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Phytoplankton nutrient status in Lake Erie: An
efficient great lake

By:

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An efficient great lake**

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ABSTRACT

Reduction of phosphorus (P) inputs to Lake Erie since the 1970's have resulted in lower mean total phosphorus (TP) concentration in the lake and lower mean chlorophyll *a* concentration. In this study we examine indicators of phytoplankton nutritional status to determine whether the observed decrease in TP concentration has resulted in a strongly P deficient phytoplankton community. Phytoplankton nutrient status measurements including alkaline phosphatase activity (APA), phosphorus (P) and nitrogen (N) debt, ³³P turnover time and particulate carbon (C), N and P stoichiometric ratios, were made in all three basins of Lake Erie from May through October in 1997. The phytoplankton in the west basin were not phosphorus or nitrogen deficient at any time over the May through October sampling season. Phytoplankton in the large central basin were moderately P deficient during the stratified season except for strong deficiency in July, the time of maximum heat content and strong stratification. The east basin became moderately P deficient with the onset of stratification and remained moderately P deficient over the entire stratified season. Light and N were also sufficient indicating that some other nutrient such as Fe may be involved. Compared to several other lakes in the same geoclimatic region as Lake Erie, including Lake Superior, the phytoplankton community was not strongly nutrient deficient. Within the same group of lakes, Lake Erie had much higher rates of integral primary production than more P deficient lakes. These results lead us to conclude that the Lake Erie phytoplankton community in 1997 was operating efficiently at the extant P concentrations and was not strongly P deficient.

État nutritionnel du phytoplancton au lac Érié :

un grand lac efficace

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RÉSUMÉ

La réduction, depuis les années 1970, des rejets de phosphore (P) dans le lac Érié a eu pour résultat une baisse des concentrations moyennes de phosphore total et de chlorophylle *a* dans le lac. La présente étude porte sur les indicateurs de l'état nutritionnel du phytoplancton et vise à déterminer si une diminution de la concentration de phosphore total entraîne une grande carence en phosphore dans la communauté phytoplanctonique. Pour déterminer l'état nutritionnel du phytoplancton, on a mesuré l'activité de la phosphatase alcaline, le déficit en phosphore et en azote, le taux de renouvellement du ^{32}P et les rapports stoechiométriques du carbone, de l'azote et du phosphore sous forme particulaire. Les mesures ont été prises dans les trois bassins du lac Érié, de mai à octobre 1997. Chez le phytoplancton du bassin Ouest, il n'y a pas eu de carence en phosphore ni en azote pendant la période d'échantillonnage. Dans le grand bassin central, on a noté une carence modérée en phosphore chez le phytoplancton pendant la période de stratification, carence qui devenait forte en juillet, période pendant laquelle le contenu thermique est maximal et la stratification forte. Dans le bassin Est, avec l'apparition de la stratification, on a observé une carence modérée en phosphore qui s'est maintenue pendant toute la période de stratification. Les quantités de lumière et d'azote étaient également suffisantes, ce qui indique que certains autres nutriments, comme le fer, peuvent être en cause. Par comparaison avec les communautés phytoplanctoniques de plusieurs autres lacs de la même région géoclimatique, notamment avec celles du lac Supérieur, celle du lac Érié ne présentait pas une grande carence en nutriments. Dans le même groupe de lacs, le lac Érié avait des taux de production primaire intégrale bien plus hauts que les lacs où la carence en phosphore était plus grande. Après examen de ces résultats, on conclut que, en 1997, la communauté phytoplanctonique du lac Érié fonctionnait efficacement aux concentrations de phosphore existantes et ne présentait pas une grande carence en phosphore.

NWRI RESEARCH SUMMARY

Plain language title

The nutritional state of algae in Lake Erie

What is the problem and what do scientists already know about it?

With the advent of alein mussels in Lake Erie and the achievement of the nutrient loading controls there was a need to find out if the expected limitations on algae still applied.

Why did NWRI do this study?

The lake is in a state of rapid change. This paper and others like it are needed as baseline studies of the new biological condition of the lake.

What were the results?

The algae in the west basin were not nutrient limited likely because the west basin is where the main nutrient sources are. The central and east basin algae were moderately phosphorus deficient most of the time with one period of strong deficiency. This means that phosphorus is still limiting algal growth and filtration by mussels, although important in shallow water, has a small effect on algae offshore where the experiments were done.

How will these results be used?

The results feed into the Lakewide management Plan in that they elucidate the present state of the algal population and lay to rest notions that the mussels had somehow disconnected the algae populations from the nutrient supply.

Who were our main partners in the study?

University of Waterloo

Sommaire des recherches de l'INRE

Titre en langage clair

État nutritionnel des algues au lac Érié

Quel est le problème et que savent les chercheurs à ce sujet?

Avec l'apparition de moules exotiques dans le lac Érié et la réduction de la charge en éléments nutritifs, il était nécessaire de vérifier la validité des limitations prévues sur les algues.

Pourquoi l'INRE a-t-il effectué cette étude?

Le lac Érié est en évolution rapide. Le présent article et d'autres recherches dans cette veine sont nécessaires pour servir d'études de base sur les nouvelles conditions biologiques du lac.

Quels sont les résultats?

Les algues du bassin Ouest n'étaient pas limitées sur le plan nutritionnel, vraisemblablement parce que s'y trouvent les principales sources de nutriments. Les algues du bassin central et du bassin Est présentaient, la plupart du temps, une carence en phosphore modérée, sauf pour une période de grande carence. Ces résultats indiquent que le phosphore est encore le facteur limitant de la croissance des algues et que la filtration par les moules, quoique importante dans les eaux peu profondes, a peu d'effet sur les algues pélagiques, là où les échantillons ont été prélevés.

Comment ces résultats seront-ils utilisés?

Les résultats s'inscrivent dans le plan d'aménagement panlacustre en ce qu'ils expliquent l'état actuel de la population algale et permettent de mettre de côté l'hypothèse que les moules auraient, en quelque sorte, isolé les populations algales de leur source de nutriments.

Quels étaient nos principaux partenaires dans cette étude?

Université de Waterloo

Introduction

In this paper we report the nutrient status of phytoplankton in Lake Erie in 1997. Implementation of the Great Lakes Water Quality agreement in 1972 has led to a decrease in total phosphorus (TP) (Charlton et al. 1999). But it is unknown whether P reduction has resulted in a strongly P deficient phytoplankton community. Lower chlorophyll *a* concentrations in response to P controls were initially, at least, perceived as a positive outcome of the Great Lakes Water Quality Agreement. Recently, however, concerns have been raised regarding the impact of lower TP concentrations on primary production and fish production of Lake Erie (Ryan et al. 1999). Although the relationship between primary production and fish production is complex, there are studies including Lake Erie demonstrating a statistically significant relationship between primary production and fish production (Downing et al. 1990). An important question to ask before responding to any requests for relaxation of P controls is: Will more P mean higher primary production and will the productivity result in higher fish production?

Algal growth in most North American temperate lakes is thought to be P limited (Schindler 1977), and lakes are routinely classified in terms of their TP concentrations, with TP less than 0.32 μM , such as found in present day Lake Erie (Charlton et al. 1999), being an oligotrophic (implying low productivity) lake. A recent comparison by Smith et al. (2003) demonstrated that in 1997 integral primary production per unit of TP in Lake Erie was higher than several other large lakes with similar or higher TP. The rates of integral primary production were higher in Lake Erie in Smith's study because the amount of organic carbon produced per unit of chlorophyll was high (Smith et al. 2003). These results imply that phytoplankton in Lake Erie in 1997 were growing at higher growth rates than in other lakes with similar TP. Measurement of phytoplankton growth rates in natural communities is difficult. However, phytoplankton growth rates are highly correlated to their nutritional status. Phytoplankton that are severely P deficient have lower growth rates than phytoplankton that are not nutrient deficient, providing they are not limited by light (Healey and Hendzel 1979a, Falkowski and Raven 1997). Phytoplankton nutrient status measurements can provide information about whether the availability of a particular nutrient element (e.g. P, N) or trace element is regulating the

rate of phytoplankton growth and also the degree to which the nutrient is limiting growth, that is degree of nutrient deficiency. The concept of phytoplankton nutrient deficiency measurements is based on the premise that the cellular constituents, nutrient uptake, and certain enzymatic activities will vary in predictable ways depending on the nutritional status of the phytoplankton cell. Nutrient status measurements are particularly useful when it is difficult to quantify "available" nutrient concentrations because growth limiting concentrations for some algae are below measurable concentrations. In combination with water chemistry measurements and physical measurements, such as light extinction and depth of stratification, nutrient status measurements can provide valuable information about the factors controlling algal growth and primary productivity in a lake.

In 1997 phytoplankton nutrient status measurements were made in all three basins of Lake Erie from early May until early October. Although many studies have published chlorophyll and nutrient chemistry for Lake Erie, we do not know of any other studies that have specifically looked at phytoplankton nutrient status over the spring, summer and fall season in all three basins of Lake Erie. Although Lake Erie is constantly changing as a result of exotic invaders and other natural and anthropogenic influences including climate change, lake level changes, erosion, agricultural and urban runoff, our measurements from 1997 should indicate the factors controlling algal growth in the post *Dreissena* invasion, post P reduction era (Charlton et al. 1999). The three distinct basins in Lake Erie and their different levels of P concentration (Charlton et al. 1999) are an ideal system for understanding the nutrient cycling and phytoplankton nutrient status dynamics of the other Laurentian Great Lakes and large lakes in general which differ in their P concentrations and dynamics.

Specifically the questions we address are: What is the nutrient status of phytoplankton in Lake Erie's three basins over the spring to fall seasons? How does the nutrient status of the phytoplankton in Lake Erie compare to other lakes? How can the information about seasonal dynamics of phytoplankton nutrient status and the dynamics of P, N and Si in the three basins help us to understand and make predictions about the health, productivity and trophic status of Lake Erie in the present and in the future?

Methods

Study Area

Lake Erie is the second smallest of the Laurentian Great Lakes with a surface area of 25,657 km² and drainage of 58,800 km². The Detroit River supplies 80% of the water input to Lake Erie. With its shallow average depth of 17 m Lake Erie has the shortest water retention time of the Laurentian Great Lakes. It is morphometrically divided into three distinct basins: the shallow west basin (mean depth 7.4 m), the large central basin (mean depth 18.5 m) which is separated from the deep east basin (mean depth 24.4 m) by the Pennsylvania ridge (Fig. 1). Detailed information about the lake can be found in two special issues of the Journal of Great Lakes Research (Boyce et al. 1987 and Makarewicz and Bertram 1993).

