NUTRIENT DYNAMICS IN GREAT LAKES COASTAL WETLANDS: FUTURE DIRECTIONS

Robert T. Heath
*Department of Biological Sciences
and
Water Resources Research Institute
Kent State University
Kent, Ohio 44242*

ABSTRACT.   The most comprehensive investigations of N and P dynamics in Great Lakes coastal wetlands have been done at Old Woman Creek National Estuarine Research Reserve (OWC); whether OWC is a good general model of coastal freshwater wetlands remains to be shown. This wetland is probably a nutrient sink, storing P in sediments (at least temporarily) and releasing N by dissimilatory denitrification. Also, its biotic community transforms dissolved inorganic N and P inputs into organic dissolved and particulate outputs, thereby altering nutrient availability to Lake Erie communities. Nutrient dynamics in coastal wetlands probably differs greatly from that of inland marshes (where slow decomposition rates permit peat to accumulate as a nutrient sink) and estuaries (where high salinity alters sediment nutrient dynamics). A conceptual model specific for coastal wetlands is presented that accounts for the wide range of redox potentials encountered over the short vertical span of the shallow OWC wetland ecosystem. Future studies need to be conducted within the context of testable hypotheses generated from this model. Future investigations should focus attention on annualized nutrient budgets, sediment-water nutrient exchanges and their dependence on organic matter generated within the ecosystem.
INDEX WORDS: Wetland, Lake Erie, cycling nutrients, phosphorus, nitrogen.

INTRODUCTION

Situated between coastal watersheds and the open water of the Laurentian Great Lakes, freshwater coastal wetlands may significantly alter the impact of nutrients released from watersheds on the receiving lakes. By comparison with large efforts to understand the structure and function of freshwater inland wetlands and coastal salt marshes and adjacent estuaries for both scientific and management purposes, relatively little is known about the influence of Great Lakes coastal wetlands on nutrient inputs. These coastal wetlands are rapidly vanishing because of their usefulness as rich agricultural land and as sites for real estate development and recreational activities. Along the southwestern coast of Lake Erie alone, they have diminished from about 4,000 km² in 1850 to less than 150 km² at the present; the predominant loss has been to agricultural development (Herdendorf 1987).

Coastal wetlands should be studied within a context of testable hypotheses. Can the paradigms developed from the great number of studies of nutrient dynamics of freshwater inland marshes or marine estuaries be transferred to formulating useful hypotheses regarding the function of coastal wetland ecosystems on the Great Lakes? My primary goal here is to address this question by summarizing current knowledge regarding nutrient dynamics in Great Lakes coastal wetlands and to compare those findings with research conducted on inland marshes and marine estuaries. My thesis is that Great Lakes coastal wetlands differ sufficiently from both freshwater marshes and marine estuaries to require their own conceptual models from which testable hypotheses can be developed.

Rather than being a comprehensive review, this paper focuses on nutrient dynamics research that has been done at Old Woman Creek National Estuarine Research Reserve (OWC) and relates it to selected studies completed on other Great Lakes coastal wetlands. As the only freshwater wetland included in the National Estuarine Research Re-

serve System under the aegis of NOAA within the U.S. Department of Commerce, OWC is managed to provide a reliable base for long-term investigation. Since 1980, both a rigorous monitoring program and various scientific investigations have studied nutrient content, dynamics, and fate within this wetland. These studies, coupled with current views of wetland and estuary function, provide a basis for identifying gaps in our current knowledge of coastal wetland ecosystems and a basis for presenting a conceptual model of nutrient dynamics for Great Lakes coastal wetlands in general.

OLD WOMAN CREEK WETLAND

General Characteristics

The OWC-NERR is located on the southern shore of Lake Erie, about 5 km east of Huron, Ohio. A 0.3 km² marsh wetland, situated along the 2.1 km drowned mouth of OWC, drains a 69.1 km² watershed with agriculture as the predominant land use (Brant and Herdendorf 1972, Woods 1987). Stream gradients of OWC were originally much faster and steeper than at present, but as the level of Lake Erie rose due to crustal rebound following glacial retreat, OWC gradients decreased, the mouth became drowned, and deposition at the mouth was increasingly dominated by finer sediments (Buchanan 1982, Woods 1987). During the past 100 years only silts and clays have accumulated, and the rate of deposition has increased due to agricultural activities in the watershed. Of the three geomorphic provinces within the watershed (Lake Plain, Berea Escarpment, and Till Plain), the majority of the deposits currently originate from agricultural land on the Till Plain in the upper regions of the watershed (Buchanan 1982).

Flow rate through OWC wetland marsh is controlled primarily by storms. During seasons of high flow and storm activity on the lake (typically November through mid-April), the mouth is open and flow progresses rapidly through the wetland marsh. During relatively quiescent times the mouth is closed by a barrier beach (typically May through September), and flow through the marsh is limited to percolation through that barrier. The barrier beach, that is probably recent, has permitted an acceleration of deposition by slowing the water flow rate (Buchanan 1982). Slower flows permitted increased growth of macrophytes, and may have led to increased sediment organic content. Sus-

pended sediment remains relatively constant (approx. 0.1 g/L) throughout the wetland marsh, increasing during storms (Buchanan 1982).

