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To cite this version:

Anne-Sophie Pavaux, Flora Drouet, Jean-Louis Jamet, Jean-Marc Ginoux, Christophe Brach-Papa, et al.. Ecological succession of pico- and nanophytoplankton in a coastal bay of NW Mediterranean sea. Continental Shelf Research, In press, pp.104948. 10.1016/j.csr.2023.104948 . hal-03985097

HAL Id: hal-03985097

https://hal.science/hal-03985097v1

Submitted on 13 Feb 2023

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Ecological succession of pico- and nanophytoplankton in a coastal bay of NW Mediterranean Sea

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Highlights (3 à 5 bullets points – 85 characters each with spaces):

- Combined use of diversity indices and RFD is relevant to study coastal ecosystems
- Ecosystems were more diversified and mature in the more polluted site
- *Synechococcus* spp. population widely dominated coastal areas from the Bay of Toulon

Abstract (100-150 words):

The long-term evolution of pico- and nanophytoplanktonic communities in two coastal contrasting sites from the bay of Toulon was studied using monthly flow cytometry analyses during a seven-year period. Results highlighted higher abundance of both pico- and nanophytoplanktonic communities in the more eutrophic site (*i. e*. the Little Bay). Moreover, even if both sites were widely dominated by *Synechococcus* spp. population, it represented more than 90 % of the population

during summer in the Large Bay. Using diversity indices and rank frequency diagrams to study ecological successions in both sites, communities from the Little Bay (the most polluted site) appeared, paradoxically, as more diversified and more mature than that from the Large Bay. Communities from the Large Bay appeared as less diversified and juvenile linked to the dominance of *Synechococcus* spp. The complementarity of diversity indices and rank frequency diagram was revealed in this present work.

Keywords: ecological succession, diversity, pico- and nanophytoplankton, Mediterranean Sea, Rank Frequency Diagram

1. Introduction

Pico- (size range < 2 µm) and nanophytoplankton (size range 2 - 20 µm) constitute an important part of the microbial loop by being the base of the trophic web (Chiang et al., 2013) and thus have been recognized as major contributors to the total primary production in marine ecosystems (Azam et al., 1983; Platt et al., 1983). Their importance is well established in open oceans, notably for picophytoplankton, but their role and succession in more coastal waters is not well documented (Mitbavkar et al., 2012). However, understanding ecosystem structure and functioning is essential to monitor and predict their evolution. In most cases, community structure and dynamics are shaped by a wide variety of environmental variables including nutrients availability, salinity or temperature (Bec et al., 2005; Sommer et al., 1986). Yet coastal waters are subject to nutrient enrichment by anthropogenic activities and freshwaters discharges (Paerl et al., 2006, 2003). Indeed, freshwater flow (i) are a main source of nutrients and (ii) cause hydrological perturbations as salinity variation or water resilience which play a determinant role in nutrients availability (Paerl et al., 2006). These anthropogenic perturbations and freshwater discharges, typical of coastal waters, may play an important role in shaping community structure and determine ecological succession in these marine systems. Indeed, according to the model of ecological succession proposed by Margalef (1951),

52 Reynolds (1984, 1980) or Sommer et al. (1986), succession of species represents a response to
53 physical, chemical and biological changes. To our knowledge, only few studies focused on ecological
54 succession in coastal waters and even less on pico- and nanophytoplanktonic succession.
55 This study was realised along a seven-year time series at the Bay of Toulon, at two linked but
56 contrasted sites, *i. e*. the Little Bay (LiB) and the Large Bay (LaB). They are subjected to the same
57 climatic conditions but differently affected by anthropogenic activities. The LiB , at the West, is semi
58 enclosed, characterised by smaller dimensions (9.8 km^2 and 15 m deep – Dang et al., 2014), a longer
59 residence time of water (3 - 6 days – Jouan et al., 2001), and is strongly affected by human activities
60 (leisure, commercial and military harbours, shipyards). Whereas the LaB, at the East, is characterised
61 by bigger dimensions (42 km^2 and 5 to 30 m deep– Coclet et al., 2018) with a shorter residence time
62 of water (1 - 2 days – Duffa et al., 2011), less impacted by anthropogenic activities and more open on
63 the Mediterranean Sea. Surface waters and sediments are strongly polluted by metalloids and trace
64 metals especially in the LiB (Tessier et al., 2011; Cossa et al., 2014; Dang et al., 2014, 2015, Coclet et
65 al., 2018). Inversely to the LaB, the LiB is considered as eutrophic, with a higher abundance of pico-
66 and nanophytoplanktonic organisms (Coclet et al., 2018; Delpy et al., 2018). The same pattern has
67 been observed for the micro phytoplanktonic and meso zooplanktonic communities (Rossi and
68 Jamet, 2008; Serranito et al., 2016). The diversity observed in the LiB is lower, due to a characteristic
69 presence of *Oithona nana* GIESBRECHT (1892) (Crustacea: Cyclopoida – Bandeira et al., 2013, Richard
70 & Jamet, 2001).
71 Regarding the functional importance of pico- and nanoeukaryotes in food webs and in carbon
72 fluxes in coastal marine waters, this study aimed at (i) investigating composition and abundance of
73 pico- and nanophytoplanktonic communities between two contrasting sites from the Bay of Toulon,
74 and (ii) defining the ecological successions of these sites using both diversity indices and Rank
75 Frequency Diagram (RFD). This study will allow us to determine if diversity indices and rank
76 frequency diagrams are relevant tools to assess the anthropogenic impact on coastal communities.
77

2. Material and Methods

2.1. Sampling

Samples were collected monthly between October 2013 and August 2020, in the Bay of Toulon, at two stations: Little Bay (LiB - S1, 43°06’30” N / 05°55’00” E) and Large Bay (LaB - S2, 43°05’45” N / 05°56’30” E). All samples were collected between 08:00 and 11:00 AM at both 3 and 10 m depth (Figure 1).

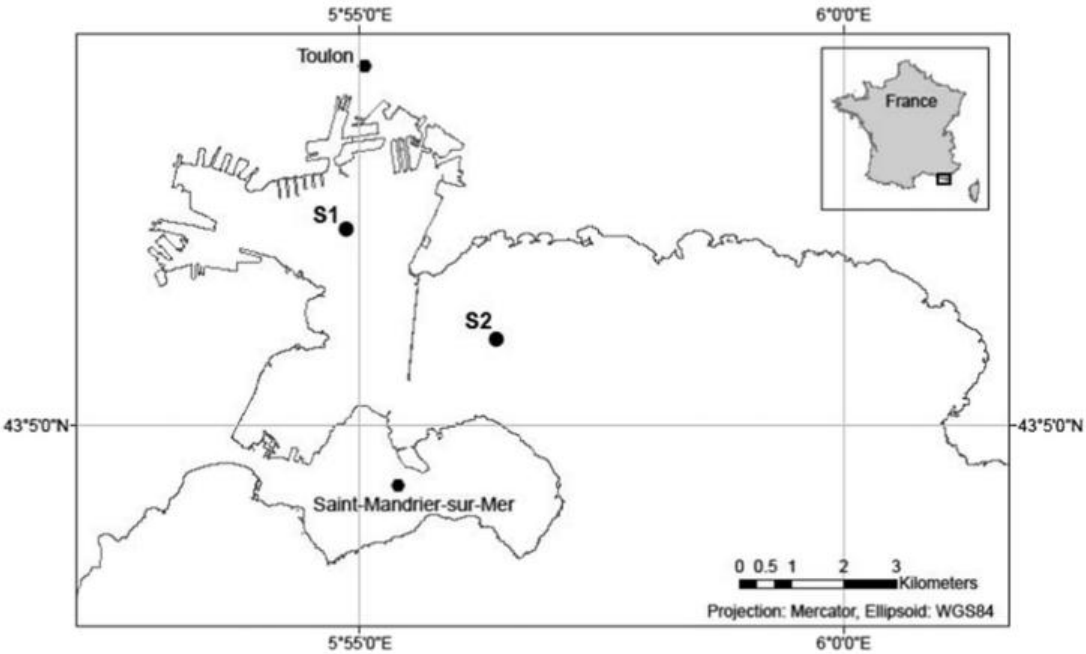

Figure 1: Localization of the two stations in the LiB (S1) and LaB (S2) in the Bay of Toulon (from Serranito et al., 2016).

Environmental variables (temperature, salinity, pH and dissolved oxygen concentration) were measured *in situ* in LiB and LaB, at 3 and 10 m deep using calibrated sensors: Hydrolab HL7® and Hydrolab Quanta® multiparametric probes. These variables were used as descriptive factors to characterize differences among the two contrasted sites.

To determine pico- and nanophytoplankton communities’ abundance, water samples were collected using a 10L Niskin bottle at 3 and 10 m depth at both sites (LiB and LaB). Samples were pre-filtered through a 90 µm mesh to remove grazers and other macroparticules. Subsamples of 4.5 mL were then immediately transferred into 5 mL cryotubes and fixed with a glutaraldehyde solution

95 (final concentration 0.25 %) and a pluronic acid solution (final concentration 0.01 %). These
96 subsamples were kept at 4°C until analysis and then thawed out just prior analysis by flow cytometry.
97
98 2.2. Flow cytometry analysis
99 Flow cytometry analyses were performed using an Accuri C6 flow cytometer (BD Biosciences®)
100 equipped with 488 and 640 nm laser. The sheath fluid used was ultrapure water filtered through 0.2
101 µm. The 488 nm blue laser induced two natural fluorescence: Chlorophyll a (red fluorescence
102 FL3 > 670 nm) and Phycoerythrin (orange fluorescence FL2: 585 +/- 20 nm). The FL4 phycocyanin (far
103 red fluorescence 675 +/- 25 nm) is induced by the 640 red laser. The forward scattered light (FSC)
104 was related to the size of the cells while Side scattered light (SSC) was related to shape and cell
105 structure; 500 µl sample were analysed at a flow rate of 60 $\mu l.min^{-1}$. Beads of 2 µm diameter
106 (Fluoresbrite YG, Polysciences) were periodically added to the samples as internal standards to
107 differentiate between Picoeukaryotes and Nanoeukaryotes.
108 Thanks to their optical properties, six different clusters of pico- and nanophytoplankton were
109 discriminated (Figure 2): (i) *Synechococcus* spp. (SYN) characterised by small cells (FSC < 12 000), rich
110 in phycoerythrin (mean FL2 ≃14 950) and low in chlorophyll a (mean FL3 ≃15 950); (ii)
111 *Prochlorococcus* spp. (PROCHL) which cells are differentiated from SYN cells by lower fluorescence
112 (mean FL2 ≃117 and mean FL3 ≃ 895); (iii) Picoeukaryotes (PICOeuk) characterized by larger cells
113 than cyanobacteria (FSC ≃ 45 000) and higher red FL3 fluorescence (Mean FL3 ≃ 29 000); (iv)
114 Nanoeukaryotes (NANOeuk) are separated from PICOeuk by higher FSC (> 200 000) and higher red
115 FL3 fluorescence (mean FL3 ≃ 167 592) ; (v) Cryptophyceae (CRYPTO) are discriminated from
116 NANOeuk thanks to higher orange FL2 fluorescence ; and (vi) Heterotrophic Protist (HtP)
117 characterized by low red and orange fluorescence (respectively < 2 000 and < 1 000) and high FSC
118 (> 900 000).
119

