COMPARATIVE POPULATION DYNAMICS OF FRESHWATER DINOFLAGELLATES OF THE GENERA *PERIDINIUM* AND *PERIDINIOPSIS*

by

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A thesis submitted to the faculty of The University of Mississippi in partial fulfillment of the requirements of the Sally McDonnell Barksdale Honors College.

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Freshwater dinoflagellates, like their marine relatives, have the potential to reach large population sizes known as blooms. Though they are not toxic like some marine forms, freshwater blooms may have a large impact in their respective ecosystem. This study investigated the temporal and spatial changes in population density of four *Peridinium* species (*P. deflandrei, P. volzii, P. wisconsinense, and P. limbatum*) and one *Peridiniopsis* species (*Peridiniopsis polonicium*) in Boondoggle Lake, a shallow lake (4.5 m) in northern Mississippi (Lafayette Co.). On each sampling date, measurements of the abiotic environment were made, including dissolved oxygen, temperature, pH, and turbidity. Also, water samples were taken from three depths: 0.25 m, 1 m, and 2 m. Estimates of total dinoflagellate density were made by enumeration of concentrated samples on LM slides. Individual species were identified using SEM, and estimates of the relative abundance of each species were made at the SEM, which allowed estimates of the actual densities of each species to be made. One species, *P. deflandrei*, was by far the most dominant in the summer bloom (90% of the total dinoflagellate population) and reached a maximum population density of $2.75 \times 10^5$ cells/ L. *P. volzii* was the most abundant species in the spring and late fall, with its maximum density being $5.7 \times 10^4$ cells/ L. The other
three species had temporal patterns similar to either *P. deflandrei* or *P. volzii* but never comprised more than 25% of the total dinoflagellate population. *P. limbatum* reached maximum densities in the spring and fall, similar to *P. volzii*. *P. wisconsinense* and *Peridiniopsis polonicium* reached maximum densities in the summer, similar to *P. deflandrei*. The species composition and population density of dinoflagellates in Boondoggle Lake are determined by many environmental factors. Those that are likely to be most important include low nutrient levels, an acidic pH (5.5-6.5), warm temperatures, summer anoxia, wind protection, and interspecific competition.
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Section 1: General Introduction

1.1 Overview of Dinoflagellates

Dinoflagellates are a monophyletic group of single-celled eukaryotes that could originally be found in the classification schemes of both zoologists and botanists. Although they share cellular features with members of both the plant and animal kingdom, they are now believed to be most closely related to either photosynthetic protists or protozoa (Carty 2003). Molecular evidence suggests they branched from the eukaryotic lineage early in the evolution of eukaryotes (Herzog 1986). At present, approximately 2000 extant species of dinoflagellates have been identified (Pfiester and Anderson 1987).

The most extensive studies of dinoflagellates have been in marine environments due to their important ecological roles and potential detrimental effects on marine biota as well as humans. Blooms of marine dinoflagellates known as red tides have the potential to cause fish kills, and dinoflagellate toxins, which are produced only by marine forms, can cause human illnesses such as toxic shellfish poisoning and ciguatera (Graham and Wilcox 2000).

Freshwater dinoflagellates, although not as dangerous to humans, can have an equally large role in their respective ecosystems. Freshwater blooms of the genera *Ceratium* and *Peridinium* have been documented in numerous lakes (Moore 1981; Pollingher and Hickel 1991; Stewart and Blinn 1976; Whiting et. al. 1978; Wu and Chou...
Certain *Peridinium* blooms have been known to reach high enough population densities to be labeled as freshwater “red tides.” One such red tide was documented in Clear Lake, California, where *Peridinium pernardii* reached densities of $5 \times 10^6$ cells/L (Horne, et. al. 1971). Another freshwater bloom of *Peridinium* with densities reaching $10^{-93} \times 10^6$ cells/L occurred in an oligotrophic reservoir near Tokyo in 1975 (Nakomoto 1975). A bloom of *Peridiniopsis polonica* was responsible for fish kills in Lake Sagami near Tokyo, one of the few cases of a toxic freshwater dinoflagellate bloom (Hashimoto, et. al. 1968).

Below, I review the basic biology of dinoflagellates, including morphology, classification, nutrition, life history, and ecology. This review focuses on motile freshwater armored dinoflagellates and the two genera that were investigated in this study, *Peridinium* and *Peridiniopsis*.

1.2 Morphology and Classification

Freshwater dinoflagellate species show diverse patterns of morphology. They are loosely grouped in the categories of thecate (armored) and athecate (naked), depending on the presence or absence of sub-membranous cellulose plates. If present, the collection of plates is known as the theca (Taylor 1987). The two genera of focus in this study, *Peridinium* and *Peridiniopsis*, are thecate genera. A diagram of a freshwater armored dinoflagellate is shown in Figure 1.1. The view is of the ventral side. Important features to note are the cingulum (girdle), sulcus, flagella, epitheca, hypotheca, and sutures. One flagellum lies in the transverse groove known as the cingulum (also girdle). The other is found in the longitudinal groove, the sulcus.
Figure 1.1: Key morphological features of freshwater armored dinoflagellates (Modified after Lefevré 1932)
The epitheca and hypotheca refer to the collection of thecal plates above and below the cingulum respectively. The ridges where thecal plates meet are known as sutures (Taylor 1987). Classification of freshwater armored dinoflagellates is based on the arrangement and number of the thecal plates (Carty 1986).

1.3 Nutrition

Dinoflagellates are also diverse in their modes of nutrition. Autotrophic, auxotrophic, mixotrophic, and heterotrophic forms have been documented (Carty 2003, Holt and Pfiester 1981). Only six freshwater species have been documented as completely autotrophic, meaning they require no organic substances for growth in the light. Four of these are species from the genus *Peridinium*: *P. cinctum* f. *ovoplanum*, *P. inconspicuum*, *P. volzii*, and *P. willei* (Gaines and Elbrächter 1987). Many photosynthetic dinoflagellates require vitamins for growth (auxotrophy). There are only three vitamins that are known to be required by auxotrophic algae: B$_{12}$, thiamine, and biotin (Graham and Wilcox 2000), and dinoflagellates have been shown to require one, two, or all three of these vitamins for growth (Gaines and Elbrächter 1987). Pure heterotrophs (living exclusively on organic compounds) comprise approximately half of all dinoflagellates. In freshwater systems, photosynthetic species dominate, but heterotrophic benthic species are not uncommon (Gaines and Elbrächter 1987).

