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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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.

Introduction

44

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

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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 Vaulot, 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_2) 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 ^{3}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 ^{3}H-leucine stock (3, 4, 5 -^{3}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 ^{3}H-leucine incorporation rates were

123   incubated shipboard at *in situ* temperatures following the ^{3}H-leucine incorporation protocol

124   described in (Kirchman et al., 1985) and (Smith and Azam, 1992). Preserved bacterial

125   abundance and killed ^{3}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). ^{3}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 ^{3}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±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"

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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^{-1} and 26°C,

187   respectively (Fig. 2). Bacterial abundance varied ~2-fold (ranging 5.73 $\times 10^5$ cells ml^{-1} to 9.13

188    $\times 10^5$ cells ml^{-1}; Fig. 2). ^{3}H-leucine incorporation rates ranged between 13 and 37 pmol Leu L^{-1}

189   h^{-1} (Fig. 2). Variation in bacterial abundance and production was overall small (SD = 0.7 $\times 10^5$

190   cells ml^{-1} and SD = 6 pmol Leu L^{-1} h^{-1}; 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 5.06and 903.45

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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 µm filter fraction) compared to

198 the total (>0.2 µm) and picoplankton fraction (0.2 and 3.0 µm; 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

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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

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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).

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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

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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 μm size fraction) and

310   picoplanktonic ($\geq$0.2 μm $\leq$3.0 μm size fraction) communities typically displayed bimodal

311   patterns, whereas the larger size class ($\geq$3.0 μm 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).

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319

320   *Environmental conditions and diversity regulate metapopulation dynamics*

321   Concomitant measurements of environmental variables, bacterial abundance and

322   ^{3}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

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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

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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.

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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 µm, >0.2 and <3.0 µm and 3.0

551 µm 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 µm, >0.2 and <3.0 µm and 3.0 µm 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 µm, >0.2 and <3.0 µm and 3.0 µm 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 µm, >0.2 and <3.0 µm and >3.0 µm 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.

	October	November	December			January		
Community	**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
Prochlorococcus sp.	YES***	YES**	YES*	YES*	NO	YES*	YES*	NO
Synechococcus 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

