Limnological Basis for Modeling Reservoir Ecosystems

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The aim of the study of reservoir ecosystems is to understand why particular conditions exist and why populations of organisms develop in a particular way. The term reservoir (i.e., impoundment or man-made lake) should be restricted to water bodies constructed by man. The importance of reservoirs for mankind and the fusion of practical and theoretical aspects during their study is obvious. To a theoretical limnologist the study of reservoir ecosystems offers a greater variety of conditions, the possibility of directed changes, and the organization of natural experiments. The scientific limnologist is led to accumulate more and more detailed data and to see the qualitative complexity of the structure of the ecosystem and the particularity of the examples studied. An engineer or applied limnologist is required to solve problems immediately by oversimplifying the quantitative expression of the behavior of the system and is looking for generality. The present degree of accumulation of data and abstraction of important relations and comparative bases on the one hand and the trend for both sufficiently accurate and widely applicable predictions on the other could induce the increasing convergence of the two approaches. If a common language is found, mutual understanding and use of results will grow.

ANALYSIS OF AQUATIC ECOSYSTEMS

The recent application of engineering techniques to the study of systems with complex interrelations also implies a close cooperation between limnologists and engineers in the use of mathematical language. Methods of systems analysis allow a limnologist to use the accumulated data for elucidating general trends, for quantitative comparisons, and for the quantitative interpretation of rather complex interactions. Results expressed as models are comprehensible to an engineer, and the limnologist is satisfied, since his results are being used immediately.

Figure 1 illustrates the stages of the analysis of aquatic ecosystems. The upper part of the flow diagram is the limnologist's participation; the bottom part is done on a computer with considerable participation by a mathematician. The trend is to understand at first the deterministic part of the relations. Obviously, the danger of obtaining false final results by neglecting at each step the evidently stochastic nature of the inputs could not be excluded.

The real aquatic ecosystem is divided into the water body and its surroundings, which include at least the surrounding landscape and atmosphere; in reservoirs the inflow and catchment area as well as the outflow and regulations by man are included. The first step of abstraction is the selection of adequate variables of the reality to be studied. Adequacy is the critical point, depending at this stage (verification being possible at the end of the procedure) on limnological experience and logical analysis of the objectives of the study. The goal of the next step of abstraction is to recognize and quantitatively formulate the main relations between variables measured by statistical techniques. The term limnological model is derived from economics literature [e.g., Gál, 1968; Rychetník, 1968], where economics models precede the transfer into purely mathematical notation. Correspondingly, the limnological model should cover both the structure and the behavior of the system. Structure means the compartments of the model and their functional relations and feedbacks, in other words, the processes forming the skeleton of the system. Behavior means the quantitative expression of the input-output relations of the model. O'Connor and Patten [1967] applied Lewins'
LIMNOLOGICAL MODELING OF RESERVOIR ECOSYSTEMS

Fig. 1. Block diagram of the analysis of aquatic ecosystems.

The quantitative formulation of the realistic models is imprecise. In my opinion they are derived mainly from comparative investigations of water bodies. Many widely accepted limnological theories can easily be transferred into symbolic mathematical notation. The reality and also the degree of practical application of such theories as Naumann’s [1932] trophic concept, Kolkwitz and Marsson’s [1908] saprobity, and others somewhat justify the failing attempts for numerical solutions, which are repeated with pigheadedness. The methodology of classical limnology was to run, by high abstraction, particular pathways through observations of many diversified water bodies. As a result classical models are unifactorial models of system behavior with no direct quantitative relation with the multifactorial nature or structure of the actual aquatic ecosystems. Until multifactorial models are designed, no hopes for adequate quantitative testing are justified.

General a priori models are based on simple mathematical formulas. They are either obtained directly by mathematical induction or induced from previous limnological observations of the ecosystems.

The classification of the three types according
to gnoseology has drawbacks just as any classification does. For example, transitions between classes or models attributable to several classes are easily found. But more important, the three types can be considered historical steps toward achieving the maximum precision, optimum reality, and maximum generalization possible for the given purpose. According to the treatment of the mathematical plankton models by O'Connor and Patten [1967] the usual historical succession in this field has been from precise to general models. Stimm and Stimm-Zollinger [1968], Szekkelda [1967, 1968], Uhlmann [1968], and Vollenweider [1969] followed in reverse the limits of validity of some general models to existing marine and freshwater ecosystems in attempts to obtain realistic models. Hypothetically, it should be possible to proceed from realistic structural models to precise models by considering the limiting conditions and multifactorial nature of the ecosystems. O'Connor and Patten [1967] stressed that realistic models have not been explored thoroughly in plankton ecology, and the same is true for reservoir limnology.

