Influence of a reservoir with surface release on the life history of the mayfly *Heterocloeon curiosum* (McDunnough) (Ephemeroptera: Baetidae)

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Received April 1, 1980

KONDRATIEFF, B. C., and J. R. VOSHELL, JR. 1981. Influence of a reservoir with surface release on the life history of the mayfly *Heterocloeon curiosum* (McDunnough) (Ephemeroptera: Baetidae). Can. J. Zool. **59**: 305–314.

The life history of *Heterocloeon curiosum* was compared in the impounded North Anna River (NAR) and the free-flowing South Anna River (SAR) in Virginia, U.S.A. The study site on the NAR was 32 km below Lake Anna, a surface-release reservoir. *Heterocloeon curiosum* was bivoltine in both rivers with two summer generations and probable overwintering in the egg stage. It passed through 10 larval instars (range 9–12) in both rivers. The density of larvae was twice as great in the SAR as the NAR. Factors which may have contributed to the lesser success of *H. curiosum* in the NAR included bottom scouring produced by sudden increases in discharge, absence of the macrophyte *Podostemum*, quality of available food, and alterations of the temperature regime. Of these four factors, temperature probably had the most significant effect. The emergence of the second generation was 1 month later in the NAR because the reservoir delayed the normal seasonal cooling of the river. The nonoptimal temperature regime appeared to significantly reduce the fecundity of *H. curiosum* in the NAR. Our data indicate that surface-release reservoirs may have subtle but significant effects on the life histories of benthic macroinvertebrates.

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La cycle biologique d'*Heterocloeon curiosum* a été étudié dans une rivière endiguée, la rivière North Anna (NAR) et dans une rivière à écoulement libre, la rivière South Anna (SAR), en Virginie, aux Etats-Unis. Dans la rivière NAR, l'échantillonnage s'est fait à 32 km en aval du lac Anna, un réservoir à écoulement de surface. Dans les deux rivières, *H. curiosum* produit deux générations d'été par année, et l'espèce semble passer l'hiver à l'état d'œuf. On peut reconnaître 10 stades larvaires (de 9 à 12) dans les deux rivières. La densité des larves est deux fois plus élevée dans la rivière SAR. Les facteurs qui ont pu entraver le succès d'*H. curiosum* dans la rivière NAR sont: le lessivage du fond par des augmentations soundaines de l'écoulement, l'absence du macrophyte *Podostemum*, la qualité de la nourriture disponible et les modifications du régime thermique. De ces quatre facteurs, la température est probablement celui qui a le plus d'effet. L'émergence de la second génération a été repoussée d'un mois dans la rivière NAR parce que la présence du réservoir retarde le refroidissement saisonnier normal des eaux de la rivière. Le régime non optimal de température semble diminuer significativement la fécondité de l'espèce dans la rivière NAR. Ces données démontrent que les réservoirs à écoulement de surface peuvent avoir des effets subtils, mais importants sur le cycle biologique des macroinvertébrés benthiques.

[Traduit par le journal]

Introduction

Man-made reservoirs constitute a significant portion of the lentic waters of the world, and streams that are influenced by reservoirs have become the most common lotic environments (Stanford and Ward 1979). The downstream effects of impoundments on benthic macroinvertebrates have been reviewed by Ward (1976) and Ward and Stanford (1979). Most studies of the downstream effects of impoundments have been conducted below deep-release reservoirs that are used for hydroelectric generation. Hypolimnial release characteristically produces thermal constancy in receiving streams (winter–warm and summer–cool conditions). Mayflies have been frequently reported to be reduced for considerable distances below reservoirs with hypolimnial release (Briggs 1948; Hilsenhoff 1971; Spence and Hynes 1971; Lehmkuhl 1972; Ward 1974; Gore 1977).

There have been very few studies of the downstream effects of reservoirs with surface release. Reservoirs of this type have been constructed to provide water for public consumption, cooling electricity generating facilities, and flood control. In the temperate region, surface-release reservoirs generally shift the seasonal temperature cycle (warm slower in spring, cool slower in fall) and increase the seasonal temperature range (warmer in summer), rather than producing thermal constancy in receiving streams. The few studies of benthic macroinvertebrates below surface-release dams have been primarily concerned with community structure (Simmons and Voshell 1978; Ward and Short 1978; Fraley 1979). In all of these studies the investigators found that surface-release reservoirs changed the relative abundance of mayflies in the receiving streams.

However, there have been no detailed studies of the life histories of mayflies below surface-release reservoirs that might provide the explanation for the changes

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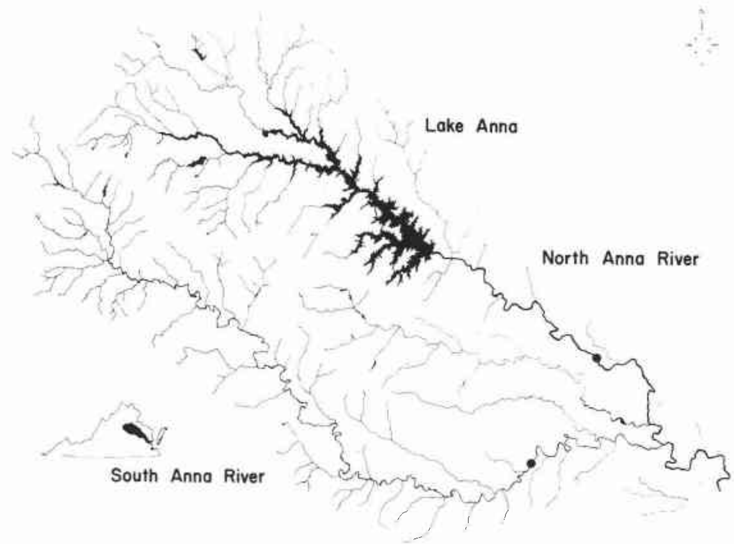

