Illinois State Laboratory

of

Natural History

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FRESH WATER FISHES AND THEIR ECOLOGY

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1914

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By Stephen A. Forbes

When we watch a summer thunder storm, which covers the earth with a sudden flood and makes rivulets by the road-side, each carrying down to the smaller streams its load of leaves and other organic debris, together with the lighter parts of the soil, and when we see these silt-laden streams unite in rivers turbid with the rich spoil of the land, we are inclined to lament the enormous and oft-repeated waste, seeing no way in which it can be recovered in any considerable measure to the use of man; but if we follow it to the lake bottom and the river bed we shall see much of it arrested there, to become an aquatic soil, partly muddy water and partly wet mud, more fertile even than the richest fields, and sustaining a new population of plants and animals, of many grades and classes, one climbing upward, as we may say, upon the shoulders of another, to reach a level which makes them accessible again to our use.

Since the waters which wash the surface of the earth fall virtually lifeless and sterile from the sky, whatever population they eventually contain must evidently be supplied from the contributions made to them by the earth, including, of course, the organic and inorganic substances dissolved out of the earth by surface wash and underground filtration. The aquatic population of a lake or stream is thus sustained by the wastes of the land—materials which would otherwise be carried down practically unaltered to the sea; and our rivers and lakes may be looked upon as a huge apparatus for the arrest, appropriation, digestion, and assimilation of certain raw materials about to pass from our control, valueless and sometimes deleterious as they leave us, but capable of being worked over, renovated, and returned to us in new and valuable forms, mainly as fishes available for food.

The raw materials thus contributed by the land vary according to their origin. In uncivilized nature they were mainly the washings and sweepings of the primitive prairie and forest, rich in carbon but with a minimum amount of nitrogen. With the occupation of the country, the cultivation of its lands, and the building of towns and cities, the animal wastes are increased, with their larger increment of nitrogen, and larger quantities of the soil itself are swept into the streams—all alike available

* Read at the University of Chicago, August 20, 1913.

in the end as containing food for aquatic plants and animals, and so finally for the support of man. Even the sewage of great cities is to be classed with the rest as an available resource, capable of being arrested, redeemed, and returned to us in acceptable form, provided that certain conditions are observed necessary to the protection of these organs of digestion against chemical poisoning and against a mechanical overloading with more food stuffs than they can continuously assimilate. From this point of view we may say that as the land loses fertility, the waters should gain; and if they do not, it is because of faulty management.

We may be helped to an analysis and understanding of the construction and operation of this aquatic apparatus of appropriation and assimilation if we so arrange the principal organisms of our Illinois waters in the form of a table of feeders and their food, of eaters and things eaten, that we may see at a glance for each group of fresh water animals both what it feeds upon and what feeds upon it in turn. (Fig. 1.)

This table, I need hardly say, might be indefinitely complicated and enlarged; but I am intending it only to show the main features of the relationship. If I had made it to include details and exceptions and organisms of secondary importance, or even internal parasites, it would have been too complex for our present purpose.

Notice especially the evident predominance of fishes in this scheme of vital relationship, shown by the fact that they feed upon everything in the bill of fare from terrestrial wastes to frogs, while they are, on the other hand, their own worst enemies, more fishes falling a prey to other fishes than to all other aquatic enemies combined. Further, if we take account not only of the food of fishes, but also of the food of their food, we shall see that it covers every item on our table excepting a few at the lower right-hand corner relating to turtles, serpents, birds, and mammals, including, of course, man; and that even these exceptional groups themselves all feed on fishes. It is thus graphically evident to us that to understand the ecology of fishes completely we must study also the ecology of every class of living things in the midst of which they live. We must even go outside the aquatic environment and analyze the relations of fishes to their terrestrial enemies, and to many terrestrial sources of their food. To handle anything so complex, we must have the aid of such groupings and classifications as our materials will permit; and for even so brief a discussion of the topic as is possible for us today, a rough classification will be useful.

Ecological classification of animals may take either one of two principal directions, or indeed both of them in turn. Ecology being the relations of interaction between organisms and their environment, if we take it up from the side of the organism we shall naturally prefer a classification based on differences of animal reactions to the same environmental conditions—differences of behavior, that is—and our classification will be a *habit* classification; if it is the environment, on the other hand, which interests us primarily, we shall assemble our animals in groups according to their environmental preferences, and our classification will be a *habitat* classification. The habit classification is fundamentally physiological and the habitat classification is primarily physical or spatial, and the two cut across each other, often at right angles, each habitat containing associated animals of various *habit,* and each habit group being distributed, as a rule, over various *habitats.* A mill pond, for instance, is a very definite habitat, but it may contain fishes of every sort of habit; strictly piscivorous fishes form a very definite habit group, one or more of which may be found in almost any kind of aquatic habitat.

I do not myself favor the attempt to reduce the facts and materials of animal ecology to one hard and fast, all-including classification, such as biologists attempt to establish, in the face of almost infinite difficulties, for descriptive botany and zoology; but I believe that our ecological classifications should be as various as the objects we have in view, being made sometimes on one basis and sometimes on another, as best serves our purpose at the time. It will serve my present purpose to classify fishes first in general terms according to the principal elements of their food, thus forming habit groups, without present reference to their habitats.

I must first acknowledge, however, that fishes can not be completely and clearly divided into mutually exclusive groups upon this basis, for their choices of food and their capacities for its appropriation are not sufficiently fixed and definite in the different species to make this practicable. I can best describe the actual situation by saying that fishes have a common body of food resources of miscellaneous character upon which many of them draw almost indiscriminately according to the circumstances at the time, but that from this common mass of resources, habits, and capacities there is a tendency to specialize in various directions, which tendency goes to its limit in some species, halts at various intermediate stages in others, and in still others is hardly discernible at all. Moreover, the food choices of scarcely any fishes are so definite and unchangeable as to be unmixed and identical under all conditions, in all parts of their habitat, and at all times of the year. We shall find, indeed, the same state of affairs when we come to deal with a habitat classification; and if we look the whole field of ecology over we shall see it rather characteristic of an ecological classification generally, especially on the animal side. We can nevertheless profit greatly by such groupings of our heterogeneous data as are still possible, if we admit the limitations of the scheme and understand their significance.

One of the most peculiar of our food habitat groups contains the gizzard-shad and the stone-roller as its most notable representatives, together with a few minnows less strictly limited to it, all of them characterized by unusually long, convoluted intestines, the gizzard-shad having also the digestive surface still further increased by the development of a very large number of finger-like cæca on its anterior section. These fishes all discard intermediary agents, and help themselves to the raw materials of their food in the form of the mere mud and slime of the bottom, which contains, of course, a considerable quantity of organic debris, mostly of vegetable origin. They form the group of the *mud-eaters.* (Figs. 2, 3, and 4.)

The gizzard-shad, although but little eaten, is one of our most valuable fishes, since it is enormously abundant in our large waters, both rivers and lakes, competes with no other species for food, and is itself the principal food of our game or predaceous fishes—the most highly valued products of our fisheries. It affords, also, a remarkable instance of a transformation or development in the food habits and resources of fishes, coincident with increase in size. From the time this fish hatches from the egg until it comes to an inch or so in length it is as slender as a minnow, with the alimentary canal a simple straight tube. Still more remarkable, although the mouth of the adult is perfectly toothless, the young have, at this stage, a row of conical, pointed teeth upon the upper jaw. (Fig. 5.) Teeth would evidently be useless to it in sucking up mud or straining out plankton from the water; but to the larva—if such it may be called—they must be very useful, for instead of being a mud-eater the fish is predaceous in this stage, its prey being the minute animals of the plankton, especially the Entomostraca, which it pursues and captures one by one as a pike might capture minnows. With its growth and transformation it changes its habits slowly, its food becoming more mixed with mud; but it develops effective gill-rakers also, and we sometimes find the stomach of the adult stuffed with a fairly clean plankton.

The stone-roller, although a mud-eater and especially equipped for that function by its long intestine, wound in a close coil around the air-bladder, nevertheless avoids muddy waters as a rule, preferring quick currents over rocky streams, from the stones of which it nibbles and sucks the sediment and slime.

The most remarkable in many ways of our American fresh-water fishes is the Polyodon or paddle-fish (Fig. 6), and in nothing is it more peculiar than in the fact that, although it is one of our largest fishes, reaching a maximum length of six feet and a weight of a hundred and sixty pounds, it is essentially a plankton-eater, feeding largely, and sometimes almost wholly, on the smallest aquatic animals and plants, for the appropriation of which it has, in its gill-rakers, a straining apparatus scarcely less effective than that of the whalebone whale. To strain out the plankton, it holds its enormous but weak-jawed mouth wide open as it swims about, permitting the water to flow through its very wide gill slits, getting thus not only the smallest animals and plants, but many insect larvæ also of kinds abundant on the open bottom in comparatively shallow water. It is, indeed, a living, fine-meshed, water-net. This fish is our only proper member of the special class of plankton-eaters, although plankton is taken in quantities at times, especially in spring, by a considerable number of other fishes of various sizes, all with long and fine gill-rakers—structures which have, in fact, no other use than to strain from the water food particles too small to be taken in any other way. The crappies and certain other sunfishes will often so gorge themselves with plankton by this means that the bulging of their stuffed stomachs can be seen from the outside. Lake herring and white-fish are other examples of this class, not dependent, however, upon plankton as their most important food.

While adult plankton-eaters are thus relatively few, it is an interesting and peculiarly important fact that plankton is almost the sole infant food of nearly all our fresh-water fishes, of whatever kind or adult food habit. The hatching season of most of our fresh-water species is, in fact, the prime season of the year for plankton production in the shallows and back-waters where most fishes spawn; and the minute mouths and gill slits of the very young are perfectly fitted, without special adaptation, for the capture of this microscopic prey.

I have already given you, in the gizzard-shad, one example of a young fish especially armed with teeth for this sort of hunting, and I may mention, in passing, another case of the kind which is even more remarkable. The common whitefish of the Great Lakes is, as you all know, quite toothless, and, as an adult, is what the Germans call a *Kleintierfresser*—a convenient word for which we can hardly substitute its literal translation—a small-animal-devourer. The recently hatched whitefish, however, is a pure plankton-eater, and it must snatch its minute prey, one at a time, from the sparsely inhabited waters of the open lake. It is very important to it, consequently, that it should not miss its catch or lose its hold, and we find it specially equipped against this accident with four acute, curved, raptatorial teeth on its lower jaw (Fig. 7), as effective against a *Cyclops* or a *Diaptomus* as the fangs of a tiger against an antelope.

