THE EFFECTS OF WATER TURBULENCE ON THE LIMNOLOGY OF A SHALLOW, PRAIRIE WETLAND

by

Brian Glenn Kotak

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"Question all things. Seek for answers,
and when you find what seems to be
an answer, question that too."

L. L'Amour

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Abstract

In the first year of this study a field survey was conducted in the Blind Channel of the Delta Marsh, Canada to determine the influence of wind-induced water turbulence on the limnology of a shallow, prairie wetland. Hourly and seasonal changes in wind stress had a marked effect on suspended particulate concentration in the water column while phytoplankton biomass was affected by wind stress on a short-term (hourly) basis only.

Research in the second field season involved a manipulative experiment. Small-diameter littoral enclosures incorporating pumps which permitted in situ control of turbulence were utilized to examine the effects of controlled water turbulence on the limnology of the marsh. Because small enclosures lack turbulence, and are therefore plagued to some extent by enclosure effects, the use of artificially-generated turbulence within enclosures was evaluated as a posible means of alleviating enclosure effects. Turbulence within enclosures influenced all limnological parameters examined (suspended particulate concentration, water clarity, oxygen and nutrient levels, phytoplankton and periphyton biomass and productivity) except water temperature. Enclsoure effects on many of these parameters were evident and turbulence within the enclosures greatly alleviated these enclosure effects. The use of small-diameter turbulent enclosures appears to provide realistic data when compared to the adjacent marsh.

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Chapter 1 : Literature Review

Aquatic Mesocosms

1.1 Introduction: Uses and Designs

Since the 1960s, the use of aquatic mesocosms such as enclosures and limnocorrals has expanded from studies concerned primarily with phytoplankton dynamics (Lund, 1972) to eloberate, manipulative experiments concerning global issues such as the eutrophication and acidification of freshwater lakes (Schindler et al., 1971;1980), heavy metal toxicity, and most recently, the environmental fate and effects of a variety of organic contaminants (e.g. dioxins, pesticides, etc.) in aquatic ecosystems (Goldsborough and Robinson, 1983; Muir et al., 1985; Corbet et al., 1988). Indeed, part of the evolution in the utility of the mesocosm has paralleled public and political motivation. Studies utilizing mesocosms have also greatly increased knowledge of ecological processes and concepts (e.g. predator/prey relationships, population biology, nutrient cycling, etc.).

There is a large diversity of types of aquatic mesocosms. Enclosure and limnocorral designs include square, triangular, and circular shapes constructed of wood, stainless steel, rubber and a wide variety of sheet plastics. Mesocosm shape, size and construction material are important considerations in both ecological studies and those involving organic contaminants. For example, since

many organic compounds are subject to sorption phenomena, care should be taken to assure that adsorption of the contaminant to the mesocosm wall material is minimized. When dealing with very hydrophobic compounds such as dioxins, adsorption to the mesocosm walls should be monitored and accounted for.

Mesocosm shape and size influence these sorption processes through surface area effects. Large diameter circular mesocosms provide the lowest surface area relative to the enclosed volume while small volume square mesocosms have a much higher surface area/volume ratio. Consequently, the risk of contaminant adsorption to the walls is increased by providing more surface area. Also, as the surface area/volume ratio is increased, additional confounding factors may become more pronounced. For example, development of periphyton on mesocosm walls may occur causing increased attenuation of light within translucent mesocosms and unnaturally high levels of nutrient consumption (Goldsborough et al., 1986). The popularity of the use of circular mesocosms may be due in part to the elimination of "corner effects". The corners of square and triangular mesocosms often lead to the concentration of large amounts of suspended inorganic and organic particulates as well as phytoplankton and zooplankton (Sanders, 1985).

1.2 Mesocosms and the Experimental Approach in Ecology

Odum (1984) distinguishes two schools of thought with respect to experimental design in ecology that are also applicable to

toxicology. The first is a reductionist view in which a complex system is reduced to a more simplified, controllable microcosm in order to accurately assess the effects of a perturbation or manipulation (e.g. change in species competition and/or predation, introduction of nutrients or a pesticide, etc.) on a selected species or compartment of the aquatic system. This commonly includes studies utilizing test tubes, flasks and small aquaria in the laboratory in which as many independent variables as possible are controlled. In direct contrast to the reductionist view, the holistic view stresses the need for ecosystem level (macrocosm) studies which incorporate a greater degree of environmental realism. Each approach has merits as well as disadvantages (e.g., Diamond, 1986).

There has been a growing tendency for ecologists and toxicologists to study discrete "sections" of the aquatic environment by utilizing mesocosms. Mesocosms bridge the gap between the more controllable and repeatable microcosms and the more realistic and complex macrocosms. Mesocosms offer an alternative that gives the best of both worlds. In addition to limnocorrals in lakes (Schindler et al., 1971; Lund, 1972; Solomon et al., 1980; Schindler et al., 1988; Servos, 1988) and in situ, littoral enclosures (Goldsborough et al., 1986), other designs such as artificial streams (Kosinski and Merkle, 1984), natural prairie sloughs (Jones and Moyle, 1963), artificial dugout ponds (Muir et al., 1985; Corbet et al.,1988) and concrete ponds have been used successfully in a number of studies. These range in size from 1 m^3 up to elaborate ecological and toxicological experiments such as MERL (Marine Ecological Research

Laboratory), CEPEX (Controlled Ecosystem Pollution Experiment; Case, 1978) and MELIMEX (Metal LIMnological EXperiment; Gachter, 1979). For example, CEPEX involves large, floating marine limnocorrals which extend below the photic zone. Although the latter mentioned examples are costly to operate, smaller versions have yielded valuable information at a cost comparable to laboratory experiments.

This review compares and contrasts the relative merits and disadvantages of the three levels of experimental design: laboratory microcosm, mesocosm and macrocosm. Mesocosm performance will be assessed by the comparisons of the results of mesocosm studies with those of both microcosm and macrocosm studies utilizing both ecological and toxicological data from aquatic systems.

1.3 Micro-, Meso- and Macrocosms: Merits and Limitations

To address the question of which type of experimental approach works best, one must compare the merits and disadvantages of mesocosms relative to both laboratory assays and macrocosm experiments on many levels. Microcosm experiments are perturbations produced by the experimenter in the laboratory while mesocosm experiments are perturbations imposed by the experimenter in isolated "sections" of the environment. Macrocosm experiments utilize a whole aquatic ecosystem (eg. a lake). It should be pointed out that mesocosms and macrocosms are not conceptually distinct but may overlap. For example, natural prairie sloughs may

be classified as either mesocosm or macrocosm experimental units. Diamond (1986) states that these three types of experiments differ greatly in the hypotheses which can be addressed by their use. Table 1-1 summarizes how the three experimental designs differ in their relative merits according to several criteria.

Table 1-1 shows that microcosm studies offer the greatest degree of control over independant variables and variation between sample sites (site matching), although Sanders (1985) states that there are examples in the literature where the coefficient of variation between replicate enclosures is comparable to that found in microcosm studies. Although a limited number of independent variables can be controlled in mesocosm studies (and still fewer in macrocosm studies) all treatments will recieve the same levels of variables such as light, temperature and wind, even if these factors are not accounted for. Thus, uncontrolled variables in mesocosm studies need not be a primary concern as long as all treatments receive them equally. Indeed, this may add greater realism to a study.

Clearly, microcosm experiments permit the largest number of replicates (and treatments) and therefore, greater statistical sensitivity and precision. Satisfactory replication is difficult to attain in macrocosm studies, for example in lakes, since no two lakes are sufficiently similar. Replication in such studies can also be expensive. Reference lakes, commonly used as controls, must be used with caution as natural seasonal and yearly variation may obscure true relationships (Schindler, 1987). Schindler et al. (1987)

Table 1-1. Comparison of three levels of experimental design in ecology and toxicology according to several criteria (modified from Diamond, 1986).

Criterion	Microcosm	Mesocosm	Macrocosm
1. Regulation of variables	High	Med	Low
2. Site matching	High	Med	Low
3. Replication	High	High/Med	-
4. Statistical precision	High	Med	Low
5. Repeatability	High	Med/Low	Low
6. Max. temporal scale[a]	Low	Med/High	High
7. Max. spatial scale[b]	Low	Med/High	High
8. Scope[c]	Low	Med	High
9. Realism	None	High	High
10. Generality	None	Med	High
11. Risk of contamination	Low	Low/Med	High

Table 1-1 (cont'd)

Criterion	Microcosm	Mesocosm	Macrocosm
12. Ease of clean up	High	High/Med	Low
13. Cost	Low	Low/Med	High

(a) length of time an experiment can be conducted in a location
(b) size of the experimental units
(c) number of manipulations and/or variables that can be examined

have been fertilizing a small, precambrian shield lake with nitrogen and phosphorus since 1969. Changes in water chemistry and biota must be compared to reference lakes receiving no external nitrogen and phosphorus. Whole-lake acidification experiments have also been done (Schindler et al., 1985). Because of a heterogeneous environment, site matching in mesocosm work is more problematic than in laboratory studies but is offset by randomization and dispersion of the mesocosms and through replication.

Natural seasonal and yearly variation in macrocosm and mesocosm studies diminishes the degree of repeatability of experiments in comparison to microcosm studies. Variation between years may constitute a large portion of the variation during long-term experiments in mesocosm and macrocosm experiments. Microcosm experiments are usually of short duration (low maximum temporal scale) while macrocosm experiments can be theoretically operated indefinitely. Mesocosm studies are intermediate in duration; the length of time being untimately dictated by the durability and size of the mesocosm. Microcosm studies lack the temporal scale needed to elucidate long-term effects. Mesocosm and macrocosm studies are usually of a sufficient duration (2-10 years) to allow determination of such long-term effects.

Microcosm experiments have the lowest spatial scale. Microcosms in the laboratory involve use of test tubes, flasks and aquaria with small volumes of water. Mesocosms offer a opportunity for larger spatial scales while maintaining easy regulation of important variables. Macrocosm experiments offer the greatest

spatial scale but are often difficult to control. The larger spatial scale of mesocosm studies allows more realistic extrapolation to the natural environment than microcosm studies. However, Diamond (1986) states that when spatial scale is increased there is usually a concomitant decrease in replication.

Perhaps the greatest shortcoming of laboratory assays is the lack of realism and the degree to which systems fail to emulate the natural environment (Table 1-1). All variables are set such that growth conditions are optimal. This is rarely the case in nature (Solomon et al., 1985). In addition, microcosm experiments commonly involve single species cultures. To offset the single species "dilemma", some investigators have included representatives of several trophic levels in their design (Metcalf et al., 1971; Harris et al., 1980 in Larsen et al., 1986). deNoyelles et al. (1982) point out that the response of any single species to a perturbation is likely to be influenced by the presence of other species and components of the abiotic system (eg. sediments). For example, the current standards (acceptable levels) for organic contaminants in the environment come mainly from data generated from single species toxicity assays performed in the laboratory. Many recognize the artificiality of such tests (Cairns, 1983; Odum, 1984; Kimball and Levin, 1985; Schindler, 1987) and consequently the applicability of such data to the natural environment is limited. Despite the lack of environmental realism in such laboratory assays, risk and hazard assessments are made from combining these laboratory toxicity data with exposure information. Exposure is predicted from monitoring

programs while toxicity data arise from extrapolation of these single species bioassays on selected, representative organisms. In addition, many laboratory assays in test tubes or flasks do not include the sediment compartment in the design. Therefore these assays do not account for processes such as adsorption of the contaminant and degradation in the sediments. Consequently these experiments cannot yield data concerning the persistence or compartmentalization of organic contaminants in the environment.

Although reduction of complex ecosystems down to simplified laboratory microcosms allows for greater control, the validity of extrapolating such data to the real world remains unanswered. The behavior of a species or contaminant in the environment cannot be easily predicted from the behavior in the subunits of the system. Impacts at one heirarchical level do not translate well into effects at other levels (Odum, 1984). For example, microcosm toxicity assays failed to predict the detrimental effects of acid rain on fish in Sweden. High mortalities of fish occurred at a pH which was not physiologically harmful by laboratory assay standards. However, these toxicity tests could not predict the pH-mediated leaching of aluminum from the watershed which caused clogging of fish gills and disruption of ionic regulation at this physiologically "safe" pH (Odum, 1984).

Community functions such as species interactions (predation and competition), immigration and emigration, or interrelationships between organisms and biogeochemical cycles are neglected in microcosm studies (Schindler, 1987). For example, although acute

microcosm tests examining the effects of copper on fish, invertebrates and periphyton correctly assessed mortality due to copper toxicity in Ohio streams, chronic tests failed to accurately predict the impact on these streams (Greckler et al., 1976). Chronic microcosm tests looked only at mortality, growth and fecundity of fish. When subjected to a concentration of 120 $ug \cdot L^{-1}$ Cu, fish migrated out of the area to avoid the high levels of copper in the stream.

Species used for toxicological testing in the laboratory are usually those which can be cultured conveniently, rather than the most sensitive or critical species in natural environments. Larsen et al. (1986) found a 10-fold difference in EC_{50} values to atrazine among 8 species of algae in laboratory single species toxicity assays. Larsen et al. (1986) also state that most toxicity protocols utilize only one species of algae. Misleading conclusions may be drawn if the representitive alga is tolerant to the toxin in question.

In contrast to the microcosm design, mesocosm studies incorporate more realism into their design (Table 1-1). Many species of different trophic levels are present and species interactions and possibly synergistic effects may occur. This is clearly an advantage over microcosm assays although synergistic effects are rarely quantified. Results can be more realistically extrapolated to the natural environment. Many species are included in the study so that the effects of, for example, a contaminant can be monitored on both resistant and vulnerable species.

In spite of the incorporation of many interacting species in the mesocosm design, the effects of a contaminant are usually monitored at the community level and not at the individual species level. This may be a disadvantage to the system as information about species tolerance to a contaminant can be lost. However, this may only be an artifact of reductionalist thinking! Gurney (1988) using littoral enclosures in the Delta Marsh, Manitoba, Canada utilized quantitative grain density microautoradiography to determine the primary production response of each species of the periphytic algal community to simazine exposure. Although this method permitted her to follow the toxicity of individual species, the technique takes considerable amounts of time (Gurney, pers. comm.) and therefore its utility in mesocosm and macrocosm studies is of limited value.

Mesocosms commonly include all the compartments found in natural aquatic environments (eg. water, sediment, biota, air-water interface, sediment-water interface) and therefore lend themselves well to investigations concerning contaminant effects, compartmentalization and environmental fate. Because all of the compartments are present, processes such as adsorption of contaminants to sediments and suspended particulates can also be monitored, something rarely studied in the lab.

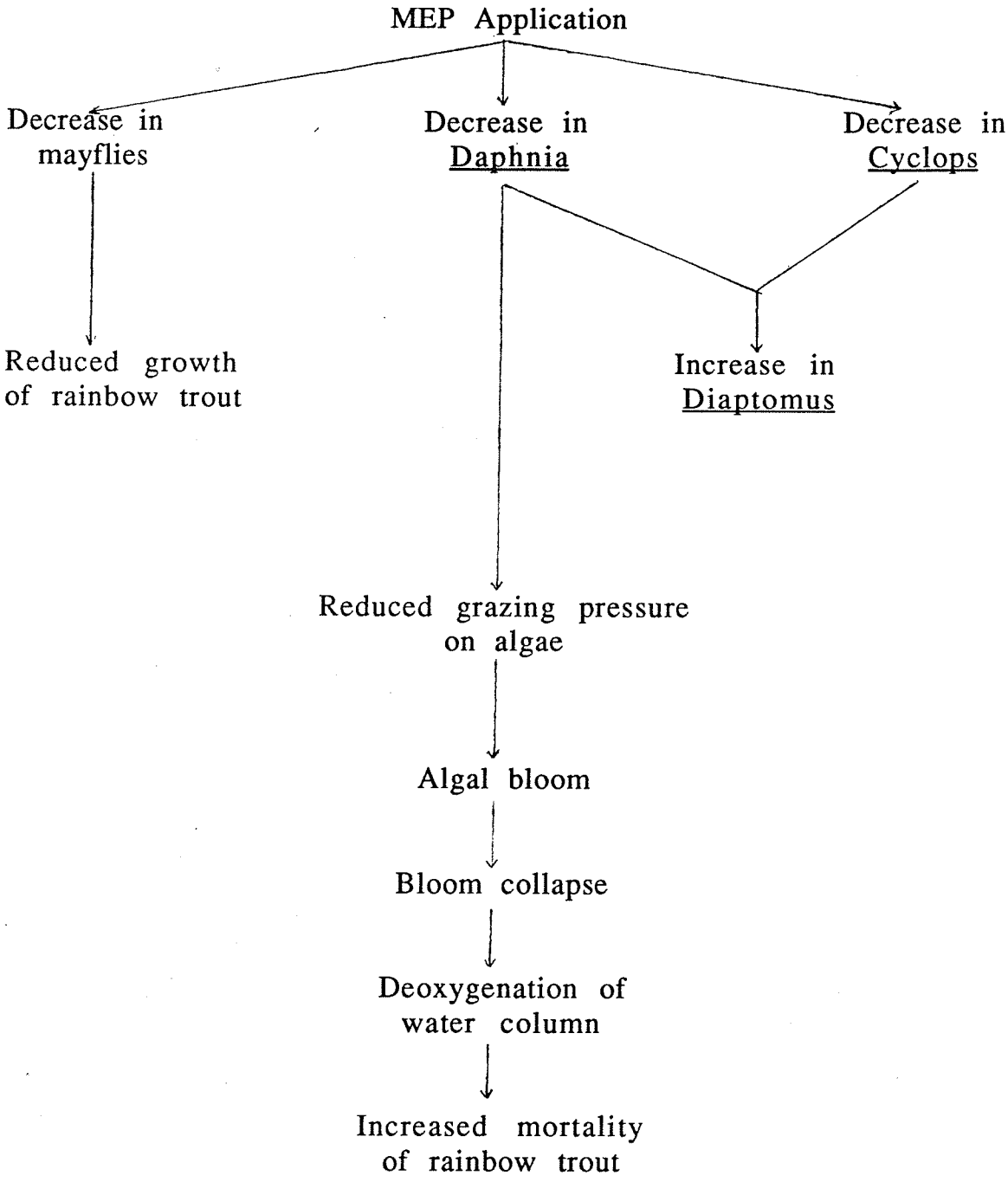
Mesocosms allow an investigation at many trophic levels simultaneously; this is rarely achieved in the laboratory. Elimination or inhibition of a species (or several species) may well have ramifications on higher trophic levels through changes in

competition or predation. Schindler (1987) refers to this as a "trophic cascading" effect. For example, Crossland (1984) examined the effects of methyl parathion (MEP) in outdoor ponds and laboratory aquaria. MEP in ponds was toxic to some species of aquatic insects and crustaceans but not to fish. This spectrum of toxicity was similar to results from laboratory tests. However, interactive, secondary effects in the ponds could not be predicted from laboratory toxicity tests. Fig. 1-1 is a flow chart depicting the sequence of secondary events after application of the ponds with MEP (100 $\mu g \cdot L^{-1}$).

