Phytoplankton dynamics and bloom events in oligotrophic Mediterranean lagoons: seasonal patterns but hazardous trends

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Abstract :

Detailed seasonal analyses of phytoplankton assemblages' composition were performed on long-term datasets (20 years) of two oligotrophic Mediterranean lagoons (Diana and Urbino), in order to test if phytoplankton community and bloom events patterns rely on a seasonal basis. Our results highlight a similar phytoplankton composition between the lagoons, but different patterns in terms of phytoplankton abundances, of timing, magnitude and occurrence of Taxonomic Units, and of bloom events occurrence. Dominant diatoms group showed a seasonal repartition, with highest contribution of Skeletonema sp. during winter and spring, some other groups emerging in warmer seasons (e.g. Chaetoceros spp.), or not showing marked seasonality (e.g. Pseudo-nitzschia spp.). Dinoflagellates' abundances were higher during autumn, besides exhibiting punctual proliferations over the year. Salinity was the strongest environmental parameter in controlling Diana lagoon phytoplankton community, while Urbino community was mostly controlled by turbidity. A worrying evolution of the toxic diatom Pseudo-nitzschia spp., linked to salinity and temperature changes, was detected in both lagoons. We further demonstrated changes in the phytoplankton community are ongoing in these lagoons, despite their contrasting human pressure contexts, indicating that serious impacts on phytoplankton dynamics and blooms triggering in Mediterranean lagoons shall be foreseen within the current and forecasted climate change scenarios.

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Competing Interests

47   The authors declare that they have not known competing financial interests or personal

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Availability of Data and Material

50   The datasets generated and/or analysed during the current study are available from the

51   corresponding author on reasonable request. The long-term datasets analysed during the current

52   study are available in the REPHY repository, https://doi.org/10.17882/47248.

53   **Code Availability – not applicable**

54   **Authors' Contributions – not applicable**

1. INTRODUCTION

The Mediterranean region is expected to be specifically affected by climate change in future projections (Giorgi, 2006; Lejeusne et al., 2010). This, together with eutrophication observed on aquatic ecosystems during the past 50 years (Cloern, 2001; De Jonge et al., 2002), results in considerable threats to Mediterranean coastal lagoons. Nevertheless, coastal lagoons are very productive ecosystems hosting a high degree of biodiversity and provide numerous ecosystem services for human wellbeing (Barbier et al., 2011). There is an urgent need to better understand the functioning of coastal lagoons and the response of biological communities to current and future global and local changes, particularly with regard to their vulnerability. Beside biomass, the relative species abundance and the community composition are the main metrics for characterizing phytoplankton assemblages; their evolution can result in cascading effects at higher trophic levels (Goberville et al., 2010). Phytoplankton dynamics are driven by multiple environmental factors, mainly temperature and salinity, turbulence, nutrient availability and irradiance (Cloern, 1999), but also by trophic strategies, allelopathic interactions and grazing, which determine together the community composition, algal populations growth and species succession (Armi et al., 2010; Garrido et al., 2016). These factors lead to recurrent patterns of phytoplankton composition observed at different temporal scales (Cloern, 1996). Most phytoplankton species can grow under a wide range of environmental conditions. The structure of the assemblage will therefore depend on the trade-off among several complex chemical, physical and biological factors (Naselli-Flores et al., 2021).

Analyses of phytoplankton composition and long-term studies on phytoplankton assemblages' variations are extremely important for a better understanding of coastal lagoons biogeochemistry. Despite a consistent amount of studies on long-term phytoplankton variations in the Mediterranean lagoon environment, most of them are focused on summer period (Bec et

80   al., 2011; Derolez et al., 2019; Derolez et al., 2020). The interest on this specific season resides

81   in its maximal productivity in lagoons, due to optimal light and temperature conditions (Souchu

82   et al., 2010; Bec et al., 2011; Leruste et al., 2016, Leruste et al., 2019; Derolez et al., 2020),

83   which frequently results in high frequency of bloom occurrence (Bec et al., 2011). However,

84   phytoplankton communities exhibit seasonal patterns that are crucial to understand, especially

85   in relation to the driving factors involved and because some bloom events can occur all year-

86   round (Bec et al., 2005; Pulina et al., 2018; Silkin et al., 2019; Trombetta et al., 2019).

87   Trombetta et al. (2019) already highlighted winter blooms as high as spring blooms and linked

88   to increase in temperature in a Mediterranean coastal lagoon (France). Pulina et al. (2012)

89   described a shift in the annual peak density from summer-autumn to winter-spring period over

90   long-term analysis in another Mediterranean coastal lagoon (Cabras Lagoon, Italy). General

91   common seasonal patterns have already been identified, with diatoms (most adapted to exploit

92   a large continuum of environmental conditions and usually exhibiting fast growth) being

93   observed during winter, spring and autumn, and dinoflagellate blooms generally occurring in

94   summer, even though spatial and temporal variability is important (Armi et al., 2010;

95   Carstensen et al., 2015). The dinoflagellates, representing 75% of toxin-producing

96   phytoplankton species (Smayda, 1997a), can also bloom in other periods than summer, and

97   often peak in autumn (Carrada et al., 1991; Caroppo et al., 2018).

98   Amongst diatoms, some groups are recurrent in a specific season due to their ecological niche:

99   winter and spring blooms are frequently dominated by *Skeletonema* spp. worldwide, while

100   *Chaetoceros* spp., *Leptocylindrus* spp., *Nitzschia* spp. and *Cerataulina* sp. are mostly found in

101   warmer seasons (Sarno et al., 1993; Dupuy et al., 2000; Gilabert, 2001; Gle et al., 2007).

102   Proliferations of diatoms are essential as they sustain trophic network and are the major resource

103   in aquaculture exploitation (Pernet et al., 2012). However, some blooms can be dangerous for

104   the environment. Such hazardous blooms, under the name of Harmful Algal Blooms (HABs),

are historically known to occur and can bring about disruption in the ecosystem functioning (e.g. disturbances in both pelagic and benthic trophic networks, damage to fish gills or oxygen depletion; Hallegraeff, 1993). These events can sometimes be especially concerning as some species are able to produce toxins which can be detrimental and even lethal for wildlife and humans (Smayda, 1997b). HABs recently gained attention, mainly due to their impact on economy, especially in respect of aquaculture exploitation (Zingone et al., 2021). Caged fish are very susceptible to non-toxic HABs provoking mechanical or chemical gills damage, but toxic HABs are even more underhand threat especially in shellfish farming, as filter-feeding molluscs can concentrate toxins through bioaccumulation in their tissues and lose their commercial values (Smayda, 1997b; Salcedo-Garduño et al., 2019). In the last few decades, HABs have shown an increasing trend in multiple environments, especially in coastal zones and noticeably around Mediterranean margins (Smayda, 1997b; Hallegraeff, 2010; Kudela et al., 2015; Cecchi et al., 2016). Indeed, proliferation of some species, mainly from the Amnesic Shellfish Poisoning (ASP) toxins-producer *Pseudo-nitzschia* genus, are known to produce blooms at all seasons in lagoon environment (Bouchouicha Smida et al., 2014; Delegrange et al., 2018; Melliti Ben Garali et al., 2020). Moreover, *Pseudo-nitzschia* spp. blooms have already been shown to be increasing in frequency and magnitude over the Mediterranean basin (Husson et al., 2016; Melliti Ben Garali et al., 2020).

At present, lagoons functioning and evolutions still remain imperfectly understood, especially with regard to phytoplankton communities' seasonal dynamics, bloom events and hazardous taxa. The main objective of this study was thus to characterize the seasonality of the phytoplankton community structure (i.e. abundance, bloom events, relation to environmental factors) in two nearby oligotrophic Mediterranean coastal lagoons using long-term data series. We hypothesized that seasonal phytoplankton community patterns can be identified and that environmental and biological long-term trajectories can be highlighted on seasonal basis. The

130   main questions addressed are the following: i) Are there seasonal environmental and

131   phytoplankton communities' long-term evolutions and which structuring environmental drivers

132   can be identified? ii) Is it possible to highlight significant trends (blooms occurrence,

133   composition and magnitude, nature of toxic taxa) by season, what are their dependence on

134   environmental factors, and which possible implications of climate change on phytoplankton

135   communities can be identified?

136

137   **2. MATERIAL AND METHODS**

138

139   2.1 Study sites

140   Diana and Urbino lagoons are located on the oriental coast of Corsica island (Mediterranean

141   Sea), not far from each other (< 10 km; Fig. 1). They share some common characteristics, such

142   as same tectonic origin, geomorphological features, hydrological functioning, oligotrophic

143   status and dominant fauna and flora (Table 1). Nevertheless, these lagoons exhibit some major

144   differences (renewal rate; watershed size and percentage of agricultural exploitation, degree of

145   the communication with the sea) while also submitted to contrasting anthropogenic histories

146   and current human impacts. Diana lagoon is owned and managed by multiple private enterprises

147   exploiting it for fishing and for shellfish and fish farming, while no aquaculture activities are

148   carried out in Urbino lagoon nowadays, as they were gradually stopped from 2000 (Table 1).

149   Moreover, Urbino lagoon, which is the property of *Conservatoire du Littoral* since 2007, is

150   recognized as Natura 2000 site since 2004 and Ramsar wetland conservation site since 2009.

151

152   2.2 Long-term analysis

153   Daily rainfall and daily mean air temperature data were collected from Météo-France at

154   Solenzara weather station (41°55'19" N, 9°24'03" E), which was chosen to represent

meteorological conditions of the area, based on its proximity to the study sites (20 km South; Fig. 1). Cumulative monthly rainfall and mean monthly air temperature were calculated to characterize meteorological conditions from January 1998 to December 2019. Environmental parameters (salinity, temperature, turbidity, dissolved oxygen concentration and nutrients (Dissolved Inorganic Nitrogen (DIN), Dissolved Inorganic Phosphorus (DIP) and silicates)) and biotic data (microphytoplankton (generally > 20 µm) abundances and chlorophyll *a* (Chl *a*) concentrations), were collected from the REPHY - French Observation and Monitoring program for Phytoplankton and Hydrology in coastal waters - monitoring network (REPHY, 2019). For each lagoon, one single surface sampling station was available: "Diana centre" and "Urbino centre", however they were considered representative of the entire basins as internal spatial homogeneity is well known for both lagoons (Frisoni, 1984). Environmental parameters datasets from January 1998 to September 2019 (Diana) and August 2018 (Urbino) based on monthly medians (Derolez et al., 2020) were used for long term analyses.

