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The "Knothead" Carp of the Illinois River

BY

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THE NATURAL HISTORY SURVEY DIVISION
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THE "KNOTHEAD" CARP OF THE ILLINOIS RIVER

David H. Thompson

FOREWORD

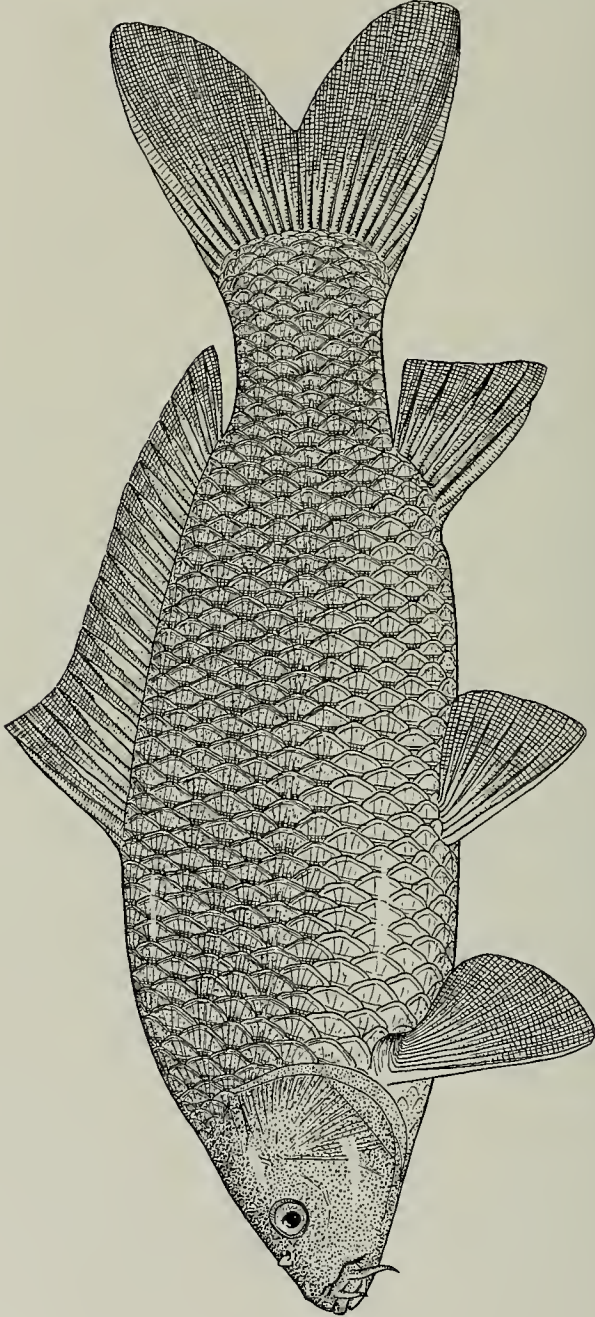
The investigation reported here was begun in collaboration with Doctor Ludwig Scheuring, of the Bayerische Biologische Versuchsanstalt für Fischerei and the University of Munich, during his visit to this country in the winter of 1926-1927. While the "knothead" carp of the Illinois River had been known to the writer for some time, no start had been made on the problem because of the lack of such a fund of information on the biology and pathology of fishes as Doctor Scheuring was equipped to furnish. During the two months when he took an active part in the work in field and laboratory, most of the important facts were brought out, and since his return to Germany he has given advice and suggestions for the continuance of the investigation and has aided in the preparation of the manuscript.

INTRODUCTION

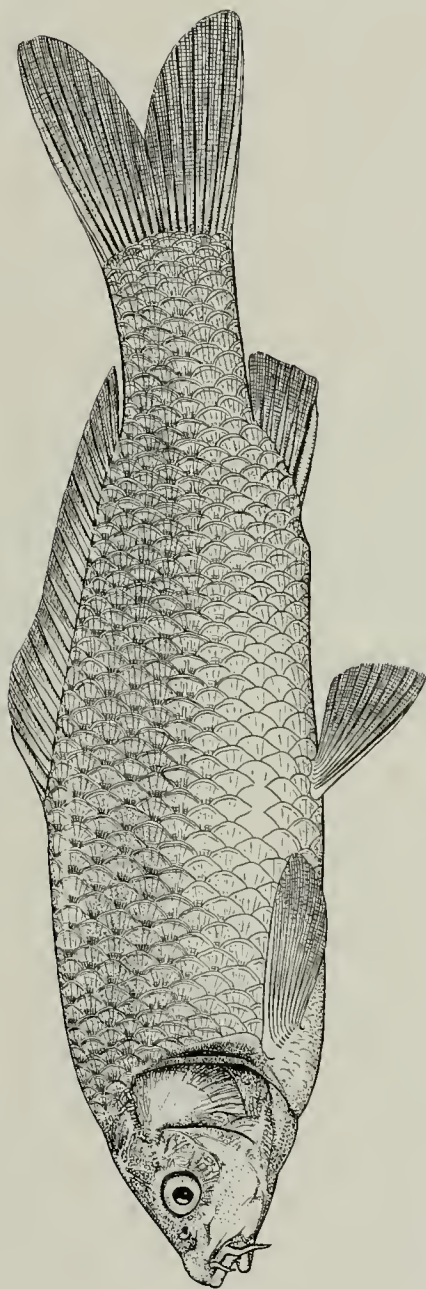
Any serious hazard to the carp of the Illinois River is of considerable economic consequence, inasmuch as the carp is by far the most important commercial fish of this stream. Introduced in 1885, out of a stock brought to the United States a few years earlier from Europe,¹ the carp first became an important item in the Illinois River fishery soon after 1890. In 1898, the Illinois Fishermen's Association reported that the carp catch exceeded the value of all other commercial fishes. Statistics gathered by the United States Bureau of Fisheries² show that in 1908 the total yield of commercial fishes of the Illinois River was 23,896,000 pounds, of which carp constituted 64 per cent, or 15,400,000 pounds. More recently, because of the decreased acreage of water due to drainage of bottomlands for agricultural uses, and because of the southward encroachment of pollution, the annual yield of the entire river has been reduced about one-half, and even more in the middle section of the stream.

¹ Forbes, S. A., and R. E. Richardson. The Fishes of Illinois. Illinois State Natural History Survey Final Report. Vol. III. Second Edition. 1920.

² Fisheries of the United States. Bureau of the Census. Special Reports. 1908.



J.F. Müller
FIG. 1. Normal carp of the Illinois River.



J. F. Miller

FIG. 2. Knothead carp of the middle Illinois River.

The carp has a greater viability under these unfavorable conditions than other fishes and now contributes between 80 and 90 per cent of the total annual catch of commercial fishes.

The plant and animal life of the middle Illinois River changed fundamentally during and immediately following large increases in the load of pollution in the years 1916-1918. One of the changes was a marked alteration in the growth form of the carp. While this alteration varied widely in degree, it was generally obvious in most of the carp and was readily recognized by the fishermen. This change has been found to resolve itself into two general outstanding differences: retardation of the rate of growth throughout the life of the carp; and marked anatomical abnormalities, especially of the bones. A number of methods have been employed to find out what factors are responsible for these structural and functional changes. Several months of painstaking search gave no evidence of an infection of a kind to have any bearing on this case. However, a variety of information has been accumulated which indicates the presence of developmental and metabolic disturbances similar in many respects to those found in rickets among the higher vertebrates, and this has been supplemented with evidence of factors, in both the early and adult food supplies of the carp, apparently capable of inducing diet-deficiency disease.

DESCRIPTION OF KNOTHEAD CARP

The carp (*Cyprinus carpio* L.) of the Illinois River are not at all broad or high-backed like the cultivated European races. The malformed carp considered in this paper are, as a rule, still more slender (see Figures 1 and 2) and have a body shape similar to the German wild carp (Bauernkarpfen). The carp of the Mississippi River, on the other hand, tend to have a more fleshy body and a "roach" back and can usually be distinguished readily from Illinois River specimens. This seems not to be an inherent difference but rather a result of more favorable conditions for growth in the Mississippi. Some of the smaller bottomland lakes of the Illinois valley occasionally have their outlets closed during seasons of low water, so that the imprisoned fishes may exhaust the available fish food. Under such conditions of starvation, carp are often found which appear stunted and have the slender form that accompanies the present abnormality, but they lack many other readily recognized and more significant characteristics of the abnormal carp described in this paper.

"Knothead" is the name that the Illinois River fishermen use most often to designate these abnormal carp, but the terms "lunkhead", "pop-gill", "clam-jaw", "lump-jaw", etc., are also heard. These names all refer to the striking malformation of the head and opercles. The sweeping streamlines of the normal carp are broken up by several irregularities in the conformation of the knotheads. The opercles, instead of being slightly convex as in normal carp, are more or less bulged or curled up, with an average curvature about like that of the bowl of a spoon. The skull is

narrowed and the cheek region is conspicuously sunken between the eye and the opercle. Many of the knotheads have a marked lateral constriction or narrowness at the pectoral girdle just back of the opercles, and a more or less well-defined wrinkle over the snout. The head appears generally emaciated, and the sclerotic ring and the sculpturings on the cranial bones can be plainly seen (see Figure 3). On the under side there is usually a depression beneath the chin and a bulge in the region of the heart. All these external peculiarities which are commonly found in the more seriously affected individuals, together with a "drooping" of the fins and general sluggishness of habit, present a very different picture from the trim, sleek, and alert normal carp.