Field sampling

All three basins of Lake Erie were sampled from the CCGS Limnos at approximately monthly intervals from May through October in 1997 (Fig. 1). Samples were routinely taken from a depth of 5 m or less if the upper mixed layer was shallower than 5 m, using an 8-L PVC Niskin bottle on a General OceanicsTM Rosette sampler. Samples were stored in dark carboys until measurements were made on board ship which was usually less than 4 hours from the time of sampling. Temperature profiles were recorded using a SeabirdTM profiler. The depth of thermal stratification was considered to be the depth where temperature change exceeded 1°C per m. Water column light attenuation (K_d) was determined from vertical profiles of photosynthetically active radiation (PAR) made using a LICOR quantum probe with a cosine sensor and mean PAR in the mixed layer was calculated as described in Smith et al. (2003).

Laboratory procedures

Nitrate (NO₃), soluble reactive phosphorus (SRP), soluble reactive silica (SRSi), total phosphorus (TP), and total dissolved nitrogen (TDN) and organic seston measurements were made at the National Laboratory for Environmental Testing (NLET) at the Canada Centre for Inland Waters (CCIW) following their preservation and analytical procedures (Environment Canada 1979). Particulate carbon (C), nitrogen (N) and silica (Si) were measured in the Analytical Laboratory at the Freshwater Institute (Stainton et al. 1977). Total N (TN) is the sum of TDN and particulate N, total Si (TSi) is

the sum of SRSi and particulate Si. Chlorophyll *a* was measured fluorometrically (Stainton et al. 1977).

Measurements to determine the nutritional status of algae consisted of three seston composition ratios and four metabolic indicators. The seston ratios were particulate carbon:particulate nitrogen (C:N), particulate carbon:particulate phosphorus (C:P), and particulate carbon:chlorophyll *a* (C:chl). Particulate N and P and chlorophyll *a* change their proportion to C in algae that are deficient in nutrients and/or light (Healey 1975). The metabolic nutrient status indicators were nitrogen debt (N debt), phosphorus debt (P debt) and alkaline phosphatase activity (APA). We also measured PO₄ turnover time, using ³³P-PO₄. Algae growing at low growth rates because they are deficient in either N or P will take up more of that nutrient per unit chlorophyll *a* than algae not deficient in that nutrient (Healey and Hendzel 1980). This uptake by N or P deficient algae was termed "N or P debt" by Healey and Hendzel (1980). Similarly, high demand for PO₄ relative to supply will cause faster phosphate turnover times (Lean and Nalewajko 1979). For the N debt assay, 100 mL of unfiltered sample was enriched with ammonium chloride to yield a final concentration of 5 μM. Ammonium was measured (Stainton et al. 1977) on triplicate sub-samples at the beginning and end of incubation in the dark at room temperature for 24 h. Nitrogen debt was calculated as the N removed over a 24-h period per unit of chlorophyll *a* (Healey 1977). Phosphorus debt was measured in a similar way to N debt except that KH₂PO₄ was added (final concentration 5 μM). Soluble reactive P (SRP) was measured on triplicate sub-samples (Stainton et al. 1977) at the beginning and end of a 24 h. incubation. Phosphate turnover time was estimated from the rate of removal of carrier-free ³³P-PO₄ from the dissolved phase (Bentzen and Taylor 1991). APA was measured fluorometrically (Healey and Hendzel 1979b) using 5-μM *o*-methyl-fluorescein-phosphate as the substrate. Parallel determinations were made of total and soluble activities in order to distinguish between APA associated with particles and APA in solution, the soluble activity being that associated with passing through 0.2-μm filters. The difference was reported as particulate activity and this was normalized to chlorophyll *a*. Values indicative of nutrient deficiency for the seston and metabolic indicators are given in Table 1.

Data analysis

Seasonal data for most of the variables are presented as box plots in order to show the spread and variability in the data as completely as possible. For each box the central horizontal line is the median, the lower and upper edges of the box comprise the interquartile range within which 50% of the values occur. The bars extending above and below the boxes can represent a range around the median 1.5 times the interquartile range or they indicate the maximum and minimum values (if they are less than 1.5 times the interquartile range). Values beyond 1.5 times the interquartile range are indicated by an asterisk (*) and values 3 times the interquartile range by an open circle (o). When only one line is plotted, this represents the median without enough data points to calculate the distribution. Data for correlations were logarithmically transformed (base 10) to achieve more normal distributions and variances independent of their means. Statistical analyses were done using SYSTAT (Wilkinson 1990).

Results

Temperature, stratification and light

To illustrate the progress and degree of thermal stratification in Lake Erie over the months of our study (May to October), we plotted temperature profiles from a centrally located offshore station from each of the three main basins (Fig. 1). We chose station 357 with a depth of 11 m in the west basin, station 84, with a depth of 24 m in the central basin and station 23, the deepest location in the lake (60 m), in the eastern basin. During the first cruise in early May, there was no significant stratification in these basins (Fig. 2). There was a slight inverse stratification evident at station 23. The temperature in the western basin was 10 degrees Celsius and this was 3 degrees greater than the central basin and 7 degrees higher than the eastern basin. A strong west to east temperature gradient was imposed by the different depths of the basins early on in the phytoplankton growing season. The west basin temperature remained 2 – 5 degrees higher than the east and central basins until the lake began to cool in September (Fig. 2). The west basin showed various degrees of thermal stratification from June to September. Station 357 and other stations in the west basin are so shallow that stratification and destratification may occur throughout the summer months depending on the wind conditions. The larger

deeper basins are slower to warm, cool and mix compared to the western basin. Temperatures in the epilimnetic waters became more similar in the three basins as the summer progressed and the depth of the epilimnion also became very similar in the central and east basins during August and September.

The light environment for phytoplankton in the upper mixed layer (Fig. 3) is determined by a combination of the light attenuation coefficient (K_d) and the mixing depth of the water column (z_{mix}). K_d was as high as 2.7 m^{-1} in the west basin in the early months of the season, when high spring stream discharges of suspended solids tends to be higher and winds tend to resuspend the sediments. By mid summer, K_d was lower in all basins, relatively constant in the central and east basins; and mean PAR in the mixed layers of the basins was determined primarily by z_{mix} (Fig. 3).

Nutrients

TN, TP and TSi represent the total pool of macronutrients potentially available for phytoplankton growth. In Lake Erie the three different basins exhibit a wide range of TN, TP and TSi concentrations (Table 2). On a lake wide basis, these plant nutrient pools were highly correlated with each other (Fig. 4) with seasonal mean concentrations of TP, TN and TSi all higher in the west than in the central and east basins (Table 2).

The dissolved fractions of N, P and Si respond to uptake and sedimentation and can suggest when a critical nutrient might be in short supply in the different basins. N as indicated by both NO_3 and TDN remained readily detectable, never falling below 15 and $28 \mu\text{mol L}^{-1}$ respectively and showed little seasonality in all three basins (Fig. 5 a, b). Unfortunately, NH_3 , which would be most available to phytoplankton was not routinely measured. TDP was highly variable in the west basin, but never less than $0.1 \mu\text{M}$ (Fig. 5 b). SRP and TDP declined with the onset of stratification in the central and east basin (Fig. 5 a, b) and concentrations less than $0.1 \mu\text{M}$ TDP persisted in the central and east basins until destratification. TDP concentration remained lower for longer in the east basin (Fig. 5 b). The SRP data are incomplete and we use the more complete TDP data to infer the relative seasonal dynamics of dissolved P.

Indicators of phytoplankton biomass

In the central and east basins of Lake Erie, chlorophyll *a* and other particulate fractions, including particulate C, N, P and Si, were highly correlated (Table 3) while in the west Basin chlorophyll *a* was not significantly correlated to any of the particulate fractions (Table 3). However, when the data from the months of May and June (periods of weakest stratification and spring runoff) were removed from the correlations for the western basin, the agreement and levels of significance between chlorophyll *a* particulate C, N, P and Si were more similar to those of the central and eastern basins (Table 3). We did not include organic seston in the table of correlations because we did not have organic seston samples from October. However it can be seen from Fig 6 a, that in general organic seston had similar patterns to the other indicators of phytoplankton biomass with striking agreement on the July minima for all particulate fractions in the central basin. In the west basin in the spring particulate C, N, P, Si and organic seston decrease from June to July but chlorophyll *a* does not (Fig. 6a, b) which suggests that much of the particulate material was non-algal organic matter derived from spring terrestrial runoff.

As was observed with the total nutrient concentrations (Table 2), mean chlorophyll *a* concentrations for the May to October period were significantly higher in the western basin than in the central and eastern basins. The other measures of particulate matter followed a similar pattern (Table 2), that is, west basin concentrations were higher than central and east basins and the central basins concentrations were slightly, but consistently, higher than the east basin.

Chlorophyll *a* in the central basin ranged from a low monthly median concentration of $1.0 \mu\text{g L}^{-1}$ in July to a high of $6.5 \mu\text{g L}^{-1}$ in Oct., exhibiting a classical spring high, summer low and fall rise pattern (Fig. 6a). In the east basin both spring and fall chlorophyll *a* concentrations were low relative to the central basin. In the western basin monthly median chlorophyll *a* concentrations varied less over the sampling period and did not exhibit distinctive peaks or minima in any month.

Indicators of phytoplankton nutrient status

In Lake Erie in 1997, the east basin C:Chl ratio was consistently in the range indicative of nutrient (either N or P) deficiency (Fig. 7). The central basin C:Chl ratios

were on average lower and still in the range indicative of nutrient deficiency. In the western basin, C:Chl ratios were high in May and June but low, below the nutrient-limited range, for the remainder of the sampling season. As discussed above, particulate C in the western basin was high and more closely correlated to organic seston than to chlorophyll *a* in May and June. We interpret that to mean that the C:chl ratios in May and June in the west basin may not be reliable indicators of phytoplankton nutrient status but that they are more representative of phytoplankton during July to Oct. Thus taken as an overall indicator of nutrient status for Lake Erie, the C:Chl ratio indicates that the west basin is not nutrient deficient and the central and eastern basin are nutrient deficient with the east being more consistently nutrient deficient than the central basin.

The N debt assay and the particulate C:N ratio are indicators for N deficiency. In the west basin in May and June particulate C:N ratios and the N debt assay in the same months indicated N deficiency (Fig. 7). As discussed above, the west basin receives a high load of organic matter in spring and the seston C:N ratios are likely influenced by this material. The high N debt may be result of nitrifying bacteria using added NH_4 in the assay as a substrate. Whitby et al. (2001) reported increased numbers of nitrifying bacteria in the southern eutrophic basin of Lake Windermere as a result of winter mixing and resuspension of organic sediments. In the central basin during the months of May to August, N deficiency was indicated at some of the stations while in September and October N debt and C:N were in the no N deficiency range at all the stations in the central basin. In the east basin, no N debt measurements were made until July. C:N was high at all the east basin stations in May indicating N deficiency (Fig. 7). Although N debt and C:N ratios remained in the "nil" to "moderate" range during the remaining months sampled in the east basin, the values did not drop to low levels in September and October as they did in the central and west basins. Overall, the measures of N deficiency indicate no strong consistent N deficiency in any of the three basins.