Such transformations in food habit with increasing size are, indeed, the rule among fresh-water fishes. Starting together as plankton-eaters, they presently diverge in habit, reaching their adult food stage through two or three degrees of change. The sheepshead (Fig. 8), for example, begins, like the rest, with plankton, becomes insectivorous when it is a few inches long, living almost wholly on the insect larvæ of the bottom, and as it reaches adult size its habits change again to those of a mollusk-eater, in adaptation to which it develops in its throat a powerful crushing apparatus, with pharyngeal jaws capable of smashing the thickest shells of our water snails, and even those of clams or mussels of considerable size.

Other mollusk-eaters are the Great Lakes sturgeon (Fig. 9) and certain species of the catfish (Fig. 10), sucker (Fig. 11), and sunfish families (Fig. 12), several of them especially equipped for crushing shells—the suckers and sunfish by stout, blunt teeth set in their strong pharyngeal jaws (Fig. 13), and the catfish by pads of sharp conical teeth in their premaxillaries (Fig. 14) and mandibles. By the use of these they seem able to crack a snail as a boy cracks a hazelnut, rejecting the broken shells to swallow the juicy meats. Among the suckers there is a curious inverse correlation in the development of certain of their feeding structures, gill-rakers and pharyngeal jaws growing, one may say, each at the expense of the other. That is, where gill-rakers are long and numerous, the pharyngeal jaws are weak and their teeth are numerous and small, and the species feeds largely on Entomostraca; while if the pharyngeal jaws are thick and strong, with strong crushing teeth, the gill-rakers are short and thick, and relatively ineffective as a straining apparatus. This is so generally true that one may even tell whether or not a sucker is a mollusk-eater by looking at its gill-rakers, although these have nothing to do directly with the collection or mastication of molluscan food.

Another terminus to the series of changes in food choice through which most fishes pass is in the piscivorous habit, characteristic of what we commonly call our game fishes; especially the pike, the pike-perch, and the Great Lakes trout; but the largest number of our fresh-water species linger in the intermediate, insectivorous stage. Indeed, taking our adult fresh-water fishes as they come, we find that insects are by far the most important general element of the food of the class, eaten more or less by nearly every kind of fish and the main dependence of a great many species which, by mere increase in size and the consequent coarser structure of their gill apparatus, have lost the original capacity of the young to strain out the plankton, without attaining to a size and strength sufficient for the capture of a prey larger and stronger than aquatic insect larvæ.

Some kinds of insects occur in such abundance in situations difficult of access, that certain groups of fishes have become especially adapted to their search and capture there. Darters, for example (Fig. 15), live mainly on insect larvæ which hide under stones in swift water, and they are enabled to get at this food by virtue of their large pectoral and anal fins, by which they can support themselves on the bottom in a swift current or make their way among the ripples of a rocky stream, and by their small heads and pointed noses which enable them to pry about under stones where worm-like *Chironomus* larvæ and larvæ of small May flies abound. A little cyprinoid fish—the sucker-mouthed minnow (Fig. 16)—is very similarly equipped and to a like advantage. Access to the same kind of food under the heavier stones of larger streams is given to a sucker known as the hammerhead (Fig. 17). It has a similar development of the paired and anal fins, and a large square head with which it can push and roll about the stones under which day-fly and stone-fly larvæ may be found in great abundance; and these are its principal food.

Besides the six food classes which I have already mentioned, namely, the mud-eaters, the plant-eaters, the plankton-eaters, the mollusk-eaters, the insect-eaters, and the fish-eaters, we may doubtfully distinguish two more—the garbage-eaters and the omnivora. There is, indeed, but one of our fresh-water fishes—the common eel—which seems to live by preference on dead food or decayed flesh; but the class of garbage-eaters may be made to include three or four of the catfishes also, which resort to such food willingly when it is convenient to them. Certainly fishes in whose stomachs we have found, from time to time, distillery slops, ham bones, dead rats, dead cats, and heads and entrails of fish thrown out from fish boats, need not complain if they are provisionally assigned to the humble class of scavengers.

These same catfishes might perhaps be better classed as omnivorous, for they eat, in fact, very nearly every kind of food which the water contains, including insects, mollusks, fishes, crawfishes, and sometimes unusual quantities of algæ and other aquatic vegetation. In this omnivorous class we may also place the common European carp, except that this fish does not eat carrion.

If, now, we review the generalities and the peculiarities of food and feeding habits which I have imperfectly sketched, seeking to understand their differentiation and succession, we may best interpret the facts by attempting to realize the food resources of an average, typical, undifferentiated fish, which should reach adult condition without acquiring any special adaptations of structure or of preference in respect to the choice, appropriation, and assimilation of its food. Such an undifferentiated fish would have a subcylindrical body with only the ordinary equipment for locomotion; it would be toothless both as to its jaws and its pharyngeal bones; its mouth would be neither suctorial nor especially protractile; and its gill-arches would be without specialized gill-rakers. In other words, it would be a simple product of growth, without progress or differentiation, from the state of the recently hatched fry. Such a fish would necessarily begin, as all our fishes now do, with a mixed plankton for its earliest food, taking the smaller organisms first and the larger ones later. As it gradually becomes too large for the pursuit of so minute a prey, and its gill structures too coarse to serve longer as a plankton strainer, it would draw next upon the insects, and mainly on the insect larvæ of the bottom and the shores—creatures especially available to it because their soft and poorly protected bodies make them fit for digestion without mastication or other special preparation; and with these it might mingle also amphipod crustaceans, and the smaller thin-shelled mollusks, especially those which could be picked from an aquatic vegetation. Next would come such young fishes as it could seize and swallow without a special armature of jaws and throat; and at this stage of growth and progress it would apparently stop. To go farther as a predaceous fish it would need the swimming capacity and the raptatorial teeth of a pike-perch or a pike; to get effective access to the abundant stores of molluscan life, gastropod and bivalve, in our streams and lakes, it would need either a suctorial mouth or strong pharyngeal jaws with crushing teeth, or both of these, and thus it might become the equivalent of a sheepshead, a sunfish, or a sucker, as other conditions should determine. To continue as a plankton-eater, it would need the numerous, long, and slender gill-rakers of a paddle-fish or a lake herring, and with these, especially if it had a suctorial mouth and a very long intestine, it might be able to sift and strain from the silt of the bottom the finer organic particles derived from the debris of aquatic vegetation and from the wash of the land. Other specialties of differentiation in structure or in habit might open to it less usual food resources, as with the darters and the top-minnows; and a mere deviation or degradation of taste might add the carrion of the stream to its menu.

Evolution of food habits must thus have taken the course of structural evolution—an advantageous specialization in various degrees and in various directions from a generalized, undifferentiated original. Sometimes added specialties of advantageous equipment have brought in their train limitations or prohibitions in other directions, which have shut a species out from certain food resources in making others more available. The same set of gill-arches, for example, can not serve at once as a plankton-net and a shell-crusher; but, generally speaking, the structural differentiations mentioned have enlarged the resources of the fish in some directions without reducing them in others. Even so definitely predaceous a fish as the Great Lakes trout, which lives habitually on the abundant herring of the lakes, has been known to devour salt pork, ham bones, chicken bones, raw potatoes, corn cobs, rags, spoons, tin cans, silver dollars, and in single instances, a watch and chain, an open jack knife seven inches long, and a two-foot piece of tarred rope.

From this it would appear that these structural differentiations have not necessarily followed upon differentiations of preference, fitting the fish to get more easily and abundantly the kind of food which it had already come to prefer; they seem to have arisen independently of any peculiarities of choice, and may, indeed, have forced the species, in a sense, into directions which it would not otherwise have been inclined to follow.

If we turn now from these examples of habit groups to a classification by habitats—from physiological to spatial ecology—from a discussion of the food of fishes to the subject of their local distribution and their assemblage in what are called animal associations, we shall find a similar state of affairs to that just noticed. Some of our fresh-water fishes are so widely and thoroughly distributed over a large variety of situations that they may be likened to the omnivorous class in the classification by habits, while others are as narrowly limited in habitat as is the carnivorous pike in respect to its food. For my detailed data of local distribution I shall have to draw almost wholly on our Illinois observations, for the reason that we have made in Illinois much larger and more intensive collections of our native fishes than have been made in any other state—larger, indeed, as I believe, than in any other area of like size anywhere in the world.

The blunt-nosed minnow (Fig. 18) is an example of what we may call omnilocal distribution, the map of its local occurrences in Illinois (Map XXVII), being a fair abstract of the map of localities for all our Illinois fish collections. It is relatively rare only in our larger rivers, the frequency of its occurrence there being, by our data, as 5 to 34 for the smaller rivers, and to 43 for creeks. That is to say, if we were to take equal numbers of fish collections from each of these classes of waters throughout the state until we found this species five times in larger rivers, we might expect to find it about thirty-four times in small rivers, and about forty-three times in creeks. It is not limited in its range or habitat by its choice of food, for it feeds mainly on mud, and that it could easily find almost anywhere in Illinois. It prefers streams with a rocky bottom, it is true, its occurrence in such waters having a frequency of 46 as compared with 27 in other places; and the kinds of vegetation mixed with the mud of its intestinal contents give us reason to think that it nibbles and sucks the slime from stones and other submerged objects.

Contrast with this, now, the distribution map of the spot-tailed minnow (Map XXXVIII), and another minnow species, *Notropis heterodon* (Map XXXIV), not well enough known to have received an English name. The spot-tailed minnow, very common in lakes and ponds and especially in the Great Lakes, occurs elsewhere mainly in the larger rivers, its average frequency in our collections in these two situations being as 33 to 3.5 in the smaller streams. That is, we have found it nearly ten times as common in the larger waters as in the smaller ones; and its food, consisting mainly of insects, crustaceans, algæ, and fragments of aquatic plants, is as different from that of the preceding species as is its distribution. The little *heterodon,* on the other hand—about two inches long—is essentially a lake and pond species, and its abundance, not only in the lake region of northeastern Illinois but also along the larger rivers, is explained by the fact that it is mainly in the lowlands of the river bottoms that lakes and ponds are to be found in Illinois. It is in such situations that it finds the bottoms of mud and sand which seem to attract it, its frequency ratio there being 71 as compared with 22 over rock and sand, and 7 over mud. The food of this species is consistent with this preference of location, being mainly Entomostraca and small larvæ of gnats. It is, indeed, essentially a plankton-eater, being of the size to make the plankton of its favorite resorts its most convenient and abundant food.

