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DIATOM COMMUNITY RESPONSES TO DEVELOPMENT AND CLIMATE CHANGE IN LAKE GEORGE, AN OLIGOTROPHIC LAKE IN THE ADIRONDACK MOUNTAINS

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Abstract: Lake George is a highly monitored, oligotrophic lake that experiences widespread tourism in the summer months. The southern basin is more developed than the northern basin, suggesting a north-south gradient of anthropogenic impairment. This study aimed to assess differences in nearshore diatom communities regarding gradients of water chemistry and watershed development throughout the lake. Using Redundancy analyses, water chemistry was found to explain more variation within diatom assemblages than watershed variables. Weighted averaging optima and tolerances specified taxa of concern, *F. gracilis* and *A. formosa*, that indicate increased phosphorus (μg/L) and conductivity (μS/cm), respectively. Two hypotheses related to the effect of climate change on phytoplankton communities are potentially affirmed with comparison to past diatom studies in the lake. Increased development and warming temperatures are predicted to cause an increase in abundance of smaller centric diatoms and benthic diatoms. Our results verify that the effects of human development and concomitant effluents can be observed in diatom communities that may be used as biological indicators or sentinels of environmental change.

Key Words: phosphorous, chloride, conductivity, temperate, freshwater, phytoplankton

INTRODUCTION

In the Adirondack region of upstate New York, Lake George remains in a relatively unaffected, oligotrophic state. The lake's watershed is largely untouched with 90 to 95 percent natural forestland and 45 percent being "forever wild" state-owned preserve (Boylen et al., 2014). Given the nearly $2 billion USD tourism industry, primarily localized in the lake's southern basin, water quality is a high concern regarding public drinking water, recreation, and shoreline property values (Boylen et al., 2014, Hintz et al., 2019, Dodds et al., 2009). Following prominent research in the 1960s and 1970s regarding nutrient loading and lake acidification, Rensselaer Polytechnic Institute began an extensive water quality monitoring program in 1980 that has resulted in one of the highest quality, long-term datasets available in North America. With over thirty years of water chemistry data, annual cycles and historical trends have become evident to researchers. Since the 1980s, chlorophyll *a* has increased by 33%, Secchi depth clarity has decreased by half a meter (-6%), and chloride (Cl^-) concentration has increased significantly (+218%), suggesting changes in the geochemical cycles and phytoplankton community may be occurring (Hintz et al., 2019).

Changes in water quality and subsequent detrimental effects, often attributed to increased anthropogenic impact, can be difficult to monitor when strictly using water chemistry. Although rapid assessments with water chemistry samples are advantageous, they often lack a long-standing representation of water quality (Bradshaw, 2002). Alternatively, biological indicators integrate stressors over time and directly assess impacts to the ecosystem (Friberg et al., 2011). The use of organisms to indicate biotic integrity has been implemented for many years with indices, sometimes spanning across multiple taxonomic groups (Patrick, 1949, Kane et al., 2009), ecological guilds (Fore et al., 1996), or limited to a single taxonomic group (Karr, 1981). Typically, developing an index and understanding biotic integrity often relies upon a healthy reference site to measure the extent of anthropogenic impact upon an ecosystem. Given that very few ecosystems remain pristine, ecologists use paleoecological records in sediment cores to reconstruct pre-civilization climatic conditions, lake trophic state, and watershed characteristics (Engstrom et al., 1985, Bourbonniere & Meyer, 1996). Specifically, changing diatom communities in sediment cores has been shown to effectively model human-caused lake acidification and cultural eutrophication (Charles et al., 1986, Dixit et al., 1999). Even in relatively pristine Lake George, diatom communities in sediment cores confirmed that water column productivity has almost doubled since European settlement, suggesting anthropogenic impairment is not a recent phenomenon (DelPrete and Park, 1981).

More recently however, the use of diatoms as bioindicators is being applied to infer pre-disturbance biological conditions in present day ecosystems, where gradients of anthropogenic impact and water chemistry (Kireta et al., 2007, Sgro et al., 2007). As dominant members of the phytoplankton and a high-quality food source for zooplankton, diatoms represent an integral part of a lake's primary energy source, leading to direct effects on upper trophic levels (Round et al., 1990). Diatoms are especially useful as bioindicators due to their high diversity, distinguishable species morphology, ubiquitous nature, and rapid response to changing environmental conditions (Stevenson et al., 2010). Although diatoms exist in nearly all aquatic environments, individual species show specific niche requirements, allowing the characterization of ecosystems (Round et al., 1990, Hall and Smol, 2010). The ease of collecting diatom samples is another advantage. In one microscope slide, thousands of diatoms may be present, creating large datasets and redundancies in information which increase the confidence of environmental inferences (Dixit et al. 1992). Relative abundances within a dataset can be analyzed by multivariate analyses or weighted averaging (WA) to understand species' optima and tolerances in reference to specific environmental variables (Marchetto et al., 2003, Sgro et al., 2007). The strong correlation of diatom models with both watersheds and water chemistry make them an excellent candidate for assessing anthropogenic impact (Kireta et al., 2007).

Lake George is a unique lake in being highly monitored, minimally impacted, and moderately large in relation to most well-studied lakes (Lathrop, 2007, Foley, 2012). Interestingly, a slight gradient of total phosphorus and Cl^- has been observed as a result of increasing human development in the southern basin (Boylen et al., 2014). Elevated Cl^- levels have likely developed due to consistent road salt deposition leaching into groundwater or entering through one of the more than 141 streams which account for 57 percent of the lake's annual hydrologic budget (Shuster, 1994). While the effects of salinization on freshwater ecosystems have not been extensively studied, bottom-up changes may occur after a decrease in diversity among plankton communities (Hintz et al., 2017). Although phosphorus levels have remained stable since the late 1980s, often increased levels of phosphorus are undetectable due to rapid uptake by the biotic community. A most recent phosphorus budget by Stearns and Wheler (2001) attributes 36 percent of total phosphorus (TP) to be from anthropogenic sources, while the most conserved estimate by Sutherland et al. (1983) suggests a 25 percent anthropogenic input. As a limiting nutrient, phosphorus is rapidly incorporated by phytoplankton, leading to decreased clarity and potential eutrophication (Lathrop et al. 1999, Cottingham et al. 2000). Furthermore, Lake George is becoming noticeably warmer (+1.8 °C) and will likely continue to do so if current trends are continued (Hintz et al., 2019). Longer warm seasons increase the duration of stratification, possibly causing anoxia in the hypolimnion and the release of phosphorus from sediments (Foley et al., 2012, Messina et al., 2020). Collectively, climate change could be an exacerbating factor promoting accelerated degradation of Lake George water quality.

