



HAL
open science

Linking Spatial and Temporal Dynamic of Bacterioplankton Communities With Ecological Strategies Across a Coastal Frontal Area

Clarisse Lemonnier, Morgan Perennou, Damien Eveillard, Antonio Fernandez-Guerra, Aude Leynaert, Louis Marié, Hilary Morrison, Laurent Mémery, Christine Paillard, Lois Maignien

► To cite this version:

Clarisse Lemonnier, Morgan Perennou, Damien Eveillard, Antonio Fernandez-Guerra, Aude Leynaert, et al.. Linking Spatial and Temporal Dynamic of Bacterioplankton Communities With Ecological Strategies Across a Coastal Frontal Area. *Frontiers in Marine Science*, 2020, 7, 10.3389/fmars.2020.00376 . hal-02938091

HAL Id: hal-02938091

<https://hal.science/hal-02938091v1>

Submitted on 5 Jan 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Linking Spatial and temporal dynamic of bacterioplankton communities with ecological strategies across a coastal frontal area

1

2 **C. Lemonnier^{1,2}, M. Perennou², D. Eveillard³, A. Fernandez-Guerra^{4,5,6}, A. Leynaert², L.**
3 **Marié⁷, H.G. Morrison⁸, L. Memery², C. Paillard² and L. Maignien^{1,8}**

4

5 ¹Univ Brest (UBO), CNRS, IFREMER, Laboratoire de Microbiologie des Environnements Extrêmes,
6 F-29280 Plouzané, France

7 ²Univ Brest (UBO), CNRS, IRD, Ifremer, Laboratoire des Sciences de l'Environnement Marin, F-
8 29280 Plouzane, France

9 ³Univ Nantes, CNRS, Centrale Nantes, IMTA, Laboratoire des Sciences Numériques de Nantes, F-
10 44322 Nantes, France

11

12 ⁴Microbial Genomics and Bioinformatics Research Group, Max Planck Institute for Marine
13 Microbiology, Bremen, Germany

14

15 ⁵ Lundbeck Foundation GeoGenetics Centre, GLOBE Institute, University of Copenhagen, Øster
16 Voldgade 5-7, 1350 Copenhagen K, Denmark

17

18 ⁶University of Bremen, Center for Marine Environmental Sciences, 28359 Bremen, Germany

19

20 ⁷Univ. Brest, CNRS, IRD, Ifremer, Laboratoire d'Océanographie Physique et Spatiale, F-29280
21 Plouzané, France

22 ⁸Marine Biological Laboratory, Josephine Bay Paul Center for Comparative Molecular Biology and
23 Evolution, Woods Hole, MA, United States

24

25 *** Correspondence:**

26 Loïs Maignien

27 lois.maignien@univ-brest.fr

28

29

30 **Keywords: Marine front, bacterial communities, dynamic, network, ecological strategies**

31

32

33 **Abstract**

34 Ocean frontal systems are widespread hydrological features defining the transition zone between
35 distinct water masses. They are generally of high biological importance as they are often associated
36 with locally enhanced primary production by phytoplankton. However, the composition of bacterial
37 communities in the frontal zone remains poorly understood. In this study, we investigate how a coastal
38 tidal front in Brittany (France) structures the free-living bacterioplankton communities in a spatio-
39 temporal survey across four cruises, five stations and three depths. We used 16S rRNA gene surveys
40 to compare bacterial community structures across 134 seawater samples and defined groups of co-
41 varying taxa (modules) exhibiting coherent ecological patterns across space and time. We found that
42 bacterial communities composition was strongly associated with the biogeochemical characteristics of
43 the different water masses and that the front act as an ecological boundary for free-living bacteria.
44 Seasonal variations in primary producers and their distribution in the water column appeared as the
45 most salient parameters controlling heterotrophic bacteria which dominated the free-living community.
46 Different dynamics of modules observed in this environment were strongly consistent with a
47 partitioning of heterotrophic bacterioplankton in oligotroph and copiotroph ecological strategies.
48 Oligotroph taxa, dominated by SAR11 Clade members, were relatively more abundant in low
49 phytoplankton, high inorganic nutrients water masses, while copiotrophs and particularly opportunist
50 taxa such as *Tenacibaculum sp* or *Pseudoalteromonas sp* reached their highest abundances during the
51 more productive period. Overall, this study shows a remarkable coupling between bacterioplankton
52 communities dynamics, trophic strategies, and seasonal cycles in a complex coastal environment.

53

54 1 Introduction

55 Bacteria dominate the marine environment in abundance, diversity and activity where they
56 support critical roles in the functioning of marine ecosystems and oceanic biogeochemical cycles
57 (Falkowski et al., Fenchel, and Delong 2008; Cotner and Biddanda 2002; Madsen 2011). In the coastal
58 environment, they are closely associated with other planktonic organisms (e.g. viruses, phytoplankton
59 and zooplankton) during the recycling of organic matter and inorganic nutrients through the so-called
60 microbial loop (Azam and Malfatti 2007; Pomeroy et al. 2007). They form complex and highly
61 dynamic assemblage (S. J. Giovannoni and Vergin 2012), with bacterioplankton diversity variations in
62 space and time linked to changes in functional diversity (Galand et al. 2018). Therefore, understanding
63 how the bacterioplankton composition varies in the environment remains one of the central question
64 to elucidate so that we can better understand coastal ecosystem functioning (Fuhrman et al. 2015).

65 Phytoplankton development represents a major source of organic matter for heterotrophic
66 bacteria in the water column. During their growth and upon bloom termination, algae release a complex
67 bulk of dissolved organic matter that is almost only available for bacteria (Azam 1998; Fenchel and
68 Jørgensen 1977). This organic matter processing requires diverse heterotrophic bacterioplankton
69 among which one could find members of *Bacteroidetes (Flavobacteriaceae)*, *Roseobacter group*,
70 *Gammaproteobacteria and Verrucomicrobia* (Buchan et al. 2014). These taxa contribute to the
71 complexity of the marine ecosystem via different adaptive strategies, owing to the unequal access to
72 their respective resource (Stocker 2012; Luo and Moran 2014). For instance, heterotrophs are generally
73 distinguished as either oligotrophs or copiotrophs that compete at low and high nutrient concentrations
74 respectively (Koch 2001; Giovannoni et al. 2014). They also present different degrees of ecological
75 specialization, with generalist bacteria able to assimilate a broad variety of substrates, while specialists
76 will compete for a narrow range of nutrients (Mou et al. 2008). Analysis of these ecological traits offer
77 a simplified view of complex microbial communities and has gained interest for better understanding
78 the dynamics of natural microbial communities and to gain insight into their role in the ecosystem
79 (Krause et al. 2014; J. Raes et al. 2011; Haggerty and Dinsdale 2017).

80 Marine fronts are common mesoscale features in the ocean and are located at the transition
81 between water masses of different physicochemical characteristics that actively shape the distribution
82 of microbial organisms (phytoplankton, zooplankton and bacteria). Driven by currents and mixing,
83 local nutrient input in the vicinity of the front generally enhances primary and secondary production,
84 making the frontal zone an area of high biological importance (Olson and Backus 1985) and of critical
85 influence on the microbial processing of organic matter (Baltar et al. 2015; Heinänen et al. 1995).
86 However, the bacterial communities' composition involved in such dynamic systems remains to be
87 investigated (Baltar et al. 2016).

88 The Ushant Front in the Iroise Sea (Brittany, France) is considered as a model for coastal tidal
89 front (Le Fèvre 1986). Its position and characteristics are highly dynamic and influenced by
90 atmospheric forcing and tidal currents which are strong in this area (Le et al. 2009). It occurs from May
91 to October and leads to contrasting physicochemical environments with higher phytoplankton biomass
92 at the frontal area (Le Fèvre et al. 1983). West of the front, stratification results in warmer oligotrophic
93 surface waters and colder nutrient-rich deeper waters separated by a marked thermocline. East of the
94 front, associated with highly variable conditions, permanently mixed coastal waters are characterized
95 by an unlimited quantity of inorganic nutrients but with highly fluctuating conditions. These

96 contrasting water masses structure the distribution of primary producers with the dominance of small
97 phytoplankton and dinoflagellates in surface stratified waters and diatoms in mixed waters (Birrien et
98 al. 1991; GREPMA 1988; Videau 1987).

99 In this study, we investigated how such contrasting physicochemical and biological parameters will
100 drive free-living bacterioplankton community structure. We then tested the hypothesis that the
101 contrasted distribution of primary producers will select for bacteria with different adaptative strategies.
102 To do so, using a network analysis we defined groups of co-varying bacterial OTUs that present the
103 same dynamic across the samples, postulating that they may share the same ecological niches.

104

105 **Materials and Methods**

106

107 1. Study site and sampling design

108

109 For this study, we completed four east-west transects of about 60 km across the Iroise sea in September
110 2014 (the 9th, 10th and 11th), March 2015 (the 10th, 11th and 12th), July 2015 (the 1st, 2nd and 3rd)
111 and September 2015 (the 8th, 9th and 10th) aboard the R/V Albert Lucas. Station positions remained
112 identical across cruises and were designed to span the front (Fig. 1A). Station **5** ($48^{\circ}25\ N$, $5^{\circ}30\ W$) is
113 the most offshore station and is characterized by a strong stratification in summer. Station **4** ($48^{\circ}25\ N$,
114 $5^{\circ}20\ W$) and Station **3** ($48^{\circ}20\ N$, $5^{\circ}10\ W$) are closer the front. Station **2** ($48^{\circ}15\ N$, $5^{\circ}00\ W$) is present
115 in the mixed area and Station **1** ($48^{\circ}16\ N$, $4^{\circ}45\ W$) is the most coastal station, near the outflow of the
116 Bay of Brest. At each station, we obtained CTD profiles to assess the physical characteristics of the
117 water column and establish the depth designed to capture the important biological and chemical
118 features of the water column at the surface, bottom and Deep Chlorophyll Maximum (DCM).

