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1 # Characterization of particle-associated and free-living bacterial and
2 # archaeal communities along the water columns of the South China Sea

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17 **Abstract**

18 There is a growing recognition of the role of particle-attached (PA) and free-living (FL) microorganisms in
19 marine carbon cycle. However, current understanding of PA and FL microbial communities is largely on
20 those in the upper photic zone, and relatively fewer studies have focused on microbial communities of the
21 deep ocean. Moreover, archaeal populations receive even less attention. In this study, we determined
22 bacterial and archaeal community structures of both the PA and FL assemblages at different depths, from the
23 surface to the bathypelagic zone along two water column profiles in the South China Sea. Our results suggest
24 that environmental parameters including depth, seawater age, salinity, POC, DOC, DO and silicate play a
25 role in structuring these microbial communities. Generally, the PA microbial communities have relatively
26 low abundance and diversity compared with the FL microbial communities at most depths. Further microbial
27 community analysis revealed that PA and FL fractions generally accommodate significantly divergent
28 microbial compositions at each depth. The PA bacterial communities mainly comprise members of
29 *Actinobacteria* and *γ-Proteobacteria*, together with some from *Bacteroidetes*, *Planctomycetes* and *δ-*
30 *Proteobacteria*, while the FL bacterial lineages are mostly distributed within *α-*, *γ-Proteobacteria*,
31 *Actinobacteria* and *Bacteroidetes,* along with certain members from *β-*, *δ-Proteobacteria*, *Planctomycetes*
32 and *Firmicutes*. Moreover, there is an obvious shifting in the dominant PA and FL bacterial compositions
33 along the depth profiles from the surface to the bathypelagic deep. By contrast, both PA and FL archaeal
34 communities dominantly consist of Marine Group II (MGII) and Marine Group I (MGI), together with
35 variable minor Marine Group III (MGIII), *Methanosarcinales*, Marine Benthic Group A (MBG-A) and
36 *Woesearchaeota*. However, the pronounced distinction of archaeal community compositions between PA and
37 FL fractions are observed at finer taxonomic level. A high proportion overlap of microbial compositions
38 between PA and FL fractions implies that most microorganisms are potentially generalists with PA and FL
39 dual lifestyle for versatile metabolic flexibility. In addition, microbial distribution along the depth profile
40 indicates a potential vertical connectivity between the surface-specific microbial lineages and those in the
41 deep ocean, likely through microbial attachment to sinking particles.
42

43 **Keywords:** particle-attached, free-living, marine microbe, vertical distribution, sinking particles, deep ocean,
44 the South China Sea.

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45 **1. Introduction**

46 The sinking of particulate organic matter (POM) formed in the photic layer is a fundamental process
47 that transports carbon and nutrient materials from the surface into the usually starved deep ocean, with
48 a significant role in structuring the distributions and activities of marine microorganisms in the dark
49 realm (Azam and Malfatti, 2007; Mestre et al., 2018; Suter et al., 2018). During sinking, the POM is
50 generally colonized and concurrently, decomposed by particle-attached (PA) prokaryotes, releasing
51 dissolved organic matter (DOM) into ambient seawater, fueling the free-living (FL) microbes (Kiorboe
52 and Jackson, 2001; Azam and Malfatti, 2007). It has been revealed that PA and FL microbial
53 populations exhibit different taxonomic composition, physiology and metabolism, corresponding to
54 their lifestyle and ecological behavior. For example, PA bacteria, compared to FL bacteria, are often
55 larger in size (Alldredge et al., 1986; Zhang et al., 2007; Lauro et al., 2009) and metabolically more
56 active (Karner and Herdl, 1992; Grossart et al., 2007). They often maintain higher levels of
57 extracellular enzymes, adhesion proteins and antagonistic compounds, and are capable of degrading
58 high-molecular-weight (HMW) organic compounds (Smith et al., 1992; Crump et al., 1998; Long and
59 Azam, 2001; Mevel et al., 2008; Ganesh et al., 2014). Recently, examination of microbial
60 metagenomes suggests that there are notable differences between PA and FL assemblages in GC
61 content, effective genome size, general taxonomic composition and functional gene categories (Smith
62 et al., 2013). In particularly, some broad key functional gene categories involved in DOM utilization
63 (Poretsky et al., 2010; Rinta-Kanto et al., 2012) and specific functional gene groups linked to
64 successive decomposition of phytoplankton blooms (Teeling et al., 2012) are significantly different,
65 indicating the fundamental differences in survival strategies in relation to potentially available
66 substrates. It is further revealed that PA microbes generally have larger genomes with a variety of
67 metabolic and regulatory capabilities of utilizing compositionally varied organic matter, while the
68 genomes of FL microbes usually are smaller with streamlined metabolic and regulatory functions that
69 enable efficient adaption to oligotrophic conditions (Smith et al., 2013; Yawata et al., 2014; Yung et
70 al., 2016). Phylogenetically, PA and FL lineages generally exhibit different compositions. The PA
71 fraction is relatively enriched in members of *γ-Proteobacteria*, *Verrucomicrobia*, *Bacteroidetes*,
72 *Firmicutes* and *Planctomycetes* (Azam and Malfatti, 2007; Milici et al., 2016; Salazar et al., 2016;
73 Suter et al., 2018), while the FL assemblages are often populated by members of *α-Proteobacteria*
74 (SAR11 clade or *Ca.* Pelagibacter) and *Deferribacteres* (DeLong et al., 1993; Crespo et al., 2013;
75 Milici et al., 2017). However, significantly overlapped compositions of PA and FL microbial
76 communities were also reported in a few studies (Hollibaugh et al., 2000; Ghiglione et al., 2007;
77 Ortega-Retuerta et al., 2013; Rieck et al., 2015; Liu et al., 2018a). Actually, most members of the PA
78 and FL clades are generalists which switch their lifestyles via attachment and detachment to particles
79 (Crespo et al., 2013; Li et al., 2015). As revealed in many marine niches, *α-Proteobacteria*, *γ-*
80 *Proteobacteria* and *Bacteriodetes* are the major overlapped phyla in both PA and FL microbial
81 fractions (Yung et al., 2016).

82 Our current knowledge of PA and FL microbial populations largely relies on the upper photic ocean,
83 whereas little information is known from the deep dark ocean, which is the largest biome and
84 accommodates more than half of the ocean's microbes (Aristegui et al., 2009; Salazar et al., 2016).
85 Recently, a number of studies have revealed the PA and FL communities in the bathypelagic waters (Li

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86 et al., 2015; Salazar et al., 2015; Milici et al., 2017; Mestre et al., 2018) or the deepest abyssal and
87 hadal environments (Eloe et al., 2011; Tarn et al., 2016; Liu et al., 2018a). It is shown that PA and FL
88 bacterial communities in the deep ocean have clear differences in abundance and composition, in
89 addition to the detection of novel, unknown prokaryotic taxa. Furthermore, although archaea are a
90 major component of the marine ecosystem and play significant roles in the degradation of organic
91 materials (Iverson et al., 2012; Suzuki et al., 2017), PA and FL archaeal communities receive less
92 attention and little is known about them. Previous limited reports have observed controversial results,
93 as several studies showed that no obvious differences in archaeal community structures between PA
94 and FL assemblages (Galand et al., 2008; Eloe et al., 2011; Suzuki et al., 2017), while a clear
95 separation was found in recent reports (Tarn et al., 2016), with PA archaeal fraction dominated by
96 Marine Group II (MGII) and Marine Group III (MGII), and FL archaeal fraction by Marine Group I
97 (MGI) and anaerobic methane-oxidizing archaea (ANME). In brief, it is not well known about the
98 changes of PA and FL prokaryotes along vertical profiles of water column, from the surface to the
99 deep bathyal, abyssal and hadal depths.

100 In this study, we analyzed and compared microbial compositions between PA and FL fractions at
101 different depths along the vertical profile in the South China Sea (SCS). The SCS is a marginal sea
102 located in the Northwest Pacific with a maximal depth of approximately 5,380 m (Fig. S1). Our results
103 reveal diverse and significantly divergent microbial compositions in PA and FL fractions, and obvious
104 community stratification at different depths along the vertical profiles.

105 2. Materials and Methods

106 2.1 Sample collection and environmental parameter measurements

107 Seawater samples were collected from two stations, G3 station, depth of 4,039 m at 117° 00.131′ E,
108 16° 59.947′ N, and J5 station, depth of 4,301 m at 114° 00.209′ E, 13° 59.958′ N, located in the central
109 deep basin of the SCS during the Open Cruise of R/V *Dongfanghong* II from July 3 to 18, 2014 (Fig.
110 S1). A Sea-Bird CTD rosette sampler (SBE 911 plus) with 12 L Niskin bottles (Seattle, Washington,
111 USA) was used to collect seawater from six different depths (50, 200, 1,000, 2,000, 3,000, and 4,000
112 m) at each station.

113 Basic environmental parameters of the water column, including depth, salinity, temperature and
114 dissolved oxygen (DO) were obtained in situ using the conductivity-temperature-depth (CTD) profiler
115 and a DO sensor during the sampling. Once water samples were collected onboard, about 0.1 L of
116 seawater was taken immediately for pH measurement with a pH meter (Mettle Toledo Inc.,
117 Switzerland).

118 Approximately 8 L of seawater was filtered onboard through a 142 mm precombusted glass fiber
119 membrane (0.7 μm nominal pore size, Whatman, USA) under a gentle vacuum of <150 mm Hg for
120 particulate organic carbon (POC) analysis. The membranes were folded and stored at -20 °C until
121 further analysis. Then about 30 mL of filtered seawater of each sample was taken into 40 mL
122 precombusted EPA vials and immediately stored at -20 °C for DOC concentration measurement in the

123 land-based laboratory. About 200 ml filtered seawater at each depth was stored at -20 °C for analysis
124 of nutrients (NO_3^-/NO_2^-, dissolved inorganic phosphate and silicate). The remaining seawater was
125 stored at -20 °C for other analyses.