Following the work of previous studies on Lake George, we aimed to assess anthropogenic impairment through diatom communities over a two-year period at a higher resolution of 27 sites throughout the lake. Modern Geographic Information Systems (GIS) were employed to classify Lake George sub-watersheds and determine potential terrestrial impact upon sites. Watershed features and *in situ* water chemistry were compared to diatom relative abundances to elucidate underlying phytoplankton trends occurring as a result of anthropogenic impairment or climate change. We hypothesized: 1) Diatom communities will be differentiated based upon gradients within watersheds or water chemistry. With the southern basin being more developed, diatom species and communities reflecting impairment will be more abundant there. 2) Weighted averaging optima and tolerances will reveal specific indicator taxa for nutrient enrichment and/or salinization regarding seasonality. 3) Species' optima and seasonal trends will allow insight into the diatom communities that may occur given increased anthropogenic impairment or increased temperatures.

METHODS

Study System

Lake George is a glacially formed lake with two deep basins of comparable volumes separated by a shallow section called the Narrows (Fenneman, 1938). Prior to glaciation, the southern basin flowed south to the Hudson River while the northern basin flowed to Lake Champlain. Following the Wisconsin Glaciation (15,000 years ago), the basin began to accumulate sediment, damming the southern flow and causing the lake to drain at a single northern outlet, the LaChute River, before descending 69 meters to Lake Champlain (Boylen et al., 2014).

The lake sits at 97.5 m above sea level with a maximum width of 3.3 kilometers and a length of 51 km, equaling a 114 km^2 surface area. An average depth of 18 m and a maximum depth of 58 m results in the lake holding a volume of 2.1 km^3 (Boylen et al., 2014). The annual hydraulic budget draws 57 percent from streams, 25 percent from precipitation, and 18 percent from groundwater in a watershed that encompasses 606 km^2 (Shuster 1994). Lake level is usually held within 1 m by the LaChute Hydro Company Inc with a dam on the northern end at the LaChute River. The lake's bedrock is primarily metamorphic gneisses which have been overlaid with glaciolacustrine clay, undifferentiated till, and Holocene lake deposits (Hutchinson et al. 1981). Hydraulic retention time is estimated to be 7 to 8 years and an average surface water velocity of 3.8 km d^{-1} (Boylen et al. 2014). Due to the shallow constriction between the two basins, commonly called the Narrows, horizontal motion below the 20 m level is reduced to spring and fall turnover (Boylen et al. 2014).

Field Sampling

27 near-shore sites were accessed via motorboat over the course of the 2018-2019 seasons (Fig. 1). Sampling efforts were performed monthly from 4 June to 25 October (excluding September) for 2018 and from 22 May to 19 September during 2019. Depths of sampling locations ranged from 2-5 meters and all sites had total water clarity to the lake's bottom. Water chemistry variables recorded included: temperature (°C), dissolved oxygen (DO; mg/L), specific conductance (SPC; µS/cm), pH,

chloride (Cl^-, mg/L), phycocyanin (PC; μg/L), chlorophyll *a* (Chl *a*; μg/L), fluorescent dissolved organic matter (FDOM; RFU), total nitrogen (TN; mg/L), total phosphorus (TP; μg/L), silica (Si; mg/L), and calcium (Ca^{2+}, mg/L). While sampling at each site, temperature, DO, SPC, Cl^-, PC, Chl *a*, and FDOM were recorded using a Exo2 Sonde from YSI. Water chemistry analysis for raw water samples (TN, TP, Si, Ca^{2+}) occurred within 24 hours at the Darrin Fresh Water Research Institute associated with Rensselaer Polytechnic University following standard methods (APHA, 1995).

Algal samples were collected with 3-4 vertical plankton tows of the entire water column using a 64 μm phytoplankton net. Samples of 54 ml were combined with 6 ml of formalin for a final 4% formaldehyde preservation. A total of 241 samples were transported to John Carroll University for diatom slide preparation. Organic material was removed from a sub-sample of 20 ml using a boiling nitric acid digest. Samples were then rinsed at least six times, pelleted using a centrifuge, and eventually diluted in disposable culture tubes with deionized water to a proper opacity. Slides were made for each sample by pipetting the diatom slurry onto coverslips, letting them dry overnight, and mounting with Naphrax® (Brunel Microscopes, Chippenham, UK). At least 400 diatoms valves were counted along random transects for each sample using an Olympus BX60 photomicroscope with Nomarski DIC optics. Diatom identification utilized the following resources: Krammer and Lange- Bertalot (1986, 1988, 1991, 1997), Camburn and Charles (2000), Siver and Hamilton (2011), and Diatoms of North America (https://diatoms.org/).

GIS Applications

A geographic database derived from the National Land Cover Dataset (NLCD), Warren County Geographic Information System Program, and the NY GIS Clearinghouse detailed 31 sub-watersheds. Five variables were chosen to succinctly describe the anthropogenic gradient present within the watershed of Lake George: Road density (km/ha), percent developed area per sub-watershed (%), percent forested area (%), average percent slope (%), and latitude (°). Each of these variables (excluding latitude) either reflects a direct human impact on a watershed or inherent features of the watershed that limit development. Latitude, recorded during sampling periods, serves as proxy for a sub-watershed's position in the lake, particularly in reference to the origin at the south and the flow of water to the north. Landcover variables (percent forested and developed) represent multiple classifications re-categorized as one encompassing classification. Street and highway shapefiles retrieved from the NY GIS Clearinghouse were used to calculate road density (km/ha) for each sub-watershed. Elevation raster files, also retrieved from NY GIS Clearinghouse, allowed average percent slope to be calculated. A preliminary principal component analysis (PCA) was performed to help classify sites with similar watersheds. Differentiated sites are detailed in the following section with additional information regarding sites potentially affecting water quality:

Highly Developed Sites – 09, English Brook (EN)

Both sites (09, EN) lie just off the shore of the town of Lake George, the most developed area along the lake's shore. Although both watersheds are relatively small, they demonstrate the highest development and road density. English Brook specifically follows Interstate 87 for several miles before emptying into the lake, leading to elevated chloride (Cl^-) levels and specific conductance (SPC) measurements. The Lake George sewage treatment facility does not directly discharge into a body of water.

Southern Basin - 01, 03, 07, 12, 13, Dunham's Bay (DB), Diamond Shallows (DS), East Brook (EB), Harris Bay (HB), Warner Bay (WB)

Sample sites within the southern basin are characterized as having highly developed, less forested watersheds. Along the western shore (01, 03, 07, DS) some of the highest road densities are found as state route 9 runs north through the towns of Lake George, Diamond Point, and Bolton. Between these municipalities, rental properties, resorts, and campgrounds consistently line the shore. Site 01 is near the Darrin Freshwater Institute in the Town of Bolton where the Bolton sewage treatment plant is less than half a mile from the shore. Site 03 is located in Basin Bay, which is south of the Town of Bolton and north of Diamond Point. Site 07 lies south of Cannon Point and may be influenced by multiple resorts along the shore. Diamond Shallows is an island site off the shore from site 07 which results in the two sites having very similar watershed influences and water chemistry.

Southeastern sites (12, 13, DB, EB, HB, WB) are all within the same watershed that is characterized by being equally developed as the western shore sites but also one of the less steep Lake George watersheds. Although the watershed contains Dunham's Bay Marsh (State Resource Management Area; IUCN Management Category VI), two golf courses in the southernmost portion may contribute to elevated phosphorus levels and dissolved organic matter. Furthermore, water quality may be homogenized leaving the watershed as the marsh empties into all three of the residentially developed bays (DB, HB, WB).

