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MODEL PREDICTIONS OF EFFECTS OF IMPOUNDMENT ON PARTICULATE ORGANIC MATTER TRANSPORT IN A RIVER SYSTEM

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INTRODUCTION

Seston may be defined as all organic and inorganic matter suspended in water (Ruttner, 1963). The organic fraction of seston, including both living and nonliving material, is generally known as particulate organic matter (POM). A substantial number of studies over the last quarter-century have demonstrated that POM is extremely important in the energetics of freshwater, marine, and estuarine ecosystems. The concern in this paper is with the dynamics of POM in stream ecosystems and the effects of impoundment on POM dynamics in a river system.

A general model of biological factors affecting POM in streams is illustrated in Fig. 1. There are two broad categories of POM: coarse particulate organic matter (CPOM), usually considered to be material greater than 1 mm diameter, and fine particulate organic matter (FPOM), particles between 1 mm and 0.45 μm in diameter. Stream POM is derived from several possible sources. In low-order, woodland streams, the major source of POM is allochthonous material, primarily leaves, falling directly or blowing and sliding into the stream from the stream margin (e.g., Cummins, 1974). In nonwoodland streams and in woodland streams sufficiently wide to allow light penetration through the canopy, periphytic algae are a major source of fixed carbon (e.g., Minshall, 1978) and algal sloughing contributes to POM (e.g., Swanson and Bachmann, 1976). In larger streams, macrophytes may provide substantial portions of autochthonous production (e.g., Cummins, 1975) and, on death, contribute to POM. Additionally, though not shown in Fig. 1, periphyton and possibly macrophytes may contribute indirectly to the seston through herbivore

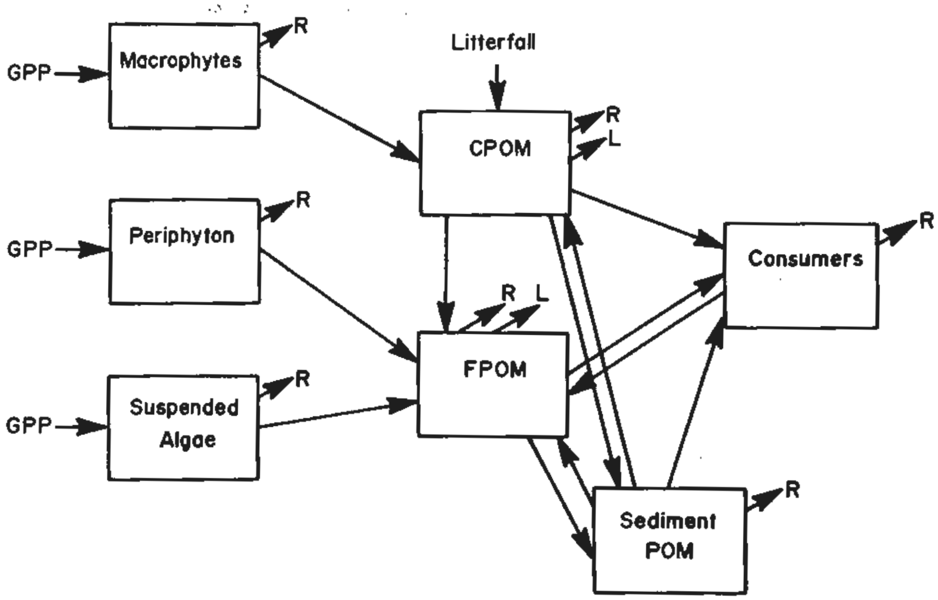

Fig. 1. General model of particulate organic matter (POM) in a stream ecosystem; GPP = gross primary production, CPOM = coarse POM, FPOM = fine POM, R = respiration, and L = leaching.

consumption and through flocculation of leachates. In large rivers, and especially in reservoirs, suspended algae are the major source of primary production and POM. Also, floodplain capture of allochthonous material may be an important source of POM. Once in the stream, POM is processed or degraded via respiration by associated microflora, leaching of dissolved organic material, capture and consumption by consumers, and sedimentation. POM is returned from sediments by increased flows, and a large fraction of the POM ingested by collectors is returned by egestion (Wallace et al., 1977).

A realization that POM is important in the energetics of stream ecosystems has led to a proliferation of investigations of POM dynamics in a variety of streams. General results of some of the more recent studies are listed in Table 1. Stream orders have been combined for the sake of convenience and because of uncertainty of the precise order of certain streams. Several difficulties encountered in attempts to derive broadly applicable models for POM dynamics in streams from the literature are immediately apparent in Table 1. Methods for sample collection varied somewhat, but that factor is probably less bothersome than variation in methods used for sample analysis.

In a comparison of POM transport in streams of various orders, both within and between geographic regions, Sedell et al. (1978) found that there was little variation in POM concentration between stream orders within specific regional basins; however, they determined that concentrations varied between basins by as much as an order of magnitude. In addition to finding no strong correlation between stream order and POM transport characteristics, Sedell et al. (1978) were unable to demonstrate strong relationships between either unit stream power or gradient and POM transport, such as has been demonstrated for inorganic particles. They suggested that differences in behavior of organic and inorganic particles can be attributed to lower specific gravities and higher surface-to-volume ratios of organic particles.

