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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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ABSTRACT

French Mediterranean coastal lagoons have been subject to huge inputs of urban nutrients for decades leading to the eutrophication of these vulnerable ecosystems. In response to new environmental regulations, some of the lagoons have recently been the subject of large-scale management actions targeting the waste water treatment systems located on their watersheds. While the eutrophication of coastal ecosystems is well described, recovery trajectories have only recently been studied. To assess the rapidity and the extent of the effect of the remediation actions, we analysed data from a 14-year time series resulting from the monitoring of nutrients, biomass and the abundance of phytoplankton in the water column of French Mediterranean coastal lagoons covering the whole anthropogenic eutrophication gradient. Following a 50% to 80% reduction in total phosphorus (TP) and total nitrogen (TN) urban loadings from the watershed of hypertrophic and eutrophic ecosystems, the integrative parameters chlorophyll *a*, TN and TP, provide evidence for a rapid response (1 to 3 years) and for an almost complete recovery, suggesting no hysteresis for the eutrophic lagoon. However, our findings also show that recovery patterns depend on the eutrophication status before remediation and may include feedback responses. The different responses revealed by our results should help stakeholders prioritise remediation actions and identify appropriate restoration goals, especially in light of the targets of the Water Framework Directive (WFD).

1. Introduction

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

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

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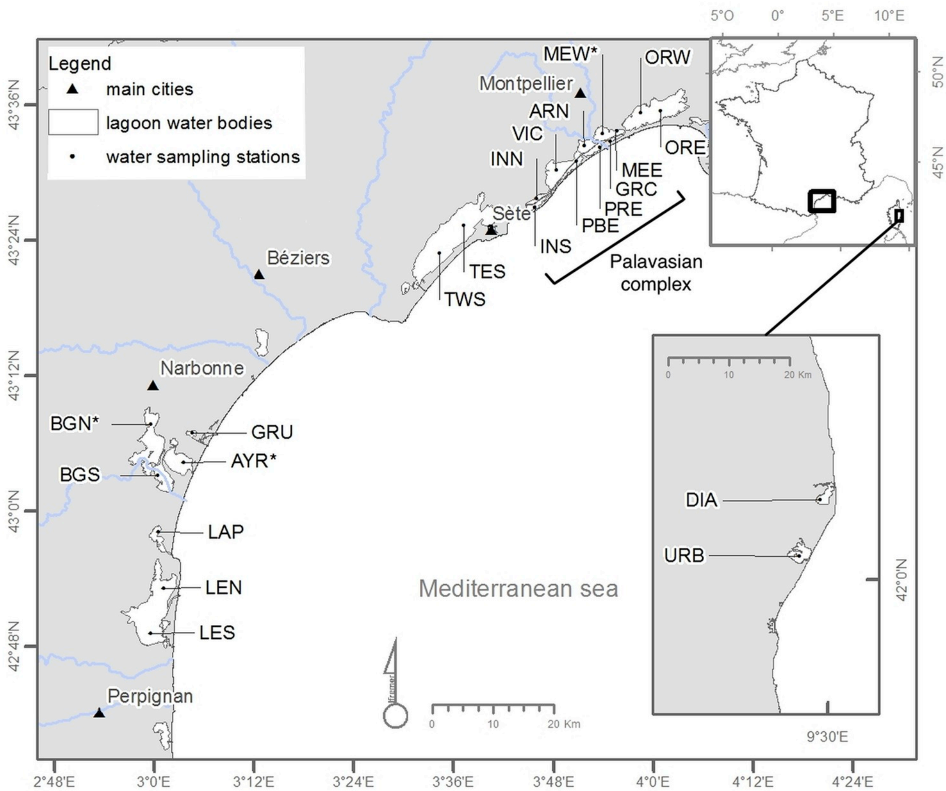

Fig. 1. Location of the 16 lagoons and the 22 water sampling stations. The three stations with asterisks were the subject of specific statistical analyses.

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

2. Materials and methods

2.1. Study sites and sampling strategy

Data from 16 French Mediterranean coastal lagoons collected between 2001 and 2014, were analysed. Fourteen of the lagoons are located in the Gulf of Lions, from north of Perpignan to Montpellier, and two in Corsica (Fig. 1). The database includes polyhaline and euhaline microtidal lagoons (annual median salinity > 18) (see Supplementary Material), with surface areas ranging from 1.4 to 75 km^2, depths ranging from 0.7 to 9 m and volumes ranging from 0.7 to 260 × 10^6 m^3 (Souchu et al., 2010). Details on the morphometric and hydrologic characteristics of the study sites are available in Souchu et al., (2010) and Bec et al., (2011). The lagoons are all connected to the Mediterranean Sea, through direct inlets, or through indirect connections via a canal or another lagoon. The database covers the anthropogenic eutrophication gradient from oligotrophic to hypertrophic lagoons (Bec et al., 2011). In each of the 16 lagoons, water was sampled at one or two stations depending on the size of the lagoon, giving a total of 22 stations: Leucate (LES, LEN), La Palme (LAP), Bages-Sigean (BGS and BGN), Ayrolle (AYR), Gruissan (GRU), Thau (TES, TWS), Ingril (INN and INS), Vic (VIC), Pierre-Blanche (PBE), Arnel (ARN), Prévost (PRE), Méjean (MEW, MEE), Grec (GRC), Or (ORE and ORW), Diana (DIA) and Urbino (URB). We first analysed changes in the anthropogenic eutrophication gradient at the 22 stations over the 14-year study period.