Northwest Bay and Shelving Rock – 16, Finkle Brook (FI), Indian Brook (IN), Shelving Rock (SR)

All four sites are located south of the Narrows, a transition point of the watersheds becoming less developed, more forested, and with much steeper topography. Indian Brook, Finkle Brook, and site 16 are along the western shore in the shallower Northwest bay. Most of the watersheds surrounding the bay, particularly in the north, are part of the Tongue Mountain Range, a preserve included in the Lake George Wild Forest. Shelving Rock is the last eastern site before entering the Narrows where Shelving Rock Brook empties into the lake and has a highly undeveloped, mountainous watershed. Water quality metrics are often similar to southern sites due to the lake's outlet to the north and mixing within the basin.

Northern Sites (Narrows included) – 18, 19, 21, 22, 24, 25, 28, 30, Sunset Bay (SB), Hague Brook (HA), Sucker Brook (SU)

Watersheds surrounding the sites in the Narrows (18, 19, 21, SB) are the most undeveloped, steep and forested watersheds along Lake George. Both site 21 and Sunset Bay are near Hulett's Bay, a small development of primarily residential properties, which sometimes results in slightly elevated phosphorus or Cl^- levels. Further north, the lake begins to deepen into the final sub-basin, Rogers Rock. State Route 9N returns to the western shoreline starting at Sabbath Point (22) for nearly 10 miles and facilitates a slight development of resorts and residences (25, HA). Eastern sites (24, SU) remain beside a steep, undeveloped shoreline, typically demonstrating the lake's lowest nutrient levels and cleanest water. At the lake's outlet (28, 30), residential and agricultural development begins to occur with the outskirts of the town of Ticonderoga. Site 30 is prone to erratic spikes in water chemistry either resulting from being the lake's final discharge or the sudden increase of development in its watershed.

Statistical Analyses

Diatoms, water chemistry, and watershed features from each site were used from each sampling for analyses. Diatom count data was calculated as relative abundance (%) to ensure standardization amongst species. Taxa were removed from analyses if not fulfilling 1 percent relative abundance in at least 3 three samples. Certain taxa were categorized together under the most common species name if discrepancies in morphology were not conspicuous or if species in question were lacking taxonomic solidarity, e.g. *Brachysira sp.* (Kütz), *Cocconeis placentula* (Ehrenberg), *Fragilaria crotonensis* (Kitton), and *Pantocsekiella comensis* (Grunow) Kiss & Ács.

All ordination methods were performed using Canoco 5.1 (ter Braak and Šmilauer, 2018). The preliminary PCA of sub-watersheds features allowed for site classification within the following analyses. For each sampling period (9 total), a redundancy analysis (RDA) was performed using diatom relative abundances as the response variables and watershed features or water chemistry as the explanatory variables. RDA is a constrained ordination method suggested when the gradient length of the first axis is less than 3 standard deviation units, indicating a homogenous dataset. After removing rare species following the protocol described above, a total of 83 diatom species were used in the analysis. Watershed variables included were road density, percent development, percent forest, average percent slope, and latitude. Water chemistry variables included were temperature (°C), DO, SPC, pH, Cl^-, PC, Chl *a*, FDOM, TN, TP, Si, and Ca^{2+}. Variables likely to interact with diatom species exponentially (TN, TP, Ca^{2+}, Cl^-, Si) were log-transformed prior to statistical tests. Significance of independent (simple) effects of explanatory variables were tested by means of a Monte Carlo permutation test with a falsediscovery rate p-value correction. Pearson correlation tests were performed to assess the effect of temperature on explained variation (%) for both watershed features and water chemistry.

Weighted averaging was performed on a subset of dominant taxa with regards to TP, SPC, and Temp (°C). Importance values (IV; average percent density x proportion frequency), which range from 0 to 100, can indicate dominance if > 1. Only eight species resulted in a dominant IV, requiring a further determination of potentially important species for weighted averaging. Using Canoco 5.1, the ten best-fitting species for each RDA were counted, concluding with 20 species chosen as dominant taxa (all species with IV > 1 were included). Weighted averaging was performed using the R 3.6.2 (R Core Team, 2019) package optimos.prime, which calculates optima and tolerances using log-transformed environmental variables (Sathicq et al. 2019).

RESULTS

Multivariate analyses

RDAs from each sample period revealed water quality measurements outperformed watershed features in explaining diatom communities (Fig. 2). Among watershed features, latitude was the most prominent variable being found significant ($p < .05$) in 7 of the 9 watershed RDAs. Other variables (Road density, % forest, % development, % slope) were found to be only significant ($p < .05$) in early season sampling (May) or late season sampling (September/October). In general, watershed explained variation (EV) of diatom communities was highest in early/late season months (May/June/October; n=4, 52.8 %) whereas midsummer months (July/August/September; n=5, 41.2%) were lower. As mentioned earlier, water chemistry variables (66.4%) had higher EV than watershed features (46.4%) in all sampling periods except for June 2018 (Fig. 3). Regressions investigating the effect of temperature (°C) on EV (%) revealed a non-significant, negative relationship (df = 7, p = 0.44, r2 = -0.29) with watershed features in contrast to the non-significant, yet positive relationship (df = 7, p = 0.19, $r^2 = 0.47$) with water chemistry. Individually, water chemistry RDAs performed well in elucidating seasonal trends and environmental variables determining diatom communities. Although water chemistry EV peaked in June (80.1%), higher EV values were found in the warmer months (69.6 %) than cooler months (62.3 %). SPC (μS), the most prominent environmental variable, was found to be significantly correlated (p = <0.05) with diatom communities in 5 of 9 sampling periods and commonly associated with sites in the southern basin (Fig. 4). DO (mg/L) and FDOM (RFU) were both found to be significantly related ($p < 0.05$) to diatom communities in 3 of 9 sampling periods, all occurring below 20 °C. FDOM was typically correlated with southern basin sites while DO appeared to be associated with northern sites when a large gradient existed, particularly at the end of both years (9/19 and 10/18). TP was also found to have a significant relationship (p = <0.05) in 3 of 9 sampling periods, but in contrast all occurred during months warmer than 20 °C. Southern sites are generally associated with TP and a higher number of dominant diatom species. Temperature was only significant (p = <0.05) in one sampling period, most likely a result of temperature variability being influenced temporally in the lake rather than geographically.

Diatoms

Within the 241 samples analyzed, 258 diatom taxa were identified. Among the 20 selected for further analysis, seven are considered benthic species (Tab. 1). WA optima and tolerances for temperature, TP, and SPC revealed similar trends among diatom taxa and water chemistry variables.

Temperature values show certain taxa to be season-specific either by physiological constraints or selective, predatory forces (Fig. 5). *Discostella stelligera* and *Cyclotella atomus* are similar-sized diatoms (<20 um) with optima at opposite ends of the measured temperature gradient, suggesting physiology may determine abundance. Small centric diatoms (*Pantocsekiella comensis* and *P. delicatula*) generally have lower temperature optima than small fragilarioids (*Pseudostaurosira parasitica* and *Staurosirella pinnata*), while large-bodied taxa (*Tabellaria quadrisepta*, *Asterionella formosa*, and *Synedra ulna var. chaseana*) have moderate optima values as a result of year-round prevalence.

