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Implications of floodgate operation for phytoplankton structure in a coastal lagoon (short-term vs mid-term)

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Implications of floodgate operation for phytoplankton structure in a coastal lagoon (short-term vs mid-term)

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Introduction

Coastal ecosystems, because of the high productivity and diversity of taxonomic groups of organisms living in them, are treated as biodiversity hotspots more and more often (Burton et al., 2004; Sierszen et al., 2012). For this reason, they were taken into account in many protection programmes, including the Natura 2000 network, as priority habitats (code 1150). This makes it necessary to introduce protection measures and maintenance of natural processes taking place in them. In this context, particularly changes in hydrological connectivity seem to be crucial for the functioning of coastal lakes. Scheffer et al. (2001) argued that both external and internal environmental factors can cause deep changes leading to destabilization of an aquatic ecosystem, and can result in one of the alternative stable states: turbid-water or clear-water state. That theory was initially based on the trophic level but it seems to be more universal and explains also some other possible relations in shallow-water lakes, e.g. the level of salinity in coastal lakes (Obolewski et al., 2018a).

Coastal lakes are ecosystems characterized by varying hydrological conditions, resulting from an opposition of terrestrial and marine influences. In the case of intermittently closed/open lakes and lagoons (ICOLL), their state is conditioned mostly by the marine influence, but in closed seas, such as the Baltic, nutrient loads from the catchment dominate (e.g. Netto et al., 2012; Grzybowski et al., 2022; Szymańska-Walkiewicz et al., 2023). Relatively low levels of seawater intrusion, implying a narrow gradient of salinity in Baltic coastal lakes, are not able to shift the ecological balance in them permanently and significantly (=change of regime) (Obolewski and Glińska-Lewczuk, 2020). For this reason, on the Baltic coast, we divided the studied water bodies into two major types in respect of salinity: brackish-water (3-7 PSU) and freshwater ones (>0.5 PSU), with a transitional state between them (Obolewski et al. 2018a).

In all the considerations concerning the mechanisms of functioning of coastal lakes, the crucial system is the one where only periodical hydrological connection between the lake and the sea is observed (Obolewski and Glińska-Lewczuk 2020). Depending on the scope of the connection, two types of transitional lakes can be distinguished: those with a dominance of fresh water (freshwater-brackish type) or of brackish water (brackish-freshwater type) (Szymańska-Walkiewicz et al. 2022). In this context, Lake Jamno for many years was a classic transitional lake, with a prevalence of fresh water, regularly interrupted by seawater intrusion. However, a decade ago it was isolated completely from the influence of seawater by construction of a floodgate at the outlet of the lake, Nurt Jamneński (Cieśliński et al., 2016). Such actions cause dysregulation of natural processes shaped by the intrusion and stress for the affected water bodies(eg. Niekerk et al. 2005; Anandraj et al. 2008; Lawrie et al. 2010; Netto et al. 2012; Obolewski et al., 2018b). The observation of ecological impact may result from an emergency (short-term effects) or monitoring of consequences for water body functioning (mid-term or long-term effects).

To assess the directions of long-term changes, caused by physical stress factors (e.g. blocking of free hydrological connectivity), many groups of aquatic organisms can be used, although in open water the preferred group is phytoplankton (Chen et al. 2010; Gillett and Steinman, 2011; Wu et al. 2019, 2023). The nutrient loads flowing into the coastal zone imply an increase in turbidity and limited access to sunlight, leading to accelerated eutrophication (Cloern and Jassby, 2010). This process in open water is connected with increased primary production, associated with phytoplankton development as well as an increased importance of cyanobacteria and a decreased biomass of diatoms (Jöhnk et al. 2008). The level of primary production can be assessed on the basis of concentrations of photosynthetic pigments, mostly chlorophyll *a* (Chl-*a*). It affects the optical properties of fresh water and seawater, as it increases the backscattering of light (Blondeau-Patissier et al., 2014). Chl-*a* in aquatic ecosystems (Cullen, 1982; Blondeau-Patissier et al., 2014) is widely applied as an important indicator of habitat quality, impact of pollution, and biophysical status (e.g. Carpenter et al., 1998; Shi et al. 2013; Cheng et al. 2013; Wozniak et al., 2014).

In this study, we hypothesized that a drastic decrease in the level of hydrological connectivity between a coastal lake and the sea (lack of seawater intrusion) affects the dispersion of phytoplankton communities (structure and Chl-*a* concentration). It could be expected that the blocking of seawater intrusion implies an increase in algal biomass and a decrease in species diversity of the community, with a growing contribution of cyanobacteria. The level of hydrological connectivity (lagoon vs. sea) does not seem to be the only factor but it can be a key predictor that determines phytoplankton structure in coastal lagoons (Obolewski et al., 2018a). Besides, phytoplankton structure can change with the duration of isolation from the sea, as short-term and mid-term effects. To check this, samples were taken in the same periods (months) in the 1st and 2nd year after floodgate construction (short-term effects) and 5–6 years after the storm surge system was implemented (mid-term effects).

Material and Methods

Study area

Lake Jamno is located in the coastal belt of the southern Baltic Sea (Fig. 1A). It is a large (area 22 km²) and shallow (mean depth <2 m) coastal lake on the Slovincian Coast, and is separated from the sea by a sandy spit (Choiński et al. 2014).

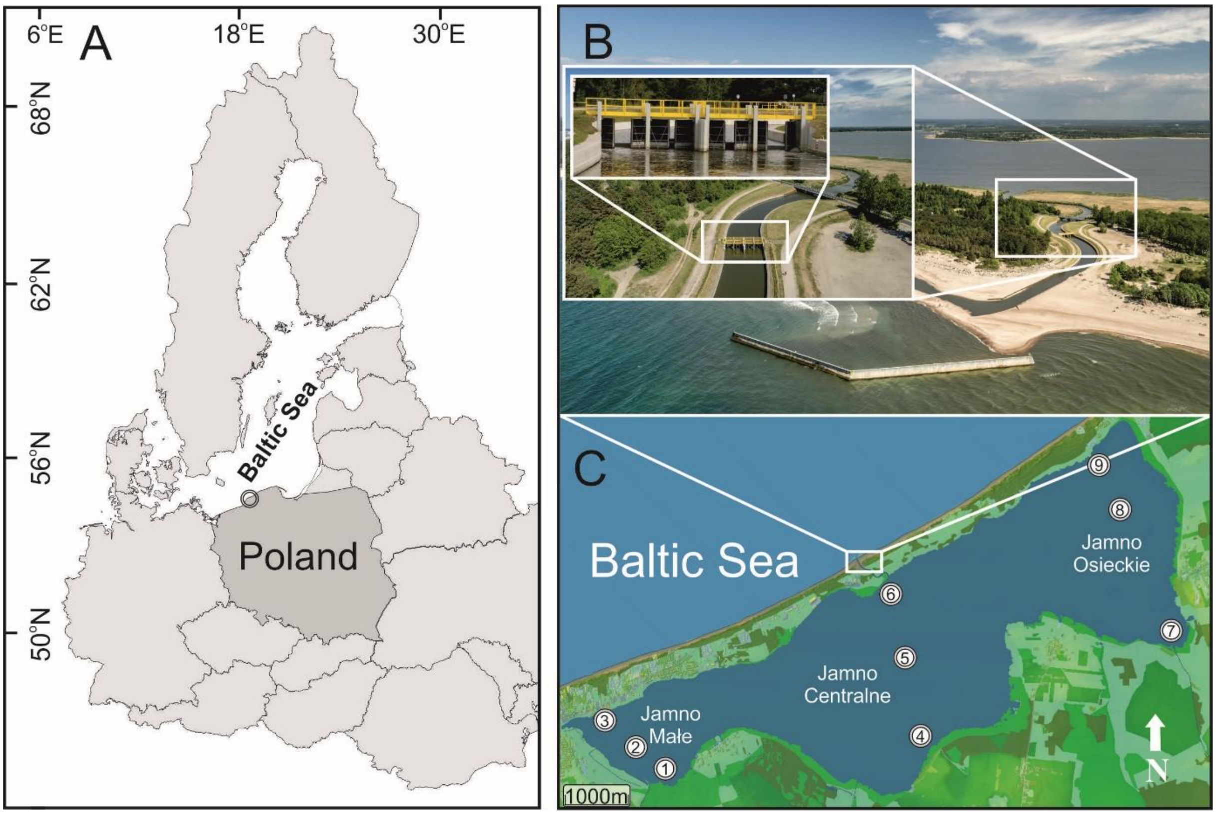

Figure 1. Location of Lake Jamno (A), Nurt Jamneński after the construction of a floodgate (B), and location of sampling sites on Lake Jamno (C).

