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VARIATIONS IN THE FRESHWATER SNAIL, GONIOBASIS LIVESCENS.

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INTRODUCTION.

In the course of some general ecological field work in the Bass Island region of Lake Erie, it was observed that the shells of the snail *Goniobasis livescens* varied considerably in shape and size. It occurred to me that it might be possible to correlate these variations with the degree of exposure to wave action. With this end in view, collections were made in this region during the summer of 1924, while in residence at The Lake Laboratory, Put-in-Bay, Ohio. By way of comparison some *Goniobasis* were collected in the Scioto and Olentangy rivers, near Columbus. The standard used as basis of comparison is the average obesity. My reason for choosing it and the definition of it are given in the section devoted to the description of the method.

On looking over the literature on the ecology of fresh-water mollusks, I have found several instances where variations within a species of mollusks are correlated with environmental factors. This evidence is based partly on actual experiments under control, partly on observations and measurements.

Colton ('08) has shown experimentally for Lymnaea columella Say, that the following factors may be the cause of dwarfing: large water plants (doubtful results), sediment, cold (indirectly through its effect upon the food supply and directly through its influence upon the physiological processes), improper aeration, volume of water, lack of exercise, and accumulation of excreted matter. He also found that in alternating favorable and unfavorable conditions, as, for instance, cold and warmth, and feeding and starving, the rate of growth exceeded the rate of those which were always under favorable conditions. This was true even when in the case of alternating temperatures the latter was reduced to the freezing point.

The following is quoted from Colton, Variations In the Dog Whelk *Thais* (*Purpura Amt.*) *lapillus*: "An examination of a large series of Thais (Purpura), the purple sea snail or dog whelk, from one hundred and six stations seems to indicate that variation in size and shape of shells is the result of the direct effect of environment." Colton found that shells collected from an exposed coast had a relatively wide aperture; (ratio of the height to the width 1.32+.004) while in those shells collected in sheltered bays with plenty of food the aperture was relatively narrow, (ratio of height to width being 1.70 +.009). Then he goes on to say, "The greater area of the foot (aperture) of those exposed to the surf is a direct reaction to the environment in preventing the animal from being destroyed by the surf. Since there is no overlapping of these characters, it is evident that we are here dealing with the direct effect of the environment." Brot observed in a lake near Geneva, Switzerland, that, "If a snail be long dwarfed and later be put under favorable conditions, the shell is often strangely distorted. Baker ('18) found that *Goniobasis livescens* varied in obesity in Lower South Bay of Oneida Lake. Some that he found were unusually long and narrow.

Ball, ('22) reports that in some species of fresh-water mussels the obesity seems to be directly proportional to the amount of waterflow. Steuer reports some very interesting variations in several species of plankton that apparently are correlated with environmental factors, namely, temperature, salinity, density of water, depth. Some of these variations occur at different localities, while others appear as seasonal variations at the same locality. Most of these variations consist in an abnormal development or a corresponding reduction of some part of the body, and seem to be a mechanism that enables the organism to float in a medium that varies in density or in salinity at different seasons of the year.

Other instances of the effect of the environment will be mentioned under the discussion of factors that may limit the distribution of mollusca.

Goniobasis livescens is a fresh-water mollusk. It belongs to the sub-class Streptoneura of the class Gastropoda and to the family Pleuroceridæ of the order Pectinobrachia. It is the only species of *Goniobasis* found in this region.