The four measures for P deficiency, C:P, APA, P debt and PO_4 turnover time indicated that phytoplankton were on average not P deficient in the west basin during the sampling season in 1997 (Fig. 8 a and b). During July and October rates of alkaline phosphatase activity were measured that indicate P deficiency in the west basin but otherwise all the indicators were in the no P deficiency indicator range. In the central

basin, all four indicators of P deficiency indicated P deficiency at most stations during August and September, with the exception of P debt in August. C:P ratios and APA in July indicated strong P deficiency in the central basin. The east basin is different from the other basins in that, with the exception of the P debt assay, all the indicators of P deficiency were in the P deficient range for all the months sampled. As we noticed with the indicators of phytoplankton biomass, the central basin experienced larger excursions of values over the sampling season. The strongest indications for P deficiency, as indicated by C:P and APA, in the lake, were measured in the central basin during July when nutrient concentrations and particulates also showed a strong minimum. Overall the measures of P deficiency indicate no P deficiency in the west basin, severe P deficiency in the central basin only during July and sustained moderate P deficiency in the eastern basin from May to October. Agreement for indicators of P deficiency was best among C:P, APA and PO_4 turnover time. P debt did not appear to be as sensitive as the other P deficiency indicators in Lake Erie. In severely P deficient oligotrophic shield lakes in northwestern Ontario, P debt was sensitive to P deficiency and highly correlated to other indicators of P deficiency (Healey and Hendzel 1980).

Discussion

West Basin

Our nutrient status measurements indicated that phytoplankton in the west basin in 1997 were not, on average, N or P deficient during May through October. The western basin, although exhibiting much reduced P concentrations since the implementation of the GLWQ agreement in the 1979 (Charlton et al. 1999), still has relatively high P concentrations (Fig. 5a, b) and continues to have high N concentrations (Fig. 5a, b). The shallow depth of the western basin ensures that stratification is not persistent (Ackerman et al. 2001) so nutrients rarely become depleted in the euphotic zone for any length of time. As well as high nutrient concentrations, the lower mean water column light conditions (Fig. 3) could explain why phytoplankton in the western basin do not develop nutrient deficiency. Mean water column light intensity in the western basin during May and June is in the range that would be expected to result in light limitation of some species of phytoplankton (Hecky and Guildford 1984, Fahnenstiel et al. 2000, Smith et al.

2003). After June the light environment in the shallow west basin improves (Fig. 3) and mean water column light intensities are generally not in the range where light limitation might occur. However given the dynamic nature of the shallow western basin it is likely that there are intermittent wind driven resuspension events that would result in short term light deficiency and at the same time contribute new nutrients to the water column, both phenomenon which would lessen nutrient deficiency.

Grazing as well as light is likely a contributing factor to the apparent lack of phytoplankton nutrient deficiency in the western basin compared to the central and eastern basins. Johannsson et al. (1999) reported mean zooplankton biomass of $73 \mu\text{g L}^{-1}$ at an offshore west basin station compared to 52 and $37 \mu\text{g L}^{-1}$ at central and east basin offshore stations respectively in 1993-1994. More recent zooplankton biomass data show a similar pattern of highest zooplankton biomass in the western basin (Stockwell et al. 2002, MacDougall et al. 2001). *Daphnia*, a most effective grazer of phytoplankton, comprises the majority of the zooplankton biomass in the offshore western basins during the months of May to July (Johannsson et al. 1999, MacDougall et al. 2001).

Although density and biomass estimates of *Dreissena* indicate that relative to the east and central basins the west basin *Dreissena* biomass is not exceptional (MacDougall et al. 2001), the shallow depth and smaller volume of the western basin compared to the central and east basin means that the ratio of water to mussels is greatest in the western basin. Of the three Erie basins, the western basin exhibited the greatest decrease in chlorophyll concentration and increase in water transparency following the invasion of the zebra mussels. Charlton et al. (1999) reported that chlorophyll decreased by almost $3.0 \mu\text{g L}^{-1}$ from 1984 to 1996 compared to 0.7 and $0.4 \mu\text{g L}^{-1}$ in the east and central basins respectively. Transparency as indicated by Secchi disk depth increased by 2.2 m in the western basin during the same post *Dreissena* invasion period and only 0.5 m in the east basin and not at all in the central basin (Charlton et al. 1999).

Nicholls et al. (1999) demonstrated that *Dreissena*-impacted nearshore locations underwent dramatic decreases in the chlorophyll:TP ratio as a response to heavy grazing. The offshore stations in our 1997 data do not exhibit exceptionally low Chlorophyll:TP ratios and this fact would argue against grazer control of phytoplankton at the offshore stations. It is likely that phytoplankton in the offshore stations have higher chlorophyll

per cell as a result of the lower mean PAR at those stations. Phytoplankton increase the cellular content of chlorophyll as a compensatory mechanism for decreased light (Healey 1985). This phenomenon could mask evidence for grazing based on a reduced chlorophyll:TP ratio in the offshore western basin.

Another indirect indication that phytoplankton in the west basin are influenced by grazing as well as light is the increasing occurrence of the cyanobacteria *Microcystis* in the western basin of Lake Erie post *Dreissena* (Vanderploeg et al. 2001, Budd et al. 2001). Vanderploeg et al. (2001) demonstrated that *Microcystis* was likely increasing because it was selectively rejected after inhalation by *Dreissena*. Lavrentyev et al. (1995) reported a similar effect with *Dreissena* from Lake Huron as did Nicholls et al. (2002) in the Bay of Quinte in Lake Ontario. A species that is not grazed has a competitive advantage over more heavily grazed species if nutrients are not limiting growth of phytoplankton in general. A further advantage for *Microcystis* is that they have a relatively low optimum N:P atomic ratio, 9, for growth (Hecky and Kilham 1988) which would give them a competitive advantage over several other phytoplankton species in a low N:P environment. Grazers regenerate N as ammonium the most useable N fraction for phytoplankton. Arnott and Vanni (1996) demonstrated that *Dreissena polymorpha* regenerates relatively more P than N, and showed that N:P ratios decreased from the surface to the bottom in water overlaying a mussel bed in western Lake Erie (Arnott and Vanni 1996). High grazing rates and low N:P of regenerated nutrients would favour *Microcystis* and other relatively inedible colonial cyanobacteria in the western basin.

Central Basin

There was a dramatic decline in particulate matter and in plant nutrients throughout the central basin in July 1997 (Fig. 6a, b and 5a, b). The strongest indicator values for P deficiency that we observed during the study were those observed in the central basin at this time. Lean et al. (1983) measured phosphate turnover time in the central basin in 1979 and found a similar pattern with long turnover times in May and June and much shorter turnover times during the strongly stratified period in July and August. Dissolved Si was drawn down as low as 0.5 μM in the Central Basin during July, which

is a concentration that would be potentially limiting for the growth of diatoms (Ragueneau et al. 2000). When diatoms become Si deficient their sinking rates increase (Waite et al. 1997). Preserved lugols samples from offshore stations in the central basin were inspected quantitatively to determine the composition of the phytoplankton community over the months when we observed the dramatic fluctuations in particulate matter in the upper mixed layer. In June diatoms made up 80 % of total phytoplankton biomass (265 mg m^{-3}). The dominant species were *Stephanodiscus hantzschii*, *Actinocyclus normanii* and *Fragilaria crotenensis*. Biomass in the samples taken in early July was down to 115 mg m^{-3} and diatoms made up only 22 % of the total biomass. By early September sample biomass increased to 170 mg m^{-3} and the diatoms, dominated by *Fragilaria crotenensis* made up over 70% of the samples biomass. Thus it appears from the indicators of nutrient deficiency (strong indications of P deficiency), measures of dissolved Si (declining to limiting concentrations) and the decrease and change in phytoplankton composition (disappearance of diatoms from the epilimnion) that the phytoplankton in the central basin were likely growing at high or positive growth rates until July when, at the period of maximum thermal stratification, P became limiting to the phytoplankton population in general and Si became limiting to the diatom population which formed a major part of the total phytoplankton population. This event of concurrent P and Si limitation, followed by sedimentation of most of the particulate matter from the epilimnion (Fig. 6 a, b) in July and the rapid rebound in biomass in August when the thermocline deepened (Fig. 2) is significant to the understanding of the productivity of the central basin, especially with respect to the changes as a result of P reductions.

Over the years of high P loading and eutrophication of Lake Erie, Si became depleted as the growth and sedimentation of diatoms exceeded the Si supply (Schelske et al. 1983). One of the results of implementation of P controls on detergents and waste treatment plants appears to be that the concentration of Si in Lake Erie is increasing. In the early 1980's average Si concentrations were $3 \mu\text{mol L}^{-1}$ in the central and east basins and $14.5 \mu\text{mol L}^{-1}$ in the west basin (Lesht and Rockwell 1985, 1987). In our study the average Si concentrations were much higher (Table 2). This increase in the Si pool in response to P reductions likely contributed to the increase in diatom abundance reported

by Makarewicz et al. (1999). A similar observation has been made in Lake Michigan by Barbiero et al. (2002). The balance of P and Si in the central basin appears to be favourable for the growth of diatoms. Kilham (1986) demonstrated that diatoms from Lake Michigan were superior competitors for P when Si supply was not limiting, and that when Si was limiting chlorophytes became dominant. With Si:P in proportions that favour diatom growth, the central basin may be more favourable for secondary production than when P was in higher concentrations. Diatoms are the preferred species of phytoplankton for grazers in a lake in terms of providing high food quality at the base of the food chain (Sterner and Elser 2002). The balance of Si, P and light in the central basin of Lake Erie may now combine to provide a very productive base for the food web.

The other factor that favours diatom growth in the central basin is a result of the basin morphometry. The central basin is a large relatively flat basin, just deep enough to stratify in summer. Stratification contributes to a high light environment which encourages phytoplankton growth. At the same time the central basin is shallow enough, with 38% of its total area under 20 m, that nutrient return to the epilimnion would occur more frequently than in the deeper east basin where only 16% of the total area is less than 20 m deep (Fig. 2). Another large shallow productive lake basin that is similar to the central basin of Lake Erie is the north basin of Lake Winnipeg. Hecky et al. (1986) demonstrated that in the north basin of Lake Winnipeg as the overlying waters cooled there was return of nutrients to the water column because of the temperature change between the water overlaying the sediments and the interstitial water in the sediments. It was not necessary to have vigorous mixing for this to occur. The fact that chlorophyll *a* concentration and other indicators of phytoplankton biomass increased immediately after the July sedimentation event, to levels as high as observed in the May sampling, demonstrates that the central basin receives a good supply of nutrients from the epilimnetic sediments and/or from the hypolimnetic water as the thermocline deepens (Fig. 2). After the July minimum (Fig. 6 a, b), phytoplankton were moderately P deficient until stratification was completely removed in October.

