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## Two decades of oligotrophication: Evidence for a phytoplankton community shift in the coastal lagoon of Thau (Mediterranean Sea, France)

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### Highlights

► The decrease in water nutrients confirms oligotrophication in the period 1998–2016. ► The decrease in phytoplankton biomass was associated with a decrease in diatom abundance. ► The dominant taxa shifted from *Skeletonema-Chaetoceros* to *Chaetoceros-Pseudo-nitzschia*. ► The median proportion of dinoflagellates relative to diatoms increased significantly. ► The total dinoflagellate abundance did not change significantly.

**Keywords :** Eutrophication, Oligotrophication, Nutrients, Recovery, Phytoplankton community shift, Mediterranean coastal lagoon

18      **1. Introduction**

19      Anthropic eutrophication and its effects on coastal ecosystems and primary producers are well  
 20     described in the literature (de Jonge and Elliott 2001; Cloern et al. 2014). The geomorphology and  
 21     functioning of transitional ecosystems, including coastal lagoons, make them inherently extremely  
 22     vulnerable to eutrophication (Newton et al. 2014). Eutrophication effects can jeopardise the natural  
 23     goods and services provided by these ecosystems, whose value is among the highest among natural  
 24     ecosystems (Basset et al. 2013). As Mediterranean coastal lagoon ecosystems are very densely  
 25     inhabited, in recent decades, they have been particularly exposed to anthropic eutrophication, mainly  
 26     due to urbanisation (Zaldívar et al. 2008; Souchu et al. 2010).

27      Thau lagoon is one of the largest Mediterranean coastal lagoons and provides many ecosystem  
 28     services including shellfish farming (*C. gigas* oysters and *M. galloprovincialis* mussels). Oyster  
 29     production dominates and represents roughly 10% of French national oyster production, with 12 000  
 30     t produced in the 2000s (Gangnery et al. 2001) and 7 300 t in 2016 (DDTM, 2017). Since the 1960s,  
 31     the increase in anthropogenic inputs, linked to the exponential growth of the human population in the  
 32     lagoon watershed, has contaminated shellfish farms and caused the eutrophication of Thau lagoon,  
 33     with significant socio-economic and ecological impacts, such as frequent bans on shellfish sales and  
 34     major anoxic events (Souchu et al. 1998; Loubersac et al. 2007). In the eutrophic conditions which  
 35     prevailed in the 1970s and 1980s, large quantities of dissolved inorganic nitrogen (DIN) and  
 36     phosphorus (DIP) inputs from the watershed resulted in high levels of dissolved nutrients in the  
 37     lagoon (up to 70 µM for  $\text{NO}_3^-$  and 10 µM for DIP, Casellas et al. 1990; Souchu et al. 1998), leading to  
 38     phytoplankton blooms associated with fast growing diatoms (up to 30 µg Chl a L<sup>-1</sup>, Tournier and  
 39     Pichot 1987; Collos et al. 2003). Thus, diatoms were long identified as the dominant phytoplankton  
 40     group in Thau lagoon (Pavillard 1905; Hénard 1978; Jarry et al. 1990). *Skeletonema costatum* and  
 41     *Chaetoceros* spp. were the most frequent diatom genera in the lagoon, *Skeletonema costatum* were  
 42     observed during winter blooms, and *Chaetoceros* spp. in spring and summer blooms (Collos et al.  
 43     1997; Collos et al. 2003; Bec et al. 2005). Dinoflagellates were also present but their contribution to  
 44     total abundances of phytoplankton communities remained low, except during autumn-winter blooms  
 45     (Collos et al. 2009; Collos et al. 2014). In the 1970s, improvements were made to waste-water  
 46     treatment systems in the watershed. A decrease in nutrient inputs to Thau lagoon has been  
 47     observed ever since, reinforced in the late 2000s, thanks to the EU Nitrates Directive and the Water  
 48     Framework Directive (WFD) (EC 1991a; 1991b and 2000), which gradually led to the  
 49     oligotrophication of the ecosystem (Deslous-Paoli et al. 1998; La Jeunesse et al. 2002; Collos et al.  
 50     2003).

51      In contrast to eutrophication, oligotrophication has rarely been described in coastal ecosystems  
 52     (Yamamoto 2003; Borkman and Smayda 2015; Riemann et al. 2016), particularly in coastal lagoons  
 53     (Collos et al. 2009; Leruste et al. 2016; Derolez et al. 2019; Le Fur et al. 2019). The literature  
 54     contains more case studies on freshwater ecosystems, especially lakes (Ruggiu et al. 1998; Ibelings  
 55     et al. 2007; Jeppesen et al. 2007). The few examples available on oligotrophication in Mediterranean  
 56     coastal lagoons report modifications in the composition and structure of phytoplankton communities  
 57     (Collos et al. 2009; Leruste et al. 2016) and macrophyte communities (Pasqualini et al. 2017; Le Fur  
 58     et al. 2019). Phytoplankton are generally the first autotrophic compartment to respond to a reduction  
 59     in the concentrations of nutrients following remediation (Leruste et al. 2016; Derolez et al. 2019). In

60 studies of the oligotrophication of lakes, phytoplankton responses to the reduction in nutrients are  
 61 reported to have resulted in considerable changes in phytoplankton biomass, as well as in the size,  
 62 structure and diversity and development of mixotrophic organisms (Gaedke 1998; Ruggiu et al.  
 63 1998; Anneville et al. 2005). During the first stages of oligotrophication in Thau lagoon (1998-2005),  
 64 some changes in phytoplankton communities were observed with the simultaneous appearance of a  
 65 dinoflagellate species (*Alexandrium catenella*) and a picocyanobacteria species (*Synechococcus*)  
 66 (Collos et al. 2009). However, the long-term trends of phytoplankton communities of coastal lagoons  
 67 under oligotrophication have been only partially studied, as most authors focused on the main algal  
 68 groups (diatoms, dinoflagellates) (Gowen et al. 2015; Leruste et al. 2016) and did not consider the  
 69 whole phytoplankton community at species level.

70 The aim of this paper is to describe long-term changes in phytoplankton abundance and community  
 71 composition in Thau lagoon in a context of oligotrophication and climate change since the late 20<sup>th</sup>  
 72 century. The specific objective of our study was to check if the expected decreases in phytoplankton  
 73 biomass and abundance were associated and concomitant with changes in community composition  
 74 and structure. To this end, we analysed long monitoring time-series (1998-2016) of phytoplankton  
 75 biomass, abundance and species composition, using univariate and multivariate statistics. The  
 76 trends were analysed in parallel with changes in nutrient levels and in climate conditions  
 77 (temperature and rainfall). Finally, based on our results, on the mandala of Glibert et al. (2016), and  
 78 on the literature, we present a conceptual scheme representing the main drivers of phytoplankton  
 79 community structure to clarify the ecosystem functioning of a Mediterranean lagoon used for shellfish  
 80 farming, under oligotrophication and climate change.

## 81 2. Materials and methods

### 82 2.1. Study site and changes in nutrient inputs

83 Thau is a microtidal and restricted coastal lagoon, connected to the Mediterranean Sea through two  
 84 permanent inlets (Fig. 1), the Sète channel in the north, which is responsible for 90% of sea water  
 85 exchanges, and the Pisses-Saumes channel in the south (Fiandrino et al. 2017). The lagoon covers  
 86 68 km<sup>2</sup>, 19.5 km long and 4.5 km wide, with a mean depth of 4 m (Fiandrino et al. 2017). A depth  
 87 gradient is observed from the south-west to the north-east of the lagoon (mean depth: 3.3 m and 5.2  
 88 m, respectively) (Souchu et al. 2001). The Mediterranean climate is characterised by hot dry  
 89 summers and mild wet winters. The Thau watershed covers about 280 km<sup>2</sup> and is drained by  
 90 numerous tributaries with intermittent flows. The Vène and Pallas rivers are the two main natural  
 91 tributaries to the lagoon and contribute more than 50% of total freshwater inflow into the lagoon (La  
 92 Jeunesse et al. 2015). Approximately half the watershed's permanent population (about 103,500 inh.  
 93 in 2015, INSEE 2016) is located in the city of Sète, situated on the southern shore of the lagoon (La  
 94 Jeunesse et al. 2015).

95 Shellfish farming structures cover about 20% of the surface of the water body in three cultivation  
 96 zones (Marseillan, Mèze and Bouzigues) along the northern shore of the lagoon (Fig. 1) (Deslouis-  
 97 Paoli et al. 1998). Thau lagoon accounts for about 10% of the production of French Pacific oyster  
 98 *Crassostrea gigas* whose growth rates at this location are among the highest in France (Gangnery et  
 99 al. 2001).

100 Since the years 1970s, important works have been undertaken to improve the waste water treatment  
 101 system in the watershed, leading to a significant decrease in microbial pathogens and nutrient inputs  
 102 (La Jeunesse et al. 2002; Loubersac et al. 2007). Recent European regulations targeting the  
 103 improvement of water quality (EC 1991a & 1991b, EC 2000) led stakeholders to implement further  
 104 remediation actions. All these management actions led to a 52% reduction in phosphorus inputs  
 105 between the 1970s and the 1990s, from 135 to 65 t y<sup>-1</sup> (La Jeunesse 2001), and consequently to a  
 106 decrease in nutrient concentrations in the water column (Fig. S2, Souchu et al. 1998; Collos et al.  
 107 2009). Between the 1990s and 2016, the decrease reached 80% for phosphorus and 48% for  
 108 nitrogen, leading to an increase in the N:P ratio from 8 to 21.8 (Table 1).

## 109           **2.2. Meteorological, hydrological and phytoplankton monitoring**

### 110           **2.2.1. Meteorological and hydrological time-series**

111 Rainfall level and air temperature data were collected from Sète meteorological station (Fig. 1)  
 112 (Météo-France station n°34301002). Daily data were cumulated (rainfall, mm.y<sup>-1</sup>) or averaged (air  
 113 temp., °C) per year from 1998 to 2016 and compared to the mean level calculated from 1970 to  
 114 2016.

115 Water samples were collected 1 m below the surface in the eastern part of the lagoon, at monthly  
 116 intervals in June, July and August. Sampling took place at TES station from 1999 to 2016 (Fig.1).  
 117 The concentrations of dissolved nutrients (dissolved inorganic phosphorus (DIP), nitrate and nitrite  
 118 (NO<sub>3</sub><sup>-</sup>+NO<sub>2</sub><sup>-</sup>) and ammonium (NH<sub>4</sub><sup>+</sup>), µM) and total nutrients (total nitrogen (TN) and total phosphorus  
 119 (TP), µM) in the water were analysed using the methods detailed in Souchu et al. (2010).

120 To allow longer-term trend analysis, meteorological data collected at Sète station from 1970 to 1997  
 121 and dissolved nutrient concentrations (DIP and NO<sub>3</sub><sup>-</sup>+NO<sub>2</sub><sup>-</sup>) measured from 1972 to 1993 at ZA  
 122 station (Fig. 1) were added to the 1999-2016 time series and presented in the supplementary  
 123 material (Figs S1 and S2).

