



Marine genomics

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1 **Marine Genomics: News and Views**

2

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19

20 **Keywords**

21 Genomics, RNAseq, targeted sequencing, RADseq, marine species, evolution

22

23 Abstract

24
25 Marine ecosystems occupy 71% of the surface of our planet, yet we know little about their diversity. Although
26 the inventory of species is continually increasing, as registered by the Census of Marine Life program, only
27 about 10% of the estimated two million marine species are known. This lag between observed and estimated
28 diversity is in part due to the elusiveness of most aquatic species and the technical difficulties of exploring
29 extreme environments, as for instance the abyssal plains and polar waters. In the last decade, the rapid
30 development of affordable and flexible high-throughput sequencing approaches have been helping to improve
31 our knowledge of marine biodiversity, from the rich microbial biota that forms the base of the tree of life to a
32 wealth of plant and animal species. In this review, we present an overview of the applications of genomics to
33 the study of marine life, from evolutionary biology of non-model organisms to species of commercial relevance
34 for fishing, aquaculture and biomedicine. Instead of providing an exhaustive list of available genomic data, we
35 rather set to present contextualized examples that best represent the current status of the field of marine
36 genomics.

37

Introduction

38 Marine ecosystems, including coral reefs, deep-sea floor, hydrothermal vents, seagrass meadows, mangroves,
39 the abyssal water column, sandy and rocky beaches, polar ice and saltmarshes, occupy a vast portion of Earth's
40 surface and harbour the majority of its biomass. As sequencing the genome of any species is now technically
41 feasible and increasingly affordable, marine scientists have been taking advantage of genomic technologies to
42 address both new and long-standing questions in evolutionary biology, as well as to explore the richness of
43 marine biodiversity for industrial purposes. Several international consortia have been established and are
44 currently pooling efforts towards producing, curating and disseminating marine genomic data (see Box 1).

45 Assembling whole genomes can still be lengthy and non-trivial, especially for most eukaryotic species. Yet, they
46 are essential to improve our understanding of species evolution. For example, the genome of the amphioxus
47 *Branchiostoma floridae* allowed the reconstruction of the gene set of the last common chordate ancestor
48 (Putnam et al., 2008), whereas the genome of the jawless fish sea lamprey *Petromyzon marinus* has shed light
49 into the development of appendages and the origin of myelin-associated proteins (Smith et al., 2013).

50 Venkatesh and colleagues revealed interesting immune system innovations in the genome of the elephant
51 shark *Callorhinichus milii* (Venkatesh et al., 2014) whereas the hitherto assumed essential vertebrate immune
52 gene, MHC class II, was shown to be missing completely from the Atlantic cod genome *Gadus morhua* (Star et
53 al., 2011). Complete genomes of model fish species have also been shown to be important tools for studying
54 general mechanisms of evolution in other species. The established model species zebra fish *Danio rerio*, and
55 emerging model systems such as the spotted gar *Lepisosteus oculatus* (Braasch et al., 2016) are being
56 increasingly used to study human genome evolution and to better understand human diseases at the genomic
57 level.

58 Marine research has also taken advantage of methods that focus on subsets of the genome, which have a
59 lower cost and therefore facilitate research on non-model organisms (da Fonseca et al., 2016). One such
60 approach is the sequencing of RNA molecules (known as RNAseq), which targets the portion of the genome
61 that is transcribed. RNAseq actually offers the advantage of detecting immediate molecular responses to

