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1 **Seasonal dynamics in microbial trace metals transporters during**
2 **phytoplankton blooms in the Southern Ocean**

3

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13

14

15 **Key words:** prokaryotic trace metals transporters; metagenomics; MAGs;

16 autonomous sampler; Southern Ocean;

17

18

19 **Abstract**

20

21 Trace metals are required as co-factors in metalloproteins that are essential in microbial
22 metabolism and growth. The microbial requirements of diverse metals and the
23 capabilities of prokaryotic taxa to acquire these metals remain poorly understood. We
24 present here results from metagenomic observations over an entire productive season
25 in the region off Kerguelen Island (Indian Sector of the Southern Ocean). We observed
26 seasonal patterns in the abundance of prokaryotic transporters of 7 trace elements (Zn,
27 Mn, Ni, Mo, W, Cu, Co) and the consecutive spring and summer phytoplankton blooms
28 were strong drivers of these temporal trends. Taxonomic affiliation of the functional
29 genes revealed that the transporters of these trace metals were associated to different
30 microbial assemblages. Our observations suggest that *Rhodobacteraceae* had a broad
31 repertoire of trace metal transporters (Mn, Zn, Ni, W, Mo) and a more restricted set was
32 observed for other prokaryotic groups, such as *Flavobacteriaceae* (Zn), *Nitrospiraceae*
33 (Ni, W) and *Thioglobaceae* (Mo). The prevalence of one or more trace metal
34 transporters within a prokaryotic group, as determined on the family level, was overall
35 confirmed in representative metagenome assembled genomes. We discuss the potential
36 involvement of prokaryotic groups in processes related to organic matter utilization that
37 require these metals and the consequences on carbon and trace metal cycling in surface
38 waters of the Southern Ocean.

39 **Introduction**

40 The metals zinc (Zn), manganese (Mn), nickel (Ni), cobalt (Co), copper (Cu),
41 molybdenum (Mo) and tungsten (W) are co-factors in metalloenzymes that drive the
42 biogeochemical cycling of major elements. Diverse metal-containing enzymes are
43 involved in the transformation and processing of dissolved organic matter (DOM), the
44 major pool of organic carbon in the ocean. The utilization of different types of organic
45 substrates within the DOM pool, covering a range of size fractions and varying degrees
46 of bioavailability, is mediated by prokaryotes through pathways with distinct metal
47 requirements. Zn is involved in carbohydrate-active enzymes (CAZymes) that play an
48 important role in the degradation of polysaccharides (Hobbs et al. 2023), while Mn is
49 required in the central carbon metabolism (Hansel 2017). Ni and Mo are both essential
50 for nitrogen fixing microbes (Kuypers et al. 2018) and these elements are further
51 involved in the utilization of nitrogen-containing substrates (Ni) and in carbon
52 monoxide oxidation (Mo) (King and Weber, 2007). Methyloprobes require W for the
53 utilization of substrates with no carbon-carbon bonds, including C1 compounds
54 (Chistoserdova 2011). Cu, a catalyst in numerous cuproenzymes, has a major
55 involvement in the respiratory enzyme cytochrome c oxidase in aerobic microbes
56 (Ridge et al. 2008), and Co is mainly used as a key component of cobalamin (vitamin
57 B12) synthesis (Bertrand et al. 2015). Despite the essential role of these elements in
58 microbial metabolism and the cycling of DOM, little is known about the capacities of
59 diverse prokaryotes to acquire these metals.

60

61 The key role of the trace element iron (Fe) for microbial communities in large parts of
62 the ocean has motivated research on trace metal uptake mechanisms. The search for
63 genes involved in the acquisition of different forms of Fe in individual genomes and
64 metagenomes revealed that Fe³⁺ transporters were common in marine prokaryotic
65 genomes, while transporters for siderophore-bound Fe and heme were more abundant
66 in *Gammaproteobacteria* and *Bacteroidetes* as compared to *Alphaproteobacteria*
67 (Hopkinson and Barbeau, 2012). Exploring metagenome assembled genomes (MAGs)

68 from the Southern Ocean extended this view to taxonomy-specific differences in Fe-
69 acquisition strategies (Sun et al. 2021). The use of distinct Fe-uptake mechanisms was
70 further supported by metatranscriptomics approaches (Debeljak et al. 2019; Sun et al.
71 2021). By contrast, the ecological strategies of prokaryotic taxa for the uptake of other
72 essential trace metals has been less investigated. A genomic study revealed pronounced
73 differences in the capacity of metal transport between *Roseobacter* and SAR11 (Hogle
74 et al. 2016). While *Roseobacter* genomes contained transporters for several metals (Fe,
75 Co, Ni, Cu, Zn), a reduced repertoire was present in SAR11 genomes (Hogle et al.
76 2016). The potential role of *Rhodobacteraceae* in trace metal cycling was confirmed
77 by gene expression patterns in experimental incubations (Debeljak et al. 2021).
78 *Rhodobacteraceae* were major contributors to the transcripts of genes associated to the
79 transport, sensing and regulation of nine metals (Zn, Mn, Cu, Co, Ni, Cd, Mo, W, and
80 Fe) in Southern Ocean microbial communities (Debeljak et al. 2021). The diverse
81 metabolisms present in marine microbial communities are likely strong drivers of the
82 acquisition strategies of prokaryotic taxa, which in turn has implications on their role
83 in the cycling of these elements in the ocean.

84 The main objectives of the present study were to identify genes encoding for the
85 transport of seven metals (Zn, Mn, Ni, Mo, W, Cu, Co) in Southern Ocean prokaryotic
86 communities, to investigate their temporal patterns over an entire productive season
87 and to identify the key microbial players for each metal considered. We therefore
88 searched for the respective genes in metagenomes obtained from microbial
89 communities collected with an autonomous sampler in surface waters of the Central
90 Kerguelen Plateau. Our observations are discussed with respect to a previous study in
91 which we investigated the seasonal dynamics of Fe and organic substrate acquisition
92 gene repertoires (Zhang et al. 2023).

93

94

95 **Experimental procedures**

96 Sample collection, DNA extraction and metagenome sequencing

97 We used 12 metagenomes obtained from seawater samples collected by the Remote
98 Access Sampler (RAS) in surface waters (40 m) above the Kerguelen plateau (Station
99 A3) in the Indian sector of the Southern Ocean (Blain et al. 2021). The details of DNA
100 extraction and metagenome sequencing are given in the study by Liu et al. (2020) and
101 Zhang et al. (2023). The data sets are available in the European Nucleotide Archive
102 (ENA) repository at <https://www.ebi.ac.uk/ena> under the project ID PRJEB56376.

103

104 Metagenome assembly

105 Quality control (QC) passed reads from each sample were individually assembled by
106 MEGAHIT v1.2.9 with default settings and metaSPAdes v3.15.2 (Nurk et al. 2017,
107 parameters used -k 21, 33, 55, 77, 99, 127). After comparing the length of N50 produced
108 by two tools (N50-MEGAHIT=690 bp, N50-metaSPAdes=935 bp), we finally used the
109 metaSPAdes assembly results for analysis.

110

111 Metagenomic functional analysis

112 Open reading frames (ORFs) were predicted using Prodigal v2.6.3 (Hyatt et al. 2010,
113 parameters used -p meta). CD-HIT v4.8.1 (Li & Godzik, 2006, parameters used -c 1 -
114 aS 1 -g 1) was used to construct a non-redundant protein database. A total of 8.9 Mio
115 non-redundant protein-coding genes were identified for all samples. Genes per kilobase
116 million (GPM) were used as a proxy for gene abundance as described in Zhang et al.
117 (2023). In order to identify the transporter sequences resulting from the individual
118 metagenomic assemblies, predicted protein sequences were aligned using eggNOG 5.0
119 (Huerta-Cepas et al. 2019) and GhostKOALA (Kanehisa et al. 2016) with default
120 parameters. All KEGG orthologous (KO) numbers defined as “Transporter” in KEGG
121 were retrieved, and metal transport-related genes were verified by reviewing previous
122 literature and manually checking the metal transport information in the KEGG database

123 (Table S1). We then focused on genes related to the transport of trace metals into the
124 cell, except for Co and Cu (see below). We used the *sitABCD* complex (Mn/Fe; Table
125 S1) to refer to Mn transporters (Papp-Wallace & Maguire, 2006), as other Mn
126 transporter proteins (e.g. *mnt*, *tro*) had low abundances or were undetectable in our
127 sequences. Zn-transporters were identified based on ZIP2 (Grass et al. 2005) and
128 *znuABC* (Hantke et al. 2001). While the ZIP family is known to contain several general
129 trace metal transporters, the ZIP2 we used has been characterised as being specific for
130 Zn (Grass et al. 2005). *Cbik* was used to refer to Ni transporters (Rodionov et al. 2006).
131 Mo-transporters were identified based on *modABC* (Grunden & Shanmugam, 1997)
132 and W-transporters were identified based on *tupAB* (Hagen, 2023). Genes for Co uptake
133 were low and no Cu uptake genes were detected in our metagenomes, we therefore only
134 considered the efflux systems of both metals and present the seasonal patterns for
135 *cusABC* (for Cu) and *cnrABC*, *czcD* (for Co) (Franke et al. 2003; Okamoto & Eltis,
136 2011).

