Algal primary production in prairie wetlands: The effects of nutrients, irradiance, temperature and aquatic macrophytes

By

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A Thesis
Submitted to the Faculty of Graduate Studies
In Partial Fulfillment of the Requirements
For the Degree of

Doctor of Philosophy

Department of Botany
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A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of Manitoba in partial fulfillment of the requirements of the degree

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Abstract

I studied algal primary production in prairie wetlands, and impacts of anthropogenic nutrient loading, changes in light and temperature, and the presence or absence of macrophytes in the water column. I manipulated nitrogen and phosphorus loading, macrophyte abundance, temperature, and photosynthetically active radiation. My study sites were two Ramsar wetlands, Delta Marsh, an 18,500 ha lacustrine marsh, and Oak Hammock Marsh, a 2,400 ha diked marsh.

I hypothesized that algae would contribute significantly to primary production in prairie wetlands, on a scale comparable to or exceeding macrophyte production. The objective in Delta Marsh was to promote a shift from an epiphyton- and submersed macrophyte-dominated marsh (clear water state) to a phytoplankton-dominated turbid state by manipulating macrophyte abundance and inorganic nutrient loading in large enclosures. One objective of my survey of algal and macrophyte abundance in Oak Hammock Marsh was to quantify the contribution of all algal and macrophyte communities to total wetland primary production. Other objectives were to develop a photosynthesis model for each wetland algal assemblage based on photosynthesis-irradiance relationships, and to determine the major limiting resource for algal primary production.

I found that algae contribute significantly to primary production in prairie wetlands. In Delta Marsh, algae contributed 34% to standing crop in unmanipulated mesocosms, and 57% to standing crop in nutrient enriched mesocosms. In Oak Hammock Marsh, algae contributed 62% and 68% of total annual primary production in two consecutive years. Phytoplankton responded to nutrient addition, both in the presence of macrophytes and when they were absent. Therefore, the nutrient addition treatments did promote a more turbid state, but the likelihood of a complete switch from

clear water to a turbid state in the enclosures was equivocal. This is because periphyton and epiphyton showed a similar magnitude of response to nutrient addition as phytoplankton did, providing an important buffering mechanism within the enclosures by sequestering large amounts of added nutrients. The photosynthesis model, developed from experimentally determined photosynthesis parameters, was able to predict accurate daily productivity estimates when compared with *in situ* measurements. Light was the single most limiting resource for algae in Oak Hammock Marsh.

Acknowledgements

There are many people who have enriched these years of my graduate student career, without whom, I could not have achieved this goal. A central person in all this has been my supervisor, Gordon Goldsborough, who first opened the doors to the scientific world for me. He has offered me support, perspective, knowledge, and a strong example of scientific curiosity and professional integrity. His facilitative style has allowed me to grow as a scientist, from a hesitant student to an optimistic colleague. He has encouraged me to work hard, aim high, and take time to enjoy the process. I could not have asked for a better teacher, and I look forward to our continuing association as friends and as colleagues in a challenging field.

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1. Introduction

Photosynthetic organisms, such as algae and aquatic macrophytes, constitute the first trophic level in complex food webs through which energy is processed (Wetzel 2001). Energy is lost in each trophic transfer, so that the size and metabolic activity of the first trophic level is a determining factor in maintaining the diversity and abundance of organisms at higher trophic levels. Therefore it is important to quantify all of the primary producers within an ecosystem in a meaningful way that allows comparison between primary producers and among aquatic ecosystems.

In aquatic ecosystems, there are deep open water (pelagic) zones and shallow water (littoral) zones, which support distinct assemblages of autotrophs. Pelagic zones are dominated by phytoplankton, the algae entrained in the water column and mainly distributed by water movements (Wetzel 2001). Littoral zones are often described as the interface between the land of the drainage basin and the open water of lakes (Wetzel 2001), but they are ecologically distinctive areas that support a diverse assemblage of hydrophytic vascular and non-vascular plants and algae. In some cases, littoral zones border lakes and are continuous with pelagic zones, with water depth acting as the controlling boundary for vegetation change. In other cases, aquatic ecosystems are mainly littoral in nature, as is the case for most wetlands and many shallow lakes. In fact, Wetzel (2001) argues that the majority of water bodies in the biosphere are small and relatively shallow, and that the metabolic activities of the littoral and wetland regions regulate the productivity of most lakes in the world. Historically, limnologists have tended to focus on processes in the pelagic zone, whereas the more complex ecology of the littoral zone has received less attention (Wetzel 1983, Beklioglu and Moss 1996) and still remains as somewhat of an undefined "black box". In particular, the mechanisms and

interactions that regulate the complex communities of shallow aquatic systems such as wetlands are not well understood (Scheffer *et al.* 1993).

My objective has been to study the primary production of algae in prairie wetlands to gain a more complete understanding of wetland algal responses to environmental factors, including light, nutrients, and temperature, and their interactions with macrophyte primary producers. I think that primary producers play a major role in maintaining the structure and function of wetland ecosystems, and that the role of wetland benthic algae, in particular, has been largely unrecognized. By studying algal primary production within the context of interactions with aquatic macrophytes in an environment of potentially limiting resources, I intend to provide new insight into the unique ecological role of wetland algae.

1.1 Prairie wetlands

Wetlands are an important feature of the prairie landscape, providing habitat for waterfowl, migratory birds, and small mammals, as well as spawning grounds for fish, reptiles, and invertebrates. The decline and degradation of freshwater wetlands has been widespread in North America (Whillans 1987, Dahl and Johnson 1991, Westcott *et al.* 1997). Degradation and loss of wetlands through human intervention is viewed as one of the major land-use issues facing both provincial and federal jurisdictions (Rubec and Rump 1985). Estimates of wetland loss in North America range from 40 to 80% of original area (Canada-United States Steering Committee 1988, in Millar 1989). It has been estimated that at least 75% of prairie wetlands in Canada have been lost through drainage for agriculture and urban development (Environment Canada 1986).

Wetland degradation has been attributed to such factors as reduced water clarity associated with nutrient enrichment, high rates of land erosion and sedimentation, and turbidity from the actions of common carp, *Cyprinus carpio* (Westcott *et al.* 1997).

Degradation of wetlands is an increasing concern, particularly in the prairie pothole region of North America where wetlands occur within the zone of intensive agricultural activity. Prairie potholes and marshes are vulnerable to increasing eutrophication from external sources of nutrients such as agricultural fertilizers, animal manure, and domestic sewage. The use of phosphorus fertilizer on the Canadian prairies has doubled since 1965, and the use of nitrogen fertilizer has increased by six times over the same time period (Figure 1) (Korol and Girard 1996). Calculations for various aquatic systems suggest that since the beginning of the 1900s, P loading to aquatic systems has increased approximately 2 – 6 times and N loads have increased 1.5 – 4.5 times (Conley 2000). Although wetlands are often thought of as 'natural filters' for excess nutrients, there may be a point where external nutrient loading begins to cause water quality degradation and ecosystem decline. It is difficult to assess the magnitude and effect of increases in nutrient loading over time because little information exists about "pristine" conditions in wetlands.

Concerns for wetland ecosystems also stem from predictions of global climate change, with most scenarios predicting increased temperatures, changes in quality and quantity of solar radiation, and fluctuations in annual precipitation patterns (Poiani and Johnson 1993, Larson 1995, Covich *et al.* 1997). In shallow systems such as prairie wetlands, the impacts to biotic organisms of changes in temperature, irradiance and water depth can be extremely significant. The light and temperature regime in shallow wetlands may differ significantly from that of deeper lakes. The water column may be more turbid in shallow wetlands because of resuspension of flocculent sediments via wind action and water motion. Wetland algae may be partially or completely shaded by the leaf canopy of both emergent and submersed macrophytes, which can absorb much of the available photosynthetically active radiation (PAR). Because of their growth habit, attached algae are necessarily located in relatively fixed positions below the water

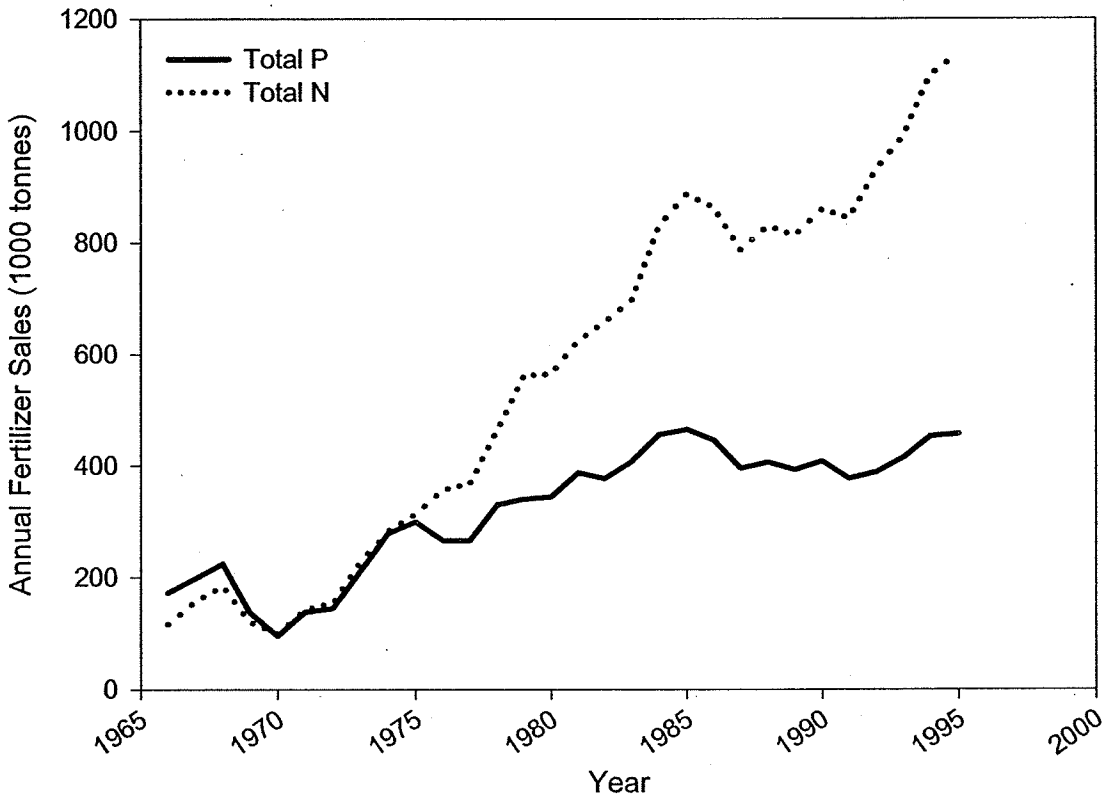

Figure 1. Phosphorus and nitrogen fertilizer sales (1000 tonnes) on the prairies (Alberta, Saskatchewan and Manitoba) over 30 years (1966-1995). (from Korol and Girard 1996).

surface where light attenuation with depth becomes a factor determining photosynthetic productivity. Temperatures in shallow water bodies such as wetlands often exhibit greater extremes than temperatures in deeper lakes. Temperature change also becomes a factor determining algal photosynthetic productivity, because photosynthesis is in part an enzyme-mediated process.

There have been few measurements of wetland algal primary production (Hecky and Hesslein 1995, Lowe 1996, Robinson *et al.* 1997). In many studies of algal production, phytoplankton are the only assemblage measured, and benthic algal assemblages (described below) are ignored. In a recent survey of major aquatic journals, phytoplankton-based research papers outnumbered benthic algal research papers by about 20 to 1 over a period of five years (Lowe 1996). Furthermore, the effects of light, temperature, and nutrients on benthic algal photosynthesis remain understudied (Hill 1996).

1.2 Introduction to wetland primary producers

1.2.1 Algae

One of the major groups of primary producers in littoral zones and wetlands are the algae. Planktonic algae, or phytoplankton, sink or remain suspended in the water column as a result of a variety of mechanisms including size, shape (spines, horns), production of gas vacuoles, and flagellar or euglenoid motion (Reynolds 1984). Benthic algae are associated with surfaces and are identified by various terms related to their specific attachment substratum (Hutchinson 1975, Goldsborough and Robinson 1996, Wetzel 2001). Benthic, from the Greek *benthos*, for bottom, refers to organisms associated with the bottom, or with any solid-liquid interface in aquatic systems (Wetzel 2001). Epipelon or epipelic algae are the motile algae growing on fine, organic sediments. The term, sediment-associated algae, is more general and includes both

epipelon and non-motile crusts (sometimes called plocon) associated with sediments. Epilithon or epilithic algae grows on rock surfaces, epipsammon or epipsammic algae is associated with sand grains, epizooic algae grows on animals, and epiphyton or epiphytic algae grows on plant surfaces. The epiphytic algal community consists of an adnate component – algae with the major cell axis in direct contact with the macrophyte – and a loosely attached component, consisting of stalked, motile, and filamentous algae that grow away from the macrophyte surface (Round 1981). Metaphyton are aggregates of algae that are not strictly attached or truly floating. They are included with benthic algae because they originate from attachment substrata such as sediments or plant surfaces. Metaphyton tend to form macroscopic mats, which may trap gases and float below or at the water surface. Finally, periphyton is a more general term intended to denote the entire community attached to any substrata, including algae, bacteria, fungi, animals, and detritus (Wetzel 2001). The use of the term periphyton to specifically denote attached algae has found its way into common usage, particularly in the USA (Stevenson 1996).

I have chosen to use the term epiphyton to refer to the algae sampled from the surfaces of macrophytes. The term periphyton will be used to refer specifically to attached algae sampled from artificial substrata. I will use the term epipelon to refer to motile sediment-associated algae, and the term plocon to refer to non-motile crusts at the sediment surface. Phytoplankton and planktonic algae will be considered interchangeable terms, whereas metaphyton will be used to refer to floating mats of filamentous algae.

Most classes of freshwater algae are well-represented in wetlands, with diatoms (Bacillariophyceae), green algae (Chlorophyceae), euglenids (Euglenophyceae) and cyanobacteria (Cyanophyceae) being most common (Round 1981, Goldsborough and Robinson 1996). Many species may be found in both benthic and planktonic

associations (Goldsborough and Robinson 1996). Benthic species may be dislodged and become entrained in the water column where they are sometimes called tychoplankton (Round 1981). Conversely, planktonic species may sink to the sediments and survive among sediment-associated algae, or become entrapped in the matrix of an epiphytic biofilm.

1.2.2 Macrophytes

Aquatic plants comprise the other major group of primary producers in prairie wetlands, and their distribution within an ecosystem is often linked to a water depth gradient (Walker 1965, Walker and Coupland 1968, Kantrud *et al.* 1989, Squires and van der Valk 1992). Macroscopic hydrophytic plants are often referred to as aquatic macrophytes, or simply macrophytes, and include vascular plants, mosses and ferns, and macroalgae such as the charophytes (Sculthorpe 1967). Aquatic macrophytes are further classified according to growth habit and attachment to the substratum (Sculthorpe 1967, Wetzel 2001). Emergent macrophytes occur on saturated or submersed soils (water depth -0.5 m to 1.5 m) and produce mature aerial leaves and aerial reproductive organs. They are attached to the substratum via rhizomes or corms and may produce some floating or submersed leaves (e.g., *Typha, Phragmites, Scirpus, Eleocharis*). Floating-leaved macrophytes attach to submersed sediments by roots, rhizomes, or holdfasts and occur in water depths ranging from 0.5 m to 3 m. They are often heterophyllous, with submersed leaves preceding floating leaves and reproductive organs that are either aerial or floating (e.g., *Nuphar, Nymphaea*). Submersed macrophytes also attach to submersed sediments via roots, rhizomes or holdfasts and occur at all depths within the photic zone. Leaf morphology is highly variable, from rosettes to finely divided, and reproductive organs may be aerial, floating or submersed (e.g., *Isoetes, Chara, Stuckenia, Myriophyllum*). Freely floating macrophytes form a diverse group living unattached within or upon sheltered or slow-flowing water. Many

have aerial or floating leaves and reproductive organs and submersed roots, (e.g., *Eichhornia, Lemna, Azolla*) and a few have all organs submersed (e.g., *Ceratophyllum*).

Some adaptations to the water environment are evident in the above description of various growth forms, including emergence of some plant organs above water for reproduction and enhanced access to CO_2, reduction and fine division of leaves in water to decrease boundary layers and increase surface area to volume ratio for enhanced diffusion and access to light, and the maintenance of root systems for access to sediment-bound nutrients (Vymazal 1995). Other adaptations include the evolution of cells with large air spaces (aerenchyma) in roots and stems, reduction or elimination of stomata on leaves, and reduction in the amount of mechanical support tissues such as lignin in submersed and floating plants (Sculthorpe 1967). Increased reliance on vegetative reproduction and the production of vegetative overwintering structures (turions) are also considered to be adaptations to the water environment (Sculthorpe 1967, Sastroutomo *et al.* 1979). Photosynthetic adaptations to decreased availability of CO_2 in water include utilization of sediment CO_2 via roots and aerenchyma, bicarbonate utilization, and C_4 or CAM metabolism (Madsen and Sand-Jensen 1991).

1.3 Introduction to my study

I undertook two approaches to my study of the algal assemblages of prairie wetlands. I used an experimental approach in Delta Marsh, Manitoba, where I employed large-scale mesocosms to manipulate nutrient loading and submersed macrophyte abundance. I used a descriptive approach in Oak Hammock Marsh, Manitoba, where I conducted an extensive survey of algal and macrophyte abundance over two growing seasons. This descriptive approach was augmented by experimental determinations of nutrient limitation, and experimental manipulations of light and temperature during

photosynthesis measurements. I used a modeling approach to quantify total annual algal primary production in Oak Hammock Marsh.

Experimental manipulations in Delta Marsh were carried out in a large enclosure complex in the Blind Channel in 1995 and 1996 (Figure 2). The survey of algal and macrophyte abundance was carried out in Cell Four of Oak Hammock Marsh in 1997 and 1998 (Figure 3). Nutrient limitation experiments and dawn to dusk *in situ* photosynthesis experiments were also performed in Cell Four in 1997 and 1998. Light and temperature manipulations of algal photosynthesis were carried out at the National Water Research Institute in Saskatoon, Saskatchewan, using algae from Cell Four of Oak Hammock Marsh.

Delta Marsh is a large (18,500 ha) lacustrine marsh situated at the south end of Lake Manitoba. The marsh is connected to Lake Manitoba by at least four channels (Wrubleski 1998), allowing the water level of the marsh to be influenced by the prevailing wind direction and seiche activity on shallow Lake Manitoba. The level of Lake Manitoba has been stabilized since 1961, when the Fairford Dam was constructed at the northern outlet of the lake. As a consequence, water levels in Delta Marsh have remained relatively stable since that time. Delta Marsh was recognized as an Important Bird Area in 1999 due to its significance as a waterfowl staging area and stopover sight for neotropical migrating songbirds. The Delta Marsh Bird Observatory tracks the migration of over 7,500 songbirds per year (DMBO 2001).

Oak Hammock Marsh is a large (2,400 ha) diked marsh reclaimed from the remnants of a much larger wetland that had previously been drained for agricultural cultivation in the 1930s. Oak Hammock Marsh has been a designated Wildlife Management Area since 1973. The marsh is divided into four diked cells in various stages of a seven-year cycle of draw-down and reflooding, managed by the provincial

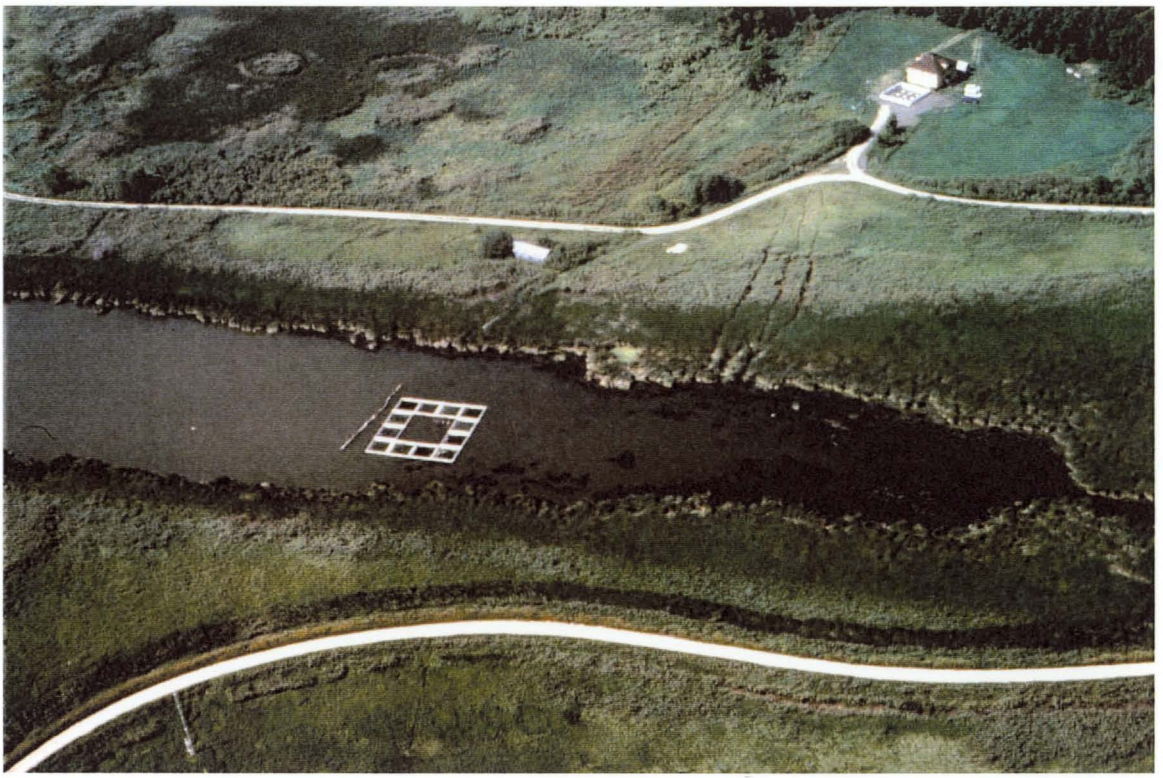

Figure 2. Aerial photograph of enclosure complex in the Blind Channel of Delta Marsh, Manitoba, taken in August 1996.

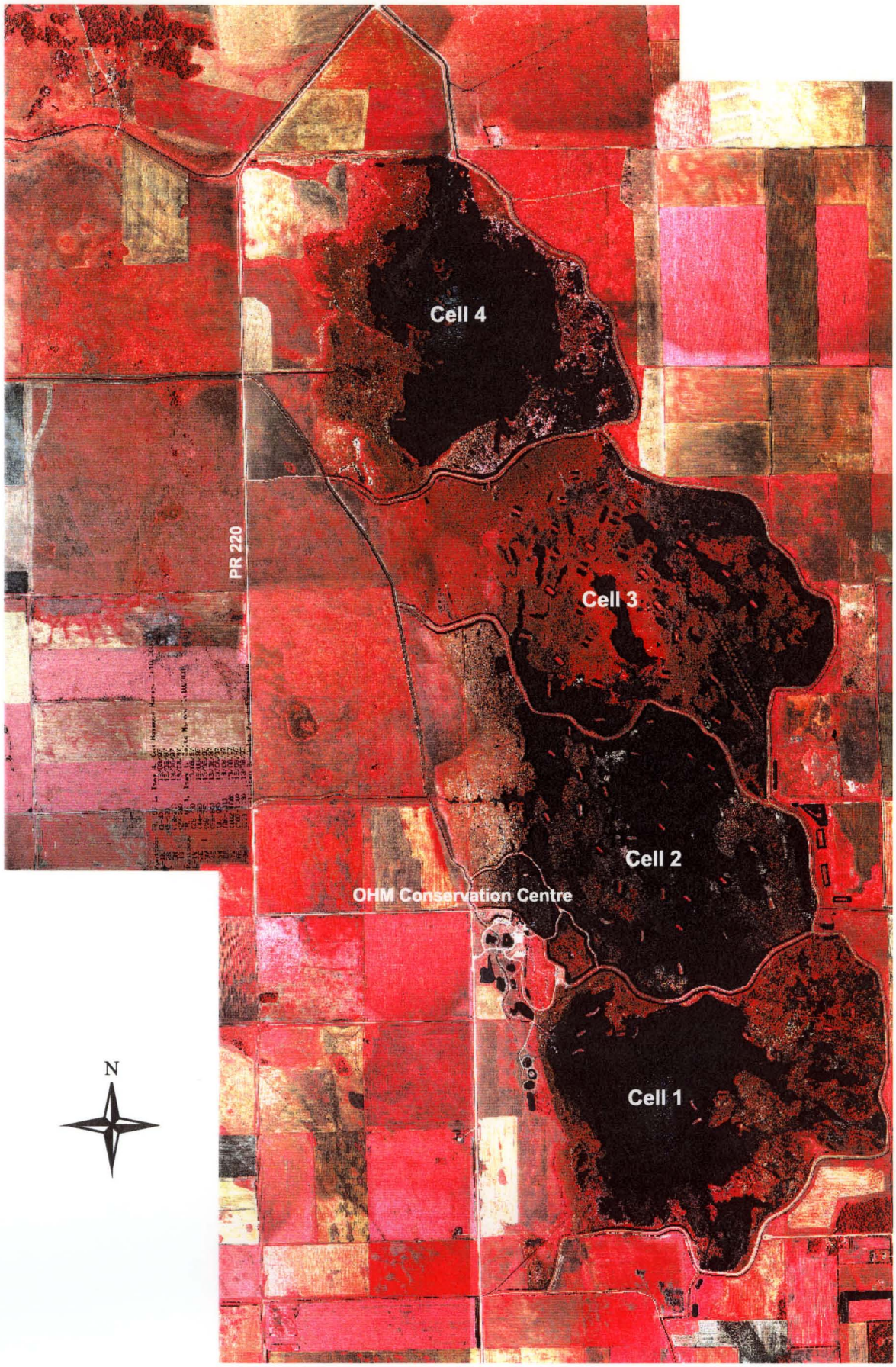

Figure 3. Aerial photograph of Oak Hammock Marsh, Manitoba, taken in August 1997.

Department of Conservation, Province of Manitoba. Water for water-level management is supplied by nearby Wavey Creek and several local artesian wells. Subsequent to reclamation, wildlife production and utilization of the marsh have increased dramatically. Provincial government biologists have estimated peak waterfowl production at 7000-9000 ducks per year. Peak staging estimates have indicated that over 50,000 ducks and 200,000 geese use the marsh during fall migration. The marsh supports a tremendous diversity of other species as well, achieving an international reputation as a bird-watching site (Anonymous 1988).

These marshes are within close geographic proximity of each other (~100 km) and both are designated Ramsar wetlands of international importance (Jones 1993). It is imperative that the primary production capabilities of these wetlands be adequately characterized because of their importance to wildlife, waterfowl, and fish production. In particular, we need to gain a clearer understanding of the complex functional roles of each of the biotic components of these ecosystems, in order to develop stronger predictive tools for future conservation and management decisions for these wetlands.

1.4 Hypotheses and specific objectives

At the outset of my research, I hypothesized that algal assemblages would contribute significantly to primary production in prairie wetlands, on a scale comparable to or exceeding aquatic macrophyte production. I further hypothesized that benthic algae were quantitatively more important than phytoplankton in prairie wetlands.

With respect to my mesocosm experiment in Delta Marsh, my objective was to promote a shift from an epiphyton- and submersed macrophyte-dominated marsh (clear water state) to a phytoplankton-dominated turbid state by manipulating submersed macrophyte abundance and inorganic nutrient loading in large enclosures. I hypothesized that phytoplankton would flourish in enclosures where macrophytes were

excluded, a response that would be enhanced if nutrients were also added concurrently. The absence of macrophytes would reduce colonization substrata for epiphyton, and consequently reduce nutrient demand by these two components of the system. This would enable phytoplankton to predominate, particularly because of its physical position near the top of the water column as first consumer of the regularly added nutrients. In enclosures where nutrients were added and macrophytes remained, I hypothesized that metaphyton would become dominant, a result that I had noted in an earlier experiment (McDougal *et al.* 1997). The macrophytes would provide ample attachment substrata from which filamentous algae could detach and the sheltering effect of the macrophytes would provide a stable environment for the maintenance of large floating algal mats. Epiphyton on submersed macrophytes were expected to remain the dominant algal assemblage in unmanipulated control enclosures.

With respect to my survey of algal and macrophyte abundance in Oak Hammock Marsh, my objective was to quantify the contribution of all algal and macrophyte communities to total wetland primary production. I hypothesized that algal production would equal macrophyte production when all algal assemblages were included and the faster turnover rate of algal biomass was taken into account. Based on the extent of colonization surfaces available within the euphotic zone of Oak Hammock Marsh, I hypothesized that benthic algal production would exceed phytoplankton production in absolute abundance.

My photosynthesis experiments were designed to determine individual photosynthesis-irradiance response relationships for each algal assemblage. Because of the extreme temperature fluctuations that wetland algae must tolerate in shallow water columns, I hypothesized that the maximum rate of photosynthesis at high irradiance (P_{max}) would increase with increasing temperature for all algal assemblages. I also hypothesized that P_{max} would be higher for phytoplankton and metaphyton than for algae

attached to surfaces at depth. I hypothesized that attached algae would exhibit higher photosynthetic efficiency (*a*), allowing them to photosynthesize more efficiently at low light levels.

With respect to nutrient limitation experiments, my objective was to determine if phytoplankton and attached algae were limited by the same major nutrient (N or P). I hypothesized that both assemblages would be N-limited, based on recent evidence that N rather than P is often the limiting nutrient in shallow lakes (Elser *et al.* 1990, Axler and Reuter 1996). Based on the potential for shading by dense stands of macrophytes, I hypothesized that light, rather than nutrients, would be the single most limiting resource for algal primary production in Oak Hammock Marsh.

2. Literature Review

2.1 Introduction

2.1.1 Interactions among primary producers

Several features of shallow aquatic ecosystems contribute to the complex interactive nature of their environment, including the presence of illuminated sediments and surfaces which provide abundant habitat for attached organisms, the unique biogeochemistry of the sediments and the water column which undergoes rapid changes in oxygen concentration from supersaturation to anoxia, and the diversity of organisms, many of which grow in close proximity to one another.

In particular, the macrophyte-epiphyte complex has been described as a unique ecological unit within shallow aquatic ecosystems, possessing complex interrelationships not found in open water zones (Allen 1971, Moeller *et al.* 1988). The nature of these interrelationships between macrophytes and their associated epiphytes has been the focus of much of the research in shallow lake and wetland ecology. Several explanations have been advanced to describe macrophyte-epiphyte interactions, including positive interactions (symbiosis or mutualism), negative interactions (competition and allelopathy), and neutrality or no interaction. Proponents of the symbiotic or mutualistic interaction argue that epiphytes benefit from the organic compounds and nutrients secreted by the macrophytes, and in return, the macrophyte is protected from grazing by the coating of epiphytes (Hutchinson 1975, Burkholder and Wetzel 1990, Wetzel 2001). The competition argument states that macrophytes and epiphytes compete for scarce resources of nutrients and light, with macrophytes maintaining the advantage for nutrients, and epiphytes out-competing macrophytes for light via dense colonization (Fitzgerald 1969, Sand-Jensen 1977, Phillips *et al.* 1978). The theory of allelopathy suggests that macrophytes or epiphytes secrete some substance that inhibits the growth

of the other (Fitzgerald 1969, Hootsmans and Blindow 1994). Finally, some proponents argue that macrophytes just provide surface area, and not inhibitory or stimulatory substances, to epiphytes. Epiphytes are kept in check by grazers and fast growth of new leaves of macrophytes, so that their relationship is for the most part biologically neutral (Cattaneo and Kalff 1979, Carignan and Kalff 1982). When considering these macrophyte-epiphyte interactions, further complexity is introduced when phytoplankton, sediment-associated algae, and metaphyton are included.

2.1.2 Roles for primary producers

Primary producers have an obvious biotic role to play in aquatic ecosystems, that of processing energy to provide food resources for themselves and for higher trophic levels. However, the algae and macrophytes of shallow systems also fulfill other chemical and physical roles in their environment. The biotic, chemical and physical roles that algae and macrophytes fill are, by their nature, intimately interconnected. For example, during photosynthesis to produce new biomass (a biotic role), algae consume CO_2 and H+ ions, driving up the pH (a chemical role), in the process causing $CaCO_3$ to precipitate as calcite, which stabilizes the sediment (a physical role). I will consider each of these roles in turn, to facilitate a comparison of macrophyte and algal roles and to evaluate the basis for algal - macrophyte interactions.

2.2 Biotic roles for algae and macrophytes

2.2.1 Primary production

Despite early recognition that the littoral regions of aquatic ecosystems represent some of the most productive communities in the world (Wetzel 1964, Allen 1971), there is still debate about the origin of this productivity. Whereas there is a proliferation of literature detailing aquatic plant productivity in shallow lakes and wetlands (Westlake 1975, van der Valk and Davis 1978a, Smith and Walker 1980, Madsen and Sand-

Jensen 1991, Madsen and Sand-Jensen 1994), and an even larger body of information about phytoplankton productivity in pelagic zones (Goldman 1965, Vollenweider *et al.* 1974, Kalff and Welch 1974, Harris *et al.* 1980, Hammer 1983, Reynolds 1984, Grobbelaar 1985), there is less known about the contributions of benthic algae to these systems (Hecky and Hesslein 1995, Lowe 1996). Benthic algae have greater visibility and have been more thoroughly studied in stream and riverine (lotic) ecosystems (Blum 1956, Stockner and Shortreed 1978, Biggs 1996), which differ ecologically from wetlands and shallow lakes in many ways, including flow velocity, light environment, substratum surface availability, and nutrient cycling. The relatively fewer studies on benthic algae of non-flow (lentic) systems may have to do with the greater difficulty of access to benthic communities, growing on flocculent sediments, within dense stands of emergent macrophytes, or on the relatively fragile surfaces of submersed macrophytes. It may be that the importance of benthic algal production in shallow systems has not been recognized (Murkin 1989, Hecky and Hesslein 1995). Or it may be that the intimate connectedness of some of these algae with their living substrata have made them "invisible", or at least, difficult to study as separate entities.

The idea is common in the literature that primary production within wetland and littoral habitats is dominated by the growth of emergent macrophytes, such as *Phragmites*, *Typha* and *Juncus* (Landers 1982, Mitsch and Gosselink 1993, Gessner *et al.* 1996, Beklioglu and Moss 1996). Direct grazing of this plant matter by invertebrates is considered negligible in most wetland habitats, because much of the carbon within macrophyte tissues (lignocellulose) is not readily digested (Mann 1988). This has lead to the widely held assumption that detritus is the basis of wetland food webs (Polunin 1984, Mann 1988, Pieczynska 1993). Murkin (1989) has contradicted this view; suggesting that herbivory and the role of algae in wetland food web support have been underestimated. Wetzel (1964, 1983a, 1993) has continually argued the case for significant contributions

to primary production by benthic algae. However, generalizations about the detrital base of wetland food webs still prevail, as, for example, in an extensive review of wetlands, Mitsch and Gosselink (2000, p. 403) state, "Herbivory is considered fairly minor in inland marshes where most of the organic production decomposes before entering the detrital food chain."

In some studies where algal contribution to primary production has been considered, only phytoplankton has been measured (Oglesby 1977, Nixon 1988), resulting in the perception that phytoplankton are the major contributors to algal primary production in lentic ecosystems (Lowe 1996). However, the controls on phytoplankton in shallow systems with abundant macrophytes are poorly understood, and the well-known pelagic ecology of phytoplankton may not apply in littoral zones (Søndergaard and Moss 1998). Phytoplankton abundance in shallow ecosystems is often low (Cole and Fisher 1978, Brammer 1979, Godmaire and Planas 1986, Gessner *et al.* 1996) and consequently, algal primary production may be dismissed as minor in comparison to macrophyte production.

There have been few measurements of benthic algal primary production (Hecky and Hesslein 1995, Lowe 1996, Robinson *et al.* 1997). However, there has been increased interest in benthic algae in the past twenty years (Stevenson 1996). The application of stable isotope techniques to food web studies has allowed researchers to identify the benthic algal origin of carbon sources in some aquatic systems. Benthic microalgae have been identified as a primary carbon source in estuarine food webs (Peterson and Howarth 1987, Sullivan and Moncreiff 1990). Studies of food webs in arctic, temperate and tropical lakes have shown that benthic algae are major contributors of fixed carbon, not only to primary consumers, but to higher trophic levels as well (Hecky and Hesslein 1995). Hecky and Hesslein (1995) noted that whereas consumers showed a near equal dependence on benthic and planktonic algal carbon

based on their carbon isotope signatures, photosynthetic productivity measurements of benthic algae (<15% of total photosynthesis) were often much lower than for planktonic algae. They questioned whether this mismatch was the result of underestimation of benthic algal production, or more efficient use of this food resource by grazers.

There are a number of methodological problems that make measurements of benthic algal production more difficult than measurements of the comparatively homogeneous phytoplankton (Wetzel 1983b, Hecky and Hesslein 1995). There are difficulties with separation of attached algae from their substrata, whether they are fine-grained, flocculent sediments, uneven rock surfaces or the fragile surfaces of leaves. Many studies only measure the loosely attached epiphyton, which may be easily dislodged and lost during sampling. The adnate epiphyton can contribute substantially to total epiphyte production (6% in spring and fall to 68% of total algal production in midsummer) (Cattaneo and Kalff 1980). Therefore, it is likely that most studies underestimate the role of epiphytes in macrophyte beds. Also, in comparisons of macrophyte vs. algal biomass, macrophyte leaves are little grazed during early and mid-summer, whereas algae are often heavily grazed, suggesting that the contribution of algae to total energy flow in shallow systems is much greater than their measured contribution to standing crop at any one time (Cattaneo and Kalff 1980, Murkin 1989). Pollard and Kogure (1993) also suggested that simultaneous measurements of algal turnover and biomass are important because, if the grazing rate is high, the algal biomass may represent only a fraction of the macrophyte above-ground biomass. In their study of a tropical seagrass bed, they found that algal and seagrass productivity was equal, each contributing 50% to total net primary productivity. However, seagrasses allocated 75% of their photosynthate to underground tissues, which means that the algae contributed more than half of the aboveground primary production of the system (Pollard and Kogure 1993).

Attempts to compare estimates of primary production among studies are fraught with difficulty, due to differences in methodology (discussed below), difficulty in comparing rates of energy processing (photosynthesis) with measurements of standing crop (chlorophyll-*a*), and differences in units of measurement used (volume vs. substratum area vs. wetland area). There are also few studies that have measured all primary producers within the same time period, making estimates of relative contributions by each producer more difficult.

Among the few studies that have measured most primary producers, it is evident that benthic algae is of major importance, contributing about 54% of annual primary production in Delta Marsh, Manitoba (Table 1) and about 70% in Lawrence Lake, Michigan (Table 2). In both of these systems, total annual algal production exceeded macrophyte annual production. Other studies that have focused on the relative contributions of epiphyton and macrophytes show a wide range of values for epiphyton contribution from 2 to 71% of combined production (Table 3). These values may represent the real range of epiphyton contribution, modified by environmental factors such as nutrient or light limitation and grazing pressure. On the other hand, the variability may be a function of methodological differences and problems obtaining reliable measurements.

Table 1. Primary production in Delta Marsh, Manitoba (estimated using photosynthesis-irradiance models) (from Robinson *et al.* 1997) (macrophyte values from van der Valk 2000).

Primary Producer	Mean Annual ($g\ C\ m^{-2}\ y^{-1}$)	Contribution (%)
Phytoplankton	28	4
Epiphyton	102	14
Metaphyton	265	36
Epipelon	3	< 1
Total Algae	398	54
Total Macrophytes (Above- and Below-ground)	338	46
Total	736	100

Table 2. Primary production in Lawrence Lake, Michigan (from Wetzel and Søndergaard 1998)

Primary Producer	Mean daily (mg C m^{-2} d^{-1})	Mean annual (kg C $lake^{-1}$ y^{-1})	Contribution (%)
Phytoplankton	119	2,154	13
Epiphytic algae < 1 m	2,001	5,512	34
Epiphytic algae 1-5 m	500	5,968	37
Submersed Macrophytes	241	2,701	16
Total		16,335	100

(Note: Epipelon constituted <1% of total primary production)

Table 3. Epiphyte production as a percentage of the total production (plant plus epiphytes) in beds of emergent, submerged macrophytes and mosses (modified from Cattaneo and Kalff (1980) by the inclusion of additional references*)

Host Plant	Location	Epiphyte Production (% of total)	Reference
Loose epiphyton on *Myriophyllum spicatum*	Lake Memphremagog, Québec-Vermont	13-53	Cattaneo and Kalff 1980
Utricularia	Everglades, Florida	>50	Brock 1970
Submersed	Kalgaard, Denmark	2	Søndergaard and Sand-Jensen 1978
Moss (*Marsupella*)	Latnajaure, Lapland	17	Bodin and Nauwerch 1969
Emergent	Mikolajskie, Poland	29	Kajak et al. 1972
Submersed	Mikolajskie, Poland	48	Kajak et al. 1972
Emergent	Pond, Czechoslovakia	21	Straškraba 1963
Submersed and Emergent	Lawrence Lake, Michigan	31	Allen 1971*
Submersed only	Lawrence Lake, Michigan	71	Wetzel and Søndergaard 1998*
Emergent	Lake Belau, Germany	6	Gessner *et al.* 1996*
Emergent	Schöhsee, Germany	65	Gessner *et al.* 1996*
Emergent	Florida Everglades	33-43	Browder *et al.* 1994*

2.2.2 Measuring algal primary production

The standing crop, or biomass, of algae can be estimated by measuring the concentration of photosynthetic pigments, especially chlorophyll-*a,* in algal sub-samples. The method is relatively easy to use and provides a sensitive approximation of algal biomass (Wetzel and Likens 1991). However, chlorophyll-*a* concentrations in algae can vary, depending on light, temperature, nutrient availability, and the physiological state of the algae (Falkowski and Raven 1997). Despite this drawback, the method is widely used, providing the basis for comparing estimations of algal biomass among a large number of studies. However, such measurements of algal standing crop provide an assessment of biomass at only one point in time. Such assessments will likely severely underestimate total annual energy processing by algae, because of such factors as intense grazing pressure and the short (hours to days) life cycle of many algal species. The magnitude of such underestimations is illustrated by this statistic: that approximately 40% of the photosynthesis on Earth each year occurs in aquatic environments and is carried out by less than 1% of the total plant biomass on Earth (Falkowski and Raven 1997).

A more accurate approach to estimating annual energy processing by algae is to determine rates of carbon fixation during photosynthesis. However, there are still difficulties in extrapolating short-term photosynthetic rates determined in small containers to large-scale spaces over long time periods. The small containers themselves introduce potential error in photosynthesis measurements, termed 'bottle effects'. These 'bottle effects', which have been noted with phytoplankton photosynthesis measurements also apply to measurements of benthic algae. These confounding effects include maintenance of algae in an unstirred high light environment, respiration and re-uptake of $^{14}CO_2$, enclosure of bacteria and microzooplankton, and possible N or P limitation (Peterson 1980, Geider and Osborne 1992). Measurements

are further complicated by the disruption of the attached algal community during sample collection. This alters the three-dimensional structure of the biofilm, as well as disrupting the boundary layer and altering the light and nutrient environment of cells within the layered community (Jones 1984). Several approaches have been developed to reduce disruption of the biofilm, including the use of artificial substrata (Allen 1971, Hooper and Robinson 1976, Goldsborough et al. 1986), the use of *in situ* plexiglass chambers (Cattaneo and Kalff1980, Loeb 1981) and the use of microelectrodes for measuring fine-scale changes in oxygen, light, and pH (Revsbech and Jorgensen 1981, Revsbech et al. 1983, Dodds 1992).

2.2.2 (a) Photosynthesis methodology

There are also problems in obtaining comparable estimates due to the use of different methods for measuring photosynthesis. Several methods are currently used for measuring algal photosynthesis, including measurement of oxygen evolution, measurement of ^{14}C uptake, and measurement of changes in dissolved inorganic carbon (DIC) using gas chromatography to measure changes in pCO_2.

The increase in oxygen in a closed system can be used as a measure of photosynthesis because approximately one molecule of carbon is fixed for every molecule of oxygen evolved (Geider and Osborne 1992). The increase in dissolved oxygen in light bottles is considered a measure of net photosynthesis, because it includes both photosynthetic evolution and respiratory consumption. The consumption of oxygen in dark bottles is considered a measure of respiration, and the difference between light bottle and dark bottle dissolved oxygen concentrations (+light - -dark) is a measure of gross photosynthesis. Problems with the O_2 method include lack of sensitivity, particularly in oligotrophic systems where the quantity of oxygen evolved is small in relation to the background concentration of the gas. On the other hand, productive samples may produce more O_2 than there is headspace in the bottle, leading

to loss of O_2 and measurement error. In addition, the O_2/CO_2 ratio, or photosynthetic quotient, is not usually 1, but can range from 1.1 to 1.4, requiring some mathematical adjustment to obtain the amount of C fixed (Geider and Osborne 1992).

The radioactive tracer, ^{14}C, has been used for many years in photosynthesis experiments since it was introduced in 1952 by Steemann-Nielsen (Geider and Osborne 1992). The tracer method is a sensitive method, which can be used in both oligotrophic and eutrophic systems. It is based on the incorporation of inorganic ^{14}C into organic algal carbon and assumes that the addition of a small amount of radio-labeled carbon does not change the DIC concentration significantly. A further assumption is that ^{14}C uptake is quantitatively proportional to ^{12}C uptake, and that the discrimination against uptake of the heavier isotope is constant at 5%, resulting in the use of an isotope discrimination factor of 1.05 in photosynthesis calculations (Strickland and Parsons 1972). The largest drawback of the ^{14}C method is that there is no measurement of respiration, so that there is some ambiguity in whether the rate of ^{14}C uptake is a measure of gross or net photosynthesis. Over a short incubation period, before a significant fraction of the organic carbon becomes labeled, the rate of uptake of ^{14}C is interpreted to be a measure of the gross photosynthetic rate (Geider and Osborne 1992). Over longer time periods, as the label of the organic portion approaches equilibrium with the labeled inorganic pool, a portion of the labeled organic carbon will be respired, and the rate of uptake of ^{14}C is taken as a measure of the net photosynthetic rate. At four hour incubation times, with a physiologically healthy mixed population of algae, ^{14}C uptake probably measures something in between gross and net photosynthetic rates, but closer to gross than net (Falkowski and Raven 1997).

The measurement of changes in DIC by using gas chromatography to measure changes in the partial pressure of CO_2 (pCO_2) is a method that has been used successfully for algal assemblages in the oligotrophic lakes of the Experimental Lakes

Area (Turner *et al.*1995). The method entails obtaining accurate measurements of initial DIC, including pCO_2, pH and carbonate alkalinity prior to incubation. Following incubation, measurements of DIC are again made, using infrared gas analysis techniques. Similar measurements are made for dark bottles for determining dark respiration. Algal photosynthesis is calculated as the measured change in DIC adjusted for incubation time and the amount of algal material incubated (Turnet *et al.* 1995). The advantage of this method is that it is a direct measure of CO_2 uptake, and includes a measure of respiration, allowing estimation of both net and gross photosynthesis.

2.2.2 (b) Photosynthesis-irradiance relationships

Photosynthesis is a biological response to light, which can be examined mathematically as a resource-response curve. In this case, irradiance (*E*) is the resource and the rate of photosynthesis (P) is the response, resulting in the term P*E* relationship or P*E* curve. According it optical physicists, *E* is the symbol for irradiance, the flux of radiant energy on an infinitesimally small surface, which is expressed in units of mol quanta m^{-1} s^{-1}. The use of *I* to denote irradiance has been dropped because *I* has been adopted to denote radiation intensity with units mol quanta s^{-1} $steradian^{-1}$ (Falkowski and Raven 1997).

There are three regions of the relationship between photosynthesis and irradiance, (1) a light-limited region in which photosynthesis increases with increasing irradiance (denoted by *a*), (2) a light-saturated region in which photosynthesis is independent of irradiance (P_{max}), and (3) a photoinhibited region in which photosynthesis decreases with further increases in irradiance (ß) (Figure 4). A fourth value, E_k, corresponds to the point at which the linear part to the initial slope intersects the plateau, and is therefore a measure of the irradiance at the onset of light saturation, calculated from P_{max}/a (Geider and Osborne 1992).

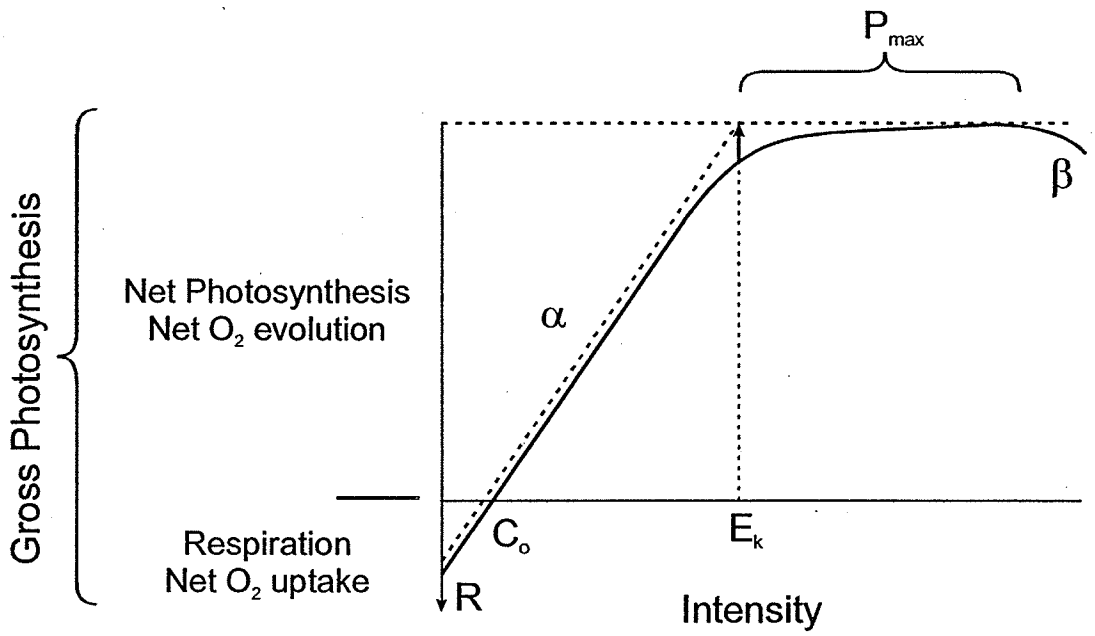

Figure 4. An example of a typical photosynthesis vs. irradiance curve. This curve could be derived from measurements of net oxygen exchange between the organism and the bulk fluid. In the dark, there is a net consumption of oxygen as a consequence of respiration. Dark respiration, R, is generally assumed to remain constant in the light. At low irradiance levels, the evolution of oxygen is approximately a linear function of irradiance, and the ratio between photosynthesis and irradiance in this portion of the photosynthesis-irradiance profile is often denoted by the symbol *a*. At some irradiance level, photosynthetic rates reach a plateau. The light-saturated rate is denoted P_{max}. The saturation irradiance, E_k, is given as intercept between *a* and P_{max}. At supra-optimal irradiance levels, photosynthetic rates frequently decline from the light-saturated value. The rate of decline, *ß*, is analogous to the initial slope, *a*, but with an opposite sign (from Falkowski and Raven 1997).

Many mathematical representations of PE curves have been developed (Talling 1957, Fee 1973, Bannister 1974, Jassby and Platt 1976, Platt *et al.* 1980). The mathematical representation of the P*E* curve requires a nonlinear mathematical function to account for the change in the rate of photosynthesis at light-saturation. Functions that have been successful to varying degrees include a rectangular hyperbolic function, a quadratic function, an exponential function, and a hyperbolic tangent function (Table 4).

The curves generated by these equations are somewhat similar, differing mainly in the abruptness of the transition from light-limited to light-saturated photosynthesis (Geider and Osborne 1992). The rectangular hyperbolic equation, taken from the Michaelis-Menton description of enzyme kinetics, generally has the poorest fit for P*E* models, because the curve bends too slowly and the light-saturation effect is not adequately described (Bannister 1974, Falkowski and Raven 1997). The quadratic function was used in early photosynthesis models (Talling 1957), but has not been widely adopted. The hyperbolic tangent and the exponential function both provide similar fit to experimental data and are the most widely used in empirical photosynthesis modeling. The exponential function is mathematically identical to the cumulative one-hit Poisson distribution used to describe the relationship between flash intensity and flash yield of oxygen in the photosynthetic unit during flash photolysis (Falkowski and Raven 1997). The hyperbolic tangent function was introduced as a purely empirical function (Jassby and Platt 1976), and has less biologically-based justification (Geider and Osborne 1992). I chose to use the exponential function because there is a physiological basis for its application to P*E* curves, it mathematically simplifies a complex process, and it has been used by other wetland researchers (e.g., Robinson *et al.* 1997), providing a stronger basis for inter-study comparison. The exponential function also makes provision for photosynthetic inhibition (*ß*), which appeared to occur at high light levels in my P*E* experiments with phytoplankton and periphyton.

Table 4. Examples of some equations used to model photosynthesis-irradiance (P*E*) relationships (from Falkowski and Raven 1997).

$P=P_m \frac{aE}{P_m + aE}$	Rectangular hyperbola
$P=P_m \frac{aE}{\sqrt{P_m^2 + (aE)^2}}$	Quadratic
$P=P_m [1 - e^{(-aE/Pm)}] \times e^{(-\beta E/Pm)}$	Exponential
$P=P_m \tanh \frac{aE}{P_m}$	Hyperbolic tangent

2.2.2 (c) Variability in PE curves

An abrupt break in a resource-response curve indicates a switch in control of the response between two different external factors (Blackman 1905, in Geider and Osborne 1992). With the P*E* curve, the initial slope, *a*, is a light-dependent process, because it is a function of the photochemical processes of photosynthesis (i.e. the light reactions) and depends on the ability of the cells to trap light and the quantum yield (the ratio of product formed per unit of light absorbed). P_{max} is a function of the enzymatic processes in photosynthesis (i.e. the dark reactions) and is thus independent of changes in irradiance. The term, *ß*, is used to denote photoinhibition, which is a physiologically-based modification of P_{max} by a reversible or irreversible inactivation of photo-system II (Geider and Osborne 1992, Falkowski and Raven 1997). Early measurements of photoinhibition were often an artifact of phytoplankton being held in high light intensities for an artificially long period of time during incubation experiments (Peterson 1980). However, even in rapidly mixing water columns, on sunny days there is often evidence of a mid-day depression in the photosynthetic rate at the water surface (Falkowski and Raven 1997).

The initial slope, *a,* is expressed as photosynthesis per unit of biomass per unit of incident irradiance and so is a measure of the efficiency with which the algae uses light, at low intensities, to fix CO_2 (Kirk 1994). The initial slope, *a*, may be controlled by cell size and shape, which affects self-shading of chlorophyll in the cell (i.e. influence of the package effect) (Taguchi 1976), pigment composition as it is affected by light quality and nutrient availability (Osborne and Geider 1986, Falkowski *et al.* 1989) or diel periodicity (Sournia 1974, MacCaull and Platt 1977). The initial slope, *a*, is usually considered to be temperature independent, but the rate of photosynthetic electron transport is dependent on the fluidity of organelle membranes, which is influenced by temperature (Falkowski and Raven 1997). Therefore, it is possible for *a* to vary with temperature, but the effect is usually minor in comparison to rate-limitation by light (Tilzer *et al.* 1986). P_{max} can vary

under the influence of temperature (Harrison and Platt 1980), nutrient availability (Cote and Platt 1984, Osborne and Geider 1986), diel periodicity (Sournia 1974), and species composition (Cote and Platt 1984).

The major source of variation in photosynthetic rates per area in aquatic systems is related to the amount and distribution of photosynthesizing biomass. In physiological terms, the rate of photosynthetic electron flow is related to the concentration of photosynthetic pigments per unit volume or area of aquatic system (Falkowski and Raven 1997). Therefore, when photosynthetic rates are normalized to chlorophyll-*a*, there is a reduction in variance by an order of magnitude. Considerable variation remains, which needs to be related to one or a combination of the factors described above that cause variation in photosynthetic parameters. Parameters that have been normalized to chlorophyll concentration are denoted by the use of the superscript ^{B}, as in P^{B}_{max}, or a^{B}.

The aim of developing quantitative photosynthesis models is to be able to use them to predict algal production from measurements of chlorophyll-*a* and daily PAR. In order to make accurate predictions, it is necessary to develop models with values for the photosynthetic parameters, P_{max}, *a*, and *ß*, which are relevant to the environmental influences on these parameters. The use of models to predict algal photosynthesis from chlorophyll and daily PAR helps to alleviate the problems involved with 'scaling up' to estimations of integrated annual primary production for an entire system. Most of the current models have been developed and tested for phytoplankton, although some modeling of wetland algae has been done (e.g., Robinson *et al.* 1997). An important contribution towards the goal of adequately characterizing primary production in wetlands is to test a photosynthesis model using algal assemblages found in a number of wetlands and to evaluate the output against measured environmental influences over time. On a global scale, measurements of chlorophyll fluorescence via remote sensing

are coupled with irradiance measurements to predict global annual algal production in oceans (Falkowski and Raven 1997).

2.2.3 Grazing and primary production

Primary production provides food resources for invertebrate and vertebrate consumers and in turn, grazers alter the biomass of the primary producers. For example, grazing by snails is able to limit the peak standing crop of epiphytic algae (Elwood and Nelson 1972, Hunter 1980). Cladocerans, copepods and chironomids have the capacity to reduce epiphytic algal biomass substantially (Mason and Bryant 1975, Hann 1991). Zooplankton, such as *Daphnia* and *Bosmina*, are also able to significantly reduce phytoplankton biomass (Schriver *et al.* 1995).

Algae are generally considered to have high nutritional value (Lamberti and Moore 1984) and are readily available to grazers with small mouthparts (Campeau *et al.* 1994). Vascular plant tissue has been argued to be a less desirable food source than algae because of low nutritional value (high C/N ratio), tough cell walls, lignified structures and secondary plant metabolites (Otto and Svensson 1981). Therefore, macrophyte tissue is more likely to enter the invertebrate diet as partially decomposed organic detritus (Porter 1977). Sand-Jensen and Borum (1991) support this view, suggesting that grazing losses are higher for planktonic and benthic algae which have a high protein content and are easy to ingest and digest for many invertebrates. They contend that invertebrate grazing on rooted macrophytes is probably lower in most aquatic systems. Campeau *et al.* (1994) found that cladocerans, copepods, and ostracods readily grazed algae, and that their abundance increased in response to increased algal production via nutrient addition. Chironomids also responded to algal production, but used decaying macrophyte litter as an important alternate food source in late summer (Campeau *et al.* 1994). Soszka (1975, reported in Brönmark 1989) found that trichopteran and lepidopteran larvae fed almost exclusively on living macrophyte

tissue, causing extensive loss of *Stuckenia* (*Potamogeton*) leaf surface area. Other researchers have found that invertebrates graze the epiphyton on the macrophyte leaves, benefiting the grazer-resistant macrophytes by reducing epiphyton competition for light and nutrients (Orth and van Montfrans 1984, Duffy 1990). This grazing interaction supports the mutualism hypothesis of Hutchinson (1975).

Whereas living macrophytes may be a minor food source for invertebrates, vertebrates graze them more extensively. Waterfowl grazing removed about 30 to 40% of the peak standing crop of *Stuckenia* foliage and 18% of the tubers during mid- to late summer (Anderson and Low 1976, Jupp and Spence 1977). Muskrats harvested 9 to 14% of the annual net biomass production of *Typha* shoots for lodge construction and feeding (Pelikan *et al.* 1971). Nutria reduced above-ground biomass of *Sagittaria* by 84% and below-ground biomass by 24-40% (Evers *et al.* 1998). Fish and crayfish are also important grazers of submersed macrophytes, with crayfish removing 50 to 90% of shoot biomass (Carpenter and Lodge 1986, Lodge 1991). Grazing by fish (rudd) on *Elodea* and *Stuckenia* and by birds (coots) on *Elodea* and *Ceratophyllum* was found to decrease total submersed macrophyte abundance and cause a shift in species composition to less edible species (van Donk and Otte 1996). Grazing by coots was also found to delay re-colonization of shallow areas by *Stuckenia* (Lauridsen *et al.* 1993).

2.3 Chemical roles for algae and macrophytes

Direct chemical roles for algae and macrophytes are based on their uptake and release of chemicals within the aquatic environment. The uptake and release of organic and inorganic nutrients that occurs during nutrient cycling is one of the key chemical roles for both algae and macrophytes. Secretion and leaching mechanisms that release chemicals into the environment may also have a number of other ecological functions besides nutrient cycling. Both algae and macrophytes have been shown to secrete low

molecular weight organic compounds into their surrounding environment (Wetzel and Manny 1972, Sharp 1977, Søndergaard and Schierup 1982, Bjørnsen 1988, Mann and Wetzel 1996). These compounds include glycolic acid, carbohydrates, polysaccharides, amino acids, peptides, organic phosphates, volatile substances, enzymes, vitamins, hormones, inhibitors and toxins (Wetzel 1983a). The physiological mechanisms and the ecological functions underlying such secretions are still poorly understood. There has been much discussion about the role of these exudates from primary producers, with evidence for support of bacterial production, provision of mucilage for protection and motility, provision of chemoreception for grazers, allelopathy and in particular, for enhancement of nutrient cycling. In addition, there is a direct chemical role for algae and macrophytes in environmental toxicant uptake, which is important in food web biomagnification of toxicants and in bioremediation and waste disposal processes. However, a discussion of toxicant uptake will not be undertaken in this paper.

Algae and macrophytes may also affect the chemical environment indirectly, through processes that alter sediment or water column chemistry. Photosynthetic and respiratory processes have impacts on sediment redox conditions, which in turn influence sediment nutrient retention, production of root phytotoxins, and regulation of gas emission and transport. Photosynthesis and respiration also affect water column dissolved oxygen concentrations, pH, and bicarbonate alkalinity equilibrium.

2.3.1 Algal secretion

For algae, it has been suggested that dissolved organic matter (DOM) or dissolved organic carbon (DOC) secretion is the active release of excess photosynthates that accumulate when carbon fixation exceeds incorporation into new cell material (Fogg 1983). More recently, DOM secretion has been re-interpreted as a continuous loss of compounds via passive diffusion across a concentration gradient through permeable cell membranes (Bjørnsen 1988). Bacteria on the exterior of algal cell walls are thought to

maintain the concentration gradient by continuously assimilating the exudates (Iturriaga and Hoppe 1977). Baines and Pace (1991) have since questioned this passive diffusion interpretation, and argue for Fogg's earlier interpretation of an excess photosynthate mechanism. At present, it appears that the underlying mechanism of DOM secretion in algae is still in question. Extracellular release from algae can range from 0 to 50% of photosynthetic carbon fixation (Sand-Jensen and Borum 1991).

2.3.2 Macrophyte secretion

The underlying physiological mechanism of macrophyte secretion is also still under debate. Evidence that secretion occurs has been provided by tracer studies that follow the translocation of a radio-labeled substance, such as ^{14}C or ^{32}P (see Nutrients below). The extracellular release comprises 0 to 4% of photosynthetically fixed carbon in macrophytes (Sand-Jensen and Borum 1991). Allen (1971) suggested that macrophyte secretions may function as chelators, allowing autotrophs access to inorganic iron, antibiotics, vitamins, hormones and sources of enzymes. Pakulski (1992) suggested a secretion mechanism for emergent halophytes involving secretion of ions from leaf salt glands, or the accumulation and subsequent leaching of salts from leaf surfaces as a result of transpiration. Acropetal mass transport of water (guttation) powered by root pressure has been demonstrated in submersed macrophytes using tritiated water as a tracer (Pedersen 1993, Pedersen and Sand-Jensen 1993). This mass transport mechanism accounts for nutrient translocation from roots to growing leaves, so it is also likely to be involved in macrophyte secretion.

2.3.3 Support of bacterial production

Macrophyte-derived organic carbon supports bacterial production, although most emergent macrophyte studies focus on leachate from decomposition rather than DOC secretion (e.g., Mann and Wetzel 1996, Boschker *et al.* 1999). Decomposition will be discussed in more detail below (see Nutrients).

Submersed macrophytes may be comparable to algae in terms of DOC secretion. Secretion of DOC by the submersed macrophyte, *Najas flexilis*, was found to equal secretion by phytoplankton in Lawrence Lake, and the total of these two sources was greater than allochthonous DOC input (Wetzel and Manny 1972). In addition, both the algal and the submersed macrophyte DOC were equally labile, and therefore more readily used by bacteria, than the allochthonous DOC. Because of continuous leaf-turnover among many submersed macrophytes, high levels of exudates originate from living, as well as senescing, macrophytes (Wetzel and Søndergaard 1998).

The significance of the contribution of phytoplankton carbon secretion to the support of bacterial production is currently under debate. A commonly held view has been that phytoplankton are the major source of organic matter for bacterioplankton, a view supported by evidence of the covariance of bacterial abundance and production with phytoplankton biomass and production (Cole and Likens 1979, Søndergaard *et al.* 1985, Friedrich *et al.* 1999). However, quantitative analyses from a number of studies have shown that phytoplankton extracellular release accounts for only about 13 to 32% of bacterial carbon requirements across aquatic systems of varying trophic status (Baines and Pace 1991). Wetzel and Søndergaard (1998) contend that in shallow aquatic systems, the abundance of phytoplanktonic carbon is totally inadequate to fuel bacterioplankton production. They argue that carbon from epiphytic algae on the surfaces of submersed macrophytes fuels the bulk of bacterial production in many small lakes and wetlands.

2.3.4 Mucilage secretion

Another type of secretion, produced by both algae and bacteria, is mucilage, which can constitute a substantial portion of attached microbial communities or biofilms (Wetzel *et al.* 1997). The composition of mucilage is varied, consisting mainly of mucopolysaccharides, with bacterial production of exopolymer fibrils important in the

initial phase of attachment to a new surface (Wetzel *et al.* 1997). Little is known about the environmental factors that determine the amount of mucilage associated with attached communities. Wetzel *et al.* (1997) observed that mucilage occurs as sheets, sometimes several layers thick, which cover both living and detrital components of the biofilm. They speculate that the mucilage film acts as a diffusion barrier to the community. The film would help decrease diffusion loss of nutrients from the community to the surrounding water and encourage efficient recycling of nutrients between the algae and bacteria within the mucilage. The mucilage film also provides a large surface area for adsorption of dissolved and particulate matter from the surrounding water, which acts to increase the diffusion gradient for nutrients into the attached community. The amount of mucilage produced by attached communities is reduced in the presence of DOC derived from the macrophyte leachate of *Typha latifolia* (Wetzel *et al.* 1997). Humic acids in the DOC appeared to alter the porosity of the mucilage, suggesting an underlying chemical basis for a possible allelopathic effect of emergent macrophyte leachate on epiphyton. Allelopathic interactions are discussed in more detail below.

Mucilage secretion in algae is also important in motility, attachment to substrata, and protection from desiccation. Some pennate diatoms extrude mucilage through a raphe, a long narrow opening in the cell wall, which imparts gliding motion to this group of algae (Sze 1993). Mucilage secreted for attachment purposes is often amorphous in green algae and cyanobacteria, and is organized into pads, stalks and tubes for diatoms (Blunn and Evans 1981, Stevenson 1996). Production of mucilage stalks allows diatoms to form a three-dimensional structure on attachment surfaces, which may impart advantages in competition for light or nutrients (Hoagland *et al.* 1982). Flexible mucilage stalks also allow diatoms to tolerate turbulence while remaining firmly attached to the substratum (Cattaneo 1990, Hoagland and Peterson 1990). Some colonial cyanobacteria can survive short periods out of water through use of a mucilage reservoir

to keep the cells hydrated (Shephard 1987). Secretion of mucilage by diatoms is also thought to enhance resistance to short-term desiccation (Hoagland *et al.* 1993). In flowing water, mucilage has been suggested to function in decreasing cell exports and retaining cell immigrants in attached communities (Peterson 1987).

2.3.5 Chemoreception

The secretion of macrophyte exudates has been proposed as a chemoreception mechanism for attracting snail grazers to reduce epiphyte colonization on macrophyte surfaces (Brönmark 1989). Brönmark (1989) argues that if the association between submersed macrophytes and their epiphytes is not symbiotic, but competitive, then the macrophytes would have evolved mechanisms to counteract the negative effects of epiphytes. An association between submersed macrophytes and snail grazers has long been noted (Krecker 1939). Pip and Stewart (1976) advanced the hypothesis that secretions of organic compounds from submersed macrophytes may attract specific snail species, reducing interspecific competition for food. They suggested, based on grazing damage to macrophytes, that the vascular plant tissue formed an important part of the snail diet. Brönmark (1985) refined this hypothesis by including epiphytes in the interaction between submersed macrophytes and snail grazers. Grazing studies had shown that detritus and algae formed the largest proportions of snail diets, with living macrophyte tissues comprising <1% of the diet (Reavell 1980, reported in Brönmark 1985). In addition, it was shown that snails selectively grazed preferred patches of epiphyton (Calow 1974, reported in Brönmark 1985). Brönmark (1985) suggested that dissolved organic matter secreted by macrophytes attracted grazers, which then removed the epiphytic covering on macrophyte leaf surfaces. The growth of the macrophytes was subsequently enhanced via decreased shading by epiphytes (Brönmark 1985) and decreased necrotic conditioning by epiphytic bacteria (Rogers and Breen 1983).

2.3.6 Allelopathy

The existence of allelopathic interactions between macrophytes and algae has been invoked many times in the literature (e.g., Hasler and Jones 1949, Hutchinson 1975, Hootsmans and Blindow 1994), but proof of the occurrence of such interactions is by no means clear-cut. Allelopathy differs from competition, in that allelopathy involves the secretion or exudation of a chemical substance into the environment, whereas competition results from the reduction of some co-required factor in the environment (Rice 1984).

