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Benthic macroinvertebrates of a fluctuating reservoir

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SUMMARY. Benthic macroinvertebrate distribution, abundance, and composition were observed in a fluctuating (7.7 m) central Wisconsin, U.S.A., reservoir during 1973–74. Chironomidae and Oligochaeta represented 98% of the total fauna by number. The chironomid, *Chironomus plumosus*, and an oligochaete, *Limnodrilus*, each averaged 36% of the total benthic biomass. Annual mean numbers and biomass in areas exposed to air, exposed to ice cover, or remaining inundated were $3025/m^2$ ($1.8 g/m^2$), $4311/m^2$ ($4.5 g/m^2$), and $8558/m^2$ ($16.0 g/m^2$), respectively. A substantial portion of the benthic fauna was stranded and subsequently decreased rapidly in drying and frozen substrates exposed to air. Total benthic numbers and biomass were greatest immediately below the drawdown limit.

Recolonization required 3 months (mid-March to mid-June, 1974) to attain pre-drawdown values for numbers and biomass, and subsequently both were greater after reinundation than before the substrate was exposed. Recolonization of areas exposed to the air was greater in substrates containing large amounts of organic matter than in sandy areas containing little organic matter. Sorting and transportation of sediments redistributed organic materials from the regulated zone to below the drawdown limit, and macrophytes were eliminated from the regulated zone. When compared to other reservoirs and lakes, the density of benthos in the Big Eau Pleine Reservoir is neither high nor low. However, when compared with non-fluctuating reservoirs the number of Ephemeroptera, Plecoptera, Trichoptera, Amphipoda, and Gastropoda was low.

Introduction

Fluctuations in water level influence benthic populations by changing water chemistry (McLachlan, 1970), eliminating macrophytes in the regulated zone (Grimas, 1965; Quennerstedt, 1958), altering substrates by erosion in the regulated zone (Grimas, 1961; Cowell & Hudson 1968), and by exposing substrates to air or ice cover (Paterson & Fernando, 1969). Successful establishment of benthic fauna in regulated zones depends upon water-level management of minimum pool levels, duration and season of drawdown, the ability of benthic fauna to adapt to water fluctuations by following receding water levels, their survival in areas exposed to air or ice cover, and their recolonization of inundated areas after refilling.

From June 1973 to August 1974, the Big Eau Pleine Reservoir fauna was studied to determine the effect of water level fluctuation on the dominant benthic macroinvertebrate populations. The reservoir is located at 44° 43′ N, 89° 45′ W, in Marathon County Wisconsin, U.S.A. The reservoir, when full,

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covers 2832 ha, is 29.8 km long, and has a maximum depth of 14 m. Flow augmentation of the Wisconsin River for generation of hydroelectric power has been the main purpose of the reservoir since its construction in the mid-1930s. During the period from 1965 to 1974, water drawdown averaged 7.5 m, ranging from 3.0 to 10.2 m, and generally began in June or July, reaching a minimum in February or March, with refilling to maximum capacity in April. This water fluctuation differentiates three benthic habitats: (1) a substrate exposed to atmospheric conditions during summer and autumn drawdown before ice cover, (2) a substrate covered with massive ice sheets during winter drawdown, and (3) a substrate that remains inundated below the drawdown limit.

Methods

Six sampling stations were selected for study (Fig. 1). Two stations (A2 and A3) in or near the old river channel, remained inundated during maximum drawdown. The remaining stations were seasonally exposed to air (A5 and A6) or to ice cover (A1 and A4) during drawdown depending on whether drawdown occurred before or after ice had formed at the surface. Each station was sampled twice a month while inundated and once a week when exposed to the air until the benthic macroinvertebrates were absent in two successive weekly samples. Stations exposed to air were again sampled twice a month after inundation during refilling.

Four replicate Ekman grabs ($232\ cm^2$) were collected to a sediment depth of about 10 cm at each station in open water, through the ice, and in unfrozen exposed substrates. A metal ice spade was used to collect duplicate $232\ cm^2$ samples from frozen, exposed substrates. Each replicate grab was washed through a U.S. Standard No. 30 sieve and preserved in a mixture of 70% ethanol and 5% formalin. Individual animals of each taxon were counted, centrifuged as a taxonomic group at a relative centrifugal force of 650 for 3 min, including acceleration and deceleration, to remove excess moisture, and weighed to the nearest 0.1 mg.

