

# 1 **There and back again – unraveling mechanisms of bacterial biogeography in** 2 **the North Pacific Subtropical Gyre to and from station ALOHA**

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15 **Running title:** Bacterial metapopulation dynamics in the North Pacific Subtropical Gyre  
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17

## 18 **Abstract**

19 Bacterially-mediated fluxes of energy and matter are dynamic in time and space coupled with  
20 shifts in bacterial community structure. Yet, our understanding of mechanisms shaping  
21 bacterial biogeography remains limited. Near-surface seawater was collected during transits  
22 between Honolulu and Station ALOHA in the North Pacific Subtropical Gyre to examine the  
23 shape of occupancy-frequency distributions (the different number of populations occupying  
24 different number of sites) and determine bacterial metapopulation dynamics. Bacterial 16S  
25 rRNA gene amplicons were sequenced from whole seawater and filter-size fractionated  
26 plankton DNA samples while also separating the community into distinct taxonomic groups  
27 at phyla/class and analyzing these compartments separately. For the total seawater (i.e. the  
28 >0.2 µm size fraction) and picoplankton communities (i.e. the size fraction >0.2 µm and < 3.0  
29 µm), but not the large size fraction community (i.e. the >3.0 µm size fraction), most  
30 individual operational taxonomic units (OTUs) occupied a single site and the number of  
31 OTUs occupying different number of sites followed a significant bimodal pattern with several  
32 core OTUs occupying all sites. Nevertheless, only Cyanobacteria (in particular  
33 *Prochlorococcus* sp.) and in a few instances also Alphaproteobacteria (in particular SAR11

34 clade and Aegan-169 marine group bacteria) exhibited bimodal occupancy-frequency  
35 patterns. As expected, *Prochlorococcus* sp. had an inversed bimodal occupancy-frequency  
36 distribution with most OTUs found at all sites. Yet, there were individual satellite OTUs  
37 affiliated with *Prochlorococcus* sp. that were phylogenetically distinct from the core OTUs  
38 and only found at a single site. Collectively, these findings indicate that different  
39 compartments (size fractions and taxa) have different metapopulation dynamics. Bimodal  
40 patterns among the low diversity total and picoplankton communities but not in the high  
41 diversity large size fraction suggest that positive feedbacks between local abundance and  
42 occupancy are important when environmental conditions are homogenous and diversity is  
43 low.

## 44 **Introduction**

45 Spatial and temporal variability in bacterial population dynamics influence nutrient cycling in  
46 aquatic systems (Crump et al., 2004; Kirchman et al., 2005; Fuhrman et al., 2006; Galand et  
47 al., 2010; Lindström et al., 2010; Östman et al., 2010; Alonso-Saez et al., 2015). Yet, despite  
48 observable biogeographical patterns among marine microbial assemblages (see e.g. Pommier  
49 et al., 2007; Ghiglione et al., 2012; Sunagawa et al., 2015; Salazar et al., 2016), the  
50 mechanisms shaping microbial biogeography remain largely unknown (Martiny et al., 2006;  
51 Hanson et al., 2012; Poisot et al., 2013).

52           With the introduction of high-throughput sequencing, and large sequence  
53 datasets enabled by these technologies, microbial ecologists are now able to test a wide  
54 variety of theoretical ecological models that are the foundation for mechanisms explaining  
55 macroecological patterns among larger taxa (Purdy et al., 2010; Poisot et al., 2013). Such  
56 theoretical models, including, but not limited to, metacommunity (Leibold et al., 2004) and  
57 metapopulation (McGeoch and Gaston, 2002) frameworks have provided mechanistic  
58 concepts in ecology among organisms ranging from birds to fish and insects to phytoplankton  
59 (Levin, 1974; Hanski, 1982; Gotelli, 1991; Tokeshi, 1992; Hanski and Gyllenberg, 1993; van  
60 Rensburg et al., 2000; Hubbell, 2001; Mehranvar and Jackson, 2001; Mouquet and Loreau M,  
61 2002; Verberk et al., 2010; Unterseher et al., 2011; Wardle et al., 2011; Hercos et al., 2013).

62           Two models; Hanski's core and satellite hypothesis (CSH; (Hanski, 1982) and  
63 Levin's model (Levin, 1974), were recently empirically tested and used to explain distribution  
64 patterns among marine bacteria that are typically assumed not to be dispersal limited (Lindh  
65 et al., 2016). In the study bimodal occupancy-frequency patterns (i.e. the number of species  
66 occupying different number of sites) were found and the CSH model agreed well with  
67 observed data in the Baltic Sea and in global datasets, indicating its applicability also for  
68 marine microbes. The CSH model provides a mechanistic basis for the observation of

69 abundant (core) and rare (satellite) species in ecosystems. In brief, the CSH makes predictions  
70 of the shape of occupancy-frequency distributions from variation in colonization and  
71 extinction rates (i.e. populations successfully dispersed to previously unoccupied sites vs.  
72 populations disappearing from previously occupied sites). In the CSH the bimodal  
73 occupancy-frequency distributions are the result of stochastic variation in colonization and  
74 extinction rates (i.e. a quadratic relationship between colonization/extinction rates and  
75 occupancy) that either push populations to become rare or abundant. Nevertheless, empirical  
76 data from examining the applicability of metapopulation models to marine bacterial  
77 assemblages are limited.

78           In the present paper the prevalence of bimodal occupancy-frequency patterns  
79 were examined in the oligotrophic North Pacific Ocean and among different taxa and/or size  
80 fractions of a bacterial community. The main hypothesis was that in this relatively  
81 homogenous oligotrophic ocean environment bimodal patterns, reflecting a coherent oceanic  
82 region without dispersal limitation and environmental filtering, could be a common feature  
83 among marine bacteria. The second hypothesis was that taxa with different dispersal  
84 capability and filtered by various environmental conditions could display different  
85 metapopulation dynamics. The third hypothesis was that since *Prochlorococcus* sp. is the  
86 dominant bacteria found in this system (Schmidt et al., 1991; Campbell and Vaultot, 1993;  
87 Eiler et al., 2011) much of the observed metapopulation dynamics could be driven by this key  
88 organism but that there may be core- and satellite distribution patterns within the same genus.  
89 To test these hypotheses, bacterial 16S rRNA amplicons were sequenced from whole  
90 seawater and filter size fractionated community DNA, sampled from the near-surface ocean  
91 on a series of cruise transects between Honolulu and station ALOHA (22.75° N, 158° W) in  
92 the North Pacific Subtropical Gyre. The observed bacterial populations were subsequently  
93 fitted to different theoretical metapopulation models.

## 94 **Material and Methods**

### 95 *Field sampling*

96 Seawater samples for subsequent extraction of plankton DNA were collected during 4  
97 research cruises (October 2015, HOT 277; November 2015, KM1519; December 2015,  
98 KM1521; and January 2016, HOT 280) offshore of the Hawaiian island of Oahu aboard the  
99 R/V Ka'imikai-O-kanaloa and R/V *Kilo Moana*. Seawater was collected from the research  
100 vessels' flow-through seawater intake systems into acid-washed, Milli-Q rinsed  
101 polycarbonate bottles. The flow-through seawater system was instrumented to include a  
102 thermosalinometer (SeaBird 911), fluorometer (Seapoint Chlorophyll Fluorometer; Seapoint  
103 Sensors, Inc.) and dissolved oxygen (O<sub>2</sub>) sensor (SBE 43; Sea-Bird Electronics). On all  
104 cruises, plankton biomass for subsequent DNA extraction was harvested by filtering 2 L of  
105 seawater on to 25 mm diameter, 0.2 µm pore size polyethersulfone filters (Supor membrane,  
106 Pall). In addition, on two of the cruises (December 2015 and January 2016) plankton biomass  
107 were also sequentially filter size-fractionated samples for subsequent extraction of DNA for  
108 information on bacterial community structure among different plankton size classes. During  
109 these cruises, seawater was filtered onto 25 mm diameter, 3.0 µm pore size polycarbonate  
110 membranes (Millipore), followed by filtration onto 25 mm diameter, 0.2 µm pore size Supor  
111 filters. The various filter size-fractionated bacterial communities were defined as: total (>0.2  
112 µm), picoplankton (>0.2 and <3 µm) and large (>3 µm), respectively. Filters were stored at -  
113 80°C until extraction.

114           Coincident samples for measurement of bacterial abundance and production  
115 were collected from the vessels' flow-through seawater system. Seawater for determination  
116 of bacterial abundance was subsampled into 2 ml cryotubes (BD Falcon) preserved with 20  
117 µL paraformaldehyde (Final concentration 0.2%; Sigma-Aldrich). Triplicate 1.5 ml samples  
118 for subsequent measurements of <sup>3</sup>H-leucine incorporation rates were aliquoted into 2.0 ml

119 microcentrifuge tubes (Axygen; (Pace et al., 2004)) and amended with 20 nM (final  
120 concentration) of <sup>3</sup>H-leucine stock (3, 4, 5 -<sup>3</sup>H-leucine, 109 Ci/mmol; Perkin-Elmer). One  
121 killed control was included from each station sampled (5% final concentration of  
122 trichloroacetic acid; Sigma-Aldrich). Samples for <sup>3</sup>H-leucine incorporation rates were  
123 incubated shipboard at *in situ* temperatures following the <sup>3</sup>H-leucine incorporation protocol  
124 described in (Kirchman et al., 1985) and (Smith and Azam, 1992). Preserved bacterial  
125 abundance and killed <sup>3</sup>H-leucine incorporation rate samples were flash frozen in liquid  
126 nitrogen and stored at -80° C until processing in the laboratory. Preserved bacterial abundance  
127 samples were thawed, and aliquoted into 250 µl wells and stained with 2.5µl µl of 100X  
128 SybrGreen (Thermo Fisher) and enumerated using an Attune™ acoustic focusing flow  
129 cytometer (Applied Biosystems). <sup>3</sup>H-leucine incorporation rates samples were processed  
130 following a modified method of the microcentrifuge method as described in (Smith and  
131 Azam, 1992). A detailed description of the <sup>3</sup>H-leucine incorporation protocol can be found in  
132 (Viviani and Church, 2017).