### 124           **2.2.2. Phytoplankton time-series**

125 Microphytoplankton data were collected from the REPHY monitoring network (REPHY, 2017). Since  
 126 1987, water samples have been collected twice a month at the station located at Bouzigues,  
 127 hereafter referred to as "REPHY" (Fig. 1), along with physical measurements of temperature (Temp.,  
 128 °C) and salinity (Sal., PSU). The water samples were collected in a standard 2 L water sampler  
 129 (Hydrobios ref: 436 132) at a depth of one metre, and kept in plastic bottles in a dark cooler for less  
 130 than 2 h before transport to the laboratory. For the identification of phytoplankton, 1 L was fixed with  
 131 Lugol's solution (1 to 10 mL per L, depending on the density of the algae) and counted using the  
 132 Ütermöhl method (Ütermöhl, 1958). A 10 mL tubular plankton chamber (Hydrobios ref: 435 022) was  
 133 filled with this fixed sample water. After decantation for at least 12 hrs, the entire chamber was  
 134 observed under an Olympus IMT2 inverted light microscope with phase contrast, according to the  
 135 method of Utermöhl (1958). A phytoplankton expert identified them to the lowest possible taxonomic  
 136 level and counted organisms bigger than 20 µm, plus smaller species that form colonies or chain  
 137 structures. Smaller species were also counted if they were potentially toxic. The species were  
 138 identified using the IOC-UNESCO taxonomic reference list of harmful microalgae (WoRMS <http://marinespecies.org/>). Chlorophyll a (µg Chl a L<sup>-1</sup>) concentrations were measured by monochromatic

140 spectrophotometry (Aminot and Chaussepied 1983; Aminot and Kérouel 2004) and were used as a  
 141 proxy for phytoplankton biomass.

### 142           **2.3. Data processing and analyses**

143 All data analyses were performed using R software (R Development Core Team 2019). In order to  
 144 characterise and quantify changes in the phytoplankton community structure following the reduction  
 145 in nutrient inputs to Thau lagoon between 1998 and 2016, we analysed the long monitoring time-  
 146 series which included the meteorological and hydrological context and phytoplankton biomass,  
 147 abundance and species composition.

#### 148           **2.3.1. Preliminary processing of phytoplankton data**

149 Because phytoplankton taxa are difficult to distinguish with optical microscopy, and a variation in  
 150 expertise during the study period could not be excluded, taxa were grouped in taxonomic units (TU),  
 151 at the lowest common taxonomic level. Grouping in this way enabled homogeneous interpretation of  
 152 phytoplankton time-series (Hernandez-Farinés et al. 2014). The data analyses were limited to  
 153 diatoms and dinoflagellates and reached a total of 56 TU over the study period (see Supplementary  
 154 Table S1). The phytoplankton dataset (1987-2016) was first examined using time-scale scatter plots  
 155 and revealed that the first years corresponded to a period of increasing taxonomic skills with several  
 156 training sessions (in 1992, 1995, 1996). Consequently, with the agreement of the people responsible  
 157 for identifying and counting the phytoplankton, data up to and including 1997 were discarded to avoid  
 158 misinterpretation, leading us to focus our analyses on the data for the period 1998-2016.

159 Phytoplankton counts are affected by a detection limit (100 cells L<sup>-1</sup>): when a taxon is not detected, it  
 160 means that its concentration in the sample ranges from 0 up to the detection limit. This was taken  
 161 into account in annual medians and in the PCA (see below), when we set undetected TU  
 162 abundances at 100 cells L<sup>-1</sup>.

#### 163           **2.3.2. Univariate analyses of phytoplankton and environmental data**

164 Temporal analyses focused on the dominant TUs. The dominant taxa were determined using a  
 165 method adapted from the Sanders index (Sanders, 2003). This index is determined by classifying the  
 166 taxonomic units from 1 to 10 according to their abundance in each sample. Rank 1 receives a value  
 167 of 10 points; rank 2 of 9 points; rank 3 of 8 points, etc. and a rank of 10 equals one point. The points  
 168 are then summed. If a TU is ranked first in all the samples, it will have the highest possible score.  
 169 The adaptation consisted in taking abundance into account by using the relative abundance of  
 170 species in the sample instead of points.

171 Annual medians were calculated using environmental and phytoplankton variables based on  
 172 bimonthly data (Sal., Temp., Chl a, diatoms and dinoflagellate abundances, proportion of  
 173 dinoflagellates relative to diatoms) or on monthly summer data (DIP, NO<sub>3</sub><sup>-</sup>+NO<sub>2</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup>, DIN=NO<sub>3</sub><sup>-</sup>  
 174 +NO<sub>2</sub><sup>-</sup>+NH<sub>4</sub><sup>+</sup>, TN, TP, and the ratios TN:TP, DIN:DIP, DIP:TP and DIN:TN).

175 A tailored method was used to calculate annual medians for phytoplankton abundances to explicitly  
 176 account for the existence of measurements below the limit of detection. Here we used the robust  
 177 regression on order statistics (robust ROS) (Helsel and Cohn, 1988; Lee and Helsel, 2007). ROS is a  
 178 semi-parametric method which models censored distributions using a linear regression model of  
 179 observed concentrations versus their normal quantiles (NADA for in R). If the proportion of data

180 below the limit of detection is greater than 80%, the estimates are considered as tenuous (Lee and  
 181 Helsel 2005). Hence, we did not use the ROS method on annual data with 80% or more censored  
 182 values.

183 We used Mann-Kendall tests (MK) on annual medians to characterise the monotonic trends of  
 184 environmental and phytoplankton time-series. To eliminate the effect of serial correlation on the MK  
 185 test, we used the modification by effective sample size, computed with only the lag-1 serial  
 186 correlation coefficient (Yue and Wang 2004, *modifiedmk* package in R). There are many different  
 187 recommendations about the minimum number of data needed to implement the Mann-Kendall test:  
 188 we decided not to apply it below 8 medians in accordance with ITRC (2013). If the test was  
 189 significant (i.e. p-values <0.05), Theil-Sen's slope estimator was calculated (Sen, 1968) and the  
 190 percentage decrease or increase in phytoplankton abundances (in cells L<sup>-1</sup>) was obtained from the  
 191 forecast values of the regression line for the first and last available years.

### 192           **2.3.3. Multivariate analyses of phytoplankton community composition**

193 To focus on the main changes in the phytoplankton community, TUs were excluded from the  
 194 analyses when their frequency of occurrence was less than 15% over the period 1998-2016. The  
 195 abundances of the 26 TU were  $\log_{10}(x+1)$  transformed to normalise the data and reduce the effect of  
 196 dominant taxa. The data were then averaged per year to identify inter-annual differences, before  
 197 principal component analyses (PCA) was performed in the *ade4* package in R. K-means cluster  
 198 analysis was then applied to identify years with similar species composition (*vegan* package in R).  
 199 The optimal number of clusters was estimated based on the simple structure index (SSI) criterion  
 200 (Dolnicar et al. 1999).

## 201           **3. Results**

### 202           **3.1. Meteorological conditions**

203 Air temperature and rainfall monitored by the Sète weather station from 1998 to 2016 revealed  
 204 changes in the meteorological conditions in the Thau lagoon watershed. Compared with the average  
 205 temperature for the period 1970-2016 (15.3 °C), annual means showed an increase in temperature  
 206 from 1998 to 2016 (Fig. 2a). During this period, below average temperatures were only recorded in  
 207 two years (2005 and 2010). The deviation from the average temperature increased over time, from  
 208 +0.2 °C in 1998 to +1.5 °C in 2014 (mean temperatures of 15.5 °C and 16.8 °C, respectively). The  
 209 years 2003 and 2006 were characterised by summer heat waves, leading to severe anoxia in Thau  
 210 lagoon associated with massive shellfish mortalities (Minghelli-Roman et al. 2011). The years 2003  
 211 and 2006 had the first and third hottest summers in the 1998-2016 period. However, the annual  
 212 mean air temperatures in the same two years were only the fourth and third hottest in the period  
 213 1998-2016 (respectively 16.1 °C and 16.4 °C).

214 The average annual rainfall in the period 1970-2016 (570.6 mm y<sup>-1</sup>) was exceeded in only 5 years  
 215 between 1998 and 2016, with deviations higher than +200 mm in 1999 and 2002 (cumulative rainfall:  
 216 967.2 and 779.5 mm y<sup>-1</sup>, respectively) (Fig. 2b). After 2005, the years were less rainy than average,  
 217 and mean rainfall was only exceeded in 2014 (619.8 mm y<sup>-1</sup>, 49.2 mm more than the average).

### 218           **3.2. Hydrological conditions**

219 Hydrological conditions measured in the water column at REPHY station from 1998 to 2016 revealed  
 220 no monotonic trend in salinity or temperature. Water temperatures ranged from 3.7 °C to 29.6 °C,  
 221 with minimum annual medians recorded in 1999, 2008 and 2000 (15.9, 16.2 and 16.25 °C,  
 222 respectively) and maximum medians recorded in 2006 and 2007, reaching 18.6 °C and 18.5 °C,  
 223 respectively (Fig. S3a). Salinity ranged from 29.6 to 40.8 PSU from 1998 to 2016 with no significant  
 224 trend (Fig. S3b). Minimum median salinity was recorded in 2003 and 2004 (33.8 and 35 PSU,  
 225 respectively) associated with high cumulative rainfall (Fig. 2b). The highest medians were recorded  
 226 in 1998 and 2012 (38.4 and 38.5 PSU, respectively) and were associated with low cumulative rainfall  
 227 (Fig. 2b). After 2005, annual salinity minima were higher than before, linked to the drier conditions  
 228 during this period.

229 Concomitantly with the reduction in phosphorus inputs from the watershed (Table 1), the DIP  
 230 concentrations measured in the water in summer decreased significantly between 1999 and 2016  
 231 (MK p<0.001), with annual summer medians falling from 0.4 to 0.04 µM (-90%) (Fig. 3a). A  
 232 significant decreasing trend was also observed in summer median concentrations of  $\text{NO}_3^- + \text{NO}_2^-$ ,  
 233 which fell from 0.3 to 0.1 µM (-67%) (MK p=0.002) (Fig. 3b). Summer annual median concentrations  
 234 of  $\text{NH}_4^+$ , which ranged from 0.05 to 0.71 µM between 1999 and 2016, also decreased over the period  
 235 (MK p=0.004) (Fig. S4a). Summer annual medians of DIN, TP and of the ratios TN:TP, DIN:TN and  
 236 DIP:TP also decreased significantly between 1999 and 2016. Conversely, trends were not significant  
 237 for TN and for the ratio DIN:DIP (see Fig. S4 for the plots of changes and for MK p-values).

### 238       3.3. Long-term phytoplankton trends

#### 239       3.3.1. Phytoplankton biomass and abundances

240 There was a 60% drop in chlorophyll a concentrations over the study period (MK p=0.002, Fig. 4a),  
 241 with annual concentrations decreasing significantly from 2.43 µg Chl a L<sup>-1</sup> in 1998 to 0.98 µg Chl a L<sup>-1</sup>  
 242 in 2016, according to Theil-Sen's regression line. The lowest annual median value was recorded in  
 243 2005 and the highest in 2003 (1.0 µg Chl a L<sup>-1</sup> and 3.0 µg Chl a L<sup>-1</sup>, respectively).

244 From 1998 to 2016, phytoplankton communities were dominated by diatoms and dinoflagellates,  
 245 which together represented 99.9% of the total abundances. Euglenoidea (*Euglenoidea*, *Eutreptia*  
 246 spp. and *Eutreptiella* spp.) and Dictyophyceae (*Dictyocha* spp.) were sporadically observed over the  
 247 period.

