ATURE CITED

RD. 1942. Studies on parasites of Reelfoot
and checklist of parasites. *J. Tenn. Acad.*

graphy of the Central Basin of Tennessee.
., Bull. 38. 268 p.
freshwater Hirudinoidea of Canada. *J. Fish.*
2.
tics, distribution, and ecology of Colorado
83:1-37.
North American freshwater fishes. U. Calif.

leeches (Annelida: Hirudinea) of North
ater Ecosystems: Identification Manual No.
ce, Washington. 53 p.
udinea): their structure, physiology, ecology,
Press, New York. 201 p.
of the leeches (Piscicolidae) living on fresh-
ica. *Trans. Am. Microsc. Soc.*, **59**:354-376.
ne leeches (Piscicolidae) living on freshwater
bid., **65**:237-249.
of the U. S. National Museum. *Proc. U. S.*

Illinois. *Bull. Ill. State Lab. Nat. Hist.*, **5**:

ROBACK. 1967. An ecosystematic study of the
vannah River. *Proc. Acad. Nat. Sci. Phila.*,

invertebrates of the United States. Ronald

es of Louisiana, with notes on some North
nea, Annelida). *Proc. La. Acad. Sci.*, **30**:

s as new hosts for the nematomorph, *Gordius*

eshwater leeches, exclusive of the Piscicolidae,
ll. Biol. Monogr. 46. 153 p.

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Distribution and Dispersal Mechanisms of Oxytrema (=Goniobasis) suturalis Haldeman (Gastropoda: Pleuroceridae) in the Yellow River, Georgia, U. S. A.

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ABSTRACT: The distribution of *Oxytrema suturalis* Haldeman in the Yellow River drainage of Georgia, U.S.A., was determined. At 10 stations along the Yellow River, dissolved oxygen, *p*H, temperature and turbidity were measured weekly from June 1968 through June 1969. The distribution of *O. suturalis* appeared to be independent of these parameters. Field and laboratory experiments indicated that the combined effects of an unstable substratum, increased stream velocity and vegetation are of paramount importance in restricting the distribution of this species to shoals and rapids. Quadrat samples revealed a highly nonuniform dispersion. *Podostemum ceratophyllum* (riverweed) mats created the optimum microhabitat for *O. suturalis* and appeared to serve as areas from which these snails emigrate to less favorable microhabitats. Positive rheotaxis and upstream migration were demonstrated on a firm substratum, and this behavior may be an effective mechanism for the upstream dispersal of *O. suturalis*. The probability of successful exploitation of new shoals habitats depends on the proximity of the shoals to the source of migration.

INTRODUCTION

Members of the freshwater prosobranch Family Pleuroceridae are found on four continents (Morrison, 1954), yet little is known concerning the effects of environment on their distribution and abundance. Dispersal mechanisms which have led to the many disjunct, but often sympatric, populations extant today are unknown.

Krecker (1924) made one of the earliest attempts to explain the distribution of pleurocerids. *Goniobasis livescens* were most abundant in Lake Erie where substratum and wave action were optimal, but he found no similar correlation with *p*H and carbon dioxide concentration. Dazo (1965) found a greater abundance of pleurocerids in the more alkaline streams that he studied.

Oxytrema proxima was found by Foin (1971) to be restricted to aggregated populations within the headwaters of three river basins. He presented evidence "that aggregation and distribution of *O. proxima* are largely functions of the complex factors influencing sufficient rate of respiration (current and depth) and consequently of the dispersal ability of populations."

Houp (1970) suggested that substratum is the most important factor influencing the distribution of *Pleurocera acuta*, with water depth and current of secondary importance. She measured several physicochemical parameters in the stream, finding a positive correlation between the presence of these snails and high dissolved oxygen, high alkalinity and lack of siltation.

By physiographically relating the distribution of postglacial fossil shells of *Goniobasis* sp. and *Pleurocera* sp. to the present distribution of these species, Wright (1932) traced the probable routes and relative rates of their migration into an Indiana river basin. He did not suggest any mechanisms by which this dispersal took place. Positive rheotaxis and upstream migration were revealed in field studies of *G. proxima* (Crutchfield, 1966) and *P. acuta* (Houp, 1970). Several workers (Allee *et al.*, 1950; Malone, 1965a, 1965b; and Dundee *et al.*, 1967) described probable dispersal mechanisms for various freshwater snails, but these have almost all involved hermaphroditic pulmonates, in which isolated individuals can more easily establish new populations than dioecious forms such as the Pleuroceridae.

Oxytrema (= *Goniobasis suturalis* Haldeman is abundant and widely distributed in Georgia Piedmont streams. However, only Nelson and Scott (1962) have included this genus (identified as *G. postellii*) in a general study on stream productivity (Walker, 1918; Goodrich, 1942). We, therefore, shall attempt to relate its distribution in one of the Piedmont drainage basins, Yellow River, to various physicochemical and geological parameters and discuss possible dispersal mechanisms based on field and laboratory studies.