Flow is one stream variable that often has been correlated positively with POM concentration (Nelson and Scott, 1962; Maciolek, 1966; Bormann et al., 1974; Wetzel and Manny, 1977; Malmqvist et al., 1978; Naiman and Sedell, 1979). Maximum concentrations of POM are usually associated with episodic high discharges related directly or indirectly to precipitation (Bormann et al., 1969; Fisher and Likens, 1973; Fisher and Minckley, 1978). Seasonal timing of high discharges has varying effects on POM concentration (Liaw and MacCrimmon, 1977; Wetzel and Manny, 1977; Bilby and Likens, 1979). For example, a June storm produced a twofold greater organic load in Catahoula Creek (Mississippi) than at a similar discharge in February (de la Cruz and Post, 1977). A peak discharge in May, equaling about half the February discharge, produced an organic loading almost equal to the June load.

One general conclusion to be derived from the various studies of POM transport in all types of streams is that most of the material is transported as extremely small particles (e.g., Maciolek, 1966; Maciolek and Tunzi, 1968; Fisher and Likens, 1973; Sedell et al., 1978; Naiman and Sedell, 1979). CPOM entering headwater streams tends to move only short distances before becoming trapped by obstructions and is usually processed in place (e.g., Peterson and Cummins, 1974; Malmqvist et al., 1978; Naiman and Sedell, 1979a). Rising discharges suspend smaller and lighter particles and transport them downstream. Receding discharges allow fine particles to be trapped by obstructions (Bilby and Likens, 1979) or to settle in low gradient reaches of the stream (Malmqvist et al., 1978). Subsequent discharge peaks repeat the process. Continued mechanical action, coupled with a variety of biological processing factors (Boling et al., 1975), reduces the particle size of POM. Naiman and Sedell (1979a) summarized the phenomenon concisely. Small streams, by virtue of their resistance to the movement of large particles, retain CPOM; thus, more FPOM is transported than other size fractions. Larger streams transport FPOM because that is the

Table 1. POM Concentrations in Streams

Location	Method[a]	POM Conc Range mg 1^{-1}	POM Conc mean annual mg 1^{-1}	Duration	Authors
Stream Order 1-3					
Augusta Creek, Mich. (1st Order)	3	0.6-6.4[b]		weekly, 24 mo	Wetzel and Manny (1977)
Augusta Creek, Mich. (3rd Order)	3	0.6-13.96[b]		weekly, 24 mo	Wetzel and Manny (1977)
Augusta Creek, Mich. (2nd Order)	1	2.4-15.0	7.13	1-2d/qtr	Sedell et al. (1978)
Augusta Creek, Mich. (3rd Order)	1	3.01-7.02	4.77	1-2d/qtr	Sedell et al. (1978)
Bear Brook, N.H.	3		0.31	monthly? 19 mo	Fisher and Likens (1973)
Camp Creek, Idaho	1	0.82-7.60	2.62	2-3d/qtr	Sedell et al. (1978)
Catahoula Creek, Miss.	1	4.80-11.85	7.0	Feb.-Aug.	de la Cruz and Post (1977)
Convict Creek, Calif.	3	0.30-2.1	0.67	weekly, 12 mo	Maciolek (1966)
Devils Creek, Ore.	1	0.54-1.35	0.97	2-3d/qtr	Naiman and Sedell (1979a)
Hubbard Brook (W-6), N.H.	1	<0.1-10.0		variable 4 yr	Bormann et al. (1974)
Hubbard Brook (W-2), N.H.	1	<0.1-10.0		variable 4 yr	Bormann et al. (1974)
Laurel Creek, Calif.	3	0.5-3.0		July, Aug.,Oct.	Maciolek and Tunzi (1968)
Mack Creek, Ore.	1	0.212-1.270	0.59	2-3d/qtr	Naiman and Sedell (1979a)
Panther Creek, Ga.	1	0.7-3.3		quarterly 12 mo	Malas and Wallace (1977)
Rhode River Watershed, Md.	1		3.7-22.7	weekly, 3 yr[c]	Pierce and Dulong (1977)
Roaring Brook, Maas.	1	0.04-3.2		bimonthly, 3 mo	McDowell and Fisher (1976)
Smith Creek, Mich.	1	2.62-10.4	5.89	1-2d/qtr	Sedell et al. (1978)
Stampen (stream), Sweden	3		4.0-22.0	monthly, 13 mo[d]	Malmqvist et al. (1978)
White Clay Creek, Penn.	1	0.97-3.65	1.36-2.29	2-3d/qtr	Sedell et al. (1978)
Stream Order 4-5					
Buck and Doe Run, Penn.	1	0.89-6.91	3.1		Sedell et al. (1978)
Kalamazoo River, Mich.	1	2.15-6.91	4.76	1-2d/qtr	Sedell et al. (1978)
Little Miami River, Ohio	1	1.0-31.0		weekly, 12 mo	Weber and Moore (1967)
Lookout Creek, Ore.	1	0.31-1.10	0.58	2-3d/qtr	Naiman and Sedell (1979a)
Middle Oconee, Ga.	4	8.4-47.0	10.0-20.0 (Ave)	monthly, 12 mo	Nelson and Scott (1962)
Palouse River, Idaho	4	2.2-3.5		weekly, 3 mo[e]	Buscemi (1969)
River Pilica, Poland	4	2.4-8.5		monthly, 12 mo	Penczak, et al. (1976)
River Rickleon, Sweden	1	0.2-5.0	1.0-1.5	5d/wk 10 mo	Karlström and Backlund (1977)
Salmon River, Idaho	1	0.72-9.4	3.68	2-3d/qtr	Sedell et al. (1978)
Shetucket River Conn.	5	0-3.0		3 h thundstm., Oct.	Klotz and Matson (1978)
Tallulah River, Ga./N.C.	1	1.5-4.4		Apr.,Oct.,Nov.	Wallace et al. (1977)
W. Br. Patuxent River, Md.	2	0.39-34.4[b]		monthly, 24 mo	Keefe et al. (1976)

