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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 ecosystem resilience and resistance, we then analysed meteorological data, eutrophication status and shellfish production to identify the triggers of summer anoxia over the 49-year period.

2. Materials and methods

2.1. Study site

Thau lagoon is a microtidal restricted coastal lagoon, connected to the Mediterranean Sea through two permanent inlets, one of which is the Sète channel located in the north-east, which is responsible for 90% of sea water exchanges (Fig. 1) (Fiandrino et al., 2017). The lagoon covers an area of 68 km², its mean depth is 4 m (Fiandrino et al., 2017). A depth gradient is observed from the south-west mean depth: 3.3 m) to the north-east (mean depth: 5.2 m) of the lagoon (Souchu et al., 2001). The Thau watershed covers 280 km² and is drained by tributaries with intermittent flows and two permanent rivers (La Jeunesse et al., 2015). Approximately half the watershed's permanent population (103,500 inh. in 2015, INSEE 2016) is located in the city of Sète (La Jeunesse et al., 2015).

Shellfish farming structures cover 20% of the lagoon surface in three cultivation zones (Fig. 1). The shellfish reared are mussels *Mytilus galloprovincialis* (*M. galloprovincialis*) and Pacific oyster, *Crassostrea gigas* (*C. gigas*), whose production accounted for about 10% of total French oyster production in the 2000s (Gangnery et al., 2003).

2.2. Biological and meteorological monitoring

The biological and meteorological data used in our study, the associated spatial and temporal strategy and the references when available, are described in detail in Table A1.

2.2.1. Hydrological, nutrients and phytoplankton time series

From 1999 to 2018, water samples were collected monthly in summer (June, July and August), which is the maximum primary production period in Mediterranean lagoons (Bec et al., 2011; Souchu et al., 2010), at three stations: TANG, TE and TW (Fig. 1A). Samples were collected a minimum of three days after any period when wind speed exceeded 12.5 m s^{-1} to allow sediments to stabilise. Temperature (*TEMP*, °C), salinity (*SAL*) and dissolved oxygen (*O2*, mg L^{-1}) were recorded *in situ* with field sensors. At each station, on each sampling occasion, one water sample was collected in a 1 L polypropylene bottle one metre below the surface for laboratory analyses, according to Souchu et al. (2010).

Laboratory analyses were carried out to measure dissolved and total nutrient concentrations (µM): dissolved inorganic phosphorus (*DIP*), dissolved inorganic nitrogen (*DIN* = NH_4^+ + NO_3^- + NO_2^-), total nitrogen (*TN*) and total phosphorus (*TP*). Nutrients were analysed using the standard protocols (Aminot and Kérouel, 2007) described in Souchu et al. (2010). Turbidity (*TURB*, NTU) was measured in the laboratory with a HACH 2100N IS sensor according to ISO 7027.

From 1972 to 1993, DIP was analysed in water samples collected monthly in summer at ZA station, located in the shellfish farming area in the north-east part of the lagoon (Fig. 1A) (Collos et al., 2009; Derolez et al., 2020; Souchu et al., 1998).

Phytoplankton analyses were performed according to Bec et al. (2011). Chlorophyll *a* concentrations (*CHLA*, µg Chl *a* L^{-1}) were measured by spectrofluorimetry (Neveux and Lantoine, 1993) with a Perkin-Elmer L650. Based on cytometric analyses, different size classes of phytoplankton were identified and counted with a FACSCalibur flow cytometer: autotrophic picoeukaryotes (≤ 3 µm) and nanophytoplankton (> 3 µm) abundances (*PEUK* and *NANO*, 10^6 cells L^{-1}). Phycoerythrin-rich picocyanobacteria (< 1 µm, *PE-CYAN*, 10^6 cells L^{-1}) were distinguished from other photosynthetic organisms by their strong orange fluorescence and light-scattering properties.

2.2.2. Macrophyte and sediment time series

Soft bottom macrophytes were monitored five times in June from 2003 to 2017 at 36 stations (Fig. 1A, Table A1). Data from four older samplings (1966 to 1998), collected using different sampling protocols and monitoring methods, were added to the macrophyte time series. Table A1 summarises the years of observation, the formats of the data and the sampling methods used for all macrophyte data. In the case of sampling carried out over several years to cover the entire surface of the lagoon, it was decided to refer to the year corresponding to the middle of the period (i.e. year 1966 for the sampling period 1963-1968, and year 1992 for the sampling period 1988-1994) in the results section 2.3.2. The methods applied in 1998 and from 2003 to 2017 are detailed in Le Fur et al. (2017).

Sediment was sampled at 28 stations in late spring or early summer in 1998, 2003, 2008 and 2014 (Fig. 1B). The top layer (0-5 cm) of sediment was collected with a sediment corer and then sifted through a 2-mm sieve (see Le Fur et al. (2019) for details). Mud content (%) corresponded to the fraction with a diameter of less < 50 µm. Organic matter content (*OM*, expressed as % of dry sediment weight), total nitrogen (*TN*) and total phosphorus (*TP*) were analysed and were expressed in g kg^{-1} and mg kg^{-1} of dry sediment, respectively.

Data on Kjeldahl-N (*KN*) and TP concentrations, analysed in sediment samples collected in 1987 at 30 stations, were taken from Péna and Picot (1991) and added to the sediment time series.

2.2.3. Shellfish production

Total annual oyster production, mussel production and total shellfish production data (in 10^3 t y^{-1}) were collected by the Departmental Direction of Maritime Affairs and gathered by Comps et al. (2000) and Gangnery (1998 & 1999) for the period 1970-2000. Data for the years 2001, 2002 and 2003 were collected by Gangnery (2003). Production data for the period 2004 to 2018, were provided by the Departmental Directorate of Territories and the Sea (French acronym DDTM). The mussel species remained the same throughout the study period (*M. galloprovincialis*), but the oyster species changed in 1973 after the epizootic linked to an iridovirus which resulted in the disappearance of the Portuguese oyster *Crassostrea angulata*, which was replaced by the Pacific oyster (*C. gigas*) (Grizel and Héral 1991).

Given that anoxia events can cause significant mortality of the shellfish cultivated in the lagoon, the total shellfish production of the preceding year was used to estimate the stock exposed to anoxia in the summer of any given year (*Q_shellfish_1*). Data were transformed into binary variables with the following values: *shellfish* = 1 for low production rates (≤ 10 000 t) and *shellfish* = 2 for higher production (> 10 000 t).

2.2.4. Meteorological data

Daily data on rainfall (mm), air temperature (°C) and wind intensity (m s^{-1}) from 1970 to 2018 were collected from the Sète meteorological station (Météo-France station n°34301002) (Fig. 1A).

Summer air temperatures and wind intensities were averaged by month (June, July and August) (*air_M*, *wind_M*). Wind intensities were then standardised according to four periods determined by shifts in the raw time series corresponding to modifications to the sensors identified by Météo-France (January 1972, August 1996, January 2008) (*wind_ST*).

Rainfall was cumulated in June, July and August (*rainfall_6*, *rainfall_7*, *rainfall_8*) corresponding to the summer months when anoxia occurrs, and from January to May (*rainfall_1-5*) corresponding to the winter and spring months preceding anoxia.

