MID-PROJECT DATA REPORT: PHYTOPLANKTON MONITORING IN THE GREAT LAKES

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Introduction

This report is intended for audiences who are familiar with the USEPA's Open Lake Water Quality Survey of the Great Lakes. Those unfamiliar with the project are directed to http://www.epa.gov/glnpo/monitoring/sop for a detailed background of the overall project goals, ideology and methods. This report fulfils the task of "Preliminary Report" (due July 28, 2009) as agreed in contract GL-00E23101-2.

Results herein focus on 2007 phytoplankton data from GLNPO's Great Lakes open water biological monitoring program. The main objectives of this report are to (1) present general characteristics of the 2007 phytoplankton assemblages, (2) reconstruct long-term phytoplankton trends in the context of phytoplankton data collected prior to 2000, and (3) use various observational and statistical techniques to confirm that data quality objectives, mainly taxonomic consistency, have been met.

Since the initiation of the University of Minnesota Duluth's (UMD) involvement in the monitoring program, significant efforts have been allocated to taxonomic assurance. Following the transition of the project to a new contractor in 2001, several data quality issues related to inconsistencies in taxonomic identifications arose resulting in temporary termination of the phytoplankton program in 2004. Part of UMD's agreement was to ensure that the new phytoplankton data collected in 2007 meet specific taxonomic criteria. In other words, taxonomy for 2007 needed to match that from pre-2000 samples so that long-term analyses were reliable. It is our opinion that we have met taxonomic criteria and that, with continued taxonomic workshops, we are building a reliable long-term phytoplankton database that will be a valuable tool to track ecological shifts in the lakes.

Subsequent sections present the following results and summaries.

1. An itemized list of significant efforts undertaken since UMD's initiation of our role in the phytoplankton work.
2. General data presentations for phytoplankton collected in 2007, including dominant taxa, seasonal and spatial trends.
3. Comparison of pre-2000 and 2007 phytoplankton assemblages for long-term trend analysis and checks on taxonomic consistency.
4. A detailed statistical investigation of pre-2000 and 2007 assemblages, intended to illustrate taxonomic similarities between "old" and "new" phytoplankton data and show fundamental changes in the assemblages over the last decade.
5. Algal indicator development. This section details the development and application of algal-inferred nutrient models for three select years: 1999, 2003 and 2007. Primary intents were to show the power of the phytoplankton as indicators and investigate consistency of species indicator coefficients among years.

Major analytical efforts are forthcoming. When additional years' phytoplankton data are available we will be performing more detailed analyses of species-specific shifts in the lakes. For instance, it appears that certain taxa have flourished, while others have been extirpated, due to recent changes in food webs and water quality conditions. There are many likely reasons for these changes, including size-specific preferences of food organisms by successful grazers, nutrient enrichment (e.g., Lake Erie) and depletion (e.g., Lake Superior), and climate-related shifts. These future results will be critical to management recommendations regarding the causes and impacts of changes in the lakes.

1. Significant efforts since March 2007

- Five sampling seasons aboard the Lake Guardian have been completed. As of June 2009 more than 600 samples have been prepared for both soft algae and diatom analyses. More than half of these samples have been fully assessed and entered into the project database
- Several meetings have been held for program quality assurance.
    - A 4-day workshop was held in July 2007 in Chicago to identify and correct taxonomic issues.
    - A quality-assurance (QA) session/workshop was held on April 11-21, 2008 at the Natural Resources Research Institute (NRRI-Duluth). Soft-algae QA counts were completed and there were detailed discussions on diatom taxonomy.
    - An audit of the University of Minnesota's Ely laboratory protocols was completed in September 2008. All reports indicate that the EPA is satisfied with our QA/QC procedures and adherence to the standard protocols. This audit was combined with a 2-day taxonomic workshop with EPA and UMD analysts.
    - A QA session/workshop was held from January 26 through February 2, 2009 at NRRI-Duluth. Soft-algae QA counts were completed and algal taxonomy was discussed in detail.
    - Reavie provided a seminar at the EPA Region 5 office to present project progress (much of which is included in this document).
- Following a major effort, a newly revised GLNPO phytoplankton species list was developed. The new species list, along with a workshop summary report, was submitted to the PO on 26 September 2007. Using the new species list, a new entry database (originally developed by the University of Wisconsin Superior personnel) was built. The algae database underwent much revision to accommodate older (1990s) data and to resolve issues with biovolume calculations.
- In preparation for phytoplankton analyses, iconographs and summary sheets have been developed for problematic algal groups (e.g., blue-greens algae, small cryptomonads, *Stephanodiscus*, *Synedra* and *Aulacoseira*). Using new and pre-2000 diatom slides, efforts have been undertaken to create photographic plates and refine diatom taxonomy using virtual communications (among Reavie, Barbiero, Agbeti and others). Continued efforts have refined these photographic plates using virtual communications and workshops.
- Preliminary multidimensional analyses indicated that taxonomic efforts have resulted in improvement in the compatibility between the 1996-1999 and 2001-2004 datasets; in particular, the analysis showed improved correspondence between 2007 and 1996-1999 data. It became clear that algal communities at the majority of sample locations are very different than they were in the 1990s.

2. 2007 Phytoplankton data, general results

A total of 324 taxa was encountered in the 2007 phytoplankton samples. The assemblages comprised centric diatoms (46 taxa), pennate diatoms (120 taxa), chrysophytes (46 taxa), green algae (72 taxa), cryptomonads (8 taxa), blue-green algae (20 taxa), euglenoids (2 taxa), dinoflagellates (6 taxa) and some unknown entities (4 taxonomic categories). A small number of these taxa are collections of very rare species or genera not identifiable to the species level (a genus followed by "sp."), or members of known divisions but with few diagnostic characteristics (e.g., "unidentifiable chrysophyte ovoid").

Table 1 presents the top 10 most common taxa encountered throughout the basin, and the top five most common taxa encountered in each lake. Figures 1a through 1d present distribution information for the top

10 most common taxa encountered throughout the basin. Taxa are presented in order of total phytoplankton, spring dominants, summer dominants and seasonally nonspecific taxa. These suites of data are largely presented for reader information, but several important observations can be made.

- Cell densities and biovolumes are several-fold higher in summer compared to spring, with the exception of Lake Erie (Figure 1a). Phytoplankton biovolumes in Lake Erie are substantially higher in spring due to an early bloom of the filamentous diatom *Aulacoseira islandica*.
- Overall spring dominants tend to be opportunistic diatom taxa (*Aulacoseira*, *Stephanodiscus*) which make use of abundant nutrients such as phosphorus and silica before nutrient limitation is established later in the year (Figure 1b).
- Spring dominant taxa are more abundant in the lower lakes (Erie and Ontario); algal abundance overall is relatively low in the upper lakes (Figure 1b).
- Summer assemblages are much more diverse than spring assemblages (Figure 1c).
- The upper lakes are dominated in the summer by diatoms, while the lower lakes contain more soft algae taxa such as cryptophytes and blue-green algae (Figure 1c).
- Three species, *Asterionella formosa*, *Gymnodinium helveticum* and *Rhodomonas lens*, have a broad seasonal and geographic tolerance (Figure 1d).

3. Long-term trends – pre-2000 versus 2007

Comparisons of pre-2000 (1996-1999) and 2007 algal assemblages (Figures 2a-2g) were used to track long-term changes in phytoplankton assemblages and to provide a cursory check on taxonomic consistency between these two groups of data. Efforts to assess and refine data for intermediate years (2000-2006) are ongoing, and detailed long-term trends will be presented in future reports.

Lake Superior (Figure 2a): In terms of cell numbers, Superior is dominated by blue-green algae throughout the year. Dominant taxa include entities comprising many small cells, such as *Oscillatoria minima*, *Oscillatoria limnetica*, *Aphanocapsa* and *Aphanothece*. However, algal biovolume in Superior is little influenced by the blue-green algae and is instead dominated by diatoms and green algae (more so in the summer). A significant drop in spring phytoplankton abundance has occurred between 1999 and 2007, whereas recent summer density and biovolume remain similar to that encountered in 1999. Superior's 2007 summer productive period was dominated by diatoms in the genus *Cyclotella*, a group of species known to favor low-nutrient conditions.

Lake Michigan (Figure 2b): Like Superior, cell density in Michigan is similarly dominated by blue-green algae such as *Oscillatoria minima* and *Oscillatoria limnetica*. In terms of biovolume, spring in Michigan is dominated by diatoms, although there has been a dramatic overall decline in spring biovolume and cell numbers since 1999. A similar decline is also observed for summer cell densities, but summer biovolume estimates are unchanged due to a continuing abundance of large, summer pennate diatoms such as *Fragilaria crotonensis*.

Lake Huron (Figure 2c): As for the upgradient lakes, Huron cell densities are usually dominated year-round by small celled blue-green algae such as *Oscillatoria minima, Oscillatoria limnetica, Aphanocapsa* and *Aphanothece*. However, since 1999 Huron has seen a significant decline in overall spring density and biovolume. Spring cell numbers in Huron are now the lowest observed throughout the basin, averaging around 200 cells/ml and a biovolume less than 50,000 μm^3/ml. Summer cell numbers have also

apparently declined somewhat since 1999, but biovolume remains similar, dominated by an assemblage of loricate chrysophytes (including *Dinobryon cylindricum*) and select diatoms (including *Cyclotella comta*).

Lake Erie West (Figure 2d): As for the cell densities in the upgradient lakes, Erie's western basin is typically dominated by blue-green algae in both spring and summer. However 2007 saw a dramatic spring decline in all taxa to an uncharacteristically low total density less than 1000 cells/ml, mostly filamentous centric diatoms that comprised most of the algal biovolume. Summer densities, biovolume and assemblage characteristics remain similar to those observed in the late 1990s.

Lake Erie Central (Figure 2e): Spring in Erie's central basin remains dominated by filamentous centric diatoms, especially *Aulacoseira islandica*. At some sites, spring 2007 saw biovolumes of *Aulacoseira* higher than 3,000,000 μm^3/ml, much higher than typical pre-2000 biovolumes. Summer assemblages in 2007 were typical of pre-2000 assemblages, the biovolume being represented by a diverse assemblage of algae.

Lake Erie East (Figure 2f): Erie's eastern basin similarly saw a significant increase in the biovolume of filamentous centric diatoms in the spring. The summer assemblages were similar to those observed in pre-2000 samples, but total biovolume in 2007 was about half what it was in 1999.

Lake Ontario (Figure 2g): Pre-2000 spring algal densities were dominated by blue-green algae, but very few blue-greens were observed in 2007. In relative terms, biovolume of the spring assemblage is dominated by centric diatoms (including *Aulacoseira islandica*) and cryptophytes (including *Rhodomonas minuta*), however the 2007 density and biovolume was much lower than observed in pre-2000 samples. Summer densities of phytoplankton are dominated by blue-green algae, and 2007 assemblages were similar in number and composition to pre-2000 records. Summer biovolumes, however, have approximately doubled since 1999, particularly with increases in pennate diatoms (including *Diatoma tenue* v. *elongatum* and *Fragilaria crotonensis*) and blue-green algae (including the large-celled *Anabaena flos-aquae*). The dinoflagellate *Ceratium hirundinella* remains an important component of Ontario's summer biovolume.

4. Multivariate relationships – pre-2000 versus 2007 (Figures 3a-3d)

To examine taxonomic comparability between the 2007 and pre-2000 phytoplankton datasets correspondence analyses (CA) were conducted. Preliminary detrended correspondence analyses indicated that the phytoplankton species were responding unimodally along environmental gradients, and so CA (a parametric, unimodal technique) was applied. Downweighting of rare species was applied to minimize their influence on analyses. Analyses were performed separately for spring and summer datasets, and for absolute abundance (cells/ml; Figure 3a) relative cell density (percent of total abundance; Figure 3b), biovolume (μm^3/ml; Figure 3c) and relative biovolume (percent of total biovolume; Figure 3d) datasets.

There are obvious differences between the 2007 and pre-2000 data in most of the ordinations (Figures 3a-3d). Given the considerable effort to ensure taxonomic consistency, we contend that these differences reflect real changes in the lakes during the eight-year gap between datasets, and that further analyses of data from the intermittent years will be important to explain the timing, causes and impacts of recent ecological shifts in the lakes.

Differences between pre-2000 and 2007 datasets are much more pronounced in the spring datasets (Figures 3a top, 3c top), and the 2007 assemblages appear less diverse as inferred from their smaller

footprint in the ordination diagrams. The spring season is clearly the period of greatest change in the phytoplankton. Overlap in the datasets during the summer indicates that the 2007 phytoplankton communities eventually stabilized to conditions similar to those observed prior to 2000.

Based on all data types, spring Lake Erie data from 2007 stand out as being substantially different from pre-2000 conditions. This difference is largely due to very low diversity and evenness in spring 2007, principally marked by a high abundance of *Aulacoseira islandica*.

In most cases scores for the first two axes lie in a triangular pattern, especially when the data are represented as relative numbers. This pattern is due to the fact that the Great Lakes phytoplankton assemblages for a particular season tend to fall into three main groups:

Spring density

- Lake Erie central and western basin assemblages dominated by filamentous centric diatoms
- A sparse, low density Lake Erie eastern basin assemblage dominated by filamentous centric diatoms
- Lakes Superior, Michigan and Huron assemblages dominated by blue-green algae

Summer density

- Lakes Superior, Michigan, Huron and Erie assemblages dominated by blue-green algae
- A small subset of Lake Erie eastern basin samples with relatively low abundance almost exclusively composed of blue-green algae
- A sparse group of samples from throughout the basin with diverse assemblages

Spring biovolume

- Lake Erie assemblages dominated by filamentous centric diatoms
- A diverse, low-biovolume assemblage in Lake Superior
- Lake Huron assemblages dominated by pennate diatoms

Summer biovolume

- A diverse Lake Erie assemblage
- Lakes Ontario and Michigan assemblages dominated by pennate diatoms, overlapping with Lake Huron samples dominated by diatoms and green algae
- Oligotrophic Lake Superior assemblages dominated by single-celled centric diatoms

5. Model development – 1999 versus 2007

Background

Modeling approaches were applied to characterize the environmental coefficients of the Great Lakes phytoplankton taxa. Developing effective indicators of ecological condition requires that indicators be calibrated to identify their responses to important environmental stressors (Karr and Chu 1999, Seegert 2001). The main goals of calibration are to identify environmental optima and tolerances of indicator taxa. Although bioindicator approaches in the Great Lakes have gained attention in the last decade (e.g., Environment Canada and U.S. EPA 2003, Uzarski et al. 2004), most indicators proposed for Great Lakes coastal environments remain uncalibrated and untested. Assemblages of algae, which are physiologically

subject to water chemistry and grazers, have the potential to provide time-integrated inferences of limnological conditions. These bioindicators are particularly needed to monitor the impacts of human activities that are increasing nutrient supplies to water bodies, introducing non-native species and changing climate. As a primary goal of GLNPO's biological monitoring program, tracking long-term change should be strongly supported by algae indicator data.

Modern datasets, also known as training sets, provide the basis for development of indicator transfer functions by relating contemporary assemblages with their corresponding environmental measurements. Algal assemblages, in particular, are proven robust indicators of stressors such as nutrients (e.g., Tibby 2004, Meriläinen et al. 2003), water clarity (Dixit and Smol 1994) and acidification (e.g., Siver et al. 2003), as well as a suite of other water quality problems in freshwater ecosystems (Smol 2002). Algae are known to have definable optima along gradients of environmental conditions. Species tend to be taxonomically distinct and abundant in almost all aquatic environments, and they respond rapidly to changing conditions. Hence, researchers can use changes in community composition to classify and quantify long-term environmental changes that result from anthropogenic activities.

A transfer function is derived by relating algae taxa assemblages in a training set of samples (in this case, pelagic samples collected throughout the Great Lakes) to an environmental variable of interest (Charles 1990). The transfer function consists of taxa coefficients (environmental optima and tolerances) that can be used to infer quantitative information about the variable of interest, based on the abundance of each taxon in a sample assemblage. Transfer function evaluation and testing typically involves the comparison of algal-inferred water quality to measured water quality to evaluate function robustness, which is usually characterized by a coefficient of determination (r^2) and a prediction error (RMSE).

In addition to developing indicator models, characterizing the environmental characteristics of Great Lakes taxa provides a means to evaluate year-to-year taxonomic consistency. Numerous taxonomic issues have resulted in re-evaluation of data collected from 2001 through 2004 (e.g., Barbiero 2006), and a significant effort was assumed to ensure taxonomic consistency between the recent 2007 dataset and pre-2000 phytoplankton collections. If taxonomic data are comparable (say, between 1999 and 2007 datasets) then the calibrated environmental optima and tolerances derived for each year's set of taxa will be similar. Fundamental Niche Theory (Vandermeer 1972) suggests that the environmental preferences of species should remain unchanged, particularly for highly diverse organisms such as algae. We would expect that taxon-specific optima and tolerances to environmental parameters would be unchanged over the last decade. Otherwise, if taxonomic consistency between years is poor (i.e., diagnostic identifications have not been consistent), we would expect the species coefficients between years to be different. More importantly, the confirmation of taxonomic inconsistencies will complicate long-term trend analyses for the lakes.

Methods

Three phytoplankton-phosphorus transfer functions were developed based on spring assemblages from 1999, 2003 and 2007. Density data were chosen because preliminary analyses suggested the strongest species-environmental relationships occurred when phytoplankton data were represented as densities. We hypothesized that model testing would show consistency between 1999 and 2007 assemblages, and we deliberately selected an "uncorrected" set of data from 2003 to illustrate the impact of taxonomic inconsistencies on species-environmental relationships. It is important to note that several issues with the

2003 phytoplankton data have been identified and corrected, and the uncorrected 2003 dataset is used specifically to test our hypotheses.

Transfer functions for Great Lakes total phosphorus (TP) were developed using weighted averaging (WA) regression with inverse deshrinking and tested using jackknife (leave-one-out) cross-validation for error estimation and lognormal taxa transformation (C2 software; Juggins 2003). Algal-inferred estimates of TP for each sample were calculated by taking the optimum of each taxon to that variable, weighting it by its abundance in that sample, and calculating the average of the combined weighted taxa optima (Birks et al. 1994). The strengths of the transfer functions were evaluated by calculating the squared correlation coefficient (r^2) and the root mean square error (RMSE) between measured TP and transfer function estimates of those values for all samples.

Results and Discussion

Several of the most common species have been further evaluated to determine their environmental characteristics (Figures 4a-4gg). Three environmental variables, total phosphorus (TP), silica and chloride (Cl^-), have been selected as the environmental gradients because of their known relationships to phytoplankton distributions. The varied distributions of taxa along the environmental gradients are interesting and illustrate how the optimum and tolerance values are derived. For instance, the abundant *Aulacoseira islandica* (Figure 4a) tends to occur in environments with high TP, low silica and high chloride. It is worth noting that *Aulacoseira* is a relatively heavy diatom that requires abundant silica for cell wall development, and the fact that it occurs in low silica conditions is likely a result of silica depletion by the diatoms themselves, particularly in Lake Erie. Contrast this with species of *Cyclotella* (Figures 4b, 4c, 4d; *comensis* "rough center with process", *comensis* var. 1, *comta*) which favor low TP, high silica and low chloride environments.

Most taxa show relatively specific optima for chemical variables, with a few exceptions. Cryptophytes such as *Rhodomonas lens* (Figure 4w) and *Rhodomonas minuta* (Figure 4x) are more cosmopolitan in the lakes, exhibiting broad tolerances to the three variables shown. Some species appear to show preferences to single variables. For instance, *Gymnodinium helveticum* (Figure 4gg) has a fairly well-defined, oligotrophic TP optimum, whereas it has a monotonous response along both the silica and chloride gradients.

Model testing indicated that each selected year's data was capable of providing a robust indicator model (Figure 5). Within itself the uncorrected dataset (2003) had a relatively high observed-inferred relationship ($r^2_{jackknife} = 0.66$), so although taxonomic discrepancies were observed between years, taxonomy was sufficiently robust within the year 2003 to provide an indicator model based on that year's taxonomic protocols. Based on model performance criteria (higher r^2 and lower prediction error) the "best" model was derived using 2007 data. Confirming that this is a better model is deceptive due to the extreme characteristics that were observed in spring 2007. In particular, 2007 exhibited a much greater rift in water quality conditions (and algal assemblages) between lakes than previously observed, especially that nutrient concentrations in Superior are getting lower, whereas those in Erie appear to be getting higher. The similar rift in algal data supported a model that had little problem, for instance, reconstructing total phosphorus based on Erie samples dominated by *Aulacoseira* (Figure 5, upper right of the 2007 plot).

As would be expected for a taxonomically consistent dataset, the species optima and tolerances are similar between 1999 and 2007 (Figure 6). Some variations in species coefficients between years are

attributed to typical analytical error associated with water quality sampling and phytoplankton sample assessment. Also, due to changes in the species assemblages, some species may have been poorly represented in one of the years, resulting in weaker calibration data. Despite the subtle variations there is a marked similarity in species coefficients between years. The importance of taxonomic consistency was underlined by species coefficients for the uncorrected 2003 dataset (data not presented), which indicated poor compatibility with 1999 and 2007.