Hydrologic differences due to the presence or absence of the barrier beach give rise to different behaviors of OWC. When the barrier beach is absent, water rapidly flushes through the marsh with a residence time of only several hours (Klarer 1988). These conditions provide a lotic scenario in which hydrology and sediment transport dominate nutrient dynamics. Presence of the barrier beach gives a lentic scenario as the water residence time extends to the order of weeks; concerns of nutrient uptake for growth and the dynamics between planktonic, benthic and littoral communities then dominate.

Nutrient dynamics in Old Woman Creek

Two categories of investigations should be addressed regarding nutrient flow through coastal wetlands: (1) the effect of available nutrients on the wetland community itself, and (2) the effect of the wetland on nutrient availability to the receiving lake community. In the first category are studies that determine the effects of various nutrients on the growth and activities of organisms within the wetland, such as studies related to growth limitation by nutrient availability (e.g., Correll and Weller 1989). In the second category are studies that determine whether the wetland ecosystem acts as a "sink," "source," or a "transformer" of given chemical compounds known to support growth and activities of organisms in the receiving lake community (e.g., Richardson 1989).

Nutrient limitation studies

Based on estimates of gross planktonic primary production (3,700 kcal m⁻² yr⁻¹) and net macrophytic primary production (750 kcal m⁻² yr⁻¹), OWC plankton community is considered to be relatively productive, but macrophyte productivity is modest by comparison to other wetlands (Mitsch and Reeder 1989). Does nutrient availability limit primary productivity? The average summer concentrations are 8.426 μM NO$_3^-$ (Wickstrom 1988) and 0.284 μM PO$_4^{3-}$ (Heath 1987), giving an average N:P atomic ratio of 29.67 of available nutrients. This atomic ratio would be expected to cause phytoplankton to be P-limited (Chiaudani and Vighi 1979), although algal productivity apparently was not P-limited in nutrient-addition bottle assays (Heath 1987). Phosphatase specific activity,

an indicator of P-limitation (Fitzgerald and Nelson 1966), remained relatively low at all times, consistent with the conclusion that plankton were not P-limited. On one occasion, early in the growing season, additions of nitrate stimulated planktonic productivity, indicating that N-availability may on occasion limit phytoplankton growth (Heath 1987). Because the turbidity of the open water was typically between 60–80 nephelometric turbidity units (NTU), planktonic productivity may ultimately be limited by light availability. Possible nutrient limitation of macrophyte growth has not been investigated in OWC.

Input-Output studies

Much of the nutrient load enters the OWC wetland either dissolved or sorbed to sediments following storm events (Klarer 1988). By comparing the relationship between turbidity and nutrient concentrations measured at sites along the flow axis following early spring storms before formation of the barrier beach, three different classes of nutrients were identified according to the way in which nutrient concentration was attenuated following the storm: Table 1 (data from Klarer 1988, Klarer and Millie 1989). Nutrient concentrations were compared with turbidity because turbidity (measured in NTU) correlated well with stormwater influx ($r^2 = 0.97$, 40 D.F.) (Krieger 1984). Positive correlations with turbidity implied that these ions (e.g., PO_4^{3-} and NH_4^+) were loaded in the creek with eroded sediments in surface runoff. Both K^+ and NH_4^+ are regularly added in agricultural fertilization practices within the watershed, and their loading probably resulted from losses from recently fertilized farmlands. The delayed increase of certain other ions (e.g., NO_3^-) following storm events implied mobilization of these ions from the subsurface soil, loaded as storm interflow (Baker 1984). Negative correlation with turbidity was interpreted to mean that ions such as Ca^{2+} and Mg^{2+} are water soluble, enter the creek at constant rates and are diluted by stormwater.

Decreases in concentration of biologically important ions such as PO_4^{3-}, NO_3^-, and Si were much greater than would be expected from geochemical processes alone (Klarer and Millie 1989). Concentration decreases due to dilution were detected by comparison with decreases in Cl^- concentrations, a biologically conservative ion. The ions Fe^{3+}, Mn^{2+}, and Zn^{2+} were probably lost from the water column by sorption to sediment surfaces (Angino

TABLE 1. Nutrient loading following storm events, Old Woman Creek Watershed (adopted from Klarer 1988).

Nutrient Ions	Output/Input Ratio	
	April	May
Class I: Positive correlation with turbidity at all sites; concentration increases are coincident with turbidity influx.		
PO_4^{3-}–P	0.49	0.20
NH_4^+–N	1.18	0.81
K^+	0.67	0.55
Fe^{3+}	0.65	0.46
Cu^{2-}	0.47	0.50
Zn^{2-}	0.50	0.40
Class II: Positive correlation with turbidity at some sites; concentration increase trails turbidity influx.		
Si	0.50	0.28
NO_3^-	0.65	0.28
NO_2^-	1.09	0.70
Class III: Negative correlation with turbidity; concentration decreases with turbidity influx.		
Ca^{2+}	0.98	0.73
Mg^{2+}	0.96	0.74
Na^+	0.95	0.67
Cl^-	0.92	—
SO_4^{2-}	0.87	0.49

et al. 1974) and subsequent sedimentation as the flow rate decreased, especially in the broad shallow lower reaches of the OWC wetland where water passed over remnant macrophyte beds. Losses of PO_4^{3-}, NO_3^-, and Si from the water column at a rate greater than loss of Fe^{3+} implied that biogeochemical processes, such as uptake by bacterioplankton and phytoplankton, were important factors in decreasing the nutrient load available in water leaving the wetland (Klarer 1988).

