Important contribution of macroalgae to oceanic carbon sequestration

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Abstract

The role of macroalgae in Blue Carbon assessments has been controversial, partially due to uncertainties on the fate of exported macroalgae. Available evidence suggests that macroalgae is exported to reach the open ocean and the deep-sea. Nevertheless, this evidence lack of systematic assessment. Here, we provide robust evidence of macroalgal export beyond coastal habitats. We used metagenomes and metabarcodes from the global expeditions Tara Oceans and Malaspina 2010 Circumnavigation. We discovered macroalgae worldwide at up to 5,000 km from coastal areas. We found 24 orders, most of them belong to Rhodophyta. Diversity of macroalgae was similar across oceanic regions, although the assemblage composition differed. The South

Atlantic Ocean presented the highest macroalgal diversity; the Red Sea was the least diverse region. Abundance of macroalgae sequences attenuated exponentially with depth at a rate of 37.3% km^{-1}, and only 24% of macroalgae available at the surface were expected to reach the seafloor at 4,000 m depth. Our findings indicate that macroalgae is exported across the open and the deep ocean, suggesting that macroalgae may be an important source of allochthonous carbon, and their contribution should be considered in Blue Carbon assessments.

Main

Coastal habitats are highly productive ecosystems that contribute greatly to global carbon sequestration[1,2]. Seagrass meadows, salt marshes and mangrove forests have complex root systems that sequester large amounts of carbon in soft sediments within their habitat[3-6]. Macroalgae have been neglected in Blue Carbon assessments[7,8], because most of them lack root systems, grow on rocky substrate, and do not accumulate carbon-rich sediments. However, macroalgae form the most extensive and productive vegetated coastal habitat, exporting over 44% of their primary production[1,7,9]. Calculations suggest that 25% of exported macroalgal carbon is sequestered in long-term reservoirs, such as coastal sediments and the deep sea[1,7].

Based on first-order calculations[7], it is hypotesized that macroalgae globally support an export of 679 Tg C $year^{-1}$. Most of this carbon is remineralized or grazed in coastal environments, or cast onshore, while 14 Tg C $year^{-1}$ is sequestered in coastal sediments and 152 Tg C $year^{-1}$ could be sequestered in the deep sea[7]. Although there is a lack of empirical data, these calculations are supported by annecdotal evidence from sightings of long-distance macroalgae rafting[10] and presence in deep-sea sediments[7]. This evidence is dominated by observation of large biomass of brown macroalgae (Phaeophyta), but observations of red (Rhodophyta) and green (Chlorophyta) macroalgae are few[10]. This evidence imbalance could be related to lineage-specific features of the macroalgae cell wall composition and differences in cell-degradation rates[11]. Furthermore, most calculations of macroalgal primary production suggest that macroalgal carbon is exported as dissolved and particulate organic carbon (DOC and POC)[12,13], which are not visually detectable. An inclusive method, such as the identification of macroalgal environmental DNA (eDNA), could provide evidence of macroalgal carbon export in the ocean, and may allow the required systematic and consistent assessments. eDNA is the DNA left behind by organisms in

53 the surrounding environment including degraded cell tissues, gametes, animal feces, etc. As
54 DNA comprises approximately 3% of cellular organic carbon[14], the presence of macroalgal DNA
55 in waters beyond macroalgal habitats is both an indicator of the presence of the species and
56 evidence (not necessarily quantitative) of the export of macroalgal carbon.
57 Here, we examined the presence and relative abundance of Rhodophyta, Phaeophyta, and
58 Chlorophyta macroalgal eDNA sequences in the ocean. The sequences were derived from
59 hundreds of metagenomes generated by two global expeditions: Tara Oceans[15] and Malaspina
60 2010 Circumnavigation[16]. These expeditions surveyed the global ocean from surface to 4,000 m
61 depth, and sequenced the particulate material present in environmental water samples[17,18] (see
62 Methods). Although the expeditions primarily assessed the microbial and planktonic diversity,
63 they also generated a global DNA resource that allows identification of multicellular eukaryotes.
64 We exploited the potential of this eukaryotic eDNA resource to explore the presence of
65 macroalgae in the global ocean. This holistic approach has not been attempted before, but is
66 semi-quantitative and consistent for evaluating the hypothesis that macroalgal material is broadly
67 exported across the global ocean.
68 We identified macroalgae using two global ocean datasets. The first one included 163
69 metabarcodes of amplicon 18S rDNA from Tara Oceans[19]. The second one included 417
70 metagenomes pooled from the Tara Oceans[20] and Malaspina[21] expeditions (see Methods). We
71 used two different strategies for the second dataset: (a) a query targeting all genes (AG), and (b)
72 restricting the query to the top four single-copy protein-encoding genes (SCG) available in the
73 gene catalogue of both expeditions. Since macroalgae taxonomy is not well covered in barcoding
74 and genome reference libraries[22], we used order instead of species as the taxonomical level for
75 macroalgae identification.

Tracing macroalgae in the oceanic particulate organic matter

Combining the results of the three independent datasets, 24 macroalgae orders were identified within the particulate organic matter (POM) of the water column. Both metagenomic approaches (AG and SCG) delivered seventeen orders, of which ten were shared among the two approaches (Table 1). Only six orders were detected in the amplicon 18S rDNA metabarcodes, all of them found in the metagenomes. Rhodophyta was the most common macroalgal lineage (18 orders: 12 in AG, 13 in SCG, and 4 in the 18S dataset), followed by Phaeophyta (4 orders: 2 unique in each metagenomic approach), and Chlorophyta (2 orders: 2 in AG, and 1 shared in both SCG and 18S datasets; Table 1).

The relative abundance of macroalgal DNA varied between oceanic basins and datasets. The Mediterranean Sea presented the highest abundance of sequences in both 18S and AG datasets, while the South Atlantic Ocean was the most abundant in the SCG dataset. The basins with the fewest sequences were the Red Sea in the 18S dataset, the Southern Ocean in AG and the Mediterranean Sea in the SCG dataset. Similarly, the relative abundance of sequences per order differed greatly. Cyanidiales (Rhodophyta) and Ectocarpales (Phaeophyta) jointly accounted for 57% of the macroalgal sequences in both metagenomic datasets, although they were absent from the amplicon 18S dataset, whose most abundant order was Prasiolales (Chlorophyta) with 53% of all macroalgal sequences (Table 1).