28

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

Figure 2

Figure 3

Figure 4

Figure 5

32

Supplementary Figure 1
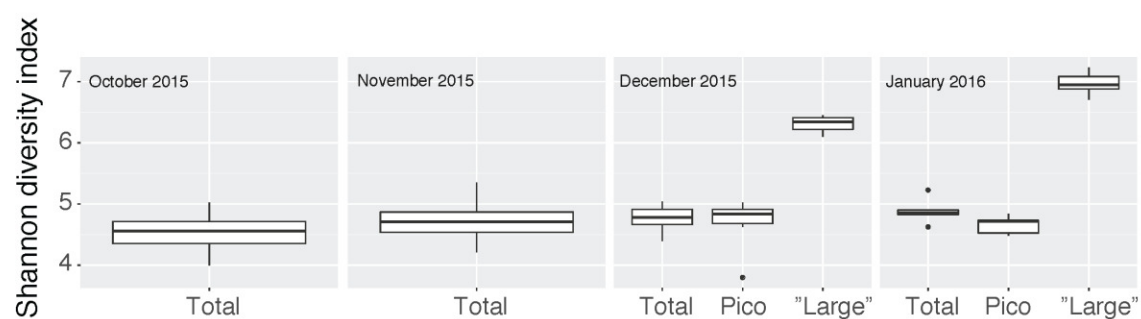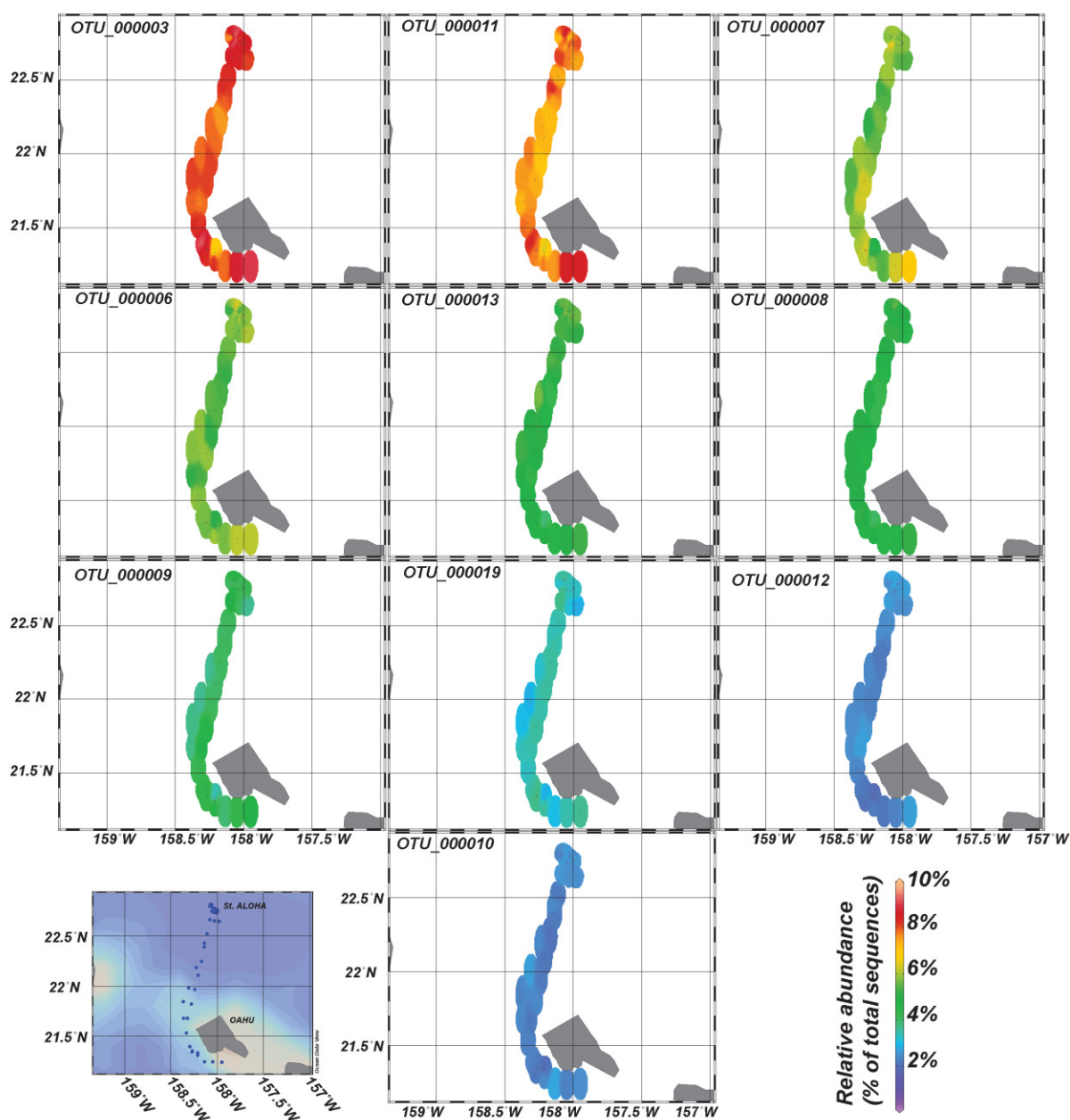