A PRELIMINARY INVESTIGATION OF BOTTOM FAUNA AND INVERTEBRATE DRIFT IN AN UNREGULATED AND A REGULATED STREAM IN ALBERTA*

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A preliminary investigation of two mountain streams in Alberta was undertaken during 1968–69, in order to assess the effect of fluctuating stream flows on standing crops and drift of benthic organisms. One of these, the Kananaskis River, was subject to flow regulation for hydroelectric purposes, while the other, a tributary, Lusk Creek, was not. Several environmental factors known to affect these phenomena were also investigated. The life histories of some of the Ephemeroptera and Plecoptera, and emergence patterns of some Plecoptera in addition to a study of insect distribution at and below the surface of the substrate have been reported elsewhere (Radford & Hartland-Rowe 1971a, b, c).

Except for studies by Neel (1963), Pearson & Franklin (1968), and Pearson, Kramer & Franklin (1968), little work has been done on rivers whose flow is regulated. Pearson & Franklin (1968) note that sudden flow increases caused rapid rises in the catastrophic drift of *Baetis* sp. and Simuliidae and found that artificial reduction of stream discharge also caused an increase in the drift, with virtually all bottom-dwelling forms being affected, as also did Minshall & Winger (1968).

Neel (1963) states that daily fluctuations in reservoir releases discourage littoral stream life and may reduce a stream's carrying capacity for many organisms. Sedentary forms of insects, clams and fixed oligochaetes find survival very difficult under such conditions, but most insects (especially those making long mating and egg-laying flights) are apparently able to cope with controlled, fluctuating discharges. Also, the normal annual temperature cycle of streams can be disrupted under regulated flows since reservoirs delay the rise in river temperature in the spring and its decline in the autumn, because more time is required for their relatively great volumes of water to approach air temperature.

Rawson (1948) undertook a biological investigation of the Kananaskis River after completion of the Upper Kananaskis Lake reservoir (Interlakes Dam), but before construction of the Lower Kananaskis Lake reservoir (Pocaterra Dam). He found a 'rich and varied fauna' (no quantitative data are given) in stream samples obtained below the Lower Kananaskis Lake. This was the only previous study of the benthic invertebrates in the Kananaskis River.

THE STUDY AREA

The Kananaskis River system is comprised of two lakes, the Upper and Lower Kananaskis Lakes (which were formerly connected by the Upper Kananaskis River), and the Lower Kananaskis River (Fig. 1). Originally the drainage was from the Upper Lake through the river to the Lower Lake and thence to the Kananaskis River, which flows in a northerly direction for about 84 km to join the Bow River at Seebe (Thomas 1955).

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The Bow River flows eastward into the Saskatchewan River system of the Hudson Bay drainage.

Two dams were built in 1936 and 1942 to impound the waters of the Upper Lake. The next power development of this watershed was the construction in 1946–47 of the Barrier Dam, 64 km downriver from the lakes. In 1955 work was completed on the Pocaterra Dam on the Lower Kananaskis River about 1 mile below its source in the Lower Kananaskis Lake.

As in all hydro power projects of this type, water is stored during the spring runoff and is gradually released during the winter to produce power. Lake levels are usually at an extreme low in May and are highest in October or November. Normally, the Upper Kananaskis Lake is the first to be lowered and when that reservoir nears its low water level the Lower Kanaskis Lake and Barrier reservoir are lowered, respectively. Frequent releases from Barrier Lake occur due to the inflow of the Kananaskis River, although the discharges are highly variable in duration and occurrence.

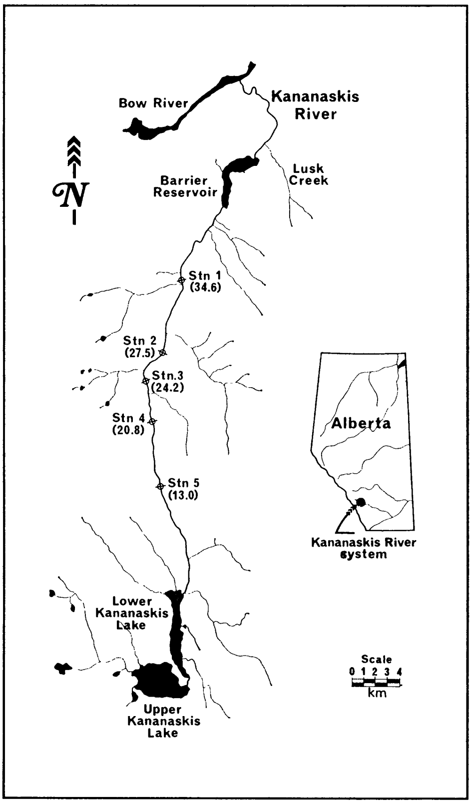


FIG. 1. Kananaskis River System. Figures in parentheses represent the distance (km) from the Lower Kananaskis Lake to the sampling site.

The Kananaskis River is a substantial stream; a mean discharge of 13·6 m^3/sec was recorded during the study, with a range of 1·4 m^3/sec in April to about 68 m^3/sec in June. An extreme low of about 0·3 m^3/sec discharge was measured in September. The extent of water level fluctuation was 83·8 cm. The stream has a mean gradient of about 10·4 m/km and in many areas has a rapid flow; rates of 1 to 2 m/sec are not uncommon. In some sections the river is shallow with a braided channel.

The mean flow in Lusk Creek was approximately 0·5 m^3/sec, with a range in discharge of 0·2 m^3/sec in November to 0·8 m^3/sec in June (excepting a June spate when an estimated high flow of about 5·7 m^3/sec occurred). The extent of water level fluctuation was at least 14 cm. The stream has a slope of about 70 m/km.

Both streams are located on the eastern slopes of the Rocky Mountains in south-west Alberta at approximately 50 N and 115 W, about 70 km west of Calgary.

Since the benthic invertebrate fauna and substrate (sand, gravel and rubble, with some large boulders) of the streams were similar, Lusk Creek was chosen as a control. Although it was not ideal (because of its smaller size) it was considered satisfactory for comparative purposes.

METHODS

Fig. 1 indicates the location of sampling sites on the Kananaskis River. Sites were selected on the basis of their distance from the Lower Kananaskis Lake, their similarity in gross physical appearance (e.g. substrate, current velocity and depth), and their ease of access. Sampling was done at a single site on Lusk Creek, about 200 m from the stream's junction with the Kananaskis River.

At approximately 4-week intervals from April until November, three Surber samples (mesh size of 9 meshes/cm) were taken from Lusk Creek and each sampling site on the Kananaskis River to obtain an estimate of standing crops of benthic invertebrates. Because of the non-random distribution of insects in streams, samples were taken at sites of similar physical nature, as suggested by Chutter & Noble (1966), in order to reduce variability in quantity and quality of fauna. While not representative of the whole stream, these are valid comparative estimates, since the physical features used in selecting sites were the same for both streams. Samples were preserved in 10% formalin in the field, hand-sorted in the laboratory and then transferred to 70% ethanol.