2.3. Data processing and analyses

2.3.1. Hydrological, nutrient and phytoplankton time series

Data collected in summer from 1999 to 2018 at the three stations TANG, TE and TW were averaged per year before performing an explanatory PCA analysis with nine variables (*DIN*, *DIP*, *TP*, *TN*, *CHLA*, *PEUK*, *NANO*, *PE-CYAN* and *O2*) (ade4 package in R). The phytoplankton variables were $\log_{10}$ transformed to normalise the data and reduce the effect of very high values. The three hydrological parameters (*TEMP, SAL and TURB*) were considered as illustrative variables in the PCA. K-means cluster analysis was then applied to identify years and stations with similar eutrophication patterns (vegan package in R). The optimal number of clusters was estimated based on the Calinski-Harabasz index (Calinski and Harabasz, 1974).

For the hydrological and phytoplankton variables (*DIN*, *DIP*, *TP*, *TN*, *CHLA*, *PEUK*, *NANO*, *PE-CYAN, O2*, *TEMP*, *SAL*, *TURB* and the ratio *PE-CYAN/PEUK*), Mann-Kendall tests (MK) were performed on the means calculated for each year from 1999 to 2018 to characterise the monotonic trends. To eliminate the effect of serial correlations on the MK test, we used the modification by effective sample size, computed with significant serial correlation coefficients (Hamed and Rao (1998), modifiedmk package in R). If the test was significant (i.e. p-values <0.05), the Theil-Sen's slope estimator was calculated (Sen, 1968). The correlation between water temperature and *PE-CYAN* was tested using Spearman's test.

In Thau lagoon, DIP is not considered to be the main limiting nutrient (Fouilland et al., 2002; Souchu et al., 2010) and its concentrations in water are well correlated with the inputs from human activities in the watershed (La Jeunesse and Elliott, 2004). Moreover, in summer, it has been shown that in deeper lagoons such as Thau, P loads from sediments are enhanced by high temperatures through the benthic remineralization process (Chapelle et al., 2000b; Souchu et al., 1998; Zilius et al., 2015). Finally, shellfish farming is known to contribute to summer remineralization (Chapelle et al., 2000a; Mazouni et al., 1996). For all these reasons, the summer concentration of DIP in the water column is a good indicator of eutrophication in the Thau lagoon. To analyse the changes in summer DIP 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 surveys carried out before 2003, it was not possible to collect information from all 36 stations. The number of stations used for each survey is given in Table A1.

Finally, the proportion of stations with bare sediment (i.e. without vegetation) or dominated by each group of macrophytes was calculated for each period as follows: Proportion of stations dominated by group *i* = number of stations dominated by group *i* ÷ total number of stations considered.

2.3.3. Sediments

To characterise the monotonic trends of sediment variables we performed Mann-Kendall tests on the medians calculated for each survey (1998, 2003, 2008 and 2014 for mud, OM and TN and 1987, 1998, 2003, 2008 and 2014 for TP).

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

Information on the frequency and intensity of the summer anoxic crises which occurred between 1970 and 2018 was collected from the scientific and grey literature (Hamon et al., 2000; Trousselier and Deslous-Paoli, 2001; Ifremer, 2004; Ifremer, 2007; Lagarde, 2018a). Since the spatial and temporal strategies of O_2 monitoring did not remain the same over the study period, we defined the occurrence of anoxia based on presence of white water caused by sulphur bacteria reoxidising the sulphur released in the water column (Minghelli-Roman et al., 2011), or on the presence of at least one measurement of O_2 concentration < 0.05 mg L^{-1}. The intensity of the anoxia crises was characterised according to their duration in months (≤ 1 to 3) and to their maximum spatial extent: 1 (one of the shellfish farming areas), 2 (two of the shellfish farming areas), 3 (all three shellfish farming areas), 5 (the whole lagoon).

Out of the total of 147 summer months in the 1970-2018 period, 12 months were characterised by the onset of an anoxia crisis (*anoxia* = 1) and 135 months had no anoxia onset (*anoxia* = 0). In order to identify the meteorological and environmental conditions involved in the triggering of anoxia, a binomial generalised linear model (glm) (McCullagh and Nelder 1989) was built with the following eight variables:

- meteorological variables: *air_M* and *wind_ST* (summer monthly averages), *rainfall_6*, *rainfall_7*, *rainfall_8* and *rainfall_1-5* (cumulative rainfalls);
- eutrophication status: *period* (1 or 2);

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

The Akaike information criterion (AIC) was used to select the significant variables and the odds ratios (OR) were calculated ($OR_x = e^{\beta x}$, with β_x the estimated coefficient for variable x) to evaluate the probability of triggering anoxia versus the probability of not triggering anoxia when modifying variables independently. The odds ratios provide information on the strength and direction of the association between the dependent and explanatory variables (OR>1: increases the probability, 0≤OR<1: decreases the probability) (Schwarz, 1978, ggeffects in R). The performance of the glm was assessed by cross validation (70% for calibration, 30% for validation). The test datasets consisted of 100 observations randomly drawn from the 135 months with no anoxia; and from the 12 months characterised by the onset of anoxia. The receiver operating characteristic (ROC), which depends on specificity and sensitivity), and the area under the curve (AUC) were calculated for the 50 test datasets drawn randomly to estimate the average and standard deviation of this criterion (DeLong et al., 1998, Presence-Absence in R). According to AUC, a model is considered as not contributing (AUC = 0.5), not very informative (0.5 ≤ AUC < 0.7), moderately informative (0.7 ≤ AUC < 0.9), very informative (0.9 ≤ AUC < 1) or perfect (AUC = 1) (Swets, 1988).

In addition, Kruskal-Wallis tests were performed on the following variables to identify significant differences in the characteristics of the two periods: *air_M*, *wind_ST*, *rainfall_6*, *rainfall_7*, *rainfall_8*, *rainfall_1-5*, *DIP_6* and *Q_shellfish_1*.

3. Results

3.1. Change in trophic status from eutrophication to oligotrophication

3.1.1. Water column

The average summer concentrations of dissolved phosphorus measured in water ranged from 6.7 µM in 1972 to 0.04 µM in 2016-2017, with a median value of 0.9 µM, and they decreased monotonically and significantly over the study period (MK p<0.001, Theil-Sen's slope = -0.1 µM y^{-1}) (Fig. 2).

When focusing on June observations, the concentrations of dissolved phosphorus ranged from 5.2 µM in 1974 to 0.04 µM in 2015-2017, with a median value of 0.3 µM, and they decreased monotonically and significantly over the study period (MK p<0.001, Theil-Sen's slope = -0.1 µM y^{-1}) (Fig. 2, black dots). The slope of the time series modelled with LOESS revealed two breaks: the first in June 1991 and the second in June 1993. Moreover, the threshold of good status according to WFD (DIP ≤ 1 µM) was no longer exceeded after June 1993, which made it possible to identify two contrasting periods based on the eutrophication status: period 1, from 1970 to 1992 and period 2, from 1993 to 2018. When considering data for each period separately, DIP concentrations also decreased significantly, but the median and the slope were higher in the first period (respectively, 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 Theil-Sen's slope = -0.005 µM y^{-1}).

PCA analysis of the data was performed on nine variables (*DIN*, *DIP*, *TP*, *TN*, *CHLA*, *PEUK*, *NANO*, *PE-CYAN* and *O2*) collected from 1999 to 2018, corresponding to PERIOD 2 defined based on eutrophic status. The PCA of this water column time series showed that the two first axes accounted for 52.6% of total variability (33.9% and 18.6% for axis 1 and axis 2, respectively). The third axis, accounted for 14.4% of the variability and was positively correlated with O2 and negatively correlated with TN (Fig. A1.A). The first axis revealed a clear temporal structure, contrasting the earliest and the most recent years (Fig. 3B). This first axis was negatively correlated mainly with TP, DIP, PEUK, CHLA and DIN (Fig. 3A). The second axis was mainly defined by PE-CYAN abundances, with a high contribution of the years 2006 and 2003 (Fig. 3A). The temperature, considered as an illustrative variable in the PCA analysis, was correlated with the second axis and consequently with PE-CYAN. The third axis isolated the samples collected at TANG station (Fig. A1.C).