The water body is fed by three rivers (Unieść, Dzierżęcinka, and Strzeżenica) and several smaller watercourses. Surface inflow from the three tributaries is estimated to reach annually: 42 million m^3 from Dzierżęcinka (which feeds the central part – Jamno Centralne), 49 million m^3 from Unieść (which feeds Jamno Osieckie), and 9 million m^3 from Strzeżenica (which feeds Jamno Małe). Outflow to the sea through Nurt Jamneński (known also as Jamneński Canal) reached 130 million m^3 per year, at a mean flow rate of 4.75 $m^3 \cdot s^{-1}$ (Heese, 2012; Cieśliński, 2016). In another report the estimated volume of water flowing out of the lake into the Baltic was about 200 million m^3 (Obolewski 2009). In contrast, seawater intrusion was estimated at about 16.1% in relation to the whole inflow balance, i.e. nearly 30 million m^3 of water. Seawater intrusion in Lake Jamno varied greatly and was limited to 280 days a year. Its intensity depended on the water level in the Baltic and Jamno. It is estimated that seawater intrusion in autumn and winter was more violent but rare. In spring and summer it was milder but more frequent. Because of its periodical connection with the Baltic, through Nurt Jamneński, the lake was classified as brackish (Obolewski et al. 2018b). The situation changed in the autumn of 2013, when the floodgate was installed, which stopped the influx of seawater (Fig. 1B). This was a response to flood damage, caused by rising water level in the lake. The floodgate consists of four pairs of swinging "doors" (5.6 m high and 17 m wide), which are closed automatically (under the influence of blowing wind) at Beaufort force 6. When the sea is calmer, then the floodgate opens itself under the influence of lake water flow to the sea (Cieśliński et al., 2016)

Sampling

The study was conducted in May, August, November in two periods: (i) 2014–2015, soon after the loss of hydrological connection with the lake (short-term effects, SE); (ii) 2019–2020 (mid-term effects, ME), i.e. 6–7 years after construction of the floodgate. Every time, samples were collected from nine sites (Fig. 1C) located in three parts of the lake: Jamno Małe (sites 1–3), Jamno Centralne (sites 4–6), and Jamno Osieckie (sites 7–9) (Fig. 1C). A total of 108 phytoplankton samples were collected.

At each site, we measured *in situ* electrolytic conductivity (EC), pH, oxygen content (DO%), dissolved oxygen (DO), salinity, total dissolved solids (TDS), oxidation-reduction potential (ORP), and water temperature, by using Aquaprobe® AP-7000 (AquaRead Instrument, England). Visibility was measured using a Secchi disc (Secchi depth). For laboratory analyses, water samples were collected from the depth of 0.5 m to 1-litre polyethylene containers (chemical analyses) and from the same depth to dark 0.5-litre containers (biological analyses). The samples for biological analyses were cold-stored in the field.

Laboratory procedure

Within 24 h after collection, water samples were analysed in the laboratory. The concentrations of phosphates and nitrates ($P\text{-}PO_4^{3-}$, $N\text{-}NO_3^{-}$) were determined in a laboratory with the use of spectrophotometry (DR-3900, Hach, US) and assessed as recommended by Hashim et al. (2018). Total organic carbon (TOC) and total inorganic carbon (TIC) were analysed after filtering the samples through nitrocellulose membranes with pore size of 0.45 μm (Millipore), using a QbD1200 analyser (Beckman Coulter, USA), which oxidises the organic carbon into carbon dioxide.

In the laboratory, biological material was poured into a glass 25-ml cuvette and analysed using a spectral ALA fluorimeter (AlgaeLabAnalyser, BBE Germany). One measurement was an arithmetic mean of three so-called fast analyses. In this way, we collected data about total Chl-*a* concentration (TChl-*a*, $\mu g\ L^{-1}$) and its concentration in four taxonomic groups: the Chlorophyta, Bacillariophyta, Cyanobacteria, and Cryptophyta ($\mu g\ L^{-1}$). For proper calculation of TChl-*a*, we corrected it for yellow substances, using the chromophoric dissolved organic matter correction. The whole procedure was performed within 72 h from sample collection in situ. For a detailed description, see Nguyen et al. (2015).

Data analysis

First, the biomass of individual groups of phytoplankton was square-root transformed ($\sqrt{x+1}$), while environmental data were log-transformed ($\log_{10}$ (x+1)) (Ter Braak and Šmilauer 2002). Environmental variables included visibility (Secchi depth), EC, pH, DO%, DO, salinity, TDS, ORP, water temperature, P-PO_4^{3-}, N-NO_3^-, TOC, TIC, chromophoric dissolved organic matter, total Chl-*a* concentration, and its concentration in four taxonomic groups: Chlorophyta, Bacillariophyta, Cyanobacteria, and Cryptophyta.

We used analysis of variance (ANOVA) with Kruskal–Wallis test (K–W), significant when p<0.05. At that stage, the data were tested for normality (Shapiro–Wilk test) and homoscedasticity (Levene test).

To assess similarities/differences in Chl-*a* concentration between the study periods, we performed an analysis of similarity (ANOSIM, 999 permutations), using Bray-Curtis distances (Clarke and Warwick, 2001). To visualize its results, we employed non-metric Multidimensional Scaling (nMDS) based on dissimilarity measured by Euclidean distances. TChl-*a* was applied as a criterion of study period classification.

At the next stage, we used the linear model of redundancy analysis (RDA) to explain the biomass of the studied groups of phytoplankton and to associate them with environmental variables. We employed the Monte Carlo test with 999 permutations. Moreover, *t*-value biplots with Van Dobben circles were generated basing on the RDA of selected physicochemical properties of water and algal groups to illustrate the statistically significant relationships between the studied organisms and environmental variables (ter Braak and Looman, 1994).

The last stage consisted in preparation of a model illustrating the influence of environmental predictors (stress factors) on Chl-*a* concentration, taking into account the time of isolation,. The data concerning this photosynthetic pigment (Y) were analysed in relation to physicochemical factors and duration of isolation: SE vs. ME (X). Partial least-squares regression (PLS-R) is a research tool applied to find links between two data matrices by using a linear multidimensional model (Wold et al., 2001). It links the explanatory variables (X) to create a new set of latent variables (LVs), which reflect the multidimensional variance in the X space correlated with Y and to calculate the vector of regression. The strength of the model was estimated on the basis of R2 and the root mean square error of cross validation (RMSECV).

Results

Environmental conditions

All the physicochemical parameters of lake water changed significantly (ANOVA, $p<0.05$), except for temperature ($p=0.60$). Secchi depth was slightly lower soon after stopping the intrusion of seawater (0.28 m) than in the second period (0.36 m). However, values of this parameter in both periods fluctuated considerably. The highest levels of EC, ORP, salinity, DO, TDS, P-PO$_4$, and chromophoric dissolved organic matter were recorded in the mid-term comparison (ME). In contrast, pH, temperature, N-NO$_3^-$, TOC, and TIC values were the highest soon after isolation (SE, Table 1). Results of the analyses show that TOC values markedly declined in ME ($p<0.0001$), reaching the lowest mean values in the last year of the study. Similarly, N-NO$_3^-$ concentration remarkably decreased in ME, as compared with SE ($p<0.0001$). Concentrations of the other studied environmental variables significantly increased in ME.

Table 1. Water quality (mean ± standard error) in Lake Jamno after blockage of seawater intrusion: short-term and mid-term effects and results of two-way ANOVA.