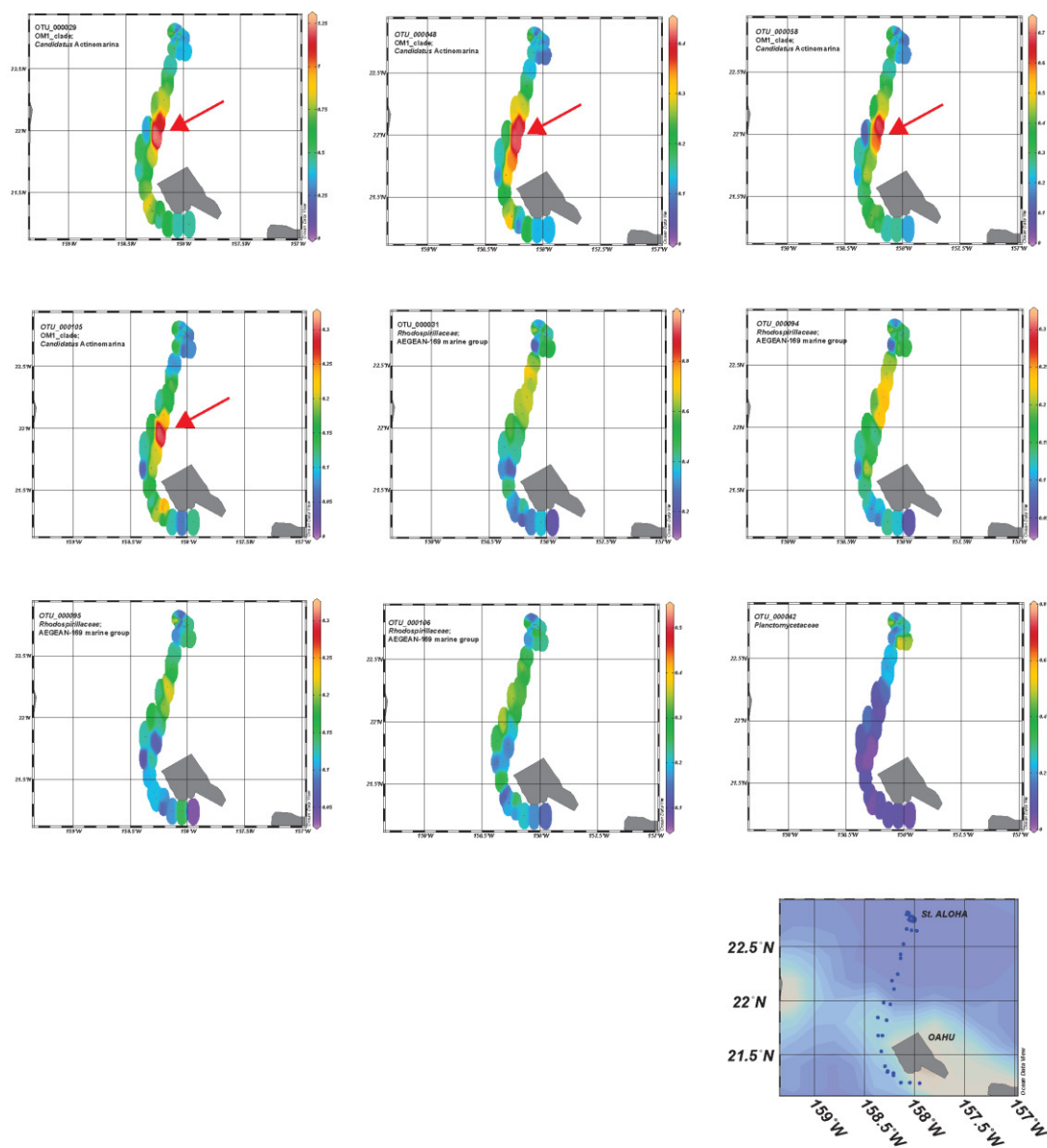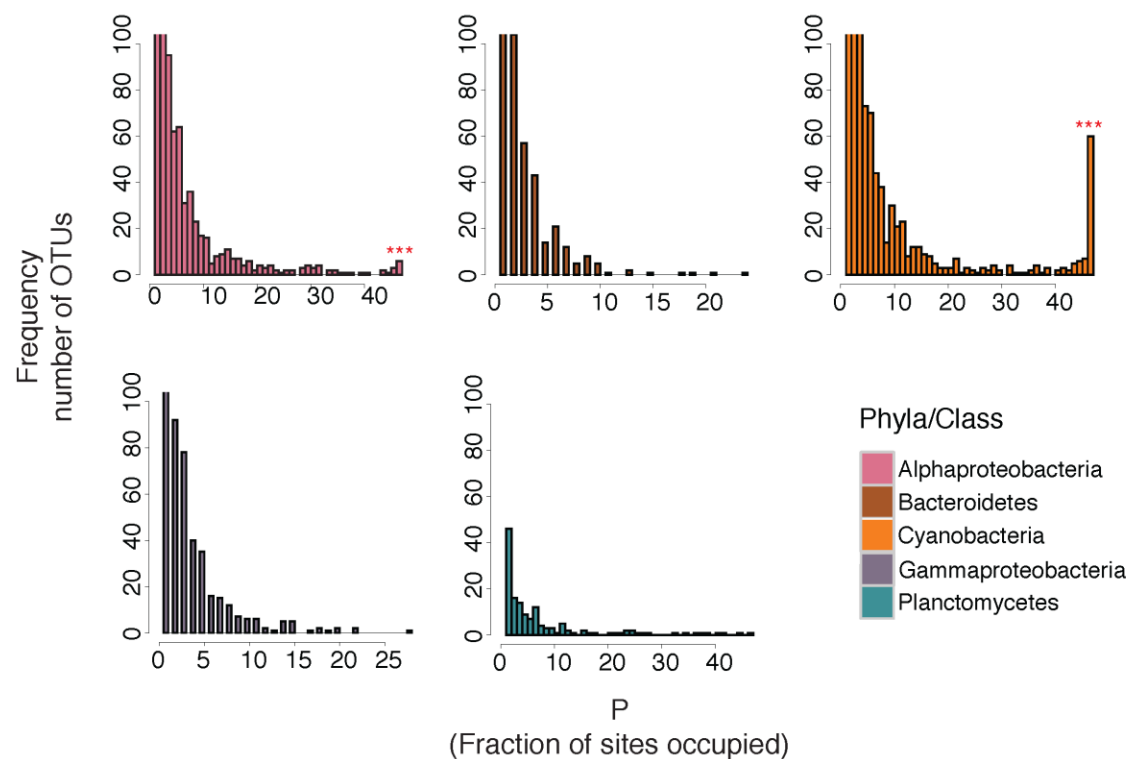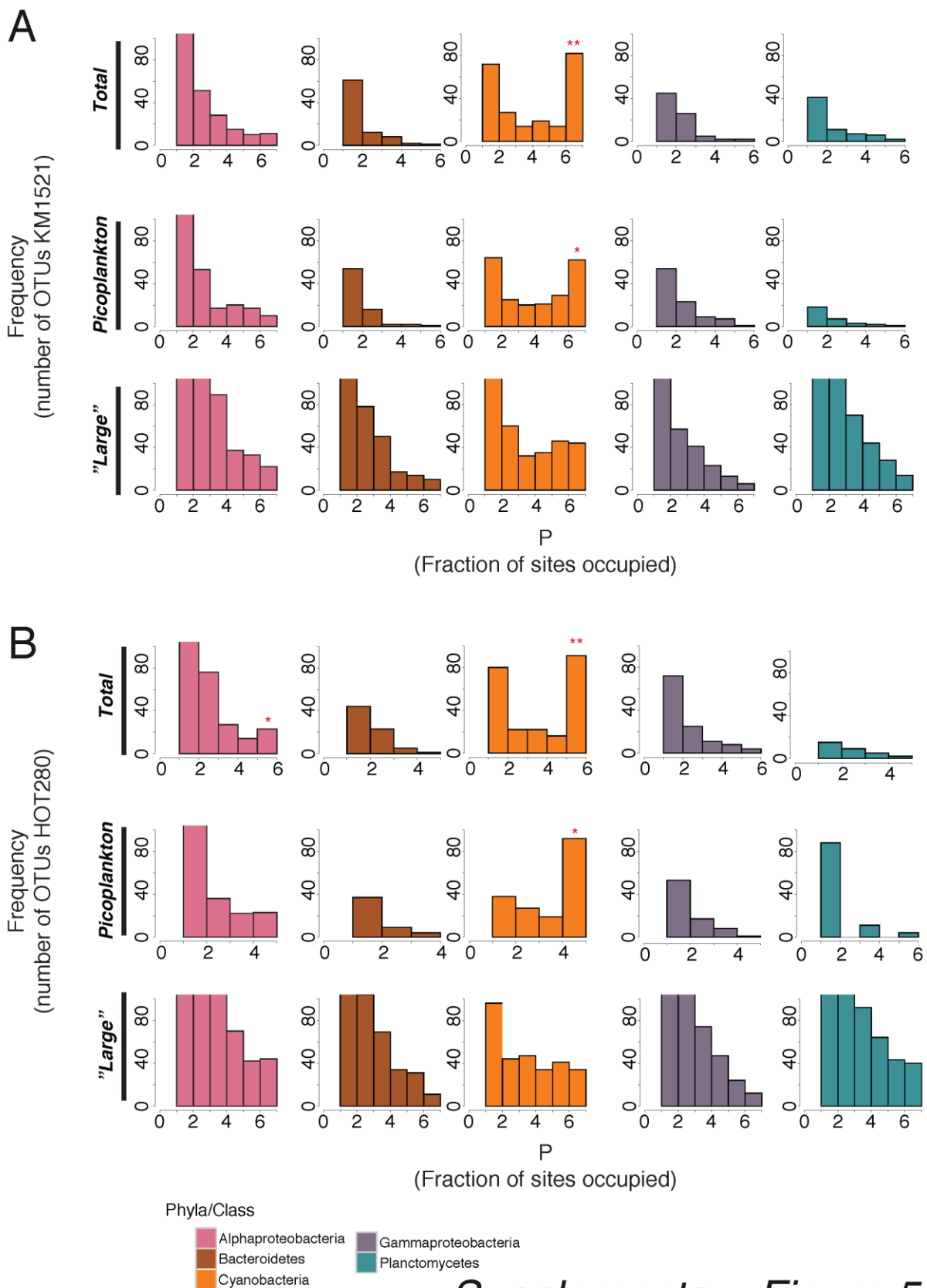