

	100 mil. amp.	200 mil. amp.	
390 meters	.11	.14	Average $\phi_1 = .126$
375 meters	.10	.15	
375 meters	.10	.15	
348 meters	.10	.14	
310 meters	.12	.14	

Decrement of decremeter with resistance introduced to reduce the current from 200 to 100 milliamperes.

100 milliamperes	375 meters
$2\phi_1$	.24
.26	.27

Average  $\phi_1 = .127$

Decrement of decremeter with damped wave 375 meters.

$$D_2 = 2d_1 + d = .36$$

$$D_1 = d_1 + d = .23$$

$$D_2 - D_1 = d_1 = .13$$

Second:

$$D_2 = 2d_1 + d = .38$$

$$D_1 = d_1 + d = .24$$

$$D_2 - D_1 = d_1 = .14$$

Thus it is shown that the above method of determining the decremetnet of a decremeter checks fairly well with the CW. method.

*Indiana University.*

## STUDIES OF THE BIOLOGY OF FRESHWATER MUSSELS.

### III. DISTRIBUTION AND MOVEMENTS OF WINONA LAKE MUSSELS.<sup>1</sup>

WILLIAM RAY ALLEN.

#### INTRODUCTION.

Many summers have been more or less devoted to the study of lake Unionidae by the writer. An account of the feeding mechanism and survey of the food materials was published in 1914. A further study of ingestion, food selection and digestion by experimental methods appeared in 1921. While attempting to account for the assortment of food material, further study was made of the distribution and effectiveness of the organs of special sense. A paper on reactions to chemical and physical stimuli is now ready for the press. Some of the statements which are made in the following pages, e. g. reactions to light and pressure sense, are based upon data fully discussed in the above paper and may here seem arbitrary. To what extent the animals assume a definite place in the lake in response to these physical and chemical stimuli, it is the province of the present paper to show.

*Previous Survey.* Headlee and Simonton's careful exploration of the mussels of Winona Lake ('03) revealed eight species—*Lampsilis luteolus*, *L. subrostratus*, *L. glans*, *Micromya fabalis*, *Quadrula rubiginosa*, *Anodonta grandis*, *A. edentula* and *Margaritana marginata*. I have translated from the synonymy of Call ('99) to that of Simpson ('99). In many summers' collecting I have added but one species and only a single specimen—*Quadrula plicata*, 175 mm. in length, taken off Yarnell's Point. It is a river form, and having no direct access from the outlet on account of the dam, it probably owes its introduction to an accidental fish host or to human agency.

Headlee and Simonton state that *Lampsilis luteolus* and *Anodonta grandis* greatly outnumber the other species. They show that the mussel zone lies upon or near sandy and gravelly banks; that distribution toward the shore is limited by waves and muskrats, and outward by the soft character of the bottom. Furthermore they believe that the "black marl" of the deeper water destroys any mussels which go too far out by stopping up the gills.

The *Anodontae* were found by Headlee and Simonton in the edge of banks where sand and mud intergrade, *edentula* being more of a mud-dweller than *grandis*. *Lampsilis luteolus* was found to be the most cosmopolitan, found principally upon sand and gravel. *Fabalis* and *glans* occurred in deeper water, on relatively firm bottom. *Subrostratus* inhabited the outer portion of the range of *luteolus*.

<sup>1</sup>Contribution from the Zoological Laboratory of Indiana University No. 188.

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These authors discuss the possible factors governing distribution, and reject all except three—enemies, wave action and bottom. I shall refer again to this portion of their paper, and discuss these factors in order.

#### THE HYDROGRAPHY OF WINONA LAKE.

Winona Lake is one of the many kettle hole lakes of the region. It lies in the center of Kosciusko County, in the mid-northern portion of Indiana. It has a maximum length of two miles, and averages three-fourths mile in width. Gently undulating moraines in alternation with flat peaty, or mucky, areas which represent in large measure extinct marsh or lake, prevail in the surrounding terrain.