126 Approximately 4 L of seawater at each depth was filtered, first through a 47 mm polycarbonate (PC)
127 membrane of 3.0 μm nominal pore size (Millipore, USA) and subsequently, through a 47 mm PC
128 membrane of 0.22 μm nominal pore size (Millipore, USA) to collect the particulate-attached and free-
129 living microbes, respectively (Eloe et al., 2011). The membranes were then frozen at -80°C until
130 further microbial analysis.

131 Concentration of POC was determined with a PE2400 Series II CHNS/O analyzer (Perkin Elmer,
132 USA) (Chen et al., 2008). DOC concentration was measured using a Shimadzu TOC-V Analyzer
133 (Shimadzu Inc., Japan) (Meng et al., 2017). Nutrients were determined using a Four-channel
134 Continuous Flow Technicon AA3 Auto-Analyzer (Bran-Lube GmbH, German).

135 **2.2 DNA extraction**

136 DNA was extracted from the membranes mentioned above for microbial analysis following the SDS-
137 based extraction method. Briefly, 800 μl DNA extraction buffer (100 mM Tris-HCl, 100 mM sodium
138 EDTA, 100 mM sodium phosphate, 1.5 M NaCl, and 1% CTAB) was added into centrifuge tubes
139 containing the PC membranes. Tubes were frozen-thawed three times by alternating in liquid nitrogen
140 and a 65°C water bath. Then, 8 μL of 20 mg mL^{-1} proteinase K was added. The solution was incubated
141 at 37°C for 30 min. Then 80 μL of 10% SDS solution was added, and samples were incubated in a
142 65°C water bath for 2 h. DNA was extracted by adding water saturated phenol/chloroform/isoamyl
143 alcohol (25:24:1) and centrifuged at 12,000 ×g for 10 min. The aqueous phase was recovered and
144 equal volume of chloroform/isoamyl alcohol (24:1) was added again and samples were centrifuged at
145 12,000 ×g for 10 min. DNA was precipitated with 0.6 volume of cold isopropanol and 0.1 volume of
146 3M sodium acetate. Samples were incubated at -20°C for 1 h and centrifuged at 12,000 ×g for 10 min.
147 Finally, DNA pellets were cleaned with 70% cold ethanol, and suspended in 50 μL of sterile deionized
148 H_2O.

149 **2.3 Pyrosequencing and analysis of 16S rRNA gene sequence amplicons**

150 The total extracted DNA was quantified with a PicoGreen dsDNA Quantitation Kit (Life
151 Technologies, USA). The extracted DNA was used as the template for PCR amplification of bacterial
152 and archaeal 16S rRNA genes with the primers 27F (5′-AGA GTT TGA TCC TGG CTC AG-3′)/533R
153 (5′-TTA CCG CGG CTG CTG GCA C-3′) containing 10-nucleotide barcodes and Arch344F (5′-ACG
154 GGG YGC AGC AGG CGC GA-3′)/Arch915R (5′-GTG CTC CCC CGC CAA TTC CT-3′)
155 containing 8-nucleotide barcodes, respectively. The PCR reactions were held in a thermocycler (Bio-
156 Rad, USA) at 94°C for 5 min to denature the DNA with amplification proceeding for 25 cycles at
157 94°C for 50 s, 53°C for 50 s, and 72°C for 50 s. A final extension of 6 min at 72°C was added to
158 ensure complete amplification. The PCR products purified with the TaKaRa Agarose Gel DNA
159 Purification Kit (TaKaRa, Japan) were quantified using a NanoDrop ND-1000 device (NanoDrop,

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160 USA) and sent to the 454 FLX Titanium System (Roche, Switzerland) for sequencing.

161 Downstream analysis of the amplicon reads was performed using QIIME 1.9.1. Reads of low quality
162 were filtered out by enforcing the following quality control criteria: (1) exclusion of reads with one or
163 more ambiguous nucleotides; (2) exclusion of reads shorter than 200 bp; (3) exclusion of reads
164 containing homopolymers of 6 bp and more; (4) exclusion of reads with an average flowgram score of
165 25 in a quality window of 50 bp. The qualified reads were clustered into operational taxonomic units
166 (OTUs) based on their sequence similarity (97%), and a representative sequence from each OTU using
167 the longest picking method was picked for downstream analysis. Taxonomy assignment was
168 conducted using the RDP classifier against the SILVA 16S rRNA gene database (Version 119).
169 Chimeric reads were identified and excluded using ChimeraSlayer in the QIIME package after
170 alignment with PyNAST.

171 **2.4 Diversity estimators and statistical analyses of microbial communities**

172 Similarities among different microbial communities were determined using similarity matrices
173 generated according to the phylogenetic distance between reads (Unifrac distance), and beta diversity
174 of principal coordinates analysis (PCoA) was computed as components of the QIIME pipeline. The
175 correlation between the microbial community structures and environmental parameters was analyzed by
176 canonical correspondence analysis (CCA) and Mantel test. All statistical analyses were performed by R
177 project (v 3.2.1) using the Vegan and Agricolae packages.

178 To assess the preference of bacterial lineages for the PA or FL lifestyles, the odds ratio was calculated
179 for specific clades as below (Ganesh et al., 2014):

180 odds ratio = log 10 (relative abundance in PA fraction / relative abundance in FL fraction)

181 a positive odds ratio represents higher relative abundance in the PA fraction, while a negative odds ratio
182 means higher relative abundance in the FL fraction

183 **2.5 Quantification of microbial 16S rRNA gene and biomass estimation**

184 Bacterial and archaeal 16S rRNA genes for particle-attached and free-living fractions were quantified
185 by fluorescence quantitative real-time PCR (Applied Biosystems, UK) with the primer sets
186 eubac341f/518r (Dilly *et al.*, 2004) and arch344f/519r (Bano *et al.*, 2004), respectively. Amplification
187 was performed in 20 μl reaction mixture that consisted of 1 μl template DNA (1 to 10 ng), a 0.15 μM
188 concentration of each primer, and 10 μl of Power SYBR green PCR master mix (Applied Biosystems,
189 UK) with ROX and SYBR green I. The negative control and gel electrophoresis after each quantitative
190 PCR experiments were also carried out. For the negative control, only primer dimer with the length of
191 about 100 bp occurred, while for the samples, just one single and bright band (~ 200 bp) appeared.
192 Melting curve analysis was performed after amplification and cycle threshold was set automatically
193 using system 7500 software (1.3). The copy number of 16S rRNA gene was calculated by the average
194 of triplicate sample. Cell abundance was calculated assuming that every bacterial and archaeal cell

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195 contained 4.08 and 1.71 copies of 16S rRNA gene on average (Lee *et al.*, 2009).

196 **3. Results**

197 **3.1 Environmental parameters of the water columns**

198 Fundamental environmental parameters, including temperature, salinity, pH, DO and POC are listed in
199 Table 1. In general, they showed similar vertical trends with the normal pelagic ocean. Salinity
200 increased gradually from ~ 33.84 PSU at 50 m to ~ 34.52 at 200 m and 1,000 m, then maintained at
201 around 34.6 PSU at greater depths until 4,000 m. DO concentration was the highest (~ 204.5 μM) at
202 surface water, and decreased gradually to the lowest (~ 83.9 μM) at 1,000 m depth, then increased
203 gradually from ~ 102 μM at 2,000 m to ~ 113.5 μM at 4,000 m. Nitrite concentrations of the water
204 columns at all depths were below the detection limit. Concentrations of nitrate, phosphate, and silicate
205 were continuously increasing from the surface to 1,000 m depth, and then remained at relatively
206 constant levels (Table 1).

207 As expected, age of the seawater determined from $\Delta^{14}C_{DIC}$ was youngest at the surface and increased
208 with depth linearly, varying from about 106 to 1650 years. The upper water layers (50 m and 200 m)
209 from the two stations had the youngest and nearly the same ages, around 106 years. Ages of 1,000 m
210 and 2,000 m in G3 station were almost identical, around 1,180 years, and increased to 1,600 years at
211 3,000 m and 1,750 years at 4,000 m. By contrast, age of 1,000 m in J5 station was ~ 1,310 years, and
212 remained relatively stable below 1,000 m with the age of about 1,650 years (Table 1). DOC
213 concentrations ranged from 63.07 to 40.34 μmol/L, with the highest at the surface and lowest at the
214 deep. However, POC concentrations varied greatly between 0.5 and 2.1 μmol/L and showed great
215 variations. The POC concentrations were highest at 3,000 m of the G3 station (1.8 μmol/L) and at
216 1,000 m of the J5 station (2.1 μmol/L) (Table 1).

217 **3.2 Microbial cell abundances**

218 The estimated abundances of bacteria and archaea were about $10^6 \sim 10^9$ cells L^{-1} and $10^6 \sim 10^7$ cells L^{-1}
219 , respectively (Fig. 1). The FL bacterial fraction generally accommodated higher cell abundances
220 (varying from 0.62×10^7 to 1.65×10^8 cells L^{-1}), several times higher than their corresponding PA
221 fraction ($1.85 \times 10^6 \sim 1.70 \times 10^9$ cells L^{-1}). However, one lower abundance of FL bacterial fraction than
222 PA fraction was detected in the surface water (50 m) of the G3 station where PA bacterial abundance
223 was up to 1.23×10^9 cells L^{-1}, two orders of magnitude higher than that of the FL fraction (1.62×10^7
224 cells L^{-1}) (Fig. 1a). The upper seawater layers (50 m and 200 m) were also inhabited with the highest
225 abundance of archaea. FL archaeal fraction had the cell abundances between 1.01×10^6 and 8.62×10^6
226 cells L^{-1}, while that of PA archaeal fraction ranged from 1.28×10^5 to 6.50×10^7 cells L^{-1}. At other
227 depths, cell densities of archaeal FL fraction varied between $1.01 \sim 3.88 \times 10^6$ cells L^{-1} and $0.74 \sim 8.62$
228 $\times 10^6$ cells L^{-1} for G3 and J5 stations, respectively. PA archaeal fraction fluctuated between 1.90×10^5
229 and 5.54×10^6 cells L^{-1}. Similar to bacteria, the FL archaeal fractions usually showed higher cell
230 abundances than their PA fractions (Fig. 1b).