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Table 1. Dominant Great Lakes taxa based on 2007 collections. Presented are the top 10 most common taxa encountered throughout the basin, and the top five most common taxa encountered in each lake. BAC = centric diatoms; BAP = pennate diatoms; CHR = chrysophytes; CRY = cryptophytes; CHL = green algae; EUG = euglenoids; PYR = dinoflagellates; CYA =blue-greens.

Species Code	Taxon	Group	Average value
ALL LAKES, AVERAGE OF BY-LAKE AVERAGES			
Spring 2007 Density (cells/ml)			
AULISLA	*Aulacoseira islandica*	BAC	166.81
STEPARV	*Stephanodiscus parvus*	BAC	109.53
OSCMINI	*Oscillatoria minima*	CYA	44.36
RHOMINU	*Rhodomonas minuta*	CRY	40.04
OSCLIMN	*Oscillatoria limnetica*	CYA	33.95
APASP	*Aphanocapsa* sp.	CYA	27.43
STEHANTH	*Stephanodiscus hantzschii* f. *hantzschii*	BAC	19.09
HAPSP	Haptophyceae	CHR	17.26
ASTFORM	*Asterionella formosa*	BAP	16.53
STEBIND	*Stephanodiscus binderanus*	BAC	16.14
Spring 2007 Biovolume (µm³/ml)			
AULISLA	*Aulacoseira islandica*	BAC	345053.38
STEALP23	*Stephanodiscus alpinus* Type II/III	BAC	15761.65
STEBIND	*Stephanodiscus binderanus*	BAC	15187.94
ASTFORM	*Asterionella formosa*	BAP	10257.39
STEPARV	*Stephanodiscus parvus*	BAC	9672.64
STENIAG	*Stephanodiscus niagarae*	BAC	7955.58
STEALP1	*Stephanodiscus alpinus* Type I	BAC	6361.37
PHASPE	*Phacus* sp.	EUG	4390.17
CRYREFL	*Cryptomonas reflexa*	CRY	4379.94
FRACROT	*Fragilaria crotonensis*	BAP	4320.90
Summer 2007 Density (cells/ml)			
APASP	*Aphanocapsa* sp.	CYA	2945.99
OSCLIMN	*Oscillatoria limnetica*	CYA	1042.10
RHOMINU	*Rhodomonas minuta*	CRY	203.22
OSCSP	*Oscillatoria* sp.	CYA	201.50
OSCMINI	*Oscillatoria minima*	CYA	118.49
MERTENU	*Merismopedia tenuissima*	CYA	118.47
MONMINU	*Monoraphidium minutum*	CHL	95.87
UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	CHR	94.07
HAPSP	Haptophyceae	CHR	86.05
FRACROT	*Fragilaria crotonensis*	BAP	86.05
Summer 2007 Biovolume (µm³/ml)			
DIATENUE	*Diatoma tenue* var. *elongatum*	BAP	36309.98
FRACROT	*Fragilaria crotonensis*	BAP	35657.66
CERHIRU	*Ceratium hirundinella*	PYR	30863.31
CYCCOMT	*Cyclotella comta*	BAC	22707.78
CRYREFL	*Cryptomonas reflexa*	CRY	20705.30
APASP	*Aphanocapsa* sp.	CYA	14844.76
OSCLIMN	*Oscillatoria limnetica*	CYA	13615.04
ANBFLOS	*Anabaena flos-aquae*	CYA	12907.90
UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	CHR	12730.21
CRYEROS	*Cryptomonas erosa*	CRY	12005.56

Table 1 (continued)

Species Code	Taxon	Group	Average value
ALL LAKES, AVERAGED BY ALL SAMPLES			
Spring 2007 Density (cells/ml)			
AULISLA	*Aulacoseira islandica*	BAC	229.68
STEPARV	*Stephanodiscus parvus*	BAC	102.29
RHOMINU	*Rhodomonas minuta*	CRY	38.11
OSCMINI	*Oscillatoria minima*	CYA	35.02
OSCLIMN	*Oscillatoria limnetica*	CYA	31.26
APASP	*Aphanocapsa* sp.	CYA	26.13
STEBIND	*Stephanodiscus binderanus*	BAC	22.23
STEHANTH	*Stephanodiscus hantzschii* f. *hantzschii*	BAC	21.14
UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	CHR	16.90
HAPSP	Haptophyceae	CHR	16.56
Spring 2007 Biovolume (µm³/ml)			
AULISLA	*Aulacoseira islandica*	BAC	475022.51
STEBIND	*Stephanodiscus binderanus*	BAC	20913.85
STEALP23	*Stephanodiscus alpinus* Type II/III	BAC	20880.17
STENIAG	*Stephanodiscus niagarae*	BAC	10770.30
ASTFORM	*Asterionella formosa*	BAP	10366.68
STEPARV	*Stephanodiscus parvus*	BAC	9210.72
STEALP1	*Stephanodiscus alpinus* Type I	BAC	7971.80
PHASPE	*Phacus* sp.	EUG	6031.04
GYMSP	*Gymnodinium* sp.	PYR	4315.38
FRACROT	*Fragilaria crotonensis*	BAP	3792.00
Summer 2007 Density (cells/ml)			
APASP	*Aphanocapsa* sp.	CYA	2727.66
OSCLIMN	*Oscillatoria limnetica*	CYA	814.24
RHOMINU	*Rhodomonas minuta*	CRY	170.55
OSCSP	*Oscillatoria* sp.	CYA	162.44
OSCMINI	*Oscillatoria minima*	CYA	118.48
MERTENU	*Merismopedia tenuissima*	CYA	95.30
UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	CHR	90.58
APOSP	*Aphanothece* sp.	CYA	85.07
MONMINU	*Monoraphidium minutum*	CHL	81.54
HAPSP	Haptophyceae	CHR	76.79
Summer 2007 Biovolume (µm³/ml)			
CYCCOMT	*Cyclotella comta*	BAC	30694.43
FRACROT	*Fragilaria crotonensis*	BAP	30043.47
DIATENUE	*Diatoma tenue* var. *elongatum*	BAP	25447.63
CERHIRU	*Ceratium hirundinella*	PYR	23573.31
CRYREFL	*Cryptomonas reflexa*	CRY	16791.43
APASP	*Aphanocapsa* sp.	CYA	13747.80
UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	CHR	12397.80
OSCLIMN	*Oscillatoria limnetica*	CYA	10605.69
ASTFORM	*Asterionella formosa*	BAP	10061.46
CRYEROS	*Cryptomonas erosa*	CRY	9771.30

Table 1 (continued)

Species Code	Taxon	Group	Average value
LAKE SUPERIOR			
Spring 2007 Density (cells/ml)			
OSCLIMN	*Oscillatoria limnetica*	CYA	44.53
APASP	*Aphanocapsa* sp.	CYA	36.73
APOSP	*Aphanothece* sp.	CYA	21.98
OSCMINI	*Oscillatoria minima*	CYA	18.35
HAPSP	Haptophyceae	CHR	9.04
Spring 2007 Biovolume (µm³/ml)			
CRYREFL	*Cryptomonas reflexa*	CRY	3337.07
CRYEROS	*Cryptomonas erosa*	CRY	2886.15
GYMHELV	*Gymnodinium helveticum*	PYR	2669.11
ASTFORM	*Asterionella formosa*	BAP	1696.76
STEPSBTR	*Stephanodiscus subtransylvanicus*	BAC	1095.76
Summer 2007 Density (cells/ml)			
APASP	*Aphanocapsa* sp.	CYA	1568.16
OSCLIMN	*Oscillatoria limnetica*	CYA	223.42
OSCMINI	*Oscillatoria minima*	CYA	101.78
OSCSP	*Oscillatoria* sp.	CYA	81.96
UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	CHR	70.85
Summer 2007 Biovolume (µm³/ml)			
CYCCOMT	*Cyclotella comta*	BAC	81729.95
CYCCOMRC	*Cyclotella comensis rough center w/ process*	BAC	10848.13
UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	CHR	10375.74
GYMHELV	*Gymnodinium helveticum*	PYR	9385.23
APASP	*Aphanocapsa* sp.	CYA	6679.17
LAKE MICHIGAN			
Spring 2007 Density (cells/ml)			
OSCMINI	*Oscillatoria minima*	CYA	189.26
OSCLIMN	*Oscillatoria limnetica*	CYA	67.67
APASP	*Aphanocapsa* sp.	CYA	61.70
FRACROT	*Fragilaria crotonensis*	BAP	26.23
RHOMINU	*Rhodomonas minuta*	CRY	23.11
Spring 2007 Biovolume (µm³/ml)			
FRACROT	*Fragilaria crotonensis*	BAP	14147.47
AULISLA	*Aulacoseira islandica*	BAC	9851.31
DIATENUE	*Diatoma tenue* var. *elongatum*	BAP	3902.58
ASTFORM	*Asterionella formosa*	BAP	3705.48
CRYREFL	*Cryptomonas reflexa*	CRY	3405.37
Summer 2007 Density (cells/ml)			
APASP	*Aphanocapsa* sp.	CYA	558.26
OSCMINI	*Oscillatoria minima*	CYA	410.18
FRACROT	*Fragilaria crotonensis*	BAP	175.55
OSCLIMN	*Oscillatoria limnetica*	CYA	158.24
UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	CHR	123.45
Summer 2007 Biovolume (µm³/ml)			
FRACROT	*Fragilaria crotonensis*	BAP	76759.28
MOUSP	*Mougeotia* sp.	CHL	22199.13
ASTFORM	*Asterionella formosa*	BAP	18543.25
UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	CHR	18136.61
SYNFILI	*Synedra filiformis*	BAP	15705.68

Table 1 (continued)

Species Code	Taxon	Group	Average value
LAKE HURON			
Spring 2007 Density (cells/ml)			
OSCLIMN	*Oscillatoria limnetica*	CYA	27.67
HAPSP	Haptophyceae	CHR	24.22
APASP	*Aphanocapsa* sp.	CYA	22.64
UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	CHR	20.12
RHOMINU	*Rhodomonas minuta*	CRY	19.20
Spring 2007 Biovolume (µm³/ml)			
ASTFORM	*Asterionella formosa*	BAP	14254.17
RHOLENS	*Rhodomonas lens*	CRY	4164.33
FRACROT	*Fragilaria crotonensis*	BAP	3796.85
CYMSOLE	*Cymatopleura solea*	BAP	3236.52
UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	CHR	2940.54
Summer 2007 Density (cells/ml)			
APASP	*Aphanocapsa* sp.	CYA	1665.30
APOSP	*Aphanothece* sp.	CYA	174.33
CYCCOME1	*Cyclotella comensis* var. 1	BAC	78.25
DINCYLI	*Dinobryon cylindricum*	CHR	68.77
UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	CHR	68.38
Summer 2007 Biovolume (µm³/ml)			
DINCYLI	*Dinobryon cylindricum*	CHR	27227.92
CYCCOMT	*Cyclotella comta*	BAC	15733.72
APASP	*Aphanocapsa* sp.	CYA	10829.39
UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	CHR	10052.90
ASTFORM	*Asterionella formosa*	BAP	9921.40
LAKE ERIE			
Spring 2007 Density (cells/ml)			
AULISLA	*Aulacoseira islandica*	BAC	828.12
STEPARV	*Stephanodiscus parvus*	BAC	234.72
STEBIND	*Stephanodiscus binderanus*	BAC	80.27
RHOMINU	*Rhodomonas minuta*	CRY	71.59
STEHANTH	*Stephanodiscus hantzschii* f. *hantzschii*	BAC	61.52
Spring 2007 Biovolume (µm³/ml)			
AULISLA	*Aulacoseira islandica*	BAC	1712403.69
STEBIND	*Stephanodiscus binderanus*	BAC	75481.39
STEALP23	*Stephanodiscus alpinus* Type II/III	BAC	72763.01
STENIAG	*Stephanodiscus niagarae*	BAC	36909.84
STEALP1	*Stephanodiscus alpinus* Type I	BAC	25919.48
Summer 2007 Density (cells/ml)			
APASP	*Aphanocapsa* sp.	CYA	9281.63
OSCLIMN	*Oscillatoria limnetica*	CYA	1354.80
MONMINU	*Monoraphidium minutum*	CHL	448.71
RHOMINU	*Rhodomonas minuta*	CRY	414.21
APOSP	*Aphanothece* sp.	CYA	193.36
Summer 2007 Biovolume (µm³/ml)			
CERHIRU	*Ceratium hirundinella*	PYR	54723.88
APASP	*Aphanocapsa* sp.	CYA	49052.29
CRYREFL	*Cryptomonas reflexa*	CRY	42980.35
CRYEROS	*Cryptomonas erosa*	CRY	29653.13
FRACROT	*Fragilaria crotonensis*	BAP	29015.19

Table 1 (continued)

Species Code	Taxon	Group	Average value
LAKE ONTARIO			
Spring 2007 Density (cells/ml)			
STEPARV	*Stephanodiscus parvus*	BAC	301.25
RHOMINU	*Rhodomonas minuta*	CRY	79.58
STEHANTH	*Stephanodiscus hantzschii* f. *hantzschii*	BAC	29.96
ASTFORM	*Asterionella formosa*	BAP	28.32
RHOLENS	*Rhodomonas lens*	CRY	26.29
Spring 2007 Biovolume (µm³/ml)			
STEPARV	*Stephanodiscus parvus*	BAC	25635.15
ASTFORM	*Asterionella formosa*	BAP	13740.16
CRYREFL	*Cryptomonas reflexa*	CRY	13218.85
GYMHELV	*Gymnodinium helveticum*	PYR	12177.58
CRYEROS	*Cryptomonas erosa*	CRY	6599.77
Summer 2007 Density (cells/ml)			
OSCLIMN	*Oscillatoria limnetica*	CYA	3450.66
APASP	*Aphanocapsa* sp.	CYA	1656.59
OSCSP	*Oscillatoria* sp.	CYA	679.64
RHOMINU	*Rhodomonas minuta*	CRY	404.45
MERTENU	*Merismopedia tenuissima*	CYA	310.38
Summer 2007 Biovolume (µm³/ml)			
DIATENUE	*Diatoma tenue* var. *elongatum*	BAP	179131.55
CERHIRU	*Ceratium hirundinella*	PYR	94462.44
FRACROT	*Fragilaria crotonensis*	BAP	64168.56
ANBFLOS	*Anabaena flos-aquae*	CYA	62888.64
CRYREFL	*Cryptomonas reflexa*	CRY	50485.87

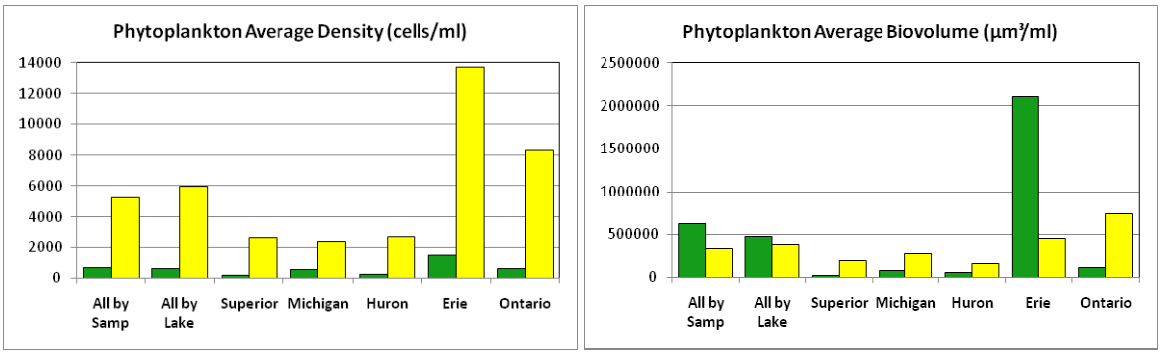

Figure 1a. Average phytoplankton densities (left) and biovolume (right) for spring (green) and summer (yellow) 2007. Total basin results are presented for an average of all samples ("All by Samp") and a master average of the by-lake average ("All by Lake").

Figure 1b. Spring 2007 dominant species: Average phytoplankton densities (left) and biovolume (right) for spring (green) and summer (yellow) 2007. Total basin results are presented for an average of all samples ("All by Samp") and a master average of the by-lake average ("All by Lake").

Figure 1b (continued). Spring 2007 dominant species: Average phytoplankton densities (left) and biovolume (right) for spring (green) and summer (yellow) 2007. Total basin results are presented for an average of all samples ("All by Samp") and a master average of the by-lake average ("All by Lake").

Figure 1c. Summer 2007 dominant species: Average phytoplankton densities (left) and biovolume (right) for spring (green) and summer (yellow) 2007. Total basin results are presented for an average of all samples ("All by Samp") and a master average of the by-lake average ("All by Lake").

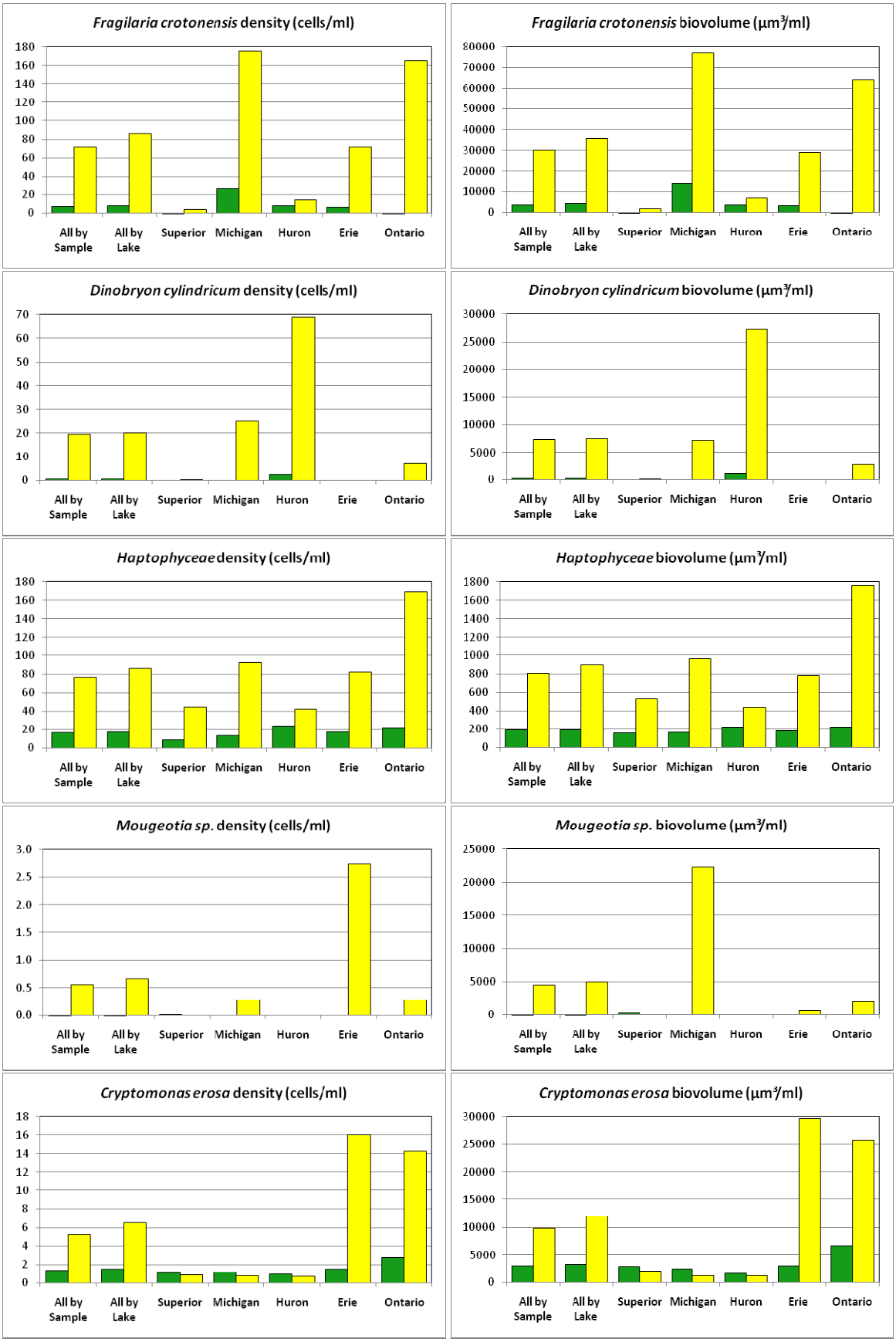

Figure 1c (continued). Summer 2007 dominant species: Average phytoplankton densities (left) and biovolume (right) for spring (green) and summer (yellow) 2007. Total basin results are presented for an average of all samples ("All by Samp") and a master average of the by-lake average ("All by Lake").