STUDY AREA

The Yellow River, which drains 1190 sq km of the Piedmont region of Georgia, is one of three major tributaries to the Ocmulgee arm of the Altamaha River system. The Yellow River arises within Gwinnett Co. about 30 km NE of Atlanta and flows 116 km to the SE to converge with the Alcovy and South rivers to form an artificial impoundment, Jackson Lake. The upper half of Yellow River drains a fast-growing metropolitan area which is intruding upon hardwood and pine forests and pastures. The lower drainage consists primarily of forests and farms.

Eleven sampling stations representative of different stream characteristics were chosen (Fig. 1). The headwaters of the river, Station I in Gwinnett Co., follow a smooth course along a narrow channel. Downstream, extensive shoals and rapids occur for 16 km, and Stations II through V (Gwinnett Co.) were in this area of granitic outcrops and boulders. Below Station V there is a smooth flow with only a few small shoals. Station VI (DeKalb Co.) was situated just below a brook which discharged small amounts of fine silt into the river from nearby granite quarries. At Station VII (Rockdale Co.), as much as 1570 ppm of fine silt were recorded until 16 August 1968 from a sand mine effluent a few km upstream. For several months thereafter, thick claylike deposits coated all objects in the streambed as far downstream as Porterdale in Newton Co. Station VIII was situated along shoals below an impoundment at Milstead (Rockdale Co.), Station IX above a second impoundment at Porterdale and Station X 1.5 km downstream near the terminus of Cedar Shoals. Only one small shoal occurs between Station X and Jackson Lake. Station XI (Newton

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Co.) was situated in this region along a sandbar 13 km below Station X. *Oxytrema* was present during this study only at Stations II, III, IV, V, VIII and X. The aquatic angiosperm, *Podostemum ceratophyllum* (riverweed), grew as thick mats on boulders and bedrock in all shoals except at Milstead, where heavy siltation apparently prevented its growth.

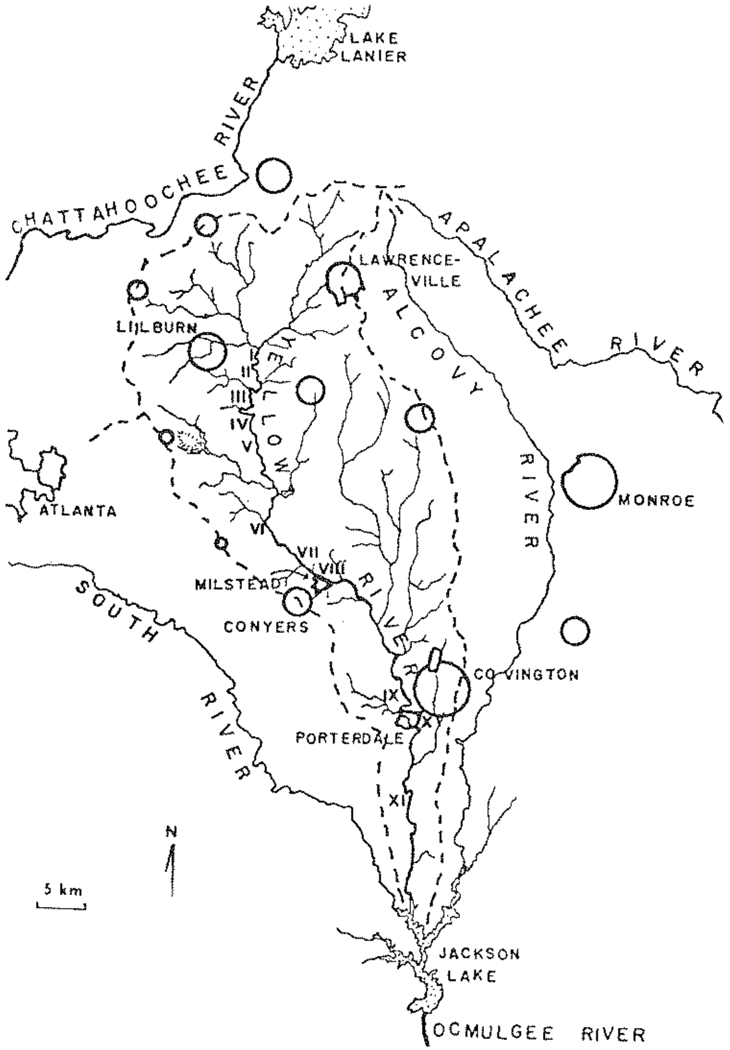


Fig. 1.—A map of the Yellow River basin, indicating the major tributaries and adjacent river basins. Roman numerals show approximate locations of sampling stations

Some organic and industrial pollution occurred at various points. Several small towns emptied treated or raw sewage into the river even though at least two towns took their drinking water from Yellow River.

MATERIALS AND METHODS

From 29 June 1968 to 27 June 1969 physicochemical parameters were measured weekly at 10 of the stations on Yellow River. Dissolved oxygen and *p*H were measured in the field with portable instruments, while max-min thermometers recorded weekly water temperatures for Stations I, III, V and VIII. A Jackson turbidimeter was employed for field determination of turbidities as low as 25 ppm.

On 22 August 1968 50 snails varying from 2.4-9.4 mm in greatest shell diam were transplanted from Station V to Station VI in a cage built of aluminum window screen on a wooden frame. After 7 months the cage at Station VI (23 March 1969) and a control cage at Station V (7 April 1969) were opened and a record made of all snails or empty shells present.