Our pioneering attempt to trace macroalgal eDNA from POM in the global ocean is challenging for two reasons. Firstly, the phylogenetic diversity of macroalgae is so great that the three lineages are as distant from each other as are mushrooms from elephants[8]. Secondly, macroalgal sequences are poorly represented in reference libraries. Metagenomic and

metabarcoding identification is restricted to previously sequenced taxa that are available in published databases. Sequencing efforts on macroalgae are rather limited, with only one full genome sequenced[23]. Half of the 24 orders identified here are not included in the SILVA 18S rDNA reference library (http://www.arb-silva.de, accessed on July 2018). Furthermore, SILVA includes only 1,068 macroalgae species, compared with 12,471 species reported in the AlgaeBase and the 27,500 described species[22]. SILVA underrepresents green and brown macroalgae in comparison with red algae: Chlorophyta and Phaeophyceae have 46 and 84 entries for macroalgae respectively, while Rhodophyta has 938 entries (searched in July 2018). Analogously, macroalgae do not have any single-copy protein-encoding gene reported in the EggNOG database (http://eggnogdb.embl.de, searched in February 2018), as most proteins are reported for model organisms such as *Oryza sativa*, *Arabidopsis thaliana* or *Saccharomyces cerevisiae*. Because of this scarcity in macroalgae reference sequences, there is an underestimation of macroalgae (false-negatives) and a bias in the taxonomic representation of the macroalgae contributing POM. There is a need for enhanced molecular resources for macroalgae, especially for single markers. A single marker (i.e. 18S rDNA gene) enhances accurate identification to species level, and could draw phylogenetic relationships among lineages. A robust genomic reference will allow the detection of species in the POC and DOC pools, enabling the use of eDNA-based approaches to assign relative contributions of species to the carbon available in the ocean.

Macroalgae taxonomical identification in all datasets was performed by matching the sequences against available DNA references. Macroalgae sequences were less abundant in the 18S metabarcoding dataset, with only 29% of orders available in the metagenomes. Thus, the

metagenomes make it easier to find macroalgal DNA in the water column, given the poor and highly unbalanced representation of macroalgae in the SILVA 18S library.

Macroalgal material is likely to be exported from their coastal habitats as whole thalli or fragments, that either degrade progressively or are rapidly delivery to the deep-sea[7]. Although marine eDNA decays within a few days[24,25], the drifting macroalgal biomass[7] is constantly leaving traces of its DNA. eDNA recovered from metagenomes is the snapshot evidence of the macroalgal biomass exported to the sampling location from the coastal habitat. However, it is uncertain whether the relative abundance of sequences per order truly reflects the contribution of each order within the macroalgal export flux. The focus on metagenomic single-copy protein-encoding genes provides a parsimonious approach for assessing relative abundance of macroalgae. A single-copy gene occurs once in the genome, accounts for a single cell, and represents one individual in microbial communities[26]. In multicellular organisms, the relative abundance of DNA sequences from SCG may be scaled to the relative number of cells (and amount of biomass) available per taxon. Thus, the abundance pattern of macroalgal SCG from different taxa may be expected to correlate with their contribution to carbon export.

Given these caveats for metagenomes, and considering that the 18S metabarcodes were limited to fewer samples, we chose the SCG dataset for further analyses of macroalgal order diversity and macroalgal biomass export in the open and deep ocean. We believe that the SCG approach is likely less biased and more informative than the other two approaches.

Macroalgal diversity in the ocean

Macroalgal taxonomic composition in the SCG dataset was similar across oceanic regions. Cyanidiales and Ectocarpales were the most ubiquitous and abundant orders across all the basins.

144 Cyanidiales represented 35% of macroalgal DNA sequences. This result was unexpected but
145 may be possibly related to the fact that Cyanidiales is the earliest Rhodophyta and other orders
146 could share enough nucleotides in the sequences that may be identified as Cyanidiales.
147 Nevertheless, we aligned these DNA sequences and the phylogeny separates Rhodophyta orders
148 (Supplementary Fig. 1). Furthermore, Cyanidiales is known for its metabolic capacities and their
149 ability to colonize extreme habitats[27]. Ectocarpales, the most diverse order of Phaeophyta (774
150 species in AlgaeBase[28]), accounted for 22% of the DNA sequences (Table 1, Fig. 1a). The
151 Atlantic and North Pacific Oceans were the most diverse regions, while the Red Sea (the smallest
152 basin sampled) was the least diverse (Supplementary Table 1, Fig. 1a). The South Atlantic Ocean
153 displayed the highest percentage of macroalgal DNA (17% of the total across all basins), while
154 the lowest was found in the Mediterranean Sea and the Indian Ocean (8% each). A high
155 abundance of macroalgae was observed poleward of 40° in both the Northern (21%) and
156 Southern (28%) Hemisphere (Fig. 1a), possibly reflecting high local production of macroalgae at
157 these latitudes. The Arctic supports abundant macroalgae populations along its extensive rocky
158 coastline[29], and the Norwegian Atlantic current may collect significant inputs of boreal
159 macroalgal detritus. Similarly, there is evidence of export of Antarctic kelps, brown macroalgae
160 of the order Laminariales, that could potentially be transported over long distances by the
161 Antarctic Circumpolar Current[30]. In addition, macroalgal material may be preserved longer at
162 low water temperatures than at the warmer found at tropical latitudes[31]. Since many species
163 contain air-vesicles that confer buoyancy, polar latitudes could be a dead end for macroalgal
164 material, as has been shown to be the case for plastic accumulation driven by surface
165 circulation[32].

One-way PERMANOVA revealed significant differences in the SCG macroalgal DNA assemblage across oceans ($p = 0.0001$; $df = 7,347$; $F = 4.7$). The Red Sea, Indian Ocean and South Pacific Ocean were significantly different to the other oceanic regions (pairwise $p < 0.005$; Supplementary Table 2). Nevertheless, cluster analysis and non-metric multi-dimensional scaling (nMDS) ordination indicated similarities in the assemblages (Fig. 1b-c). Most regions were above 75% similarity, with the exceptions of the Red Sea (60%) and the Mediterranean Sea (65% similarity). Differences between overall PERMANOVA and ordination indicate a dispersion effect, as confirmed with significant difference in variance between groups (PERMDISP $p < 0.0001$; $df = 7,347$; $F = 5.7$).

Export of macroalgae throughout the water column

The Malaspina expedition sampled eDNA from surface to 4,000 m, while for Tara the maximum sampling depth was 1,000 m. Consequently, analyses of oceanic macroalgal abundance include only the Malaspina dataset. Macroalgae order diversity varied between depth (PERMANOVA $p = 0.001$; $df = 2,352$; $F = 43.6$; pairwise $p < 0.05$; PERMDISP $p < 0.0001$; $df = 2,352$; $F = 31.7$). The epipelagic zone (0-200 m) was the most diverse, while the least diverse was the mesopelagic zone (200-1,000 m, Supplementary Table 3). The relative abundance of macroalgal DNA (and likely macroalgal carbon) attenuates exponentially with depth at a rate of 37.3% km^{-1} (Fig. 2a). This value is much lower than the attenuation rate of sinking POC flux in the Northeast Pacific Ocean down to 5,000 m (86% km^{-1}, based on data from Martin et al.[33]). However, a lower value for the global-ocean attenuation rate is fairly expected due to the refractory nature of macroalgae carbon which degrade slower in comparison to degradation of