East Basin

The phytoplankton biomass and nutrient status patterns in the eastern basin are puzzling when compared to the central basin. Phytoplankton biomass as indicated by chlorophyll *a* and particulate matter remained low in the eastern basin relative to the central basin (Fig. 6a, b and Table 2). Concentrations of dissolved nutrients in the east basin epilimnion were on average lower than the central basin (Fig. 5 a, b). If phytoplankton biomass was lower in the east basin as a result of nutrient limitation it was expected that the nutrient status indicators would reflect this. The pattern we observed was that of moderate and consistent nutrient deficiency but not as strong as we observed in the central basin in early July. (Fig. 8a). The central and east basin are both very different from the west basin. Differences between the central and east basin are much more subtle, but nevertheless present. There is a lag in temperature, with the east warming later and never quite reaching the maximum temperature found in the central basin. In 1997 the east basin stratified shallower than the central basin, and although for August and September the depth of stratification was similar in the two basins, the central basin was mixing to the bottom by October and entraining nutrients, while the east did not mix throughout its greater depth during our observational period. The thick, cold hypolimnion underlying much of the epilimnetic eastern basin does not appear to provide nutrients at the same rate or concentration as in the central basin when thermocline deepening begins.

The phytoplankton in the east basin became moderately P deficient by July and remained, on average, moderately P deficient through October. The persistent thermocline overlaying the deep, cold east basin hypolimnion can explain why nutrient deficiency is not relieved as the summer progresses. Lean et al. (1983) noticed a similar pattern in the east basin of Lake Erie in 1979. Evidence for P deficiency extended into October. As noted in the discussion of the central basin, the proportion of the basins that overlays water less than 20 m deep is quite different, with the east basin having only 16% of its total area over water shallower than 20 m, compared to 38% of the central basin and 100% of the western basin. What is puzzling about the east basin is the lack of extreme P deficiency. In the central basin in July C:P ratios, alkaline phosphatase activity, and P debt at some stations did indicate extreme P deficiency. Although moderate P deficiency persists on into October in the east basin, it does not become as severe as we observed in

the central basin. It is possible with the smaller number of stations in the east basin compared to the central basin that we may have missed periods or stations with indications of severe nutrient deficiency. Alternatively, this lack of extreme P deficiency in the stratified east basin may indicate that phytoplankton were controlled by a factor or factors other than P.

In spring cool temperatures and deeply mixed water prevent the mean water column light intensity from being high enough to result in rapid drawdown of nutrients. For the remainder of the sampling season low light extinction and shallow stratification ensured the epilimnion had adequate light (Fig. 3). Why then did we not see stronger P deficiency? Guildford et al. (1994) posed a similar question about the degree of P deficiency in Lake Superior. Lake Superior has on average even lower TP ($0.15 \mu\text{M}$) than the east basin of Lake Erie. Indicators of P deficiency were stronger in Lake Superior (Guildford et al. 1994) than in Lake Erie, but not nearly as strong as the indicators of P deficiency in many other smaller lakes in the same geoclimatic region (Fig. 9). It was suggested that Lake Superior was not as strongly nutrient deficient as the smaller lakes because the deeper epilimnion allowed more time for regeneration of nutrients within the upper mixed layer compared to smaller lakes with shallow epilimnions where nutrients were lost early in the stratified season with sinking particles (Fee et al. 1994; Guildford et al. 1994). This "large lakes hypothesis" was cited by Levine et al. (1999) as a possible explanation for lack of strong nutrient limitation in Lake Champlain. It is difficult to reconcile this explanation in Lake Erie as the central and east basin epilimnetic depths were similar for much of the summer. Recent experiments in Lake Erie (Twiss et al. 2000, North, unpublished data) indicate that Fe can be a limiting nutrient at times for phytoplankton in the Lake Erie. Guildford et al. (2003) similarly demonstrated the importance of Fe in a series of enrichment experiments in tropical African Great Lake Malawi. Because the hypolimnion of the eastern basin is deep and does not experience anoxia, there is no mechanism for sedimentary release and return of P or Fe to the water column. The oxygenated hypolimnion also ensures that NO_3 , rather than NH_4 , remains high throughout the year. Low Fe and other trace metals may retard the development of strong P deficiency in the east basin of Lake Erie.

Grazing may also limit the development of extreme P deficiency by rapidly recycling P to sustain phytoplankton growth. The phytoplankton abundance in the offshore waters of the eastern basin would not be as strongly affected or controlled by *Dreissena* grazing as in the shallow west basin. The nearshore littoral in the eastern basin has a high proportion of bedrock which provides ideal habitat for *Dreissena polymorpha* and *Dreissena bugensis* and the abundance of *Dreissena bugensis* became very high in the eastern basin during the years since the invader was first observed in 1989 (Johannsson et al. 2000). However thermal stratification essentially isolates the epilimnion from the effects of benthic filter feeders for the majority of the phytoplankton growing season (Ackerman et al. 2001). There are no data that would indicate that zooplankton or the pelagic veliger stage of *Dreissena* are abundant enough to impact phytoplankton in the eastern basin (Johannsson et al. 2000).

Based on our 1997 indicators of nutrient status and phytoplankton biomass, it is difficult to conclude what nutrient or factor is controlling phytoplankton growth in the eastern basin. One problem is that we have fewer data in the eastern basin compared to the central and west. This is important because the east is morphometrically more variable than either the central or the western basin and more stations may be needed to achieve an accurate representation of the biotic and abiotic processes. However we do note that the coefficient of variation for most of the variables in the eastern basin are actually lower than for the central or western basin (Table 2, 4) suggesting sampling variability is not distorting our results.

Lake Erie in perspective

On average the phytoplankton of Lake Erie were not strongly N or P deficient in 1997. With the exception of early July in the central basin, our measures of phytoplankton nutrient status indicated that phytoplankton were only moderately P deficient during the stratified season in the central and east basin and not P deficient at all in the mainly unstratified western basin. All of the indicators of nutrient status used in this study have been used in similar long term, whole lake studies in several large lakes within the same geoclimatic region of Canada. In order to place Lake Erie results in perspective with these other lakes, two of the P deficiency indicators (C:P and APA)

were plotted for Lake Erie, Southern Indian Lake (Hecky and Guildford 1984), and eight lakes from the Northwestern Ontario Lakes Size Series Study (NOLSS) (Guildford et al. 1994). Fig 9 shows that the values for C:P and APA for Lake Erie fall in the middle to low range of this group of lakes, and the values for TP for Lake Erie fall in the middle to high range for the group. Among the group of lakes there is a trend for increasing P deficiency with decreasing TP concentration. However there are lakes with TP concentrations very similar to the Lake Erie central and eastern basin average concentrations that are more P deficient as indicated by both APA and C:P. Compared to these other lakes it appears that per unit of TP, the phytoplankton in Lake Erie are not as P deficient as the phytoplankton in the other lakes (Fig. 9 a, b).

It is expected that if phytoplankton are not severely N or P deficient and if no other factor is controlling growth, then the phytoplankton should be growing at a higher growth rate than phytoplankton that are strongly nutrient deficient. Although we do not have actual growth rates, we are able to compare photosynthetic parameters P_m^b and α^b , from the same group of lakes. Lake Erie phytoplankton had higher P_m^b and α^b than any of the other lakes (Table 5). The lakes from the Northwestern Ontario Lakes Size Study (NOLSS), including Lake Superior that had similar or lower TP, were more P deficient than Lake Erie (Fig. 9 a, b), and had lower photosynthetic parameters (Table 5). Stations from the Southern Indian Lake study (4B, 6C and 6E) had high concentration of TP and had higher values for P_m^b and α^b than NOLSS but lower than Lake Erie. Light extinction was high in Southern Indian Lake (Table 5) and the phytoplankton were light limited (Hecky and Guildford 1984). Smith et al. (2003) compared integral production for the same group of lakes and we have included his values in Table 6 to illustrate how much higher rates of integral production are in the less P deficient, non light limited lakes (Table 5).

Lake Erie phytoplankton productivity is higher per unit of TP than other lakes because the phytoplankton are not strongly P deficient nor light limited. It appears that P is regenerated more efficiently in Lake Erie than in other lakes. The mechanism explaining this more efficient regeneration is beyond the scope of this study. However, we speculate that Lake Erie, especially the central basin, has an optimal combination of

light, nutrient supply rates and ratios, and benthic regeneration imposed by the morphometry of this large, open, shallow lake.

Conclusions

Reductions in TP in Lake Erie have not resulted in a strongly P deficient phytoplankton community. During 1997, phytoplankton in the west basin were neither P or N deficient and experienced light deficiency only in May. The central and eastern basins remained moderately P deficient as long as stratification persisted except for early July when phytoplankton in the central basin became severely P deficient. At this time the predominately diatom community sedimented from the mixed layer but rebounded by the end of the month. Phytoplankton in the eastern basin, where we measured the lowest TP concentrations and where stratification persisted for the longest period, never became strongly P or N or light deficient. This led us to speculate that in the east basin some other nutrient such as Fe or some other factor such as grazing may be important. Compared to several other lakes from the same geoclimatic area as Lake Erie, with a wide range of TP concentrations, Lake Erie stands out as being less nutrient deficient and having higher rates of integral primary production per unit TP than many of the lakes. These results lead us to conclude that the Lake Erie phytoplankton community in 1997 was operating efficiently at the extant P concentrations. If P loading to the lake were increased it may well lead not to enhanced primary productivity but rather to proliferation of less desirable and less efficient phytoplankton, replacing the apparently efficient community that has developed after several decades of P controls.

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Table 1. Values indicative of presence or absence or degree of nutrient deficiency for nutrient status indicators used in this study. C = particulate carbon; N = particulate nitrogen; P = particulate phosphorus; chl = chlorophyll *a*; TT=turnover time. Values are based on Healey and Hendzel (1979) except for PO₄ TT which is based on Lean et al. (1983).

Indicator	Nutrient	No Deficiency	Moderate Deficiency	Extreme Deficiency	Deficient
C:N ^a	N	<8.3	8.3-14.6	>14.6	
C:P ^a	P	<129	129-258	>258	
C:Chl ^b	N or P	<4.2	4.2-8.3	>8.3	
N debt ^c	N	<0.15			>0.15
P debt ^d	P	<0.075			>0.075
APA ^e	P	<0.003	0.003-0.005	>0.005	
PO ₄ TT ^f	P	>60	<60	<10	

^a atomic ratio

^b $\mu\text{mol C } \mu\text{g chl}^{-1}$

^c $\mu\text{mol N } \mu\text{g chl}^{-1}$

^d $\mu\text{mol P } \mu\text{g chl}^{-1}$

^e $\mu\text{mol P } \mu\text{g chl h}^{-1}$

^f min

Table 2. Mean and standard deviation (*italics*) for total (T) and particulate (P) C, N, P and Si, ($\mu\text{mol L}^{-1}$) and chlorophyll *a* ($\mu\text{g L}^{-1}$). Number of samples is given in parentheses.