Perhaps, the gnoseology followed in this paper could be adequately classified as a progression from empirical studies of a few ecosystems and derived precise models toward attempts to distinguish the compatibility of the relations to comparative observations on several water bodies and derived realistic models. Thomann [1969] called for using all possible analytical techniques before proceeding to simulation. Surely, this deeply justified appeal deserves more than just being misused by the present author to cover his mathematical impotency.

APPLICATION TO RESERVOIRS

Before applying any limnological or oceanograhic model (approach or method) to reservoirs, we should clarify the a priori limits of such a transfer because of the hydrologic differences between lakes and reservoirs.

In Figure 2, reservoirs from a geographically sufficient representative area for which data were easily available (the United States) are arranged in different size categories according to annual mean retention times (i.e., storage ratio or discharge-volume rate). Reservoirs with retention times >1 year, which are comparable to lakes in the sense of classical limnology, represent only ~20% of the reservoirs or ~40% of the large reservoirs (reservoirs >1.000 · 10⁴ m³). The majority of reservoirs have retention times below this figure. Reservoirs with retention times <110 days represent almost one half of all reservoirs, and only in the large reservoirs do the figures drop to 20%.

Obviously, large modifications, if not other bases, will be necessary to cover reservoirs with shorter retention times. The search for an adequate basis is a major goal in this paper. Particularly helpful in this respect were the long-term data gathered during the Slapy Reservoir ecosystem study, made independently on the model approach. For the sake of brevity, direct data are mentioned here only in reviewing the basis for the models of reservoir ecosystems and subsystems and as reasons for the suggested additions.

The Slapy Reservoir is of medium size (270·10⁴ m³), and the annual mean theoretical retention times ranged during the 10-year study from 24 to
83 days (the mean being 38.5 days). Fifteen years ago Hrbáček designed intuitively a project of limnological study of reservoirs closely resembling the first steps of the present systems analysis. Two years of detailed hydrologic, physical limnological, chemical, microbiological, phytoplankton, zooplankton, and benthos studies (Hrbáček and Straškraba, 1966; Hrbáček et al., 1966; Háruška, 1966, 1973; Javornický et al., 1962; Javornický, 1966; Straškraba and Hrbáček, 1966) were conducted when a free river was flowing into the reservoir. During another 8-year study a similar reservoir (Orlik Reservoir with a volume of 720·10⁶ m³, observed retention times that ranged from 57 to 170 days, and a mean of 100 days) was operating close upstream. As a result the data for the Slapy Reservoir ecosystem are more suitable for systems analytical techniques than those for any other ecosystem in the country in which systems analysis originated. The method of distinguishing regular annual cycles and correlating their extremes was developed for evaluating relations between observed variables. The philosophy of this procedure is to avoid the drawbacks of a direct application of correlation and regression techniques to natural phenomena that result from the assumption that the independent variables are not randomly variable (Eshett, 1969; Kozák, 1968) and from complications with the seasonally changing correlation and regression coefficients (for temperatures see McCombie [1959] and Moore [1964]). An approximation of seasonal trends by harmonic analysis was preferred to the approximation by polynomials suggested by Eshett because of the direct usefulness of the modeling processes for deriving differential equations. Extreme values were interpreted as integrals of opposing processes for a particular preceding period. For extremes, correlation coefficients that were greater than correlations of all untreated data were obtained. High correlation coefficients are very useful for an adequate test of the hypotheses on the nature of relations and for predictions.

The structure of the Slapy Reservoir ecosystem as studied by a team of scientists (Javornický and Komárková, 1973; Procházková et al., 1973; Straškraba, 1966, 1970; Straškraba et al., 1973) is evident from Figure 3. Since the system is eutrophic, a few species are dominant, a characteristic that is favorable for study. Obviously, the part of the figure marked by a dotted line is relatively isolated from the rest and might be considered a subsystem and therefore be treated separately, but it must be understood to interpret the whole system.

**SUBSYSTEM TEMPERATURE AND INTERNAL MIXING**

The modeling of temperatures is of leading importance for the limnological modeling of reservoir ecosystems as a basic input affecting all chemical and biological processes and as a guide for proper physical structuring and a measure of mechanical transfer within the reservoir system. The two goals are achieved in present models by either the empirical sinusoidal approximation of the annual temperature cycle or the heat budget approach.