Application of MEP resulted in the rapid loss of Daphnia spp. and a less severe decline in the populations of Cyclops spp. and mayflies. A large increase in the populations of Diaptomus spp. occurred in the treated ponds 20-90 d. after treatment due to the loss of its competitors (Daphnia spp.) and preditors (Cyclops spp.). Loss of mayflies from the ponds treated with MEP reduced the growth rate of rainbow trout as the trout's principle food source was eliminated. Loss of herbivorous zooplankton and mayflies also resulted in a reduction in grazing pressure on algae. An algal bloom formed as a reuslt. Collapse and subsequent decomposition of the bloom increased biological oxygen demand (BOD) in the water such that oxygen levels in the water could no longer sustain rainbow trout. Trout mortality increased dramatically.

Mesocosms also have limitations. Schindler (1987) points out that aquatic mesocosms fail to incorporate phenomena such as water turbulence and/or nutrient cycling. When using enclosures and

Fig. 1-1. Flow chart showing secondary effects of application of methyl parathion to ponds (derived from Crossland, 1984).


MEP Application
Decrease in mayflies
Decrease in Daphnia
Decrease in Cyclops
Reduced growth of rainbow trout
Increase in Diaptomus
Reduced grazing pressure on algae
Algal bloom
Bloom collapse
Deoxygenation of water column
Increased mortality of rainbow trout

limnocorrals in lakes and ponds, one must be sure that enclosure effects (the effect of isolating a water column from the rest of a water body in the absence of a treatment) are minimized (Kuiper, 1977).

Macrocosm studies provide the most realistic data in terms of what occurs in the natural environment. Results from these experiments need only be extrapolated to the general case since a macrocosm is part of a natural system (not a subset of a system). However, obtaining government and public consent, for example to intentionally introduce a contaminant into part of a natural ecosystem, can be a major challenge.

The popularity of laboratory microcosms, particularly in screening potentially harmful chemicals, is derived from the rapid generation of data and low operating cost relative to macrocosms. If one is to obtain representative samples from macrocosm studies, the cost of such chemical appraisal could greatly exceed its utility. The cost of conducting an experiment in a "dugout" pond mesocosm only slightly exceeds that of a microcosm experiment. Additional expense may include the cost of pond excavation and transportation to and from the study site. Goldsborough et al. (1986) describe 0.3 m^3 littoral enclosures costing $30 Can. while Solomon et al. (unpubl.) describe limnocorrals with volumes of 20, 125 and 1000 m^3 costing $360, $1620 and $3000 respectively.

Another factor contributing to the popularity of microcosm studies is that the data obtained yield standard end points such as

growth rates and mortality rates as well as LD_{50}, LC_{50} and EC_{50} values and NOEC (No Observable Effect Concentration) and MATC (Maximum Allowable Toxicant Concentration). These end points are rarely quantified in mesocosm studies and even less so in macrocosm studies. However, non-biological end points such as half life values of contaminants in various compartments of the aquatic environment are common to both mesocosm and macrocosm studies (Hesslein et al., 1980; Muir et al., 1980; Schindler et al., 1980; Rawn et al., 1982; Servos, 1988).

When investigating the effect of a perturbation on the environment, the decision to perform the study in the laboratory, in mesocosms or in natural ecosystems should incorporate a measure of the ease of site cleanup after use and the risk of contaminating nearby areas. Rapid cleanup is accomplished easily in the laboratory, but becomes more challenging in mesocosm or macrocosm studies. For example, in laboratory toxicology studies, flasks are easily cleaned whereas mesocosms such as dugouts may require removal of water and hydrosoil to a landfill site. Mesocosm experiments using enclosures may require disposal of the enclosures upon termination of the experiment or even enclosure removal from lakes or ponds before winter freeze up. Solomon et al. (unpubl.) however, state that their large limnocorrals could remain in the lake all year and receive no damage from winter ice.

The risk of releasing a contaminant into the environment during or after an experiment is relatively easily controlled in laboratory studies, but can prove difficult in ecosystem studies,

particularly if a lake has an outflow or significant groundwater recharge. Risk of movement of the contaminant to other areas can also be a factor in mesocosm studies. Limmocorrals which do not contact the sediments increase the risk of contamination to the entire lake during vernal or autumnal overturn. Littoral enclosures with a good seal at the sediments lessen the chance of contaminating the adjacent unenclosed water. Dugouts lined with polyethylene plastic perhaps represents the best alternative for containment. Providing no rips or tears are present in the polyethylene pond liner, risk of spreading the contaminant is low due to isolation of the pond from groundwater flow.

Table 1-2 indicates the relative sensitivity of each type of experimental design to the level of organization to be studied. The utility of microcosm experiments at the organism level and at higher resolution is better than for the other two experimental designs. However, the validity of extrapolating to the population, community and ecosystem levels (levels desired by environmental toxicologists, lake managers, field ecologists, etc.) remains in doubt. Mesocosms have the resolution to detect responses at the population and community levels although techniques such as microautoradiography make resolution at finer levels possible . Extrapolation of data from the mesocosm design to the natural environment is more realistic than from the microcosm design.

Table 1-2. Comparison of the scale of resolution that is commonly studied in three experimental designs in ecology and toxicology.

Biological Level Of Organization	Microcosm	Mesocosm	Macrocosm
Biochemical processes	Yes	No	No
Cell	Yes	No	No
Tissue	Yes	No	No
Organ	Yes	No	No
Organism	Yes	No	No
Population	No	Yes	Yes
Community	No	Yes	Yes
Ecosystem	No	No	Yes

As Diamond (1986) has suggested, the question as to which experimental design is superior is inappropriate. The specific needs of each study will generally dictate which type of design best serves those needs. In many cases more than one design will work well, and several ecologists (Hurlbert, 1984; Diamond, 1986; McIntosh, 1987) urge a pluralistic approach , which compare results from similar experiments utilizing different experimental designs.

1.4 The Performance of Mesocosms Relative to Micro-and Macrocosms.

The performance of mesocosms in ecological and toxicological studies of aquatic ecosystems can be evaluated on many levels. Variation between replicate mesocosms should ideally be comparable to that achieved in the laboratory. This may be investigated by comparing the coefficient of variation (CV) between replicate mesocosms with that of laboratory results regarding physical (e.g., light attenuation, temperature), chemical (e.g., nutrient levels, contaminant half lives) and biological (e.g., phytoplankton biomass and productivity) parameters measured in the study. In studies utilizing limnocorrals or littoral enclosures, one should be sure that enclosure effects are minimized. One cannot expect results of the effect of a perturbation to be realistic if the behavior of the various components within the mesocosm does not emulate what is occurring outside the mesocosm. Lastly, information obtained from mesocosm studies should supplement results obtained from laboratory work as

well as fill in gaps where laboratory assays cannot provide information.

Mesocosms provide defensible data with respect to among-replicate variability when compared to laboratory studies. In mesocosm studies, among-replicate variability may be a function of the volume of enclosed water; the larger the mesocosm, the smaller the CV between replicate mesocosms. However, the effect of mesocosm size on among-replicate variability remains an untested hypothesis. Larger mesocosms may increase spatial heterogeneity within the mesocosm, thus making sampling more problematic and increasing the within-enclosure CV. Sanders (1985) suggests that the relationship between mesocosm size and among-replicate variability may be manifested through size-dependent aggregation effects (e.g., reduced wall effects via lower surface area/volume ratios, etc.).

Pilson et al. (1979) found that nutrient concentrations, phytoplankton and zooplankton species composition and biomass were similar between replicated, on-shore tanks. Sanders' (1985) survey of the literature found that biomass indices (e.g., phytoplankton, zooplankton, benthic invertebrates, etc.) in enclosures had a mean CV of 25 % (n=15) and biological flux rates (e.g., primary productivity) were comparable at CV= 21 % (n=16). Abiotic variables (e.g., dissolved oxygen, temperature, light, secchi depth, etc.) replicated much better (CV= 13 %, n=7) than biotic variables although data were limited. These values agree well with laboratory microcosms (Sanders, 1985).

Table 1-3 summarizes the among replicate CV values for various physical, chemical and biological parameters in enclosures at Delta Marsh, Canada during a five week experiment in 1989 (data obtained from Chapter 3). Enclosures were of two types: enclosures with artificially-induced water turbulence (Turbulent) and enclosures lacking such turbulence (Control). CVs of biological indices within 1.5 m diameter enclosures at Delta marsh are generally higher than those reported elsewhere in the literature (Sanders, 1985), although the values from Delta marsh fall within the reported range. CVs for physical and chemical parameters (Table 1-3) are more representative of the values reported in the literature review by Sanders (1985).

Mesocosms also provide defensible data when compared to macrocosm studies. For example, Baccini et al. (1979) examined the deposition of trace metals added to enclosures and an open lake. Deposition rates replicated better in enclosures than along unenclosed sediment transects (CV= 36 % vs 68 % respectively). Equivalent comparable data for organic compounds in aquatic ecosystems are lacking. Solomon et al. (1985) examined the dissipation of permethrin in limnocorrals. The mean CV between replicate limnocorrals for the concentration of permethrin in the water column over a 94 d period was 29 %. Herman et al. (1986), using similar limnocorrals in the same lake, examined the effects of atrazine on periphyton biomass, carbon assimilation and species composition. The mean CV between replicate limnocorrals for atrazine in the water column was 9 % (n=10). This value compares

Table 1-3. Among-replicate coefficient of variation (CV) from enclosures at Delta marsh during a five week experiment.

Parameter/Treatment	Coefficient of Variation				
Week	1	2	3	4	5
Temperature (°C.)					
Turbulent	-	3.6	0.9	0.0	1.8
Control	-	2.0	0.7	1.0	1.8
Light extinction coefficient (m^{-1})					
Turbulent	-	36.9	43.6	16.4	24.1
Control	-	16.4	36.3	20.2	31.4
Turbidity (NTU)					
Turbulent	-	64.6	56.8	51.0	33.4
Control	-	106.7	15.3	41.9	106.8
Suspended Particulates ($mg \cdot L^{-1}$)					
Turbulent	6.1	52.2	61.1	60.5	34.5
Control	50.2	30.3	33.5	51.9	107.2
Organic Content of Particulates (%)					
Turbulent	11.6	-	61.5	34.2	17.5
Control	7.9	-	24.1	9.3	18.9
Dissolved Reactive Silicon ($\mu g \cdot L^{-1}$)					
Turbulent	36.1	34.8	50.8	52.6	47.7
Control	42.9	53.4	58.1	19.3	37.1
Soluble Reactive Phosphorus ($\mu g \cdot L^{-1}$)					
Turbulent	0.0	94.1	35.8	40.2	79.7
Control	0.0	100.0	8.1	26.4	73.1

Table 3 (cont'd)

Parameter/Treatment	Coefficient of Variation				
Week	1	2	3	4	5
Particulate Phosphorus ($\mu g \cdot L^{-1}$)					
Turbulent	19.1	19.6	50.9	36.2	47.7
Control	48.8	72.8	48.0	54.5	29.6
Ammonia ($\mu g \cdot L^{-1}$)					
Turbulent	55.5	75.2	32.9	29.8	49.5
Control	14.9	89.2	12.1	33.8	98.1
Oxygen ($mg \cdot L^{-1}$)					
Turbulent	-	27.2	39.5	30.7	23.2
Control	-	12.5	25.3	34.4	25.7
Phytoplankton Biomass (μg Chla$\cdot L^{-1}$)					
Turbulent	55.8	103.8	101.3	55.8	99.0
Control	70.9	94.8	95.0	23.6	96.6
Phytoplankton Max. Gross Productivity (μg C$\cdot L^{-1} \cdot h^{-1}$)					
Turbulent	71.0	2.9	72.1	95.9	107.0
Control	89.1	82.5	84.5	67.9	108.5
Phytoplankton Max. Specific Productivity (μg C$\cdot$(μg Chla)$^{-1} \cdot h^{-1}$)					
Turbulent	65.9	74.4	58.8	39.1	39.1
Control	39.9	67.6	29.1	51.0	18.7
Phytoplankton I_k ($\mu mole \cdot m^{-2} \cdot sec^{-1}$)					
Turbulent	38.6	21.1	61.5	21.7	51.4
Control	31.3	7.9	29.3	16.1	26.7
Phytoplankton alpha (μg C$\cdot$(μg Chla)$^{-1} \cdot h^{-1} \cdot$($\mu mole \cdot m^{-2} \cdot sec^{-1}$)$^{-1}$)					
Turbulent	92.7	88.8	62.5	33.0	56.6
Control	36.0	61.2	37.8	40.7	32.2

Table 3 (cont'd)

Parameter/Treatment	Coefficient of Variation				
Week	1	2	3	4	5
Phytoplankton E_{max} ($\mu g\ C \cdot (mg\ Chla)^{-1} \cdot h^{-1} \cdot (\mu mole \cdot m^{-2} \cdot sec^{-1})^{-1}$)					
Turbulent	65.2	78.6	61.6	38.2	35.1
Control	39.7	52.7	25.4	39.1	34.1
Periphyton Biomass ($\mu g\ Chla \cdot cm^{-2}$)					
Turbulent	-	119.6	57.7	34.7	59.9
Control	-	121.6	74.3	34.5	37.6
Periphyton Max. Gross Productivity ($\mu g\ C \cdot cm^{-2} \cdot h^{-1}$)					
Turbulent	-	41.1	33.1	21.3	41.4
Control	-	34.9	27.9	21.8	24.2
Periphyton Max. Specific Productivity ($\mu g\ C \cdot (\mu g\ Chla)^{-1} \cdot h^{-1}$)					
Turbulent	-	70.1	48.9	28.0	29.0
Control	-	62.8	52.6	62.0	52.2
Periphyton I_k ($\mu mole \cdot m^{-2} \cdot sec^{-1}$)					
Turbulent	-	35.1	55.3	33.2	24.0
Control	-	26.8	23.4	24.9	31.6
Periphyton alpha ($\mu g\ C \cdot (\mu g\ Chla)^{-1} \cdot h^{-1} \cdot (\mu mole \cdot m^{-2} \cdot sec^{-1})^{-1}$)					
Turbulent	-	43.5	27.4	34.3	35.5
Control	-	39.2	59.9	34.9	82.8

Table 3 (cont'd)

Parameter/Treatment	Coefficient of Variation				
Week	1	2	3	4	5
Periphyton E_{max} ($\mu g\ C \cdot (mg\ Chla)^{-1} \cdot h^{-1} \cdot (\mu mole \cdot m^{-2} \cdot sec^{-1})^{-1}$)					
Turbulent	-	48.9	21.5	29.4	28.4
Control	-	51.6	59.2	28.3	70.8

Number of replicates per treatment=5
Units in brackets=units of measurement for parameter
I_k=light intensity at which max. specific productivity is attained
alpha=initial slope of the photosynthesis vs. light intensity curve
E_{max}=maximum photosynthetic efficiency

well with the loss of methyl parathion (MEP) from outdoor ponds (CV= 11 %, n=6; Crossland and Bennett, 1984). This also agrees well with the CV between replicate enclosures for the aqueous half life of MEP in small enclosures in ponds (CV= 14 %, n=3; Stephenson and Kane, 1984).

If littoral enclosures and limnocorrals are to provide realistic data one must be sure that the effect of isolating the water column, sediments and attendant biota from the adjacent water body is minimal. Physical, chemical and biological processes should be unaltered by the isolation caused by the mesocosm. Enclosure effects are common to studies using limnocorrals and enclosures, although these effects are rarely quantified. Sanders (1985) suggests that enclosure effects are directly related to the degree of scaling down of the natural environment.

Small diameter mesocosms limit the fetch across the waters surface (Sanders, 1985) and therefore reduce wind-induced turbulent mixing of the water column within the mesocosm. This problem can be alleviated by increasing the mesocosm size or by orienting the mesocosms such that the greatest fetch across the mesocosm is exposed to prevailing winds.

Enclosure effects can be manifested in a number of ways. Of primary importance is the loss of horizontal and vertical turbulence. This may result in unnaturally high sedimentation rates, increased light penetration (decreased turbidity), altered temperature profiles in the water column and changes in nutrient cycling. In addition,

the combination of reduced water circulation and exclusion of biological material (phytoplankton, zooplankton) from its source of inoculum (the adjacent water body) may significantly alter the structure and functioning of these planktonic communities. The effect of this isolation on benthic communities is unknown.

Loss of turbulence within enclosures has been cited more often than any other factor as the primary cause of enclosure effects. However, little attempt has been made to quantify this supposition, perhaps owing to the general lack of knowledge by ecologists of the processes involved in turbulent flow in aquatic ecosystems. Davies and Gamble (1979) have given evidence that vertical eddy diffusivity could be decreased 10-fold by isolation of the water column. Eppley et al. (1978) found that vertical eddy diffusivity was only 0.6 $cm^2 \cdot s^{-1}$ in $68m^3$ marine enclosures while values typical for the open ocean are 5-50 $cm^2 \cdot s^{-1}$.

Because enclosures physically isolate a column of water from an adjacent water body, wind events which may cause resuspension of sediments (and therefore increase the concentration of suspended particulates) in the adjacent water rarely have an impact on the water quality within the enclosure. Twinch and Breen (1978) found that elevated levels of suspended particulates in the adjacent water associated with wind storms were not found in enclosures.

Increased light penetration and lower turbidities are commonly reported as enclosure effects (Lund, 1972; Kuiper, 1977; Twinch and Breen, 1978; Landers, 1982). Increased water transparency caused

surface temperatures in enclosures to be 11°C. higher than the adjacent water of Midmar Dam during periods of warm weather (Twinch and Breen, 1978).

Similarity of temperature profiles between enclosures and adjacent waters are commonly given as evidence for the lack of enclosure effects on vertical turbulence (Goldman, 1962; Kemmerer, 1968; Kistritz, 1978; DeCosta et al., 1983). However, Boyce (1974) showed mathematically that temperature profiles inside and outside enclosures can be expected to be similar due to horizontal heat transfer across the enclosure walls. Therefore the similarity of temperature profiles need not be indicative of the commensurability of vertical flux rates.

The effect of enclosure on the water chemistry in enclosures is more variable than that of physical parameters. Although some workers have shown no enclosure effects (Klussman and Inglis, 1968; Kistritz, 1978; Twinch and Breen, 1981; DeCosta et al., 1983; Shires, 1983) others have shown pronounced effects on water chemistry (Kuiper, 1977; Twinch and Breen, 1978). DeCosta et al. (1983) found that some chemical parameters (total phosporus) followed trends in the adjacent water while others did not (nitrate, pH). Sanders (1985) suggests that the degree of enclosure effects on water chemistry can be expected to be influenced by the ratio of sediment surface area to the volume of the enclosed water; therefore enclosure diameter.

The isolation of a body of water can also have a profound effect on the biological communities and processes occurring in the

enclosure. Smyly (1976) found that physical isolation changed the biomass of zooplankton communities within enclosures but did not alter the species composition. Moss (1981) found that periphyton in control enclosures contained species typical of the phytoplankton community of the adjacent lake water. Moss suggested that this may be due to a lack of turbulence in enclosures which resulted in phytoplankton sedimentation into the periphyton. Periodic turbulence in the enclosures also caused dislodgement of epiphytic algae from their macrophyte hosts and a resultant increase in epiphyte species and numbers in the plankton (Moss, 1981). Changes in community composition has also been reported by Lund (1972), Twinch and Breen (1978) and DeCosta et al. (1983), while Kuiper (1977) found an excellent correspondence between the timing and magnitude of phytoplankton biomass and species composition in enclosures and the open sea.

Loss of turbulence and subsequent sedimentation has also been responsible for changes in phytoplankton community metabolism. Bender and Jordon (1970) found that phytoplankton production in a 0.5 m diameter tube enclosure was initially similar to the surrounding lake but decreased by 50 % by the end of the 25 day experiment.