Input-output studies conducted during quiescent times when the mouth of the wetland was closed indicated that inorganic nutrients were lost from the water column. Orthophosphate concentration (detected as SRP) was two to five times lower at the outlet than at the inlet (Reeder and Mitsch 1989, Heath 1987, respectively) when the barrier beach closed the mouth of OWC. The proportion of dissolved and particulate organic forms increased as inorganic P was removed from the water column. Dissolved organic phosphorus compounds (DOP) and particulate P were elevated at sites studied within the wetland, but overall their

concentrations were only slightly elevated at the outlet compared to DOP and particulate P at the inlet station (Heath 1987, Reeder and Mitsch 1989). Similarly, dissolved inorganic N (DIN) concentrations decreased five-fold along the flow axis from the inlet to the outlet (Wickstrom 1988). Nitrate concentrations decreased markedly, while nitrite and ammonium concentrations showed about two-fold decreases during passage through the wetland. Dissolved organic nitrogen (DON) and particulate N have not yet been studied in OWC.

Despite consistently lower concentrations of important inorganic nutrients at the outlet, these findings have a limited value in assessing the performance of the wetland ecosystem because they include considerations neither of total amounts transported nor of possible removal processes. When nutrient concentrations are coupled to hydrologic flows, nutrient fluxes across the inlet and outlet boundaries can be calculated and mass balance budgets estimated. Using observations of P-loading from the OWC watershed and transfer rates estimated within OWC, a simulation model was constructed that included phosphate uptake by plankton and macrophytes, exchanges between the sediments, phytoplankton, macrophytes, and dissolved P compounds (Mitsch and Reeder 1991). Especially important, this model included considerations of the influence of different hydrologic scenarios and the implicit dependence on primary production.

This model estimated that 10 percent of P entering the marsh was retained in sediment accumulation, and the remainder left as dissolved P and plankton. Simulations from early spring through autumn indicated that the ecosystem is a slight P-sink in the summer. This model considered that there was no efflux in the presence of the barrier beach, although recent studies using lysimeters show a percolation of water through the barrier beach (Matisoff and Eaker 1989), implying that this model may have underestimated efflux. Analysis of this model indicated that sedimentation was the most important sink for P and that release of "unavailable P" from plankton, macrophytes, and sediments was also significant in diminishing the availability of P. "The Old Woman Creek wetland clearly has a major role to play in the nutrient dynamics of its watershed, but it is more likely as a nutrient transformer than as a nutrient sink"; the marsh retained from 17–52 percent of P entering; retention was strongly influenced by hydrology (Reeder and Mitsch 1989).

Biogeochemical processes within OWC wetland

"Transformations" of dissolved nutrients entering the wetland into less readily available particulate and dissolved organic materials are largely a consequence of a complex array of geochemical and biological processes that are not fully understood. The rate of phosphate uptake by particles caught on a Millipore 0.45 μm filter increased along the flow axis through the wetland (Heath 1986, 1987, 1992). Using short-term radiometric experiments and inhibiting metabolic activities with cyanide or CCCP, these studies also showed that the fraction of phosphate taken up "actively" (i.e., dependent on metabolic energy) also increased toward the mouth of the wetland during the growing season. Dissolved organic phosphorus compounds increased in concentration at sites within the wetland during the growing season. Phosphomonoesters, a class of low molecular weight DOP compounds that can be hydrolyzed by phosphatase enzyme activity (Francko and Heath 1979), consistently increased along the flow axis through the OWC wetland, approximately compensating for the loss of phosphate from the water column (Heath 1987). Bacterial and algal phosphatase also increased through the wetland and through the growing season, indicating that plankton recycled this important class of DOP compounds (Heath 1986, 1987). Alteration of P from predominantly dissolved inorganic compounds to dissolved and particulate organic compounds further indicated that the OWC wetland acted as a "transformer" of nutrient availability (Heath 1987).

Large quantities of nitrate (0.36–2.81 mg/L) from the OWC agricultural watershed entered the marsh but diminished by about 95 percent in transit through the wetland during times of slow flow, while the quantity of ammonium increased 1.5 to 2 fold during transit through the wetland (Wickstrom 1988). Ammonium concentrations entering the marsh in mid-summer 1986 were typically 0.12 mg N/L and concentrations leaving the marsh were typically 0.19 mg N/L. Ammonium was the only DIN component that was in substantially greater concentration in sediment pore water than the overlying waters (0.19 mg N/L in the overlying water and 0.29 mg N/L in the pore water), suggesting that significant ammonification occurred at the sediment surface and that sediments could be a source of ammonium to the water column. Although nitrogenase activity is present in the plankton (largely *Anabaena* sp.), on the stems of rooted

macrophytes (probably due to epiphytic *Gloeotrichia*) and at the sediment surface (due to heterotrophic azotrophic bacteria), N-fixation represented considerably less than one percent of the N-budget of the estuary (Wickstrom 1988).