Invertebrate drift was measured with a modified high-speed plankton sampler (enclosing a coarse plankton net with 1·34 meshes/mm) of the variety used by Elliott (1967a). The volume of water sampled was determined indirectly by periodically measuring the water velocity with a Gurley flow-meter at the intake end of the tube. The velocity was determined at six-tenths of the vertical depth of the water column, this being equivalent to the mean velocity of the vertical (Corbett 1962; Grover & Harrington 1966). Since the area of the intake was known it was a simple matter to calculate the amount of water sampled.

Sampling was done for 24 h in most instances and the nets were usually emptied every 3 h in Lusk Creek and every 4–6 h in the Kananaskis River. All samples were preserved in the same manner as Surber samples. Light intensity (ft-candles) was measured with a Sekonic Light Meter (Model L-28C) when nets were emptied.

Drift samples were taken at approximately 4-week intervals from May to September, inclusive; additional samples were taken at other times to assess drift under certain flow conditions. Drift was sampled at Lusk Creek and three sites (Stations 1, 4, and 5) on the Kananaskis River, although Station 1 was sampled most frequently because it was easily accessible.

A stream-gauging station was established at Station 1 on the Kananaskis River; discharge was determined by methods outlined in Corbett (1962), and Grover & Harrington (1966). A Stevens Water Level Recorder (Type A35) recorded the amount of water level fluctuation. In Lusk Creek, a series of computed discharge measurements were related to periodic staff gauge readings for discharge analysis. Although a continual record of water level fluctuation was not available this method was adequate for flow measurement since the discharge in Lusk Creek was fairly stable.

Both air and water temperatures were recorded at Lusk Creek and Stations 1 and 5 on the Kananaskis River, and water temperature only was recorded at Station 3. Rigosha thermographs (enclosed in weather screens) were used in the former case and a Belfort Instrument Company thermograph recorder in the latter. Because of the similarity of the temperature recordings for all stations on the Kananaskis River only data for Station 1 will be presented (Fig. 2). The pattern of water temperature paralleled air temperature except during spates and reservoir releases. Although Nelson (1965) found that the daily maximum stream temperatures between Pocaterra plant and Barrier Reservoir varied only between 10 and 12° C in the summer of 1961, temperatures of 14–15° C were recorded for this period during 1969.

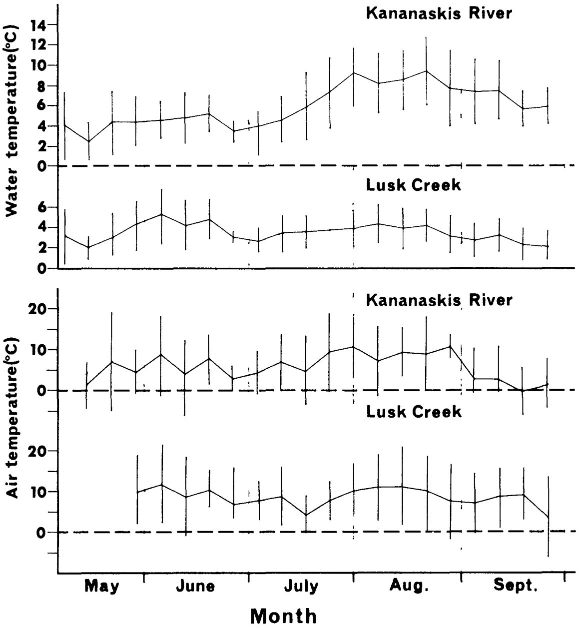


FIG. 2. Mean and range of weekly air and water temperatures for Station 1 on the Kananaskis River and Lusk Creek.

RESULTS

General discharge pattern

The general discharge pattern of the Kananaskis River (Fig. 3) was as follows. Initial high flows (42·5 m^3/sec) occurred during the second and third week of May following a low discharge in April. Reduced flows in mid-May resulted from a slowing of the spring melt by a late snowfall. However, fair weather in late May caused another increase in discharge. The peak flows (50 m^3/sec) during early June are a result of a series of reservoir releases combined with a high runoff (which ceased by mid-June). Peaks in early July and August were due to heavy rains and reservoir releases, respectively, while the increasing discharge after mid-September was a result of almost daily reservoir releases.

Few releases occurred during low flow periods in mid-July, and late August to mid-September.

In Lusk Creek the spring runoff spanned the month of May and ceased by June, at which time flows subsided. The May snowfall also reduced discharge. Heavy rains (Fig. 3) caused extreme flooding in late June–early July. From mid-July onwards discharge declined to flows approximating 0·23 m^3/sec.

The annual discharge pattern of unregulated streams in this region differs from that of the Kananaskis River in several respects. Whereas relatively high flows occur during the autumn and winter in regulated rivers, discharge is at its lowest at this time in unregulated streams. Also, summer discharge peaks of the magnitude experienced in the Kananaskis River are exceptional in unregulated streams.

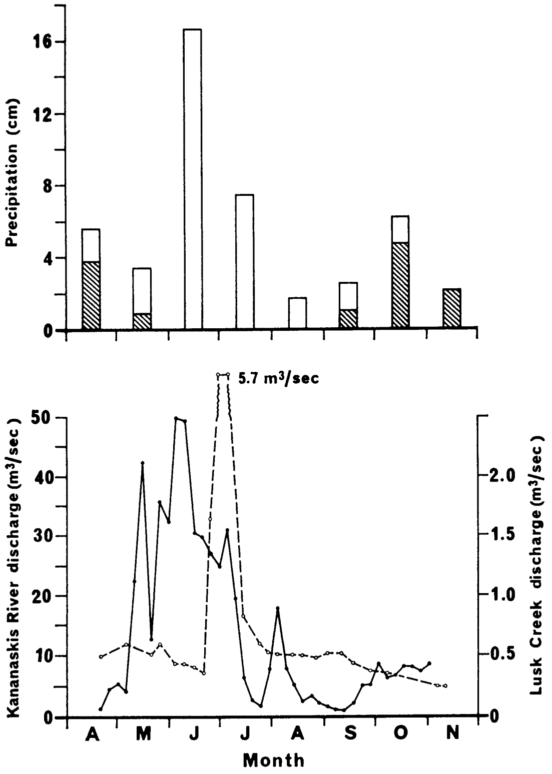


FIG. 3. Discharge of the Kananaskis River (●, average of 5-day intervals) and Lusk Creek (○, average of approximately 7-day intervals) and monthly precipitation. Open columns, rain; hatched columns, snow.

Description of reservoir releases

Typical reservoir releases are not definable although they do have certain characteristic features (Fig. 4). Releases from the Pocaterra Dam generally consist of a 27 m^3/sec discharge through the penstock. If the Kananaskis River is not naturally fluctuating at the time, the release reaches a peak (the height of which is related to the release magnitude) within 0·5–4 h, depending on the amount of water in the channel. The peak is maintained for the duration of the release. When the release is stopped the water level gradually subsides until reaching its former height, unless another release is initiated before this can occur. During the June releases, the discharged water passed Stations 5, 4, and 1 after about 2, 3·5, and 6 h, respectively, travelling about 6·44 km/h.

Usually only one release per day occurs during the spring and summer. However, during the autumn two releases per day are normal, one in the morning and another in the evening to satisfy the requirements of power peaking in nearby Calgary.