119

120

121 2. Nutrients, phytoplankton counts and pigment analyses

122

123 Seawater was sampled at each depth for nutrients, biogenic silica (BSi), chlorophyll a (Chl a),
124 particulate organic carbon and nitrogen (POC/PON) concentrations, and microscopic phytoplankton
125 cell counts and identification. Dissolved inorganic phosphate (DIP) and silicate (DSi) concentrations
126 were determined from seawater filtered on Nucleopore membrane filters (47 mm) and dissolved
127 inorganic nitrogen (DIN) on Whatman GF/F filters (25 mm). Filters for DIN and DIP were then frozen,
128 whereas filters for DSi were kept at 4 °C in the dark. Concentrations were later determined in the
129 laboratory by colorimetric methods using segmented flow analysis (Auto-analyser AA3HR Seal-
130 Analytical) (Aminot and K erouel 2007). BSi was determined from particulate matter collected by
131 filtration of 1 L of seawater through 0.6 µm polycarbonate membrane filter. The analysis was
132 performed using the alkaline digestion method (Ragueneau and Tr guer 1994). Total Chl a and
133 phaeopigments (Pheo) were determined in particulate organic matter collected on 25 mm Whatman
134 GF/F filters. The filters were frozen (-20°C) and analyzed later by a fluorometric acidification

135 procedure in 90% acetone extracts (Holm-Hansen et al. 1965). Particulate material for POC/PON
136 measurements was recovered on pre-combusted (450 °C, 4 h) Whatman GF/F filters. Samples were
137 then analyzed by combustion method (Strickland and Parsons 1972), using a CHN elemental analyzer
138 (Thermo Fischer Flash EA 1112). Phytoplankton samples were fixed with Lugol's solution and cell
139 counts were carried out using the Lund et al. (1958) method (Lund et al. 1958).

140

141

142 3. Bacterioplankton community sampling

143

144 Seawater for bacterial diversity analysis was collected at different depths using Niskin bottles and
145 directly poured in 5 L sterile carboys previously rinsed three times with the sample. For each depth,
146 three biological replicates samplings were done, consisting of three different Niskin deployments,
147 except Station 4 in September 2014. Filtrations started in the on-shore laboratory 3 to 4 hours after
148 sampling. Water samples were size-fractionated using three in-line filters of different porosity: 10 µm,
149 3 µm (PC membrane filters, Millipore®) and 0.22 µm (Sterivex® filters, with PES membrane). In this
150 study, we focused only on the 0.22-3 µm free-living fraction. All filters were frozen in liquid nitrogen
151 before storage at -80 °C. In total, 2 to 5 liters of seawater were filtered each time, depending on filter
152 saturation.

153

154

155 4. DNA extraction and sequencing

156

157 Half-filters were directly placed in Matrix B® tubes (filled with 0.1 mm silicate beads, MP
158 Biomedicals) with lysis buffer (Tris pH 7.0, EDTA pH 8.0 and NaCl), SDS 10% and Sarkosyl 10%
159 and subjected to physical lysis for 5 minutes on a vortex plate. The liquid fraction was then collected
160 in order to perform a phenol-chloroform extraction using PCI (Phenol, Chlorophorm Isoamyl alcohol
161 with a ratio of 25:24:1) and a precipitation step with isopropanol and 5 M sodium acetate. DNA was
162 resuspended in 100 µL of sterile water.

163 Bacterial diversity was assessed by targeting the v4-v5 hypervariable regions of 16S rDNA with the
164 primers 518F (CCAGCAGCYGCGGTAAN) / 926R (CCGTCAATTCNTTTRAGT-
165 CCGTCAATTTCTTTGAGT - CCGTCTATTCCTTTGANT) (Nelson et al. 2014). PCR products
166 were purified using Ampure XP® kit and DNA quantity was measured using Picogreen® staining and
167 a plate fluorescence reader (TECAN® infinite M200 Pro). Each sample was diluted to the same
168 concentration and pooled before sequencing on an Illumina MiSeq sequencer at the Marine Biological
169 Laboratory (Woods Hole MA, USA).

170

171

172 5. Bioinformatics analysis

173

174 We obtained 22,523,398 raw reads, with a range from 31,583 to 2,001,687 reads per sample. Reads
175 were merged and quality-filtered according to recommendations in Minoche et al. (Minoche et al.,

176 2011) using the Illumina-utils scripts (Eren et al. 2013). Those steps removed 17 % of all the sequences.
177 We used the Swarm algorithm (Mahé et al. 2014) to cluster the 18,876,655 remaining sequences into
178 1,611,447 operational taxonomic unit OTUs. Chimera detection was done using vsearch *de novo*
179 (Rognes et al. 2016) resulting in 281,825 filtered OTUs. Taxonomic annotation for each OTU was
180 done with the SILVA database v123 (Quast et al. 2012) using the mothur classify.seqs command
181 (Schloss et al. 2009). 19,516 OTUs (1,247,339 sequences) were affiliated with non-bacterial taxa (e.g.
182 archaea, chloroplasts, mitochondria, eukaryota) and removed from the dataset. As a result, we obtained
183 262,308 OTUs for 134 samples, with a large number of singletons (205,292 OTUs), that were kept
184 along the statistical analysis.

185

186

187 6. Statistical analysis

188

189 Libraries were normalized for read number using DESeq package in R (Anders and Huber 2010). A
190 visualization of the bacterial community structure similarity was assessed with an NMDS based on
191 Bray-Curtis dissimilarities using vegan R package (Oksanen et al. 2007). Influence of depth, station
192 and sampling time on bacterial communities was investigated using a permutational multivariate
193 analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities and 999 permutations. We
194 used principal coordinate analysis (PCA) ordination to characterize water samples environmental
195 parameters. Finally, we examined the presence of biomarker OTUs (i.e. OTUs with a significant higher
196 relative abundance in a given condition) of the different stations within each cruise using the LefSe
197 software (Segata et al. 2011).

198

199 7. Network analysis

200

201 Network analysis was done based on a truncated matrix only containing the most abundant OTUs with
202 more than 50 sequences in at least three samples. The filtered matrix contained 681 OTUs that
203 accounted for 79% of all the sequences. This filtering step was necessary to avoid false positive
204 correlations in the network analysis. Our module detection analysis followed part of the pipeline of
205 Chafee *et al.* (Chafee et al. 2018). First, the application of SPIEC-EASI computes pairwise co-variance
206 based correlation between OTUs in order to address the sparsity and composition issues inherent to
207 microbial abundance data (Kurtz et al. 2015). The possible interaction was then inferred using the
208 glasso probabilistic inference model with a lambda.min.ratio of 0.01. Based on this model, only the
209 significant covariance values were extracted and transformed into a correlation matrix using the
210 cov2cor() function.

211 We then delineated network modules as groups of highly interconnected OTUs that presented very
212 close variations in relative abundances across the studied samples. Those modules were defined using
213 the Louvain algorithm (Blondel et al. 2008). We used Gephi (Bastian et al. 2009) and Force Atlas 2
214 layout algorithm to generate a visualization of the main correlations (>0.3). Module eigengenes (ME,
215 the first principal component, considered a representative of the OTUs distribution of a given module)
216 were calculated based on the relative abundance matrix using WGCNA function moduleEigengenes()
217 (Langfelder and Horvath 2008). Those ME were used to calculate Pearson correlations between the

218 different modules and the environmental variables, using the WGCNA commands `moduleTraitCor()`,
219 `moduleTraitPvalue()`.

220 We used the methods proposed by Newton et al. to infer the trophic strategy of OTUs within each
221 modules (Newton and Shade 2016). In that study, they differentiated opportunist taxa with high
222 abundance variability in space and time, and marathoners with low abundance variability. They
223 distinguished these using the Coefficient of Variation (CV) of OTU dynamic combined with their
224 abundance and prevalence in the samples. Based on their method, we defined high CV opportunist
225 OTUs (or HCV) as OTUs above 5% upper boundary of the linear modeling 95% confidence interval
226 in a CV plot against OTU occurrence. Conversely, we defined low CV marathoners OTUs (or LCV)
227 as OTUs below the 5% lower boundary of the linear modeling. In our analysis, OTU occurrence was
228 defined by a relative abundance > 0.05%.

229
230 All the scripts used for this analysis are available at: <https://loimai.github.io/BBobs/>

231

232 **Results**

233 1. Environmental settings

234 This study was carried out between September 2014 and September 2015 in the Iroise Sea, off
235 Brittany (Northeast Atlantic), in the vicinity of the Ushant island. The Ushant front position and
236 characteristics were estimated using Satellite Surface Temperature (SST) maps (Fig. 1) and CTD data
237 collected at the dates of sampling (suppl. data 1). The March 2015 sampling took place before the onset
238 of the Ushant front and presented a homogeneous temperature around 10 °C across all the stations.
239 High nutrient concentrations at all stations (Si(OH)_4 : 1.82 to 4.38 μM , nitrates: 5.88 to 12.13 μM ,
240 suppl. data 2), low surface Chl a (<1 $\mu\text{g}\cdot\text{L}^{-1}$ except for Station 1, suppl. data 3) and overall low
241 phytoplankton cells counts observed during this cruise (suppl. data 2) indicated that sampling occurred
242 prior to the development of the phytoplankton spring blooms. In summer (September 2014, July 2015
243 and September 2015), SST maps showed a sharp transition between coastal and offshore temperatures
244 confirming the presence of a frontal system. The different observed stratification regimes (suppl. data
245 1) coincided with distinct physicochemical patterns and phytoplanktonic patterns across seasons (Fig.
246 1B, suppl. data 2). In late summer (September samples), offshore deep waters shared close
247 characteristics with winter waters (March sample, Temperature: 11.7 to 12.3 °C), with few
248 phytoplankton cells, similar concentration of Si(OH)_4 (1.61 to 3 μM) and nitrates (3.99 to 6.41 μM).
249 Conversely, surface waters presented high temperatures (14.7 to 18.2 °C), a nutrient depletion
250 (Si(OH)_4 : 0.02 to 1.65 μM , NO_2+NO_3 : 0.00 to 0.09 μM) and high phytoplankton cell counts. In early
251 summer (July), inorganic nutrient concentrations were overall lower than in September, probably
252 consumed by the spring bloom coinciding with the onset of the front around May-June. A significant
253 bloom occurred at stations 2 and 3, on the 27th of June, five days before the sampling period as seen
254 in the satellite surface Chl a observations (suppl. Data 3 B.).