	TN	TP	TSi	Chl <i>a</i>	PC	PN	PP	PSi
Whole Lake	49.5	0.45	32.7	4.1	33.4	3.9	0.25	6.7
(52)	24.9	0.29	26.1	3.3	20.7	2.2	0.20	6.9
West	64.8	0.71	60.5	5.9	47.6	5.5	0.41	11.1
(17)	38.5	0.36	23.4	3.9	29.5	2.6	0.24	9.6
Central	42.2	0.35	18.8	3.7	27.9	3.4	0.20	5.7
(23)	9.5	0.14	12.0	2.9	10.2	1.6	0.11	4.0
East	42.6	0.30	17.3	2.0	24.1	2.7	0.12	2.5
(12)	8.0	0.14	12.4	0.8	6.4	1.0	0.09	1.5

Table 3 Pearson correlation matrix for indicators of biomass. PC = particulate C, PN = particulate N, PP = particulate P, P_{Si} = particulate Si. Data were log transformed. Bolded values represent data with p values less than the significance level 0.05.

		Chl <i>a</i>	PC	PN	PP
West	PC	0.04			
	PN	0.31	0.92		
	PP	0.25	0.76	0.66	
	P _{Si}	0.11	0.72	0.54	0.90
West July- Oct	PC	0.71			
	PN	0.85	0.96		
	PP	0.70	0.91	0.90	
	P _{Si}	0.32	0.70	0.60	0.76
Central	PC	0.88			
	PN	0.90	0.98		
	PP	0.75	0.60	0.66	
	P _{Si}	0.73	0.67	0.67	0.69
East	PC	0.81			
	PN	0.94	0.91		
	PP	0.81	0.70	0.90	
	P _{Si}	0.40	0.21	0.28	0.30

Table 4. Mean and standard deviation (*italics*) for indicators of nutrient status. Number of samples for most of the indicators in parentheses. C:Chl ($\mu\text{mol ug}^{-1}$), N debt ($\mu\text{mol N } \mu\text{g Chl}^{-1}$), C:N (molar), C:P (molar), APA ($\mu\text{mol P } \mu\text{g Chl h}^{-1}$), P debt ($\mu\text{mol P } \mu\text{g Chl}^{-1}$), PO_4 TT (min). TT = turnover time

	C:Chl	N debt	C:N	C:P	APA	P debt	PO_4 TT
Whole Lake	11.3	0.167	8.6	175	0.015	0.048	1801
(52)	<i>9.6</i>	<i>0.316</i>	<i>1.6</i>	<i>119</i>	<i>0.017</i>	<i>0.047</i>	<i>4256</i>
West	12.6	0.178	8.4	129	0.007	0.062	1418
(17)	<i>16.0</i>	<i>0.402</i>	<i>1.8</i>	<i>47</i>	<i>0.009</i>	<i>0.043</i>	<i>1344</i>
Central	9.3	0.191	8.5	189	0.018	0.034	2563
(23)	<i>3.3</i>	<i>0.294</i>	<i>0.9</i>	<i>145</i>	<i>0.020</i>	<i>0.040</i>	<i>5574</i>
East	13.4	0.074	9.3	212	0.021	0.058	51
(12)	<i>4.5</i>	<i>0.123</i>	<i>2.3</i>	<i>119</i>	<i>0.015</i>	<i>0.065</i>	<i>48</i>

Table 5. Comparison of photosynthesis parameters, TP and chlorophyll *a* for several lakes in the same geoclimatic area as Lake Erie. SIL is the Southern Indian Lake study (Hecky and Guildford 1984), NOLSS is the Northwest Ontario Lake Size Study (Guildford et al 1994), Lake Erie data are from this study (Smith et al submitted). TP ($\mu\text{mol L}^{-1}$), P_m^b is the light saturated photosynthesis parameter (g C g chl h^{-1}), α^b is the light utilisation efficiency parameter ($\text{g C g chl}^{-1} \text{E}^{-1} \text{m}^2$), P_{int} is seasonal primary production (g C m^{-1} , May to Oct), K_d is the light extinction coefficient (m^{-1}).

Lake/site	Study	TP	P_m^b	α^b	P_{int}	Chl <i>a</i>	K_d
Wood	SIL	0.41	2.6	4.2	81	3.3	0.75
6C	SIL	0.73	3.2	4.8	49	3.0	1.30
6E	SIL	0.97	3.0	5.1	35	3.4	2.29
4B	SIL	0.55	3.1	5.9	99	3.6	0.80
Green	NOLSS	0.24	2.6	2.5	34	1.8	0.46
Orange	NOLSS	0.27	2.2	3.5	35	2.7	0.61
Linge	NOLSS	0.33	2.5	4.1	41	3.5	0.62
Musclow	NOLSS	0.40	2.5	4.4	53	4.2	0.61
Sydney	NOLSS	0.32	2.4	3.9	48	2.8	0.48
Trout	NOLSS	0.24	2.6	3.9	43	1.8	0.35
Nipigon	NOLSS	0.25	2.7	4.0	47	2.4	0.44
Superior	NOLSS	0.15	1.9	3.2	31	0.9	0.17
West	ERIE	0.71	5.3	7.5	111	4.9	1.12
Central	ERIE	0.35	4.3	8.1	120	3.3	0.43
East	ERIE	0.30	3.9	7.9	109	2.1	0.33

Figure Captions

Fig. 1. Map of Lake Erie showing location of sampling stations and the 20 m contour. Not all stations were sampled on each cruise.

Fig. 2. Representative monthly temperature profiles from each basin for each of the cruises. The stations were 357 (west basin), 84 (central basin) and 23 (east basin). The dates were May (May 6-9), June (June 2-5), July (July 1-3), August (July 29-31), September (August 26-28) and October (October 6-8).

Fig. 3. Box plots of vertical attenuation coefficient (K_d), mixing depth (z_{mix}), and mean PAR in the surface mixing layer by basin and month in 1997 for each of the five cruises from May to October 1997. For each box the central horizontal line is the median, the lower and upper edges of the box comprise the interquartile range within which 50% of the values occur. The bars extending above and below the boxes can represent a range around the median 1.5 times the interquartile range or they indicate the maximum and minimum values (if they are less than 1.5 times the interquartile range). Values beyond 1.5 times the interquartile range are indicated by an asterisk (*) and values 3 times the interquartile range by an open circle (o). When only one line is plotted, this represents the median without enough data points to calculate the distribution.

Fig. 4. Total nitrogen (TN) vs total phosphorus (TP), total Si (TSi) vs TP and TSi vs TN. Units are $\mu\text{mol L}^{-1}$, log scale. Symbols are • (west basin), o (central basin), + (east basin).

Fig. 5a. Box plots by month for each basin of nitrate (NO_3), soluble reactive phosphorus (SRP) and soluble reactive silica (SRSi). Units are $\mu\text{mol L}^{-1}$.

Fig. 5b. Box plots by month for each basin of total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP). Units are $\mu\text{mol L}^{-1}$.

Fig. 6a. Box plots by month for each basin of chlorophyll *a* ($\mu\text{g L}^{-1}$), organic seston (mg L^{-1}) and particulate carbon (C) ($\mu\text{mol L}^{-1}$).

Fig 6b. Box plots by month for each basin of particulate nitrogen (N), particulate phosphorus (P) and particulate silica (Si) ($\mu\text{mol L}^{-1}$).

Fig. 7a Box plots by month for each basin for indicators of phytoplankton nutrient deficiency C:Chl *a* ($\mu\text{g L}^{-1}$), N debt ($\mu\text{mol N } \mu\text{g chl}^{-1}$) and particulate C:N (molar).

Fig. 8a. Box plots by month for each basin for indicators of phosphorus deficiency. Particulate C:P (molar), Alkaline phosphatase activity (APA) ($\mu\text{mol P } \mu\text{g chl h}^{-1}$), Pdebt ($\mu\text{mol P } \mu\text{g chl}^{-1}$).

Fig. 8b. PO_4 turnover time (minutes).

Fig 9. Comparison of P deficiency indicators for several lakes in the same geoclimatic region as Lake Erie. Alkaline phosphatase activity (APA) ($\mu\text{mol P } \mu\text{g chl h}^{-1}$) vs TP ($\mu\text{mol L}^{-1}$) and particulate C:P (molar) vs TP ($\mu\text{mol L}^{-1}$). West, central and east refer to Lake Erie data from this study. The references for the data for the remaining lakes and sites are given in the text.