248 The decrease in the phytoplankton biomass was associated with that of diatom abundance. There  
 249 was a significant 60% drop in the annual median concentrations of diatoms from 166 000 cells L<sup>-1</sup> in  
 250 1998 to 56 000 cells L<sup>-1</sup> in 2016, according to Theil-Sen's regression line (MK p<0.001, Fig. 4b). In  
 251 contrast, dinoflagellate abundances revealed no significant monotonic trend over the study period  
 252 (MK p=0.897, Fig 4c), with a median abundance of 4 400 cells L<sup>-1</sup>, varying annually from 2 300 cells  
 253 L<sup>-1</sup> (in year 1999) to 9 800 cells L<sup>-1</sup> (in 2008). The median proportion of the abundance of  
 254 dinoflagellates in the sum of abundances of diatoms was 4.9% (mean=13.6%), highlighting a  
 255 significant increase over the study period (MK p=0.008), with annual medians ranging from 1% in  
 256 1998 and 2000 to 12% in 2015.

#### 257       3.3.2. Changes in the phytoplankton community

258 After exclusion of the 30 TUs whose frequency of occurrence was less than 15%, 26 TUs remained,  
 259 representing 99.9% of total phytoplankton abundance (Table 2).

260 A PCA analysis was performed on these 26 most frequent TUs. The first three axes accounted for  
 261 47.6% of total variability (23.7%, 13% and 10.9% for axis 1, axis 2 and axis 3, respectively). The first  
 262 axis showed a clear temporal structure, in contrast to the earliest and the most recent years (Fig. 5b  
 263 and Fig. S5). This first axis was negatively correlated mainly with the abundances of four diatom taxa  
 264 (group NAVI, *Skeletonema* spp., group *Thalassiosira-Porosira* (THAP) and *Cocconeis* spp.) and  
 265 positively correlated mainly with the abundances of two dinoflagellate taxa (*Gonyaulax* spp. and  
 266 *Prorocentrum* spp.) and three diatom taxa (group THAL, *Cylindrotheca* spp. and group *Pleurosigma*-  
 267 *Gyrosigma* (PLEU)) (Fig. 5a). The second axis was mainly defined by *Nitzschia-Hantzschia* (NITZ)  
 268 and *Gonyaulax* spp. (negative correlations) versus *Rhizosolenia* spp. and *Alexandrium* spp. (positive  
 269 correlations). The third axis was mainly defined by *Dinophysis* spp. and *Grammatophora* spp.  
 270 (positive correlations) versus *Leptocylindrus* spp. and to a lower extent *Nitzschia-Hantzschia* (NITZ)  
 271 (negative correlations) (Fig. S5). Clustering distinguished six groups of years, distributed in  
 272 chronological order from the left to the right along axis 1, highlighting the shift in the composition of  
 273 the phytoplankton community (Fig. 5b and Fig. S5).

274 On the left side of the PCA, the first period was from 1998 to 2004. The year 1999 was isolated in  
 275 the first cluster and was characterised by high annual abundances of the following diatom taxa:  
 276 NAVI, *Thalassiosira-Porosira* (THAP), *Cocconeis* spp., *Skeletonema* spp. and *Licmophora* spp. and  
 277 of the dinoflagellate *Alexandrium* spp. Another cluster grouped the years 1998 and 2000 to 2004 and  
 278 was characterised by particularly high abundances of the diatom taxa *Cerataulina* spp., *Skeletonema*  
 279 spp. and *Thalassiosira-Porosira* (THAP), and of the dinoflagellate group SCRI. During this first  
 280 period, in terms of contributions to total phytoplankton abundances, the two main taxa were (i) from  
 281 1998 to 2002, *Skeletonema* spp. and *Chaetoceros* spp. (on average 44.7% and 30.3% of the total  
 282 abundances, respectively); (ii) in 2003, *Nitzschia-Hantzschia* and *Chaetoceros* spp. (67% and 7.8%,  
 283 respectively); (iii) in 2004, *Leptocylindrus* spp. and *Pseudo-nitzschia* spp. (48.2% and 19.9%,  
 284 respectively) (Fig. 6). The years 2003-2004 marked a shift in the phytoplankton community, after  
 285 which *Skeletonema* spp. ceased to be the dominant taxon, most often replaced by *Chaetoceros* spp.  
 286 or *Pseudo-nitzschia* spp. (except in 2006 and 2012).

287 After this shift, a second period can be seen on the PCA with a cluster grouping the years 2005 to  
 288 2008. This cluster was characterised by high abundances of the diatom taxa *Chaetoceros* spp.,  
 289 *Nitzschia-Hantzschia*, and *Leptocylindrus* spp. and of the dinoflagellate *Gonyaulax* spp. From 2005  
 290 to 2008, the genera *Chaetoceros* spp. and *Pseudo-nitzschia* spp. represented the highest  
 291 contributions to phytoplankton abundances (on average 37.5% and 25.1% of the total abundances,  
 292 respectively) (Fig. 7).

293 The third period was identified by a cluster grouping the years 2009 to 2013. This cluster was  
 294 characterised by high abundances of the diatom taxa *Nitzschia-Hantzschia* (NITZ) and of the  
 295 dinoflagellate taxa *Gonyaulax* spp., *Prorocentrum* spp., *Protoperidinium-Peridinium* (PROP) and  
 296 *Dinophysis* spp.

297 Finally, a fourth period was identified from 2014 to 2016. The years 2014 and 2015 were grouped in  
 298 a cluster characterised by high abundances of the diatom taxa *Cylindrotheca* spp. and *Cocconeis*

299 *spp.* and of the dinoflagellate genus *Dinophysis spp.* The year 2016 was separated from the other  
 300 years by high annual abundances of the diatom taxa *Rhizosolenia spp.*, THAL, *Leptocylindrus spp.*,  
 301 *Dactyliosolen fragilissimus*, *Grammatophora spp.*, *Guinardia spp.* and *Pseudo-nitzschia spp.*

302 During the third and fourth period, the genera *Chaetoceros spp.* and *Pseudo-nitzschia spp.* still  
 303 contributed the most to phytoplankton abundances (on average 37.6% and 25.8% of total  
 304 abundances from 2009 to 2013 and 38% and 33.9% from 2014 to 2016, respectively) (Fig. 7).

### 305 3.3.3. Trends of the dominant taxonomic units

306 According to the modified Sanders index, from 1998 to 2016, the three most dominant taxa were  
 307 diatoms of the genera *Chaetoceros*, *Pseudo-nitzschia* and *Skeletonema* (see Table S1 for details on  
 308 frequency of occurrence, relative abundance and Sanders index of each TU). These three taxa  
 309 cumulated over 73% of total abundance. The dinoflagellates were dominated by *Prorocentrum spp.*,  
 310 the group SCRI and *Gymnodinium spp.* according to the modified Sanders index. These three  
 311 dinoflagellate taxa cumulated only 1.5% of total abundance.

312 Of the three dominant diatom taxa, only the abundances of *Skeletonema spp.* decreased  
 313 significantly over the study period (MK p<0.001, Fig. 6c). Sen's regression line revealed a 97%  
 314 decrease, from 4 000 cells L<sup>-1</sup> in 1998 to 100 cells L<sup>-1</sup> in 2016. A maximum annual median of 65 700  
 315 cells L<sup>-1</sup> of *Skeletonema spp.* was reached in 2000. The annual medians of *Chaetoceros*  
 316 abundances varied from 5 300 cells L<sup>-1</sup> to 73 300 cells L<sup>-1</sup> (in 2013 and 1999, respectively), with no  
 317 significant monotonic trend (Fig. 6a). The abundances of *Pseudo-nitzschia spp.* varied from 1 100  
 318 cells L<sup>-1</sup> to 9 300 cells L<sup>-1</sup> (annual medians of 2001 and 2007, respectively) with no significant trend  
 319 (Fig. 6b). There was a significant decrease in another diatom taxon between 1998 and 2016, the  
 320 abundance of group NAVI (MK p<0.001) dropped by 86% (from 700 cells L<sup>-1</sup> to 100 cells L<sup>-1</sup>,  
 321 according to Theil-Sen's regression line) (see Table S1 for MK-test results). In contrast, the  
 322 abundances of the genus *Licmophora* and the group THAL increased significantly (MK p=0.04 and  
 323 p=0.03, respectively) during the study period. However, their median abundance remained close to  
 324 the detection limit (from 100 cells L<sup>-1</sup> to 140 cells L<sup>-1</sup> for *Licmophora* and from 170 cells L<sup>-1</sup> to 360  
 325 cells L<sup>-1</sup> for the group THAL).

326 The genus *Prorocentrum*, the dominant dinoflagellate according to the modified Sander's index, was  
 327 characterised by a significant increase in median abundance (MK p=0.03, Fig. 6d), from 200 cells L<sup>-1</sup>  
 328 in 1998 to 500 cells L<sup>-1</sup> in 2016 (+150%). The abundance of the two other dominant dinoflagellate  
 329 taxa varied throughout the study period, but no significant trend was identified, their annual medians  
 330 ranging respectively from 400 to 2 000 cells L<sup>-1</sup> for the group SCRI (in 2009-2016 and 2001,  
 331 respectively) and from 170 to 3 400 cells L<sup>-1</sup> for *Gymnodinium spp.* (in 1999-2002 and 2006,  
 332 respectively) (Fig. 6e and 6f).

## 333 4. Discussion

### 334 4.1. Shift in the phytoplankton community during oligotrophication

#### 335 4.1.1. Decrease in chlorophyll a biomass and diatom abundance

336 Remediation actions in the watershed of an originally eutrophic lagoon over a period of more than 40  
 337 years led to a significant reduction in nutrient inputs (La Jeunesse et al. 2002). Previous studies  
 338 showed that the effect of these actions was a decrease in nutrient concentrations in the water

339 column of Thau lagoon from the 1970s to the early 2000s (Fig. S2, Collos et al. 2009; Gowen et al.  
 340 2015). Our study, based on the analysis of 19-year monitoring time-series revealed that the long-  
 341 term decrease in nutrient concentrations is continuing. The significant decrease in nutrients in the  
 342 water column led to a gradual decrease in chlorophyll a biomass and in diatom abundances from  
 343 1998 to 2016. Only a few long-term studies have been conducted on the recovery process of coastal  
 344 lagoons (Leruste et al. 2016; Derolez et al. 2019; Le Fur et al. 2019). These studies emphasised  
 345 rapid shifts in communities of primary producers after mitigation actions, in agreement with the order  
 346 of magnitude and with the time-lags reported in estuaries (Greening and Janicki 2006; Lie et al.  
 347 2011; Boynton et al. 2013). What is remarkable about our results is that the recovery process which  
 348 started for 40 years ago is still continuing. Thau lagoon, which was eutrophic in the 1970s, shifted to  
 349 a moderately eutrophic state in the 1990s and to a mesotrophic state in the 2000s (Collos et al.  
 350 2009; Souchu et al. 2010; Gowen et al. 2015). Such long-term observations of oligotrophication are  
 351 only available for temperate lakes, where there is evidence for gradual decreases in phytoplankton  
 352 biomass and community shifts mainly related to phosphorus limitation (Anneville et al. 2005; Ibelings  
 353 et al. 2007; Jeppesen et al. 2007). Monitoring of nutrients in Thau lagoon in the 1990s showed that P  
 354 and Si were not the main limiting nutrients and that N-limitation occurred in spring and summer  
 355 (Souchu et al. 1998; Collos et al. 2009). More recent data obtained from monitoring in the 2010s  
 356 revealed that Si is still not limiting ( $\text{SiOH}_4 > 2 \mu\text{M}$ , REPHY 2017-2018) but that N and P co-limitation  
 357 may now occur in summer and autumn. A similar shift from N-limitation to P-limitation or N-P co-  
 358 limitation has already been observed in coastal ecosystems during oligotrophication (Philippart et al.  
 359 2007; Souchu et al. 2010; Paerl et al. 2014), and can favour shifts in the phytoplankton community  
 360 (Collos et al. 2009).

