# Differences in Benthos Upstream and Downstream of an Impoundment[1]

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Pronounced differences were found in the macroinvertebrate riffle fauna upstream and downstream of a flood control impoundment. Downstream differences were comparable with those occurring after mild organic enrichment. Plecoptera were absent, but numbers of *Baetis* and *Caenis* (Ephemeroptera) increased, and the abundance and number of species of *Stenonema* were considerably reduced. Numbers of Chironomidae, Simuliidae, *Optioservus* (Coleoptera), Hydropsychidae, and *Hyalella azteca* (Amphipoda) increased downstream. These changes are associated with downstream increase in the availability of detritus, a lag of about 4 weeks in the early summer rise in water temperature and a maximum temperature more than 6 degrees C lower than upstream, and alteration of other environmental factors.

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Il existait des différences considérables dans la faune macroinvertébrée, en amont et en aval d'un barrage sur une rivière. En aval, des différences étaient comparables à ceux qu'occasionne l'occurrence d'un faible enrichissement organique: disparition complète des Plécoptères, augmentation du nombre de *Baetis* et de *Caenis* (Ephéméroptère), et diminution dans le nombre d'espèces et individus de *Stenonema*. L'accroissement en aval du nombre de Chironomidae, Simuliidae, *Optioservus* (Coléoptère), Hydropsychidae, et *Hyalella azteca* (Amphipoda) semblait lié à l'augmentation du détritus disponible et aux autres changements de l'habitat, un retard de quatre semaines environs dans le réchauffement printanier des eaux et une température maximale d'au moins 6 C. inférieure qu'en aval, et l'altération des autres facteurs d'environs.

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THE object of this study was to investigate the influence of a dam on the benthos of the river downstream. Though dams have many individual characteristics, they all impose a lentic environment on a lotic one, and in this respect the situation resembles that found in natural lake basins whose outflowing streams have biological and limnological characteristics attributable to the influence of the lake. Impoundments, however, exert influences not encountered in natural lake–river systems. The present study concerns a flood control dam in which the water is released from the hypolimnion.

Neel (1963) considered the important effects of mainstream dams to be alteration of flow patterns, reduction of turbidity, changes in temperature regime, and the development of attached masses of algae, which are so characteristic of rivers below dams.

Studies on the biological effects of impoundments on rivers have been of limited scope. Most of them deal with the downstream changes in the plankton that originated in the reservoir. Stober (1963) found that a mainstream reservoir in Montana supported an extremely low plankton population, and that the potamoplankton downstream was largely indigenous and arose from the benthic communities of the river. Coutant (1963) carried out a simultaneous study of plankton populations upstream and downstream of an impoundment when it was thermally stratified and found distinctly different populations. The plankton downstream contained many bacteria and moribund phytoplankters derived from the hypolimnion of the impoundment.

## Study Area

The Shand Dam and its impoundment, Belwood Lake, on the Grand River, Wellington County, Ont., was selected for three reasons: (1) it was

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necessary to have comparable reaches of river and comparable habitats. The riffles upstream and downstream, separated by 8 km of reservoir, must have been quite similar before the dam was constructed. Temperature and flow regimes were probably nearly identical, as they have similar gradients, on a bedrock covered with glacial till, and the land bordering the river in both regions is agricultural with stands of mixed deciduous trees and white cedar. Thus, the biocoenoses were probably similar before the dam was built; (2) the dam was completed in 1942 and thus had existed for 22 years before the study started in September 1965; any long-term influence of Belwood Lake on the life cycles of fish and invertebrates in the river downstream would have become established in this time; (3) this upper region of the Grand River is virtually unpolluted and not controlled, apart from the construction of the Shand Dam.

