Fifty years of ecological changes: Regime shifts and drivers in a coastal Mediterranean lagoon during oligotrophication

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FIFTY YEARS OF ECOLOGICAL CHANGES: REGIME SHIFTS AND DRIVERS IN A COASTAL MEDITERRANEAN LAGOON DURING OLIGOTROPHICATION

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1. Introduction

Eutrophication is one of the most severe anthropic pressures faced by coastal ecosystems (de Jonge and Elliott, 2001; Nixon, 1995). Coastal lagoons are particularly exposed to anthropogenic eutrophication because of their relative isolation from the sea, their close links with watersheds, and their geomorphological features which enable high biological productivity (Newton et al., 2014; Pérez-Ruzafa et al., 2019b; Zaldívar et al., 2008). Anoxia is triggered by eutrophication and by hydro-climatic factors such as high temperatures, and can seriously affect ecosystem functioning and the provision of ecosystem services (Iriarte et al., 2014; Jager et al., 2018; Newton et al., 2018) as they lead to the collapse of aquatic communities (Elliott and Quintino, 2007; Friedrich et al., 2014).

Thau lagoon is one of the largest Mediterranean coastal lagoons and supports traditional fishery and shellfish farming and, more recently, tourism and recreational activities (Deslous-Paoli et al., 1998; Gangnery et al., 2001). At the beginning of the 20th century, Thau lagoon was dominated by seagrass beds associated with gastropods, while bare bottom areas were dominated by bivalves (Calvet, 1910). Since the 1960s, facing the exponential growth of the human population in the French Mediterranean coastal region and the resulting increase in anthropogenic inputs, Thau lagoon has suffered eutrophication and degradation of water quality (La Jeunesse and Elliott, 2004; Picot et al., 1990; Souchu et al., 2010). Among the ecological and socio-economic impacts of this degradation, eutrophication caused major anoxic events leading to massive mortality of shellfish stocks with significant economic impacts (Chapelle et al., 2000a; Souchu et al., 1998).

In the 1970s, improvements were made to waste-water treatment systems in the watershed. Ever since, a decrease in nutrient inputs to Thau lagoon has been recorded (Deslous-Paoli et al., 1998; La Jeunesse et al., 2002), reinforced in the late 2000s by the European regulations (EC 1991a; 1991b and 2000), which gradually led to the oligotrophication of the ecosystem (Bec et al., 2011; Collos et al., 2009). In our study, « oligotrophication » refers to the process associated with the depletion of nutrient in aquatic ecosystems, as used in other studies analysing the process of recovery of coastal or freshwater ecosystems after a decrease in nutrient loads (De Wit et al., 2020; Kamenir and Morabito, 2009; Mozetič et al., 2010). The recovery of the ecosystem was associated with a significant decrease in phytoplankton biomass, linked to a decrease in diatom abundance, and to a taxonomic shift in the microphytoplankton community, raising shellfish farmers' concerns about the limit of the lagoon's carrying capacity (Gowen et al. 2015; Derolez et al., 2020). In parallel, climate

forcings in the Mediterranean region changed between the 1970s to the 2010s, with an increase in mean air temperature and in the frequency of summer heat waves, and a decrease in the frequency of wet years (Derolez et al., 2020; Jouzel et al. 2014). This raised the hypothesis that the shift in phytoplankton communities could be the result of the effects of a reduction in nutrient inputs combined with climatic-related variables.

Oligotrophication has only recently been characterised in coastal lagoons and existing studies mainly focus on a single community of primary producers: phytoplankton (Collos et al., 2009; Derolez et al., 2020; Leruste et al., 2016) or macrophytes (Le Fur et al., 2019; Tsiamis et al., 2013). Some of these studies showed that oligotrophication can lead to significant community shifts: from the dominance of diatoms to that of Chlorella-like algae and dinophytes (Leruste et al., 2016) and from the dominance of opportunistic species to that of perennial macrophyte species (Le Fur et al., 2019; Tsiamis et al., 2013). However, few studies have described coastal lagoons at the ecosystem level and over a long period to identify ecological changes (Pasqualini et al., 2017; Pérez-Ruzafa et al., 2019a). In coastal lagoons, assessing ecological status regarding eutrophication requires data on both pelagic and benthic compartments, as recommended by several authors (Newton et al. 2003; Zaldivar et al. 2008), most of which are identified in the Water Framework Directive (WFD) (EC, 2000): nutrients in the water column, phytoplankton biomass and abundance, macrophyte abundance and composition, and finally nutrients and organic matter in the sediment. However, regarding the dynamics of ecosystems recovery under global change, integrated long-term studies are needed to better understand the trajectories of lagoons focused on (i) changes in the ecosystem status, (ii) the capacity of ecosystems to withstand changes during environmental stresses (hereafter referred to as "resistance"), and (iii) their ability to return to predisturbance levels (hereafter referred to as "resilience") (Elliott et al., 2007; Gladstone-Gallagher et al., 2019).

The aim of the present study was first to determine how the decrease in nutrient inputs has resulted in ecological changes in the Thau lagoon ecosystem, by analysing five decades of time-series (1970-2018) of observations of the pelagic (nutrients and phytoplankton in the water column) and benthic (macrophytes and sediment) compartments. We hypothesise that the process of oligotrophication has led to ecosystem regime shifts and to changes in the drivers of summer anoxia, making the ecosystem more resistant to the threat of climate change. Considering anoxia crises as indicators of

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60   ecosystem resilience and resistance, we then analysed meteorological data, eutrophication status

61   and shellfish production to identify the triggers of summer anoxia over the 49-year period.

62   **2. Materials and methods**

63   **2.1. Study site**

64   Thau lagoon is a microtidal restricted coastal lagoon, connected to the Mediterranean Sea through

65   two permanent inlets, one of which is the Sète channel located in the north-east, which is responsible

66   for 90% of sea water exchanges (Fig. 1) (Fiandrino et al., 2017). The lagoon covers an area of 68

67   km², its mean depth is 4 m (Fiandrino et al., 2017). A depth gradient is observed from the south-west

68   mean depth: 3.3 m) to the north-east (mean depth: 5.2 m) of the lagoon (Souchu et al., 2001). The

69   Thau watershed covers 280 km² and is drained by tributaries with intermittent flows and two

70   permanent rivers (La Jeunesse et al., 2015). Approximately half the watershed's permanent

71   population (103,500 inh. in 2015, INSEE 2016) is located in the city of Sète (La Jeunesse et al.,

72   2015).

73   Shellfish farming structures cover 20% of the lagoon surface in three cultivation zones (Fig. 1). The

74   shellfish reared are mussels *Mytilus galloprovincialis* (*M. galloprovincialis*) and Pacific oyster,

75   *Crassostrea gigas* (*C. gigas*), whose production accounted for about 10% of total French oyster

76   production in the 2000s (Gangnery et al., 2003).

77   **2.2. Biological and meteorological monitoring**

78   The biological and meteorological data used in our study, the associated spatial and temporal

79   strategy and the references when available, are described in detail in Table A1.

80   2.2.1. Hydrological, nutrients and phytoplankton time series

81   From 1999 to 2018, water samples were collected monthly in summer (June, July and August), which

82   is the maximum primary production period in Mediterranean lagoons (Bec et al., 2011; Souchu et al.,

83   2010), at three stations: TANG, TE and TW (Fig. 1A). Samples were collected a minimum of three

84   days after any period when wind speed exceeded 12.5 m s^{-1} to allow sediments to stabilise.

85   Temperature (*TEMP*, °C), salinity (*SAL*) and dissolved oxygen (*O2*, mg L^{-1}) were recorded *in situ* with

86   field sensors. At each station, on each sampling occasion, one water sample was collected in a 1 L

87 polypropylene bottle one metre below the surface for laboratory analyses, according to Souchu et al.

88 (2010).

89 Laboratory analyses were carried out to measure dissolved and total nutrient concentrations (µM):

90 dissolved inorganic phosphorus (*DIP*), dissolved inorganic nitrogen (*DIN* = NH_4^+ + NO_3^- + NO_2^-), total

91 nitrogen (*TN*) and total phosphorus (*TP*). Nutrients were analysed using the standard protocols

92 (Aminot and Kérouel, 2007) described in Souchu et al. (2010). Turbidity (*TURB*, NTU) was measured

93 in the laboratory with a HACH 2100N IS sensor according to ISO 7027.

94 From 1972 to 1993, DIP was analysed in water samples collected monthly in summer at ZA station,

95 located in the shellfish farming area in the north-east part of the lagoon (Fig. 1A) (Collos et al., 2009;

96 Derolez et al., 2020; Souchu et al., 1998).

97 Phytoplankton analyses were performed according to Bec et al. (2011). Chlorophyll *a* concentrations

98 (*CHLA*, µg Chl *a* L^{-1}) were measured by spectrofluorimetry (Neveux and Lantoine, 1993) with a

99 Perkin-Elmer L650. Based on cytometric analyses, different size classes of phytoplankton were

100 identified and counted with a FACSCalibur flow cytometer: autotrophic picoeukaryotes (≤ 3 µm) and

101 nanophytoplankton (> 3 µm) abundances (*PEUK* and *NANO*, 10^6 cells L^{-1}). Phycoerythrin-rich

102 picocyanobacteria (< 1 µm, *PE-CYAN*, 10^6 cells L^{-1}) were distinguished from other photosynthetic

103 organisms by their strong orange fluorescence and light-scattering properties.

104   2.2.2.   Macrophyte and sediment time series

105 Soft bottom macrophytes were monitored five times in June from 2003 to 2017 at 36 stations (Fig. 1A,

106 Table A1). Data from four older samplings (1966 to 1998), collected using different sampling protocols

107 and monitoring methods, were added to the macrophyte time series. Table A1 summarises the years

108 of observation, the formats of the data and the sampling methods used for all macrophyte data. In the

109 case of sampling carried out over several years to cover the entire surface of the lagoon, it was

110 decided to refer to the year corresponding to the middle of the period (i.e. year 1966 for the sampling

111 period 1963-1968, and year 1992 for the sampling period 1988-1994) in the results section 2.3.2. The

112 methods applied in 1998 and from 2003 to 2017 are detailed in Le Fur et al. (2017).

113 Sediment was sampled at 28 stations in late spring or early summer in 1998, 2003, 2008 and 2014

114 (Fig. 1B). The top layer (0-5 cm) of sediment was collected with a sediment corer and then sifted

115 through a 2-mm sieve (see Le Fur et al. (2019) for details). Mud content (%) corresponded to the

116   fraction with a diameter of less < 50 µm. Organic matter content (*OM*, expressed as % of dry

117   sediment weight), total nitrogen (*TN*) and total phosphorus (*TP*) were analysed and were expressed in

118   g kg^{-1} and mg kg^{-1} of dry sediment, respectively.

119   Data on Kjeldahl-N (*KN*) and TP concentrations, analysed in sediment samples collected in 1987 at

120   30 stations, were taken from Péna and Picot (1991) and added to the sediment time series.

121   2.2.3.   Shellfish production

122   Total annual oyster production, mussel production and total shellfish production data (in 10^3 t y^{-1})

123   were collected by the Departmental Direction of Maritime Affairs and gathered by Comps et al. (2000)

124   and Gangnery (1998 & 1999) for the period 1970-2000. Data for the years 2001, 2002 and 2003 were

125   collected by Gangnery (2003). Production data for the period 2004 to 2018, were provided by the

126   Departmental Directorate of Territories and the Sea (French acronym DDTM). The mussel species

127   remained the same throughout the study period (*M. galloprovincialis*), but the oyster species changed

128   in 1973 after the epizootic linked to an iridovirus which resulted in the disappearance of the

129   Portuguese oyster *Crassostrea angulata*, which was replaced by the Pacific oyster (*C. gigas*) (Grizel

130   and Héral 1991).

131   Given that anoxia events can cause significant mortality of the shellfish cultivated in the lagoon, the

132   total shellfish production of the preceding year was used to estimate the stock exposed to anoxia in

133   the summer of any given year (*Q_shellfish_1*). Data were transformed into binary variables with the

134   following values: *shellfish* = 1 for low production rates (≤ 10 000 t) and *shellfish* = 2 for higher

135   production (> 10 000 t).

136   2.2.4.   Meteorological data

137   Daily data on rainfall (mm), air temperature (°C) and wind intensity (m s^{-1}) from 1970 to 2018 were

138   collected from the Sète meteorological station (Météo-France station n°34301002) (Fig. 1A).

139   Summer air temperatures and wind intensities were averaged by month (June, July and August)

140   (*air_M*, *wind_M*). Wind intensities were then standardised according to four periods determined by

141   shifts in the raw time series corresponding to modifications to the sensors identified by Météo-France

142   (January 1972, August 1996, January 2008) (*wind_ST*).

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143   Rainfall was cumulated in June, July and August (*rainfall_6*, *rainfall_7*, *rainfall_8*) corresponding to the

144   summer months when anoxia occurrs, and from January to May (*rainfall_1-5*) corresponding to the

145   winter and spring months preceding anoxia.

146   **2.3. Data processing and analyses**

147   2.3.1.   Hydrological, nutrient and phytoplankton time series

148   Data collected in summer from 1999 to 2018 at the three stations TANG, TE and TW were averaged

149   per year before performing an explanatory PCA analysis with nine variables (*DIN*, *DIP*, *TP*, *TN*,

150   *CHLA*, *PEUK*, *NANO*, *PE-CYAN* and *O2*) (ade4 package in R). The phytoplankton variables were

151    $\log_{10}$ transformed to normalise the data and reduce the effect of very high values. The three

152   hydrological parameters (*TEMP, SAL and TURB*) were considered as illustrative variables in the PCA.

153   K-means cluster analysis was then applied to identify years and stations with similar eutrophication

154   patterns (vegan package in R). The optimal number of clusters was estimated based on the Calinski-

155   Harabasz index (Calinski and Harabasz, 1974).

156   For the hydrological and phytoplankton variables (*DIN*, *DIP*, *TP*, *TN*, *CHLA*, *PEUK*, *NANO*, *PE-CYAN*,

157   *O2*, *TEMP*, *SAL*, *TURB* and the ratio *PE-CYAN/PEUK*), Mann-Kendall tests (MK) were performed on

158   the means calculated for each year from 1999 to 2018 to characterise the monotonic trends. To

159   eliminate the effect of serial correlations on the MK test, we used the modification by effective sample

160   size, computed with significant serial correlation coefficients (Hamed and Rao (1998), modifiedmk

161   package in R). If the test was significant (i.e. p-values <0.05), the Theil-Sen's slope estimator was

162   calculated (Sen, 1968). The correlation between water temperature and *PE-CYAN* was tested using

163   Spearman's test.

164   In Thau lagoon, DIP is not considered to be the main limiting nutrient (Fouilland et al., 2002; Souchu

165   et al., 2010) and its concentrations in water are well correlated with the inputs from human activities in

166   the watershed (La Jeunesse and Elliott, 2004). Moreover, in summer, it has been shown that in

167   deeper lagoons such as Thau, P loads from sediments are enhanced by high temperatures through

168   the benthic remineralization process (Chapelle et al., 2000b; Souchu et al., 1998; Zilius et al., 2015).

