Seascape genomics: assisting marine biodiversity management by combining genetic knowledge with environmental and ecological information

PERSPECTIVE PAPER

ABSTRACT

Biodiversity, including genetic diversity, is the foundation of ecosystems and the well-being of all organisms, including humans. Determining how the marine environment shapes genetic diversity and developing best practices to conserve it requires a multi-disciplinary approach incorporating genomic and environmental information. Seascape genetics and genomics combine spatially resolved ecological, genomic and environmental data coupled with modeling to explore past, present and future patterns of diversity and connectivity. Seascape genetics and genomics provide scientists and managers with a multi-faceted tool that can be applied across a wide range of species and can be incorporated into marine spatial management. Despite the known importance of genetic diversity, the incorporation of genetic and genomic data is grossly underrepresented in policy, decision-making and conservation measures. We aim to support the understanding and access to seascape genetics and genomics information for conservation and management practitioners. We explain how integrating environment, space, traits, and genetics or genomics can advance marine spatial management. We also outline the scientific and policy context of seascape genomics and the corresponding methodology and concepts, exemplified by two specific case studies. Lastly, we review the present status of seascape genomics research and discuss present challenges, strengths, and future opportunities by providing a road map that could aid the integration of seascape genomics into management.

Keywords

Biodiversity, Conservation management, Genetic diversity, Predictive modeling, Seascape genomics

Running title

Opportunities for marine biodiversity management with seascape genomics

1. OUTLINE OF SEASCAPE GENOMICS’ SCIENTIFIC AND POLICY CONTEXT

The conservation of genetic diversity is imperative as anthropogenic pressures (Halpern et al., 2015) and biodiversity loss continue to increase (Pinsky et al., 2020). However, most conservation policies and management programs rarely include genetic and genomic aspects (Allendorf et al., 2022), although international biodiversity policies already started recognizing the importance of marine genetic diversity in the early 1990s. For example, the 1992 United Nations Convention on Biological Diversity highlighted the importance of marine biodiversity and genetic diversity and launched a conservation program in 1998 (COP 4 Decision IV/5, 1998). These early CBD intentions are reflected in many current multi-national policies such as the EU Habitat and Marine Strategy Framework Directives (Directives 92/42/EEC, 2008/56/EC) and the UN Sustainable Development Goal 14 that highlights the need to conserve and make any use of marine resources sustainable (UN, 2022). Despite the early ambitions, it took almost 20 years before the global biodiversity crisis started making headlines (Díaz et al., 2019) and gave rise to political debates worldwide (Lees et al., 2020). In 2020, a series of joint calls from environmental NGOs, businesses, religious groups, local and regional governments, indigenous people, and youth organizations mobilized hundreds of millions of people to demand action on nature conservation (WWF, 2020). Convincing published scientific evidence (Lotze, 2021) and governmental reports by the International Panel on Climate Change (IPCC) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (Brondízio et al., 2019; Pörtner et al., 2021) portray the importance of genetic diversity.

Although first steps have been taken to address genetic diversity gaps in policy, the widespread inclusion of genetic diversity in conservation practice still lags, and the goals are far from being met. By 2022, few targets stipulated in the CBD and adjacent documents have been met because of inadequate national policy responses, lack of funding, science-policy gaps, and imperfect review mechanisms (Brondízio et al., 2019; Xu et al., 2021). The same applies to marine biodiversity (Cavanagh et al., 2016), genetic diversity (Hoban et al., 2020; Laikre et al., 2020), and, specifically, the genetic diversity of marine ecosystems (Laikre et al., 2016). Genetic diversity is essential for adaptive capacity, evolutionary potential, and community function, and it plays a significant role in ecosystem services (Allendorf et al., 2022). However, ambitions regarding genetic diversity are more articulated in general conservation policies and strategies targeting terrestrial systems than in marine policies (Laikre et al., 2016). For example, the UN Decade of Ocean Science for Sustainable Development 2021-2030 fails to stress the importance of monitoring and maintaining intraspecific genetic diversity (Thomson et al., 2021).

The research field of seascape genomics uses multidimensional approaches to study how the marine environment shapes genetic diversity and connectivity of populations and can be incorporated into marine spatial management. Seascape genomics and seascape ecology are based on the theories of population and conservation genetics (Allendorf et al., 2022; Hartl and Clark, 2007) and landscape ecology (Wu and Hobbs, 2007), respectively. Seascape genomics combines environmental and genomic information to study how environmental factors shape genetic diversity, connectivity, and evolutionary processes of populations and species (BOX 1 and 2; Figures 1, 2 and 3). In certain examples, we refer to seascape genetics, which uses a small set of genetic markers in contrast to seascape genomics, which are studies using genome-wide marker sets, reference genomes, and/or high-throughput genomic sequencing (Selkoe et al., 2008; van Oppen and Coleman, 2022; see BOX 1). The integration of seascape ecology (Pittman, 2018) and seascape genomics methods are increasing in research studies (Jahnke and Jonsson, 2022; Pittman et al., 2021), and the multi-faceted application of seascape genomics (BOX 1) makes it a valuable tool for a wide range of applications. However, it is not often included in the spatial management of ecosystems or in driving other policy decisions for future planning. Here we aim to illustrate that the integration of seascape ecology (focused on species and communities) and seascape genetics/genomics (focused on diversity within and between populations) (BOX 1; Figures 1, 2 and 3) represents a valuable tool for a wide range of scenarios, such as spatial management of ecosystems, for instance when introducing protected areas or defining fishing regulations (quotas and exclusion zones) (Murphy et al., 2021). We review the present status of seascape genomics exemplified in two case studies and discuss the present challenges, strengths and future opportunities by providing a road map that could aid the integration of seascape genomics into management.

>> BOX 1

>> BOX 2

2. SEASCAPE GENOMIC CASE STUDIES ON GLOBAL THREATS

In this section, we outline two of the five global drivers of biodiversity loss, namely habitat loss and resource overexploitation, apart from pollution, climate change, and non-indigenous species, to illustrate what knowledge seascape genomics can provide and how it could be embedded in conservation and resource management (Mazor et al., 2018). Our aim in this section is to describe the current state of the scientific field of seascape genomics. We have selected well-documented cases of genotyped populations that incorporated spatio-temporal and environmental information. The first example deals with an iconic ecosystem engineer whose long-term survival needs urgent management measures (tropical coral reefs). The second example details how managing (over)exploited marine living resources benefits from spatially structured population genomics knowledge (fisheries). While most described studies used a single-species approach, in the future, the focus should shift to communities (Knutsen et al., 2022; Nielsen et al., 2020b) for more holistic ecosystem-based management (Pikitch et al., 2004).