Three physically similar sampling stations were chosen on the river (see Fig. 1). They are riffles about 7 m wide and 15–70 cm deep, depending on the flow, with beds of large stones interspersed with gravel and sand. Station 2 was chosen to exemplify the extreme effects of the dam. However, there are considerable differences superimposed on this basic physical similarity. Downstream, the substrate was always covered with dense layers of diatoms, and from June to mid-September these communities became covered by growths of *Ulothrix zonata* with associated genera of epiphytic diatoms such as *Diatoma, Navicula, Acnanthes, Gyrosigma, Cymbella, Gomphonema,* etc. Amongst this matrix of *U. zonata, Mougeotia* sp., *Nostoc sphaericum,* and *Rivularia* sp., various euglenoids, and Ciliophora were found. Above the impoundment, however, winter populations of epilithic diatoms were replaced in spring by encrusting marl-forming communities. Blum (1960) describes *U. zonata* as a rheobiont of cool, well-oxygenated streams, with population maxima in spring and late summer. The comparably cool water temperatures found downstream of the dam till mid-July (Fig. 2) partly explains its summer growth there.

The annual flow patterns at stations 1 and 2 are shown in Fig. 3. The noon water temperatures

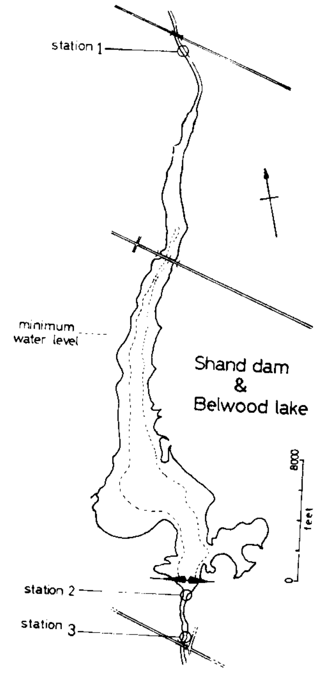


FIG. 1. Study area, Shand Dam and Belwood Lake on the Grand River, Ont., showing the three sampling stations.

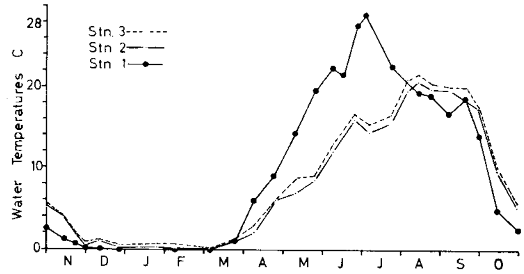


FIG. 2. Temperature regime (noon water temperatures) 1 mile downstream (station 3), immediately downstream (station 2), and ½ mile upstream (station 1) of the impoundment, November 1965–November 1966.

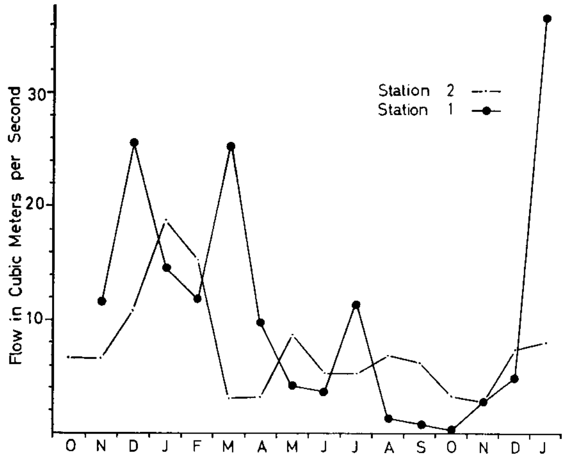


FIG. 3. Flow of water above and below the Shand Dam, October 1965–January 1967.

on sampling days at stations 1, 2, and 3 are shown graphically in Fig. 2. Upstream of the dam at station 1, the diurnal temperature cycle is characteristic of that of an exposed shallow river some distance from its source, with a minimum at dawn and maximum in the late afternoon. Thus, the present measurements made at noon are several degrees below the maximum. At station 2, the diel cycle is completely suppressed, since the outflowing water comes from the deeper strata of the lake. The only temperature fluctuation occurring there is the seasonal cycle. The same almost holds true for station 3, though there was a slight rise in the midday temperature here. There is also a considerable lag downstream in the spring rise of water temperature.

Water samples were collected at the three river stations and analysed for *p*H, bicarbonate, alkalinity, specific conductivity, organic phosphate, and nitrate nitrogen by the same methods as Duthie (1968) used in his study of the impoundment, Belwood Lake. The results are summarized in Table 1.