1.4 Life History

An important characteristic of the motile freshwater dinoflagellate life cycle is the alternation between a swimming, vegetative form and a resting stage known as a cyst.
Cyst formation is associated with most sexually reproducing forms and occurs after a zygote ceases to be motile and forms a thick cell wall. Encystment is believed to be an adaptation for surviving environmental stress, and it usually occurs in conjunction with specific environmental conditions (Pollingher 1988). Some of the possible environmental factors that can lead to encystment include temperature, nutrient depletion, light intensity, and changes in concentration of dissolved gasses. Of these, nutrient depletion of nitrogen has been best demonstrated to induce encystment in cultures (Pfiester and Anderson 1987). Sexual reproduction followed by encystment was shown to be induced by nitrogen depletion in cultures of four *Peridinium* species: *Peridinium cinctum, Peridinium willei, Peridinium gatunense, and Peridinium volzii* (Pfiester 1975; Pfiester 1976; Pfiester 1977; Pfiester and Skvarla 1979).

Dinoflagellates undergo asexual reproduction and sometimes sexual reproduction depending on the species and environmental conditions. The vegetative (also called assimilative) stage of freshwater armored dinoflagellates is haploid and divides asexually through mitosis (Pfiester and Anderson 1987). Cells increase their size before dividing, which is accomplished by expanding the theca at the sutures between thecal plates. These expanded areas are referred to as intercalary bands (Taylor 1987).

Sexual reproduction begins when the haploid vegetative stage forms gametes through mitosis. Gametes then fuse to form a planozygote. The planozygote is motile, with two longitudinal flagella, and can remain motile to continue cell growth (Pfiester and Anderson 1987). Planozygotes accomplish cell enlargement in the same manner as vegetative cells by expansion at the sutures between thecal plates (Pfiester and Skvarla 1980). Formation of a hypnozygote occurs when the planozygote loses motility and
forms a thick cell wall. Hypnozygotes rest on the lake bottom until conditions are right for excystment, at which time vegetative cells are returned to the water column. Meiosis must occur between formation of the planozygote and excystment of the hypnozygote, and when it occurs varies among taxa.

The causes and mechanisms of sexual reproduction have been studied in only 22 of all 2000 dinoflagellate species (Pfiester and Anderson 1987). As previously mentioned, many environmental factors are thought to induce sexual reproduction and subsequent encystment. In previous studies of freshwater dinoflagellates, environmental cues have been shown to influence the emergence of vegetative cells from resting stages (Pfiester and Anderson 1987; Kawabata and Ohto 1989; Anderson et al. 1987).

Life history traits are an important deterministic component of the population dynamics and ecology of dinoflagellates because reproductive strategies influence temporal and spatial patterns in dinoflagellate abundance. Figure 1.2 shows the basic sexual and asexual life cycle of freshwater armored dinoflagellates.

1.5 Ecology

Dinoflagellates usually reach their maximum population size in the summer months. Though they are usually found in low numbers, some species may form large blooms given the correct environmental conditions. Members of the genera Ceratium and Peridinium are well studied bloom formers (Carty 2003; Pollingher 1988). The population ecology of freshwater dinoflagellates is widely thought to be influenced by many bottom-up and top-down control factors. Bottom-up factors include pH, temperature, organic matter, inorganic ions (Ca, Cl, N, P), light intensity, vitamins, and
Figure 1.2: Basic life cycle of sexually reproducing freshwater armored dinoflagellates (Modified after Carty 2003)
inoculum from cysts. Top-down factors include predation, disease, life history traits (cyst formation), lake outflow, and turbulence (Carty 2003; Pollingher 1988; Popovsky and Pfiester 1990). The effects of bottom-up and top-down factors on patterns of freshwater dinoflagellate abundance have been investigated in many studies. A brief review of the well-studied control factors is now presented.

Lake pH has been demonstrated to influence the growth rate of freshwater dinoflagellates. However, the effect of pH on growth rate is variable across species. In the genus *Peridinium*, studies of laboratory cultures have shown species with maximum growth occurring at a pH ranging from 5.5 (*P. limbatum*) to 8 (*P. cinctum*), and one species, *Peridinium inconspicuum*, showed little change in growth rate over a range of 5.5-8.5 (Holt 1981; Pollingher 1988).

The influence of temperature on freshwater dinoflagellate populations is only a general trend. Most dinoflagellates show maximum growth during the summer, but there is a wide tolerance range for temperature. That is, dinoflagellates are not strong stenotherms (Carty 2003; Pollingher 1988). Though most freshwater dinoflagellates form cysts during the winter, some have been found in the water column throughout an entire year. These include *Peridinium bipes* and *Peridinium willei* (Pollingher 1988).

Freshwater dinoflagellates are not tolerant of oxygen stress. Low oxygen levels can cause *Peridinium cinctum* fa. *Westii* to shed its flagella, shed its theca, and become immobile. Insufficient oxygen has also been shown to induce encystment in *Peridinium* species from Lake Kinneret (Pollingher 1987). *In situ* observations of *Peridinium* in Lake Kinneret and *Ceratium* in Esthwaite Water have revealed that these freshwater
dinoflagellates are rarely, if ever, found in anoxic hypolimnic waters (Pollingher 1988; Harris et. al. 1979).

The concentrations of inorganic nutrients, particularly nitrogen and phosphorus, are important in determining the growth of dinoflagellates. Freshwater dinoflagellates are generally more abundant relative to other algal taxa when nutrients are low. It is thought that the resilience of dinoflagellates under low nutrient conditions along with reduced competition from other algae is largely responsible for their summer success in nutrient poor systems (Pollingher 1987; Pfiester 1971). Mechanisms for tolerance of low nutrient levels have been studied. These include luxury consumption of phosphorus, long generation times, and vertical migration to obtain nutrients (Heany and Eppley 1981; Carty 2003; Pollingher 1988). As mentioned earlier, low nitrogen levels may contribute to sexual reproduction and encystment of freshwater dinoflagellates (Pfiester and Anderson 1987; Pfiester 1975, 1976, 1977; Pfiester and Skvarla 1979).