2.1. Rescue from habitat loss - saving the high diversity of coral reefs

Tropical warm-water coral reefs cover only 0.1 % of the oceans, but harbor 25 % of all marine species (Fisher et al., 2015), and approximately 500 million people depend on coral reefs for their livelihoods (Spalding et al., 2017). Coral reefs consist of calcium carbonate skeletons built up by living corals over tens of thousands of years. Corals and their symbionts face many threats, two major ones being warming and ocean acidification (Harvey et al., 2018; Pendleton et al., 2016). Global change is predicted to severely deplete reef systems and diversity by 2030 (Dietzel et al., 2021). Unfortunately, the spatial scale of these global changes is outside the jurisdiction of most managers (Hoegh-Guldberg, 1999). Identifying the most promising avenues for local to regional coral reef restoration actions and conservation management is even more important and can be supported by seascape genomics.

Many coral species and their symbionts have a low tolerance to warming, resulting in coral bleaching - a phenomenon where the density of symbiotic algae declines severely when the host coral is overheated (Gates et al., 1992). However, some coral and symbiont genotypes have evolved to persist at higher temperatures, such as life in shallow lagoons or in a generally warmer region (Bay et al., 2017; Sampayo et al., 2008). In a few compelling studies, coral seascape genomics has been applied to assess the effects of global warming on corals by examining connectivity between subpopulations. These studies have incorporated spatially explicit genomic and oceanographic data to identify populations that can act as sources for other populations and identify routes of larval dispersal (Matz et al., 2018; Padrón et al., 2018). In theory, as long as these source populations are preserved, the metapopulation can be maintained. For example, eco-evolutionary modeling confirmed that the corals of the Great Barrier Reef still maintain a high level of genetic diversity, despite the loss of coral cover in recent years (Matz et al., 2018). Realistically, creating genomic data at spatial scales and resolutions that are directly applicable for spatial management may often be too costly. However, predictive modeling may be a promising avenue to predict the persistence and adaptive potential of the future (Matz et al., 2020). An alternative approach aims to correlate specific genotypes and environments to pinpoint candidate sites within the genome (and, in some instances, genes) that potentially enable heat resistance. Geographically localized efforts used this approach by linking distributions of genetic variants to specific environmental conditions, which were first measured in the field and then modeled at different spatial scales (Selmoni et al., 2021, 2020). This information can then be used for indexing - based on the present status of a management unit and its predicted health - and allows managers to rank populations according to the urgency of intervention. Hence, population genetic measures and their integration in a spatially explicit context are important tools for designing and managing marine protected areas (MPAs) (Riginos and Beger, 2022). In addition, seascape genomics on large scales may be able to identify candidate heat-resistant genotypes or candidate adaptive genes in source populations, which may allow these populations to be used for selective breeding (Drury et al., 2022), thus providing a potential climate adaptation strategy.

2.2. Future-proof fisheries - empowering living resource management to counteract overexploitation

Worldwide marine catches have yielded around 80 million tonnes per year since the 1990s and account for 17 % of the dietary animal protein intake of the world population (FAO, 2022). However, in 2019, 35.4 % of fish stocks were either overexploited or depleted (FAO, 2022). In addition, climate change is altering the distribution and productivity of many commercial species (Pinsky et al., 2013; Poloczanska et al., 2013). Furthermore, in response to climate change, where populations either acclimate, adapt, move poleward, or go extinct (Hastings et al., 2020), the continuation of overfishing globally may lead to ecosystem imbalances at regional scales, potentially affecting population diversity, food web structure, resilience, and productivity (du Pontavice et al., 2020; Schindler et al., 2010). Therefore, adequate fisheries management is necessary for socio-economic, ecosystem resilience and conservation purposes.

Fisheries management often operates on spatio-temporal scales that are not an ideal match for biological realities (Kerr et al., 2017). Firstly, spatial management units are not always congruent with genetic units or, in other words, genetic population structure. For example, overexploitation of the smaller of two populations with overlapping management units may lead to their extirpation (Hutchinson et al., 2003). Secondly, fisheries assessment models are mostly based on relatively short-term changes in abundance or biomass and rarely consider long-term evolutionary implications (Laugen et al., 2014). Conserving genetic diversity and, more specifically, candidate adaptive genetic variants has the potential to support resilience of populations in changing environments (Harrison et al., 2014; Rochat et al., 2021).

Seascape genomics has provided highly resolved information on biological boundaries for management and the relation of populations to environmental variables, such as temperature and salinity (e.g., in stripey snapper, common sole and European hake; DiBattista et al., 2017; Diopere et al., 2018; Milano et al., 2014). In the case of Atlantic cod, both low-salinity genetic adaptation and age-specific distribution of coastal and offshore ecotypes are now considered in population-level managed fisheries (Barth et al., 2019; Synnes et al., 2021). Seascape genomics has also provided correlative evidence for spatial population structure associated with environmental clines in invertebrate target species such as American lobster, eastern oyster, and sea scallop, which may eventually benefit the management of these resources (Benestan et al., 2016; Bernatchez et al., 2019; Lehnert et al., 2019; Table 1). Another example is highly migratory fish stocks, which are challenging to manage due to their transboundary nature and knowledge gaps regarding connectivity and population structure. Seascape genomics has rarely been applied to highly migratory fish species, partly because it may have been difficult to collect sufficient data. However, with decreasing sequencing costs and increasing availability of large-scale environmental data layers, seascape genomics offers great prospects, for example, to identify migratory "highways," spawning and nursery grounds of migratory species. Spatially resolved seascape and/or population genomics data is starting to become available, for instance, for Atlantic bluefin tuna (Puncher et al., 2018; Rodríguez-Ezpeleta et al., 2019), Greenland halibut (Ferchaud et al., 2022), and grey reef sharks (Boussarie et al., 2022).

Overall, fisheries management is expected to benefit from increasingly using seascape genomics approaches, which can supply crucial information about population structure, connectivity, migration patterns, and putative adaptive variation. Considering spatial and evolutionary information from seascape genomics in fisheries management policies (including quotas but also no-take zones) could thus lead to more future-proof fisheries management.