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231 **3.3 Estimation of microbial diversity**

232 Totally 92,041/81,761 and 73,094/97,611 valid sequences of bacterial 16S rRNA gene were obtained
233 for FL/PA fractions of G3 and J5 stations, respectively. The average valid sequences, including both
234 PA and FL bacteria were 14, 354 sequences per depth. Based on the 97% similarity, these FL and PA
235 bacterial sequences were defined into a total of 6,666 operational taxonomic units (OTUs). The
236 number of OTUs in the FL and PA bacterial fractions at each depth ranged from 214 to 1,470 (Table
237 S1). Correspondingly, 50,736/41,719 and 44,456/38,333 archaeal sequences were determined for
238 FL/PA archaea fractions of G3 and J5 stations. Attempt to determine PA archaeal sequence from 3,000
239 m depth of G3 station and 4,000 m depth of J5 station failed because of technical reasons. The average
240 number of archaeal sequences (including PA and FL archaea) were 7,966 sequences per depth. A total
241 of 1,071 archaeal OTUs were defined and the number of OTUs for the FL and PA archaeal fractions
242 varied from 82 to 275 (Table S2).

243 Shannon's diversity (H) and Chao1 were calculated to estimate microbial diversity of both PA and FL
244 fractions at all depths (Fig. 2 and Fig. S2). In most cases, the H indices of the bacterial FL fractions
245 were always higher than their PA counterparts at each depth (Fig. 2). H index of FL and PA bacterial
246 fractions gradually increased from 50 to 1,000 m, decreased from 1,000 to 2,000 m, and increased
247 again from 2,000 to 4,000 m (Fig. 2a). Similar to bacteria, FL archaea had higher H index values than
248 the PA fraction. The H index was usually the lowest at the surface, increased to the highest value at
249 200 m or 1,000 m and decreased continuously into the deep (Fig. 2b). Chao1 index showed similar
250 variation trends for both PA and FL microbial fractions (Fig. S2).

251 PCoA analysis revealed that there were significant differences in bacteria and archaea community
252 structures over the depth profiles and between the FL and PA fractions. Overall, three groups were
253 distinguished, the surficial 50 m group, the FL group, and the PA group (Fig. 3). One incompact group,
254 consisted exclusively of samples at 50 m depth, separated the microbes in the surface from those in the
255 rest of the water column of both stations, irrespective of microbial lifestyles (FL or PA). However, the
256 other two groups were separated mainly based on the FL and PA lifestyles. It is interesting to note that
257 the FL bacterial samples clustered into one group where samples were further partitioned with respect
258 to depth (Fig. 3a). Canonical correspondence analysis (CCA) showed that fundamental environmental
259 parameters including depth, DO, salinity, seawater age, DOC and POC concentration, and silicate
260 exerted potential impact on variations of FL and PA microbial communities along the water column
261 (Fig. 4, Fig. S3). Mantel test further indicated that all those factors , except POC concentration (P
262 =0.164), were the statistically significant variables associated with variation of PA and FL fractions (P
263 =0.001).

264 **3.4 Taxonomic compositions of the PA and FL bacterial and archaeal fractions**

265 Taxonomic compositions of FL and PA bacterial fractions and their relative abundances are presented
266 in Fig. 5. At phylum level, bacterial sequences were mainly assigned into *Proteobacteria* (α-, β-, γ-,
267 and δ-), *Actinobacteria*, *Cyanobacteria*, *Planctomycetes*, *Bacteroidetes*, *Marinimicrobia* (SAR406
268 clade), *Chloroflexi*, *Firmicutes*, *Gemmatimonadetes*, *Gracilibacteria* and *Verrucomirobia*. The taxa at

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269 family level with relatively high abundances on average in either PA or FL fraction were further shown
270 in Fig. 6.

271 It is clear that α- and *γ-Proteobacteria* were the dominant lineages in both the FL and PA fractions at
272 nearly all depths. In most cases, the sum of α- and *γ-Proteobacteria* accounted for ~ 40% to nearly
273 90%. Moreover, their relative abundances in different PA and FL fractions and different stations also
274 varied widely. Within the *α-Proteobacteria*, the dominant families included *Methylobacteriaceae*,
275 *Phyllobacteriaceae*, *Rhodobacteraceae* and *Erythrobacteraceae* (Fig. 6). Members of the families
276 *Methylobacteriaceae* and *Erythrobacteraceae* occurred commonly in both fractions at almost all
277 depths but usually with higher proportions in PA fractions. The family *Rhodobacteraceae* occurred
278 commonly in both fractions at every depth (1 % ~ 20%), while the *Phyllobacteriaceae* was dominantly
279 distributed in the PA fraction of 2,000 m depth of J5 station with > 60% proportions. In addition,
280 another important lineage within *α-Proteobacteria* is SAR11 clade (now named as *Pelagibacterales*)
281 (Grote et al., 2012). It was clearly revealed that SAR11 clade showed relative higher abundances in FL
282 fractions than PA fractions. Moreover, at depths above 1000 m, SAR11 clade had a far higher
283 proportion than the deep ocean and the maximum levels occurred at 200 m depth (20% ~ 24%) (Fig. 6,
284 Table S1). *γ-Proteobacteria* is another lineage with the highest abundance overall. Its relative
285 abundances change significantly with depths and in different fractions. The minimum abundances
286 were only 1% ~ 5%, while the maximum were up to 73% ~ 80% (Fig. 5 and Table S1). Moreover, G3
287 station generally had higher *γ-proteobacteria* proportions than that of J5 station on average. As shown
288 in Fig. 6, although sequences of *γ-Proteobacteria* were classified into multiple families, actually only
289 two families *Alteromonadaceae* and *Pseudoalteromonaodaceae* exhibited dominant prevalence in the
290 bacterial populations. The *Pseudoalteromodaceae* populated predominantly the PA fractions in 50 m
291 and 200 m depths (66% ~ 75%), while the *Alteromonadaceae* mainly dominated the PA fractions in
292 the deep water, particularly at 2,000 m and 3,000 m depths. *δ-Proteobacteria* also had a common
293 distribution in both fractions of all depths, usually accounting for less than 10% proportions in most
294 samples (Fig. 5), and SAR324 clade members contributed significantly to the dominance of the *δ-*
295 *Proteobacteria* (Fig. 6). *Actinobacteria* and *Cyanobacteria* were abundantly distributed only in the
296 surficial 50 m depth, and by sharp contrast, their proportions in other depths were less than 5%. Other
297 bacterial lineages which had a wide distribution in all depths but only with minor abundances in both
298 fractions included *Planctomycetes*, *Bacteroidetes*, *Marinimicrobia* (SAR406 clade), *Chloroflexi*, *β-*
299 *Proteobacteria*, *Firmicutes*, *Gemmatimonadetes* and *Verrucomicrobia* (Fig. S4).

300 Majority of archaeal amplicons were mainly fallen into several uncultured taxonomic lineages (Fig. 7
301 and Fig. S5). Both FL and PA archaeal fractions at all depths were principally populated by Marine
302 Group I (MGI) of the *Thaumarchaeota* and Marine Group II (MGII) of the *Euryarchaeata*. Members
303 from MGI and MGII lineages generally contributed more than 80% relative abundances in their
304 respective clone libraries. MGI was always one of the most abundant clades along the vertical profiles
305 except in the topmost FL and PA fractions. Within the MGI group, only a small part of members were
306 annotated into the cultured genus *Nitrosopumilus* and *Candidatus* Nitrosopelagicus, while the majority
307 of them fell into those uncultured subclades (Table S2). MGII clade exhibited a wide distribution
308 along the water columns, and it usually accounted for the large proportions in both archaeal size
309 fractions. The photic layer (~ 50 m depth) contained the highest abundances of MGII clade,
310 particularly in FL fractions with up to ~ 80% proportions. By sharp contrast, the lowest abundances of
311 MGII occurred at 2,000 m (G3 station) and 3,000 m (J5 station) depths, making up <20% percentages.

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312 The third most abundant clade overall is Marine Group III (MGIII) of the *Euryarchaeata*. MGIII
313 representatives were mainly dispersed in the FL fractions with 5% ~ 18% abundances, while they were
314 absent from most of the PA fractions. The order *Methanosarcinales* of *Euryarchaeata* was detected
315 commonly in most PA fractions, but it had the higher abundance only in the upmost 50 m depth (~
316 29.7%) (Fig. 7). Another sample accommodating relatively much *Methanosarcinales* was the PA
317 faction of 3,000 m in J5 station with 9.1% proportion. Within the *Euryarchaeata*, another clade of
318 methanogens, *Methanobacteriales*, was also detected from both size fractions but with low relative
319 abundances (<5%) (Fig. 7, Fig. S5, Table S2). In addition, other archaeal lineages included
320 *Woesearchaeota* (formerly known as the DHVEG-6 group), Miscellancous Crenarchaeotic Group
321 (MCG, now named as *Bathyarchaeota*), the *Halobacteriales* of the *Euryarchaeata* and Marine Benthic
322 Group A (MBG-A) of the *Thaumarchaeota*. They just provided a limited contribution to archaeal
323 populations (Fig. S5).

324 **3.5 Bacterial preference to PA or FL lifestyles**

325 Odds ratio was used to assess the preference of bacterial taxonomic lineages to the PA or FL lifestyle.
326 A positive odds ratio indicates PA preference or higher abundance in the PA fraction, while a negative
327 value suggests FL preference or higher abundance in the FL fraction. The bacterial lineages
328 dominating the PA fractions come exclusively from *α*- and *γ-Proteobacteria* (Fig. 6). At family level,
329 the dominant clades comprised of the *Phyllobacteriaceae*, *Methylobacteriaceae*, *Erythrobacteraceae*,
330 *Rhodobacteraceae* (*α-Proteobacteria*), and *Pseudoalteromonadaceae*, *Alteromonadaceae* (*γ-*
331 *Proteobacteria)* (Fig. 6) and they show a clear preference to PA lifestyle at different depths (Fig. 8).
332 Except for these prevalent families, there is a wide range of lineages also showing preference to
333 particle-attached lifestyle but with relatively low abundance (Fig. 6 and Fig. 8). These minor lineages
334 are mainly populated by the families *Oceanospirillaceae* and *Alcanivoracaceae* (*γ-Proteobacteria*),
335 *Sandaracinaceae* and *Bdellovibrionaceae* (*δ-Proteobacteria*), *Burkholderiaceae* (*β-Proteobacteria*),
336 *Saprospiraceae* (*Bacteroidetes*), *Planctomycetaceae* and *Phycisphaeraceae* (*Planctomycetes*),
337 SAR406 clade (*Marinimicrobia*), *Cryomorphaceae* and *Flavobacteriaceae* (*Bacteroidetes*),
338 *Propionibacteriaceae*, *Nocardioidaceae* and *Corynebacteriaceae* (*Actinobacteria*).