Among the three clusters identified by the Calinski-Harabasz index on the PCA, a first group, located on the left side of the PCA, grouped 23 samples collected from 1999 to 2008, with the years 1999 to 2001 and 2003 to 2005 only found in this cluster (Fig. 3B). On the right side of the PCA, the second cluster (29 samples) was characterised by low levels of nutrient and phytoplankton biomass and abundance and isolated the samples collected exclusively from 2007 to 2018 (Fig. 3B). Finally, the third cluster was isolated according to the third axis and grouped seven samples collected at TANG station in 2002, 2006, 2008 to 2011 and 2018 (Fig. A1.B and A1.C).

From 1999 to 2018, the phytoplankton community was marked by changes in chlorophyll *a* biomass and pico- and nano-phytoplankton abundances at TW-TE stations (averaged data) and TANG stations (Fig. 4). A significant decreasing trend was found for chlorophyll *a* biomass from 1999 to 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}). Moreover, two phases are identifable in the evolution of CHLA: the period 1999-2006, when maximum values were reached (respectively 6.2 and 15.7 µg L^{-1} at TW-TE and TANG), and the period 2007-2018 characterised by lower values (< 2 µg L^{-1}) (Fig. 4A).

Like chlorophyll *a*, picoeukaryote abundances revealed a decreasing trend (MK p=0.006 and 0.001 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), with the exception of the maximum values reached in 2003 and 2004 (respectively 120 10^6 cells L^{-1} at TW-TE and 113 10^6 cells L^{-1} at TANG) (Fig. 4C). On the contrary, nanophytoplankton revealed no significant monotonic trend (MK p>0.05). Nanophytoplankton levels peaked in 2006 (41.6 10^6 cells L^{-1} at TANG) and increased to reach a second maximum in 2011 (28.4 10^6 cells L^{-1} at TW-TE), then decreased and remained below 3.7 10^6 cells L^{-1} (Fig. 4B).

Changes in phycoerythrin-rich picocyanobacteria were contrasted, with no significant monotonic trend (MK p>0.05). PE-CYAN abundances exhibited three peaks in 2003, 2006 and 2018 (respectively 283.7, 295 and 282.3 10^6 cells L^{-1} at TW-TE), associated with water temperatures above 25.6°C (Fig. 4D). Water temperatures and PE-CYAN abundances were significantly correlated at TW-TE stations (Spearman p=0.002, rho=0.65) but not at TANG station. Finally, the PE-CYAN/PEUK ratio increased 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 not at TANG station.

Among the other hydrological parameters, decreasing monotonic trends were found for TP, DIP and DIN at TW-TE and TANG stations from 1999 to 2018 (Fig. A2.B, A2.D and A2.C) and for TN and O2 only at TW-TE stations (Fig. A2.A and A2.F). An increasing trend was found for TEMP only at TANG station (Fig. A2.H).

3.1.2. Benthic compartment

a) Macrophyte composition

The percentage of benthic stations not covered by soft bottom macrophytes tended to decrease from 1966 to 2017, with the highest percentages measured in the 1980s and 1960s (28.6 and 22%, respectively), and null values from 2011 on (Fig. 5).

The macrophyte community consisted mainly of seagrass beds in the 1960s, dominating coverage at 40% of the benthic stations (Fig.5). Seagrass cover declined between the 1960s and the 1980s in favour of red algae, which became the second dominant group after seagrass in 1986 and 1992. The percentage of stations dominated by seagrass continued to decline until 2003, when it reached its minimum (11.4%), then increased from 15.4% in 2008 to 22.5% in 2011 and 2014. After dominance by seagrass, red algae dominated the macrophyte community from 1998 to 2017 (between 42.5% of benthic stations were dominated by this group in 2011 and 2014 and 55.6% in 2017).

Brown algae dominated 18% of the stations in 1966, but rarely dominated between 1986 and 2008 (0 to 15.4% of the benthic stations were dominated by this group); brown algae reached 22.5% to 25% between 2011 and 2017. The contribution of green algae to macrophyte cover was low to zero (in 2017) and did not change significantly over the study period (from 11.4% of benthic stations dominated by this group in 1966 and 2003 to 19.2% in 1999).

Regarding the composition of each group of macrophytes, seagrass beds were composed of two *Zostera* species: *Zostera noltei* and *Z. marina*, both species being observed in all samples collected from 1966 to 2017.

Red algae consisted of *Polysophonia* and *Halopitys* genera in 1966 (Dubois, 1972; Lauret, 1967 & 1970). Then, *Halopitys* and *Gracilaria* genera were the two most frequent red algae observed in 1986, 1992 and 1998 (Gerbal and Verlaque, 1995; Lauret, 1990 & 1994; Verlaque, 2000). *Gracilaria* and *Alsidium* were the most frequent red algae in 2003 and *Gracilaria* and *Polysiphonia* in 2008 (Ifremer, 2004 & 2007). Finally, from 2011 to 2017, *Gracilaria* and *Halopitys* again became the most frequent red algae, with a shift in dominance from *Gracilaria* to *Halopitys* in 2017 (Bouchoucha et al. 2019; Derolez et al. 2015; Ifremer 2009 & 2012).

Codium genera was the only green algae listed in 1966, while *Ulva* and *Monostroma* genera were the most frequently observed green algae in 1986 (Dubois, 1972; Gerbal and Verlaque, 1995; Lauret, 1967 & 1970). *Ulva* and *Chaetomorpha* were the most frequent genera in 1992 (Lauret, 1990 & 1994). Finally, the most frequent green algae were *Ulva* and *Cladophora* in 2008 and 2011 and *Chaetomorpha* and *Cladophora* in 1998, 2003 and 2014 (Derolez et al. 2015; Ifremer 2004, 2009, & 2012; Verlaque, 2000).

Cystoseira and *Sargassum* were the only brown algae genera listed in 1966 and 1998, respectively, whereas both genera were cited in 1986 (Dubois, 1972; Gerbal and Verlaque, 1995; Lauret, 1967 & 1970). *Colpomenia* and *Cutleria* and *Colpomenia* and *Cystoseira* were the most frequently observed in 1998 and 2003, respectively, (Ifremer, 2004; Verlaque, 2000). Finally, *Dictyota* genera and the family *Ectocarpaceae* were the most frequent brown algae observed from 2008 to 2017 (Bouchoucha et al. 2019; Derolez et al. 2015; Ifremer 2009 & 2012).

b) Sediment

Median concentrations of mud and organic matter in the surface sediment ranged from 61.8% in 1998 to 83.5% in 2008 and from 6.6% in 1998 to 13% in 2014, respectively, but did not change significantly from 1998 to 2014 (MK p=0.67 and p=0.051, respectively) (Fig. A3-A and A3-B). On the contrary, a significant increasing trend was revealed for total nitrogen from 1998 to 2014, with medians ranging 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 2014 when KN values measured in 1987 (2.7 g kg^{-1}) were included (MK p<0.001, Theil-Sen's slope=0.49 g kg^{-1} y^{-1}) (Fig. A3-C). In contrast to the other parameters, although the medians of total phosphorus did not show a monotonic trend from 1987 to 2014 (MK p=0.81), the maximum was reached in 2003 (771 mg kg^{-1}) and the minimum in 2014 (577 mg kg^{-1}) (Fig. A3-D).

