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Recovery trajectories following the reduction of urban nutrient inputs along the eutrophication gradient in French Mediterranean lagoons

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1

2 **1. Introduction**

3 Mediterranean coastal lagoons are often surrounded by densely populated areas and
4 are consequently subject to strong anthropogenic pressure, and particularly high levels
5 of inputs of domestic sewage (Viaroli et al. 2008; Zaldívar, Cardoso, et al. 2008;
6 Souchu et al. 2010). In addition to this urban pressure, the transitional status of these
7 waters makes these ecosystems particularly vulnerable to eutrophication (de Jonge &
8 Elliott 2001; Newton et al. 2014). Eutrophication of coastal ecosystems is a worldwide
9 issue which has been described for decades (Nixon 1995; Cloern 2001). The increase
10 in nutrient inputs, enhanced by urbanisation, agriculture or industry, leads to a complex
11 cascade of both direct and indirect responses by ecosystems (Schramm 1999; Viaroli
12 et al. 2008). Anthropogenic eutrophication causes ecological damage including anoxic
13 crises, toxic algal blooms, even loss of species, and more widely, deterioration of
14 ecosystem functions and the services they provide (Cloern 2001; Zaldívar et al. 2008).

15 In recent decades, several legal and managerial frameworks have been designed to
16 reduce human pressure on aquatic ecosystems and to establish ambitious ecological
17 quality targets, e.g., EC Nitrate Directive and Water Framework Directive (WFD) (EC
18 1991; EC 2000) or the US Clean Water Act (USEPA 2002). In particular, mitigation
19 actions have targeted sewerage networks in estuarine watersheds, and have resulted
20 in their recovery at varying speeds and with various patterns (Lie et al. 2011; Saeck et
21 al. 2013; Staehr et al. 2017). While the degradation trajectories of coastal ecosystems
22 subjected to eutrophication have been extensively described (Schramm 1999; Cloern
23 2001; de Jonge et al. 2002; Viaroli et al. 2008), recovery trajectories have only recently
24 been studied (Duarte et al. 2009; Borja et al. 2010; McCrackin et al. 2017). Moreover,
25 the rate of improvement after mitigation works on coastal ecosystems is not well
26 known, even though this information is indispensable to assess recovery effectiveness

1 and to guide future management actions (McCrackin et al. 2017). Only a few studies
2 have been conducted on the recovery process of French coastal lagoons, and they
3 focused on selected water bodies (Collos et al. 2009; Leruste et al. 2016; Pasqualini et
4 al. 2017). These studies emphasised shifts in communities of primary producers after
5 mitigation actions. The originality of our study is that we used a large set of data
6 collected from 2001 to 2014 from 16 French Mediterranean coastal lagoons, thereby
7 covering the whole eutrophication gradient from oligotrophic to hypertrophic. Some of
8 these lagoons have been receiving large quantities of urban nutrient inputs for
9 decades, leading to extremely high levels of phytoplankton biomass, associated with
10 high pico- and nano-phytoplankton abundances in the most degraded lagoons (annual
11 median values $>100 \mu\text{g Chl } a.L^{-1}$, $>10^9$ and $>10^{10} \text{ cell}.L^{-1}$, respectively, Souchu et al.
12 2010; Bec et al. 2011). Large-scale management actions were recently undertaken on
13 waste water treatment systems to restore the quality and the functioning of the
14 ecosystems (De Wit et al. 2015; Leruste et al. 2016). The unprecedented range of
15 anthropogenic eutrophication and the remediation works carried out during the 14-year
16 study period allowed us to analyse recovery trajectories. First we analysed changes in
17 the eutrophication gradient over the study period and identified key parameters. We
18 then focused on three contrasted ecosystems to test the following hypotheses: (i)
19 reducing inputs of urban nutrients has a rapid effect on the nutrient levels and
20 phytoplankton biomass in Mediterranean lagoons; and (ii) the pattern of the recovery
21 trajectories depends on the degree of anthropogenic eutrophication before the
22 remediation actions were undertaken. Analysis of available historical data provided
23 useful information to improve our understanding of the patterns of change in the
24 ecological functioning of coastal lagoons after remediation.

25 **2. Materials and methods**

26 **2.1. Study sites and sampling strategy**

1 Data from 16 French Mediterranean coastal lagoons collected between 2001 and 2014,
2 were analysed. Fourteen of the lagoons are located in the Gulf of Lions, from north of
3 Perpignan to Montpellier, and two in Corsica (Fig. 1). The database includes polyhaline
4 and euhaline microtidal lagoons (annual median salinity > 18) (see Supplementary
5 Material), with surface areas ranging from 1.4 to 75 km², depths ranging from 0.7 to 9
6 m and volumes ranging from 0.7 to 260 x 10⁶ m³ (Souchu et al. 2010). Details on the
7 morphometric and hydrologic characteristics of the study sites are available in Souchu
8 et al. 2010 and Bec et al. 2011. The lagoons are all connected to the Mediterranean
9 Sea, through direct inlets, or through indirect connections via a canal or another
10 lagoon. The database covers the anthropogenic eutrophication gradient from
11 oligotrophic to hypertrophic lagoons (Bec et al. 2011). In each of the 16 lagoons, water
12 was sampled at one or two stations depending on the size of the lagoon, giving a total
13 of 22 stations: Leucate (LES, LEN), La Palme (LAP), Bages-Sigean (BGS and BGN),
14 Ayrolle (AYR), Gruissan (GRU), Thau (TES, TWS), Ingril (INN and INS), Vic (VIC),
15 Pierre-Blanche (PBE), Arnel (ARN), Prévost (PRE), Méjean (MEW, MEE), Grec (GRC),
16 Or (ORE and ORW), Diana (DIA) and Urbino (URB). We first analysed changes in the
17 anthropogenic eutrophication gradient at the 22 stations over the 14-year study period.
18 Next, three stations were selected for specific statistical analyses based on their
19 degree of anthropogenic eutrophication according to the descriptions provided by
20 Souchu et al. (2010): Ayrolle (AYR station): oligotrophic, Bages-Sigean (BGN station):
21 eutrophic, Palavasian complex (MEW station): hypertrophic (represented by asterisks
22 in Fig. 1). At the beginning of monitoring in 2001, AYR station was characterised by
23 transparent waters with dominance of marine phanerogams and associated
24 macroalgae, whereas BGN station was characterised by phanerogams and
25 proliferating macroalgae (stations AY and BN in Souchu et al. 2010). MEW station was
26 almost entirely dominated by phytoplankton (station MW in Bec et al. 2011). Details on