255

256 2. Bacterial community dynamics in the Iroise Sea

257 In the Iroise Sea, free-living bacterial communities structure presented clear time and spatial
258 patterns as shown in the NMDS ordination plot (Fig. 1C, for each cruise separately see suppl. Data 4).
259 Firstly, community structure displayed strong seasonality, with sample primarily grouping by sampling
260 cruises. We also observed similar communities in stratified waters of September 2014 and 2015
261 samples (Fig. 1C), suggesting that these seasonal pattern were recurring .

262 Besides, we also observed an important spatial influence, as within each sampling cruise,
263 communities were markedly different between stations. In winter samples, communities were highly
264 similar throughout the water column (Depth was non-significant, Permanova $Pr(>f) = 0.225$), but
265 presented a coastal to offshore gradient (Station was significant, Permanova $Pr(>f) = 0.001$, suppl. Data
266 4) that followed a gradient of salinity, temperature and inorganic nutrient (sup. data 2). Conversely, in
267 September, when the front was the strongest, free-living bacterial communities were much more
268 heterogeneous with clear patterns associated to the set-up of the front : stratification resulted in highly
269 diverging communities with depth (Depth $Pr(>f) = 0.004$), while this pattern was not seen for the mixed
270 and coastal samples (Depth was not significant, $Pr(>f) = 0.222$ and 0.434 , suppl. Data 4). In July, the
271 patterns were mostly associated with depth for all the stations, except station 1 (suppl. Data 4).

272 Overall, bacterial communities structure followed the different water masses, mirroring environmental
273 physicochemical variations represented in the PCA plot of environmental variables (Fig. 1B): deep
274 water communities in the summer crews remained more similar to winter communities (Fig. 1C). In
275 contrast, surface bacterial communities in stratified regimes and in most of the stations in July departed
276 from this typical winter structure. In addition, for these summer cruises, the DCM samples either cluster
277 with surface or deep samples. This could be explained by the difficulty to sample the DCM precisely,
278 as its depth can vary between the CTD measurements and the biological sampling.

279 Using the LefSe algorithm (Segata et al. 2011), we found that some stations displayed specific
280 biomarker OTUs within each sampling time (suppl. Data 5). Biomarkers such as OTU1 (*Amylibacter*)
281 and OTU4 (*Planktomarina*) were found at the most near-shore station (Station 1) in September 2014
282 and March 2015 and other biomarkers were found in surface stratified waters in early summer (OTU29
283 *NS4 marine group*) and late summer (OTU10 *Synechococcus*) cruises, but no biomarker was identified
284 for the mixed and frontal stations except in July 2015 at Station 2 with OTU35 (*Aliivibrio*) and OTU74
285 (*Pseudoalteromonas*).

286 287 8. Description of modules

288 We further investigated groups of co-varying OTUs that could potentially share the same
289 ecological niches in this partitioned marine environment via a co-occurrence network analysis. In the
290 inferred network, we were able to identify 14 sub-networks (Fig. 2A and 2B) defining groups of OTUs
291 (termed modules) with similar distribution patterns across the entire study. Two modules (5 and 4)
292 were dominant in our dataset and respectively accounted for 32.7% and 20.9% of all sequences. Eight
293 modules represented between 1.6% and 14.2%, and four were rarer with less than 1% abundance. The
294 OTU taxonomy in each module is summarized in suppl. Data 6 and Fig. 4 presents the distribution of
295 the dominant families among each module.

296 Since its eigengene could characterize each module, we investigated to which extent module
297 distribution could be correlated (i.e. Pearson correlation) with environmental parameters (Fig. 2C).
298 Correlation patterns partitioned modules into three significant sub-networks. The first one mostly
299 comprises modules 5 and 13 representing 32.7 and 6.8% of the dataset respectively that correlated
300 positively to inorganic nutrient concentrations and negatively to temperature and Particulate Organic
301 Matter (POC, PON) values. Their relative abundance in the different samples showed that they were
302 dominant in oligotrophic waters: together they ranged from 39% at Station 1 to 72% at Station 5 of the
303 late winter communities, and 54% to 59% of the deep stratified waters in September (Fig. 3). SAR11
304 Surface 1 (46.7% of the module sequences), *ZD0405 marine group* (12%) and SAR86 Clade (6.4%)
305 dominate the main module (module 5). Module 13 showed a different diversity as being dominated by
306 members of *Marinimicrobia* (15.8%), *SAR11 Deep 1* (12%), *SAR11 Surface 1* (8.9%) and
307 *Salinisphaeraceae* (7.9%).

308 Modules 4, 8, 2 and 1 contributed to the second sub-network, representing 20.9, 14.2, 5.5 and
309 5.4% of the dataset respectively. They presented clear inverse correlations compared with modules of
310 the first group: they correlated positively with temperature, POM and Diatoms but negatively with
311 inorganic nutrient concentrations. In relative abundance, they dominated the samples of July and in the
312 surface and coastal stations. Their taxonomy was distinct from the first group; i.e. together they
313 gathered the majority of *Flavobacteriaceae* (70%) and *Rhodobacteraceae* (88%). Also, module 9 was
314 enhanced in July 2015 but was almost exclusively present in Station 2 and strongly correlated with
315 ammonium (0.72, $p < 0001$). Its taxonomy was also particular as dominated by *Vibrionaceae* (58%)
316 and *Pseudoalteromonadaceae* (30%).

317 The third sub-network (modules 6 and 3) was less abundant and presented different correlations
318 with environmental parameters. They respectively account for 1.6 and 2.6% of the dataset, were
319 correlated with specific phytoplankton groups (dinoflagellates, nanophytoplankton) and were
320 dominant in the surface and DCM of stratified waters in September where they made up to 34% of the
321 community. Among them, module 3 was constituted almost exclusively of Cyanobacteria (94%)
322 affiliated with the *Synechococcus* genus.

323 To examine whether the modules gather OTUs that exhibited different ecological behavior (i.e.
324 marathoners or opportunist), we computed the coefficient of variation (CV) for all OTU used in the
325 network analysis and plotted this metric against OTU occurrence as proposed in Newton et al. (Newton
326 and Shade 2016). We then examined their module membership (suppl. Data 7 and Fig. 4B): modules
327 showed a clear gradient ranging from relatively low CV (LCV) OTUs (modules 4, 11, 14, 5 and 13) to
328 high CV (HCV) OTUs (modules 9, 10, 7 and 2).

329

330 Discussion

331

332 *The spatial and temporal dynamics of bacterial communities associated with a coastal tidal front*

333

334 In this study, we investigated the spatiotemporal variations of free-living bacterial community
335 composition over one year across contrasting coastal water masses characterized by a seasonal tidal
336 front structure. For each cruise (season) we observed a spatial influence on bacterioplankton
337 community composition. However, in the studied area, winter communities were comparatively much
338 more homogeneous with only an influence from coast to the offshore. At this time of the year, the river
339 debit were at the highest and this is known to influence free-living bacterial communities in coastal
340 area (Tréguer et al. 2014; Pizzetti et al. 2016). In summer, bacterial communities diverged according
341 to the station and depth, highlighting the importance of the onset of a tidal front and open ocean
342 stratification for bacterioplankton community structure. This was mainly due to the sharp divergence
343 of summer surface samples, as deep summer samples remained closer to winter ones (Fig. 1C). The
344 existence of two contrasting types of bacterioplankton dynamics (winter and deep vs. summer surfaces)
345 reflects similar patterns in sample ordination based on biogeochemical parameters and can be
346 associated to phytoplankton development, temperature increase or lowering in inorganic nutrient
347 concentrations, which are key parameters influencing bacterial communities dynamic in marine coastal
348 environment (Fuhrman et al. 2015 ; Giovannoni and Vergin 2012).

349 These observations of a frontal zone as a sharp ecological transition for bacterioplankton
350 among different water masses are consistent with reports in stratified waters (Cram et al. 2015;
351 Ghiglione et al. 2008) and from other frontal areas (Baltar et al. 2016) confirming their role as
352 ecological boundaries in the oceans (Raes et al. 2018). Interestingly, the frontal area itself around
353 station 3-4 did not exhibit a specific bacterial composition (Fig. 2C and Fig 4), but could rather result
354 from mixing between adjacent communities, as already suggested for the phytoplankton and
355 zooplankton (Sournia 1994) and in another marine boundaries such as a shelf break (Zorz et al. 2019).
356 We could not identify any biomarker OTUs associated with frontal stations. Hence, bacterioplankton
357 communities associated with enhanced productivity at the Ushant front (Videau 1987) could result
358 from an increase in resident plankton density (Franks 1992) rather than the emergence of distinct
359 communities.

360 In addition, we observed a remarkable seasonal recurrence between the two September cruises,
361 within each station and depth. This pattern was comparatively more accentuated toward the open ocean
362 (station 4 and 5) than near shore (stations 1 to 3). This temporal dynamic is coherent with previous
363 reports of seasonal patterns in single stations as shown in the North Sea (Chafee et al. 2018) or the
364 English Channel (Gilbert et al. 2012) time series. Our results suggest that despite a substantial
365 heterogeneity in our system, such seasonal recurrence patterns also extend to stations along
366 geographical and bathyal gradients.

367

368

369 *Distinct bacterioplankton trophic strategies associated with tidal front temporal and spatial dynamics*

370 Using network analysis on samples exhibiting strong temporal and spatial variations, we could
371 define modules of ecologically coherent OTUs. As suggested elsewhere, such modules can be

372 considered as OTUs potentially sharing the same environmental niches with coherent ecological
373 strategies (Eiler et al. 2012). In association with previously characterized dominant taxa in each
374 module, we aim at identifying higher order bacterioplankton community organization and revealing
375 ecological drivers of community dynamics in the frontal zone.