133

134 *DNA extraction, PCR, sequence processing and analysis.*

135 DNA was extracted from the filters using the DNeasy Plant MiniKit (Qiagen) following slight  
136 modifications of the manufacturer's suggestions. Modifications included the addition of  
137 Proteinase K to the lysis buffer followed by bead-beating with 0.1 mm and 0.5 mm glass beads  
138 (Biospec products) for additional cell disruption prior to the extraction. DNA concentrations were  
139 determined using the Qubit 2.0 Fluorometer and Qubit dsDNA High Sensitivity Assay kit  
140 (Molecular Probes), with DNA quality checked using 1.5% agarose gel electrophoresis. Extracted  
141 DNA was stored at -80°C.

142 Amplicon processing for all samples was performed as described in (Lindh et al., 2015).

143 Bacterial 16S rRNA was amplified using primers 341F and 805R (Herlemann et al., 2011)

144 following the PCR protocol of (Hugerth et al., 2014). Amplicons were purified by spin-column  
145 centrifugation using E.Z.N.A.® Cycle Pure kit (Omega Biotek). The resulting purified amplicons  
146 were pooled in equimolar concentration and sequenced on an Illumina Miseq (Illumina, USA)  
147 platform at the Hawai'i Institute for Marine Biology (HIMB), Hawaii, USA using the 300 bp  
148 paired-end setting. Raw sequence data generated from Illumina Miseq were processed using the  
149 UPARSE pipeline (Edgar, 2013). Taxonomy was determined against the SINA/SILVA database  
150 (SILVA123; (Quast et al., 2013)). After quality filtering and discarding plastid and archaeal  
151 sequences a total of 1.25 million bacterial sequences were utilized for subsequent analyses. Thus,  
152 the final OTU table consisted of 96 samples with 27340 OTUs delineated at 99% 16S rRNA gene  
153 identity with an average of  $13093 \pm 5644$  sequences per sample. For all alpha diversity measures  
154 the OTU table were subsampled to 10,000 sequences per sample. DNA sequences have been  
155 deposited in the National Center for Biotechnology Information (NCBI) Sequence Read Archive  
156 under accession number SRP091841.

157

### 158 *Statistical tests*

159           Occupancy-frequency distributions (the number of OTUs occupying different  
160 number of sites) were analyzed as described in (Lindh et al., 2016). In brief, an equivalent to  
161 Tokeshi's test of bimodality was performed using Mitchell-Olds' and Shaw's test (Mitchell-  
162 Olds and Shaw, 1987) for the location of quadratic extremes. Colonization and extinction  
163 rates of OTUs were determined by calculating the change in fraction of sites occupied  
164 between two cruises where the same stations were sampled with <1 month interval. Non-  
165 linear least squares analysis of observed colonization and extinction rates was performed  
166 using the equations of Levin's model, the CSH hypothesis and Gotelli's propagule rain model  
167 (Levin, 1974; Hanski, 1982; Gotelli, 1991).

168           All statistical tests were performed in R 3.3.3 (Team, 2014) using the package "Vegan"

169 (Jari Oksanen et al., 2010). Graphical outputs were made in R 3.3.3 using the package “ggplot2”  
170 (Wickham, 2009).

171

## 172 **Results**

173 In the present study bacterial population dynamics and biogeography were examined during 4  
174 research cruises in the North Pacific Subtropical Gyre (Fig. 1). For all four transects (total 96  
175 samples) 27,340 operational taxonomic units (OTUs) were detected. A more exhaustive  
176 sampling was performed in the October 2015 cruise with measurements of a larger set of  
177 biotic and abiotic measurements and is thus the focus in the present paper. An additional  
178 cruise with a different transect (November 2015) to the Southwest of Oahu were performed to  
179 compare patterns observed in the October 2015 cruise. Finally, on two cruises (December  
180 2015 and January 2016), samples were filter size-fractionated for information on bacterial  
181 diversity associated with differing size classes of plankton (>3 µm, >0.2 and <3.0 µm, and  
182 >0.2 µm, large, picoplankton and total, respectively).

183

### 184 *Physicochemical conditions, community abundance, production and biodiversity*

185 Across the 200 km transect to Station ALOHA (October 2015) concentrations of Chl *a* and  
186 sea surface temperatures were relatively stable in space, averaging 0.6 µg L<sup>-1</sup> and 26°C,  
187 respectively (Fig. 2). Bacterial abundance varied ~2-fold (ranging 5.73 x10<sup>5</sup> cells ml<sup>-1</sup> to 9.13  
188 x10<sup>5</sup> cells ml<sup>-1</sup>; Fig. 2). <sup>3</sup>H-leucine incorporation rates ranged between 13 and 37 pmol Leu L<sup>-1</sup>  
189 h<sup>-1</sup> (Fig. 2). Variation in bacterial abundance and production was overall small (SD = 0.7 x10<sup>5</sup>  
190 cells ml<sup>-1</sup> and SD = 6 pmol Leu L<sup>-1</sup> h<sup>-1</sup>; Fig. 2).

191 The number of OTUs varied between 371 and 1037 but appeared relatively  
192 stable in space and time (SD = 145.34). Estimation of alpha diversity followed a similar trend  
193 where Shannon diversity index and Chao 1 richness varied between 3.99 and 5.06 and 903.45



194 to 2256.88, respectively. Alpha diversity for the total community was also stable within all  
195 other cruises around the same range as observed during October 2015 (Fig. S1A). During the  
196 December 2015 and January 2016 transect, size fractionation of plankton DNA samples  
197 revealed higher alpha diversity in the larger size fraction (3.0  $\mu\text{m}$  filter fraction) compared to  
198 the total ( $>0.2 \mu\text{m}$ ) and picoplankton fraction (0.2 and 3.0  $\mu\text{m}$ ; Fig. S1A).

199

### 200 *Bacterial community composition*

201 In all cruises the total and picoplankton communities were dominated by Cyanobacteria  
202 (averaging ~50% of total sequences), with bacteria that were affiliated with several other  
203 phyla or classes not included in the taxonomic analysis or unclassified OTUs comprising  
204 nearly 25% of the total sequences (Fig. 3). Actinobacteria and Alphaproteobacteria each  
205 typically contributed to ~5% of total sequences in these communities. In the December 2015  
206 and January 2016 cruises the large size class bacterial assemblages were more diverse than  
207 other size classes of bacteria, with notable increases in relative abundances of  
208 Alphaproteobacteria, Planctomycetes, Chloroflexi and Bacteroidetes (Fig. 3B). However,  
209 Cyanobacteria were also dominating the large size class communities. Cluster analysis of  
210 Bray-Curtis distances obtained from samples in the October 2015 cruise showed a largely  
211 similar community structure (~15% dissimilarity), resulting in samples from near-shore  
212 coastal sites clustering with samples from the open ocean sites (Fig. 3).

213           Among the top ten most abundant OTUs all were affiliated with  
214 *Prochlorococcus* sp., demonstrating homogenous relative abundances along the transect (Fig  
215 S2). Other less abundant OTUs that exhibited variance in relative abundance along the  
216 transect, included the OM-1 clade bacteria (*Candidatus Actinomarina*) and OTUs within the  
217 family *Rhodospirillaceae* affiliated with AEGEAN-169 marine group. Notably, the OM-1  
218 clade bacteria appeared relatively enriched in a localized region north of Oahu (22° N, see

219 arrows Fig. S3). Nevertheless, the variation in relative abundance among these OTUs was  
220 low.

221

### 222 *Occupancy-frequency distributions*

223 The number of different species occupying different number of sites sampled during the  
224 transects were also examined to evaluate the shape of occupancy-frequency distributions.  
225 Bacterial communities sampled during the October 2015 cruise displayed a significant  
226 bimodal occupancy-frequency pattern. Most OTUs were found at a single site followed by a  
227 monotonical decrease in the number of OTUs occupying increasing number of sites but with a  
228 peak in the number of OTUs occupying all sites (Fig. 4A; Table S1). As this transect  
229 contained several samples obtained from around Station ALOHA this dataset were  
230 subsampled to only show stations 3, 6, 9, 13, 33 and 47 to keep a clear transect trajectory  
231 profile with distinct sites (see insert Fig. 4A). This subsampling exercise confirmed the  
232 significant bimodal pattern. In addition, samples from completely different stations in a  
233 trajectory 30 km Southeast of Honolulu were collected to validate the shape of occupancy-  
234 frequency distribution found in the Honolulu-Station ALOHA transect. Also for this transect  
235 a significant bimodal pattern were found (see insert Fig. 4A).

236 The main hypotheses were that different parts of a bacterial community may  
237 exhibit different metapopulation dynamics; for example, taxa distributed among the  
238 picoplankton and larger bacterial assemblages might have different dispersal capabilities and  
239 be subjected to different environmental filters. To elucidate differences between such  
240 compartments the total community from the October 2015 cruise and size-fractionated  
241 communities from the December 2015 and January 2016 cruises were examined and taxa  
242 were analyzed at different taxonomic levels. Similar to the “total” community, the  
243 picoplankton assemblage demonstrated significant bimodal patterns (Fig. 4B; Table S1); in

244 contrast, for the “large” bacterial size classes most OTUs were found at a single site followed  
245 by a monotonical decrease in the number of OTUs occupying increasing number of sites.  
246 Thus, in contrast to the picoplankton and total communities, the large size fractions exhibited  
247 unimodal occupancy-frequency patterns (Fig. 4B; Table S1). In addition, for particular OTUs  
248 binned at the phyla/class level detected in the October 2015 cruise varying occupancy-  
249 frequency distributions were observed. In fact, only Planctomycetes, Alphaproteobacteria,  
250 and Cyanobacteria contained OTUs that were found at all sites and only the latter two  
251 displayed bimodal patterns (Fig. S4; Table S1). Cyanobacteria had the most substantial  
252 bimodal pattern with a strong peak in number of OTUs occupying all sites. Moreover, most  
253 OTUs binned at the phyla/class level exhibited unimodal patterns for picoplankton and large  
254 size class communities (Fig. S5; Table S1).