1 the main hydro-morphologic characteristics of these stations and the reductions in
2 nutrient inputs are listed in Table 1. The three stations are located in shallow lagoons
3 (mean depth < 1.5 m) (Bec et al. 2011) with comparable ranges of salinities (median
4 values: AYR=31.1, BGN=25.9, MEW=28.1; see Supplementary Material) and climatic
5 conditions. MEW station is located on Méjean lagoon, which is part of the Palavasian
6 complex, south of Montpellier (Fig. 1). Méjean lagoon has no direct connection to the
7 sea and the water renewal is driven by the inputs of brackish waters coming from the «
8 Rhône to Sète Canal » (Leruste et al. 2016). The Palavasian complex watershed is
9 highly urbanised due to the presence of the city of Montpellier (250,000 inhabitants).
10 The construction of an upgraded wastewater treatment plant (WWTP) in 2005, followed
11 by the diversion of its effluents via an outfall in the Mediterranean Sea located 11 km
12 off-shore led to a sudden dramatic reduction in anthropogenic inputs of nitrogen and
13 phosphorus into the lagoons. This included an estimated 83% reduction in total N and
14 a 73% reduction in total P from the watershed (Meinesz et al. 2013). Before
15 remediation works, the contribution of WWTPs to total inputs to the Palavasian
16 complex was lower for P than for N (respectively 78% and 89% of the total inputs),
17 thanks to the physicochemical treatment of Montpellier's WWTP allowing better
18 phosphorus abatement. As a consequence, the diversion of discharges from this
19 WWTP in 2005 resulted in a larger decrease in N than in P total inputs. This difference
20 in reduction rates between N and P is also explained by the increase in urban run-offs
21 from the watershed, leading to an increase in P total inputs. Bages-Sigean lagoon is
22 located south of the city of Narbonne (53,000 inhabitants). At BGN station, the water is
23 mainly renewed by brackish waters coming from the southern part of the lagoon, which
24 is directly connected to the sea (Fiandrino et al. 2017). The construction of an
25 upgraded WWTP in Narbonne in 2003 enabled a 55% reduction in total N and a 64%
26 reduction in total P inputs from the watershed. Before remediation, the contribution of
27 WWTPs to total inputs to Bages-Sigean lagoon was higher for P than for N

1 (respectively 82% and 76% of the total inputs), this being explained by the lack of
2 physicochemical treatment on Narbonne's WWTP before its refurbishment. The
3 improvement of this WWTP in 2003, including additional treatment to ameliorate
4 phosphorus binding, resulted in a larger decrease of P total inputs than in N total
5 inputs. Oligotrophic Ayrolle lagoon has a permanent connection to the Mediterranean
6 Sea and its watershed is not directly concerned by urban inputs (Bec et al. 2011).

7 **2.2. Laboratory analyses and data collection**

8 Between 2001 and 2014, water was sampled each year at monthly intervals (June,
9 July and August) in summer, when primary production is at maximum in Mediterranean
10 lagoons (Souchu et al. 2010; Bec et al. 2011). We avoided collecting samples during
11 periods of sediment resuspension by not sampling for three days after any period in
12 which wind speed exceeded 12.5 m s^{-1} . Temperature (Temp., °C), salinity (Sal.) and
13 dissolved oxygen (O_2 , mg L^{-1}) were recorded *in-situ* with field sensors. At each station,
14 on each sampling occasion, one water sample was collected in a 1 L polypropylene
15 bottle at the subsurface (in the middle of the water column for depths below 2 m and at
16 -1 m from the surface at deeper stations) for laboratory analysis. The following
17 parameters were analysed in the laboratory: dissolved inorganic nitrogen ($\text{DIN} = \text{NH}_4^+$
18 $+ \text{NO}_3^- + \text{NO}_2$, μM), dissolved phosphorus (DIP, μM), dissolved silicate (Si, μM), total
19 nitrogen and phosphorus (TN and TP, μM) and turbidity. Nutrients were analysed using
20 standard protocols (Aminot and K erouel, 2007), as described in Souchu et al. (2010).
21 Turbidity (Turb., NTU) was measured with a HACH 2100N IS sensor following ISO
22 7027 protocols. Chlorophyll *a* concentrations ($\mu\text{g Chl } a \text{ L}^{-1}$) were measured by
23 spectrofluorimetry (Neveux and Lantoin e 1993) with a Perkin-Elmer L650. Based on
24 cytometric analyses, different size classes of phytoplankton were identified and
25 counted with a FACSCalibur flow cytometer: autotrophic picoeukaryotes ($\leq 3 \mu\text{m}$) and

1 nanophytoplankton ($> 3 \mu\text{m}$) abundances (PICO and NANO, $10^6 \text{ cells L}^{-1}$) (see Bec et
2 al., 2011 for phytoplankton analyses).

3 **2.3. Statistical analyses**

4 Before statistical analyses, Chl *a* data were \log_{10} transformed to homogenise the
5 variances. We used non-parametric Spearman's rank correlation (ρ) analyses to
6 identify potential relationships between the 12 environmental variables: Temp., Sal.,
7 O_2 , DIN, DIP, Si, TN, TP, Turb., Chl *a*, PICO and NANO.

8 Five environmental variables were selected for further analyses because of their key
9 role in anthropogenic eutrophication processes in coastal lagoon waters (Souchu et al.
10 2010): DIN and DIP both cause eutrophication; Chl *a* represents phytoplankton
11 biomass resulting from eutrophication; TP and TN correspond to causes and
12 consequences and are used as integrated parameters for phytoplankton biomass and
13 for organic matter. The five selected variables were standardised before between- and
14 within-group principal component analyses (PCA), using time and space as
15 instrumental variables to control multivariate analysis (Blanc et al. 2001). The within-
16 group PCA of the dataset was centred by group (same dimensions as the original
17 dataset: 5 columns (environmental variables), 924 lines). The within-group analysis
18 searched for information shared by the groups, while the between-group analysis
19 searched for differences between groups. For example, in our study, between-station
20 analysis was a PCA of the dataset containing of station means: 5 columns
21 (environmental variables) and 22 lines (stations). In order to highlight the annual
22 variability of each station with respect to its average position on the inertia axes, the
23 initial data were used as supplementary individuals in the between-station PCA.
24 Between-group and within-group PCAs were performed to study station, year and
25 month effects, using a reduced dataset with five selected parameters (Chl *a*, TN, TP,
26 DIN and DIP). These PCAs made it possible to split the total inertia (i.e. the total

1 information contained in the dataset) into between- and within-group inertia. Monte
2 Carlo permutation tests were conducted on stations, sampling years and sampling
3 months to identify the statistical significance of between-group analyses (Manly 2007).
4 The distances of the trajectories recorded year to year (d_i , with i : period from year i to
5 $i+1$) were calculated at MEW, BGN and AYR stations using the first two dimensions of
6 the between-station PCA. The cumulative year-to-year distance on the first two
7 dimensions was calculated ($\Delta_{\text{total}} = \sum |d_i|$, from $i=2001$ to 2013). At MEW and BGN,
8 annual average distances were also compared for the periods before (Δ_{before}) and after
9 (Δ_{after}) the works on the sewerage systems were completed.