188 planktonic POC[34]. These results provide the first large-scale quantitative evidence of macroalgal
189 transport to the to the deep sea, validating previous assumptions of vertical export[7].
190 Most macroalgae grow in coastal areas. Exceptions are the drifting Sargasso Sea, and
191 macroalgae living on shallow oceanic seamounts[35,36]. Oceanic and biological processes (e.g.
192 storms, senescence) promote coastal detachment, dispersion and export of macroalgae to the
193 open ocean[7,37]. Contrary to the exponential attenuation by depth, there was no difference in
194 macroalgal abundance from the shoreline to distances up to 4,860 km (PERMANOVA p =
195 0.194; df = 6,223; F = 1.2; Fig. 2b). This observation corroborates the estimated widespread
196 export of macroalgal material to the open ocean, hitherto based on anecdotal evidence.
197 Rhodophyta can tolerate long periods of darkness and remain photosynthetic at great
198 depths[38,39]. Furthermore, these macroalgae cover the largest geographical extent and support the
199 largest global production[38]. Thus, Rhodophyta would be estimated to export more material than
200 Phaeophyta and Chlorophyta. Our results confirm these assertions: several red algae were
201 present at high depths, and 63% of the DNA sequences belonged to Rhodophyta, compared with
202 26% for Phaeophyta and 11% for Chlorophyta (Table 1, Fig. 3). Likewise, Rhodophyta were
203 taxonomically more abundant than Phaeophyta and Chlorophyta (13>3>1 order, respectively).
204 This richness is expected: the AlgaeBase shows a greater diversity of red algae (6,245 classes, 30
205 orders,) than brown (1,792 classes, 13 orders) or green algae (546 classes, 15 orders)[8,22]. The low
206 oceanic richness of Chlorophyta in the exported POM could be related to morphological and
207 biochemical features. Rhodophyta and Phaeophyta contain taxon-specific polysaccharides that
208 provide structural complexity and recalcitrancy[40]. Fucoidans (in brown algae) and carrageenans
209 (in red algae) bind to the cell wall and protect from desiccation and microbial cell-invasion,
210 hence delaying degradation[11,41-43]. These features are absent in green algae[41]. Such recalcitrance-

promoting compounds may enhance long-distance transport of Rhodophyta and Phaeophyta, as supported by their prevalence in the oceanic particulate organic matter pool.

Implication for Blue Carbon assessment

Our findings demonstrate the ubiquitous presence of macroalgal DNA in the ocean up to 4,000 m depth and 4,860 km away from the nearest coastline. The attenuation rate of macroalgae (37.3% km^{-1}) implies that 69% of the macroalgal DNA available at the surface will sink below 1,000 m. Oceanic models demonstrate that the carbon reaching 1,500 m depth is sequestered close to permanent time-scales[44] in terms of climate change mitigation. Hence, the macroalgal material (and organic carbon) that reaches 1,000 m (the boundary between mesopelagic and bathypelagic layers[45]) will be sequestered and prevented from exchanging with the atmosphere over extended timescales[7,44]. Moreover, 24% of macroalgal DNA sequences sinking from the surface will be expected to reach the seafloor (assuming mean oceanic depth of 3,800 m). Our results also revealed an increase in the relative abundance of Laminariales (i.e. kelp) DNA in POM between 3,000 and 4,000 m (Fig. 3a), consistent with the reported bedload bulk-transport of kelp to the deep sea[7]. This transport is influenced by episodic storm-driven events[7,46] that detach and rapidly sink macroalgae; this rapid sink is due to the presence of heavy rocky substrate retained by macroalgae in their holdfast. Submarine canyons support intense bedload fluxes of kelp, thereby delivering macroalgae (along with their DNA sequences and carbon) directly into the deep sea[7,47-49]. Through this mechanism, a larger biomass of Laminariales is delivered to the deep sea, while the remaining orders progressively degrade into smaller and smaller fragments, thus attenuating exponentially with increasing depth.

While the global ocean metagenomes analyzed here were produced to explore the oceanic microbiome, the data also allow detection of eukaryotic organisms such as macroalgae. Metagenomes are an unexplored tool for fingerprinting the contributions of different organisms to POM in the ocean. This research is a first step supporting the role of macroalgae as an important allochthonous source of Blue Carbon sequestered in the deep sea. Our eDNA approach provides robust evidence of the widespread oceanic presence of macroalgae, and our data support the hypothesis of macroalgae export to the open and deep ocean hitherto based on estimations[1,7]. As DNA is also cellular organic carbon[14], we infer that the presence of the taxa evidences the export of macroalgal carbon. Nevertheless, calculations of the macroalgal carbon exported to the ocean require experimentally-determined ratios between carbon and DNA content per taxon, which are currently unknown. Although the ultimate fate of oceanic macroalgal material remains uncertain, it is clear that a significant fraction reaches oceanic sinks while another is grazed and degraded by bacteria, thus subsidizing oceanic food webs.

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Author Contributions

CMD and DKJ conceived the research; JMG, SA, RL, RM, IA and AAK produced and curated the data; AO, CMD, NRG and IA conducted the data analysis; AO and CMD wrote the manuscript. All coauthors contributed to improve the manuscript and approved the submission.

Competing interests

The authors declare no competing interests.

Figure captions

Fig. 1: Assemblage of macroalgae in the ocean. a, Global distribution of macroalgae. Pie size represents DNA abundance per region: highest abundance in South Pacific Ocean (17%), lowest abundance in Mediterranean Sea and Indian Ocean (8%). Bar-graph shows latitudinal distribution of total macroalgal DNA, with 50% abundance beyond 40° N and 40° S (RPM, reads per million ± SE). **b,** Bray-Curtis similarity cluster and **c**, nMDS comparing macroalgal assemblage across oceanic regions.

Fig. 2: Export of macroalgae to the deep and open ocean. a, Vertical attenuation profile of macroalgal DNA in the Malaspina single-copy protein-encoding genes (SCG) dataset. Dashed line shows fitting curve based on power law equation of *y*. The calculated attenuation coefficient is indicated by *b* (see Methods). **b**, Horizontal export of macroalgal DNA from shoreline (continent or island) to open ocean (sampling point), based on Tara and Malaspina epipelagic metagenomes (0-200 m depth; RPM, reads per million ± SE).

Fig. 3: Oceanic export of macroalgal DNA relative abundance per order. **a**, Depth attenuation of macroalgae from surface to bathypelagic zone (4,000 m), using Malaspina metagenomes. Most orders attenuated with depth, with the exception of Prasiolales and Laminariales. **b**, Macroalgal DNA export from shoreline to open ocean, based on Tara and Malaspina epipelagic metagenomes (0-200 m depth). Presence of macroalgae is ubiquitous in the open ocean. RPM, reads per million.