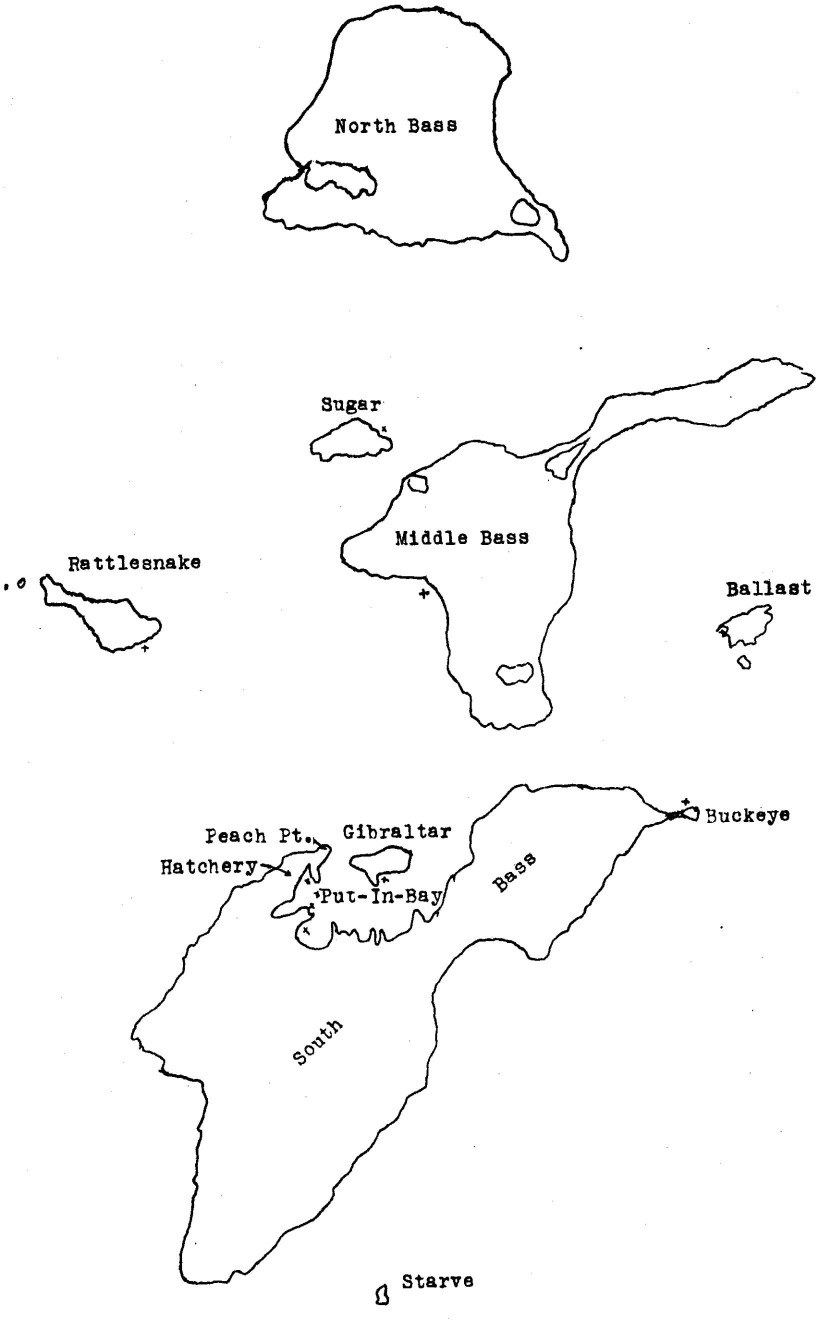
I want to take this opportunity to thank Dr. F. H. Krecker, under whose direction this work was done, for suggesting the problem and for helpful criticism as the work progressed. The identification of the snail was made by Mr. Bryant Walker in connection with some work done by Dr. Krecker. Mr. Walker's kindness is greatly appreciated.

Method.

The first step in the solution of the problem was the selection of a number of stations from which material could be collected. In the selection of stations special attention was paid to the degree of exposure to wave action. The first series of five stations is in the vicinity of the State Fish Hatchery, which is situated on the west shore of Hatchery Bay, a subdivision of Put-in-Bay. The first station, Peach Point, is at the entrance to Hatchery Bay; the second station is an old dock a short distance beyond the entrance to Hatchery Bay and almost in front of the State Fish Hatchery. The third station is along the shore of Hatchery Bay from the U. S. Fish Hatchery, which adjoins the State Fish Hatchery to Smith's Point at the entrance of Squaw Harbor, another subdivision of Put-in-Bay; the fourth station is the west shore of Squaw Harbor; the fifth station is on the Put-in-Bay side of Gibraltar Island, which lies across the entrance to Put-in-Bay. These five stations represent a definite series with respect to wave action. From Peach Point to Squaw Harbor there is a gradual decrease in the degree of exposure. At Gibraltar the degree of exposure increases again.

The remaining six stations are selected near the following islands and are named after them in the tables: Ballast, Middle Bass, Buckeye, Rattlesnake, Sugar, and Hen. All stations except the one on Hen Island, are indicated on the map of the Put-in-Bay region.

In the collection of snails special care was taken to secure mature individuals. In the young shells the spires are sharp, conical, and the whorls distinctly keeled. While the old shells have obtuse spires and the whorls are not carinated except in some of the very long individuals where the last 2 or 3 whorls may be carinated.



Map of the Bass Island Region of Lake Erie
Scale: 4 cm. = 1 mile. Stations are indicated by +.

One hundred of the largest specimens from each station were carefully measured to determine the length and the width. The distance from the apex to the lower edge of the lip was taken as the length, while the diameter just above the apex of the aperture was chosen as the width. This width is not quite the same as the greatest diameter, but it is more easily measured and for a comparative study it is just as good. All measurements were made to the tenth of a millimeter with a vernier caliper.

The unit chosen as a standard for comparison is the average obesity. It was chosen because it involves both the length and the width of the shells and is therefore a convenient standard of comparison. The average obesity is defined as the quotient of the average width by the average length. If $0=$ave. obesity, $W=$average width, and $L=$ average length, we get the equation $O= W/L$.

From this formula it follows that the average obesity varies directly as the average width and inversely as the average length.

The average length is the sum of the lengths of one hundred shells divided by one hundred. Similarly the average width is the sum of the diameters of a hundred individuals divided by one hundred.