10 A Mann-Kendall test was performed to assess monotonic temporal trends in
11 environmental variables at MEW, BGN and AYR stations. Non-parametric Kruskal-
12 Wallis one-way analysis of variance was also performed at these stations to identify
13 significant differences between sampling years. At MEW and BGN stations, Wilcoxon
14 rank sum tests enabled comparison of concentrations before (respectively, 2001-2005
15 and 2001-2003) and after (respectively, 2006-2014 and 2004-2014) works on the
16 sewage systems.

17 Tests were considered significant at $p < 0.05$. All statistical analyses were performed
18 with R software (R CoreTeam 2017).

19 **3. Results**

20 3.1. Key parameters highlighted a eutrophication gradient

21 The dataset revealed several significant correlations (Table 2) (see Supplementary
22 Material for the ranges of the environmental parameters). Temperature, salinity, O_2 , Si,
23 DIN and NANO were weakly correlated with other parameters ($\rho < 0.5$). Chl a
24 concentrations were highly correlated with TP ($\rho = 0.82$, $n = 900$), TN ($\rho = 0.70$, $n =$
25 899), autotrophic picoeukaryote abundances ($\rho = 0.67$, $n = 886$) and turbidity ($\rho = 0.66$,
26 $n = 903$). These five variables were significantly correlated with each other,

1 demonstrating their link with the primary production process. Total phosphorus was
2 significantly and much more strongly correlated with its inorganic forms DIP ($\rho = 0.61$,
3 $n = 902$) than total nitrogen with DIN ($\rho = 0.23$, $n = 901$). The contribution of DIP to TP
4 had a median value of 11.4%, while the contribution of DIN to TN was only 1.7%,
5 highlighting the dominance of organic forms, especially of nitrogen. Ammonium (NH_4^+)
6 was the main form of dissolved inorganic nitrogen (median 69.2%, $n = 908$).
7 Percentages of other inorganic forms of nitrogen were 18.2% for nitrates and 8.4% for
8 nitrites. The weakest correlations with other environmental parameters were found for
9 dissolved oxygen concentrations.

10 Permutation tests of between-group PCAs performed on the five selected parameters
11 (Chl *a*, TN, TP, DIN and DIP) were all significant (Monte-Carlo's $p < 0.001$), but
12 between-month inertia only accounted for a very low percentage of total inertia (0.7%),
13 much lower than the percentages represented by the between-year and between-
14 station inertias (respectively 8.5% and 41.5%). This led us to average the dataset per
15 year and per station for the five water quality parameters. Then, as the spatial pattern
16 was stronger than the temporal pattern (percentages of total inertia of 52.3% and
17 10.2%, respectively, Table 3), between-station PCA was selected to identify an
18 anthropogenic eutrophication gradient among the 22 sampling stations and to reveal
19 trajectories of change over the study period.

20 The first factorial axis of the between-station PCA (PC1, 81% of the between-station
21 inertia) was highly correlated with Chl *a*, TN, TP, and to a lesser extent with DIP (Fig.
22 2a). This axis ordinated stations according to a clear anthropogenic eutrophication
23 gradient (Fig. 2b). The second axis (PC2) accounted for only 11.5% of the between-
24 station inertia and was correlated with DIN (Fig. 2).

25 3.2. Recovery trajectories after remediation actions

1 The following statistical analyses focused on three stations distributed along the
2 anthropogenic eutrophication gradient identified by the between-station PCA: MEW -
3 hypertrophic station, BGN - eutrophic station - and AYR - oligotrophic station - (stations
4 in colour in Fig. 2b). Figure 3 illustrates the trajectories of the three stations between
5 2001 and 2014 on the plane defined by the first two axes of the between-station PCA.
6 During the study period, the variability of AYR station trajectory was low along the first
7 axis and the first plane of the between-station PCA. The cumulative year-to-year
8 distance on the first plane for AYR was the lowest ($\Delta_{\text{total}}=2.9$). Conversely, BGN station
9 shifted significantly along the first axis (PC1) towards oligotrophy after mitigation works
10 were completed. The cumulative distance on the first plane was more than two times
11 greater than that of AYR ($\Delta_{\text{total}} = 6.4$) and the average annual distance decreased after
12 mitigation works, indicating a reduction in ecosystem variability ($\Delta_{\text{before}} = 1.2$ and $\Delta_{\text{after}} =$
13 0.4). From 2001 to 2014, the MEW trajectory also shifted significantly along PC1
14 towards oligotrophy. The cumulative year-to-year distance on the first plane for MEW
15 was nearly eight times greater than that of AYR ($\Delta_{\text{total}}=21.5$). The average annual
16 distance of MEW station also decreased after mitigation works ($\Delta_{\text{before}}=2$ and $\Delta_{\text{after}}=1.5$).
17 However, from 2011 to 2014, the trajectory oscillated back and forth (Fig. 3), revealing
18 instability of the ecosystem, especially from 2013 to 2014, when the trajectory
19 displayed notable backtracking.

20

21 Figure 4 shows the time series of DIP, DIN, TP, TN, Chl *a*, PICO and NANO for the
22 three stations (AYR, BGN and MEW) used for a detailed examination of changes in
23 trajectories. Between 2001 and 2004, i.e. before the remediation actions in the
24 watershed containing the Palavasian complex, MEW station remained in its initial
25 hypertrophic state, with average Chl *a* concentrations of $134 \mu\text{g L}^{-1}$. The recovery
26 process started in 2005 with no lag time, immediately after the construction of the