The northern and eastern shores of Winona Lake lie close to gravelly moraines, and the middle of the western side even more closely. The southern and northwestern shores are separated from high ground by more extensive flat areas, which are but little above lake-level, and have gone through the lake-marsh succession. In the case of this lake the process of degradation through the erosion of the outlet has been arrested by a dam. Just prior to the mussel survey by Headlee and Simonton much dredging had been done at the east, south, and northwestern portions of the lake. (Fig. 1.) This resulted in a rather profound alteration of the bottom in some parts, and the elimination of some mussel beds.

Sugar Creek, Cherry Creek, and Pocahontas Creek, springs, and artesian wells are the principal sources of the incoming water. The outlet is a creek two miles in length which enters the Tippecanoe River below Warsaw. Since the tributaries are small, though steady, mussels have not gone above the lake. The latter is purely lacustrine in form and marks the upper limit in its drainage system for all bivalves except Sphaeriidae. Such has not always been the case, for I have found shells at least two miles up Pocahontas Creek. We should expect a rather small number of species so near the headwaters of Walnut Creek. Nor should we expect to find river mussels so far up.

Since the lake level has been held nearly constant for many years, the shore line has been well stabilized. Also the wave cut terrace is now well established, and in most parts of the lake its margin is sharply set off from the abysmal portion of the lake in accordance with the angle of rest of its component materials. Thus the ten and twenty foot contours parallel the shore most closely of all. (Fig. 1.) Wave action is still at work reducing the sharp points of the shore line, and the most sandy and gravelly parts of the terrace are these exposed points; while in the coves the bottom merges into mud at a much slighter depth. The prevailing storms are northwest. This is correlated with the fact that the wave cut terrace of the east shore is everywhere wider than others, and that the contours of the west shore lie closer together. Except for the sheltered situations the east terrace is swept freer of mud, which is distributed farther out in the lake. The southern corners of the lake have not yet recovered from the dredging of twenty years ago. The south shore receives the wind and waves obliquely from the northwest,

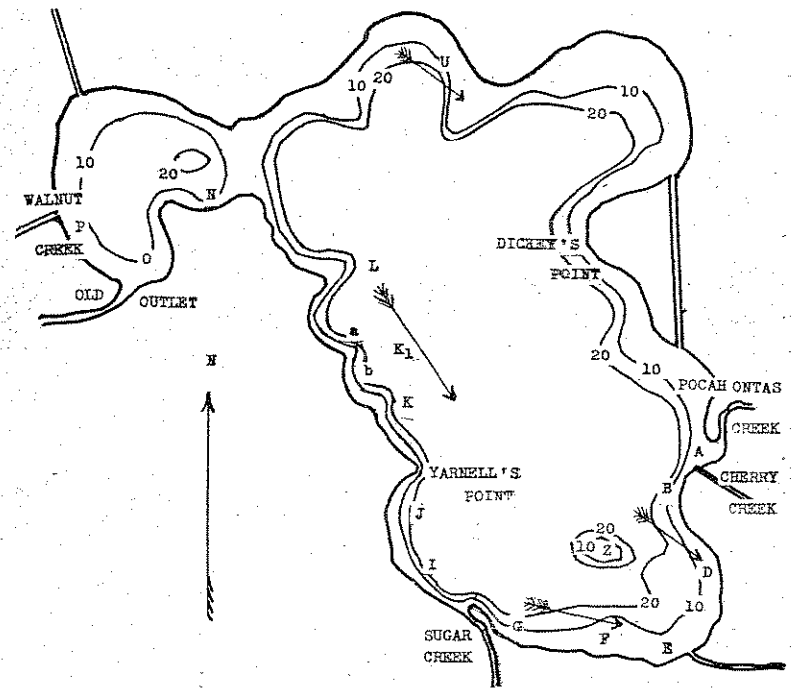


Fig. 1. Winona Lake, Indiana. Ten and twenty-foot contours shown. Letters represent stations referred to in text. Arrows are shore currents.

hence a slow distribution of its mud toward Boys' City Bay (Scott, '16, p. 14, map) and a rather firm bottom results.