255           More than 50% (64 out of 108) of the core OTUs detected from the October  
256 2015 cruise was affiliated with *Prochlorococcus* sp. (Fig. 3; S6A). When analyzed separately,  
257 *Prochlorococcus* sp. OTUs exhibited a strong right-skewed occupancy-frequency distribution  
258 in the total and picoplankton size classes, with most OTUs occupying all sites. There were  
259 satellite phylotypes among the *Prochlorococcus* sp. affiliated OTUs detected at only a single  
260 site (Fig. S6). Notably, for the *Prochlorococcus* sp. OTUs in the large size class communities,  
261 neither unimodal nor bimodal occupancy-frequency patterns were detected (Fig. S6B). By  
262 analyzing phylogenetically distinct *Prochlorococcus* sp. OTUs and comparing those OTUs  
263 detected at all sites (core) vs. the OTUs only found in a single site (satellite) phylogenetic  
264 differences in core/satellite characteristics among closely related populations were examined.  
265 This analysis revealed that the most abundant core *Prochlorococcus* sp. OTUs were  
266 phylogenetically distinct from the most frequently observed satellite OTUs within the same  
267 genus (Fig. S7).

268

269 *Colonization and extinction rates*

270 In the CSH (Hanski, 1982) predicted bimodal occupancy-frequency distributions of species  
271 based on stochastic variation in colonization and extinction rates following a quadratic  
272 relationship between these rates and occupancy. By calculating the number of OTUs  
273 successfully dispersed to new sites compared to the number of OTUs that disappeared from  
274 occupied sites colonization and extinction rates was estimated (Fig. 5). These calculations  
275 were performed using the December 2015 and January 2016 cruises where the same stations  
276 were sampled allowing for the observation of temporal changes in the number of occupied  
277 sites ( $dP/dt$ ).

278           The total bacterial community was characterized by a quadratic curve for both  
279 colonization and extinction rates. Notably, extinction rates were higher than colonization rates  
280 with a more distinct quadratic curve (Fig. 5A). Both colonization and extinction rates fitted  
281 well with the quadratic relationship described by the CSH (Hanski, 1982). For the  
282 picoplankton and large size class communities, the relationship between colonization rates  
283 and occupancy were more difficult to determine and none of the models tested resulted in  
284 robust fits to the observations (Fig. 5A). However, for the large plankton size class, extinction  
285 rates aligned well with the expectation of a linear relationship between extinction rates and  
286 occupancy as described in Levin's model (Levin, 1974).

287           At the Phyla/Class level rates of colonization and extinction were plotted against  
288 occupancy for major bacterial lineages (Fig. 5B). Both Alphaproteobacteria and  
289 Cyanobacteria demonstrated quadratic relationships between extinction rates and occupancy  
290 in the total community. However, as above, colonization rates were more difficult to  
291 characterize. It was noteworthy that the extinction rates were both higher and more  
292 pronounced compared to colonization rates. Planctomycetes, Bacteroidetes and  
293 Gammaproteobacteria demonstrated curves that initially appeared to follow a quadratic

294 relationship between extinction rates and occupancy, but either decreased followed by an  
295 increase in extinction rates with occupancy (Planctomycetes and Gammaproteobacteria)  
296 and/or did not decrease rapidly at maximum occupancy (Bacteroidetes). Unlike the patterns  
297 for all of the OTUs in the overall community analysis, resulting patterns among the  
298 picoplankton and large size class bacterial communities at phyla/class level were more  
299 difficult to validate using the different metapopulation models. Nevertheless, extinction rates  
300 among OTUs binned at phyla/class for the larger size class communities displayed a tendency  
301 toward a linear relationship between extinction rates and occupancy thus following Levin's  
302 model (Levin, 1974) (Fig. 5B).

303

## 304 **Discussion**

305 In the present paper metapopulation models were applied to describe bacterial  
306 community dynamics observed in the North Pacific Subtropical Gyre to elucidate  
307 mechanisms shaping biogeography. The results highlight that bimodal occupancy-frequency  
308 patterns are prominent in the North Pacific Subtropical Gyre but only among specific size  
309 classes and taxa of the bacterial communities. Total ( $\geq 0.2 \mu\text{m}$  size fraction) and  
310 picoplanktonic ( $\geq 0.2 \mu\text{m} \leq 3.0 \mu\text{m}$  size fraction) communities typically displayed bimodal  
311 patterns, whereas the larger size class ( $\geq 3.0 \mu\text{m}$  filter fraction) community exhibited unimodal  
312 patterns. In instances where bimodal patterns were found quadratic relationships between  
313 rates of colonization/extinction and occupancy were observed. These findings indicate a  
314 strong positive feedback mechanism between local abundance and occupancy and the  
315 observed patterns generally fit Hanski's metapopulation model, the CSH (Hanski, 1982). In  
316 agreement, significant bimodal occupancy-frequency distributions linked with quadratic  
317 colonization and extinction rates have been found among bacterial assemblages in the Baltic  
318 Sea Proper (Lindh et al., 2016).

319

320 *Environmental conditions and diversity regulate metapopulation dynamics*

321           Concomitant measurements of environmental variables, bacterial abundance and  
322 <sup>3</sup>H-leucine incorporation rates in the present paper allowed for linking mechanisms shaping  
323 biogeography with the prevailing environmental conditions and community functioning.  
324 Overall, the environment and community dynamics was highly stable throughout each of the  
325 transects performed coupled with core and satellite metapopulation dynamics. Bimodal  
326 patterns were typically coupled with lower community diversity and quadratic relationships  
327 between colonization/extinction rates and occupancy of OTUs in the total and picoplankton  
328 communities. In contrast, the large size fraction communities exhibited unimodal patterns  
329 linked with higher diversity and linear colonization and extinction rates of OTUs. These data  
330 suggest that positive feedbacks between local abundance and occupancy are important in  
331 structuring picoplankton bacterial communities when environmental conditions are  
332 homogenous and diversity is low. Still, it is noteworthy that the metadata in this study was  
333 derived from whole seawater and total community and the environmental conditions  
334 characterizing the size fractionated “large” communities are unknown. Further more focused  
335 studies coupling size fractionated community composition and functioning would be very  
336 rewarding for our understanding of metapopulation dynamics and ultimately provide a deeper  
337 mechanistic understanding of biogeography of both picoplankton and large size fraction  
338 communities.

339

340 *Metapopulation dynamics of Prochlorococcus sp.*

341           OTUs affiliated with *Prochlorococcus* sp. contributed up to 50 % of total  
342 sequences for the total and picoplankton communities. A majority of the detected core  
343 populations were in fact affiliated with *Prochlorococcus* sp., thus driving much of the

344 observed metapopulation dynamics. In agreement with these findings, *Prochlorococcus* sp. is  
345 the dominant bacteria found in this system (Schmidt et al., 1991; Campbell and Vaulot, 1993;  
346 Eiler et al., 2011) and are ubiquitous in the oligotrophic ocean (Flombaum et al., 2013).  
347 However, this is the first study to examine metapopulation models for *Prochlorococcus* sp.  
348 and finding core- and satellite dynamics for this key organism. Although many of the  
349 *Prochlorococcus* sp. OTUs found in this study were distributed over all stations, OTUs within  
350 the same taxa had more restricted ranges geographically. Such OTUs with restricted  
351 distributions also added to the dominance of the left-skewed majority of rare satellite  
352 populations indicating dispersal and environmental filtering of particular *Prochlorococcus*  
353 ecotypes. Although this bacterium is ubiquitously distributed in the oligotrophic surface  
354 ocean, ecotypes within the same species have been suggested from variations in genome  
355 content and functional potential (Rocap et al., 2003). In fact, ecotypes of *Prochlorococcus* sp.  
356 have been observed in the Atlantic Ocean along environmental gradients with varying  
357 conditions implicating niche partitioning of closely related 16S rRNA sequences derived from  
358 the same species (Johnson et al., 2006). Single-cell genomic approaches have further  
359 emphasized that subpopulations of the same *Prochlorococcus* sp. are likely adapted to  
360 different environmental conditions (Kashtan et al., 2014). Taken together, *Prochlorococcus*  
361 sp. metapopulations exhibited core and satellite dynamics indicative of positive feedback  
362 mechanisms between local abundance and occupancy suggesting a rescue effect of core  
363 populations (Hanski, 1982; Hanski and Gyllenberg, 1993).

364

#### 365 *Disentangling community compartments*

366 Individual taxonomic groups and particular OTUs displayed different metapopulation  
367 dynamics suggesting that taxa likely have different dispersal capability and are subjected to  
368 environmental filtering. Further studies at deeper taxonomic levels are however warranted to

369 examine dynamics of “large” communities at different spatial scales to determine the  
370 mechanisms that regulate their biogeographical distribution. From observing variation in the  
371 shape of occupancy-frequency distributions among complex assemblages studied in  
372 macroecology (Mehranvar and Jackson, 2001) and colleagues have suggested that pooling all  
373 taxa into the same metapopulation model obscured taxonomic differences. Such taxonomic  
374 differences in compartments of communities may ultimately be linked with different dispersal  
375 capabilities and assembly of distinct species (Lindström and Langenheder, 2012).  
376 Conclusions made on community structure from high-throughput sequencing of microbial  
377 assemblages coupled with community functioning should thus be done with care and relative  
378 to individual compartments.

379

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388

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536

## 537 **Figures and Tables**

538 **Figure 1.** Map illustrating the four transects performed with the locations of Station ALOHA  
539 and Station Kahe marked. Asterisks denote the same station sample repeatedly.

540

541 **Figure 2.** Variation bacterial community abundance, production and alpha diversity during  
542 the October 2015 cruise, including variation in Chl *a* (green open circles) and average sea  
543 surface temperature (blue dotted line).

544

545 **Figure 3.** Variation in community composition during the October 2015 cruise (A), and  
546 November 2015, December 2015 and January 2016 cruises (B). Barcharts denote relative  
547 abundance (% of total sequences) among major bacterial groups at phyla/class. Dendrogram  
548 in (A) denote cluster analysis of variation in beta diversity estimated from Bray-Curtis  
549 distances. For the cruises in December 2015 and January 2016 in (B) total, picoplankton and  
550 “large” denote size-fractionated community DNA from  $>0.2 \mu\text{m}$ ,  $>0.2$  and  $<3.0 \mu\text{m}$  and  $3.0$   
551  $\mu\text{m}$  filters, respectively.

