

MATHEMATICAL MODELLING OF PRIMARY PRODUCTION IN
GREEN BAY (LAKE MICHIGAN, USA),
A PHOSPHORUS - AND LIGHT-LIMITED SYSTEM

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ABSTRACT

Application of mathematical models in the design and evaluation of lake restoration programmes must include due consideration of three basic concepts of model development; 1) that the model framework is appropriately matched to the intended management use, 2) that selection of the proper degree of model complexity is fundamental to the achievement of model credibility and 3) that field and laboratory studies must be designed and interpreted with the aid of the model to insure development of a comprehensive, integrated tool.

These concepts are demonstrated for the case of lake restoration efforts in Green Bay (Lake Michigan, USA). Striking gradients in water quality (transparency, algal standing crop, hypolimnetic oxygen depletion) and trophic state occur along the major axis of the bay in response to phosphorus loaded from the Fox River. A simple model for gross primary production is developed to permit calculation of the relative importance of internal carbon production to the total organic carbon budget of the bay. Primary production varies from high rates over a limited photic depth in the turbid, phosphorus-rich waters of the eutrophic portions of the bay to low rates over an extensive photic depth in the transparent, phosphorus-poor reaches of the oligotrophic regions. Internal production accounts for approximately 90 % of the total organic carbon loaded to the system over the summer growing season. Water quality management strategies must address the stimulation of primary production by phosphorus loaded from the Fox River in any attempt to lower the standing crop of nuisance algae, improve water clarity, and reduce rates of hypolimnetic oxygen depletion in Green Bay.

LAKE RESTORATION - AN INTEGRATED APPROACH

Matching model framework and management application.

A fundamental tenet of mathematical modelling is that models must be designed in consideration of their intended use or application. Two markedly different approaches may be utilized in designing models for analysis of lake restoration programmes, *viz.* simple, 'bottom up' models which rely on a careful quantification of key inputs, outputs and internal processes for simulation of pollutant dynamics and complex, 'top down', models which call for a comprehensive and detailed description of many ecosystem components. Simple models are routinely employed to quantify the response of surface water systems to water quality management plans and thus are identified with applied interests. The simple, applied models incorporate both mechanistic and empirical features, building from elementary mass balance considerations and drawing upon statistical relationships between decision variables (*e.g.* pollutant concentrations) and control variables (*e.g.* pollutant loadings) (RECKHOW and CHAPRA, 1983). Simple management models fail to improve our understanding of the effects

of remedial actions on fundamental ecosystem characteristics, *e.g.* plankton species composition or rates of nutrient and biomass turnover; further, the treatment of sources and sinks as net or collective processes in simple models provides little information on the relative importance of individual mechanisms to the overall mass balance. A more complex, ecosystem approach may be used to provide such information and to deal with environmental problems which may not be adequately characterized by a simple approach (CHAPRA and RECKHOW, 1983). The complex, ecosystem models are highly mechanistic in nature and are often identified with research interests. Identification of the appropriate level of model complexity is an initial hurdle commonly encountered by most modellers. Programme goals and objectives are the key points to consider in dealing with this question.

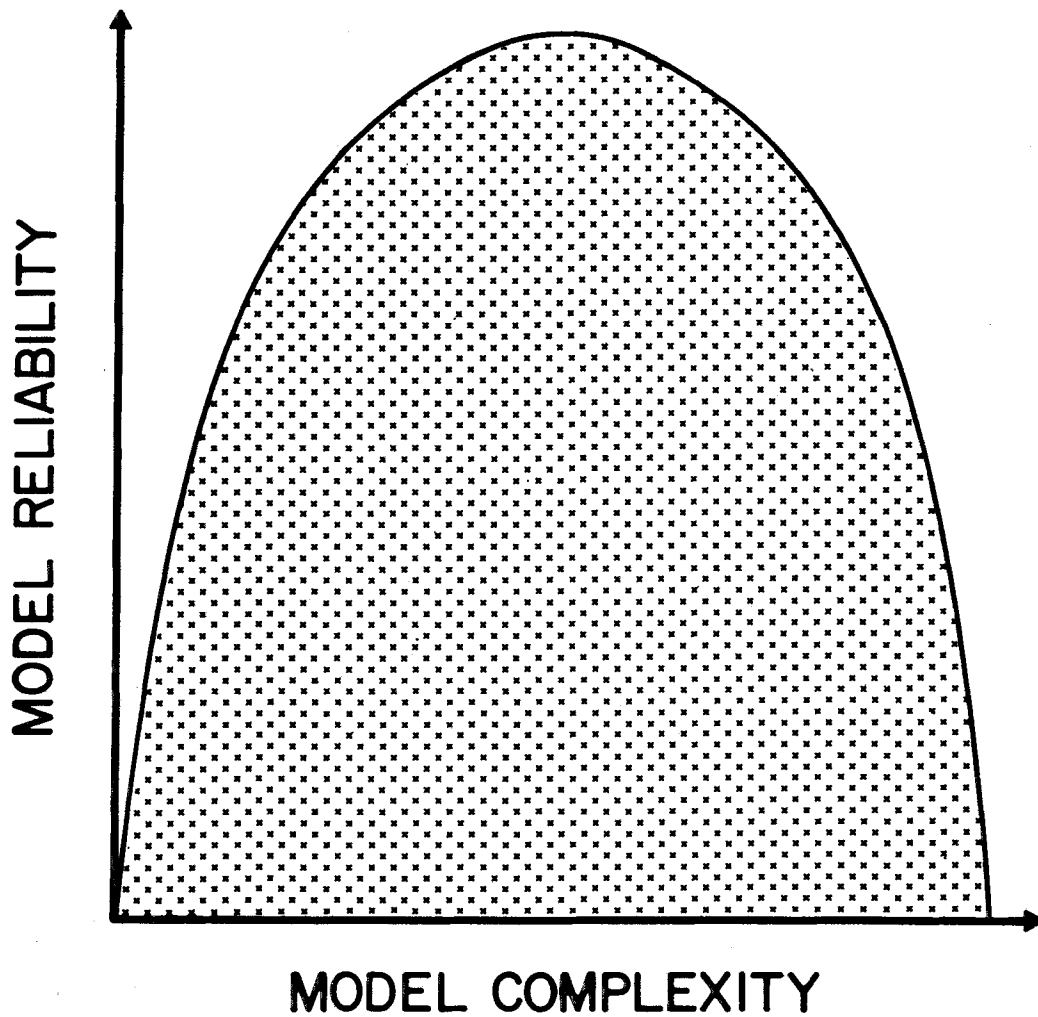


Fig. 1. The relationship between model complexity and model reliability.