The Walkley–Black (1934) method was used for determining organic carbon in the sediment fraction that was smaller than 2 mm diameter. A hydrometer method (Bouyoucos, 1927) was used for determining the percentage, by weight, of sand, silt, and clay fractions. Detritus was considered to be the percentage by weight of non-mineral matter retained by a 2 mm mesh sieve.

Geometric mean values and 95% confidence limits for numbers and biomass are based on logarithmic transformations ($\log_{10}$) of the original data.

Results

Drawdown began on 21 June 1973, and minimum pool depth was reached 256 days later on 3 March 1974. The water level dropped 7.7 m leaving a minimum head of 2.1 m at the dam. Two stations (A5 and A6) were

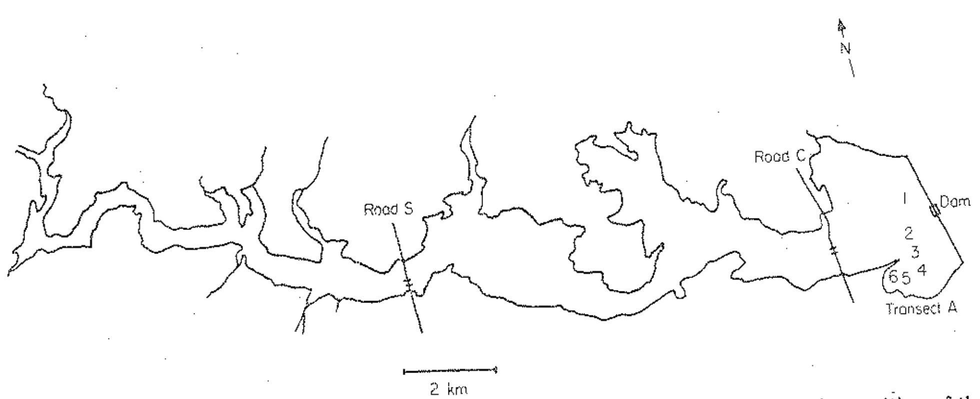

FIG. 1. Map of the Big Eau Pleine Reservoir showing sampling stations and the relative position of the dam and major roadways.

TABLE 1. Geome…
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Date		Stati… 1
August	N	514 (17…
	B	5.2 (2.8
September	N	523 (46
	B	3.2 (0.…
October	N	539 (10
	B	6.2 (2.
November	N	11 (78
	B	10 (3.
December	N	69 (2…
	B	4.… (0
January	N	–
	B	–
February	N	7 (…
	B	0 (…
March	N	–
	B	–
April	N	7 (
	B	1 (
May	N	(
	B	
June	N	
	B	
July	N	
	B	
August	N	
	B	

TABLE 1. Geometric means (and 95% confidence limits) for numbers (N) and biomass (B) at each station in the Big Eau Pleine Reservoir from August 1973 to August 1974

