



## **The ocean genome and future prospects for conservation and equity**

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# 1 The Ocean Genome and Future Prospects for Conservation and Equity

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5 **Life has evolved in the ocean for 3.7 billion years, resulting in a rich “ocean genome”, the**  
6 **ensemble of genetic material present in all marine biodiversity, including both the physical**  
7 **genes and the information they encode. Rapid advances in sequencing technologies and**  
8 **bioinformatics have enabled exploration of the ocean genome and are informing innovative**  
9 **approaches to conservation and a growing number of commercial biotechnology applications.**  
10 **However, the capacity to undertake genomic research and to access and use sequence data is**  
11 **inequitably distributed among countries, highlighting an urgent need to build capacity,**  
12 **promote inclusive innovation, and increase access to affordable technologies.**

13 The ocean is a vast and diverse habitat that covers 70% of the Earth’s surface. Although estimates of  
14 extant species are based on indirect approaches and extrapolations can vary widely, some 2.2  
15 million (range 0.3-10 million) eukaryotic marine species likely exist in the ocean, of which 230,000  
16 are confirmed<sup>1,2</sup>. Comparisons with terrestrial life underscore the striking diversity of marine life: for  
17 instance, of the 34 major animal phyla, only 12 are found on land, while 33 have been recorded in the  
18 ocean<sup>3</sup>. The abundance and diversity of marine prokaryotes (bacteria and archaea) and viruses  
19 reaches monumental orders of magnitude, collectively accounting for the majority of living mass in  
20 the ocean, with estimates, extrapolated from mean values per unit volume of seawater, of  $1.2 \times 10^{29}$   
21 prokaryote cells and  $1.3 \times 10^{30}$  virus particles found in ocean waters<sup>4,5</sup>. Some 24-98% of eukaryotic  
22 marine species, depending on the taxon group, remain undescribed, while even less is known about  
23 prokaryotic marine life, with estimates extrapolated using scaling laws, ranging from  $1.0 \cdot 10^6$  to  
24  $3.0 \cdot 10^{27}$  operational taxonomic units comparable, in taxonomic terms, to species<sup>2,6,7</sup>.

25 The diversity of marine life is closely associated with and dependent upon underlying genetic  
26 diversity, namely the total number of genetic characters in the genetic makeup of each species.  
27 Genetic diversity encodes the functional attributes of species, and their distribution and adaptability.  
28 Conserving genetic diversity provides more opportunities for evolution, and helps to foster the  
29 fitness of populations and their potential to recover from and adapt to threats ranging from disease  
30 to environmental changes<sup>8</sup>.

31 We define the “ocean genome” as the ensemble of genetic material present in all marine  
32 biodiversity, including both the genes and the information they encode<sup>9</sup>. The explicit reference to  
33 the physical resources and informational component of genes reflects technological advances as  
34 well as the regulatory efforts striving to govern them. In recent decades, it has become possible not  
35 only to store the nucleotide sequences of DNA and RNA as digital information, but to then use this  
36 information to synthesize proteins, create molecular processes and innovation, and modify or even  
37 create organisms<sup>10,11</sup>. Genetic sequence data and innovations based on such digital information are  
38 now the subject of patent and ownership claims<sup>12</sup>. The complexity of regulating access to both  
39 informational and physical resources and equitably sharing benefits from the vast potential

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40 applications of these genetic resources across multiple industries remains unresolved and is the  
41 subject of negotiations in multiple international fora<sup>13</sup>.

42 In this review, we address three questions. What are the benefits to the biosphere, to humanity and  
43 to other living organisms that arise from the ocean genome? What are the threats eroding genetic  
44 diversity in the ocean? How can the ocean genome be conserved and used in a more sustainable, fair  
45 and equitable manner?

## 46 Ecological benefits

47 Most attributes of organisms are encoded within their genomes, which determine much of their  
48 morphology, biology, behavior and physiology. High levels of genetic variability and the presence of  
49 multiple genotypes within a species can result in functional redundancy that supports species  
50 resilience and adaptive capacity under environmental pressures and anomalous conditions<sup>14,15</sup>.  
51 Within the context of complex and dynamic systems, genetic diversity is therefore a crucial  
52 stabilizing factor. Such benefits have been of interest to fishery managers, as genetically diverse fish  
53 populations are better positioned to exploit a range of habitats, which adds flexibility in their  
54 responses to environmental change<sup>16</sup>. Alaska's Bristol Bay salmon, for instance, is a highly  
55 heterogeneous population that includes over 100 discrete sub-populations, resulting in a portfolio  
56 effect, whereby the associated diversity has led not only to a more stable population, but also less  
57 frequent closures for fishing communities<sup>15</sup>. Elsewhere, the benefits of genetic variability have been  
58 recorded in restoration projects. For instance, in North America and Indonesia, plots of seagrass  
59 with higher levels of genetic diversity also exhibited higher rates of survival, plant density and  
60 growth<sup>17</sup>. The ecological benefits of genetic diversity extend beyond the resilience of individual  
61 populations. In both of the above cases, positive impacts were recorded – in the stability of  
62 populations feeding on salmon during spawning, and in increased levels of primary production and  
63 nutrient retention in restored seagrass beds in the Chesapeake Bay<sup>15,18</sup>.