62 stressors (e.g. climatic, pollution or even presence of predators or competitors), while DNA sequence data
63 provides information regarding relatively long-term evolutionary adaptive changes. Transcriptomes can be
64 produced from a specific tissue (Li et al., 2014), a whole individual (Rodriguez et al., 2012), a pool of individuals
65 (Helm et al., 2013) or even a microbial community [i.e. metatranscriptomics (Alex and Antunes, 2015; Sun et
66 al., 2014)]. The flexibility of RNAseq has allowed marine scientists to explore the basal non-bilaterian metazoan
67 lineages (Fernandez-Valverde et al., 2015; Pooyaei Mehr et al., 2013; Stefanik et al., 2014; Wenger and Galliot,
68 2013), providing insight into the evolution of special developmental features such as head regeneration in
69 *Hydra magnipapillata* (Krishna et al., 2013), or life cycle events as they happen with the scyphozoan jellyfish
70 *Aurelia aurita* (Brehm et al., 2015) and Porifera family members (Perez-Porro et al., 2013; Qiu et al., 2015).
71 RNAseq has also been used to investigate mechanisms of evolutionary processes, such as the basis for the
72 repeated evolution in independent populations of the copepods *Tigriopus californicus* (Pereira et al., 2016).
73 Other popular approaches targeting limited portions of the genome are restriction-site associated DNA
74 sequencing (RADseq) and targeted sequencing. RADseq is a reduced-representation method where a
75 restriction enzyme is used to digest the whole genome into small fragments that are then sequenced in both
76 directions from enzyme cut sites (Baird et al., 2008; Etter et al., 2011). RADseq provides a cost-efficient way to
77 simultaneously detect and genotype hundreds to thousands of SNPs in non-model species because does not
78 require a reference genome (Andrews et al., 2016). Targeted sequence capture is the method of choice when
79 the sequence of the regions of interest are known, and it implies the sequencing of the DNA that hybridizes
80 with a set of probes (Grover et al., 2012). Capture probes are designed from anonymous, genic and/or ultra-
81 conserved regions from a reference genome of the same or a closely-related species, depending on the
82 required variation for the downstream analysis (da Fonseca et al., 2016).
83 Unlike for most multicellular organisms, genome size and complexity are not a limitation in microbial genomics.
84 Microbial organisms have small genomes and hence it is no surprise that the first marine bacterial genome
85 (thermophilic methanogenic archaeon *Methanococcus jannaschii*, genome size: 1.7Mb) was sequenced in
86 1996, five years prior to the human genome. Microbial genomics methods include sequencing of isolates and

87 cultivation-independent techniques. The latter are of particular importance to sample the unknown marine
88 diversity and encompass single-cell genomics (SCG; reviewed in (Gawad et al., 2016; Lasken and McLean, 2014)
89 and metagenomics [e.g. (Escobar-Zepeda et al., 2015)]. SCG recovers genomic information from single,
90 uncultured cells. This enables, for example, the discovery of microbes that grow in nutritionally poor
91 environments [oligotrophs; (Swan et al., 2013)], the identification of viral material in single cells and the study
92 of the interactions between marine microorganisms (Labonté et al., 2015; Roux et al., 2014). Metagenomics
93 implies a simpler laboratory setup than SCG, and has become a popular approach. Metagenomic data is mainly
94 produced by two approaches: amplicon- and shotgun-sequencing [(Poretsky et al., 2014) and (Ranjan et al.,
95 2015) for details about each approach] of DNA extracted using specific methods (Taberlet et al., 2007). The
96 goals of marine metagenomic projects vary considerably: from characterizing community composition, mostly
97 using the 16S ribosomal RNA sequences, to discovering the functional potential of genes found in genomes
98 from a specific environment. Metagenomics provides insight into the whole genomic composition of an
99 environment, as one obtains full or partial genomes of co-inhabiting microorganisms from an environmental
100 sample, including microbial communities living within and on the body of a larger host organism. The collection
101 of microbial genomes obtained from a single environmental sample is referred to as a ‘metagenome’, although
102 originally this word was specifically used to describe ‘the collective genomes of soil microflora’ (Handelsman et
103 al., 1998). Furthermore, metagenomics has also shed light on community function when backed-up with
104 metatranscriptomic data (RNAseq of environmental samples), which can hold information regarding what is
105 essential for microbial survival in particular conditions. This dual approach has revealed that some groups of
106 Archaea, generally known as ammonia-oxidizers, have the physiological machinery to digest proteins,
107 carbohydrates, and lipids (Li et al., 2015), prompting a complete re-thinking of the carbon-cycle in marine
108 environments.

109 In the following sections, we provide examples on how genomic studies using the approaches described above
110 (whole-genome sequencing, RNAseq, RADseq, target capture, metagenomics, SCG and metatranscriptomics),

111 are helping to resolve the tree of life, contributing to a better understanding of marine biogeography, revealing
112 adaptions to marine conditions and fostering the discovery new bioactive compounds.

