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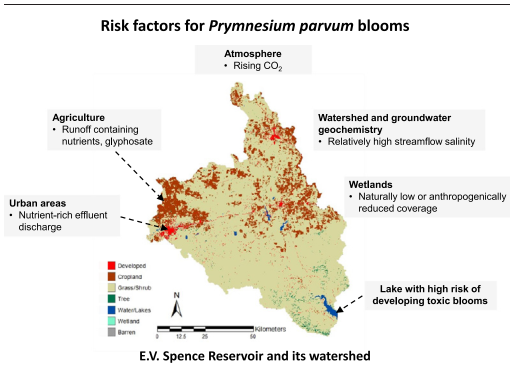
HIGHLIGHTS

- Increased air CO_2 and glyphosate coincided with *P. parvum* HAB recurring appearance.
- HAB-impacted reservoirs were of higher salinity.
- Watersheds of HAB-impacted reservoirs had far smaller wetland areas.
- Increased air CO_2 and glyphosate may partly drive establishment of *P. parvum* HAB.
- Higher salinity and wetland deficiency may have facilitated HAB establishment.

GRAPHICAL ABSTRACT



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ABSTRACT

This study examined the association of air, land, and water variables with the first historical occurrence and current distribution of toxic *Prymnesium parvum* blooms in reservoirs of the Brazos River and Colorado River, Texas (USA). One impacted and one reference reservoir were selected per basin. Land cover and use variables were estimated for the whole watershed (WW) and a 0.5-km zone on either side of streams (near field, NF). Variables were expressed in annual values. Principal component and trend analyses were used to determine (1) differences in environmental conditions before and after the 2001 onset of toxic blooms in impacted reservoirs (study period, 1992–2017), and (2) traits that uniquely discriminate impacted from reference reservoirs (2001–2017). Of thirty-three variables examined, two positively aligned with the reoccurring appearance of blooms in impacted reservoirs (air CO_2 and herbicide Glyphosate) and another two negatively aligned (insecticides Terbufos and Malathion). Glyphosate use was observed throughout the study period but a turning point for an upward trend occurred near the year of first bloom occurrence. While the relevance of the decreased use of insecticides is uncertain, prior experimental studies reported that increasing concentrations of air CO_2 and water Glyphosate can enhance *P. parvum* growth. Consistent with prior findings, impacted reservoirs were of higher salinity than reference reservoirs. In addition, their watersheds had far lower wetland cover at NF and WW scales. The value of wetlands in reducing harmful algal bloom incidence by reducing nutrient inputs has been previously recognized, but wetlands can also capture pesticides. Therefore, a diminished wetland cover

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could magnify Glyphosate loads flowing into impacted reservoirs. These observations are consistent with a scenario where rising levels of air CO_2 and Glyphosate use contributed to the establishment of *P. parvum* blooms in reservoirs of relatively high salinity and minimal wetland cover over their watersheds.

1. Introduction

Prymnesium parvum is a unicellular, mixotrophic haptophyte of worldwide distribution found in marine waters, estuaries, and brackish inland waters (Granéli et al., 2012; Roelke et al., 2016). This species can produce compounds that are toxic to fishes and other aquatic organisms. In the USA, harmful algal blooms (HABs) of *P. parvum* were first documented in the Pecos River and other locations in Texas in the 1980s, but a large range expansion and intensification of the blooms were observed throughout the south-central region of the country in the 2000s (Roelke et al., 2016). Impacts to the economy and ecological integrity of affected areas have been considerable (Oh and Ditton, 2005, 2008; Southard et al., 2010; VanLandeghem et al., 2013).

Various abiotic environmental variables are known to influence *P. parvum* growth and bloom formation. Its abundance has been positively correlated with salinity in the range of ~1 to 10–12 psu (Guo et al., 1996; Hambright et al., 2010, 2014; Lemley et al., 2019; Patiño et al., 2014; Roelke et al., 2011; VanLandeghem et al., 2015a). As salinity rises further, however, the salinity-abundance association becomes negative (Guo et al., 1996; Israël et al., 2014; Lemley et al., 2019; Rashel and Patiño, 2017). The concentration of certain ions in brackish waters, such as sulfate, also may influence *P. parvum* growth independently of salinity (Moestrup, 1994; Patiño et al., 2014; Rashel and Patiño, 2019). Other water quality factors known to influence *P. parvum* growth are nutrient levels and temperature, as most toxic blooms in the USA occur in eutrophic waters during the cooler months of the year (Roelke et al., 2016). Among atmospheric variables, there is evidence suggesting that the timing (relative to bloom season) and intensity of precipitation may influence the development of blooms (Clayton et al., 2021), and that rising levels of atmospheric CO_2 could enhance their intensity (Rashel, 2020).

Pesticides carried into streams and lakes by precipitation runoff could also influence the spatial distribution and development of HABs. Various pesticides are known to inhibit phytoplankton growth (DeLorenzo et al., 2001; Halstead et al., 2014; Rumschlag et al., 2022; Smedbol et al., 2018; Staley et al., 2015) and potentially could suppress *P. parvum* abundance. However, *P. parvum* is relatively resistant to the herbicide Atrazine (Flood and Burkholder, 2018; Yates and Rogers, 2011), suggesting that surface waters containing Atrazine could selectively favor *P. parvum* growth. Moreover, *P. parvum* is not only tolerant to Glyphosate – the most widely used herbicide in the USA and globally (Benbrook, 2016) – but its growth is enhanced by low, environmentally relevant concentrations of this herbicide (Dabney and Patiño, 2018).

Little information is available concerning the association between HAB occurrence and the types of land use over the watersheds of affected water bodies. The few studies available that examined this association focused primarily on nutrient sources (Beaver et al., 2014; Marion et al., 2017; Rose et al., 2019) or their spatial coverage was limited to a single lake (Ware, 2012). Harmful algal blooms commonly occur within or downstream of urban or agricultural areas, in part because these areas are major sources of nutrients (Beaver et al., 2014; Clayton et al., 2021; Marion et al., 2017; Rose et al., 2019; Ware, 2012). In the Southern Great Plains of the USA, which includes Texas, however, many major reservoirs are eutrophic or hypereutrophic regardless of their status as having been impacted or not by *P. parvum* (Patiño et al., 2014). The latter observation suggests that a nutrient-rich condition is by itself insufficient to explain the distribution of *P. parvum* blooms.

This study provides a comprehensive multivariate analysis of the association of air, land, and water variables with the first historical appearance and current spatial distribution of toxic blooms of *P. parvum* in major reservoirs of the Southern Great Plains. Study sites include *P. parvum*-impacted and reference (non-impacted) reservoirs of the Brazos River and Colorado River basins (Texas), which are among the most severely affected basins in North America (VanLandeghem et al., 2013, 2015a). Other studies of these two basins examined associations of water quality, lake inflow, and selected biotic variables with *P. parvum* presence and bloom formation (Clayton et al., 2021; Dawson et al., 2015; Patiño et al., 2014; Roelke et al., 2007, 2011, 2013, 2016; VanLandeghem et al., 2012, 2015a, 2015b, 2015c), and a study of Lake Texoma (Red River, Texas and Oklahoma, USA) reported the association of near-field land cover types with *P. parvum* (Ware, 2012). However, watershed-scale studies of total-environmental associations (including pesticides) have not been conducted for *P. parvum*.