Usually, photosynthetic dinoflagellates prefer abundant light and are concentrated in the upper layers of the water column (Pollingher 1987). Their motility makes them able to move to an optimal depth for photosynthesis as well as nutrients. Dinoflagellates have been shown to undergo vertical diel migrations, which are thought to be most influenced by light, temperature, and nutrient availability. However, these migrations are frequently variable for different species (Heany and Eppley 1981). One study of vertical migration in Ceratium hirudinella suggests that a compromise between light availability from the surface and nutrients concentrated at depth will determine the depth where maximum densities of dinoflagellates will occur (Heany and Furnass 1980). Irradiation
is important not only in how productive dinoflagellates will be but also where they will be found in the water column.

The role of top-down factors in the population ecology of freshwater dinoflagellates also has been investigated, but to a lesser extent. Measurements of physiological death of *Peridinium* in Lake Kinneret showed a decrease of 8-10% during exponential growth and 40-80% at the end of the summer bloom (Serruya et al. 1975). Large freshwater dinoflagellates, such as some species of *Peridinium and Ceratium*, are subject to grazing only by certain species of rotifers and in some cases, fish. Parasitism by chytrid fungi has been documented in *Peridinium* (Pollingher 1988). Other factors contributing to loss include turbulence, which was associated with a 62.5% death rate in continuously shaken *Peridinium* cultures (Pollingher and Zemel 1981), and lake outflow, which was observed to remove $7.65 \times 10^{13}$ dinoflagellate cells/ day from a lake population (Heany and Talling 1980).

1.6 This Study

The objective of this study was to describe the population dynamics of the freshwater armored dinoflagellates in Boondoggle Lake (Oxford, Mississippi). This objective was accomplished by collecting physical and chemical data from the lake, identifying the species of freshwater armored dinoflagellates present, and estimating population densities of dinoflagellates throughout the study period.

There is a paucity of information on the ecology and distribution of freshwater dinoflagellates. This study will provide some of the much needed information on the dinoflagellates in Mississippi.
Section 2: Materials and Methods

2.1 Sampling site and surrounding area

Boondoggle Lake is a man-made lake located approximately 10 miles east of Oxford, MS on the edge of Holly Springs National Forest and is approximately 70 yrs old. The lake has an elevation roughly 120 m above sea level and is surrounded by mixed bottomland forest on all sides. It is about 1.5 hectares in surface area and has a maximum depth of approximately 4.5 m. It undergoes one major period of stratification in the summer and has been observed to go through a mixing and restratification in the fall after intense rain. The lake experiences anoxia in the summer that may begin as high as 1.5 m from the surface, and it exhibits a dark reddish-brown color during summer months, which becomes clearer upon cooler temperatures and mixing.

2.2 Water Sampling, Temperature and Oxygen Measurements

Water samples were collected on 44 dates between March 2002 and September 2003. For each sampling date, water samples and measurements were taken at a marked point near the middle of the lake (depth ~4 m). Sampling was performed during mid-day (between 11:00 a.m. and 1:00 p.m.) each date and took approximately 45 minutes to complete. Samples were returned to the lab and processed within approximately one hour of sampling time.
Two replicates of water samples were taken at 0.25 m, 1 m, and 2 m using 2-liter Nalgene® plastic bottles. A peristaltic pump was used to obtain samples from 1 m and 2 m. Water was run through the pump at each depth before filling the bottles in order to prevent contamination of samples by water from a different depth.

Along with collection of water samples, basic physical and chemical data from the lake were collected on each sampling date. Secchi depth measurements were used to estimate light penetration. A YSI model 57 oxygen meter was used to measure dissolved oxygen and temperature profiles with readings taken every 0.25 m from the surface to a depth of 4 m.

2.3 Water Sample Measurements and Preservation

In the lab, 200 mL of each water sample were vacuum filtered through a 47 mm Whatman® GF/F-filter. The filters were wrapped in aluminum foil and saved in a -80°C-freezer until needed for HPLC pigment analysis. The filtrate was saved in Whirl pak® bags in a -20°C-freezer for nutrient measurements.

Turbidity was measured for all unfiltered water samples using a Hach model 2100A Turbidimeter. The turbidimeter was calibrated using a 9.9 NTU Gelex® secondary turbidity standard.

The pH of unfiltered water samples was determined using a Fisher Scientific Accumet® 1001 pH meter. The pH meter was standardized using a pH 4 potassium biphthalate buffer solution and a pH 7 potassium phosphate monobasic-sodium hydroxide buffer solution.
Water samples to be used for enumeration of dinoflagellates were concentrated before being preserved. One liter of water from each of two replicates from each depth was filtered through a 20 µm mesh filter and concentrated to a volume of approximately 20 mL. These water samples were placed into plastic vials and fixed with 200 µL of acid Lugol’s solution so that they could be used later for enumeration and identification. Also, for most dates, 100 mL of unconcentrated sample water from .25 m, 1 m, and 2 m was preserved with 1mL of Acid Lugol’s for potential later use.

2.4 Population Counts

Slides were prepared for population counts of dinoflagellates at each depth according to the following procedure. 2-3 mL of previously concentrated sample was filtered onto an 8 µm-nitrocellulose filter. Filters were dried briefly on top of an upside down petri dish that was placed on a hotplate set to the lowest heat setting. 2-3 drops of immersion oil were placed on a microscope slide, and the filter was placed on top of the immersion oil. The filters cleared upon contact with the immersion oil. A cover slip was placed on each slide and all slides were refrigerated until counted.