I know well that these specific details are hardly fit for a general lecture, but they are the materials of my generalizations, and I must ask you to indulge me to the extent of two more examples, chosen from another family of fishes—that most interesting division of the perches commonly known as the darters. These are the johnny darter (Fig. 19; Map XC), and another species, *Cottogaster shumardi* (Fig. 20; Map LXXXVIII), which has no English name. They are particularly interesting, because the johnny darter, although very abundant all over the state, seems to avoid the larger streams, having a frequency there of only 3 as against 53 for creeks, while the *Cottogaster,* although comparatively rare, occurs almost wholly in the larger rivers and in the bottom-land lakes in their immediate neighborhood. Whether there are differences in food corresponding to their distribution we cannot tell, because the food of the rarer species has not been studied.

Many other instances might be given of the fact that fishes can be separated into groups according to their habitats as well as by differences in their food, but that the groups so formed are of very unequal scope. It is as if, in classifying fishes structurally, we should find that there were some families which combined the characteristics of nearly all the others; that other kinds present many such common characters, but a smaller number; and that only a few had differentiated so far from the common mass as to have fixed distinguishing characters of their own. An ecological classification, while quite possible, and indispensable also, ought not to be framed in imitation of the classifications of the taxonomist, but must have objects and methods of its own.

You are all familiar, no doubt, with the idea of animal associations—groups of species habitually associated in the same environments; and these are as recognizable among fishes as among the animals of the land; and here again, substantially as in the other cases, we find animals which, taken by themselves, may be seen to form associate groups with a large extension, covering many distinguishable kinds of situations, and others which are rather narrowly limited to a single sort of habitat, characterized by quite special conditions. There is a group of creek fishes, for example, made up of species which may be found almost anywhere in a creek and in almost any kind of a creek, and another group, like certain of the darters and the stone-roller, which are thoroughly at home only in rocky streams with a relatively rapid flow of at least fairly clear water. If we analyze the aquatic environment into all the situations clearly distinguishable, we shall find, perhaps, a group of certain species distinctive for each situation, but for other species our analysis will be seen to have gone too much into detail; it will distinguish differences of condition to which they are indifferent. Even the distinction between small river and creek, and between river and lake, is too narrow for some fishes, which are found with almost equal frequency in both. The grass pickerel (Fig. 21), which we have taken in one hundred and eleven Illinois collections, is almost equally abundant in creeks and in ponds; and the river-chub (Fig. 22) has been found about equally common in creeks and in small rivers, and virtually absent from the larger rivers and from lakes. Nevertheless, the distinction of animal associations is very helpful to our grasp and understanding of the system of living nature, and will become much more so as our knowledge becomes both more comprehensive and more precise.

An organization of the animal population of a region into associations may be approached either from the side of the *environment* or from that of the *animal inhabitants;* either by an analysis of the environment into habitats and situations, and a critical survey of the inhabitants of each, or by an analysis of the animal population into groups of most frequent associates, and a study of the local and ecological distribution of each such group. By the first method, spatial units—so-called *units of environment*—are first distinguished and delimited, and the animals contained in each such unit are then identified, listed, and enumerated. By the second method, the associate groups are first distinguished, defined, and analyzed, and the territory under examination is mapped in a way to mark the area of distribution of each such group. The first method is primarily geographical, and the second is essentially biological. Both methods are useful and the product of both is necessary to a full knowledge of our complex subject; but of the two, the biological method seems to me much the more useful and significant.

The most general division of the environment of fresh-water fishes into habitats distinguishes large rivers, small rivers, creeks, upland lakes, lowland lakes, marshes, and stagnant ponds. Streams are still further divisible into those with rocky bottoms, bottoms of sand, and bottoms of mud; into those with a swift or with a sluggish current; and into those with clear or with turbid waters. Even parts of streams are distinguishable into different habitats—the rippled reaches of rocky streams differ materially from the deep, still pools between. In the larger rivers, like the Illinois, we may sometimes distinguish between the opposite margins, where, as at Havana, one has a muddy bank and the other a sandy one. In lakes there are notable differences between the marginal shoals and the deep interior waters, between sandy bars and mud flats; between open waters and those filled with weeds; and in the weedy parts, between those in which reeds, rushes, and other coarse, rooting plants are present and those in which the plants are mostly submerged. These present their characteristic differences in the fishes which resort to them—differences clearly discernible, however, only by the use of quantitative methods, which give us the relative numbers of each species found in each situation over a sufficient length of time and variety of external conditions to make us sure that we are getting fair and stable averages.

The first thoroughly practical work of this kind that I know of was done at Havana, Illinois, under my direction, in 1898-99, by Wallace Craig, later a doctor of philosophy of the University of Chicago, but at that time a temporary assistant on the Illinois Natural History Survey and also a graduate student in the University of Illinois. He began in August, 1898, a detailed study of the local distribution and the movements of fishes, with a view to making out preferences of situation or choices of environment of the various species of fish under varying conditions and at different times of the year. Using identical apparatus by uniform methods at regular intervals in the waters of the locality, it was possible to get totals and averages by a comparison of which the striking features of the different situations were made manifest when the statistical tests were compared with each other. By this method it was shown that the Illinois River gave us different data of frequency for the different species on the two sides of the stream, one of which was muddy and the other clear; but the most interesting conclusion was a notable difference in degree of specialization in the fishes inhabiting the different sections of a stream system. Those from the larger river were, as a rule, not only the largest, but the most primitive, or the least specialized; those preferring the bottomland lakes were, on the whole, more highly differentiated; and those from the creeks were smallest and the most highly specialized of all.

It is perhaps what we ought to expect, that the creek species should be more diverse and highly organized than any other fishes, for they must have had longer experience of fresh-water life. As the continent first began to rise from the sea, all its streams were necessarily small, and its first fishes were consequently those adjusted to life in creeks. As the process continued, as the surface of the land became more diversified, as the small stream systems of the coast ate their way back, with many lateral branches, and united to form large rivers, and these again to make rivers of the largest size, new habitats would be formed, both in the uplands and along the coast, and new adaptations of fishes to them would naturally lead to about the kind of classifiable diversity which we actually find.

That ecological differentiations and divisions among fresh-water fishes are, as a rule, of no very compelling force is shown in a remarkable manner by the fact that the whole system of such distinctions breaks down almost completely at least once a year, when a great migration movement up-stream and into shallow water seizes all species alike, under the overpowering impulse of the breeding instinct. At this time fishes of the most varied habit and habitat seem temporarily to desert or forget their favorite places of resort, and throng together, indifferent to their individual welfare, in search of places for the deposit of their eggs, and, with many species, for the subsequent care and protection of their young. Even under less extraordinary circumstances I have found, in fact, that a large river like the Illinois becomes a sort of metropolis of the fish population of its drainage basin, in which representatives of the various groups or associations, separate and distinct in its headwaters and smaller tributaries, may be found indiscriminately commingled, just as in this great city we see people from scores of smaller cities and hundreds of smaller towns and thousands of rural communities. Sunfish species, for example, which rarely occur in each other's company in collections from the smaller tributaries, were found together twice as often in collections from the larger streams.

Such are some of the products of a study of the populations of predetermined habitats. It remains to be seen to what extent these habitat populations coincide with real ecological groups of most frequent associates—to what extent our habitat characters are the real determiners of the actual associative distribution of our fishes. It may be that the effective sensibilities of fishes are not altogether what we have supposed them to be, *a priori;* that things we have not thought of in that connection have much to do with their assemblage in more or less definite and in more or less permanent societies. This is especially possible with fishes, because we can see so little of them as a rule, and because their power of free and rapid locomotion enables them to assemble and to disperse so readily and so rapidly. To get at the fundamental facts we must find a means of learning what and where definite associations among fishes really exist; what is the local center and what are the optimum conditions of each such associate assemblage; and what are its most typical and constant components—what species, that is to say, are the most clearly and constantly characteristic of it. This means that we must study the details of the distribution, and hence of the associate grouping of fishes, with reference at first to their location only; and then, when our associations have thus been determined, located, and described,. we must see how they compare with the habitat system arrived at by our preliminary analysis of the environment.

This sort of critical study of the essential details of ecological distribution has almost never been made, at least for animals, and even the methods of it are scarcely agreed upon. Those which I shall briefly describe to you were devised for the purpose of utilizing, for ecological description and inference, the product of extensive collections of Illinois fishes, made in the long course of the natural history survey of the state. They are based upon the obvious fact that a biological association is made up of species which are associated with one another more frequently than they are with other species; from which it follows that to find an association one must find a group of such most frequent associates; and to determine the center of its location and the extent of its range we must find where this associative frequency—this frequency of joint occurrence—of the several species of the group is greatest, and how far in each direction each species of it continues to be more frequently associated with the other members of the group than with any other species. If, for example, we make a hundred collections over a given area of complex ecological composition, and find that we have fifty species of fish represented in these collections, it is easy for us to tell, by a simple examination of our numerical data, which of these fifty species have come out in our nets in each other's company the most frequently, and in what situation or habitat each of these most frequent associates has been found most abundant. In so far as frequency of habitat occurrences and frequency of associate occurrences coincide, we have evidently a local association distinguished, together with its characteristic and accustomed habitat.

I tested the utility of these simple ideas during the summer vacation of 1905, by an application of them to our Illinois collections of the so-called darters—species of the subfamily Etheostominæ—in a way to prove, what, indeed, we already knew as a matter of common observation, that, taken as a whole, these darters are an associate group, and that their characteristic habitat is what also we already knew it to be—the rocky rapids of small streams. The essential correctness of the method was thus verified; and I was also able to distinguish six species of darters peculiarly typical of the group, to be regarded as especially characteristic of it because they were found more than two and a fourth times as frequently associated with each other as they were with the seven remaining species; and likewise because they were about two and a half times as frequently associated with each other as were the seven remaining species among themselves.

It was easy to show, on the other hand, by similar methods, that the sunfishes (see Fig. 23 and 24), although as much alike to a general observation as the darters, are not a homogeneous ecological group, but that they are so variously related to different habitats—to different features of their environment—that several of the sunfish species are much more frequent associates of fishes widely different from themselves than they are of each other; that the various sunfish species often belong, in fact, to different zoological associations. Indeed, it was found by repeated use of this method of analysis that it was a rather common thing for closely related species of fishes—near neighbors in the taxonomic system—to be in some sense averse to each other's company—to avoid each other, seemingly, and to find their closest and most familiar associates in fishes far removed from them in taxonomic relationship.