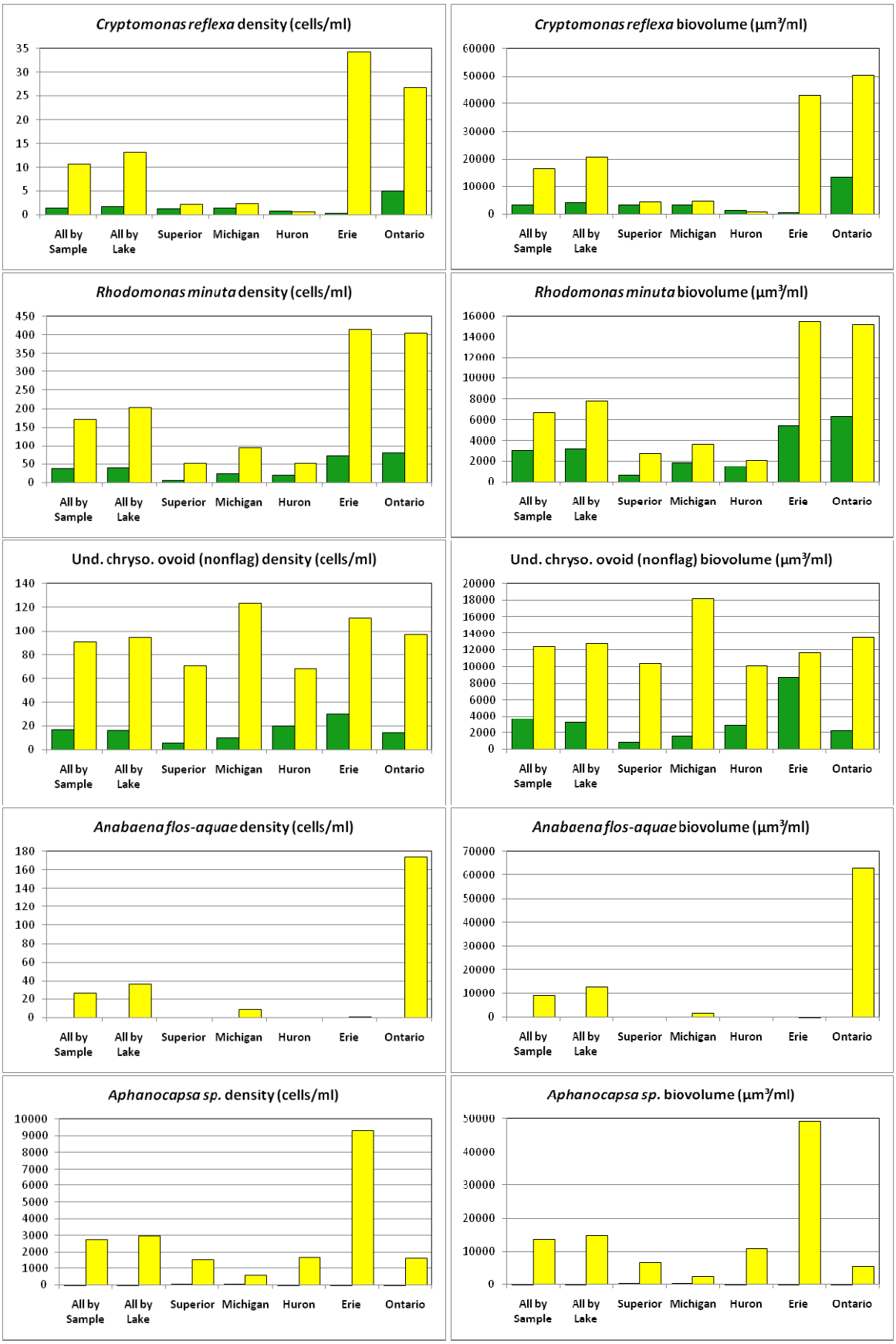

Figure 1c (continued). Summer 2007 dominant species: Average phytoplankton densities (left) and biovolume (right) for spring (green) and summer (yellow) 2007. Total basin results are presented for an average of all samples ("All by Samp") and a master average of the by-lake average ("All by Lake").

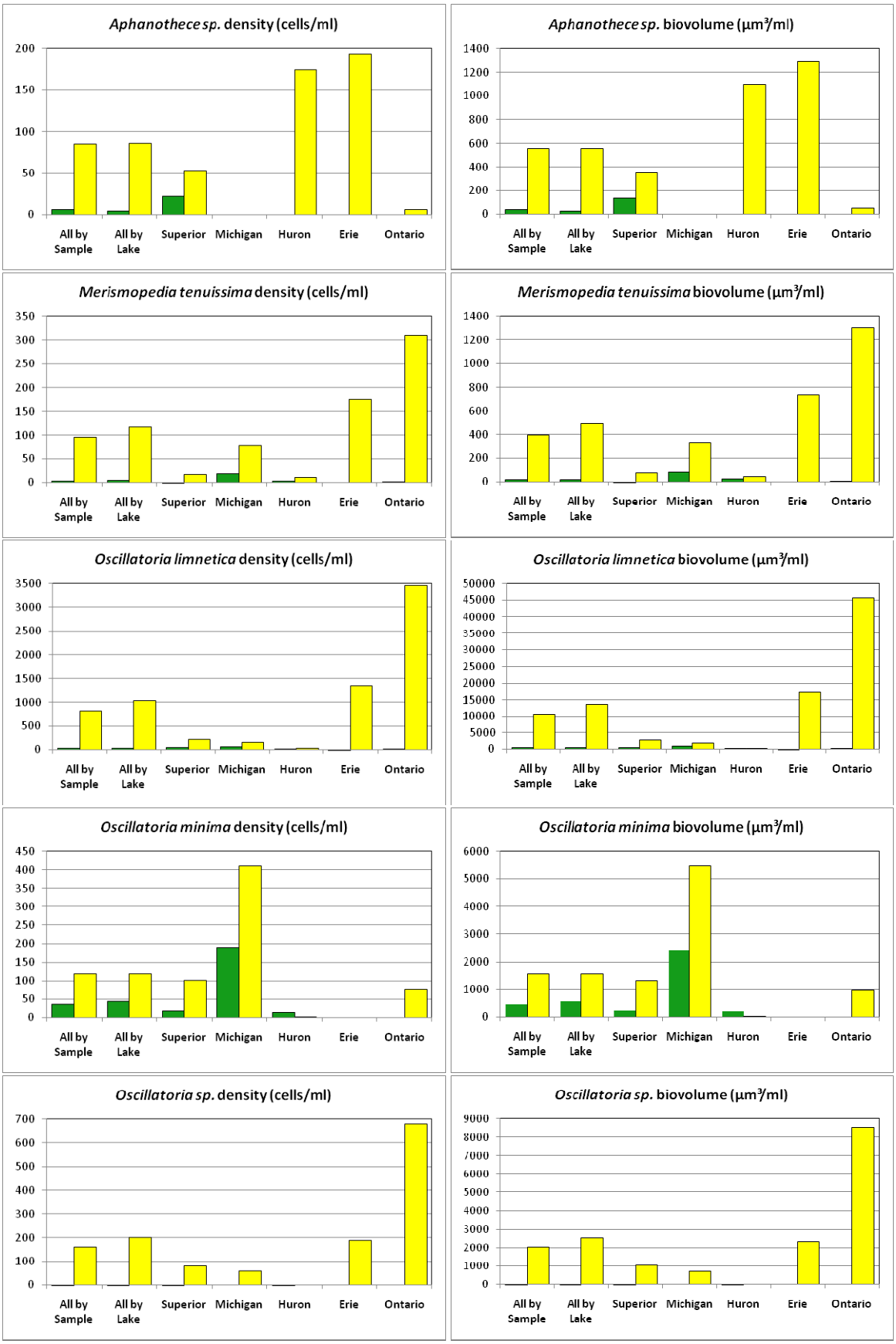

Figure 1c (continued). Summer 2007 dominant species: Average phytoplankton densities (left) and biovolume (right) for spring (green) and summer (yellow) 2007. Total basin results are presented for an average of all samples ("All by Samp") and a master average of the by-lake average ("All by Lake").

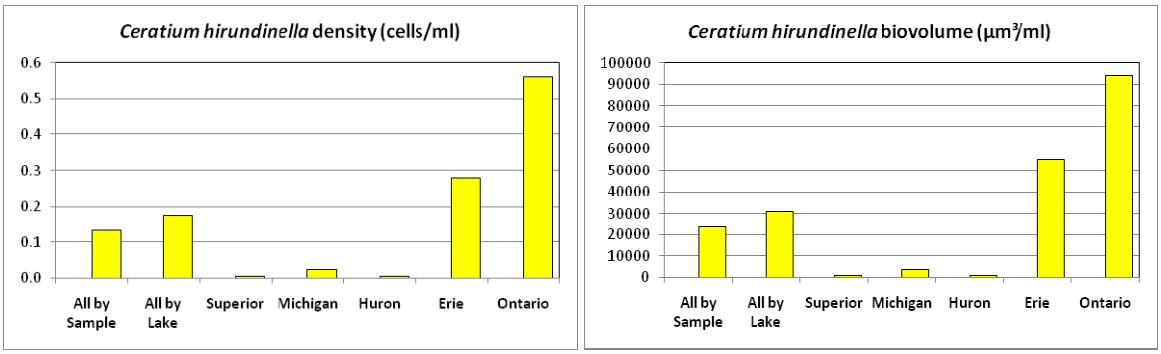

Figure Xc (continued). Summer 2007 dominant species: Average phytoplankton densities (left) and biovolume (right) for spring (green) and summer (yellow) 2007. Total basin results are presented for an average of all samples ("All by Samp") and a master average of the by-lake average ("All by Lake").

Figure 1d. Seasonally non-specific 2007 dominant species: Average phytoplankton densities (left) and biovolume (right) for spring (green) and summer (yellow) 2007. Total basin results are presented for an average of all samples ("All by Samp") and a master average of the by-lake average ("All by Lake").

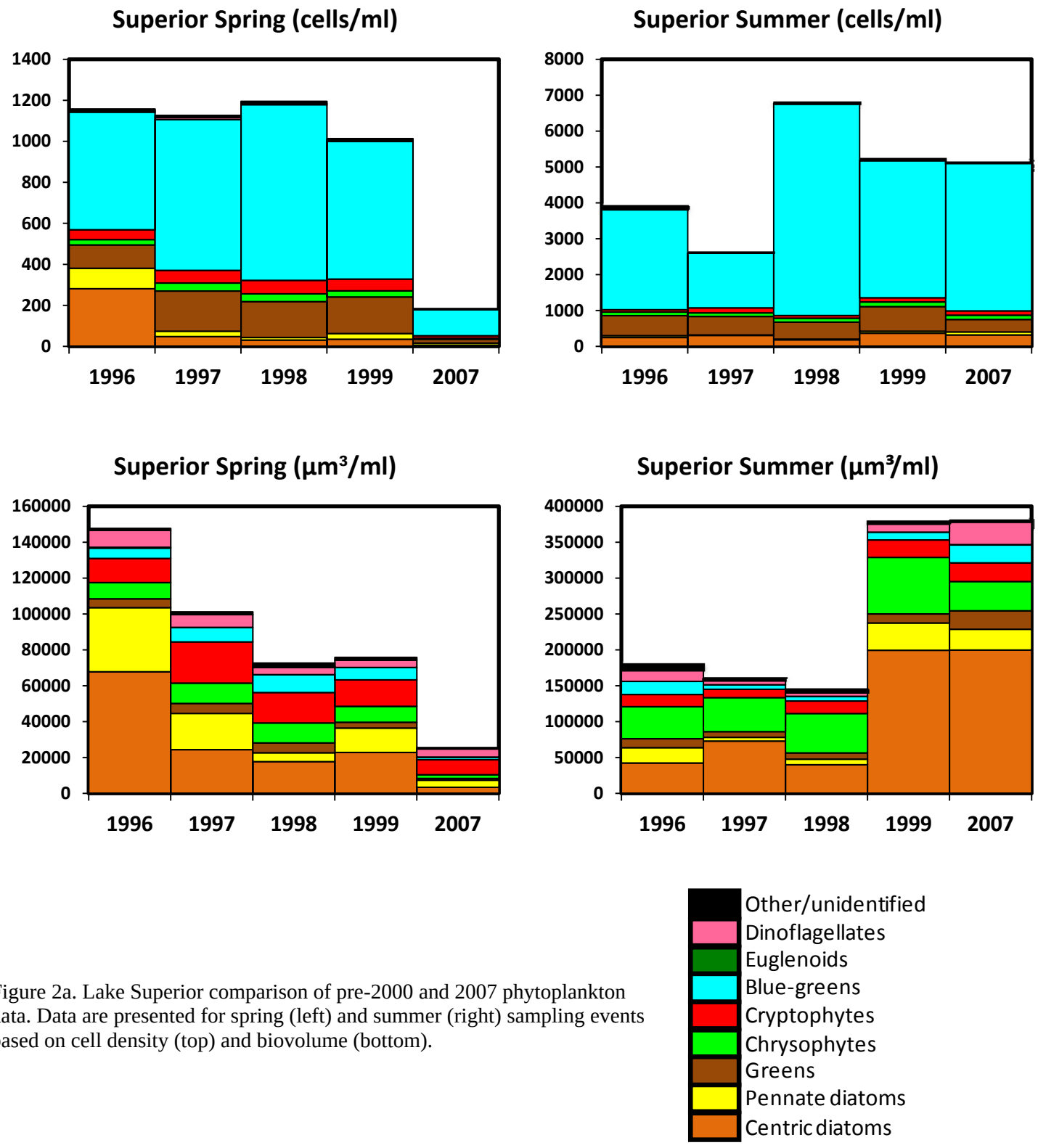

Figure 2a. Lake Superior comparison of pre-2000 and 2007 phytoplankton data. Data are presented for spring (left) and summer (right) sampling events based on cell density (top) and biovolume (bottom).

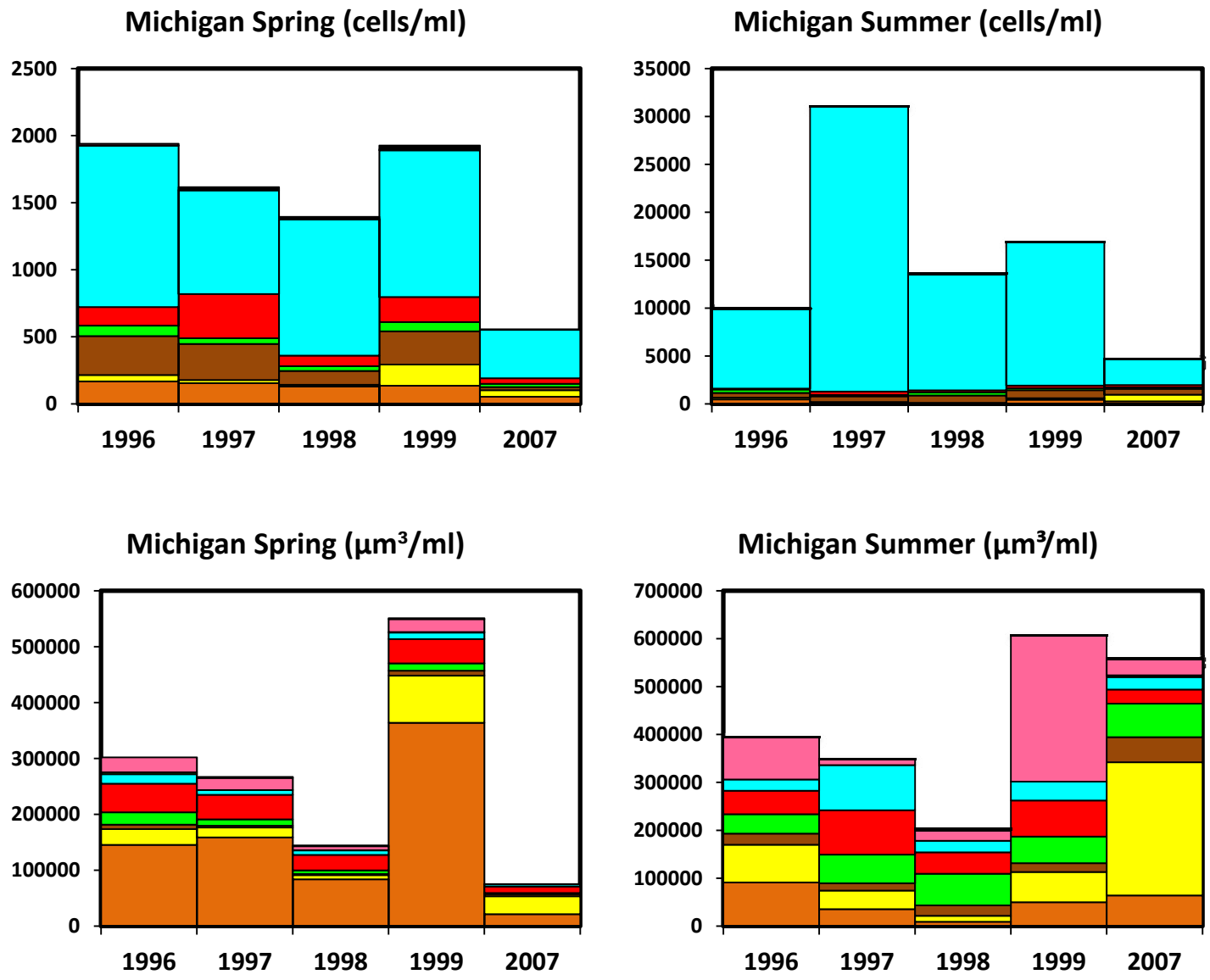

Figure 2b. Lake Michigan comparison of pre-2000 and 2007 phytoplankton data. Data are presented for spring (left) and summer (right) sampling events based on cell density (top) and biovolume (bottom).

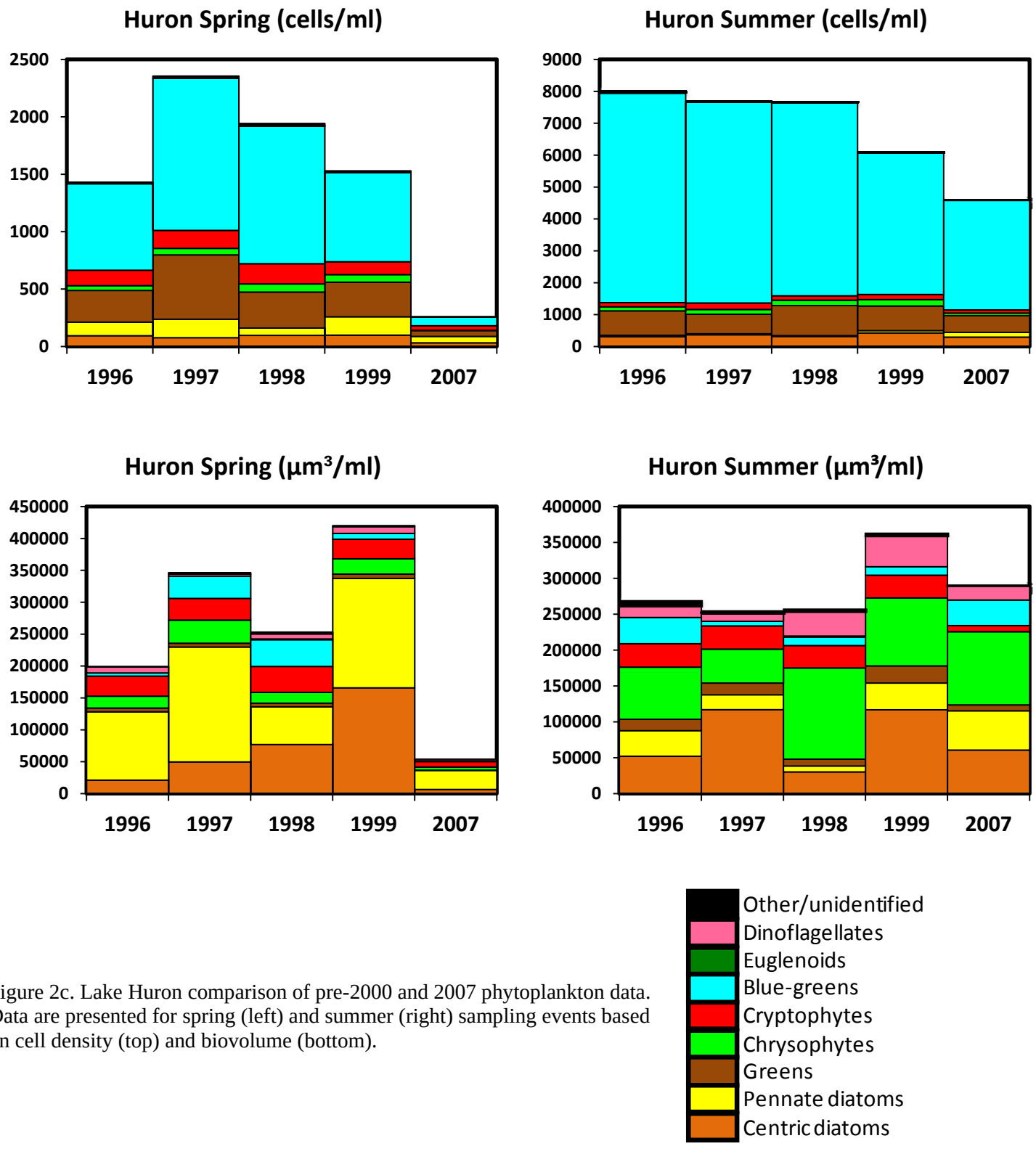

Figure 2c. Lake Huron comparison of pre-2000 and 2007 phytoplankton data. Data are presented for spring (left) and summer (right) sampling events based on cell density (top) and biovolume (bottom).