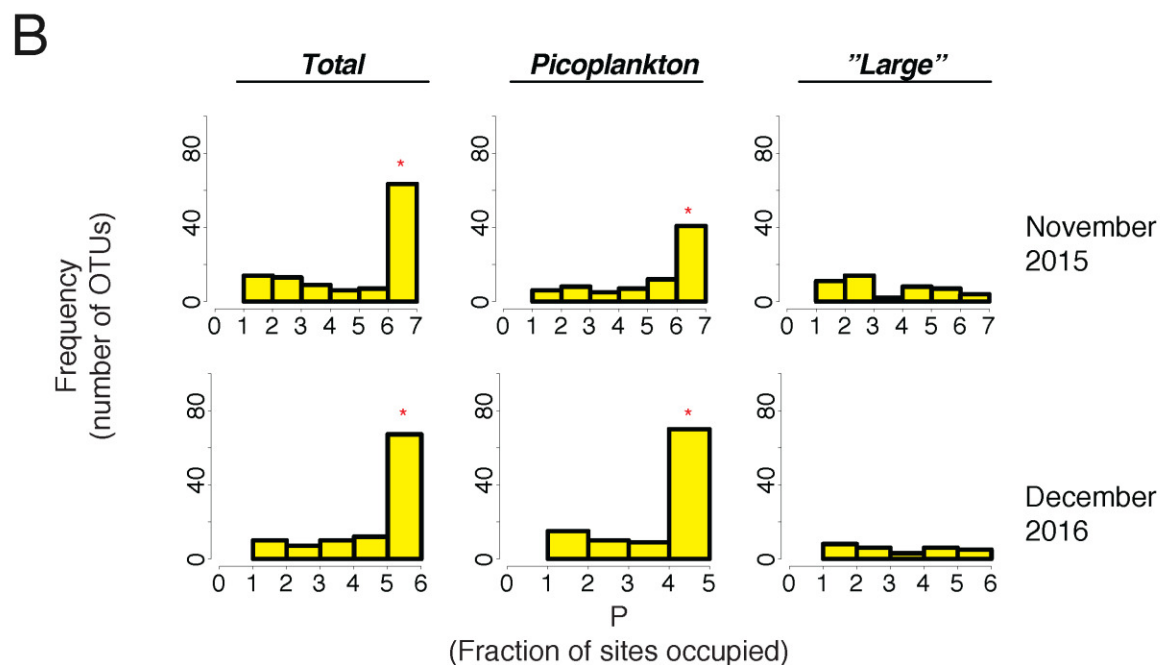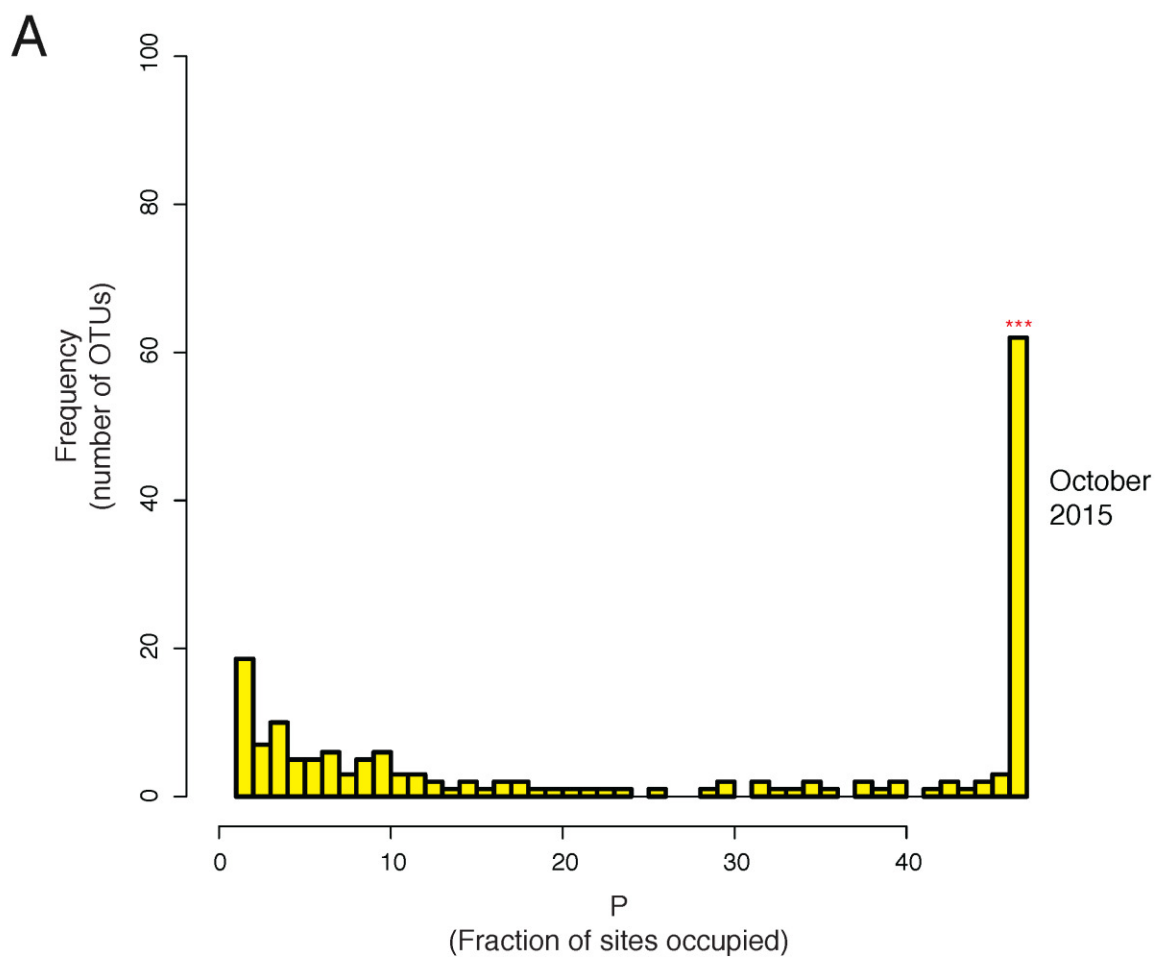
Supplementary Figure 2

