SEASONAL AND SPATIAL VARIATION IN PHYTOPLANKTON COMMUNITY DYNAMICS IN SARDIS RESERVOIR, NORTHEASTERN MISSISSIPPI.

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ABSTRACT

Reservoirs, formed by river impoundment, can exhibit longitudinal spatial gradients in physical and chemical characteristics such as water transparency, chemical availability, and depth. Development and maintenance of these gradients is influenced by reservoir management operation affecting the rate at which water flows through the reservoir (hydrologic residence time). This research was conducted in Sardis Reservoir, in northeastern Mississippi. When flux of water out of the reservoir is restricted, as during the summer, hydrologic residence time increases and gradients develop in physicochemical characteristics along a transect from the riverine to the lacustrine (near dam) end of the reservoir. We hypothesized that, associated with these gradients, there would develop spatial variation in phytoplankton community composition, biomass, and productivity. To test this hypothesis, we made measurements over an annual cycle along the main longitudinal axis of Sardis Reservoir as well as in the embayment of three major tributaries. This reservoir, built for flood control, functions more like a lake during spring and summer when flood control gates are nearly closed, but more like a river during fall and winter. For examination of phytoplankton biomass and community composition we measured concentrations of taxon-specific photosynthetic pigments using high pressure liquid chromatography. Total phytoplankton biomass generally increased from spring through summer into fall. Based on indicator pigment concentrations, chlorophyte biomass peaked in summer, cyanobacteria were most common in summer and fall, and chrysophyte biomass peaked in both spring and fall. There were three distinct peaks in diatom abundance, one each in spring, summer and fall. Spatial heterogeneity in phytoplankton communities was most distinct in summer, especially between the two most distant sampling stations. The proportion of the total phytoplankton community of chlorophyll b, an indicator of chlorophytes, was consistently higher at the riverine end of the reservoir than at the lacustrine end. In contrast, the proportion of

diatoxanthin, a diatom indicator pigment, was consistently higher nearest the dam in the lacustrine portion of the reservoir. Seasonal variation in phytoplankton community biomass, composition and productivity can be linked to seasonal changes in water temperature, light and nutrient conditions, along with hydrologic changes associated with reservoir operation.

INTRODUCTION

Development of heterogeneous aquatic communities within a lake is a common phenomenon due to spatial and temporal variation in physical and chemical processes acting in the lake. The complexity of processes occurring in man-made systems like reservoirs, built by damming a river, is further compounded by their operating conditions. Reservoirs often exhibit spatial and temporal diversity in plankton distribution, composition, productivity and biomass due to longitudinal gradients in morphology, water inflow, retention time, and light and nutrient conditions (Kimmel et. al 1990). There is a general increase in light availability and residence time, and general decrease in nutrient availability and abiogenic turbidity along the longitudinal transect from up-lake to down-lake regions of a reservoir. River and lake interactions form a basis of such heterogeneity, where riverine conditions are prevalent in up-lake section whereas lacustrine conditions occur in the areas near the dam. But every reservoir is a unique system due to differences in operating conditions, size, morphology and location. Any changes in water conditions would be expected to reflect in phytoplankton community responses. A reservoir can harbor phytoplankton populations having different growth requirements, and communities often being continuously replaced in the course of time. Knowledge about the extent of diversity occurring within a system and how the variation in external factors affects the phytoplankton community dynamics would be valuable for an aquatic ecologist and a useful management tool for a reservoir resource manager.

Furthermore, studies of phytoplankton communities in reservoirs often focus on a single sampling location, usually the deepest point in the reservoir (Chrzanowski 1985; McGaha 1966). But a single sampling location may not be a representative condition to make inferences for the whole reservoir.

The purpose of this study was to evaluate the seasonal patterns in phytoplankton community characteristics along the longitudinal transect of Sardis reservoir. This is a descriptive study where the physicochemical factors and phytoplankton responses are measured in the natural setting. We study major factors relevant to the reservoir, especially nutrient availability, light conditions and water residence time that can limit phytoplankton biomass, production and composition. The phytoplankton composition was determined for six major taxonomic groups by measuring their characteristic pigment signatures with high performance liquid chromatograph. HPLC can detect pigments for fragile or small phytoplankton that are difficult to identify with microscopic counts (Roy et al. 1996).

METHODS

Study site

Sardis Reservoir is a flood control reservoir built in 1940 by damming the Little Tallahatchie River located in north eastern Mississippi. It lies in the Little Tallahatchie Watershed of the Yazoo river basin and covers a drainage area of 526 sq. miles (Fig. 1). Flood control operations and variable amounts of runoff from flowing streams results in large seasonal changes in water level and flow rates (Aumen et al. 1992). The surface area of the lake is greater than 12000 ha in summer which is reduced to less than 5000 ha by winter due to hypolimnetic water releases beginning in early fall and the water level starts to gradually rise from early spring. The water residence time is longest in summer and shortest in winter (Ochs and Rhew 1997).

Sampling

The lake was sampled for a suite of limnological parameters including phytoplankton community characteristics from March 2004 to April 2005 with one to two site visits per month. Samples were collected from three stations along the longitudinal transect of the reservoir and three major tributary embayment. Station 1 is the down-lake station representing the lacustrine zone, Station 3 is the mid-lake station representing a transitional zone, Station 6 is the up-lake station

representing the riverine zone, Station 2 is Clear Creek embayment area, Station 4 is Toby Tubby Creek embayment area and Station 5 is Hurricane Creek embayment area (Fig. 1).

Field samples were taken from March 2004 to November 2004 with a total of thirteen sampling dates. The first four dates in March, April and May represent spring samples, the next five dates in June, July and August represent summer samples, and the last four dates in September, October and November represent fall samples.