FIG. 1. Map of the North and South Anna rivers in Virginia, U.S.A., indicating location of sampling stations (●).

reported in community structure. Recent studies have shown that subtle differences in temperature (Sweeney and Vannote 1978) and food (Anderson and Cummins 1979) can affect life histories of aquatic insects. Surface-release reservoirs are likely to produce subtle differences in both of these parameters. The purpose of this study was to analyze the effects of a surface-release reservoir on a baetid mayfly by comparing its life history in an impounded and a free-flowing river.

Study area

The North and South Anna rivers (NAR and SAR, respectively) drain approximately parallel watersheds within the York River Basin (37°45′ N, 77°30′ W) in central and eastern Virginia, U.S.A. (Fig. 1). Both rivers begin in the Piedmont Plateau Province and flow southeastwards over the Fall Line before they join to form the Pamunkey River in the Coastal Plain Province. The Fall Line is the boundary between the Piedmont Plateau and Coastal Plain physiographic provinces; it is a narrow zone where the granitic rocks pass below tide level and the streams drop abruptly over a succession of ledges. There are no major population centers in the York River Basin. Approximately 70% of the basin is forested; approximately 22% is in cropland and pasture (Anonymous 1970).

The NAR was impounded in 1972 to provide cooling water for a nuclear-powered electricity generating facility. Lake Anna is a mainstream impoundment with a maximum depth of 27 m, average depth of 8 m, and area of 5261 ha. Studies of the limnology of Lake Anna have been reported by Armitage and Simmons (1975), Hall (1976), Reed and Simmons (1976), Saunders (1975), and Voshell and Simmons (1977). Under normal flow conditions water is released entirely from gates at the top of the dam. Legal requirements stipulate the release of at least 1.13 m^3/s into the NAR. There are also gates lower in dam, but these are only used occasionally for flood control. Average input into Lake Anna from the NAR is 7.65 m^3/s, and the average release from the dam is 6.22 m^3/s.

We established one study site on each river at the Fall Line. The study site on the NAR is approximately 32 km below Lake Anna. Simmons and Voshell (1978) and Voshell (unpublished) found that mayflies were not abundant below Lake Anna until the Fall Line. We selected the Fall Line because it was the site closest to the dam where we could collect adequate numbers of a mayfly to analyze its life history, and we speculated that if there were any subtle effects upon its life history they would still be detectable at this distance downstream. For example, the average annual temperature of the NAR at the Fall Line is slightly warmer than the SAR, and the NAR cools slower in the fall and warms slower in the spring. The elevation of the NAR study site is 20 m, the gradient is 21.8 m/km, and the width is 75 m. At this point the NAR is a fifth-order stream that drains approximately 1.14×10^5 ha. The substrate consists primarily of coarse pebble (32–64 mm), cobble (64–256 mm), and boulder (> 256 mm). The aquatic macrophyte, *Justicia americana* (L.) (water willow), is very abundant along the edges and in shallow areas with slow current in midstream. Mine drainage affected the overall ecology of the NAR prior to its impoundment, but community structure and diversity of benthic macroinvertebrates were not affected as far downstream as the present study site (Simmons 1972*a*, 1972*b*; Simmons and Reed 1973). The impoundment of the NAR appears to have completely ameliorated the effects of the mine drainage in downstream areas (Simmons and Voshell 1978).

The study site on the SAR was established at the Fall Line because the habitat is the most similar to the NAR study site. The sampling area included 0.2 km of riffles between two large pools. The elevation is 38 m, the gradient is 3.4 m/km, and the width is 100 m. At this point the SAR is also a fifth-order stream, and its watershed is approximately 1.02×10^5 ha. The substrate is similar to the NAR, but the aquatic macrophyte *Podostemum ceratophyllum* (Michaux) (river weed) is very abundant in the SAR in addition to *Justicia*. The *Podostemum* often forms a thick carpet on large rocks in fast water during the summer, but it dies back considerably in the winter.