552

553 **Figure 4.** Core and satellite populations detected among occupancy-frequency distributions  
554 during the October 2015 cruise (A), and December 2015 and January 2016 cruises (B). Insert  
555 in (A) shows occupancy-frequency distributions of populations in a subset of the October  
556 2015 cruise with the same stations sampled in the December 2015 and January 2016 cruises  
557 and the additional cruise in November 2015. Total, picoplankton and “large” denote size-  
558 fractionated community DNA from  $>0.2 \mu\text{m}$ ,  $>0.2$  and  $<3.0 \mu\text{m}$  and  $3.0 \mu\text{m}$  filters,  
559 respectively. The y-axis is scaled at maximum 500 OTUs. Bimodality tests was performed  
560 using Mitchell-Olds and Shaw’s test for quadratic extremes (Mitchell-Olds and Shaw, 1987),  
561 a proxy for Tokeshi’s test (Tokeshi, 1992). ND=Not Determined. Significance level is  
562 indicated with “\*\*\*\*”, “\*\*\*” and “\*\*” for p-values  $<0.001$ ,  $<0.01$  and  $<0.05$ , respectively.

563

564 **Figure 5.** Measured colonization and extinction rates for all OTUs collectively (A), and for  
565 all OTUs within major bacterial groups and particular OTUs within the same genus (B).  
566 Observed rates in (A) were fitted with theoretical predictions from different metapopulation  
567 models.

568

## Supporting information

### Supplementary Figures and Tables

**Figure S1.** Variation in observed Shannon diversity index for all cruises.

**Figure S2.** Relative abundances of the top ten most abundant OTUs found during the October 2015 transect. All OTUs were affiliated with *Prochlorococcus sp.* Colour shows interpolated relative abundances using the weighted-average gridding algorithm in Ocean Data View (<http://odv.awi.de>; version 4.7.8).

**Figure S3.** Relative abundances of the top ten OTUs exhibited the highest variance during the October 2015 transect. Colour shows interpolated relative abundances using the weighted-average gridding algorithm in Ocean Data View (<http://odv.awi.de>; version 4.7.8). Arrows denote hotspots in relative abundance detected for OM-1 clade *Candidatus Actinomarina*.

**Figure S4.** Occupancy-frequency distributions of populations binned by phyla/class during the October 2015 cruise. Bimodality tests was performed using Mitchell-Olds and Shaw's test for quadratic extremes (Mitchell-Olds and Shaw, 1987), a proxy for Tokeshi's test (Tokeshi, 1992). ND=Not Determined. Significance level is indicated with "\*\*\*\*", "\*\*\*" and "\*\*" for p-values <0.001, <0.01 and <0.05, respectively.

**Figure S5.** Occupancy-frequency distributions of populations binned by phyla/class during the December 2015 and January 2016 cruises. Total, picoplankton and "large" denote size-fractionated community DNA from >0.2  $\mu\text{m}$ , >0.2 and <3.0  $\mu\text{m}$  and 3.0  $\mu\text{m}$  filters, respectively. Bimodality tests was performed using Mitchell-Olds and Shaw's test for



quadratic extremes (Mitchell-Olds and Shaw, 1987), a proxy for Tokeshi's test (Tokeshi, 1992). ND=Not Determined. Significance level is indicated with "\*\*\*\*", "\*\*\*" and "\*\*" for p-values <0.001, <0.01 and <0.05, respectively.

**Figure S6.** Occupancy-frequency distributions of OTUs affiliated with *Prochlorococcus* sp. during the October 2015 (A), and December 2015 and January 2016 cruises (B). Total, picoplankton and "large" in (B) denote size-fractionated community DNA from >0.2  $\mu\text{m}$ , >0.2 and <3.0  $\mu\text{m}$  and >3.0  $\mu\text{m}$  filters, respectively. Bimodality tests was performed using Mitchell-Olds and Shaw's test for quadratic extremes (Mitchell-Olds and Shaw, 1987), a proxy for Tokeshi's test (Tokeshi, 1992). ND=Not Determined. Significance level is indicated with "\*\*\*\*", "\*\*\*" and "\*\*" for p-values <0.001, <0.01 and <0.05, respectively.

**Figure S7.** Maximum-likelihood tree of OTUs affiliated with *Prochlorococcus* sp. exhibiting core or satellite metapopulation dynamics obtained from 16S rRNA gene data from all cruises. The evolutionary history was inferred by using the Maximum Likelihood method based on the Tamura-Nei model (Tamura and Nei, 1993). The bootstrap consensus tree inferred from 999 replicates is taken to represent the evolutionary history of the taxa analyzed (Felsenstein, 1985). Branches corresponding to partitions reproduced in less than 50% bootstrap replicates are collapsed. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. The analysis involved 18 nucleotide sequences. All positions containing gaps and missing data were eliminated. There were a total of 427 positions in the final dataset. Evolutionary analyses were conducted in MEGA7 (Kumar et al., 2016).



**Table S1.** Prevalence of significantly bimodal occupancy-frequency patterns in different community compartments (size fractions and taxa) in the present paper. Bimodality tests was performed using Mitchell-Olds and Shaw’s test for quadratic extremes (Mitchell-Olds and Shaw, 1987), a proxy for Tokeshi’s test (Tokeshi, 1992). ND=Not Determined. Significance level is indicated with ”\*\*\*\*”, ”\*\*\*” and”\*\*” for p-values <0.001, <0.01 and <0.05, respectively.

Community	October	November		December		January		
	Total	Total	Total	Picoplankton	“Large”	Total	Picoplankton	“Large”
All	YES***	YES***	YES**	YES**	NO	YES**	YES*	NO
Cyanobacteria	YES***	YES***	YES**	YES**	NO	YES*	NO	NO
Bacteroidetes	NO	NO	NO	NO	NO	NO	NO	NO
Actinobacteria	NO	NO	NO	NO	NO	NO	NO	NO
Verrucomicrobia	NO	NO	NO	ND	NO	NO	ND	NO
Alphaproteobacteria	YES***	NO	NO	NO	NO	YES*	NO	NO
Betaproteobacteria	NO	ND	ND	ND	NO	ND	ND	NO
Gammaproteobacteria	NO	NO	NO	NO	NO	NO	NO	NO
Planctomycetes	NO	NO	NO	NO	NO	NO	ND	NO
Acidobacteria	ND	ND	ND	ND	NO	ND	ND	NO
Deltaproteobacteria	NO	NO	NO	NO	NO	NO	NO	NO
Chloroflexi	NO	NO	NO	NO	NO	NO	NO	NO
<i>Prochlorococcus</i> sp.	YES***	YES**	YES*	YES*	NO	YES*	YES*	NO
<i>Synechococcus</i> sp.	NO	NO	NO	NO	NO	NO	ND	NO
SAR11 clade	YES**	YES**	NO	NO	NO	YES*	NO	NO
SAR86 clade	NO	NO	NO	NO	NO	NO	NO	NO
Aegan-169	YES***	YES**	NO	NO	NO	NO	NO	NO

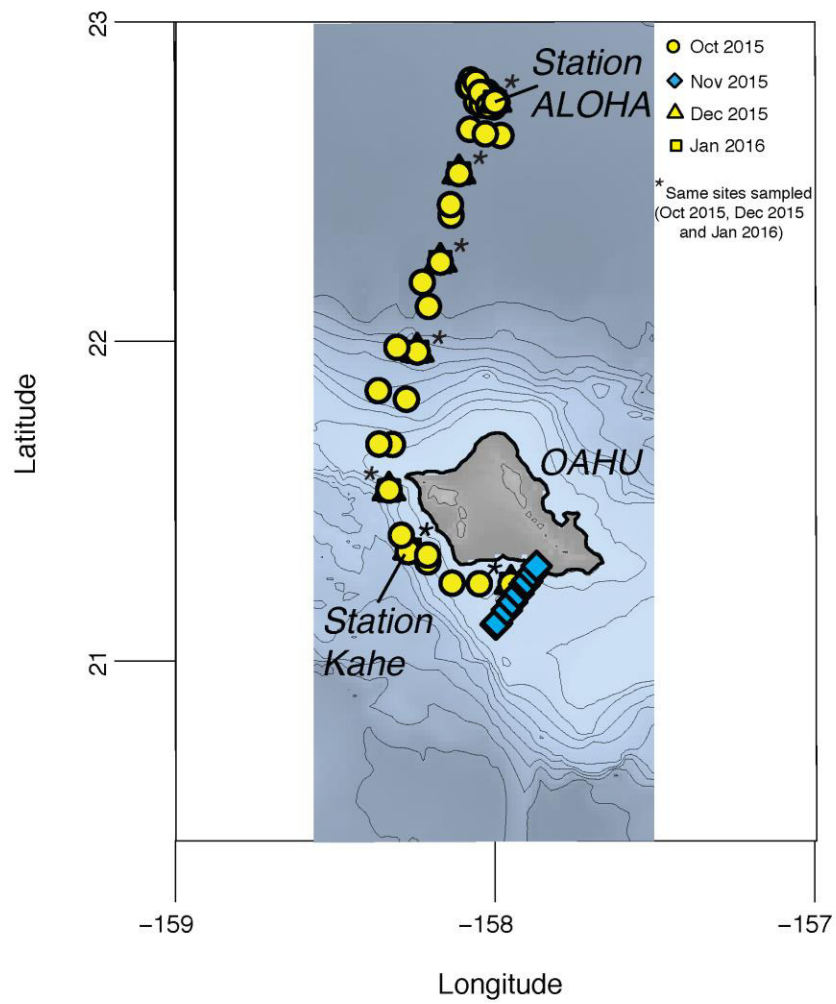
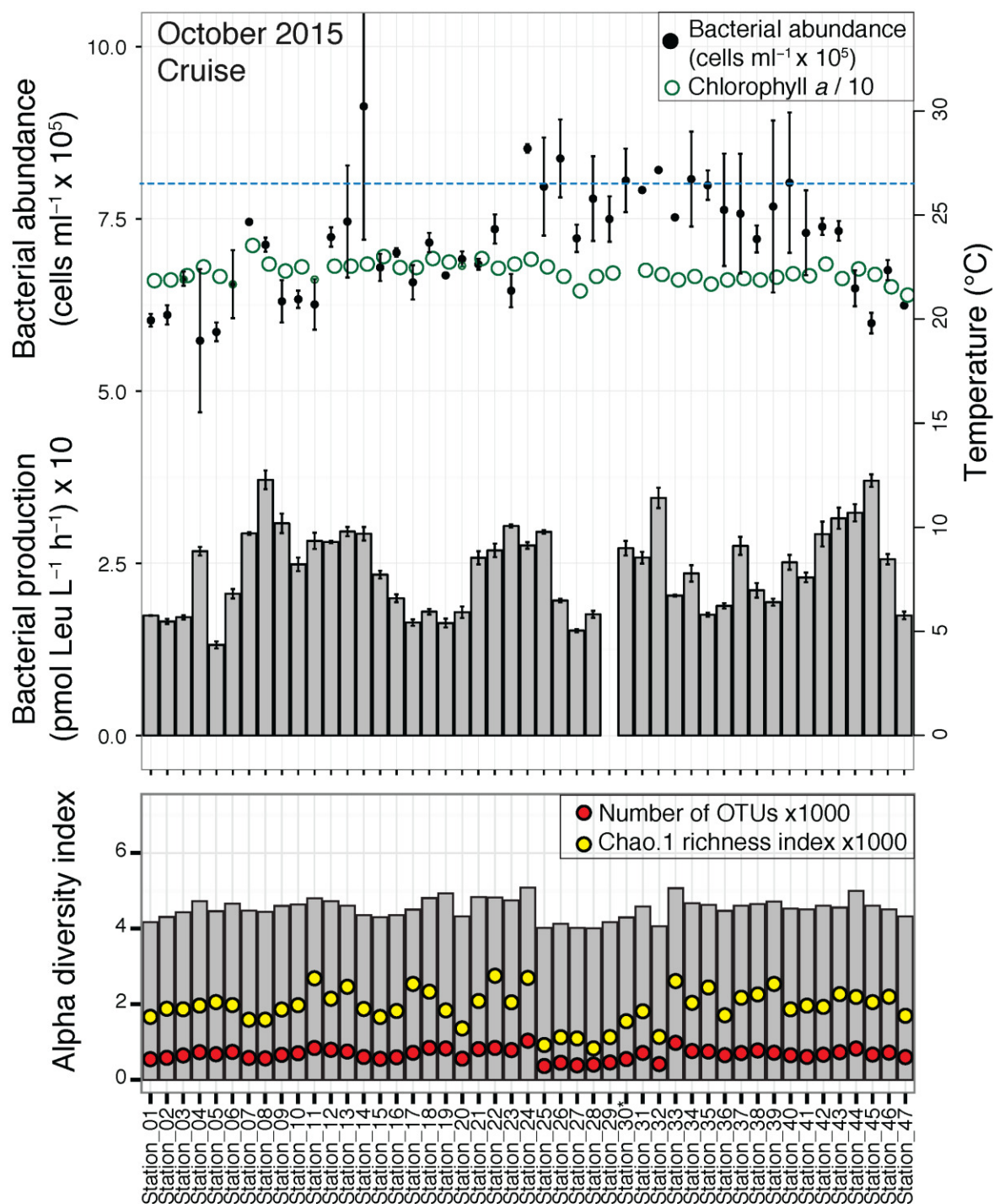