376 Our study gives evidence of module partitioning into two major heterotrophs-dominated sub-
377 networks, exhibiting distinct inverse covariance patterns (Fig. 2A and 2B). Their correlations with
378 environmental variables also clearly separated conditions between water masses with active primary
379 producers (low nutrients and high POM values) that were present in summer surface samples, and
380 conditions with overall low development of phytoplankton typical of winter and deep samples.
381 Development and decay of phytoplankton lead to the release of dissolved organic matter, which is
382 almost only available for heterotrophic bacteria (Azam and Malfatti 2007). Thus, these two different
383 conditions likely selected for copiotrophic or oligotrophic heterotrophic free-living bacteria adapted to
384 different concentrations of organic matter in the environment (Giovannoni et al. 2014). The taxonomic
385 affiliation was highly coherent with these observations. Modules 5 and 13 are dominated by SAR11
386 clades, which typically thrive in basal concentrations of organic matter (Morris et al. 2002) or members
387 of taxa typical of the sub-euphotic zones such as *Marinimicrobia*, or SAR11 Deep 1 (Agogue et al.
388 2011). Conversely, modules 4, 8, 2, 1 and 9 were dominated by members of the *Rhodobacteraceae* and
389 *Flavobacteriaceae*, typically associated with phytoplankton-derived organic matter (Buchan et al.
390 2014; Teeling et al. 2012). Thus, the availability of phytoplankton-derived organic matter will drive
391 heterotroph dynamics.

392 The last sub-network with module 3, dominated by *Synechococcus*, highlights the contribution
393 of phototrophic bacteria. These cyanobacteria became strongly dominant in the surface of well
394 stratified-waters in late summer, which is already known to favor these small phytoplanktonic cells
395 (Taylor and Joint 1990; Cadier et al. 2017).

396 Interestingly, known chemoautotrophs involved in the nitrification such as *Nitrospinaea* did
397 not form a separate module and were included in the oligotrophic module 13. Nitrification in the water
398 column is typically found in the sub-euphotic zone as nitrite-oxidizing bacteria could be light-sensitive
399 (Lomas and Lipschultz 2006) and can be outcompeted by phytoplankton for the uptake of nitrite (Smith
400 et al. 2014; Wan et al. 2018). This fact could explain why they exhibit a dynamic similar to oligotrophic
401 bacteria.

402

403

404 *Differential bacterioplankton responses to organic matter availability*

405

406 Using the OTU coefficients of variation to distinguish rather marathoners or opportunist taxa,
407 we examined whether heterotrophic bacteria had different responses to organic matter availability in
408 summer samples. Their dynamic and composition was highly coherent with a partitioning of the
409 microbial loop between different taxa (Bryson et al. 2017). For instance, several modules presented a
410 majority of HCV OTUs (Fig. 4B): *Tenacibaculum sp.* (a *Flavobacteriaceae* dominating Module 2) was
411 highly abundant reaching up to 20.7% of the sequences in the 2015 July surface waters shortly after
412 significant phytoplankton bloom. One single *Tenacibaculum* OTU dominated the surface of 4 stations
413 over a 40km distance just a few days after a phytoplankton bloom. This dynamic of *Tenacibaculum*

414 genus is coherent with previous observations of a recurrent population increase after seasonal
415 phytoplankton blooms in coastal water (Teeling et al. 2016) while being part of the rare biosphere
416 otherwise (Alonso-Sáez, Díaz-Pérez, and Morán 2015). During the same period, module 9, dominated
417 by *Vibrionales* (*Aliivibrio sp*) and *Alteromonadales* (*Pseudoalteromonas sp.*) class, was especially
418 abundant at Station 2, reaching up to 27% of the sequences (Fig. 3). These taxa are known copiotroph
419 bacteria that can sharply increase in abundance in response to high substrate loading (Tada et al. 2012).
420 These results strongly support an opportunist lifestyle of bacteria in modules 2 and 9. When they are
421 dominant, bacteria with such an opportunist strategy have a critical role as they can contribute to a
422 substantial fraction of organic matter recycling (Pedler et al. 2014).

423 In contrast, module 4 was mostly composed of LCV OTUs with a cosmopolitan distribution
424 across time, depth and geography. The dominant family in module 4, the *Rhodobacteraceae*, are known
425 as generalist bacteria with a versatile substrate utilization (Moran et al. 2004; R. J. Newton et al. 2010).
426 Some of the free-living *Rhodobacteraceae* grow on low molecular weight organic compounds and
427 numerous studies pointed out that they compete for the same substrate as SAR11 Clade, but are more
428 competitive at higher organic matter concentrations. They can be very successful in coastal waters, an
429 example being a representative of the genus *Planktomarina* that is dominant in the North Sea (Voget
430 et al. 2015). Other dominant taxa of this module, such as SAR86 Clade, *Methylophilaceae* or members
431 of SAR116 Clade are widespread in marine environments and are also known to target small organic
432 molecules (Dupont et al. 2012; Huggett et al. 2012; Oh et al. 2010).

433 Module 8 presented mixed CV values among its OTUs. Many members of this module, such
434 as *Flavobacteriaceae* (Buchan et al. 2014), *Verrucomicrobiacea* (Martinez-Garcia et al. 2012) or
435 *Cryomorphaceae* (Bowman 2014), can use complex algal-derived substrates and present a typical
436 increase in abundance after phytoplankton blooms (Teeling et al. 2016). We interpret these
437 observations to be a result of the relatively low sampling time resolution that probably fails to resolve
438 rapid OTU variations of other opportunistic bacteria.

439 Overall, this study allowed us to delineate several groups of bacterioplankton trophic strategies and
440 their variations in response to biogeochemical cycles in a highly dynamic coastal environment.
441 Oligotrophs, typically represented by SAR11 OTUs, were present in all water masses. They
442 outcompete other heterotrophic organisms in low labile organic matter environments such as winter
443 and deep offshore water masses, while copiotrophs communities develop during the high productivity
444 period. Within copiotrophs, several taxa show patterns of adaptation to rapidly changing conditions in
445 their substrate availability: opportunist taxa can rapidly become highly dominant (represented by
446 *Tenacibaculum* and *Alteromonadales*) after local events such as phytoplankton bloom, while more
447 generalist taxa such as *Rhodobacteraceae* exhibit a ubiquitous distribution. It is likely that this
448 dichotomy between oligotroph and copiotroph is an over-simplification in trophic strategies, as
449 suggested by numerous studies (Bryson et al. 2017; Mayali et al. 2012). Heterotrophs could instead
450 follow a gradient from oligotrophy to copiotrophy, and only finer analysis such as growth rate
451 measurements or dissolved organic matter quantification could help to better describe the trophic
452 strategies of heterotrophs (Kirchman 2016). However, these complex heterotrophic community
453 dynamics observed in this study highlight the central role of free-living bacteria in organic matter
454 cycling. Indeed, previous studies of the Iroise Sea nutrient cycling demonstrated that after the initial
455 depletion of winter nutrients pool, phytoplankton growth strongly relies on nutrients recycled through

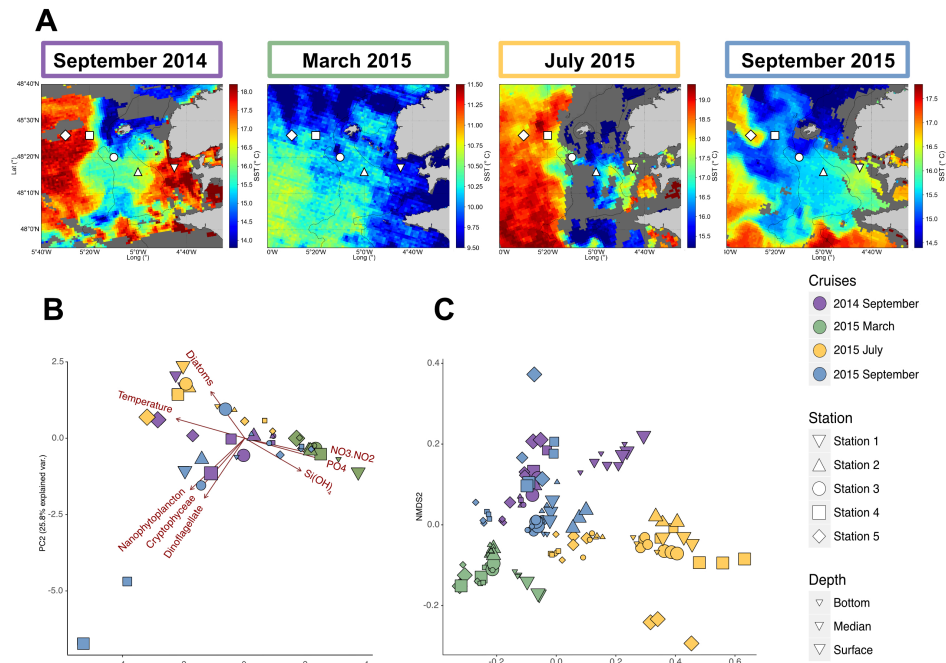
456 the microbial loop (LHelguen et al. 2005), through which they are remineralized several times in a
457 seasonal cycle (Birrien et al. 1991). In this system, bacteria could be directly responsible for up to 25%
458 of urea with the remaining originating from ciliates mainly, which also mostly feed on bacteria
459 (LHelguen et al. 2005)

460

461 **Conclusion**

462 Here, using a complex 3D (vertical, horizontal, and temporal) survey of free-living bacterial diversity
463 in correlation with the seasonal dynamics of a coastal tidal front, we have shown that such complex
464 mesoscale features controls the dynamic of free-living bacterial communities. The Ushant tidal front
465 acts as an ecological boundary for those communities. We illustrated the link between different water
466 masses on this dynamic with for instance photosynthetic bacteria enriched in oligotrophic stratified
467 waters in late summer. Using a network analysis, we were able to gain insight on ecologically coherent
468 modules of free-living bacteria driven by the availability of organic matter produced by the
469 phytoplankton. This has major implication for our understanding of the microbial loop in coastal
470 systems. In the future, these observations should be confirmed with measurements and characterization
471 of dissolved organic matter quantity and quality in the water column as well as direct measurement of
472 growth rates in order to more precisely describe bacterial trophic strategies. Moreover, to better
473 understand these systems, future studies should include the characterization of other key members of
474 the planktonic communities such as viruses, ammonium oxidizing archaea, eukaryotic phytoplankton
475 and grazers, as well as particle-attached bacteria that are central for organic matter and biogeochemical
476 cycles.