113

114 **Biodiversity and Biogeography**

115
116 The vast majority of earth's microorganism diversity (*sensu latum*: Virus, Bacteria and Archea) is found in
117 marine ecosystems. A big share of this diversity was uncovered by the use of SCG and metagenomics
118 approaches, which revealed an expanded version of the tree of life as compared to the one recovered by using
119 solely cultured isolates (Hug et al., 2016). Despite being a recent field, metagenomics has advanced our
120 knowledge in a variety of marine biology domains. A new archaeal lineage reconstructed from metagenomic
121 samples from deep marine sediments has provided information about the nature of the eukaryotic ancestor
122 (Spang et al., 2015). We now can distinguish the microbial communities across the majority of marine
123 environments: from the ocean surface [e.g. (Kent et al., 2016)] to deep-sea hydrothermal vents [e.g. (Anderson
124 et al., 2015)] through mangroves [e.g. (Andreote et al., 2012)] and coral reefs (Blackall et al., 2015).

125 Furthermore, metatranscriptomics has been used to characterize the diversity in sponge associated
126 microorganisms (Moitinho-Silva et al., 2014; Radax et al., 2012; White et al., 2012). This means that it is now
127 possible to combine meta-omics data and environmental data sources with concepts from the well-established
128 field of microbial biogeography (Hanson et al., 2012), and borrow landscape genetics methods (Dudaniec and
129 Tesson, 2016) to determine the importance of environmental and or historical events in generating and
130 shaping the astonishing marine micro-biodiversity.

131 Genomics has also revealed many aspects of the evolution of green plants in marine environments, including
132 green algae and flowering plants (about 60 species of flowering plants, all alismatid monocots, are considered
133 marine species). The analysis of genomic data under a phylogenetic framework (i.e. phylogenomics) has shed
134 light on topics as exciting as the transition to land (Wicket et al., 2014), the mechanisms that allowed such
135 transition (Delaux et al. 2015; Li et al., 2015), and relationships amongst early-diverging clades in plant
136 evolution. Also, phylogenomic studies using whole-plastid genomes has provided new insights into the early

137 origin of green algae (Leliaert et al., 2016), helped clarify the origin of marine flowering plants, or seagrasses
138 (Chen et al., 2004; Les et al., 1997; Ross et al., 2016) and concluded that the colonisation of marine
139 environments happened on three separate occasions from freshwater lineages of flowering plants (Benzecry
140 and Brack-Hanes, 2016).

141 Great contributions to understanding the origin and early evolution of animals have been provided by whole
142 genome sequences of Porifera (sponges), Placozoa, Cnidaria (e.g., sea anemones, corals, hydroids, and jellyfish)
143 and Ctenophora (comb jellies) (Pan et al., 2013; Putnam et al., 2007; Ryan et al., 2013, 2010; Smith et al., 2012;
144 Srivastava et al., 2010). The details regarding the genetic complexity of sponges and the fact they share more
145 genes with bilaterians than with non-bilaterian metazoans have been uncovered by RNAseq data (Riesgo et al.,
146 2014). Transcriptomes of several invertebrate species helped resolve the deep evolutionary relationship within
147 molluscs (Kocot et al., 2011; Smith et al., 2011). RADseq approaches have also been successfully applied to
148 uncover the phylogeographic and demographic history of the sea anemone *Nematostella vectensis* (Reitzel et
149 al., 2013).

150 The development of new data analysis methods has also enabled population genomics studies of marine
151 mammals despite their large genomes, which were previously prohibitively expensive. Two compelling studies
152 were successful at combining the power of new statistical methods with low-coverage sequencing data [see
153 (O’Rawe et al., 2015)] to elucidate the demographic and evolutionary history of killer whale ecotypes (Foote et
154 al., 2016), and polar bear *Ursus maritimus* and brown bear *Ursus arctos* (Liu et al., 2014).

155

156 **Adaptive Evolution**

157 Understanding how organisms adapt to changing conditions in their environment has been facilitated by the
158 availability of the new genomic tools. By studying the transcriptome (Kong et al., 2014) and the genome
159 sequencing of *Zostera marina* (Olsen et al., 2016), researchers revealed gene losses related to marine
160 adaptation, such as stomatal genes (Benzecry and Brack-Hanes, 2016), ultraviolet resistance genes and genes
161 associated with biosynthesis of the exine pollen layer (Cooper et al., 2000). Some volatile-compound synthesis

162 pathways, such as ethylene synthesis, were also found missing in *Z. marina* and in the Australian seagrass
163 *Nanozostera muelleri* (Golicz et al., 2015). Furthermore, transcriptome profiles of *Z. marina* and the heat
164 tolerant *Nanozostera noltii* allowed the identification of 78 genes directly related to heat stress (Franssen et al.,
165 2014).