3.2. Changes in shellfish production

Shellfish production varied significantly between 1970 and 2018 (Fig. 7). Total annual production ranged from 6 650 t in 1982 to 18 000 t in 2001 to 2003. Mussel production ranged from 1 038 t in 1990 to 11 550 t in 1970 and dominated Thau shellfish production from 1970 to 1983 (45-93% of total production). From 1972 to the 1990s, mussel production declined in favour of oyster production (*Crassostrea angulata* until 1972 and *Crassostrea gigas* ever since). Thus, oyster production has accounted for most shellfish production since 1983 (53 to 90% of total production). Oyster production revealed two peaks: a first peak in 1994 (15 000 t) and a second peak during the period 2000-2008 (12 000 to 13 000 t). In 2009, oyster production declined sharply due to the OsHV-1 µvar epizootic (Pernet et al., 2012). It slowly increased from 2012 to 2017, while remaining below 8 000 t. Finally in 2018, oyster production again decreased to 6 030 t.

Figure 6 also shows the years in which a summer anoxic event occurred (in grey). From 1970 to 2018, 12 anoxic events were recorded in the lagoon. About half of these crises occurred in the 1980s and 1990s. Some of these years were characterised by significant a decline in production (e.g. 1975, 1982, 1990, 1997, 2018), associated with shellfish mortalities.

3.3. Triggering factors of summer anoxia

Figure 7 shows the duration and spatial extent of summer anoxia in Thau lagoon from 1970 to 2018. The 1970 anoxia event lasted three months and the 1983 and 1994 anoxia events each lasted two months. The anoxia events in 1975, 1982, and 1987 lasted six weeks and the other anoxia events, between 1990 and 2018 lasted one month or less. The most extensive anoxia event occurred in 1975, when the entire lagoon was under hypoxic conditions (Troussellier and Deslous-Paoli, 2001). The 1982, 1983, 1990, 2006 and 2018 anoxia events affected all three shellfish farming areas, while the others affected only one or two. The duration and spatial extent of the seven anoxia events which occurred in period 1 (from 1970 to 1992) were greater than those of the five last anoxia events which occurred in period 2 (from 1993 to 2018) (respective median duration ranged from four to six weeks and the median spatial extent from two to three areas).

The Kruskal-Wallis tests performed to differentiate the characteristics of *periods 1* and *2* were significant for the following variables (p-values < 0.05): mean monthly air temperature increased (*air_M*, median from 22.3 to 23.1°C), rainfall from January to May and rainfall in June decreased (respectively *rainfall_1-5:* median from 253 mm to 219 mm, *rainfall_6*: median from 21 mm to 16 mm), the concentration of DIP in June decrased (*DIP_6*, median from 2.3 to 0.1 µM) and total annual shellfish production increased (*Q_shellfish_1*, median from 8.7 10^3 to 13.4 10^3 t y^{-1}). The other three variables (*wind_ST*, *rainfall_7*, *rainfall_8*) did not differ significantly between the two periods.

Among the eight variables included in the glm predicting the triggering of summer anoxia, four were considered as significant based on the AIC: summer monthly averages of air temperature and wind intensity, rainfall in July and the period determined according to the eutrophication status (*air_M*, *wind_ST*, *rainfall_7* and *period 2*). According to the AUC criterion, the performance of this glm was good (mean=0.81, sd=0.1), corresponding to moderately to very informative models. *Period 2* and *rainfall_7* were associated with, respectively, the highest and the lowest absolute values ot the estimated coefficients in the glm (Table A2). Air temperature and rainfall in July were associated with positive coefficients, in contrast to wind intensity and to the less eutrophic period (*period 2*: from 1993 to 2018). The odds ratio associated with the period corresponding to the eutrophication status is 0.17 ($e^{-1.78}$), meaning that the fact of being in period 2 divided the risk of triggering anoxia by 5.9 (1/0.17) compared to the risk in period 1. The odds ratio of the summer monthly average wind intensity was 0.27 ($e^{-1.32}$), meaning that an increase of 1 unit of wind intensity (the variable *wind_ST* being standardised) divided the risk by 3.7. The odds ratio associated with air temperature ($e^{1.03}$=2.8) means that an 1°C increase multiplies the risk of triggering anoxia by by 2.8. Finally, the odds ratio of rainfall in July indicates that a 10 mm increase multiplies the risk by 1.5 ($e^{10*0.04}=1.5$). Figure 8 shows the predicted probabilities of triggering anoxia according to the three significant meteorological variables of the glm for period 1 and period 2, showing that the highest probabilities of the highest temperature were reached in period 1.

4. Discussion

4.1. Ecological changes and regime shifts during oligotrophication

Our results, based on long time series, show that the pelagic and benthic communities in Thau lagoon changed during the course of oligotrophication. Previous studies of the lagoon from the 1990s to the 2000s showed that the gradual decrease in nutrient inputs from the watershed resulted in a continuous decrease in nutrients and Chl *a* concentrations in the water column (Collos et al., 2009; Derolez et al. 2020; Deslous-Paoli et al., 1998; Gowen et al., 2015). Our study revealed the continuation of oligotrophication over the past 20 years (1999-2018), and the recovery of the ecosystem, through nutrient and phytoplankton parameters. Thus, based on changes in the summer concentration of DIP in the water, which is a good indicator of the eutrophication status of Thau lagoon (La Jeunesse and Elliott, 2004; Souchu et al., 1998), we identified a progressive shift from a bad quality status to a high quality status, according to the thresholds of the WFD (METS, 2018). Reaching the good DIP status (DIP < 1 µM, METS, 2018), which was no longer exceeded after June 1993, divided the time series into two periods (1:1970-1992 and 2:1993-2018). At the same time, dissolved nitrogen concentrations also decreased significantly ($NO_3^-+NO_2^-$ in June: MK $p<0.01$, slope=-0.01 µM y^{-1}). In period 2, when nutrient levels were already low, phytoplankton shifted with a time lag in year 2006. After 2006, the levels of Chl *a* biomass (< 5 µg L^{-1}) and picoeukaryote abundances (< 50 10^6 cells L^{-1}) corresponded to those reported in oligotrophic coastal waters of the Mediterranean (Massana 2011). Coastal lagoons often host blooms of picophytoplankton that can continue for months to years (Glibert et al 2010; Bec et al. 2011). In Thau lagoon, phycoerythrin-rich picocyanobacteria abundances did not increase significantly but their relative contribution (PE-CYAN/PEUK ratio) to picophytoplankton did.The numerical dominance of picocyanobacteria in summer may reflect the oligotrophic conditions of the lagoon linked to low phosphorus levels (Collos et al., 2009; Bec et al. 2011). We also found a positive correlation between temperature and the abundance of phycoerythrin-rich picocyanobacteria. Positive effects of temperature on the growth rate 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., 2000b) - led to stabilisation, or even to the beginning of a decrease in the quantities of phosphorus in the sediments (lowest median of TP was observed in 2014).