A total of 105 reservoir releases were recorded during the study but only those occurring over short intervals (i.e. during the course of a week) were similar. The average release lasted for 6·1 h and the duration ranged between about 0·5–16 h, depending on the power demand. The range of water level fluctuation was 32 cm. Two distinct ranges of absolute water level fluctuation occurred, the first encompassing 20 cm (initial thirty discharges) and the second 32 cm (remaining discharges). This pattern is probably correlated with the seasonal variations of flow and channel configuration associated with the release.

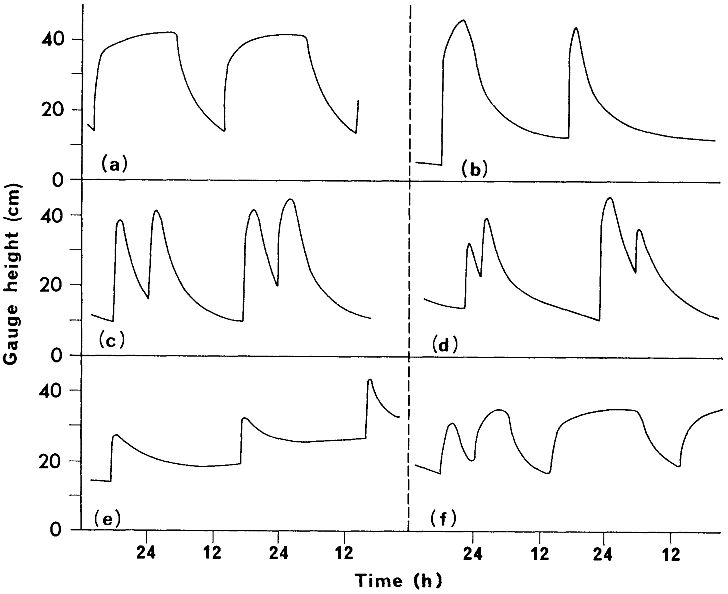


FIG. 4. Discharge pattern of the Kananaskis River (Station 1) during a variety of reservoir releases. (a) Consecutive single releases of equal magnitude, (b) consecutive single releases of unequal magnitude, (c) consecutive double releases of approximately equal magnitude, (d) consecutive double releases of unequal, reversed, magnitude, (e) consecutive single releases during the spring runoff, (f) combination of consecutive double and single releases of unequal magnitude.

The stream was very turbid during releases and carried a high silt load, much wood debris, with sand and small gravel. The abrasive effect of the rapidly moving water (e.g. greater than 2 m/sec) on algae was considerable as was the problem of silting.

Relationship between temperature and discharge

It does not appear that increased discharges from normal spring runoff lowers water temperature because this was seen to rise continually during the spring (Figs. 2 and 3).

However, the June rains (which caused a high discharge) reduced water temperatures in Lusk Creek and the Kananaskis River by approximately 1·8–2·0° C, with resultant lessened daily temperature fluctuations (e.g. 1·0–2·0° C rather than the usual 3·0° C plus).

During the runoff, reservoir releases seemed to have a negligible effect on water temperatures at Station 1 although a slight effect was noticeable at Station 5 (i.e. the release appeared to lower the water temperature slightly). These results are probably explicable on the basis of the mixing action of the current over this distance. Unseasonal releases (eleven consecutive discharges) in late July and early August lowered the mean stream temperature throughout the Kananaskis River by about 1·6° C for the release duration; they also appeared to depress stream-side air temperature (Fig. 2). Reductions in temperature in Lusk Creek are not noticeable at this time. It is difficult to interpret the biological effect of such a subtle temperature decline.

There does not appear to be any evidence for a delay of river temperature rise in the spring due to releases, or a marked disruption of summer stream temperatures, as described by Neel (1963), although there seems to be a delayed decline in the autumn. It is possible, however, that the temperature pattern characteristic of southern regulated rivers would occur in some years in the Kananaskis River. Certain reservoirs in southern latitudes (e.g. in Utah and Colorado) have a pronounced cooling effect on streams via releases and have created waters inhabitable by trout which were previously unsuitable for such fish (Pearson & Franklin 1968). Being a headwater stream, the Kananaskis River is naturally cold because of its elevation, latitude, and current velocity. Reservoir releases did not appreciably further depress stream temperatures; rather, the absence of regular releases during the summer, when potential river water was stored, caused increased temperatures in the constricted channel.

BOTTOM FAUNA

Seasonal fluctuations

The abundance of benthic invertebrates in numbers and calculated dry weights for the study is illustrated in Fig. 5. Biomass was generally similar at all sites on the Kananaskis River although the greatest amount occurred at Station 5; this may be correlated with substrate stability which was high at the site. Aberrant values for some months (e.g. Station 4, 10 September) are a result of collection of species with unusual attributes (e.g. extreme weight); others may be due to enlargement or reduction of inhabitable water caused by fluctuating stream flows. The exceptionally high values for Kananaskis River sites in August are probably partly a result of sampling when discharge was low, which could effectively concentrate stream insects in a narrow channel.

The seasonal trend of standing crops in the Kananaskis River is partially explicable as follows. The reduction in standing crops between April and June is largely a result of Plecopteran emergence; this is the time of their maximum emergence in these latitudes (Radford & Hartland-Rowe 1971c). Part of the decline may also be due to mortality from increased flows during the spring runoff. Emergence of stonefly and mayfly populations is then gradual, although continual, until the fall when many stoneflies of the genus *Alloperla* emerge, with concurrent emergence of some mayflies (Radford & Hartland-Rowe 1971a). This causes a decline from high summer densities.

The sequence of bottom fauna abundance in Lusk Creek parallels that of the Kananaskis River with one notable exception, this being the very low density recorded in July.

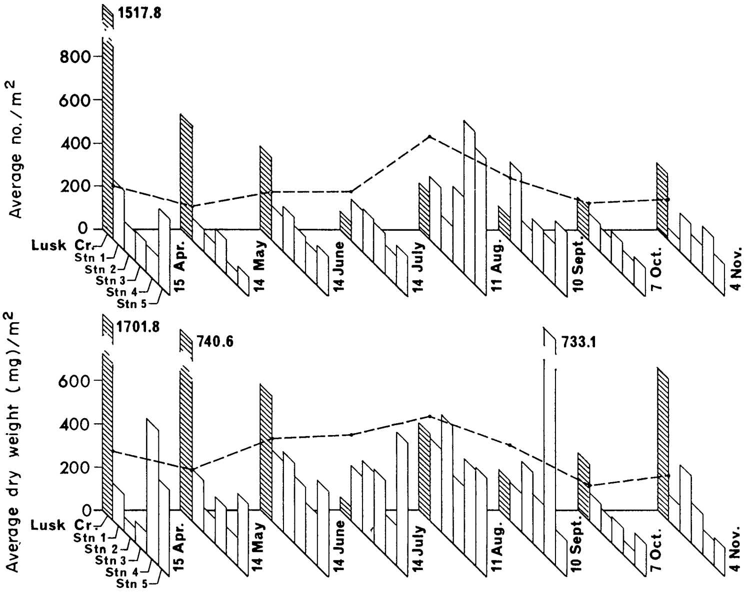


FIG. 5. Standing crops of bottom fauna (average number and dry weight per three Surber samples) in the Kananaskis River (open areas) and Lusk Creek (hatched areas). Dry weights calculated from wet weights assuming 80% loss in weight on drying. Broken-line graphs represent the mean values for the stations on the Kananaskis River.