Methods

The life history of *Heterocloeon curiosum* (McDunnough) was elucidated and compared in the impounded NAR and free-flowing SAR from June 1977 to June 1978. Quantitative samples (three replicates) were collected in riffle areas at each study site with an Ellis–Rutter portable invertebrate box sampler (0.1 m^2 area, 351 μm net). Samples were collected monthly from November to March and every 2 weeks for the remainder of the year. A coarse brush was used to dislodge the organisms from each rock in the sampler. Rocks larger than 32 mm were examined individually to make sure that no organisms were left clinging to them. The *Podostemum* was removed from each rock with a paint scraper and placed in the sample. The substrate was thoroughly stirred to a depth of 10 cm to make sure that all organisms were dislodged and washed into the net. Samples were preserved in the field in 5% formalin. The substrate in each sample was analyzed according to the methods of Cummins (1962) and Hynes (1970). Rocks larger than 32 mm were sorted into size categories and weighed in the field. The remaining substrate in the sampler was scooped out and returned to the laboratory for drying, sieving, and weighing. Most sand, silt, and clay were lost through the net, but several complete analyses indicated that the substrate contained very little in these size categories. The vegetation in the sample was also dried and weighed in the laboratory. The depth of each sample was measured with a metre stick, and the current was measured with a General Oceanics, Inc., model 2030, Mark II, digital flowmeter.

Additional larvae were collected with a kick net for gut analyses and rearing. Larvae were reared in screen cages in a model LS-700 Living Stream (Frigid Units, Inc., Toledo, Ohio, U.S.A.). Dechlorinated tap water was used in the rearing apparatus which was maintained at the approximate temperature of the NAR and SAR. To assist in determining emergence and flight periods, a black-light trap and (or) a white light (Coleman lantern) placed on a white sheet of cloth were used to collect subimagoes and adults during appropriate months. Additional adult material was obtained with an aerial net. Other data such as timing, place of emergence, and flight patterns were recorded from direct observation in the field. The duration of the subimaginal stage was determined by timing specimens reared in the laboratory.

The following physical–chemical parameters were measured at each station according to the methods of the American Public Health Association et al. (Anonymous 1975): temperature, dissolved oxygen, total alkalinity, pH, conductivity, major cations, and major anions. Cation and anion concentrations were measured monthly; all other parameters were measured on every benthic sampling date. Mean daily discharge for each river was obtained from the closest gauging station (NAR, Virginia State Water Control Board at Doswell; SAR, United States Geological Survey at Ashland).

In the laboratory organisms were removed from debris by the flotation technique described by Hynes (1970). Head widths were measured with an ocular micrometer on a dissecting microscope; larvae were measured immediately below the occipital sulcus to the nearest 0.025 mm. Sex was determined for larvae with head widths > 0.5 mm. Size–frequency histograms were constructed to determine the number of generations per year and emergence times. The number of instars was estimated by the method of Janetschek (1967). McClure and Stewart (1976) and Newell and Minshall (1978) have explained the use of Janetschek's method in life history studies of mayflies. To compare fecundity, eggs were counted from last-instar larvae (indicated by dark, swollen wing pads) in each generation from each river.

Feeding habits were analyzed by the methods of Shapas and Hilsenhoff (1976). The percent by volume in each of four categories (detritus, diatoms, filamentous algae, and animal) was estimated to the nearest 10%. Results were calculated by averaging five fields from each of three replicate slides.

To determine habitat preferences of larvae each benthic sample was classified as follows: depth < 20 cm or ≥ 20 cm; current ≤ 100 cm/s or > 100 cm/s; substrate > −7 mean phi or ≤ −7 mean phi; vegetation present or absent. The relative importance of individual habitat factors in determining distribution was analyzed by the indexing system of Williams and Hynes (1973).

Results

Subimagoes

The subimagoes of *H. curiosum* emerged late morning (ca. 11:00 a.m.) to late afternoon (ca. 4:00 p.m.) from riffle regions. Observation of specimens in the laboratory indicated that turbulent water was necessary for successful emergence. *Heterocloeon curiosum*, like many other baetid mayflies, used the larval skin as a momentary raft at the surface of the water. The average duration of the subimago stage at laboratory temperature (ca. 24°C) was 17.5 h.

Adults

There was seasonal size variation among adults from both rivers. The total body length was greater for the first generation (male 5.40 ± 0.55 mm, female 4.92 ± 0.51 mm) than the second generation (male 3.90 ± 0.35 mm, female 3.92 ± 0.33 mm). Seasonal size variation has been frequently reported among multivoltine mayflies (Ide 1935; Macan 1957; Elliott 1967; Clifford 1970; McClure and Stewart 1976).

A nuptial flight was observed on the NAR at 6:45 a.m. (Eastern Daylight Savings Time) on 3 August 1978. The flight consisted of six to eight males and two to four females, rhythmically performing an undulating, nonsynchronous flight pattern. At first the group was 3–4 m above the surface of a riffle, but then it quickly soared out of sight. Although little life history information is available on the members of the genus *Heterocloeon*, there have been studies of some species in the closely related genus *Baetis*. A similar type of flight behavior was described for *B. vagans* by Murphy (1922); Needham et al. (1935) described the nuptial flight of *B. flavistriga* as being more irregular. No copulation or oviposition was observed even though the river was searched for 4 h, 200 m upstream and downstream of where the nuptial flight had been first sighted. *Heterocloeon curiosum* females may migrate much farther upstream to oviposit or simply be missed because of their small size.