Water samples were collected at 0.5 m depth at all stations as three replicates in 2 liter HDPE Nalgene bottles and kept cool and in the dark until sample processing, usually within 2-4 hours after collection.

Physical and chemical properties

Temperature and oxygen profiles were measured using a YSI Model 57 oxygen meter. Light extinction profiles were obtained using LI-1000 radiometer with spherical quantum sensor and deck mounted reference cell. Water transparency was measured with a 20-cm diameter Secchi disc. Turbidity was measured in the laboratory with Hach Model 2100A turbidimeter.

Total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) were measured with an Astoria auto-analyzer in water filtered through Whatman GF/F filters (0.75μm), after digestion with alkaline persulphate (Charles et al. 2003).

Phytoplankton community analysis

Phytoplankton pigment extraction and determination was carried out using the method outlined in Jeffery et al. (1997) (modified). The water samples (200-400ml) were filtered through Whatman GF/F filters (0.75-μm) under low vaccum (<380 mm Hg) and the filters stored in a ultra-cold freezer (-70^{o}C) until pigment extraction. For extraction, the filters were cut into small pieces and soaked in 90% acetone for 2 hrs at 4^{0}C in the dark. The samples were sonicated under

low light and in an ice-bath for 30-60 seconds. The sonicated filters with the acetone were emptied into plastic test tubes pierced at the bottom and placed in a scintillation vial and centrifuged at 2000 rpm for 3 minutes. The supernatant was filtered through a 0.4-µm Millex hydrophilic LCR (PTFE) filter prior to pigment separation by high performance liquid chromatograph.

Phytoplankton community composition was identified for major taxonomic groups (Table. 1) by pigment analysis using reverse phased Dionex HPLC. The HPLC system consisted of a photodiode array detector (Dionex PDA 100), pump (Dionex P580) and silica C8 column (Alletech Allsphere ODS-2 5 µ). The system used a 1 ml/ min flow rate and 3-solvent gradient system (see Jeffery et al. 1997 for details). Pigments were identified by retention time and absorption spectrum and their concentration analysed using Dionex Chromeleon software. The HPLC had been calibrated with pigment standards obtained from the International Agency for ^{14}C Determination (DHI Water and Environment), Hørsholm, Denmark.

Volumetric primary production was measured in all sites at all dates by the ^{14}C-method as explained in Wetzel and Likens (1991). Twenty-four ml of water sample in glass serum vials loosely topped with rubber stoppers were inoculated with 25 µl of $NaH^{14}CO_3$ (20 µCi/ml) and incubated in a laboratory incubator at in situ temperature and at saturating light levels (560 µmolar irradiance) for 2-3 hours. The total dissolved inorganic carbon (DIC) assimilated was estimated from the radiolabeled carbon assimilated and available DIC in water (Ochs and Rhew 1997).

RESULTS

Light and nutrient conditions

There was steady decrease in turbidity from spring to summer and increase during fall (Fig. 2A). There were statistically significant differences in turbidity at five of the six sites in summer with the up-lake station (station 6) having the highest and the down-lake station (station 1) having the

lowest mean values (Table 2). During spring, the turbidity conditions were similar at all stations and in fall, the up-lake and down-lake stations were the only sites different from each other (Table 2). TDN and TDP concentrations did not show any statistically significant differences among the sites in any season (Table 2), but there was a seasonal difference with high spring values and generally low summer values (Fig 2C, 2D). TDP was reduced to negligible amounts in summer.

Phytoplankton biomass, production and Production:Biomass (P:B) ratio

Phytoplankton biomass, estimated as chlorophyll a (chl a) pigment, tended to increase steadily from spring to fall with two distinct peaks in spring and summer and maximum values in late fall (Fig. 3A). The mean values were highest at the up-lake station and lowest at the down-lake station. These two stations were significantly different at all times whereas station 2 and 3 were similar to down-lake and station 4 and 5 were similar to the up-lake station (Table 2).

Productivity decreased from spring to summer and rose again in fall (Fig. 3B). Photosynthetic capacity (P:B ratio) was highest in spring, and least during summer and slowly increased during fall at all stations (Fig. 3C). There were no statistically significant differences in spring and fall at all stations. The only difference was between station 1 and 6 in summer.

Phytoplankton community composition by HPLC pigment analysis

The amount of chlorophyll b (chl b), a signature pigment for chlorophytes, was higher in summer than spring and fall at all stations (Fig. 4A). Differences in chl b concentration between up-lake and down-lake stations were statistically significant in all three seasons (Table 2). The three stations near the dam (Station 1, 2, 3) were different than three stations near the river (Station 4, 5, 6) but there was similarity among the three in both groups.

The amount of diatoxanthin, a signature pigment for diatoms, showed three distinct peaks in spring, summer and fall (Fig. 4B). Spatial differences in diatoxanthin were not obvious in all three seasons (Table 2).

The amount of fucoxanthin, a signature pigment for chrysophytes, declined from spring to summer and increased in fall at all stations (Fig. 4C). The differences between the up-lake and down-lake station were statistically significant in spring and summer but not in fall (Table 2). The other stations had intermediate mean values.

The amount of zeaxanthin, a signature pigment for cyanobacteria, was only detected during late spring with high mean values in summer at all stations (Fig. 4D). Zeaxanthin concentrations were not statistically different among sites in all three seasons (Table 2).