As a further aid to understanding the distribution of *O. suturalis* in Yellow River, snails were placed in a laboratory stream with various combinations of stream velocity, temperature and substratum. This stream consisted of a Plexiglas trough measuring 91 x 25 x 11 cm. The floor of the trough was marked lengthwise on the sides and bottom in 5-cm intervals from 0 to ± 40 cm. At the "upstream" end, water issued from holes on the underside of a Plexiglas tube, and a removable section of Plexiglas created a small reservoir of water which overflowed across and down the runway at a uniform velocity. At the "downstream" end a glass rod was placed across the trough to prevent sediment from washing into the main reservoir.

Dechlorinated tap water was pumped into the trough from the reservoir and was maintained at desired temperatures by a Bronwill Constant Temperature Circulator. By adjusting screw clamps on the two arms of a Y-joint leading from the circulator, water velocity in the trough was controlled by shunting different amounts of water directly back into the reservoir. All experiments were conducted inside a totally darkened walk-in-type refrigerator.

As the Plexiglas presented an exceptionally smooth surface not found in the natural habitat, white Scot towel was placed on the floor of the trough to serve as a stable but rough-textured substratum. The towelling was replaced after every three runs. For unstable substrata, river sediment from Station III was dried and sifted through U. S. Standard sieves to obtain separate sand sizes of 1.0 mm, 0.71 mm, and 0.125 mm. Each was spread evenly over the trough bottom sufficiently deep to prevent crawling snails from contacting the plastic surface. After each run the sand was mixed to disperse any mucus.

Each experiment consisted of six runs using a particular combination of physical parameters. Twelve snails were observed for each run, and three runs employed large snails (6.4-7.1 mm diam) while the other three runs employed small snails (2.8-3.4 mm diam). Individuals were arranged at "0 cm" on the grid with three facing each quadrant of the compass to preclude bias of the results due to their initial orientation. Each run lasted 30 min, after which the orientation and longitudinal position of each snail were recorded.

Quadrat samples were taken near Stations III, V, VIII and X using a modified Surber stream-bottom sampler with a square sampling area measuring 0.5 m on a side. All vegetation and the upper several centimeters of sediment, if any, were removed from the enclosed area, and all snails were graded according to greatest shell diameter. Quadrats were taken in 1968 on the following dates: V-1, 1 July; V-2, V-3, 7 August; V-4, V-5, V-6, 14 August; V-7, V-8, 24 August; III-1 through III-4, 3 September; X-1 through X-4, 5 September; and V-9, V-10, 2 November. Quadrats V-1 through V-8 and III-1 through III-4 were taken along transects at varying distances due to the unsuitability of the sampler on uneven substrata. The four quadrats near Station X were selected as sampling areas with probable maximum densities of *Oxytrema.*

RESULTS AND DISCUSSION

Distribution.—*Oxytrema* first appeared between Stations I and II and occurred downstream through most of the region to the termination of the shoals below Station V and in the lower reaches of three of the six major tributaries within this section. Turkey and Watson creeks, which empty into a 0.8 km section of the river above Station III, occasionally have exposed bedrock and boulders in the streambeds except within about 75 m of the mouth, where there is a sandy substratum. On the undersides of the boulders were large numbers of small- and medium-sized *Oxytrema,* but snails were absent from the sandy substratum.

Garner Creek, about 0.5 km below III, has a shelving rock base over much of its streambed, which forms a series of cascades and pools with sandy or rocky bottoms. The final 400 m of this stream is a very soft and unstable sand and gravel substratum with actively eroding banks. In contrast to Turkey and Watson creeks, no *Oxytrema* were found on or beneath stones upstream or in the final 400 m except on submerged logs about 20 m above the mouth.

The next two tributaries downstream, Pounds and Jacks creeks between IV and V, have primarily alluvial substrata without *Oxytrema.* A sixth stream empties onto shoals at their termination below Station V. Immediately above the mouth of this small stream a sandy substratum extends about 65 m upstream succeeded by a small ravine. A storm conduit at this point completely blocks movement of snails. However, since *Oxytrema* occurred on bedrock and boulders both above and below the conduit, it is apparent that the population just upstream had survived and reproduced for a number of years in this isolated situation.

Between Stations V and VIII two small but dense populations were found in small shoals. In the extensive shoals below the Milstead dam (VIII) a very sparse population was present during this study apparently due to the heavy siltation. The most downstream population occurred in the lower portions of Cedar Shoals (X).