Concerning the benthic macrophyte community, our results showed that the proportion of seagrass decreased in favour of red algae from the 1960s to the 1990s. This trend corresponds to the generic eutrophication trajectory described by many authors: a shift from dominance of seagrass and perennial macrophytes to dominance of macroalgae (Schramm, 1999; Viaroli et al., 2008; Zaldívar et al., 2008). Seagrass meadows only started to slightly recover between 2003 and 2008, but their contribution to benthic vegetation did not reach the level observed in the 1960s, or the historical conditions describing Thau lagoon dominated by seagrass at the beginning of the 20th century (Calvet, 1910). Despite the significant and continuous decrease in nutrient inputs observed since the 1970s, the beginning of the recovery of the Thau lagoon macrophyte community lagged behind that of the phytoplankton community. This time lag and partial recovery suggest hysteresis during oligotrophication in the Thau lagoon and correspond to partial resilience observed in aquatic ecosystems (Borja et al., 2010; Duarte et al., 2009; Elliott et al., 2007). Continuous nutrient fluxes from sediments could promote phytoplankton or macroalgae growth and delay the recovery process of perennial macroalgae and seagrasses (Kosten et al. 2011). Accordingly, internal phosphorus loading from sediments has frequently been reported as a cause of hysteresis in lakes (Gulati and Van Donk, 2002; Jeppesen et al., 2007; Søndergaard et al., 2003) and more recently in coastal or estuarine ecosystems (Lillebø et al., 2007; Ní Longphuirt et al., 2016; Ratmaya et al., 2018; Riemann et al., 2016).

During five decades of changes from eutrophication to oligotrophication, contrasting periods in the pelagic and benthic compartments of the Thau lagoon were identified. This evolution is represented in the conceptual model (Figure 9), showing the changes in several indicators of ecosystem status (DIP concentration in water, phytoplankton and macrophyte) in response to changes in the levels of pressures which affect the ecosystem (nutrient loads and temperature). Although the decrease in nutrient loads was accompanied by a decrease in nutrient concentrations and phytoplankton biomass in water, period 1 (1970-1992) can be considered as a eutrophic period due to the shift from seagrass to red macroalgae and to the frequent and critical anoxic crises during that period. Period 2 (1993-2018) was characterised by a better eutrophic status, less frequent and less intense anoxia crises and by the continuation of the recovery process. This second period can be divided into three steps: 2a) a transition phase (1993-2003) during which the pelagic compartment continued to recover from eutrophication with stabilisation of the benthic community; 2b) a regime shift between the year 2003, (before which seagrass continued to decline), and the year 2006, after which low chlorophyll *a* values were reached in the water column. Since the summers of 2003 and 2006 were both characterised by major heat waves and anoxias events, we hypothesise that this regime shift is the result of the combination of an internal oligotrophication process and external forces linked to high summer temperatures (Sheffer and Carpenter, 2003). After the regime shift, 2c) the ecosystem shifted to oligotrophy (2006-2018), the water column became characteristic of an oligotrophic state and the marine grass began to recover.

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

To analyse the trajectory of Thau lagoon ecosystem over five decades, the effects of reduced nutrient inputs and of climatic-related variables, especially the gradual increase in temperature, which was evidenced in the Mediterranean and Thau regions (Bec et al., 2018; Cramer et al., 2018), need to be taken into account. Indeed, oligotrophication and warming may have combined effects on biodiversity and ecosystem functioning (Glibert, 2016; Kosten et al. 2011; Verbeek et al., 2018). Thus, we focused particularly on the occurrence and intensity of anoxia crises as indicators of ecosystem resilience and resistance and on what triggers these disturbances (Coffin et al., 2018).

The model used to predict the triggering of summer anoxia revealed that four variables were significant (three meteorological variables and one corresponding to the eutrophication status). The strongest effect was induced by air temperature, followed by the effect of the eutrophication period, by the negative effect of wind, and to a lesser extent by the positive effect of rainfall in July. These results highlight the effects of climate variables and confirmed a previous study underlying the effects of increasing temperature and decreasing winds on the probability of the occurrence of anoxia in the Thau lagoon (Harzallah and Chapelle, 2002). In coastal ecosystems, decreased wind speed could play an important role in triggering anoxia by decreasing vertical water mixing and oxygenation at the air-water interface (Chen et al., 2015; Du et al., 2018; Zilius et al., 2015). In northern temperate estuaries, increased frequency of extreme summer rainfall events could increase the frequency of anoxia events because floods can mobilize significant quantities of organic matter and suspended solids which are subsequently deposited in estuaries and/or due to more intense stratification (Iriarte et al., 2014; Oviatt et al., 2017).

We showed a 6-fold higher risk of triggering anoxia in the first period (1970-1992), considered to be the eutrophic period. It is known that anthropogenic nutrient inputs affect both the oxygen supply and uptake (Conley, 2000; Friedrich et al., 2014; Souchu et al., 1998) and that eutrophication-related parameters (chlorophyll *a* biomass or nutrient concentrations or loadings) can trigger anoxia in coastal areas (Coffin et al. 2018; Du et al. 2018; Zilius et al., 2015). What is remarkable about our result is the marked effect of the eutrophication status, so that the oligotrophication process observed during our study period led to increasing resistance of the Thau lagoon ecosystem to climate stress. Among the climatic-related variables, the effect of air temperature on triggering anoxia was the strongest. Indeed, the functioning of the lagoon could be particularly threatened by warming since increases in the annual average temperature and in the frequency of summer heat waves were recorded in the Mediterranean region from the 1970s to the 2010s (Bec et al., 2018; Cramer et al., 2018). However, oligotrophication lead to the decreased risk of triggering anoxia in the Thau lagoon. This is consistent with a previous study in the mid-estuarine waters (Bilbao, Spain) showing that anthropogenic-mediated pollution mitigation was more important than climatic factors in driving inter-annual variations in dissolved oxygen saturation (Iriarte et al., 2014). In Narragansett Bay (USA), Oviatt et al. (2017) showed that a 60% reduction in nutrient concentrations resulted in a 34% reduction in summer hypoxia. In Chesapeake Bay (USA), authors suggested that reductions in nutrient loads would also reduce hypoxic volumes (Testa et al., 2014), but biological conditions (linked to nutrient loading) and physical conditions (vertical exchange and temperature) could play an equally important role in seasonal and inter-annual variations in the hypoxic condition of this ecosystem (Du et al., 2018). Among the climatic-related variables, we also showed a decrease in the rainfall levels from period 1 to period 2, due to the decrease in the occurrence of wet years recorded since 2005 (Bec et al., 2018). This trend may have facilitated the oligotrophication process by decreasing nutrient inputs resulting from watershed runoff (Bec et al., 2018).

With climate change trends already demonstrated by regional meteorological experts and predicted for the future (Jouzel et al., 2014), we would expect the effects of climate warming to slow down or even reverse the recovery process observed in the Thau lagoon. At regional scale, meteorological datas revealed that 2003, 2017 and 2018 were the three hottest summers in the 1970-2018 period (Météo-France, 2018). In the present study, the last anoxia crisis occurred in 2018 when the water 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

Zostera spp. The delay in reaching the WFD good status for macrophytes in comparison to phytoplankton is related to the time lag evidenced by several authors in the recovery of the benthic compartment (Borja et al., 2010; Le Fur et al., 2019). A recent study carried out on several French Mediterranean lagoons (Derolez et al., 2019) hypothesised that the level of recovery after the reduction of nutrient inputs could be affected by: (i) external drivers, such as completeness of nutrient reduction, marine connectivity, or climate change; (ii) internal factors such as physical traits, sediment nutrient stocks or the presence of residual seagrass patches or seed stocks; and interactions between the two drivers. Among the three strategies identified for the lagoons which have not fully achieved the objectives set by the European WFD ("Wait and see", "Go further", "Give a helping hand"), the first seems to be the most relevant for the Thau lagoon according to the importance of the works performed on the depuration system and their efficiency observed in the ecosystem. One could hypothesise that eutrophication pressure is now sufficiently low to allow the benthic compartment to recover its ecological functions and structure of the reference conditions, after a period of hysteresis.