Model complexity and model reliability.

Good management models must offer ease of application and must have a high degree of reliability or credibility, *e.g.* impart a degree of confidence to the decision-maker. Two model characteristics are fundamental to the reliability/complexity question, *viz.* the model must provide a good description of the system under study and the modeller must minimize the uncertainty associated with model input. Unfortunately, these two goals are often at odds. Fig. 1 illustrates the relationship between model complexity and model reliability. Overly-simple models may fail to provide an adequate description of the system and thus have poor reliability. Similarly, complex models may suffer from difficulties in providing accurate estimates for the large numbers of model inputs required for this approach. A 'bottom up' approach is recommended here for lake restoration purposes - earlier work with complex frameworks has resulted in a well-developed body of knowledge on the topic.

By restricting model complexity, investigators may focus their resources on reducing the uncertainty associated with model inputs and on verifying the applicability of previously described mechanisms and empirical models to their system. The simple, 'bottom up' approach to modelling for lake restoration offers a high probability for success in satisfying the interests of water quality managers, government officials and public interest groups. For additional discussion of these topics, especially in relation to detailed ecosystem models, the reader is referred to the literature on ecosystem analysis (*cf.* O'NEILL, 1975 and MANKIN *et al.*, 1975).

The Integrated Approach.

Application of mathematical models to the solution of water quality problems offers a special opportunity for interaction and synergy among modellers and experimentalists. Models are extremely valuable aids in the design of field sampling programmes and for identifying key processes and mechanisms which merit further study. The role of models in programme design is seldom recognized; modellers are then faced with the difficult, if not impossible, task of retrofitting models to previously acquired data sets and estimates of model coefficients. It is vital that the modeller and the experimentalist work together from the outset to develop a comprehensive programme of field and laboratory study compatible with model requirements.

Fig. 2 illustrates an integrated approach to the solution of water quality problems using mathematical models. The conceptual framework is developed initially based on existing theory (paradigms) and data. A quantitative capability is introduced to the conceptual framework by applying algorithms which define system interactions. The model is calibrated by comparison with field measurements; model coefficients may be adjusted within the bounds of their uncertainty in the calibration process. Problems encountered in calibration may point to a need for additional monitoring or a better description of processes and mechanisms. Feedback to the model framework from the calibration process permits field and laboratory programmes to evolve simultaneously with the model. Model verification is performed by conducting simulations with a different set of model inputs (altered loads, meteorological conditions), but with no change in model coefficients permitted. The confirmed or verified model may then be used to make projections of the impact of management actions on water quality.

The integrated approach has been successfully applied to the analysis of several water pollution problems in the Great Lakes region (dissolved oxygen depletion (AUER and CANALE, 1985), nonpoint sources of pollution (AUER *et al.*, 1985), nuisance growth of attached algae (CANALE and AUER, 1982), aquatic macrophytes (FREEDMAN and CANALE, 1977) and coliform bacteria (CANALE *et al.*, 1973).

AN INTEGRATED APPROACH

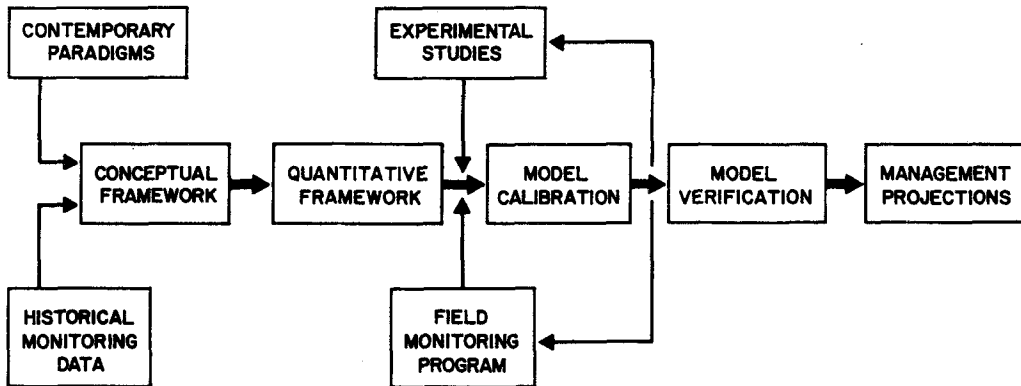


Fig. 2. Flow chart for an integrated approach to the solution of water quality problems using mathematical models.

THE GREEN BAY ECOSYSTEM

Morphology and Water Quality.

Green Bay is a major gulf located in the northwest corner of Lake Michigan (Fig. 3). The bay is 160 km in length along its major NE/SW axis, has a mean width of 22 km, a mean depth of 15.8 m, holds approximately 67 km³ of water and has a mean hydraulic residence time of 6 years (MORTIMER, 1978). According to the typology of AUER *et al.* (1986), trophic state in Green Bay ranges from eutrophic in the inner bay near the city of Green Bay, to oligotrophic near the bay's junction with Lake Michigan, approximately 120 km to the north. The strong gradients in water quality observed along the major axis of the bay (Fig. 4) occur in response to discharges of phosphorus, chlorophyll-*a*, and suspended sediment from the Fox River, Green Bay's major source of pollutant inputs. Summer average total phosphorus levels range from in excess of 100 $\mu\text{g P.l}^{-1}$ near the Fox River mouth to < 10 $\mu\text{g P.l}^{-1}$ near the junction with Lake Michigan. Chlorophyll-*a* levels show similar variation, ranging from approximately 80 $\mu\text{g.l}^{-1}$ to < 2 $\mu\text{g.l}^{-1}$ over the length of the bay.