Fig. 1

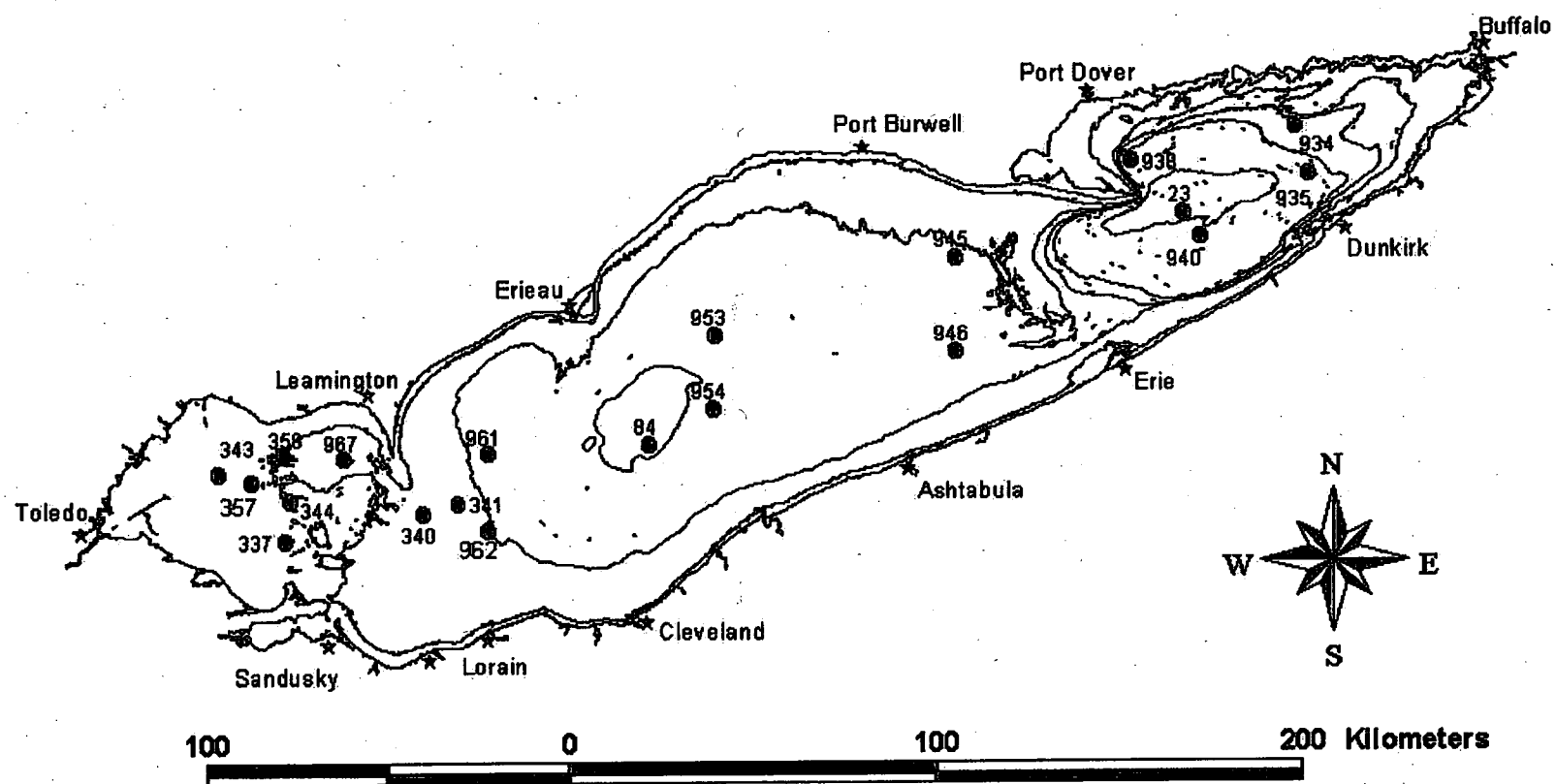


Fig. 2

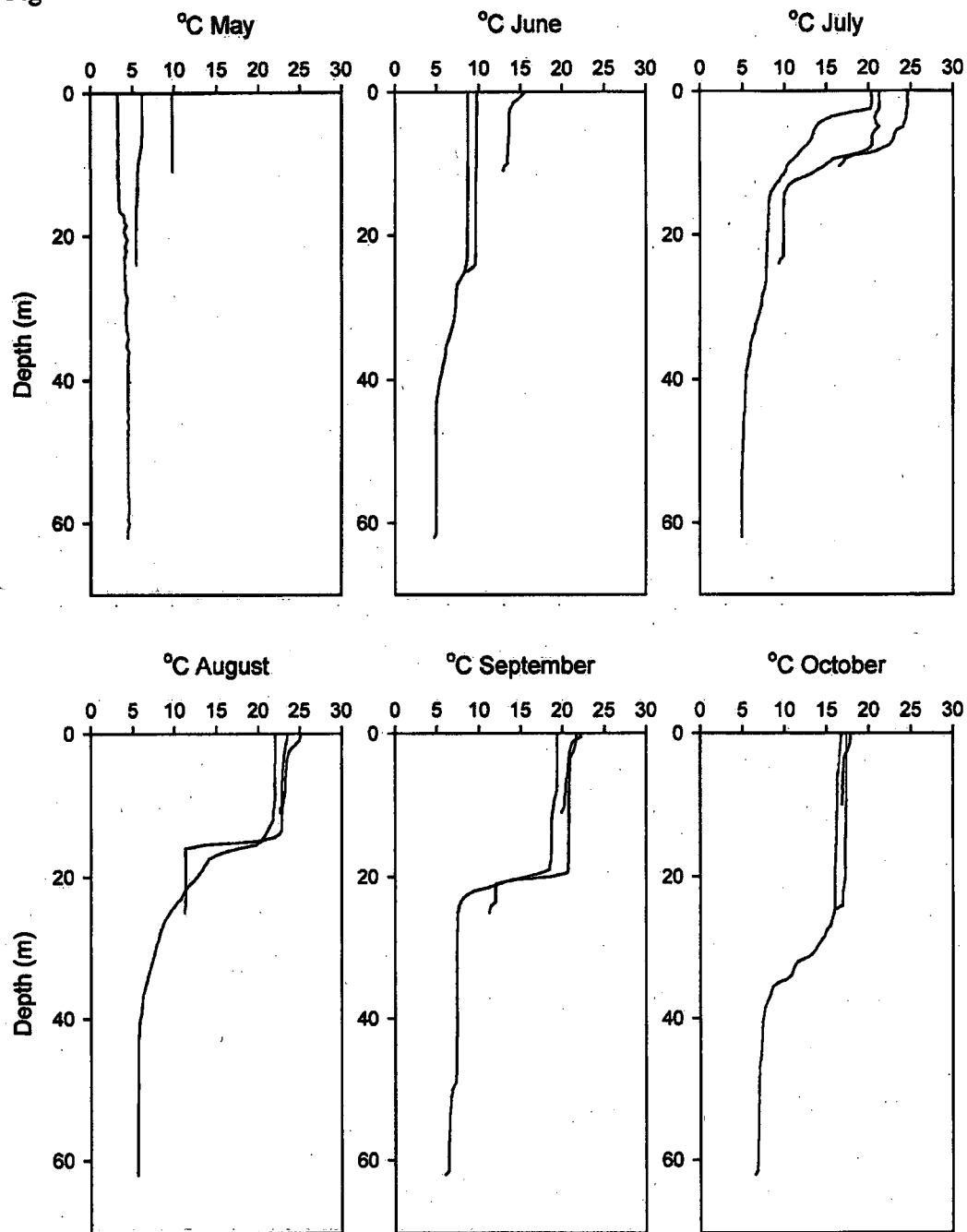


Fig. 3

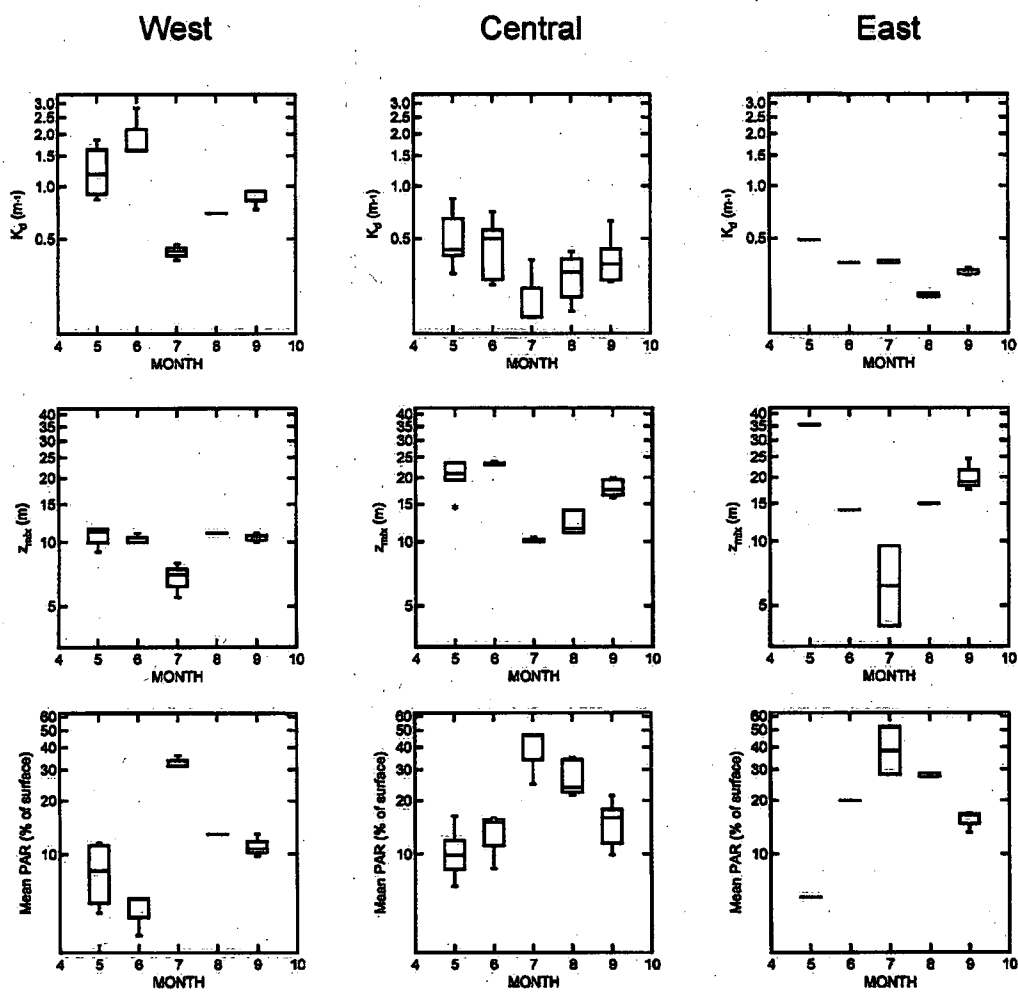


Fig. 4

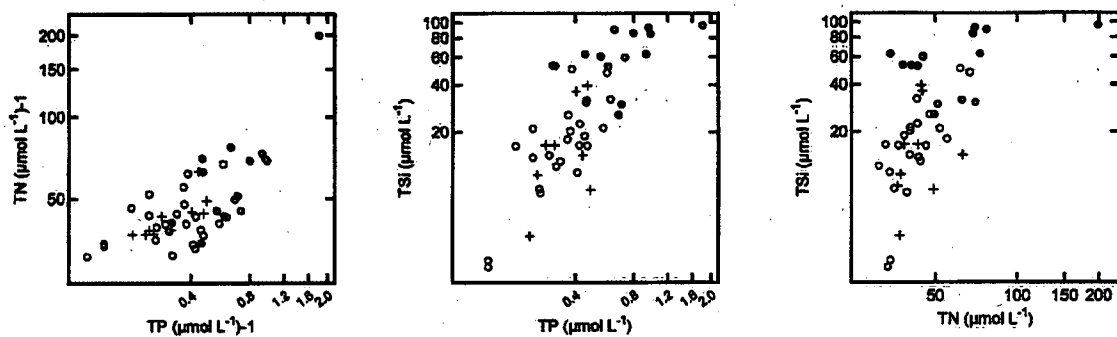


Fig. 5a

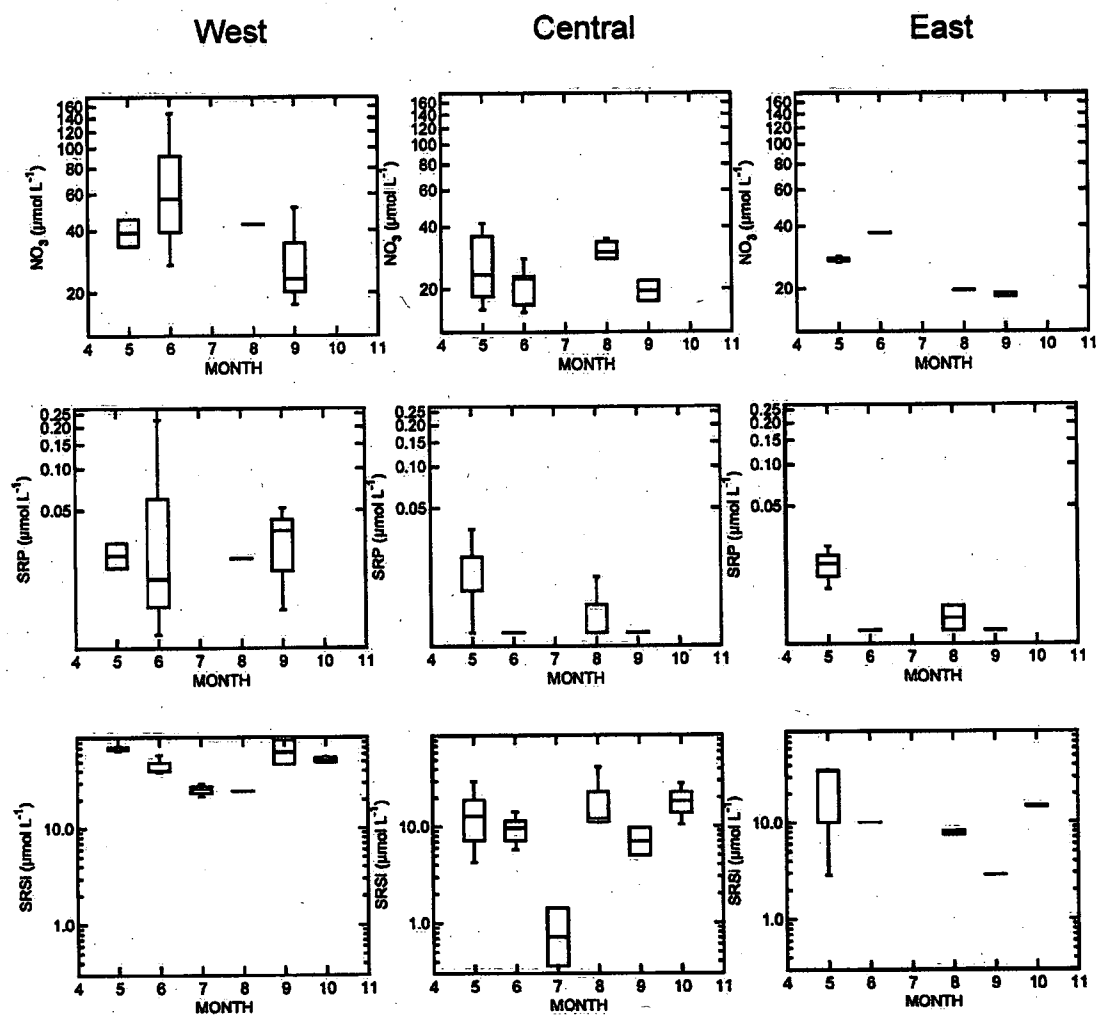