64 Genetic variability also drives adaptive potential, which not only enhances resilience to anomalous  
65 conditions, but also enables persistence as environmental conditions change and evolve over time.  
66 Recent studies have demonstrated that this adaptive potential is of relevance even over short  
67 timeframes, for instance within the span of 200 to 600 generations (6 months) of certain tropical  
68 diatoms<sup>19</sup>. Due to the prominence of coral reef ecosystems as hotspots of marine biodiversity and a  
69 crucial element of marine food webs, the bleaching and loss of corals is of special concern. There is  
70 evidence suggesting that some corals may already have begun adapting to ocean warming caused  
71 by anthropogenic activity, rendering them more resistant in the context of mass-bleaching events.  
72 This relatively rapid response is a function of genetic diversity and phenotypic plasticity at the  
73 holobiont level. Likewise, current changes in ocean conditions could alter the functional  
74 composition of marine phytoplankton communities, the foundation of virtually all marine food webs  
75 and the source of roughly half of the oxygen on the planet. In an experimental setting, cultures of  
76 marine phytoplankton with higher genetic diversity outperformed less diverse cultures with regard  
77 to their ability to withstand low salinities and maintain nitrogen uptake levels<sup>23</sup>.

78 Closely studied ecosystems and commercial fisheries are already providing some evidence of how  
79 genetic diversity contributes to ecosystem function and enhances adaptive potential. Yet the full  
80 value of marine genetic diversity for the ocean and the biosphere will become increasingly apparent  
81 as ocean systems continue to change and additive and synergistic impacts are better understood.

82

## 83 Commercial benefits

84 While the ocean genome provides the ecological foundation that sustains major commercial  
85 industries such as marine fisheries and tourism, commercial benefits are also derived directly from  
86 marine genes. Marine organisms, from microbes to large vertebrates, establish complex intra- and  
87 interspecific interactions mostly mediated by a variety of chemicals. These chemicals serve multiple  
88 purposes, including communication, chemical defense to predators, allelopathy, antifouling and  
89 many others<sup>24,25</sup>. These chemicals, also called secondary metabolites, are small molecules of a  
90 diverse nature (e.g. peptides, sterols, phenols, terpenoids, alkaloids) often with a biological function  
91 yet to be resolved. The continuum of “omic” approaches, extending from genomics and functional  
92 genomics to transcriptomics, proteomics and metabolomics provides a mechanistic pathway linking  
93 the ocean genome to the metabolites that play an important role as potential natural products for  
94 human applications, as well as a key role in modulating interactions among organisms. Much  
95 research has focused on finding useful biological activities for biomedical, cosmetic and other  
96 commercial purposes. With the recent advances in analytical techniques (mass spectrometry,  
97 nuclear magnetic resonance), new high throughput metabolomics approaches are able to  
98 simultaneously unravel hundreds of novel compounds. When coupled to other omics technologies,  
99 such as Next-Generation Sequencing (NGS), in a systems biology approach, insights of the complex  
100 picture of interaction among organisms can be obtained. Furthermore, the pathways for production  
101 of the metabolites can be obtained, which opens the way to their mass production using  
102 biotechnological methods<sup>26</sup>.

103 Perhaps the hallmark of human benefit from a marine gene is the discovery of green fluorescent  
104 protein, which produces bioluminescence in the jellyfish *Aequorea victoria* and has been used across  
105 a range of applications from protein tagging to identifying levels of environmental toxicity,  
106 contributions ultimately recognized with the 2008 Nobel Prize in Chemistry<sup>27</sup>. Further examples  
107 include bioprospecting for novel antifoulants and adhesives, and the search for novel antibiotics,  
108 which has increasingly focused on the bioactive compounds produced by marine invertebrates and  
109 microorganisms associated with sea sponges<sup>28-30</sup>. Other marine microorganisms produce a type of  
110 naturally occurring polymer (extracellular polymeric substance) that is of interest in bioremediation  
111 efforts due to its capacity to detoxify pollutants such as heavy metals<sup>31</sup>, while *Pseudomonas spp.* and  
112 *Ideonella sakaiensis* have the capacity to biodegrade certain plastics<sup>32</sup>. Additional categories of  
113 commercial activity focused on marine genetic resources are briefly introduced below.  
114 Controversies over the ownership and exclusive use of these genetic resources have persisted and  
115 present some unique challenges to existing international frameworks, as well as to potential pace of  
116 discovery.