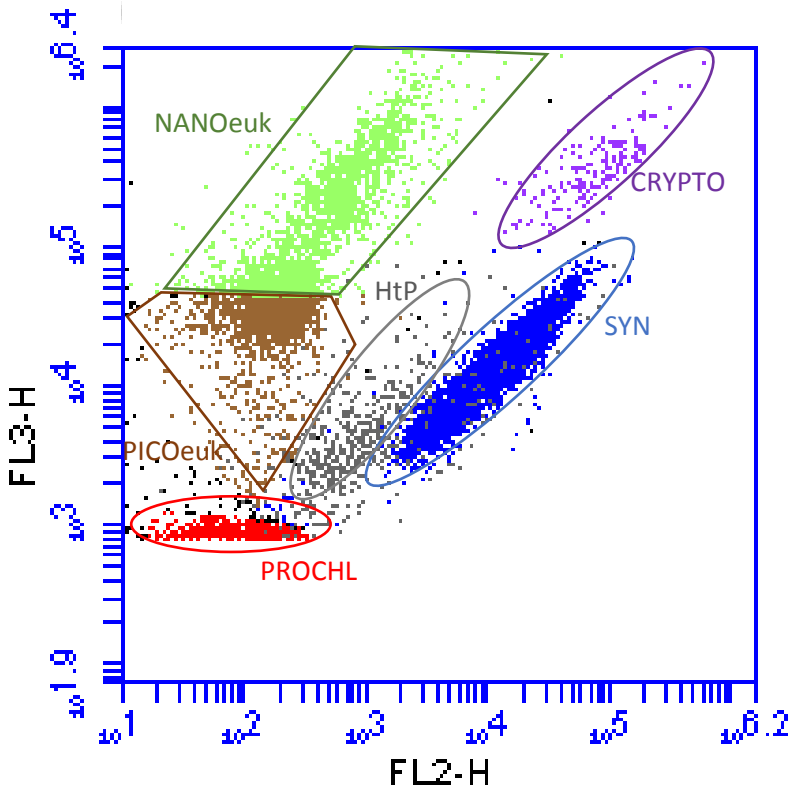

Figure 2 : Resolution by flow cytometry of ultraphytoplankton assemblage composition during the study period.

2.3. Statistical analysis

Differences of pico- and nanophytoplanktonic abundances, and abiotic factors between sites (LiB and LaB) and depth (3 m and 10 m) were assessed by Kruskal-Wallis analysis. As no significant difference was observed for abiotic factors and abundances between 3 m and 10 m deep ($p > 0.05$), values were averaged.

A Principal Components Analysis (PCA) was used to assess the relationships between pico- and nanophytoplankton abundances and their hydrological environment. The dataset consisted of 81-month values, from October 2013 to August 2020, described by 36 biological variables (abundances, FL2, FL3, FL4, SSC and FSC of SYN, PROCHL, PICOeuk, NANOeuk, CRYPTO, HtP) and 4 hydrological variables (temperature, salinity, pH, dissolved oxygen concentration). The multifactorial treatment was made using R software with FactoMineR package. To determine the number of

principal components used in this analysis, a scree plot was used to represent eigenvalues ordered from the largest to the smallest (Peres-Neto et al., 2005). Only the first two components were used since more than 64 % of the variances were explained by these components. As a second step, correlation of Bravais-Pearson was used to assess the relation between abiotic factors and abundances of the communities.

Using the classification of diversity indices proposed by Bandeira et al. (2013), 2 types of indicators were chosen: (i) Shannon and (ii) Piélou indicators which were monthly calculated to investigate the diversity of both sites. Shannon index (H') is one of the most frequently used biodiversity indexes. It originates from the information theory as a measure of entropy (Shannon, 1948) and is used to estimate the specific diversity of planktonic communities and calculated as follow:

$$H' = -\sum_{i=1}^{S} p_i \, log_2 p_i$$

with $p_i = n_i/N$; p_i is the frequency of each class, S the total number of classes, n_i the number of individuals from the i class and N the total abundance. The minimum value of the index is 0 when all the observations belong to a single class. The maximum value equals ln (1/S) and it can be reached when the observations are equally divided between all the classes.

Piélou regularity index (J') (1966) reflect the evenness of a community and is calculated as follow:

$$J' = \frac{H'}{H'_{max}} = \frac{H'}{log_2(S)}$$

This index represents a standardization form of the Shannon index, displaying the relations between the class frequencies (Piélou, 1966). The evenness equals one when the class frequencies are similar and it approaches zero when the majority of observations belong to a single class.

Succession of pico- and nanophytoplanktonic communities were assessed using Rank Frequency Diagrams (RFD, Frontiers 1976). Status of the community were empirically defined according to the trend of the RFD curves; various models of species distributions have been described in the past as Broken Stick model (MacArthur, 1957), lognormal (Preston, 1948), geometric (Motomura, 1932) or even Zipf-Mandelbrot (Frontier, 1985). No fitting to any model is intended here since RFD are only

used to describe ecological succession, following Frontier's description for planktonic ecosystem (Frontier, 1985, 1983, 1976). Depending on the shape of the curve, three main stages have been described. In stage 1, beginning of the succession, the curve is concave at the top left and become convex on the right part, typical of a young community with low diversity structure. In stage 2, the curve is entirely convex and the diversity at its maximum. In stage 3, end of the succession, the curve becomes straight and diversity is intermediate.-The determination of the stage was done using the linear trend curve in excel: when the determination coefficients were higher than 0.82 and 0.87 for LaB and LiB respectively, the curve was determined as convex; for lower determination coefficients, curve was determined as concave or straight.

3. Results

3.1. Temporal variability of abiotic variables, pico- and nanophytoplanktonic abundances

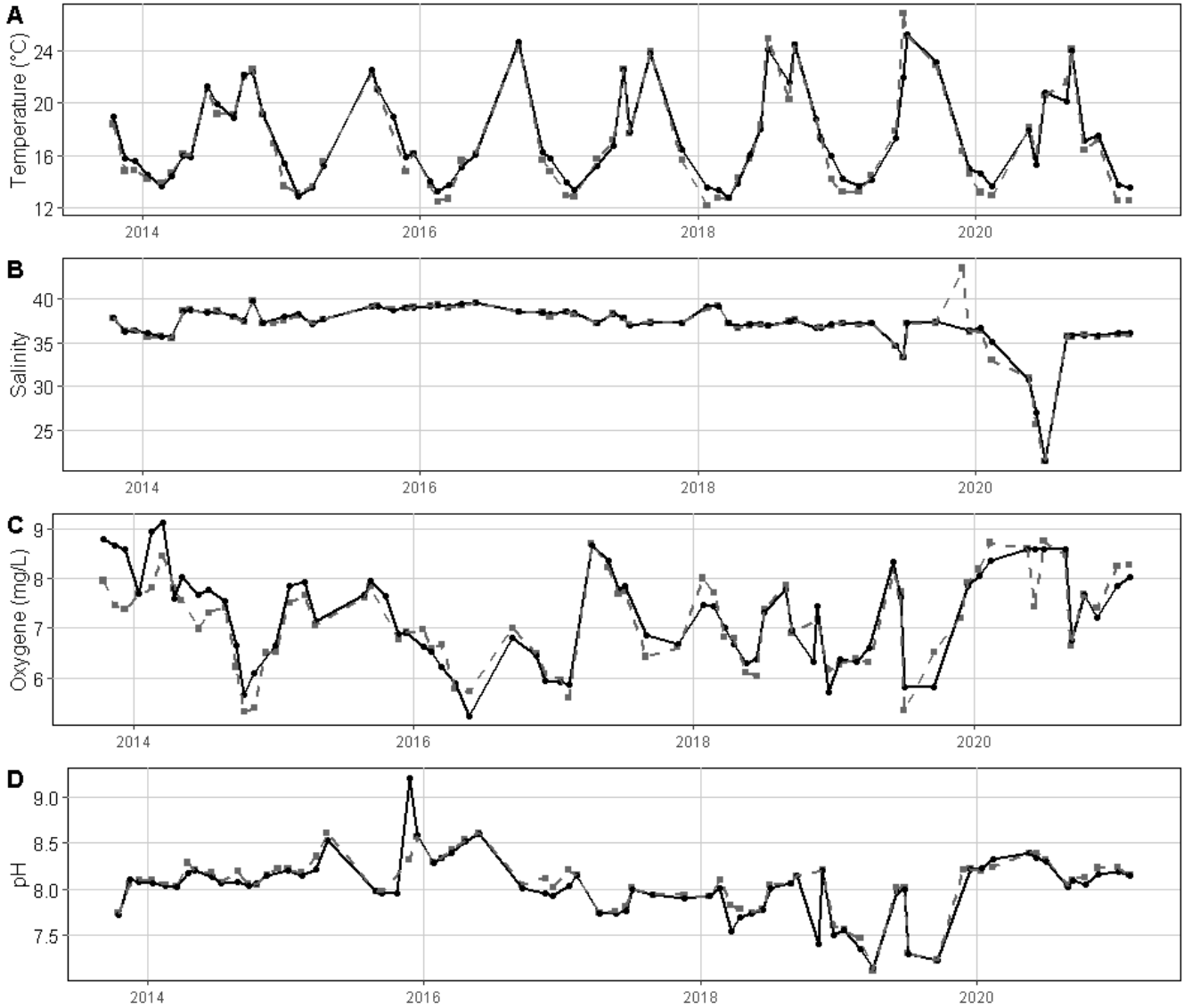

Figure 3: Abiotic variables in the Little Bay (dashed lines) and the Large Bay (solid lines): (A) Temperature (°C), (B) Salinity, (C) Dissolved Oxygen ($mg.L^{-1}$), (D) pH. Data are acquired as an average of values measured at 3 m and 10 m of depth.

The annual variations of the hydrological variables (*i. e*. temperature, salinity, dissolved oxygen and pH) were presented in the Figure 3. No significant difference was observed between LiB and LaB, whatever the considered variables (Kruskal-Wallis; $p > 0.05$).

182 Seasonal variations of temperature were observed in LiB and LaB (Figure 3A): maximal values

183 (> 20°C) were recorded during summers and minimal ones during the winter period (< 15°C).