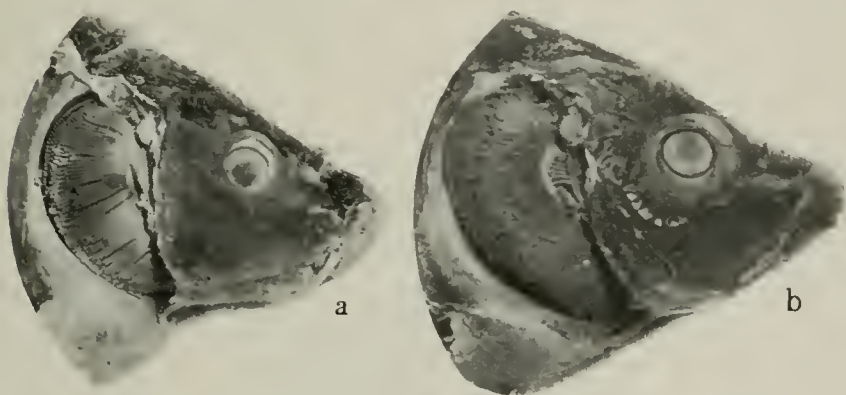
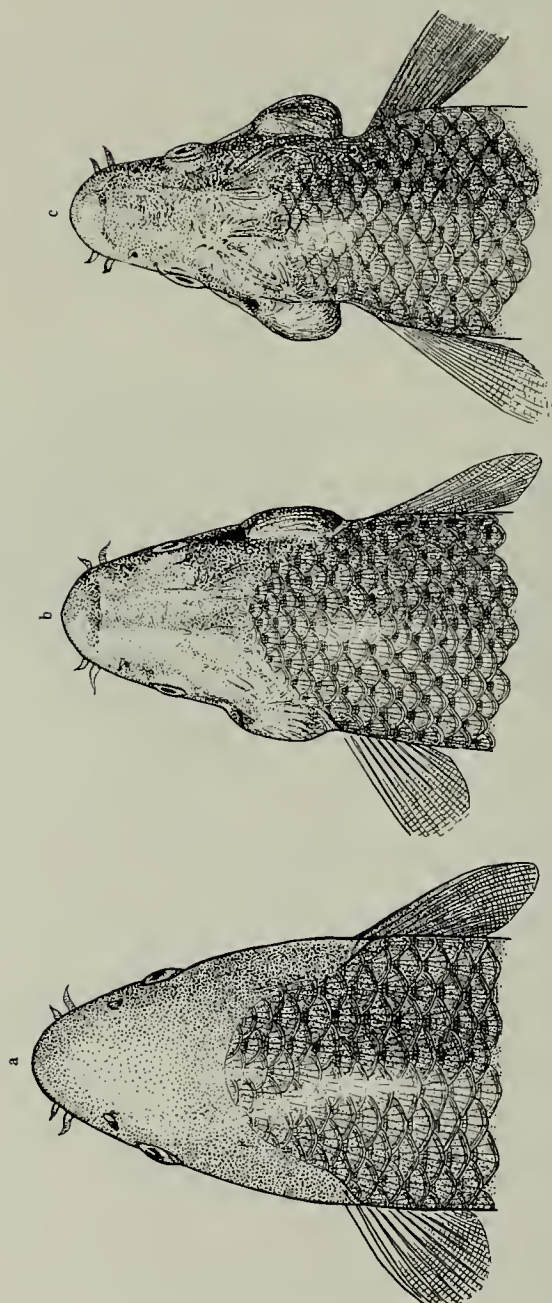


FIG. 3. Carp with their opercles removed: a, normal; b, knothead.

The knothead malformation is variable, and all degrees of it have been found up to monstrous, emaciated individuals three times as old as normals of the same weight. (See Figure 4.) There seems to be a close correlation in the degrees of malformation of the previously mentioned parts; that is, individuals with slightly bulging opercles have all these parts affected slightly; those of moderate degree have them all moderately affected, and so on. The bulging of the opercle is the most practical criterion of the knothead malformation, at least for use in the field, but it is so variable that among any dozen carp from the middle Illinois River one or more are usually difficult to classify as normal or abnormal (see Figure 10a). All references to the frequency of knotheads in this paper are based on specimens exhibiting obvious malformation; and specimens that were doubtful or only slightly malformed were commonly included with the normals.

When a number of living carp from the middle Illinois River are observed in a crib or pond or aquarium, the knotheads are seen to be some-



J.F. Müller

FIG 4. Heads of carp; a, normal; b, moderate knobhead; c, extreme knobhead.

what darker and less uniform in color than the normals, the darkest of them usually being the most malformed.

The large serrated spines of the dorsal and anal fins are strikingly altered in most knothead carp, being more or less reduced in length, sometimes to vestiges scarcely one-fourth the normal length, and having fewer and shorter serrations, or none at all. The dorsal spine of a normal carp is a little longer than the anal spine, but the reverse is usually true in knothead carp. The spines of knothead carp are often thicker laterally than those from normal carp of the same size, especially in the more distal portions. The right and left halves of these malformed spines are not so closely fused as in the normal spines, and in some instances they can be readily pulled apart. The dorsal spines of the knothead carp are not held erect as in normal carp, but are inclined backward, sometimes lying flat. (See Figures 1, 2, and 5.)

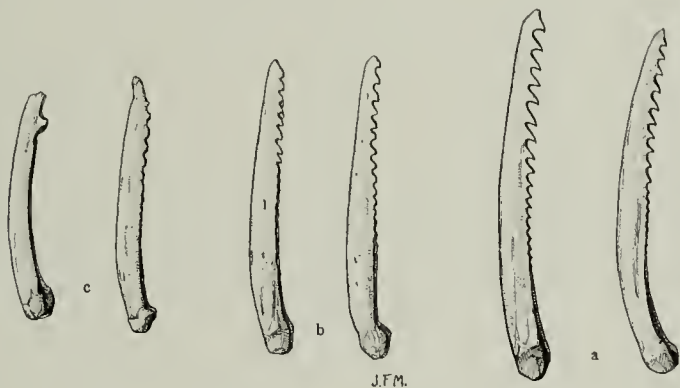


FIG. 5. Dorsal and anal spines of carp of the same length: a, normal; b, moderate knothead; c, extreme knothead. In each pair the dorsal spine is at the left and the anal spine at the right.

Many of these abnormal carp have the opercle so highly arched that it fails to reach the posterior margin of the gill chamber; in consequence, the opercular membrane does not lap flat on the body wall as in normal fishes, but extends inward or is curled under the edge of the opercle, seriously hampering the mechanics of respirations. In extreme cases considerable portions of the gills are always exposed, and the ragged and irregular arrangement of the lamellae in some knotheads may be the result of constant irritation by the edges of opercles that fall short of the posterior margin of the gill chamber. In such cases some of the lamellae have club-like thickenings at their tips (see Figure 3); less often they are partly grown together and show evidence of branching.

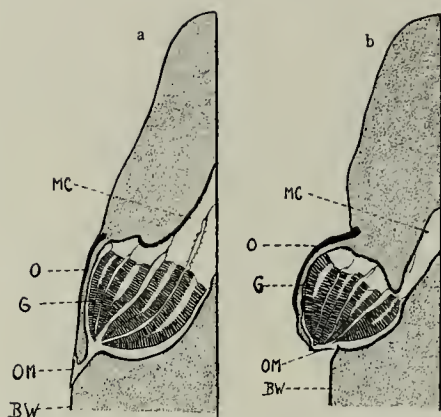


FIG. 6. Frontal sections through carp heads of the same length: a, normal; b, knothead. MC—mouth cavity; O—opercle; G—gills; OM—opercular membrane; BW—body wall.

To ascertain whether the bulging of the opercles might be due to an enlargement of the gills as an adaptation to diminished concentration of dissolved oxygen, counts and measurements of the lamellae on each gill were made on one normal and another malformed head, with the result that the lamellae were found to be both smaller and less numerous on the malformed head—averaging 15.5 mm. long on the normal head and 11.0 mm. on the malformed, with numbers of the lamellae to each gill as shown in Table I. Moreover, the gill chamber in the knothead was smaller than in the normal, as can be seen in Figure 6.

TABLE I.
NUMBERS OF LAMELLAE ON THE GILL ARCHES OF NORMAL AND KNOTHEAD CARP

	First gill arch	Second gill arch	Third gill arch	Fourth gill arch
Normal	138	133	117	118
Knothead	132	122	105	100

A close study of the opercles and the bones of an abnormal head showed no traces of an infection of the bones, either at present or in the past, which could be responsible for this malformation. Some of the bones of the abnormal head were thicker and heavier than those of the normal head, but this may have been due partly to the greater age of the knothead, which was 6 summers old as against 3 summers for the normal carp.

Age determination in knothead carp is more difficult than in normal ones, not only because the rings are more crowded as a result of the greater age, but also because there are numerous secondary rings in the scales. This is also true for the growth rings of the cranial bones and the vertebrae. It is possible, however, according to the criteria given by Hoffbauer,³ to distinguish the winter rings from secondary rings, since at the division line of the scale the annuli of the winter ring

³ Hoffbauer, C. Die Altersbestimmung des Karpfen an seiner Schuppe. Allgemeine Fischerei Zeitung. Vol. 23, p. 341. 1898. Vol. 25, pp. 135, 150, 297. 1900.

diverge, but those of the secondary ring do not. Most knothead carp have scales that are granular and opaque, and it is often necessary to examine large numbers to get a few showing the rings clearly—a condition found also among cultivated carp that have been starved.

