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Source: American Midland Naturalist, Vol. 57, No. 2 (Apr., 1957), pp. 371-402

Published by: The University of Notre Dame Stable URL: http://www.jstor.org/stable/2422405

Accessed: 02/11/2008 23:58

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The Ecology of the Macroscopic Bottom Fauna in Lake Texoma (Denison Reservoir), Oklahoma and Texas

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With the advent of extensive flood control and hydroelectric projects, the field of limnology has had a new and imperfectly understood facet added in the form of numerous impoundments. While several studies have been made on smaller impoundments, few have been done on the larger and deeper ones of the Southwest. This is particularly true of studies of benthic organisms, as Greenbank's (1937) results from Elephant Butte Reservoir in New Mexico were the only ones suitable for comparison with the work presented here. Emphasis of this study has been on horizontal and vertical distribution and seasonal succession of the macroscopic bottom animals. A cursory examination of the other limnological features was also made (Sublette, 1955).

The major community which Klugh (1923) referred to as the lake bottom association has commonly been divided by limnologists into the littoral, sublittoral, and profundal zones. These zones are defined as follows: littoral, from the lake margin to a depth which marks the lakeward limits of the rooted aquatic vegetation; sublittoral, the area bounded by the littoral above and the profundal below; and profundal, roughly, the area of the bottom in contact with the hypolimnion. An examination of the literature shows the extreme variability of zones so described, not only between different bodies of water, but within a lake itself. This variability is primarily the result of two One of these is the lakeward extension of rooted aquatic plants. It has been demonstrated (vide Welch, 1952) that different plant species have differing depth tolerances. Are two bodies of water, similar in every respect except that one has a shallow water and the other a deep water flora, to be considered as having entirely different littoral zones? The other variable factor is that of hypolimnion depth distribution. When a hypolimnion is present it varies in depth from season to season. Are the profundal zone limits then to change with the fluctuations of the hypolimnion? And what of the lake which rarely or never has a hypolimnion? Many writers, in order to avoid such poorly defined categories, have instead used the categories mentioned (littoral, sublittoral, and profundal) but have defined them by stating the exact depth limits of each zone. A more logical system would be to designate the zones on the basis of sediment substratum as has been pointed out by Pearse (1939) for marine communities.

The two major divisions, littoral and profundal, can readily be recognized as major communities since each exhibits a very different assemblage of organisms. What is not usually recognized is that within each major community ("zone") there are minor communities. Observations on these minor

communities (i.e., close agreement between bottom type, number of species and number of individuals) have been made by Baker (1918), Muttkowski (1918), Adamstone (1924), Rawson (1930), Krecker and Lancaster (1933), and Shelford and Boesel (1942). However, few of these workers recognized the components of each substratum type as a definite community and the results of those that did are not directly comparable because of lack of uniformity in terminology on bottom sediments and the associated communities.

The following is a classification of the major and minor communities as observed in Lake Texoma. The basic ecological terminology is that of Klugh (1923) with some additions. The classification of substratum is based on sediment terminology according to the Bureau of Soils Classification as modified by the U.S. Engineers Office, Ft. Peck, Mont., 1938 (vide Turnbull, 1945). Certain elements of Roelofs' (1944) hydrosols classification have also been incorporated.

Lake Bottom Association

Littoral bottom (chilile systasis)—from 0 to 6 meters

Gravel cenosis—gravel and sand greater than 70%, gravel predominates Sand cenosis—sand and gravel greater than 80%, sand predominates Emophyte cenosis—occurs within either gravel or sand cenosis (submerged aquatic vegetation)

Clay consociation—occurs only as hardpan

Ecotone—transition area between cenoses. The one between littoral and profundal cenoses (=sublittoral) shifts with seasons, local conditions; roughly corresponds to the 6 to 8 meter zone in Lake Texoma.

Profundal bottom (mesophthmile systasis)—8 to 20 meters (maximum depth sampled)

Mud cenosis—clay greater than 20%, organic content high chiefly as peat or muck.

This paper is the second report on the limnology of Lake Texoma. The first, (Sublette, 1955), described the physical and chemical features of the lake. The research was made possible by an Oklahoma Game and Fish Council fellowship which was subsidized by the U. S. Army, Corps of Engineers, a member agency of the Council. Grateful acknowledgment is made to the late Dr. A. O. Weese, Department of Zoology, University of Oklahoma, for his invaluable assistance in research direction. The University of Oklahoma Biological Station, the Department of Zoology, University of Oklahoma, and the U. S. Army, Corps of Engineers contributed much needed equipment and supplies. The author wishes to thank Dr. Carl D. Riggs who made available the facilities of the Biological Station during the latter part of the study. To my wife, Mary Smith Sublette, especial thanks are due for indispensable aid in many features of the investigation and preparation of the report. Dr. Harold M. Hefley, Panhandle A&M, Goodwell, Oklahoma, read the manuscript and made many helpful suggestions.

Apparatus and Methods

The study was made during June and July, 1949, and from June, 1950 to May, 1951. The first two months study was a preliminary survey of the fauna of the lake as sampled at random at eight areas of the lake: Rock

Creek, Newberry Creek; Big Glasses Creek; Cold Spring Creek; Hickory Creek; Buncombe Creek; the Islands; and Caney Creek. This survey is the source of most of the horizontal and vertical distribution of the benthos. The second period of the study, June, 1950-May, 1951, was concerned with securing data on seasonal succession of the benthos.

A six-inch square Ekman dredge was used as a bottom sampler, except for six samples taken with a nine inch square Ekman dredge. During the preliminary survey one dredging constituted a sample; during the seasonal study, four dredgings in the littoral and three in the profundal constituted a sample.

A total of 350 dredgings making up 158 samples was taken.

Several sampling methods were employed to study the faunal distribution caused mainly by the inefficient functioning of the Ekman dredge in many situations. In shallow water with a fine sand or sand-silt bottom the Ekman was hand operated (forced into the substratum by hand instead of being lowered by a rope). In other places in the upper littoral, qualitative sampling was done with a heavy duty, fine mesh, aquatic dip net. Such samples were supplemented with those taken with a six foot fry seine which secured many motile forms that could not otherwise be taken. The details of sampling procedure have been presented in an earlier paper (Sublette, 1955) and will not be repeated here.

AUTECOLOGY

PORIFERA

Spongilla lacustris (Linné).—This sponge was taken once, December 8, 1950, on a rocky headland shore east of the University of Oklahoma Biological Station. The habitat was a ledge of limestone bed rock overlain with boulders, gravel, and some sand and silt normally under several feet of water but at the time was just awash because of low water level. The area is subjected to slight wave action as evidenced by the accumulation of sand and silt in the interstices of the gravel-boulder ledge. The individual sponges were rather small and were abundantly distributed over most of the ledge. The habit of this species is incrusting; the coloration brown with a faint greenish tinge, probably caused by the large number of diatoms found living among the cells.

Asteromeromeyenia radiospiculata (Mills).—This sponge was collected by W. J. Harman of Louisiana Polytechnic Institute on submerged timbers of the boat house of the University of Oklahoma Biological Station, July, 1954. One specimen, roughly oval in outline, was low mound-shaped and measured approximately four centimeters by one centimeter. Dr. Minna E. Jewell, who determined the species, stated that there were a few flesh spicules of Spongilla lacustris included with the material of A. radiospiculata. This may be an indication of a much wider dispersal in the lake for S. lacustris than was found during the original study period, 1949-1951.

NEMATODA

On several occasions small free living nematodes were recovered from the samples. No attempt was made to determine species. No apparent depth or sediment preference was found.

BRYOZOA

Plumatella repens Linné.—This bryozoan flourished in several situations in the reservoir and was common on the undersides of floating leaves of Potamogeton americanus, on submerged sticks and logs, and along rocky shores which were subjected to little or no wave action. The colonies varied in size from less than one centimeter to a maximum of more than five centimeters. Statoblasts averaged a dimension ratio of one to three. Colonies consisted almost entirely of repent branches and were collected from late in June until the middle of December.

ANNELIDA

OLIGOCHAETA

Because of methods of collection and preservation, annelids collected were

in poor condition for specific identification.

The group showed a decided preference for soft bottoms composed of mud or silty sand, and were dredged from practically all depths throughout the year. The distribution of Oligochaeta showed a bimodal curve when numbers were plotted against depth. One peak occurred in the littoral and the other in the profundal; the distributional pattern probably was caused by different species having different depth tolerances.

HIRUDINEA

One small undetermined specimen of a leech was taken during the investigation. This was at Rock Creek (Station I) in seven meters of water on a mud bottom.

Mollusca

PELYCEPODA

Freshwater mussels were rather sparsely represented in Lake Texoma by five species: Quadrula q. apiculata (Say), Truncilla donaciformis (Lea), Leptodea laevissima (Lea), Anodonta corpulenta (Cooper), and A. imbecillis (Say). Leptodea laevissima was the most prevalent species probably due to its ability to migrate with fluctuating water levels as described by Isely (1924). Collections at periods of extremely low water levels rarely yielded living specimens of L. laevissima and then only in deep pockets left by the receding waters, but the relative dominance in numbers of this species over other pelecypods was clearly indicated by the number of shells found along the shore line. The empty shells probably resulted from normal mortality within the population at high water levels.