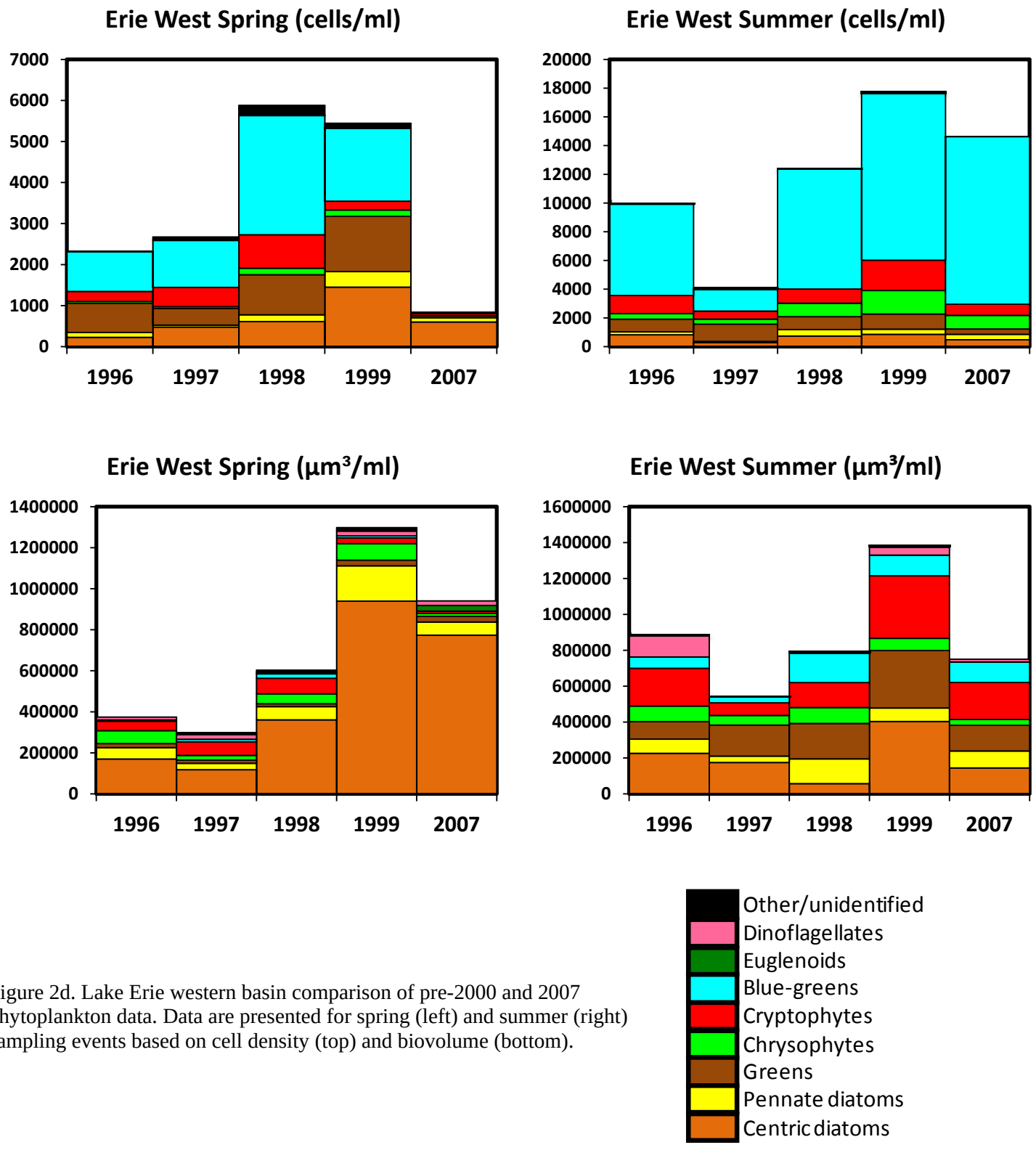

Figure 2d. Lake Erie western basin comparison of pre-2000 and 2007 phytoplankton data. Data are presented for spring (left) and summer (right) sampling events based on cell density (top) and biovolume (bottom).

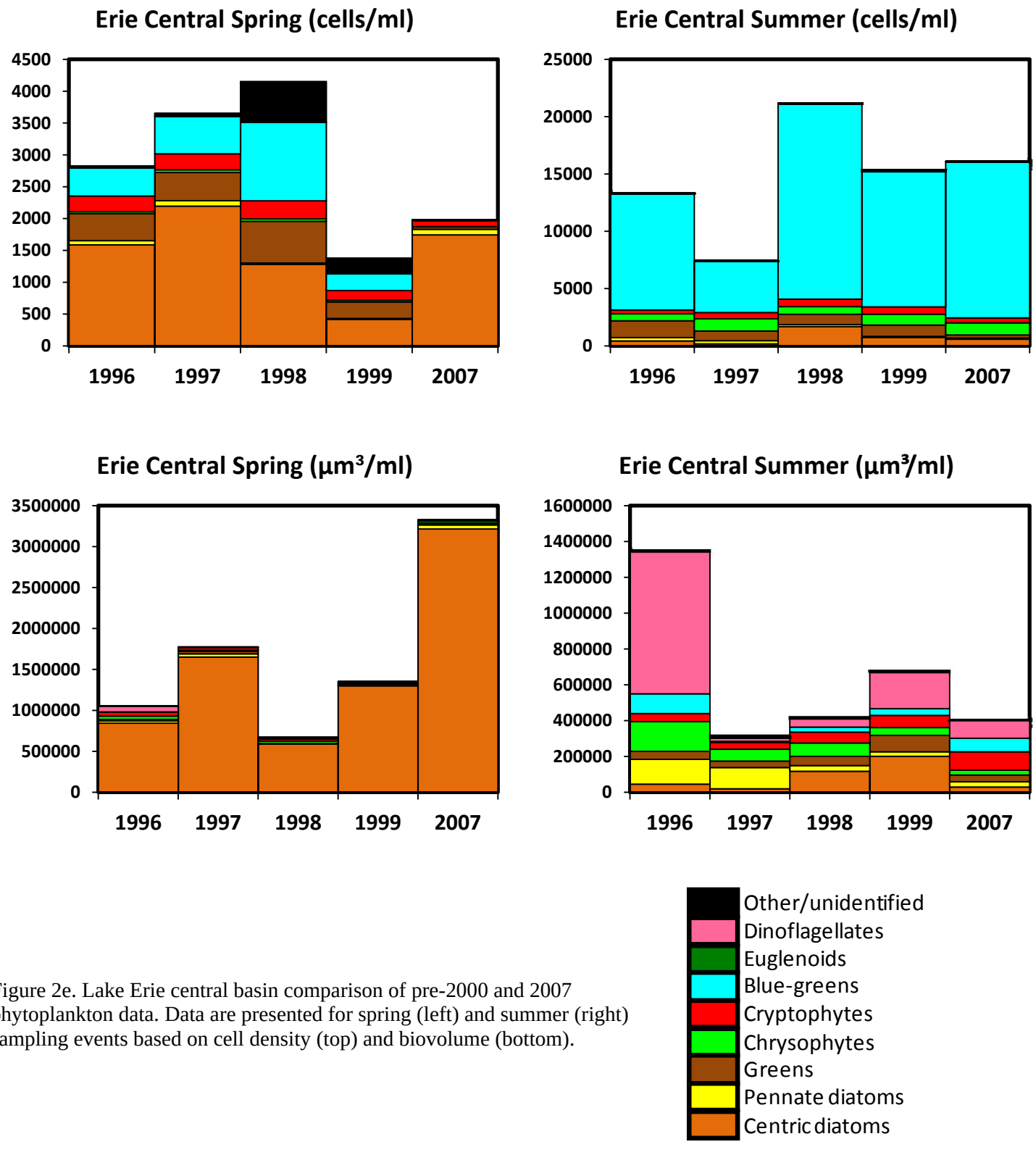

Figure 2e. Lake Erie central basin comparison of pre-2000 and 2007 phytoplankton data. Data are presented for spring (left) and summer (right) sampling events based on cell density (top) and biovolume (bottom).

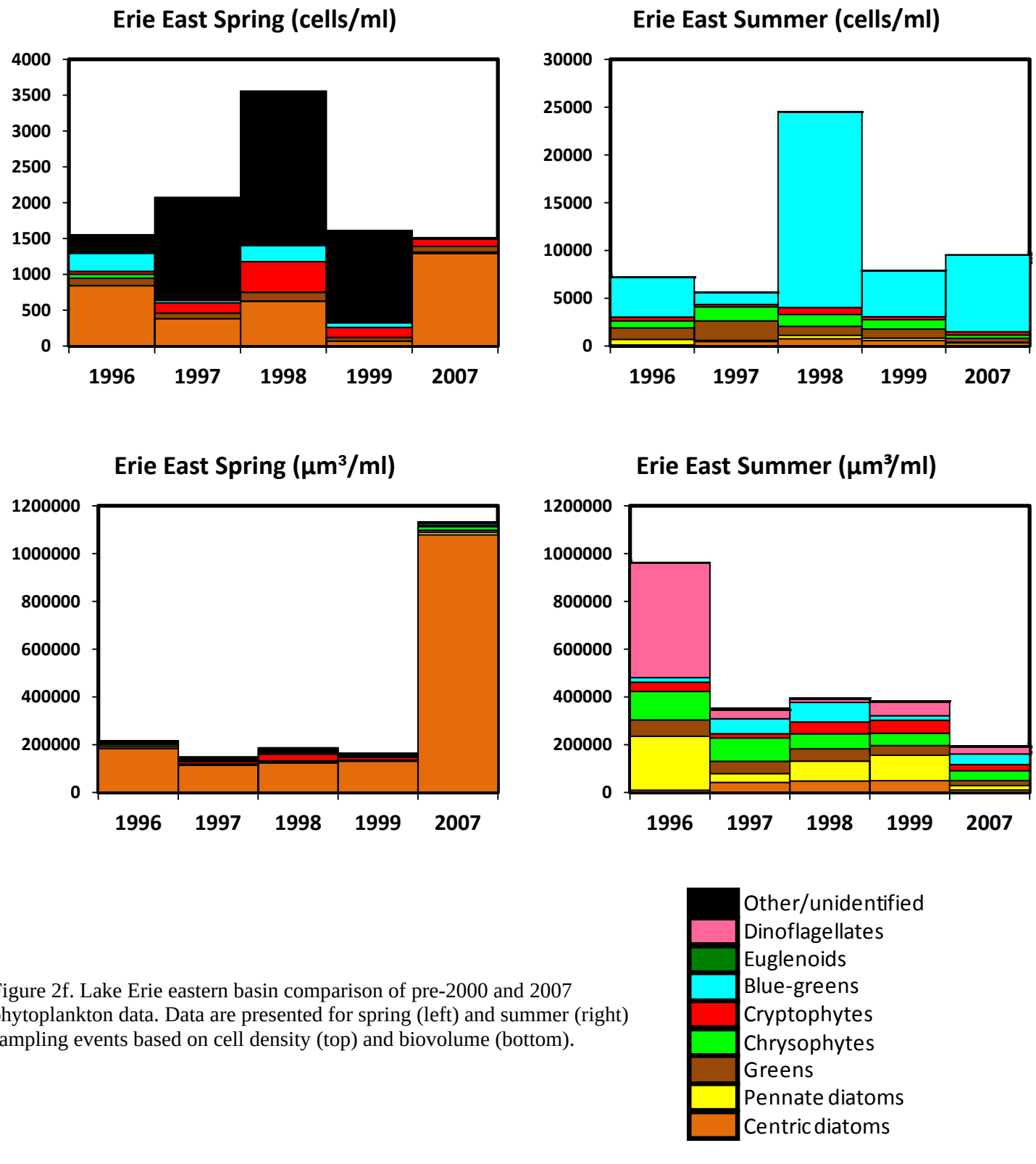

Figure 2f. Lake Erie eastern basin comparison of pre-2000 and 2007 phytoplankton data. Data are presented for spring (left) and summer (right) sampling events based on cell density (top) and biovolume (bottom).

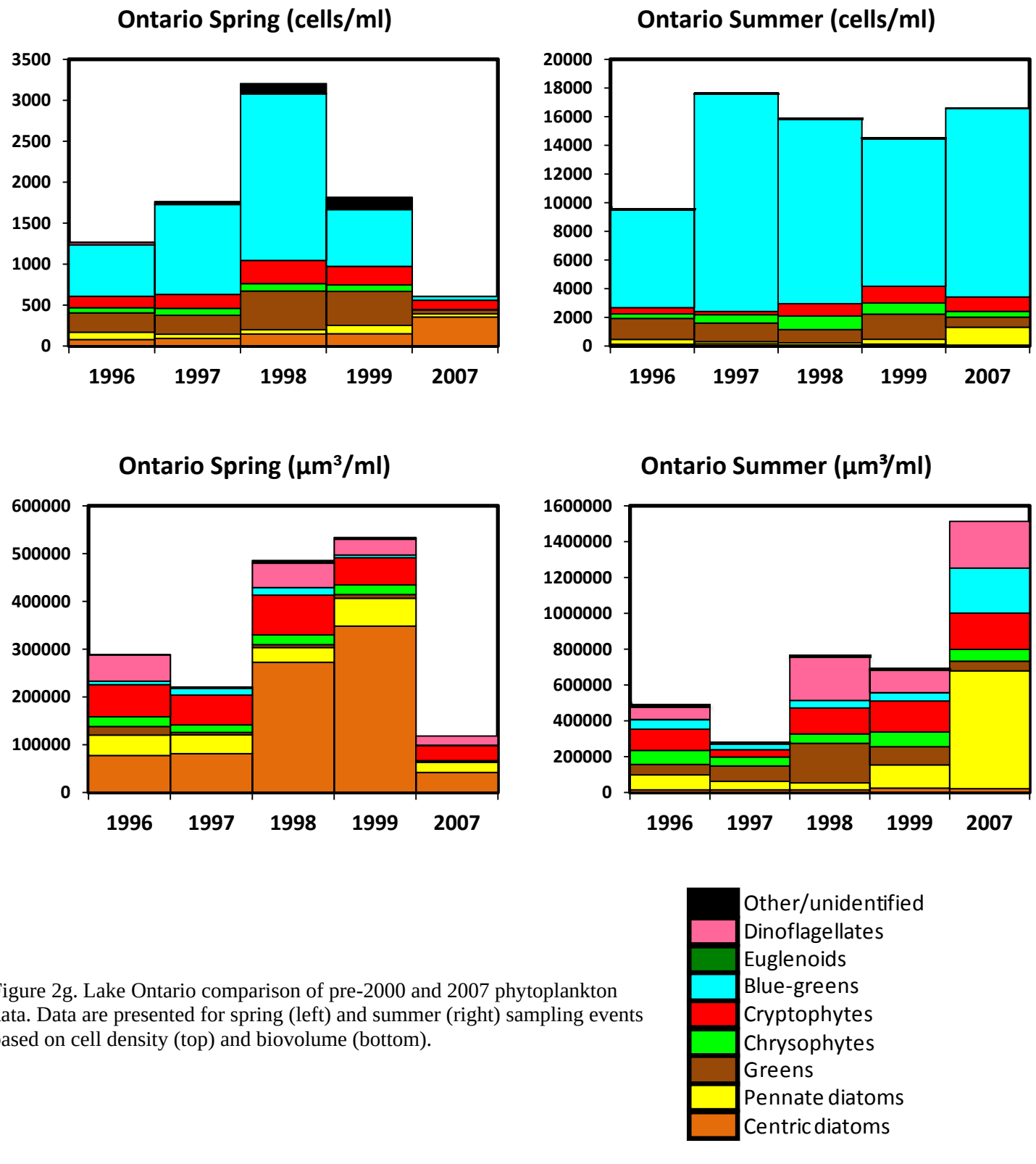

Figure 2g. Lake Ontario comparison of pre-2000 and 2007 phytoplankton data. Data are presented for spring (left) and summer (right) sampling events based on cell density (top) and biovolume (bottom).

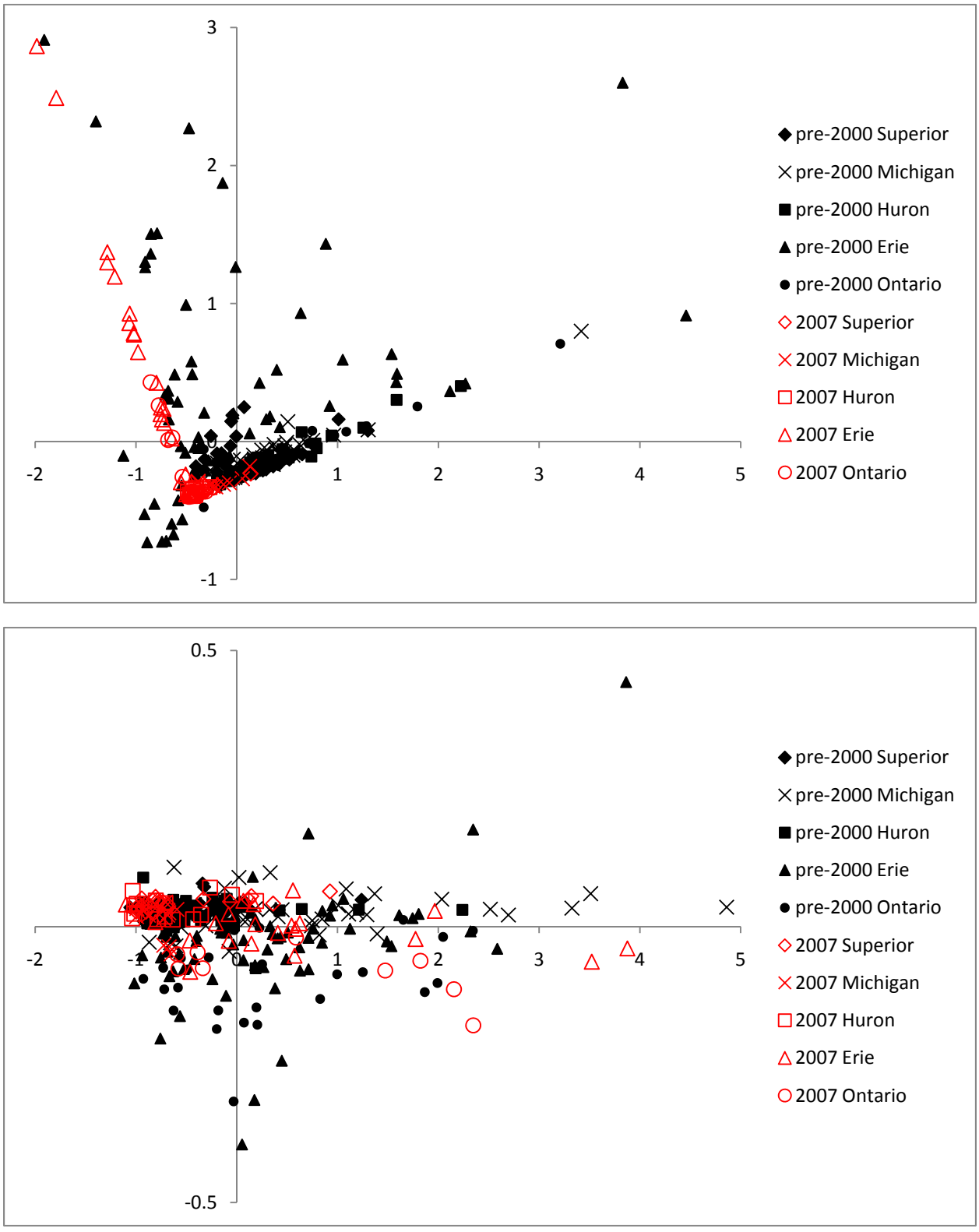

Figure 3a. Correspondence analysis (CA) of pre-2000 and 2007 phytoplankton data. Data are presented for spring (top) and summer (bottom) cell density (cells/ml). All symbols represent sample scores. The ranges of axis scores roughly reflect the importance of that axis in capturing variation in the phytoplankton data.