Dissection and examination of normal and abnormal specimens showed that the skin, gill surfaces, and internal organs were free from infection or parasites; and the color of the gills in the living carp was bright red in both. There is less fat on the mesenteries and pericardium in the abnormal than in the normal ones, but fat is never altogether lacking. The flesh of the knotheads is softer than that of normal carp, although it is not as flabby and watery as in starved carp. Fishermen

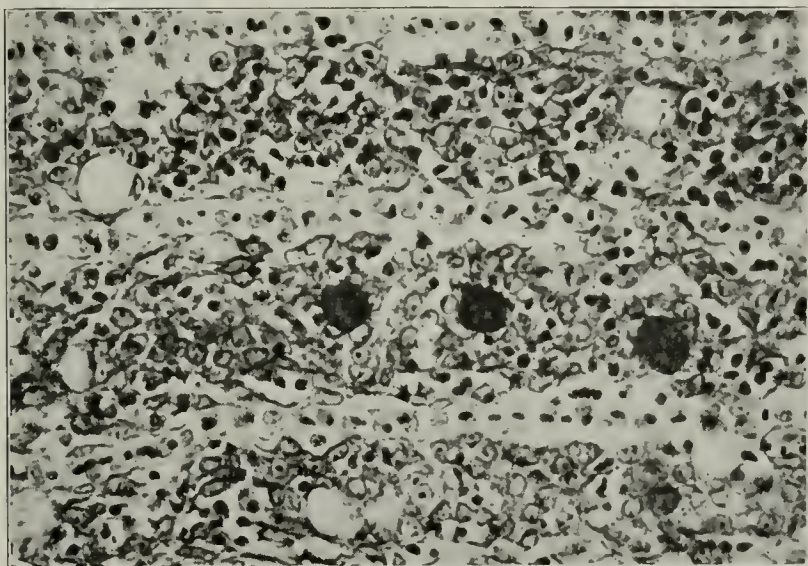


FIG. 7. Microphotograph of gill tissue of knothead carp.

of the middle Illinois River say that it is difficult to dress these carp for the market without seriously tearing the flesh and removing portions of it with the scales and skin when they are "fleeced". This softness of the flesh is well known to fish culturists and has been produced artificially in the experiments of Podhradsky and Kostomarov.⁴

Examination of the gill tissues of knothead carp gave no evidence of an infection, but sections of the gills showed varying numbers of bodies larger than ordinary tissue cells (10 to 20 microns in diameter) and staining differently. (See Figure 7.) These bodies were observed throughout the epithelium of the lamellae and gill arch and occasionally

⁴ Podhradsky, J., and B. Kostomarov. Das Wachstum der Fische beim absoluten Hungern. Archiv für Entwicklungsmechanik und Organismen. Vol. 105, p. 587. 1925

in the connective tissue, but most often in the deeper proximal parts of the lamellae. They were found in each of the several normals and knot-heads examined, but were more abundant in the latter. For a time they were thought to be parasites, with perhaps some connection with the knothead disease, but after considerable study it was seen that they had no characteristic resemblance to microscopic parasites of any known kind. They are quite different from mucous cells. They evidently belong to the tissues of the carp itself, but their place in its histology has not been determined.

A knothead carp of moderate degree and a normal one of the same age were selected for comparison from a collection made at Peoria in November, 1927, which was kept alive and under observation several days in large aquaria, in order to make sure that the selected individuals were representative of the two kinds and not obviously injured or affected differently by other factors. By taking these precautions, differences due to age, environment, parental stock, etc., were largely eliminated, so that any observed differences were probably effects of the disease. Data on these two carp are given in Table II.

TABLE II
MEASUREMENTS OF CARP USED FOR COMPARISON

	Normal	Knothead
Age	4 summers	4 summers
Length	14.2 inches	12 4 inches
Depth (at front of dorsal fin) .	5.0 inches	3.9 inches
Width (at front of dorsal fin) .	2.9 inches	2.5 inches
Weight	57 ounces	30 ounces

These two carp were anaesthetized, and dorsal and lateral X-ray photographs were made of them by Dr. C. S. Bucher at the Bucher Clinic, Champaign, both being rayed at the same time and on the same sensitized surface in order to maintain conditions as uniform as possible. These X-ray photographs, reproduced in Figures 8 and 9, show many of the malformations already described—the bulged opercles, sunken cheeks, narrow pectoral girdle, etc. Examination of the original negatives by strong light also shows a difference in the thickness of flesh on top of the head. In the normal specimen the median ethmoid, frontals, parietals, and pterotics, are overlaid by flesh 1 to 2 millimeters in thickness, while in the knothead practically none is visible over the frontals, parietals, and pterotics and a layer only $\frac{1}{2}$ to 1 millimeter thick over the median ethmoid.

These X-ray pictures, besides confirming observations already made and revealing further malformations, give a clue to the more intimate nature of these malformations; for, other factors being substantially equal, the depth of the “shadow” cast by a bone depends mainly on the thickness of that bone and its degree of mineralization.

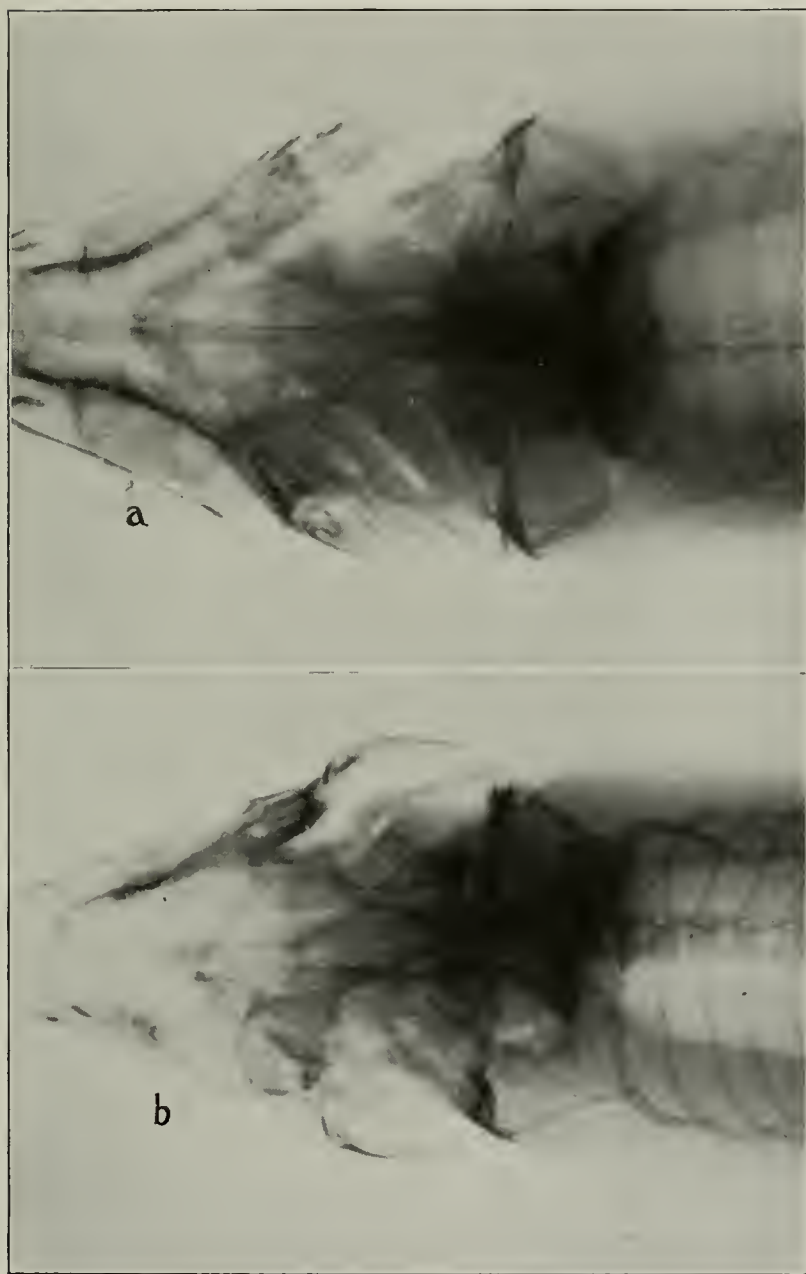


FIG. 8. Dorsal X-ray photographs of 4-year-old carp: a, normal; b, knothead.

The heads of the two 4-year-old carp used in the above comparison were heated almost to boiling, and the flesh was cleaned off the skulls and the bones of the pectoral girdle. The right opercle, the right cleithrum, and the right pharyngeal bearing the teeth were selected from each for chemical analysis. These bones were weighed and their percentages of ash and calcium determined by Mr. O. W. Rees, chemist of the Illinois State Water Survey, and the weights and percentages are given in Table III as an indication of the degree of mineralization.