		Stream Order 6-7			
Altamaha River, Ga.	1	0.66-1.2		Apr.,Oct.,Nov.	Wallace et al. (1977)
Brazos River, Tex.	2	2.76-11.04[b]	7.2[b]	monthly, 12 mo	Malcolm and Durum (1976)
Grand River, Ont.	3	1.0-26.2	6.9	monthly, 24 mo	Liaw and MacCrimmon (1977)
McKenzie River, Ore.	1	0.616-0.919	0.742	2-3d/qtr	Naiman and Sedell (1979a)
Nanaimo River, B.C.	2	0.28-0.68[b]		quarterly, 12 mo	Seki et al. (1969)
Nanaimo River, B.C.	1	0.10-1.2[b]		bimnthly, 12 mo	Naiman and Sibert (1978)
Neuse River, N.C.	2	0.396-9.8[b]	5.64[b]	monthly, 12 mo	Malcolm and Durum (1976)
Patuxent River, Md.	2	0.67-10.3[b]		monthly, 24 mo	Keefé et al. (1976)
River Thames, England	1	2.09-19.83	5.47	Apr.-Mar,	Berrie (1972)
Salmon River, Idaho	1	0.51-1.98	1.24	2-3d/qtr[f]	Sedell et al. (1978)
Sopchoppy River, Fla.	2	0-8.04[b]	3.2[b]	monthly, 3 mo	Malcolm and Durum (1976)
South Platte River, Colo.	1		0-40.7	monthly, 12 mo[g]	Ward (1974)
South Platte River, Colo.	1		0.8-5.7	monthly, 12 mo[h]	Ward (1976)
		Stream Order >7			
Ohio River, Ill.	2	1.56-8.76[b]	3.60[b]	monthly, bimonthly, 11 mo	Malcolm and Durum (1976)
Mississippi River, La.	2	2.16-12.24[b]	7.56[b]	monthly, 6 mo[i]	Malcolm and Durum (1976)
Missouri River, Neb.	2	0.96-380.0[b]	18.36[b]	monthly, 16 mo	Malcolm and Durum (1976)

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[a] 1-filtration; loss on ignition
2-filtration; carbon analysis via machine
3-filtration; dichromate oxidation
4-centrifugation; loss on ignition
5-other

[b] POM computed as $\frac{POC}{0.5}$

[c] Data summarized for 9 small streams in watershed

[d] Data summarized for 17 sites

[e] Data summarized for 4 sites

[f] Data summarized for 2 sites

[g] Data summarized for 4 sites

[h] Data summarized for 8 sites

[i] Data summarized for 3 sites

predominant fraction they receive from tributaries. These authors conclude that FPOM is probably generated continuously and rapidly.

Goldman and Kimmel (1978) state that dams are barriers to natural drainage and result in interruptions of organic matter transport that may profoundly affect downstream food webs. The few studies available concerning reservoir effects on POM show that different reservoirs have different effects. Some papers point to serious disruption in the flow of organic matter, while others point to limnetic production in reservoirs as a positive influence downstream. Perhaps the central difficulty is that few studies have been sufficiently broad to encompass large reaches of stream in which reservoirs are integral components. Our objective in this study was to construct a model of POM dynamics in a river system that would reflect, as much as possible, known mechanisms of POM transport and utilization. We then placed an impoundment on the model river and observed the effects on POM dynamics.

MODEL DEVELOPMENT

General Modeling Approach

In building the model to assess effects of impoundment, we considered the entire river system above an impoundment and for some distance downstream. The interdependence of reservoirs and their parental rivers clearly indicates that they should be studied as a single functional unit, a river-reservoir ecosystem. Vannote (unpublished manuscript) and Cummins (1975) point out that the general framework within which stream ecosystems should be viewed is as a continuum from headwaters to mouth.

Present biologically oriented models of stream ecosystems are essentially point models (e.g., Hall, 1972; McIntire, 1973; Boling et al., 1975; Webster et al., 1975; McIntire and Colby, 1978). The fundamental difference between a stream and a lake is the unidirectional flow of water, which, for the most part, precludes feedback from downstream components (Webster and Patten, 1979). This essential feature is lacking in point models. Point models, in effect, treat streams as lakes. O'Neill et al. (unpublished manuscript) and Boling (personal communication) are attempting to avoid this error by modeling stream ecosystems as series of point models. This approach is certainly an improvement, but still treats streams as linearly connected lakes. In our model development we used the civil engineering approach, pioneered by Streeter and Phelps (1925) and further developed by O'Connor (1962), Dobbins (1964), and Thomann (1972), in which stream distance is treated as an independent variable. The model equation for POM is a partial differential equation describing the rates of change of POM with respect to both time and distance. We combined concepts from current biological and civil engineering models and placed them on a framework of geomorphological models that describe the physical conditions for biological functions. In addition, we used hydraulic engineering principles in developing several parts of the model.

We attempted to develop a general model of POM transport in streams. All inputs were functions, rather than empirical values, in order to minimize the number of site specific parameters. Where it was necessary to numerically parameterize the model, we used data from the New River and Claytor Lake. The section of river used extends from the headwater near Boone, North Carolina, north 400 km to Glen Lyn, Virginia, near the West Virginia border. Over this reach the river goes from first to sixth order. Human impact on the New River includes impoundment, industrial and urban effluents, and agricultural runoff. Upper reaches of the river, though far from pristine, have received minimal impact, and one section has been designated for protection under the Scenic Rivers Act. Approximately 290 km below the headwaters, the New River is impounded by a hydroelectric power dam, which forms Claytor Lake. We emphasize that our model is not meant to be a simulation of the effects of Claytor Lake on POM transport in the New River. Rather, at this time, we intend the model to be a means of summarizing current knowledge of POM dynamics in a river-reservoir ecosystem and a means of identifying areas where essential information is lacking.