All five species were collected in the shallow, protected inlets and bays in the sand cenosis. The exact limits in depth are not known, but were probably from one to six meters. Beyond this depth the amount of sand in the substratum decreased to a point where the bottom will no longer support the weight of a mussel. There was no indication of a shell zone. Compared with other bodies of water Texoma was a poor mussel lake, possibly because of

wide seasonal fluctuation of water levels.

Dr. Henry Van der Schalie, University of Michigan, determined the species of Pelecypoda.

GASTROPODA

Three species of Gastropoda, *Physa halei* Lea, *Lymnaea* (=Fossaria) modicella (Say), and *Ancylus* sp. were found in the lake. Determination of the first two species was made by Mr. R. Tucker Abbott, formerly of the U.S. National Museum, now at the Academy of Natural Sciences, Philadelphia.

The only specimens of *L. modicella* collected were taken while seining the recently overflowed margins of the lake near the border of a permanent marsh. This is in agreement with Baker's (1928) statement that this species does not normally live in large bodies of water but prefers mud flats or small pools. It seems likely that the species is not usually found in Lake Texoma.

Physa halei was widely distributed in the lake. Specimens were collected in a variety of situations including gravel substratum with moderate wave action; sand substratum with much debris and little wave action; and on Potamogeton americanus. Most individuals were collected on clumps of Potamogeton.

Several specimens of an undetermined species of *Ancylus* were collected along with *Physa halei* on *Potamogeton*.

Arthropoda

CRUSTACEA

PALAEMONIDAE

Palaemonetes (Palaemonetes) paludosus (Gibbes).—This freshwater prawn was typically collected in the Potamogeton beds in Texoma although it occurred also among debris along the shore. Creaser and Ortenburger (1933) characterized this prawn as an inhabitant of slowly moving streams and ponds periodically overflown by rivers. These habitat preferences were reflected by its distribution in the reservoir, where it was taken only in well protected bays and inlets which were subjected to little or no wave action. It was a normal component of the emophyte cenosis and did not occur in dredgings. Ovigerous females were taken in June and July.

ARGULIDAE

Argulus lepidostei (Kellicott).—The presence of an argulid in bottom samples is of interest since normally it is an ectoparasite of fish. One specimen of this species was taken on a gravel shore in approximately one and one-half meters of water on the east side of Buncombe Creek Bay on September 6, 1950.

ARCHNOIDEA

HYDRACARINA

Since the water mites were represented in Lake Texoma by few individuals no attempt was made to determine them to species. The group was restricted to the places in the littoral having firm gravel or sand bottoms. The greatest concentration of individuals occurred near the deeper portion

of the depth range. A peak in number of individuals (42 per square meter) occurred in late fall (October 23) with a population minimum occurring in summer.

INSECTA

EPHEMEROPTERA

The following species of mayflies were collected: Caenis sp., Brachycercus lacustris (Needham), Stenonema femoratum tripunctatum Banks, Callibaetis montanus Eaton?, Siphlonurus sp., Hexagenia munda elegans Traver, and H. limbata venusta Eaton. Dr. Lewis Berner of the University of Florida determined the species of Hexagenia.

The mayfly fauna was distinctly divided into two components, the mudburrowing forms (*H. munda elegans* and *H. limbata venusta*) and the firm bottom (including *Potamogeton americanus*) inhabitants.

The two species of Hexagenia were very distinct as adults, H. munda elegans being larger with reddish-brown to black coloration and H. limbata venusta smaller with a creamy yellow coloration. The immature stages were not so distinct although there was a size difference. The mature naiad of H. munda elegans was definitely larger. However, since many collections consisted of mature and immature specimens, producing a size range overlap between the two species, size was not a useful taxonomic criterion. It was found that the most reliable taxonomic characteristic was the coloration of the imago which showed through the thin cuticula of the naiad. Length and shape of frontal prominence as well as length of mandibles, extent of mandibular cross over, and various head ratios were found to be of little value in separating these species in the earlier instars. The shape of the frontal prominence was diagnostic, however, in naiads approaching maturity (Spieth, 1941).

Hexagenia munda elegans Traver.—H. munda elegans was more common than H. limbata venusta both in naiad and adult collections. In Lake Texoma its distribution was chiefly profundal, although considerable numbers occurred in the lower littoral area. The population maximum was near the eight meter contour on the lake bottom with gradually diminishing numbers both shoreward and lakeward. As Lyman (1943) has demonstrated Hexagenia naiads are sensitive to decreasing amounts of oxygen and are intolerant of sediments with high sand content. The distribution of H. munda elegans was, therefore, a normal one in that the organisms were seemingly located in response to these two factors.

The seasonal distribution for *H. munda elegans* was typical of many benthic organisms. The period of adult emergence was from late May to August. At this time the number of naiads was at its lowest point. The numbers appearing in the dredgings increased from the summer minimum to a maximum in February. The maximum number recorded was 625 per square meter on February 10, 1951. Following this, there was a gradual decline until the population minimum was reached in midsummer.

Hexagenia limbata venusta Eaton.—This species differed little from the preceding in ecological characteristics. It was not nearly as numerous nor as tolerant to depth since the maximum numbers (32 per square meter, February

10) occurred near the six meter contour. Its seasonal history was similar in every respect except that the season of emergence was about two weeks later

than of H. munda elegans and apparently lasts slightly longer.

There has been some question as to the validity of the subspecies *H. limbata venusta*. Spieth (1941) divided *H. limbata* into five subspecies which he maintained were distinct although interbreeding where overlap occurs. He says, "for all of these subspecies intergrading specimens of geographically adjoining subspecies have been found." Hunt (1951) says that this species is extremely variable as to color phases with all phases freely interbreeding. He therefore dismissed Spieth's subspecies as invalid. It would appear that Spieth's subspecies could be accepted if at any one geographic location the subspecies remained constant, that is, without variation in the subspecific characteristic (in this case, coloration). Since this apparently was the case at Texoma, the author feels justified in retaining the subspecies *H. limbata venusta*.

Caenis sp.—The naiad of this small two-winged mayfly was the most characteristic inhabitant of the littoral zone. It occurred in all littoral cenoses except bare sand. It was not numerous and contributed little to the community. Caenis exhibited a normal seasonal distribution with maximum numbers (21 per square meter) in midwinter and a minimum in summer.

Brachycercus lacustris Needham.—The sprawling naiad of this mayfly was collected only four times during the study from the littoral bottom on silty sand or gravelly sand. Adults were not associated.

Stenonema femoratum tripunctatum Banks.—Literature records for Oklahoma have included the species S. tripunctatum and S. birdi Traver. According to Spieth (1947), these are not valid species but only color phases of the subspecies S. femoratum tripunctatum. Although both forms of Stenonema occurred in Lake Texoma, they are considered here as one. It was one of the characteristic lentic benthic forms and was found in the rapids of all clear gravel bottom tributary streams examined. Its location in a lotic cenosis can be attributed to the gravel cenosis in Lake Texoma duplicating, at least partially, the conditions in a stream. Specimens were collected on three dates at three different rocky promontories. Adults were not taken.

Callibaetis montanus Eaton?.—Naiads were collected on two occasions in the upper sand (silty sand) cenosis. C. montanus? appeared to prefer very quiet waters, having been collected in well protected, deep inlets. Adults were collected in July.

Siphlonurus sp.—An undetermined species of Siphlonurus was collected on two occasions from the same cenosis as Callibaetis montanus?. Adults were not collected.

ODONATA

Suborder Anisoptera

Pantala hymenea Say, Erpetogomphus sp., and Gomphus plagiatus Selys were the dragonflies collected. Dr. George H. Bick, Tulane University, deter-

mined the first two species listed. The specific placement of G. plagiatus is after Garman (1927).

Pantala hymenea Say.—The naiad of this species was taken only twice, both times in water of about a meter in depth on a sand bottom overlayed with much debris. Adults were collected on August 11, 1950.

Erpetogomphus sp.—Naiads were collected only from the littoral zone in the sand cenosis, in water less than three meters deep. It was the most common dragonfly in the benthic communities.

Gomphus plagiatus Selys.—This species, collected only once, occurred on a sand bottom at three meters. Adults were not taken.

Suborder ZYGOPTERA

Enallagma civile (Hagen).—Naiads were apparently confined to sand bottoms. Specimens were collected by dip net only. Adults were not collected.

Ischnura sp.—This form showed the least preference for substratum type. The collections were as follows: sand (2), gravel (1), and Potamogeton americanus (1). Species of this genus recorded from the Red River drainage are I. denticollis Bur., I. posita Hagen, I. kellicotti Williamson, and I. verticalis Say (Bird, 1932).

Argia moesta (Hagen)?.—This species was one of the most characteristic benthic inhabitants of the gravel cenosis, being found in no other situation. Like S. femoratum tripunctatus, this form was apparently a typical stream form that was able to survive in this cenosis because of the duplication of the environment of the normal habitat. Adults were collected: February 10, July 12 and 31, 1950.

Argia spp.—Several specimens differing from A. moesta? were collected, most of them from the gravel cenosis.