#### 361        4.1.2. Shift in phytoplankton taxonomic composition

362 In Thau lagoon, the response of the phytoplankton community to oligotrophication in the period  
 363 1998-2016 mainly concerned diatoms, which was the main group of microphytoplankton and largely  
 364 exceeded dinoflagellate abundance. Among the dominant diatom taxa, a shift from *Skeletonema*-  
 365 *Chaetoceros* to *Chaetoceros-Pseudo-nitzschia* dominance was observed over the study period.  
 366 *Skeletonema* spp., the main diatom genus in terms of contribution to total abundances over the  
 367 period, showed a strong decreasing trend, confirming observations made on *S. costatum* during the  
 368 early stages of oligotrophication in Thau lagoon (1998-2005, Collos et al. 2009).

369 In coastal temperate waters, *Skeletonema* spp. represents a high proportion of the phytoplankton  
 370 community, particularly in winter and spring (Borkman and Smayda 2009; Hernández Fariñas et al.  
 371 2015). In French coastal waters, this chain-forming diatom mainly occupies an ecological niche with  
 372 low light, high nutrient concentrations and cool environmental conditions, and can be considered as  
 373 a generalist species due to its high tolerance to environmental conditions (Hernández Fariñas et al.  
 374 2015). In Thau lagoon, under the eutrophic conditions which prevailed in the 1970s and 1980s,  
 375 diatom blooms mainly occurred after episodic rainfall events transported dissolved inorganic nitrogen  
 376 and phosphorus (DIN and DIP) from the watershed (Jarry et al. 1990; Collos et al. 2014). Fast  
 377 growing diatoms such as *Skeletonema* spp. and *Chaetoceros* spp. were well adapted to this nutrient  
 378 regime because they are both known to process nutrients rapidly into new biomass (Collos, 1986;  
 379 Collos et al. 2003). However, in contrast to *Skeletonema* spp., *Chaetoceros* abundances showed no  
 380 significant trend over the 19-year time-series. These two genera are characterised by different

381 nitrogen uptake kinetics and ability to accumulate internal nitrate pools (Collos et al. 1997). In  
 382 contrast to *Skeletonema*, *Chaetoceros* does not accumulate large internal nitrate pools but has a low  
 383 half-saturation constant K<sub>s</sub> (0.33-0.36 µM) in situations with very low nitrate levels (Collos et al.  
 384 1997), suggesting that this genus is better adapted than *Skeletonema* to the low nitrogen level which  
 385 prevail during oligotrophication. In contrast to DIN and DIP, silicate concentrations appeared to have  
 386 remained unchanged over the time-series, indicating that the decrease in diatom abundance was not  
 387 linked to Si limitation (Souchu et al. 2010; Gowen et al. 2015).

388 *Pseudo-nitzschia* spp. did not display any significant monotonic trends over the study period.  
 389 However, this taxon became the second major contributor to total phytoplankton abundance starting  
 390 in 2005. Long-term trends of phytoplankton communities in French Atlantic coastal waters revealed  
 391 an increase in the abundance of *Pseudo-nitzschia* over the period 1992-2011 and could have been  
 392 favoured by increasing salinity and temperature (Hernandez-Farinés et al. 2014). Thus, along the  
 393 French Atlantic coast, the ecological niche of *Pseudo-nitzschia* was characterised by high irradiance,  
 394 and high water temperatures and salinity levels, but low nutrient concentrations and turbidity  
 395 (Husson et al. 2016). *Pseudo-nitzschia* has also been associated with decreased nutrient  
 396 concentrations and high salinity in Old Tampa Bay (Florida) (Corcoran et al. 2017). In the Ebro Delta  
 397 (NW Mediterranean Sea), high molecular weight dissolved organic matter enrichment has been  
 398 shown to contribute positively to the growth of *Pseudo-nitzschia* species in low inorganic N  
 399 environments (Loureiro et al. 2009), highlighting the potential role of organic nutrients in the  
 400 development of this genus.

401 In our study, the median proportion of dinoflagellates relative to diatoms increased significantly over  
 402 the period 1998-2016, although total abundances continued to be dominated by diatoms. In contrast  
 403 to chlorophyll a concentrations and diatom abundance, dinoflagellate abundance did not decrease  
 404 significantly. In coastal waters, some authors have reported that, under oligotrophication,  
 405 phytoplankton communities can shift from dominance of fast-growing diatoms to that of  
 406 dinoflagellates (Yamamoto 2003). This shift could be associated with some dinoflagellates with low  
 407 growth and that are usually mixotrophic and can consequently use dissolved organic phosphorus  
 408 (DOP) instead of DIP (e.g. *Alexandrium catenella/tamarensense*) (Yamamoto 2003; Collos et al. 2009;  
 409 Collos et al. 2014; Gowen et al. 2015). In Thau lagoon, a dichotomy has been observed in the  
 410 environmental factors influencing diatom and dinoflagellate blooms (Collos et al. 2014). Diatom  
 411 blooms are consistent with traditional patterns of phytoplankton blooms associated with episodic  
 412 rainfall events leading to nutrient inputs, whereas dinoflagellate blooms are influenced by water  
 413 temperature and can occur even in the absence of rainfall (Collos et al. 2014). A study of Thau  
 414 phytoplankton time-series that ended in 2009, suggested that the balance between the two lifeforms  
 415 diatom/dinoflagellate (characterised by the “Plankton Index for phytoplankton” (Plp)) responded to  
 416 changes in DIP in the water column, but identified no long-term trend in the Plp related to  
 417 oligotrophication (Gowen et al. 2015). In our study, which included an additional seven years of data,  
 418 among the community changes we identified, a transient change in favour of a community  
 419 characterised by higher dinoflagellate concentrations (*Gonyaulax*, *Prorocentrum*, *Protoperidinium* and  
 420 *Dinophysis* genera) was observed in the period 2009-2013. These dinoflagellate genera are not  
 421 strictly autotrophic and could have ecological advantages over other phytoplankton groups due to  
 422 their ability to use dissolved organic matter (DOM) during oligotrophication. Only the dinoflagellate  
 423 taxa *Prorocentrum* spp. increased significantly during the study period. However, the concentrations

424 observed in Thau lagoon were often close to the detection limit and much lower than those  
 425 measured in other ecosystems ( $10^2$  cell L $^{-1}$  in Thau vs  $10^5$  and  $10^6$  cell L $^{-1}$  in the Baltic Sea and  
 426 Biguglia lagoon) (Olenina et al. 2010; Cecchi et al. 2016).

427 We identified no significant monotonic trends in the abundances of the three harmful species  
 428 observed in Thau lagoon (*Pseudo-nitzschia*, *Alexandrium* spp. and *Dinophysis* spp.). Although  
 429 concentrations of the diatom genus *Pseudo-nitzschia* have regularly exceeded sanitary alert  
 430 thresholds ( $300\,000$  cell L $^{-1}$ ), no ASP toxicity was observed in shellfish during the study period (Bec  
 431 et al. 2018). After its appearance in Thau lagoon in the late 1990s, the dinoflagellate *Alexandrium*  
 432 *catenella* bloomed often, leading to frequent PSP toxicity events among shellfish exploited in the  
 433 early 2000s (Collos et al. 2009; Gowen et al. 2015). PSP concentrations in shellfish ceased to  
 434 exceed sanitary thresholds between 2008 and 2014, but toxic events associated with *A. catenella*  
 435 blooms have re-emerged in recent years (2015-2016-2017, Bec et al. 2018). *Dinophysis* spp.  
 436 increased transiently in the period 2009-2013 but only led to DSP toxicity in shellfish twice (2002 and  
 437 2014) in our study period. Hence, these observations only partially support hypotheses based on  
 438 previous studies of Thau lagoon or other coastal ecosystems which linked oligotrophication with an  
 439 increase in potentially toxic phytoplankton species (Yamamoto 2003; Collos et al. 2009; Glibert  
 440 2016). Other authors produced evidence showing that in nutrient depleted coastal ecosystems,  
 441 excess light could favour the production of toxins by *Pseudo-nitzschia* (Terseleer et al. 2013) and  
 442 that higher salinity could increase its allelopathic effects on cryptophytes and diatoms (Van  
 443 Meerssche et al. 2018).

#### 444       **4.2. Long-term evolution of phytoplankton communities and links with bottom-up and** 445       **top-down controls**

446 When studying long-term monitoring time-series of phytoplankton communities, the effects of local  
 447 factors, such as changing anthropogenic nutrient inputs, are difficult to distinguish from the effects of  
 448 long-term climate variation (Borkman and Smayda 2009; Paerl et al. 2014). During our 19-year study  
 449 period (1998-2016), we found no evidence of significant trends in annual average water temperature  
 450 or salinity. However, when considering longer meteorological time-series (1998-2016), we found an  
 451 increase in mean air temperature and a decrease in the occurrence of wet years. These trends were  
 452 even more pronounced when we looked at the longer-term series (1970-2018, Fig. S1), and they are  
 453 in accordance with the tendencies of climate change process demonstrated by regional  
 454 meteorological experts (Jouzel et al. 2014). We hypothesise that the shift in phytoplankton  
 455 communities observed in this Mediterranean lagoon could be the result of the effects of a reduction  
 456 in nutrient inputs combined with climatic-related variables. The mixture of warming and  
 457 oligotrophication has led to shifts in freshwater phytoplankton communities (Pomati et al. 2012;  
 458 Verbeek et al. 2018). These authors showed that biomass initially increased with warming but  
 459 decreased with nutrient depletion. They also highlighted the fact that warming reduced phytoplankton  
 460 richness and evenness, whereas the reduction in nutrient inputs at ambient temperature had positive  
 461 effects on diversity. Other authors have demonstrated in a marine diatom species that nutrient  
 462 deprivation is likely to exacerbate the effects of environmental warming by decreasing its tolerance of  
 463 extreme temperatures (Thomas et al. 2017). A long-term study of the phytoplankton community  
 464 along the French Atlantic coast linked the increase in the proportion of dinoflagellates relative to

465 diatoms with a decrease in nutrient concentrations, an increasing trend in salinity, and changes in  
 466 the Atlantic Multidecadal Oscillation index (Hernandez-Farinás et al. 2014).

467 We summarised the main changes in phytoplankton in Thau lagoon by re-examining the revisited  
 468 "Margalef Mandala" proposed by Glibert (2016) (Fig. 8), and representing the bottom-up control (Fig.  
 469 8, central square), their potential impact on the main phytoplankton community traits (Fig. 8, middle  
 470 square) and the possible links with competition and top-down control (Fig. 8, outer square). The main  
 471 change in the environmental bottom-up drivers observed in Thau lagoon during the study period was  
 472 a decrease in nutrient inputs from the watershed, which was more significant for phosphorus than for  
 473 nitrogen. This trend led to an increase in the N:P supply ratio (Fig. 8, axis 1). This increase was  
 474 associated with an increase in the TN:TP ratio in the water column, and reflects the decreasing  
 475 influence of sewage inputs on the total nutrient load, which has already been observed in French  
 476 Mediterranean lagoons (Souchu et al. 2010; Derolez et al. 2019). The decrease in the concentrations  
 477 of DIN and DIP observed in the water column increased the contribution of organic forms to total  
 478 nutrients (axis 2) (decrease in summer DIP:TP and DIN:TN). In the long term, climate related factors  
 479 highlighted an increase in temperature and a decrease in total rainfall. A decrease in total rainfall can  
 480 increase salinity (axis 3) and reduce water turbulence (axis 4) due to less mixing of the water  
 481 column.