1 upgraded WWTP, when the Chl *a* biomass fell sharply (Fig. 4c). TP and TN decreased
2 synchronously with chlorophyll *a*. This was followed by a decrease in DIP and PICO
3 concentrations in 2006 and 2007 (Fig. 4a and 4d). From 2007 to 2010, the Chl *a* and
4 PICO concentrations continued to decline, whereas DIP concentrations increased
5 significantly. The 2011-2014 period was characterised by sporadic increases in
6 phytoplankton biomass and abundances, and in DIP levels (Fig. 4) of the same order of
7 magnitude or even higher than those measured before 2005 (years 2009 to 2012 and
8 2014, $p = 0.013$). However, chlorophyll *a* biomass declined significantly ($p = 0.012$)
9 throughout the study period and average Chl *a* concentrations measured before and
10 after remediation works were divided by 15.7 (134 before and $8.6 \mu\text{g L}^{-1}$ after, $p <$
11 0.0001) (Fig. 4c). TP and TN followed the same trend, with a significant decrease ($p =$
12 0.009 and 0.002) and average concentrations divided respectively by 2.5 and 3.1 (20
13 before and $8.1 \mu\text{M}$ of TP after, $p < 0.0001$; 339 before and $109 \mu\text{M}$ of TP after, $p <$
14 0.0001) (Fig. 4b). As PICO abundances were highly correlated with Chl *a* ($\rho = 0.65$, $p <$
15 0.0001 , $n = 42$), they also decreased significantly over the study period ($p = 0.037$),
16 and their concentrations decreased by a factor of 2.4 after WWTP refurbishment (4.01
17 $\times 10^9$ before and $1.65 \times 10^9 \text{ cell L}^{-1}$ after, $p = 0.005$). Abundances of nanophytoplankton
18 underwent significant variations depending on the year, with a peak in 2006 (average
19 $7.63 \times 10^9 \text{ cell L}^{-1}$). The decrease in phytoplankton biomass was accompanied by a
20 decrease in turbidity and oxygen levels ($p=0.0014$ and 0.0017). Changes in DIN
21 concentrations revealed no particular pattern over time.

22 The pattern of change at BGN station differed from that at MEW. From 2001 to 2003,
23 i.e. before the upgraded WWTP began operating, the BGN station was eutrophic,
24 according to Souchu et al. (2010). From 2003 to 2005, BGN started recovering, but
25 less abruptly than MEW (Fig. 3). DIP concentrations dropped the year after the
26 remediation works were completed (Fig. 4a) and a significant decrease was observed

1 over the study period ($p = 0.007$), with levels divided by 5.2 (from 1.6 to 0.3 μM , $p =$
2 0.004) after completion of the works. Changes in TP followed the same trend as DIP,
3 with mean levels divided by 2.4 (from 3.3 to 1.4 μM , $p = 0.01$), but chlorophyll *a*
4 concentrations only started decreasing after a lag time of two years. DIN increased
5 after completion of the WWTP works and reached a maximum in 2005 (Fig. 4a).

6 After the delay in ecosystem response, the pattern of change suggested a gradual
7 continuation of the recovery process from 2006 until 2014, with a decrease in Chl *a* and
8 DIP. Chlorophyll *a* concentrations decreased significantly throughout the study period
9 ($p=0.001$) and were divided by 1.6 after remediation works (from 4.5 to 2.8 $\mu\text{g L}^{-1}$,
10 $p=0.03$). Chl *a* concentrations decreased after remediation works, with average levels
11 divided by 1.2 (from 47.8 to 38.5 μM , $p = 0.004$). TN concentrations decreased rapidly
12 from 2002 to 2006, but then increased again and stabilised below the level observed
13 before remediation works. However, picoeukaryotes, nanophytoplankton and dissolved
14 and organic forms of N did not decrease significantly and no significant between-year
15 differences were observed.

16 At AYR station, despite a decrease in Chl *a*, DIN and DIP over the course of the study
17 period (from 1.6 to 0.5 $\mu\text{g L}^{-1}$, $p = 0.016$; from 1.2 to 0.32 μM , $p = 0.02$; from 0.04 to
18 0.03 μM , $p = 0.03$, respectively), the orders of magnitude of the concentrations were
19 much lower than those at BGN and MEW stations (mean levels respectively from 1.6
20 and 4.6 times lower (DIN) to 3.8 and 28.2 times lower (Chl *a*)) (Fig. 4). Phytoplankton
21 abundances showed no significant trends over time.

22 The average TN:TP and DIN:DIP ratios at MEW station were already the lowest and
23 decreased significantly after remediation works (from respectively 17.4 to 14.6, $p=0.02$;
24 and from 4.2 to 2.2, $p = 0.02$). TN:TP ratios were below 20, suggesting N limitation
25 according to the total nutrient based approach (Guilford & Hecky 2000 in Souchu et al.
26 2010). The average TN:TP ratio at BGN station (31.1) was farther from the Redfield

1 ratio and did not change significantly after remediation works. The TN:TP ratio at BGN
2 station highlighted a limitation by both P and N. Moreover, the average DIN:DIP ratio
3 (9.5) characterised a limitation by N according to the dissolved nutrient based criteria
4 (Justic et al. 1995 in Souchu et al. 2010). The average TN:TP and DIN:DIP ratios were
5 the highest at AYR station (respectively 46.8 and 17.6) and highlighted a P limitation.

6

7 **4. Discussion**

8 4.1. Integrative parameters revealed a eutrophication gradient

9 The rare dataset we used to monitor coastal lagoons whose status ranged from
10 oligotrophic to hypertrophic (Souchu et al. 2010; Bec et al. 2011), allowed us to analyse
11 eutrophication and oligotrophication phenomena in these ecosystems. Some of these
12 lagoons received large inputs of urban nutrients for several decades, but major
13 management actions have recently been implemented on the waste water treatment
14 systems in most of their watersheds (Meinesz et al. 2013; Gowen et al. 2015; Leruste
15 et al. 2016). Fourteen years after the monitoring of French Mediterranean lagoons
16 began (Souchu et al. 2010), an anthropogenic eutrophication gradient is still highlighted
17 by the water quality parameters. The five parameters selected in our study to identify
18 the anthropogenic eutrophication gradient are representative of nutrient cycling in the
19 water column of coastal lagoons as they incorporate either the causes (DIN and DIP),
20 or the consequences of the eutrophication process (Chl *a*), or both (TP and TN, which
21 were closely correlated with each other and with Chl *a*). DIN and DIP represented very
22 low percentages of total nutrients in summer (median 1.68% and 11.4%, respectively).
23 Dissolved nutrient concentrations were very low because of continuous uptake by
24 massive phytoplankton blooms, which occur mainly in summer (Bec et al. 2011). These
25 results are in agreement with observations made in shallow lakes (Ibelings et al. 2007;
26 Jeppesen et al. 2007), where the integrative parameters TN, TP and Chl *a* appear to

1 be good complements to the dissolved nutrients usually measured in transitional and
2 coastal ecosystems (Claussen et al. 2009; Ferreira et al. 2011; McLaughlin et al. 2013;
3 Lemley et al. 2015). These parameters appear to be suitable for monitoring
4 programmes, such as WFD assessment programmes, whose aim is to evaluate the
5 effectiveness of management measures.