Eggs

Eggs measured 0.125 × 0.075 mm in diameter. For the first generation the average fecundities (n = 10) of mature larvae (dark, swollen wing pads) were 216 eggs per female in the NAR and 518 eggs per female in the SAR. For the second generation the average fecundities were 175 and 240 eggs per female in the NAR and SAR, respectively. Analysis of variance indicated that there were significantly more eggs in larvae from the first generation than the second generation, and significantly more eggs in larvae from the SAR than the NAR (P = 0.0001). Females of the first generation were significantly larger than those of the second generation (P = 0.0001); however, there was no significant difference in the size of females from the two rivers (P = 0.10).

Larvae

The head capsule width of recently hatched first-instar larvae was 0.100–0.130 mm. Sex could be reliably determined for larvae with head width > 0.5 mm. The sex ratio of larvae that could be determined (690) was 1 male:1.3 females. From June to November the density of *H. curiosum* averaged 144 organisms/m^2 in the NAR and 298 organisms/m^2 in the SAR (Fig. 2).

Analysis of the larval habitat preferences according to the method of Williams and Hynes (1973) indicated that *H. curiosum* preferred shallow water with fast current and substrate consisting of fine cobble (64–128 mm) or coarse pebble (32–64 mm). In the NAR, larvae preferred sites without vegetation, whereas in the SAR larvae preferred sites with vegetation. The difference in their preference can be explained by the type of vegetation in each river. In the NAR the vegetation consisted entirely of *Justicia* which occurred as loosely arranged, vertical stalks; in the SAR the vegetation consisted almost entirely of *Podostemum* which occurred in dense, irregular tangles. Apparently, *Justicia* does not provide as suitable a microhabitat for *H. curiosum* larvae as *Podostemum*.

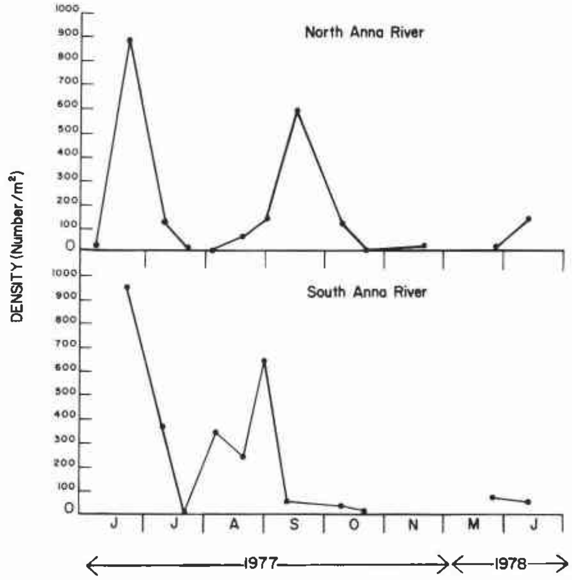

FIG. 2. Seasonal abundance of *Heterocloeon curiosum* larvae in the North and South Anna rivers.

Seasonal cycle

Heterocloeon curiosum had two summer generations in succession with some overlap in both rivers (Figs. 3 and 4). This developmental cycle corresponds with type B-2 of Landa (1968). The larvae persisted longer in the NAR, with the second emergence pulse occurring in mid-September to late October. Mature larvae were still collected in November, but they probably failed to emerge because of seasonal low temperatures as Ide (1935) reported for *Epeorus humeralis*. In the SAR the second emergence pulse was middle to late August with some individuals emerging into late October. Peak larval densities occurred at emergence periods, and larval densities were higher at the first emergence in both rivers (Fig. 2). In the NAR very few larvae were collected in July and August between the emergence peaks. In the SAR larvae became abundant more quickly after the first emergence. After the second emergence very few larvae were collected in either river until late May. Many of the larvae collected in May were ready to emerge, especially in the SAR. It appears that the larvae collected in May hatched in late March to early April from diapausing eggs that were deposited in the fall. Most of this brood emerged in middle to late June in both rivers. Eggs from the first brood probably hatched within 30 days, and the larvae grew through the summer. Macan (1979) lists two species of *Baetis* that have similar life histories in Great Britain.

Development

Determination of the number of instars by the Janetschek method (1967) indicated that there were usually 10 larval instars (range 9–12) for the combined summer