166 Re-sequencing (shotgun sequencing genomic DNA for a species that has a reference genome) multiple
167 individuals from populations inhabiting different environments can also provide insight into adaptation to local
168 environmental conditions, and uncover genes responsible for optimizing individual fitness. Noteworthy
169 examples include adaptation of marine threespine stickleback *Gasterosteus aculeatus* populations to
170 freshwater habitats (Jones et al., 2012), and adaptation to low salinity conditions in sea bass *Dicentrarchus*
171 *labrax* (Tine et al., 2014) and Atlantic herring *Clupea harengus* (Martinez Barrio et al., 2016). The use of the
172 reduced representation method RADseq can also reveal ongoing natural selection, as it was the case of the
173 highly migratory Atlantic eel *Anguilla anguilla* where selection was detected within a generation (Pujolar et al.,
174 2014).

175 Genomic data has also revealed the targets of natural selection during the secondary colonisation of the
176 oceans from the terrestrial environments by marine mammals. Genomics has pinpointed the importance of
177 genes associated with hypoxia, lipid metabolism, muscle and brain function, the control of blood pressure and
178 salt concentration and sensory function (Foote et al., 2015; McGowen et al., 2012; Yim et al., 2014; Zhou et al.,
179 2013). These genomic adaptations in cetaceans were shown to occur after they split from their shared ancestor
180 with the Hippopotamidae, and are thus likely to be associated with adaptation to a fully aquatic existence
181 (Tsagkogeorga et al., 2015). Furthermore, whole genome data on killer whales ecotypes (Foote et al., 2016) and
182 bears [polar and brown bears; (Liu et al., 2014)], found evidence for selection on genes associated with adipose
183 tissue development, in the polar bear and in the killer whale inhabiting in the Antarctic pack-ice. This suggests
184 that polar bear and local populations of killer whales have adapted to a cold environment and a high fat diet.

185

186 **Effects of anthropogenic-induced changes in marine habitat**
187 Several marine ecosystems are being severely affected by anthropogenic actions, from increasing water
188 temperature, leading to recent bleaching of the Great Coral Reef in Australia, to the oil spills as the 2010 Gulf
189 of Mexico event. RNAseq has been used extensively by marine researchers to assess the effect of permanent
190 and transient changes in the environment (Todd et al., 2016), including bleaching in corals (Anderson et al.,
191 2016) and exposure to heavy metals in cnidarian (Elran et al., 2014). This approach has allowed the detection
192 of local adaptation in genes involved with biomineralization and growth due to ocean acidification, a
193 consequence of increased atmospheric CO₂ concentrations (Pespeni et al., 2013a, 2013b). Additionally,
194 transcriptomic data has demonstrated that genes associated with detoxification proteins (that protect from
195 xenobiotic stressors) are underrepresented in marine bacteria, indicative of low capacity to deal with pollution
196 (Bengtsson-Palme et al., 2014), which is a major concern given the rising levels of pollution in marine
197 environments and the role of bacteria as primary producers.

198 Genotyping of meadows of Australian seagrasses *Posidonia oceanica* (included in the 1000 Plants project; see
199 Box 1) has revealed a whole range of intraspecific levels of diversity: from complete clonality to high variability
200 (Arnaud-Haond et al., 2012; Micheli et al., 2015; Serra et al., 2012a). Their extreme sensitivity to human impact
201 and temperature changes makes them important bioindicators for the conservation of marine habitats
202 (Mazzuca et al., 2013). For this reason, adaptive responses to environmental factors, such as light gradients,
203 CO₂ stress, or heat shock, have been extensively assessed in seagrasses with EST approaches or reverse
204 transcription quantitative polymerase (RP-qPCR) of target genes (Dattolo et al., 2014; Serra et al., 2012b).
205 RNAseq tools were also used to investigate how the sudden and dramatic change in environment caused by
206 the *Deepwater Horizon* oil spill altered the expression patterns across all genes in the marsh minnow *Fundulus*
207 *grandis* (Garcia et al., 2012).