The summer phytoplankton community is dominated by green algae (*Pediastrum*, *Staurastrum*, *Oocystis*), 22 %, and diatoms (*Fragilaria*, *Melosira*, *Stephanodiscus*), 53 %. A shift to blue-green algae (*Oscillatoria* and *Polycystis*), 23-73 %, occurs in the inner bay in August and September, but these forms remain minor components of the phytoplankton community in the mid- and outer-bay regions. Light penetration increases with distance from the Fox River mouth; the 1 % light level ranging from < 1 m in the extreme inner bay to 15 m (approximately the epilimnion thickness) near the junction with Lake Michigan. The lakeward extent of water quality problems is directly related to pressure applied to the system by pollutant loadings from the Fox River. Remedial measures for water pollution control are expected to alter the gradient, bringing good water quality closer to the city of Green Bay.

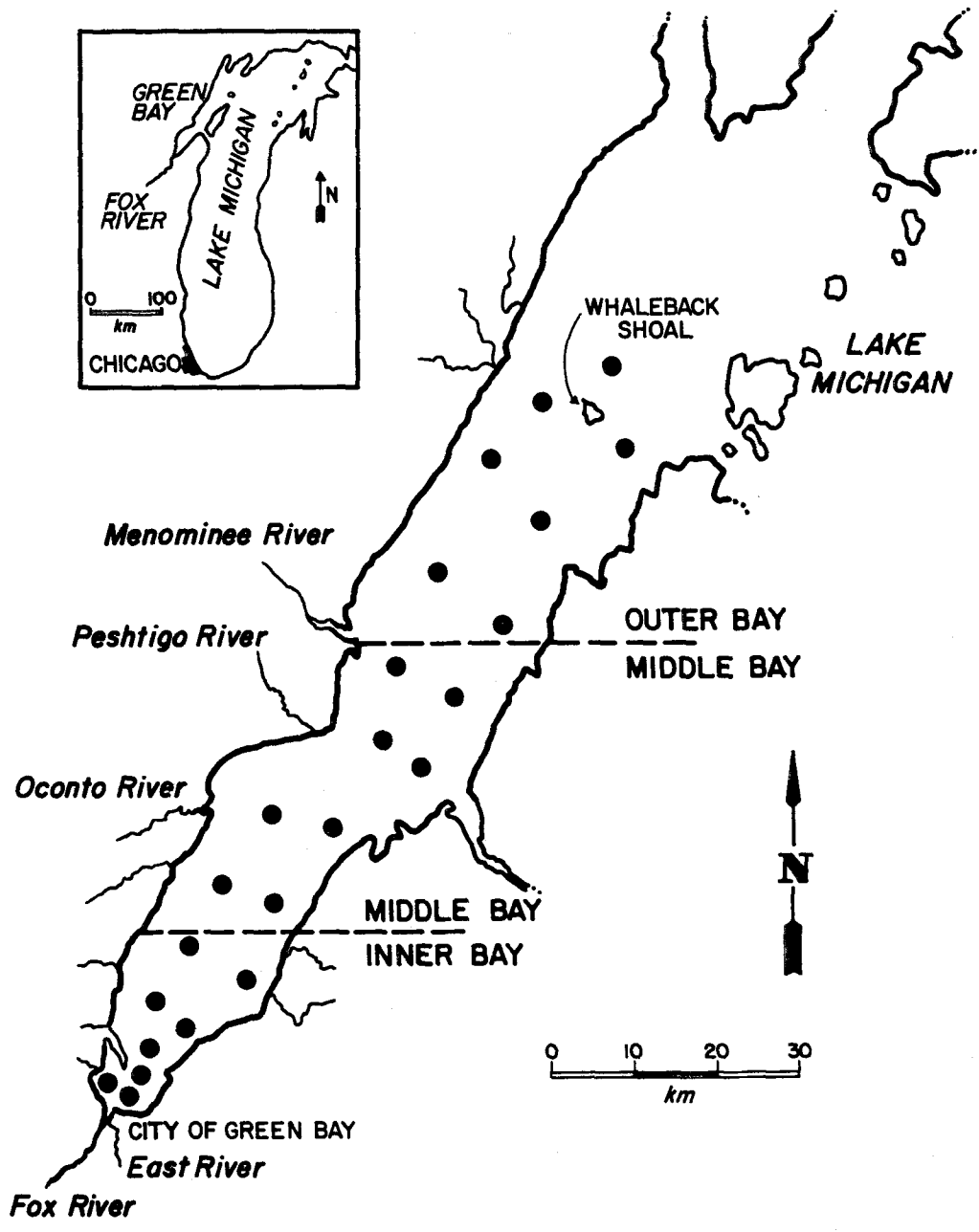


Fig. 3. Green Bay : location, sampling stations, regional divisions, and key morphological features.