For microphytoplankton, two different datasets are available, according to the strategy applied for cell counting. A first strategy consisted in the counting of all identifiable taxa present in a sample, regardless of their concentration: the associated Total Flora database (FLORTOT) contains thus a representative estimate of all taxa present, so of community diversity and composition (Belin and Neaud-Masson, 2017). The second strategy aimed at monitoring a certain number of taxa on a selected list defined by the Water Framework Directive (WFD): the associated Indicator Flora database (FLORIND) produces thus a restricted description of the community present in the sample. A regular monitoring of certain selected toxic taxonomic groups (*Pseudo-nitzschia*, *Alexandrium*, *Dinophysis*, *Ostreopsis*) was systematically carried out, regardless of their concentration (FLORTOX), while some other non-toxic taxa were included only when their concentration exceeded the threshold of 100 000 cell L^{-1}, defining a bloom event (Belin and Neaud-Masson, 2017).

180 Based on the extensiveness of REPHY databases, our work allowed different long-term

181 analyses of phytoplankton communities, depending on the availability of monitoring strategies

182 data, for the two lagoons studied (a summary description of the databases used is available in

183 Supplementary Material, Table S1):

184 1) Diana lagoon analysis on total phytoplankton community has been performed, as FLORTOT

185 dataset was available between January 2001 and September 2019, with monthly to three times

186 per month sampling frequency. FLORTOT dataset was used to describe seasonal evolution of

187 total phytoplankton community over a longer time-scale, as well as to identify driving

188 environmental parameters involved;

189 2) In order to analyse and compare phytoplankton communities in the two lagoons (Diana and

190 Urbino), the FLORIND database was used. FLORIND data were available all year-round from

191 January 2008 to December 2015 and sampling frequency varied from monthly to five times per

192 month. FLORIND dataset exploitation allowed to compare bloom events between lagoons over

193 a longer time-scale and to investigate potential relation with environmental drivers;

194 3) FLORIND strategy is constantly evolving in time to satisfy sanitary regulations evolution

195 and WFD requirements. Hence, longer series concerning only selected toxic species were

196 available, from January 1998 to September 2019 for Diana lagoon and to April 2017 for Urbino

197 lagoon; sampling frequency varied from monthly to five times per month. This longer series,

198 hereafter referred to as FLORTOX, allowed to target and analyse the evolution of the

199 potentially toxic taxon *Pseudo-nitzschia* spp. in the two lagoons (Diana and Urbino).

200 For all datasets, phytoplankton cellular densities were grouped in Taxonomic Units (T.U.s) in

201 order to homogenize data and reduce classification confusion, as suggested by other studies

202 involving REPHY datasets (Gailhard et al., 2002; Guarini et al., 2004; Hernández-Fariñas et

203 al., 2014). Taxonomic groups were aggregated to the lowest common taxonomic level (Table

204 2).

205

206 2.3 Statistical analysis

207 All data were analysed with the statistical R software (RStudio Team, 2016; version 4.0.2).

208 To evaluate long-term changes of the two lagoons, a seasonal approach was carried out to

209 analyse the historical databases obtained. Seasons were determined as follows: *Winter* as

210 December, January and February, *Spring* as March, April and May, *Summer* as June, July and

211 August and *Autumn* as September, October and November.

212 For both lagoons, deviations of mean annual values from averages over the period were

213 considered for cumulative rainfall, mean air temperature, salinity and water temperature. Mann-

214 Kendall (MK) trend tests (*modifiedmk* package in R, (Patakamuri and O'Brien, 2020)) were

215 also applied on seasonal annual medians of the same parameters with the aim of detecting

216 potential monotonic trends over the period considered for each season separately. To avoid

217 serial autocorrelation drawbacks, a modified Mann-Kendall test was performed (Hamed and

218 Rao, 1998). If the MK test was significant (*i.e.* p-value < 0.05), Theil-Sen's slope estimator was

219 provided.

220 In order to describe temporal evolution of phytoplankton communities in the two lagoons,

221 multiple approaches were carried out. Before analysis, as phytoplankton counts are generally

222 subjected to a limit in cell detection, a threshold of 100 cell L^{-1} was set up and used to describe

223 abundances of non-detected T.U.s, whose concentration was then considered to be below this

224 threshold (Derolez et al., 2020). This detection limit was taken into account when the

225 calculation of annual seasonal medians was needed, thanks to the application of the Robust

226 Regression on Order Statistics method (ROS) (Helsel and Cohn, 1988; Lee and Helsel, 2007).

227 A first in depth analysis was performed on Diana lagoon on FLORTOT dataset to investigate

228 total phytoplankton community seasonal evolution on the long-term and to identify potential

229 environmental drivers. Long-term changes in Chl *a* concentrations and total cellular densities

230   of dominant classes, i.e. diatoms and dinoflagellates, were analysed with Mann-Kendall trend

231   test applied to annual medians by season. Then, for each season separately, annual contribution

232   of most frequent T.U.s (frequency of occurrence > 15% on total samples and for each season)

233   to total microphytoplankton abundance was studied. Relationships between phytoplankton

234   community and environmental variables were analysed through Canonical Correspondence

235   Analysis (CCA) on the overall dataset: cellular densities of the 25 most frequent T.U.s

236   (frequency of occurrence > 15% and total abundance > 80% in each season) were $\log_{10}(x+1)$

237   transformed and analysed together with four environmental variables (rainfall, salinity, water

238   temperature and turbidity). Mean air temperature was not included in the analysis as it showed

239   strong significant correlation with water temperature. Seasonal differences were demonstrated

240   through Permutational Multivariate Analysis Of Variance (PERMANOVA) test. Significant

241   effects were furtherly investigated through PAIRWISE test and similarity percentages test

242   (SIMPER), in order to identify differences between groups and major T.U.s contributing to

243   these differences.

244   Further analysis focusing on bloom events on both lagoons was based on FLORIND databases

245   over the 2008-2015 period, in order to compare long-term bloom events seasonal patterns and

246   potential links to environmental factors in the two lagoons. In this study, "bloom events"

247   corresponded to blooms of one T.U. with concentrations exceeding 100 000 cell L^{-1}. Frequency

248   of occurrence of blooms was analysed (number of blooms over total number of samplings),

249   considering each season separately, and contribution of each T.U. to bloom occurrence was

250   expressed in terms of percentage proportion. To analyse and compare magnitude of blooms

251   occurring in the lagoons, mean bloom densities were calculated for each season on overall

252   bloom events. Maximal bloom-forming T.U.s were also noted, as well as the abundances

253   reached. A similar approach was applied to analyse blooms produced by the potentially toxic

254   taxon *Pseudo-nitzschia* on the overall FLORTOX period. Then, seasonal monotonic trends on

255 the abundance of this taxon were also investigated through Mann-Kendall trend tests applied

256 on annual medians. For significant MK test (*i.e.* p-value < 0.05), Theil-Sen's slope estimator

257 was provided.

258 General Linear Model (GLM) was used in order to assess possible links between environmental

259 parameters (salinity, water temperature and turbidity) and bloom events at different seasons and

260 to describe the triggering factors in the two lagoons. A first GLM model was used to test the

261 effects of the three environmental parameters, of season (winter, spring, summer or autumn)

262 and of site (Diana or Urbino lagoon). Separate GLM models were then applied for each lagoon

263 in order to test the effects of environmental factors and season. Interactions between variables

264 were also tested and the best models were selected according to the Akaike information criterion

265 (AIC).

266

267 **3. RESULTS**

268

269 3.1 Environmental variables

270 The long-term analysis (from 1998 to 2019) of meteorological conditions revealed that major

271 rainfall events were concentrated in autumn, winter and spring depending on the year but with

272 an important interannual variability in terms of intensity (Fig. S1a, S1b). No monotonic trend

273 could be identified over the period (Mann-Kendall trend test). Mean air temperature showed a

274 typical seasonal trend (Fig. S1c) and positive anomalies occurred almost systematically at all

275 seasons from 2014 (data not shown). Significant monotonic increasing trends in mean air

276 temperature were detected in spring (MK p = 0.005) and summer (MK p = 0.028) over the

277 period, with an annual increase of 0.08 °C and 0.07 °C respectively (Sen's Slope = 0.08 and

278 0.07) (Table 3). The two lagoons showed different salinity patterns, with variations of higher

279 amplitude at Urbino lagoon (Fig. S1d). Mann-Kendall trend tests did not reveal any significant

280 monotonic trends for this parameter (Table 3). Water temperatures followed typical seasonal

281 trend with similar variation patterns for both lagoons (Table S2). Significant monotonic

282 increasing trends were detected for water temperature in winter at Diana lagoon (MK p = 0.03,

283 Sen's Slope = 0.07) and spring for both lagoons (Diana: MK p < 0.001, Sen's slope = 0.13;

284 Urbino: MK p < 0.001, Sen's Slope = 0.22) (Table 3). Highest mean turbidity and lowest mean

285 dissolved oxygen values were found in autumn and summer respectively at both lagoons (Table

286 S2) that were not different to each other. Nutrient data were available only for summer season

287 (Table S2). Dissolved Inorganic Phosphorus (DIP) and Dissolved Inorganic Nitrogen (DIN)

288 concentrations showed a similar temporal pattern for both lagoons (not shown), except a peak

289 of DIP at Diana lagoon in 2008 (1.69 μM). A sharp increase in DIN was registered between

290 2017 and 2018, reaching over 1.00 μM on annual median at both lagoons. Silicate concentration

291 was more elevated in Urbino lagoon over the period (Table S2), especially after 2010, reaching

292 a seasonal peak in 2013 at 92.70 μM. Maximal Silicate concentration values were found in July

293 2013 for both lagoons.