However, it should be noted that in the 1990s, some authors mentioned the threat of reaching the limits of the trophic capacity of the Thau lagoon if the depuration works became too drastic (Deslous-Paoli et al., 1998; Souchu et al., 1998). During the recovery, shellfish production in Thau lagoon has evolved due to changes in the main reared species from mussels to oysters from the 1970s to the 1990s for epizootic and economic reasons (Hamon and Tournier, 1984; Le Brun, 1985); the removal of some shellfish structures located along the shoreline in the early 2000s following the recommendations of scientists made after the critical anoxia events of the 1990s (Deslous-Paoli et al., 1998; Souchu et al., 2011); and changes in farming techniques following epizootics such as OsHV-1 in 2008 (Pernet et al., 2014). This last epizootic reduced oyster production by half. More recently, fishermen and shellfish farmers have been facing economic difficulties and they worry about the potential limiting capacity of the ecosystem (Derolez et al. 2020). In the context of emerging marine diseases related to climate change, recent studies have shown that the impact of oyster diseases can be limited by maintaining the good ecological status of coastal waters (Harvell et al., 1999; Pernet et al., 2018). To reach a satisfactory trade-off between uses, ecosystem services and maintaining biodiversity and ecological functions under global change, there is a need to use ecosystem-based models (Filgueira et al. 2015; Guyondet et al., 2014; McKindsey et al., 2006). Such a model has been developed for Thau lagoon and showed that lagoon productivity significantly depends on hydrometerology, with higher oyster production in wet years than in dry years (Pete et al., 2020). Using a modeling approach based on scenario comparisons would help (i) disentangle the effects of anthropogenic forcings and of climate driven variables such as increasing temperature or decreasing rainfall and (ii) determine the limits of ecological tolerance. By testing different management and climate scenarios, this modelling approach would also help decision-makers better target their actions to improve the ecosystem's resistance to increasing climate pressure. It is will also be necessary to increase high-frequency oxygen measurements in real time (Friedrich et al., 2014; Schmidt et al., 2017) to help managers and shellfish farmers better anticipate the appearance of hypoxia/anoxia and design and apply mitigation actions (e.g. emersion of oysters at night) to mitigate environmental and economic impacts. Finally, in the context of global change, Breitburg et al. (2018) recommend an integrated framework, combining modelling, observations and experiments and involving all stakeholders (scientists, local governments, shellfish farmers) to facilitate the development and implementation of the most ecologically and economically effective management strategy to reduce anoxia.

5. Conclusions

The processes and consequences of oligotrophication have been poorly studied in coastal lagoons from a long-term perspective and at ecosystem scale. By analysing time series over 5 decades of observations on pelagic and benthic autotrophic communities, our study shows how the decrease in nutrient inputs led to major ecological changes in a Mediterranean coastal lagoon used for shellfish farming. Considering anoxia crises as indicators of ecosystem resilience and resistance, the combined analysis of meteorological data, eutrophication status and shellfish production over these 5 decades allowed us to identify air temperature and eutrophication status as the two main triggers of summer anoxia.

We identified successive periods in ecosystem functioning during the oligotrophication process: a eutrophic period characterised by a shift from dominance by seagrass to dominance by red macroalgae; a 3-step period characterised by a better eutrophication status i.e. a transition phase with a stable benthic community, a regime shift between two heat waves and anoxic crises; and finally the achievement of oligotrophic conditions. Our analyses also show that oligotrophication has led to changes in the drivers of summer anoxia, making the ecosystem more resistant to climatic stress caused by high summer temperatures.

However, with predicted climate change trends, we would expect the effects of climate warming to slow down or even to reverse the observed recovery process. The development and use of ecosystem-based models are now needed to better understand the functioning of the ecosystem and to help stakeholders find a trade-off between uses, ecosystem services and the maintenance of 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.

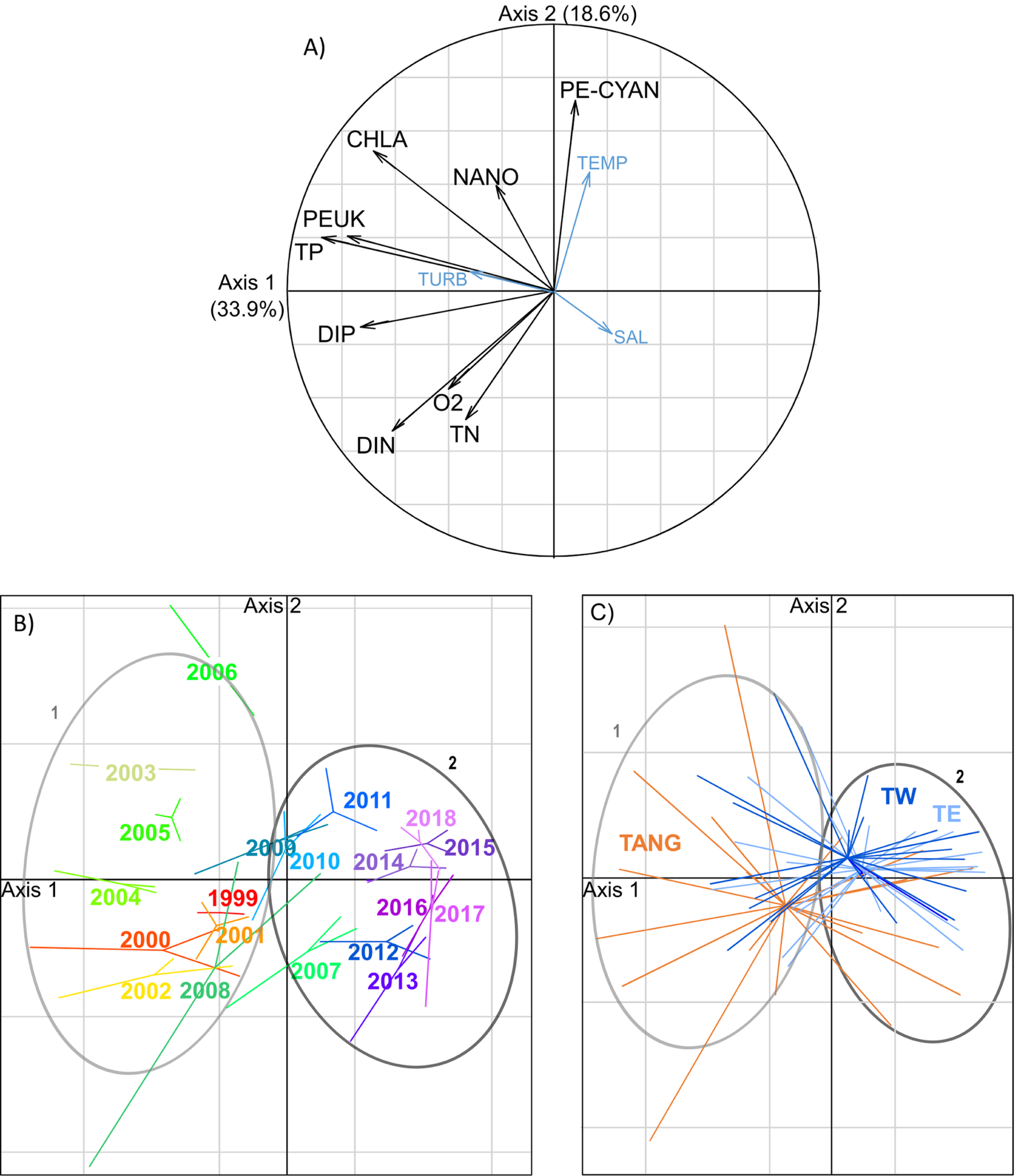
Fig. 7. Duration and intensity of summer anoxia crises from 1970 to 2018. The y-axis corresponds to the duration (months) of the crises and the size of the bubbles corresponds to the spatial extent of the anoxia.