A number of compounds have been isolated from macrophyte leaf extracts that have demonstrated negative effects on algal growth and photosynthesis. Two sulfur-containing compounds isolated from several characean species (*Chara globularis*, *C. hispida* L., *C. baltica*) inhibited both epiphytic diatom and pond phytoplankton photosynthesis (Wium-Andersen *et al.* 1982). Whereas charophytes are botanically classified as algae of the Class Charophyceae in the Division Chlorophyta (Sze 1993), they are included here with macrophytes because of their macroscopic structure and their similar growth habit to vascular submersed macrophytes. Three organic compounds were isolated from *Ceratophyllum demersum* L. that inhibited the growth of green algae (Larson 1983). Water-soluble extracts of eelgrass (*Zostera marina*) leaves, thought to contain phenolic compounds, were found to reduce the rate of photosynthesis of diatom epiphytes (Harrison and Durance 1985). Sterol and fatty-acid extracts from *Typha latifolia*, an emergent macrophyte, were demonstrated to selectively inhibit cyanobacteria, but not green algae or chrysophytes (Aliotta *et al.* 1990). Jasser (1995) tested extracts from several macrophytes, and found that *Ceratophyllum demersum* L. and *Myriophyllum spicatum* L. extracts had significant inhibitory effects on cyanobacteria but not on green algae. Nakai *et al.* (1996) found that a fraction of highly polarized compounds extracted from *M. spicatum* L. produced an inhibitory effect on both green

algae and more strongly on cyanobacteria, but were rapidly biodegraded. These studies indicate that some macrophytes contain compounds that have the potential to inhibit algal growth. However, the existence of these compounds within macrophytes is not proof that they are exuded or secreted to interact with algae in the environment (Wium-Andersen 1987).

In fact, the occurrence of allelopathy in the field has yet to be demonstrated conclusively (Scheffer 1998). Direct evidence of secretion of phytotoxic compounds in macrophyte stands is lacking. Instead, the absence or sparseness of phytoplankton in macrophyte-dominated water bodies has been used as evidence of allelopathic interactions (Hasler and Jones 1949, Jasser 1995, Mjelde and Faafeng 1997). In most of the studies where allelopathy is suggested, other factors are not completely ruled out that may provide alternative and equally plausible explanations (Hootsmans and Blindow 1994). These factors include competition for nitrogen (Fitzgerald 1969), competition for phosphorus and changes in water chemistry (conductivity and carbonate alkalinity) (Brammer 1979), presence of a thick hydrophobic cuticle on *Scirpus validus* culms (Goldsborough and Hickman 1991), and competition for light (Grimshaw *et al.* 1997). It is possible that cyanobacteria may experience allelopathic inhibition by *Ceratophyllum* and *Myriophyllum*, allowing other algae such as greens and diatoms to gain a competitive advantage (Jasser 1995, Scheffer 1998). However, Forsberg *et al.* (1990) argue that *Chara* does not have allelopathic effects on phytoplankton, based on "normal" phosphorus-chlorophyll relationships found in *Chara*-dominated lakes that compare favorably to the range of these relationships published for other lakes worldwide. They also point to the observations by several workers of charophyte stands covered by visible coatings of epiphytes as an indication of the absence of allelopathy by *Chara in situ*. Godmaire and Planas (1986) found that *Myriophyllum spicatum* L. stimulated rather than inhibited phytoplankton production in enclosures, a result that they attributed to

some factor other than nutrient or light conditions, although they then proceeded to speculate about phosphorus release from epiphyton.

Other examples of allelopathy have also been reported, including algal/algal, algal/macrophyte, and macrophyte/macrophyte interactions. Cyanobacterial toxins were tested for allelopathic effects on green algae, producing mixed results, including stimulation, inhibition, and no effect (Wolfe and Rice 1979). Cyanobacterial secretions were also shown to have negative effects on the growth and photosynthesis of the macrophyte *Zannichellia peltata*, although nutrient competition was not completely eliminated as an alternative explanation (van Vierssen and Prins 1985). Allelopathic effects of the spikerush (*Eleocharis* spp.) on pondweeds (*Potamogeton* spp.) and on common duckweed (*Lemna minor*) were investigated and found to be of minor importance (Frank and Dechoretz 1980, Wooten and Elakovich 1991).

Despite the lack of clear evidence for allelopathy in field studies, it cannot be completely ruled out as a possible interaction between macrophytes and algae, because of the existence of phytotoxic metabolites found in some macrophytes. Rather, the suggestion is that allelopathy may occur in concert with other antagonistic effects (Hootsmans and Blindow 1994). At the ecosystem level of interaction, allelopathy is thought to be of lesser importance than other factors such as nutrient, light, and grazing effects (Søndergaard and Moss 1998).

2.3.7 Toxin production

Some species of cyanobacteria are known to produce potent neurotoxins and hepatotoxins (Gurney and Jones 1997). These toxins can be detected by protein phosphatase bioassays (Lambert *et al.* 1994) and are thought to enter the water when algal cells rupture or die. Whereas these toxins are not known to affect other algae or macrophytes, they are toxic to fish (Tencalla *et al.* 1994), animals (Galey *et al.* 1987, Gurney and Jones 1997), and humans (Falconer *et al.* 1983). Neurotoxins affect the

nervous system causing muscle twitching, cramping, fatigue, paralysis and often death (Carmichael 1994). *Anabaena, Aphanizomenon*, and *Oscillatoria* sp. are genera known to produce neurotoxins. The most common algal hepatotoxin is microcystin-LR, which was first isolated from *Microcystis aeruginosa*, but can also be found in *Oscillatoria*, *Anabaena* and *Aphanizomenon* sp. (Carmichael 1994). This hepatotoxin causes extensive necrosis of the liver, resulting in death by hemorrhagic shock or liver failure. Sublethal long-term ingestion of hepatotoxin has been implicated in the promotion of liver cancer in humans (Falconer 1991).

Whereas these toxins may not have direct relevance to a discussion of algal/macrophyte interactions, their existence provides another reason for managers of aquatic ecosystems to understand and monitor conditions that might promote massive cyanobacterial blooms. The conditions under which toxic cyanobacterial blooms most commonly occur are quite variable and not all cyanobacterial blooms produce toxins (Kotak *et al.* 1993). Environmental factors such as high nutrient concentrations, low N to P ratios, persistent warm water temperatures and high pH are thought to promote both cyanobacterial growth and toxin production. Conventional water treatment technology (flocculation, filtration and chlorination) does not remove significant amounts of these toxins (Gurney and Jones 1997). Therefore, awareness of the existence of these toxins is crucial for individuals using wetlands, reservoirs and shallow lakes for human and livestock water supplies, trout farms, or recreational bathing.

2.3.8 Nutrients

2.3.8 (a) Sources of nutrients

In shallow ecosystems, nutrient pools in water and sediment are interconnected, via sedimentation and adsorption to sediments and via diffusion, resuspension, and macrophyte-mediated transfer to the water column. Both macrophytes and algae are dependent on the inorganic nutrients cycling between these two pools and through the biotic components of

the ecosystem, including invertebrates, fish, and the macrophytes and algae themselves. The positioning of primary producers within the ecosystem may control competitive access to nutrients.

The water column is the major source of nutrients for phytoplankton. Because P is often the macro-nutrient in shortest supply in the water column, phytoplankton are often considered to be P-limited in freshwaters (Wetzel 1983a, Hecky and Kilham 1988). Phytoplankton tend to have thin diffusive boundary layers, due to sinking motion or locomotion, and large surface area to volume ratios, which aid in rapid nutrient uptake (Sand-Jensen and Borum 1991). However, concentrations of available forms of inorganic nutrients in the water column are often extremely low. For example, orthophosphate (PO_4^-) normally comprises <10% of total P in most water bodies and is rapidly assimilated by autotrophs (Wetzel 1983a). Inorganic nitrogen forms often constitute <50% of total soluble N in freshwaters. Concentrations of ammonium (NH_4-N) are generally low in aerobic water columns because of algal and macrophyte uptake and bacterial nitrification to nitrate (NO_3^-). Nitrate is the predominant form of inorganic N in aerobic water columns, but its concentration may be rapidly reduced by autotrophic uptake and by some denitrification to N_2 in anoxic microzones (Wetzel 1983a).

Sediments may sometimes become sources of nutrients to phytoplankton in shallow water columns. This happens when sediments are resuspended into the water column by wind or wave action (Mayer *et al.* 1999), or by sediment disturbances caused by carp (King *et al.* 1997) and burrowing insects (Gallepp 1979). Flocculent, fine-grained organic sediments are particularly susceptible to resuspension (D'Angelo and Reddy 1994), particularly in the absence of stabilizing algal biofilms or submersed macrophytes (see Physical Roles below). Nutrients may also be released from sediments into the water column during periods of anoxia at the sediment-water interface (see Indirect Chemical Effects below). Carignan and Kalff (1982) calculated that soluble P release from epiphyton accounted for a 2.2% daily increase in P concentration in the water column. They suggested

that this release represented a new supply of P to phytoplankton from sediments, through macrophytes and epiphyton.

The nutrient uptake dynamics of macrophytes have been studied extensively, with the conclusion that the sediments are a more important source of nutrients for rooted macrophytes than the water column (Barko and Smart 1980, Howard-Williams and Allanson 1981, Carignan 1982, Moeller *et al.* 1988, Barko *et al.* 1991). Twilley *et al.* (1977) found that in the heterophyllous macrophyte, *Nuphar luteum,* the roots absorbed P from the sediments, which was translocated acropetally. The submersed leaves of *Nuphar* absorbed P from the water column, which was translocated both acropetally and basipetally, whereas the floating leaves functioned mainly as photosynthetic organs. They noted that root P absorption was greater than submersed leaf P absorption by a factor of 10 (Twilley *et al.* 1977). Various studies have reported that sediment-derived P accounts for 50% (Carignan 1982), 70% (Chambers *et al.* 1989), and 100% (Carignan and Kalff 1980) of source P for macrophytes. Attempts to stimulate submersed macrophyte growth by P addition to the water column have generally been unsuccessful (Moeller *et al.* 1988, Barko *et al.* 1991). The greater reliance of macrophytes on sediments, rather than the water column, as a source of P may be related to the low concentrations of available soluble reactive phosphorus (SRP) in the water column. Carignan (1982) developed an empirical model that related macrophyte use of P to the ratio of sediment pore-water SRP to water column SRP concentrations. At a ratio of approximately 3:1, macrophytes obtained equal amounts of P from the two sources. At higher ratios, sediments were the principle source of P for macrophytes, which at lower ratios, water was the principle source (Carignan 1982).

Both sediments and the water column may supply N to submersed macrophytes, depending on which source has the higher N concentration (Nichols and Keeney 1976). However, submersed macrophytes preferentially take up ammonium over nitrate, which indicates that the reducing environment of the sediments may be the predominant source for N (Nichols and Keeney 1976). Available N is depleted from sediments more rapidly than P

because of smaller exchangeable N pools in the sediments (Barko *et al.* 1991), suggesting that N is more likely to limit submersed macrophyte growth. In fact, fertilization experiments using N have resulted in significantly increased growth of submersed macrophytes (Anderson and Kalff 1986, Moeller *et al.* 1988).

Nutrient sources to benthic algae, particularly to epiphyton, have been the subject of much debate. The role of macrophytes in supplying nutrients to their epiphytes has been at the center of this debate. Some researchers have argued that macrophytes pump nutrients from sediments to epiphytes (Jackson *et al.* 1994), a role that will be discussed in more detail below (see Macrophytes as nutrient sources). Eminson and Moss (1980) hypothesized that macrophytes act as a major nutrient source for epiphyton in nutrient-poor systems, but in eutrophic systems, the water column becomes the major nutrient source. It is clear that epiphytes have access to nutrients in the water column, but the thickness of the biofilm and the stagnant boundary layer around the epiphyte-macrophyte complex may limit diffusion of nutrients into the matrix (Borchardt 1996). Epiphytes may also rely on rapid cycling of nutrients between the algal and bacterial constituents within the biofilm itself (Mulholland *et al.* 1991, Wetzel 1993). For sediment-associated algae, both the sediments and the water column have been shown to be nutrient sources (Hansson 1989, Portielje and Lijklema 1994). Metaphyton may have access to sediment nutrient sources as long as mats remain attached to either sediments or macrophytes. However, these mats also have access to nutrients in the water column (Fong *et al.* 1993) where some species (e.g., *Enteromorpha* spp) are efficient scavengers of nitrate (Harlin 1978) and others (e.g., *Cladophora glomerata*) prevail at high P concentrations (Dodds 1991a).

2.3.8 (b) Macrophytes as nutrient sources

One facet of the proposed symbiotic relationship between macrophytes and epiphytes is that epiphytes may benefit from the organic compounds and nutrients secreted

by the macrophytes. Early work was aimed at determining whether there was some chemically-driven host specificity for particular epiphyte species on macrophytes. Prowse (1959) placed 'clean' (epiphyte-free) plants in a large fishpond, allowed colonization for a fortnight and found that there appeared to be some host specificity, although he did not speculate on the nature of this relationship. Allen (1971) speculated that epiphytic diatoms that have a growth requirement for silicon might preferentially colonize the silica-rich stems of *Phragmites* sp. Eminson and Moss (1980) suggested that host specifity of epiphytic algae may be regulated by nutrient deficiency, where the necessary nutrients are supplied by macrophyte exudates. Goldsborough and Robinson (1985) noted host specifity of epiphytes on the free-floating macrophyte *Lemna minor* in midsummer, but did not attribute this to simple nutrient deficiency. They argued that nutrient limitation within a *Lemna* mat should exert a similar selective pressure as nutrient limitation associated with artificial substrata, resulting in similar epiphytic communities. Since the epiphytic communities on *Lemna* and artificial substrata were distinctly different in composition they suggested some more specific physical or chemical (possibly facultative heterotrophy of macrophyte exudates?) link involved in host specificity. Burkholder and Wetzel (1989) also argued for specific metabolic interactions between macrophytes and their epiphytes, citing the differing algal community composition on plastic plants compared to real macrophytes. They concurred with the hypothesis of Eminson and Moss (1980) that macrophyte sources of nutrients are important to epiphytes in oligotrophic systems, but less so in eutrophic systems where water column nutrients are more important.

The argument that epiphytes gain nutritional benefits from their host macrophytes gained credence as tracer studies identified translocation of substances from one to the other. Allen (1971) traced the translocation of ^{14}C through macrophytes to epiphytes and found evidence of increased DOM secretion when epiphytes were present versus when

they were not. He found that macrophyte secretion of ^{14}C accounted for 15 to 19% of carbon fixed by epiphytic algae. He argued for the occurrence of chemo-organotrophy in epiphytic algae, enhanced by the close association of bacteria and algae on macrophyte surfaces rich in DOM secretions (Allen 1971). Goering and Parker (1972) described a nutritional link from algae to the host macrophyte. They found that some species of epiphytic cyanobacteria fixed molecular nitrogen and the resulting soluble nitrate found its way into the seagrass host. Harlin (1973) demonstrated the translocation of both ^{32}P and ^{14}C from macrophyte leaves into algal epiphytes. She also demonstrated the transfer of labeled photosynthate from the algae back into the host plant and to other nearby epiphytes. She suggested that nutrient transfer might occur through the basal attachment disks of the epiphyton (Harlin 1973). McRoy and Goering (1974) found that labeled N and C were transferred from sediments to epiphytes via the seagrass *Zostera marina*. They separated the root/sediment compartment from the leaf/water compartment to ensure that the only pathway of transfer was via translocation through *Zostera* stems. They suggested that transfer to epiphytes occurred through secretion by macrophytes and subsequent uptake by the algae, rather than by any direct absorption mechanism (McRoy and Goering 1974). Moeller *et al.* (1988) found that macrophyte P accounted for a larger proportion of epiphyton P supply when only live algal cells were taken into account (Table 5). They used track autoradiography to distinguish metabolically active cells from the bulk epiphyte layer, which was found to contain a large amount of unlabelled detrital P. They argued that other researchers (e.g., Carignan and Kalff 1982, Table 5) had underestimated the importance of macrophyte P to epiphytes because of the overestimation of viable algal cells in the epiphytic biofilm. They also found evidence to support the idea that algal growth form may be related to nutrient acquisition strategy. With track radiography they found that adnate diatoms (*Acnanthes, Navicula*) and larger attached (*Synedra, Fragilaria*) obtained 60% of their P

Table 5. Estimated contribution of phosphorus from macrophytes to epiphyton.

Source Macrophyte	% P Contribution	Reference
Zostera marina	33 – 70	McRoy *et al.* (1972)
Nuphar luteum (submersed leaves)	86	Twilley *et al.* (1977)
Myriophyllum spicatum	3 - 9	Carignan and Kalff (1982)
Najas flexilis	15 – 24 in bulk layer 20 – 60 for individual cells	Moeller *et al.* (1988)

from host macrophytes, whereas filamentous greens (*Mougeotia*), blue-greens (*Lyngbya*) and long-stalked diatoms (*Gomphonema*) obtained most of their P from the water column and only 20% from macrophytes (Moeller *et al.* 1988).

The measurement of alkaline phosphatase activity (APA, see below) in epiphytic algae has been used to demonstrate P supply from host macrophytes, because alkaline phosphatase activity is inversely correlated with P availability (Burkholder and Wetzel 1990). Burkholder and Wetzel (1990) found that APA was consistently higher for epiphytes on plastic plants as compared to epiphytes on real macrophytes. They suggested that macrophytes provide a continuous source of P for epiphytes throughout the growing season. Pakulski (1992) measured the release of SRP from the leaves of *Spartina alterniflora* in a salt marsh, and calculated that the annual secretion of P from macrophyte leaves was equivalent to 61% of the annual release of P via decomposition. Unfortunately, epiphytic algae were not mentioned in this study, so there is no way to know if the release into the water column was directly from the macrophytes or possibly from the epiphytes by way of the macrophytes. In fact, Pakulski (1992) could not relate the seasonal pattern of macrophyte P release to any environmental variables, perhaps because the pattern of P release was governed by the dynamics of epiphyte growth on the *Spartina* plants. Jackson *et al.* (1994) demonstrated that both essential and nonessential trace elements were translocated from sediments through roots to shoots and then to epiphytes. They ensured that these elements were not available to the shoots or the epiphytes from the water column. Their work suggests not only a nutrient source for epiphytes, but also a mechanism for transferring both nutrients and contaminants from the sediments into the water column of littoral zones (Jackson *et al.* 1994).

2.3.8 (c) Alkaline phosphatase activity

In addition to macrophyte secretions, algal secretions are also involved in nutrient interactions in aquatic environments. Algae secrete enzymes, which enhance

nutrient uptake ability. Acid and alkaline phosphatase enzymes are located on either the cell surface or on the plasmalemma, and are excreted when P limits growth (Burkholder and Wetzel 1990). Phosphatases are nonspecific esterases that catalyze the breakdown of organic P compounds, releasing orthophosphate for algal and macrophyte uptake (Jansson *et al.* 1988). Phosphatases are also secreted by bacteria and invertebrates. It has been shown that both acid and alkaline phosphatase enzymes that are released into the water through extracellular release or cell lysis are subsequently bound and inactivated by dissolved humic compounds (Boavida and Wetzel 1998). These humic-complexed enzymes are then dispersed throughout the ecosystem via water movement, and eventually reactivated by breakdown of the complexes as they are exposed to natural UV radiation. This provides a mechanism to help account for the ubiquitous supply of dissolved phosphatase enzymes found in most freshwater systems (Boavida and Wetzel 1998).

2.3.8 (d) Macrophytes as neutral substrata

Some researchers have argued for a neutral role for macrophytes in terms of nutrient supply to epiphytes (Cattaneo and Kalff 1978, Carignan and Kalff 1982). Cattaneo and Kalff (1978) compared the growth of epiphytes on macrophytes with that of epiphytes on plastic plants and found similar seasonal trends for epiphyton biomass on both substrata. They found that the major effect of the macrophyte, *Potamogeton richardsonii*, was on epiphyton species diversity, due to photosynthetically induced precipitation of $CaCO_3$ on the leaves. This precipitate helped to reduce the development of adnate forms, while securing the loosely attached filamentous and long-stalked epiphyton, thus maintaining species diversity throughout the growing season. Conversely, on plastic plants, whereas epiphyton biomass was comparable, species diversity was strongly reduced as adnate forms dominated later in the season. Cattaneo and Kalff (1979) also compared chlorophyll-normalized epiphyton primary production and found no difference between real versus plastic plants. They argued

that whereas some macrophyte P might be transferred to the epiphyton, it was insufficient to afford them any real competitive advantage. They stated that the primary role of macrophytes was a physical one, providing a suitable support, high in the water column, where leaf movements in water currents might provide a superior exposure to light and nutrients (Cattaneo and Kalff 1979). Carignan and Kalff (1982) calculated that epiphytes derived only a small portion of their P from *Myriophyllum spicatum* (Table 4) and concluded that macrophytes were more important as physical supports rather than as nutrient sources. They argued that the most important role of macrophytes was as physical supports for the epiphyton/bacterial communities that play an important role in P cycling in the littoral zone (Carigan and Kalff 1982).

2.3.8 (e) Nutrient competition

Competition for scarce resources plays an important role in structuring natural communities (Roughgarden 1983). Nutrient competition between algal species has been demonstrated (Tilman 1977) and models have been proposed that invoke competition for limiting resources as a mechanism of interaction among phytoplankton (Tilman *et al.* 1982). Fong *et al.* (1993) suggested that few studies have specifically quantified competition between different groups of algae. Despite this, competition is often invoked as a mechanism of interaction between algae and macrophytes (Fitzgerald 1969, Brammer 1979, Kufel and Ozimek 1994) or between algal assemblages, such as phytoplankton and epiphyton (Hwang *et al.* 1998), or phytoplankton and sediment-associated algae (Hansson 1989, Fong *et al.* 1993). Sand-Jensen and Borum (1991) argued that competition for nutrients is evident because both benthic algae and rooted macrophytes stabilize the sediments, reducing sediment nutrient availability to phytoplankton in the water column, in addition to competing for the same water-nutrient pool as phytoplankton. In this competition for nutrients, it is commonly thought that phytoplankton are best placed to acquire surface or advective inputs of nutrients, whereas sediment-associated algae have the first opportunity to take up nutrients released from the sediments. In a proposed model of alternative stable states in

wetlands, Goldsborough and Robinson (1996) have suggested that nutrient competition is one of the mechanisms of interaction between algal communities that may promote a shift between alternative stable states.

Epiphyton may achieve a competitive advantage over phytoplankton due to the ability to access nutrients from both the sediments (via macrophytes) and the water column (Hwang *et al.* 1998). Epiphyton may also rely less on water column concentrations of nutrients because of efficient internal cycling within the mucilaginous algal/bacterial complex (Mulholland *et al.* 1991). Epipelon may be able to compete efficiently with rooted macrophytes for nutrients in both the water column and the sediments (Hansson 1989). Hansson (1990) demonstrated that algae growing on the sediments reduced total P concentration in the overlying water by 44%, suggesting that sediment-associated algae could competitively reduce phytoplankton growth in shallow water.

Brammer (1979) cited intense competition for essential nutrients with the submersed macrophyte, *Stratiotes aloides*, as the major factor in the decline of phytoplankton in eutrophic shallow lakes in Sweden and Poland. He suggested that the macrophytes were responsible for depleting assimilatory CO_2 due to photosynthetically induced increases in pH and decreases in carbonate alkalinity. Concentrations of potassium, sodium, and calcium were also reduced, and water column SRP concentration was low (Brammer 1979). Unfortunately, there was no recognition of the possible role of epiphytic algae in this study. Kufel and Ozimek (1994) noted that charophytes have a large storage capacity for P and faster uptake rates for P than phytoplankton. They argued that it is this competitive advantage for P uptake, rather than allelopathy, which accounts for reduced phytoplankton in charophyte stands. Filamentous *Cladophora*, which forms metaphyton mats, also has large intracellular P storage capacity, enabling it to remain competitive even when external P sources have been depleted (Auer and Canale 1982). Dodds (1991b) noted a lack of nutrient competition between *Cladophora glomerata* and its epiphytes, because *Cladophora* was N-limited whereas the epiphytes were P-limited. Other filamentous mat-forming species,

Enteromorpha spp., have extremely high uptake rates for nitrate, enabling them to outcompete marine red algae, particularly under conditions of high temperature and irradiance (Harlin 1978).

Phytoplankton have high specific uptake rates for phosphorus, comparable to bacterioplankton, and much higher than the specific uptake rates for benthic algae (epiphyton and epipelon) (Hwang *et al.* 1998). Hwang *et al.* (1998) found that phytoplankton V_m/K_s (quotient of maximum uptake rate to half saturation constant) increased significantly during periods of P-limitation, suggesting that not only are phytoplankton more efficient at taking up phosphorus than benthic algae, they are also more efficient at adapting to a scarce P supply. Phytoplankton may have a competitive edge over macrophytes in uptake of scarce CO_2, owing to lower diffusive resistance and a 100-fold lower half-saturation constant for CO_2 uptake in phytoplankton compared to rooted macrophytes (Sand-Jensen and Borum 1991). Filamentous algae that form metaphytic mats tend to have high nutrient uptake rates similar to those of phytoplankton (Borchardt 1996). However, Borchardt (1996) cautioned that comparisons of nutrient uptake kinetics are confounded by differences in flow velocities and boundary layers between planktonic and benthic algae and macrophytes (see Physical Roles below).

Macrophytes may change their growth allocation patterns in response to nutrient limitation or nutrient competition. Under fertile sediment conditions, submersed macrophytes tend to maximize shoot production and minimize the allocation of energy into roots (Barko *et al.* 1991). Conversely, under infertile conditions, submersed macrophytes have the ability to increase their root to shoot (R:S) ratio, thus increasing the absorptive surface area exposed to sediments for scarce nutrient uptake. In general, emergent and floating leaved macrophytes exhibit R:S ratios that are much greater than those for submersed macrophytes (Barko *et al.* 1991). Emergent macrophytes with high R:S ratios appear to be less affected by unfavorable sediment nutrient concentrations than submersed species with low R:S ratios (Sand-Jensen and Søndergaard 1979, Barko and Smart 1986). Even with reduced root

development, submersed macrophytes are capable of rapidly depleting pools of N and P in sediments (>90% of exchangeable N and >30% of extractable P over a six week growth period) (Barko *et al.* 1991). This suggests that even in fertile systems, submersed macrophytes have the capability to reduce sediment nutrient availability, increasing competition amongst other biotic components such as bacteria, epipelon, and phytoplankton. However, submersed macrophyte nutrient uptake from sediments may enhance nutrient availability to epiphyton.

Canfield *et al.* (1984) examined the possibility of competitive interactions between submersed aquatic macrophytes and phytoplankton by using a macrophyte abundance term in a nutrient-chlorophyll regression equation for predicting phytoplankton chlorophyll. They suggested that percent volume of a lake infested (PVI) by macrophytes might be an important source of variability in nutrient-chlorophyll regressions. They found that chlorophyll-*a* and PVI were inversely related in 32 Florida lakes and that predictions of chlorophyll-*a* were improved by including a PVI term. They predicted that major reductions in chlorophyll-*a* do not occur until PVI values exceed 30%, but that in most lakes, public perception of macrophytes as nuisance weeds occurs around 15% PVI (Canfield *et al.* 1984). Underlying causative factors for the inverse relationship were not addressed in this study, but were suggested to include (1) competition for nutrients by macrophytes and epiphytes, (2) reduction in nutrient cycling because macrophytes reduce wind mixing and the resuspension of nutrients from the bottom sediments, and (3) increased sedimentation of planktonic algae due to a reduction in water turbulence by macrophytes (Canfield *et al.* 1984).

2.3.8 (f) The metabolic gate function

Wetlands and littoral zones have been described as metabolic gates to adjacent pelagic zones or rivers (Wetzel 1992). This metabolic gate function consists of physical sieving or trapping of particulate matter (see Physical Roles below) and nutrient recycling. Nutrient recycling between primary producers, primary consumers, particulate and dissolved organic detritus, and bacteria, is an important process in aquatic ecosystems. Recycling

increases the amount of organic matter produced per P atom present in the system and accelerates the rate of sediment accumulation (Carpenter 1981).

Wetzel (1993) argues that rapid recycling of nutrients and organic carbon occurs at a micro-environmental scale and is necessary for sustained high productivity in shallow systems. He suggests that the close spatial arrangement of heterotrophs and autotrophs in biofilms is an evolutionarily-driven adjustment to a nutrient-limited environment, allowing immediate access to fixed carbon or inorganic nutrients.

In addition to such micro-scale nutrient cycling, systems that support large stands of submersed macrophytes may experience greater effects of macrophyte-driven nutrient recycling. Many submersed macrophytes (e.g., *Myriophyllum*, *Potamogeton*, and *Elodea*) have high biomass turnover during the growing season when temperatures are high and decomposition is accelerated (Barko *et al.* 1991). Large stands of submersed macrophytes may alter the N:P ratio of nutrients exported to the pelagic zone, which may in turn affect phytoplankton community composition (Barko *et al.* 1991). Macrophytes have greater access to P in the sediments, and are generally limited by the smaller available N pools. Thus, the N:P ratio of macrophyte-derived detritus is decreased, resulting in greater P than N export to the pelagic zone.

In addition to altering N:P ratios, macrophyte stands may also substantially reduce the export of nutrients to the pelagic zone. Howard-Williams and Allanson (1981) suggested that once phosphorus is cycling within a macrophyte community, it is unlikely to be transferred to the pelagic zone. They found that as soon as labeled P was released in the littoral zone, it was taken up again by filamentous epiphytes, the adnate epiphyte/leaf complex, and filter feeding animals via phytoplankton. Of a given input of P to the water, 32% went to loosely attached epiphytic algae, 17% went to the *Potamogeton* leaf/adnate epiphyte complex, 16% to phytoplankton, 28% to sediments and 7% to microbes associated with detritus (Howard-Williams and Allanson 1981). Similar partitioning was found in a more

recent P tracer study where 31% of added P went to phytoplankton, 26% to the macrophyte-epiphyte complex, 37% to sediments and 6% to bacterioplankton (Hwang *et al.* 1998).

The ability of macrophytes and algae to take up nutrients far in excess of growth requirements is known as luxury consumption (Gerloff and Krombholz 1966). Luxury consumption rapidly depletes ambient nutrient concentrations and allows increased primary productivity over a much longer period because of continued availability of internally stored P (Portielje and Lijklema 1994). The combined effect of luxury consumption, rapid recycling, and sedimentation is that the littoral zone acts as a sink for dissolved inorganic material (Howard-Williams and Allanson 1981).

Other researchers have also noted that aquatic macrophyte beds serve as effective sieves and traps for inflowing dissolved and particulate materials (Wetzel 1979, Carpenter 1981) (see Physical Roles below). Mickle and Wetzel (1978a, b, c) investigated the role of the submersed macrophyte-epiphyte complex in regulating the flow of labile DOC, refractory DOC, and inorganic nutrients through the littoral zone to the pelagic zone. They found that the flow of DOC and inorganic nutrients was significantly dampened when macrophytes were present versus when there were no macrophytes. More importantly, they found that the composition of DOC was changed as it passed through the littoral zone, with the result that labile, low molecular weight compounds (<1000 MW) were not exported from the littoral zone when macrophyte-epiphyte complexes were metabolically active. The DOC exported to the pelagic zone was of higher molecular weight and was more refractory and therefore less available to the phytoplankton. They attributed this to utilization of the labile portion by the epiphytes in the littoral zone (Mickle and Wetzel 1978a, b, c). The littoral zone also reduced the absolute quantity of refractory organic compounds passing through to the pelagic zone, mainly due to adsorption to precipitating $CaCO_3$ induced by high rates of photosynthesis in the littoral zone (see Physical Roles below).

Mitsch and Reeder (1991) found that a macrophyte-dominated wetland bordering Lake Erie retained 17 to 52% of inflowing P, attributed mainly to active algal uptake and subsequent sedimentation. In this way, algae play a quantitatively important role in transforming inorganic P to organic P and transporting it to the sediments during senescence. Sedimentation of organic matter provides an important mechanism for nutrient renewal to the littoral sediments, which may balance nutrient losses due to macrophyte uptake (Barko *et al.* 1991). Sedimentation of phytoplankton, epiphytic algae from leaf surfaces, decomposing filamentous algal mats, and leaves sloughed by actively growing macrophytes can provide major inputs of N and P from water column to sediments (Howard-Williams 1981, Barko *et al.* 1991).

Conversely, processes in sediment-associated biofilms can control chemical fluxes of nutrients from the sediment to the overlying water (Woodruff *et al.* 1999). Silicon concentration in the overlying water was controlled by diatom uptake of silicon in a sediment-associated biofilm (Woodruff *et al.* 1999). Epipelon has been shown to influence phosphorus exchange between the sediment and the water column (Carlton and Wetzel 1988, Hansson 1989, Woodruff *et al.* 1999). Hansson (1989) found that the presence of epipelon reduced the P content of both the overlying water and the underlying sediments. In aquaria experiments, he found that the increase in P content of the epipelon closely matched the decrease in water and sediment P combined. This demonstrates that there is a direct role for algae and bacteria, linked to nutrient uptake, in the control of P flux between sediment and water (Hansson 1989). There is also an indirect role for sediment-associated algae, linked to modification of redox conditions, which will be discussed below (see Indirect chemical effects).

Nutrient regeneration by invertebrate grazers and planktivorous fish is another important process in shallow systems (Lehman 1980, Hessen and Andersen 1992, Vanni and Layne 1997). Grazer nutrient regeneration is rapid and can supply 10 times more P and

3 times more N to phytoplankton than all external sources combined during mid-summer (Lehman 1980). Rapid grazer-mediated nutrient regeneration occurs through a number of mechanisms, including 'sloppy feeding' (which promotes algal cell lysis and leaching of N and P), gut passage of live algal cells (which exposes the cells to the nutrient-enriched environment of the gut), and direct excretion of nutrients (Vanni and Layne 1997). Zooplankton grazers have the capacity to maintain the N:P ratios of their body tissues by altering the N:P ratio of their excretions (Andersen and Hessen 1991, Sterner *et al.* 1992). Daphnid grazers have a low tissue N:P ratio, and tend to excrete nutrients at a relatively high N:P ratio. Conversely, smaller copepod grazers have high tissue N:P ratios and excrete nutrients at a lower N:P ratio (Sterner *et al.* 1992). Zooplanktivorous fish may have an indirect impact on N:P ratios of recycled nutrients by altering the composition of the zooplankton through differential predation of large-bodied grazers. Fish also influence algal nutrient supply by direct excretion of nutrients (Vanni and Layne 1997). When P is limiting, algae tend to have high C:P ratios, resulting in relatively low P excretion rates by zooplankton grazers as they attempt to conserve tissue P (Sterner *et al.* 1992). In this case, P recycling by fish may be more important than recycling by zooplankton in regenerating P supply to primary producers. Vanni *et al.* (1997) found that total water column P increased with increasing planktivorous fish biomass and argued that the presence of fish increases the relative retention of P in the water column. Nutrient recycling by fish is most important when the biomass of small zooplanktivorous fish is high and piscivorous fish are absent or rare, which is often the case in shallow littoral areas and wetlands (Vanni and Layne 1997). Grazer damage to submersed and emergent macrophytes also contributes to nutrient regeneration by promoting increased leaching of nutrients and accelerating senescence and decomposition of macrophyte tissue (Lodge 1991, Lauridsen *et al.* 1993, Evers *et al.* 1998). Nutrient supply is generally considered a bottom-up control mechanism for primary production (Carpenter *et al.* 1985). However, significant nutrient regeneration and alteration of N:P supply ratios by invertebrates and fish, which are generally considered top-down

agents of control via grazing, adds an additional element of complexity to trophic interactions.

2.3.8 (g) Decomposition

Macrophytes and algae contribute DOC and inorganic nutrients through leaching during decomposition (Otsuki and Wetzel 1974). Decomposition is an integral part of nutrient recycling, which may result in the regeneration of nutrients to the water column and the surface sediments, or the loss of nutrients through incomplete mineralization and burial deep in the sediments. Several researches have found that 30 to 40% of net production of macrophytes and phytoplankton is released as dissolved organic matter on autolysis (Otsuki and Hanya 1972, Otsuki and Wetzel 1974, Godshalk and Wetzel 1977).

Wrubleski *et al.* (1997a) studied the decomposition of several mudflat annual species of macrophytes and found that most of the nutrient loss took place in the first year when the litter was unflooded. An additional study of the decomposition of emergent macrophyte roots and rhizomes indicated that flooded or draw-down conditions had little impact on the rate of decomposition, which was comparable to the rate of shoot litter decomposition (Wrubleski *et al.* 1997b). A three-stage pattern of mass loss during decomposition has been described by several researchers (Davis and van der Valk 1978, Polunin 1982, Barko *et al.* 1991, Wrubleski *et al.* 1997b). The first stage is a short (1-2 day) period of rapid mass loss by physical leaching, followed by a longer (90-120 day) period of lower but sustained mass loss via microbial decomposition. The third stage is an indefinite period of slow mass loss, attributed to the recalcitrance of the remaining structural materials (Wrubleski *et al.* 1997b). Kuehn and Suberkropp (1998) studied the standing dead litter of emergent *Juncus* spp. and determined that submergence and collapse to the sediment surface was not necessary for substantial decomposition to occur. They suggested that during decomposition, most of the N and P

was immobilized in microbial biomass. They stress that the biomass of fungal decomposers is often overlooked, or underestimated due to inadequate measurement techniques. They calculated that fungal decomposers could retain 99% of the available N from decomposing macrophytes (Kuehn and Suberkropp 1998).

Vargo *et al.* (1998) found that the application of sediment to emergent plant litter significantly reduced decomposition rates, probably through inhibition of microbial access and action. This calls into question the practice of burying litter to enhance degradation rates by increasing moisture availability. The high rates of sedimentation common in highly productive wetlands (0.5 cm to > 3-4 cm per year) are a factor in the incomplete decomposition of organic matter in these systems, which may result in burial prior to complete release of nutrients to the water column or top layer of flocculent sediments (Vargo *et al.* 1998). Several studies have shown that anaerobic decay proceeds at slower rates than aerobic decay and generally does not proceed to completion owing to the lack of oxidizing power and alternative electron acceptors (nitrate, oxidized iron, manganese and sulfate) (Godshalk and Wetzel 1977, Schlesinger 1997). These processes enhance the role of wetlands and littoral zones as nutrient and carbon sinks. The build-up of breakdown products such as organic acids, alcohols, lignins, tannins and phenolics in the sediments may eventually create an environment that is inhibitory or toxic to continued macrophyte growth (Barko *et al.* 1991).

2.3.8 (h) Decomposition supports production

Nutrients derived from algal and macrophyte decomposition can support both heterotrophic and autotrophic production. Boschker *et al.* (1999) found that leachate from the emergent macrophyte, *Spartina* spp. contributed little to bacterial production when algal carbon was available. They found that the stable carbon isotope ratio of bacteria was depleted relative to *Spartina*, and more closely matched the ratio of algal-derived carbon, except in areas where algal production was sparse. Mann and Wetzel

(1996) found that the leachate from emergent macrophytes (*Typha latifolia* and *Juncus effuses*) was less labile and supported lower growth efficiencies of bacteria than the more labile leachate from algae. Macrophyte particulate detritus was even less labile than macrophyte leachate, with conversion efficiencies to new organic tissue via bacterial production of 10-20% for detritus and 50% for macrophyte leachate (Findlay *et al.* 1986).

Leaching of nutrients from senescing macrophyte leaves may be accelerated by the presence of periphyton communities (Howard-Williams *et al.* 1978). They found that the rough-walled bacterial component of the periphyton caused cuticular erosion and epidermal pitting to leaves, which was suggested to enhance leaching rates and hasten leaf death. This process would increase the access to nutrients for the algal component of the periphyton and for nearby phytoplankton. Neely (1994) also found that there were positive interactions between epiphytic algae and heterotrophic bacteria on decomposing *Typha latifolia*. Growth of heterotrophs was enhanced in treatments with high algal abundance, probably because of increased availability of labile DOC secreted from the algae. In turn, high algal abundance resulted in increased autotrophic oxygen production, which enhanced the rate of decomposition of *Typha*. In the treatments with high algal abundance and enhanced heterotroph abundance, there was a significantly greater reduction (41 to 50% less) in TP released to the surrounding water column (Neely 1994). The presence of epiphytic algae on senescing or dead macrophyte tissue has been reported many times (Muelemans 1988, Neely 1994). Rho and Gunner (1978) found that decomposing *Myriophyllum heterophyllum* released ammonia and phosphate in concentrations sufficient to promote an initial growth response by epiphytic algae, including euglenoids, diatoms and filamentous greens. This was subsequently followed by an increase in planktonic green algae.

Landers (1982) found that decomposing stands of *Myriophyllum spicatum* supplied significant inputs of N and P to surrounding waters, stimulating phytoplankton biomass. With many submersed macrophytes, two-thirds of the annual production senesces during the growing season, resulting in continual cycling of sediment P to surrounding water because of leaf sloughing, in addition to the pulse of P released during annual fall die-back. Landers (1982) calculated that 70% of the P and 50% of the N from submersed macrophytes would enter the water column during decomposition. In terms of overall contribution to the ecosystem, this would represent 18% of the annual P loading and 2.2% of N loading.

2.3.9 Indirect chemical effects

The metabolic processes of submersed macrophyte-epiphyte complexes affect biogeochemical cycling within shallow ecosystems (Wetzel and Søndergaard 1998). In particular, the processes of photosynthesis and respiration govern fluctuations in dissolved oxygen, carbon dioxide and hydrogen ion (pH) concentrations in the water and the surface sediments. In turn, dissolved oxygen concentrations control nutrient cycling from sediments via reduction-oxidation potential, or redox (Schlesinger 1997). Chemical speciation of several nutrients is determined by pH, including precipitation of aluminum and iron phosphates and hydroxides, and speciation of ammonium ions to undissociated ammonia (Kadlec and Knight 1996). Carbon dioxide is usually present in greater quantities as bicarbonate (HCO_3^-) rather than dissolved CO_2, which may favor plants and algae that are able to utilize HCO_3^- in photosynthesis (Allen and Spence 1981, Boston *et al.* 1989).

2.3.9 (a) Importance of oxygen

Oxygen is not very soluble in water and diffuses 10,000 times more slowly in water than in air (Schlesinger 1997). Therefore, aquatic organisms must be adapted to surviving periods of low oxygen concentration and rapid fluctuations from near-anoxia to

supersaturation. Underwater photosynthesis provides crucial supplies of oxygen to invertebrates and fish, particularly in stagnant water or water under ice cover (Kadlec and Knight 1996). Browder *et al.* (1994) suggested that benthic algae might be as important for its role in providing an oxygenated habitat for aquatic animals as for its role in the food web. Oxygen is evolved as a by-product of photosynthesis when water molecules are hydrolyzed in photosystem two (Falkowski and Raven 1997). Oxygen is consumed during photorespiration and dark respiration in autotrophs, and in heterotrophic respiration (Raven and Beardall 1981). The presence of oxygen (an electron acceptor or oxidizing agent) gives an environment a high redox potential. As oxygen is depleted, redox potential drops and other chemical species may act as electron acceptors (e.g., NO_3^-, Mn^{+4}, Fe^{+++}, $SO_4^=$) (Schlesinger 1997).

2.3.9 (b) Redox potential

Redox potential is biologically significant because it plays a part in nutrient cycling, organic matter decomposition, anaerobic production of gases, and long-term organic matter storage (coal and peat). Organic matter is one of the most reduced substances in the littoral environment, and decomposition (oxidation) of organic matter is the major process that can quickly lower redox potential. When organic matter oxidation does not proceed to completion, organic matter may be buried and stored for long periods of time as peat or coal. The anaerobic microbial processes of denitrification, sulfate reduction, and methanogenesis are responsible for the release of gases to the atmosphere, including N_2, N_2O (a major greenhouse gas), H_2S (highly toxic to humans, fish and plants), and CH_4 (another major greenhouse gas). The biological availability of iron, manganese, sulfur and nitrogen are directly affected by redox conditions, whereas phosphorus is indirectly affected through iron complexation. Nitrogen is available in both its oxidized (NO_3^-) and reduced (NH_4^+) form, with nitrate being more prevalent in aerobic environments and ammonium being more prevalent in anaerobic environments.

Manganese and iron are more available in their reduced forms, whereas sulfur is generally taken up in its oxidized form (sulfate). Phosphorus is immobilized in complexes with ferric iron under aerobic conditions. In anaerobic conditions, phosphorus is released during reduction of iron to more soluble ferrous compounds. The availability of phosphorus is complicated by other physicochemical reactions besides redox, including adsorption to clay particles, changes in pH, and changes in carbonate equilibrium, which causes coprecipitation with calcium carbonate crystals or the formation of insoluble calcium phosphate salts (Schlesinger 1997).

2.3.9 (c) Carbonate equilibrium, pH, and alkalinity

Both photosynthesis and respiration have effects on carbonate equilibrium and pH. Carbon dioxide and H^+ ions are consumed during photosynthesis, and regenerated during respiratory processes (Raven and Beardall 1981, Falkowski and Raven 1997).

Carbon dioxide exists in water as free CO_2 or as bicarbonate (HCO_3^-) or carbonate ($CO_3^=$) anions, according to equilibrium reactions described by this equation:

$H_2O + CO_2 \; ? \; H_2CO_3 \; ? \; H^+ + HCO_3^- \; ? \; 2H^+ + CO_3^=$ (from Wetzel 2001).

The speciation of carbon is pH dependent with CO_2 the predominant form at pH<6, HCO_3^- at pH 6 to 9, and $CO_3^=$ at pH>9. Carbonate equilibrium and pH are interconnected, because the pH of natural waters is governed largely by the interaction of H^+ ions arising from the dissociation of H_2CO_3 and from OH^- ions produced during hydrolysis of HCO_3^- (Wetzel 2001). Alkalinity refers to the compounds that shift the pH of water to the alkaline (>7) side of neutrality. Alkalinity is also interconnected with carbonate equilibrium, because it is usually imparted by the presence of bicarbonates, carbonates, and hydroxides in fresh water (Wetzel 2001). Water tends to resist changes in pH as long as bicarbonate reactions remain in equilibrium. Because bicarbonate and carbonate do not contribute to the vapor pressure of the gas, the concentration of dissolved inorganic carbon in water can greatly exceed the atmosphere/water

equilibrium of gaseous CO_2 (Falkowski and Raven 1997). Thus, the solubility of CO_2 increases with increasing carbonate content in the water, and this aggressive CO_2 (Wetzel 2001) will maintain large amounts of calcium carbonate ($CaCO_3$) in solution. Photosynthesis by aquatic autotrophs is the primary means for rapid depletion of aggressive CO_2 in fresh waters, causing precipitation of $CaCO_3$ on the sediments and the surfaces of plants and algae. These marl encrustations can be massive, exceeding the weight of the plant (Wetzel 2001). Photosynthesis also consumes H^+ ions during the reduction of CO_2 to carbohydrate, driving the pH up (often >9) in surrounding waters or sediments. During nocturnal respiration, CO_2 production reduces pH (Falkowski and Raven 1997).

2.3.9 (d) Sediment and water column chemistry

The immediate effect of aquatic photosynthesis is an increase in dissolved oxygen concentration in the water column. However, an indirect effect of massive primary production is the generation of high biological oxygen demand during senescence and decomposition of plants and algae (Kadlec and Knight 1996). Collapsing algal blooms can cause rapid depletion of dissolved oxygen, resulting in massive fish kills (summerkill) in shallow systems (Barica 1978). Decomposition of primary production under ice can also result in depletion of oxygen and winterkill of fish and other aquatic organisms (Wetzel 1983a). Wide diurnal fluctuations in oxygen concentrations and pH were cited as reasons for the low abundance of sunfish foraging in dense stands of macrophytes (Miranda and Hodges 2000).

Dense phytoplankton blooms were found to inhibit the growth of rooted macrophytes and attached algae by generating high pH, thus hampering inorganic carbon uptake as CO_2, and making it more dependent on the light-driven utilization of HCO_3^- (Maberly and Spence 1983). A similar inhibitory effect by epiphyton on rooted macrophytes has also been noted (Sand-Jensen *et al.* 1985). Eiseltová and Pokorný

(1994) found that *Cladophora* spp. were efficient HCO_3^- users and were able to tolerate high pH within photosynthesizing mats. By rapid growth and resultant shading, depletion of CO_2, and increases in pH, *Cladophora* was able to outcompete all other autotrophs. Simpson and Eaton (1986) found that filamentous algae, *Cladophora* and *Spirogyra,* had deleterious effects on macrophyte growth through their impact on the chemical environment. They increased pH, decreased CO_2 and induced supersaturation with O_2, all of which seriously impaired the photosynthesis of *Elodea Canadensis.*

Morin and Kimball (1983) documented a reverse pattern of macrophyte-epiphyte relationships, with *Myriophyllum heterophyllum* structuring the seasonal succession of epiphyte species through physical and chemical alteration of the environment. Early in the season, before *Myriophyllum* shoots had reached the water surface, pH was low (~6) and diatoms dominated the epiphyton. By midsummer, *Myriophyllum* stems filled the water column, which impeded water mixing and allowed vertical physicochemical gradients to develop. At this time, *Myriophyllum* photosynthesis occurred predominantly in the top 20 cm of the water column, surface pH rose above 7 and cyanobacteria and filamentous green algae replaced diatoms on the top portion of macrophyte stems. Diatoms were confined to lower stems where macrophyte photosynthesis was absent and pH remained low. Morin and Kimball (1983) argued further that observations of little difference in colonization between plastic and real plants might be questionable because of macrophyte-induced conditions in the water column. They suggested that plastic plants placed *in situ* in macrophyte beds are subject to the same influences as the real macrophytes, and therefore their epiphytes will be similarly affected. These influences include a reduction in light availability, decreased water circulation, and changes in water chemistry due to plant photosynthesis and respiration.

Dense mats of floating leaf macrophytes can also influence the chemical environment of associated epiphyton and phytoplankton (Goldsborough 1993). Low

dissolved oxygen (<1 mg L^{-1} within 1-2 cm of the water surface) was measured below a mat of the common duckweed, *Lemna minor*. In the reduced environment below the *Lemna* mat, ammonium was able to accumulate in the water column (Goldsborough 1993). Lower dissolved oxygen concentrations and pH were also measured beneath the canopy of overlapping leaves of the floating leaf macrophyte, *Brasenia schreberi* (Frodge *et al.* 1990).

During photosynthetically-induced calcium carbonate precipitation, other solutes are also removed from solution, including dissolved organic carbon and inorganic phosphorus (Woodruff *et al.* 1999). Some of the calcite precipitate attaches to algal cells, increasing their weight and consequently their rate of deposition into sediments, a mechanism that might help account for the decline of phytoplankton amidst actively photosynthesizing epiphyte-macrophyte complexes. Woodruff *et al.* (1999) found that an algal biofilm on the sediment surface regulated dissolved calcium, SRP, and alkalinity concentrations in the surface sediment pore water and the bulk water above the biofilm. They noted a large increase in dissolved oxygen and pH that corresponded with photosynthetic activity during the day. At night, net release of calcium and alkalinity corresponded with high respiration activity. They calculated that the presence of the photosynthetic biofilm induced nine times more mineral precipitation compared to precipitation under strictly abiotic conditions (Woodruff *et al.* 1999).

Carlton and Wetzel (1988) showed that epipelon influences the concentration of water column P by regulating redox potential at the sediment water interface. They demonstrated that the magnitude of P flux changed rapidly and was closely tied to the pattern of oxidation and anoxia in the sediment microzone. The mechanism for P regulation is related to the formation and breakdown of an oxidized microzone at the sediment surface as a result of diel photosynthesis patterns. In the light, epipelic photosynthesis oxygenates the surface sediments, and P release from the sediments is

inhibited. This inhibition is likely attributable to precipitation of insoluble phosphates with ferric iron (Fe(III)), calcium, and aluminum under aerobic conditions (Schlesinger 1997). In the dark, respiration proceeds, the sediment microzone becomes anoxic, insoluble phosphates are reduced to soluble forms and phosphate is released into solution. Under sustained anaerobic conditions, the resulting P-release caused a decrease in the P-pool of the surface sediments of well over 30% during a few weeks (Portielje and Lijklema 1994). Carlton and Wetzel (1988) suggested that the net effect of diurnal epipelic regulation of sediment P flux was to conserve P in the sediment. This role for epipelic algae, as the sediment P regulator, may reduce P availability to phytoplankton and consequently reduce phytoplankton productivity.

Some submersed macrophytes also function as sediment P regulators, particularly in oligotrophic systems, which may lack large sources of reductants (Jaynes and Carpenter 1986). Macrophytes are able to release oxygen into the rhizosphere by passive molecular diffusion, following concentration gradients (Brix 1993, Flessa 1994). Oxygen release via roots into the surrounding sediment can elevate redox potential causing P to precipitate in insoluble complexes and reducing the availability of soluble P in the sediment pore-water (Barko *et al.* 1991). In oligotrophic systems, submersed macrophytes such as isoetids may significantly oxidize sediments so that availability of nutrients to other autotrophs is reduced (Jaynes and Carpenter 1986). Macrophytes may also enhance their ability to take up P over large areas of the sediments through associations with fungal mycorrhizae (Wigand and Stevenson 1994). The ability of freshwater primary producers to retain P in sediments is a major factor contributing to the general condition of P limitation in freshwater systems (Conley 2000).

Flessa (1994) suggests that the oxidizing power of macrophyte roots is an essential adaptation to the stress of living in a highly reduced environment. He notes that reduced sulfide and iron oxides can reach phytotoxic concentrations in the sediments.

Therefore, the maintenance of an oxidized microzone around root tips acts as a protective barrier against toxic substances. Such oxidized microzones will also accelerate organic matter decomposition in the root vicinity, perhaps improving access to labile organic carbon or inorganic nutrients (Flessa 1994).

Emergent macrophytes may exert an even greater influence on sediment redox. The shallow water in dense emergent stands may be anoxic due to lack of water movement and shading, which inhibits algal photosynthesis. Coupled with a large volume of slowly decomposing litter, these conditions may result in low redox potential. On the other hand, emergent macrophytes can operate as effective conduits of oxygen from the atmosphere to the sediments by convective flow of oxygen driven by thermal transpiration and humidity-induced pressurization (Brix 1993).

2.3.9 (e) Gas emissions

Macrophytes can consist of 60% aerynchyma (Vymazal 1995). The aerynchyma conduit in stems can operate in both directions, providing a route for oxygen to the roots and for gases to escape from the sediment to the atmosphere. Often there is a separation of function with green, living shoots conducting air (oxygen) downward and old, broken, or dead shoots releasing gases to the atmosphere (Brix *et al.* 1996). A number of gases have been shown to be emitted to the atmosphere via macrophytes, including carbon dioxide (Thomas *et al.* 1996), methane (Sebacher *et al.* 1985), nitrous oxide and dinitrogen (*Reddy et al.* 1989), hydrogen (Schütz *et al.* 1988), and carbon monoxide (Conrad *et al.* 1988).

Gas flux through macrophytes occurs via humidity-induced convection, otherwise known as pressurized ventilation, or simply, pressure flow (Armstrong *et al.* 1996). The common reed, *Phragmites australis*, possesses a large capacity to vent gases via pressure flow. Emissions of carbon dioxide from *Phragmites* stands ranged from 2.9 to 5.1 liters m^{-2} day^{-1} (Brix *et al.* 1996). Macrophtyes with roots embedded in methane-

saturated anaerobic sediments were found to have elevated concentrations of methane in their mesophyll cells (Sebacher *et al.* 1985). Methane is transported from the roots via mechanisms of transpiration, diffusion, and pressure-induced flow. Methane emissions from 20 species of macrophytes ranged from 0.1 to 14.8 g plant^{-1} day^{-1} (Sebacher *et al.* 1985). The common cattail, *Typha latifolia*, produced the second highest emissions, at 9.8 g plant^{-1} day^{-1}, and the white water lily, *Nymphaea odorata*, produced the highest emissions (Sebacher *et al.* 1985). Methane emissions from non-rooted macrophytes were undetectable. Low vegetation, such as *Sphagnum* sp., with no or small root systems, are thought to be insignificant plant pathways in terms of gas emissions to the atmosphere (Thomas *et al.* 1996).

Conversely, macrophtyes may reduce methane emissions by the maintenance of an oxygenated rhizosphere in the sediments. This oxygen-rich zone in otherwise anaerobic sediments allows for the oxidation of methane by methanotrophic bacteria, obligate aerobes that oxidize methane to CO_2 for energy production. Methane oxidation in the rhizosphere of macrophytes can account for between 65 and 90% of potential methane emissions from sediments (Reddy *et al.* 1989). High rates of methane oxidation in the rhizosphere of rice plants in rice fields (80 to 90%) have also been reported (Holzapfel-Pschorn *et al.* 1986). Oxygen flow to the root zone of *Phragmites* ranged from 4.9 to 5.7 liters m^{-2} day^{-1}, 20% of which was consumed in plant respiration, the remainder being used for oxygenating the sediments or for efflux upward to the atmosphere (Brix *et al.* 1996). In the presence of an oxygenated rhizosphere around *Phragmites*, the methane concentration of the sediments dropped from 75% to 58% of total gas volume (Brix *et al.* 1996). The oxygenated rhizosphere of macrophtyes also provides a source of oxygen for the oxidation of Fe(II) to Fe(III) oxide. Subsequent Fe(III) oxide reduction and organic carbon oxidation by anaerobic bacteria provides a competing mechanism to methanogenic bacterial production of methane, consequently

reducing methane emissions (Roden and Wetzel 1996). Benthic algae may also reduce methane emissions to the atmosphere through photosynthetic increases in oxygen concentrations at the sediment water interface, increasing the potential for methane oxidation (King 1990).

2.4 Physical roles for algae and macrophytes

2.4.1 Regulation of sediment structure

"Sediment physical characteristics are as much a product of aquatic macrophyte growth as they are delimiters of macrophyte growth," (Barko *et al.* 1991, p. 58). Submersed macrophytes help to stabilize sediments in large wind-swept basins and reduce inorganic turbidity (Hosper and Meier 1993). Mycorrhizal fungi associated with submersed macrophytes help to improve substratum physical stability through the development of an extensive mycelium growing outwards from the roots (Barko *et al.* 1991, Wigand and Stevenson 1994). The potential stabilizing effect of submersed macrophytes is dramatically illustrated when the macrophytes are suddenly removed from the system. After a flood event destroyed macrophyte beds in a shallow lake in Wisconsin, wind-driven turbidity greatly altered the ecosystem (Engel and Nichols 1994). The wind suspended soft sediments, uprooted surviving macrophytes, and increased nutrient circulation through the water column, leading to an increase in dense phytoplankton blooms. These algal blooms occurred early in the season, shading the water column before macrophytes had a chance to sprout and reach the water surface. Engel and Nichols (1994) noted that these conditions triggered a switch to macrophyte species that can overcome early shading effects by growing quickly from tubers and forming a leaf canopy on the water surface (e.g., sago pondweed and water lilies).

The stabilizing effects of submersed macrophytes are also important for the development and maintenance of films of sediment-associated algae (Lassen *et al.*

1997). Layers of benthic algae and settled phytoplankton on flocculent sediments are easily resuspended by wind action in shallow lakes (Hosper and Meier 1993). The greatest negative effect to the algae of such resuspension is the risk of burial deep in non-photic sediments.

Emergent vegetation is also effective in reducing wind-induced sediment resuspension of shallow water bodies. Dieter (1990) found that sediment resuspension in several wetlands was 2.5 times higher in open areas than in areas protected by emergent macrophyte stands. Submersed macrophyte beds also reduced resuspension but not with the same effectiveness as the emergent stands. By reducing turbulence, aquatic macrophytes serve an important role in sediment stabilization and accretion (Madsen and Warncke 1983). Sedimentation rates in littoral zones have been shown to be about two times greater than rates of sedimentation in adjacent pelagic zones (James and Barko 1990). This may be a function of both increased production and reduced turbulence in littoral zones.

The composition of accumulating sediments can affect the macrophyte community. With increased sedimentation of fine-textured inorganic materials, submersed macrophyte growth is stimulated, but with increased sedimentation of refractory organic matter submersed macrophyte growth declines (Barko *et al.* 1991). The increased erosion of the fine-textured sediments on steeper littoral slopes results in nutrient deficiency and promotes the decline of submersed macrophytes in these areas (Duarte and Kalff 1988). As sediment organic matter accumulates in shallow systems, submersed macrophytes are often replaced by nutritionally more conservative floating-leaved and emergent species with higher root to shoot ratios (Carpenter 1981, Barko *et al.* 1991).

Calcite precipitation, which results from algal and macrophyte photosynthesis stabilizes flocculent sediments (Woodruff *et al.* 1999). Continued deposition of calcite by

algae results in the formation of stromatolites, which are laminated sedimentary formations produced by sediment trapping and binding as a result of the growth and metabolic activity of sediment-associated algae (Freytet and Verrecchia 1998). These crystalline structures were originally thought to be produced mainly by cyanobacteria, but Freytet and Verrecchia (1998) have also identified chrysophytes, chlorophytes, rhodophytes and diatoms that contribute to stromatolite formation. The formation of a cohesive mucilaginous biofilm of algae on sand grains also stabilizes sediments (Holland *et al.* 1974). Grant *et al.* (1986) found that an extracellular diatom film inhibited resuspension by 33 to 100%. They stressed that the diatom film benefited not only the structure of the sediments, but also the retention of viable algal cells during turbulent events.

2.4.2 Regulation of water flow and temperature

Macrophyte beds are known to reduce water flow in streams and are often removed to prevent flooding due to flow restriction (Sculthorpe 1967). However, in lentic environments water flow has rarely been the focus of study. One study of modeled flow showed that *Myriophyllum spicatum* beds in Lake Wingra decreased water flow through the littoral zone by 36% (Carpenter and Lodge 1986). Evidence of enhanced deposition of fine sediments in macrophyte stands suggests that reduced water flow is likely occurring.

Water loss to the atmosphere, although not strictly a flow process, is one of the major components of water balance in shallow water bodies (Winter 1989). Emergent macrophytes can mediate such water loss through the process of evapotranspiration. However, the effect of vegetation on water loss to the atmosphere is unclear, due to conflicting study results (Mitsch and Gosselink 2000). The presence of vegetation retards the rate of evaporation from the open water surface by up to 50%, as a result of shading, increased humidity near the surface, and reduction of wind motion (Kadlec and

Knight 1996). Some studies have found that evapotranspiration from macrophyte stands is 20 to 80% greater than open water evaporation, whereas others have found that it is 10 to 20% less (Kadlec and Knight 1996, Mitsch and Gosselink 2000). Bernatowicz *et al.* (1976) found little difference among the transpiration rates of reeds, sedges, and cattails. Evapotranspiration through vegetation does have a significant effect in wetland and riparian areas with no standing water and therefore no evaporative water loss. The roots of macrophytes can extend down into the groundwater zone and pump water up to the leaf surfaces. For this reason, riparian vegetation is often removed along streambeds in arid parts of the world (Mitsch and Gosselink 2000). Winter (1989) noted that few studies have been done on evapotranspiration in northern prairie wetlands and little is known about the long-term effects of this process on shallow water levels.

Extensive covers of macrophytes can restrict water mixing and promote thermal stratification, resulting in high surface water temperatures during sunny days, and extreme diurnal fluctuations in temperature (Frodge *et al.* 1990). Goldsborough (1993) noted that the temperature below a dense *Lemna* mat remained cool, never exceeding 15°C even in midsummer. However, there was wide diurnal temperature fluctuations of up to 15° in the top cm of the water surface, with temperatures >30°C at midday. Metaphyton mats floating at the water surface have a similar effect on underlying and surface water temperature (Dodds 1991b, Fong *et al.* 1993). Because of the different physical and chemical characteristics above and below a macrophyte canopy, Frodge *et al.* (1990) argued that these should be considered fundamentally different habitats.

Dale and Gillespie (1977) found that the vertical temperature gradient within a macrophyte stand was 10°C m^{-1}, compared to a gradient of 0.2°C m^{-1} in nearby unvegetated areas. They suggested that this drop in temperature would decrease by half the metabolic rates of macrophytes and algae with each meter of depth. This type of cooling effect under floating mats and in dense macrophyte stands will also decrease the

efficiency of metabolically temperature-dependent heterotrophic decomposers (Wetzel 1983a). Coates and Ferris (1994) describe a mechanism for replenishment of nutrient-depleted water under floating leaf macrophytes by temperature-driven convective flow. They describe how differential heating of an open and a shaded part of a water body will generate a surface flow from the illuminated water to the shaded water. They suggest that this intrusion will bring nutrient-rich water into the floating root zone of the plants (Coates and Ferris 1994).

Another consequence of reduced water flow is the development of greater diffusive boundary layers around macrophyte leaves and algae. The diffusive boundary layer is a relatively nutrient depleted region adjacent to the leaf surface, generated by nutrient uptake by the macrophyte leaf (Stevens and Hurd 1997). A common view is that phytoplankton have thin diffusive boundary layers (Reynolds 1984). Boundary layers around macrophyte blades are thought to be larger, with macrophytes having the additional diffusion barrier of an epiphytic biofilm (Sand-Jensen and Borum 1991). However, Borchardt (1996) suggests that because benthic algae are in fixed positions relative to water motion, they may be subject to flow velocities from 10 to 100,000 times greater than the sinking rates of phytoplankton, thus reducing their boundary layers. Stevens and Hurd (1997) have also suggested that the boundary layers around macrophyte leaves (and thus epiphytic algae) might be less of a barrier to nutrient diffusion than commonly thought, because of slight movements which momentarily reduce boundary layers significantly. Even slight motion in a wavy, directionally variable fluid can strip the diffusive boundary layer of macrophytes, increasing nutrient uptake by a factor of 10 (Stevens and Hurd 1997). On the other hand, Wetzel (1993) argues that turbulent flows are rare at surface interfaces. Losee and Wetzel (1993) state that previous estimates of non-turbulent boundary thicknesses (10 μm) are too small, and that boundary layer thicknesses for attached communities are in the range of 10^2 to 10^4 μm. Wetzel (1993) argues further that reliance on diffusion of carbon and nutrients

through boundary layers of this thickness would severely limit growth and productivity. Based on measured high, sustained rates of productivity in surface biofilms, he argues for the internal recycling mechanism between phototrophs and autotrophs described earlier. The effectiveness of this internal recycling is enhanced by the relatively impervious mucilage coating that decreases diffusion loss to the surrounding water.

Another physical role related to alteration of water flow is the trap or sieve function attributed to wetlands and littoral zones (Wetzel 1992). Cattaneo and Kalff (1978) found that in early summer, the abundant loosely attached filamentous and long-stalked epiphyton on submersed macrophytes can trap a significant amount of phytoplankton (up to 37% of the community), a mechanism that might help to account for the reduction of phytoplankton in macrophyte beds. Mickle and Wetzel (1978c) found that the macrophyte-epiphyte complex was effective at removing particulate organic and inorganic carbon from inflowing water, physically trapping and sieving it in the loose structure of the algal-bacterial-mucilage matrix on the surface of macrophytes. The effectiveness of removal varied, with finely dissected species such as submersed *Myriophyllum* more effective than linear-leaved emergent *Scirpus* with less surface area for epiphyte colonization (Mickle and Wetzel 1978c).

2.4.3 Regulation of light penetration

Besides nutrients, light is the resource most likely to limit the growth of primary producers. Light attenuation in water is the result of absorption and scattering by water itself, and by dissolved and particulate substances, including algae (Kirk 1983). Light extinction by macrophyte canopies is also an important factor altering the light environment in a water column (Carpenter and Lodge 1986). Limitation of vertical light penetration is one of the main controlling factors in models of alternative stable states in shallow systems (Scheffer *et al.* 1993, Faafeng and Mjelde 1998) (see stable states below). High light intensity extending to the sediment surface within shallow water

bodies allows for greater structural complexity of the autotrophic community (Hudon and Bourget 1983). Structural complexity is achieved by the development of many different growth forms (floating, attached, adnate, stalked, rosette, caulescent, emergent) able to exploit the light environment. Round (1961) described the positive influence of light intensity on the total biomass and diversity of benthic diatoms. Hudon and Bourget (1983) found that the development of vertical structure and the diversity of growth forms in a diatom community were influenced by increasing availability of light. Development of vertical structure in algal communities, including an under story and an upper stratum, has been noted by others (Hoagland *et al.* 1982, Sand-Jensen and Revsbech 1987). High light intensity and long daylight hours have been cited as factors in the midsummer seasonal succession of floating metaphyton mats over attached algae and phytoplankton (Fong and Zedler 1993).

Because light is often a limiting resource in aquatic systems, competition for light has been the focus of extensive study. Sand-Jensen and Borum (1991, p. 155) contend that competition for light is the most important factor in the balance among primary producers, stating that, "Competition for light between phytoplankton and submersed macrophytes is mutual, but macrophyte shading on phytoplankton is only effective in shallow regions, whereas phytoplankton shading on macrophytes always takes place."

More light is needed to maintain stands of rooted macrophytes compared with populations of unicellular algae (Sand-Jensen and Borum 1991). This is because self-shading or package effects are less in unicells than in macrophytes with overlapping leaves that are many cell layers thick. Macrophytes have large quantities of non-photosynthetic tissue, which must be maintained by the photosynthetic organs, whereas in unicellular algae, all cells are photosynthetic. Macrophytes also require more energy during reproductive stages, compared to unicells (Sand-Jensen and Borum 1991). Light

limitation may also be more prevalent than nutrient limitation in rooted macrophytes, because of macrophyte access to nutrient-rich sediments.

Because of early emphasis on phytoplankton ecology, coupled with the observation of macrophyte absence in areas of dense phytoplankton blooms, a working hypothesis developed that increasing phytoplankton biomass limits the light environment for submersed macrophytes (Phillips *et al.* 1978). However, Phillips *et al.* (1978) noted that epiphytic and filamentous algal growth increased significantly in response to increasing nutrient supply in eutrophic water bodies. They hypothesized that epiphyton and metaphyton shading caused a decline in macrophyte growth and that the increase in phytoplankton followed this decline, either because of release from nutrient competition or release from allelopathy.

Epiphyton shading of macrophytes has also been demonstrated in other studies. A thick crust of adnate diatoms reduced host eelgrass photosynthesis by 31% at optimum light levels and by 58% at low light levels (Sand-Jensen 1977). He suggested that macrophyte response to such shading involved the production of a new leaf every fourteen days and the sloughing of older, encrusted leaves.