TABLE III

	Weight of bone in grams Dried at 105°C.	Ash Per cent of bone weight	Calcium Per cent of bone weight
Right opercle			
Normal	1.2705	56.0	21.2
Knothead	1.0243	54.7	21.3
Right cleithrum			
Normal	0.9700	50.0	19.6
Knothead	0.6262	53.3	21.3
Right pharyngeal bearing teeth			
Normal	0.7562	51.3	15.8
Knothead	0.3489	54.1	17.7

The analyses show that the percentage of ash is about the same in both the normal and the knothead and that the percentage of calcium is slightly greater in the bones of the knothead. The calcium determination is of greater significance for comparison of X-ray "shadows", since calcium is the only element of importance in bone which produces the shadow. The percentages of calcium, however, are so similar that any considerable differences in the X-ray shadows of corresponding bones of the two heads are probably due to differences in the thickness of bone penetrated.

The shadows cast by the various bones of each head in the present comparison differ greatly in density. The roentgenograms show that the frontals, parietals, pterotics, opercles, and a few other bones of dermal origin on the top and sides of the knothead skull are more opaque to X-rays than the corresponding bones in the normal. The denseness of these malformed bones is not evenly distributed, but is most pronounced near the ossification centers, while other parts of the same bones often cast lighter shadows than the corresponding parts of normal bones.

The deeper-lying bones of the knothead skull, both of dermal and chondral origin, throw lighter shadows than corresponding normal bones because they are generally thinner. Many of the longer bones of the skull are not only thinner in the knothead but are often much narrower than the ratio of the lengths of the two would indicate. The greatest difference in the shadows cast by the bones of the two skulls is to be found in those about the base of the skull, which are perhaps the deepest-lying bones of the head.

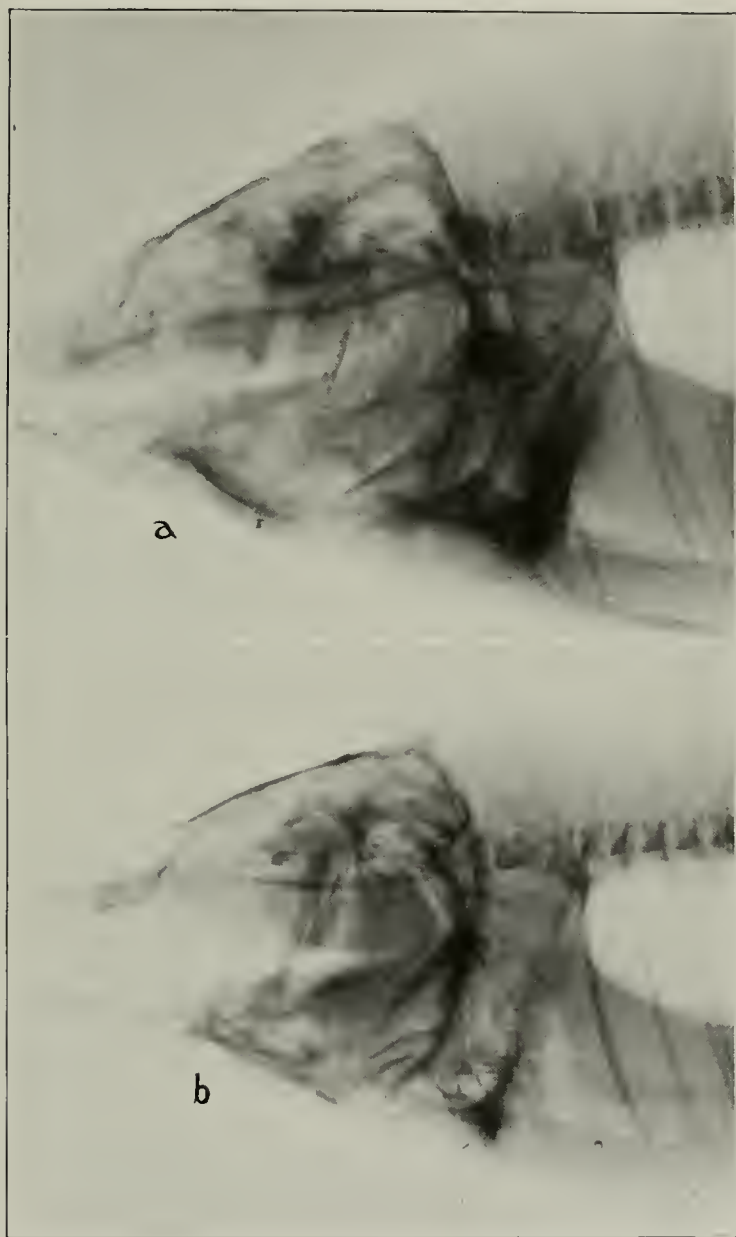


FIG. 9. Lateral X-ray photographs of 4-year-old carp: a, normal; b, knothead.

The relation of the weight of the bones of the head to their depth beneath the surface is well shown in Table III. The opercles are covered by only a thin skin and are taken as representative of the peripheral bones. The ratio of the weight of the normal to the knothead opercle is 1:0.81. The cleithra form part of the pectoral girdle and are of intermediate depth. The ratio of their weights is 1:0.64. The pharyngeals that bear the teeth are fairly large and more easily removed entire than the other deeper-lying bones. Their ratio is 1:0.46.

This pronounced thinness of the bones of the occipital region of the knothead skull is quite obvious in the cleaned skulls. While the knothead skull is actually smaller than the normal, its foramina for the passage of nerves and blood vessels are almost always actually larger. The two heads had been heated in the same vessel of water and cleaned and treated throughout in the same manner, and the skulls had been air dried in the same box; but the thinner bones forming the brain case of the knothead skull opened at the sutures, leaving gaps occasionally more than a millimeter in width. These gaps are not due to a general disarticulation of the skull, because it is still held firmly together by the heavy bones on top of the head and the parasphenoid. No such gaps appeared in the normal skull as it dried. Those of the knothead skull are apparently produced by differential shrinkage of the heavy, dense bones forming the roof of the cranium and the thin, lightly mineralized bones lying deeper in the head.

X-ray photographs of knotheads of different degrees of malformation, from slight to extreme, made for comparison with the one of moderate degree we have been considering, are shown in Figure 10. The extreme knothead (Figure 10d) shows heavier and denser bone at the ossification centers of the peripheral bones of the skull than those in Figure 8b, and these centers of heavy ossification are lacking in the head with only a slight degree of malformation (Figure 10a).

Photographs of the skulls from these two heads are reproduced in Figure 11. The difference in conformation is greater than would have been suspected from the appearance of the living fishes or from their X-ray photographs. The areas of heavy mineralization found in the peripheral bones of the knothead are visible in its skull as unusually heavy sculpturing and ridging at the ossification centers. The anterior margins of the malformed opercles have a slightly inflated appearance, and, when freshly cleaned, they had the red color of cancellated bone tissue. There are further alterations in shape and details of structure in every bone of the knothead skull, but a detailed description of them is hardly justified in this account.

In proportion to the length of the spinal column, the head in these malformed carp is 2 to 5 per cent shorter than normal. This is understandable in view of the fact that there is no malformation visible in the vertebrae of the knotheads, either by direct examination of the bones or from their X-ray shadows.

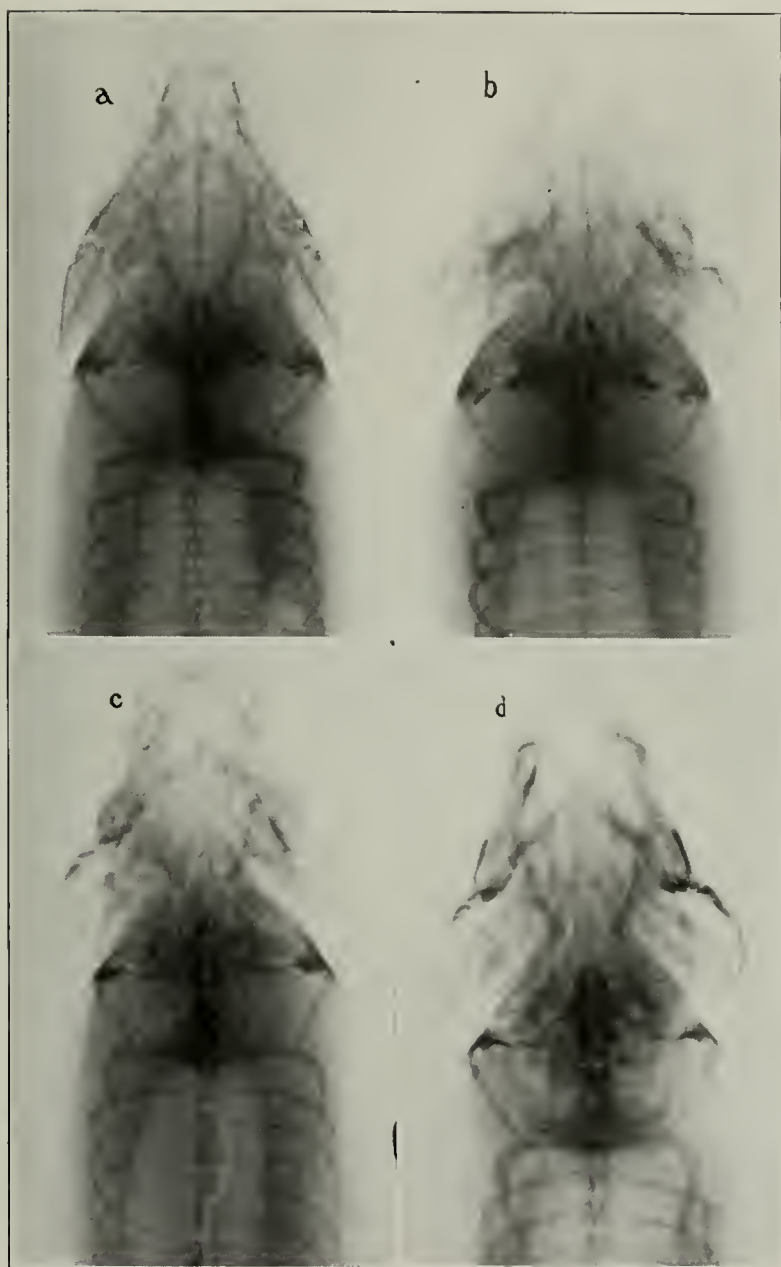


FIG. 10. Dorsal X-ray photographs of knotheads showing different degrees of malformation: a, slight; b, moderate; c, moderate; d, extreme.