Table 1 Relative abundance of macroalgal DNA. IO Indian Ocean (*n* = 87, 11; 87 SCG and AG metagenomes, 11 metabarcodes for 18S), MS Mediterranean Sea (*n* = 19, 18); NAO, SAO North (*n* = 44, 2) and South Atlantic Ocean (*n* = 101, 21); NPO, SPO North (*n* = 51, 0) and South Pacific Ocean (*n* = 88, 18), RS Red Sea (*n* = 13, 2), and SO Southern Ocean (*n* = 14, 6). Order Abundance indicates percentage of each order among total macroalgal DNA sequences per dataset. Order Prevalence indicates percentage of metagenomes/metabarcodes (*n*) where the order was present. Cyanidiales represented 35% of the SCG dataset (reads per million ± SE) and was present in 72% of the metagenomes. Prasiolales dominated the 18S dataset: 53% of the total sequences (metagenomic Illumina tags ± SE) and found in 66% of the metabarcodes

Methods

Macroalgae taxa are included in two of the eight major lineages of the Eukaryota domain[50], where they belong to 4 kingdoms, 15 phyla and 54 classes[22]. Marine macroalgae are found in three phyla (Rhodophyta, Phaeophyta, Chlorophyta), which also contain microalgae. Chlorophyta (green algae) are closer to vascular plants than to Rhodophyta (red algae) or to Phaeophyta (brown algae), which are closer to molds than to other macroalgae[22,50,51]. Macroalgae groups have broad differences in cell wall composition[11]. Even the same order of algae can have strong divergences among genera[52]. Thus, macroalgae classification is very diverse, and the term *macroalgae* describes functional groups that are not necessarily related phylogenetically to each other even at phylum level. Identification of macroalgal DNA sequences is a challenging process: there is no universal gene marker[53], and barcoding attempts are limited to certain groups[53,54]. 18S rDNA barcoding resources are poorly represented: only 3.8 % of macroalgae are reported in the SILVA database (1,068 of 27,500 described species[22], http://www.arb-silva.de, searched on July 2018). Nevertheless, the available (and limited) molecular resources based on a single gene marker are an important tool for accurately identifying macroalgae, and also for drawing phylogenetic conclusions about these taxa.

However, less strict approaches can also be used to identify marine macroalgae groups when resolution at species level is not required. Since DNA represents 3% of cellular organic carbon[14], here we infer the carbon export of marine macroalgae phyla with the presence of macroalgal DNA in the water column. We investigated occurrence of macroalgae in the open and deep ocean, using global metagenomes and metabarcodes generated by the Tara Oceans[15] and Malaspina 2010 Circumnavigation[16] expeditions.

Sample description

Tara sampling covered epipelagic and mesopelagic zones (5-1,000 m) across eight oceanic regions, with a total of 210 sampling stations: North Atlantic Ocean, South Atlantic Ocean, North Pacific Ocean, South Pacific Ocean, Indian Ocean, Southern Ocean, Mediterranean Sea, and Red Sea. Each location was sampled at different depths (surface water layer 3-7 m, deep chlorophyll maximum layer 30-70 m, mesopelagic zone 400-1.000 m), using CTD and Niskin bottle Rosette sampling system[17,18,20]. We used 243 metagenomic samples that targeted the gene pool of viral to metazoan plankton, using multiple filters to isolate distinct size-fractions of the suspended particle pool (0.1-0.22 μm 20 samples, <0.22 μm 45 samples, 0.22-0.45 μm 18 samples, 0.45-0.8 μm 21 samples, 0.22-1.6 μm 36 samples, and 0.22-3 μm 103 samples)[20]. We used 163 metabarcodes from the 18S rDNA aimed at *piconano*- to *meso*-plankton communities (size-fractions: <0.8 μm 28 samples, 0.22-3 μm 1 sample, 0.8-5 μm 60 samples, 0.8-20 μm 6 samples, 5-20 μm 23 samples, 20-180 μm 31 samples, and 180-2000 μm 14 samples)[19]. Water samples were kept at -20 °C on board and at -80 °C in the laboratory until DNA extraction, then DNA was kept at -20 °C until sequencing[55]. Detailed sampling and methods are available for metagenomes in Pesant et al.[20], and for 18S rDNA amplicons in De Vargas et al.[19].

The Malaspina expedition sampled open-ocean waters from surface to 4,018 m depth, with emphasis on the bathypelagic zone (1,000-4,000 m)[16]. Water samples were collected using CTD and Niskin bottle Rosette sampling system, at 70 sampling stations across the oceans and grouped into the eight oceanic regions used by Tara (see above). Filters containing the particle pools sampled in the water were flash frozen in liquid nitrogen and stored at -80 °C until DNA extraction and further sequencing[56]. We used 174 metagenomic[21] samples that targeted free-

452 living bacteria to picoeukaryotes and nanoeukaryotes (size-fractions: 0.2-0.8 μm 29 samples, 0.2-
453 3 μm 100 samples, 0.8-20 μm 31 samples, and 3-20 μm 14 samples).
454 Together, these expeditions used massive DNA sequencing and generated hundreds of
455 metagenomes to assess oceanic microbial and planktonic diversity[18]. Tara also generated a global
456 Eukaryotic DNA resource based on 18S-V9[11] rDNA amplicons. This data collection did not aim
457 to survey macro-organisms. Nevertheless, we exploited their potential to reveal macroalgal
458 genes. Data came from 153 Tara and 65 Malaspina sampling stations across the oceans, from the
459 surface to 4,000 m (Supplementary Fig. 2).
460 We identified DNA sequences of Rhodophyta, Phaeophyta, and Chlorophyta using two
461 datasets: (1) amplicon 18S rDNA-based metabarcodes from Tara Oceans, and (2) metagenomes
462 that contain the whole gene pool from both Tara Oceans and Malaspina. These macroalgal DNA
463 sequences belonged to 20,212 unique genes available in the reference gene catalogs of both
464 expeditions (Supplementary Table 4). We believe this holistic approach has not been tried
465 before.
466
467 *Amplicon 18S data extraction*
468 For the first dataset, denoted 18S, single amplicon reads were extracted from 163 Tara[57]
469 metabarcodes of the 18S rDNA V9 hyper-variable loop. Metabarcodes were blasted against
470 SILVA 18S rDNA database (SILVA Release 132, http://www.arb-silva.de). Macroalgae
471 taxonomy is not well described[22], and sequences from the 18S rDNA are scarce in the SILVA
472 database (only 3.8 % representation, searched on July 2018); thus, to avoid false-negative results,
473 we chose order rather than species as the taxonomical level. The search was taxonomically
474 restricted to taxa Viridiplantae, Stramenopiles and Rhodophyta. The resulting taxonomical list

was filtered manually by choosing all macroalgae orders whose sequences presented an identity percentage cut-off >90%. A cut-off of 90% is above the accepted threshold for order level (84-90%[58-62]).

Malaspina 18S rDNA metabarcodes, though available[63], were excluded for several reasons: Malaspina sequenced the 18S rDNA V4 region, and the sampling and sequencing effort was much lower than in Tara. The contribution of Malaspina to the amplicon 18S dataset was limited to only 7 samples presenting any macroalgae sequence, in contrast to 78 samples from Tara.

