APPLIED ASPECTS OF MAYFLY BIOLOGY

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ABSTRACT

Mayflies have been of interest to man for centuries. This paper will trace the history of this interest from its earliest beginnings in crude piscatorial entomology, through more recent application of the group as water quality indicators and research tools to present and future uses in modern aquatic technology.

Frost and Brown (1967) state that the use of artificial baits to catch trout by means of rod and line dates back to twelfth century Europe, although Leonard and Leonard (1962) report that it was practised by the ancient Greeks. Documentation of this occurred first in 1496 in the form of "The Treatyse of Fysshynge wyth an Angle" by Dame Juliana Berners. Doubtless, tempting fish with freshly caught aquatic insects would have preceded this, but the delicate nature of insect bodies would probably soon have led to the making of more robust imitations from a variety of readily available materials such as fur, feathers and wool. Presumably, the more realistic the artificial insect, the more successful its user would be. This fact alone probably led to a more careful scrutiny of lake or riverside insects and their habits, bringing the first aquatic entomologists into being.

A considerable literature on this topic, in both scientific journals and the popular press, now exists. I do not propose to review the state of the art of angling here, but to summarize some of the basic good descriptive entomology that has led to the refinement of

fly fishing as illustrated by the Ephemeroptera. Figure 1 shows the stages in the life cycle of a typical mayfly (left) and the artificial flies that are meant to imitate these stages (right). The aquatic nymphs is fished as a wet fly beneath the water surface. Dominant features of the nymph, such as the cerci, segmented abdomen, legs and darkened, pre-emergent wingpads are all duplicated in the fly. The emerging subimago is also fished as a wet fly, though just below the surface; most mayflies emerge at or near the water surface (Needham et αl . 1935). The characteristic rumpled wings are simulated on the artificial fly by a small portion of feather. The fully emerged subimago, now a terrestrial stage, is represented by a dry fly fished on the water surface. The subimago is similar in appearance to the adult, but has duller colours, the legs and cerci are shorter, and heavy pigmentation along the veins may produce a dark pattern on the wings (Leonard and Leonard 1962). The latter rarely persists in the imago but is faithfully copied in the fly (called a dun) by use of a mottled feather. features of the imago are seen in its counterpart - the spinner which is again fished on the water surface. The colours in this lure are brighter than in the dun, and the wings are made from a non-mottled feather. Segmentation in the abdomen is duplicated by a silk thread binding. Many hundreds of patterns are known for this fly depending on the species of mayflies occurring in local waters. The final stage of mimicry is that of the prostrate, spent female floating on the water surface. This change in posture is again reflected in the dry fly counterpart.

Why should the art of deceiving fish have developed to such a high degree? Tebo and Hasler (1963) state that availability and not abundance is the most important factor determining what foods are eaten by trout. The Ephemeroptera are most easily accessible as prey at emergence (Frost 1939). This accounts for the findings of Frost and Went (1940) that young atlantic salmon stomachs (Salmo salar L.) contained larger numbers of Baetis spp. than ${\it Ephemerella}$ spp. even though their densities in the benthos were almost identical; Baetis has a longer emergence period than Ephemerella. A certain amount of selectivity while feeding therefore appears evident. Bryan and Larkin (1972) reached a similar conclusion for brook trout (Salvelinus fontinalis (Mitchill)), cutthroat trout (Salmo clarki Richardson) and rainbow trout (Salmo gairdneri Richardson). This specialization is more evident in fish with full stomachs than in those with only a few items in their guts where feeding is more random (Allen 1941). Food constancy is of advantage to a fish in that it enables it to temporarily set its feeding behaviour for a transient but abundant supply of identical organisms (Frost and Brown 1967). This promotes efficiency in foraging, with a considerable safety benefit and has parallels in flower selection constancy documented for worker honeybees (Michener A fish may reset its feeding for successively available insect species (Williams and Coad 1979 have shown this for cyprinids).