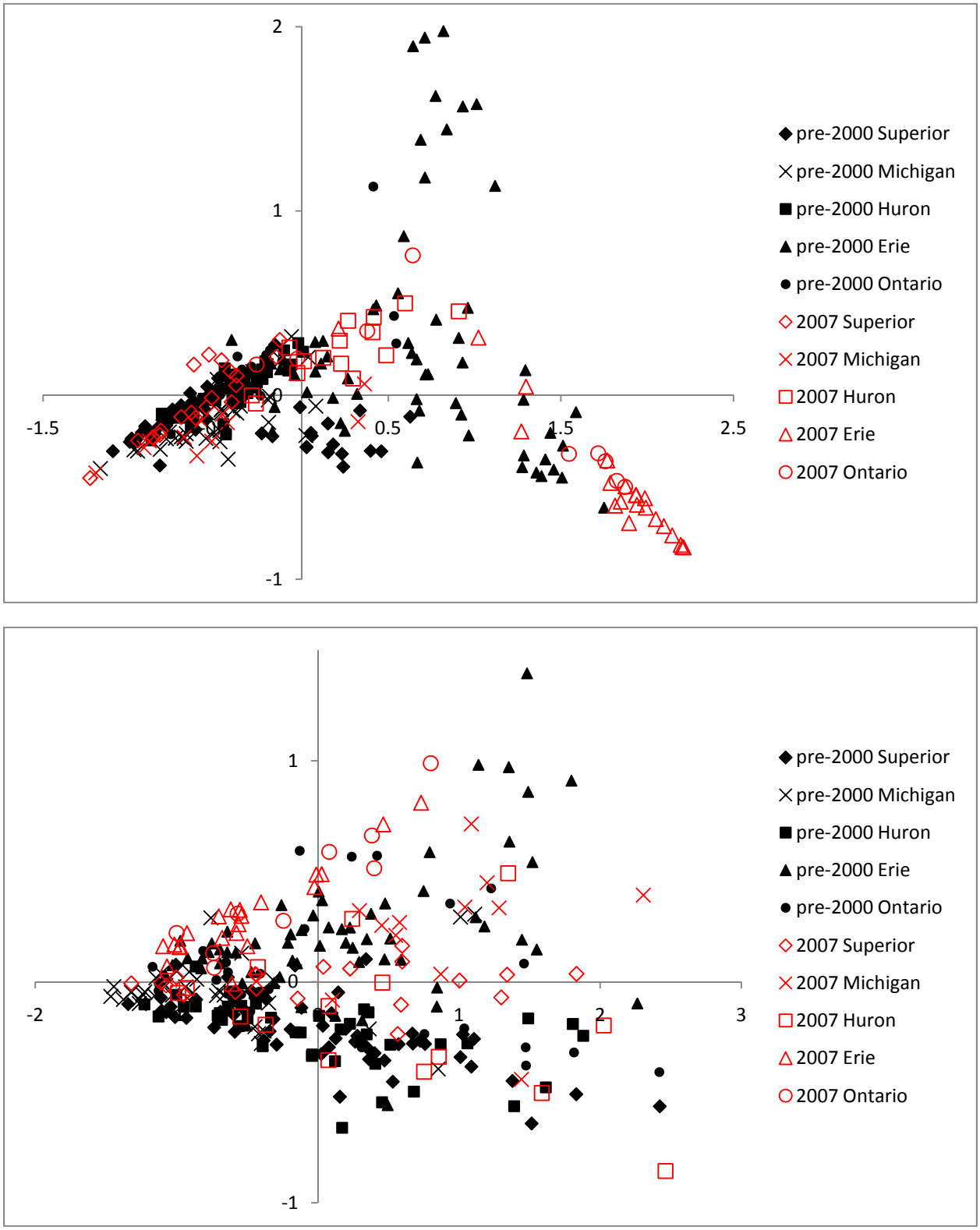

Figure 3b. Correspondence analysis (CA) of pre-2000 and 2007 phytoplankton data. Data are presented for spring (top) and summer (bottom) relative cell density (% of total cells/ml). All symbols represent sample scores. The ranges of axis scores roughly reflect the importance of that axis in capturing variation in the phytoplankton data.

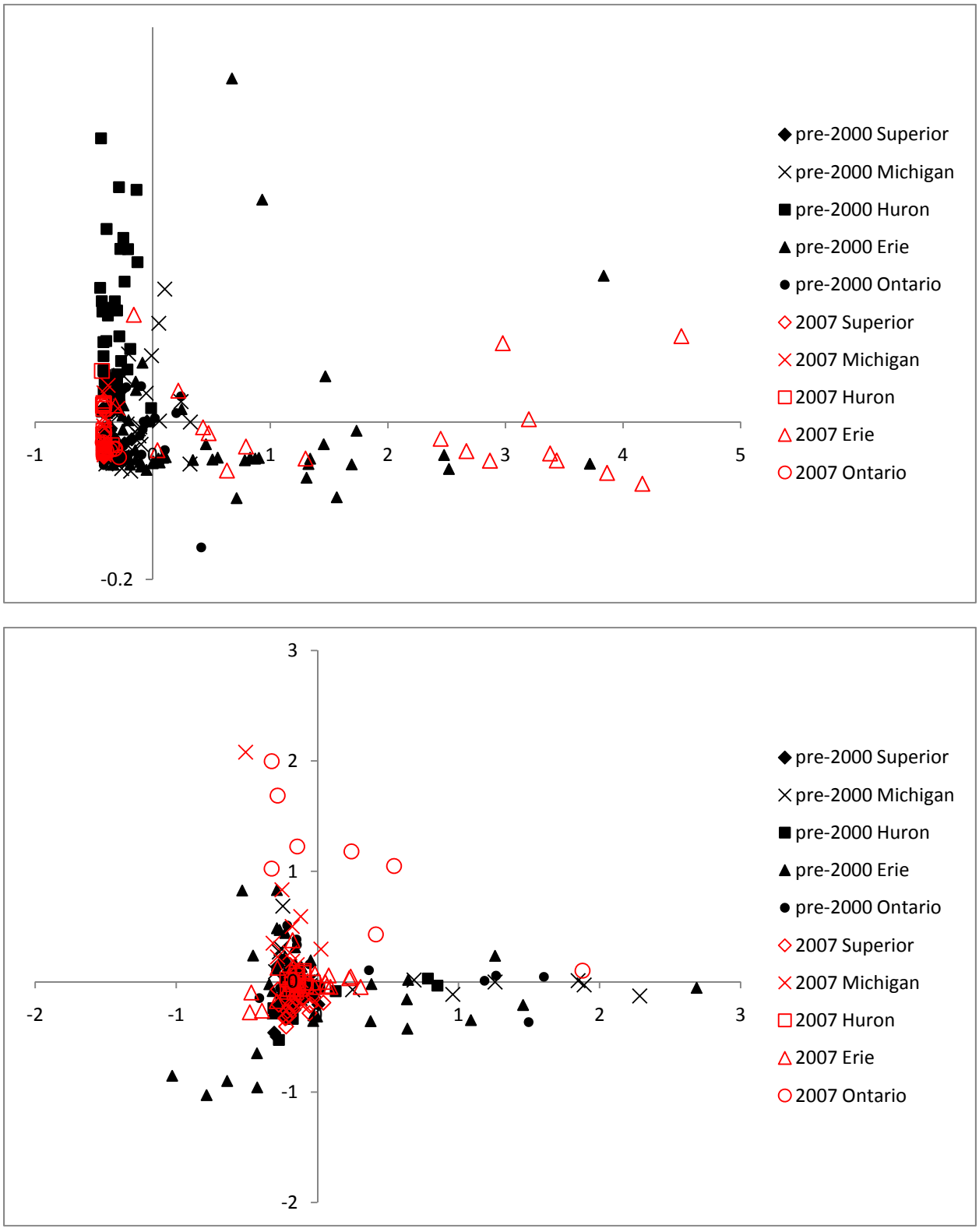

Figure 3c. Correspondence analysis (CA) of pre-2000 and 2007 phytoplankton data. Data are presented for spring (top) and summer (bottom) biovolume (μm^3/ml). All symbols represent sample scores. The ranges of axis scores roughly reflect the importance of that axis in capturing variation in the phytoplankton data.

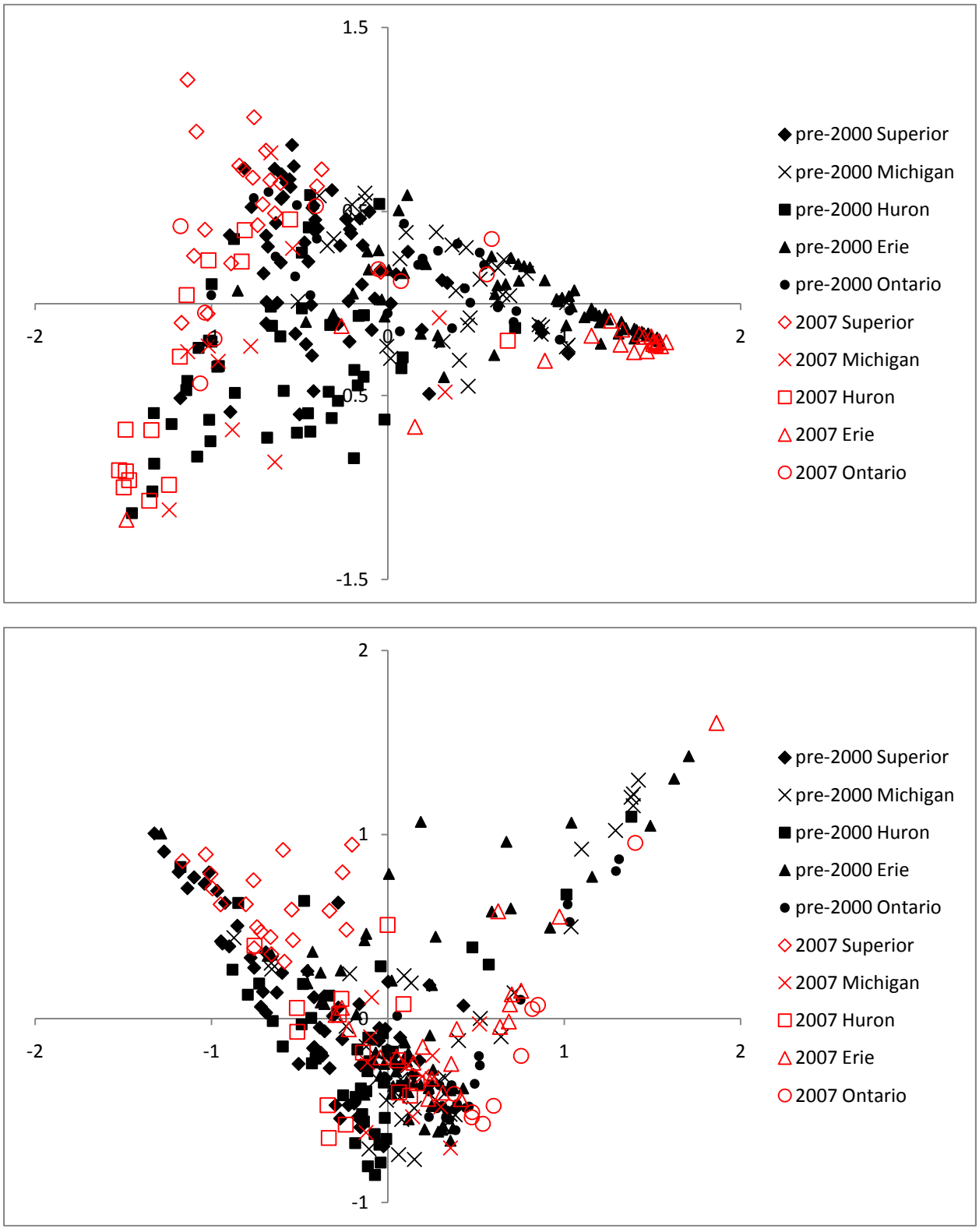

Figure 3d. Correspondence analysis (CA) of pre-2000 and 2007 phytoplankton data. Data are presented for spring (top) and summer (bottom) relative biovolume (% of total μm^3/ml). All symbols represent sample scores. The ranges of axis scores roughly reflect the importance of that axis in capturing variation in the phytoplankton data.

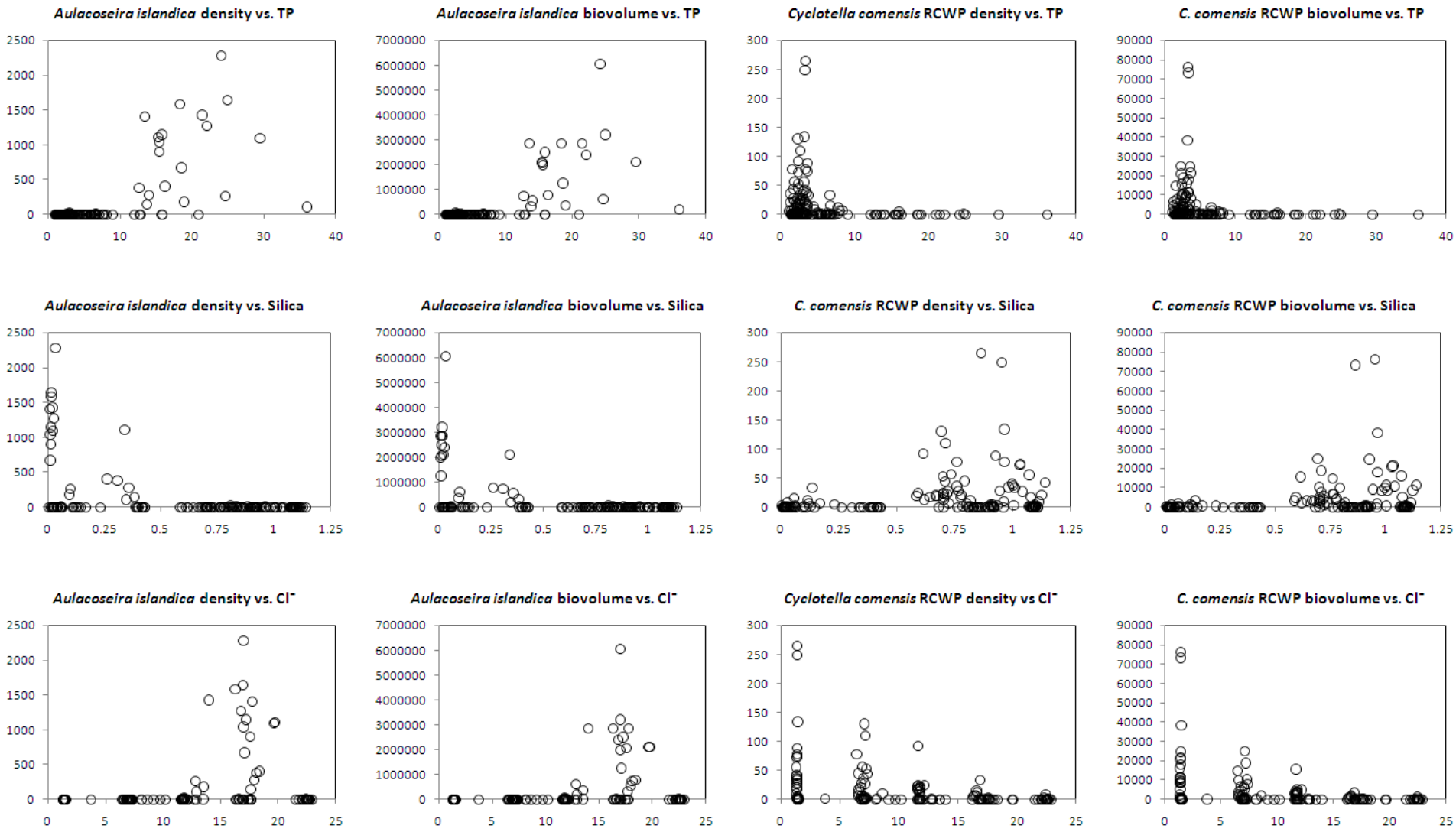

Figure 4a. Distribution of density (left) and biovolume (right) data for *Aulacoseira islandica* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4b. Distribution of density (left) and biovolume (right) data for *Cyclotella comensis* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

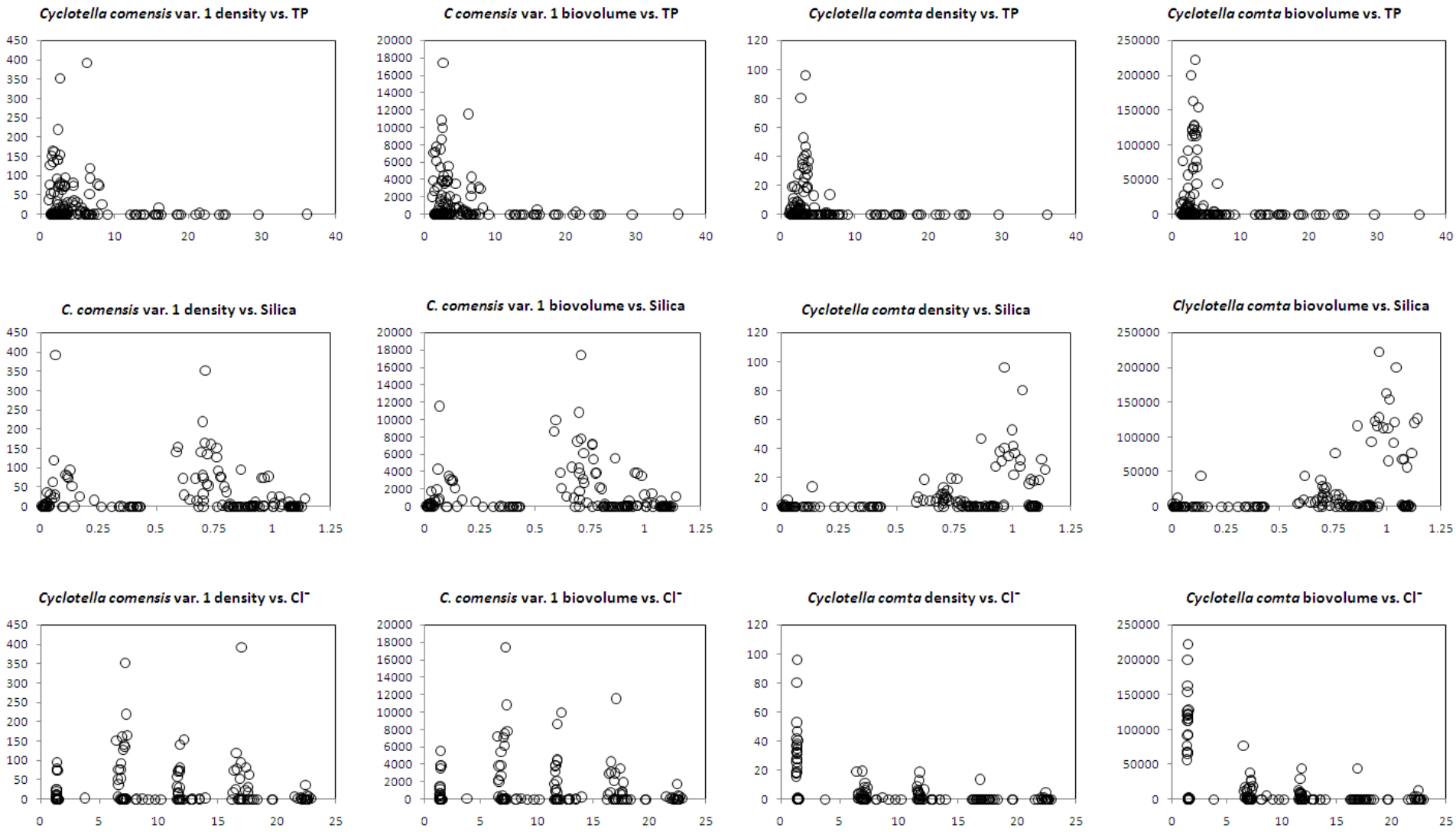

Figure 4c. Distribution of density (left) and biovolume (right) data for *Cyclotella comensis* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4d. Distribution of density (left) and biovolume (right) data for *Cyclotella comta* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

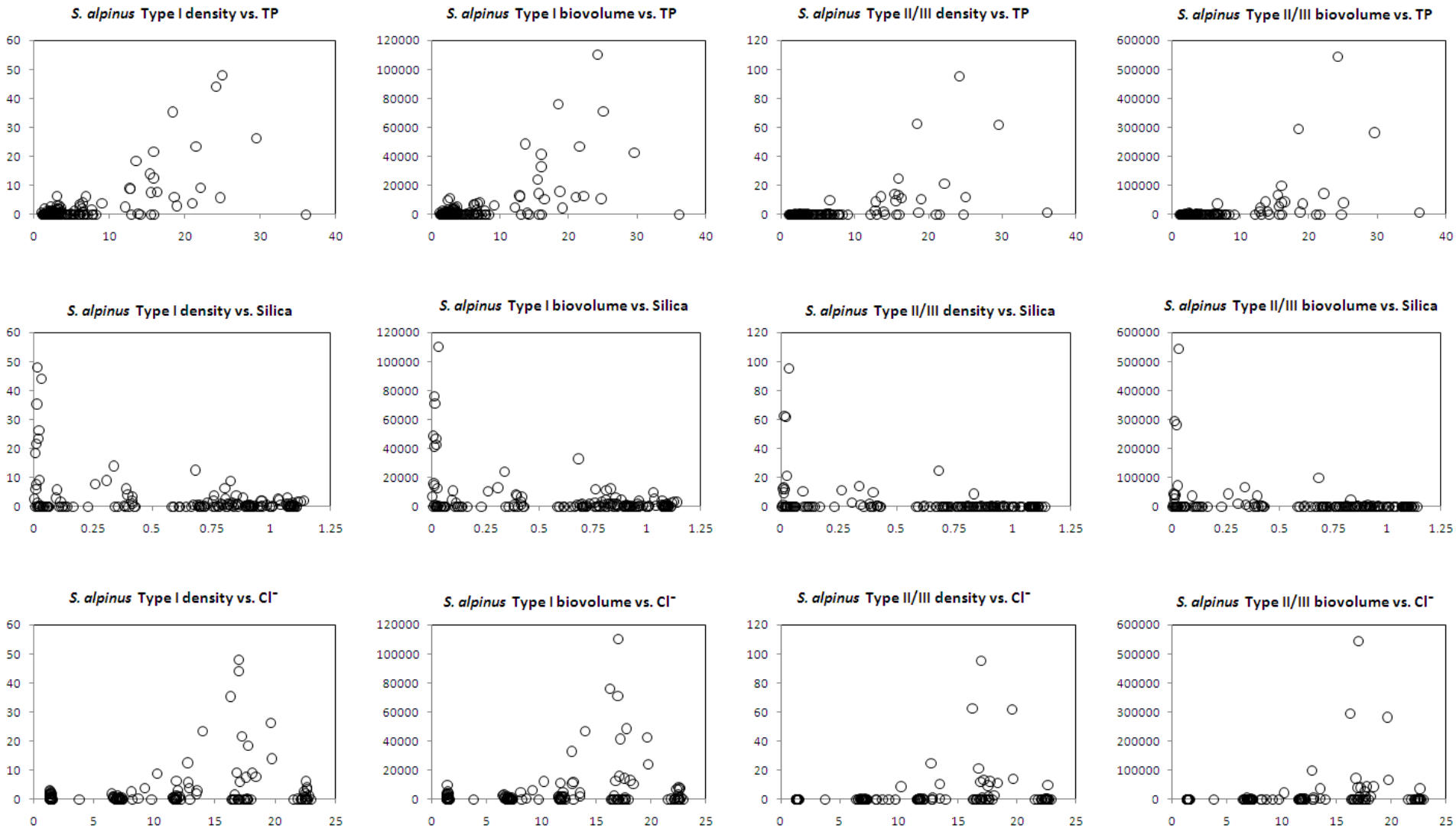

Figure 4e. Distribution of density (left) and biovolume (right) data for *Stephanodiscus alpinus* Type I in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4f. Distribution of density (left) and biovolume (right) data for *Stephanodiscus alpinus* Type II/III in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