	Short-term effects (SE) n=54		Mid-term effects (ME) n=54	
	2014	**2015**	**2019**	**2020**
Visibility (m)**	0.3±0.0	0.3±0.0	0.3±0.0	0.4±0.0
Temp (°C)	17.7±0.2	14.8±0.0	17.3±0.3	17.0±0.1
pH****	8.62±0.02	8.91±0.01	8.63±0.03	7.93±0.04
EC (µS cm^{-1})****	226±1	395±5	400±14	513±2
ORP (mV)****	87.3±2.3	-13.4±2.2	126.0±4.5	177.1±1.5
Salinity (PSU)****	0.07±0.00	0.18±0.00	0.26±0.00	0.22±0.00
DO%****	112.4±0.1	98.4±0.6	131.8±0.8	125.7±0.7
DO (mg L^{-1})****	9.8±0.6	8.6±0.1	12.6±0.1	11.3±0.0
TDS (mg L^{-1})****	146±0	256±2	411±1	327±2
N-NO$_3^-$ (mg L^{-1})****	0.95±0.02	0.83±0.03	0.39±0.01	0.31±0.00
P-PO$_4^{3-}$ (mg L^{-1})****	0.187±0.003	0.092±0.001	0.202±0.028	0.405±0.029
TOC (mg L^{-1})****	20.80±0.19	19.34±0.31	10.40±0.06	9.78±0.05
TIC (mg L^{-1})****	10.99±0.11	9.34±0.15	8.44±0.06	9.30±0.03
CDOM (µg L^{-1})****	3.75±0.10	0.58±0.04	3.55±0.03	4.75±0.09

p values modified by the Bonferroni procedure for multiple comparisons show significant effect at $p<0.05^{*}$; $p>0.01^{**}$; $p<0.001^{***}$; $p<0.0001^{****}$. EC= conductivity; ORP=oxidation-reduction potential; DO=dissolved oxygen; TDS=total dissolved solids; TOC=total organic carbon; TIC= total inorganic carbon; CDOM= chromophoric dissolved organic matter

Phytoplankton structure

In the first study period (SE), the mean phytoplankton biomass reached 48.5 μg L^{-1}, so it was 3.6-fold higher than in the second period (ME). Cyanobacteria were a major component of phytoplankton in Lake Jamno, as they accounted for 91% and 93% of the total phytoplankton biomass in SE and ME, respectively. This increase between the two study periods was significant ($p<0.0001$). Blockage of seawater intrusion to the lake caused statistically significant changes in the biomass of also other groups of phytoplankton (Table 2). TChl-*a* content was the highest soon after the floodgate was installed (SE) and its values continuously decreased, reaching the lowest values in the last year of the study (ME). During the blockage, the biomass of individual groups of phytoplankton gradually declined ($p<0.0001$). As early as at the end of the first study period (SE), Cryptophyta biomass rapidly decreased and the Bacillariophyta were completely eliminated (Table 2). Additionally, in ME, green algae were absent in the collected lake water samples.

Table 2. Phytoplankton structure (mean ± standard error) in Lake Jamno after blockage of seawater intrusion: short-term and mid-term effects and results of two-way ANOVA.

Chlorophyll *a* concentration (as an estimate of biomass)	Short-term effects (SE) n=54		Mid-term effects (ME) n=54	
	2014	**2015**	**2019**	**2020**
Total Chl-*a* (μg L^{-1})****	85.1±3.8	11.8±1.0	17.1±0.0	9.4±0.9
Chlorophyta (μg L^{-1})****	0.65±0.04	1.01±0.1	0±0	0±0
Cyanobacteria (μg L^{-1})****	78.08±3.51	10.31±0.89	16.0±0.02	8.71±0.78
Bacillariophyta (μg L^{-1})**	0.26±0.02	0±0	0±0	0±0
Cryptophyta (μg L^{-1})****	6.14±0.29	0.19±0.4	1.54±0.12	0.72±0.08

p values modified by the Bonferroni procedure for multiple comparisons show significant effect at $p<0.05^{*}$; $p>0.01^{**}$; $p<0.001^{***}$; $p<0.0001^{****}$

The qualitative-quantitative analysis of similarities (ANOSIM), based on the Bray−Curtis index, showed that Chl-*a* concentrations differed significantly between the study periods (Global $R_{ANOSIM}=0.435$, $p=0.0001$). ANOSIM was confirmed by non-metric multidimensional scaling (nMDS). It indicated the presence of clusters of points representing individual study periods, corresponding to differences in Chl-*a* concentration (Fig. 2). In the second period (ME), small distances between points attested to a high similarity of the results.

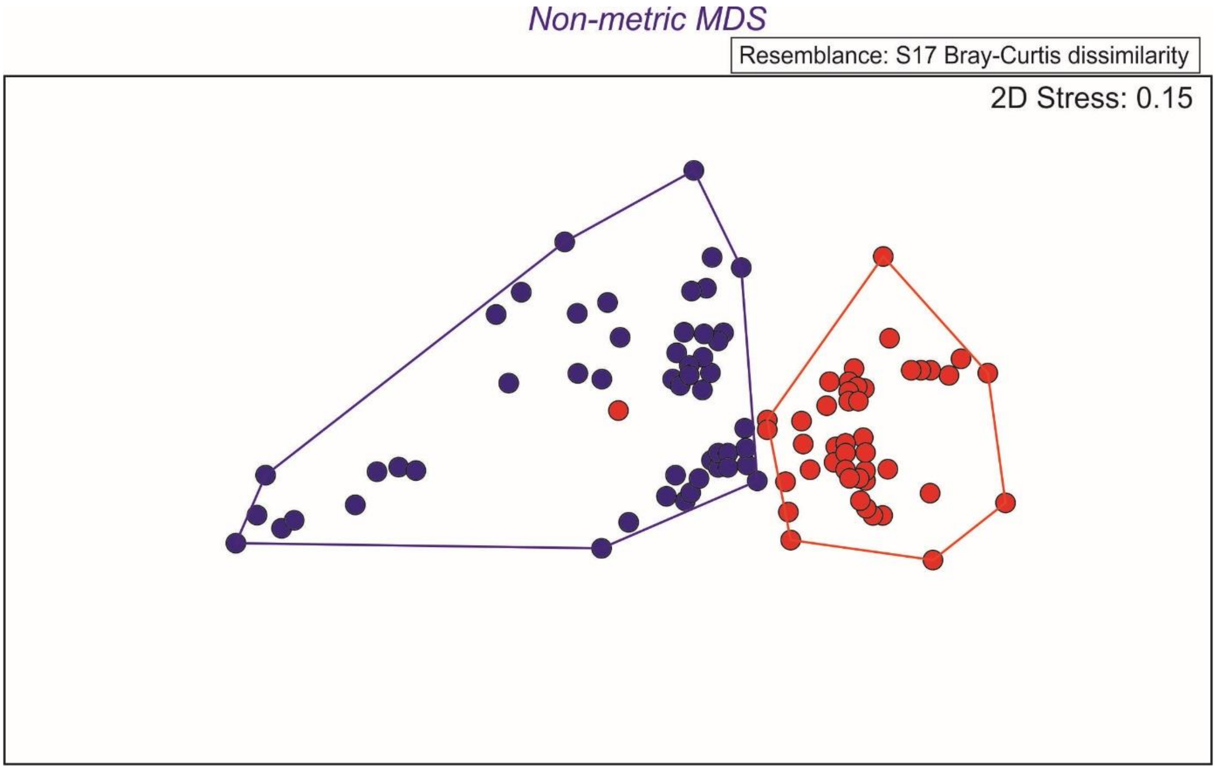

Figure 2. Results of non-metric multidimensional scaling (nMDS) ordinations of Chl-*a* concentration (mg L^{-1}) after isolation of Lake Jamno from seawater intrusion: short-term effects (blue) and mid-term effects (red).

Out of the analysed environmental variables associated with hydrological isolation and analysed initially in the RDA model, we finally selected 12, which markedly affected model quality. The final model explained 46.1% of the total variation in phytoplankton structure and all the canonical axes were significant (Monte Carlo test, p=0.001). The generated model was most strongly influenced by three factors: salinity and EC negatively affected individual groups of algae, while temperature positively affected TChl-*a* concentration as well as cyanobacteria and cryptophytes. Additionally, in these groups, we noticed some non-significant positive effects of higher concentrations of carbon compounds (TIC, TOC) and chromophoric dissolved organic matter. Simultaneously, the biomass of these groups tended to decrease at higher levels of ORP, EC, and water salinity. In the case of the Chlorophyta and Bacillariophyta, we did not observe any considerable associations between their biomass and physicochemical properties of water (Fig. 3A). Simultaneously, van Dobben circles indicated that to a large extent the biomass of cyanobacteria and cryptophytes was affected by water temperature, Secchi depth and TOC concentration (Figs. 3B-D). Only in the Chlorophyta, biomass growth was slowed down by increasing water temperature in Lake Jamno (Fig. 3B).