482 In our study, the main shifts observed in the phytoplankton composition (2003-2004 and 2005-2008)  
 483 were concomitant with two major summer anoxia events associated with heatwaves (Minghelli-  
 484 Roman et al. 2011), which could have heightened the effect of oligotrophication. In Mediterranean  
 485 lagoons, the temperature increase during summer anoxic crises has already been associated with  
 486 phytoplankton blooms of *Chaetoceros*, *Nitzschia* and *Thalassionema* genera and with an increase in  
 487 chlorophyll a biomass (Souchu et al. 1998). Indeed, high temperatures and anoxic conditions have a  
 488 significant effect on benthic fluxes of  $\text{NH}_4^+$  and DIP, which in turn support phytoplankton blooms  
 489 (Souchu et al. 1998; Zilius et al. 2014). Conversely, other authors have produced evidence for an  
 490 indirect positive correlation between dinoflagellate blooms and a drop in water temperature, which  
 491 they assumed to represent turbulence (Collos et al. 2014). The same authors reported that the  
 492 appearance of both picocyanobacteria (mostly *Synechococcus*) and the toxic dinoflagellate  
 493 *Alexandrium catenella* in Thau lagoon appeared to be related to reduced nutrient loading and to the  
 494 increase in water temperature (Collos et al. 2009).

495 Like Glibert (2016), we hypothesise that the effects of the bottom-up factors related to climate and  
 496 nutrient inputs led to a shift from new production to regenerated production of phytoplankton (axis  
 497 13). In terms of functional traits, this shift has been accompanied by a decrease in cell size (axis 5),  
 498 and in the growth rate (axis 6), and a shift from taxa with an r- ecological strategy (typically diatoms  
 499 according to Glibert (2016)) to taxa with a K- ecological strategy (typically dinoflagellates and  
 500 picophytoplankton such as *Synechococcus* according to Glibert (2016)) (axis 7) and from autotrophy  
 501 to mixotrophy (axis 8). These trends are consistent with our observations and with those of previous  
 502 studies of Thau lagoon (Bec et al. 2005; Collos et al. 2009) and of other coastal ecosystems (Bec et  
 503 al. 2011; Glibert 2016; Pulina et al. 2018), which produced evidence for a change among the  
 504 microphytoplankton community from large diatom dominance to a larger proportion of dinoflagellates,  
 505 and among the pico- and nano-phytoplankton community, a shift from the dominance of autotrophic  
 506 picoeukaryotes to that of picocyanobacteria such as *Synechococcus*. In the oligotrophication context

507 of Thau lagoon, combined with the climate scenarios predicting higher temperatures, particularly in  
 508 Mediterranean regions (IPCC, 2013), the increase in regenerated production, especially of  
 509 picophytoplankton and dinoflagellates is expected to continue (Herrmann et al. 2014).

510 In coastal lagoons, sediments play a key role in nutrient budgets through storage and recycling  
 511 processes (Giordani et al. 2008; Zaldívar et al. 2008). During oligotrophication, the continuing  
 512 nutrient fluxes from the sediment are an internal load that may support phytoplankton or macroalgal  
 513 growth, thus delaying the recovery process (Viaroli et al. 2008; Le Fur et al. 2019). This release of  
 514 nutrients from the sediment into Thau lagoon in summer has been shown to be the main source of  
 515 nitrogen and phosphorus in the water column, especially during anoxia events (Souchu et al. 1998).  
 516 The impacts the sediment has on phytoplankton communities, as can be seen in Fig. 8 (axis 9), are  
 517 expected to increase during oligotrophication and with the predicted climate change.  
 518 Oligotrophication also leads to a shift from a phytoplankton-dominated state to a macroalgae and  
 519 seagrass dominated state (Souchu et al. 2010; Bec et al. 2011; Derolez et al. 2019; Leruste et al.  
 520 2016; Le Fur et al. 2019), in turn leading to competition for nutrients in the water column (Fig. 8, axis  
 521 10). Further analyses including pico- and nano-phytoplankton and macrophyte communities and  
 522 using functional approaches would help identify the changes in the function of primary production  
 523 during the different trophic states of the ecosystem (Cibic et al. 2018; Leruste et al. 2018).

524 In addition to the possible bottom-up effects of changes in nutrient concentrations and climate-  
 525 related variables, top-down control of filter-feeding bivalves (Fig. 8, axis 11) may affect both  
 526 phytoplankton production and community structure (McKinsey et al. 2006; Filgueira et al. 2015). In  
 527 estuarine and coastal areas, the feeding activity of cultivated shellfish can deplete the phytoplankton  
 528 populations and their excrements may favour the production of smaller phytoplankton cells (Vaquer  
 529 et al. 1996; Abbiati et al. 2010; Souchu et al. 2001). Moreover, in ecosystems used to rear filter-  
 530 feeding bivalves, like Thau lagoon, chlorophyll a depletion has been demonstrated in shellfish farms  
 531 (Jarry et al. 1990; Souchu et al. 2001). Conversely, since microphytoplankton primary producers,  
 532 and particularly diatoms, have been identified as the main food sources for bivalve suspension  
 533 feeders (Dupuy et al. 2000; Pernet et al. 2012), in the long term, oligotrophication and its  
 534 consequences for the phytoplankton community it would be expected to reduce shellfish production,  
 535 as suggested by authors on the Mar Piccolo of Taranto in Italy (Caroppo et al. 2015; Karuza et al.  
 536 2015). Among the possible bottom-up effects of the oligotrophication process, some authors have  
 537 identified cascading alterations to the structure of the food web (Fig. 8, axis 12), from a standard  
 538 productive food web to poor fish production with large quantities of inedible jellyfish (Yamamoto  
 539 2003), which are frequently observed in Thau lagoon (Marques et al. 2016).

540 In parallel with the recovery of the Thau lagoon ecosystem, fishermen and shellfish farmers have  
 541 been facing economic difficulties and they worry about the potential limiting carrying capacity of the  
 542 ecosystem. The issue of the possibility of reaching the limit of the carrying capacity of Thau lagoon  
 543 ecosystems needs to be addressed, as well as associated impact on oyster farming and fisheries. In  
 544 order to address the problem of finding a trade-off between uses, ecosystem services and the  
 545 maintenance of biodiversity and ecological functions, there is a need to use ecosystem-based  
 546 models to help stakeholders make appropriate decisions (Philippart et al. 2007). Such models have  
 547 been developed to guide the management of several coastal areas, through the use of ecological  
 548 carrying capacity or GIS-based mapping tools (McKinsey et al. 2006; Guyondet et al. 2014; Paerl et

549 al. 2014). The use of these kinds of tools, integrated in a socio-ecosystem based approach, is  
550 indispensable: (i) to improve our understanding of the functioning of the systems, (ii) to compare  
551 management scenarios and climate change scenarios, (iii) to facilitate dialogue among stakeholders  
552 and hence to contribute to decision-making on coastal areas.

553

554

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564

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869 **Fig. 1.** Location of Thau lagoon and of the phytoplankton and hydrological monitoring stations: REPHY station  
 870 (phytoplankton); ZA station and TES station (nutrients); Sète meteorological station. Shellfish farming structures  
 871 are located along the northern shore of the water body.

872 **Fig. 2.** Comparison of the average level (1970-2016) of (a) annual mean air temperature ( $^{\circ}\text{C}$ ) and (b) annual  
 873 cumulative rainfall levels ( $\text{mm y}^{-1}$ ), monitored at Sète meteorological station from 1998 to 2016 (data: Météo-  
 874 France).

875 **Fig. 3.** Monthly concentrations (dots) of summer levels (June to August) of (a) DIP ( $\mu\text{M}$ ) and (b)  $\text{NO}_3^- + \text{NO}_2^-$  ( $\mu\text{M}$ )  
 876 in the water column from 1999 to 2016 at TES station.

877 **Fig. 4.** Box-and-whisker plots of annual variations in chlorophyll a concentrations (a), diatom (b) and  
 878 dinoflagellate (c) abundances between 1998 and 2016 at REPHY station. Orange dashes represent annual  
 879 medians. Theil-Sen's slope is represented by a green line when MK is significant (i.e. p-value < 0.05).

880 **Figure 5.** Results of PCA of phytoplankton community data from Bouzigues station in Thau lagoon from 1998 to  
 881 2016. (a) First and second axes for taxonomic units (dinoflagellates in orange, diatoms in green). (b) Years on  
 882 the plane defined by the first and second axes and clusters highlighted by clustering. The plot shows 23.7% and  
 883 13% of the variance on the first and second axes, respectively. The codes for the taxonomic units are detailed in  
 884 Table 2.

885 **Fig. 6.** Box-and-whisker plots of the variation in annual abundance of the three dominant diatom taxonomic  
 886 units (top panel: (a) *Chaetoceros spp.*, (b) *Pseudo-nitzschia spp.* and (c) *Skeletonema spp.*) and the three  
 887 dominant dinoflagellate taxonomic units (bottom panel: (c) *Prorocentrum spp.*, (d) SCRI - *Scrippsiella spp.* +  
 888 *Ensicalifera spp.* + *Pentapharsodinium spp.* + *Bysmatrum spp.* - and (e) *Gymnodinium spp.*) between 1998 and  
 889 2016 at REPHY station. Orange dashes represent annual medians. Theil-Sen's slope is represented by a green  
 890 line when the MK p-value is significant. Grey lines represent the detection limit ( $10^2 \text{ cells L}^{-1}$ ).

891 **Fig. 7.** Annual mean contribution of the main phytoplankton taxonomic units to total phytoplankton abundances  
 892 between 1998 and 2016 at REPHY station. The codes for the taxonomic units are detailed in Table 1.

893 **Fig. 8.** Conceptual scheme representing the phytoplankton community in Thau lagoon according to the revised  
 894 phytoplankton Mandala proposed by Glibert (2016). Variables are ordered according to 3 categories  
 895 represented in 3 squares: bottom-up control (central square), the main phytoplankton community traits (middle  
 896 square) and competition and top-down control (outer square). Variables are depicted along 12 axes (identified  
 897 by the small numbers in the corner of each axis). The axes include: (1) the N:P supply ratio; (2) the contribution  
 898 of organic forms to total nutrients in the water column; (3) climate-related variables: temperature and salinity; (4)  
 899 water turbulence; (5) cell size; (6) growth rate; (7) ecological strategy along the r to K spectrum (8) tendency to  
 900 be autotrophic vs mixotrophic; (9) impact of sediment; (10) competition with macrophytes; (11) potential impact  
 901 of shellfish farming; (12) potential impact of trophic web/grazing. The oligotrophication process is represented by  
 902 changes in phytoplankton biomass and mirrors the shift from new production to regenerated production. Note  
 903 that all the scales are relative and no dimensions are implied; (13) propensity for phytoplankton production to  
 904 cycle through regenerated production or to constitute new production. All responses within relative space are  
 905 representative and are not meant to imply that all species or individuals in a given response zone will respond  
 906 similarly.

907 **Table 1.** Nitrogen and phosphorus inputs ( $\text{t y}^{-1}$ ) from the Thau lagoon watershed from 1990 to 2016 (data from  
 908 La Jeunesse 2001 (1) and Bec et al. 2018 (2)), and associated N:P ratios (by moles).

Period	N inputs from the watershed (t y <sup>-1</sup> )	P inputs from the watershed (t y <sup>-1</sup> )	N:P ratio of inputs from the watershed (by moles)
1990s <sup>(1)</sup>	236.0	65.0	8.0
2009 <sup>(2)</sup>	109.7	39.7	6.1
2016 <sup>(2)</sup>	122.0	12.4	21.8

909 **Table 2.** List and codes of the 26 most frequent taxonomic units of diatoms (in green) and dinoflagellates (in  
910 orange) observed from 1998 to 2016 at REPHY station. Groups with more than 2 genera are referred to by their  
911 code in the text.