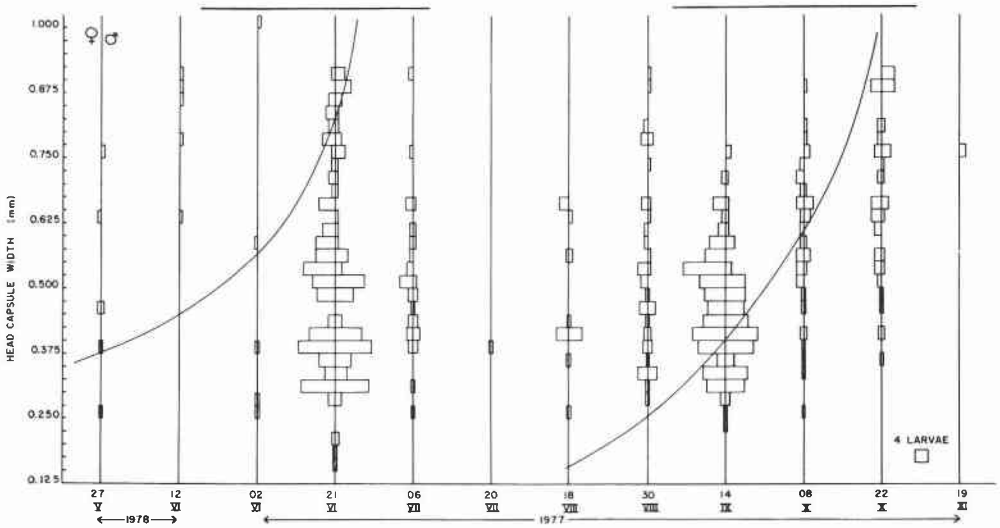

FIG. 3. Size frequency distribution of head capsule widths of *Heterocloeon curiosum* in the North Anna River. Curved lines indicate proposed generations. Horizontal lines indicate adult flight periods. The head capsule width of recently hatched first-instar larvae was 0.100–0.130 mm. Sex could be determined for larvae with head width > 0.5 mm.

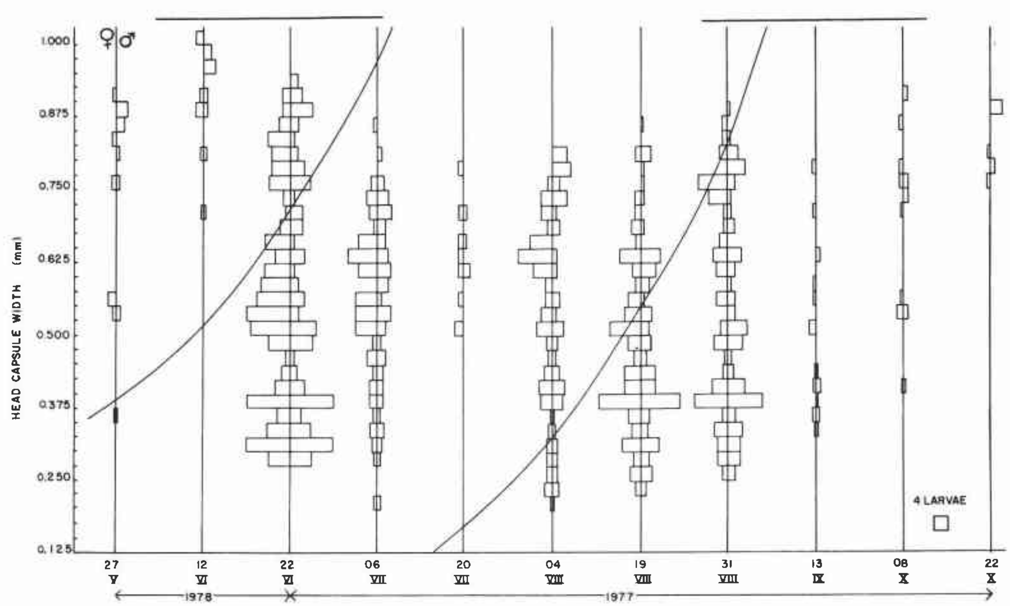

FIG. 4. Size frequency distribution of head capsule widths of *Heterocloeon curiosum* in the South Anna River. Curved lines indicate proposed generations. Horizontal lines indicate adult flight periods. The head capsule width of recently hatched first-instar larvae was 0.100–0.130 mm. Sex could be determined for larvae with head width > 0.5 mm.

generations. This interpretation was aided by rearing and noting head capsule widths of molting individuals in the last five instars. The number of instars was the same in both rivers. Also, there was no difference in the number of instars between sexes. The number of instars for *H. curiosum* was considerably less than that reported for other mayflies: 16–19 for *Choroterpes mexicanus* (McClure and Stewart 1976), 19–23 for *Tricorythodes minutus* (Newell and Minshall 1978), and 27 for *Baetis vagans* (Murphy 1922). Our data are most similar to those of Benech (1972), who studied *Baetis rhodani* in a trout stream in the Pyrenees, and noted 9–14 larval instars with 11 or 12 being most common.

Dyar's rule (1890) was not followed by larvae in either river, because a curved line resulted when the logs of the mean head capsule width were plotted versus instar number. However, growth appeared to be consistent at both study sites. There was a factor of increase of 1.16 and 1.13 in the NAR and SAR, respectively. McClure and Stewart (1976) reported a progression factor of 1.16–1.20 for *Choroterpes mexicanus*.

Feeding habits

A comparison of the feeding habits of *H. curiosum* larvae in each river (Figs. 5 and 6) showed that detritus was the major component of the diet followed by diatoms in the NAR, in contrast with diatoms followed by detritus in the SAR. In the NAR gut contents consisted of 56% detritus (range 40–85%), 42% diatoms (range 10–65%), and 3% filamentous algae (range 0–5%). In the SAR diatoms constituted 58% of the gut contents (range 25–85%), detritus 38% (range 15–75%), and filamentous algae 3% (range 0–15%). The differences in feeding habits of *H. curiosum* in the two rivers probably reflected differences in species composition and seasonal trends of periphyton communities occurring on different substrates. In the SAR larvae probably fed more on the epiphytic diatom growths and detrital accumulations on strands of *Podostemum*, but in the NAR larvae fed on epilithic algae and detritus.