The approximation of temperatures by harmonic analysis is currently used as a basic input to hydrobiological models (Davidson and Clymer [1966] for the ocean, Parker [1968] for a reservoir, and Karpov et al. [1966], Krogius et al. [1969], and Menshutkin and Umnov [1970] for a lake). The application for air temperatures is included in mathematical textbooks [Alger, 1963]. Ward [1963] introduced the method to systematic studies of stream and reservoir temperatures. He showed high correlation coefficients of the observed values versus a simple sinusoidal curve calculated from monthly averages:

$$ T = T + a \sin (x + b) $$

(1)

![Diagram](image.png)

**Fig. 3.** Structure of the ecosystem of one particular eutrophic reservoir (Slapy Reservoir ecosystem) from Straškraba [1970].
where $T$ is the annual mean temperature, $a$ is the amplitude of the wave, $x$ is the number of days from November 1 expressed in degrees, and $b$ is the phase coefficient.

This simple curve holds for inflow temperatures and surface temperatures of reservoirs assumed to have no lateral heat transfer. For reasons shown below for reservoir and outflow temperatures the inclusion of the second harmonics is necessary for a proper approximation [Stráškraba and Javornický, 1973]. No statistical techniques were used to test the significance of the higher harmonics, but no systematic effect was obtained by the inclusion of the third harmonics.

Evidently, the inclusion of much higher harmonics is necessary when daily cycles must be covered in addition to annual cycles. Thomann [1963, 1969] applied power spectrum analysis to water quality records in tidal streams. A source of references for the application of the technique to aquatic sciences is given by Gunnerson [1967].

Essentially, the approximation of temperature by harmonic analysis is included in oceanographic techniques (applied later for lake studies) for determining diffusion coefficients, these techniques being based on the time lag of temperature maxima in the deeper strata of a water mass [e.g., Dutton and Bryson, 1962, references]. For water bodies assumed to have no lateral heat transfer the depth distribution of temperature is given by:

$$T = A_n e^{-2\pi(z/z_n)\sin 2\pi \frac{t - (z/z_0)t_0}{t_o}} \quad (2)$$

where

- $A_n$: diffusion coefficient;
- $z$: depth of the surface;
- $z_n$: depth of the bottom;
- $t$: phase shift at depth $z$;
- $t_0$: 365 days.

The approach based on energy transfer through a boundary between the atmosphere and the water can be applied accurately for prediction of highly turbulent water masses (such as streams and unstratified reservoirs). Recent methods of calculating different terms of the analytical heat budget equation from standard meteorological data and empirical equations are given by Wright and Horrell [1967] and, in Russian literature, Nesina [1967]. For the most recent oceanographic application, see Seckel [1970]. Important earlier reservoir applications are those by Anderson [1954], Sauer and Anderson [1956], Raphael [1962], and Delay and Seaders [1966].

Nielsen [1967] pointed out that for application to stratified reservoirs present ideas should be expanded to include advective heat transfer by reservoir inflow and outflow. This line is followed under natural conditions by the Tennessee group [Wunderlich and Elder, 1968] and under laboratory conditions particularly by Harleman and Huber [1968] and Brooks and Koh [1968].

The basic assumptions of the graphic temperature model by Wunderlich and Elder [1968] are listed in the first column of Table 1. The assumptions reflect conditions in the prototype reservoir for this model, the Fontana Lake, which has a mean theoretical retention time of 150 days. The numerical model by Orlob and Selin [1968] is intended to be more widely applicable; nevertheless, most of the assumptions above are implied if not stated explicitly. The difficulties with understanding turbulent diffusion in reservoir conditions are avoided by using an effective diffusion coefficient obtained from field data on temperature profiles, discharges, and inflow temperatures. It will be shown elsewhere that diffusion coefficients are correlated with the mean depth in lakes. In a reservoir the complexity of currents, as shown in Figure 4, contributes to turbulent diffusion. In reservoirs with peaking operations, complicated daily changes in turbulence due to changes in currents have to be expected. A hydrodynamic solution of this complex situation is difficult if all these currents have to be included. Field observations suggest some guidelines to decide on the importance of particular currents.

Schroder [1958] showed in detail for reservoirs in Thuringer Wald that stratification conditions are affected by retention times. The same is implied in the empirical relations between the mean theoretical retention times and the annual mean difference of the reservoir inflow and outflow temperature derived by Bratrancyk [1953, 1961] from observations on Czechoslovak reservoirs.