TRICHOPTERA

The following caddis flies were collected: Cyrnellus marginalis (Banks), Oecetis inconspicua (Walker), O. cinerascens (Hagen), Hydroptila sp., and Orthotrichia sp. Dr. H. H. Ross of the Illinois Natural History Survey examined all but the last two species listed.

Cyrnellus marginalis (Banks).—This species, along with Oecetis inconspicua (Walker), was collected in considerable numbers in the light traps. In larval collections two species were prevalent, Oecetis inconspicua and a previously undescribed psychomyiid larva. Since the only adult species of Psychomyiidae collected was C. marginalis, this larva is described by supposition as C. marginalis.

Mature larva: This larva will key to couplet 5, page 53 of Ross' (1944) key to the Psychomyiidae. It differs from Genus A as described by Ross on the basis of mandibular pattern.

Cyrnellus marginalis showed a decided preference for a firm bottom substratum, being most frequently found in the gravel or sand (gravelly sand) cenoses. It occurred occasionally on *Potamogeton americanus* and clay hardpan shoals. It was a littoral form being found at a maximum depth of four meters. Maximum numbers (172 per square meter) were dredged on October 23 with a gradual decline in numbers until late spring, when emergence occurred. Adults were collected from June to September.

Oecetis inconspicua (Walker).—Like Cyrnellus marginalis, this caddis fly was a littoral form. Its substratum preference was slightly different, however, with individuals most frequently occurring on a sand substratum and only rarely on Potamogeton and gravel. Individuals were collected in depths as great as nine meters, indicating a greater depth tolerance than C. marginalis. Maximum numbers (21 per square meter) occurred on November 12.

Oecetis cinerascens (Hagen).—This caddis fly, easily identified in the field by means of its log-cabin type of case, occurred in Texoma only among clumps of Potamogeton. Specimens were collected only at one site. Adults were not collected.

DIPTERA

CULICIDAE

Subfamily CHAOBORINAE

The distribution of *Chaoborus punctipennis* in Lake Texoma agreed in every particular with the results found by investigators of natural lakes (Muttkowski, 1918; Juday, 1921, 1922; Eggleton, 1932). It was the most typical profundal benthic organism in Texoma, being restricted to the soft sediments of deep water. When numbers are plotted against depth, *Chaoborus* shows a sloping curve with minimal numbers occurring in the littoral and maximal in the profundal regions. Numerically, it was the predominant benthic organism making up roughly fifty percent of summer standing crop. Its seasonal numerical dominance is graphically shown in fig. 1, in which the number of *C. punctipennis* are plotted with the total number of organisms.

TABANIDAE

Chrysops sp. and Tabanus sp.—Horsefly larvae were collected only upon one occasion, while seining along the recently inundated shore in the vicinity of a marsh. It is improbable that these species were normal inhabitants of the lake. Adults were not associated.

STRATIOMYIIDAE

Stratiomyia sp.—Only one soldier-fly was collected, along with the Tabanidae. Adults were not associated.

EPHYDRIDAE

Hydrellia sp. — The one shore-fly larva represented in Texoma by only one species was restricted to the *Potamogeton* (emophyte) cenosis. Adults were not associated.

HELEIDAE

Culicoides was the only genus identified from the material collected. Since the immature stages are imperfectly known no further taxonomic treatment was considered.

Members of this family were found in practically all substratum types and depths, although a maximum number occurred at eight meters with gradually diminishing numbers lakeward and shoreward.

Although this group was insignificant in numbers of individuals, it is probably important in the ecology of the benthic assemblages because of the predaceous habits of the larvae. Quantitative results indicated little seasonal variation in the number of larvae. A slight peak was reached on November 12 (48 larvae per square meter) with only slightly lowered numbers for the remainder of the year. Adults were not separated from the light trap material.

TENDIPEDIDAE

Subfamily PELOPIINAE

Pentaneura basalis (Walley)?.—An examination of the adult tendipedid fauna over a ten months period revealed two species of Pentaneura present, P. annulata (Say) and the species referred to as P. basalis (Walley)? by Johannsen (1946). The bottom fauna collection disclosed two distinct larval types, one of which is P. annulata (as described by Malloch, 1915) and the other a form which the writer associated with P. basalis?. This latter form has been briefly described by Malloch as Tanypus sp. A. The two species may be separated on the basis of a difference in lingula patterns (Malloch, 1915, Plate XXV, figures 2 and 7) and a difference in mandibles. The mandible of P. basalis? is much more strongly hooked, the tip being at right angles to the base; the auxiliary tooth is prominent in P. annulata while it is indistinct or absent in P. basalis?

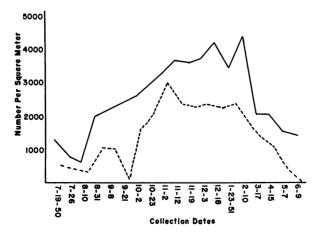


Fig. 1.—Annual standing crop of bottom organisms (solid line) showing numerical dominance of *Chaoborus punctipennis* (dash line).

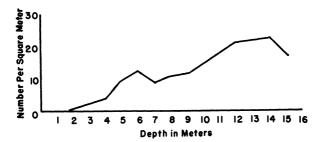


Fig. 2.—The depth distribution of *Pentaneura basalis?* as shown by a smoothed curve of the summer population (June, July, 1949).

The pupa of *P. annulata* was not distinguished from that of *P. basalis*?. The larvae of the Pelopiinae are not tubicolous as are most Tendipedidae. Instead they are predacious, feeding largely upon other Tendipedidae and smaller aquatic animals (Johannsen, 1937). This predatory habit is reflected in the horizontal distribution of *P. basalis*?. Specimens were collected on all cenoses beyond two meters with the greatest concentration in deep water. The distribution trend is shown in fig. 2. According to quantitative results, this form was predominantly profundal. The distribution into the littoral bottom is explainable on the basis of its predatory habits. The seasonal maximum was reached on February 10 with 27 organisms per square meter recorded. Adults were collected from May 7 to September 1.

Pentaneura annulata (Say).—The immature stages of this species were described as Pentaneura monilis (Malloch, 1915, not Linné). The specimens collected agreed in all details with Malloch's description.

Larvae of *P. annulata*, while similar in feeding habits to *P. basalis*?, were distinctly littoral forms, occurring in all littoral cenoses to a depth of six meters. A maximum number of individuals was found at two meters, occurring with less frequency than *P. basalis*?. The relatively few individuals collected made accurate seasonal fluctuations impossible to determine. Probably it agreed with the majority of the tendipedids in having a midwinter maximum and a summer minimum. Adults were collected from April 15 to September 1.

Pelopia stellata Coq.—The characteristics of this larva agreed with those given by Johannsen (1937). The habitat preference was the same as Pentaneura basalis? P. stellata was found in much larger numbers, being the most prevalent profundal tendipedid and the second most prevalent benthic organism. The seasonal distribution of the larvae was most unusual, with maximum and minimum numbers occurring in reverse to most tendipedids. The maximum numbers collected (1625 organisms per square meter) was on September 29. The population was smallest in late winter and early spring. Adults were collected from March 17 to November 19.

Procladius bellus (Loew).—The larva has been described by Malloch (1915) and Johannsen (1937). It was a member of the profundal assemblage,

having been collected from three to fifteen meters depth with a maximum occurring at about eight meters. *P. bellus* was a poorly represented predatory tendipedid with an atypical seasonal distribution. A seasonal maximum occurred in the spring (590 organisms per square meter on April 18). Adults were collected from April 15 to October 23.

Procladius culiciformis (Linné).—The larva of Procladius culiciformis was not distinguished from that of Procladius bellus. Since adult specimens of P. bellus were most common, it was assumed that practically all larval specimens were of the latter species. For this reason, all Procladius larvae collected were included under P. bellus. This contention was further strengthened by Morrissey's (1950) work in Iowa where he found P. culiciformis emerging from clumps of aquatic vegetation. The absence of distinguishable P. culiciformis larvae could then be explained on the basis of a sparse population and a cursory examination of the emophyte cenosis. Adults were collected from April 15 to June 9.

Coelotanypus.—Three species of Coelotanypus were collected as adults in the light traps: C. tricolor (Loew), C. concinnus (Coq.), and scapularis (Loew). While three species of adults were collected, only one larval form could be distinguished, that of C. concinnus, the only species described in the larval stage. Presumably the other two species were present as larvae but were indistinguishable from C. concinnus. These three morphologically indistinguishable species presumably had slightly different substratum preferences as shown when numbers of Coelotanypus spp. were plotted against depth. The resulting curve was a trimodal one with one small peak at one meter, a much larger one at eight meters, and still another, slightly smaller, at fifteen meters. The seasonal distribution as sampled in the mud cenosis was a normal one with a seasonal maximum of 625 individuals per square meter on February 10. The minimum for this substratum occurred in July.

Adults of *C. tricolor* were collected from July 6 to September 1; those of *C. scapularis* from February 2 to September 22; and *C. concinnus* from July 6 to September 22.

