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The ecology and distribution of *Hexagenia munda* Eaton (Ephemeroptera) in Stone Mountain Lake, Georgia, U. S. A.

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With 5 figures in the text

In 1969 when work was begun on the distribution of the nymphs of *Hexagenia munda* Eaton living in Stone Mountain Lake, Georgia (Fig. 1), an unexpected problem was discovered. All of the large nymphs showing abdominal color patterns appeared to be intergrades (Walker 1970). Before work could begin on the parameters affecting

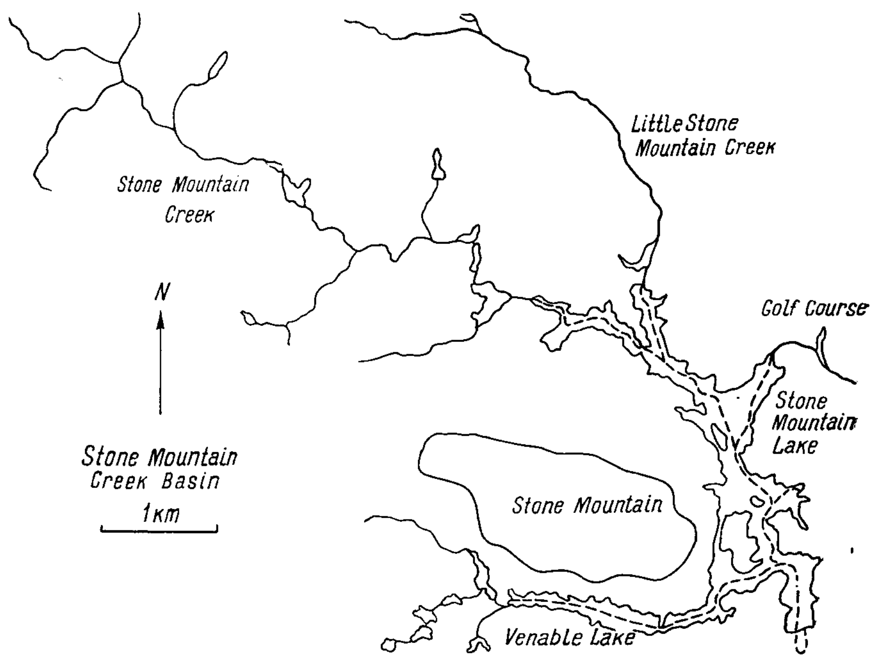

Fig. 1. A map of the Stone Mountain Creek basin, indicating the major Stone Mountain Creek tributaries and major lakes.

the distribution of the nymphal population, it was necessary to decide which of five subspecies of *H. munda* were responsible for an apparent hybrid swarm. In 1941 Spieth reported that when populations of two subspecies of *H. munda*, *H. m. marilandica*, the southern highlands burrowing mayfly, and *H. m. elegans*, the coastal plains subspecies, are geographically in contact, hybridization may occur. Since the intergrades at Stone Mountain resembled *elegans* and *marilandica*, it was thought that they might be hybrids of these two subspecies. It is known that *Hexagenia* nymphs were in Stone Mountain creeks before the lake was filled but no record of the subspecies classification is known (R a u l e r s o n 1960). However, according to B e r n e r (1950), *H. m. elegans* were collected in Decatur, Georgia, a few kilometers west of Stone Mountain.

Stone Mountain Lake lies about 16 km east of Atlanta, Georgia, at an altitude of 255 m. It is a young lake which was filled for the first time in 1964. One arm, still called by its original name, Venable Lake, which is over 100 years old, is separated from the rest of the lake by a dam, but water from Venable Lake flows by a waterfall into the lower basin. Stone Mountain Lake (including Venable Lake) has an area of 156 hectares, a maximum depth of 13 m, and is 3.4 km long. During warm months it becomes strongly stratified with a bottom temperature of 10° C and with dissolved oxygen below the thermocline of less than 1 ppm (Fig. 2). In the winter the bottom temperature may drop to 3° C and ice may form on the surface of the lake. With one exception during the last six years, every winter the lake has been drawn down from 2.4 to 4.3 m below its summer level.