294

295 3.2 Long term phytoplankton dynamics in Diana lagoon

296 The FLORTOT series available for Diana allowed the long-term analysis of phytoplankton

297 assemblages (Table S1). From 2001 to 2019, Chl a concentration ranged between 0.03 μg L^{-1}

298 in January 2004 and 13.4 μg L^{-1} in February 2001 (Table S3), and a significant increasing trend

299 was detected in winter (Table 3; MK p < 0.001, Sen's slope = 0.03). From 2001 to 2019,

300 Diana's phytoplankton community was largely dominated by diatoms representing up to 90 %

301 of total abundances at all seasons except autumn, where they represented 69.8 % of total

302 abundances. In autumn, dinoflagellates exhibited their highest contribution to total abundances

303 of the 2001-2019 period, reaching 19.2 %. The long-term analyses on diatoms' abundances

304 highlighted high intra- and inter-annual variations (Fig. 2a). Nevertheless, a significant

305   increasing trend could be identified in summer season (Table 3; MK p = 0.001, Sen's slope =

306   2.5 x 10^4), where median total diatom abundances increased from 1.8 x 10^4 cell L^{-1} in 2001 to

307   1.8 x 10^6 cell L^{-1} in 2019 (Fig. 2a). No monotonic long-term trends in abundances were detected

308   for dinoflagellates, although higher densities for this class were observed in the most recent

309   years at all seasons, reaching up to 3.2 x 10^6 cell L^{-1} in September 2019 (Fig. 2b).

310   The composition of phytoplankton assemblages has also experienced a wide variability among

311   years and seasons (Fig. 2c). In winter, *Skeletonema* sp. was the major contributor to total

312   abundances in 2001 and 2002. Other T.U.s, mainly *Leptocylindrus* spp., *Pseudo-nitzschia* spp.

313   *Chaetoceros* spp., Thalassionemataceae and *Nitzschia* spp. were alternatively dominant over

314   the period. From 2005 to 2009, the Cryptophyceae class showed high contribution to total

315   abundances, reaching a peak in December 2007, at 2.7 x 10^6 cell L^{-1}. Some T.U.s of the

316   dinoflagellates (*Prorocentrum* spp., *Protoperidinium* spp. and *Scrippsiella* spp.) were present

317   in 2005, 2006 and 2009, but their abundances never reached the bloom threshold (i.e. 100 000

318   cell L^{-1}).

319   During spring, *Skeletonema* sp. exhibited again high dominance in 2008, 2015 and 2019.

320   *Chaetoceros* spp. was systematically present from 2010, constituting an important part of total

321   abundances especially between 2010 and 2012 (> 29 %). Dinoflagellate contribution was also

322   quite important especially in 2003, 2007 and 2009, were multiple taxa like Gymnodiniales,

323   *Protoperidinim* spp. and *Scrippsiella* spp., and potentially toxic taxa such *Dinophysis* spp. and

324   *Prorocentrum* spp., appeared, but they did not reach bloom density threshold. The years 2006

325   and 2007 showed greater diversity in terms of composition but no single T.U. clearly dominated

326   the community, while in 2007 the lowest concentrations of diatoms (Fig. 2a) and dinoflagellates

327   (Fig. 2b) over the entire study period were recorded. The only bloom of Euglenophyceae (over

328   the entire period) occurred in March 2013 (1.1 x 10^5 cell L^{-1}).

Summer season was characterised by a dichotomous distribution: the phytoplankton community showed higher diversity before 2012 (except for 2004 and 2005 with a total *Skeletonema* sp. dominance). Then, after 2012, *Nitzschia* spp., *Chaetoceros* spp., *Leptocylindrus* spp. and *Pseudo-nitzschia* spp. were systematically the most dominant T.U.s. This structural shift corresponds to the increasing dominance trend of diatoms underlined in Fig. 2a for this season. Some dinoflagellates were also detected, particularly in 2002, 2006 and 2008, when *Scrippsiella* spp. also bloomed at 1.8×10^5 cell L^{-1}. Other dinoflagellate blooms were recorded in 2012 (*Prorocentrum* spp.) and 2017 (*Prorocentrum* spp. and Gymnodiniales). Most of dinoflagellate blooms were observed in autumn. Particularly, between 2004 and 2011, this class highly contributed to total abundances and was sometimes dominating. Multiple *Prorocentrum* spp. blooms occurred in 2004, 2005, 2006, 2010 and 2011, reaching up 1.4×10^6 cell L^{-1} in November 2011. Other punctual bloom events were due to rarer taxa, such as Gymnodiniales and *Gyrodinium* spp. in 2006, *Heterocapsa* spp. in 2013 and *Heterocapsa* spp. and *Tripos* spp. in 2019. From 2012, diatoms were always dominant and *Nitzschia* spp. and *Chaetoceros* spp. showed a marked presence. The Cryptophyceae class also bloomed in 2003, 2013 and 2019 (reaching its maximum on the overall period at 3.0×10^5 cell L^{-1} in September 2019) and appeared to be important on total abundance, as well as in 2008 even if no bloom density was reached.

Relationships between Diana phytoplankton community and environmental variables (rainfall, water temperature, salinity and turbidity) were investigated through CCA (Fig. 3). The model was significant (p = 0.001) and the first two significant canonical axes (p < 0.01) explained 52.5 and 21.3 % of the total variance respectively and were used to summarize variation in community composition. The first axis was positively correlated with salinity and water temperature, corresponding to samples collected during summer and autumn, while the second axis was positively correlated with turbidity and rainfall, corresponding to samples collected

during spring and autumn. In the CCA tri-plot, four main quadrants can be identified that corresponded to the four seasons represented by their centroids (Fig. 3). Diatoms were almost centred on the tri-plot as they were dominant whatever the season. A seasonality can be identified for the main diatom T.U.s: on the left part *Pseudo-nitzschia* spp. and *Skeletonema* sp. seemed to be favoured by lower salinity and temperature and associated to spring and winter seasons. At the opposite side, *Leptocylindrus* spp. and *Nitzschia* spp. were favoured by higher temperatures and salinity and mostly associated with the summer season. Gymnodiniales and *Scrippsiella* spp. appeared also to be more favoured by higher salinities and temperatures, without clear influence of rainfall and turbidity. *Chaetoceros* spp. and Thalassionemataceae were positioned in the bottom part of the plot, in opposition to high turbidity and rainfall levels, unlike *Prorocentrum* spp. and *Gyrodinium* spp. which seemed to be mainly driven by turbidity and rainfall. Dinoflagellates were also located in the top-right quadrant, indicating their importance in autumn.

PERMANOVA investigation on phytoplankton assemblages highlighted significant effect of the season ($p = 0.001$) (Table S4). PAIRWISE test confirmed each season differed from the others ($p < 0.01$) (Table S4). From SIMPER test, spring showed overall 12 % difference from other seasons, while other contrasts all showed 13 % difference. *Chaetoceros* spp. *Pseudo-nitzschia* spp., *Nitzschia* spp., *Skeletonema* sp., Thalassionemataceae, diatoms, *Leptocylindrus* spp. and *Prorocentrum* spp. were systematically within the 10 more important contributors to diversity between seasons, representing at least 59 % of the difference between groups. The general seasonal characterization emerging from the test showed that diatoms in general, *Skeletonema* sp. and *Pseudo-nitzschia* spp. in particular, as well as Cryptophyceae, were most important during cooler and rainy seasons, i.e. winter and spring. Other T.U.s like *Chaetoceros* spp. and *Leptocylindrus* spp. were generally more abundant in summer. Globally, dinoflagellates were most abundant during autumn and summer, like *Prorocentrum* spp.,

379   *Scrippsiella* sp. and Gymnodiniales, this latter being however important in winter due to bloom

380   formation. In the contrast between summer and autumn, other dinoflagellates as

381   *Protoperidinium* spp., *Gyrodinium* spp., *Karenia* spp., *Diplopsalis* spp., *Dinophysis* spp. and

382   *Amphidinium* spp. showed higher importance during autumn, despite being contributing less to

383   overall difference between seasons.

384

385   3.3 Bloom events in Diana and Urbino lagoons

386   Blooms analysis over the 2008-2015 period for the two lagoons relied on the FLORIND dataset

387   (Table S1). 212 events have been recorded, i.e. 26.5 blooms per season and per site on average,

388   but with a lower occurrence in Urbino than in Diana (84 and 128 events, respectively) (Fig. 4).

389   High interannual variability, both in terms of bloom occurrence and T.U.s contributions to the

390   blooms, was highlighted for both lagoons (Fig. 4). Highest bloom frequency (number of blooms

391   over total samplings per season) was found in winter at Diana lagoon (0.59) and in autumn and

392   spring at Urbino lagoon (0.46 and 0.42, respectively) (Fig. 4). At Diana lagoon, no bloom was

393   recorded in 2008 during summer and autumn, in spring and autumn 2009 and in spring 2010.

394   Urbino lagoon did not exhibit bloom events in winter for three consecutive years (2012, 2013

395   and 2014) and in summer 2012 (Fig. 4). However, both lagoons reached the maximal bloom

396   occurrence in winter 2008, with 11 and 7 bloom events for Diana and Urbino respectively. In

397   Urbino lagoon, the maximal bloom occurrence (7 events) was also found in autumn 2013.

398   Overall, despite seasonal variability, the regular occurrence of several dominant T.U.s was

399   similar for the two lagoons. Blooms of *Nitzschia* spp. have been systematically observed at both

400   lagoons whatever the season (Fig. 4). *Pseudo-nitzschia* spp. occurrence was particularly

401   important in winter and spring, together with *Skeletonema* sp. (Fig. 4). *Chaetoceros* spp. also

402   constituted an important proportion of bloom events in both lagoons, all year round except in

403   winter, and especially stood out in summer, together with *Leptocylindrus* spp. (Fig. 4).

17

404 Thalassionemataceae group seemed to be more important at Urbino lagoon but occurred at both

405 lagoons in summer (Fig. 4). Dinoflagellate blooms (*Prorocentrum* spp. and Gymnodiniales)

406 constituted punctual events at both lagoons and were found only in autumn and winter.

407 However, dinoflagellate blooms could reach important magnitude, like Gymnodiniales, which

408 were responsible for the highest winter bloom recorded in Diana lagoon, at 6.9×10^6 cell L^{-1} in

409 January 2008 (Fig. 4). Generally, mean seasonal bloom magnitude for both lagoons was in the

410 order of 10^5 cell L^{-1}, except for spring at Diana lagoon, were it was up to 10^6 cell L^{-1}, with

411 multiple dense blooms of *Skeletonema* sp., reaching up to a maximum of 2.1×10^7 cell L^{-1} in

412 March 2015 (Fig. 4). During summer season, bloom frequency and mean magnitude were lower

413 at Urbino lagoon (Fig. 4).

414 Amongst the selected toxic taxa listed in the FLORIND dataset (2008-2015), *Pseudo-nitzschia*

415 spp. was systematically present at both lagoons and contributed strongly to blooms occurrence.