Subfamily Hydrobaeninae

Hydrobaenus (Psectrocladius) sp.—This previously undescribed larva most closely resembles H. (P.) sp. a Roback (1953a). The larva is characterized thus: The length is 4 mm. Only the tips of the mandibles and labium are brown, the rest of the head and body is light yellow. The eyespots are contiguous, the smaller being only one-third the diameter of the larger one. Antennal ratio, 36:14:2:1:1; the blade reaches the base of the third segment. The labrum appears glabrous; the epipharyngeal area is margined with several blade-like bristles. The mandibles are slender and rather straight. The accessory tooth and bristles appear to be absent. The labial plate is strongly arched so that the lateral teeth appear only on a depressed plate. The plate bears 12 teeth, 5 dark laterals on each side, a median colorless area (fig. 20, Roback, 1953a) is very similar. The posterior prolegs bear a series of dark brown retractile claws. The preanal papillae are only slightly

longer than wide, distinctly dark brown and apparently scleritized. On the specimens studied the papillae bear only one terminal bristle.

The pupa and adult were unassociated.

This species was another of the littoral assemblage occurring from the water's edge to a depth of seven meters. There was little evidence to indicate a substratum preference since specimens were collected in sand, gravel, and emophyte cenoses. Paucity of individuals prohibited a discussion of seasonal distribution.

Hydrobaenus (Hydrobaenus) sp.—This previously undescribed larva is apparently most closely related to the species figured by Roback (1953a) as H. (H.) sp. b. Larva: The body is 3 to 4 mm in length with a greenish coloration. The head is yellowish with only the lateral teeth of the labial plate and the tips of the mandibles brown. The antennae are very short, five segmented, and about half the length of the mandibles; the segments bear to one another the ratio 20:8:5:10:6; the blade exceeds the apex by a distance equal to the length of the last antennal segment. Details of the labral and epipharyngeal areas could not be distinguished on the specimens at hand. The mandible is slender and rather acutely tipped with three dark teeth; the accessory tooth is apparently absent; a mandibular brush is present, composed of several basally fused rays. The labial plate has 11 teeth, the central one broadly rounded and colorless (fig. 16-B—Roback, 1953a). A paralabial beard may be present but could not be seen with certainty. The preanal papillae are about 11/2 times as long as broad, each bearing 7 bristles. The posterior prolegs are very short, the claws appearing to arise from the segment itself. The claws are about 24 on each leg, all are yellowish and apparently oriented in the same plane. The anal gills are 4 in number; the dorsal pair are widely separated and conspicuous, the ventral pair very short, close together, and inconspicuous. The gills are tapered broadly and are rounded. The dorsal pair are as long as the preanal papillae; the ventral pair are about half

The adults and pupa were unassociated.

This larva was collected only on one date, May 7, 1951, from the gravel cenosis of the littoral bottom. Since mature larvae were collected, it is probable that emergence took place shortly after this date.

Hydrobaenus (Smittia) sp.—In the absence of associated adults, the subgeneric placement was based on Johannsen's (1937) description of Hydrobaenus (Smittia) sp. E, Group Epoicocladius Zavrel. Malloch (1915) briefly described this larva as genus Incertus B. Roback (1953b) has illustrated a labial plate of a species designated as H. (S.) ephemerae (Kief.). The larva described as follows may be identical. Mature larva: The length is 4.5 to 5 mm. The body has a greenish cast. The antennae are slightly longer than the mandibles. The antennal ratio is 14:4:1:1:1; the blade exceeds the tip of the antenna by a distance equal to the last three segments. The eyes are roughly reniform. The maxillary palp is short with the basal segment ringlike. The labial plate is strongly arched with the lateral margins black, the central area colorless, a strong bristle at each posterior-lateral angle. (See Malloch, Plate XXIX, fig. 23.) These lateral black margins were irregular,

possibly indicating lateral teeth; however, none could be seen with certainty on the specimen at hand. The body segments are very distinct, each bearing 4 strong bristles and 2 to 6 finer, less distinct bristles. The preanal papillae are slightly more than $1\frac{1}{2}$ times as long as broad. Each papilla bears 7 strong terminal bristles with an additional shorter bristle located on the anterior median aspect of the papilla. The 2 anal gills are long and tapering to a point. Each gill is basally constricted. The posterior prolegs are long with brown retractile claws.

The pupa and adult were unassociated.

Hydrobaenus (Smittia) sp. was always found in littoral sediments with a slight overlap into the profundal as defined herein. Specimens were collected from three to eight meters. This distribution was coextensive with that of Hexagenia limbata venusta. Although Hydrobaenus (Smittia) sp. was not collected on Hexagenia limbata venusta, there is a possibility that it was a commensal (or ectoparasite) on that form having been dislodged during screening. The species which most closely resembles Hydrobaenus (Smittia) sp. was described by Johannsen (1937) as Hydrobanus (Smittia) sp. E. This sp. E of Johannsen was found clinging to the legs and gills of Hexagenia recurvata. Johannsen's placement was based on Hexagenia ephemerae which was described by Sulc and Zavrel (1924) as a symbiont on Ephemera vulgata.

Hydrobaenus (Eukiefferiella) sp.—This previously undescribed larva belongs to the subgenus Eukiefferiella as restricted by Johannsen (1937).

One adult male, in poor condition, was identified for this genus.

Mature larva: The length is 3.5 to 4.5 mm. The body is yellowishgreen. The head, which is slightly tapered anteriorly, is light yellow except for the occipital margin, the tips of the mandible, and the 4 lateral teeth of the labial plate which are dark. The antennal ratio is 16:5:2:1:1; the blade reaches the apex of the 4th joint. The antennae are only slightly more than half as long as the mandibles. The labrum has a pair of bristles on the dorso-anterior margin; a pair of small forked bristles, and a group of small pointed blades on the ventro-anterior margin. The epipharyngeal area bears 10 to 12 curved blades, a pair of which appear bifid at the tip. The mandibles are brownish with the teeth black; the inner basal portion is practically colorless and bears the 3 to 4 serrations characteristic of the subgenus. The labial plate has 13 teeth; the lateral 4 on each side are dark. The central tooth is about 4 times the first laterals in width, and in mature larvae, slightly shorter. The anterior eye spot is about half the size of the posterior and is separated from it by a distance less than a third its own diameter. The preanal papillae are small, about as long as wide; each bears 5 bristles. There are 4 anal gills; the dorsal pair is one third longer and broader than the ventral. Posterior prolegs are about as long as the dorsal pair of gills; each leg has about 20 yellowish-brown claws.

The pupa and adult were unassociated.

H. (Eukiefferiella) sp. was another of the littoral assemblage. Individuals were collected from zero to six meters only on gravel and sand substrata.

Cricotopus tricinctus (Meig.).—The larvae of this genus that were collected keyed in Johannsen (1937) to C. trifasciatus (Panzer). Johannsen states that C. tricinctus cannot be distinguished from C. trifasciatus in the

larval and pupal stages. As C. tricinctus was the only adult of the genus collected at Texoma, this larva was associated with it.

This species was most frequently collected as larvae on *Potamogeton*; however, it was collected not too infrequently on other substrata, namely, gravel, and clay hardpan. It was taken only in the littoral zone on these substrata.

Adults were collected from April 15 to November 2.

Subfamily Tendipedinae Tribe Calopsectrini

Calopsectra (Calopsectra) neoflavellus (Malloch).—The larva and pupa of this species have been briefly described by Hauber (1944) as Calopsectra (Calopsectra) sp. B. The dead pupa from which the description was drawn contained the male hypopygium which was in poor condition. Associated material (mature pupae with clearly distinguishable hypopygia) was collected on several occasions in Lake Texoma indicating the affinities of the stages. The following description is given to supplement Hauber's description.

Mature larvae: The length is 3 to 3.5 mm. The color is yellowish brown; head, pale yellow except the mandibular teeth and the teeth of the labial plate. The antennal socket is elevated, with the inner side bearing a low tubercle but without a spine. The antennae are elongate; ratio, 36:6:4:5:2. The Lauterborn organs are extremely long-petiolate, 2 times the 3 distal antennal segments. The labial plate is 11-toothed; the middle tooth, which is trilobed, is rather broad and variable depending on age and amount of abrasion. The paralabial plates are separated on the midline by a distance less than 1/3 the width of the central tooth. The posterior prolegs are short; the claws massive with a yellowish coloration. There are 2 anal gills which are slightly shorter than the preanal papillae. Preanal papillae are robust, longer than wide; each bears 6 strong, dark brown bristles. The larva inhabits a tube constructed from sand grains.

Pupa: The respiratory organs are very similar to fig. 24 of Hauber (1944). The frontal tubercle is long and conical with an apical bristle. The comb of the 8th segment has 7 large sharp marginal teeth with a variable number of shorter teeth on the disk, usually around 10 in the specimens examined. Hauber (1944) gives a number of 16 to 20 for these.

Adult: These are as described by Malloch (1915), Hauber (1944), and

Johannsen and Townes (1952).

Calopsectra neoflavellus was another of the tendipedid fauna restricted to the littoral zone. It occurred principally in the sand cenosis. A maximum number of larvae (155 per square meter) was collected on April 15.

Adults were collected from April 4 to September 1.

Calopsectra (Calopsectra) dissimilis (Joh.).—The immature stages of C. dissimilis are as described by Johannsen (1937). The ecology of the species was very similar to that of Calopsectra neoflavellus except that it exhibited a much greater latitude of substratum preferences. It normally occurred in the sand cenosis but was also taken in gravel and Potamogeton. A maximum number of 75 per square meter was found on January 23.