Sand-Jensen and Søndergaard (1981) showed that the shading effect of epiphyton became more important with increasing nutrient supply, and that increased epiphyte colonization limited the depth distribution of the macrophytes. In oligotrophic lakes, the water column itself accounted for 65-72% of the light attenuation, with phytoplankton and epiphyton accounting equally for the remaining attenuation. In lakes where silicon and nitrogen were more abundant, epiphyton were responsible for 50% of the light attenuation, whereas in an eutrophic lake, epiphyton accounted for 86% of light attenuation to macrophytes (Sand-Jensen and Søndergaard 1981). Sand-Jensen and Søndergaard (1981) also suggested that epiphyton were a more sensitive indicator of eutrophication, as the biomass of epiphyton increased 200 times in response to higher

nutrient levels, compared to a 9 times increase by phytoplankton biomass. They hypothesized that increasing eutrophication, with attendant increases in epiphyton colonization, would favor a shift from slow-growing rosette species to caulescent macrophyte species with long stems, capable of forming leaf canopies at the water surface (e.g., *Potamogeton* and *Myriophyllum* spp). Sand-Jensen (1990) argued that the dominance of elodeid (long-stemmed) species in eutrophic lakes and isoetid species in oligotrophic lakes may be attributed as much to differences in the light climate as to differences in the availability of carbon or inorganic nutrients.

Epiphyton shading limited the depth distribution of the submersed macrophtye, *Lobelia dortmanna,* to 1 m in a mesotrophic lake, although the calculated light-compensation point for *Lobelia* in that lake occurred at 3.5 m depth (Sand-Jensen and Borum 1984). Light attenuation by the epiphyton accounted for 67-82% of total attenuation at 0.5 m depth. Sand-Jensen and Borum (1984) noted seasonal patterns in light attenuation, with the spring diatom maximum attenuating 95-99% of incident light, dwindling to 30-60% attenuation in midsummer. During the critical spring period of high epiphyte colonization, Sand-Jensen and Borum (1984) suggested that macrophytes at 0.5 m depth were living close to their light-compensation point, putting their continued survival at risk if other growth conditions (e.g., temperature, nutrients) became less favorable.

Using oxygen microelectrodes to distinguish between the photosynthetic activity of the loosely attached epiphyton and the adnate epiphyton/leaf complex, Sand-Jensen and Revsbech (1987) were able to demonstrate that loosely attached epiphyton reduced the leaf complex photosynthesis by 65% in low light. The amount of light reaching the adnate epiphyton/leaf surface was about 30% of the incident light reaching the top of the loosely attached layer. At high light intensities characteristic of midday, the photosynthetic rates of loose epiphyton and the leaf were comparable. Sand-Jensen and

Revsbech (1987) suggested that the low E_k (irradiance for onset of saturated photosynthesis) of *Potamogeton* leaves indicated a low photosynthetic capacity and a possible adaptive mechanism for growth in a shaded environment.

De La Vega *et al.* (1993) explained the seasonal patterns of macrophyte and epiphyton abundance in a South Florida water body based on the interactions of shading and nutrient availability. They found an inverse relationship between epiphyton and the submersed macrophyte, southern naiad, suggesting that increased shading by epiphyton promoted the senescence of the macrophyte. During senescence, southern naiad released inorganic nutrients, which stimulated greater epiphyton growth.

Macrophyte shading of algae also occurs, particularly for algal communities located near the bottom of the water column or on the sediment surface. Lassen *et al.* (1997) found that there was a trade-off in the submersed macrophyte habitat between increased light attenuation by macrophyte leaves and increased water transparency due to decreased phytoplankton and less sediment resuspension. Phytoplankton may also shade sediment-associated algae, particularly in eutrophic lakes where high levels of nutrients support high biomass of phytoplankton in the water column (Hansson 1992).

Emergent macrophytes also play a role in shading the water columns of shallow systems, although there appears to be less extensive research in this area. Light limitation can occur in dense stands of emergent macrophytes even at midday, limiting photosynthesis in the water column, the lower portions of the plants, and the epiphytic algae (Frodge *et al.* 1990). Grimshaw *et al.* (1997) compared light penetration in cattail (*Typha*) and sawgrass (*Cladium*) stands and found that photosynthetically active radiation (PAR) was reduced 85% in cattail, but only 35% in the more open stands of sawgrass. A comparison of benthic algal photosynthetic rates showed that they were reduced by 30% in sawgrass and by 80-90% in cattail, compared to open water areas. Water in the cattail stands was more nutrient-rich than in the sawgrass stands, so the

suppression of epiphyton photosynthesis was attributed to light limitation by the broader leaved, more densely packed macrophytes (Grimshaw *et al.* 1997).

2.4.4 Provision of habitat

Macrophytes and algae in wetlands and littoral zones provide ideal habitat because of their high rates of primary production for food web support, coupled with the spatial structure provided by a variety of complex growth forms. Macrophytes provide an extensive attachment surface area for epiphytic bacteria as well as epiphytic algae. Wetzel and Søndergaard (1998) emphasize that the majority of autotrophic production and bacterial metabolism in shallow ecosystems is concentrated within the extensive surface area of the macrophyte attachment habitat. This indicates a pivotal role for both submersed macrophytes and attached algae in sustaining the "bacterial loop" in aquatic systems.

Macrophytes provide refuges against fish predation for crustacean grazers, which, in turn, can control phytoplankton populations (Timms and Moss 1984, Schriver *et al.* 1995). This is because increased structural complexity leads to a decrease in the foraging ability of the predator concerned. This refuge effect also benefits phytophilous grazers, who feed on epiphyton, and pelagic grazers, who migrate horizontally to the littoral zone refuge during the day (Lauridsen *et al.* 1996). Smaller prey fish such as juvenile rudd, perch and roach also use macrophyte beds as refugia from piscivorous fish (Persson and Crowder 1998). Piscivorous adult perch and largemouth bass will change from an active pursuit mode to an ambush sit-and wait mode in dense macrophyte beds. In addition to providing refugia from predators, macrophytes provide invertebrate grazers with a sheltered environment where reduced turbidity and water motion aids in efficient invertebrate filter-feeding (Beckett and Aartila 1992).

Wetlands and littoral areas also provide habitat for waterfowl, migratory birds, and small mammals, as well as spawning grounds for fish, reptiles, and invertebrates.

Emergent vegetation provides nesting and escape cover for waterfowl, and nearby open water areas with abundant algae, submersed vegetation and invertebrates provide adequate food resources (Swanson and Duebbert 1989). Bird use is associated with the structure and the cover pattern of the vegetation. The percentage of a wetland covered with emergent macrophytes is a significant predictor of bird species richness, as is the total area of adjacent wetland habitat (Fairbairn and Dinsmore 2001).

Muskrats are the most common semi-aquatic mammals in wetlands, where they use the roots and basal portions of macrophyte shoots for food and the tougher leaves and stems for lodge construction (Fritzell 1989). Muskrat "eat-outs" can decimate emergent macrophytes and alter the structure of an ecosystem dramatically. Other small mammals in wetland and littoral habitats include shrews, voles, mice, and squirrels. Many larger mammals such as the fox, raccoon, mink, skunk, and deer also use the wetland habitat for cover and food resources (Fritzell 1989). Fathead minnows and brook sticklebacks are usually the only fishes that can survive the low dissolved oxygen concentrations in shallow water bodies in winter (Peterka 1989). However, littoral areas bordering deeper lakes can provide spawning cover and food resources for many pelagic fish species. Amphibians and reptiles that use littoral habitats include salamanders, lizards, snakes, frogs, toads and turtles. Many of these animals use wetlands and small lakes for cover and food resources in a landscape that is increasing agricultural or urban in nature (Millar 1989).

2.4.5 Human relevance

Many wetlands and littoral areas also play a role in providing habitat and recreation for humans. There are many non-consumptive recreational and educational functions, such as bird-watching, hiking, canoeing, and public education about ecosystem diversity and development. Other recreational and economic activities supported by these areas include hunting, fishing, trapping, rice production, peat

harvesting, cottage and resort location, and camping. The contribution of macrophytes is obvious in some of these activities, such as peat harvesting and rice production. Algae and macrophytes also play a role in defining the aesthetics of water bodies, based on the human perception of algal blooms as "slime" and of macrophyte beds as "nuisance weeds". The occurrences of rare species of plants such as orchids, mosses, ferns, and liverworts (Sculthorpe 1967, Novacek 1989) enhance the value of such habitats to conservationists and tourists alike. At the landscape scale, vegetation also plays an important role in classification systems of wetlands and lakes. The successive zones of littoral areas of lakes, from open water to upland, are defined by the vegetation types that inhabit each zone (Wetzel 1983a). Most wetland classifications systems rely on vegetation type as a major determinant of inclusion in a particular category (Stewart and Kantrud 1971, Zoltai 1988, Mitsch and Gosselink 2000).

2.5 Summary

2.5.1 Primary production as a central functional role

Primary production is the major biotic role for both algae and macrophytes. However, in the process of performing this role, algae and macrophytes regulate many of the chemical and physical aspects of their environment, which in turn affects the future productive output, in a continuous interacting network. Some of the internal feedback loops in this network are negative, such as increased shading by macrophytes, increased turbidity, or decreased nutrient availability. Other internal feedback loops are positive, such as enhanced access to nutrients or sediment stabilization. In this way, algae and macrophytes have interacting, complementary, and competitive roles in shallow ecosystems, but they cannot necessarily functionally replace each other without causing major changes in the system. Thus the removal of macrophyte beds and consequent loss of epiphytic algae may have severe consequences for the support of

the littoral food web. When the balance shifts, for example from macrophyte-epiphyte dominance to phytoplankton, the result is changed food web structure, nutrient cycling, oxygen dynamics, and frequently a decline in recreational value and in commercially important fish (Sand-Jensen and Borum 1991).

2.5.2 Alternative stable state models provide a framework

I have found that the underlying theme in most of the ecological research in aquatic ecosystems is interaction. There are interactions among algae and macrophytes, interactions with grazers and fish, and interactions with abiotic components of the system. Several researchers have tried to incorporate these interactions into hypotheses and models to better describe shallow ecosystem function. Hypotheses and conceptual models such as these emphasize, to a greater or lesser degree, the interaction of the many biotic and abiotic components within shallow ecosystems. These models are useful tools to use to approach a better understanding of ecosystem function. The predictive success that these models have is likely to depend on the depth of understanding of the roles of interacting components.

One conceptual model of degraded and "healthy" wetland states has been developed by Chow-Fraser (1998), based on observations of Cootes Paradise Marsh in Ontario, Canada. A number of interacting components are proposed for these two states, which are largely characterized by the presence or absence of submersed and emergent macrophytes, and to a lesser degree, by the abundance of phytoplankton and epiphyton. Chow-Fraser (1998) hypothesizes that high water levels, high turbidity, high nutrient levels, high algal biomass, high carp and planktivore biomass, and low invertebrate grazing pressure due to smaller bodied invertebrates maintain the degraded state. She suggests that the "healthy" state might be maintained by the reversal of these characteristics (Chow-Fraser 1998).

Van der Valk and Davis (1978b) have proposed a model of vegetation succession in wetlands, which includes the dry marsh (germination of annuals and emergents), the regenerating marsh (dominance of emergents), the lake marsh (dominance of submersed vegetation), and the degenerating marsh (loss of vegetation). The wet-dry cycle of hydrology in wetlands has been proposed as the underlying mechanism for stage change in this model (van der Valk and Davis 1978b).

Goldsborough and Robinson (1996) have proposed a conceptual model of four alternative stable states in wetlands, characterized by their predominant algal component. The dry marsh state is characterized by low water levels that occur following a drought or deliberate drawdown. Because irradiance at the sediment surface is high, epipelon tend to be the predominant algal assemblage. The open marsh state is maintained by periodic natural disturbances in the wetland, leading to epiphyton predominance on the surfaces of submersed and emergent macrophytes. The sheltered marsh state develops if there is protection from wind action, or there are enough macrophytes in the water column to reduce water movement, allowing metaphyton to predominate. The lake marsh is characterized by high water levels, abundant nutrients in the water column and low grazing pressure, leading to phytoplankton predominance. Suggested interacting mechanisms that promote stability or change between states include water level, nutrient loading, grazing pressure, and abundance of submersed and emergent macrophytes (Goldsborough and Robinson 1996).

Another model that has gained considerable support proposes that alternative clear and turbid stable states may exist in shallow systems (Irvine *et al.* 1989). The turbid stable state is characterized by high concentrations of phytoplankton and other suspended solids, whereas the clear water state is characterized by an abundance of submerged vegetation (Scheffer 1998). Some interacting components have been identified for the alternative states, but many of the underlying ecological mechanisms

are still poorly understood (Scheffer *et al.* 1993). Suggested mechanisms include macrophyte and phytoplankton abundance, level of nutrient loading, turbidity and shading, and densities of invertebrate grazers and planktivorous fish (Irvine *et al.* 1989, Moss 1990, Scheffer *et al.* 1993, Hosper 1998). Recent studies of shallow lakes have focused on phytoplankton and submersed macrophytes as identifying components of these alternative stable states (Irvine *et al.*, 1989, Scheffer, 1990, Blindow *et al.*, 1993, Scheffer *et al.*, 1993, Beklioglu & Moss, 1996). Benthic diatoms are noted, but not discussed, as a buffering mechanism for the clear water stable state (Hosper, 1998).

2.5.3 Other knowledge gaps

There is some general lack of understanding of the ecological differences between planktonic and benthic algae. This became most evident as I reviewed the literature on allelopathy. Apart from the fact that nutrient and light competition are often not ruled out in studies showing apparent allelopathy, the interpretation of macrophyte/algal interactions is further hampered by a general lack of recognition of the role of attached algae in macrophyte stands. Although there is a large body of literature on aquatic photosynthesis, most of it focuses on the phytoplankton. More detailed explorations of areal benthic photosynthesis and the factors that control its variability are needed. In particular, more work is needed in the development of wetland-specific photosynthetic parameters that can be used in modeling wetland algal production across long time spans and geographically large areas.

More information is needed about the effect of vegetation on evapotranspiration and water loss from shallow systems. Quantification of gas fluxes through vegetation is a related area of research that needs more attention. Algal mediation of gas fluxes is also important, particularly benthic algal effects on the oxidation of methane. These areas of research may become particularly important in providing predictive information for global climate change modeling.

One of the most difficult tasks in writing this review was selecting the organizational approach to take in discussing the various roles and interactions of algae and macrophytes. This is because of the fact that in shallow aquatic systems "everything is connected to everything else", making any separation of topics for the purposes of explanation seem awkward and artificial. However, during this attempt to understand the roles of algae and macrophytes, I have identified some knowledge gaps in the research literature. One major gap is that accurate quantification of all contributions to primary production within shallow wetland ecosystems is lacking. In particular, more comprehensive studies of benthic algal contributions to primary production are needed. In many cases there is implied, if not explicit, dismissal of the significance of algal primary production.

3. Methods

3.1 Delta Marsh study

3.1.1 Study site

The mesocosm experiment was carried out in a sheltered channel of Delta Marsh, Manitoba, Canada (98° 23' W, 50° 11' N). The site was a shallow (~1 m depth) river paleochannel situated within the marsh on the south shore of Lake Manitoba. The 45 m wide channel was maintained by natural disturbances, including wind, herbivory, and nutrient limitation, in an open marsh state characterized by abundant epiphyton on the surfaces of submersed and emergent macrophytes (Goldsborough & Robinson, 1996). The submersed macrophyte flora included sago pondweed (*Stuckenia pectinatus* (L.) Boerner) (formerly *Potamogeton*), water-milfoil (*Myriophyllum sibiricum* Komarov), and free-floating hornwort (*Ceratophyllum demersum* L.), whereas the two main emergent macrophytes were cattail (*Typha* x *glauca* Godr. (pro sp.)) and reed grass (*Phragmites australis* (Cav.) Trin. Ex Steud.) (Shay 1999, ITIS 2001). Free-floating macrophytes such as duckweed (*Lemna minor* L.) and bladderwort (*Utricularia macrorhiza* L.) occur mainly along the sheltered channel edges. The marsh supports abundant zooplankton, micro and macroinvertebrates (Hann 1999), small fish species, mainly fathead minnows (*Pimephales promelas*) and brook sticklebacks (*Culaea inconstans*) and large benthivorous (*Cyprinus carpio*) and piscivorous fish (*Perca flavescens*) (Suthers & Gee 1986).

3.1.2 Experimental enclosures and treatments

Floating enclosures (5m x 5m), constructed of 40 cm wide plywood frames supported on high density foam, were installed at the study site on 23 May 1995 and 11 June 1996. A translucent 6 mil plastic curtain was secured to the inside of each enclosure and embedded into the sediments with metal bars, enclosing a sediment area

of 25 m^2 and a total water volume of about 20,000 L. Water depth at the site varied from 80 to 100 cm during the study. The enclosure mesocosms were allowed to recover from the disturbance of installation for four weeks in 1995 and three weeks in 1996, designated as the pretreatment period for each year.

Enclosures were assigned as replicates, of one of three treatments in 1995 and one of four treatments in 1996, to maximize interspersion of treatments and minimize structural edge effects. The experimental treatments in 1995 included (1) submersed macrophyte removal (henceforth referred to as xMac), (2) macrophyte removal plus addition of inorganic N and P thrice weekly (xMacNP) and (3) unmanipulated procedural controls (Control) (Figure 5). I was unable to examine the effects of inorganic N and P addition alone in 1995, because of the lack of available enclosures for additional treatment replicates. The experimental treatments in 1996 included (1) exclusion of macrophytes (henceforth referred to as Ex), (2) addition of inorganic N and P thrice weekly (NP), (3) exclusion of macrophytes plus addition of inorganic N and P thrice weekly (ExNP), and (4) unmanipulated procedural controls (Control) (Figure 6).

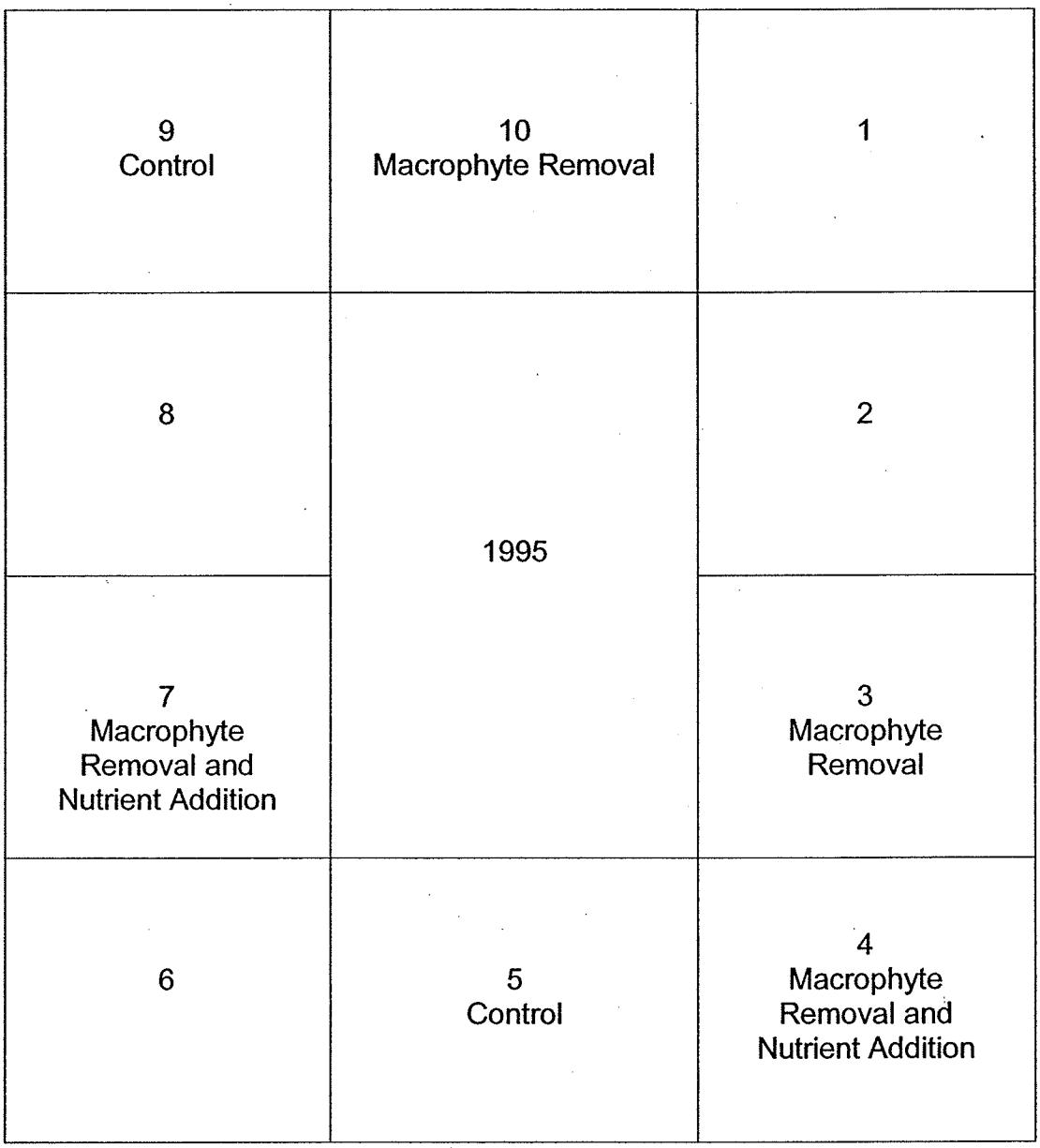

Figure 5. Schematic diagram of the treatment enclosures used in Delta Marsh in 1995. Enclosures 1, 2, 6, and 8 were used in another experiment.

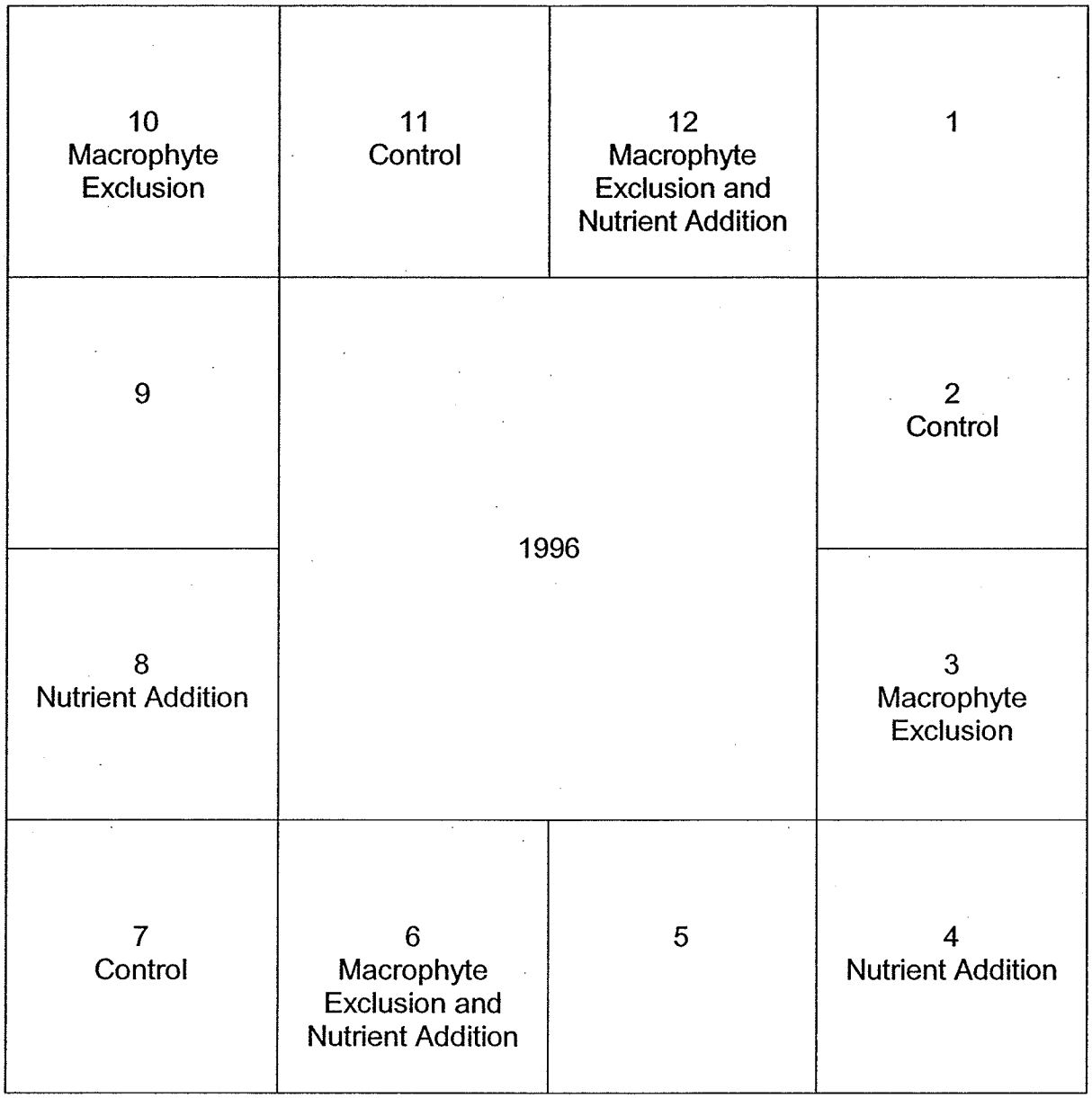

Figure 6. Schematic diagram of the treatment enclosures used in Delta Marsh in 1996.

Enclosures 1, 5, and 9 were used in another experiment

In 1995, macrophyte removal in each of the xMac and xMacNP treatment enclosures was performed by clipping the submersed macrophytes at the sediment surface using long-handled grass clippers. A long-handled rake and a sieve were used to remove the clipped macrophytes from the enclosures. In 1996, exclusion of submersed macrophytes was accomplished in each of the Ex and ExNP treatment enclosures by anchoring a porous black polypropylene fabric (DeWitt Pro-5 Weed Barrier) over the sediments (Schriver *et al.* 1995). This fabric was perforated to facilitate exchange of metabolic gases and nutrients at the sediment/water interface.

Forty-two solid acrylic rods (0.64 cm diameter, 90 cm length) were positioned vertically in each enclosure as algal colonization substrata (Goldsborough *et al.* 1986). The uppermost 60 cm of each substratum was pre-scored to sub-sample algae for analysis of chlorophyll-*a*, photosynthetic C fixation, and algal particulate phosphorus, and the lower 30 cm was pushed firmly into the sediments.

Nutrient addition commenced on 28 June 1995 and 3 July 1996. Inorganic N (as $NaNO_3$) and P (as $NaH_2PO_4 \cdot 2H_2O$) were added every Monday, Wednesday and Friday until 28 August 1995 and 1996, for a total of 27 additions over ten weeks in 1995, and 25 additions over nine weeks in1996. The ratio of N to P was approximately 8:1 by weight, chosen from previous measurements of the sediment interstitial N:P ratio to simulate a nutrient flush such as might occur following dry-down and reflooding of the marsh (Kadlec 1986). The total nutrient load was doubled in 1996 over that applied in 1995. Cumulative nutrient load for the experiment in 1995 was 10.4 g m^{-2} N and 1.4 g m^{-2} P, and 20.6 g m^{-2} N and 2.7 g m^{-2} P in 1996. Nutrients were dispensed by dissolving the inorganic chemical in 10 L of enclosure water and distributing the solution uniformly over the enclosure surface. Occasional vertical sampling indicated the absence of vertical nutrient profiles in the shallow water column.

Gee-type minnow traps were placed in each enclosure immediately after the curtains and fabric macrophyte barriers were put in place. During the pretreatment period, fish caught in traps were removed from the enclosures daily. Post-addition in 1995, I attempted to exclude fish by removing them from the traps in the enclosures daily. Post-addition in 1996, the minnow traps were used to track the fish population in each enclosure. They were checked twice daily, with their contents being counted and released back into their enclosure of origin.

3.1.3 Sampling and analyses

3.1.3 (a) Water chemistry

Depth-integrated water samples were collected with a stoppered acrylic tube (6.4 cm inner diameter, 50 cm length) twice weekly and filtered through a 100-µm mesh to remove zooplankton. Water samples were transported to the field lab in opaque plastic bottles, where they were analyzed for pH, alkalinity (acid titration), ammonium-N (NH_4-N) (hypochlorite method), nitrite+nitrate-N (NO_3-N) (UV spectrophotometry), total reactive P (TRP) (acid molybdate method), soluble reactive silicon (SRS) (acid molybdate method), and, in 1996, turbidity (Hach model 2100A turbidimeter) (APHA 1995, Stainton *et al.* 1977). Water samples were not filtered to remove particulate matter, so TRP included soluble reactive phosphorus (SRP) plus phytoplankton particulate P that reacted to acid molybdate analysis. The acid molybdate method for inorganic P determination may hydrolyze a fraction of organic P, so TRP may overestimate inorganic P (APHA 1995). Weekly water samples were analyzed for total phosphorus (TP) and total Kjeldahl nitrogen (TKN) (APHA 1995). Water depths and temperatures of each enclosure were measured daily. Morning and evening dissolved oxygen (DO) concentrations at 10 and 50 cm depth were determined weekly with an oxygen meter (YSI model 51). Weekly extinction profiles of photosynthetically active radiation (PAR) through the water column

were measured using a Li-Cor LI-189 meter with an LI-192SA submersible quantum sensor.

3.1.3 (b) Algal and macrophyte biomass

All algal assemblages in each enclosure were sampled weekly for chlorophyll-*a* content, including phytoplankton from the water column, epiphyton from the surfaces of submersed macrophytes, periphyton from artificial substrata, epipelon from sediments, and metaphyton from the water column. Epipelon, the motile algae in the sediments, was not sampled in 1996 because the plant barrier fabric in two of the treatments precluded access to the sediments and, presumably, growth of epipelon.

Triplicate phytoplankton samples (500 mL) were collected from depth-integrated water samples as described above, and filtered onto 1.2 µm pore size glass microfiber filters (grade GF/C, Whatman International Ltd., England). The filters were neutralized with saturated $MgCO_3$ solution and frozen for at least 24 hours to lyse cell membranes prior to chlorophyll analysis. Thawed filters were then placed in 90% methanol for 24 hours in the dark to extract chlorophyll pigments. Spectrophotometric measurements (Spectronic 601, Milton Roy Company, Rochester, New York) of the pigment extract were made at 665 nm and 750 nm (1-cm path length) for chlorophyll-*a* and its derivatives, before and after acidification with 10^{-3} N HCl to facilitate correction for pheophytin. Calculation of chlorophyll concentration (µg/L) followed Marker *et al.* (1980). Three additional 100 mL aliquots of each phytoplankton water sample were filtered onto pre-weighed dried glass microfiber filters and dried to constant weight at 104°C for determination of phytoplankton dry weight and total P content (in 1996) (see method below). Phytoplankton chlorophyll values (µg L^{-1}) were multiplied by estimates of enclosure volume (based on depth measurements) at the time of sampling and divided by enclosure surface area (25 m^2) to extrapolate to units of wetland area (µg m^{-2}).

Triplicate acrylic rods were randomly sampled without replacement from each enclosure for determination of periphyton chlorophyll-*a*, photosynthetic carbon uptake, and periphyton particulate P content. The pre-scored rods were separated into segments (10 cm, 2.5 cm, and 5 cm, respectively) in the field using two pairs of needle-nosed pliers. Segments (2.5 cm) for photosynthesis were placed in paired clear and blackened glass incubation tubes filled with 25 mL of pre-filtered marsh water (see methods below). Segments (5 cm) for total P content (in 1996) were placed in labeled vials and transported back to the lab for processing. Periphyton was removed from the rod segments by scraping with a rubber blade and rinsing with distilled water. The resulting slurry was filtered onto glass microfiber filters (Whatman GF/C), which were dried to constant weight at 104°C and analyzed for total P (see methods below). Segments (10 cm) for chlorophyll-*a* were placed in glass vials and frozen for at least 24 hours prior to analysis. Chlorophyll analysis was the same as for phytoplankton, except that each colonized rod segment was placed in 90% methanol, and chlorophyll-*a* was calculated per unit area (cm^2) of rod surface. Periphyton colonization and snail density on the submersed curtain walls was determined in 1996 in a concurrent study by sub-sampling strips of the polyethylene curtain material suspended vertically along the enclosure edges (Mundy & Hann 1996).

Submersed macrophytes, epiphyton and associated invertebrates were collected weekly with a Downing box sampler (Downing 1986). The sampler, a hinged plexiglass case enclosing 4-L volume, was lowered into the water column and closed around the top 30 to 40 cm of macrophyte. The contents of the box were then poured through a 100-µm mesh net to collect microinvertebrates for analysis in a concurrent study (Sandilands *et al.* 2000). The macrophyte sample was then shaken vigorously in 1 L of pre-filtered water to dislodge epiphyton. Three aliquots of the resulting epiphyton slurry (100 mL) were then filtered onto glass microfiber filters (Whatman GF/C) and processed

and frozen as for phytoplankton, described above. Three additional 100 mL aliquots of each epiphyton slurry were filtered onto pre-weighed dried glass microfiber filters and dried to constant weight at 104°C for determination of epiphyton dry weight. Downing box macrophyte samples were sorted by species and dried to constant weight at 104°C. Prior to drying, sub-samples of each species were measured (leaf, stem and flower length and width or circumference). The dry weight of each corresponding macrophyte sub-sample was recorded separately from the rest of the macrophyte sample to enable extrapolation of epiphyton colonization to the entire macrophyte sample and to the marsh bottom area (m^2) occupied by the macrophyte sample. The conversion of macrophyte dry weight (g m^{-2}) to surface area (cm^2 macrophyte surface area m^{-2} marsh bottom area) was calculated using a species specific empirical relationship between dry mass and surface area developed over four years (1995-98) of concurrent measurements (Figure 7). This calculation of macrophyte surface area (cm^2 m^{-2}) was used to convert epiphyton chlorophyll values (µg cm^{-2}) to units of wetland area (µg m^{-2}). Sub-samples of dried macrophytes were also analyzed for total P content in 1996 (see methods below).

Entire above-sediment portions of submersed macrophytes were collected in each of June, July, and August for determination of areal macrophyte biomass (g m^{-2}). An open-ended plastic cylinder was used to delineate a known bottom area (0.45 m^2) and long-handled shears were used to cut the enclosed macrophytes at the sediment surface. These macrophyte samples were processed as above.

Triplicate metaphyton samples were collected from each enclosure where metaphyton was present using methods described by Gurney and Robinson (1988) and Robinson *et al.* (1997). Percent cover (m^{-2}) of metaphyton was estimated for each enclosure. At three randomly chosen locations within enclosures where metaphyton was present, a foam block (625 cm^2) was used to raise all of the metaphyton suspended

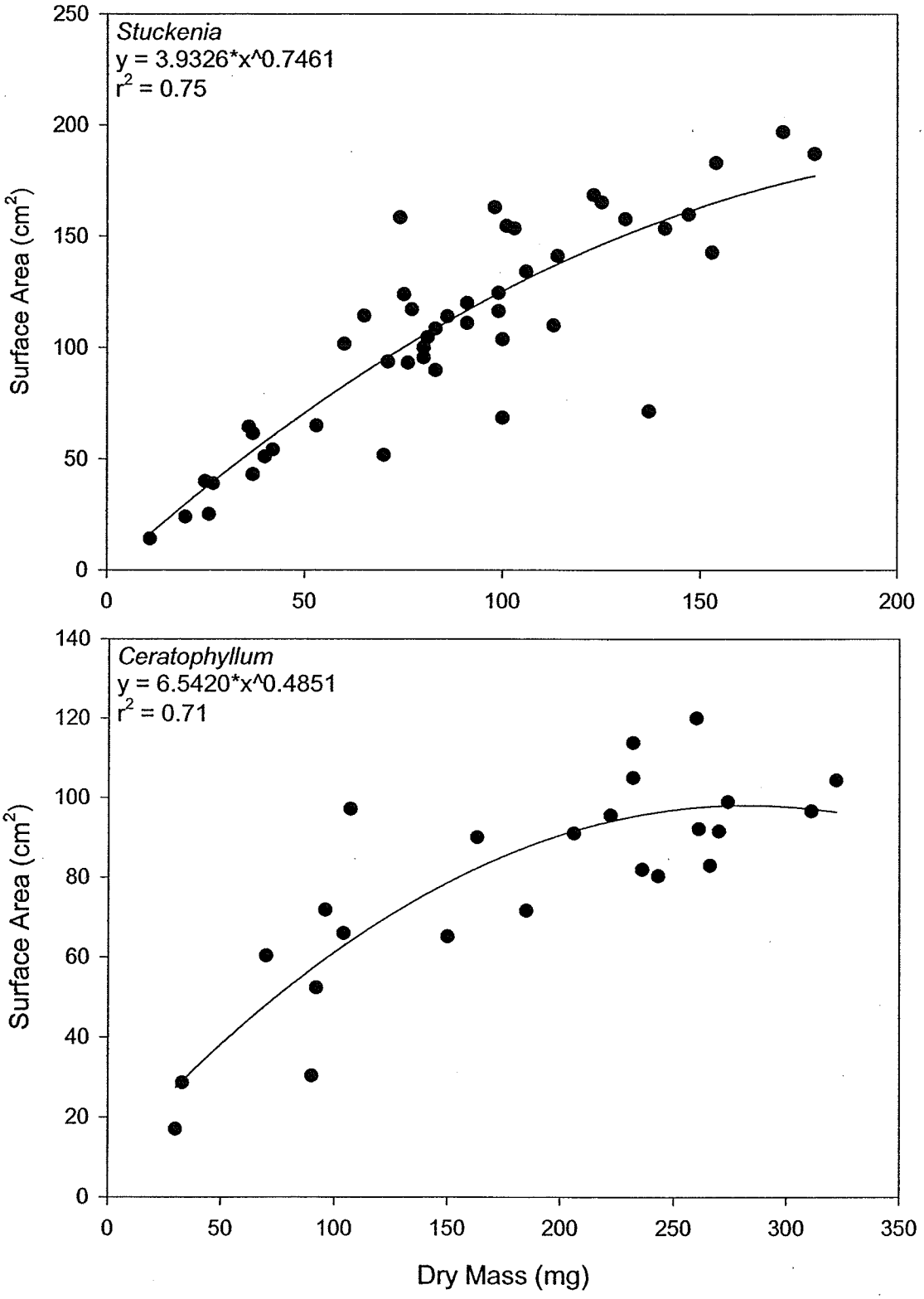

Figure 7. Relationship between submersed macrophyte dry mass (mg) and surface area (cm^2) of macrophyte by species (1995 to 1998).

through the water column to the water surface. A copper corer (1 cm inner diameter) was used to remove three metaphyton cores from each block. Each metaphyton core was placed in a labeled glass vial and frozen for at least 24 hours prior to chlorophyll analysis. Chlorophyll analysis followed the same method as for phytoplankton, except that the entire metaphyton core was placed in 90% methanol. Three additional metaphyton cores were taken from each block and dried to constant weight at 104°C for determination of metaphyton dry weight. A weighed sub-sample of each dried metaphyton sample was analyzed for total P content in 1996 (see below).

Triplicate epipelon samples were obtained from all enclosures in 1995 according to methods described by Eaton and Moss (1966). A coring tube was lowered through the water column to delineate a known area (82 cm^2) of the sediment. A hand-operated vacuum apparatus was used to aspirate the top 0.5 cm of the sediment within the tube. The resulting slurry was transferred to a blackened beaker and allowed to settle for 24 hours in the dark. The overlying water was drawn off without disturbing the settled sediment. The beakers were then transported to an outdoor site where they would receive natural irradiance for at least 18 hours. A circle of untreated lens paper the same diameter as the beaker was placed on each sediment surface to trap the algae migrating toward the light. The blackened sides of the beakers prevented light penetration through the sides. After 18 hours, the lens paper circles were carefully removed from the beakers and placed in 100 mL of pre-filtered (Whatman GF/C) marsh water. These samples were vigorously shaken for two minutes to dislodge the epipelic algae, which had migrated up from the sediment into the lens paper. Sub-samples of the epipelon slurry were filtered onto glass microfiber filters (Whatman GF/C) and processed and frozen as for phytoplankton. The remaining sub-samples of the slurry were used to measure epipelon photosynthesis.

3.1.3 (c) Algal photosynthesis

Phytoplankton and periphyton photosynthesis were measured weekly. Epipelon was measured four times throughout the summer in 1995. Algal photosynthesis was determined by adding one mL of $NaH^{14}CO_3$ (37 kBq mL^{-1}) solution to each sample, including dark samples, prior to incubation. Samples were incubated in a water bath maintained at 25°C at an irradiance of ~500 µmol m^{-2} s^{-1} for four hours (Sylvania high pressure sodium lamp). Immediately following incubation, samples were collected on 1.2 µm pore size glass microfiber filters (Whatman GF/C) using a gentle vacuum. For periphyton, the entire colonized rod segment was collected on the filters. The filters containing the samples were fumed over concentrated HCl to release any residual inorganic radio-labeled bicarbonate as carbon dioxide. The filters were then placed in 5 mL glass vials of liquid scintillation cocktail (Beckman Ready Safe™, Fullerton, California). Radioactivity (dpm) of the samples was determined by liquid scintillation counting in a Beckman LS3801 (Beckman Instruments, Irvine, California) scintillation counter programmed for H-number color quench correction. After correcting for dark uptake, the carbon fixation rate (µg C L^{-1} h^{-1} for phytoplankton, µg C cm^{-2} h^{-1} for periphyton) was calculated using the dissolved inorganic C content of the incubation water, determined from measurements of temperature, pH, and titratable alkalinity. Specific (Chl-*a* normalized) photosynthesis (Ps^B) was then calculated using the Chl-*a* values measured at time of sampling, according to the following equation:

$$Ps^B\ (\mu g\ C\ \mu g^{-1}\ Chl\text{-}a\ h^{-1}) = \frac{dpm_s \times DIC \times 1.05}{dpm_t \times T \times Chl}$$

where dpm_s is the radioactivity of each sample corrected for dark uptake; DIC is the dissolved inorganic carbon concentration (µg L^{-1}) of the marsh water as determined from alkalinity, pH, and temperature; 1.05 is an isotope discrimination factor (Strickland and Parsons 1972); dpm_t is the radioactivity of added $NaH^{14}CO_3$; T is the incubation time

(hours); and Chl is Chl-*a* (μg L^{-1} for phytoplankton, μg cm^{-2} for periphyton) at time of sampling (Robinson *et al.* 1997).

3.1.4 Phosphorus budget

A phosphorus budget was calculated in 1996 to identify phosphorus partitioning among the various biotic and abiotic pools within the treatment enclosures, and to identify the fate of added phosphorus in NP and ExNP treatments. Weekly samples of phytoplankton, periphyton and metaphyton, and bi-weekly samples of macrophytes, invertebrates, fish and sediment were analyzed for total phosphorus content and data were extrapolated to comparable units of wetland area (mg m^{-2}). Total P was analyzed using the method of Andersen (1976). The samples were combusted at 550°C and then boiled in 1 N HCl to convert polyphosphates to orthophosphate. Total phosphorus was then quantified using the acid molybdate method (Stainton *et al.* 1977). Dissolved inorganic phosphorus (DIP) was determined by subtracting phytoplankton total P from TRP (because TRP includes particulate (i.e. phytoplankton) P). Sediment samples for P analysis were aspirated from a known area (81.7 cm^2) to a depth of 2 cm using a hand vacuum pump. The resulting slurry was allowed to settle in the dark for 24 hours and the overlying water was drawn off prior to sub-sampling the sediment. Because sediment P could not be measured in treatments with plant barrier fabric, the sediment P value from NP enclosures was used in calculating ExNP total P, whereas the sediment P value from Control enclosures was used in calculating Ex total P. Mean numbers of fish per enclosure were estimated from weekly minnow trap counts and mean invertebrate densities were provided by Sandilands *et al.* (2000).

3.2 Oak Hammock Marsh Study

3.2.1 Site description

My second study was carried out in Cell Four of Oak Hammock Marsh (97° 7' W, 50° 11' N) (Figure 8), a 596 ha wetland nearing the end of its flooded cycle, with approximately half its area in shallow open water (1-m depth or less) and half in vegetation coverage by submersed, emergent, or free-floating macrophytes. Eight study sites were established in Cell Four by stratified random sampling with vegetation type (presence or absence of *Typha*) as the first subset, and water depth (less than or greater than 50 cm) as the second subset. Sites 2 and 7 were replicates of Open Shallow (no emergent vegetation, water depth < 50 cm), sites 3 and 6 were replicates of Open Deep (no emergent vegetation, water depth > 50 cm), and sites 1, 4, 5, and 8 were replicates of *Typha* Shallow (*Typha* present, water depth < 50 cm). There were four *Typha* Shallow replicates because there were no *Typha* sites in the marsh with water depths greater than 50 cm. Two additional sites (9 and 10, both *Typha* Shallow) were established in the tertiary sewage treatment lagoon adjacent to the Oak Hammock complex to assess possible effects of nutrient loading. The position of each site was recorded using the global positioning system (GPS, Eagle Explorer twelve-channel parallel, Eagle Electronics, Catoosa, Oklahoma). To facilitate repeated sampling at each site over two years, permanent transects (2-m width, 10-m length) were established using flagged stakes. At the beginning of each ice-free season, forty-eight pre-scored (10-cm interval) solid acrylic rods (0.64 cm diameter, 90 cm length) for periphyton sampling were vertically positioned (50 cm apart) within each transect by pushing the lower 30 cm of each rod firmly into the sediment.

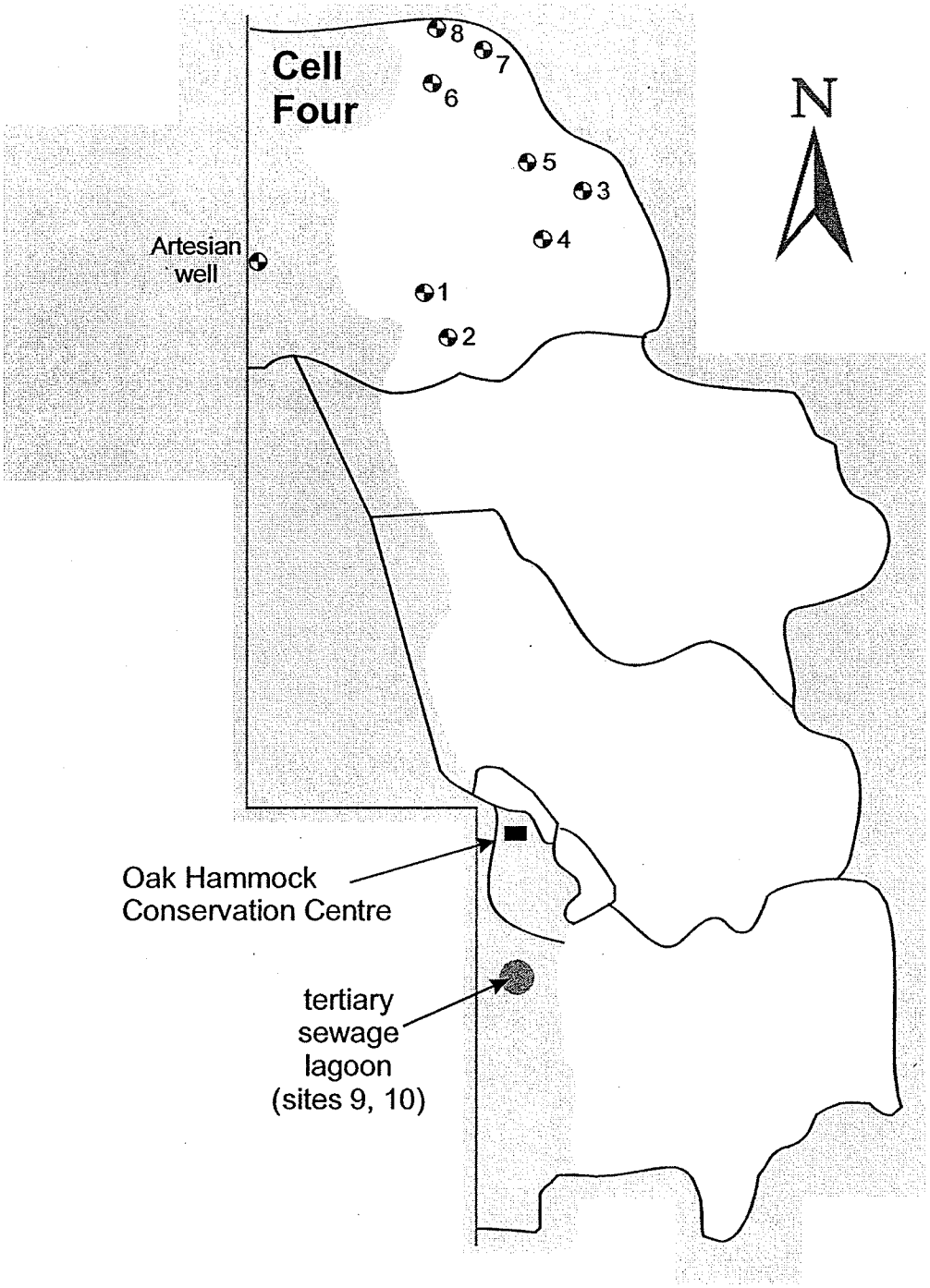

Figure 8. Location of sampling sites in Cell Four and the tertiary sewage lagoon of Oak Hammock Marsh, Manitoba.

The tertiary sewage lagoon was a cattail-dominated constructed wetland (0.5 ha) with a clay-lined bottom covered by gravel. The water level (mean 50 cm depth) of the tertiary lagoon was managed throughout the ice-free season as treated water was released by gravity flow into Oak Hammock Marsh Cell One after meeting provincial water quality standards for fecal coliforms (200 MPN/100 mL), total coliforms (1500 MPN/100 mL), biological oxygen demand (BOD) (30 mg L^{-1}), and sodium (300 mg L^{-1}) (Williamson 1988). Subsequently, effluent water from the secondary sewage lagoon was then released by gravity flow into the tertiary lagoon. This cycle was repeated several times until all of the previous year's effluent water from the secondary lagoon had been treated and released through the tertiary lagoon.

Free-floating vegetation in Cell Four consisted mainly of common duckweed (*Lemna minor* L.), some star duckweed (*Lemna trisulca* L.), and hornwort (*Ceratophyllum demersum* L.). Submersed aquatic vegetation was dominated by sago pondweed (*Stuckenia pectinatus* (L.) Boerner) (formerly *Potamogeton*). Although *Ceratophyllum* is classified as free-floating (Sculthorpe 1967), it is entirely submersed and provides attachment substrata for attached algae in a fashion similar to *Stuckenia.* Therefore, I have included *Ceratophyllum* with *Stuckenia* whenever I have used the term 'submersed macrophytes' within this study. The two main emergent macrophytes fringing the marsh were hybrid cattail (*Typha* X *glauca* Godr. (pro sp.)) and reed grass (*Phragmites australis* (Cav.) Trin. Ex Steud.) (ITIS, 2001). The tertiary sewage lagoon was dominated by hybrid cattail and a minor component of sago pondweed (< 10 m^2).

3.2.2 Sampling and analysis

3.2.2 (a) Environmental variables

All sampling was carried out at bi-weekly intervals over the course of two ice-free seasons, 01 April to 20 November 1997 and 25 March to 05 November 1998. Water depths and temperatures were measured at each site at each sampling time. Bi-weekly

extinction profiles of photosynthetically active radiation (PAR) at 10-cm intervals through the water column were measured at each site using a Li-Cor meter (Li-189) with a submersible quantum sensor (Li-192SA). A Li-Cor quantum datalogger (Li-1000, Li-Cor Inc., Lincoln, Nebraska) installed on the roof of the building adjacent to Oak Hammock Marsh recorded incident irradiance ($\mu mol\ m^{-2}\ s^{-1}$) at 15-minute intervals over the course of the ice-free season in both 1997 and 1998. Mean monthly estimates of air temperature and wind speed were calculated from data obtained from the Environment Canada weather station located at the Winnipeg International Airport, 25 km south of Oak Hammock Marsh.

3.2.2 (b) Water chemistry and nutrient analyses

Bi-weekly depth-integrated water samples were collected with a stoppered acrylic tube (6.4 cm inner diameter, 50 cm length) at random intervals along the 10-m transect established at each site. The water samples were filtered through a 100-µm mesh to remove zooplankton, and transported to the lab in opaque plastic bottles. Water samples were analyzed for pH, alkalinity, ammonium-N, nitrite+nitrate-N, and total reactive P (TRP) as described earlier. Mid-summer water samples were analyzed in both 1997 and 1998 for soluble reactive silicon (SRS) (described earlier). Mid-summer water samples were analyzed in 1997 for total phosphorus (TP), total Kjeldahl nitrogen (TKN), and dissolved organic carbon (DOC) (persulfate-ultraviolet oxidation method) (APHA, 1995).

Three experiments were undertaken to assess nutrient limitation of algal assemblages in Cell Four. Nutrient-diffusing substrata placed on the sediment surface were used to assess periphyton nutrient limitation (Fairchild *et al.* 1985). Phytoplankton nutrient status in Cell Four and the tertiary sewage lagoon was determined using assays of nitrogen debt (Healey 1977) and alkaline phosphatase activity (Healey and Hendzel 1980).

3.2.3 Nutrient-diffusing assay

3.2.3 (a) Nutrient diffusion rates

In order to determine rates of diffusion of nitrate (NO_3-N) (measured as nitrate+nitrite-N) and total reactive phosphorus (TRP) from the nutrient diffusing substrata, a laboratory experiment was conducted prior to the *in situ* study. Clay plant pots (outside diameter = 8.8 cm, height = 8.0 cm) were prepared according to Fairchild *et al.* (1985). Silicon adhesive was used to attach a plastic Petri dish to the large opening of each pot, producing an internal chamber volume of 245 cm^3. Four nutrient treatments, 0.05 and 0.5 mol L^{-1} P (as $NaH_2PO_4 \cdot H_2O$); and 0.05 and 0.5 mol L^{-1} N (as $NaNO_3$) in agar were used. Each treatment was poured into three pots (n = 12) through the small opening in each pot and sealed with a neoprene stopper.

After allowing sufficient time for the agar to gel, each pot was placed into a widemouth 4 L glass jar with 1.5 L of deionized water. The water was sampled for diffused nutrients and replaced with 1.5 L of deionized water each day for 23 days (Fairchild *et al.* 1985). NO_3-N and TRP analyses were performed daily (Stainton *et al.* 1977, APHA 1992). At the conclusion of the experiment, the agar was scraped from the interior chamber of each pot, heated, immediately diluted to 1 L with deionized water, and analyzed for NO_3-N and TRP content. Daily release rates were calculated and verified by the measurement of remaining nutrients.

3.2.3 (b) In situ *periphyton study*

The nutrient-diffusing assay took place in Oak Hammock Marsh from 4 July to 21 August (48 days) in 1997 and 1998. Nine treatment combinations of N:P (0/0, 0/0.05, 0/0.5, 0.05/0, 0.05/0.05, 0.05/0.5, 0.5/0, 0.5/0.05, 0.5/0.5) were used, with four replicates per treatment.

The clay pots were positioned 2-3 cm above the sediments near Site 3 using a 20 cm length of wooden dowel affixed to the bottom of each substrata and pushed down

into the sediments. The pots were randomly placed 40 cm apart in a grid at a depth of 60 cm. Surface water samples were collected weekly above the nutrient-diffusing grids and at nearby Sites 3 and 5 to determine ambient levels of NH_4-N, NO_3-N, and TRP.

The substrata were slowly brought to the surface at the end of each experiment. Each pot was gently removed, scrubbed with a toothbrush and rinsed with deionized water to dislodge all periphytic growth. The volume of this algal slurry was made up to 500 mL with distilled, deionized water and returned to the laboratory. Three sub-samples were filtered from each sample for chlorophyll-*a* analysis (methods described earlier).

3.2.4 Nutrient deficiency experiments

3.2.4 (a) Nitrogen debt

Nitrogen debt experiments for phytoplankton were undertaken in Oak Hammock Marsh during the same time periods as the nutrient-diffusing assays. Nitrogen debt was determined as the amount of ammonium-N taken up by whole water column samples in the dark over a 24-hour period (Solorzano 1969, Healey 1977). Integrated water column samples were collected from Site 3, Site 6, and the tertiary sewage lagoon. Three subsamples were analyzed for phytoplankton chlorophyll-*a,* as per methods described below, and three additional subsamples received a known amount of ammonium chloride (NH_4Cl). Aliquots of these enriched N subsamples were removed immediately (0 hours) and 24 hours later for spectrophotometric determination of NH_4-N concentration. The greater the amount of NH_4Cl taken up by the phytoplankton (chlorophyll normalized) over the course of 24 hours, the greater the degree of nitrogen deficiency. A value greater than 0.15 µmol N μg^{-1} Chl-*a* 24-hr^{-1} indicates severe N deficiency (Healey 1975).

3.2.4 (b) Alkaline phospatase activity

Alkaline phosphatase activity (APA) was measured on whole water column samples at Oak Hammock Marsh concurrently with the nitrogen debt experiments. Three

unfiltered aliquots (5 mL) of the water column sample were set aside for determination of total APA (Healey and Hendzel 1980). Three aliquots (5 mL) were filtered under gentle vacuum through 0.45 µm cellulose nitrate filters for determination of soluble APA and an additional three aliquots (5 mL) were filtered through 0.20 µm cellulose nitrate filters for determination of bacterial APA. All aliquots were enriched with 3-*o*-methylfluorescein phosphate (*o*-MFP) and held in a water bath at 35° C while fluorescence was determined at 3 minute intervals using a Turner fluorometer (Model 110, G. K. Turner and Assoc., Palo Alto, California). Alkaline phosphatase activity was normalized to phytoplankton chlorophyll-*a* and calculated, with reference to concurrently run standards, as µmoles of *o*-methylfluorescein phosphate hydrolyzed to *o*-methylfluorescein per unit of chlorophyll per hour.

The alkaline phosphatase bioassay (Healy and Hendzel 1980) is based on the premise that algae produce an enzyme, alkaline phosphatase, that cleaves phosphate from larger organic particles, and that this activity increases when algal cells experience P deficiency. In the bioassay, the P source fluoresces as phosphate is hydrolyzed. Therefore, the more fluorescence there is, the more alkaline phosphatase activity and the higher the likelihood of P deficiency. A value greater than 0.005 µmol *o*-MFP μg^{-1} Chl-*a* hr^{-1} is indicative of severe P deficiency (Healey and Hendzel 1980). Non-bacterial APA generally ranges from 5 to 50% of total alkaline phosphatase activity in cultures and natural phytoplankton assemblages (Healey and Hendzel 1979).

3.2.5 Algal and macrophyte sampling and analyses

Aerial colour infrared photographs (Wild 15/4 UA6-S large format camera, Kodak Aerochrome Infrared film) of Cell Four were taken in August 1997 when plant development and biomass was near peak potential. These photographs were flown at a height of 1847 m and produced at a scale of 1:10,000, providing a ground resolution of about 1 meter. The photographs were digitized using a geographic information system

(ArcView GIS 3.2, Environmental Systems Research Institute, Inc., Redlands, California) to assess the area of vegetation cover. Ground surveys of vegetation cover were carried out in August 1997 to corroborate identification of vegetation types and locations on the aerial photographs.

Algal assemblages, including phytoplankton, periphyton, epiphyton, and metaphyton were sampled bi-weekly at each site for chlorophyll-*a* determinations. Epipelon and plocon were sampled monthly. Submersed, emergent and floating leaf macrophytes were sampled bi-weekly for biomass determinations (g dry weight m^{-2} of marsh bottom area).

Triplicate phytoplankton samples (500 mL) were collected from depth-integrated water samples and analyzed for chlorophyll-*a* as per methods described earlier. Triplicate acrylic rods were randomly sampled without replacement from each site for determination of periphyton chlorophyll-*a*. The pre-scored rods were separated into segments (10 cm) in the field using two pairs of needle-nosed pliers. Each segment was labeled according to its original depth in the water column (surface:0-20 cm, mid:20-40 cm, deep:40-60 cm) and frozen for at least 24 hours prior to chlorophyll analysis.

Triplicate submersed epiphyton samples were collected from sub-samples of submersed macrophytes during macrophyte sampling at sites 3 and 6. At three randomly chosen locations along each 10-m site transect, an open-ended cylindrical macrophyte sampler (0.55 m inner diameter) was carefully lowered through the water column to delineate a known area of the marsh bottom. Long-handled shears were used to cut the enclosed above-ground portions of the macrophytes at the sediment surface. The macrophytes were gently removed with a small plastic rake and placed in a labeled plastic bag. If more than one species of macrophyte was present, the sample was sorted, each species was processed separately, and the values were summed to determine total biomass (g dw m^{-2}) and total epiphyton chlorophyll-*a* (µg g^{-1} dw of

macrophyte). For chlorophyll analysis, a sub-sample of each macrophyte sample was shaken vigorously in 1 L of filtered water to dislodge epiphyton. Three aliquots of the resulting epiphyton slurry (100 mL) were then filtered onto glass microfiber filters (Whatman GF/C) and processed and frozen as for phytoplankton, described above. The remaining portion of each macrophyte sample was shaken in filtered water to remove epiphyton and then dried to constant weight at 104° C. The dry weight of each corresponding macrophyte sub-sample was recorded separately from the rest of the macrophyte sample to enable extrapolation of epiphyton colonization to the entire macrophyte sample and to the marsh bottom area (m^2) occupied by the macrophyte sample. The conversion of macrophyte dry weight (g m^{-2}) to surface area (cm^2 macrophyte surface area m^{-2} marsh bottom area) was calculated using the empirical relationship described earlier (Figure 7). Epiphyton was not sampled in the tertiary sewage lagoon, as removal of vegetation was not permitted by site managers.

Triplicate emergent epiphyton samples were collected from the submerged lower portions (0-20 cm above sediment surface) of *Typha* stems during macrophyte sampling at sites 1, 4, 5, and 8. Stem counts (stems m^{-2}) of *Typha* were recorded along the 10-m transect at each site. This was done by placing a floating quadrat sampler (0.67 m^2 inner area) on the water surface four times in a non-overlapping square pattern and counting the number of stems within the quadrat area each time. I then advanced 2 m along the transect and repeated the four quadrat stem counts. This process was repeated 6 times, yielding 24 quadrat stem counts along each 10-m transect. At three randomly chosen intervals along the transect, the above-ground portions of the stems within the quadrat area were harvested by shearing them at the sediment surface. Just prior to this bulk harvesting, three *Typha* stems were chosen at random for epiphyton analysis. Each of these stems was first sheared at the surface of the water and the emergent portion of the stem was labeled and bagged. Then, each stem was sheared at the sediment

surface, and each 10 cm segment was cut off and bagged separately and labeled with their original depth in the water column. The remaining *Typha* stems within the quadrat were then harvested and bagged. The epiphyton was removed from each 10-cm stem portion by scraping the stem with a rubber blade and rinsing with distilled water. The resulting epiphyton slurry was processed and frozen as for phytoplankton. The circumference and the length of each stem portion were recorded to enable calculation of epiphyton chlorophyll per surface area of stem and extrapolation to surface area of stems per marsh bottom area ($cm^2\ m^{-2}$). The *Typha* stems were dried to constant weight at 104°C.

Triplicate metaphyton samples were collected from each site where metaphyton was present using methods described earlier. Percent cover (m^{-2}) of metaphyton was estimated along the 10-m transect at each site. This was done by placing a floating quadrat sampler (0.25 m^2 inner area) on the water surface four times in a non-overlapping square pattern and observing the percent cover within the quadrat area each time. I then advanced 2 m along the transect and repeated the four percent cover observations. This process was repeated 6 times, yielding 24 percent cover estimates along each 10-m transect. At three randomly chosen intervals along each 10-m site transect, a foam block (625 cm^2) was used to raise all of the metaphyton suspended through the water column to the water surface. A copper corer (1 cm inner diameter) was used to remove three metaphyton cores from each block. Each metaphyton core was placed in a labeled glass vial and frozen for at least 24 hours prior to chlorophyll analysis.

Triplicate epipelon samples were obtained at all sites and processed according to methods described earlier. Triplicate samples of plocon were collected from all shallow sites (1,2,4,5,7,8) where it was present. Presence/absence of plocon on the sediment surface was estimated using the same method as for estimating percent cover of

metaphyton, except that instead of walking the transect, I canoed the length, being careful not to touch the paddle to the sediment surface. When plocon was present, I estimated the percent area of sediment bottom within the floating quadrat sampler (0.25 m^2 inner area) that was covered by plocon. Following the percent area estimate, I canoed the length again, randomly touching the paddle to the sediment surface to dislodge patches of plocon, which would float to the water surface. Using the same coring method as for metaphyton, a foam block (625 cm^2) was placed under the plocon patch at the water surface and a copper corer (1 cm inner diameter) was used to obtain three plocon cores. Each plocon core was placed in a labeled glass vial and frozen for at least 24 hours prior to chlorophyll analysis.

Triplicate samples of common duckweed were collected at sites 1, 4, 5, and 8. Percent cover was estimated using the same method as for metaphyton. At three randomly chosen intervals along each 10-m site transect, a plastic mesh sieve (17 cm inner diameter) was raised slowly through the water column to collect a known area of duckweed. The duckweed was dried to constant weight at 104°C.

3.2.6 Dawn to dusk *in situ* photosynthesis experiments

Dawn to dusk phytoplankton and periphyton photosynthesis was measured *in situ* at Site 3 in Oak Hammock Marsh three times in 1997 (11 July, 20 August, and 15 September) and three times in 1998 (8 June, 27 July, and 15 September). The apparatus for *in situ* photosynthesis consisted of pairs of slotted clear plastic collars that allowed glass incubation tubes (30 mL volume) to be secured horizontally in the water column (Goldsborough and Brown 1986) (Figure 9). The plastic collars were suspended on cord from a floating polyurethane foam frame. The length of the cord was adjusted so that each row of incubation tubes was suspended at 10-cm depth intervals. Using this apparatus, three replicates of phytoplankton and 3 replicates of periphyton could be incubated at 5, 15, and 25 cm depth in ambient water temperature and ambient levels of

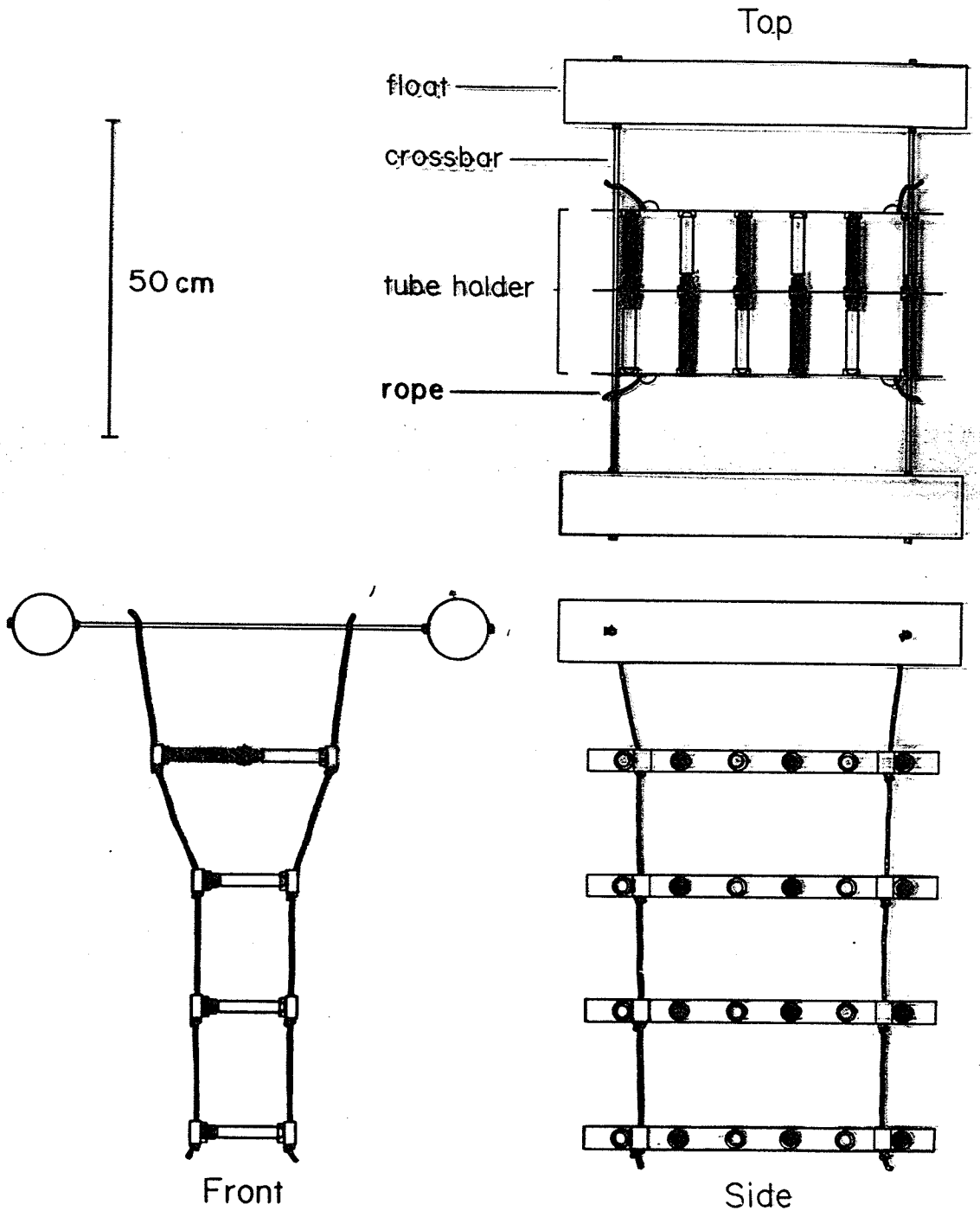

Figure 9. Apparatus for measurement *of in situ* photosynthesis (Goldsborough and Brown 1986).

PAR. Three additional slots held three darkened incubation tubes. The floating apparatus was anchored near Site 3 and samples were incubated for four-hour intervals, beginning at sun-up and continuing until sundown. I used a second floating apparatus to prepare the next set of samples, so that the next incubation period was timed to begin 5 minutes before the previous incubation ended.

Depth-integrated phytoplankton samples were collected with a water column sampler and filtered through a 100-µm mesh to remove zooplankton. Three 25 mL aliquots per depth interval (5, 15, and 25 cm) were dispensed into labeled clear glass incubation tubes, and three aliquots were placed in darkened tubes. Three additional phytoplankton samples were collected for chlorophyll analysis. Periphyton was sampled from randomly chosen vertical acrylic rods (0.64 cm diameter, 90 cm length), pre-scored at 2.5 cm intervals, which had been deployed at Site 3 three weeks previous to each sampling date. The colonized rods were sectioned using needle-nose pliers and chosen rod segments were placed in 25 mL of pre-filtered (Whatman GF/C) marsh water in labeled incubation tubes. The rod segments were placed in the incubation apparatus according to their original depth in the water column (surface:0-10 cm, mid:10-20 cm, deep:20-30 cm), and one segment from each of these depths was placed in three darkened tubes. I added one mL of $NaH^{14}CO_3$ (37 kBq mL^{-1}) solution to each sample, including dark samples, just prior to placing the tubes in the suspension apparatus for incubation. Additional 2.5 cm segments were collected for chlorophyll analysis. Triplicate marsh water samples were also collected and analyzed for temperature, pH and alkalinity. Light extinction profiles were measured at 10-cm intervals through the water column at the start of each four-hour incubation period.

