of marine mammal habitat in the considered region; (ii) a regional expert workshop where Aols deemed to fulfil the IMMA criteria and supported by adequate evidence are put forward as candidate IMMAs (cIMMAs); (iii) peer-review of cIMMAs by an independent review panel and assignment of IMMA status; and (iv) communication of results, including the population of an electronic atlas (eAtlas; <https://www.marinemammalhabitat.org/imma-eatlas/>) available for users of the IMMA knowledge product. All Aols and cIMMAs are archived to promote research activities to achieve the future determination of IMMA status.

1.5.2 | How genetics inform the IMMA criteria and process

Genetic tools are among the primary means of delineating population units and are useful for developing estimates of abundance, both of which form the basis of the IMMA criteria. Genetic diversity metrics are also useful in informing conservation prioritization for species and populations, for example by providing insights on evolutionary potential or vulnerability to perturbation. Specific intersections between genetic tools and the individual IMMA criteria and format of the data that would be employed are summarized in Table 1. A wide array of analytical approaches and genetic marker types are useful to support the identification of IMMAs, from: (i) species-level analyses to inform IMMA criteria A (Species or population vulnerability) and D (Special Attributes; e.g. phylogenetic trees based on mitochondrial or nuclear gene sequences, genetic diversity metrics); to (ii) population-level analyses to inform IMMA criteria A (Species or population vulnerability), B (Distribution and abundance), C (Key life cycle activities), and D (Special attributes; e.g. population distinctiveness and diversity metrics based on restriction site-associated sequencing); to (iii) individual-level analysis to inform IMMA criteria B (Distribution and abundance) and C (Key life cycle activities; e.g. site fidelity based

on unique microsatellite genotypes; Table 1). This demonstrates the utility of genetic data and associated information in supporting IMMA identification and highlights this area of applied research as one with significant potential for expansion.

Different types of genetic markers have different properties that directly affect their interpretation. For example, mitochondrial sequences are maternally inherited and provide insights into female-mediated gene flow, whereas Y chromosome markers provide information about male-mediated gene flow, and biparentally inherited markers, such as nuclear microsatellites provide information regarding gene flow for both sexes. The mutation rate of a genetic marker also influences the temporal scale of the inference that can be made. Rapidly mutating microsatellites provide insights into contemporary (e.g. genotypic matches of the same individual) or more recent evolutionary processes (e.g. emerging population units), whereas moderately evolving mitochondrial sequences provide a more historical perspective (e.g. established population differentiation), and slowly evolving nuclear coding genes provide insights into the distant past (e.g. speciation events). High-throughput DNA sequencing technologies are being increasingly used for conservation, protection and spatial planning questions: these technologies allow researchers to conduct analyses using thousands of genetic markers across the genome (e.g. single nucleotide polymorphisms), thereby significantly increasing the statistical power of inference when compared to traditional approaches, which typically relied on 10–20 markers (Allendorf, Hohenlohe & Luikart, 2010). Genome-wide analyses also have potential to provide insight into genomic adaptation of populations to local habitats, which could be informative for predicting how populations will respond to future environmental change (Hoelzel, Bruford & Fleischer, 2019). However, best practices for incorporating adaptive genomic information into management decision-making are still being developed (Funk et al., 2019). In the context of a marine protection and MSP process, understanding the different types of research questions that can be addressed with different types of genetic markers is critical to ensure that the appropriate genetic tool is employed to meet the conservation objective(s) of that particular process.

2 | METHODS

2.1 | Developing a geospatial genetics approach

To meet the need for the integration of genetic data and associated information into marine protection and MSP, an approach to geospatially represent genetic data and associated information in a way that can be more easily understood and readily integrated by practitioners was developed. Genetic data (e.g. measures of population differentiation, connectivity) are transformed to simple geospatial data layers that are easy to interpret by non-geneticists (i.e. through colour coding, symbology, etc.) and can be mapped alongside other spatial genetic (e.g. landscape and seascape genetic analyses) and non-genetic (e.g. satellite telemetry, habitat models)

TABLE 1 How genetic data and analyses inform the individual Important Marine Mammal Area (IMMA) criteria

IMMA criterion	Genetic tool(s)	Data format
A) Species or population vulnerability	Identification of species	Phylogenetic trees Coalescent-based trees Diagnostic sequence characters (DNA barcodes)
	Identification of stocks and populations	Coalescent-based trees Genetic differentiation indices (e.g. F_{ST} , Φ_{ST}) Clustering algorithms Assignment probabilities PCA-based analyses
	Changes in abundance through time	Allele frequency distribution Time since bottleneck Changes in population size over time
	Effective population size (N_e)	Measure of effective population size (N_e)
	Population diversity	Genetic diversity indices (continuous measures, e.g. H_o , H_e , A_R) Inbreeding level
	Species diversity	Phylogenetic trees Coalescent-based trees Clustering algorithms Species diversity measures
B) Distribution and abundance (<i>sub-criterion B(i) Small and resident populations</i>)	Number and distribution of populations	Genetic differentiation indices (e.g. F_{ST} , Φ_{ST}) Clustering algorithms Assignment probabilities PCA-based analyses Seascape genetics spatial analysis
	Effective population size (N_e)	Measure of effective population size (N_e)
	Changes in abundance through time	Allele frequency distribution Time since bottleneck Changes in population size over time
	Site fidelity	Genotypic matches Relatedness analyses
C) Key life cycle activities	Connectivity between different areas (e.g. breeding and feeding areas)	Sex-biased population structure and dispersal Genotypic matches Seascape genetics spatial analysis
	Site fidelity	Genotypic matches Relatedness analyses
	Sex-specific differences	Sex-biased population structure and dispersal Genotypic matches Relatedness analyses
	Mixing on migratory routes	Mixed stock analysis Genotypic matches
D) Special attributes	Evolutionary distinctive species (<i>sub-criterion D(i) Distinctiveness</i>)	Phylogenetic trees Coalescent-based trees Diagnostic sequence characters (DNA barcodes)
	Highly isolated populations within a species (<i>sub-criterion D(i) Distinctiveness</i>)	Phylogenetic trees Coalescent-based trees Diagnostic sequence characters (DNA barcodes) Genetic differentiation indices (e.g. F_{ST} , Φ_{ST}) Clustering algorithms Assignment probabilities PCA-based analyses
	Species diversity (<i>sub-criterion D (ii) Diversity</i>)	Phylogenetic trees Coalescent-based methods Clustering algorithms Species diversity measures