Adults were collected from July 6 to October 10.

Calopsectra (Stempellina) bausei (Kieffer)?.—The immature stages agreed in every detail with the description given by Johannsen (1937). This tendipedid was taken only in the littoral zone in the sand cenosis.

Tribe TENDIPEDINI

Pseudochironomus pseudoviridis (Malloch).—The adult specimens of this species agreed with the description given by Townes (1945) for a variant from Lugert, Oklahoma, in that the ventral appendages of the hypopygium were divided slightly over halfway to the base. Since only one species of this genus was collected at Texoma in the adult stage, the larva described below as new is assumed to be associated with this species.

Larva: The generic placement is based on Hauber's (1947) description of *P. fulviventris* (Joh.). In describing this species as new he overlooked Johannsen's (1937) description of *Tanytarsus* [=*Pseudochironomus*] (sens. lat.) sp. J. This sp. J is unmistakably a member of the genus if not the

species described.

The larva herein associated as *P. pseudoviridis* is similar in almost every respect to *P.* sp. J (Joh.) and *P. fulviventris* (Joh.) Hauber. The length is 5 mm. The antennal ratio is 16:5:3:3:1. The blade extends to the tip of the 4th segment. The mandible is long and heavy; the inner margin with 4 uniformly dark teeth, of which the basal one appears to be fused with the mesio-proximal shelf of the mandible. The labial plate and other features are as in *Pseudochironomus* sp. J. (Joh.) and *P. fulviventris* (Joh.) Hauber.

Pupa: One cast skin which is probably associated with this species was found at the water's edge. The skin was 6 mm long and practically colorless. A prominent cephalic tubercle with a long preapical bristle was present. Respiratory organs could not be seen, so presumably they were lost. The lateral margins of segments 7 and 8 bore 4 bristles. The caudo-lateral angle the 8th segment was broadly rounded and supported 10 broadbased spines. The swim fin had about 40 bristles.

The larvae of *P. pseudoviridis* were characteristic of the upper littoral, being found in water less than three meters in depth. The largest number of individuals occurred on silty sand, but specimens were also collected from gravelly sand and gravel. This species was poorly represented in the dredgings but sufficient numbers of larvae were collected to indicate that a maximum (21 per square meter) occurred around December 18, with a minimum occurring in midsummer.

Adults were collected from July 6 to August 29.

Polypedilum (Tripodura) digitifer Townes.—Adult specimens of two species in the genus Polypedilum were collected at Texoma, P. (T.) digitifer Townes and P. illinoense (Malloch). Adults were collected in a ratio of about forty P. digitifer to one P. illinoense. Upon examining the larval material, only one apparent larval type was encountered; this appeared to be P. illinoense. Later in the investigation, two mature pupae were collected with attached larval skins. These pupae were clearly P. digitifer (as evidenced by the visible male genitalia in the cleared specimen) although the larval exuviae resembled the P. illinoense type. Although these larvae are superficially identical with P. illinoense, one is led to infer that they are actually

P. digitifer. This contention is further strengthened by the work of Berg (1950), who found the larvae of P. (P.) illinoense living in Potamogeton natans.

In Lake Texoma most of these *P. illinoense* type larvae were collected from the lake bottom, not on *Potamogeton*. This would indicate a different species. The paucity of larvae on *Potamogeton* is a reflection of the population density of adults.

A critical examination of the Texoma material of *P. digitifer* showed these differences when compared to the descriptions of the larvae of *P. illinoense* as given by Hauber (1947) and Berg (1950).¹ The antennal ratio is 14:6:1:3:1 as compared to Hauber's ratio (for *P. illinoense*) of 14:4:2:2:1. The blade exceeds the antennal tip by a distance as great as the length of the last segment. The various features of the labium, labrum, and epipharynx, seem to be identical in the two species.

The pupa of P. (T.) digitifer appears to differ from that of P. (P.) illinoense in the character of the caudo-lateral spur on the 8th segment in that P. illinoense has four main apical spines and several smaller subapical ones while P. digitifer has only three apical spines and two equally large subapical ones. Polypedilum digitifer has a smaller number of bristles in the swim fin (27 to 32 as compared to 40 to 45 described by Hauber) and distinct cephalic tubercles, which are small and nipple-like with a preapical bristle.

P. digitifer was another of the littoral forms found typically on a silty sand substratum (sand cenosis). Its seasonal distribution was atypical with the population maximum occurring in the spring and a minimum in the late fall. The maximum number of larvae dredged was 410 per square meter on May 7. This species apparently had several generations per year as evidenced by the collection of adults.

Adults were taken from February 9 to September 22.

Polypedilum (Polypedilum) illinoense (Malloch).—The immature stages were collected in sparse numbers on Potamogeton. The stages were as described by Hauber (1947) and Berg (1950).

Adults were collected from May 4 to August 9.

Tanytarsus (Tribelos) sp.—Adults of two species of the genus were collected, Tanytarsus (Tribelos) fuscicornis (Malloch) and T. (Stictochironomus) palliatus (Coq.). During the course of the investigation a larvae of Tanytarsus was collected which very much resembled, yet differed from, the described larvae of T. (Tribelos) jucundus var. dimorphus. At the time of the study, of the two species of adults collected, only the larva of T. palliatus had been described (Malloch, 1915; Johannsen, 1937). It was assumed that this undescribed larva was T. fuscicornis since the described T. palliatus larva differed considerably. However, Roback (1955) has since described the larva of T. fuscicornis, based on a reared female, which differs in several particulars from the Texoma species of Tanytarsus. From the scarcity of this

¹ Berg (1950) described the larva of *P. (P.) illinoense* (Mall.) as new, apparently having overlooked Hauber's earlier paper.

previously undescribed larva it is concluded that the adult stage was not taken in the light traps so that a logical association cannot be made.

Mature larva: The length is 7 mm. The head is pale yellow except the occipital margin which is light brown and the labial and mandibular teeth which are black. The antennal socket is rounded and fairly prominent. Antennal ratio, 30:8:4:4:2; the blade reaches the middle of the 4th segment. The labrum has many curved bristles, 2 of which are pectinate. The epipharyngeal comb has 7 large teeth, most of which are trident due to the presence of basal denticles. The tips of the premandibles are strongly hooked. The mandibles and labial plate are as in T. dimorphus var. jucundus; and T. nigricans (Joh., 1937, Plate V, figs. 65 and 70). The paralabials are long, slightly curved and widely separated on the midline. The inner anterior tip of the paralabials are produced into a long filament-like structure which reaches the base of the 1st lateral tooth. The preanal papillae are very short, about as wide as long; each bears 8 bristles. There are 4 anal gills; the dorsal and ventral pair approximate in size.

The pupa was not associated.

Larvae occurred only in one collection from Potamogeton.

Tanytarsus (Tribelos) fuscicornis (Malloch).—Adults were collected from July 6 to September 1.

Tanytarsus (Stictochironomus) palliatus (Coq.).—The immature stages were not collected during the investigation. This was attributed to a very low population density and/or inadequate sampling of certain cenoses.

Adults were collected only on August 19 and 20.

Stenochironomus macateei (Malloch).—During this investigation, a larva was collected and keyed in Johannsen (1937) to Stenochironomus taenia-pennis, the only described larva for this genus (Townes, 1945). On close inspection, the larva showed characteristics different from those described for S. taeniapennis. Since only one adult, S. macateei (Mall.), was collected at Texoma, this previously undescribed larva was associated with it.

Larva: The length is 3.5 to 4 mm. The head is brown and subcircular in outline. The antennae are six-segmented, the segments having a ratio of 13:5:5:2:3:2. The blade extends to the middle of the 6th segment. Other features are indistinguishable from *S. taeniapennis*.

The pupa was unassociated.

Adults were collected from July 12 to September 1.

Larvae occurred on silty or gravelly sand in the littoral zone down to a maximum depth of eight meters.

Xenochironomus festivus (Say).—This larva was very briefly described by Malloch (1915) as Chironomus sp. B from material dredged in the Illinois River. The following is given to supplement his description: Larva: The length is 20 mm. The color is reddish in life, fading to a yellowish-brown upon alcoholic preservation. The head capsule is yellow-brown. The tips of the mandibles and labium are dark brown to black. Antennal ratio, 63:18:5:7:3; the blade reaches the apex of the 3rd segment; the basal segment distinctly curved (Malloch, 1915, Plate XXX, fig. 6). The maxillary palp

as illustrated by Malloch (1915, Plate XXX, fig. 5); the basal joint arising from a low rounded tubercle. This tubercle is covered with numerous hairs which are as long as the basal joint of the palpus. The labrum and epipharyngeal area as figured by Malloch (1915, Plate XXIII, fig. 7). The epipharyngeal comb bears about 22 sharp teeth; the premandibles are distinctly toothed and bear a heavy brush. The labial plate as shown by Malloch (1915, Plate XXIX, fig. 5). The paralabial plates are very wide, coarsely striated, and separated by about a distance equal to the width of the trilobed central tooth.