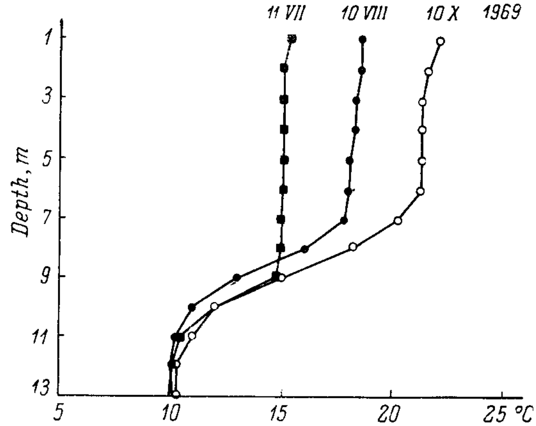

Fig. 2. Thermal profile of Stone Mountain Lake during the fall, 1969.

The lowering of the lake level leaves the bottoms of both Arm 1 and Arm 2 out of water. In Arm 2 (Fig. 3) a 12 square meter depression remained filled with water from November 1969 to March 1970 and contained a concentrated aggregation of *Hexagenia*.

To prove that an intergrade population occupied Stone Mountain Lake, it was necessary to collect male *Hexagenia* for taxonomic identification. Repeated efforts resulted in the capture of only one male in the field. Consequently, large *Hexagenia* nymphs with dark wing ads were collected and kept in laboratory cultures. Eventually, after vigorously undulating their abdomens for up to thirty minutes, the exoskeleton split dorsally and the alate subimagoes emerged in 5 sec. Although there was some mortality in the transformations from nymph to subimago and from subimago to adult, a series of male imagoes was obtained. To verify the diagnosis that they were morphological intergrades, specimens were sent to a mayfly expert, Dr. L e w i s B e r n e r, of the University of Florida. He confirmed that all the adult males showed various degrees of intergradation based on the hind wing coloration and abdominal markings.

In addition to morphological comparisons of male *Hexagenia*, laboratory and field studies showed that the Stone Mountain mayflies could not be separated into distinct subspecies. First, using a modified S c h o l a n d e r technique (S c h o l a n d e r, 1950), comparisons of respiratory rates were made of nymphs resembling *elegans* and *marilandica* (Fig. 4) and at 20° C there was no statistical difference between the two groups, but the results compare favorably with those of E r i k s e n (1963) at 13.0 ± 1.14° C for *H. limbata*. Second, young nymphs were successfully hatched in the laboratory from eggs from *marilandica*-type females artificially fertilized by sperm from *elegans*-type males. Third, no separation could be made into subspecies on the basis of habitat; nymphs collected in all parts of the lake

Fig. 3. The 12 sq. m. pool remaining in Arm 2 after winter drawdown of 1969. It contained 1199 nymphs per square meter.

were intergrades with no correlation of morphological types of intergrades with particular habitats.

When it was understood that all *Hexagenia* nymphs of Stone Mountain Lake were intergrades, 71 stations were established. Collections were made repeatedly using a Hayward dwarf orange peel grab and nymphs were found ranging in densities up to 304 per sq. m. (Fig. 5).

To determine the environmental parameters influencing the distribution of *Hexagenia* intergrade nymphs in the lake, field observations and laboratory experiments were made. These included responses of the nymphs

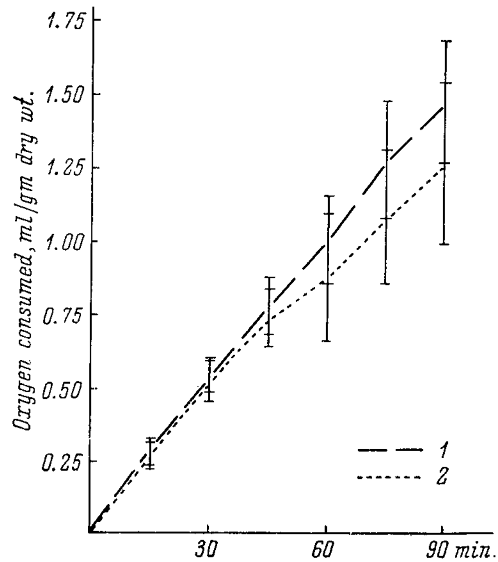

Fig. 4. Cumulative oxygen consumption at 20° C for *Hexagenia munda elegans* (*1*) and *H. m. marilandica* (*2*).

to pH, water temperature, dissolved oxygen, light, wind, depth of water, and the character of the substratum. Of these parameters, neither pH nor water temperature appeared to limit the distribution of the intergrade nymphs in the lake, which is also true of *H. limbata* (Hunt 1953; Eriksen 1963).