169   Finally, shellfish farming is known to contribute to summer remineralization (Chapelle et al., 2000a;

170   Mazouni et al., 1996). For all these reasons, the summer concentration of DIP in the water column is

171   a good indicator of eutrophication in the Thau lagoon. To analyse the changes in summer DIP

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concentrations in the water of Thau lagoon from 1970 to 2018, we pooled the data collected in

summer at ZA and TE stations, located in the same well mixed zone according to Millet (1989) and

Fiandrino et al. (2017). To avoid the impact of high temperatures and anoxia on DIP due to increased

discharge from sediment (Chapelle et al., 2000b; Mazouni et al., 1996), data collected in the late

summer (July and August) were removed from the dataset. Thus, DIP data collected in June (*DIP_6*)

were modelled using LOESS (polynomial degree=2, smoothing degree=0.75). The first derivative of

the modelled data was first used to identify the breaking points characterising changes in the slope in

the curve. Then, the measured concentrations of DIP in June were compared with the threshold of the

good status for DIP according to the WFD (DIP ≤ 1 µM; MTES, 2018), in order to identify the year

after which this threshold was no longer exceeded. These two criteria were used to divide the time

series into two contrasting periods in terms of eutrophication status: *period 1* and *period 2*. We

performed MK tests on the total time series and for both periods to characterise monotonic trends.

2.3.2. Macrophyte community

The phylum taxonomic scale was chosen to enable us to compare macrophyte data from the nine

available surveys conducted between 1966 and 2018 (Table A1). The macrophytes were distributed

in four groups: red algae (Rhodophyta), green algae (Chlorophyta), brown algae (Ochrophyta) and

seagrass (Tracheophyta). An additional group corresponding to bare sediment was created for

stations with no vegetation. For data whose measurements were sporadic, the percentage of cover or

biomass was calculated for each group of macrophytes. The group with the highest percentage of

cover was selected as "dominant". When the difference in the percentages between the first two

groups was ≤ 2%, both groups were considered to be dominant. This pre-treatment enabled

comparison of data on dominant groups shown on the maps collected from 1966 to 1992. The first

two most frequent genera in each group are given for each survey.

The spatial representation of the macrophyte was homogenised over the nine vegetation surveys in

order to retrieve the data corresponding to the 36 benthic stations monitored in the five most recent

surveys (Fig. 1). Concerning the three surveys conducted between 1986 and 1998, the macrophyte

data were retrieved from 100 m buffer zones created around the 36 stations projected onto the three

available maps. The publications used to construct the map of the 1960s consisted of a description of

macrophyte distribution in the literature, without precise spatial coordinates. Consequently, we

localised the information on the dominant species in the locations described in the literature. In the

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202 surveys carried out before 2003, it was not possible to collect information from all 36 stations. The

203 number of stations used for each survey is given in Table A1.

204 Finally, the proportion of stations with bare sediment (i.e. without vegetation) or dominated by each

205 group of macrophytes was calculated for each period as follows: Proportion of stations dominated by

206 group i = number of stations dominated by group i ÷ total number of stations considered.

207   2.3.3. Sediments

208 To characterise the monotonic trends of sediment variables we performed Mann-Kendall tests on the

209 medians calculated for each survey (1998, 2003, 2008 and 2014 for mud, OM and TN and 1987,

210 1998, 2003, 2008 and 2014 for TP).

211   2.3.4. Occurrence and intensity of anoxia events, meteorological and environmental
212   conditions

213 Information on the frequency and intensity of the summer anoxic crises which occurred between 1970

214 and 2018 was collected from the scientific and grey literature (Hamon et al., 2000; Trousselier and

215 Deslous-Paoli, 2001; Ifremer, 2004; Ifremer, 2007; Lagarde, 2018a). Since the spatial and temporal

216 strategies of O_2 monitoring did not remain the same over the study period, we defined the occurrence

217 of anoxia based on presence of white water caused by sulphur bacteria reoxidising the sulphur

218 released in the water column (Minghelli-Roman et al., 2011), or on the presence of at least one

219 measurement of O_2 concentration < 0.05 mg L^{-1}. The intensity of the anoxia crises was characterised

220 according to their duration in months (≤ 1 to 3) and to their maximum spatial extent: 1 (one of the

221 shellfish farming areas), 2 (two of the shellfish farming areas), 3 (all three shellfish farming areas), 5

222 (the whole lagoon).

223 Out of the total of 147 summer months in the 1970-2018 period, 12 months were characterised by the

224 onset of an anoxia crisis (*anoxia* = 1) and 135 months had no anoxia onset (*anoxia* = 0). In order to

225 identify the meteorological and environmental conditions involved in the triggering of anoxia, a

226 binomial generalised linear model (glm) (McCullagh and Nelder 1989) was built with the following

227 eight variables:

228   • meteorological variables: *air_M* and *wind_ST* (summer monthly averages), *rainfall_6*,
229   *rainfall_7*, *rainfall_8* and *rainfall_1-5* (cumulative rainfalls);

230   • eutrophication status: *period* (1 or 2);

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231   •   shellfish production: *shellfish* (1: low or 2: high).

232 The Akaike information criterion (AIC) was used to select the significant variables and the odds ratios

233 (OR) were calculated ($OR_x=e^{\beta_x}$, with β_x the estimated coefficient for variable x) to evaluate the

234 probability of triggering anoxia versus the probability of not triggering anoxia when modifying variables

235 independently. The odds ratios provide information on the strength and direction of the association

236 between the dependent and explanatory variables (OR>1: increases the probability, $0 \leq OR < 1$:

237 decreases the probability) (Schwarz, 1978, ggeffects in R). The performance of the glm was assessed

238 by cross validation (70% for calibration, 30% for validation). The test datasets consisted of 100

239 observations randomly drawn from the 135 months with no anoxia; and from the 12 months

240 characterised by the onset of anoxia. The receiver operating characteristic (ROC), which depends on

241 specificity and sensitivity), and the area under the curve (AUC) were calculated for the 50 test

242 datasets drawn randomly to estimate the average and standard deviation of this criterion (DeLong et

243 al., 1998, Presence-Absence in R). According to AUC, a model is considered as not contributing

244 (AUC = 0.5), not very informative ($0.5 \leq AUC < 0.7$), moderately informative ($0.7 \leq AUC < 0.9$), very

245 informative ($0.9 \leq AUC < 1$) or perfect (AUC = 1) (Swets, 1988).

246 In addition, Kruskal-Wallis tests were performed on the following variables to identify significant

247 differences in the characteristics of the two periods: *air_M*, *wind_ST*, *rainfall_6*, *rainfall_7*, *rainfall_8*,

248 *rainfall_1-5*, *DIP_6* and *Q_shellfish_1*.

249 **3. Results**

250   **3.1. Change in trophic status from eutrophication to oligotrophication**

251   **3.1.1. Water column**

252 The average summer concentrations of dissolved phosphorus measured in water ranged from 6.7 μM

253 in 1972 to 0.04 μM in 2016-2017, with a median value of 0.9 μM, and they decreased monotonically

254 and significantly over the study period (MK p<0.001, Theil-Sen's slope = -0.1 μM y^{-1}) (Fig. 2).

255 When focusing on June observations, the concentrations of dissolved phosphorus ranged from 5.2

256 μM in 1974 to 0.04 μM in 2015-2017, with a median value of 0.3 μM, and they decreased

257 monotonically and significantly over the study period (MK p<0.001, Theil-Sen's slope = -0.1 μM y^{-1})

258 (Fig. 2, black dots). The slope of the time series modelled with LOESS revealed two breaks: the first

259 in June 1991 and the second in June 1993. Moreover, the threshold of good status according to WFD

260 (DIP ≤ 1 µM) was no longer exceeded after June 1993, which made it possible to identify two

261 contrasting periods based on the eutrophication status: period 1, from 1970 to 1992 and period 2,

262 from 1993 to 2018. When considering data for each period separately, DIP concentrations also

263 decreased significantly, but the median and the slope were higher in the first period (respectively,

264 median=2.3 µM, MK p<0.001 and Theil-Sen's slope = -0.3 µM y^{-1}; median=0.1 µM, MK p=0.002 and

265 Theil-Sen's slope = -0.005 µM y^{-1}).

266 PCA analysis of the data was performed on nine variables (*DIN*, *DIP*, *TP*, *TN*, *CHLA*, *PEUK*, *NANO*,

267 *PE-CYAN* and *O2*) collected from 1999 to 2018, corresponding to PERIOD 2 defined based on

268 eutrophic status. The PCA of this water column time series showed that the two first axes accounted

269 for 52.6% of total variability (33.9% and 18.6% for axis 1 and axis 2, respectively). The third axis,

270 accounted for 14.4% of the variability and was positively correlated with O2 and negatively correlated

271 with TN (Fig. A1.A). The first axis revealed a clear temporal structure, contrasting the earliest and the

272 most recent years (Fig. 3B). This first axis was negatively correlated mainly with TP, DIP, PEUK,

273 CHLA and DIN (Fig. 3A). The second axis was mainly defined by PE-CYAN abundances, with a high

274 contribution of the years 2006 and 2003 (Fig. 3A). The temperature, considered as an illustrative

275 variable in the PCA analysis, was correlated with the second axis and consequently with PE-CYAN.

276 The third axis isolated the samples collected at TANG station (Fig. A1.C).

277 Among the three clusters identified by the Calinski-Harabasz index on the PCA, a first group, located

278 on the left side of the PCA, grouped 23 samples collected from 1999 to 2008, with the years 1999 to

279 2001 and 2003 to 2005 only found in this cluster (Fig. 3B). On the right side of the PCA, the second

280 cluster (29 samples) was characterised by low levels of nutrient and phytoplankton biomass and

281 abundance and isolated the samples collected exclusively from 2007 to 2018 (Fig. 3B). Finally, the

282 third cluster was isolated according to the third axis and grouped seven samples collected at TANG

283 station in 2002, 2006, 2008 to 2011 and 2018 (Fig. A1.B and A1.C).

284 From 1999 to 2018, the phytoplankton community was marked by changes in chlorophyll *a* biomass

285 and pico- and nano-phytoplankton abundances at TW-TE stations (averaged data) and TANG

286 stations (Fig. 4). A significant decreasing trend was found for chlorophyll *a* biomass from 1999 to

287 2018 (respectively MK p=0.003 and p=0.02, Theil-Sen's slope = -0.17 µg L^{-1} and -0.15 µg L^{-1}).

288 Moreover, two phases are identifable in the evolution of CHLA: the period 1999-2006, when maximum

289   values were reached (respectively 6.2 and 15.7 µg L^{-1} at TW-TE and TANG), and the period 2007-

290   2018 characterised by lower values (< 2 µg L^{-1}) (Fig. 4A).

291   Like chlorophyll *a*, picoeukaryote abundances revealed a decreasing trend (MK p=0.006 and 0.001

292   and Theil-Sen's slope = -1.6 10^6 L^{-1} and -2.8 10^6 cells L^{-1} at TW-TE and TANG stations respectively),

293   with the exception of the maximum values reached in 2003 and 2004 (respectively 120 10^6 cells L^{-1} at

294   TW-TE and 113 10^6 cells L^{-1} at TANG) (Fig. 4C). On the contrary, nanophytoplankton revealed no

295   significant monotonic trend (MK p>0.05). Nanophytoplankton levels peaked in 2006 (41.6 10^6 cells L^{-1}

296   at TANG) and increased to reach a second maximum in 2011 (28.4 10^6 cells L^{-1} at TW-TE), then

297   decreased and remained below 3.7 10^6 cells L^{-1} (Fig. 4B).

298   Changes in phycoerythrin-rich picocyanobacteria were contrasted, with no significant monotonic trend

299   (MK p>0.05). PE-CYAN abundances exhibited three peaks in 2003, 2006 and 2018 (respectively

300   283.7, 295 and 282.3 10^6 cells L^{-1} at TW-TE), associated with water temperatures above 25.6°C (Fig.

301   4D). Water temperatures and PE-CYAN abundances were significantly correlated at TW-TE stations

302   (Spearman p=0.002, rho=0.65) but not at TANG station. Finally, the PE-CYAN/PEUK ratio increased

303   significantly, from 0.01 in 1999 to 15.7 in 2018 at TW-TE (MK p<0.001 Theil-Sen's slope = 0.16), but

304   not at TANG station.

305   Among the other hydrological parameters, decreasing monotonic trends were found for TP, DIP and

306   DIN at TW-TE and TANG stations from 1999 to 2018 (Fig. A2.B, A2.D and A2.C) and for TN and O2

307   only at TW-TE stations (Fig. A2.A and A2.F). An increasing trend was found for TEMP only at TANG

308   station (Fig. A2.H).

309   ### 3.1.2.   Benthic compartment

310   **a) Macrophyte composition**

311   The percentage of benthic stations not covered by soft bottom macrophytes tended to decrease from

312   1966 to 2017, with the highest percentages measured in the 1980s and 1960s (28.6 and 22%,

313   respectively), and null values from 2011 on (Fig. 5).

314   The macrophyte community consisted mainly of seagrass beds in the 1960s, dominating coverage at

315   40% of the benthic stations (Fig.5). Seagrass cover declined between the 1960s and the 1980s in

316   favour of red algae, which became the second dominant group after seagrass in 1986 and 1992. The

317   percentage of stations dominated by seagrass continued to decline until 2003, when it reached its

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318   minimum (11.4%), then increased from 15.4% in 2008 to 22.5% in 2011 and 2014. After dominance

319   by seagrass, red algae dominated the macrophyte community from 1998 to 2017 (between 42.5% of

320   benthic stations were dominated by this group in 2011 and 2014 and 55.6% in 2017).

321   Brown algae dominated 18% of the stations in 1966, but rarely dominated between 1986 and 2008 (0

322   to 15.4% of the benthic stations were dominated by this group); brown algae reached 22.5% to 25%

323   between 2011 and 2017. The contribution of green algae to macrophyte cover was low to zero (in

324   2017) and did not change significantly over the study period (from 11.4% of benthic stations

325   dominated by this group in 1966 and 2003 to 19.2% in 1999).

326   Regarding the composition of each group of macrophytes, seagrass beds were composed of two

327   *Zostera* species: *Zostera noltei* and *Z. marina*, both species being observed in all samples collected

328   from 1966 to 2017.