3. PRESENT CHALLENGES, STRENGTHS, AND FUTURE OPPORTUNITIES OF SEASCAPE GENOMICS

3.1 Obstacles and potential solutions

The uptake of seascape genomics in conservation management has been slow. It is presently facing some challenges, such as technical knowledge gaps and a lack of collaboration networks, platforms for communication, and knowledge transfer between parties (Benestan, 2019; Sandström et al., 2019). The methods used to gather genetic information are complex, and conservation agencies are often understaffed regarding personnel trained to analyze and interpret such data. Additionally, quickly advancing technologies widen the gap between conservation genomics and management (Cook and Sgrò, 2018; Shafer et al., 2015). For example, chromosomal variant analyses were recently introduced to characterize populations, and even though the analysis of such data can be challenging, this valuable information can aid with *in situ* stock discrimination (Berg et al., 2021; Dorant et al., 2020). Molecular assignment in wild and farmed Atlantic salmon has been steadily integrated into management, achieved by appointing fisheries managers trained in genomics (Glover, 2010). These collaborations have allowed managers, who view scientific research as critical to the decision process, to have the support and access to genomic data required to make decisions (Benestan, 2019). Ambitious efforts to build bridges and establish platforms between science and management exist, and inspiration can be found in both terrestrial (Holderegger et al., 2019) and aquatic cases (Klütsch and Laikre, 2021).

Other obstacles are the lack of consistency in seascape genomic methodologies (Jahnke and Jonsson, 2022). While access to high-throughput sequencing has cleared the genotyping bottleneck, high-quality reference genomes, data storage, and analysis remain to be some limiting factors (Liggins et al., 2019). Computational power is also a limiting factor for high-resolution oceanographic modeling. In addition, researchers and DNA sequence repositories, such as GenBank, struggle with processing and storing high volumes of data. To improve the implementation of seascape genomic results, scientists need to increase their understanding of what data is required for managers to make their decision (Klütsch and Laikre, 2021) and ensure that the methodology is adequately evaluated and validated.

Additionally, conservation managers face operational challenges that hinder policy implementation and must handle uncertainties and complexities related to vague and sometimes conflicting policy goals. Limited resources for implementation make it challenging to decide on appropriate management measures (Sandström et al., 2019). Even though it is widely accepted that genetic diversity contributes to healthy and resilient marine ecosystems (Díaz et al., 2020), the significance of genetic diversity is neither always adequately understood nor is the priority between conflicting conservation goals given (Beger et al., 2014; Nielsen et al., 2020a; Sandström et al., 2016). Knowledge communication efforts (lectures/deliberative discussions) are effective in increasing managers' perception of genetic diversity (Heyden et al., 2014; Lundmark et al., 2017) but need to be continued over time to maintain effects (Lundmark et al., 2019).

Furthermore, there are often discrepancies between the appreciation of genetic diversity at a higher policy level (e.g., international and national) and its implementation in strategies and actions at regional or local levels. For example, the environmental impact statements of coastal infrastructures, such as wind farms and oil rigs, do not or cursorily mention genetic change (e.g., Belgium: Degraer et al., 2020; Draget, 2014; EU, 2020). Nevertheless, these introduced infrastructures may play an important role by acting as novel stepping stones in population spread. As a result of this lack of trickle-down effect, conservation management is not moving forward as fast as desirable, with negative impacts on biodiversity. One potential solution would be to facilitate increased policy coherence concerning objectives, instruments, and practices (Nilsson et al., 2012) and improve communication and collaboration between decision-makers at different levels.

Finally, while there is a lot of scientific data (Table 1), applications are still lacking or are in their infancy. For instance, Sweden has started a likely powerful program for temporal genetic monitoring for several marine species, but the information is too novel to integrate into conservation management procedures (Laikre, pers. comm.).

3.2 Strengths and future opportunities of seascape genomics

The outcomes of seascape genomics translate well into management processes and provide a valuable perspective on the global biodiversity challenges (see Table 1 for examples). Technological advancements have advanced seascape genomics in recent years by providing access to high-quality spatially and temporally structured digital repositories. For example, the European Union's Earth observation program Copernicus (copernicus.eu), the British Oceanographic Data Centre (BODC), the ICES data portal, data archiving repositories such as Dryad, the Microbe Atlas Project (https://microbeatlas.org), the European Nucleotide Archive, and GEOME (Riginos et al., 2020), can all provide genetic, environmental, and oceanographic data required for correlation and association studies. In addition, automated high-throughput data collection, the growing applicability of "genetic nets" through environmental DNA (eDNA), and developments with *in-situ* tool automation open perspectives for continuous sampling and remote observatories (Danovaro et al., 2020; Gilbey et al., 2021).

3.2.1 Roadmap to integrate seascape genomics into management

Recent developments in genomics and modeling have provided scientists with a versatile and powerful set of tools for monitoring marine populations, such as providing information regarding their demographic and adaptive history (Kelley et al., 2016; van Oppen and Coleman, 2022). Applied seascape genomics examples cover habitats from the inshore dispersal of cockle larvae in the Irish Sea (Table 1) to the genetic connectivity of adult reef sharks without larval dispersal across the tropical Indo-Pacific Ocean (Boussarie et al., 2022). Other ongoing examples include the implementation of an MPA in Scotland for the critically endangered flapper skate *Dipturus intermedius* (Bache-Jeffreys et al., 2021); Marine Scotland, 2022); the real-time follow-up of the Northeast Atlantic cod *Gadus morhua* fishery in a marine protected area (Johansen et al., 2018), and the adaptive management of eelgrass *Zostera marina* meadows along the Swedish west coast (see below). However, despite the considerable amount of published seascape genomic studies (Table 1), the implementation of research outcomes into management is still lagging. Therefore, we highlight a set of steps in a roadmap fashion to aid in implementing seascape genomics in management (Figure 4). We use the Swedish seagrass case, in which several authors of this paper are involved, as an example.

