Change in Thermal Regime as a Cause of Reduction of Benthic Fauna Downstream of a Reservoir

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The kinds and numbers of Ephemeroptera and other insects in the Saskatchewan River are greatly reduced downstream of a dam. This is attributed to changes in river temperatures caused by the reservoir. The river is warmed in winter and cooled in summer. Consequently, mayflies and other insects with strict thermal requirements cannot hatch and grow successfully. The effect is evident 70 miles downstream.

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Le nombre d'espèces et d'individus d'éphéméroptères et autres insectes est grandement réduit en aval d'un barrage dans la rivière Saskatchewan. Nous attribuons ce phénomène aux changements de température de la rivière, réchauffement en hiver et refroidissement en été, causés par le bassin de retenue. L'éclosion et la croissance des éphémères et autres insectes sténothermes en sont affectées. Les effets se font sentir à 70 milles en aval du barrage.

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RECENT investigations have shown striking reductions in invertebrates downstream from the outlets of reservoirs (Pearson et al. 1968; Lehmkuhl 1970; Hilsenhoff 1971; Spence and Hynes 1971a, b). The cause of the reduction has not been demonstrated, but lowered water temperature, altered water chemistry, and increase in siltation have been implicated. The objective of this study was to determine the cause of the reduction of fauna, and this report provides evidence that an alteration of the total seasonal temperature regime prevents reproduction of many benthic organisms.

A reservoir results when any watercourse is dammed. In North America, virtually no large temperate river remains that is not regulated to some degree. The Missouri and Tennessee are examples of rivers that have been brought entirely under control by reservoirs (Neel 1963), and other large programs are in the planning stages (Anon. 1969). When a dam is constructed, the upstream riverine environment changes into a lake-like reservoir with associated alteration of the fauna. Changes also occur on the downstream side, because as water flows into the reservoir the sediment load is lost, dissolved materials may be gained or lost, and thermal stratification usually occurs. Reservoirs in temperate climates normally discharge from the bottom (in contrast to natural lakes) a summer cool but winter warm, chemically altered, sediment-free outflow into the downstream channel at

pared to the original river or the river upstream, not the reservoir itself) have been predicted (Edmunds and Musser 1960; Edmunds 1972) and have now been documented (see above), but the mechanism causing the reduction had not been demonstrated.

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Effects on Study Area

In the present study I have found a marked reduction of macro-invertebrates downstream from a reservoir on the South Saskatchewan River (Fig. 1), and the reduction is evident 70 miles downstream from the dam, at which point sewage and industrial pollution from Saskatoon mask the effect of the reservoir and prevent further downstream monitoring. The conclusion that there was a reduction in the fauna 70 miles downstream from the outlet is based on the following observations. During 1970 and 1971, extensive collections were made in the Saskatchewan River; 19 species of mayflies (Ephemeroptera) were found in the control area upstream from the reservoir (Fig. 1, Station I), and 20 species were collected at or near the control station on the North Saskatchewan River (Fig. 1, Station VII). In contrast, no species were collected below the dam outlet (Station II), one species was collected at Station III. two species were collected at Station IV, three species were collected at Station V, and seven

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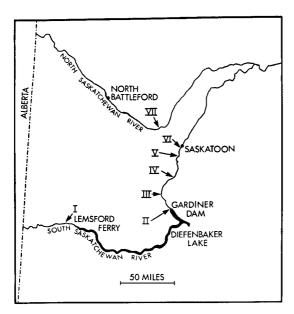


Fig. 1. Study area in west central Saskatchewan. Stations I and VII provide a base for comparison with stations II-VI, which are influenced by the reservoir.

species were collected at Station VI, 70 miles downstream from the outlet. Thus, even 70 miles downstream the incidence of mayfly species was less than 40% compared to the upstream control area and the control area in the north branch of the river.