The terrace constitutes a shelf of rather moderate depth surrounding the lake. This is the principal habitat of the mussel population. Baker ('16) and others have recorded the occurrence of the maximum population on the most exposed points of the shores of lakes. This generalization holds for Winona Lake except at its extreme leeward corner—Boys' City Bay—where the drift, marl, and mud from all parts of the lake accumulate and are graded out within a short distance from the shore. Kosciusko beach (Map, B) is the most exposed part of the shore line. Here in spite of much intensive collecting it continues to be one of the most populous areas of the lake bottom.

#### FACTORS GOVERNING DISTRIBUTION IN WINONA LAKE.

Having in mind the character of the lake it will now be pertinent to examine the facts of distribution and the possible factors limiting the same. We will first consider the three accepted by Headlee and Simonton.

(1) *Muskrats*. These animals are known to depopulate small areas of mussel beds. Where occurring in sufficient number it is possible that they very definitely limit the shoreward extension of the same. However at the present time there are too few muskrats here to have a significant effect, except locally, about the mouths of creeks in particular.

(2) *Wave action.* Despite the lack of predatory enemies, mussels are uncommon on wave-swept beaches or elsewhere at two feet depth or less. Headlee and Simonton found numerous individuals thrown up on the beach following storms, and concluded that this is the manner in which their shoreward distribution is limited. The writer has seen very few such cases except those thrown up by human agency. Recently dead *Anodonta* sometimes float to the surface and are swept ashore, thus entitling them to the vernacular name of "floater."

The writer placed mussels experimentally in water of a few inches depth near the shore at various points about the lake. Sooner or later they were sure to turn and seek greater depths, oriented by a pressure sense. This movement is expedited in times of storm and high waves. The explanation is a matter of stimulation or annoyance by the moving water and sand in suspension. In protected areas the return to deep water is more leisurely.

(3) *Bottom.* The above authors have very clearly shown how the several species are limited to the respective types of bottom in the lake. The matter of preference of certain types of bottom is a function of shell weight, at least in part. The *Anodonta* alone are found sometimes on muddy substrata, while the other species are sand dwellers, all having also moderate shell weight and erect posture. In the paper referred to in the introduction experiments along these lines will be described.

During recent years no *Margaritana marginata* have been obtained from the lake. Almost no *glans* and *fabalis* have been seen. Rather few *subrostratus* and *rubiginosa* have been taken, and in both cases have been confined to small groups of individuals in a few localities. *Subrostratus* has been collected always in rather deep water off exposed points. Since so few localities of the favored type occur, we may thus account in part for their small numbers.

The western shore is so inclined to the prevailing northwesterlies that southward shore currents are set up. (Fig. 1, arrows.) Thereby even the wind has a share in determining mussel distribution, locally. (Scott, '16, map opp. p. 14.) On every point of land this shore current picks up the mud from the northern margin and deposits it on the southern fringe of the same point, in the quieter water of the lee slope. Thus the beach has an alternation of sand and mud bottom on the west shore, arranged in serrate outline. The effect on mussel distribution may be seen with the help of the map (Fig. 1) and the table. A census of the two dominant species at various points demonstrates that not only general distribution, as shown by Headlee and Simonton, but also the minute local distribution is largely a matter of the character of the bottom.

In the following table the records represent all the mussels found at a depth of from three to four feet, for a distance of a few rods, and on bottom areas selected at random. In all cases where sand is abundant *luteolus* predominated, and was nearly wanting on soft bottoms. *Anodonta* occurs often on sand, but oftener on mud or marly sand. Headlee and Simonton's zones are thus shown not to correspond at all to contour lines, for the physiographic agencies which assort the bottom materials are complicated on the west shore by the action of the shore currents.

This is also observable at one point on the east shore—the north side of Boys' City Bay—(Map, D) and at one point on the north shore, (Map, U) which lie somewhat parallel to the prevailing winds.

TABLE I  
Correspondence of Species to Type of Bottom.