Role of sediments in nutrient dynamics of OWC

Frizado *et al.* (1986) conducted an extensive chemical and physical survey of the structure of OWC sediments. Analyzing 12 sediment cores, 18 surface sediment samples, and 31 suspended sediment samples taken throughout the wetland area, they conducted quantitative studies of the size, mineralogy, and elemental composition of sediments and pore waters. Sediments in the region of the major stream flux were coarser and had lower clay composition than sediments taken from more quiescent regions of the marsh, likely due to the continual resuspension and washing out of the finer clay material in the more turbulent areas. They noted greater organic content of surface sediments taken from vegetated areas, but did not report large storage of peat, as generally would be found in an inland marsh. Pore water composition was not related to the bulk mineralogy of adjacent sediments. Trace elements were in higher concentration in pore waters than in overlying water, indicating that sediment was a source of these elements to the wetland community.

Phosphate content (measured as SRP), DOP, and total P content of the pore water became progressively more similar to the overlying water along the flow trajectory (Heath 1987, 1992). Also in this study, continuously suspended sediment slurries took up phosphate under aerobic conditions but released it under anaerobic conditions. At the entry to the OWC wetland, uptake of phosphate by sediments was largely due to abiotic geochemical reactions in the sediment sample, but phosphate uptake became progressively more dependent on biotic processes and was largely dependent on biotic processes (i.e., greater than 90 percent) in the sample taken from the mouth of estuary (Heath 1987).

Sediments are likely to be actively involved in N-dynamics in the OWC estuary, as well. Large quantities of incoming nitrate are either taken up by biota for growth or denitrified by sediment microbes (Wickstrom 1988). As organisms senesce, die, and decompose in the sediments, ammonium is produced largely by ammonifying bacteria (Bu-

chanan and Gibons 1974). Whether ammonium is released to the surrounding pore water or assimilated for production of amino acids is a function of the C:N ratio of available nutrients. At high C:N, ammonium is utilized for amino acid production and growth. At low C:N, ammonium is released to the pore water and diffuses to the overlying waters (Hardy and Holsten 1973), where it can be assimilated by growing plankton populations or exit the wetland.

Ammonium can also be utilized by obligate aerobic autotrophic nitrifiers: Group I, ammonium-oxidizing bacteria, and Group II, nitrite-oxidizing bacteria. In freshwater habitats these are generally species of *Nitrosomonas* (Group I) and *Nitrobacter* (Group II) (Watson *et al.* 1981). These genera are seldom planktonic but are attached to surfaces of sediments and suspended particles (Matulewich and Finstein 1978). Nitrite and nitrate produced by these nitrifiers can be released to overlying aerobic waters, re-assimilated by growing organisms, or reduced to N_2 by dissimilatory denitrifiers. In freshwater habitats, facultatively anaerobic species of the genera *Alcaligenes, Bacillus*, and *Pseudomonas* are the most common denitrifiers (Jeter and Ingraham 1981). Each of these processes may play a role in the N-dynamics of OWC, yet none of these processes has been observed or measured. However, relatively high quantities of nitrite occurred in the pore and overlying waters (0.08 mg $N L^{-1}$ in both pore water and overlying water) and bacteria capable of dissimilatory denitrification existed in the sediments ($1-12 \times 10^5$ cells mL^{-1}, MPN) (Wickstrom 1988).

Conceptual model of OWC wetland nutrient dynamics

Research conducted at OWC has represented the interests of the individual investigators more than a programmed investigation of testable hypotheses formulated around a conceptual model (Krieger *et al.* 1990). Such a model is presented here as a hypothetical synthesis based on studies conducted at OWC and elsewhere (Fig. 1). This model emphasizes the importance of sediment-water interactions owing to the shallowness of the marsh. Microbial activity in the water column, at the sediment-water interface, and within the sediments likely is intense because of the high temperatures resulting from this shallowness. The water column is treated without vertical structure because com-
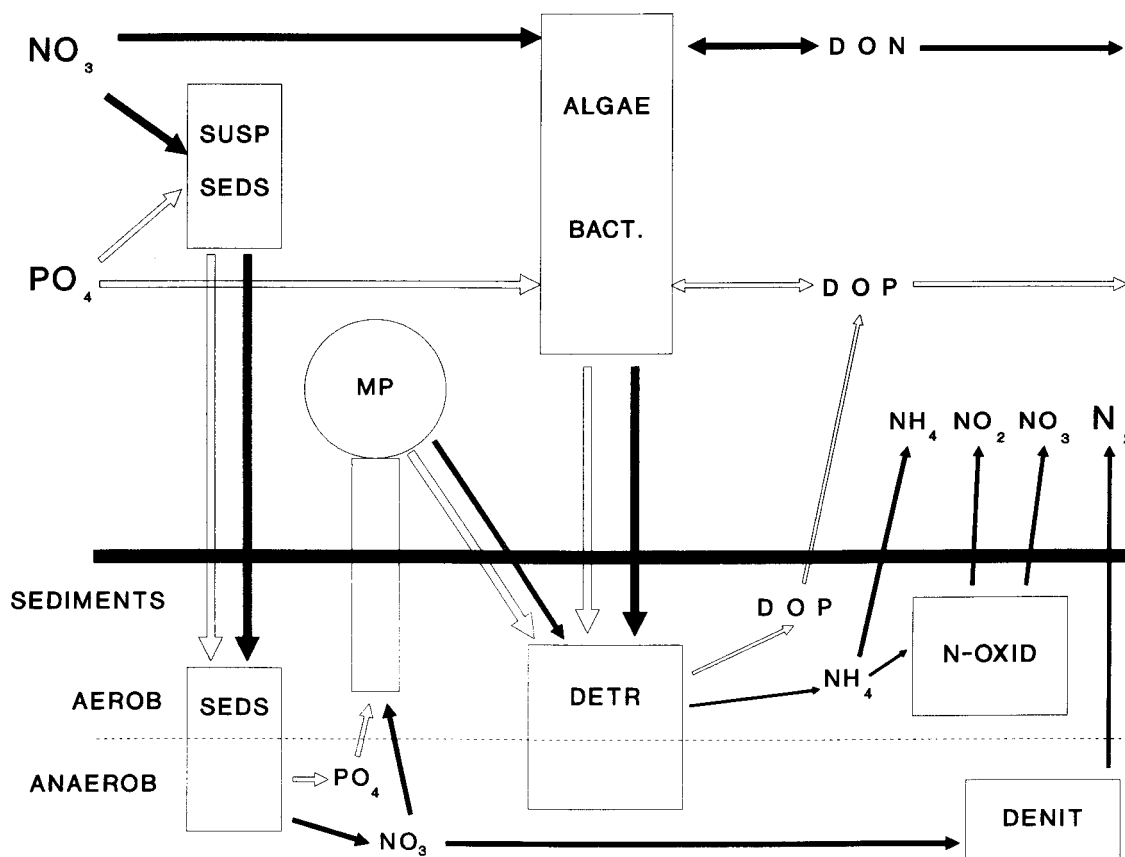
FIG. 1.   Conceptual model of N and P dynamics in OWC wetland. N-flux shown in solid arrows; P-flux in open arrows. Particulate quantities in boxes, dissolved quantities unboxed. SUSP SEDS, suspended sediments; SEDS, sediments, aerobic sediments above dashed line, anaerobic sediments below dashed line; water column above the heavy solid line. Algae and bacterioplankton shown together; MP, rooted macrophytes; DETR, detritus; N-OXID, nitrogen oxidizing bacteria (Group I and Group II grouped together); DENIT, denitrifying bacteria.