TP optima values reveal taxa with affinities for ecologically impaired or healthy sites (Fig. 6). *Fragilaria gracilis* and *C. atomus* are two of the higher TP-associated species, potentially coinciding with their early season abundance. The taxa with the lowest TP optima, *Fragilaria crotonensis*, is the most common diatom within the lake (Tab. 1) and often occupies > 60% of the community during the summer in northern sites (Fig. 4). Wide tolerances among most taxa confirms that only a small gradient of phosphorus occurs in the lake, causing TP optima to be partially related to seasonality.

SPC values are the most useful where tolerances are distinct between species, suggesting certain taxa (*A. formosa*, *S. pinnata*, and *D. stelligera*) may be indicators of increased salinization (Fig. 7). *A. formosa*, the highest SPC optima, was a dominant taxon in southern sites during the August and October 2018 sampling efforts but not during the 2019 sampling periods.

DISCUSSION

This study aimed to investigate differences in diatom communities and the underlying, influential environmental variables throughout Lake George. Previous diatom studies in the lake demonstrated that primary productivity has increased since the onset of human settlement (DelPrete and Park 1981) but lacked the geographic replication necessary to determine areas of concern. This study addresses that deficiency. Diatom communities, water chemistry, and watershed features were evaluated across 27 sites in Lake George (Fig. 1), resulting in distinct clustering within multivariate analyses. Water chemistry EV showed a weak positive relationship ($r^2 = 0.47$) with temperature, which suggests once strong stratification occurs, diatoms become highly determined by epilimnion characteristics. In comparison, watershed EV demonstrated a negative relationship ($r^2 = -0.29$) with temperature, suggesting cooler months with higher precipitation may result in more nutrient runoff, leading to watershed features such as development and percent impervious surfaces to have more of an impact upon water quality (Watson et al., 1981). Sites in the Narrows (18, 19, 21 and SB) offer a unique demonstration of stratification and runoff dynamics within the lake. Hulett's Bay, a small development located near sites 21 and SB, may drive water chemistry and subsequently diatom communities to be similar to southern, impaired sites (Fig. 2). On the other hand, sites 18 and 19 have very little immediate development, yet occasionally show water chemistry and diatoms reflecting development. In particular, site 18 shows similarities to impacted sites in six sampling periods, at the end of 2018 and beginning of 2019, possibly demonstrating the effect of epilimnion water moving north towards the lake's outlet. In contrast, sites 12, 13, DB, HB, and WB are all located in the southern basin and generally fall into the southern, impacted cluster despite having Dunham's Bay Marsh as an effluent source. However, during the 2018 sampling season, some of these sites showed healthier diatom compositions, suggesting the successful effect of wetlands in removing nutrients in 2018 but not so in 2019 (Johnston et al., 1990). Beyond these few intricacies, diatom communities consistently confirm a general north-south gradient of anthropogenic impact within Lake George.

Although water chemistry gradients within the lake are small, abundances of dominant taxa can be used to determine ecological impairment during different seasons. In spring, centric diatoms (*C. atomus*, *L. lemanensis*, *P. comensis*, and *P. delicatula*) are present throughout the entire lake. With mixing occurring, bringing nutrients to the surface and homogenizing the lake, spring taxa must be adaptable and competitive (Lotter et al. in Smol and Stoermer 2010). Upon closer investigation, select diatoms have affinities to locations in the lake, such as *L. lemanensis*, which is universally present throughout cooler months, yet has consistently nearly double the abundance in southern sites compared to northern sites (Fig. 4). *C. atomus*, typically a eutrophic indicator (van Dam et al., 1994), is more abundant in the ecologically pristine, northern sites. This trend is further confused by the diatom taxa *F. gracilis*, typically a meso-oligotrophic indicator according to van Dam et al. (1994), being more abundant in southern sites. The southern basin is shallower and generally experiences ice melt sooner than the northern basin. Coupled with phosphorus enrichment, marginal areas are optimal habitat for increased periphyton, potentially leading to tychoplankton blooms (*F. gracilis* or *A. minutissimum*; Tab. 1) in disturbed areas (Lotter and Bigler 2000).

During summer months, trends between basins are best observed by following *F. crotonensis* as an overwhelmingly dominant species (Fig. 4). The consistency of *F. crotonensis* as a "clean" taxon in the northern sites is evident throughout both years from July to October. In past research, *F. crotonensis* has a mixed reputation of being a healthy but tolerant indicator (Sgro et al 2007, van Dam et al. 1994) in the Great Lakes to an anthropogenic pollution indicator in Lake Washington (Stockner and Woodruff 1967). In part, the decrease in *F. crotonensis* in the southern basin may be a result of increased conductivity or Cl^- levels which give a competitive advantage to *A. formosa*. Mechanisms behind this interaction are speculative at best, but increased Cl^- may interact with food web dynamics surrounding *A. formosa*'s obligate fungal parasite, *Zygorhizidium sp.*, and zooplankton (Kagami et al., 2007). Changes in osmoregulation may affect fungal and/or zooplankton survival, releasing selective pressures and allowing *A. formosa* blooms in sites with high conductivity or Cl^- levels (Hintz et al., 2017). Additionally, competition with smaller tychoplanktonic or benthic diatom species developing in the southern basin's periphyton community may limit dominance of *F. crotonensis* in planktonic communities (Sochuliaková et al., 2018).

The continuing effect of climate change upon Lake George can be addressed in two ways: how has it already been affected and how will warmer temperatures further impact the lake? Previous studies offer a glimpse into the diatom communities existing prior to the 1.8 °C increase over the last 30 years. Clesceri and Williams (1972) reported dominant taxa and comparisons between periphyton and plankton communities over a three-year period (1967-1969). Many of their reported taxa are also included in our study with one exception: *Stephanodiscus astraea* which was reported to be more abundant than *Tabellaria* sp. Although *Stephanodiscus* has undergone extensive revision and fragmentation since that time, we assume that their *S. astraea* is the same *Stephanodiscus* species observed in our study at very minimal abundances (< 6%). Since that time, smaller centric diatoms (e.g. *P. comensis*, *P. delicatula*, *D. stelligera*, and *C. atomus*) have become more abundant, potentially affirming the hypothesis that intensifying thermal stratification caused by climate change can be advantageous to smaller cell-sized organisms (Falkowski and Oliver 2007). Similar changes have been observed in Lake Tahoe, with larger sized species such as *Stephanodiscus sp.* and *A. formosa* decreasing in abundance and smaller, faster growing centric species replacing them (Winder et al. 2009). Another less favored hypothesis suggests longer warm periods will deplete the epilimnion of nutrients, effectively decreasing planktonic species and allowing tychoplankton and/or benthic species to become dominant within the lake (Sochuliaková, et al. 2018). According to Delprete and Park (1981), benthic species once dominated the lake over 3000 years ago, which may have signified a nutrient-depleted epilimnion. Although we are unable to directly compare the abundance in previous studies, benthic species (e.g. *Nitszchia* sp., *Cocconeis* sp., *Psammothidium* sp.) have become a considerable portion of the community (~7%) with no geographical preference in the lake. Given both hypotheses, the further effects of climate change on diatom communities in Lake George may be recognized by the dominance of smaller centric diatoms or benthic species in nearshore plankton communities.