I have supposed this to be an expression of the disadvantages of close competition between closely similar species, and of the advantage, consequently, of such differentiations in habit and such separations in ecological preference as would carry these natural competitors into noncompeting ecological groups. Such an apparent evasion of competition by near relatives is well illustrated by our observations on the top-minnows (Fig. 25)—very small fishes of the killifish family, of which we have three species in Illinois. Two of these species are distributed throughout the state, but the third is southern in its distribution, lapping over on the Illinois area of the other two only in the southern part of the state. Now it was to me an extremely interesting fact that we found this southern species much more frequently in company with the two more widely distributed top-minnows than these two were with each other. It was as if those which occupy the same area conjointly had found themselves compelled to an ecological division of it, such as would keep them largely out of each other's way, while those of an essentially unlike geographical distribution had found no such mutual avoidance necessary. It seems quite possible that this intra-local separation of competitive groups, this effective isolation of forms inhabiting the same territory, may be one of the early steps—sometimes the very first step, perhaps—in the differentiation and fixation of species. A difference in respect to choice of breeding grounds especially, by preventing the interbreeding of two diverging groups, would separate them as effectually as an impassable mountain chain running through the area of their original distribution.

This principle of an evasion of competition seems to apply to associations also, as well as to species, and to explain in part the composition of neighboring associations. Similarly endowed species, similarly disposed towards their environment, would profit mutually by a *geographical* separation, which should give to each a range not entered by the other; and adjacent associations might thus be formed, alike in their ecological make-up but different in their species. It is in some such way that we may perhaps explain a few otherwise unexplained limitations of the distribution of our Illinois fishes. Six of our one hundred and fifty Illinois species are so definitely limited to the Wabash drainage as to suggest that there must be some ecological barrier against their spread, since there is certainly no geographical one, namely: brindled stonecat, *Schilbeodes miurus* (Fig. 26 and Map LIX); green-sided darter, *Diplesion blennioides* (Fig. 27 and Map LXXXIX); *Notropis illecebrosus* (Fig. 28 and Map XXXVII); silver-mouthed minnow, *Ericymba buccata* (Map XLVI); long-eared sunfish, *Lepomis megalotis* (Fig. 29 and Map LXXVI); and *Boleichthys fusiformis* (Fig. 30 and Map XCVIII).

These are all species whose general distribution throughout the country would lead us to expect to find them anywhere in Illinois.

Even more interesting is another series of limitations upon the local distribution of our Illinois fishes, because it seems to be clearly explainable as due to an ecological factor of geological origin—to the physical character of the surface soils of a large part of southern Illinois corresponding to the area known as the lower Illinoisan glaciation. This area is notable for the extremely fine division of its soil particles, due to its geological history, and for the consequent persistent and even permanent muddiness of its waters, such that the suspended particles cannot be completely separated by repeated filtering with the finest filter paper, and do not subside even after long intervals of stagnation. This persistent turbidity of the waters might well be expected to have an effect to repel or exclude certain kinds of fishes, particularly those having a special preference for the clean water and hard bottom of the lakes or streams which they inhabit. Other species, on the other hand, which are found in muddy situations elsewhere, might be expected to tolerate the persistently muddy waters of this southern Illinois district. An analysis of our data bears out this assumption in a remarkable way, a fact most clearly shown by examples of the distribution of species selected from our lists of those tolerant, and those intolerant, of muddy waters generally. Compare, for example, our Illinois distribution maps of the stone-cat (Map LVII), the common sucker (XVIII), the hogsucker (XIX), the stone-roller (XXIII), the common shiner (XLI), and the river chub (LI), all rare or wanting in the lower Illinois glaciation, with the following six other species freely distributed there, namely: the black bullhead (LV), the tadpole cat (LVIII), the chub-sucker (XVI), the bluntnosed minnow (XXVIII), the golden shiner (XXXI), and the long-eared sunfish (LXXVI) ; and also the fact that our statistics of ecological distribution, crude as they are, serve to distinguish these two groups strongly with respect to their relation to muddy situations. The fishes of the first group, for example, have occurred over muddy bottom only once to nearly four times over a bottom of mud and sand, while those of the second group have occurred with about equal frequency in the two situations.

With these merely miscellaneous illustrations of method and product, I must leave this subject, much too large and too complex for any fairly comprehensive treatment, at least by me, within an hour's lecture. I am the less disturbed by the fragmentary character of this discussion because I know that you have in charge of your ecological studies a leader in this line of progress, abundantly able to make good its deficiencies, and especially competent to describe to you the aims, methods, and results of an intensive experimental study of separate problems in animal ecology, quite in contrast to the broad reconnaissance and general orientation work which naturally falls to the director of a biological survey of so large an area as the state of Illinois.

PLATE I

Principal FOOD RELATIONS of Aquatic Organisms (Illinois)	Bacteria	Algae	Higher Plants	Protozoa	Rotifers	Entomostraca	Worms	Crawfishes	Insects	Mollusks	Fishes	Frogs; tadpoles	Turtles	Serpents	Birds	Man
Terrestrial Wastes	X	X	X	X	X	X	X	X	X	X	X	X				
Bacteria				X	X	X	X		X	X	X					
Algae				X	X	X	X		X	X	X	X				
Higher Plants								X	X		X		X		X	
Protozoa				X	X	X	X			X	X					
Rotifers				X		X				X	X					
Entomostraca			X		X	X	X		X		X		X			
Worms								X	X		X	X				
Crawfishes							X				X	X		X	X	
Insects			X					X	X		X	X		X	X	
Mollusks							X	X			X		X		X	
Fishes						X	X	X	X		X	X	X	X	X	X
Frogs											X	X	X	X	X	X
Turtles							X									X
Serpents															X	
Birds													X			X

Fig. 1. Table of Foods (at the left) and Feeding Organisms (upper list).

PLATE II

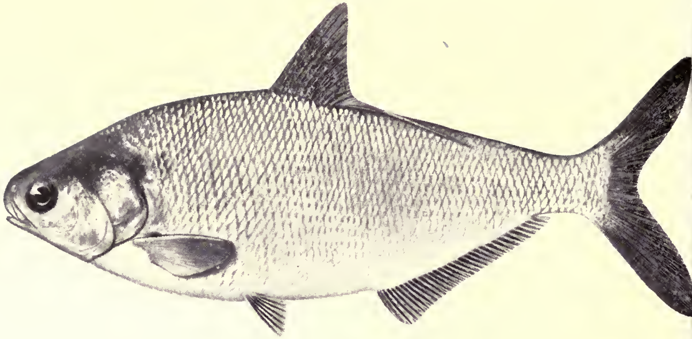


Fig. 2. Gizzard-shad (*Dorosoma cepedianum*). ×⅓

Fig. 3. Stone-Roller (*Campostoma anomalum*). ×1½

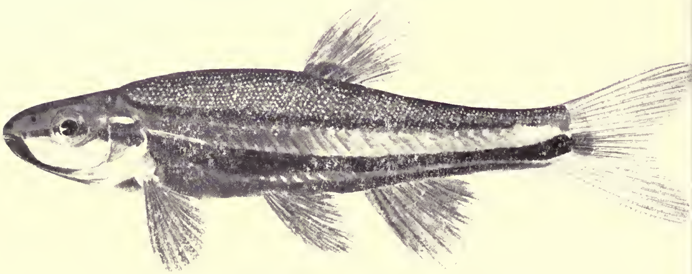


Fig. 4. Red-bellied Dace (*Chrosomus erythrogaster*). ×2

PLATE III

Fig. 5. Upper jaw of young Gizzard-shad (*Dorosoma cepedianum*), showing minute teeth. $\times 30$

Fig. 7. Lower jaw of young Whitefish (*Coregonus clupeiformis*), showing raptatorial teeth. $\times 30$

Fig. 6. Paddle-fish (*Poloydon spathula*). $\times 1/18$

Fig. 8. Sheepshead (*Aplodinotus grunniens*). $\times 1/8$

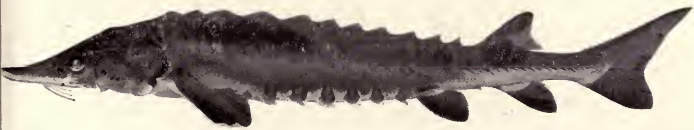


Fig. 9. Lake Sturgeon (*Acipenser rubicundus*). $\times 1/10$

PLATE IV

Fig. 10. Common Bullhead (*Ameiurus nebulosus*). ×⅓

Fig. 11. Common Sucker (*Catostomus commersonii*). ×¼

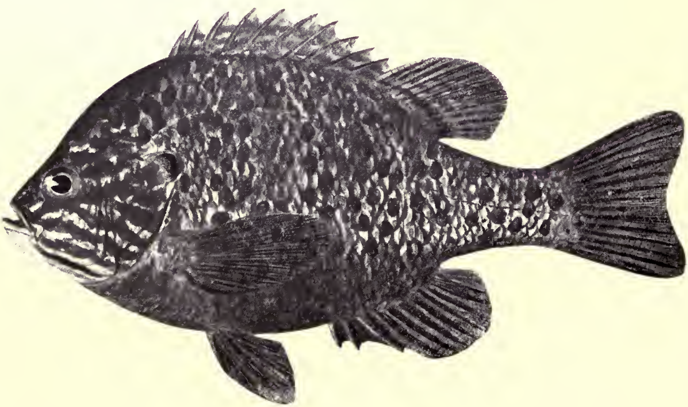


Fig. 12. Pumpkinseed (*Eupomotis gibbosus*). ×⅘

PLATE V

Fig. 13. Lower left pharyngeal jaw of Pumpkinseed (*Eupomotis gibbosus*): (a), from above; (b), from outside