Finally the obesity of each shell separately was calculated to get the maximum obesity, the minimum obesity and the difference between these two.

Description of the Stations.

No. 1. This station is at the western edge to the entrance of Hatchery Bay. The most characteristic feature of this station is a bar extending into Hatchery Bay in a southeastern direction. The substratum on the northeast side of the bar consists in part of pebbles and small stones and in part of a smooth rock bottom. The shore on this side is subject to almost continual wave action from the open lake. It is exposed to waves coming in from the southwest and also to some coming from the northeast. The substratum on the southeast side of the bay consists of stones varying from a few cubic inches to several hundred cubic inches. This part of the shore is exposed to much less wave action because most of the waves break against the bar or on the shore below the bar. *Goniobasis livescens* were quite common in a few inches of water on the protected side of the bar, while on the exposed side very few individuals were found and those in deeper water. The water over this area varied in depth from a few inches to a depth of four feet.

No. 2. This is a part of an old dock about 50 yards southeast of Station No. 1, just beyond the entrance to Hatchery Bay and almost in front of the State Fish Hatchery. The dock is built up of horizontal timbers and then filled up with stones of considerable size. In some places the stones are covered with a few inches of water, while in others they extend above the surface of the water. The water surrounding the dock is about 13 feet deep. This station is less exposed to wave action than Number 1, because much of the effect of the waves is lost when they hit the bar at Peach Point. On both the timbers and the stones *Goniobasis* were found in a few inches of water.

No. 3. The edge of Hatchery Bay from the U. S. Fish Hatchery, which adjoins the State Fish Hatchery, to Smith's Point, at the entrance to Squaw Harbor, another subdivision of Put-in-Bay. The water is uniformly shallow; in most places it is less than 3 feet in depth. The substratum is varied; in part it is composed of a smooth rock bottom, partly of smaller and larger stones, and partly of larger boulders. The shore for some distance consists of a cement wall. Wave action is relatively small, since only waves coming from the northwest could break on this shore and some of these are broken at Peach Point bar, at Gibraltar, and at docks just beyond the entrance to the bay. This makes the part of Put-in-Bay known as Hatchery Bay, a well protected situation. *Goniobasis* are common on the larger stones and boulders, and are plentiful on the cement wall. But everywhere they are in very shallow water, rarely exceeding a foot in depth.

No. 4. A subdivision of Put-in-Bay called Squaw Harbor. The water averages around 3 feet in depth and is very turbid. In many places the bottom is covered with mud or silt. Close to the western edge of the shore where the collecting was done, are many large stones barely covered with water. The bank consists in part of large stones piled up artificially and in part of a cement wall. Wave action of any degree is very rare as Gibraltar Island cuts off the waves coming in from the northwest, and South Bass cuts off all waves from the west, south, and practically all that come from the east. *Goniobasis* are very plentiful on the stones along the bank as well as on the cement wall. I found a number of *Goniobasis* on one stone about 15 feet from the shore and in 3 feet of water.

No. 5, Gibraltar Island, situated at the entrance to Put-in-Bay. The north side of the island faces the open lake and all the waves that pass between Middle Bass and Rattlesnake break either at Peach Point or on the north side of Gibraltar. Consequently the north side is exposed to a great deal of wave action. The south side faces Put-in-Bay and has very little wave action. The station No. 5 is along the protected side of the island. It is not as well protected as Squaw Harbor, because some waves from the northeast may wash this shore. The substratum is composed of stones varying from a few cubic inches to several hundred cubic inches. The water varies in depth from a few inches to about 5 feet. *Goniobasis* are very abundant both on the stones and on the timbers of a small dock, but they always occur in a few inches of water.

No. 6, Ballast Island, northeast of the eastern end of South Bass and east of Middle Bass. The island as a whole is exposed to the full force of wave action from the open lake. But on the side facing Middle Bass there is a little cove protected from the northwest by an old dock and from the southeast by a bar. This protection is not sufficient to cut off all wave action. The station is freely exposed to waves from the southeast and also, though to a less extent, to those from the southwest. A look at the map will indicate that Ballast is more exposed than the south side of the bar at Peach Point. But because of this cove, Ballast is less exposed than Buckeye, which will be described next. The substratum is made up of larger stones. *Goniobasis* are abundant on the stones in a few inches of water.

No. 7. This station is located on the north side of Buckeye Island. The substratum is mostly a smooth rock bottom over which a few boulders have been strewn. The water is very shallow and gets deeper only very gradually. The island is just as much exposed to wave action as Ballast is; and the station here is more exposed than the one at Ballast, because there is neither bar nor dock to break the force of the waves. *Goniobasis* are rather rare and are found on the larger boulders only.

No. 8, Rattlesnake Island, about a mile northwest of Peach Point. The entire shore is well exposed to wave action from the open lake. The station is a pile of rock and timber on the side facing Peach Point. This side is least exposed. This station is more exposed than Buckeye, but it has also a more favorable substratum. A few *Goniobasis* of an unusually small size were found on the larger stones and the timbers in a few inches of water.