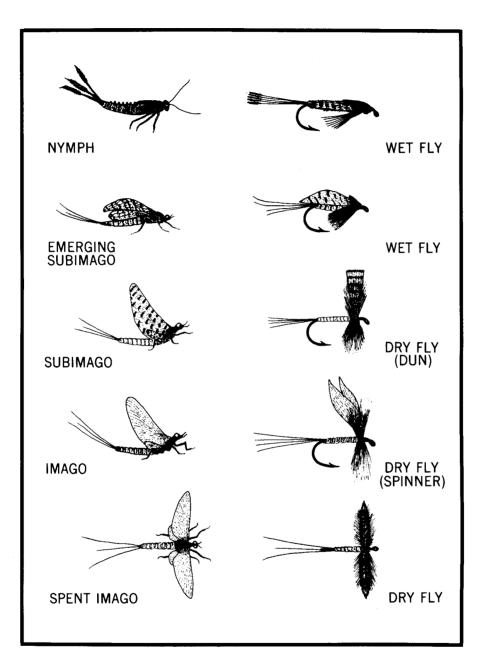


Figure 1. Comparison of the stages in the life cycle of a mayfly and the artificial flies that imitate them.

The angler takes advantage of this fact by presenting a suitable imitation of a particular mayfly during the time when the fish's feeding behaviour is set for that species; the so-called technique of "matching the hatch".

More recently, mayflies, along with other benthic macroinvertebrates, have been looked to as possible indicators of aquatic pollution (e.g. Britt 1975). Studies have shown that many pollutants have a marked affect on mayfly abundance and this can readily be de-Table 1 cites some examples of mayfly abundance above and below various sources of pollution. It shows different degrees of of response by nymphs of different families. Even the same genus, Baetis, responded differently to organic pollution in the Rivers Dee and Tees. This could well have been due to a difference in species or in the exact nature of the pollutant, however. case, that of Tricorythodes in Deer Creek, a build up of guarry stonedust on a riffle resulted in an increase in density. perhaps not surprising as the genus typically prefers a silty substrate (Burks 1953). Other studies have found species apparently preferentially selecting polluted conditions. Snow and Rosenberg (1975), for example, in an experimental study of colonization of artificial substrates coated with crude oil, found Baetidae only in oily substrates. These examples clearly indicate that mayflies do respond to environmental change, but because of insufficient identification the conclusions are somewhat limited, in application, to the individual studies. Although mayflies are generally considered to be very sensitive to pollutants, particularly those of organic origin, Roback (1974) provided data to show that this, as a generality, is not so. He cites examples of common genera, like Stenonema, that may occasionally be found in extreme conditions, and concludes that although there may be differences at the species level, nymphal taxonomy is not sufficiently advanced, at present, to allow reliable prognostications to be made. Resh and Unzicker (1975) similarly point out the importance of species identification in the meaningful biological assessment of water quality.

Roback's argument, would, therefore, seem to preclude widespread application of mayflies as biological indicators in North America at present. However, where the nymphs of certain nearctic genera are separable, e.g., Stenonema, Cloeon, Heterocloeon, Ephemerella, Neoephemera, and Hexagenia (Edmunds et al. 1976), or where keys to local species are available (e.g., Flowers and Hilsenhoff 1975) then the group becomes valuable as a biotic index. Hilsenhoff (1977), for example, used a modified version of Chutter's (1972) empirical biotic index to evaluate the water quality of Wisconsin's streams. Familiarity with the local fauna allowed him to assign values to species, many of them mayflies. These values ranged between 0 and 5, with 0 assigned to species collected only in streams of very high water quality, and 5 assigned to species collected in badly polluted streams. Table 2 gives some examples

Table 1. Examples of mayfly abundance above and below various sources of stream pollution.

Taxon	Number/sample upstream pollution(x)	Number/sample immediately downstream of Type of pollution (y) Pollutant	Type of Pollutant	Location	Data source
Ephemeridae Baetidae Heptageniidae	237 16 2.6	188 2.5 0	Sewage "	Red Cedar River Michigan, U.S.A	Leonard (1962) "
Baetis Ephemerella Ecdyonurus Rhithrogena	5 18 33	サイヤ		River Tees England "	Butcher <i>et al.</i> (1937) " "
Baetis Ecdyonurus venosus Rhithrogena se colorata Heptagenia sulphurea	205 5 5 8	36 0 2	Mild or- ganic pollution "	River Dee Wales "	Hynes(1960) " "
Stenonema frontale Baetisca callosa	195 18a 35	0 0	Acid mine waste	Margaret Creek /Sandy Run, Ohio, U.S.A.	Napier and Hummon (1976)
Caenis Baetis Tricorythodes	y/x ratio = 0 0 1	0.1 Deposit 0.7 stor 1.7	Deposited quarry stonedust	Deer Creek Indiana, U.S.A.	Gammon (1970) "

of the values he assigned to the mayflies. The biotic index was calculated according to the formula:

B.I. =
$$\frac{\sum n_i a_i}{N}$$

where n_i is the number of individuals in each species, a_i is its assigned value, and N is the total number of individuals in the sample. The biotic index for a given stream was then compared with a standard scale of values calculated for Wisconsin streams. Values of less than 1.75 indicated excellent water quality, characterizing clean, undisturbed streams; values of between 2.25 and 3.00 indicated fair quality, associated with moderate enrichment or disturbance; and greater than 3.75 indicated very poor water quality with gross enrichment or disturbance. Not only can mayflies be used to detect and categorize pollution, but, as Edmunds et αl . (1976) have suggested, they may help to remove some of the organic material by incorporating it into their body tissues which may later decompose on land.

An increasing nymber of laboratory studies are being reported in the literature in which mayfly nymphs are used as experimental animals. For example, Fremling and Schoening (1973) advocated the use of the burrowing nymphs of Hexagenia for the study of behaviour and for bioassay work, and designed a special artificial substrate for these purposes. Mayflies may have considerable potential in this kind of research, particularly as many species are easy to collect and maintain in the laboratory. These facts may also make them useful educational material in the classroom (Needham $et\ al.\ 1935$).

Mayflies provide an important food source for a great many predators, in both aquatic and terrestrial environments. Some, such as fish, are immediately obvious, others are perhaps not so obvious. For example, Leonard and Leonard (1962) cite adult dragonflies, hornets and spiders as well as a variety of birds, bats and other mammals, many of which are attracted to areas of mass emergence. In the aquatic phase, mayfly nymphs are eaten by waterfowl and may be an important component of the diet of their young (Krull and Boyer 1976). By far the most studied aspect of the food potential of the Ephemeroptera is that for fish, and salmonids in particular. New ideas are presently opening up in this area and attempts are being made to apply principles of stream ecology to increasing salmonid stocks.

As part of the Canadian Federal Government's Pacific Salmon Enhancement Programme, Mundie (1974) proposed the feasibility of raising salmon smolts (primarily coho salmon, Oncorhynchus kisutch (Walbaum)) in high density in seminatural streams. The approach was to combine some of the desirable features of rivers with the

Examples of water quality values assigned to mayflies by Hilsenhoff in a study of Wisconsin streams (0 = excellent water quality, 5 = extremely poor water quality).	BAETIDAE	2 3 4 5	Baetis frondalis B. levitans osum B. vagans B. pygmaeus Pseudocloeon dubium	HEPTAGENIIDAE	2 3 4 5	m S. terminatum S. exiguum s S. mediopunctatum H. diabasia	EPHEMERIDAE	2 3 4 5	Hexagenia limbata	EPHEMERELLIDAE	2 3 4 5	E. temporalis
Examples of water quality values Wisconsin streams (0 = excellent	BAETID	1 2	Cloeon alamance Baetis frondalis Heterocloeon curiosum B. vagans Pseudocloeon dubium	HEPTAGEN	1 2	Stenonema fuscum H. lucidipermis S. n	EPHEMER	1 2	Ephemera simulans Hexagenia limb	EPHEMEREL	1 2	E. simplex E. needhami
Table 2. E		0			0	Heptagenia pulla S. rubrum		0			0	Ephemerella atternata E. bicolour E. excrucians E. subvaria E. funeralis

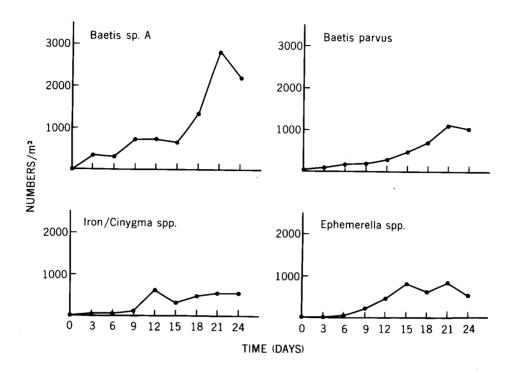


Figure 2. Colonization curves for mayfly nymphs.

productive capacity of hatcheries, but at a reduced cost. He considered the basic environmental unit for young coho to be a riffle/pool sequence at a meander. The unit provides an area of fast—moving, shallow water that supports benthic invertebrates, an area of deeper, slow-moving water for the fish, and an overhanging bank which provides their shelter. Central to the theory is the use of benthos on the riffles as part of the fry's diet, the invertebrates conveniently being transported from the riffles to the waiting fish in the pools by drift, and the recycling of excess manufactured food and fish faeces into the benthic food chain.