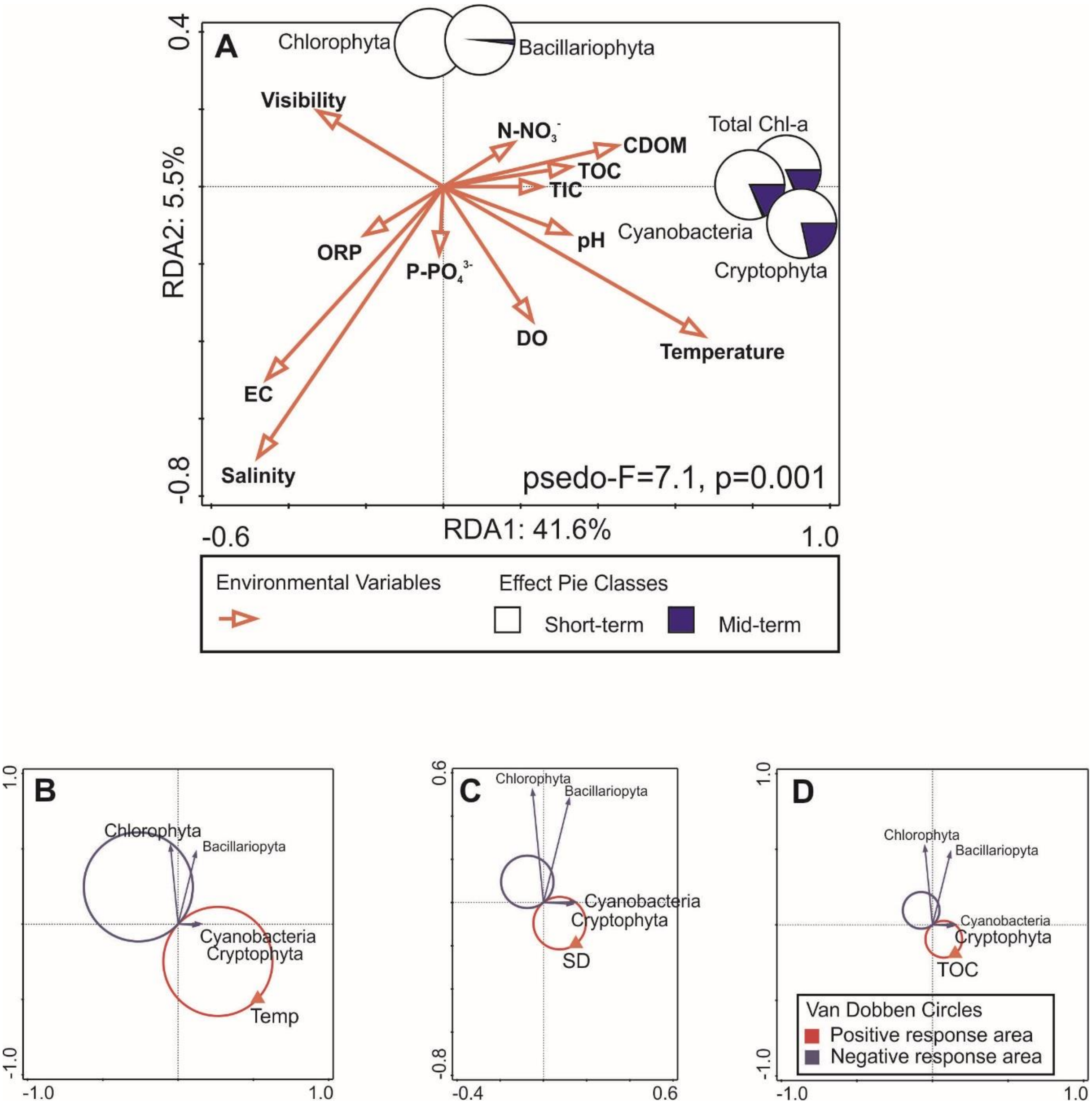

Figure 3. Results of redundancy analysis (RDA): (A) a biplot of significant environmental variables and phytoplankton structure in Lake Jamno (p<0.05); (B–D) t-value biplots with Van Dobben circles based on the RDA of phytoplankton structure and environmental variables: (B) temperature; (C) visibility (Secchi depth); and (D) total organic carbon. CDOM= chromophoric dissolved organic matter; DO=dissolved oxygen; EC= conductivity; ORP=oxidation-reduction potential; SD=Secchi depth; TIC= total inorganic carbon; TOC=total organic carbon

To illustrate the multidimensional structure of data, on the basis of the PLS-R model, we generated biplots of scores and correlation loads. The biplot in Fig. 4A summarizes contributions of predictors (explanatory variables, X): of the time of study and physicochemical parameters of water, which control TChl-*a* concentration (dependent variables, *Y*) in the coastal lake.

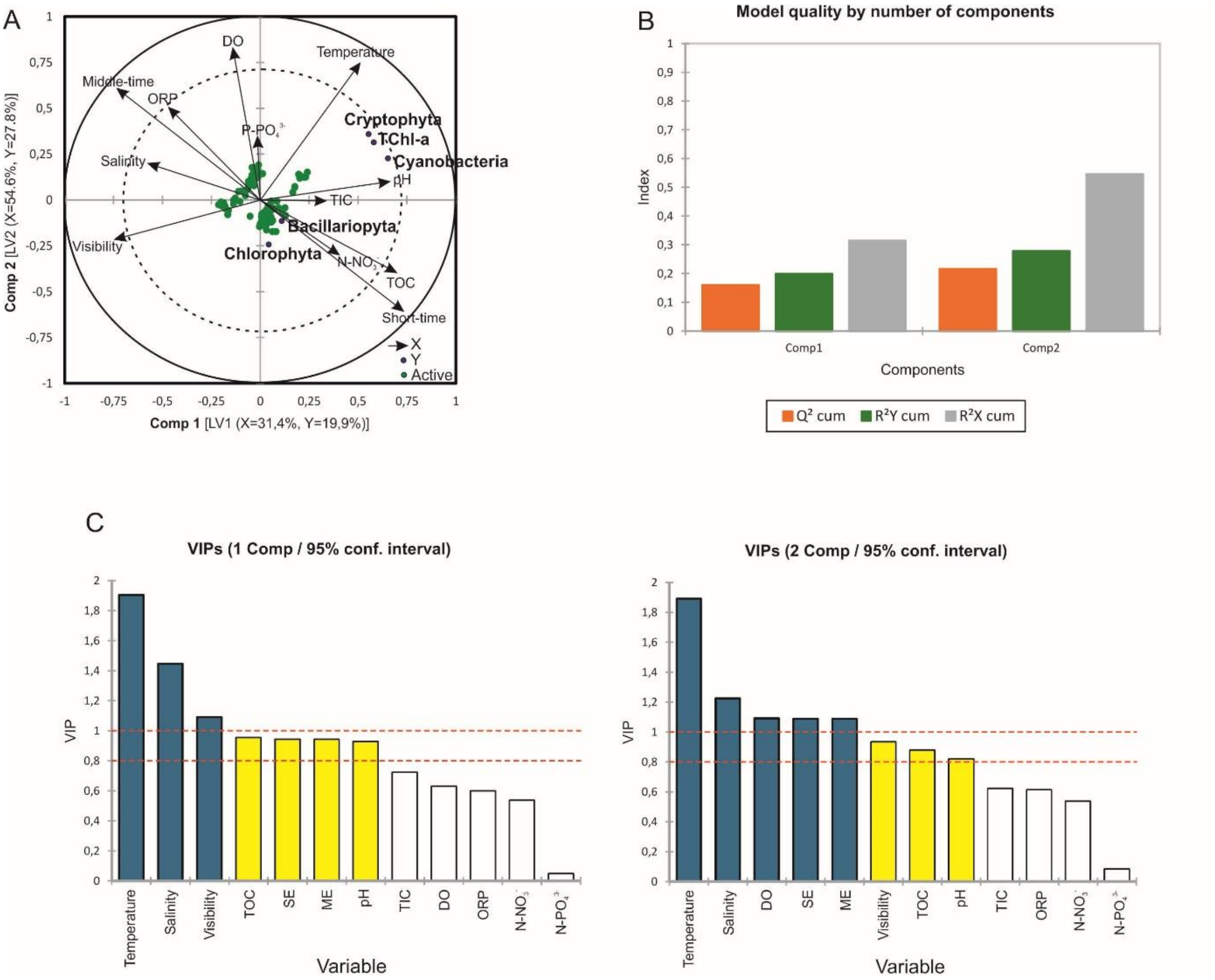

Figure 4. (A) Biplot of partial least-squares regression (PLS-R), reflecting the influence of water quality parameters and study period, as explanatory variables (*X*), on Chl-*a* (*Y*) in Lake Jamno. Percentages of variance in *X* and *Y* explained by each variable (as latent variables LV1 and LV2) are shown on the axes. Internal broken circle denotes correlation coefficient *r*=0.75. (B) Quality of the PLS-R model. (C) Variable influence on projection (VIP) plots for each explanatory variable: LV1 and LV2. VIP plots show the relative importance of predictors. VIPs>0.8, based on Wold's criteria, indicate that the predictor variable is regarded as significant for the corresponding dependent variable. DO=dissolved oxygen; ORP=oxidation-reduction potential; SD=Secchi depth; TIC= total inorganic carbon; TOC=total organic carbon.