Lack of turbulence should not only be a concern to the ecologist, but also to those who utilize enclosures in studying the fate and effects of organic contaminants in aquatic ecosystems. The use of aquatic mesocosms for this purpose is a recent addition to the process of registration of pesticide products in Canada, which require

manufacturers to provide a data base showing the environmental fate and effects of such products on aquatic resources using the mesocosm protocol. Common to many pesticide studies of this nature are reports of the rapid loss of active pesticide from the water column to the sediments (Stephenson and Kane, 1984; Solomon et al., 1985; Gurney and Robinson, 1989). Because of the lack of turbulence in such situations enclosure studies conducted in shallow water bodies may underestimate not only the persistence of the herbicide in the water column, but the biological impact (toxic effect) as well. Mauk et al. (1976) found that levels of simazine in the water column could be elevated substantially by strong winds. This suggests that simazine can easily dissociate from the sediments with physical disturbance.

It is clear that the use of small enclosures in both ecological and toxicological studies may yield misleading results due to the elimination of the turbulence factor. Incorporation of some means by which to contol water turbulence within enclosures may provide more realistic data. Studies are needed in which water mixed artificially within enclosures can be compared to enclosures lacking such turbulence. This will be addressed in Chapter 3 of this thesis.

Chapter 2

The Effect of Wind-induced Turbulence on the Limnology of a Shallow, Prairie Wetland: a Mensurative Study

2.1 Abstract

A field study was conducted in a shallow channel of the Delta Marsh, Canada to determine the effect of wind-induced water turbulence on various limnological parameters. Wind-induced water turbulence had a marked effect on suspended particulate concentration by resuspending surficial sediments into the water column. The concentration of suspended particulate matter in the water column was influenced by changes in the hourly and seasonal wind regime while phytoplankton biomass was positively related to wind stress on an hourly basis only. The influence of water turbulence on the fidelity of algal species to specific communities is suggested and the common practice of defining discrete algal communities rather than a community continuum concept is questioned.

Two mathematically simple equations are presented to quantitatively describe wind stress conditions at the waters surface. Both equations accurately predicted the concentration of suspended particulates in the water column between two week periods throughout the sampling season.

2.2 Introduction

Wind has long been cited as a key factor influencing the limnology of shallow water bodies. However, quantitative expressions decribing wind-related events have rarely been attempted. This should, perhaps, not be surprising as the understanding of the processes involved in water circulation has evolved slowly (Hutchinson, 1967). Mathematically-simple expressions are urgently needed by ecologists.

Many prairie wetlands and lakes in central Canada are shallow. Because of the lack of tall vegetation surrounding these water bodies, situations of wind stress over the waters surface may occur frequently, inducing turbulent waves and circulations. The effectiveness of wind as an agent of water turbulence has been suggested to be a function of fetch, duration above a critical wind speed, and water depth (Viner and Smith, 1973; Knoechel and Kalff, 1975; Wetzel, 1983) as well as the density of submersed and emergent macrophytes in the water column (Van der Valk and Davis, 1978) which create boundary layer effects.

Wind-induced turbulence in shallow water bodies commonly results in the resuspension of surficial sediments (Wetzel, 1970; Davis, 1973; Viner and Smith, 1973; Walmsley et al., 1980; Carper and Bachmann, 1984) and consequently affects underwater light penetration (Tyler, 1961; Grobbelaar and Stegmann, 1976; Walmsley, 1978; Kirk, 1980, 1985; Walmsley et al., 1980). In addition, turbulence in shallow lakes may inhibit the recovery of water

quality of many shallow lakes from cultural eutrophication (Ryding and Forsberg, 1977; DeGroot, 1981) by mixing nutrient-rich porewater within surficial sediments into the overlying water (Viner, 1977). Although Viner's study involved a tropical lake, the mechanism of turbulent displacement of porewater may be expected to be similar in temperate water bodies.

The importance of water turbulence in the maintainance of phytoplankton communities is widely recognized. Reports of the appearance of typically planktonic species of algae in the periphyton under calm conditions and the appearance of typically benthic species in the plankton under windy conditions (Moss, 1981) suggest the importance of turbulence. Indeed, the process of seasonal succession in phytoplankton communities has been suggested to be closely linked to water turbulence (Hutchinson, 1967; Knoechel and Kalff, 1975).

The marked increase in phytoplankton biomass during periods of wind stress (Ganf, 1974) questions the dogma of defining specific algal communities when wind-stressed or completely calm conditions exist. Fidelity of one or more species to a particular community may be a function of the degree of water turbulence. For example, under periods of wind stress, algal communities in littoral zones may form more of a continuum rather than existing as separate entities.

This study investigated the influence of wind-induced turbulence on the resuspension of surficial sediments and the biomass of suspended algae. Two mathematically simple and

intuitively appealing equations are presented which quantitatively describe the hourly and seasonal changes in wind stress on a shallow, prairie wetland.

2.3 Methods and Materials

Study Site

A field study was conducted in the Blind Channel of the Delta Marsh, located on the southern end of Lake Manitoba, Canada (99° 19'W, 50° 7'N) from 25 May to 09 August, 1988. Delta marsh is a shallow (< 2m.), postglacial prairie wetland. The geologic character and history has been described by Teller and Last (1981).

Hourly wind data (speed and direction) were obtained from meteorological data collected at the Environment Canada MET Station, University of Manitoba Field Station (Delta Marsh).

Suspended Particulates

Triplicate water samples were taken every 2-4 hours (0900-1500 hrs. daily) from the Blind Channel of Delta Marsh at irregular intervals throughout the sampling season using a 3 L. Van Dorn water sampler. Samples were split into two subsamples. One set was filtered onto preweighed, ignited (16 h. @ 550° C.) Whatman GFC filters for weight determinations of suspended particulates. Filters were dried in an oven (approx. 12 h. @ 105° C.) and weighed on a Cahn Gram Electrobalance to give dry weight measurements ($mg \cdot L^{-1}$).

Samples were then ignited in a Fisher muffle furnace (1 h. @ 550° C.) and reweighed to give ash weight measurements ($mg \cdot L^{-1}$).

Phytoplankton Biomass

Phytoplankton biomass, estimated as chlorophyll a ($\mu g \cdot L^{-1}$), was monitored by filtering the second set of water samples onto Whatman GFC filters. Chlorophyll a (CHLA) was extracted overnight in 90 % methanol and analyzed after the method of Lorenzen (1967) as described by Marker et al. (1981). CHLA values were corrected for phaeophytin.

Indices of Wind Stress

Two indices of wind stress were developed to quantitatively described the hourly and seasonal change in the wind climate at Delta Marsh. The first index, referred to as %AC (Percent Above Critical) is the number of hours for which the wind speed exceeded 3.1 $m \cdot s^{-1}$ during the 24 hour period preceeding each sampling period for suspended particulates, expressed as a percentage of all hourly wind speeds.

In order for sediment resuspension to occur, wind speed must exceed a critical velocity (Viner and Smith, 1973; Carper and Bachmann, 1984). Wetzel (1983) states that the minimum wind speed necessary to create Langmuir circulations in the water column is 3.1 $m \cdot s^{-1}$. This critical wind speed was chosen as a basis for one of the quantitative expressions of wind stress (%AC) at Delta marsh. In addition, data obtained from enclosures at Delta Marsh have

indicated that under complete calm conditions, sedimentation of particles out of the water column takes 24 hours on average. Therefore, the quantity of suspended particulates in the water column at one moment will be influenced by wind events within this time period. The 24 hour wind prehistory was therfore included into the index.

The second index of wind stress, termed WSI (Wind Stress Index) is described by the equation

$$WSI = \frac{\sum_{i=1}^{24} (Si)(ds)}{D}$$

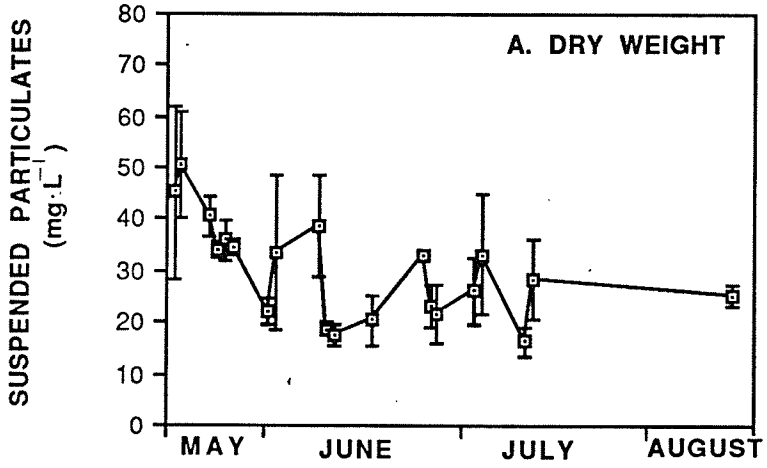
where Σ (Si)(ds) is the product of wind speed and the duration at each wind speed for each hour during the 24 hour period preceeding the sampling time. Wind speed (Si), duration (ds) and water depth (D) are given in $m \cdot s^{-1}$, sec. and m. respectively. The effectiveness of wind as an agent of sediment resuspension is known to be a function of water depth, wind speed and duration (Viner and Smith, 1973; Knoechel and Kalff, 1975; Wetzel, 1983). These parameters were therefore combined to generate the second quantitative expression of wind stress: the Wind Stress Index (WSI). Again, the 24 hour wind prehistory was included in the equation.

2.4 Results

Fig. 2-1a depicts the seasonal change in the concentration of suspended particulates in the water column (expressed as dry weight·L^{-1}). A great degree of variation in suspended particulate concentration (represented by the standard deviation of the daily mean) is evident for many sampling days. There was a general decrease in the concentration of suspended particulates throughout the sampling period from maximum levels in spring (40-60 mg·L^{-1}) to lower levels in late summer (20-30 mg·L^{-1}). The daily and seasonal distribution of suspended particulates expressed on an ash weight per litre basis shows a similar trend (Fig. 2-1b). The two parameters are highly correlated (r^2=0.97, $p < 0.0001$, n=454).

A seasonal trend can also be seen in the distribution of phytoplankton biomass (Fig. 2-2). Mean biomass increased from 53 μg·L^{-1} in May to 70 and 72 μg·L^{-1} in June and July respectively, and then decreased to 47 μg·L^{-1} in August. The seasonal trend in phytoplankton biomass is opposite to that of Figs. 2-1a + 2-1b, suggesting that phytoplankton biomass contributed little to the weight of particulates in suspension. As with the hourly changes in the concentration of suspended particulates on many days, the phytoplankton biomass data also show a great deal of variation.

Fig. 2-1. Daily and seasonal changes in suspended particulate concentration at Delta Marsh. a) Dry weight, b) Ash weight. Vertical bars represent the standard deviation (Sd) of the daily mean.


A. DRY WEIGHT
SUSPENDED PARTICULATES
(mg·L⁻¹)
80
70
60
50
40
30
20
10
0
MAY
JUNE
JULY
AUGUST

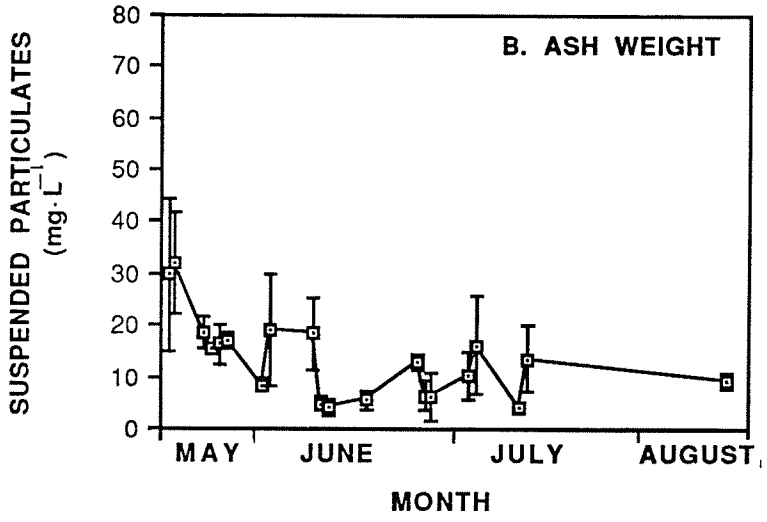
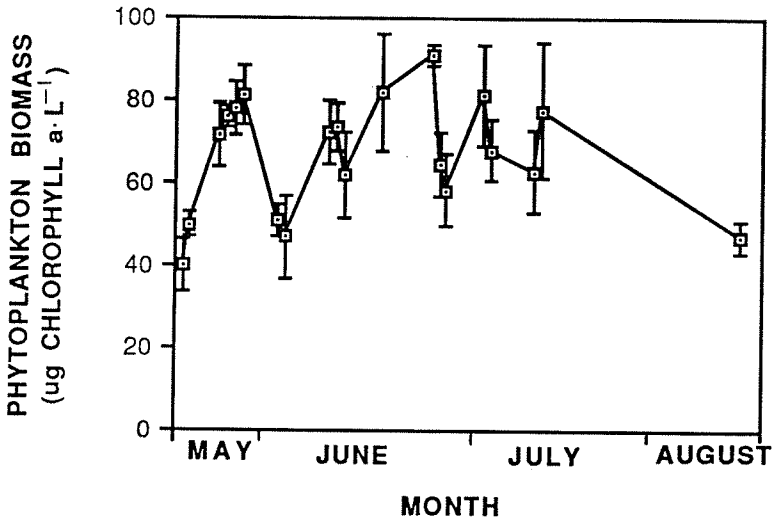

B. ASH WEIGHT
SUSPENDED PARTICULATES
(mg·L⁻¹)
80
70
60
50
40
30
20
10
0
MAY
JUNE
JULY
AUGUST
MONTH

Fig. 2-2. Daily and seasonal changes in phytoplankton biomass at Delta marsh. Vertical bars represent the standard deviation (Sd) of the daily mean.

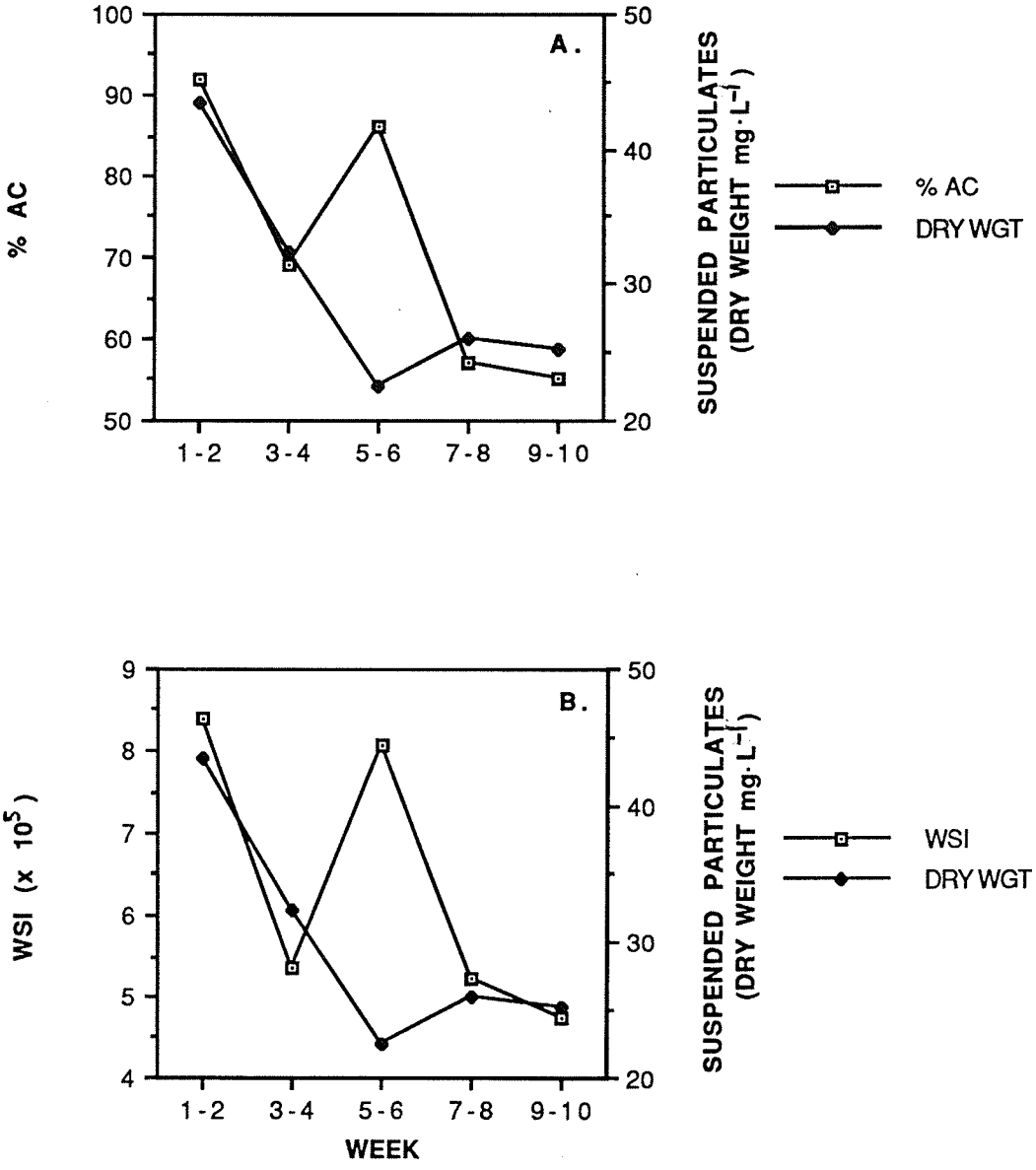

PHYTOPLANKTON BIOMASS
(ug CHLOROPHYLL a·L⁻¹)
100
80
60
40
20
0
MAY
JUNE
JULY
AUGUST
MONTH

Algal biomass increased by 60 % on several days within the span of 3-4 hours (e.g., June 12, July 12 and 13).

The seasonal change in wind stress (represented as %AC) paralleled the seasonal change in the concentration of suspended particulates (dry weight·L^{-1}) in the water column at Delta Marsh (Fig. 2-3a) with one exception. During the two week period of June 16-30 (week 5-6) the concentration of suspended particulates was low while the %AC was relatively large.

The deterioration of the relationship between suspended particulates and both %AC and WSI during week 5-6 can be accounted for by two factors: the location of the anemometer relative to the adjacent marsh and, the direction of the prevailing winds during this period. The Blind Channel of the Delta marsh is situated south of, and is isolated from, Lake Manitoba by a forested beach-ridge. During the summer months, when the trees of the ridge are fully foliated, north winds off the lake are effectively blocked and wind stress on the marsh is minimal, even during periods of strong north winds (pers. obs.). The anemometer is situated on this ridge and therefore is measuring wind speed on the ridge, not on the marsh. Therefore, during summer months, %AC and WSI values may overestimate wind stress on the marsh during periods of north winds. This is the case for week 5-6 when strong north winds dominated the wind regime at Delta marsh. This problem of overestimation would be expected to be minimal during the rest of the sampling season as north winds were either rare or insufficiently

Fig. 2-3. Seasonal relationship between, a) %AC and dry weight of suspended particulates, and b) WSI and dry weight of suspended particulates at Delta Marsh.