Geomorphic Foundation

The geomorphic foundations of our model rest on three empirical equations relating elevation, stream width, and mean annual stream flow to distance.

Elevation and slope. The longitudinal profile of a river (a plot of elevation versus distance) typically has the shape of a negative exponential; that is, it is usually concave (e.g., Leopold et al., 1964; Morisawa, 1968). Data from the New River very closely approximate this relationship ($r^2 = 0.99$, $N = 46$). Slope (or gradient) of the stream was calculated as the derivative of the elevation curve:

$$E = 966.9\ e^{-0.00197x} \qquad (1)$$

and

$$G = -1.907\ e^{-0.00197x}, \qquad (2)$$

where E is the elevation (m), x is distance measured from the headwaters (km), and G is channel gradient (m km^{-1}).

Streamflow. Mean annual streamflow was assumed to be directly proportional to stream distance in the analysis by Leopold and Maddock (1953). Using data from seven gaging stations on the New River [Kanawha River Basin Coordinating Committee (KRBCC), 1971], we found a better approximation ($r^2 = 0.98$, $N = 7$) by using a power function:

$$Q = 0.0054\ x^{1.718}, \tag{3}$$

where Q is mean annual discharge ($m^3 s^{-1}$). We introduced seasonal fluctuation in flow, using a sine function with a wavelength of one year, a mean equal to the mean annual flow, an amplitude of 1.2 times the mean, and a peak in mid-March. These parameters are based on data from the New River (KRBCC, 1971). In addition, an annual flood occurring in mid-March, lasting approximately 3 days, and with a flow of 20 times the mean annual flow was included in the model.

Stream width. Stream width approximates a power function of discharge both for temporal variation of streamflow at one point and spatial variation of mean annual flow (Leopold and Maddock, 1953). Because mean annual flow is a power function of distance (Equation 3), width can be treated as a power function of distance. Using measurements taken from Geologic Survey 15 minute series topographic maps, we found a significant power function relationship between width and distance ($r^2 = 0.89$, $N = 22$):

$$W = 2.18\ x^{0.740}, \tag{4}$$

where W is stream width (m). Temporal variability in stream width was not incorporated into our model.

Hydraulic Parameters

Derivations of other model hydrodynamic parameters are based on the Manning equation:

$$V = \frac{1}{n}\ R^{2/3} G^{1/2}, \tag{5}$$

where V is stream velocity (m s^{-1}), n is Manning's roughness coefficient, and R is hydraulic radius (m); and on the flow continuity equation:

$$Q = WDV, \tag{6}$$

where D is mean depth (m). In the Manning equation (Equation 5), we have approximated hydraulic radius with mean depth, a good approximation for natural river channels (Leopold and Maddock, 1953). We used n = 0.04 for the entire river.

Solving Equations 5 and 6 simultaneously, we obtained an equation for mean depth as a function of empirically derived parameters:

$$D = \left(\frac{Qn}{WG^{1/2}}\right)^{3/5}. \tag{7}$$

We then calculated velocity and cross-sectional area (A) from these parameters:

$$V = \frac{Q}{WD} \tag{8}$$

and

$$A = WD. \tag{9}$$

Reservoir Parameters

Our model reservoir began at a dam 300 km below the river headwater and extended upstream 25 km. From Equation 1, the surface elevation of the reservoir was 562.3 m. Reservoir depth was calculated as

$$D = 562.3 \; -E, \; 275 < x \leq 300, \tag{10}$$

where E was calculated from Equation 1. Width of the reservoir was calculated from a linear equation derived from regression of map-measured widths of Claytor Lake on distance:

$$W = 268.0 + 18.4\;(x - 275), \; 275 < x \leq 300. \tag{11}$$

The fit of this equation was not strong but statistically significant ($r^2 = 0.48$, $N = 25$). After calculating width and depth, we calculated velocity and cross-sectional area from Equations 8 and 9, as before.

Biological Parameters

In our model development we have so far used only a much simplified version of Fig. 1. As shown in Fig. 2, we considered a single, combined category of POM with a single input from litterfall and an output due to breakdown. Suspended POM interacted with sediment POM through deposition and erosion.

Litterfall dynamics were based on the model of litterfall into a lake, developed by Gasith and Hassler (1976), in which litterfall decreased linearly with distance from the shoreline to zero at 10 m. We assumed a forest literfall rate of 300 g m^{-2} y^{-1}, which is about average for deciduous forests (Bray and Gorham, 1964). Our litterfall equation was:

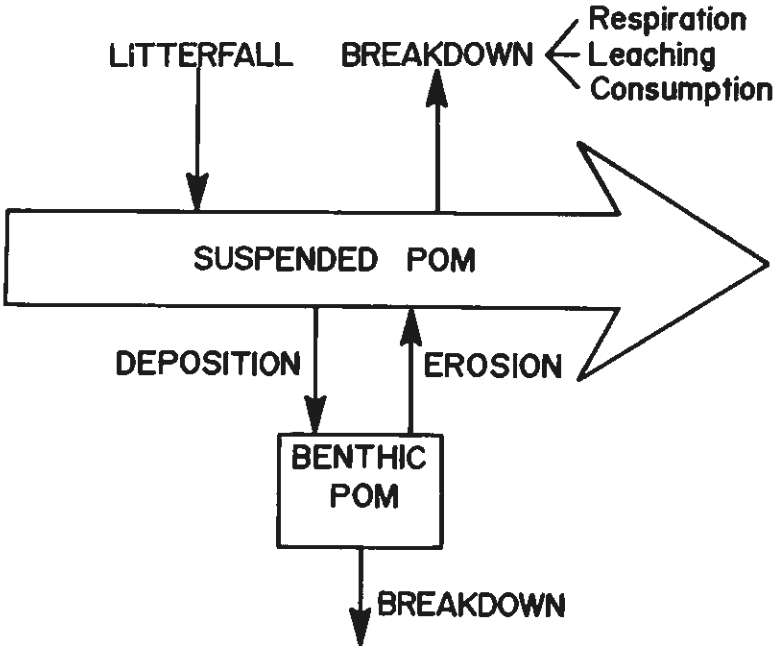

Fig. 2. Simplified model of particulate organic matter (POM) in a stream ecosystem.