Supplementary Figure 3
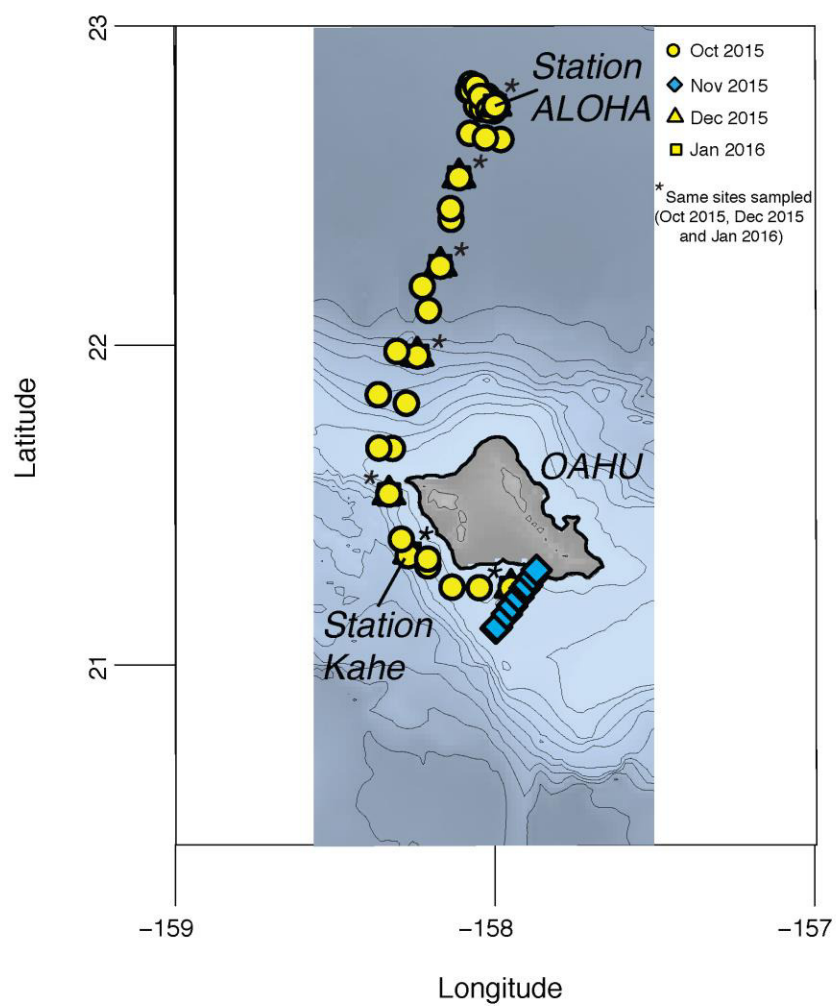
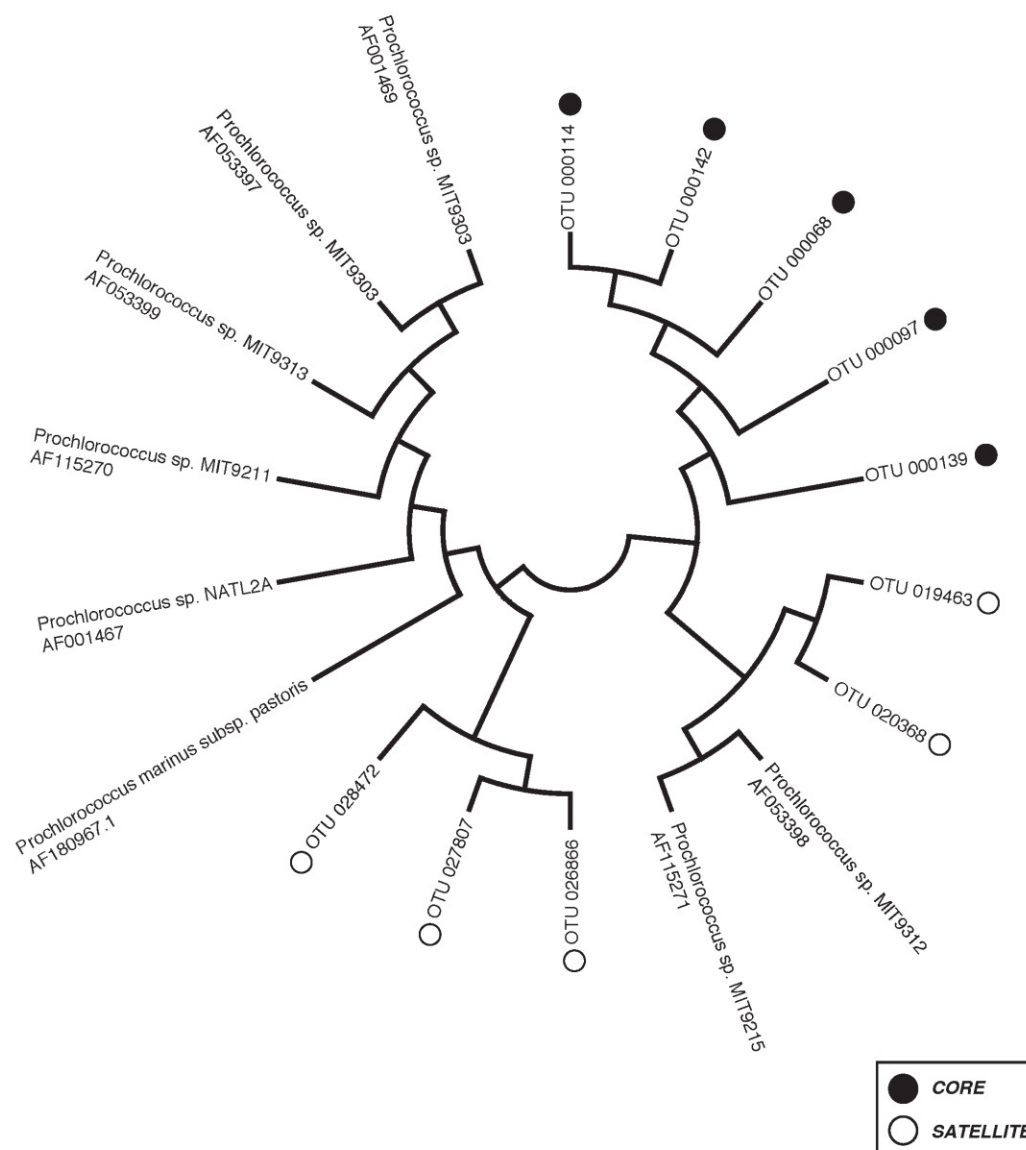*Supplementary Figure 4*