339 The predominant lineages of FL fractions mainly consisted of members of *Actinobacteria*,
340 *Cyanobacteria*, *Bacteroidetes*, *α*- and δ-*Proteobacteria*, as shown in Fig.5. At family level, the
341 phylogenetic lineages with showing a FL preference are mainly populated by the families OM1 clade
342 and Sva0996 marine group (*Actinobacteria*), SAR324 clade and *Nitrospinaceae* (*δ-Proteobacteria*),
343 *Cyanobacteria*, *Comamonadaceae* (*β-Proteobacteria*), *Erythrobacteraceae*, SAR11 clade,
344 *Methylobacteriaceae*, *Bradyrhizobiaceae*, *Rhodobacteraceae*, *Hyphomonadaceae* (α-Proteobacteria),
345 *Phycisphaeraceae* and *Phycisphaeraceae* (*Planctomycetes*), SAR406 clade, *Saprospiraceae*,
346 *Chitinophagaceae*, *Cryomorphaceae*, *Flavobacteriaceae*, *Flammeovirgaceae* (Bacteroidetes) (Fig. 8).
347 However, compared with counterparts of PA fractions, their abundances in FL fractions are low
348 without absolute dominance.

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349 ## 4. Discussion

350 ### 4.1 Comparison of microbial abundance and diversity between PA and FL fractions

351 PA bacterial and archaeal fractions show generally lower abundance and taxonomic richness than their
352 FL counterparts and constitute a small fraction of the total abundances. Our results are consistent in
353 principle with previous reports on various pelagic environments, in either the euphotic zone, twilight
354 or the dark deep ocean (Turley and Stutt, 2000; Simon et al., 2002; Ghiglione et al., 2007; Rieck et al.,
355 2015). However, in some eutrophic and notably particle-rich marine ecosystems, for example, marine
356 snow or estuaries, PA bacterial fractions were present in higher local concentrations and greater
357 diversity than FL bacteria (Caron et al., 1982; Karner and Herndl, 1992; Turley and Mackie, 1994;
358 Garneau et al., 2009). In upper photic zone, PA bacterial abundance and their contribution to total
359 bacterial biomass are highly variable, and depend largely on the quantity and quality of suspended
360 organic particles (Cammen and Walker, 1982; Simon et al., 2002; Doxaran et al., 2012). This is indeed
361 the case in the South China Sea. As shown in Fig. 1, at 50 m and 200 m depths of G3 station, PA
362 bacterial abundances outnumbered FL bacteria by nearly 2 ~ 100 times, whereas J5 station has an
363 opposite trend. However, as shown in Table 1, these two stations have almost the same environmental
364 parameters, particularly in POC concentrations. One possibility may be that G3 and J5 have different
365 POC compositions, attributable to different origins of organic matter. Although bacteria attaching to
366 particles are of relatively lower abundance compared to free-living cells in the pelagic ocean, they are
367 consistently metabolically more active with higher extracellular enzymatic activities (Karner and
368 Herndl, 1992) and cell-specific thymidine incorporation rates (Turley and Mackie, 1994; Turly and
369 Stutt, 2000). Therefore, PA bacteria often play a comparable role to free-living bacteria in hydrolysis
370 or decomposition of marine organic matter, biomass production and carbon cycling (Griffith et al.,
371 1994; Turly and Stutt, 2000; Liu et al., 2015). The decline of bacterial abundance and richness along
372 the depth profile is largely owing to the gradual decreasing availability of usable organic carbon
373 (Smith, 1992; Turly and Stutt, 2000; Jiao et al., 2014). In contrast, archaea are commonly much lower
374 in cell abundance and community diversity compared with their bacterial counterparts at the same
375 depths (Fig. 1-2 and Fig. S2). The relative abundance of archaeal populations in total prokaryotes
376 increases gradually with depth, indicative of a potential rising impact on biogeochemical cycle in
377 marine environments. In addition, pronounced distinction in microbial community structures of PA
378 and FL assemblages were observed along the depth profile, which were well supported by results of
379 statistical analyses (Fig. 3). It is expectable that PA fraction differs taxonomically from FL fraction,
380 considering their discrepant activity patterns for survival. Related discussions are shown below.

381 ### 4.2 Environmental factors potentially shaping microbial community structure

382 Several environmental parameters were supposed to play a pivotal role in structuring microbial
383 communities of seawater. Depth, together with age and salinity of water mass, are a key subset of
384 environmental drivers (Fig. 4). Recent studies have shown that microbial populations in the meso-/
385 bathypelagic ocean are largely dissimilar to those of the epipelagic zone (Salazar et al., 2015; Milici et
386 al., 2017; Liu et al., 2018a), indicative of a crucial environmental selection process exerted by depth.

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387 In our study, PCoA analysis revealed that PA and FL fractions from the surficial zone (50 m) were
388 clustered into a separate but relatively loose group distant from other depths (Fig. 3), indicative of the
389 influence imposed from depth in shaping microbial community structures. Several bacterial lineages,
390 including *Cyanobacteria*, *Actinobacteria*, *δ-Proteobacteria*, *Marinimicrobia* (SAR406 clade) and
391 *Firmicutes* with distinct distributing stratification contribute to this dissimilarity. *Cyanobacteria* and
392 *Actinobacteria* belong to typical phototrophs (Mizuno et al., 2015) and they are prevalently distributed
393 in euphotic zones. By contrast, δ-proteobacterial SAR324 clade, as shown in our results, are primarily
394 found in mesopelagic waters (200 ~ 1,000 m) (Fuhrman and Davis, 1997; Wright et al., 1997).
395 SAR406 clade has a ubiquitous distribution across diverse marine niches, however, its high abundance
396 always occurs within the mesopelagic zones, ~ five times or higher than in surface ocean (Yilmaz et
397 al., 2016). Archaeal population components also reflect the impaction of depth. Euphotic zones hold
398 less abundant thaumarchaeotal MGI and more euryarchaeotal *Methanosarcinales* and *Woesearchaeota*
399 (Fig. 7), while marine thaumarchaeotal groups are more abundant in meso- and bathypelagic waters
400 (Karner et al., 2001; Mincer et al., 2007; Varela et al., 2008). In addition, Salazar et al. (2016) found
401 that sampling depth appears to have a more direct impact on free-living bacterial communities. Our
402 results are highly consistent with this observation in that FL bacterial fractions from the same depth
403 grouped together irrespective of their sampling locations (G3 or J5 station) (Fig. 3a).

404 DO concentration is observed to strongly affect particle flux and particle transfer efficiency from
405 euphotic zone to the deep sea since remineralization of organic particles appears to be oxygen-
406 dependent (Laufkotter et al., 2017; Cram et al., 2018). It is considered as one of the best subsets of
407 environmental variables for shaping the compositions of particle-attached bacterial assemblages
408 (Salazar et al., 2016). Some taxonomic lineages are directly affected by oxygen. For example, a most
409 recent study found that oxygen is one of the key factors driving the distribution and evolutionary
410 diversity of *Woesearchaeota* (Liu et al., 2018b). POC and DOC can be substrates for both PA and FL
411 communities, respectively (Azam and Malfatti, 2007; Zhang et al., 2016; Liu et al., 2019). However,
412 POC concentration in the present study is not statistically significantly correlated with either bacterial
413 or archaeal community abundances ($P > 0.05$). We hypothesize that the quality rather than the quantity
414 of POC imposes a decisive influence on microbial populations, especially in the deep, dark ocean.
415 During the POC sinking from surface through the water column, the labile organic matter becomes
416 increasingly decomposed, while the more refractory material remains and resists degradation (Simon
417 et al., 2002). In such cases, utilization of refractory POC by microorganisms depends on the quality of
418 POC. Among common nutrients, silicate exhibited statistically significant correlation with microbial
419 distributions (Fig. S3), and this is out of our expectation because the SCS generally shows N- or P-
420 limit in phytoplankton production (Wu et al., 2003; Chen et al., 2004). However, recent research found
421 that near the sampling site of this study, there is a clear silicon deficiency in the euphotic zones
422 shallower than 75 m (Huang et al., 2015), which directly influences the diversity and biomass of
423 phytoplankton, and consequently, the quantity and quality of POM transported to the deep along the
424 vertical water columns, and finally exerts a potential impact on microbial communities. Actually,
425 microbial community structure and their distribution along the water column profile are a
426 comprehensive combination impacted by multiple environmental variables.