6 4.2. Remediation works triggered a rapid and significant response by lagoon 7 ecosystems

8 In our study, the hypothesis that the reduction in urban nutrient inputs would have a
9 rapid effect on the water total nutrient levels and phytoplankton biomass was confirmed
10 in hypertrophic and eutrophic lagoons. After a reduction of more than 50% in TP and of
11 80% in TN loadings from the watershed of these ecosystems, a recovery trajectory was
12 rapidly identified using the integrative parameters Chl *a*, TN and TP. The
13 concentrations of these parameters in the water column decreased significantly within
14 one to three years. The response lag times and ranges observed after remediation
15 actions in the eutrophic lagoon are in agreement with those reported in other coastal
16 lagoons by Pasqualini et al. (2017) and in estuaries by Lie et al. (2011), Boynton et al.
17 (2013) or Ní Longphuirt et al. (2016). Our results demonstrate that even hypertrophic
18 coastal lagoons can recover following substantial reduction in nutrient loads and
19 confirm the rare observations available on such degraded ecosystems, whose main
20 nutrient sources are WWTPs (Leruste et al. 2016), or on temperate lakes (Jeppesen et
21 al. 2005; Ibelings et al. 2007; Jeppesen et al. 2007). What is remarkable about our
22 results is the speed (one to two years) and the extent of the recovery of the
23 hypertrophic lagoon, the decreases in the concentrations of Chl *a* and TP being 10 fold
24 greater than in the eutrophic lagoon. This difference may be due to the more drastic
25 reduction in nutrient loading, which reached 83% for total N and a 73% for total P in the
26 hypertrophic lagoon versus 55% and 64% in the eutrophic lagoon. We observed

1 shorter recovery lag times than those observed by many authors in transitional water
2 ecosystems, who reported 10 to 18 years (García et al. 2010; Gee et al. 2010; Saeck
3 et al. 2013). We also observed stronger effects than those reported by other authors on
4 water column quality after remediation works of comparable magnitude (Kronvang et
5 al. 2005; Williams et al. 2009).

6 The TN:TP ratios were the lowest for the hypertrophic lagoon and the closest to the
7 Redfield ratio, intermediate for the eutrophic lagoon and the highest for the oligotrophic
8 lagoon. Such increases in the TN:TP ratios from the most to the least eutrophic
9 ecosystem may also reflect a reduction in the dominance of primary production by
10 phytoplankton and also a limitation of phytoplankton growth by phosphorus, which is
11 more frequently observed in undisturbed ecosystems (Souchu et al. 2010; Paerl et al.
12 2014). The increase in the DIN:DIP ratio from the hypertrophic to the oligotrophic
13 lagoon confirms this shift from DIN limitation to DIP limitation. This result is in
14 agreement with observations of coastal lagoons (Zirino et al. 2016) and also of
15 freshwater ecosystems (Jeppesen et al. 2005; Jeppesen et al. 2007; Yan et al. 2016).
16 In the hypertrophic lagoon, the decrease in the TN:TP and DIN:DIP ratios corresponds
17 to a decrease in urban nutrient inputs, which was greater for nitrogen (-83%) than for
18 phosphorus (-73%). The decrease is also due to the higher DIP concentrations
19 observed four years after remediation actions were completed. The increase in DIP
20 concentrations could be caused by phosphorus released into the water column from
21 highly enriched bottom sediments (Gikas et al. 2006), which is facilitated by the strong
22 benthic-pelagic nutrient coupling in shallow coastal lagoons (Kennish & de Jonge,
23 2011). But this increase in DIP could also be the result of non-consumption by
24 phytoplankton as a consequence of strong nitrogen limitation in summer (Souchu et al.
25 2010).

26 4.3. Recovery trajectories in coastal lagoons

1 The pathways of change in the three coastal lagoons in our study covered a wide
2 range of anthropogenic eutrophication, from oligotrophic to hypertrophic ecosystems.
3 Environmental monitoring of hypertrophic and eutrophic lagoons for respectively nine
4 and 11 years after significant reductions in urban nutrient loading made it possible to
5 identify different recovery patterns. The conceptual models of changes to the status of
6 an ecosystem with pressure proposed by Elliott et al. 2007 and Tett et al. 2007, were
7 used to represent the trajectories of the oligotrophic, eutrophic and hypertrophic
8 lagoons, at different phases of anthropogenic eutrophication and recovery processes
9 (Fig. 5). The concentration of Chl *a* in the water in summer was chosen as the
10 ecosystem status metric (for shared periods: before (years 2001 to 2003) and after
11 remediation works (years 2012 to 2014), as this integrative parameter has been shown
12 to be a relevant indicator of eutrophication status (Cloern et al. 2001; Bec et al. 2011;
13 Ferreira et al. 2011). Moreover, our results are in agreement with those of Bec et al.
14 (2011), showing that Chl *a* is closely correlated with autotrophic picoeukaryotes, which
15 comprise the majority of the phytoplankton community in French Mediterranean
16 lagoons. TN total inputs from the watersheds (before and after remediation works,
17 Table 1) were chosen as the pressure metrics, as N is typically the limiting factor in
18 eutrophic lagoons in summer (Souchu et al. 2010).

19 Like in many studies of the recovery of coastal ecosystems (except e.g. Kemp et al.,
20 2005 or Ibelings et al. 2017), the states of the eutrophic and hypertrophic lagoons
21 before degradation were not fully described. The observations on the oligotrophic
22 lagoon revealed a high ecological status, with low Chl *a* concentrations in accordance
23 with the reference conditions laid down by European WFD (MEDDE, 2015), and
24 revealed slight inter-annual variations (Fig. 5-1). This pattern reflects the inherent
25 variability of undisturbed coastal lagoons (Elliott and Quintino 2007), dominated by
26 perennial benthic macrophytes (Schramm et al. 1999; Viaroli et al. 2007).

1 The eutrophic lagoon, in which the presence of macrophytes had been demonstrated
2 before remediation (Fig. 5-2), recovered to a mesotrophic state, with primary
3 production less dominated by phytoplankton and more by phanerogams (Ifremer 2014).
4 If we hypothesise that the reference conditions attainable for the eutrophic lagoon were
5 similar to those of the oligotrophic lagoon, the recovery was almost complete, indicating
6 complete resilience, because the ecosystem status after remediation was close to the
7 reference state (Elliott et al. 2007). Such shifts from pelagic-dominated to more
8 benthic-dominated communities based on macroalgae and seagrasses during the
9 oligotrophication process have already been reported in coastal and estuarine
10 eutrophic ecosystems after remediation actions (Lie et al. 2011; Cebrian et al. 2013;
11 Saeck et al. 2013).