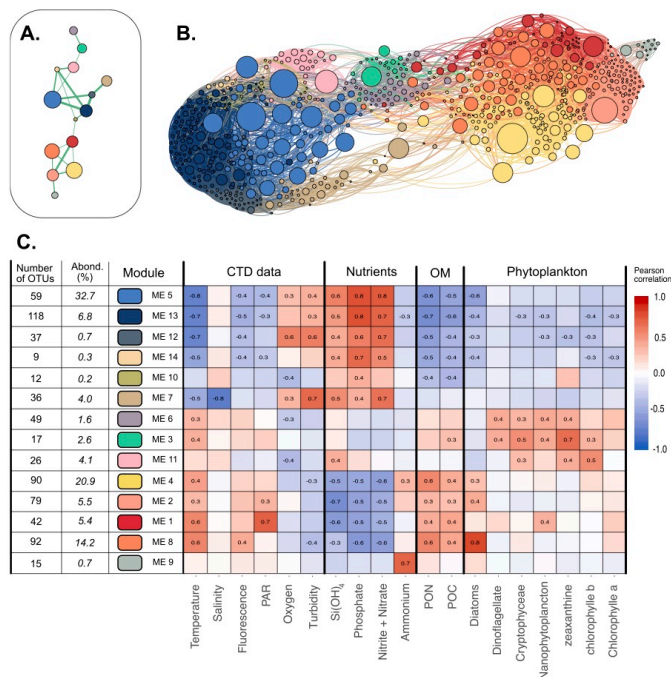
477



479

480 **Figure 1 | Environmental and bacterial communities characteristics of the Iroise Sea for the different**
 481 **cruises.**

482 **A.** Map of the Satellite Sea Surface Temperatures (SST) in the Iroise Sea for each cruise (September 2014 the
 483 8th, March 2015 the 6th, July 2015 the 2nd and September 2015 the 8th), highlighting in the summer cruises the
 484 presence of the Ushant front that separates offshore warm stratified waters and coastal cooler mixed waters. The
 485 shape corresponds to the different stations sampled, with at each time 2 or 3 depths. Surface waters are highly
 486 dynamic and some eddies are conspicuous during September 2015, bringing cold water into surface stratified
 487 waters. Thus SST map are not enough to define the frontal area and vertical profiles are needed to characterize
 488 the different water masses (suppl. Data 1) **B.** Principal Component Analysis of the environmental characteristics
 489 for the different samples (n=49) based on temperature, inorganic nutrients (Si(OH)₄, NO₃+NO₂, PO₄)
 490 concentrations and microscopic count of the different phytoplanktonic groups (*Diatom*, *Nanophytoplankton*,
 491 *Cryptophyceae* and *Dinoflagellate*) **C.** NMDS of the bacterial diversity based on Bray-Curtis dissimilarities
 492 among the different cruises, stations and depth (stress=0.091). For bacterial diversity, biological triplicates were
 493 done for each station and depth, explaining the higher number of samples (n=135).



494

495

Figure 2 | Visualization of the different modules and their main characteristics

496

A. Representation of the main connectivity between the different modules detected with the Louvain algorithm.

497

Each node represent a module, each edge represents the median of the positive correlations between two

498

modules. Only the strongest connections are shown.

499

B. Network visualisation of the dataset. Each node represents an OTU, while each edge represent a positive

500

correlation (>0.3) obtained from the covariance matrix calculated with SPIEC-EASI. The node size depends on

501

the abundance of one OTU (in number of sequences) in the entire dataset. The edge size depends on the value

502

of the correlation. Nodes colors represent the OTU affiliation to the different Louvain communities. Network

503

was represented using Gephi and Force Atlas layout algorithm. **C.** Presentation of the 14 modules detected.

504

Pearson correlations between each module eigengene and the different environmental data are presented in the

505

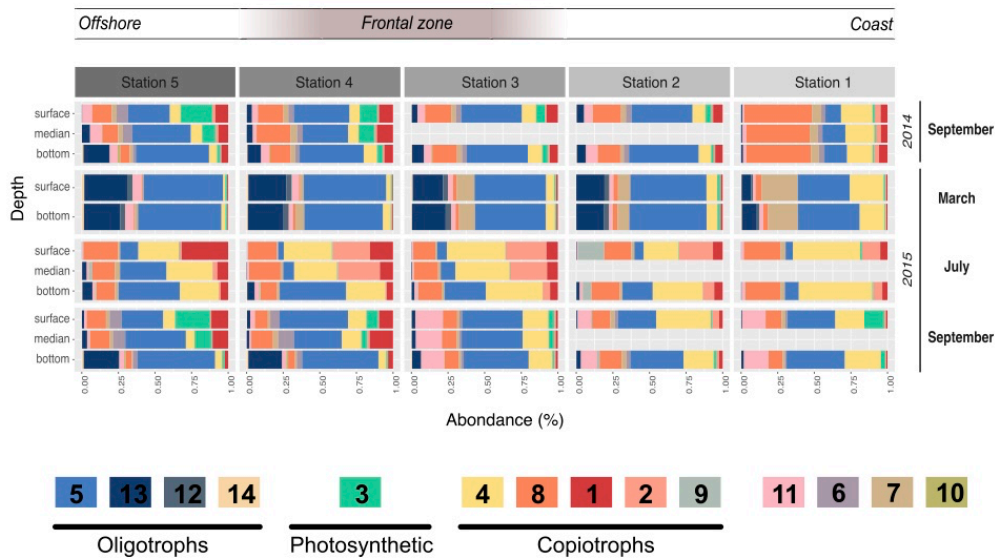
heatmap. OM : Organic Matter, PAR: Photosynthetically Available Radiation, PON : Particulate Organic

506

Nitrogen, POC: Particulate Organic Carbon. Only the significant correlations (p.value > 10⁻⁴) are shown. The

507

number of OTUs in each module and the relative abundance of each module (in % of all the reads) are detailed.

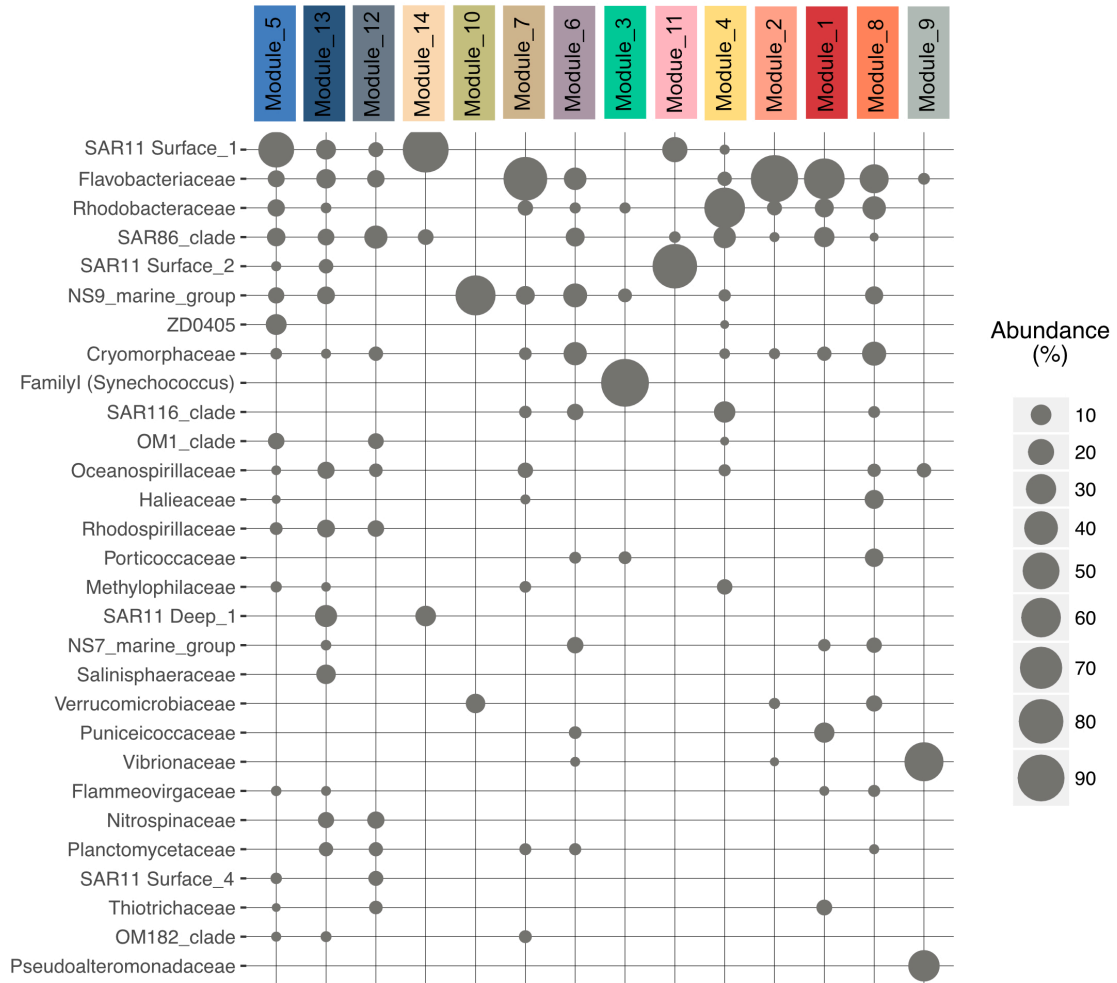


508

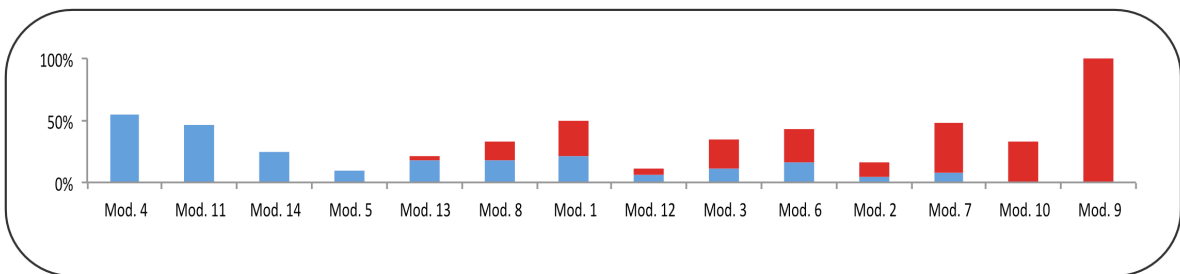
509 **Figure 3 | Module dynamics across the different campaigns, stations and depths**