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427 **4.3 Specialist or generalist for PA and FL lifestyle: clues from bacterial community compositions**

428 It was suggested that PA and FL bacterial fractions accommodated different phylogenetic
429 compositions along the depth profiles (Fig. 3), consistent with previous reports in various marine
430 niches (Acinas et al., 1997; Moeseneder et al., 2001; Ghiglione et al., 2009; Salazar et al., 2015).
431 However, in most cases, taxonomic compositional disparity between the two filtration fractions does
432 not seem much apparent at phylum level (Fig. 5). Actually, a few studies also confirmed that at high
433 taxonomic ranks, bacteria show conserved lifestyles either in association with particles or as free-
434 living microorganism (Eloe et al., 2011; Salazar et al., 2015; Liu et al., 2018a). The pronounced
435 contrast in population compositions of the two filtration fractions was unveiled only at greater
436 taxonomic level and a considerable number of phylogenetic taxa exhibited different preferences to PA
437 or FL lifestyles. As shown in Fig.5 and Fig.6, as the most abundant members, *α*- and *γ-Proteobacteria*
438 occurred prevalently in both filtration fractions, but at the family level, most of predominant bacterial
439 lineages of PA and FL fractions were significantly divergent, indicating their preference to different
440 microhabitats shaped by organic particles and environmental parameters. The dominant lineages in PA
441 fractions were mainly associated with the families *Pseudoalteromonadaceae* and *Alteromonadaceae*
442 within *γ-Proteobacteria*, and the *Methylobacteriaceae* within *α-Proteobacteria*. These *γ-*
443 *proteobacterial* members are usually retrieved from diverse marine habitats as the typical PA clades,
444 and they are believed to have the abilities to degrade/utilize HMW organic compounds with higher
445 nutrient requirements (DeLong et al., 1993; Crespo et al., 2013). The adhesion to particles could make
446 them increase nutrients acquisition and avoid the nutrient-depleted conditions (Crespo et al., 2013). By
447 contrast, members of *α-Proteobacteria* are rarely reported as the dominant lineages of PA fraction or
448 particle-attached preference (Crespo et al., 2013; Rieck et al., 2015; Suzuki et al., 2017), which is
449 inconsistent with our results revealing α-proteobacterial lineages frequently prevail as PA members.
450 Further phylogenetic assignment revealed that the majority of α-proteobacterial PA members
451 exclusively belong to the genus *Methylobacterium* which are strictly aerobic, facultatively
452 methylotrophic bacteria, and can grow on a wide range of carbon compounds (Green, 2006). They
453 probably benefit from the particle-attached lifestyle, making their high requirements for organic
454 matters easily to achieve. Compared with bacterial PA counterparts, FL bacterial communities are
455 more diverse, and dominant populations are scattered in more phylogenetic taxa with relatively
456 homogeneous proportions. Among the predominant lineages, the actinobacterial OM1 cade and
457 cyanobacteria dominantly govern the upper surficial waters (Fig. 6), likely attributed to their
458 phototrophic behaviors. Although actinobacteria are recognized as ubiquitous members of marine
459 bacterioplankton (Giovannoni and Stingl, 2005), they are scarcely reported with predominance (Milici
460 et al., 2016a). Recently, Ghai et al. (2013) revealed the OM1 clade members possess the smallest cell
461 sizes with streamlined genome, representing a typical adaption to oligotrophic condition (Giovannoni
462 et al., 2014) which well agrees with the oligotrophic environments in the SCS (li). Other predominant
463 FL lineages include α-proteobacterial SAR11 clade, δ-proteobacterial SAR324 clade, and
464 *Marinimicrobia* (SAR406 clade), all usually being the most ubiquitous free-living bacterial lineages
465 and dominantly distributed in epi- and mesopelagic zones (Grote et al., 2012; Tarn et al., 2016; Yilmaz
466 et al., 2016; Milici et al., 2017; Liu et al., 2018a). Genomic information underlines that although these
467 clades have a flexible metabolism utilizing multiple hydrocarbon compounds, they generally lack of
468 carbohydrate-active enzyme genes for the attachment to and the degradation of particulate organic
469 matter (Peoples et al., 2018), consistent with their preference to free-living lifestyle rather than

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470 particle-attachment (Eloe et al., 2011; Salazar et al., 2015; Tarn et al., 2016).

471 In addition to those predominant lineages mentioned above, there are a couple of bacterial taxa
472 showing evident PA or FL preferences. At ~ family level, these PA- or FL-preferred taxa are well
473 hinted by their odds ratio between PA and FL fractions. These bacterial lineages are characterized by
474 low abundances or occasional occurrence in water columns (Fig. 6) but high odds ratio (absolute
475 value) (Fig. 8), indicating their strong preferential divergence in the two size fractions. As shown in
476 Fig. 8, such families with PA preference were mainly derived from the phyla/classes *Actinobacteria*
477 and *γ-Proteobacteria*, together with several families from *Bacteroidetes*, *Planctomycetes* and *δ-*
478 *Proteobacteria*, while FL-preferred lineages are mostly distributed within *α-*, *γ-Proteobacteria*,
479 *Actinobacteria* and *Bacteroidetes,* along with certain groups of *β-*, *δ-Proteobacteria*, *Planctomycetes*
480 and *Firmicutes*. The majority of these lineages are recorded consistently about their PA- or FL
481 preferences in previous studies, and commonly possess the ability to hydrolyze and utilize complex
482 carbon sources. Although their abundance is low, these minor populations can still effectively
483 influence local microhabitats because of their high specificity for organics. In contrast, there are still
484 some populations which are scarcely reported. For example, Sva0996 marine group, an actinobacterial
485 group, is retrieved occasionally from marine sediments and upper ocean (Bano and Hollibaugh, 2002;
486 Wang et al., 2018). Orsi et al. (2016) first found this group prefers to free-living lifestyle in upper
487 seawater and have the ability to assimilate phytoplankton-derived dissolved protein. Our present
488 results suggest that Sva0996 group are flexible to adapt PA or FL lifestyles at the surface seawater
489 because two lifestyles occur concurrently. Moreover, the distribution of Sva0996 group is not
490 restricted only in upper photic ocean, and they can survive in meso- and bathypelagic seawaters with
491 the significant preference for free-living lifestyle (odds ratio for FL-preference is up to 3.93).
492 However, nothing is available to elaborate the selection between PA and FL lifestyles due to lack of
493 pure culture or their genome information.

494 A high proportion of bacterial lineages are revealed to co-occur in both PA and FL fractions. At OTU
495 level, more than 1/3 of total OTU numbers (2402 out of 6964 OTUs) are shared by PA and FL
496 fractions (Fig. 9). Phylogenetically, these PA/FL-shared OTUs are mainly fallen into *α-*, *γ-*, *δ-*
497 *Proteobacteria*, *Planctomycetes*, *Bacteroidetes* and *Actinobacteria*. Moreover, taxonomic components
498 of PA/FL-shared OTUs at different levels are primarily similar to those of OTUs retrieved exclusively
499 from PA fractions or FL fractions (Table S1, Fig. 9), indicating that a considerable amount of bacterial
500 lineages potentially have PA and FL dual lifestyle strategies (Bauer et al., 2006; Gonzalez et al., 2008).
501 On the one hand, a few lineages such as *Flavobacteriaceae*, *Planctomycetaceae*, *Rhodobacteraceae*,
502 *Erythrobacteraceae*, *Burkholderiaceae*, *Nitrospinaceae*, SAR324 clade, *Alteromonadaceae*,
503 *Pseudomonadaceae* and *Salinisphaeraceae* co-occur in PA and FL fractions at least at one of the same
504 depths with approximately equivalent abundances. In such cases, their odds ratios are close to zero or
505 minor range, indicating that bacteria are able to employ two different survival strategies at the same
506 time. On the other hand, some taxa including the families Sva0996 marine group, *Flavobacteriaceae*,
507 *Phycisphaeraceae*, *Rhodobacteraceae Methylobacteriaceae*, *Erythrobacteraceae*,
508 *Pseudoalteromonadaceae*, *Halomonadaceae* and *Moraxellaceae*, show divergent preferences to PA or
509 FL lifestyles at different depths or different locations. This is clearly evident by the shift or conversion
510 of their odds ratios at different depths along the vertical profiles of water column (Fig. 9), indicative of
511 their different adaption tactics to different environments. One possible explanation is that most of the
512 marine bacteria are generalists with dual life strategies (Bauer et al., 2006; Gonzalez et al., 2008), and

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513 able to grow in suspension as well as on particles (Lee et al., 2004; Grossart et al., 2006, 2010). For
514 instance, PA bacteria must be capable of surviving freely in the water column to migrate and colonize
515 new organic particles (Ghiglione et al., 2007; Crespo et al., 2013). Bacterial populations may switch
516 their lifestyles between free-living and particle-attachment, depending on substrate availability and the
517 surrounding chemical triggers (Grossart, 2010; D'Ambrosio et al., 2014). To date, one exception, the
518 genus *Scalindua* in the *Planctomycetes* phylum, which is a known marine chemoautotroph involved in
519 anammox, is exclusively observed in FL fractions in previous studies (Fuchsman et al., 2012; Ganesh
520 et al., 2014; Suter et al., 2018). However, it is absent from our water columns.

521 **4.4 Archaeal community preferences to PA and FL lifestyles**

522 Samples of PA and FL archaeal fractions were also separated into different groups by statistical
523 analysis (Fig. 3b), indicating their phylogenetically different community structures. However, because
524 most of OTUs belonged to uncultured archaeon, it is impossible to assign them into taxonomic
525 lineages at finer level. Thus, the distinction of archaeal population compositions between PA and FL
526 fractions was unnoticeable (Fig. 7). The MGI and MGII are the most abundant taxa in both PA and FL
527 archaeal fractions. The MGI thaumarchaea are one of the most abundant and cosmopolitan
528 chemolithoautotrophs in the dark ocean (Karner et al., 2001) and responsible for much of the ammonia
529 oxidation in this environment for their common metabolism of aerobic ammonia oxidation.
530 Corresponding to their autotrophic metabolism, MGI generally exhibit free-living preference and are
531 the prevalent archaeal taxa in free-living fractions below euphotic zone (Smith et al., 2013; Salazar et
532 al., 2015; Tarn et al., 2016). However, different from our results, a few studies showed that MGI
533 dominated both the PA and FL archaeal populations and no obvious distinction was observed in
534 abundance and ecotype of MGI (Eloe et al., 2011; Jin et al., 2018). To date, only a few pure cultures of
535 marine MGI, small rods with a diameter of 0.15~0.26 μm and a length of 0.5 ~ 1.59 μm and no
536 flagella were observed (Könneke et al., 2005; Qin et al., 2014), suggesting that their occurrence in PA
537 fraction is not caused by pore size of filter to fractionate different assemblages. One possibility is that
538 decomposition of organic particles continuously releases ammonia and MGI can easily acquire high
539 concentrations of ammonia by attaching to particles, especially in oligotrophic area. Recent studies
540 provide another explanation to particle-attached MGI that some MGI cultures are obligate mixotrophy
541 that rely on uptake and assimilation of organic compounds (Alonso-Sáez et al., 2012; Qin et al., 2014).
542 In such case, PA lifestyle is in favor of their nutrient requirements. MGII have a wide distribution in
543 the open ocean and as shown in our results, they are the dominant archaeal community generally
544 within the upper euphotic zone (Massana et al., 2000; Martin-Cuadrado et al., 2015). Recently, they
545 have been found, however, to be also abundant in deep-sea waters (Baker et al., 2013; Tarn et al.,
546 2016; Liu et al., 2018a), showing a wider adaption to diverse marine habitats in addition to the photic
547 zone. MGII are thought to be heterotrophs, and have the ability of degrading proteins and lipids
548 (Iverson et al., 2012; Orsi et al., 2015). Metagenomes revealed a number of genes encoding cell
549 adhesion, degradation of high molecular weight organic matter and photoheterotrophy (Rinke et al.,
550 2019; Tully et al., 2019), evidencing their potentiality to utilize organic particles as important growth
551 substrates. All these findings imply MGII's preference to particle-attached lifestyle, and they are
552 frequently detected from PA fractions in size-fractionated studies (Iverson et al., 2012; Orsi et al.,
553 2015; Tran et al., 2016). However, in a few studies including our present study, MGII are also
554 identified as the dominant archaeal components from FL fractions, with equal or even more abundance