A prototype channel was constructed in 1975 alongside the Big Qualicum River, Vancouver Island, British Columbia. It is 400 m long by 4.5 m wide and consists of 25 riffles and 25 pools arranged alternately. The pools are 9 m long by 1 m deep and the riffles are 5 m long by 15 cm deep. An optimum discharge of 0.4 m 3 /s gives a surface velocity of 60 cm/s on the riffles and 9 cm/s in the pools. Water is drawn from the river at the top end of the channel and is

returned at the bottom end. Screens prevent the loss of fry and the entry of predatory fish at either end. Other screens divide the channel into five sections so that the effects of downstream accumulation of wastes can be assessed.

In coastal streams of B.C., several factors limit natural smolt production. Foremost amongst these are extremes of discharge, limited benthic production, and predation. Discharge is controlled in the channel and predation from birds and mink has been countered with a fence and net canopy. The fry are fed on prepared pellet food, in order to increase the capacity of the system, but receive a natural supplement of benthic invertebrates and aerial insects (Mundie and Mounce 1978).

The contribution potential of benthos to the diet of the fry and the possibility of recycling fish wastes and excess pellet food into edible benthos were evaluated experimentally. Much of this work has already been published (Williams $et\ al.$ 1977) but I propose to present here data specifically involving the role of mayflies in these processes.

Drifting mayflies often form a substantial part of the natural diet of salmonids (e.g. Elliott 1973). Not only may a steady intake of these insects provide vitamins and essential trace elements. but a necessary natural feeding experience that may be lacking in hatchery-reared fish (Fenderson et al. 1968). As drift occurs mostly at night, fish cannot fully exploit this food source. a semi-natural channel, however, insects can be dislodged artificially during the day. In order to establish a regime for doing this without completely depleting areas of benthos, the cropping potential of insects on a unit area of riffle must be calculated. Williams et αl . (1977) set out troughs of sterile gravel and collected all the invertebrates that had colonized at three day intervals, up to 24 days. Colonization curves were then drawn for dominant groups. Figure 2 shows the curves for the four main groups of mayflies. The response was not the same in each group, but within 2-3 weeks the standing crop of mayflies had levelled out. results suggested that under winter conditions, small areas of the channel's riffles could be disturbed every 15 days to yield about 80,000 invertebrates/m², weighing about 0.62 g dry weight; this contains a mayfly component of around 2,400/m². This yield should be sustainable provided that undisturbed areas are left to serve as production sites.

The possibility of recycling wastes in the channel was investigated as follows: troughs of gravel were loaded with different amounts of food pellets (Oregon Moist Pellets, Formula II) and pure fish faeces and left for 4 weeks. The response of the mayflies to 0.M.P. is shown in Figure 3. Baetis sp. A responded favourably initially with a 36% increase in its numbers between the clean

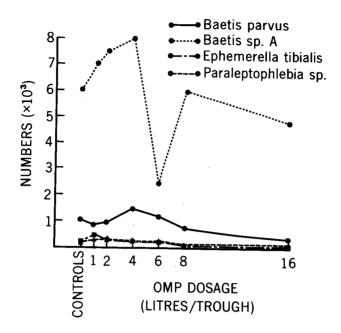


Figure 3. Response of mayflies to fish pellets (0.M.P.).

gravel control trough and the trough loaded with 4 L of pellets. A gradual decline followed. The other mayflies varied in their initial responses but gradually declined with increasing dosage. Rhithrogena, Cinygma and Iron were eliminated entirely. Figure 4 shows the response of Baetis parvus Dodds and Baetis sp. A to fish faeces. A steady decline is evident.

The response of the total benthos to these wastes was more one of increased numbers (Figure 5), although this was mostly due to chironomids. It appears, therefore, that the mayflies would only play an important part in recycling wastes in the channel if the wastes consisted primarily of a limited excess of food pellets and provided that the level of fish faeces could be kept to a minimum. The standing crop of mayflies on the channel riffles could, however, be increased by other means. For example, Mundie $et\ al$. (1973) obtained an increase in the numbers of several species after enriching gravel with wheat grain, and Williams and Mundie (1978) showed that selection of a suitable size for the riffle gravel could promote desirable elements in the fauna.