Abbreviations: A_R , allelic richness; F_{ST} , fixation index that measures population differentiation due to genetic structure; H_e , expected heterozygosity; H_o , observed heterozygosity; Φ_{ST} , fixation index that weights genetic distance among alleles; PCA, principal component analysis.

data types. Non-spatial genetic information is presented through simple graphics (e.g. bar charts, pairwise matrices) that can be viewed in tandem with the geospatial genetic data. Consideration of non-spatially transformed genetic data is crucial for accurate interpretation and contextualization of the simple graphical representations that form the basis of the geospatial genetics approach. All geospatial genetic data layers and graphics are paired with simple explanations to increase accessibility to practitioners. Following this approach, geneticists can transform and present their findings in a way that practitioners can integrate more easily into decision making. Geospatial genetic information is particularly powerful when combined with a collaborative MSP tool, such as SeaSketch (<https://www.seasketch.org/>; a free and open source version of SeaSketch will be available in early 2022), which enables practitioners to easily map and explore different genetic and non-genetic data layers, access graphics and supporting information, test different MSP scenarios, and actively engage with stakeholders throughout the planning process (see Pınarbaşı et al., 2017, and Janßen, Göke & Luttmann, 2019, for reviews on spatial and web-based tools that support marine spatial planning). This work was developed and refined through a series of meetings (including panel discussions and workshops at the 3rd International Marine Protected Areas Congress in 2013, the 3rd and 4th International Marine Conservation Congress in 2014 and 2016, and the 21st Biennial Conference of the Society of Marine Mammalogy in 2015), published papers (Kershaw & Rosenbaum, 2014; Mendez et al., 2014; IUCN Marine Mammal Protected Areas Task Force, 2018), and development of interactive, expert-reviewed case studies. As described below, this work is currently serving in the policy arena by informing the identification of IMMAs, an initiative led by the IUCN Marine Mammal Protected

Areas Task Force, which has cultivated an intersectional community of geneticists, spatial ecologists, and practitioners interested in collaborating to advance this approach.

2.2 | Case study development and expert consultation

Prototype case studies demonstrating the geospatial mapping of genetic data to support the identification of IMMAs were developed through a collaborative process using the MSP tool SeaSketch. To date, case studies have been developed for the highly migratory humpback whale in the South-East Atlantic and Western Indian Ocean (Figure 1; <https://humpbacks.seasketch.org/>; Kershaw, 2015; Kershaw et al., 2017), the spinner dolphin in Hawaiian waters (Figure 2; <https://spinners.seasketch.org/>; Andrews et al., 2010), and the common bottlenose dolphin in the Wider Caribbean (Figure 3; <https://tursiops.seasketch.org/>; Caballero et al., 2011), to demonstrate how genetic data may need to be mapped and interpreted differently for species with different life histories and habitat preferences. The humpback whale and spinner dolphin case studies were reviewed by a group of experts to assess the utility of the overall approach and gather specific feedback for improvement. The Hawaiian spinner dolphin case study falls within the Pacific Islands IMMA region and, due to the still incomplete global coverage of IMMAs, the humpback whale case study partially falls within the Western Indian Ocean and Arabian Seas IMMA region. The Wider Caribbean region has not yet been assessed through the IMMA process.

Genetic data and associated information were transformed for each of the three case studies using a standard set of relatively

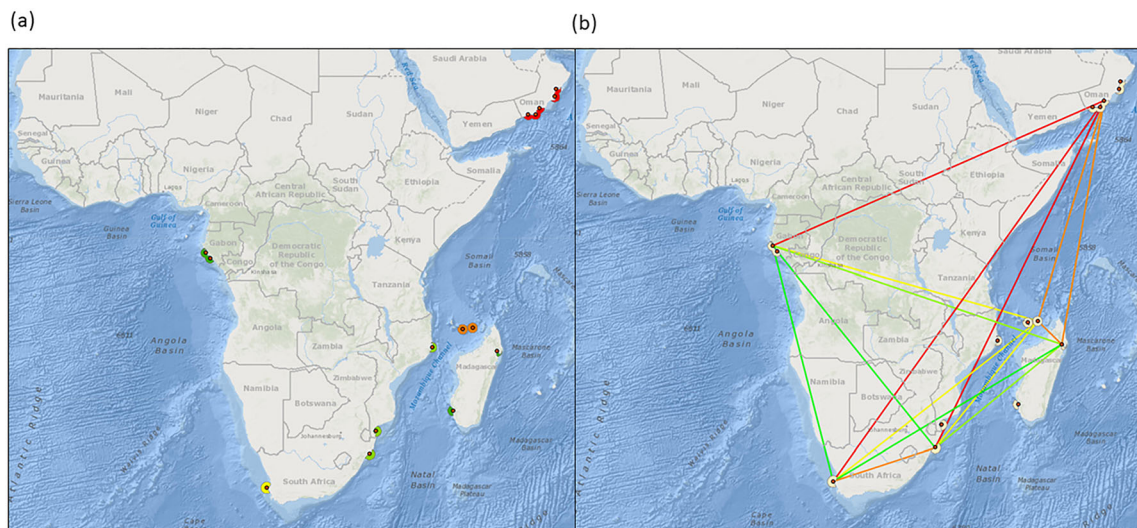


FIGURE 1 Two examples of geospatial genetic data layers from the humpback whale case study in SeaSketch: (a) Magnitude of east to west genetic connectivity based on nine nuclear microsatellite markers for humpback whales between six major sampling sites in the South Atlantic and Western Indian Ocean (Kershaw et al., 2017; green: high connectivity; yellow: medium connectivity; red: low connectivity); (b) Genetic diversity (number of haplotypes) for humpback whales across 10 sampling sites based on a 484-bp sequence of the mitochondrial control region (Kershaw et al., 2017; green: high genetic diversity; yellow/orange: moderate genetic diversity; red: low genetic diversity)

