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Temporal and spatial variability of an invasive toxigenic protist in a North American subtropical reservoir

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ABSTRACT

The toxigenic marine flagellate *Prymnesium parvum* was first recorded in Lake Texoma, OK-TX, USA, an impoundment of the Red and Washita Rivers, following a massive fish kill in January 2004. Results of a 4.5-year monitoring program, spanning five bloom periods, revealed that *Prymnesium* abundances in the lake were temporally and spatially variable—densities were higher in winter, near-shore, and in Red River-associated sampling sites; the largest blooms were in Lebanon Pool, a large backwater basin often disconnected from the main reservoir. *Prymnesium* blooms appeared to have been fueled by high nutrient concentrations, and winter-spring densities were positively correlated with chlorophyll *a*, conductivity, total phosphorus, total nitrogen, and microzooplankton biomass, and negatively correlated with molar total nitrogen:total phosphorus and cladoceran and total crustacean zooplankton biomass. Comparison of *Prymnesium* densities with hydrological data suggested that *Prymnesium* blooms in Lebanon Pool were highest when the pool was disconnected from the main reservoir; no bloom occurred in the winter of 2004–2005, the only year since the 2003–2004 invasion in which Lebanon Pool and Lake Texoma were connected during the winter months.

1. Introduction

Harmful algae are those that can cause a variety of deleterious effects on aquatic ecosystems, including beach fouling, water oxygen deficiency, clogging of fish gills, or poisoning of various organisms (Granéli and Turner, 2006). Blooms of harmful algae (commonly referred to as HABs) are increasingly becoming a major impediment to the normal ecological and economical functioning of aquatic ecosystems world wide. For example, in coastal marine systems, blooms of *Pseudo-nitzschia* spp., *Alexandrium* spp., and *Karenia brevis* and their associated toxins (domoic acid, saxitoxin, and brevetoxin, respectively) have resulted in increasing numbers of cases of human shellfish poisoning, and blooms of *Pfiesteria* spp. and *Heterosigma* sp. have been linked to fish and bird mortalities (Burkholder, 1998; Granéli and Turner, 2006; Shumway et al., 2003). Such dramatic events are not usually associated with harmful algae in freshwater systems. Rather, freshwater harmful algae are most commonly cyanobacteria and generally are associated more with aesthetics and nuisance, creating surface scums and imparting bad tastes and odors to water (Paerl, 1988). Fish kills can result from cyanobacterial blooms, but these tend to be related more to oxygen depletion, rather than direct toxicity. Notable and increasingly common exceptions to the marine-freshwater HAB dichotomy are freshwater blooms of golden algae of the genus *Prymnesium*. Although generally confined to coastal marine systems, *Prymnesium*, particularly *P. parvum*, have created havoc in freshwater aquaculture ponds in Israel and China, and in coastal broads in England since the 1950s, 1960s, and 1970s, and is now rapidly becoming a growing threat in freshwater ecosystems in North America (Grover et al., 2007; Roelke et al., 2007).

Prymnesium parvum, hereafter *Prymnesium,* is a toxigenic marine haptophyte that has seemingly expanded its range into freshwater systems throughout the world (Edvardsen and Imai, 2006; Lutz-Carrillo et al., 2010). The first North American record of *Prymnesium* is from the 1980s in the Pecos River system of southern Texas (Baker et al., 2007). During the subsequent two decades, *Prymnesium* gradually expanded its distribution northward, reaching the Red River basin in 2001, the Canadian River basin in 2003, and Lake Texoma in 2004 (Watson, 2001). *Prymnesium* blooms and fish kills have also been reported as far eastward as North Carolina, and westward to Arizona (Texas Parks

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and Wildlife Department, 2009b). While this progression marks a relatively fast spread for an invasive species (Lockwood et al., 2007), its invasion per se or its simple occurrence in a given system is not the primary concern for lake and fisheries managers, environmentalists, or the general public. Moreover, given recent debate in ecology of the concept that "everything is everywhere, but, the environment selects," and the role of dispersal in community assembly (see de Wit and Bouvier, 2006), *Prymnesium* may not be invasive at all, but simply has shifted from being a rare to a dominant member of the plankton following environmental changes (Countway et al., 2005). Nevertheless, *Prymnesium*'s toxigenic nature, its ability to bloom (i.e., produce massive outgrowths) in newly invaded systems, and the typical outcome of these blooms – widespread and massive fish kills – are clearly the more pressing issues with respect to ecosystem health, water quality, recreational status of lakes, and even the economic wellbeing of communities dependent on lakes and reservoirs susceptible to *Prymnesium* outbreaks.

Though the continued range expansion of *Prymnesium* will depend ultimately on dispersal, to better understand conditions conducive to *Prymnesium* establishment and bloom formation, we have routinely monitored (weekly to monthly, during bloom and non-bloom periods, respectively) important physical, chemical, and biological variables at eight near-shore (littoral) and five open-channel (pelagic) stations extending from near the mouths of the Washita and Red Rivers to the Denison Dam. Here we describe the appearance and seasonal dynamics of *Prymnesium* in Lake Texoma over the course of four and a half years. Our data suggest that *Prymnesium* blooms are fueled by excessive nutrient loading to the lake, although bloom size within a given area in the lake seems to depend more on salinity and molar TN:TP.

2. Methods

2.1. Study site

Lake Texoma is a freshwater impoundment of the Red and Washita Rivers on the border of Texas and Oklahoma, USA (Fig. 1). The lake was constructed in 1944 to serve for flood control, hydropower generation, and recreation. At normal pool elevation, Lake Texoma is the 12th largest reservoir in the US with a surface area of 360 km^2, and mean and maximum depths of 8.7 and 26 m. The lake drains a watershed of 87,500 km^2 and is therefore highly susceptible to watershed influences (Thornton et al., 1990). The majority of the Lake Texoma's watershed lies in the high plains of Texas and the rolling plains of Texas and Oklahoma, regions containing rich deposits of calcium carbonate, halite, gypsum, anhydrite and other Permian-Salado evaporites (Ground and Groeger, 1994). As such, salinity is relatively high for fresh waters. During 1959–2008, specific conductance in Lake Texoma's discharge averaged (±SD) $1685 \pm 285\ \mu S\ cm^{-1}$ (United States Geological Survey, 2009). The watershed is also extensively agricultural and rural, although urban centers (e.g., Gainesville, Denison, and Sherman, TX and Ardmore, Madill, Kingston, and Durant, OK) and recreational facilities and resorts around the lake have grown considerably within the last few decades (Army Corps of Engineers-Tulsa District, 2009b).

Lake Texoma provides habitat for more than 50 fish species, many of which are recreationally important (Matthews et al., 2004). From 1965 to 1974, Lake Texoma was stocked with striped bass (*Morone saxatilis*) which have since established a self-sustaining reproductive population and supports a recreational striped bass fishery that generates tens of millions of dollars annually (Matthews et al., 1989; Schorr et al., 1995). A unique combination of high nutrient loading and turbidity, fisheries management, and sub-tropical seasonality has created a system containing a diverse array of daphniid zooplankton species co-occurring and/or alternating with a small cladoceran-copepod-rotifer assemblage more typical of lakes with high fish planktivory (Franks et al., 2001; Threlkeld, 1986; Work and Gophen, 1995). The phytoplankton assemblage is characterized by an abundant and diverse assemblage of chlorophytes, diatoms, and cyanobacteria, with summers often dominated by filamentous and colonial cyanobacteria and large chlorophytes.