Phytoplankton community composition, as indicated by indicator pigments as a ratio of total phytoplankton biomass, differed at the two spatially extreme stations of up-lake and down-lake, during summer (Fig. 5). The chl b/chla ratio, the chlorophyte indicator, was higher at the up-lake station than the down-lake station (Fig. 5A). The fucoxanthin/chl a ratio, the chrysophyte indicator, was consistently higher at the up-lake station than the down-lake station even though the differences were smaller (Fig 5C). In contrast, the diatoxanthin/chl a ratio, the diatom indicator, was higher at the down-lake station than up-lake station (Fig. 5B). The zeaxanthin/chl a ratio, the cyanobacteria indicator, was similar at both stations (Fig. 5D).

CONCLUSION

As indicated by the four signature pigments of chl b, diatoxanthin, fucoxanthin and zeaxanthin representing chlorophytes, diatoms, crysophytes and cyanobacteria respectively, the phytoplankton groups showed distinct and consistent differences both seasonally and spatially. Their abundance changed on a seasonal basis (Fig. 4). The proportion of each pigment to total phytoplankton biomass showed distinct spatial variation at the two most extreme stations of up-lake and down-lake during summer (Fig. 5). Chlorophytes were an important part of the phytoplankton population in summer (Fig. 4A) whereas cyanobacteria only appeared in summer and were not prevalent in fall (Fig. 4D). Chrysophytes were abundant in spring and fall (Fig.

4C). Diatoms were an important part of the phytoplankton population at all times with three distinct seasonal peaks for spring, summer and fall (Fig. 4B).

These changes in the phytoplankton community might be linked to seasonal changes in temperature (Fig. 2B) and changes in light (Fig. 2A) and/or nutrient (Fig. 2C, 2D) conditions. Phytoplankton with differing growth responses to nutrient concentrations, mixing and turbidity will produce taxonomically distinct populations and the effect of each factor will shift the community composition, even though there might not be any consistent pattern (Pickney et al. 2001). The seasonal changes in abundance of differing phytoplankton groups (Fig. 4) are also parallel to reservoir operation. Water was turbid with lower surface temperature in spring and fall whereas water was clearer with higher surface temperature in summer throughout the reservoir (Fig.2). The dam gates are opened at the beginning of fall and closed at the beginning of spring which creates turbid conditions in fall, winter and early spring. The water level gradually rises through spring and summer. As a result of this, the reservoir is expected to be more heterogeneous in summer when stations near the dam are more like a lake and stations near the river are more like a lotic system. Spatial variation in physicochemical conditions of water and phytoplankton response characteristics was most distinct in summer when the reservoir is heterogeneous, especially at the two extreme stations of up-lake and down-lake.

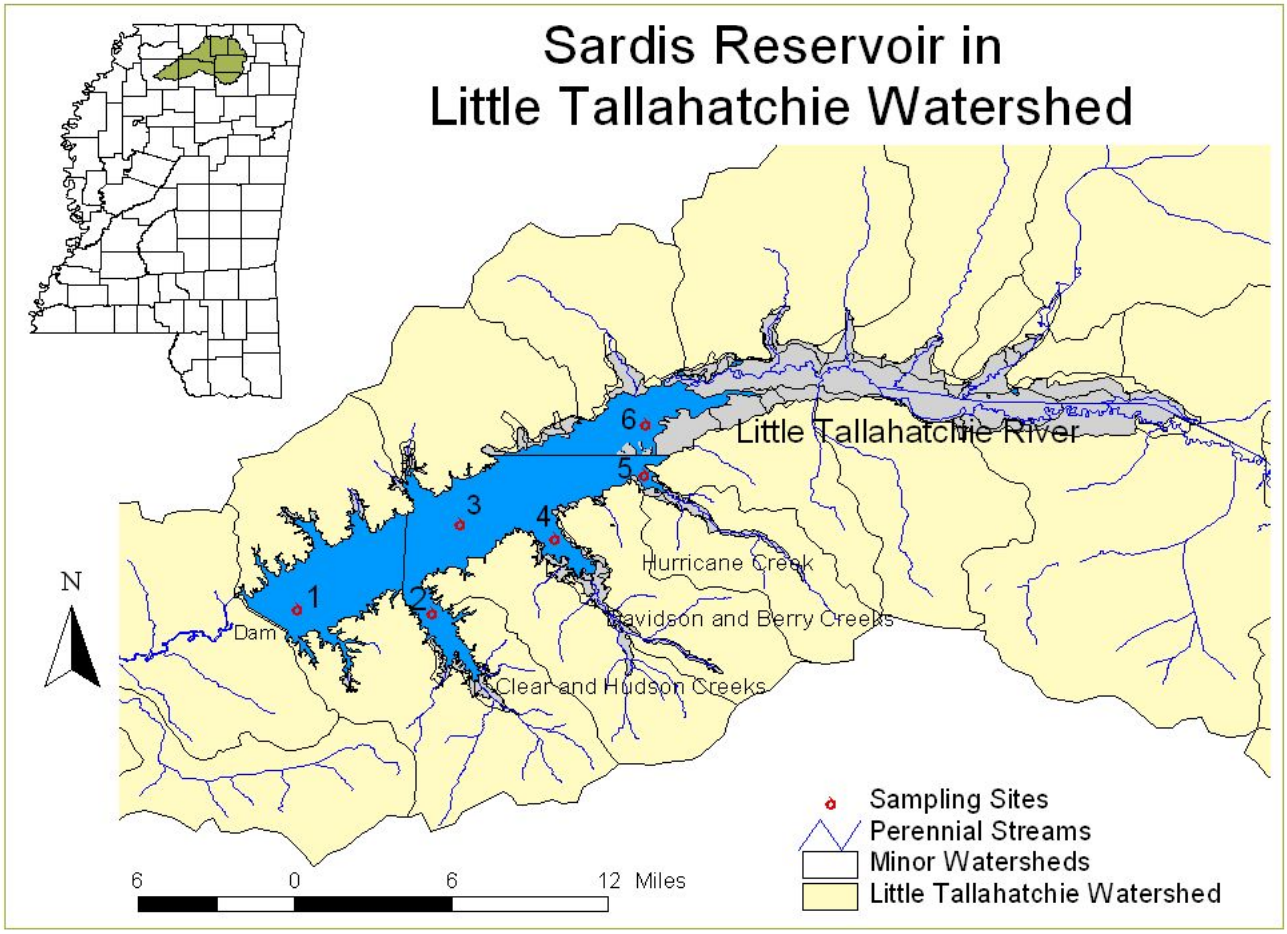
Phytoplankton biomass generally increased from spring to fall with peaks in spring and summer and a less evident peak in fall (Fig 3A). At some stations, there was a decline in phytoplankton biomass at the end of spring and possibly lesser decline at the end of summer (Fig. 3A). The decline in phytoplankton biomass at the end of spring might be due to a decline in mainly crysophytes and diatoms (Fig. 4B, 4C), favored by lower temperature, higher turbidity and higher nutrient conditions of early spring (Fig. 2). The decline in phytoplankton biomass at the end of summer might be due to a decline in population of mainly chlorophytes, cyanobacteria and possibly a different population of diatoms (Fig. 4A, 4B, 4C), favored by higher temperature, lower turbidity and probably lower nutrient conditions of summer (Fig. 2). The abundance of chlorophytes and cyanobacteria decreased at the beginning of fall with the regain of turbid