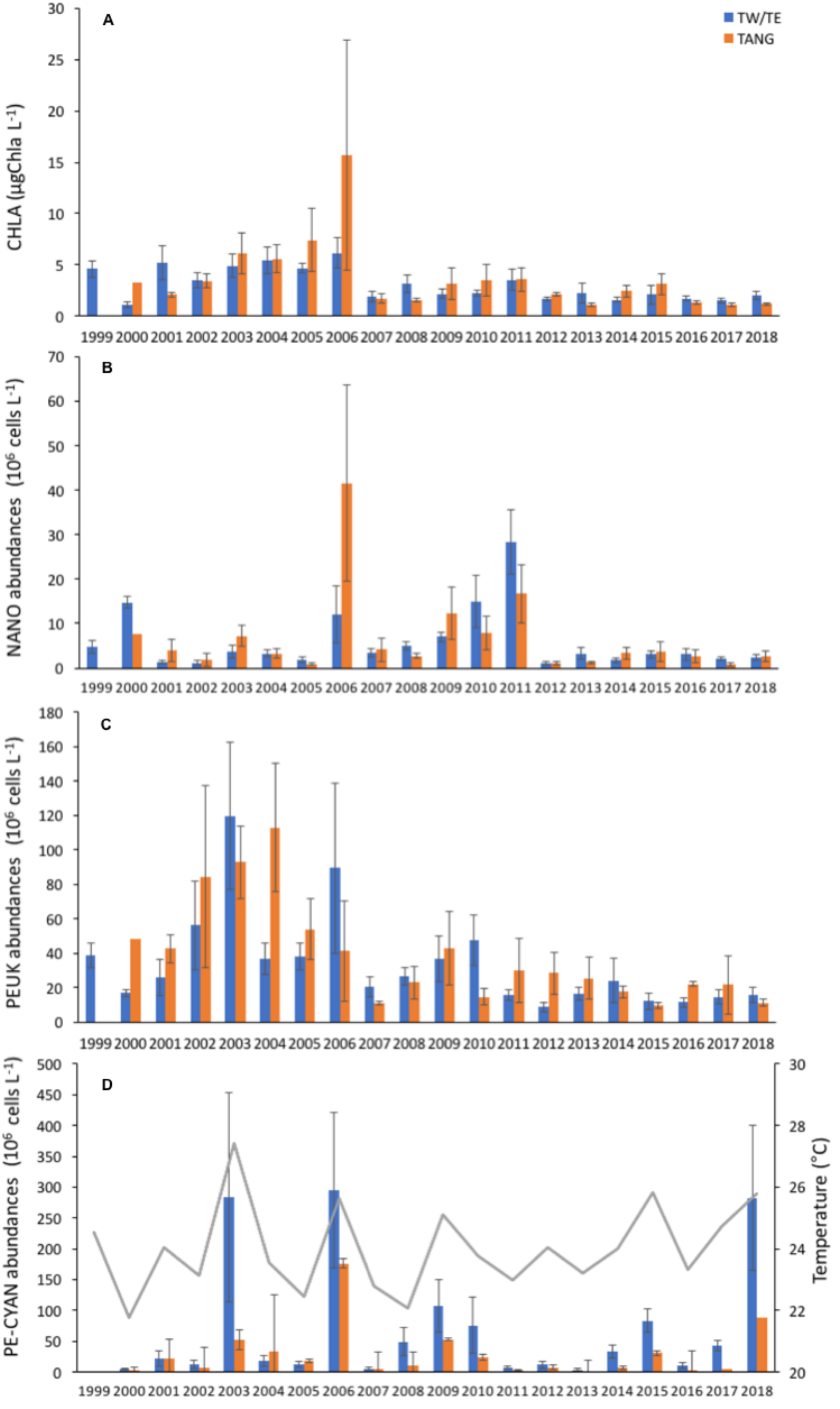
Fig. 8. Effects of the 3 meteorogical variables included in the glm predicting the probability of triggering summer anoxia (%: mean and confidence interval): wind intensity (wind_ST, standardised unit), air temperature (air_M, °C), rainfall in July (rainfall_7, mm), based on the period determined according to the eutrophication status (period 1 or period 2).

Fig. 9. Schematic synthesis of the oligotrophication process in Thau lagoon from 1970 to 2018 (period 1 and the 3 steps in period 2) and a possible scenario for the period 2020-2030 (stabilization of the nutrient load and increase in temperature). Pressures: nutrient inputs from the watershed and climate driver (temperature). Impact: the size of the bubbles represents the spatial extent and the intensity of the colour grey the intensity of the summer anoxia crises. Changes in mussel and oyster production: the size of the shellfish represents the level of production. Abundance of DIP and Chl *a* in the lagoon water and the abundance of seagrass, green algae and red algae in the soft-bottom sediment. Ecosystem status: the eutrophication status of the water column according to the WFD thresholds determined for DIP in French coastal lagoons (MTES, 2018). All variables are represented within relative space.


A)
TANG
ZA
TE
TW
Mediterranean Sea
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


DIP (µM)
0
2
4
6
8
1971
1975
1979
1983
1987
1991
1995
1999
2003
2007
2011
2015


A)
Axis 2 (18.6%)
Axis 1 (33.9%)
PE-CYAN
TEMP
CHLA
NANO
PEUK
TP
TURB
DIP
SAL
O2
TN
DIN
B)
Axis 2
Axis 1
1
2
2006
2003
2005
2004
1999
2000
2001
2002
2008
2009
2010
2011
2007
2012
2013
2014
2015
2016
2017
2018
C)
Axis 2
Axis 1
1
2
TANG
TW
TE