TABLE 1. Chemical analyses. Annual means and range of values. (Total alkalinity, phosphate, and nitrate are expressed in milligrams per liter.)

| | Station | | |
|---|---|---|---|
| | 3 | 2 | 1 |
| | | *p*H | |
| Mean | 8.29 | 8.25 | 8.41 |
| Range | 7.95–8.60 | 7.72–8.50 | 7.78–9.30 |
| | | *Total alkalinity* | |
| Mean | 170 | 176 | 169 |
| Range | 133–205 | 135–205 | 85–227 |
| | | *Specific conductivity* | |
| Mean[a] | 346 | 350 | 366 |
| Range | 120–461 | 120–444 | 105–504 |
| | | $PO_4$ | |
| Mean | .032 | .028 | .035 |
| Range | .001–.059 | .001–.059 | .002–.073 |
| | | $NO_3$ | |
| Mean | .390 | .259 | .225 |
| Range | .01–.77 | .01–.74 | .01–.50 |

[a]Figures for November 1965–May 1966 only.

Considering the annual mean values of the chemical analyses (Table 1), the differences above and below the impoundment were slight. Over the year of study, there was a slight drop in *p*H, no significant difference in the levels of total alkalinity, conductivity, and phosphate, but nitrate levels were slightly higher. There was, however, less fluctuation of the various ionic concentrations below the dam, undoubtedly because of the mixing in the lake of the highly variable inflowing water.

Estimates of the total weight of suspended particulate matter and its fractions were obtained by filtration of water samples through Millipore filters of pore size 8, 0.8, and 0.22 μ. Results were expressed as milligrams air dry weight per liter.

During the summer there was more suspended matter in the river above the impoundment (Fig. 4). The decreased levels below the dam can be attributed to sedimentation and stratification in the lake. However, as the level of the lake fell during the summer and the lacustrine plankton died off, the amounts of suspended matter below the dam increased and eventually exceeded those above the impoundment, so that from mid-September to December there was several times as much below the impoundment as above. The suspended matter below the dam consisted largely of moribund plankters, in particular planktonic Cyanophyceae, that formed a succession of blooms in the lake through the summer (Duthie 1968). This increase in suspended matter downstream was probably of considerable importance to the filter feeders and other components of the communities here. The period when it occurred (September–December) is an important one for many aquatic arthropods, since it is then that most early instars have their major period of growth and possibly compete for food.

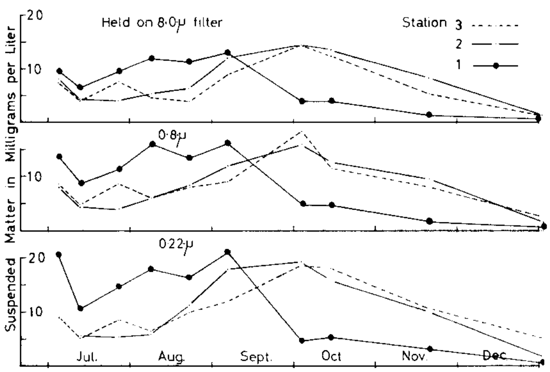


FIG. 4. Suspended matter fractions retained by membrane filters of pore size 8.0, 0.8, and 0.22 μ.

## Differences in the Benthos

The invertebrate fauna was sampled at each of the three stations by the kick sample technique of Hynes (1961) and Morgan and Egglishaw (1965). This technique is not quantitative in that it does not sample a known area of substrate, nor the animals living deep in the substrate. It is, however, sufficient to enable rough quantitative and qualitative comparisons between the three stations to be made.

For each station the numbers of the 24 major taxa occurring per sample were averaged for the year to give the average number per sample. This number, plotted in Fig. 5, it is realized, has no absolute quantitative meaning, but it does enable comparisons of the relative density of each of these 24 taxa to be made.

Differences in the ephemeropteran, trichopteran, dipteran, crustacean, and molluscan macroinvertebrates upstream and downstream of the dam are summarized in Tables 2–5. In the Odonata, nymphs belonging to four genera — *Argia, Ischnura, Calopteryx*, and *Enallagma* — were found downstream. These genera, except for *Enallagma*, were also found upstream.

