# NOTES ON THE FOOD OF THE PADDLEFISH AND THE PLANKTON OF ITS HABITAT.*

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The paddlefish or spoonbill cat, *Polyodon spathula* (Wal.) has long been recognized as a fish of very peculiar structure. It has a long, broad, paddle-like snout and an enormous mouth, almost toothless. Its alimentary canal is very short and consists chiefly of a very capacious stomach emptying into an intestine which is not much more than a spiral valve. Its gills also are large and are equipped with gill rakers or strainers nearly twice as long as the corresponding gill filaments.

A fish of such structure obviously cannot eat other fish but must depend for food on smaller organisms. Forbes (1878), in his pioneer studies of the food of fish, first recognized the paddlefish as feeding entirely on plankton. Other investigators, as Jordan and Evermann (1896), Imms (1904), and Stockard (1907), have regarded it as partly a bottom feeder. Fishermen have always confused the fine mass of plankton in its stomach with mud and consequently have considered this fish as being a mud feeder. An examination of the contents of a number of paddlefish stomachs shows an exclusive diet of microscopic organisms, most of which are normally found in the plankton.

Little is known of the life history or habits of the paddlefish. It is widely distributed in the larger streams and lakes of the Mississippi valley from Wisconsin to Louisiana, being quite abundant in the larger lakes and bayous of the lower Mississippi valley, but it does not occur in the Great Lakes drainage basin. Next to the sturgeon the paddlefish has the highest market value of any fish of this region. It is priced locally as high as 75c per pound under the name of "Boneless Cat."

Some paddlefish reach a very large size. Individuals have been reported by Jordan and Evermann (1896) from Manitou Lake, Indiana, as weighing 163 pounds. It is surprising that so large a fish can secure enough food of microscopic size to maintain itself. Its gills have to strain a prodigious volume of water in order to catch enough plankton for one square meal.

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If we wish to understand the feeding habits of this fish in relation to the quantity of available plankton in the waters of its habitat, we must make quantitative collections of the plankton and compare the number and abundance of the constituent organisms with those found in the stomach of the fish.

The present paper is based on data obtained from a study of the stomach contents of 30 paddlefish which were taken from McIntyre Lake near Money, Mississippi, in the spring and summer of 1927. In addition to these, ten stomachs which were secured from the Illinois River at Meredosia in June, 1927, by Doctor D. H. Thompson of the Illinois State Natural History Survey, were also used for comparison.

McIntyre Lake is four miles long and one-fourth mile wide and has an average depth of thirty feet. Plankton collections were made from the lake at the same time that the fish were taken. Both the stomach contents and the plankton collections were carefully preserved and examined microscopically to determine the constituent organisms and their relative abundance. A striking uniformity was found to exist in the constituents of the stomach contents at any one period.

Of the 26 stomachs which were obtained from McIntyre Lake between the 18th and the 24th of August, some were full and others were apparently empty. Those that seemed empty were opened and scraped, yielding food and a considerable amount of detritus which appeared to be stomach lining. Several collections were also made of scrapings from the gill rakers. These collections were composed entirely of plankton organisms in a fine state of preservation.

The contents of the different regions of the intestinal tracts were saved separately and preserved in formalin for examination. In the cardiac region of the stomach the contents resembled freshly caught plankton, with a gray color depending on the nature of the constituent organisms. The collections from the Illinois River had a reddish color due to the presence of certain species of Entomostraca which formed the bulk of the stomach contents. In the pyloric region of the stomachs from McIntyre Lake, the contents were still in a fair state of preservation although somewhat broken. In the spiral valve a decided change had occurred, the contents having the appearance of brown mud and bearing a very disagreeable odor. In the material from this region only fragments of empty skins were recognizable, the bulk of the contents consisting of a mass of opaque detritus, apparently digested or disintegrated food.

Two organisms which formed the bulk of the food in the material collected in August at McIntyre Lake were *Cyclops leuckarti* Claus and the larvae of an undetermined species of Corethra. From eighty to ninety percent of the bulk of the contents was composed of these two organisms. A variable amount of detritus was always present and occurred most abundantly in those stomachs which seemed empty. This did not resemble mud but looked like particles of digested food or bits of stomach lining. A smaller and generally immature copepod, *Cyclops bicuspidatus* Claus was found in twelve of the twenty-six stomachs but was never abundant. Mosquito larvae occurred in nine of the stomachs but were common in only one where they composed about fifteen percent of the bulk. Larval copepods were scarce, occurring in very few numbers in seven stomachs. Rotifers were never abundant and occurred in only very small numbers in less than half of the stomachs examined. A very few *Anuraea cochlearis* Gosse occurred in eleven stomachs while a single *Brachionus calyciflorus* Pallas was found in one stomach. Another stomach contained a few specimens of *Conochiloides dossuaris* (Hudson) and *Diurella stylata* Eyferth. Cladocerans were more abundant than rotifers. *Moina micrura* Kurz occurred in ten stomachs and although never occupying much bulk, it was sometimes fairly abundant. Small numbers of *Diaphanasoma brachyurum* (Liéven) were found in seven stomachs. Protozoa were very scarce and were limited to two species. *Pleodorina californica* Shaw occurred in seven stomachs and was abundant only in one, but because of its small size occupied only about five tenths of one percent of the bulk. Two specimens of *Difflugia globulosa* Duj. were found in one stomach. The only algae found in the stomachs consisted of several *Scenedesmus quadricauda* (Turpin) Breb. in one stomach and a few cells of *Lysigonium* (*Melosira*) *granulata* (Ehr.) Ralfs in another.