184 Maximal temperature was reached in June 2019, in LiB.

185 No variation of salinity was observed along the study period (LiB: 37.07 ± 2.89; LaB: 37.11 ± 2.70)

186 excepted in July 2020, when salinity reached respectively 21.53 and 21.54 for LiB and LaB (Figure 3B).

187 Dissolved oxygen concentrations varied from 5.23 $mg.L^{-1}$ (October 2014) and 9.11 $mg.L^{-1}$ (March

188 2014) without following a seasonal trend (Figure 3C).

189 pH values were stable across the study period (LiB: 8.12 ± 0.36; LaB: 8.09 ± 0.40) and varied between

190 7.11 (April 2019 – LiB) and 9.22 (July 2015 – LaB – Figure 3D).

191

192 Table 1 : Mean annual abundances of each communities ($cells.mL^{-1}$) in both sites (LiB and LaB)

Date	Site	CRYPTO	NANOeuk	PICOeuk	HtP	PROCHL	SYN
2013	LiB	854	4033	16486	3134	6425	12708
2013	LaB	173	2222	4072	1049	3443	21256
2014	LiB	725	5438	10284	4260	4865	10094
2014	LaB	231	2616	4786	1276	2380	17489
2015	LiB	402	4789	9021	2948	2622	15643
2015	LaB	110	2283	4316	1129	1427	18045
2016	LiB	479	2385	6773	2309	2475	6808
2016	LaB	196	1982	7391	1002	1193	21935
2017	LiB	338	3345	6412	1569	238	14774
2017	LaB	82	1995	2924	611	332	13243
2018	LiB	596	4001	10567	4745	888	16952
2018	LaB	273	3296	7362	1942	616	31004
2019	LiB	469	5294	7934	3123	825	14585
2019	LaB	172	2805	5750	910	429	15049
2020	LiB	447	4637	9482	1939	579	13606
2020	LaB	80	2445	6474	579	278	16490

193

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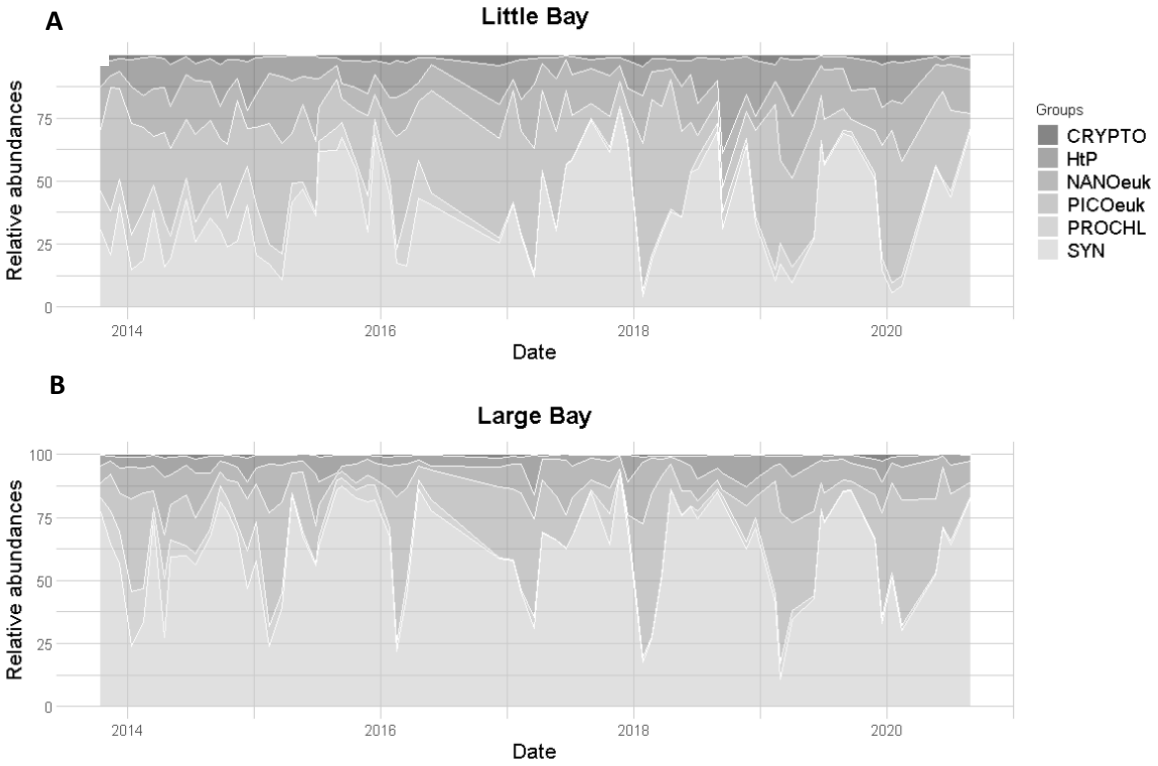


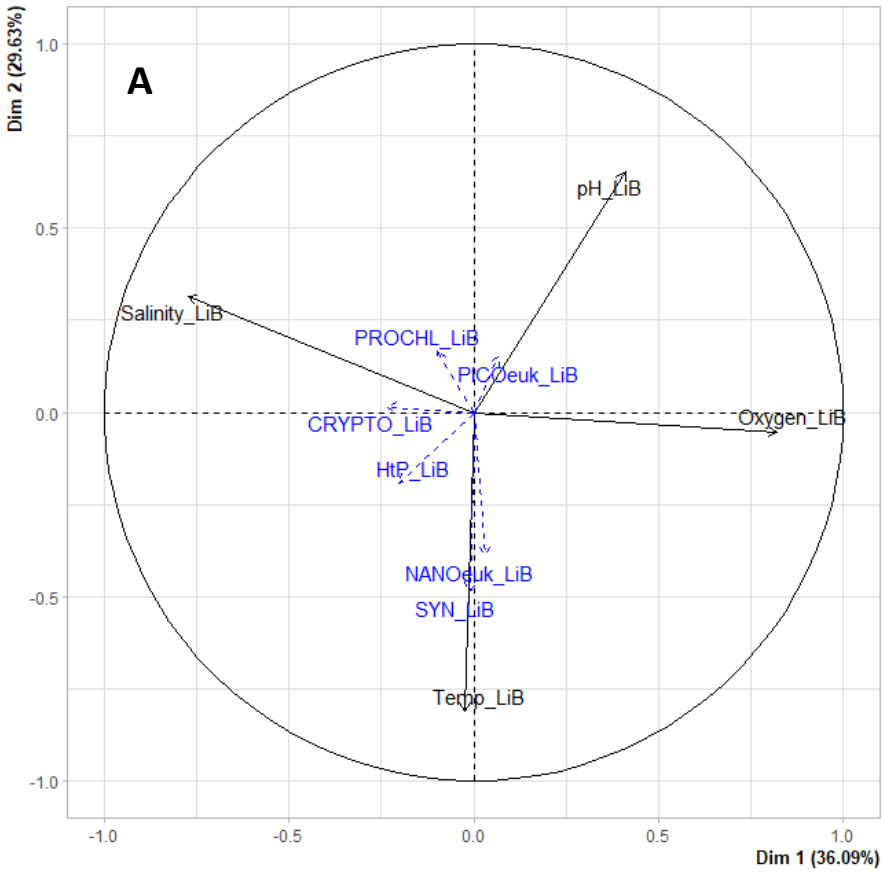
Figure 4: Repartition of *Synechococcus* spp., *Prochlorococcus* spp., Heterotrophic Protist, Picoeukaryotes, Nanoeukaryotes and Cryptophyceae and in LiB (A) and LaB (B).

The mean annual abundances of the communities identified by flow cytometry are presented in the Table 1; the composition of the communities is represented in the Figure 4. Total abundances of the 6 communities were significantly different between the 2 studied site (Kruskal-Wallis, $p < 0.05$) with in average higher values in LiB (32 419 cells.mL^{-1}) than in LaB (28 747 cells.mL^{-1}). Both sites are largely dominated by SYN: in average, SYN represents respectively 38 % and 61 % of total abundances in LiB and LaB.

Strong variations of SYN abundances was observed between October 2013 and February 2015 in LiB, not linked with seasonality: abundances peaked between 35 and 40 % in December 2013, March, June, August and December 2014. Apart from that, abundance was between 10 and 26 %. PICOeuk was especially abundant during this period and varied between 17 % in September 2014 and 48 % in November 2013. PROCHL and HtP abundances varied between 9 to 19 % and 6 to

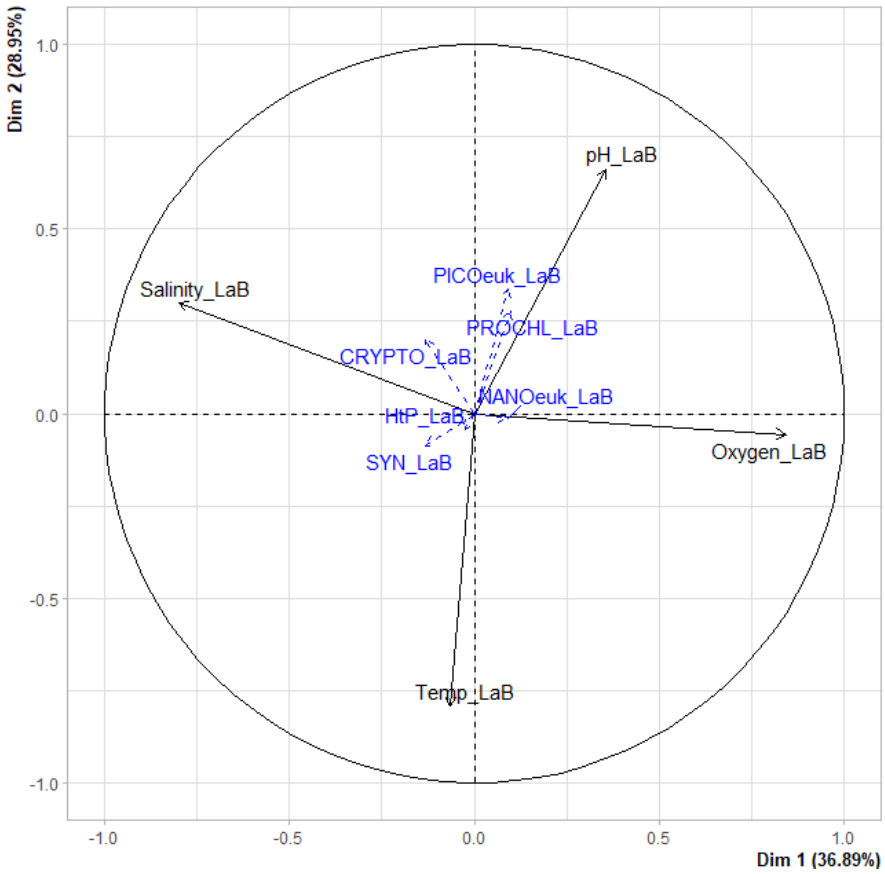
12 % respectively. NANO represented less than 20 % of the community. CRYPTO abundance varied between 0.3 and 3 %. In 2015, SYN proportion increased and reached 67 % in September 2015; at the same date, PICOeuk abundance substantially decreased to 9 %. From 2016, seasonal variation of SYN abundances was observed: its proportion reached up to 80 % during spring and decreased to less than 15 % in winter (4 % in January 2018). In the meantime, proportion of PICOeuk was minimal during summer (5 % in August 2017) and maximal during winter (62 % in February 2018). PROCHL, HtP, NANO and CRYPTO represented respectively 3, 10, 14 % and less than 3 % of the community.