329   Red algae consisted of *Polysophonia* and *Halopitys* genera in 1966 (Dubois, 1972; Lauret, 1967 &

330   1970). Then, *Halopitys* and *Gracilaria* genera were the two most frequent red algae observed in 1986,

331   1992 and 1998 (Gerbal and Verlaque, 1995; Lauret, 1990 & 1994; Verlaque, 2000). *Gracilaria* and

332   *Alsidium* were the most frequent red algae in 2003 and *Gracilaria* and *Polysiphonia* in 2008 (Ifremer,

333   2004 & 2007). Finally, from 2011 to 2017, *Gracilaria* and *Halopitys* again became the most frequent

334   red algae, with a shift in dominance from *Gracilaria* to *Halopitys* in 2017 (Bouchoucha et al. 2019;

335   Derolez et al. 2015; Ifremer 2009 & 2012).

336   *Codium* genera was the only green algae listed in 1966, while *Ulva* and *Monostroma* genera were the

337   most frequently observed green algae in 1986 (Dubois, 1972; Gerbal and Verlaque, 1995; Lauret,

338   1967 & 1970). *Ulva* and *Chaetomorpha* were the most frequent genera in 1992 (Lauret, 1990 &

339   1994). Finally, the most frequent green algae were *Ulva* and *Cladophora* in 2008 and 2011 and

340   *Chaetomorpha* and *Cladophora* in 1998, 2003 and 2014 (Derolez et al. 2015; Ifremer 2004, 2009, &

341   2012; Verlaque, 2000).

342   *Cystoseira* and *Sargassum* were the only brown algae genera listed in 1966 and 1998, respectively,

343   whereas both genera were cited in 1986 (Dubois, 1972; Gerbal and Verlaque, 1995; Lauret, 1967 &

344   1970). *Colpomenia* and *Cutleria* and *Colpomenia* and *Cystoseira* were the most frequently observed

345   in 1998 and 2003, respectively, (Ifremer, 2004; Verlaque, 2000). Finally, *Dictyota* genera and the

346 family *Ectocarpaceae* were the most frequent brown algae observed from 2008 to 2017 (Bouchoucha

347 et al. 2019; Derolez et al. 2015; Ifremer 2009 & 2012).

348 **b) Sediment**

349 Median concentrations of mud and organic matter in the surface sediment ranged from 61.8% in 1998

350 to 83.5% in 2008 and from 6.6% in 1998 to 13% in 2014, respectively, but did not change significantly

351 from 1998 to 2014 (MK p=0.67 and p=0.051, respectively) (Fig. A3-A and A3-B). On the contrary, a

352 significant increasing trend was revealed for total nitrogen from 1998 to 2014, with medians ranging

353 from 2.8 to 4.7 g kg^{-1} (MK p=0.001, Theil-Sen's slope=0.54 g kg^{-1} y^{-1}) and confirmed from 1987 to

354 2014 when KN values measured in 1987 (2.7 g kg^{-1}) were included (MK p<0.001, Theil-Sen's

355 slope=0.49 g kg^{-1} y^{-1}) (Fig. A3-C). In contrast to the other parameters, although the medians of total

356 phosphorus did not show a monotonic trend from 1987 to 2014 (MK p=0.81), the maximum was

357 reached in 2003 (771 mg kg^{-1}) and the minimum in 2014 (577 mg kg^{-1}) (Fig. A3-D).

358 **3.2. Changes in shellfish production**

359 Shellfish production varied significantly between 1970 and 2018 (Fig. 7). Total annual production

360 ranged from 6 650 t in 1982 to 18 000 t in 2001 to 2003. Mussel production ranged from 1 038 t in

361 1990 to 11 550 t in 1970 and dominated Thau shellfish production from 1970 to 1983 (45-93% of total

362 production). From 1972 to the 1990s, mussel production declined in favour of oyster production

363 (*Crassostrea angulata* until 1972 and *Crassostrea gigas* ever since). Thus, oyster production has

364 accounted for most shellfish production since 1983 (53 to 90% of total production). Oyster production

365 revealed two peaks: a first peak in 1994 (15 000 t) and a second peak during the period 2000-2008

366 (12 000 to 13 000 t). In 2009, oyster production declined sharply due to the OsHV-1 µvar epizootic

367 (Pernet et al., 2012). It slowly increased from 2012 to 2017, while remaining below 8 000 t. Finally in

368 2018, oyster production again decreased to 6 030 t.

369 Figure 6 also shows the years in which a summer anoxic event occurred (in grey). From 1970 to

370 2018, 12 anoxic events were recorded in the lagoon. About half of these crises occurred in the 1980s

371 and 1990s. Some of these years were characterised by significant a decline in production (e.g. 1975,

372 1982, 1990, 1997, 2018), associated with shellfish mortalities.

373 **3.3. Triggering factors of summer anoxia**

13

374   Figure 7 shows the duration and spatial extent of summer anoxia in Thau lagoon from 1970 to 2018.

375   The 1970 anoxia event lasted three months and the 1983 and 1994 anoxia events each lasted two

376   months. The anoxia events in 1975, 1982, and 1987 lasted six weeks and the other anoxia events,

377   between 1990 and 2018 lasted one month or less. The most extensive anoxia event occurred in 1975,

378   when the entire lagoon was under hypoxic conditions (Troussellier and Deslous-Paoli, 2001). The

379   1982, 1983, 1990, 2006 and 2018 anoxia events affected all three shellfish farming areas, while the

380   others affected only one or two. The duration and spatial extent of the seven anoxia events which

381   occurred in period 1 (from 1970 to 1992) were greater than those of the five last anoxia events which

382   occurred in period 2 (from 1993 to 2018) (respective median duration ranged from four to six weeks

383   and the median spatial extent from two to three areas).

384   The Kruskal-Wallis tests performed to differentiate the characteristics of *periods 1* and *2* were

385   significant for the following variables (p-values < 0.05): mean monthly air temperature increased

386   (*air_M*, median from 22.3 to 23.1°C), rainfall from January to May and rainfall in June decreased

387   (respectively *rainfall_1-5:* median from 253 mm to 219 mm, *rainfall_6*: median from 21 mm to 16 mm),

388   the concentration of DIP in June decrased (*DIP_6*, median from 2.3 to 0.1 µM) and total annual

389   shellfish production increased (*Q_shellfish_1*, median from 8.7 10^3 to 13.4 10^3 t y^{-1}). The other three

390   variables (*wind_ST*, *rainfall_7*, *rainfall_8*) did not differ significantly between the two periods.

391   Among the eight variables included in the glm predicting the triggering of summer anoxia, four were

392   considered as significant based on the AIC: summer monthly averages of air temperature and wind

393   intensity, rainfall in July and the period determined according to the eutrophication status (*air_M*,

394   *wind_ST*, *rainfall_7* and *period 2*). According to the AUC criterion, the performance of this glm was

395   good (mean=0.81, sd=0.1), corresponding to moderately to very informative models. *Period 2* and

396   *rainfall_7* were associated with, respectively, the highest and the lowest absolute values ot the

397   estimated coefficients in the glm (Table A2). Air temperature and rainfall in July were associated with

398   positive coefficients, in contrast to wind intensity and to the less eutrophic period (*period 2*: from 1993

399   to 2018). The odds ratio associated with the period corresponding to the eutrophication status is 0.17

400   ($e^{-1.78}$), meaning that the fact of being in period 2 divided the risk of triggering anoxia by 5.9 (1/0.17)

401   compared to the risk in period 1. The odds ratio of the summer monthly average wind intensity was

402   0.27 ($e^{-1.32}$), meaning that an increase of 1 unit of wind intensity (the variable *wind_ST* being

403   standardised) divided the risk by 3.7. The odds ratio associated with air temperature ($e^{1.03}=2.8$)

404   means that an 1°C increase multiplies the risk of triggering anoxia by by 2.8. Finally, the odds ratio of

405   rainfall in July indicates that a 10 mm increase multiplies the risk by 1.5 ($e^{10*0.04}$=1.5). Figure 8 shows

406   the predicted probabilities of triggering anoxia according to the three significant meteorological

407   variables of the glm for period 1 and period 2, showing that the highest probabilities of the highest

408   temperature were reached in period 1.

409   **4. Discussion**

410   **4.1. Ecological changes and regime shifts during oligotrophication**

411   Our results, based on long time series, show that the pelagic and benthic communities in Thau lagoon

412   changed during the course of oligotrophication. Previous studies of the lagoon from the 1990s to the

413   2000s showed that the gradual decrease in nutrient inputs from the watershed resulted in a

414   continuous decrease in nutrients and Chl *a* concentrations in the water column (Collos et al., 2009;

415   Derolez et al. 2020; Deslous-Paoli et al., 1998; Gowen et al., 2015). Our study revealed the

416   continuation of oligotrophication over the past 20 years (1999-2018), and the recovery of the

417   ecosystem, through nutrient and phytoplankton parameters. Thus, based on changes in the summer

418   concentration of DIP in the water, which is a good indicator of the eutrophication status of Thau

419   lagoon (La Jeunesse and Elliott, 2004; Souchu et al., 1998), we identified a progressive shift from a

420   bad quality status to a high quality status, according to the thresholds of the WFD (METS, 2018).

421   Reaching the good DIP status (DIP < 1 µM, METS, 2018), which was no longer exceeded after June

422   1993, divided the time series into two periods (1:1970-1992 and 2:1993-2018). At the same time,

423   dissolved nitrogen concentrations also decreased significantly (NO_3^-+NO_2^- in June: MK p<0.01,

424   slope=-0.01 µM y^{-1}). In period 2, when nutrient levels were already low, phytoplankton shifted with a

425   time lag in year 2006. After 2006, the levels of Chl *a* biomass (< 5 µg L^{-1}) and picoeukaryote

426   abundances (< 50 10^6 cells L^{-1}) corresponded to those reported in oligotrophic coastal waters of the

427   Mediterranean (Massana 2011). Coastal lagoons often host blooms of picophytoplankton that can

428   continue for months to years (Glibert et al 2010; Bec et al. 2011). In Thau lagoon, phycoerythrin-rich

429   picocyanobacteria abundances did not increase significantly but their relative contribution (PE-

430   CYAN/PEUK ratio) to picophytoplankton did.The numerical dominance of picocyanobacteria in

431   summer may reflect the oligotrophic conditions of the lagoon linked to low phosphorus levels (Collos

432   et al., 2009; Bec et al. 2011). We also found a positive correlation between temperature and the

433   abundance of phycoerythrin-rich picocyanobacteria. Positive effects of temperature on the growth rate

15

and abundance of picocyanobacteria have previously been demonstrated in Thau lagoon (Bec et al. 2005, 2011). These results confirmed the trends expected in coastal ecosystems under oligotrophication and global warming (Glibert, 2016; Pulina et al., 2018; Trombetta et al., 2019). This shift period observed in picophytoplankton in 2006 mirrors the shift in the microphytoplankton community identified in a previous study (decrease in diatom abundance and shift dominance from *Skeletonema‑Chaetoceros* to *Chaetoceros‑Pseudo-nitzschia* in the community between 2005 and 2008) (Derolez et al. 2020). Our results showed a rapid and significant response of the pelagic compartment to the decrease in nutrient loadings comparable to the responses observed in other coastal ecosystems (Boynton et al., 2013; Derolez et al., 2019; Leruste et al., 2016; Lie et al., 2011; Ní Longphuirt et al., 2016) and in lakes (Anneville et al., 2005; Jeppesen et al., 2007).

Decreases in nutrient concentrations and phytoplankton biomass and abundances were associated with a decrease in dissolved oxygen concentrations in summer from 1999 to 2018. This decrease could be induced by warming which is known to reduce the solubility of oxygen in water and to enhance microbial activity (Breitburg et al., 2018; Conley, 2000; Jager et al., 2018). Moreover, the respiration of shellfish coupled to the decrease in phytoplankton biomass could impact oxygen concentrations in water. Oligotrophication has also been shown to induce changes in trophic functioning, shifting from autotrophic regime to mixotrophic and heterotrophic regimes (Collos et al., 2009; Gowen et al., 2015; Lagarde et al., 2018b), and thus leading to changes in oxygen balance.

Our results provide for the first time a long-term analysis of the benthic compartment of the Thau lagoon. In the sediments, total nitrogen concentrations increased significantly from the 1980s to the 2010s, suggesting that the benthic compartment stored these nutrients during the eutrophication period. In contrast, we found no significant trend in total phosphorus, whose maximum value was reached in 2003 and whose minimum value was reached in 2014. Such contrasted evolution has already been reported in coastal ecosystems, where the presence of sulphate reduces the efficiency retention of DIP by the sediments and favours recycling of DIP over that of DIN (Caraco et al., 1990; Conley, 2000; Lehtoranta et al., 2009). Moreover, high temperatures and anoxic conditions have a significant effect on benthic fluxes of NH_4^+ and DIP (Souchu et al. 1998; Zilius et al. 2015). In Thau lagoon, we hypothesise that releases from the sediments, coupled with the decrease in inputs from the watershed - corresponding to internal and external nutrient loadings, respectively, (Chapelle et al.,

463   2000b) - led to stabilisation, or even to the beginning of a decrease in the quantities of phosphorus in

464   the sediments (lowest median of TP was observed in 2014).

465   Concerning the benthic macrophyte community, our results showed that the proportion of seagrass

466   decreased in favour of red algae from the 1960s to the 1990s. This trend corresponds to the generic

467   eutrophication trajectory described by many authors: a shift from dominance of seagrass and

468   perennial macrophytes to dominance of macroalgae (Schramm, 1999; Viaroli et al., 2008; Zaldívar et

469   al., 2008). Seagrass meadows only started to slightly recover between 2003 and 2008, but their

470   contribution to benthic vegetation did not reach the level observed in the 1960s, or the historical

471   conditions describing Thau lagoon dominated by seagrass at the beginning of the 20th century

472   (Calvet, 1910). Despite the significant and continuous decrease in nutrient inputs observed since the

473   1970s, the beginning of the recovery of the Thau lagoon macrophyte community lagged behind that of

474   the phytoplankton community. This time lag and partial recovery suggest hysteresis during

475   oligotrophication in the Thau lagoon and correspond to partial resilience observed in aquatic

476   ecosystems (Borja et al., 2010; Duarte et al., 2009; Elliott et al., 2007). Continuous nutrient fluxes

477   from sediments could promote phytoplankton or macroalgae growth and delay the recovery process

478   of perennial macroalgae and seagrasses (Kosten et al. 2011). Accordingly, internal phosphorus

479   loading from sediments has frequently been reported as a cause of hysteresis in lakes (Gulati and

480   Van Donk, 2002; Jeppesen et al., 2007; Søndergaard et al., 2003) and more recently in coastal or

481   estuarine ecosystems (Lillebø et al., 2007; Ní Longphuirt et al., 2016; Ratmaya et al., 2018; Riemann

482   et al., 2016).