2.2. Lake monitoring

Lake Texoma monitoring data reported here extend from the period of the first *Prymnesium* bloom (January 2004) through July 2008 and consists of data collected by several research groups. During 2004 (January–April), 2005 (January–December), and 2006 (January–April) sampling of littoral sites on the Oklahoma side of the lake was conducted by the South Central Regional Fisheries Division of the Oklahoma Department of Wildlife Conservation (live, refrigerated samples for *Prymnesium* counts; performed by J. Glass, Texas Parks and Wildlife Department, TPWD) and by the Water Quality Division of the Oklahoma Water Resources Board (surface deployments of a Hydrolab sonde that recorded water temperature, conductivity, dissolved oxygen, and pH). Beginning February 2006, monitoring was conducted by the research staff of the University of Oklahoma Biological Station. The sampling program (parameters sampled and sampling frequency) was designed to maximize information gained relative to the temporal and spatial features of the *Prymnesium* bloom: we monitored weekly during the winter months (the expected *Prymnesium* bloom period), bi-weekly in the spring and autumn, and monthly during summer; with higher sampling effort at near-shore (littoral) sites ($N = 8$) relative to open-water (pelagic) sites ($N = 5$). On average, we sampled 13 sites 32 times per year.

We sampled eight near-shore stations along the northern (Oklahoma) side of Lake Texoma (Fig. 1) in marinas and creek mouths, including L1-Wilson Creek, L2-Lebanon Pool, L3-Brier Creek, L4-Keeton Creek, L5-Buncombe Creek, L6-Soldier Creek, L7-Catfish Bay Marina, and L8-Johnson Creek. We also sampled five pelagic stations including P1-Red River, the upper Red River main channel south of Lebanon Pool, P2-Buncombe Creek, the Red River main channel between the mouths of Buncombe and Big Mineral Creeks, P3-Islands, the Red River main channel south of Treasure Island, P4-Denison Dam, the main basin adjacent to Denison Dam, and P5-Washita River, the Washita River main channel just south of the railway bridge.

Near-shore samples were taken in shallow (usually <1 m) waters, usually from boat ramps. Temperature, dissolved oxygen, chlorophyll *a* (a proxy for total algal biomass), and conductivity (a useful proxy for salinity) were measured *in situ* with either a YSI (6820 Multi-parameter Water Quality Monitor) or Hydrolab (H2O Submersible Water Quality Data Transmitter) sonde. Water samples (250 mL) were collected in Nalgene bottles, stored on ice in the field, and refrigerated in the laboratory for subsequent sub-sampling for phytoplankton and microzooplankton (protists and rotifers) enumeration, laboratory chlorophyll *a* analysis, pH, and nutrient chemistry. Crustacean zooplankton were collected by pouring 20 L of water through a 325-μm-mesh conical plankton net and preserving the filtrate in 4% sugar-formalin.

The five pelagic stations ranged in depth from 6 to 27 m. Depth, temperature, dissolved oxygen, chlorophyll *a*, and conductivity were measured with sondes as for near-shore stations, but at 1-m intervals. Water samples for phytoplankton, microzooplankton, chlorophyll *a*, pH, and water chemistry were taken as an integrated sample for the upper 10 m, (6 m for the upper Red River station), by lowering a weighted 19 mm (ID) flexible pipe to 10 m, closing the top end and hauling up the pipe with a rope attached to the lower

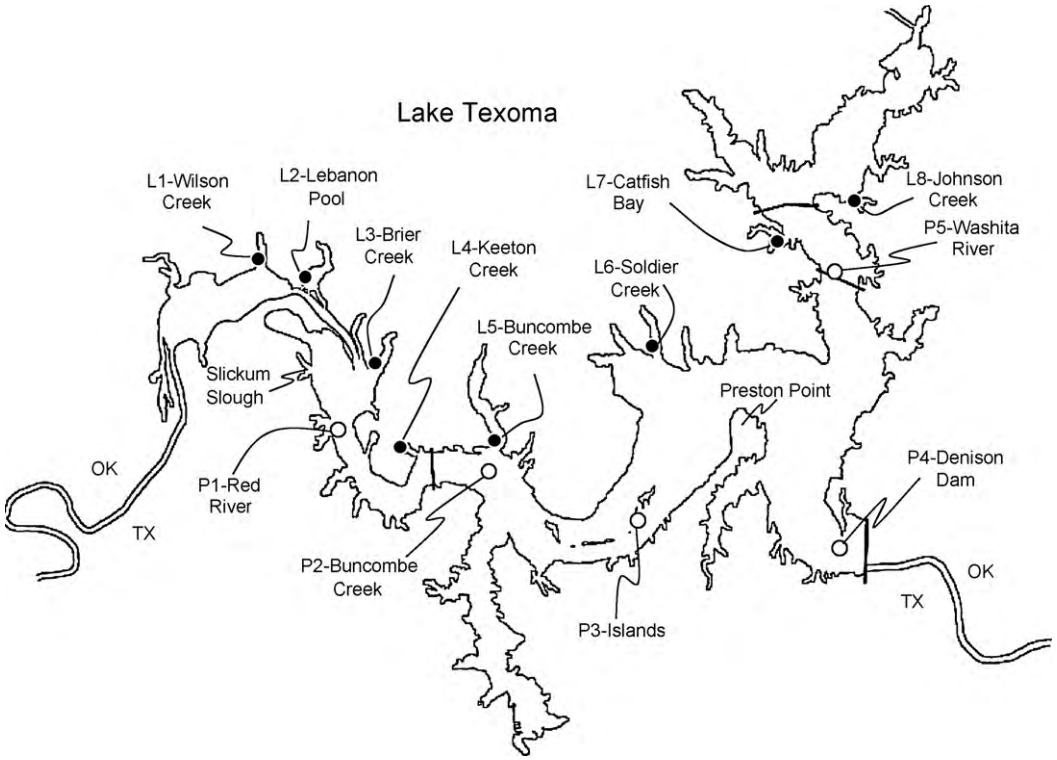

Fig. 1. Map of Lake Texoma showing littoral (solid circles) and pelagic (open circles) monitoring stations.

end. The 2 L of water collected were poured into a plastic beaker and a 250-mL sample was collected and stored on ice as above for littoral stations. Zooplankton samples were collected using vertical tows of the entire water column with a 325-μm-mesh conical plankton net and preserved as above for near-shore samples.