Next, three stations were selected for specific statistical analyses based on their degree of anthropogenic eutrophication according to the descriptions provided by Souchu et al. (2010): Ayrolle (AYR station): oligotrophic, Bages-Sigean (BGN station): eutrophic, Palavasian complex (MEW station): hypertrophic (represented by asterisks in Fig. 1). At the beginning of monitoring in 2001, AYR station was characterised by transparent waters with dominance of marine phanerogams and associated macroalgae, whereas BGN station was characterised by phanerogams and proliferating macroalgae (stations AY and BN in Souchu et al., 2010). MEW station was almost entirely dominated by phytoplankton (station MW in Bec et al., 2011). Details on the main hydromorphologic characteristics of these stations and the reductions in nutrient inputs are listed in Table 1. The three stations are located in shallow lagoons (mean depth < 1.5 m) (Bec et al., 2011) with

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

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 $t.year^{-1}.10^6 m^{-3}$				N and P total inputs from the watershed, in $t.year^{-1}.10^6 m^{-3}$			
						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

comparable ranges of salinities (median values: AYR = 31.1, BGN = 25.9, MEW = 28.1; see Supplementary Material) and climatic conditions. MEW station is located on Méjean lagoon, which is part of the Palavasian complex, south of Montpellier (Fig. 1). Méjean lagoon has no direct connection to the sea and the water renewal is driven by the inputs of brackish waters coming from the « Rhône to Sète Canal » (Leruste et al., 2016). The Palavasian complex watershed is highly urbanised due to the presence of the city of Montpellier (250,000 inhabitants). The construction of an upgraded wastewater treatment plant (WWTP) in 2005, followed by the diversion of its effluents via an outfall in the Mediterranean Sea located 11 km off-shore led to a sudden dramatic reduction in anthropogenic inputs of nitrogen and phosphorus into the lagoons. This included an estimated 83% reduction in total N and a 73% reduction in total P from the watershed (Meinesz et al., 2013). Before remediation works, the contribution of WWTPs to total inputs to the Palavasian complex was lower for P than for N (respectively 78% and 89% of the total inputs), thanks to the physicochemical treatment of Montpellier's WWTP allowing better phosphorus abatement. As a consequence, the diversion of discharges from this WWTP in 2005 resulted in a larger decrease in N than in P total inputs. This difference in reduction rates between N and P is also explained by the increase in urban run-offs from the watershed, leading to an increase in P total inputs. Bages-Sigean lagoon is located south of the city of Narbonne (53,000 inhabitants). At BGN station, the water is mainly renewed by brackish waters coming from the southern part of the lagoon, which is directly connected to the sea (Fiandrino et al., 2017). The construction of an upgraded WWTP in Narbonne in 2003 enabled a 55% reduction in total N and a 64% reduction in total P inputs from the watershed. Before remediation, the contribution of WWTPs to total inputs to Bages-Sigean lagoon was higher for P than for N (respectively 82% and 76% of the total inputs), this being explained by the lack of physicochemical treatment on Narbonne's WWTP before its refurbishment. The improvement of this WWTP in 2003, including additional treatment to ameliorate phosphorus binding, resulted in a larger decrease of P total inputs than in N total inputs. Oligotrophic Ayrolle lagoon has a permanent connection to the Mediterranean Sea and its watershed is not directly concerned by urban inputs (Bec et al., 2011).

2.2. Laboratory analyses and data collection

Between 2001 and 2014, water was sampled each year at monthly intervals (June, July and August) in summer, when primary production is at maximum in Mediterranean lagoons (Souchu et al., 2010; Bec et al., 2011). We avoided collecting samples during periods of sediment resuspension by not sampling for three days after any period in which wind speed exceeded $12.5 m s^{-1}$. Temperature (Temp., °C), salinity (Sal.) and dissolved oxygen (O_2, 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 at the subsurface (in the middle of the water column for depths below 2 m and at −1 m from the surface at deeper stations) for laboratory analysis. The following parameters were analysed in the laboratory: dissolved inorganic nitrogen (DIN = $NH_4^+ + NO_3^- + NO_2$, µM), dissolved phosphorus (DIP, µM), dissolved silicate (Si, µM), total nitrogen and phosphorus (TN and TP, µM) and turbidity. Nutrients were analysed using standard protocols (Aminot and Kérouel, 2007), as described in Souchu et al. (2010). Turbidity (Turb., NTU) was measured with a HACH 2100N IS sensor following ISO 7027 protocols. Chlorophyll *a* concentrations (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 (PICO and NANO, 10^6 cells L^{-1}) (see Bec et al., 2011 for phytoplankton analyses).