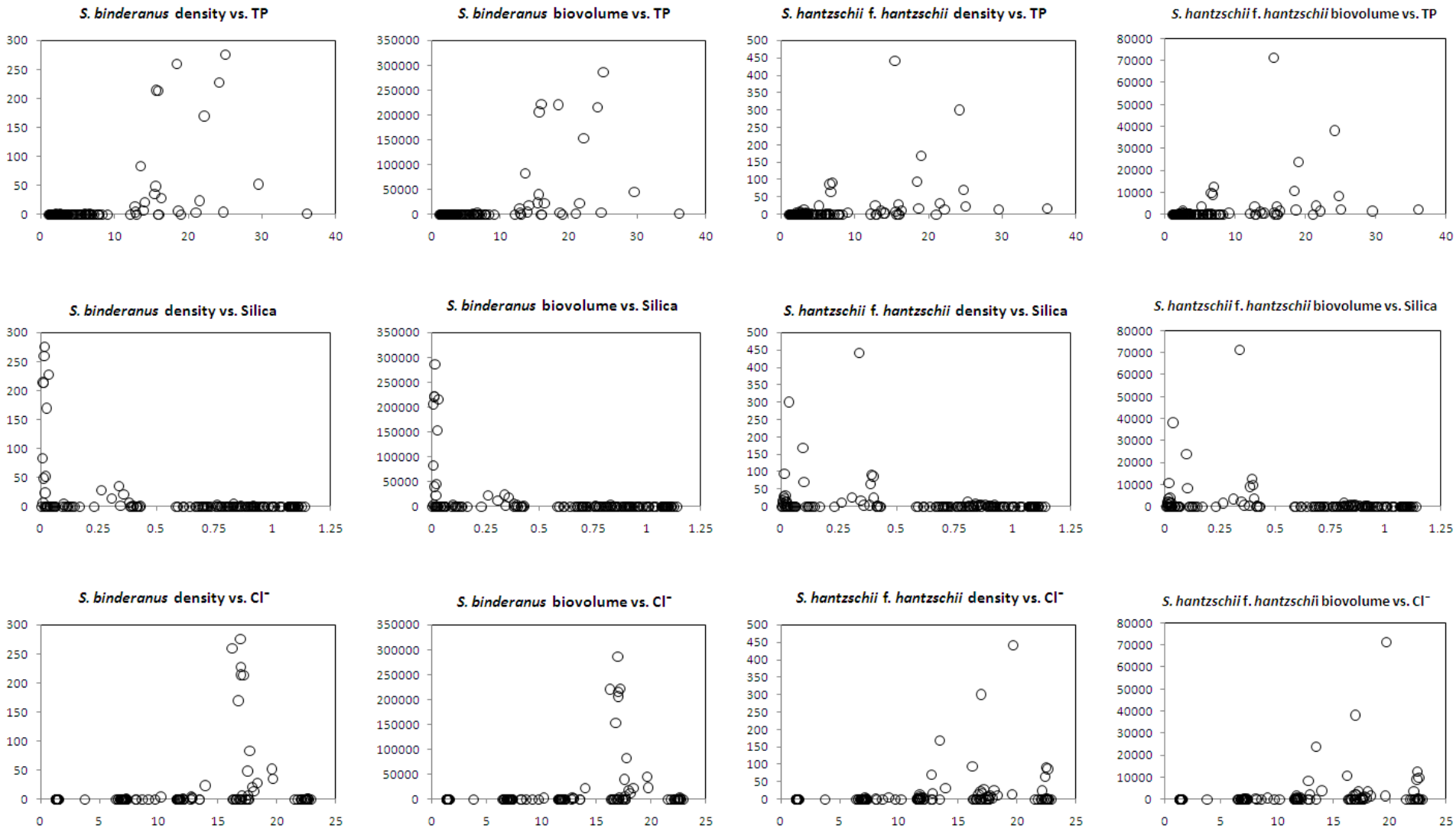

Figure 4g. Distribution of density (left) and biovolume (right) data for *Stephanodiscus binderanus* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4h. Distribution of density (left) and biovolume (right) data for *Stephanodiscus hantzschii* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

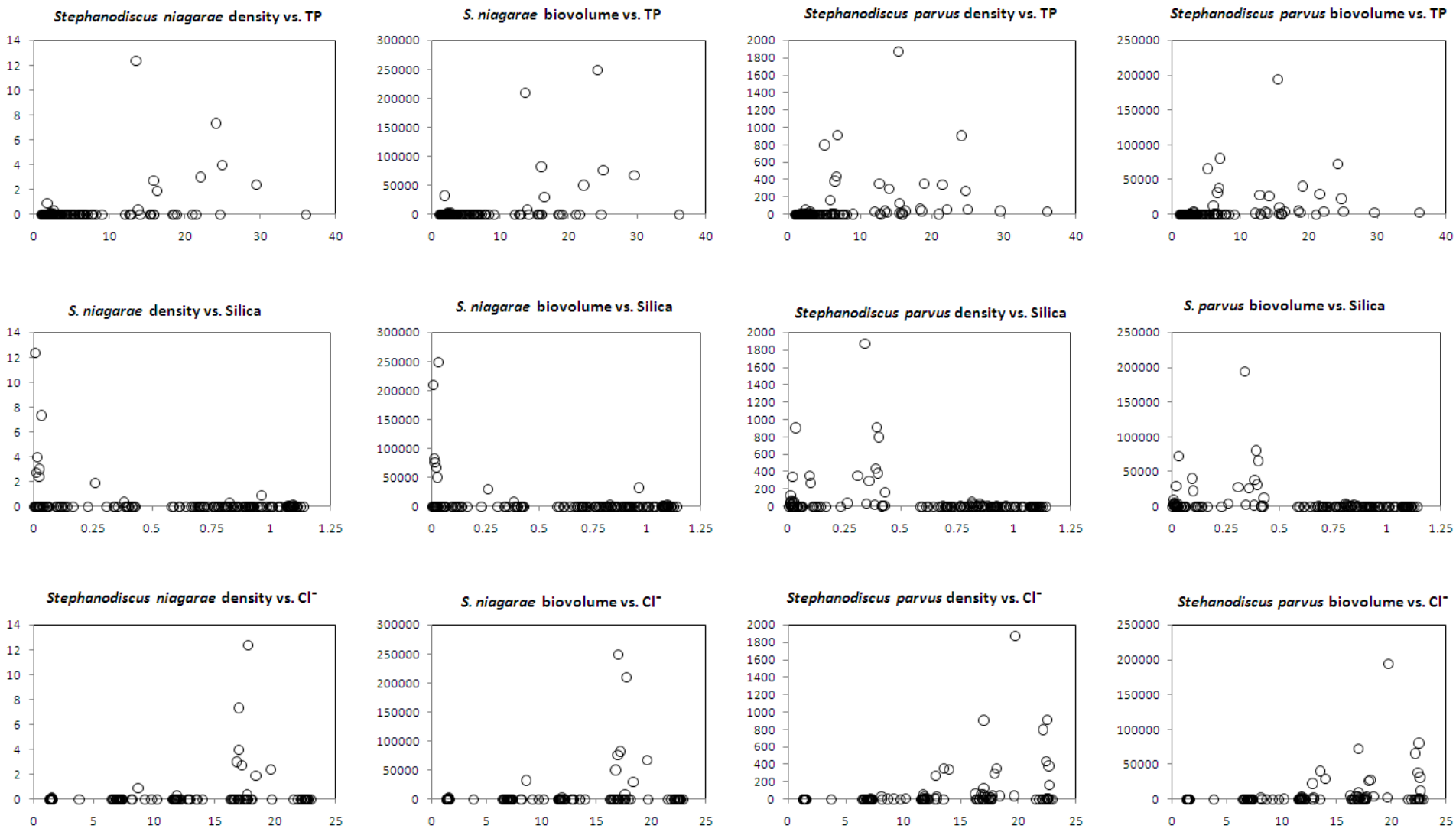

Figure 4i. Distribution of density (left) and biovolume (right) data for *Stephanodiscus niagarae* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4j. Distribution of density (left) and biovolume (right) data for *Stephanodiscus parvus* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

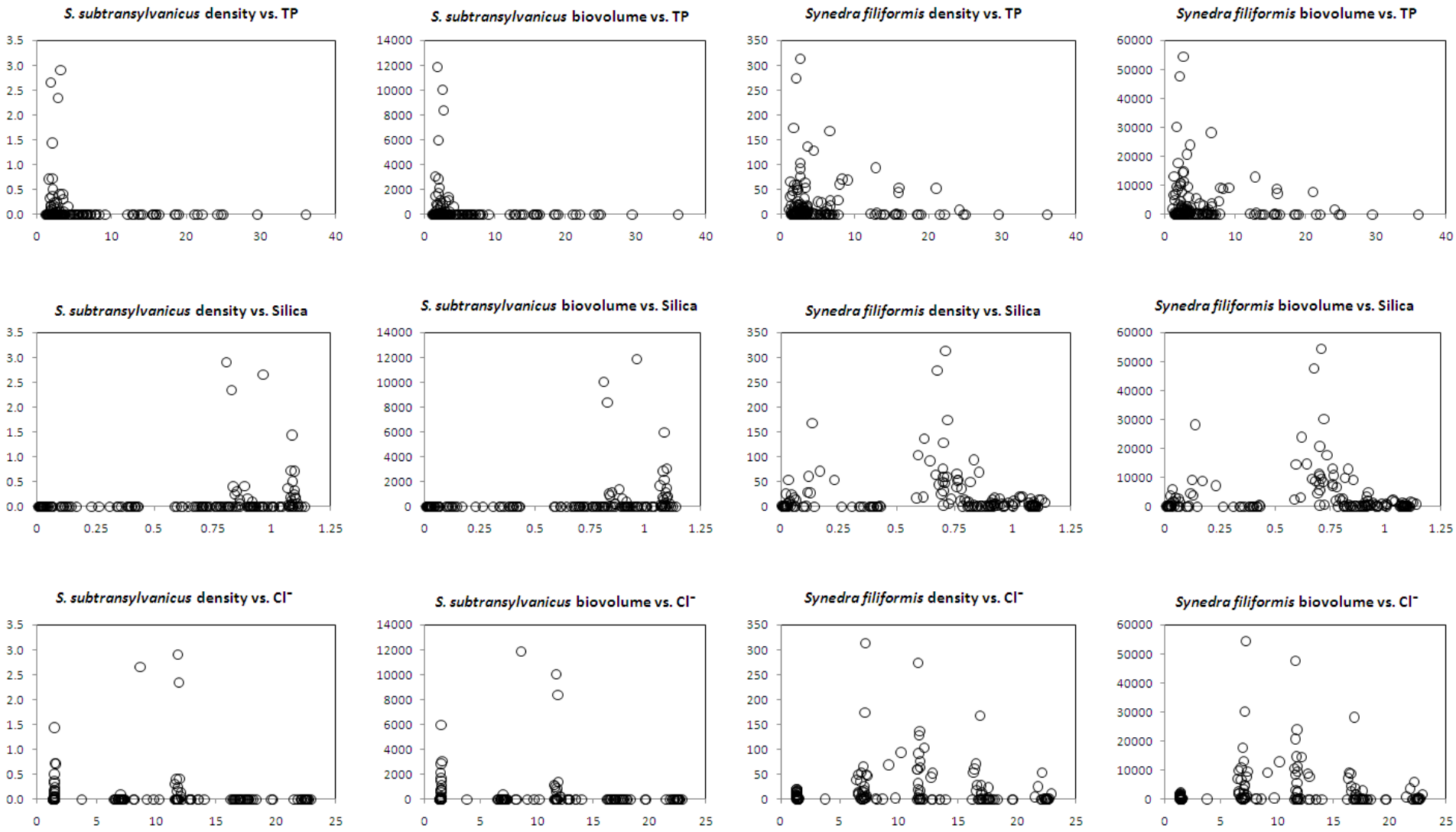

Figure 4k. Distribution of density (left) and biovolume (right) data for *Stephanodiscus subtransylvanicus* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4l. Distribution of density (left) and biovolume (right) data for *Synedra filiformis* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

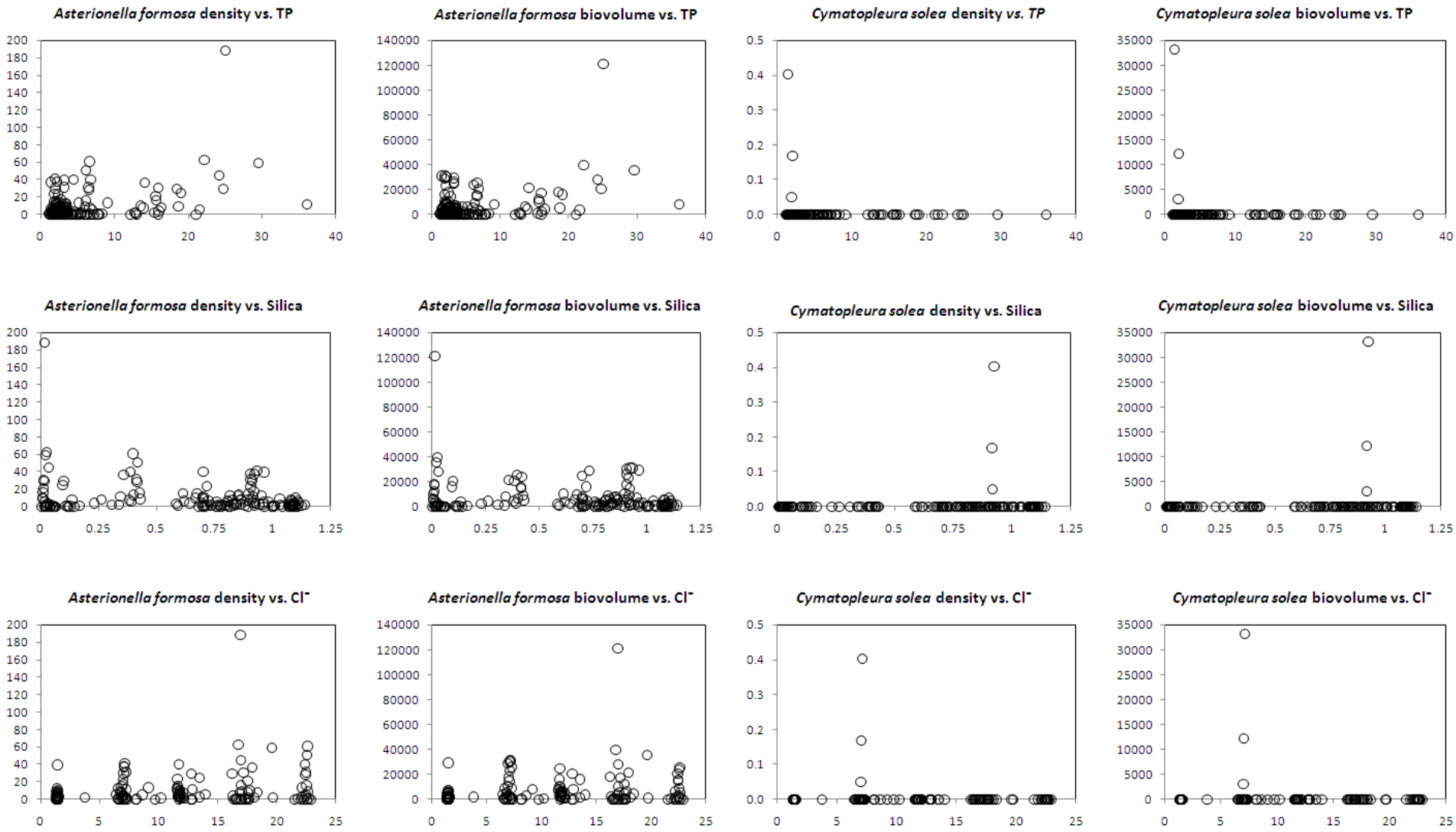

Figure 4m. Distribution of density (left) and biovolume (right) data for *Asterionella formosa* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4n. Distribution of density (left) and biovolume (right) data for *Cymatopleura solea* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

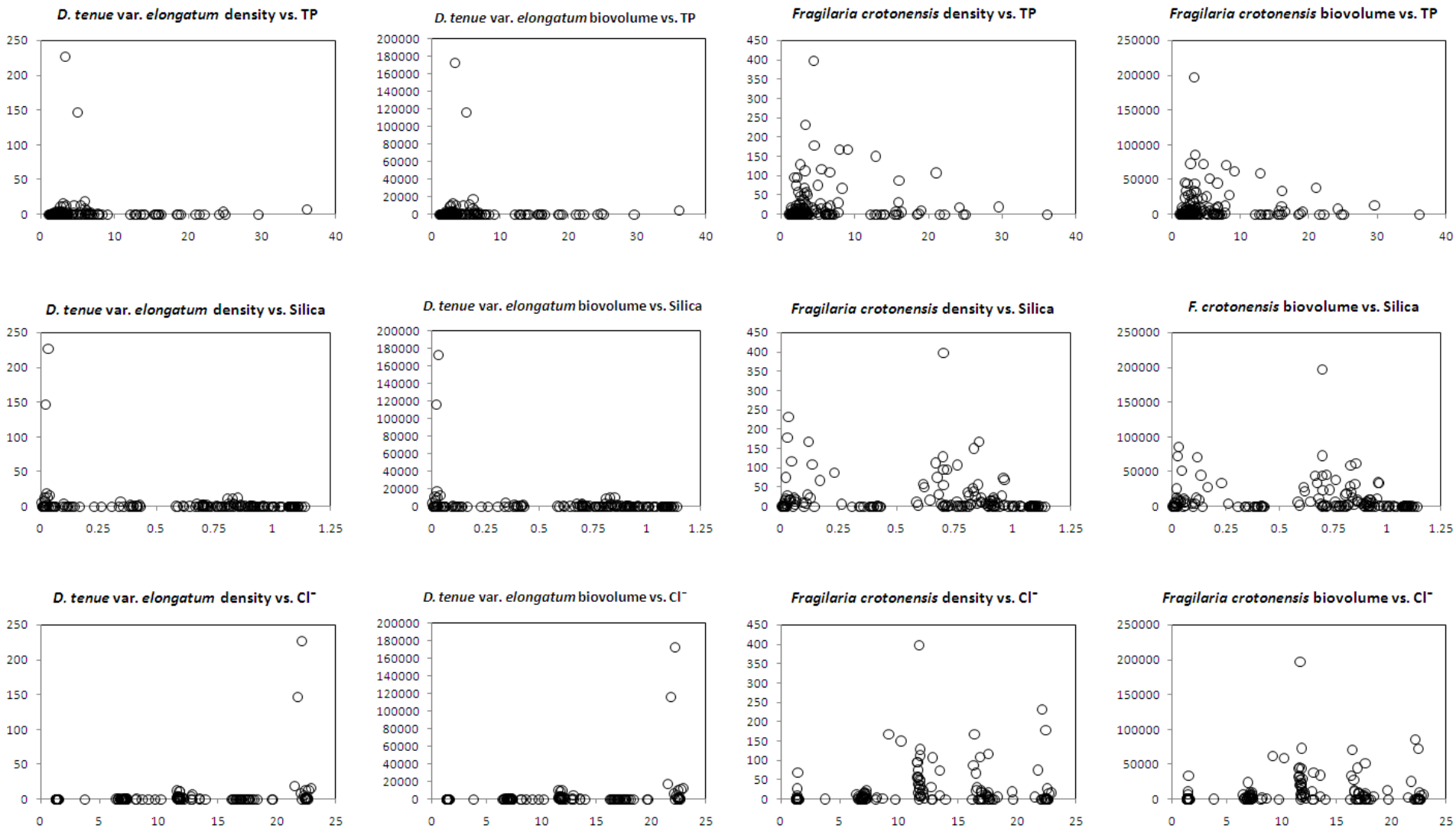

Figure 4o. Distribution of density (left) and biovolume (right) data for *Diatoma tenue* var. *elongatum* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4p. Distribution of density (left) and biovolume (right) data for *Fragilaria crotonensis* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