137

138 Metagenomic taxonomic analysis and MAGs analysis

139 Taxonomic classification of metal-related genes was performed according to the
140 Genome Taxonomy Database (Parks et al. 2022) using Centrifuge v1.0.4 (Kim et al.
141 2016) and the alignments with highest score were kept. We mainly considered the
142 family level and used metagenome-assembled genomes (MAGs) for a more fully
143 resolved description. One MAG assigned to *Flavobacterium*, *Nitrincolaceae*,
144 *Porticoccaceae*, SAR11, *Sphingomonadaceae* and *Thioglobaceae*, and two MAGs
145 assigned to *Polaribacter* as well as four MAGs assigned to *Rhodobacteraceae* were
146 downloaded from data previously published by Sun et al. (2021). Following the method
147 described in the analysis of MAGs by Zhang et al. (2023), functional annotations of
148 MAGs were performed and the abundances of MAGs and their metal transport-related
149 genes across the 12 metagenomes were calculated. The coverage of the MAGs in each
150 metagenome sample was determined by aligning reads from each sample back to the
151 MAGs using Bowtie2 (Langmead & Salzberg, 2012). The mean coverage for each

152 MAG was then calculated from these alignments using anvio v7.1. This mean
153 represents the average depth of coverage across contig, calculated as the coverage of
154 each nucleotide in a contig divided by the length of the contig. Visualization of data
155 was performed using the packages ggplot2 in the R v4.2.1 and SigmaPlot v14.5
156 software.
157

158 **Results**

159 Environmental context

160 The remote autonomous sampler (RAS) was deployed at station A3, located above the
161 Kerguelen plateau southeast of Kerguelen Island (50.63°S, 72.06°E; overall depth
162 527 m) in the Indian Sector of the Southern Ocean (Fig. 1). Samples were collected at
163 40 m depth from 25 October 2016 to 24 February 2017 covering the entire productive
164 season. During this time period temperature increased steadily from 4°C in early spring
165 to 6° late summer (Fig. S1). The high concentrations of silicic acid at the beginning of
166 the season (20 μM) rapidly decreased during spring (to 5 μM), while concentrations of
167 nitrate remained elevated over the course of the season (20 to 30 μM) (Blain et al. 2021)
168 (Fig. S1). Two consecutive phytoplankton blooms occurred during the sampling period,
169 a spring bloom with a peak in mid-November and a summer bloom in early January
170 (Fig. 1). Diatoms were the main contributors to phytoplankton biomass and revealed
171 pronounced successional changes in community composition (Blain et al. 2021).
172 Seasonal dynamics in prokaryotic community composition were strongly related to
173 phytoplankton biomass and composition (Liu et al. 2020).

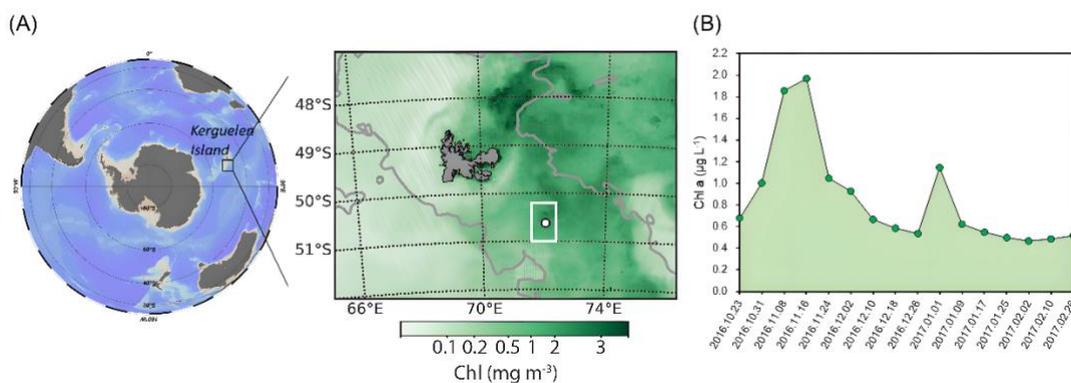


Figure 1. (A) Regional view of the mooring site on the Central Kerguelen plateau. The white dot denotes the position of the RAS mooring overlaying monthly chlorophyll for November 2016. Grey lines are the 1000 m isobaths. (B) Temporal changes of Chlorophyll *a* (green shaded area) during the period of the RAS deployment. Modified from Blain et al. (2021) and Liu et al. (2020).

175 Seasonal dynamics in trace element transporters

176 In a previous study we determined the temporal patterns of genes related to the uptake
177 of different forms of iron (Fe) and of genes involved in the cleavage and uptake of
178 organic substrates (Zhang et al. 2023). We focus here on genes related to the transport
179 of the metals Mn, Zn, Ni, Mo, W, Co and Cu. A total of 89 metal transport related
180 KEGG orthologous (KO) genes were retrieved from the KEGG database. Among these,
181 67 KO genes were detected in our dataset and their normalized abundances varied
182 between 0.2 to 760 genes per kilobase million (GPM) (Table S1, Fig. S2). We set a
183 threshold for the further analyses with the aim to consider only the most abundant genes.
184 We therefore considered only those KO genes for which the sum of the respective GPM
185 in the 12 metagenomes was > 45 GPM; this resulted in 26 KO genes (Table S1). The
186 majority (84 %) of these transporters are metal uptake genes, and we also detected
187 several efflux genes. In the case of Co, uptake genes had low abundance (< 40 GPM)
188 in our metagenomes, and no Cu uptake genes were detected.

189 Seasonal patterns of *sitABCD* (Mn/Fe transporters) revealed a sharp increase in GPM
190 during the spring bloom and remained high until the summer bloom, followed by a
191 rapid decline and a second smaller peak after the summer bloom (Fig. 2A). Transporters
192 of Zn (*znuABC* and *ZIP2*), Ni (*cbiK*) and W (*tupAB*) increased after the spring bloom
193 and their temporal patterns matched those of Mn over the remaining season (Fig. 2B,
194 C, D). By contrast, transporters of Mo (*modABC*) had low GPM during the spring
195 period, and revealed a small increase prior to and a marked peak after the summer
196 bloom (Fig. 2E). As for Cu and Co, their efflux genes (*cusABC* for Cu and *cnrABC*,
197 *czcD* for Co) had seasonally high GPM prior to and after the spring and summer blooms
198 (Fig. 2F).