The first objective of this study was to determine overall differences in environmental conditions before and after the 2001 onset of toxic blooms in the impacted reservoirs of the study area (Southard et al., 2010), under the working hypothesis that some of these temporal differences may be causally associated with the first appearance and subsequent recurrence of blooms. The period of record (POR) for this objective (1992–2017) was delimited by the availability of pesticide data (Section 2.3.3), which is an important variable for this study. The second objective was to characterize environmental traits that discriminate or separate impacted from reference reservoirs since the first appearance of toxic blooms (POR, 2001–2017), under the working hypothesis that attributes that are exclusively shared by impacted reservoirs may explain their susceptibility to *P. parvum*. The temporal scale of the environmental data used in this study was annual and also determined by the available scales of two important variables – pesticides and land cover (Section 2.3). While the annual scale of these data precluded their close integration with infra-annual bloom occurrences (sometimes lasting only a few weeks), environmental data at annual scales are adequate to address the present study objectives, which are framed within long-term temporal and landscape scales of toxic *P. parvum* bloom distributions. The goal of this study is to inform efforts of land and water managers to improve reservoir water quality and reduce the risk of HAB incidence.

2. Methods

2.1. Study sites

Four reservoirs and their watersheds within two river basins of the Southern Great Plains (Texas) were evaluated in this study. They are Possum Kingdom Lake and Waco Lake on the Brazos River, and E.V. Spence Reservoir and Twin Buttes Reservoir on the Colorado River (Table 1). Possum Kingdom Lake and E.V. Spence Reservoir are mainstem reservoirs that have experienced recurring blooms of *P. parvum* and associated fish-kill events or toxicity detections since 2001 (Southard et al., 2010; VanLandeghem et al., 2013, 2015b; Table S1). Waco Lake and Twin Buttes Reservoir are on tributaries of their respective mainstems and have not experienced toxic blooms, and thus were designated as reference sites (Table 1). These four reservoirs were selected based on prior studies of the ecological impacts of *P. parvum* on fish communities (VanLandeghem et al., 2013) and of long-term trends in hydrological variables and their association with *P. parvum* at the landscape scale (Dawson et al., 2015; Patiño et al., 2014). These earlier studies, however, did not address the influence of land cover or pesticide use within the reservoir watersheds.

Possum Kingdom Lake was built in 1941 on the Brazos River (Archer, 2015). Its primary functions include municipal water supply, flood control, recreation services, and hydropower generation (Texas Water Development Board, 2022). The reference reservoir, Waco Lake, is on the North Bosque River, a tributary to the Brazos River. Waco Lake was built in 1930 and

Table 1
Characteristics of reservoirs from the upper Colorado River and Brazos River basins in Texas used in this study.

Reservoir	River basin	Surface area at full pool (ha)	Storage at full capacity ($m^3 \times 10^6$)	Whole watershed area (ha)	Stream network near field area (ha)
Possum Kingdom	Brazos	7250	663	965,928	171,527
Waco	Brazos	3314	234	421,930	160,271
E. V. Spence	Colorado	5924	632	663,392	230,325
Twin Buttes	Colorado	3675	229	866,172	168,481

its functions include provision of water to the City of Waco, flood control, and recreational services (Conry, 2010).

E.V. Spence Reservoir was built in 1969 on the Colorado River, primarily as a source of municipal water and for recreation (Hunt and Leffler, 2019). Twin Buttes Reservoir, the reference reservoir, was built in 1963 and is located on the Middle Concho River, a tributary to the Concho River which, in turn, merges with the Colorado River at O.H. Ivie Reservoir (Nickels and Mauldin, 2001). Its primary uses are as a source of water for the City of San Angelo and for irrigation, power plant cooling, and recreation (Texas Water Development Board, 2022; VanLandeghem et al., 2013).

2.2. Watershed definitions

Reservoir watersheds were defined by hydrologic unit codes (HUC; https://water.usgs.gov/GIS/huc.html) in ArcGIS version 10 (Fig. 1). The 10-digit HUC was used in most cases, but a 12-digit HUC was also used for the Twin Buttes watershed in order to exclude the City of San Angelo, which is downstream of the dam and therefore does not contribute inflow (runoff) to the reservoir (Table S2).

The downstream end of all watersheds was the reservoir dam. For E.V. Spence, the upstream end of its watershed was defined as the dam of the next upstream reservoir on the mainstem, Lake J.B. Thomas, at approximately 200 river kilometers from the E.V. Spence dam. There is no upstream reservoir on the Brazos River mainstem for Possum Kingdom Reservoir and in this case, a point approximately 200 river kilometers upstream of the dam was considered as the watershed's upstream end. All stream systems draining into the mainstem segments (Possum Kingdom, E.V. Spence) or into the reference tributaries (Waco Lake, Twin Buttes) were included within their respective watersheds.

2.3. Data acquisition

Variables used in this study included atmospheric data, land cover, agricultural pesticide use, and lake hydrology including water quality. Available periods of record (POR) differed among the various data types. To allow inclusion of all variables in the analyses, the shortest POR available became the POR for the study – this was for pesticides (1992 to 2017). For the purpose of imputing missing data, however, longer PORs were selectively used for some variables to increase data density and enhance the reliability of imputed values (Section 2.4). Land cover and agricultural pesticide use data are available only in annual values; therefore, all variables for this study are presented in annual formats. Although annual values do not allow evaluation of seasonal drivers or correlates of bloom formation, the primary interest of this study was to characterize ambient conditions associated with spatial and long-term temporal distributions of toxic blooms. Hydrological variables were initially organized at seasonal scales for the purpose of imputing missing seasonal values before estimating annual values. Seasons were defined according to an earlier study of Colorado River and Brazos River reservoirs (Dawson et al., 2015) as follows: Winter, December–February; Spring, March–May; Summer, June–August; and Fall, September–November.

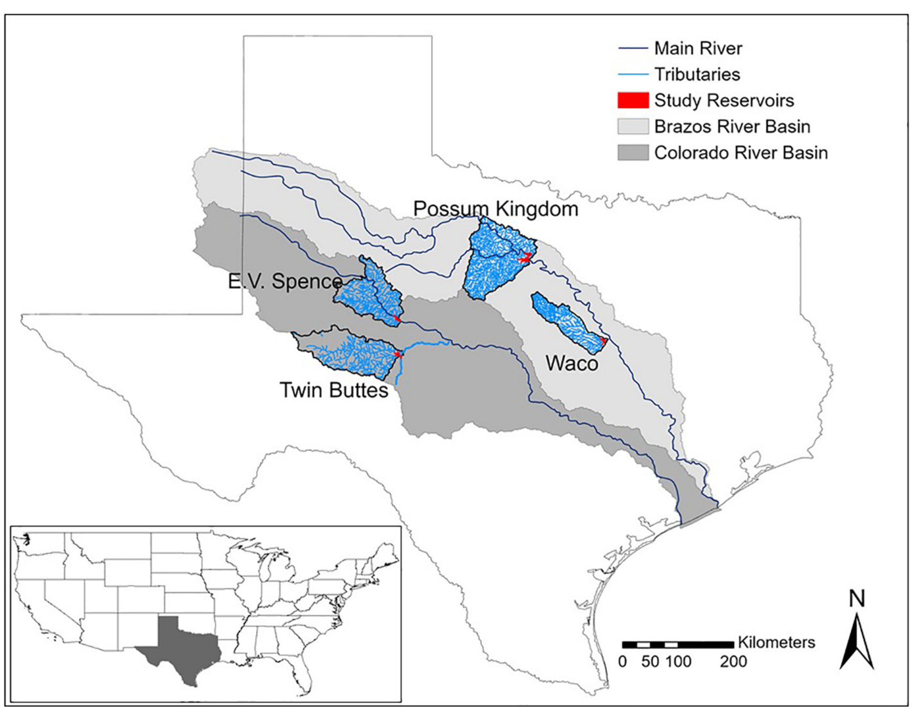

Fig. 1. Map of Texas showing the location of the Brazos River and Colorado River basins and the study watersheds with their stream networks (blue areas). The small red areas on the downstream end of the watersheds show the reservoir locations, and the inset map shows the conterminous United States highlighting the state of Texas.