No. 9. This station is on the western side of Middle Bass Island near a point where the shore makes a sharp turn towards the west. The station is so situated that the wave action is greatly reduced by this curve in the shore. Still the station is exposed freely to the waves from the northwest and from the west. Rattlesnake, which is due west of this station, helps to reduce the amount of exposure from the west. Hence this station is considerably less exposed than the one at Rattlesnake.

The station proper is an old dock built up of timbers and then filled in with stones. The end farthest out in the lake was only partly filled, so that the water covered the stones to a depth of from 12 to 20 inches. A few *Goniobasis* were found on the sides of the dock, but on the inside on stones as well as on the timbers they were quite plentiful in a few inches of water.

No. 10, Sugar Island, due west of Middle Bass. The station is along the northeastern shore of the island. While Sugar Island on the whole is less exposed to wave action than is Rattlesnake, the station proper is more exposed than the one at Rattlesnake. It gets the full force of waves from the open lake passing between Middle Bass and North Bass and also waves passing to the west of North Bass. It is therefore well exposed and gets the full force of both the east and northeast winds. The substratum is partly a smooth rock bottom and partly smaller and larger boulders. The water varies in depth from a few inches to about 3 feet. *Goniobasis* are rather rare and are found only on the larger stones and boulders and at a depth averaging about 18 inches.

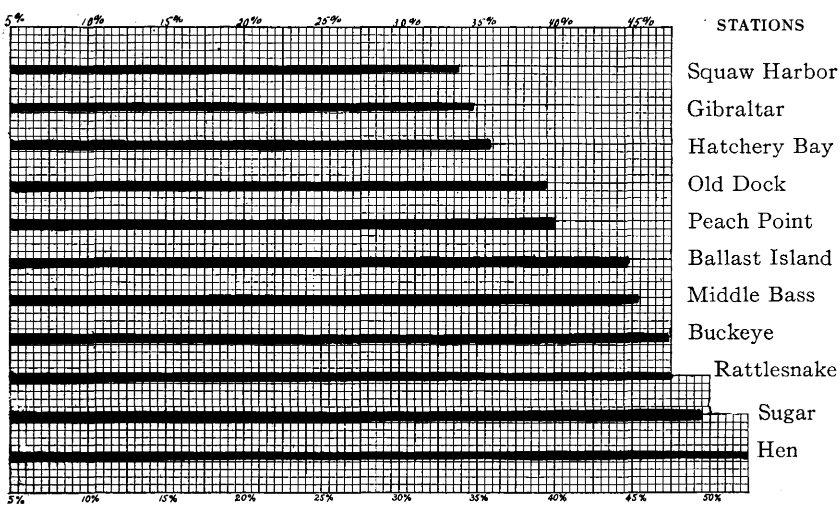
No. 11, Hen Island, about 10 miles south of South Bass. It is out in the open lake and is exposed to the full force of wave action from all directions. There are no islands near enough to break the force of the waves as there are at Sugar Island. Hen has therefore, a higher degree of exposure than any other station in this series. The station proper is a dock built in the shape of a capital L. It extends for about 30 feet into the lake and then for about an equal distance it extends parallel with the shore. The average depth of the water surrounding the dock is about 4 feet. A few *Goniobasis* were found on all sides of the dock and also on the larger stones between the dock and the shore. However, at the bend in the dock where the floor and the side of the dock had been partly torn up, and where large stones were submerged in shallow water, *Goniobasis* were quite plentiful. The description of the dock might create the impression that this station is after all fairly well protected. It must be remembered, however, that when the winds come from the right direction the dock and boulders are exposed freely to waves from the open lake. Again snails migrate into less protected areas during fair weather, then when it gets rough they seek a sheltered place.

In the description of the stations three factors have been emphasized, namely, substratum, depth of water, and degree of exposure to wave actions. It is readily apparent that these stations differ principally with respect to exposure to wave action.

RESULTS.

Measurements and calculations made as suggested in the paragraphs on method, soon yielded some very definite results. These results are embodied in Tables I–IV. The average obesities are also represented graphically.

GRAPHIC REPRESENTATION OF OBESITIES AT



Percentages of Obesities represented by horizontal lines. One square = 5%.
(The first five percent are not shown.)

Table I shows the average obesity, mean obesity, minimum obesity, maximum obesity, and the difference between the last two. All are in terms of percent.

The first column of Table I is the most important, since the average obesity is the standard of comparison. It might be well to recall at this point that the stations in Tables I–III are arranged with reference to the degrees of exposure. From Peach Point to Squaw Harbor the degree of exposure is decreasing, while from Gibraltar to Hen Island it is again increasing. Squaw Harbor has the lowest degree of exposure.

TABLE I.