3.2.1.1 Co-creation to define gaps and questions

Defining the gaps, questions, and aims of the project is the first step to determining if a project aligns with researchers' and managers' goals. Sometimes, this common ground is hindered by the fact that different partners are required to meet different aims. For example, researchers are constrained by academic goals, such as the requirement to publish or develop projects that fit grant application goals, while state or federal aims define managers' tasks. Additionally, management scales are often more local than at a seascape scale (e.g., MPA management; Young et al., 2018). Despite these limitations, common aims can still be established through co-creation in an interdisciplinary team consisting of, but not limited to, researchers, conservation practitioners, stakeholders, and governmental agencies. Once the interdisciplinary team is established, the formulation of detailed aims and planning of the project can begin.

For the implementation of seascape genomics in the management and restoration of eelgrass meadows along the Swedish coast, the research group ZORRO (gu.se/en/research/zorro) at the University of Gothenburg and conservation practitioners at the County Administrative Board (CAB) of Västra Götaland and other regions, as well as the Swedish Agency of Marine and Water Management (SwAM) came together with the common goal to reduce seagrass loss and improve seagrass conservation. All parties acknowledged the importance and value of the ecosystem services provided by these meadows', such as countering erosion, improving water quality, and acting as carbon and nitrogen sinks (Duarte et al., 2005; Moksnes et al., 2021). It was also acknowledged that underpinning genetic diversity of these populations plays a crucial role in conserving and restoring these meadows. A key factor for the success of this collaborative project is open and frequent communication and discussion on implementation and specific needs of the different groups.

3.2.1.2 Data collection and analysis

Data collection and integration into generally spatially referenced data is integral to a seascape genomics assessment (Figure 3, BOX 1). For example, data collection can be in the form of a field study, or data can be mined from data repository sites; often, there is a combination of methods.

In the eelgrass example, seascape genetic, biophysical, and environmental data were collected and generated and then used to identify valuable and vulnerable meadows along the Swedish west coast, allowing for a ranking of urgency and cost-effectiveness of intervention (Jahnke et al., 2020). The results showed that genetic diversity within these populations was still high despite recent declines. Therefore, once the genetic differentiation on small spatial scales has been established, local populations with high genetic diversity, similar genetic background, and that are not isolated from the recipient population to a high degree, can act as donor material for future restoration efforts (Jahnke et al., 2018). Moreover, priority restoration sites were suggested based on biophysical modeling of dispersal, which predicted candidate restoration sites where the entire eelgrass metapopulation would profit most from increased dispersal (Jahnke et al., 2020).

Many marine species have more complex life histories than eelgrass, involving passively or actively drifting larval stages and actively moving (sub)adults. Even complicated life histories might become better understood through statistical models, such as correlational genetic niche and dynamic energy budgets (DEB) (van de Wolfshaar et al., 2021). Seascape genomics can also be used to understand the spatio-temporal dynamics of rare species (Delaval et al., 2021) and emblematic communities such as coral reefs (see above; Table 1). On a life-history scale, seascape genomics applies to short-lived microbes (Laso-Jadart et al., 2021) up to millenary seagrass clones (Edgeloe et al., 2022).

3.2.1.3 Integration of seascape genomics into policy

Integrating seascape genomic findings into management protocols and policy is the least developed part of the management cycle but fundamentally the most crucial step (Figure 4). Expanding on adaptive management to meet the challenges of the future is particularly urgent (Wåhlström et al., 2022), and scenarios that help to develop a capacity for dealing with the unknown and unpredictable, or the unlikely but possible, are essential to realistic forecasting. Such scenarios should be developed with stakeholders' input and guide scientists and managers to develop forecasting models. The opportunity to assess a range of spatial and temporal scales in seascape genomics makes it possible to advise on spatial scales relevant for management and design adaptive management plans that account for future predicted changes (see also Table 1). For instance, in the eelgrass example, eco-evolutionary modeling was used to predict the effect of halting eelgrass decline on future genetic diversity and persistence of these meadows (Jahnke et al., 2020). Integrating eelgrass seascape genetic data into management is ongoing in the areas of protection, restoration, and monitoring. Regarding implementing seascape genomics results in protection, priority areas with high genetic diversity and high connectivity identified in Jahnke et al. (2020) have been communicated to the County Administrative Board. Additionally, the European Commission has highlighted the importance and applicability of the approach) for assessing the efficiency of the EU's network of marine protected areas (MPAs) and defining management units (EU, 2020b). To our understanding, these suggestions will be considered in the present efforts to expand protected areas specifically for eelgrass meadows. Furthermore, in terms of eelgrass restoration, test planting has already been performed at several sites suggested in Jahnke et al. (2020) as optimal restoration candidate sites (Moksnes et al., 2021).

Finally, as eelgrass is a priority species, monitoring efforts are ongoing under different policies, for instance, the European Water Framework Directive (WFD), Marine Strategy Framework Directive (MSFD), and Habitat Directive. Monitoring of genetic diversity has now also been initiated and financed by SwAM (Johannesson and Laikre, 2020). Efforts are being carried out to have some spatial overlap with sites monitored under different directives (e.g., EU Habitat Directive, EU MSFD, and EU WFD), with the aim to incorporate data from different monitoring efforts into a seascape genomics approach. In a similar spirit to the eelgrass example and also in analogy to scenarios supporting the mitigation of global CO_2 emissions (IPCC, 2014), scenarios are under development for fisheries management (Merrie et al., 2018), marine ecology under climate change (Gattuso et al., 2015), coral reef resilience (Delevaux et al., 2018), future-proofing underwater forests (Wood et al., 2021) and the expansion of MPAs (Cashion et al., 2020).

4. CONCLUSIONS

The multi-disciplinary combination of environmental and genomic data coupled with different modeling approaches represents a powerful approach to generate relevant knowledge in support of biodiversity conservation (BOX 1, Table 1). Whereas conducting assessments at different spatio-temporal scales makes it possible to develop management plans at a spatially relevant scale and consider genetic adaptability under future environmental changes.

Seascape genomics approaches are applicable from an ecosystem-based policy perspective, which aims to integrate the management of land, water, and living resources (e.g., EU MSFD; Sturludottir et al., 2018). Realized and potential applications involve, amongst others, the design of protected areas, coastal zoning, habitat restoration, predicting species invasions, and living resource stock assessment. The most advanced applications currently come from coral reefs, seagrass meadows, and commercial fish stocks in coastal settings. Still, the potential applications in the deep-sea, offshore pelagic seas, polar seas, poorly studied oceans, and highly migratory species are promising. While present applications of seascape genomics in MPAs and ocean zoning focus on source-sink metapopulation dynamics and connectivity, these can be extended and supported by global change scenarios impacting ecosystem services. Recent applications in living resource management focus on connectivity, matching fish stocks and populations, and the impact of fishing (Table 1). Scenarios that show the effects of climate and habitat change on fisheries-related biodiversity will be promising for ecosystem-based climate adaptation.