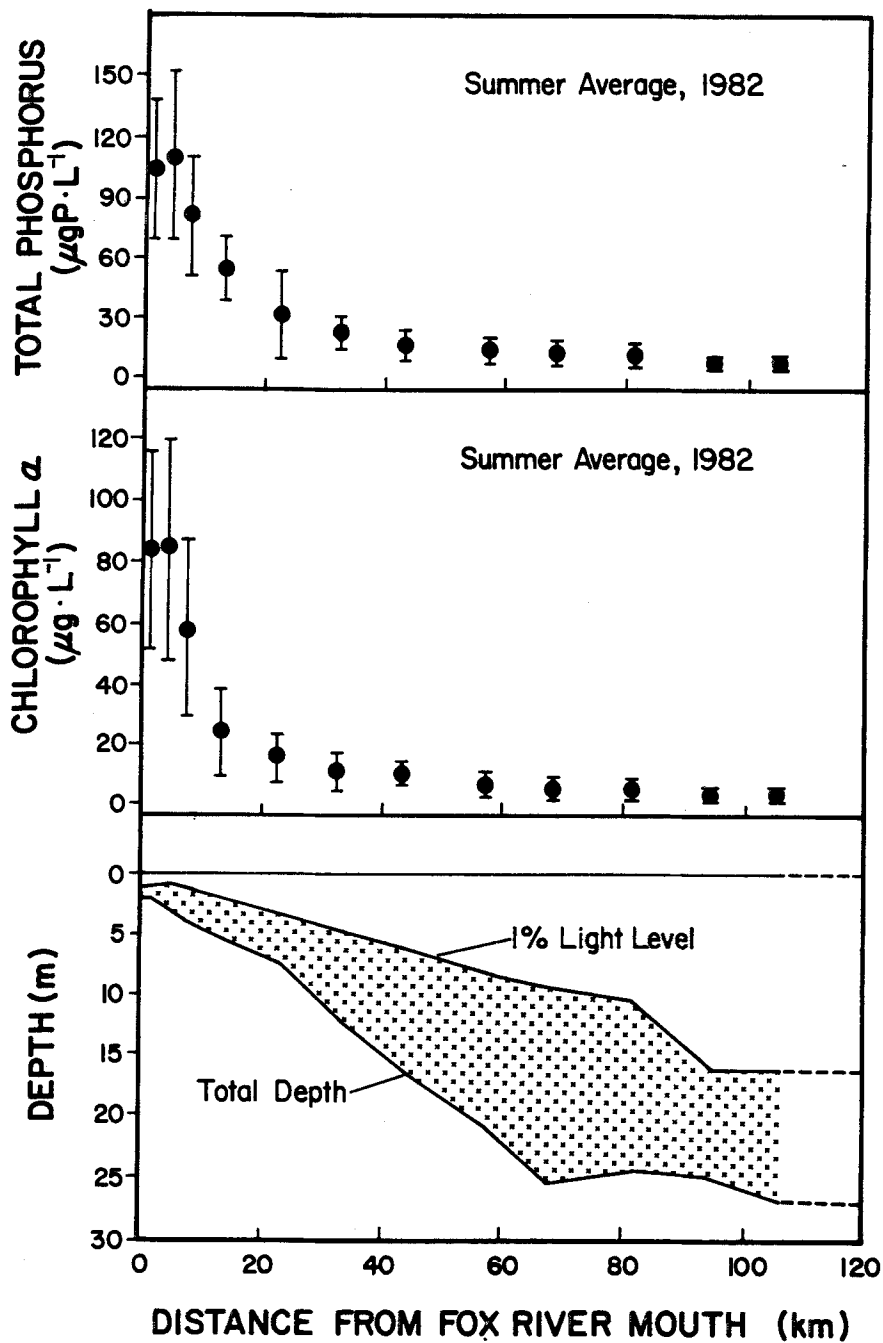


Fig. 4. Gradients in total phosphorus, chlorophyll-a, and light penetration along the major axis of Green Bay; summer average conditions 1982. Bars reflect seasonal variation for individual locations.

Rehabilitation Efforts.

Green Bay has been identified as one of the major water quality problem areas in the Great Lakes. High levels of suspended sediment, excessive algal growth, poor water clarity, and hypolimnetic oxygen depletion are characteristic of the system. Green Bay receives the greatest part of its external loading of organic matter and algal nutrients from agricultural, industrial (pulp and paper), and municipal discharges via the Fox River. Water quality conditions in the Fox River and inner Green Bay have been severely degraded for over forty years (WSCWP, 1939). Cooperative efforts among citizens, industry, and state, regional and local governments have resulted in improved dissolved oxygen conditions in the Fox River (DAY *et al.*, 1980), however, suspended sediment and algal nutrient loads remain high and impact water uses in Green Bay (HARRIS *et al.*, 1982).

Recent surveys indicate that extensive areas of the bay's hypolimnion experience dissolved oxygen depletion in the summer. The occurrence of dissolved oxygen depletion in Green Bay at sites far removed from the direct impact of the Fox River indicates that water quality restoration efforts should focus upon 'secondary' pollution (nutrients and internal carbon production) rather than on direct tributary loadings of oxygen-demanding substances. AUER and CANALE (1985) estimated that approximately 90 % of the organic carbon loaded to Green Bay during the growing season is produced internally. In this paper we refine that estimate, making use of improved expressions for algal growth kinetics in developing a mathematical model which relates internal carbon production to the total phosphorus concentration of the water column. The mechanistic primary production model described here may be coupled to a mass balance model for phosphorus and empirical functions relating phosphorus to chlorophyll and water clarity to support the development of a basin-wide water quality management plan.

MODEL DEVELOPMENT

THOMANN (1972, p. 7) defines environmental systems analysis as, 'the art of disassembling complex phenomena into smaller, more readily understood, subsystems and then reassembling relevant subsystems into a meaningful whole'. The goal of the submodel presented here is to quantify the contribution of internal primary production to the total summer loading of organic carbon to Green Bay. This phosphorus-driven submodel will later be coupled to a mass balance model for total phosphorus in Green Bay, permitting evaluation of the impact of changes in phosphorus loading on internal carbon production. Ultimately, the phosphorus and carbon submodels will, in sequence, drive a model for dissolved oxygen dynamics in the bay. Our understanding of the complex phenomenon of dissolved oxygen depletion will be developed from studies and modelling of the factors which drive the process.

In the model framework, Green Bay is divided into twelve cells (Fig. 5), each containing at least two monitoring stations and each representing a region of relative homogeneity in water quality along the gradient from the Fox River mouth to the junction with Lake Michigan. Spatially variable model inputs (total phosphorus, epilimnion temperature, cell and photic zone depth) are averaged over the summer season (June through September) for each model cell; system-wide model inputs (incident light, photoperiod) represent summer average conditions as well. Characteristics of cell geometry, cell-specific model inputs and system-wide model inputs are summarized in Table 1.