Although populations of *O. suturalis* in Yellow River were limited to well-defined areas, there appeared to be no real relation to the physicochemical parameters, which are summarized in Table 1 and Figure 2. Percent dissolved oxygen (D.O.) was high throughout the year at all stations, and only at Stations I, II and XI were saturations below 80% ever recorded. The t statistic showed highly significant differences ($P < .01$) of D.O. between all adjacent stations except between II and III and VI and VII, which were not significant. *Oxytrema* occurred in the lower Yellow River only in areas (VIII and X) which tended toward a supersaturated D.O. level, but in upper Yellow River it was found also in areas (II and III) with mean D.O. values below saturation. Thus, the occurrence of *Oxytrema* in areas where

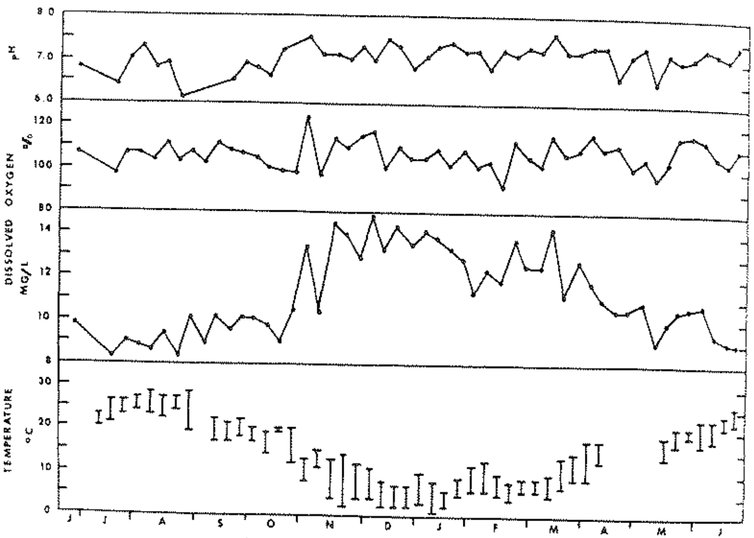


Fig. 2.—Temperature ranges, dissolved oxygen, and *p*H at Station V measured weekly from June 1968 through June 1969

Table 1.—Mean physicochemical parameters measured weekly during 1968-1969 at 10 stations along the Yellow River. Asterisks indicate *Oxytrema* populations present

	I	II*	III*	V*	VI	VII	VIII*	IX	X*	XI
D.O. (mg/l)	9.58	10.19	10.48	11.17	10.29	10.54	10.91	9.84	10.40	9.90
D.O. (%)	88.9	95.0	98.0	105.3	98.8	99.4	105.2	95.2	101.5	95.9
*p*H	7.02	7.03	6.98	7.08	6.93	6.89	7.23	6.78	7.00	6.88
C	13.41	....	13.79	14.41	....	....	14.35	....	......	....

D.O. approached or exceeded saturation appears to have been only coincidental with increased aeration caused by a high gradient of the river.

Hydrogen ion concentrations were related somewhat better to the presence of *Oxytrema* populations than was D.O. These snails were usually found where neutral or slightly alkaline conditions prevailed, but in a few cases, Station I and Garner and Big Haynes creeks, where conditions were slightly alkaline, no *Oxytrema* were found. Differences in *p*H were highly significant between Stations VII and VIII, VIII and IX, IX and X, III and VIII, V and IX and VIII and XI; and significant between V and VI, V and VIII, and X and XI. The *p*Hs obtained in this study tend to agree with the range of 6.9-7.9 reported by Nelson and Scott (1962) for a station on the Middle Oconee River populated by *Goniobasis postellii* about 60 km E of this study area, although the present study revealed a wider range (6.1-8.4) in areas populated by *O. suturalis*.

Since similar temperatures and turbidities were recorded for all stations, apparently these parameters have little influence on the distribution of *Oxytrema*. Mean temperatures were not significantly different among the stations. Temperatures varied from 0 C in winter to 30 C in summer, a wider range than was found in the Middle Oconee (5.8 to 27.3 C) by Nelson and Scott (1962), but they did not take continuous readings as was done in this study.

The available calcium content of Yellow River water was not measured, but Cherry (1961) reported a hardness below 60 ppm, and Nelson and Scott (1962) reported a bicarbonate alkalinity from 16.15 to 21.15 ppm in the Middle Oconee. Herrmann (1954) found up to 14% CaO in analysis of horneblende gneisses, granites and schists exposed within the Yellow River drainage, but calcium becomes available only upon the slow weathering of these minerals. Sufficient amounts of calcium for *O. suturalis* may be provided through weathering and this may then be used by *aufwuchs* upon which the snails feed. This may be another reason why they are limited in their distribution to regions of extensive boulders and outcrops.

The transplantation of *Oxytrema* within the drainage system provided a further clue that some parameter other than physicochemical factors governs the distribution of this species. After 7 months, 95% of the snails at Station VI were alive compared to 97% of the control snails at Station V. Although both cages were full of sand and muck, the high survival rates indicate that *O. suturalis* can live indefinitely beneath this type of substratum. The suitability of this type of habitat for reproduction and establishment of permanent populations was not determined.

Experiments.—Analysis of variance revealed significant variation in the displacement of *Oxytrema* in a laboratory stream at different velocities and highly significant variation in displacement on different substrata (Table 2). The rate of upstream migration was greatest at a water velocity of 5 cm/sec for both large and small snails, although the substratum was different for each size snail. At 10 cm/sec considerable movement upstream was limited to the large snails on the paper towel substratum, while on the sand substrata upstream movement in both sizes was reduced or downstream displacement was increased. By contrast, downstream displacement of both sizes of snails was greater and most consistent on 1.0 mm sand. Downstream displacement of the large snails was least on the paper towel and 0.125 mm sand substrata while downstream displacement of the small snails was least on paper towel.