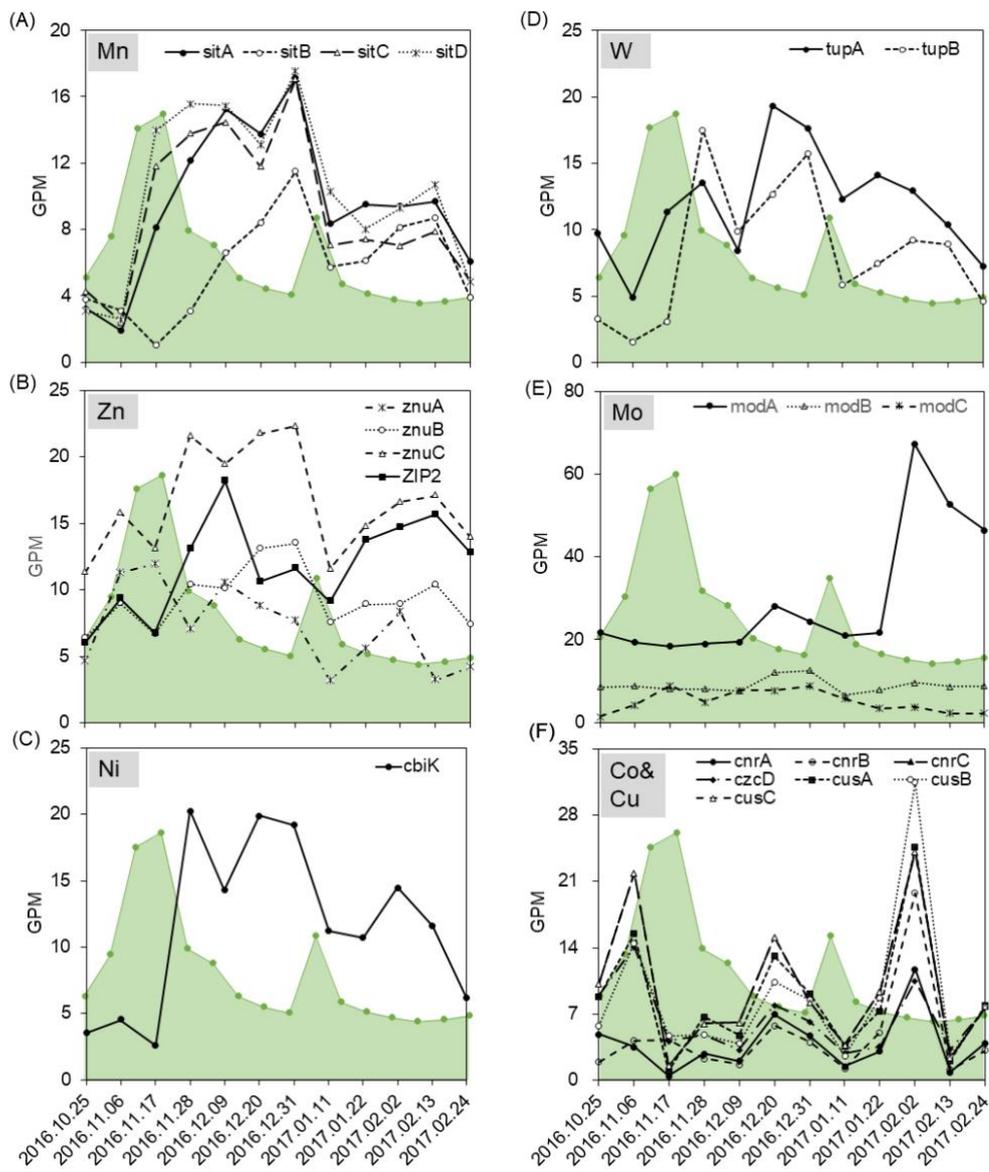


Figure 2. Temporal changes of Chlorophyll a (green shaded area) and abundance of genes for Mn transporters (A), Zn transporters (B), Ni transporters (C), W transporters (D), Mo transporters (E), and Co and Cu efflux transporters (F). Normalized gene abundances are given in genes per kilobase million (GPM).

199

200 Taxonomic affiliation of transporter genes

201 The taxonomic affiliations revealed pronounced differences in the relative contribution
 202 of prokaryotic groups, at the family level, to the transporters of different trace metals
 203 (Fig. 3). *Porticoccaceae* were the dominant contributors to *sitABCD* (Mn/Fe) during

204 the peak of the spring bloom and its early declining phase and *Rhodobacteraceae* had
 205 an equal share during the remaining season. In the case of Zn, a contrasting picture was
 206 obtained for the two types of transporters identified in our metagenomes. ZIP2 were
 207 predominantly attributed to *Flavobacteriaceae*, with the exception of the start of the
 208 spring bloom when *Pseudomonadaceae* had high contributions to ZIP2 transporters.
 209 By contrast, taxonomic affiliations were more diverse for *znuABC* with seasonally
 210 changing contributions of *Pseudomonadaceae*, *Porticoccaceae*, *Rhodobacteraceae* and
 211 *Pelagibacteraceae*. The taxonomic assignments of *cbiK* (Ni) were dominated by
 212 *Nitrincolaceae* after the spring bloom and *Rhodobacteraceae* and *Pelagibacteraceae*
 213 were dominant contributors during the remaining season. Taxonomic assignments of
 214 *tupAB* (W) were similar to those of *cbiK*. Transporters of Mo (*modABC*) were affiliated
 215 to *Thioglobaceae*, *Pseudomonadaceae*, *Porticoccaceae*, and *Rhodobacteraceae*
 216 throughout the season. *Pseudomonadaceae* and *Sphingomonadaceae* had similar
 217 contributions to Co and Cu efflux transporters (Fig. S3).

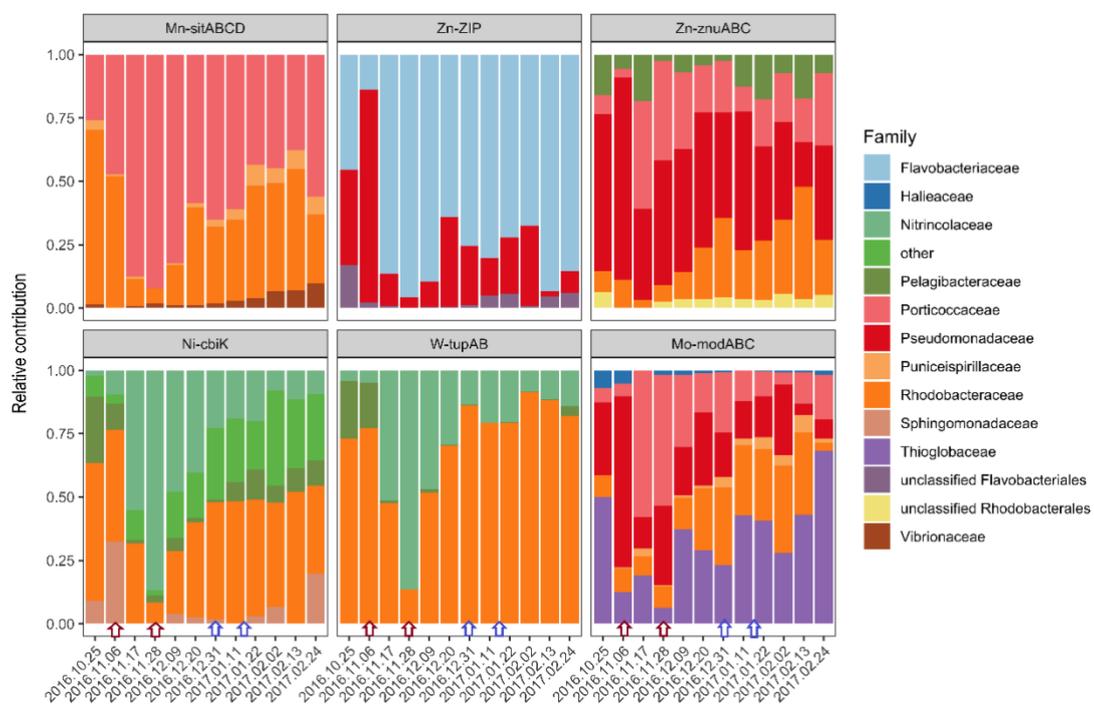


Figure 3. Relative contribution of prokaryotic groups to specific genes associated with Mn (*sitABCD*), Zn (ZIP2 and *znuABC*), Ni (*cbiK*), W (*tupAB*) and Mo (*modABC*) transporters. Prokaryotic groups are based on the family level. Red arrows

indicate the spring phytoplankton bloom, and blue arrows indicate the summer phytoplankton bloom.

218

219 Metal acquisition genes in metagenome assembled genomes (MAG)

220 To identify the inventories of metal acquisition genes in individual prokaryotic taxa, we
221 used previously published MAGs obtained from samples collected in the Kerguelen
222 region, including our study site at the time point of the RAS deployment (Sun et al.
223 2021). We chose 12 MAGs belonging to *Flavobacteriaceae*, *Nitrincolaceae*,
224 *Porticoccaceae*, *Rhodobacteraceae*, SAR11, *Sphingomonadaceae* and *Thioglobaceae*
225 (Fig. 4). These MAGs were chosen because they belong to prokaryotic groups with a
226 substantial contribution to the different gene categories (Fig. 3). Moreover, ASVs
227 belonging to these prokaryotic groups were shown to be abundant and have distinct
228 seasonal relative abundance patterns (Liu et al. 2020). For some abundant prokaryotic
229 groups with contributions to the genes of interest, as for example *Pseudomonadaceae*,
230 no MAGs were previously annotated (Sun et al. 2023). Our results indicate that the
231 *Rhodobacteraceae* MAGs (MAG 20, 23, 52, 106) had the most diverse and abundant
232 metal transport gene inventories, including transporters of Mn, Zn, Ni, W, Mo, and Co,
233 while MAGs belonging to other families had a reduced set of transporter genes. Two of
234 the *Rhodobacteraceae* MAGs (20 and 52) had relatively high read-based coverage
235 during the late declining stage of the spring bloom, while MAG106 had a less
236 pronounced seasonal pattern. We detected Zn transporters (*znuABC* and *ZIP2*) in two
237 *Flavobacteriaceae* MAGs (*Flavobacterium* MAG16 and *Polaribacter* MAG88) that
238 had both highest coverage after the spring bloom. In addition, *Flavobacteriaceae*
239 MAG16 harbored genes for Cu and Co efflux transporters. *Nitrincolaceae* MAG115
240 contained transporters for Zn (*znu*), Ni (*cbik*) and W (*tup*) and had the highest coverage
241 of all MAGs considered here, peaking during the early spring bloom decline. A
242 contrasting seasonal coverage was observed for SAR11 MAG133 for which the W
243 transporter *tup* was detected. *Sphingomonadaceae* MAG116 and *Thioglobaceae*
244 MAG136 harbored both the Ni transporters (*cbik*), and MAG116 also contained *mod*.