Communities from LaB were largely dominated by SYN which represented in average 61 % of the communities. Seasonal variations of its proportion were observed; it is minimal during winter (25 % in February 2015) and maximal during summer (92 % in September 2017). PICOeuk was the second more abundant group and represents 7 to 50 % of the community. NANO, PROCHL, CRYPTO and HtP represents less than 15 % of the total communities.



B

Figure 5: Principal Components Analysis (PCA) applied to data from LiB (A) and LaB (B).



The results of the PCA variables representing the 7 years sampling years are shown in Figure 5. The first two axes accounted for 36 % and 29 % of the total variance for both LiB and LaB, demonstrating that, the major factor affecting our data was temperature. But, most likely due to photosynthesis, oxygen was also highlighted by the PCA as a variable affecting the communities' structure.

In LiB, abundances of both SYN and NANOeuk were strongly influenced by high temperature, explaining SYN peaks during summer (Bravais-Pearson, respectively $p < 0.00001$ and $p < 0.01$). On the contrary, PICOeuk from both LiB and LaB, were influenced by low temperature since it peaked during winter.

In LaB, no clear relations could be determined; abiotic factors used in this analysis seems insufficient to explain the variances of abundances from all studied communities.

3.2. Diversity indices

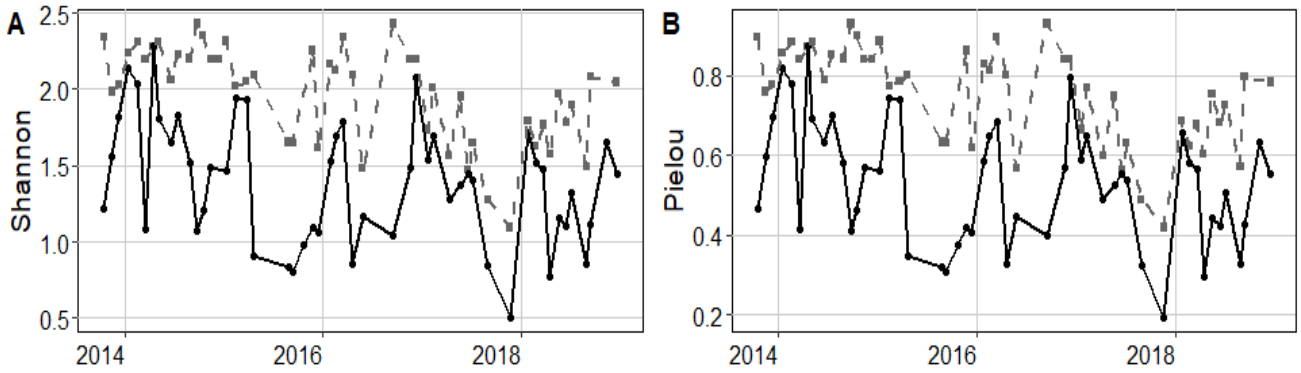


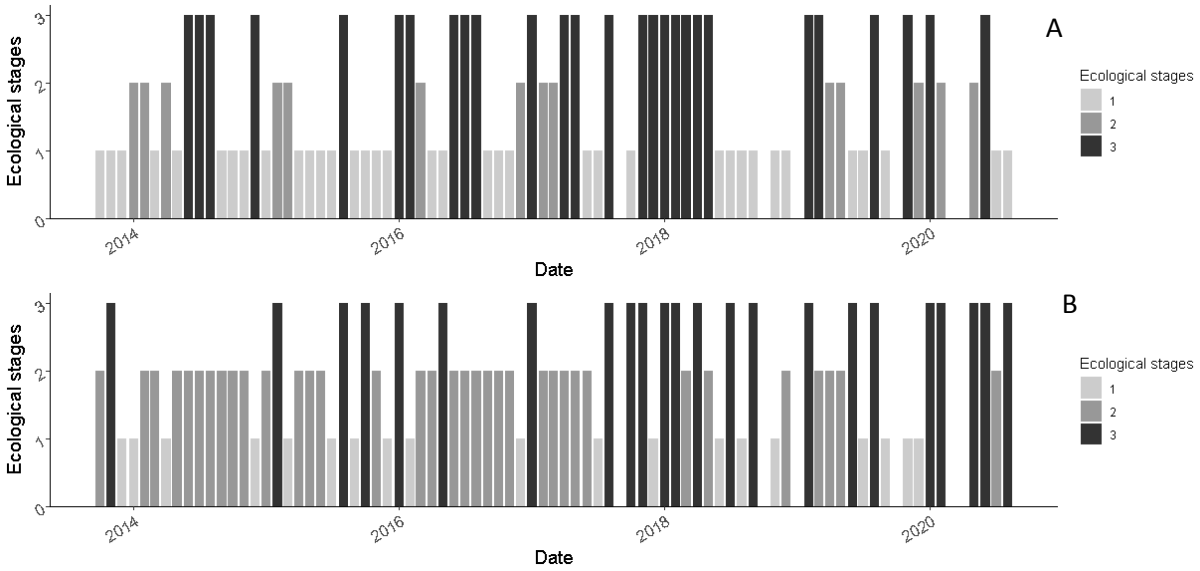
Figure 6: Evolution of plankton indices along the study period: Shannon (A) and Piélou indices (B) for LiB (dashed grey lines) and LaB (solid black lines).

Diversity indices are presented in Figure 6. Shannon index was significantly lower in LaB than in LiB (Mann Whitney, $p < 0.05$). In LiB, Shannon index varied from 1.1 (November 2017) to 2.43 (September 2016) without a seasonal trend; in LaB, this index peaked at the beginning of the year (it reached 2.08 in December 2016) and is minimal during summer (0.84 in August 2015).

Equitability index or Piélou index has the same trend as Shannon index since its calculation derives from Shannon's one.

247

248 3.3. Community assemblage



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250

251 Figure 7: Ecological stages determined for LiB (A) and LaB (B)

252

253 Ecological stages determined following Frontier's descriptions (1985) are presented in the
254 Figure 7. In LiB, a total of 19 stages 1 have been determined; 35 months have been determined as
255 stage 2 and 23 as stage 3. Three complete successions are observed between December 2014 to
256 February 2015, February and May 2016, and November and February 2019. In LaB, 36 months were
257 determined as stage 1, 14 as stage 2 and 27 as stage 3. Only one complete succession was
258 determined in November 2016 to January 2017.

259

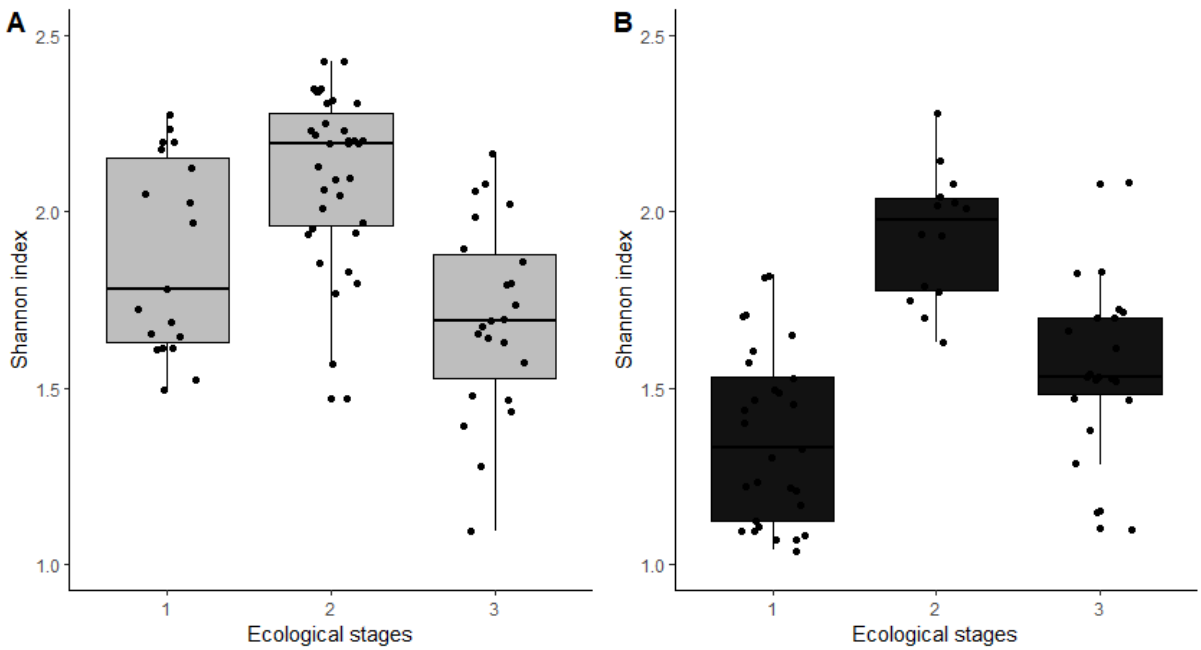

Figure 8: Evolution of Shannon index and ecological stages for both LiB (A) and Lab (B). Stages were determined following Frontier's recommendations (see Frontier 1985, 1983, 1976).

Shannon indices varied with ecological stages. In LiB, Shannon index varied between 1.50 and 2.28 in stage 1, between 1.47 and 2.43 in stage 2 and decrease to 1.10 and 2.17 in stage 3. In LaB, Shannon indices was between 0.81 and 1.82 for stage 1. They increased at stage 2 to reach the minimum of 1.63 and the maximal value of 2.28. At stage 3, this index decreased and was between 0.51 and 2.08 (Figure 8).