Counting was performed using a Jena-Lumar© light microscope. All counts were made at 125X magnification. Two different counting methods were employed depending on the abundance of organisms. If few dinoflagellates were present, then slides were counted by two transects across the diameter of the filter: one horizontal and one vertical. The width of one transect was the width of the eyepiece grid at 125X magnification (790 µm). When many dinoflagellates were present, the slides
were counted by random fields. Counts were made in ten random fields giving a total number of organisms per the area of 10 fields (each field was 0.624 mm$^2$). Slide counts and concentration factors for each sample were used to back-calculate the population density of all dinoflagellates. Estimates of actual densities (given in cells/L) were made using the following formula:

\[
\frac{\text{# of cells counted}}{\text{area counted (mm}^2\text{)}} \times \frac{\text{area of filter (mm}^2\text{)}}{\text{mL filtered}} \times \text{Concentration Factor}
\]

where the area counted was equal to 0.6241 mm$^2$ per field $\times$ 10 fields $= 6.241$ mm$^2$ or when transects were used, the length $\times$ width of a transect. The area of the filter was 227 mm$^2$. The concentration factor was given by:

\[
\frac{\text{volume of sample after concentrating (L)}}{\text{volume of field sample concentrated (L)}}
\]

2.5 Species Identification and Population Proportion Counts using SEM

In order to identify species of dinoflagellates, scanning electron microscopy was used to visualize the morphological features used to classify freshwater dinoflagellates. Dinoflagellates were identified by the number and pattern of thecal plates and also by the presence of reticulation on thecal plates. Species were identified using three taxonomical keys to the freshwater dinoflagellates (Popovsky 1990; Starmach 1974; Lefevre 1932).

Scanning electron microscope stubs were prepared by filtering between 2 and 5 mL of concentrated sample water (see section 2.3) onto a 0.8µm-membrane filter.
The filter was dried by the same method as section 2.5. After drying, filters were affixed to the stubs using double-sided tape and gold coated using a sputter coater. The specimens were examined using a JEOL® JSM-5600 scanning electron microscope. The magnification was changed as needed to examine morphological features.

In addition to identification of species present in the water samples, scanning electron microscopy was employed to estimate the proportion of the total dinoflagellate population contributed by each species throughout the 16 month sampling period. SEM stubs were prepared by the same method used for species identification for two sampling dates from each month. For each date, stubs were prepared from all three sampled depths (.25 m, 1 m, 2 m). Relative abundances were determined by counting a series of transects across the stub until 100 cells were counted. All counts were made at 300X magnification. The percent of total dinoflagellates represented by each species was multiplied by the total density obtained from the light microscope counts (see section 2.4) in order to estimate individual species densities on each sampling date.

2.6 Dissolved Inorganic Nutrient Measurements

Ion chromatography was used to quantify dissolved inorganic nutrients. In particular, concentrations of nitrate, orthophosphate, and ammonium were measured to estimate trophic status of the lake. Measurements of sulfate were also made. Filtrate from the GF/F-filters (see section 2.3) was analyzed on a Dionex® 600 system with an AS14 column and conductivity detector. Peaknet® 6 software was
used for analysis. The detection limits were 10 ppb for nitrate and phosphate. The
detection limits for ammonium and sulfate were 5 ppb and 3 ppb, respectively.

2.7 Pigment Measurements using HPLC

High performance liquid chromatography (HPLC) was used to quantify pigments from the GF/F-filters (see section 2.3). Chlorophyll a was quantified to estimate total phytoplankton biomass. Peridinin was quantified because it is a pigment unique to dinoflagellates. Sample preparations were performed after the method of Wright and Jeffrey (1997). The filters were extracted with 5 mL of 90% acetone, sonicated, and the resulting pulp was filtered again using centrifugation. Samples were run using a Dionex® reversed phase HPLC column with both UV-Vis and photodiode array detectors. Chromeleon® software was used for data analysis.
Section 3: Physical and Chemical Characteristics of Boondoggle Lake

This section presents the physical and chemical data recorded over the study period, including measurements of temperature, dissolved oxygen, pH, Secchi depth, dissolved inorganic ions, and photosynthetic pigments.

3.1 Temperature

Throughout the study period, water surface temperatures ranged from 7.5 to 31°C, with an average of value of 21°C. Vertical temperature profiles show that the lake has well defined temperature stratification that lasts throughout the summer months. It mixes completely during the remainder of the year and rarely, if ever, experiences ice cover. Therefore, according to the classification scheme of Lewis (1983), Boondoggle Lake is a warm monomictic lake (Kalff 2002).

Figure 3.1 presents temperature profiles for selected dates from each month sampled. For the profiles from 2002, stratification began in March, and the thermocline remained poorly defined through April and May. In June, a well defined thermocline was seen beginning at 1.5 m. By October, the lake was mixing again.

A similar trend was seen in the 2003 temperature profiles. The lake began to stratify in March and showed weak stratification from April through May. A well defined thermocline was seen in June and July.
Figure 3.1: Temperature and dissolved oxygen profiles for selected dates beginning March 2002 and ending July 2003
3.2 Dissolved Oxygen

A stratification of dissolved oxygen levels accompanied temperature stratification in the summer. Anoxic conditions were present during the summer months, which began near the lake bottom and rose to depths just below the epilimnion.

Dissolved oxygen in surface waters (0.25 m) ranged from 6 mg/L to 11.5 mg/L during the study period. When the lake was mixing, dissolved oxygen was between 7-10 mg/L at all depths.

Figure 3.1 presents dissolved oxygen profiles for selected dates from each month sampled. In 2002, stratification of dissolved oxygen began in mid April, and by mid May, anoxia developed below 4 m. The depth at which anoxia began became shallower during June and July and receded during August and September. The shallowest depth at which anoxia began was recorded on August 22, 2002 and was 1.25 m. By October, the lake was mixing and the dissolved oxygen concentration was approximately 6 mg/L. Dissolved oxygen increased during the colder winter months, reaching a maximum of 10 mg/L in December.

Data from 2003 showed a similar trend in dissolved oxygen concentration. Again, strong stratification and anoxia began in May. In the profiles from June and July, oxygen concentration dropped quickly after a depth of 1 m, with complete anoxia occurring between 1.25 m and 1.5 m.
3.3 pH

For all dates and depths, pH was always between 5.5 and 6.5. Figure 3.2 shows the temporal changes in pH values measured at three depths. The data suggest a stratification of pH that corresponds to the temperature and oxygen stratification mentioned in sections 3.1 and 3.2.

In Figure 3.2, from May 2002 through September 2002, a clear separation was seen between the pH values of each depth. The pH measured at .25 m remained the highest and the pH measured at 2 m remained the lowest through the stratification period, with the pH at 1 m falling in between. This pattern of decreasing pH with depth is likely due to buildup of carbon dioxide and carbonic acid associated with anoxia at deeper depths. Measurements of pH remained similar between depths during lake mixing (October 2002- April 2003).

3.4 Secchi Depth

Figure 3.3 shows temporal patterns in Secchi depth. Secchi depth ranged from 2.1 m in the early spring to 0.72 m in late summer. Average Secchi depth was 1.2 m over the study period.