### 117 **Marine drug discovery**

118 The marine environment has been an attractive source of bioactive compounds for the development  
119 of novel drugs. The approximately 34,000 marine natural products<sup>33</sup> that have been reported have  
120 resulted in 8 clinically-approved drugs, with a further 28 in clinical trials and 250 under preclinical  
121 investigation<sup>34</sup>. Compared with drug development from terrestrial natural products, this is a  
122 remarkable success rate<sup>35</sup>. A driving force behind the development of marine drugs has been  
123 extensive funding from the US National Cancer Institute and prospective efforts by private  
124 companies, as well as a focus on the collection of marine genetic resources globally, particularly  
125 from shallow tropical reefs and marine invertebrates. Consequently, five of the eight clinically-  
126 approved drugs are treatments for cancer, with the remainder comprising treatments for  
127 neuropathic pain, the *Herpes simplex* virus and hypertriglyceridemia. Seven of the eight drugs were  
128 derived from sessile marine invertebrates, whose tendency to produce highly bioactive compounds  
129 – a virtual chemical arsenal – may be related to their lack of an adaptive immune system, predation  
130 pressure, and intense competition for space and resources, although the majority of these  
131 compounds have no apparent defensive function<sup>36</sup>.

## 132 **Nutraceuticals and cosmeceuticals**

133 With properties that provide medical or health benefits and also serve cosmetic or nutritional  
134 purposes, cosmeceuticals and nutraceuticals are a growing industry, with marine resources  
135 comprising an attractive source due to the wide range of exhibited metabolic pathways. The  
136 resulting diversity of bioactive compounds includes vitamins, carbohydrates, proteins and peptides,  
137 and – perhaps most prominently – omega-3 fatty acids<sup>37</sup>. While fish and crustaceans have long been  
138 exploited as sources of eicosapentaenoic acid and docosahexaenoic acid, overexploitation of fish  
139 stocks has led to research in alternative sources of omega-3 fatty acids, and the subsequent  
140 development of algal oils that can be produced in industrial quantities using phototrophic  
141 microalgae<sup>38,39</sup>. Cosmeceutical skin creams with purported anti-inflammatory and detoxifying  
142 agents have been developed from species as diverse as the Caribbean gorgonian (*Pseudopterogorgia*  
143 *elisabethae*) and bacteria isolated from deep-sea hydrothermal vents (*Altermonas macleodi* subsp.  
144 *fijiensis* biovar *deepsane*; *Thermus thermophilus*)<sup>40,41</sup>.

## 145 **Aquaculture and new food products**

146 While genetic modification has been used on a variety of commercial land crops, it remains in its  
147 infancy in the aquaculture industry. To date, only the Atlantic salmon (*Salmo salar*) has been  
148 commercialized using genetic engineering, namely through the insertion of growth hormone cDNA  
149 from Chinook salmon (*Oncorhynchus tshawytscha*) and regulated with antifreeze protein promoter  
150 sequences from the Ocean pout (*Zoarces americanus*) that enable it to survive in near-freezing  
151 temperatures<sup>42</sup>. The resulting transgenic salmon, which reached the market for the first time in  
152 2017<sup>43</sup>, can reach a marketable size within 16-18 months, as opposed to the three years it would  
153 otherwise require. But with just 40 fish species having fully sequenced genomes, and the recent  
154 advent of tools such as CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats) and  
155 associated enzymes (e.g. Cas9) allowing selective gene editing, the number of transgenic  
156 aquaculture species is expected to increase, particularly due to a growing demand for seafood and  
157 increasing focus on lower trophic level species like seaweeds and bivalve molluscs<sup>44</sup>. However,  
158 questions of consumer acceptability, environmental risk and social desirability remain paramount  
159 and unresolved, alongside an uncertain regulatory framework<sup>45,46</sup>. Parallel research has also  
160 developed, focused on novel functional food ingredients with the potential to extend shelf-life and  
161 prevent spoilage (e.g. chitosan and protein hydrolysates)<sup>47</sup>, and the use of enzymes from marine  
162 microorganisms as natural food processors<sup>48</sup>.

## 163 **Bulk chemicals**

164 Products and processes derived from marine genetic resources are of growing importance for the  
165 bulk chemical market, with applications ranging from novel laundry detergents to their use as  
166 emulsifiers and stabilizers in food production. Bioplastics derived from seaweed polymers are being  
167 used across a range of applications from straws and flip-flops to edible alternatives to plastic  
168 packaging<sup>48,49</sup>. The enzymes allowing species to flourish in extremely cold and hot marine  
169 environments have also attracted commercial interest. For example, a genetically modified version  
170 of a thermostable enzyme collected from a hydrothermal vent organism has been used for  
171 bioethanol production due to its capacity to function across wide pH and temperature ranges<sup>50</sup>. The  
172 addition of certain red seaweeds (*Asparagopsis taxiformis* and *Asparagopsis armata*) to ruminant  
173 feed has been shown to more than halve methane emissions, although concerns exist about the  
174 ozone-depleting properties of bromoform, a secondary metabolite produced by these seaweeds, if  
175 industrial-scale production for animal feed is pursued<sup>51,52</sup>.