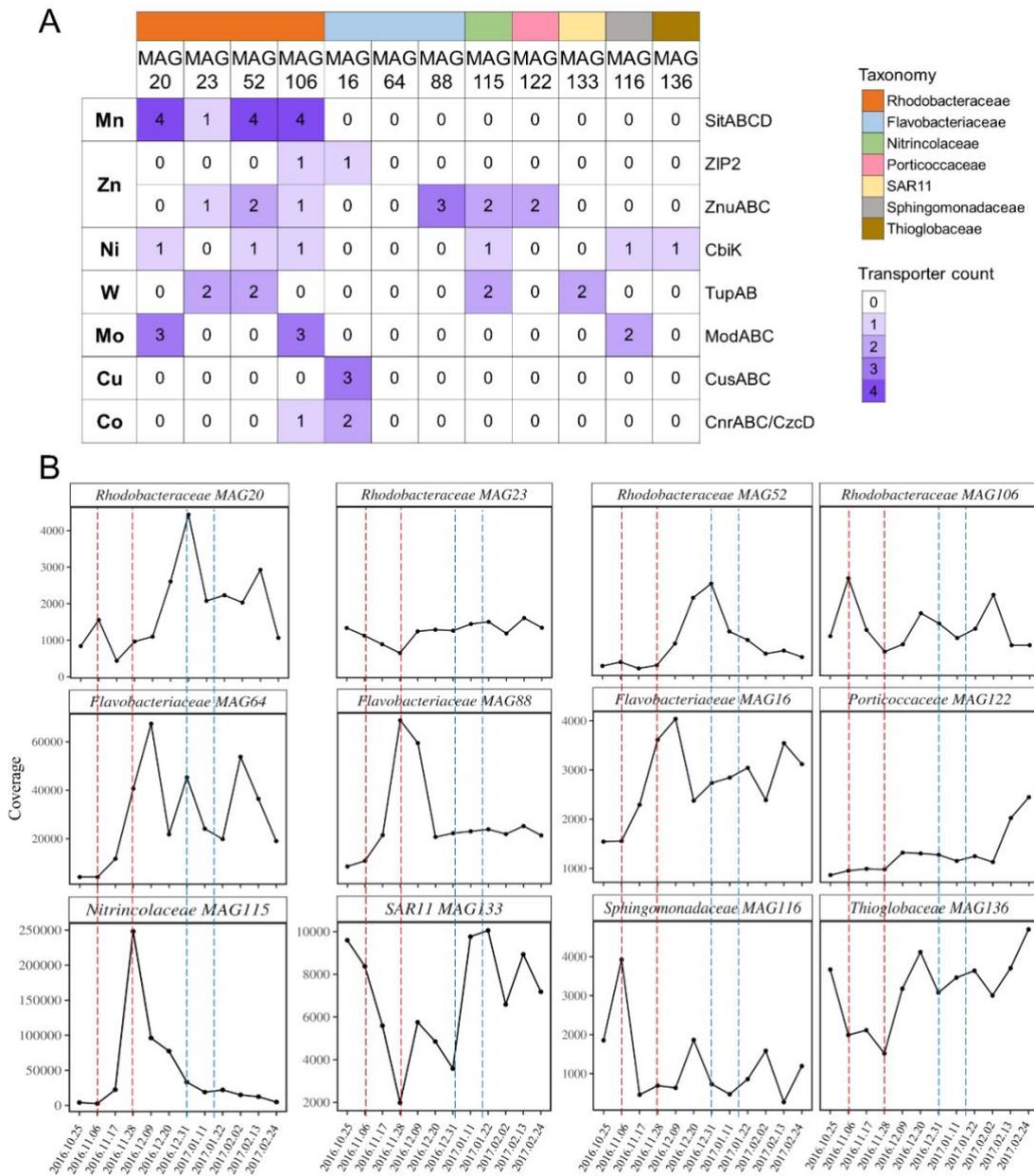


Figure 4. The distribution of specific genes related to Mn, Zn, Ni, W, Mo, Cu and Co transporters in the twelve MAGs. The square blocks are colored according to the gene counts (A). The coverage of MAGs in the twelve samples. The red lines represent the first spring phytoplankton bloom, and blue lines represent the second summer phytoplankton bloom. (B).

245

246

247 **Discussion**

248

249 We observed marked seasonal patterns of prokaryotic transporter genes for the metals
250 Mn, Zn, Ni, W and Mo in the Southern Ocean. These metals are key for metalloenzymes
251 involved in diverse metabolic pathways. Among these are pathways linked to the
252 degradation, uptake and processing of the diverse pool of organic substrates that
253 constitute the main source of carbon and energy for heterotrophic microbes.
254 Concentrations of dissolved Fe ($\sim 0.1\text{-}0.3$ nM) (Blain et al. 2007, Qu  rou   et al 2015),
255 Mn (~ 0.3 nM; Zhang et al., under revision) are in the picomolar range in surface waters
256 at our study site, and those of Zn (~ 2 nM) and Ni (~ 6 nM) in the lower nanomolar
257 range (Wang et al. 2019). Mo is present at higher concentrations in marine surface water
258 (~ 100 nM) (Matsuoka et al. 2023) than W (~ 50 pM; Matsuoka et al. 2023). Iron is
259 essential for microbial respiration, and it has been shown that this element can be
260 limiting for microbial growth in Southern Ocean surface waters (Obnersterer et al.
261 2015, Baltar et al. 2018). However, whether this is the case for the metals considered
262 here is not known. Due to their overall higher concentrations and probably lower
263 cellular requirements due their utilization in specific pathways, as opposed to the wider
264 use of Fe as a redox catalyst, it is unlikely that they are direct limiting factors of
265 microbial growth (Baltar et al. 2018). The seasonal patterns observed in our study
266 therefore rather reflect the requirements of a given trace element for the processing of
267 the seasonally changing amount of DOM and the diversity of organic substrates present
268 within this pool. Our results further allow us to identify abundant prokaryotic groups
269 with the capacity to transport a given trace element. A high contribution of a given
270 prokaryotic group to a trace metal transporter could illustrate its competitiveness driven
271 by trace-metal acquisition under a specific bloom stage. Given the key role of DOM in
272 driving prokaryotic growth and community composition in this ocean region (Landa et
273 al. 2016), we will focus our discussion on a few prominent biogeochemical processes
274 within the marine carbon cycle involving trace metals and the potential microbial key
275 players.

276

277 Zn and Mn are contained in enzymes with distinct roles in the cleavage and processing
278 of organic carbon. Zn plays an important role in catalytic processes to access organic
279 matter. About half of the Zn-bound proteins are enzymes, among which hydrolases
280 make up more than 50% (Andreini et al. 2012). The Zn enzymes alcohol dehydrogenase
281 and carboxypeptidase belong to glycoside hydrolase (GH) families of CAZymes, and
282 include GH18 and GH19 responsible for the decomposition of chitin (Nguyen et al.
283 2019). We identified both the high-affinity Zn-uptake system, encoded by the *znuABC*
284 genes (Hantke 2001) and the low-affinity ZIP2 transporter (Grass et al. 2005). ZIP2
285 transporters had a seasonal trend that closely matched that of CAZymes (Fig. S4)
286 (Zhang et al. 2023) pointing to increased Zn-requirements for the degradation of
287 complex substrates. *Flavobacteriaceae*, including *Flavobacterium* and *Polaribacter*,
288 were the main contributors to ZIP2 (Fig. 3 and Fig. S5) and this family accounted for
289 up to 30% of the CAZymes during the bloom decline (Zhang et al. 2023). The 3
290 *Flavobacteriaceae* MAGs all peaked after the spring bloom (Fig. 4B) and 2 MAGs
291 (MAG16 and MAG88) harbored genes for Zn transporters (Fig. 4A). These results
292 highlight that *Flavobacteriaceae*, through their well-documented capacities to degrade
293 various polymeric substrates (Xing et al. 2015; Krüger et al. 2019) could play an
294 important role in the cycling of Zn.

295

296 Mn is involved in the central carbon metabolism, phosphorylation and peptide cleavage
297 (Hansel 2017). Phosphoenolpyruvate synthase uses Mn as a cofactor and pyruvate
298 carboxylase is a Mn-containing enzyme, and both are critical in gluconeogenesis
299 (Hansel 2017). We detected the gene *sitABCD* in our metagenomes, a protein transport
300 system that is not specific to Mn, but can potentially transport also Fe (Sabri & Dozois,
301 2006). Using a set of transporters of Fe³⁺ (*fbp*, *futA1/A2*, *fbpB-futB*) and Fe²⁺ (*feo*,
302 *efeUOB*) (Fig. S8, Zhang et al. 2023) revealed a seasonal pattern that differed from that
303 observed for *sit* in the present study (Fig. 2A), suggesting that the temporal dynamics
304 of *sit* likely reflect Mn transporters. The rapid increase in Mn transporters during the
305 spring bloom and their continuously high levels throughout the declining phase is likely

306 related to the processing of readily accessible phytoplankton-derived organic substrates.
307 *Porticoccaceae* and *Rhodobacteraceae* were identified as main contributors to *sit*
308 transporters, but at distinct time periods (Fig. 3). The temporal pattern of the
309 contribution of *Porticoccaceae* to *sit* transporters closely matched the dynamics of an
310 ASV belonging to SAR92 (*Porticoccaceae*) that revealed a rapid increase in relative
311 abundances (to up to 10%) during the spring bloom (Liu et al. 2020). These
312 observations suggest a fast response of SAR92 to phytoplankton-derived substrates, an
313 idea that is further supported by previous observations pointing to SAR92 as an
314 abundant and active member of the microbial community during the peak and spring
315 bloom decline (West et al. 2008; Obernosterer et al. 2011). Using the same
316 metagenomic dataset, we observed that *Porticoccaceae* had a low contribution to
317 CAZymes (2-15%) (Zhang et al. 2023), suggesting that this group had a minor
318 implication in the degradation of complex compounds (Kim et al. 2019; He et al. 2023).
319 *Rhodobacteraceae* accounted for a large share of *sit* transporters during the transition
320 phase to the summer bloom consistent with the seasonal patterns of *Rhodobacteraceae*
321 MAGs and abundant ASVs (Liu et al. 2020), suggesting their increased contribution to
322 the processing of DOM at the final stage of the spring bloom decline (Buchan et al.
323 2019).