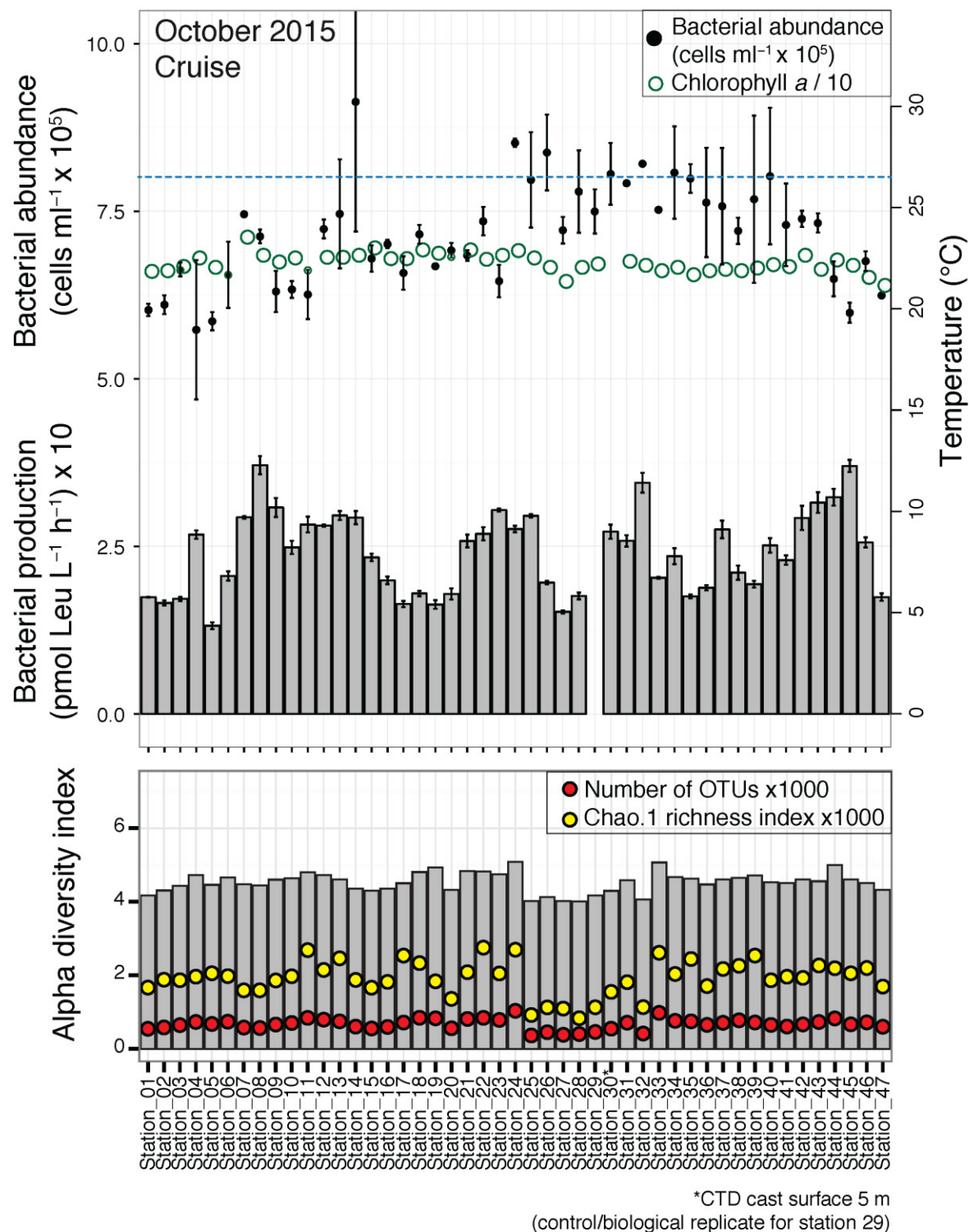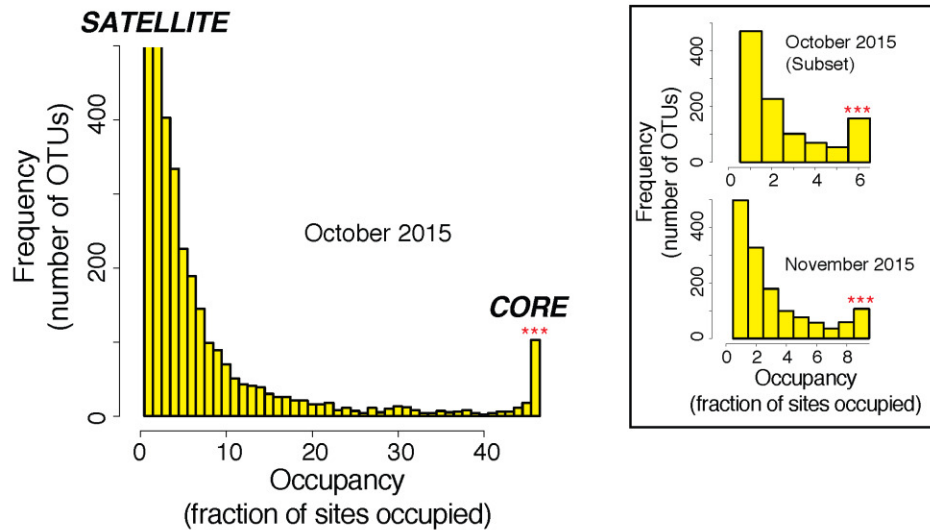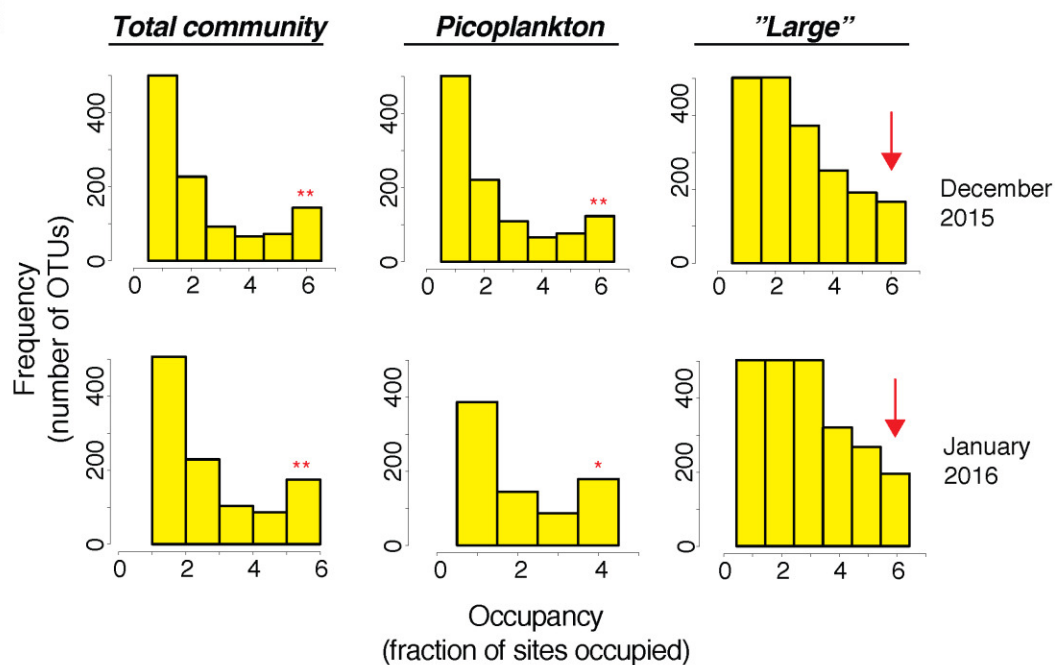