A second experiment compared the displacement of *Oxytrema* at 7 C and 20 C and at three stream velocities (Table 3). Analysis of variance revealed a significant difference in displacement between the two temperatures, but no significant differences among the velocities. There appeared to be little displacement of the small snails at any

TABLE 2.—Mean displacement in cm of *O. suturalis* upstream (+) or downstream (—) in 30 min at 20 C using different combinations of substratum velocity and snail size

		Substratum			
		Towel	1.0 mm sand	0.71 mm sand	0.125 mm sand
Small					
	0	+3.0	—0.9	—0.4	+0.5
velocity	5	+2.6	—4.4	+2.9	+13.3
(cm/sec)	10	+4.8	—9.4	—0.6	—3.9
	15	*	—5.3	—6.7	—9.2
Large					
	0	+4.9	+2.2	—1.0	—0.1
velocity	5	+30.8	—2.8	+2.9	+4.9
(cm/sec)	10	+19.1	—9.3	+0.5	+0.8
	15	*	—13.4	—1.9	+0.8

* Snails washed out of trough

TABLE 3.—Mean displacement in cm of *O. suturalis* upstream (+) or downstream (—) in 30 min on a paper towel substratum using different combinations of velocity, temperature and snail size

Temperature		7 C	20 C
Small			
	0	—0.4	+3.0
velocity (cm/sec)	5	+1.3	+2.6
	10	—0.4	+4.8
Large			
	0	+0.4	+4.9
velocity (cm/sec)	5	—0.1	+30.8
	10	—2.0	+19.1

velocity at either 7 C or 20 C, but the large snails showed a distinct upstream migration at 20 C.

Observations on the orientation of the test snails were inconclusive. The only definite positive orientation after 30 min occurred with the large snails on the paper towel substratum, when only two of 36 snails were not oriented upstream at 5 cm/sec, and when only five of 36 were not oriented upstream at 10 cm/sec.

These experiments revealed effects of increased velocities on the stability of both the snail and the substratum. Snails of both sizes were washed downstream occasionally at the beginning of experiments at velocities of 10 and 15 cm/sec but never at 5 cm/sec. At the termination of most experiments at all velocities, one or several snails were oriented and crawling downstream. At 15 cm/sec all three of the sand substrata shifted very slowly downstream, and sand was washed from around and beneath the snails. These results, showing greatest stability on the stable artificial substratum and relative instability on the sand substrata, were supported by the quadrat samples which revealed only a few snails on sand substrata in the river channel but many snails on the rock substratum. Substratum, then, seems to exert a major influence on the distribution of *O. suturalis*.

In his Lake Erie study, Krecker (1924) observed that *Goniobasis livescens* was more abundant in still water than in water disturbed by waves. In rough water it occurred on large stones, while in calm areas it was found on comparatively small stones. He also noted that waves might influence snails by moving the substratum or the snails themselves, and he considered movement of the substratum through wave action to be "a very important factor controlling distribution" (Krecker, 1924). His observations apply quite well to Yellow River, with the wave action of the lake having an effect comparable to stream currents. In pools without strong currents, *Oxytrema* can be found on vertical mud banks and on sloping sandy sediments where it apparently fares successfully until periods of high water, when the pools and stream banks are scoured and sediment is eroded or deposited.

Oxytrema occurred on rocks and in *Podostemum* mats in the river at velocities much greater than those employed in the laboratory but, as Krecker (1924) explained, these snails undoubtedly had been subjected, or had subjected themselves, to a gradual increase in stream velocity and so were able to withstand these stronger currents.

In conclusion, it seems that substratum alone does not limit the distribution of *O. suturalis* to shoals, but that both alluvial substratum and stream velocity create an unstable condition to which this species is not adapted.

Dispersion.—Of the 18 quadrats at three stations where *O. suturalis* was found, all except V-6, V-7, V-8 and X-1 were on thick *Podostemum* mats covering bare rocks and gravel in the stream; V-6 had both *Podostemum* and sand substrata; V-7 and V-8 had entirely a sand substratum, being located in the main stream channel; X-1 had a shallow sand substratum on bare rock. The quadrats yielded the following total numbers of *Oxytrema* (1.4 mm diam or larger): V-1, 53; V-2, 56; V-3, 467; V-4, 397; V-5, 236; V-6, 7; V-7, 21; V-8, 11; V-9, 215; V-10, 745; III-1, 408; III-2, 206; III-3, 129; III-4, 290; X-1, 61; X-2, 10; X-3, 6; X-4, 37.