208

209 **Genome Evolution**
210 The analysis of microbial genome evolution, seemingly trivial because of the very small genome sizes involved,
211 has become complex because of the technical and computational challenges of the aforementioned

212 cultivation-independent methods (SCG and metagenomics). Often a combination of both methods is necessary
213 for a comparative analysis (Mende et al., 2016). Metagenomic contigs need to be binned into putative species,
214 a process that might result in chimeric bins (Sangwan et al., 2016). Furthermore, genomes recovered from
215 metagenomes are community genomes that might possess gene variation and allelic composition not present
216 in a natural individual. Strain resolution can be improved by single-molecule real-time sequencing, which when
217 combined with high-throughput sequencing has revealed genome heterogeneity and mobile elements in
218 Bivalve symbiont species (Dmytrenko et al., 2014; Ikuta et al., 2016).

219 Genomic studies have uncovered the extreme complexity in genome organization and evolution in marine
220 organisms. Such complexity in the sea urchin *Strongylocentrotus purpuratus* (Sodergren et al., 2006) and the
221 Pacific oyster *Crassostrea gigas* (Zhang et al., 2012) resulted in a difficulty to distinguishing between haplotypes
222 and paralogs (that arise from genome duplication events). The California two-spot octopus *Octopus*
223 *bimaculoides* was also shown to have a quite complex genome organization, with massive expansions of two
224 gene families related to neural function and extensive RNA editing (Albertin et al., 2015), while the
225 consequences of ongoing re-diploidization after whole genome duplication events have been highlighted by
226 research on salmonid genomes (Berthelot et al., 2014; Lien et al., 2016). Reduced-representation methods such
227 as RADseq have enabled the generation of high density linkage maps (i.e. positioning of genes along
228 chromosomes) in non-model fish species. These linkage maps have been used to explore and understand
229 meiotic recombination patterns in non-model species at unprecedented detail such as in the sockeye salmon
230 *Oncorhynchus nerka* (Limborg et al., 2015).

231

232 **Aquaculture and Bioprospecting**

233 Aquaculture has highly benefited from the development of genomic technologies. Genomic data has enabled
234 the identification of gene variants associated with advantageous traits such as growth, health and disease
235 resistance in species of commercial interest. For example, candidate genes that can be used for selective
236 breeding have been identified in the Pacific oyster (Zhang et al., 2012) and the Mediterranean mussel *Mytilus*

237 *galloprovincialis* (Murgarella et al., 2016). A mutation was also found in a gene controlling age of maturation in
238 Atlantic salmon *Salmo salar* (Barson et al., 2015); such information can be of great commercial value since the
239 gene can be used to inform selective breeding for later maturation, and thereby increased growth in captivity.
240 Another interesting application of genomic approaches includes the search for bioactive compounds with
241 potential to become novel drugs, nutritional supplements or applications for industrial biotechnology (Frazão
242 and Antunes, 2016; Urbarova et al., 2012). As an example, metagenomics has uncovered that a sponge
243 symbiont is the producer of most polyketides and peptides that have been isolated from its host; these
244 molecules are known to be medically important (Wilson et al., 2014).
245 Sequencing the transcriptomes of Cnidaria revealed to be an alternative to traditional *in vivo* and *in vitro*
246 analyses that targeted venoms or secreted proteins (Frazão and Antunes, 2016; Johansen et al., 2010).
247 Bioprospecting of neurotoxic drugs using deep sequencing of transcriptomes has been performed in sea
248 anemones (Kozlov and Grishin, 2011; Urbarova et al., 2012), tentacles of the jellyfish *Chrysaora fuscescens*
249 (Ponce et al., 2016), and from acrorhagi (specialized tentacles) of the polyps of the aggressive and non-
250 aggressive anemone *Anthopleura elegantissima* (Macrander et al., 2015).
251 Another fascinating target of bioprospecting research are the sea snails of the superfamily Conoidea. These
252 snails possess the most sophisticated poisoning strategies of the animal kingdom (Kohn, 1956) and are widely
253 renowned for synthesizing a very specific peptide family of sedating and paralyzing venoms termed conotoxins
254 (Olivera, 1997; Olivera et al., 1999). Recent studies allowed for a better understanding of the function and
255 diversity of conopeptides and indicated that conopeptide genes likely evolve under repeated pulses of strong
256 positive selection (Barghi et al., 2015; Dutertre et al., 2014). Genomic, transcriptomic and proteomic
257 approaches are being carried out to characterize cone snail genomes and discover potentially bioactive
258 compounds (Bianchi et al., 2010; Hu et al., 2011; Leonardi et al., 2012; Lluisma et al., 2012; Terrat et al., 2012).
259 In addition, a recent phylogeny of cone snails from the genus *Conus* (Puillandre et al., 2014) revealed highly
260 divergent lineages not found in the limited set of cone snail lineages analyzed thus far. This implies that