416 The analysis of FLORTOX data (1998-2019 at Diana and 1998-2017 at Urbino) revealed a

417 higher *Pseudo-nitzschia* spp. bloom frequency at Urbino lagoon than at Diana lagoon in winter

418 and spring seasons (Table 4). In general, blooms of *Pseudo-nitzschia* spp. were denser at Urbino

419 site, with maximum blooms reaching 10^6 cell L^{-1} at all seasons except summer, while the same

420 densities were reached only at the winter maximal bloom for Diana (Table 4). The Mann-

421 Kendall trend test on annual median abundances detected significant increasing trends for this

422 T.U. over the studied periods for winter and spring seasons at Diana lagoon (p = 0.006 and p =

423 0.034 respectively) and for autumn season at Urbino lagoon (p = 0.034) (Table 4).

424 GLM models helped to understand bloom determinism. The first best GLM model tested on

425 entire dataset (AIC = 710) highlighted a significant effect of the lagoon factor (Diana *vs* Urbino)

426 in interaction with season and turbidity, and of the season factor in interaction with salinity

427 (Table 5). Separate GLM models were then applied for each lagoon in order to better understand

428 seasonal bloom dynamics and to identify major environmental factors involved. The best GLM

429   for Diana lagoon (AIC = 401) indicated a significant effect of the interaction between the season

430   and salinity. In particular, a decrease in salinity values during spring season significantly

431   enhanced the probability of blooms occurrence (p = 0.018), while the opposite effect was found

432   for autumn season (p = 0.037) (Table 5). Best GLM model for Urbino lagoon (AIC = 297)

433   identified an important and significant role of turbidity on bloom events, in interaction with

434   seasonal factor (Table 5). A negative effect of turbidity was found for both spring (p = 0.003)

435   and autumn (p = 0.005), indicating an increase in bloom occurrence with decreasing turbidity

436   at these seasons (Table 5). Temperature did not show any significant effect on bloom triggering

437   for Diana and Urbino. Overall, bloom determinism seemed to be differently regulated within

438   the two lagoons: mainly by salinity in Diana and mainly by turbidity in Urbino.

439

440   **4. DISCUSSION**

441

442   4.1 Seasonal patterns and key taxonomic units

443   The two studied lagoons are set in a Mediterranean climate context, with two main rainy periods

444   corresponding to autumn and spring, separated by a winter drier cold period, and an arid and

445   hot period during summer (Aubin et al., 2019). Over the study period, some exceptionally rainy

446   winters occurred (e.g. in 2008 and 2017), and the 2008-2015 period was generally cooler, with

447   especially wet spring. Overall, the two lagoons exhibited some shared traits, like similar

448   seasonal environmental dynamics and oligotrophic status, which is their main characteristic.

449   From a general point of view, Chl a concentrations were consistent with observations relative

450   to other Mediterranean oligotrophic lagoons (Souchu et al., 2010; Bec et al., 2011; Leruste et

451   al., 2019). Microphytoplankton community was dominated by diatoms and dinoflagellates,

452   which are known to be the dominant classes and major contributors to the phytoplankton

453   communities of Mediterranean lagoons (Armi et al., 2010; Frisoni, 1984, Derolez et al . 2020).

19

454 The oligotrophic nature of these systems implies a tight dependence of phytoplankton dynamics

455 on nutrient fluctuations, typical for the Mediterranean region (Paches et al., 2019). Seasonal

456 nutrient patterns are therefore important for the understanding of phytoplankton seasonality.

457 Several studies have described a typical DIN pattern in Mediterranean coastal lagoons (Bec et

458 al., 2005; Collos et al., 2003). NO_3^- concentrations rising occurs mostly in humid seasons and

459 is conventionally linked to inputs from rainfall and runoff, while a major contribution of NH_4^+

460 is observed in summer, and classically associated with *in situ* regenerated production (Bec et

461 al., 2005) and/or release from the sediment sediment production in warm period (Garrido et al.,

462 2016).

463 Such shifts in nutrient sources could have affected the microphytoplankton composition we

464 observed in our study. In winter, *Skeletonema* sp. showed an important contribution to total

465 abundance at Diana lagoon, together with *Pseudo-nitzschia* spp. and *Nitzschia* spp. This is in

466 accordance with other observations that detected especially *Skeletonema* spp. as an important

467 contributor to winter blooms in coastal systems, linked to NO_3^- inputs from watershed following

468 rainfall events (Sarno et al., 1993; Gle et al., 2007; Collos et al., 2014). *Skeletonema* sp. success

469 during winter might reside in its preference for high NO_3^- loads and for low temperatures

470 (Collos et al., 2003; Derolez et al., 2020). In Diana lagoon, an association between *Skeletonema*

471 sp. and *Pseudo-nitzschia* spp. abundances and lower salinity and temperature values emerged,

472 related to winter conditions. *Skeletonema* spp. is considered a generalist taxon that is highly

473 tolerant to salinity variations. However, the link between *Pseudo-nitzschia* spp. and lower

474 salinity is in contrast to other studies that have underlined positive correlation of this genus with

475 salinity and temperature (Balzano et al., 2011; Bouchouicha Smida et al., 2014; Hernández

476 Fariñas et al., 2015; Husson et al., 2016; Van Meerssche et al., 2018), although this may vary

477 depending on species or genotype (Armi et al., 2008; D'Alelio et al., 2008).

Winter conditions detected in long-term analysis on Diana lagoon are also consistent with the presence and high contribution of Cryptophyceae class during this season, as they are known to be linked to freshwater inputs and turbid waters in other natural systems and lagoon environment (Gregor and Maršálek, 2004; Catherine et al., 2012; Garrido et al., 2016, 2019). Winter observations are also in accordance with Sarno et al. (1993), who found important abundances of small Cryptophyceae during winter together with *Skeletonema costatum* in an Italian coastal lagoon.

Spring microphytoplankton composition showed redundant high dominance and blooms of *Pseudo-nitzschia* spp. in both lagoons, together with *Chaetoceros* spp. and *Skeletonema* sp., which is in line with typical timing of these taxa (Gle et al., 2007; Sarno et al., 1993). Some dinoflagellates were also found at Diana lagoon, even if not blooming, mainly of the taxa *Dinophysis* spp., *Prorocentrum* spp., Gymnodiniales and *Scrippsiella* sp. This is in accordance with other observations stating that some of these organisms can be found all year round in oligotrophic waters, due to metabolic advantages of mixotrophy (Bec et al., 2011; Derolez et al., 2020).

The microphytoplankton observed during summer season was mainly characterised by *Chaetoceros* spp., Thalassionemataceae, *Cerataulina* spp.*, Nitzschia* spp. and *Leptocylindrus* spp. Dominant T.U.s detected were favoured by high temperature and salinity values, which can also explain the presence of some dinoflagellates, like *Scrippsiella* sp., sometimes associated with these conditions in Mediterranean lagoons (Dhib et al., 2013). Generally, the summer phytoplankton composition described in this study was similar to that found in this season in other lagoon environments and especially in the French Mediterranean Thau lagoon, showing similar characteristics to the two studied lagoons (Dupuy et al., 2000; Collos et al., 2003; Souchu et al., 2010). Thalassionemataceae group was also found to increase over long-term summer survey in these different ecosystems (Derolez et al., 2020; Dupuy et al., 2000).

503   A long-term increasing trend in diatom total densities was detected for Diana lagoon during

504   summer. Parallel to diatom abundances rise during summer, an increasing trend in air

505   temperature was observed on the long-term, suggesting a possible role of climatic factors in

506   phytoplankton structure shifting. As summer is considered to be the most affected season by

507   climate change in the Mediterranean region, with global temperature predicted to increase by

508   4-5°C over the century (Giorgi and Lionello, 2008), possible effects of this factor seem already

509   detectable on phytoplankton community structure and will probably intensify in the future.

510   Temperature rise could also lead to increasing frequency of potentially toxic dinoflagellates

511   already detected in this season, i.e. *Scrippsiella* spp., *Prorocentrum* spp. and Gymnodiniales

512   (Reñé et al., 2011; Dhib et al., 2013; Sahraoui et al., 2013). Both community composition

513   modification and the emergence of toxic taxa correspond to an alarming threat in sight of future

514   climate change. A similar increasing trend in mean air and water temperature was also detected

515   for spring. Even if no significant trend emerged from phytoplankton analysis, it may not be too

516   long to see similar changes to those observed in summer with the exacerbation of climate

517   change.

518   Autumn microphytoplankton community was mainly characterized by a stronger contribution

519   of dinoflagellates. Despite being usually associated with summer conditions, some studies

520   already underlined the presence and importance of dinoflagellates in oligotrophic lagoons, like

521   Thau and Leucate lagoons (France, Mediterranean Sea), and especially in autumn, thanks to

522   their trophic abilities (Collos et al., 2009, 2014; Cecchi et al., 2016).

523

524   4.2 Bloom dynamics and concerning trends

525   For both lagoons, some years did not present blooms at each season, but there is no

526   correspondence between lagoons nor with specific meteorological events, suggesting that local

527   factors are primarily involved. Overall, despite high silicate concentrations and diatoms

528 dominance, lower phytoplankton biomass and bloom occurrence were observed at Urbino than

529 at Diana lagoon over the study. Generally, in oligotrophic lagoons, major primary producers

530 are aquatic angiosperms and macroalgae (Duarte, 1995; Schramm, 1998; Souchu et al., 2010).

531 Urbino lagoon is dominated by especially well-developed *Cymodocea nodosa* meadows

532 (Garrido et al., 2013). The important presence of these phanerogams has already been proven

533 to negatively impact the phytoplankton compartment due to competitive advantage over

534 microalgae for environmental resource exploitation and through allelopathic regulation (de Wit

535 et al., 2012; Laabir et al., 2013). However, this phenomenon could also be associated with the

536 different exploitation carried out on the two lagoons. Indeed, intensive aquaculture performed

537 in Diana lagoon certainly induces high inputs of organic matter (faecal pellets, other external

538 food inputs) which can sustain a higher phytoplankton production (Mazouni et al., 1998).

539 Concerning the T.U.s seasonal repartition, a stronger contribution of *Skeletonema* sp. to blooms

540 was found in spring at Diana than at Urbino lagoon. Parallel to that, an association between

541 lower salinity and higher bloom probability was detected, diatoms being the most involved

542 group in these events. This contrasts with previous studies, which highlighted positive

543 correlation between diatom blooms and salinity (Mukherjee et al., 2018).