$$Z = \begin{cases} 300\ W - 15\ W^2, & W \leq 10 \\ 1500, & W > 10, \end{cases} \tag{12}$$

where Z is litterfall (g per linear meter). According to this equation, litterfall input increased rapidly with stream distance to the point where stream width exceeded 10 m (7.8 km downstream). From there downstream, litterfall input was constant at 1500 g m^{-1}. To simulate seasonal litterfall, we modeled all input to occur as a pulse in October and November.

Paul (1978) measured leaf breakdown rates in the New River, using mesh bags of box elder, sycamore, sugar maple, and dogwood. For these species, which represent a broad spectrum of breakdown rates, we estimated an average breakdown rate (Jenny et al., 1949; Olson, 1963) of 2.74 y^{-1}. This constant was used for breakdown of both suspended and sediment POM.

Sedimentation and Erosion

Because information concerning sedimentation and resuspension of organic particles is lacking, our model is based on the stream power approach developed by Bagnold (1966) for inorganic particles. In the equation

$$I_s = \Omega(a\ V/V_f), \tag{13}$$

I_s is the suspended sediment load a stream can carry, Ω is available stream power, a is a constant, and V_f is fall velocity of the suspended particles. Available stream power is given by

$$\Omega = \rho g Q G, \tag{14}$$

where ρ is the density of water and g is the force of gravity. The suspended sediment load can also be written as

$$I_s = \frac{\sigma - \rho}{\sigma}\, mgVW, \tag{15}$$

where σ is the density and m is the mass of the suspended particles, so that $\frac{\sigma - \rho}{\sigma}$ is the immersed weight of the suspended sediment. Substituting Equation 14 into Equation 13 and solving 13 and 15 simultaneously for m yields

$$m = \frac{c\ Q\ G}{W}, \qquad (16)$$

where c is a constant combining a, V_f, ρ, and σ. The units of m are mass per unit area. Converting m to concentration by dividing by depth yields

$$S = c\ V\ G, \qquad (17)$$

where S is suspended sediment concentration (g m^{-3}).

Equation 17 can be compared to empirically derived equations. Combining Equations 7 and 8 gives

$$V \propto Q^{2/5}. \qquad (18)$$

Converting S, sediment concentration, to sediment load, L = SQ, we obtained

$$L \propto Q^{1.4}. \qquad (19)$$

Leopold and Miller (1956) state that the exponent of this equation is between 1.5 and 2.0 for natural river channels [citing Leopold and Maddock (1953)]. However, Leopold and Maddock (1953) and Leopold et al. (1964) report that the exponent is between 2 and 3. Müller and Förstner (1968) found values of the exponent from 0 to 2.5.

We used Equation 17 to calculate maximum POM load in the river. We evaluated c with data from Newbern (1978) for the New River. In late fall 1976 the New River at Galax, Virginia, was at approximately mean annual flow (50 m^3 s^{-1}). POM concentrations during this period ranged between 2 and 3 mg l^{-1}. We calculated c = 3.44, based on the assumption that POM was maximal at that time of year.

In our model, if the POM concentration was above the maximum (S_{max}) calculated from Equation 17, POM was transfered from suspension to sediment at the rate

$$DR = 4335\ \frac{S - S_{max}}{S_{max}}, \qquad (20)$$

which gives a deposition rate (y^{-1}) of 50% of the excess per hour when the POM concentration is twice the maximum. Actual deposition (DP) was then calculated as

$$DP = DR(S - S_{max}). \tag{21}$$

Similarly, resuspension occurred when the POM concentration was less than the maximum and POM was available in the sediment according to the equation

$$E = 90(S_{max} - S), \tag{22}$$

where E is resuspension input ($g\ m^{-3}\ y^{-1}$). This equation is based on the assumption of 25% uptake of the deficit per day.

Simulation Equations

Our simulation equation for the rate of change of POM concentration (S) with respect to time (t) and distance (x) came from Thomann (1972) and was based on mass balance:

$$\frac{\partial S}{\partial t} = \frac{1}{A}\frac{\partial (QS)}{\partial x} - KS + \frac{Z}{A} + \frac{S_T}{A}\left(\frac{\partial Q}{\partial x}\right) + E - DP, \tag{23}$$

where K is breakdown rate, S_T is the POM concentration of tributary inputs, and other symbols are as above. For tributary inputs we used:

$$S_T = \begin{cases} S(x), & x \leq 275 \\ S(275), & x > 275. \end{cases} \tag{24}$$

That is, above the point where the lake starts, all tributary POM concentrations equaled the main river POM concentrations. From 275 km on downstream, tributary inputs remained constant.