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555 than PA fractions (Fig. 7). Further studies confirm that genome contents and populations of free-living
556 MGII are distinct from those of particle-attached MGII (Orsi et al., 2015; Rinke et al., 2019),
557 suggesting their metabolic evolution and adjustment to niche partitioning. In addition, MGIII also
558 occurred commonly in both fractions (Fig. 7). MGIII are usually retrieved as minor components of
559 deep mesopelagic and bathypelagic communities (Galand et al., 2009; Tarn et al., 2016). Like MGII,
560 to date no cultured representative of MGIII leads to little is known about their ecological and
561 physiological characteristics. Function prediction from metagenomes suggest that MGIII are aerobic
562 (or facultative anaerobic), motile, and heterotrophic, and potentially can utilize lipid, proteins and
563 polysaccharides as major energy source (Martin-Cuadrado et al., 2008; Haro-Moreno et al., 2017).
564 Recently, a novel lineage of MGIII genomes preferring to live in the photic zone was recovered,
565 consistent with previous few studies and our present results in which MGIII populations are obtained
566 from the euphotic zone with a considerable abundance (Galand et al., 2009, 2010). Moreover, recent
567 findings also indicate that MGIII are inclined to be attached to other microorganisms (particle-attached
568 preference) and only sporadically be released to the surrounding environments (free-living lifestyle)
569 (Haro-Moreno et al., 2017).

570 In addition, there are several other archaeal lineages with remarkable differences in abundance
571 between PA and FL fractions. The order *Methanosarcinales* and *Methanobacteriales*, affiliated to the
572 phylum *Euryarchaeota* and retrieved exclusively from PA fractions (Fig. 7), belong to strictly
573 anaerobic methanogens. Their preference to particle-attached lifestyle in water column environments
574 is intelligibly convinced. Within normal water column, seawater is oxic in spite of low oxygen
575 concentration and only on or inside the particles where heterotrophic microbes attach and digest
576 organic matter using oxygen as electron acceptor, local anoxic niches are developed with the
577 exhaustion of ambient oxygen and become suitable for the survival of methanogens. Members of the
578 *Woesearchaeota* were abundantly derived from the PA fraction of the upper seawater. In marine
579 environments, *Woesearchaeota* are distributed restrictively in marine sediments (Lipsewers et al.,
580 2018) or deep-sea hydrothermal vents (Takai et al., 1999), and are scarcely detected from pelagic
581 seawater masses. Recent studies suggest that woesearchaeotal lineages are mostly retrieved from
582 anoxic environments (Castelle et al., 2015; Liu et al., 2018b). Moreover, genomic metabolic analysis
583 indicates *Woesearchaeota* have an anaerobic heterotrophic lifestyle with conspicuous metabolic
584 deficiencies (Probst et al., 2017; Liu et al., 2018b), implying a potential syntrophic or mutualistic
585 partnership with other organisms (Castelle et al., 2015; Liu et al., 2018b). It is further demonstrated
586 that *Woesearchaeota* tend to co-occur with typical anaerobic methanogens from the *Methanomicrobia*
587 and *Methanobacteria* constituting a potential consortia (Liu et al., 2018b). In our present results, at
588 several depths, the *Methanosarcinales* of the *Methanomicrobia* and the *Methanobacteriales* of the
589 *Methanobacteria*, together with *Woesearchaeota*, were detected concurrently, implying to a large
590 extent their potential syntrophic partnership.

591 **4.5 Potential vertical connectivity of microbial populations along the depth profile**

592 Microbial distribution at different depths to a certain extent implicates their potential vertical
593 connectivity along the water column profile. It has been suggested that the sinking of organic particles
594 formed in upper euphotic zone is a main vector in transferring prokaryotes from the surficial ocean to
595 deep waters (Mestre et al., 2018). Those surficial lineages, usually belonging to putative

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596 photosynthetic/photoheterotrophic, Bchl a-containing microorganism or strict epipelagic/euphotic
597 inhabitants, are reliable indicators to hint their downward transportation if they are detected from
598 meso- or bathypelagic waters. For example, cyanobacteria are typical photosynthetic bacteria and their
599 distribution is thought to be confined to the euphotic zone, with commonly observed maximum depths
600 of about 150 ~ 200 m. In the present study, however, cyanobacterial lineages were retrieved
601 throughout the whole water column (Fig. 5 and Fig. 6), especially at 4,000 m depth where
602 cyanobacteria account for nearly 12% of the PA communities. Although a recent study revealed that
603 cyanobacteria can dominate the deep continental subsurface microbial communities with the potential
604 for a hydrogen-based lithoautotrophic metabolism instead of photosynthesis (Puente-Sanchez et al.,
605 2018), these indigenous deep cyanobacteria were classified into the genera *Calothrix*, *Microcoleus* and
606 *Chroococcidiopsis*, phylogenetically different from those prevailing in our study (*Prochlorococcus*,
607 *Synechococcus*). Jiao et al. (2014) observed substantial *Prochlorococcus* populations at 1,500 m depth
608 in the South China Sea, and suggested that multiple physical processes, including internal solitary
609 waves and mesoscale eddies were responsible for the occurrence of these “deep *Prochlorococcus*”.
610 However, in our study area, ages of seawater increase gradually from the surface to the deep along the
611 water column profile in a normal time sequence (Table 1), refuting this possibility. Thus, a reasonable
612 postulation here is that the sinking particles function as vectors and convey cyanobacteria attaching on
613 particle surfaces from epipelagic zone into deep-sea waters. Likewise, members of the family
614 *Erythrobacteraceae*, which are largely represented by OTUs within the genus *Erythrobacter*, are also
615 present abundantly in both PA and FL fractions at 4,000 m depth (Fig. 6). *Erythrobacter* spp. belong to
616 putative Bchl a-containing, aerobic anoxygenic photoheterotrophic bacteria and are thought to be
617 distributed only in the euphotic upper ocean (Kolber et al., 2000; Koblížek et al., 2003). SAR11 clade,
618 are potentially photoheterotrophic (Gomez-Pereira et al., 2013; Evans et al., 2015) and ubiquitous in
619 global photic zones as one of the most abundant bacteria (Morris et al., 2002). We observed that
620 members of SAR11 clade are distributed across the whole water columns, especially in mesopelagic
621 aphotic depths with relatively high proportions. Other lineages specializing in inhabiting surface
622 seawater but was also retrieved from the deep ocean include γ-proteobacterial SAR86 clade, SAR116
623 clade of marine Roseobacter and SAR202 clade within *Chloroflexi*. The majority of the OTUs within
624 these “surface lineages” have been retrieved from the meso-/bathypelagic ocean and can be traced
625 back simultaneously to those present in surface waters, suggesting their potential origin from the upper
626 epipelagic zones.

627 5. Conclusions

628 In this study, we systematically compared bacterial and archaeal community structures within two
629 different filtration fractions representing particle-attached and free-living lifestyles at different depths
630 in the South China Sea. As revealed in previous studies, whatever bacteria or archaea, the FL fractions
631 usually show higher cell abundance and diversity than their PA counterparts at most depths. A set of
632 environmental factors including depth, salinity, seawater age, DOC, POC, DO and silicate are
633 considered playing important roles in structuring PA and FL microbial communities along the depth
634 profile. On the one hand, as the result of adapting to different organic substrates available, PA and FL
635 fractions generally accommodate significantly divergent microbial compositions at each depth. At fine
636 taxonomic levels, a considerable number of microbial lineages exhibit pronounced preferences to PA
637 or FL lifestyles, also with distinct distributing stratification along the depth profile. A few microbial

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638 taxa show potentially PA and FL dual lifestyle strategies, able to switch according to substrate
639 availability an environmental variation and implying versatile metabolic flexibility. In addition,
640 according to some special microbial lineages supposed to be restricted in upper euphotic zones, we
641 found that the sinking organic particles likely function as vectors to transfer prokaryotes from surficial
642 ocean to deep waters, indicative of the potential vertical connectivity of prokaryotes along water
643 column profile.

644

645 **Data availability**

646 The pyrosequencing data obtained from the 454 sequencing of 16S rRNA genes were deposited in the
647 Sequence Read Archive (SRA) database under accession ID PRJNA546072 for bacterial sequences
648 and PRJNA546071 for archaeal sequences.

649

650 **Author contribution**

651 JL and JF designed the experiments, and JL, LG, JW and BW carried them out. JL, SB, LZ and LS
652 treated and analyzed the sequence data. JL and JF wrote the manuscript with contributions from all co-
653 authors.