Invertebrates other than mayflies were also reduced downstream near the outlet. In 1971, the uniform sampling technique used at stations II-VI was a modification of the kick sample method (Spence and Hynes 1971a) and involved sweeping with a long-handled net while one stirs the bottom with the feet and walks backward against the water current. The dislodged organisms are captured in the net. The sample at each station consisted of two 20-ft samples near the shore and one 50-ft sample in a sand bar. The results were as follows: nine chironomid larvae (Diptera) and no other invertebrates were found below the outlet (Station II); stations III-VI, respectively, yielded 39, 42, 277, and 289 specimens of aquatic invertebrates; in terms of diversity, the number of major groups represented (Chironomidae, other Diptera, Corixidae, Dytiscidae, Gomphidae, Plecoptera, Trichoptera, Ephemeroptera, leeches, molluscs, and Crustaceans) were, respectively, 1, 6, 6, 7, and 11 for stations II-VI. The data support the earlier mentioned reports that there is an alteration of the benthic fauna near the outlet of the reservoir, and, further, that the effect extends a number of

miles (in this study, 70) downstream from the outlet (also noted by Pearson et al. 1968).

Possible Environmental Factors

What factor or factors cause the reduction of the fauna? Since an increase in the density and diversity of the fauna was observed with increasing distance downstream from the outlet (from 0 to 7 species of mayflies, from 1 to 11 groups of invertebrates, and from 9 to 289 total specimens per sample), it is argued that the causal factor should change with the recovery of the fauna. It should be possible to measure environmental factors at points downstream from the outlet. eliminate as insignificant those factors that remain constant at all stations, and retain as significant those factors that change (become more favorable) with the increase in the faunal community. Measurements were taken on total dissolved solids, pH, total alkalinity, P alkalinity, Ca hardness, Mg hardness, sulfide, chloride, nitrate, CO₂, phosphate, silica, ammonia, turbidity, oxygen, and temperature. All physical and chemical factors measured except temperature were nearly constant at the stations downstream from the reservoir. Organic matter and plant growths for the base of the food chain were available at all stations. The water was saturated with O2 at all stations at midday in summer, and because of the turbulence of the outflow and absence of unusual BOD, there is no reason to believe that O2 levels would be low in other seasons. Total dissolved solids were always near 265 ppm and there were no significant differences in dissolved materials among the stations. Water color and turbidity increased downstream with the increase in organisms but this is probably a result of increased algal growth and agricultural run-off, and not a cause of faunal depletion. Differences among stations were slight and the published literature provided no evidence that minor variations of these factors can cause broad elimination in all groups from a habitat. Temperature, however, does appear to be an important factor.

EFFECT ON WATER TEMPERATURE

Temperature was obviously altered by the reservoir (Fig. 2). No upper lethal temperatures were involved, so temperature per se at a given time must not be the limiting factor. When the total seasonal temperature pattern is considered and correlated with the life cycles of organisms, it will be shown that it is impossible for certain organisms to reproduce near the dam outlet.

Figure 2 shows the seasonal pattern of warming and cooling at points downstream from the dam

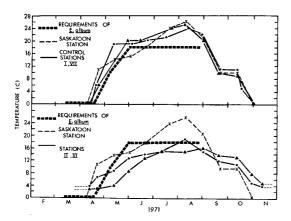


FIG. 2. Seasonal temperature pattern at the control stations (upper) and at stations downstream from Diefenbaker Lake (lower). The pattern for Saskatoon (VI) is repeated to facilitate comparison. Temperatures are the daily maximum — i.e. readings were taken in the afternoon during clear weather; the heavy line summarizes the requirements of *Ephoron album*; exposure of eggs to freezing; an increase to 10–13 C, a further increase to 18 C; $2\frac{1}{2}$ months at or above 18 C.

and the control stations (I and VII, Fig. 1). At stations I and VII (the controls) the temperature increased rapidly in April after ice break-up and dropped sharply in the autumn, leading to freezing of the river. The temperature was 0 C (ice) from November until April. In contrast, within 20 miles of the outlet (stations II and III, Fig. 1) the water temperatures did not drop sufficiently to form an ice cover and the spring rise and autumn decline in temperature were gradual. Summer maxima were lower and winter minima were higher at stations II and III than at I and VII.

