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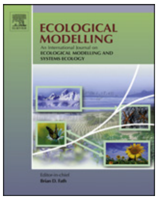

# Modeling of plankton community dynamics characterized by algal toxicity and allelopathy: A focus on historical *Prymnesium parvum* blooms in a Texas reservoir

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ABSTRACT

A model is formulated to explore the dynamics of the harmful alga *Prymnesium parvum*, in a reservoir typical of those in the south-central U.S. where fish-killing blooms of this species frequently occur. Based on a previous model of growth in a well-mixed system, *P. parvum* competes for nutrients with cyanobacteria, which also excrete allelopathic cyanotoxin(s) that inhibit the growth of *P. parvum*. A new feature added here is a population of small-bodied zooplankton grazing on both types of algae, with the grazing rate on *P. parvum* inhibited by dissolved toxin(s) excreted by this species. In contrast to previous models that did not produce convincing calibrations, the new model is successfully calibrated using one year of forcing data on hydraulic flow, water temperature, salinity and nutrient supply from Lake Granbury, Texas. The calibrated model successfully reproduces the seasonal dynamics of *P. parvum*. Both allelopathy from cyanobacteria and toxic inhibition of grazers are necessary for fitting the calibration data, and produce dynamics in which blooms of *P. parvum* occur at low temperatures, below those optimal for growth. Long-term historical simulations of the new, calibrated model predict the observed occurrence of *P. parvum* blooms in cool weather, and suggest that low water flows during the late 1980s and early 2000s predisposed reservoirs to having such blooms. Respectively, these time periods correspond to the first known fish kills due to *P. parvum* in Texas, and to a series of annually recurrent blooms in several reservoirs.

## 1. Introduction

Harmful algal blooms (HABs) have been characterized as increasing in many coastal and inland waters (Hallegraeff, 1993). Associated impacts include disruption of food webs and ecosystem functions (Sunda et al., 2006), contamination of human food supplies and other health effects (Van Dolah, 2000), and poisoning of wildlife and fish (Bricelj and Lonsdale, 1997; Turner and Tester, 1997). One species particularly associated with fish kills and food web disruption is *Prymnesium parvum* (Brooks et al., 2011; Edvardsen and Imai, 2006). This unicellular, haptophyte flagellate has caused numerous HABs in coastal and brackish inland waters (Edvardsen and Paasche, 1998; Johnsen et al., 2010; Southard et al., 2010), is lethal to fish and has toxic effects on many other aquatic organisms (Brooks et al., 2010; Manning and La Claire, 2010).

A scientific consensus has not emerged regarding causes of HABs. Connections to eutrophication involve increases in nutrient supply and possibly, changes in supply ratios of different nutrients (Cloern, 2001; Heisler et al., 2008; Smayda, 1989; Smith et al., 1999). Climate change may have recently rendered some locations suitable for invasion and proliferation of harmful species from elsewhere (Briand et al., 2004; Hallegraeff, 2010; Paerl and Huisman, 2008), which might be further facilitated by transport due to shipping, aquaculture and other human activities (Hallegraeff and Gollasch, 2006; Lutz-Carillo et al., 2010). Altered flow regimes appear to be an aspect of climate change particularly important to bloom formation in some inland waters (Mitrovic et al., 2011; Roelke et al., in press, 2011). Mathematical modeling can help untangle the complex factors affecting HABs, and provide insight that can guide mitigation and management.

Mathematical modeling of algal dynamics is a mature subject in theoretical ecology (e.g. Andersen, 1997; Lehman et al., 1975) and water quality research and management (Chapra, 1997; Thomann and Mueller, 1987). Historically, much of this modeling has been directed at eutrophication and aimed at understanding total algal biomass in relation to nutrient supply. Effort has also been devoted to understanding dominance by particular higher taxa of algae, such as cyanobacteria, green algae, or diatoms. Modeling of HABs

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grows out of this tradition, but must address dynamics of particular species, rather than or in addition to dynamics of total biomass or higher taxa (e.g. Hood et al., 2006). A number of processes usually absent from conventional eutrophication models must often be represented, including production and degradation of toxins, allelopathy, zooplankton grazing and its inhibition by toxins produced by other organisms.

Nevertheless, conventional eutrophication models are a point of departure for HAB models, which share a common ecophysiological kernel representing the reproductive growth of algae as a function of nutrients and other environmental factors. For the ecophysiological kernel, much information is available from laboratory experiments to assign functions and parameters for diverse taxa of algae (Bowie et al., 1985; Grover, 1989). Fortunately, there are many studies that provide suitable information on *P. parvum* (Baker et al., 2007, 2009; Larsen et al., 1993; Larsen and Bryant, 1998).

To date, only a small number of published models address *P. parvum*. Some of these (Chakraborty et al., 2008; Grover et al., 2011; Martines et al., 2009) aim primarily at theoretical understanding, focusing on particular processes while neglecting others, and do not attempt site-specific calibrations or simulations of observed blooms. Only one study attempts to calibrate more comprehensive, many-parameter models to bloom dynamics in a natural habitat (Grover et al., 2010). Convincing fits to one year of calibration data from Lake Granbury, Texas, were not obtained, because models predicted population minima for *P. parvum* during winter, a time of year when the maximal populations were observed. This failure did not appear to be a shortcoming of the ecophysiological kernel of the models, because the same mathematical functions successfully predicted population dynamics over the shorter time scale of about a month during a hydraulic flushing event (Roelke et al., 2010a).