Metagenomic data extraction

For the second dataset, denoted as metagenomes, we used 243 Tara[20] and 174 Malaspina[21] metagenomes to find macroalgal DNA sequences in the open ocean. We used two different strategies: (a) targeting all genes (AG), and (b) restricting the query to the top four single-copy protein-encoding genes (SCG) available in the gene catalogs of both expeditions. Each strategy generated its own new dataset. Metagenomic data were analyzed using the Dragon Metagenomics analysis platform (DMAP, http://www.cbrc.kaust.edu.sa/dmap). DMAP re-annotated Tara Oceans and Malaspina metagenomic gene catalogs, keeping the original reads that are based on gene abundance for each sample (units are in reads per million, RPM).

DMAP uses UniProt Knowledgebase as a reference database to compare genes from Tara and Malaspina's gene catalogs. To assign taxonomy and generic functional role, DMAP uses high-throughput BLASTp that are examined to traverse lowest common ancestor along the best hits. Specific functional role is assigned using BLASTp against KEGG Orthologs from KEGG database. This taxonomic and functional role information is indexed for all genes, and made available for lookups and sample comparisons in the *Compare* module of DMAP. In this module,

498 we restricted both metagenomic strategies (AG and SCG) to taxa Viridiplantae (DMAP filter
499 taxID: 33090), Stramenopiles (taxID: 33634) and Rhodophyta (taxID: 2763); the search was
500 restricted to coverage and identity percentage cut-offs greater than or equal to 90%. A higher cut-
501 off recovers fewer sequences (false-negatives). Identification of macroalgae in the metagenome
502 dataset is based on protein similarity. Proteins are very conserved at higher taxonomic levels,
503 thus a threshold of 90% is above the mean percentage identity for proteins (70%)[64].
504 The SCG strategy (b) included additional steps. Initially, we wanted to restrict the search to
505 single-copy protein-encoding genes specifically from Chlorophyta, Rhodophyta or Phaeophyta,
506 but there were none available in the reference database (EggNOG[65], searched on February 2018).
507 Thus, we searched for the top four single-copy protein-encoding genes present in Viridiplantae,
508 Stramenopiles and Rhodophyta within the expeditions' gene catalogs; we used the *KEGG*
509 *Ortholog* module of DMAP. Back to the *Compare* module, we individually restricted the SCG
510 search to each one of these top four protein-encoding genes: NADH:ubiquinone reductase (EC:
511 1.6.5.3), N-acetyl-gamma-glutamyl-phosphate reductase (EC: 1.2.1.38), DNA-directed RNA
512 polymerase (EC: 2.7.7.6), and non-specific serine/threonine protein kinase (EC: 2.7.11.1).
513 Order was used as the level for taxonomical assignment, because most macroalgae species
514 have an incomplete genome reference library and undescribed taxonomy[22]. The initial search
515 using species as taxonomical level returned false-negative BLAST hits. For instance, when the
516 search was restricted to a few species of the order Ectocarpales, DMAP did not return any
517 sequence because the dataset is incomplete; sequences were returned when we searched directly
518 for the order. The databases include *unknown* or *uncultured* sequences that are assigned to higher
519 taxonomic ranks, e.g. order. The search generated a taxonomical list, where we manually filtered
520 all macroalgae orders that returned sequences.

Data analyses

A list of macroalgae orders and the relative abundance of the sequences was obtained from each dataset (18S metabarcodes, metagenomes AG and metagenomes SCG). Relative abundance is reported in the metagenomes as reads per million (RPM), and as Illumina tags ($_{mi}$Tags) for the 18S dataset. Each sample included information on depth, size-fraction and location. To account for unequal sampling effort within each oceanic region, the relative abundance of sequences was standardized by dividing the total number of sequences of each order in each oceanic region by the number of samples within each oceanic region.

We performed Bray-Curtis Similarity clustering and non-metric multidimensional scaling (nMDS) ordination to elucidate differences in macroalgal assemblage among oceanic regions. One-way permutational multivariate analysis of variance (PERMANOVA) and analysis of homogeneity of multivariate dispersion (PERMDISP) based on Bray-Curtis similarities were performed to test for differences in macroalgal assemblage composition across oceanic basins; data were log-transformed prior these analyses. These analyses were done in R using the Vegan[66] package. To evaluate how taxonomic richness and relative abundance of the sequences is distributed among oceanic regions, we calculated the indices of Pielou equitability (J), Dominance (D) and Shannon (H); these indices assess evenness, dominance and diversity at order level. To compare observed order richness with estimated richness, we calculated the index CHAO 2. Indices were calculated in PAST[67]. Order diversity was also evaluated through the water column from surface to 4,000 m using only the Malaspina dataset; the Tara dataset is limited to 1,000 m depth.

The global distribution of macroalgal DNA sequences was analyzed by assessing export and relative abundance with depth from the surface to the deep ocean (vertically), and with distance from the sampling point to the closest shoreline (horizontally). Vertical export was analyzed by comparing Malaspina macroalgae sequences through the water column zones: epipelagic (0-200 m), mesopelagic (200-1,000 m) and bathypelagic zone (1,000-4,000 m). Attenuation of macroalgae sequences with depth was modeled by fitting relative abundance of each zone to a normalized power function, following the coefficient[33] for particulate organic carbon flux:

$$y = ax^{-b},$$

where y is macroalgae relative abundance, a is the intercept, x is the depth, and b is the macroalgae attenuation coefficient (sequences in RPM m^{-1}). Relative abundance of macroalgal DNA by depth was standardized, dividing the total number of sequences per depth category by the number of samples within each depth category (0-200 m; 500 m; 1,000 m; 2,000 m; 3,000 m; and 4,000 m; maximum depth recorded was 4,018 m).

Horizontal export was analyzed by comparing relative abundance of macroalgae sequences with distance from the sampling point to the closest shoreline (continent or island) using one-way permutational multivariate analysis of variance (PERMANOVA). These data consisted of Tara and Malaspina metagenomes that belong to the epipelagic zone (0-200 m). The relative abundance of macroalgal DNA was standardized, dividing the total number of sequences per distance category by the number of samples within each distance category (0-200 km; 500 km; 1,000 km; 2,000 km; 3,000 km; 4,000 km; and 5,000 km; maximum distance recorded was 4,860 km).

Data availability

The data that support the findings on this study are available in: Pesant et al.[20] (Tara Oceans metagenomes, doi: 10.1038/sdata.2015.23), De Vargas et al.[57] (Tara Oceans 18S rDNA V9 metabarcodes, doi: 10.1126/science.1261605); and Zenodo (Malaspina metagenomes, doi: 10.5281/zenodo.2596829)[21].