A.
% AC
SUSPENDED PARTICULATES (DRY WEIGHT mg·L⁻¹)
100
90
80
70
60
50
50
40
30
20
1-2
3-4
5-6
7-8
9-10
% AC
DRY WGT
B.
WSI (x 10⁵)
9
8
7
6
5
4
WEEK
WSI
DRY WGT

strong (< 3.1 $m \cdot s^{-1}$) or the trees on the forested ridge were not foliated (particularly in May).

With the omission of week 5-6 from the analysis, an excellent linear relationship existed between the seasonal change in %AC and the dry weight of suspended particulates (r^2=0.99, p=0.002, n=4). A similar relationship existed between %AC and the ash weight of suspended particulates (r^2=0.99, p=0.003, n=4).

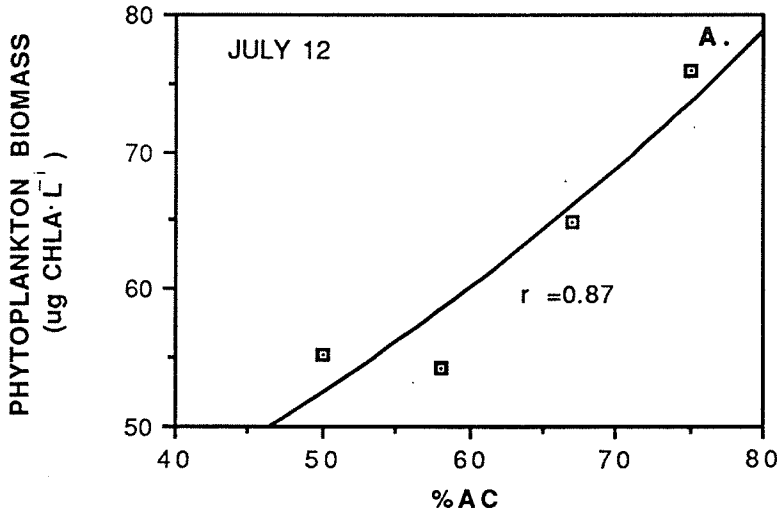
WSI also predicted the seasonal change in the dry weight of suspended particulates (Fig. 2-3b). Omission of week 5-6 resulted in an excellent linear correlation between the two variables (r^2=0.92, p=0.05, n=4). This relationship was slightly weaker for WSI vs. ash weight (r^2=0.90, p=0.05, n=4). An excellent relationship existed between the two estimators of wind stress: %AC and WSI (r^2=0.94, p=0.007, n=5).

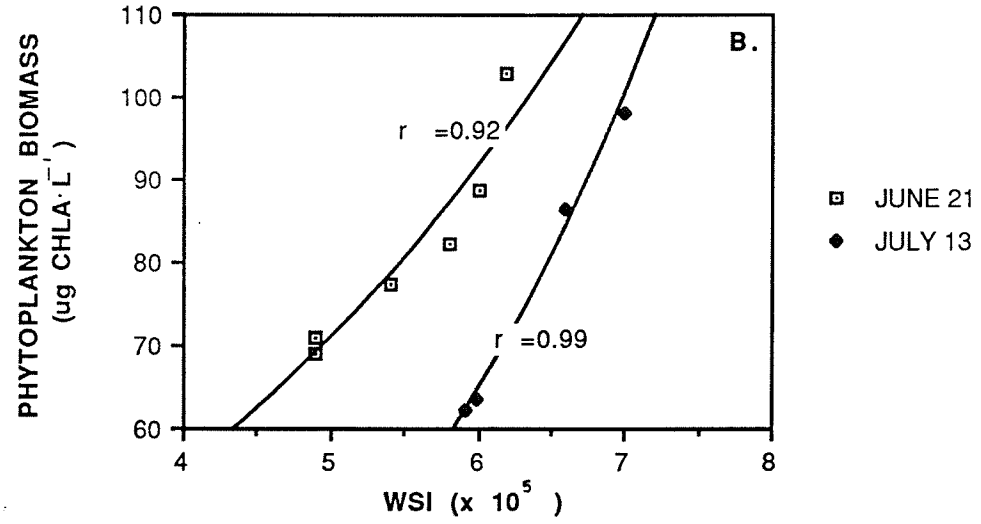
The seasonal trend in phytoplankton biomass did not appear to follow the seasonal decrease in wind stress. However, on days in which large hourly changes in phytoplankton biomass occurred (e.g., June 21, July 12 and 13), hourly changes in wind stress were related to the changes in phytoplankton biomass (Figs. 2-4a+b).

2.5 Discussion

Wind stress may play a major role in shaping the limnology of shallow water bodies. Shearing forces, created when wind blows across the surface of the water, may be sufficient to create waves and Langmuir circulations. Both cause circular vortices in the water

Fig. 2-4. The effect of hourly changes in a) %AC and b) WSI on phytoplankton biomass at Delta Marsh.


JULY 12
A.
r =0.87
PHYTOPLANKTON BIOMASS
(ug CHLA·L⁻¹)
%AC
80
70
60
50
40
50
60
70
80


B.
r =0.92
r =0.99
JUNE 21
JULY 13
PHYTOPLANKTON BIOMASS
(ug CHLA·L⁻¹)
WSI (x 10⁵)
110
100
90
80
70
60
4
5
6
7
8

column (Wetzel, 1983; Carper and Bachmann, 1984). These vortices decrease in strength and diameter with increasing depth. If the wind is sufficiently strong, or the water sufficiently shallow, these vortices become elliptical in shape as the circulations "feel" the sediments. Under such conditions horizontal transport of sediments can occur.

The minimum wind speed necessary to create Langmuir circulations in the water column cited by Wetzel (1983) agrees well with that estimated by Carper and Bachmann (1984). The minimum wind speed necessary to cause sediment resuspension in a shallow (Z_{max}=1.7) Iowa lake was 4 $m \cdot s^{-1}$. Viner and Smith (1973) however, found the critical wind speed to be 12.5 $m \cdot s^{-1}$ at Lake George, Uganda. This large value may be due to the deeper nature of the lake basin, difference in sediment characteristics and the duration of wind storms in this area. Wind storms on Lake George typically last only 1-2 hours while those at Delta Marsh can exceed 24 hours.

The two assumptions concerning 1) the critical wind speed, and 2) the influence of the 24 hour wind prehistory, appear to be valid given the good relationships between the seasonal change in %AC and the concentration of suspended particulates on both a dry and ash weight basis (Fig. 2-3a). Although not based upon a critical wind speed value, Moore (1935) based his estimates of water turbulence on the number of days (per 100) during which onshore winds were blowing.

WSI was also an excellent predictor of the seasonal change in the concentration of suspended particulates (Fig. 2-3b). In addition, WSI accurately predicted suspended particulate concentration on an hourly basis. For example, hourly changes in the concentration of suspended particulates were greatest on May 25 and parallelled changes in WSI.

The effect of water turbulence on sediment resuspension has been reported in a number of aquatic ecosystems. Sediment resuspension has been linked to tidal hydraulics in marine systems (Oretel and Dunstan, 1981), vernal and autumnal turnover in deep lakes (Davis, 1973) and through wind-induced turbulence in shallow water bodies (Davis, 1973; Viner and Smith, 1973; Walmsley et al., 1980; Carper and Bachmann, 1984). Wind-induced water turbulence has been shown to physically disturb sediments down to a sediment depth of 14 cm. (Davis, 1973; Viner and Smith, 1973).

Wetzel (1970) has demonstrated that the influence of wind-induced circulations can be very pronounced. Surface sediments on a submerged lakemount island in a northern Indiana lake were found to be over 2700 years old. Wetzel attributed this age to the continual wave-mediated resuspension of recent surficial sediments from the littoral shelf to deeper areas of the lake.

Wind-induced water turbulence effects underwater light penetration directly and indirectly. Wetzel (1983) states that wave action can increase surface reflectivity, and therefore light attenuation, by up to 20 %. Light attenuation within the water

column is a function of light absorption and light scattering. These in turn are carried out by four components: the water itself, trypton, phytoplankton and the color of the water (Kirk, 1980). Since wind stress has a marked effect on the concentration of suspended particulates, water clarity should also be affected.

Walmsley et al. (1980) found that resuspension of silt by wave action and flooding events strongly affected the secchi disc transparency, turbidity and mean attenuation coefficient in an African impoundment. In a laboratory experiment Jones and Wills (1956) demonstrated the effects of increasing concentrations of kaolin sediment on light extinction. A concentration of only 10 mg·L caused over 80 % extinction. Suspended particulate concentration at Delta marsh varied from 10-70 $mg \cdot L^{-1}$ throughout the sampling season and would therefore be expected to greatly influence water clarity.

Phytoplankton also contribute to light attenuation. Kirk (1973) showed that cell or colony shape and size can greatly influence light attenuation. It should not be surprising, therefore, that light attenuation will be seasonally variable, based on changes in phytoplankton community composition (Kirk, 1980) through changes in cell/colony dimensions and pigment content (Kirk, 1973). However, given the low seasonal biomass ($< 100\ \mu g \cdot L^{-1}$), phytoplankton may not be expected to contribute greatly to light attenuation at Delta marsh.

The seasonal changes in phytoplankton biomass (Fig. 3) do not appear to follow the seasonal decrease in wind stress (%AC, WSI) at Delta marsh. Other factors may have an overriding influence. For example, low biomass in May are likely due to low water temperature. Higher biomass in the summer may reflect optimum water temperature, nutrients and light conditions. The low biomass values on August 9 may be due to low nutrient availability. This has been shown to limit epiphyton biomass during late summer (Hooper-Reid and Robinson, 1978). Based on five assay techniques (protein to carbohydrate and lipid ratios, silica debt, extractable cellular phosphate, alkaline phosphatase activity and, nitrogenase activity) Hooper-Reid and Robinson (1978) concluded that extreme nutrient deficiency was evident for all major nutrients.

Increases in wind stress on an hourly scale elevated phytoplankton biomass by up to 60 % in the water column at Delta marsh (Figs. 2-4a+b). Therefore, on a short time frame the influence of wind-induced turbulence was very marked. The source of this additional biomass was not investigated, but may be twofold. The sediments at Delta Marsh support an extensive community of epipelic algae (Robinson, pers. comm.). Under windy conditions, viable cells may be resuspended from within surficial sediments into the water column. This hypothesis is supported by the work of Ganf (1974) who found that under windy conditions, the sediments could supply a source of viable benthic algae to increase planktonic biomass by 56 %. This increase in biomass could not be accounted for by growth processes alone.

A second source of algae to the plankton of Delta marsh may be from the detachment of epiphytes associated with the large standing crop of Typha sp., Potamogeton pectinatus, Utricularia vulgaris and Myriophyllum spicatum within the marsh. The appearance of typically epiphytic algal species in the plankton due to the dislodgement from their macrophyte host during windy conditions has been reported by Moss (1981) and is a common occurrence in the Delta Marsh (Robinson, pers. comm.).

The fidelity of species to any one community (plankton, epiphyton, epipelon) may be a function of the degree of water turbulence. Sedimentation of cells from the phytoplankton under calm conditions is widely reported (Moss, 1969; Brown and Austin, 1973; Ganf, 1974; Knoechel and Kalff, 1975; Moss, 1981) as well as the appearance of typically benthic species in the plankton under windy conditions. Under wind stressed-conditions algal communities may form more of a continuum rather than existing as discrete entities. This led Sladeckova (1962) to prefer the term psuedoperiphyton to describe periphyton with a planktonic origin.

Wind-induced water turbulence has been a key factor in the lack of recovery of some shallow lakes from cultural eutrophication. The success of a lake recovery program can not only be attributed to sewage/nutrient diversion or treatment plants but also in the contribution of internal phosphorus loading to the overall nutrient budget. Reduced nutrient loading from external sources has been successful as a management tool in deep lakes but rarely is an

adequate solution for shallow, wind-swept lakes (Ryding and Forsberg, 1977). Release of nutrients into the overlying water from nutrient-rich sediments by turbulent mixing can constitiute a large proportion of the nutrient budget in shallow lakes (Petterson and Bostrom, 1984).

2.6 Conclusions

The results of this study suggest that wind-induced water turbulence is an important factor shaping the limnology of Delta marsh. The concentration of suspended particulates in the water column was influenced by both hourly and seasonal changes in wind stress. Phytoplankton was affected by short-term (hourly) changes in wind stress only. Although not quantified in this study, changes in suspended particulate concentration may be expected to have a marked influence on water clarity and therefore the attenuation of light within the water column. This was qualitatively evident in the increased turbidity of the water under wind-stressed conditions.

Chapter 3

The Effect of Water Turbulence on the Limnology of a Shallow, Prairie Wetland: a Manipulative Study Utilizing Enclosures

3.1 Abstract

A field study was conducted in a shallow channel of the Delta Marsh, Canada within small-diameter (1.5 m.), in situ littoral enclosures to determine the effect of artificially-induced water turbulence on physical, chemical and biological features of a shallow wetland. In addition, enclosure effects were monitored and the use of artificially-induced water turbulence as a means of alleviating enclosure effects was evaluated.

Controlled water turbulence within enclosures had a marked effect on suspended particulate concentration and water clarity. Enclosure effects concerning these parameters were severe but were alleviated by induced turbulence. Mean water column temperature was not affected by controlled turbulence while oxygen levels in turbulent enclosures were lower than in control enclosures. Nutrient levels in turbulent enclosures were higher than in control enclosures although inferences concerning enclosure effects on water chemistry or the use of turbulence to alleviate enclosure effects on water chemistry cannot be made due to nutrient loading events that

occurred in all enclosures through the introduction of feces by perching gulls.

Biomass of two algal communities, the phytoplankton and the periphytic community colonizing acrylic substrata, were affected by both water turbulence and nutrient (feces) input. The photosynthetic performance of each algal community was assessed by measuring ^{14}C uptake over a range of light intensities (0-2500 $\mu mole \cdot m^{-2} \cdot s^{-1}$). Photosynthetic parameters (SP_{max}, I_k, α , E_{max}) derived from P vs. I curves collected from 99 productivity experiments indicated that short-term (2 h.) controlled turbulence in enclosures had little effect on algal community photosynthesis.

The use of small-diameter turbulent enclosures appears to provide realistic data when compared to an adjacent marsh while doing so at a fraction of the cost of constructing large-scale enclosures or limnocorrals.

3.2 Introduction

Aquatic mesocosms such as enclosures and limnocorrals have been utilized in a wide variety of studies in order to provide data to either supplement laboratory and ecosystem-level (macrocosm) studies or to provide insight into processes and mechanisms which cannot be easily addressed by laboratory or macrocosm studies. Enclosures bridge the gap between the more controllable and repeatable laboratory studies and the more environmentally realistic

and complex ecosystem manipulations (Odum, 1984). Enclosures and limnocorrals have provided valuable information concerning phytoplankton dynamics, nutrient cycling and the eutrophication and acidification of freshwater lakes. The use of the aquatic mesocosm protocol has also recently been added to the registration process of pesticide products in Canada. Despite its widespread applicability, enclosures have short-comings which must be addressed.

If enclosure studies are to provide environmentally realistic data one must be sure that the effects of isolating the water column, sediments and attendant biota from the adjacent water body is minimal. "Enclosure effects" result from the isolation of a water column in the absence of an experimental treatment and are common to many studies. Some enclosure effects are thought to be a function of the degree of down-scaling of the aquatic environment and the resultant loss of turbulence within the enclosure (Sanders, 1985).

Small-diameter enclosures limit the fetch across the surface of the water (Sanders, 1985) and therefore reduce wind-induced water turbulence within the enclosure. Large-diameter enclosures have been used to eleviate this problem (Lund, 1972; Smyly, 1976; Case, 1978) but are costly to construct and operate. Increased enclosure size also introduces unwanted sampling problems caused by a more heterogeneous environment within the enclosure. A more cost effective way of alleviating the turbulence problem may lie in the use of small diameter enclosures which incorporate a means of controlling water turbulence.

Given the importance of wind-induced turbulence in affecting physical (Walmsley et al., 1980; Carper and Bachmann, 1984; see also Chapter 2), chemical (Ryding and Forsberg, 1977; Petterson and Bostrom, 1984) and biological (Ganf, 1974; see also Chapter 2) parameters in shallow water bodies, the use of enclosures which severely limit or eliminate such turbulence may not yield reliable data. This is particularly crucial in the environmental testing of organic contaminants (e.g. pesticides, dioxins) in the aquatic environment. Is the commonly reported rapid loss of a contaminant from the water column to the sediments (Stephenson and Kane, 1984; Solomon et al., 1985; Gurney and Robinson, 1989) an artifact of enclosure protocol? Does wind-induced turbulence have an effect on the persistence and therefore impact of a contaminant in aquatic ecosystems? The information obtained from such studies is only as good as the assessment protocol that is used.

The objectives of this study are threefold: 1) to determine the effects of artificially-induced water turbulence within small-diameter enclosures on various limnological parameters, 2) to identify enclosure effects by comparing control enclosures to an adjacent body of water, and 3) to evaluate the use of turbulence in alleviating these enclosure effects.

3.3 Methods and Materials

Study Site

The field study utilizing in situ littoral enclosures was conducted in the Blind Channel of the Delta Marsh, located on the south end of Lake Manitoba, Canada (99°19' W, 50°7' N). The duration of the experiment was 5 weeks (July-August, 1989). Water depth at the study site is commonly less than 1 m. Marked changes in water level can however, occur frequently due to invasion of water from Lake Manitoba through connecting channels into Delta Marsh during periods of strong north winds. This necessitated the use of telescoping enclosures capable of accommodating such water level changes.

Enclosure Design

An enlarged (150 cm. diameter, 120 cm. height) version of the telescoping enclosure design described by Goldsborough et al. (1986) was utilized. This version could accommodate water level changes up to 120 cm. The enclosure design consisted of two overlapping PVC tubes (0.15 cm. wall thickness) joined by means of a flexible vinyl curtain. The lower section was slightly smaller (145 vs. 150 cm) in diameter and taller (120 vs. 90 cm.) than the overlapping, upper section. A vinyl curtain was attached to the outside of each section by means of a water-tight Poly Zip (Curry Industries, Winnipeg) tracking (Cruikshank et al., 1983). Six flexible flotation collars (15 cm. diameter, 85 cm. length) were attached to the outside

of the telescoping section to maintain the upper edge of the enclosure 20 cm. above the water surface. This eliminated any dilution effects arising from the addition of water to the enclosure by wave action. Twelve enclosures were constructed and deployed.

Enclosures were transported to the study site separately in a 12 foot aluminum boat, gently lowered into the water, and imbedded into the sediments to a depth of 30 cm. This provided a water-tight seal. Aquatic macrophytes (Potamogeton pectinatus, Myriopyllum spicatum) were removed from the study site prior to enclosure placement and were periodically harvested from enclosures during the experiment as was feasible without disrupting the integrity of the sediments. Total enclosed water volume of each enclosure was approximately 1800 L.

Six enclosures were experimentally manipulated by means of controlled water turbulence. Artificially-induced water turbulence in each experimental enclosure was generated by a 12 volt Proven Pony Pump (Proven Pony Pump Corp., California) located on an adjacent floating raft. Water turbulence was generated by drawing enclosure water from near the sediments and returning it to the surface of the water in the enclosure. Pumps were operated 2 h. each day prior to sampling. Six enclosures served as controls (no turbulence).