2.3. Laboratory procedures

In the laboratory, pH of the 250-mL water samples was measured with a VWR 8025 pH meter, and *in vivo* chlorophyll was measured (as a back-up and check for the field sonde) with a TD 700 bench-top fluorometer. The water samples were then subsampled and filtered (GF/F) for nutrient determinations by flow injection auto analysis (Lachat 8500 Quickchem FIA). Soluble reactive phosphate, ammonia, and nitrate were determined on filtered samples; total dissolved phosphorus and total dissolved nitrogen on filtered samples digested in acid (P) and alkaline (N) persulfate at 120 °C for 1 h; and total phosphorus and total nitrogen on unfiltered samples digested as above for total dissolved phosphorus and nitrogen.

Prymnesium (in whole unpreserved water samples) were counted immediately upon return to the laboratory on a haemocytometer (minimum of six subsamples) using a stereomicroscope with DIC Nomarsky illumination at 200–400× magnification. Additional analyses, made with selected samples using the Ütermohl sedimentation method and by flow cytometry (BD-FACSCalibur) were conducted in order to calibrate and optimize the haemocytometer method. Samples for phytoplankton and microzooplankton (50 mL) were preserved with Lugol's iodine solution (1% final concentration) for subsequent microscopic enumeration under an inverted microscope. Zooplankton samples were rinsed through a 100-μm-mesh net to remove Formalin and re-preserved using 70% ethanol and 1% glycerin in 20-mL glass scintillation vials for subsequent microscopic identification, counting, and measuring under a dissecting microscope.

2.4. Data analysis

To date we have compiled a 4.5-year (five *Prymnesium* bloom periods) data base for *Prymnesium* abundances from 4 January 2004 through 19 June 2008 for the littoral stations (104 sampling dates) and from 4 February 2006 to 19 June 2008 *Prymnesium* abundances and environmental conditions for littoral and pelagic stations (37 sampling dates). For the purposes of this report and to allow efficient presentation of important findings, all time series data were used to calculate monthly means for each station (and for the upper 10 m only, for pelagic stations) for the period January 2004 through June 2008. Regression and correlational statistics were analyzed with SPSS (v16).

3. Results

Prymnesium was first recorded in Lake Texoma during the winter of 2004 (January–March), following substantial fish kills in Lebanon Pool, an often isolated 61-ha lagoon on the northern (OK) side of the lake, and from Slickum Slough to Preston Point on the southern (TX) side of the lake (Fig. 1). Since then, *Prymnesium* has been recorded in Lake Texoma every year, and at least once at every station monitored (Table 1).

Toxicity and the extent of fish kills varied annually, with the most extensive kill occurring during 2004 (Oklahoma Department of Wildlife Conservation, 2009; Texas Parks and Wildlife Department, 2009a). There was no bloom or kill observed in 2005. The 2006 and 2007 blooms were primarily restricted to Lebanon Pool, although *Prymnesium* was observed throughout the lake, and minor fish kills occurred in Lebanon Pool and Buncombe Creek, as well as in several Texas sites. During 2008, the bloom in Lebanon Pool was the second largest bloom recorded and very similar to the 2006 bloom, with *Prymnesium* densities reaching 162,000 cells mL^{-1} and remaining above 100,000 cells mL^{-1} for nearly two months. However, unlike the 2006 bloom, the 2008 bloom did not appear to produce toxins.

Table 1
Maximum density of *Prymnesium* (cells mL^{-1}) and number of sampling dates present of total sampling dates (in parentheses) recorded at each sampling site in Lake Texoma during January 2004 through June 2008; n.d. = no data available.

Sample site	2004	2005	2006	2007	2008
L1-Wilson Creek	6,000 (2/5)	1,000 (1/8)	6,000 (10/20)	2,000 (10/25)	12,333 (6/18)
L2-Lebanon Pool	144,000 (5/6)	4,000 (2/8)	161,000 (12/20)	183,000 (22/28)	162,000 (24/27)
L3-Brier Creek	58,000 (5/6)	12,000 (2/8)	38,000 (13/20)	23,000 (17/24)	48,000 (15/18)
L4-Keeton Creek	18,000 (5/7)	1,000 (1/8)	10,000 (9/20)	10,000 (12/23)	4,333 (9/18)
L5-Buncombe Creek	22,000 (7/7)	6,000 (2/8)	7,000 (10/20)	45,000 (10/23)	3,667 (7/18)
L6-Soldier Creek	3,000 (3/7)	0 (0/8)	0 (0/20)	1,281 (6/23)	333 (1/18)
L7-Catfish Bay	1,000 (1/7)	0 (0/8)	1,000 (1/20)	563 (5/23)	0 (0/18)
L8-Johnson Creek	0 (0/6)	0 (0/8)	2,000 (2/20)	1,000 (4/23)	0 (0/18)
1P-Red River	n.d.	n.d.	6,500 (3/15)	5,000 (7/14)	9,000 (4/9)
2P-Buncombe Creek	n.d.	n.d.	1,000 (1/16)	2,000 (3/14)	5,000 (4/9)
3P-Islands	n.d.	n.d.	4,000 (1/15)	1,000 (4/13)	67 (2/9)
4P-Dennison Dam	n.d.	n.d.	0 (0/14)	1,000 (1/12)	0 (0/7)
5P-Railroad Bridge	n.d.	n.d.	0 (0/14)	1,000 (1/12)	0 (0/8)

No fish kills were observed there or at any other site around the lake. Laboratory fathead minnow toxicity bioassays throughout the bloom period confirmed the absence of toxicity.

Typically, but with the exception of 2004–2005 during which there was no bloom, the *Prymnesium* population began to increase in abundance in fall (October) when water temperatures dropped below 20 °C, peaked in February–March at temperatures between 10 and 15 °C, crashed in April–May when water temperatures exceeded 20 °C, and remained at very low densities during summer (June–September) (Fig. 2). The seasonal pattern of dissolved oxygen tracked temperature inversely at all stations, while most other chemical parameters monitored, such as conductivity, pH and nutrient concentrations, showed little seasonally-related patterns (Hambright, 2008). By contrast, and like *Prymnesium* abundances, most other biological parameters (e.g., chlorophyll *a*, zooplankton biomass) exhibited strong seasonality (Fig. 3). Crustacean zooplankton biomass was highest in winter-spring months, and in the littoral sites, comprised of roughly equal biomasses of cladocerans (mostly *Daphnia lumholtzi*, *D. parvula*, and *D. mendotae*) and copepods (*Eurytemora affinis*, *Diaptomus* sp. and various Cyclopoida). During the peak abundance of *Prymnesium*, *D. lumholtzi* became relatively rare and *D. parvula* and *D. mendotae* became more important contributors to total crustacean biomass. In pelagic sites, the spring crustacean biomass was predominantly in the form of the cladocerans *D. parvula* and *D. mendotae*. Summer and fall crustacean biomass was much lower. *Daphnia lumholtzi* was prevalent in the littoral sites, while cyclopoids and small cladocerans (predominantly *Bosmina longirostris*, *Ceriodaphnia cornuta*, and *Diaphanosoma birgei*) became important contributors to overall biomass in the summer pelagic assemblages. Microzooplankton (ciliated protists and rotifers), a minor component of total herbivorous zooplankton biomass throughout the year, except in late summer, exhibited mild seasonality, with peaks in biomass in winter (January–March) and summer (August–September). During July–August in the littoral sites and July in the pelagic sites, microzooplankton constituted 24–79% and 23%, respectively, of the total grazer biomass.