2.3. Statistical analyses

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

Five environmental variables were selected for further analyses because of their key role in anthropogenic eutrophication processes in coastal lagoon waters (Souchu et al., 2010): DIN and DIP both cause eutrophication; Chl *a* represents phytoplankton biomass resulting from eutrophication; TP and TN correspond to causes and consequences and are used as integrated parameters for phytoplankton biomass and for organic matter. The five selected variables were standardised before between- and within-group principal component analyses (PCA), using time and space as instrumental variables to control multivariate analysis (Blanc et al., 2001). The within-group PCA of the dataset was centred by group (same dimensions as the original dataset: 5 columns (environmental variables), 924 lines). The within-group analysis searched for information shared by the groups, while the between-group analysis searched for differences between groups. For example, in our study, between-station analysis was a PCA of the dataset containing of station means: 5 columns (environmental variables) and 22 lines (stations). In order to highlight the annual variability of each station with respect to its average position on the inertia axes, the initial data were used as supplementary individuals in the between-station PCA. Between-group and within-group PCAs were performed to study station, year and month effects, using a reduced dataset with five selected parameters (Chl *a*, TN, TP, DIN and DIP). These PCAs made it possible to split the total inertia (i.e. the total information contained in the dataset) into between- and within-group inertia. Monte Carlo permutation tests were conducted on stations, sampling years and sampling months to identify the statistical significance of between-group analyses (Manly, 2007). The distances of the trajectories recorded year to year (d_i, with i: period from year i to i + 1) were calculated at MEW, BGN and AYR stations using the first two dimensions of the between-station PCA. The cumulative year-to-year distance on the first two dimensions was calculated ($\Delta_{total} = \Sigma|d_i|$, from i = 2001 to 2013). At MEW and BGN, annual average distances were also compared for the periods before (Δ_{before}) and after (Δ_{after}) the works on the sewerage systems were completed.

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

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

Table 3
Inertia and first eigenvalues (PC1) associated with global, between- and within-group Principal 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

3. Results

3.1. Key parameters highlighted a eutrophication gradient

The dataset revealed several significant correlations (Table 2) (see Supplementary Material for the ranges of the environmental parameters). Temperature, salinity, O_2, Si, DIN and NANO were weakly correlated with other parameters ($\rho < 0.5$). Chl *a* concentrations were highly correlated with TP ($\rho = 0.82$, n = 900), TN ($\rho = 0.70$, n = 899), autotrophic picoeukaryote abundances ($\rho = 0.67$, n = 886) and turbidity ($\rho = 0.66$, n = 903). These five variables were significantly correlated with each other, demonstrating their link with the primary production process. Total phosphorus was significantly and much more strongly correlated with its inorganic forms DIP ($\rho = 0.61$, n = 902) than total nitrogen with DIN ($\rho = 0.23$, n = 901). The contribution of DIP to TP had a median value of 11.4%, while the contribution of DIN to TN was only 1.7%, highlighting the dominance of organic forms, especially of nitrogen. Ammonium (NH_4^+) was the main form of dissolved inorganic nitrogen (median 69.2%, n = 908). Percentages of other inorganic forms of nitrogen were 18.2% for nitrates and 8.4% for nitrites. The weakest correlations with other environmental parameters were found for dissolved oxygen concentrations.