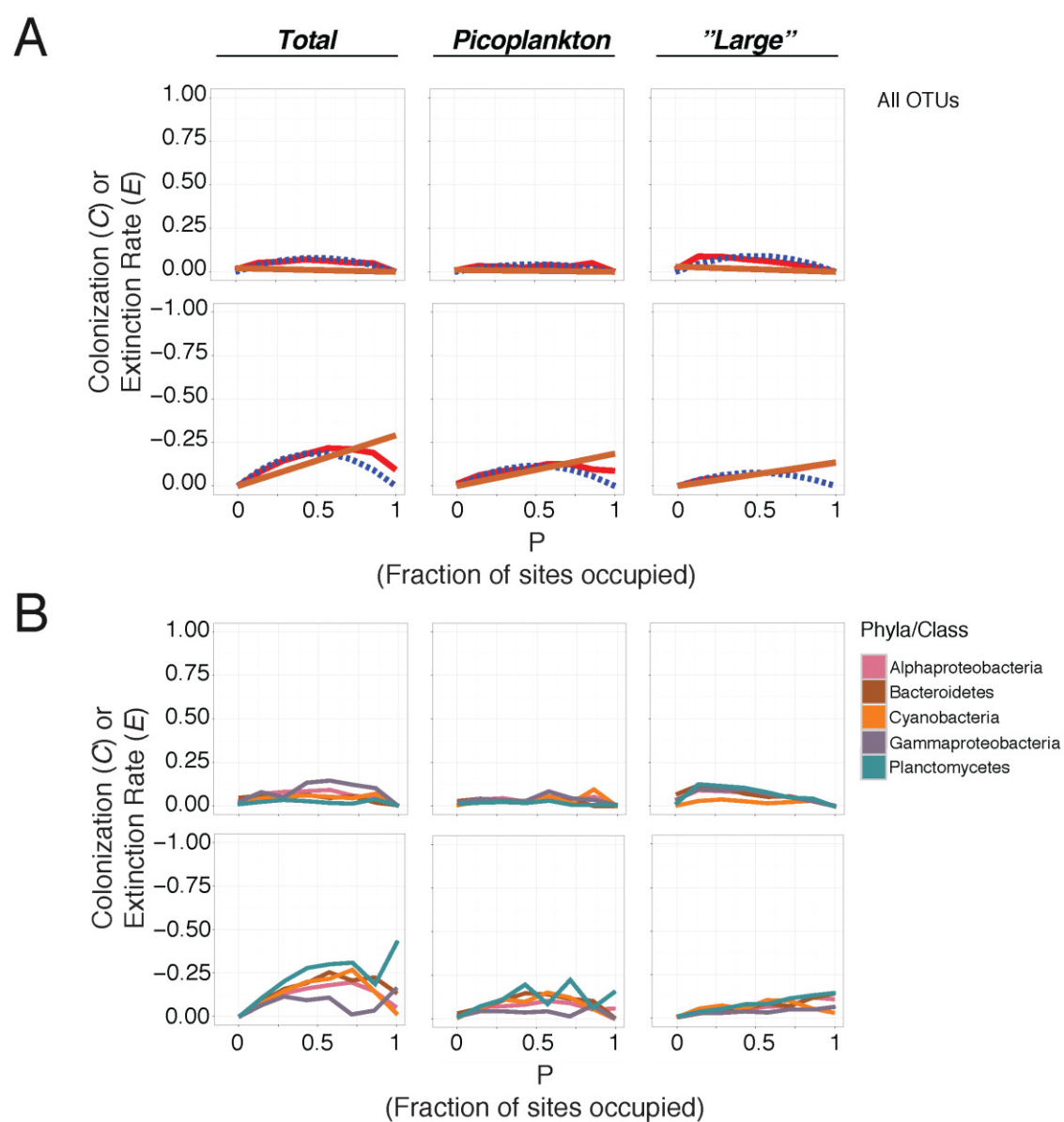
Supplementary Figure 5

Supplementary Figure 6

Supplementary Figure 7