CONCLUSION

Lake George is a unique study system being highly monitored and only partially impacted. As the first in-depth diatom study of Lake George, our study can be used to verify future changes as a result of anthropogenic impairment or climate change. Using multivariate analyses, nearshore diatom communities differentiated based upon water chemistry measurements and watershed variables (Fig. 4) demonstrating a general gradient of ecological impairment from the southern basin to the north. Diatom communities were best explained by water chemistry in warmer months (Fig. 3) which suggests further sampling of diatoms in July or August would return optimal results. WA optima and tolerance values present potential species that may become dominant if trends of development within the watershed continue. Blooms of specific taxa, such as *A. formosa* or *F. gracilis*, may be harbingers of impact specifically in the southern basin. Two hypotheses related to effect of climate change: 1) a decrease in diatom cell-size and 2) an increasing abundance of benthic diatoms have been potentially observed but need further verification (Falkowski and Oliver, 2007, Sochuliaková et al., 2018). Although we provide results from two years of monitoring, our study reveals the subtle changes that have been occurring in the phytoplankton community for many years and will likely continue to occur in the oncoming decades.

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Table 1. Dominant diatom taxa of Lake George determined from Importance Values (IV) and redundancy analysis best-fit species. Species code corresponds with Figure 4 abbreviations used in RDA. WA optima and tolerances for total phosphorus (TP), specific conductivity, and temperature.

			TP (µg/L)		SPC (µS/cm)		Temp. (°C)	
Code	Species	IV	Opt.	Tol.	Opt.	Tol.	Opt.	Tol.
FRCR	*Fragilaria crotonensis* Kitton	38.27	4.2	±1.4	147.9	±7.3	20.0	±4.5
TAFE	*Tabellaria quadrisepta* B.M. Knudson	9.58	4.7	±1.6	146.3	±9.2	18.7	±4.0
LILE	*Lindavia lemanensis* (Chodat) T.Nakov et al.	7.74	5.0	±1.5	145.0	±8.3	16.5	±3.7
ASFO	*Asterionella formosa* Hassall	7.20	4.7	±1.4	153.4	±6.0	16.9	±4.4
ACMI	*Achnanthidium minutissimum* (Kützing) Czarnecki	5.22	4.7	±1.4	147.8	±7.1	19.7	±4.7
PACO	*Pantoceskiella comensis* (Grunow) K.T.Kiss & E.Ács	5.19	5.1	±1.6	146.9	±9.9	16.5	±3.9
STPI	*Staurosirella pinnata* (Ehrenberg) D.M.Williams & Round	4.08	4.6	±1.4	149.4	±7.7	19.9	±4.8
PADE	*Pantocsekiella delicatula* (Hustedt) K.T.Kiss & E.Ács	1.08	4.8	±1.7	150.6	±13.7	16.9	±4.3
PSPA	*Pseudostaurosira parasitica* (W.Smith) E.Morales	0.81	4.5	±1.3	148.2	±6.0	20.7	±4.7
ACGR	*Achnanthidium gracillimum* (F.Meister) Lange-Bertalot	0.51	4.6	±1.4	147.2	±6.0	18.6	±5.0
ULCH	*Synedra ulna var. chaseana* Thomas	0.26	4.7	±1.8	147.6	±10.2	17.8	±4.0
CYAT	*Cyclotella atomus* Hustedt	0.23	5.2	±1.6	144.0	±9.5	13.7	±3.0
ROPU	*Rossithidium pusillum* (Grunow) Round & Bukhtiyarova	0.22	4.6	±1.3	148.0	±5.5	20.7	±4.5
DIST	*Discostella stelligera* (Cleve & Grunow) Houk & Klee	0.20	4.6	±1.5	148.6	±5.8	21.9	±3.0
FRGR	*Fragilaria gracilis* Østrup	0.16	5.8	±1.6	144.2	±6.7	14.7	±3.9
NISI	*Nitzschia sinuata var. tabellaria* Grunow	0.15	4.5	±1.4	147.0	±4.8	18.7	±5.2
ULDE	*Ulnaria delicatissima* (W.Smith) Aboal & P.C.Silva	0.10	5.5	±1.8	145.8	±6.5	17.3	±4.5
NATR	*Navicula trivialis* Lange-Bertalot	0.08	4.8	±1.5	147.3	±4.5	20.1	±4.5
NACR	*Navicula cryptonella* Lange-Bertalot	0.07	4.4	±1.3	146.5	±4.5	20.2	±4.4
NIBA	*Nitzschia bacillum* Hustedt	0.03	4.6	±1.3	147.5	±7.9	18.7	±4.7

FIGURE CAPTIONS

Figure 1. Sixteen sub-watersheds of Lake George, NY paired with adjacent sampling locations to assess anthropogenic impact and topography on diatom communities. Gradient of color represents classification of sites for later analyses. White = Northern Basin and Narrows, Light grey = Northwest Bay and Shelving Rock, Medium grey = Southern Basin, Dark grey = Highly developed watersheds. Projected in NAD 1983 UTM Zone 18N.

Figure 2. Principal component analyses (PCA) based on physical and chemical characteristics of site. a) PCA for watershed features among 27 different sampling sites. Clustering and latitudinal position in lake provided classification of sites in further analyses. b) PCA for water chemistry measurements at each site in June 2019 (sampling period with the highest explained variation). Squares: most developed sites (EN, 09); Diamonds: southern basin sites; Circles: Northwest bay and Shelving Rock sites; Triangles: northern and narrows sites.

Figure 3. Redundancy analysis (RDA) percentage of explained variation for both watershed features and water chemistry variables of diatom communities. Nine sampling periods occurred over two years (6/18-9/19) at 27 nearshore sites in Lake George. Filled circles: water chemistry; Empty circles: watershed features.