Group	Taxonomic unit	Code
<b>Diatoms</b>	<i>Cerataulina</i> spp. <i>Chaetoceros</i> spp. <i>Coccconeis</i> spp. <i>Cylindrotheca</i> spp. <i>Dactyliosolen fragilissimus</i> <i>Grammatophora</i> spp. <i>Guinardia</i> spp. <i>Leptocylindrus</i> spp. <i>Licmophora</i> spp. <i>Navicula</i> spp., <i>Fallacia</i> spp., <i>Haslea</i> spp., <i>Lyrella</i> spp., <i>Petroneis</i> spp. <i>Nitzschia</i> spp., <i>Hantzschia</i> spp. <i>Pleurosigma</i> spp., <i>Gyrosigma</i> spp. <i>Pseudo-Nitzschia</i> spp. <i>Rhizosolenia</i> spp. <i>Skeletonema</i> spp. <i>Thalassionema</i> spp., <i>Thalassiothrix</i> spp., <i>Lioloma</i> spp. <i>Thalassiosira</i> spp., <i>Porosira</i> spp.	CERA CHAE COCC CYLI DACT GRAM GUIN LEPT LICM NAVI NITZ PLEU PSEU RHIZ SKEL THAL THAP
<b>Dinoflagellates</b>	<i>Alexandrium</i> spp. <i>Dinophysis</i> spp. <i>Gonyaulax</i> spp. <i>Gymnodinium</i> spp. <i>Gyrodinium</i> spp. <i>Heterocapsa</i> spp. <i>Prorocentrum</i> spp. <i>Protoperidinium</i> spp., <i>Peridinium</i> spp. <i>Scrippsiella</i> spp., <i>Ensicalifera</i> spp., <i>Pentapharsodinium</i> spp., <i>Bysmatrum</i> spp.	ALEX DINO GONY GYMN GYRO HETE PROR PROP SCRI

912  
913

914 **Supplementary material**

915 **Table S1.** List of the 56 taxonomic units (TU) of diatoms and dinoflagellates observed from 1998 to 2016 at  
 916 REPHY station. Frequency of occurrence and the contribution to the total abundance over the study period (in  
 917 %), order according to the Sanders index and codes of each TU. Results of the Mann-Kendall test (MK test): the  
 918 p-value is given for phytoplankton time-series with 8 or more annual medians. When  $p < 0.05$ , Theil-Sen's slope  
 919 and 1998 and 2016 values according to Theil-Sen's regression line are given. Lines in bold correspond to the 26  
 920 most frequent TUs (frequency of occurrence > 15%).

Group	Taxonomic unit	Code	Occurrence frequency (%)	Contribution to total abundance (%)	Order according to the modified Sanders index	MK-tests		
						p-value	Theil-Sen's slope	1998–2016 values from Theil-Sen's regression line ( $\log_{10}$ )
<b>Diatoms</b>	<i>Achnanthes</i> spp.	ACHN	0.8	0.0007	46	-	-	-
	<i>Asterionella</i> spp., <i>Asterionellopsis</i> spp., <i>Asteroplanus</i> spp.	ASTE	11.4	0.7	25	-	-	-
	<i>Bacteriadrum</i> spp.	BACT	4.9	0.05	27	-	-	-
	<i>Biddulphia</i> spp.	BIDD	0.6	0.0004	45	-	-	-
	<i>Cerataulina</i> spp.	CERA	31.6	0.2	23	0.96	-	-
	<i>Chaetoceros</i> spp.	CHAE	81	25	1	0.08	-	-
	<i>Cocconeis</i> spp.	COCC	44.7	8.8	10	0.11	-	-
	<i>Coscinodiscus</i> spp., <i>Stellarima</i> spp.	COSC	7.8	0.005	36	-	-	-
	<i>Cylindrotheca</i> spp.	CYLI	17	4.9	5	-	-	-
	<i>Dactyliosolen fragilissimus</i>	DACT	27.4	0.5	17	0.34	-	-
	<i>Diploneis</i> spp.	DIPL	0.4	0.0003	47	-	-	-
	<i>Ditylum</i> spp.	DITY	6.4	0.035	29	-	-	-
	<i>Eucampia</i> spp., <i>Climacodium</i> spp.	EUCA	3.9	0.005	38	-	-	-
	<i>Grammatophora</i> spp.	GRAM	21.4	0.039	24	1.00	-	-
	<i>Guinardia</i> spp.	GUIN	19	0.3	21	-	-	-
	<i>Hemiaulus</i> spp.	HEMI	12.9	0.05	30	-	-	-
	<i>Lauderia</i> spp., <i>Detonula</i> spp.	LAUD	4.7	0.02	26	-	-	-
	<i>Leptocylindrus</i> spp.	LEPT	54.7	3.7	4	0.49	-	-
	<i>Licmophora</i> spp.	LICM	40.2	0.03	18	0.04	0.01	1.99 – 2.15
	<i>Melosira</i> spp.	MELO	3.3	0.01	28	-	-	-
	<i>Navicula</i> spp., <i>Fallacia</i> spp., <i>Haslea</i> spp., <i>Lyrella</i> spp., <i>Petroneis</i> spp.	NAVI	66.1	0.1	11	<0.001	-0.04	2.86 – 2.09
	<i>Nitzschia</i> spp., <i>Hantzschia</i> spp.	NITZ	71	10.3	6	0.34	-	-
	<i>Odontella</i> spp.	ODON	0.2	0.00007	56	-	-	-
	<i>Pleurosigma</i> spp., <i>Gyrosigma</i> spp., <i>Pseudo-Nitzschia</i> spp.	PLEU	18.2	0.009	31	-	-	-
	<i>Rhizosolenia</i> spp.	PSEU	81.4	20.4	2	0.76	-	-
	<i>Skeletonema</i> spp.	RHIZ	42.5	1	16	0.73	-	-
	<i>Striatella</i> spp.	SKEL	50	27.9	3	<0.001	-0.09	3.61 – 2.02
	<i>Thalassionema</i> spp., <i>Thalassiothrix</i> spp., <i>Lioloma</i> spp., <i>Thalassiosira</i> spp., <i>Porosira</i> spp.	STRIA	4.3	0.002	37	-	-	-
		THAL	50.8	1.3	9	0.03	0.02	2.24 – 2.56
		THAP	20	0.7	13	0.71	-	-

<b>Dinoflagellates</b>								
<i>Akashiwo sanguinea</i>	AKAS	1.8	0.0008	40	-	-	-	
<i>Alexandrium spp.</i>	ALEX	20.7	1.5	15	<b>0.70</b>	-	-	
<i>Ceratium spp.</i>	CERA	0.2	0.0001	55	-	-	-	
<i>Cochlodinium spp.</i>	COCH	0.6	0.001	49	-	-	-	
<i>Dinophysis spp.</i>	DINO	18.2	<b>0.009</b>	33	-	-	-	
<i>Diplopsalis spp.,</i> <i>Diplopelta spp.,</i> <i>Diplopsalopsis spp.,</i> <i>Preperidinium spp.,</i> <i>Oblea spp.</i>	DIPL	0.9	0.002	44	-	-	-	
<i>Gonyaulax spp.</i>	GONY	19.6	0.3	22	-	-	-	
<i>Gymnodinium spp.</i>	GYMN	72.9	0.4	12	<b>0.63</b>	-	-	
<i>Gyrodinium spp.</i>	GYRO	49.6	<b>0.07</b>	19	<b>0.72</b>	-	-	
<i>Hermesinum spp.</i>	HERM	1.8	0.003	43	-	-	-	
<i>Heterocapsa spp.</i>	HETE	15.9	0.2	14	-	-	-	
<i>Karenia mikimotoi</i>	KARE	2.7	0.004	42	-	-	-	
<i>Katodinium spp.</i>	KATO	12.5	0.01	32	-	-	-	
<i>Kryptoperidinium foliaceum</i>	KRYP	0.2	0.0006	54	-	-	-	
<i>Lingulodinium spp.</i>	LING	0.4	0.0003	53	-	-	-	
<i>Neoceratium spp.</i>	NEOC	5.9	0.002	41	-	-	-	
<i>Oxyrrhis marina</i>	OXYR	0.2	0.00007	52	-	-	-	
<i>Oxytoxum spp.</i>	OXYT	12.7	0.01	34	-	-	-	
<i>Phalacroma spp.</i>	PHAL	2.3	0.001	39	-	-	-	
<i>Podolampas spp.</i>	PODO	0.2	0.00004	51	-	-	-	
<i>Polykrikos spp.</i>	POLY	6.1	0.008	35	-	-	-	
<i>Prorocentrum spp.</i>	PROR	61.2	<b>0.8</b>	7	<b>0.03</b>	<b>0.02</b>	<b>2.27 – 2.73</b>	
<i>Protoceratium reticulatum</i>	PROT	0.2	0.0001	50	-	-	-	
<i>Protoperidinium spp., Peridinium spp.</i>	PROP	62.7	<b>0.15</b>	20	<b>0.26</b>	-	-	
<i>Scripsiella spp.,</i> <i>Ensiculifera spp.,</i> <i>Pentapharsodinium spp., Bysmatrum spp.</i>	SCRI	81.8	0.3	8	<b>0.28</b>	-	-	
<i>Triplos spp.</i>	TRIP	1.9	0.0004	48	-	-	-	

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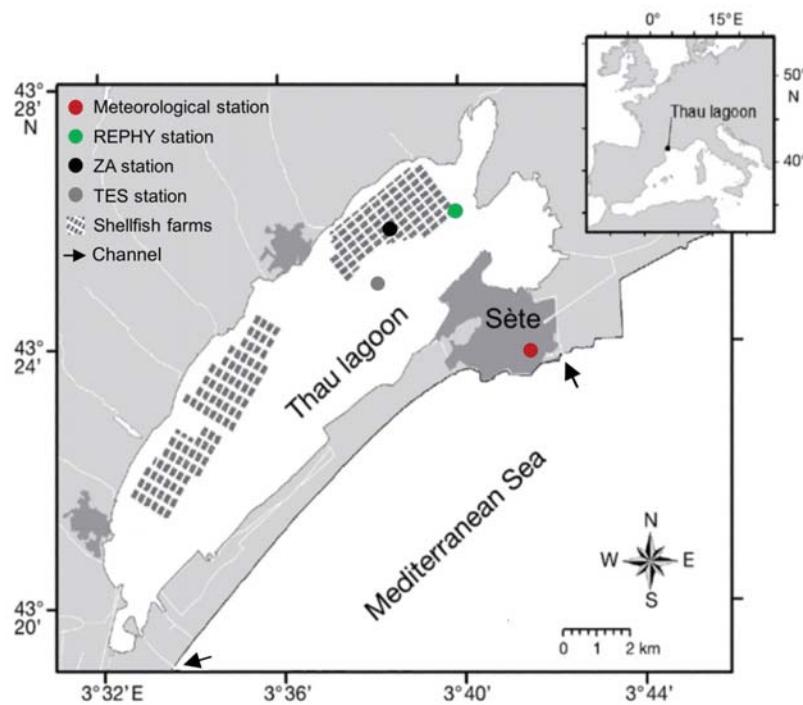
922 **Fig. S1.** Comparison of the average level (1970-2016) of (a) annual mean air temperature ( $^{\circ}\text{C}$ ) and (b) annual  
 923 cumulative rainfall levels ( $\text{mm y}^{-1}$ ), recorded at Sète meteorological station from 1970 to 2016 (data: Météo-  
 924 France).