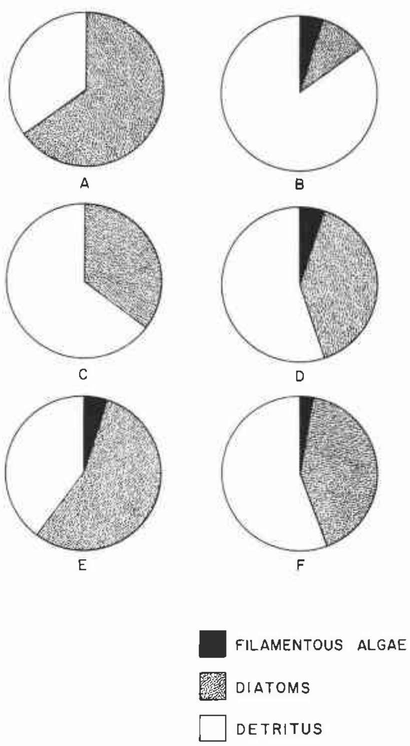

FIG. 5. Feeding habits of *Heterocloeon curiosum* in the North Anna River. Results are expressed as the percent of the total volume of gut contents. Larvae were grouped into two size categories by head capsule widths (millimetres) and three temporal categories as follows: A, 0.525–0.725, 2 June 1977 (N = 5); B, 0.750–1.000, 2 June 1977 (N = 1); C, 0.525–0.725, 6 July 1977 (N= 6); D, 0.525–0.725, 14 September 1977 (N = 5); E, 0.750–1.000, 14 September 1977; F, average of all larvae.

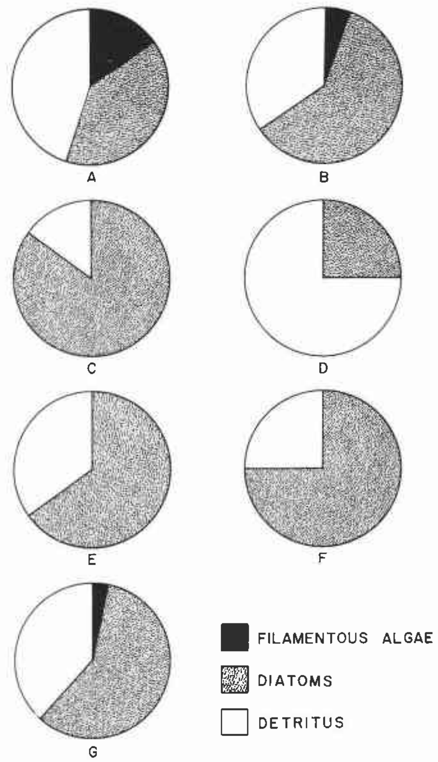

FIG. 6. Feeding habits of *Heterocloeon curiosum* in the South Anna River. Results are expressed as the percent of the total volume of gut contents. Larvae were grouped into two size catogories by head capsule widths (millimetres) and three temporal categories as follows: A, 0.525–0.725, 12 June 1978 (N = 5); B, 0.750–1.000, 12 June 1978 (N = 4); C, 0.525–0.725, 4 August 1977 (N= 3); D, 0.750–1.000, 4 August 1977 (N = 2), E, 0.525–0.725, 13 September 1977 (N = 4); F, 0.750–1.000, 13 September 1977 (N = 3); G, average of all larvae.

Physical–chemical parameters

Results of physical–chemical analyses are summarized in Table 1. The mean annual temperature of the NAR was approximately 1°C higher than the SAR. The NAR was 1–4°C warmer from May to December and 1.5°C cooler from January to April as compared with the SAR (Fig. 7). During August, water temperature dropped suddenly in the SAR from 27.0 to 23.0°C. On the same date the temperature was 27.0°C in the NAR, unchanged from the previous reading.

There were dramatic differences in the mean daily discharges of the two rivers during the study period (Table 1 and Fig. 8). Drought occurred during the summer of 1977. The discharge of both rivers was very low, and there was a significant drop in the water level of

TABLE 1. Basic physical and chemical properties of the North and South Anna rivers from June 1977 to June 1978

Parameter	North Anna River Mean	North Anna River Range	South Anna River Mean	South Anna River Range
Mean daily discharge (m^3/s)	12	1–260	7	2–77
Temperature (°C)	18.7	2.5–29.0	17.6	4.0–28.0
Dissolved oxygen (ppm)	9.8	6.0–13.5	9.5	6.5–13.0
Dissolved oxygen saturation (%)	105	79–127	100	78–120
Total alkalinity (ppm $CaCO_3$)	18	12–29	26	15–35
Total hardness (ppm $CaCO_3$)	38.6	6.7–70.3	42.8	14.0–71.9
Hydrogen ion concentration (pH)	7.00	5.90–7.70	7.07	6.40–8.05
Specific conductance (μmho*/cm)	61	40–93	69	12–120
Orthophosphate (ppm)	0.3	0.00–0.06	0.08	0.00–0.40
Total phosphate (ppm)	0.52	0.00–3.56	0.51	0.07–2.64
Nitrate nitrogen (ppm)	0.615	0.000–3.420	0.443	0.127–0.707
Ammonia nitrogen (ppm)	0.042	0.000–0.096	0.018	0.000–0.954
Sulfate (ppm)	11	8–15	11	5–19
Calcium (ppm)	2.66	1.70–3.70	1.75	1.10–2.40
Iron (ppm)	0.30	0.20–0.50	0.90	0.50–1.20
Magnesium (ppm)	7.66	0.50–15.00	9.1	2.30–16.00
Manganese (ppm)	0.06	0.00–0.20	0.08	0.00–0.10
Sodium (ppm)	3.38	1.50–5.00	5.13	3.30–9.00
Potassium (ppm)	2.68	1.50–7.00	2.28	1.10–5.00
Zinc (ppm)	0.02	0.00–0.10	0.01	0.00–0.03

*1 mho = 1 S.