Date		Station 1	2	3	4	5	6
August	N	5146 (1752–8469)	861 (236–2115)	5107 (1465–9937)	5889 (2438–11 395)	3680 (926–8437)	5687 (1003–9720)
	B	5.2 (2.8–9.6)	3.0 (0.9–10.3)	10.1 (0.6–19.6)	5.0 (0.1–14.4)	2.2 (0.3–8.7)	4.1 (1.8–9.4)
September	N	5231 (4675–5853)	1477 (847–3172)	4746 (1030–9136)	4158 (3053–5662)	3625 (988–6391)	0
	B	3.2 (0.2–9.9)	5.5 (0.2–12.6)	4.7 (1.1–9.3)	2.5 (1.5–4.1)	1.6 (0.6–4.3)	0
October	N	5395 (1003–8947)	2359 (983–5451)	8337 (1334–13 593)	2553 (1011–4859)	1909 (1067–3416)	0
	B	6.2 (2.1–10.3)	13.1 (4.3–19.0)	10.0 (2.4–18.6)	3.4 (0.6–6.7)	1.0 (0.6–1.3)	0
November	N	11 366 (7820–14 865)	2160 (993–3965)	12 213 (8651–18 463)	3847 (892–8253)	735 (405–1218)	0
	B	10.9 (3.5–19.9)	15.4 (4.6–19.0)	16.1 (9.8–22.4)	2.6 (1.1–5.9)	0.4 (0.05–8.6)	0
December	N	6934 (2837–11 947)	3957 (1008–8385)	9073 (2499–13 029)	2180 (752–6321)	0	0
	B	4.5 (0.9–7.9)	19.6 (12.2–31.6)	15.0 (11.3–21.5)	2.8 (0.5–15.7)	0	0
January	N	–	2583 (1363–3476)	14 811 (9473–17 099)	2584 (879–5394)	0	0
	B	–	14.0 (8.6–21.0)	15.4 (11.3–23.4)	2.5 (0.6–8.2)	0	0
February	N	75 (34–325)	3303 (1121–5784)	14 811 (10 032–33 190)	2584 (88–231)	0	0
	B	0.2 (0.02–8.5)	11.4 (3.0–28.7)	22.8 (5.0–43.1)	0.2 (0.01–4.0)	0	0
March	N	–	1765 (847–2975)	19 848 (9334–29 775)	301 (202–475)	0	0
	B	–	5.0 (0.9–12.2)	25.6 (9.9–37.6)	0.8 (0.1–5.4)	0	0
April	N	717 (392–1274)	2669 (1076–3989)	22 072 (19 056–25 312)	3506 (1638–5398)	194 (103–254)	0
	B	1.3 (0.3–9.3)	17.2 (4.3–38.5)	27.0 (12.4–51.6)	3.8 (0.8–13.2)	0.14 (1.1–0.005)	0
May	N	1926 (1367–2673)	3155 (1122–7686)	23 758 (15 546–57 396)	4447 (3845–5143)	475 (328–674)	376 (134–1057)
	B	2.4 (0.8–7.4)	25.1 (20.6–30.5)	34.7 (15.0–81.2)	4.5 (0.9–23.0)	0.6 (0.03–7.8)	1.7 (0.1–11.3)
June	N	5989 (3174–8979)	4495 (1839–7936)	14 884 (7469–19 746)	5825 (3112–9488)	3413 (1005–6498)	6374 (4328–10 833)
	B	5.3 (1.1–25.6)	15.5 (2.5–27.4)	18.2 (4.0–44.7)	6.8 (1.1–17.7)	2.0 (0.4–8.5)	3.6 (0.2–9.4)
July	N	6433 (784–37 930)	6934 (3944–12 191)	13 192 (7596–48 652)	6874 (4830–10 473)	6369 (5097–7958)	8117 (6743–11 864)
	B	7.2 (1.0–16.2)	19.0 (3.1–41.7)	15.4 (9.0–26.0)	9.6 (0.9–24.1)	5.5 (2.0–15.0)	6.0 (3.0–12.0)
August	N	5433 (3829–9578)	4238 (2477–7249)	9414 (9040–9803)	3128 (2193–5471)	4883 (2178–8789)	23 147 (6543–45 382)
	B	5.4 (4.7–6.2)	16.1 (10.5–24.5)	11.0 (6.4–18.9)	5.6 (1.7–15.8)	3.0 (2.6–3.5)	11.1 (1.1–24.1)

exposed to air during the summer and the substrates at two others (A1 and A4) were covered with massive ice sheets during winter. The two deeper stations (A2 and A3) remained inundated throughout the study. Total surface area at maximum drawdown was 16.7% (472 ha) of the full pool area of 2832 ha.

The reservoir was eutrophic with dissolved oxygen supersaturation in summer and fish dying in winter (Bartelt *et al.*, 1973; Joy, 1975). Secchi disc transparency was 1 m or less during most of the study period but it increased to 2 m during refilling in late May. A rapid decrease in transparency after refilling was completed probably resulted from a bloom of blue-green algae in the reservoir (Bartelt *et al.*, 1973) rather than turbidity caused by erosion in the regulated zone. Sheltered bay areas supported terrestrial plants when the substrate was exposed to air. Aquatic macrophytes were virtually non-existent in the reservoir because of water fluctuations.

Dominant benthos

The benthic macroinvertebrate fauna of the reservoir was dominated by the Chironomidae and worms of the subclass Oligochaeta, comprising 98% of the total benthic fauna by number. *Chironomus plumosus* (Meigen), and an oligochaete, *Limnodrilus*, averaged 37 and 35% respectively of the total benthic biomass for all stations during the study.

Benthos exposed to air, ice cover, or remaining inundated

A substantial portion of the benthic fauna did not follow receding waters but remained *in situ*, and subsequently numbers and biomass decreased rapidly in drying and frozen substrates (A5 and A6) exposed to air. The greatest geometric mean number and biomass of benthos stranded and destined to die in exposed substrates was $5687/m^2$ ($4.1\ g/m^2$) at station A6 (Table 1). Total benthos at station A6 decreased from $5687/m^2$ 7 days after the substrate was exposed, to zero within 35 days. The chironomid, *Polypedilum* sp., and *Limnodrilus*, decreased in number from 1496 and $8137/m^2$, respectively, to zero within 35 days after the substrate was exposed to air on 2 August 1973, (Fig. 2). During the same period, semi-aquatic Diptera (Ceratopogonidae) and terrestrial Diptera increased from zero to $3024/m^2$ (Fig. 2).