2.3.1. Atmospheric variables

Data for cumulative daily precipitation and average daily air temperature were collected for a total of eight weather stations from the National Climatic Data Center (http://www.ncdc.noaa.gov/), two in each watershed. One of the stations chosen for Possum Kingdom was discontinued in 2015 (Graham); however, a new nearby station started recording data that same year (Graham 0.9; Table S3). The selection of stations was based on Dawson et al. (2015) and on their available POR. Daily precipitation summaries were added to obtain cumulative monthly precipitation for each station, and the average of the two stations was used to estimate cumulative annual precipitation for each watershed. Months with more than five consecutive days of missing data were considered incomplete (missing value). Average daily temperature was used to calculate average monthly and annual temperatures. Average annual atmospheric CO_2 data were downloaded from the National Oceanic and Atmospheric Administration (Mauna Loa, Hawaii; https://gml.noaa.gov/ccgg/trends/data.html). Values for atmospheric CO_2 are global in scope, but they were included with site-specific variables to evaluate their potential relative contribution to the first appearance and spatial distribution of *P. parvum* blooms.

2.3.2. Land cover

Annual land cover data were obtained from the Land Change Monitoring, Assessment, and Projection (LCMAP, Collection 1) of the U.S. Geological Survey (USGS) (https://www.usgs.gov/core-science-systems/eros/lcmap). This collection is composed of raster (30-m resolution) land cover maps that classify land into seven types: cropland, developed, grass/shrub, barren, tree cover, water, and wetland. Because land cover near to the streams may have higher influence on water quality than more distant areas (Medalie et al., 2020; Tran et al., 2010), a near-field zone (NF) with a width of 0.5 km on either side of all streams within each watershed was developed and land cover data for those zones were extracted. The LCMAP maps were masked by the NF zone and whole-watershed (WW) zone polygons, and area fields were added to the attribute tables to calculate the area of each cover type for each zone using the field calculator. (Note: the term "near field" used in this study refers to proximity to the stream network within the watershed, and not solely to distance from or around the reservoir.)

2.3.3. Pesticide use

The five most widely used agricultural herbicides, insecticides, and fungicides in Texas (total of 15 pesticides) at the beginning of the study period (Gianessi and Anderson, 1995) were selected for this study (Table S4). County-level annual use data were obtained from the Pesticide National Synthesis Project (PNSP) of the USGS (https://water.usgs.gov/nawqa/pnsp/usage/maps/county-level/). The maximum available POR for pesticide data at the time of this study was from 1992 to 2017. The PNSP provides two datasets, one with low-estimates (EPest-low) and the other with high-estimates (EPest-high). They differ in that when a Crop Reporting District (CRD) is surveyed but a particular pesticide is not reported for a given pesticide by crop combination, their values are assumed to be zero for the EPest-low estimates and missing for the EPest-high estimates. The EPest-high is then calculated based on values reported by neighboring CRDs (Baker and Stone, 2015). For this study, EPest-high estimates of each pesticide were collected for all counties within or overlapping with the study watersheds (Table S5). After data processing (Section 2.4), annual pesticide values for each watershed were assessed as the sum of all county values corrected by the fraction of the county area within the watershed (WW zone). Agricultural pesticide use within the NF zone was estimated by correcting for the fraction of cropland cover within the NF zone.

2.3.4. Reservoir storage and discharge

Daily storage data were obtained from the Texas Water Development Board (https://www.twdb.texas.gov/surfacewater/rivers/reservoirs/) and daily discharge data from the National Water Information System Mapper Interface of the USGS (https://maps.waterdata.usgs.gov/mapper/). Discharge gages below the dam of each reservoir were used, except for Twin Buttes Reservoir, which does not have a gage below the dam (Table S3). Average monthly values were calculated from daily values and used to obtain average seasonal data, and when values were available for only one month, the single value was used as representative for the season. Seasons without data were considered missing values.

2.3.5. Reservoir water quality

Surface water quality variables initially considered include chlorophyll, pheophytin, orthophosphate, specific conductance, dissolved oxygen, pH, transparency, total alkalinity, total phosphorus, nitrate, ammonia nitrogen, total Kjeldahl nitrogen, chloride, and sulfate. Data were obtained from the Surface Water Quality Web Reporting Tool of the Texas Commission on Environmental Quality (https://www80.tceq.texas.gov/SwqmisPublic/index.htm). Two stations were selected and averaged for each reservoir except for Twin Buttes where only one station was available (Table S3). One station was located in the upstream reach of the reservoir and the other in the downstream reach, typically by the dam. Available monthly data were averaged to obtain seasonal values, and when values were available for only one month, the single value was used as representative for the season. As noted by Dawson et al. (2015), temporal biases caused by uneven within-year distribution of water quality data are assumed to occur randomly in any given year and thus become unbiased over the long term. Seasons without any data were considered missing values. Air temperature was used as a proxy for surface water temperature to avoid the need for imputation (Sections 2.3.1 and 2.4).

2.4. Imputation of missing data

There were no missing data for air CO_2 and temperature (Table S6). In regard to precipitation, the Waco Lake watershed had complete datasets and other watersheds only had 0.4–4% missing values. Waco Lake and Possum Kingdom Lake had complete storage datasets and other lakes had only small fractions of missing data (1–2%; Table S6). There is no flow gage immediately downstream of Twin Buttes and discharge data for this reservoir are unavailable; other reservoirs had 0–15% missing discharge data (Table S6). Among pesticides, Glyphosate and 2,4-D had no missing observations and several additional pesticides had near-complete datasets (Table S6). Various other variables, however, had larger fractions of missing observations. Alkalinity, ammonia, orthophosphate, pheophytin, total Kjeldahl nitrogen, Copper, and Maneb were excluded from further analysis because they had >75% missing data (Table S6). Similar cut-off levels for imputation have been used by other studies (Madley-Dowd et al., 2019; VanLandeghem et al., 2015b).

Missing monthly precipitation data were imputed with the average of all available values for the missing month within discrete 10 year-intervals between 1990 and 2019. For example, if precipitation of May 2015 was missing for the E.V. Spence watershed, the average of May precipitation values from 2010 to 2019 was used to impute the missing value for this watershed. Time intervals for this analysis were 1990–1999, 2000–2009, and 2010–2019.

For water quality variables and lake discharge and storage data, missing observations in seasonal data (i.e., when all three months of a season had no data) were imputed for each reservoir separately using a multiple imputation (MI) approach in IBM SPSS Statistics for Windows, Version 26 (IMB Corp., Armonk, NY, USA). Ten complete-case datasets were created, and their averages were used to calculate annual values. The MI procedure uses a Markov Chain Monte Carlo Gibbs' sampling algorithm that assumes data are missing randomly (Hopke et al., 2001; Yuan, 2011). A POR of 1985 to 2020 was used for these imputations, which is slightly longer than the study POR (1992–2017). The extended POR increased the density of data and was assumed to enhance the reliability of the imputed values. For annual pesticide use values, original datasets were organized by county for all 15 pesticides, and county-wise MI was performed as described for water variables to impute missing values.