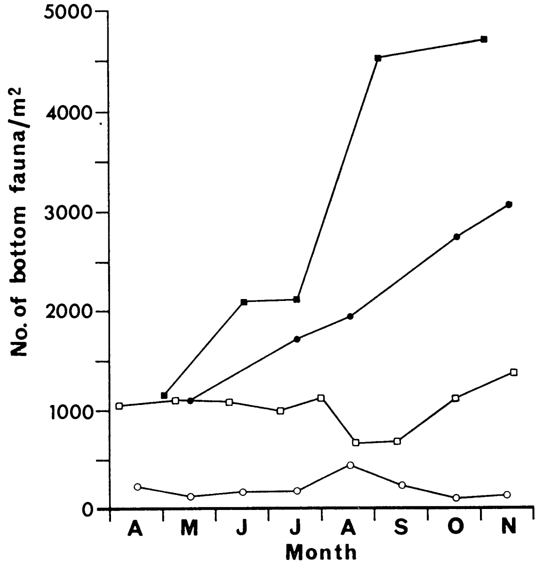


FIG. 6. Comparison of standing crops of bottom fauna in the Kananaskis River (○) and other western North American streams. ■, Provo River, Utah, Gaufin (1959); ●, Bridger Creek, Montana, Logan (1963); □, Wampus Creek, Alberta, Zelt (personal communication).

From mid-April to mid-June standing crops declined and this was due primarily to stonefly emergence (particularly those species belonging to the genus *Nemoura*). Another peak emergence period occurred during August and early September involving the same species as in the Kananaskis River. The spate of late June–early July (Fig. 3) caused a reduction in numbers from about 377 to 86/m^2. Heavy rains caused a rise in discharge from about 0·4 to 5·7 m^3/sec during this period and extreme scouring and channel shifting was evident. The abrasive effect of the suspended load, and bed movement, removed all algae.

It is significant that although the spate in Lusk Creek seriously reduced the numbers of benthic invertebrates this was not evident in the Kananaskis River; there, the numbers remained almost unchanged at every station. It is possible that because of numerous reservoir releases over a period of many years the river's channel has adapted to flood-like conditions and the substrate is less markedly affected than in unregulated streams; the stream bottom may be more stable and conducive to the maintenance of insect populations at a steady level.

A comparison of standing crops of benthos between the Kananaskis River and several other streams in western North America (Fig. 6) illustrates the former's low productivity. Although the standing crop is consistently low and relatively stable in the Kananaskis River a similar situation does not occur in other waters. Rather, numbers may increase several fold over short periods and large fluctuations appear common. Compared with other streams the Kananaskis River ranks very low regarding average densities and weight over extended periods (Table 1).

Species composition

The species composition of the benthos is illustrated in Fig. 7; some of the rare members are not shown. The data illustrate several interesting features.

Three ephemeropteran species (*Epeorus longimanus* (Eaton), *Ephemerella doddsi* (Needham), and *Rhithrogena doddsi* (McDunnough)) comprised about 65% of the insect fauna of the Kananaskis River; these species share related adaptations to a torrential existence. They are robust forms with strong legs and are able to cling to stones in swift currents by means of an adhesive disc employing the ventral side of the abdomen. In *Ephemerella doddsi* the adhesive disc is bounded by a setaceous cutaneous fold; in the genus *Rhithrogena* the characteristic gills form the boundary. Nielsen (1950) feels that the latter apparatus is even better developed in the genus *Epeorus*, where the lateral margins of the gill lamellae are thickened. These species comprised only about 20% of the insect fauna in Lusk Creek, a stream with a greater slope (70 m/km) than the Kananaskis River (10 m/km), yet less pronounced current velocities. It appears that there is selection for torrential species in the river and this is likely to be related to high flows and corresponding high velocities.

Another significant point is the fact that whereas *Nemoura* spp. made up about 20% of the benthic fauna in Lusk Creek, they comprised less than 1% of the total in the Kananaskis River (although they were not sampled during their highest densities). This genus characteristically inhabits aggregations of litter and leaves in Lusk Creek and these niches are rare in the river because rapid, turbulent flows sweep the bottom of allochthonous matter, especially during the autumn when leaves fall into the stream. The data for pre- and post-impoundment years on the Green River, Utah (Pearson *et al.* 1968) indicate that *Nemoura* spp. similarly disappeared from its fauna.

This type of comparison is difficult to pursue much further on a specific level, since

Table 1. *The standing crop of the Kananaskis River and Lusk Creek compared with stream benthos in other streams*

Stream	No./m^2	Wet weight (g/m^2)	Dry weight (g/m^2)	Substrate	Remarks
West Creek, Quebec, a	3110	11·07	2·21	Mixed	Annual average Net with 16 meshes/cm
River Endrick, Scotland, b	2840	11·28	(2·35)*	Bare stones	Annual average Net with 65 meshes/cm
Bridger Creek, Montana, c	2253	–	–	Mixed	Annual average Net with 9 meshes/cm
Provo River, Utah, d	2077	–	–	Mixed	Annual average Net with 9 meshes/cm
Firehole River, Wyoming, e	1215	9·9	(1·98)	Stones	Spring, summer only. Net with 16 meshes/cm
Montreal River, Saskatchewan, f	1146	–	–	Rubble and boulders	Summer only. Net with 9 meshes/cm
Lusk Creek, Alberta	417	2·91	(0·58)	Rubble and stones	Spring, summer and fall only. Net with 9 meshes/cm
Kananaskis River, Alberta	203	1·37	(0·27)	Rubble and stones	Spring, summer and fall only. Net with 9 meshes/cm

* Values in parentheses calculated assuming 80% loss in weight on drying.

a, MacKay & Kalff (1969); b, Maitland (1964); c, Logan (1963); d. Gaufin (1959); e, Armitage (1958); f, Cushing (1963).

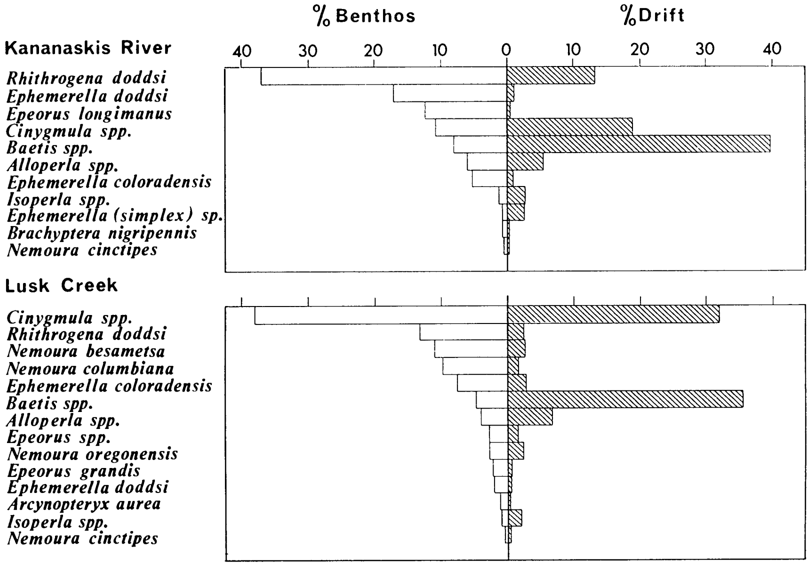


Fig. 7. Species composition of the bottom fauna (representing average numbers of organisms collected by Surber samples) and the drift in the Kananaskis River and Lusk Creek. Rare species are not shown.