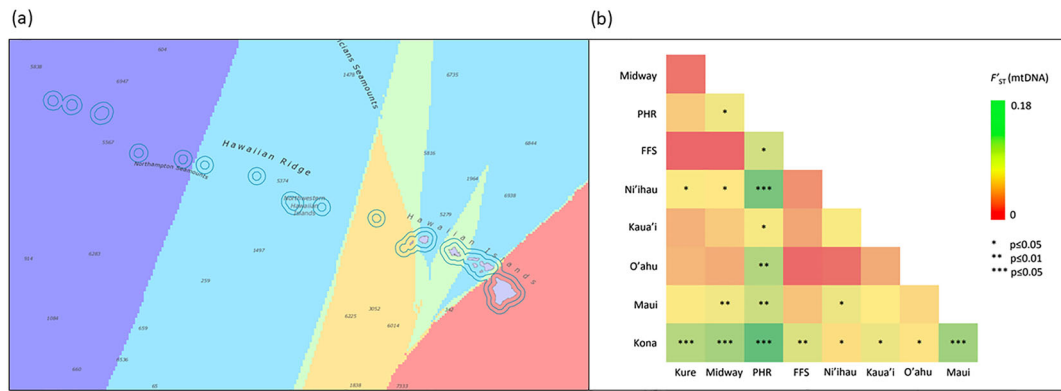


FIGURE 2 Two examples of geospatial genetic data layers and graphical analyses from the spinner dolphin case study in SeaSketch: (a) Pairwise population differentiation (F_{ST}) for spinner dolphins between Hawaiian Islands based on 10 nuclear microsatellites (Andrews et al., 2010; green: low differentiation; red: high differentiation); (b) Interpolated local F_{ST} (population differentiation) for spinner dolphins across the Hawaiian Archipelago based on a 474-bp sequence of the mitochondrial control region (Andrews et al., 2010; genetically different groupings are indicated by the red, orange, and blue shading)

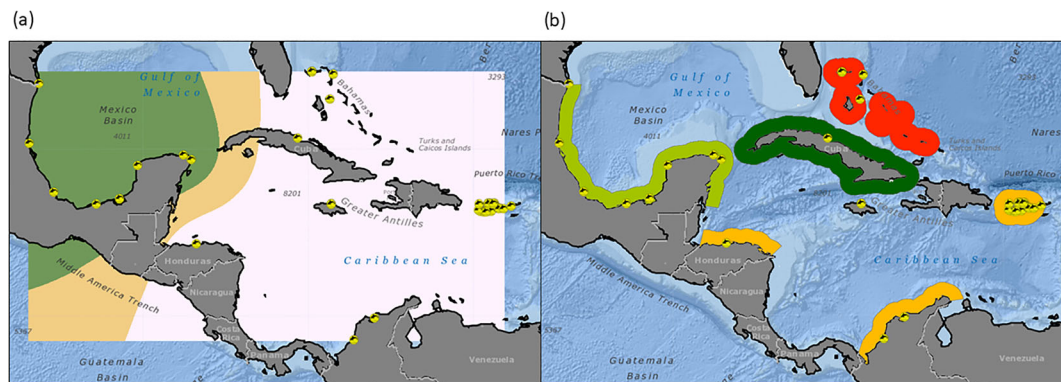


FIGURE 3 Two examples of geospatial genetic data layers from the bottlenose dolphin case study in SeaSketch: (a) Sampling locations (yellow symbols) and interpolated local F_{ST} (population differentiation) for common bottlenose dolphins across the Wider Caribbean based on a 386-bp sequence of the mitochondrial control region (Caballero et al., 2011). The colour bands indicate sampling locations that are differentiated from one another (i.e. samples within the green band are most genetically different from those in the yellow band; samples within the tan band show intermediate genetic differentiation); (b) Genetic diversity (number of alleles) for common bottlenose dolphins for nine sampling regions in the Wider Caribbean based on nine nuclear microsatellites (Caballero et al., 2011; green: high genetic diversity; yellow: moderate genetic diversity; red: low genetic diversity)

simple GIS techniques (Table 2) and uploaded to the MSP tool SeaSketch. Detailed descriptions of each of the genetic data layers and their meaning were added to each SeaSketch project to increase accessibility to non-geneticists, provide context, and support accuracy of interpretation. Additional graphics of key ‘analytics’ (e.g. pairwise population differentiation matrices, haplotype networks) were also uploaded to the SeaSketch project to provide additional non-spatial information required for accurate interpretation of the simple genetic data layers. The original peer-reviewed manuscripts and supporting materials describing the genetic data were also posted on SeaSketch. The holistic consideration of each of these sources of information is necessary for robust inference about genetic data, needed for effective conservation decision making and identification of what further research is required.

2.3 | Expert evaluation of the geospatial genetics case studies

Initial feedback on the geospatial genetic data layers in SeaSketch were gathered from the scientific community at a workshop held during the 21st Biennial Conference of the Society of Marine Mammalogy in San Francisco (CA, USA). A self-selecting group of 12 workshop attendees with expertise in marine mammal genetics and spatial ecology reviewed both the humpback whale and spinner dolphin case studies and answered a series of multiple choice and long-form questions on the data layers and supporting analytics (see Supporting Information). Data layers and analytic measures that were reviewed included indices of pairwise genetic differentiation (i.e. mean local F_{ST} , pairwise F_{ST}), population structure, genetic diversity, contemporary genetic connectivity, and historical gene

TABLE 2 Summary of geographic information systems (GIS) techniques used to develop the three geospatial genetics case studies illustrated in SeaSketch

Data type	Geospatial technique(s)
Sampling locations Point of departure of survey vessels used to collect the biopsy samples used in the genetic analysis	Latitude and longitude point locations.
Sampling areas Approximate boundary of the area that biopsy samples were collected based on the maximum distance of the survey vessel from shore. This data layer is also helpful to aid visualization of other geospatial genetic layers (e.g. genetic diversity)	Layer polygons created using: (i) a radial buffer representing maximum distance from latitude longitude <i>sampling locations</i> ; clipped to offshore; (ii) the island where samples were collected.
Genetic diversity Various measures of genetic diversity for each sampling location	<i>Sampling areas</i> colour-coded as a traffic light system: red = low diversity; green = high diversity; orange = intermediate diversity. Categories of absolute values provided in the legend. 'High,' 'medium' and 'low' levels represent natural breaks, or 'jenks,' in the determined by ArcGIS. The layer's attribute table containing additional information (e.g. sample size, data collection year(s), male to female ratio, absolute value of diversity) available when user right-clicks on sampling location.
Population structure Includes a range of measures that demonstrate how genetically different each of the sampling locations are from one another (e.g. Local F_{ST} , haplotype network, genetic cluster analyses such as STRUCTURE or PCA).	Indices of population structure (e.g. Local F_{ST}): <i>Sampling areas</i> colour-coded as a gradient from high levels of population structure (i.e. isolation) to low levels of structure. Categories of absolute values provided in the legend. Matrix of statistical significance between sampling areas provided as a supplementary graphic. Interpolation of indices of population structure (e.g. Local F_{ST}) created by kriging. Kriging settings should be adjusted to best fit the data (SeaSketch projects use ArcGIS standard settings for demonstration purposes only). Haplotype network: <i>Sampling areas</i> colour coded to reflect the geographic locations included in the haplotype network. Haplotype network provided as a supplementary graphic. Cluster analyses: <i>Sampling areas</i> colour coded to reflect the identified clusters. More information on clusters (e.g. STRUCTURE or PCA output provided as a supplementary graphic.
Connectivity Series of measures of connectivity between different sampling locations. Data may range from contemporary connectivity based on genetic matching of individuals (interchange index) to long-term (many generations) population connectivity.	Layer linear connections created between each <i>sampling location</i> and provided with the connectivity value recorded between those two locations. All lines within the layer are then joined and colour coded based on a traffic light system reflecting the level of connectivity: red = low connectivity; green = high connectivity; orange = intermediate connectivity. Levels of connectivity represent natural breaks, or 'jenks,' in the data, as determined by ArcGIS. Categories of absolute values are provided in the legend. Bar charts of magnitude and directionality of genetic connectivity may also be provided as a supplementary graphic.