To make full use of the integration of genetic diversity in marine ecosystems, scientists, policymakers, and managers would benefit from joining forces to create multi-disciplinary collaborations to ensure that:

- International and national policy is translated into practical guidance for implementation
- Best available scientific knowledge on seascape genomics is used in practical management
- New knowledge is continuously incorporated into biodiversity management
- The audience and users of seascape genomic studies are broadened.

Seascape genomics combines essential genomic knowledge with spatial, temporal and environmental information required for biodiversity management. However, it needs to be better integrated into conservation and management practices to maintain genetic diversity and stop the ongoing biodiversity loss to provide future generations with a more sustainable planet.

BOX 1: The art of seascape genomic analysis

Seascape genomics combines tools developed in several disciplines (e.g., evolutionary biology and genetics, ecology, oceanography, climatology, and computational sciences) to obtain a comprehensive picture of the interactions between the marine environment and its inhabitants at various spatial and temporal scales (Selkoe et al., 2016; Figure 3). The data generally used in seascape genomics can be classified into two main categories: (i) biological data, e.g., genomic sequences, species/population occurrence data, phenotypes, experimental data; and (ii) environmental data, e.g., spatio-temporally structured seawater temperature and salinity. These two data types can be correlated statistically with appropriate sampling design to identify potential locally adapted populations, spatial population structure, or connectivity patterns. In addition, oceanographic modeling may be used to estimate dispersal probabilities among populations (Jahnke and Jonsson, 2022; Legrand et al., 2022). Finally, predictive modeling can show how observed patterns may change in the future. However, not all seascape genomic studies follow the same approach and use all available data types and methods. For example, dispersal simulations and predictive modeling are only sometimes used, although these can arguably, in some cases, provide the most powerful results for management applications. Seascape genomics can be thought of as the art of assembling vastly different data into a coherent output that illustrates the interactions of organisms with their environment and their evolution over time.

Further reading: For a recent review on seascape genomics, see Liggins et al. (2019), and for the broader discipline of population genomics, see Luikart et al. (2018). For an overview of molecular tools and statistical techniques, consult Holliday et al. (2018) and Grummer et al. (2019). For knowledge sharing initiatives we refer to the Genomics Observation MetaDatabase (GEOME) which captures metadata of biological samples with associated genomics data (Riginos et al., 2020), the network of researchers and practitioners SEA-UNICORN to advance knowledge and unify concepts and approaches on marine functional connectivity (www.sea-unicorn.com), the G-bike network of researchers and practitioners to enable tools for assessing, monitoring, and managing the genetic resilience and adaptive potential of wild and captive populations https://g-bikegenetics.eu (Holderegger et al., 2019), the Symphony 2.0 tool for ecosystem-based marine spatial planning (https://www.msp-platform.eu/practices/symphony-tool-ecosystem-based-marine-spatial-planning), the US-based project on cataloging migratory connectivity in the ocean (MiCO) (https://mico.eco/system), and the BaltGene project on Baltic Sea Genetics for managers https://www.gu.se/en/cemeb-marine-evolutionary-biology/management-conservation/baltgene).

BOX 2: Glossary

Biodiversity: the diversity of ecosystems, species, populations and genes, and the processes related to the diversity of life.

Dispersal: movements of individuals or propagules that have potential consequences for gene flow within and between populations and across space.

[Fish] stock: a group of individuals (fish) of the same species occupying a well-defined spatial range independent of other groups of the same species. A stock can be regarded as an entity for management or assessment purposes.

Genetic connectivity: transfer of genetic material (via individuals or gametes) between populations.

Genetic diversity: the number of different genetic variants within a population or species.

Genotype: the entire genetic constitution of an organism or the genetic composition at a specific gene locus or set of loci.

Management unit: entity (such as a coastline or fish stock) that has been given the mandate by a State to perform specific management functions

Metapopulation: a group of connected populations of a species.

Migration: the ecological, behavioral and evolutionary implications of the act of moving from one spatial unit to another.

Phenotype: the physical, physiological and behavioral appearance of an organism.

Population: a group of individuals of a given species in a defined area, genetically distinct from other such groups.

Restoration: the process of assisting the recovery of a degraded, damaged, or destroyed ecosystem.

Seascape: spatially heterogeneous and dynamic spaces in the ocean that can be delineated at a wide range of scales in time and space.

Seascape genetics: a research field combining environmental and genetic information to study how environmental factors shape genetic diversity, connectivity, and evolutionary processes of populations and species (see Figure 3).

Seascape genomics: similar to seascape genetics, but by using genome-wide (i.e., thousands) of genetic loci/markers and/or reference genomes and/or high-throughput sequencing technology, seascape genomics often also allows the assessment of adaptive processes (see Figure 3).

COMPETING INTERESTS

The authors declare no competing interests.

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Table 1: Examples of seascape genomics interpreted from a management perspective, driver of global biodiversity change, topic, outcome, organisms, habitat and reference.

Management practice	Global change	Topic	Outcome	Organism [Classification]	Habitat	Reference
Conservation management and spatial planning	Climate change	Identification of adaptive potential based on environmental characteristics and genotype frequencies, combined with connectivity analysis	Identification of reefs carrying potential heat stress adaptation and dispersal potential to neighboring reefs	Coral [Cnidaria]	Coastal	(Selmoni et al., 2020)
Conservation management	Climate change	Future proofing' efforts rely on predicting how neutral and adaptive genomic patterns will change under future climate scenarios	Range-edge populations harbor beneficial adaptations	Crayweed [Macroalgae]	Coastal - Benthos	(Wood et al., 2021)
Conservation and living resource management	Climate change	The viability of remnant populations could be impacted by continued fishing, by-catch pressure, and climate change	Climate change could inflict a strong selective force upon remnant populations	Blue skate [Fish]	Open ocean - Pelagic	(Delaval et al., 2021)
Conservation management	Habitat loss	Environmental factors may influence the evolutionary potential of populations and species	Species-specific habitat requirements and responses to environmental stresses may be better predictors of evolutionary patterns than strong environmental gradients	Crab [Crustacea], Sea urchin [Echinodermata], Limpet [Mollusca]	Coastal	(Nielsen et al., 2020b)
Living resource management	Habitat loss/resource overexploitation	Study of fine-scale spatial genetic structure and comparison to environmental variables and current-mediated larval dispersal within a modelling framework	Oceanographic currents and geographic proximity explain over 20% of the variance observed at neutral loci, while genetic variance at outlier loci was explained by sea surface temperature extremes.	Cockle [Mollusca]	Coastal - Plankton	(Coscia et al., 2020)
Conservation management	Habitat loss	Artificial structures function as stepping stone connectivity to suitable habitats	The marine steppingstone effect is obviously important for the distribution of sessile taxa	Mussel [Mollusca]	Coastal	(Coolen et al., 2020)