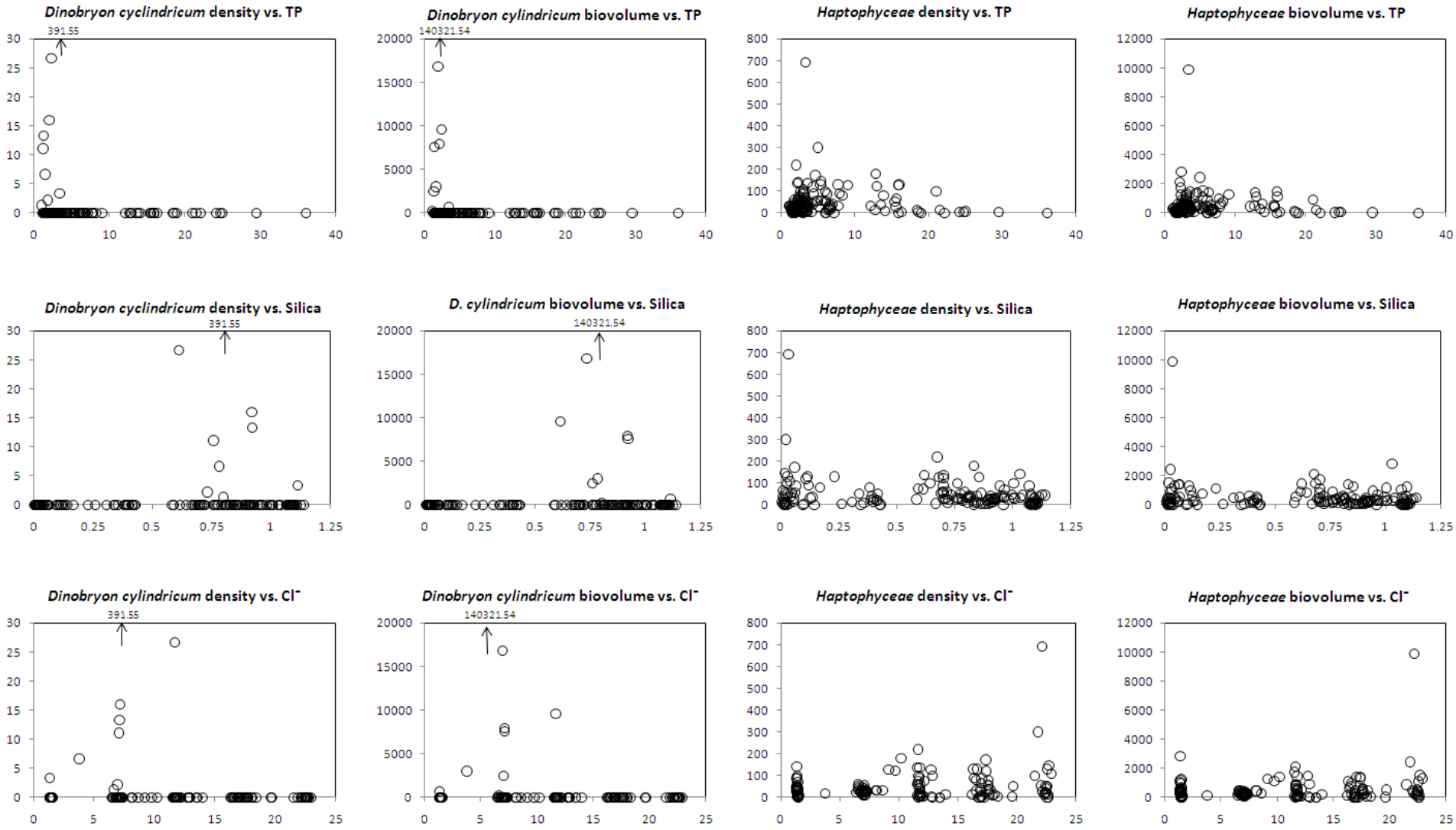

Figure 4q. Distribution of density (left) and biovolume (right) data for *Dinobryon cylindricum* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4r. Distribution of density (left) and biovolume (right) data for Haptophyceae in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

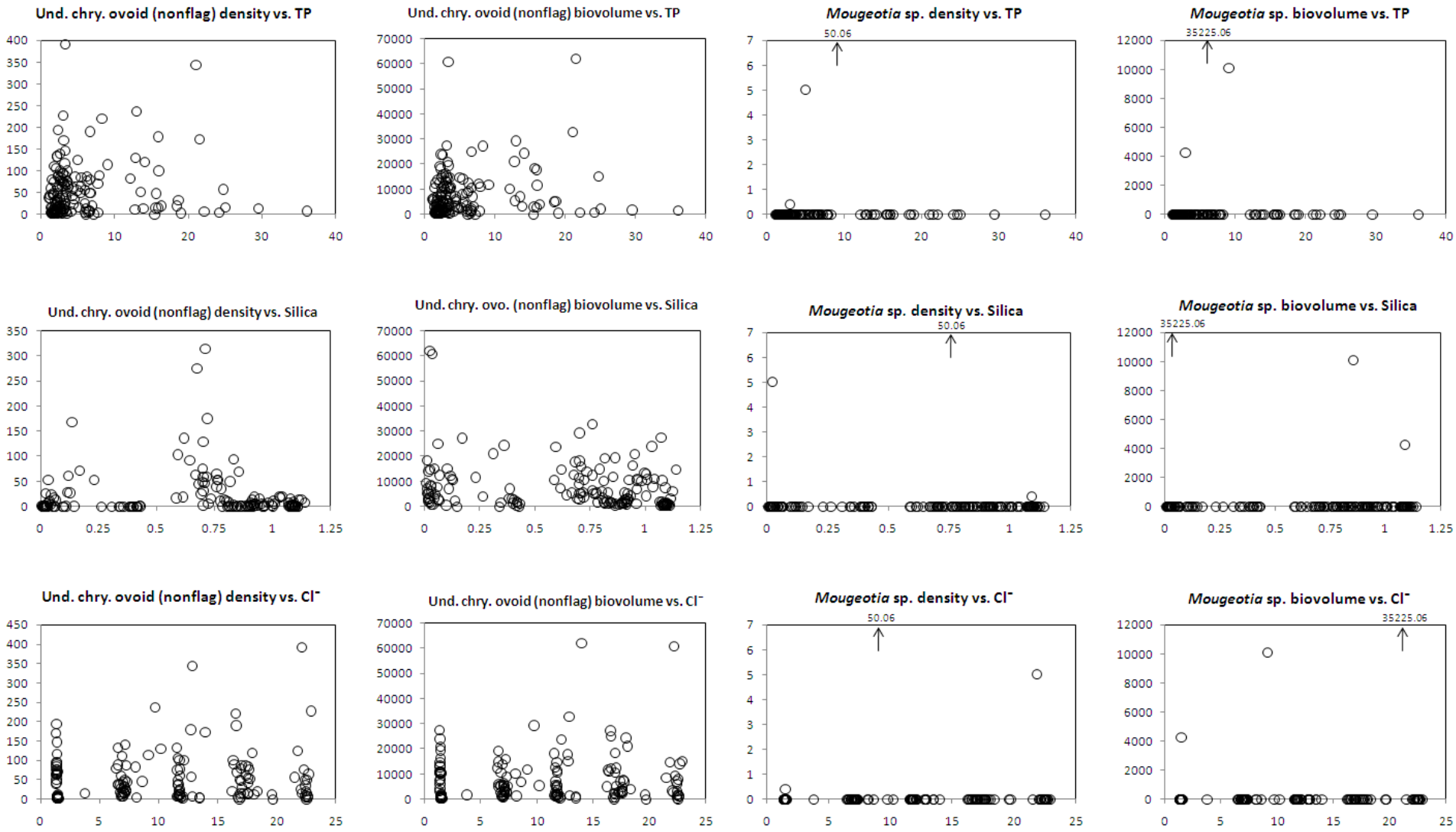

Figure 4s. Distribution of density (left) and biovolume (right) data for nonflagellated, unidentified chrysophyte ovoids in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4t. Distribution of density (left) and biovolume (right) data for *Mougeotia* sp. in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

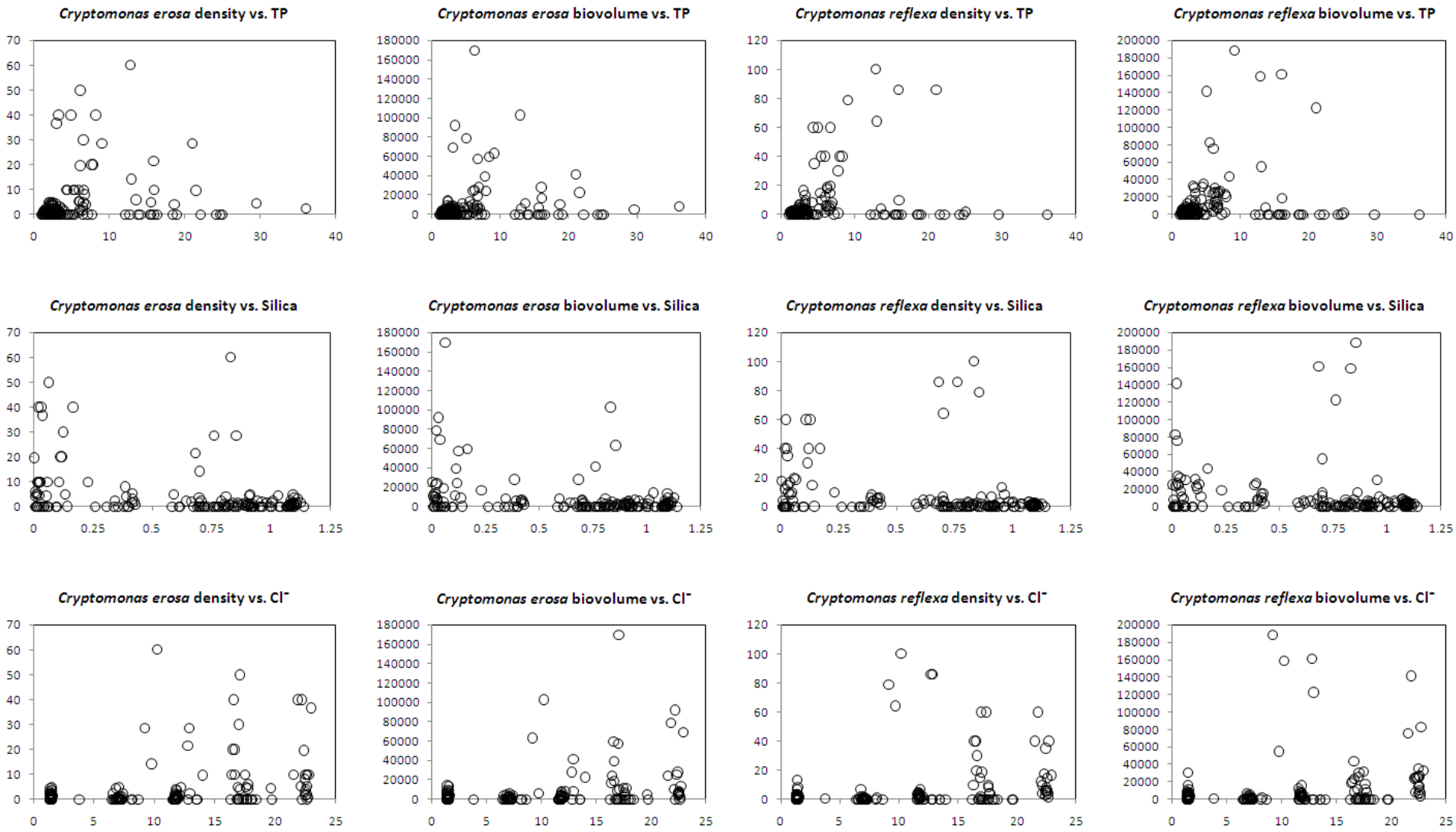

Figure 4u. Distribution of density (left) and biovolume (right) data for *Cryptomonas erosa* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4v. Distribution of density (left) and biovolume (right) data for *Cryptomonas reflexa* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

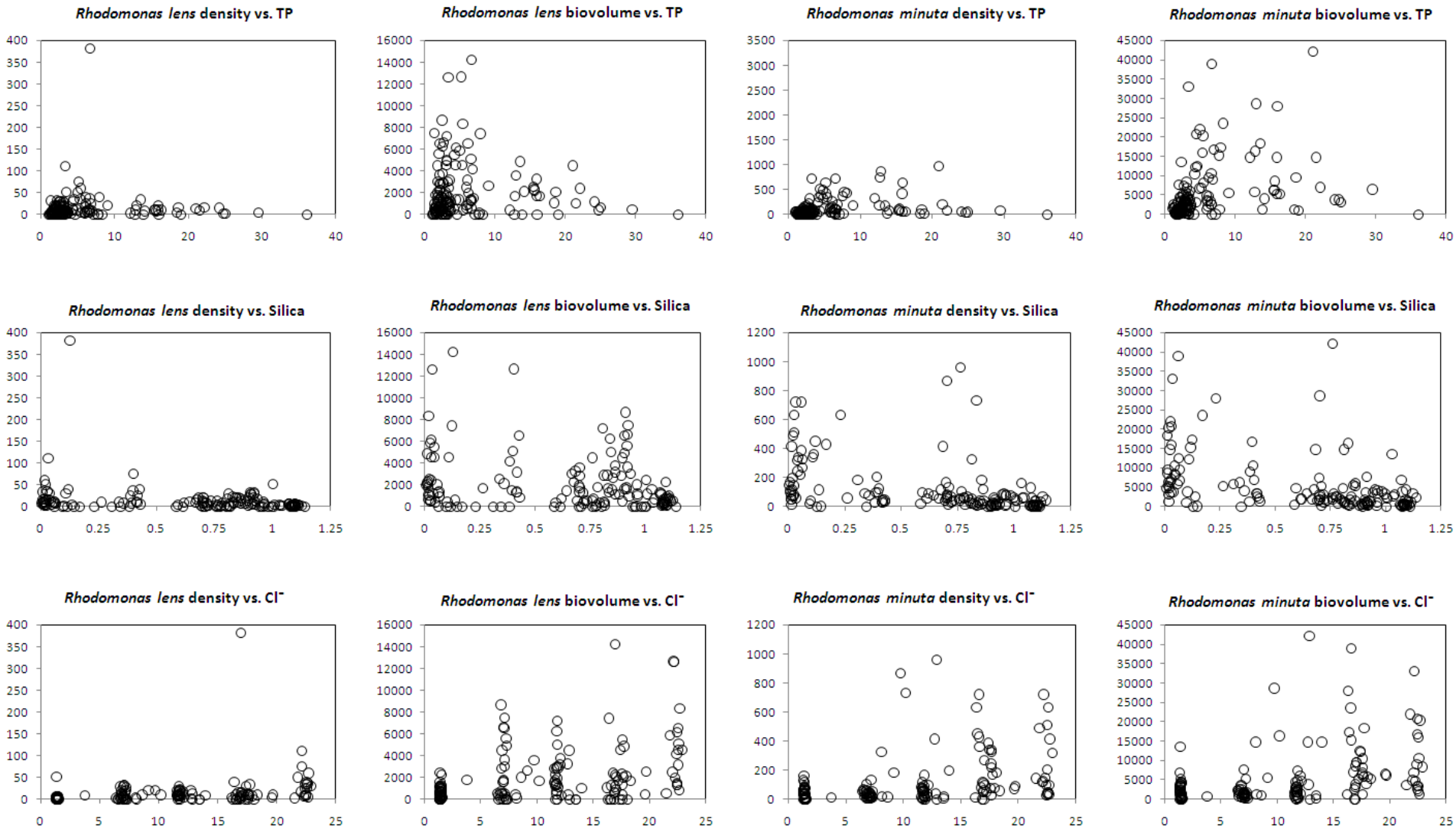

Figure 4w. Distribution of density (left) and biovolume (right) data for *Rhodomonas lens* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4x. Distribution of density (left) and biovolume (right) data for *Rhodomonas minuta* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

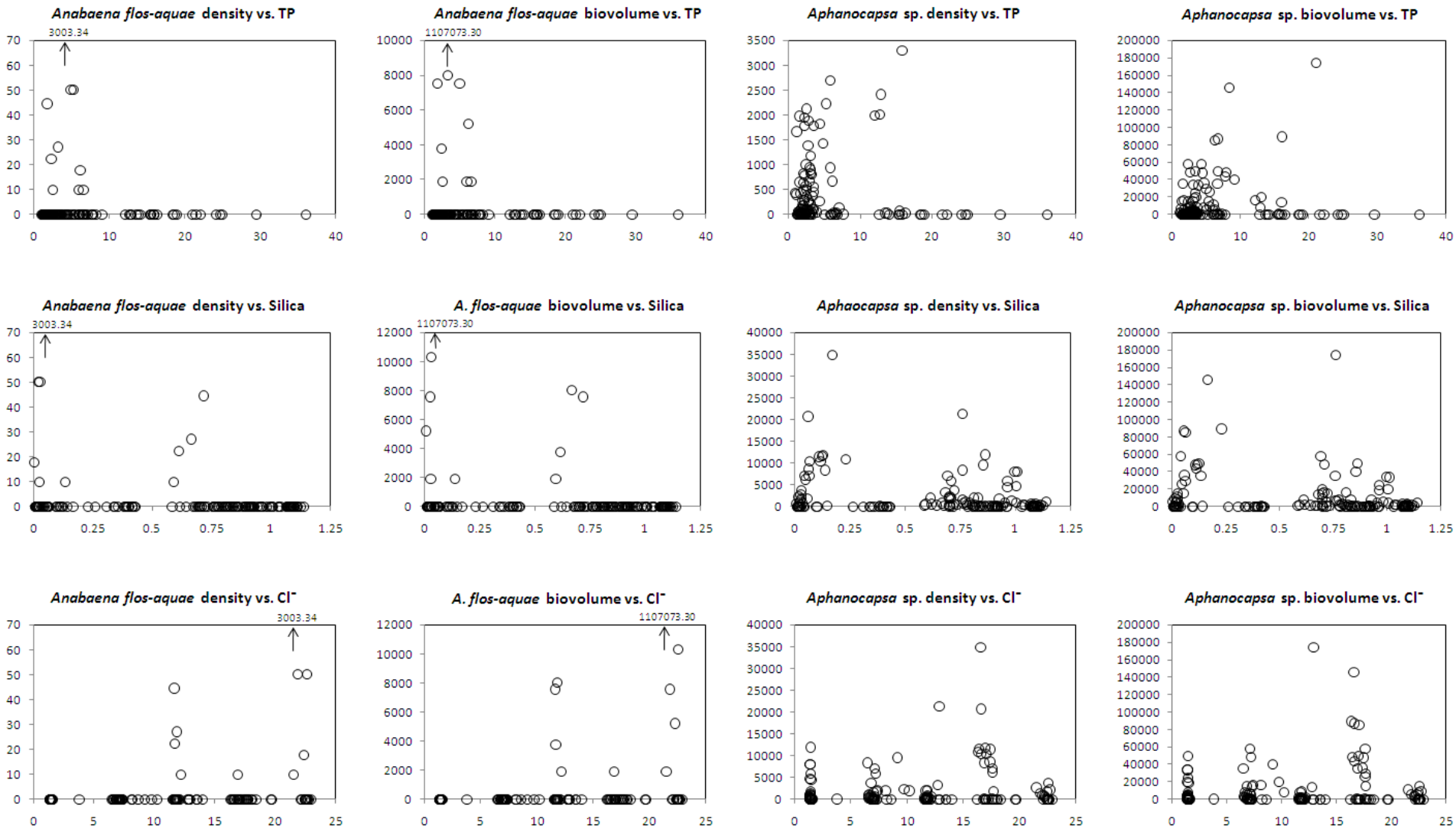

Figure 4y. Distribution of density (left) and biovolume (right) data for *Anabaena flos-aquae* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4z. Distribution of density (left) and biovolume (right) data for *Aphanocapsa* sp. in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