3.2.6 (a) Measurements of photosynthesis

After the four-hour incubation period, the incubation tubes were immediately placed on ice in closed coolers and transported to the lab for processing. The samples were

immediately collected on 1.2 µm pore size glass microfiber filters (Whatman GF/C) using a gentle vacuum. The filters containing the samples were fumed over concentrated HCl to release any residual inorganic radio-labeled bicarbonate as carbon dioxide. Photosynthetic carbon uptake was determined using methods described earlier.

3.2.7 Sample collection for photosynthesis-irradiance experiments

Photosynthesis-irradiance experiments were conducted in 1997 (28 July, 17 October) and in 1998 (26 May, 08 July). Triplicate algal samples for P*E* experiments were collected on these dates, from Site 3 (Open Deep) for phytoplankton and periphyton, and from Site 5 (Typha Shallow) for metaphyton. Depth-integrated phytoplankton samples were collected at random intervals along the 10-m site transect. The water samples were filtered through a 100-µm mesh to remove zooplankton, and stored in opaque plastic bottles. Periphyton was sampled from randomly chosen vertical acrylic rods (0.64 cm diameter, 90 cm length), pre-scored at 2.5 cm intervals, which had been deployed at Site 3 three weeks previous to each sampling date. The colonized rods were sectioned in the field and each rod segment was placed in 25 mL of pre-filtered (Whatman GF/C) marsh water. The rod segments were labeled according to their original depth in the water column (surface:0-17.5 cm, mid:17.5-35 cm, deep:35-50 cm). Metaphyton was sampled at random intervals along the 10-m site transect using the coring method described earlier. Each sample (1-cm diameter) was placed in 25 mL of pre-filtered (Whatman GF/C) marsh water.

At each sampling time, water temperature, depth and light extinction profiles through the water column were recorded. Three additional sets of samples for phytoplankton, periphyton and metaphyton were collected and processed for chlorophyll analysis. Triplicate marsh water samples were also collected and analyzed for pH and alkalinity. All algal samples for P*E* experiments were immediately packed on ice in

darkened coolers and transported to the National Water Research Institute (NWRI) in Saskatoon, Saskatchewan.

3.2.8 Photosynthesis-irradiance experiments

3.2.8 (a) Phototron

Photosynthesis-irradiance experiments were performed in the phototron (Rai and Krambeck 1992) at NWRI in Saskatoon, Saskatchewan. The phototron consisted of a machined aluminum block holding 36 (75 mL) glass incubation chambers, closed at the bottom but open at the top to permit sampling. The incubation chambers were illuminated from below by individual high intensity halogen bulbs (Philips Spot Lamps Model GBE, 18° arc, 12 volts, 20 watts). The intensity of light was controlled by placing individual neutral density screens made of steel or brass in a tray centered between the bulbs and the chambers (Arts and Rai, 1997). Excess heat from the bulbs was removed by a fan that blew between the bulbs and the chambers. The aluminum block was cooled internally by ethylene glycol pumped from a refrigeration unit (Julabo, Model F20, Ultra-Temp 2000) allowing precise temperature control within the incubation chambers (±0.5°C). The entire aluminum block sat on a shaker table, which provided gentle motion to maintain the algal cells in circulation within the incubation chambers. A light fixture to supply ultraviolet-B (UV-B) radiation was suspended above the phototron on a moveable pulley system. A black roller blind was pulled down around the phototron to contain the UV-B rays and to minimize outside light interference (Arts and Rai, 1997).

3.2.8 (b) Design of experiments

The design of the phototron allowed incubation of four replicate P*E* curves simultaneously, each with eight intensities of photosynthetically active radiation (PAR), which I set at 25, 50, 100, 300, 500, 900, 1500, and 2000 µmol m^{-2} s^{-1}. The remaining four chambers were opaque at the bottom and were fitted with black caps, providing four replicate dark incubation chambers. PAR in the incubation chambers was measured with

a quantum scalar irradiance meter (Biospherical Instruments Model QSL-100) equipped with a 1.9 cm diameter solid Teflon sphere irradiance collector (Biospherical Instruments, California, USA). A four-hour incubation period was used for all experiments. Algal photosynthesis was determined by adding one mL of $NaH^{14}CO_3$ (37 kBq mL^{-1}) solution to each sample, including dark samples, prior to incubation. Samples were collected on 1.2 µm pore size glass microfiber filters (Whatman GF/C) using a gentle vacuum. For periphyton, the entire colonized rod segment was collected on the filters, whereas for metaphyton the entire metaphyton core was retained on the filters. The filters containing the samples were fumed over concentrated HCl to release any residual inorganic radio-labeled bicarbonate as carbon dioxide. Sample radioactivity was measured and specific photosynthesis (Ps^B) was calculated using the same methods described earlier.

Incubations were started immediately upon arrival at NWRI and were completed within 48-56 hours of sample collection from Oak Hammock Marsh. Incubations of each algal assemblage were conducted at 7°, 14° and 21°C on each date, to encompass the range of water temperatures found in nature over the course of the growing season. Although algae may grow at lower or higher temperatures than these, the chosen 7° and 21° temperatures were just within the mechanical limits of the phototron's cooling/heating system to ensure maintenance of consistent temperatures. The spring metaphyton samples for the 7° P*E* curve were lost due to equipment failure. The fall metaphyton samples for the 7° P*E* curve were lost when the cooling system of the phototron malfunctioned during the incubation. Therefore I was only able to use metaphyton P*E* curves for 14°and 21° in my model. I had also planned to conduct experiments in 1998 using 8 levels of UV-B radiation, ranging from 0 to 120% of mean ambient UV-B. Unfortunately, the phototron was unavailable at this time.

3.2.8 (c) Photosynthesis model parameters

The photosynthetic parameters, P^B_{max}, *a*, and ß were determined by non-linear regression (SAS v. 8.2, SAS Institute Inc., 1997) using all Ps^B values and their corresponding irradiances for each algal assemblage. Once photosynthetic parameters were calculated for all P*E* curves, I evaluated a series of nested non-linear models (SAS v. 8.2, SAS Institute Inc., 1997) to determine the best parameter values to use in my photosynthesis model. I compared the sum of squares, the mean square, and the F statistic of three models, (1) a 3-parameter constant model using a single estimate for each parameter, (2) a temperature-specific model using unique parameters for 7°, 14° and 21°C, and (3) a sample-specific model using individual parameters for each P*E* curve.

3.2.9 Photosynthesis modeling

I estimated total daily productivity for 1997 and 1998 for each algal assemblage in Cell Four of Oak Hammock Marsh using my calculated photosynthetic parameters, mean hourly incident PAR, and mean daily chlorophyll-*a*. I did not extend my calculations through the winter (ice-on) period, assuming zero productivity during this time in my estimations of total annual productivity. Within the model, I used the temperature-specific P^B_{max} value that corresponded most closely to the measured water temperature for each day of the season. The volume of each 10-cm isobath was calculated using a stage-area curve of Cell Four of Oak Hammock Marsh (Oak Hammock W. M. A. General Plan, Ducks Unlimited Canada). The volume within emergent vegetation, submersed vegetation, and open water was calculated using the stage-area curve and the vegetation map that I produced from aerial photographs. The area of metaphyton and plocon colonization was calculated from the vegetation map and percent cover estimates over time at each site.

Hourly PAR was calculated using the mean of the measured incident PAR values one-half hour before and after each hour (CST). Incident PAR values were corrected for light loss due to surface reflection. Mean seasonal surface reflectance (% loss = [surface PAR-PAR below-surface] / surface PAR x 100) was calculated from bi-weekly measurements of surface and just-below-surface PAR in 1997 and 1998. Light extinction through the water column was expressed as % attenuation per 10 cm of depth (Wetzel and Likens 1991). Light extinction at the mid-point of each isobath was calculated as the mean of the measured values at the top and bottom of each isobath.

Daily chlorophyll-*a* (μg L^{-1} or μg cm^{-2}) values were interpolated between bi-weekly measured values using linear regression. Chlorophyll-specific algal productivity (Ps^B) for phytoplankton, periphyton, and metaphyton was derived using the exponential equation:

$$Ps^B = P^B_{max} [1 - e^{(-aE/PBmax)}] \times e^{(-\beta E/PBmax)},$$

where P^B_{max}, a, and β were my calculated parameters, and E was hourly PAR corrected for surface reflectance and extinction with depth. Submersed and emergent epiphyton productivity was calculated using my periphyton parameters. Epipelon and plocon productivity was also derived from this equation, using P^B_{max}, a, and β values from Robinson *et al.* (1997).

Daily productivity (mg C m^{-2} d^{-1}) was estimated as the sum of all hourly productivity values for each isobath. All daily productivity estimates were expressed per m^2 of marsh bottom area to facilitate comparison among assemblages. Total annual algal production in Cell Four (kg C ha^{-1} y^{-1}) was calculated from the mean daily productivity of each algal assemblage and the estimated area of each assemblage in each isobath. Macrophyte productivity was estimated from measurements of peak plant biomass in mid-summer. Macrophyte biomass (g dw m^{-2}) was converted to carbon (g C m^{-2}) by assuming a 45% carbon content of macrophyte tissue (Davis and van der Valk

1978, Madsen and Sand-Jensen 1991). Total annual macrophyte production in Cell Four (kg C ha^{-1} y^{-1}) was calculated from the area of each vegetation type.

3.3 Statistical analyses

Statistical analyses were performed using SAS for Windows 95 software (v. 8.2, SAS Institute Inc., 1997). Data were log-transformed where necessary to stabilize the variance and to approximate a normal distribution of the errors prior to performing statistical tests. All statistical tests were evaluated at a=0.05 level of probability. Repeated measures two-factor analysis of variance (ANOVA) was used to evaluate significant temporal trends over the weeks of the experiments. The use of two-factor ANOVA allowed me to evaluate treatment effects for each factor, as well as interactions between these variables and time. I used PROC GLM (SAS Institute Inc., 1997) when a compound symmetric error structure could be assumed. PROC MIXED (SAS Institute Inc., 1997) was used to evaluate competing error structures. Akaike's Information Criterion (AIC) (Burnham and Anderson 1998) was used to select the appropriate error structure from among three co-variance models. I considered the compound symmetry model, which assumes equal association between the measures obtained on the same units repeatedly over time, the auto-regressive order 1 model, which assumes that correlations between repeated measures decay as the time lag between them increases, and the independence model, which assumes independence of measures taken on the same unit over time (Milliken and Johnson 1984). Non-linear regression analysis (Bates and Watts 1988) was used to fit photosynthesis and light data and to determine photosynthetic parameters for modeling algal productivity. Post-hoc tests of statistically significant main effects were performed using comparisons of least squares means, and temporally sliced treatment contrasts of the least square means to examine significant interaction terms (Winer 1971). Linear relationships were evaluated statistically using the

Pearson product-moment correlation coefficient and reported as the coefficient of determination (r^2) (Neter *et al.*, 1996). Forward step-wise multiple regression was used to examine correlations between environmental variables and algal productivity, and between environmental variables and photosynthetic parameters. This analysis computes a series of regression equations by successively adding variables that increase the correlation coefficient until a 'best set' of independent variables is obtained and added variables do not improve the predictive power significantly (Neter and Wasserman 1974). Selection of variables by this method does not imply cause and effect relationships; it merely identifies similar variation over the range of measured units.

4. Delta Marsh Study

4.1 Results

4.1.1 1995 experiment

4.1.1 (a) Nutrients

Nutrient levels were low (<0.1 mg L^{-1}) in all enclosures during the four-week period of pre-treatment (Figure 10). Post-addition, TRP concentrations in the xMacNP treatment diverged significantly ($F_{(2,3)}$=139.26, p=0.001) from the Control and xMac treatments, which did not differ from each other. Elevated levels of TRP were detectable in the xMacNP treatment from the time of first nutrient addition, increasing to ~1.4 mg L^{-1} by the end of the experiment. Post-addition concentrations of ammonium-N (NH_4-N) and nitrate+nitrite-N (NO_3-N) also differed significantly in the xMacNP treatment ($F_{(2,3)}$=21.23, p=0.017, $F_{(2,3)}$=233.55, p=0.001), whereas the Control and xMac treatments did not differ from each other. Increases in NH_4-N concentrations (to 0.5 mg L^{-1}) in the xMacNP treatment only occurred in the last three weeks of August (Figure 10), whereas NO_3-N concentrations were slightly elevated from the time of first nutrient addition. NO_3-N concentrations in the xMacNP treatment increased steadily to a peak of 3 mg L^{-1} in late August, before declining to <1 mg L^{-1} by the end of the experiment. The mass ratio of ambient post-addition inorganic N to P in the xMacNP treatment was much lower (2.2) than the input ratio (7.6) of inorganic nutrients, indicating greater N than P uptake or conversion in the water column.

The total phosphorus to dissolved inorganic phosphorus molar ratio (TP:DIP) in the water column was 2:1 in xMac and Control treatments throughout the experiment, and in the xMacNP treatment prior to nutrient addition (Table 6). Post-addition, TP:DIP was 1:1 in the xMacNP treatment. The total nitrogen (sum of TKN and NO_3-N) to

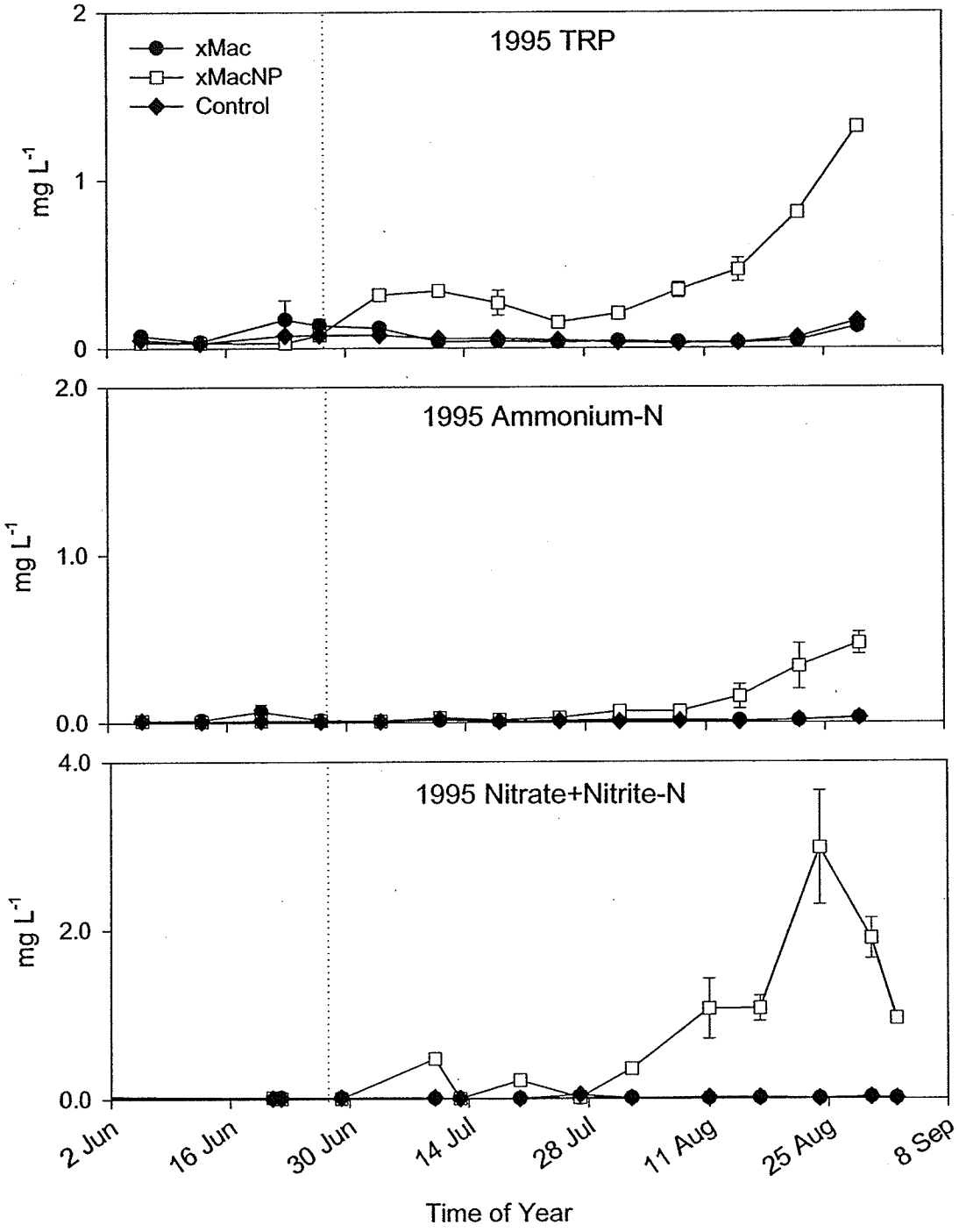

Figure 10. Total reactive phosphorus (TRP) (mg L^{-1}, ±SE, n=2), ammonium-N (mg L^{-1}, ±SE, n=2), and nitrate+nitrite-N (mg L^{-1}, ±SE, n=2) in experimental enclosures in 1995. Vertical dotted line denotes the start of nutrient addition on 28 June, 1995. (Note change in scale of y axis.)

Table 6. Molar ratios of total phosphorus to dissolved inorganic phosphorus (TP:DIP) and total nitrogen to dissolved inorganic nitrogen (TN:DIN) in treatment enclosures before and after nutrient addition in 1995.

1995 TP:DIP	xMac	xMacNP	Control
Pre-addition	2	2	2
Post addition	2	1	2
1995 TN:DIN	**xMac**	**xMacNP**	**Control**
Pre-addition	53	57	51
Post addition	58	10	55

dissolved inorganic nitrogen (sum of NO_3-N and NH_4-N) molar ratio (TN:DIN) was >50:1 in all treatments prior to nutrient addition, and in xMac and Control treatments for the remainder of the experiment (Table TP). Post-addition, TN:DIN was 10:1 in the xMacNP treatment. TN:TP ratios were variable over the course of the experiment, and were sometimes indicative of P limitation (TN:TP>15) (Figure 11). TN:TP ratios dropped dramatically (<15) in all treatments in mid-summer and again in early fall, indicating possible N limitation. TN:TP ratios did not differ significantly between treatments ($F_{(2,3)}$=1.10, p=0.438) but were noticeably lower in the xMacNP treatment from mid-summer to the end of the experiment.

Soluble reactive silicon (SRS) concentrations did not differ significantly between treatments over time ($F_{(2,3)}$=3.71, p=0.155) (Figure 11). Concentrations of SRS ranged from 2-3 mg L^{-1} in spring to ~0.5 mg L^{-1} at the end of summer. There was a mid-summer decline in SRS concentrations in all treatments, particularly in xMacNP and xMac treatments where levels were as low as 0.2 mg L^{-1} for a brief period.

4.1.1 (b) Other environmental variables

Water column alkalinity did not differ significantly between treatments $F_{(2,3)}$=2.91, p=0.198), probably because of large within-treatment variability. Alkalinity decreased steadily over the summer to ~150 mg L^{-1} in xMac and Control treatments, whereas the xMacNP treatment began to increase slightly in late summer to ~240 mg L^{-1} (Figure 12). The pH in all treatments was high, ranging from 8 to almost 10 in early summer (Figure 12). There was no significant difference between treatments ($F_{(2,3)}$=6.87, p=0.076), but pH was lower in the xMac treatment in the first half of the summer. Turbidity was highest in all treatments (2-3 NTU) in the pre-treatment period of the experiment, then decreased and remained low (~1 NTU) for the remainder of the summer (Figure 12). Turbidity did not differ significantly between treatments ($F_{(2,3)}$=4.24, p=0.178)

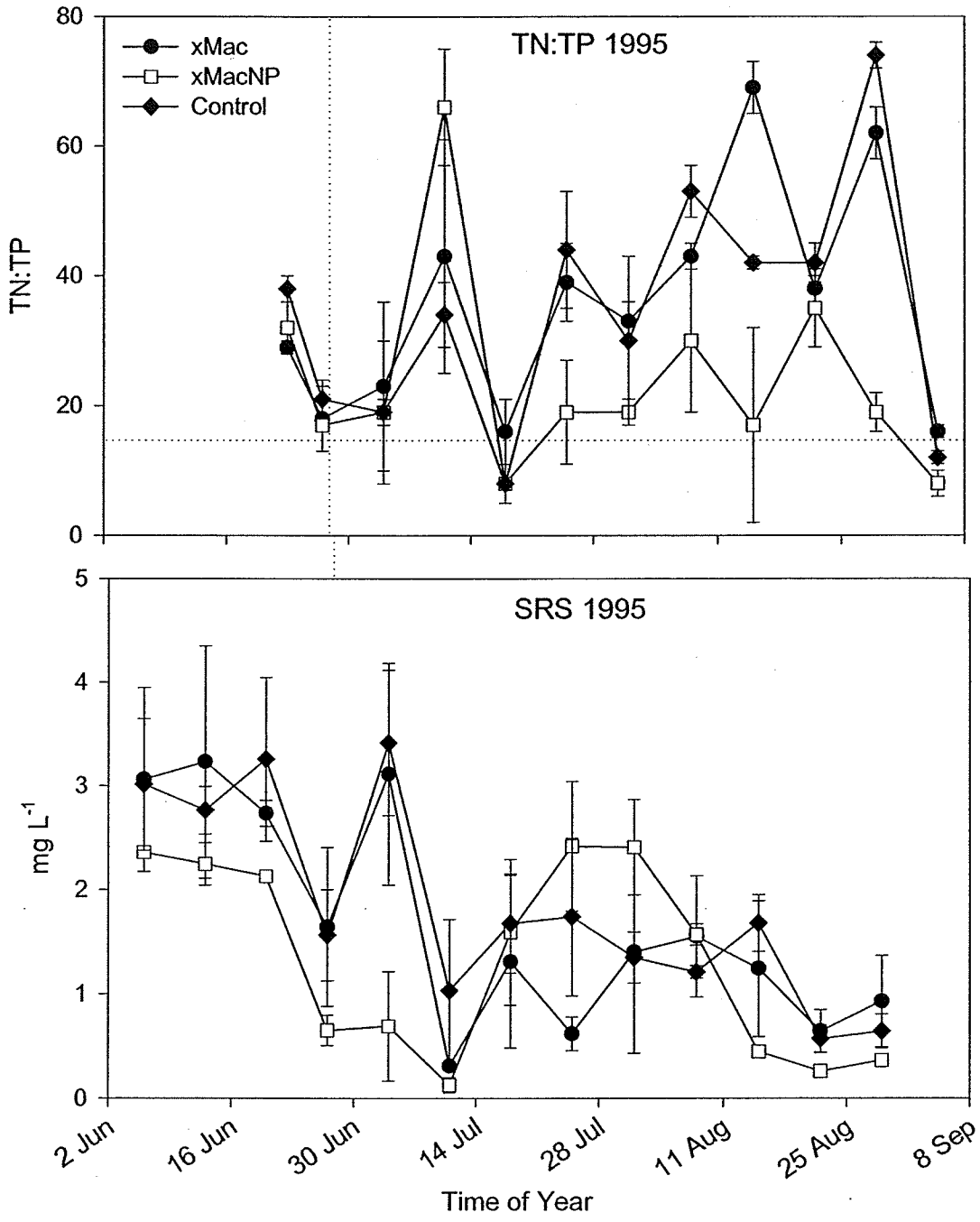

Figure 11. Soluble reactive silicon (mg L^{-1}, ±SE, n=2) and total nitrogen to total phosphorus ratios (TN:TP, ±SE, n=2) in experimental enclosures in 1995. Vertical dotted line denotes the start of nutrient addition on 28 June, 1995. Horizontal line denotes TN:TP<15. (Note change in scale of y axis.)

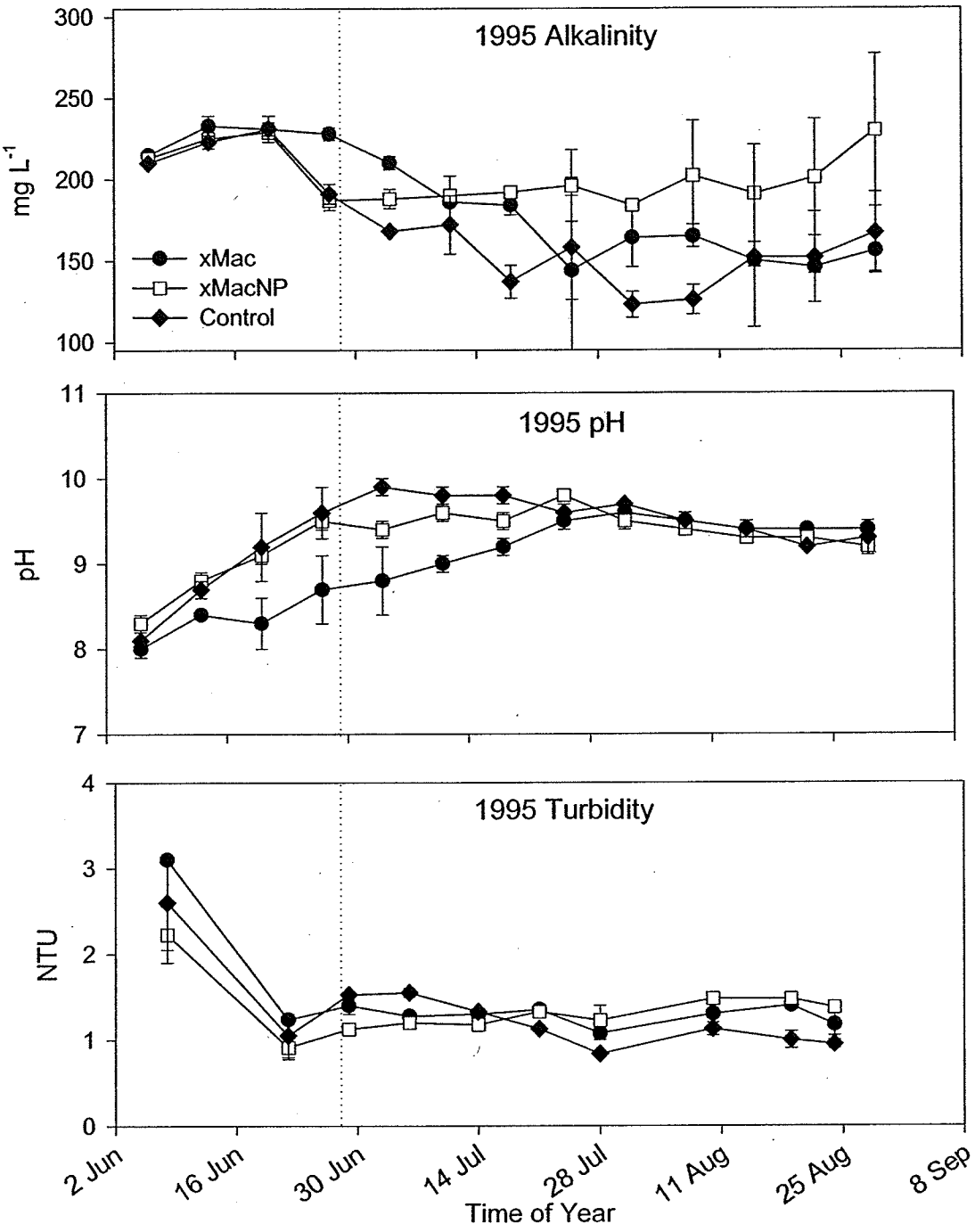

Figure 12. Alkalinity (mg L^{-1}, ±SE, n=2), pH (±SE, n=2), and turbidity (NTU, ±SE, n=2) in experimental enclosures in 1995. Vertical dotted line denotes the start of nutrient addition on 28 June, 1995. (Note changes in scale of y axes.)

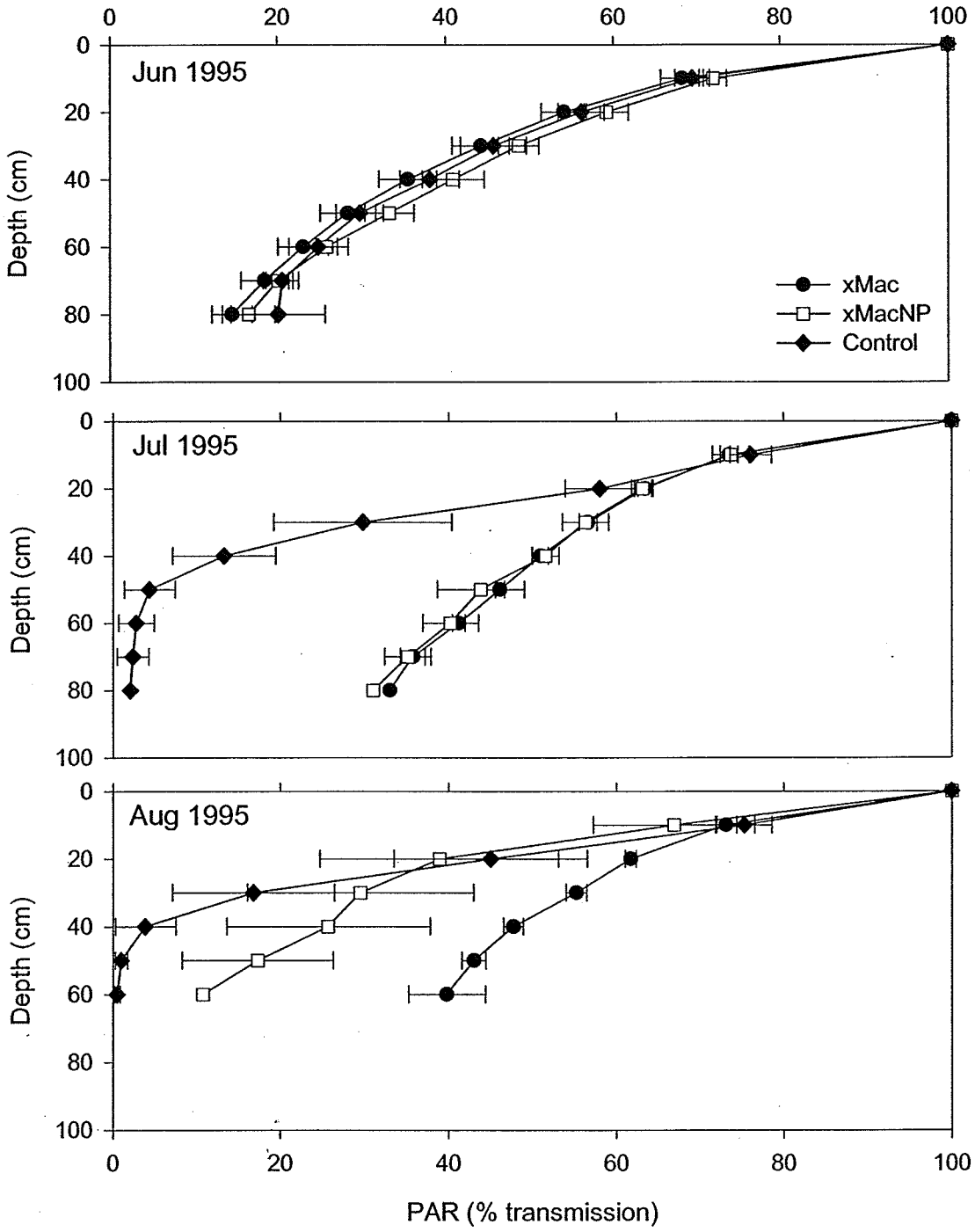

Figure 13. Light extinction profiles (PAR % transmission, ±SE, n=4) with depth in experimental enclosures in 1995.

During the pre-treatment period in June, light extinction with depth in the water column did not differ significantly between treatments ($F_{(2,26)}$=0.08, p=0.926) (Figure 13). At least 20% of surface PAR reached the sediment surface at 80-cm depth. In July, there was a significant difference in light extinction between treatments ($F_{(2,23)}$=3.24, p=0.016). Post-hoc tests revealed that light extinction was significantly greater in the Control than in either xMac or xMacNP, which did not differ from each other. About 2% of surface PAR reached the sediment surface in Controls, whereas more light (~30%) reached the sediments in xMac and xMacNP treatments (Figure 13). By August, light extinction was significantly different in each of the treatments ($F_{(2,18)}$=2.33, p=0.046). The proportion of surface PAR reaching the sediment surface at 60 cm depth was <1% in Control enclosures, ~10% in xMacNP enclosures, and ~40% in xMac enclosures.

Daily mean water column temperatures differed less than 1°C among enclosures and the surrounding marsh. Mean water temperatures were 18.6, 21.9, and 21.6°C, in June, July and August respectively. The water column in each enclosure was generally well oxygenated. Mean oxygen saturation, (calculated from oxygen concentration (mg L^{-1}) and temperature) in xMac, xMacNP, and Control enclosures ranged from morning lows of 25-45% to mid-afternoon highs of 110-130% and was generally higher than the surrounding marsh (daily range 13 to 121% saturation), although the difference was not significant (F=43.61, df= 5, p=0.098).

4.1.1 (c) Biotic variables

I was unable to detect a treatment response by algal assemblages in the experiment in 1995. Neither phytoplankton nor epipelon increased in response to removal of macrophytes or to combined macrophyte removal and nutrient addition. The appearance of metaphyton in the xMacNP treatment was transient and short-lived.

Phytoplankton chlorophyll-*a* was highest (10-15 mg m^{-2}) in all enclosures in the pre-treatment period in early spring, immediately following installation of the enclosures

in the marsh (Figure 14). Phytoplankton chlorophyll-*a* declined to low levels (1 mg m^{-2}) just prior to the start of nutrient addition and macrophyte removal, and remained low for the remainder of the experiment. Phytoplankton chlorophyll-*a* did not differ significantly between treatments ($F_{(2,3)}$=0.88, p=0.499). Mean concentrations of phytoplankton chlorophyll-*a* in original units of measurement were 80-100 µg L^{-1} in the pre-treatment period, and 20-40 µg L^{-1} post-addition (see Appendix A). Mean seasonal phytoplankton chlorophyll-*a* in the surrounding marsh was 25 µg L^{-1}.

A transient metaphyton mat (40-75% cover) developed in xMacNP enclosures in mid-August, whereas metaphyton was not detected in appreciable abundance (<5% cover) in xMac or Control treatments. Metaphyton chlorophyll-*a* was high (300-600 mg m^{-2}) during the time it was present in the xMacNP treatment (Figure 14).

Epipelon chlorophyll-*a* declined from a pre-treatment high of 4-6 mg m^{-2} to low levels of 1-2 mg m^{-2} through July and early August (Figure 15). Epipelon chlorophyll-*a* did not differ significantly between treatments ($F_{(2,3)}$=0.34, p=0.737).

Periphyton on the surfaces of acrylic substrata responded significantly ($F_{(2,3)}$=11.13, p=0.041) to treatment (Figure 15). Periphyton chlorophyll-*a* in xMac and xMacNP treatments was significantly higher than in Controls, and xMacNP periphyton chlorophyll-*a* was significantly higher than in the xMac treatment. Periphyton chlorophyll-*a* was low (<1 µg cm^{-2}) in all enclosures during the pre-treatment period and remained at this level in Control enclosures throughout the experiment. Periphyton chlorophyll-*a* in xMac and xMacNP treatments began to increase at the start of the treatment period. Periphyton chlorophyll-*a* in the xMacNP treatment decreased to <1 µg cm^{-2} by the end of July. The increase in periphyton chlorophyll-*a* in the xMac treatment was sustained until mid-August, during which time, chlorophyll-a levels on acrylic substrata were ~3 µg cm^{-2} (Figure 15).

Mean chlorophyll-normalized light-saturated photosynthesis (Ps^B) was highest for phytoplankton (4 µg C μg^{-1} Chl-*a* h^{-1}), followed by periphyton (3 µg C μg^{-1} Chl-*a* h^{-1}), and then epipelon (1µg C μg^{-1} Chl-*a* h^{-1}) (Table 7). The rate of Ps^B did not differ significantly between treatments for phytoplankton ($F_{(2,3)}$=1.43, p=0.163), periphyton ($F_{(2,3)}$=7.04, p=0.759), or epipelon ($F_{(2,3)}$=0.54, p=0.767). The photosynthetic productivity (Ps) of phytoplankton and epipelon was strongly correlated with algal chlorophyll-*a* (r^2=0.74, r^2=0.82, respectively) (Figure 16). There was less evidence of a strong relationship between photosynthetic productivity and chlorophyll-*a* for periphyton (r^2=0.48). There appeared to be an inverse relationship between periphyton Ps and Chl-*a* in the xMac treatment, in that Ps was higher when Chl-*a* was low, and decreased as Chl-*a* increased (Figure 16). This was probably a consequence of self-shading within the thicker biofilm of periphytic algae on the acrylic substrata in xMac enclosures.

Submersed macrophytes in the Control treatment reached peak biomass (125 g m^{-2}) in mid-July (Figure 17), concurrent with flowering. Macrophyte senescence began to occur toward the end of August. The increase in epiphyton chlorophyll-*a* in Control enclosures was closely linked to the increase in mass, and therefore, colonizable surface area of developing macrophytes. Epiphyton chlorophyll-*a* reached a maximum of 45 mg m^{-2} in Control enclosures in mid-summer (Figure 17). The complete removal of submersed macrophytes from xMac and xMacNP enclosures was never accomplished. Even with extensive efforts to clip and remove macrophytes every second day, regrowth of macrophytes continued to occur. The removal method was able to prevent the caulescent macrophytes from extending up through the water column to the water surface, but the macrophytes remained in a short, extensively-branched condition in the bottom of all treatment enclosures. The clipping method also prevented flowering, effectively maintaining the macrophytes in a metabolically active juvenile state.

The abundance of zooplankton increased rapidly in the water column of all enclosures during the pre-treatment period (to 500-700 cladocerans L^{-1} and to 250-300 copepods L^{-1}) (Sandilands and Hann 1995). Zooplankton populations subsequently decreased to low abundance by the second week post-addition (to 150 cladocerans L^{-1} and 50 copepods L^{-1}), and remained low in all treatments for the remainder of the experiment (Sandilands and Hann 1995).

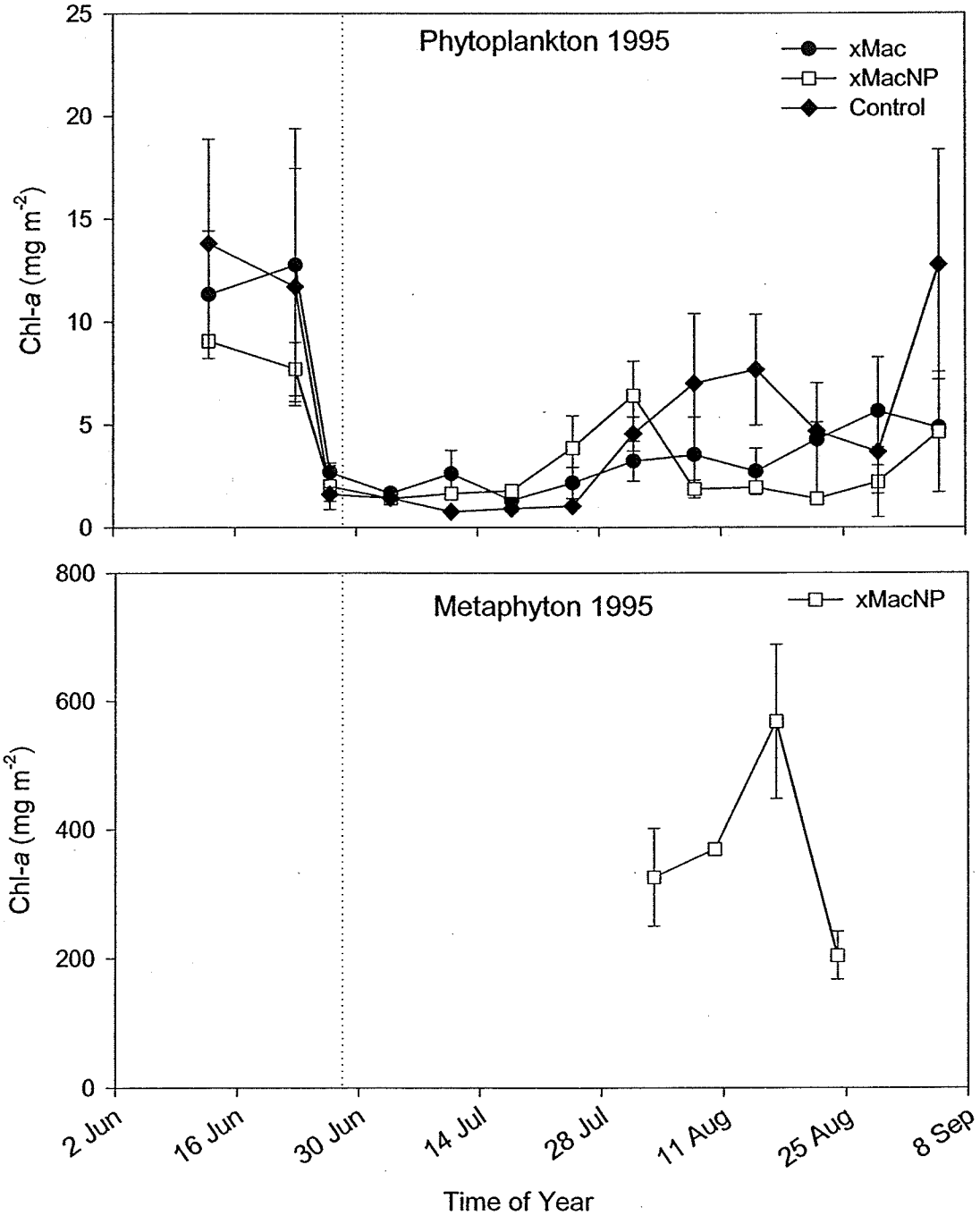

Figure 14. Phytoplankton chlorophyll-*a* (mg m^{-2}, ±SE, n=2) and metaphyton chlorophyll-*a* (mg m^{-2}, ±SE, n=2) in experimental enclosures in 1995. Vertical dotted line denotes the start of nutrient addition on 28 June, 1995. (Note change in scale of y axis.)

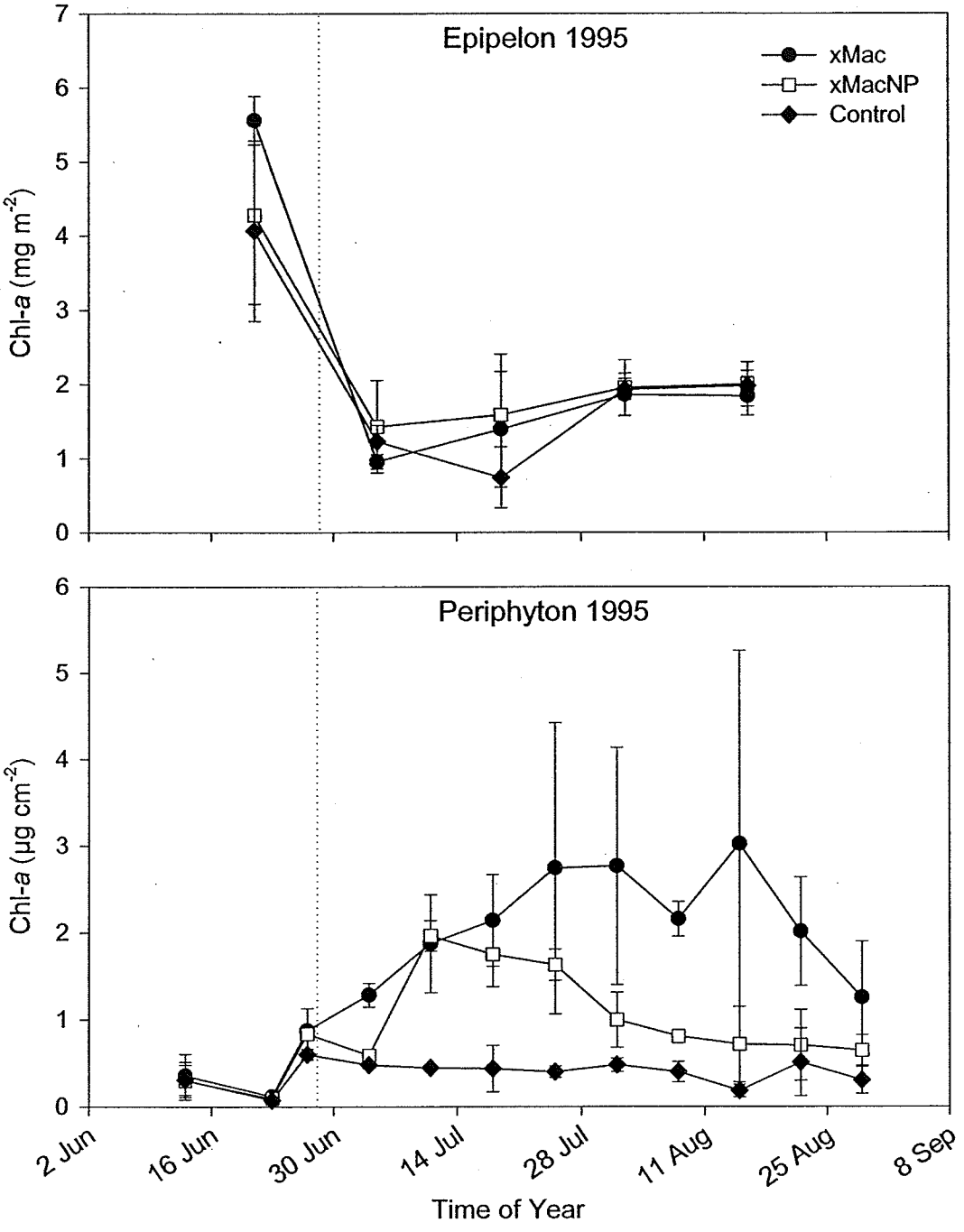

Figure 15. Epipelon chlorophyll-*a* (mg m^{-2}, ±SE, n=2) and periphyton chlorophyll-*a* (µg cm^{-2}, ±SE, n=2) in experimental enclosures in 1995. Vertical dotted line denotes the start of nutrient addition on 28 June, 1995. (Note change in scale and units on y axis.)

Table 7. Mean rates of chlorophyll-normalized light-saturated photosynthesis (Ps^B) (µg C $µg^{-1}$ Chl-*a* h^{-1}) for phytoplankton, periphyton and epipelon in experimental enclosures in 1995.

Assemblage	xMac	xMacNP	Control
Phytoplankton	4.1	3.6	4.2
Periphyton	3.3	3.0	3.1
Epipelon	1.0	1.0	0.9

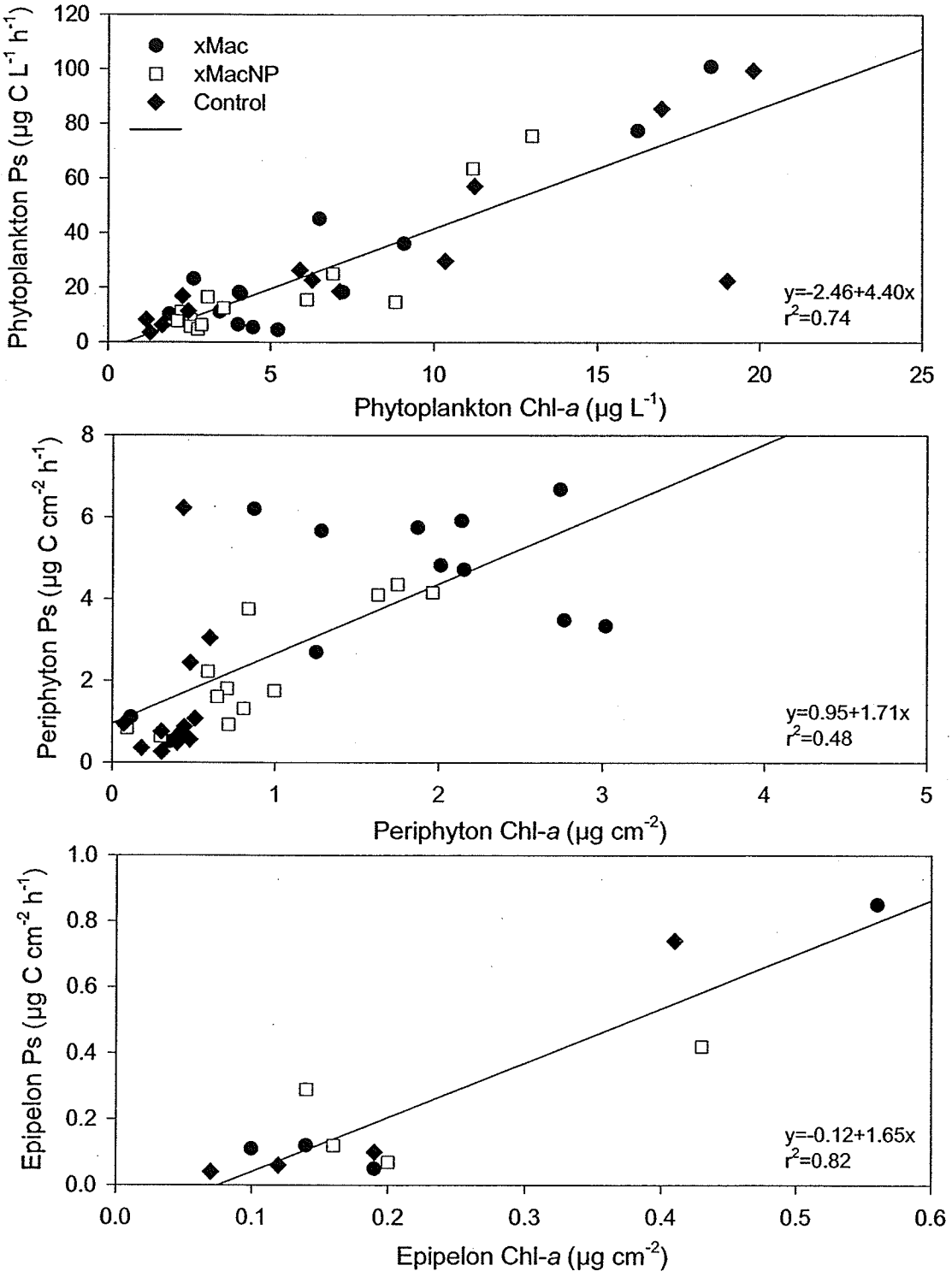

Figure 16. Variation in photosynthetic productivity (Ps) correlated with variation in chlorophyll-*a* for algal assemblages in experimental enclosures in 1995.

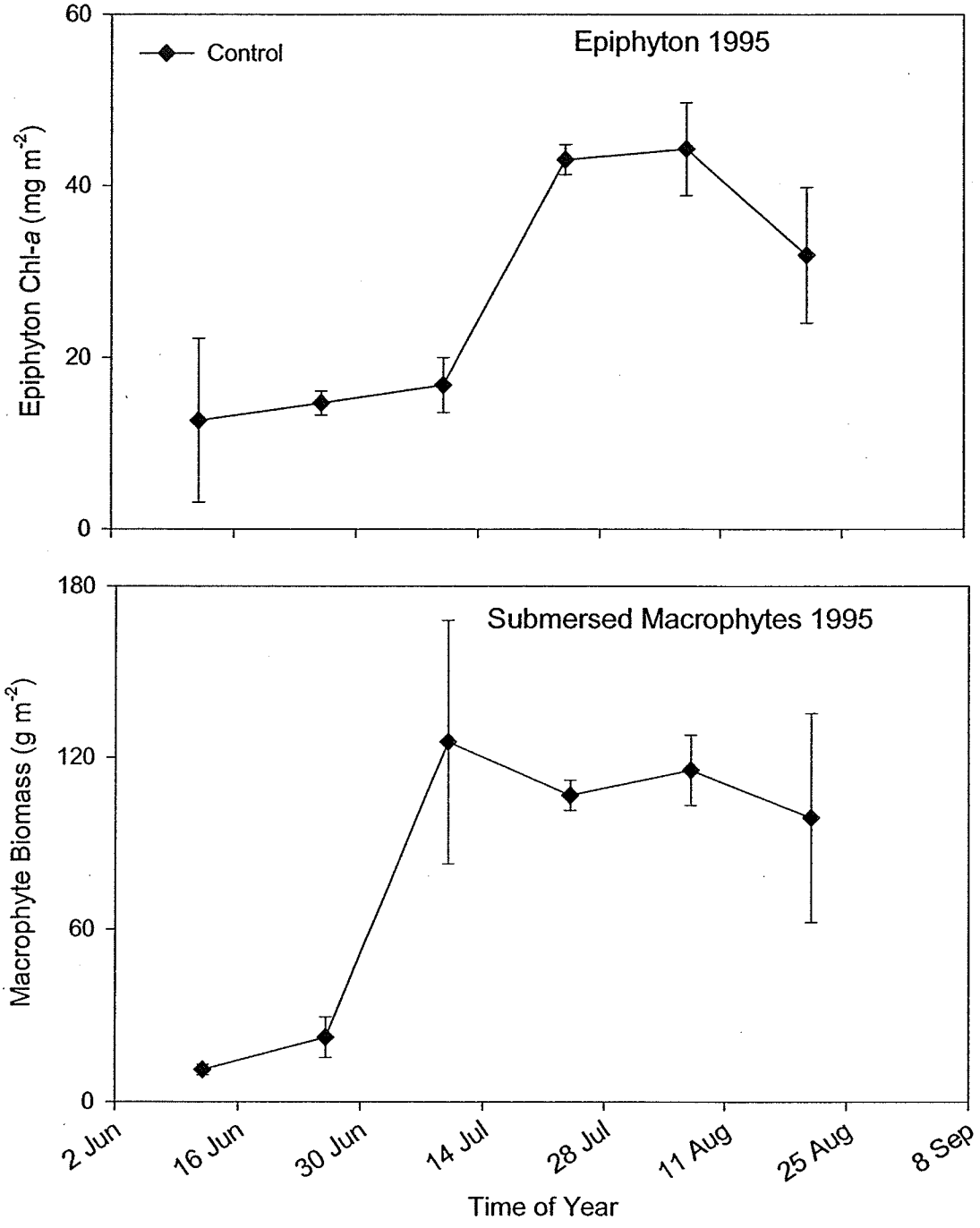

Figure 17. Epiphyton chlorophyll-*a* (mg m^{-2}, ±SE, n=2) and submersed macrophyte biomass (g m^{-2}, ±SE, n=2) in experimental enclosures in 1995. (Note change in scale of y axis.)

4.1.2 1996 experiment

4.1.2 (a) Nutrients

Pretreatment water column nutrient concentrations were low (<0.2 mg L^{-1}) and did not differ between treatments prior to 3 July (Figure 18). Mean concentrations of N and P remained low and did not differ in Control and Ex treatments throughout the remainder of the experiment. In NP and ExNP treatments, concentrations of TRP and NO_3-N increased post-addition and were significantly higher ($F_{(3,5)}$=9.06, p=0.029; $F_{(3,5)}$=52.24, p=0.000) than in Ex and Control treatments. Concentrations of TRP increased more in the NP treatment (mean 0.8 mg L^{-1}) than in ExNP (mean 0.5 mg L^{-1}), particularly through August. Post-addition NO_3-N concentrations were similar in NP and ExNP treatments (~1 mg L^{-1}) (Figure 18). Concentrations of NH_4-N remained low in NP and ExNP treatments post-addition, until mid- August when NH_4-N levels peaked at 0.64 mg L^{-1} in the NP treatment (Figure 18). Post-addition, the mass ratio of ambient inorganic N to P was much lower (1.7 for NP and 2.3 for ExNP) than the input ratio (7.6) of inorganic nutrients.

The TP:DIP molar ratio in the water column was 2:1 in Ex and Control treatments throughout the experiment, and in ExNP and NP treatments prior to nutrient addition (Table 8). The ratio of TP:DIP was 1:1 in both ExNP and NP treatments post-addition. The TN:DIN molar ratio was ~50:1 in all treatments prior to nutrient addition, and in Ex and Control treatments for the remainder of the experiment (Table 8). Post-addition, TN:DIN was 4:1 in both ExNP and NP treatments. Molar ratios of total nitrogen to total phosphorus (TN:TP) did not differ significantly between treatments ($F_{(3,5)}$=2.05, p=0.212), but were lower in NP and ExNP treatments (~ 12 to 15) than in Ex and Control treatments (~ 15 to 25) throughout the post-addition period (Figure 19). An abrupt switch from high molar TN:TP (45 to 50) to low TN:TP (14 to 20) occurred in all treatments in mid-July.

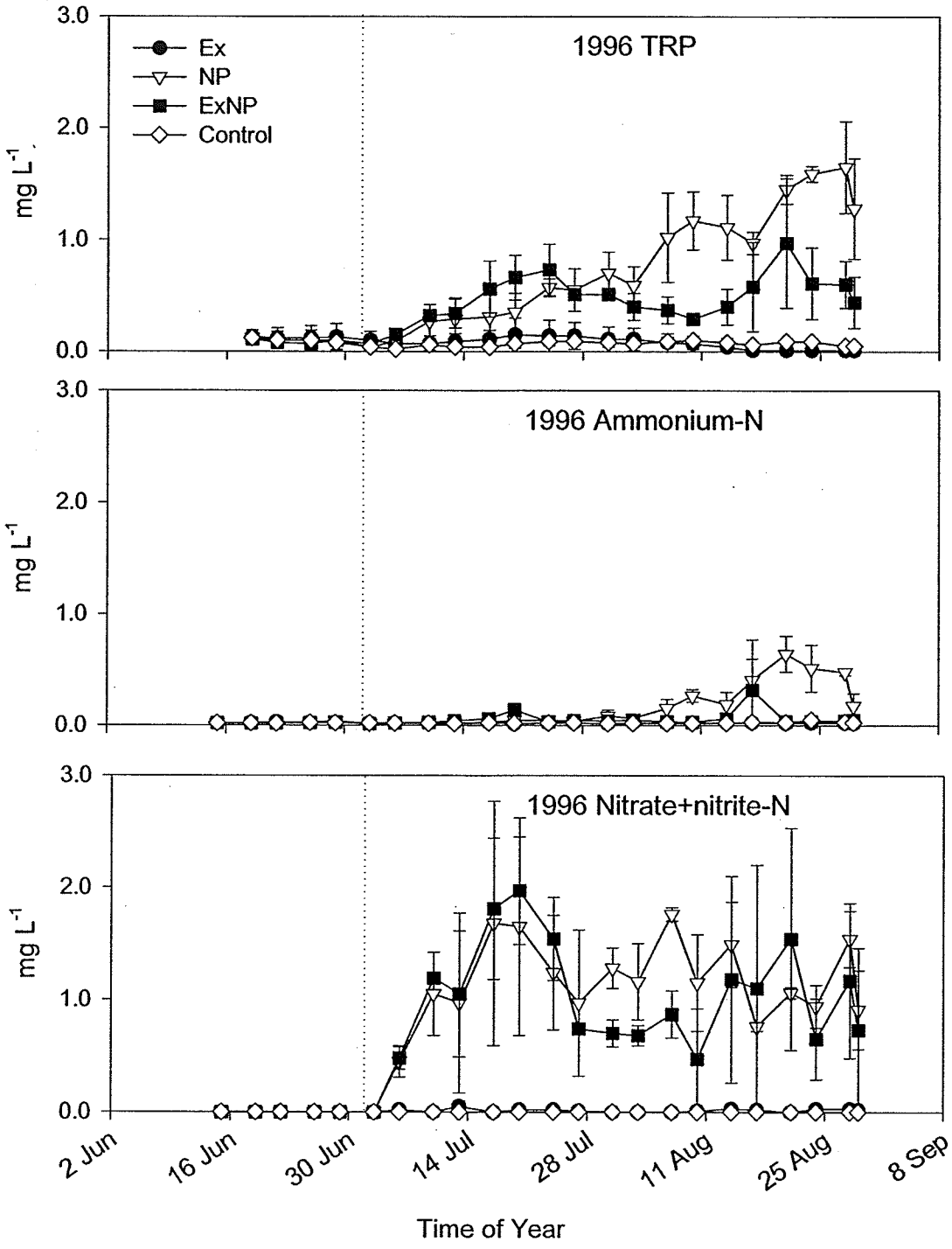

Figure 18. Total reactive phosphorus (TRP) (mg L^{-1}, ±SE, n=2), ammonium-N (mg L^{-1}, ±SE, n=2), and nitrate+nitrite-N (mg L^{-1}, ±SE, n=2) in experimental enclosures in 1996. Vertical dotted line denotes the start of nutrient addition on 3 July, 1996.

Table 8. Molar ratios of total phosphorus to dissolved inorganic phosphorus (TP:DIP) and total nitrogen to dissolved inorganic nitrogen (TN:DIN) in treatment enclosures before and after nutrient addition in 1996.

1996 TP:DIP	Ex	NP	ExNP	Control
Pre-addition	2	2	2	2
Post addition	2	1	1	2
1996 TN:DIN	**Ex**	**NP**	**ExNP**	**Control**
Pre-addition	47	55	49	50
Post addition	44	4	4	53

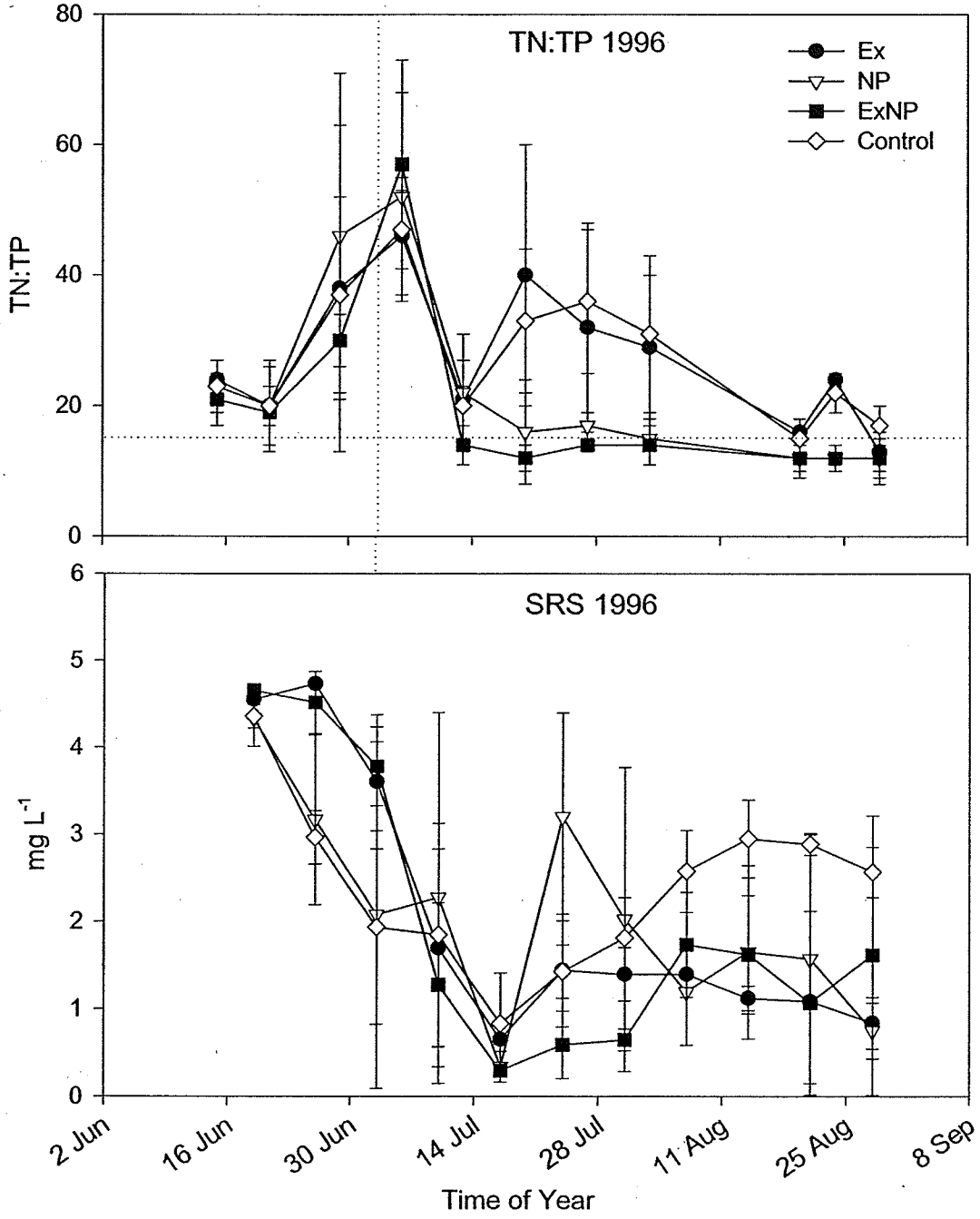

Figure 19. Soluble reactive silicon (mg L^{-1}, ±SE, n=2) and total nitrogen to total phosphorus ratios (TN:TP, ±SE, n=2) in experimental enclosures in 1996. Vertical dotted line denotes the start of nutrient addition on 3 July, 1996. Horizontal line denotes TN:TP<15. (Note change in scale of y axis.)

Concentrations of soluble reactive silica (SRS) in the water column did not differ significantly between treatments ($F_{(3,5)}$=1.97, p=0.219) (Figure 19). Concentrations of SRS were highest in early June (4.5 mg L^{-1}) declining to a low of 0.2-0.6 mg L^{-1} in mid-July in all treatments, then increasing to ~2 mg L^{-1} by late July and remaining at this level for the remainder of the experiment.

4.1.2 (b) Other environmental variables

Water column pH differed significantly between treatments ($F_{(3,5)}$=22.82, p=0.005) with NP and Control treatments diverging from Ex and ExNP treatments early in the pretreatment period (Figure 20). Post-addition, pH in ExNP treatment increased and was similar to pH in NP and Control (~9.3), whereas pH in Ex treatment (~8.4) remained significantly lower throughout the experiment. Water column alkalinity showed a similar, but opposite, pattern of divergence in the pretreatment period, with NP and Control (243 mg L^{-1}) diverging from Ex and ExNP treatments (257 mg L^{-1}) (Figure 20). Mean alkalinity continued to decrease in Control (180 mg L^{-1}) during the post-addition period and was significantly different ($F_{(3,5)}$=14.45, p=0.012) than mean alkalinity in the other three treatments (242 mg L^{-1}). Turbidity was similar in all treatments (2-3 NTU) prior to nutrient addition (Figure 20). Post-addition, turbidity did not differ significantly between treatments over time ($F_{(3,5)}$=5.47, p=0.066), likely related to large within treatment variability. Ex and Control decreased in turbidity (1-2 NTU), whereas NP (7 NTU) and ExNP (3 NTU) became more turbid.

Light extinction did not differ significantly between treatments during the pre-treatment period ($F_{(3,5)}$=6.83, p=0.168) when about 10-20% of surface PAR reached the sediment surface. Corresponding with higher post-addition turbidity in NP, light extinction in NP enclosures was higher in July than in the other three treatments (Figure 21), but did not differ significantly ($F_{(3,5)}$=1.34, p=0.299). The significant difference in light extinction in August ($F_{(3,5)}$=3.76, p=0.248) was attributable to the Ex treatment, as

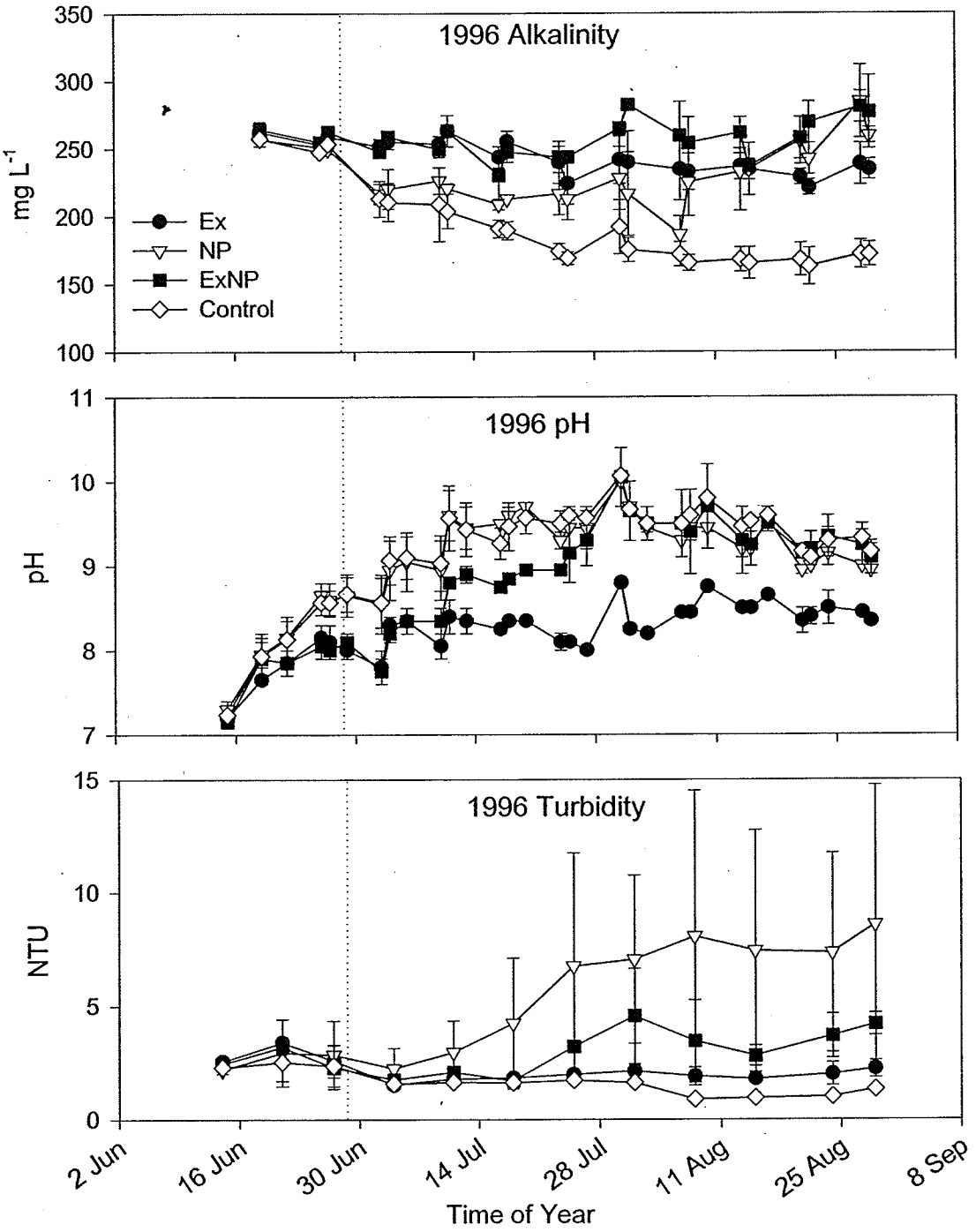

Figure 20. Alkalinity (mg L^{-1}, ±SE, n=2), pH (±SE, n=2), and turbidity (NTU, ±SE, n=2) in experimental enclosures in 1996. Vertical dotted line denotes the start of nutrient addition on 3 July, 1996. (Note changes in scale of y axes.)