Among the Plecoptera, *Acroneuria lycorias*, *Paragnetina media*, and *Phasgonophora capitata* nymphs were common upstream, and during the winter *Allocapnia pygmaea*, *Taeniopteryx maura*, and *Amphinemura delosa* were also found. Plecoptera were absent, however, from the reach of river studied downstream.

In the Coleoptera, no differences were found downstream of the dam, though the Psepheniidae, represented by *Ectopria* and *Psephenus*, were absent from station 2. There were, however, noticeable quantitative differences in the distribution of the Elminthidae. Upstream, larvae of *Stenelmis* were twice as numerous as those of *Optioservus*. Downstream, *Optioservus* were four to five times more numerous than *Stenelmis*.

The only aquatic lepidopteran larvae found were those of a species of *Cataclysta* (=*Paragyractis*) at station 1 only.

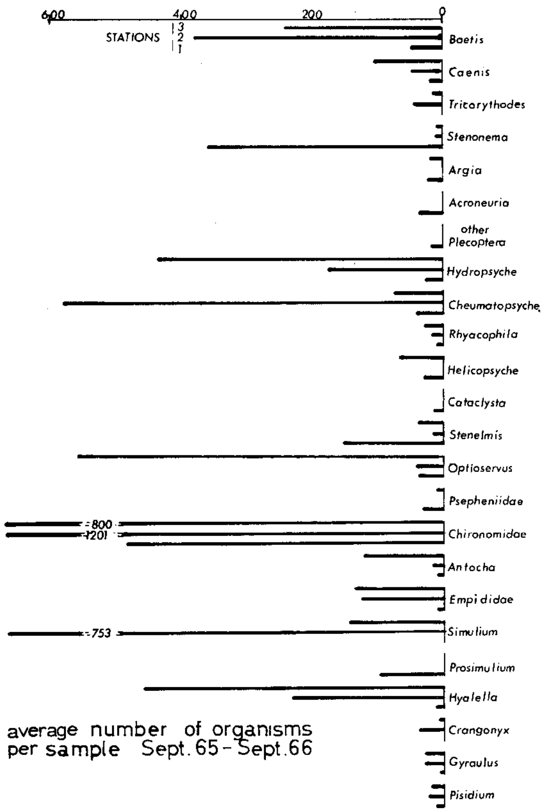


Fig. 5. Average number of organisms per sample at stations 3, 2, and 1 for the 24 main taxonomic groupings.

Table 2. Differences in the ephemeropteran fauna upstream and downstream of the dam.

| Species | Station 3 | Station 2 | Station 1 |
|---|---|---|---|
| *Baetis rusticans* Mc Dunnough | + | + | − |
| *B. levitans* McDunnough | + | + | + |
| *B. pygmaeus* Hagen | + | + | − |
| *B. vagans* McDunnough | + | + | + |
| *B. herodes* Burks | − | − | + |
| *Caenis* sp. | + | + | + |
| *Tricorythodes* sp. | + | + | − |
| *Ephemerella bicolor* Clemens | + | + | + |
| *E. deficiens* Morgan | − | − | + |
| *E. needhami* McDunnough | − | − | + |
| *Pseudocloeon* sp. | − | − | + |
| *Heterocloeon* sp. | − | − | + |
| *Paraleptophlebia mollis* Eaton | − | − | + |
| *Centroptilum* sp. | − | − | + |
| *Stenonema tripunctatum* Banks | + | + | + |
| *S. bipunctatum* McDunnough | − | − | + |
| *S. femoratum* Say | − | − | + |
| *S. canadense* Walker | − | − | + |
| *S. neopotellum* McDunnough | − | − | + |
| *S. fuscum* Clemens | − | − | + |
| *S. heterotarsale* McDunnough | − | − | + |
| *S. rubomaculatum* Clemens | − | − | + |
| Total of 23 species | 8 | 8 | 19 |

TABLE 3. Differences in the trichopteran fauna upstream and downstream of the dam.