483   During five decades of changes from eutrophication to oligotrophication, contrasting periods in the

484   pelagic and benthic compartments of the Thau lagoon were identified. This evolution is represented in

485   the conceptual model (Figure 9), showing the changes in several indicators of ecosystem status (DIP

486   concentration in water, phytoplankton and macrophyte) in response to changes in the levels of

487   pressures which affect the ecosystem (nutrient loads and temperature). Although the decrease in

488   nutrient loads was accompanied by a decrease in nutrient concentrations and phytoplankton biomass

489   in water, period 1 (1970-1992) can be considered as a eutrophic period due to the shift from seagrass

490   to red macroalgae and to the frequent and critical anoxic crises during that period. Period 2 (1993-

491   2018) was characterised by a better eutrophic status, less frequent and less intense anoxia crises and

492   by the continuation of the recovery process. This second period can be divided into three steps: 2a) a

17

493 transition phase (1993-2003) during which the pelagic compartment continued to recover from

494 eutrophication with stabilisation of the benthic community; 2b) a regime shift between the year 2003,

495 (before which seagrass continued to decline), and the year 2006, after which low chlorophyll *a* values

496 were reached in the water column. Since the summers of 2003 and 2006 were both characterised by

497 major heat waves and anoxias events, we hypothesise that this regime shift is the result of the

498 combination of an internal oligotrophication process and external forces linked to high summer

499 temperatures (Sheffer and Carpenter, 2003). After the regime shift, 2c) the ecosystem shifted to

500 oligotrophy (2006-2018), the water column became characteristic of an oligotrophic state and the

501 marine grass began to recover.

502 **4.2. Triggers of anoxia, resistance and resilience of the ecosystem**

503 To analyse the trajectory of Thau lagoon ecosystem over five decades, the effects of reduced nutrient

504 inputs and of climatic-related variables, especially the gradual increase in temperature, which was

505 evidenced in the Mediterranean and Thau regions (Bec et al., 2018; Cramer et al., 2018), need to be

506 taken into account. Indeed, oligotrophication and warming may have combined effects on biodiversity

507 and ecosystem functioning (Glibert, 2016; Kosten et al. 2011; Verbeek et al., 2018). Thus, we focused

508 particularly on the occurrence and intensity of anoxia crises as indicators of ecosystem resilience and

509 resistance and on what triggers these disturbances (Coffin et al., 2018).

510 The model used to predict the triggering of summer anoxia revealed that four variables were

511 significant (three meteorological variables and one corresponding to the eutrophication status). The

512 strongest effect was induced by air temperature, followed by the effect of the eutrophication period, by

513 the negative effect of wind, and to a lesser extent by the positive effect of rainfall in July. These

514 results highlight the effects of climate variables and confirmed a previous study underlying the effects

515 of increasing temperature and decreasing winds on the probability of the occurrence of anoxia in the

516 Thau lagoon (Harzallah and Chapelle, 2002). In coastal ecosystems, decreased wind speed could

517 play an important role in triggering anoxia by decreasing vertical water mixing and oxygenation at the

518 air-water interface (Chen et al., 2015; Du et al., 2018; Zilius et al., 2015). In northern temperate

519 estuaries, increased frequency of extreme summer rainfall events could increase the frequency of

520 anoxia events because floods can mobilize significant quantities of organic matter and suspended

521 solids which are subsequently deposited in estuaries and/or due to more intense stratification (Iriarte

522 et al., 2014; Oviatt et al., 2017).

523   We showed a 6-fold higher risk of triggering anoxia in the first period (1970-1992), considered to be

524   the eutrophic period. It is known that anthropogenic nutrient inputs affect both the oxygen supply and

525   uptake (Conley, 2000; Friedrich et al., 2014; Souchu et al., 1998) and that eutrophication-related

526   parameters (chlorophyll a biomass or nutrient concentrations or loadings) can trigger anoxia in coastal

527   areas (Coffin et al. 2018; Du et al. 2018; Zilius et al., 2015). What is remarkable about our result is the

528   marked effect of the eutrophication status, so that the oligotrophication process observed during our

529   study period led to increasing resistance of the Thau lagoon ecosystem to climate stress. Among the

530   climatic-related variables, the effect of air temperature on triggering anoxia was the strongest. Indeed,

531   the functioning of the lagoon could be particularly threatened by warming since increases in the

532   annual average temperature and in the frequency of summer heat waves were recorded in the

533   Mediterranean region from the 1970s to the 2010s (Bec et al., 2018; Cramer et al., 2018). However,

534   oligotrophication lead to the decreased risk of triggering anoxia in the Thau lagoon. This is consistent

535   with a previous study in the mid-estuarine waters (Bilbao, Spain) showing that anthropogenic-

536   mediated pollution mitigation was more important than climatic factors in driving inter-annual

537   variations in dissolved oxygen saturation (Iriarte et al., 2014). In Narragansett Bay (USA), Oviatt et al.

538   (2017) showed that a 60% reduction in nutrient concentrations resulted in a 34% reduction in summer

539   hypoxia. In Chesapeake Bay (USA), authors suggested that reductions in nutrient loads would also

540   reduce hypoxic volumes (Testa et al., 2014), but biological conditions (linked to nutrient loading) and

541   physical conditions (vertical exchange and temperature) could play an equally important role in

542   seasonal and inter-annual variations in the hypoxic condition of this ecosystem (Du et al., 2018).

543   Among the climatic-related variables, we also showed a decrease in the rainfall levels from period 1 to

544   period 2, due to the decrease in the occurrence of wet years recorded since 2005 (Bec et al., 2018).

545   This trend may have facilitated the oligotrophication process by decreasing nutrient inputs resulting

546   from watershed runoff (Bec et al., 2018).

547   With climate change trends already demonstrated by regional meteorological experts and predicted

548   for the future (Jouzel et al., 2014), we would expect the effects of climate warming to slow down or

549   even reverse the recovery process observed in the Thau lagoon. At regional scale, meteorological

550   datas revealed that 2003, 2017 and 2018 were the three hottest summers in the 1970-2018 period

551   (Météo-France, 2018). In the present study, the last anoxia crisis occurred in 2018 when the water

552   column was characteristic of an oligotrophic state (Figure 9) and after a 12-years period without

anoxic event. This support the conclusions drawn in the Mediterranean Basin where accelerated climate change could exacerbate existing environmental problems (Cramer et al 2018). Similar results have been reported these limits in Lake Zurich, where, despite the success achieved in fighting eutrophication, a recent increase in hypoxia has been observed (Friedrich et al., 2014). In Chesapeake Bay, it has been shown that the expected climate changes will exacerbate physical conditions, which would also amplify the negative impact of human-induced eutrophication, requiring greater efforts to reduce nutrient inputs in order to reach a satisfactory level of water quality (Du et al., 2018). Finally, a recent study (Jager et al., 2018) reviewed ways to enhance the resilience of coastal aquatic ecosystems in the face of future, unnatural hypoxic regimes. In addition to efforts to slow climate change, the measures identified by these authors include: reducing nutrient and carbon loadings from rivers, restoring aquatic vegetation, increasing oxygen exchange in sediments and water clarity via the management of key species such as seagrass, or the protection of oyster and mussel beds (Jager et al., 2018). The restoration of the health of oyster reefs and the expansion of tidal marshes were also shown to reinforce the improvement of water and habitat quality along a restoration trajectory in Chesapeake Bay (Kemp et al., 2005). The choice of management options first requires the definition of a desirable state for the ecosystem. Jager et al. (2018) defined desired states as ecosystems with long trophic chains and slow nutrient and carbon dynamics that provide many ecosystem services. Other authors have shown that different levels of Mediterranean coastal lagoon restoration may be desired by society in terms of recovery of ecosystems, and that some discrepancies can be observed between social representations and ecological diagnoses (Audouit et al., 2017; de Wit et al., 2015).

4.3. Management of restoration and shellfish farming

In Thau lagoon, the significant efforts invested by public stakeholders and managers to mitigate eutrophication which began in the 1970s have succeeded in reducing the occurrence of anoxia events by increasing ecosystem resistance and achieved the good water column status targeted by the WFD. Official assessments of the biological quality elements in application of the WFD have only been carried out since 2009 in Thau lagoon. According to these diagnoses, the phytoplankton has reached the good status in 2009 and shifted to a high status in 2018 (Andral and Sargian, 2010; Bouchoucha et al., 2019). However, the macrophytes remained in a medium status from 2009 to 2018, although an improvement was observed, associated with the increase in the coverage of

583   *Zostera spp*. The delay in reaching the WFD good status for macrophytes in comparison to

584   phytoplankton is related to the time lag evidenced by several authors in the recovery of the benthic

585   compartment (Borja et al., 2010; Le Fur et al., 2019). A recent study carried out on several French

586   Mediterranean lagoons (Derolez et al., 2019) hypothesised that the level of recovery after the

587   reduction of nutrient inputs could be affected by: (i) external drivers, such as completeness of nutrient

588   reduction, marine connectivity, or climate change; (ii) internal factors such as physical traits, sediment

589   nutrient stocks or the presence of residual seagrass patches or seed stocks; and interactions between

590   the two drivers. Among the three strategies identified for the lagoons which have not fully achieved

591   the objectives set by the European WFD ("Wait and see", "Go further", "Give a helping hand"), the first

592   seems to be the most relevant for the Thau lagoon according to the importance of the works

593   performed on the depuration system and their efficiency observed in the ecosystem. One could

594   hypothesise that eutrophication pressure is now sufficiently low to allow the benthic compartment to

595   recover its ecological functions and structure of the reference conditions, after a period of hysteresis.

596   However, it should be noted that in the 1990s, some authors mentioned the threat of reaching the

597   limits of the trophic capacity of the Thau lagoon if the depuration works became too drastic (Deslous-

598   Paoli et al., 1998; Souchu et al., 1998). During the recovery, shellfish production in Thau lagoon has

599   evolved due to changes in the main reared species from mussels to oysters from the 1970s to the

600   1990s for epizootic and economic reasons (Hamon and Tournier, 1984; Le Brun, 1985); the removal

601   of some shellfish structures located along the shoreline in the early 2000s following the

602   recommendations of scientists made after the critical anoxia events of the 1990s (Deslous-Paoli et al.,

603   1998; Souchu et al., 2011); and changes in farming techniques following epizootics such as OsHV-1

604   in 2008 (Pernet et al., 2014). This last epizootic reduced oyster production by half. More recently,

605   fishermen and shellfish farmers have been facing economic difficulties and they worry about the

606   potential limiting capacity of the ecosystem (Derolez et al. 2020). In the context of emerging marine

607   diseases related to climate change, recent studies have shown that the impact of oyster diseases can

608   be limited by maintaining the good ecological status of coastal waters (Harvell et al., 1999; Pernet et

609   al., 2018). To reach a satisfactory trade-off between uses, ecosystem services and maintaining

610   biodiversity and ecological functions under global change, there is a need to use ecosystem-based

611   models (Filgueira et al. 2015; Guyondet et al., 2014; McKindsey et al., 2006). Such a model has been

612   developed for Thau lagoon and showed that lagoon productivity significantly depends on

613 hydrometerology, with higher oyster production in wet years than in dry years (Pete et al., 2020).

614 Using a modeling approach based on scenario comparisons would help (i) disentangle the effects of

615 anthropogenic forcings and of climate driven variables such as increasing temperature or decreasing

616 rainfall and (ii) determine the limits of ecological tolerance. By testing different management and

617 climate scenarios, this modelling approach would also help decision-makers better target their actions

618 to improve the ecosystem's resistance to increasing climate pressure. It is will also be necessary to

619 increase high-frequency oxygen measurements in real time (Friedrich et al., 2014; Schmidt et al.,

620 2017) to help managers and shellfish farmers better anticipate the appearance of hypoxia/anoxia and

621 design and apply mitigation actions (e.g. emersion of oysters at night) to mitigate environmental and

622 economic impacts. Finally, in the context of global change, Breitburg et al. (2018) recommend an

623 integrated framework, combining modelling, observations and experiments and involving all

624 stakeholders (scientists, local governments, shellfish farmers) to facilitate the development and

625 implementation of the most ecologically and economically effective management strategy to reduce

626 anoxia.

627 **5. Conclusions**

628 The processes and consequences of oligotrophication have been poorly studied in coastal lagoons

629 from a long-term perspective and at ecosystem scale. By analysing time series over 5 decades of

630 observations on pelagic and benthic autotrophic communities, our study shows how the decrease in

631 nutrient inputs led to major ecological changes in a Mediterranean coastal lagoon used for shellfish

632 farming. Considering anoxia crises as indicators of ecosystem resilience and resistance, the

633 combined analysis of meteorological data, eutrophication status and shellfish production over these 5

634 decades allowed us to identify air temperature and eutrophication status as the two main triggers of

635 summer anoxia.

636 We identified successive periods in ecosystem functioning during the oligotrophication process: a

637 eutrophic period characterised by a shift from dominance by seagrass to dominance by red

638 macroalgae; a 3-step period characterised by a better eutrophication status i.e. a transition phase with

639 a stable benthic community, a regime shift between two heat waves and anoxic crises; and finally the

640 achievement of oligotrophic conditions. Our analyses also show that oligotrophication has led to

641 changes in the drivers of summer anoxia, making the ecosystem more resistant to climatic stress

642 caused by high summer temperatures.

643 However, with predicted climate change trends, we would expect the effects of climate warming to

644 slow down or even to reverse the observed recovery process. The development and use of

645 ecosystem-based models are now needed to better understand the functioning of the ecosystem and

646 to help stakeholders find a trade-off between uses, ecosystem services and the maintenance of

647 biodiversity and ecological functions in the context of global change.

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Fig. 1. A) Location of Thau lagoon and of water and macrophyte sampling stations (*the macrophyte station not sampled in 2003). B) Location of sediment sampling stations. The three shellfish farming areas are represented by polygons.

Fig. 2. Changes in summer DIP concentrations (µM) in the water in Thau lagoon from 1972 to 2018 at ZA station (1972-1993) and TE station (1999-2018). Data for June are represented by black dots and the LOESS curve in DIP in June by a black line. Data for July and August are represented by grey dots. The blue line represents the threshold of the good status according to the WFD (DIP ≤ 1 µM; MTES, 2018).

Fig. 3. Results of PCA analysis of water column parameters monitored from 1999 to 2018 at the three stations TW, TE and TANG. A) First and second axes for the nine environmental variables (dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), total phosphorus (TP), total nitrogen (TN), chlorophyll *a* (CHLA), autotrophic picoeukaryotes (PEUK), nanophytoplankton (NANO), phycoerythrin-rich picocyanobacteria (PE-CYAN) and dissolved oxygen (O2)). Illustrative hydrological variables (temperature (TEMP), salinity (SAL) and turbidity (TURB)) are in blue. B) Years and C) sampling stations on the plane defined by first and second axes accounted for 52.6% of the total variability. The first cluster is represented by a grey ellipse and the second cluster by a black ellipse.