## 176 **Erosion of the ocean genome**

177 All of these benefits—including products from marine genetic resources and ecosystem services  
178 delivered by diverse and fully functioning ocean systems—are predicated on the existing ocean  
179 genome. Yet this is threatened by the intensification of human activity around the world, which is  
180 contributing to a rapid loss of biodiversity in marine life and accelerating trends that are evident  
181 across multiple ocean-based industries<sup>53</sup>. Marine capture fisheries, coastal development and  
182 pollution have contributed to the loss of (sub-) populations and in extreme cases, species extinction,  
183 although these are rare in marine environments<sup>54</sup>. This leads to a decline in genetic diversity in the  
184 ocean, mostly concentrated, thus far, at the level of within species variability. The economic  
185 importance of the salmon industry has spurred close monitoring of the population dynamics of  
186 salmon, helping to understand the impact of human activities: within the Columbia River basin, for  
187 example, dam construction has resulted in the extinction of several sockeye salmon subpopulations,  
188 while chinook salmon have lost up to two-thirds of their genetic diversity<sup>55</sup>. The decline in genetic  
189 diversity has resulted in smaller and more variable salmon returns<sup>55</sup>. Even within subpopulations  
190 that persist, overfishing can result in the loss of genetic diversity over time, most likely reflected in  
191 loss of allelic diversity for specific genes, as the prominence of certain genotypes fluctuates and  
192 genetic drift reduces genetic diversity and lowers the capacity of species to persist and adapt to  
193 changing conditions.

194 Although documented species extinction has been rare in the ocean compared with recent rates of  
195 terrestrial species loss, climate change is expected to result in disproportionate levels of species loss  
196 in the ocean due to the narrow thermal range tolerated by marine ectotherms<sup>54,56</sup>. As the ocean  
197 warms and becomes more acidic and less oxygenated with climate change, the geographic  
198 distribution of species is also changing as they track their environmental niche<sup>57</sup>. At a genetic level,  
199 this implies an altered distribution of genetic variants in space and time, impacts on levels of  
200 phenotypic plasticity and changes to connectivity and population size<sup>58</sup>. Genetic variation is not  
201 uniform across species ranges, with populations in historic refuges often characterized by greater  
202 genetic diversity, and likewise threatened by shifts in distribution due to climate change<sup>59</sup>.

203 Efforts to optimize marine aquaculture have included the selective breeding of species and their  
204 introduction into non-native habitats. Careful monitoring and containment helps to maintain the  
205 integrity of local ecosystems, but escape events do occur, and have led to farmed species  
206 outcompeting native populations as well as the interbreeding of farmed and native species<sup>60</sup>. This  
207 results in genetic introgression and can lead to a rapid and irreversible loss of genetic diversity  
208 among the native fish populations, thereby lowering their adaptive capacity<sup>61</sup>. Such impacts could  
209 be accelerated by the accidental release of genetically modified strains in the ocean.

210 Much of the deep ocean and seabed remain unexplored, and scientific expeditions regularly result in  
211 the discovery of new species. A tendency for deep-sea life to exhibit slow growth rates and long  
212 lifespans renders deep-sea ecosystems particularly vulnerable to environmental disturbance<sup>62</sup>. The  
213 potential for large-scale commercial mining of the international seabed has therefore drawn  
214 particular concern within the scientific community due to uncertainty about the scale of physical and  
215 geochemical disturbance caused by mining operations and resulting sediment plumes in the deep  
216 sea, which are expected to lead to the loss of habitat and a potentially irreversible loss of  
217 biodiversity<sup>62</sup>. The scaly-foot snail (*Chrysomallon squamiferum*), for instance, is found exclusively on  
218 three hydrothermal vent systems in the Indian Ocean at depths of over 2400 meters, and was placed  
219 on the IUCN Red List in June 2019 due to two of the three systems falling within the boundaries of  
220 exploratory mining licenses granted by the International Seabed Authority<sup>63</sup>.

221 The acceleration of human activities on land and in the sea means that many marine species and  
222 communities are simultaneously facing multiple pressures with cumulative or synergistic effects on  
223 genetic structure and gene flow. Well-studied examples include the twin pressures of wild capture

224 salmon fisheries and aquaculture escapement, which undermine the genetic variability of wild  
225 populations<sup>64</sup>. Looking beyond individual populations or species, multiple pressures can also result  
226 in a complete reordering of ecosystems into novel regimes. For instance, the combined and  
227 interlinked pressures from eutrophication, overfishing and the introduction of invasive species into  
228 the Black Sea led to abrupt transitions and the emergence of a new stable regime characterized by a  
229 low-energy food web dominated by jellyfish and the dinoflagellate *Noctiluca scintillans*.<sup>65</sup>

## 230 **A more sustainable and equitable future**

231 How can a growing understanding of the ecological and commercial benefits associated with the  
232 ocean genome be leveraged to promote conservation efforts and mitigate the drivers of genetic  
233 diversity loss in the ocean? Below, we detail not only what can be done to conserve the ocean  
234 genome, but also avenues through improved regulatory frameworks and models of inclusive  
235 innovation that can render use of the ocean genome more sustainable, equitable and fair.