flow. Guidance was sought on how understandable and easy to interpret the data layers and analytics were in their current form relative to the experts' knowledge of the underlying data and species, and how they might be improved.

3 | RESULTS

3.1 | Case study 1: Humpback whales in the South-East Atlantic, Western Indian Ocean, and Arabian Sea (Figure 1a,b)

One of the best studied migratory marine species is the humpback whale (*Megaptera novaeangliae*), which typically migrates annually

from low-latitude breeding areas to high-latitude feeding areas (Gambell, 1976). Humpback whale genetic structure at the ocean basin scale is driven by a combination of natal philopatry to breeding areas and maternal fidelity to feeding areas (Baker et al., 1998; Baker et al., 2013). This implies that demographically discrete populations return to the same breeding areas each year, and that low levels of exchange between breeding areas occurs; a pattern that is supported by genetic studies at the ocean basin scale (Baker et al., 1998; Rosenbaum et al., 2009; Baker et al., 2013; Rosenbaum et al., 2017). The fidelity of humpback whale populations to specific breeding areas has formed the basis for management of the species. Demographically discrete 'breeding stocks' are designated by the International Whaling Commission (IWC) globally for assessment purposes. In the Southern Hemisphere, these include Breeding Stock B in the South-East

Atlantic and Breeding Stock C in the Western Indian Ocean. The highly endangered, resident, and genetically isolated 'Arabian Sea humpback whale' is a putative subspecies (Pomilla et al., 2014) that is often discussed in the context of Southern Hemisphere stocks, even though it is located in the Northern Hemisphere. Breeding Stocks B and C have been further divided into 'substocks' (B1, B2, C1, C2, and C3) due to genetic differentiation in samples taken from within the stock being suggestive of a level of demographic independence (IWC, 2006).

As observed for other migratory species in both hemispheres (Alter, Newsome & Palumbi, 2012; Kershaw et al., 2013), genetic studies of humpback whales continue to reveal more complex structure at finer spatial scales than accounted for in current stock designations (Kershaw et al., 2017). For example, the relatively small number of genetically distinct whales observed feeding and migrating off west South Africa, referred to as Breeding Substock B2 by the IWC (whales have not been observed breeding in this area), may consist of whales that migrate north to a major breeding area off Gabon (Breeding Substock B1) and also whales that undertake inter-oceanic migration to breed in the Western Indian Ocean (Breeding Substock C1) (Pomilla & Rosenbaum, 2005; Carvalho et al., 2014; Kershaw et al., 2017). Genetic structure and connectivity for Breeding Stock C also appears to be highly complex and challenging to generalize. For example, levels of historical gene flow were found to be particularly high for females rather than males, calling the general model of maternally driven natal philopatry to breeding areas into dispute (Palsbøll et al., 1995; Baker et al., 1998; Baker et al., 2013). Estimations of gene flow also suggest higher levels of potential exchange between the three substocks of Breeding Stock C for both females and males than previously detected (IWC, 2009). Collectively, these results indicate that the typically presumed biological or management boundary of Breeding Stock B and C may be more 'porous' than previously assumed. This apparent complexity indicates that the definition of management units requires further evaluation, particularly as new evidence becomes available.

Several IMMAs have been identified in the Western Indian Ocean and Arabian Seas IMMA region based on, at least in part, humpback whale habitat (<https://www.marinemammalhabitat.org/immas/immas-searchable-database/>). Eleven IMMAs include habitat for Breeding Stock C (Aldabra Atoll; Comoros Island Chain and Adjacent Reef Banks; Kisite-Shimoni; Madagascar Central East Coast; Mascarene Islands and Associated Oceanic Features; Mozambique Coastal Breeding Grounds; North-west Madagascar and North-east Mozambique Channel; Shelf Waters of Southern Madagascar; South-East African Coastal Migration Corridor; Toliara, St. Augustine Canyon and Anakaio; Watumu-Malindi and Watumu Banks) and five IMMAs include habitat of the highly endangered Arabian Sea humpback whale (Dhofar; Gulf of Masirah and Offshore Waters; North-East Arabian Sea; Oman Arabian Sea; Maldives Archipelago and Adjacent Oceanic Waters). Consideration of findings derived from mitochondrial sequences and nine microsatellite markers and other associated information on humpback whales and Case Study 1 with the identified IMMAs (Figure 4) shows, for example, that habitats