Fig. 4. Changes in mean summer chlorophyll *a* biomass (µg Chla L^{-1}) (A), nanophytoplankton (B), picoeukaryote (C) and phycoerythrin-rich picocyanobacteria abundances (10^6 cells L^{-1}) with changes in water temperature (°C) (D) from 1999 to 2018 at TW and TE (averaged) and TANG stations (respectively in blue and orange).
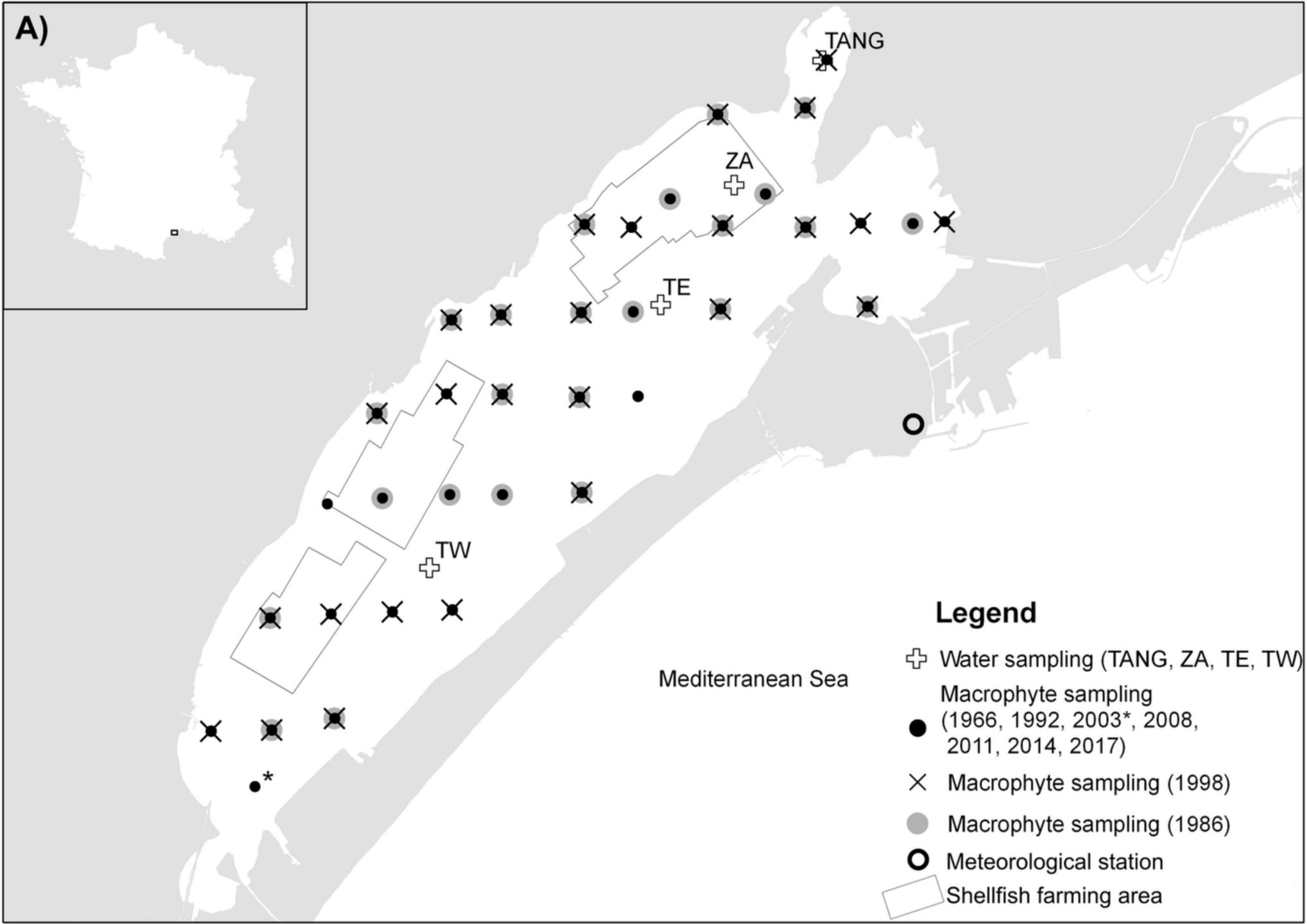
Fig. 5. Proportion of stations dominated by four groups of macrophytes (seagrass, brown algae, red algae and green algae) or bare sediment from 1966 to 2017 (data from Bouchoucha et al. 2019; Derolez et al. 2015; Dubois 1972; Gerbal and Verlaque 1995; Ifremer 2004, 2009 & 2012; Lauret 1967, 1970, 1990 & 1994; Verlaque, 2000). *NB: 1966 refers to the sampling period 1963-1968; 1992 refers to the sampling period 1988-1994.*
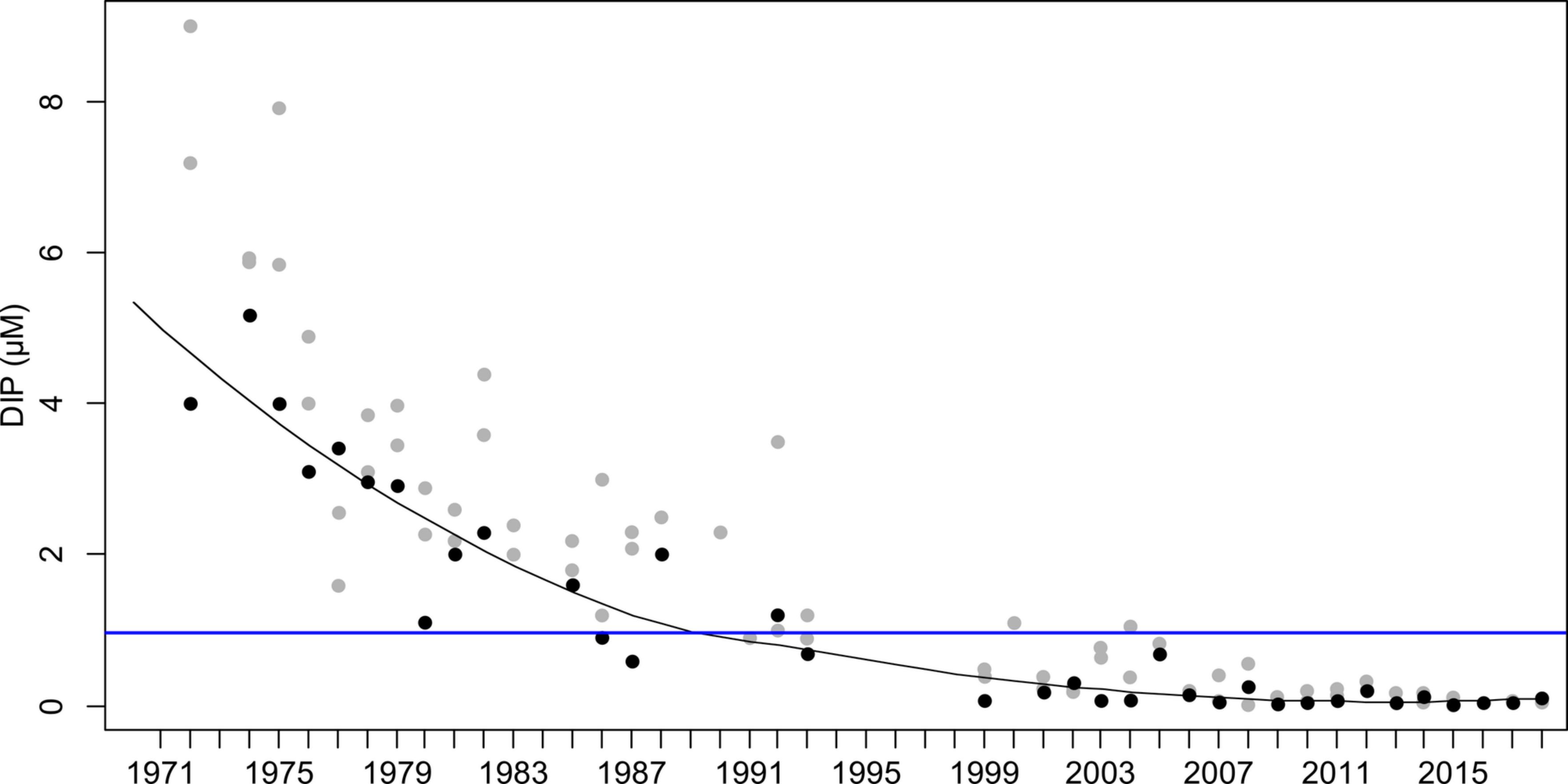
Fig. 6. Oyster (in brown), mussel (in grey) and total shellfish production (in black) in 10^3 t $year^{-1}$ from 1970 to 2018 and the occurrence of summer anoxia events (vertical grey bands) in Thau lagoon.
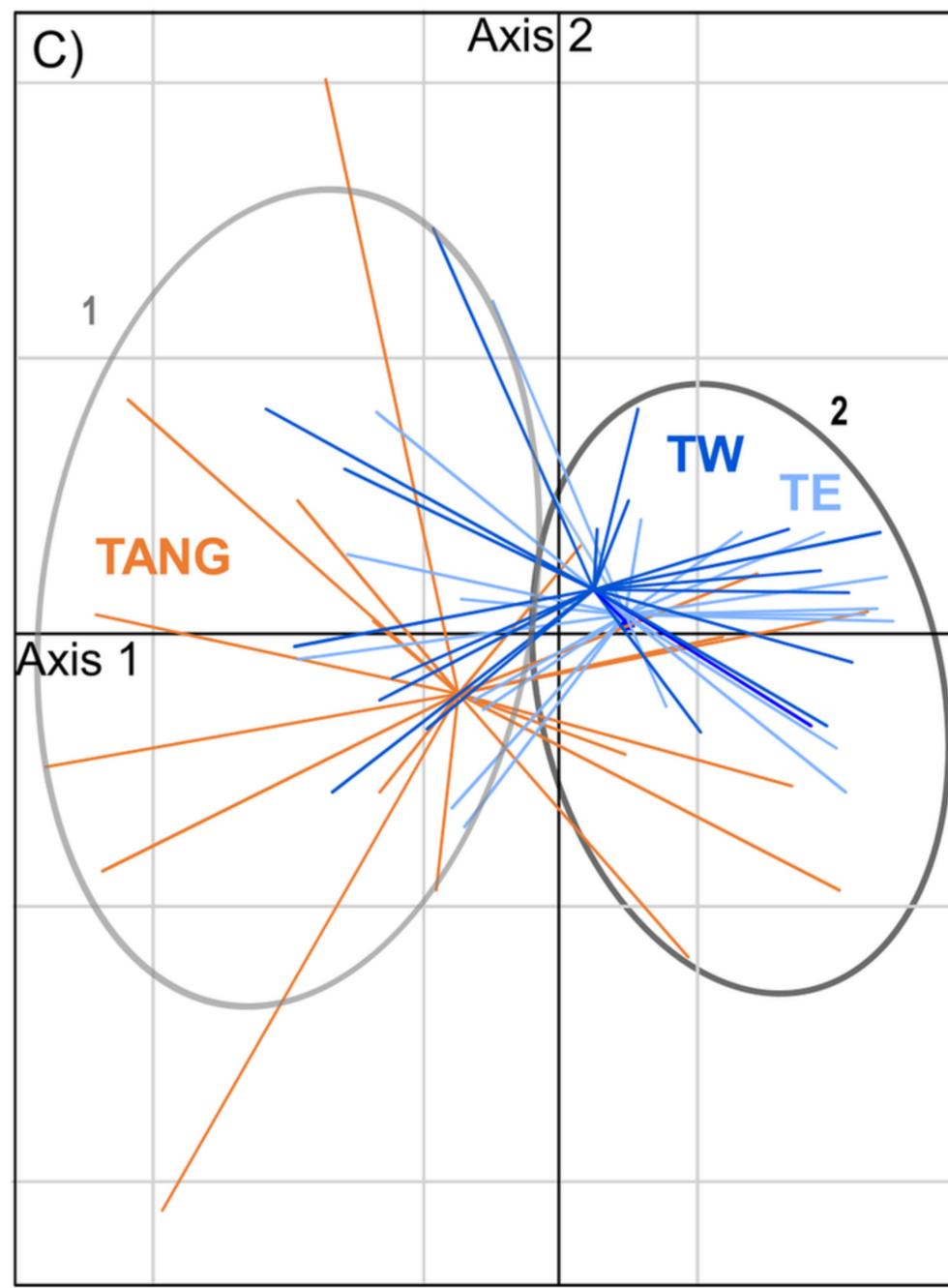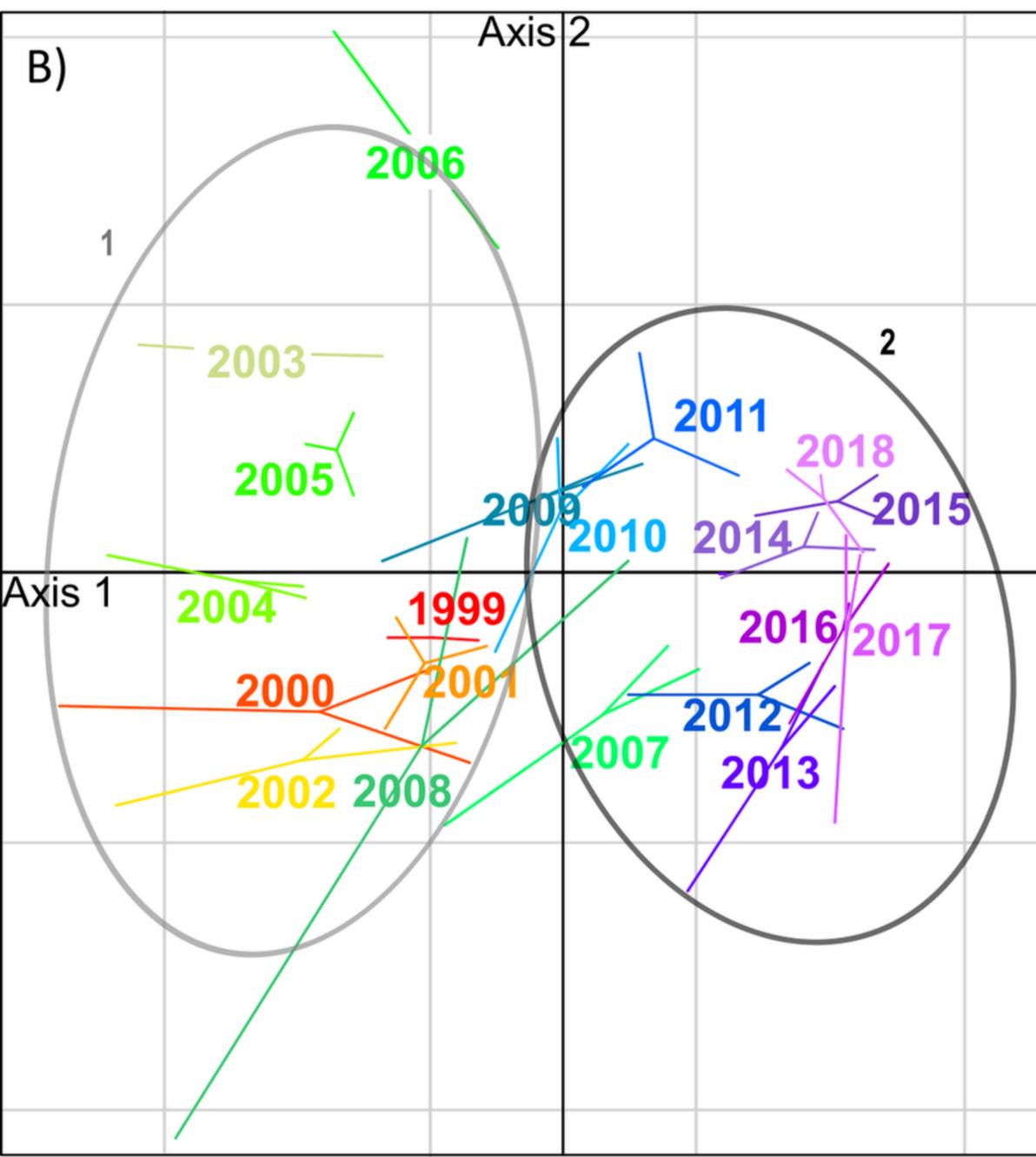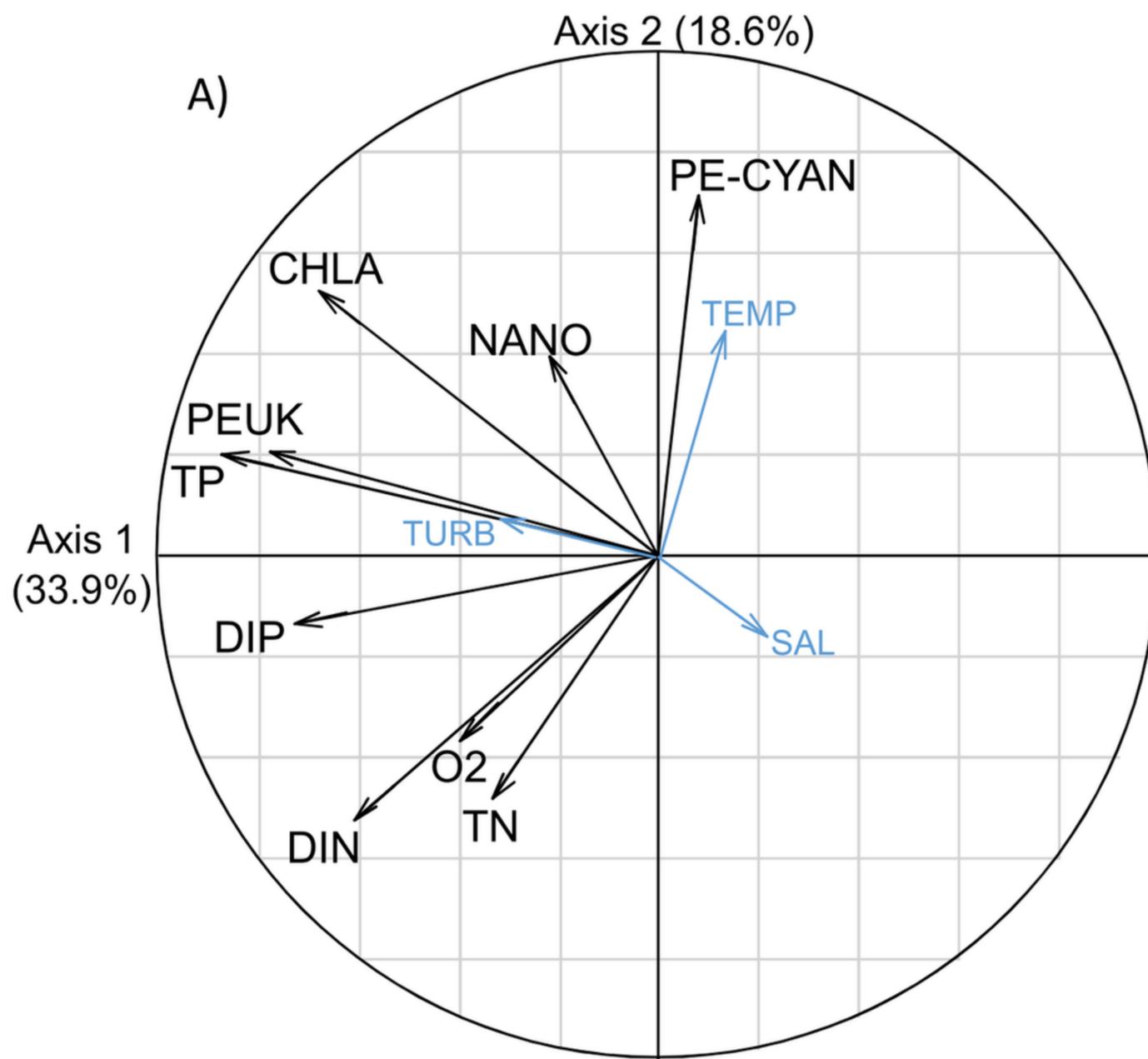
1104   **Fig. 7.** Duration and intensity of summer anoxia crises from 1970 to 2018. The y-axis corresponds to