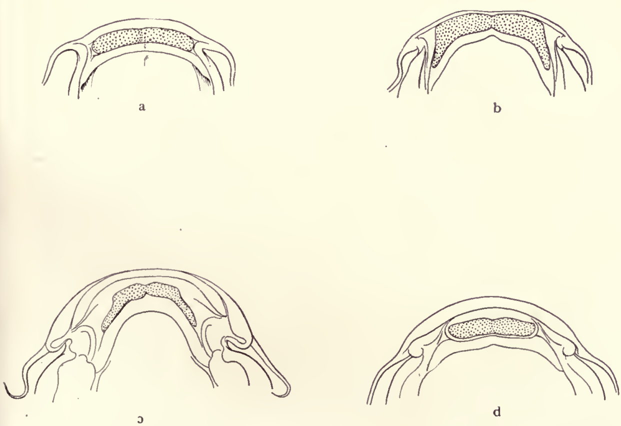


Fig. 14. Premaxillary Teeth of Catfishes: (a). Noturus flavus: (b). Leptops olivaris: (c). Schilbeodes gyrinus: (d). Ameiurus melas

PLATE VI

Fig. 15. Sand Darter (*Ammocrypta pellucida*). $\times 2$

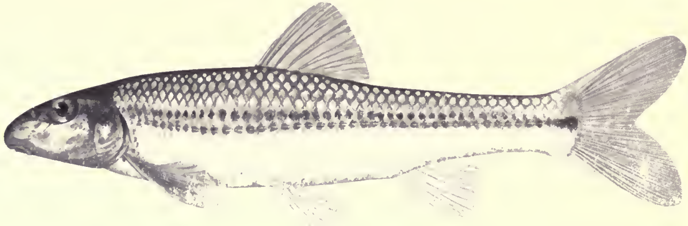


Fig. 16. Sucker-mouthed Minnow (*Phenacobius mirabilis*). $\times 1^2/_7$

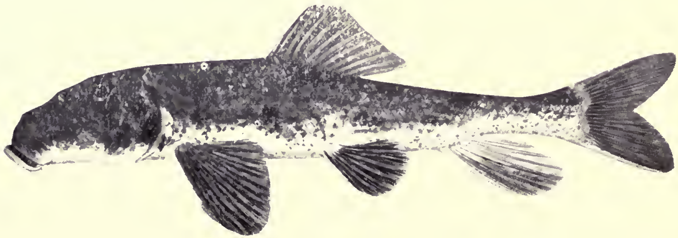


Fig. 17. Hammerhead (*Catostomus nigricans*). $\times ^1/_5$

Fig. 18. Blunt-nosed Minnow (*Pimephales notatus*). $\times ⅞$

PLATE VII

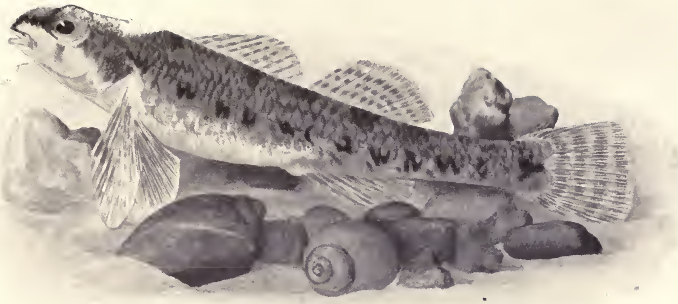


Fig. 19. Johnny Darter (*Boleosoma nigrum*). ×2

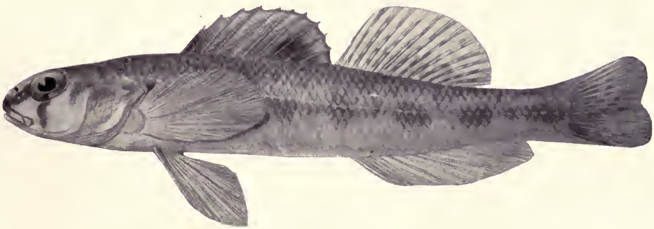


Fig. 20. Cottogaster shumardi ×2

Fig. 21. Grass Pickerel (*Esox vermiculatus*). ×⅜

PLATE VIII

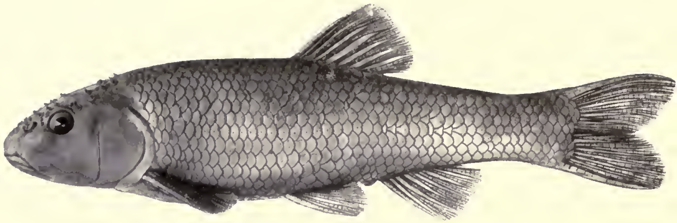


Fig. 22. River Chub (*Hybopsis kentuckiensis*). ×¾

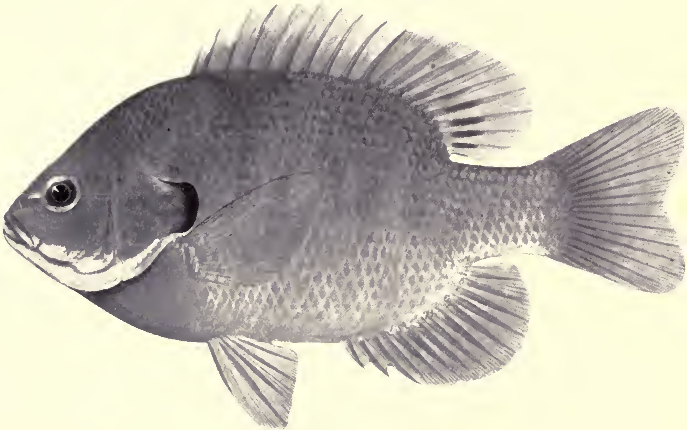


Fig. 23. Bluegill (*Lepomis pallidus*). ×¾

Fig. 24. Blue-spotted Sunfish (*Lepomis cyanellus*). ×¾

PLATE IX

Fig. 25. Top Minnow (*Fundulus dispar*) male. ×2

Fig. 26. Brindled Stonecat (*Schilbeodes miurus*). ×1²/₇

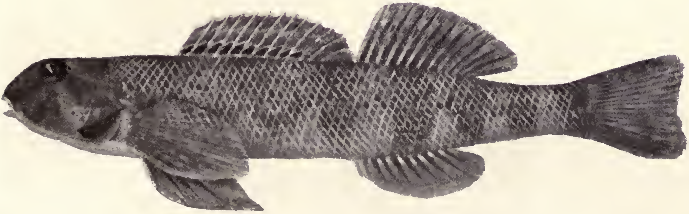


Fig. 27. Green-sided Darter (*Diplesion blennioides*). ×1½

PLATE X

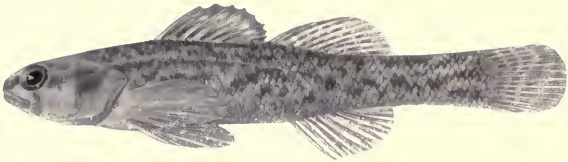


Fig. 28. *Notropis illecebrosus.* ×1½

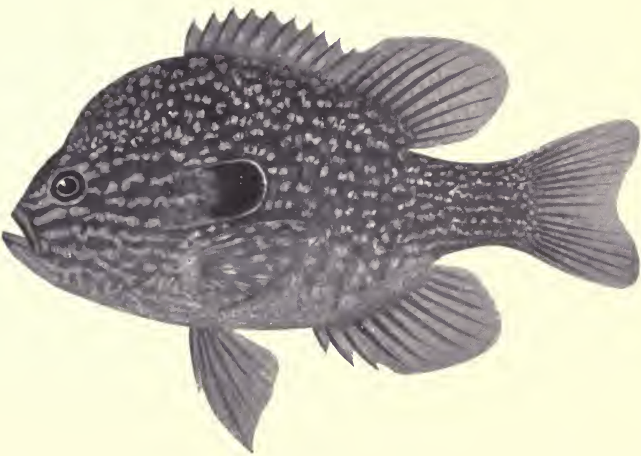
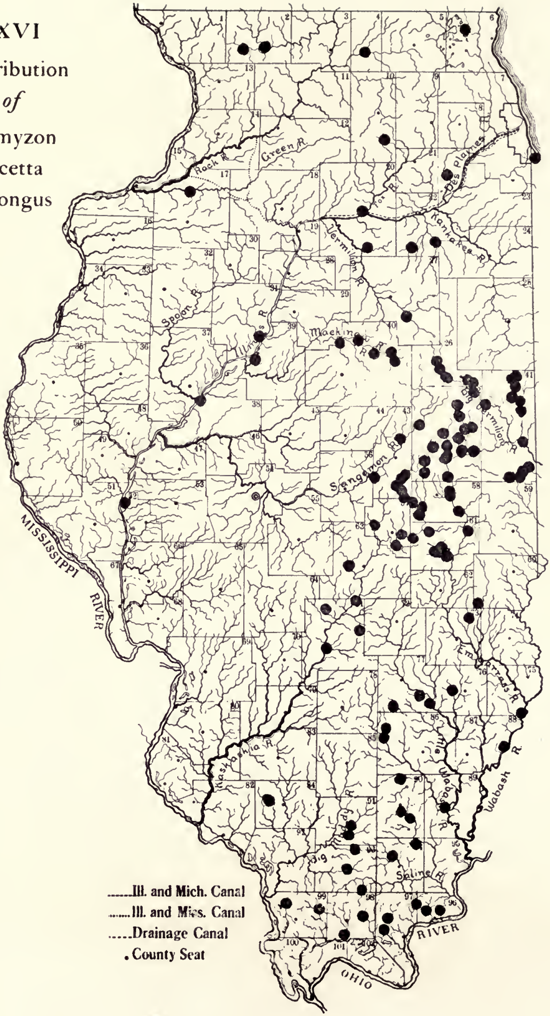
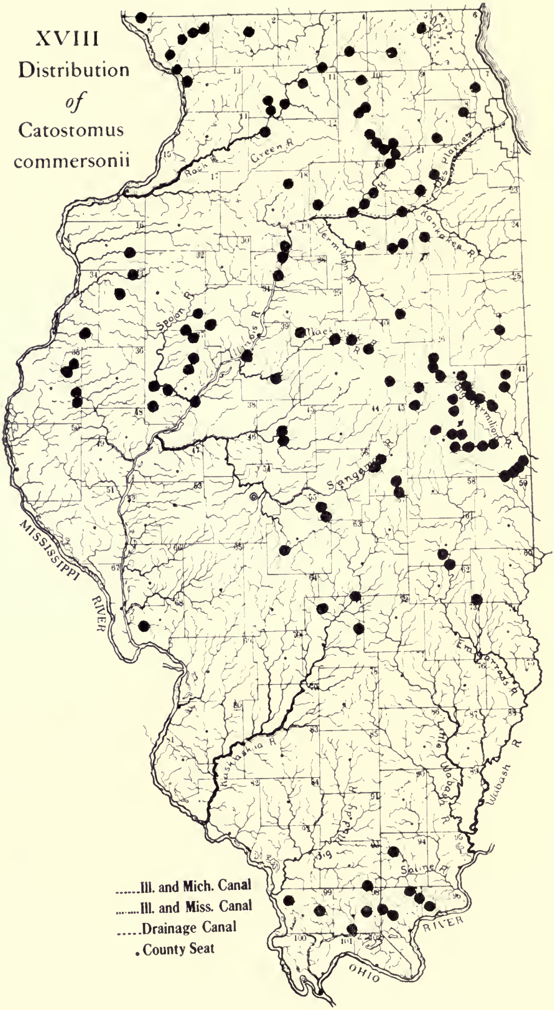