2.5. Data analysis

2.5.1. Principal component analysis

Principal component analysis (PCA) is a multivariate analytical procedure that reduces complex datasets of multiple variables to a lesser number of orthogonal variables, or principal components (PCs), while retaining most of the original variation in the data. The importance of the original variables to each PC is measured by their factor loading value (0–|1|). This procedure is especially useful for visual exploration of data patterns in PC biplots, where data points that group together in multivariate space share similar characteristics (Jolliffe, 2002, 2005). The PC or combination of PCs that best separates data according to a grouping factor of interest can then be used to evaluate which original variables contribute the most to the separation. PCA was used to examine spatiotemporal patterns in the distribution of multivariate environmental data without drawing statistical inferences. The statistical significance of temporal trends in individual variables was assessed by trend analysis (Section 2.5.2).

Some of the variables used in this study were correlated with each other; for example, the salinity-associated variables specific conductance, chloride, and sulfate. Inclusion of correlated (colinear) variables can inflate estimates of the variance explained for the PC on which the variables load. We did not eliminate correlated variables from the analysis because this would require assuming that all associations involving these variables can be represented in nature by any one of the correlated variables. In the case of salinity-associated variables, however, specific effects of chloride (Talarski et al., 2016) and salinity-independent effects of sulfate (Rashel and Patiño, 2019) have been shown for *P. parvum*. This study thus reports but does not interpret the variance explained by the selected PCs.

The first objective of this study was to establish differences in environmental conditions in the impacted reservoirs before and after 2001, the year when toxic *P. parvum* blooms were first reported in the impacted lakes. To address this objective, PCA was conducted with data from E.V. Spence Reservoir and Possum Kingdom Lake using the time periods before (1992–2000) and after (2001–2017) the onset of blooms (POR, 1992–2017) as grouping factor. Prior to analysis, variables were normalized (proc rank) using the Blom method (Blom, 1958) in SAS 9.4 (SAS Institute Inc., Cary, NC, USA). The PCA was done in GraphPad Prism 8.4.0 (GraphPad Software, San Diego, California, USA), which allows PC selection based on Parallel Analysis – a selection method that objectively determines how many PCs to retain. Original variables with factor loading values ≥|0.60| in the selected PCs were interpreted in this study. Separate analyses were done using WW and NF estimates of land cover and pesticide use.

The second objective of the study was to characterize environmental traits that uniquely discriminate impacted from reference reservoirs since toxic blooms began in 2001. To address this objective, data from all four reservoirs were included in a PCA with the POR of 2001–2017, and the grouping factor was reservoir classification as having been historically impacted or not by toxic blooms. Data processing, PCA procedures, and data pattern evaluations were conducted as previously described. Discharge data were not included in this analysis because it was unavailable for Twin Buttes Reservoir.

2.5.2. Trend analysis

Temporal trends (environmental variable vs year) were estimated to complement and aid in the interpretation of PCA results. The nonparametric Kendall's Tau *b* test was calculated using Tibco Statistica 13.3 (Tibco Software, Inc., Palo Alto, CA, USA). Kendall's Tau *b* coefficient (τ) provides a measure of the strength and direction of the temporal association (Helsel and Hirsch, 2002). This analysis was done on untransformed data (POR, 1992–2017) and separately for each site. Statistical significances of trends within each site were estimated in GraphPad Prism using the False Discovery Rate approach (Benjamini et al., 2006), which reports *q*-values (generated from the original *p*-values) with a significance threshold of 0.05 (discoveries). For land cover and pesticide use, trends were estimated using WW and NF data. Heat maps of τ-values were developed in GraphPad Prism to evaluate general patterns of change across the landscape.

3. Results

Principal component analysis of data from the two impacted sites (Possum Kingdom, E.V. Spence) included a total of thirty-three variables and resulted in the selection of two PCs in both the NF and WW analyses (Tables 2, S7). With few exceptions, factor loading values and patterns were similar between the NF and WW analyses. The first component clearly separated data from the two reservoirs and was defined by air (e.g., precipitation), reservoir water quantity (e.g., storage), water quality (e.g., salinity), and land cover variables (Fig. 2). (Salinity is used here to collectively refer to specific conductance and the two major anions that contribute to salinity in the study reservoirs – chloride and sulfate.) Several pesticides also contributed to the separation along PC1, some as strongly (e.g., factor loading values > |0.60|) as the other variable types (Table 2). Principal component 2 separated data grouped according to temporal period (1992–2000 vs 2001–2017) – and is therefore the primary interest of this study – but the clustering of data was not as distinct as it was along PC1 (Fig. 2). Atmospheric CO_2 was the strongest contributor to PC2 (Table 2). Among the pesticides, Glyphosate, Malathion, and Terbufos were the strongest contributors to data separation along PC2 (Table 2; Table S7). Atmospheric CO_2 and Glyphosate use values were higher since the start of toxic blooms in 2001, while Malathion and Terbufos use were lower (Fig. 2). Land cover, hydrological and water quality variables on PC2 did not meet the interpretation criterion (Tables 2, S7; Fig. 2).

Table 2

Principal component analysis of near-field and whole-watershed environmental data from *Prymnesium parvum*-impacted study reservoirs in Texas (period or record, 1992–2017). Factor loadings ≥ |0.6| are shown for variables in the first two principal components (PC) retained by the analysis. Eigenvalues, and proportional and cumulative variance are also shown for each PC. See Table S7 for full listing of loading factors.

Variable	Near field		Whole watershed	
	PC1	PC2	PC1	PC2
Atmospheric CO_2		−0.87		−0.89
Air temperature				
Precipitation	−0.69		−0.69	
Discharge	−0.89		−0.88	
Storage	−0.90		−0.90	
Specific conductance	0.86		0.86	
Chloride	0.69		0.68	
Sulfate	0.90		0.90	
Dissolved oxygen	0.67		0.66	
pH				
Total phosphorus	0.75		0.75	
Chlorophyll	0.80		0.80	
Transparency	−0.72		−0.71	
Barren	0.75		0.77	
Cropland			0.77	
Developed	0.74		0.75	
Grass/shrub	0.89		0.88	
Tree cover	−0.80		−0.81	
Water cover	−0.91		−0.90	
Wetland	−0.80		−0.81	
2,4-D	−0.66		−0.66	
Atrazine				
Glyphosate	0.67	−0.61	0.66	−0.63
Metolachlor				
Trifluralin	0.72		0.73	
Carbaryl				
Chlorpyrifos	−0.65		−0.65	
Dimethoate				
Malathion		0.75		0.74
Terbufos		0.86		0.86
Chlorothalonil				
Quintozene	0.72		0.73	
Sulfur	−0.60			
Eigenvalue	13.9	4.8	14.4	4.5
Proportion of total variance (%)	42.0	14.6	43.7	13.7
Cumulative variance (%)	42.0	56.6	43.7	57.4