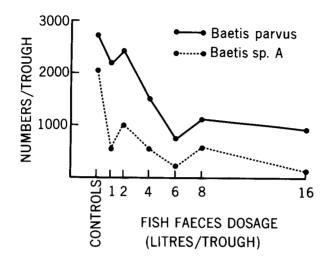


Figure 4. Response of mayflies to fish faeces.

Warren $et\ al.$ (1964) produced an increased mayfly biomass in a small Oregon creek by adding sucrose, primarily by increasing the growth of Sphaerotilus as food for the herbivorous insects. Along the same lines, additions of soluble plant nutrients, such as nitrates and phosphates, to channel water may, where light and other nutrients are non-limiting, increase periphyton which in turn would promote the mayfly fauna. It would, of course, be desirable to maintain high water quality in the system as this would probably promote mayflies naturally.

The results of the Big Qualicum channel's first few years of operation are encouraging. It was stocked with 400,000 swim-up fry in May, 1976 and these were released to the sea as 15 g smolts in May, 1977. During this time, they obtained sufficient natural food (from unaided drift) to necessitate a reduction to 25% hatchery rations of their pelleted food to prevent waste. The percentage of mayflies in their diet is given in Table 3. As might be expected, there were seasonal differences in the numbers of mayflies eaten. 1800 h seemed to be the time when most were eaten but this peak was not well marked. Only total numbers were assessed with the result that the size difference between those drifting in the day (very small ones) and those at night (large

nymmbs in the diet of coho fry (based on sampling 25 fish four

Table 3. Percentage of times in 24 I	t mayily nymphs hours in each se	Percentage of mayily nymphs in the diet of cono if times in 24 hours in each section of the channel).	cono iry (based annel).	Percentage of mayily nymphs in the diet of cono fry (based on sampling 2) fish four times in 24 hours in each section of the channel).
Date	Section 2 (upstream)	Section 3	Section 4	Section 5 (downstream)
May 11, 1976	13	. 50	œ	13
June 24	15	2	∞	9
July 15	2	7	က	E
August 23	6	6	13	12
September 2	∞	13	7	12

ones) was not adequately recorded (see Allan 1978). Fish in all sections of the channel were eating mayflies. Even though the percentages in the guts were never high (20% maximum) each fish had the chance to develop a normal feeding behaviour that would help prepare it for a free-ranging existence once released from the channel.

The 1977 released fish returned to the river in the fall of 1978 and results indicate a return percentage similar to that of a local hatchery. However, this was the first complete cycle and increased yields can reasonably be expected in subsequent returns. The first batch of smolts was, however, raised at substantially less cost than hatchery fish and some of this is attributable to natural food (Mundie, personal communication).

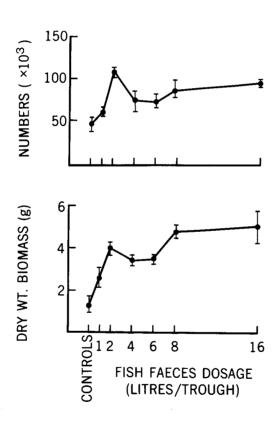


Figure 5. Response of total benthos to fish faeces (vertical lines represent range of three subsamples).

To conclude, a possible future use of mayflies is given. (1964) reviewed the potential of using animal remains in Quaternary lake and bog sediments as an aid to reconstructing past environments and their ecological interrelationships. He listed a great many groups of insects and other invertebrates but indicated that information on many of them is limited. One of the most commonly used groups is the Coleoptera and this is probably because they may constitute over 85% of insect remains in Pleistocene sediments (Shotton So far as mayflies are concerned, Frey listed three records of either nymphal or adult remains (Brehm et~al.~1948; Swain 1961 and Tasch and Zimmerman 1961). He concluded by saying that "this general dearth of records suggests that fragments of nymphs either are not generally preserved or else have not yet been generally recognized. I suspect that the latter is correct, not only for this order but also for a number of other orders in which the immature forms are aquatic." The Ephemeroptera, with its ancient lineage and specialization to different aquatic habitats could probably make significant contributions to paleoecology. certainly proved to be the case for the Trichoptera as they are now being used with considerable success (e.g., Williams and Morgan 1977, Moseley 1978).

In retrospect, mayfly biology has the potential to be applied in many areas. Perhaps the inability to identify many of the nymphs is the chief factor currently impeding this.