## 236 **Towards conservation of the ocean genome**

237 In marine systems, there are opportunities for the conservation of genetic diversity via key tools,  
238 among them ecosystem-based approaches to fisheries management, spatial planning, effective  
239 quotas, marine protected areas (MPAs), protecting and managing key marine biodiversity areas,  
240 reducing run-off pollution into oceans, and working closely with producers and consumers of ocean  
241 products<sup>66</sup>. Among these, the imperative of conserving the ocean genome would appear to be on  
242 firm footing in existing international frameworks: the importance of genetic diversity was already  
243 emphasized in the Convention on Biological Diversity (CBD) (1992), while the target of protecting at  
244 least 10% of the ocean is found in both Sustainable Development Goal 14 and Aichi Target 11. Yet  
245 genetic diversity has been largely overlooked in conservation policies and action plans, and only 8%  
246 of the ocean is set aside for biodiversity conservation, while just 2.5% is considered fully or highly  
247 protected<sup>68</sup>.

248 MPAs are considered one of the most effective tools for achieving the conservation of genetic  
249 diversity on an ecosystem scale<sup>69</sup>. Fully or highly-protected large-scale MPAs and networks of MPAs  
250 can encompass multiple sites of importance for the life-cycle of marine species. Well-managed  
251 MPAs with adequate protection levels function as storehouses of genetic diversity that  
252 simultaneously serve as important reference points for understanding changes to the ocean<sup>70</sup>. MPA  
253 networks can be designed with a specific focus on areas where genetic diversity is exceptionally high,  
254 or where particular adaptation potential lies. Such MPA adaptation networks are relevant for  
255 instance in coral reef systems<sup>71</sup>, which have been the focus of empirical work to map their  
256 adaptation potential<sup>72</sup>. The capacity for a single coral species to inhabit a range of environments  
257 characterized by high genetic diversity and on scales of less than 100 meters underscores the need  
258 for protected areas to be designed with a consideration not only for potential shifts in species  
259 distribution across latitudes, but also different water depths<sup>34,73</sup> (Figure 1).

260 Recognizing the importance of MPAs and other effective area-based conservation measures  
261 (OECMs) as tools for conserving the ocean genome, there is a particular need to optimize design to  
262 also conserve the genetic component of marine biodiversity. This remains a substantial challenge  
263 due to the rarity of temporal genetic diversity datasets or baselines, although a number of novel  
264 genetic technologies are becoming available with the potential to overcome this barrier. These  
265 include Sanger sequencing, with a history of applications ranging from wildlife conservation and  
266 management to the identification of mislabeled seafood<sup>74</sup>, as well as Next-Generation Sequencing  
267 (NGS), a high-throughput DNA-sampling tool that can provide large-scale spatial and temporal  
268 syntheses for both individual species and community assemblages<sup>75</sup>. Several community initiatives

269 using NGS are starting to change this landscape, such as the Earth BioGenome Project which aims  
270 to sequence, catalog, and characterize the genomes of all of Earth's eukaryotic biodiversity over a  
271 period of 10 years<sup>76</sup>, the sponge microbiome project a comprehensive resource of sponge-  
272 associated microbial communities based on 16S rRNA gene sequences that can be used to address  
273 overarching hypotheses regarding host-associated prokaryotes<sup>77</sup>, and the Earth Microbiome Project  
274 to characterize microbial life on the planet using DNA sequencing and mass spectrometry<sup>78</sup>.  
275 Emerging data on diversity within the microbiome of marine holobionts is revealing a vast reservoir  
276 of hitherto largely ignored microbial biodiversity<sup>79</sup>.

277 When coupled with another novel molecular approach, environmental DNA (eDNA) analysis, NGS  
278 has also been used for the detection and monitoring of marine invasive species<sup>80,81</sup>. The passive  
279 sampling techniques employed for eDNA analysis provide multiple benefits of interest to marine  
280 conservation. Due to the constant shedding of DNA by species as they interact with their  
281 environment, analysis of eDNA samples can indicate whether certain species are present in a given  
282 geography<sup>82</sup>. As a result of the rapid decomposition of eDNA over the span of days or even hours in  
283 seawater, eDNA analysis provides an almost real-time picture of species presence, including rare or  
284 elusive species, and invasive species<sup>83,84</sup>. The flexibility of the approach allows for simultaneous  
285 identification of hundreds of species in a single sample, providing insight into areas of particular  
286 species richness and potential priority for area-based protection. Recent advances in interpreting  
287 eDNA are also enabling quantification of population genetic structure and insights into trophic  
288 connectivity<sup>85</sup>. Sampling and analysis of eDNA is most powerful in well-studied marine ecosystems  
289 with substantial barcode reference collections, but may become an increasingly useful tool for the  
290 design of marine conservation interventions.

291 Some have touted the potential of new genome-editing techniques such as CRISPR for conservation,  
292 but their application remains theoretical. Extensive work done on corals, for example, reveals  
293 limited knowledge about potential candidate genes to target, whether this would result in  
294 phenotypic changes, whether the modified genome would be stable, and what unintended  
295 consequences gene editing could generate<sup>86,87</sup>. Moreover, a scarcity of information about the  
296 environmental, social and ethical risks of existing and new genetic engineering tools, especially in  
297 marine environments, have raised important questions about the governance and regulation of such  
298 technologies, necessitating a precautionary approach to the introduction of such technologies for  
299 conservation and fisheries management.