Section	<i>Anodonta grandis</i> present	<i>Lampsilis luteolus</i> present	Bottom character	Remarks
D	18	23	Marly sand	
O	31	2	Marly mud	
I-K	14	39	Very soft	
E	10	6	Sandy	All small
K <sub>1</sub>	a 9	12	Soft marl	
	b 31	16	Marly sand	See Figure 1
L	42	52	Marl, mud	
Z	3	33	Firm, marly sand	"Sunken Island"

Section K<sub>1</sub> will illustrate very well how the gradation in bottom is followed in the distribution of the two species. (Table I and Fig. 1.) The sandy portion has fewer *Anodonta* than *Lampsilis*, while the adjacent muddier part has twice as many *Anodonta* as *Lampsilis*. Section L is subject to similar comparison. Such comparisons can be made between areas in the above table, except Section E.

Headlee and Simonton relate that mussel beds at Stations E to I were covered twenty years ago with mud from dredging operations. To this day many dead shells are found in those areas, and few living mussels. I was long at a loss to explain the occurrence of so many dead shells where there were almost no live ones. Even today they have secured a new foothold only in the more or less exposed places (e.g. Section G.)

The extremely soft bottoms of the canals and Section N of the lake are inhabited by Sphaeriids, but not by Unionids. In the latter some dead shells are found.

Evermann and Clark's observations of the distribution in Lake Maxinkuckee ('17) show that there the greater part of the bivalve population lies within the shoreward contours, and that deeper dredgings bring up more *Anodonta* than *Lampsilis*. Baker ('18) finds by far the greater part of the invertebrate life of Oneida Lake within the six foot contour, the bivalves lying more deeply than the other invertebrates. My collecting in Winona Lake shows that the mussel zone of Winona Lake is in somewhat shallower water. We might expect this in a small kettle hole lake, whose littoral is chiefly a wave cut terrace, going off sharply into deeper water at its outer margin, and itself averaging less in depth than in such a lake as Oneida. Being formed by waves and currents, it tends to be shallower and narrower in lakes too small for large waves. Headlee and Simonton's map indicates that the mussel life belongs predominantly within the ten-foot contour. While they found live mussels out to a depth of twenty-two feet, the deeper ones were all narrowly limited to exposed points, which the undertow keeps swept clean, and on the lee shore, where the thermocline may sometimes be depressed. Aeration and food must be better at such points than at others of equal depth.

Needham and Lloyd's Figure 191 is likely to mislead one to regard the 10-20 foot zone as the most productive in Winona Lake.

River mussels, as well as lake forms, have preferred types of bottom, hence "shoals."

Having in the main corroborated Headlee and Simonton's analysis, with respect to the three factors given above, and compared the present situation with that of fifteen years ago, let us consider some of the factors ignored or rejected by them.

(4) *Sex* can be eliminated. Both males and females seem to occur over the entire range.

(5) *Age* is probably pertinent. First because juveniles are rarely collected on the grounds where adults are most abundant. In the second place, while adults are prevalent on certain types of bottom, some of them must have migrated thither, for the host fishes of course do not drop the young mussels upon selected bottom. It will be interesting to learn the evolution of the parasitic habit of the bivalves, the origin of specific infection, and the correspondence in preferred habitat between given mussels and their respective hosts. The matter of age is very uncertain due to the rare finding of juveniles.

(6) *Pressure* has been shown (in paper No. II of this series) to initiate and to govern the movements of mussels. Their distribution is partly due to this factor. It is probably of greater importance inshore than in deep water. The pressure difference within a few inches of the surface must be greater than differences of several feet in deep water, at the outer limit of the range. Physiologically the change from twelve inches to six inches should be the equivalent to a change from twelve feet to six feet. The most active movements of mussels actually take place in water of slight depth.

(7) *Light* has a directive influence upon the movements which may sometimes affect distribution. The experimental demonstration is discussed in the above named paper.

(8) *Relation to the Epilimnion*. The above factors without further additions are sufficient to account for the adjustment to favorable environment. Yet it is at least a happy coincidence that the most suitable bottom, depth, etc., occur in the epilimnion. Otherwise mussel life would have been impossible. Food supply, temperature, and oxygen are at the optimum where the bottom is also most favorable. Furthermore these conditions are best fulfilled during the summer months, the time of highest metabolic activity of the animals.