Conservation management	Non-indigenous species and populations	Species introductions promote secondary contacts between taxa with long histories of geographically separate divergence	The outcomes of species introductions are diverse, from introgression swamping to strong barriers to gene flow; lead to local containment or widespread invasion	Sea squirt [Tunicata] and Mussel [Mollusca]	Coastal	(Viard et al., 2020)
Conservation management	Non-indigenous species and populations	During range expansions, strong genetic drift through repeated founder events may decrease genetic diversity with increased distance from the point of invasion or the center of the historic range	Patterns of genetic diversity correlate with invasion pathway	Lionfish [Fish]	Coastal	(Bors et al., 2019)
Conservation management	Non-indigenous species and populations	Rapid climate-driven evolution might shift biogeographic distributions in response to global change	Rapid evolutionary adaptation has played a pivotal role in enabling the successful invasion of a wide range of habitats	Mussel [Mollusca]	Coastal	(Han and Dong, 2020)
Environmental management	Pollution	Specific evolutionary circumstances and mechanisms might rescue species at risk of decline from lethal levels of pollution	High nucleotide diversity might have been a crucial substrate for selective sweeps to stimulate rapid adaptation	Killifish [Fish]	Estuary	(Reid et al., 2016; Whitehead et al., 2017)
Conservation management	Pollution	Two types of point sources of aquatic environmental pollution affect gene diversity, genetic differentiation, and adaptation differently	Genetic effects are associated with exposure to sewage treatment plant effluents on wild populations	Mussel [Mollusca]	Baltic Sea; Coastal	(Larsson et al., 2016)
Living resource management and spatial planning	Resource overexploitation	Investigation of the influence of environment, geographic isolation, and larval dispersal on the variation in allele frequencies	Important to consider spatial scale in the design of a protected area network	Mullet [Fish]	Coastal	(Dalongeville et al., 2018)
Living resource management	Resource overexploitation	Testing for the presence of genetic discontinuities and spatial processes influencing spatial structure	Depletion of one population also affects recruitment of other populations	Sea cucumber [Echinodermata]	Benthos	(Xuereb et al., 2018a)
Living resource management	Resource overexploitation	Environmental association analysis to identify bioclimatic variables correlated with putatively adaptive genetic variation	Environmental variables play a role as drivers of spatially varying selection	Sea cucumber [Echinodermata]	Benthos	(Xuereb et al., 2018b)

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Figure 1: Seascape genomics is a multi-disciplinary research field. It starts from the individual genetic code of populations of wild organisms. Populations live in communities in a three-dimensional habitat and are influenced by a wide range of physical and biological drivers. The novel insights in population diversity and structure in a habitat setting assist with the conservation and management of natural populations.

Figure 2: Seascape genomics incorporates geo-referenced oceanographical information along environmental gradients structured vertically and horizontally (illustrated here with temperature and salinity). The evolutionary processes of genetic connectivity, genetic drift (depending on population size) and adaptation shape genetic diversity within and between populations. Illustration by Jerker Lokrantz/Azote.

Figure 3: Definitions and visual illustrations of the scientific disciplines of genetics, genomics, seascape genetics and seascape genomics (also see BOX 1 and 2).

Figure 4: Seascape genomics can be embedded in the management cycle of biodiversity protection. In a first step, an interdisciplinary team defines gaps and questions. Once a consensus is reached on a research question, data are mined and collected, analyses are prepared, and models are designed to integrate the results and embed the new understanding from seascape genomics into policy. At this stage, new gaps are identified, and a new set of questions are generated, while management practices and policies can be updated to allow the incorporation of the findings.