4. Discussion

Because of its topography and anthropogenic pressure this site is currently facing, the Bay of Toulon is relevant to explore annual variability of zooplankton (Jamet et al., 2001; Richard and Jamet, 2001) and microphytoplankton (Bogé et al., 2006; Jamet et al., 2005; Rossi and Jamet, 2009). A previous study (Delpy et al., 2018) has investigated pico and nanoplanktonic dynamics during a two year cycle (October 2013 to December 2015). By using a longer time series (2013-2020), our study

276 explores the evolution of pico- and nanophytoplanktonic communities to determine ecological
277 successions in the two contrasting sites of the Bay of Toulon.
278
279 4.1. Variations of abiotic variables and pico- and nanophytoplanktonic abundances
280 The monitoring of abiotic variables (*i. e*. temperature, salinity, pH and oxygen) did not reveal a
281 stratification phenomenon in both sites since no significant difference was observed between depths
282 of 0 and 10 m, probably due to wind which can disturb vertical stratification in coastal waters
283 (Charles et al., 2005). Moreover, no significant difference in abiotic variables have been revealed
284 between the both studied sites.
285 Water temperature showed a clear seasonal pattern as usually found in coastal sites from the
286 Mediterranean sea (Rossi and Jamet, 2009). Salinity and pH were quite stable along the sampling
287 period excepted in July 2020 when salinity reached 21, related to the summer storms.
288 Pico- and nanophytoplankton abundances are significantly higher in LiB than in LaB, as previously
289 described by Delpy et al. (2018). It reflected the trends observed for other higher planktonic species
290 such as mesozooplankton or microphytoplankton (Jamet et al., 2001; Serranito et al., 2016). Such
291 differences of abundances between sites were attributed to eutrophic conditions characterising LiB
292 (Rossi and Jamet, 2009). Indeed, mean chlorophyll a concentration in the Mediterranean Sea ranges
293 between 0,1 to 0,5 $\mu g.L^{-1}$ although values measured in LiB are significantly higher (1 to 1,5 $\mu g.L^{-1}$ -
294 Jamet et al., 2001) and characterize eutrophic waters according to Jacques and Tréguer (1986) and
295 Psyllidou-Giouranovits et al. (1997).
296 Seasonal variations of abundances were observed in both sites: abundances of SYN
297 significantly increased during late spring/summer with maximum abundance of 127 300 $cells.mL^{-1}$ (in
298 2017, at LaB), close to maxima observed for Mediterranean coastal systems (Agawin and Agusti,
299 1997; Cerino et al., 2012; Ferrier-Pages and Rassoulzadegan, 1994); in winter, PROCHLO became
300 dominant and represented 50 % of the total communities (34 648 $cells.mL^{-1}$), close to values
301 observed by Grégori et al. (2001) in Marseille. Such seasonality in pico- and nanophytoplanktonic

302 communities was in agreement with previous observations in the Gulf of Lion (Lefevre et al., 1997)
303 and in Marseille (Grégori et al., 2001).
304 Seasonal changes in both abiotic variables and groups abundances were analysed using a
305 PCA. Paradoxically, a clear relation between temperature and SYN abundances was only determined
306 in LiB but not on LaB. As previously described by Sohm et al. (2016), two different ecotypes may
307 occupy these two different bays; SYN occupying LiB could largely be defined by temperature
308 contrarily to the SYN ecotype from LaB.
309 Moreover, no clear relation was observed for the other communities with abiotic variables
310 presented here. Previous studies have demonstrated that abundance of these different groups is
311 driven by nutrient availability and species growth rate. Indeed, LiB is considered as more eutrophic
312 than LaB due to higher Chlorophyll a and nutrient concentrations (Rossi et al., 2008; Rossi and Jamet,
313 2009). LaB exhibited lower P-PO_4^{3-} concentrations due to (i) a more regularly mixing of waters and
314 (ii) the predominance of SYN which can contribute up to 35 % of the total Pi uptake (Delpy et al.,
315 2018). It is important to note that biotic interaction such as grazing pressure or competition for
316 nutrient and space by larger phytoplankton could also play an important role in shaping community
317 structure and need to be clarified.
318
319 4.2. Composition of pico- and nanophytoplanktonic community
320 Even if SYN was dominant in both LiB and LaB, this group was largely more abundant in LaB as
321 previously described by Delpy et al. (2018). It represented between 25 to 92 % of total communities
322 in LaB, although communities of the LiB were represented by 2 major codominant groups *i. e*. SYN
323 (representing between 15 to 75 % of the total communities) and PICOeuk (5 to 62 % of the
324 community). The dominance of SYN in terms of abundance and contribution to primary productivity,
325 has now been widely recognised (Johnson et al., 1982; Morris and Glover, 1981). Because of their
326 small size and higher surface to volume ratios, SYN are more competitive than other to acquire
327 nutrients and explained their dominance in both sites (Bec et al., 2011). The ability of SYN to acquire

328 soluble reactive phosphorus (notably in P-limited zones) provides an ecological advantage over other
329 phytoplankton classes (Collos et al., 2009). Differences of abundances between sites could be
330 explained by higher trace metals' concentration in LiB (Rossi and Jamet, 2008). Indeed, a strong
331 inhibition of SYN growth rate was observed when exposed to Copper (EC_{50} = 4 µg.L^{-1} - Debelius et al.,
332 2011, 2009). Moreover, pico- and nanophytoplanktonic communities collected in LaB exposed to
333 trace metal cocktail, revealed a shift from SYN dominated community (typical of LaB) to a less SYN
334 dominated community (with higher proportion of picoeukaryotes) as observed in LiB (Coclet et al.,
335 2018). Codominance of PICOeuk and SYN (as observed in LiB) has been previously observed in other
336 coastal waters (Changjiang Esturay - Pan et al., 2007), where PICOeuk can even surpass
337 cyanobacteria in terms of biomass. Other groups (NANOeuk, HtP) represented less than 20 % of total
338 communities. Differences between both cyanobacteria biomass (*i. e.* PROCHL and SYN) was
339 consistent with previous study since PROCHL abundance vary inversely with SYN ones (Partensky et
340 al., 1996) and is predominantly abundant in oligotrophic waters (Pan et al., 2007; Partensky et al.,
341 1999).

342 In previous studies (Agawin et al., 1998; Delpy et al., 2018; Moisan et al., 2010), successions of
343 pico- and nanophytoplanktonic communities appeared mainly driven by the ability to acquire
344 nutrients and species growth rate. However, communities of the Bay of Toulon showed SYN
345 dominated the communities, suggesting bottom up processes as key variables in the structuring of
346 communities. Indeed, the dominance of SYN during the spring/summer period in LaB explained the
347 seasonal variations of Shannon (and Piélou) index with a clear decrease of this index during summer;
348 in winter, diversity increased again, notably linked to the fall in SYN proportion. In LiB, no clear
349 seasonal variation of Shannon index was observed. However, diversity was significantly higher in LiB
350 than LaB and thus, confirmed by RFD analysis (with more month described as in LiB than in LaB),
351 contrary to the previous results obtained at the same site for zooplankton and phytoplankton
352 suggesting that diversity was higher in LaB (Jamet et al., 2005; Rossi and Jamet, 2009; Serranito et al.,
353 2019). Such contradiction could be induced by the dominance of SYN in the Bay of Toulon: in LaB,

354 SYN largely drive the community's dynamic; in LiB, SYN was still very abundant but due to high trace
355 metals concentration, it became less competitive than in LaB, and other groups, as PICOeuk, became
356 more abundant. Moreover, in LiB, the proportion of HtP is higher than in LaB and could also control
357 SYN population by grazing pressure (Christaki et al., 1999; Dolan and Šimek, 1999; Guillou et al.,
358 2001).

359 Interestingly, according to Frontier (1985, 1983), a chronic pollution induces a recover to a stage
360 1 (typical of a juvenile population) since few species are able to maintain themselves in such
361 conditions of stress. However, our results indicated more stage 1 in LaB than LiB, and even, more
362 evolution to a complex ecosystem typical of a stage 2 in LiB than in LaB. The LaB is characterized by
363 stage 1 corresponding to a little evolution of the population, whose structure and organisation are
364 deeply affected by disturbances, here the domination of SYN population linked to its ability to better
365 acquire nutrients. Paradoxically, populations from LiB naturally evolved towards more mature and
366 diversified ecosystems. This is explained by anthropogenic activities increasing trace metals'
367 concentrations limiting SYN domination in LiB, by (i) decreasing SYN growth rate (Debelius et al.,
368 2011, 2009) and (ii) increasing grazing pressure by ciliates and other heterotrophic protists (Christaki
369 et al., 1999; Dolan and Šimek, 1999; Guillou et al., 2001).

370

371 4.3. The combine use of RFD and diversity index to monitor pico- and nanophytoplanktonic
372 assemblage

373 To better understand the structure and the functioning of ecosystems, ecologists have worked
374 on principals establishing theorical ecology. Among these are the diversity indices used to complete
375 the description of a community by describing the richness or the evenness of species. The whole idea
376 was to obtain quantitative information to compare biological entities (Heip et al., 1998). In our study,
377 we used two different indices based on their mathematical convergence highlighted by the work of
378 Bandeira et al. (2013). Shannon and Piélou revealed important variations of diversity and evenness in
379 agreement with our observations.

Another method used to determine ecological succession of an ecosystem is to build Rank Frequency Diagram, establishing “the numerical repartition of individuals by species within a biocenosis” (Frontier, 1976). Considered as a fuller description of biological communities than diversity indices (although not independent from them), it introduces maturity degrees of the populations divided in 3 stages. First, stage 1, the beginning of the succession, is dominated by high ranked taxa. The community is composed by one or a few small species with predominantly *r* selected species described as invasive, fast growing and prolific (Reynolds, 1997). In stage 2, the abundance of rare species continues to decrease and common species become more numerous. This community is characterized by K selected species, with bigger size, lower growth rate, favoured by physiological capabilities allowing their survival towards the supportive capacity of the resource available (Reynolds, 2006). According to Khemakhem et al. (2010), this favoured retroactive loops within the trophic network, allowing a more stable ecosystem where the diversity is maximal. And, in stage 3, the end of the succession, the numbers of the most abundant species increase whereas the diversity decreases, characterising the maturity of the community.This tool, notably used in other field of application as language study (Mandelbrot, 1953), or socio-economy (Petruszewicz, 1972), were widely used fifty years ago in ecology notably by Margalef (1957) and Frontier (1985, 1983, 1976). According to these authors, ecosystems have a structure in terms that they are composed by different species arranged in a define pattern according to the availability of resources. Stages are described following different fitting models: broken stick model (MacArthur, 1957), general lognormal (Preston, 1948), geometric (Motomura, 1947) or Zipf-Mandelbroat (Mandelbrot, 1977). This method wasn’t used much during these past decades, notably linked to the difficulty in interpreting results. However, the relevance of this method has been well documented in both marine (Davoult et al., 1993; Fromentin et al., 1997; Frontier, 1985; Jamet et al., 2005; Sanvicente-Añorve et al., 2002) and terrestrial ecosystems (Kevan et al., 1997; Vahid et al., 2013; Watkins and Wilson, 1994; Wilson et al., 1998, 1996; Wilson and Gitay, 1995).