Station	Average Obesity	Mean Obesity	Maximum Obesity	Minimum Obesity	Difference
	Percent	Percent	Percent	Percent	Percent
Peach Point....	40.00	40.45	49.70	31.20	18.5
Old Dock......	39.30	40.00	50.30	29.70	20.6
Hatchery Bay..	35.8	36.65	44.5	28.8	15.7
Squaw Harbor.	33.6	32.2	43.3	27.1	16.2
Gibraltar......	34.1	38.45	48.1	28.8	19.3
Ballast.........	44.6	46.05	52.4	39.7	12.7
Middle Bass....	45.20	44.55	54.7	34.4	20.3
Buckeye.......	47.4	48.5	55.9	41.1	14.8
Rattlesnake....	47.5	49.05	58.2	38.9	19.3
Sugar Island...	49.3	48.25	55.6	40.9	14.7
Hen Island.....	52.44	56.2	67.3	45.1	22.2

On examining the figures of the first column of Table I, it is at once apparent, that (1) a very distinct difference in the average obesity exists, (the total variation amounting to 18.84%, and (2) that these variations in average obesity follow the variations in the degree of exposure to wave action, i. e., from Peach Point to Squaw Harbor the average obesity decreases and from Gibraltar to Hen Island it again increases. In short the average obesity seems to be directly proportional to the degree of exposure.

Column 2 shows the mean obesity and with the exception of Middle Bass and Sugar Island, it follows the same trend as the average obesity.

The maximum obesity varies in case of Sugar Island and Old Dock. The minimum obesity varies in the case of Middle Bass and Rattlesnake.

The greatest difference between the maximum and the minimum occurs at Hen Island and amounts to 22.2%. The least difference occurs at Ballast and amounts to 12.7%.

Table II gives the average lengths, mean lengths, maximum lengths, the minimum length, and the difference between the maximum and the minimum.

Column one shows that with a few exceptions the average lengths follow the same trend as did the average obesities, namely, the average length increases from Peach Point to Squaw Harbor, when it reaches the maximum, then at Gibraltar it begins to decrease until a minimum is reached at Rattlesnake. For Sugar and Hen Islands the average length is again slightly greater.

TABLE II.

Station	Average Length in mm.	Mean Length in mm.	Minimum Length in mm.	Maximum Length in mm.	Difference
Peach Point....	17.86	18.1	14.5	21.7	7.2
Old Dock......	18.12	19.85	15.0	24.9	9.9
Hatchery......	19.76	20.4	16.4	26.4	10.0
Squaw Harbor.	20.86	21.2	16.4	26.0	9.6
Gibraltar......	20.25	21.9	16.8	27.0	10.2
Ballast Island .	19.26	20.5	16.0	25.0	9.0
Middle Bass....	16.01	16.85	13.5	20.2	6.7
Buckeye Isl....	15.6	16.5	12.4	20.6	8.2
Rattlesnake....	13.89	15.65	11.3	20.0	8.7
Sugar Island...	14.62	16.5	12.4	19.9	7.5
Hen Island.....	14.87	16.5	12.4	20.6	8.2

The mean lengths follow the same trend as the average lengths and presents the same deviations from the average obesities.

The greatest maximum length, 27 mm., is found at Gibraltar and the least, 19.9 mm., at Sugar Island. The greatest minimum length, 16.8 mm., occurs at Gibraltar, and the least, 11.3 mm., at Rattlesnake.

The greatest variation in length, 10.2 mm., occurs at Gibraltar, the least, 6.7 mm., at Middle Bass.

The specimens from Squaw Harbor and Gibraltar are exceptionally long for *Goniobasis livescens.* In a private letter to Dr. Krecker, Dr. Bryant Walker stated that the *Goniobasis livescens* he (Dr. Krecker) sent him, were the longest he had ever seen, with the exception of specimens from Presque Isle, and that these specimens almost warranted description as a special variety.

Table III shows the width, mean widths, maximum widths, minimum widths, and the difference between the last two.

The average widths differ from the order followed by the average obesities in case of Middle Bass and Rattlesnake. The mean widths vary in the case of Hatchery Bay, Middle Bass, and Rattlesnake. The maximum widths vary in the case of Squaw Harbor, Gibralter, Middle Bass and Rattlesnake. The minimum width differs in the case of Hatchery Bay, Middle Bass and Rattlesnake.

TABLE III.

Station	Average Width in mm.	Mean Width in mm.	Maximum Width in mm.	Minimum Width in mm.	Difference
Peach Point....	7.16	7.25	8.5	6.0	2.5
Old Dock......	7.13	7.25	8.5	6.0	2.5
Hatchery Bay..	7.08	7.35	8.4	6.3	2.1
Squaw Harbor.	6.95	7.15	8.6	5.7	2.9
Gibraltar......	7.01	7.35	8.5	6.2	2.3
Ballast Isl.....	8.69	9.0	10.5	7.5	3.0
Middle Bass....	7.25	7.1	8.7	5.5	3.2
Buckeye.......	7.40	7.7	9.4	6.0	3.4
Rattlesnake....	6.60	6.65	8.3	5.0	3.3
Sugar Island...	7.22	7.65	9.0	6.3	2.7
Hen Island.....	7.80	8.25	10.1	6.4	3.7

Not including column five of Table III all the maxima occur at Ballast and all the minima at Rattlesnake. The shells from the former place were exceptionally large and those from the latter were unusually small.