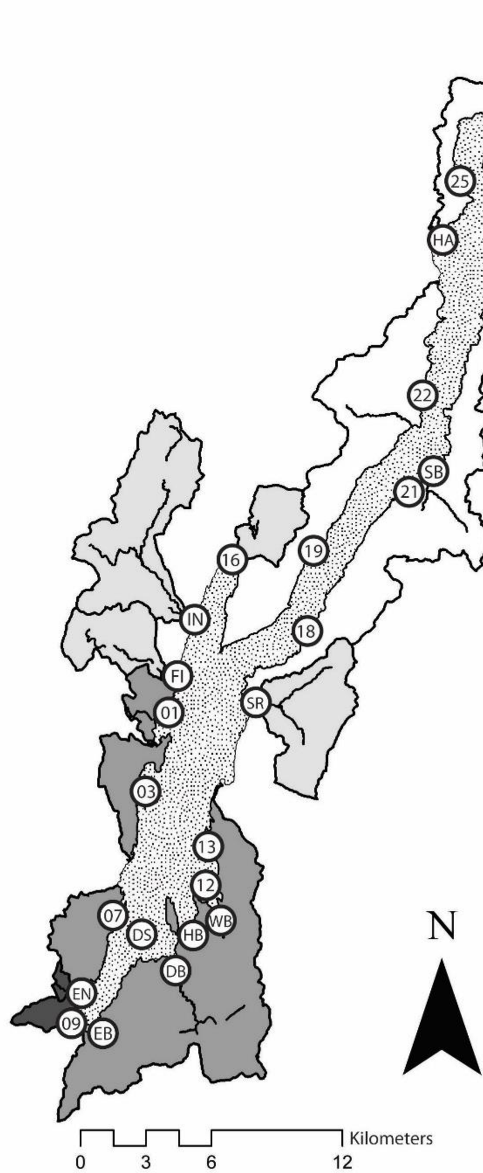
Figure 4. Redundancy analysis (RDA) for nearshore diatom communities explained by water chemistry measurements over two years in Lake George. Ten best-fitting species were included and abbreviated as first two letters of genus and species (codes are available in Table 1). Squares: most developed sites (EN, 09); Diamonds: southern basin sites; Circles: Northwest bay and Shelving Rock sites; Triangles: northern and narrows sites.

Figure 5. Caterpillar plot of temperature (°C) weighted-average optima and tolerance values for dominant diatom taxa in Lake George.

Figure 6. Caterpillar plot of total phosphorus (TP) weighted-average optima and tolerance values for dominant diatom taxa in Lake George.

Figure 7. Caterpillar plot of specific conductivity (SPC) weighted-average optima and tolerance values for dominant diatom taxa in Lake George.

Figure 1.


30
28
25
SU
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EN
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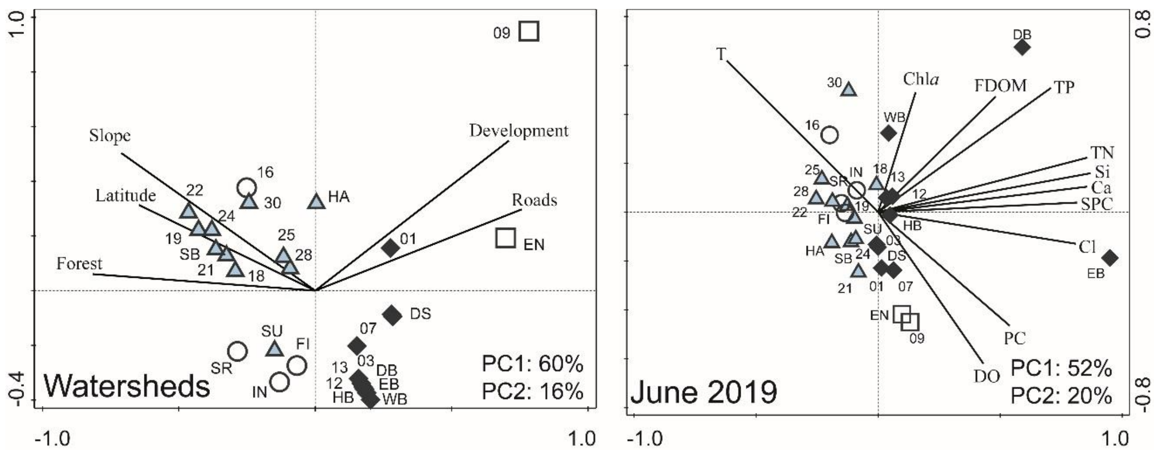
3
6
12
Kilometers

Figure 2.



Watersheds
PC1: 60%
PC2: 16%
Slope
Latitude
Forest
Development
Roads
June 2019
PC1: 52%
PC2: 20%
T
Chla
FDOM
TP
TN
Si
Ca
SPC
Cl
PC
DO

Figure 3.