plete mixing is frequent, providing sediment resuspension and wide diurnal variations in oxygen concentration at the sediment surface (ranging from 2 to 14 mg O_2 L^{-1}) (Mitsch and Reeder 1991).

This model is intended to represent OWC during a time of relatively slow flow, as occurs after formation of the barrier beach. The model is also built on the assumption that after formation of the barrier beach biotic nutrient assimilation becomes progressively more significant during passage of incoming nutrients through the wetland marsh, although sedimentation likely also represents a major sink of incoming P (Reeder and Mitsch 1989). When the barrier beach is open and flow through the wetland occurs, nutrient loss from the water column is probably largely due to sorption to sediment surfaces followed by settling as flow rate decreases over the broad shallow expanse of the wetland (Frizado et al. 1986).

Ironically, the most important part of this conceptual model is the least studied at OWC. Sediments have been characterized chemically and physically (Buchanan 1982, Woods 1987, Frizado et al. 1986), but biological characteristics have been performed only cursorily as a part of other studies (Heath 1987, Wickstrom 1988, Reeder and Mitsch 1989). Yet these studies, taken together, suggest that the high productivity of the plankton community and of macrophytes drives an active benthic microbial community.

Phosphate is rapidly sorbed to aerobic sediments and assimilated by plankton (algae and bacteria) or assimilated from aerobic sediments by macrophytes (Carignan and Kalff 1980). In turn, DOP is released from plankton, possibly as a result of grazing activities (Ivancic and Degobbis 1987). Also, bioavailable P can be released from living macrophytes (Burkholder *et al.* 1990) and by decomposition in the sediments (Smith and Adams 1986). Following release from sediments, DOP can be recycled by bacteria and some phytoplankton (Tarapchak and Moll 1990).

Similarly, nitrate entering OWC wetland is either rapidly sorbed to inorganic suspended sediments or assimilated by plankton; macrophytes can assimilate nitrate from aerobic sediments (Barko *et al.* 1986). Plankton can release DON or decompose in the sediments and release ammonium. Large deposits of detritus from plankton and macrophytes likely drive active metabolism in the sediments. Although some ammonium may be released to overlying waters because of turbulence that resuspends sediments (Binnerup *et al.* 1992), most ammonium is likely taken up rapidly by ammonium-oxidizing bacteria that may release nitrite which in turn is probably taken up by nitrite-oxidizing bacteria (Gardner *et al.* 1987). Nitrate released in the sediments is then used by denitrifying bacteria in the anaerobic sediments which release N_2 to the overlying waters (Gardner *et al.* 1991).

IS OWC TYPICAL OF OTHER GREAT LAKES COASTAL WETLANDS?

Wetlands differ from each other and vary over time primarily as a function of hydrologic sources and flow rates. Rather than a constant source of water entering at a constant rate, Great Lakes coastal wetlands are storm-driven ecosystems, as the hydrology of coastal wetlands is dominated by storm events that radically alter the flow rate and can even alter the primary source of the water (Herdendorf and Krieger 1989). Two different types of coastal wetlands can be identified according to their structure that permits them to persist after major storms: (1) the "barrier and lagoon" wetland, and (2) the "embayment" wetland (Geis 1985, Herdendorf and Krieger 1989).