Figure 1

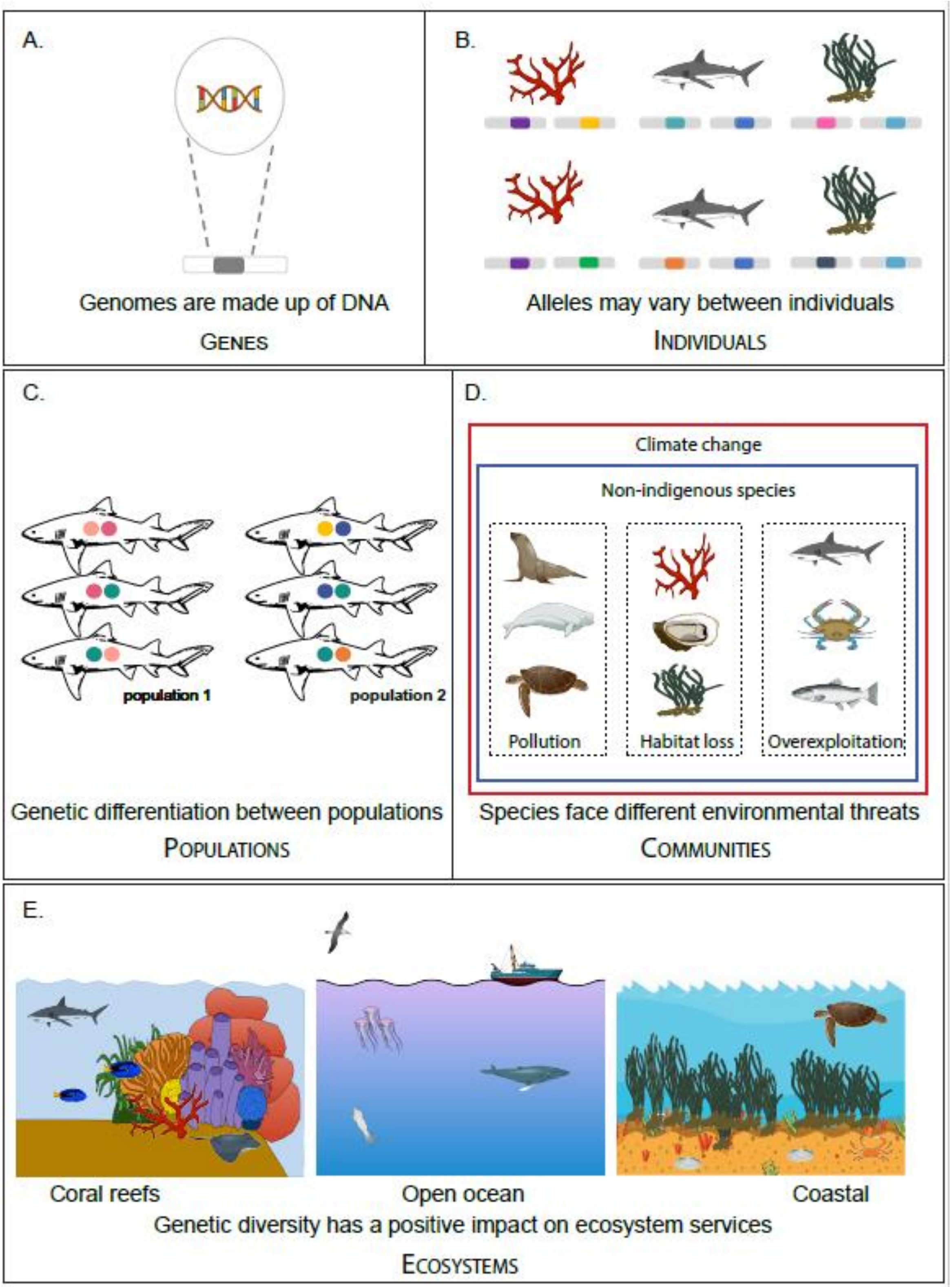
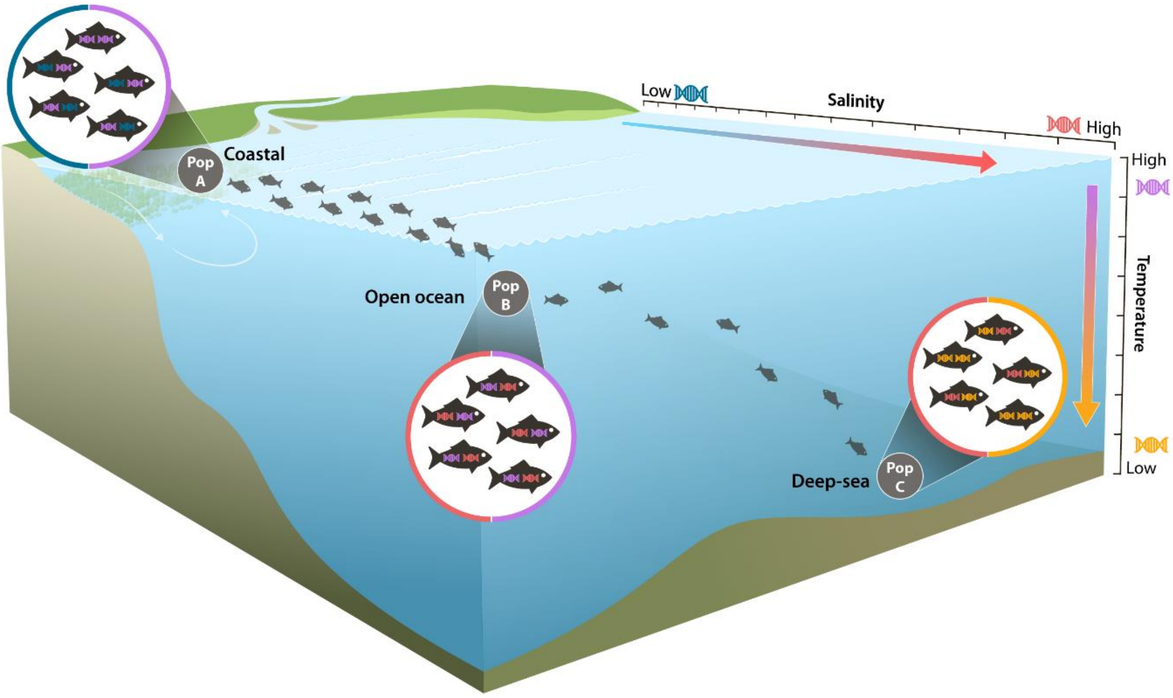
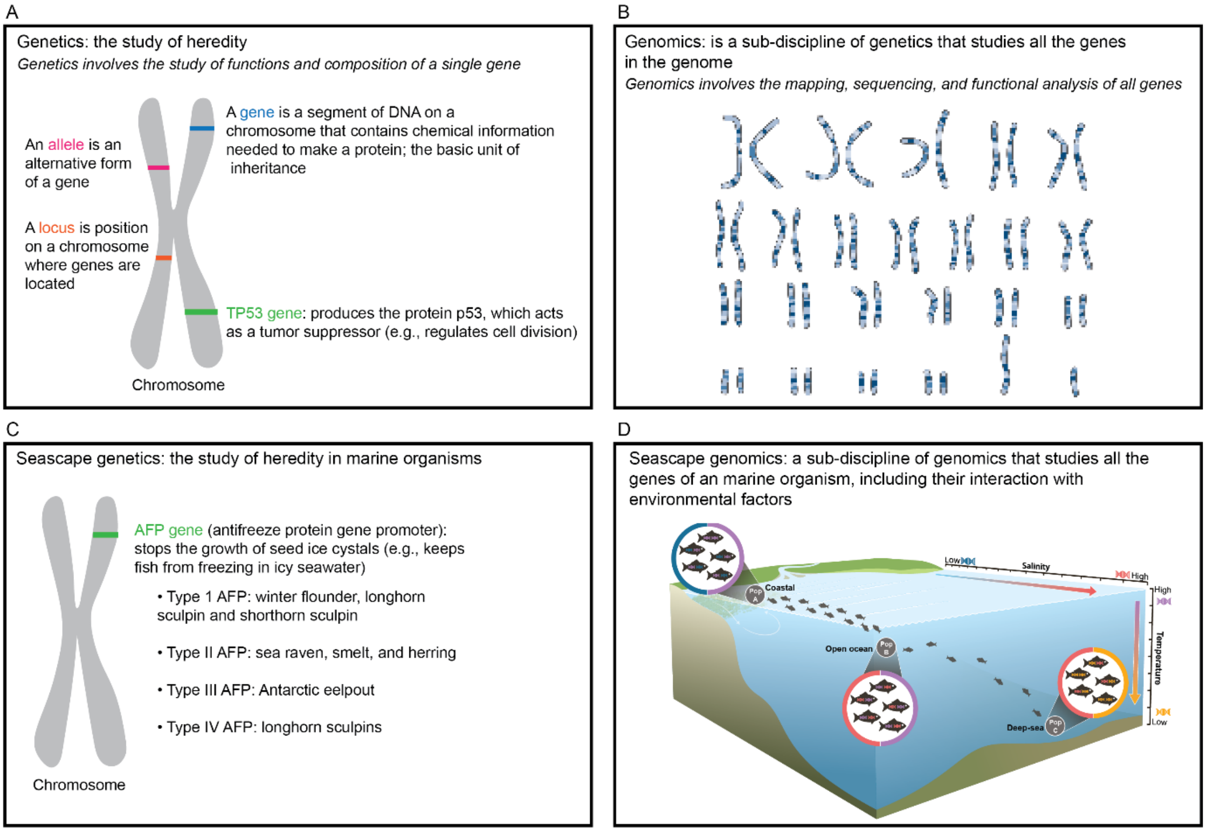