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615 **Table 1.**

Dataset	Lineage	Order	IO	MS	NAO	NPO	RS	SAO	SO	SPO	% Order Abundance	% Order Prevalence
SCG	Chlorophyta	Prasiolales	1.3 (±0.6)	0.9 (±0.4)	2.2 (±0.5)	0.7 (±0.4)	0.3 (±0.3)	1.6 (±0.3)	2.5 (±1.4)	1.2 (±0.2)	11.46	40.05
SCG	Phaeophyta	Ectocarpales	1.1 (±0.3)	4.1 (±1.4)	2.1 (±0.5)	3.7 (±1.2)	0.9 (±0.3)	2.1 (±0.3)	4.3 (±1.5)	2.1 (±0.4)	21.87	49.40
SCG	Phaeophyta	Fragilariales	0.2 (±0.1)	0.4 (±0.1)	0.9 (±0.3)	0.1 (±0.0)	0.4 (±0.2)	0.6 (±0.2)	-	0.3 (±0.2)	3.11	17.75
SCG	Phaeophyta	Laminariales	0.2 (±0.1)	-	-	0.2 (±0.2)	-	0.2 (±0.1)	-	-	0.77	4.56
SCG	Rhodophyta	Bangiales	-	-	-	-	-	-	0.1 (±0.1)	-	0.14	1.44
SCG	Rhodophyta	Batrachospermales	-	-	-	-	-	0.4 (±0.3)	1.0 (±0.9)	-	1.47	2.88
SCG	Rhodophyta	Bonnemaisoniales	-	-	-	0.1 (±0.1)	-	-	-	-	0.12	0.72
SCG	Rhodophyta	Ceramiales	-	-	-	-	-	-	-	-	0.05	0.96
SCG	Rhodophyta	Corallinales	0.1 (±0.0)	0.1 (±0.1)	0.3 (±0.2)	0.1 (±0.0)	-	1.3 (±0.5)	-	0.1 (±0.0)	2.14	15.83
SCG	**Rhodophyta**	**Cyanidiales**	**3.0 (±0.7)**	**1.8 (±0.7)**	**3.6 (±0.8)**	**2.5 (±0.5)**	**7.6 (±4.9)**	**4.8 (±1.1)**	**2.6 (±0.7)**	**7.1 (±1.2)**	**35.31**	**72.42**
SCG	Rhodophyta	Gelidiales	0.1 (±0.0)	0.2 (±0.2)	-	0.1 (±0.0)	-	0.5 (±0.2)	0.1 (±0.1)	0.1 (±0.0)	1.14	6.24
SCG	Rhodophyta	Gigartinales	1.2 (±0.2)	0.1 (±0.1)	0.8 (±0.2)	1.1 (±0.3)	0.6 (±0.3)	0.7 (±0.2)	0.9 (±0.6)	1.1 (±0.2)	6.90	46.52
SCG	Rhodophyta	Halymeniales	0.1 (±0.1)	-	0.2 (±0.1)	0.4 (±0.2)	-	0.3 (±0.1)	0.2 (±0.2)	0.2 (±0.1)	1.58	9.35
SCG	Rhodophyta	Nemaliales	0.5 (±0.2)	0.1 (±0.0)	2.3 (±0.8)	1.1 (±0.4)	0.1 (±0.1)	2.3 (±0.6)	2.4 (±2.1)	3.6 (±0.7)	13.22	32.61
SCG	Rhodophyta	Palmariales	-	-	-	-	-	-	0.1 (±0.1)	-	0.18	1.44
SCG	Rhodophyta	Plocamiales	-	-	-	-	-	-	-	-	0.01	0.24
SCG	Rhodophyta	Rhodymeniales	-	-	-	-	-	0.3 (±0.1)	-	0.2 (±0.0)	0.54	13.19
AG	Chlorophyta	Prasiolales	0.0 (±0.1)	-	0.0 (±0.1)	-	-	0.1 (±0.3)	0.2 (±0.2)	-	1.21	7.91
AG	Chlorophyta	Ulvales	-	-	-	-	-	0.1 (±0.1)	-	-	0.28	1.44
AG	Phaeophyta	Ectocarpales	0.4 (±1.5)	0.1 (±0.4)	0.7 (±2.5)	0.6 (±1.8)	0.7 (±2.0)	0.9 (±2.0)	0.3 (±0.5)	0.7 (±3.1)	25.10	30.22
AG	Phaeophyta	Fucales	-	-	-	-	-	-	-	-	0.06	0.48
AG	Phaeophyta	Laminariales	-	-	-	-	-	-	-	-	0.07	6.71
AG	Rhodophyta	Balliales	0.4 (±0.6)	-	-	0.1 (±0.1)	-	0.6 (±0.8)	0.2 (±0.3)	0.4 (±0.6)	4.33	6.71
AG	Rhodophyta	Bangiales	0.8 (±1.5)	0.3 (±0.5)	0.1 (±0.5)	0.3 (±0.8)	0.1 (±0.1)	0.3 (±1.0)	0.9 (±1.4)	0.2 (±0.7)	11.87	33.09
AG	Rhodophyta	Ceramiales	-	-	-	-	-	-	0.1 (±0.1)	-	0.15	0.48
AG	Rhodophyta	Corallinales	-	-	-	-	-	-	-	-	0.04	0.48
AG	**Rhodophyta**	**Cyanidiales**	**0.2 (±0.6)**	**8.3 (±9.0)**	**0.4 (±1.6)**	**0.4 (±1.4)**	**0.4 (±0.7)**	**0.5 (±1.5)**	**0.6 (±1.8)**	**0.2 (±1.3)**	**32.41**	**44.12**
AG	Rhodophyta	Gigartinales	0.1 (±0.2)	-	0.1 (±0.1)	0.2 (±0.2)	-	0.1 (±0.2)	0.1 (±0.1)	0.1 (±0.1)	1.72	5.28
AG	Rhodophyta	Gracilariales	0.1 (±0.1)	-	-	0.3 (±0.3)	-	0.1 (±0.2)	-	-	1.05	1.92
AG	Rhodophyta	Hapalidiales	-	-	-	-	-	-	-	-	0.08	0.48
AG	Rhodophyta	Nemaliales	0.1 (±0.2)	0.1 (±0.2)	0.3 (±0.9)	0.1 (±0.3)	0.6 (±1.3)	0.5 (±1.2)	-	0.1 (±0.3)	7.94	24.22
AG	Rhodophyta	Palmariales	-	-	-	0.2 (±0.2)	2.4 (±4.6)	-	-	-	8.93	3.84
AG	Rhodophyta	Porphyridiales	-	-	-	-	-	-	-	-	0.04	0.24
AG	Rhodophyta	Stylonematales	0.0 (±0.1)	0.2 (±0.3)	0.2 (±0.5)	0.1 (±0.2)	0.1 (±0.2)	0.3 (±1.0)	-	0.1 (±0.4)	4.71	19.42
18S	**Chlorophyta**	**Prasiolales**	**9.7 (±2.8)**	**1.0 (±0.6)**	**0.8 (±0.5)**	**-**	**1.5 (±0.5)**	**13.5 (±7.2)**	**10.7 (±3.5)**	**4.2 (±1.1)**	**53.20**	**66.23**
18S	Rhodophyta	Ceramiales	-	16.8 (±14.6)	-	-	-	-	-	-	21.63	12.99
18S	Rhodophyta	Gigartinales	-	0.2 (±0.2)	-	-	-	-	-	-	0.29	2.60
18S	Rhodophyta	Porphyridiales	0.4 (±0.3)	8.4 (±8.0)	1.8 (±3.5)	-	-	4.3 (±3.4)	0.5 (±0.3)	0.4 (±0.1)	20.16	35.06
18S	Rhodophyta	Rhodymeniales	-	3.7 (±3.5)	-	-	-	-	-	-	4.73	3.90