The thermocline of Winona Lake begins at a depth of fifteen to twenty feet. Therefore the contours which represent its contact with the lake bottom are quite near the boundary of the wave-cut terrace. The terrace is thus washed by the epilimnion only, and the hypolimnion lies wholly outside the terrace. Conversely, the greater part of the lake bottom lies beneath the hypolimnion. These facts are of importance to the mussels in the ways mentioned above.

(a) *Temperature*. The development of a thermocline due to the thermal resistance of water to mixture results in the maintenance throughout summer of low temperatures below its level. Instead of a distribution of the heat of summer throughout the water, the epilimnion

receives most of it. Its temperature is therefore much higher than if the heat became distributed vertically, and higher than when the lake becomes holothermous in autumn. This results in a heightened metabolic rate on the part of the inhabitants of the epilimnion, while the abysmal bottom on the contrary is rendered unfit for the production of many living things.

(b) *Oxygen, Carbon Dioxide, and Carbonates*. The water of the epilimnion receives most of the sun's energy that is not reflected from the surface. Only here is photosynthesis effective, and here the phytoplankton has evolved methods of flotation which keep the lake's minute inhabitants mostly near the surface. For these reasons oxygen production is virtually limited to the epilimnion. Currents due to wind are set up which distribute the epilimnetic water from one part of a lake to another. The return currents pass underneath, next to the thermocline. For mussels the situation is perfectly adapted to secure well oxygenated water so long as they remain above the level of the thermocline. Yet even more striking than the oxygen curve of Winona Lake is the increase of the carbon dioxide. (Scott '16, p. 34.)

Were a lake bottom in the hypolimnion entirely suited in other particulars to support mussel life, the conditions of temperature and oxygen would make it virtually uninhabitable. *Sphaerium* has been collected from bottom of various depths down to eighty feet, where, during summer, it exists under almost anaerobic conditions.

The increase in acidity as we read downward in a lake means a corresponding reduction of the available carbonates, which is of importance in shell formation. Most of the marl deposition occurs in shallow water. The lime cycle is a function of the epilimnion almost wholly.

In all respects we may say that the stratification of a lake tends toward increasing the habitability of the epilimnion at the expense of the hypolimnion. The turnover in autumn is rendered harmless to mussels through the thorough mixing, and through the temperature reduction.

(c) *Food Supply, etc.* The currents of the epilimnion are no less important to the Unionidae in that a constant renewal of the food supply is effected. That it is entirely sufficient is shown by the fact that freshly collected mussels are never without plankton in the intestine, or without a crystalline style. (Allen, '14, and '21.)

Evermann and Clark ('17) have stated as a foregone conclusion that rivers are the abode of mussels *par excellence*. And it is true that there are more species and larger individuals. But I cannot wholly agree with their explanation. They say it is due to the changing water of the current, abundance of food and dissolved oxygen. Yet it is not explained why lake beaches are inferior in these respects to river shoals. In the former we have a slower, though no less steady, movement of water. The dissolved oxygen exists in great concentration, even to supersaturation. The plankton content of a lake surface is far in excess of that of most rivers. The average temperature of the lake habitats through the year is probably higher than in rivers, due to temperature discontinuity. Since these things are true, the metabolic

rate should be higher. Then, with higher metabolism, more food, and more oxygen, lake mussels should be the larger, if these were the determining factors. In the upper reaches of lake-fed rivers the mussels may profit to a certain extent by the water flowing from the lakes above.

It is likely that the Najades originally populated the fresh waters through the rivers rather than originating in the lakes. The lakes are younger, more transient, less extensive, at greater altitudes, and at the extremes of the drainage systems, and mussels have had less time in which to grow adjusted to them than to rivers.