conditions and decreasing temperature, when crysophytes and diatoms, as in the spring, became more abundant (Fig. 4B, 4C).

The proportion of chlorophytes to total phytoplankton biomass was more important at the up-lake station than the down-lake station in summer, suggesting their ability to thrive in more turbid and a possibly nutrient richer environment (Fig. 5A, 2). The pattern was similar but less prominent for crysophytes (Fig. 5C). In contrast, the proportion of diatoms to total phytoplankton biomass was more important at the down-lake station than up-lake station in summer, suggesting their ability to thrive in the less turbid and possibly more nutrient deficient environment of down-lake (Fig. 5B, 2). Even though the dissolved nutrient concentration was not different at these two stations in summer (Table 2), nutrient availability at the up-lake station might be higher, as suggested by the substantial difference in phytoplankton biomass. The proportion of cyanobacteria to total phytoplankton biomass was important at both stations in late summer and early fall, suggesting nitrogen deficiency in the reservoir during those periods (Fig. 5D). The per capita productivity of the phytoplankton was low in summer as illustrated by the P: B ratio (Fig. 2C). This can most likely be attributed to the deficiency in nutrients.

In this descriptive study of changes in phytoplankton community dynamics in a reservoir, we found that, on an annual basis, seasonal variation is more distinct than spatial variation. During summer the spatial separation is more distinct, especially between the two most distant stations. The seasonal variation can be linked to seasonal changes in water temperature, light and nutrient conditions, along with dramatic changes causes by with the reservoir operation.

List of Figures:



Station 1: Down-lake (DL)
Station 2: Clear creek embayment (CC)
Station 3: Mid-lake (ML)
Station 4: Toby Tubby (Davidson and Berry) embayment (TT)
Station 5: Hurricane creek embayment (HC)
Station 6: Up-lake station (UL)