| Family and species | Station 3 | Station 2 | Station 1 |
|---|---|---|---|
| Rhyacophilidae | | | |
| *Rhyacophila fuscula* Walker | + | + | + |
| *Agapetus* sp. | − | − | + |
| *Glossosoma* sp. | − | − | + |
| Philopotamidae | | | |
| *Chimarra aterrima* Hagen | + | + | + |
| *Chimarra obscura* Walker | − | − | + |
| Hydropsychidae | | | |
| *Hydropsyche bifida* Banks | + | + | − |
| *H. slossonae* Banks | + | + | + |
| *H. betteni* Ross | − | − | + |
| *H. recurvata* Banks | − | − | + |
| *Cheumatopsyche minuscula* Banks | + | + | + |
| Hydroptilidae | | | |
| *Agraylea multipunctata* Curtis | + | + | + |
| *Myatrichia ayama* Mosely | − | − | + |
| *Ochrotrichia* sp. | − | − | + |
| Phryganeidae | | | |
| *Ptilostomus* sp. | + | + | − |
| Limnephilidae | | | |
| *Limnephilus consocius* Walker | + | − | + |
| *Neophylax autumnus* Vorhies | − | − | + |
| *Pycnopsyche lepida* Hagen | − | − | + |
| *Pycnopsyche* sp. | − | − | − |
| Leptoceridae | | | |
| *Leptocella candida* Hagen | + | + | − |
| *Athripsodes tarsipunctatus* Vorhies | + | + | − |
| *Athripsodes* sp. | − | − | + |
| *Oecetis avara* Banks | − | − | + |
| *O. inconspicua* Walker | − | − | + |
| Brachycentridae | | | |
| *Micrasema* sp. | + | + | − |
| *Brachycentrus americanus* Banks | − | + | − |
| Helicopsychidae | | | |
| *Helicopsyche borealis* Hagen | + | − | + |
| Total of 26 species | 10 | 9 | 20 |

TABLE 4. Differences in the dipteran fauna upstream and downstream of the dam.

| Family and species | Station 3 | Station 2 | Station 1 |
|---|---|---|---|
| Tipulidae | | | |
| *Antocha* sp. | + | + | + |
| *Tipula* spp. | + | + | − |
| *Pedicia* | − | − | + |
| *Dicranota* | + | − | − |
| Empididae | | | |
| *Hemerodromia* sp. | + | + | + |
| Other species | + | + | + |
| Ceratopogonidae | + | + | + |
| Simuliidae | | | |
| *Simulium vittatum* Zetterstedt | + | + | − |
| *Prosimulium fuscum* Syme and Davis | − | − | + |
| *P. mixtum* Syme and Davis | − | − | + |
| Tanypodinae | | | |
| *Procladius* sp. | + | + | + |
| *Thienemannimyia* sp. | − | − | + |
| Diamesinae | | | |
| cf. *Pagastia* sp. | + | − | + |
| Orthocladiinae | | | |
| *Adactylocladius* sp. | − | + | − |
| *Cricotopus* sp. | + | + | − |
| *Eukiefferiella* spp. | + | + | + |
| *Orthocladius* sp. A | + | − | + |
| sp. B | − | − | + |
| sp. C | − | − | + |
| *O.* (*Euorthocladius*) sp. | + | + | + |
| *Paracricotopus* sp. | + | + | − |
| *Trissocladius* sp. | + | − | + |
| Chironomini | | | |
| *Dicrotendipes* | + | + | + |
| *Glyptotendipes* (*Phytotendipes*) | − | + | − |
| *Microtendipes* | − | − | + |
| *Stictochironomus* | + | − | + |
| Tanytarsini | | | |
| *Tanytarsus* sensu strictu spp. | + | + | + |

Differences in the ostracod, water mite, and oligochaete faunas were not dealt with.

In a stream above and below a natural lake, Illies (1956) found a fourfold increase in the number of a *Baetis* sp. below the lake, and this was paralleled by increases in the numbers of *Heptagenia* nymphs, filter-feeding Trichoptera, and Simuliidae. He attributed these differences to an increase in available food. Egglishaw (1964) found a close correlation between the distribution of plant detritus and *Baetis* spp. in stream riffles, and in the present study the increase in numbers of *Baetis* spp. nymphs downstream of the dam (Table 2) can be attributed to the luxurious growths of attached filamentous algae. These provide a large number of microhabitats for the nymphs and hold more detritus than can the marl-covered stones in the river above the dam.