*Feeding Conditions upon Stream Deltas.* Northwesterly winds have diverted the mouth of Pocahontas Creek southward into a shallow bay. The bivalve population of this bay were observed at times to have an almost complete change of diet. Ordinarily the food is lake plankton. After heavy rainfall the increased volume of creek water usually spreads out in a sheet of a few inches depth over the entire bottom of the bay. On such occasions the food of the mussels is greatly altered. The same phenomenon was sometimes observed to take place when there had been no rainfall, and at first it was puzzling to explain the sudden changes of diet from lake to stream plankton. The explanation turned out to be simple, when it was found to correspond to the diurnal or cyclonic temperature changes. The creek is shallow and its temperature changes more rapidly than that of the lake. After a cold period, its cooler water sinks into the water of the lake and spreads out in a thin layer at the bottom of the embayment. Its planktons become the food of the mussels there, and they are excluded from their normal food supply. When the creek water is turbid and cold at the same time, it may easily be seen to underlie the warmer clearer lake water. It follows the bottom closely until the edge of the terrace is reached, where it spreads out horizontally in the region of the thermocline, in water of virtually equal temperature.

This alternation in temperature and food does not show evidence of inciting movement. But, during freshets, when the lake level is greatly changed upon the littoral, movements shoreward begin, due to pressure change.

In streams one may often see the siphonal regions of living shells used as holdfasts by such filamentous stream algae as *Cladophora*. This does not ordinarily occur in the lake. Yet it is a common observation in the above-mentioned bay where the water of the creek lies next to the substratum, even well out from the mouth of the creek.

Evermann and Clark acknowledge the greater food content of lakes. They suggest that fertilization is favored in the current of rivers and take no cognizance of the movements of lake water which accomplish the same purpose. Their explanation of the distribution of mussels upon riffles and other parts of a river bed lays emphasis upon the current as the distributional factor. Since lake species tend also to seek out gravelly or sandy beds and few choose soft bottom, the correspondence to river forms is exact. In lakes it is certainly the character of the bottom which is of most importance, and this factor can as readily explain distribution on river bottom. The current has of course produced the form of the bottom, and is thus an indirect factor.

These authors point to the possible reduction of vitality in small lakes through inbreeding—hence less size. They also show that a given lake species reaches its maximum growth only in the more fluviatile lakes. The writer has often noted this inequality between the mussels of the isolated, headwater lakes such as Winona and those of the elongated, fluviatile Oswego and Tippecanoe lakes.

Mussels are by no means unique in the occurrence of the smaller members of a family in smaller bodies of water, the larger members grading in size with the size of the stream or lake. Fishes are notable in this regard.

#### MOVEMENTS AND MIGRATIONS.

Isely ('13) through the checking up of marked mussels arrived at the conclusion that well-grown river forms are virtually sedentary. Evermann and Clark ('17) have often observed the tracks of mussels moving in shallow water. They state that the fixed habit increases with the increase in age and with increased depth. These observations are doubtless true in spite of the seemingly anomalous fact that younger individuals burrow more deeply than the older. The limey crust on the former rarely covers more than the siphon region of the shell, indicating the extent of submergence.

As told above, the writer has checked the movements of Winona Lake species, and finds an inshore or offshore movement corresponding to the stage of the lake water.

Observations on White River in late spring, and after summer freshets, show that sand bars newly exposed after having been submerged for a time, are more or less populated. Furthermore, mussels are stranded sometimes by receding water, and often tracks are seen which show that an effort has been made to reach deeper water.

Mussels upon rather permanent gravelly bars bounded by rock or mud bottom, are much limited in their movements. Shifting channels and shifting sand bars imply a corresponding movement of their population.

During the summer of 1915 the writer marked sixty or more *Lampsilis luteolus*, somewhat after Isely's method, and planted them at several points in the lake. Still others were planted during the following summer. Forty were put in water of three and one-half feet depth in Boys' City Bay, on bottom of marly sand. In the summers of 1916, 1917, 1919, and 1921 systematic efforts to recover these mussels were made. Many others of similar size were found, and many empty shells, but no marked mussels or shells were ever picked up. Others were put out in front of the Biological Station. Only two of these were found subsequently. Three years later one was found that had moved fifty feet from the starting point and had shifted from water of two feet depth to four. The other record was about the same in distance without change in depth, in six years. In six years the latter had increased in length scarcely one-fourth inch.

From the above it is clear that movements do take place. In some cases they are more or less seasonal, and of considerable magnitude deserving to be called migrations.

"Sunken Island" (Fig. 1) consists of several acres at 4-10 feet below the surface, having a sand-marl bottom, and only small areas not covered with Potamogeton. Little evidence of movement of its abundant mussel population is ever seen.