Figure 1



\*CTD cast surface 5 m  
(control/biological replicate for station 29)

**Figure 2**

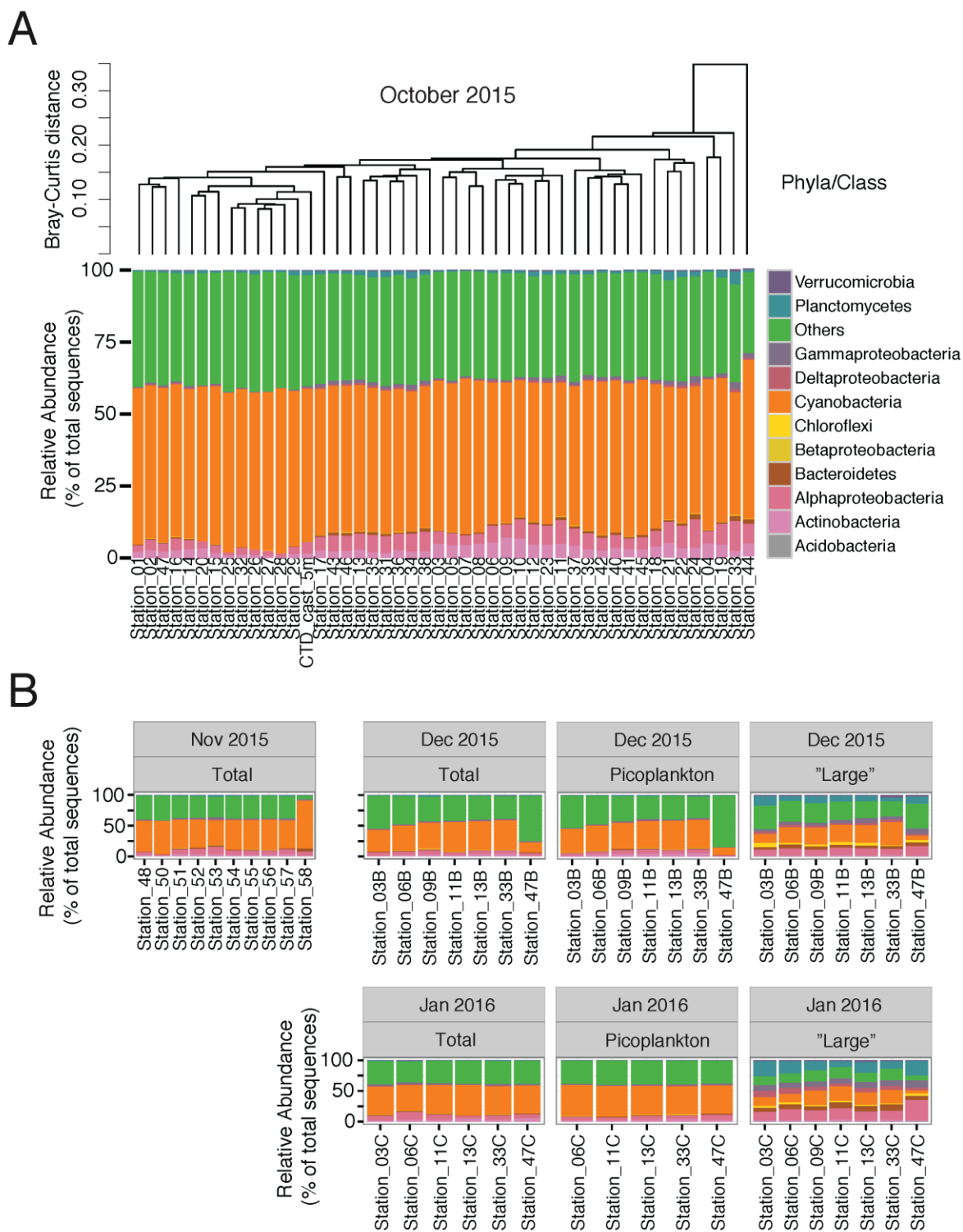
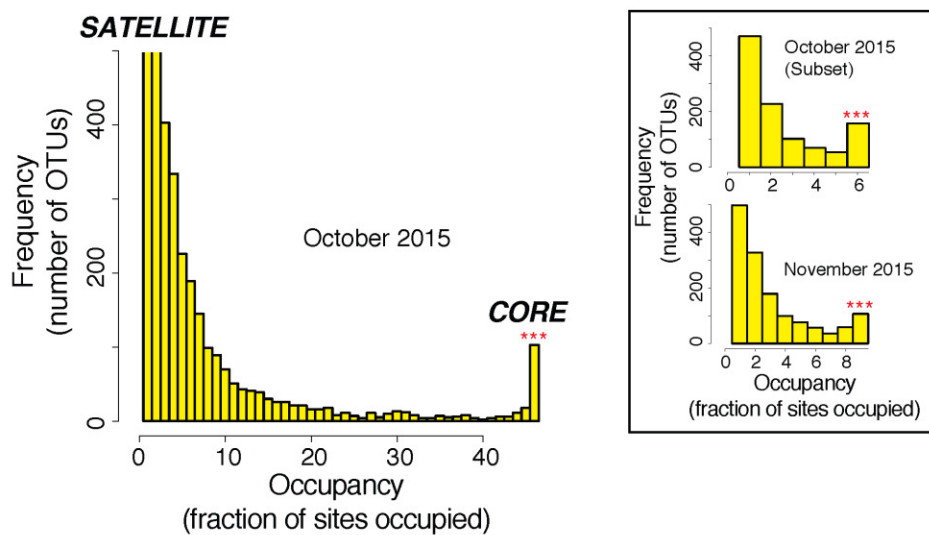
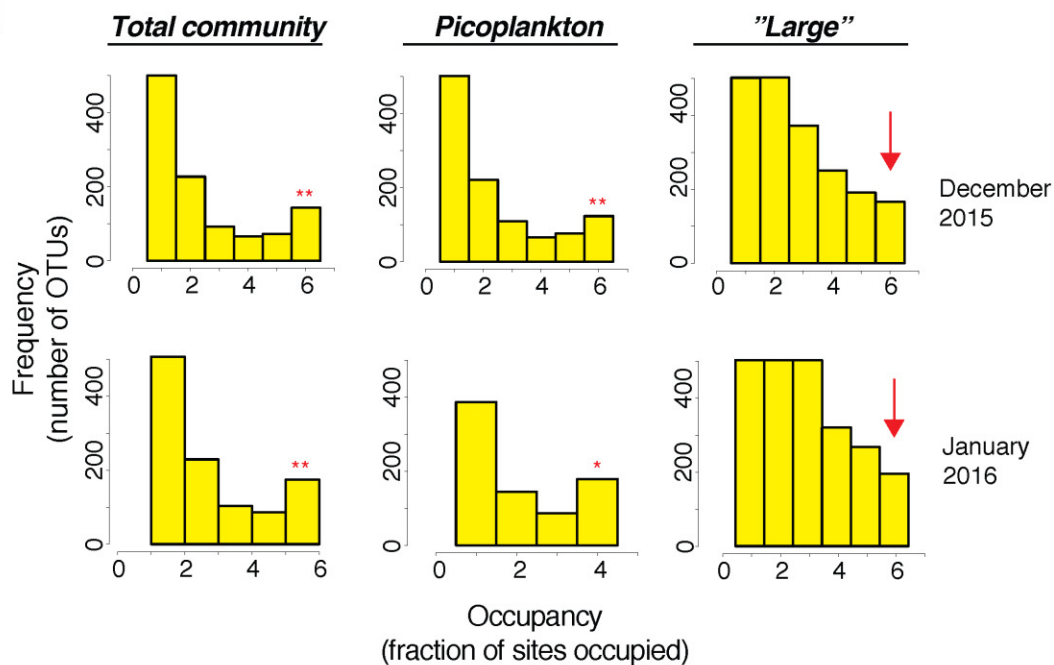