our sample sizes are small and probably not satisfactory for statistical analysis. There is an additional observation on the group level, however, which deserves attention. This is the fact that trichopteran populations were exceedingly low in the Kananaskis River (less than 1% of the total) yet relatively high in Lusk Creek (about 15% of the total). This may be due to an inability of some net-spinning forms (e.g. *Parapsyche elsis* Milne) to maintain their abode in fluctuating water levels and velocities, since their nets would probably not be operative over a wide range of flow conditions. Some species require very specific current velocities for net maintenance (Hickin 1967). *Glossosoma pterna* Ross feeds on algae and did not appear in the Kananaskis River until low, more or less regular, discharges occurred, at which time (mid-September) algae had increased in abundance. Since this species characteristically inhabits the tops of stones and does not migrate to their undersides in daylight (Hynes 1970) it would be at a particular disadvantage during turbulent and turbid reservoir releases.

INVERTEBRATE DRIFT

General considerations

Although regular drift samples were taken in Lusk Creek it was not possible to sample the Kananaskis River regularly, or achieve uniformity in sampling conditions, due to the nature of reservoir releases. To test the effect of releases on drift one should sample the river for a 24-h period prior to, and during a release. Only by this method are comparisons possible. It would also be desirable that no releases precede such sampling for a period of at least several days to allow the river to reach some level of constancy. These conditions occurred only once during the study.

Discharge fluctuations are a reflection of power demands and since these are not regular, an infinite variety of types and combinations of release duration, magnitude, sequence, and frequency is possible (Fig. 4). Usually when releases are relatively uniform it is because the thermal power plant at Wabamum, Alberta is unserviceable and such occasions are also unpredictable. Therefore, it is extremely difficult to test hypotheses on the nature of drift in regulated streams. Nevertheless, some interesting data were obtained.

Species composition

All species collected in the bottom fauna were also taken in the drift, although two species which occurred in the drift (*Paraleptophlebia rufivenosa* (Eaton) and *Siphlonurus occidentalis* (Eaton)) were not found in the stream benthos. Both were rarely sampled. Nymphs of *S. occidentalis* normally inhabit small isolated pools along the river's bank; these are sometimes connected with the stream channel thus some individuals could be introduced into the river via the outlets. They could also be introduced by reservoir releases which usually engulf such locations, and since both species were normally taken only during releases this explanation seems more likely. Nymphs of *Paraleptophlebia rufivenosa* probably also occupy riverside pools although no specimens were obtained from these areas.

The percentage composition of stream insects taken in the drift in Lusk Creek and the Kananaskis River is presented in Fig. 7. A few species comprised 75% of the drifting invertebrates in Lusk Creek, these being *Baetis* spp. (35·6%), *Cinygmula* spp. (32·7%), and *Alloperla* spp. (6·6%). The remaining species were usually poorly represented including those forms with ventral abdominal holdfasts modified as adhesive discs (e.g.

Rhithrogena doddsi, 2·5%, *Epeorus* spp., 1·5% and *Ephemerella doddsi*, 0·3%). The species showing the greatest contribution lack these morphological adaptations and may be behaviourally more inclined to drift. It is likely that a different pattern of drift would have occurred had winter samples been obtained, because this is a period of high plecopteran density. This group was at low densities throughout the drift sampling period.

The basic pattern of drift in the Kananaskis River was very similar to that of Lusk Creek and the same three genera were roughly as frequent (e.g. *Baetis* spp. 39·9%, *Cinygmula* spp. 18·8%, and *Alloperla* spp. 5·5%; total 64·2%). However, it appears that *Rhithrogena doddsi* drifted more frequently (13·3%) than in Lusk Creek although *Ephemerella doddsi* (1·2%) and *Epeorus longimanus* (0·6%) did not. It is possible that the high frequency of *Rhithrogena doddsi* resulted partly from a contribution of a tributary, or as a result of greater activity in the river. There does not appear to be any marked difference between the drift rates of the remaining species for the two streams.

Daily fluctuations

The drift sample records for Lusk Creek were chosen for analysis of daily fluctuations since they are probably more representative of the phenomena than those of the Kananaskis River (because the nets were emptied more frequently). However, in general the daily fluctuations were not unlike those observed in Lusk Creek.

In all months more aquatic invertebrates were taken at night than in the day, the greatest number most often being obtained in the second 3-h sample after sunset, and the smallest during the late afternoon (Fig. 8). In a small moorland stream in England Elliott (1967a) found the greatest numbers to be in the first 3-h period after sunset. However, the duration and the timing of the sampling periods could account for this discrepancy, as has been pointed out by Elliott (1969).

The daily fluctuations of a given species in the drift paralleled that of total numbers for all species where sample size was sufficient (Table 2). Generally, some members of each of the more common species were in the drift throughout the day although there were periods when no individuals of some species were sampled. The rare members of the benthos were seldom taken in the drift.

Proportion of benthos in the drift

In order to estimate the proportion of the benthos in the drift at any instant in time Elliott (1967a) employed the formula:

$$P = \frac{xD \cdot 100}{X - xD}$$

where the number of animals in the drift is x individuals/m^3 and in the benthos X individuals/m^2, and where D is the average depth of the stream. Two assumptions are necessary if the formula is to be correct: (1) the sampling areas must be representative of the cross section of the stream; (2) equilibrium of the benthos must exist (i.e. the rate of settlement is approximately equal to the rate of erosion). Ulfstrand (1968) used a similar formula except that xD was not subtracted from X, probably because this amount is extremely small.

The first assumption is unwarranted in Lusk Creek since the sampling area can probably never be representative of a cross section of the stream. This is an extremely variable parameter in the uneven terrain of the Kananaskis Valley and is not directly related to the mean depth if the width and configuration of the bottom are excluded.

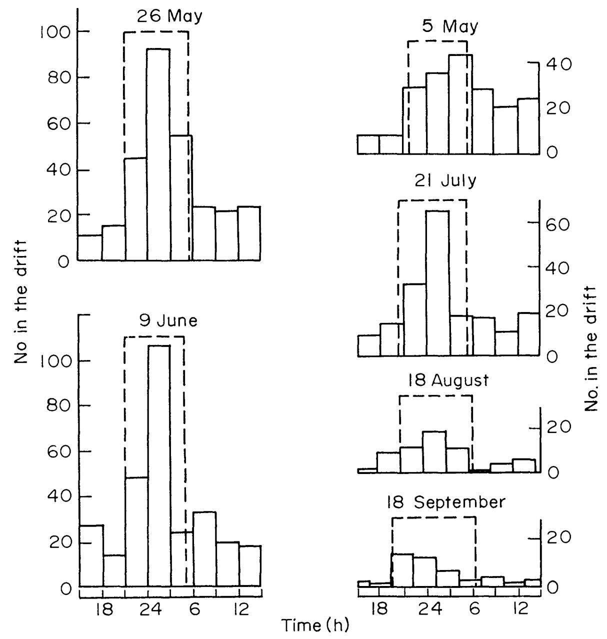


FIG. 8. Numbers of stream insects taken in the drift (per three hour sample) in Lusk Creek. Dotted line represents the period of darkness.