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

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

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

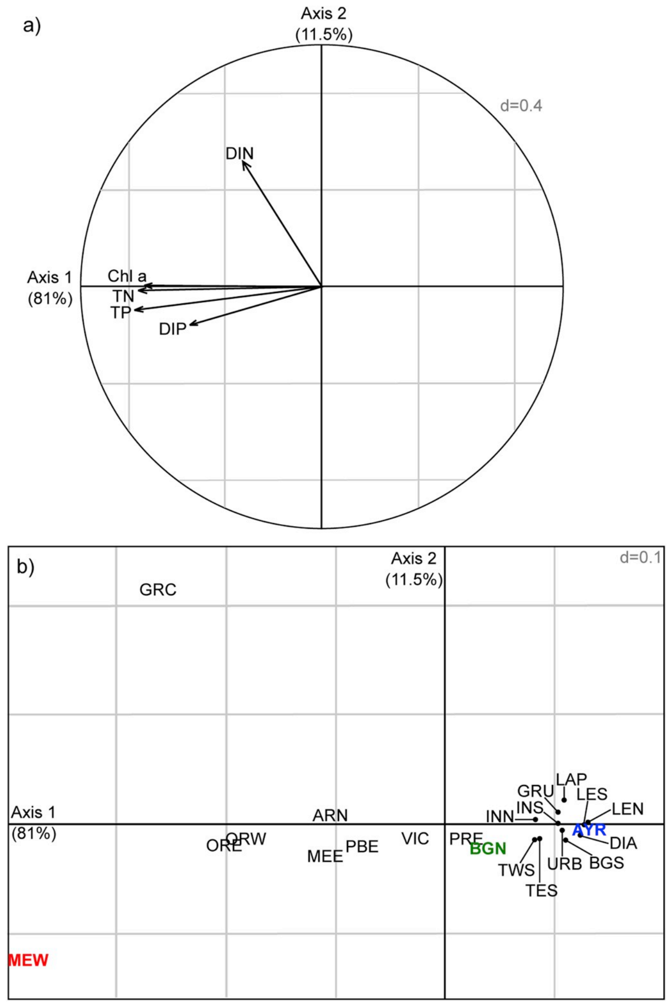

Fig. 2. Between-station PCA of 5 water column variables from the 22 stations and the 14 years of sampling. **a)** Loadings of the 5 active variables on the plane defined by PC1 and PC2. **b)** Location of stations on the PC1-PC2 plane. The colours show the degree of eutrophication of three of the stations: oligotrophic (AYR, blue), eutrophic (BGN, green) and hypertrophic (MEW, red). The d-values give the scale (i.e. the size of the grid is shown in grey). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

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

3.2. Recovery trajectories after remediation actions

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

Fig. 4 shows the time series of DIP, DIN, TP, TN, Chl *a*, PICO and NANO for the three stations (AYR, BGN and MEW) used for a detailed examination of changes in trajectories. Between 2001 and 2004, i.e. before the remediation actions in the watershed containing the Palavasian complex, MEW station remained in its initial hypertrophic state, with average Chl *a* concentrations of 134 µg L^{-1}. The recovery process started in 2005 with no lag time, immediately after the construction of the upgraded WWTP, when the Chl *a* biomass fell sharply (Fig. 4c). TP and TN decreased synchronously with chlorophyll *a*. This was followed by a decrease in DIP and PICO concentrations in 2006 and 2007 (Fig. 4a and d). From 2007 to 2010, the Chl *a* and PICO concentrations continued to decline, whereas DIP concentrations increased significantly. The 2011–2014 period was characterised by sporadic increases in phytoplankton biomass and abundances, and in DIP levels (Fig. 4) of the same order of magnitude or even higher than those measured before 2005 (years 2009–2012 and 2014, $p = 0.013$). However, chlorophyll *a* biomass declined significantly ($p = 0.012$) throughout the study period and average Chl *a* concentrations measured before and after remediation works were divided by 15.7 (134 before and 8.6 µg L^{-1} after, $p < 0.0001$) (Fig. 4c). TP and TN followed the same trend, with a significant decrease ($p = 0.009$ and 0.002) and average concentrations divided respectively by 2.5 and 3.1 (20 before and 8.1 µM of TP after, $p < 0.0001$; 339 before and 109 µM of TP after, $p < 0.0001$) (Fig. 4b). As PICO abundances were highly correlated with Chl *a* ($\rho = 0.65$, $p < 0.0001$, $n = 42$), they also decreased significantly over the study period ($p = 0.037$), and their concentrations decreased by a factor of 2.4 after WWTP refurbishment (4.01×10^9 before and 1.65×10^9 cell L^{-1} after, $p = 0.005$). Abundances of nanophytoplankton underwent significant variations depending on the year, with a peak in 2006 (average 7.63×10^9 cell L^{-1}). The decrease in phytoplankton biomass was accompanied by a decrease in turbidity and oxygen levels ($p = 0.0014$ and 0.0017). Changes in DIN concentrations revealed no particular pattern over time.

The pattern of change at BGN station differed from that at MEW. From 2001 to 2003, i.e. before the upgraded WWTP began operating, the BGN station was eutrophic, according to Souchu et al. (2010). From 2003 to 2005, BGN started recovering, but less abruptly than MEW (Fig. 3). DIP concentrations dropped the year after the remediation works were completed (Fig. 4a) and a significant decrease was observed over the study period ($p = 0.007$), with levels divided by 5.2 (from 1.6 to 0.3 µM, $p = 0.004$) after completion of the works. Changes in TP followed the same trend as DIP, with mean levels divided by 2.4 (from 3.3 to 1.4 µM, $p = 0.01$), but chlorophyll *a* concentrations only started decreasing after a lag time of two years. DIN increased after completion of the WWTP works and reached a maximum in 2005 (Fig. 4a).