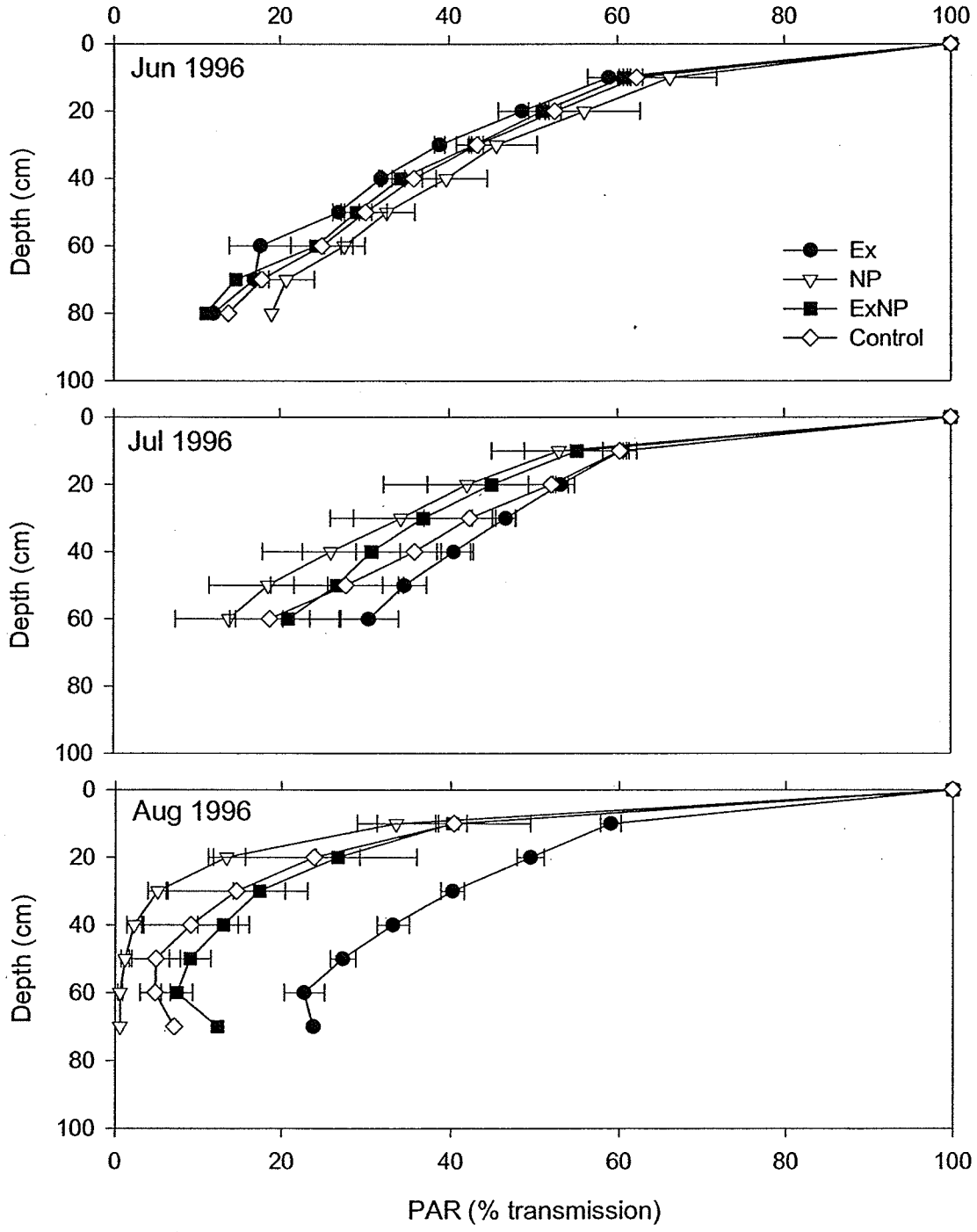

Figure 21. Light extinction profiles (PAR % transmission, ±SE, n=4) with depth in experimental enclosures in 1996.

identified by post-hoc tests, whereas the ExNP, NP and Control treatments did not differ significantly from one another. About 27% of surface PAR reached the sediments at 70-cm depth in Ex enclosures, and 9%, 5%, and 1% of surface PAR reached the sediments in ExNP, Control and NP enclosures, respectively.

Daily mean water column temperatures differed less than 1°C among enclosures and the surrounding marsh again in 1996. Mean June, July and August water temperatures were 19.0, 21.6, and 20.6°C, respectively. The water column in each enclosure was generally well oxygenated, although temporary evening anoxia (0.4 to 4.4% saturation) developed near the sediment surface in NP enclosures in mid-August. Mean oxygen saturation in Ex, NP, and Control enclosures ranged from morning lows of 50% to mid-afternoon highs of 110% and was significantly higher ($F_{(3,5)}$=8.34, p=0.000) than the surrounding marsh (daily range 10 to 87% saturation). Mean oxygen saturation in ExNP was significantly higher ($F_{(3,5)}$=5.18, p=0.001) than in the other three treatments, with a daily range from 62 to 168% saturation.

4.1.2 (c) Biotic variables

There was observable variability among replicates of the same treatment in 1996. This variability resulted from the natural heterogeneity that occured in the marsh over areas as large as that encompassed by the enclosure complex (400 m^2). Initial conditions such as macrophyte abundance, presence of algal innoculum, or numbers of fish or invertebrates may have varied slightly from enclosure to enclosure, contributing to the resulting variability over time. However, over and above this within-treatment variability, I observed some strongly significant main effects of treatment.

Mean phytoplankton chlorophyll-*a* differed significantly between treatments ($F_{(3,5)}$=41.26, p=0.001). Phytoplankton chlorophyll-*a* was similar in Control and Ex (~17 mg m^{-2}) throughout the experiment and differed from NP and ExNP treatments post-addition (Figure 22). Phytoplankton chlorophyll-*a* increased in NP and ExNP from a

mean of 14 mg m^{-2} pre-treatment to 125 mg m^{-2} by late July, and finally to a maximum of 136 mg m^{-2} (NP) and 190 mg m^{-2} (ExNP) in late August. Mean concentrations of phytoplankton chlorophyll-*a* in original units of measurement were 20 µg L^{-1} in Control and Ex treatments throughout the experiment, and 120 µg L^{-1} in NP and ExNP post-addition (see Appendix A). Mean seasonal phytoplankton chlorophyll-*a* in the surrounding marsh was 28 µg L^{-1}.

Metaphyton was absent in NP and Control treatments and infrequently present (< 5 mg m^{-2}) in Ex and ExNP treatments (Figure 22).

Periphyton chlorophyll-a per unit of surface area (cm^2) did not differ significantly on acrylic substrata and enclosure curtain walls ($F_{(1,19)}$=18.26, p=0.623). Therefore, I used the area of the curtain walls below the water surface to calculate periphyton chlorophyll-*a* on an areal basis for each enclosure. Periphyton chlorophyll-a increased over time in all treatments and was significantly different in ExNP relative to the other three treatments ($F_{(3,5)}$=8.39, p=0.033) (Figure 22). In Control, NP and Ex treatments, mean periphyton chlorophyll-*a* increased steadily, ranging from 10 mg m^{-2} at the beginning of July to a maximum of 100 mg m^{-2} in late August. In ExNP, periphyton chlorophyll-*a* increased from 10 mg m^{-2} to a maximum of 170 mg m^{-2} in late July and August. Mean periphyton chlorophyll-*a* from acrylic substrata, in original units of measurement, was 2.1, 2.6, 4.3, and 1.4 µg cm^{-2} in Ex, NP, ExNP, and Control treatments, respectively (see Appendix A).

Mean chlorophyll-normalized light-saturated photosynthesis (Ps^B) was higher for phytoplankton (5 µg C μg^{-1} Chl-*a* h^{-1}) than for periphyton (2 µg C μg^{-1} Chl-*a* h^{-1}) (Table 9). The rate of Ps^B for phytoplankton was significantly higher in NP and ExNP treatments than in Ex and Control treatments ($F_{(3,5)}$=6.61, p=0.012). There was no significant difference between treatments in the rate of Ps^B for periphyton ($F_{(3,5)}$=1.34, p=0.362).

The photosynthetic productivity (Ps) of phytoplankton was strongly correlated with algal chlorophyll-*a* (Chl-*a*) (r^2=0.91) (Figure 23). There was little relationship between photosynthetic productivity and chlorophyll-*a* for periphyton (r^2=0.17). In particular, increases in periphyton chlorophyll-*a* in the ExNP treatment did not result in increased periphyton Ps.

Mean epiphyton chlorophyll-*a* increased significantly in NP treatment relative to Control treatment ($F_{(1,3)}$=6.58, p=0.042) (Figure 24). Epiphyton chlorophyll-*a* was 10 mg m^{-2} in the pre-treatment period, and remained at that level in Controls for the post-addition period. Epiphyton chlorophyll-*a* in the NP treatment increased steadily to ~40 mg m^{-2} by the end of the summer, a response that was not tied solely to increases in the colonization surface area of macrophytes (see below).

There was no significant difference in submersed macrophyte biomass between Control and NP treatments throughout the experiment ($F_{(1,3)}$=0.27, p=0.640) (Figure 24). Macrophyte surface area was 1.1 m^2 m^{-2} in Control and 0.5 m^2 m^{-2} in NP treatments. The two major species were *Stuckenia pectinatus* and *Ceratophyllum demersum*, with *C. demersum* comprising 71% of total biomass but only 21% of surface area in Control, and 87% of total biomass but only 38% of surface area in NP treatments. In both treatments, peak macrophyte biomass occurred in mid-July, concurrent with flowering. Macrophyte senescence in NP was evident by 24 July, at least two weeks earlier than the onset of senescence in Control.

Algal chlorophyll-*a* was converted to equivalent dry weight (Goldsborough 2001) to facilitate a direct comparison of algal and macrophyte production in Control and NP treatments (Table 10). In the Control treatment, mean macrophyte biomass (50 g m^{-2}) exceeded algal biomass (26 g m^{-2}) whereas in the NP treatment, mean algal biomass (66 g m^{-2}) exceeded macrophyte biomass (50 g m^{-2}). Together, benthic and planktonic algae represented 34-57% of total primary producer biomass in the water column.

Based on weekly minnow trap catches, estimated mean density of fish was 1 m^{-2} and did not differ significantly ($F_{(3,5)}$=1.74, p=0.130) between treatments. Additional young-of-the-year fathead minnows were observed in all enclosures but they were too small to be retained in the minnow traps.

The abundance of zooplankton increased in the water column of all enclosures during the pre-treatment period (to 150 cladocerans L^{-1} and 800 copepods L^{-1}) (Sandilands *et al.* 2000). Zooplankton populations subsequently decreased to low abundance by the second week post-addition (to <10 cladocerans L^{-1} and ~100 copepods L^{-1}) and remained low in all treatments for the remainder of the experiment (Sandilands *et al.* 2000).

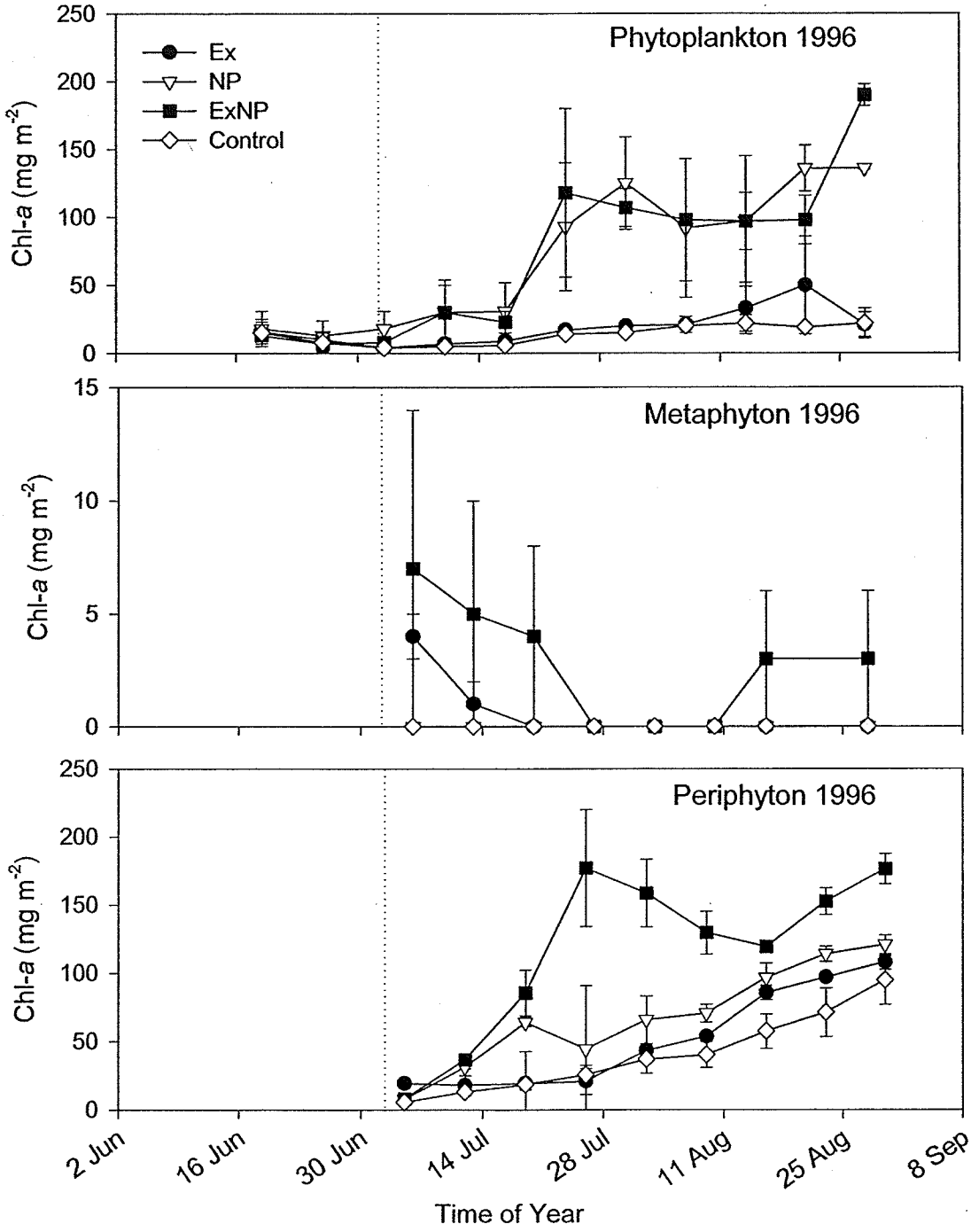

Figure 22. Phytoplankton chlorophyll-*a* (mg m^{-2}, ±SE, n=2), metaphyton chlorophyll-*a* (mg m^{-2}, ±SE, n=2), and periphyton chlorophyll-*a* (mg m^{-2}, ±SE, n=2) (on curtain walls) in experimental enclosures in 1996. Vertical dotted line denotes the start of nutrient addition on 3 July, 1996. (Note changes in scale of y axes.)

Table 9. Mean rates of chlorophyll-normalized light-saturated photosynthesis (Ps^B) (µg C μg^{-1} Chl-*a* h^{-1}) for phytoplankton and periphyton in experimental enclosures in 1996.

Assemblage	Ex	NP	ExNP	Control
Phytoplankton	4.2	6.3	5.3	3.6
Periphyton	2.5	1.6	1.5	2.2

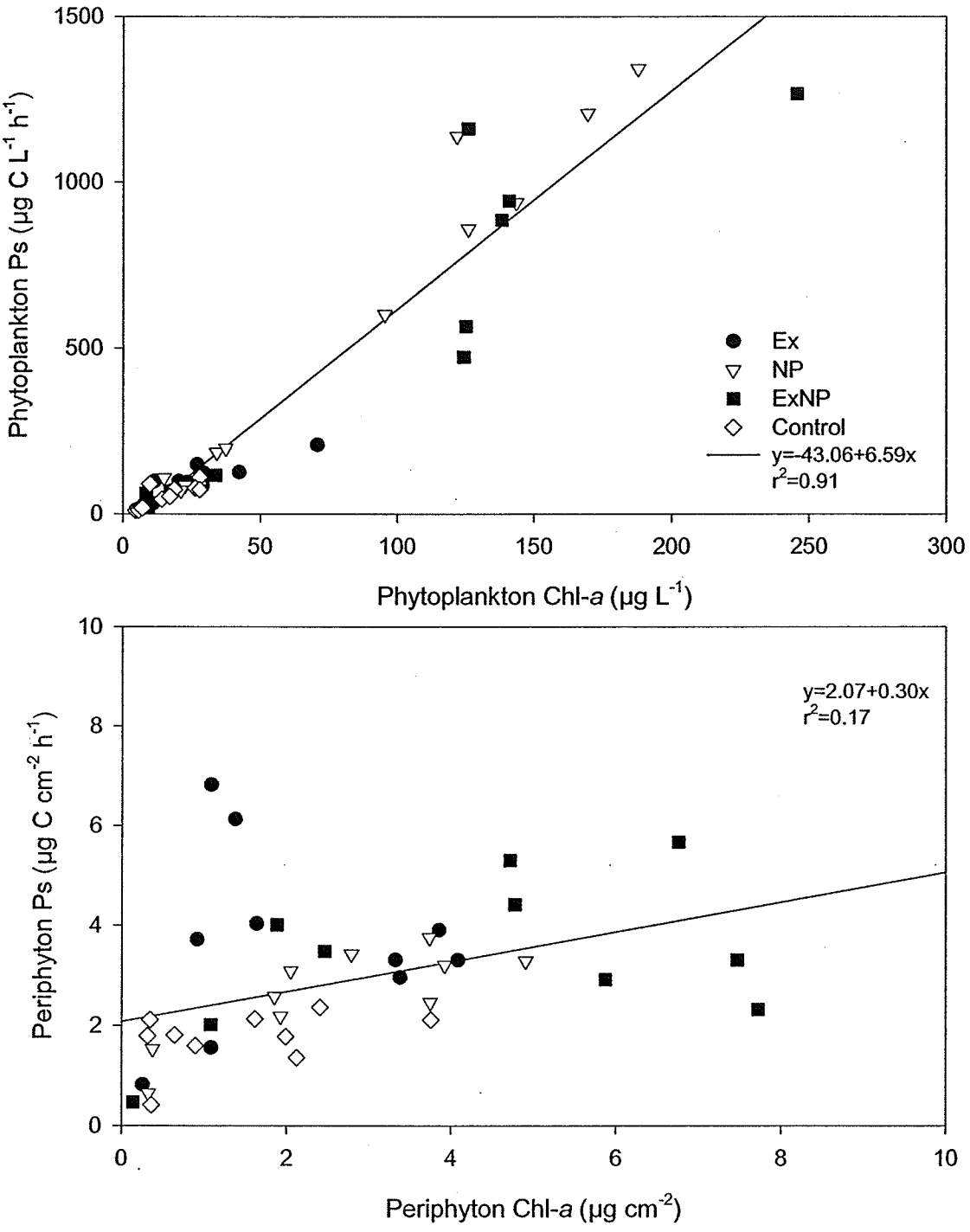

Figure 23. Variation in photosynthetic productivity (Ps) correlated with variation in chlorophyll-*a* for algal assemblages in experimental enclosures in 1996.

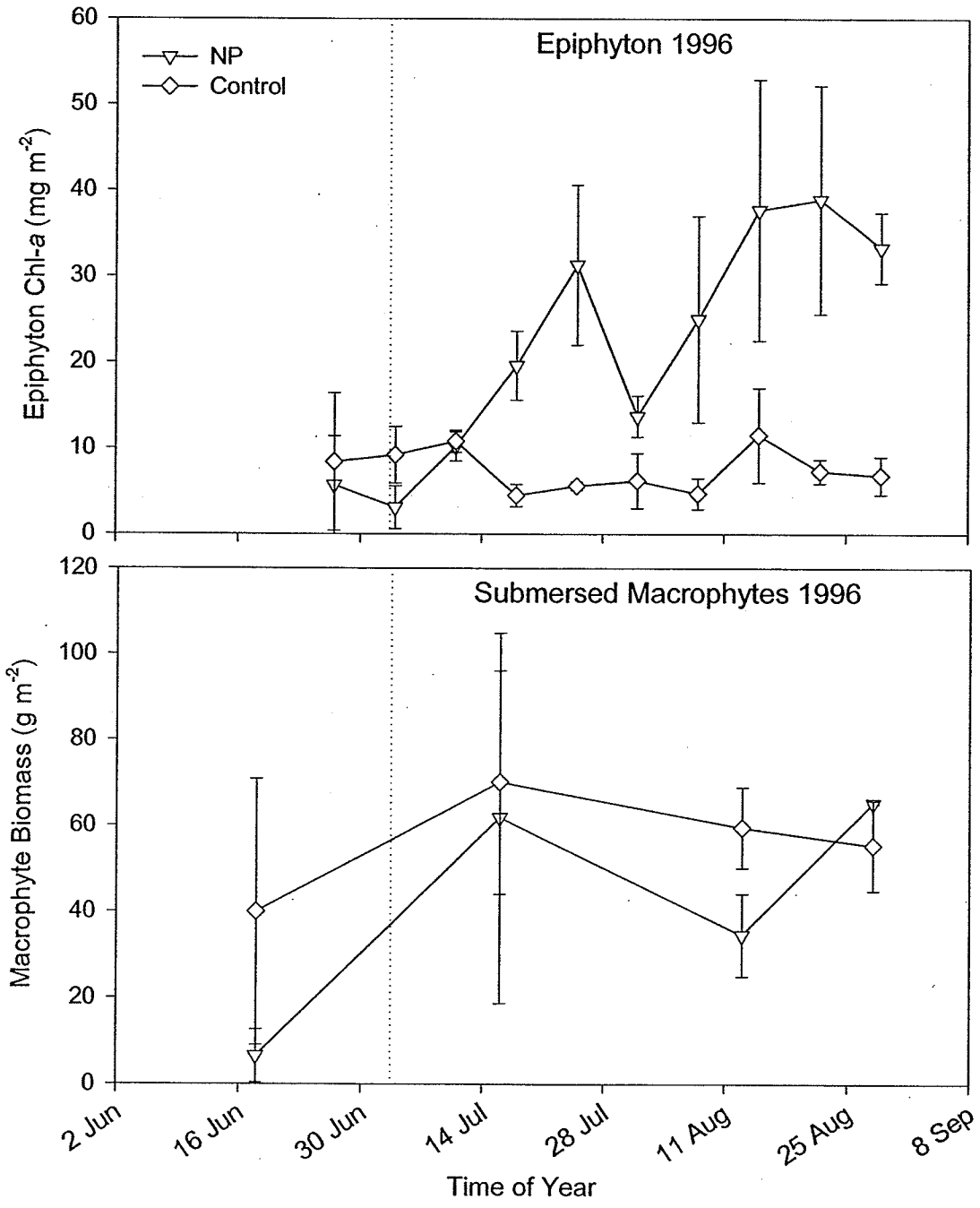

Figure 24. Epiphyton chlorophyll-*a* (mg m^{-2}, ±SE, n=2) and submersed macrophyte biomass (g m^{-2}, ±SE, n=2) in experimental enclosures in 1996. Vertical dotted line denotes the start of nutrient addition on 3 July, 1996. (Note change in scale of y axis.)

Table 10. Mean algal biomass (g dw m^{-2}) and mean macrophyte biomass (g dw m^{-2}) in Control and NP treatments in 1996. Algal chlorophyll-a was converted to equivalent dry weight using a conversion factor (g chl-a / 0.25% = g dw) from Goldsborough (2001).

Primary Producer	Control (g m^{-2})	NP (g m^{-2})
Phytoplankton	6	29
Benthic Algae	20	37
Submersed Macrophytes	50	50
Total	76	116

4.1.3 Phosphorus budget

There was a significant positive correlation between TP in the water column and phytoplankton chlorophyll-*a* (r^2=0.81, p<0.001) (Figure 25). TP in the water column and periphyton chlorophyll-*a* were also positively correlated (r^2=0.53, p<0.001) (Figure). There was no significant correlation between TP and metaphyton chlorophyll-*a* (r^2=0.00, p>0.05) or between TP and macrophyte biomass (r^2=0.03, p>0.05).

Algal total phosphorus was strongly correlated with algal chlorophyll-*a* (r^2=0.87, p<0.001 for phytoplankton; r^2=0.68, p<0.001 for periphyton) (Figure 26). There was no significant correlation between metaphyton total phosphorus and metaphyton chlorophyll-*a* (r^2=0.53, p>0.05). Phytoplankton total phosphorus, normalized per unit of chlorophyll-*a*, averaged 0.3 µg P μg^{-1} Chl-*a* in all treatments, and there was no significant difference between treatments ($F_{(3,5)}$=0.02, p=0.930). Chlorophyll-normalized periphyton total phosphorus averaged 0.2 µg P μg^{-1} Chl-*a* in all treatments, and there was no significant difference between treatments ($F_{(3,5)}$=1.39, p=0.338). There was no significant treatment effect on the total phosphorus content of macrophytes ($F_{(1,3)}$=3.38, p=0.163), invertebrates ($F_{(3,5)}$=0.52, p=0.248), or fish ($F_{(3,5)}$=0.39, p=0.259). The phosphorus content of the sediment was significantly higher ($F_{(1,3)}$=17.85, p=0.000) in NP (398 µg g^{-1} dw) than Control (149 µg g^{-1} dw) treatments.

Macrophytes, periphyton and phytoplankton were the largest biotic pools of P in the enclosures, whereas the pools of P in metaphyton, invertebrates, and fish were small (Table 11). The sum of all biotic pools represented only 1-4% of the total P measured in the system. The largest P pools were the two abiotic components, with sediments constituting 71-79% of total P, and the water column containing 18 to 26% of total P. When just the biotic pool of phosphorus is considered, the proportion of P in biotic components varied with treatment. In the Ex treatment, the largest biotic P pool was in periphyton (50%), followed by phytoplankton (30%) and then invertebrates (10%) and

fish (10%). In ExNP, the largest biotic P pool was in phytoplankton (65%), followed by periphyton (26%), and then metaphyton (3%), invertebrates (3%) and fish (3%). In NP, the largest biotic P pool was in macrophytes (51%), followed by phytoplankton (36%), and then epiphyton (9%), invertebrates (2%) and fish (2%). In Control, the largest biotic P pool was in macrophytes (82%), followed by phytoplankton (7%), and then epiphyton (5%), invertebrates (3%) and fish (3%).

The sum of all P pools in Ex (746 mg m^{-2}) and Control (757 mg m^{-2}) treatments represents the background level of total P (mean 750 mg m^{-2}) in the system. When the mean of P additions (1169 mg m^{-2}) was subtracted from NP and ExNP totals, the remaining P for NP (751 mg m^{-2}) and ExNP (649 mg m^{-2}) was comparable to the background level, suggesting that the budget accounted adequately for all components of the phosphorus pool.

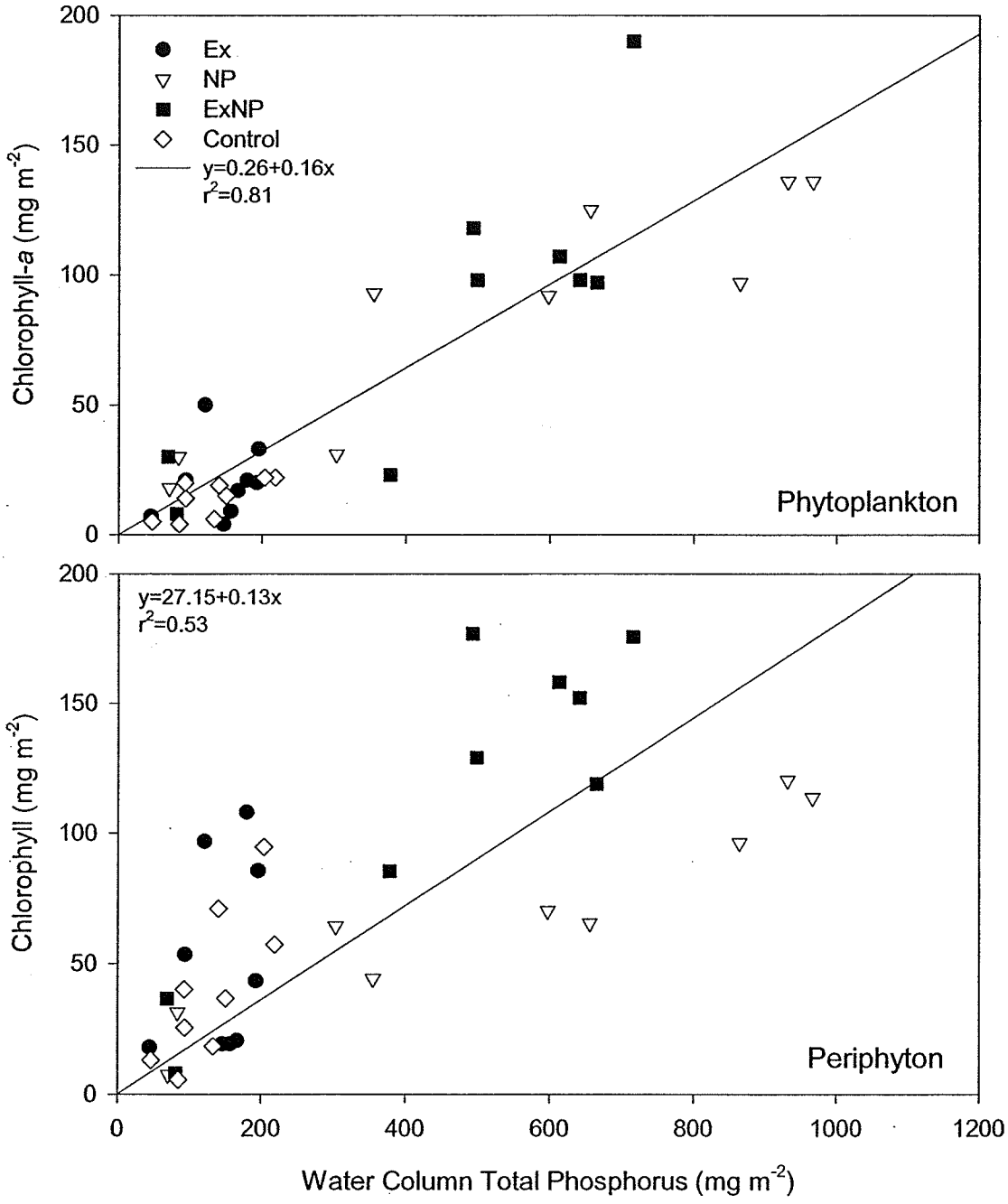

Figure 25. Relationship between water column total phosphorus (mg m^{-2}) and chlorophyll-*a* content of phytoplankton and periphyton in experimental enclosures in 1996.

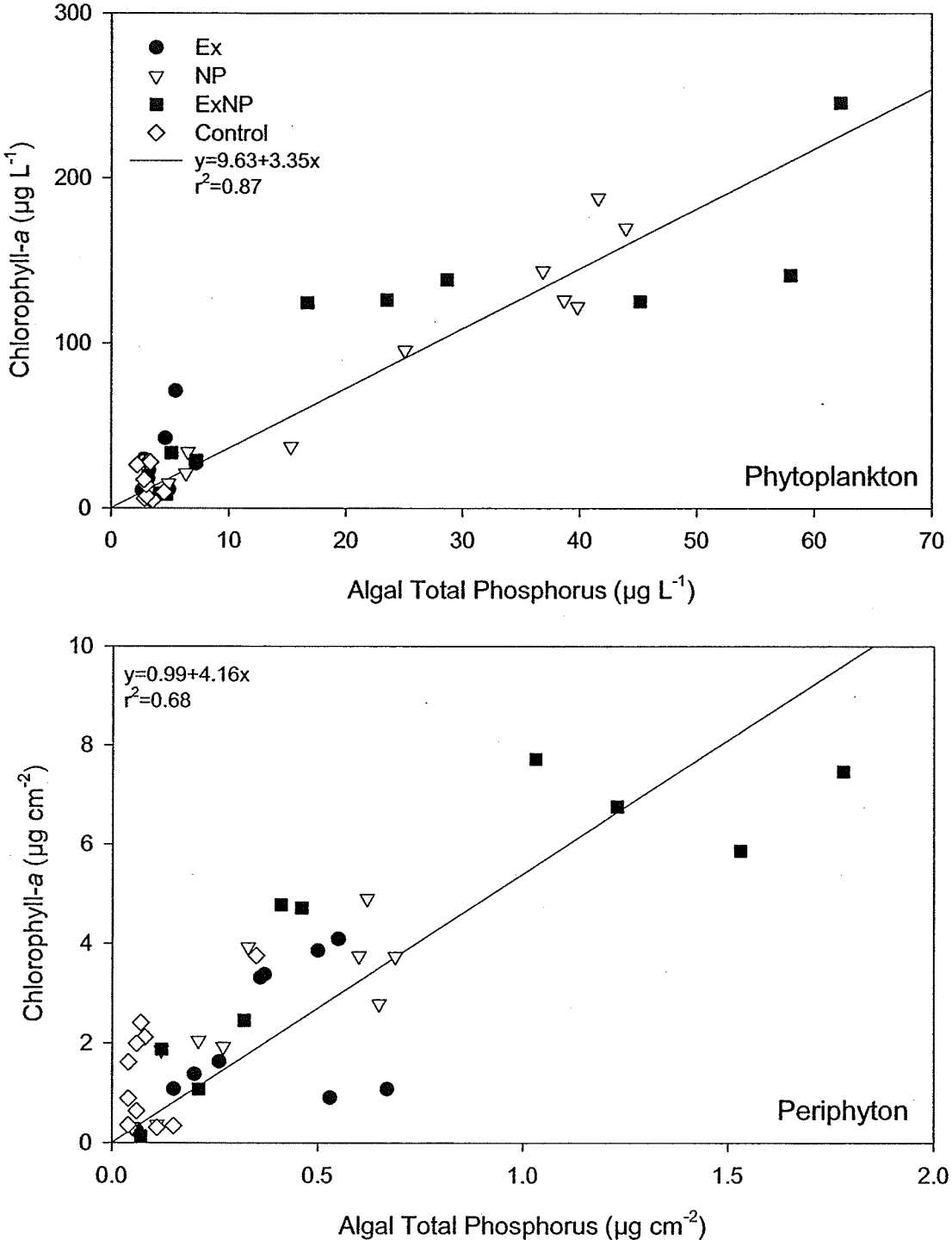

Figure 26. Relationship between algal total phosphorus and chlorophyll-*a* content of phytoplankton and periphyton in experimental enclosures in 1996.

Table 11. Mean phosphorus content (mg m^{-2}) in biotic (macrophytes, periphyton, epiphyton, phytoplankton, metaphyton, invertebrates and fish) and abiotic (sediment and water column) pools within wetland enclosures in 1996.

Phosphorus Pool	Ex	NP	ExNP	Control
Macrophytes	0	29	0	33
Periphyton/Epiphyton	5	5	8	2
Phytoplankton	3	21	20	3
Metaphyton	0	0	1	0
Invertebrates	1	1	1	1
Fish	1	1	1	1
Sediment	(585)	1353	(1353)	585
Water Column	151	500	434	133
Total P Pool	746	1920	1818	757

4.2 Discussion

4.2.1 Nutrient addition effects

Delta Marsh is presently classified as an eutrophic water body (TP range 30-100 μg L^{-1}, Wetzel 2001). A shift to hypereutrophic conditions (TP>100 μg L^{-1}), such as was created in nutrient addition treatments in these experiments, may conceivably occur in prairie marshes, depending on the agricultural and municipal practices within the watershed. Nutrient concentrations in spring runoff in a watershed adjacent to Delta Marsh ranged from 6-22 mg L^{-1} for N, and 4 to 9 mg L^{-1} for P, when animal manure was applied to fields over the winter season (Green 1996). In comparison, the cumulative loading during these experiments was 10 and 1.5 mg L^{-1} for N and P in 1995, and 20 and 3 mg L^{-1} for N and P in 1996, respectively.

With this shift to hypereutrophic conditions via nutrient addition, I had predicted an increase in phytoplankton in the treatments with no macrophytes present (xMacNP in 1995 and ExNP in 1996), and an increase in metaphyton in the treatment with macrophytes present (NP in 1996). There was no increase in phytoplankton in xMacNP in 1995, relative to Control and xMac treatments. The closest thing to the development of a phytoplankton bloom was a thin film of neuston that developed for several days in the xMacNP treatment in late July 1995. Neuston is a unique algal community that develops at the air/water interface and is often noticeable as a thin oily film on the surface of the water on calm days (Round 1981). Microscope examination of the neuston film from the xMacNP treatment showed that it was about 90% *Chlamydomonas* sp., but also contained *Lyngbya* sp., *Pseudanabaena* sp., *Nitzschia* sp., *Tabellaria* sp., and *Cryptomonas* sp.

There was a response by phytoplankton in both NP and ExNP treatments in 1996, with three times more phytoplankton produced in NP and five times more in ExNP relative to Control and Ex treatments. However, there was a concurrent response by the

periphyton and epiphyton, of a similar magnitude to that of phytoplankton (three times more attached algae in NP and ExNP than in Controls).

Metaphyton responded to nutrient addition for a brief period in the xMacNP treatment in late summer of 1995. A similar, delayed response to fertilization by metaphyton in unvegetated treatments was noted in another wetland study (Murkin *et al.* 1994). In the xMacNP treatment in my study, it is likely that the continued existence of short macrophytes in the enclosures provided initial attachment substrata for the filamentous algae. Metaphyton did not respond to nutrient addition during the 1996 experiment, despite a large response to nutrient addition (mean 260 mg m^{-2} for 7 weeks) in a previous experiment at this site in 1994 (McDougal *et al.* 1997). Metaphyton may require additional conditions of high irradiance and calm water conditions for optimum productivity (Whitton 1970, Fong and Zedler 1993, Goldsborough and Robinson 1996). I speculate that lower irradiance and windier conditions during the summer of the 1996 experiment, relative to the earlier experiment in 1994, may account for some of the difference in metaphyton response. In addition, it is possible that in 1996, the abundant phytoplankton population was able to out-compete metaphyton for nutrients, particularly as the phytoplankton contained nitrogen-fixing cyanobacteria (see below).

The equal magnitude of the response by phytoplankton, epiphyton and periphyton in 1996 suggests that the benthic algae were strong competitors with phytoplankton for added nutrients. In shallow water columns like this, benthic algae are nearly as well-distributed as phytoplankton, and therefore placed strategically to compete as first consumers of surface-added nutrients or surface run-off. For example, epiphyton on the leaves of canopy-forming macrophytes such as *S. pectinatus* can be positioned near the top of the water column, as well as being situated on lower stems and leaves. In this experiment, periphyton on the acrylic substrata and on the curtain walls were also suspended within the water column, and had the advantage over

phytoplankton, via attachment to substrata, of being able to maintain their position without energy expenditure. Natural analogues, besides submersed and emergent macrophytes, to the rod and curtain attachment sites in this experiment would include rocks, fallen logs, floating branches and other debris. Benthic algae associated with the sediments, or the plant barrier cloth in this experiment, have the added advantage of accessing nutrients that have sedimented through the water column. For example, Hansson (1990) demonstrated that sediment-associated algae could reduce phosphorus availability in the overlying water by up to 44%. Algae at the sediment surface alters the availability of phosphorus to phytoplankton by producing oxygen at the sediment/water interface, causing the chemical binding of phosphorus in the sediments (Carlton and Wetzel 1988). Benthic algae are often found in mats or films in close association with bacteria capable of nitrate reduction to ammonium-N (Wetzel 1993, Axler and Reuter 1996). This may allow benthic algae to more readily access added nitrate-N at the expense of phytoplankton, which preferentially use N in the form of ammonium-N (Priscu *et al.* 1985). Axler & Reuter (1996) found that benthic algal uptake and bacterial denitrification, not phytoplankton assimilation, accounted for 70 to 90% of nitrate uptake in a shallow lake and concluded that benthic algae could out-compete phytoplankton for water-column nutrients.

Evidence of the ability of benthic algal mats (which are often dominated by diatoms) to convert and take up large quantities of N is present in this study. The sharp decline in TN:TP ratios in both 1995 and 1996 was coincident with a sharp decrease in concentrations of soluble reactive silicon in the water column, suggesting that high diatom productivity prior to the decline may have been involved in the reduction of available N in the water column. Around the time of the decline in silicon each year, the colour of the periphyton on acrylic substrata changed from brown to 'grass' green, a qualitative indication that the population had changed from a predominantly brown-

pigmented diatom assemblage to an assemblage of green algae, many of which were filamentous, imparting a 'fuzzy' appearance to the acrylic substrata. The decline in TN:TP ratios was also concurrent with increasing submersed macrophyte biomass in treatments where macrophytes were present. Submersed macrophytes have a high requirement for nitrogen and macrophyte stands have been known to reduce the N:P ratio of water flowing through them (Barko *et al.* 1991).

Phytoplankton may have been N-limited in nutrient addition enclosures, even though nitrate-N was present in the water column, as other studies have found that even at saturating nitrate concentrations, phytoplankton ammonium-N uptake exceeds nitrate uptake by a factor of 2 to 10 (Goldman & McCarthy 1978, Priscu *et al.* 1985). In late July of 1996, the colour of the phytoplankton bloom in the NP and ExNP treatments changed from a 'grass' green to an 'aqua' green, a qualitative indication of a switch from green algae to cyanobacteria. Observations of this aqua green bloom under a microscope found that it contained a high proportion of *Microcystis aeruginosa*, a common bloom-forming cyanobacteria that maintains its position near the top of the water column through the use of internal gas vesicles, and *Anabaena flos-aquae*, a known nitrogen-fixer (Round 1981, Sze 1986). When ammonium-N concentrations increased in the water column of xMacNP(1995) and NP(1996) enclosures in mid to late August, there was a concurrent increase in the rate of phytoplankton photosynthesis. The rise in ammonium-N concentrations may have been due to the release of inorganic nutrients through advanced macrophyte senescence (e.g., Kistritz 1978, Landers 1982) or, in 1996, the result of ammonium-N release from the sediments during temporary anoxia that developed just above the sediment/water interface at this time.

The mean molar TN:TP ratio in the surrounding channel dropped from 28-30 in June to 18-20 in early July of both years (from 13 to 8 by mass ratio), coincident with the decrease in the TN:TP ratios in the enclosures, suggesting that the surrounding benthic

algal-dominated marsh is normally a nitrogen-limited system. The low N:P mass ratio of added nutrients (8:1) is in the range that is likely to promote nitrogen limitation (Schindler, 1998). Increasing the N:P mass ratio of added nutrients to a ratio greater than 15:1 would possibly have enhanced the phytoplankton response to nutrient addition, but would have been less indicative of a natural flush of nutrients from the N-limited sediments of this marsh, as described earlier.

There was no increased growth response of macrophytes to water column nutrient addition, suggesting that submersed macrophytes were not nutrient limited or obtained their nutrients from the sediments. Other studies have also found little or no increase in macrophyte biomass in response to nutrient enrichment (Howard-Williams 1981, Granéli and Solander 1988, McDougal *et al.* 1997). Macrophytes in NP and Control treatments contained similar levels of phosphorus, suggesting that macrophytes were not luxury-consuming added phosphorus in NP enclosures. It is possible that macrophytes were indirectly affected by nutrient addition in a negative manner, given the earlier onset of macrophyte senescence in nutrient addition treatments. Increased epiphyton colonization on the surfaces of macrophytes in these enclosures may have limited the amount of light impinging on leaf surfaces, as has been noted elsewhere (Sand-Jensen and Borum 1991, Granéli and Solander 1988, Philips *et al.* 1978).

4.2.2 Macrophyte exclusion effects

Macrophytes affected the physical environment when they were present in the water column. As macrophytes developed in Control and NP enclosures, the reduction in water motion was evident. Shading by the macrophyte canopy at the water surface reduced heat penetration through the water column, setting up temporary afternoon thermoclines, which further reduced turbulent mixing and increased the settling loss of suspended particles, including phytoplankton (*cf.* Scheffer, 1998). Light transmission through the water column to the sediment surface was higher in xMac and xMacNP

treatments in 1995 and in Ex and ExNP treatments in 1996, a function of the absence of macrophytes, and also in xMac and Ex, less phytoplankton in the water column. The combined effects of macrophyte and algal photosynthesis also altered the chemical environment in NP and Control treatments in 1996, causing significantly higher pH values and lower alkalinity values in these two treatments. This effect was also noticeable, although dampened, in Control treatments in 1995. By driving up pH, macrophytes may have had an indirect effect on competition between periphyton and phytoplankton. High pH reduces the capacity of iron to bind phosphorus in the sediments (Lijklema, 1977) so this condition coupled with temporary anoxia in NP enclosures in 1996, might have accounted for the higher levels of TRP present in the water column in August, compared to levels in ExNP. Denitrification would also be enhanced in enclosures with macrophytes (Scheffer, 1998), because of the occurrence of temporary anoxia near the sediment surface in these enclosures. In this way, macrophytes may have been indirectly involved in increasing the N-limitation for phytoplankton.

There was no noticeable effect of macrophyte removal alone on phytoplankton abundance in either 1995 or 1996. I speculate that reductions in water turbulence caused by enclosure walls may have adversely affected the environment for phytoplankton, mimicking the sheltering effect of submersed macrophyte stands, and causing faster settling times for phytoplanktonic cells.

There was an effect of macrophyte removal alone on periphyton abundance in the xMac treatment in 1995. The increase in periphyton on acrylic substrata in xMac enclosures was clearly a response to light and not nutrients, because periphyton in xMac enclosures increased two times more than the periphyton in xMacNP enclosures, which had access to additional nutrients, but less light in the water column. Therefore, it seems likely that benthic algae in this system might be primarily light-limited, whereas planktonic algae are primarily N-limited.

In 1996 there was some evidence of a synergistic effect of combined nutrient addition and macrophyte exclusion that was not predictable from the effect of either treatment alone. Whereas phytoplankton chlorophyll-*a* values did not differ significantly from week to week between NP and ExNP treatments, the magnitude of change in phytoplankton abundance post-addition compared to pre-treatment levels was 10 times higher in ExNP and only 6 times higher in NP. This suggests that the phytoplankton in ExNP were also responding positively to the reduction in macrophyte-mediated effects such as water column stability, shading, or grazing refugia for zooplankton from fish. This same trend was more evident for periphyton, where the magnitude of change in periphyton abundance post-addition compared to pretreatment levels was 16 times higher in ExNP and only 8 times higher in NP. The significantly higher level of dissolved oxygen in ExNP, relative to the other treatments, also provides evidence of higher photosynthetic activity by both phytoplankton and periphyton in this treatment.

4.2.3 Interpretation of the 1995 experiment "failure"

The lack of response by phytoplankton in 1995 to macrophyte removal alone, and to macrophyte removal combined with nutrient addition, was an interesting outcome, which prompted some changes in experimental design for the following year, including increasing the total loading of nutrients, adding in the nutrient addition plus macrophytes (NP) treatment, employing a different method of macrophyte removal, quantifying periphyton on curtain walls, and allowing fish to remain in the system. Phytoplankton in 1995 did not appear to be light-limited, because the more favorable light environment in the xMac treatment did not elicit an increased response relative to the more shaded Control treatment. Phytoplankton also did not appear to be phosphorus-limited, as there was no increased response in the xMacNP treatment, and there was an elevated concentration of TRP in the water column for most of the summer. Phytoplankton were probably N-limited and may have been unable to compete successfully for the added N

with the short, but metabolically active submersed macrophytes that remained in the system. Although not measured, these macrophytes were probably coated with epiphyton, judging by the increased periphyton on acrylic substrata in the xMacNP treatment. An unquantified amount of periphyton was also growing on the curtain walls. This unmeasured epiphyton, along with macrophytes, epipelon and metaphyton, may have provided phytoplankton with strong competition for nutrients in the xMacNP treatment. Grazing pressure on phytoplankton was high during the pre-treatment period, and the level of nutrients that was provided may not have been high enough to allow phytoplankton production to outstrip grazing pressure, or even sustain high levels of secondary production. Other studies have noted that their level of nutrient loading may have been too low to have a substantial impact on sustained phytoplankton production (Murkin *et al.* 1994, R. Hecky 1996, pers. comm.). The exclusion of fish in 1995 may have been another factor influencing phytoplankton abundance. The exclusion of fish allowed zooplankton, particularly the larger cladocerans, to remain in the enclosures at a level of abundance that may have been able to keep the N-limited phytoplankton in check through efficient grazing. This became clearer in 1996, when fish were maintained in the enclosures and zooplankton numbers, particularly large cladocerans, were reduced to much lower levels than in 1995 by predation. Low numbers of zooplankton were found in all treatments in 1996 (Sandilands *et al.* 2000), suggesting that the refuge effect of submersed macrophytes for zooplankton was not effective, due to the fact that the enclosed fish had no place else to forage other than within the macrophyte stands.

4.2.4 Benthic vs. planktonic algal production

Contributions to total algal production by planktonic and benthic (epiphyton, periphyton, and metaphyton) algae varied among treatments. In all treatments but one, benthic algae were the largest contributors to total algal production, bearing out Wetzel's (1993) assertion that the dominant primary productivity of shallow aquatic ecosystems is

not planktonic but is associated with surfaces. In 1995, planktonic to benthic proportions were 30% to 70% in Control, 86% to 14% in xMac, and 3% to 97% in xMacNP treatments. Planktonic to benthic proportions in 1996 were 23% to 77% in Control, 28% to 72% in Ex, 48% to 52% in NP and 42% to 58% in ExNP treatments.

Both planktonic and benthic algae in 1996 were affected more by nutrient addition than by the manipulation of macrophyte biomass. The presence of benthic algae, with its ability to compete effectively for added nutrients, acted to dampen the response by phytoplankton. In ExNP enclosures, where benthic algal colonization surfaces were reduced significantly by the absence of macrophytes, periphyton was still the largest contributor to total algal production. Even in a macrophyte-free natural system with no curtain walls as colonization surfaces, the high potential for growth and nutrient uptake by sediment-associated algae and algae attached to other hard surfaces (rocks, debris) suggests that phytoplankton dominance may not be the inevitable outcome for a shallow nutrient-enriched water column. Other studies have also noted this increased shift toward benthic primary production, thus reducing phytoplankton responses to enrichment (Blumenshine *et al.* 1997, Havens *et al.* 1999).

4.2.5 Phosphorus budget

The majority of the P (71-79%) was found in the sediments, which supports speculation in other studies that fractions of P unaccounted for (30 to 59%, Havens *et al.* 1999; 47 to 74%, McDougal *et al.* 1997) were probably sequestered in the sediments. Sediments can be an effective sink for phosphorus because of the substantial adsorption capacity of clay minerals and organic matter and the processes of chemical binding and coprecipitation with iron, manganese and carbonate (Kadlec & Knight 1996), particularly when there is an oxidized microzone at the sediment/water interface (Wetzel 2001). However, with continued external P loading, the capacity of sediments to sequester phosphorus will eventually be overwhelmed (Howard-Williams 1981, Kadlec & Knight

1996). In addition, the development of anoxia at the base of submersed macrophyte stands, along with the higher pH resulting from macrophyte photosynthesis, promote the release of iron-bound phosphorus from the sediments (Scheffer 1998).

Sequestration of added P in the biotic components of the system was small relative to the total input load and the proportion sequestered in sediments. However the measurement of small storage pools in biotic organisms such as algae, zooplankton and fish, does not mean that these organisms are unimportant in the P cycle in aquatic systems. Rather, these organisms promote higher productivity in aquatic environments, by cycling P rapidly and efficiently (Carpenter 1981, Wetzel 1993) from one biotic compartment to the next. For example, rapid nutrient regeneration from zooplankton grazers can supply 10 times more P to phytoplankton than all external sources combined in mid-summer (Lehman 1980). The concentration of inorganic P in a water body can be altered by algal uptake of the nutrient in shortest supply, by zooplankton alteration of the N:P ratios of their excretions, and by horizontal diurnal migrations and differential predation of large-bodied zooplankters by fish (Sterner *et al.* 1992, Vanni *et al.* 1997, Hwang *et al.* 1998, Brazner *et al.* 2001).

Periphyton, phytoplankton and epiphyton were the major biotic recipients of added P because their production increased in response to enrichment whereas macrophyte biomass did not change. As in the earlier nutrient addition experiment (McDougal *et al.*1997), I found that periphyton, phytoplankton, and metaphyton accumulated P in proportion to their increasing chlorophyll-*a* content, in contrast to other studies where P content of algae increased with P enrichment (Portielje & Lijklema 1994, Havens *et al.* 1999). This suggests that algae in nutrient addition treatments were not luxury-consuming the excess phosphorus, a contention that is supported by the elevated concentrations of TRP in the nutrient addition treatments. This lack of luxury-consumption of P and the fact that elevated levels of available TRP were detectable in

the water column throughout the experiment are further evidence that algal growth was limited by N availability at this site.

The strong correlation between water column TP and phytoplankton chlorophyll-*a* was expected, given that the water column is the major source of nutrients for phytoplankton. The correlation between water column TP and periphyton chlorophyll-*a* suggests that periphyton sustain much of their nutrient demand from the water column. The stronger relationship between total algal P and chlorophyll-*a*, than between water column TP and chlorophyll-*a*, is consistent with the Droop model which relates algal growth to the internal nutrient concentration rather than the nutrient concentration in the environment (Droop 1974). However, Scheffer (1998) suggested that a portion of the TP that is actually available to algae in shallow water columns includes part of the phosphorus in the sediments, which makes the interpretation of regression models explaining algal production from TP in shallow systems more difficult.

The lack of relationship between metaphyton chlorophyll-*a* and P was unexpected, as metaphyton would be expected to sequester P from the water column (Auer and Canale 1982, Borchardt 1996). However, if metaphyton were N-limited, perhaps they had no requirement for luxury-uptake of P from the water column. The lack of relationship between macrophyte biomass and P was expected, as macrophyte growth is rarely correlated with phosphorus content. Peak macrophyte biomass occurs after the period of peak P uptake. While biomass is still increasing, P is already being sequestered to the roots or rhizomes or is being lost due to an increase in "leakiness" with the onset of senescence (Granéli and Solander 1988). In addition, if submersed macrophytes get most of their P from the sediments, a strong relationship between water column P and macrophyte biomass would not be expected.

5. Oak Hammock Marsh Study

5.1 Results

5.1.1 Environmental variables

The ice-free season in 1997 was cooler and windier than in 1998, particularly in the early spring and late fall (Table 12). In 1997 there were18 days where wind speeds exceeded 50 km hr^{-1}, compared to 9 days in 1998. Water column depth showed a similar trend of decreasing depth with evaporation and transpiration over the season in both 1997 and 1998 (Figure 27). Open Deep sites ranged from about 65 cm early in the season to 40 cm in the fall. Open Shallow sites ranged from 45 cm down to 25 cm, whereas *Typha* Shallow sites ranged from 30 cm down to 5 cm over the season. Changes in water level in the tertiary lagoon were related to effluent release from the secondary lagoon as described earlier. Maximum daily PAR followed a similar trend over both years (Figure 28), although there were 10 days in May to August 1997 where maximum daily PAR was less than 600 µmol m^{-2} s^{-1}, compared to only 3 days for the same period in 1998. Average daily maximum PAR for the ice-free season was 1247 µmol m^{-2} s^{-1} in 1997 and 1258 µmol m^{-2} s^{-1} in 1998. Reflection of PAR from the water surface was higher (24%) in 1997 than in 1998 (17%).

Light extinction profiles through the water column were similar in both years, but differed significantly in open water versus vegetated sites (Figure 29). Repeated measures two factor ANOVA indicated that both main effects of marsh-type and depth were significant ($F_{(2,52)}$=12.65, p<0.0001; $F_{(4,78)}$=100.21, p<0.0001), as was the interaction term ($F_{(4,78)}$=3.43, p=0.0124), suggesting that the effect of marsh-type was dependent on depth. Post-hoc comparisons performed on the marsh-type*depth interaction using sliced contrasts of the least square means showed that the effect of depth was significant at 10, 20, and 30 cm, but not at 40 cm, where the effect of marsh-

Table 12. Monthly mean air temperature (°C), water temperature (°C), and wind speed (km hr^{-1}) at Oak Hammock Marsh in the ice-free seasons of 1997 and 1998, based on data collected from Winnipeg International Airport, 25 km to the south.

Month	1997 Air Temp (°C)	1997 Water Temp (°C)	1997 Wind Spd (Km hr^{-1})	1998 Air Temp (°C)	1998 Water Temp (°C)	1998 Wind Spd (Km hr^{-1})
May	9.0	8.4	19.5	12.8	15.8	17.2
Jun	19.3	20.5	17.5	15.7	16.5	15.2
Jul	19.8	21.5	17.3	19.7	23.3	14.0
Aug	18.3	20.5	15.1	20.7	21.8	14.5
Sep	14.3	16.2	18.5	14.5	16.2	16.3
Oct	5.4	6.3	19.6	6.7	7.2	18.7
Season Mean	**14.3**	**15.6**	**17.9**	**15.1**	**16.8**	**14.3**

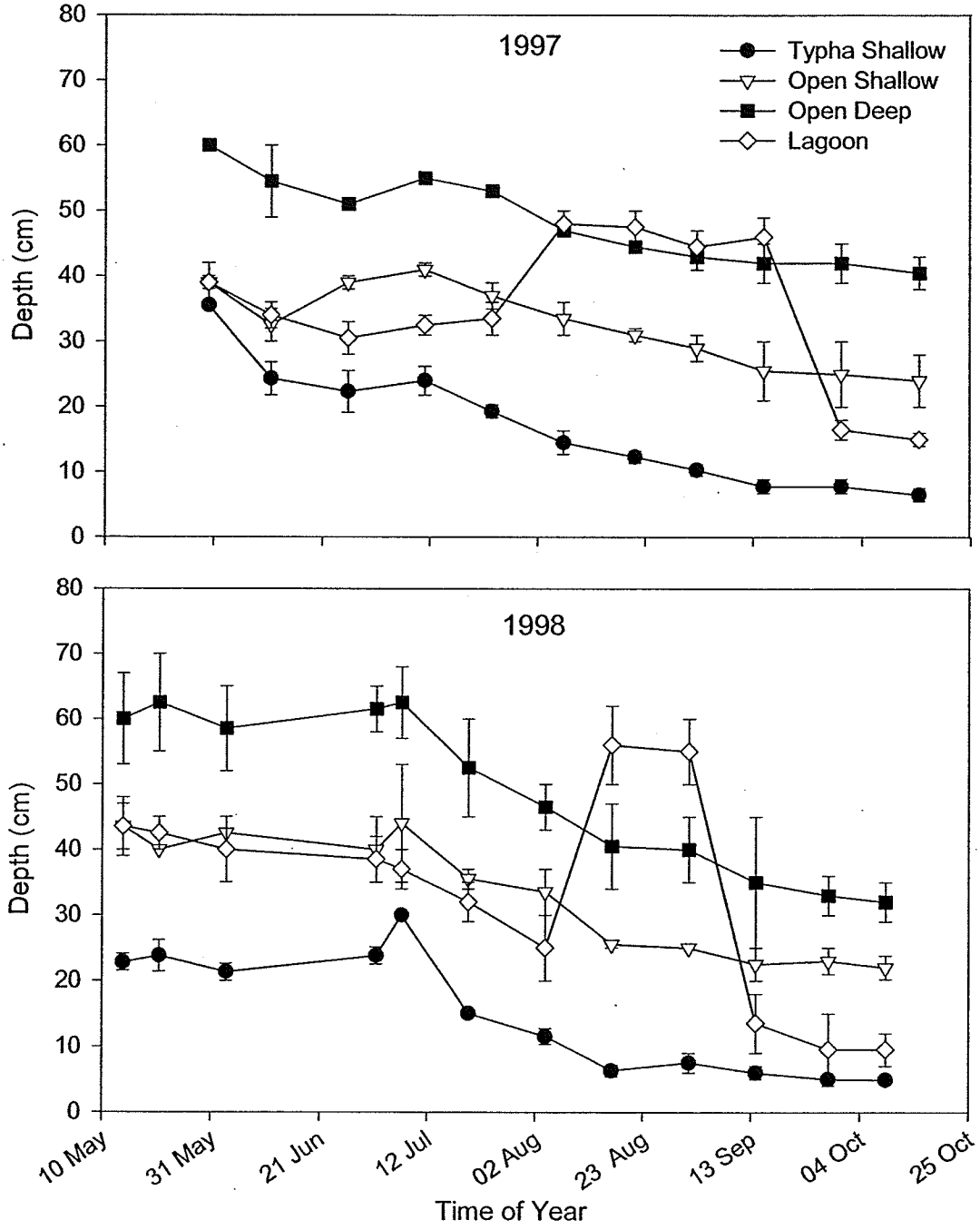

Figure 27. Mean water column depth (cm, ±SE, n(TS)=4, n=2) at sites in Cell Four of Oak Hammock Marsh and the tertiary sewage lagoon in 1997 and 1998.

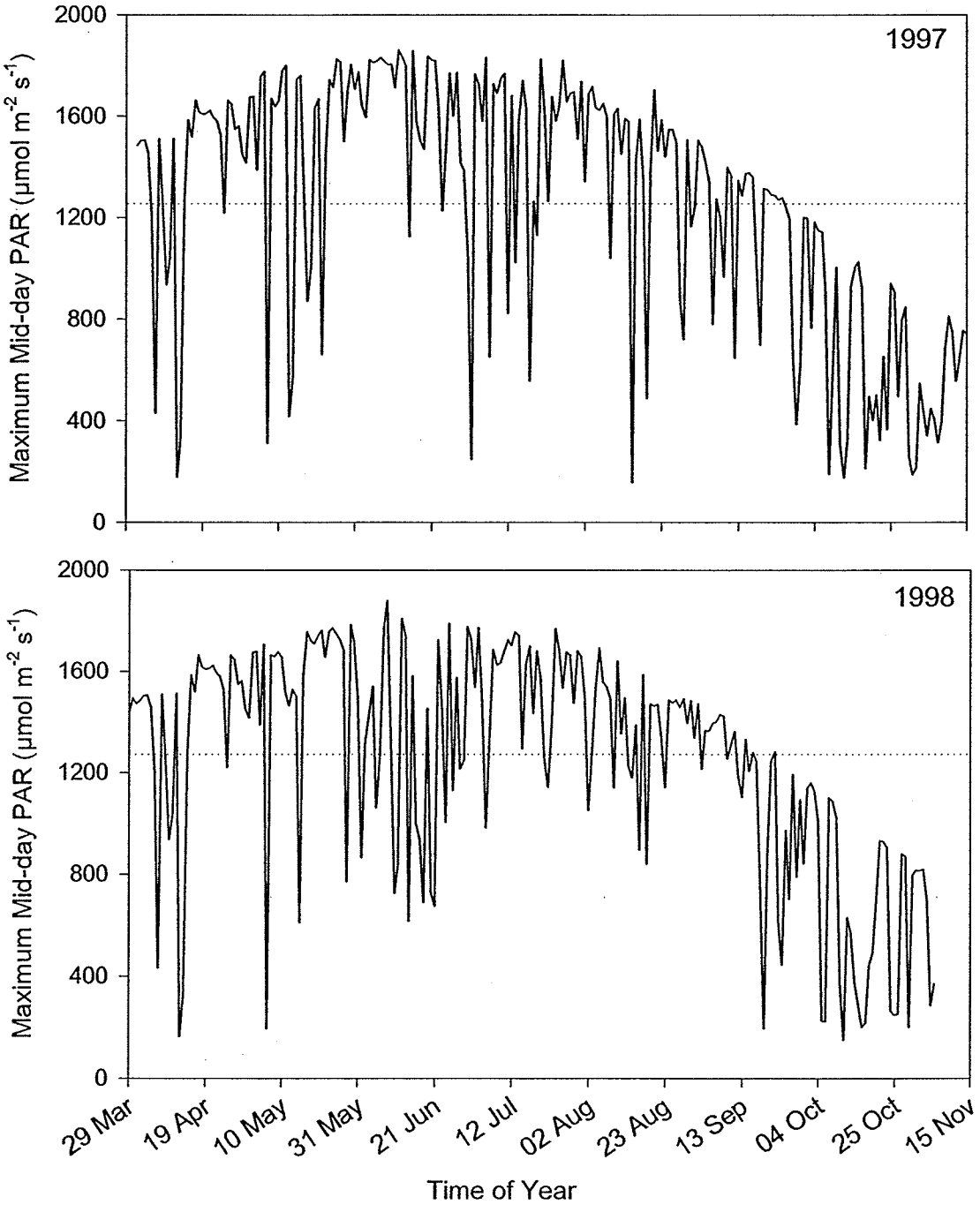

Figure 28. Maximum daily surface PAR (µmol m^{-2} s^{-1}) at Oak Hammock Marsh in 1997 and 1998. Horizontal dotted line represents the overal mean PAR for the period measured (1997: 1247 µmol m^{-2} s^{-1}; 1998: 1258 µmol m^{-2} s^{-1}).

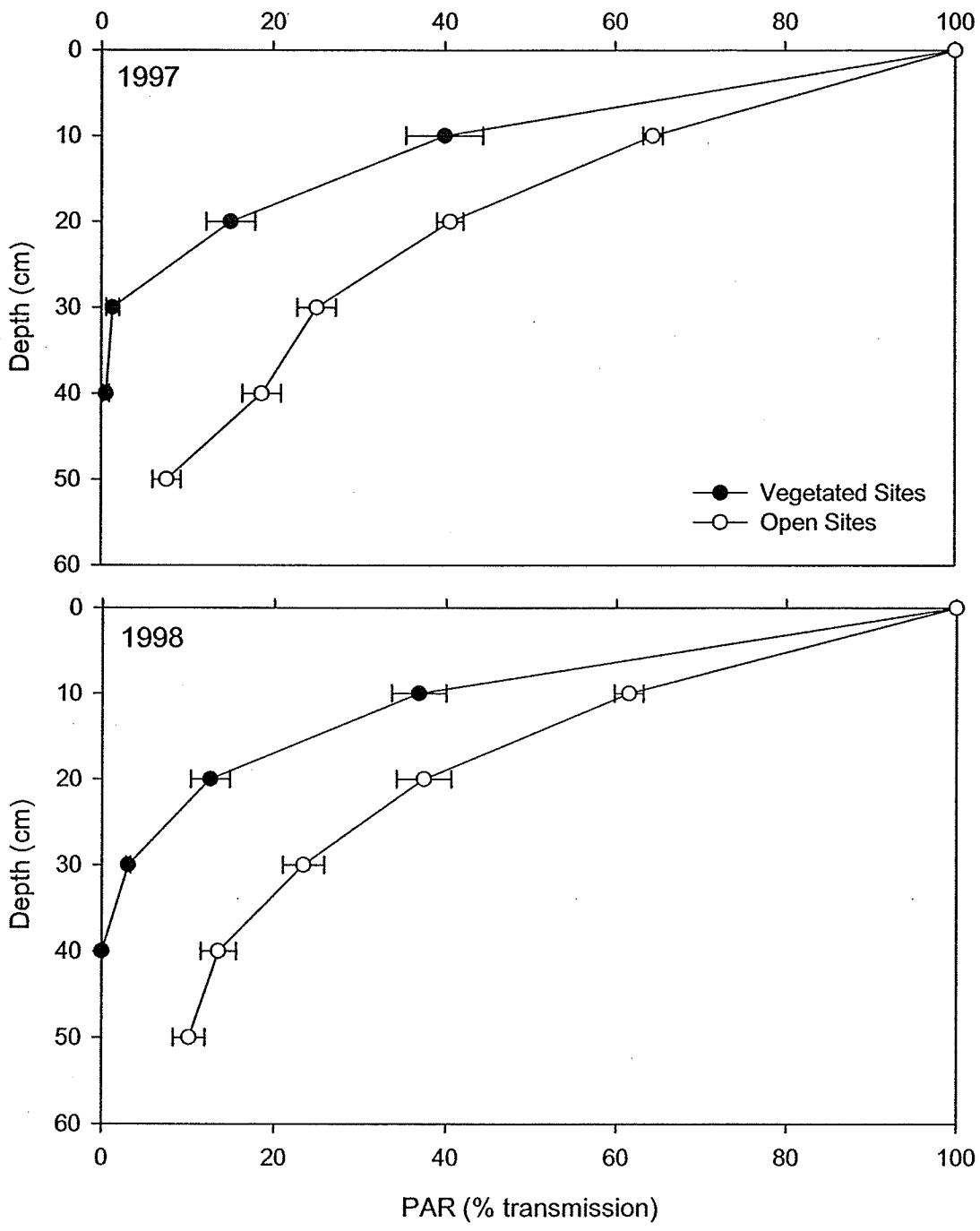

Figure 29. Light extinction profiles (% transmission, ±SE, n=8) with depth in vegetated and open water sites in Cell Four of Oak Hammock Marsh in 1997 and 1998.

type was more important. Because of this difference in light extinction profiles, I employed both profiles in my photosynthesis model, using the vegetation extinction profile to adjust PAR with depth in the vegetated areas, and the open water extinction profile to adjust PAR with depth in the open water areas of Cell Four.