Pupa: One pupal exuvia was recovered which, because of its size, may be associated with this species. The length is 22 mm. The cephalic tubercles are small, acute, and with a preapical bristle. The respiratory organs are numerous white filaments. The swim fin has in excess of 150 white bristles. The lateral margins of the 8th segment bears 3 large and 2 small filaments. The posterior-lateral angle bears a spur made up of about 30 coalesced spines, the spines distinct at the tips. Except for the large number of spines in the spur and the size, this description would fit several typical members of

Tendipes (Tendipes).

The ecology of X. festivus was more unusual than that of any other tendipedid species encountered in Lake Texoma. This is the only large tendipedid found in the vicinity of the lake. Since its larval stages had not been described, the author sought a large larva to associate. For a greater part of the investigation, none was found. On March 17, 1951, while examining a shoal area exposed by low water, it was noticed that numerous keyhole-shaped burrows honeycombed a clay hardpan area. Each of these burrows was found to contain a large reddish larva which undulated its body in the characteristic movements of a plankton feeding, tubicolous tendipedid. Upon examination, these proved to be identical with Chironomus sp. B (of Malloch). Since X. festivus was the only large adult tendipedid found on the lake, this large larva is associated with it.

Malloch (1915) records his sp. B as having been dredged from the Illinois River and Townes (1945) says, "according to my experience, this species breeds only in large rivers." The presence of X. festivus in Texoma can be explained by its habitat location, i.e., wind swept clay hardpan shoals. These areas duplicate the conditions of a large river just as do the gravel

areas for Stenonema, a typical swift stream mayfly.

Since the hardpan could not be dredged (with the Ekman used) seasonal distribution of the larvae cannot be given.

Adults were collected from July 6 to November 19.

Cryptochironomus.—Four species of this genus were collected as adults at Texoma: C. blarina Townes, C. sorex Townes, C. fulvus (Johannsen) and an apparently undescribed species. However, only one discernible larval type was collected. This type does not differ in any of the particulars described by Johannsen (1937) for C. digitatus (Mall.) and C. fulvus (Joh.). Since an association cannot be logically given this larval type is designated C. sp.

C. sp. was found to be a distinct littoral form occurring down to a depth of six meters. The substratum preference was silty sand and gravel with a few individuals occurring in gravelly sand. A seasonal distribution curve

plotted for this species showed a distinct bimodality with the two peaks occurring at December 18 and May 7. This bimodal curve is suggestive of a multiple species composition.

Adults of C. fulvus were collected from May 4 to September 1; C. blarina, from July 6 to September 1; C. sorex, May 4 to September 1; and C. sp.,

July 6 to September 1.

Cryptochironomus, sens. lat. sp. b Joh.—A larva which agreed in all particulars with Johannsen's (1937) description was taken from the stomach of a blue sucker, Cycleptus elongatus (LeS.). This larva, while not actually collected from the lake floor, was found associated with several typical sand and gravel cenosis inhabitants in the fish's stomach. Its absence in dredging samples can be explained by its known habitat, i.e., under bark of submerged logs (Johannsen, 1937; Roback, 1953a).

Tendipes (Limnochironomus) neomodestus (Mall.).—The larval, pupal, and adult stages of this species that were collected agreed with the description given by Johannsen (1937) and Hauber and Morrissey (1945) for the larva and pupa, and Townes (1945) and Hauber and Morrissey (1945) for the adult. The larvae, which were restricted to the littoral, exhibited a definite substratum preference with the largest numbers occurring on silty sand. Although a preference was shown for this substratum, individuals were taken in other cenoses. The order in decreasing abundance of individuals collected was gravelly sand, Potamogeton, and gravel. The larvae had a regular seasonal distribution with a maximum number of 825 individuals per square meter being recorded on December 18.

Adults were collected from April 16 to September 23.

Tendipes (Limnochironomus) nervosus (Staeger).—The distribution of this species agreed with the preceding species in all particulars except that the maximum number of larvae was much smaller, 75 per square meter.

Adults were collected from February 2 to November 12.

Tendipes (Tendipes) decorus (Joh.).—In Texoma, this species showed the least depth preference of any studied. Specimens were collected from the water's edge to the maximum depth studied, twenty meters. The species showed a decided substratum preference, however, being restricted to mud and sandy silt bottoms. Although Tendipes decorus occurred in the littoral zone, it should be considered a profundal inhabitant since maximum numbers were found there. The seasonal distribution of T. decorus was very regular with a maximum number of 575 individuals per square meter recorded on December 3 and a minimum of less than 10 per square meter from July 19 to September 8.

Adults were collected from March 17 to November 19 with maximum emergence in early July.

Tendipes (Tendipes) plumosus (Linné).—Two specimens of the variety T. (T.) plumosus var. ferrugineovittatus (Zett.) were collected during the study. These were at Station I, Rock Creek bay, Washita arm. Since no other specimens have been dredged or adults taken in light traps, it probably

was a river form occurring in the lake only in the immediate vicinity of the inflowing Washita River. The two specimens were collected from a silty-mud bottom at seven meters depth.

Adults were not collected.

Glyptotendipes (Phytotendipes) paripes (Edw.)—This previously undescribed larva is very similar to G.(P.) lobiferus (Say) as described by Johannsen (1937). It differs in the following particulars: The tips of the premandibles are heavily chitinized and blackened. Antennal ratio, 28:10:6:5:2; the blade extends almost to the tip of the 4th segment. The accessory tooth is short and broad but not notched. The labial bristle is in line with the last lateral tooth of the labial plate.

The pupa is also similar to that of G. (\dot{P} .) lobiferus. It differs as follows: The length is 8 mm. The length of maces on tergites 2 to 6 in their respective orders are, 0.135, 0.15, 0.165, 0.21, and 0.375 mm.

The larvae of *G. paripes* occurred most frequently on *Potamogeton*, being one of the most typical forms in the cenosis. Specimens were also collected from sand and gravelly sand bottoms. It was restricted to the littoral.

Adults were collected from July 6 to November 2.

Harnischia (Harnischia).—The genus Harnischia was divided into the subgenera Cladopelma and Harnischia by Townes (1945). In his check list he listed ten species under Cladopelma and 27 under Harnischia. The immature stages of nearctic Cladopelma are unknown; two species of Harnischia have been described.

During this investigation adults of four species of Harnischia (Harnischia) were collected, H. (H.) incidata Townes, H. (H.) carinata Townes, H. (H.) nigrovittata (Mall.), and H. (H.) monochromus (Van der Wulp). None of these species have been described in the immature stages. Larval collections revealed two distinct forms herein described as H. (H.) monochromus and H. (H.) sp. The association of larva and adult of H. (H.) monochromus was based on these four reasons (1), H. (H.) monochromus was by far the most common adult; (2), the larva herein described as H. monochromus was the most common type of larva present in collections; (3), the herein described larva of H. monochromus was very similar to the described larva of H. (H.) tenuicaudata (Mall.); and (4), the adult of H. monochromus together with H. tenuicaudata and H. potamogeti Townes form a closely related group.

The larva described here as *Harnischia* sp. was clearly a member of the genus and subgenus and, undoubtedly, it is the immature stage of one of the remaining three species; however, no plausible association could be worked out.

The pupae of three of the four species were definitely associated by means of the visible male genitalia. These are H. monochromus, H. incidata, and H. nigrovittata.

Harnischia (Harnischia) monochromus (Van der Wulp).—Larva: The length is 3.5 to 4 mm. The head of the larva is yellow except for the labium which is dark brown and the mandibles which are yellowish-brown. The antennal ratio is 25:12:3:1:1. The blade extends to the middle of the 3rd

segment. The mandibles are rather strongly hooked, the mandibular teeth appearing as slight notches. A mandibular comb could not be detected in any of the specimens; however, the mandibles of this species are in an oblique plane, so this characteristic could have been overlooked. A compound brush is present, the branches being rather indistinct. A strong bristle is present on the convex side of the mandible, located at the basal fifth. The labial plate is similar to H. (H.) tenuicaudata differing in these respects (1), the central tooth is broadly trilobed; (2), the tips of the 1st lateral teeth reach only to the base of the indentation of the central tooth; and (3), the 4th and 6th lateral teeth are much shorter and smaller than the remaining teeth. The paralabials are slightly over 3 times as wide as long. Each preanal papilla has 8 bristles. At the base of each dorsal anal gill is a strong bristle.

Pupa (positive association, male genitalia visible): The respiratory organs consist of tufts of about 20 white filaments each, arising from 6 main branches. The cephalic tubercles are small, slender, and acutely tipped; each bears an apical bristle. Segment 8 has 4 lateral bristles, with neither comb nor a spur. Lateral fringe of swim fin with about 30-35 bristles.

The depth distribution of *H. monochromus* was rather unusual. Specimens were collected from two to fifteen meter depth with a maximum number of 30 per square meter occurring at seven meters. From the distribution of the larvae and the structure of the larval mandibles a logical inference would be that these are predatory forms. A seasonal maximum of 80 larvae per square meter was recorded on May 7.

Adults were collected from July 26 to September 23.

Harnischia (Harnischia) sp.—The generic placement is based on the close similarity to H. (H.) abortiva (Mall.) as described by Johannsen (1937). This larva is probably the immature stage of one of the three species as discussed under Harnischia (Harnischia).