In addition to seasonality, most parameters, including *Prymnesium* abundances showed strong spatial variation which can be best observed in the winter mean and summer mean values (Figs. 4 and 5). Heavy blooms (>100,000 cells mL^{-1}; >90% of total phytoplankton assemblage) of *Prymnesium* were restricted to Lebanon Pool (L2), minor blooms (up to 50,000 cells mL^{-1}; 50–90% total phytoplankton) to Brier, Keeton, and Buncombe Creeks (L3,

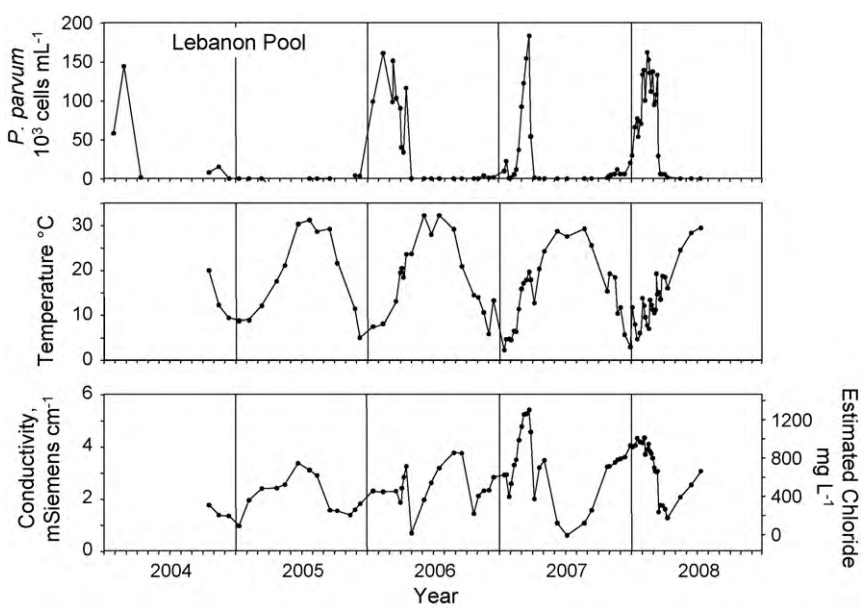

Fig. 2. Abundance of *Prymnesium*, water temperature, conductivity, and estimated chloride concentrations in Lake Texoma at the Lebanon Pool sampling site during 2004–2008. Chloride concentrations were estimated from conductivity according to the equation, Chloride, mg L^{-1} = 0.285 × specific conductivity, μS cm^{-1}) − 194, N = 193, r^2 = 0.995 (scanned figure 5.101 in, Atkinson et al., 1999). Although densities of *Prymnesium* were typically much lower in other littoral and pelagic sampling sites (see Fig. 4), the seasonal patterns in abundance were similar to the data shown above.

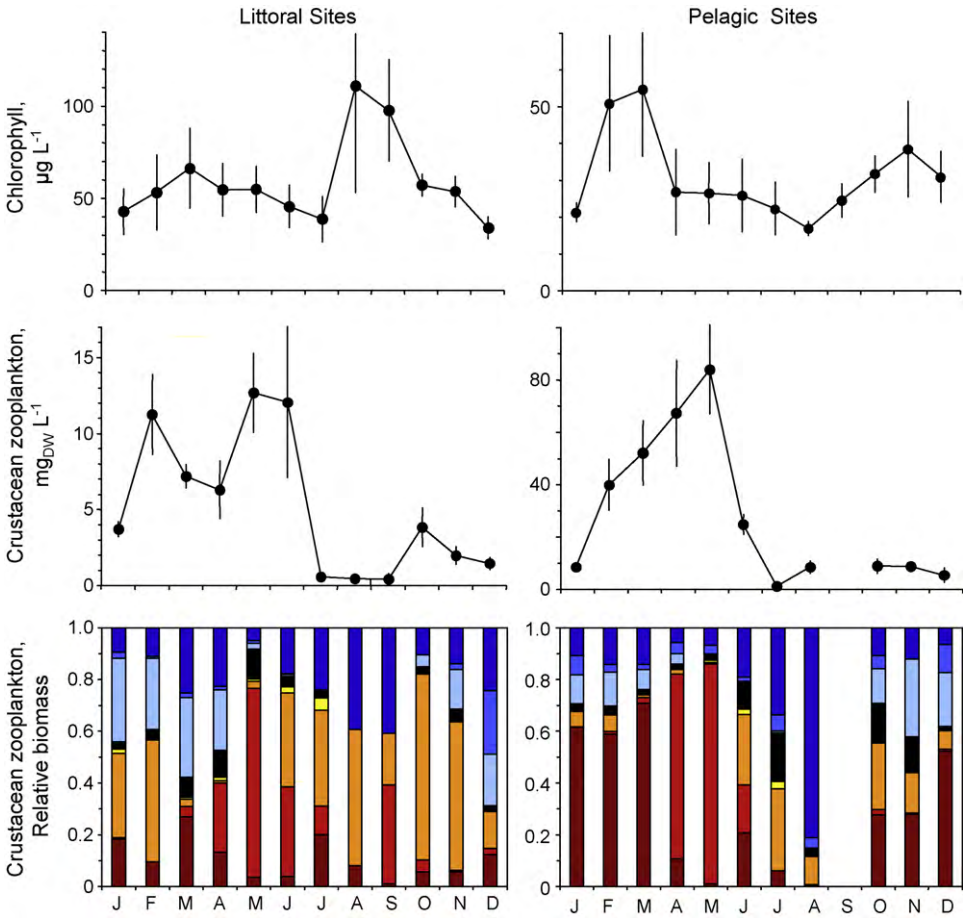

Fig. 3. Mean (±SE) monthly chlorophyll concentrations and crustacean zooplankton biomass and mean relative abundances of major crustacean taxa in the littoral (left-hand panels) and pelagic (right-hand panels) sampling sites of Lake Texoma during 2006–2008. *Daphnia parvula*, *D. mendotae*, *D. lumholtzi*, other *Daphnia*, small cladocerans, *Eurytemora affinis*, *Diaptomus* sp., cyclopoid copepods.

L4, and L5) and the pelagic Red River station (P1). Only trace or rare occurrences ($\leq$5000 cells mL^{-1}; other algae abundant) were recorded for Wilson, Soldier, and Johnson Creeks (L1, L6, L8), Catfish Bay (L7), and the pelagic Buncombe Creek, Islands, Denison Dam, and Washita River stations (P2–P5). Littoral stations on the Red River arm of the lake (Wilson Creek, Lebanon Pool, Brier Creek, and Keeton Creek; L1–L4) showed higher levels of salinity (i.e., higher conductivity) and trophic status (e.g., higher chlorophyll, phosphorus and nitrogen concentrations) compared with the littoral stations on the Washita arm of the lake (Catfish Bay,

Table 2
Correlation matrix (showing Pearson's *R* and probability *P*) for *Prymnesium* and various environmental and biological parameters in eight littoral and five pelagic stations during winters (January–April) of 2006–2008.