It could hardly be expected that the average lengths and the average widths would run exactly parallel with the average obesities. What I mean is this, that there may be instances where the average obesity increases even if the average width decreases, or that the average obesity may increase even when the average length increases. This is true because the average obesity depends on both the average length and the average width. But as Tables I and II show, this does not happen very often.

More deviations would be expected in the means of either obesity, length or width, since they represent the average of only two individuals in each case. And in the maxima and minima deviations could be still more frequent in as much as they are measurements of only one individual in each case. With this in mind one can easily see how Squaw Harbor can have the lowest obesity and yet not have the greatest maximum length. Or, that Ballast can have the maximum average width and yet not have the greatest average obesity. Or, again that Rattlesnake, with the least average width, still can have the third largest average obesity.

The average obesity, since it is dependent upon both the average length and the average width of at least one hundred shells in each case, would seem to be the most reliable criterion as far as the results embodied in Tables I to III are concerned.

Table IV is a record of the results obtained on the *Goniobasis livescens* in the Olentangy and the Scioto Rivers near Columbus. It seems to show that there is some difference in obesity in the rivers and that the obesity is correlated with the rate of flow. However, the amount of data is too limited to draw any conclusion.

TABLE IV.

	OLENTANGY			SCIOTO		
Station	Av. L.	Av. W.	Ave. O.	Av. L.	Av. W.	Av. O.
Rapids	15.53	6.37	41.01	17.73	7.11	40.10
Pool	18.8	7.12	37.86	18.29	7.22	39.47

The volume of water in the rapids in the Olentangy was much greater than that in the rapids on the Scioto. This is probably the reason why the difference in obesity in the Olentangy is greater than in the Scioto. Another reason for the small difference in obesities at the Scioto is that, in my judgment, the snails in the pools might at times be subject to draught.

It might be well to point out here that wave action and rate of water-flow expressed in volumes are not quite identical. Wave action is more nearly identical with the rate of flow and the volume of flow combined. The volume of flow might be relatively large, but if its flowing is slowly and steadily, it would jar the snails less than would a much smaller volume if flowing at a greater rate.

DISCUSSION.

On examining Tables I–III it becomes at once apparent that the degree of obesity is very definitely correlated with the degree of exposure to wave action. This is especially well illustrated by the first six stations, namely, Peach Point, Old

Dock, Hatchery Bay, Squaw Harbor, Gibraltar and Ballast. It is again quite striking when any two of the remaining five stations are compared or when any one of them is compared with any one of the first six, but especially when compared with Gibraltar and Squaw Harbor.

The differences in obesity are produced in two ways: (1) in some shells the top is worn off so that several whorls are missing; (2) many shells are very bulbus, which makes the ratio of width to length high.

Before attempting to explain the relation of obesity to exposure some other factors that might limit the distribution and development of *Goniobasis livescens*, or any other gill-breathing mollusk, will be considered. These are: temperature, oxygen supply, Co_2 in the water, nature of substratum, depth of water, and exposure to wave action.

TABLE V.

Station	Squaw Harbor	Gibraltar	Peach Point
Average Temperature..........	75.5° C.	73° C.	74° C.

Temperature cannot be of much direct influence and cannot account for the differences in size and shape of *Goniobasis livescens*. All these stations are frozen over during the winter months and hence the snails must in all cases be able to endure a temperature not above 4° C. The average temperature is probably slightly lower in the more exposed area, because of the water being mixed with water from the deeper and cooler portions of the lake. While the average temperature for Squaw Harbor is, perhaps, more favorable, it is equally true that Squaw Harbor is subject to great diurnal changes in temperature as well as in alkalinity. Temperature readings are here given for the north side of the bar at Peach Point, for Squaw Harbor, and for Gibraltar. These readings were made during July, 1923.

Table V shows the average temperature for the month is very nearly the same, for all the three stations considered. Then in comparing Table I and V, we note that while the average temperature at Peach Point is more favorable than that at Gibraltar, the average obesity at Peach Point is 5.9% greater than that at Gibraltar. If temperature were a determining factor, we would expect that the obesity at Gibraltar would be greater than at Peach Point.

Table VI brings out the great daily variations in temperature in a protected place, like Squaw Harbor, and the relatively small variations in a more exposed place, like Peach Point. The conditions at Peach Point and at Squaw Harbor may be taken as representative of all exposed and protected stations respectively—provided the depth of the water is the same.