261 conotoxin study is only in its infancy, and hence warrants further studies to prospect new conotoxins and new
262 therapeutic applications.

263 Currently, a very promising research avenue on marine genomics is to use marine invertebrates as models to
264 investigate the clonal transmission of cancers. Metzger and colleagues (Metzger et al., 2015) recently
265 confirmed the monoclonal origin of hemic neoplasia in the soft shell clam *Mya arenaria* and also in the
266 common-cockle *Cerastoderma edule*. Potentially widespread in the marine environment, affecting other
267 bivalves, and with an important economic impact (Carballal et al., 2015), the massive study of these
268 phenomena can also potentially shed light on transmissible cancers and the metastization process in general.

269

270 **Concluding remarks**

271 The study of marine biology has gained powerful allies with the genomics revolution. As shown in this review, a
272 diverse array of methodological approaches has already been applied to several lines of research in marine
273 biology. It has been explored by scientists interested in fundamental questions in biology and biomedical
274 research, as well as by industrial engineers in search of biomaterials. The more we accumulate genomes and
275 transcriptomes, the better we will be able to: i) uncover the full biodiversity in the marine environments
276 including the placement of new specimens in their evolutionary context, ii) understand the processes that
277 originated marine biodiversity, and iii) develop new materials and drugs. Looking forward, it is pressing that the
278 scientific community makes an effort to curate this wealth of information in a standardized way, along with the
279 effort to make the data publically available in common platforms (see Box 1).

280 As per Captain Nemo revelation to professor Annorax, in Jules Verne 2000 leagues under the seas (1870)
281 “Astonishment and stupefaction will probably be your normal state of mind. You will not easily become blasé
282 about the sights continually offered to your eyes (...) and our planet, through my efforts, will deliver up its last
283 secrets”, we will certainly be amazed with the secrets that marine genomics will disclose in the future.

284

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BOX 1. Genomic resources for next-generation marine biologists

Public repositories of genomic data

NCBI – Genbank: USA National Center for Biotechnology Information: www.ncbi.nlm.nih.gov

EMBL-ENA: European Nucleotide archive: <http://www.ebi.ac.uk/ena>

DDBJ: DNA Data Bank of Japan: www.ddbj.nig.ac.jp

Curation guidelines for genomic data

GSC – Genomic Standards Consortium: guidelines towards a better description of the genomes being produced: from accurate reporting of sampling sites, to laboratory sequencing procedures, through detailed environmental description; <http://gensc.org/>

Marine circumnavigation expeditions launched to collect metadata (biological samples, physico-chemical variables)

Sorcerer II (2003-2009): <http://www.jcvi.org/cms/research/projects/gos/overview>

Tara Ocean (2009-2012): <http://www.embl.de/tara-oceans/start/research/index.html>

Malaspina (2010-2011): <http://www.expedicionmalaspina.es/>

Galathea 3 (2006-2007): <http://www.galathea3.dk/uk>

International Consortiums aimed to generated large-scale gene sequencing data including marine species

OneKP: 1000 Plants project: <https://sites.google.com/a/ualberta.ca/onekp/>

Global Invertebrate Genomics Alliance (GIGA): <http://giga-cos.org/>

Transcriptomes of 1000 Fishes: <http://www.fisht1k.org/>

Marine Mammal Genome Project: <https://www.hgsc.bcm.edu/marine-mammals>

Ocean sampling day: <https://www.microb3.eu/osd>

291

292

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