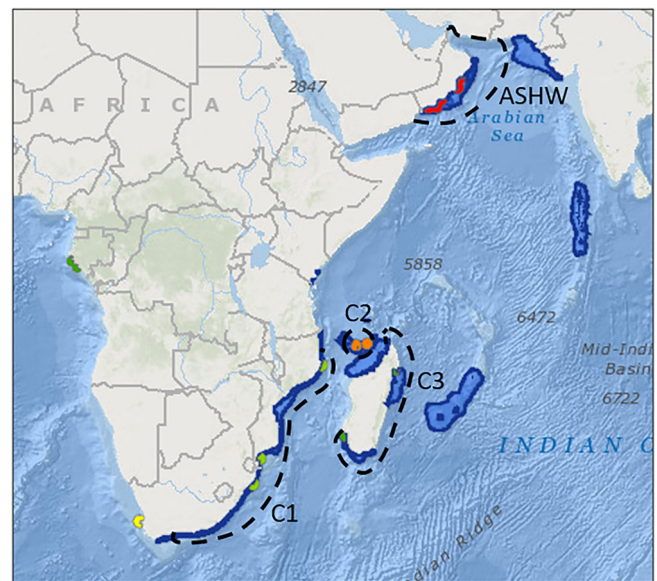


FIGURE 4 Genetic diversity (number of haplotypes) for humpback whales across 10 sampling sites based on a 484-bp sequence of the mitochondrial control region (Kershaw et al., 2017; green: high genetic diversity; yellow/orange: moderate genetic diversity; red: low genetic diversity) overlaid in SeaSketch with the 15 Important Marine Mammal Areas (IMMAs) in the Western Indian Ocean identified as having importance, at least in part, for humpback whales (blue polygons). The hypothesized boundaries of the demographically discrete breeding substocks C1, C2, and C3, and the genetically isolated Arabian Sea humpback whale population (ASHW) are indicated by dashed lines (IWC, 2011; Rosenbaum et al., 2017). The overlay shows how different genetic groups are represented by different IMMAs and how IMMAs may provide greater resolution of important habitat areas within the broad-scale ranges of demographically discrete populations

corresponding to the geographic distribution of the three genetically differentiated substocks of Breeding Stock C are represented in multiple IMMAs. The strong genetic isolation of the critically endangered Arabian Sea humpback whale supports the designation of multiple IMMAs within the Arabian Sea. Due to the highly migratory nature of humpback whales, the distribution of genetically distinct populations and habitats of higher relative importance are difficult to resolve and may be defined at too great a spatial scale to be directly useful for marine protection and MSP efforts. By combining genetic data and associated information with other data types (e.g. habitat parameters, behaviour, direct observations)—as carried out through the IMMA process—habitat areas that are representative of the genetic diversity of the species can be identified at management-relevant scales.

For humpback whales, translation of the complex genetic patterns into a geospatial form enables both the researcher and practitioner to more easily appraise humpback whale genetic patterns at multiple scales, more rapidly evaluate levels of genetic differentiation and connectivity between breeding stocks and substocks, and easily compare genetic information with other forms

of spatial data indicative of important humpback whale habitat (e.g. bathymetry, distance from shore). Moreover, geospatial genetics provides an effective tool to communicate genetic results. For example, colour-coding demonstrates the lack of connections between the Arabian Sea humpback whale putative subspecies to other breeding stocks, making its isolation more easily apparent to non-geneticists and therefore useful in communicating why urgent conservation action is needed. That said, complexities inherent in humpback whale population genetic structure are difficult to convey in their entirety via graphical spatial overlays. This case study highlights the importance of appraising geospatial genetic information in tandem with non-spatial genetic information (e.g. matrices of population differentiation), and developing a common understanding of the constraints of each data type so any apparently contradictory data can be identified, explained, and factored into decision making.

3.2 | Case Study 2: Spinner dolphins in the Hawaiian Archipelago (Figure 2a,b)

Spinner dolphins (*Stenella longirostris*) are a major target of the wildlife tourism industry in the Hawaiian Archipelago due to the predictable daytime occurrence of this species in calm, nearshore waters. This has led to frequent and close human interactions with Hawaiian spinner dolphins and has raised concerns regarding potential negative impacts on the dolphins (Heenehan et al., 2017; Tyne et al., 2018). Hawaiian spinner dolphins are nocturnal, feeding offshore at night and resting in nearshore waters during daylight hours. Because human activity affects spinner dolphins during daylight hours, this may disrupt sleep patterns and lead to decreased fitness for the dolphins.

Genetic data can be used to help assess the impact of human activity on Hawaiian spinner dolphins by providing information regarding population structure and genetic diversity across the archipelago. A population genetic study of spinner dolphins was conducted across the Hawaiian Archipelago with samples collected from all islands where this species is regularly sighted, using 10 microsatellite markers and mtDNA control region sequences. This study revealed significant genetic divergence between most islands, with the strongest genetic breaks separating three groups of islands: (i) the three most westerly islands (Kure Atoll, Midway Atoll, and Pearl & Hermes Reef); (ii) the most easterly island (Hawai'i Island or 'the Big Island'); and (iii) the central archipelago (from Maui westward to the French Frigate Shoals; Andrews et al., 2010). Surprisingly, population structure did not always correspond with expectations based on geographic distance between islands; for example, Maui was more distinct from the Big Island, which is less than 50 km away at the Alenuihāhā Channel's narrowest point, than it was from French Frigate Shoals, which is almost 1,000 km away. In contrast, patterns of genetic diversity more closely followed predictions, with the highest diversity occurring for dolphins sampled at the island with the largest population size (the Big Island) and the lowest diversity occurring for dolphins sampled at the islands with the smallest population sizes (the three most westerly islands). These genetic data were used to define

five island-associated stocks for management of spinner dolphins in the Hawaiian Archipelago (Hill, Oleson & Andrews, 2010).

The Main Hawaiian Archipelago IMMA comprises 61,950 km² of continuous waters surrounding the Big Island westwards to Ni'ihau and encompasses the home ranges of 11 small, resident, island-associated cetacean species, including the Hawaiian spinner dolphin (<https://www.marinemammalhabitat.org/portfolio-item/main-hawaiian-archipelago/>). Comparison of the genetic information on spinner dolphins presented in Andrews et al. (2010) and Case Study 2 with the boundaries of the IMMA shows that the habitat of the genetically distinct population found off the Big Island is included within the IMMA. However, the IMMA includes only partial habitat of the central archipelago group of islands for which genetic similarity was observed from Maui westward to French Frigate Shoals, as French Frigate Shoals falls beyond the IMMA's western boundary. Furthermore, the IMMA does not include the spinner dolphins in the three most westerly islands of the archipelago. Nonetheless, the IMMA does include the region within the Hawaiian Archipelago where the majority of human activity occurs that is likely to impact spinner dolphins. While the intent of the Main Hawaiian Archipelago IMMA is to be comprehensive in terms of its inclusion of marine mammal habitat for multiple species, as per the IMMA criteria, the genetic results described in Andrews et al. (2010) have provided valuable information for defining management units *within* the IMMA (Hill, Oleson & Andrews, 2010). In addition, the archipelago-wide analysis of genetic structure for spinner dolphins provides a potential future basis for extending the IMMA westwards to encompass more habitat for this and other marine mammal species.