Mussels changed from one habitat to another usually exhibited greater unrest than undisturbed ones. A number were first accustomed to stream conditions, then subjected to the following experiment. They were placed, ten together in a rectangle, two siphoning upstream, two down, and the remaining six transversely to the current, in the mouths of Sugar and Pocahontas creeks. On succeeding days their positions were checked, with especial reference to tropic movements in response to current, depth, obstacles, distance moved, etc. The experiment was repeated many times.

There were 101 identifiable reactions considered, as follows, in those cases in which some movement had occurred:

(1) Remained transverse to current	25 out of 72 possible
(2) Turned transversely to current	5 out of 48 possible
(3) Remained faced downstream, siphoning up	23 out of 24 possible
(4) Turned downstream, to siphon up	23 out of 96 possible
(5) Remained facing upstream, siphoning down	13 out of 24 possible
(6) Turned upstream to siphon down	12 out of 96 possible

There was some tendency to remain transverse to the stream when placed that way originally, but much less tendency to assume a new position in opposition to current. There was a greater tendency to remain siphoning downstream than to turn that way. Of those set to siphon upstream nearly all retained that orientation, and one-fourth of the others assumed it, a much higher proportion than of those which chose to siphon in any other direction. This seems to bear out the tradition that mussels prefer to siphon upstream. Yet I am encouraged to believe that the orientation is as much a reaction to the pressure sense and a desire to reach deeper water, as it is a rheotropic reaction. Almost all the cases under item six took place after rains when the creeks rose; the depth of the water was doubled and the velocity increased. The reaction was more probably due to increased depth than to current. These cases are few but selected, and there were many rejected cases that seemed to point the same way. Yet an *Anodonta* placed in an eddy pool three feet deep did not move until a freshet raised the creek. Then it moved round and round the pool at the same depth, against the current of the eddy, not attempting to get out, and doubtless oriented by the eddy.

The bottom of Sugar Creek consists of much finer sand, gravel, and mud than Pocahontas. Hence the movements of *Lampsilis* were much more frequent and pronounced in the former. This despite the fact that Sugar Creek is cleaner and colder.

Movements were observed also in the outlet of the lake—Walnut Creek. When the dam was raised and the creek lowered most of its mussels sought deeper water, and more or less downstream movement took place. After periods of higher water the direction of movement was more random. Here again the amount of movement was coextensive with the favored bottom.

Obstacles on the bottom divert a mussel from its course. In the lake or in slight current the original course is often not resumed; but in a brisk current the mussel tends to fall back into the same angle with the flow of water regardless of what that angle may have been. Obstacles may include an alternation of sand, gravel, and mud. Drift-wood, plant roots, rubble, or stones are the more obvious ones. The concave walls of an aquarium may be followed a little way, but will soon bring the mussel to a halt. Ripple marks upon sandy bottom may be seen to have diverted a mussel more or less shoreward.

The prevalence of mussels upon favored type of bottom is in itself an argument for greater or less migration. Juveniles do not remain where left by their fish hosts at random, but find their way to suitable substratum.

Besides the common lake species there occurred in the outlet not far below the dam the following additional: *Symphynota costata*, *Quadrula undulata*, and *Lampsilis anodontoides*. *Quadrula plicata* doubtless occurs; it has been mentioned that one individual has been taken in the lake.

#### MISCELLANEOUS OBSERVATIONS.

In addition to the production of a shell the Unionidae may constitute a geological agent of a sort not usually recognized. The total amount of water siphoned and the amount of material taken out of suspension are surprising. Both mud and organic matter are separated out and precipitated in mucous clots. An aquarium jar filled with muddy water is cleared entirely in the course of a few hours by a single mussel.

Beneath the posterior end of a mussel which is actively siphoning in a lake the ground may be seen to be carpeted with a conspicuous amber-green slimy coating.

Due to the considerable deposition of marl on the plant grown terrace, through the reduction of the bicarbonates to carbonates in photosynthesis, there is much less lime present in the water of the outlet of Winona Lake. Prof. Scott has determined the carbonate ratio to be about thus: Springs : upper lake : outlet :: 3 : 2 : 1.