Larva: The length is 5 mm. The head is colorless except the labial plate and mandibular teeth which are black. The antennal segments have a ratio of 27:5:4:3:1. The 1st segment bears a blade and an accessory blade, both of which reach beyond the middle of the 3rd segment. The labial plate has 15 black teeth, the middle one almost twice as wide as the 1st lateral. The last lateral tooth of the plate is less than half the length of the adjacent tooth; other teeth of the plate gradually diminishing in size (as in Johannsen, 1937, Plate VII, fig. 100). The paralabial plate is slightly crenate on the anterior margin, about 2/5ths as long as wide. The striations are very coarse, each paralabial having about 10 striae. The anal gills are about 1/3 as long as the anal legs. The legs have strong yellowish brown claws. Each preanal papilla bears 7 long brown bristles.

This rarely collected larva was confined to the littoral zone and was found

on gravel, gravelly sand, and Potamogeton substrata.

Pupa and adult were not associated.

Harnischia (Harnischia) incidata Townes.—The larva was unassociated. Pupa? (association based on visible male genitalia which apparently belong to this species). The length is 3 mm. The abdomen is green; the thorax, dark brown. The cephalic tubercles are long and slender, each with a short

preapical bristle. The respiratory organs are dichotomously branched, with over 20 ultimate branches to each organ. The 8th segment has 4 lateral bristles and a slender yellow spine on the posterior lateral border. Swim fin has about 40 bristles.

Adults were collected from May 7 to August 26.

Harnischia (Harnischia) nigrovittata (Malloch).—The larva was unassociated.

Pupa (association based on visible male genitalia): It differs from H. (H.) incidata? in that there are 2 spines on the posterio-lateral angle of the 8th segment, of which the anterior is smaller and straight; the posterior, rather long and sinuate. The swim fin has about 35 lateral bristles.

Adults were collected from May 7 to October 23.

Harnischia (Harnischia) carinata Townes—One adult of this species was collected on August 7. Larvae and pupae were not associated.

HEMIPTERA

Members of four families of aquatic bugs were collected: Ranatra sp. (immature) (Nepidae); Belostoma testaceum (Belostomatidae); Rheumatobates hungerfordi (Gerridae); and Corixidae. The first three species mentioned were found only on Potamogeton or on a silty sand shore with much detritus (over it in the case of R. hungerfordi). The corixids did not exhibit any substratum preference and were found in all littoral cenoses.

Hemiptera determinations were made by Dr. Leslie E. Ellis, Mississippi

State College.

MEGALOPTERA

SIALIDAE

Sialis sp.—Only one specimen was collected. This was at Station V on a silty sand bottom in 2.3 meters of water.

Adults were not collected.

COLEOPTERA

Representatives of three families of aquatic beetles were collected: Dineutus sp. (Gyrinidae), Haliplus sp. (Haliplidae), Berosus pugnax (LeC.) and Tropisternus sp. (Hydrophilidae). All species typically occurred on silty sand bottoms with considerable detritus. Depth distribution was zero to three meters.

Benthic Communities

LITTORAL BOTTOM (Chilile Systasis)

This group of communities or systasis has been defined as extending from the water's edge to a depth of six meters. This depth was selected as the limits for the systasis because the author felt that the criterion most frequently used, i.e., lakeward limits of rooted macrophytic aquatics, was too variable. The criterion used for this study was depth of wave action as demonstrated by the depth of major sand deposition (Sublette, 1955, fig. 5). While it is recognized that the depositional pattern will vary from situation to situation and from lake to lake, in the author's opinion it is more satis-

factory than the one of plant distribution. Even the limitations of percentage composition of the substratum would be arbitrary if it were not for the ultimate criterion, that is close agreement between substratum type and numbers and species of inhabitants (cf. Baker, 1918; Muttkowski, 1918; Adamstone, 1924; Rawson, 1930; Krecker and Lancaster, 1933; Shelford and Boesel, 1942).

Gravel Cenosis.—Because of the conditions of the substratum and the type of dredging equipment available, this community was sampled only qualitatively at irregular intervals.

Of all the many factors of the hydroclimate (Wasmund, 1934, *vide* Clements and Shelford, 1939) none is more operative in determining the extent and duration of the gravel cenosis than wave action and associated currents. The gravel shoal or bar is maintained by continual water movements which tend to remove the finer sediments to areas of lesser activity. It would appear that in the absence of more than moderate water movement, residual boulders, cobble, and pebbles of the original lake basin are soon covered with allochthonous and autochthonous sediments. This condition was observed at Lake Texoma since the gravel cenosis was found only facing open water of considerable extent. All of the small deep bays and inlets had the original boulder and gravel bottom covered to a variable extent with sand, silt, and detritus. The only apparent exception was where the shoreline tended to be precipitous.

The criterion of community difference (or similarity) is both a qualitative and quantitative difference of species composition as well as environmental difference. Qualitatively, this community differed in the presence of three species found in no other community within the lake. These were Argia moesta?, Stenonema femoratum tripunctatum, and Spongilla lacustris. Although a quantitative difference was not recorded due to inadequacy of sampling apparatus, frequency occurence (i.e., the number of collections in which a particular organism was collected) and observations indicated that certain species were abundantly represented most seasons of the year. These were Physa halei, Caenis sp., Cyrnellus marginalis, Tendipes neomodestus, Cricotopus tricinctus, and Argia spp. It seems that the majority of these latter species occurred in the gravel cenosis because the substratum offered a firm place for attachment, locomotion, feeding, or other vital processes. This was inferred because the other communities in which these animals also occurred, i.e., gravelly sand and Potamogeton, offered the same thing and little more.

Sand Cenosis.—Sampling indicated that this was the most extensive community of the littoral zone. The substratum varied from almost pure sand to sand with an admixture of silt, clay, and detritus. The homogeneous sand substratum occurred only on windswept shores, principally those facing south. Almost invariably, sampling from this area gave negative results. The only animal collected was Oecetis inconspicua, one of the sand-case inhabiting caddis flies.

The usual sand cenosis substratum consisted predominantly of sand with admixtures of silt, some clay, and autochthonous and allochthonous detritus.

A total of 59 species (or groups such as Heleidae, Corixidae, Hydracarina) was collected from the sand cenosis. Of these 59 species (or groups), 25 occurred in no other situation. These are: Quadrula q. apiculata, Truncilla donaciformis, Leptodea laevissima, Anodonta corpulenta, A. imbecillis. Lymnaea modicella, Hydracarina, Brachycercus lacustris, Callibaetis montanus?, Siphlonurus sp., Panatala hymenea, Enallagma civile?, Erpetogomphus sp., Gomphus plagiatus, Chrysops sp., Stratiomyia sp., Tabanus sp., Heleidae, Calopsectra neoflavellus, C. bausei?, Stenochironomus macateei, Sialis sp., Dineutus sp., Haliplus sp., Tropisternus sp. Six of the 59 species were typically found in the profundal and are recorded as present only because of a slight community overlap in the vicinity of the ecotone. This assemblage of animals, while showing variation in species composition from one site to another, maintained a recognizable identity. The same is true for the profundal assemblage, although showing less variability. Where the two communities come in contact there is some overlap for many species. This zone of transition from one community to the other is the sublittoral, of authors. The following from Eggleton (1934) demonstrates this. He says of Lancaster Lake:

"... there were 6,585 animals per square meter of bottom at the 2 meter depth, which were recorded in the column for 'All others.' This category contained all animals present except Corethra, Chironomus, Protenthes, Tubificidae, and Sphaeriidae. It was a heterogeneous group and contained representatives from several phyla and from many orders of invertebrates. At 3 meters this group had decreased to a total of 308 individuals per square meter, and these were restricted to a very few orders, whereas at 4 meter depth none of them were present, and the entire benthic fauna had changed to the typical profundal benthic types."

In the author's opinion such a line of separation between distinct assemblages as described by Eggleston would constitute an ecotone between communities in the sense used in terrestrial or marine ecology (cf. Allee, et.al., 1949). Fig. 3 is presented to demonstrate the position of the ecotone between this and the mud cenosis. The depth distributions shown are those of a typical sand cenosis inhabitant, *Polypedilum digitifer*, and a typical mud inhabitant, *Pelopia stellata*.

This was the only littoral community in which both qualitative and quantitative sampling was done. Since it was the most typical littoral situation, remarks concerning this community are also generalizations about the littoral systasis. The sand community limits fluctuated considerably with changing water levels. The direct effect of this on most of the forms was not noticeable. Moon (1940) demonstrated that when hydrosols are denuded they acquire a fauna in a very short time. An observation at Texoma confirmed this. On June 9, 1951, a series of eight dredgings was made along a shoreline recently inundated by a rise in lake level. These samples showed an average of 139 organisms per square meter present in this recently flooded area indicating that there had been a recent invasion.

The indirect effects of water fluctuations on the fauna are more pronounced. An obvious effect on the fauna is the distribution of aquatic plants. Large fluctuation tends to eliminate many species of aquatic plants. A reduced flora is reflected in a reduced fauna while extensive growths of macrophytic aquatics tend to produce an abundant fauna (cf. Ball, 1948).