324

325 Nickel is an essential cofactor of enzymes in nitrogen fixation, nitrogen uptake and
326 carbon fixation. Among nickel-dependent enzymes are urease, carbon monoxide
327 dehydrogenase (CODH) and superoxide dismutase (NiSOD). *Nitriolaceae* had a
328 dominant contribution to the Ni transporters *cbik* during the early spring bloom decline
329 when the respective GPMs were high (Fig. 2). This pattern could be due to the presence
330 of two *Nitriolaceae* ASVs that together reached 40% relative abundance (Liu et al.
331 2020), coherent with the remarkably high coverage of *Nitriolaceae* MAG115 that
332 harbored *cbik* (Fig. 4). *Nitriolaceae* are specialized in the utilization of amino acids
333 and peptides (Francis et al. 2021; Debeljak et al. 2023) which could explain the high
334 contribution of this family to the peptide/nickel transport system in early spring (*ddp*,
335 PE.P, PE.P1, PE.S) (Fig. S6A). Urea is a nitrogen containing compound and its

336 utilization requires the Ni-containing enzyme urease. Urea can account for a substantial
337 fraction of the prokaryotic nitrogen demand in marine systems (Jørgensen 2006),
338 including the Southern Ocean (Hollibaugh et al. 2023) and diverse prokaryotic taxa are
339 implicated in this process (Connelly et al. 2014). The increase in the concentrations of
340 ammonium during the bloom decline (Fig. S1) could indicate that reduced forms of
341 nitrogen, including urea, become important sources of this nutrient for certain
342 prokaryotes, potentially including *Nitriocolaceae*. Further in-depth studies are required
343 to confirm this idea.

344

345 Tungstoenzymes are required by methylotrophic prokaryotes to metabolize organic
346 substrates containing no carbon-carbon bonds, such as single-carbon (C1) compounds
347 (e.g. methane, methanol), methylated amines and methylated sulfur species (DMS,
348 DMSO) by specialized pathways (Chistoserdova 2011; Maia et al. 2017). W-containing
349 formate dehydrogenase (FDH) catalyzes the oxidation of formate, an intermediate
350 product in methylotrophy, to carbon dioxide and therefore plays an important role in
351 the processing of these compounds (Chistoserdova 2011). Methylotrophy appears to be
352 widespread in marine microbial communities (Sun et al. 2011; Lidbury et al. 2014). In
353 the present study, *Rhodobacteraceae* were the main contributors to W-transporters
354 throughout the season, except for the peak of the spring bloom when W-transporters
355 were mainly affiliated with *Nitriocolaceae* (Fig.3). *Rhodobacteraceae* are known
356 utilizers of methylated sulfur compounds (Buchan et al. 2005) and amines (Chen 2012;
357 Lidbury et al. 2014, Taubert et al. 2017), which could explain their W requirements.
358 Recent observations point to a potential role of *Nitriocolaceae* in C1 metabolism
359 (Francis et al. 2021). The full set of methanesulfonate monooxygenase genes, required
360 for the utilization of methanesulfonate as carbon source and for the oxidation of DMS
361 were present and expressed in *Nitriocolaceae* MAGs from the Southern North Sea
362 (Francis et al. 2021). These observations could point to a possible role of *Nitriocolaceae*
363 members in methylotrophy, but further genome-based investigations would be required
364 to identify the pathways involving W-containing enzymes in members belonging to this
365 family.

366

367 Mo is widely known for its role in nitrogenase, the enzyme responsible for N₂ fixation
368 (Tuit, 2003). Another metabolism in which Mo is involved is carbon monoxide (CO)
369 oxidation. Mo-containing CO dehydrogenase (CODH, *coxSML*) is an enzyme in
370 aerobic CO oxidizers that can use CO as their carbon source (King and Weber, 2007).
371 The seasonal trend in Mo transporters, peaking in late summer, matched those of *nifH*
372 and CODH (Fig. S4) and suggests that both pathways could potentially be taking place.
373 The main contributors to the *nifH* genes were *Xanthobacteraceae* (Fig. S6C), a family
374 that is widely known to have N₂ fixing capacity (Brenner et al. 2005; González-Cortés
375 et al. 2022). *Thioglobaceae*, important contributors to Mo transporters throughout the
376 season, have the potential for carbon fixation (Morris et al. 2022), however, in the
377 present study *cox* was not affiliated with this group. By contrast, *Rhodobacteraceae*
378 contributed to both *mod* and *cox*, suggesting that members of this group could make
379 use of this pathway. Genomic insights (Moran et al. 2004, Simon et al. 2017) and uptake
380 experiments (Tolli et al. 2006) have shown that *Roseobacter* oxidize CO. These Mo-
381 requiring processes are likely to occur concurrently, but carried out by different
382 microbial groups.

383

384 Several trace metals could further play a role in superoxide dismutases (SODs). SODs
385 are metalloenzymes that catalyze the conversion of superoxide molecules to hydrogen
386 peroxide and molecular oxygen. SODs are one of the main defense mechanisms of cells
387 against oxidative stress (McCord and Fridovich, 1969). Three types of SODs were
388 described in prokaryotes, that are Ni-containing SODs (NiSOD), Fe- or Mn-containing
389 SODs (FeSOD and MnSOD), and Cu- and Zn-containing SODs (Cu,ZnSODs) (Wang
390 et al. 2018). In our metagenomes, all types of SODs were identified and they peaked
391 during the early spring bloom decline (Fig. S7). Microbial respiration is linked to the
392 formation of reactive oxygen species (ROS) that can be neutralized by SODs (Tiwari
393 et al. 2002). The sharp increase in SODs could be a result of the enhanced microbial
394 metabolism in response to the phytoplankton bloom, including respiration of large

395 amounts of DOM (Lesser 2006). Our results indicate that different metals could be used
396 for SODs concurrently. The involvement of diverse taxa in this key process in
397 combination with the different capacities of these prokaryotes of transport metals could
398 explain this pattern.

399

400 The seasonal dynamics of the contribution of prokaryotic groups to trace metal
401 transporters as observed in the present study point to distinct capabilities in the
402 acquisition of these elements. In combination with the temporal trends in the
403 abundances of a given trace metal transporter, our findings provide insights to the
404 potential roles of abundant prokaryotic groups in the cycling of trace metals during
405 consecutive spring and summer phytoplankton blooms in the Southern Ocean.
406 *Rhodobacteraceae* had a broad repertoire of trace metal transporters (Mn, Zn, Ni, W,
407 Mo) a feature that likely reflects the large diversity of metabolic functions present in
408 this prokaryotic group. Our data suggest a more restricted repertoire for
409 *Flavobacteriaceae* (Zn) and *Nitrospiraceae* (Ni, W), which could point to a more
410 specialized functional role possibly associated with requirements of a reduced set of
411 trace metals. The temporal variability in the abundances of genes encoding for trace
412 metal transporters provides insight on the bloom stages that are favorable for diverse
413 metal-requiring pathways to occur. Our results, based on trace metal transporter
414 capacities, represent a novel perspective on the functional role of prokaryotes in the
415 biogeochemical cycling of elements in the ocean.

416

417 **Author contributions**

418 Yanhui Kong, Stephane Blain and Ingrid Obernosterer designed the research.
419 Bioinformatic analyses were performed by Yanhui Kong and Rui Zhang. Yanhui Kong
420 and Ingrid Obernosterer wrote the first draft of the manuscript. All authors contributed
421 to editing the manuscript.

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435 **Competing interests**

436 The authors declare no competing interests.

437 **Data availability statement**

438 The data sets generated and analyzed during the current study are available in the
439 European Nucleotide Archive (ENA) repository at <https://www.ebi.ac.uk/ena> under
440 the project ID PRJEB56376.