5.1.2 Water chemistry

Nutrient levels in Cell Four followed similar trends among marsh sites and between years (Figure 30 and 31). Unfortunately, the nitrate+nitrite-N samples for the fall of 1997 were lost due to sample contamination. Nutrient levels were lowest in mid-summer and higher in early spring and again in late fall. There was a significant difference between sites for total reactive phosphorus (1997: $F_{(4,7)}=68.01$, $p<0.0001$; 1998: $F_{(4,7)}=11.14$, $p=0.004$), ammonium-N (1997: $F_{(4,7)}=7.14$, $p=0.013$; 1998: $F_{(4,7)}=23.00$, $p=0.0004$), and nitrate+nitrite-N (1997: $F_{(4,7)}=79.72$, $p<0.0001$; 1998: $F_{(4,7)}=37.88$, $p<0.0001$). Post-hoc comparisons of least squares means revealed that Cell Four sites (*Typha* Shallow, Open Shallow and Open Deep) did not differ from each other. Lagoon and Spring sites were significantly different from the sites in Cell Four, but did not differ from each other. Nutrient levels in the tertiary sewage lagoon were extremely low in both years, comparable to the nutrient levels in the artesian spring feeding into Cell Four (Figure 30 and 31). Alkalinity, pH, and soluble reactive silicon levels were similar in 1997 and 1998 (Table 13). Mean alkalinity was slightly lower and pH was greater in the tertiary lagoon compared to sites in Cell Four. Soluble reactive silicon levels were low (0.3 mg L^{-1}) in the tertiary sewage lagoon in mid-summer in both years. Dissolved organic carbon (DOC) concentration in Cell Four was 47.4 mg L^{-1} in mid-summer 1997.

Dissolved inorganic N to P molar ratios (DIN:DIP) were variable in 1997 and 1998 (Figure 32), but were mainly indicative of N-limitation in the water column (ratio<15), except in Open Shallow sites in late summer of 1998. Conversely, total N to P

ratios (TN:TP) were indicative of P-limitation (ratio>15) in the water column in 1997 (Table 14). The TP:DIP ratios indicated that virtually all of the P in Cell Four was present in inorganic form, whereas the TN:DIN ratios indicated that more N was present as organic N than inorganic N (Table 14). In the tertiary sewage lagoon, both TP:DIP and TN:DIN were an order of magnitude greater than in Cell Four, indicating that proportionately more organic N and P were present in the sewage lagoon.

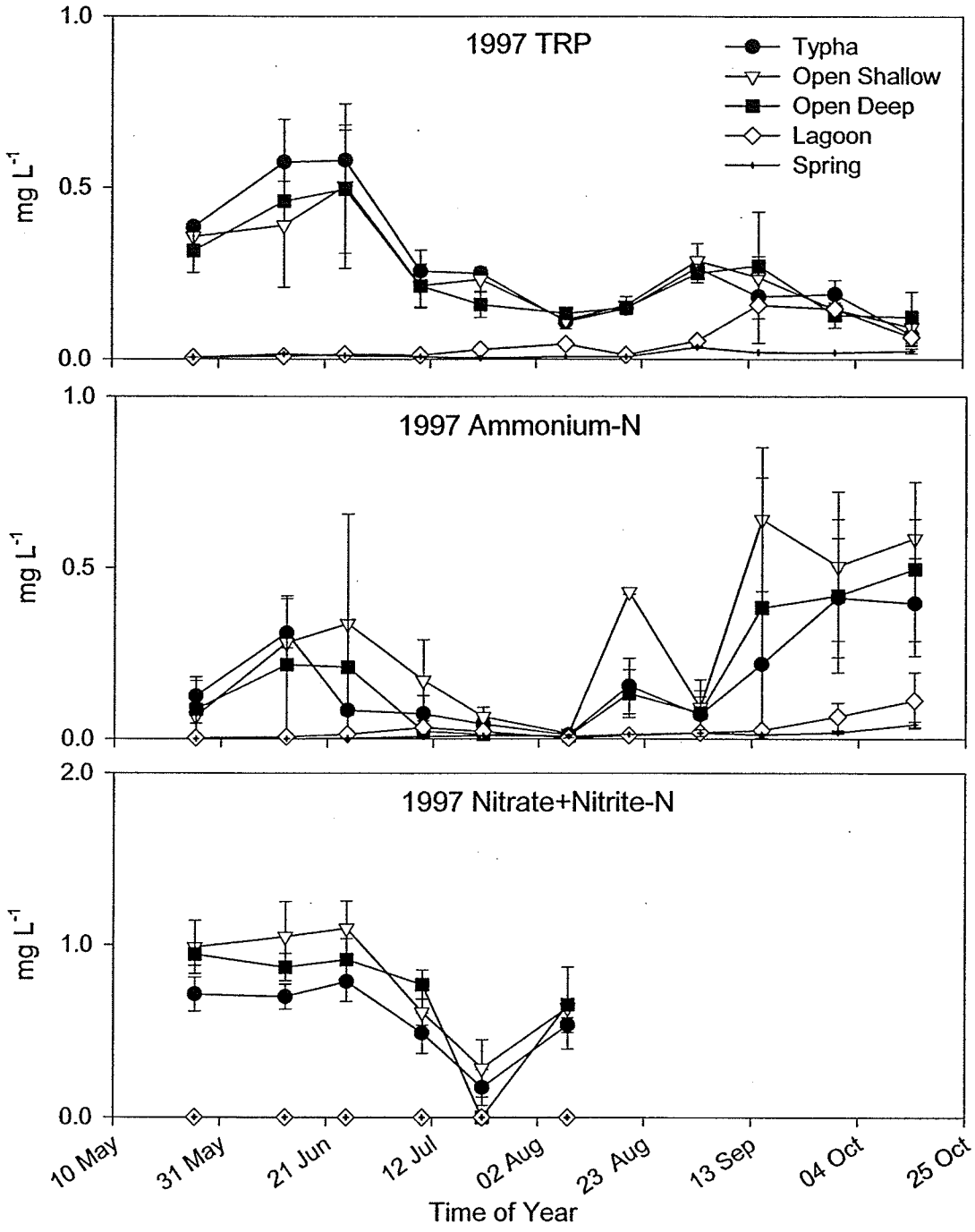

Figure 30. Total reactive phosphorus (TRP) (mg L^{-1}, ±SE, n(TS)=4, n=2), ammonium-N (mg L^{-1}, ±SE, n(TS)=4, n=2), and nitrate+nitrite-N (mg L^{-1}, ±SE, n(TS)=4, n=2) in 1997 in Cell Four sites, the tertiary sewage lagoon, and the artesian well (Spring) that feeds into Cell Four.

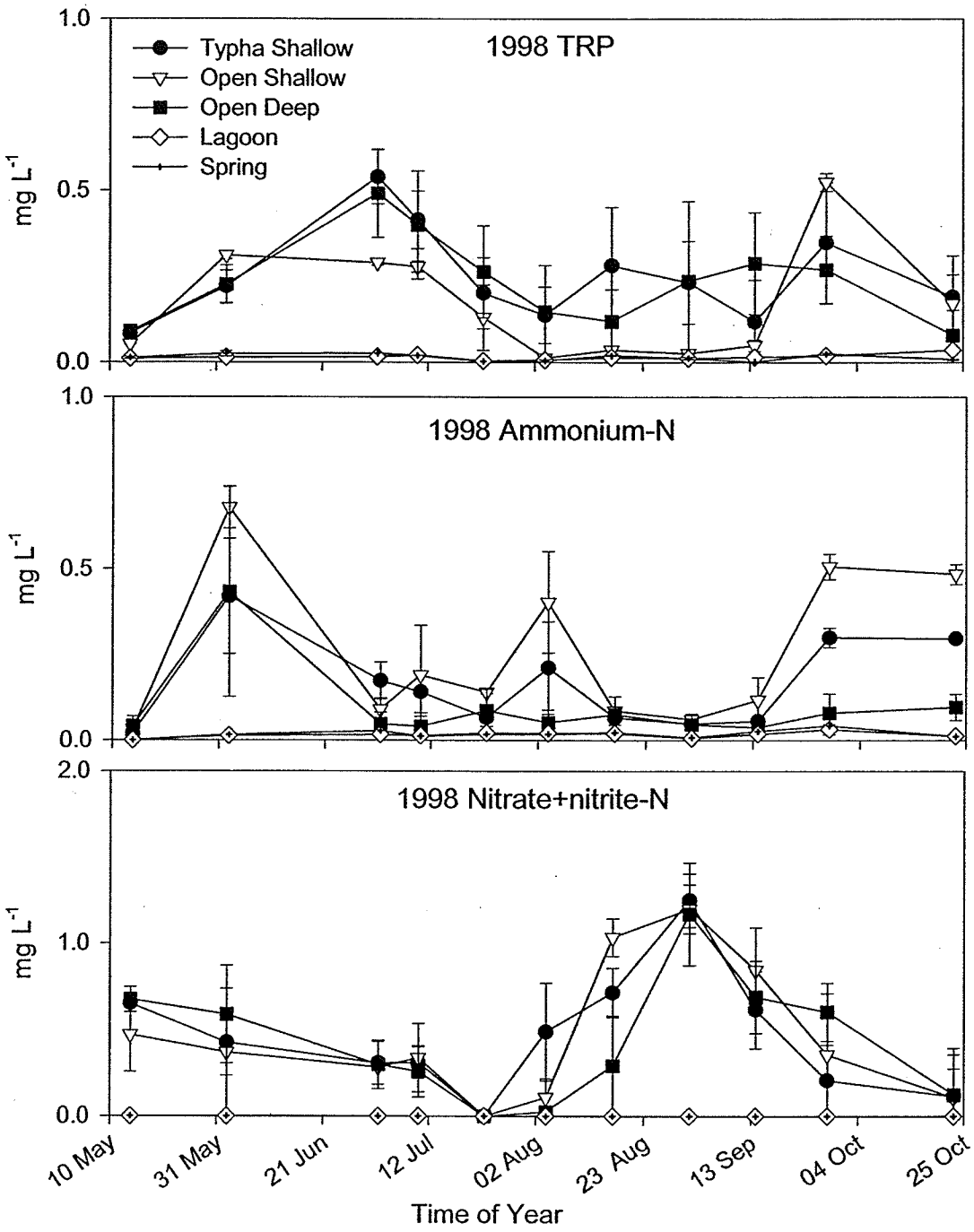

Figure 31. Total reactive phosphorus (TRP) (mg L^{-1}, ±SE, n(TS)=4, n=2), ammonium-N (mg L^{-1}, ±SE, n(TS)=4, n=2), and nitrate+nitrite-N (mg L^{-1}, ±SE, n(TS)=4, n=2) in 1998 in Cell Four sites, the tertiary sewage lagoon, and the artesian well (Spring) that feeds into Cell Four.

Table 13. Mean soluble reactive silicon (SRS) (mg L^{-1}, ±SE, n=8), alkalinity (mg L^{-1}, ±SE, n=8), and pH (±SE, n=8) in Cell Four of Oak Hammock Marsh and the tertiary sewage lagoon in 1997 and 1998.

	1997		1998	
	Cell Four	Lagoon	Cell Four	Lagoon
pH	8.5 (±0.1)	8.9 (±0.1)	8.5 (±0.1)	8.8 (±0.1)
Alkalinity (mg L^{-1})	398 (±9)	333 (±14)	439 (±18)	398 (±21)
Silicon (mg L^{-1})	1.4 (±0.5)	0.3 (±0.0)	1.1 (±0.2)	0.3 (±0.1)

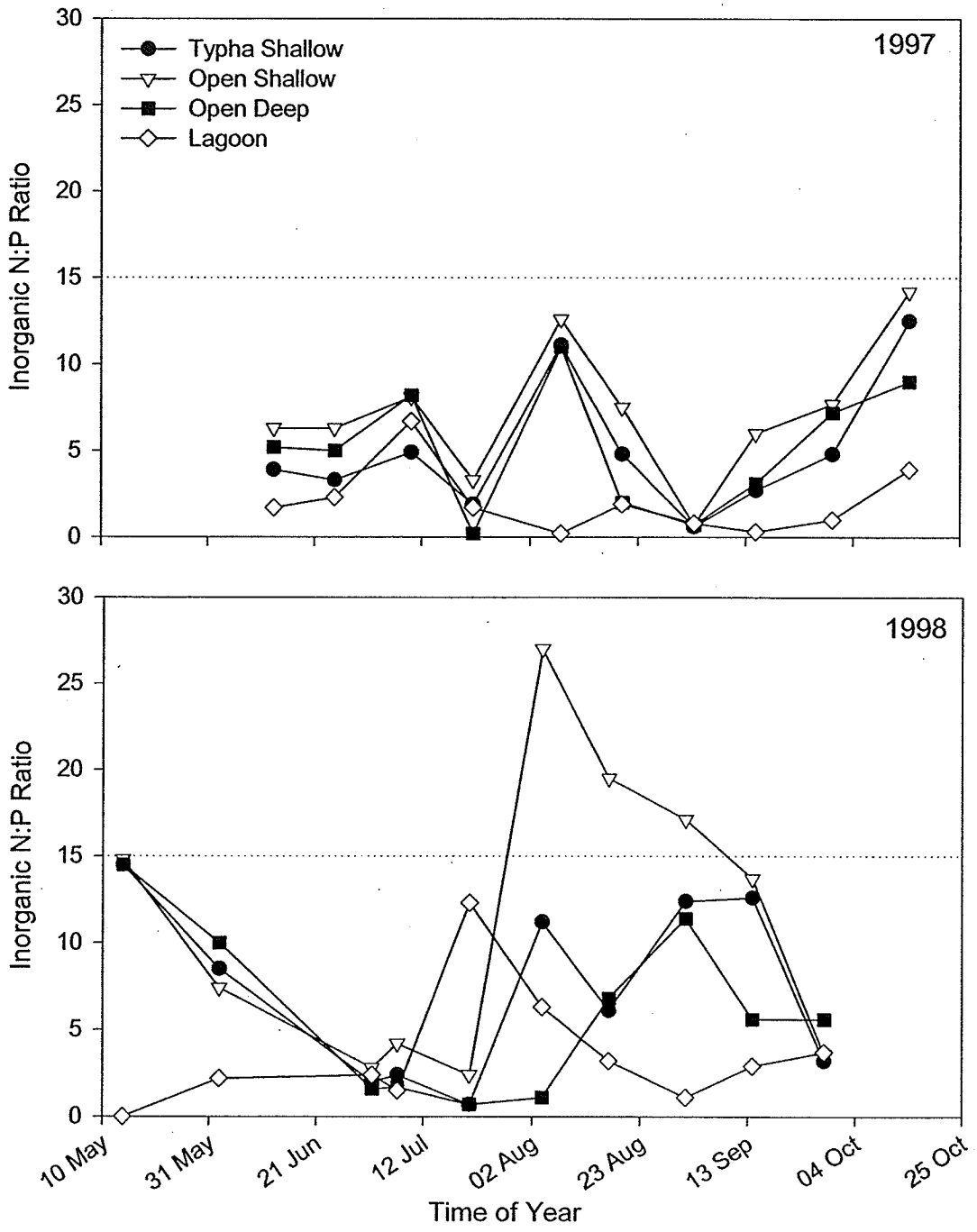

Figure 32. Dissolved inorganic N to P molar ratios (DIN:DIP) in the water column in Cell Four of Oak Hammock Marsh and the tertiary sewage lagoon in 1997 and 1998. (Dotted line indicates N:P<15 - N limitation, N:P>15 - P limitation.)

Table 14. Molar ratios of total N to total P (TN:TP), total P to dissolved inorganic P (TP:DIP), and total N to dissolved inorganic N (TN:DIN) in Cell Four and the tertiary sewage lagoon in 1997.

Location	TN:TP	TP:DIP	TN:DIN
Typha Shallow	23	1	4
Open Shallow	32	1	4
Open Deep	23	1	4
Lagoon	28	11	44

5.1.3 Nutrient diffusion rates

The mean diffusion rates for NO_3-N and PO_4-P ions from clay pots under laboratory conditions varied according to concentration (0.5 and 0.05 M), with no significant differences between replicate substrata ($F_{(2,27)}$=0.00, p=0.999; $F_{(2,27)}$=0.00, p=0.870). Release of NO_3-N from P-pots and of PO_4-P from N-pots was undetectable. Mean diffusion rates for 0.5 M and 0.05 M N substrata were 4.6 and 0.3 mmol d^{-1}, respectively. Mean diffusion rates for 0.5 M and 0.05 M P substrata were 3.7 and 0.3 mmol d^{-1}.

5.1.4 *In situ* periphyton study

In both 1997 and 1998, the periphyton assemblage showed some evidence of co-limitation by N and P (Table 15). Periphyton chlorophyll-*a* on substrata increased significantly with increasing N concentration ($F_{(2,27)}$=11.100, p=0.0003; $F_{(2,27)}$=120.190, p<0.0001) in both years. Periphyton chlorophyll-*a* increased significantly with increasing P concentration ($F_{(2,27)}$=3.920, p=0.032) in 1997, but not in 1998 ($F_{(2,27)}$=1.030, p=0.371), due to the low response of periphyton on 0.5/0.05 N:P substrata. The interaction between N and P was not significant in either year ($F_{(4,27)}$=1.200, p=0.332; $F^{(4,27)}$=1.210, p=0.332).

Nutrients diffusing from the substrata did not affect ambient nutrient concentrations. There was no significant difference between water column nutrient concentrations above the substrata grids and nutrient concentrations at nearby sampling sites ($F_{(3,11)}$=0.000, p=0.907). Mean concentrations of TRP, NH_4-N, and NO_3-N above the grid averaged 0.29, 0.03 and 0.18 mg L^{-1}, respectively, which was within the ambient range for these nutrients at nearby sites.

5.1.5 Nutrient deficiency experiments

Nitrogen debt for phytoplankton from Cell Four was well below the level of N-deficiency (0.15 µmol N μg^{-1} Chl-*a* 24-h^{-1}) throughout the season in both 1997 and 1998

(Figure 33). However, phytoplankton in the tertiary sewage lagoon was strongly N-limited in 1997 and for most of 1998, except for a short period in mid-summer and again in late fall (Figure 33). Alkaline phosphatase activity in phytoplankton in Cell Four was greater than 0.005 μmol *o*-MFP μg^{-1} Chl-*a* h^{-1} in July of 1997, and for much of the season in 1998, indicating severe P limitation (Figure 34). Phytoplankton in the tertiary sewage lagoon exhibited a level of alkaline phosphatase activity indicative of severe P limitation throughout most of 1997 and 1998. Bacterial alkaline phosphatase activity accounted for 68% of total APA on average, indicating that 32% of total APA was associated with algal particles or with soluble phosphatase enzymes released by algae.

Table 15. Mass of periphyton chlorophyll-*a* (µg cm^{-2}) that accumulated on nutrient diffusing substrata containing nine combinations of N and P (± SE, n=4) in Cell Four of Oak Hammock Marsh.

Phosphorus Concentration (mol L^{-1})		Nitrogen Concentration (mol L^{-1})		
		0.0	**0.05**	**0.5**
0.0	1997	0.4 (±0.1)	0.7 (±0.2)	1.5 (±0.6)
	1998	0.2 (±0.0)	1.3 (±0.1)	4.2 (±0.7)
0.05	1997	0.6 (±0.2)	1.4 (±0.3)	2.3 (±0.9)
	1998	0.5 (±0.1)	1.4 (±0.3)	4.3 (±0.5)
0.5	1997	1.0 (±0.4)	1.3 (±0.5)	3.9 (±0.7)
	1998	0.6 (±0.1)	1.1 (±0.2)	5.3 (±0.4)

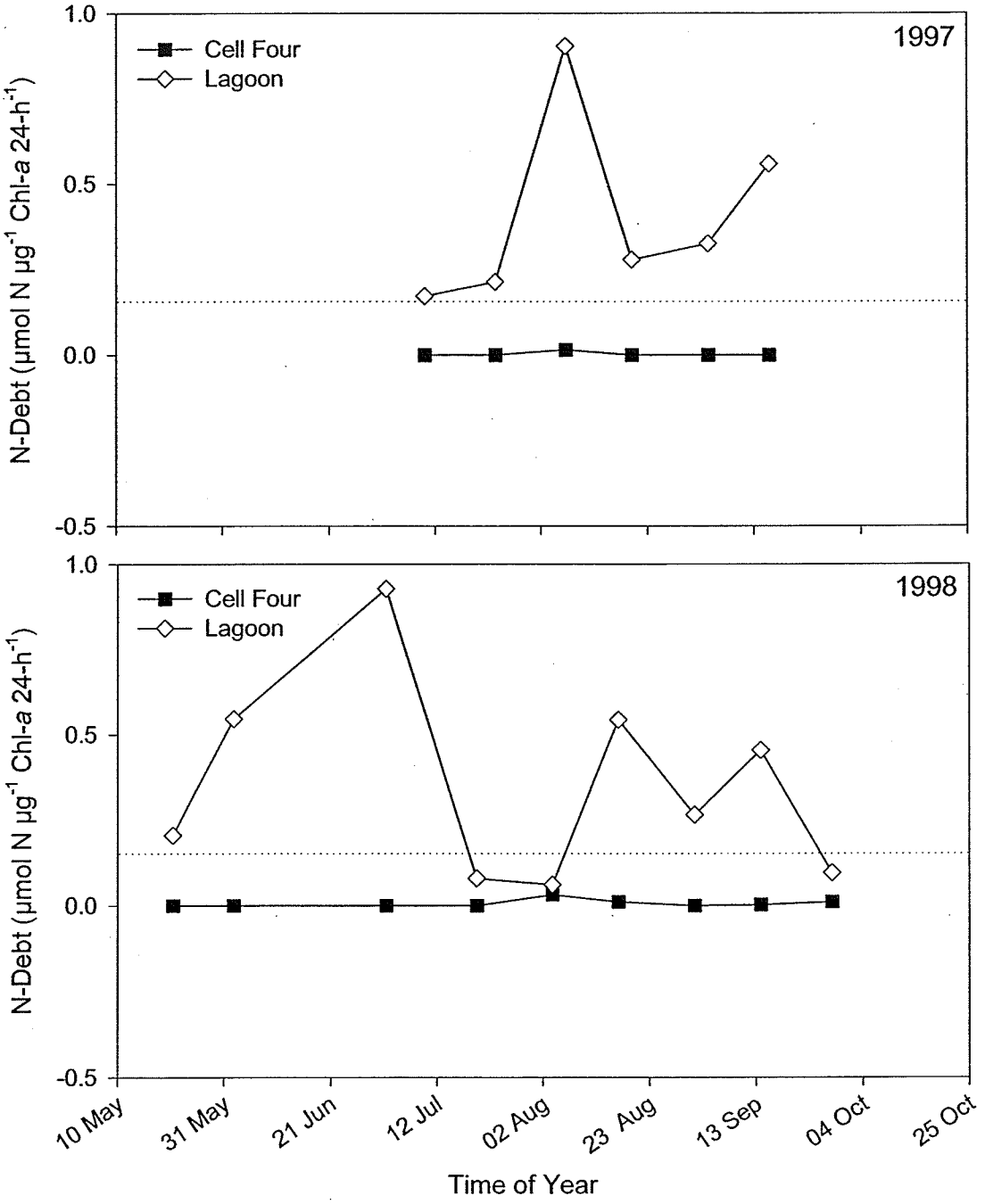

Figure 33. Nitrogen debt as an indicator of phytoplankton nitrogen deficiency in Cell Four of Oak Hammock Marsh and the tertiary sewage lagoon in 1997 and 1998. N-debt values above the dotted line at 0.15 µmol N μg^{-1} Chl-*a* 24-h^{-1} indicate severe N deficiency.

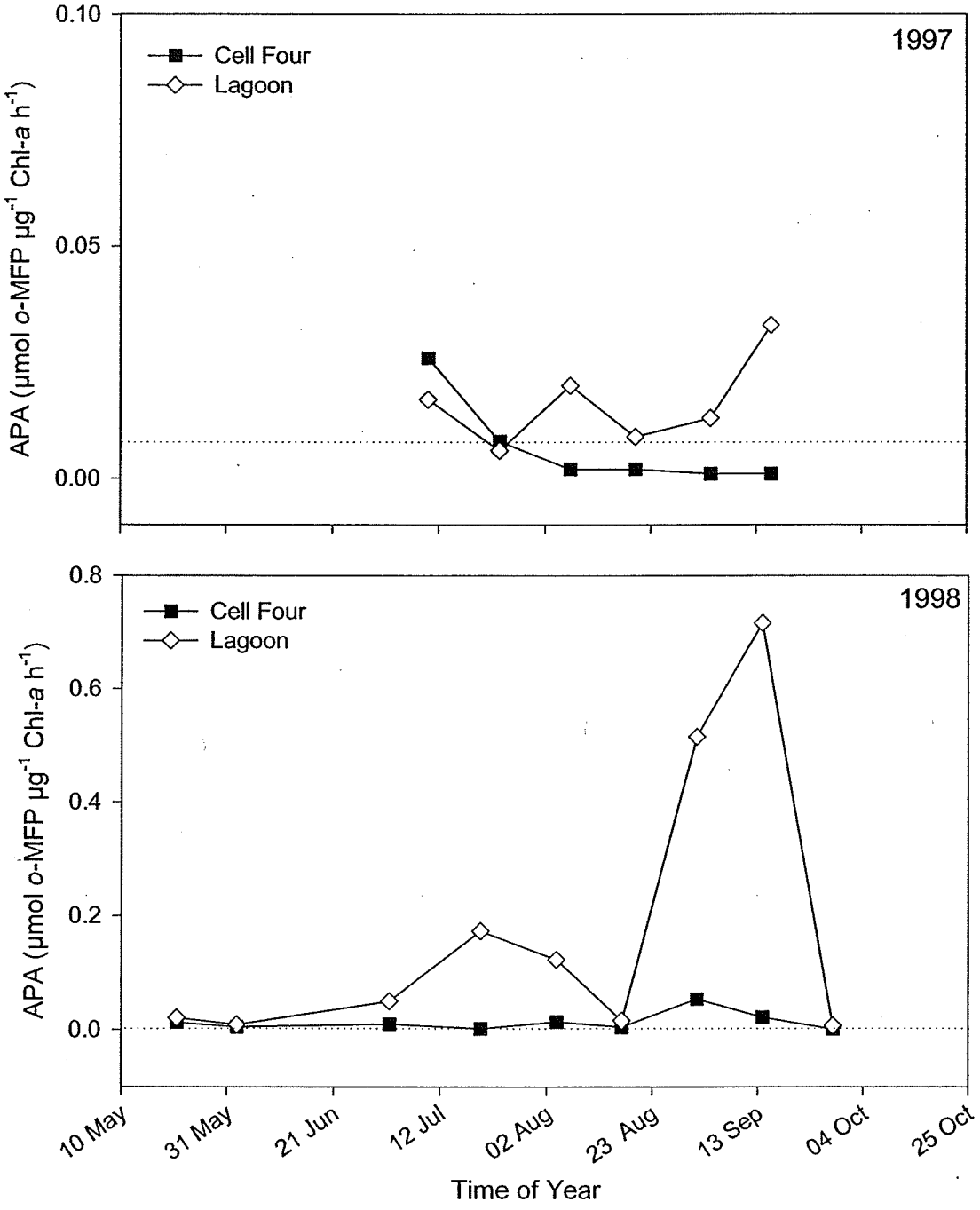

Figure 34. Alkaline phosphatase activity as an indicator of phytoplankton phosphorus deficiency in Cell Four of Oak Hammock Marsh and the tertiary sewage lagoon in 1997 and 1998. APA values above the dotted line at 0.005 µmol *o*-MFP μg^{-1} Chl-*a* h^{-1} indicate severe P deficiency. (Note change in scale of y axis.)

5.1.6 Vegetation cover in Cell Four

Emergent vegetation was dominated by *Typha* X *glauca*, which occurred in the shallowest areas of Cell Four, generally around the periphery of the cell (Figure 35). Duckweed and metaphyton tended to occur within sheltered areas of emergent vegetation, or sometimes associated with patches of submersed vegetation. Metaphyton dominated (90-100% cover) the sheltered areas in spring and early summer, then gradually gave way to duckweed cover, which dominated (90-100% cover) these areas in mid-summer and early fall. Submersed vegetation was confined to deeper areas of the cell that had some shelter from nearby emergent macrophyte stands. Very few submersed macrophytes grew in open areas at the south end of the Cell, which were exposed to the long north to south wind fetch across the Cell.

Part of the area of Cell Four (189.5 ha) was above the level of standing water and was characterized by grasses and shrubs. This area of upland was not included in my study. Of the water-covered area, 47% of Cell Four was unvegetated open water, whereas 53% was vegetated with submerged, emergent, or free-floating macrophytes (Table 16). The spatial distribution of macrophytes within Cell Four did not change significantly from 1997 to 1998. Therefore, I used the vegetation map developed from 1997 aerial photographs to calculate areal abundance in 1998.

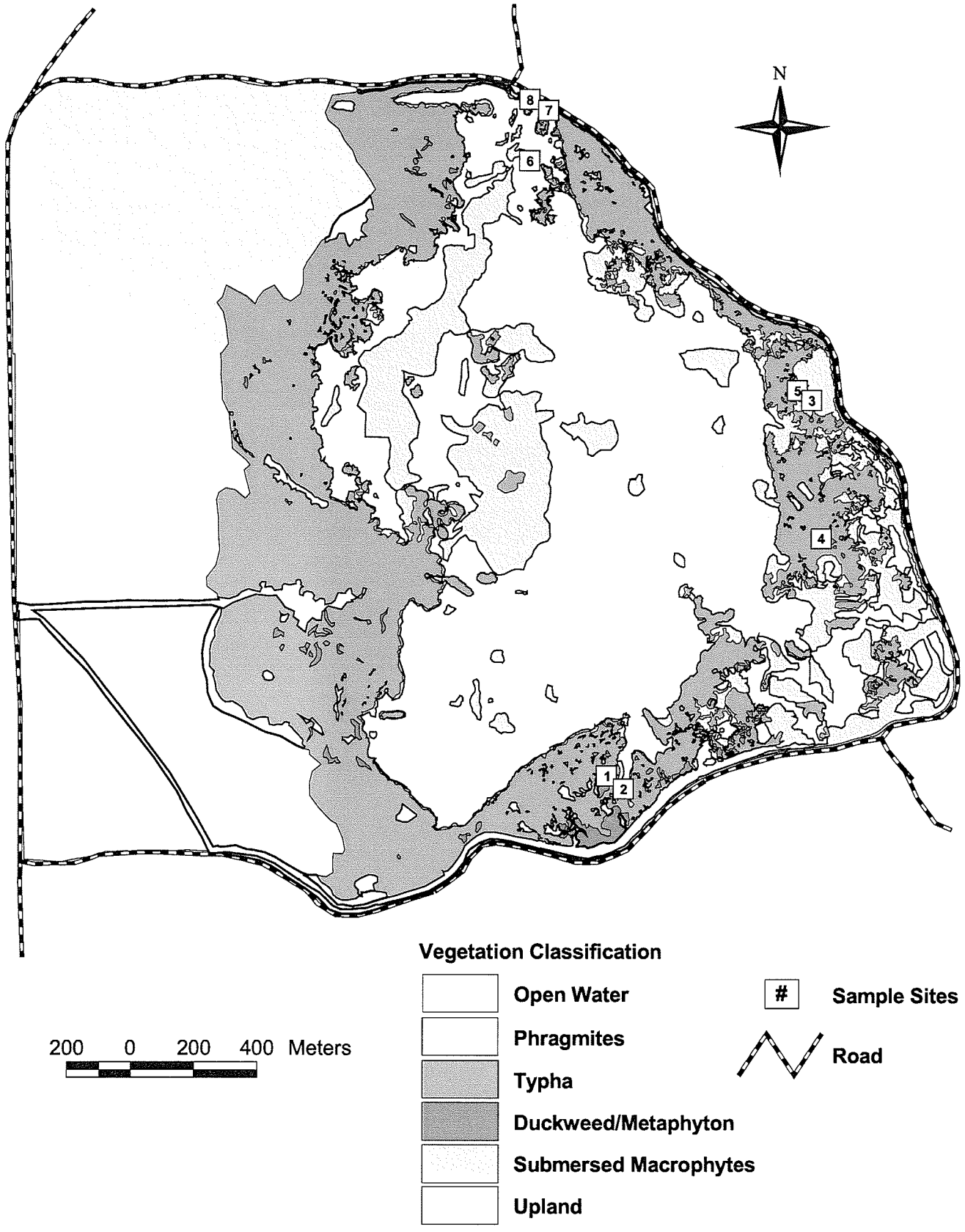

Figure 35. Vegetation map of Cell Four, Oak Hammock Marsh, Manitoba in mid-summer 1997.

Table 16. Area (ha) of each vegetation type in Cell Four of Oak Hammock Marsh in August 1997.

Vegetation Type	Area (ha)	% of Water-Covered Area
Upland	189.5	0
Open Water	193.1	47
Submersed	59.6	15
Duckweed/Metaphyton	5.8	1
Emergent Cattail	140.4	35
Emergent Reed Grass	7.4	2
Total	595.8	100

5.1.7 Algal and macrophyte biomass

Phytoplankton chlorophyll-*a* concentrations were an order of magnitude greater in Cell Four than in the tertiary sewage lagoon in both 1997 and 1998 (Figure 36). There was a significant difference in chlorophyll-*a* concentrations between sites in both years ($F_{(3,6)}$=18.820, p=0.002; $F_{(3,6)}$=12.370, p=0.006). Post-hoc tests revealed that the Lagoon was significantly different than the sites in Cell Four, which were not significantly different from each other. Phytoplankton chlorophyll-*a* concentrations at Open Shallow, Open Deep, and *Typha* Shallow sites ranged from 5 to 150 µg L^{-1} over the course of the season. Phytoplankton chlorophyll-*a* concentrations in the tertiary lagoon were ~5 µg L^{-1} over the entire season in both years. When phytoplankton chlorophyll-*a* was converted to mg Chl-*a* per m^2 of marsh bottom area (Figure 37), the seasonal trends looked slightly different, especially for *Typha* Shallow sites, because of the low volume of water per m^2 in these sites.

Periphyton chlorophyll-*a* was generally higher in Cell Four (mean 3.6 µg cm^{-2}) than in the tertiary sewage lagoon (mean 1.2 µg cm^{-2}); however, there were different trends among sites in Cell Four (Figure 38). In 1997, periphyton in Open Deep sites increased steadily from 3 µg cm^{-2} in mid-August to 16 µg cm^{-2} by mid-October, a trend that was not evident in these sites the following year. Periphyton substrata colonization was not significantly different between sites in 1997 ($F_{(3,5)}$=3.330, p=0.114), probably because of the large within site variability. In 1998, the significant difference between sites ($F_{(3,5)}$=6.000, p=0.041) was attributable to periphyton response at Open Shallow sites, as revealed by post hoc comparisons of least squares means. Periphyton in Open Shallow sites began to increase from 3 µg cm^{-2} in early July to a maximum of 10 µg cm^{-2} in mid to late August, then began to decline steadily through September and October in both years.

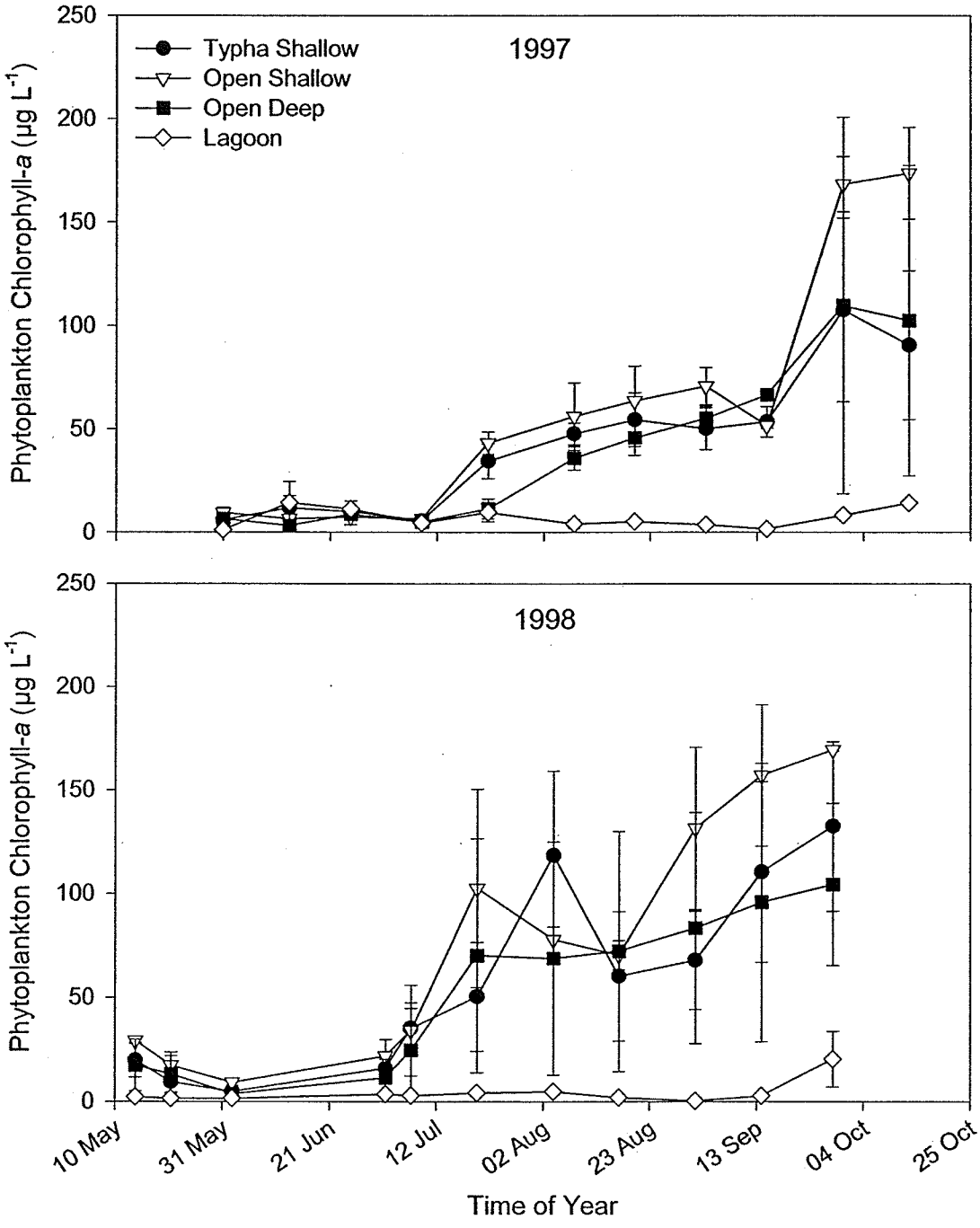

Figure 36. Phytoplankton chlorophyll-*a* (µg L^{-1}, ±SE, n(TS)=4, n=2) in Cell Four of Oak Hammock Marsh and the tertiary sewage lagoon in 1997 and 1998.

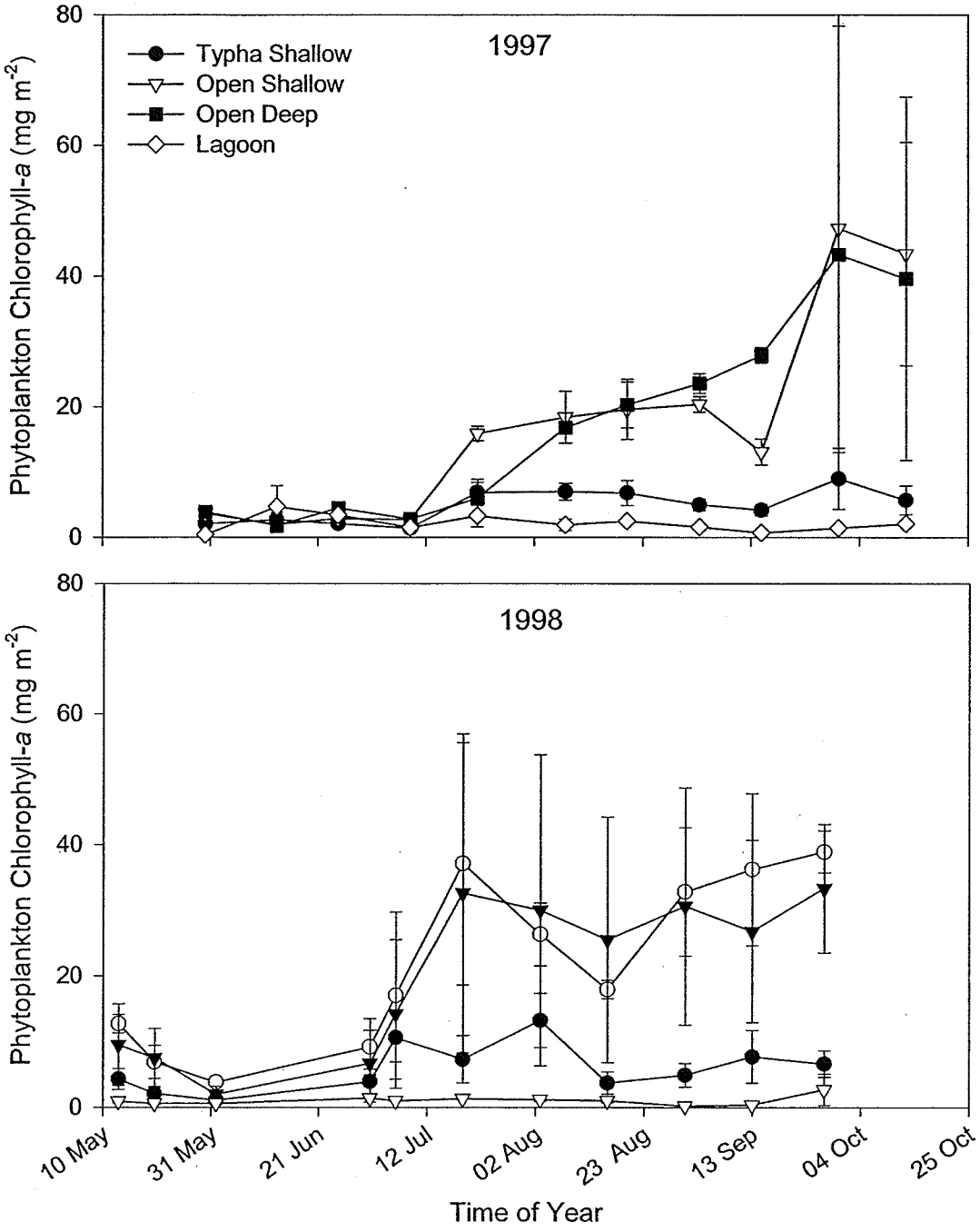

Figure 37. Phytoplankton chlorophyll-*a* (mg m^{-2}, ±SE, n(TS)=4, n=2) in Cell Four of Oak Hammock Marsh and the tertiary sewage lagoon in 1997 and 1998.

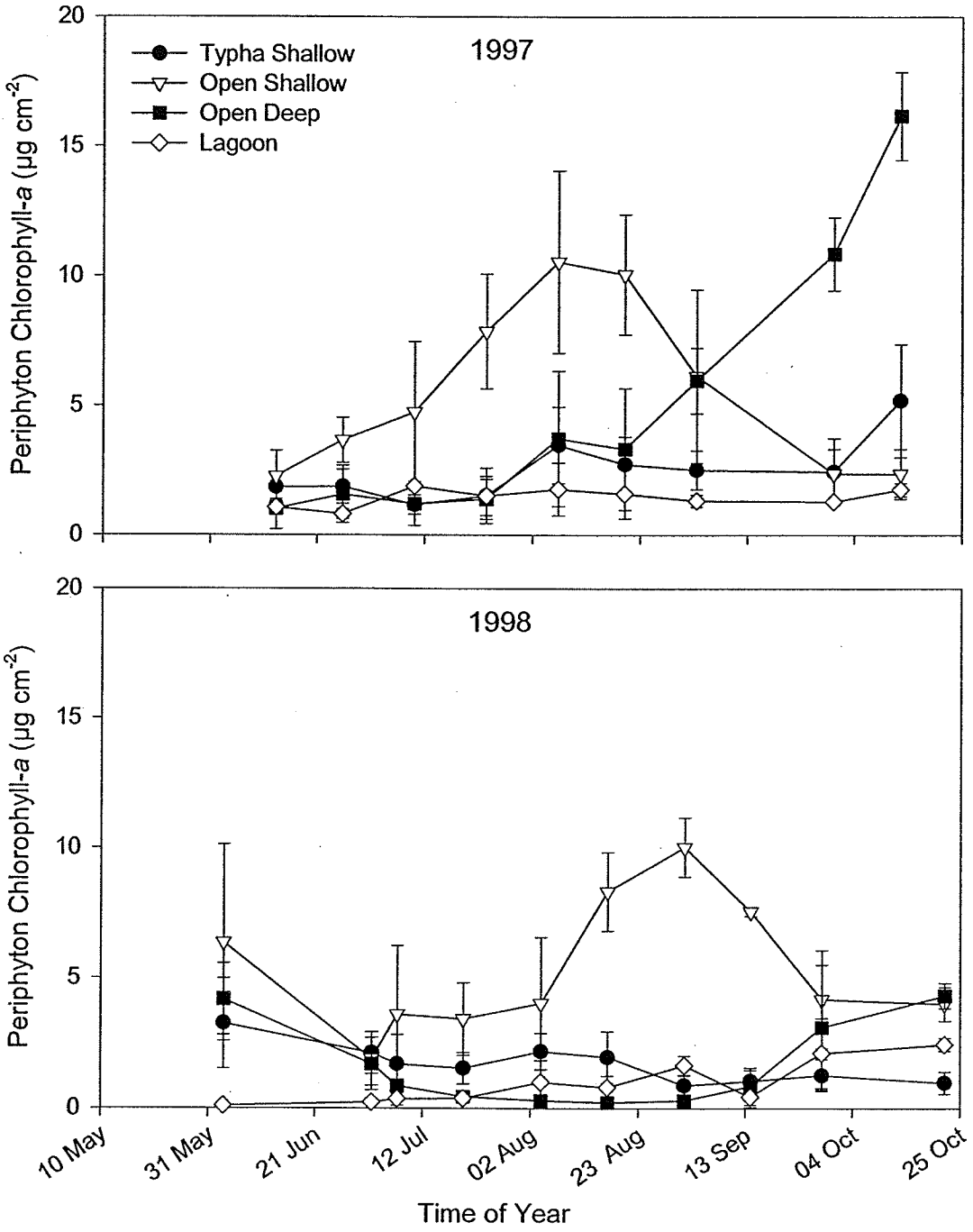

Figure 38. Periphyton chlorophyll-*a* (µg cm^{-2} SE, n(TS)=4, n=2) in Cell Four of Oak Hammock Marsh and the tertiary sewage lagoon in 1997 and 1998.

Epiphyton was expressed as units of chlorophyll-*a* per area of calculated submersed macrophyte plant surface area within one m^2 of marsh bottom area (mg m^{-2}). Because of this relationship with available plant surface area, the absolute abundance of epiphyton was dependent on the abundance of submersed macrophytes within the marsh (Figure 39A). Epiphyton abundance closely followed the increase and subsequent decline of submersed macrophyte biomass at each Open Deep site in 1997 and 1998 (Figures 40 and 41). Epiphyton chlorophyll-*a* from submersed macrophytes was similar at both Open Deep sites in 1997, ranging from 1 mg m^{-2} up to 10 mg m^{-2} by late summer (Figure 40A). Submersed macrophyte peak biomass at Open Deep sites in 1997 was 100 to 140 g dry weight m^{-2} (Figure 40B). In 1998, submersed macrophyte biomass at Site 6 was low (peak at 50 g m^{-2}) compared to biomass at Site 3 (peak at 180 g m^{-2}) (Figure 41B). Consequently, epiphyton chlorophyll-*a* was much lower at Site 6 (<3 mg m^{-2}) than at Site 3 (3 to 14 mg m^{-2}) (Figure 41A).

Periphyton colonization on acrylic rods per unit surface area was not significantly different than epiphyton colonization on submersed macrophytes ($F_{(1,2)}$=6.990, p=0.118) at the same sites in 1997, although periphyton was always higher (mean 2.69 µg cm^{-2}) than epiphyton (mean 0.61 µg cm^{-2}) (Figure 42). The interaction term (measurement type*time) was also not significant ($F_{(4,8)}$=0.62, p=0.6620), suggesting that there was a similar trend between periphyton and epiphyton over time. In 1998, periphyton colonization (0.70 µg cm^{-2}) and epiphyton colonization (0.51 µg cm^{-2}) were not significantly different ($F_{(1,2)}$=0.260, p=660), nor was the interaction (measurement type*time), indicating that periphyton and epiphyton also followed similar growth trends over the time in 1998 (Figure 42).

The absolute abundance of epiphyton on emergent macrophytes per area of marsh bottom was dependent on emergent macrophyte surface area, but the relationship was not a linear increase in epiphyton with increased macrophyte biomass

(Figure 39B). Epiphyton chlorophyll-*a* from *Typha* was highest in June in both 1997 (5.5 mg m^{-2}) and 1998 (3.5 mg m^{-2}) and then dropped off to <1 mg m^{-2} for the remainder of the season (Figure 43A and 44A). Conversely, above-ground *Typha* biomass increased from 200 g m^{-2} in early spring to peak mid-summer biomass of 600 g m^{-2} in 1997 and 800 g m^{-2} in 1998 (Figure 43B and 44B).

Epiphyton colonization of *Typha* stems and periphyton colonization of acrylic rods within *Typha* sites varied significantly with depth in both 1997 and 1998 ($F_{(1,76)}$=23.680, p<0.0001; $F_{(1,76)}$=19.260, p<0.0001). There was consistently higher mean algal chlorophyll on *Typha* stems and acrylic rods 0-10 cm below the water surface, compared to 10-20 cm depth (Table 17). Mean annual periphyton colonization on rods was always significantly greater than mean annual epiphyton colonization on *Typha* stems ($F_{(1,76)}$=15.91, p=0.0002; $F_{(1,76)}$=10.01, p=0.0022) (Table 17). Periphyton colonization on acrylic rods per unit surface area (mean 2.05 µg cm^{-2}) was significantly higher than epiphyton colonization on plants (mean 0.37 µg cm^{-2}) at the same sites in both years ($F_{(1,6)}$=16.21, p=0.007; $F_{(1,6)}$=28.82, p=0.0017) (Figure 45). However, the interaction term (measurement type*time) was not significant in either year ($F_{(5,30)}$=4.34, p=0.143; $F_{(4,24)}$=0.79, p=0.541), indicating that periphyton and epiphyton followed similar growth trends in 1997 and again in 1998 (Figure 45).

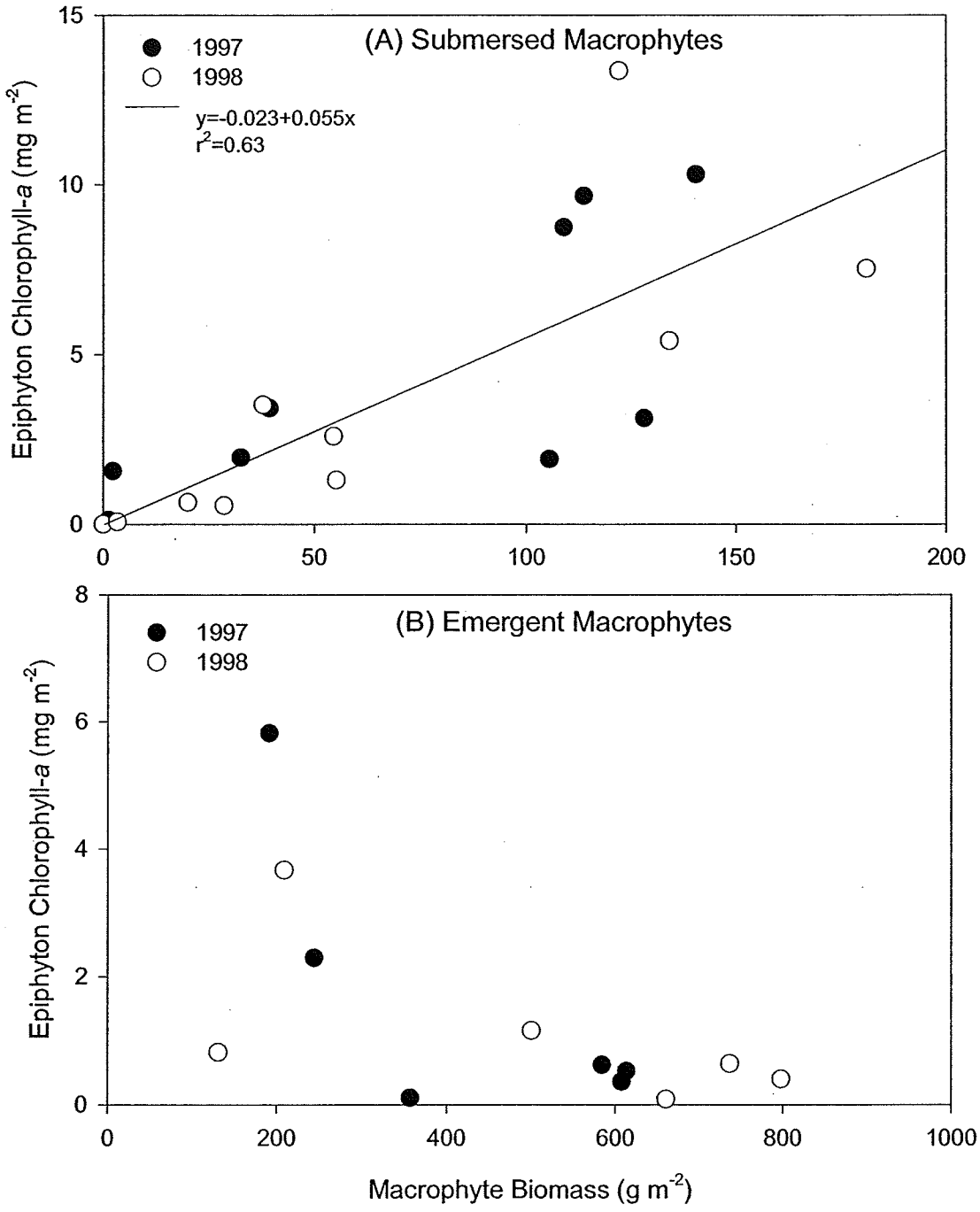

Figure 39. Relationship between (A) submersed macrophytes (g m^{-2}) and epiphyton (mg m^{-2}) and between (B) emergent macrophytes (g m^{-2}) and epiphyton (mg m^{-2}) in Cell Four of Oak Hammock Marsh in 1997 and 1998. (Note changes in scale of x and y axes.)

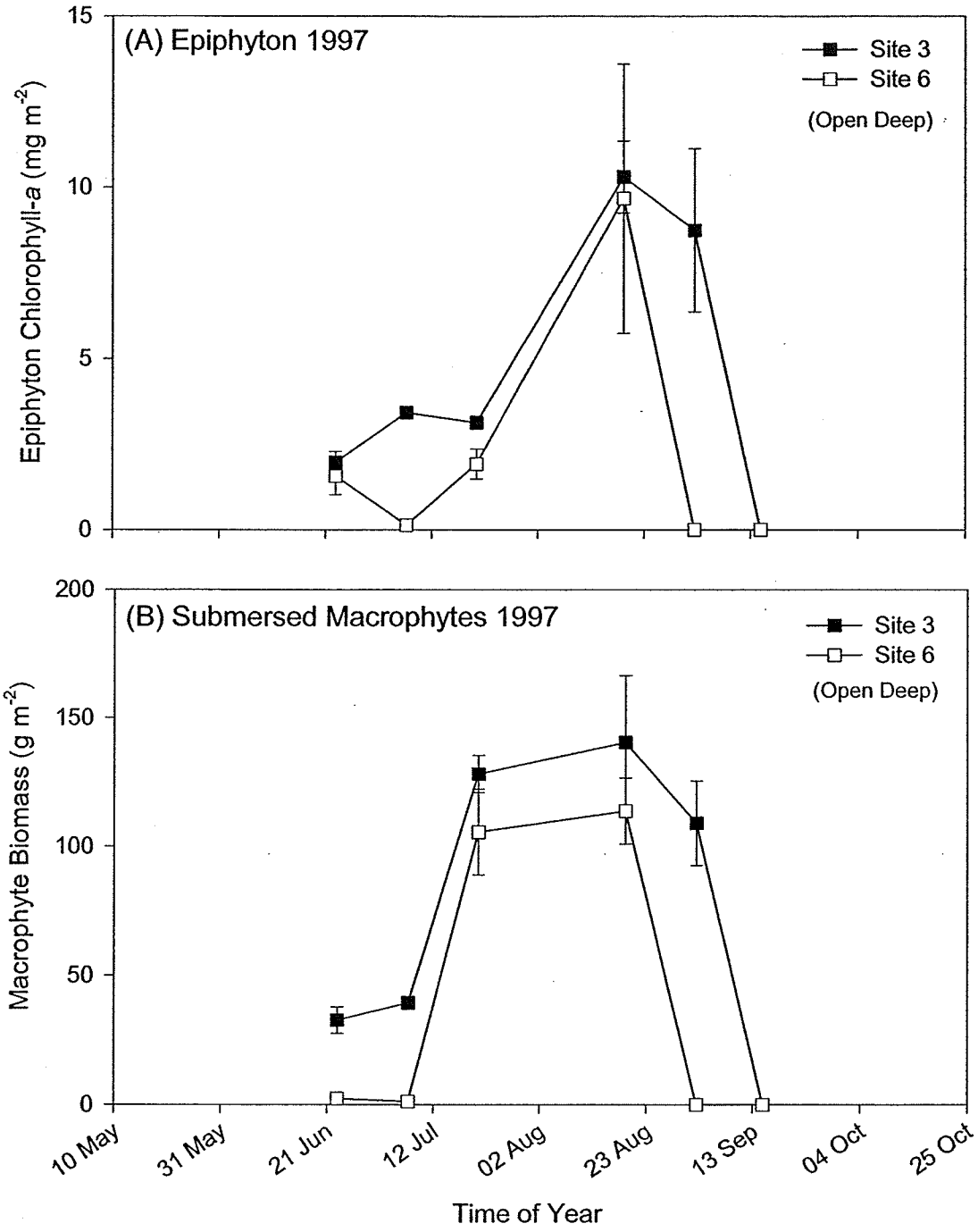

Figure 40. (A) Epiphyton chlorophyll-*a* (mg m^{-2}, ±SE, n=3) and (B) submersed macrophyte biomass (g m^{-2}, ±SE, n=3) from Open Deep sites in Oak Hammock Marsh in 1997.

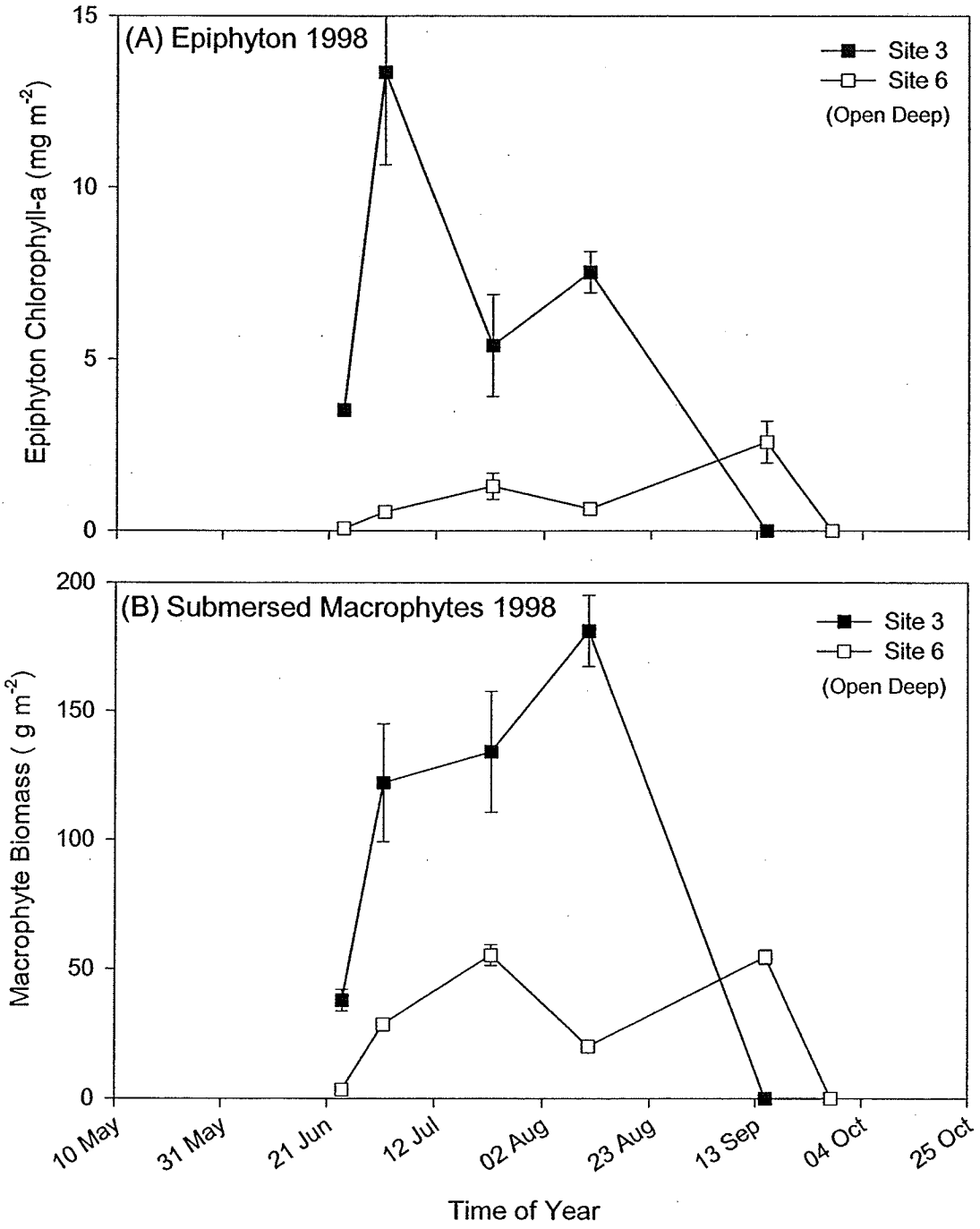

Figure 41. (A) Epiphyton chlorophyll-*a* (mg m^{-2} SE, n=3) and (B) submersed macrophyte biomass (g m^{-2} ±SE, n=3) from Open Deep sites in Oak Hammock Marsh in 1998.

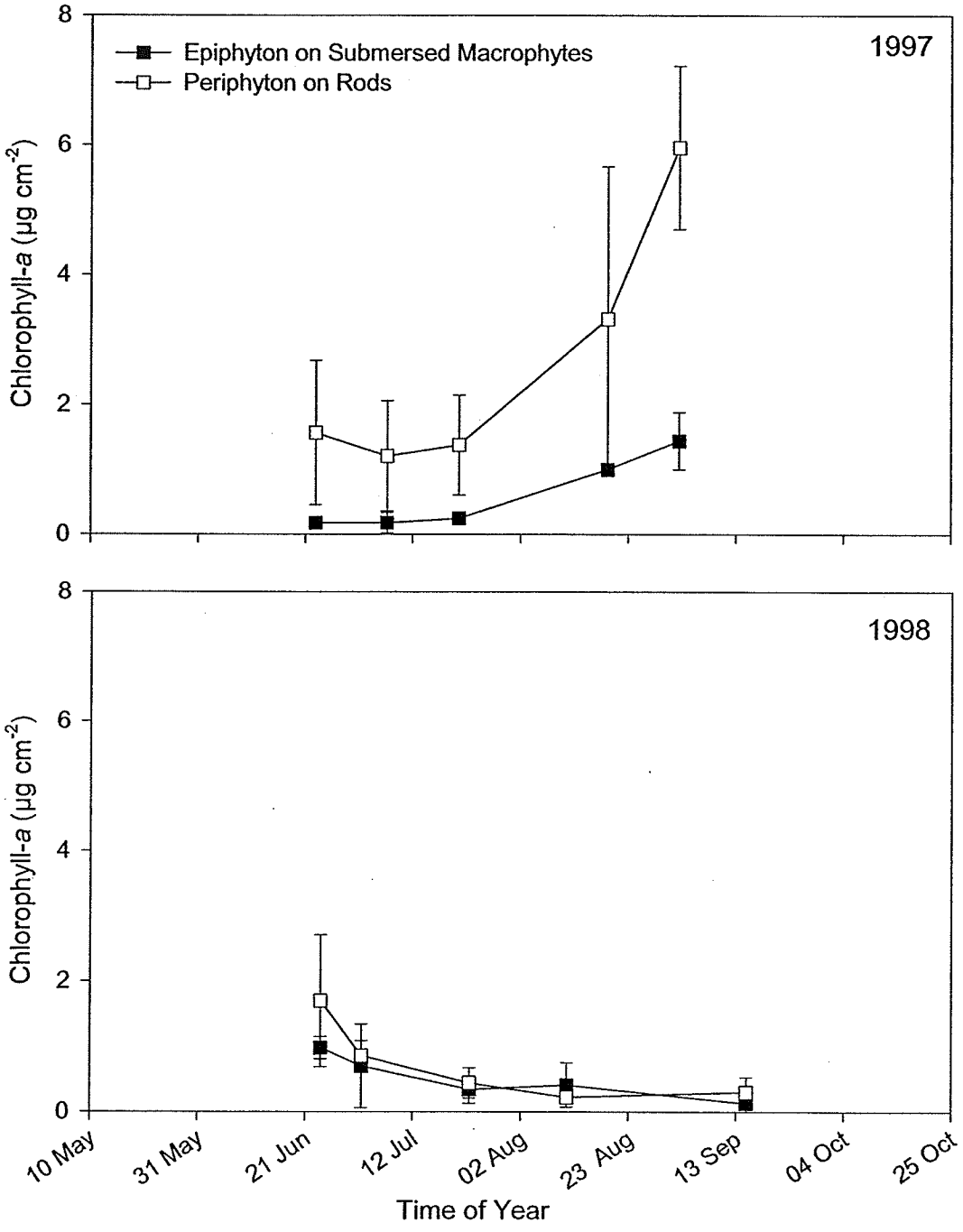

Figure 42. Comparison of epiphyton chlorophyll-*a* (µg cm^{-2} ±SE, n=2) sampled from submersed macrophytes, with periphyton chlorophyll-*a* (µg cm^{-2} ±SE, n=2) sampled from acrylic substrata at Sites 3 and 6 (Open Deep) in 1997 and 1998.

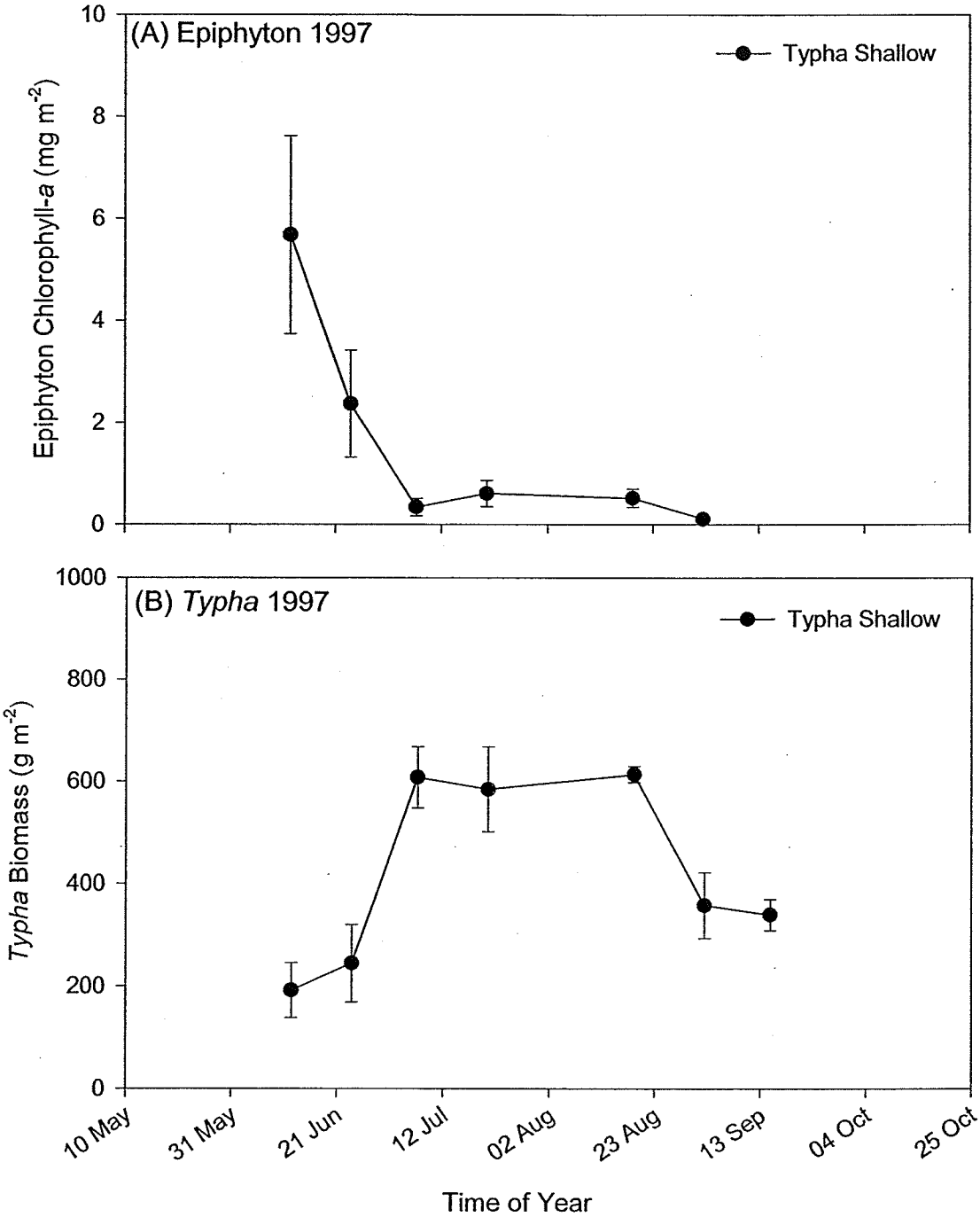

Figure 43. (A) Epiphyton chlorophyll-*a* (mg m^{-2}, ±SE, n=4) and (B) *Typha* biomass (g m^{-2}, ±SE, n=4) from *Typha* Shallow sites in Oak Hammock Marsh in 1997.