Very few reported studies of nutrient dynamics in Great Lakes coastal wetlands have been sufficiently comprehensive to provide an adequate comparison with OWC. Nutrient concentrations have been reported from many coastal wetlands,

indicating similarity with OWC, but seldom have studies been organized around questions such as whether the wetland is a "sink, source or transformer," nutrient limitation of wetland species, or detailed examination of specific nutrient processes. Concentrations of SRP typically range widely in coastal marshes throughout the year. Especially in barrier and lagoon type wetlands, concentrations can vary from barely detectable to greater than 1,000 μg SRP-P L^{-1}; the annual variation of SRP in OWC ranges from < 1–283 μg L^{-1} (Krieger 1989). Nitrate + nitrite also can range from barely detectable to over 10 μg L^{-1}, as OWC varies from 0–13.8 μg $(NO_3 + NO_2)$-N L^{-1} (Krieger 1989).

Calculations of nutrient discharges from Big Creek Marsh into Long Point Bay indicate that coastal wetland is a nutrient sink that contributes negligible amounts of N and P to Lake Erie (Mudroch 1981). Big Creek runs along the northern boundary of a marsh that opens into the bay, but it is unclear how much of the creek water actually passes through the wetland. Because the water residence time within the marsh is uncertain, the actual load to Long Point Bay remains unclear (Krieger 1989). A strong positive correlation between total N load and above-ground production of *Typha latifolia* indicated that macrophytes in Big Creek Marsh may be N-limited. Although nitrate was the predominant form of N in the creek, most of the N within the marsh was organic-N, indicating that the marsh may transform N inputs to forms less available to lake organisms.

The relation between seiche periods and nutrient content in a coastal marsh on Green Bay indicated that a coastal marsh generally acted as a nutrient transformer (Sager *et al.* 1985). Peter's Marsh exchanges water as Green Bay seiches with an average period of about 10 hours. Nutrient-rich hypereutrophic water containing large quantities of algae enters during flood periods. The performance of the wetland on these inputs can be estimated by comparing the water content leaving the marsh during the ebb periods with that entering it. Comparison of chemistry of the water column between ebb and flood periods indicated that this *Typha* dominated wetland generally imported particulate N as algae and exported dissolved nitrate, nitrite, and ammonium. Likewise, Peter's Marsh retained "total P" and exported DOP, in general. The marsh had a net retention of particulate carbon and a net release of inorganic carbon, presumably as respired CO_2. Activity of the marsh appeared to be most intense at the end of summer.

Sandusky Bay is a 30 km long drowned river mouth that receives considerable nutrient and sediment loads from a large agricultural watershed. The bay is constricted about 10 km from the mouth, creating an upper and a lower bay; the constriction prevents lake intrusions from entering the upper bay. Sandusky Bay has a water residence time ranging from days to months, depending on precipitation in the watershed (Richards and Baker 1985). It is a broad, shallow and turbid water mass, with an average depth of 2.6 m, a Secchi transparency in summer that ranges from 15 cm in the silt-laden upper reaches of the bay to about 0.8 m in the lower regions of the bay that support large cyanobacterial populations (Garono and Heath 1992). Comparison of incoming stormwater with outgoing water quality indicated that suspended solids decreased 97%, total P decreased 86%, SRP decreased 77%, and nitrate + nitrite decreased 51%, yet chlorophyll content of suspended solids increased greatly. Following large storms, high SRP concentrations were rapidly attenuated in the upper bay, but total P loads from the watershed were much less attenuated as the water mass proceeded through the bay into Lake Erie (Richards and Baker 1985). Likewise, nitrate + nitrite concentrations were rapidly attenuated on entering the bay.

In contrast with the marshy wetlands such as Big Creek Marsh or Peter's Marsh that are dominated by macrophyte production, Sandusky Bay's productivity is largely in phytoplankton. The phytoplankton community is unique to the embayment and differs from that of either Sandusky River or nearshore Lake Erie (Garono and Heath 1992). Examination of physiological variables characteristic of nutrient limitation indicated that phytoplankton were not growth limited by the availability of either N or P. Phosphatase specific activity of the phytoplankton was low and phosphate turnover times were long in comparison with P-limited communities. Also, Nostocalean cyanobacteria (largely *Anabaena* sp.) exhibited very low proportions of heterocysts relative to the number of vegetative cells, indicating that these populations were not N-limited (Heath, unpub. obs.). Also, bacterial and rotifer populations were generally ten-fold higher in the bay than in Lake Erie, suggesting an active microbial metabolism of dissolved and particulate organic matter in the bay (Hwang and Heath 1992). Although Richards and Baker (1985) regarded Sandusky Bay as a nutrient sink, the large phytoplankton and bacterioplankton populations that develop in summer indicate that this embayment may act more as a nutrient "transformer" than as a permanent sink, transforming inorganic nutrients into dissolved and particulate matter that is retained in the bay until flushed into the lake by storms or seiches.

These examples of coastal wetlands demonstrate the variety of structure encountered at the land margin interface with the Great Lakes. They also illustrate the difficulty of categorizing these wetlands into distinct types or of finding a "typical model wetland." None is a good example of either the "barrier and lagoon" type or the "embayment" type of wetland; even Sandusky Bay has been termed "entirely anomalous in contrast to all other tributary confluences in . . . the Great Lakes" (Bedford 1989). None is similar in structure to OWC, and OWC itself is unlike either of the general coastal wetland types. OWC exhibits characteristics of both types of wetland but at different times of the year. During quiescent times in the summer when the barrier beach is present, OWC is similar to the "barrier and lagoon" wetland type, except that its major source of water and nutrients is from the watershed, whereas, when the creek mouth is open, OWC is an "embayment" wetland, where water and nutrients from the watershed can mix with lake water during seiches.