This equation was solved by the method of characteristics (e.g., Chester, 1971). By changing to another independent variable, ξ, we broke down Equation 23 into a set of three ordinary differential equations:

$$\frac{dt}{d\xi} = 1$$

$$\frac{dx}{d\xi} = \frac{Q}{A} \tag{25}$$

$$\frac{dS}{d\xi} = \frac{S_T - S}{A} \quad \frac{\xi Q}{\xi x} - KS + \frac{Z}{A} + E - DP.$$

The first equation was solved analytically: $t = \xi + t_o$, where t_o is the initial time. The rate of change of discharge with respect to distance was calculated by differentiating Equation 3. The other two equations were then solved numerically by the fourth-order Runge-Kutta integration technique, with initial conditions t_o = variable, $x_o = 0.001$, and $S_o = 0$. The generated solution was a downstream series of POM concentrations, with time also increasing with downstream distance.

Because sediment POM does not move downstream, the same solution technique could not be used. We found it necessary to treat sediment POM as a series of compartments. We used a total of 70 compartments, distributed at decreasing intervals downstream. Between downstream simulation runs, each sediment POM compartment was updated according to the equation

$$\frac{dB_i}{dt} = (DP_i - E_i)\ D - K\ B_i, \tag{26}$$

where B_i is the sediment POM concentration (g m^{-2}) in compartment i, and DP_i and E_i are the deposition inputs and erosion outputs to compartment i. DP_i and E_i were calculated as the average values of DP (Equation 21) and E (Equation 22) over the distance represented by compartment i. Multiplication by depth (D) converted from concentrations to area units.

RESULTS AND DISCUSSION OF SIMULATION

Some of the output from a 14-month simulation produced by our model is shown in Figs. 3 and 4. With respect to the river above the reservoir, the model produced the following results:

1. POM concentration was highest during leaf fall and decreased through the rest of the year. It is difficult to separate seasonal effects from flood effects in published data; however, there are studies with which the model results can be compared. In studies of low-order

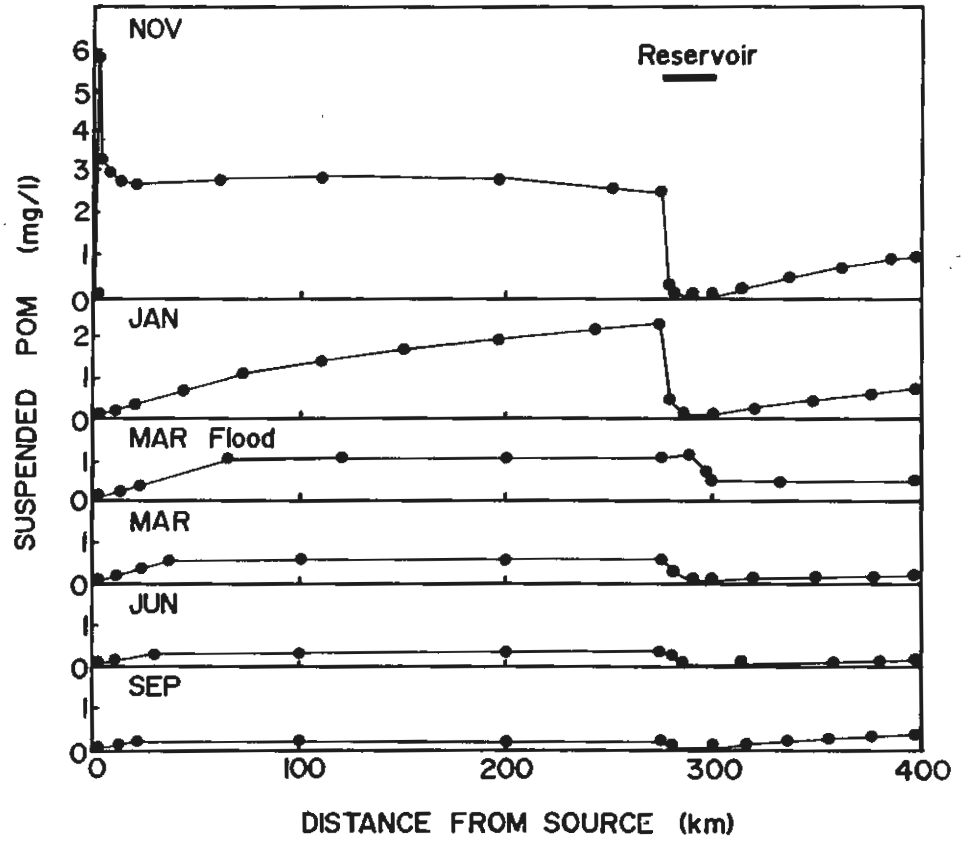

Fig. 3. Model-predicted suspended particulate organic matter (POM) as a function of distance from the river source.

woodland streams Naiman and Sedell (1979) found a winter POM concentration peak. Using a continuous sampler in a woodland stream, Malmqvist et al. (1978) found a POM peak in winter associated with high flows. FPOC concentrations in small streams at Hubbard Brook were highest during summer, when flows were highest (Hobbie and Likens, 1973). Wetzel and Manny (1977) found a summer peak, associated with rapid vegetative growth, and an early winter peak associated with high flows. Minimum POC concentration occurred during leaf fall. Data from small forested watersheds at Coweeta Hydrologic Laboratory (Wallace et al., unpublished) show that base flow POM concentrations are consistently lower in winter than summer. In general, these studies suggest that POM is retained in low-order streams much longer than predicted by our model.