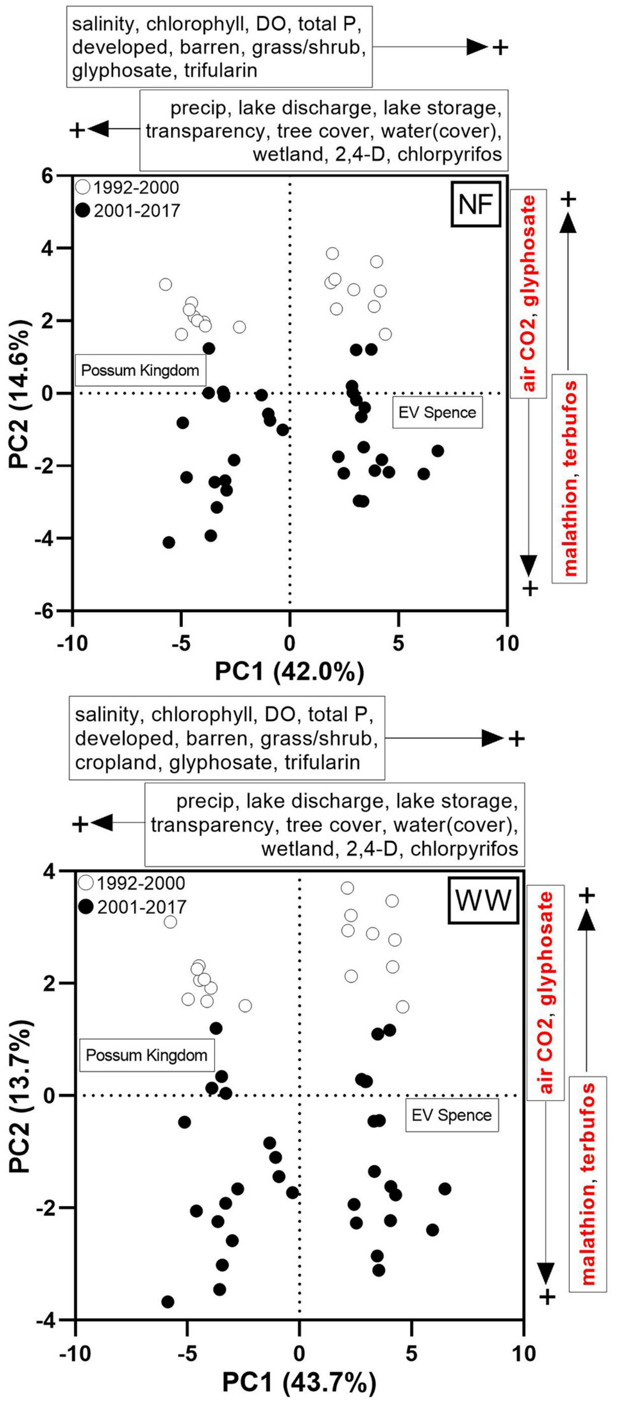

Fig. 2. Biplots of principal components (PC) 1 and 2 from analysis of environmental data for *Prymnesium parvum*-impacted reservoirs, Possum Kingdom Lake and E.V. Spence Reservoir in Texas (period of record, 1992–2017). Data are grouped according to time period before (1992–2000) and after (2001–2017) the first appearance of toxic blooms. NF, near field; WW, whole watershed; DO, dissolved oxygen, P, phosphorus.

Analysis of data from all four reservoirs (POR, 2001–2017) included a total of thirty-two variables (discharge was excluded from this analysis because it was unavailable for Twin Buttes) and resulted in the selection of four PCs in the NF and WW analyses. The original variables that contributed to each PC and the distribution of data in the biplots, however, varied between the NF and WW analysis (Tables 3, S8; Fig. 3). In the NF analysis, separation of impacted from reference reservoirs was primarily associated with PC2 for the Colorado River basin (E.V. Spence and Twin Buttes) and primarily with PC3 for the Brazos River basin (Possum Kingdom and Waco Lake) (Fig. 3). Salinity-associated variables (specific conductance, chloride, sulfate), chlorophyll, wetland cover, and several pesticides contributed to PC2, whereas storage, transparency, and barren areas contributed to PC3 (Table 3). The overall separation of impacted from reference reservoirs was therefore not based on a single PC but on the combination of PC2 and PC3 (Fig. 3). To facilitate visualization of the original variables that contributed to the separation of impacted from reference reservoirs in both basins combined, a polygon was traced around each of the two data groups and factor loading vectors that best separate the polygons were included in the biplot (Fig. 3; see Fig. S1 for the full vector plot). Inspection of the biplot indicated that the primary variables associated with the overall separation of impacted from reference reservoirs are salinity-associated variables (higher values in impacted reservoirs) and wetland area (lower values in impacted reservoirs) (Fig. 3). Principal component 1 was dominated by a number of land cover and pesticide variables and PC4 was driven primarily by air CO_2 (Table 3), but neither of these PCs individually or in combination with other PCs yielded information useful for addressing the study objectives.

Table 3
Principal component analysis of near-field and whole-watershed environmental data from all fours study reservoirs in Texas (period of record, 2001–2017). Factor loadings ≥ |0.6| are shown for variables in the first four principal components (PC) retained by the analysis. Eigenvalues and proportional and cumulative variance are also shown for each PC. See Table S8 for full listing of factor loadings.

Variable	Near field				Whole watershed			
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
Atmospheric CO_2				−0.88				−0.85
Air temperature								
Precipitation	0.68				−0.73			
Storage	0.62		−0.63		−0.66	−0.62		
Specific conductance		−0.81			0.66	−0.63		
Chloride		−0.76				−0.63		
Sulfate		−0.85			0.68	−0.60		
Dissolved oxygen								
pH								
Total phosphorus								
Chlorophyll		−0.67						
Transparency			−0.76			−0.75		
Barren			0.72					
Cropland	0.88						0.77	
Developed	0.79						0.79	
Grass/shrub	−0.94				0.80			
Tree cover	0.94				−0.80			
Water cover	0.71				−0.66	−0.70		
Wetland		0.83			−0.70	0.64		
2,4-D	0.88				−0.69			
Atrazine	0.85					0.62		
Glyphosate		−0.73			0.74			
Metolachlor	0.73							
Trifluralin		−0.79			0.83			
Carbaryl	0.90				−0.80			
Chlorpyrifos	0.81							
Dimethoate								
Malathion	0.68							0.80
Terbufos	0.81							
Chlorothalonil	0.79							
Quintozene		−0.69			0.72			
Sulfur	0.80							
Eigenvalue	11.7	5.9	3.6	2.2	9.1	4.8	3.8	3.0
Proportion of total variance (%)	36.6	18.3	11.3	6.8	28.6	15.1	11.9	9.3
Cumulative variance (%)	36.6	54.9	66.2	73.0	28.6	43.7	55.6	64.9