Table 2. *Examples of the daily fluctuations of aquatic species (number of organisms/3-h sample) in the drift in Lusk Creek*

Sample no.	1	2	3	4	5	6	7	8	Date
Emptying time (h)	15	18	21	24	3	6	9	12	
Ephemerella (*simplex* gp.) sp.	1	0	0	4	5	3	2	2	6 May
Alloperla spp.	3	2	1	7	12	6	1	1	6 May
Cinygmula spp.	10	4	9	12	39	34	12	10	26 May
Rhithrogena doddsi McDunnough	0	2	0	2	6	0	0	0	26 May
Baetis spp.	4	2	9	33	41	9	7	4	21 July
Nemoura oregonensis Claassen	0	0	3	5	5	0	0	1	17 Sept.

Date	Sunset (hours)	Sunrise (hours)	Night samples
6 May	20.30	05.25	3–6
26 May	20.35	04.30	3–6
21 July	20.40	04.45	4–5
17 Sept.	18.45	06.15	3–6

For instance, sections representative of 0·78 and 0·76 m^2 in Lusk Creek had mean depths of 0·162 and 0·357 m, respectively, depending on the cross section. If these mean depths are used in Elliott's formula with the same x and X values, two very different proportions will result.

Also the assumption that equilibrium in the benthos exists, with the rate of settlement about equal to the rate of erosion is not always correct. For example, when current velocities increase, not only will animals travel longer distances per unit time, but also settling will become more difficult. Thus even if the proportion of the benthic population drifting remained the same, there will be an increased rate of population loss due to animals drifting out of suitable biotopes (Ulfstrand 1968).

Because of the fact that Elliott's formula is inappropriate for our streams, a simplified formula has been devised:

$$P = \frac{x}{X-x}$$

where x is the number of drifting organisms/m^3 and X the number of bottom fauna/m^2. Although this formula makes no attempt to equate the proportion to the entire stream it does provide a satisfactory estimate.

Thus calculated, the proportion of the bottom fauna in the drift in Lusk Creek was usually small (as low as 0·01 %) and at no time exceeded 0·35 %, this being the highest value obtained (Table 3). The proportion seems to increase from May to July, and declines thereafter. However, there is not a strong correlation between numbers of drifting organisms/m^3 and the average density/m^2. Possibly the proportion of drifting organisms is more a reflection of their life histories than of prevailing density, although other factors are probably important. Elliott (1967b) found that a comparison of the density of most species in the drift with their life histories revealed a strong correlation between peaks in the density of the drift and periods of rapid growth. He suggests that the density of nymphs in the drift depends to some extent on the stages in their life histories, because, although all instars occur in the drift, mature nymphs are especially common. This was also noted in our study. Elliott adds that the number of late instars in the benthos is probably more significant than total numbers in determining proportions.

Proportions of bottom fauna in the drift have been calculated for some samples from the Kananaskis River (Table 3); these values are extremely low. Similar results were obtained in stream studies in England and Norway (Elliott 1965, 1967a) and Sweden (Ulfstrand 1968) with the use of Elliott's formula.

Effect of stream flow reduction

The amount of invertebrate drift sampled in the Kananaskis River was normally less than 200 organisms/24 h except in cases of accrual from tributaries. An exceptionally high rate of drift was recorded at Station 1 on 6 August when a total of 1460 organisms/24 h were recorded. The species composition of the sample is presented in Table 4.

The five most abundant species in the drift were ephemeropterans. The agreement is not complete, but there is some correlation between the abundance of these species in the drift and their density in the benthos. All species reached their highest density in the drift during the period of darkness. The proportion of fauna in the drift was also greatest during this time and extreme values of 0·109 for *R. doddsi* and 0·181 for *Ephemerella* (*simplex* gp.) sp. were recorded. It seems that the density in the drift was declining by 7 August.

Table 3. *Proportion of bottom fauna (based on Surber samples) in the drift in Lusk Creek and the Kananaskis River*

Stream	Date	Bottom fauna (no./m^2)	Drift (no./m^3	Proportion of bottom fauna in drift
Lusk Creek	5 May	541	0·2662	0·0005
	26 May	541	0·3947	0·0007
	9 June	394	0·4601	0·0012
	24 June	394	0·2772	0·0007
	21 July	82	0·2896	0·0035
	18 Aug.	219	0·1143	0·0005
	17 Sept.	108	0·0672	0·0006
Kananaskis River				
Station 1	5 May	103	0·0291	0·0003
	5 May	103	0·0402	0·0004
	26 May	162	0·1899	0·0012
	24 July	190	0·0965	0·0005
	6 Aug.	301	1·9690	0·0066
	16 Sept.	369	0·6101	0·0017
	17 Sept.	369	0·1920	0·0002
Station 4	5 May	57	0·0177	0·0003
	6 May	57	0·0179	0·0003
	22 July	132	0·0117	0·0001
	22 July	132	0·1091	0·0008
Station 5	6 May	93	0·0167	0·0002
	27 May	183	0·0205	0·0001
	22 July	183	0·0432	0·0002

Table 4. *Composition of the drift following reduction of stream flow in the Kananaskis River at Station* 1

	6 August							7 August	
Duration (hours)	11.00–15.00	15.00–18.15	18.15–21.00	21.00–04.00	04.00–09.00	09.00–11.00	Total	11.00–15.00	15.00–18.15
Sample no.	1	2	3	4	5	6			
Species									
Ephemerella spinifera Needham				1	1		2	2	
Arcynopteryx spp.				2			2		
Epeorus grandis McDunnough				2			2		
Ephemerella coloradensis Dodds	1		1	2			4		4
Isoperla spp.				5			5		
Nemoura oregonensis Claassen				7			7		
Ameletus sp.		1		10	2		13		
Siphlonurus occidentalis Eaton				17			17		
Alloperla spp.		1	1	16			18		
Cinygmula spp.	6	6	3	76	2		93	5	6
Ephemerella doddsi Needham				97			97		
E. (*simplex* gp.) sp.		1	1	101	3	1	107		
Baetis spp.	17	17	4	82	10	1	131	4	8
Epeorus longimanus (Eaton)	12	4	2	431	12	2	463	2	2
Rhithrogena doddsi McDunnough			2	501	4		507	1	1
Others						1	1	1	
Total	36	30	14	1350	34	6	1469	15	21

It is notable that on each of the 10 days prior to the drift sample there was a reservoir release which resulted in an average flow of about 17·8 m^3/sec, with a range in discharge of about 29·7 m^3/sec to 9·3 m^3/sec. Except for a small release on 6 August flow was steady at about 3·7 m^3/sec, i.e. 14·1 m^3/sec less than the previous discharges. It is probable that this reduced discharge resulted in the unusually high density of invertebrate drift, for this has been observed by other workers (Minshall & Winger 1968; Pearson & Franklin 1968). Minshall & Winger found that all bottom-dwelling invertebrates were affected by reduced flows and observed that the normal avoidance response to light was reversed. Similar observations have been made on mayfly nymphs by Elliott (1968). Neither Pearson & Franklin nor ourselves noted a reversal of the negative phototactic response. Morning and afternoon drift rates were not different from those observed at other times. After sunset, however, drift rates of all species reached the highest levels recorded for the rivers.