544 At Urbino lagoon, low turbidity was found to favour bloom occurrence during spring and

545 autumn. Turbidity variations can either indicate water column stabilization or alternatively

546 mixing with sediment inducing nutrients resuspension; thus, they greatly impact on fitness and

547 composition of phytoplankton assemblages (Trombetta et al., 2021). The observed inverse

548 relationship between blooms and turbidity in Urbino lagoon is in contrast with the common

549 knowledge regarding diatom preference for well mixed waters, however, light penetration could

550 play a role in this case, as spring blooms can be triggered by combined effects of temperature

551 and irradiance variations (Sommer et al., 1986; Winder and Sommer, 2012). In particular, at

552 Urbino site the highest contribution to bloom occurrence in spring was due to *Pseudo-nitzschia*

spp., which already showed positive correlation of its growth rate with irradiance (Terseleer et al., 2013; Thorel et al., 2014; Husson et al., 2016) and this taxon showed a significant density increase in autumn. Similarly, both in winter and spring, *Pseudo-nitzschia* spp. abundance significantly increased on the long-term at Diana lagoon and showed maximal bloom frequency in both lagoons in winter. Parallel water and air temperature increases were detected for both lagoons in spring. Despite the fact that temperature was not found to be a statistically significant factor in bloom triggering in this study, detected trends are particularly concerning with regard to global climate change in the future, as this taxon is frequently correlated with high temperatures (Bouchouicha Smida et al., 2014; Husson et al., 2016; Delegrange et al., 2018). Although the constant presence of this taxon and its regular exceeding of bloom-threshold in the studied lagoon has never been associated to toxin production until now, a persistence in water temperature increase in winter or spring could not only potentially increase *Pseudo-nitzschia* spp. blooms occurrence and intensity, but also their toxicity since high temperatures can boost their Domoic Acid production (Thorel et al., 2014). Climate change implications already discussed above can be even exacerbated in spring season, as nutrient inputs, frequent during spring rainfall, can also influence the toxicity of bloom events (Nezan et al., 2006; Terseleer et al., 2013; Van Meerssche et al., 2018). Moreover, this genus can potentially modify community structure as it was found to induce allelopathic inhibition on many species, notably diatoms and *Skeletonema marinoi* in particular, as well as Cryptophyceae (Van Meerssche et al., 2018).

In a scenario of future temperature increase, water temperature rise in winter could also lead to unbalance in timing, frequency and magnitude of bloom events, especially with lower biomass accumulation during spring blooms, as hypothesized by Trombetta et al. (2019) following the observation in the French Mediterranean Thau lagoon. These authors found indeed that high winter blooms, triggered by mild winter temperature, induced a cascade effect on the following

season by provoking blooms of lower intensity during spring. This phenomenon, already known to occur in coastal environment is expected to increase in the future (Martens, 2001; van Beusekom et al., 2009) and can then potentially affect the whole food-web of coastal lagoons at some point (Trombetta et al., 2021). All these events can also affect specifically aquaculture exploitation, both in terms of toxicity and community shifting. Many studies have already reported that a change in phytoplankton size structure or species composition can affect shellfish farming and aquaculture exploitation in the long term (Collos et al., 2003; Ribera d'Alcalà et al., 2004; Derolez et al., 2020). Shifting in diatom dominance (such as *Skeletonema* sp. and *Chaetoceros* spp.), an important resource for aquaculture (Dupuy et al., 2000; Pernet et al., 2012), in favour to other less interesting species for this purpose or even potentially toxic, as it has been the case in Thau lagoon (Derolez et al., 2020), might be particularly detrimental. In summer, *Chaetoceros* spp. produced blooms of the highest seasonal magnitude and largely contributed to bloom occurrence in both lagoons. This taxon, which is typically encountered in summer blooms thanks to its ability to exploit regenerated production and to rapidly accumulate nutrients in new biomass, even in low NO_3^- concentration, is fundamental in shellfish farming sustain (Collos et al., 2003; Bec et al., 2005; Derolez et al., 2020).

Punctual proliferations of dinoflagellates were highlighted during the study, especially in autumn. In general, harmful dinoflagellate blooms are commonly occurring during summer season (Fraga et al., 1995; Armi et al., 2010; Reñé et al., 2011), however some studies report dinoflagellate preference to late-summer/autumn conditions (Carrada et al., 1991; Sarno et al., 1993; Gilabert, 2001; Carstensen et al., 2015). Despite the low dinoflagellate contribution in winter, a punctual bloom of Gymnodiniales was detected at extremely high density at Diana lagoon in 2008. Species of this group are generally associated with summer-autumn conditions, characterized by high salinity and temperature (Carrada et al., 1991; Fraga et al., 1995; Reñé et al., 2011). However, lower salinity and temperature associated with high nutrient input can

favour harmful dinoflagellate blooms (Bouchouicha Smida et al., 2014) and during winter 2008 a positive rainfall anomaly was found, indicating the possibility of nutrient high load from the watershed. In autumn, two potentially toxic taxa stood out for their intensity in bloom events: Gymnodiniales and *Gyrodinium* spp. Both are known to frequently bloom in coastal and lagoon environment and in the Mediterranean region (Carrada et al., 1991; Fraga et al., 1995; Reñé et al., 2011). Some species of the Gymnodiniales group, like *Gymnodinium catenatum*, can produce Paralytic Shellfish Poisoning toxins, depending on the cellular density reached, suggesting that this may rise concern during bloom events (Carrada et al., 1991; Sarno et al., 1993). *Gyrodinium* genus comprises some toxic species, notably *G. corsicum*, firstly identified in Diana lagoon and responsible for fish mass mortality and neurotoxin production (da Costa et al., 2005). The observation of blooms of these T.U.s during autumn season is in accordance with their established correlation with high salinity values (Fraga et al., 1995), as for both lagoons maximal salinity values were found at this season. In addition, in Diana lagoon, a significant positive effect of salinity was found for bloom triggering, and Urbino lagoon showed a similar tendency. A potential increase in salinity during this season could enhance bloom frequency, these latter also being known to be positively correlated with salinity in autumn (Armi et al., 2010). Our results show the dominance of dinoflagellates in autumn and a slight increase in abundances of this class in most recent years at all seasons, though not significant, maybe linked to large scale climatic processes. Compared to other similar lagoons, another study identified the importance of dinoflagellate blooms in autumn in Thau lagoon, highlighting their emergence in the context of long-term oligotrophication and especially the rise of toxic HAB-forming *Alexandrium catenella* (Collos et al., 2009).

4.3 Final large-scale considerations

627   Diana and Urbino lagoons show an oligotrophic regime and are not subjected to strong

628   artificialization such as increasing urbanization. They may therefore be considered close to a

629   hypothetical reference state for similar Mediterranean lagoons, in particular Urbino, which is

630   clearly dominated by seagrass meadows as primary producers and reflects a quasi-pristine

631   condition. Observations in these environments can thus give an idea of future evolutions in

632   oligotrophication processes, despite the difficulty in their prediction, as well as giving

633   information on shellfish farming-exploited environments. On the whole, the two studied

634   lagoons showed similar trajectories and are evolving over time, despite different exploitation

635   carried out, left aside some dissimilarities linked to specific local environmental conditions. In

636   fact, major differences could be identified. Urbino lagoon showed slightly wider range in

637   salinity variations and a more variable salinity evolution on the long-term as well as higher

638   silicate content and far longer residence time than Diana lagoon. In contrast, turbidity was

639   generally higher and more variable in Diana lagoon. The origin of these phenomena is not

640   known, yet it can be suggested that salinity variations may depend on local differences in

641   exchanges with the sea, watershed inputs or local meteorological factors. Groundwater

642   exchanges with the lagoon can also play an important role in local conditions and may be

643   involved in the differences in silicate content between the two lagoons (Erostate et al., 2020).

644   This, together with high developed seagrass meadows, can also determine lower turbidity in

645   Urbino lagoon, due to sediment trapping. Aquaculture exploitation in Diana lagoon can also

646   provoke higher turbidity through the release of suspended organic matter. Lastly, some local

647   climatic factors not investigated in this study can be involved, like the different exposure to

648   winds relative to surface, as the two lagoons show different shapes and surfaces. These

649   observations could suggest dissimilarities in hydrological functioning and local regulation of

650   the two lagoons and explain different major driving factors acting on phytoplankton dynamics

651   previously discussed: Diana's highest stability in terms of salinity values could imply a stronger

652 response of the community to minor variations, while the same would happen at Urbino site,

653 but regarding turbidity.

654 Despite the complexity of the systems at local scale, overall seasonal dynamics discovered by

655 this study for Diana and Urbino lagoons are supported by other observations in similar lagoon

656 environments (Bec et al., 2005; Collos et al., 2009; Leruste et al., 2019; Derolez et al., 2020).

657 In particular, winter and spring importance of *Skeletonema* sp. (Borkman and Smayda, 2009;

658 Hernández Fariñas et al., 2015; Derolez et al., 2020; Collos et al., 2014), and general

659 *Chaetoceros* spp. dominance were also found in other oligotrophic lagoons, like Ayrolle lagoon

660 in South of France (Leruste et al., 2019). Even if the studied lagoons are relatively preserved

661 from anthropic pressure and show oligotrophic status, some changes in phytoplankton

662 community structure and trends are already ongoing, indicating that the changes depicted

663 during the study must be related to large-scale processes, such as climate influence.

664 Despite their relatively preserved conditions, the two studied lagoons showed some worrying

665 trends, like Chl *a* increase over winter and the occurrence of blooms of potential harmful algae.

666 In both lagoons, the presence, magnitude, frequency and trends of harmful *Pseudo-nitzschia*

667 spp. blooms seem to be the most alarming point, especially given the fact that their intensity

668 and frequency are already known to be increasing over the Mediterranean basin (Bouchouicha

669 Smida et al., 2014; Husson et al., 2016; Melliti Ben Garali et al., 2020). Other punctual

670 proliferations of potentially toxic groups (like Gymnodiniales) should be considered a potential

671 risk, since similar HAB emergences were already found in other similar lagoon environments

672 at oligotrophic state (Collos et al., 2009). Moreover, potential effects of salinity and temperature

673 variations on these two lagoons were highlighted. Even at regional scale, climate change should

674 then be taken into account for future monitoring and conservation of these environments, since

675 expected future variations in temperature, salinity, precipitations and nutrient loads are likely

676 to play a role in favouring potentially harmful phytoplankton proliferations, changing size

677 structuring and provoking bloom shifts, with all consequent economic, social and sanitary

678 drawbacks (Tatters et al., 2012; Sahraoui et al., 2013).