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RESUME

Cela fait des siècles que l'homme s'intéresse aux éphéméroptères. L'auteur retrace l'histoire de cet intérêt dupuis les premières tentatives entomologiques de l'homme se rapportant à la pêche jusqu'aux usages présents et futurs de ce groupe d'insectes en hydrologie, en passant par ses applications plus récentes comme indicateur de la qualité des eaux et comme outil de recherches.

ZUSSAMENFASSUNG

Eintagsfliegen sind seit mehreren Jahrhunderten für den Menschen von Interesse. Die vorliegende Arbeit verfolgt die Geschichte dieses Interesses von den ersten Anfängen in einfacher, früher Fischerei-Entomologie über die neuzeitlichere Verwendung der Fliegen als Indikatoren für die Qualität des Wassers und ferner als Forschungs-

werkzeuge für gegenwärtige und zukünftige Nutzung in der modernen aquatischen Technologie.

REFERENCES

- Allan, J.D. 1978. Trout predation and the size composition of stream drift. *Limnol. Oceanogr.* 23: 1231-1238.
- Allen, K.R. 1941. Studies on the biology of the early stages of the salmon (Salmo salar). 2. Feeding habits. J. Anim. Ecol. 10: 47-76.
- Berners, Dame Juliana. 1496. The Treatyse of Fysshynge wyth an Angle. Reprinted from the book of St. Albans. London. Pickering, 1827.
- Brehm, V., G. Krasske and W. Krieger. 1948. Subfossile tierische Reste und Algen im Schwarzsee bei Kitzbühel. *Oesterr. bot.* Z. 95: 74-83.
- Britt, N.W. 1975. Mayflies (Ephemeroptera) as biological indicators of water quality. Ohio Biol. Surv., Inf. Circ. 8: 52-54.
- Bryan, J.E. and P.A. Larkin. 1972. Food specialization by individual trout. J. Fish. Res. Board Can. 29: 1615-1624.
- Burks, B.D. 1953. The mayflies, or Ephemeroptera, of Illinois. Ill. Nat. Hist. Surv. Bull. 26: 1-216.
- Butcher, R.W., J. Longwell and F.T.K. Pentelow. 1937. Survey of the river Tees, III. The non-tidal reaches. Chemical and Biological. Tech. Pap. Wat. Pollut. Res. Lond. 6: 1-187.
- Chutter, F.M. 1972. An empirical biotic index of the quality of water in South African streams and rivers. Water Res. 6: 19-30.
- Edmunds, G.F., Jr., S.L. Jensen and L. Berner. 1976. The Mayflies of North and Central America. Univ. Minnesota Press, Minneapolis.
- Elliott, J.M. 1973. The food of brown and rainbow trout (Salmo trutta and S. gairdneri) in relation to the abundance of drifting invertebrates in a mountain stream. Oecologia 12: 329-347.
- Fenderson, O.C., W.H. Everhart and K.M. Muth. 1968. Comparative agonistic and feeding behaviour of hatchery reared and wild salmon in aquaria. J. Fish. Res. Board Can. 25: 1-14.
- Flowers, R.W. and W.L. Hilsenhoff. 1975. Heptageniidae (Ephemeroptera) of Wisconsin. *Great Lakes Entomol.* 8: 201-218.
- Fremling, C.R. and G.L. Schoening. 1973. Artificial substrates for *Heptagenia* mayfly nymphs. p. 209-211. *In:* Proc. 1st Int. Conf. Ephemeroptera.W.L. Peters and J.G. Peters, eds. E.J. Brill, Leiden.
- Frey, D.G. 1964. Remains of animals in Quaternary lake and bog sediments and their interpretation. *Ergeb. Limnol.* 2: 1-114.
- Frost, W.E. 1939. River Liffey Survey II. The food consumed by the brown trout (Salmo trutta Linn.) in acid and alkaline

- waters. Proc. R. Irish Acad. 46B. 139-206.
- Frost, W.E. and M.E. Brown. 1967. The Trout. Collins, London.
- Frost, W.E. and A.E.J. Went. 1940. River Liffey Survey III. The growth and food of young salmon. *Proc. R. Irish Acad.* 46B: 53-80.
- Gammon, J.R. 1970. The effect of inorganic sediment on stream biota. Rep. Wat. Qual. U.S.E.P.A. No. 5501-0074, 141 p.
- Hilsenhoff, W.L. 1977. Use of arthropods to evaluate water quality of streams. Wis. Dep. Nat. Resour. Tech. Bull. 100: 1-15.
- Hynes, H.B.N. 1960. The Biology of Polluted Waters. Liverpool Univ. Press.
- Krull, J.N. and R.L. Boyer. 1976. Abundance and diversity of benthos during the spring waterfowl migration. Am. Midl. Nat. 95: 459-462.
- Leonard, J.W. 1962. Environmental requirements of Ephemeroptera.