Figure 1

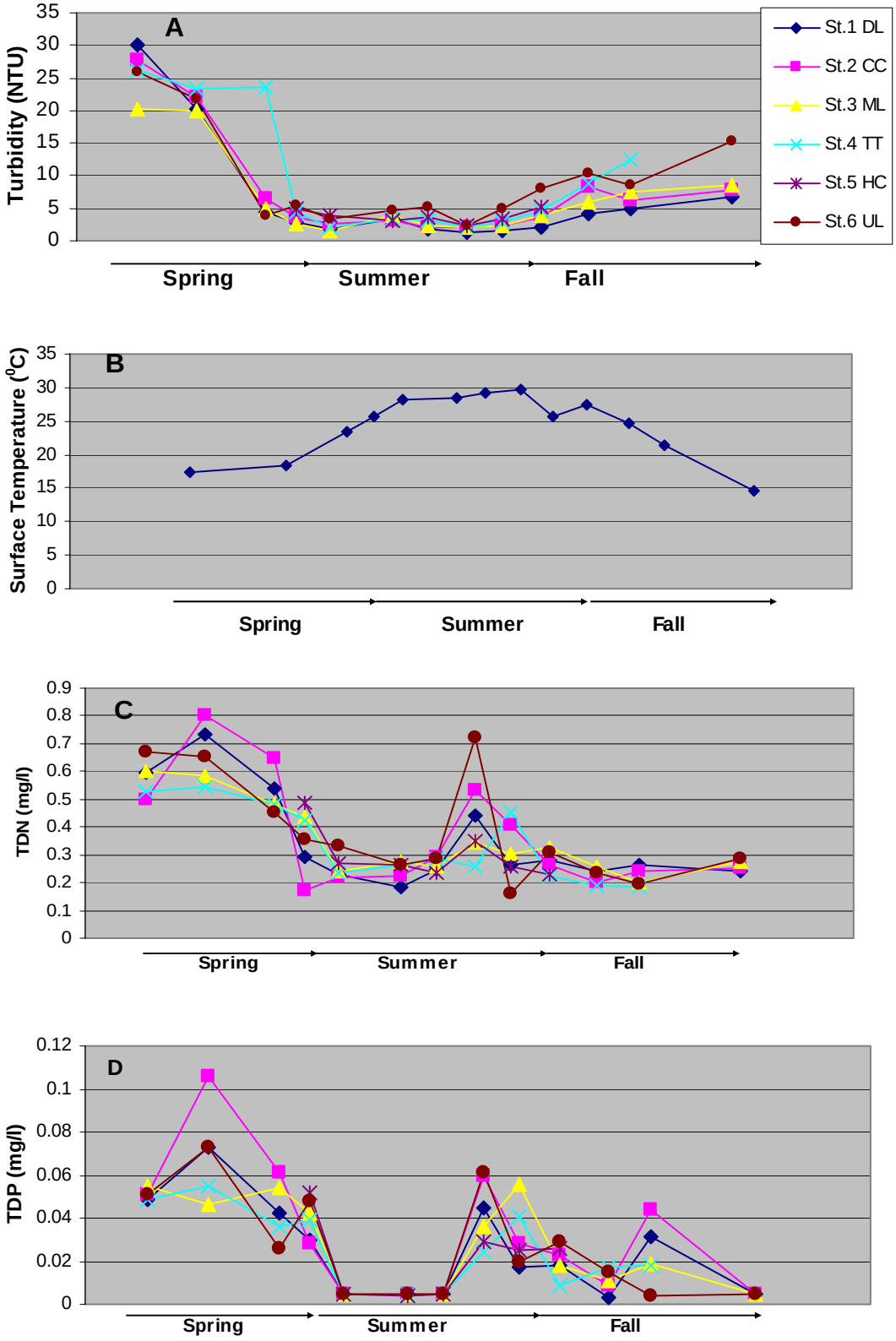

A
Turbidity (NTU)
35
30
25
20
15
10
5
0
St.1 DL
St.2 CC
St.3 ML
St.4 TT
St.5 HC
St.6 UL
Spring
Summer
Fall
B
Surface Temperature (0C)
35
30
25
20
15
10
5
0
Spring
Summer
Fall
C
TDN (mg/l)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Spring
Summer
Fall
D
TDP (mg/l)
0.12
0.1
0.08
0.06
0.04
0.02
0
Spring
Summer
Fall

Figure 2

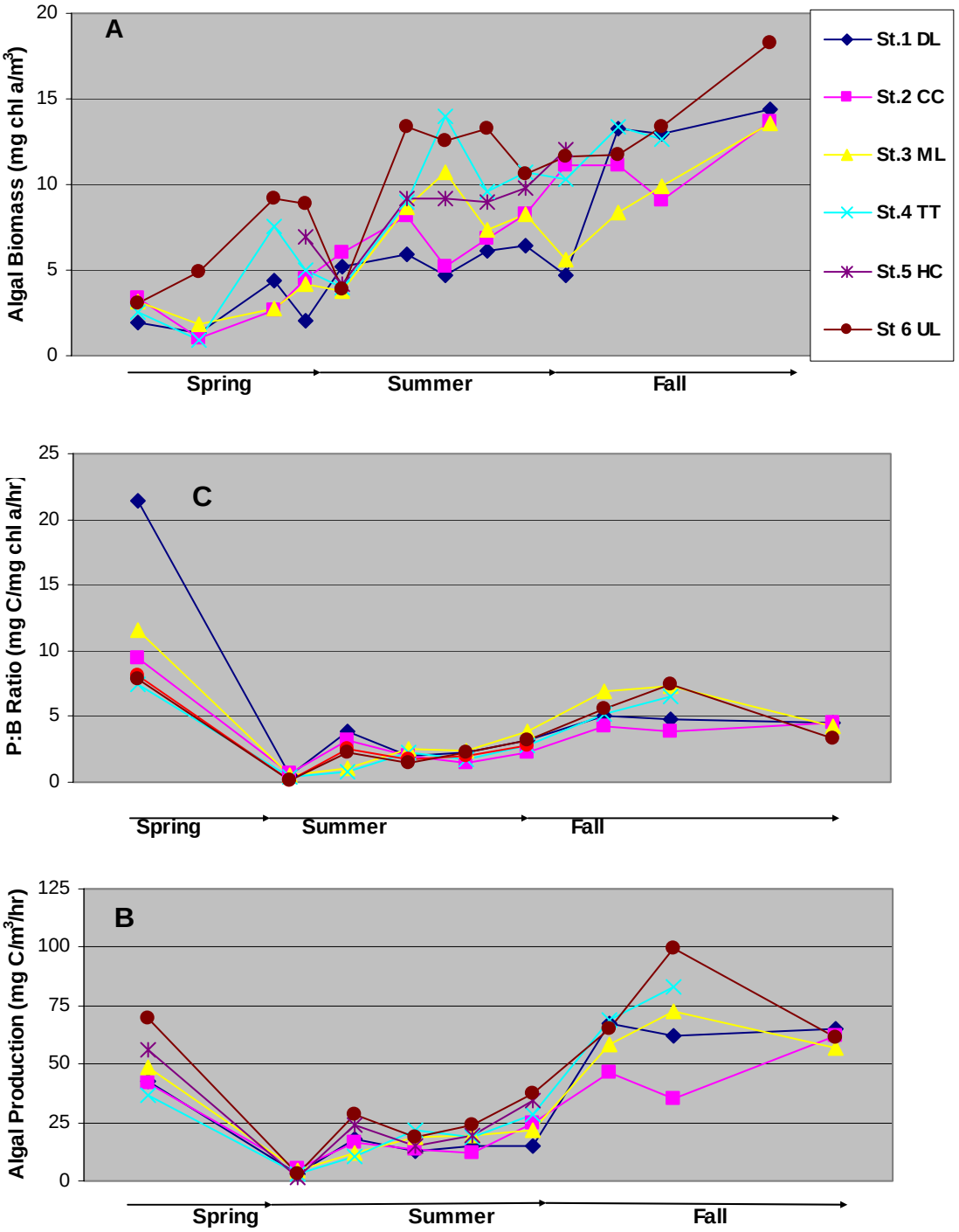

A
Algal Biomass (mg chl a/m3)
20
15
10
5
0
Spring
Summer
Fall
St.1 DL
St.2 CC
St.3 ML
St.4 TT
St.5 HC
St 6 UL
C
P:B Ratio (mg C/mg chl a/hr)
25
20
15
10
5
0
Spring
Summer
Fall
B
Algal Production (mg C/m3/hr)
125
100
75
50
25
0
Spring
Summer
Fall