1105   the duration (months) of the crises and the size of the bubbles corresponds to the spatial extent of the
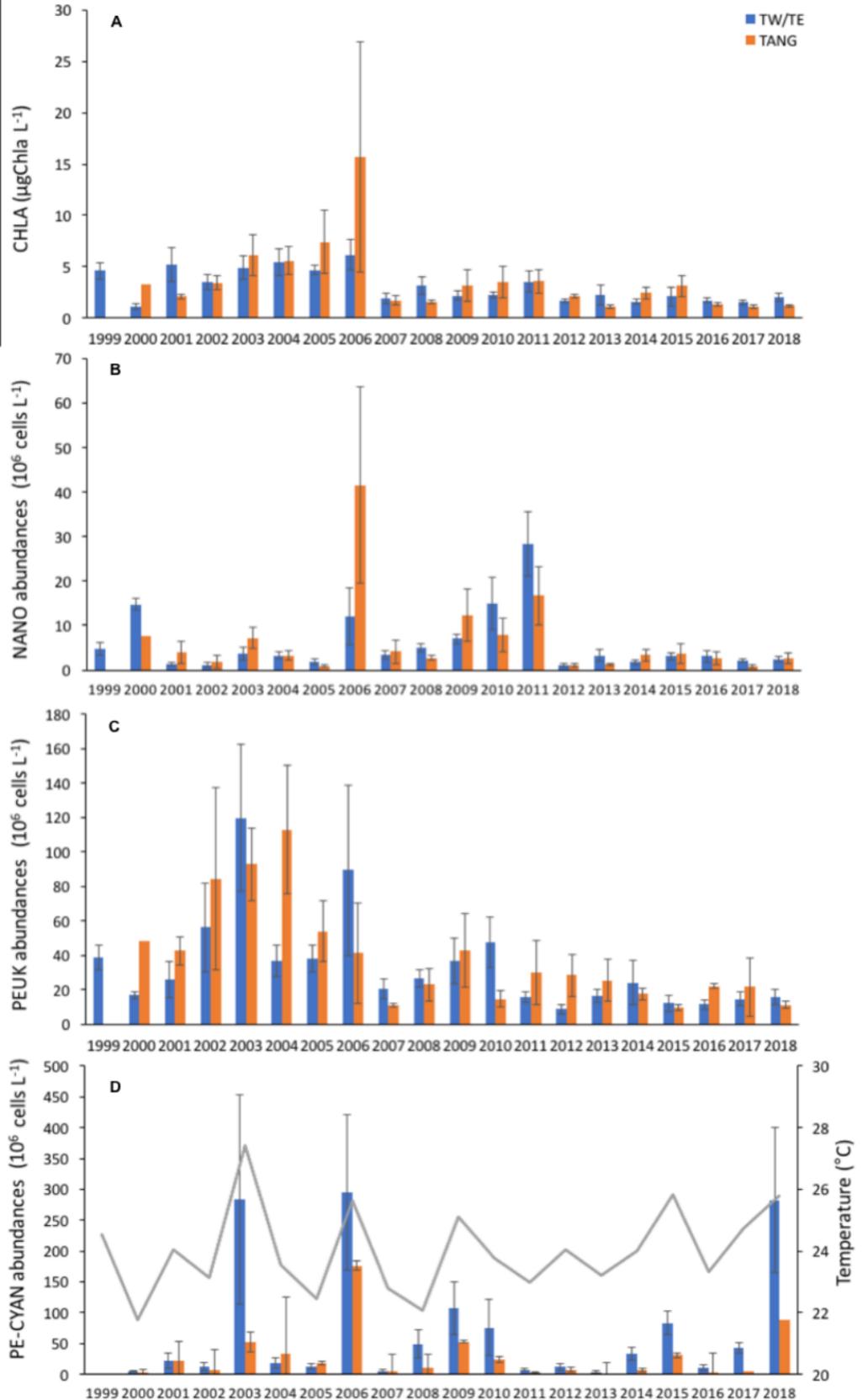
1106   anoxia.

1107   **Fig. 8.** Effects of the 3 meteorogical variables included in the glm predicting the probability of

1108   triggering summer anoxia (%: mean and confidence interval): wind intensity (wind_ST, standardised

1109   unit), air temperature (air_M, °C), rainfall in July (rainfall_7, mm), based on the period determined

1110   according to the eutrophication status (period 1 or period 2).

1111   **Fig. 9.** Schematic synthesis of the oligotrophication process in Thau lagoon from 1970 to 2018 (period

1112   1 and the 3 steps in period 2) and a possible scenario for the period 2020-2030 (stabilization of the

1113   nutrient load and increase in temperature). Pressures: nutrient inputs from the watershed and climate

1114   driver (temperature). Impact: the size of the bubbles represents the spatial extent and the intensity of

1115   the colour grey the intensity of the summer anoxia crises. Changes in mussel and oyster production:

1116   the size of the shellfish represents the level of production. Abundance of DIP and Chl *a* in the lagoon

1117   water and the abundance of seagrass, green algae and red algae in the soft-bottom sediment.