Differences in the intimate structure of the skull bones of normal and diseased carp were studied by means of X-ray photographs made by Dr. G. L. Clark of the University of Illinois by the monochromatic pin-hole method,⁵ showing the degree of diffraction of a beam of X-rays passed through the bone. The crystals of both were found to have a random orientation and to be within the range of size of colloidal particles, those of the knothead being slightly larger than those of the normal—a fact which substantiates previous observations of the greater brittleness of knotheads' bones.

DISTRIBUTION OF KNOTHEAD CARP

Carp fingerlings with bulging opercles were first noticed in the fall of 1918 in the Illinois River at Peoria. Fishermen report that knothead

⁵ Clark, G. L. Applied X-rays. McGraw-Hill Book Co. 1927.



FIG. 11. Skulls of 4-year-old carp: a, normal; b, knothead.

carp began to appear in the catch of market-size fishes in 1920, and that the percentage of knotheads increased rapidly, reaching about 50 per cent in 1922 at several points on the river. In order to find out more definitely the distribution of the malady and the percentage of market-size carp affected, many points on the river were visited during 1926 and 1927, and catches of carp were examined and information was obtained from fishermen. A summary of the data is given in Table IV, and the location of sampling stations is shown in Figure 12. These data were all obtained during the winter of 1926-1927 except the Peoria and Meredosia numbers, which are for the summer and fall of 1927. The rather high percentage of knotheads at Peoria is largely due to the recognition of slight degrees of malformation in individuals such as had formerly been included with the normals. The observed percentages are based on hoop-net catches and give a more accurate measure of the proportion of knothead carp than hauls made with seines which have larger meshes and allow many of the stunted and slender knotheads to go through.

In the course of several years work on the fishes of Rock River, less than a dozen knotheads have been noticed among the many thousands of carp taken. Careful examination of catches of carp from various parts of the Mississippi Valley in the Chicago markets has occasionally revealed a few individuals with distinctly knothead characteristics. Indirect reports have been received of large numbers of knothead carp being taken in Lake Pepin on the Upper Mississippi, but no direct information has been available as yet on this point.

RELATION TO POLLUTION

The beginning of this malformation among the carp was coincident with a period of very rapid increase in pollution, due partly to an increase in the population of Chicago and other cities which pour their wastes into the river, but still more to the war-time boom in many industries, particularly those engaged in the packing and manufacture of food products. The subsequent fundamental alteration of the character of the bottom fauna of the Illinois River has been described by Richardson in the various publications of the Illinois Natural History Survey.

As indicated in Table IV, knothead carp range from Utica (Starved Rock) down to the Copperas Creek Dam with only occasional individuals below that point. There are no fishes of any kind above Utica, since, because of pollution, the amount of dissolved oxygen in that part of the river is so low throughout most of the year that fishes can not live. As long ago as 1912 Utica was the upper limit of most of the species of fishes in the Illinois.⁶ The few species that were occasionally found above that point disappeared completely, according to the reports of fishermen, in the years between 1912 and 1917.

⁶Forbes, S. A., and R. E. Richardson. Studies on the Biology of the Upper Illinois River. Ill. Nat. Hist. Surv. Bull. Vol. IX, Art. X. 1913.

In the years since 1917, pollutional conditions have prevailed over a hundred-mile stretch of the middle Illinois River, and the fishery yield of this section has shown marked reduction as compared with the yield before 1917. The fishes themselves are largely restricted to the cleaner bottomland lakes and backwaters of this section. The carp, being of more tolerant habit than other fishes, have continued to range over a large part of this pollutional area except during periods of severe oxygen depletion

TABLE IV
DISTRIBUTION AND PERCENTAGE OF KNOTHEAD CARP IN THE ILLINOIS RIVER
DURING 1926 AND 1927

Stations going downstream	Number of carp examined	Observed percentage of knotheads	Information and estimates of local fishermen
Utica	none	About 50 per cent of the carp are knotheads. This is the upper limit of fish life in the Illinois River.
LaSalle-Peru	none	About 50 per cent of the carp are knotheads.
Depue	23	91	Not as many knotheads as this sample indicates. 60 to 75 per cent is more nearly correct.
Henry	316	75	60 per cent is more nearly correct as a year-round average.
Chillicothe	117	64	About the correct proportion.
Spring Bay	302	46	Hardly as many knotheads as usual from this place.
Averyville	149	57	About the correct percentage.
Peoria	256	78	The carp in Lower Peoria Lake average 50 to 60 per cent knotheads.
Pekin	about 500	about 30	About average percentage of knotheads. Knotheads are found downstream as far as the Copperas Creek Dam. The knotheads here are not slender and many even tend to be pot-bellied.
Havana	539	none	An occasional knothead carp is taken which is believed to have straggled down the river from where they are plentiful. The percentage is extremely low, as only a few individuals are taken among many tons of carp.
Beardstown	3	none	No knothead carp have been seen here.
Meredosia	42	2	Fishermen have not noticed knothead carp here. The one taken was of moderate degree and pot-bellied.

in summer and under heavy ice in winter. The distribution of knothed carp coincides, both in main features and in detail, with the areas of greatest change in sanitary condition.

Below the Copperas Creek Dam the carp are all normal except for occasional knotheds that have straggled down the river. Natural purification of the sewage load of the upper and middle river is approaching completion in midsummer by the time this lower section is reached:



FIG. 12. Sketch map of the Illinois River.

and there has been no general or serious alteration in the character of the food supply of the carp.

The observed percentages of knotheds at various points on the Illinois River indicate that the proportion of affected carp decreases downstream, as is to be expected if the malformation is correlated with pollution.

The knothead malformation appears among those races of carp with reduced scalation (mirror and leather carp) to the same extent as among the scaled variety. The proportion of these mutant races of carp in the original stock of the Illinois River was quite large, but their numbers soon decreased to the present proportion of one or two per cent of mirror carp and still fewer leather carp. The carp populations of other waters of the Mississippi Valley show these varieties in about the same proportions.

The occasional occurrence of a few knotheads in the Rock River and other waters seems to have no relation to pollution.

No malformations similar to those of the knothead carp have been found in other species of fishes of the middle Illinois River. During the course of this and other investigations considerable numbers of about twenty species of larger fishes from this section of the river were handled without any appearance of alteration in their growth form, but an examination of other cyprinoid fishes (minnows) of this area might discover an abnormality like that of the knothead carp.⁷

CHANGES IN THE FOOD SUPPLY OF THE CARP

The following statement by Mr. R. E. Richardson concerning recent changes in the natural food supply of the carp in the middle river is based on various field observations and unpublished plankton data in the possession of the Natural History Survey, accumulated between 1910 and 1925.

The most significant changes in the plant and animal food supply of the carp in the middle Illinois River in recent years had to do either directly or indirectly with the plankton and the coarse aquatic vegetation. That the latter usually serves to some extent as green forage for carp above the late fingerling stage can hardly be doubted, though the exact extent to which either the roots or the stems or other parts of coarse aquatic plants enter into the normal food supply of these fishes has not been quantitatively determined. The almost complete extermination of the Potamogetons and other large plants in Peoria Lake and also in the river and in its connecting lakes and sloughs far below that point, between 1915 and 1920, left large numbers of carp practically without any green forage at all for several seasons. Since 1922 or thereabout, restoration of the Potamogetons particularly has proceeded rather

⁷Some young goldfish, spawned in the summer of 1927 in the University of Illinois lily pond, were brought indoors in October and kept in a large aquarium, which was supplied with running tap-water and aerated with compressed air. They were fed commercial goldfish food occasionally, and there was no other food available except mud on the bottom. There were no algae or other green plants present. The fishes were an inch to an inch and a half long when they were brought indoors, and they did not grow perceptibly afterwards. In December some of them showed signs of emaciation and an occasional one died. About half of the 50 fishes in the aquarium on December 15 had distinctly arched opercles, most frequent on the emaciated fishes but present also on some of the fleshier ones. Those with arched opercles also showed the sculpturing of the skull bones, the drooping fins, the narrow pectoral girdle, and the general sluggishness characteristic of knothead carp.

More recently a few golden shiners with strongly bulged opercles have been found in the Salt Fork River in Champaign County.

rapidly in many sections of Peoria Lake as measured by the areas affected, though the growths are yet generally very sparse as compared with those of the pre-1920 years, and the areas covered are still decidedly smaller.