Parameter	Distance, W to E	ln(*Prymnesium* density + 1)	Conductivity	Chlorophyll	TN	TP	Molar TN:TP,	Clad. biomass	Crust. biomass
ln(*Prymnesium* density + 1)	−0.732**								
	<0.001								
Conductivity	−0.465**	0.660**							
	0.003	0.001							
Chlorophyll	−0.708**	0.664**	0.517**						
	<0.001	<0.001	0.001						
TN	−0.544**	0.393*	0.145	0.573**					
	<0.001	0.013	0.378	<0.001					
TP	−0.676**	0.580**	0.162	0.682**	0.825**				
	<0.001	<0.001	0.324	<0.001	<0.001				
Molar TN:TP	0.553**	−0.672**	−0.229	−0.436**	−0.385*	−0.659**			
	<0.001	<0.001	0.160	0.006	0.016	<0.001			
Cladoceran biomass	0.383*	−0.483**	−0.127	−0.303	−0.277	−0.445**			
	0.016	0.002	0.441	0.061	0.088	0.005			
Crustacean biomass	−0.380*	−0.445**	−0.079	−0.319*	−0.284	−0.456**	0.717**	0.990**	
	0.017	0.005	0.634	0.048	0.08	0.004	<0.001	<0.001	
Microzooplankton biomass	−0.666**	0.625**	0.579**	0.644**	0.356	0.685**	−0.653**	−0.394	−0.327
	<0.001	0.001	0.002	<0.001	0.074	<0.001	<0.001	0.046	0.103

Asterisks indicate that correlation is significant at the 0.05 level (*) or 0.01 (**) levels (2-tailed); all $N = 39$, except for microzooplankton biomass correlations, where $N = 26$.

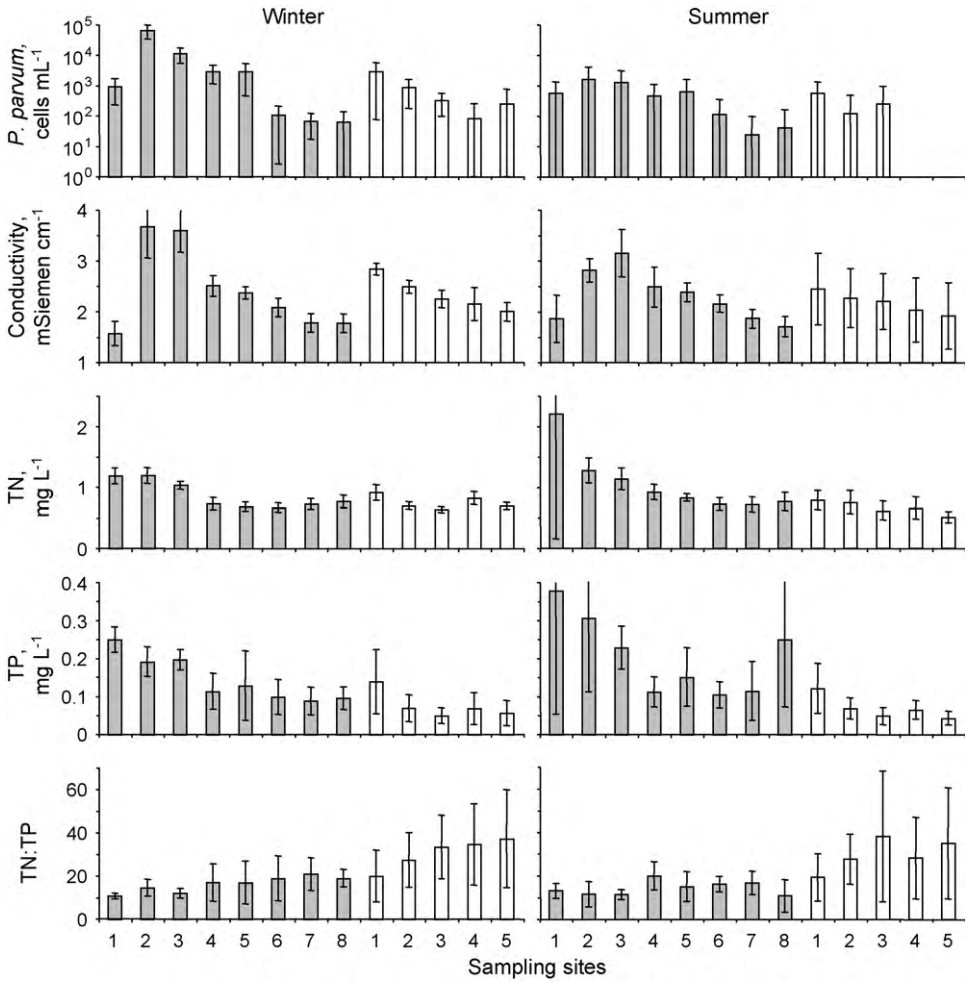

Fig. 4. Mean (±SE) winter (January–April; left-hand panels) and summer (May–December; right-hand panels) abundances of *Prymnesium*, conductivity, concentrations of TP and TN, and molar TN:TP for the eight littoral (gray bars) and five pelagic (open bars) sites in Lake Texoma during 2006–2008.

Johnson Creek; L7 and L8). High chlorophyll concentrations in winter often reflected high *Prymnesium* densities, but the late summer and fall peaks typically reflected high densities of colonial (*Microcystis* sp.) and filamentous (*Aphanizomenon* sp., *Anabaena* sp., *Cylindrospermopsis* sp.) cyanobacteria. Chlorophyll and nutrient concentrations were also relatively high in the pelagic stations, again indicating high trophic status, but were typically lower compared with concentrations in the littoral stations. The general trend of higher salinities, chlorophyll, and nutrient concentrations in the Red River arm versus the Washita River arm of the lake was similar to that seen in the littoral stations, though the magnitude of difference was lower. With a few exceptions (e.g., February and November, P3; November, P4 and P5), mean pelagic TN:TP molar ratios were typically well below 64:1, a value indicating ecosystem-level nitrogen limitation (e.g. Smith, 1983; Smith and Bennett, 1999). In the littoral stations, mean TN:TP molar ratios were always below 35:1, indicating even stronger nitrogen limitation. General nitrogen limitation in Lake Texoma is corroborated by frequent and persistant blooms of N_2-fixing cyanobacteria during much of the year (K.D.H., unpublished data). In general both crustacean zooplankton (cladocerans and calanoid and cyclopoid copepods) and microzooplankton (ciliates and rotifers) were more abundant in winter and spring months. Cladocerans and copepods were typically more abundant in pelagic sampling sites and microzooplankton more abundant in littoral sites. There was an apparent inverse relationship between microzooplankton and cladoceran and cyclopoid biomass.