1118   Ecosystem status: the eutrophication status of the water column according to the WFD thresholds

1119   determined for DIP in French coastal lagoons (MTES, 2018). All variables are represented within
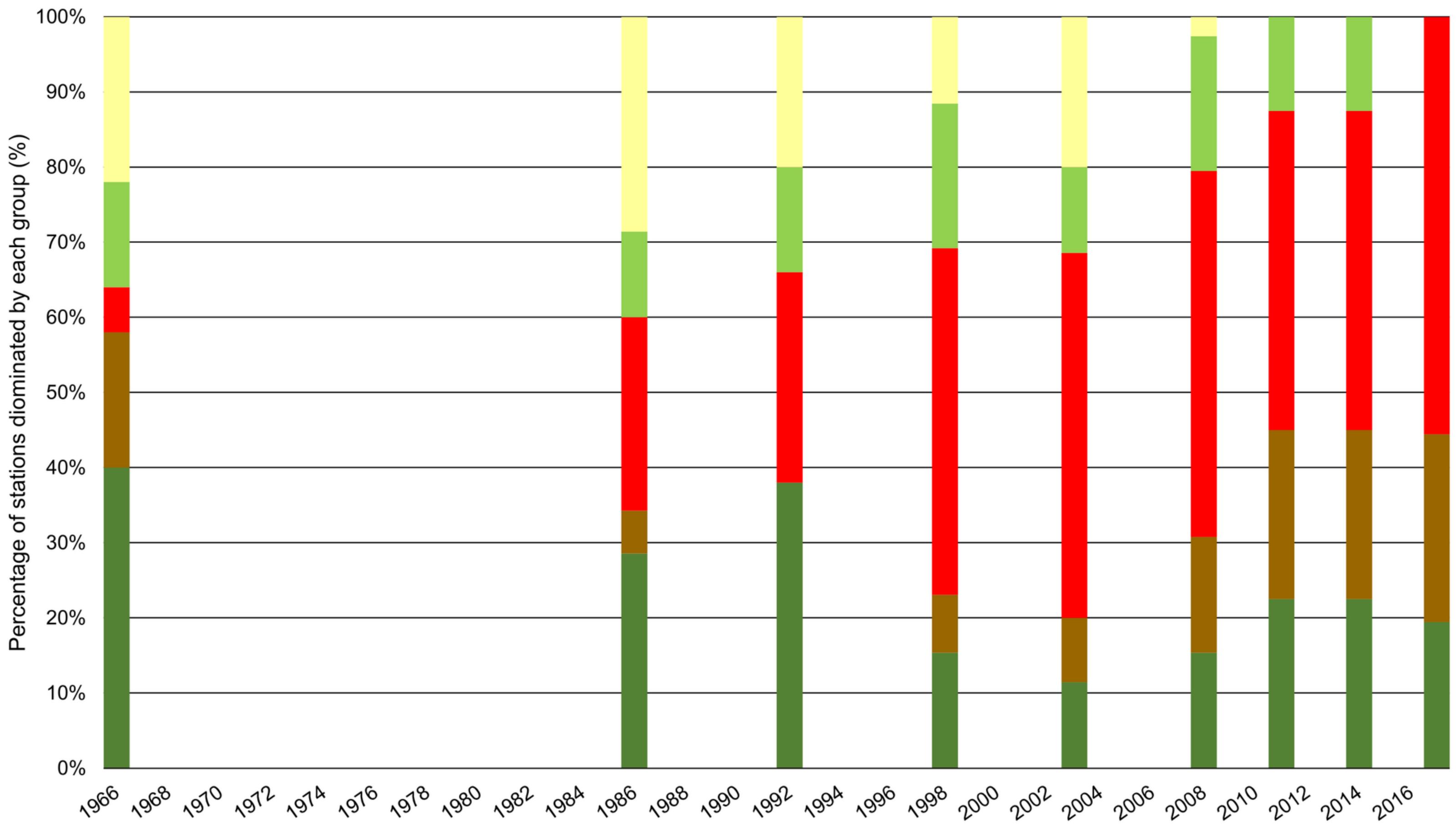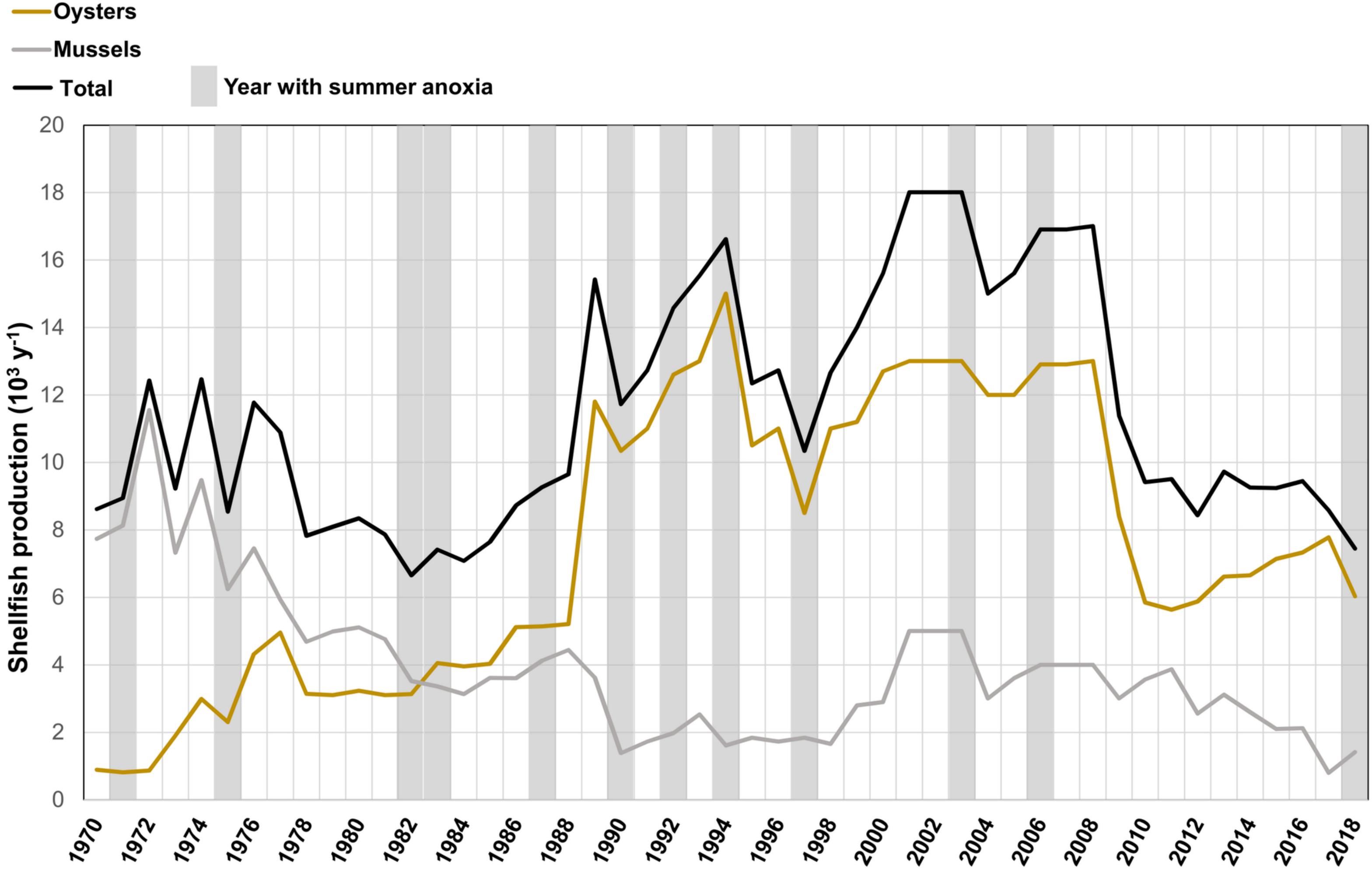
1120   relative space.
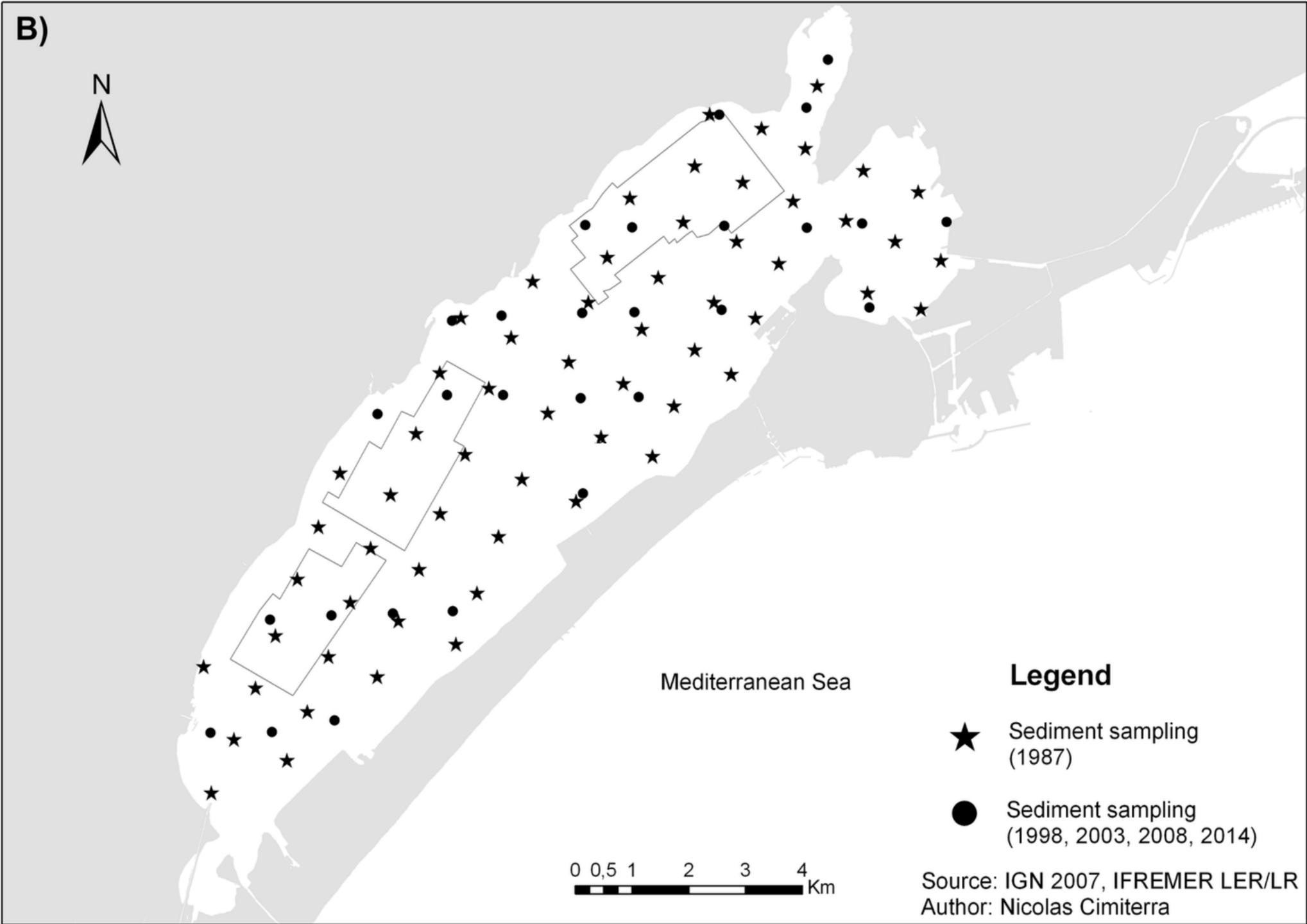
A)

TANG

ZA

TE

Mediterranean Sea

TW

Legend

✚ Water sampling (TANG, ZA, TE, TW)

Macrophyte sampling
● (1966, 1992, 2003*, 2008,
2011, 2014, 2017)

✕ Macrophyte sampling (1998)

● Macrophyte sampling (1986)

◯ Meteorological station

▭ Shellfish farming area

B)

N

Mediterranean Sea

Legend

★ Sediment sampling
(1987)

● Sediment sampling
(1998, 2003, 2008, 2014)

0 0,5 1   2   3   4
━━━━━━━━━━━━ Km

Source: IGN 2007, IFREMER LER/LR
Author: Nicolas Cimiterra

Period 1. Eutrophic period

Period 2
2a. Transition 2b. Regime shift 2c. Towards oligotrophy

PRESSURES

NUTRIENT LOAD

+

TEMPERATURE

−

IMPACT Anoxia

?

Shellfish production

Abundance

+

Seagrass

Chl *a*

DIP

Green algae

Red algae

−

?