Overall, the multi-layered colour-coded map illustrating the genetic structure and diversity analyses described in Andrews et al. (2010) for the Hawaiian spinner dolphin provides a visually appealing tool to quickly observe the genetic results, and enhances the ease of visualizing the striking lack of correspondence between genetic structure and geographic distance between some islands. This map has strong potential as a practical tool to inform future IMMA delineations or revisions and for managers seeking to use scientific evidence to effectively define and prioritize management units of spinner dolphins within the Hawaiian Archipelago.

3.3 | Case Study 3: Bottlenose dolphins in the Wider Caribbean Sea (Figure 3a,b)

The common bottlenose dolphin (*Tursiops truncatus*) is a well-researched cetacean with worldwide distribution occurring in tropical to temperate waters. The species has been categorized as 'Least Concern' by the IUCN (Wells, Natoli & Braulik, 2019); however, three populations (called 'subpopulations' by the IUCN) are rated variously as Vulnerable (Mediterranean), Endangered (Black Sea) or Critically Endangered (Fiordland, New Zealand) (Birkun, 2002; Bearzi, Fortuna & Reeves, 2008; Currey, Dawson & Slooten, 2009; Bearzi, Fortuna & Reeves, 2012). This conservation status applies particularly to coastal populations that are under threat from human activities, such as

habitat loss or degradation, direct and incidental mortality from fisheries, direct and indirect disturbance and harassment by vessels and vessel noise, and exposure to contaminants such as PCBs and DDT (Wells & Scott, 1999; Kannan et al., 2000; Wells et al., 2008; Vollmer & Rosel, 2013; May-Collado & Quiñones-Lebrón, 2014).

Across their worldwide distribution comprising many separate populations, common bottlenose dolphins have shown great individual morphological plasticity that has resulted in different 'forms' in relation to the areas they inhabit. Their evolutionary history suggests independent colonization processes from oceanic animals into coastal habitats, with independent adaptation processes (Moura et al., 2013). As a response to adaptation to different environmental conditions, two forms, referred to as 'inshore' and 'offshore' or 'worldwide distributed' ecotype forms, have been described, but a full review of the taxonomy of this genus is still needed (Wells & Scott, 2018). The Small Cetaceans Sub-Committee of the International Whaling Commission undertook a revision of the taxonomy of this genus for three consecutive years, and their findings suggest the recognition of two species, *Tursiops truncatus* and *Tursiops aduncus*, with multiple potential subspecies (IWC, 2018), and suggest the use of at least mitochondrial DNA in order to define such subspecies (Taylor et al., 2017). Genetic analyses of mitochondrial control region sequences for 158 individuals and nine microsatellite loci for a subset of 123 individuals sampled from dead stranded dolphins, captive animals (with known origin), and free-ranging dolphins, indicate that two bottlenose dolphin ecotypes were identified in the Caribbean Sea: the 'inshore' ecotype form, characterized by the use of coastal habitats and showing comparatively lower levels of genetic diversity, and an 'offshore' or 'worldwide distributed' ecotype form, characterized by the use of oceanic habitats and showing higher levels of genetic diversity in comparison with the inshore ecotype form (Caballero et al., 2011). Genetic differentiation at the mitochondrial level between inshore and offshore ecotype forms was significant; however, the distribution of the two ecotype forms appears to overlap in most of the locations sampled. Some significant differentiation was also detected at the nuclear level for both ecotype forms between the four population units identified: (i) Honduras/Colombia/Puerto Rico; (ii) Bahamas; (iii) Cuba; and (iv) Mexico (Caballero et al., 2011).

For common bottlenose dolphins, the SeaSketch platform allows visualization of the genetic differentiation and diversity of these populations at a geographic level around the Wider Caribbean. The MSP tool is user-friendly to decision makers and, for example, aids in the understanding of how common bottlenose dolphins belong to genetically distinct populations on independent evolutionary paths (particularly around Cuba). The case study is highly informative for future efforts to identify IMMA in the Wider Caribbean region. Illuminating genetic differences between morphologically similar ecotypes of dolphin that could not have been detected by other means informs Criteria A (Species and population vulnerability) and B (Distribution and abundance). Separate IMMA may need to be identified for the offshore and coastal ecotypes if they are to accurately reflect important habitat. In addition, the ecotypes may

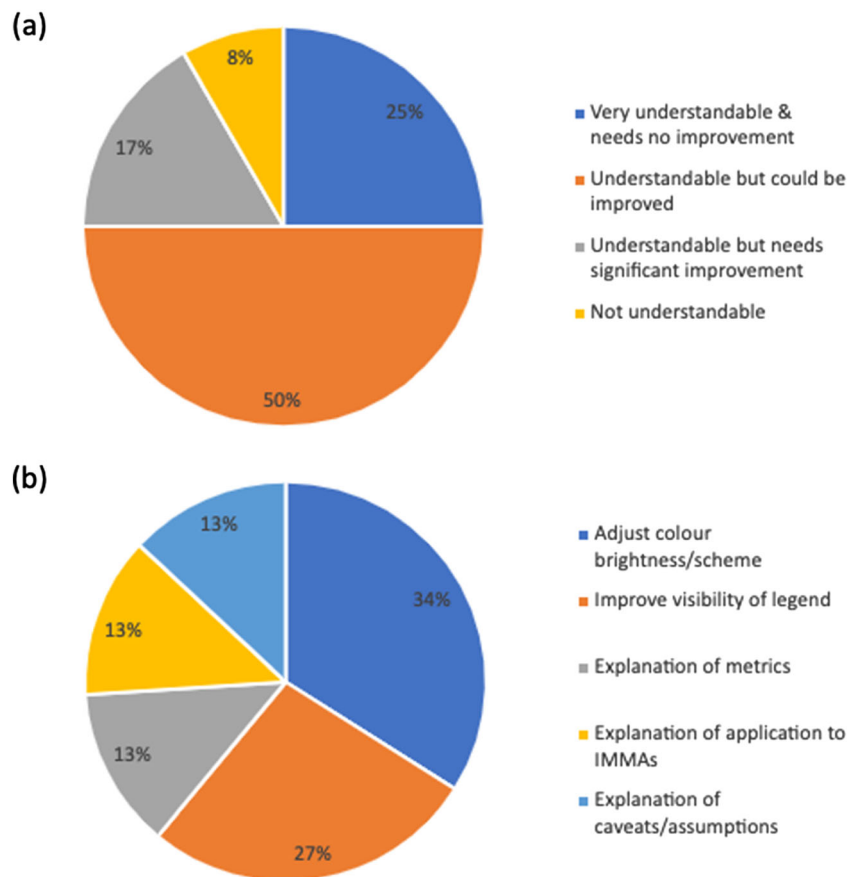
experience different relative vulnerabilities that should be taken into account as part of the IMMA evaluation. Beyond IMMA, it is important that captive breeding programmes take these genetic differences into account, even if no evidence on genetic effects of outbreeding (i.e. captive crosses between *T. aduncus* and *T. truncatus*) currently exists (Martien et al., 2012).