The major pattern observed in Secchi depth was the sharp decrease in early June to a depth of approximately 1 m. Secchi depth then gradually decreased through the summer and remained shallow until November, when a sharp increase in depth occurred.
Figure 3.2: Temporal patterns of pH for three depths: .25m, 1m, and 2m
Figure 3.3: Temporal patterns in Secchi depth
3.5 Dissolved Inorganic Ions

Table 3.1 presents monthly measurements of nitrate, phosphate, ammonium, and sulfate for samples from each depth between May 2002 and March 2003. Entries labeled “ND” represent ion concentrations below the detection limit (see section 2.7).

Nitrate concentrations were higher in the fall and winter, and were highest in February (0.12- 0.15 ppm). An average concentration of 0.16 ppm was recorded in the surface samples from June. Orthophosphate concentrations remained under the detection limit from June 2002 – September 2002. The highest concentrations were recorded in fall and spring (0.15- 0.20 ppm). The highest ammonium concentrations were recorded in September, October, and November 2002. The highest sulfate concentrations were recorded in winter and spring.

3.6 Photosynthetic Pigments (chlorophyll a and peridinin)

Table 3.2 presents monthly measurements of chlorophyll a and peridinin for samples from each depth between June 2002 and February 2003. Entries labeled “ND” represent samples where the pigment was not detected.

Chlorophyll a concentrations ranged from 0.8- 8.6 ppb, with the highest concentrations occurring in the summer and fall. Peridinin concentrations were highest in July, August, and September (1.37- 9.39 ppb). Peridinin was either detected in low concentrations or not detected in the fall and winter samples.
Table 3.1: Monthly measurements of nitrate, phosphate, ammonium, and sulfate concentrations. Values for months with more than one measurement (n>1) have been averaged.
<table>
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<th>Month</th>
<th>n</th>
<th>Chlorophyll a (ppb)</th>
<th>Peridinin (ppb)</th>
</tr>
</thead>
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<td></td>
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</table>

**Table 3.2:** Monthly measurements of chlorophyll a and peridinin concentration. Values for months with more than one measurement have been averaged.
Section 4: Identification of Dinoflagellate Species from Boondoggle Lake

Six species of freshwater armored dinoflagellates were identified from the water samples taken from Boondoggle Lake. They include *Peridinium deflandrei*, *Peridinium volzii*, *Peridinium wisconsinense*, *Peridinium limbatum*, *Peridinium inconspicuum*, and *Peridiniopsis polonicium*. This section highlights the main morphological features that are unique to each species, and presents data on cell size and geographical distribution.

4.1 *Peridinium deflandrei*

*P. deflandrei* belongs to the subgenus *Poroperidinium*, meaning it possesses an apical pore. The general epithecal plate formula for this subgenus according to the Kofoid system of plate designation is 4′, 3a, 7″ (Taylor 1987; Popovsky and Pfiester 1990). However, *P. deflandrei* has the epithecal plate formula of 4′, 2a, 7″ (Popovsky and Pfiester 1990). Popovsky and Pfiester (1990) classify this species as *Peridinium umbonatum* var. *deflandrei*, grouping it with a number of other species. The taxonomic schemes of Lefevré (1932) and Starmach (1974) have it listed as a separate species, *Peridinium deflandrei*.

Distinguishing features used to positively identify *P. deflandrei* included epithecal plate pattern, absence of reticulation on thecal plates, presence of rows of
small points on thecal plates, and two antapical spines (Popovsky and Pfiester 1990; Lefevré 1932, Starmach 1974).

Vegetative cells of *P. deflandrei* are between 28-35 µm long and 26-32 µm wide. This species has been reported in Spain and in New York (Lefevré 1932; CSLAP 2002).

Scanning electron micrographs of *P. deflandrei* are presented on Plate 4.1.

### 4.2 *Peridinium volzii*

*P. volzii* is the only *Peridinium* species in this study belonging to the subgenus *Cleistoperidinium*. This subgenus name has now been changed to *Peridinium* and includes all *Peridinium* species lacking an apical pore (Popovsky and Pfiester 1990; Carty 1986). The general epithecal plate formula for this subgenus according to the Kofoid system of plate designation is 4′, 3a, 7/\( \text{a} \) (Taylor 1987; Popovsky and Pfiester 1990).

Distinguishing features used to positively identify *P. volzii* included symmetrical arrangement of the three intercalary plates, a small 1′ plate, sulcal penetration into the epitheca, and reticulation on the thecal plates (Carty 1986; Susan Carty pers. Comm.).

*P. volzii* vegetative cells are between 38-42 µm long and wide. It has been previously reported in the United States in Oklahoma, North Carolina, Minnesota, Maryland, and Massachusetts. It has also been reported in Canada, Australia, Europe, Asia, and Africa (Carty 1986).

Scanning electron micrographs of *P. volzii* are presented on Plate 4.2.
4.3 Peridinium wisconsinense

*P. wisconsinense* belongs to the subgenus *Poroperidinium*. Cells of this species are pointed at each end, giving them a spindle shape. The two bottom plates on the hypotheca (1 and 2) form a horn-like structure, with the 1 plate extending to the tip of this structure. The sulcus only penetrates slightly into the epitheca, and reticulation is present on the thecal plates (Carty 1986; Popovsky and Pfiester 1990). These features were used to positively identify *P. wisconsinense*.

Vegetative cells of *P. wisconsinense* are between 55-64 µm long and 48-56 µm wide (Popovsky and Pfiester 1990). It has previously been reported in the United States and Canada. Within the United States, there have been reports from Alabama, Georgia, Louisiana, Massachusetts, Michigan, Minnesota, New Jersey, North Carolina, South Carolina, Texas, West Virginia, and Wisconsin (Carty 1986).

Scanning electron micrographs of *P. wisconsinense* are presented on Plate 4.3.

4.4 Peridinium limbatum

*P. limbatum* belongs to the subgenus *Poroperidinium*. The most distinctive features of this species are the pair of horn-like thecal projections on the hypotheca and the conical, pointed epitheca. The sulcus widens on the hypotheca and reaches the antapex of the cell. Reticulation is present on the thecal plates (Popovsky and Pfiester 1990).