After the delay in ecosystem response, the pattern of change suggested a gradual continuation of the recovery process from 2006 until 2014, with a decrease in Chl *a* and DIP. Chlorophyll *a* concentrations decreased significantly throughout the study period ($p = 0.001$) and were divided by 1.6 after remediation works (from 4.5 to 2.8 µg L^{-1}, $p = 0.03$). Chl *a* concentrations decreased after remediation works, with average levels divided by 1.2 (from 47.8 to 38.5 µM, $p = 0.004$). TN concentrations decreased rapidly from 2002 to 2006, but then increased again and stabilised below the level observed before remediation works. However, picoeukaryotes, nanophytoplankton and

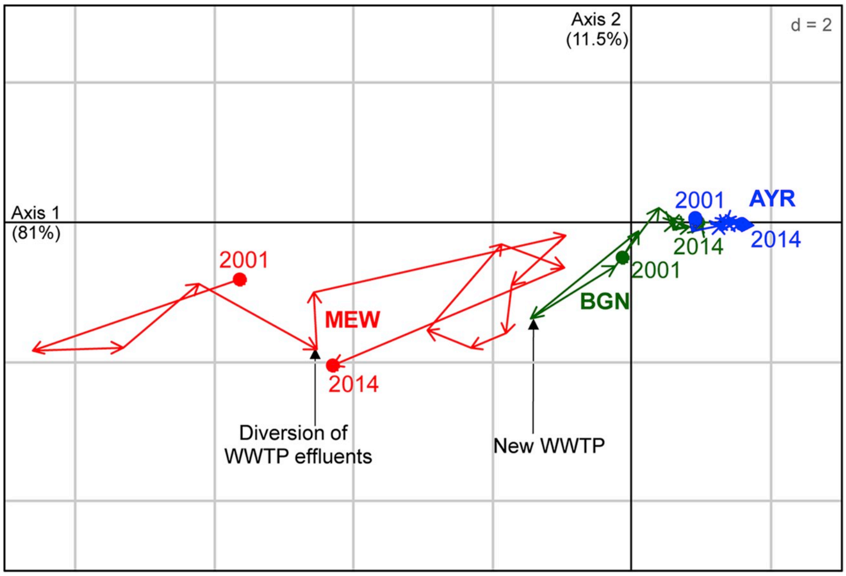

Fig. 3. Trajectories between 2001 and 2014 of the AYR (oligotrophic, in blue), BGN (eutrophic, in green) and MEW (hypertrophic, in red) stations on the plane defined by PC1 and PC2 of the between-station PCA. The d-value gives the scale (i.e. the size of the grid is shown in grey). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

dissolved and organic forms of N did not decrease significantly and no significant between-year differences were observed.

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

The average TN:TP and DIN:DIP ratios at MEW station were already the lowest and decreased significantly after remediation works (from respectively 17.4 to 14.6, $p = 0.02$; and from 4.2 to 2.2, $p = 0.02$). TN:TP ratios were below 20, suggesting N limitation according to the total nutrient based approach (Guildford & Hecky 2000 in Souchu et al., 2010). The average TN:TP ratio at BGN station (31.1) was farther from the Redfield ratio and did not change significantly after remediation works. The TN:TP ratio at BGN station highlighted a limitation by both P and N. Moreover, the average DIN:DIP ratio (9.5) characterised a limitation by N according to the dissolved nutrient based criteria (Justic et al. 1995 in Souchu et al., 2010). The average TN:TP and DIN:DIP ratios were the highest at AYR station (respectively 46.8 and 17.6) and highlighted a P limitation.

4. Discussion

4.1. Integrative parameters revealed a eutrophication gradient

The rare dataset we used to monitor coastal lagoons whose status ranged from oligotrophic to hypertrophic (Souchu et al., 2010; Bec et al., 2011), allowed us to analyse eutrophication and oligotrophication phenomena in these ecosystems. Some of these lagoons received large inputs of urban nutrients for several decades, but major management actions have recently been implemented on the waste water treatment systems in most of their watersheds (Meinesz et al., 2013; Gowen et al., 2015; Leruste et al., 2016). Fourteen years after the monitoring of French Mediterranean lagoons began (Souchu et al., 2010), an anthropogenic eutrophication gradient is still highlighted by the water quality parameters. The five parameters selected in our study to identify the anthropogenic eutrophication gradient are representative of nutrient cycling in the water column of coastal lagoons as they incorporate either the causes (DIN and DIP), or the consequences of the eutrophication process (Chl *a*), or both (TP and TN, which were closely correlated with each other and with Chl *a*). DIN and DIP represented very low percentages of total nutrients in summer (median 1.68% and 11.4%, respectively). Dissolved nutrient concentrations were very low because of continuous uptake by massive phytoplankton blooms, which occur mainly in summer (Bec et al., 2011). These results are in agreement with observations made in shallow lakes (Ibelings et al., 2007; Jeppesen et al., 2007), where the integrative parameters TN, TP and Chl *a* appear to be good complements to the dissolved nutrients usually measured in transitional and coastal ecosystems (Claussen et al., 2009; Ferreira et al., 2011; McLaughlin et al., 2013; Lemley et al., 2015). These parameters appear to be suitable for monitoring programmes, such as WFD assessment programmes, whose aim is to evaluate the effectiveness of management measures.