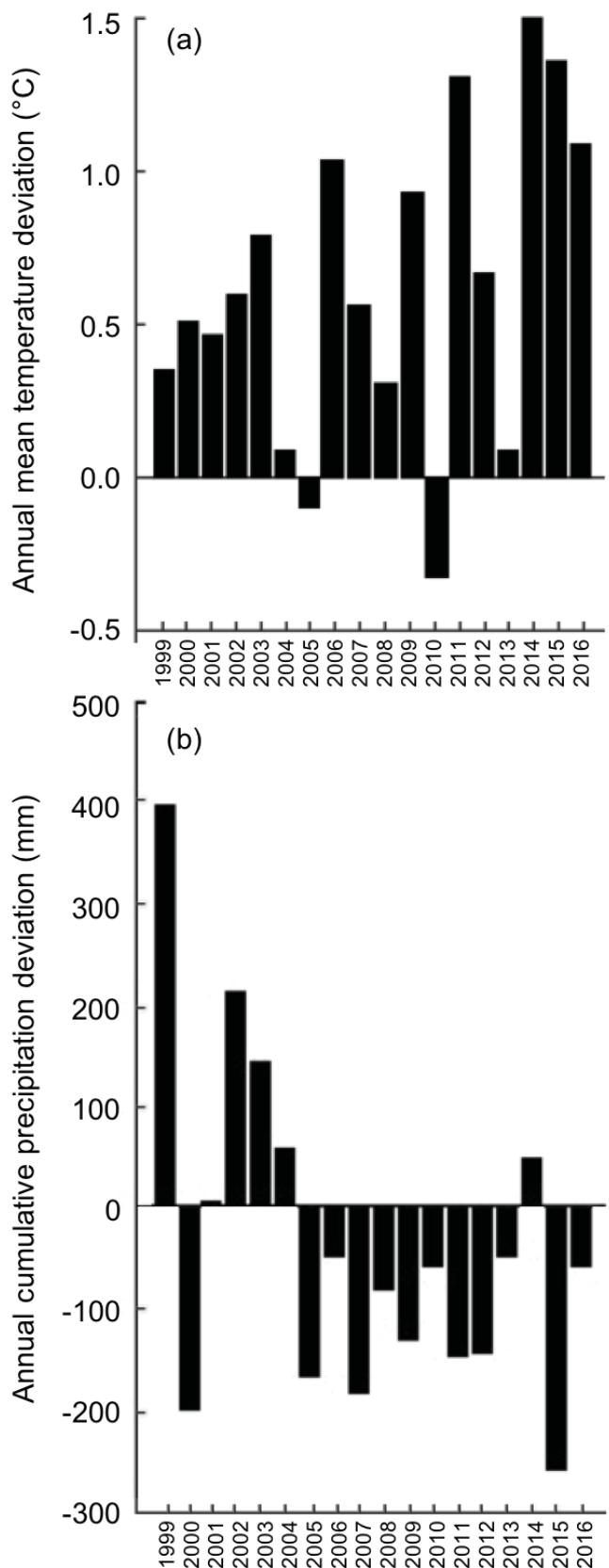
925 **Fig. S2.** Monthly concentrations (dots) of summer levels (June to August) of (a) DIP ( $\mu\text{M}$ ) and (b)  $\text{NO}_3^- + \text{NO}_2^-$   
 926 ( $\mu\text{M}$ ) in the water column from 1972 to 1993 at ZA station (in black) and from 1999 to 2016 at TES station (in  
 927 grey).

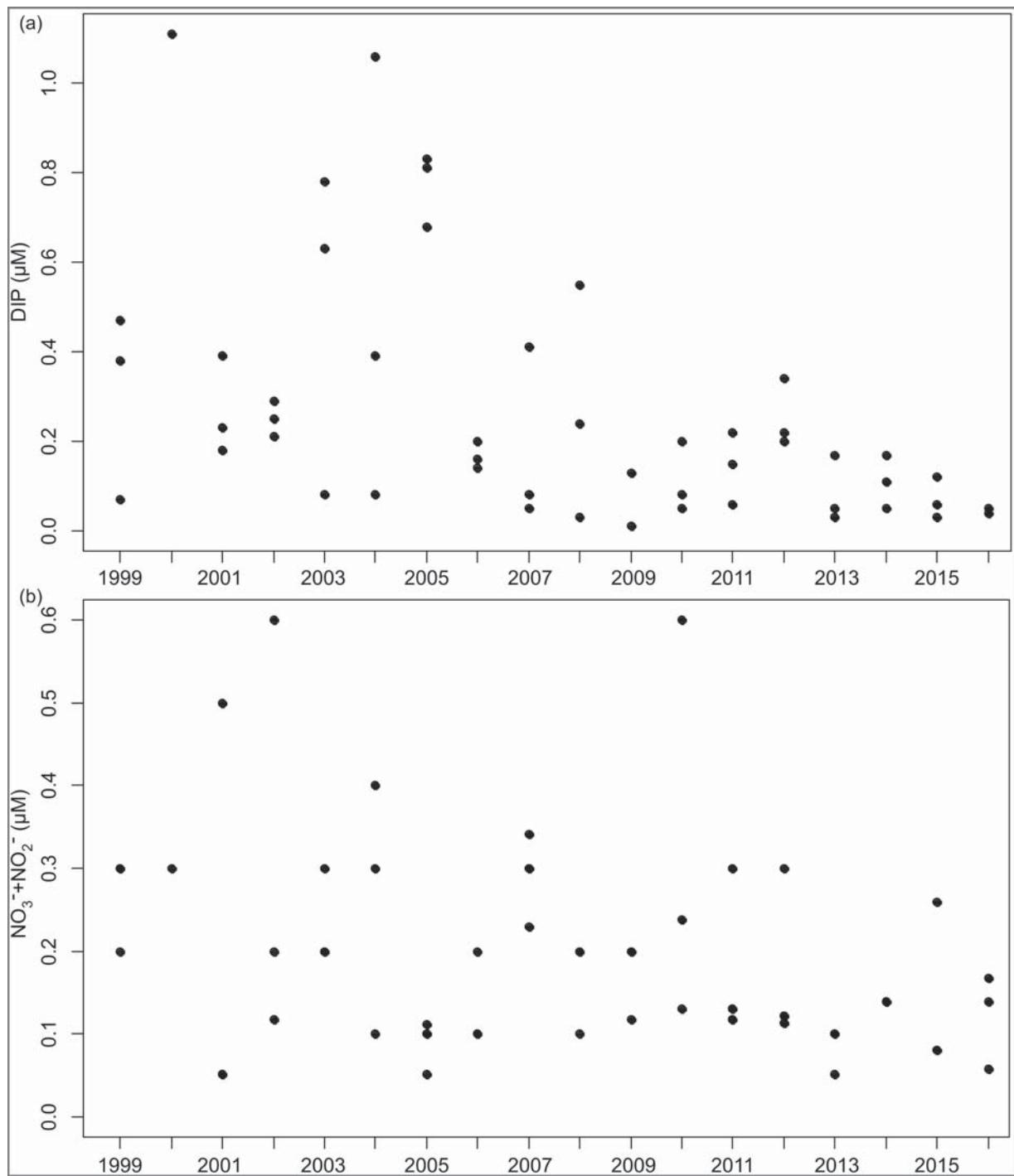
928 **Fig. S3.** Box-and-whisker plots of annual variations in water temperature (a) and salinity (b) from 1998 to 2016  
 929 at REPHY station. Orange dashes represent annual medians. MK p-values are given.

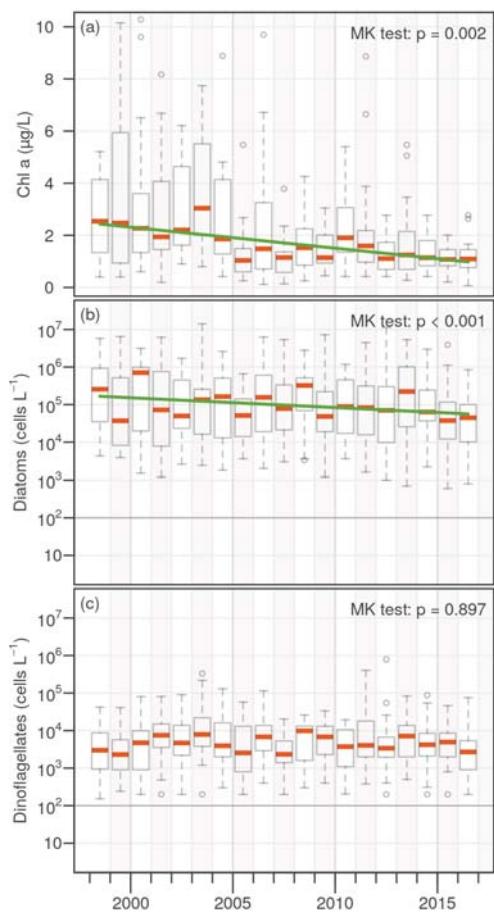
930 **Fig. S4.** Changes in the summer concentrations (June, July, August) of  $\text{NH}_4^+$  (a), DIN (b), TN (c), TP (d), TN:TP  
 931 (e), DIP:TP (f), DIN:TN (g) and DIN:DIP (h) between 1999 and 2016 at TES station. MK p-values are given (\*in  
 932 bold when the MK test is significant, i.e.  $p < 0.05$ ).

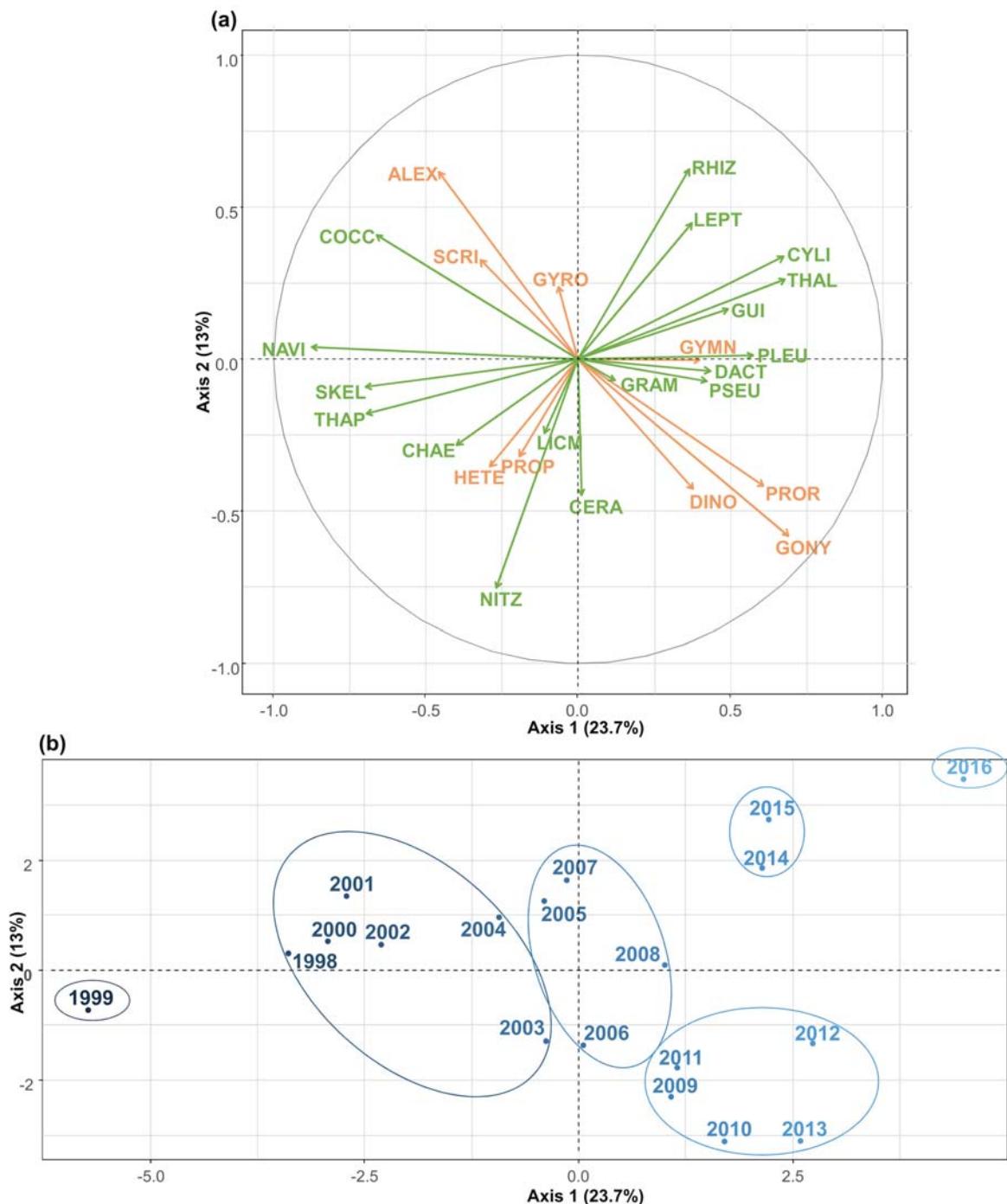
933   **Fig. S5.** Results of PCA of phytoplankton community data from Bouzigues station in Thau lagoon from 1998 to  
934   2016. (a) First and third axes for taxonomic units (dinoflagellates in orange, diatoms in green). (b) Years on the  
935   plane defined by first and third axes and clusters highlighted by clustering. The plot shows 23.7% and 10.9% of  
936   the variance on the first and third axes, respectively.