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664

Supplementary Information for
“Seasonal dynamics in microbial trace metals transporters during
phytoplankton blooms in the Southern Ocean”

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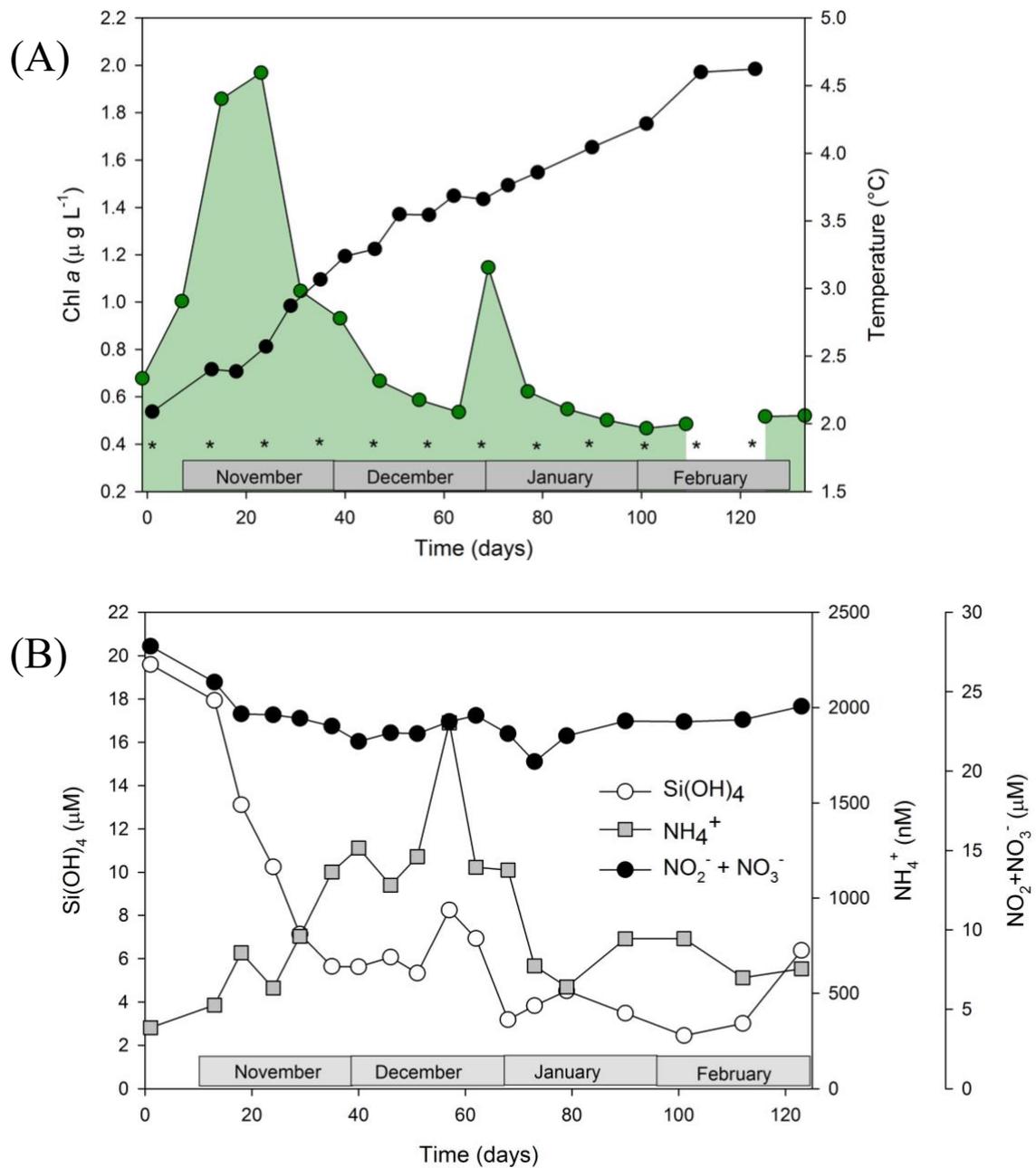
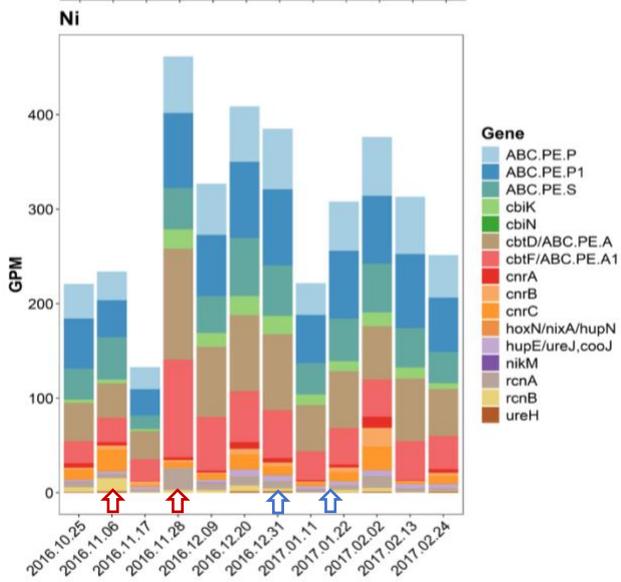
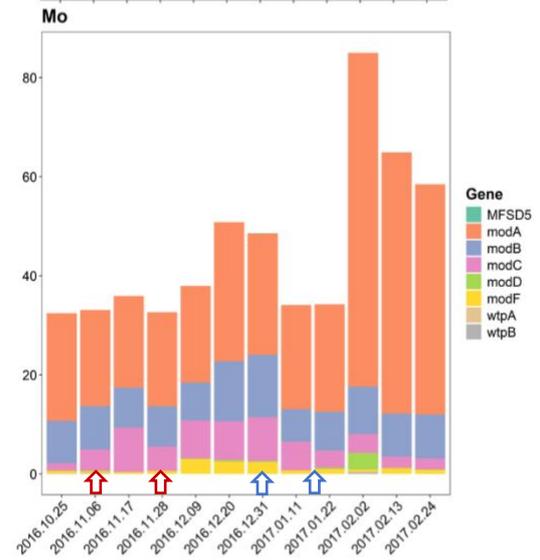
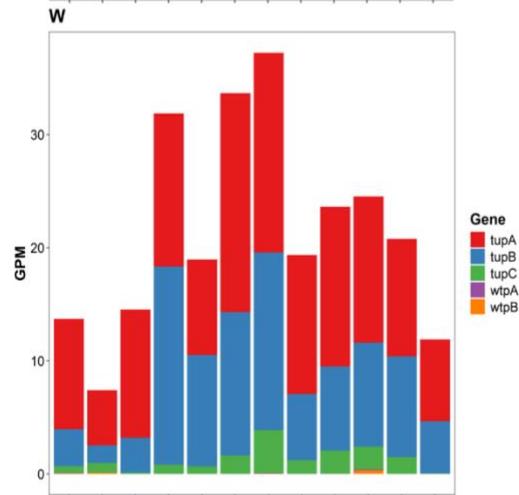
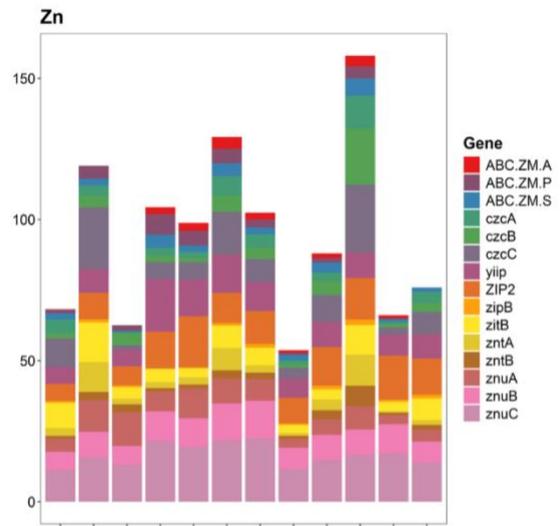
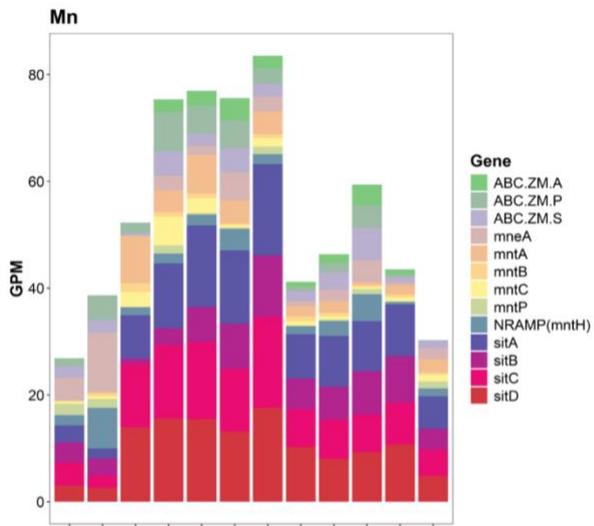


Figure S1 Temporal changes of Chlorophyll a (green shaded area) and temperature (black circles) during the period of RAS deployment (A). Temporal changes of silicic acid (Si(OH)_4), ammonium (NH_4^+) and nitrite+nitrate ($\text{NO}_2^- + \text{NO}_3^-$) during the period of sampling (25 October 2016 to 24 February 2017) (B). Data are from Blain *et al.* (2021).