654

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658

659 **Competing interests**

660 The authors declare that they have no conflict of interest.

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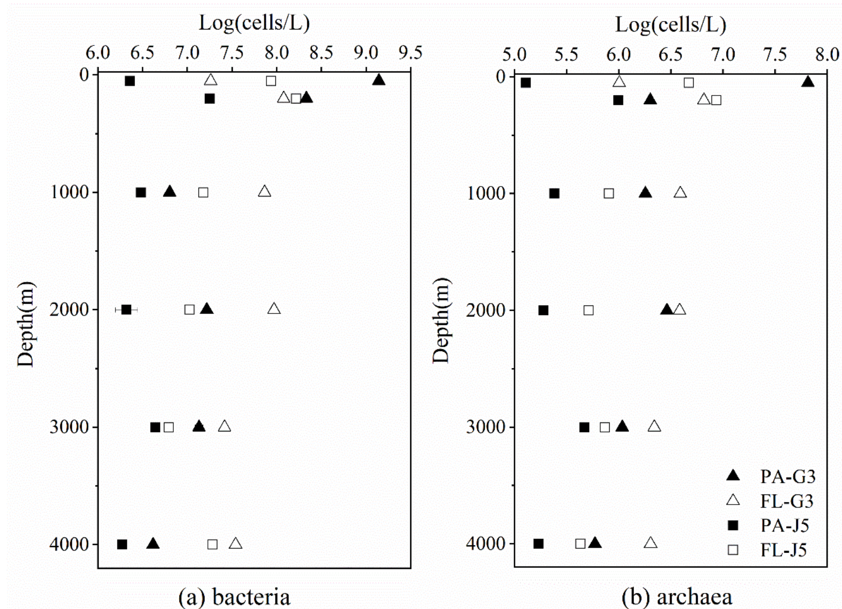

943

944 **Figure 1.** Bacterial and archaeal cell abundances in seawaters at different depths from G3
945 station and J5 station in the South China Sea, estimated from 16S rRNA gene copy
946 abundances.

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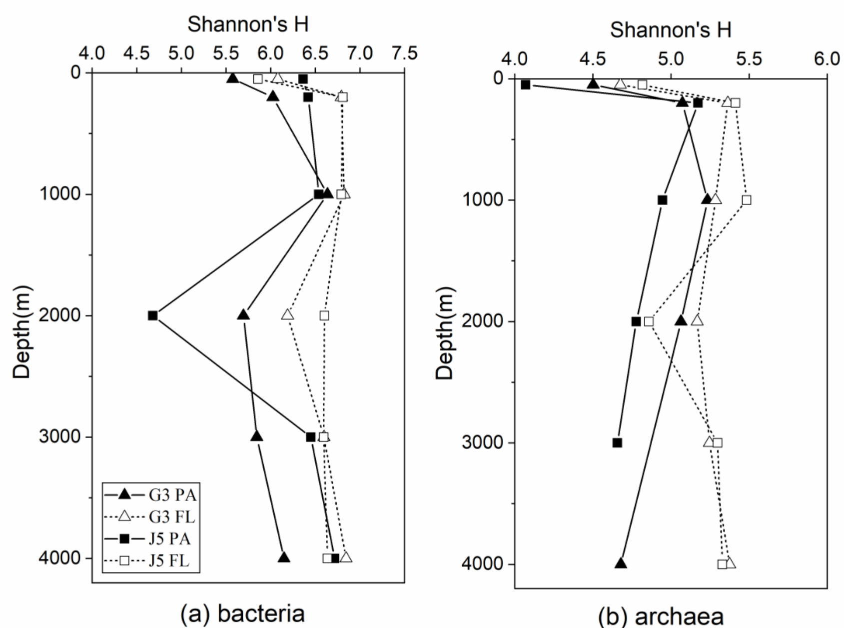

948

949 **Figure 2.** Shannon's diversity index calculated for all bacterial and archaeal communities of
950 seawaters collected from G3 station and J5 station in the South China Sea.

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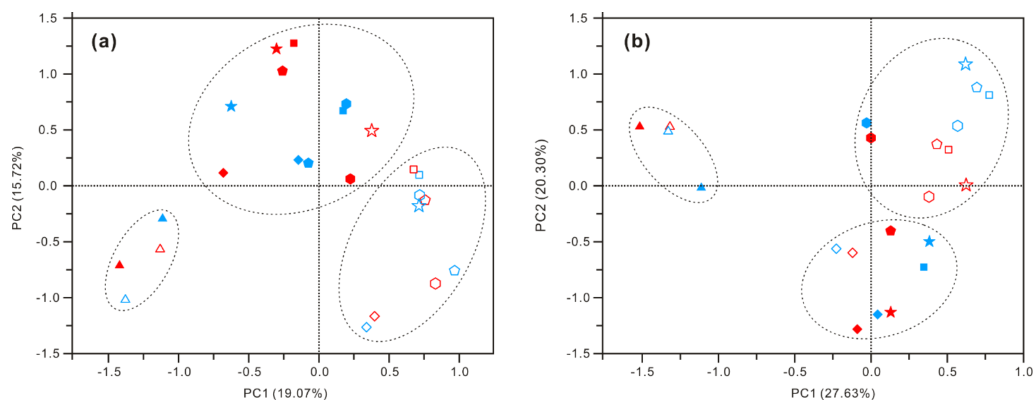

951

952 **Figure 3.** Results of PCoA analysis for particle-attached and free-living microbial fractions collected from
953 seawater columns of the South China Sea. (a) PA and FL bacteria; (b) PA and FL archaea. Triangle: 50 m;
954 rhombus: 200 m; hexagon: 1000 m; star: 2000 m; square: 3000 m; pentagon: 4000 m. Blue color: J5 station;
955 red color: G3 station. Filled: particle-attached fraction; open: free-living fraction.

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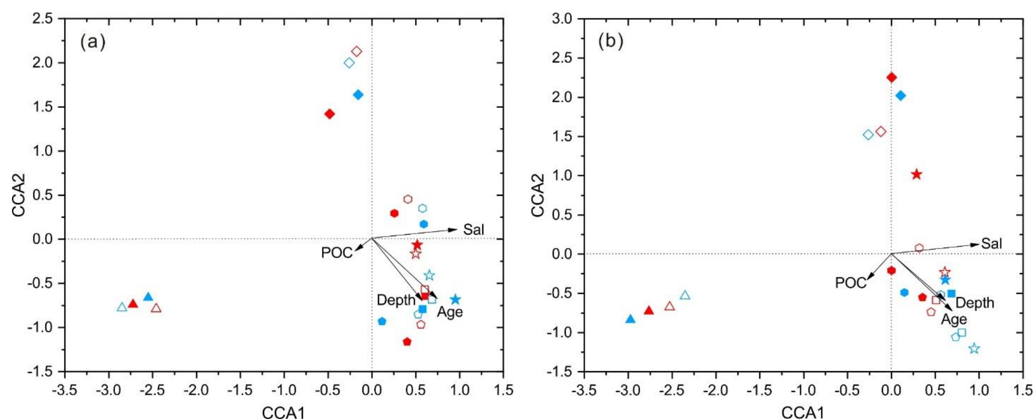

957

958 **Figure 4.** Results of CCA analysis to correlate several environmental factors including POC, seawater age,
959 salinity and depth to PA and FL microbial communities collected from seawater columns of the South China
960 Sea. (a) PA and FL bacteria; (b) PA and FL archaea. Triangle: 50 m; rhombus: 200 m; hexagon: 1000 m; star:
961 2000 m; square: 3000 m; pentagon: 4000 m. Blue color: J5 station; red color: G3 station. Filled: particle-
962 attached fraction; open: free-living fraction.

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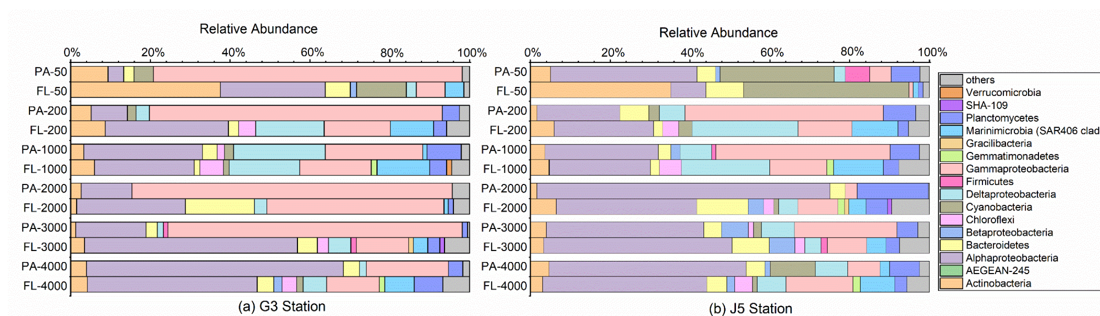
963 

964 **Figure 5.** Taxonomic compositions of particle-attached and free-living bacterial communities of seawaters at
965 different depths along two different water columns in the South China Sea. (a) G3 station; (b) J5 station. The
966 phylum or class which has less than 1% proportions is classified into "others" (Fig. S4).

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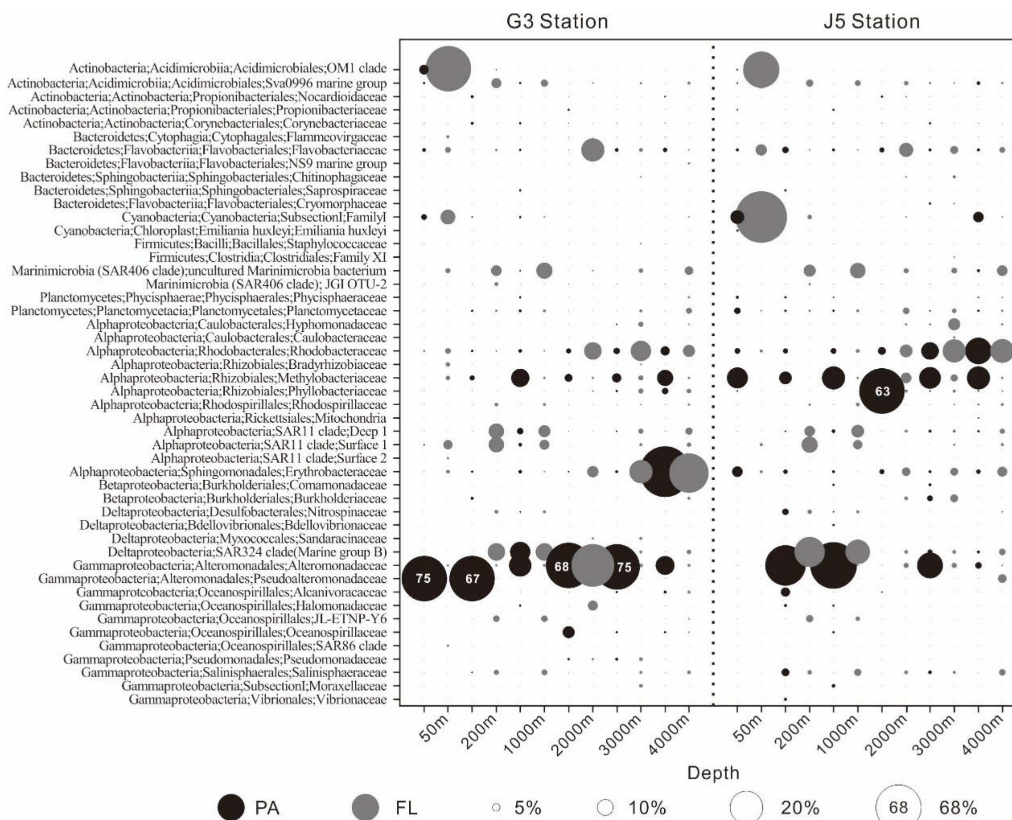

967

968 **Figure 6.** The relative abundances of families in particle-attached and free-living bacterial communities. Dark
969 grey bubbles are the average relative abundances in the PA fraction, while light grey bubbles are the average
970 relative abundances in the FL fractions. Scale is shown in the bottom, and the cycle with a number inside
971 indicates actual relative abundance.