Fig. 5b

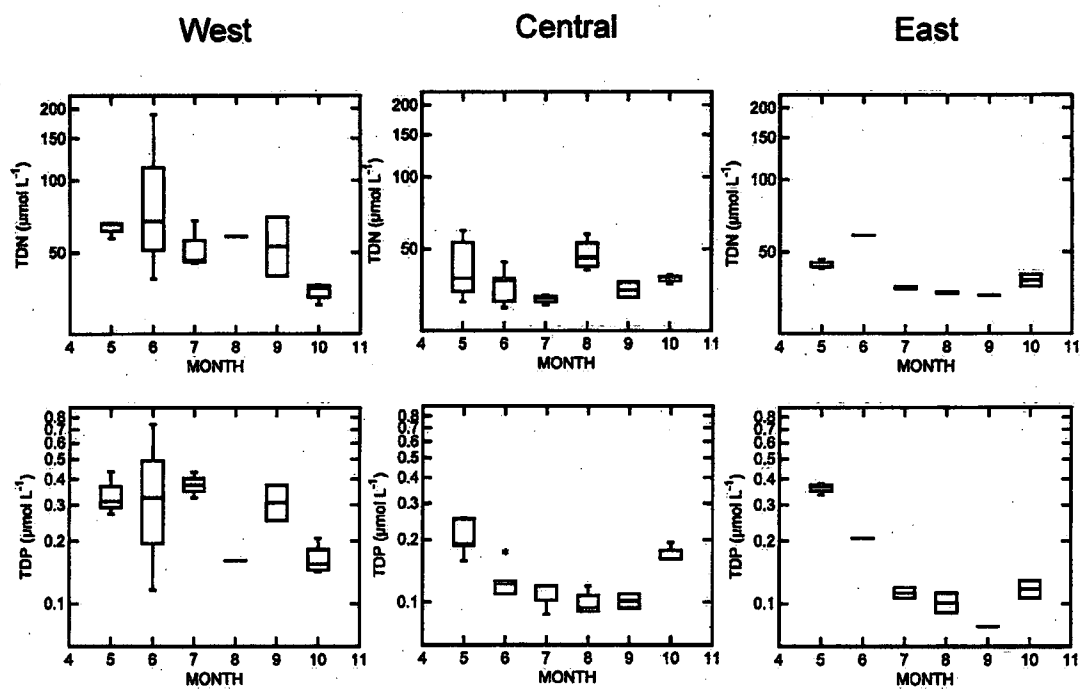


Fig. 6a

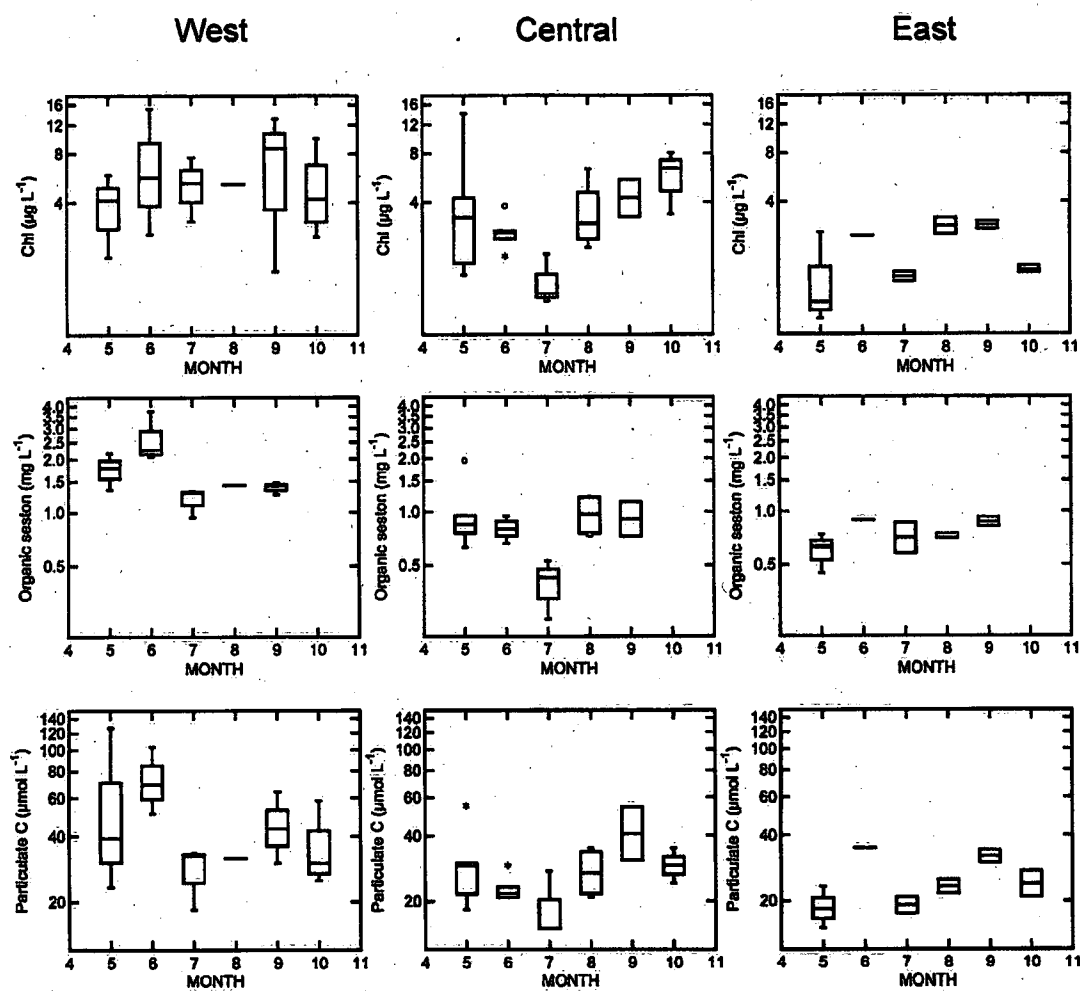


Fig. 6 b

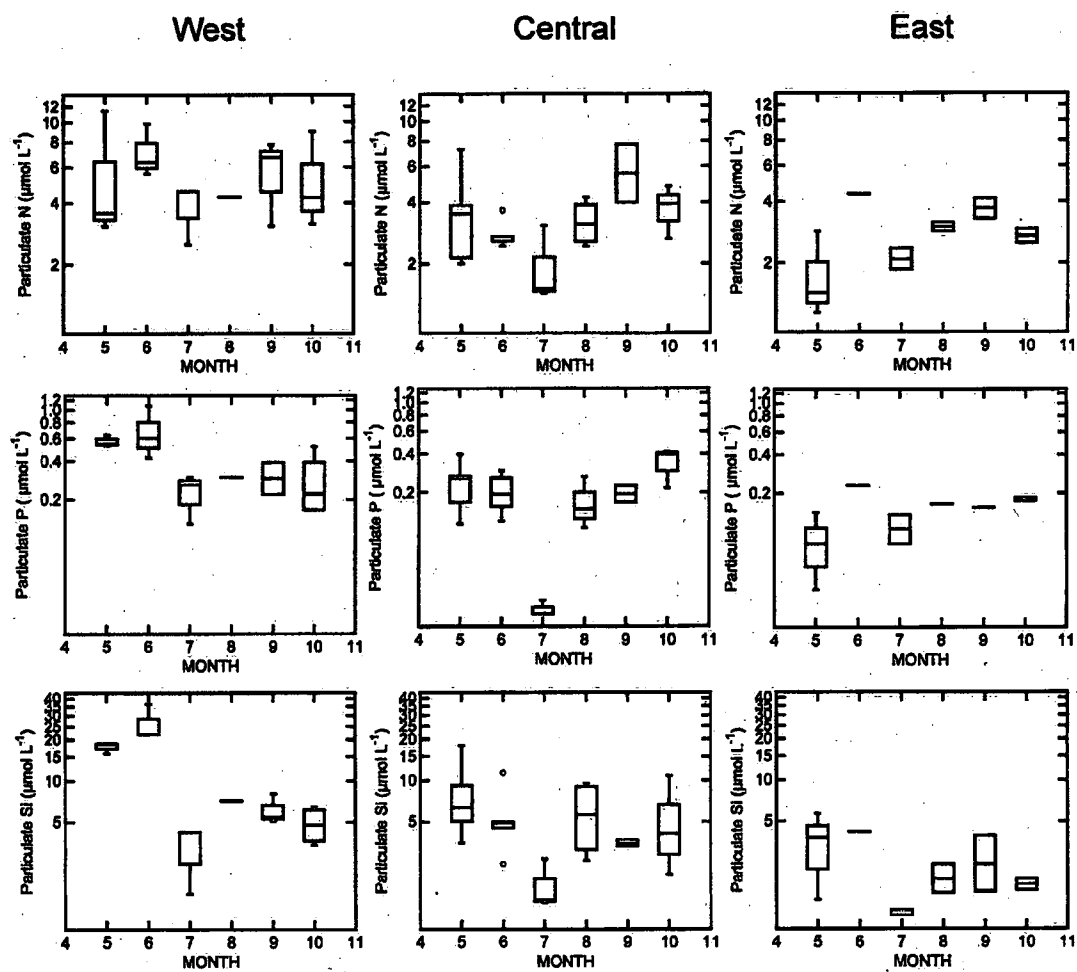


Fig. 7

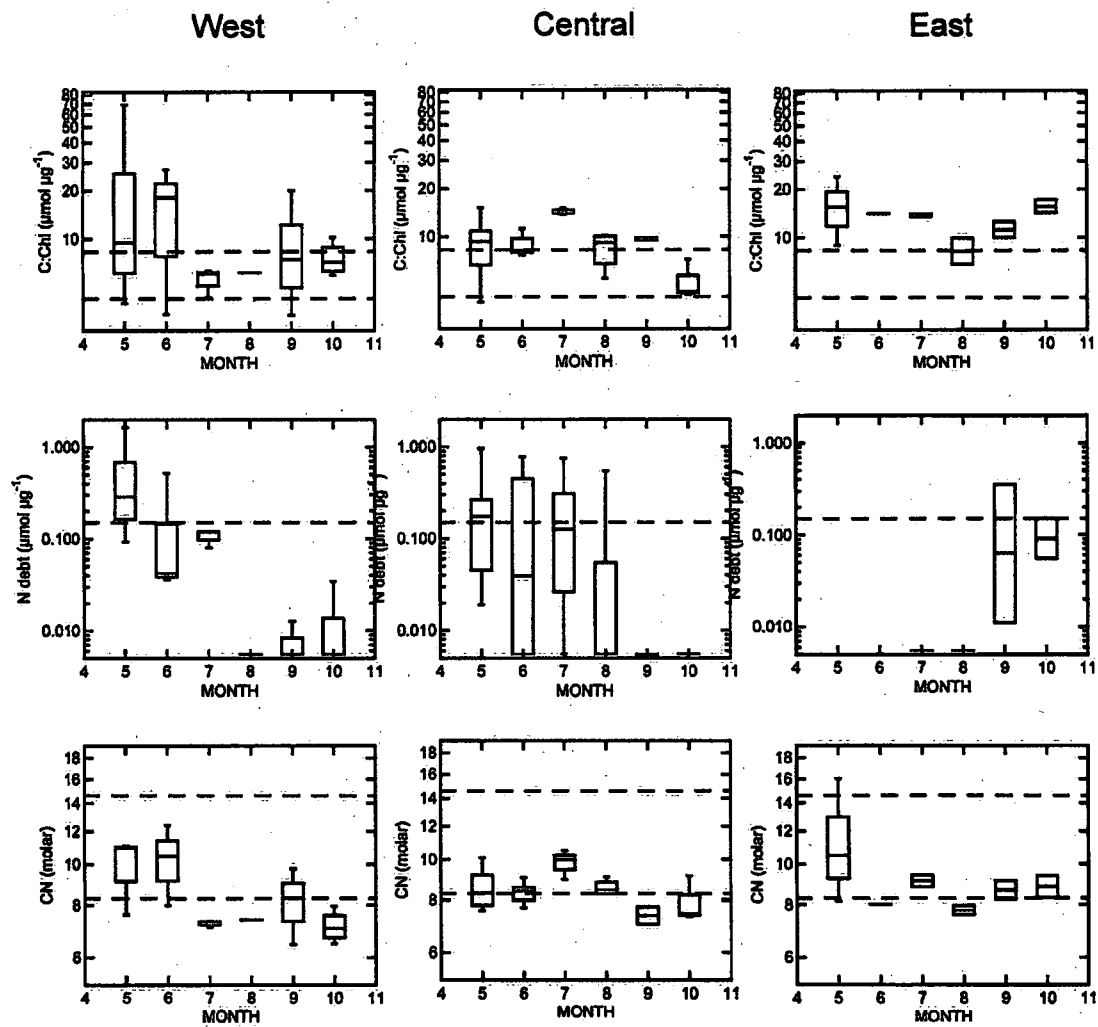


Fig. 8 a