The conclusion that substratum type is the chief factor regulating distribution of *Hexagenia* nymphs agrees with the findings of Lyman (1943), Hunt (1953), Eriksen (1964), and others. Locations of the nymphs in the field and in substratum selection experiments both indicate that 96% of the *Hexagenia* selected a mud or sandy mud substratum with particles having a diameter of 0.05 to 2.0 mm. In no case were nymphs, neither experimentally nor in the field, found in a substratum containing more than 55% sand by weight. Apparently, substrata that were too sandy would not support the establishment of burrows. Also, nymphs would not burrow into suitable mud when it was covered with 2 cm of sand. Ninety per cent of the nymphs, both large and small, burrowed to depths of 10 cm, but only large nymphs, with an average length of 29.25 mm, burrowed to depths of 15 cm.

An interesting experiment was conducted which gives some insight into the importance of burrows to the tubiculous nymphs. Both in the field and in laboratory experiments, nymphs were negatively phototactic as previously reported by Hunt (1953). However, when provided with artificial burrows in the form of transparent glass tubes, they remained in the

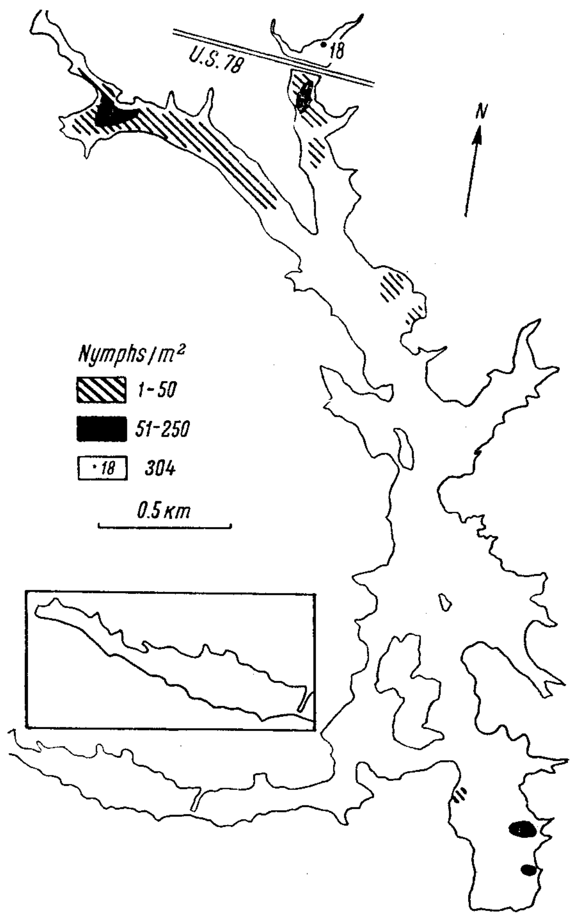

Fig. 5. Distributional map of *Hexagenia munda* nymph populations in Stone Mountain Lake showing approximate population sizes and densities.

glass tubes in the light even though cover providing darkness was available (Walker 1970).

Distribution of nymphs is also affected by biotic factors. Since nymphs are non-selective detritus feeders or «swallowers» (Turpaeva 1959), they frequent muddy bottoms that are rich in decomposing plant and animal debris. They transfer energy to consumers and in areas where predators are numerous, the distribution and density of nymphs are reduced. As found by Hunt (1953) and in this study not only do nymphs make up an important part of the diet of the crappie, *Pomoxis nigromaculatus* (Le Seur) and the bluegill *Lepomis macrochirus* (Cope), but they are also eaten by Odonata nymphs. No *Hexagenia* nymphs were found in the 100-year old Venable Lake which is confluent with an adjacent arm of Stone Mountain Lake. Since Venable Lake is regularly stocked with fish, all nymphs may have been eaten.

Nymphs were not only removed by predators at all times of the year, but their numbers were greatly reduced from June through September after large nymphs underwent transformation and left the lake as subimagoes. Upon emergence, their chief predators were birds which caused a reduction in population potential as many females were eaten before they could mate and oviposit. Strong prevailing southerly winds may have kept all but the strongest flyers from ovipositing in southern reaches of the lake, with a resultant greater concentration of nymphs in the shallow Arms 1 and 2 at the northern end of the lake.

The frequent winter drawdowns of from 2.4 to 4.3 m and an oxygen tension of less than 1.0 ppm at 7.0 m imposed severe spatial constraints on the distribution of the nymphs (Britt 1955; Eriksen 1964). Although nymphs were never found below 6.5 m, they were found in shallow areas of the lake margins that had been uncovered during the winter. The only way they could have become established in these shallow margins and in arms of the lake having a depth of less than 2.4 m (the minimum drawdown level) is by migration from deeper water after normal summer levels were reestablished which is also true for other species of *Hexagenia* (Fremling 1960; Swanson 1967).