The effects of controlled water turbulence on various physical, chemical and biological parameters were monitored weekly throughout the experiment by comparing enclosures with artificially-

induced turbulence to control enclosures. The adjacent marsh was also monitored so that: 1) comparisons of control enclosures and the adjacent marsh would identify any enclosure effects, and 2) comparisons between turbulent enclosures and the adjacent marsh would allow for an assessment of the relative success of the use of artificial turbulence as a means of reducing any enclosure effects.

Physical Parameters

The effect of controlled water turbulence on the physical limnology of Delta Marsh was monitored through examinations of the concentration and organic content of suspended particulates, changes in the underwater light climate, and water temperature. The concentration of suspended particulates was determined from water samples taken from the surface of the water of each replicate enclosure using 4 L. plastic jugs. Water samples from the adjacent marsh were not replicated. Triplicate 250 mL. subsamples were filtered onto ignited (16 h. @ 550°C.) Whatman GFC filters. Filters were dried in an oven (approx. 12 h. @ 105°C.) and weighed on a Cahn Gram Electrobalance to give dry weight measurements ($mg \cdot L^{-1}$). Samples were then ignited in a Fisher muffle furnace (1 h. @ 550°C.) to give ash weight measurements ($mg \cdot L^{-1}$). The organic content of the particulates (expressed as a percentage of the original dry weight) was detrermined by the equation

$$\% \text{ Organic} = \frac{(\text{Dry weight} - \text{Ash weight})}{\text{Dry weight}} \times 100$$

Changes in the underwater light climate was assessed by two parameters. Turbidity of triplicate water samples was measured using a DRT-15B turbidimeter (H.F. Instruments). Turbidity was expressed as Nephalometric Turbidity Units (NTU). In addition to turbidity, underwater light penetration was estimated by determination of the light extinction coefficient. Light profiles were constructed from P.A.R. irradiance values ($\mu mole \cdot m^{-2} \cdot s^{-1}$) recorded at 5 cm. intervals from the water surface to the sediments using a LiCor cosine-corrected quantum sensor attached to a LiCor Data Logger. Two quantum sensors were used: a surface (deck) unit and an underwater unit. Irradiance values at depth were standardized to a percentage of the surface illumination. The light extinction coefficient (m^{-1}) was determined as the slope of the lnI vs. depth plot. Correlation coefficients (r^2) were never less than 0.88.

Water temperature was recorded at 5 cm. intervals from the water surface to the sediments using a YSI 51B temperature/oxygen meter. Since water temperature was nearly constant from the surface to the sediments, only mean water column temperatures are compared.

Chemical Parameters

The effect of water turbulence on the chemical environment was monitored through weekly examinations of dissolved oxygen and nutrient levels in the water column. Dissolved oxygen was measured at 5 cm. intervals in the water column using a YSI 51B temperature/oxygen meter. Mean water column oxygen

concentration ($mg \cdot L^{-1}$) was calculated from oxygen values in the upper 50 cm. of the water column to avoid low oxygen levels near the sediments. Concentration of nutrients (soluble reactive phosphorus, particulate phosphorus, ammonia and dissolved reactive silicon) were determined spectrophotometrically following the methods of Stainton et al. (1968) from triplicate surface water subsamples.

Biological Parameters

The effects of turbulence on biological parameters was monitored through weekly examinations of algal biomass and productivity. Two algal communities were studied: periphyton colonizing artificial substrata and the phytoplankton. The artificial substrata employed were extruded acrylic rods (Goldsborough and Robinson, 1983).

Twelve acrylic rods (0.6 cm. diameter, 90 cm. length) were vertically positioned in each enclosure and the adjacent marsh 10 days prior to periphyton biomass and productivity sampling. This period of time allowed for adequate colonization of the rods by periphytic algae. Rods were pushed 20 cm. into the sediments to provide anchorage. Substrata were prescored at 2 cm. intervals with a hacksaw to facilitate subsampling. Each rod segment had a surface area of 4.2 cm^2. Sampling was accomplished by snapping off segments from the rods using needle-nosed pliers.

Algal Biomass

Periphyton biomass (μg chlorophll a· cm^{-2}) was monitored weekly from weeks 2-5. Eight rods segments were sampled from 2 randomly chosen acrylic rods from each enclosure and the adjacent marsh. Rod segments positioned 30-70 cm. below the surface of the water were placed individually into 20 mL. polyethylene vials and frozen within 1 h. of sampling until chlorophyll a (CHLA) extractions were performed. CHLA was extracted overnight in 90 % methanol and analyzed after the method of Lorenzen (1967) as described by Marker et al. (1981). CHLA values were corrected for phaeophytin.

Phytoplankton biomass (μg CHLA·L^{-1}) was monitored weekly by filtering 250 mL. water samples onto Whatman GFC filters. Five replicates were used per enclosure. Filters were frozen immediately until CHLA extraction was performed. Extraction procedures were identical to those described for the periphyton community.

Primary Productivity Experiments

Primary productivity experiments were conducted weekly for both algal communities. Experiments were conducted in a water filled incubator which allowed for a range of light intensities. A high-pressure sodium lamp (Sylvania LU70) was used to generate P.A.R. intensities up to 2500 μmole·m^{-2}·s^{-1}. A LiCor spherical quantum sensor attached to a LiCor Data Logger was used to measure light intensities.

Periphyton productivity estimates were made from twelve rod segments from two randomly chosen rods per enclosure. Eight rod segments were incubated at different light intensities while four rod segments served as dark controls. Each rod segment was placed into 20 mL. of filtered (Whatman GFC) enclosure/marsh water and injected with 0.5 mL. of standardized $NaH^{14}CO_3$. Incubations were 2 h. in duration. Incubator water temperature varied between weeks (23-27°C.).

Phytoplankton productivity estimates were made from eight 20 mL. light incubated samples per enclosure and four dark incubated samples per enclosure.

Following incubation, samples were filtered onto membrane filters (25 mm diameter, 0.45 µm pore size) and rinsed with distilled water. Filters (and colonized rod segments in the case of the periphyton) were fumed over concentrated HCl for one minute to remove residual inorganic ^{14}C and placed in vials containing scintillation fluor. A Beckman LS3801 scintillation counter with H-Number quench correction was used to determine sample radioactivity. ^{14}C assimilation rates were calculated by the equation:

$$\mu g\ C\ fixed \cdot cm^{-2}\ or\ L^{-1} \cdot h^{-1} = \frac{DPM(S) \times C \times 1.05}{DPM(T) \times M \times T}$$

where

DPM(S) = specific radioactivity of sample, corrected for dark uptake
DPM(T) = specific radioactivity added to the sample

C = total inorganic carbon in incubation water derrived from alkalinity (APHA, 1980), pH and temperature
1.05 = ^{14}C discrimination factor
M = area (cm^2) for periphyton or volume (L) for phytoplankton
T = incubation time (h).

Specific productivities (μg C fixed$\cdot(\mu g$ CHLA$)^{-1}\cdot h^{-1}$) were calculated by dividing gross productivity values by the CHLA content of the community. Photosynthesis/irradiance (P vs. I) curves were generated using the nonlinear regression model described by Platt et al. (1980) and the standardized specific productivities. Several photosynthetic parameters were obtained from this analysis. These include maximum specific productivity (SP_{max}), the light intensity at SP_{max} (I_k), the initial slope of the P vs. I curve (α) and maximum photosynthetic efficiency (E_{max}). In addition, maximum productivity (P_{max}) was calculated from the product of SP_{max} and CHLA content.

A t-test was used to compare the two enclosure treatments: turbulent enclosures and control enclosures with respect to the various limnological parameters. Two enclosures developed tears in the vinyl curtain during the experiment. Data from these enclosures were not used in the analysis so that there were only 5 replicate enclosures per enclosure treatment. The adjacent marsh could not be statistically compared to the two enclosure treatments using a t-test since marsh samples were not replicated.

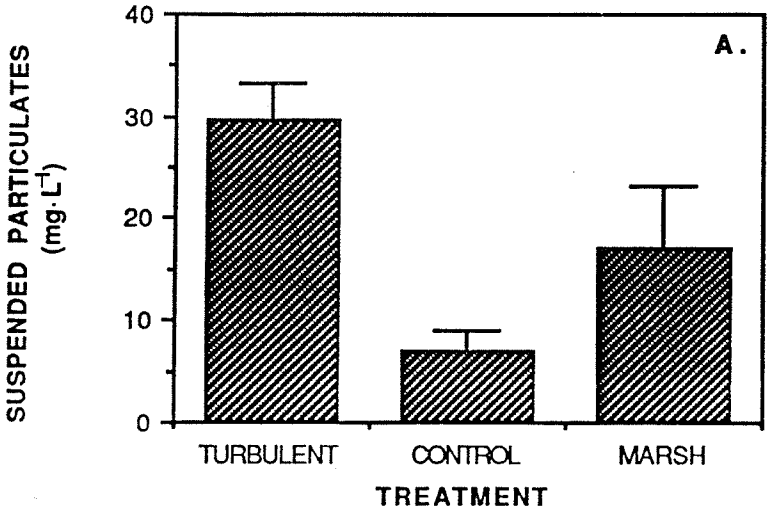
3.4 Results

Water turbulence had a pronounced effect on the concentration of suspended particulates (expressed as dry weight·L^{-1}) in the water column (Fig. 3-1a). Dry weight of suspended particulates throughout the experiment was significantly higher in turbulent enclosures than in control enclosures throughout the experiment (Table 3-1). The concentration of particulates in the adjacent marsh was also higher than in control enclosures (Fig. 3-1a) and was related to the degree of wind stress (%AC and WSI; see Chapter 2) on the marsh (%AC vs. dry weight r^2=0.80, n=5; WSI vs. dry weight r^2=0.68, n=5).

Although the concentration of suspended particulates was much lower in the control enclosures than in the adjacent marsh, the organic content of the particulates was almost identical (Fig. 3-1b). The organic content of the suspended particulates from control enclosures and the adjacent marsh was rarely less than 60 %. In contrast, the organic content of the suspended particulates in the turbulent enclosures rarely exceeded 35 %.

Controlled water turbulence also had a marked effect on water clarity in enclosures. Turbidity of water in turbulent enclosures was consistently higher than in control enclosures throughout the experiment (Table 3-1; Fig. 3-2a), on one occasion up to 10 times higher. Turbidity in the adjacent marsh varied between weeks, the mean value falling between that of the turbulent and control enclosures. Water turbulence had a less pronounced effect on light extinction than on turbidity (Fig. 3-2b). Light extinction values from

Fig. 3-1. a) Mean concentration and b) organic content of suspended particulates at Delta Marsh in two enclosure treatments and the adjacent marsh averaged over the experiment. Vertical bars are the SE of the mean.


A.
SUSPENDED PARTICULATES
(mg·L⁻¹)
40
30
20
10
0
TURBULENT
CONTROL
MARSH
TREATMENT

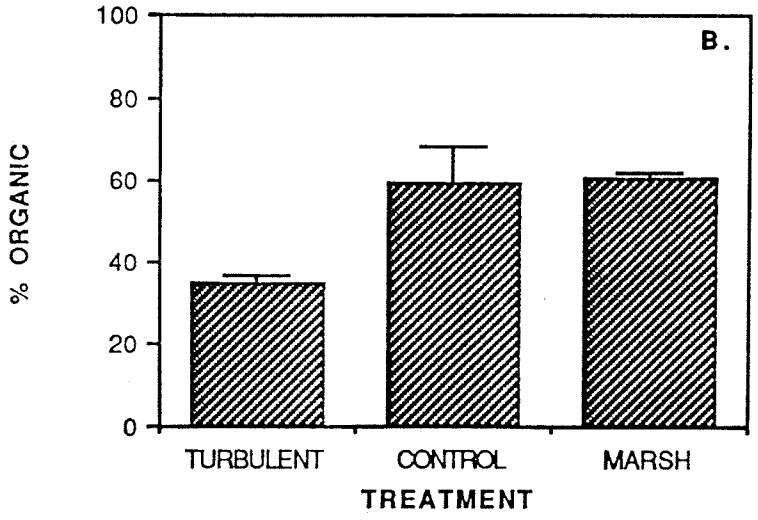
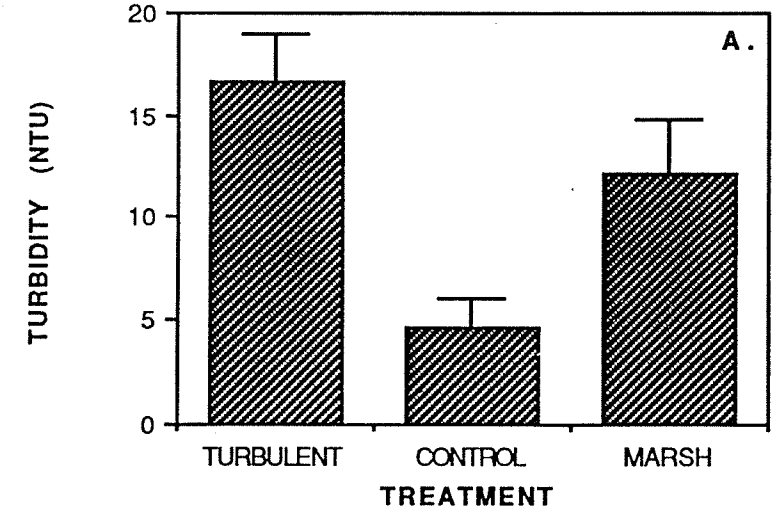

B.
% ORGANIC
100
80
60
40
20
0
TURBULENT
CONTROL
MARSH
TREATMENT

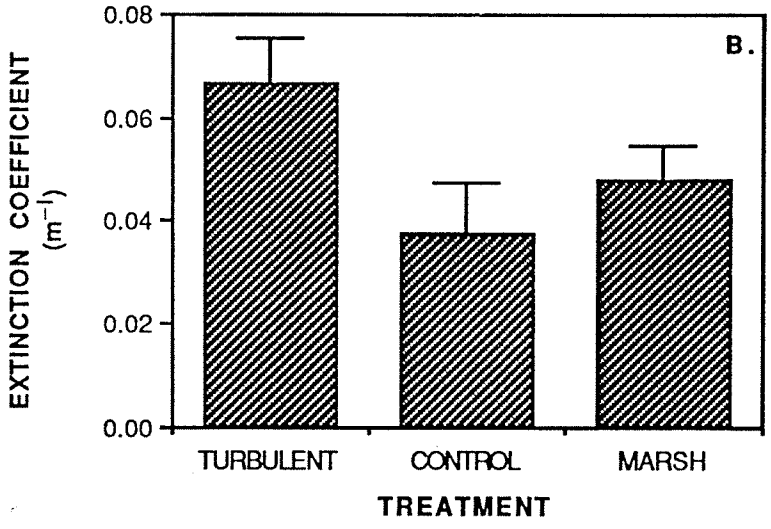
Table 3-1. Comparison of t and p values with their associated degrees of freedom for various physical parameters obtained from t-tests comparing turbulent and control enclosures at Delta Marsh.

	Suspended Particulates			Organic Content			Turbidity			Extinction Coefficient			Water Temp.		
WEEK	t	p	df	t	p	df	t	p	df	t	p	df	t	p	df
1	12.74	.001	8	14.50	.001	8	-	-	-	-	-	-	-	-	-
2	3.85	.004	8	-	-	-	1.98	.07	8	3.23	.01	8	2.13	.06	8
3	3.32	.01	8	2.94	.02	8	3.51	.007	8	3.31	.01	8	3.79	.005	8
4	2.59	.03	8	3.76	.005	8	3.18	.01	8	2.23	.05	8	1.00	.35	8
5	2.31	.05	8	.14	.88	8	2.37	.04	8	2.62	.03	8	0.00	1.00	8

Units:
Suspended Particulates ($mg.L^{-1}$)
Organic Content (%)
Turbidity (NTU)
Extinction Coefficient (m^{-1})
Water Temperature (^{o}C)

Fig. 3-2. The effect of water turbulence on a) turbidity, and b) light extinction at Delta Marsh in two experimental enclosure treatments and the adjacent marsh averaged over the experiment. Vertical bars are the SE of the mean.


A.
TURBIDITY (NTU)
20
15
10
5
0
TURBULENT
CONTROL
MARSH
TREATMENT


B.
EXTINCTION COEFFICIENT
(m⁻¹)
0.08
0.06
0.04
0.02
0.00
TURBULENT
CONTROL
MARSH
TREATMENT

turbulent enclosures were only slightly higher than those from control enclosures (Table 3-1). Light extinction values in the adjacent marsh were more similar to those of turbulent enclosures than from control enclosures.

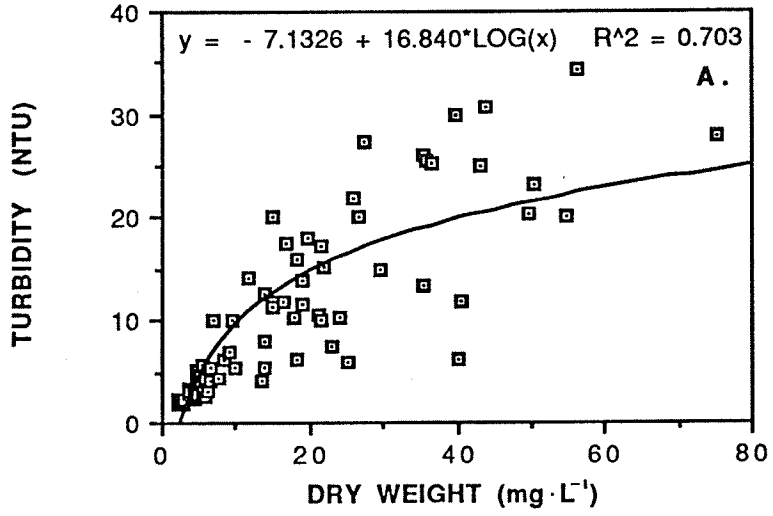
Figs. 3-3a+b show the relationships between the concentration of suspended particulates and either turbidity or light extinction. A good curvilinear relationship existed between suspended particulates and turbidity (r^2=0.70, Fig. 3-3a) while the relationship between suspended particulate concentration and light extinction was weaker (r^2=0.29).

Water turbulence had no effect on mean water column temperature between turbulent and control enclosures (Table 3-1) except during week 3. However, temperature differed by only 1° C. and this difference would not be expected to be biologically significant. Water temperature in the adjacent marsh was similar to that of both enclosure treatments.

Oxygen concentrations in turbulent enclosures were lower than in control enclosures (Table 3-2) rarely exceeding 6.0 $mg \cdot L^{-1}$ while that in control enclosures reached 11.5 $mg \cdot L^{-1}$. Despite the varying degree of turbulence in the adjacent marsh, mean oxygen levels were similar to control enclosures.