The distinct change in the general composition of the normal summer plankton in the section of river extending from Spring Valley to a point in Peoria Lake only a few miles above Peoria Narrows, between 1913-1915 and 1920, was probably no less important in its final effects than the reduction in the coarse aquatic vegetation as an item in the general reduction of the green forage supply that took place during the period as a result of pollution; and this has continued substantially without visible relief up to the date of our latest observations. This change involved the substitution on a large scale of non-chlorophyll-bearing *Protozoa* for chlorophyll-bearing kinds, and the replacement of vast numbers of DIATOMACEAE and CHLOROPHYCEAE by filamentous or non-filamentous blue-green algae. The change was so marked in the summer of 1920 between Chillicothe and the foot of Upper Peoria Lake that the water, which in former years had shown a normal pale-green tint when relatively free of silt during the hot season, took on a distinctly blackish tinge, apparent to the unaided eye in bright sunlight. The recovery of the diatoms and CHLOROPHYCEAE as well as of other green microscopic forms, was quite rapid both that summer and in the summer of 1922 below the upper third or half of Middle Peoria Lake—a fact enabling us to make fairly satisfactory, though rough, colorimetric determination on given days of the location of the boundary line between preponderance of blue-green and green plankton by observing the change in color of the plankton samples in the bottle in the field a few minutes after pouring on the alcohol-formalin mixture used for preservation. A similar boundary line between the greens and the blue-greens of the plankton could be made out in the same way in the summers of 1911 and 1912 at points usually lying only a short distance below Spring Valley.

These changes in the plankton could obviously affect directly the fry of carp and other fishes depending upon it for their first food. A far more important effect upon the carp between the fingerling and adult stage could apparently be exerted through the medium of the bottom, shore, and limnetic organisms of microscopic size, which had fed upon the plankton and had later entered into the carp's rations in the same or adjacent areas. During the same period (1913-1915 to 1920-1922) the changes in the principal constituent organisms of the small bottom fauna,⁸ though also great in degree, appear to have been in themselves of no particular importance to the health of the carp and other bottom-ranging fishes. The increased restriction of the diet of the small bottom animals above Peoria to microscopic organisms lacking in chlorophyll or food elements, such as vitamins, directly or indirectly derived from it can easily be believed, however, to have been capable of caus-

⁸ Richardson, R. E. The bottom fauna of the middle Illinois River, 1913-1925; its distribution, abundance, valuation, and index value in the study of stream pollution. Ill. State Nat. Hist. Surv. Bull. Vol. XVII, Art. XIII. (In press.)

ing disturbances both in the growth and metabolism of fishes confined to these small bottom animals for food, if the requirements in that respect of man and many lower animals above the grade of fishes are to be accepted as in any sense a usable criterion.

RATE OF GROWTH OF KNOTHEADS

During the winter of 1926-1927, representative samples of carp, obtained from fishermen at various points on the Illinois River, were weighed to the nearest ounce and measured for length and for depth at the front of the dorsal fin, and about twenty scales were taken from the left side of each fish between the dorsal fin and the lateral line. The carp were classified into normals and knotheads, but many with doubtful or slight degrees of malformation were included with the normals. The scales were cleaned and age determinations were made by counting the winter rings of at least ten scales from each fish. Scales which have been regenerated, and consequently have smaller numbers of winter rings, can usually be recognized by their irregular shape, and avoided. The data on the age and weight of normal and knothead carp at various points on the Illinois River are given in Table V.

Differences in age of normals and knotheads of the same size are shown in Table VI, the data of which have been arranged in twelve 5-ounce weight classes and the ages of the two kinds compared in each class. The knotheads average older than the normals in each of the twelve classes. Arithmetical averages (not weighted) of the ages of the two kinds in the first six and the last six classes show that the difference in age between normals and knotheads of the same size is much greater in the heavier classes.

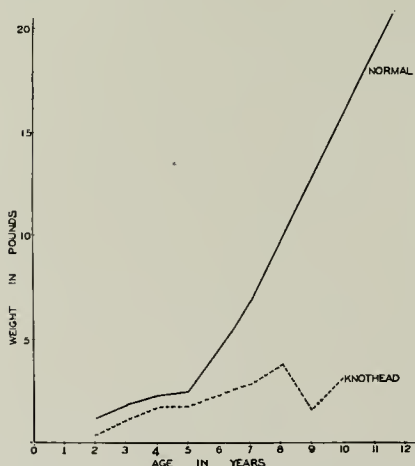
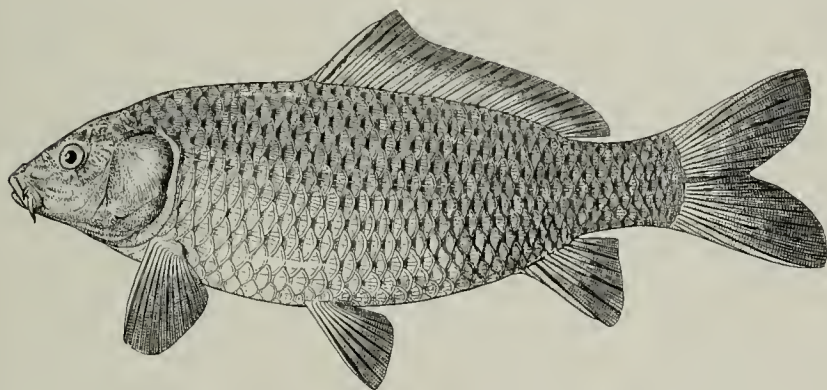


FIG. 13. Growth curves of normal and knothead carp of the Illinois River.

Growth curves plotted from the data in Table VI are shown in Figure 13. These curves indicate that the stunting effect of the disease is cumulative and stops growth altogether in the knotheads at the time when normals are growing most rapidly. Since it has been obvious throughout the investigation that growth is retarded in proportion to the degree of malformation, it seems probable that carp with slight degrees of malformation have a growth rate intermediate between normals and knotheads, and the inclusion of knotheads of slight degree with the normals has probably resulted in an appreciable lowering of both the curves between the third and sixth years.

Calculated from the data in Table VI, the average individual growth rate of normal carp is about 11 ounces a year⁹ and that of knothead carp is only about 6 ounces a year. There is no considerable variation in the growth rate of the former from one end of the river to the other, but the growth rate of the latter tends to increase downstream. Thus the lowest rate for knotheads, 3.8 ounces a year is at Depue, while the highest rate, 9.1 ounces a year is at Pekin.

The greater growth rate down the river is strikingly reflected in the body contours of the knotheads. A large number of them were seen at Pekin and practically all, instead of being more slender than the normal, were pot-bellied—a condition strikingly illustrated in a single knothead taken at Meredosia in July, 1927, a drawing of which is shown in Figure 14. An examination of the gonads of this fish showed that it was a spent female. Its scales showed that it was four years old, and the relatively greater width of the last two growth rings indicated that in those years growth had gone on at a relatively rapid rate.



J.E. Miller

FIG. 14. Pot-bellied knothead carp from the lower Illinois River.

The 30 per cent or so of pot-bellied knotheads seen in catches from the stretch between Pekin and the Copperas Creek Dam may indicate either that the conditions associated with pollution and inducing malformation were of short duration or else that these fishes migrated downstream, perhaps from the Peoria Lake region, after their growth form had been altered by exposure to the knothead-inducing conditions during their early life. The development of the pot-belly seems to indicate that, under non-pollutional and hence more favorable conditions, the viscera tend to grow at a normal rate while the growth of the skeleton and muscles of the carp is permanently retarded.

⁹ Doctor Scheuring says that the growth of normal carp in the Illinois River is about as rapid as under fairly good cultivation in Germany.

TABLE V
 WEIGHT (IN OUNCES) OF NORMAL AND KNOTHEAD CARP OF DIFFERENT AGES
 Based on random samples obtained from fishermen during the winter of 1926-1927. The data on knothead individuals
 are in bold-face type.

Locality	Miles below Lake Michigan	Age in years											
		Year spawned											
		2	3	4	5	6	7	8	9	10	11	12	
DÉPUE Depue Lake	114.3	1925	1924	1923	1922	1921	1920	1919	1918	1917	1916	1915	
		3	12	10	11	15		18					
		3	13	13	11	24							
		8	14	30	14	28							
			16		15								
					20								
					21								
HENRY Sawmill Lake	129.5				23								
					23								
					26								
					32								
HENRY Sawmill Lake	129.5	26	25	23	15	65	31						
		28	28	33	28								
			31		28								
					28								
					33								
					37								
					46								

CHILLICOTHE Rice Pond	145.3			25 37 46 50	18 22 24 25 31 31 33 33 36	26 26 43 25 68	33 108	73		
SPRING BAY Spring Bay	153.2	34		19 32 34 44	16 17 36 38	27 33	37	48 65 80	48 53	
AVERYVILLE Peoria Narrows	161.0	42		47 106	39 42	33 47	80	75		352
PEORIA Peoria Slough	163.7				29	17 24 37	43	26		
PEKIN Down the river	180.5					55 59				

TABLE V—*Concluded*

Locality	Miles below Lake Michigan	Age in years											
		Year spawned											
		2	3	4	5	6	7	8	9	10	11	12	
HAVANA	Clear Lake 195.3	1925	1924	1923	1922	1921	1920	1919	1918	1917	1916	1915	
				35	65 68								
Quiver Lake	202.4		22	19 19 27 29	27 33 37 37	30 64 133							
				32 32 33 39 47 50 56									
Cook's Ditch	206.0		22 24	22 26 30 31 32 34 35 67	22 35 41 43 54								
BEARDSTOWN													
Ditch below town	241.6			50 74	62								

BEHAVIOR OF KNOTHEAD CARP

The reactions of knothead carp to their environment differ from those of normal carp in many details. Our present information, although rather fragmentary, shows that some of the differences in behavior are of considerable importance, and that they are attributable to various manifestations of three defects found in the knotheads—an inefficient respiratory apparatus, a general flaccidity of the body that implies a lack of muscular tone, and a comparatively low sensitivity to stimuli.