Using means for winter-spring months (January–April) of all data monitored in 2006–2008, we detected strong correlations between most environmental and biological parameters (Table 2). Most notably, *Prymnesium* density (ln cells mL^{-1}) was positively correlated with conductivity, chlorophyll, total phosphorus and nitrogen, and microzooplankton biomass and negatively correlated with molar TN:TP, cladoceran and copepod biomass. Multiple

Table 3
Results from multiple regression analysis examining the effect of multiple independent variables (conductivity and molar TN:TP) on ln-transformed site-specific mean winter *Prymnesium* densities during 2006–2008.

Source	Sum of squares	df	Mean square	*F*	*P*
ANOVA					
Regression[a]	359.34	3	119.78	36.44	<0.001
Residual	115.06	35	3.29		
Total	474.40	38			
Model predictors	**Coefficient**	**Std. error**	**Std. Coef.**	***t***	***P***
Coefficients					
Constant	3.383	1.342		2.521	0.016
Conductivity	0.003	0.001	0.534	5.923	<0.001
TN:TP	−0.160	0.026	−0.550	−6.094	<0.001

Addition of chlorophyll (as a measure of total algal biomass and useful indicator for total nutrient availability) slightly improved the model ($R^2 = 0.737$). Addition of TN, TDN, TP, or TDP concentrations or cladoceran, crustacean, or microzooplankton biomass failed to improved the model.

[a] $R^2 = 0.722$ (adjusted $R^2 = 0.707$).

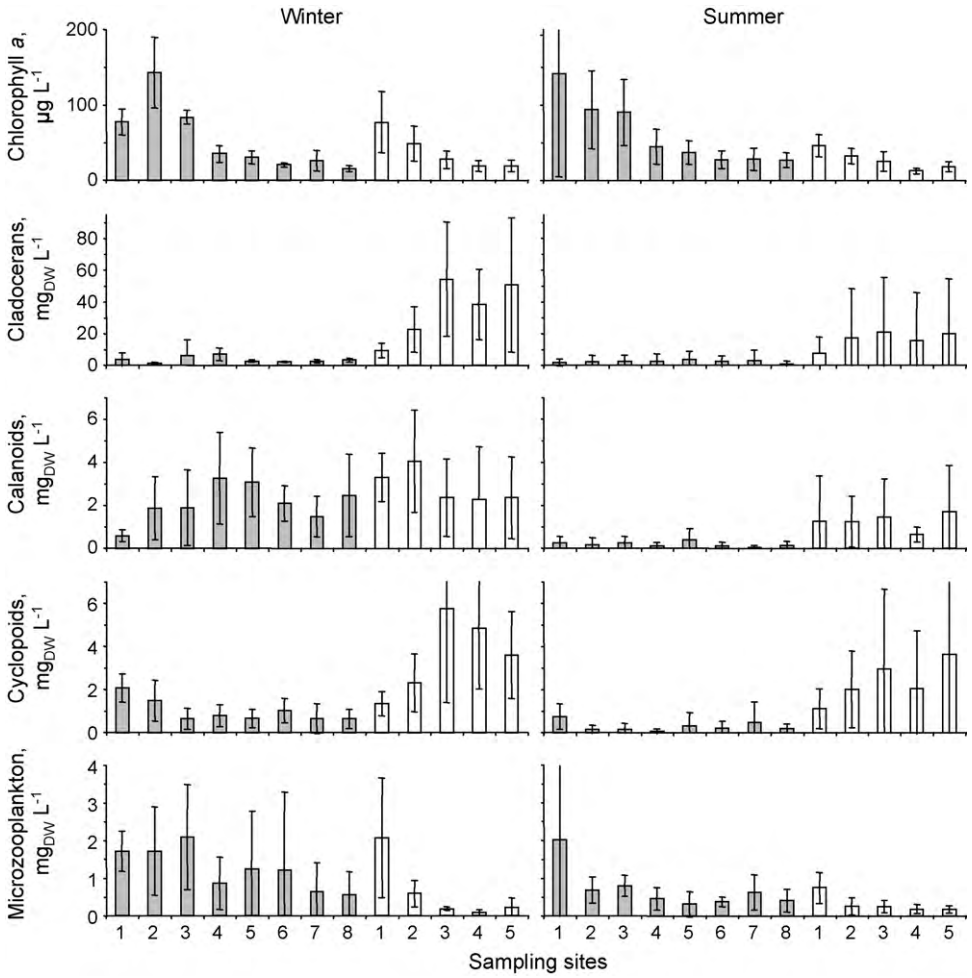

Fig. 5. Mean (±SE) winter (January–April) and summer (May–December) concentrations of chlorophyll, and biomasses of cladocerans, calanoid copepods, cyclopoid copepods, and microzooplankton for the eight littoral (gray bars) and five pelagic (open bars) sites in Lake Texoma during 2006–2008.

regression analysis found that the best model describing *Prymnesium* abundances during winter in Lake Texoma included conductivity and molar TN:TP (Table 3).

4. Discussion

Prymnesium parvum is an invasive, marine, mixotrophic haptophyte that has been responsible for fish kills in waters throughout the world since the early 20th century (Granéli and Turner, 2006; Lutz-Carrillo et al., 2010). *Prymnesium parvum* generally occurs in brackish inshore or coastal waters of temperate and tropical regions, with growth rates highest in moderate salinities (10–20 practical salinity units, psu; equiv. ~16,000–32,000 µS cm^{-1}) and relatively warm temperatures (20–30 °C) (Baker et al., 2007; Edvardsen and Imai, 2006). However, since appearing in North America, *Prymnesium* blooms more typically occur in relatively low salinities (<3 psu; equiv. ~4800 µS cm^{-1}) and during the winter at water temperatures ranging from 10 to 20 °C (Baker et al., 2007; Grover et al., 2007; Roelke et al., 2007). Lake Texoma is no exception—maximum conductivities were recorded in the Red River arm of the lake and ranged 830–3494 µS cm^{-1} in the pelagic stations and 318–8830 µS cm^{-1} in the littoral sites. Excluding three outliers recorded for Lebanon Pool (5230–5410 µS cm^{-1}) and one for Brier Creek (8830 µS cm^{-1}), conductivities remained below ~4500 µS cm^{-1}. Washita River-associated sites had lower conductivities, ranging 610–2711 and 376–2755 µS cm^{-1} in the pelagic and littoral sites, respectively.