Several years of relevant data on the temperature conditions of one reservoir (Slapy Reservoir) with annual mean theoretical retention times that varied in different years within broad limits were analyzed by Straškraba et al. [1973]. The data are particularly relevant to a quantitative study of the relations between retention times and thermics for two reasons. First, in part of the study period the reservoir was
TABLE 1. Comparison of the Main Assumption Used in the Temperature Model by Wunderlich and Elder [1968] and the Results of the Slapy Reservoir Ecosystem Study

<table>
<thead>
<tr>
<th>Subject</th>
<th>Wunderlich and Elder Assumption</th>
<th>Slapy Reservoir Ecosystem Study</th>
<th>Evidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density of water</td>
<td>Dependent primarily on temperatures</td>
<td>Dependent primarily on temperatures</td>
<td>***</td>
</tr>
<tr>
<td>Thickness of the layer heated by solar energy</td>
<td>Constant (~3 meters)</td>
<td>Function of retention time</td>
<td>Figure 6d</td>
</tr>
<tr>
<td>Heat transfer from the upper layer downward</td>
<td>Negligible</td>
<td>Important, function of retention time</td>
<td>Figure 6b</td>
</tr>
<tr>
<td>Temperature of the upper layer</td>
<td>Equilibrium temperature, approximation by analytical heat budget</td>
<td>Does not correspond to equilibrium temperature, cannot be approximated by analytical heat budget</td>
<td>Figure 8</td>
</tr>
<tr>
<td>Temperature of the inflow</td>
<td>Constant</td>
<td>Changing depending on the hydrologic differences between years</td>
<td>equation 3</td>
</tr>
<tr>
<td>Mixing of the inflow with reservoir water</td>
<td>No</td>
<td>Intensive, particularly in the backwater reach</td>
<td>***</td>
</tr>
<tr>
<td>Depth of the inflow stream jet</td>
<td>Constant, from year to year changing seasonally</td>
<td>Changing with retention time and seasonally</td>
<td>Figure 6a</td>
</tr>
<tr>
<td>Withdrawal layer</td>
<td>Limited by the upper and lower plane of intake</td>
<td>Changing with discharges and shape of intakes</td>
<td>Omatek [1955]</td>
</tr>
<tr>
<td>Water from the upper layer</td>
<td>Sinking gradually deeper</td>
<td>Sinking gradually deeper</td>
<td>***</td>
</tr>
<tr>
<td>Fall isotherms</td>
<td>Vertical lines from the surface to corresponding temperature levels</td>
<td>Vertical lines from the surface to corresponding temperature levels</td>
<td>***</td>
</tr>
<tr>
<td>Date of mixing</td>
<td>Constant</td>
<td>Function of retention time</td>
<td>***</td>
</tr>
</tbody>
</table>

fed by the bottom waters of a similar reservoir upstream. The effect of the discharges is given by summing up the influence of the two reservoirs. Second, the mixing of the inflow and reservoir water can be easily observed owing to the marked temperature difference between the cold inflow and the warm upper layers.

Figure 5 illustrates summer temperature profiles at comparable dates in successive years with different discharges. Evidently, when other factors are reduced to a minimum (the same reservoir with similar volumes of water), basic differences in both the absolute temperatures of different layers and the shape of temperature profiles occur. An analysis by the method of extremal correlations showed that the inflow temperatures (deepwater temperatures of the upstream reservoir slightly modified by a reregulation reservoir) are a function of the discharges. For illustration the April-July temperatures are

\[ T_4(IV - VII) = -1.8 + 5.4 \log Q(IV - VII) \] (3)

The annual course of air temperatures reflecting the heat budget of a water body when the lateral heat income is negligible correlates with the discharges \( T_a \), the maximum monthly mean, is equal to \( 22.8 - 3.32 \log Q(IV - VII) \), \( r = -0.776 \); \( T_d(I - III) = -11.6 + 5.74 \log Q(I - III), r = 0.980 \). Rainy years have, on the average, much colder summers than sunny years, but cold winters are dry.

Figure 6 shows a few of the most critical correlations found between temperatures, stratification, and discharges. During the period when Slapy Reservoir is fed by the upstream reservoir, the maximum heat content of the reservoir (calculated on a biergan basis from temperature readings in the lower reach of the reservoir) (Figure 6a) increases less rapidly than the lateral heat inflow for the period of rising temperatures. The lateral heat inflow is calculated as a product of monthly mean discharges and inflow temperatures. (Biergan basis, distinct from foreclan basis, is calculated per unit of volume below
Fig. 4. Block diagram of the web of the thermal relations within a reservoir. The various currents in a reservoir are grouped in four main categories according to the driving force, seiches being separated because of mixed origin. Several characteristic currents can be named within the groups, e.g., among gravity currents the balancing currents in a particular depth from the dam upstream. Three main parameters of the currents to which the turbulence is related are indicated only for density currents (\(V\) being volume, \(u\) being velocity, and \(\rho\) being density). The analytical heat budget equation shows the heat transfer on the air-water interface. For details, see Straškraba et al. [1973].