Figure 3

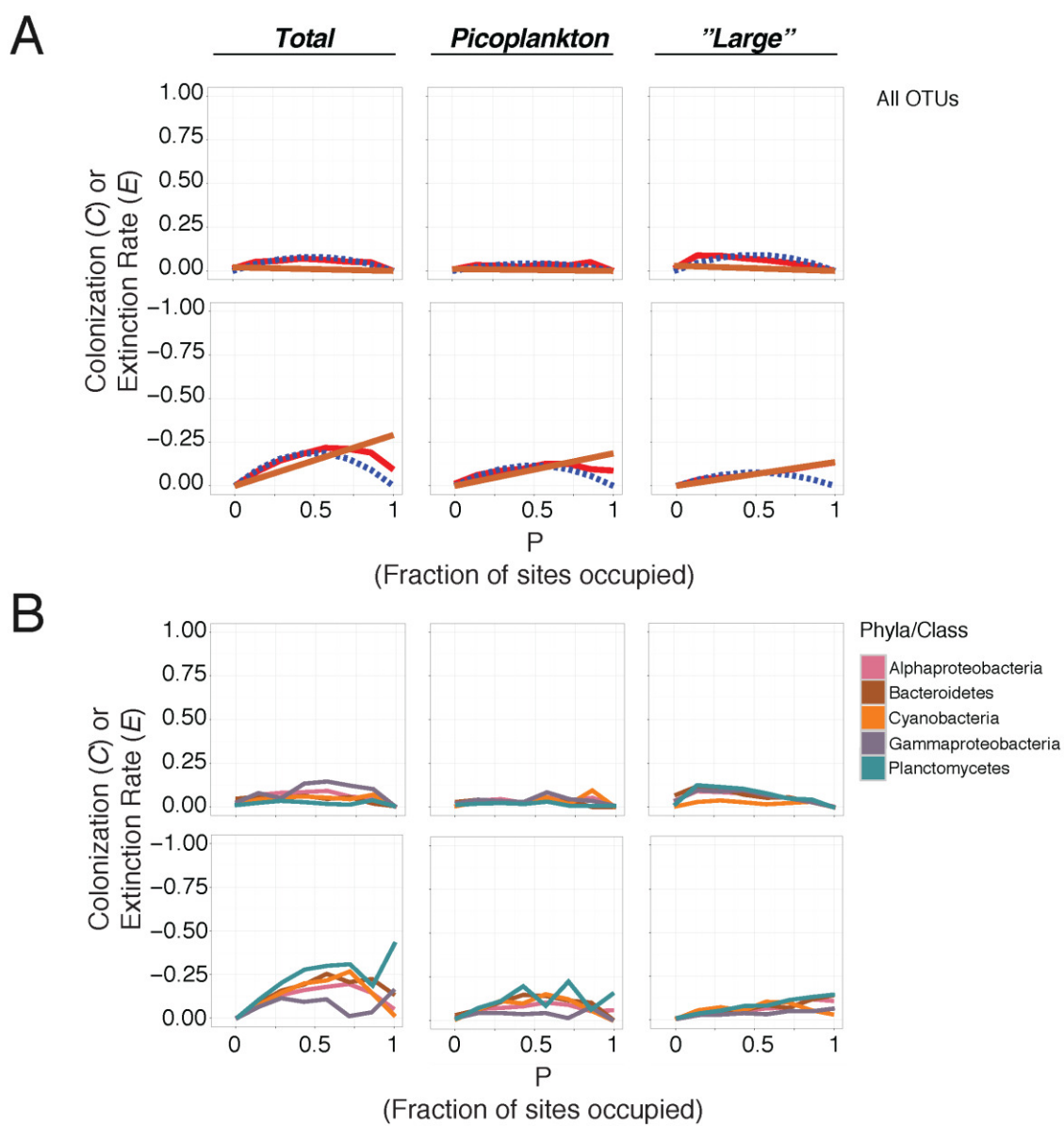
**A**



**B**

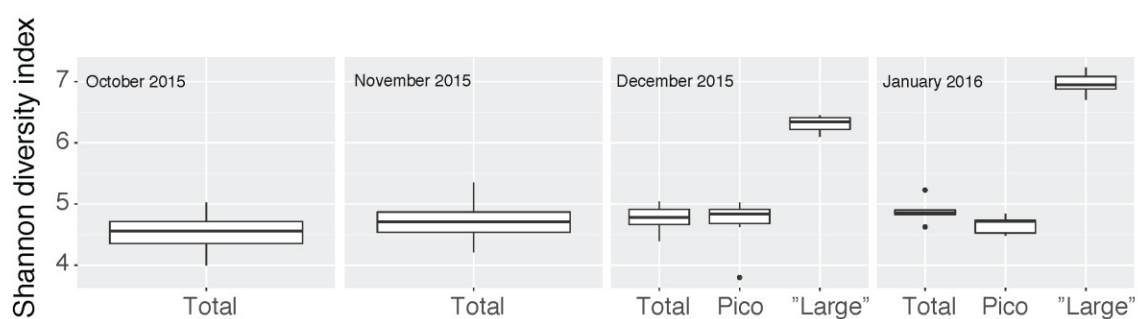


*Figure 4*

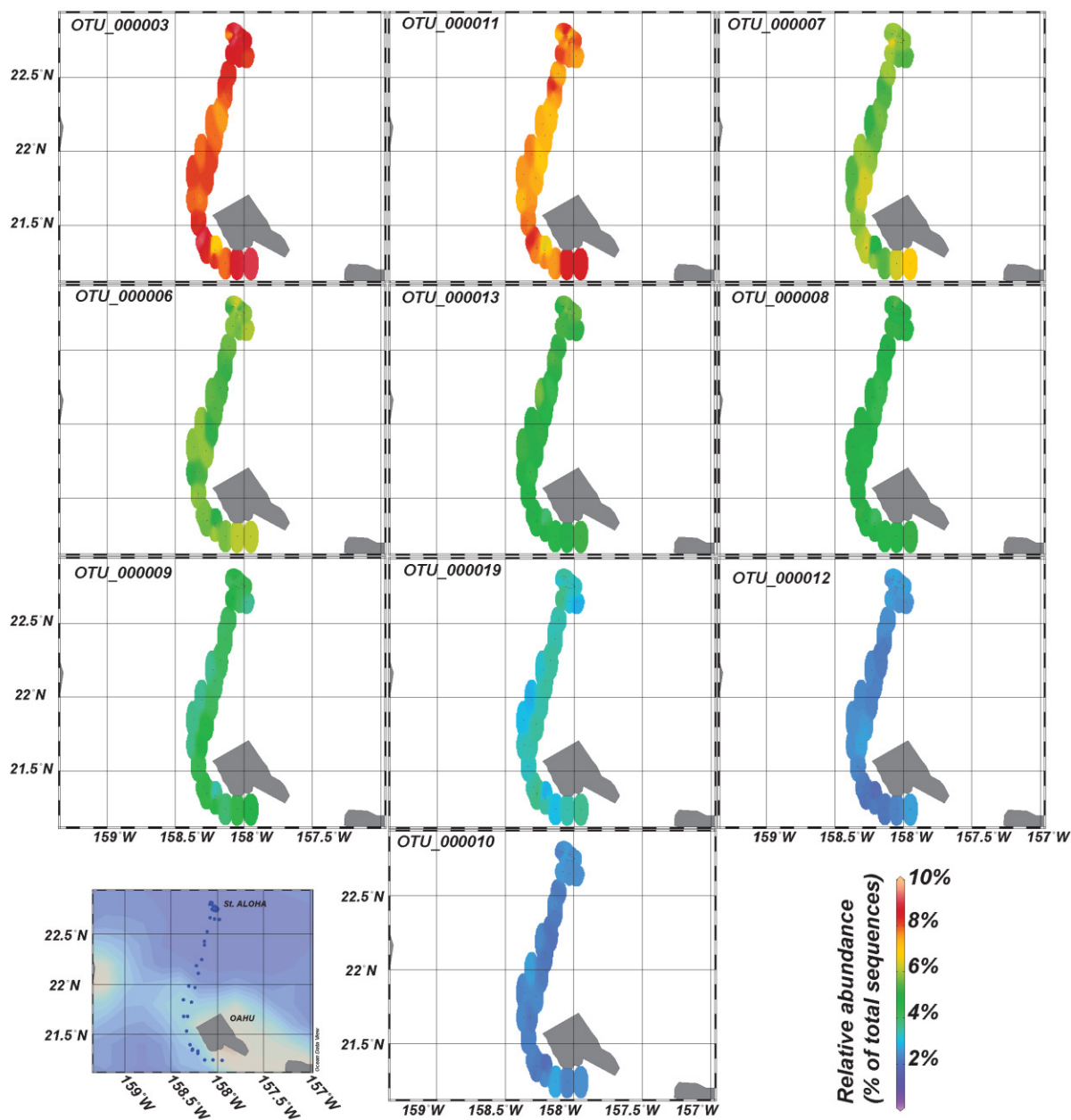


*Figure 5*

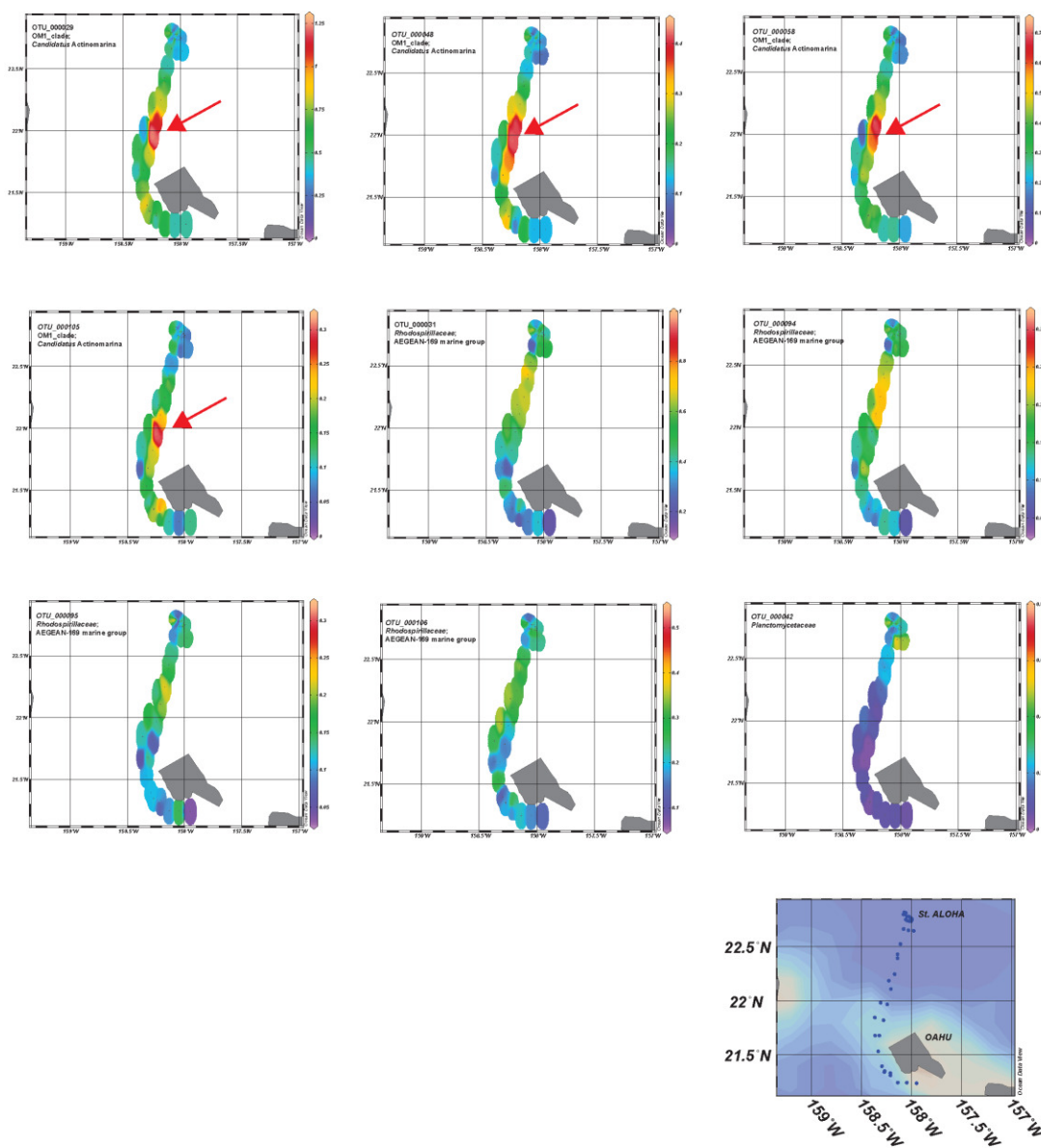