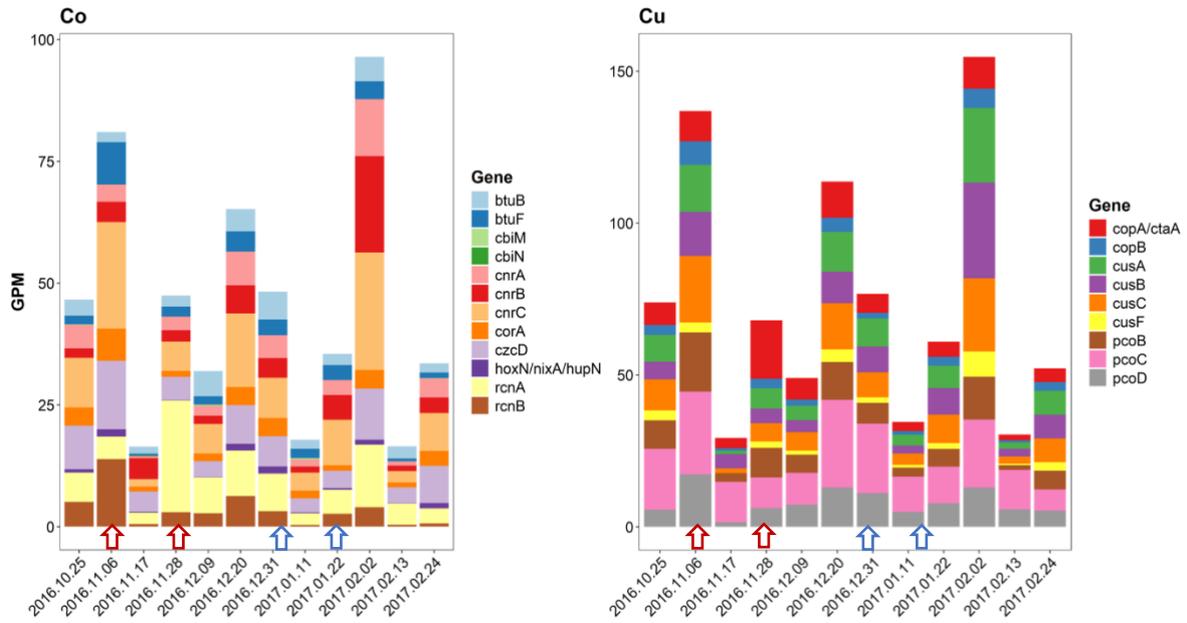


Figure S2 Abundance of genes related to Mn, Zn, W, Mo, Ni, Co and Cu transport at the 12 time points. Gene abundance is represented by genes per kilobase million (GPM). Red arrows indicate the first spring phytoplankton bloom, and blue arrows indicate the second summer phytoplankton bloom.

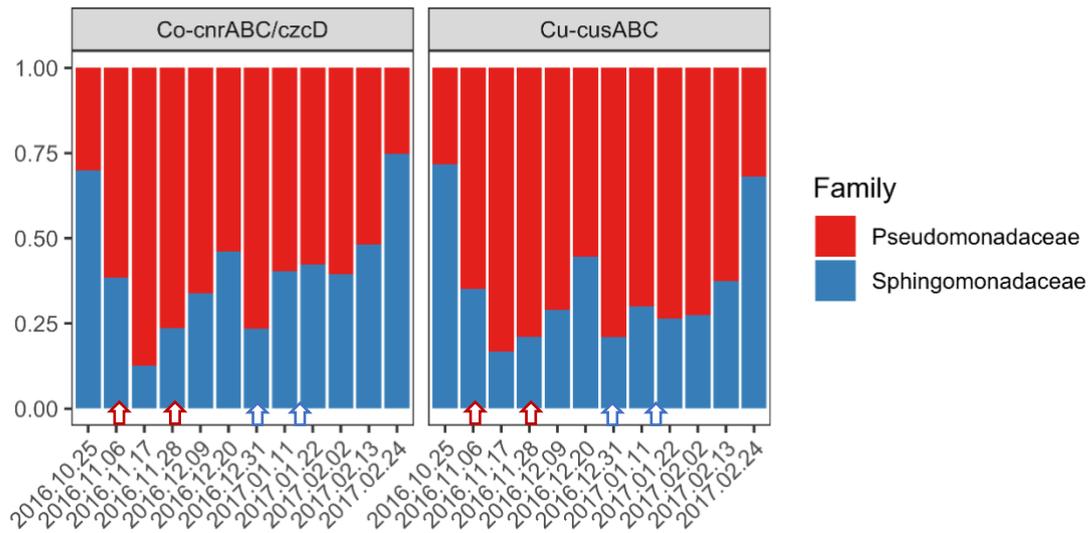


Figure S3 Relative contribution of prokaryotic groups to specific genes associated with Co and Cu efflux transporters. Prokaryotic groups are based on the family level. Red arrows indicate the first spring phytoplankton bloom, and blue arrows indicate the second summer phytoplankton bloom.

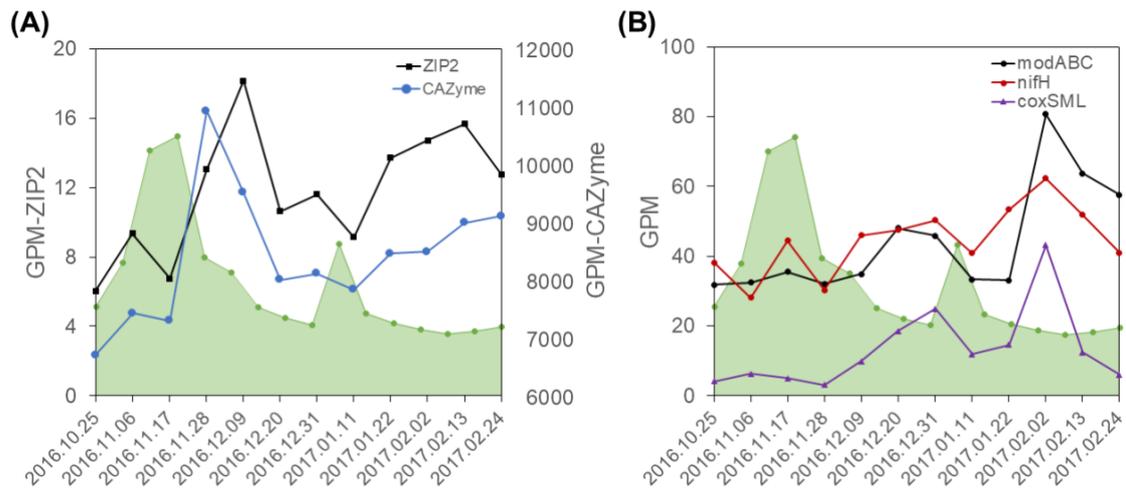


Figure S4 Temporal changes of Chlorophyll a (green shaded area) and abundance of genes for Zn transporter (ZIP2) and carbohydrate-active enzymes (CAZymes) (**A**), Mo transporters (*modABC*), nitrogen fixation gene (*nifH*) and carbon monoxide dehydrogenase (*coxSML*) (**B**). Normalized gene abundances are given in genes per kilobase million (GPM).