If it is true that a constant temperature is more favorable for growth and normal development than one that varies considerably, it would appear, as far as temperature is concerned, that Peach Point is the more favorable environment of the two stations, for here the variation is only 4° C., while it is 16° C. at Squaw Harbor. The difference in the amount of variation is easily explained; the water at Peach Point, though shallow, is continually mixed with water from the cool portions of the lake, while the water at Squaw Harbor, also shallow, is ordinarily not mixed with lake water.

TABLE VI.

Station	Time of Day	Temperature	Ph.
Squaw Harbor	9 A. M.	70° C.	8
	11 A. M.	78° C.	8
	4 P. M.	86° C.	9
Peach Point	10 A. M.	72° C.	8
	11 A. M.	73° C.	8
	4 P. M.	76° C.	8

Note: These readings were taken July 9, 1923.

Temperature has undoubtedly an effect upon the rate of growth. Howard has shown that the growth in fresh-water mussels occurs during the warm summer months. This is likely also true for *Goniobasis livescens*, but the variations in temperature as shown above are hardly sufficient to produce any change in the rate of development. Much less could it be the cause of the remarkable differences in shape and consequently the obesity.

Temperature could also have an indirect effect through the food supply. That it is not a limiting factor in this respect is evidenced (1) by the growth of filamentous algae on the stones where snails were collected, (2) in most instances the shells were heavily covered with algae, and (3) that if they feed on plankton at all—which according to Baker is doubtful—my plankton studies in (23) show that diatoms, desmids, and several unicellular algae are quite abundant even in places that are exposed to the full force of the waves from the open lake, as for instance, the western shore of South Bass.

The oxygen supply cannot be a limiting factor, because most stations are in shallow water, and where this is not the case, as at Old Dock, the snails live near the surface of the water. The wind stirs the water sufficiently to keep it well supplied with oxygen.

Carbon dioxide may affect Mollusks in two ways. If present in large quantities it becomes toxic and thus kills them. Again, if mollusks live in soft water or in water containing only small amounts of Ca Co_3 and Co_2 is present in considerable quantities, it might combine with Ca Co_3 of the prismatic layer, (when the periostrum is ruptured), and the nacre to form the soluble Ca $(HCO_3)_2$, (Cooker, Shira, Clark, and Howard); (Hegner). Ca Co_2 is abundant in all these stations.

My determinations of the concentrations of free CO_2 and the hydrogen ion in this region of Lake Erie show that the water contains at the most very minute traces of CO_2. This of course would be expected, for the water is shallow and almost continually stirred by slight winds, making it easier for the CO_2 to escape. Again as the temperature increases, the capacity of the water to hold CO_2 is decreased. The hydrogen-ion concentration in any of these places is not above PH=8. This means that the water is very decidedly alkaline. Before CO_2 in solution could attack the mineral components of the shell it must neutralize the excess OH-ion of the water. But CO_2 dioxide is not chemically active until it has combined with water to form H_2CO_3, which in turn is ionized to form $H+HCO_3$, and because if it had done this, the H-ion would first combine with OH-ion to neutralize the water, and again because we find the water decidedly alkaline, it follows that an excess of dissolved CO_2 does not exist.

The nature of the substratum is also of great importance in the distribution of mollusks. Adamstone ('21) has shown it to be of importance in the distribution of Mollusca in Lake Nipigon; Cooker, Shira, Clark and Howard have called attention to the importance of the character of the substratum in the case of fresh-water mussels. Howard again in the artificial rearing of fresh-water mussels has ascribed great significance to the nature of the bottom. Krecker ('24) has shown that the substratum is an important factor in the distribution of

Goniobasis livescens. Baker reports *Goniobasis livescens* from 15 stations in Oneida Lake, but in every instant he states that they are found on boulders.

Undoubtedly the substratum does play an important part in the distribution of different species of Mollusca, including *Goniobasis livescens.* But in my opinion it does not account for the great variations in obesities as shown in Table I, column one. Take, for instance, the substrata of Old Dock, Middle Bass, and Hen Island, which are as nearly alike as any three substrata could be. Yet the average obesity at Old Dock is 39.3%, that at Middle Bass is 45.2%, and that at Hen Island is 42.44%. Again the substratum at Sugar Island, on account of the many large boulders, is really more favorable than the substratum at Buckeye. Still the average obesity at Sugar is 49.3%, while that at Buckeye is 47.4%. Apparently the substratum does not account for the differences in obesities.

The depth of the water is another factor that may limit the distribution of Mollusca and they are accordingly divided into deep water species and shore species. No variations in my snails can be ascribed to a difference in depth, since all collections were made in approximately the same depth of water. The water at all the stations except Old Dock does not vary more than two feet in depth, and even here the snails were near the surface.