Figure 3

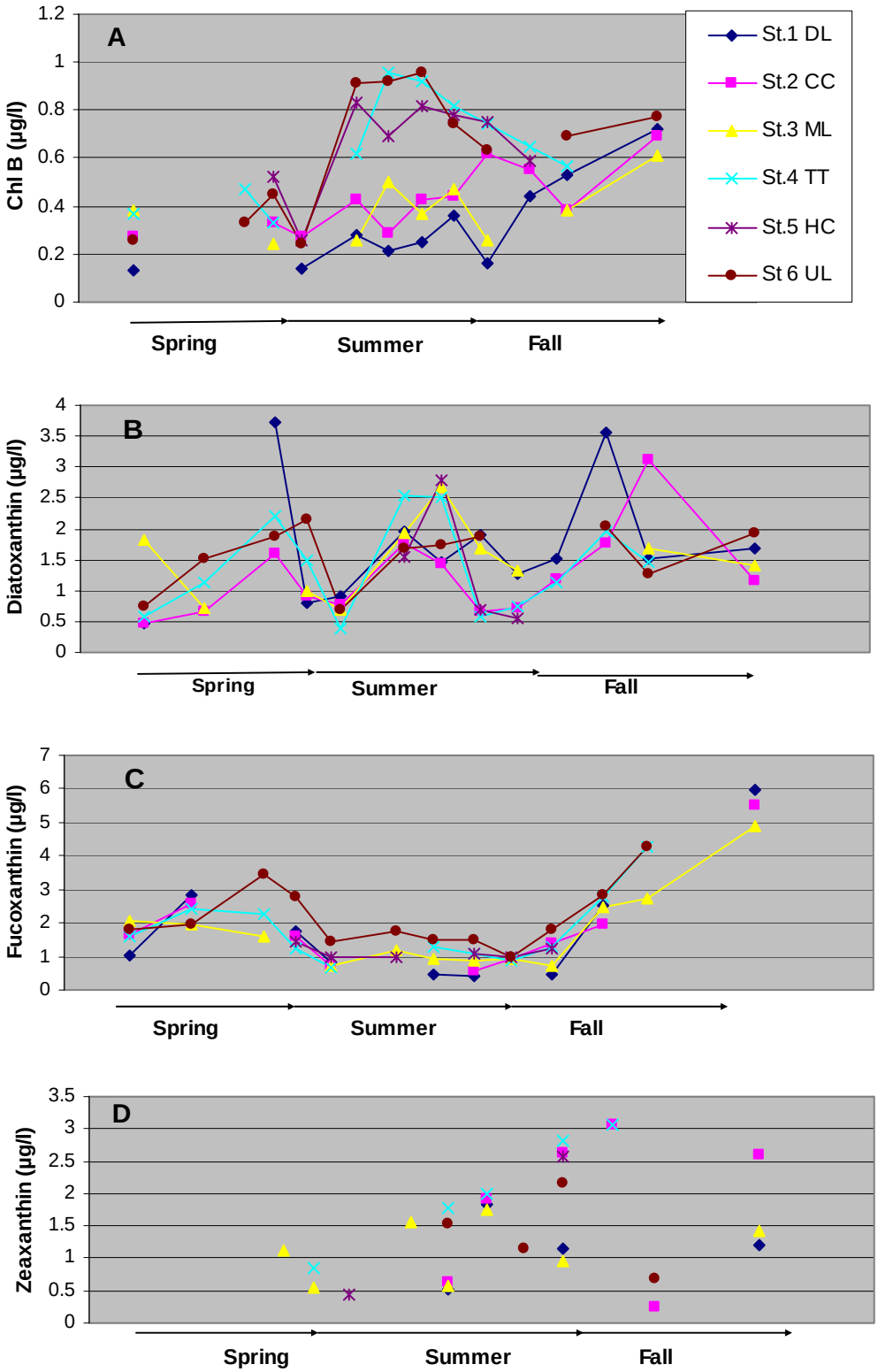

A
Chl B (µg/l)
1.2
1
0.8
0.6
0.4
0.2
0
St.1 DL
St.2 CC
St.3 ML
St.4 TT
St.5 HC
St 6 UL
Spring
Summer
Fall
B
Diatoxanthin (µg/l)
4
3.5
3
2.5
2
1.5
1
0.5
0
Spring
Summer
Fall
C
Fucoxanthin (µg/l)
7
6
5
4
3
2
1
0
Spring
Summer
Fall
D
Zeaxanthin (µg/l)
3.5
3
2.5
2
1.5
1
0.5
0
Spring
Summer
Fall