12 The hypertrophic lagoon, which was dominated by phytoplankton and where the
13 bottom was bare sediments before remediation (Fig. 5-4), shifted to a eutrophic state
14 (Fig. 5-3), with the appearance of fast-growing macroalgae after mitigation actions
15 (Ifremer 2010). In contrast to the eutrophic lagoon, the recovery trajectory of the
16 hypertrophic lagoon appears to be not yet complete, suggesting that all compartments
17 of the ecosystem have not yet recovered, particularly the benthic compartments (Elliott
18 et al. 2007; Tett et al. 2007). Moreover, the trajectory of the hypertrophic lagoon
19 displayed high variability and feedback responses, suggesting that the ecosystem
20 regime had become unstable (Scheffer and Carpenter 2003; Ibelings et al. 2007;
21 Kennish and de Jonge 2011). Shortly after remediation actions, the hypertrophic
22 lagoon displayed a renewed increase in DIP concentrations, mimicking the immediate
23 decrease in Chl *a*, and later the appearance of macroalgae (observed between 2006
24 and 2009 (Ifremer 2010)). The increase in DIP could correspond to the release of
25 phosphate accumulated in the sediments, which is favoured by summer conditions
26 (Kemp et al. 2005), and also to their incomplete consumption by phytoplankton in the

1 water column. Another possible explanation is recycling of the organic matter
2 originating from macroalgae degradation and leading to an increase in dissolved
3 inorganic nutrients in the water column. In lakes, internal loading of phosphates from
4 sediments has frequently been reported to delay recovery from anthropogenic
5 eutrophication (Gulati and Van Donk 2002; Jeppesen et al. 2005; Jeppesen et al.
6 2007), more rarely in coastal or estuarine ecosystems (Lillebø et al. 2007; Ní
7 Longphuirt et al. 2016; Riemann et al. 2016). The recent renewed increases in Chl *a*
8 and DIP persisting in 2015 and 2016, confirmed the incomplete recovery of the
9 hypertrophic ecosystem, which alternates blooms of macroalgae and phytoplankton
10 depending on the monitoring year (Schramm 1999; Viaroli et al. 2008). Although a
11 significant decrease was observed, Chl *a* concentrations after remediation still
12 correspond to a bad status according to the European WFD (MEDDE, 2015).

13 Figure 5 suggests that there is a common restoration scheme in the studied lagoons
14 following an equivalent decrease in anthropogenic pressure (nitrogen inputs). To what
15 extent factors such as depth or salinity could modify this pattern remains to be
16 determined. Following a significant reduction in nutrient inputs, hypertrophic or
17 eutrophic coastal lagoons showed an almost immediate positive response in their
18 environmental conditions. However, the oligotrophication trajectory and the likelihood of
19 recovery, even partial, remain statistically difficult to predict (Duarte et al. 2009;
20 McCrackin et al. 2017). Given the costs and difficulties in implementing management
21 plans for nutrient reduction, managers and policy-makers should consider uncertainty
22 and ecosystem specificity as their main guides when designing any remediation actions
23 targeting oligotrophication of coastal lagoons. Indeed, as exemplified in this study, the
24 level of recovery and the trajectory could be affected by: (i) external drivers, such as
25 completeness of nutrient reduction, other stressors, connectivity, or climate change; (ii)
26 internal factors such as physical traits (i.e. water renewal time; de Jonge et al. 2002;

1 Fiandrino et al. 2017), lagoon history, sediment nutrient stocks (Duarte et al. 2009;
2 Borja et al. 2010) or the presence of residual seagrass patches or seed stocks (Ibelings
3 et al. 2007; Le Fur et al. 2017); and interactions between the two drivers. All of these
4 may cause time lags, regime shifts and non-linearities (Ibelings et al. 2007; Duarte et
5 al. 2009; Riemann et al. 2016) in ecosystem responses following remediation efforts.
6 Specifically in the case of hypertrophic coastal lagoons, we showed that even 10 years
7 after major reduction in nutrient loads, the environmental conditions necessary to
8 restore the ecological functions and structure of the ecosystem, and the objectives laid
9 down by the European WFD have not fully been achieved. It was not possible to
10 estimate the recovery times needed to reach a good ecological status by all the
11 lagoons studied. Further analyses of a larger number of lagoons will be necessary and
12 should be completed by modelling to determine the effects of each factor and feedback
13 interactions (positive or negative) with an impact on recovery trajectory and recovery
14 time. At the time of writing, three strategies are feasible:

- 15 • “Wait and see”: one could hypothesise that eutrophication pressure is now
16 sufficiently low to allow the ecosystem to recover its ecological functions and
17 structure of the reference conditions, after a period of hysteresis;
- 18 • “Go further” in reducing nutrient inputs: this is economically and technically hard
19 to implement, and the likelihood of ecological recovery, even partial, is not
20 guaranteed for the same reasons as discussed previously;
- 21 • “Give a helping hand”: implementing active restoration programmes to enhance
22 internal factors could facilitate ecological recovery (Verdonschot et al. 2013).
23 Examples of possible active restoration actions are: restoration of seagrass
24 meadows (Orth et al. 2012; de Wit et al. 2017) to reduce nutrient sediment
25 fluxes or limit turbidity; development of passive aquaculture for top-down

1 phytoplankton control and/or nutrient export (Ferreira and Bricker 2016; Ahmed
2 et al. 2017; Reitsma et al. 2017).

3 Two common results in studies of oligotrophication trajectories are the unpredictability
4 of the degree of ecological recovery and its duration (at best 10 years) in the case of
5 success (Duarte et al., 2009; Verdonschot et al. 2013; McCrackin et al. 2017). Both call
6 for continued long-term monitoring and research programmes (see list of priorities in
7 Verdonschot et al. 2013) as well as adaptive recovery management plans, which
8 emphasize institutional experimentation and learning by doing (Jentoft 2007).

9 **Author contributions**

10 All authors contributed to the conception and design of the study, to the selection,
11 analyses and interpretation of the data and relevant literature. VD led the writing of the
12 manuscript. BB, DM, AF, RP, MS, PS, TL, CA and NM critically revised the manuscript.
13 All authors approve the manuscript in its current form and agree to be accountable for
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8

1 **Table 1.** Summary characteristics of the three sampling stations studied covering the eutrophication
 2 gradient. Lagoon and watershed areas, eutrophication status in 2001 (from Souchu et al., 2010), residence
 3 time (Fiandrino et al. 2012) and year of the remediation works. Annual N and P inputs originating from
 4 WWTPs located in the watershed and annual N and P total inputs from whole watershed (including inputs
 5 from the WWTPs), before and after remediation works (Meinesz et al. 2013). N and P inputs were
 6 standardized by lagoon volume (values in $\text{t}\cdot\text{year}^{-1}\cdot 10^6\text{m}^{-3}$).