The data matrices for the lake are well described by two meaningful latent variables (LVs) in components 1 and 2 (Fig. 4A). In LV1, 31.4% of the variance in the *X* matrix explain 19.9% of the variance in the *Y* matrix. In LV2, 54.6% of the variance in the *X* matrix explain 27.8%

of the variance in the *Y* matrix. In the whole model (LV1 and LV2), 86% of the variance in the *X* matrix were used to explain 47.7% of the variance in the *Y* matrix. Q^2, as a measure of predictive accuracy, showed that component 1 (axis 1), explaining TChl-*a* concentration (Q^2=0.314) was significant (threshold Q^2>0.160, which corresponds to p<0.05) (Fig. 4). Variable influence on projection (VIP) plots (Fig. 4C) show the relative importance of predictors for components 1 and 2. Among VIPs>0.8, based on Wold's criteria, significant effects of temperature, salinity, Secchi depth, TOC, pH, and DO% were observed for the corresponding dependent variables (*Y*). The greatest impact on the biomass of cyanobacteria and cryptophytes was exerted by three factors: temperature, pH (both positive), and Secchi depth (negative). Biomass of the chlorophytes and diatoms was negatively influenced by salinity and oxygen concentration, while positively by TOC concentration. It is noteworthy that the sets of results linked with SE and ME are at opposite ends of the plot, so this suggests that they are very different.

Discussion

Permanent human interventions in the systems of open river mouths are known worldwide, also in coastal lakes. In their case, the limited level of hydrological connectivity decreases the possibility of lake flushing, so it potentially lowers their resistance to human impact and their natural potential. In the long run, the lack of awareness of the lake-sea system functioning, combined with the observed unfavourable directions of climate change, have led in many cases to interventions into their hydrological systems by artificial transformations of their mouths. For this purpose, many solutions were planned and implemented, including the construction of floodgates blocking seawater intrusion into lagoons. These actions were assumed to improve water quality, increase fishing efficiency, and prevent flooding of the neighbouring areas (e.g. Dye and Barros 2005; Gladstone et al. 2006; Heese et al. 2012). However, the responses of coastal ecosystems proved to be rather unpredictable and dependent on many specific factors (Schallenberg et al. 2010). Moreover, in the long run, artificial disturbance of the hydrological connection of the lagoon with the sea indicated a possibility to accelerate ecological succession, which leads to shallowing of lake basins due to deposition of allochthonous sediments (Bate 2007). Thus short-term effects can be observed, which are associated with a strong impact on the environment, but also mid- and long-term ones, resulting from "attempts" of the ecosystem to reach a new ecological balance (Lorenz et al. 2012).

The analysis of the ecological status of Lake Jamno indicates that for decades it has remained in the stable turbid-water state in the phytoplankton dominance regime (Carpenter, 2001). This is a commonly observed trend also in other Baltic coastal lakes (Kornijów, 2018; Obolewski et al. 2018a). The varying intensity of seawater intrusion into these ecosystems led to nullifying this state as a result of marine dispersion phase (Colling et al. 2007; Obolewski 2009). Nevertheless, seawater intrusion was not sufficient, as compared to lake size, to result in the more favourable, stable clear-water state, with a dominance of aquatic vegetation. Because of this, in Lake Jamno, seawater intrusion did not have any significant effect on eutrophication rate and improvement of its ecological status (Obolewski 2009). As a result, lakes in such a situation are characterized by high productivity, associated with nutrient supply from both auto- and allochthonous matter, accumulated in sediments for many years (Schernewski et al., 2011; Verdonschot et al., 2013; Viaroli et al., 2008).

Artificial blockage dramatically changed the dynamics of the aquatic environment, causing stress at many levels of ecosystem organization. Already the first results, soon after the hydrotechnical construction was created, show a strong response of the ecosystem, caused by stress factors (Lawrie et al., 2010). The first factor is a change in water balance, because of a different volume of water input, and the second one is the change in water chemistry. It can be assumed that (i) water volume in the lake basin decreased; (ii) the pollution loads from the catchment were not compensated for by any input of better oxygenated, clean seawater.

During the blockage of seawater intrusion, phytoplankton structure changed significantly (Table 2). In the study lake, we observed a loss and/or a lower diversity of some components of phytoplankton structure because of the lack of seawater input. This confirms observations reported by Lang-Yona et al. (2018). In Lake Jamno, in the second study period, phytoplankton biomass greatly decreased (to about 25% of the former level), whereas diatoms and green algae were completely eliminated. Simultaneously, the dominance of cyanobacteria gradually increased from 91% soon after floodgate construction to 93% in the mid-term comparison (Table 2). Individual species or even genera of cyanobacteria are attributed various features that help them to be successful in interactions with other groups of planktonic algae (Wilk-Woźniak 2009, Bonilla et al. 2011, O'Neil et al. 2012). As a group, cyanobacteria usually reach the highest growth rate at relatively high temperatures (Robarts and Zohary, 1987; Coles and Jones, 2000). In such conditions, they most successfully compete with eukaryotic primary producers, such as diatoms, green algae or cryptophytes (De Senerpont Domis et al., 2007; Jöhnk et al., 2008). Their expansion can be linked with an increase in water temperature, which was evidenced by the analyses (Figs. 4A and C) and *t*-value biplots

(Fig. 3B). These findings are consistent with earlier studies in marine and freshwater ecosystems (Ibelings, 1996; O'Neil et al., 2012; Walls et al., 2018). Isolation of the lake from seawater input intensifies this process, as seawater intrusion stops the increase in lake water temperature and shapes the level of the low temperature threshold of algal existence, thus limiting the growth of cyanobacteria and their toxin production (Robarts and Zohary, 1987; Liu et al., 2011). This was confirmed by our results, as water temperature was the key predictor of phytoplankton biomass. This factor was more significant than study period (Fig. 4C). However, an unexpected result was the progressing decline of cyanobacteria after the construction of the floodgate and the slow increase in their dominance (Table 2). Similar findings were reported by Kosten et al. (2011), as warmer climate did not cause a higher total phytoplankton biomass, but the contribution of total cyanobacteria biomass increased with temperature.

The disturbance caused also changes in values of all the measured abiotic parameters (Table 1). This applies particularly to phosphate concentration, which doubled between SE and ME, indicating that the process of lake degradation was accelerated. It is generally presumed that when a hydrological connection is blocked artificially, nutrient concentrations increase (Santos et al. 2006), implying an overproduction of autotrophs (Twomey and Thompson 2001; Gobler et al. 2005; Netto et al. 2012). Surprisingly, in the mid-term comparison, the greater availability of nutrients was not reflected in phytoplankton growth. Additionally, the generated PLS model indicates that concentrations of $P\text{-}PO_4^{3-}$ and $N\text{-}NO_3^{-}$ only negligibly affected biological results (Fig. 4A-C). An interesting finding was also the decrease in pH in 2020. We suppose that it was caused by the decline of cyanobacteria biomass, as their noxious blooms often increase the pH of the water column to alkalinity (Kosten et al. 2011). Supposedly, the elevated pH helps cyanobacteria to outcompete other algal groups (Feng et al. 2014).