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

In our study, the hypothesis that the reduction in urban nutrient inputs would have a rapid effect on the water total nutrient levels and phytoplankton biomass was confirmed in hypertrophic and eutrophic lagoons. After a reduction of more than 50% in TP and of 80% in TN loadings from the watershed of these ecosystems, a recovery trajectory was rapidly identified using the integrative parameters Chl *a*, TN and TP. The concentrations of these parameters in the water column decreased significantly within one to three years. The response lag times and ranges observed after remediation actions in the eutrophic lagoon are in agreement with those reported in other coastal lagoons by Pasqualini et al. (2017) and in estuaries by Lie et al. (2011), Boynton et al. (2013) or Ní Longphuirt et al. (2016). Our results demonstrate that even hypertrophic coastal lagoons can recover following substantial reduction in nutrient loads and confirm the rare observations available on such degraded ecosystems, whose main nutrient sources are WWTPs (Leruste et al., 2016), or on temperate lakes (Jeppesen et al. 2005, 2007; Ibelings et al., 2007). What is remarkable about our results is the speed (one to two years) and the extent of the recovery of the hypertrophic lagoon, the decreases in the concentrations of Chl *a* and TP being 10 fold greater than in the eutrophic lagoon. This difference may be due to the more drastic reduction in nutrient loading, which reached 83% for total N and a 73% for total P in the hypertrophic lagoon versus 55% and 64% in the eutrophic lagoon. We observed shorter recovery lag times than those observed by many authors in transitional water ecosystems, who reported 10–18 years (García et al., 2010; Gee et al., 2010; Saeck et al., 2013). We also observed stronger effects than

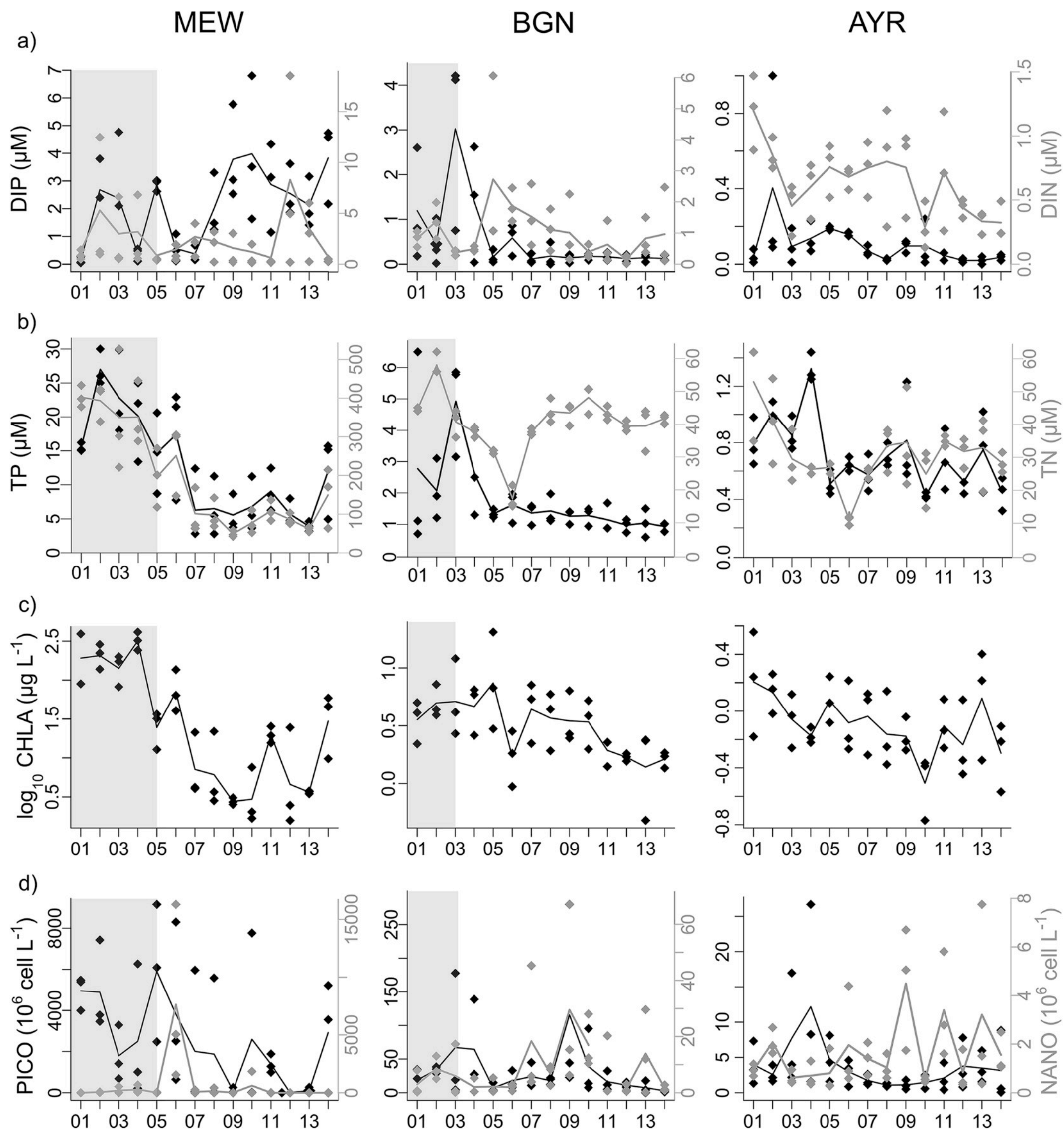

Fig. 4. Monthly concentrations (diamonds) and means (curves) of summer concentrations (June–August) of: **a)** DIP and DIN (µM), **b)** TP and TN (µM), **c)** Chl *a* (µg L^{-1}, $\log_{10}$ scale) and **d)** picoeukaryote and nanoeukaryote abundances (10^6 cell L^{-1}) from 2001 to 2014 at MEW (left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