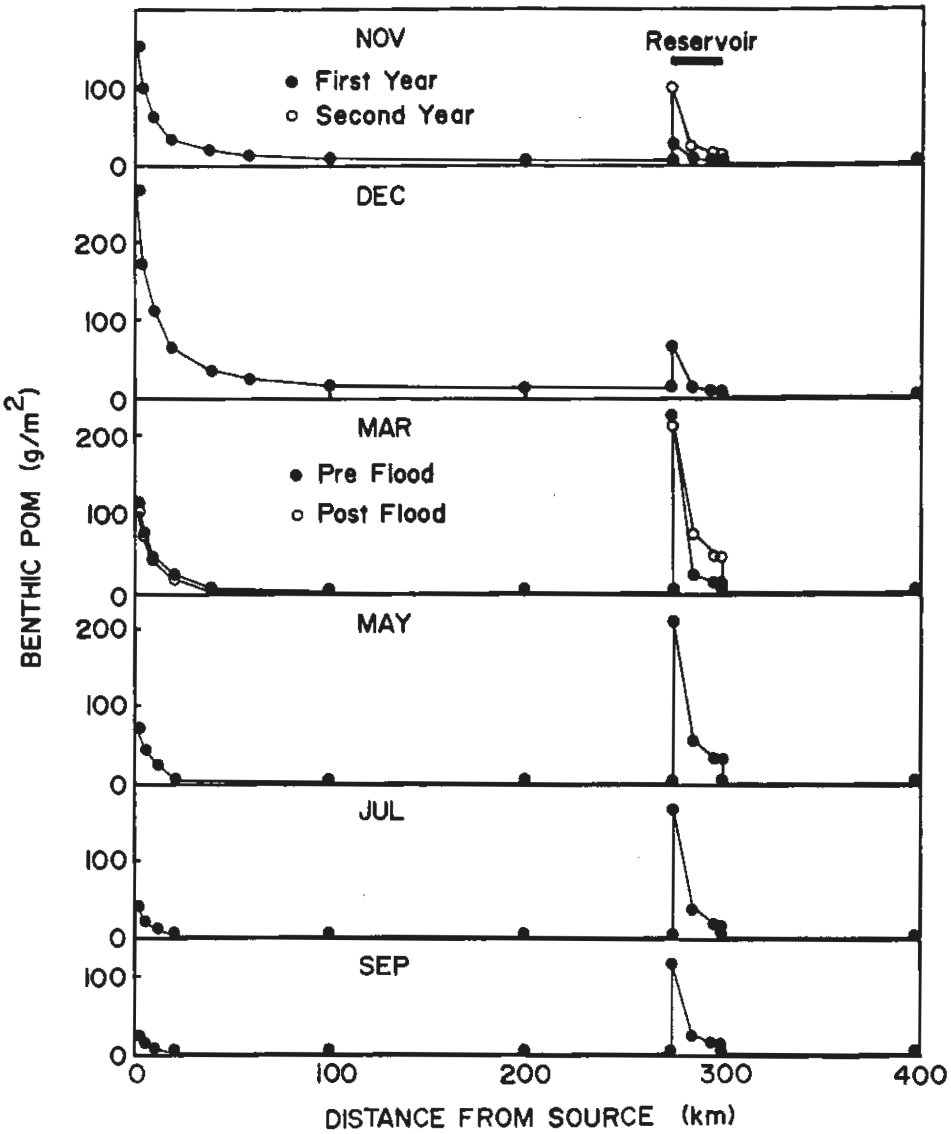

Fig. 4. Model-predicted benthic particulate organic matter (POM) as a function of distance from the river source.

Also, as a number of studies have shown, the input of allochthonous leaf material to headwater streams continues beyond leaf fall because of blow-in (e.g., Fisher and Likens, 1973; McDowell and Fisher, 1976; Comiskey et al., 1977; Webster, 1977). In studies of larger streams not immediately affected by lakes, high POM concentrations during low-flow periods are often reported and are usually associated with autochthonous production (Weber and Moore, 1967; Berrie, 1972; Naiman and Sedell, 1979).

2. During leaf fall, POM concentration peaked a short distance downstream from the headwaters, then decreased downstream. At other times of the year POM concentration increased or remained constant downstream. Data from first- to fourth-order streams at Coweeta Hydrologic Laboratory (Wallace, unpublished) show peak concentrations within the first 2 km for all seasons except spring, when POM concentration increased slightly from the headwaters to a point 6 km downstream. Malmqvist et al. (1978) found that POM concentration in a small woodland stream in Sweden increased to a peak 5-6 km downstream from the headwaters, then decreased downstream. Data from the River Continuum Study (Sedell et al., 1978; Naiman and Sedell, 1979) show a variable pattern. At each of four sites in Oregon, Pennsylvania, Michigan, and Idaho, samples were collected from four streams spanning first to seventh order. In Oregon the peak annual average POM concentration was in the lowest-order stream; in Michigan and Idaho it was in the next-to-lowest order stream. In Pennsylvania the peak was in the highest-order stream. In a more thorough analysis of the Oregon data, Naiman and Sedell (1979) found that POM concentration was always higher in the first-order stream than in the third- and fifth-order streams, which were generally similar. POM concentrations in the seventh-order streams were higher than in the third- and fifth-order streams in spring, summer, and autumn, but lower in winter. In spring, POM concentration in the seventh-order stream was higher than in the first-order stream. It is evident from these studies that an understanding of the longitudinal distribution of POM in stream basins is not yet possible. Such factors as autochthonous production and increased downstream inputs from nonforested areas produce a more complex system than currently depicted in our model.

3. Benthic POM was greatest just after leaf fall and was gradually depleted over the rest of the year. This pattern is generally consistent with studies of low-order streams, where inputs are primarily allochthonous (e.g.,

Minshall, 1967), though some studies also show a spring peak (e.g., Nelson and Scott, 1962; Tilly, 1968; Webster and Patten, 1979).