510 Relative abundance of the different modules in each campaign, station and depth. The value shown resulted of
 511 the mean of the triplicates done for each sampling. The legend includes the different hypotheses of the modules'
 512 trophic strategies based on their correlations to the environmental parameters, their taxonomy and their dynamic.
 513 Oligotrophic modules are likely to present heterotrophic bacteria adapted to low organic matter levels, while
 514 copiotrophic bacteria are likely more competitive under higher organic matter levels. Finally the photosynthetic
 515 module is almost only composed of Cyanobacteria.
 516

A.



B.



518 **Figure 4 | Modules' taxonomy and Coefficient of Variation of their OTUs**

519 A. Relative abundance of the 30 main families in each module. B. Proportion of OTUs (in % of all the OTUs
520 in a module) that present a High Coefficient of Variation (HCV) in red, or a Low Coefficient of Variation
521 (LCV) in blue defined based on Newton method (Newton et al., 2016).

- 522 Agogu , H l ne, Dominique Lamy, Phillip R. Neal, Mitchell L. Sogin, and Gerhard J. Herndl. 2011.
523 “Water Mass-Specificity of Bacterial Communities in the North Atlantic Revealed by Massively
524 Parallel Sequencing.” *Molecular Ecology* 20 (2): 258–74. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-294X.2010.04932.x)
525 294X.2010.04932.x.
- 526 Alonso-S ez, Laura, Laura D az-P rez, and Xos  Anxelu G. Mor n. 2015. “The Hidden Seasonality
527 of the Rare Biosphere in Coastal Marine Bacterioplankton.” *Environmental Microbiology* 17 (10):
528 3766–80. <https://doi.org/10.1111/1462-2920.12801>.
- 529 Aminot, Alain, and Roger K rouel. 2007. *Dosage Automatique Des Nutriments Dans Les Eaux*
530 *Marines: M thodes En Flux Continu*. Editions Quae.
- 531 Anders, Simon, and Wolfgang Huber. 2010. “Differential Expression Analysis for Sequence Count
532 Data.” *Genome Biology* 11 (10): R106.
- 533 Azam, Farooq. 1998. “Microbial Control of Oceanic Carbon Flux: The Plot Thickens.” *Science* 280
534 (5364): 694–96. <https://doi.org/10.1126/science.280.5364.694>.
- 535 Azam, Farooq, and Francesca Malfatti. 2007. “Microbial Structuring of Marine Ecosystems.” *Nature*
536 *Reviews Microbiology* 5 (10): 782–91. <https://doi.org/10.1038/nrmicro1747>.
- 537 Baltar, Federico, Kim Currie, Esther Stuck, St phanie Roosa, and Sergio E Morales. 2016. “Oceanic
538 Fronts: Transition Zones for Bacterioplankton Community Composition: Fronts Delimit
539 Bacterioplankton Communities.” *Environmental Microbiology Reports* 8 (1): 132–38.
540 <https://doi.org/10.1111/1758-2229.12362>.
- 541 Baltar, Federico, Esther Stuck, Sergio Morales, and Kim Currie. 2015. “Bacterioplankton Carbon
542 Cycling along the Subtropical Frontal Zone off New Zealand.” *Progress in Oceanography* 135
543 (June): 168–75. <https://doi.org/10.1016/j.pocean.2015.05.019>.
- 544 Bastian, Mathieu, Sebastien Heymann, and Mathieu Jacomy. 2009. “Gephi: An Open Source
545 Software for Exploring and Manipulating Networks.” *Icwsn* 8 (2009): 361–362.
- 546 Birrien, J.L., M.V.M. Wafar, P.Le Corre, and R. Riso. 1991. “Nutrients and Primary Production in a
547 Shallow Stratified Ecosystem in the Iroise Sea.” *Journal of Plankton Research* 13 (4): 721–42.
548 <https://doi.org/10.1093/plankt/13.4.721>.
- 549 Blondel, Vincent D., Jean-Loup Guillaume, Renaud Lambiotte, and Etienne Lefebvre. 2008. “Fast
550 Unfolding of Communities in Large Networks.” *Journal of Statistical Mechanics: Theory and*
551 *Experiment* 2008 (10): P10008. <https://doi.org/10.1088/1742-5468/2008/10/P10008>.
- 552 Bowman, John P. 2014. “The Family Cryomorphaceae.” In *The Prokaryotes*, edited by Eugene
553 Rosenberg, Edward F. DeLong, Stephen Lory, Erko Stackebrandt, and Fabiano Thompson, 539–50.
554 Berlin, Heidelberg: Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-38954-2_135.
- 555 Bryson, Samuel, Zhou Li, Francisco Chavez, Peter K. Weber, Jennifer Pett-Ridge, Robert L. Hettich,
556 Chongle Pan, Xavier Mayali, and Ryan S. Mueller. 2017. “Phylogenetically Conserved Resource
557 Partitioning in the Coastal Microbial Loop.” *The ISME Journal* 11 (12): 2781–92.
558 <https://doi.org/10.1038/ismej.2017.128>.

- 559 Buchan, Alison, Gary R. LeCleir, Christopher A. Gulvik, and José M. González. 2014. “Master
560 Recyclers: Features and Functions of Bacteria Associated with Phytoplankton Blooms.” *Nature*
561 *Reviews Microbiology* 12 (10): 686–98. <https://doi.org/10.1038/nrmicro3326>.
- 562 Cadier, Mathilde, Thomas Gorgues, Marc Sourisseau, Christopher A. Edwards, Olivier Aumont,
563 Louis Marié, and Laurent Memery. 2017. “Assessing Spatial and Temporal Variability of
564 Phytoplankton Communities’ Composition in the Iroise Sea Ecosystem (Brittany, France): A 3D
565 Modeling Approach. Part 1: Biophysical Control over Plankton Functional Types Succession and
566 Distribution.” *Journal of Marine Systems* 165 (January): 47–68.
567 <https://doi.org/10.1016/j.jmarsys.2016.09.009>.
- 568 Chafee, Meghan, Antonio Fernandez-Guerra, Pier Luigi Buttigieg, Gunnar Gerdt, A. Murat Eren,
569 Hanno Teeling, and Rudolf Amann. 2018. “Recurrent Patterns of Microdiversity in a Temperate
570 Coastal Marine Environment.” *The ISME Journal*, 2018, sec. 12.
- 571 Cotner, James B., and Bopaiah A. Biddanda. 2002. “Small Players, Large Role: Microbial Influence
572 on Biogeochemical Processes in Pelagic Aquatic Ecosystems.” *Ecosystems* 5 (2): 105–21.
573 <https://doi.org/10.1007/s10021-001-0059-3>.
- 574 Cram, Jacob A, Cheryl-Emiliane T Chow, Rohan Sachdeva, David M Needham, Alma E Parada,
575 Joshua A Steele, and Jed A Fuhrman. 2015. “Seasonal and Interannual Variability of the Marine
576 Bacterioplankton Community throughout the Water Column over Ten Years.” *The ISME Journal* 9
577 (3): 563–80. <https://doi.org/10.1038/ismej.2014.153>.
- 578 Dupont, Chris L., Douglas B. Rusch, Shibu Yooseph, Mary-Jane Lombardo, R. Alexander Richter,
579 Ruben Valas, Mark Novotny, et al. 2012. “Genomic Insights to SAR86, an Abundant and
580 Uncultivated Marine Bacterial Lineage.” *The ISME Journal* 6 (6): 1186–99.
581 <https://doi.org/10.1038/ismej.2011.189>.
- 582 Eiler, Alexander, Friederike Heinrich, and Stefan Bertilsson. 2012. “Coherent Dynamics and
583 Association Networks among Lake Bacterioplankton Taxa.” *The ISME Journal*, 2012, sec. 6.
- 584 Eren, A. Murat, Joseph H. Vineis, Hilary G. Morrison, and Mitchell L. Sogin. 2013. “A Filtering
585 Method to Generate High Quality Short Reads Using Illumina Paired-End Technology.” *PLoS One* 8
586 (6): e66643.
- 587 Falkowski, P. G., T. Fenchel, and E. F. DeLong. 2008. “The Microbial Engines That Drive Earth’s
588 Biogeochemical Cycles.” *Science* 320 (5879): 1034–39. <https://doi.org/10.1126/science.1153213>.
- 589 Fenchel, T. M., and B. Barker Jørgensen. 1977. “Detritus Food Chains of Aquatic Ecosystems: The
590 Role of Bacteria.” In *Advances in Microbial Ecology*, edited by M. Alexander, 1–58. *Advances in*
591 *Microbial Ecology*. Boston, MA: Springer US. https://doi.org/10.1007/978-1-4615-8219-9_1.
- 592 Franks, Pjs. 1992. “Sink or Swim, Accumulation of Biomass at Fronts.” *Marine Ecology Progress*
593 *Series* 82: 1–12. <https://doi.org/10.3354/meps082001>.
- 594 Fuhrman, Jed A., Jacob A. Cram, and David M. Needham. 2015. “Marine Microbial Community
595 Dynamics and Their Ecological Interpretation.” *Nature Reviews Microbiology* 13 (3): 133–46.
596 <https://doi.org/10.1038/nrmicro3417>.