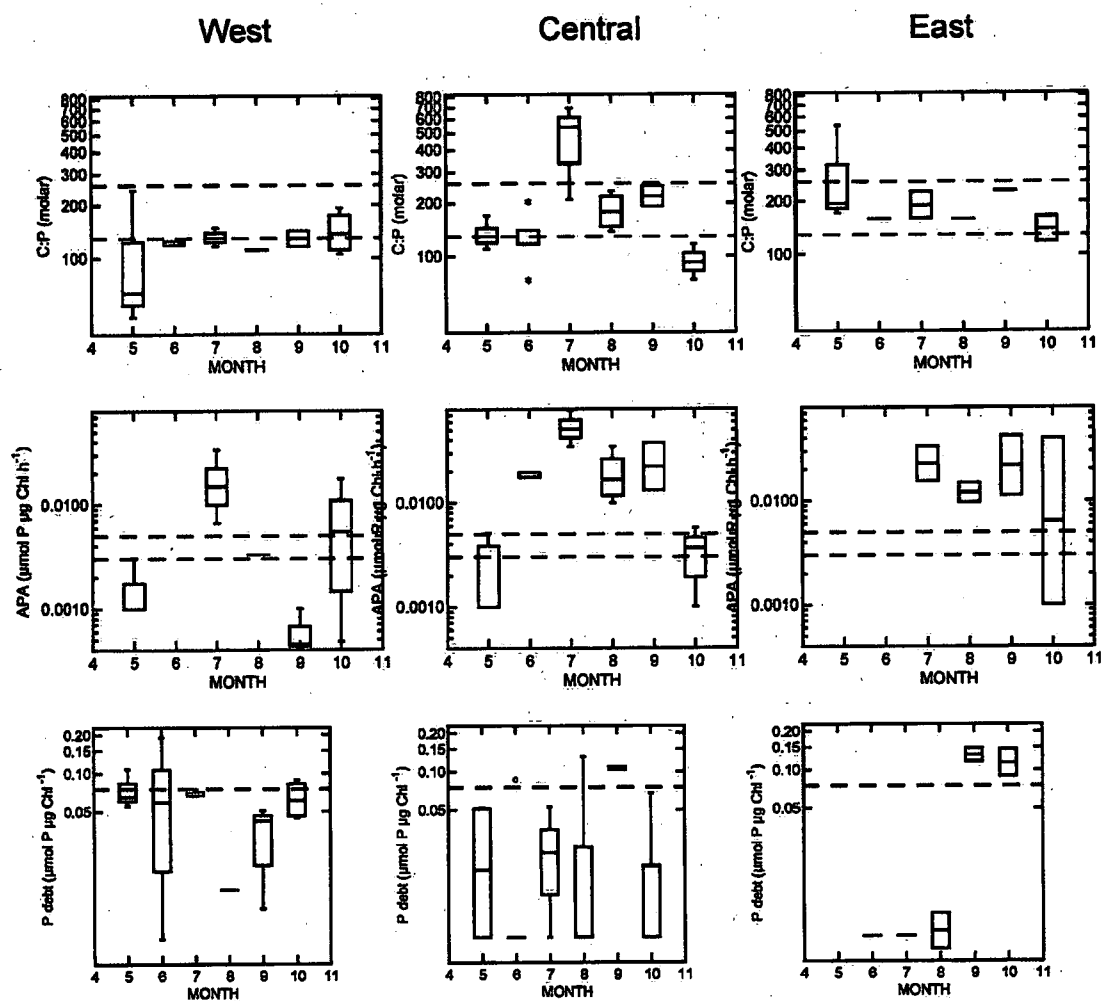


Fig. 8 b

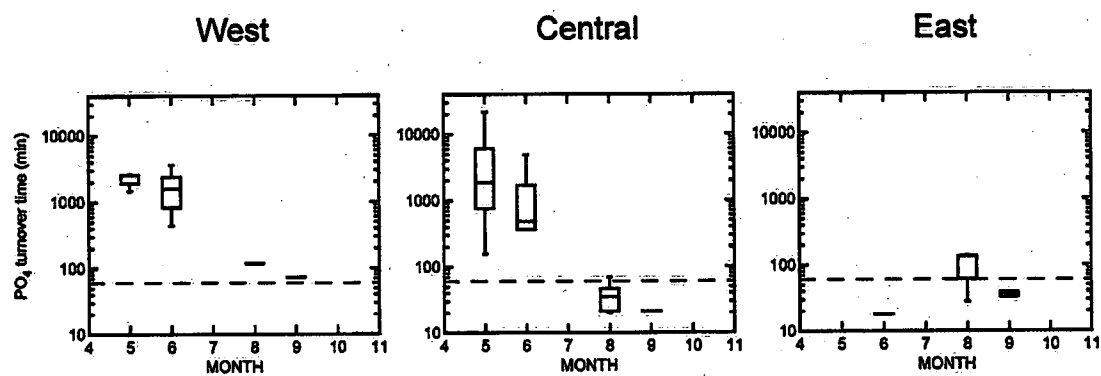
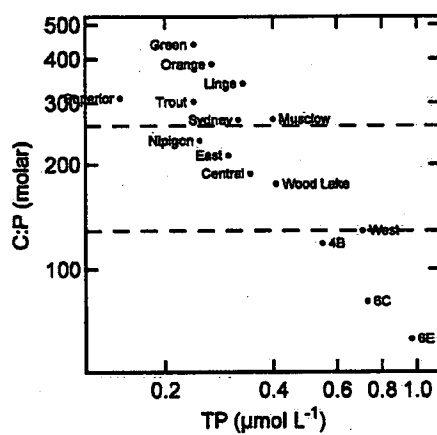
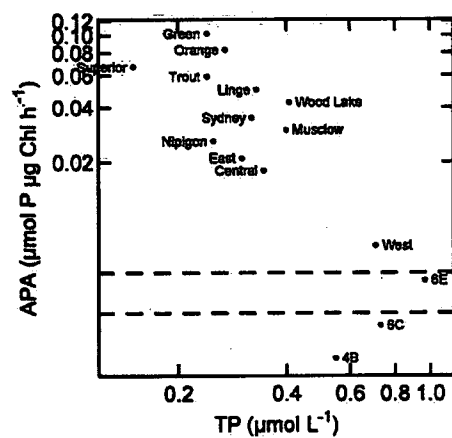


Fig. 9



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