The last surviving larvae of *C. plumosus* collected from a depth of 8 cm in exposed

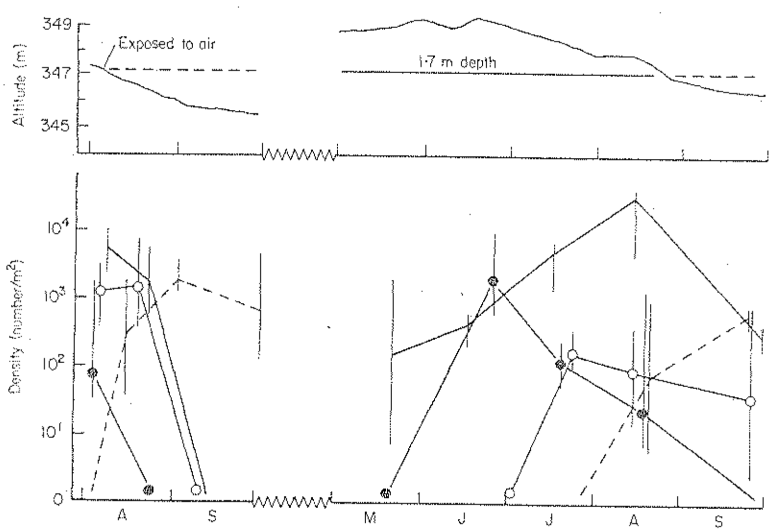

FIG. 2. Relation of benthic fauna density (geometric mean numbers/m^2) and water level at station A6. *Limnodrilus* ———; *C. plumosus* —●—; *Polypedilum* —○—; Terrestrial dipterans – – – –. The vertical lines represent 95% confidence limits.

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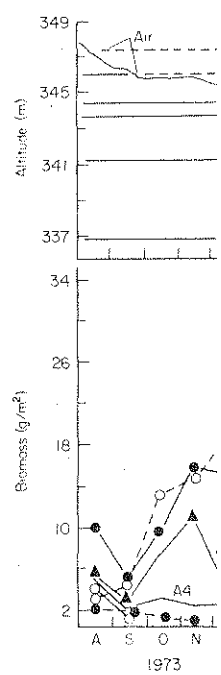

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substrate at station A6 were all in the fourth instar, which indicates the increased ability of larvae in this instar to survive in substrates exposed to air. The mean individual wet weight of *C. plumosus* increased from 0.4 mg, 5 days before exposure, to 35.8 and 37.4 mg, 7 and 14 days respectively after being exposed to the atmosphere.

Chironomid and oligochaete density decreased in frozen substrates exposed to ice cover (A1 and A4), but because of the insulation value of ice and snow, some individuals survived and increased their density through reproduction during reservoir refilling. Survival of benthos under ice cover increased from 2 to 4% and 4–21% as the depth of frozen substrate decreased from 45 to 7 cm and 7–3 cm, respectively. Three months (mid-March to mid-June, 1974) were required for numbers to increase to pre-drawdown values.

Numbers (Table 1) and biomass (Fig. 3) of benthic fauna were greatest at stations remaining inundated (A2 and A3), and were least at stations exposed to air (A5 and A6). At stations exposed to air (A5 and A6), exposed to ice cover (A1 and A4), or remaining inundated (A2 and A3) the arithmetic mean values, with 95% confidence limits, were 1.8±0.8, 4.5±3.1, and 16.0±7.0 g/m^2 respectively. The arithmetic mean numbers of benthos at stations exposed to atmosphere, exposed to ice cover, or remaining inundated, averaged 3025±372, 4311±863, and 8558±1629/m^2 respectively. The numbers of benthos later decreased to zero at stations exposed to air while there was a smaller reduction in numbers at stations exposed to ice cover (Table 1). Numbers at inundated stations remained relatively constant.