Fig. 5. Comparable summer plots of temperature against depth in Slapy Reservoir in successive years from thermistor readings.
Fig. 6. Correlations between temperatures, stratification, and discharges in different years in Slapy Reservoir. (a) Maximum heat content (birgean basis) plotted against mean heat inflow for April–July. (b) Mean surface temperatures for April–June correlated with discharges for the period. (c) Depth of the mean theoretical inflow stream jet for May–September plotted against discharges for the period. (d) Thickness of the epilimnion in July–August plotted against discharges for April–July. Numbers at points indicate years. Crosses denote years not included in the regressions, particularly those before the upstream reservoir operated. This figure is modified from Strakkrabe et al. [1973].

Illustrate simply this complex web of cause and effect pathways, highly schematized drawings generalizing the summer conditions during 3 selected years with mean theoretical retention times for the period when stratification develops (April–July) of about 15, 30, and 90 days are shown in Figure 7. The result of dynamic seasonal changes during such conditions is reflected in the different annual courses of temperatures approximated by harmonic analysis for two critical depths (surface and intake level) in Figure 8. In addition to the lower surface level and higher intake level temperatures in July at lower retention times (Figure 7), note the slower rise and retarded peak of the surface temperatures during low retention times. In
deeper layers the peak is advanced, and temperatures are increased, much earlier autumnal homothermy resulting during low retention times. Winter temperatures are also highly different: the inversion evident during dry years results in the freezing of the reservoir surface, whereas in wet years water is almost homothermal below 2°C with no ice cover.

In a series of reservoirs such as that studied here this situation is striking and is easily analyzable. To a reduced extent it is valid for a solitary reservoir too. The relations shown between reservoir temperatures and discharges, particularly the negative logarithmic relations to deepwater temperatures, suggest a justification for devoting the early steps of reservoir hydrodynamics modeling to density currents as the most probable adequate approximation [Smutek, 1955; Deblar, 1959; Otsuoboto and Fukushima, 1959; Levi, 1959; Jaske and Snyder, 1967].

The findings above result in basic changes of the assumptions useful for a model of stratification conditions of reservoirs below some critical

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**Fig. 7.** Schematic representation of the summer stratification conditions in Slapy Reservoir during dry, medium, and wet years. The April–July mean temperature of the inflow is \( T_1 (IV - VII) \); the mean July (August) temperatures of the air, surface level, and intake level are \( T_A, T_0, \) and \( T_{in} \); the mean April-July discharge into the reservoir is \( Q_d(IV - VII) \); the depth of the epilimnion is \( ED \); the May–September mean theoretical inflow stream jet (depth of the reservoir corresponding to the inflow temperature) is \( ISJ \); and the coefficient of effective turbulence is \( A_z \).
mean theoretical retention time. From present evidence the critical retention time will be somewhere <1 year, but the exact value has to be clarified. In the shortest possible way the assumptions are listed in the last column of Table 1. The suggestion of the corresponding physical structure of a temperate deep reservoir model is given in Figure 9. (An adequate classification of deep and shallow reservoirs will be $D < H$ and $D > H$, where $D$ is the effective depth of mixing and $H$ is the total depth. An empirical relation for $D$ in a particular region, the Baltic lowland in northern Poland, was developed by Patalas [1968].) Figure 9b is the most general model, Figure 9a represents its derivative by $\lim \rightarrow \infty$ the backwater stretch, and Figure 9c represents its derivative by

![Fig. 8. Sinusoidal annual temperature curves for the surface level and intake level in Sąpy Reservoir during a dry, medium, and wet year from November to October.](image)

![Fig. 9. One-dimensional idealization of the physical structure of hypothesized deep temperate reservoirs with different retention times.](image)
in flowing waters are based on the Streeter and Phelps application of the equation of continuity or mass balance. Although the equations are appealing in their simplicity, numerous physical and biological processes severely limit their practical usefulness [Frankel and Hansen, 1968].

To reconsider briefly the applicability of this approach to reservoirs, two aspects are separated: (1) the hydrologic aspect, representing not only the distribution within the water body but also one major source (or sink) of oxygen that is exchanged with the atmosphere, and (2) the biological (biochemical) aspect, including the associated physical processes.