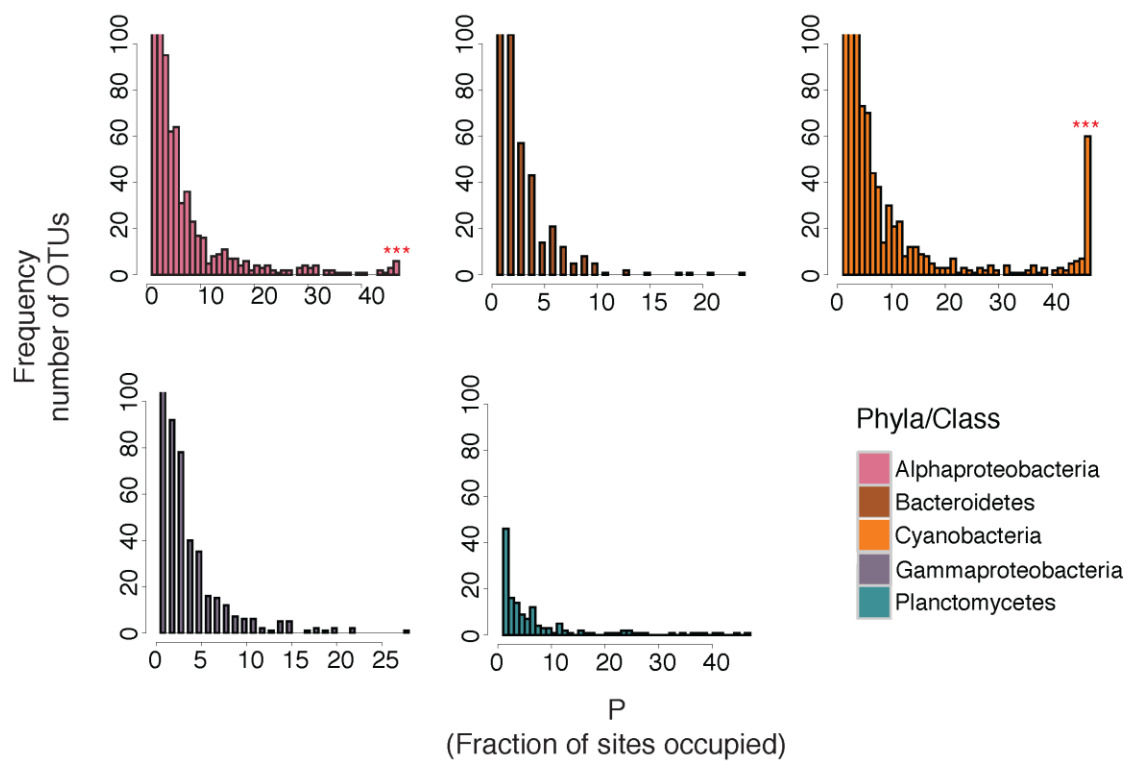
*Supplementary Figure 1*



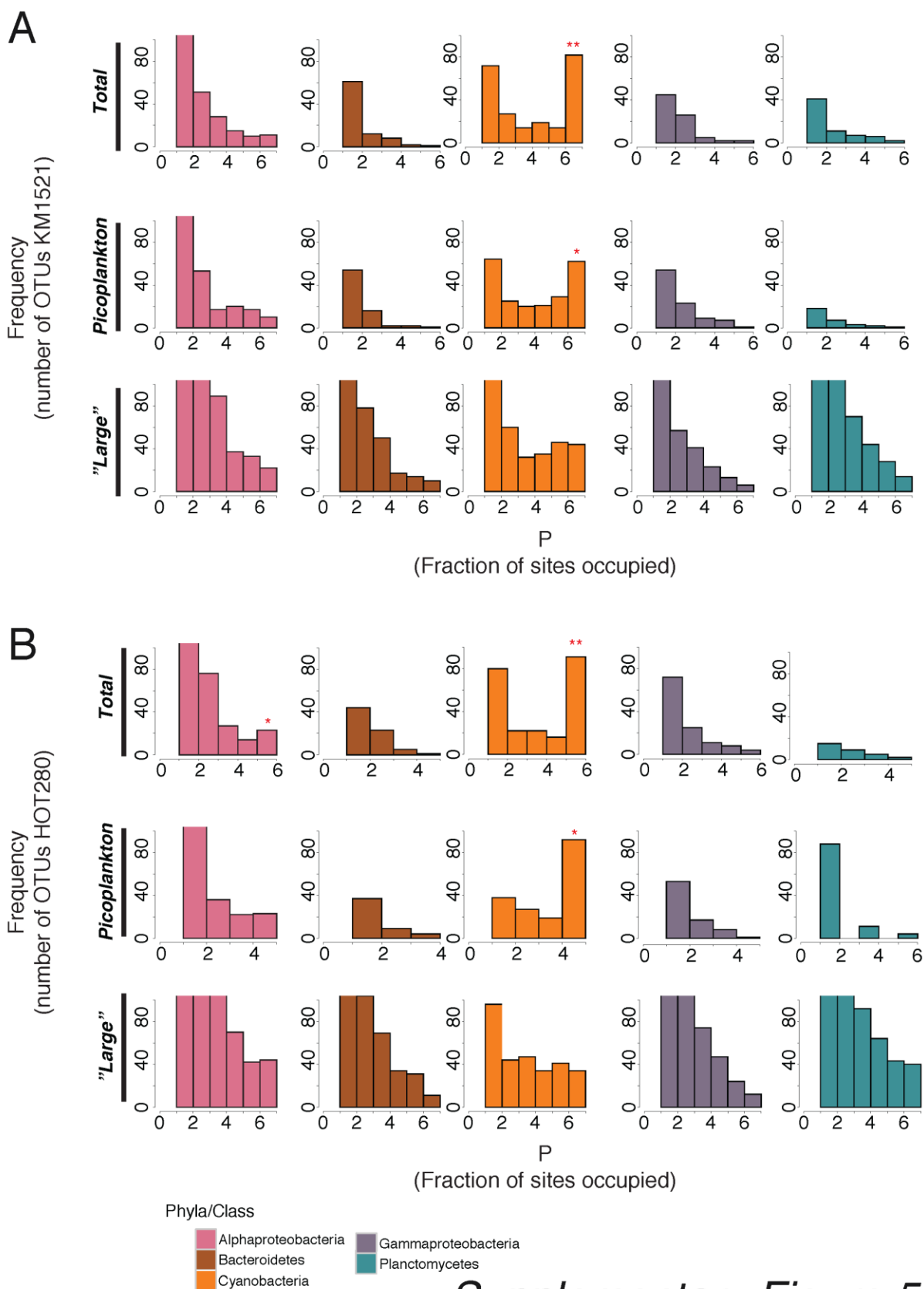
*Supplementary Figure 2*



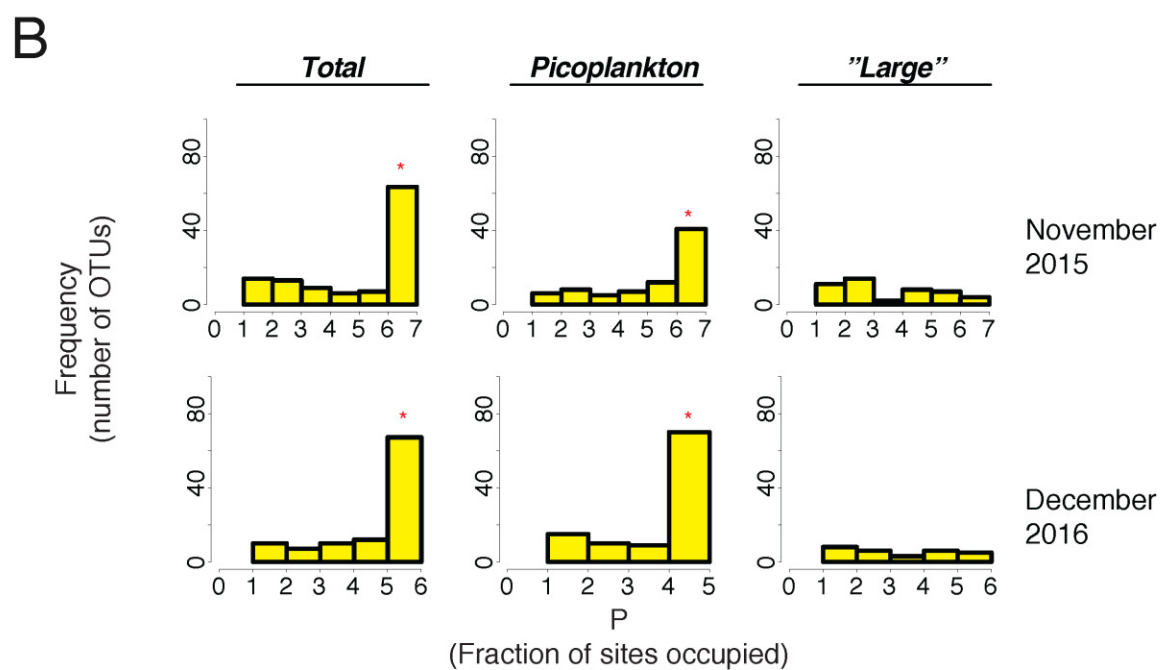