 In: Biological Problems in Water Pollution. Third seminar.

 U.S. Public Health Serv. Publ. 999-WP-25: 110-117.
- Leonard, J.W. and F.A. Leonard. 1962. Mayflies of Michigan trout streams. Cranbrook Inst. Sci. Bull. 43: 1-139.
- Michener, C.D. 1974. The Social Behaviour of the Bees: a Comparative Study. Belknap Press, Harvard Univ., Massachusetts, 404 p.
- Moseley, K.A. 1978. A preliminary report on Quaternary fossil caddis larvae (Trichoptera) Quat. Newsletter 26: 2-12.
- Mundie, J.H. 1974. Optimization of the salmonid nursery stream. J. Fish. Res. Board. Can. 31: 1827-1837.
- Mundie, J.H. and D.E. Mounce. 1978. Application of stream ecology to raising salmon smolts in high density. *Int. Verein. theor. angew. Limnol. Verh.* 20: 2013-2018.
- Mundie, J.H., D.E. Mounce and L.E. Smith. 1973. Observations of the response of zoobenthos to additions of hay, willow leaves and cereal grain to stream substrates. Fish. Res. Board Can. Tech. Rep. 387: 1-123.
- Napier, S., Jr. and W.D. Hummon. 1976. Survival of mayfly larvae under mine acid conditions. Int. Rev. gesamten Hydrobiol. 61: 677-682.
- Needham, J.G., J.R. Traver and Y.C. Hsu. 1935. The Biology of Mayflies with a Systematic Account of North American Species. Comstock, Ithaca.
- Resh, V.H. and J.D. Unzicker. 1975. Water quality monitoring and aquatic organisms: the importance of species identification. J. Water Pollut. Contr. Fed. 47: 9-19.
- Roback, S.S. 1974. Insects (Arthropoda: Insecta). p. 313-376.

 In: C.W. Hart, Jr. and S.L.H. Fuller, eds. Pollution Ecology of Freshwater Invertebrates. Academic Press, N.Y.
- Shotton, F.W. 1959. Insects in Pleistocene deposits. J. Inst. Biol. 6: 63-65.
- Snow, N.B. and D.M. Rosenberg. 1975. The effects of crude oil on the colonization of artificial substrates by zoobenthos

- organisms. Can. Fish. Mar. Serv. Res. Dev. Tech. Rep. 553: 1-35.
- Swain, F.M. 1961. Limnology and amino-acid content of some lake deposits in Minnesota, Montana, Nevada, and Louisiana. *Bull. geol. Soc. Am.* 72: 519-546.
- Tasch, P. and J.R. Zimmerman. 1961. Fossil and living conchostracan distribution in Kansas-Oklahoma across a 200-million year time gap. Science (Wash. D.C.) 133: 584-586.
- Tebo, L.B. and W.W. Hassler. 1963. Food of brook, brown and rainbow trout in streams of W.N. Carolina. J. Elisha Mitchell Sci. Soc. 79: 44-53.
- Warren, C.E., J.H. Wales, G.E. Davis and P. Doudoroff. 1964.
 Trout production in an experimental stream enriched with sucrose. J. Wildlf. Manage. 28: 617-660.
 Williams, D.D. and B.W. Coad. 1979. The ecology of temporary
- Williams, D.D. and B.W. Coad. 1979. The ecology of temporary streams III. Temporary stream fishes in southern Ontario, Canada. Int. Rev. gesamten Hydrobiol. (In press).
- Williams, D.D. and J.H. Mundie. 1978. Substrate size selection by stream invertebrates and the influence of sand. Limnol. Oceanogr. 23: 1030-1033.
- Williams, D.D., J.H. Mundie and D.E. Mounce. 1977. Some aspects of benthic production in a salmonid rearing channel. *J. Fish.*Res. Board Can. 34: 2133-2141.
- Williams, N.E. and A.V. Morgan. 1977. Fossil caddisflies (Insecta: Trichoptera) from the Don Formation, Toronto, Ontario, and their use in paleoecology. Can J. Zool. 55: 519-527.