According to sources published about 50 years ago, the range of visibility during the growing season in Lake Jamno rarely exceeded 50 cm and often was close to zero (Michalski and Januszkiewicz, 1967; Malej, 1974). In Obolewski’s (2009) study, Secchi depth was small and did not exceed 50% of lake depth. This was probably linked with strong phytoplankton development and high primary production in this water body (PIOŚ, 2001). Similarly, in our study, Secchi depth did not exceed 0.4 m (Table 1) and was strongly associated with cyanobacteria biomass and TChl-*a* levels (Figs. 3C and 4). The higher visibility in 2020 could be directly linked with a decrease in phytoplankton biomass in open water.

Our results, as well as a growing number of laboratory and field studies (De Senerpont Domis et al., 2007; Jeppesen et al., 2009; Wagner & Adrian, 2009) suggest that rising water temperature may increase the dominance of cyanobacteria. They can benefit more from warming than other groups of phytoplankton because of their higher optimum temperatures for growth. Additionally, their global expansion increases due to climate change: the growing potential threat to surface waters is linked with cyanobacteria activity (Lang-Yona et al., 2018; Walls et al., 2018). Another possibility is that the isolation, associated with deterioration of environmental conditions in Lake Jamno, disturbs the existence of even this, so commonly observed group, treated as an indicator of strong eutrophication. Thus the combination of many unfavourable natural and anthropogenic predictors leads to degradation of the transformed estuaries, including Lake Jamno. In this case, the monitoring data collected starting from the 1960s showed its poor ecological status or even indicated that the ecosystem was dying (Szmidt 1967; Malej 1974). Our results revealed that floodgate creation accelerated this process, leading to reduced phytoplankton diversity. The mid-term results are particularly worrying, as this was the time of shaping a new ecological balance in this ecosystem.

Conclusions

Results of this study show that phytoplankton communities in Lake Jamno were shaped primarily by salinity and to a smaller extent by other physicochemical parameters of water, which because of the lack of contact with the sea were not influenced by brackish water input. Knowledge about hydroecological conditions of functioning of the lakes on the southern coasts of the Baltic Sea is a basis for their management and protection. Baltic coastal water bodies are usually components of small river catchments, so they are particularly vulnerable to human impact. Our results unambiguously confirmed that the prolonged lack of seawater input is unfavourable for coastal lakes. It contributes to biodiversity loss and allows the existence of nearly exclusively cyanobacteria, which can negatively influence the functioning of other ecosystems. The situation is aggravated by the recently observed rapid climate change, which is a strong stress factor affecting water temperature –the major predictor shaping phytoplankton biomass in the lake. In light of this, blockage of hydrological connections between estuaries and the sea cause greater environmental damage in the long run than their short-term financial benefits. Nevertheless, a reliable comparison of profits and losses is possible after long-term monitoring. Pilot studies of short-term effects can be misleading because of inadequacy of results of severe environmental stress, which usually fades with time, when a new ecological balance is shaped in the ecosystem.

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02 June 2023

Dear Editor,

Please find attached here the typescript of our paper: “Implications of floodgate operation for phytoplankton structure in a coastal lagoon (short-term vs mid-term” authors: Monika Szymańska-Walkiewicz and Krystian Obolewski, which we would like to publish in Ecological Engineering.

In the presented paper the consequences of the floodgate closure between a coastal lagoon and the Baltic Sea for phytoplankton were analyzed. It was found out that an intensive and prompt decrease in water salinity with related concentrations of chlorides and sodium, due to floodgate closure, eliminates the majority of diversity of plankton algae incapable to adopt to new habitat conditions. The study results show the case, where the floodgate management, not considering the ecological requirements, leads to abrupt and inappropriate effects onto the different functional groups that provide ecological integrity in coastal ecosystem.

The work is new and original and not under consideration elsewhere. Submission for publication has been approved by all of the authors. There are no conflicts of interests between Authors.
I hope that the form and contest of this paper will satisfy reviewers and you as well.
To facilitate our future contacts please use e-mail: obolewsk@ukw.edu.pl or k.obolewski73@gmail.com

Yours sincerely,
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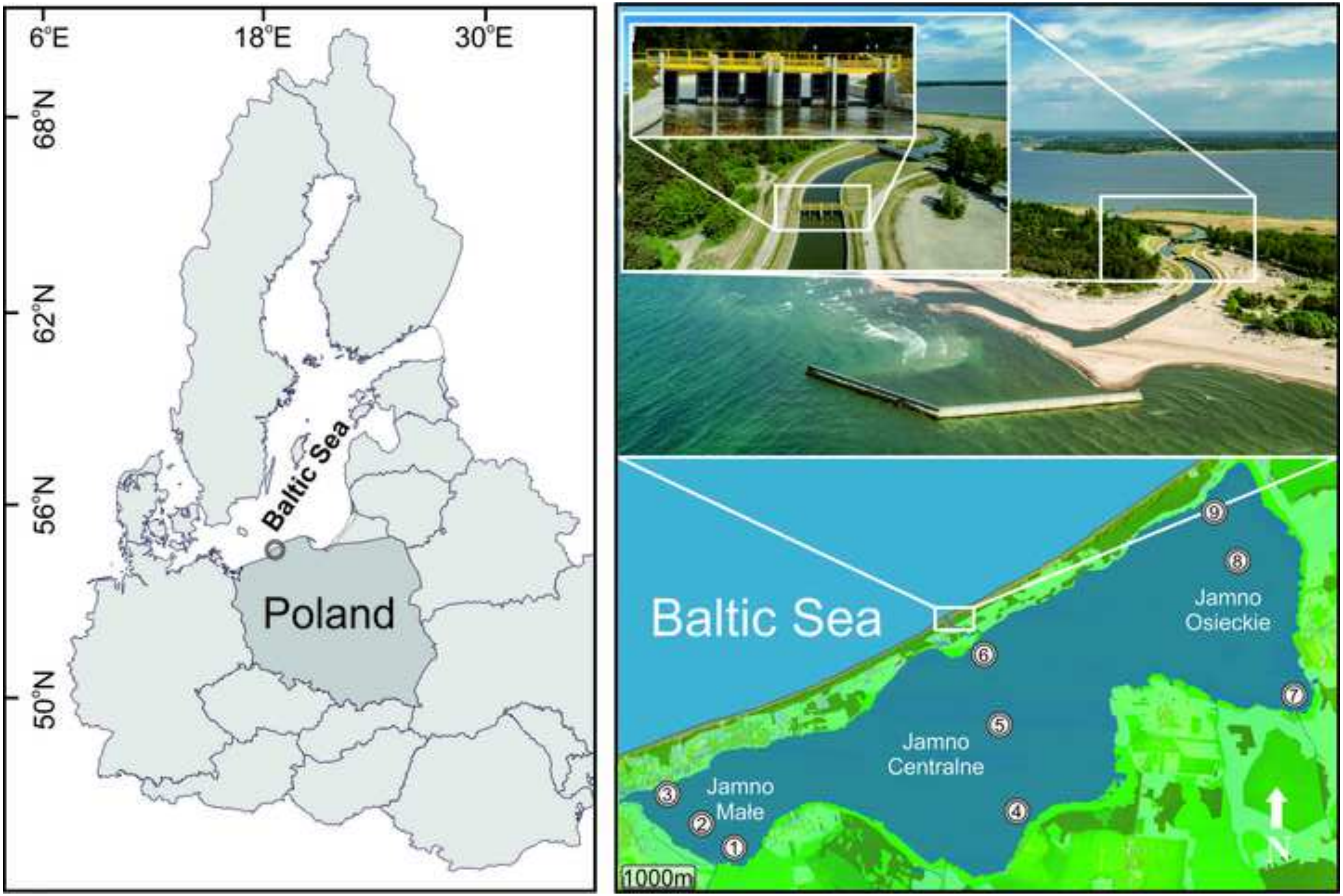
Declaration of interests

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

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

Figure 1


6°E
18°E
30°E
68°N
62°N
56°N
50°N
Baltic Sea
Poland
Baltic Sea
Jamno Osieckie
Jamno Centralne
Jamno Małe
①
②
③
④
⑤
⑥
⑦
⑧
⑨
N
1000m