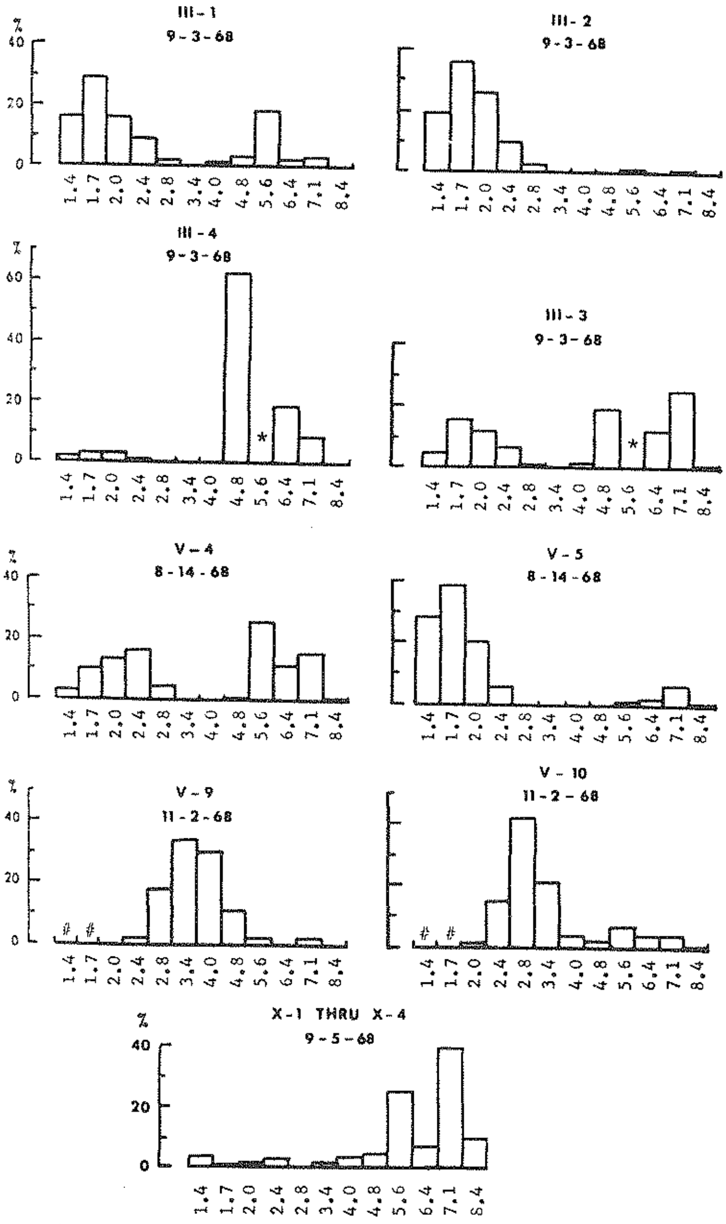
There was wide variation in total numbers of individuals taken from the quadrats within each population. For example, although the microhabitats of quadrats V-3 and V-5 appeared identical, V-3 produced twice as many individuals as V-5. However, quadrats V-3 through V-8 formed a transect across the river with the main channel and strongest currents in the area of quadrats V-6, 7 and 8. Hence, the disparity between quadrats V-3 and V-5 may reflect a trend toward less density as the quadrats become deeper and approach the stream channel. Similarly, quadrat V-10, located only 0.5 m from the stream bank, yielded more than three times as many snails as quadrat V-9, located 3.5 m from the edge.

Numbers of snails collected from different populations also showed important differences. The quadrats at Stations III and V yielded by far the most individuals, while a quadrat at Station VIII yielded no *Oxytrema.* However, random collections at Station VIII of the first 100 snails observed within a 2-hr period in October 1968 produced no individuals smaller than 7.1 mm in shell diam. Widely dispersed quadrats at Station X yielded only relatively few *Oxytrema* but large numbers of the operculate *Somatogyrus alcoviensis* (Krieger, 1972). Thus, the general area of Stations III and V apparently most nearly approaches the optimum environmental conditions for this species in Yellow River.

At Station VIII poor conditions for survival and reproduction were indicated in 1968 and 1969. The only noticeable difference between Stations V and VIII which might have affected the density of *Oxytrema* was the temporary heavy siltation of the river below Station VI until mid-August 1968. The absence of snails smaller than 7.1 mm diam at Station VIII suggests that reproduction had failed entirely for one season or more, particularly during the summer of 1968. Because *Oxytrema* deposits its eggs on stones and on the shells of other snails (Morrison, 1954; Bickel, 1968), the heavy siltation during 1968 probably suffocated the eggs and any newly hatched juveniles. By May 1974, however, this population had increased noticeably and juveniles were present.

In areas of Yellow River such as the Milstead shoals, where catastrophic events have almost or completely extinguished large populations of *Oxytrema,* tributaries in the immediate vicinity with surviving populations should be of extreme value in reestablishing the species in the river, for without these population reserves reestablishment would be dependent upon the success of other dispersal mechanisms. No populated tributaries exist around the Milstead shoals.

Organic pollution, though present in small amounts at various



* Included in 4.8 mm size group.

\# These size classes were not collected.

Fig. 3.—Histograms showing size distribution of *O. suturalis* taken from 25 m^2 quadrats. Each size class, representing greatest shell diameter in mm, is shown as percentage of the total sample

points along the river, is not believed to be responsible for the relative differences among the populations.