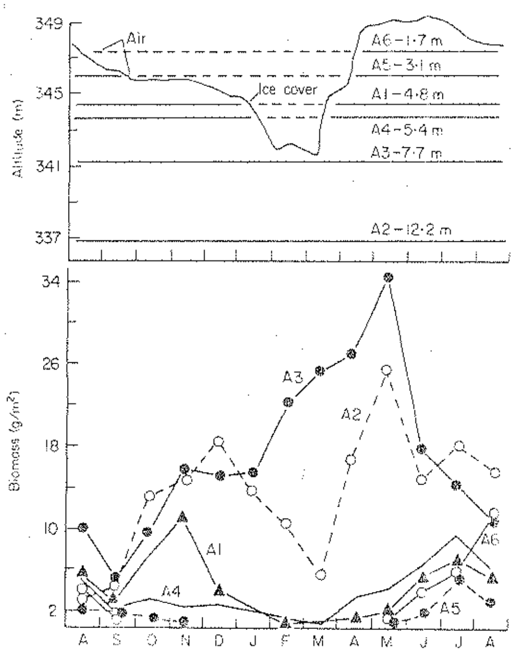

FIG. 3. Relation between the arithmetic mean benthos biomass and water level at stations A1–A6. Geometric means and 95% confidence limits for biomass and numbers are given in Table 1.

Total numbers of benthos and biomass were greatest immediately below the drawdown limit (A3). The annual arithmetic mean numbers and biomass during the 13-month study period were 13 781±4276/m^2 and 17.6±6.3 g/m^2 at station A3, just below the drawdown limit. This station was exposed to ice cover during the 1970–72 drawdowns but remained inundated during the 1973 and 1974 drawdowns. At the deepest station (A2) in the old river channel, 4.6 m below the 1974 drawdown limit, the arithmetic mean numbers and biomass were 3336±1024/m^2 and 14.3±5.7 g/m^2.

All genera collected before the drawdown were present after refilling, and total density and biomass were greater after refilling, in the spring of 1974, than before drawdown at all stations exposed to air and ice cover.

During drawdown, pelecypods became stranded in substrate exposed to air. The clam, *Lasmigona complanata* (Barnes), failed to move with the receding water. It burrowed into the substrate after exposure to air, and some individuals died within 5 days. The clams had adequate mobility to follow receding water but many failed. Many of the clams were observed moving consistently toward land rather than to deeper waters. In 1 h I collected by hand 50 clams stranded near station A6. Only one individual of *L. complanata* was captured during the study in an Ekman grab sample.

Chironomids and oligochaetes other than *C. plumosus* and *Limnodrilus* decreased to zero in substrates exposed to the air and were usually found in greater numbers than before the drawdown. The oligochaetes *Stylaria* and *Pristina* are active swimmers capable of moving with receding waters. Both were collected from inundated substrate but not after the substrate was exposed to air.

Vertical movement of benthos in substrates

The vertical movement of *C. plumosus* to deeper layers of substrate exposed to the atmosphere at station A6 was accompanied by a decrease in activity and darkening of body colour. In substrates exposed to air, *C. plumosus* were collected only at depths of 2, 5, and 8 cm after 7, 14, and 21 days respectively, indicating downward movement which was accompanied by a darkening of the red body colour. Benthos was not found below 9 cm in substrates exposed to air; however, *C. plumosus* was found alive at 15 cm in substrate exposed to ice cover.

When exposed to air, *Limnodrilus* may have burrowed into the substrate to avoid desiccation. Larger *Limnodrilus* decreased in abundance more rapidly than smaller *Limnodrilus* when the substrate was exposed. The mean individual weight of *Limnodrilus* was 0.6 mg, 4 days before and 7 days after the substrate was exposed to air, and then it decreased to 0.3 mg after 15 days and to 0.1 mg 30 days after the substrate was exposed.

After spring refilling was completed, *Limnodrilus* reproduced, which resulted in a large increase in population density during the following 4 months. All *Limnodrilus* collected at station A6 during the first sampling period, 17 May 1974, were sexually mature with an average individual weight of 6.6 mg. Average weight decreased rapidly on succeeding sampling dates because reproduction resulted in a large number of small worms. The greatest increase in numbers occurred from 9 July to 12 August, 1974, a 34-day period in which the geometric mean number of *Limnodrilus* increased from $861/m^2$ (538–1378, 95% confidence limits) to $21\,011/m^2$ (11 058–39 921, 95% confidence limits). This considerable increase was related to the large number of mature worms present in May 1974. Kennedy (1966) found that *Limnodrilus* hatched from its cocoon in 3–4 months. Mature *Limnodrilus* at stations remaining inundated (A2 and A3) were present throughout the year.