The large populations of *Stenonema* spp. above the lake are characteristic of clean streams in this region of North America. Ide (1935) has shown that the number of species of *Stenonema* increases

TABLE 5. Differences in the crustacean and molluscan fauna.

| Family | Station 3 | Station 2 | Station 1 |
|---|---|---|---|
| Crustacea | | | |
| *Hyalella azteca* Saussure | + | + | + |
| *Crangonyx gracilis* Smith | + | + | − |
| *Cambarus bartonii* Fabricus | + | − | + |
| *Orconectes virilis* Hagen | + | + | + |
| Total of four species. | 4 | 3 | 3 |
| Mollusca | | | |
| *Sphaerium simile* Say | − | − | + |
| *S. striatinum* Lamarck | − | − | + |
| *Pisidium* sp. | + | + | + |
| *Alasmidonta calceolus* Lea | − | − | + |
| *Ferrissia rivularis* Say | + | + | − |
| *Physa* sp. | + | + | + |
| *Fossaria* sp. | + | − | − |
| *Valvata tricarinata* Say | + | + | − |
| *Helisoma anceps* Minke | + | + | + |
| *Gyraulus parvus* Say | + | + | + |
| Total of 10 species | 7 | 6 | 7 |

with the increasing temperature range of a stream. At station 1 the temperature range is from 0 to above 28 C and a total of eight species occurred there. *Stenonema tripunctatum* was the only species occurring downstream; it also occurred upstream. This species is known to have wide environmental tolerances, and Burks (1953) observed that it is characteristic of sluggish creeks and small silted rivers from which other *Stenonema* sp. are absent. The absence of two other *Stenonema* species from the two downstream stations would seem to be due to the lower summer temperatures found there, though the abundant Aufwuchs may also be a factor.

The absence of Plecoptera from the reach of river studied below the dam is notable. Neither the temperature regime nor the availability of food can explain the absence either of the predatory forms such as *Acroneuria*, *Phasgonophora*, and *Paragnetina* or of the herbivorous *Allocapnia* and *Taeniopteryx*. Several factors may be implicated, but most critical is likely to be the amount of oxygen available to the nymphs. The sensitivity of Plecoptera to a slight diminution of dissolved oxygen is well-documented, and Rodhe (1962) has noted that they are never found in streams that have more assimilation than dissimilation. The respiratory demand at night of heavy Aufwuchs communities can also cause oxygen exhaustion in the surface microlayers of the substrate (McIntire 1966). Such conditions are present in the downstream region of the stream studied and could explain the absence of Plecoptera.

When the Trichoptera found in the study are classified according to feeding habits, a grouping similar to that of Scott (1958) becomes apparent, that is, detritus feeders, algal scrapers, active predators, and net spinners, which are mainly predatory.

*Rhyacophila fuscula*, *Ocoetis avara*, and *O. inconspicua* are conventional predators (Ross 1944), and their distribution and density would be expected to be closely correlated with the availability of prey. The distribution and abundance of *R. fuscula* in the present study is clearly related to availability of prey. This is not so for *Ocoetis*, and some unknown factors related to the dam must be responsible for the absence of this genus from stations 1 and 2.

Three net-spinning families were found in the present study. The Hydropsychidae represented by *Hydropsyche* and *Cheumatopsyche* and the Philopotomidae represented by *Chimarra* occurred at all three stations. The Polycentropidae represented by *Polycentropus interruptus* occurred only upstream. The abundance of both *Hydropsyche* and *Cheumatopsyche* downstream (Fig. 3) can be related to both the availability of food and the lack of extreme current fluctuations. Although the standing crops of Hydropsychidae at stations 3 and 2 are comparable, there was a difference in species dominance at these stations. The two *Hydropsyche* species were dominant at station 3, whereas *Cheumatopsyche miniscula* was dominant at station 2. This situation undoubtedly reflects some microhabitat differences between these two stations.

The remaining Trichoptera (Table 3) are detritus and Aufwuchs feeders, but none of them, surprisingly, increased in numbers downstream of the dam. In general, the effect of the dam was to reduce the number of species and to increase the abundance of some. Out of a total of 26 species, 20 were found at station 1, 10 at station 3, and 9 at station 2. In pristine streams, the trichopteran communities show great diversity and stability. However, the ecological balance between these communities and the environment is delicate. A slight alteration of the environment could eliminate certain members of the community, and this would seem to be what has happened downstream of the dam.