The calculation of internal carbon production is based on estimates of chlorophyll-specific rates of gross photosynthesis ($\text{mg O}_2 \cdot \mu\text{g Chl}^{-1} \cdot \text{d}^{-1}$) by nutrient saturated phytoplankton. Those estimates are then sequentially modified to account for the effects of light attenuation, water temperature, photoperiod, and phosphorus availability. The modified chlorophyll-specific rate of gross photosynthesis is converted to a volumetric basis ($\text{mg O}_2 \cdot \text{l}^{-1} \cdot \text{d}^{-1}$) using the chlorophyll level of the model cell. Finally, the photosynthetic quotient is applied to yield the volumetric rate of gross primary production. Areal primary production is estimated by

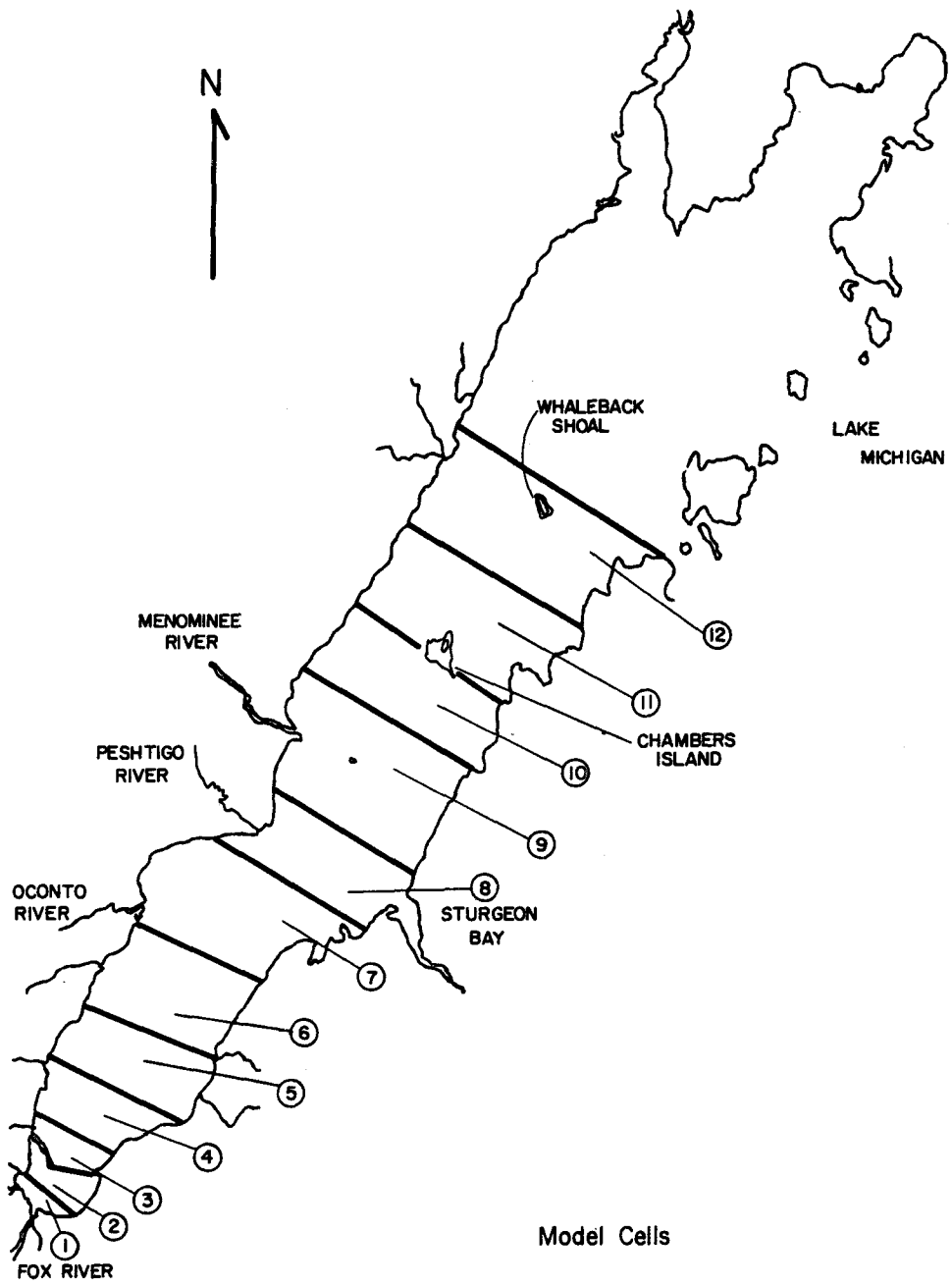


Fig. 5. Cell geometry for the Green Bay primary production model.

GROSS PHOTOSYNTHESIS

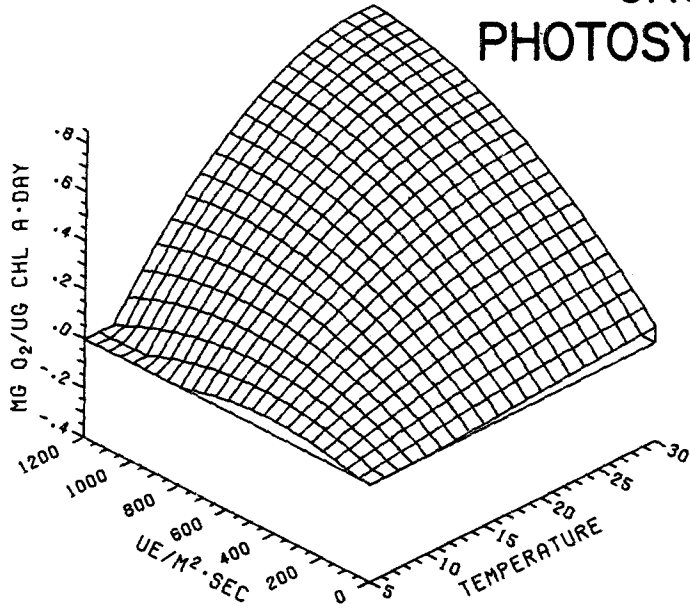


Fig. 6. Three-dimensional response surface illustrating the relationship among light, temperature and the chlorophyll-specific rate of gross photosynthesis in Green Bay phytoplankton.