*P. limbatum* is the largest species identified in this study. Vegetative cells are between 80-93 µM long and 60-82 µm wide (Popovsky and Pfiester 1990). An
incomplete list of where it has been documented includes Canada and Oklahoma (Holt 1981; Yan and Stokes 1978; Yung 1991).

Scanning electron micrographs of *P. limbatum* are presented on Plate 4.4.

4.5 *Peridinium inconspicuum*

*P. inconspicuum* belongs to the subgenus *Poroperidinium* and is recognized by its small size as well as shape. The cingulum divides the epitheca into almost equal halves, and the sulcus penetrates slightly into the epitheca. There is no reticulation on the thecal plates, but there is ornamentation in the form of longitudinal rows of dots. Spines may be found on the antapex (Carty 1986). These features, along with the expertise of Dr. Susan Carty, were used to identify *P. inconspicuum* (Susan Carty pers. comm.).

*P. inconspicuum* is the smallest freshwater dinoflagellates species, with vegetative cells ranging from 15-30 µm long and 12-25µm wide. It is a widely reported species. Reports come from most European countries, Cuba, and the United States. Within the United States, it has been reported in 25 states, including Mississippi. The range within the continental United States includes far western (California) to eastern (South Carolina) and southern (Mississippi, Louisiana) to northern (Wisconsin, North Dakota) (Carty 1986).

Scanning electron micrographs of *P. inconspicuum* are presented on Plate 4.5.
4.6 *Peridiniopsis polonicium*

The genus *Peridiniopsis* is distinguished from *Peridinium* because species possess 0-1 anterior intercalary plates. *Peridiniopsis polonicium* was identified by its oval shape, large 1/ plate, reticulation on thecal plates, and sulcal extension to the antapex (Popovsky and Pfiester 1990). Identification was also confirmed with Dr. Susan Carty (Susan Carty pers. comm.). Variations are known to occur in the number of anterior intercalary plates in this species, and cells observed in this study had two anterior intercalary plates (Popovsky and Pfiester 1990).

Vegetative cells of *Peridiniopsis polonicium* are between 33-54 µm long and 30-51 µm wide. Areas where this species has been documented include Europe and North America (Popovsky and Pfiester 1990).

Scanning electron micrographs of *Peridiniopsis polonicium* are presented on Plate 4.5.

4.7 Other Phytoplankton and Zooplankton

Other phytoplankton identified included cryptomonads, diatoms, green algae, and the chrysophyte *Dinobryon*. Although it was not quantified, *Dinobryon* was found in high densities in the spring. This alga is phagotrophic and feeds on bacteria (Graham and Wilcox 2000). Scanning electron micrographs of diatoms are presented on Plate 4.6. Scanning electron micrographs of *Dinobryon* and the green alga *Micrasterias* are presented on Plate 4.7.

The zooplankton identified included rotifers, cladocerans, and copepods. A scanning electron micrograph of a *Keratella* rotifer is included on Plate 4.7.
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Section 5: Spatial and Temporal Patterns in Population for Dinoflagellates in Boondoggle Lake

This section presents the results of the counts of total dinoflagellate abundance, and for five of the six species identified, population proportion of species and estimates of population sizes for individual species are presented. One species, *Peridinium inconspicuum*, could not be quantified because it is smaller than the size of the mesh used to concentrate the water samples (see methods, section 2.3).

5.1 Total Dinoflagellate Abundance

The temporal changes in combined population density for all dinoflagellates greater than 20 µm in size is shown for each depth sampled in Figure 5.1. It should be noted that the X-axis is not to scale.

Maximum population densities occurred between July 26 and September 13, 2002 for all three depths. The maximum population density for 0.25 m occurred on August 22, 2002 and was $2 \times 10^5$ cells/L. The maximum density recorded for 1 m occurred two weeks later on September 6 and was $2.96 \times 10^5$ cells/L. For the 2 m samples, the maximum density occurred on September 13, 2002 and was $1.78 \times 10^5$ cells/L.

In addition to the summer maxima, other smaller peaks of density occurred. At 0.25 m, there were two small peaks, one two months before and one a month after the main summer maximum. These peaks were between $5-7 \times 10^4$ cells/L. Two peaks
Figure 5.1: Total dinoflagellate population density
between 6-8 \( \times 10^4 \) cells/L were seen in the spring at 1 m. Also at 1 m, a peak in June of 1.2 \( \times 10^5 \) cells/L and a peak in October of 7 \( \times 10^4 \) cells/L were seen.

5.2 Population Proportion

Figures 5.2-5.4 show the patterns in proportion of the total population for each species at all dates and depths sampled. Clear temporal patterns of population proportion were observed for all species. However, no clear differences in population proportion were seen between sample depths.

Individual species showed one of two temporal patterns in percent of the total population. The first pattern was a higher percentage in the summer and fall, and the second pattern was a higher percentage in the winter and spring. *P. deflandrei*, *P. wisconsinense*, and *Peridiniopsis polonicium* all were a higher percentage of the total population between mid-May and mid-November. *P. volzii* and *P. limbatum* were all a higher percentage between November and April.

The two species that represented the highest proportion at all three depths and for all dates sampled were *P. deflandrei* and *P. volzii*. None of the other three species ever comprised more than 25% of the total dinoflagellate abundance. *P. deflandrei* was 50% or more of the total dinoflagellates on approximately 63% of the days sampled, especially in the summer and early fall. *P. volzii* was 50% or more of the dinoflagellates on approximately 32% of the days sampled, especially in the late fall, winter, and spring. Since *P. volzii* occurs in the winter and spring when total dinoflagellates abundance is low, its high proportion at these times does not necessarily mean it has a high population
Figure 5.2: Population proportion at 0.25 m
Figure 5.3: Population proportion at 1 m
Figure 5.4: Population proportion at 2 m (circles represent no data)
density. *P. deflandrei*, however, reaches a maximum proportion of the population in the summer when total density is high and is responsible for 90% of the summer maximum.

5.3 Individual Population Trends

Calculated estimates of population density for each species over the sampling period are shown in Figures 5.5-5.7. Y-axes are scaled differently for each species in order to clearly show trends in population density. The X-axis is not to scale.