Fig. 29. Long-eared Sunfish (*Lepomis megalotis*). ×¾

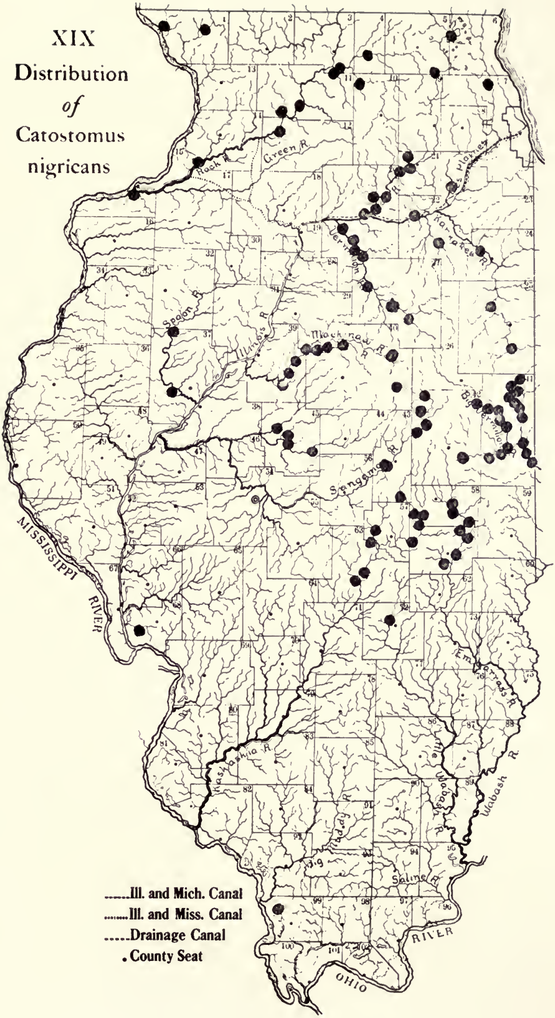
Fig. 30. *Boleichthys fusiformis* ×2

XVI
Distribution
of
Erimyzon
sucetta
oblongus

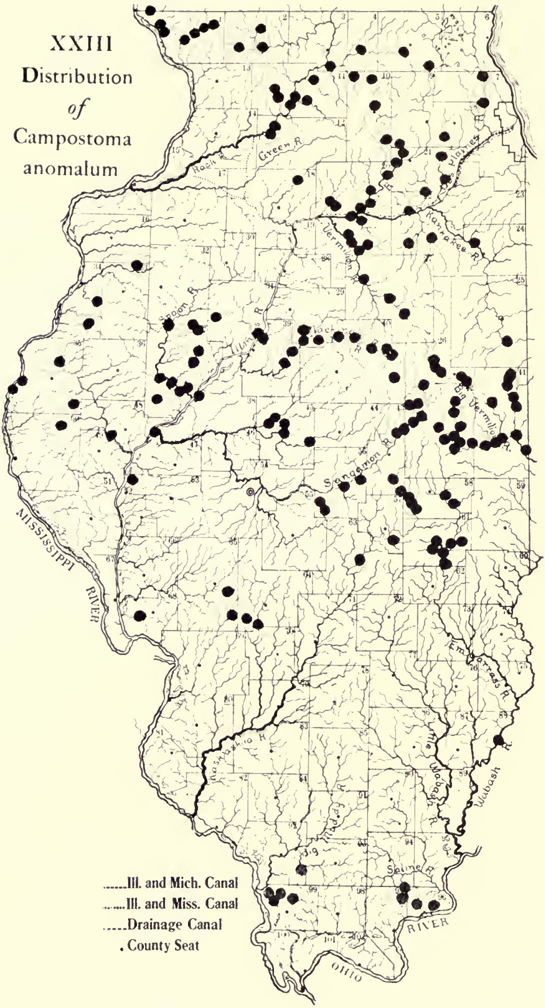




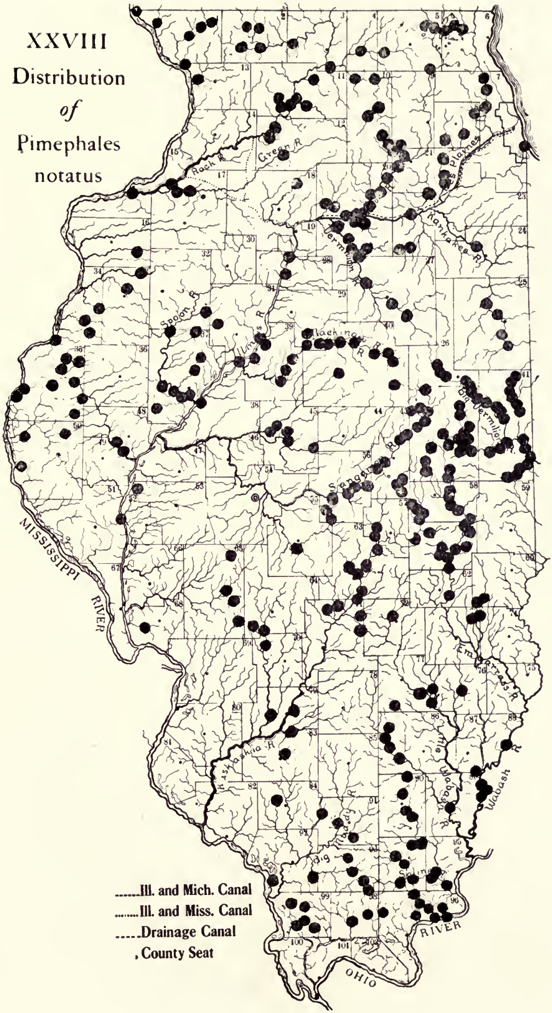
XVIII
Distribution
of
Catostomus
commersonii

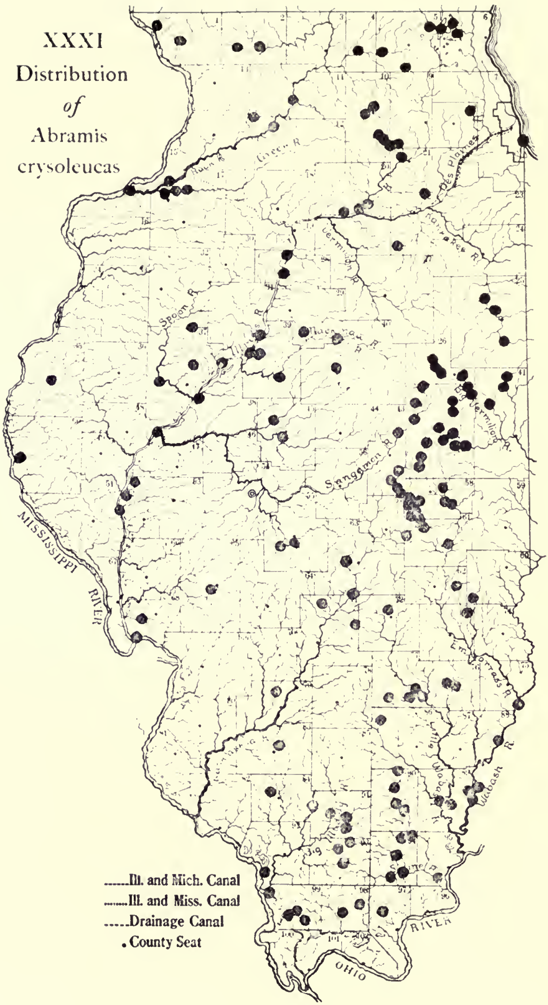

XIX
Distribution
of
Catostomus
nigricans
Rock R.
Green R.
Des Plaines
Kankakee R.
Vermilion R.
Spoon R.
Illinois R.
Mackinaw R.
Big Vermilion
Sangamon R.
MISSISSIPPI
RIVER
Embarrass R.
Kaskaskia R.
Little Wabash R.
Wabash R.
Big Muddy R.
Saline R.
OHIO
RIVER
......Ill. and Mich. Canal
.........Ill. and Miss. Canal
.....Drainage Canal
. County Seat