For shallow unstratified streams, classical objects of the engineering approach, the solution of the exchange rates with the atmosphere (in the absence of supersaturation equal to reaeration rates) is relatively well known [Owens et al., 1964; Thackston and Krenkel, 1969]. The first application for deep unstratified slowly flowing rivers is of relatively recent date [O’Connor and Dobbins, 1956]. In a historical sequence to very slowly moving water masses, Owens et al. [1964] and Znamenskii [1965] suggested that the same approach should be applicable for stratified conditions, the depth of the thermocline being used instead of total depth for calculations of the reaeration coefficient. Calculations on this basis were made by O’Connel and Thomas [1965]. The difficulties with applying empirical hydrologic equations to reservoirs were stressed by Kittrell [1959]. Nielson [1967] suggested the derivation of the reaeration coefficient from hydrologic parameters in terms describing reservoir conditions by substituting the usual parameters of wind speed for flow velocity and effective mixing depth for total depth. No proof of the applicability is known to me, and I see a major drawback in the functional relation between wind speed and effective mixing depth in reservoirs and also in the additional effect of currents, as discussed previously.

The biological aspect was fairly simple in the original Streeter and Phelps model in connection with considering polluted streams as diluted sewage. Only the temperature-dependent oxygen consumption by bacteria was included, and the corresponding equation read

\[ L_t = L_0 \cdot \exp(-kt) \]  

(4)

in the integrated form, where \( L_t \) was the concentration of biochemical oxygen demand (BOD) at time \( t \), \( L_0 \) was the same at the beginning, and \( k \) was the depletion coefficient. Development of the concept resulted from independent limnological studies on clean waters [e.g., Odum, 1956]. The participation of the other members of the community metabolism was quantified. Systematic long-term studies on the biological sources and sinks of oxygen in streams were made by a group of English applied limnologists (summarized by Owens et al. [1964, 1969]). Recently, the list of important oxygen sources and sinks increased to 13 items [Frankel and Hansen, 1968], which can be grouped as listed in the appendix.

Evaluating oxygen conditions in particular reservoirs was attempted from two sides, a limnological side [Wright, 1961; Parker, 1968] and an engineering one [Symons et al., 1967; Wunderlich and Elder, 1968]. The professions of Wright and Wunderlich and Elder clearly dictated the models used, but I see no professional or reservoir-bound reason why the first author should neglect advection and the second author should neglect turbulence. Nevertheless, according to the authors’ reports, both models resulted in satisfactory agreement between measured and calculated values. Wright’s [1961, 1967] purpose was to obtain a measure of the phytoplankton oxygen production independent of the light and dark bottle technique for Canyon Ferry Lake (\( R \approx 220 \) days). Therefore the very simplified model

\[ (dO_2/dt) = A_s(dO_2/dz) + R \]  

(5)

from Hutchinson [1957] was evaluated numerically, where \( A_s \) was the coefficient of vertical eddy diffusivity and \( R \) was the biological rate of change. The difference between the calculated and the observed rate of change in oxygen concentrations in deeper strata was assumed to be counterbalanced by diffusion from the equivalent oxygen production of the euphotic zone.

Wunderlich and Elder [1968] assumed during the first evaluation of the oxygen model for deeper strata of Fontana Lake (\( R = 150 \) days) that vertical eddy diffusion was negligible. The exponential decay law (4) was applied to changes in dissolved oxygen (DO). The organic loading of the advected water mass was neglected. Basically different depletion coefficients at similar temperatures were noted for waters of different nutrient contents.
The need to include phytoplankton photosynthesis and respiration as major oxygen sources and sinks is generally recognized in engineering studies of reservoirs [e.g., Krenkel et al., 1968] and does not need to be explained here. The O’Connel and Thomas [1965] model used by Symons et al. [1967] is intended to cover the euphotic zone of a water body, where sedimentation is negligible. In addition to terms for reaeration and the exponential decay law for the DO deficit, symbolic terms covering phytoplankton photosynthesis and respiration in general were included.

More sophisticated models of the phytoplankton changes with time relevant to DO and water quality changes in reservoirs are those derived from marine observations as reviewed by Patten [1968]. All actually bear traces of the ingenuity of Riley (particularly Riley et al. [1949]), who in 1946 included the principles of feedback before it was generally recognized in cybernetics:

![Diagram of nutrient, phytoplankton, and zooplankton relationships]

The qualitative formulation of the models includes, following Patten [1968]:

$$\frac{dB}{dt} = f_1 (\text{influx of producer biomass}) + f_2 (\text{photosynthesis}) + f_3 (\text{efflux of biomass from all trophic levels}) - f_4 (\text{respiration}) + f_5 (\text{grazing})$$

Terms $f_1$ and $f_2$ are equivalent to the hydrologic term for redistribution of mass within the water body in the appendix. Active migrations of phytoplankters are neglected. Term $f_3$ is covered in essence in the engineering models by the exponential decay law. In connection with a low organic matter content this term is grossly neglected in marine studies and limnological models. Phytoplankton photosynthesis ($f_2$) is assumed to depend on one limiting nutrient, light, temperature, and algal standing crop, and these are included in the models. Nielson [1967] suggested that for application to reservoirs this relation be modeled by a statistical empirical equation similar to that applied for estuaries and rivers by Bailey [1967]. In generalized notation this can be written as

$$\frac{dP}{dt} = (k_t I k_4 N k_3 T) B$$

where $I$ is the light intensity, $N$ is the critical nutrient, $T$ is the temperature, and $k_t$ are the empirically derived coefficients.