3.4 | Expert evaluation of the geospatial genetics case studies

Twelve individual responses were submitted regarding the overall accessibility of the geospatial genetic data layers for the humpback whale and spinner dolphin case studies and 18 individual responses were submitted regarding suggested improvements to each case study (humpback whale: $n = 7$; spinner dolphin: $n = 11$). Overall, three quarters of responses indicated that the genetic data and associated information included in the case studies was either "very understandable and needed no improvement" (25% of the responses) or "understandable but required some improvement" (50% of the responses). The remaining responses flagged that some geospatial data needed "significant improvement" in order to make a layer understandable (25% of the responses; Figure 5a). Recommended improvements to the overall accessibility of the case studies (Figure 5b) centred around a preference for further explanation, including of the metrics (e.g. what colours represent, statistics), how metrics were calculated (e.g. significant differences in diversity, thresholds of diversity), information on caveats and limitations of the data and analytics on the SeaSketch project site (e.g. sample size, spatial and temporal scales, genetic marker considerations, and statistical significance), and how metrics can support IMMA delineations (53% responses). Recommended improvements to how individual geospatial genetic data layers are presented on SeaSketch included changes to the colour scheme (34% responses), the addition of a legend that is visible in conjunction with the data layers (13% responses), and the inclusion of additional tools to help identify IMMA. This initial feedback from a relatively small group of self-selecting experts served to inform the development of the Wider Caribbean case study and will continue to inform future case studies and their iterations, as well as overall improvements to the geospatial genetics approach. Our goal is to carry out a larger-scale, systematic evaluation in the future, following review of the case studies by the broader scientific community.

The visualization of genetic data also led the experts to specify additional data types that would aid in the identification of IMMA. More abundance data, such as satellite tag or mark/recapture data, were suggested to illustrate movements of individual humpback whales. Historical/contemporary migration rates between sampling sites, habitat use, behaviour, and abundance were identified as useful additions for spinner dolphins. The inclusion of other types of data in the case studies will require additional time and collaborative efforts. However, the case studies may provide a helpful research prioritization tool.

FIGURE 5 Results of the expert consultation on the geospatial genetic data and associated information presented in the humpback whale and spinner dolphin case studies on SeaSketch: (a) feedback on how understandable the genetic data and associated information is in its current form ($n = 12$ responses); (b) areas for suggested future improvement to increase accessibility and ease of interpretation of the data ($n = 18$ responses)



4 | DISCUSSION

4.1 | Key considerations when using geospatial genetics to support policy decisions

As with any type of data, there are a range of caveats and uncertainties that require consideration when interpreting geospatial genetic data and analyses for the identification of IMMAs or as part of an MSP or conservation planning process. The geospatial presentation of genetic data may lead to inaccuracies in interpretation if certain aspects of the underlying genetics study are not taken into account. Simplification necessarily leaves out details that may be useful, and the strength of inference will depend on the accuracy and power of the available data. The most pertinent considerations include those related to spatial and temporal sampling, the extent and resolution of the data, the properties of the genetic marker used, and the definition of ‘thresholds of difference.’ In addition, every aspect of genetic analysis carries some component of uncertainty and it is essential that practitioners have these uncertainties clearly presented so they can be considered in parallel with the genetic data and associated information within the context of the marine protection and MSP process. Expert synthesis of genetic information, and its inherent caveats and uncertainties, should therefore be undertaken in a

standardized manner understandable to non-geneticists prior to its use in marine protection and MSP efforts. Methods and techniques from the fields of landscape and seascape genetics should be employed to bolster the strength of inference underlying observed geospatial patterns, as appropriate. Geospatial genetics offers opportunities to develop new methods to communicate uncertainty to practitioners and the wider community in a way more readily translatable into conservation action.

4.1.1 | The importance of uncertainty

The results generated, and conclusions drawn, from any genetic analysis are highly sensitive to the sampling scheme adopted. How individuals are sampled spatially and temporally has a direct influence on the determination of populations or management units, inferences regarding the dynamism of those units through time, and estimates of genetic diversity. These issues are particularly pertinent for highly mobile or migratory species, where a genetic study may only capture a snapshot of the patterns existing at a specific life history stage. Comprehensive spatial and temporal sampling is extremely arduous for marine species, meaning that details of the sampling scheme and associated levels of uncertainty need to be made available in an

understandable way to inform marine protection and MSP efforts. Frameworks to account for uncertainty in data and models have been developed to support spatial conservation priority setting. For example, Kujala et al. (2013) explicitly assessed uncertainty and potential risks associated with planning conservation areas under an incorrect climate scenario. Gissi et al. (2017) proposed a three-level methodology to perform a general uncertainty analysis of cumulative impact assessment aimed at informing marine spatial planning in the Adriatic and Ionian region. It would be valuable to develop similar frameworks to support the application of genetics in conservation, beyond accounting for taxonomic uncertainty (e.g. Rosauer et al., 2018).

Related to the issue of sampling is that of the extent and resolution of the data used. Inferences regarding the delineation of management units and the connectivity between those units in a study region of 10 km² may significantly differ if an extent of 100 km² were considered, for example. Similarly, a coarse analytical resolution may overlook management units that have boundaries at a finer resolution. In lieu of a robust methodology to account for these scaling issues, the process of identifying important areas should employ, when possible, an exploration of the sensitivity of the results to the scale of analysis (e.g. Dungan et al., 2002).