Figure 4

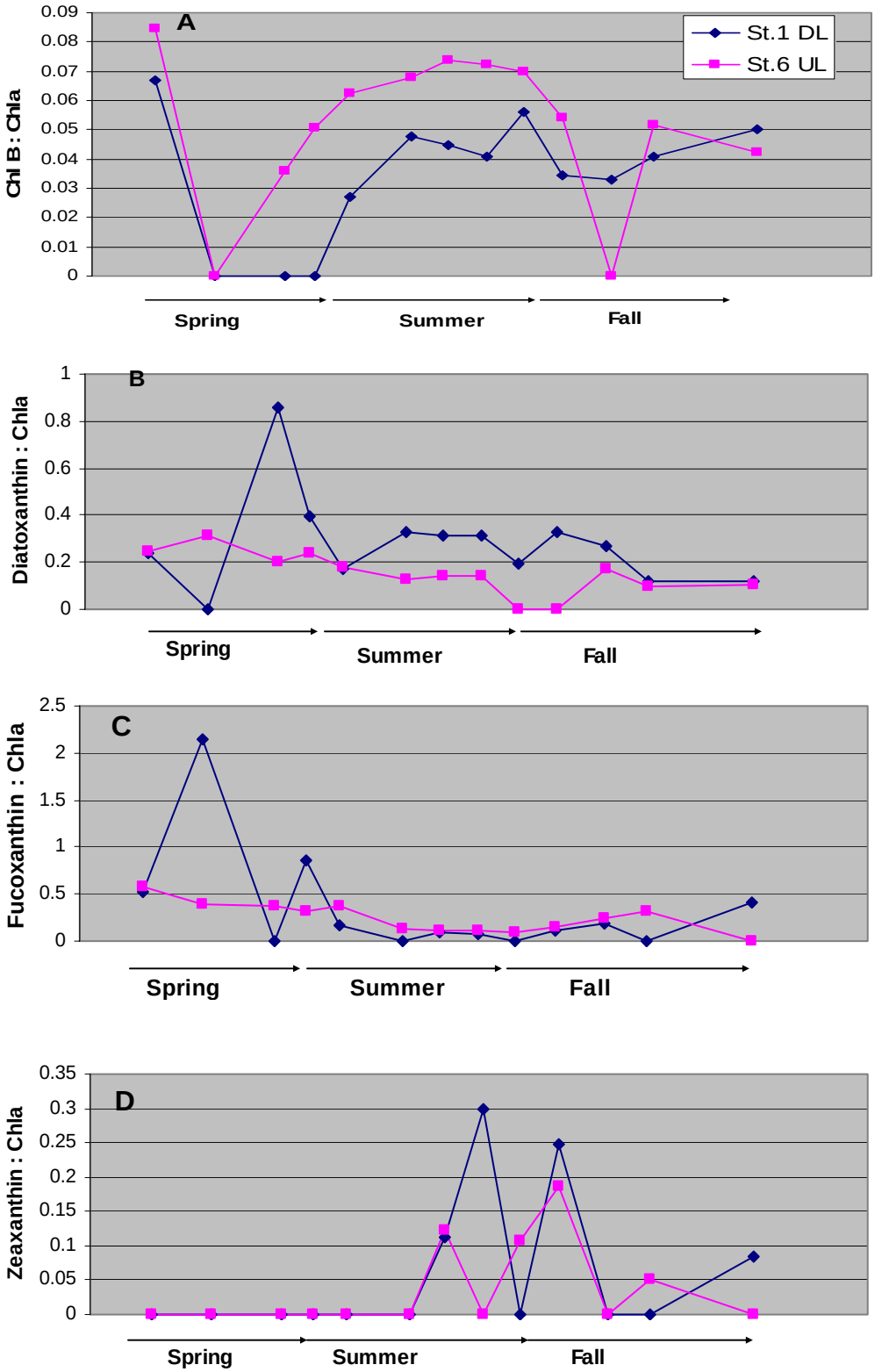

A
St.1 DL
St.6 UL
Chl B : Chla
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
Spring
Summer
Fall
B
Diatoxanthin : Chla
1
0.8
0.6
0.4
0.2
0
Spring
Summer
Fall
C
Fucoxanthin : Chla
2.5
2
1.5
1
0.5
0
Spring
Summer
Fall
D
Zeaxanthin : Chla
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Spring
Summer
Fall

Figure 5

Table 1: Taxonomic diagnostic pigments (chlorophylls and carotenoids) used in classifying phytoplankton composition (modified from Vinebrooke and Leavitt 1998)

Pigment	**Phytoplankton Group**
Chla	All phytoplankton
Chl b	Chlorophytes
ß-carotene	All phytoplankton
Alloxanthin	Cryptophytes
Diatoxanthin	Diatoms, few Chrysophytes
Fucoxanthin	Chrysophytes, diatoms, and some dinoflagellates
Lutein	Chlorophytes
Zeaxanthin	Cyanobacteria
Peridinin	Dinoflagellates

Table 2. Two way ANOVA for parameters listed in the study. Two main effects of date and station location were tested for the given variables. Station means having the same subscript are not significantly different from each other at $P<0.05$. NS = not significant. Cells lacking values indicate no measurements. Zero values indicate no detection.