Many fishermen of the middle Illinois River have given us information concerning knothead carp and their habits, one of the most important items of which is a difference in the habitat of normal and knothead carp. Carp are distributed throughout many kinds of situations in the Illinois River proper, in the connecting bottomland waters, and in Peoria Lake, which is a widening of the river. Those taken from situations where there is a considerable flow, and where it is probably necessary for them to swim more or less constantly to hold their position, are almost invariably normals. The catch from the deeper quiet waters includes both normal and slightly deformed carp. Most of those taken from the shallower backwaters of the section between LaSalle and Peoria, extensive areas of water choked with brush and vegetation, have moderate degrees of malformation. The writer has examined single catches with as many as 200 carp from these shallow backwaters without finding a single entirely normal individual, although during periods of high water, normal carp are taken there in fair numbers along with knotheads.

In summer extremely malformed and emaciated knotheads can often be picked up by hand where they are lying quiescent in shore vegetation. These are known to fishermen as "grass" carp. Their behavior suggests that extreme malformation has so embarrassed respiration that they can live only in relatively high concentrations of dissolved oxygen, and that they are so occupied with getting sufficient oxygen that they do not feed or react to ordinary stimuli. Such individuals are often found dead in nets and along the shores.

A large part of the commercial catch of carp is taken by means of hoop-nets set along the shores and in other shallow waters from 2 to 8 feet deep. The openings of these nets are directed downstream and are flanked by wings to guide the fishes into the openings. Such nets capture, of course, only those fishes that swim into them, and their usefulness depends on the fact that the fishes react to small changes in environmental factors, such as stage of water, temperature, turbidity, rate of flow, waves, light, ice movement, dissolved oxygen, and food supply. Since minor changes in these factors occur from day to day, some fishes are always moving from place to place, and a more or less constant number of them are taken daily in these hoop-nets. The catch of knotheads, however, is more irregular than that of normal

carp and other fishes. This indicates that the knotheads do not so readily react to these minor changes in condition, but are quiescent for long periods of time. When major variations of environmental factors cause them to move, they are taken in large numbers, because they are less alert and more blundering than normal carp. For example, an upstream wind apparently drives these knotheads before it along the shores, where they are taken in large numbers by hoop-nets.

The first fingerling knothead carp seen by the writer had been washed ashore in late August, 1923, while the laboratory boat was tied up at Peoria Narrows. An upstream wind which blew continuously for several days, producing waves a foot or more in height, caused thousands of small carp and a sprinkling of other small fishes to be thrown up on the beach, along with uprooted vegetation and miscellaneous debris. These little carp were apparently uninjured, and a quantity of them were gathered up and kept alive for several weeks in the large aquarium on the laboratory boat. They were from 1 to 3 inches long and were obviously of the brood spawned during May and June of that year. At that time the local fishermen pointed out that many of these young carp had the bulged opercles characteristic of the knothead fish that had been numerous in their catches. They further remarked that it was very unusual for carp to be driven ashore, inasmuch as the carp, of all fishes in the river, are the most alert and best able to take care of themselves.

Occasionally the Illinois River is frozen over for a few weeks in winter and a condition of stagnation develops which is accompanied by a decrease in the amount of dissolved oxygen in the water.¹⁰ When the amount of dissolved oxygen in the heavily polluted channel waters drops to 3 parts per million or less, the fishes begin to retreat into the back-water lakes, spring holes, mouths of tributaries, and other places where there is more oxygen. At such times large hauls of fishes are taken by fishermen in certain spring holes, the best known of which is at Spring Bay in Upper Peoria Lake, where 200,000 pounds of carp were taken in December and January, 1917-1918. Large numbers were taken there also in the winter of 1924-1925, and a fair number in the winter of 1926-1927. The early hauls from this spring hole are almost all knothead carp, but later hauls, made after stagnation in the river is more advanced, are mostly normal carp. This is further evidence that the knotheads are more quickly affected by low oxygen concentrations than are normal carp.

Illinois River fishes often have a very disagreeable "gassy" taste or odor, which seriously lessens their palatability, and these gassy fishes are definitely associated with periods of prolonged ice on the river, mortality in nets and traps, and other indications of a scanty oxygen supply. Fishermen find that this gassy taste occurs more often and is more pronounced in knothead than in normal carp, and for this reason

¹⁰ Thompson, David H. Some observations on the oxygen requirements of fishes in the Illinois River. Ill. Nat. Hist. Surv. Bull. Vol. XV, Art. VII. 1925.

the knotheads are culled out when carp are shipped to New York from the Illinois River, because it is very costly to ship such long distances by express and any defect in the quality of the fish is likely to cause them to be docked in price to a point where the money received will not pay the transportation charges. To remove this gassy taste, fishermen place their fishes for a week or two in cribs or ponds fed by spring or other well-aerated water.

A spring-fed pond of about half an acre has been constructed by a fishing firm on the east shore of Lower Peoria Lake as storage space for live carp. In warm weather the carp are hardened in this cold spring water before they are shipped alive in tank cars to New York, and in winter they are left in this clean, well-aerated water for a few weeks to improve the flavor. The first live carp were put in this pond for storage during the latter part of the summer of 1927, and by the middle of September about 120,000 pounds had been accumulated.

During a fortnight of very warm weather in September some of these fishes died of suffocation, and it was noticed that the first to die were almost all knotheads, and that those dying a few days later were both normals and knotheads. A few dissolved-oxygen determinations made at this time indicated that the knotheads began to die in numbers as soon as the dissolved oxygen fell to about 2.8 parts per million, and that the normals began to die when it had fallen to about 2.45 parts per million.

The weather turned cool, the aeration of the spring water was improved, and the carp stopped dying. Some determinations made a little later showed about 5 parts per million of dissolved oxygen in various parts of the pond. At this time many of the knotheads were lying in the shallow water at the margin, while the normals were moving about in the deeper parts of the pond or making repeated attempts to ascend the stream of spring water as it poured in. These normals kept their fins fully extended and were seldom quiet for more than 2 to 5 seconds, but the knotheads would lie on the bottom for many minutes at a time, seldom moving unless they were nudged by other fishes. Their fins were rarely fully extended, and the dorsal was usually inclined backward or lying flat.

Three normals and six knotheads, each weighing between $1\frac{1}{2}$ and $3\frac{1}{2}$ pounds, were hauled from this pond to the laboratory at Urbana in 10-gallon cans and kept in a large aquarium in well-oxygenated water at about 62°F. The average numbers of respiratory movements per minute of five of the knotheads were 61, 63, 67, 69, and 87. Although accurate counts could not be made on any of the normals because they were constantly moving about, their respiratory movements were obviously slower than those of any knotheads and were estimated to be about 50 per minute. The relative viability of the two kinds is indicated by the fact that 4 of the 6 knotheads died during the first three days while none of the normals died. The death of the former could not have been due to over-crowding or lack of oxygen, because the aquarium was

large and was supplied with a good flow of well-aerated water which was further oxygenated by bubbling compressed air through the tank. This greater loss of the knotheads is experienced by fishermen who ship carp to New York in tank cars that are constantly aerated by air compressors.

The supernumerary rings on the scales seem to indicate that the knotheads stop feeding for considerable periods of time during the growing season, perhaps because of embarrassment in respiration during periods of dissolved-oxygen deficiency in summer.

ETIOLOGY OF KNOTHEAD DISEASE

The possible causes of malformation in fishes are usually considered as falling into three classes: (1) hereditary defects, (2) infections, and (3) environmental changes that disturb the normal metabolic and developmental processes. There is no reason to suppose that the knothead malformation of carp is hereditary; neither has any evidence been obtained, during several months of work on the histology and morphology of knotheads, of an infection of any kind that could produce it. The first two possible causes of malformation being thus eliminated, it seems probable that we have to deal with some external influence which has interfered with the developmental processes or the metabolism of these carp and has altered their growth form.

No significant similarity has been discovered between the knothead malformation and any of the many abnormalities that have been produced in fishes by various workers by changing the physical and chemical conditions of the medium during the egg and early embryonic stages. Double-headed monsters, multiplication of parts, coalescence of parts, supernumerary organs, etc., such as have been described by O. Hertwig, G. and P. Hertwig, Mielewski, Stockard, Tornier, Werber, and others, obviously have nothing in common with the malformation we are considering. The explanation of knotheads, therefore, is to be sought in terms of metabolic disturbance.

The marked difference in the growth rates of normal and knothead carp is direct evidence of some metabolic change, the production of large numbers of knotheads in a certain part of the river indicates some general environmental cause, and the fact that growth is retarded throughout the life of these fishes indicates, further, that the causative conditions are persistent in this area. The few pot-bellied knotheads, which we have found farther downstream, are individuals that partly recovered after they had escaped from the waters in which the causative conditions obtained.