XXIII
Distribution
of
Campostoma
anomalum

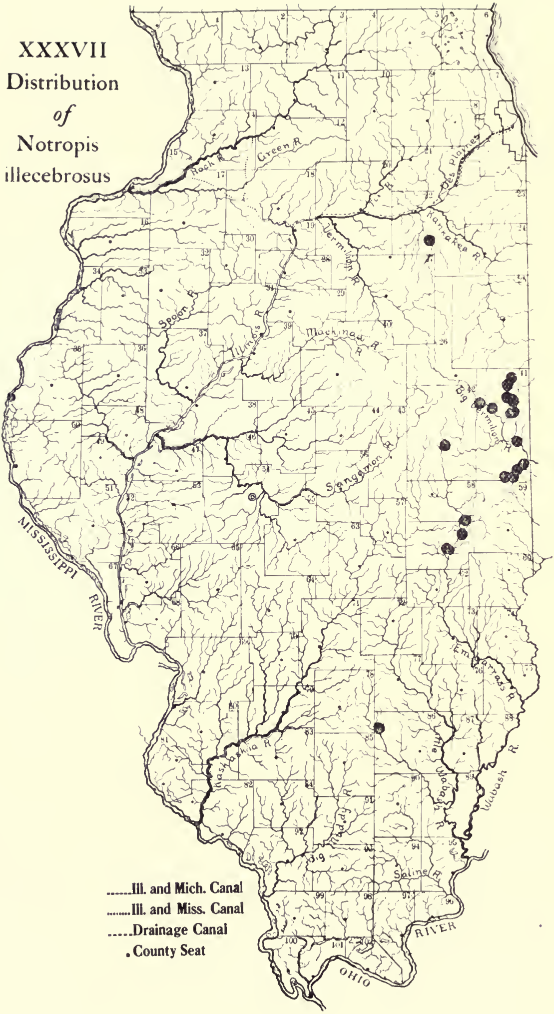


XXVIII
Distribution
of
Pimephales
notatus



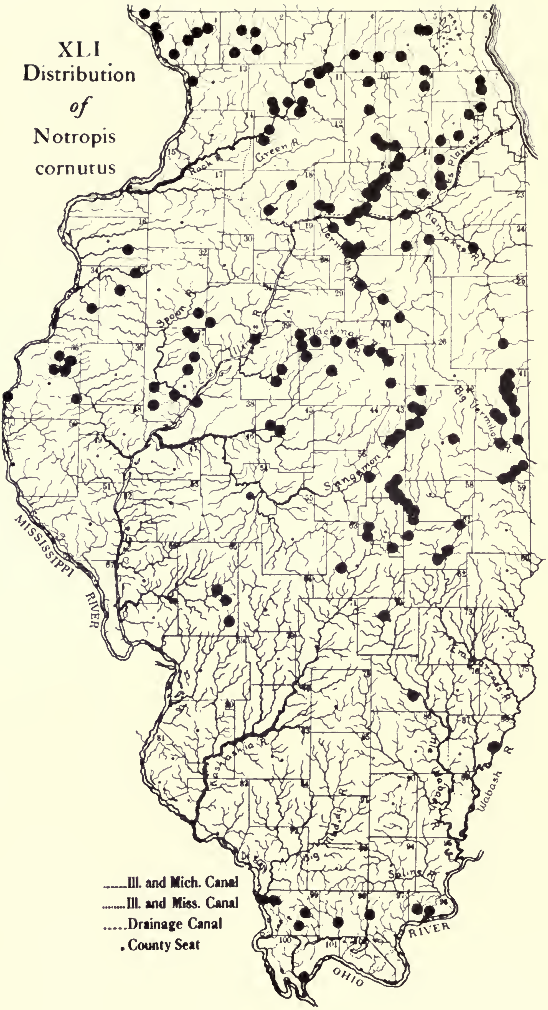

XXXI
Distribution
of
Abramis
crysoleucas
Ill. and Mich. Canal
Ill. and Miss. Canal
Drainage Canal
County Seat
MISSISSIPPI
RIVER
OHIO
RIVER
Sangamon R.
Spoon R.
Des plaines
Kankakee R.
Vermilion R.
Wabash R.

XXXIV
Distribution
of
Notropis
heterodon

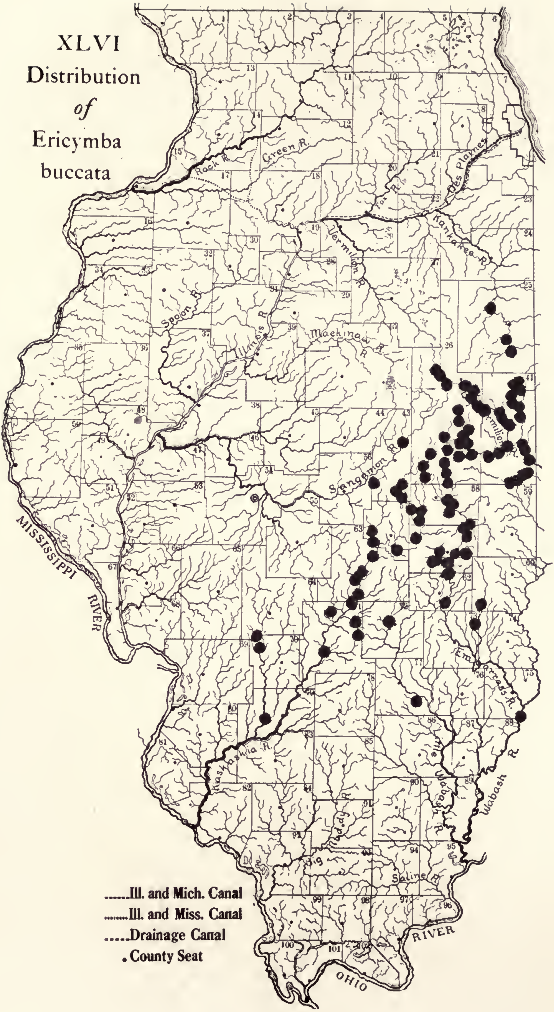


XXXVII
Distribution
of
Notropis
illecebrosus
......Ill. and Mich. Canal
........Ill. and Miss. Canal
.....Drainage Canal
. County Seat
MISSISSIPPI RIVER
OHIO RIVER
Rock R.
Green R.
Des Plaines R.
Kankakee R.
Vermilion R.
Illinois R.
Spoon R.
Mackinaw R.
Big Vermilion R.
Sangamon R.
Kaskaskia R.
Embarrass R.
Little Wabash R.
Wabash R.
Big Muddy R.
Big Saline R.

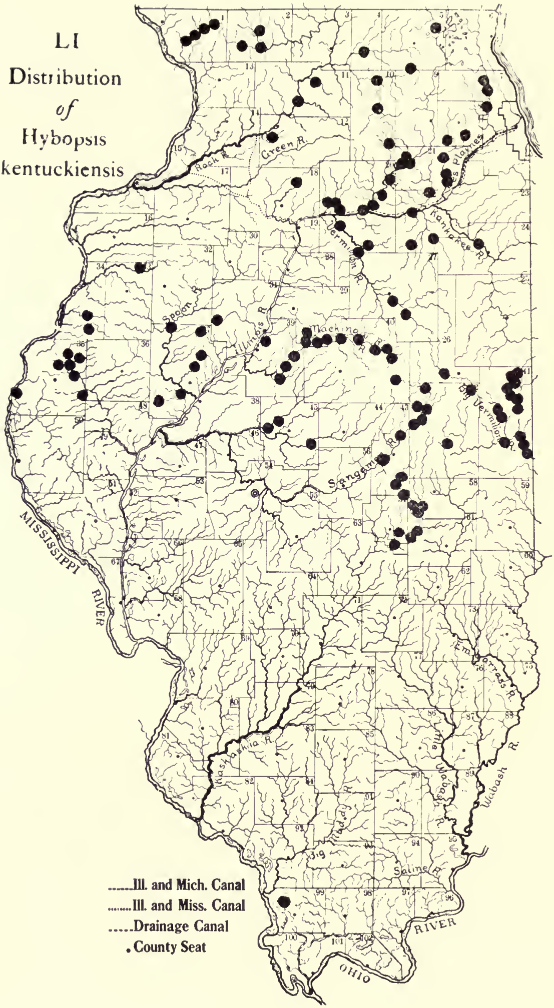
XXXVIII
Distribution
of
Notropis
hudsonius


XLI
Distribution
of
Notropis
cornutus
Rock R.
Green R.
Des Plaines
Kankakee R.
Spoon R.
Illinois R.
Mackinaw R.
Big Vermilion R.
Sangamon R.
Kaskaskia R.
Embarrass R.
Little Wabash R.
Wabash R.
Big Muddy R.
Saline R.
MISSISSIPPI RIVER
OHIO RIVER
......Ill. and Mich. Canal
........Ill. and Miss. Canal
.....Drainage Canal
. County Seat

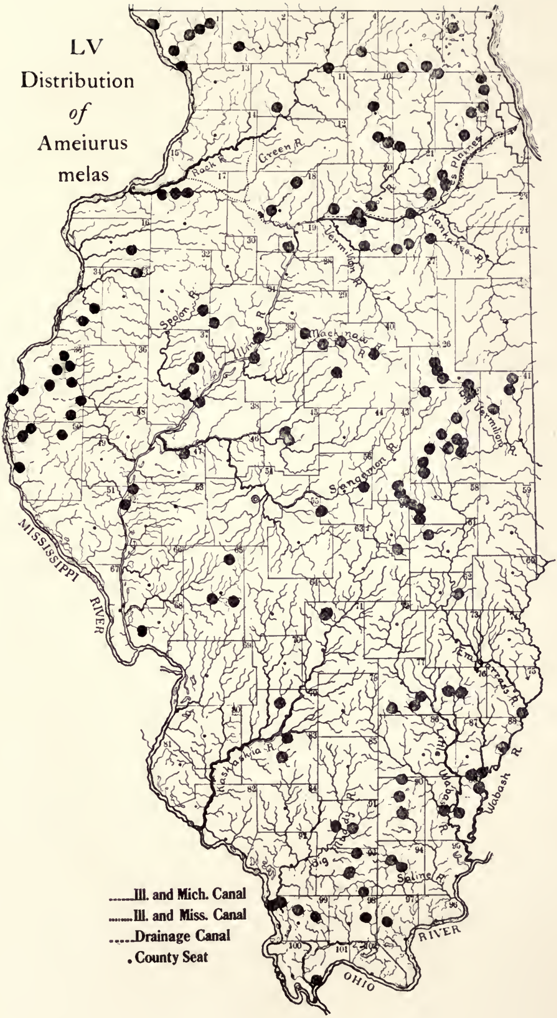
XLVI
Distribution
of
Ericymba
buccata



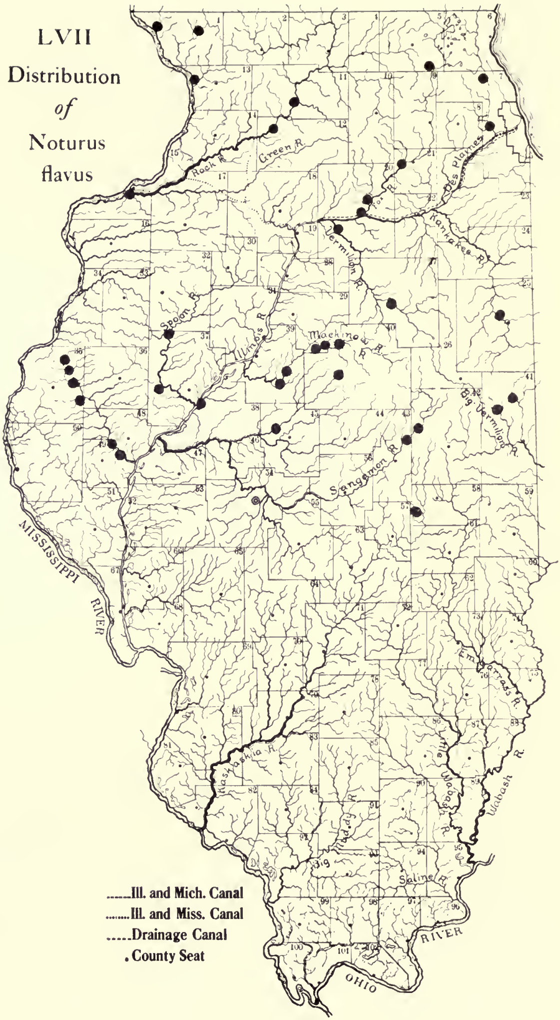
LI
Distribution
of
Hybopsis
kentuckiensis