4.1.2 | Defining 'difference'

Prioritization efforts often require information regarding thresholds of 'difference.' As population genetic metrics are generally continuous parameters, there exists a need to incorporate the ability to explore different thresholds into the marine protection and MSP process so that users can make inferences based on thresholds appropriate for the specific conservation objective they are working towards, or to explore how inferences may change across a range of thresholds. For example, at what level of genetic differentiation are management units considered to be different in an applied context? To what extent would they be considered to be connected demographically? What level or composition of genetic diversity is considered necessary for conservation action (e.g. evolutionary potential to cope with environmental change, or conservation of genetically unique populations)? Importantly, genetic metrics (e.g. diversity, differentiation, etc.) result from the complexities of the evolutionary history of a species; there is, therefore, no 'one size fits all' genetic metric that can be applied across all taxa. For example, spinner dolphins within the eastern Tropical Pacific have minimal population genetic structure across thousands of kilometres, despite the presence of strong spatial variation in morphology and behaviour, which has led to the designation of different subspecies within the region (Leslie & Morin, 2016; Leslie, Archer & Morin, 2019). This weak population genetic structure contrasts with the strong population genetic structure across short geographic distances for spinner dolphins in the Hawaiian Archipelago (as described above), and probably results from the continuous nature of the dolphins' pelagic habitat in the eastern tropical Pacific, as well as the presence

of very large population sizes in this region, since the strength of genetic drift is inversely correlated with population size. Despite the weak genetic structure, spinner dolphins in the eastern tropical Pacific are managed as three separate stocks due to the strong spatial phenotypic variation in this region. This example highlights the importance of understanding the evolutionary processes influencing genetic variation when defining management units, as well as the importance of including morphological, ecological, and other forms of data when assessing spatial variation in biological diversity.

Thresholds may also differ in relation to specific management goals. Threshold values should therefore be defined in relation to current knowledge of the species in question and should be explicitly selected in the context of the particular conservation objective. Analysis tools that allow the user to define 'classes' of high/low divergence and diversity (e.g. Marxan) will be particularly useful in this regard.

4.2 | Research needs and future prospects

The field of geospatial genetics has a basis in land- and seascape genetics as well as a number of existing tools; however, techniques to spatially visualize genetic data are still just emerging and, as the questions raised in the previous section highlight, there are several methodological and policy-related questions that require further, targeted research. From a methodological standpoint, questions remain regarding the most effective way to communicate genetic information so that it is both ecologically meaningful and useful for practitioners. Methods have been presented here through three case studies to serve as a starting point and framework for further exploration into more advanced geospatial techniques (e.g. time series that show how the frequency of alleles in a population may change over time, dynamic management units that reflect the changing spatio-temporal distribution of taxa, uncertainty visualization), as well as further study into the sociological (e.g. receptivity to genetic information and expertise) and communications (e.g. data visualization, platform accessibility, developing a simple common language to describe genetic information) aspects of this work to ensure that geospatial genetics products have real utility for practitioners. Further, there are important research questions related to applying geospatial genetic data and associated information at scales relevant to management, the development of 'distinctiveness' criteria for different conservation contexts or study systems, the application and interpretation of geospatial genetic data and associated information within a multi-species context, and if there is a role for systematic conservation planning approaches and tools (e.g. MARXAN) to optimize protection of genetic diversity under different MSP scenarios. There also exist outstanding questions of how management units identified by geospatial genetic means might align with other types of units defined by legal terminologies in the management and policy arena. Investigation is also needed into how geospatial genetic data, as presented here, are visualized and interpreted alongside other data types being considered by

practitioners. For example, how do simple maps of habitat areas align with genetically distinct populations? How is genetic connectivity data compared with direct movements inferred from satellite telemetry? And, most importantly, how should practitioners approach these different geospatial data and use them collectively to make policy and management decisions? A further analytical step is to integrate different data types within a quantitative framework. The field of landscape genetics has much to offer in terms of methods and techniques to test the explanatory power of environmental characteristics or anthropogenic impact in the context of genetic data (e.g. 'latent factor mixed models', Frichot et al., 2013; and 'redundancy analysis', Kierepka & Latch, 2015), and advances are being made in integrating genetic data with acoustic, satellite telemetry and stable isotopes (e.g. Townsend et al., 2018; Viengkone et al., 2018; Sremba et al., 2019; Montanari, Kershaw & Rosenbaum, 2020). The advancement of these often-complex analytical approaches should occur in parallel with the development of communication strategies to support the interpretation of analytical methods, results, and conservation applications by non-specialists.

What is clear from this work to date is that geneticists must be included among the range of scientific experts invited to contribute to and/or advise on a marine protection and MSP process. Geospatial genetics offers an approach with the potential to foster increased collaboration among geneticists and practitioners. For example, geneticists can design genetics studies to be useful at scales specific to priority management questions. This increased opportunity for dialogue and cooperation will serve to advance the field of geospatial genetics more rapidly and help ensure that evolutionary processes are factored into marine protection and MSP. Lastly, the potential for geospatial genetics to inform policy decisions extends beyond marine mammals to other marine species, including sessile species and those with a larval dispersal phase, and potentially to terrestrial systems, and has particular utility for conservation priorities that concern species or habitats with complex population structure, such as sharks and rays (Domingues, Hilsdorf & Gadig, 2018), brown bears (e.g. Fedorca et al., 2019), and European sweet chestnut (Mattioni et al., 2017).

ACKNOWLEDGEMENTS

Many thanks to the participants of the panel discussions and workshops at the 3rd International Marine Protected Areas Congress in 2013, the 3rd and 4th International Marine Conservation Congress' in 2014 and 2016, and the 21st Biennial Conference of the Society of Marine Mammalogy in 2015; without their input and expert feedback the development of the geospatial genetics approach and refinement of the case studies presented here would not have been possible.

AUTHOR CONTRIBUTIONS

F.K. conceived the idea and designed and coordinated the project. W.M. developed and hosted the SeaSketch case studies and provided technical support at the expert workshops. F.K., K.A., F.R.S., and

S.C. developed the case studies in SeaSketch and drafted the manuscript. M.J.T., G.N.D.S., and E.H. co-hosted the Society of Marine Mammalogy expert workshop, drafted the manuscript, and guided the project. G.G. drafted the manuscript. E.C. analysed the expert feedback on the case studies. K.K.R. conducted background research and drafted the manuscript. H.C.R. guided the overall study. All authors gave final approval for publication.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Kershaw, F., McClintock, W., Andrews, K.R., Riet-Sapirza, F.G., Caballero, S., Tetley, M.J. et al. (2021). Geospatial genetics: Integrating genetics into marine protection and spatial planning. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 1–19. <https://doi.org/10.1002/aqc.3622>