*Simulium vittatum* was the only member of the Simuliidae below the dam, and Sommerman et al. (1954) mention that this species is characteristic of lake outflows. It can be seen from Fig. 6 that

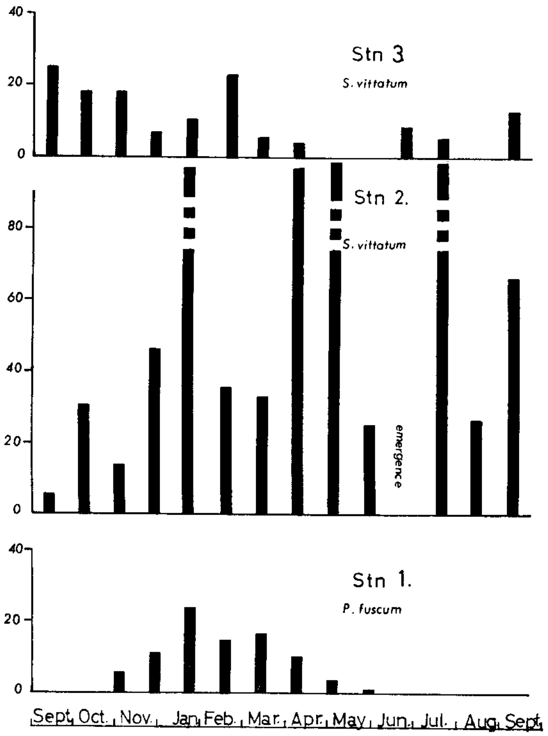


FIG. 6. Numbers of simuliid larvae per sample, September 1965–September 1966, at stations 3, 2, and 1.

it passed through two generations in the year. Overwintering larvae pupated and emerged through the latter half of April and most of May, and larvae were then absent from samples till July 15 when an abundance of minute early instars was found. These grew rapidly and were emerging in the last week of August. The numbers in the samples do not show this clearly, however, because of the staggered development rates of larvae. Davies et al. (1962) describe *S. vittatum* as being a multivoltine species and Sommerman et al. (1954) found that it had two or three generations a year in Alaskan streams, which were considerably colder (maximum of about 13 C) than the Grand River under the Shand Dam.

*Prosimulium mixtum* and *P. fuscum*, the only species upstream of the dam, had only one generation, which emerged in late May and early June. All species in the *Prosimulium hirtipes* complex appear to be obligately univoltine. Davies and Syme (1958) found that they had a single attenuated generation that probably spent the warm summer months in egg diapause. This would explain their total absence from samples taken between June and October but, judging from the ecological data presented by Davies and Syme (1958), there is no reason why *P. mixtum* and *P. fuscum* should not be found downstream. The temperature regime and other environmental conditions all fall within their range. The explanation would seem to be that the multivoltine *S. vittatum* builds up its numbers with summer generations so that all available suitable substrate is colonized with larvae long before the univoltine *Prosimulium* sp. have hatched.

The absence of *S. vittatum* larvae from station 1 is not due to the high midsummer temperatures reached there, since they are known to tolerate temperatures in excess of 27 C (Davies et al. 1962). It may be related to the uneven flow and scouring action of flash floods at this station.

No chironomid larvae were reared out; thus, a detailed analysis of this important group was impossible. However, even at the generic level, differences are evident.

*Procladius* sp., *Eukiefferiella* spp., *Orthocladius* (*Euorthocladius*) sp., and *Tanytarsus* (*s.s.*) spp. seemed to be fairly eurytypic, occurring at all three stations. One of the dominant forms upstream, *Pagastia* sp., did not occur in the extreme conditions of station 2, but reappeared at station 3. Three species of *Orthocladius* (*s.s.*) were confined to station 1 upstream, and *Cricotopus* sp. and *Eucricotopus* sp. were associated with the growths of Aufwuchs downstream.

## CRUSTACEA

*Hyalella azteca*, though abundant downstream, occurred only sporadically upstream of the dam. *Hyalella* is a eurythermal detritus feeder, and its abundance downstream can be explained by the availability of microhabitats and food amongst the algal growths.