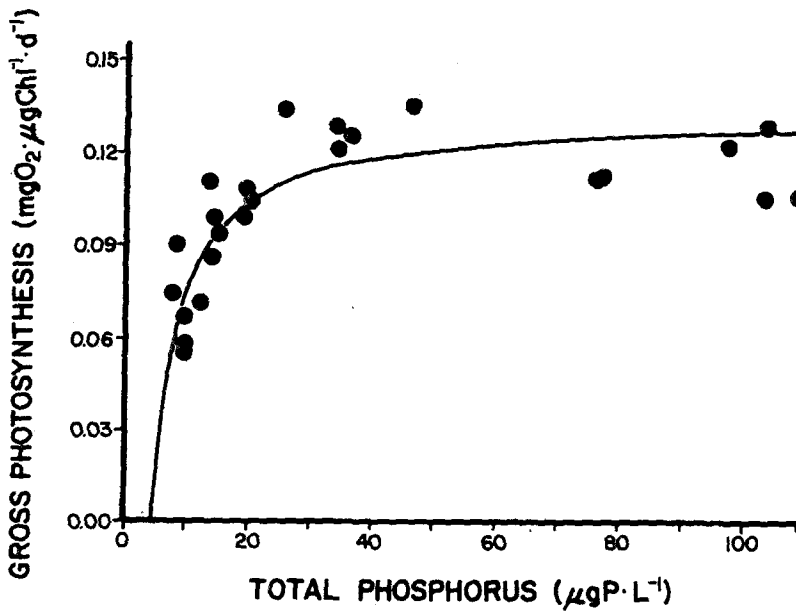


Fig. 7. Chlorophyll-specific gross photosynthesis as a function of total phosphorus concentration over the range of conditions observed in Green Bay.

Temperature is the cell-specific, summer-average value presented in Table 1. Light at depth is calculated from the summer-average incident light according to Equation 3

$$I(z) = I_0 * e^{-K_e * z} \quad (3)$$

where I_0 = incident light ($\mu E \cdot m^{-2} \cdot s^{-1}$)
 K_e = vertical extinction coefficient (m^{-1})
 z = depth (m)

Incident light is the summer-average value presented in Table 1. The vertical extinction coefficient is calculated from the regression of cell-specific, summer-average K_e versus cell-specific, summer-average total phosphorus concentration shown as Equation 4 (total phosphorus, TP as in Table 1)

$$K_e = (0.0498929 * TP) - 0.1914935 \quad (4)$$

The nutrient-saturated, chlorophyll-specific rate of gross photosynthesis is multiplied by the average photoperiod (Table 1) to account for daylength effects

$$PGROSS = PGROSS * PP \quad (5)$$

where PP = photoperiod (dimensionless).

Nutrient limitation is addressed for this phosphorus-limited system by multiplying the nutrient-saturated, chlorophyll-specific daily rate of gross photosynthesis by a phosphorus limitation function

$$PGROSS = PGROSS * f(TP) \quad (8)$$

where $f(TP)$ = function relating the rate of gross photosynthesis to the total phosphorus concentration (dimensionless).

The phosphorus limitation function presented as Equation 9 and illustrated in Fig. 7 was developed from measurements of gross photosynthesis by the Green Bay phytoplankton assemblage over a wide range of total phosphorus concentrations (AUER *et al.*, 1986)

$$f(TP) = (TP - P_{t,u}) / ((K_s - P_{t,u}) + (TP - P_{t,u})) \quad (9)$$

where $P_{t,u}$ = threshold phosphorus concentration for the commencement of growth ($\mu g TP \cdot l^{-1}$)
 K_s = Monod-type half-saturation constant for chlorophyll-specific gross photosynthesis ($\mu g TP \cdot l^{-1}$).

Values for total phosphorus are those of Table 1; $P_{t,u} = 4.3 \mu g TP \cdot l^{-1}$, $K_s = 8.5 \mu g TP \cdot l^{-1}$.

Chlorophyll-specific rates of gross photosynthesis are multiplied by the chlorophyll concentration to yield a volumetric rate of gross photosynthesis.

$$\text{PGROSS} = \text{PGROSS} * \text{CHL} \quad (10)$$

where CHL = chlorophyll concentration ($\mu\text{g.l}^{-1}$).

The chlorophyll concentration is calculated from the regression of cell-specific, summer-average chlorophyll concentration versus cell-specific, summer-average total phosphorus concentration presented as Equation 11 (total phosphorus, TP, as in Table 1)

$$\text{CHL} = (0.7989247 * \text{TP}) - 6.442454 \quad (11)$$

Finally, the rate of gross photosynthesis is multiplied by the photosynthetic quotient to yield the rate of primary production. A photosynthetic quotient of 1 is assumed ($\text{PQ} = 0.375$; 12 mg C fixed per 32 mg O_2 evolved)

$$\text{GPROD} = \text{PGROSS} * \text{PQ} \quad (12)$$

where GPROD = the daily rate of gross primary production ($\text{mg C.l}^{-1}.\text{d}^{-1}$)

PQ = photosynthetic quotient (mg C/mg O_2).

The areal rate of gross primary production ($\text{mg C.m}^{-2}.\text{d}^{-1}$) is calculated by integrating the production profile over the photic zone ($I(z) > 10 \mu\text{E.m}^{-2}.\text{s}^{-1}$, approximately 1 % of I_0) using Simpson's 1/3 Rule (CHAPRA and CANALE, 1985). The mass of organic carbon produced in each cell over the growing season is calculated by multiplying cell-specific areal production rates by the surface area of the model cell and the duration of the growing season (120 days); cell-specific values are summed to yield regional or bay wide totals.