Lagoon (sampling station - eutrophication status in 2001)	Lagoon area (km ²)	Lagoon volume (10 ⁶ m ³)	Watershed area (km ²)	Residence time (d) (volume/residence time, 10 ⁶ m ³ d ⁻¹)	Year of the remediation works	N and P inputs from the WWTPs, in $\text{t}\cdot\text{year}^{-1}\cdot 10^6\text{m}^{-3}$				N and P total inputs from the watershed, in $\text{t}\cdot\text{year}^{-1}\cdot 10^6\text{m}^{-3}$			
						N before works	N after works	P before works	P after works	N before works	N after works	P before works	P after works
Ayrolle (AYR - oligotrophic)	13.4	9.9	119.8	ND	-	0	0	0	0	0.05	0.05	0.006	0.006
Bages (BGN - eutrophic)	24.4	47	468.6	210 (0.23)	2003	6.2	0.9	0.9	0.09	8.2	3.7	1.1	0.4
Palavasian complex (MEW - hypertrophic)	7.2	9.1	662	32 (0.28)	2005	157.7	3.9	13.5	0.6	177.2	30.2	17.3	4.6

7

8 **Table 2.** Spearman's rank correlations (ρ) between environmental variables measured monthly at the 22
 9 stations from 2001 to 2014 (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; *ns*: not significant; strong correlations
 10 ($|\rho| \geq 0.5$) in bold and underlined). Temp.: temperature, Sal.: salinity, O2: dissolved oxygen, Turb.: turbidity,
 11 Si: dissolved silicate, DIN: dissolved inorganic nitrogen, TN: total nitrogen, TP: total phosphorus, DIP:
 12 dissolved inorganic phosphorus, Chl *a*: chlorophyll *a*, NANO: nanophytoplankton, PICO: autotrophic
 13 picoeukaryotes

	Temp.	Sal.	O2	Turb.	Si	DIN	TN	TP	DIP	Chl <i>a</i>	NANO
Sal.	0.07*										
O2	-0.10**	-0.24***									
Turb.	<i>ns</i>	-0.32***	<i>ns</i>								
Si	0.14**	-0.24***	-0.09	0.31***							
DIN	<i>ns</i>	-0.19***	0.14***	0.24***	<i>ns</i>						
TN	0.13***	-0.36***	<i>ns</i>	0.73***	0.46***	0.23***					
TP	0.22***	-0.27***	<i>ns</i>	0.74***	0.36***	0.20***	0.81***				
DIP	0.16***	-0.10**	<i>ns</i>	0.34***	0.34***	0.09**	0.38***	0.61***			
Chl <i>a</i>	0.29***	-0.19***	<i>ns</i>	0.66***	0.38***	0.12***	0.70***	0.82***	0.45***		
NANO	0.10**	-0.11***	<i>ns</i>	0.35***	<i>ns</i>	0.10**	0.31***	0.36***	0.13***	0.41***	
PICO	0.12***	-0.22***	<i>ns</i>	0.57***	0.28***	0.13***	0.56***	0.65***	0.28***	0.67***	0.38***

14

15 **Table 3.** Inertia and first eigenvalues (PC1) associated with global, between- and within-group Principal
 16 Component Analyses (PCA) of the environmental dataset (DIN, DIP, Chl *a*, TN, TP)

PCA	Global	Within-year	Between-year	Within-station	Between-station
Inertia	5	4.49 (89.7%)	0.51 (10.2%)	2.38 (47.7%)	2.62 (52.3%)
PC1	3.12	2.75	0.41	1.07	2.12

17

18

19

1 Figure captions:

2

3 **Fig. 1.** Location of the 16 lagoons and the 22 water sampling stations. The three stations with
4 asterisks were the subject of specific statistical analyses.

5

6 **Fig. 2.** Between-station PCA of 5 water column variables from the 22 stations and the 14 years of
7 sampling. **a)** Loadings of the 5 active variables on the plane defined by PC1 and PC2. **b)** Location of
8 stations on the PC1-PC2 plane. The colours show the degree of eutrophication of three of the
9 stations: oligotrophic (AYR, blue), eutrophic (BGN, green) and hypertrophic (MEW, red). The d-values
10 give the scale (i.e. the size of the grid is shown in grey).

11

12 **Fig. 3.** Trajectories between 2001 and 2014 of the AYR (oligotrophic, in blue), BGN (eutrophic, in
13 green) and MEW (hypertrophic, in red) stations on the plane defined by PC1 and PC2 of the between-
14 station PCA. The d-value gives the scale (i.e. the size of the grid is shown in grey).

15

16 **Fig. 4.** Monthly concentrations (diamonds) and means (curves) of summer concentrations (June-
17 August) of: **a)** DIP and DIN (μM), **b)** TP and TN (μM), **c)** Chl *a* ($\mu\text{g L}^{-1}$, \log_{10} scale) and **d)**
18 picoeukaryote and nanoeukaryote abundances (10^6 cell L^{-1}) from 2001 to 2014 at MEW (left column),
19 BGN (middle column) and AYR (right column) stations. The shaded areas represent the period before
20 the waste water treatment systems were improved.

21

22 **Fig. 5.** Changes in chlorophyll *a* in the water at stations BGN and MEW measured before (years 2001-
23 2002-2003) and after mitigation actions (years 2012-2013-2014) versus TN total inputs from the
24 watersheds (dots: average; crosses: outliers). Boxplot of Chl *a* at AYR station represents data
25 measured in 2001-2002-2003 and in 2012-2013-2014. Data are represented in the conceptual model
26 of changes in the ecosystem status with pressure (adapted from Elliott et al. 2007 and Tett et al.
27 2007). Illustrations of ecosystem status: oligotrophic (1) mesotrophic (2), eutrophic (3) and
28 hypertrophic (4) (© Réseau de Suivi Lagunaire).