616 **Relative abundance of macroalgal DNA.**

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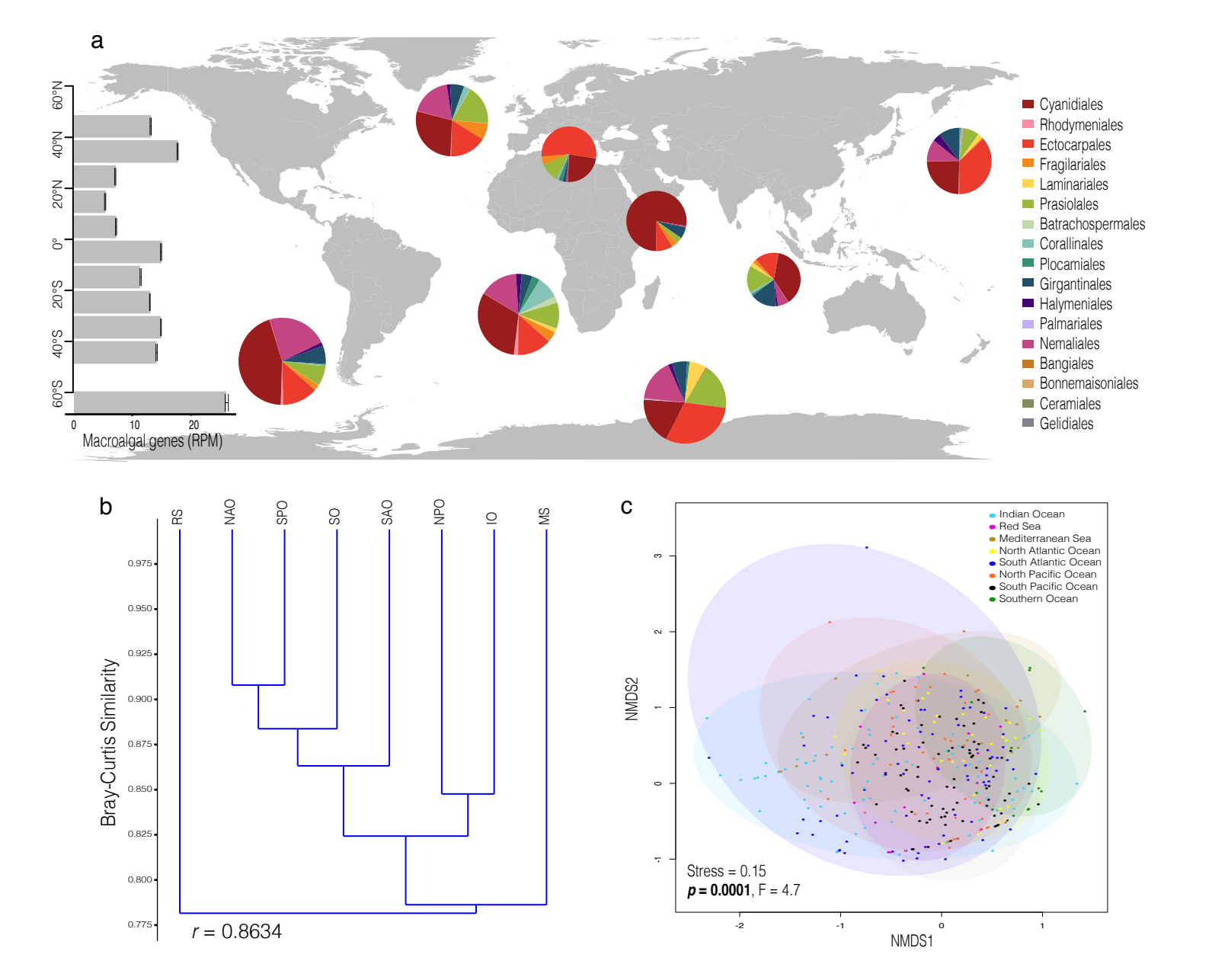
618