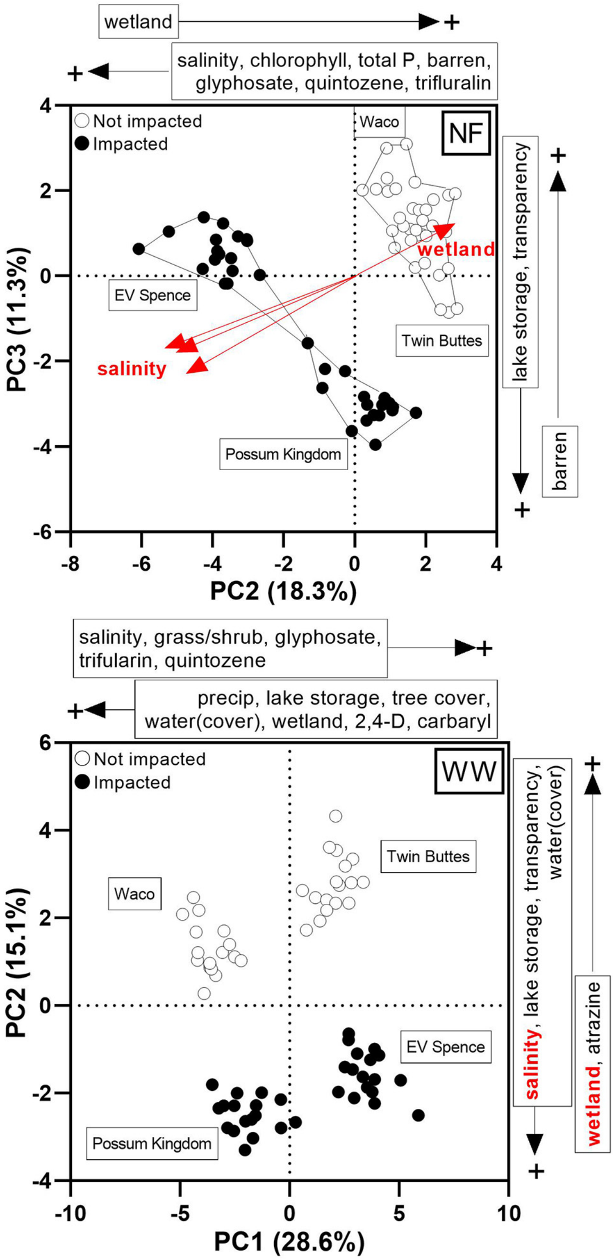

Fig. 3. Biplots of principal components (PC) 2 and 3 from near-field (NF) and PC 1 and 2 from whole-watershed (WW) analysis of environmental data for all study reservoirs in Texas (period of, 2001–2017). *Prymnesium parvum*-impacted reservoirs include Possum Kingdom Lake and E.V. Spence Reservoir, and reference reservoirs include Waco Lake and Twin Buttes Reservoir. Data are grouped by type of reservoir as *P. parvum*-impacted (Impacted) or reference (Not impacted). Polygons were traced around each group in the NF plot and factor loading vectors that best separate the polygons are shown (see also Fig. S1). The salinity vectors include specific conductance, chloride, and sulfate. P, phosphorus.

In the WW analysis of all four reservoirs, PC1 separated river basins and PC2 separated impacted from reference reservoirs (Fig. 3). The PC1-PC2 biplot thus provided clear separation of multivariate data by basin and by lake status (impacted vs reference). Notable differences between basins (PC1 axis) included lower values of precipitation, lake storage, water and wetland cover, and higher values of salinity in the Colorado River than the Brazos River (Fig. 3). Variables associated with PC2, which clearly separated impacted from reference reservoirs, included the same variables that separated reservoir groups in the NF analysis; namely, wetland area (higher values in reference reservoirs) and salinity-associated variables (higher values in impacted reservoirs) (Fig. 3). In addition, impacted reservoirs had higher levels of transparency and storage, and their watersheds had higher levels of water cover and lower application rates of Atrazine. The other two PCs did not associate with separation of basin or reservoir groups – PC3 was defined by cropland and developed areas and PC4 by air CO_2 and Malathion (Table 3).

Heat maps of trend coefficients for individual variables during the period between 1992 and 2017 showed that Glyphosate use increased, and Malathion and Terbufos use decreased at the WW and NF scales not only in the impacted-lake watersheds but also the reference watersheds (Fig. 4), and these trends were statistically significant (Tables S9–S12). Scatterplots of Glyphosate use in watersheds of impacted and reference reservoirs showed this herbicide was already in use since the early 1990s. However, a turning point for an upward trend was observed in the late 1990s to early 2000s at NF or WW scales in all watersheds, except the trend was of much lesser magnitude in the Twin Buttes reservoir, where a clear turning point was not observed until late in the POR (Fig. S2). Carbaryl showed a consistent negative trend in all watersheds at the NF or WW scales (Fig. 4) but was not statistically significant at the NF scale in the Twin Buttes watershed (Tables S9–S12). Trends for other pesticides were inconsistent or not statistically significant between the impacted-lake watersheds or among all watersheds (Fig. 4; Tables S9–S12). Wetland cover generally decreased in all watersheds at the NF and WW scales (Fig. 4), except the trend was not significant at the NF scale in the Possum Kingdom and Twin Buttes watersheds (Tables S9–S12). Water cover significantly decreased in watersheds of impacted reservoirs and at the NF scale in the watershed of Twin Buttes, but significantly increased at both scales in the Waco watershed (Fig. 4; Tables S9–S12). Cropland cover significantly decreased at the NF and WW scales in the E.V. Spence watershed but did not significantly change in the other watersheds at either scale (Fig. 4; Tables S9–S12); it should be noted, however, that Twin Buttes cropland cover at the NF scale was 3–4 times higher in 2017 than in the preceding

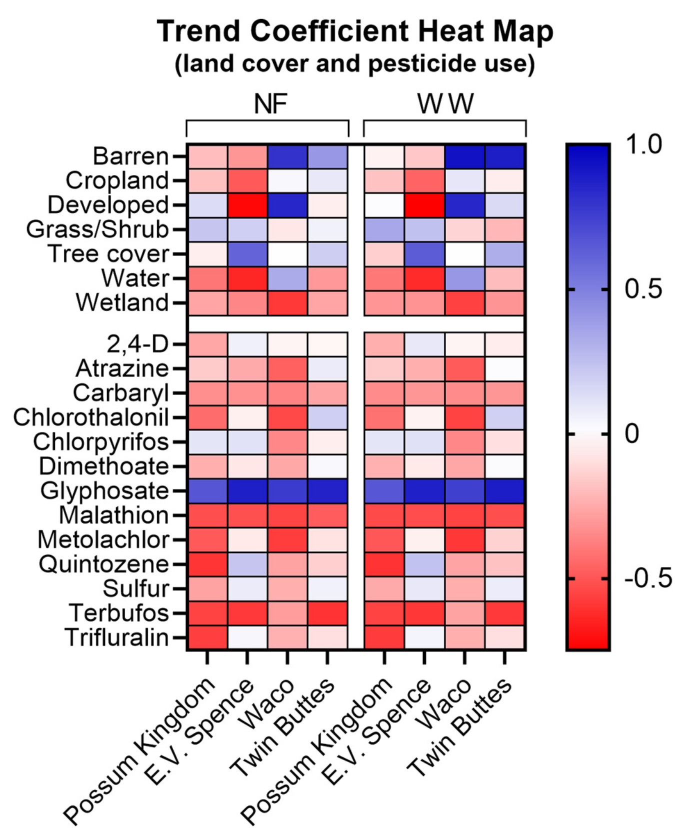

Fig. 4. Kendall Tau correlation coefficient heat map for land cover and pesticide use variables for all four study sites in Texas at the whole-watershed (WW) and near-field (NF) scales.

years (not shown), which at least partly explains why NF-corrected Glyphosate use increased considerably in 2017 (Fig. S2). Trends in the other land cover types were either not consistent between impacted sites or not significant (Fig. 4; Tables S9–S12). Among water variables, the only trend that was statistically significant and changing in the same direction (negative) in the two impacted reservoirs and in Twin Buttes was transparency (Fig. 5; Table S13). Other water quality trends were either changing in the opposite direction (chlorophyll) among impacted reservoirs or were not statistically significant (Fig. 5; Table S13). Air CO_2 showed a significant positive trend from 1992 to 2017 (Fig. 5; Table S13).

Summaries of descriptive statistics for all variables analyzed in this study are presented in Tables S14–S18.