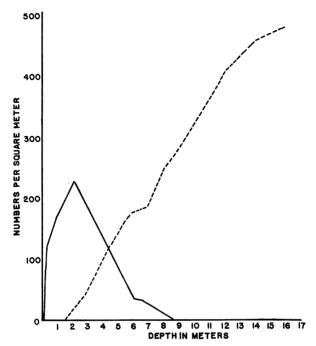


Fig. 3.—The depth distribution of two species of Tendipedidae (*Pelopia stellata*, dash line; *Polypedilum digitifer*, solid line) showing overlap of respective populations. This overlap is construed to be an ecotone. The distributions shown are smoothed curves of summer populations (June, July, 1949) as sampled at eight different localities in the lake.

Clay Consociation.—This community had a very limited distribution in the lake, being found only on windswept shores that were made up of residual clay hardpan. Away from windswept shores the absence of wave action soon caused the residual clay to become covered with sediments.

The Ekman dredge could not sample this substratum; hence, all results obtained by hand examinations were qualitative. Extensive examination revealed that only one species, *Xenochironomus festivus*, a large blood-red midge larva, normally inhabited this community. The distribution of this larva was unusual in that it showed distribution was clearly discernible on clay banks after the water level had receded. It appeared that the first (or early) instar larvae excavated their burrows shortly after leaving the site of ovoposition. That the "colonies" were usually circular in outline would indicate that the larvae randomly wandered away from the site before the motivation for burrow construction terminated their wanderings. On large clay banks the "colony" pattern tended to disappear apparently due to overlapping individual broods. The distinct bunched "colony" was typical of small isolated patches of clay hardpan.

Potamogeton (Emophyte) Cenosis.—This discontinuous community which was found to be only locally prevalent was widely distributed in the lake.

It exhibited the least stability of any present in the lake, as a result of water draw down and winter die-back.

Samples taken in the *Potamogeton* beds disclosed the presence of 28 species of animals, of which only six were restricted to that particular habitat. These are: *Ancylus* sp., *Argia* sp., *Oecetis cinerascens*, *Orthotrichia* sp., *Hydrellia* sp., and *Tanytarsus* sp.

PROFUNDAL BOTTOM (Mesopthmile Systasis)

Mud Cenosis.—Of all substratum situations present in a lake, none is more adverse to most benthic species than the soft mud bottoms of deep water. In a temperate lake of the second order some of the adverse factors are: soft flocculent bottoms that will not support heavy bodied animals; low concentration or absence of dissolved oxygen; and high concentrations of carbon dioxide and other noxious substances. Since Texoma is a lake of the third order, most of these factors should not be operative. The physical and chemical data revealed that transistory thermal and chemical stratification occurred in many areas of the lake. However, the stratification pattern was not continuous but occurred only in areas with sufficient protection from the wind. Complete oxygen depletion did not occur although it was approached at Station IV. These transitory thermal stratifications and near stagnation in certain areas indicated that, while Lake Texoma was classified as a third order lake, it was very near the borderline between the second and third order. The distribution of the profundal fauna also supported the view. The normal sequence of distribution of bottom fauna for second order lakes was described by Eggleton (1931) while that of a third order was described by Adamstone (1924). The characteristic feature of the summer benthic fauna of a second order lake is a concentration zone (i.e., large numbers of individuals) in the upper profundal or lower littoral, while in a third order lake the fauna is more evenly distributed throughout the year. This has been explained for the

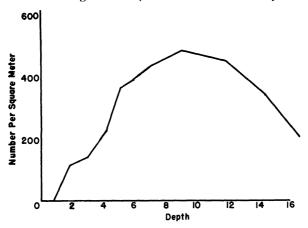


Fig. 4.—Depth distribution and relative abundance of *Chaoborus punctipennis* as shown by a smoothed curve of the summer population (June, July, 1949) of eight stations located throughout the lake.

second order lakes as a response to decreased oxygen content of the hypolimnion; the animals migrating upward to escape the effects of decreased oxygen. Since oxygen was not exhausted, only lowered in the lower profundal region, it would be expected that the fauna would not show this distributional sequence as clearly as in lakes where a stratification sequence is well established. Two types of horizontal distribution were observed in the profundal area; one, exemplified by *Chaoborus punctipennis*, where the animals are apparently sensitive to lowered amounts of oxygen and the other, shown by *Pelopia stellata*, where the only distributional pattern was a response to depth and not to oxygen content of the water. These distributional patterns are given in figs. 3 and 4.

The species composition of the profundal fauna of Lake Texoma was very similar to that described for natural lakes of the second order (Welch, 1952). This deep water fauna was characterized by a relatively large number of individuals and by few species. Animals which have extensive distribution in the profundal area are: Oligochaeta, Pelopia stellata, Pentaneura basalis?, Procladius bellus, Tendipes decorus, Harnischia sp., Hexagenia munda elegans, Chaoborus punctipennis, Coelotanypus spp.

BOTTOM FAUNA PRODUCTION

Four stations were sampled at frequent intervals throughout the year. The figures expressing annual crop have been derived from 267 dredgings representing 75 samples taken at these stations, two samples having been taken in the littoral (sand cenosis) and two in the profundal systasis on each collecting date.

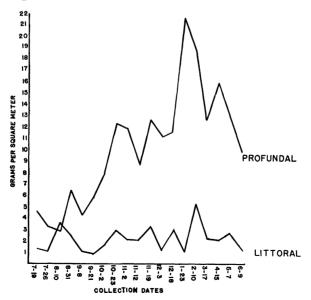


Fig. 5.—Annual standing crop from two communities, the sand cenosis (littoral) and mud cenosis (profundal).

Fig. 5 gives the annual standing crop of bottom fauna expressed in grams per square meter, and shows that Texoma has a winter maximum and summer minimum characteristic of many natural bodies of water. When total number of bottom organisms (fig. 1) is compared to weight (fig. 5) it will be seen that there is a close relationship.

Texoma had an annual mean standing crop of 21.75 kilograms of bottom fauna per hectare in the littoral community and 102.9 kilograms per hectare in the profundal. Townes (1938) considers a natural lake yielding 300 kilograms per hectare of bottom fauna to be "at least normally rich." When compared to such a standard Texoma appears to be rather poor. However, this standard may show a supposed, rather than a real, poorness. In Texoma three factors modify this standard: (1) Most of the submerged bottom is producing macroscopic benthic organisms because of a lack of stagnation, (2) the rate of turnover is much higher in southern waters, and (3) many of the benthic organisms are large enough to be readily available (Hexagenia spp., Coelotanypus spp., Pentaneura spp., Tendipes spp., and others). Townes (1938) says concerning this size-availability relationship:

"Chautauqua is a lake unusually rich in invertebrate fish food . . . with an average of 39 grams per square meter [390/kgm/ha] . . . in spite of its richness, Chautauqua is poor in certain features. Its profundal fauna contains less *Chironomus* [=Tendipes] plumosus than does that of many lakes. There are practically no burrowing mayflies, few polycentropid caddisflies and surprisingly few dragonflies in the lake."

His implication was that although Chautauqua supported a large benthic biomass, it did not contribute proportionally to the next consumer level, the fish population. The reverse may be true at Texoma, where a small benthic biomass is present contributing a much larger proportion to the next trophic level(s).

SUMMARY

The results of a fifteen months study on Lake Texoma, Oklahoma and Texas, are presented. Emphasis has been placed on the horizontal distribution and seasonal changes of the benthic invertebrates.

The waters circulate almost continuously throughout the year, with some tendency for stratification to occur, at least in areas that have some protection from the prevailing winds. This tendency is reflected to some extent in the composition and distribution of the bottom fauna, at least in the profundal area. In this region of the lake floor, the benthos is of a limited quality (indicative of lessened amounts of oxygen—only a few species are tolerant to lowered oxygen content) and compared to other cenoses of the lake, of relatively large quantity throughout the year (showing the absence of complete stagnation). In addition, this profundal community does not develop a concentration zone, again showing a lack of complete stagnation.

A total of eighty-seven species (or groups) of macroscopic benthic invertebrates was collected. Of this number, the insects predominate with seventy species. Brief autecological notes are presented for each species or group. To determine many insect species in the larval or nymphal stages, adults were collected by light traps and sweepings and associated. The immature stages of twelve species and one genus are described for the first time. Three additional species are associated from previous incertae sedis descriptions.

The benthic communities are classified according to a modification of Klugh's (1923) outline. These communities are named after the substratum composition for which criteria were modified from Roelofs (1944) and the Bureau of Soils Classification (vide Turnbull, 1944). It was found that the distribution of the bottom fauna followed closely the character of the substratum with each principal substratum type showing both qualitative and quantitative differences. The substratum type in turn was dependent upon the nature of the original lake basin as modified by certain environmental factors, notably depth and wave action.

Data are presented to demonstrate the presence of ecotones. Those between adjacent cenoses are rather poorly defined, but those between the littoral and profundal systases are well defined. This latter ecotone is considered to be the equivalent of the sublittoral zone, of authors.

The annual standing crop of bottom fauna from two cenoses is given. The minimum standing crop was found in the late summer and the maximum in late winter and early spring. It is suggested that although this production figure is low, the lake is probably more productive in the next trophic level (fish) due to certain of the modifying factors that would be expected from the amount of benthos produced.

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