Discussion

Benthos recolonization of areas inundated after refilling probably was partially dependent on the nature of the substrate. From shallow to deep water the substrate composition changed from sand, muddy sand, sandy mud, and organically enriched mud, with the exception of sheltered bays which progressed from sandy mud to muddy sand. Macrobenthos distribution was primarily in sand and organic silt-clay substrates. Benthos recolonized more rapidly and was of greater density in substrates containing large amounts of detritus or organic matter (A6) than in sandy substrates (A5). Sandy bottoms are ordinarily considered unstable habitats for most benthos.

Survival of benthos in frozen substrates (A1 and A4) was related to the substrate type or the depth to which the substrate was frozen or both. Substrates composed of much detritus froze deeply. The greatest benthos survival under ice cover was 21% of the monthly average. Grimas (1961) reported that 80% of the benthic fauna was alive after 3 months of exposure to ice cover during mid-winter drawdown in Lake Blasjon, Sweden.

There is indication that some chironomids and possibly some oligochaetes survive long periods of desiccation or burrow deeper into the substrate to avoid desiccation or freezing. *C. plumosus* generally inhabits the upper 6 cm of substrate (Kajak & Dusoge, 1971) but it was collected from the Big Eau Pleine Reservoir at a depth of 15 cm in substrate exposed to ice cover (A1). Chironomid tunnels were found deeper than 20 cm.

The small numbers of larval chironomids surviving drawdown at station A5 and A6 were probably of little importance in recolonization because of the large numbers of chironomid larvae surviving below the drawdown limit. The near shore swarming behaviour of adults during breeding (Hilsenhoff, 1966) resulted in rapid recolonization to the littoral area by egg deposition.

The rate of recolonization of oligochaetes could be greatly increased if mature individuals survived the drawdown in the exposed substrate and reproduced after the substrate was again inundated.

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Large *Limnodrilus* burrow into the substrate (Kajak & Dusoge, 1971) and are probably capable of surviving for several months (Paterson & Fernando, 1969). In the Big Eau Pleine Reservoir the presence of only mature *Limnodrilus* after refilling in spring suggests either the movement of mature *Limnodrilus* to the shallow water, or the survival of mature worms deep in the exposed substrate (A6), which had emerged to breed when the substrate was inundated.

Benthos generally decreases in density from the littoral to the profundal zone in lakes and non-fluctuating reservoirs, but in fluctuating reservoirs the greatest abundance of benthos is found immediately below the drawdown limit (Grimas, 1961; Fillion, 1967) as in the Big Eau Pleine Reservoir. During April–August, 1974, the weight distribution of benthos in the Big Eau Pleine Reservoir increased with an increase in water depth. Benthos biomass represented 8% by weight at the 2.5 m depth zone, 20% at the 5 m depth zone, and 72% at the 10 m depth zone. The distribution of benthos was nearly reversed in non-fluctuating Lake Ashtabula Reservoir, North Dakota, in which animals in the 0–3 m depth zone accounted for 53% by weight of all animals from April to August, 1969, 37% in the 3–8 m depth zone, and 9% in the 8–12 m depth zone (Peterka, 1972).

The greatest number of genera (21) in the Big Eau Pleine Reservoir was collected just below the drawdown limit (A3). The least number of genera (13) was collected from the old river channel, the deepest station (A2). Grimas (1961) found the majority of species in the upper littoral zone of unregulated Lake Ankarvattnet contrasting with regulated Lake Blasjon where the majority of species occurred below the drawdown limit. Fillion (1967) found more taxa of Chironomidae species above the drawdown limit in the littoral zone of Barrier Reservoir, Canada.

The density of benthos in the Big Eau Pleine Reservoir can be regarded as neither high nor low. However, when compared with non-fluctuating reservoirs in North America, the number of major taxa (Ephemeroptera, Plecoptera, Trichoptera, Amphipoda, Gastropoda) is low. The range of benthos densities reported in the literature for reservoirs and lakes varies greatly. In Keystone Reservoir, Oklahoma, the average monthly density was $1319/m^2$ (Ransom & Dorris, 1972). This contrasts with the lowest average monthly density of $2018/m^2$ and the greatest average monthly density of $13781/m^2$ in the Big Eau Pleine Reservoir. Cowell & Hudson (1968), however, recorded Chironomidae larvae alone at $60620/m^2$ in Lake Francis Case Reservoir, part of the Missouri River System.

Acknowledgments

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