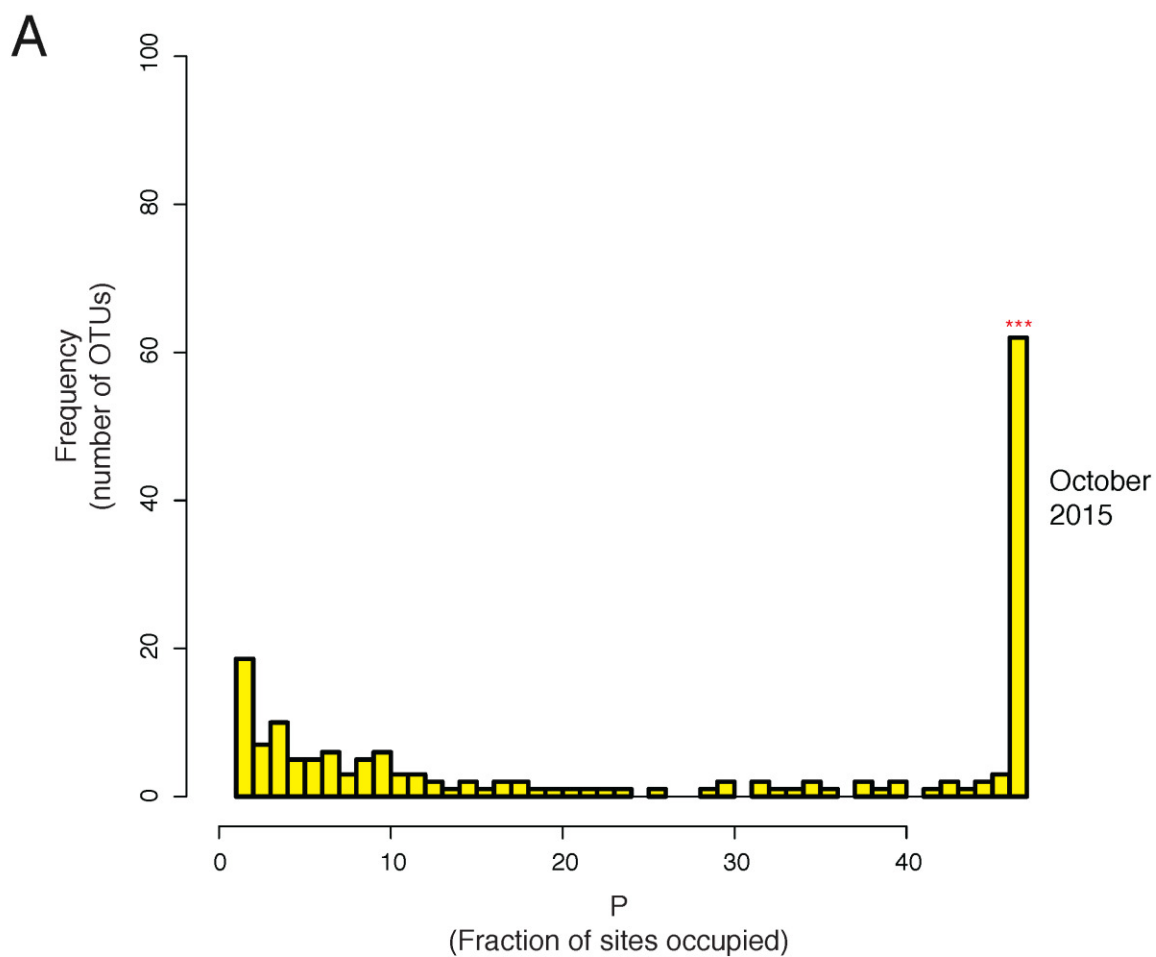
*Supplementary Figure 3*



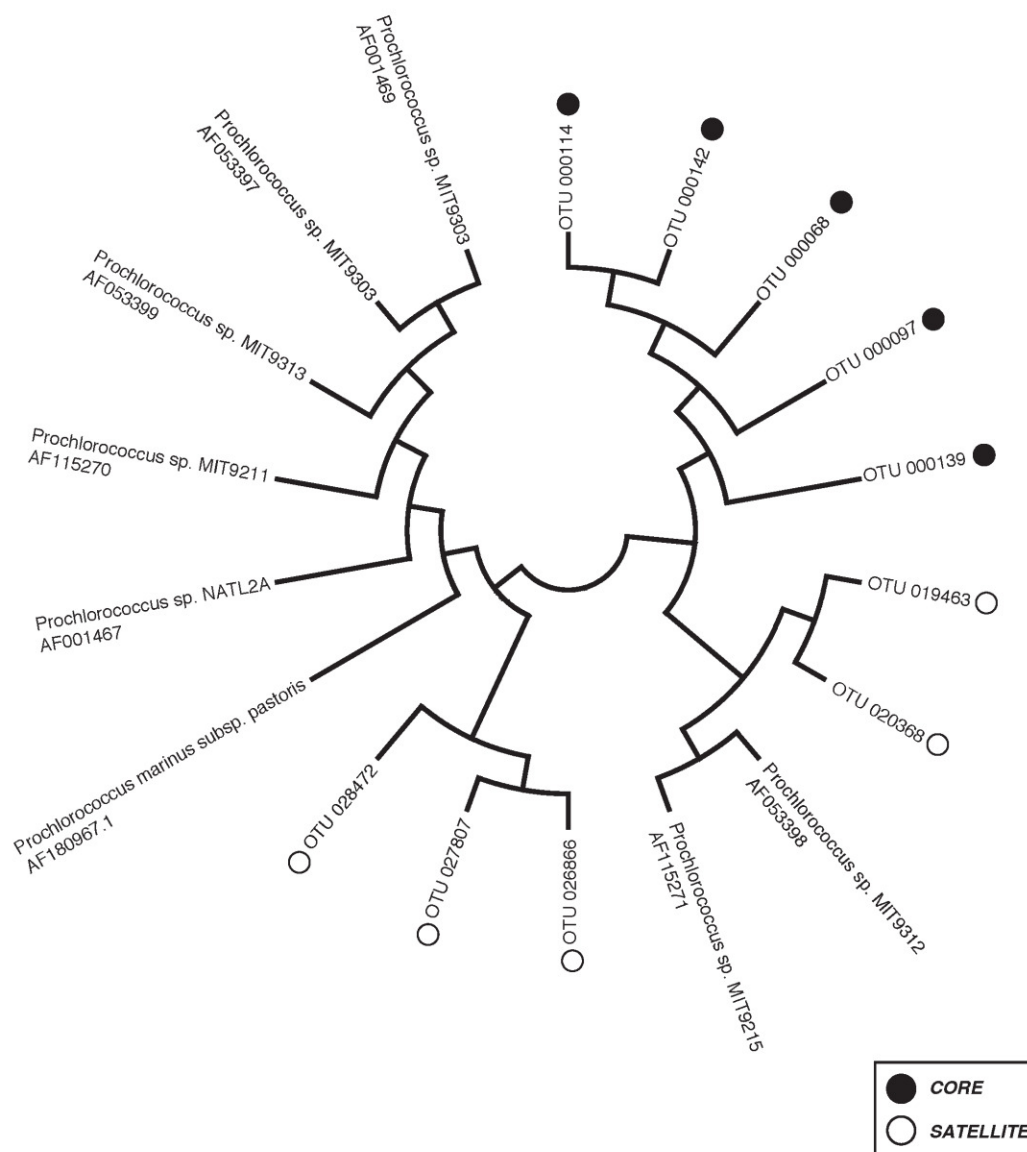
*Supplementary Figure 4*



*Supplementary Figure 5*



*Supplementary Figure 6*



Supplementary Figure 7