Food is not only an important factor, but it may become a limiting factor for any form of life, especially animal life. Yet it is not probable that the difference in obesity could be explained on a basis of food. It is certain, as Colton has shown, that a shortage of food may produce dwarfing, but as far as I can tell there exists no shortage of either organic or inorganic food. It has already been emphasized in connection with temperature that organic food is abundant. And under the discussion of CO_2 it has been shown that there is no shortage of $Ca\ Co_3$. Yet if there were a shortage of $CaCo_3$, the only difference that would be likely to be produced would be a reduction in the thickness of the prismatic and the mother-of-pearl layers, and would not necessarily affect the shape nor the length of the shell. Even a total absence of these layers would not produce a great difference in the ratio of the width divided by the length. Incidentally it happens that the obesity is least in Squaw Harbor where the alkalinity is greatest.

Wave action. Adamstone ('21) concludes that aside from the food supply the degree of exposure to wave action is the principal factor that limits the distribution of mollusca in Lake Nipigon. Krecker ('24) has shown that the distribution of *Goniobasis livescens* is definitely correlated with wave action. I have had ample opportunity to confirm Krecker's conclusions. Baker states that in Lake Oneida *Goniobasis livescens* are more abundant on a bouldery shore than on a bouldery point. Perhaps this could be explained on a basis of exposure.

My results as recorded in Table I, show as far as they go conclusively, (1) that variations in obesity are correlated to the exposure to wave action, and (2) that the obesities are directly proportional to the degree of exposure to wave action, i. e., the obesity is increased whenever the degree of exposure is increased.

This is in line with the results obtained by Ball ('22) in the case of certain species of fresh-water mussels. Ball found that in certain species the obesity increased, with an increase in the volume of water flow. It is perhaps well to note that wave action and volume of water-flow, as used by Ball, are comparable, but are by no means identical. Jarring and vibrations play a much greater part in wave action than it necessarily would in a stream. This would probably make no difference in the case of mud-burying mussels, but it makes a big difference for *Goniobasis livescens.* My results also agree with those obtained by Colton ('22) in the case of the Dog Whelk, as indicated in the introduction.

If obesity is a function of wave action, how is this relationship brought about? It has already been indicated that the great differences in obesities are produced in two ways, (1) in some shells in the more exposed situations, the apex is worn off considerably, and (2) the shells in the exposed situations are very bulbous at the base and then taper sharply while in the protected situations the base is no more bulbous than any other part of the shell and they taper off very gradually. The wearing off of the apex accounts only for a small amount of the increase in obesity, for even some specimens from the most protected stations have the apex worn off. It is true, as Table II shows, that there is a decrease in the average lengths in the more exposed stations. But this decrease in lengths is due largely to the fact that in specimens from the exposed places the whorls above the first one are very much narrower than corresponding whorls of the specimens from the protected stations. Again in referring to Table III, we note that the increase in the ratio of the width to the length is due not alone to a decrease in length, but also to a decided increase in the width.

Number (1) can easily be accounted for by the mechanical action of the waves—the wearing off of the apex is analogous to the erosion of rock strata by streams. Number (2) is either a germinal difference or it is the result of the direct effect of the environment—in this case thought to be the wave action.

The assumption that these variations in shape are hereditary and that the whole thing is a matter of natural selection is open to the following objection. If it is a matter of a survival of the fittest—best fitted to the environment—why is there so little overlapping in the protected situations?

Why are practically all the shells at Squaw Harbor and Gibraltar for example elongate, while all the shells at Middle Bass or Sugar Island are of the bulbous or obese type? If conditions at Gibraltar or Squaw Harbor are favorable for the snails with a long slender shell, why would not that same environment be favorable for snails with a short bulbous shell and a larger foot? (The ratio of the length of the aperture to the width of aperture in Squaw Harbor is 167.0, while at Sugar Island the same ratio is 150.2).

Again the assumption that the differences are environmental variations is open to criticism for lack of experimental evidence to that effect. It is true Colton has shown that various environmental factors—see introduction—may cause dwarfing, but it has not been shown for *Goniobasis livescens.* The final answer then will have to wait until breeding experiments can be carried out to show whether these variations are hereditary or not.

Supposing that these variations are not hereditary and that they are the result of wave actions, how could this relationship be explained? The effect of wave action is perhaps of two kinds, (1) it may be the cause of dwarfing, i. e., a snail develops so slowly that it might never develop the full number of whorls. (It is pointed out by Colton that shells of the same size, but of different age have the same number of whorls, (2) it may change the direction of growth; shells instead of becoming long and slender become short and obese.

Just how wave-action produces this effect is not known, neither is it known how other environmental factors produce temporary variations. But it is entirely possible that this jarring coming at some critical period in the development changes the direction of growth.

SUMMARY.

1. The average obesity is directly proportional to the degree of exposure to wave action.

2. The differences in obesity are due to a wearing off of the apex and to a difference in the shape of the shell. The latter accounting for the main part of the difference.

3. The more obese shells have a larger aperture and hence a larger foot.

4. What is true as to the relation between obesity and exposure to wave action in the lake is probably also true for the Scioto and Olentangy rivers near Columbus.

5. It cannot at present be decided whether these differences in shape are due to heredity or whether they are the result of the direct effect of the environment.

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