Variables		**Date**		**Station**		**Station Means**					
		P	**df**	**P**	**df**	**1**	**2**	**3**	**4**	**5**	**6**
Biomass (mg chl a /m^3)											
	Spring	0.0001	3	0.0001	4	2.41 ^{a}	2.87 ^{a}	2.99 ^{a,b}	4.01 ^{b}		6.52 ^{c}
	Summer	0.0001	4	0.0001	5	5.12 ^{a}	6.31 ^{a,b,d}	7.76 ^{b,c,d}	9.45 ^{c,d,e}	8.27 ^{d}	10.73 ^{e}
	Fall	0.0001	3	0.0001	4	11.35 ^{a}	11.25 ^{a}	9.38 ^{b}	12.28 ^{a,c}		13.76 ^{c}
P:B (mg C /chl a/hr)											
	Spring	0.0001	3	NS	4	2.48 ^{a}	1.51 ^{a}	1.93 ^{a}	1.22 ^{a}		1.29 ^{a}
	Summer	0.0001	4	0.019	5	1.85 ^{a}	1.37 ^{a,b,c}	1.37 ^{a,b,c}	1.02 ^{b,c}	1.23 ^{a,b,c}	1.08 ^{c}
	Fall	0.0001	3	0.0001	4	4.42 ^{a,c}	3.74 ^{c}	5.72 ^{b}	5.25 ^{a,b}		4.93 ^{a,b}
TDN (mg/l)											
	Spring	0.005	3	NS	4	0.54 ^{a}	0.53 ^{a}	0.53 ^{a}	0.49 ^{a}		0.52 ^{a}
	Summer	0.01	4	NS	5	0.27 ^{a}	0.32 ^{a}	0.28 ^{a}	0.3 ^{a}	0.28 ^{a}	0.31 ^{a}
	Fall	0.0001	3	0.0001	4	0.26 ^{a}	0.24 ^{a,b}	0.27 ^{a}	0.19 ^{b}		0.26 ^{a}
TDP (mg/l)											
	Spring	0.04	3	NS	4	.05 ^{a}	.06 ^{a}	.05 ^{a}	.04 ^{a}		.05 ^{a}
	Summer	0.0001	4	NS	5	.02 ^{a}	.03 ^{a}	.02 ^{a}	.02 ^{a}	0.18 ^{a}	.02 ^{a}
	Fall	0.0001	3	NS	4	.01 ^{a}	.02 ^{a}	.013 ^{a}	.016 a		.013 ^{a}
Turbidity (NTU)											
	Spring	0.0001	3	0.0001	4	14.43 ^{a}	14.95 ^{a}	11.97 ^{a}	19.36 ^{b}		12.16 ^{a}
	Summer	0.001	4	0.0001	5	1.87 ^{a}	2.34 ^{b}	2.45 ^{b}	2.73 ^{c}	3.25 ^{d}	4.08 ^{e}
	Fall	0.0001	3	0.0001	4	4.44 ^{a}	6.48 ^{b}	6.46 ^{b}	9.62 ^{c}		10.56 ^{c}
Chl B (µg/l)											
	Spring	0.0001	3	0.003	4	0.02 ^{a}	0.1 ^{a,b,c,d}	0.15 ^{b,c,d}	0.18 ^{c,d}		0.19 ^{d}
	Summer	0.0001	4	0.0001	5	0.16 ^{a}	0.29 ^{a}	0.25 ^{a}	0.66 ^{b}	0.62 ^{b}	0.74 ^{c}
	Fall	0.001	3	0.0001	4	0.38 ^{a}	0.56 ^{b}	0.31 ^{a}	0.63 ^{b}		0.62 ^{b}
ß-carotene (µg/l)											
	Spring	NS	3	NS	4	0	0	.004 ^{a}	0		.03 ^{a}
	Summer	0.0001	4	0.004	5	0.08 ^{a}	0.11 ^{a,b}	0.09 ^{a}	0.1 ^{a}	0.2 ^{b}	0.12 ^{a,b}
	Fall	0.0001	3	NS	4	0.09 ^{a}	0.2 ^{a}	0.07 ^{a}	0.14 ^{a}		0.2 ^{a}
Alloxanthin (µg/l)											
	Spring	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Summer	NS	4	NS	5	0.19 ^{a}	0.03 ^{a}	0	0.1 ^{a}	0.03 ^{a}	0.13 ^{a}
	Fall	NS	3	NS	4	0	0.06 ^{a}	0	0		0.17 ^{a}
Diatoxanthin (µg/l)											
	Spring	NS	3	NS	4	0.73 ^{a}	1.09 ^{a}	0.74 ^{a}	0.65 ^{a}		1.18 ^{a}

	Summer	0.0001	4	0.03	5	1.2 [a,b,c]	0.79 [a,b,c]	1.3 [b]	0.45 [c]	0.69 [a,b,c]	0.92 [a,b,c]
	Fall	0.0001	3	0.014	4	1.81 [a]	1.47 [a,b]	0.76 [b]	1.14 [a,b]		0.98 [a,b]
Fucoxanthin (µg/l)											
	Spring	0.0001	3	0.0001	4	1.11 [a]	1.32 [a,b]	1.14 [a,b]	1.66 [b]		2.49 [c]
	Summer	NS	4	0.0001	5	0.26 [a]	0.26 [a]	0.59 [a,b,c]	0.7 [b,c]	0.67 [c]	1.3 [d]
	Fall	0.0001	3	0.002	4	2.21 [a]	1.18 [a]	2.41 [a,b]	3.04 [a,b]		1.2 [a]
Zeaxanthin (µg/l)											
	Spring	NS	3	NS	4	0.0002 [a]	0	0.0001 [a]	0.00001 [a]		0
	Summer	0.0001	4	0.003	5	0.0002 [a]	0.0004 [a,b]	0.0002 [a,b]	0.0006 [b]	0.00003 [a]	0.0005 [a]
	Fall	0.011	3	0.006	4	0.0002 [a]	0.001 [b]	0.0002 [a,b]	0.001 [a,b]		0.0002 [a,b]
Lutein (µg/l)											
	Spring	0.0001	3	NS	4	0.2 [a]	0.16 [a]	0.17 [a]	0.41 [a]		0.36 [a]
	Summer	0.001	4	0.005	5	0.17 [a,b,c]	0.21 [a,b,c]	0.1 [b]	0.55 [c]	0.57 [c]	0.38 [a,b,c]
	Fall	0.0001	3	0.034	4	0.72 [a,b]	0.62 [a]	0.78 [a,b]	0.8 [a,b]		1.32 [b]

References

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