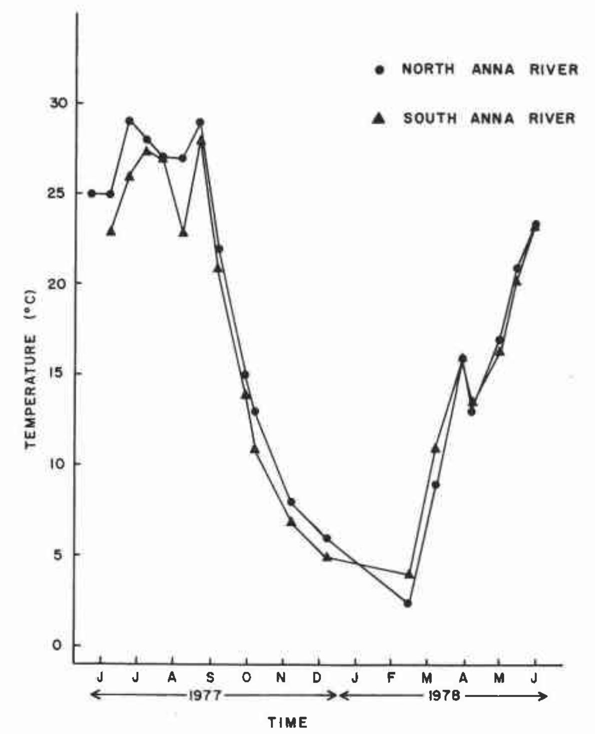

FIG. 7. Water temperatures in the North and South Anna rivers.

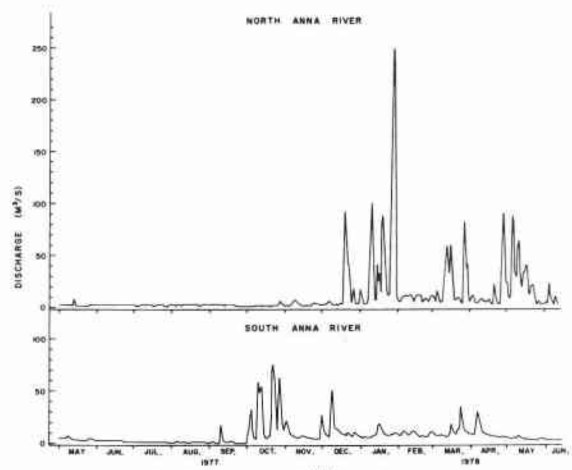

FIG. 8. Mean daily discharges of the North and South Anna rivers.

Lake Anna. There was ample rainfall again in the fall, and both rivers and the reservoir returned to normal levels. While the level of Lake Anna was below normal only the minimum amount of water required by law was released from the dam into the NAR, resulting in very uniform discharge. However, during the same period the discharge of the SAR still fluctuated according to precipitation in the basin, even though the overall discharge was below normal. During the winter after Lake Anna returned to its normal level, the NAR was characterized by rapid, large fluctuations in discharge. Apparently, the management practice is to release excess water from Lake Anna as quickly as possible, rather than releasing it slowly over a longer period. During the same period the discharge of the SAR was more constant, with moderate fluctuations indicative of local precipitation patterns.

Dissolved oxygen concentrations averaged at or above saturation, and both rivers contained soft water with circumneutral pH. Specific conductance was similar in both rivers. A detailed discussion of water chemistry is beyond the scope of this paper because there are so many factors that can interact to affect the chemistry of water. Although there were differences in nutrient and metal concentrations between the two rivers, it would be difficult to determine whether these differences were caused by the impoundment of the NAR, or whether they reflected differences in geology or human activities in the two basins. Although very little information is available on water quality criteria for insect life, it appears that neither the NAR nor the SAR exhibits any chemical properties which would be limiting factors for insect life (Anonymous 1976).

Discussion

Based upon the significantly higher density ($P = 0.01$) of larvae in the SAR, we hypothesize that there must be some factor or factors limiting the success of *H. curiosum* in the impounded NAR. Other studies have shown that mayflies are adversely affected by the flushing and scouring effects of water flow fluctuations below dams (Radford and Hartland-Rowe 1971; Trotsky and Gregory 1974). Although the erratic discharge pattern of the NAR is probably detrimental to *H. curiosum*, we do not believe that this factor alone accounts for the twofold difference in standing crop. In the studies by Radford and Hartland-Rowe (1971) and Trotsky and Gregory (1974) the discharge fluctuations occurred daily throughout the year because the dams were used for hydroelectric power generation. In the NAR the erratic discharges occurred in the winter and spring when natural spates are more likely to occur. Hynes (1970) described many anatomical and behavioral adaptations that enable invertebrates to endure temporary spates, including the fusiform body shape of baetid mayflies and the habit of using the hyporheic zone as a refugium.