The effect of water turbulence on water chemistry was less pronounced than on the physical parameters outlined. External nutrient loading events encountered in all enclosures during a three day period between weeks 2-3 necessitate the description of not

Fig. 3-3. Curvilinear relationships between a) suspended particulate concentration and turbidity, and b) suspended particulate concentration and light extinction. Data from the two enclosure treatments were combined with data from the adjacent marsh.


y = - 7.1326 + 16.840*LOG(x) R^2 = 0.703
A.
TURBIDITY (NTU)
DRY WEIGHT (mg·L⁻¹)
0
10
20
30
40
0
20
40
60
80

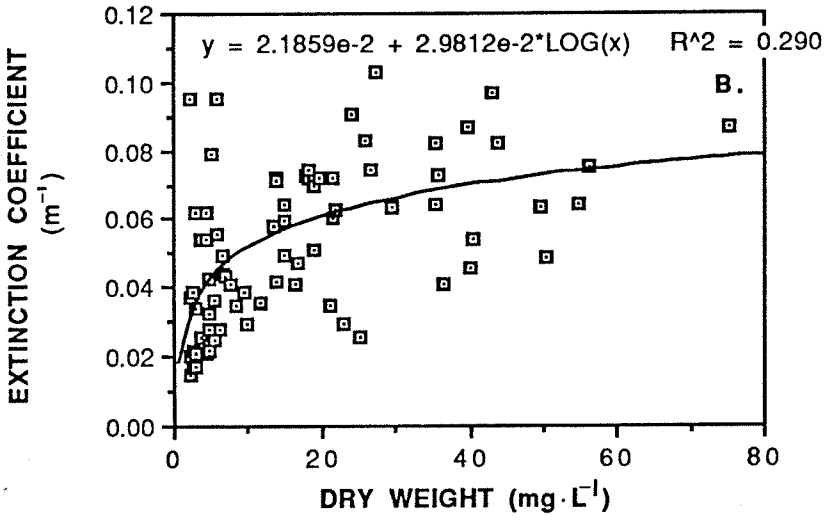

y = 2.1859e-2 + 2.9812e-2*LOG(x) R^2 = 0.290
B.
EXTINCTION COEFFICIENT (m⁻¹)
DRY WEIGHT (mg·L⁻¹)
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0
20
40
60
80

Table 3-2. Comparison of t and p values with their associated degrees of freedom for various chemical parameters obtained from t-tests comparing turbulent and control enclosures at Delta Marsh.

	Oxygen			Soluble Phosporus			Ammonia			Particulate Phosphorus			Silicon		
WEEK	t	p	df	t	p	df	t	p	df	t	p	df	t	p	df
1	-	-	-	1.00	.35	8	2.65	.03	8	.91	.39	8	.99	.35	8
2	3.26	.01	8	1.89	.09	8	2.00	.07	8	1.94	.08	8	2.45	.03	8
3	2.10	.06	8	1.63	.14	8	.77	.46	8	1.65	.13	8	3.05	.01	8
4	2.20	.06	8	2.76	.02	8	2.27	.05	8	1.68	.13	8	1.99	.08	8
5	3.66	.006	8	.42	.68	8	1.44	.18	8	2.46	.04	8	2.40	.04	8

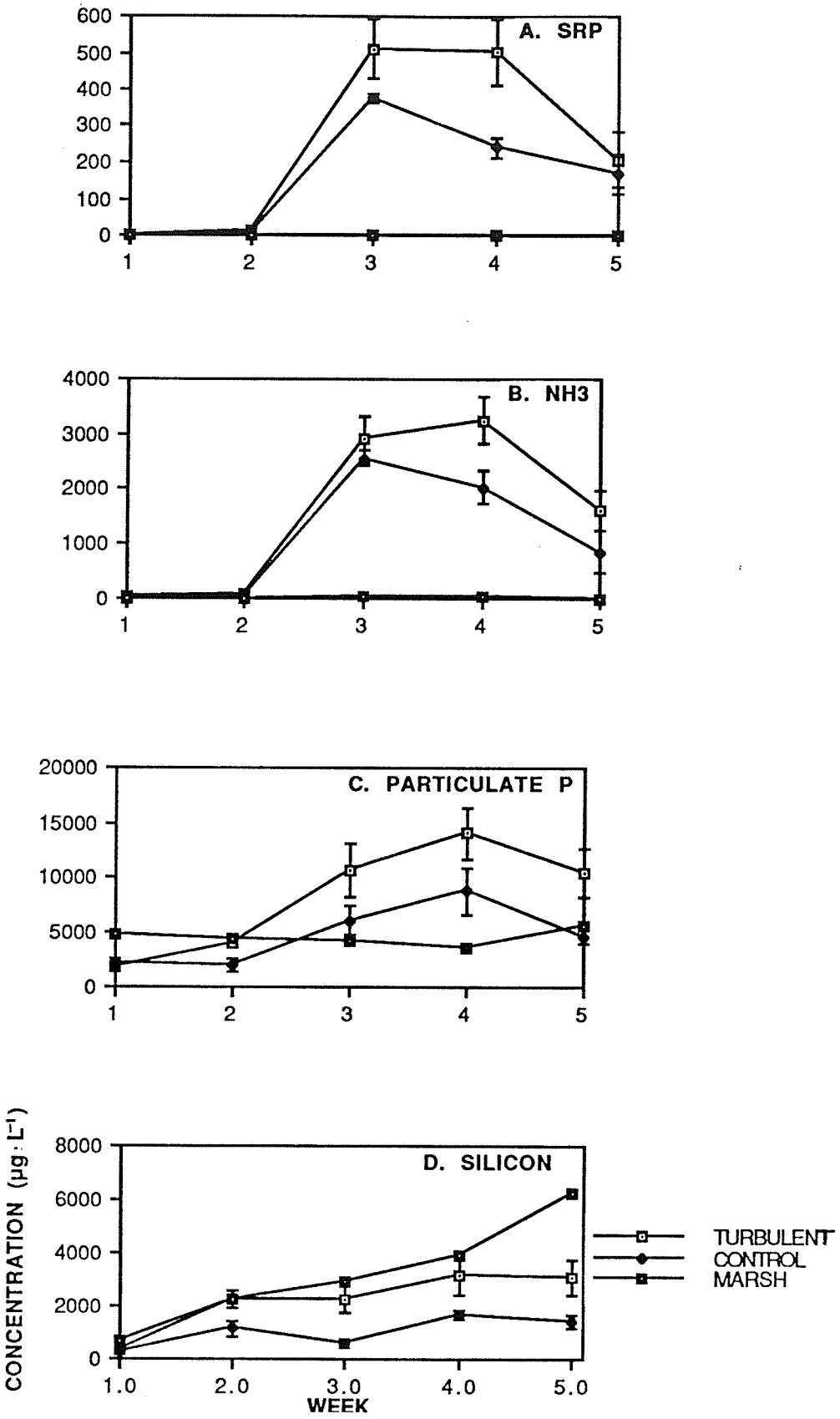
Units:
Oxygen ($mg.L^{-1}$)
Other nutrients ($\mu g \cdot L^{-1}$)

only the absolute differences in nutrient levels between enclosure treatments but also the temporal change in nutrient levels throughout the experiment.

Levels of soluble reactive phosphorus (SRP) were low (<10 $\mu g \cdot L^{-1}$) in all treatments during the first two weeks of the experiment (Fig. 3-4a). However, by week 3 levels of SRP in turbulent enclosures increased to a maximum of 512.0 $\mu g \cdot L^{-1}$. A similar trend occurred in the control enclosures although the peak in SRP was lower (375.5 $\mu g \cdot L^{-1}$). During this period of rapid increase in SRP levels, gulls were observed perching on wooden stakes within all enclosures. Introduction of feces into the enclosures by the gulls was also visibly apparent. Stakes were immediately broken off at the waters surface to remove the perch sites. Levels of SRP in turbulent and control enclosures declined by week 5 to approximately 200 $\mu g \cdot L^{-1}$. Levels of SRP in turbulent enclosures were always higher than in control enclosures throughout the experiment, although these differences were rarely significant at the 0.05 level (Table 3-2). In contrast to SRP levels in the enclosures, concentrations of SRP in the adjacent marsh rarely exceeded 2.0 $\mu g \cdot L^{-1}$ (Fig. 3-4a).

The temporal change in ammonia (NH_3) levels in the enclosures paralelled that of SRP (Fig. 3-4b). The concentration of NH_3 in turbulent enclosures was low during the first two weeks of the experiment and then increased sharply to maximum (3246.0 $\mu g \cdot L^{-1}$) levels during week 4. NH_3 levels decreased during week 5. Temporal changes in NH_3 in control enclosures followed a pattern

Fig. 3-4. Temporal changes in a) soluble reactive phosphorus (SRP), b) ammonia (NH_3), c) particulate phosphorus, and d) silicon levels in the water column of two enclosure treatments and the adjacent marsh at Delta Marsh. Vertical bars are the SE of the mean.


A. SRP
600
500
400
300
200
100
0
1
2
3
4
5
B. NH3
4000
3000
2000
1000
0
C. PARTICULATE P
20000
15000
10000
5000
D. SILICON
8000
6000
4000
2000
CONCENTRATION (µg·L⁻¹)
1.0
2.0
3.0
4.0
5.0
WEEK
TURBULENT
CONTROL
MARSH

similar to turbulent enclosures. NH_3 levels in control enclosures were always less than those in turbulent enclosures (Fig. 3-4b) although these differences were rarely significant at the 0.05 level (Table 3-2). Levels of NH_3 in the adjacent marsh did not exceed 25 $\mu g \cdot L^{-1}$.

Temporal changes in the concentration of particulate phosphorus (PP) in enclosures (Fig. 3-4c) paralleled changes in both SRP and NH_3. Again, PP concentrations in turbulent enclosures were consistantly higher than in control enclosures although the differences were not statistically significant at the 0.05 level (Table 3-2). Maximum PP levels of 14062.7 and 8807.8 $\mu g \cdot L^{-1}$ were found in turbulent and control enclosures respectively in week 4. PP levels in the adjacent marsh remained between 4000-5000 $\mu g \cdot L^{-1}$ throughout the experiment and were not statistically different from either enclosure treatment.

Concentrations of silicon (Fig. 3-4d) in turbulent and control enclosures generally increased throughout the experiment reaching maximum levels of 3208.8 and 1675.8 $\mu g \cdot L^{-1}$ respectively by week 4. Levels decreased slightly in week 5. As with the other nutrients, silicon levels were higher in turbulent enclosures than in control enclosures, and these differences were statistically significant at the 0.05 level (Table 3-2) on several ocassions. Concentrations of silicon in the adjacent marsh increased throughout the experiment (Fig. 3-4d), reaching a maximum of 6241.3 $\mu g \cdot L^{-1}$ by week 5. Levels of silicon in the adjacent marsh were much higher than control enclosures but similar to levels in turbulent enclosures.

The temporal changes in phytoplankton biomass are shown in Fig. 3-5a. Biomass was low (5.3 μg CHLA·L^{-1}) in turbulent enclosures during week 1 and increased to reach a maximum level by week 5 (273.2 μg CHLA·L^{-1}). Mean phytoplankton biomass in control enclosures increased throughout the experiment at a much lower rate, attaining a maximum of 45.7 μg CHLA·L^{-1} by week 5. Although not always statistically higher (Table 3-3), phytoplankton biomass in turbulent enclosures was generally higher than in control enclosures throughout the experiment. Phytoplankton biomass in the adjacent marsh was variable throughout the experiment. Biomass was 53.1 μg CHLA·L^{-1} during week 1, decreased to < 10 μg CHLA·L^{-1} during weeks 2 and 3 and then increased to 40.8 μg CHLA·L^{-1} by week 5.

Biomass of periphytic algae colonizing artificial substrata (Fig. 3-5b) in turbulent enclosures increased throughout the experiment from near-undetectable levels in week 2 (< 0.5 μg CHLA·cm^{-2}) to a maximum of 24.6 μg CHLA·cm^{-2} during week 4. Periphytic biomass then decreased slightly to 21.7 μg CHLA·cm^{-2} by week 5. Periphytic biomass accumulation in control enclosures followed a similar pattern to that of the periphyton in turbulent enclosures, reaching a maximum biomass accumulation in week 5 (21.7 μg CHLA·cm^{-2}). Periphyton biomass was generally higher in turbulent enclosures than in control enclosures, although these differences were rarely statistically significant at the 0.05 level (Table 3-4) except during week 4. Net biomass accumulation of periphyton in control enclosures was identical to turbulent enclosures by week 5. Periphyton biomass in the adjacent marsh increased at a much lower

Fig. 3-5. Temporal changes in a) phytoplankton and b) periphyton biomass in two enclosure treatments and the adjacent marsh in Delta Marsh over a 5 week period. Vertical bars are the SE of the mean.

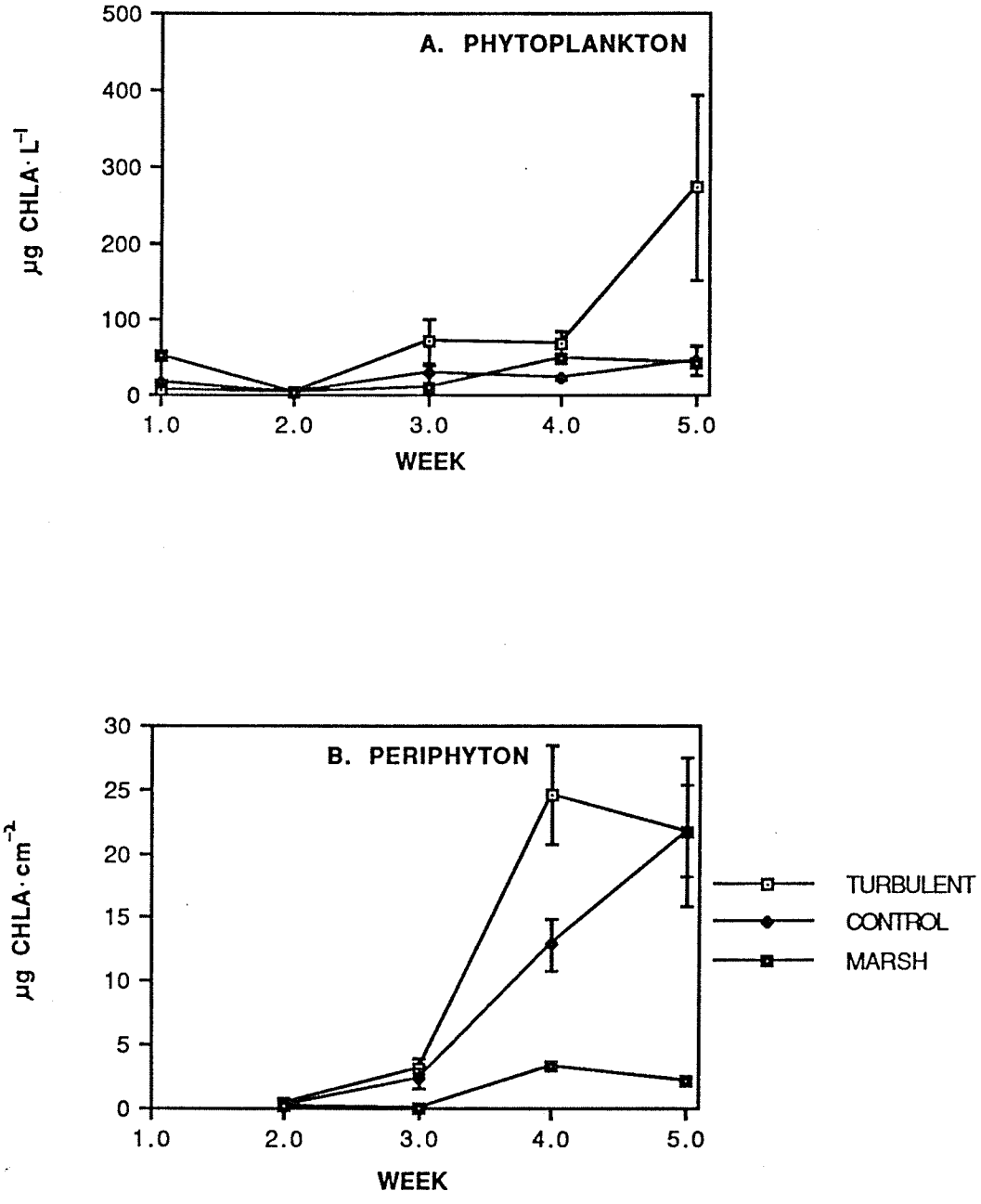

A. PHYTOPLANKTON
μg CHLA·L⁻¹
500
400
300
200
100
0
1.0
2.0
3.0
4.0
5.0
WEEK
B. PERIPHYTON
μg CHLA·cm⁻²
30
25
20
15
10
5
0
1.0
2.0
3.0
4.0
5.0
WEEK
TURBULENT
CONTROL
MARSH

Table 3-3. Comparison of t and p values with their associated degrees of freedom for various parameters of the phytoplankton community obtained from t-tests comparing turbulent and control enclosures at Delta Marsh.

	Biomass			P_{max}			SP_{max}			I_k			Alpha		
WEEK	t	p	df	t	p	df	t	p	df	t	p	df	t	p	df
1	1.99	.08	8	1.02	.34	7	.17	.87	7	2.22	.03	7	.75	.24	7
2	.91	.39	8	1.01	.42	2	.30	.78	2	.43	.35	2	.55	.32	2
3	1.19	.27	8	1.28	.24	8	.33	.75	8	.36	.36	8	.33	.37	8
4	2.65	.02	8	1.66	.15	6	1.97	.09	6	.53	.31	6	2.27	.03	6
5	1.85	.01	8	2.35	.05	6	.10	.93	6	1.61	.08	6	1.53	.09	6

Units:
Biomass ($\mu g\ Chla \cdot L^{-1}$)
P_{max}: maximum photosynthetic rate ($\mu g\ C \cdot L^{-1} \cdot h^{-1}$)
SP_{max}: maximum specific productivity ($\mu g\ C \cdot (\mu g\ Chla)^{-1} \cdot h^{-1}$)
I_k: light intensity at which SPmax is attained ($\mu mole \cdot m^{-2} \cdot s^{-1}$)
Alpha: initial slope of the P vs I curve ($\mu g\ C \cdot (\mu g\ Chla)^{-1} \cdot h^{-1} \cdot (\mu mole \cdot m^{-2} \cdot s^{-1})^{-1}$)

Table 3-4. Comparison of t and p values with their associated degrees of freedom for various parameters of the periphyton community obtained from t-tests comparing turbulent and control enclosures at Delta Marsh.

	Biomass			P_{max}			SP_{max}			I_k			Alpha		
WEEK	t	p	df	t	p	df	t	p	df	t	p	df	t	p	df
1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	1.32	.22	8	1.54	.22	3	.14	.89	3	.21	.42	3	.37	.37	3
3	.67	.52	8	.30	.77	8	1.15	.28	8	.15	.44	8	1.26	.12	8
4	2.70	.03	8	1.30	.23	8	2.42	.04	8	1.13	.14	8	1.09	.15	8
5	.62	.56	8	1.69	.13	8	.74	.48	8	.40	.35	8	.41	.34	8

Units:
Biomass ($\mu g\ Chla \cdot cm^{-2}$)
P_{max}: maximum photosynthetic rate ($\mu g\ C \cdot cm^{-2} \cdot h^{-1}$)
SP_{max}: maximum specific productivity ($\mu g\ C \cdot (\mu g\ Chla)^{-1} \cdot h^{-1}$)
I_k: light intensity at which SPmax is attained ($\mu mole \cdot m^{-2} \cdot s^{-1}$)
Alpha: initial slope of the P vs I curve ($\mu g\ C \cdot (\mu g\ Chla)^{-1} \cdot h^{-1} \cdot (\mu mole \cdot m^{-2} \cdot s^{-1})^{-1}$)

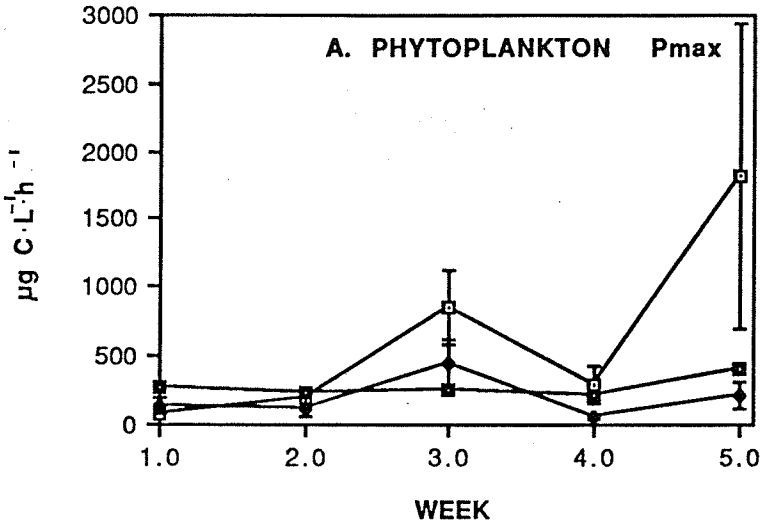
rate than in either enclosure treatment (Fig. 3-5b), never exceeding a level of 4.0 μg CHLA·cm^{-2}.