4. There was a consistent downstream decrease in POM standing crop. This is consistent with a few available studies. Naiman and Sedell (in press) showed a downstream decrease in POM standing crop in streams from first to seventh order in the Oregon Cascades. Webster (1977) found a similar pattern for first- to fourth-order streams in the southern Appalachians. Our model shows a complete depletion of benthic POM in all but the upper reaches of the river by late spring. This suggests a needed refinement in the part of the model concerned with resuspension of deposited POM.

The following results of the simulation refer to changes occurring within and below the impoundment.

5. POM concentrations decreased as the river flowed through the reservoir. There is little question that substantial amounts of suspended organic material settle from reservoir waters. Armitage (1977) estimated that up to 91% of the total solids transported by the River Tees (England) was retained by the Cow Green Reservoir. Lind (1971) reported that Lake Waco (Texas) trapped 71% of the particulate organics entering from the Bosque River catchment area, and Maciolek (1966) reported that microseston in the Convict Creek (California) catchment was seriously disrupted by Convict Lake. This phenomenon is associated with the loss of stream power and ability to transport even small low-density organic particles. One exception to this generalization occurred in our simulation during the spring flood, when material was picked up in the shallow end of the lake and deposited farther down the lake.

6. Deposition in the reservoir increased POM standing crop primarily during high winter-spring flows, especially the early spring flood. During summer and early fall, benthic POM was depleted by decomposition. Our 14-month simulation showed a realistic year-to-year increase in reservoir benthic POM.

7. There was no deposition of benthic POM below the reservoir. In a review of downstream reservoir effects, Neel (1963) noted that reservoir releases to smaller streams may remove small sediment particles, leaving a bottom composed of larger particles. One problem of the Aswan Dam has

been downstream erosion caused by silt-free, high-velocity flows (Sterling, 1971). Those observations suggest that, in some cases, POM would not be deposited below a reservoir. In other cases, where flow below the reservoir is less than reservoir input because of water diversion or where a more constant flow is maintained, the opposite effects occur. Gravels may become compacted and the interstices filled with fines (Fraser, 1972).

8. POM concentration increased with distance downstream from the dam. This effect was caused by tributary inputs and, in autumn, was accentuated by inputs from riparian vegetation. This increase has been documented in several studies conducted below reservoirs with hypolimnial releases. Ward (1974, 1976) found that water discharged from the hypolimnion of Cheesman Lake on the South Platte River (Colorado) was very low in organic particles. POM gradually increased downstream due to a combination of allochthonous and autochthonous sources. Ward also noted that the rich community of filter-feeding invertebrates frequently reported downstream from reservoirs was substantially reduced downstream from Cheesman Dam. Gore (1977) found a similar situation downstream from the Tongue River Reservoir (Montana), which has a hypolimnial release. Although low temperature of water released from these dams was implicated as contributing to depressed macroinvertebrate communities, absence of a suitable food source was cited as another factor.

Dams with releases nearer the surface may have essentially opposite effects downstream to those with deep releases. Maciolek and Tunzi (1968) reported that microseston in the outlet of Lurel Lake (California) was 85% greater than at the inlet and that the bulk was limnoplankton generated in the lake. In Belwood Lake on the Grand River (Ontario), Spence and Hynes (1971) reported that more suspended organic matter was entering than leaving the lake in summer. However, lake level fell in late summer, and there was a large die-off of limnoplankton, which were washed into the river through the dam. Suspended organic matter downstream increased to several times that carried by the river into the reservoir. Cushing (1963), Simmons and Voshell (1978), and Merkley (1978) reported that, although the reservoirs they studied had a clarifying effect on water as it passed through the lakes, there were sufficient exports of both living and moribund limnoplankters in the discharges to support large populations of filter-feeding macroinvertebrates. Lind (1971) reported that POM entering Lake Waco (Texas) from the Bosque River catchment was chiefly "sestonic detritus," while that leaving the system was living and dead limnoplankton.

9. The reservoir increased overall processing efficiency of the river. We defined processing efficiency as the difference between total particulate input to the river and total particulate output (Webster, 1977; Webster and Patten, 1979). Total input to the river estimated from the model was 1.84×10^5 T y^{-1}. Output without the reservoir was 6.60×10^3 T y^{-1}, a processing efficiency of 96.4%. With the reservoir in place, the output was 3.07×10^3 T y^{-1}, a 98.3% processing efficiency. Output from the river system was reduced to less than half. Only 240 T y^{-1} of the extra 3.53×10^3 T y^{-1} processed was stored permanently on the reservoir bottom. Because of the ability of reservoirs to trap and decompose POM, total processing of organic material in a river with a reservoir is greater than in an undammed river. This effect is not evident in published studies, because of increased autochthonous (limnoplankton) and anthropogenic (sewage) inputs. Lind (1971) estimated that Lake Waco had little effect on total organic matter transport in the Bosque River. Sedimented POM was equaled by limnoplankton production. From a study of the New River, Newbern (1978) found that annual organic matter transport at a point 90 km upstream from Claytor Lake was approximately equal to transport at a point 90 km downstream from the dam. However, in addition to the reservoir, between these two sites were a number of towns with sewage effluents to the river, so that total organic-matter processing within the reach was considerable.

CONCLUSIONS

Through our modeling effort, we identified several areas where our model does not accurately reflect current knowledge of POM behavior in river-reservoir ecosystems. These include: appropriate seasonality of allochthonous inputs, autochthonous sources of POM, filter-feeder utilization of POM, and deposition and resuspension characteristics of POM. Despite the inadequacies of our model, we feel it is an advance over previous stream-ecosystem models because it includes the longitudinal or continuum aspect. By including a reservoir as part of this system, we have been able to analyze reservoir effects on POM dynamics within this larger framework.

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