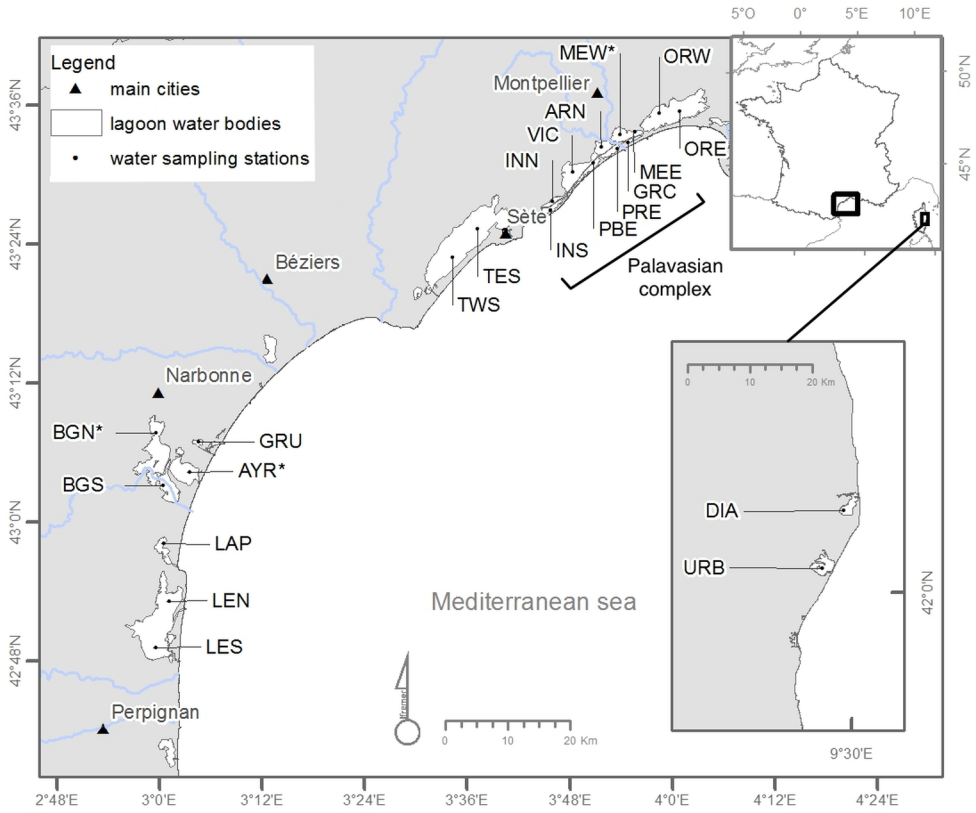
29

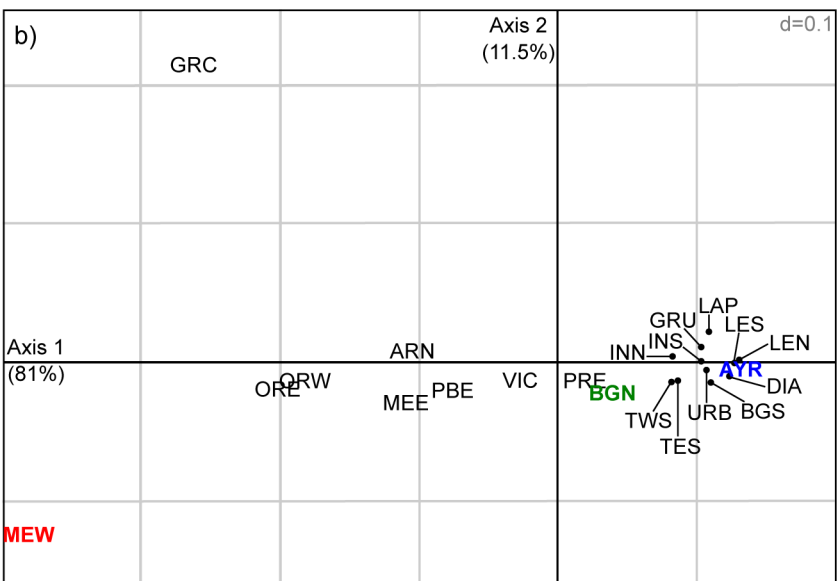
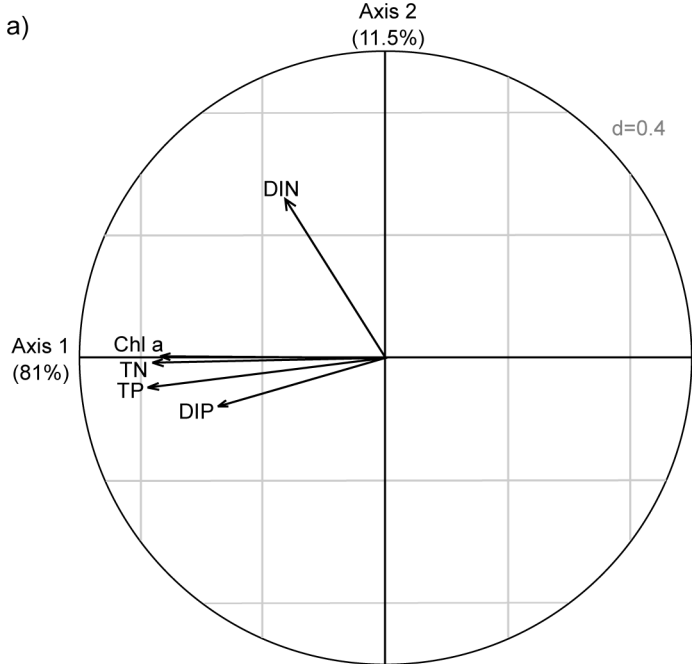
30 **Supplementary material**

31 Distribution of the 12 environmental parameters (temperature (Temp.), salinity (Sal.), dissolved
32 oxygen (O₂), turbidity (Turb.), dissolved silicate (SiOH), dissolved inorganic nitrogen (DIN), total
33 nitrogen (TN), total phosphorus (TP), dissolved inorganic phosphorus (DIP), chlorophyll *a* (Chl *a*),
34 nanophytoplankton (NANO), autotrophic picoeukaryotes (PICO)) measured in the 22 stations. Box
35 and whiskers plots from summer data (June, July, and August) of year 2001 to year 2014 (n=42 for
36 each station): the whiskers represent the 5th and the 95th percentiles, the outer edges of the boxes
37 represent the 25th and 75th percentiles, the horizontal lines within the boxes represent the medians
38 and the black points represent the averages. The colours show the degree of eutrophication of three
39 of the stations: oligotrophic (AYR, blue), eutrophic (BGN, green) and hypertrophic (MEW, red).

40 The variability of parameters of the 22 stations are within the observed ranges of coastal
41 Mediterranean lagoons. According to the whole variability observed in these 22 stations, the 3
42 selected lagoons cover the range of observed trophic status. AYR and MEW stations represent the
43 observed minima & maxima for most of the 12 parameters studied.

44





Axis 2
(11.5%)

d = 2

Axis 1
(81%)