Results thus far of the Lake Texoma monitoring program have revealed both predictable and stochastic patterns in *Prymnesium* dynamics in the lake. For example, as is obvious from anecdotal observation, *Prymnesium* blooms have so far been limited to the cooler winter months. Additionally, *Prymnesium* research in Texas (e.g. Baker et al., 2007), as well as globally (e.g., Guo et al., 1996; Holdway et al., 1978), has indicated that *Prymnesium* requires relatively high salinities (i.e., compared to more typical fresh waters). Such a requirement is logical given that *Prymnesium* in North America is believed to have originated from marine populations (Lutz-Carrillo et al., 2010). While, *Prymnesium* abundances have been typically higher in the Red River arm of the lake where salinities are generally higher than in the Washita River arm of the lake, there were no statistically significant relationships between *Prymnesium* abundance and salinity across the entire data set or within only the littoral stations where densities have been highest. However, in restricting the analysis to the bloom months of Jan–Apr, a significant relationship was revealed between *Prymnesium* abundances and salinities that suggests that *Prymnesium* bloom size may indeed scale with salinity. However, Wilson Creek (L1) generally had lower salinities than Soldier Creek (L6) or the two Washita River littoral stations, Catfish Bay and Johnson Creek (L7, L8) during the bloom season, but always had higher abundances of *Prymnesium* than those three stations. Thus salinity may be an important factor in *Prymnesium* occurrence and bloom size, but it is not likely the only, or even principal, factor involved, as multiple other significant correlations

were observed between *Prymnesium* abundances and various environmental parameters. Moreover, the best predictor of *Prymnesium* abundance was a multiple regression model including molar TN:TP. The model was slightly improved (R^2 = 0.737) with the addition of chlorophyll (as a measure of total algal biomass and useful indicator for total nutrient availability). It is not surprising that *Prymnesium* abundances might be predicted by total chlorophyll given that the two parameters are not independent (i.e., chlorophyll would be expected to be high during a *Prymnesium* bloom). However, there is some utility to the relationship–specifically, that it demonstrates that other taxa do not bloom even when nutrients are exceedingly high. The predicted role of TN:TP in *Prymnesium* blooms is somewhat unexpected, given that TN:TP is more typically invoked to explain dominance and blooms of N_2-fixing cyanobacteria (e.g., Smith, 1983; Smith and Bennett, 1999). However, we suspect that low N:P environments may give *Prymnesium* a competitive edge over its competitors, as well as its predators. Several studies have shown that haemolytic activity, allelopathic toxicity to other algae, and toxicity to brine shrimp are higher in P- or N-deficient cultures of *P. parvum* (Granéli and Johansson, 2003; Johansson and Granéli, 1999; Uronen et al., 2005). However, simultaneous manipulation of N, P and N:P in these studies, confounds any interpretation of the role of N:P. Using cultures of *P. parvum* grown in chemostat with similar P availabilities, but differing N availabilities, we have found a strong relationship between toxicity (as measured in standard LC_{50} bioassays with fathead minnows, *Pimephales promelas*) and N:P of the culture medium, with highest toxicities observed in cultures with low N:P supplies compared with cultures grown under higher N:P availabilities (K.D.H., unpublished).

Both nitrogen and phosphorus levels in Lake Texoma are very high. According to Wetzel (2001), lakes with total phosphorus concentrations between 30 and 100 $\mu g\ L^{-1}$ are considered to be eutrophic and those exceeding 100 $\mu g\ L^{-1}$ are considered to be hypertrophic. Lake Texoma littoral stations, particularly those in the western, Red River-associated arm of the lake, typically have total phosphorus concentrations in excess of 100 $\mu g\ L^{-1}$, and can often approach 1000 $\mu g\ L^{-1}$. Nitrogen levels are also extremely high in these stations, with TN always exceeding 0.5 mg L^{-1}, and often exceeding 1.0 mg L^{-1}. Pelagic nutrient concentrations are also high, with TP concentrations >30 $\mu g\ L^{-1}$ and TN > 0.5 mg L^{-1} in most pelagic stations; TP often exceeded 100 $\mu g\ L^{-1}$ in the P1-Red River station. Thus Lake Texoma ranges between eutrophic and hypertrophic. High nutrient concentrations are prerequisites for algal blooms, regardless of species (Reynolds, 1997), and in the case of Lake Texoma in which TN:TP ratios are quite low, for cyanobacterial blooms. Indeed, colonial *Microcystis*, and filamentous *Anabaena*, *Aphanizomenon*, and *Cylindrospermopsis* are commonly abundant in the lake, particularly in late summer and fall (K.D.H., unpublished data). Since the first *Prymnesium* bloom in the winter of 2003–2004, we only have nutrient chemistry and salinity data available for the winters of 2005–2006 through 2007–2008. In those three winter-spring periods, we have only seen *Prymnesium* blooms and/or fish kills in sampling sites in which TP has exceeded 0.1 mg L^{-1}, molar TN:TP has been below 25, and conductivity has been above 2000 $\mu S\ cm^{-1}$ (i.e., Lebanon Pool, Brier Creek, Keeton Creek, and Buncombe Creek; L2–L5). Thus it appears that extremely high nutrient levels with a relatively low N:P, in addition to relatively high salinities, are the primary agents behind the *Prymnesium* blooms and subsequent fish kills.

Little data are available comparing *Prymnesium* abundances to zooplankton. Our results thus far indicate that both cladoceran and copepod populations are negatively affected by *Prymnesium*, presumably due to toxicity, while microzooplankton populations are enhanced, possibly due to the reductions in crustaceans, the major predators and competitors with protist and rotifer assemblages (Gilbert, 1989; Hansen, 2000). Preliminary experimentation has revealed that while daphniid zooplankton readily consume *Prymnesium* with little acute toxicity effects, there are severe long-term life history consequences including reductions in juvenile growth rates, fecundity, and survivorship (E.J.R., unpublished).

The winter 2003–2004 *Prymnesium* bloom extended from Lebanon Pool and Slickum Slough in the west eastward to Preston Point, but the 2005–2006, 2006–2007, and 2007–2008 blooms were limited to Lebanon Pool, with relatively low abundances and only minor fish kills in other areas of the lake. Thus Lebanon Pool seems to foster *Prymnesium* more than other areas of the lake. Interestingly, Lebanon Pool and Brier Creek have similar high winter conductivities, but Wilson and Brier Creeks have higher phosphorus levels during the winter, suggesting again the relative roles of salinity and nutrients are not clear (i.e., there is not one set of predictors for *Prymnesium* abundance across the lake). There is, however, one aspect of Lebanon Pool that does appear related to the lack of a *Prymnesium* bloom in winter 2004–2005—its seasonal isolation from the main lake body.

Lebanon Pool is separated from Lake Texoma by a sandbar that has been deposited over the past 60+ years by the Red River. Two channels connect Lebanon Pool to the main reservoir (a southeastern channel representing the original channel of Hauni Creek which was flooded by the initial Red/Washita River impoundment and a southwestern channel cut through the sandbar during flood events). Because Lake Texoma is used primarily for downstream flood control by the US Army Corps of Engineers, the lake undergoes fluctuations of 1–3 m during any given year, with maximum fluctuations of nearly 7 m possible in some years (e.g., 2007) (Fig. 6). Anecdotal evidence and observation suggest that water flows downstream in the Hauni Creek-Lebanon Pool system when Lake Texoma water levels (measured at