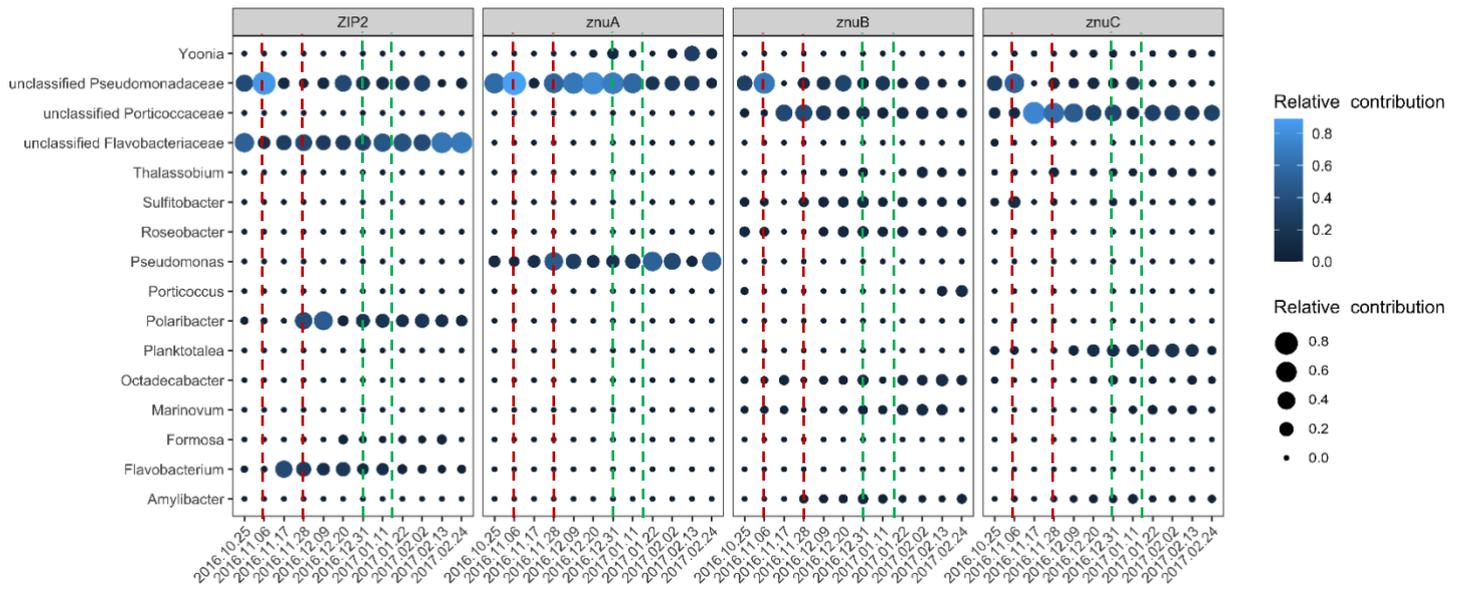


Figure S5 Relative contribution of prokaryotic groups to specific genes associated with Zn transport. Prokaryotic groups are based on the genus level. The red lines represent the first spring phytoplankton bloom, and green lines represent the second summer phytoplankton bloom.

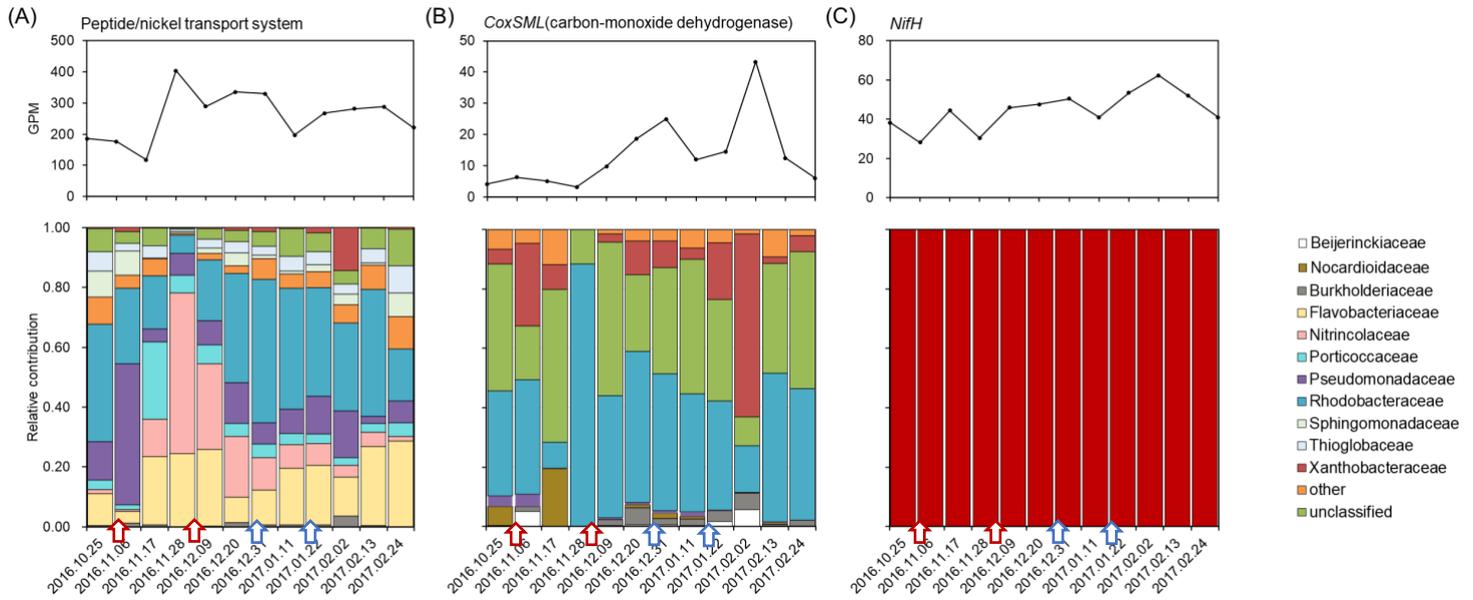


Figure S6 Temporal changes of normalized gene abundance (GPM) and relative contribution of prokaryotic groups to peptide/nickel transport system (*ddp*, PE.P, PE.P1, PE.S) (A), carbon monoxide dehydrogenase (*coxSML*) (B) and nitrogen fixation gene (*nifH*) (C). Prokaryotic groups are based on the family level. Red arrows indicate the first spring phytoplankton bloom, and blue arrows indicate the second summer phytoplankton bloom.

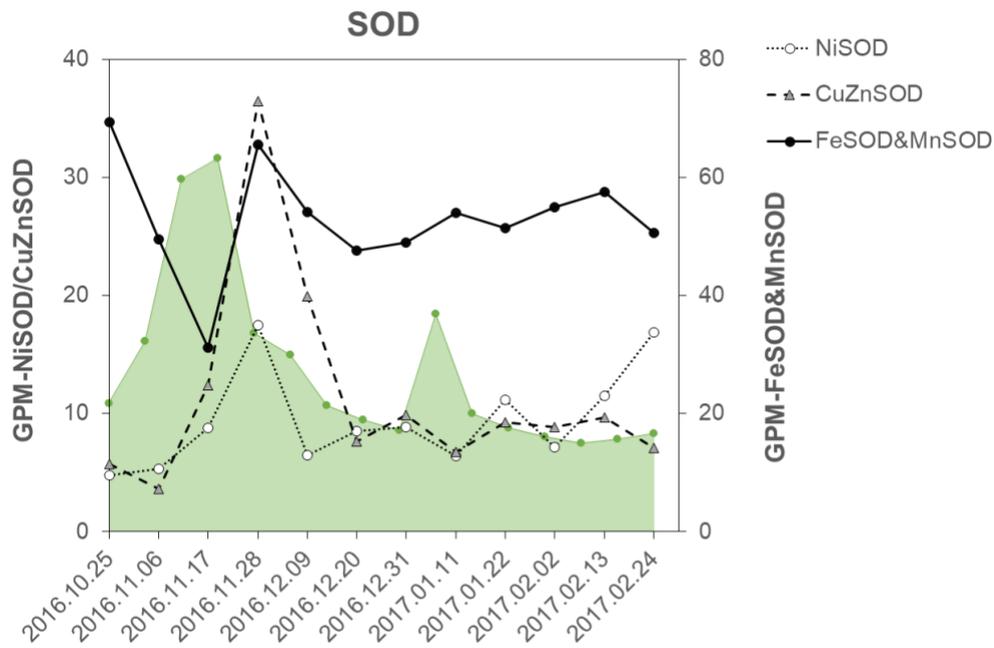


Figure S7 Temporal changes of Chlorophyll a (green shaded area) and abundance of genes for different types of superoxide dismutases (SODs). Normalized gene abundances are given in genes per kilobase million (GPM).

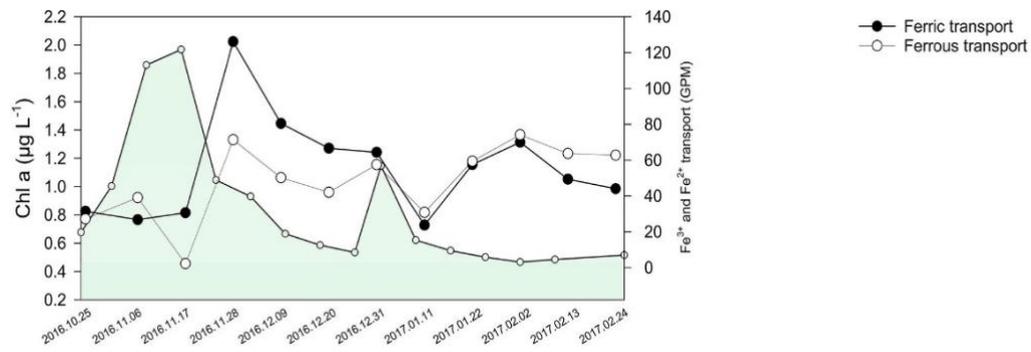


Figure S8 Temporal changes of Chlorophyll *a* (green shaded area) and abundance of genes for Fe^{3+} and Fe^{2+} transporters. Normalized gene abundances are given in genes per kilobase million (GPM). Data are from Zhang *et al.* (2023).

Reference

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- Zhang, R., Debeljak, P., Blain, S., & Obernosterer, I. (2023). Seasonal shifts in Fe-acquisition strategies in Southern Ocean microbial communities revealed by metagenomics and autonomous sampling. *Environmental Microbiology*, **25**(10), 1816-1829.