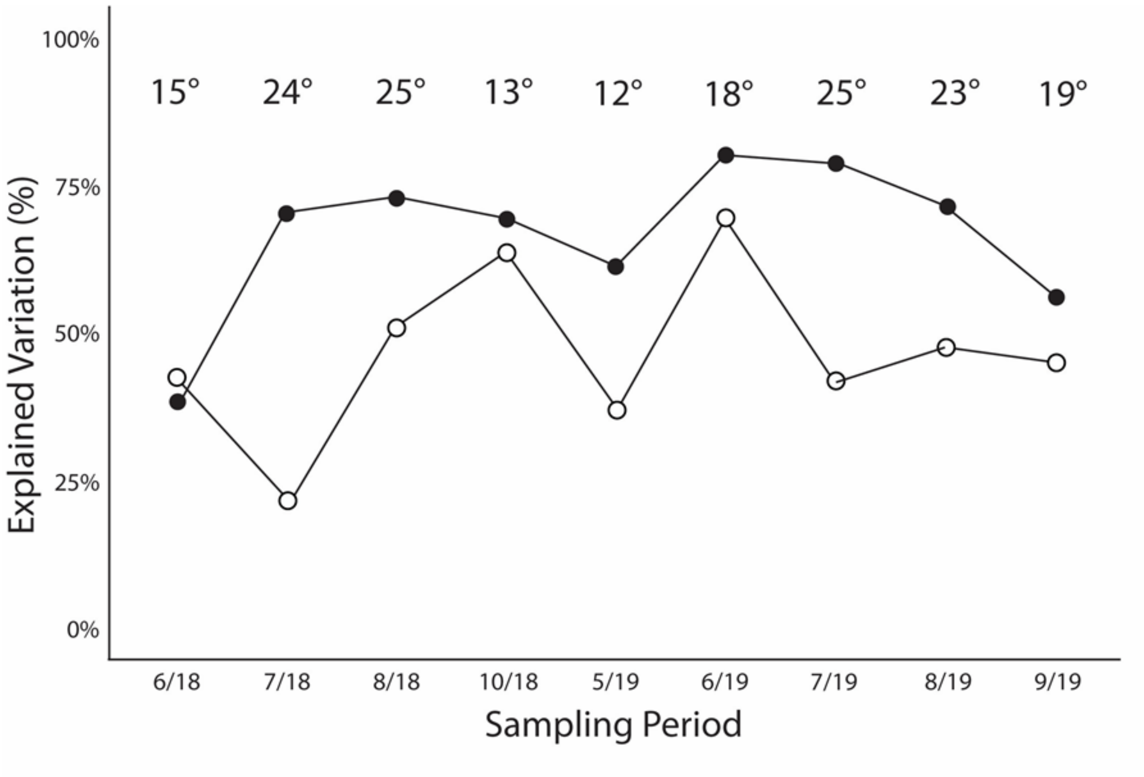
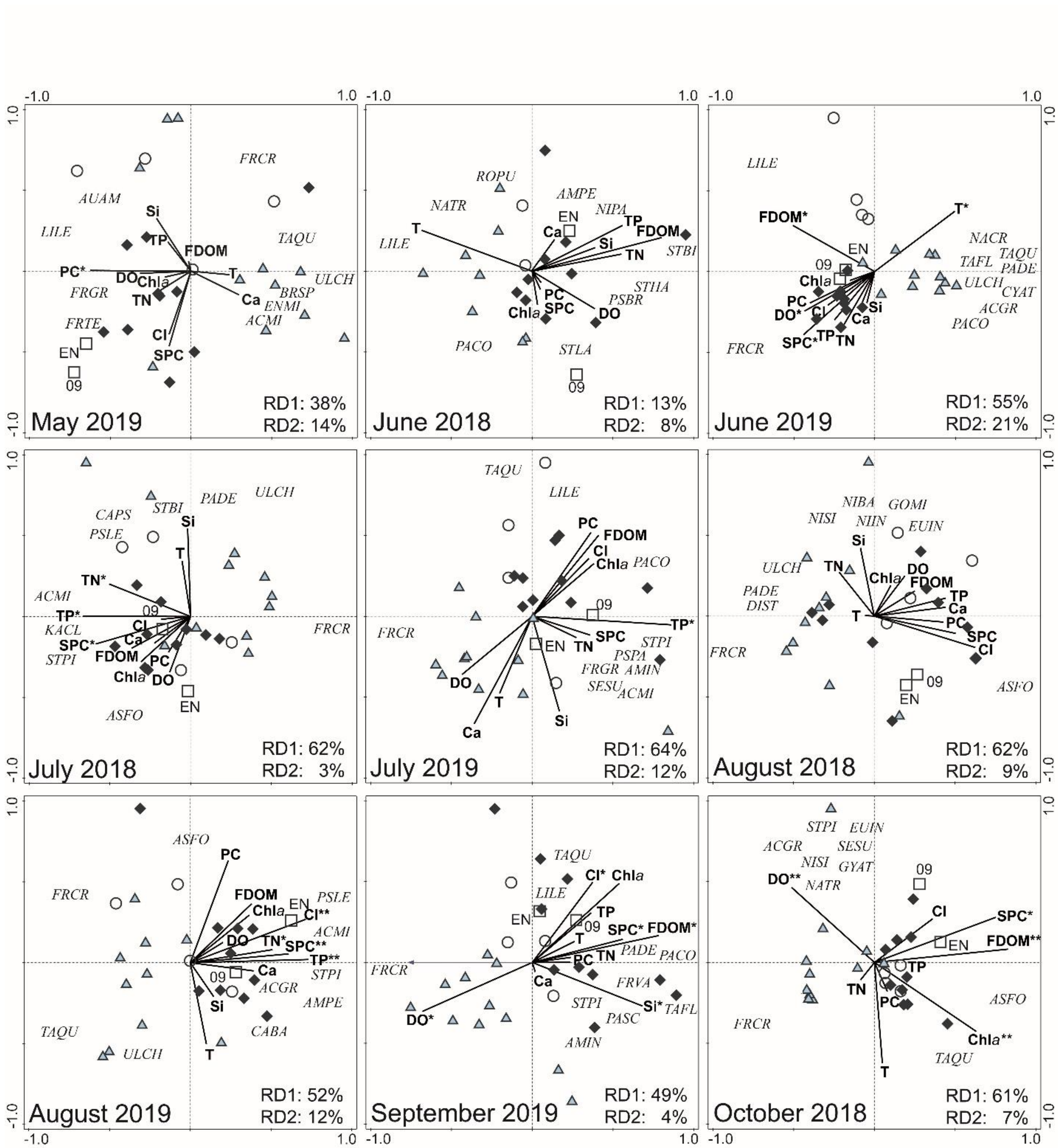

100%
75%
50%
25%
0%
Explained Variation (%)
15°
24°
25°
13°
12°
18°
25°
23°
19°
6/18
7/18
8/18
10/18
5/19
6/19
7/19
8/19
9/19
Sampling Period

Figure 4.



May 2019
RD1: 38%
RD2: 14%
June 2018
RD1: 13%
RD2: 8%
June 2019
RD1: 55%
RD2: 21%
July 2018
RD1: 62%
RD2: 3%
July 2019
RD1: 64%
RD2: 12%
August 2018
RD1: 62%
RD2: 9%
August 2019
RD1: 52%
RD2: 12%
September 2019
RD1: 49%
RD2: 4%
October 2018
RD1: 61%
RD2: 7%

Figure 5.

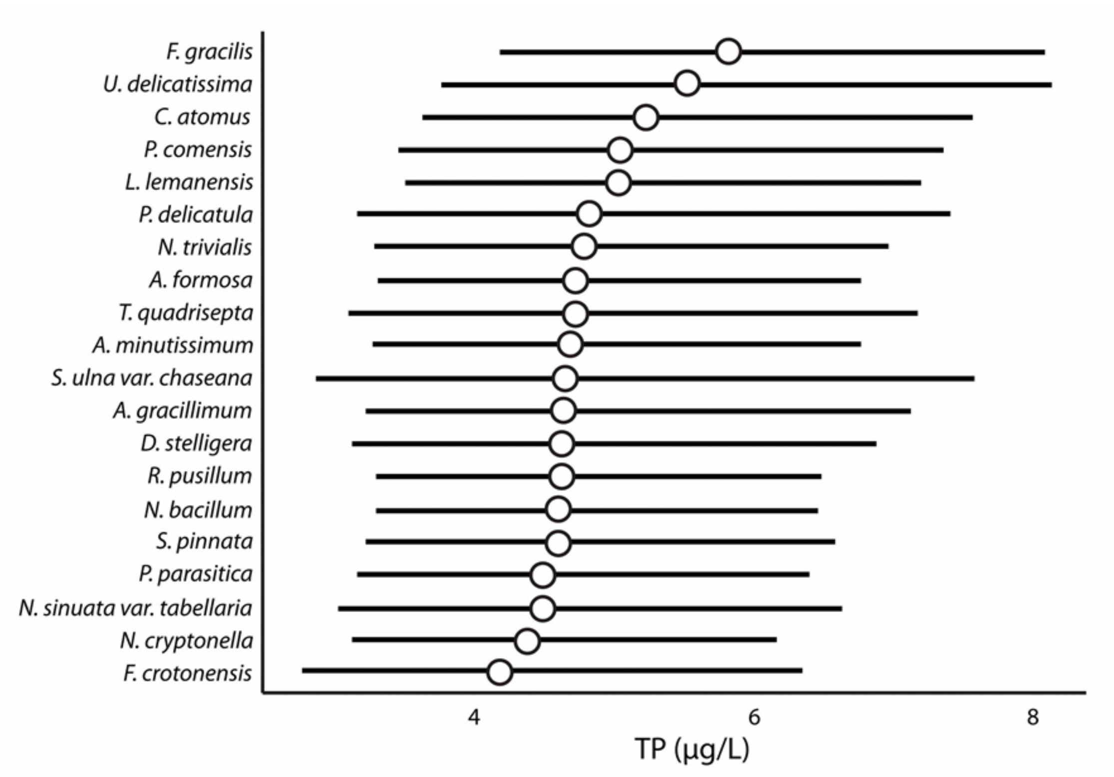

F. gracilis
U. delicatissima
C. atomus
P. comensis
L. lemanensis
P. delicatula
N. trivialis
A. formosa
T. quadrisepta
A. minutissimum
S. ulna var. chaseana
A. gracillimum
D. stelligera
R. pusillum
N. bacillum
S. pinnata
P. parasitica
N. sinuata var. tabellaria
N. cryptonella
F. crotonensis
4
6
8
TP (μg/L)

Figure 6.