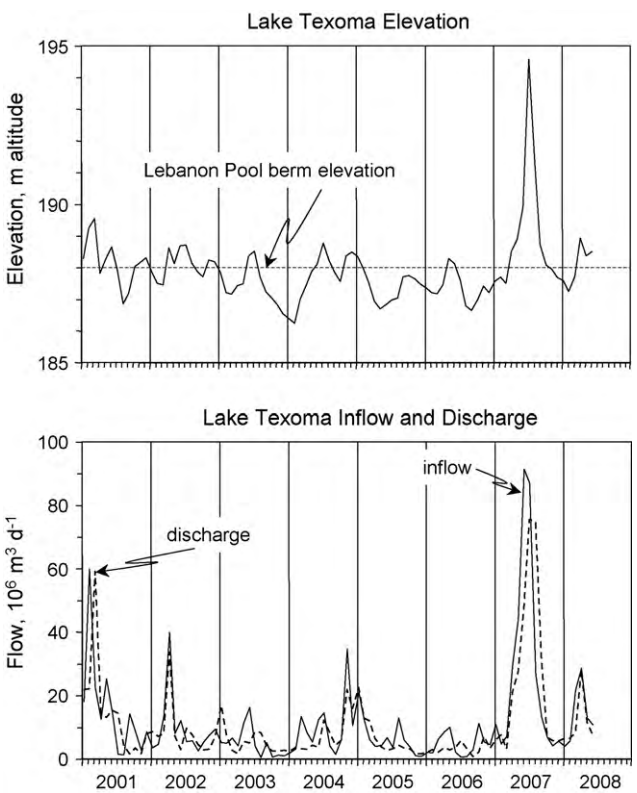

Fig. 6. Mean monthly Lake Texoma water levels (meters elevation at the Denison dam) and inflows and discharges ($10^6\ m^3\ d^{-1}$) during 2001–2008 (Army Corps of Engineers-Tulsa District, 2009a).

the Denison dam) are below 188 m altitude, but that at higher water levels, water can flow from Lake Texoma into Lebanon Pool (i.e., Lebanon Pool becomes part of Lake Texoma), suggesting that the current elevation of the isolating sandbar is approximately 188 m altitude. Examination of the hydrological data for Lake Texoma reveals that the winter of 2004–2005 was the only winter period between 2003–2004 and 2007–2008 in which the elevation of Lake Texoma exceeded 188 m altitude at the beginning of the bloom season. Interestingly, even though *Prymnesium* presence has been recorded upstream in the Red River basin since 2001, the first bloom in Lake Texoma was not recorded until the winter of 2003–2004. In other words, the Lebanon Pool blooms of *Prymnesium* occurred when Lebanon Pool was relatively isolated from Lake Texoma (winter of 2003–2004, 2005–2006, 2006–2007, and 2007–2008), while no blooms occurred during the winters that Lebanon Pool was not isolated from Lake Texoma (2000–2001, 2001–2002, 2002–2003, 2004–2005). While this does not provide a direct causative agent for the blooms (for example, *Prymnesium* occurred in other less-isolated sampling site during the bloom years), it does suggest that some factor related to high winter water elevation may have been important in preventing the development of *Prymnesium* blooms, particularly in the winter of 2004–2005. Unfortunately we have no environmental data available from the 2004–2005 winter, but given that salinity and nutrient concentrations during 2006–2008 in Red River (P1) were typically lower than those in Lebanon Pool (L2), it is possible that Lebanon Pool salinity and nutrient concentrations were reduced by dilution when the pool was connected to Lake Texoma, thereby preventing a *Prymnesium* bloom. The high water levels of winter 2004–2005 were related to increased inflowing waters following heavy precipitation in the watershed, suggesting that advective losses to the *Prymnesium* population could also be a factor involved in bloom prevention that year. Kaartvedt et al. (1991) suggested that *Prymnesium* blooms in Norwegian fjords may be favored during times of relatively low currents that resulted in increased residence time of brackish waters in the fjords and reduced advective losses (e.g., see Pace et al., 1992) to the *Prymnesium* population. Roelke et al. (2010) suggest advective losses also play an important role in the termination of the *Prymnesium* bloom in Lake Granbury, a large meandering river-like reservoir in Texas, USA. Its mobility would afford *Prymnesium* a competitive advantage in still, poorly mixed waters (i.e., a structured environment), while high turbulence, mixing, and advection (i.e., a non-structured environment) would be expected to benefit other phytoplankters (Chao and Levin, 1981; Reynolds, 1984). Indeed, such physical stresses like high advective losses may explain, in part, the relatively low abundances of *Prymnesium* in pelagic stations, even though salinities and nutrient concentrations can be quite high. Unfortunately, the high water levels and inundation of Lebanon Pool in 2004–2005 were not due to operation of the Denison Dam by the Army Corps of Engineers, but instead were related to the amount of inflowing waters (a parameter generally outside human control). Nevertheless, increased winter water levels or a deepening of the Lebanon Pool outlet channels, may be issues worth exploring for possible future *Prymnesium* bloom control in Lebanon Pool.

There still remain the questions of whether *Prymnesium* has long been present or only recently invaded and established a population in Lake Texoma; will *Prymnesium* continue to bloom and cause fish kills in the western, Red River-associated areas of the lake and will it continue to remain restricted to these areas; are downstream waterbodies in danger of future blooms; and will *Prymnesium* continue to spread northward into other drainage basins? Toward addressing the first of these questions, we are presently developing molecular tools for detecting and quantifying *Prymnesium* (R.M.Z., unpublished) and are planning to collect a series of sediment cores throughout the lake that will be used to establish a chronology of *Prymnesium* presence in the lake. We are also examining longer-term water quality in the lake in order to discern any possible trends in salinity or nutrients that may have factored into the recent *Prymnesium* blooms. Preliminary analyses of US Geological Survey data from the outflow of Lake Texoma, suggest little change in lake salinity over the past four decades, but there appears to have been long-term increases in TP and subsequent decreases in TN:TP—two factors that our present analysis suggest are important in bloom formation (K.D.H. unpublished). Answers to the remainder of the questions are less obvious and certainly not readily available at this point. However, experience gained from the study of *Prymnesium* blooms in Texas (e.g., see Watson, 2001), as well as the study of invasive species in general (Lockwood et al., 2007), suggests that *Prymnesium* is likely now a permanent resident of Lake Texoma and will likely expand its distribution downstream, as well as into adjacent watersheds.

Reservoirs provide essential services to human populations worldwide, including principally, increased flood control, electricity, and availability of water and fisheries resources, but also the enhancement of the quality of life through increased recreational and aesthetic values. Reservoirs can also serve as critical stepping stones or hubs for range expansion of invasive and often highly destructive species (Johnson et al., 2008). We here documented the temporal and spatial dynamics of an invasive and highly destructive protist species in a south-central US reservoir. Lake Texoma serves vitally important services to the surrounding area, including, but not limited to, flood control, power generation, recreational fisheries, and boating. A predominant service of Lake Texoma revolves around the self-sustaining, inland striped bass fishery, the loss of which could amount to tens of millions of dollars annually to the region (see Schorr et al., 1995). More importantly continued and increasing eutrophication stands to adversely affect countless ecological, economic, and social services provided by Lake Texoma. While we are unable to definitively pinpoint the cause of *Prymnesium* blooms in Lake Texoma, it is clear that these blooms, just like any other algal bloom, are made possible by excessive nutrient availabilities. Reductions in nutrient loading to Lake Texoma are predicted to lessen the threat of future *Prymnesium* blooms.

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