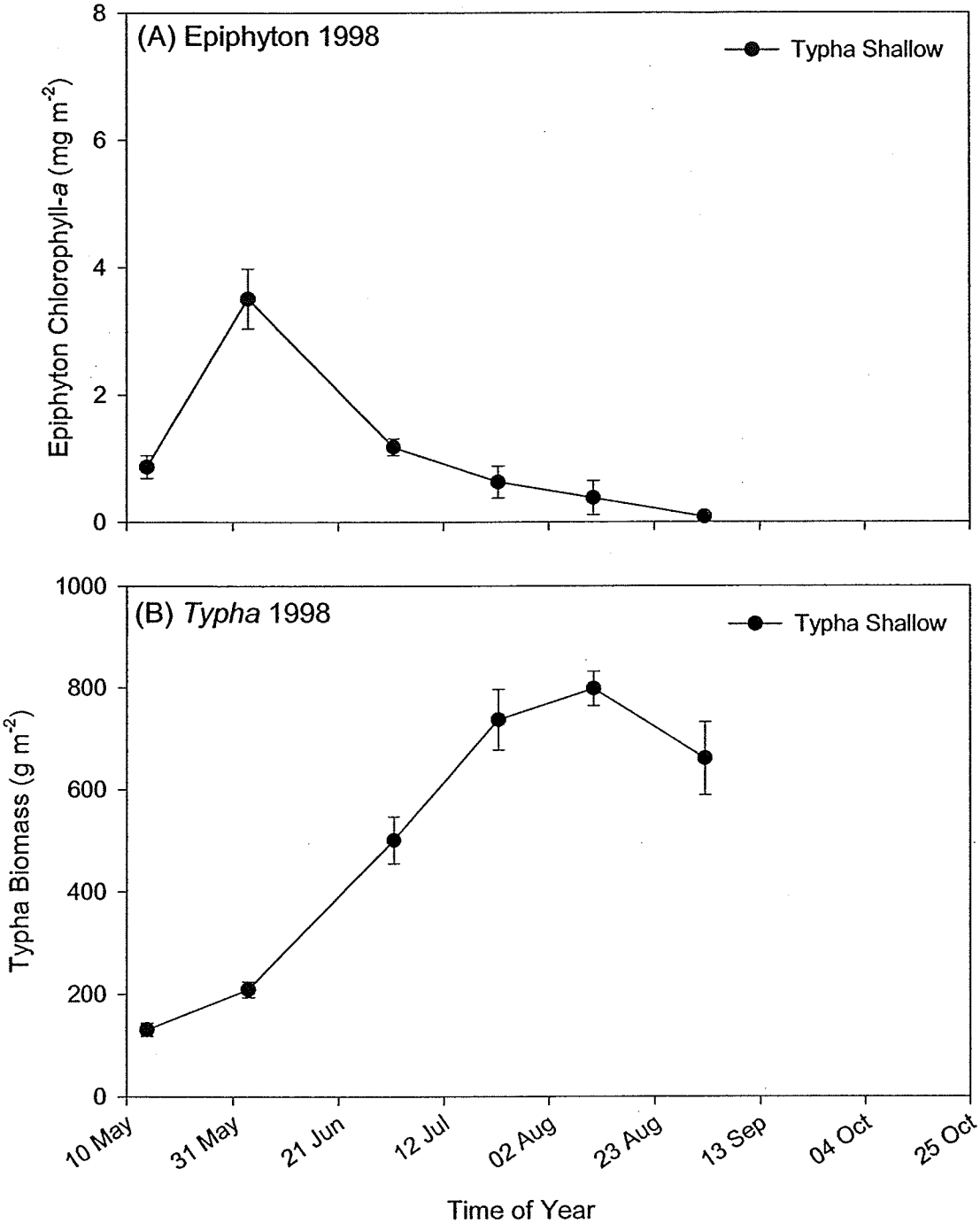

Figure 44. (A) Epiphyton chlorophyll-*a* (mg m^{-2}, ±SE, n=4) and (B) *Typha* biomass (g m^{-2}, ±SE, n=4) from *Typha* Shallow sites in Oak Hammock Marsh in 1998.

Table 17. Mean annual epiphyton (on *Typha*) and periphyton (on rods) colonization (µg cm^{-2}, ±SE, n=7) with depth in Cell Four of Oak Hammock Marsh in 1997 and 1998.

	1997		1998	
Depth (cm)	Epiphyton (µg cm^{-2})	Periphyton (µg cm^{-2})	Epiphyton (µg cm^{-2})	Periphyton (µg cm^{-2})
0 - 10	0.62 ±0.11	3.12 ±0.35	0.47 ±0.06	2.85 ±0.29
10 - 20	0.19 ±0.05	1.22 ±0.19	0.13 ±0.03	0.93 ±0.11

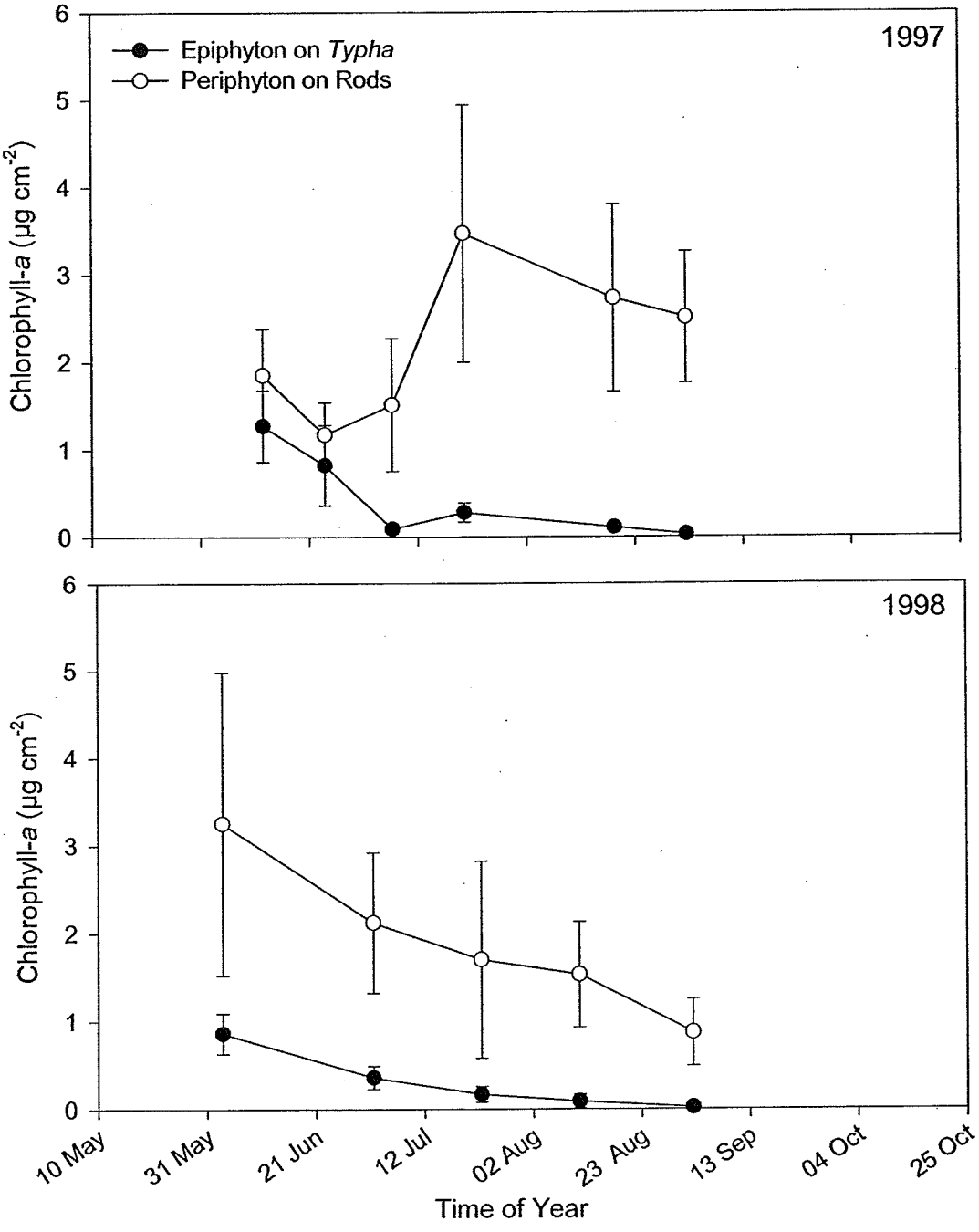

Figure 45. Comparison of epiphyton chlorophyll-*a* (µg cm^{-2} ±SE, n=4) sampled from *Typha* stems, with periphyton chlorophyll-a (µg cm^{-2} ±SE, n=4) sampled from acrylic substrata at Sites 1, 4, 5, and 8 (*Typha* Shallow) in 1997 and 1998.

Metaphyton chlorophyll-*a* was variable at all sites in both years and did not differ significantly between sites ($F_{(3,6)}$=1.21, p=0.383; $F_{(3,4)}$=2.72, p=0.179) (Figure 46). Generally, mean metaphyton chlorophyll-*a* was higher at *Typha* Shallow (204.4 mg m^{-2}) and Open Shallow (255.3 mg m^{-2}) sites than at Open Deep (89.6 mg m^{-2}) or Lagoon (165.7 mg m^{-2}) sites in 1997. The same trend was evident in 1998, with mean metaphyton chlorophyll-*a* higher in *Typha* Shallow (223.6 mg m^{-2}) and Open Shallow (280.8 mg m^{-2}) sites than in Open Deep (124.3 mg m^{-2}) or Lagoon (215.7 mg m^{-2}) sites. In both years, metaphyton in the Lagoon increased through late summer and early fall to its highest levels at that site (Figure 46).

Epipelon chlorophyll-*a* was low at all sites in 1997 (mean 1.3 mg m^{-2}) and in 1998 (mean 1.8 mg m^{-2}) (Figure 47). There was no significant difference in epipelon chlorophyll-*a* between sites in either year ($F_{(2,5)}$=2.30, p=0.1961; $F_{(2,5)}$=1.410, p=0.3272). In early fall, epipelon chlorophyll-*a* at Open Deep sites was lower than at Open Shallow or *Typha* Shallow sites. The same trend was evident in 1998 in early fall, when epipelon chlorophyll-*a* at Open Deep sites was again lower than at Open Shallow or *Typha* Shallow sites.

Plocon chlorophyll-*a* showed similar seasonal trends as epipelon chlorophyll-*a* (Figure 48). Plocon chlorophyll-*a* was higher in 1998 (mean 684 mg m^{-2}) than in 1997 (mean 373 mg m^{-2}), but there was no significant difference ($F_{(1,4)}$=3.200, p=0.146; $F_{(1,7)}$=1.44, p=2.69) in plocon chlorophyll-*a* between sites in 1997 or in 1998.

Duckweed cover was sparse (<10% m^{-2}) in May and June in both years. In July and August each year, duckweed cover ranged from 60-100% m^{-2} in *Typha* Shallow sites. Mean duckweed biomass in 1997 (53 g m^{-2}) and in 1998 (54 g m^{-2}) was similar (Figure 49). As duckweed cover approached 100% in Typha Shallow sites, metaphyton disappeared.

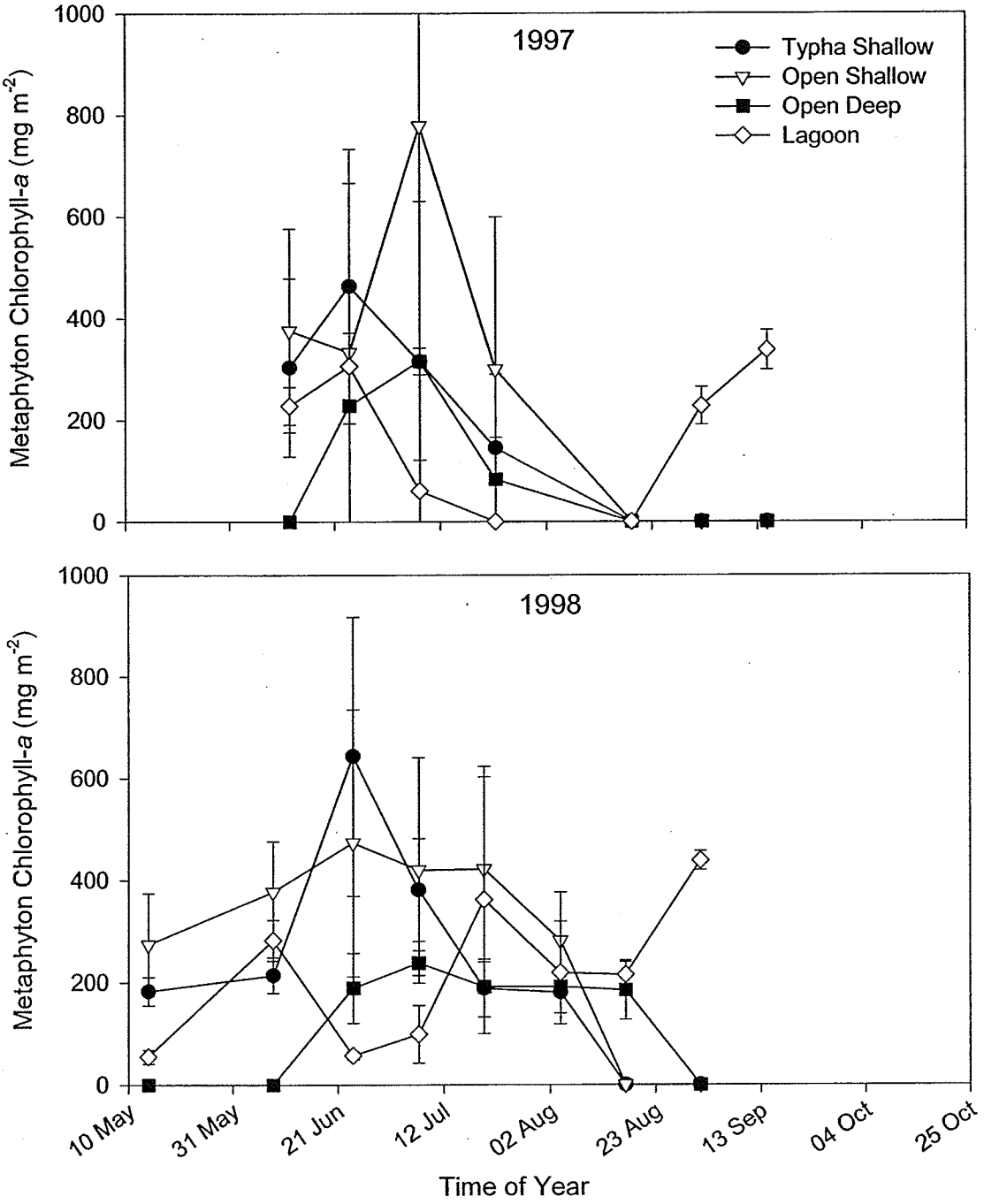

Figure 46. Metaphyton chlorophyll-*a* (mg m^{-2}, ±SE, n(TS)=4, n=2) in Cell Four of Oak Hammock Marsh in 1997 and 1998.

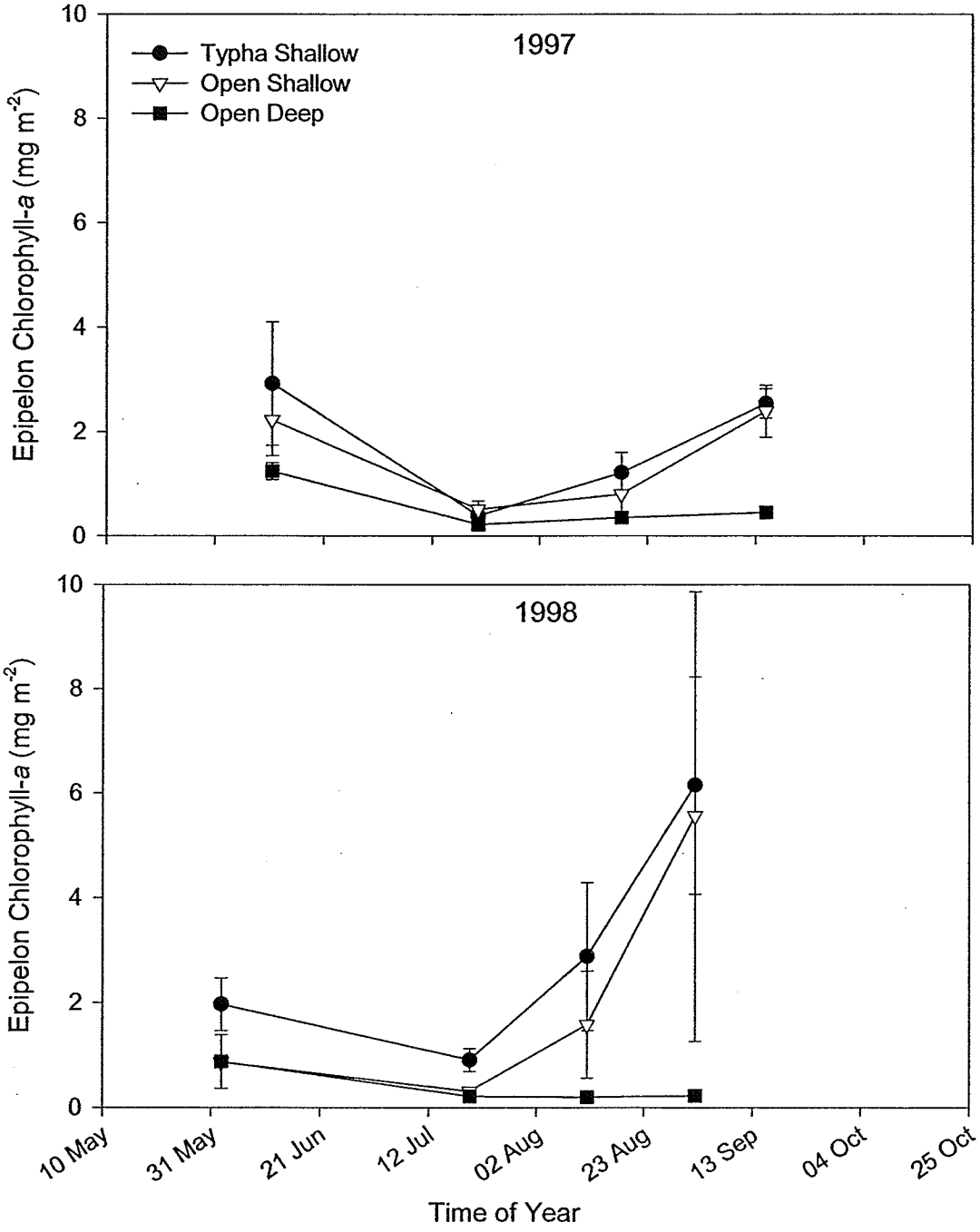

Figure 47. Epipelon chlorophyll-*a* (mg m^{-2}, ±SE, n(TS)=4, n=2) in Cell Four of Oak Hammock Marsh in 1997 and 1998.

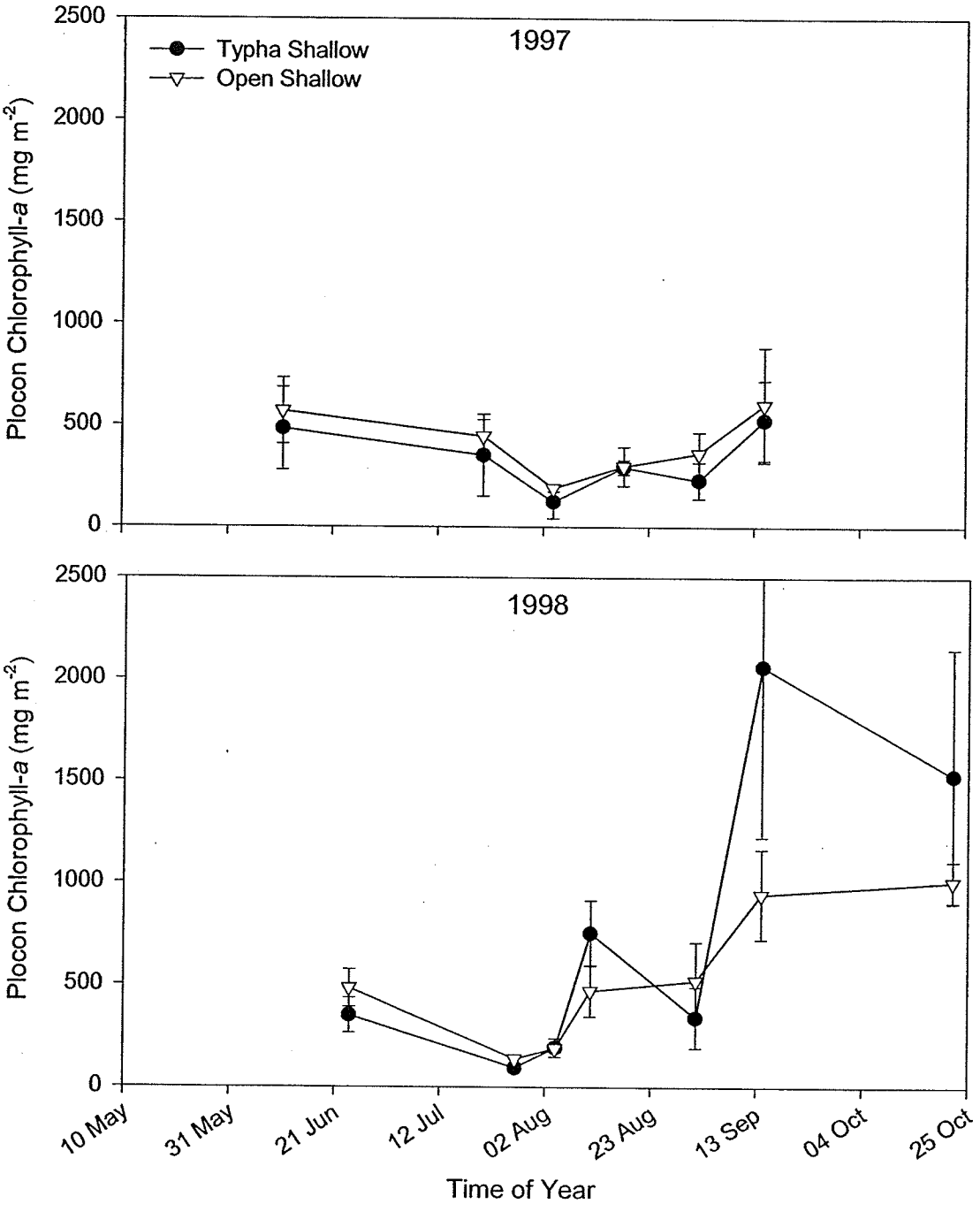

Figure 48. Plocon chlorophyll-*a* (mg m^{-2}, ±SE, n(TS)=4, n=2) in Cell Four of Oak Hammock Marsh in 1997 and 1998.

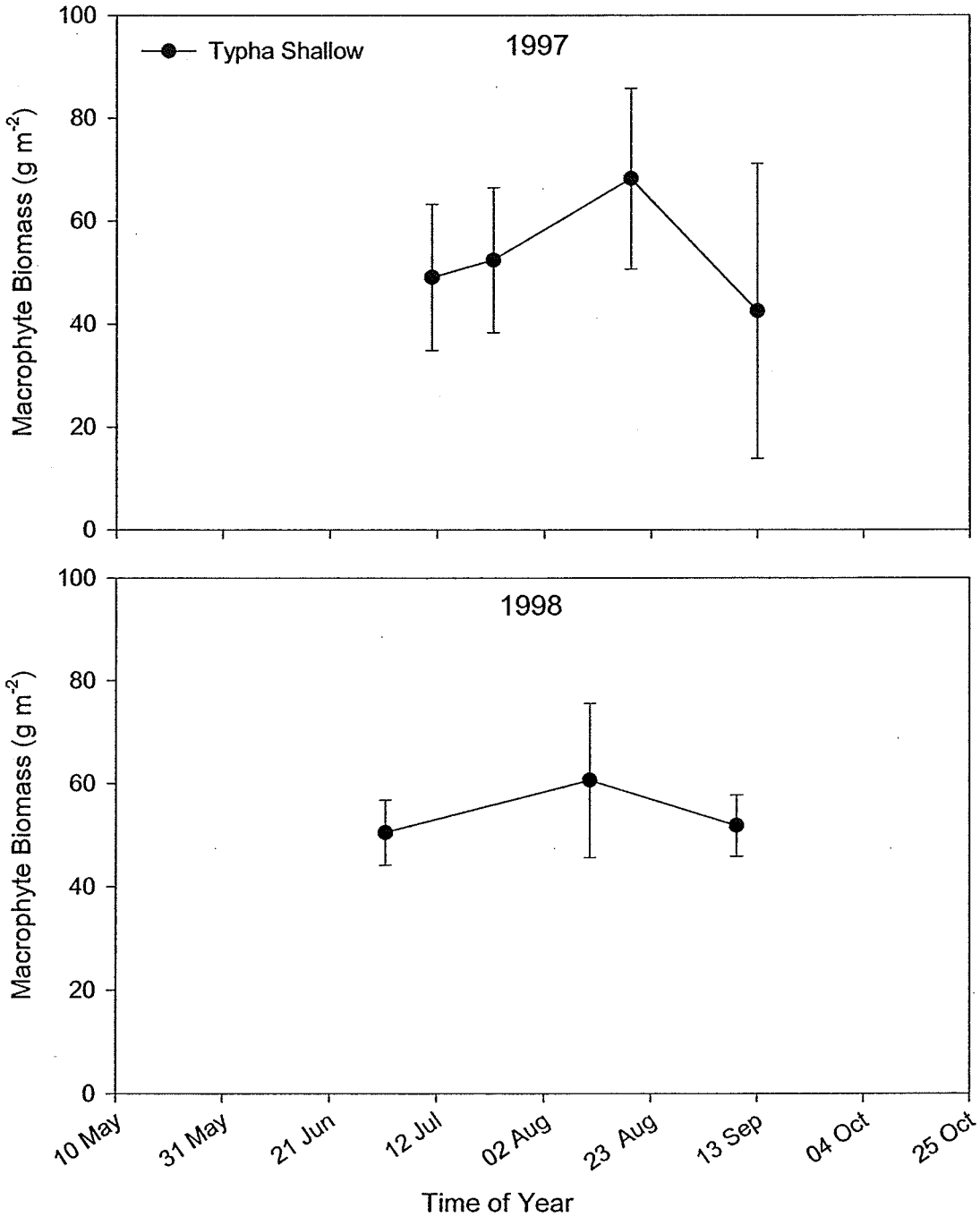

Figure 49. Free-floating macrophyte (duckweed) biomass (g m^{-2}, ±SE, n=4) in Cell Four of Oak Hammock Marsh in 1997 and 1998.

5.1.8 Photosynthesis model development

I found that temperature-specific values for P^B_{max} and constant values for *a* and *ß* were the best parameters to describe my photosynthesis data for phytoplankton, epiphyton and metaphyton (Table 18). A comparison of actual specific photosynthesis (Ps^B) to Ps^B predicted by the calculated parameters demonstrated goodness of fit (Fig. 50), particularly in the upper PAR range where actual and predicted values overlapped. Plots of the residuals were randomly scattered around zero, indicating that the parameter fit was not skewed in any direction. P^B_{max} and *ß* were highly correlated (>0.9) in many of the PE curves, suggesting that there was not much improvement in fit with *ß* once P^B_{max} and *a* were fit to the data. In some curves, *ß* was small and encompassed zero, suggesting that photoinhibition was minor or non-existent. However, there were other curves where *ß* appeared to be important, so I decided to maintain the term in my model. I tried fitting the PE curves using only two parameters (P^B_{max} and *a*) and found that there was no consistent change in the magnitude of P^B_{max} or in the fit of predicted Ps^B versus actual Ps^B values.

The temperature-specific model for phytoplankton fit the data significantly better than the constant model ($F_{(6,164)}$=111.03, $p<0.0001$), but was not significantly different than the sample-specific model ($F_{(51,113)}$=1.25, $p=0.1648$). Therefore, I chose the temperature-specific model as the most parsimonious model for my data set. Within the temperature-specific model, the confidence intervals for 7° and 14° overlapped, suggesting that these two temperatures could be grouped within one P^B_{max} parameter. This lack of separation between 7° and 14° may be a real physiological phenomenon, or it may be the result of the low number of replicates (n=4) for the 7°C curves. However, P^B_{max} at 7°C was consistently lower than at 14°C, so I decided to include the lower 7°C parameter for P^B_{max} in my model. Water temperatures in the marsh are 7°C or lower for a

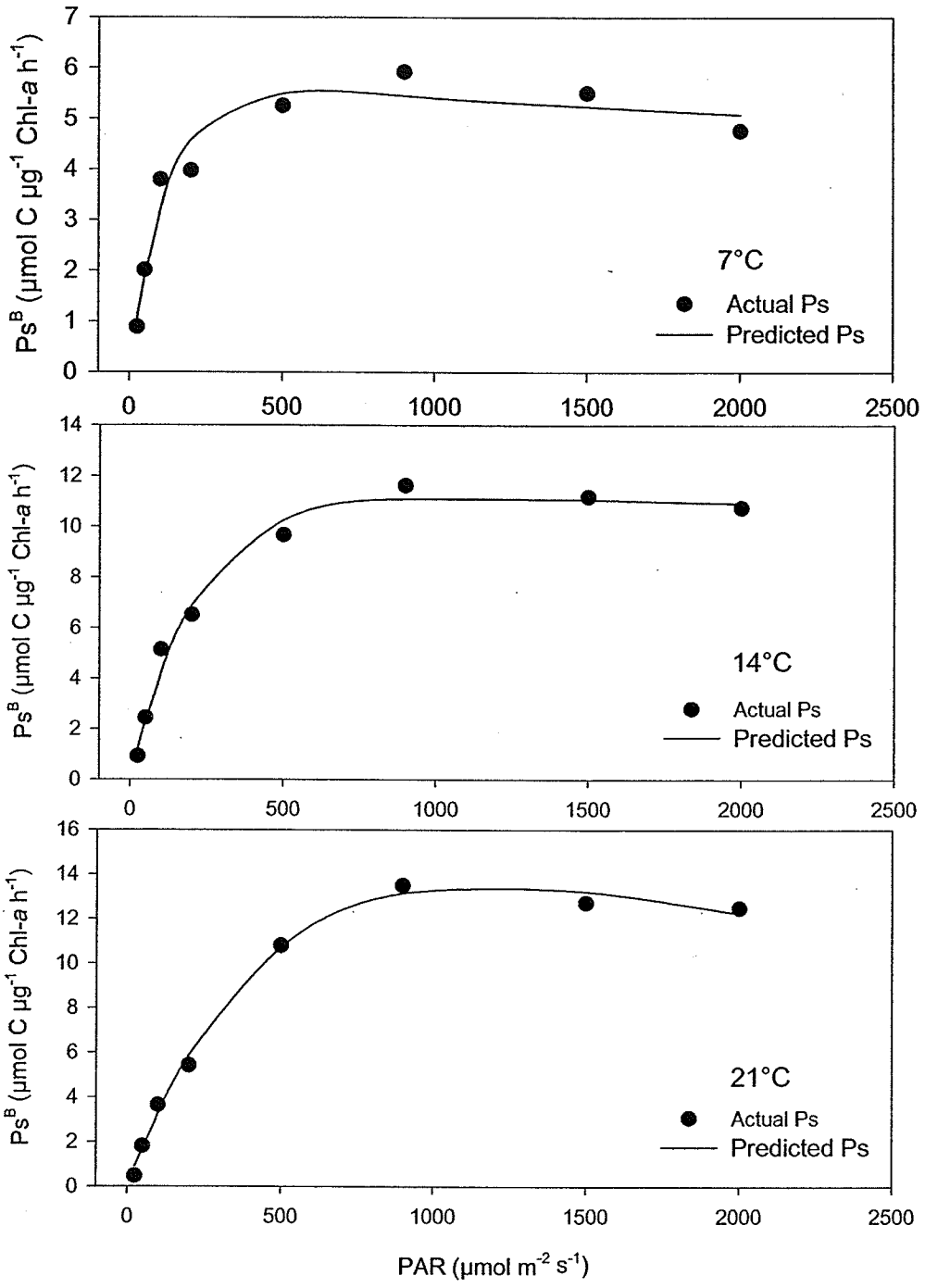

Figure 50. Actual versus predicted specific photosynthesis (Ps^B) model fit at 7°, 14°, and 21°C for phytoplankton P*E* curves used to calculate photosynthetic parameters. (Note change in scale of y axis.)

significant portion of the year, and using a higher P^B_{max} value for this time period might substantially over-estimate annual photosynthesis. The confidence intervals for both *a* and ß encompassed zero as a plausible value, whereas those for P^B_{max} did not, suggesting that P^B_{max} was the major parameter that varied with temperature. There is a strong physiological basis for temperature variability in P^B_{max}, but not in *a* or ß. Therefore, I chose to use temperature-specific values for P^B_{max}, and constant values for *a* and ß in my phytoplankton photosynthesis model (Table 18).

The temperature-specific model for periphyton was a significantly better fit than the constant model ($F_{(4,163)}$=72.93, p=0.0000), and the sample-specific model was a significantly better fit than the temperature-specific model ($F_{(35,128)}$=6.54, p<0.0001). Because the amount of additional information gained by using the sample-specific model was small (F=6.54), compared to the increased complexity of model construction using individual parameters, I chose the temperature-specific model for best fit with reasonable simplicity of application. As with phytoplankton, the periphyton model confidence intervals for *a* and ß encompassed zero, whereas those for P^B_{max} did not. Therefore, I used temperature-specific values for P^B_{max}, and constant values for *a* and ß in the periphyton photosynthesis model (Table 18).

The temperature-specific model for metaphyton was a significantly better fit than the constant model ($F_{(3,26)}$=30.43, p<0.0001), but was not different than the sample-specific model ($F_{(6,20)}$=1.22, p=0.3372). Even though there were a small number of replicates (n=4) for each temperature, there was no overlap in the confidence intervals for 14 and 21°C. Therefore, I used the temperature-specific model for my dataset. As with phytoplankton and periphyton, I used temperature-specific values for P^B_{max}, and constant values for *a* and ß in the metaphyton photosynthesis model (Table 18).

Table 18. Specific parameters of the carbon assimilation/irradiance relationships of the three algal assemblages in Oak Hammock Marsh (± SE; range in brackets). *a* = slope of light-limited specific photosynthesis (efficiency) (µg C µg^{-1} Chl-a h^{-1} µmol^{-1} m^{-2} s^{-1}); ß = slope of inhibition (units as for *a*); P^B_{max} = light-saturated specific photosynthetic rate (µg C µg^{-1} Chl-a h^{-1}); E_k = irradiance at the onset of P^B_{max} (P^B_{max}/ *a*) (µmol m^{-2} s^{-1}); n = number of individual determinations on which parameters were derived. Specific parameters for epipelon are from Robinson *et al.* (1997).

Algal Assemblage	P^B_{max}	*a*	ß	E_K
Phytoplankton 7° (n=4)	5.43 ± 0.18 (5.10-5.77)	0.048 ± 0.003 (0.032-0.084)	0.0008 ± 0.0003 (-0.0007-0.0048)	113 ± 4
Phytoplankton 14° (n=10)	10.43 ± 0.30 (8.99-11.91)	(n=20)	(n=20)	216 ± 6
Phytoplankton 21° (n=6)	16.30 ± 0.86 (14.62-20.23)			338 ± 18
Epiphyton 7° (n=4)	1.17 ± 0.14 (0.89-1.33)	0.025 ± 0.002 (0.006-0.047)	-0.0001 ± 0.0001 (-0.0008-0.0014)	48 ± 6
Epiphyton 14° (n=9)	1.61 ± 0.06 (1.32-1.89)	(n=20)	(n=20)	66 ± 2
Epiphyton 21° (n=7)	4.01 ± 0.81 (2.25-8.37)			163 ± 33
Metaphyton 14° (n=4)	1.27 ± 0.03 (1.24-1.29)	0.015 ± 0.001 (0.013-0.017)	-0.0003 ± 0.0002 (-0.0001- -0.0006)	84 ± 2
Metaphyton 21° (n=4)	1.73 ± 0.43 (1.31-2.16)	(n=8)	(n=8)	115 ± 23
Epipelon (Robinson *et al.* 1997a)	2.30 ±0.30	0.006 ± <0.001	0.00005±0.00014	383 ± 75

5.1.9 Photosynthesis - irradiance relationships

Of the algal assemblages I measured, phytoplankton had the highest photosynthetic efficiency (*a* = 0.0482) and the highest maximum photosynthetic rates (P^B_{max} = 5.43 to 16.30) (Table 18). Metaphyton had the lowest photosynthetic efficiency (*a* = 0.0151) and the lowest maximum photosynthetic rates (P^B_{max} = 1.27 to 1.73), and epiphyton was intermediate (*a* = 0.0246; P^B_{max} = 1.17 to 4.01). The point of onset of light-saturated photosynthesis (E_k) was lower for epiphyton (48-163 µmole m^{-2} s^{-1}) and metaphyton (84-115 µmole m^{-2} s^{-1}) than for phytoplankton (113-338 µmole m^{-2} s^{-1}) (Table 18). I used the epipelon parameters calculated by Robinson *et al.* (1997) because they were within the same order of magnitude as my parameters and they were also calculated for wetland algae from a nearby wetland, Delta Marsh.

Multiple linear regressions between photosynthetic parameters and environmental variables such as chlorophyll, ambient water temperature, average daily wind speed, maximum daily PAR, and water column nutrient concentrations (TRP and DIN) indicated some possible bases for variation in P_{max} and *a*. The ß parameters for phytoplankton, epiphyton and metaphyton were not well correlated with any of the environmental variables (r^2=0.00-0.296, p>0.05). The variation in *a* parameters for phytoplankton was accounted for by maximum daily PAR (58-77%) and chlorophyll-*a* (10%) (Table 19). Chlorophyll-*a* (19-37%) and water column TRP (28%) accounted for some of the variation in *a* parameters for epiphyton. Most of the variation in *a* parameters for metaphyton was accounted for by chlorophyll-*a* (99%) and water column TRP (98%). Chlorophyll-*a* (80-85%), maximum daily PAR (11%) and average daily wind speed (6%) accounted for some of the variation in P_{max} parameters for phytoplankton (Table 19). Variation in P_{max} parameters for epiphyton was accounted for by water column TRP (62%), chlorophyll-*a* (36%), and maximum daily PAR (18-34%). Variation in P_{max} parameters for metaphyton was accounted for by ambient water temperature (87-97%).

Table 19. Variation in photosynthetic parameters (P_{max}, *a*, ß) correlated with variation in environmental variables as identified by forward stepwise multiple regression. (Alpha set at 0.150 to accept or remove variables from regression.)

Assemblage	Parameter	Variable (step)	r^2	p value
Phytoplankton	P_{max} (1997)	Chl-*a* (1)	0.803	0.000
		Wind (2)	0.864	0.119
	P_{max} (1998)	Chl-*a* (1)	0.850	0.000
		PAR (2)	0.958	0.004
Epiphyton	P_{max} (1997)	TRP (1)	0.621	0.018
		PAR (2)	0.805	0.025
	P_{max} (1998)	Chl-*a* (1)	0.360	0.008
		PAR (2)	0.702	0.016
Metaphyton	P_{max} (1997)	Water Temp (1)	0.871	0.067
	P_{max} (1998)	Water Temp (1)	0.972	0.014
Phytoplankton	*a* (1997)	PAR (1)	0.774	0.017
		Chl-*a* (2)	0.875	0.049
	a (1998)	PAR (1)	0.578	0.011
Epiphyton	*a* (1997)	Chl-*a* (1)	0.369	0.005
		Water Temp (2)	0.740	0.010
	a (1998)	TRP (1)	0.282	0.062
		Chl-*a* (2)	0.465	0.136
Metaphyton	*a* (1997)	Chl-*a* (1)	0.993	0.003
	a (1998)	TRP (1)	0.978	0.011
Phytoplankton	ß	-	0	-
Epiphyton	ß (1997)	-	0	-
	ß (1998)	PAR (1)	0.296	0.083
Metaphyton	ß	-	0	-

5.1.10 Photosynthesis experiments

Measurements of dawn to dusk *in situ* photosynthesis provided a test of model predictions of daily photosynthesis. *In situ* phytoplankton specific photosynthesis (Ps^B) was not significantly different ($F_{(1,4)}$=1.047, p=0.364; $F_{(1,4)}$=0.008, p=0.932) than modeled specific photosynthesis in 1997 and 1998 (Table 20.) *In situ* periphyton Ps^B was not significantly different ($F_{(1,4)}$=0.019, p=0.934; $F_{(1,4)}$=0.748, p=0.436) than modeled Ps^B in 1997 and 1998 (Table 20). The model was least successful at predicting actual Ps^B for both phytoplankton and periphyton late in the season in both years.

Table 20. Comparison of model predictions of total daily chlorophyll-specific photosynthesis with measurements of dawn to dusk *in situ* specific photosynthesis in Cell Four of Oak Hammock Marsh in 1997 and 1998.

Date	Phytoplankton ($\mu g\ C\ \mu g^{-1}$ Chl-*a* $L^{-1}\ d^{-1}$)		Epiphyton ($\mu g\ C\ \mu g^{-1}$ Chl-*a* $cm^{-2}\ d^{-1}$)	
1997	Model	*In Situ*	Model	*In Situ*
11 July	366	441	393	224
20 August	689	722	277	245
15 September	543	1033	210	434
1998	Model	*In Situ*	Model	*In Situ*
8 June	313	243	298	576
27 July	481	437	118	80
15 September	643	809	431	779

5.1.11 Algal primary productivity

Maximum daily productivity occurred in July-August in both 1997 and 1998 for phytoplankton, epiphyton, and metaphyton (Figures 51 and 52). For epipelon and plocon, July-August was a time of lower daily productivity, with maximum daily productivity occurring in June (1997) or in September (1998) (Figure 52).

Phytoplankton daily productivity followed similar trends in both years (Figure 51), but mean daily productivity was higher in 1998 (1788 mg C m^{-2}) than in 1997 (1048 mg C m^{-2}) (Table 21). Conversely, epiphyton mean daily productivity was higher in 1997 (1447 mg C m^{-2}) than in 1998 (868 mg C m^{-2}) (Figure 51 and Table 21). Metaphyton daily productivity followed a similar trend from year to year (Figure 52), with higher mean daily productivity in 1998 (2794 mg C m^{-2}) than in 1997 (1411 mg C m^{-2}) (Table 21). Plocon mean daily productivity was higher in 1997 (2096 mg C m^{-2}) than in 1998 (1823 mg C m^{-2}), whereas epipelon mean daily productivity was higher in 1998 (12 mg C m^{-2}) than in 1997 (9 mg C m^{-2}) (Table 21). Plocon daily productivity was at least an order of magnitude larger than epipelon productivity, but both algal assemblages followed similar seasonal trends in 1997 and 1998 (Figure 52).

Possible control of daily algal productivity was explored using multiple linear regressions to relate variability of environmental parameters such as maximum daily PAR, chlorophyll-*a*, ambient water temperature, average daily wind speed, water column nutrient concentrations (TRP and DIN), and indicators of nutrient limitation (N Debt and APA) to variability in algal productivity. Variation in phytoplankton productivity in 1997 and 1998 was accounted for mainly by chlorophyll-*a* (91-92%) and ambient water temperature (6-7%) (Table 22). PAR (1.6%) and APA (0.4%) were also minor factors in the 1997 phytoplankton regression. Epiphyton productivity was correlated with different environmental variables in each year (Table 22), but chlorophyll-*a* (24-54%), ambient water temperature (3-22%), and water column TRP (4-16%) were important to a

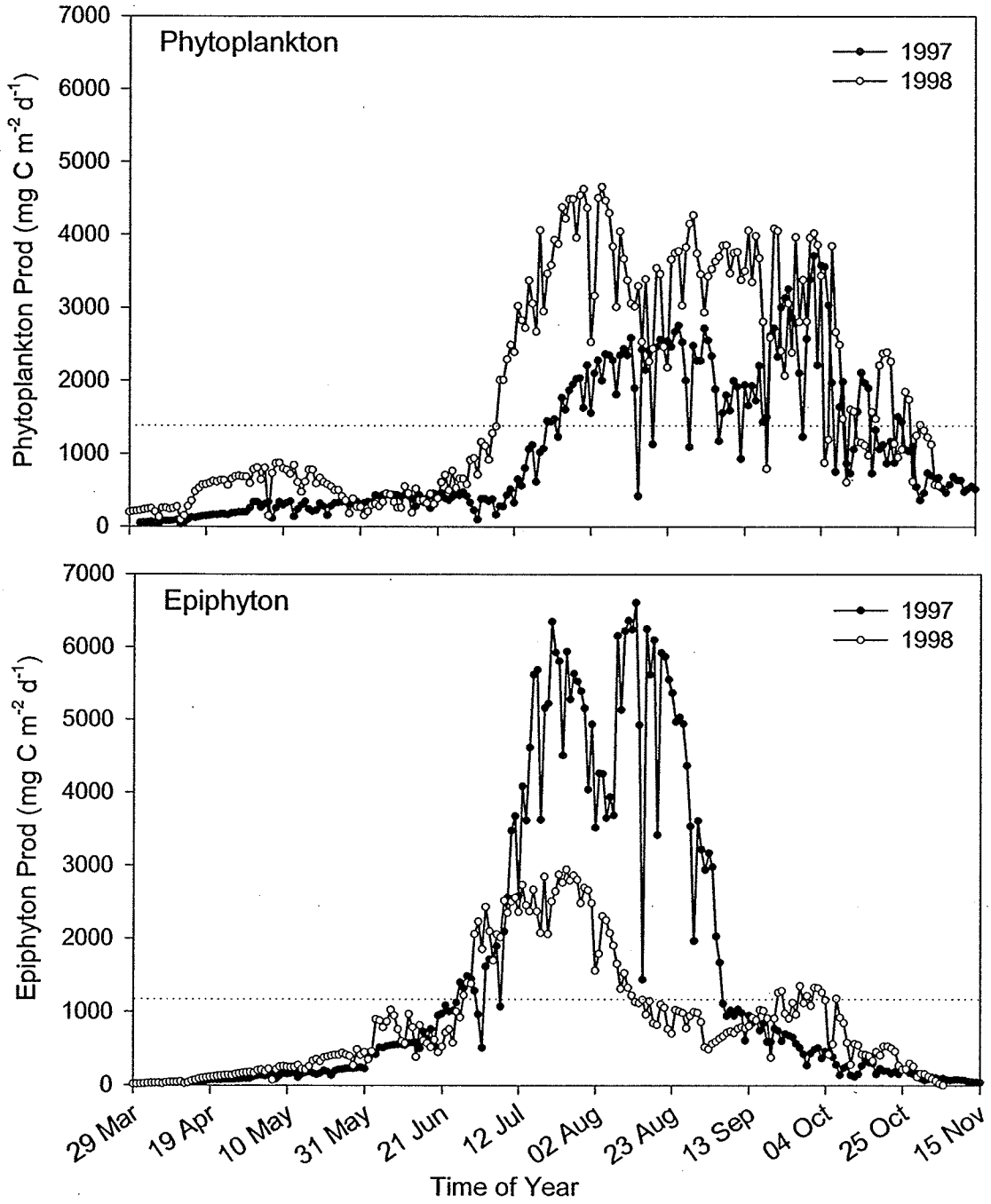

Figure 51. Mean daily productivity (mg C per m^2 wetland area d^{-1}) of phytoplankton and epiphyton in Cell Four of Oak Hammock Marsh during the ice-free periods in 1997 and 1998. Horizontal dotted line represents the overall mean productivity (phytoplankton: 1418 mg m^{-2} d^{-1}; epiphyton: 1158 mg m^{-2} d^{-1}).

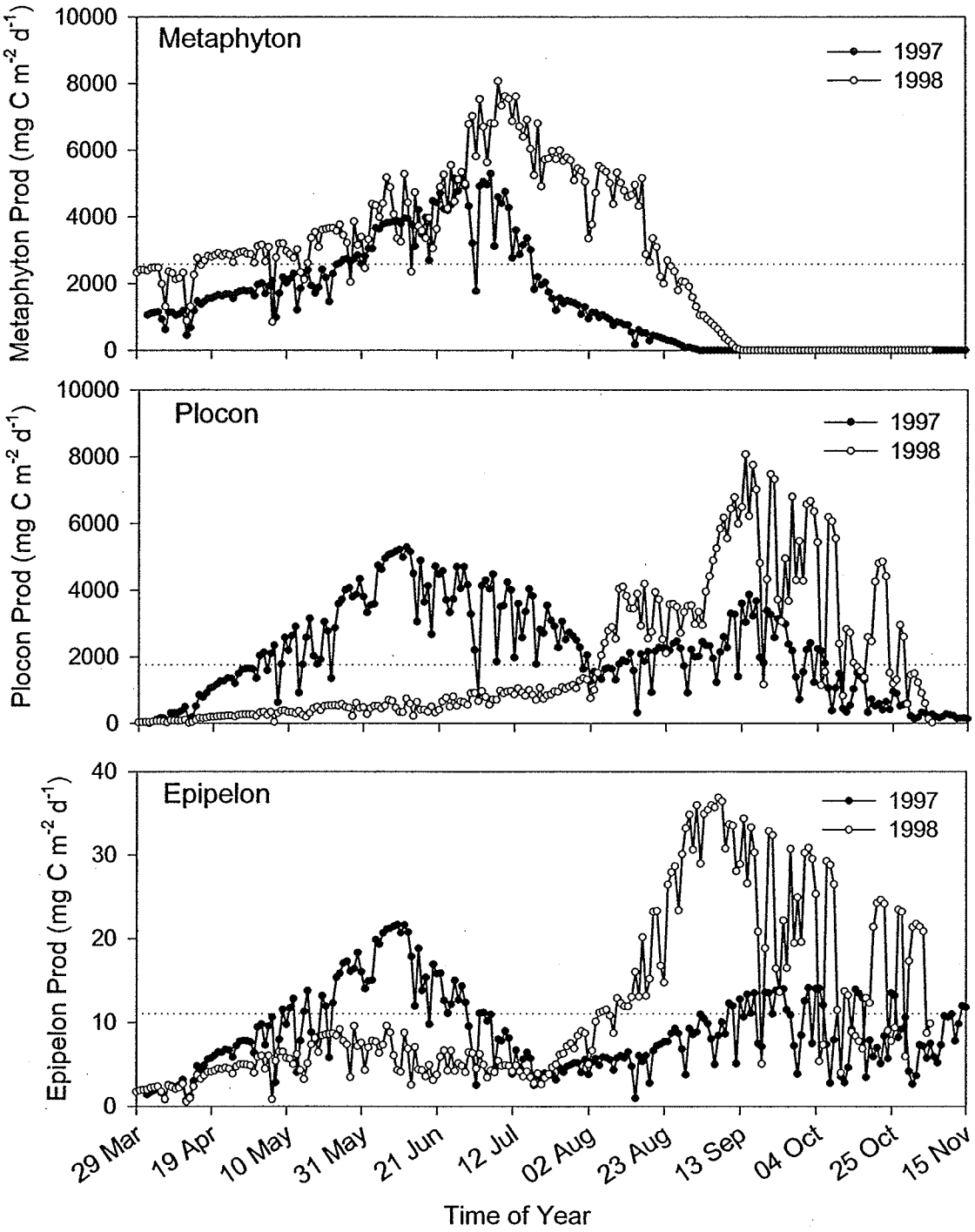

Figure 52. Mean daily productivity (mg C m^{-2} wetland area d^{-1}) of metaphyton, plocon, and epipelon in Cell Four of Oak Hammock Marsh during the ice-free periods in 1997 and 1998. Horizontal dotted line represents the overall mean productivity (metaphyton: 2516 mg m^{-2} d^{-1}, plocon: 1960 mg m^{-2} d^{-1}, epipelon: 11 mg m^{-2} d^{-1}). (Note change in scale of y axis for epipelon).

Table 21. Mean and range of daily productivity (mg C m^{-2} wetland area d^{-1}) of planktonic and benthic algae in Cell Four of Oak Hammock Marsh (OHM) in 1997 and 1998. Mean daily productivity values from Delta Marsh (DM) wetland cells are included for comparison (Robinson *et al.* 1997a).

Year	Phytoplankton	Epiphyton	Metaphyton	Plocon	Epipelon
OHM 1997	1048 (32-3712)	1447 (2-6609)	1411 (0-5293)	2096 (0-5291)	9 (1-14)
OHM 1998	1788 (97-4657)	868 (0-2944)	2794 (0-8073)	1823 (0-8078)	12 (1-37)
OHM Mean (1997-98)	1418	1158	2103	1960	11
DM Mean (1985-89)	201	723	2191	n/a	31

Table 22. Variation in daily algal productivity (mg C m^{-2} d^{-1}) correlated with variation in environmental variables as identified by forward stepwise multiple regression. (Alpha set at 0.150 to accept or remove variables from regression.)

Assemblage	Year	Environmental Variable$_{(step)}$	r^2	p value
Phytoplankton	1997	Chl-*a*$_{(1)}$	0.916	0.000
		Water Temp$_{(2)}$	0.978	0.000
		PAR$_{(3)}$	0.994	0.002
		APA$_{(4)}$	0.998	0.012
	1998	Chl-*a*$_{(1)}$	0.914	0.000
		Water Temp$_{(2)}$	0.984	0.000
Epiphyton	1997	Chl-*a*$_{(1)}$	0.536	0.001
		Water Temp$_{(2)}$	0.756	0.000
		APA$_{(3)}$	0.886	0.021
		Wind$_{(4)}$	0.935	0.021
		TRP$_{(5)}$	0.977	0.030
	1998	DIN$_{(1)}$	0.322	0.001
		Chl-*a*$_{(2)}$	0.560	0.007
		TRP$_{(3)}$	0.716	0.000
		N Debt$_{(4)}$	0.940	0.000
		Water Temp$_{(5)}$	0.970	0.047
Metaphyton	1997	Chl-*a*$_{(1)}$	0.987	0.000
		TRP$_{(2)}$	0.992	0.005
		APA$_{(3)}$	0.995	0.011
		DIN$_{(4)}$	0.998	0.014
	1998	Chl-*a*$_{(1)}$	0.983	0.000
		APA$_{(2)}$	0.994	0.001
		Water Temp$_{(3)}$	0.996	0.080
Epipelon	1997	Chl-*a*$_{(1)}$	0.726	0.000
		PAR$_{(2)}$	0.985	0.000
		Water Temp$_{(3)}$	0.989	0.146
	1998	Chl-*a*$_{(1)}$	0.857	0.000
		PAR$_{(2)}$	0.910	0.047
Plocon	1997	TRP$_{(1)}$	0.734	0.042
		PAR$_{(2)}$	0.821	0.000
		Chl-*a*$_{(3)}$	0.985	0.000
		N Debt$_{(4)}$	0.994	0.029
	1998	Chl-*a*$_{(1)}$	0.952	0.000
		APA$_{(2)}$	0.977	0.014

varying degree in both years. In addition, APA (13%) and average daily wind speed (5%) were evident in 1997, whereas in 1998, water column DIN (32%) and N Debt (22%) were important to the epiphyton regression. Variation in metaphyton productivity was correlated with chlorophyll-*a* (98-99%) and APA (0.3-1.1%) in both years (Table 22). Water column TRP (0.3%) and DIN (0.3%) in 1997, and ambient water temperature (0.2%) in 1998 were also of minor importance to the metaphyton regression. Variation in epipelon productivity was related to chlorophyll-*a* (73-86%) and PAR (5-23%) in both years (Table 22). In 1997, ambient water temperature (3%) was also a minor factor. Variation in plocon productivity was also related to chlorophyll-*a* (17-95%) in both years (Table 22). In addition, water column TRP (73%), PAR (9%), and N Debt (1%) were evident in 1997, whereas in 1998, APA (2%) was included in the plocon regression.

Metaphyton mean annual productivity was highest, followed by plocon, phytoplankton, and epiphyton (Table 23). Epipelon mean annual productivity was lowest of all algal assemblages measured. Mean annual algal productivity was about three times higher in Oak Hammock Marsh (1527 g C m^{-2} y^{-1}) than comparable annual productivity estimates in Delta Marsh (514 g C m^{-2} y^{-1}) (Table 23). One third of this difference can be accounted for by plocon (451 g C m^{-2} y^{-1}), which was measured in Oak Hammock Marsh, but not in the Delta Marsh study. Epiphyton annual productivity was two times higher, and phytoplankton annual productivity was ten times higher in Oak Hammock Marsh compared to Delta Marsh. Metaphyton and epipelon annual productivity were similar in both marshes.

Metaphyton and sediment-associated algae (plocon and epipelon) contributed proportionately more to total algal primary productivity (~40% and ~50%, respectively) In spring and early summer in 1997 (Figure 53). Epiphyton was the most important contributor to total algal productivity (~50%) in mid-summer. Phytoplankton and

Table 23. Mean and range of annual productivity (g C m^{-2} y^{-1}) of algal assemblages in Cell Four of Oak Hammock Marsh. Comparable values for Delta Marsh are from Robinson *et al.* (1997).

Algal Assemblage	Oak Hammock Marsh (g C m^{-2} y^{-1})	Delta Marsh (g C m^{-2} y^{-1})
Phytoplankton	325 (245-404)	34 (7-60)
Epiphyton	269 (197-339)	124 (28-358)
Metaphyton	481 (330-631)	348 (63-790)
Plocon	451 (412-490)	n/a
Epipelon	3 (2-3)	5 (0-15)
Total	1527 (1406-1647)	514 (105-1135)

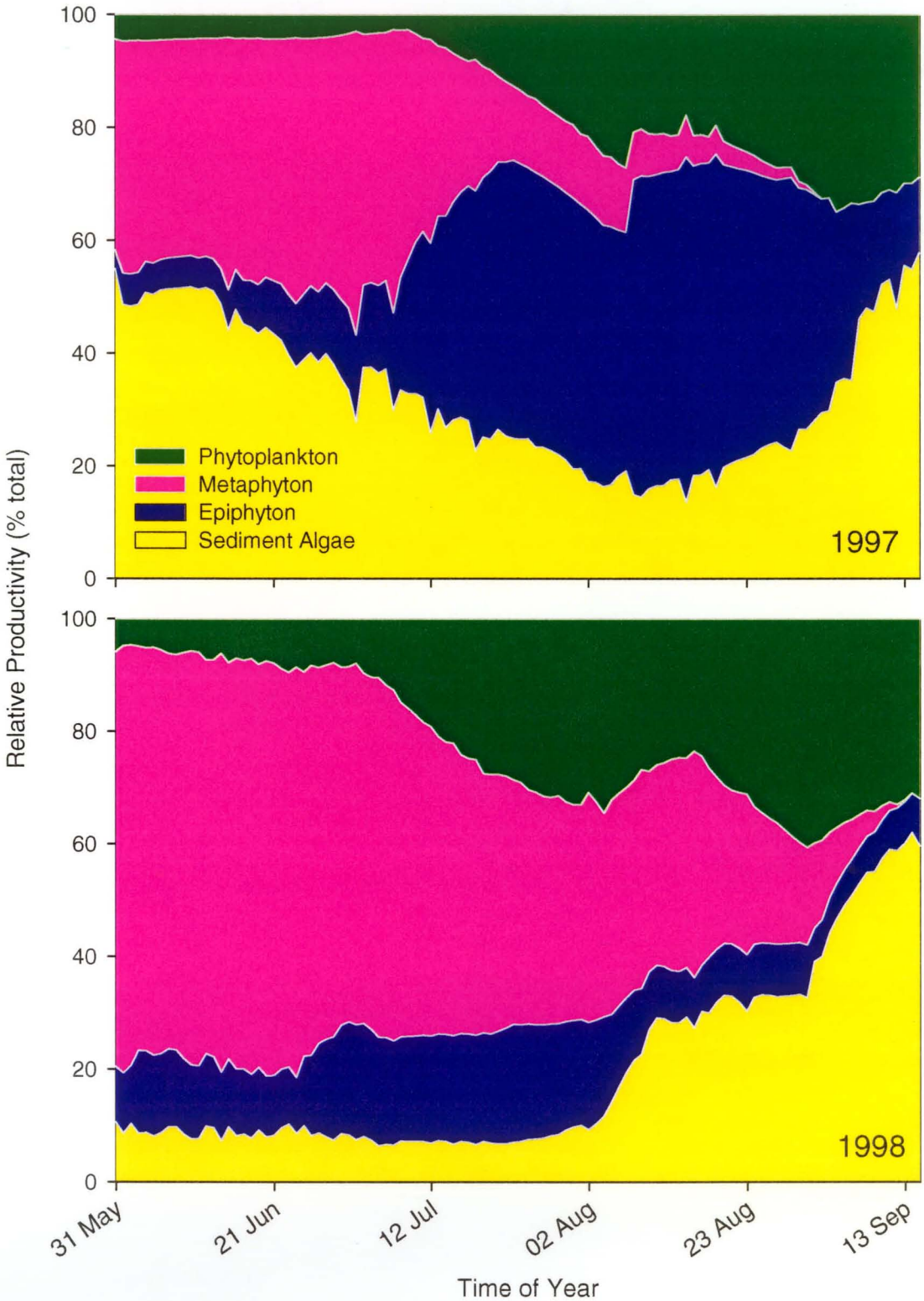

Figure 53. Relative productivity (% of total algae) of phytoplankton, metaphyton, epiphyton, and sediment-associated algae (epipelon + plocon) in Cell Four of Oak Hammock Marsh in 1997 and 1998.

sediment-associated algae were the major contributors (~60% and ~30%, respectively) in the late summer and fall.

In 1998, metaphyton was the dominant primary producer (~70%) in spring and early summer, with phytoplankton, epiphyton and sediment-associated algae each contributing about 10% to total productivity during this time (Figure 53). In mid-summer, metaphyton remained dominant (~40%), whereas phytoplankton (~30%) and epiphyton (~20%) increased in relative abundance. Phytoplankton and sediment-associated algae were the major contributors (~30% and 60%, respectively) in the late summer and fall.

5.1.12 Macrophyte primary production

Peak biomass of macrophytes occurred in mid-August in both 1997 and 1998. Emergent macrophytes produced the highest above-ground biomass, followed by submersed macrophytes, and then free-floating macrophytes (Table 24). Below-ground biomass of emergent macrophytes was not measured in this study, but an average of values from other studies (van der Valk and Davis 1978, Neely and Davis 1985, van der Valk 2000) was included to ensure that total macrophyte biomass was not underestimated. The estimated ratio of below-ground to above-ground biomass for my study was 2.1 in 1997 and 1.6 in 1998.

Proportionate contributions to total macrophyte production by *Typha*, submersed macrophytes and duckweed were similar in both 1997 and 1998 (Figure 54). *Typha* contributed ~90% in spring, and ~80% over the rest of the season, to total macrophyte production in both years. Submersed macrophytes contributed ~10% to total macrophyte production over the entire season in each year. Duckweed was absent in spring, but contributed ~10% to total macrophyte production over the rest of the season in both years.

Table 24. Mean and range of annual production of macrophytes (g dw m^{-2} y^{-1} and g C m^{-2} y^{-1}) in Cell Four of Oak Hammock Marsh in 1997 and 1998. Macrophyte biomass was converted to g C by assuming a 45% carbon content of plant tissue (Davis and van der Valk 1978, Madsen and Sand-Jensen 1991). Below-ground biomass of macrophytes was averaged from values in van der Valk and Davis (1978), Neely and Davis (1985), and van der Valk (2000).

Macrophyte	1997 (g dw m^{-2} y^{-1})	1998 (g dw m^{-2} y^{-1})	1997 (g C m^{-2} y^{-1})	1998 (g C m^{-2} y^{-1})
Free-floating	68 (28-113)	61 (21-98)	31	27
Submersed	127 (91-152)	101 (23-208)	57	45
Emergent	613 (576-714)	798 (531-885)	276	359
Above-ground				
Below-ground	1,289 (840-1679)	1,289 (840-1679)	580	580
Total	2,097	2,249	944	1,011

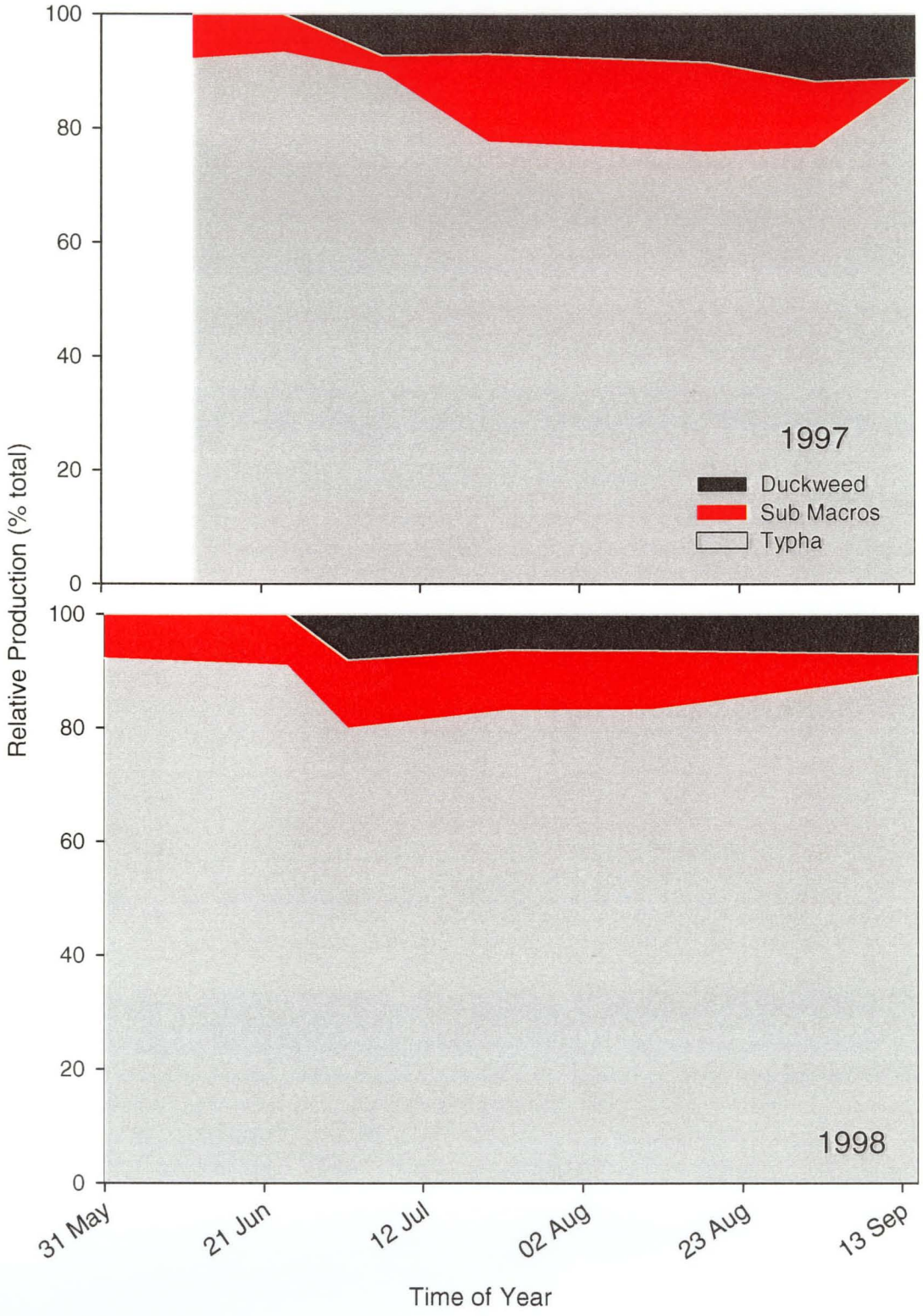

Figure 54. Relative production (% of total macrophytes) of duckweed, submersed macrophytes and Typha in Cell Four of Oak Hammock Marsh in 1997 and 1998.

5.1.13 Total primary production in Cell Four of Oak Hammock Marsh

Total annual primary production in Cell Four was 8,068 kg C ha^{-1} y^{-1} in 1997 and 10,260 kg C ha^{-1} y^{-1} in 1998 (Table 25). In terms of above-ground biomass, phytoplankton were the largest contributors to total primary production, followed by plocon, metaphyton, and *Typha*. When below-ground biomass was also considered, *Typha* was the second largest contributor to total primary production, after phytoplankton. Total algal production was almost twice as high as total macrophyte production, particularly in 1998.

When the relative productivity of each primary producer was considered over time, macrophytes (*Typha*, submersed macrophytes, and duckweed) contributed ~10% to total productivity over the entire season in both 1997 and 1998 (Figure 55). Sediment-associated algae (epipelon and plocon) and metaphyton were the largest contributors in spring and early summer in 1997, with epiphyton and phytoplankton becoming more important in mid-summer and fall (Figure 55). Metaphyton dominated in spring and summer in 1998, with epiphyton becoming more important in mid-summer. Phytoplankton and sediment-associated algae were greater relative contributors to total productivity in the fall (Figure 55). In both years, metaphyton contributions began to decrease as duckweed relative productivity increased.

Table 25. Total annual primary production (kg C ha^{-1} y^{-1}) for water-covered area (406.3 ha) of Cell Four of Oak Hammock Marsh in 1997 and 1998. Macrophyte biomass was converted to kg C by assuming a 45% carbon content of plant tissue (Davis and van der Valk 1978, Madsen and Sand-Jensen 1991). Below-ground biomass of macrophytes was averaged from values in van der Valk and Davis (1978), Neely and Davis (1985), and van der Valk (2000).