*Peridinium deflandrei* showed a temporal pattern in population density almost identical to the total abundance of dinoflagellates because it was such a high percentage of the dinoflagellate assemblage in the summer. Spatial and temporal patterns were seen in this summer bloom of *P. deflandrei* that suggested rapid initial growth followed by the sinking of the bloom. A sharp increase in population at 0.25 m was seen beginning in July 2002, and an initial maximum density of $1.6 \times 10^5$ cells/L occurred at 0.25 m in late August (see Figure 5.5). By the beginning of September, a maximum density of $2.75 \times 10^5$ cells/L was observed at 1 m, accompanied by an 80% decrease in density at 0.25 m (see Figures 5.5 and 5.6). The maximum at 1 m decreased 98% by mid September, at which time a maximum of $1.75 \times 10^5$ cells/L was seen at 2 m (see Figure 5.7).

*Peridinium volzii* had maximum densities mostly in the spring. At 0.25 m, it had a maximum density of $2 \times 10^4$ cells/L in April 2002 and another peak of $1.2 \times 10^4$ cells/L in August 2002 (see Figure 5.5). At 1 m, a maximum of $5.7 \times 10^4$ cells/L occurred in April 2002. This high density was not seen in samples from April 2003 (see Figure 5.6). At 2 m, clear peaks were seen in population density in mid to late April for 2002 and 2003 (see Figure 5.7). These peaks were between $2.2 - 2.8 \times 10^4$ cells/L.
Figure 5.5: Individual population trends at 0.25 m
Figure 5.6: Individual population trends at 1 m
Figure 5.7: Individual population trends at 2 m (circles represent no data)
*Peridinium limbatum* stayed at relatively low population densities throughout the sampling period. At both 0.25 m and 1 m, a peak in population density was seen in late April with a density of approximately $2 \times 10^3$ cells/L (see Figure 5.5 and 5.6). At 1 m, another peak of $2.5 \times 10^3$ cells/L was seen in mid March (see Figure 5.6). *P. limbatum* never reached a density higher than 300 cells/L in the 2 m samples.

*Peridinium wisconsinense* reached maximum population densities in the late summer. At 0.25 m, maximum density occurred in August and was $1 \times 10^4$ cells/L (see Figure 5.5). The maximum population density at 1 m occurred in September and was $2.1 \times 10^4$ cells/L (see Figure 5.6). Densities at 2 m were low for *P. wisconsinense*. The highest density at 2 m occurred in late July and was $5 \times 10^3$ cells/L (see Figure 5.7).

*Peridiniopsis polonicium* was only found at high density in the summer and in the surface water. The maximum density at 0.25 m occurred in August and was $1.6 \times 10^4$ cells/L (see Figure 5.5). At 1 m, the density was low except in July, when it was $3 \times 10^3$ cells/L (see Figure 5.6). At 2 m, a maximum of $3.5 \times 10^3$ cells/L occurred in mid September.

5.4 Correlations Between Temperature and Population Density

Correlations between dinoflagellate population density and temperature are presented in Figures 5.8 and 5.9. Figure 5.8 shows the correlation of total dinoflagellate density to temperature for each sampling depth through the entire sampling period. Figure 5.9 shows the correlation of the most abundant dinoflagellate, *P. deflandrei*, to temperature for each sample depth through the entire sampling period.
For the total dinoflagellate density, a positive correlation between density and temperature was seen at all three depths. This correlation was stronger for samples from 1 m ($r^2=0.61$) than for samples from 0.25 m and 2 m ($r^2=0.40$ and 0.34, respectively).

*P. deflandrei* density was also positively correlated with temperature at all three sample depths. This correlation was slightly stronger for samples from 0.25 m ($r^2=0.70$) and 2 m ($r^2=0.77$) than for samples from 1 m ($r^2=0.67$).
Figure 5.8: Correlation of total dinoflagellate density to temperature
Figure 5.9: Correlation of *P. deflandrei* density to temperature
Section 6: Discussion

Dinoflagellates have potentially large roles in freshwater ecosystems, yet there is still a paucity of information on the ecology of freshwater dinoflagellates. Many studies of dinoflagellate ecology have been conducted in areas other than the United States. Information on dinoflagellate diversity and abundance is especially lacking in the southeastern United States.

To my knowledge, all species identified in this study, with the exception of *P. inconspicuum*, have not been previously reported in Mississippi. There seems to be little information on the distribution of *P. deflandrei*. Lefevré (1932) reported this species in Spain, and a report from Echo Lake in New York was the only occurrence I could find in the United States (CSLAP 2002). *P. volzii* is a cosmopolitan species, with reports from the southeastern, northeastern, and midwestern United States, and it has also been reported in Europe, Asia, Africa, and Austrailia (Carty 1986; Starmach 1974; Lefevré 1932). Given this information, it is not surprising that it is also found in Mississippi. *P. limbatum* has been reported mostly in Canada, but one report comes from Oklahoma (Holt 1981; Yan and Stokes 1978, Yung 1991). To my knowledge, this is the furthest south *P. limbatum* has been identified. *P. wisconsinense* is a common species in the eastern United States. It has been documented in at least 11 states, including two that border Mississippi (Carty 1986). *Peridiniopsis polonica* may also be a cosmopolitan species since it has been documented in Europe, North America, and Japan (Popovsky and Pfiester 1990; Hashimoto et. al. 1968).
By far, the dominant species of dinoflagellate in the summer bloom in Boondoggle Lake is *P. deflandrei*. This species comprised an average of 90% of the total dinoflagellates during the bloom period that began in June and ended in September. The shift in the population density maximum from 0.25 m in late August to 1 m in early September and to 2 m in mid September suggests that the bloom formed in the surface waters and moved downward. Whether this downward movement was due to migration or sinking is unclear.

*P. volzii* was the second most abundant species of dinoflagellate in Boondoggle Lake. However, the maximum density observed for *P. volzii* was only 20% of the size of maximum density for *P. deflandrei*. *P. volzii* also had a different temporal pattern in abundance than *P. deflandrei*; larger populations were observed in months with cooler temperatures. This pattern is consistent with a previous study that found population maxima of *P. volzii* at temperatures between 17\(^0\)C and 21\(^0\)C (Olrik 1992). In this study, *P. volzii* reached maximum densities in March and April, was mostly absent in the summer, and was at low densities (< 5000 cells/L) from October through December. One exception to this pattern was a summer peak of *P. volzii* at 0.25 m on August 22 (see Figure 5.5). On this date, water temperature at 0.25 m was 25\(^0\)C, about 5 degrees cooler than measurements before and after, which may account for the brief summer peak of *P. volzii*.