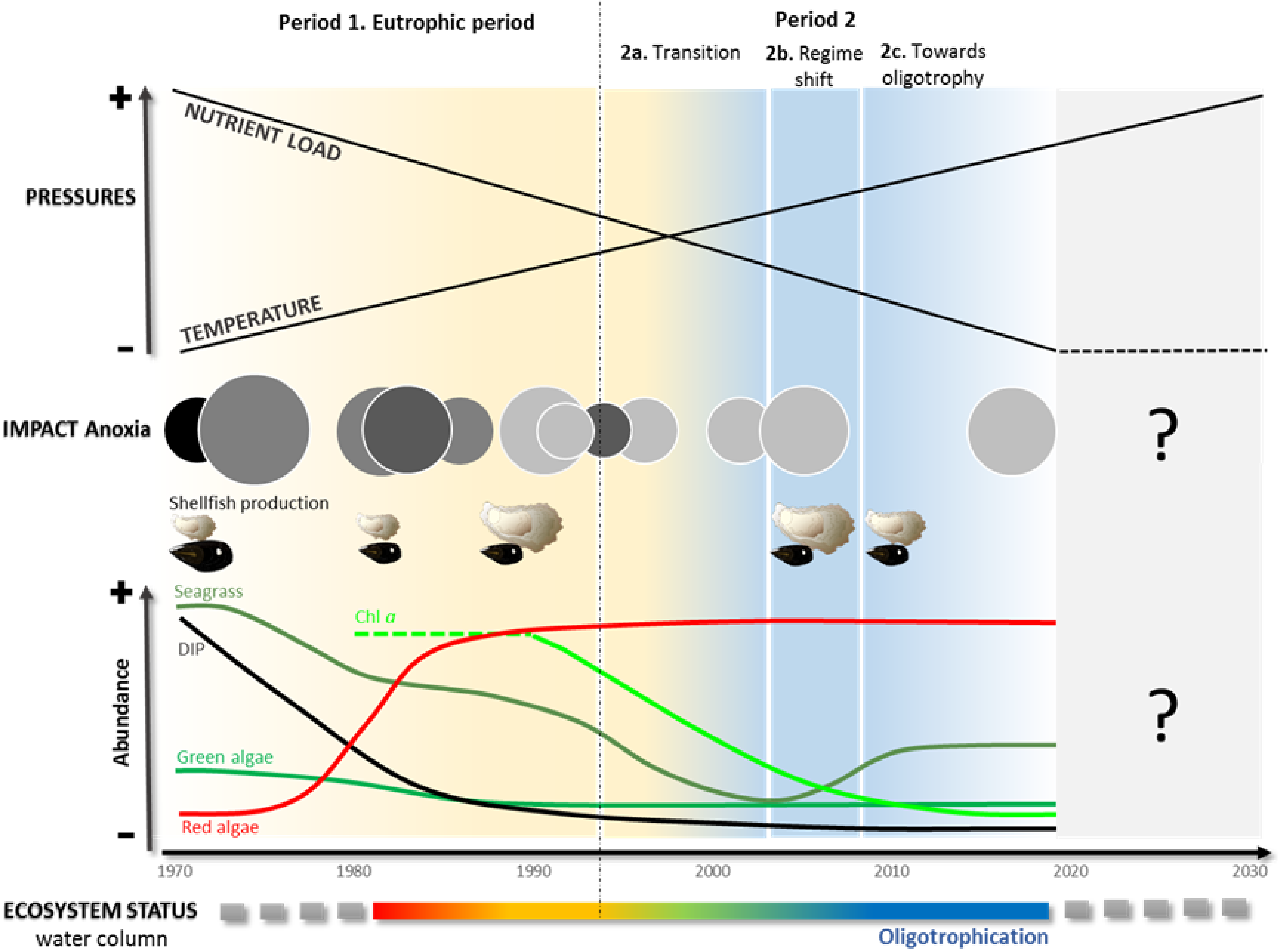

A
TW/TE
TANG
CHLA (µgChla L-1)
0
5
10
15
20
25
30
1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018
B
NANO abundances (10⁶ cells L-1)
0
10
20
30
40
50
60
70
1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018
C
PEUK abundances (10⁶ cells L-1)
0
20
40
60
80
100
120
140
160
180
1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018
D
PE-CYAN abundances (10⁶ cells L-1)
0
50
100
150
200
250
300
350
400
450
500
Temperature (°C)
20
22
24
26
28
30
1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018

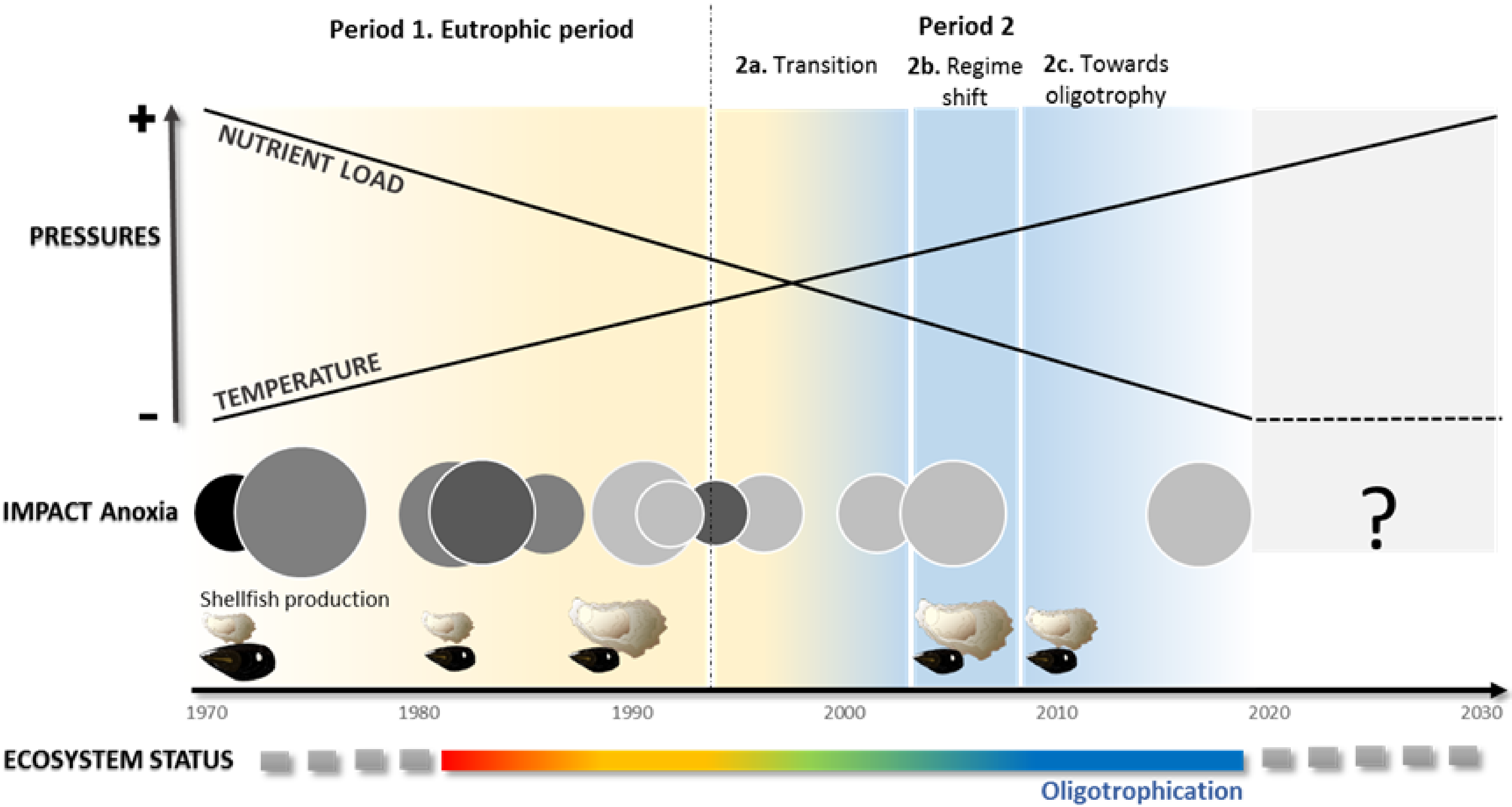

Seagrass
Brown algae
Red algae
Green algae
Bare
Percentage of stations diominated by each group (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1966
1968
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016


Oysters
Mussels
Total
Year with summer anoxia
Shellfish production (10^3 y^{-1})
0
2
4
6
8
10
12
14
16
18
20
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016
2018

Spatial extent of anoxia:
the entire lagoon
3 areas
1 area
Duration of anoxia avents (months)
3
2
⩽1
1970
1975
1980
1985
1990
1995
2000
2005
2010
2015
2018


period 1
period 2
A)
100%
75%
50%
25%
0%
p(anoxia=1)
17.5
20.0
22.5
25.0
27.5
air_M (°C)
B)
80%
60%
40%
20%
0%
p(anoxia=1)
-2
-1
0
1
2
wind_ST
C)
80%
60%
40%
20%
0%
p(anoxia=1)
0
20
40
60
rainfall_7 (mm)


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