- 597 Galand, Pierre E., Olivier Pereira, Corentin Hochart, Jean Christophe Auguet, and Didier Debroas.
598 2018. "A Strong Link between Marine Microbial Community Composition and Function Challenges
599 the Idea of Functional Redundancy." *The ISME Journal*, June. [https://doi.org/10.1038/s41396-018-](https://doi.org/10.1038/s41396-018-0158-1)
600 0158-1.
- 601 Ghiglione, J F, C Palacios, J C Marty, G Mével, C Labrune, P Conan, M Pujo-Pay, N Garcia, and M
602 Goutx. 2008. "Role of Environmental Factors for the Vertical Distribution (0–1000 m) of Marine
603 Bacterial Communities in the NW Mediterranean Sea," 35.
- 604 Gilbert, Jack A., Joshua A. Steele, J. Gregory Caporaso, Lars Steinbrück, Jens Reeder, Ben
605 Temperton, Susan Huse, et al. 2012. "Defining Seasonal Marine Microbial Community Dynamics."
606 *The ISME Journal* 6 (2): 298–308. <https://doi.org/10.1038/ismej.2011.107>.
- 607 Giovannoni, S. J., and K. L. Vergin. 2012. "Seasonality in Ocean Microbial Communities." *Science*
608 335 (6069): 671–76. <https://doi.org/10.1126/science.1198078>.
- 609 Giovannoni, Stephen J, J Cameron Thrash, and Ben Temperton. 2014. "Implications of Streamlining
610 Theory for Microbial Ecology." *The ISME Journal* 8 (8): 1553–65.
611 <https://doi.org/10.1038/ismej.2014.60>.
- 612 GREPMA. 1988. "A Physical, Chemical and Biological Characterization of the Ushant Tidal Front."
613 *Internationale Revue Der Gesamten Hydrobiologie Und Hydrographie* 73 (5): 511–36.
614 <https://doi.org/10.1002/iroh.19880730503>.
- 615 Haggerty, John Matthew, and Elizabeth Ann Dinsdale. 2017. "Distinct Biogeographical Patterns of
616 Marine Bacterial Taxonomy and Functional Genes." *Global Ecology and Biogeography* 26 (2): 177–
617 90. <https://doi.org/10.1111/geb.12528>.
- 618 Heinänen, Anne, Kaisa Kononen, Harri Kuosa, Jorma Kuparinen, and Kalervo Mäkelä. 1995.
619 "Bacterioplankton Growth Associated with Physical Fronts during a Cyanobacterial Bloom." *Marine*
620 *Ecology Progress Series*, 1995, sec. 116.
- 621 Holm-Hansen, Osmund, Carl J. Lorenzen, Robert W. Holmes, and John DH Strickland. 1965.
622 "Fluorometric Determination of Chlorophyll." *ICES Journal of Marine Science* 30 (1): 3–15.
- 623 Huggett, Megan J., Darin H. Hayakawa, and Michael S. Rappé. 2012. "Genome Sequence of Strain
624 HIMB624, a Cultured Representative from the OM43 Clade of Marine Betaproteobacteria."
625 *Standards in Genomic Sciences* 6 (1): 11. <https://doi.org/10.4056/sigs.2305090>.
- 626 Kirchman, David L. 2016. "Growth Rates of Microbes in the Oceans." *Annual Review of Marine*
627 *Science* 8 (1): 285–309. <https://doi.org/10.1146/annurev-marine-122414-033938>.
- 628 Koch, Arthur L. 2001. "Oligotrophs versus Copiotrophs." *BioEssays* 23 (7): 657–61.
629 <https://doi.org/10.1002/bies.1091>.
- 630 Krause, Sascha, Xavier Le Roux, Pascal A. Niklaus, Peter M. Van Bodegom, Jay T. Lennon, Stefan
631 Bertilsson, Hans-Peter Grossart, Laurent Philippot, and Paul L. E. Bodelier. 2014. "Trait-Based
632 Approaches for Understanding Microbial Biodiversity and Ecosystem Functioning." *Frontiers in*
633 *Microbiology* 5. <https://doi.org/10.3389/fmicb.2014.00251>.

- 634 Kurtz, Zachary D., Christian L. Müller, Emily R. Miraldi, Dan R. Littman, Martin J. Blaser, and
635 Richard A. Bonneau. 2015. “Sparse and Compositionally Robust Inference of Microbial Ecological
636 Networks.” *PLoS Computational Biology* 11 (5): e1004226.
- 637 Langfelder, Peter, and Steve Horvath. 2008. “WGCNA: An R Package for Weighted Correlation
638 Network Analysis.” *BMC Bioinformatics* 9 (1): 559.
- 639 Le, Boyer, G. Cambon, N. Daniault, S. Herbette, Cann Le, L. Marié, and P. Morin. 2009.
640 “Observations of the Ushant Tidal Front in September 2007.” *Continental Shelf Research* 29 (8):
641 1026–37. <https://doi.org/10.1016/j.csr.2008.12.020>.
- 642 Le Fèvre, J. 1986. “Aspect of the Biology of Frontal Systems.” *Advances in Marine Biology*, 1986,
643 sec. 23.
- 644 Le Fèvre, Jacques, Pierre Le Corre, Pascal Morin, and Jean-Louis Birrien. 1983. “The Pelagic
645 Ecosystem in Frontal Zones and Other Environments off the West Coast of Brittany.” *Oceanologica
646 Acta*, 1983, sec. Actes 17ème Symposium Européen de Biologie Marine,.
- 647 LHelguen, Stéphane, G. Slawyk, and Pierre Le Corre. 2005. “Seasonal Patterns of Urea Regeneration
648 by Size-Fractionated Microheterotrophs in Well-Mixed Temperate Coastal Waters.” *Journal of
649 Plankton Research*, 2005, sec. 27.
- 650 Lomas, Michael W., and Fredric Lipschultz. 2006. “Forming the Primary Nitrite Maximum:
651 Nitrifiers or Phytoplankton?” *Limnology and Oceanography* 51 (5): 2453–2467.
- 652 Lund, J. W. G., C. Kipling, and E. D. Le Cren. 1958. “The Inverted Microscope Method of
653 Estimating Algal Numbers and the Statistical Basis of Estimations by Counting.” *Hydrobiologia* 11
654 (2): 143–170.
- 655 Luo, Haiwei, and Mary Ann Moran. 2014. “Evolutionary Ecology of the Marine Roseobacter Clade.”
656 *Microbiology and Molecular Biology Reviews* 78 (4): 573–87.
657 <https://doi.org/10.1128/MMBR.00020-14>.
- 658 Madsen, Eugene L. 2011. “Microorganisms and Their Roles in Fundamental Biogeochemical
659 Cycles.” *Current Opinion in Biotechnology* 22 (3): 456–64.
660 <https://doi.org/10.1016/j.copbio.2011.01.008>.
- 661 Mahé, Frédéric, Torbjørn Rognes, Christopher Quince, Colomban de Vargas, and Micah Dunthorn.
662 2014. “Swarm: Robust and Fast Clustering Method for Amplicon-Based Studies.” *PeerJ* 2: e593.
- 663 Martinez-Garcia, Manuel, David M. Brazel, Brandon K. Swan, Carol Arnosti, Patrick S. G. Chain,
664 Krista G. Reitenga, Gary Xie, et al. 2012. “Capturing Single Cell Genomes of Active Polysaccharide
665 Degradors: An Unexpected Contribution of Verrucomicrobia.” *PLOS ONE* 7 (4): e35314.
666 <https://doi.org/10.1371/journal.pone.0035314>.
- 667 Mayali, Xavier, Peter K Weber, Eoin L Brodie, Shalini Mabery, Paul D Hoeplich, and Jennifer Pett-
668 Ridge. 2012. “High-Throughput Isotopic Analysis of RNA Microarrays to Quantify Microbial
669 Resource Use.” *The ISME Journal* 6 (6): 1210–21. <https://doi.org/10.1038/ismej.2011.175>.
- 670 Minoche, André E., Juliane C. Dohm, and Heinz Himmelbauer. 2011. “Evaluation of Genomic High-