For terrestrial ecosystems, Grime (1974, 1977) described three primary strategies in plants and their relevance to ecological and evolutionary theory. The first one, C-selection, were growth is maximized in productive and relatively undisturbed conditions. The second one, S-selection, is characterized by environmental stresses and resource depletion. The last one, R-selection, is associated to organisms with a short lifespan and high reproduction rates in severely perturbed environments. Following Smayda & Reynolds (2001) adaptations of the Grime's triangle (1974) and within the framework of this study, Frontier's (1976) stage 1 could be hypothesized as an equivalent of Grime's (1977) R-selection with fast growing, predominantly *r* selected species. The stage 2 characterized by K selected species could be considered as an equivalent of the S-selection with stress tolerant species and stage 3 that of the C-selection with highly competitive species. In the current context of global change, future environmental conditions could largely affect marine coastal ecosystems, resulting in an increase of their entropy creating stronger perturbations affecting the structure, diversity and functioning of communities. Subsequently, future monitoring of such ecosystems could more frequently highlight communities transitioning towards a composition of fewer smaller, fast growing r selected species as observed in Frontiers' stage 1 (1976) and Grime's (1977) R-selection.

Our study combines quantitative information from diversity indices and qualitative information given by RFD to study two contrasted sites from Toulon. The strong correlations between Shannon indices and ecological stages highlighted the relevance to use both methods in the analysis of ecosystems structure and ecological stages of pico- and nanophytoplankton in the NW Mediterranean Sea. Previous studies (Dugenne et al., 2014; Fuchs et al., 2021; Thyssen et al., 2014, 2008) showed that pico- and nanophytoplanktonic communities react rapidly to climatic conditions variations and wind-driven events. By dint of their short turnover time, pico- and nanophytoplanktonic communities could be used as a pertinent biological indicator to conduct future ecosystem monitoring. This study's combined use of RFD and diversity indices to determine the ecological successions stages in marine coastal ecosystems provides a better understanding of their

functioning. Our contribution through regional databases, French national observation networks (RESOMAR - Réseau des Stations et Observatoires Marins - IR ILICO) and at European scale (MSFD - Marine Strategy Framework Directive - European Commission - MSFD, 2008/56/EC) grants more tools for reflexion on management and conservation of marine coastal ecosystems to decision makers and public politics administrators.

5. Conclusion

Our result showed that, even if the two sites are geographically close and exposed to the same environmental conditions, the structure of the community completely differed. Paradoxically, communities from the most polluted site (LiB) were more diversified (in terms of Shannon index) and more often evolved to mature ecosystem. LaB is characterized by juvenile ecosystems with lower diversity index. Such differences are attributed to the dominance of *Synechococcus* in the Bay of Toulon which completely drives community structure: widely dominant in LaB, SYN induced a decrease of diversity and contributed to stay in a juvenile ecosystem. Regulated by grazing pressure and trace metal contaminant in LiB, the diversity increased and ecosystem became more mature. The two methods used in this work to study coastal ecosystems (*i. e*. diversity indices and rank frequency diagram) were complementary and allowed us to adopt a better global vision of the organisation and the structure of the populations from the bay of Toulon. Our multiscale contribution through regional, national and European networks grants more tools for reflexion on management and conservation of marine coastal ecosystems to decision makers and public politics administrators.

Acknowledgements

This work was supported by PLANETE (Relations trophiques et séries temporelles planctoniques End-To-End dans deux écosystèmes côtiers en Méditerranée nord-Ouest, financed by the University of Toulon) and DROPLETT (Dynamique et Role du PLancton lors dES Transferts de contaminants vers les

réseaux Trophiques) projects. Authors would like to thank the anonymous reviewer for its suggestions that improved this manuscript and increase its' value.

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Supplementary data

Table 1 : Ecological stages of each month for LiB and LaB. Determination coefficient (r^2) of the linear trend line are also represented. When r^2 is higher than 0.82 and 0.87 for respectively LaB and LiB, the curve is determined as convex; when r^2 is lower, the curve is determined as straight or concave. Complete succession is represented in bold.

Date	LiB		LaB	
	Stage	r^2	Stage	r^2
oct-13	2	0.97	1	0.49
nov-13	3	0.8	1	0.65
déc-13	1	0.83	1	0.69
janv-14	1	0.71	2	0.97
févr-14	2	0.9	2	0.91
mars-14	2	0.88	1	0.54
avr-14	1	0.83	2	0.93
mai-14	2	0.87	1	0.63
juin-14	2	0.9	3	0.72
juil-14	2	0.94	3	0.71
août-14	2	0.93	3	0.61
sept-14	2	0.88	1	0.49
oct-14	2	0.97	1	0.51
nov-14	2	0.96	1	0.61
déc-14	1	0.85	3	0.82
janv-15	2	0.92	1	0.69
févr-15	3	0.82	2	0.91
mars-15	1	0.85	2	0.9
avr-15	2	0.9	1	0.51
mai-15	2	0.87	1	0.67
juin-15	2	0.95	1	0.79
juil-15	1	0.63	1	0.6
août-15	3	0.68	3	0.5
sept-15	1	0.53	1	0.46
oct-15	3	0.73	1	0.49
nov-15	2	0.93	1	0.5
déc-15	1	0.53	1	0.49
janv-16	3	0.8	3	0.62
févr-16	1	0.79	3	0.75
mars-16	2	0.92	2	0.84
avr-16	2	0.88	1	0.48
mai-16	3	0.81	1	0.55
juin-16	2	0.93	3	0.76
juil-16	2	0.94	3	0.71
août-16	2	0.93	3	0.61
sept-16	2	0.88	1	0.5
oct-16	2	0.97	1	0.51
nov-16	2	0.96	1	0.61
déc-16	1	0.85	2	0.82
janv-17	3	0.78	3	0.78
févr-17	2	0.94	2	0.84
mars-17	2	0.92	2	0.95
avr-17	2	0.88	3	0.67
mai-17	2	0.96	3	0.63

Date	LiB		LaB	
	Stage	r^2	Stage	r^2
juin-17	2	0.91	1	0.8
juil-17	1	0.74	1	0.66
août-17	3	0.57	3	0.51
oct-17	3	0.68	1	0.62
nov-17	3	0.54	3	0.47
déc-17	1	0.62	3	0.6
janv-18	3	0.69	3	0.81
févr-18	3	0.69	3	0.79
mars-18	2	0.87	3	0.78
avr-18	3	0.76	3	0.52
mai-18	2	0.95	3	0.58
juin-18	1	0.81	1	0.54
juil-18	3	0.73	1	0.54
août-18	1	0.54	1	0.49
sept-18	3	0.73	1	0.5
nov-18	1	0.65	1	0.65
déc-18	2	0.9	1	0.55
févr-19	3	0.54	3	0.77
mars-19	2	0.98	3	0.7
avr-19	2	0.96	2	0.93
mai-19	2	0.93	2	0.91
juin-19	3	0.69	1	0.56
juil-19	1	0.78	1	0.6
août-19	3	0.63	3	0.51
sept-19	1	0.78	1	0.5
nov-19	1	0.75	3	0.65
déc-19	1	0.75	2	0.87
janv-20	3	0.63	3	0.79
févr-20	3	0.85	2	0.87
mai-20	3	0.81	2	0.87
juin-20	3	0.82	3	0.66
juil-20	2	0.91	1	0.7
août-20	3	0.62	1	0.52

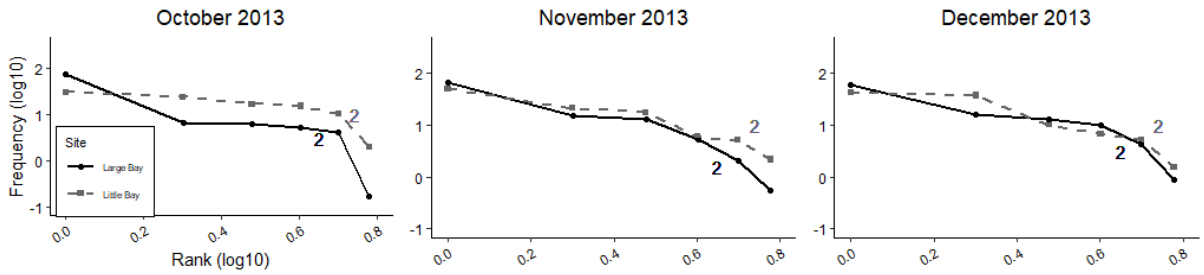


Figure 1: Rank frequency diagrams of pico- and nanoplankton assemblage in the Little Bay (dashed grey lines) and the Large Bay (solid black lines) in 2013. Both axes are on a logarithmic scale.

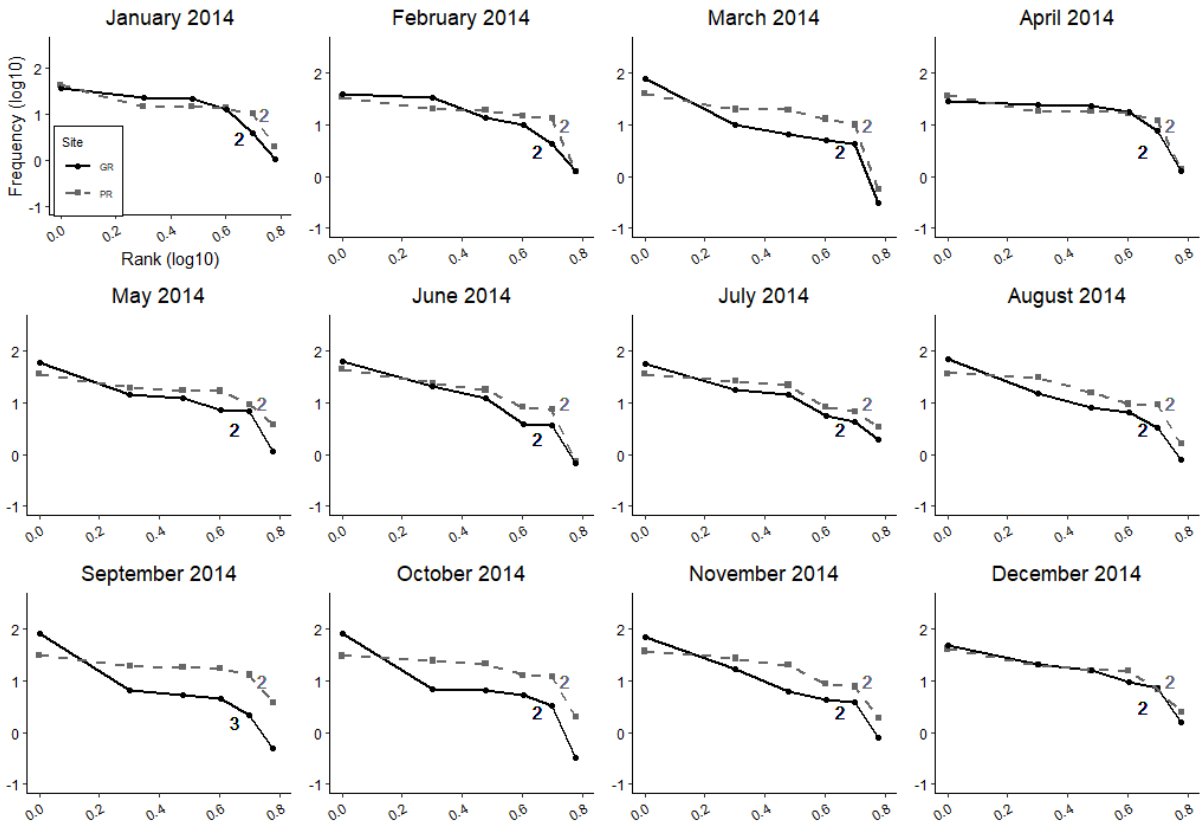


Figure 2: Rank frequency diagrams of pico- and nanoplankton assemblage in the Little Bay (dashed grey lines) and the Large Bay (solid black lines) in 2014. Both axes are on a logarithmic scale.