679 **5. CONCLUSIONS**

680 Through our study, we demonstrated that significant changes are ongoing in two oligotrophic

681 Mediterranean coastal lagoons in the Corsica Island. Our study, based on a detailed seasonal

682 characterization over long-term time span, consists in a good starting point for a better

683 understanding of the phytoplankton communities' dynamics within oligotrophic Mediterranean

684 coastal lagoons and suggested key relationships linking HAB events to the ecological

685 functioning of water bodies.

686 However, we highlighted some limitations: the available environmental data seem insufficient

687 to fully explain phytoplankton dynamics. The high complexity of the coastal lagoon functioning

688 makes it hard to detect clear relationship between phytoplankton and few environmental

689 variables, as many different factors are involved. For future long-term studies, the lack of

690 seasonal nutrients monitoring should be filled and regular counting and identification of total

691 phytoplankton community should be continued. Also, quantification of smaller phytoplankton

692 size classes should be performed on a seasonal basis, especially with regard to their importance

693 in oligotrophic lagoons and in a climate change perspective (Derolez et al., 2020). Moreover,

694 top-down control through zooplankton grazing and fish predation was not considered in the

695 study due to lack of long-term information and complexity of the relations in these

696 environments, despite them being important in the regulation of phytoplankton communities

697 (Frisoni, 1984; Bouchoucha, 2010). Despite these limitations, the results of this study proved

698 ongoing changes in the phytoplankton community structure and bloom events and worrying

699 evolution of the potentially toxic diatom *Pseudo-nitzschia* spp., linked to salinity and

700 temperature changes, in both lagoons.

Hence, this highlights the need of long-term seasonal studies to escort the implementation of prospective management of lagoon environments at regional and Mediterranean scales, taking into account their exploitation and the forecasted climate change scenario.

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1053   **Fig. 1** Location of the two study sites: Diana and Urbino lagoons. The white star indicates

1054   Solenzara meteorological station (Météo-France)

1055   **Fig. 2** Box and whiskers plots showing long-term seasonal evolution of dominant

1056   phytoplankton classes of 2a) diatoms and 2b) dinoflagellates at Diana lagoon, based on

1057   FLORTOT dataset (2001-2019). Mann-Kendall trend test significant p-value and Sen's slope

1058   value are reported for diatoms in summer (2a). Contributions (%) of major T.U.s (frequency of

1059   occurrence > 15% in each season; see Table 2 for T.U.s codes) to total annual abundance is

1060   shown for each season (2c): diatoms are shown with colours only, dinoflagellates with hatched

1061   coloured bars and other classes with dotted coloured bars

1062   **Fig. 3** Tri-plot of the Canonical Correspondence Analysis (CCA) for samplings (points),

1063   environmental variables (arrows) and major phytoplankton T.U.s (triangles). Major T.U.s were

1064   selected as those showing frequency of occurrence > 15% all over the period, and representing

1065   at least 80 % of total phytoplankton abundance in each season. Labels are displayed only for

1066   some selected T.U.s (representing > 70% of total abundance for each season), which were

1067   chosen inside the dominant classes of diatoms (regular font) and dinoflagellates (italic font) as

1068   those showing at least 20% frequency of occurrence in each season (see Table 2 for codes,

1069   DIAT and DINO indicate total diatoms and dinoflagellates respectively). The points

1070   representing the samples are color-coded based on season: blue for winter, green for spring,

1071   gold for summer, red for autumn. Centroids for each season are represented by large coloured

1072   and hollowed circles

1073   **Fig. 4** Blooms occurrence and contribution to annual and seasonal bloom events of FLORIND

1074   Taxonomic Units over the study period (2008-2015) in Diana and Urbino lagoons (See Table 2

1075   for codes). Number of blooms per year and season are reported on top of corresponding bars.

1076   Percentage contribution of main dominant T.U.s on overall seasonal bloom events are shown.

1077   On the right, the maximal bloom magnitude (cell L^{-1}) and responsible T.U. are stated for each

1078   season, as well as the overall mean bloom magnitude and seasonal blooms frequency (number

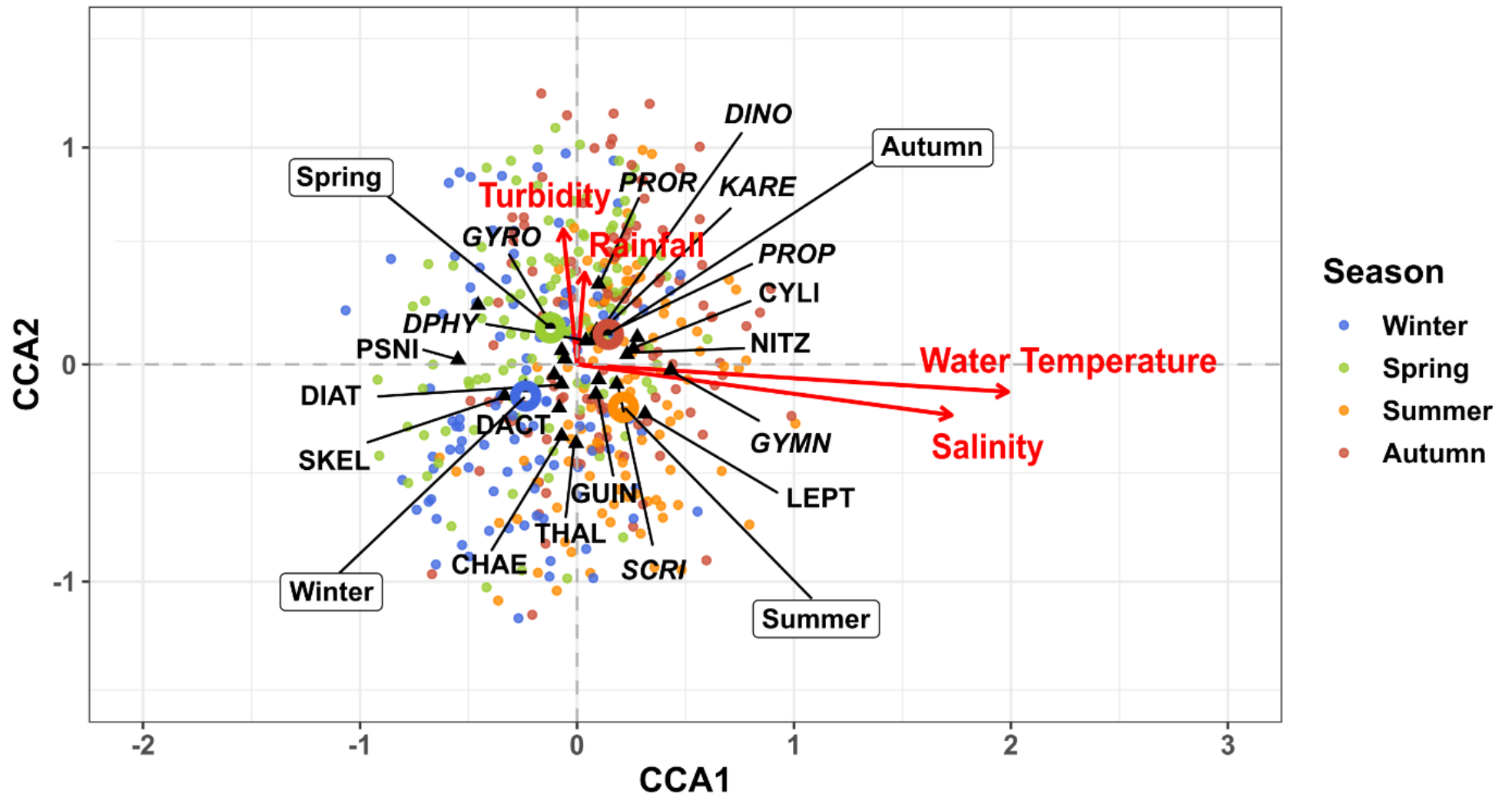1079   of blooms/total number of samples). Values over 1 000 000 cell L^{-1} are highlighted in boldu
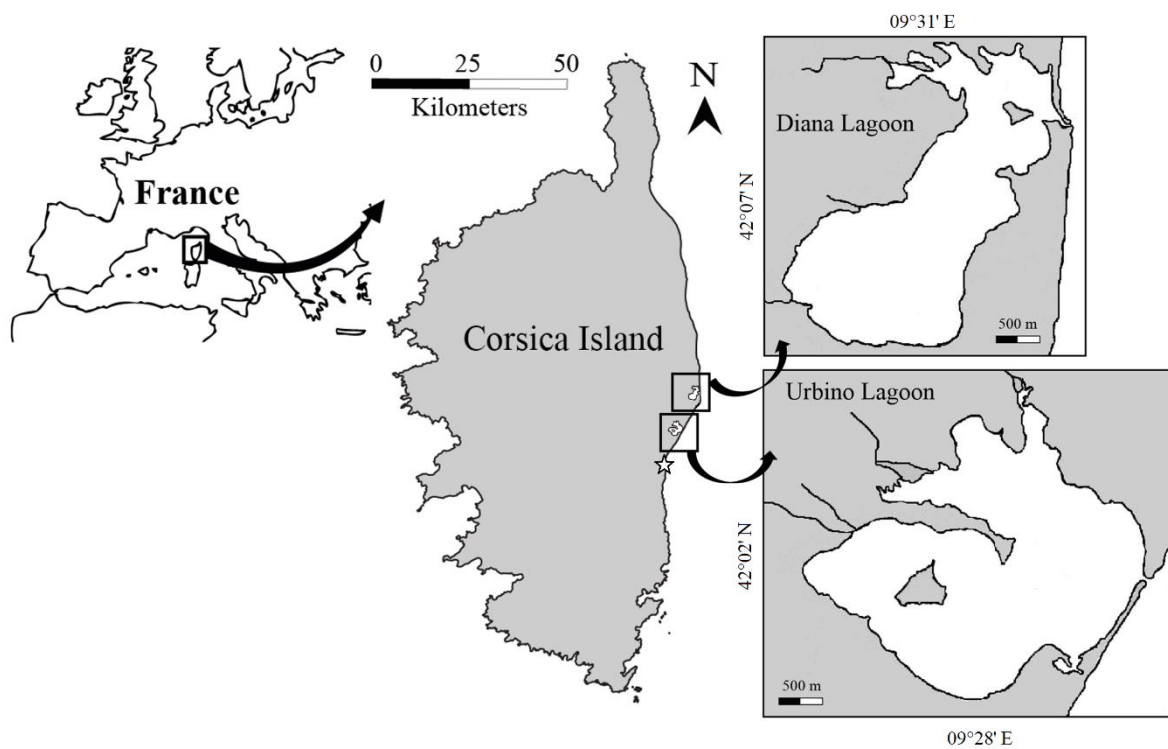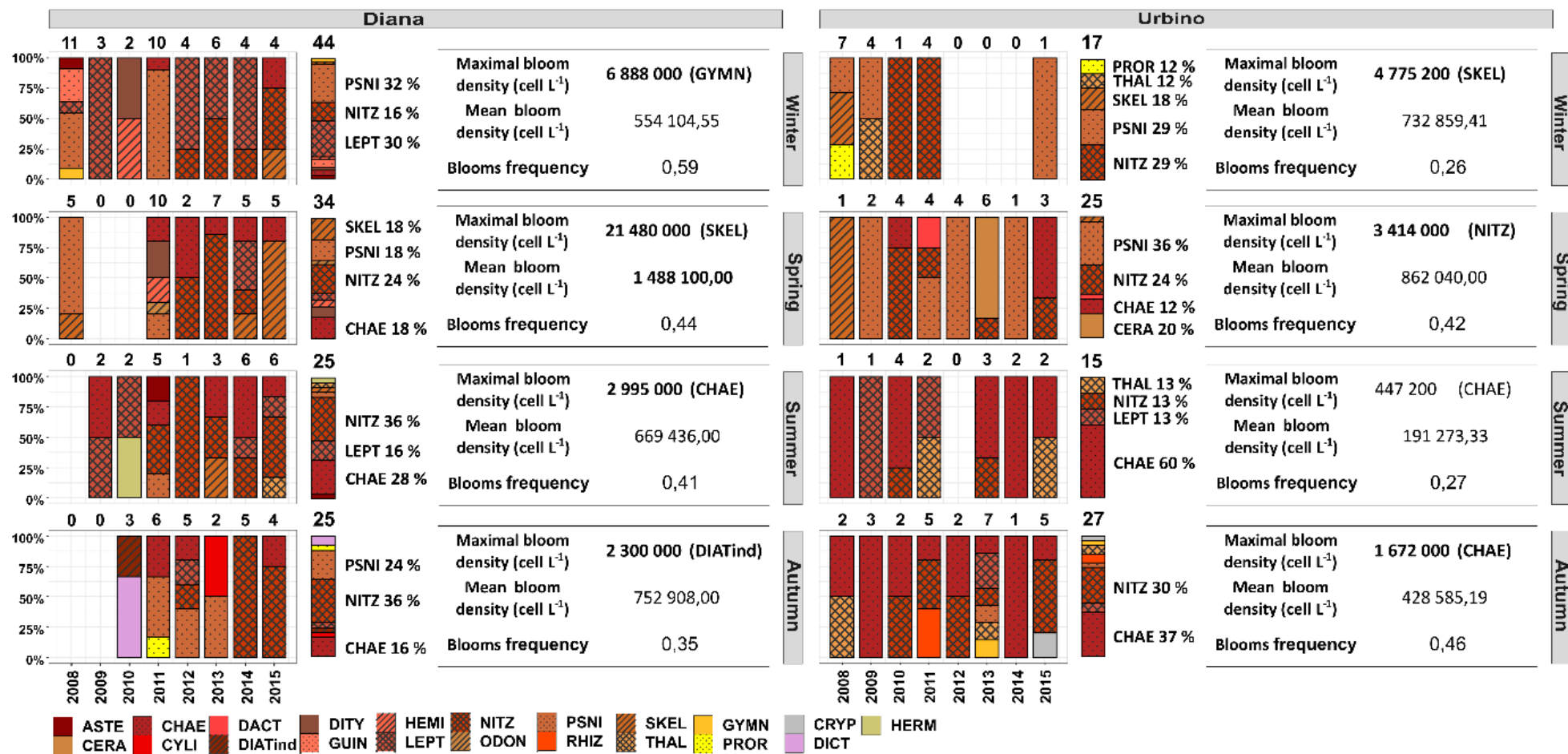
1080