1970 1980 1990 2000 2010 2020 2030
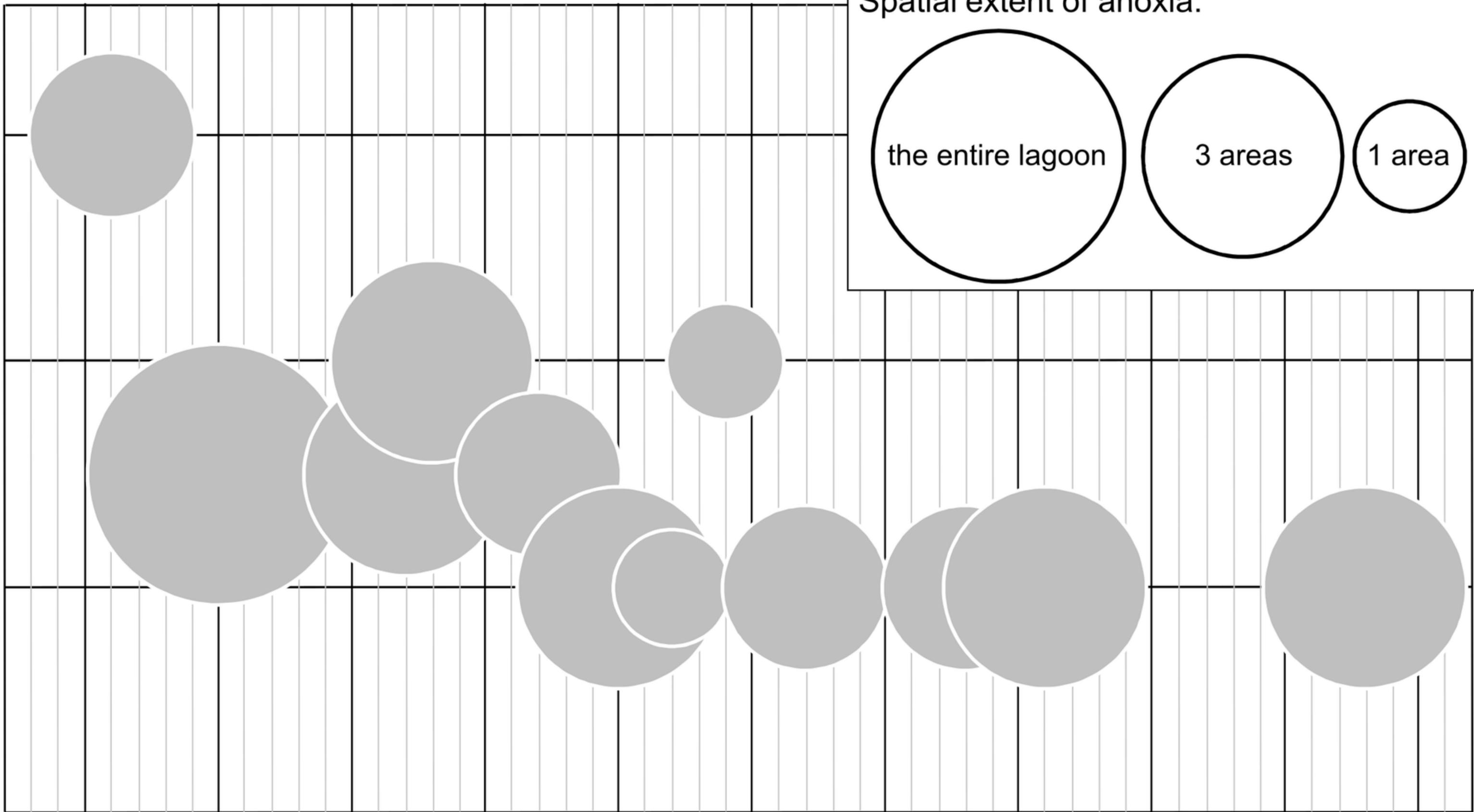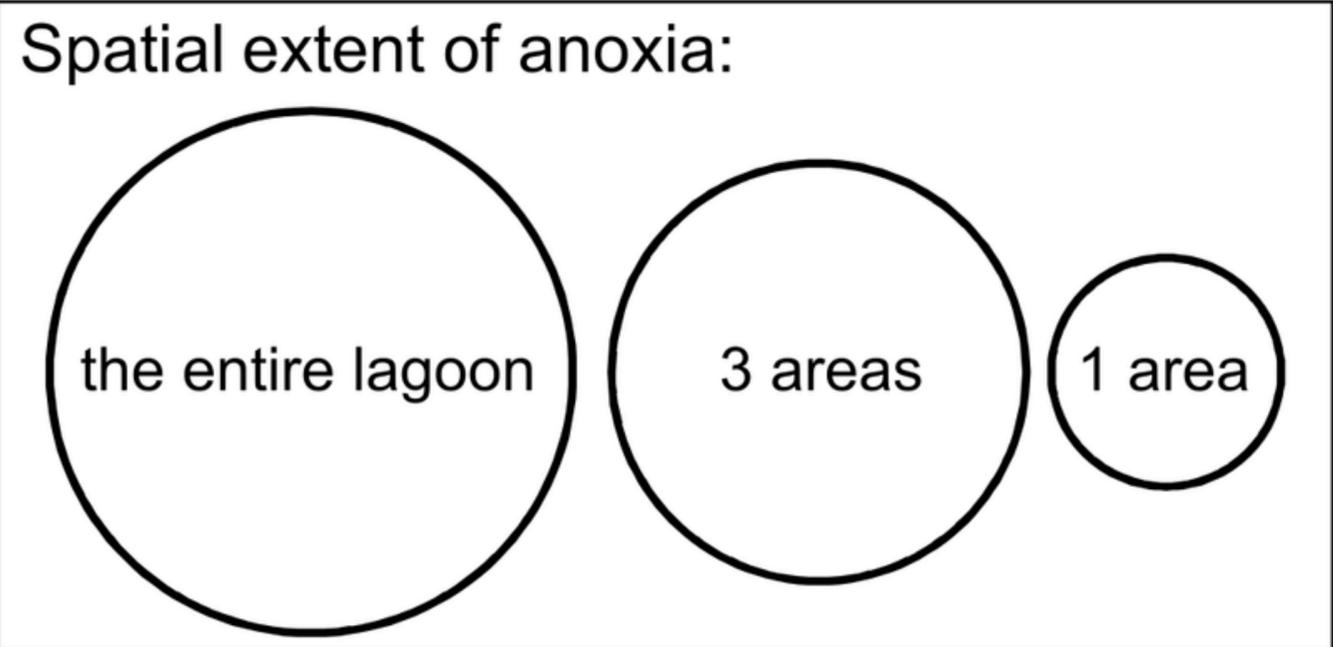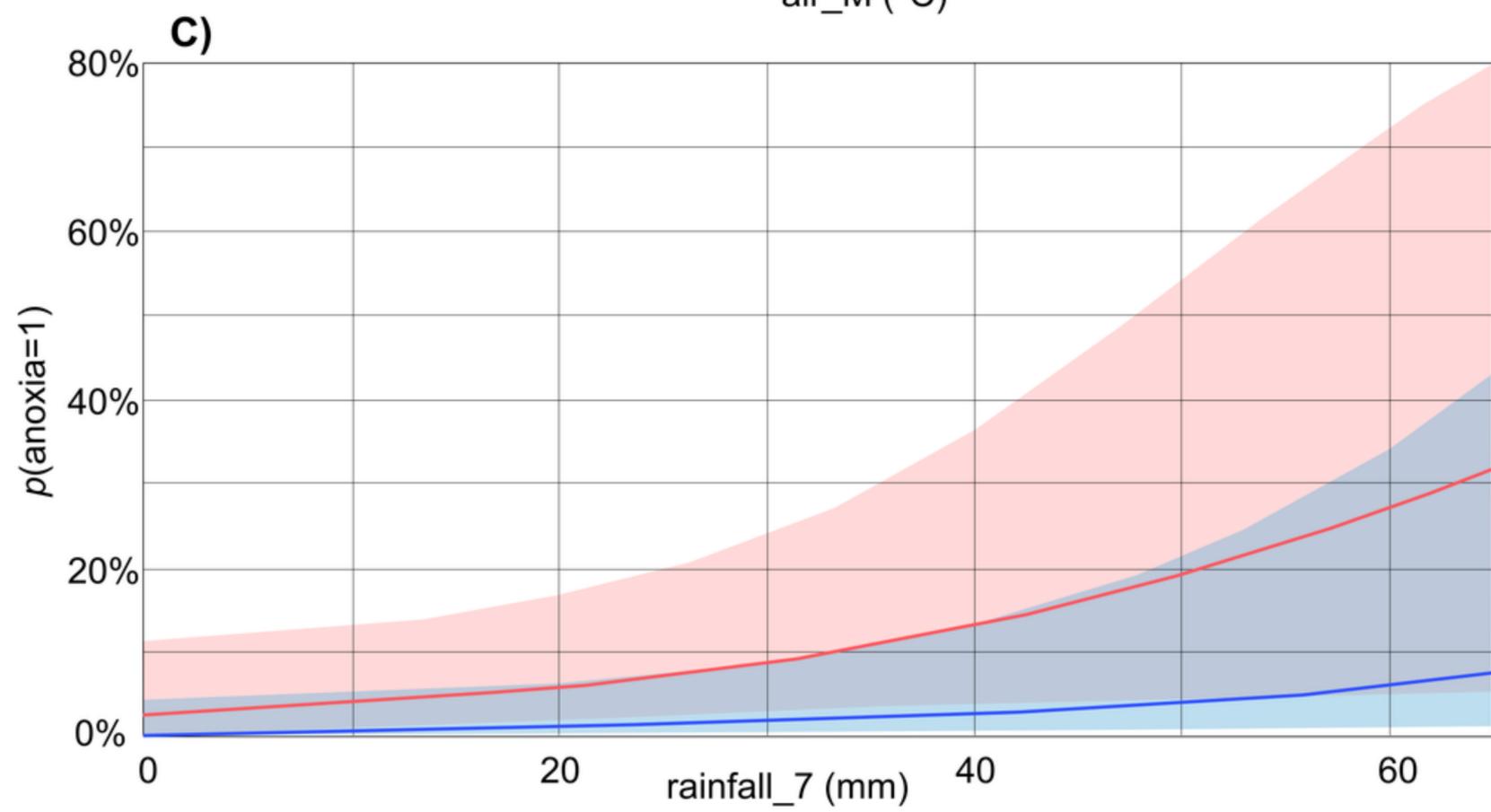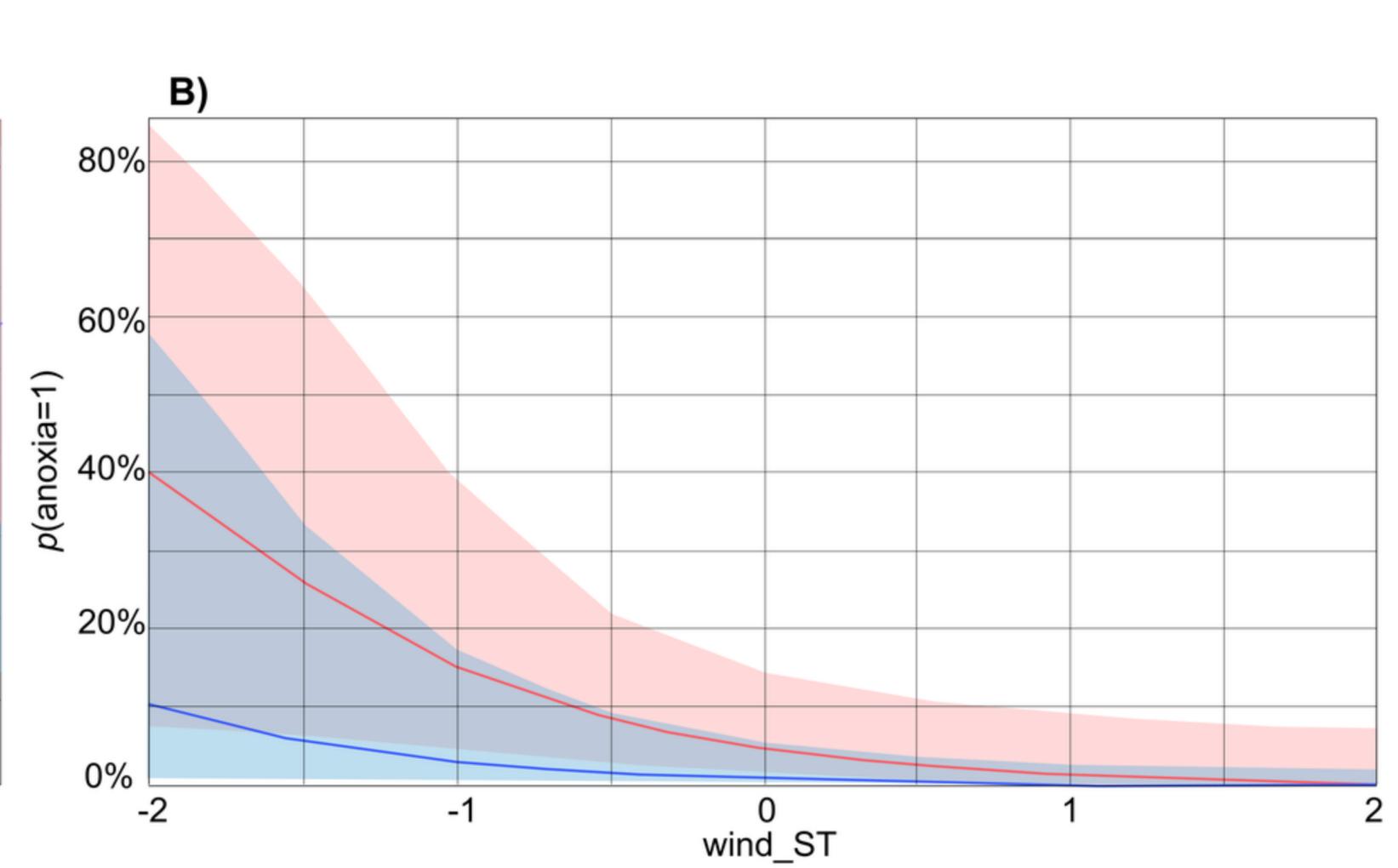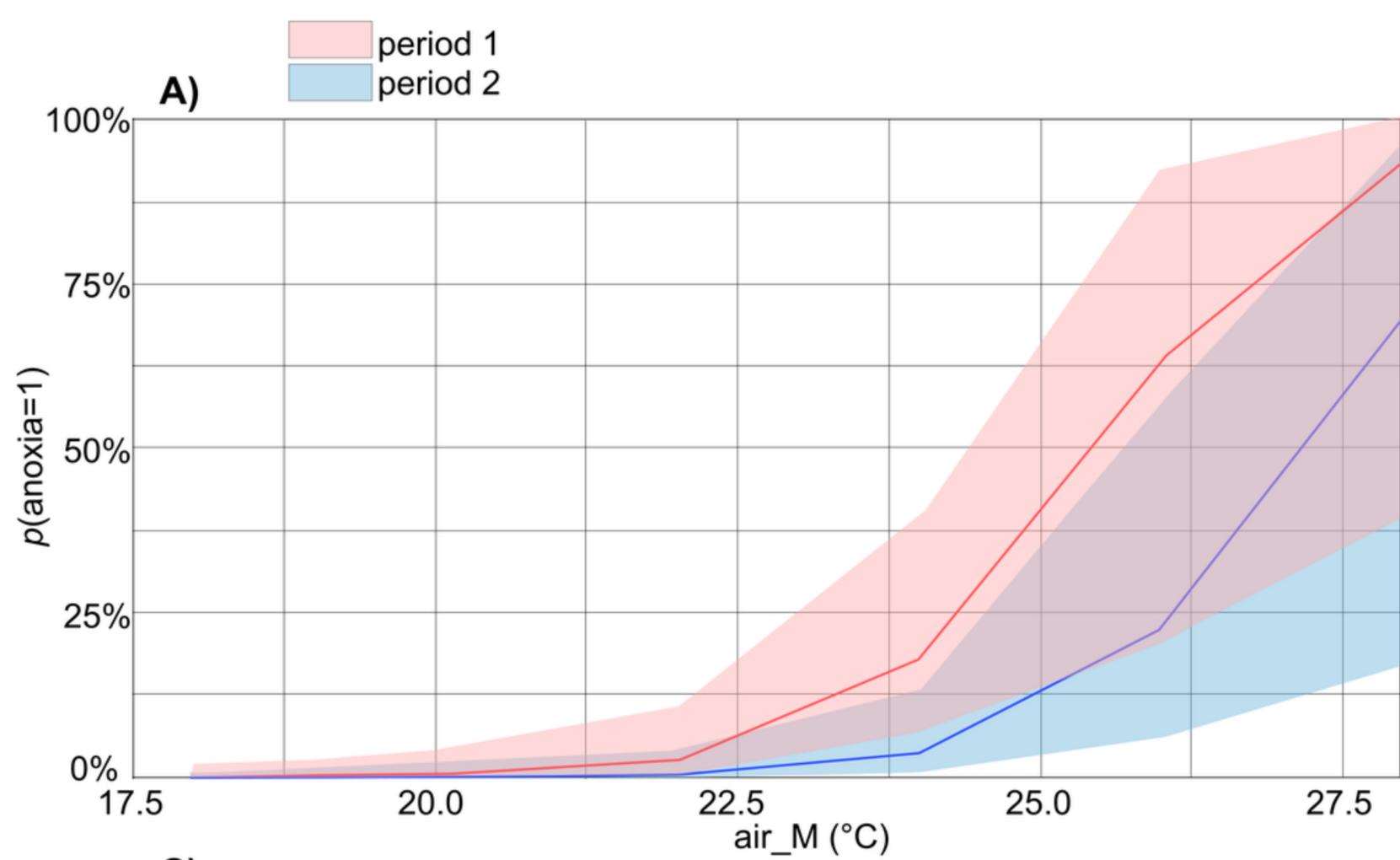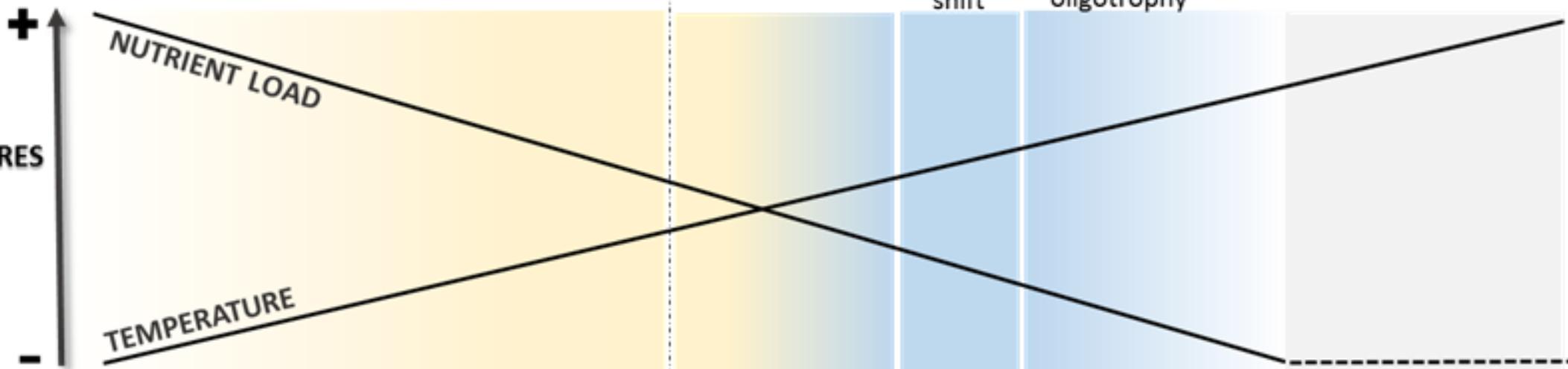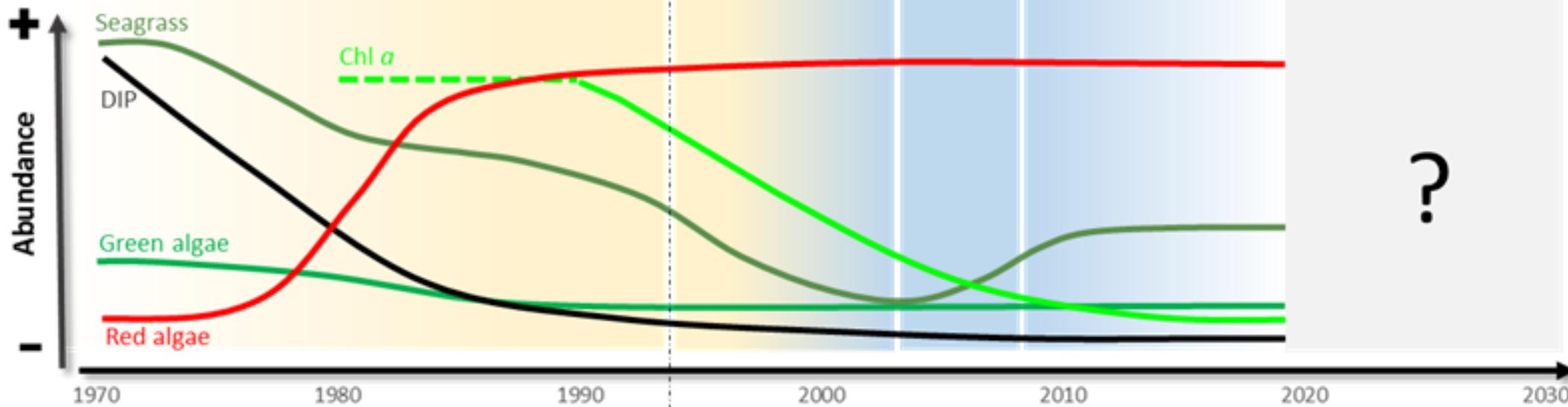
ECOSYSTEM STATUS
water column

Oligotrophication

Period 1. Eutrophic period

Period 2

2a. Transition

2b. Regime shift

2c. Towards oligotrophy

PRESSURES

NUTRIENT LOAD

TEMPERATURE

IMPACT Anoxia

Shellfish production

1970   1980   1990   2000   2010   2020   2030

?

ECOSYSTEM STATUS

Oligotrophication