Algal Assemblage	1997 (kg C ha^{-1} y^{-1})	1998 (kg C ha^{-1} y^{-1})
Phytoplankton	2,452	4,040
Epiphyton (on submersed)	478	280
Epiphyton (on emergent)	44	20
Metaphyton	822	1,572
Plocon	1,221	1,026
Epipelon	5	7
Total Algal Production	5,022	6,945
Free-floating Macrophytes	4	4
Submersed Macrophytes	84	66
Emergent Macrophytes		
Above-ground Biomass	954	1,241
Below-ground Biomass	2,004	2,004
Total Macrophyte Production	3,046	3,315
Total Annual Production	8,068	10,260

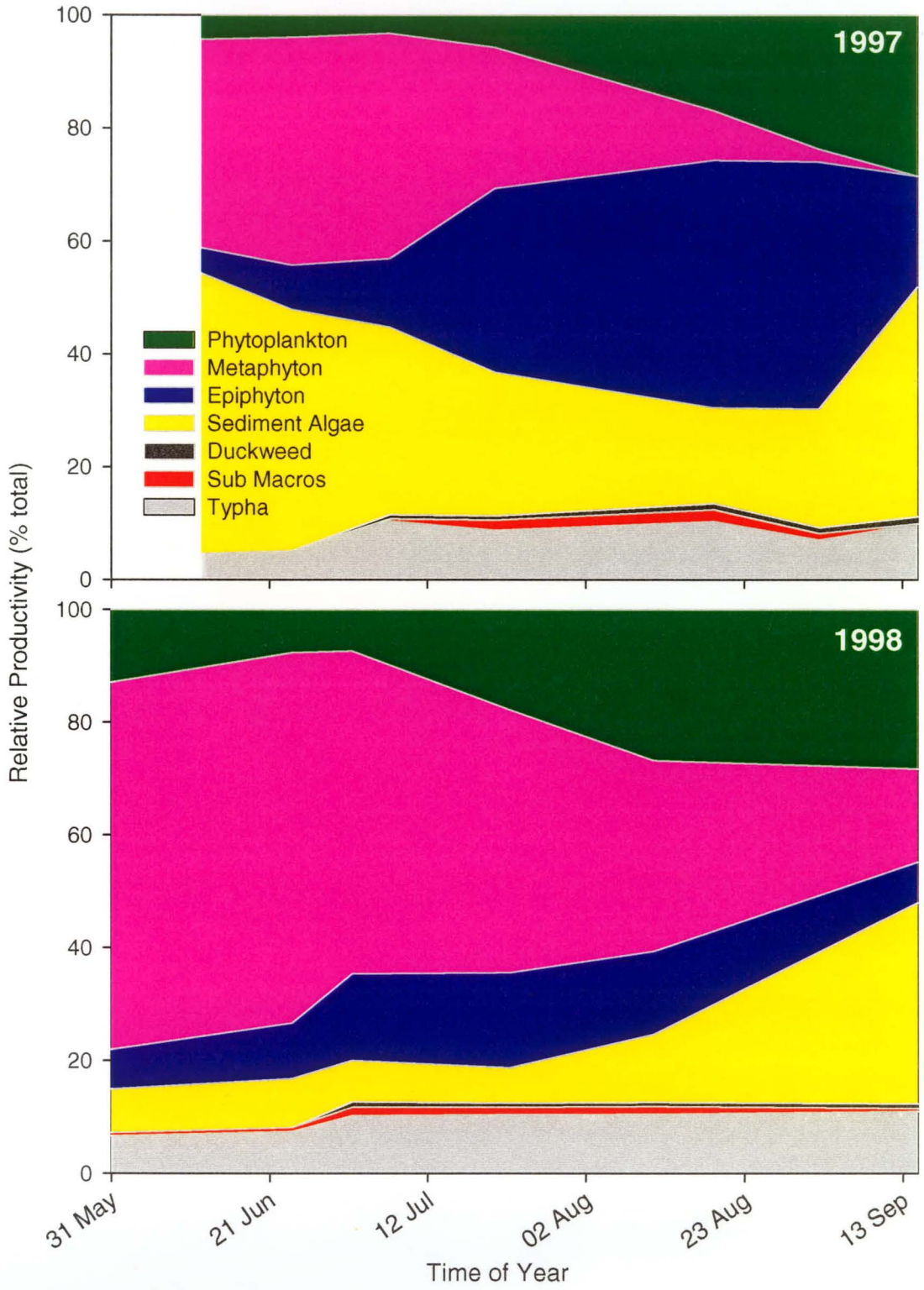

Figure 55. Relative productivity (% of total productivity) of all primary producers in Cell Four of Oak Hammock Marsh in 1997 and 1998.

5.2 Discussion

Cell Four of Oak Hammock Marsh is presently an hypereutrophic water body on the basis of its water column nutrient concentrations (TP>100 μg L^{-1}, DIN: 500-1500 μg L^{-1}) (Wetzel 2001), and its high algal productivity (Ps > 1000 mg C m^{-2} d^{-1}) (Wetzel 2001). The marsh is currently in a clear water state (cf. Irvine *et al.* 1989, Scheffer *et al.* 1993), but episodic resuspension of sediments, periodic phytoplankton blooms, and decreases in submersed macrophyte biomass are indications that a shift to a turbid state may be imminent. The interplay of competition for nutrients and light among primary producers may be one of the mechanisms determining the stability of the clear water state in Cell Four of Oak Hammock Marsh.

5.2.1 Nutrients

Inorganic N and P are detectable at relatively high levels in the water column over most of the ice-free season, but are still in the range for unpolluted surface waters (0-5 mg L^{-1} for NH_4-N; 0-10 mg L^{-1} for NO_3-N; 0-200 mg L^{-1} for TP) (Wetzel 2001). Organic N accounts for about 60% of TN in Cell Four, which is typical in most aquatic systems where organic N commonly accounts for more than half of the TN. The TP:DIP ratio of 1:1 is surprising, as inorganic phosphorus is often a small fraction (<5%) of TP, even in eutrophic systems. It is likely that the method of using unfiltered water samples to determine total reactive phosphorus is an overestimate of inorganic phosphorus, because a portion of particulate organic P is readily hydrolyzed during analysis. However, this reactive particulate organic P is also rapidly cycled by bacteria to inorganic P in nature, so that TRP is probably a fairly reasonable estimate of the P that is available for uptake by algae.

There was no active surface inflow of water to Cell Four in 1997 and 1998, so the nutrients in the water column were internally generated. Most of the water for the

flooding of Cell Four three years previous had been diverted from Wavey Creek, rather than pumped from the nearby artesian well. Wavey Creek runs through a large pasture grazed by ~50 horses and >100 head of cattle each year, which may have contributed to the nutrient levels of the inflowing water. The basin of the marsh is probably also nutrient-rich because it was reclaimed from agricultural production in the early 1970s. Spring turnover was likely responsible for the initial high levels of water column nutrients in both years. In addition, sediments were periodically re-suspended by wind-induced turbulence of the shallow water column, providing a source of P to the water column from time to time. Cycling of P between algae, invertebrates, minnows and bacteria would also function to maintain available P in the water column.

Ammonium-N is usually not present in significant amounts in oxygenated water columns, but in Cell Four, the proximity of the sediments, where a massive amount of organic matter was decomposing, would account for the persistence of NH_4-N in the shallow water column. The presence of significant quantities of NH_4-N in the water column would stimulate algal growth, but would also create a toxic environment for the biota from time to time. Algae preferentially take up N in the form of NH_4-N, but proportionately more of the NH_4-N would be in the form of undissociated ammonia at high pH (NH_4OH) (NH_4-N:NH_4OH is 1:1 at pH 9) (Wetzel 1983). This condition would likely occur on calm, sunny days when high rates of both algal and macrophyte photosynthesis would consume H^+ ions and drive up the pH. Toxic effects of undissociated ammonia on plants, algae, and invertebrates range from accelerated senescence to death.

The high concentrations of nitrate-N in the water column in late summer of 1998, coincident with low concentrations of ammonium-N, were probably the result of high rates of nitrification of NH_4-N to NO_3-N by heterotrophic nitrifying bacteria. Cell Four provided optimal conditions for nitrifying bacteria, including a ready supply of labile C

from algal secretion and decomposition, a constant source of reduced N, and ample colonization surfaces on the leaves of submersed macrophytes suspended in a warm, well-oxygenated water column.

Additional N may also have entered Cell Four in late summer via nitrogen fixation by cyanobacteria, and subsequent reduction to ammonium-N. I observed short-lived blooms of *Aphanizomenon flos-aquae* in late August of both years. *Aphanizomenon* blooms can add as much as 2 kg ha^{-1} of N to a lake (Barica 1990). In addition, this was the time of greatest plocon productivity, particularly in 1998. Plocon assemblages are often dominated by cyanobacteria, many of which produce heterocysts for nitrogen fixation (Round 1981). The increase in ammonium-N concentrations in late fall was also related to the onset of senescence of submersed macrophytes, which can release 50% of their N and 70% of their P to the water column during senescence (Landers 1982). The water column P concentration does not show evidence of this additional P release, but it is likely that all of the released P was taken up by phytoplankton, epiphyton and sediment-associated algae.

5.2.2 Nutrient limitation

It is unlikely that phytoplankton were limited by N in either year in Cell Four, based on their lack of response to added N in N-debt assays, and the water column TN:TP ratios indicative of P limitation. The water column inorganic N:P ratios are not generally reliable indicators of nutrient limitation, as they represent transient conditions that do not reflect the intra-cellular N:P ratios of algae (Barica 1990). In addition, the inorganic N:P ratios were probably skewed because inorganic P is overestimated as TRP. Phytoplankton were more consistently limited by P in 1998 than in 1997, based on their elevated level of alkaline phosphatase activity in 1998. Phosphorus variables (TRP and APA) were correlated to variability in phytoplankton productivity by multiple linear regression, a relationship that had some real (cause-effect) basis for Oak Hammock

Marsh phytoplankton. Luxury consumption of P released by senescing macrophytes might explain why P-limited algal chlorophyll could continue to increase into late fall, even as TRP levels in the water column appeared to be dropping.

Attached algae in Cell Four appeared to be co-limited by N and P on the basis of their response to nutrient-diffusing substrata. Co-limitation of a mixed algal assemblage is not unusual, indicating that some species in the assemblage are limited by nitrogen (e.g., *Achnanthidium minutissimum, Stigeoclonium tenue*), whereas others are limited by phosphorus (e.g., *Rhopalodia gibba*, *Epithemia* spp.) (Borchardt 1996). Epiphyton can be limited by N even when phytoplankton are not, because epiphyton are relatively stationary by virtue of their growth habit, unlike phytoplankton which can move through the water column. Epiphyton were growing in close association with submersed macrophytes, which also have a high requirement for N (Sand-Jensen and Søndergaard 1979), perhaps reducing the available N to the algae. Both phosphorus variables (TRP and APA) and nitrogen variables (N-debt and DIN) were correlated, in multiple linear regression analysis, with some of the variability in epiphyton productivity, perhaps as a result of co-limitation of epiphyton productivity by N and P.

The use of nutrient-diffusing substrata to determine nutrient limitation has some shortcomings, including supplying nutrients in great excess, and at unknown concentrations through the depth of the algal mat, making it difficult to determine the nutrient limitation of specific taxa within the mat (Borchardt 1996). However, they are often useful for identifying nutrient limitation at the scale of the whole assemblage and they are more successful than water column N:P ratios at predicting benthic algal nutrient limitation (Francoeur *et al.* 1999). The over-all magnitude of the attached algal response to increased N and P was quite low (an increase of 1 to 4 μg cm^{-2} at the highest enrichment levels), indicating that some other factor was probably limiting attached algal growth in Cell Four.

5.2.3 Light limitation

Competition for light between primary producers was likely to occur in Cell Four, particularly within areas of submersed and emergent vegetation, where light attenuation at 20-cm depth was 25% greater than light attenuation in open water. These vegetated areas were also the areas of greatest metaphyton abundance, as the macrophytes provided attachment substrata and shelter from wind disturbance. It is likely that light levels were limiting for epiphyton, sediment-associated algae, and phytoplankton in submersed macrophyte beds and emergent macrophyte stands, where 99% of incident light was attenuated by 30-cm depth. Even in the open water of Cell Four, light attenuation was greater with mean depth (75-92%) than values that I measured in Delta Marsh in 1996 (46-60%) or those reported by Robinson *et al.* (1997) (55-65%). It is likely that the high biomass of phytoplankton in the open water column of Oak Hammock Marsh contributed to increased light attenuation here.

5.2.4 Interactions among primary producers

Phytoplankton in Cell Four did not exhibit the 'typical' nutrient-driven periodicity described for deeper lakes, which commonly experience a spring maximum of diatom production, followed by a period of low production through mid-summer and a late-season bloom of cyanobacteria (Reynolds 1984, Wetzel 2001). The mid-summer decline typical of pelagic phytoplankton is related to nutrient depletion in a stratified epilimnion, which is not the case in the shallow water column of Cell Four where periodic mixing occurs throughout the summer.

Instead, phytoplankton production in Cell Four may have been regulated by competition with metaphyton for nutrients and light. Metaphyton peak daily productivity occurred about three weeks earlier than phytoplankton peak daily productivity; with the result that phytoplankton did not start to increase until metaphyton was on the decline. It is possible that spring-blooming diatoms were not able to reach or maintain exponential

growth because of low silicon levels in Cell Four, although the mid-summer concentrations of silicon were still above growth-limiting concentrations of 0.4 to 0.8 mg L^{-1} noted for diatoms in other studies (Nicholls 1976, Toetz 1999). In addition, the two major constituents of the metaphyton, *Cladophora glomerata* and *Enteromorpha intestinalis*, are strong nutrient competitors when nutrient concentrations are high (Borchardt 1996), as they were in Cell Four in the spring. *Cladophora* and *Enteromorpha* have particularly high uptake rates for nitrate (Harlin 1978, Dodds 1991b), which was readily available in the water column in early spring.

Epiphyton daily productivity peaked about three weeks later than metaphyton productivity in both years, and epiphyton chlorophyll-*a* on submersed macrophytes (on a per unit leaf area basis; μg cm^{-2}) only began to increase concurrent with metaphyton decline in 1997. This trend suggests that epiphyton were also involved in competition for light and nutrients with the large early season occurrence of metaphyton at Open Deep sites. In 1998, per unit leaf area epiphyton chlorophyll-*a* declined steadily over the entire season, perhaps because high metaphyton production was persistent at these Open Deep sites until mid-September. Competition between phytoplankton and epiphyton may have been a factor in 1998, as both phytoplankton productivity and chlorophyll-*a* were higher in 1998, whereas epiphyton productivity and chlorophyll-*a* were noticeably lower. Silicon limitation of epiphyton may also have been a factor, given the low level of silicon in the marsh and the fact that epiphytic algae are comprised of a large component of diatoms.

The pattern of sediment-associated algal productivity was more plausibly related to light limitation than nutrient limitation, because both epipelon and plocon can be shaded by all other primary producers, and because they had ready access to nutrients sequestered in the sediments. Peak sediment-associated algal productivity occurred late in the season when phytoplankton, epiphyton and metaphyton were declining and

submersed macrophytes were undergoing senescence. Conversely, sediment-associated algal productivity was low in mid-summer at the height of submersed macrophyte and epiphyton production.

A combination of factors was likely at work in affecting the decline of epiphyton chlorophyll-*a* on the bases of *Typha* stems, including light limitation, steep localized chemical gradients, and lower temperatures in the shaded water column. The decline in epiphyton chlorophyll-*a* occurred just as the *Typha* canopy was beginning to leaf out. Epiphyton in these sites also experienced shading from dense mats of metaphyton early in the season, replaced by dense mats of duckweed later in the year. Light attenuation at the sediment surface (20-cm depth) in *Typha* sites was 85-87% at mid-day when the sun was directly overhead, suggesting that even less light reached the sediments during most of the day when the sun's rays were angled. Light limitation was likely one of the factors that accounted for the three-fold reduction in epiphyton chlorophyll-*a* within 10-cm depth. Toxicity related to elevated concentrations of NH_4OH and H_2S was likely an additional factor negatively impacting epiphyton chlorophyll-*a* at these sites, particularly at the lowest depths. There was little water movement in the sheltered, plant- or metaphyton-covered water column of *Typha* stands, which would hamper the dispersion of NH_4-N produced during litter decomposition. Daytime photosynthesis would raise the pH, causing speciation of NH_4-N to undissociated ammonia. The toxic effects of NH_4OH have already been noted. In addition, in mid-summer there was often a pink ring around the base of the *Typha* stems, indicating the presence of purple sulfur bacteria (Thiorhodaceae) (Wetzel 2001). These photosynthetic bacteria use H_2S as an electron donor in photosynthesis and are often found at the interface of anaerobic zones where they can maximize their access to light and H_2S. Hydrogen sulfide has toxic effects on both algae and plant roots and rhizomes.

A clear reason for the submersed macrophyte decline at Site 6 in 1998 is not readily evident. Epiphyton colonization and nutrient concentrations were similar at both Open Deep sites, so were unlikely to affect submersed macrophytes differently at one site over the other. The decline in biomass was mainly the result of the disappearance of *Ceratophyllum* from this site, when it had been there in roughly equal abundance with *Stuckenia* the year before. It is likely that a number of factors were involved in the disappearance of *Ceratophyllum*. The potential for nutrient competition with phytoplankton and epiphyton is greater for *Ceratophyllum*, as it is not rooted in the sediment nutrient pool. In addition, the higher wind speeds in the fall of 1997 may have caused greater dispersal of the free-floating *Ceratophyllum* at Site 6, which was more exposed to the north and west winds than was Site 3. I had also observed that the north end of Cell Four generally experienced greater bird-use during fall staging periods, suggesting that the macrophytes at Site 6 may have experienced greater disturbance by herbivory than the macrophytes at Site 3.

5.2.5 A test of attached algal sampling substrata

The deployment of artificial substrata at each site for periphyton colonization provided me with a consistent, easily accessible sample of attached algae of known surface area, which I could sub-sample and analyze without disruption of the three-dimensional structure of the biofilm. In addition, these data provided me with an *in situ* test of the accuracy with which artificial substrata reflect the 'real' colonization on plants. I think that the acrylic rods provided a reasonably good facsimile of submersed macrophytes, in terms of comparable chlorophyll-*a* per unit area, and the trend in chlorophyll-*a* over time. The acrylic rods were less representative of *Typha*, particularly in terms of comparable chlorophyll-*a* per unit area, although they did tend to exhibit the same trend over time. Epiphyton chlorophyll-*a* tended to be higher on the artificial substrata, and so might provide an overestimate of epiphyton production when used as

a proxy. However, I would argue that this is not so, because of differences in the methodological error associated with each type of sampling. With the acrylic rods, analysis of the entire biofilm is assured because the entire colonized rod segment is immersed in the solvent for chlorophyll-*a* analysis. With submersed macrophyte leaves and *Typha*, removal of the epiphyton is necessary, by shaking in water or by manual scraping. These methods are known to underestimate epiphyton chlorophyll-*a*, because complete removal of the adnate portion of the biofilm is rarely achieved. The adnate portion of an epiphytic biofilm can comprise 6-68% of the total biofilm (Cattaneo and Kalff 1980). Other, more biologically-based, reasons for differences in colonization could include: differential grazing of plants vs. acrylic rods, the ability of submersed macrophytes to slough older, heavily colonized leaves, taxonomic differences in colonization, and the possibility of some allelopathic or competitive interaction at the epiphyton/macrophyte interface. Based on the outcome of my artificial substrata/macrophyte comparison, I would continue to use artificial substrata for sampling the production of attached algae. Sampling of both live plant tissues and artificial substrata, as I have done here, would provide the best measurements of epiphyton. However, for ease of accessibility, replication, and for least disruption of the epiphytic matrix, the use of artificial substrata provides a useful and reliable sampling method for attached algal chlorophyll-*a*.

5.2.6 The tertiary sewage lagoon

The tertiary sewage lagoon provided a nutrient contrast with Cell Four, but in the opposite direction of that expected. The water in the tertiary sewage lagoon and the pristine artesian well were virtually indistinguishable on the basis of N and P concentrations. Phytoplankton in the lagoon were severely N and P limited in both years of my study, according to N-debt and APA assays. Silicon levels were within the range of silicon limitation for diatoms in mid-summer of both years, which indicated either that

spring diatom production had depleted silicon levels, or that silicon levels were consistently low in the clay-lined lagoon. It is likely that nutrient limitation controlled phytoplankton and attached algal production throughout the season in both years. Metaphyton were the major algal contributor to primary production in the lagoon, again suggesting that metaphyton were better competitors for water-column nutrients than phytoplankton or epiphyton. The upswing in metaphyton chlorophyll-*a* in late August of both years coincided with the influx of effluent from the secondary sewage lagoon, again pointing to the competitive ability of metaphyton to take up available nutrients. In addition to nutrient limitation, the combination of metaphyton mats and emergent *Typha* shading the water column probably imposed secondary light limitation on phytoplankton and epiphyton.

The tertiary sewage lagoon was designed to supplement the nutrient-removal capabilities of the primary and secondary lagoons. The tertiary lagoon appeared to be performing its function of nutrient-removal from the water-column. The growth response by metaphyton indicated that there were elevated N and P concentrations in the inflowing effluent from the secondary lagoon. In addition to nutrient uptake by algae and macrophytes in the tertiary lagoon, the clay lining of the bottom would also provide numerous adsorption sites for sedimenting P. The water that was eventually released from the tertiary lagoon into Oak Hammock Marsh was certainly not increasing the nutrient loading to the marsh proper.

5.2.7 Photosynthesis model

The model, developed from experimentally determined photosynthesis parameters, was able to use daily PAR and chlorophyll-a values to predict remarkably accurate daily productivity estimates for both phytoplankton and epiphyton. The close agreement with measured daily *in situ* productivity suggests that the experimentally

determined photosynthesis parameters are good approximations of the relationship between light, temperature and algae in Oak Hammock Marsh.

The photosynthesis parameters that I determined for phytoplankton, epiphyton and metaphyton in Oak Hammock Marsh were similar to parameters developed for wetland algae, using the same exponential model equation, in nearby Delta Marsh by Robinson *et al.* (1997) (Table 26). All algal assemblages in Oak Hammock Marsh exhibited high photosynthetic efficiency (*a*), indicating long-term adaptation to photosynthesizing at lower light levels. Algae grown under low light have relatively higher photosynthetic efficiencies because of their higher relative chlorophyll content and subsequent improved capacity to absorb light (Steeman-Nielsen and Jørgensen 1968, Reynolds 1984). Mainly as a function of higher *a* values, E_k values for all algal assemblages were lower in Oak Hammock than in Delta Marsh, particularly for epiphyton and metaphyton. The light use efficiency of phytoplankton (*a* = 13) in Oak Hammock Marsh was higher than at Delta Marsh (7), but still within the range for phytoplankton reported in the literature (6-18 mg C mg^{-1} Chl-*a* mol^{-1} m^{-2}) (Reynolds 1984). Higher light use efficiencies for epiphyton (7) and metaphyton (4) at Oak Hammock Marsh, compared to Delta Marsh (2.2 and 0.8) (Robinson *et al.* 1997a), indicate that the algae at Oak Hammock Marsh were more efficient at using low levels of light to produce organic carbon. Benthic algae may have lower light use efficiencies than phytoplankton because of the three-dimensional structure of epiphytic biofilms or the overlapping filaments of metaphyton; situations where not every algal cell is optimally positioned to trap light.

P^B_{max} varied over the same range for phytoplankton and epiphyton in both Oak Hammock Marsh and Delta Marsh, whereas P^B_{max} for metaphyton varied over a larger range in Delta Marsh than in Oak Hammock Marsh. The parameters, *a* and *ß*, were more variable for all of the algal assemblages in Delta Marsh, compared to those for

Table 26. A comparison of photosynthetic parameters developed for P*E* relationships for wetland algae; *a* = photosynthetic efficiency (μg C μg^{-1} Chl-*a* h^{-1} μmol^{-1} m^{-2} s^{-1}); E_k = irradiance at onset of P_{max} (μmol m^{-2} s^{-1}); P^B_{max} = light saturated specific photosynthetic rate (μg C μg^{-1} Chl-*a* h^{-1}). Delta Marsh values from Robinson *et al.* (1997).

Assemblage	Location	*a*	E_k	P^B_{max}
Phytoplankton	Oak Hammock	0.048 (0.032-0.084)	222	10.7 (5.1-20.2)
	Delta Marsh	0.025 (<0.001-0.056)	282	7.2 (0.2-23.4)
Epiphyton	Oak Hammock	0.025 (0.006-0.047)	92	2.3 (0.9-8.4)
	Delta Marsh	0.008 (<0.001-0.022)	292	2.4 (0.1-7.9)
Metaphyton	Oak Hammock	0.015 (0.013-0.017)	100	1.5 (1.2-2.2)
	Delta Marsh	0.003 (<0.001-0.010)	399	1.1 (0.1-10.9)

algal assemblages in Oak Hammock Marsh. This may be a function of the much larger number of replicates (600-2,500) over a longer time frame (5 years) in the Delta Marsh study, which would have reflected a greater range in environmental variability as it affects these parameters. It is also possible that the use of the phototron in this study, with its precise control of temperature and PAR levels, allowed for reduction in experimental variability in determining these parameters. Regardless, the parameters for Oak Hammock show a similar trend as those for Delta Marsh, with phytoplankton having the highest photosynthetic efficiency and P^B_{max}, and benthic algae having the lowest.

Variation in photosynthetic parameters has been variously attributed to light or light history (Reynolds 1984, Tilzer *et al.* 1986, Kirk 1994), nutrient availability (Cote and Platt 1984, Osborne and Geider 1986), pigment composition (Taguchi 1976, Falkowski *et al.* 1989), and a variety of other environmental variables. Variation in *a* parameters in this study was most consistently related to chlorophyll-*a*, which suggests that pigment composition had strong influences on photosynthetic efficiency. Correlations of variation in *a* parameters with PAR and average daily wind speed could be explained by the dependence of *a* on light availability. The strong correlation between metaphyton *a* parameters and TRP may indicate a dependence of metaphyton photosynthetic efficiency on nutrient availability, particularly as it affects pigment composition. Variation in P_{max} for epiphyton that was correlated with variation in TRP may indicate the dependence of P_{max} on nutrient availability for attached algae. The strong correlation between variations in metaphyton P_{max} and temperature are indicative of the strong relationship observed in nature between warm temperatures and high metaphyton production (Dodds 1991, Fong and Zedler 1993).

5.2.8 Primary production in Oak Hammock Marsh

The amount and distribution of algal chlorophyll-*a* was a strong predictor of areal photosynthetic rates in Oak Hammock Marsh. In fact, multiple linear regression analysis

identified chlorophyll-*a* as the most important environmental variable correlated with productivity 7 times out of 10. The variation in productivity accounted for by variation in chlorophyll-*a* was 92% for phytoplankton, 24-54% for epiphyton, 98% for metaphyton, 73-86% for epipelon, and 16-95% for plocon.

Cell Four of Oak Hammock Marsh was a productive wetland. On an annual per unit area basis, metaphyton was the most productive algal assemblage (481 g C m^{-2} y^{-1}), followed by plocon (451 g C m^{-2} y^{-1}), then phytoplankton (325 g C m^{-2} y^{-1}), and then epiphyton (269 g C m^{-2} y^{-1}). Epipelon was a minor contributor to production (3 g C m^{-2} y^{-1}).

Emergent, submersed and free-floating macrophytes all attained peak seasonal biomass in mid to late August in both years of my study. Above-ground macrophyte biomass in Cell Four was within the range of values reported elsewhere for freshwater marshes (Table 27).

In Oak Hammock Marsh, algae, not macrophytes, were the major contributors to total annual primary production. Algae contributed 62% of total primary production in 1997, and 68% of total primary production in 1998. Phytoplankton production in Oak Hammock Marsh was similar to reported phytoplankton production in other shallow water bodies (Table 28). The lower values for macrophyte and benthic algal production in these shallow lakes are mainly related to the lower proportion of the lake that is littoral (i.e. supports macrophytes and benthic algae), although in some cases, it also appears that not all benthic assemblages were sampled.

5.2.9 Oak Hammock Marsh and the global perspective

Wetland ecosystems have been described as the most productive ecosystems in the world on a per unit area basis, with estimates of mean annual production ranging from 900 to 1800 g C m^{-2} y^{-1} (Whittaker 1970, Schlesinger 1997). These global estimates are based on macrophyte biomass and do not make reference to algal biomass. Mean

annual primary production in Oak Hammock Marsh, on a per unit area basis, was 2,505 g C m^{-2} y^{-1} (total algae: 1,527 g C m^{-2} y^{-1}; total macrophytes: 978 g C m^{-2} y^{-1}). My estimation of primary production in Oak Hammock Marsh supports the contention that wetland ecosystems are among the most productive in the world, but it also underscores the probable degree of underestimation of productivity in prairie wetland ecosystems.

Table 27. Biomass estimates from selected studies for macrophyte primary producers in prairie marshes.

Macrophyte	Biomass ($g\ m^{-2}$)	Reference
Typha sp.	378-1336	McNaughton (1966)
Typha x *glauca*	758-1549	van der Valk and Davis (1978)
	816-1351	Neely and Davis (1985)
	87-160	van der Valk (2000)
	623-817	This study
Submersed	11-249	Anderson (1978)
	91-260	van der Valk and Davis (1978)
	54-189	This study
Duckweed	50-250	Goldsborough (1993)
	53-54	This study

Table 28. Annual areal primary productivity of phytoplankton (Phyto), benthic algae (Benthic), and macrophytes (Macros) in selected other water bodies compared to Oak Hammock Marsh.

Water Body	Area (ha)	Annual Mean (mg C m^{-2} d^{-1})			kg C ha^{-1} of Lake Surface Area y^{-1}			Remarks
		Phyto	Benthic	Macros	Phyto	Benthic	Macros	
Oak Hammock Marsh, MB	406	1,418	5,232	1,088	3,246	2,738	3,181	Alkaline eutrophic marsh; benthic algae epiphytic, metaphytic, and sediment-associated (this study)
Borax Lake, CA	40	249	732	77	926	692	12	Saline lake; benthic algae mostly epilithic, some epiphytic, metaphytic (Wetzel 1964)
Eagle Lake, CA	12,150	356	1,427	1,249	1,168	142	51	Hard-water eutrophic lake; benthic algae epilithic and epiphytic (Huntsinger and Maslin 1976)
Lake Wingra, WI	140	1,200	9	321	4,380	31	1,170	Hard-water eutrophic lake; benthic algae epiphytic and metaphytic (McCracken *et al.* 1974)
Lawrence Lake, MI	5	119	2,003	241	434	399	879	Hard-water oligotrophic lake; benthic algae epiphytic (Wetzel 2001)
Marion Lake, BC	13	22	110	49	8	310	180	Soft-water oligotrophic lake; benthic algae epipelic (Hargrave 1969)

6. Conclusion

6.1 Hypotheses revisited

My objective has been to study the primary production of algae in prairie wetlands to gain a more complete understanding of wetland algal responses to environmental factors, including light, nutrients, and temperature, and their interactions with macrophyte primary producers. My use of two study approaches, experimental manipulations of wetland mesocosms in one wetland, followed by an extensive exploratory survey in another wetland, has been informative. The use of mesocosms within Delta Marsh allowed me to manipulate biotic and abiotic variables in an attempt to simulate a shift from a clear water to a turbid water state within the confines of the mesocosms. The information gained from these experiments provided the framework with which to evaluate the stable state of an entire wetland at Oak Hammock Marsh. In the first approach, I used nutrient addition to achieve a hypereutrophic level of enrichment, whereas in the second approach I was able to evaluate the biotic components of an existing hypereutrophic system. The differences between the two studies, in terms of resource limitation and the responses of primary producers, were as illuminating as the similarities.

As I had hypothesized, algae do contribute significantly to primary production in prairie wetlands. In Delta Marsh, algae contributed 34% to standing crop in unmanipulated mesocosms, and 57% to standing crop in nutrient enriched mesocosms. In Oak Hammock Marsh, algae contributed 62% of total annual primary production in one year and 68% of total annual primary production in the second year. Just on the basis of abundance, it is clear that benthic algal metabolic processes will have a measurable impact on other biotic and abiotic components of these wetlands. It is also clear that estimations of algal production based only on phytoplankton can

underestimate total wetland primary production by as much as one third. Certainly, estimates of primary production based only on macrophytes are grossly underestimating the capacity of these wetlands to fix carbon and provide extensive food web support.

My hypothesis that benthic algae would be quantitatively more important than planktonic algae was true for Delta Marsh, but was not supported by my findings at Oak Hammock Marsh. Benthic algal production was 56-77% of total algal production in Delta Marsh mesocosms, and only 42-51% of total algal production in Oak Hammock Marsh Cell Four. I think that the balance of benthic to planktonic production in these marshes is related to differential algal response to different limiting nutrients in these two marshes, coupled with the existence of light limitation in Oak Hammock Marsh. These differential responses by benthic and planktonic algae have implications for the stability of wetland stable states, an argument which I will discuss in more detail below (see: A functional role for benthic algae in stable state dynamics).

6.1.1 Outcome of the Delta Marsh experiment

My hypothesis that phytoplankton would increase in response to macrophyte removal was not supported. Neither the partial removal, nor the complete exclusion of macrophytes was enough to stimulate increased phytoplankton production, suggesting that competition interactions with macrophytes for light or water column nutrients were not major factors influencing phytoplankton. Macrophytes may have been influencing phytoplankton by stabilizing the water column and promoting increased sinking of algal cells. However, I was unable to 'remove' this effect of macrophytes in my enclosures, because the floating curtain walls performed the same sheltering function. In addition, the curtain walls and the well-illuminated bottom of the enclosures provided attachment sites for an abundance of benthic algae, which may have acted as an alternative stabilizing mechanism once macrophytes were removed from the system. Some support for a relationship between decreasing macrophytes and increasing phytoplankton was

seen in Oak Hammock Marsh, where in the second year, submersed macrophyte abundance was 22% lower and phytoplankton was 65% higher than the previous year.

The second part of this hypothesis, that phytoplankton would increase in response to combined macrophyte removal and nutrient addition was supported in 1996, but not in 1995 in Delta Marsh. The greatest phytoplankton response (to 10 times pre-treatment levels) was observed in this manipulation in 1996, suggesting that once nutrient limitation was alleviated, the phytoplankton were able to take advantage of the higher light levels achieved by the removal of macrophytes from the system. The lack of phytoplankton response in 1995 was most likely related to the incomplete removal of macrophyte (and their associated epiphyton) competitors, coupled with insufficient N-loading to allow algal production to outstrip grazer control.

Contrary to my hypothesis, metaphyton did not become dominant when nutrients were added and macrophytes were present, suggesting that factors other than high nutrient concentrations and attachment substrata are necessary to promote metaphyton proliferation. Factors that may have negatively influenced metaphyton in 1996 included lower ambient light levels, disturbance by wind, and competition for scarce inorganic N by phytoplankton, epiphyton and submersed macrophytes.

As hypothesized, epiphyton dominated the algal assemblage (70% of algal chlorophyll) in Control treatments, where macrophyte colonization substrata were abundant, and the absence of planktonic turbidity allowed a clear view through the water column to the sediment surface. A similar clear water state has persisted in the Blind Channel of Delta Marsh for several years.

Phytoplankton did respond to nutrient addition, both in the presence of macrophytes and more so, when they were absent. Therefore, the nutrient addition treatments did promote a more turbid state, but the likelihood of a complete switch from clear water to a turbid state in the enclosures was equivocal. This is because periphyton

and epiphyton showed a similar magnitude of response to nutrient addition as phytoplankton did, providing an important buffering mechanism within the enclosures by sequestering large amounts of added nutrients. In shallow N-limited water columns with ample surface area for attached algae, it is unlikely that phytoplankton will quickly or easily outcompete periphyton and epiphyton.

6.1.2 Outcome of the Oak Hammock Marsh study

My objective in Cell Four of Oak Hammock Marsh was to quantify the contribution of all algal and macrophyte communities to total wetland primary production. I was able to accomplish this objective with a fair degree of success by using a combination of direct biomass sampling, extensive transect surveys, the production of a detailed vegetation map, and the development of assemblage- and wetland-specific photosynthetic parameters for use in modeling annual integrated algal primary production. In the process of pursuing this objective, I also gained information on the light and nutrient environment experienced by algae in Cell Four, and some insights into algal macrophyte interactions.

The photosynthesis model, developed from my experimentally determined photosynthesis parameters, was able to predict remarkably accurate daily productivity estimates for both phytoplankton and epiphyton. Therefore, I assume that the model also produced reasonable estimates for metaphyton and sediment-associated algae, although I was unable to test this with *in situ* experiments.

As I had hypothesized, the P_{max} photosynthesis parameter was temperature-dependent, and increased with increasing temperature. P_{max} for phytoplankton was higher than for the other algal assemblages, but, contrary to what I had hypothesized, P_{max} for metaphyton was lower than P_{max} for epiphyton. Also contrary to my hypothesis, *a* for epiphyton was lower than *a* for phytoplankton, although it was higher than *a* for metaphyton.

My hypothesis that Cell Four was an N-limited wetland was not supported. Nutrient ratios (TN:TP) indicated that phosphorus was probably the limiting nutrient. Nutrient deficiency assays confirmed that phytoplankton was P-limited, whereas results from nutrient-diffusing substrata indicated co-limitation of attached algae by N and P.

My hypothesis that light was the single most limiting resource for algae in Cell Four was supported by several lines of evidence, including high light extinction in the shallow water column, the presence of dense mats of metaphyton or duckweed within already shaded *Typha* sites, and the relatively high *a* values for all algal assemblages that may indicate some adaptation to low light levels.

6.2 Structure and function related to algal primary production

I think that algae play a major role in the structuring and functioning of shallow prairie wetlands. The role of food web support is an obvious one that impacts both structure and function of wetland ecosystems, although not all researchers are convinced of its importance. For example, Mitsch and Gosselink (2000, p. 404) completely ignore algae in their review of freshwater marsh structure and function, other than to concede that, "several links in the food chain may precede those that provide the commonly visible birds and other carnivores with their dinners." Researchers who study invertebrate dynamics in aquatic systems (e. g. Dvorak & Best 1982, Cattaneo 1983, Campeau *et al.* 1994, Hessen and Andersen 1992, Sterner *et al.* 1992) have long recognized the importance of nutritionally superior algal food sources. Recent food web tracer studies using stable isotopes have identified the benthic algal origin of carbon sources in a number of aquatic systems (Peterson and Howarth 1987, Sullivan and Moncrieff 1990, Hecky and Hesslein 1995).

Structural roles are, perhaps, less obvious for algae, because of the more visible macro-structure of aquatic plants. However, structural roles for benthic algae have been

identified in the literature, related to the three-dimensional architecture of attached algae (e.g., Hoagland *et al.* 1982, Hudon and Bourget 1983). The structures of filamentous and long-stalked greens, cyanobacteria and diatoms perform as a sieve or trap for in-flowing or sedimenting particulate matter (Cattaneo and Kalff 1978, Mickle and Wetzel 1978c). This trapping function is generally attributed to macrophyte beds, but in reality should be viewed as a coordinated interaction between algae and macrophytes, with macrophytes providing the large-scale resistance to turbulence, and benthic algae providing the fine scale of the 'mesh'. The existence of complex structure at the micro-scale also provides vast areas of habitat for the diversity of other micro-organisms in aquatic systems, including bacteria, fungi, nematodes, ciliates, and other meiobenthos (Wetzel and Søndergaard 1998). Large mats of metaphyton, which formed a significant portion of the benthic algal assemblage in the hypereutrophic Oak Hammock Marsh, also provide structural habitat. The vast surface area of filamentous green algae provides attachment substrata for other smaller epiphytic algae and bacteria (Dodds 1991a). In addition, the thick layers provide a temperature- and light-regulated refuge for many invertebrates, who graze on the epiphyton attached to the larger filaments. Sediment-associated mats of plocon, another algal assemblage of significance in Oak Hammock Marsh, play a previously identified role in sediment stabilization (Holland *et al.* 1974, Freytet and Verrecchia 1998, Woodruff *et al.* 1999). Whereas I did not directly investigate these roles for benthic algae in my study, I argue that the significance of the structural role for algae is not well appreciated because of the widespread lack of understanding of the sheer abundance of attached algae in these shallow systems.

6.3 A functional role for benthic algae in stable state dynamics

I think that there is a role for benthic algae in alternative stable state literature that is under-recognized, in part because few studies have assessed benthic algal

production in relation to planktonic algal production in shallow systems experiencing external nutrient loading (Murkin *et al.* 1994, Blumenshine *et al.* 1997, McDougal *et al.* 1997, Havens *et al.* 1999).

I suggest that benthic algae play an important ecological role in the stabilizing mechanism that is at present designated as due to "submersed macrophytes", based on evidence from this study and from others, that benthic algae are abundant in macrophyte stands (Cattaneo & Kalff 1980, Lalonde & Downing 1991, Robinson *et al.* 1997b) and have a large capacity for nutrient uptake (Portielje & Lijklema 1994, Axler & Reuter 1996, Hwang *et al.* 1998). Increases in the proportion of benthic to planktonic algae in response to nutrient addition can reduce substantially the availability of nutrients for phytoplankton (Axler & Reuter 1996, Blumenshine *et al.* 1997, McDougal *et al.* 1997), a mechanism thus far attributed mainly to submersed macrophytes in stable state discussions. When macrophytes become sparse or disappear, the presence of crust-forming sediment-associated algae bound in a gelatinous matrix can help to stabilize the sediments (Goldsborough and Robinson 1996). Abundant benthic algae on sediments or other surfaces may continue to effectively outcompete phytoplankton for nutrients (Carlton & Wetzel 1988, Hansson 1990), helping to compensate for the loss of submersed macrophytes in the short term by keeping phytoplankton chlorophyll low.

Based on my observations in Delta Marsh and Oak Hammock Marsh, I think that differences in the competitive ability of phytoplankton and benthic algae to take up N and P may be one of the mechanisms underlying stable state dynamics. In Delta Marsh mesocosms in 1995, phytoplankton did not respond to increased concentrations of added nutrients at the low N:P mass ratio of 8:1, but benthic algae (periphyton and metaphyton) did respond. In 1996, when the absolute load, but not the N:P mass ratio, was increased, phytoplankton did respond, but so did benthic algae in equal magnitude. This suggests that benthic algae are better competitors for scarce nitrogen than

phytoplankton, and may become more abundant than phytoplankton in N-limited environments. The enhanced ability of benthic algae to access NO_3-N, because of their close association with ammonifying bacteria on surfaces, may be particularly important in systems experiencing external nitrate loading. The occurrence of a steep decline in TN:TP ratios in Delta Marsh in both years, just after the period of high diatom productivity and initial growth by submersed macrophytes, provides evidence that macrophytes and benthic algae act together in regulating the N:P ratio of their environment. The ability of both benthic algal mats and submersed macrophytes to take up large quantities of inorganic nitrogen probably provides these primary producers with a competitive advantage over phytoplankton, particularly after the spring flush of phosphorus from the sediments has been depleted. This nutrient advantage for N, coupled with the effects of shading and turbulence reduction contributed by both submersed macrophytes and benthic metaphyton mats, may constitute a more complete explanation for the ability of macrophyte beds to maintain a clear water state in shallow systems.

Oak Hammock Marsh is a P-limited, rather than N-limited system, which influences the competitive interactions for nutrients among primary producers. Not only are phytoplankton more efficient at taking up P than benthic algae, because of higher specific uptake rates, they are also more efficient at adapting to a scarce P supply (Hwang *et al.* 1998). Rooted submersed macrophytes obtain most of their P supply from sediments, so are not as likely to be affected by the P-limitation of the water column. The exception to this generalization would be *Ceratophyllum*, which, as a non-rooted macrophyte, must obtain its P supply from the water column. Macrophytes have lower surface-area to volume ratios than phytoplankton, and generally have lower specific uptake rates for nutrients (Sand-Jensen and Borum 1991), suggesting that unsuccessful P-competition with phytoplankton may have been one of the factors affecting

Ceratophyllum decline in the second year of my study. Higher phytoplankton-related turbidity in 1998 may have been an additional factor, causing shading of *Ceratophyllum* and enhancing its decline.

Whereas the TN:TP ratio may have favored phytoplankton over benthic algae in a competition for nutrients, the persistent high concentrations of both N and P in the water column indicated that the algae in Oak Hammock Marsh were probably not primarily limited by nutrients. In fact, the high availability of N and P in the spring, coupled with lower availability of silicon, appeared to give filamentous green algae the advantage over spring phytoplankton, which is often composed of diatoms. Once established, the metaphyton mats appeared to suppress the growth of phytoplankton and sediment-associated algae through light limitation. Light limitation was also a factor limiting growth of epiphyton in emergent macrophyte stands, where metaphyton and duckweed mats also shaded the shallow water column.

I contend that there is an important ecological role for benthic algae in stable state dynamics through these interacting mechanisms of light and differential nutrient competition with phytoplankton. I think that this hitherto unidentified ecological role for benthic algae within the stable state model may help to explain the stability of the clear water state over a wide range of nutrient levels (*cf.* Beklioglu and Moss 1996). At some critical point of nutrient loading and benthic algal colonization, epiphyton may also contribute to the suddenness of the 'reverse switch' (Hosper 1998) to the turbid state, by accelerating macrophyte decline via light limitation and competition for nitrogen (Phillips *et al.* 1978, Sand-Jensen and Borum 1991).

6.4 Development of the littoral ecology of algae in wetlands

Despite early recognition of the unique and complex ecology of benthic algae by some researchers (e.g., Wetzel 1964, Allen 1971, Allanson 1973, Hutchinson 1975,

Round 1981), the science of littoral algae in lentic systems has never attained the same level of recognition or development as the science of pelagic algae. As a consequence, well-known constructs from phytoplankton ecology and deep-lake limnology are often applied to shallow lake and wetland ecosystems, with varying degrees of success. For example, a typical pattern of seasonal periodicity in phytoplankton productivity and succession is often observed in deep lakes, related to summer stratification and isolation of algae in a nutrient-depleted epilimnion (Reynolds 1984). This periodicity is not necessarily typical of phytoplankton patterns in shallow lakes and wetlands, as I found in Oak Hammock Marsh, and others have also noted (Steinman *et al.* 1997, Wetzel 2001). This lack of "typical" periodicity does not indicate problems of ecosystem health, as lake managers with training in deep-lake limnology might suspect. Rather, it suggests that there has been no concerted effort to develop a descriptive model of "typical" algal periodicity and succession in littoral-dominated systems. Much of the information needed to develop such a model is probably available in the literature, but it has not been recognized in any organized way.

Three themes, which should be central to a model of prairie wetland algal ecology, have become evident to me through my experience at Delta Marsh and Oak Hammock Marsh. With the information that I have gained from this study, I have identified several directions for future work, centering on these three themes. The first is a detailed examination of the competition for nutrients between algal assemblages in early spring, particularly in relation to the prevailing N:P ratio and any subsequent changes in that ratio. The effects of invertebrate and fish interactions and their impacts on N:P ratios are also important here. It is also necessary to re-examine the common assumption that P is the limiting nutrient in freshwaters. As some researchers have noted, this is not necessarily true for wetlands or shallow lakes, where optimal conditions for bacterial nitrification and denitrification may result in greater losses of N from these

systems (Elser *et al.* 1990, Wetzel and Søndergaard 1998). The second theme is an examination of light limitation, its prevalence and its pattern of change as it relates to changes in dominant algal assemblages (for example, from metaphyton to phytoplankton to plocon). The development of fiber optic and micro-electrode technology to measure light and oxygen in millimeters of depth has allowed a more accurate assessment of the light environment and its effects on epiphyton within a three-dimensional matrix, or on macrophyte leaves coated with epiphytes (Revsbech *et al.* 1983, Dodds 1992). The third theme is the elucidation of algal-macrophyte interactions in shallow ecosystems, a task I have attempted in a small way in this study. Finally, central to the development of wetland algal ecology, there needs to be clear recognition of the magnitude and importance of algal production in relation to macrophyte production, and in particular, an understanding of the central role of benthic algae in these shallow systems.

I keep coming back to this lack of recognition of the magnitude of algal production in shallow ecosystems, but it is specifically because of the prevalent dogma that wetlands and shallow lakes are detrital or macrophyte-dominated systems that investigators continue to discount the significance of benthic algae in food web support, regulation of N:P ratios, and competition for light and nutrients with both macrophytes and phytoplankton. If the contributions of algae, particularly benthic algae, to shallow aquatic systems are believed to be minor, then there is no reason to investigate their role in influencing stable state dynamics, regulating biogeochemistry and greenhouse gas emission, or contributing to global carbon cycling and storage.

I think I have made a contribution to the development of wetland algal ecology by quantifying comparative primary production in two prairie wetlands and demonstrating the significant potential for benthic algae as a major determinant of wetland structure and function.

6.5 Implications for Delta Marsh and Oak Hammock Marsh

Both the Blind Channel of Delta Marsh and Cell Four of Oak Hammock Marsh exhibited conditions characteristic of the clear water stable state, including abundant stands of submersed and emergent macrophytes and clear water columns that allowed an excellent view of the sediment surface 60 to 100 cm below. The abundance of benthic algae associated with macrophytes and sediments was also an important characteristic of these systems.

Although the Blind Channel has existed in a clear water state for several years, there has been an observable decline in the density of submersed macrophytes in recent years. This may be an early sign of the declining stability of the clear water state. This gradual decline in submersed macrophytes may be a function of increased competition for light and nitrogen with benthic algae. It may also be exacerbated by the presence of large benthivorous carp, which can perturb the flocculent sediments, increasing water column turbidity and uprooting macrophytes.

Signs that Cell Four of Oak Hammock Marsh was moving toward a shift from clear water to a turbid state were evident. The large increase in phytoplankton production and the decreases in submersed macrophyte biomass from one year to the next could have been due simply to inter-annual variability. However, when coupled with the high nutrient concentrations in the water column and the occurrence of periodic cyanobacterial blooms, I think there was ample cause for concern. As Scheffer (2001) commented, one of the major difficulties in the evaluation of stable states is the "hysteresis of problem recognition" (M. Scheffer, pers. comm.). The possibility of an imminent shift to a turbid state was avoided due to the timing of the scheduled draw-down of Cell Four, which occurred in 1999. This draw-down phase should act as a reset function for the wetland, allowing regeneration of macrophytes from the seedbank and

re-establishment of macrophyte and benthic algal dominance upon re-flooding. The seven-year time period for management of water levels in the cell was probably chosen to optimize habitat diversity for waterfowl, but it is also beneficial as a management tool preventing a shift to a turbid state, which would promote the loss of macrophytes and increase the likelihood of phytoplankton bloom formation.

6.6 A final comment

As I have mentioned before, the macrophyte-epiphyte complex is regarded as functionally inseparable, leading some researchers to suggest that the inclusion of epiphytic algae is inferred when they use the term "macrophyte" (Gasith and Hoyer 1998). However, I argue that the existence of the attached algae should be explicitly acknowledged and studied, because of differences in growth rates, food web roles, scales of nutrient cycling and other functional roles. Whereas epiphytic algae are sometimes invisible in the literature, they are hardly invisible in shallow lakes and wetlands where "epiphytic algae form a thick attached sward over which free-living cells move, and skeins of filamentous algae may also stretch from leaf to leaf and plant to plant" (Phillips *et al.* 1978, p.120).

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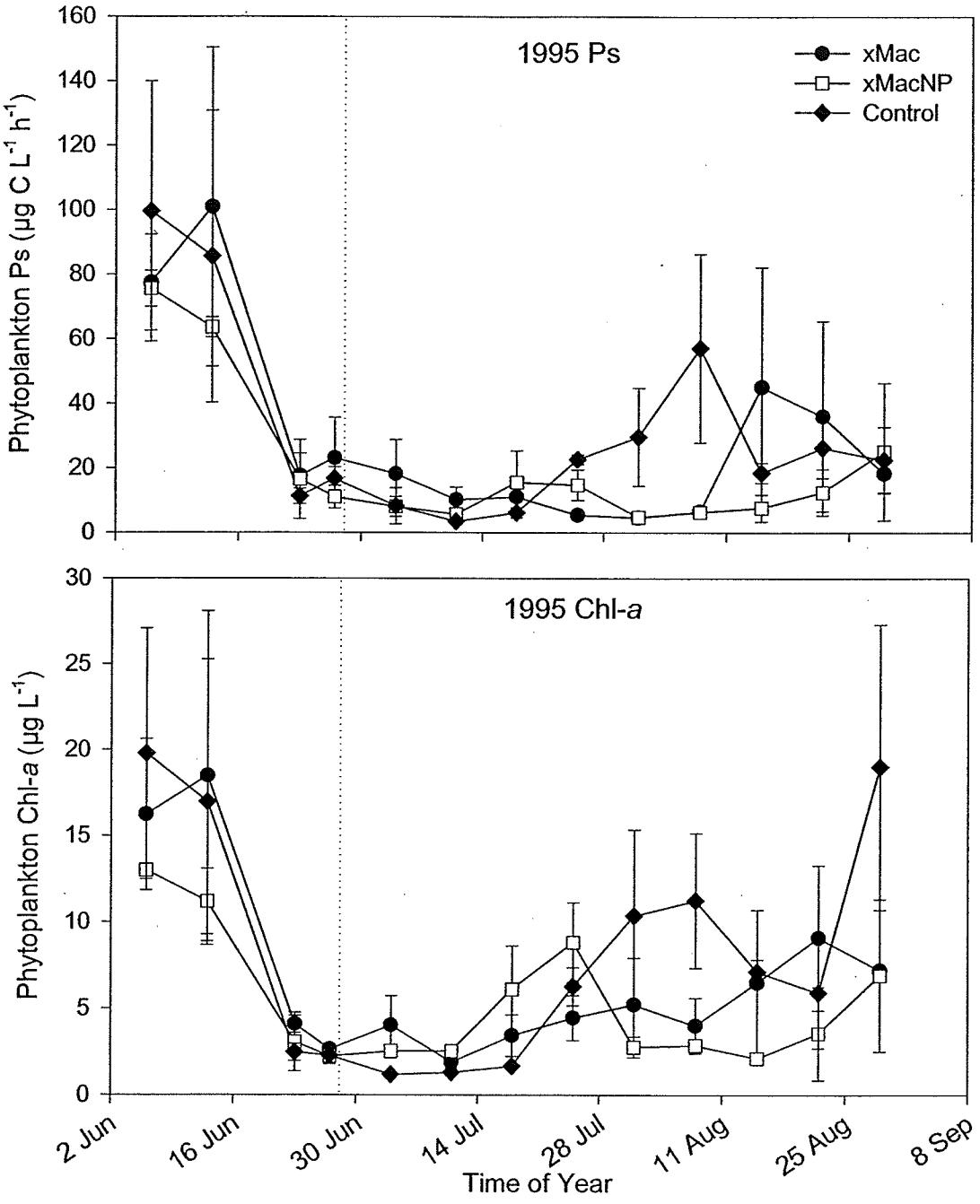

Figure 56. Phytoplankton chlorophyll-*a* (µg L^{-1}, ±SE, n=2) and phytoplankton photosynthesis (µg C L^{-1} h^{-1}, ±SE, n=2) in experimental enclosures in 1995. Vertical dotted line denotes the start of nutrient addition on 28 June, 1995. (Note changes in scale of y axes.)

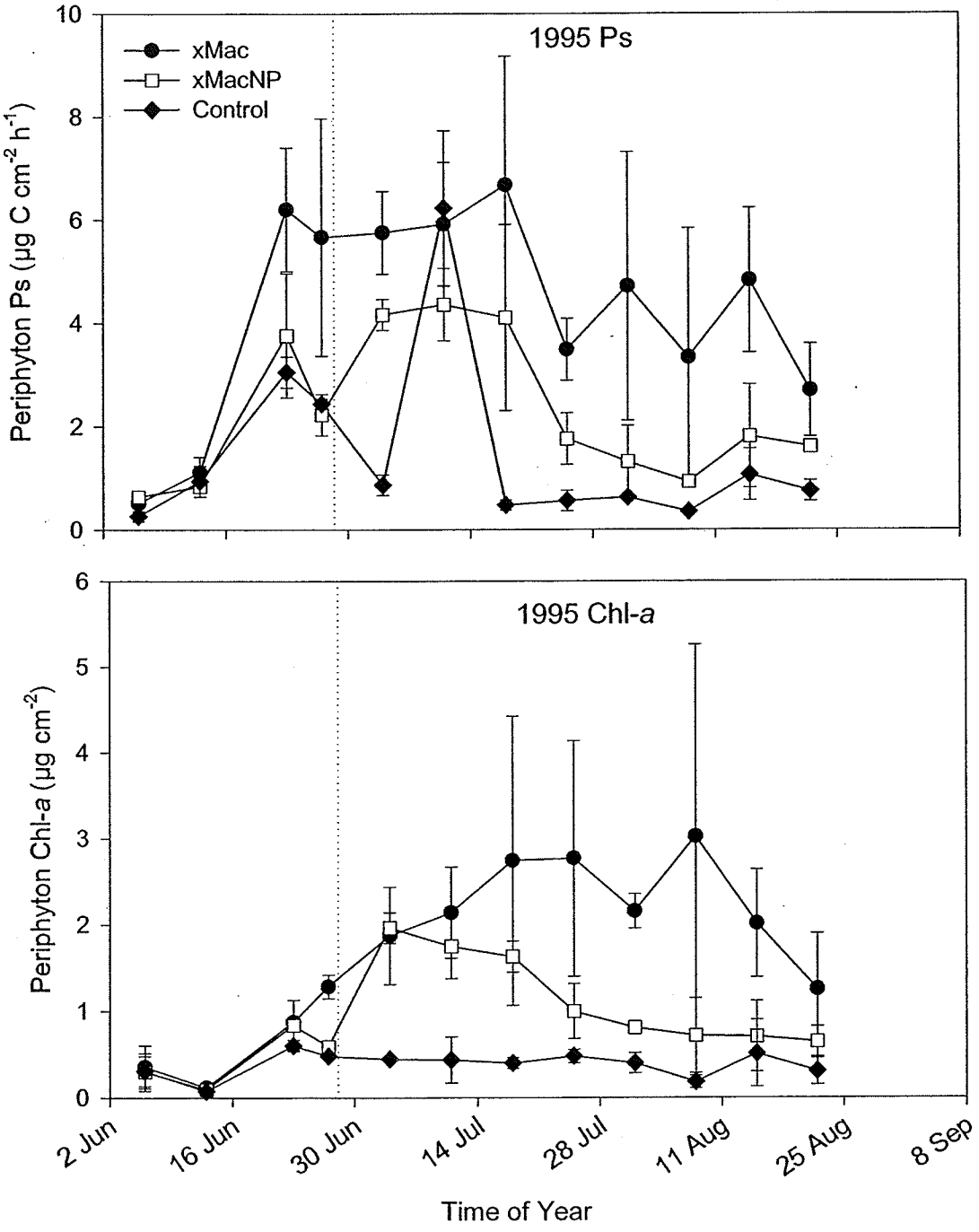

Figure 57. Periphyton photosynthesis (µg C cm^{-2} h^{-1}, ±SE, n=2) and periphyton chlorophyll-*a* (µg cm^{-2}, ±SE, n=2) in experimental enclosures in 1995. Vertical dotted line denotes the start of nutrient addition on 28 June, 1995. (Note change in scale of y axis.)

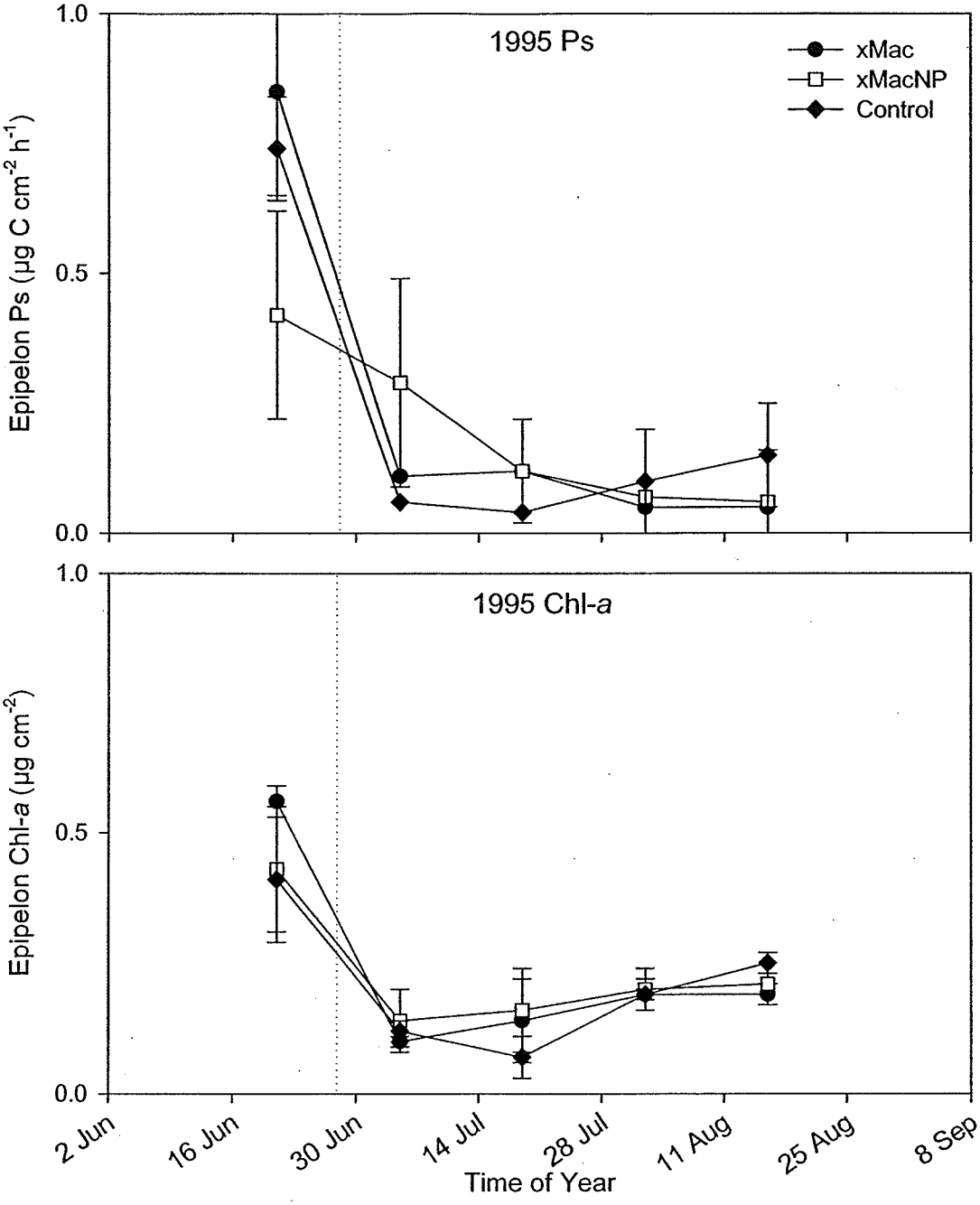

Figure 58. Epipelon photosynthesis (µg C cm^{-2} h^{-1}, ±SE, n=2) and epipelon chlorophyll-*a* (µg cm^{-2}, ±SE, n=2) in experimental enclosures in 1995. Vertical dotted line denotes the start of nutrient addition on 28 June, 1995.

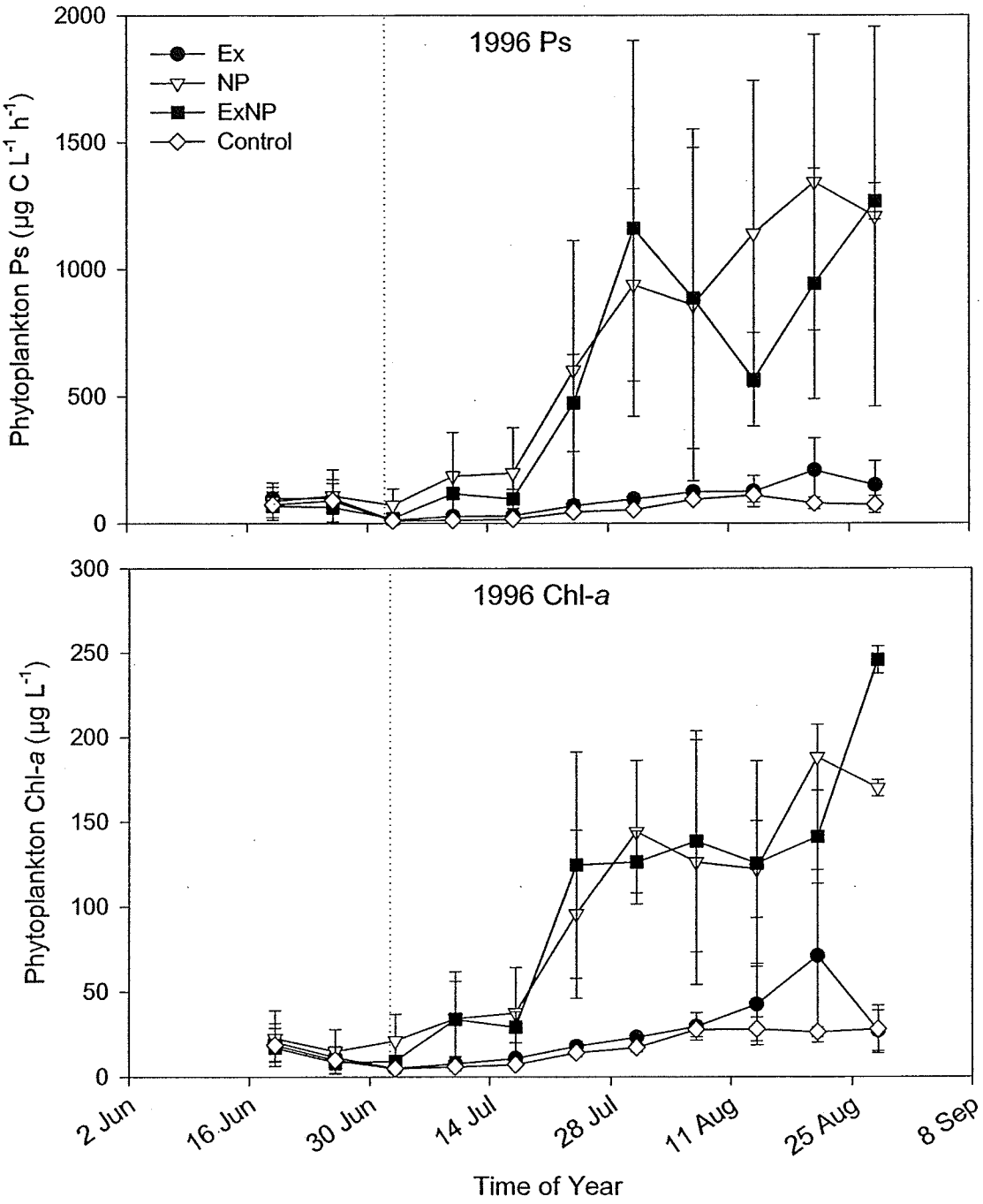

Figure 59. Phytoplankton chlorophyll-*a* (µg L^{-1}, ±SE, n=2) and phytoplankton photosynthesis (µg C L^{-1} h^{-1}, ±SE, n=2) in experimental enclosures in 1996. Vertical dotted line denotes the start of nutrient addition on 3 July, 1996. (Note change in scale of y axis.)

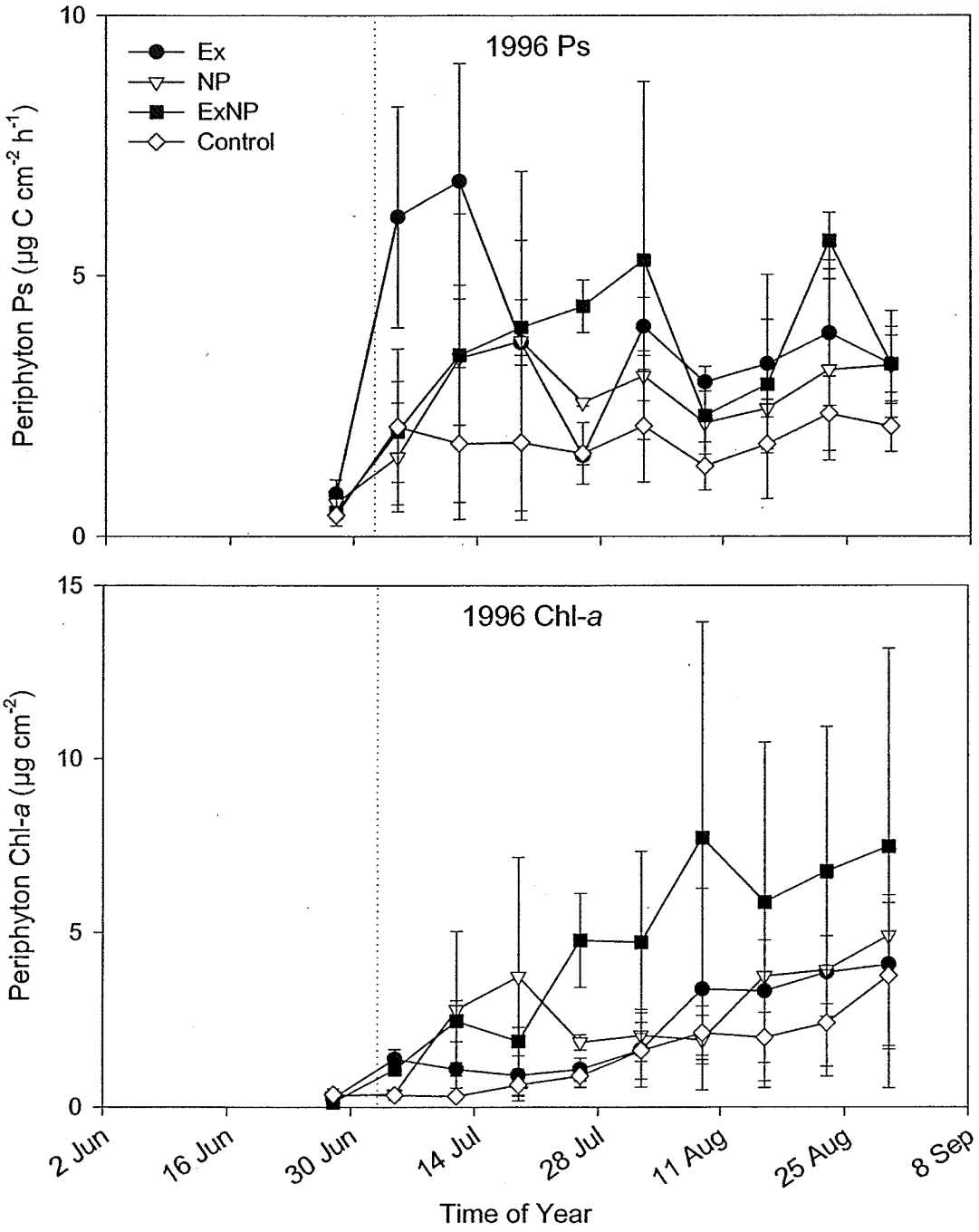

Figure 60. Periphyton photosynthesis (µg C cm^{-2} h^{-1}, ±SE, n=2) and periphyton chlorophyll-*a* (µg cm^{-2}, ±SE, n=2) in experimental enclosures in 1996. Vertical dotted line denotes the start of nutrient addition on 3 July, 1996. (Note change in scale of y axis.)