A.
Genomes are made up of DNA
GENES
B.
Alleles may vary between individuals
INDIVIDUALS
C.
population 1
population 2
Genetic differentiation between populations
POPULATIONS
D.
Climate change
Non-indigenous species
Pollution
Habitat loss
Overexploitation
Species face different environmental threats
COMMUNITIES
E.
Coral reefs
Open ocean
Coastal
Genetic diversity has a positive impact on ecosystem services
ECOSYSTEMS

Figure 2


Pop A
Coastal
Open ocean
Pop B
Deep-sea
Pop C
Low
Salinity
High
High
Temperature
Low

Figurre 3



A

Genetics: the study of heredity

Genetics involves the study of functions and composition of a single gene

An allele is an alternative form of a gene

A locus is position on a chromosome where genes are located

A gene is a segment of DNA on a chromosome that contains chemical information needed to make a protein; the basic unit of inheritance

TP53 gene: produces the protein p53, which acts as a tumor suppressor (e.g., regulates cell division)

B

Genomics: is a sub-discipline of genetics that studies all the genes in the genome

Genomics involves the mapping, sequencing, and functional analysis of all genes

C

Seascape genetics: the study of heredity in marine organisms

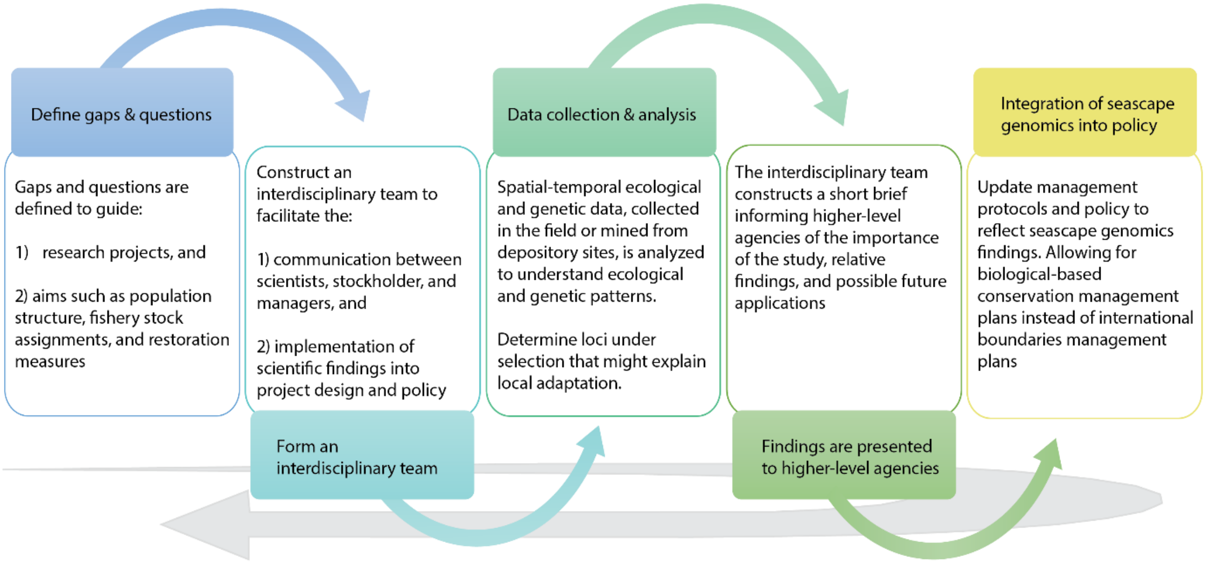
AFP gene (antifreeze protein gene promoter): stops the growth of seed ice cystals (e.g., keeps fish from freezing in icy seawater)

- Type 1 AFP: winter flounder, longhorn sculpin and shorthorn sculpin
- Type II AFP: sea raven, smelt, and herring
- Type III AFP: Antarctic eelpout
- Type IV AFP: longhorn sculpins

D

Seascape genomics: a sub-discipline of genomics that studies all the genes of an marine organism, including their interaction with environmental factors

Figure 4


Define gaps & questions
Gaps and questions are defined to guide:
1) research projects, and
2) aims such as population structure, fishery stock assignments, and restoration measures
Form an interdisciplinary team
Construct an interdisciplinary team to facilitate the:
1) communication between scientists, stockholder, and managers, and
2) implementation of scientific findings into project design and policy
Data collection & analysis
Spatial-temporal ecological and genetic data, collected in the field or mined from depository sites, is analyzed to understand ecological and genetic patterns.
Determine loci under selection that might explain local adaptation.
Findings are presented to higher-level agencies
The interdisciplinary team constructs a short brief informing higher-level agencies of the importance of the study, relative findings, and possible future applications
Integration of seascape genomics into policy
Update management protocols and policy to reflect seascape genomics findings. Allowing for biological-based conservation management plans instead of international boundaries management plans