EFFECTS ON MAYFLIES

The life cycles of most of the mayflies (Ephemeroptera) of the area were determined, and it is possible to correlate these life cycles with the temperature patterns. Ten species of mayflies from the study area (Isonychia sicca (Walsh), Lachlania saskatchewanensis Ide, Anepeorus rusticus McDunnough, Epeorus sp., Choroterpes albiannulata McDunnough, Traverella albertana (McDunnough), Ephemerella sp., Brachycercus prudens (McDunnough), and Ephoron album (Say.) Pseudiron centralis? McDunnough) fall clearly into Hynes' (1970) fast seasonal cycle, in which the eggs have a long period of diapause (arrested development) and hatch after the appropriate environmental stimuli. Following hatching there is rapid growth of the nymphs leading to emergence of adults.

The above-listed mayflies pass the winter in the egg stage; depending on the species, the nymphs hatch in June, July, or August and the adults appear in August or September of the same year. Experimental results are available for E. album (Britt 1962). With reference to temperature the species has three requirements: the eggs will not complete their development unless they are exposed to a period of temperature at or near freezing (breaking of diapause) (Britt 1962, found that 1.3 C was not sufficiently low to allow normal development); second, the eggs will not hatch to nymphs unless the near-zero temperature is folowed by temperatures of 10-13 C; third, the nymphs will not reach maturity unless exposed to $2\frac{1}{2}-4$ months of warm temperatures (not specified by Britt, but apparently 18-28 C). As can be seen in Fig. 2, all these requirements were met in the control areas where all the above species of the fast seasonal type were present, but the requirements for both freezing and warmth were not present near the dam where the above species were absent. Even if the freezing requirement was met, the requirements for hatching and growth were not. I conclude that the species are eliminated by an altered water temperature pattern.

Five species of mayflies (Ephemera simulans Walker, Ametropus neavei McDunnough, Siphloplecton sp., Baetisca bajkovi Neave, and a species belonging to an undescribed genus) fall into Hynes' (1970) slow seasonal cycle, wherein the eggs hatch soon after they are laid (no diapause) and maturation of the immature stages requires approximately 1 year. In the case of the above species at Station I, eggs were laid and hatched in summer, much growth occurred during the warm period of late summer and autumn, and nymphs wintered under the ice, at which time growth was limited, and adults occurred the following summer. It has been observed that Ephemera simulans Walker requires a specific number of degree-days (sum of mean daily temperatures) in spring before the nymphs emerge to adults (Britt 1962). At the control stations I and VII, warm periods were present for the development of these species (Fig. 2), and the species were present. In areas near the dam the warm periods were much curtailed (Fig. 2), and the species under consideration were absent. I conclude that these species are also eliminated by the altered temperature pattern.

Discussion

I conclude that the 15 species listed above cannot successfully reproduce and thus are absent near the dam outlet for one or both of two reasons: the required temperature sequence for breaking

diapause and stimulating egg hatching and growth is absent, or the total degree-days (especially in spring) needed for growth and adult emergence are not attained. Solid data are presented for two species (*Ephoron album* and *Ephemera simulans*), and inferences based on the presented data are made for 13 additional mayfly species. This same argument apparently applies to a wide range of organisms. Hynes (1970) shows that aquatic invertebrates other than mayflies, in fact most insects, have *fast* and *slow* seasonal life cycles, and would have similar requirements.

Consequently, I make the inference that the non-mayflies were eliminated by the same process as were the mayflies. Finally, I infer that all deep reservoirs in temperate climates (i.e. reservoirs that stratify thermally) that have a hypolimnion drain will cause similar downstream faunal depletion, and this explains the faunal depletion in other areas of North America.

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