*Crangonyx gracilis* occurred only downstream of the dam. This restriction would seem to be due to the cooler temperatures found here in the summer. Judging from ecological notes in Bousfield (1958), *C. gracilis* is a cold stenothermal species. Downstream, the temperatures exceeded 20 C only for a short time in August, whereas upstream of the impoundment the noon temperature exceeded 20 C during June, July, and early August, reaching a recorded maximum of 29 C in early July. *Crangonyx gracilis* was most abundant at station 2. This may reflect an accumulation of upstream migrating individuals whose progress was impeded by the dam. Such upstream movements have been reported before by Hynes (1955) who noted that small dams prevented the upstream movements of *C. pseudogracilis* Bousfield, and by Minckley (1964) for several *Crangonyx* species.

MOLLUSCA

Most of the gastropod species recorded are not found in the rapid areas of streams but are usually associated with shoreline vegetation and backwaters. Thus, little can be inferred from their occurrence in the present samples. One exception is the ancylid *Ferrissia rivularis*, which was found only below the dam. It seems to be a species that is assisted by human interference with its environment. Goodrich (1932) noted that it occurred in great numbers below the Superior dam on the Huron River, Michigan, whereas other molluscs that had once been common were absent.

The Pelecypoda, however, were considerably affected by the dam. Only one, a *Pisidium* species, occurred below it although *Sphaerium striatinum*, common above, and the naiad *Alasmidonta calceolus* did not. Stream-dwelling naiads are known to be sensitive to human interference (cf. van der Schalie 1938, and others), but the reasons are not clear. Pollution, substrate changes, alteration of flow patterns, and loss of fish hosts of the glochidia are undoubtedly implicated. One of the two known fish hosts of *A. calceolus* is *Cottus bairdi* (Clarke and Berg 1959), which occurs above but is more abundant below the impoundment. Thus, the absence of *A. calceolus* cannot be explained by lack of a specific glochidial host; possibly there is some effect related to the dense growths of Aufwuchs.

## Discussion

Having assumed that stations 1, 2, and 3 sustained similar biocoenoses before 1940, it is evident that construction of the dam has caused great changes in the community structure of the benthos. This is reflected particularly in the Ephemeroptera and Trichoptera, in which three types of changes are discernible downstream: a reduction in the total number of species (see Tables 2–5), an increase in the numbers of some species (see Fig. 3), and the replacement of yet other species by closely related ones (see Tables 2–5). These faunal changes are the result of alterations of the stream environment by the dam. Physical, chemical, and biological factors could be involved. It is highly unlikely that the slight variations in water chemistry exerted any influence on the distribution of the fauna. At all times the *p*H was above 7 and the range of variation of cationic concentrations was much less than that that is considered critical in the literature. Macan (1955) found only vague correlations between the ionic concentrations of lakes and their invertebrate faunas. His conclusion, that the distribution of the fauna would show a correlation to the more particular conditions of a habitat, can be applied here.

The difference in temperature regime is considered to be of importance. It can explain the distribution of the *Stenonema* species as discussed and of some of the fish species (Spence and Hynes 1971), but it is impossible to ascertain its effect on the other invertebrate species in the absence of data on their temperature requirements and other environmental factors. The remaining investigated effects are all biological in nature, such as the downstream development of attached algae and the increase in suspended matter during certain seasons. The increases downstream in the density of *H. azteca*, *Caenis* sp., *Baetis* spp., *Optioservus*, and Chironomidae are undoubtedly related to the greater availability of detritus and the more uniform flow here.

In attempting to answer the question of what factors caused the biocoenotic changes below the dam, one must remember that many environmental factors affect invertebrates and that several are interrelated. It is, therefore, perhaps rash to single out a few as responsible for the changes, but at least three primary factors are important: (1) alteration of the temperature regime so that water temperatures are considerably lower in summer; (2) abundant development of Aufwuchs, partly resulting from lower summer temperatures and even discharge, and involving radical alteration of the substrate surface; and (3) outflow of organic matter, particularly zooplankton and phytoplankton, from the impoundment.

The significant point of this study is, however, that collectively these factors tend to change the benthos in the same general way as does mild organic pollution.

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