The writer compared the total weights and shell weights of 16 *Lampsilis luteolus* from Dickey's Point in the lake with an equal number from Walnut Creek. The results follow:

	From lake	From outlet
Average length	90.8 mm.	87.4 mm.
Average weight	127.0 gm.	107.0 gm.
Average shell weight	69.0 gm.	51.0 gm.
Ratio shell to total weight	54.0%	48.0%

The lake specimens were heavily encrusted with the usual marl deposit, and were cleaned for comparison. The total weights were then taken with the mantle chambers full of water. The number used was small, hence subject to error. The matter will be followed further. So far as the present data go we have a significant difference due to either the lime content of the lake, or to some other factor. This difference in shell weight amounts to six per cent of the total weight of the body, or about twelve per cent of the shell weight itself. Comparative data are not yet available from lakes of greater or less hardness.

## SUMMARY.

Headlee and Simonton's survey of Winona Lake, Evermann and Clark's of Maxinkuckee, and Baker's of Oneida show great similarity in the mussel distribution. The first named authors ascribe the limitation of mussel beds in their narrow shore zone to the encroachment of enemies, to wave action, and to the character of the bottom. The writer finds that enemies are of less importance in Winona Lake than formerly, yet the shoreward distribution continues to be held within bounds, that wave action is pertinent chiefly as a stimulus to movement, and that the character of the bottom is probably the most important of all distributional factors.

The present writer agrees with Headlee and Simonton in disregarding sex as a distributional factor, and to some extent age. Pressure incited certain more or less seasonal movements, and light is a stimulus to movement.

Since the time of the foregoing paper on Winona Lake, much has been learned concerning the physical and chemical conditions of that body, the work chiefly of Scott. While the stimuli mentioned are largely responsible for confining the lake mussels to their narrow zone, yet the deeper parts of the lake are much less habitable to freshwater mussels for reasons which were necessarily disregarded in 1903. Due to the thermocline the conditions of temperature and dissolved gases are both unfavorable to mussel life. Furthermore the food supply is principally confined to the epilimnion, which bathes the lake bottom only along the shore.

A set of experiments show that the movements in creeks of mussels transplanted from the lake are due both to pressure and to current, the latter chiefly directive.

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A STUDY OF THE LIFE HISTORY AND PRODUCTIVITY OF *HYALELLA* *KNICKERBOKERI* BATE.<sup>1</sup>

DONA GAYLOR.

- I. Introduction.
- II. Methods.
- III. Reproduction.
  1. Relation of reproduction to season.
  2. Time between broods.
  3. Distribution of size of broods.
    - a. Relation of number in a brood to age.
    - b. Seasonal distribution of number in brood.
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## INTRODUCTION.

My first work with the arthrostracan crustacean, *Hyaella knickerbokeri* Bate was in the summer of 1920 at the Indiana University Biological Station at Winona Lake, Indiana, and its study was continued throughout the winter of 1920-1921.

The first problem was to determine, if possible, the contribution made by *Hyaella knickerbokeri* Bate to the food of higher animals. I soon found I could not get very far in my studies until I had worked out the life cycle of the amphipod in some detail.

*Hyaella knickerbokeri* is widely distributed. It is found in every state but at widely scattered localities. It is especially abundant in southern Canada, southern Minnesota, northern Iowa, Illinois, and Indiana. Miss Weckel ('11) extends its range to Lake Titicaca, Peru, South America. Its distribution is also discussed by Jackson ('12), Weckel ('07), and Della Valle ('93).

## METHODS.

*Hyaella* can be collected easily by washing *Chara* or other water plants in water contained in a small basin. They were then transferred to other vessels. The moving of individuals was done entirely with a small pipette and when the young were extruded they were transferred to a separate dish from that in which the mother was located, one at a time. It was next to impossible to count them when all together in one dish with the mother, due to the continual movement of all of them. Paired individuals were kept in separate dishes where they could be examined at will. The dishes were numbered and the data for each

<sup>1</sup> Contribution from the Zoological Laboratory of Indiana University No. 187.