Here, we extend one of the models considered previously for Lake Granbury, in which *P. parvum* competes for nitrogen and phosphorus with another population of algae, taken as a proxy for a diverse community dominated by cyanobacteria. The cyanobacteria also produce allelopathic toxin(s) that inhibits the growth of *P. parvum*, as suggested by experimental studies (James et al., 2011a; Roelke et al., 2010b). This model originally included mortality of *P. parvum* and cyanobacteria due to zooplankton grazing at a rate determined by observational data on zooplankton abundance. Here, the description of grazing mortality is altered by adding a dynamically coupled zooplankton population, as is commonly done in theoretical models of plankton systems (e.g. Andersen, 1997; Grover, 2002; Litchman et al., 2006). The grazing rate is determined by zooplankton abundance and their functional response of ingestion rate to algal population density. The mortality that *P. parvum* suffers due to grazing is also reduced by its production of toxin(s) that inhibit zooplankton activity (Granéli and Johansson, 2003; Remmel et al., 2011; Sopanen et al., 2006). We find that the extended model can be more successfully calibrated to data from the same field site (Lake Granbury). Further exploration shows that the new representation of grazing inhibited by toxins of *P. parvum* is essential to successful calibration, as are representations of competition and allelopathy between *P. parvum* and cyanobacteria. The calibrated model predicts the occurrence and seasonality of historical blooms of *P. parvum* in a reservoir representative of those in the south-central U.S. where such blooms are problematic. The calibrated model also agrees with observations that low hydraulic flow raises the risk of such blooms.

## 2. Field site

This study focuses on Lake Granbury, Texas (97.8°W, 32.4°N), a reservoir built in 1969 with an elongated, sinuous basin 45 km long, an average width of 0.6 km, and an area of 3378 ha. The volume is $167.4 \times 10^6$ m$^3$, with a mean depth of 4.98 m. The shoreline follows the meandering channel of the Brazos River, oriented northwest to southeast. About half (47%) of the shoreline has residential, commercial or industrial land use. Most of the remaining shoreline is agricultural, consisting of croplands, pastures and rangelands. Annual average rainfall in the lake's watershed is 88 cm year$^{-1}$, but seasonal and interannual variation is high. The headwaters of the Brazos River are in a more arid climate (<20 cm year$^{-1}$), and the river is brackish from upstream through Lake Granbury, for at least another 100 km as it passes into a more humid climate (>120 cm year$^{-1}$). There are large, interannual variations in salinity, which has ranged from <0.5 to about 3 during the period 2001–2010 (Roelke et al., 2011).

The brackish inland waters of western Texas experienced their first confirmed, fish-killing bloom of *P. parvum* in 1985 (James and De La Cruz, 1989). In the late 1980s and 1990s, blooms occurred in upstream reaches of the Brazos River (Southard et al., 2010), but did not occur in larger reservoirs on this river, such as Lake Granbury until the winter of 2000–2001 (Roelke et al., 2011). From 2001 to 2007, blooms recurred annually during cooler months, with varying degrees of toxicity to fish, while *P. parvum* blooms occurred in an increasing number of river basins and reservoirs in Texas (Southard et al., 2010). From 2007 to 2010, blooms in several reservoirs on the Brazos River, including Lake Granbury, were absent or of lower magnitude than during 2001–2007. The interannual variations in *P. parvum* abundance that occurred from 2001 to 2010 have been attributed to changes in river flow and salinity, with blooms likely when flow is under, and salinity over, particular thresholds that vary from lake to lake (Roelke et al., 2011). Projected reductions of flow due to ongoing climate change are likely to make Lake Granbury more susceptible to blooms of *P. parvum* in the future (Roelke et al., in press).

The frequency of data collection varied during the decade of recurring *P. parvum* blooms in Lake Granbury. Observations of blooms are anecdotal until 2003, when monitoring by various agencies commenced (Roelke et al., 2011). A systematic schedule of monthly monitoring at ten fixed locations in the main reservoir body began in August of 2006. The first year of these data documented a large, fish-killing bloom through the winter of 2006–2007 that was terminated by a high flow event (Roelke et al., 2010a). It also provided data used to develop and calibrate models of *P. parvum* dynamics (Grover et al., 2010), and a similar approach was taken in this study.

## 3. Model formulation

The model examined here extends an earlier model constructed to describe the dynamics of *P. parvum* in a reservoir (designated PP1A in Grover et al., 2010). Notation follows and extends that of the earlier work (Table 1). For simplicity, the model treats the reservoir as a continuously stirred tank reactor or chemostat. Blooms of *P. parvum* in Lake Granbury are not spatially uniform, but patch sizes range 1–6 km suggesting relatively strong mixing over large scales. Two dissolved nutrients potentially limit the population growth of *P. parvum* and one other algal population, assumed to represent cyanobacteria. Growth of these algal populations also depends on temperature, salinity and light. The cyanobacteria excrete dissolved cyanotoxin(s) that inhibits the growth of *P. parvum*. New features added to the model for this study include grazing on both types of algae by a dynamically growing zooplankton population, excretion of dissolved toxin(s) by *P. parvum*, and inhibition of grazing on this species by the toxin(s) (Fig. 1). Governing equations are

$$\frac{dZ}{dt} = D(Z_{\text{in}} - Z) + \mu_Z Z - m_Z Z \tag{1a}$$