RESULTS AND DISCUSSION

Calculated volumetric and areal rates of gross primary production and season-total production estimates are presented for each cell in Table 2. Gradients in primary production along the major axis of Green Bay reflect related patterns in light penetration and total phosphorus concentration. Volumetric rates, averaged over the photic zone, ranged from approximately $3 \text{ mg C.l}^{-1}.\text{d}^{-1}$ in the phosphorus-rich, turbid waters of the inner bay to $0.02 \text{ mg C.l}^{-1}.\text{d}^{-1}$ under the phosphorus-poor, well lit conditions of the outer bay. It is instructive to compare positions along the gradient in water quality and primary production observed for Green Bay with values for systems of similar trophic state elsewhere in the Great Lakes. The comparison is complicated by differences in measurement techniques (radiocarbon uptake versus oxygen evolution, also incubation light and temperature) and calculation procedures (methods for depth integration) (*cf.* VOLLENWEIDER *et al.*, 1974). WETZEL (1983) suggests that radiocarbon techniques measure net photosynthesis and that respiration generally accounts for 20-30 % of the total carbon fixed. On this basis it is noted that volumetric production rates averaged over the first metre for inner Green Bay are comparable to the maximum values reported for the western basin of Lake Erie and Saginaw Bay (VOLLENWEIDER *et al.*, 1974), while those of outer Green Bay are quite

Cell	Volumetric* (mg C.l ⁻¹ .d ⁻¹)		Areal (mg C.m ⁻² .d ⁻¹)	Season Total (MT - C)
	(1)	(2)		
1	2.96	3.32	2512	6800
2	3.03	3.60	2429	7600
3	2.11	2.39	2323	11000
4	1.22	1.85	2130	28800
5	0.57	1.16	1798	36000
6	0.35	0.81	1551	34700
7	0.22	0.56	1304	41900
8	0.14	0.37	1041	29900
9	0.10	0.28	898	27200
10	0.08	0.22	773	29200
11	0.02	0.06	331	10400
12	0.02	0.06	329	8000

Table 2. Cell-specific gross primary production estimates.
* Column (1) Mean for photic zone, Column (2) Mean for first meter.

Bay-wide comparison				
Inner Bay	(Cells 1 - 5)	90,200	MT - C/season	(33 %)
Mid-Bay	(Cells 6 - 9)	133,700	MT - C/season	(49 %)
Outer Bay	(Cells 10 - 12)	47,600	MT - C/season	(18 %)
Total Internal Production		271,500	MT - C/season	(100 %)
Compared with tributary loads				
Internal Carbon Loading		271,500	MT - C/season	(90 %)
External Carbon Loading		29,782	MT - C/season	(10 %)
Total Carbon Loading		301,282	MT - C/season	(100 %)

Table 3. Relative contributions to the Green Bay organic carbon load.

similar to those of the open waters of Lake Michigan (SCHELSKE and ROTH, 1973, VOLLENWEIDER *et al.*, 1974). The transitional region represented by the middle bay exhibit production rates similar to those of the central basin of Lake Erie and the nearshore waters of Lake Ontario (VOLLENWEIDER *et al.*, 1974): The range of water quality characteristics and trophic state observed across the Great Lakes is well matched by the gradients in phosphorus, phytoplankton standing crop and calculated primary production in Green Bay.

Vertical profiles of volumetric gross primary production for stations representing the inner, middle, and outer bay regions are presented in Fig. 8. Two trends are evident - first, volumetric rates of primary production decrease with distance from the Fox River mouth as phosphorus availability is reduced and secondly, the depth of the photic zone increases with

distance from the Fox River mouth as standing crop decreases and terrigenous materials settle out improving light penetration. Areal rates of gross primary production ($\text{mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) also decrease with distance from the Fox River mouth (Fig. 9); points along the areal production gradient in Green Bay generally correspond to areal rates at Great Lakes sites as described above for volumetric production.

The relative contribution of internal production to the organic carbon budget for Green Bay may be determined by multiplying cell-specific areal production rates by the surface area of the model cell. Cell totals are summed for the three bay regions (inner, cells 1-5, middle, cells 6-9, and outer, cells 10-12) and compared with estimates of tributary loads of organic carbon. Loads of organic carbon for the four major tributaries (see Fig. 3 for location) are calculated as the product of the mean annual flow (ROZNOWSKI and AUER, 1984) and the summer-mean total organic carbon concentration at the river mouth. Results of this analysis are presented in Table 3 and Fig. 10. It is clear from these calculations that internal production (autochthonous sources) provide the major portion of the total organic carbon load to Green Bay - approximately 90%. Despite the fact that areal rates are highest in the inner bay (high phosphorus levels), the greatest contribution to the total internal carbon loading is from the middle bay region, an area with a large photic volume and adequate phosphorus resources.

The role of phosphorus in driving processes that impact water quality in Green Bay is apparent in the character of spatial gradients for total phosphorus, chlorophyll, light penetration, and gross primary production. Basin-wide phosphorus management programmes that lower the water-column phosphorus concentration have the potential to reduce gross primary production and phytoplankton standing crop, and increase transparency in Green Bay.

Rehabilitation potential is especially significant in the middle bay region where depths are sufficient to prevent the resuspension of nutrient-bearing soil particles and sedimented algae. Reduction in the internal production of organic carbon in the middle bay region may importantly impact the oxygen depletion problem. Moving north from the Fox River mouth, it is not until the middle bay that depths sufficient for thermal stratification are achieved. These waters are relatively warm and have the thinnest hypolimnion; thus hypolimnetic oxygen reserves are smallest in the middle bay region. Finally, the sensitive middle bay region receives sedimented organic carbon from the waters that generate the largest fraction of the bay's internal carbon loading. Thus phosphorus management programmes aimed at reduction of primary production may be expected to improve not only conditions of water clarity and nuisance algal growth, but also to reduce rates of oxygen consumption in the hypolimnion.