300 Although genetic techniques are rapidly evolving, policymakers do not have the luxury of waiting to  
301 make interventions until comprehensive inventories of marine genetic diversity are available, or  
302 until the extent of varied threats are fully understood. A delayed response risks resulting in the loss  
303 of rapidly deteriorating storehouses of genetic information due to over-harvesting of species and  
304 habitat degradation. Scientific recommendations to protect 30% of the ocean from all but the most  
305 minimal extraction focus on encompassing sufficient biodiversity, species biomass, and  
306 representative habitats<sup>88</sup>. This requires that ongoing management outside protected areas  
307 complements these efforts by ensuring sustainable use, minimizing habitat destruction and  
308 avoiding overexploitation of resources. Such strategies include sustainable management of fisheries  
309 with a focus on ecosystem-based fisheries management, affording special protections for rare,  
310 vulnerable, threatened or endangered genotypes, populations and species, and using precautionary  
311 approaches when initiating exploitation of previously unexploited species or places.

### 312 **Towards equitable benefit sharing**

313 Investments in marine biodiscovery are typically extremely costly and risky due in part to the high  
314 costs of sampling in areas like the deep sea, the low chances of success, the technical, financial and



315 scientific investments required, and the significant regulatory hurdles for product approval (Figure  
316 3)<sup>89,90</sup>. The nature of the research enterprise is also changing, as research shifts towards  
317 bioinformatics and the mining and exploration of these vast and growing datasets of genetic  
318 information, which requires advanced computational resources that are not broadly available<sup>91</sup>. As a  
319 result, most exploration has been undertaken by high-income countries, especially with regard to  
320 deep-sea research<sup>36,92,93</sup>. Disparities in research capacity, technology, finances and intellectual  
321 property rights represent major constraints that prevent the inclusion of low and middle-income  
322 countries in marine biotechnology efforts. Biodiversity and molecular expertise is unevenly spread<sup>94</sup>,  
323 and research vessels or submersibles are typically owned only by a few high-income nations, and  
324 require substantial operational costs<sup>95</sup>, representing a major barrier to sampling of the deep ocean  
325 or in areas beyond national jurisdiction (see Box 1). While there are growing numbers of  
326 collaborations between high-income and lower-income countries<sup>96</sup>, the model of international  
327 collaboration is still characterized by a pharmaceutical or biotech company working with established  
328 centers of excellence located in high-income countries.

329 A number of international governance instruments and bodies provide an important platform where  
330 new models of equitable benefit sharing and research partnerships can evolve, and conservation of  
331 the ocean genome can be strengthened. These include the CBD, its Nagoya and Cartagena  
332 (Biosafety) Protocols, the International Treaty on Plant Genetic Resources for Food and Agriculture,  
333 the United Nations Convention on the Law of the Sea (UNCLOS) and the World Intellectual Property  
334 Organization (WIPO). Among other provisions, these agreements place the responsibility on states  
335 to conserve their biological diversity or to enter into meaningful management discussions with other  
336 countries with which they share resources (e.g. transboundary fish stocks). In the context of genetic  
337 resource use, the CBD's Nagoya Protocol sets forth the requirement for provider countries (where  
338 genetic resources are located) and user countries (those accessing and developing the genetic  
339 resources) to enter into mutually agreed terms based on prior informed consent before access to  
340 genetic resources is granted. In areas beyond national jurisdiction (ABNJ), roughly 64% of the ocean,  
341 no restrictions currently exist on access to genetic resources, or regulations for the sharing of  
342 benefits based on their potential commercialization. However, this is one of four main elements of  
343 ongoing UN treaty negotiations of cross-cutting importance for the ocean genome (Box 1).

344 A further complication is the so-called "definitional mistake" of the CBD and Nagoya Protocol,  
345 whereby focus is placed on genetic resources in terms of their physical form rather than explicitly  
346 including the intangible informational aspects<sup>97</sup>. The development of novel genomic techniques has  
347 contributed to a 4,000-fold drop in sequencing costs over the past decade<sup>98</sup>, and has resulted in vast  
348 and exponentially growing databases of genetic sequence data and hundreds of millions of  
349 predicted genes (Figure 2)<sup>99-101</sup>. While many of these databases are in the public domain and freely  
350 accessible, the growing tendency towards "big data" applications means that leveraging novel  
351 genomic techniques for conservation or other uses is becoming increasingly dependent on  
352 computational and bioinformatics capacity, including access to technologies protected by  
353 intellectual property rights. Additionally, the private appropriation of genetic resources through  
354 intellectual property rights such as patents, because they result in exclusivity of use, can exacerbate  
355 existing gaps in the ability to benefit from their exploitation<sup>102</sup>. Because countries of the global  
356 North and South do not have equal capacities or technologies to exploit these resources, there is a  
357 risk of inequitable outcomes out of sync with the 2030 Agenda for Sustainable Development and the  
358 CBD and its Nagoya Protocol<sup>103</sup>.