a
60°N
40°N
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0°
20°S
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60°S
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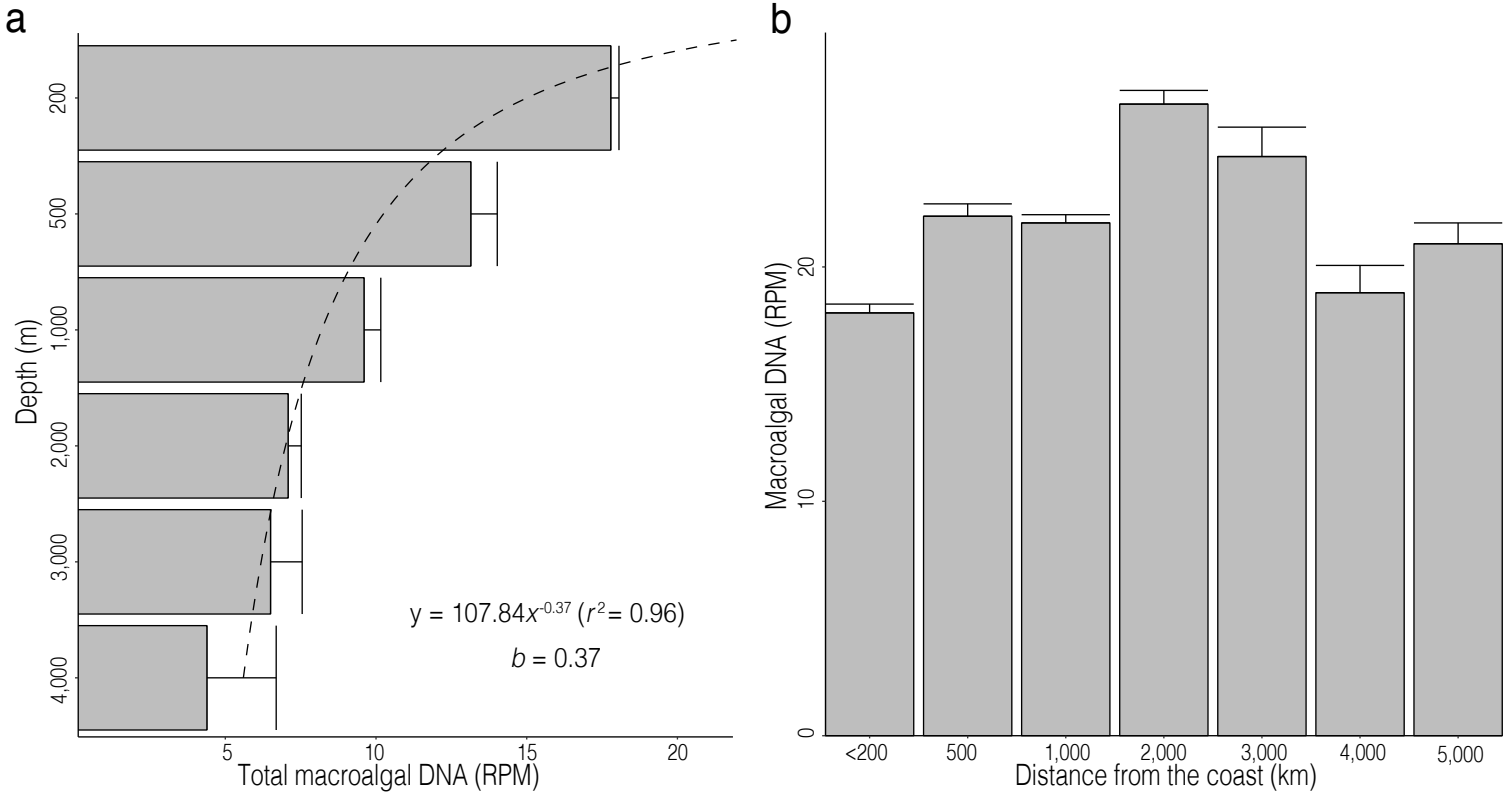
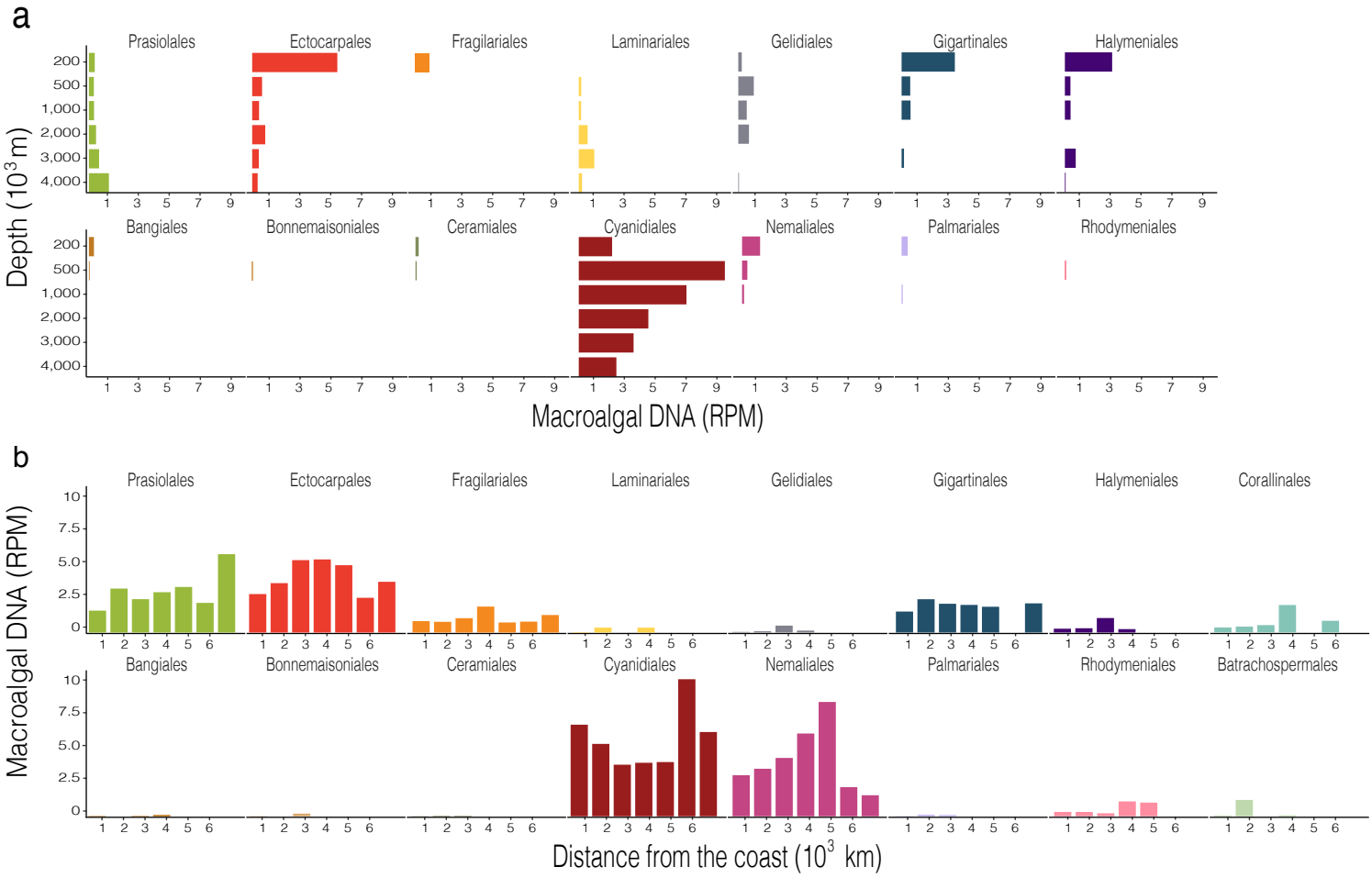
10
20
Macroalgal genes (RPM)
Cyanidiales
Rhodymeniales
Ectocarpales
Fragilariales
Laminariales
Prasiolales
Batrachospermales
Corallinales
Plocamiales
Girgantinales
Halymeniales
Palmariales
Nemaliales
Bangiales
Bonnemaisoniales
Ceramiales
Gelidiales
b
RS
NAO
SPO
SO
SAO
NPO
IO
MS
Bray-Curtis Similarity
0.975
0.950
0.925
0.900
0.875
0.850
0.825
0.800
0.775
r = 0.8634
c
Indian Ocean
Red Sea
Mediterranean Sea
North Atlantic Ocean
South Atlantic Ocean
North Pacific Ocean
South Pacific Ocean
Southern Ocean
NMDS2
3
2
1
0
-1
-2
-1
0
1
NMDS1
Stress = 0.15
p = 0.0001, F = 4.7


a
Depth (m)
200
500
1,000
2,000
3,000
4,000
5
10
15
20
Total macroalgal DNA (RPM)
y = 107.84x^-0.37 (r^2 = 0.96)
b = 0.37
b
Macroalgal DNA (RPM)
0
10
20
<200
500
1,000
2,000
3,000
4,000
5,000
Distance from the coast (km)


a
Prasiolales
Ectocarpales
Fragilariales
Laminariales
Gelidiales
Gigartinales
Halymeniales
Bangiales
Bonnemaisoniales
Ceramiales
Cyanidiales
Nemaliales
Palmariales
Rhodymeniales
Depth (10^3 m)
200
500
1,000
2,000
3,000
4,000
Macroalgal DNA (RPM)
b
Corallinales
Batrachospermales
Macroalgal DNA (RPM)
Distance from the coast (10^3 km)