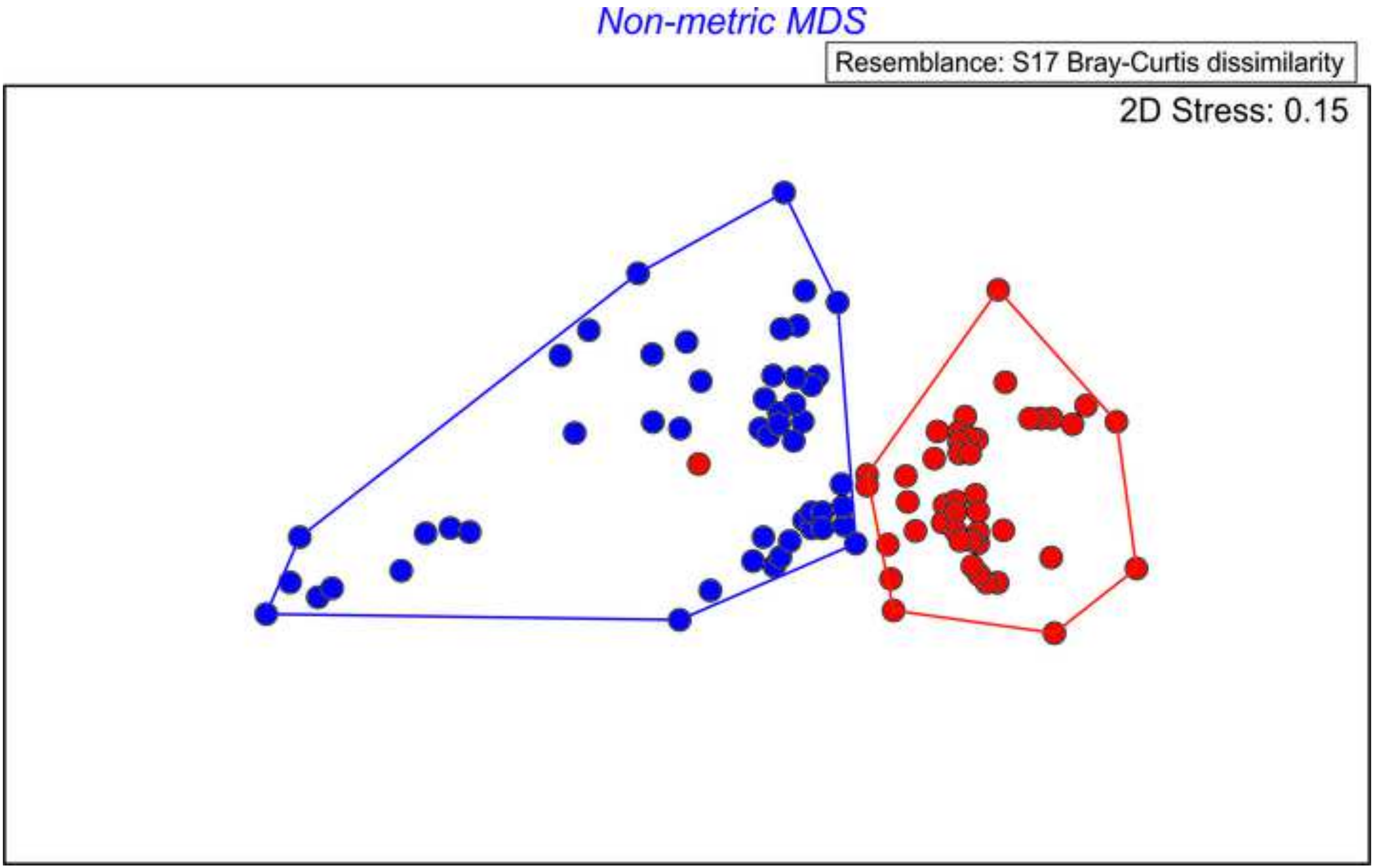

Non-metric MDS
Resemblance: S17 Bray-Curtis dissimilarity
2D Stress: 0.15

Figure 3

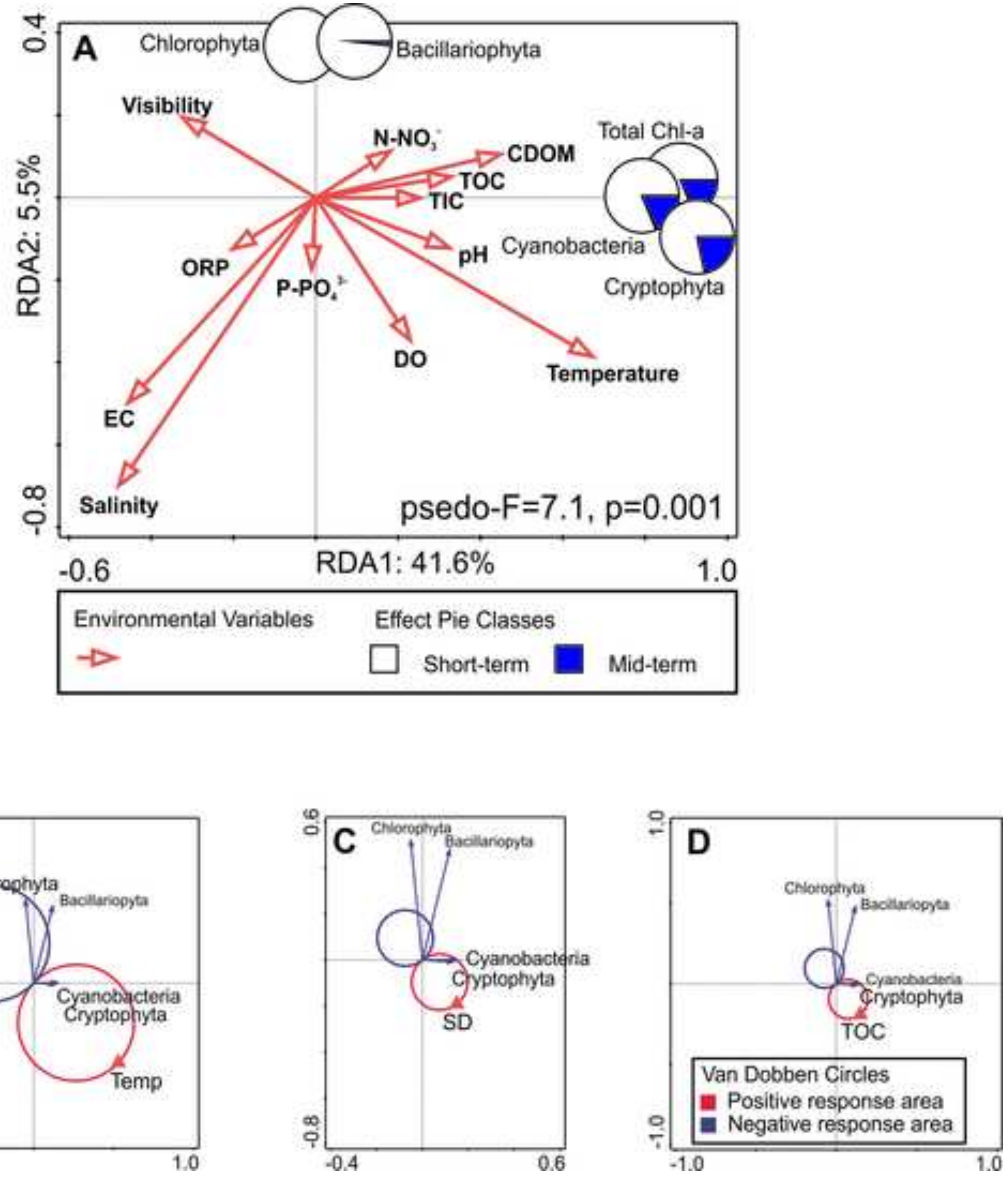

A
Chlorophyta
Bacillariophyta
Visibility
N-NO3-
CDOM
Total Chl-a
TOC
TIC
pH
Cyanobacteria
Cryptophyta
ORP
P-PO4 3-
DO
Temperature
EC
Salinity
psedo-F=7.1, p=0.001
0.4
-0.8
RDA2: 5.5%
-0.6
RDA1: 41.6%
1.0
Environmental Variables
Effect Pie Classes
Short-term
Mid-term
B
Chlorophyta
Bacillariopyta
Cyanobacteria
Cryptophyta
Temp
1.0
-1.0
-1.0
1.0
C
Chlorophyta
Bacillariopyta
Cyanobacteria
Cryptophyta
SD
0.6
-0.8
-0.4
0.6
D
Chlorophyta
Bacillariopyta
Cyanobacteria
Cryptophyta
TOC
Van Dobben Circles
Positive response area
Negative response area
1.0
-1.0
-1.0
1.0