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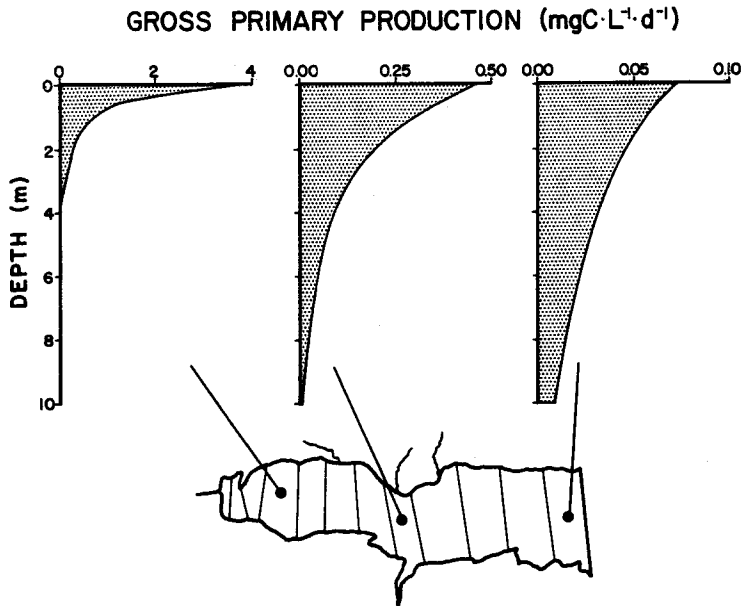


Fig. 8. Vertical profiles of volumetric primary production at stations representing the inner, middle and outer regions of Green Bay. Note differences in scale on the x-axis.

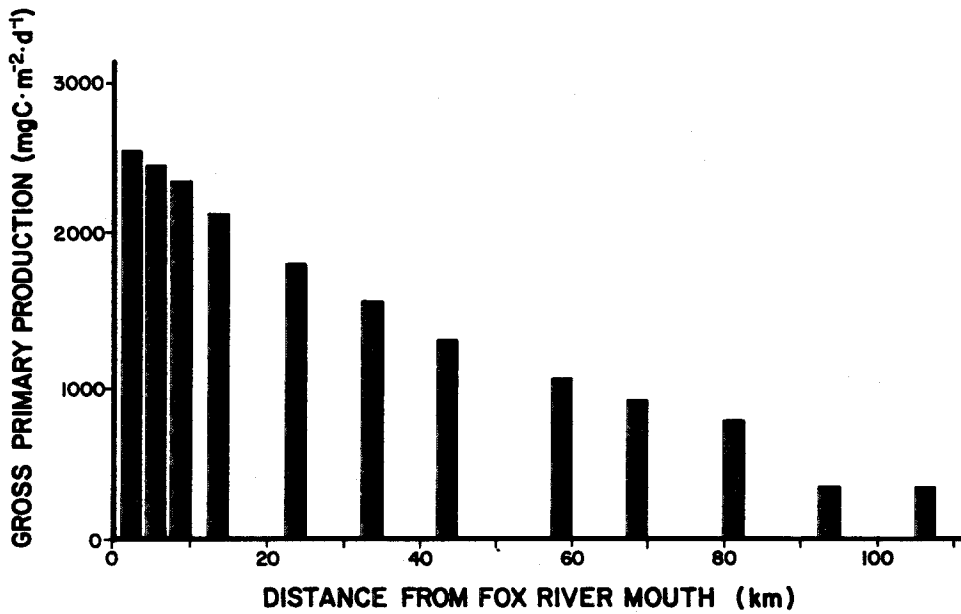


Fig. 9. Variation in areal rates of gross primary production as a function of distance from the Fox River mouth.

ORGANIC CARBON LOADING

10^3 metric tons / growing season

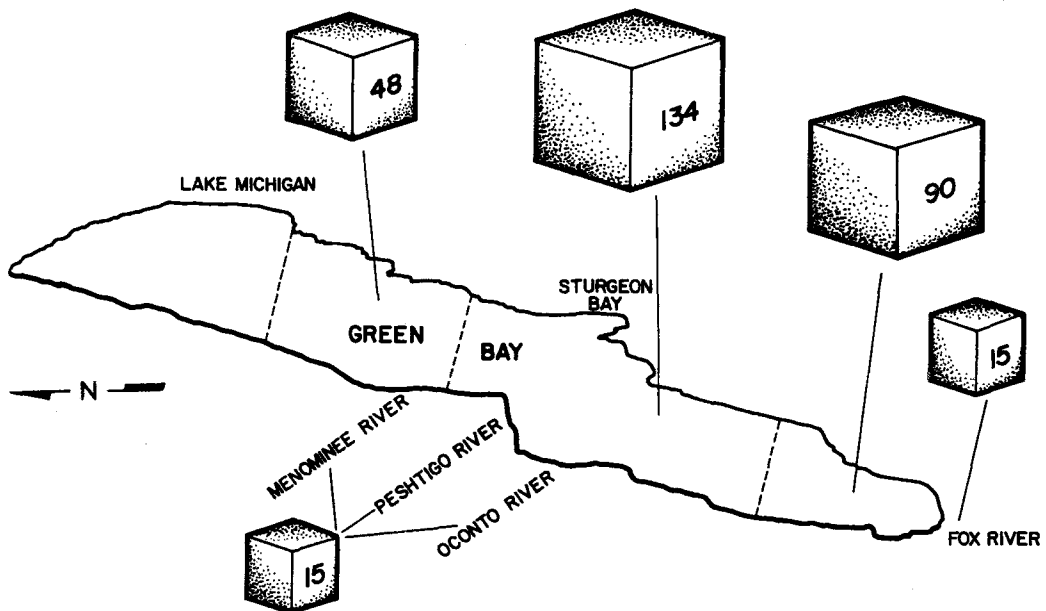


Fig. 10. Internal carbon production for the inner, middle and outer regions of Green Bay compared with tributary loads of organic carbon over the summer growing season.

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