The effect of reduced discharge might result from a response to decreases in any or all of velocity, depth or width. Although Minshall & Winger (1968) tend to disregard reduction of stream width as a causal agent and emphasize the importance of depth and velocity, the three are so related in the Kananaskis River as to be inseparable. A reduction in velocity can cause a reversal of the positive thigmotaxis of stream invertebrates (Elliott 1967a) and initiate swimming, while decreased depth and width can concentrate benthos to a degree which might increase their activity and cause entry into the current. The latter would seem more plausible because the current velocity for the Kananaskis River was not excessively low. Also, the fact that many immature nymphs of *E. doddsi* (97) and *Rhithrogena doddsi* (501) drifted during the period of darkness suggests that density is probably important, since these nymphs were likely to be interacting for space and food at this time. Both species were normally rare in the drift, but increased crowding could initiate drifting. Bishop & Hynes (1969) state that 'part of the fauna lost to the drift is probably the result of activity by the insects, that exposes them to the current forces, and competition for space and food. These factors depend on the density of insects in the optimal stone-top forage areas, current velocity and total discharge'.

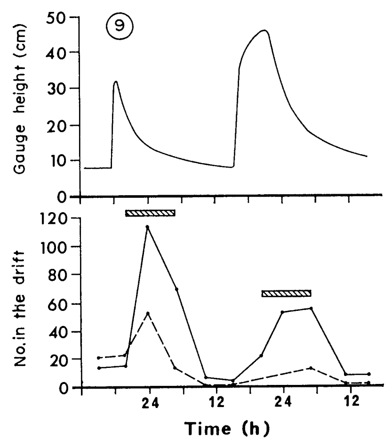
Effect of reservoir releases

As was previously discussed one should sample the river for a 24-h period prior to, and during, a release, to test its effect on drift. Also, this should be done only if no releases have preceded the sample for at least several days, to allow the river to reach some semblance of regularity. This was accomplished during the September sample as only two releases had occurred during the several weeks previous. The data for this date are shown in Fig. 10.

Unfortunately it was not realized until too late that the sampling nets became clogged with debris during a major release, though this never happened in Lusk Creek nor in the river at other times. In consequence, the results for September (and also for August, Fig. 9) are anomalous. One would expect, as Elliott (1967a) and Pearson & Franklin (1968) have observed, that more drift would be present in a greater water volume. The fact that a decrease was observed clearly indicates that the samples must be rejected as invalid.

It has been shown (Pearson & Franklin 1968) that sudden increases in flow, or in turbidity, will result in increases in the amount of drift (even if water levels remain unchanged) should upstream densities be high enough to induce behavioural drifting. Under these conditions quantitative differences between 24-h drift samples are a reflection of the different amounts of water passing a sampling point and a linear relationship exists between the two variables (Elliott 1967a). Simply stated, the greater the volume of water sampled, the greater the amount of invertebrates taken, and vice versa. This feature is of considerable importance during reservoir releases (and spates); if more insects occur in more water, then increased flows should introduce more of the benthos into the drift, with concomitant depletion in the long run (i.e. unless the proportion of benthos in the drift is in equilibrium which is unlikely over a short-term release). Also, since the number of pools is reduced during releases, settling of drifting invertebrates would be greatly reduced.

As was previously discussed, reservoir releases may introduce non-riverine species into the drift (e.g. *Paraleptophlebia rufivenosa* and *Siphlonurus occidentalis*) if these inhabit riverside pools which are periodically engulfed by rising waters. Lake plankton was also associated with releases and two zooplankters (*Diaptomus arcticus* Marsh and *D. sicilis* Forbes) were usually taken in the drift during releases. Their numbers fluctuated seasonally with a high of 0·77 organisms/m^3 in September and a low of none during July.



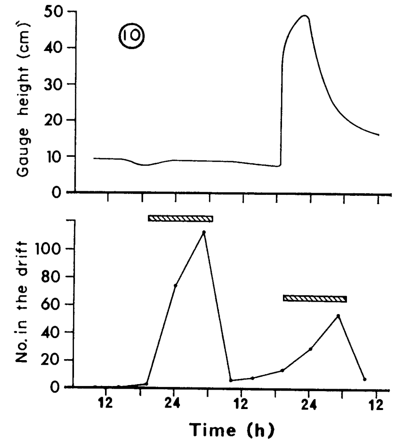


FIG. 9. Number of benthic invertebrates in the drift during two consecutive reservoir releases in the east (—) and west (– – –) channels of the Kananaskis River at Station 1, 21 and 22 August. The hatched rectangles represent the periods of darkness.

FIG. 10. Numbers of benthic invertebrates in the drift prior to, and during, a reservoir release on the Kananaskis River at Station 1, 16 and 17 September. The hatched rectangles represent the periods of darkness.

DISCUSSION

The Kananaskis River is an oligotrophic stream characterized by low standing crops of bottom fauna, a high proportion of which is composed of three torrential ephemeropteran species (*Epeorus longimanus*, *Ephemerella doddsi* and *Rhithrogena doddsi*) and two genera of Plecoptera (*Alloperla* and *Paraleuctra*) as indicated by surface and subsurface sampling techniques. It is probable that the low productivity of the river is mainly a result of extremes in flow conditions (0·3–70·0 m^3/sec). Rawson (1948) states that the extreme seasonal variation in discharge in mountain streams is one of the most unfavourable factors in limiting their productivity. The Kananaskis River has the added handicap of artificial control for hydro-power development.

There is no evidence of 'the rich and varied fauna in samples taken below the Lower Kananaskis Lake' observed by Rawson (1948) prior to the development of Pocaterra Dam. Rather, the standing crop of benthos is uniformly low throughout the Lower Kananaskis River from the lakes to Barrier Reservoir.

Although the seasonal temperature pattern is not unlike that of other mountain streams, no indirect benefits, such as creation of favourable fish habitats, are evident. Rather, the summer water temperatures are probably too high in some years during low discharge periods to be conducive to fish habitation.

The nature of reservoir releases has all but eliminated certain benthic species from the stream's fauna. Net-building Trichoptera and algal grazers are rare and they were only collected during stable flow periods, although Rawson (1948) found substantial trichopteran populations in pre-impoundment samples taken below the Lower Kananaskis Lake.

It was noted that *Nemoura* spp. were common in Lusk Creek, but were rare in the Kananaskis River; the genus has been found to be entirely herbivorous, feeding largely on decaying leaf material (Chapman & Demory 1963). Autumn-shed leaves are abundant in Lusk Creek and provide a suitable habitat, but periodic reservoir releases in the Kananaskis River (which are especially frequent during the autumn and winter) sweep the bottom of allochthonous matter. The effect is obvious. Some studies (Chapman & Demory 1963; Ulfstrand 1968) have emphasized that allochthonous plant material is the most important primary source of energy for the stream fauna.