Parker [1968] simulated phytoplankton photosynthesis in the epilimnion of Kootenay Lake, a reservoir on the U.S.-Canadian border ($R = \sim 150$ days). In addition to terms $f_3, f_4,$ and $f_5$ above the population of the major zooplankton consumer was included. Limnological observations and experiments [e.g., Hrbáček et al., 1961] demonstrated a high feedback from the fish population structure to zooplankton and phytoplankton metabolism via species composition. Hrbáček [1965, 1969] demonstrated the direct relevancy of the fish population structure to the DO content of standing waters.

The review above of the application of both the engineering models and the limnological models to reservoirs shows that no verification of the basic assumptions is obtained. Progress in this respect is to be expected from advanced field studies.

The main factors of oxygen variations have been analyzed by the method of extremal correlations and regressions during the Slapy Reservoir ecosystem study. Two aspects were followed: the regular annual variations and the relation of these variations to changes in retention times (discharges). Figure 10 represents the mean of several years of DO variations at the surface and intake levels based on moving averages [Stráškába et al., 1973]. The peaks and drops indicated in the figure occur every year, but the numerical values are different. Similar shapes were obtained for other Czechoslovak reservoirs, and evidence from several published records suggests that trinodal curves are widely distributed.

Application of a similar technique to data by Procházková et al. [1973] revealed regular annual cycles for variables presumably related to DO variations (Figure 10). Secchi disk transparency reflects the light conditions. Gross phytoplankton production expressed in grams of DO produced below a unit of surface was obtained directly from oxygen readings in suspended light and dark bottles. The values closest to natural bacterial respiration rates are considered to be those obtained in filtered water during 24 hours under reservoir temperatures. Phosphate phosphorus was recognized as the major limiting nutrient for phytoplankton production (nitrogen limitation being recognized at times). The validity of zooplankton respiration
values is not comparable with that of the other curves, since the values are based on 1-year data [Straškraba, 1966]. Indirect evidence from regular filtrator and predator standing crop data indicates that the order of magnitude but not the shape is representative.

A direct inspection of the curves suggests that several possible interrelations between the phenomena have to be examined. The winter oxygen peak coincides with the highest saturation value, and the vernal and summer oxygen peaks coincide with pulses of phytoplankton produc-
tion. The BOD variations follow the two peaks of photosynthesis, both being seasonally slightly postponed. The shift is in the intervals between samplings and hence is affected by considerable bias but is nevertheless significant. The relation of these peaks to the decomposition of organic matter produced during photosynthesis is suggested. The maximum amount of phosphate phosphorus occurs in the period of no photosynthetic activity and at the winter oxygen peak. Not only is the minimum amount of phosphate phosphorus coincident with the summer phytoplankton pulse, but a break in the rate of uptake is observed during the spring phytoplankton peak. The maximum amount of zooplankton respiration coincides with a drop in phytoplankton. The summer minimum of transparency coincides with the phytoplankton pulse.

Results of an analysis of some of the suggested relations are summarized in Figure 11 (for a description, see Straškraba et al. [1973]). The idealized surface and intake level DO curves resulting from the approach above for retentions of about 15, 30, and 90 days (identical with those characterized in Figures 7 and 8) are shown in Figure 12. The surface dots are derived from regressions in Figure 11, and the curve is a graphic simulation of the mean shape derived in Figure 10.

CONCLUSIONS

Coupling the review of the existing models to suggestions resulting from the Slapy Reservoir ecosystem study, I must first stress that engineering and limnological approaches can be considered supplementary in many respects. In reser-