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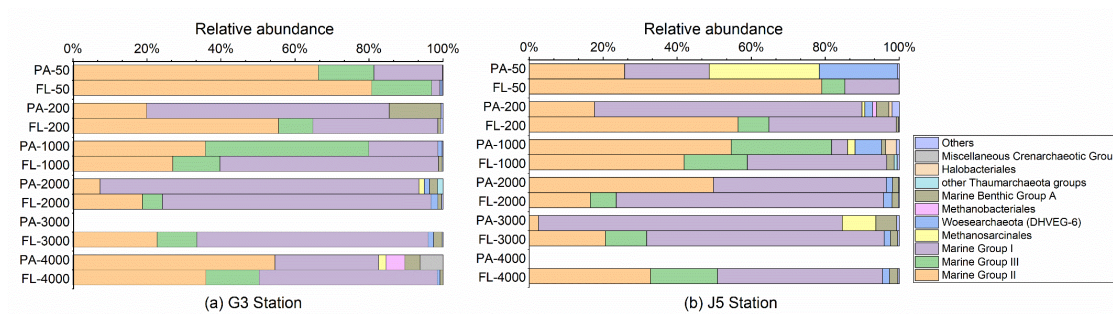

972

973 **Figure 7.** Taxonomic compositions of particle-attached and free-living archaeal communities of seawaters at
974 different depths along two different water columns in the South China Sea. (a) G3 station; (b) J5 station. The
975 archaeal lineages, at ~ phylum or class level, with less than 1% proportions is classified into "others" (Fig. S5).

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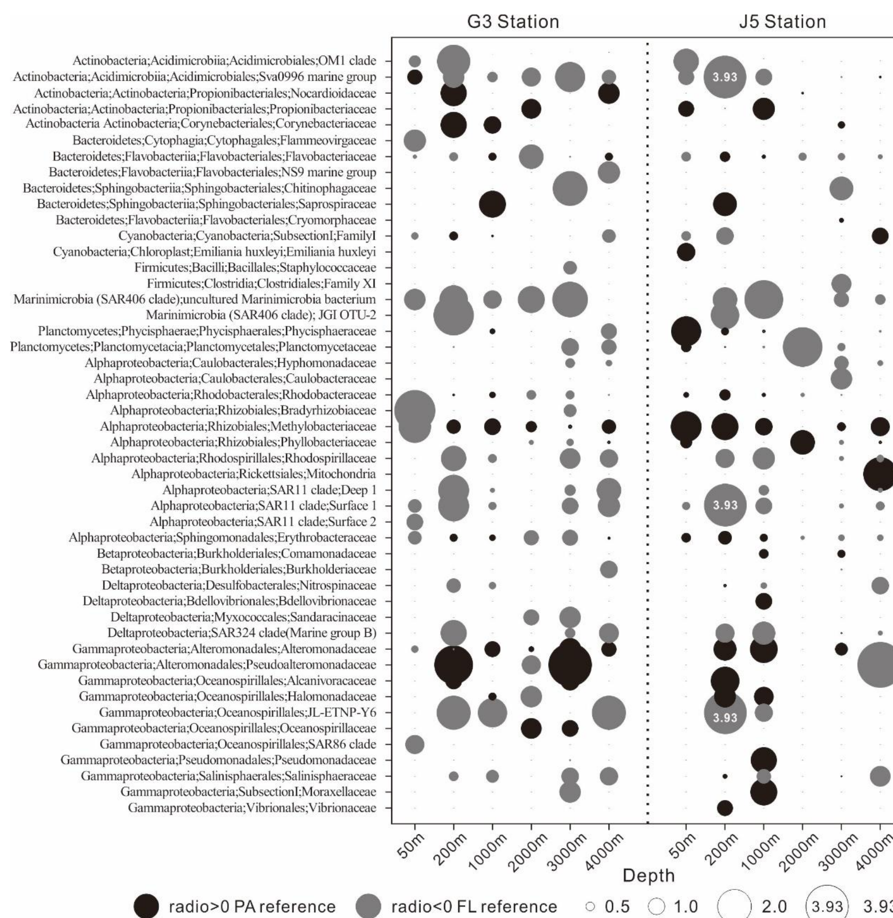

976

977 **Figure 8.** Odds ratio for each of the families with relatively abundant proportions in each sample.
978 Dark grey bubbles represent clades with a positive odds ratio, meaning higher relative abundance in
979 the PA fraction. Light grey bubbles represent clades with a negative odds ratio, or higher relative
980 abundance in the FL fraction. Scale is shown in the bottom, and the circle with a number inside
981 indicates actual ratio (not proportional).

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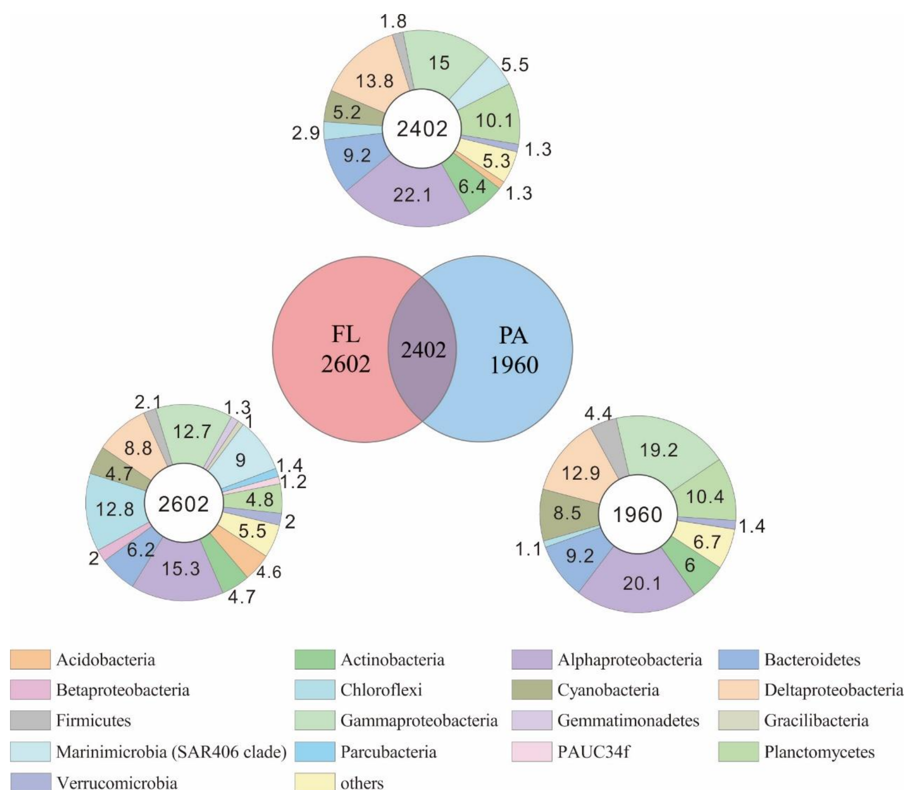

983 **Figure 9.** Numbers of each OTU sets including those exclusively found in PA fraction, FL fraction,
984 and those shared by PA and FL fractions. Pie charts represent relative proportions of each bacterial
985 lineages at phylum/class level.

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987 **Table 1.** Environmental parameters of the water columns at different depths of G3 and J5 stations in the South China Sea

Depth (m)	G3 station										J5 station									
	T (°C)	Sal. (‰)	pH	DO (uM)	DOC (μM)	POC (μM)	Ages* (yr)	NO_3^- (μM)	PO_4^{2-} (μM)	Silicates (μM)	T (°C)	Sal. (‰)	pH	DO (uM)	DOC (μM)	POC (μM)	Ages* (yr)	NO_3^- (μM)	PO_4^{2-} (μM)	Silicates (μM)
50	25.80	33.81	8.02	204.3	63.07	1.5	109	BD	BD	2.27	23.60	33.88	8.02	204.8	67.77	1.6	108	0.12	BD	2.36
200	15.46	34.54	7.75	115.1	53.02	0.8	106	17.98	1.20	21.06	14.27	34.52	7.72	116	49.99	0.9	106	19.13	1.30	26.56
1000	4.68	34.51	7.51	85.5	49.34	1.2	1170	37.16	2.72	114.40	4.46	34.53	7.51	82.3	45.62	2.1	1310	37.04	2.73	121.93
2000	2.52	34.61	-	-	-	1.1	1190	-	-	-	2.49	34.61	7.52	102	41.67	0.9	1670	38.41	2.81	151.46
3000	2.36	34.62	-	-	42.94	1.8	1600	-	-	-	2.36	34.62	7.52	109.7	40.34	0.7	1680	38.16	2.79	145.03
4000	2.39	34.63	7.52	115.1	42.44	0.7	1750	38.48	2.82	141.81	2.43	34.62	7.53	111.8	46.52	1.2	1610	38.58	2.78	145.06

988 *$\Delta^{14}C$ ages; BD: Below detection; -: no measurement.