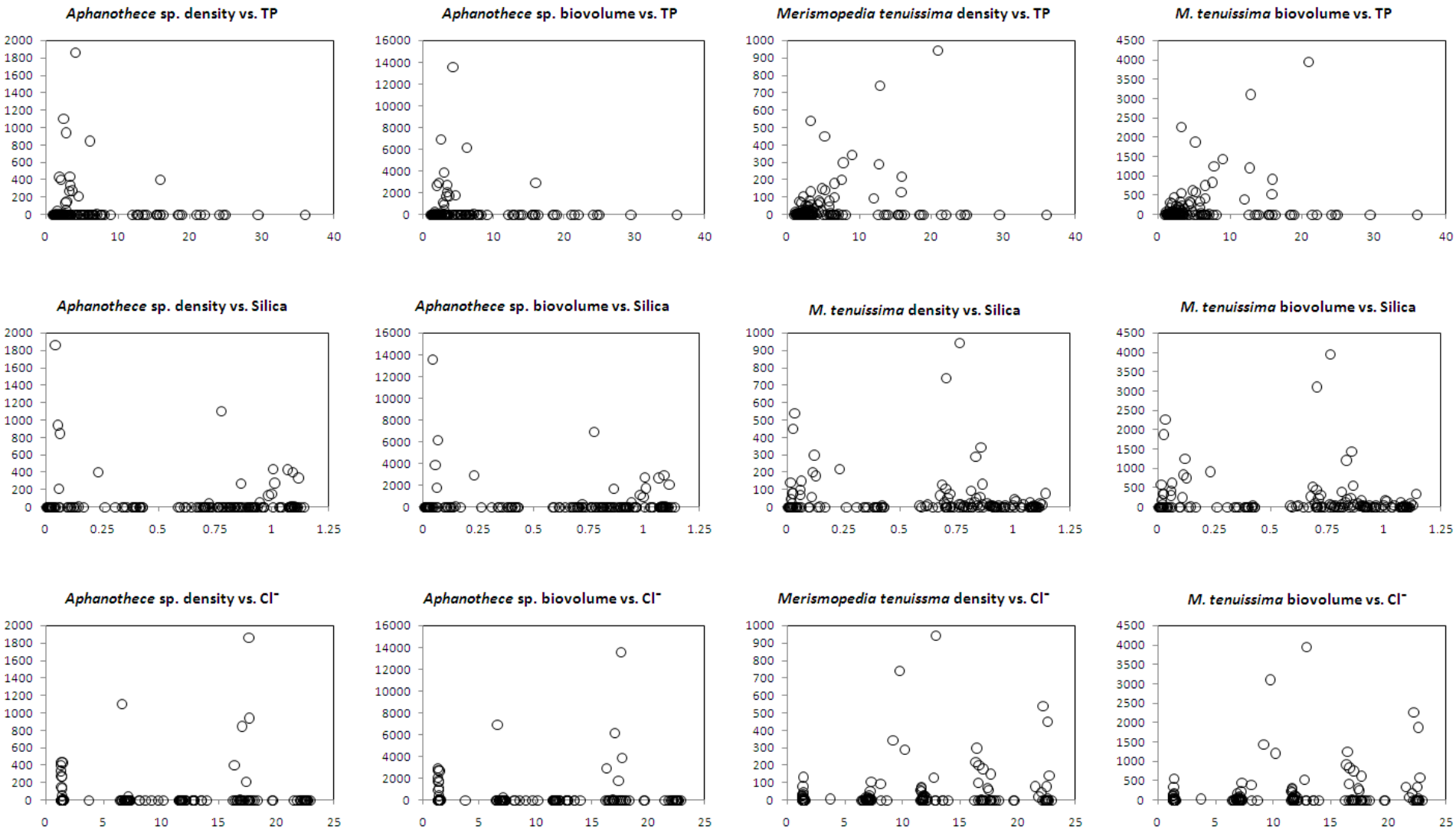

Figure 4aa. Distribution of density (left) and biovolume (right) data for *Aphanothece* sp. in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4bb. Distribution of density (left) and biovolume (right) data for *Merismopedia tenuissima* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

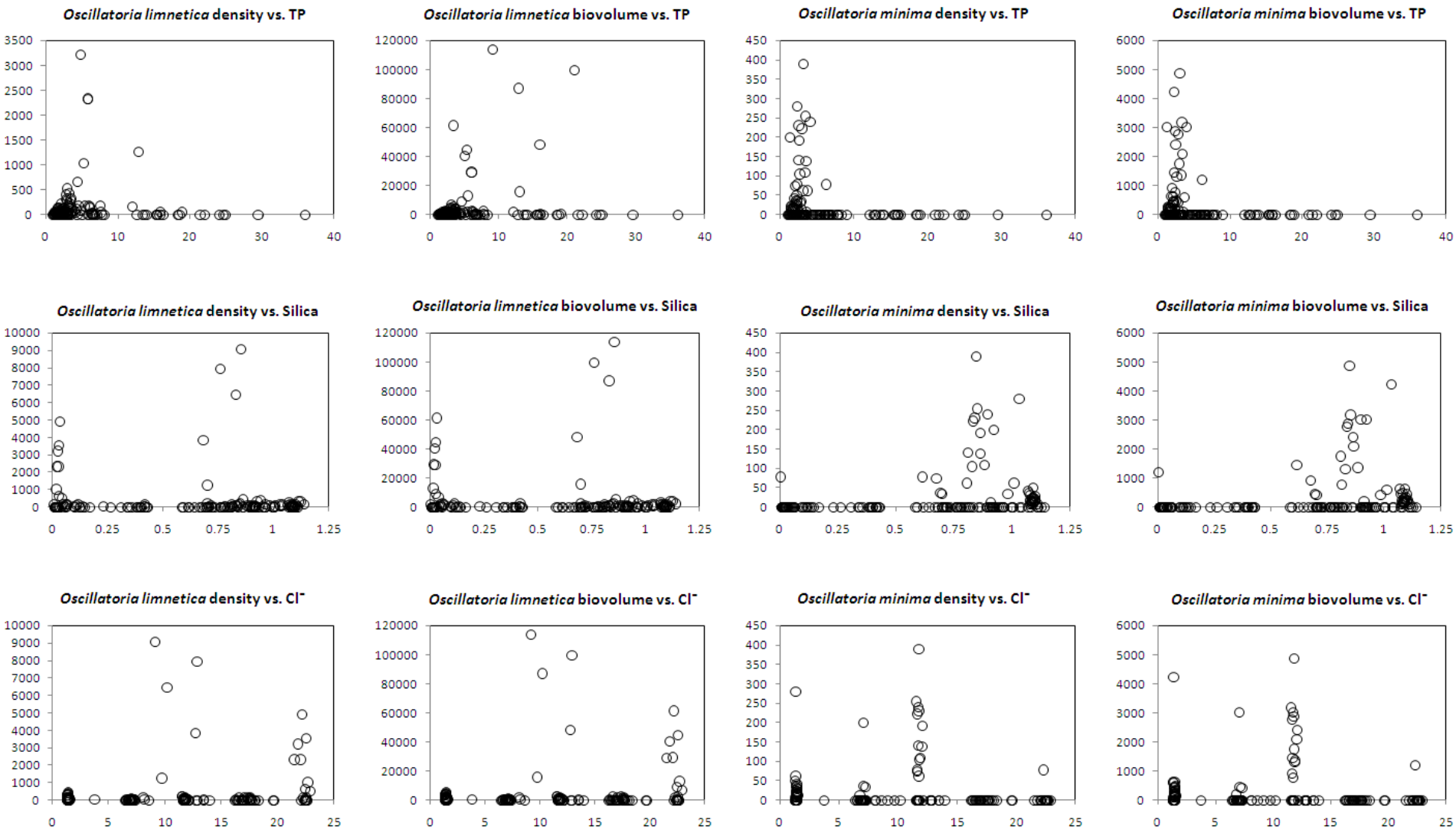

Figure 4cc. Distribution of density (left) and biovolume (right) data for *Oscillatoria limnetica* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4dd. Distribution of density (left) and biovolume (right) data for *Oscillatoria minima* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

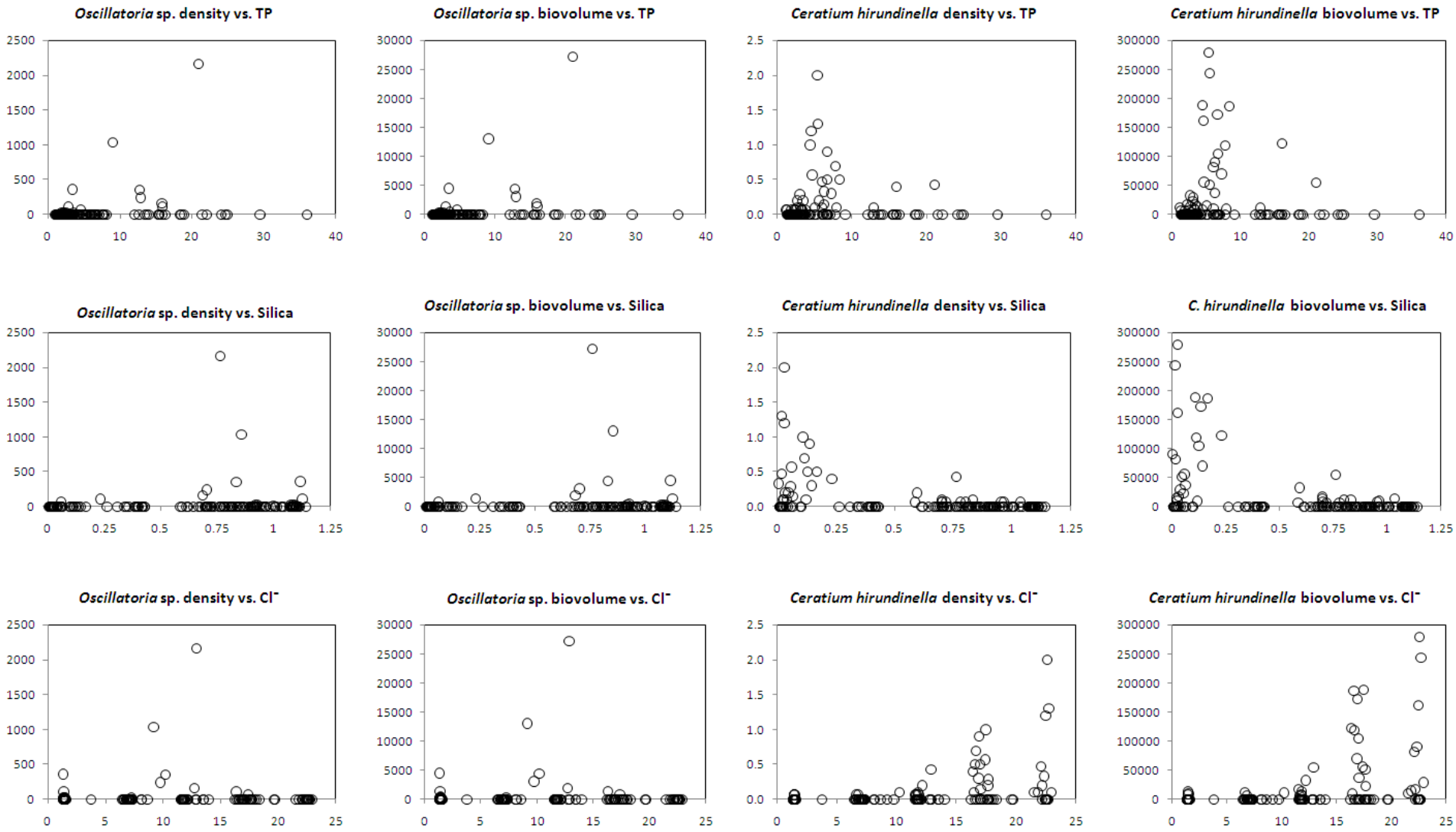

Figure 4ee. Distribution of density (left) and biovolume (right) data for *Oscillatoria* sp. in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

Figure 4ff. Distribution of density (left) and biovolume (right) data for *Ceratium hirundinella* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

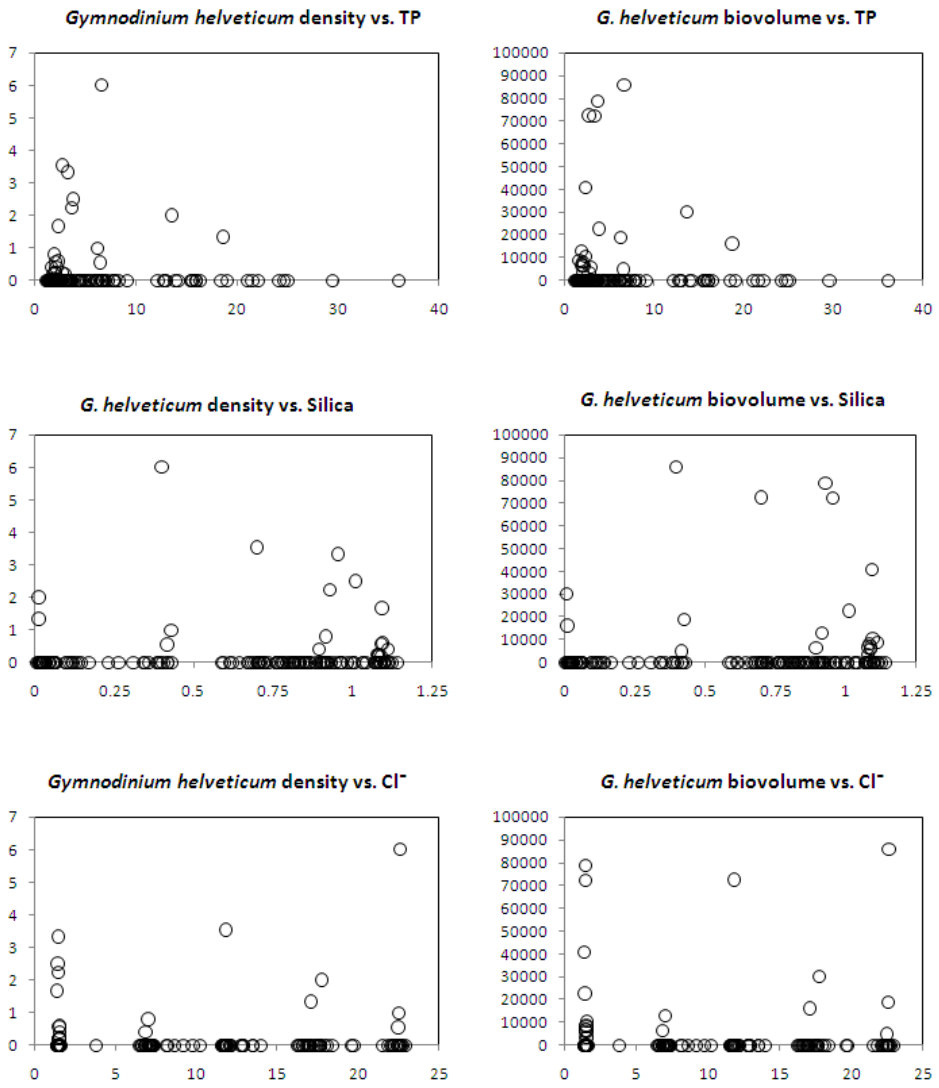

Figure 4gg. Distribution of density (left) and biovolume (right) data for *Gymnodinium helveticum* in 2007 along environmental gradients for total phosphorus (top) silica (middle) and chloride (bottom).

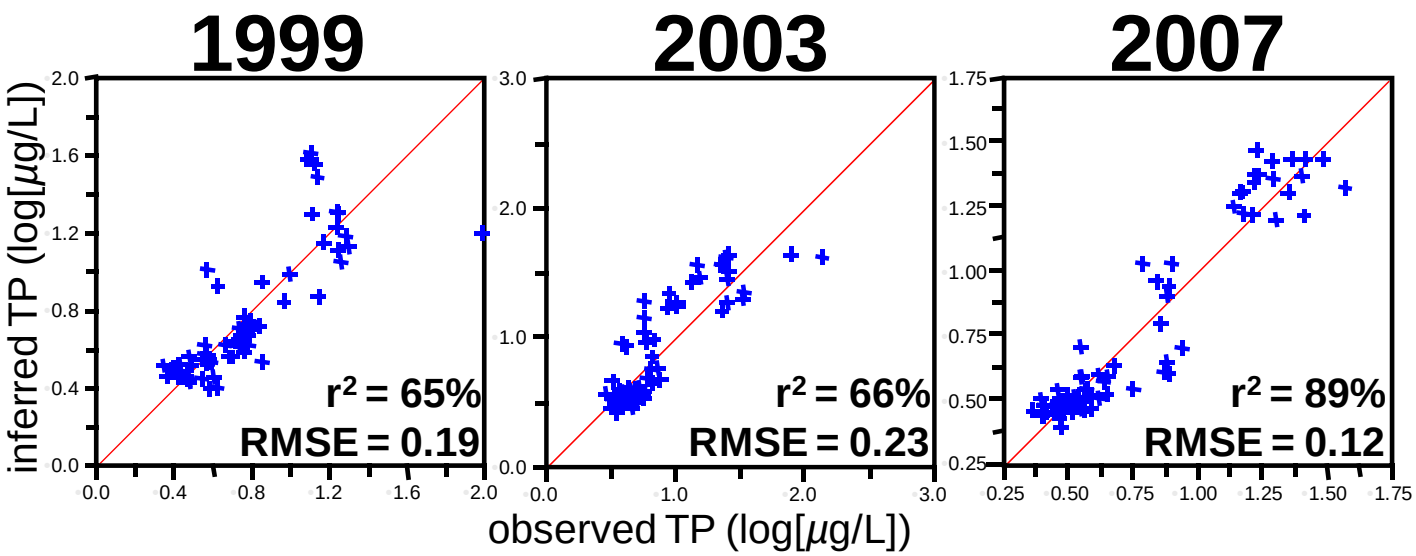

Figure 5. Total phosphorus (TP) model performance assessed by comparing measured TP to algal-inferred TP. Models were based on algal density data collected in 1999, 2003 and 2007. Performance measures are presented as the squared correlation coefficient (r2; representing the percent variation in observed data captured by the algal-inferred dataset) and the root mean square error of prediction (RMSE) around the 1:1 line (shown as the diagonal line).

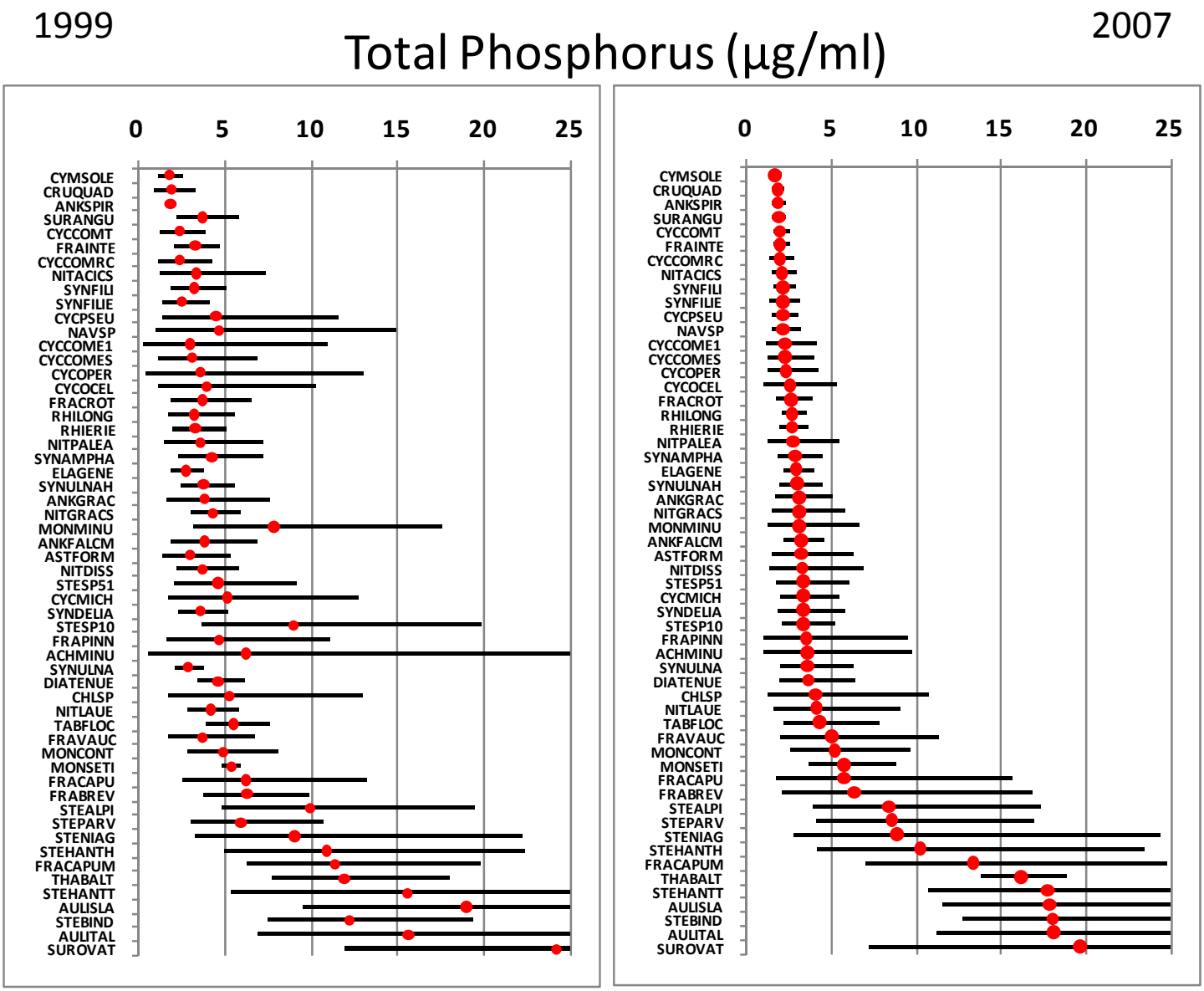

Figure 6. Comparison of total phosphorus species coefficients between 1999 and 2007 Great Lakes assemblages. Red dots are species optima and horizontal lines are tolerances. Taxa shown represent those that were in common for all years tested (1999, 2003, 2007). Taxa are sorted in order of 2007 optima.