Histograms showing summer size classes as percentages of the total sample (Fig. 3) revealed a highly nonuniform dispersion of *Oxytrema* by size. With only one exception (III-4), all the quadrats at Stations III and V yielded high proportions of snails smaller than 3.4 mm which may indicate high productivity in this population. Quadrat V-3, on 7 August 1968, may have been taken during or just after the peak of the egg-laying season, as hundreds of snails smaller than 1.1 mm and many of microscopic size were obtained from this sample. In quadrats at Station X, however, a majority of the snails were of the largest sizes and only a small proportion or none represented small sizes. In contrast to the upper river population, these results may indicate less favorable environmental conditions for reproduction or for survival of eggs or juveniles.

Except for quadrats V-9 and V-10, all quadrats at Stations III, V and X possessed very few or no snails in the size range 2.8 to 4.0 mm (Fig. 3), which indicates at least two age groups of *O. suturalis.* Dazo (1965) reported a 3- to 4-year life span for two pleurocerid species in Michigan, with a single egg-laying period each year. Histograms (Fig. 3) for quadrats V-9 and V-10, taken in November 1968, reveal an increase in the size of the smaller snails, with the largest proportion occupying the 2.8-4.0 mm range.

Dispersion and relative density within each population suggest that substratum and stream velocity affect the microhabitats occupied by this species. *Podostemum* mats contain many more *Oxytrema* than the other shoals microhabitats, and these dense areas appear to serve as "population loci" from which the snails migrate to less favorable areas. During periods of low water and relative stability of the river bottom, *O. suturalis* may emigrate from these loci into temporarily suitable microhabitats until the next period of high water, when they are washed away or are buried under new silt deposits. The greater density of snails in *Podostemum* mats probably may be partially explained by the fact that this plant usually grows on stones which are permanently submerged but never silted. Furthermore, stream velocities are reduced within these mats of vegetation which protect snails from extreme currents which otherwise might dislodge them. Thus, these plants occupy or possibly create the only microhabitat which satisfies the stability requirements of *Oxytrema* on a year-round basis. Stones without *Podostemum* almost always are frequently exposed, receive a torrential current, or are permanently or periodically silted.

Dispersal.—The dispersal mechanisms of the freshwater Gastropoda, many species of which are wide-ranging or occur in temporary or isolated aquatic habitats, have been a subject of much speculation. Malone (1965a) demonstrated possible transport of *Lymnaea obrussa* and *Promenetus exacuous* on waterfowl but concluded (1965b) that dispersal of *Physa anatina* and *Helisoma trivolis* as egg masses, juveniles or adults via the intestinal tract of birds is unlikely. *Succinea* spp. and *Physa* sp. were found on several species of waterfowl (Dundee *et al.*, 1967). Allee *et al.* (1950) surmised that wind may transport tiny snails over considerable distances, and Purchon (1968) recorded the deposition of a large number of the freshwater mussel, *Anodonta* sp., on land during a rainstorm.

The occasional transport of *Oxytrema* by birds or wind is a possible mechanism for the successful exploitation of new areas by this species. Dazo (1965) reported that the pleurocerid, *Goniobasis livescens,* mates during autumn but does not lay eggs until spring. The reproductive cycle of *O. suturalis* has not yet been determined, but if it is similar to *G. livescens,* then a single fertilized female arriving in a suitable location, through whatever means, could conceivably give rise to a new population. Some unknown mechanism also may operate to transfer viable eggs to new locations.

Within single river drainages, the present study suggests two mechanisms for dispersal: displacement downstream by water currents, and migration upstream. Recent field studies have revealed migration and positive rheotaxis in the pleurocerids, *O. proxima* (Crutchfield, 1966) and *Pleurocera acuta* (Houp, 1970). *Oxytrema suturalis* demonstrated these characteristics both in the laboratory and in the field, where individuals near the mouths of small tributaries would be expected to migrate up these streams. Nevertheless, in this study *Oxytrema* occurred above the mouths of only three tributaries, even though many streams enter the river in populated areas, because only these three tributaries possessed a bedrock or boulder-filled streambed within 75 m of their confluence with the river. All the other tributaries had sedimentary substrata extending long distances upstream. As the other physicochemical parameters of the tributaries were very similar to those of Yellow River, substratum appears to be the only factor preventing the establishment of populations in most of these streams.

A good example of the importance of substratum is illustrated by Garner Creek, which has shoals and *Podostemum* but not *Oxytrema,* and which has an unstable substratum in its final 400 m. On a solid substratum this snail conceivably might progress indefinitely upstream from the river; but in Garner Creek the extent of upstream migrations would be limited to the distance that could be traveled between periods of high water, when the sandy bottom is relatively stable. At a maximum rate of 43 cm/30 min observed in the laboratory, or 21 m/day, *O. suturalis* must travel directly upstream for 19 days to reach the extensive shoals 400 m above the mouth of Garner Creek. A depth gauge at Station III, just upstream, indicated over 40 days without an increased stream flow. However, the probability of a snail reaching these shoals over even a longer period seems extremely remote due to such variables as feeding and eddy currents. Moreover, the chance that sufficient numbers would reach these shoals to establish and maintain a population seems minute indeed.

Similarly, Big Haynes Creek, the largest Yellow River tributary, seems highly suited for *O. suturalis*, but swamps in the lower reache of this stream apparently have provided an effective barrier withou the successful operation of other dispersal mechanisms.