The fluctuations in flow expose much of the substrate for varying lengths of time with desiccating effects on algal populations. Since most ephemeropteran species (e.g. *Baetis* spp., *Ephemerella* spp. and *Epeorus* spp.) feed on algae, their numbers are probably limited by the scarcity of algae.

The power company which owns and operates the Pocaterra Plant is subject to no restrictions on maximum or minimum permissible flows on the Kananaskis River (nor on any stream on which they have hydro-developments). With the exception of a small amount of seepage, no water passes from the Lower Kananaskis Lake into the river except during releases. Nine small tributaries between the dam and Station 1 normally maintain its flow, but the river has been known to go dry in some areas. Although no records are available for these periods, it may be assumed that water temperatures would be high. With coincident low flows, dissolved oxygen concentrations could be so low as to be physiologically disastrous for stream insects and fish. Many stream insects are unable to tolerate low oxygen tensions and some have lost the ability to ventilate, by flapping gills or by undulating their abdomens, and rely upon the current to renew the oxygen supply at their body surfaces (Hynes 1970).

Because of the logistic limitations which existed in this study, it was not always possible to undertake extensive experimentation in certain areas. This was often the case in the analysis of invertebrate drift and only tentative conclusions can be drawn from some of the data. It is probably correct, though, that most indicate the general pattern.

As in other studies (Minshall & Winger 1968; Pearson & Franklin 1968) it was found that reductions in flow cause increases in drift. Also recorded were the daily fluctuations of both total numbers and individual species in the drift (in relation to light intensity especially, and secondarily other environmental factors). These results were expected since the phenomenon of high drift rates at night has been reported many times (Elliott 1967a; Holt & Waters 1967; Ulfstrand 1968). Almost all the species recorded have not previously been reported to drift, but belong to groups known to drift elsewhere.

Also established was the importance of selection of drift sample sites in relation to tributary streams since these may contribute substantial numbers during high summer densities and peak runoff periods. Tributaries should merit attention in future work for they add a significant amount of biomass to a parent stream. The data for Lusk Creek indicate a range of contribution from 2465 to 19 760 organisms/day with a rough average of 13 000/day for the study period. A contribution of 186 000 macro-invertebrates (many of which were maturing *Baetis* spp.) was also recorded from a tributary upstream from Station 1 (Ribbon Creek, at which time the flow was 1·27 m^3/sec) during a 16-h sampling period on 24 July.

Technical problems prevented careful analysis of the effect of reservoir releases on drift, but it seems improbable that the effect is different from that observed by Maitland (1964), Elliott (1967a), and Pearson & Franklin (1968), all of whom found that increased flow results in increased drift. Considering the high velocities associated with releases one would expect that much of the fauna would be transported into unfavourable habitats (e.g. Barrier Lake) which could represent a considerable loss (Dendy 1944). Also, there was an association of lake plankton with releases. *Diaptomus* spp. were taken in drift samples at Station 1, a distance of about 35 km from Pocaterra Dam, and probably arrive reasonably intact in Barrier Reservoir about 6 h after leaving the Lower Kananaskis Lake. Non-riverine species (*Paraleptophlebia rufivenosa* and *Siphlonurus occidentalis*) were also introduced into the drift from riverside pools during releases.

As pointed out by Ulfstrand (1968), although the proportion of benthos in the drift at any instant of time is small, it is found to be important when the time during which most drift occurs is fully taken into account. Perhaps the significance of drift should be re-evaluated, but only after the probable proportions of benthic populations participating in drift have been determined. In light of our results of subsurface samples of benthic invertebrates (Radford & Hartland-Rowe 1971b), it seems that since estimates of standing crops of benthos are too low this aspect must also be introduced into the calculations. It is likely that the proportion of benthos drifting is even lower than previously believed, but it assumes considerable importance when viewed on a seasonal basis because it can represent an immense population loss, especially where rivers empty into lakes.

Ulfstrand (1968) notes that the fraction of the stream populations passing a sampling site per 24 h was in the order of 1–2% in a Lapland stream. This estimate, however, seems unreasonably high since it could lead to a loss of most of the population in a short while. For instance, only 75% of an initial population would remain after 14 days, and 50% after 34 days, if one assumes a constant faunal loss of 2%. If the proportions of benthos in the drift in Lusk Creek for June, August and September, are recalculated using densities/m^2 recorded for the subsurface cylinder samples (Radford & Hartland-Rowe 1971b) rather than Surber samples, the values are 0·0071, 0·0056 and 0·0031% (rather than 0·07, 0·05 and 0·06% based on the Surber sample data). These figures seem more credible since the population loss would not be too large over short time periods.

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SUMMARY

A preliminary investigation was made of two streams on the eastern slopes of the Rocky Mountains in south-west Alberta. One stream (the Kananaskis River) was subject to flow regulation for hydroelectric purposes while the other (a tributary, Lusk Creek) was not. Water discharge rates, stream temperatures, and the nature and composition of the benthos and drift were all investigated.

High flows occur during the fall and winter in the Kananaskis River (in addition to occasional summer peaks) in contrast to low flows in unregulated rivers at this time. The nature of reservoir releases, which were highly variable in character, is discussed. The temperature regime of the river is presented; its pattern does not differ greatly from that of other streams.

The species composition and the seasonal trends of standing crops of bottom fauna are discussed. The Kananaskis River is described as oligotrophic. Low standing crops are attributed to extremes in discharge as is the nature of the species composition, which is characterized by torrential forms. A high percentage of the bottom fauna is composed of three torrential ephemeropteran species (*Epeorus longimanus*, *Ephemerella doddsi* and *Rhithrogena doddsi*) and two genera of Plecoptera (*Alloperla* and *Paraleuctra*) as indicated by surface and subsurface sampling techniques. *Nemoura* spp. and two species of Trichoptera (*Parapsyche elsis* and *Glossosoma pterna*) were found to be adversely affected by the fluctuating stream flows.

The daily fluctuations of both total numbers and individual species in the drift were recorded. More individuals were always taken during periods of darkness with the greatest number most often obtained in the second 3-h period after sunset and the least in the late afternoon. Those species described as torrential were found to drift less frequently than others. Tributaries were found to add substantial amounts of biota to the Kananaskis River; the data for Lusk Creek indicate a range of contribution from 2465 to 19 760 organisms/day with a rough average of 13 000/day for the study. The validity of Elliott's (1967a) formula for determining the proportion of benthos in the drift in our streams is questioned and a substitute provided. The highest proportion recorded under normal conditions was 0·35% and the lowest 0·01%. *Diaptomus* spp. and two species of non-riverine aquatic insects (*Paraleptophlebia rufivenosa* and *Siphlonurus occidentalis*) were introduced into the Kananaskis River during reservoir releases from the Lower Kananaskis Lake and riverside pools, respectively. It was found that

reductions in stream flow caused increases in invertebrate drift and, although evidence is lacking, it is suspected that reservoir releases cause increased rates of drift as has been noted in other studies.

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