1081   **Figure 1**
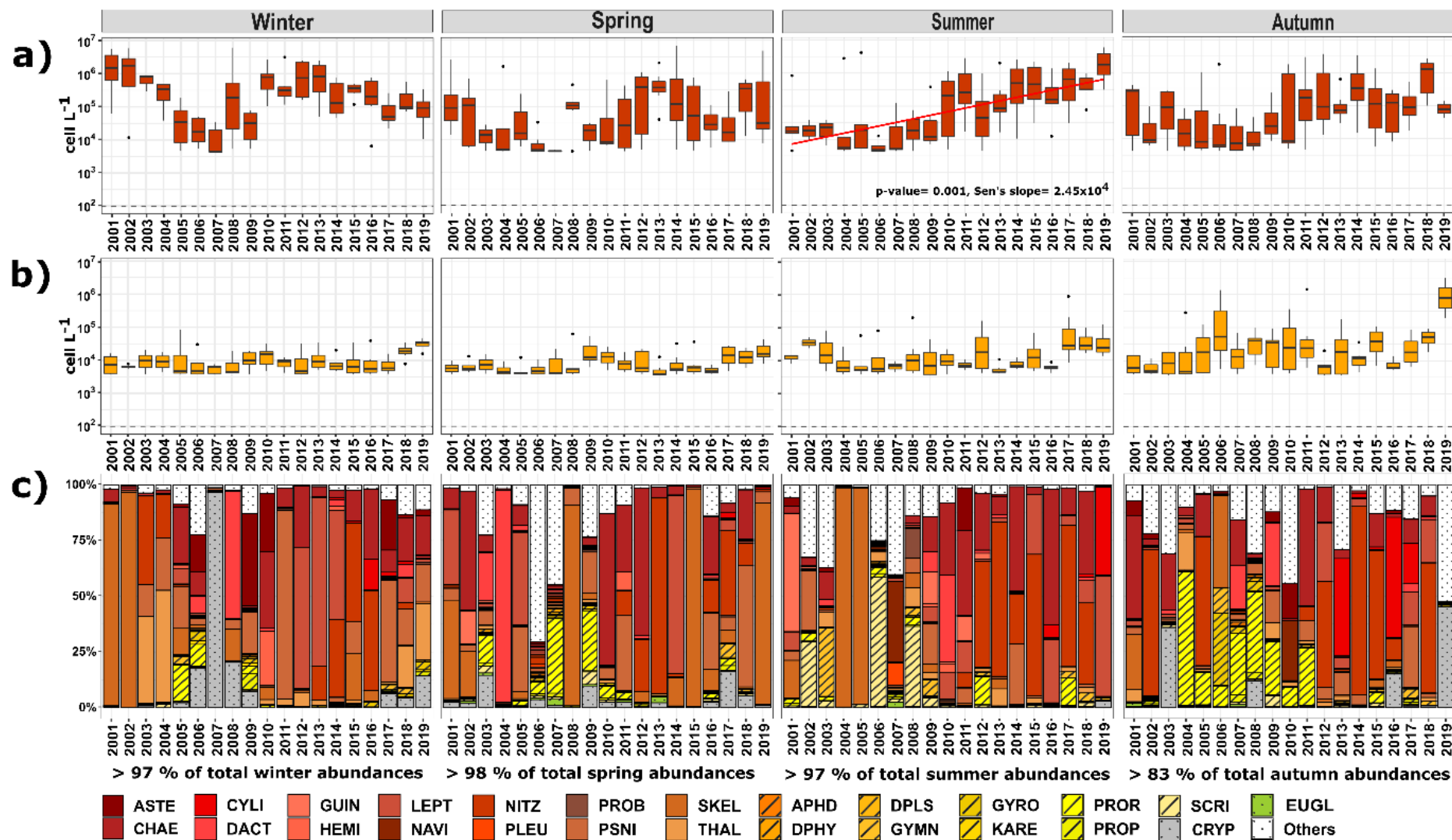
1082

1083   **Figure 2**

1084

1085   **Figure 3**

Figure 4

1088 **Table 1.** Characteristics of Diana and Urbino lagoons. Data were obtained from different
1089 sources: (1) Bouchoucha, 2010, (2) Pergent-Martini et al., 1997, (3) Souchu et al., 2010, (4)
1090 Orsoni et al., 2003, (5) Garrido et al., 2013, (6) Orsoni, 2004, (7) Orsoni et al., 2001, (8)
1091 Frisoni, 1984.

		Diana (42°07' N, 09°31' E)	Urbino (42°02' N, 09°28' E)
General features (1), (2), (3)	Surface	570 ha	790 ha
	Volume	33×10^6 m³	38×10^6 m³
	Mean depth	6 m	5 m
	Maximal depth	11 m	9 m
	Salinity	35-39 PSU	35-39 PSU
	Property	Private	Public (*Conservatoire du Littoral*)
	Management	By aquaculture exploiters	By managers of Corsican region
	Main protection status	ZNIEFF site, Natural site	Natura 2000 Site, Ramsar site
Hydrology (1), (4)	Watershed	62 km²; Some dwelling and factories have individual sanitary systems (sewage leaking into the soil)	31 km²; Some dwelling and factories have individual sanitary systems (sewage leaking into the soil)
	Freshwater	Three main streams, runoff from watershed	Two main streams, runoff from watershed and peripheral marshes
	Sea channel	Located in the northern part, regularly entertained by the aquaculture exploiters.	Located in the northern part, occasionally cleaned by managers
	Renewal	19 months	57 months
Dominant fauna & flora (2), (5)	Aquatic fauna	Mullets, seabass, sole, eels, …	Mullets, seabass, eels, *Aphanius spp*, …
	Terrestrial fauna	Great cormorants, laridae, shorebirds, large waders, …	Great cormorants, shorebirds, waders, black-headed gulls, …
	Aquatic flora	Aquatic phanerogams (*Cymodocea nodosa*) and macroalgae	Aquatic phanerogams (*Cymodocea nodosa*) and macroalgae
	Terrestrial flora	Shores composed of glasswort, inulas, reeds, phragmites.	Shores composed of glasswort, tamarisks, reeds.
Human activities (1), (6), (7), (8)	Watershed	Agriculture (about 10%), mainly vineyard, low urbanization.	Agriculture (about 45%), mainly vineyards, low urbanization.
	Lagoon	The lagoon is exploited for shellfish (oysters, mussels) and fish farming (seabream, seabass) and fishing activities. Estimated production in 2020: 150t oysters and 800t mussels.	Intensive shellfish farming was carried out from 1990 to 2000. Nowadays, activities on the lagoon are limited to traditional fishing. Mean production during exploitation: 100t/year oysters and 130t/year mussels.