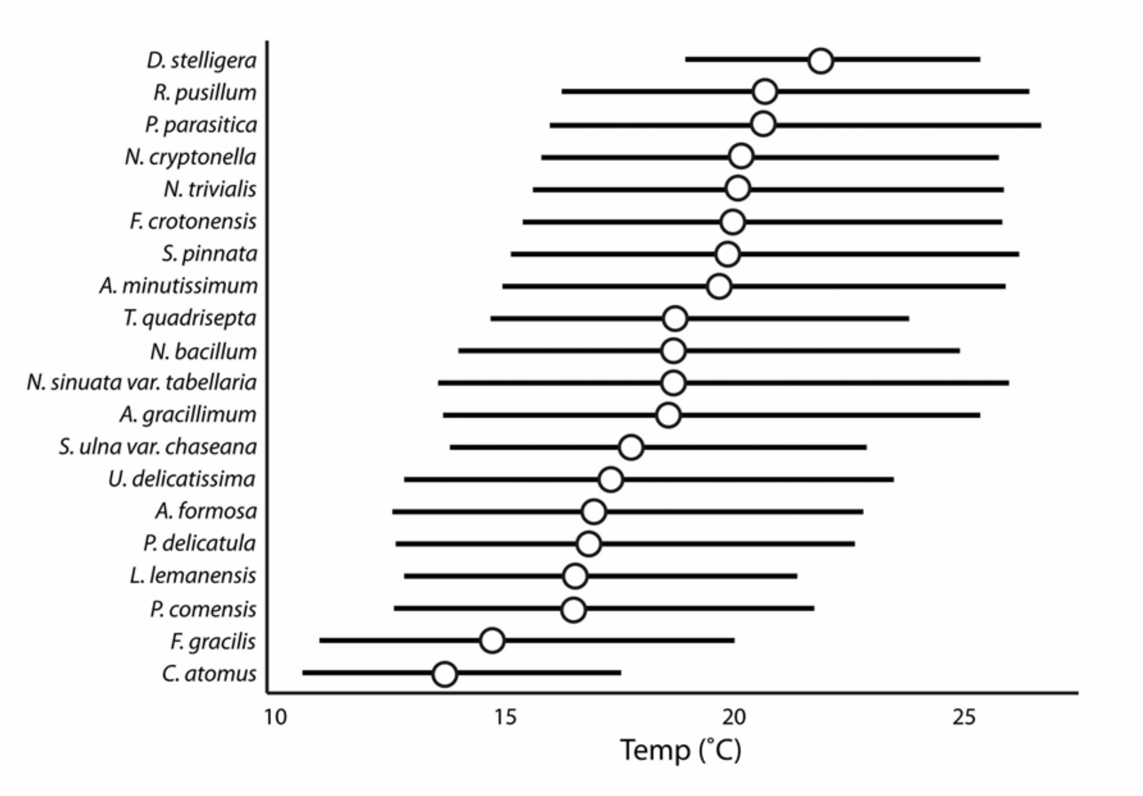
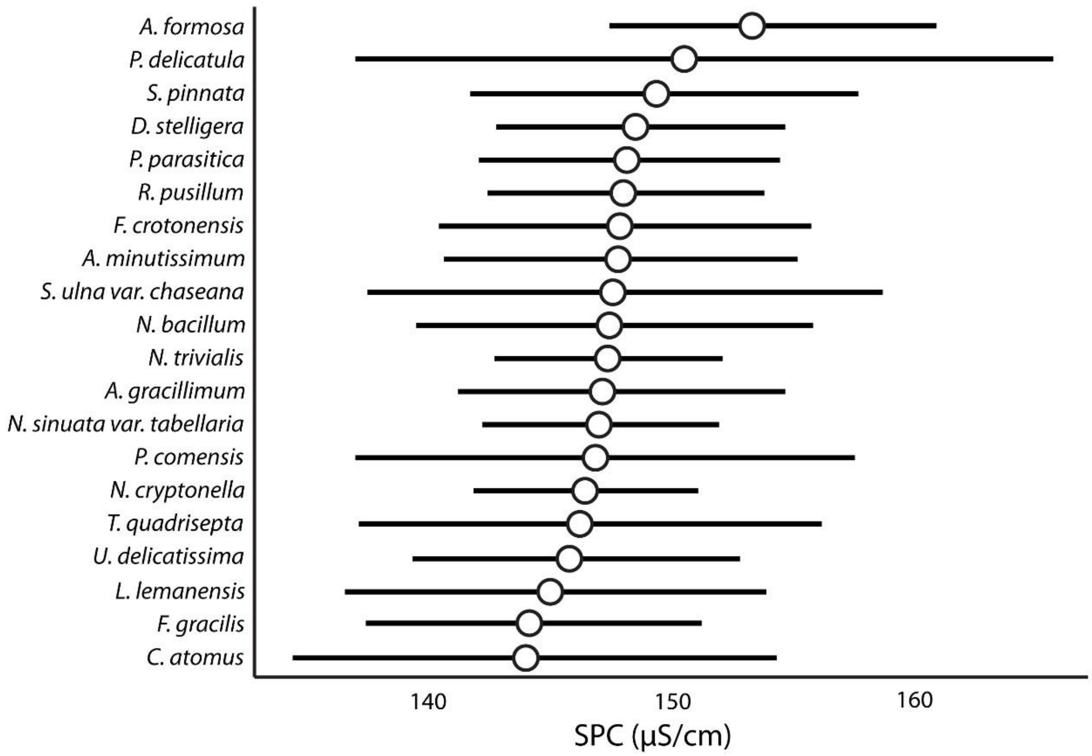

D. stelligera
R. pusillum
P. parasitica
N. cryptonella
N. trivialis
F. crotonensis
S. pinnata
A. minutissimum
T. quadrisepta
N. bacillum
N. sinuata var. tabellaria
A. gracillimum
S. ulna var. chaseana
U. delicatissima
A. formosa
P. delicatula
L. lemanensis
P. comensis
F. gracilis
C. atomus
10
15
20
25
Temp (˚C)

Figure 7.


A. formosa
P. delicatula
S. pinnata
D. stelligera
P. parasitica
R. pusillum
F. crotonensis
A. minutissimum
S. ulna var. chaseana
N. bacillum
N. trivialis
A. gracillimum
N. sinuata var. tabellaria
P. comensis
N. cryptonella
T. quadrisepta
U. delicatissima
L. lemanensis
F. gracilis
C. atomus
140
150
160
SPC (µS/cm)