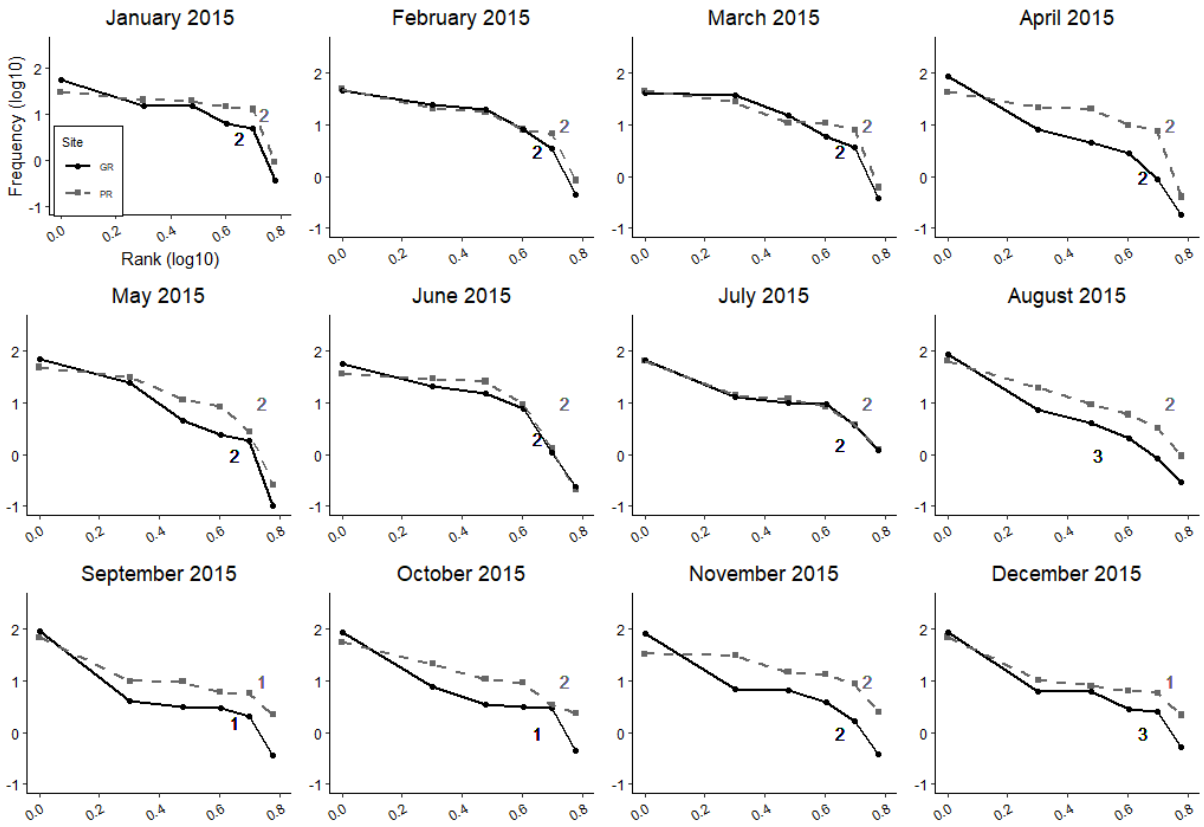
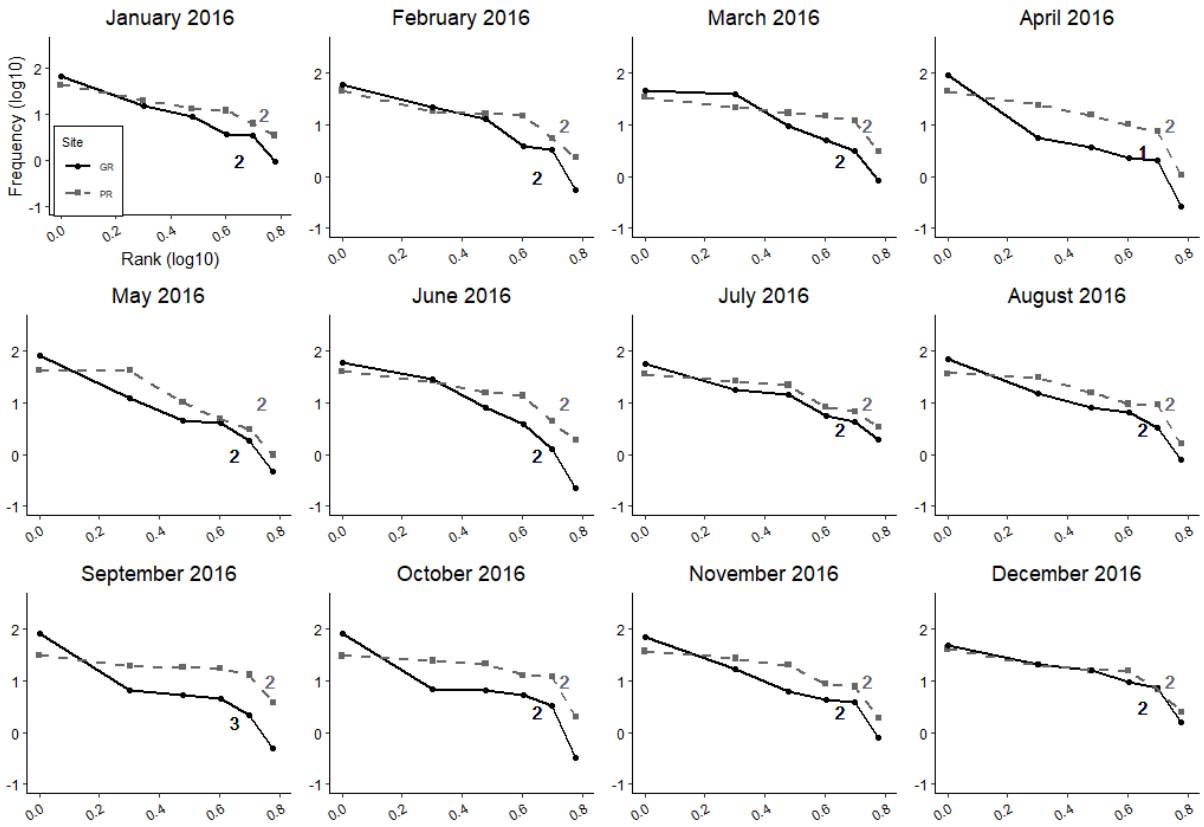


Figure 3: Rank frequency diagrams of pico- and nanoplankton assemblage in the Little Bay (dashed grey lines) and the Large Bay (solid black lines) in 2015. Both axes are on a logarithmic scale.



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715 Figure 4: Rank frequency diagrams of pico- and nanoplankton assemblage in the Little Bay (dashed

716 grey lines) and the Large Bay (solid black lines) in 2016. Both axes are on a logarithmic scale.

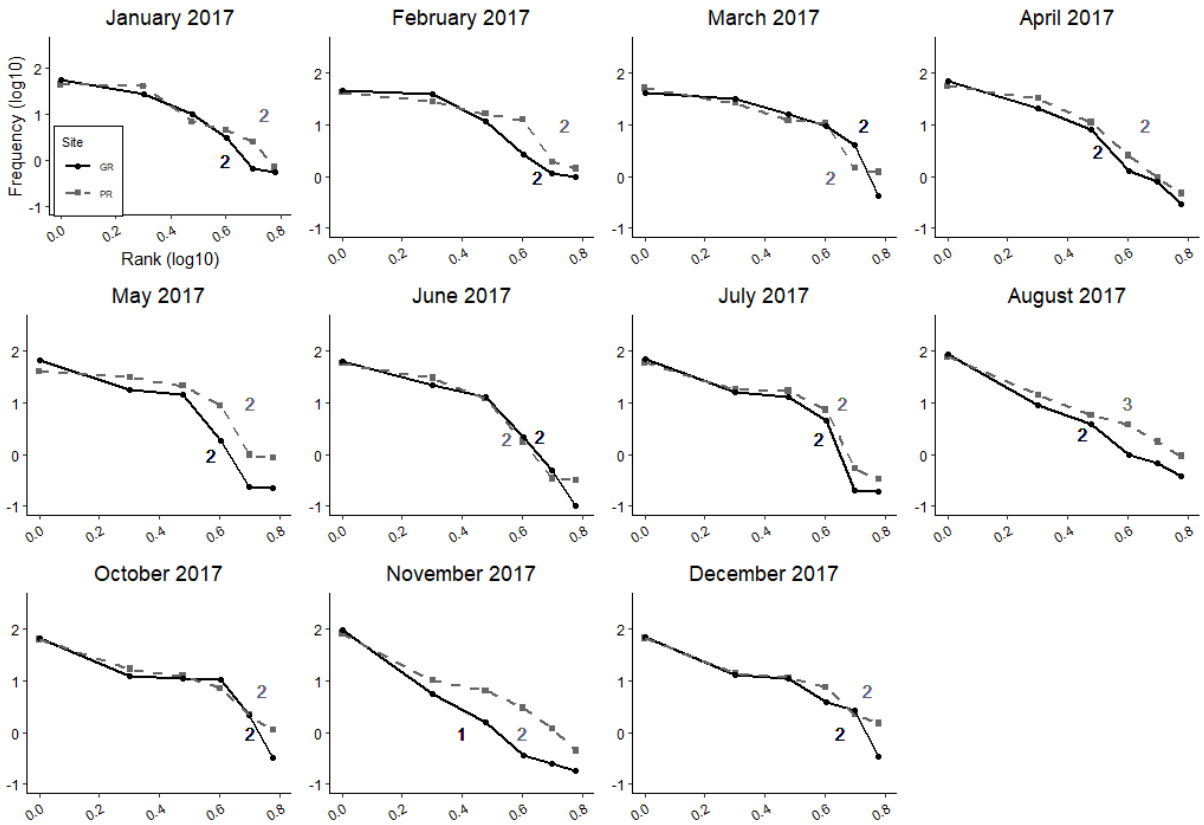

Figure 5: Rank frequency diagrams of pico- and nanoplankton assemblage in the Little Bay (dashed grey lines) and the Large Bay (solid black lines) in 2017. Both axes are on a logarithmic scale.