It has been shown that the distribution of this abnormality coincides with a certain pollutional area of the river, and this limits the causative agent to conditions which accompany pollution. The fact that carp alone show abnormality delimits the cause to some condition which affects carp and not other fishes of the area—on the supposition that

the innate liability of all fishes of the area to abnormality is the same. In the middle Illinois River under pollutional conditions, carp constitute a much higher percentage of the total catch of fishes than in the cleaner waters of the lower river. This is mostly because the carp are more tolerant of pollution and feed over much larger areas than the other less tolerant fishes, which are mostly restricted to the cleaner backwaters of the region. The character of the food supply available to the carp in this region has been strikingly altered by the pollutional conditions which have prevailed during the past decade. Since the other fishes have been restricted to the cleaner backwaters, probably no marked change in their diet has been produced. Since no other condition affecting only the carp is known which could conceivably induce metabolic disturbances, food is taken to be the causative agent of the abnormality. In recent years, many metabolic disturbances traceable to food have been found to be due to the lack of certain food elements, or vitamins. To date, very little is known about diet-deficiency diseases except in man and a few other warm-blooded animals, but in the latter the changes resulting from the lack of the different vitamins have been fairly well worked out.

The knothead malformation shows definite changes in calcium metabolism, since the bones are altered in shape and thickness; the bones of the skull are malformed while the vertebrae are unaffected; there is also a marked lack of muscular tone, as indicated by the flaccid body and general sluggishness of the affected fishes. In warm-blooded animals such symptoms have been found to be associated with the lack of vitamin D. Growth curves for experimental rachitic and normal rats¹¹ are practically identical with the growth curves for knothead and normal carp. In the higher vertebrates, where the etiology of rickets has been worked out most completely, the most characteristic symptoms are found in the long bones of the appendages and in the ribs. Critical comparison with rickets as known in these higher animals is made difficult, however, by reason of the fact that the carp has no long appendicular bones and its ribs are haemal bones, not homologous with the pleural ribs of the TETRAPODA. In the long bones of the latter a very characteristic indication of rickets is to be found in the tissues about the line of calcification in the epiphyses,¹² but there are no epiphyses in the skeleton of the carp.

Sunlight or ultra-violet rays seem to be essential to the production of the antirachitic factor, vitamin D. A number of workers¹³ have pointed out that our richest sources of vitamin D are animals, such as the cod, which feed directly or indirectly on chlorophyll-bearing, and hence sunlight-loving, plankton and other green organisms. Rickets is

¹¹ Cahan, M. H. Studies of cholesterol in prevention of rickets. Thesis, University of Illinois Graduate School. 1927.

¹² McCollum, E. V., and N. Simond. The new knowledge of nutrition. Macmillan Co. Third Edition. 1925.

¹³ Coward, K. H., and J. C. Drummond. On the significance of vitamin A in the nutrition of fish. Biochemical Journal, Vol. 16. 1922.

commonly cured either by the direct effect of sunlight or ultra-violet light, or else by a diet containing vitamin D. The fact that the peripheral bones of the knothed skull are thickened suggests the direct effect of sunlight on the local deposition of bone. The origin of the knothed abnormality among the carp of the middle Illinois River seems, then, to be due to the replacement of chlorophyll-bearing plankton by non-chlorophyll-bearing kinds and to the loss of the coarser aquatic vegetation from the dietary of the carp and of the organisms upon which they feed; but extensive feeding experiments under carefully controlled conditions would be required to determine positively whether or not the knothed malformation is due to a lack of vitamin D.

Experimental work on fishes has not produced anything similar to knotheds. Among the entire group of cold-blooded vertebrates, the only known abnormality comparable to the knothed malformation was seen by Klatt¹⁴ in *Triton* and *Rana* which he had fed exclusively with mussel flesh. The heads of these amphibians were short, broad, and oedematic, and their bones were not normally calcified.

Coward and Drummond (*op. cit.*) found that brown trout fry fed on a diet deficient in vitamins A and D did not grow much or show the vigor of those which received a diet rich in A and D.

In Germany, a carp disease characterized by a softness of the bones (Knochenweiche) is occasionally seen in artificial ponds in which the carp have been heavily fed with cereals (corn and lupines). The calcium content of the bones of such fishes does not differ from the normal.¹⁵

Schäperclaus¹⁶ describes two carp which had several of the anatomical characteristics of knothed carp. They were found among a population of older carp and other fishes which had been fed on barley in a pond free from plant life. The rings of the scales of these two carp showed normal growth during their first year, before they were placed in this pond, and very little growth during their second year, when they were in the pond.

Davis and James,¹⁷ of the U. S. Bureau of Fisheries, have made experiments showing the effects of deficient diets on carp, and report as follows:

"Since the discovery of vitamins by Funk a little over a decade ago, marvelous strides have been made in our knowledge of these elusive food factors, but until very recently we had no information as to their importance in the metabolism of lower vertebrates. It was recently found by

¹⁴ Klatt, B. Fütterungsversuche an Tritonen. Verhandl. d. Deutsch. Zool. Ges. 30 Vers. Jena, Leipzig. 1925.

— Fütterungsversuchen an Tritonen. I. (1926) II. (1927). Arch. f. Entwicklungsmechanik. Vols. 107 and 109.

¹⁵ Personal communication from Doctor Scheuring.

¹⁶ Schäperclaus, W. Kiemendeckelaufwölbung bei zweisommerigen Karpfen. Fischerei Zeitung. Nr. 24, Bd. 29. 1926.

¹⁷ Davis, H. S., M. C. and James. Some experiments on the addition of vitamins to trout foods. Trans. Am. Fisheries Soc. Vol. 54. 1924.

Drummond that trout eggs are very rich in vitamin A while several investigators have shown that cod-liver oil is far richer in this vitamin than any other known substance. The fact that fish tissues contain such large quantities of vitamin A¹⁸ is in itself an indication that it must be just as essential to them as to higher animals. However, we had no knowledge of the effect of vitamin deficiency on fishes and in order to supply this want feeding experiments were carried on at the Fairport, Iowa, station for about two months during the summer of 1923. In these experiments young carp from the Mississippi River were confined in troughs supplied with running water and fed diets deficient in one or more vitamins. The results clearly indicate the importance of these accessory food factors in the diet of fishes. In every case there was a high mortality, ranging from 40 to 67 per cent among the fish fed vitamin-deficient diets while there were no deaths among the controls which were fed a diet rich in these substances. The most striking results were obtained with the fish fed a ration containing no water-soluble B. After 3 or 4 weeks these fish became very nervous and a number developed convulsions which were especially noticeable whenever the covers were removed from the troughs. During these convulsions the fish would dart rapidly from side to side, twisting and whirling about and striking their heads violently against the sides of the trough. At intervals they would leap some distance from the water until finally, with a last convulsive shudder, the fish would sink quietly to the bottom where they would gradually recover and after a few minutes would swim about in a perfectly normal manner. These convulsions became more and more frequent and more intense from day to day until the fish succumbed to the inevitable. Conclusive proof that they were due to absence of B is shown by the fact that in several instances fish which had developed convulsions and would certainly have died if continued on a vitamin-deficient diet were fed considerable quantities of yeast and fully recovered within a few hours.

"Fish given diets deficient in fat-soluble A showed no distinctive lesions although the mortality was very heavy. As is well known the absence of A causes a disease of the eyes in rats and other mammals known as xerophthalmia, and its failure to affect the eyes in this case may cause surprise. However, it is generally believed that the xerophthalmia is really due to the fact that the tear glands do not function properly in the absence of A so that the results in this case are, after all, only what we should expect. A deficiency of water-soluble C resulted in high mortality with white spots on the gills caused by the development of necrotic areas."

It seems probable that the reason Davis and James did not find malformation caused by the diet deficient in vitamin A (and D) was either that the carp were too old and their growth form was fixed or else that the experiments were not continued long enough for malformation to become apparent.

¹⁸ Since the publication of this paper, vitamin D has been distinguished from vitamin A, both of which are found in codliver oil. D. H. T.

CONCLUSION

The knothed malformation of carp described here is believed to be the first known instance of rickets among fishes. Its resemblance to rickets in man and other higher vertebrates is as close as can be expected in view of the anatomical difference between a fish and a mammal. Carp may be affected by it from the fingerling stage through life. Their sluggishness of habit and their retarded growth are further indications of a rachitic condition. These rachitic carp are recognized by the bulging of the opercles, which is often so extreme that respiration is seriously embarrassed.

Rickets in the higher vertebrates is due to a lack of vitamin D in the food, and there is evidence that this is also true in the present case, inasmuch as the green aquatic vegetation which supplies vitamin D has been depleted in the same area and during the same period of time that the carp have been thus malformed. The depletion of the green aquatic vegetation took place following upon large increases in the sewage load of the Illinois River in the years 1916 to 1918. In the latter year knothed carp appeared, and they have continued up to the present time. They are numerous in the Illinois River from the upper limit of fish life near Utica (Starved Rock) down as far as the Copperas Creek Dam, a distance of about ninety miles. The average frequency of knotheds in this stretch is over 50 per cent, and in certain waters near the upper end it is well over 90 per cent. Other fishes of the area are unaffected, probably because they are less tolerant of pollution than the carp and feed in the cleaner backwaters.

The retardation of growth of the knothed carp contributes to the general reduction in yield of the river by pollution, which, in recent years, has probably run into millions of pounds per year, but the present studies give no reason for believing that the value of these carp as food for man is in any way impaired.