LV
Distribution
of
Ameiurus
melas

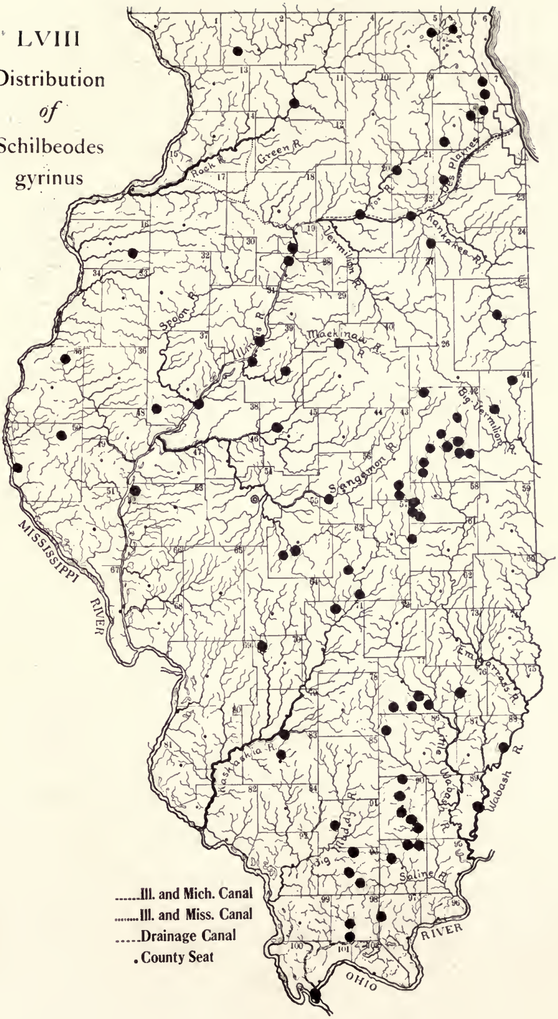


LVII
Distribution
of
Noturus
flavus



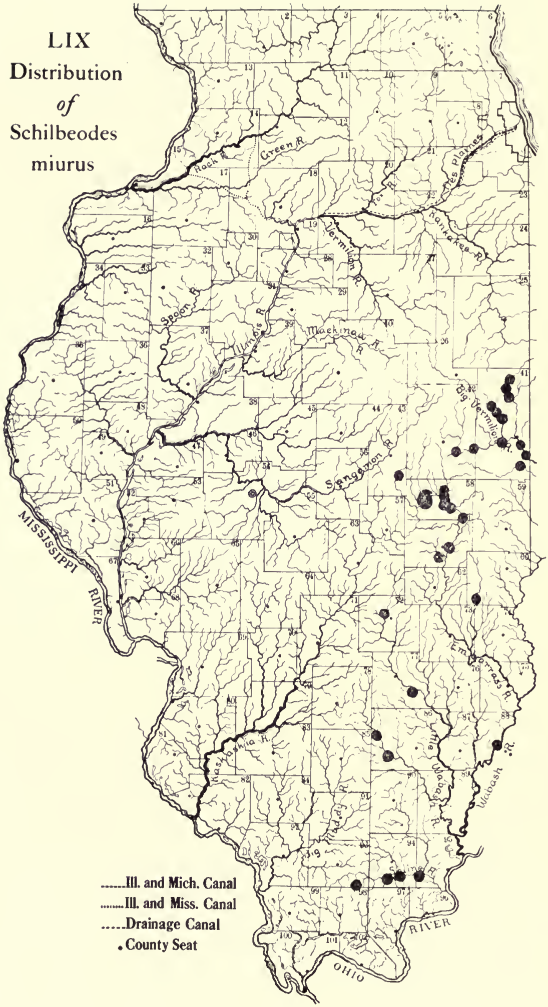
LVIII

Distribution *of* Schilbeodes gyrinus

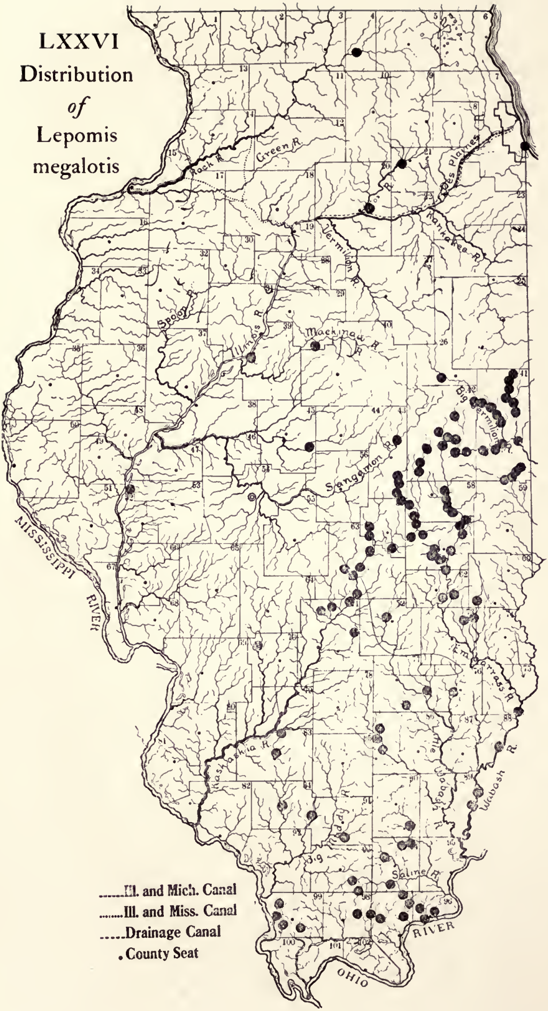


......Ill. and Mich. Canal
........Ill. and Miss. Canal
.....Drainage Canal
. County Seat

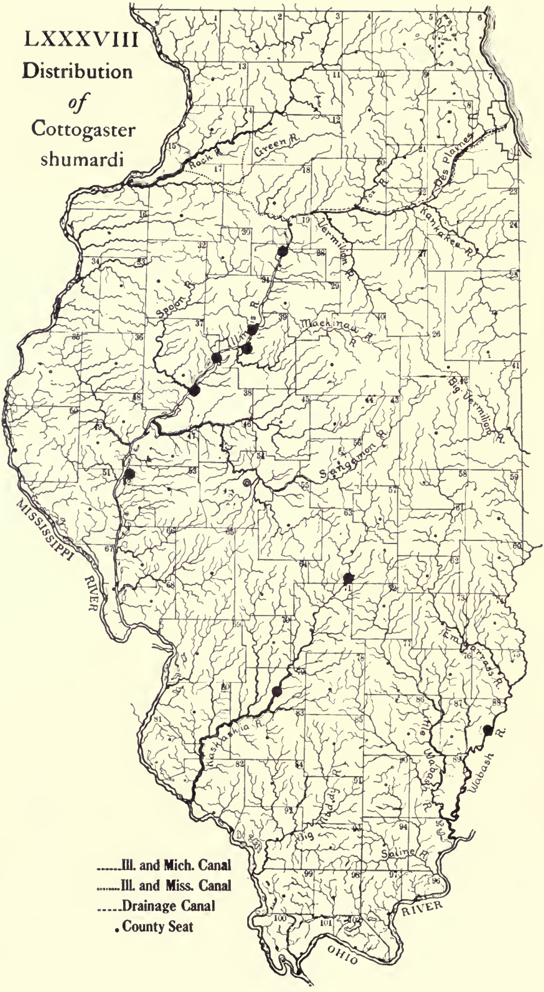
LIX
Distribution
of
Schilbeodes
miurus



LXXVI
Distribution
of
Lepomis
megalotis



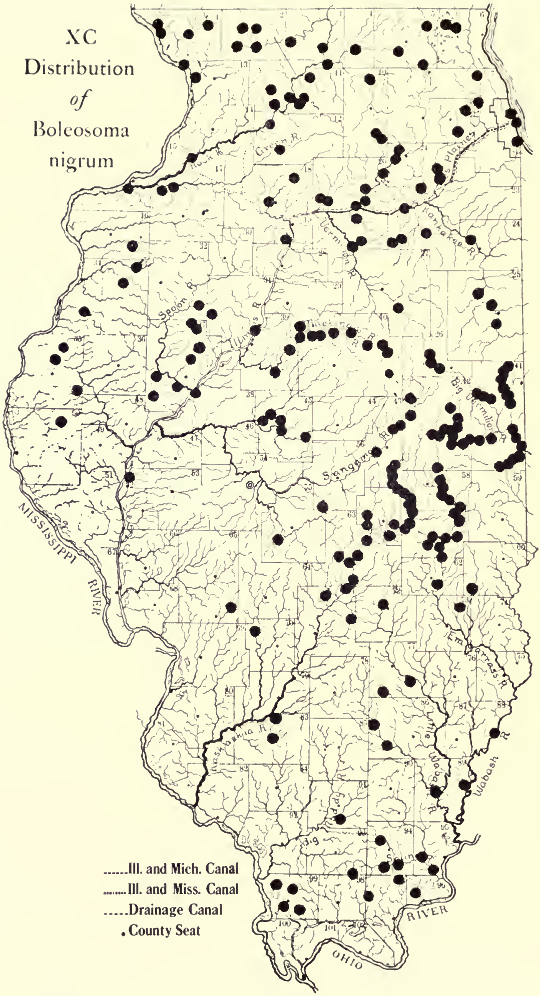
LXXXVIII
Distribution
of
Cottogaster
shumardi



LXXXIX
Distribution
of
Diplesion
blennioides

......Ill. and Mich. Canal
.......Ill. and Miss. Canal
.....Drainage Canal
. County Seat

XC
Distribution
of
Boleosoma
nigrum



XCVIII
Distribution
of
Boleichthys
fusiformis