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LITERATURE CITED

ALLEE, W. C., O. PARK, A. E. EMERSON, T. PARK AND K. P. SCHMIDT. 19 Principles of animal ecology. W. B. Saunders Co., Philadelphia. 837 p

BICKEL, D. 1968. *Goniobasis curreyana* Lyoni, a pleurocerid snail of wes central Kentucky. *Nautilus*, **82**:13-18.

CHERRY, R. N. 1961. Chemical quality of water of Georgia streams, 1957-58 a reconnaissance study. *Ga. Geol. Surv. Bull. No. 69*. 100 p.

CRUTCHFIELD, P. J. 1966. Positive rheotaxis in *Goniobasis proxima*. *Nautilu* **79**:80-86.

DAZO, B. C. 1965. The morphology and natural history of *Pleurocera acuta* an *Goniobasis livescens* (Gastropoda: Cerithiacea: Pleuroceridae). *Mala cologia*, **3**:1-80.

DUNDEE, D. S., P. H. PHILLIPS AND J. D. NEWSOM. 1967. Snails on migrato birds. *Nautilus*, **80**:89-91.

FOIN, T. C. 1971. The distribution pattern of the freshwater prosobran gastropod *Oxytrema proxima* (Say). *J. Elisha Mitchell Sci. Soc.*, 87 1-10.

GOODRICH, C. 1942. The Pleuroceridae of the Atlantic Coastal Plain. *Occ. Pap. Mus. Zool. Univ. Mich. No. 456*:1-6.

HERRMANN, L. A. 1954. Geology of the Stone Mountain-Lithonia Distri Georgia. The Geological Survey Bull. No. 61. Ga. State Div. of Co servation, Dep. Mines, Mining and Geology. 139 p.

HOUP, K. H. 1970. Population dynamics of *Pleurocera acuta* in a central Ke tucky limestone stream. *Am. Midl. Nat.*, **83**:81-88.

KRECKER, F. H. 1924. Conditions under which *Goniobasis livescens* occurs the Island Region of Lake Erie. *Ohio J. Sci.*, **24**:299-310.

KRIEGER, K. A. 1972. *Somatogyrus alcoviensis*, new gastropod species fr Georgia (Hydrobiidae). *Nautilus*, **85**:120-125.

MALONE, C. R. 1965a. Killdeer (*Charadrius vociferus* Linnaeus) as a means dispersal for aquatic gastropods. *Ecology*, **46**:551-552.

———. 1965b. Dispersal of aquatic gastropods via the intestinal tract of wa birds. *Nautilus*, **78**:135-139.

MORRISON, J. P. E. 1954. The relationships of old and new world Melanian *Proc. U. S. Natl. Mus.*, **103**:357-394.

uralis, but swamps in the lower reaches
e provided an effective barrier withou
er dispersal mechanisms.

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e U. S. National Museum for assistance in
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RATURE CITED

MERSON, T. PARK AND K. P. SCHMIDT. 1950
gy. W. B. Saunders Co., Philadelphia. 837 p.

arreyana Lyoni, a pleurocerid snail of wes
s, **82**:13-18.

quality of water of Georgia streams, 1957-58.
a. *Geol. Surv. Bull. No. 69*. 100 p.

ve rheotaxis in *Goniobasis proxima. Nautilus*

gy and natural history of *Pleurocera acuta* and
tropoda: Cerithiacea: Pleuroceridae). *Malo-*

AND J. D. NEWSOM. 1967. Snails on migratory
.

ution pattern of the freshwater prosobranch
xima (Say). *J. Elisha Mitchell Sci. Soc.*, **87**:

oceridae of the Atlantic Coastal Plain. *Occas.
ich. No. 456*:1-6.

ogy of the Stone Mountain-Lithonia District
Survey Bull. No. 61. Ga. State Div. of Con-
ining and Geology. 139 p.

dynamics of *Pleurocera acuta* in a central Ken-
Am. Midl. Nat., **83**:81-88.

ons under which *Goniobasis livescens* occurs in
e Erie. *Ohio J. Sci.*, **24**:299-310.

gyrus alcoviensis, new gastropod species from
Nautilus, **85**:120-125.

(*Charadrius vociferus* Linnaeus) as a means of
tropods. *Ecology*, **46**:551-552.

uatic gastropods via the intestinal tract of water
-139.

relationships of old and new world Melanians.
103:357-394.

NELSON, D. J. AND D. C. SCOTT. 1962. Role of detritus in the productivity of a rock-outcrop community in a Piedmont stream. *Limnol. Oceanogr.*, **7**: 396-413.

PURCHON, R. D. 1968. The biology of the Mollusca. Pergamon Press, New York. 560 p.

WALKER, B. 1918. A synopsis of the classification of the fresh-water Mollusca of North America, north of Mexico, and a catalogue of the more recently described species, with notes. *Misc. Publ. Mus. Zool. Univ. Mich. No. 6*: 1-213.

WRIGHT, H. P. 1932. Aquatic Mollusca of the Tippecanoe River System. Part I. Post-glacial migration and present distribution of four species of snails. *Ecol. Monogr.*, **2**:233-259.

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