4. Discussion

4.1. Environmental differences between the Brazos River and Colorado River basins

The Brazos River and Colorado River basins vary in their underlying geology, land cover and use, and climate. As expected from prior knowledge, differences between the two basins over the study watersheds were observed for precipitation (higher in the Brazos River; Dawson et al., 2015) and land cover patterns (different ecoregions; Elliott et al., 2014). When reservoirs within each group (i.e., impacted or reference) were separately compared between basins, some differences in water quantity (e.g., storage; respectively higher in Brazos River reservoirs) and quality (e.g., salinity; higher in Colorado River reservoirs) also were noted. In addition, some differences were observed between basins in the use of several agricultural pesticides (e.g., higher use of 2,4-D and Carbaryl in the Brazos watersheds and higher use of Glyphosate, Trifluralin, and Quintozene in the Colorado watersheds at the WW scales; Fig. 3). These landscape differences between basins are not directly relevant to the study objectives but they provide additional context to evaluate those variables associated with the first appearance and subsequent reoccurrence of *P. parvum* blooms

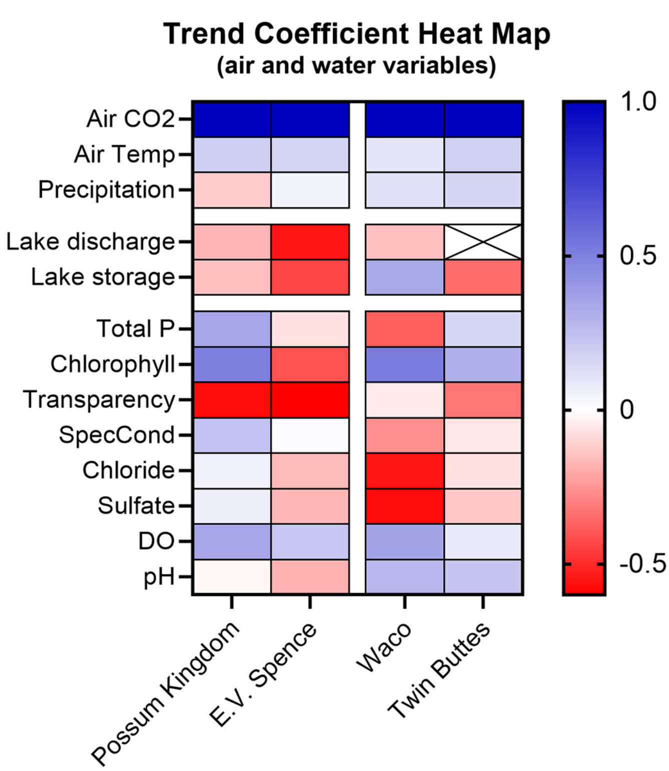

Fig. 5. Kendall Tau correlation coefficient heat map for air and water variables for all four study sites in Texas. P, phosphorus; DO, dissolved oxygen.

in impacted reservoirs (Objective 1) and with overall differences in environmental conditions between impacted and reference reservoirs (Objective 2).

4.2. Environmental variables associated with the first appearance of toxic P. parvum booms in impacted reservoirs

Associations among a total of thirty-three air, land, and water variables were examined for Possum Kingdom Lake (Brazos River) and E.V. Spence Reservoir (Colorado River) watersheds. The 26-year period of analysis (1992–2017) bracketed the year of first appearance of toxic blooms, 2001, which was then followed by a range expansion and bloom intensification over the next 10+ years (Roelke et al., 2016). Reports of fish-kill events seemed to decline in the 2010s, but toxic conditions linked to *P. parvum* continued to develop through the end of the study period (Table S1). Because of the temporal nature of the grouping variable for this analysis, results represent multivariate temporal trends. Air CO_2 was one of four variables that showed a strong temporal alignment with data group separation, and its alignment was positive. Although causal mechanisms cannot be ascertained from associational studies, there is experimental evidence indicating that bloom intensity in *P. parvum* (Rashel, 2020) – and also in the harmful cyanobacterium *Microcystis aeruginosa* (Verspagen et al., 2014) – can be enhanced by rising levels of atmospheric CO_2 within an environmentally relevant range. In nutrient-rich waters, intense algal blooms can cause the depletion of dissolved inorganic carbon, which consequently can become the growth-limiting nutrient. Under these conditions, higher levels of air CO_2 are likely to provide relief from carbon limitation and allow the formation of even denser blooms (Verspagen et al., 2014). Impacted reservoirs of this study are eutrophic/hypereutrophic (Patiño et al., 2014). Therefore, a role for increasing levels of air CO2 as a contributor to the intensification of *P. parvum* blooms during the first 10+ years since their first appearance seems plausible (Table S1). This proposed relationship, however, may not be linear before or after 2001. Variability in other conditions may also be at play. Alkalinity and nutrient (N, P) levels, for example, can influence the development of carbon limitation during blooms (Verspagen et al., 2014).

Three pesticides ranked equal or close to air CO_2 in their strength of alignment with temporal data separation at both NF and WW scales. They were the herbicide Glyphosate and the insecticides Terbufos and Malathion. The association was positive for Glyphosate and negative for the insecticides. Most herbicides (Halstead et al., 2014; Rumschlag et al., 2022) including Glyphosate (Smedbol et al., 2018) are generally toxic to algae. However, *P. parvum* is not only resistant to Glyphosate but its growth is enhanced by environmentally relevant concentrations of this herbicide (Dabney and Patiño, 2018). Notably, Glyphosate at low concentrations also enhances growth of *M. aeruginosa* (Zhang et al., 2016). Glyphosate has been commercially available in the USA since 1974 and its application rate increased dramatically after Glyphosate-tolerant crops became available in 1996 (Benbrook, 2016). In the impacted watersheds of the present study, Glyphosate was already in use for at least 10+ years prior to 2001 and upward trends were observed in the late 1990s (E.V. Spence watershed) or early 2000s (Possum Kingdom watershed). These trends coincide with the time when major range expansions and intensification of *P. parvum* blooms were observed in the south-central USA (Roelke et al., 2016). These observations are consistent with a scenario where the increased use of Glyphosate over the study POR (1992–2017), and especially since the turn of the century, may have contributed to the development of intense *P. parvum* blooms in impacted reservoirs.

Terbufos and Malathion can be directly toxic to some algal species (DeLorenzo et al., 2001; Rämö et al., 2016; Staley et al., 2015; Tien and Chen, 2012). A mesocosm study, however, found that these two insecticides indirectly caused phytoplankton abundance to increase, via their toxic effects on grazers (Rumschlag et al., 2022). Clarification of the relevance to *P. parvum* blooms of the decreased use of Terbufos and Malathion during the study period would require an understanding of their toxicity against this harmful alga. It should be noted that trend analysis confirmed the statistical significance and direction of change for the three pesticides during the study period – positive for Glyphosate and negative for the insecticides.

Variables that failed to meet interpretation criteria in the multivariate analysis but individually showed statistically significant and consistent trends (changing in same direction) in the two impacted reservoirs or their watersheds include use of the insecticide Carbaryl (negative trend), which can be toxic to algae (Rumschlag et al., 2022); water cover (negative trend) at NF and WW-scales and wetland at WW-scale, which may suggest a degree of watershed desertification during the study period; and water transparency (negative trend). The relevance of decreased transparency is difficult to interpret because our data are reported in annual scales and large fluctuations in transparency due to flooding (increased suspended material) or changes in algal biomass can occur at shorter, infra-annual scales. Transparency was not an important variable in the PCA and is not further discussed.

Changes in the aforementioned environmental conditions in impacted reservoirs and their watersheds were also generally observed in at least one of the reference sites, and rising levels of air CO_2 are a global phenomenon. Therefore, any scenario where these environmental changes are proposed to have contributed to the first appearance and reoccurrence of blooms in impacted reservoirs would also have to consider reasons why blooms have not occurred in reference reservoirs. This question was addressed by identifying environmental conditions that are exclusively found in impacted reservoirs and by exploring their potential association with *P. parvum*.