Figure 4

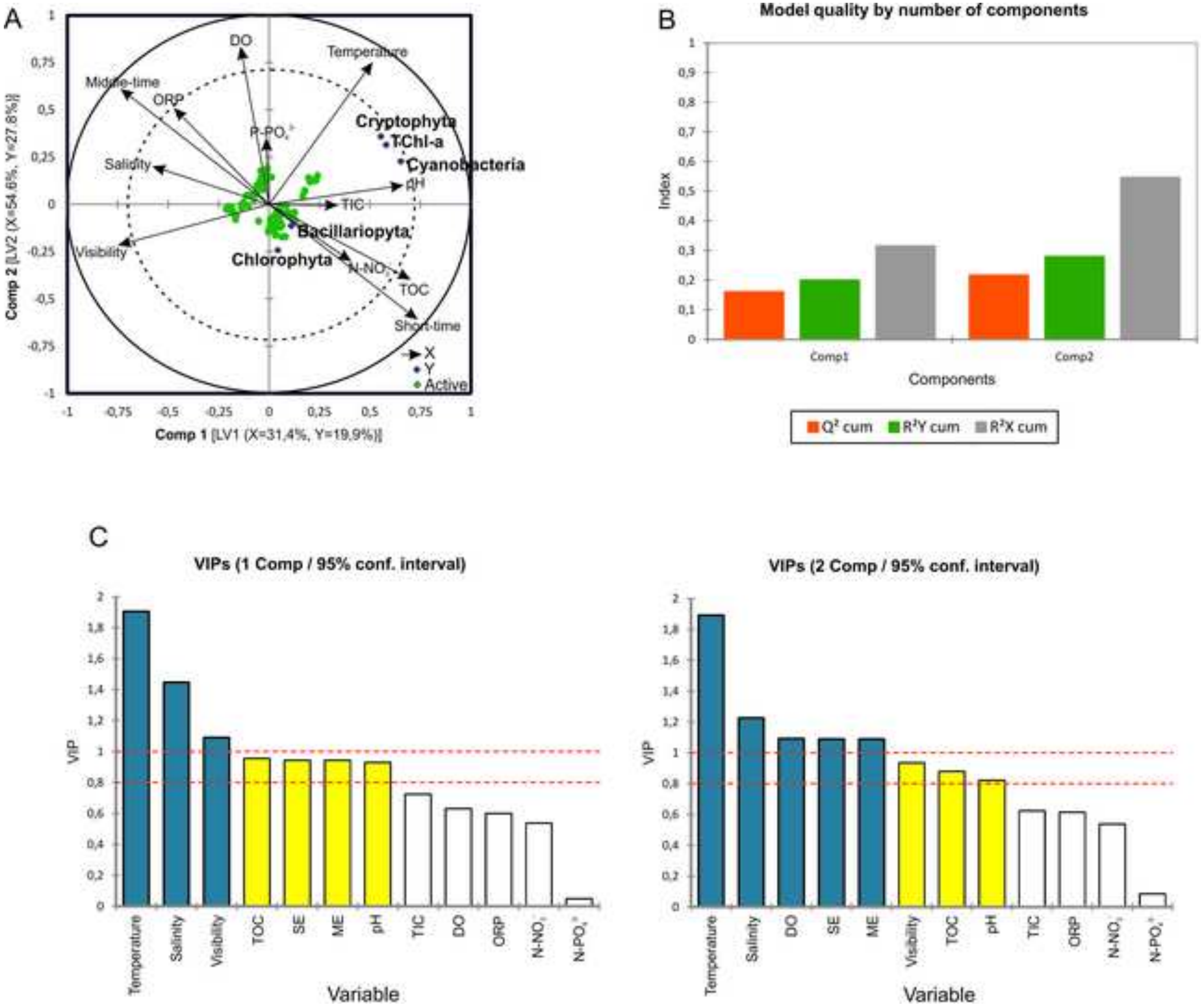

A
Comp 2 [LV2 (X=54.6%, Y=27.8%)]
Comp 1 [LV1 (X=31.4%, Y=19.9%)]
1
0,75
0,5
0,25
0
-0,25
-0,5
-0,75
-1
DO
Temperature
Middle-time
ORP
P-PO$_4^{3-}$
Cryptophyta
T.Chl-a
Cyanobacteria
Salinity
pH
TIC
Visibility
Bacillariopyta
Chlorophyta
N-NO$_3^-$
TOC
Short-time
X
Y
Active
B
Model quality by number of components
Index
Comp1
Comp2
Components
Q² cum
R²Y cum
R²X cum
0,1
0,2
0,3
0,4
0,5
0,6
0,7
0,8
0,9
C
VIPs (1 Comp / 95% conf. interval)
VIP
Temperature
Salinity
Visibility
TOC
SE
ME
pH
TIC
DO
ORP
N-NO$_3^-$
N-PO$_4^{3-}$
Variable
1,8
1,6
1,4
1,2
2
VIPs (2 Comp / 95% conf. interval)
VIP
Temperature
Salinity
DO
SE
ME
Visibility
TOC
pH
TIC
ORP
N-NO$_3^-$
N-PO$_4^{3-}$
Variable

Table 1. Water quality (mean ± standard error) in Lake Jamno after blockage of seawater intrusion: short-term and mid-term effects and results of two-way ANOVA.

	Short-term effects (SE) n=54		Mid-term effects (ME) n=54	
	2014	**2015**	**2019**	**2020**
Visibility (m)**	0.3±0.0	0.3±0.0	0.3±0.0	0.4±0.0
Temp (°C)	17.7±0.2	14.8±0.0	17.3±0.3	17.0±0.1
pH****	8.62±0.02	8.91±0.01	8.63±0.03	7.93±0.04
EC (µS cm^{-1})****	226±1	395±5	400±14	513±2
ORP (mV)****	87.3±2.3	-13.4±2.2	126.0±4.5	177.1±1.5
Salinity (PSU)****	0.07±0.00	0.18±0.00	0.26±0.00	0.22±0.00
DO%****	112.4±0.1	98.4±0.6	131.8±0.8	125.7±0.7
DO (mg L^{-1})****	9.8±0.6	8.6±0.1	12.6±0.1	11.3±0.0
TDS (mg L^{-1})****	146±0	256±2	411±1	327±2
N-NO$_3^-$ (mg L^{-1})****	0.95±0.02	0.83±0.03	0.39±0.01	0.31±0.00
P-PO$_4^{3-}$ (mg L^{-1})****	0.187±0.003	0.092±0.001	0.202±0.028	0.405±0.029
TOC (mg L^{-1})****	20.80±0.19	19.34±0.31	10.40±0.06	9.78±0.05
TIC (mg L^{-1})****	10.99±0.11	9.34±0.15	8.44±0.06	9.30±0.03
CDOM (µg L^{-1})****	3.75±0.10	0.58±0.04	3.55±0.03	4.75±0.09

p values modified by the Bonferroni procedure for multiple comparisons show significant effect at $p<0.05^{*}$; $p>0.01^{**}$; $p<0.001^{***}$; $p<0.0001^{****}$. EC= conductivity; ORP=oxidation-reduction potential; DO=dissolved oxygen; TDS=total dissolved solids; TOC=total organic carbon; TIC= total inorganic carbon; CDOM= chromophoric dissolved organic matter

Table 2. Phytoplankton structure (mean ± standard error) in Lake Jamno after blockage of seawater intrusion: short-term and mid-term effects and results of two-way ANOVA.

Chlorophyll *a* concentration (as an estimate of biomass)	Short-term effects (SE) n=54		Mid-term effects (ME) n=54	
	2014	**2015**	**2019**	**2020**
Total Chl-*a* (µg L^{-1})****	85.1±3.8	11.8±1.0	17.1±0.0	9.4±0.9
Chlorophyta (µg L^{-1})****	0.65±0.04	1.01±0.1	0±0	0±0
Cyanobacteria (µg L^{-1})****	78.08±3.51	10.31±0.89	16.0±0.02	8.71±0.78
Bacillariophyta (µg L^{-1})**	0.26±0.02	0±0	0±0	0±0
Cryptophyta (µg L^{-1})****	6.14±0.29	0.19±0.4	1.54±0.12	0.72±0.08

p values modified by the Bonferroni procedure for multiple comparisons show significant effect at $p<0.05^{*}$; $p>0.01^{**}$; $p<0.001^{***}$; $p<0.0001^{****}$