Despite the differences among Great Lakes coastal wetlands, broad general characteristics of these ecosystems can be recognized, and testable hypotheses can be formulated within the limits of these generalities. They share a temperate climate; their nutrient regimes are closely linked to their hydrologic regimes; they are pulse-fed on irregular schedules (Kaiser 1985). They support highly productive macrophyte and phytoplankton communities that appear to support large populations of bacteria and zooplankton (Klarer 1989, Havens 1991, and Krieger and Klarer 1991). They are relatively shallow, so exchange between the water column and the sediments probably is rapid, and interactions between the sediments and the water column probably are important in determining the rate and extent of individual processes of nutrient dynamics. As King (1985) noted, "much of the variability on surface earth . . . is encompassed in a (vertical) foot or less of a Great Lakes wetland," referring to the wide range of pH and oxidation potentials from the productive, alkaline, oxygen-supersaturated water column to the acidic, highly reducing condition of the sediments. Within the context of these generalities, OWC is typical of Great Lakes coastal wetlands.

COMPARISON OF OWC WITH NUTRIENT DYNAMICS OF STATIC INLAND MARSHES

Because of the very slow flow through OWC wetland in the growing season, those inland marshes through which water passes slowly may serve as good models of OWC in particular and coastal wetlands in general. Many studies have shown that available dissolved inorganic nutrients are rapidly removed from hydrologic inputs into static inland marshes (e.g., fens and bogs). In consideration of possible application of inland studies to coastal wetlands, Tilton et al. (1978) compiled a good review of nutrient dynamics in marshes. Uptake of phosphate by various submergent species showed that uptake was a function of two processes, each conforming to Michaelis–Menten kinetics, with K_t ranging from 0.006 to 37 μM, and V_{max} ranging from 0.03 to 2.2 mmol PO_4/kg. dry wt./20 min (Gerloff 1975). Radiotracer techniques showed that dissolved inorganic P rapidly turned over, suggesting that this pool is the main contributor of P in a Michigan fen (Richardson and Marshall 1986). Dinitrogen fixation and atmospheric deposition of nitrate and ammonium were the major N inputs to a temperate freshwater bog in Massachusetts; dissolved nitrate and ammonium were rapidly assimilated by macrophytes (Hemond 1983). Because of the rapid turnover of dissolved inorganic forms of these nutrients, the water column contained only negligible quantities of total wetland N and P (Verhoeven 1986).

Inland marshes generally are nutrient sinks, accumulating peat and removing nutrients from availability either by storing them in litter and peat, or releasing them to the atmosphere in gaseous form (Richardson 1989). Examination of a swamp, a marsh, and a fen indicated that greater than 90% of the total N and P was stored in peat and litter, less than 10% was in living plants (Verhoeven 1986). Likewise, over 97% of the N and P was stored in a bound organic form, not readily available to plants growing in a Michigan fen (Richardson et al. 1978). Phosphorus was lost from availability by storage in peat in a Michigan fen (Richardson and Marshall 1986). In a Massachusetts freshwater wetland, nitrogen was lost by dissimilatory denitrification, releasing nitrogen to the atmosphere, and by ion exchange adsorption of ammonium to peat, relatively smaller amounts of ammonium and DON were lost in runoff water (Hemond 1983). In some systems ammonification and subsequent loss of ammonium in runoff or diffusive release of ammonia at high pH may constitute significant losses, and the contribution of dissimilatory denitrification to losses may often be greatly overestimated (Bowden 1987).

Differences in hydrology between inland marshes and coastal wetlands likely cause fundamentally different behaviors and make it doubtful that views developed from inland marshes will provide valid models for investigation of coastal wetlands. Inland marshes typically have slow runoff, and water is predominantly lost through evapotranspiration. For example, a Michigan peatland balanced 73 cm of precipitation input with 61 cm loss through evapotranspiration and 12 cm runoff loss; that is, 84% of incoming water was lost by evapotranspiration (Kadlec 1977). By contrast in OWC, even in a year of severe drought, evapotranspiration accounted for only 9% of the water loss; predominant inputs were from the upland watershed and the lake, and outflow to Lake Erie accounted for 87% of water loss (Mitsch et al. 1989). This difference in hydrology likely prevents significant accumulation of peat. Rather, much of the organically bound nutrients are probably washed out of the OWC wetland during seasons of rapid flow.

COMPARISON OF OWC WITH ESTUARINE NUTRIENT DYNAMICS

Great Lakes coastal wetlands are similar to marine estuaries in the sense that physical events (i.e., storms on the Great Lakes in lieu of ocean tides) drive gradient formation and exchange of material from the surrounding terrestrial community. These similarities have led to the suggestion that Great Lakes coastal wetlands be designated "estuaries" (Herdendorf 1990), a view not accepted by all (Schubel and Pritchard 1990). Beyond semantics, the important issue is whether viewing these as freshwater estuaries is helpful in gaining insights about their function from studies of estuaries, or conversely that studies conducted at OWC may be useful in understanding estuarine processes (Odum 1990).