Another factor that could be causing the difference in density of *H. curiosum* is the difference in the aquatic macrophytes of the two rivers. In the SAR, *Podostemum ceratophyllum* averaged 220 g dry weight/m^2 during its growing season (April–November) and ranged as high as 700 g dry weight/m^2. *Podostemum* probably used to occur throughout the NAR but was eliminated many years ago by a source of acid and metal mine drainage. Lake Anna inundated the source of the mine drainage and significantly improved the quality of downstream water by acting as a sink for sediment and metals (Simmons and Voshell 1978), but *Podostemum* has not recolonized the NAR. The macrophyte probably contributes to the success of *H. curiosum* by providing both protection and food. In the only other reference to the ecology of *H. curiosum*, Müller-Liebenau (1974) reported that the larvae were associated with mats of *Podostemum* and Edmunds et al. (1976) suggest that this macrophyte is the typical habitat for all three species in the genus. However, we cannot entirely attribute the difference in density of *H. curiosum* to the difference in the macrophytes of the two rivers. In the SAR, where all of the choices in habitat were readily available to *H. curiosum*, the indices of preference for depth, current, and substrate size were all higher than the index for vegetation. This indicates that vegetation may be of secondary importance to other habitat factors which are equally available in the NAR.

Food is a factor which cannot be overlooked in an attempt to explain the lesser success of *H. curiosum* in the NAR. Larvae in the SAR fed primarily upon diatoms, whereas larvae in the NAR fed primarily upon detritus which has a lower caloric content and contains more refractile components. Anderson and Cummins (1979) convincingly demonstrated that food quality and quantity affects growth rate, and that growth rate affects survivorship by determining size at maturity (fecundity is positively correlated with female size). Since the exact nutritional requirements of most aquatic insects have not been established, we cannot conclude whether the diet of *H. curiosum* in the NAR is adequate for its normal growth rate. Cummins and Klug (1979) reported that many collectors and scrapers are rather facultative and merely increase the consumption of low quality food to compensate for its decreased nutritional benefit. The similarity in the number of instars and growth progression factors between larvae in the two rivers would seem to indicate that the diet of *H. curiosum* larvae was adequate in both rivers.

Temperature seems to be the factor most likely to be causing the differences in the success of *H. curiosum* in the two rivers. The delayed emergence of the second generation of *H. curiosum* from the NAR illustrates the effect of temperature on its life history. In the NAR, the second generation emerged in October rather than in August as in the SAR. The August emergence in the SAR was probably initiated by a sudden drop in temperature that did not occur in the NAR (Fig. 7). The release from the warm surface waters of Lake Anna delayed the normal cooling of the NAR until fall. When *H. curiosum* emerged from the NAR in October, the temperature was about the same as it was in the SAR in August.

Sweeney and Vannote (1978) have shown that changes of only 1–2°C, either warmer or cooler, from the normal temperature regime can reduce adult size and fecundity, and they have suggested that temperature increases of 2–3°C could eliminate species. They have hypothesized that the distribution of hemimetabolous aquatic insects, both locally within drainage systems and over large geographic areas, may be partly limited by lowered fecundity as adult size decreases in nonoptimal temperature regimes.

In our study we found that the fecundity was very significantly higher ($P = 0.0001$) for the first generation than the second generation and for both generations from the SAR. In bivoltine species, members of the first generation are often larger and contain more eggs than members of the second generation (Benech 1972; Clifford and Boerger 1974; Sweeney 1978). Benech (1972) reported that members of *Baetis rhodani*'s spring generation contained up to 4500 eggs, but members of the summer generation contained as few as 200 eggs.

However, it seems very unnatural for a species to contain significantly different numbers of eggs in two rivers located only about 10 km from each other. The fecundity of *H. curiosum* from the NAR was only 42 and 73% of those from the SAR for the first and second generations, respectively. Because of the large volume of water retained in Lake Anna, the NAR was slightly warmer in the summer and fall and slightly cooler in the winter and spring. Although the temperature differences were small, we believe that they were sufficient to cause significant differences in fecundity and, hence, density of *H. curiosum* in the two rivers.

The long-term effects of the reduced fecundity of *H. curiosum* in the NAR remain to be investigated. It seems likely that there is a minimum threshold for fecundity, below which a species would be eliminated from the community. In summary, we have shown that surface-release reservoirs may have subtle but significant effects on the life histories of mayflies. We suggest that the effects of surface-release reservoirs on life histories of benthic macroinvertebrates should be incorporated into the environmental impact assessment of future reservoir projects and the management practices below existing projects.

Acknowledgements

We thank Dr. Charles R. Parker, Department of Entomology, Royal Ontario Museum, for his assistance during this study, particularly with data analysis. Dr. George M. Simmons, Jr., Department of Biology, Virginia Polytechnic Institute and State University, was kind enough to loan us several pieces of sampling equipment and to permit us to conduct our water chemistry analyses in his laboratory.

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