those reported by other authors on water column quality after remediation works of comparable magnitude (Kronvang et al., 2005; Williams et al., 2009).

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

4.3. Recovery trajectories in coastal lagoons

The pathways of change in the three coastal lagoons in our study covered a wide range of anthropogenic eutrophication, from oligotrophic to hypertrophic ecosystems. Environmental monitoring of hypertrophic and eutrophic lagoons for respectively nine and 11 years after significant reductions in urban nutrient loading made it possible to identify different recovery patterns. The conceptual models of changes to the status of an ecosystem with pressure proposed by Elliott et al., (2007) and Tett et al., (2007), were used to represent the trajectories of the oligotrophic, eutrophic and hypertrophic lagoons, at different phases of anthropogenic eutrophication and recovery processes (Fig. 5). The concentration of Chl *a* in the water in summer was chosen as the ecosystem status metric (for shared periods: before (years 2001–2003)

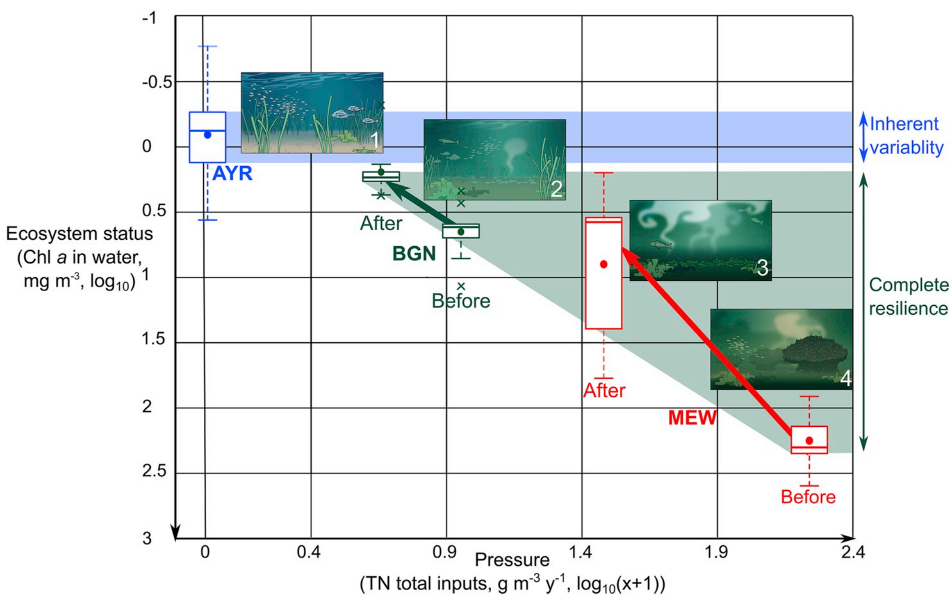

Fig. 5. Changes in chlorophyll *a* in the water at stations BGN and MEW measured before (years 2001-2002-2003) and after mitigation actions (years 2012-2013-2014) versus TN total inputs from the watersheds (dots: average; crosses: outliers). Boxplot of Chl *a* at AYR station represents data measured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

and after remediation works (years 2012–2014), as this integrative parameter has been shown to be a relevant indicator of eutrophication status (Cloern, 2001; Bec et al., 2011; Ferreira et al., 2011). Moreover, our results are in agreement with those of Bec et al. (2011), showing that Chl *a* is closely correlated with autotrophic picoeukaryotes, which comprise the majority of the phytoplankton community in French Mediterranean lagoons. TN total inputs from the watersheds (before and after remediation works, Table 1) were chosen as the pressure metrics, as N is typically the limiting factor in eutrophic lagoons in summer (Souchu et al., 2010).

Like in many studies of the recovery of coastal ecosystems (except e.g. Kemp et al., 2005 or Ibelings et al. 2017), the states of the eutrophic and hypertrophic lagoons before degradation were not fully described. The observations on the oligotrophic lagoon revealed a high ecological status, with low Chl *a* concentrations in accordance with the reference conditions laid down by European WFD (MEDDE, 2015), and revealed slight inter-annual variations (Figs. 5–1). This pattern reflects the inherent variability of undisturbed coastal lagoons (Elliott and Quintino, 2007), dominated by perennial benthic macrophytes (Schramm, 1999; Viaroli et al., 2008).