4.3. Environmental traits unique to P. parvum-impacted reservoirs

The primary variables that served to discriminate impacted from reference reservoirs were salinity-associated variables (specific conductance, chloride, sulfate) and wetland area at the NF scale, and they were also among the primary variables at the WW scale. Namely, impacted reservoirs were of higher salinity and their watersheds had smaller wetland areas both in proximity to their stream systems and over their entire watersheds. Salinity has been previously recognized as an important variable for *P. parvum* growth (Baker et al., 2007, 2009; Hambright et al., 2014; Rashel and Patiño, 2017). Thus, the higher salinity of impacted reservoirs may be among the most relevant of their unique traits that allowed the establishment of *P. parvum* blooms. This conclusion is consistent with that of an earlier retrospective field study that was based solely on an assessment of water quality variables (Patiño et al., 2014). Minimum levels for bloom occurrence in reservoirs of the Brazos and Colorado River basins are 0.5–0.6 psu (Patiño et al., 2014; Roelke et al., 2011), and in this study the average salinity values estimated from specific conductance (POR, 2001–2017) were above and below this threshold for impacted (Possum Kingdom Lake, 1.7 psu; E.V. Spence Reservoir, 2.5 psu) and reference (Waco Lake, 0.2 psu; Twin Buttes Reservoir, 0.4 psu) reservoirs, respectively. Also consistent with an earlier field study (Patiño et al., 2014) is the higher level of sulfate in impacted reservoirs, which suggests a role for this anion as a factor contributing to the establishment of toxic blooms independently of salinity (Rashel and Patiño, 2019).

The difference in wetland cover between reference and impacted study sites was substantial. In the Colorado River, the average wetland cover (2001–2017) in the reference site (Twin Buttes) was 28-times larger than in the impacted site (E.V. Spence) at the NF scale (1.42 vs 0.05%) and 17-times larger at the WW scale (0.66 vs 0.04%) (summarized in Table S19). In the Brazos River, wetland cover was 10- and 11-times larger in Waco Lake than Possum Kingdom Lake watersheds at the NF (4.37 vs 0.43%) and WW (2.34 vs 0.21%) scales, respectively. Wetlands can retain nutrients carried by stormwater runoff (Zedler, 2003), and previous studies describing negative associations between wetland cover and HAB occurrence (Bullerjahn et al., 2016; Ware, 2012) explained these associations primarily on the basis of nutrient loading. Most reservoirs within the present study region, however, are eutrophic or hypereutrophic regardless of *P. parvum*-impacts (Patiño et al., 2014). Also, total phosphorus concentration (annual averages) did not contribute to the separation of impacted from reference reservoirs. Therefore, the negative association between wetland cover and *P. parvum* distribution in the present study may not be due to the long-term differential effect of wetlands on reservoir nutrient loading. At smaller time scales, however, greatly reduced wetland cover could still influence the likelihood of *P. parvum* HAB formation in the impacted sites. Wetlands can capture nutrients (from runoff or during flooding) in near real time and therefore acutely influence nutrient loads at specific time points (Mitsch and Gosselink, 2000). Watersheds with smaller wetland areas would therefore generate stormwater runoff carrying relatively large amounts of nutrients, which in turn could enhance the risk of blooms if the precipitation event occurs at the appropriate time of the year. For example, a recent study of an impounded urban stream system reported a real-time association between a large flooding event at the beginning of the fall bloom season and the formation of a dense *P. parvum* bloom (Clayton et al., 2021).

Wetlands can also capture a wide variety of pesticides from agricultural runoff, including Glyphosate (Vymazal and Březinová, 2015). Although the application rate of Glyphosate also generally increased in reference watersheds during the study period (see also Section 4.2), their much larger wetland cover may retain correspondingly larger fractions of the herbicide compared to impacted reservoirs. Given Glyphosate's positive effect on *P. parvum* growth (see Section 4.2), the smaller wetland cover of impacted sites may have served a permissive or facilitatory role in the establishment of *P. parvum* blooms by allowing higher amounts of Glyphosate to reach the reservoirs. Validation of this scenario would require direct measurement of Glyphosate and its metabolites in the study reservoirs, as their absolute and relative concentrations depend on distance from the application sites (Medalie et al., 2020).

Multivariate analysis at the WW scale also showed a lower use of Atrazine in watersheds of impacted sites, but the relevance of this observation is uncertain because *P. parvum* seems to be resistant to this herbicide (Flood and Burkholder, 2018; Yates and Rogers, 2011). Also, while watershed water cover and lake storage were larger in impacted sites, these observations may be spurious as *P. parvum* blooms have been observed in water bodies far smaller than those of the present study (VanLandeghem et al., 2012; Clayton et al., 2021). Lastly, transparency was positively associated with impacted reservoirs (WW scale only) but as already noted (Section 4.2), in the present study the association of transparency with *P. parvum* is difficult to interpret.

5. Summary and conclusions

From a pool of thirty-three air, land, and water variables examined in a multivariate context, this study identified four that are strongly aligned in a temporal manner with the first appearance of *P. parvum* blooms in major reservoirs of the Southern Great Plains. Namely, air CO_2 concentration and agricultural use of the herbicide Glyphosate increased during a 26-year period bracketing the first appearance of toxic *P. parvum* blooms in 2001, and use of the insecticides Terbufos and Malathion decreased. Although there is insufficient information to judge the relevance of the decreased use of insecticides, prior experimental studies have found that increasing concentrations of air CO_2 (Rashel, 2020; Verspagen et al., 2014) and water Glyphosate (Dabney and Patiño, 2018; Zhang et al., 2016) can enhance growth of harmful algae, including *P. parvum*.

Salient differences between impacted and reference sites were the higher salinity and far smaller wetland cover of the former at both the NF and WW scales. The finding of higher salinity in impacted reservoirs is consistent with earlier observations about minimum salinity requirements for *P. parvum* bloom development in the study basins (Patiño et al., 2014; Roelke et al., 2011). However, the relevance of minimal wetland coverage to the establishment of *P. parvum* blooms in impacted sites may not be related to the watershed's decreased ability to retain nutrients (even if it occurred), as is generally assumed for HABs elsewhere (Bullerjahn et al., 2016). Reference reservoirs of the present study have been classified as eutrophic and are considered capable of supporting high algal biomasses

(Patiño et al., 2014). An alternative scenario suggested by this study is the decreased ability of wetland-deficient watersheds to retain other HAB-enhancing factors, such as Glyphosate.

In conclusion, results of this study are consistent with a scenario where the first occurrence and current distribution of toxic *P. parvum* blooms in reservoirs of the Southern Great Plains are the result of a combination of changing (driving) and long-existing (permissive) factors which together increased the risk of bloom establishment and recurrence. Driving factors may include the rising level of air CO_2 and increased use of Glyphosate. Individual associations between driving factors and *P. parvum* blooms may not be linear, however, as they could be influenced by various other conditions thus requiring that these associations be evaluated in multivariate context. Permissive factors may include relatively high reservoir salinity and greatly diminished wetland cover. Research needs suggested by this study include assessments of carbon deficiency during peak bloom conditions to confirm the likelihood of future intensification of *P. parvum* blooms due to the continuing rise in air CO_2 concentrations, and measurements of Glyphosate and its metabolites in reservoir environments to determine the level of exposure to this pesticide experienced by *P. parvum*. Studies of other reservoirs in the region and elsewhere would also be useful to evaluate the general applicability of the proposed scenario and to potentially reveal additional driving and permissive conditions.

CRediT authorship contribution statement

Shisbeth Tábora-Sarmiento: Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing - original draft, Writing - review and editing. **Reynaldo Patiño**: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Validation, Visualization, Writing - original draft, Writing - review and editing. **Carlos Portillo-Quintero**: Investigation, Methodology, Supervision, Visualization, Writing - review and editing. **Cade Coldren**: Investigation, Methodology, Writing - review and editing.

Declaration of competing interest

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.155567.

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