359 One opportunity rests in the development of research partnerships that connect countries that have  
360 high molecular research capacity and biotechnology infrastructure with those that do not, with such  
361 partnerships guided by norms of inclusive innovation and those of responsible research and  
362 innovation<sup>90,104</sup>. Taking an explicit focus on those excluded from the development mainstream,  
363 inclusive innovation is a conceptual approach for ensuring that innovation both addresses the

364 problems faced by the poorest and most marginalized communities, and also involves these  
365 communities in crafting a range of legal, technical and governance-based solutions<sup>101,102</sup>. The related  
366 concept of responsible research and innovation (RRI) envisages a transparent, interactive process by  
367 which societal actors and innovators become mutually responsive to each other with a view to the  
368 (a) ethical acceptability, (b) sustainability and (c) societal desirability of the innovation process and  
369 its marketable products<sup>106</sup>.

370 Historically, the majority of exploration of the ocean genome has been funded by high-income  
371 countries such as the USA, Japan, Russia and EU states, and commercial activities and benefits  
372 continue to be concentrated within a handful of highly-industrialized countries<sup>12,50</sup>. However,  
373 sustained commitments to research partnerships and inclusive and responsible research and  
374 innovation, including through capacity building and the transfer of marine technology, could result  
375 over time in a growing number of dynamic knowledge hubs and diffuse scientific collaborations  
376 outside the Global North<sup>107</sup>. Indeed, it may well be that enabling virtual access to data and the ability  
377 to use it might prove an easier task than equalizing physical access to marine genetic resources.

378 While the concept of inclusive and responsible research and innovation is appealing and in line with  
379 existing governance and regulatory frameworks, there are substantial and unresolved legal and  
380 ethical issues related to the use and sharing of genomic information. The science bodies of the EU,  
381 USA and Australia, for instance, require genomic data collected over the course of funded projects  
382 to be deposited in open access databases. While regulations on disclosure of origin and other  
383 measures aimed at increasing transparency in the use of genetic sequence data are being  
384 negotiated within multiple international fora<sup>108</sup>, the informational component of the ocean genome  
385 is increasingly entering the public domain and becoming a *de jure* universal resource, that is *de facto*  
386 only accessible to those with corresponding capacity. The capacity for industry actors to access  
387 public databases, while remaining unbound by benefit-sharing requirements, has compounded  
388 concerns among some countries of both a loss of control over national patrimony and the  
389 management of global resources and a loss of opportunity to reap benefits<sup>109</sup>.

390 Scientists and policymakers have noted the importance of respecting such concerns and avoiding  
391 inequitable exploitation – commercial or otherwise – while also ensuring that scientific progress can  
392 continue with as few impediments as possible. Some have criticized the Nagoya Protocol for  
393 inadvertently hampering taxonomic research and international collaborations<sup>110</sup>, while being unable  
394 to enforce meaningful benefits sharing. Others have underscored that UNCLOS ensures freedom to  
395 undertake scientific research, including in ABNJ (Articles 256-257)<sup>111</sup> while still others have rejected  
396 the legitimacy of legal claims that arise from marine scientific research (Article 241), including in the  
397 form of intellectual property rights<sup>112</sup>. The outcome of the BBNJ negotiations (see Box 1) has the  
398 potential to not only strike this balance for ABNJ, but also to illustrate alternative pathways for  
399 regulating the use and circulation of genetic resources internationally.

## 400 Conclusion

401 The future state of ocean ecosystems will depend in large part on recognizing that human activity  
402 has already substantially eroded the ocean genome and that this has been to the detriment of the  
403 biosphere, humanity and other life forms. Encouraging signals are emerging, including recent calls  
404 to move beyond current international targets by ensuring that in the future at least 30% of the  
405 ocean is fully or highly protected<sup>88</sup>, the declaration of a UN Decade of Ocean Science for Sustainable  
406 Development (2021-2030), and the consensus decision among UN member states to move forward  
407 with negotiating a legally-binding instrument for conservation and sustainable use of BBNJ. Yet  
408 human impacts on the ocean are growing alongside accelerating commercial use of its resources  
409 and space<sup>53,113</sup>, while the potential for new industries such as mining of the international seabed and

410 methane hydrates pose vast risks for the ocean genome<sup>62</sup>. Ensuring that the ocean genome is  
411 conserved will require effective regulation and governance based on inclusive and iterative dialogue  
412 processes that connect diverse stakeholders, are based on principles of fairness, equity and  
413 inclusivity, and are informed by the latest scientific techniques and knowledge of the ocean genome.