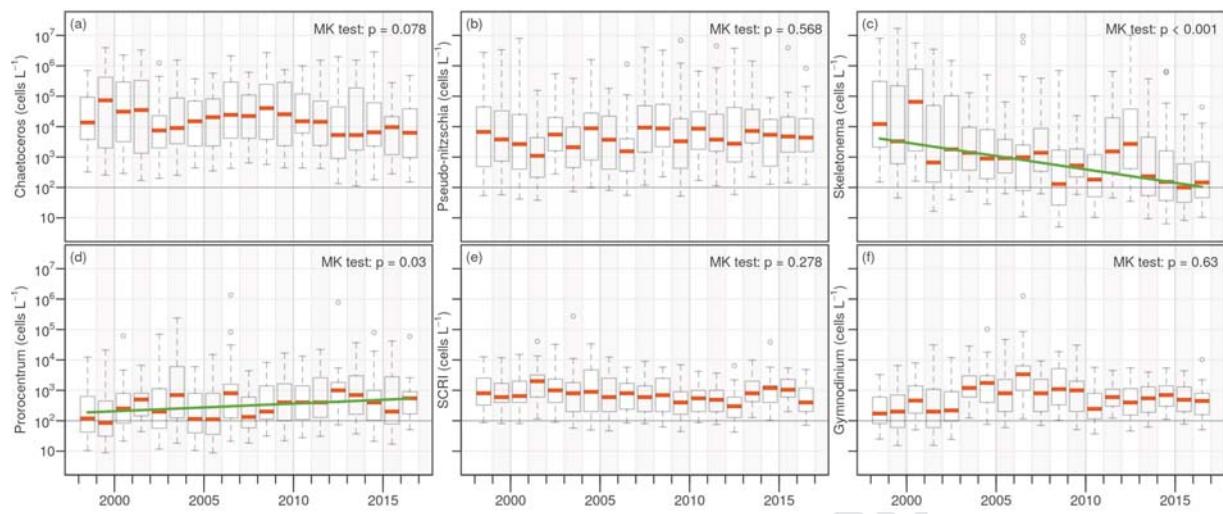


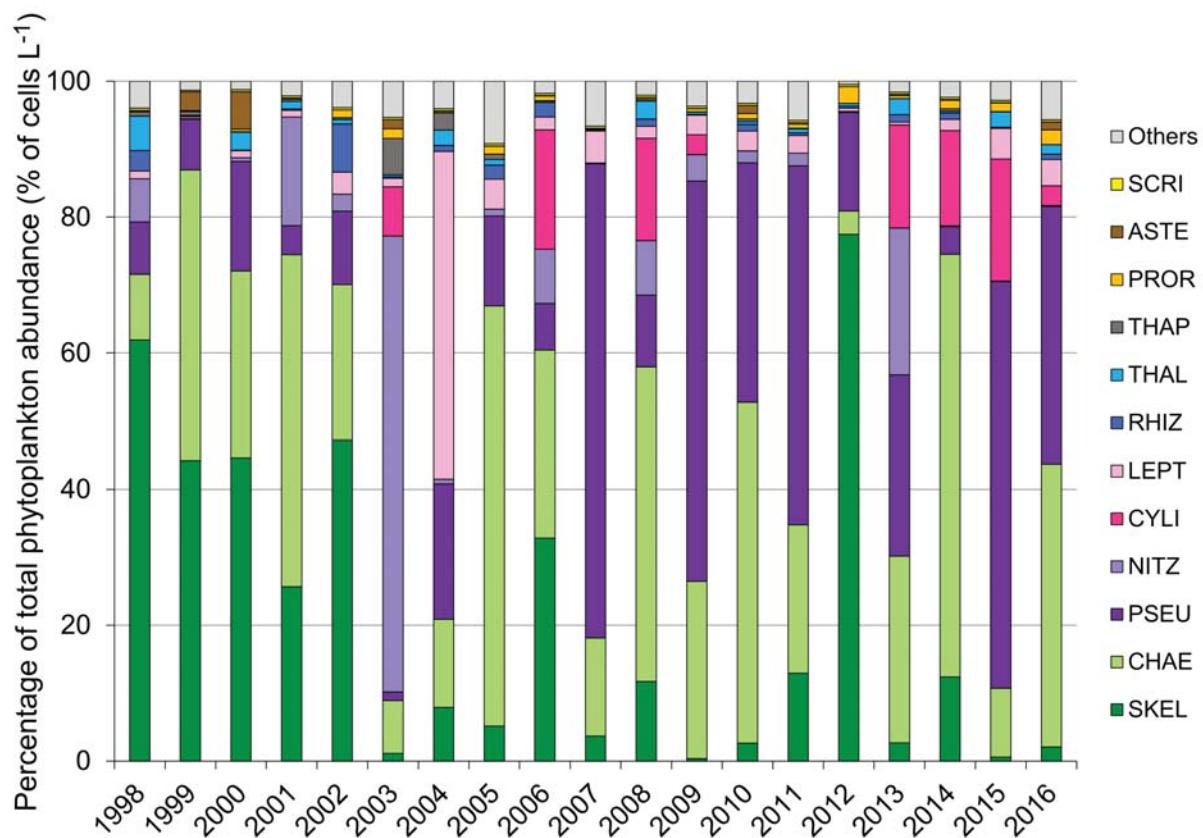


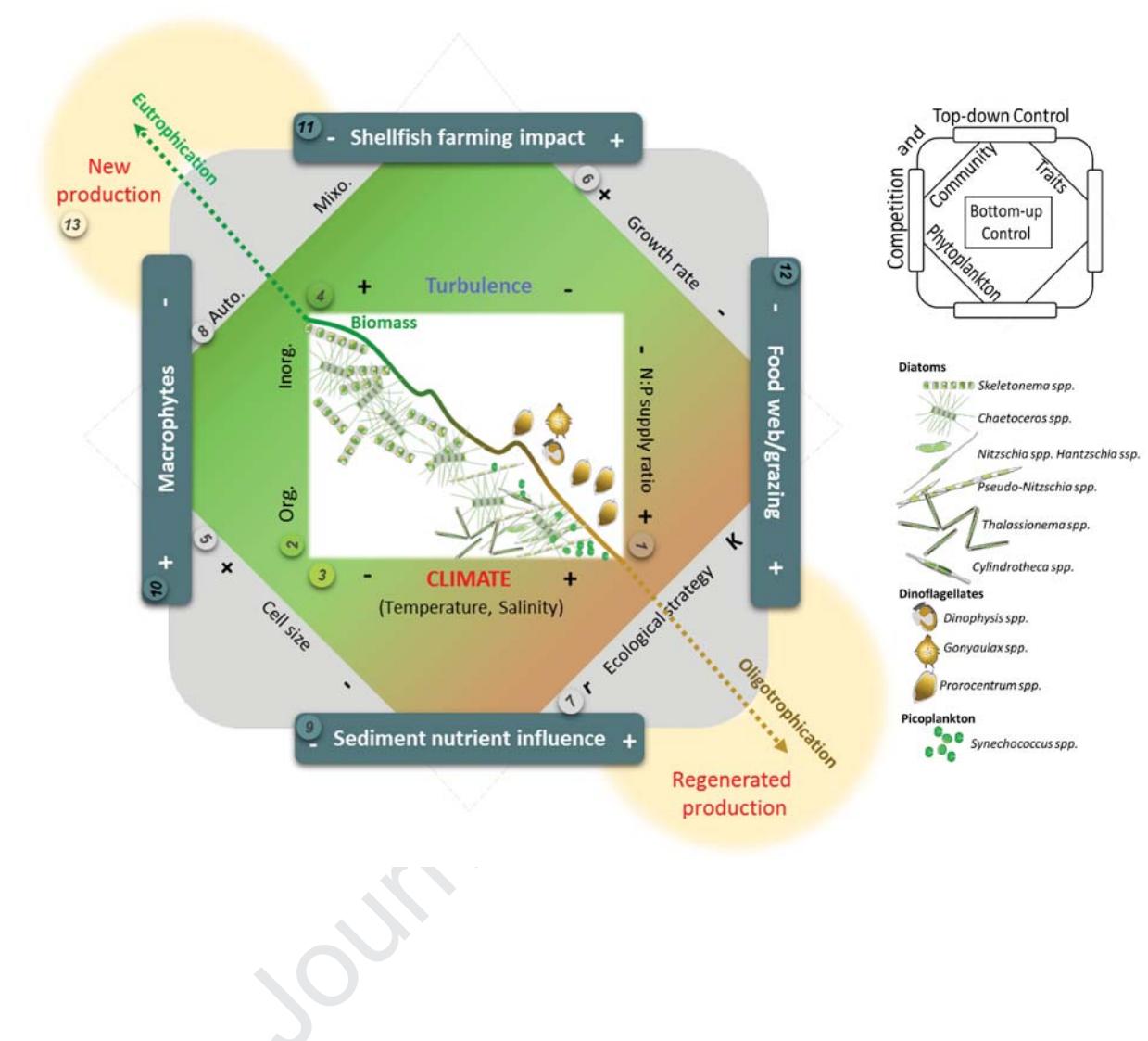












**Highlights:**

- The decrease in water nutrients confirms oligotrophication in the period 1998-2016.
- The decrease in phytoplankton biomass was associated with a decrease in diatom abundance.
- The dominant taxa shifted from *Skeletonema-Chaetoceros* to *Chaetoceros-Pseudo-nitzschia*.
- The median proportion of dinoflagellates relative to diatoms increased significantly.
- The total dinoflagellate abundance did not change significantly.

**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