1092

1093 **Table 2.** List and codes of the most frequent taxonomic units of major groups observed at

1094 Diana and Urbino stations (bloom-forming taxa for the FLORIND dataset, and taxa with

1095 frequency of occurrence > 15% in each season for the FLORTOT dataset).

Group	Code	Taxonomic unit	Grouping Taxonomic level
Diatoms	ASTE	*Asterionella* spp.	Family: Fragilariaceae
Diatoms	CERA	*Cerataulina* spp.	Genus: *Cerataulina*
Diatoms	CHAE	*Chaetoceros* spp.	Genus: *Chaetoceros*
Diatoms	CYLI	*Cylindrotheca* spp.	Family: Bacillariaceae
Diatoms	DACT	*Dactyliosolen* spp.	Genus: *Dactyliosolen*
Diatom	DIATind	Unidentified diatoms	Class: Bacillariophyceae
Diatoms	DITY	*Ditylum brightwellii*	Species: *D. brightwellii*
Diatoms	GUIN	*Guinardia* spp.	Genus: *Guinardia*
Diatoms	HEMI	*Hemiaulus* spp.	Genus: *Hemiaulus*
Diatoms	LEPT	*Leptocylindrus* spp.	Genus: *Leptocylindrus*
Diatoms	NAVI	*Navicula* spp., *Fallacia* spp., *Haslea* spp., *Lyrella* spp., *Petroneis* spp.	Superorder: Bacillariophycanae
Diatoms	NITZ	*Nitzschia* spp., *Hantzschia* spp.	Family: Bacillariaceae
Diatoms	ODON	*Odontella* spp.	Genus: *Odontella*
Diatoms	PLEU	*Pleurosigma* spp., *Gyrosigma* spp.	Family: Pleurosigmataceae
Diatoms	PROB	*Proboscia* spp.	Genus: *Proboscia*
Diatoms	PSNI	*Pseudo-nitzschia* spp.	Genus: *Pseudo-nitzschia*
Diatoms	RHIZ	*Rhizosolenia sp*p.	Genus: *Rhizosolenia*
Diatoms	SKEL	*Skeletonema costatum*	Species: *S. costatum*
Diatoms	THAL	*Thalassionema* spp., *Thalassiothrix* spp., *Lioloma* spp.	Family: Thalassionemataceae
Dinoflagellates	APHD	*Amphidinium* spp.	Genus: *Amphidinium*
Dinoflagellates	DPHY	*Dinophysis* spp.	Genus: *Dinophysis*
Dinoflagellates	DPLS	*Diplopsalis* spp., *Diplopelta* spp., *Diplopsalopsis* spp. *Preperidinium* spp., *Oblea* spp.	Family: Protoperidiniaceae
Dinoflagellates	GYMN	Gymnodiniales, *Gymnodinium* spp.	Order: Gymnodiniales
Dinoflagellates	GYRO	*Gyrodinium* spp.	Genus: *Gyrodinium*
Dinoflagellates	KARE	*Karenia* spp., *Centrodinium* spp.	Genus: *Karenia*
Dinoflagellates	PROR	*Prorocentrum* spp.	Genus: *Prorocentrum*
Dinoflagellates	PROP	*Protoperidinium* spp., *Peridinium* spp., *Protoperidinium* spp., *Archaeperidinium minutum*	Order: Peridiniales
Dinoflagellates	SCRI	*Scrippsiella* spp., *Ensiculifera* spp., *Pentapharsodinium* spp.	Family: Peridiniaceae
Euglenophyceae	EUGL	*Euglena* spp., Euglenoidea, *Eutreptia* spp.	Class: Euglenophyceae
Cryptophyceae	CRYP	Cryptophyceae	Class: Cryptophyceae
Others	HERM	*Hermesinum adriaticum*	Species: *H. adriaticum*
Others	DICT	*Dictyocha* spp., Dictyochaceae, Dictyochophyceae, Pedinellales	Class: Dictyochophyceae

1096

Table 3. Summary of statistical results of Mann Kendall trend tests performed on annual

medians of meteorological variables (cumulative rainfall, mean air temperature), salinity and

water temperature for Diana and Urbino lagoons, chlorophyll *a* concentrations, diatoms and

dinoflagellates abundances from FLORTOT dataset of Diana lagoon. Significant p-values of

Mann-Kendall tests are reported in bold and trend direction represented by arrows.

Mann Kendall trend test						
	p-value	Sen's slope	Trend			
Cumulative rainfall 1998-2019	Winter	0.398	-1.65			
	Spring	0.955	-0.04			
	Summer	0.756	0.14			
	Autumn	0.822	-0.47			
Mean air temperature 1998-2019	Winter	0.236	0.05			
	Spring	**0.005**	0.08	↗		
	Summer	**0.028**	0.07	↗		
	Autumn	0.055	0.05			

		Diana			**Urbino**		
		p-value	Sen's slope	Trend	p-value	Sen's slope	Trend
Salinity 1998-2019 (Diana) 1998-2018 (Urbino)	Winter	0.088	0.07		0.315	0.08	
	Spring	0.099	-0.06		0.243	-0.13	
	Summer	0.638	-0.02		0.867	0.01	
	Autumn	0.432	0.02		0.401	0.06	
Water temperature 1998-2019 (Diana) 1998-2018 (Urbino)	Winter	**0.032**	0.07	↗	0.069	0.07	
	Spring	**0.000**	0.13	↗	**0.000**	0.22	↗
	Summer	0.264	0.04		0.070	0.08	
	Autumn	0.904	0.01		0.649	0.05	
Diatoms abundance 2001-2019	Winter	0.294	-23461.54				
	Spring	0.208	1764.29				
	Summer	**0.001**	24460.00	↗			
	Autumn	0.093	6316.67				
Dinoflagellates abundance 2001-2019	Winter	0.528	81.82				
	Spring	0.079	210.00				
	Summer	0.506	200.00				
	Autumn	0.054	1511.11				
Chlorophyll *a* 2001-2019	Winter	**0.000**	0.03	↗			
	Spring	0.272	0.02				
	Summer	0.256	-0.02				
	Autumn	0.471	0.02				

1102

1103 **Table 4.** Summary description of *Pseudo-nitzschia* spp. bloom events in Diana and Urbino

1104 lagoons, based on available FLORTOX data (left). Maximal density and mean density (sum of

1105 bloom densities over number of blooms) calculated on all bloom events registered during the

1106 considered period are reported (values over 1 000 000 cell L^{-1} in bold). Bloom frequency was

1107 calculated as number of *Pseudo-nitzschia* spp. blooms (n) over the total number of samples (N)

1108 recorded for each season. Seasonal long-term trends of *Pseudo-nitzschia* spp. cellular densities

1109 over the sampling period are shown on the right (with significant p-values of Mann-Kendall

1110 trend tests in bold and trend direction represented by arrows).

			Blooms description					*Mann-Kendall trend test*		
			Maximal bloom density (cell/L)	Mean bloom density (cell/L)	N	n	Bloom frequency	*p-value*	Sen's slope	Trend
Diana	FLORTOX 1998 - 2019	Winter	**1 236 800**	248 044	156	16	0.10	**0.006**	1043.199	↗
		Spring	334 400	182 211	182	9	0.05	**0.034**	214.084	↗
		Summer	117 100	112 000	139	2	0.01	0.449	32.948	
		Autumn	283 800	160 017	147	6	0.04	0.348	50. 000	
Urbino	FLORTOX 1998 - 2017	Winter	**8 060 000**	**3 013 756**	167	23	0.14	0.093	190.614	
		Spring	**3 185 600**	819 774	175	23	0.13	0.185	311.400	
		Summer	201 200	158 100	137	2	0.01	0.449	-29.045	
		Autumn	**2 543 000**	912 500	142	6	0.04	**0.034**	144.881	↗

1111

Table 5. Summary of statistical results from GLMs performed on binomial variable "bloom *vs*

1113 non-bloom events" against environmental variables (salinity: SALI, water temperature: TEMP

1114 and turbidity: TURB) for Diana and Urbino lagoons. Interactions are represented with the code

1115 "x". Best models formulas and significant effects are reported. Based on the significance level,

1116 variables are reported with the following codes for p-values: '***' 0,001; '**' 0,01; '*' 0,05. The

1117 best models were selected based on lowest Akaike information criterion (AIC).

Two Lagoons	best model = blooms ~ Lagoon + Season + SALI + TEMP + TURB + LagoonxSeason + LagoonxSALI + SeasonxSALI + LagoonxTEMP + LagoonxTURB + SeasonxTURB + SALIxTURB + LagoonxSeasonxSALI + LagoonxSeasonxTURB (AIC: 710)		
	Estimate	p-value	
Season Spring	15.74	0.012	*
Season Autumn	-29.38	0.043	*
Season SpringxSALI	-0.44	0.011	*
Season AutumnxSALI	0.75	0.046	*
Lagoon UrbinoxSeason AutumnxTURB	-1.41	0.030	*
Diana	best model = blooms ~ Season + SALI + TEMP + SeasonxSALI (AIC: 401)		
	Estimate	p-value	
Season Spring	12.92	0.021	*
Season Autumn	-30.66	0.034	*
Season SpringxSALI	-0.38	0.018	*
Season AutumnxSALI	0.79	0.037	*
Urbino	best model = blooms ~ Season + TURB + SeasonxTURB (AIC: 297)		
	Estimate	p-value	
(Intercept)	-2.80	0.000	***
Season Spring	2.88	0.000	***
Season Autumn	3.72	0.000	***
TURB	0.99	0.003	**
Season SpringxTURB	-1.24	0.003	**
Season AutumnxTURB	-1.73	0.000	***

1118