- 671 Throughput Sequencing Data Generated on Illumina HiSeq and Genome Analyzer Systems.”
672 *Genome Biology* 12: R112. <https://doi.org/10.1186/gb-2011-12-11-r112>.
- 673 Moran, Mary Ann, Alison Buchan, José M. González, John F. Heidelberg, William B. Whitman,
674 Ronald P. Kiene, James R. Henriksen, Gary M. King, Robert Belas, and Clay Fuqua. 2004. “Genome
675 Sequence of *Silicibacter pomeroyi* Reveals Adaptations to the Marine Environment.” *Nature* 432
676 (7019): 910.
- 677 Morris, Robert M., Michael S. Rappé, Stephanie A. Connon, Kevin L. Vergin, William A. Siebold,
678 Craig A. Carlson, and Stephen J. Giovannoni. 2002. “SAR11 Clade Dominates Ocean Surface
679 Bacterioplankton Communities.” *Nature* 420 (6917): 806.
- 680 Mou, Xiaozhen, Shulei Sun, Robert A. Edwards, Robert E. Hodson, and Mary Ann Moran. 2008.
681 “Bacterial Carbon Processing by Generalist Species in the Coastal Ocean.” *Nature* 451 (7179): 708–
682 11. <https://doi.org/10.1038/nature06513>.
- 683 Nelson, Michael C., Hilary G. Morrison, Jacquelynn Benjamino, Sharon L. Grim, and Joerg Graf.
684 2014. “Analysis, Optimization and Verification of Illumina-Generated 16S rRNA Gene Amplicon
685 Surveys.” *PLOS ONE* 9 (4): e94249. <https://doi.org/10.1371/journal.pone.0094249>.
- 686 Newton, Rj, and A Shade. 2016. “Lifestyles of Rarity: Understanding Heterotrophic Strategies to
687 Inform the Ecology of the Microbial Rare Biosphere.” *Aquatic Microbial Ecology* 78 (1): 51–63.
688 <https://doi.org/10.3354/ame01801>.
- 689 Newton, Ryan J, Laura E Griffin, Kathy M Bowles, Christof Meile, Scott Gifford, Carrie E Givens,
690 Erinn C Howard, et al. 2010. “Genome Characteristics of a Generalist Marine Bacterial Lineage.”
691 *The ISME Journal* 4 (6): 784–98. <https://doi.org/10.1038/ismej.2009.150>.
- 692 Oh, Hyun-Myung, Kae Kyoung Kwon, Innam Kang, Sung Gyun Kang, Jung-Hyun Lee, Sang-Jin
693 Kim, and Jang-Cheon Cho. 2010. “Complete Genome Sequence of ‘Candidatus Puniceispirillum
694 Marinum’ IMCC1322, a Representative of the SAR116 Clade in the Alphaproteobacteria.” *Journal*
695 *of Bacteriology* 192 (12): 3240–41. <https://doi.org/10.1128/JB.00347-10>.
- 696 Oksanen, Jari, Roeland Kindt, Pierre Legendre, Bob O’Hara, M. Henry H. Stevens, Maintainer Jari
697 Oksanen, and MASS Suggests. 2007. “The Vegan Package.” *Community Ecology Package* 10: 631–
698 637.
- 699 Olson, Donald B., and Richard H. Backus. 1985. “The Concentrating of Organisms at Fronts: A
700 Cold-Water Fish and a Warm-Core Gulf Stream Ring.” *Journal of Marine Research*, 1985, sec. 43.
- 701 Pedler, B. E., L. I. Aluwihare, and F. Azam. 2014. “Single Bacterial Strain Capable of Significant
702 Contribution to Carbon Cycling in the Surface Ocean.” *Proceedings of the National Academy of*
703 *Sciences* 111 (20): 7202–7. <https://doi.org/10.1073/pnas.1401887111>.
- 704 Pizzetti, Ilaria, Giuliano Lupini, Fabrizio Bernardi Aubry, Francesco Acri, Bernhard M. Fuchs, and
705 Stefano Fazi. 2016. “Influence of the Po River Runoff on the Bacterioplankton Community along
706 Trophic and Salinity Gradients in the Northern Adriatic Sea.” *Marine Ecology* 37 (6): 1386–97.
707 <https://doi.org/10.1111/maec.12355>.
- 708 Pomeroy, Lawrence, Peter leB. Williams, Farooq Azam, and John Hobbie. 2007. “The Microbial

- 709 Loop.” *Oceanography* 20 (2): 28–33. <https://doi.org/10.5670/oceanog.2007.45>.
- 710 Quast, Christian, Elmar Pruesse, Pelin Yilmaz, Jan Gerken, Timmy Schweer, Pablo Yarza, Jörg
711 Peplies, and Frank Oliver Glöckner. 2012. “The SILVA Ribosomal RNA Gene Database Project:
712 Improved Data Processing and Web-Based Tools.” *Nucleic Acids Research* 41 (D1): D590–D596.
- 713 Raes, Eric J., Levente Bodrossy, Jodie van de Kamp, Andrew Bissett, Martin Ostrowski, Mark V.
714 Brown, Swan L. S. Sow, Bernadette Sloyan, and Anya M. Waite. 2018. “Oceanographic Boundaries
715 Constrain Microbial Diversity Gradients in the South Pacific Ocean.” *Proceedings of the National
716 Academy of Sciences* 115 (35): E8266–75. <https://doi.org/10.1073/pnas.1719335115>.
- 717 Raes, Jeroen, Ivica Letunic, Takuji Yamada, Lars Juhl Jensen, and Peer Bork. 2011. “Toward
718 Molecular Trait-based Ecology through Integration of Biogeochemical, Geographical and
719 Metagenomic Data.” *Molecular Systems Biology* 7 (1): 473. <https://doi.org/10.1038/msb.2011.6>.
- 720 Ragueneau, Olivier, and Paul Tréguer. 1994. “Determination of Biogenic Silica in Coastal Waters:
721 Applicability and Limits of the Alkaline Digestion Method.” *Marine Chemistry* 45 (1–2): 43–51.
- 722 Rognes, Torbjørn, Tomáš Flouri, Ben Nichols, Christopher Quince, and Frédéric Mahé. 2016.
723 “VSEARCH: A Versatile Open Source Tool for Metagenomics.” *PeerJ* 4: e2584.
- 724 Schloss, Patrick D., Sarah L. Westcott, Thomas Ryabin, Justine R. Hall, Martin Hartmann, Emily B.
725 Hollister, Ryan A. Lesniewski, Brian B. Oakley, Donovan H. Parks, and Courtney J. Robinson. 2009.
726 “Introducing Mothur: Open-Source, Platform-Independent, Community-Supported Software for
727 Describing and Comparing Microbial Communities.” *Applied and Environmental Microbiology* 75
728 (23): 7537–7541.
- 729 Segata, Nicola, Jacques Izard, Levi Waldron, Dirk Gevers, Larisa Miropolsky, Wendy S. Garrett, and
730 Curtis Huttenhower. 2011. “Metagenomic Biomarker Discovery and Explanation.” *Genome Biology*
731 12 (6): R60. <https://doi.org/10.1186/gb-2011-12-6-r60>.
- 732 Smith, Jason M., Karen L. Casciotti, Francisco P. Chavez, and Christopher A. Francis. 2014.
733 “Differential Contributions of Archaeal Ammonia Oxidizer Ecotypes to Nitrification in Coastal
734 Surface Waters.” *The ISME Journal* 8 (8): 1704–1714.
- 735 Sournia, Alain. 1994. “Pelagic Biogeography and Fronts.” *Progress in Oceanography* 34 (2–3): 109–
736 20. [https://doi.org/10.1016/0079-6611\(94\)90004-3](https://doi.org/10.1016/0079-6611(94)90004-3).
- 737 Stocker, Roman. 2012. “Marine Microbes See a Sea of Gradients.” *Science (New York, N.Y.)* 338
738 (6107): 628–33. <https://doi.org/10.1126/science.1208929>.
- 739 Strickland, John DH, and Timothy Richard Parsons. 1972. “A Practical Handbook of Seawater
740 Analysis.”
- 741 Tada, Yuya, Akito Taniguchi, Yuki Sato-Takabe, and Koji Hamasaki. 2012. “Growth and Succession
742 Patterns of Major Phylogenetic Groups of Marine Bacteria during a Mesocosm Diatom Bloom.”
743 *Journal of Oceanography* 68 (4): 509–19. <https://doi.org/10.1007/s10872-012-0114-z>.
- 744 Taylor, Ah, and I Joint. 1990. “A Steady-State Analysis of the ‘microbial Loop’ in Stratified
745 Systems.” *Marine Ecology Progress Series* 59: 1–17. <https://doi.org/10.3354/meps059001>.

746 Teeling, Hanno, Bernhard M. Fuchs, Dörte Becher, Christine Klockow, Antje Gardebrecht, Christin
747 M. Bennke, Mariette Kassabgy, Sixing Huang, Alexander J. Mann, and Jost Waldmann. 2012.
748 “Substrate-Controlled Succession of Marine Bacterioplankton Populations Induced by a
749 Phytoplankton Bloom.” *Science* 336 (6081): 608–611.

750 Teeling, Hanno, Bernhard M Fuchs, Christin M Bennke, Karen Krüger, Meghan Chafee, Lennart
751 Kappelmann, Greta Reintjes, et al. 2016. “Recurring Patterns in Bacterioplankton Dynamics during
752 Coastal Spring Algae Blooms.” *ELife* 5 (April). <https://doi.org/10.7554/eLife.11888>.

753 Tréguer, Paul, Eric Goberville, Nicolas Barrier, Stéphane L’Helguen, Pascal Morin, Yann Bozec,
754 Peggy Rimmelin-Maury, et al. 2014. “Large and Local-Scale Influences on Physical and Chemical
755 Characteristics of Coastal Waters of Western Europe during Winter.” *Journal of Marine Systems* 139
756 (November): 79–90. <https://doi.org/10.1016/j.jmarsys.2014.05.019>.

757 Videau, C. 1987. “Primary Production and Physiological State of Phytoplankton at the Ushant Tidal
758 Front (West Coast of Brittany, France.” *Marine Ecology Progress Series* 35: 141–51.
759 <https://doi.org/10.3354/meps035141>.

760 Voget, Sonja, Bernd Wemheuer, Thorsten Brinkhoff, John Vollmers, Sascha Dietrich, Helge-Ansgar
761 Giebel, Christine Beardsley, et al. 2015. “Adaptation of an Abundant Roseobacter RCA Organism to
762 Pelagic Systems Revealed by Genomic and Transcriptomic Analyses.” *The ISME Journal* 9 (2): 371–
763 84. <https://doi.org/10.1038/ismej.2014.134>.

764 Wan, Xianhui Sean, Hua-Xia Sheng, Minhan Dai, Yao Zhang, Dalin Shi, Thomas W. Trull, Yifan
765 Zhu, Michael W. Lomas, and Shuh-Ji Kao. 2018. “Ambient Nitrate Switches the Ammonium
766 Consumption Pathway in the Euphotic Ocean.” *Nature Communications* 9 (1): 915.
767 <https://doi.org/10.1038/s41467-018-03363-0>.

768 Zorz, Jackie K., Ciara Willis, André M. Comeau, Morgan GI Langille, William KW Li, Catherine
769 Johnson, and Julie LaRoche. 2019. “Drivers of Regional Bacterial Community Structure and
770 Diversity over Depth and Time in the Northwest Atlantic Ocean.” *Frontiers in Microbiology* 10: 281.

771

772

773

774

775

776

777