The other three species exhibited a temporal pattern similar to either *P. deflandrei* or *P. volzii*. *P. limbatum* was most abundant in the spring and fall. *P. wisconsinense* and *Peridiniopsis polonicium* were most abundant in the summer. These differing patterns
may be attributable to a number of dynamic environmental variables or interactions of those variables.

Many environmental variables contribute to the bottom-up and top-down control of dinoflagellate populations in freshwater systems. Those that are likely to be important in determining the temporal and spatial patterns in abundance and species composition of the dinoflagellates in Boondoggle Lake include, but are not limited to, low nutrient levels, an acidic pH, summer anoxia, warm temperatures, wind protection, and interspecific competition.

The low phosphate levels in Boondoggle Lake may be a major contributor to the relative success of dinoflagellates species. Low concentrations of orthophosphate, between 1-10 ppb, are often found in freshwater systems where dinoflagellate blooms occur (Pollingher 1987). The persistence of *Peridinium* at low phosphate levels is thought to be due to its ability to take up and store phosphate in an internal pool of polyphosphates during times of higher phosphate concentrations (Serruya and Berman 1975; Elgavish et. al. 1980). Because the detection limit for orthophosphate in this study was 10 ppb, it is probable that orthophosphate was not detected simply because it was below the detection limit.

The pH range of Boondoggle Lake (5.5-6.5) influences species diversity because it excludes species of dinoflagellates that are not tolerant of acidic environments. Acid tolerant species are not necessarily acidophilic and may remain at low population sizes because of reduced growth rates in acidic environments. According to Pollingher (1987), most freshwater dinoflagellates prefer alkaline environments. Since the pH in Boondoggle Lake is always acidic, the six species identified in this study must tolerate or
prefer acidic environments. The effect of pH on growth rate has been investigated in four of the six species of this study. Experiments with pure cultures showed *P. inconspicuum* did not vary in growth rate across a wide range of pH (5.5-8.5), but *Peridiniopsis polonicium* had reduced growth rates under slightly acidic (6.5) and basic (8.5) conditions. The same study found that *P. volzii* and *P. limbatum* had higher growth rates under acidic conditions (Holt 1981). A water quality assessment for Echo Lake in New York found *P. deflandrei* to be the most abundant species (40% of the phytoplankton), with lake pH values being between 6.7 and 7.7 (CSLAP 2002). Although there are no studies of the effect of pH on growth rate of *P. deflandrei*, it is clear from this study that it can thrive in at least a slightly acidic environment.

Bottom water anoxia is likely to be one of the key factors controlling vertical distribution of dinoflagellates in Boondoggle Lake. As mentioned earlier, dinoflagellates are thought to be intolerant of low oxygen concentrations. If this is true for all species, then dinoflagellates should be restricted to the epilimnion during the summer when anoxic conditions are present below the oxygen chemocline. Indeed, the total dinoflagellate density remained low at 2 m during the anoxic period, with the exception of a large peak on September 13 (see Figure 5.1). On this date, anoxia was present at 2 m, whereas oxygen at 1.75 m was 4.25 mg/L. This high density value recorded at 2 m under anoxic conditions is likely due to an error in sampling around the depth of the oxygen chemocline. This pattern suggests a high density of dinoflagellates at the oxic-anoxic boundary. If conditions are favorable for growth of dinoflagellates at 2 m before the onset of anoxia, then development of anoxia in the bottom waters could be forcing an
upward vertical migration and subsequent concentration of dinoflagellates in the top 1 m of the lake.

Temperature likely plays a general role in determining species abundance. Most dinoflagellates show maximum growth during the summer (Carty 2003). This pattern was seen for *P. deflandrei*, *P. wisconsinense*, and *Peridiniopsis polonicium* but not for *P. volzii* and *P. limbatum*. *P. volzii* and *P. limbatum* may be inhibited by warm summer temperatures, or other factors may be responsible for their absence in the summer.

Another potential advantage for dinoflagellates in Boondoggle Lake is that the lake is protected from wind by hills to the west and south. Wind protection favors dinoflagellates in two ways. First, phytoplankton that do not actively swim are lost more rapidly from the water column through sedimentation in wind protected lakes, reducing their level of competition with dinoflagellates (Pollingher 1988). Second, dinoflagellates are likely to suffer less mortality from turbulence under wind protected conditions (Pollingher and Zemel 1981).

Interspecific competition between dinoflagellate species may be important in determining which species dominate the summer bloom. Physiological features may confer advantages to certain species. For instance, species that are facultative heterotrophs may be able to obtain carbon and nutrients to which obligate autotrophs have no access. It is difficult to estimate how much effect interspecific competition may have since few studies have investigated this topic with freshwater dinoflagellates.

More information on the physiology and ecology of the dinoflagellate species from Boondoggle Lake is needed to understand which factors are most important in the development of the large summer population of *P. deflandrei* and to understand why the
other species do not reach such high population densities. Priorities for future research include more sensitive and comprehensive measurements of nitrogen and phosphorus and measurements of dissolved organic carbon. Vertical profiles of light intensity are also needed in order to determine a light extinction coefficient and estimate the depth of the euphotic zone. A quantification of *P. inconspicuum* should be made in order to include its seasonal abundance as part of the total armored dinoflagellates in Boondoggle Lake. Because horizontal heterogeneity is often observed in freshwater dinoflagellate blooms (Pollingher 1988), samples from more than one site are needed to describe the horizontal spatial variation associated with these populations. Lastly, measurements of diel vertical migration should be made.

Resources permitting, more extensive studies would be able to provide an even more comprehensive data set on the ecology of Boondoggle Lake dinoflagellates. Using sediment traps, measurements of the time of encystment and the amount of cysts formed for each species could be made. Enumeration of cysts from sediment samples and an attempt to induce excystment in a laboratory could also yield important data. All of these measurements would be important in determining the role of cyst recruitment in population dynamics. If these dinoflagellates could be brought into culture, estimates of peridinin to chlorophyll a ratios within cells could be made, allowing an accurate estimate of the percent of total algal biomass due to dinoflagellates using HPLC pigment analysis.
LIST OF REFERENCES