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#### **BOX 1: Negotiations on Biodiversity in Areas Beyond National Jurisdiction (BBNJ)**

Some 36% of the ocean falls within exclusive economic zones (EEZs) within which states are granted a broad range of sovereign rights to make decisions related to the conservation and management of resources (UNCLOS, Article 57). The remaining 64% of the ocean is described as areas beyond national jurisdiction (ABNJ), comprised of the water column (“The High Seas”) and the seabed and ocean floor beyond the limits of national jurisdiction (“The Area”). Multiple sectoral organizations exist with mandates to govern resources or activities in ABNJ, including a network of regional fisheries management organizations (RFMOs) under the Food and Agriculture Organization of the UN, the International Seabed Authority (for seabed mining), and the International Maritime Organization (for shipping). Recognizing that this landscape of sectoral organizations has been insufficient for addressing the full range of issues of relevance to BBNJ, states reached consensus with a UN General Assembly resolution (72/249) in December 2017 to initiate an intergovernmental conference with the aim to “elaborate the text of an international legally-binding instrument on the conservation and sustainable use of [BBNJ]”. The BBNJ negotiations are focused around a “package” of four topics, all of relevance to the ocean genome, namely:

- marine genetic resources (MGR), including questions on the sharing of benefits;
- measures such as area-based management tools, including MPAs;
- environmental impact assessments;
- capacity-building and the transfer of marine technology.

Negotiations related to MGR have proven complex due to the issues covered in this review relating to informational and physical aspects of MGR and conditions for equitable access and benefit sharing. The latter has been further hampered by a tendency for States to view MGR through the lens of contrasting regimes, namely “freedom of the high seas” or the “common heritage of [hu]mankind”. The former implies a continuation of the liberal access regime that currently prevails in ABNJ and an absence of benefit-sharing obligations, while the latter would see changes to both to reflect a view that MGR from ABNJ are owned by all. Pragmatic approaches have sought to establish common ground between these positions, particularly by shifting focus from sharing of potential monetary benefits of commercial activity to emphasize the range of associated non-monetary benefits. For a detailed account of the BBNJ negotiations, their history, and negotiating positions, see Wright et al<sup>91</sup>.

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## BOX 2: The future of the ocean genome

Ensuring that the ocean genome is both preserved and used in a sustainable, fair and equitable manner is critical and requires effective conservation in both protected areas and beyond. It will also depend on operative national and transnational legal measures being in place to ensure incentives for research and development as well as equitable technology diffusion. Within this space, emerging opportunities exist for exploration, research, innovation, and investment. These include:

- 1) **Building knowledge of the ocean genome:** Increasing governmental and philanthropic support for basic taxonomic research as well as comprehensive assessments of the risks of transgenic marine organisms and other uses of new technologies to facilitate both effective conservation and sustainable use.
- 2) **Protecting marine genetic diversity and monitoring outcomes:** Management efforts that conserve marine genetic diversity should be supported by existing international commitments, including a particular focus on protecting areas of high biodiversity via fully and highly protected areas. Strategic Environmental Assessments and monitoring programs provide opportunities to report and revise national biodiversity strategies and action plans.
- 3) **Embedding ocean genome conservation within research and commercialization:** Benefits from ocean genome exploration and use would be enhanced by requiring equitable research partnerships between high- and low-income countries and through disclosure of the origin of genetic material as well as an explanation of the potential conservation and equity outcomes of commercialization.
- 4) **Supporting greater equity in genomics research and commercialization:** Incorporating marine science capacity building, information exchange, collaboration, and appropriate technology transfer into national research policies, plans and programs can benefit from the involvement of users and providers of marine genetic resources, who can work to set fair agreements on benefit sharing and technology transfer.
- 5) **Promoting inclusive and responsible research and innovation:** A transparent and interactive process can facilitate benefit-sharing and equitable outcomes by engaging multiple stakeholders, including private sector entities and scientists, with a view to the ethical acceptability, environmental sustainability and social desirability of the innovation process, and a focus on benefits for under-represented, marginalized, and vulnerable communities.

421

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434 **Competing interests**

435 M.J. is founder of, shareholder in and consultant for 'GyreOx Ltd' which uses marine and terrestrial  
436 enzymes for the rapid production of complex molecules to target protein-protein interactions  
437 involved in disease. S.T. has participated in the BBNJ negotiations as a Pacific Islands Forum Adviser.

438 **Author contributions**

439 R.B., R.W., K.G.-C., S.T., N.M.B., A.V.M.C., J.D.S., C.M.D., M.J., A.R., K.S. and C.C.C.W. all  
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721 **Figure captions**

722 **FIGURE 1: A portfolio approach for conserving the ocean genome and its associated benefits.**  
723 *Effective conservation hinges on using multiple tools, including area-based conservation measures such*  
724 *as fully and highly protected marine protected areas (MPAs), that provide the greatest protection from*  
725 *the impacts of extractive and destructive activities. Coupling these with effective management of*  
726 *sustainable use can ensure wide-ranging benefits that are ecological, sustaining, provisional and*  
727 *commercial.*

728

729 **FIGURE 2: (A) Decline in average sequencing costs (cost per raw megabase of DNA sequence)<sup>114</sup>; (B)**  
730 **Growth in GenBank Sequence Read Archive (cumulative number of open access base pairs)<sup>115</sup>**

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732 **FIGURE 3: Risk profit margins and timelines for commercial activities based on marine genetic resources**



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