A striking example of migration occurred in Arm 2 during late 1969 and early 1970 when the lake was drawn down 4.3 m. In Arm 2 (Fig. 3) a 12 sq. m depression remained filled with water and in it nymphs were found in densities of 1.199 per sq. m. Prior to the drawdown, between 51 and 250 nymphs per sq. m had been found so the great change in numbers must have been the result of nymphs migrating from other parts of the arm to the small depression. After the lake again filled with water from the creeks and run-off from Stone Mountain, the depression filled with sand and no nymphs were subsequently found in the sand-filled depression. The absence of nymphs from shifting sand agrees with the findings of Hunt (1953) and Swanson (1967).

It would appear that the type of substratum, the amount of dissolved oxygen, depth of water, and the fluctuations of the lake level are the most important environmental factors affecting the distribution of the intergrades of *Hexagenia* in Stone Mountain Lake. However, predation, prevailing winds, and the ability of nymphs to migrate also play a part in regulating their distribution.

It will be of interest to note in years to come the fate of this hybrid population of *H. munda*. Will the intergrade population remain? Will either the *H. m. marilandica*-type or *H. m. elegans*-type prevail? Or, as in old Venable Lake, will all *Hexagenia* nymphs disappear? Time alone will tell.

Acknowledgment

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References

Berner, L. 1950. The mayflies of Florida. — *Biol. Sci. Ser. Univ. Fla.* 4, 1—267.

Britt, N. W. 1955. Stratification in Western Lake Erie in summer of 1953: effects on the *Hexagenia* (Ephemeroptera) population. — *Ecology* 36, 293—244.

Eriksen, C. H. 1963. The relation of oxygen consumption to substrate particle size in two burrowing mayflies. — *J. Exp. Biol.* 40, 447—453.

Eriksen, C. H. 1964. The influence of respiration and substrate upon the distribution of burrowing mayfly naiads. — *Verh. Int. Ver. Limnol.* 15, 903—911.

Fremling, C. R. 1960. Biology of a large mayfly, *Hexagenia bilineata* (Say), of the upper Mississippi River. — *Iowa St. Univ. Agr. and Home Econ. Exp. Sta. Res. Bull.* 482, 841—852.

Hunt, B. P. 1953. The life history and economic importance of a burrowing mayfly, *Hexagenia limbata*, in southern Michigan lakes. — *Mich. Cons. Dept., Bull. Inst. Fish Res.* 4, 1—151.

Lyman, F. E. 1943. Swimming and burrowing activities of mayfly nymphs of the genus *Hexagenia*. — *Ann. Ent. Soc. Amer.* 36, 250—256.

Raulerson, C. L. 1960. The ecology of a small Georgia mountain stream, with special emphasis on the mussel *Elliptio hopetonensis* Lea. Master's Thesis, Emory University.

Scholander, P. F. 1950. Volumetric plastic microrespirometer. — *Rev. Sci. Instruments* 21, 378—380.

Spieth, H. T. 1941. Taxonomic studies on the Ephemeroptera. II. The genus *Hexagenia*. — *Am. Midland Nat.* 26, 233—280.

Swanson, G. A. 1967. Factors influencing the distribution and abundance of *Hexagenia* nymphs (Ephemeroptera) in a Missouri River reservoir. — *Ecology* 48, 216—225.

Turpaeva, E. P. 1959. Food interrelationships of dominant species in marine benthic biocoenoses. — In: *Marine Biology*, ed. by B. N. Nikitin. Am. Inst. Biol. Sci. Washington, D. C. 137—148.

Walker, W. H., JR. 1970. A study of the ecology and distribution of burrowing mayfly nymphs (Ephemeroptera: *Hexagenia munda* Eaton) in Stone Mountain Lake, Georgia. Master's thesis, Emory University.

Discussion

Marzolf: I have observed migration of *H. limbata* in a Kansas Reservoir and feel that substrate selection and predation control the distribution. What do you feel serves as the environmental cue which stimulates migration?

Burbanck: I believe that the nymphs congregated in the pool because the lake was drawn down slowly, but they had to leave their burrows to get into the pool. Drying of the substratum may have stimulated them to move.

Fremling: Did you ever find live nymphs in the hypolimnion when the dissolved oxygen concentration decreased to 1 mg/l?

Burbanck: No, fewer below 6.5 m which had a D. O. of 1 mg/l. On this field observation we believed that reduced oxygen was limiting.

Zwick: Was there no oxygen depletion in those ponds where the nymphs aggregated per thousands in winter?

Burbanck: No, the 12 sq. m pool was very shallow and the wind kept the water well oxygenated.