Using in situ procedures in estuaries has shown that sediment interactions are critical to the overall nutrient dynamics through those coastal systems. Three North Carolina estuaries showed significant sediment releases of phosphate and ammonium, but not of nitrate, and indicated that sediments contributed 28–35 percent of the N and P required for algal production in the estuary (Fisher et al.

1982). These nutrient releases depended on the organic content of the sediments and did not occur in estuarine sediments low in organic content. Phosphate, DOP, nitrate, and ammonium behaved similarly and were released from sediments of a shallow coastal embayment at temperatures above 15° C (Nowicki and Nixon 1985a). This temperature dependence indicated that estuarine sediment function depended on microbial activity in the sediments and required organic content for metabolic support (Nowicki and Nixon 1985b).

Comparison of results from freshwater and estuarine systems indicates an apparent fundamental difference between the two environments in the fate of ammonium. In estuarine sediments ammonium, nitrate, and N_2 all constituted significant portions of the nitrogen flux across the sediment-water interface, whereas in freshwater systems, ammonium and nitrate losses were small and most of the nitrogen was released as N_2 (Seitzinger 1988). These findings imply that the fraction of ammonium available for nitrification and subsequent denitrification is greater in freshwater sediments than in marine estuaries. Recent studies indicated that these differences can be explained by the influence of sea salts on the mobility of ammonium produced in the sediments (Gardner et al. 1991, Seitzinger et al. 1991). In coastal marine sediments blockage of cation exchange sites by seawater cations and the ion pairing of ammonium with seawater anions apparently permit a significant portion of ammonium to diffuse from the sediments before nitrification can occur. In freshwater sediments, in general, ammonium apparently largely remains bound to sediment surfaces until it is nitrified, subsequently denitrified, and released as N_2 gas. Even in very productive systems, where some ammonium is released (e.g., Peter's Marsh), dissimilatory denitrification may also be very active, driven by large amounts of detritus, leading to substantial N-losses. Great Lakes coastal wetlands likely do not function as estuaries, largely because salinity causes different sediment characteristics.

CURRENT NEEDS AND FUTURE PERSPECTIVES

Understanding nutrient dynamics in coastal wetlands needs to be conducted in the context of testable hypotheses based on a plausible conceptual framework. In this paper I have presented a synthesis of work conducted at OWC. Evaluation of the usefulness of the conceptual model presented here awaits studies that test the hypothetical transfers presented. Such studies should consider mass balance flows on an annual basis, and they need to be specifically aimed at determining activities and transfers into, within, and out of the OWC sediments. Also, studies need to test the hypotheses that OWC is a "sink" and a "transformer" of P-availability resulting from rapid uptake of inorganic P, retention in suspended sediments, detritus and eventual release as less metabolically active DOP. The most likely losses of N are as N_2 through dissimilatory denitrification or in particulate organic material, flushed from OWC during times of high flow.

Subsequent investigations need to consider hydrology and productivity, because water flow and reduced carbon compounds are the primary sources of energy that drive nutrient dynamics in these ecosystems. Hydrologically, these pulse-fed systems can fill slowly from precipitation and watershed runoff, yet empty rapidly, carrying large amounts of detritus and sediment to the receiving lake. Because they are temperate systems with different hydrological characteristics in different seasons their investigation needs to be annualized: perhaps acting as nutrient sinks in the summer, yet becoming sources of nutrients in the winter, as storms remove materials in spates. Whether annual nutrient budgets are balanced remains to be determined and should be the focus of future investigations. Recently published models of phosphorus dynamics in OWC (Mitsch and Reeder 1991) include considerations of various hydrologic scenarios encountered in OWC and implicit dependence on primary production, making a major contribution toward that goal.

Because they are shallow productive systems, the functional relationship between the water column and the sediments needs to be investigated intensively. Being shallow, the water column and the sediments rapidly warm in the summer, stimulating high metabolic activity, supported by detritus and DOC. Primary productivity likely makes the water column oxidizing, wind mixing of the water column likely keeps the surface of the sediments aerobic, and benthic community metabolism likely depletes oxygen below the mixed zone (King 1985).

This wide range of redox potentials over the short vertical span possibly has both important thermodynamic and kinetic effects on nutrient dynamics (King 1985). Many chemical equilibria can affect nutrient availability, yet because these eco-

systems are open dynamic systems, not all reactions may reach equilibrium, necessitating a kinetic approach to these studies. A sufficient explanation of the coastal wetland ecosystem as a nutrient "transformer" requires that the rates of individual reactions and fates of biochemical compounds within the system be determined. The range of redox potentials implies that a variety of biologically important processes can proceed at kinetically significant rates. Sediment processes that depend on aerobic conditions (e.g., nitrification) can proceed rapidly at the sediment surface, while those dependent on anaerobic conditions (e.g., dissimilatory denitrification) can be performed only a short distance removed in adjacent micro sites (Jenkins and Kemp 1984), or deeper within the sediments.

Much past research on nutrient dynamics in these ecosystems has been accomplished largely piecemeal and out of the context of related investigations. Reports of results too often have been left in the "gray literature" of government reports and symposium proceedings. A *de facto* purpose of this paper has been to consolidate much of that "gray literature" in the hope that with a broader awareness of past accomplishments will come a greater interest in addressing future needs for understanding the functions of these ecosystems before they are damaged beyond reclamation or lost entirely from the coastal landscape.

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