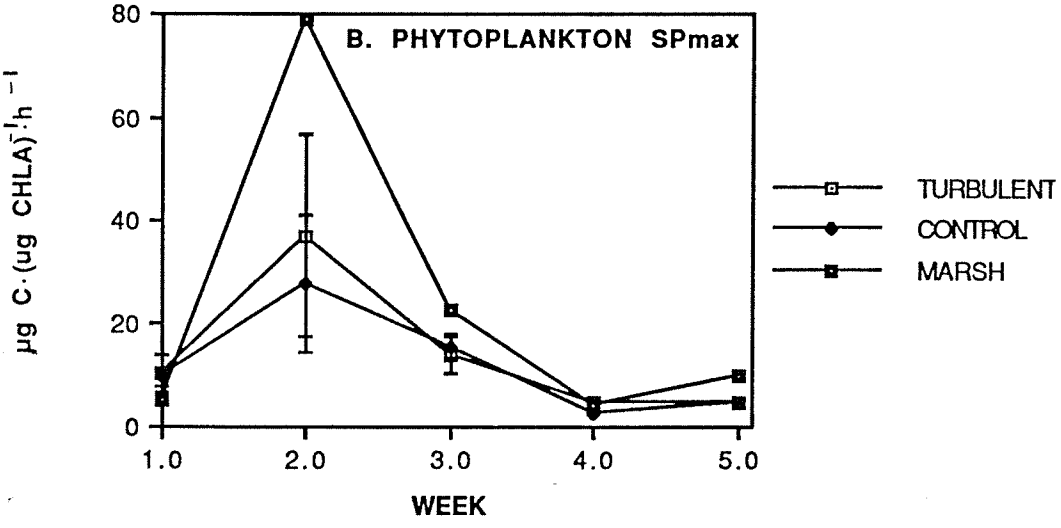
Figs. 3-6 to 3-8 summarize the differences in the various photosynthetic parameters obtained from the curvilinear P vs. I plots. A total of 55 P vs. I plots were examined for the phytoplankton community, 44 of which could be used to obtain estimates of the photosynthetic parameters. Eleven of these plots did not fit the curvilinear criteria of the model used and therefore, estimates of the photosynthetic parameters could not be made. Similarly, 6 of 44 plots could not be used to obtain estimates of the photosynthetic parameters for the periphyton community.

Fig. 3-6a depicts the temporal change in P_{max} for the phytoplankton community between treatments. With the exception of week 4, P_{max} in turbulent enclosures increased from 70.92 to a maximum of 1821.3 μg C·L^{-1}·h^{-1} during week 5, following closely the trend in biomass (Fig. 3-5a). P_{max} of the phytoplankton community from control enclosures peaked at 443.69 μg C·L^{-1}·h^{-1} during week 3, decreasing thereafter. P_{max} was generally higher in turbulent enclosures than in control enclosures throughout the experiment although the differences were not statistically significant at the 0.05 level (Table 3-3). P_{max} of the phytoplankton community in the adjacent marsh was relatively constant at 200-300 μg C·L^{-1}·h^{-1} throughout the experiment, similar to both enclosure treatments.

The phytoplankton SP_{max} curves are very different from the P_{max} curves (Fig. 3-6b). SP_{max} reached a peak during week 2 in all

Fig. 3-6. Temporal changes in a) maximum photosynthesis (P_{max}) and b) maximum specific photosynthesis (SP_{max}) of the phytoplankton communities in two enclosure treatments and the adjacent marsh over a 5 week period. Vertical bars are the SE of the mean.


A. PHYTOPLANKTON Pmax
3000
2500
2000
1500
1000
500
0
µg C·L⁻¹·h⁻¹
1.0
2.0
3.0
4.0
5.0
WEEK

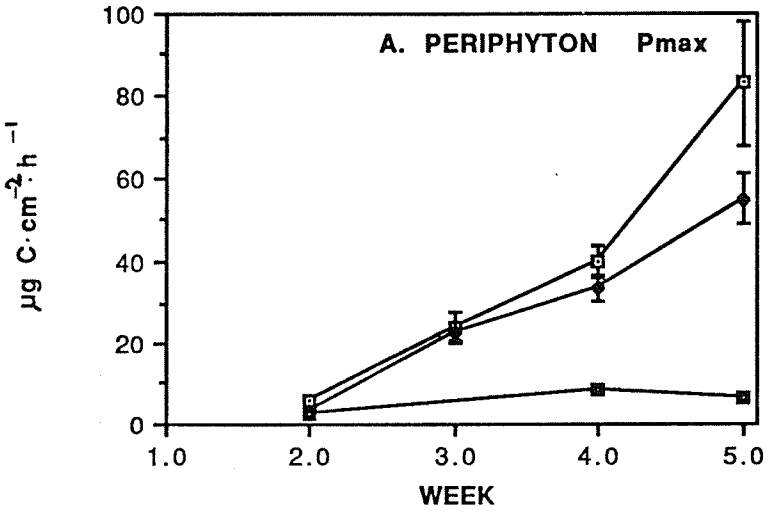

B. PHYTOPLANKTON SPmax
80
60
40
20
0
µg C·(ug CHLA)⁻¹·h⁻¹
1.0
2.0
3.0
4.0
5.0
WEEK
TURBULENT
CONTROL
MARSH

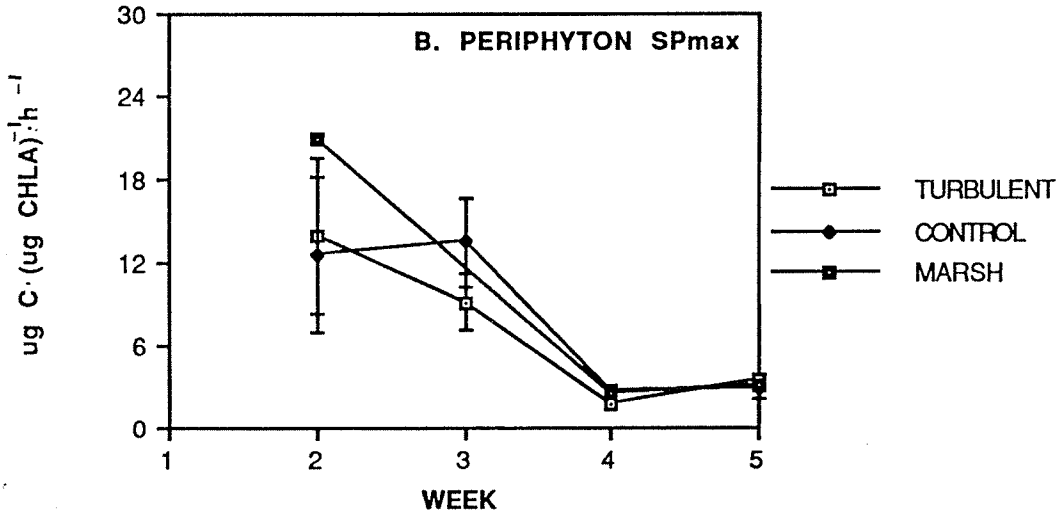
treatments, decreasing thereafter. Phytoplankton SP_{max} was generally higher in turbulent enclosures compared to control enclosures. Highest phytoplankton SP_{max} (79.06 µg C·(µg CHLA)$^{-1}$·h^{-1}) was attained by the community of the adjacent marsh during week 2.

Fig. 3-7a depicts the temporal change in P_{max} of the periphyton community throughout the experiment. The increase in P_{max} throughout the experiment parallels that of the periphyton biomass curves. Periphyton P_{max} in turbulent enclosures increased from 5.98 (week 1) to 82.94 µg C·cm^{-2}·h^{-1} during week 5. A similar trend is also seen in the control enclosure treatment, although final values were much lower (55.01 µg C·cm^{-2}·h^{-1}). Productivity of the periphyton community of the adjacent marsh remained relatively constant at approximately 5 µg C·cm^{-2}·h^{-1} throughout the experiment.

The temporal change in periphyton SP_{max} (Fig. 3-7b) is also opposite to that of the P_{max} curve. With the exception of the control enclosure treatment during week 3, the highest SP_{max} values are attained during the first sampling period (week 1) and decrease throughout the experiment. Highest SP_{max} for the periphyton in turbulent and control enclosures were very similar (approx. 13.5 µg C·(µg CHLA)$^{-1}$·h^{-1}). While having the lowest P_{max} values, the periphyton community of the adjacent marsh had the highest SP_{max} value of all treatments (20.96 µg C·(µg CHLA)$^{-1}$·h^{-1}). The phytoplankton community of the adjacent marsh also had the highest SP_{max} value (Fig. 3-6b). Specific productivity was generally higher

Fig. 3-7. Temporal changes in a) maximum photosynthesis (P_{max}) and b) maximum specific photosynthesis (SP_{max}) of the periphyton communities in two enclosure treatments and the adjacent marsh over a 4 week period. Vertical bars are the SE of the mean.


A. PERIPHYTON Pmax
µg C·cm⁻²·h⁻¹
100
80
60
40
20
0
1.0
2.0
3.0
4.0
5.0
WEEK


B. PERIPHYTON SPmax
ug C·(ug CHLA)⁻¹·h⁻¹
30
24
18
12
6
0
1
2
3
4
5
WEEK
TURBULENT
CONTROL
MARSH

for all phytoplankton communities than for the periphyton communities.

Fig. 3-8 shows the difference in phytoplankton and periphyton I_k values averaged over the experiment. Mean I_k was identical for phytoplankton from turbulent and control enclosures (452 $\mu mole \cdot m^{-2} \cdot s^{-1}$) while the phytoplankton community from the adjacent marsh had a lower average I_k (303 $\mu mole \cdot m^{-2} \cdot s^{-1}$). Mean I_k of the periphyton community (Fig. 3-8) from the turbulent treatments was slightly lower than from the control enclosures. Mean I_k of the periphyton community from the adjacent marsh was higher than the two enclosure treatments (Fig. 3-8) although a large degree of variation was observed. The periphyton had a lower mean I_k than the phytoplankton communities from the enclosure treatments.

Differences in the initial slope of the P vs. I curves (α) between treatments for the phytoplankton community are shown in Fig. 3-9. A great deal of variation existed within each treatment so that there were no significant differences between treatments (Table 3-3). However, mean α for the marsh community was almost double that of the two enclosure treatment communities. A different trend is seen in the periphyton data (Fig. 3-9) in which all three treatments had similar α values. The phytoplankton communities had a slighly lower initial slope than the periphyton communities.

Maximum photosynthetic efficiency (E_{max}) of the phytoplankton community from the adjacent marsh was almost twice as high as the phytoplankton communities of the other two

Fig. 3-8. The effect of short-term turbulence on I_k (the light intensity at $SP_{max.}$) on the phytoplankton and periphyton communities from two enclosure treatments and the adjacent marsh. Vertical bars are the SE of the mean.

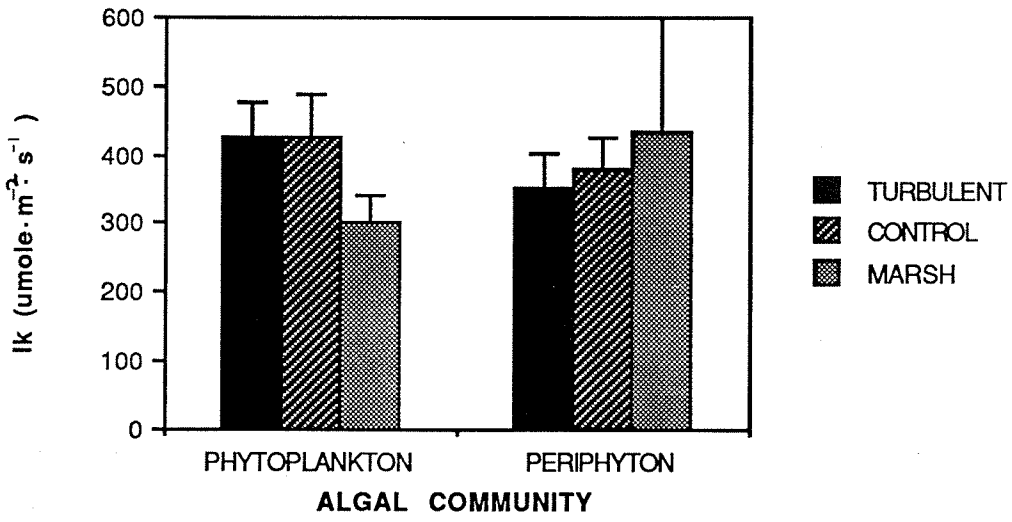
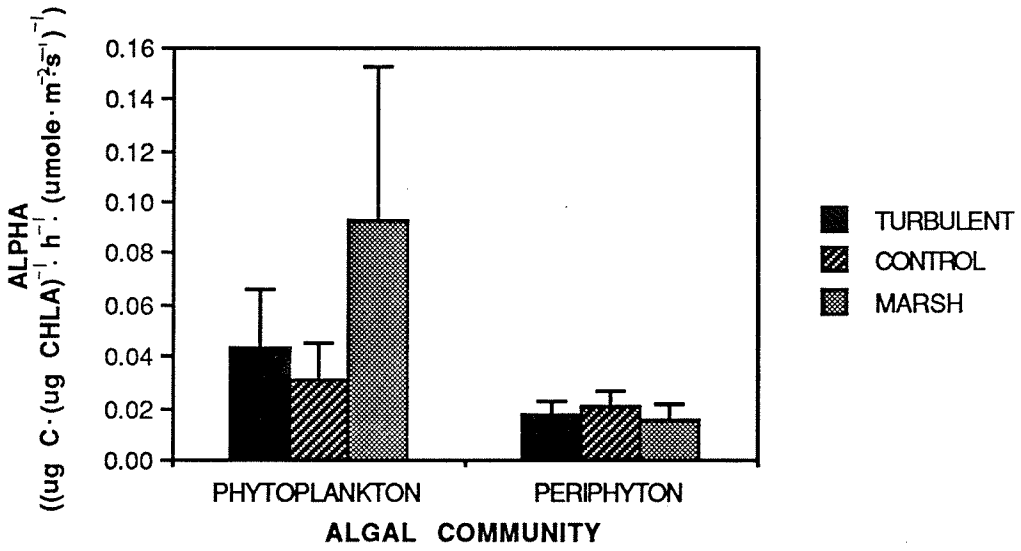

600
500
400
300
200
100
0
Ik (umole·m⁻²·s⁻¹)
PHYTOPLANKTON
PERIPHYTON
ALGAL COMMUNITY
TURBULENT
CONTROL
MARSH

Fig. 3-9. The effect of short-term turbulence on α (the initial slope of the P vs. I curve) on the phytoplankton and periphyton communities from two enclosure treatments and the adjacent marsh. Vertical bars are the SE of the mean.


ALPHA
((ug C·(ug CHLA)$^{-1}$·h^{-1}·(umole·m^{-2}s^{-1})$^{-1}$)
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
PHYTOPLANKTON
PERIPHYTON
ALGAL COMMUNITY
TURBULENT
CONTROL
MARSH

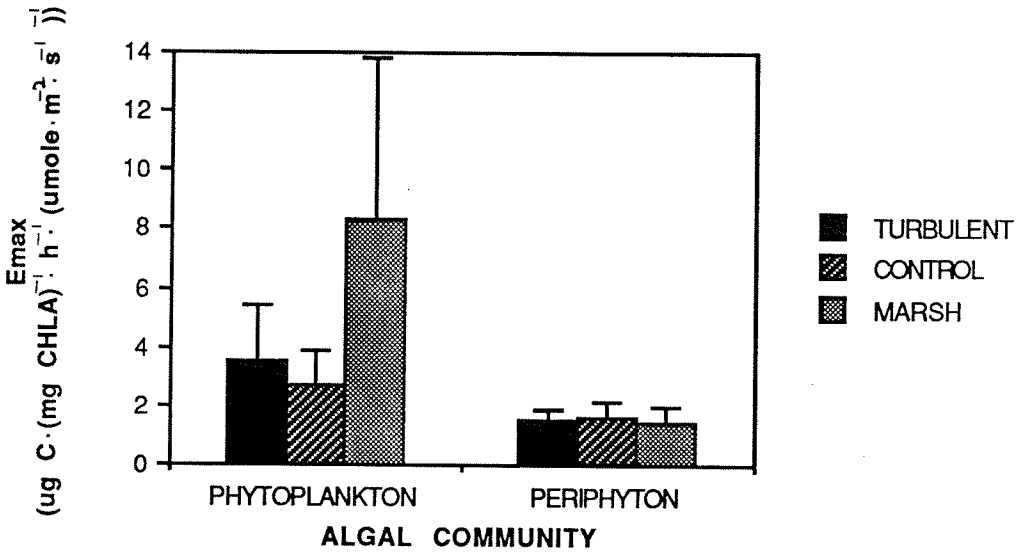
treatments (Fig. 3-10). Average E_{max} of the periphyton communities from the three treatments were almost identical (approx. 1.5 μg $C \cdot (mg\ CHLA)^{-1} \cdot h^{-1} \cdot (\mu mole \cdot m^{-2} \cdot s^{-1})^{-1}$. E_{max} values were generally higher for the phytoplankton communities than the periphyton communities (Fig. 3-10).

Photosynthetic inhibition of the phytoplankton community at high light intensities (> 2000 $\mu mole \cdot m^{-2} \cdot s^{-1}$) was found in 75, 80 and 50 % of the P vs. I curves from the turbulent, control and marsh treatments respectively. Incidence of photosynthetic inhibition of the periphyton communities was substantially lower than for the phytoplankton communities (42, 38 and 0 % for the turbulent, control and marsh treatments respectively).

3.5 Discussion

Water turbulence is known to have a profound influence on the limnology of shallow water bodies. If enclosures are to provide environmentally realistic data, then enclosure effects should be minimal. Given the large costs of constructing large diameter enclosures to alleviate enclosure effects, the use of small enclosures with artificially-induced water turbulence may provide a much more cost-effective alternative. The success of such a protocol is discussed below within the framework of the limnological parameters monitored in this study.

Fig. 3-10. The effect of short-term turbulence on maximum photosynthetic efficiency (E_{max}) of the phytoplankton and periphyton communities from two enclosure treatments and the adjacent marsh. Vertical bars are the SE of the mean.