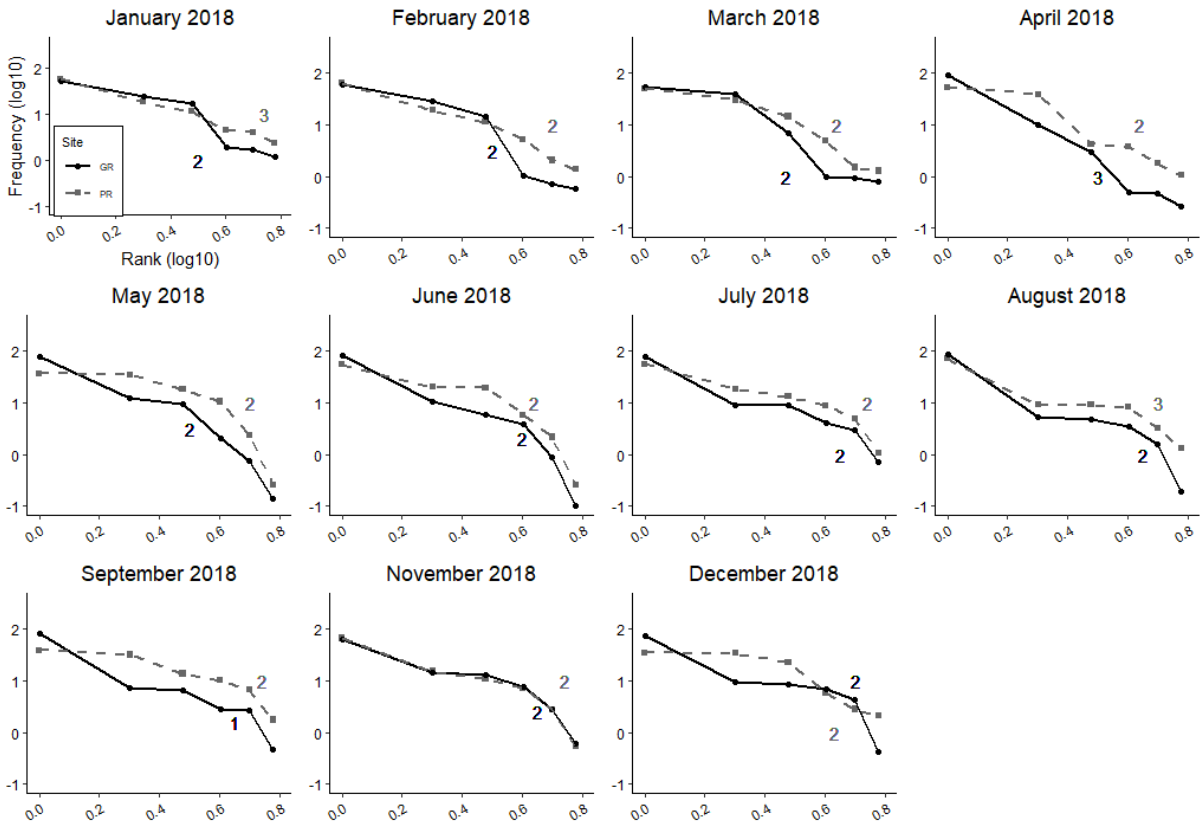

Figure 6: Rank frequency diagrams of pico- and nanoplankton assemblage in the Little Bay (dashed grey lines) and the Large Bay (solid black lines) in 2018. Both axes are on a logarithmic scale.

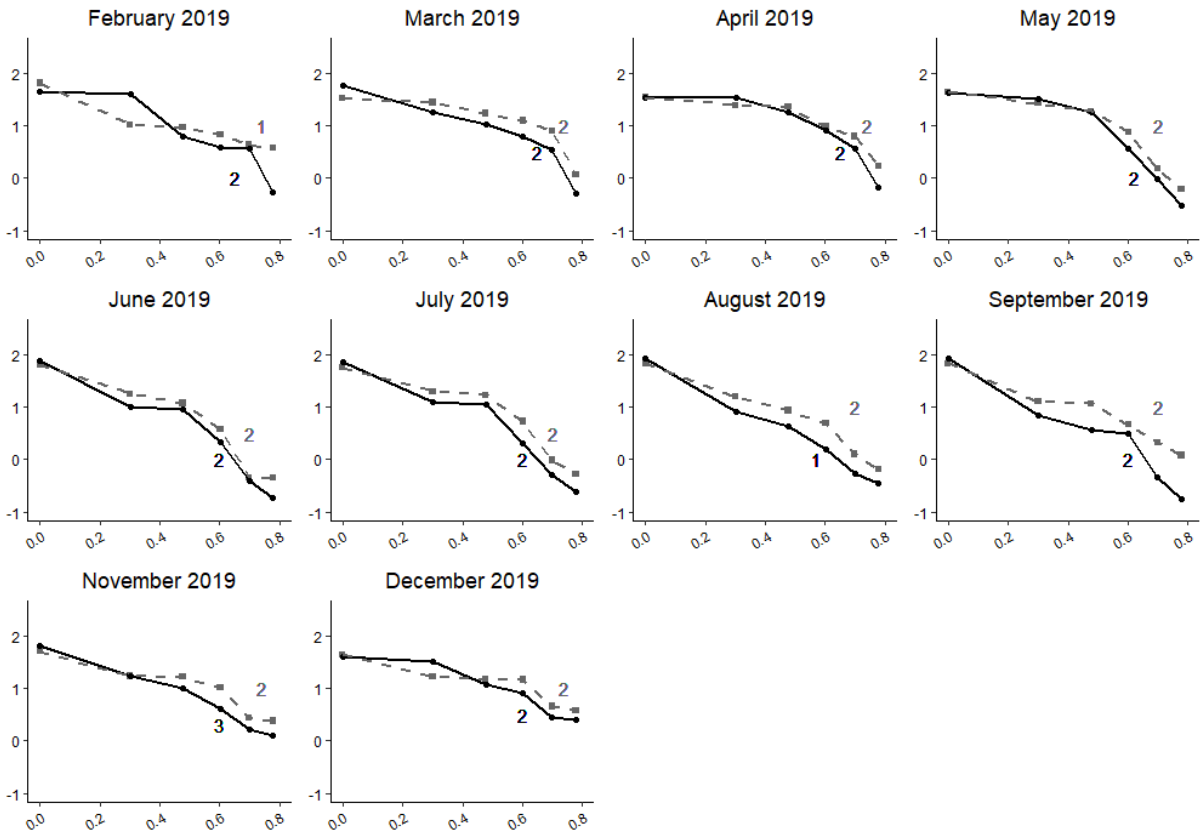

Figure 7: Rank frequency diagrams of pico- and nanoplankton assemblage in the Little Bay (dashed grey lines) and the Large Bay (solid black lines) in 2019. Both axes are on a logarithmic scale.

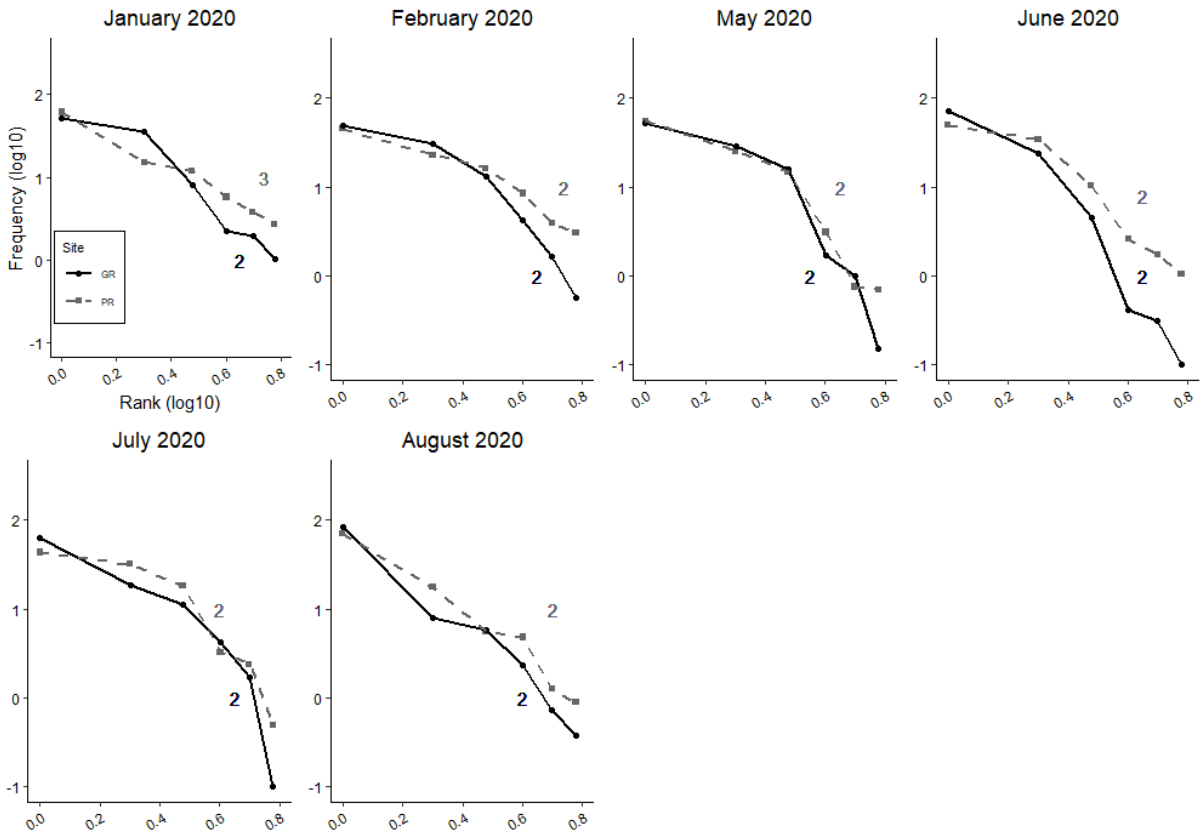

Figure 8: Rank frequency diagrams of pico- and nanoplankton assemblage in the Little Bay (dashed grey lines) and the Large Bay (solid black lines) in 2020. Both axes are on a logarithmic scale.