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

The hypertrophic lagoon, which was dominated by phytoplankton and where the bottom was bare sediments before remediation (Figs. 5–4), shifted to a eutrophic state (Figs. 5–3), with the appearance of fast-growing macroalgae after mitigation actions (Ifremer, 2010). In contrast to the eutrophic lagoon, the recovery trajectory of the hypertrophic lagoon appears to be not yet complete, suggesting that all compartments of the ecosystem have not yet recovered, particularly the benthic compartments (Elliott et al., 2007; Tett et al., 2007). Moreover, the trajectory of the hypertrophic lagoon displayed high variability and feedback responses, suggesting that the ecosystem regime had become unstable (Scheffer and Carpenter, 2003; Ibelings et al., 2007; Kennish and de Jonge, 2011). Shortly after remediation actions, the hypertrophic lagoon displayed a renewed increase in DIP concentrations, mimicking the immediate decrease in Chl *a*, and later the appearance of macroalgae (observed between 2006 and 2009 (Ifremer, 2010)). The increase in DIP could correspond to the release of phosphate accumulated in the sediments, which is favoured by summer conditions (Kemp et al., 2005), and also to their incomplete consumption by phytoplankton in the water column. Another possible explanation is recycling of the organic matter originating from macroalgae degradation and leading to an increase in dissolved inorganic nutrients in the water column. In lakes, internal loading of phosphates from sediments has frequently been reported to delay recovery from anthropogenic eutrophication (Gulati and Van Donk, 2002; Jeppesen et al., 2005; Jeppesen et al., 2007), more rarely in coastal or estuarine ecosystems (Lillebø et al., 2007; Ní Longphuirt et al., 2016; Riemann et al., 2016). The recent renewed increases in Chl *a* and DIP persisting in 2015 and 2016, confirmed the incomplete recovery of the hypertrophic ecosystem, which alternates blooms of macroalgae and phytoplankton depending on the monitoring year (Schramm, 1999; Viaroli et al., 2008). Although a significant decrease was observed, Chl *a* concentrations after remediation still correspond to a bad status according to the European WFD (MEDDE, 2015).

Fig. 5 suggests that there is a common restoration scheme in the studied lagoons following an equivalent decrease in anthropogenic pressure (nitrogen inputs). To what extent factors such as depth or salinity could modify this pattern remains to be determined. Following a significant reduction in nutrient inputs, hypertrophic or eutrophic coastal lagoons showed an almost immediate positive response in their environmental conditions. However, the oligotrophication trajectory and the likelihood of recovery, even partial, remain statistically difficult to predict (Duarte et al., 2009; McCrackin et al., 2017). Given the costs and difficulties in implementing management plans for nutrient reduction, managers and policy-makers should consider uncertainty and ecosystem specificity as their main guides when designing any remediation actions targeting oligotrophication of coastal lagoons. Indeed, as exemplified in this study, the level of recovery and the trajectory could be affected by: (i) external drivers, such as completeness of nutrient reduction, other stressors, connectivity, or climate change; (ii) internal factors such as physical traits (i.e. water renewal time; de Jonge et al., 2002; Fiandrino et al., 2017), lagoon history, sediment nutrient stocks (Duarte et al., 2009; Borja et al., 2010) or the presence of residual seagrass patches or seed stocks (Ibelings et al., 2007; Le Fur et al., 2017); and interactions between the two drivers. All of these may cause time lags, regime shifts and non-linearities (Ibelings et al., 2007; Duarte et al., 2009; Riemann et al., 2016) in ecosystem responses following remediation efforts. Specifically in the case of hypertrophic coastal lagoons, we showed that even 10 years after major reduction in nutrient loads, the environmental conditions necessary to restore the ecological functions and structure of the ecosystem, and the objectives laid down by the European WFD have not fully been achieved. It was not possible to estimate the recovery times needed to reach a good ecological status by all the lagoons studied. Further analyses of a larger number of lagoons will be necessary and should be completed by modelling to determine the effects of each factor and feedback interactions (positive or negative) with an impact on recovery trajectory and recovery time. At the time of writing, three strategies are feasible:

- "Wait and see": one could hypothesise that eutrophication pressure is now sufficiently low to allow the ecosystem to recover its ecological functions and structure of the reference conditions, after a period of hysteresis;
- "Go further" in reducing nutrient inputs: this is economically and technically hard to implement, and the likelihood of ecological recovery, even partial, is not guaranteed for the same reasons as discussed previously;
- "Give a helping hand": implementing active restoration programmes to enhance internal factors could facilitate ecological recovery (Verdonschot et al., 2013). Examples of possible active restoration actions are: restoration of seagrass meadows (Orth et al., 2012; de Wit et al., 2015) to reduce nutrient sediment fluxes or limit turbidity; development of passive aquaculture for top-down phytoplankton control and/or nutrient export (Ferreira and Bricker, 2016; Ahmed et al., 2017; Reitsma et al., 2017).

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

Author contributions

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2019.01.012.

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