Emax
(ug C·(mg CHLA)$^{-1}$· h^{-1}· (umole·m^{-2}· s^{-1}))
14
12
10
8
6
4
2
0
PHYTOPLANKTON
PERIPHYTON
ALGAL COMMUNITY
TURBULENT
CONTROL
MARSH

Controlled water turbulence had a marked effect on suspended particulate concentration (Fig. 3-1a). Levels of suspended particulates in turbulent enclosures were up to 5-fold higher than in control enclosures. A severe enclosure effect of suspended particulate concentration was evident. These enclosure effects can be attributed to the loss of water turbulence within control enclosures. Artificially-induced water turbulence in turbulent enclosures alleviated this enclosure effect. The loss of particulates from the water column within enclosures has been widely reported as an enclosure effect and is suggested to be caused by a lack of turbulence (Kuiper, 1977; Twinch and Breen, 1978). Davies and Gamble (1979) have given evidence that vertical eddy diffusivity could be decreased 10-fold by isolation of the water column. Eppley et al. (1978) found that vertical eddy diffusivity was 0.6 $cm^2 \cdot s^{-1}$ in 68 m^3 marine enclosures while values typical for the open sea are 5-50 $cm^2 \cdot s^{-1}$.

Wind has been shown to have a profound influence on water turbulence and therefore, the concentration of suspended particulates (Davis, 1973; Viner and Smith, 1973; Walmsley et al., 1980; Carper and Bachmann, 1984). In an earlier field survey (see Chapter 2) two quantitative expressions of wind stress were highly correlated to the concentration of suspended particulates in the water column at Delta Marsh. The effect of wind stress on suspended particulate concentration is also evident in this study. Suspended particulate concentration in the adjacent marsh was correlated to both %AC and WSI.

In addition to wind-induced turbulence, resuspension of surficial sediments has been linked to tidal hydraulics (Oretel and Dunstan, 1981) and vernal and autumnal turnover in deep lakes (Davis, 1973).

The lower organic content of the suspended particulates (Fig. 3-1b) from turbulent enclosures may be due to the resuspension of deeper-buried, largely inorganic sediments compared to the adjacent marsh. Wind-induced turbulence in the adjacent marsh may only have been capable of resuspending the surficial, organic-rich layer of the sediments.

Water turbulence also had a marked effect on water clarity (Figs. 3-2a+b). An enclosure effect on turbidity was evident. An enclosure effect based on light extinction was less evident. This may be due to difficulties in obtaining accurate light readings in the water column in control enclosures. Reduced water turbulence and increased water clarity in control enclosures favored the growth of aquatic macrophytes (primarily P. pectinatus). Shading of the quantum sensor by the macrophytes may have resulted in artificially high light extinction values in control enclosures, thus reducing the apparent enclosure effect on light attenuation.

Increased light penetration and lower turbidities are commonly reported enclosure effects (Lund, 1972; Kuiper, 1977; Twinch and Breen, 1978; Landers, 1982). Artificially-induced water turbulence in turbulent enclosures eliminated enclosure effects on water clarity with respect to both turbidity and light extinction.

Wind-induced turbulence in shallow water bodies can dramatically alter underwater light penetration and water clarity (Grobbelaar and Stegmann, 1976; Walmsley, 1976; Walmsley et al., 1980; Kirk, 1980; 1985) by increasing the concentration of suspended particulates in the water column. Kirk (1985) has suggested that suspended particulates can greatly reduce the depth of the euphotic zone such that productivity of a water body may be substantially overestimated if based on nutrient availability alone. Changes in water clarity in the present study were directly related to changes in suspended particulate concentration (Figs. 3-3a+b). A good curvilinear relationship existed between suspended particulate concentration and turbidity. The weaker relationship between suspended particulate concentration and light extinction may be a function of high light extinction values at low suspended particulate concentrations in control enclosures.

Water turbulence had no effect on mean water temperature between turbulent and control enclosures. This would be expected since the change in water transparency in turbulent enclosures was only short-term and thus heat uptake by enclosure water would not change substantially within this period. Mean water column temperature was similar between control enclosures and the adjacent marsh indicating no enclosure effect on temperature. Boyce (1974) showed that temperature profiles inside and outside enclosures can be expected to be similar because of horizontal heat transfer across the enclosure walls.

Many have cited the similarity of temperature profiles between enclosures and adjacent water bodies as a lack of evidence of enclosure effects on vertical turbulence (Goldman, 1962; Kemmerer, 1968; Kistritz, 1978). Boyce (1974) states that the similarity of temperature profiles need not be indicative of the commensurability of vertical flux rates. This view is supported by the data of the present study in which temperature profiles between all three treatments were similar while the degree of turbulence in each treatment was clearly very different.

Turbulence within enclosures had a marked effect on the mean oxygen concentration in the water column. Low oxygen levels in turbulent enclosures may be due to the physical mixing of anoxic sediment porewaters into the overlying water. Oxygen levels in control enclosures were statistically similar to those in the adjacent marsh indicating no enclosure effect on mean oxygen levels. Slightly higher oxygen levels in control enclosures than in the adjacent marsh may have been caused by oxygen production by aquatic macrophytes within the volume-limited space. Lateral difusion of this oxygen would be restricted by the enclosure walls, thus allowing oxygen accumulation in the control enclosures. This has also been reported by Kistritz (1978).

The effect of water turbulence on water chemistry was less well-defined than that of the physical parameters discussed. Levels of all nutrients (Figs. 3-4a-d) were consistantly higher in turbulent enclosures throughout the experiment than in control enclosures.

The large increase in SRP, NH_3 and PP levels in all enclosures between weeks 2-3 was a consequence of the introduction of feces by gulls perching on wooden stakes within the enclosures. Altered nutrient regimes within enclosures arising from introduction of bird guano has been reported elsewhere (Leah et al., 1978; Moss, 1981). Manny et al. (1975) have shown that nutrient release from the feces of migrant Canada geese can profoundly alter the trophic status of a lake.

If one were to assume equal nutrient (feces) loading rates in each enclosure, then a turbulent effect on water chemistry is supported by this study. Nutrient levels were consistantly higher in turbulent enclosures than in control enclosures. In addition, removal of perch sites (wooden stakes) caused a decrease in SRP and NH_3 levels in control enclosures while nutrient levels either remained constant (SRP) or increased (NH_3) during the following week (Fig. 3-4a+b) in turbulent enclosures. Levels of SRP and NH_3 in the adjacent marsh were consistantly low (Fig. 3-4a+b) indicating severe enclosure effects on water chemistry. However, since the trophic status of the control enclosures was clearly altered while the marsh was not, neither inferences concerning enclosure effects nor the utility of turbulence in alleviating enclosure effects on SRP and NH3 can be made. Enclosure effects on water chemistry have been shown in other studies (Kuiper, 1977; Twinch and Breen, 1978).

Physical mixing of sediments through bioturbation (Tessenow, 1966; Neame, 1977) and wind-induced water turbulence (Viner, 1977; DeGroot, 1981; Peters and Cattaneo, 1984; Hamilton and

Mitchell, 1988) has been shown to increase nutrient levels in the water column by releasing nutrients from sediment porewaters (Viner, 1977). This internal nutrient loading is targetted as a key factor contributing to the lack of success of lake eutrophication recovery programs in shallow, windswept lakes in Europe (Petterson and Bostrom, 1984). In addition, Dillon and Rigler (1974) used Vollenweider's model (1969) to predict phosphorus concentrations in the water column with the model working well with deep lakes but not with shallow lakes.

Silicon levels (Fig. 3-4d) in turbulent enclosures were higher than in control enclosures. In addition, silicon levels in turbulent enclosures tracked changes in the silicon levels in the adjacent marsh better than did control enclosures. This indicates that enclosure effects on silicon levels was evident and that in situ turbulence alleviated the enclosure effect. The source of the silicon was probably the sediments.

Phytoplankton biomass (Fig. 3-5a) was consistantly higher in turbulent enclosures than in control enclosures. This may be explained by two factors. Higher nutrient levels in turbulent enclosures may well have maintained a higher standing crop of phytoplankton than in control enclosures. In addition, water turbulence appeared to play an important role in biomass levels. Despite much higher nutrient levels in control enclosures than in the adjacent marsh phytoplankton biomass in control enclosures was either equal to or less than levels in the marsh. Loss of turbulence and subsequent sedimentation of planktonic and pseudoplanktonic

algae to the sediments in control enclosures may have inhibited the phytoplankton community from utilizing the high levels of available nutrients. Water turbulence is thought to increase algal growth by maintaining planktonic cells within the euphotic zone (ie. offsetting the process of sedimentation) and by replenishing nutrient levels in the microzone surrounding the cells (Whitford, 1960).

The importance of water turbulence in the maintainance of the phytoplankton community is widely recognized. Lack of water turbulence has been shown to have a profound effect on phytoplankton communities by causing changes in community composition (Lund, 1972; Brown and Austin, 1973; Twinch and Breen, 1978). For example, Moss (1981) has reported the appearance of typically planktonic species of algae in the periphyton under calm water conditions and states that this is due to a lack of water turbulence and resultant sedimentation of cells. Indeed, the process of seasonal succession in phytoplankton communities has been suggested to be closely linked to water turbulence (Hutchinson, 1967; Knoechel and Kalff, 1975).

The presence of water turbulence also has a marked effect on phytoplankton biomass and composition. In an earlier study (see Chapter 2) phytoplankton biomass was increased in the water column by up to 60 % in the Delta Marsh on several occasions throughout the sampling season. These short-term changes in biomass were positively correlated to changes in hourly wind stress on the marsh. The source of this biomass may be the epipelon or the detachment of epiphytes from their macrophyte hosts. Ganf (1974)

found that under windy conditions, the sediments could supply a source of viable benthic algae to increase suspended biomass by 56%. The increase in biomass could not be accounted for by growth processes alone. Moss (1981) has also noted the appearance of typically periphytic species in the phytoplankton under windy conditions and suggests that this too may be attributed to the physical detachment of epiphytes from their macrophyte hosts.

Controlled turbulence also influenced the biomass of the periphytic algal community (Fig. 3-5b) colonizing acrylic substrata. Biomass was consistently higher on substrata from turbulent enclosures than from control enclosures and may be due to higher nutrient levels and the presence of water turbulence. Periphytic algal biomass in control enclosures was not inhibited to the same degree as that of the phytoplankton from control enclosures. Periphyton biomass in control enclosures was always higher than in the adjacent marsh. This may have been a result of higher nutrient levels in the control enclosures and a lack of turbulence.

Lack of turbulence within control enclosures may favor periphyton development by providing cells of planktonic origin through sedimentation. Species colonizing substrata in turbulent enclosures may be truely periphytic while the periphyton community colonizing substrata in control enclosures may be largely derived from cells of planktonic origin. Although community composition was not monitored, the periphyton of the control enclosures appeared to be dominated by diatoms (brown color) while the periphyton in turbulent enclosures appeared to have more

chlorophytes present (green color). This would be consistent with the literature (Hutchinson, 1967; Lund, 1972) in which heavier, more dense diatoms sediment out of the water column under calm conditions more rapidly than chlorophytes.

Moss (1981) has also reported the appearance of typically planktonic species in the periphyton under calm conditions. The importance of water turbulence has serious implications on how successfully we can utilize enclosure studies involving algal communities and also on how we define these communities. Under turbulent conditions, algal communities may form more of a continuum rather than existing as discrete entities. This concept has led Sladeckova (1962) to prefer the term pseudoperiphyton to describe periphyton with a planktonic origin.

Many have recognized the importance of turbulence when conducting primary productivity experiments. Some investigators have used incubation chambers which incorporate a degree of turbulence to avoid the "static system" disadvantages (McIntire et al., 1964; Thomas and O'Connel, 1966; Marker, 1976; Rodgers et al., 1978). Suspensions of phytoplankton and epipelon are commonly used in productivity experiments while suspensions of peripyton are rarely used. Physical detachment of the periphyton from its associated substratum destroys the physical structure of the community and may alter nutrient and light penetration into the community. However, mixing of the samples during incubation was not undertaken in this study.

Temporal trends in P_{max} for both algal communities follow closely the temporal changes in biomass. The SP_{max} curves are almost opposite to the temporal changes in P_{max} for both algal communities. SP_{max} in each treatment (Figs. 3-6b+7b) generally decreased throughout the experiment while P_{max} and biomass increased. Biomass has been shown to have a marked negative effect on photosynthesis (Ramus et al., 1976; Carpenter, 1985; Jasper and Bothwell, 1986). Increased biomass may severely limit the amount of light and nutrients reaching each cell so that the community photosynthetic rate is limited.

Although nutrient levels in the turbulent enclosures were higher than in the control enclosures, SP_{max} of the phytoplankton and the periphyton in both enclosure treatments was similar. This finding agrees with Jasper and Bothwell (1986) who found no difference in SP_{max} in treatments with different phosphorus additions. However, this contrasts other studies in which SP_{max} was dependent on nutrient levels (Thomas, 1969; Glooschenko et al., 1974; Falkowski, 1981).

Water turbulence (mixing) has been shown to influence photosynthetic rate (Whitford and Schumacher, 1961; McIntire, 1968; Hunding, 1971; Colijn and Van Buurt, 1975; Rodgers et al., 1978; Bott and Ritter, 1981; Jasper and Bothwell, 1986) presumably by improving light penetration and nutrient diffusion into the community so that each cell potentially receives optimal levels. Given this argument, it is not surprising that SP_{max} of algal

communities from turbulent enclosures was similar to that from control enclosures since the productivity experiments were not made in situ, but rather in a static laboratory incubator.

SP_{max} of the two algal communities from the adjacent marsh was generally higher than that of the two enclosure treatments. In a static system incubator, a community with a lower biomass would ensure that more light and nutrients are available to each cell within the community compared to a community with a higher biomass. Therefore, the higher SP_{max} values of the algal communities from the adjacent marsh are probably due to lower biomass compared to the two enclosure treatments. SP_{max} values found in this study are generally higher than those reported in other studies but fall within the reported range for phytoplankton (Platt and Jasby, 1976; Harris, 1980; Platt et al., 1980; Jasper et al., 1983) and periphyton (McIntire and Phinney, 1965; Marker, 1976; Bott and Ritter, 1981; Jones and Adams, 1982; Jasper and Bothwell, 1986; Gurney and Robinson, 1989).

Differences in the photosynthetic parameters (I_k, α, E_{max}) were evident between turbulent and control enclosures, although they were not statistically significant at the 0.05 level. These differences were not attributable to turbulence per se, but to the alteration of the underwater light climate (turbidity) caused by the turbulence. Many photosynthetic adaptations to changes in light intensity occur in algae. Algae have the ability to change the P vs. I curves to adapt to changing light conditions (Ramus et al., 1977; Li and Titlyanov, 1978; Rosenberg and Ramus, 1982).

I_k is the light itensity at which SP_{max} is attained. Algal communities (or species) with lower Ik values are said to be better adapted to low light conditions since they saturate (attain SP_{max}) at lower light intensities. Algal cells, colonies or communities grown in low light conditions have lower I_k values than those grown at higher light intensities (King and Schramm, 1976; Ramus et al., 1976; Carpenter, 1985; Jasper and Bothwell, 1986). Controlled water turbulence in this study appeared to have no effect on I_k values between turbulent and control enclosures (Fig. 3-8). Phytoplankton I_k's of the two enclosure treatments were identical whereas mean periphyton I_k from turbulent enclosures were only slightly less than that of periphyton from control enclosures. The similarity in I_k values between turbulent and control algal communities may be a result of the short duration in which the light regime was altered. Short-term (2 h.) changes in the light climate may have been insufficient to allow for photosynthetic adaptation although Gallegos et al. (1977) could detect changes in in situ oxygen evolution over 1 minute intervals resulting from rapid changes in light intensity caused by passing clouds.

Phytoplankton from the adjacent marsh appear to be better adapted to changing light conditions (lower Ik) compared to the phytoplankton communities from the enclosures while the periphyton community of the adjacent marsh shows the opposite trend. Overall, the periphyton communities from the enclosure treatments appear to be better adapted to low light intensity than are the phytoplankton communities. This may be due to the location

of the two communities sampled (surface water vs. closer to the sediments).

Changes in the initial slope of the P vs. I curve (α) is also an indication of photosynthetic adaptation (Carpenter, 1985). An increase in α is a common adaptation to reduced light conditions (King and Schramm, 1976; Ramus et al., 1976; Li and Titlyanov, 1978; Falkowski and Owens, 1978; 1980) and is thought to be a function of an increase in size of the photosynthetic units (PSUs) rather than number of PSUs (Carpenter, 1985).

Phytoplankton from the adjacent marsh had a much higher α than either enclosure treatment although a great deal of variation was evident (Fig. 3-9). Phytoplankton from turbulent enclosures also had a slightly higher α than from control enclosures suggesting an adaptation to lower light conditions in the turbulent enclosures. The opposite trend occurred in the periphyton in which periphyton from control enclosures had the highest α. Maximum photosynthetic efficiency (E_{max}) shows a very similar trend (Fig. 3-10).

In general, the short duration of time (2 h.) in which water clarity was altered in turbulent enclosures appears to have been insufficient to allow for photoadaptative changes to occur in the algal communities. The marked differences in I_k, α, and E_{max} between phytoplankton of the adjacent marsh and phytoplankton from the two enclosure treatments may be a function of differences in community composition. This was qualitatively apparent in the pigment color of the communties (pers. obs.).

The reduced incidence of photosynthetic inhibition of algal communities grown at high light intensities is indicative of photoadaptation to high light intensities (Platt et al., 1980; Ramus and Rosenberg, 1980; Falkowski and Dubinsky, 1981; Carpenter, 1985). The lower incidence of photosynthetic inhibition of both the phytoplankton and the periphyton communities from the adjacent marsh compared to the enclosure treatment communities suggests that the natural marsh communities are better adapted to changing light environment. Short-term turbulence within turbulent enclosures was insufficient to change the incidence of inhibition relative to control enclosures. Overall, the periphytic community seems to be better adapted to lower light conditions than the phytoplankton community based on I_k, α and the incidence of photosynthetic inhibition.

3.6 Conclusions

Controlled water turbulence within enclosures had a marked effect on all limnological parameters monitored in this study. Physical parameters (suspended particulates, water clarity) were affected the greatest. Enclosure effects on the physical parameters (except water temperature) were evident and were alleviated by the incorporation of water turbulence.

Controlled turbulence had a less-well defined effect on water chemistry. Valid inferences concerning enclosure effects on water

chemistry and the successful use of turbulence to alleviate the enclosure effects cannot be made as a consequence of external nutrient loading events. This is also the case for periphyton biomass. Enclosure effects on phytoplankton biomass was evident and was alleviated by the incorporation of turbulence.

Primary productivity of the phytoplankton and periphyton communities was generally higher in turbulent enclosures than in control enclosures. The similarity of SP_{max} rates and other photosynthetic parameters (I_k, α, E_{max}, inhibition) between the two enclosure treatments may have been a result of the sort duration of the turbulence generated in the turbulent enclosures and the use of a static productivity incubator.

The use of the turbulent enclosure protocol in ecological studies utilizing enclosures appears to be justified although future work is needed to evaluate the utility of this protocol in alleviating enclosure effects on water chemistry and algal biomass, productivity and community structure. Small diameter enclosures with a means of controlling turbulence offer an economical alternative to using the more costly large diameter enclosures. This work should also find application in the testing of organic contaminants in aquatic ecosystems given the importance of a more realistic protocol for these types of experiments.

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