Fig. 11. Extremal correlations for DO and related variables in Slapy Reservoir. (a) The DO concentration during the winter peak at intake level plotted against the mean discharges from the previous October to March. (b) The DO concentration during the winter peak at the surface plotted against the surface temperature at the time of the peak; 61 is not included in the calculations owing to the exceptionally high amount of DO connected with filling the upstream reservoir. (c) The DO increase from vernal drop to vernal peak plotted against the gross phytoplankton production below a unit of surface; 63 is not included in the calculations. (d) The surface DO content during the vernal peak plotted against the log temperature at the surface during the vernal peak. (e) The April–September mean BOD (1 day at the reservoir surface temperature) plotted against the mean gross primary production for the same period (modified from Procházková et al. [1973]). (f) The surface DO decrease from vernal peak to summer drop plotted against the surface DO concentration during the vernal peak. (g) The surface DO increase from summer drop to summer peak plotted against the gross primary production; 64 is not included in the calculations owing to the exceptionally high surface concentration connected with the extremely shallow epilimnion. (h) The rate of DO decrease from the April value to a concentration of 1 mg/l at the intake level plotted against the mean April–September theoretical retention times; 65 is not included in the calculations. This figure is modified from Straškraba et al. [1973] unless another source is stated.
voirs, physical processes and decomposition of organic matter are coupled with phytoplankton production and its use.

For a proper application of models from other environments and as a base for reservoir ecosystem models the following should be considered.

1. The proper physical structuring of the reservoir model (discussed in the section on temperature) is important. Changes in DO associated with the backwater reaches of reservoirs were discussed particularly by Krenkel et al. [1968]. The proportion of oxygen transferred advectively increases greatly as retention times decrease, but turbulent transfer also increases.

2. Parameters of the models for reservoirs are shown to vary as a function of retention times. The biological changes associated with the direct physical effects show the dependence of the variables on retention times.

3. The understanding of the relation of phytoplankton photosynthesis and respiration to nutrients, light, and temperature is necessary not only because phytoplankton photosynthesis and respiration are important sources and sinks of oxygen but also because, in addition to organic matter advected, phytoplankton production is an additional important source. The organic matter produced in this way is immediately decomposed.

4. Historically, the evidence for significant feedback between variables of the ecosystem increases. In addition to the feedbacks recognized earlier and those implicit in (2) and (3), at least two highly important ones should be included. Not only is zooplankton respiration at times an important DO sink, but also the consumption of phytoplankton may at times exceed its production. Carnivores and zooplankton induce considerable changes in the phytoplankton composition and associated production and respiration rates. Surprisingly, the high feedback mechanism is not obvious per se, nor is it obvious in all the recent oceanographic models (as shown by Patten [1968]) or in all the recent limnological models (cf. the Lake Dalneye ecosystem model [Karpov et al., 1966; Krogius et al., 1969; Menshutkin and Umnov, 1970]).

5. Regular seasonal changes of limnological variables are recognized in reservoirs. Inclusion of the seasonality in the models increases their precision highly. The approximation of seasonal curves by harmonic analysis points to the differentiation of variables by time. Before a full understanding of the cyclicity for all variables is obtained, the approximated curves can be used as input for the predictive models. Extreme periods of peaks and drops result from a domination of one particular process. The values reached can be interpreted as integrals of the processes for the periods between successive extremes. Thus the phase shift of the corresponding extremes of interrelated variables can be included in the analysis.

6. In the present models the effect on the processes indicative of water quality changes of associations other than planktonic is neglected. Speculatively, the effect of the mud-water interface and associated organisms should be higher in reservoirs than in lakes in connection with the increased turbulence. This effect cannot be neglected, particularly in the backwater reaches, which have increased sedimentation rates. The effect of increased contact phenomena due to ebullition of gases from bottom sediments should be considered. No estimate is available about the participation of production and use by organisms on solid surfaces of the reservoir slopes. Macrophytes can usually be considered absent in deep temperate usually fluctuating reservoirs, but under certain circumstances this assumption may not be valid.

APPENDIX: LIST OF PROCESSES CONSIDERED IN RECENT MODELS FOR DO CHANGES IN RIVERS

I. Hydrologic processes
   A. Reaeration
      1. Turbulent mixing
      2. Effect of suspended and dissolved matter

   B. Distribution within the rivers
      1. Turbulent mixing
      2. Longitudinal dispersion
      3. Effect of channel configuration, weirs, and so on

   C. Local runoff

II. Biochemical processes: Decomposition of organic matter (variability of $k$, during nitrification stage)

III. Higher biocenosis processes
   A. Phytoplankton
      1. Photosynthesis
      2. Respiration

   B. Macrophyta
      1. Photosynthesis
      2. Respiration

   C. Benthos (respiration)
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IV. Sediment processes
   A. Sedimentation of organic matter
   B. Adsorption of organic matter by sediments
   C. Resuspension of deposits
   D. Diffusion of oxygen into sediments
   E. Diffusion of oxygen from sediments
   F. Purging action of gases rising from bottom

Considered are daily variations of flow, temperature, BOD, photosynthesis, and respiration.

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