The contents of two stomachs collected in the spring from McIntyre Lake were examined. One stomach taken March 7, 1927, contained the usual diet of plankton origin, *Cyclops bicuspidatus* (68%) constituting the bulk of the contents, and *Daphnia longispina* O. F. Muller occupying about 20% of the contents. The remainder consisted of an occasional *Bosmina* *longispina* Leydig, eggs of Cladocerans and a few *Chydorus sphaericus* O. F. Muller and Synedra.

A stomach taken April 15, 1927 contained a common assortment of plankton organisms although different from those previously described. Large specimens of *Cyclops bicuspidatus* formed most of the bulk (60%) of the contents. *Diaptomus stagnalis* Forbes composed 20 percent, and the remainder consisted of *Bosmina longispina*, 10 percent, and detritus 8 percent. A very few specimens of *Chydorus sphaericus*, *Pleodorina californica* Shaw, *Pediastrum simplex* (Bail..), and *Lysigonium (Melosira) varians* Agassiz were present but composed only about 2 percent of the bulk. The difference in the assortment of species indicated that a different plankton was present from that found later in August.

A collection of food made March 19, 1927 from the gills contained an assortment of organisms somewhat different from any found in the stomachs. Insect eggs constituted the bulk of the food (78%). Detritus was abundant (20%). Ostracods and a very few Bosmina and *Chydorus sphaericus* constituted the balance of the food. This collection showed the only evidence observed that the paddlefish fed in vegetation or on the bottom.

The contents of the stomachs obtained from the Illinois river were of the same nature as those from McIntyre Lake. Entomostraca formed the bulk of the food differing, however, in species from those found in the stomachs from Mississippi. *Cyclops bicuspidatus* composed nearly 90% of the contents of all the stomachs. Sometimes *Diaptomus sililoides* Lilljeborg was present. A few specimens of *Leptodora kindtii* (Focke), *Bosmina obtusirostris* Sars, and *Daphnia longispina* were common in six stomachs although they did not occupy much bulk. Cladoceran eggs occurred in most of the stomachs. A few specimens of Ostracods were present in three stomachs and a chironomid larva occurred in one. Both of these latter organisms normally live on the bottom although occasionally they form an adventitous element of the plankton. Only a single rotifer, *Brachionus angularis* Gosse occurred in one stomach. The smaller plankton forms were exceedingly rare just as in the stomachs from McIntyre lake. *Fragilaria virescens* Ralfs, *Scenedesmus quadricauda* (Turpin) Breb., Cyclotella, *Lysigonium (Melosira) granulata* (Ehr.) Ralfs, *Eudorina elegans* Ehr., Anabaena, and a few undetermined diatoms were present in several stomachs but formed such a slight proportion of the food as to be quite negligible.

Parasites often appeared in the stomach contents as well as in the collections from other regions of the intestinal tract. The pyloric region of the stomach usually contained a large number of nematodes, and these forms also occurred in smaller numbers in all parts of the digestive canal. The most common parasites were cestodes, both larvae and adult. These were found in practically every fish from McIntyre Lake, and at times numbered well over one thousand in a single individual host. Cestode parasites have been reported for this fish by Stockard (1907) and Beach (1902), but only the single species, *Marsipometra hastata* (Linton) has been described. This study shows that there are in reality three distinct species of this genus present; an undescribed species of moderate size occurring mostly in the pyloric caeca; a small species found most commonly in the spiral valve, also undescribed; and *M. hastata* which occurs throughout the posterior three quarters of the intestinal tract. Larval forms of these cestodes as small as 0.3 mm. and ranging to adult size were present in enormous quantities throughout the entire digestive canal. Trematodes were also found in this host but with the exception of a very common gill polystome occur only rarely.

Kofoid (1900), observing the feeding habits of a paddlefish in captivity, found that the fish apparently located the plankton or finely chopped meat which was fed to it and swam rapidly in circles occasionally opening and closing its mouth until all the food had disappeared. Weed (1925) made observations quite similar, and later suggested (Norris 1923) that the mode of swimming of the paddlefish may aid in jarring loose aquatic animals from the vegetation.. Stockard (1907), Jordan and Evermann (1896), Alexander (1914), and Imms (1904) have asserted that the paddle is used for stirring up the mud of the bottom through which the fish then swims backwards, straining out all food. If this were the case one would expect bottom organisms which do not occur normally in the plankton, to be found more often in the stomach contents. Beach (1902) thinks the paddlefish elevates the paddle above water and swims into water plants, manipulating and guiding the water plant into its mouth. He suggests that such procedure tends to cause a current of water containing food to pass out the gill openings and the gill rakers are thus enabled to catch a great deal of food. He adds further, that according to his observations, the fish is almost if not entirely vegetative in its habits. Norris (1923) states that one function of the long bill is to dislodge aquatic animals which form the chief food supply of this fish.

Our observations on the feeding habits of the paddlefish, both in its natural habitat and in confined areas, confirm those of Kofoid and Weed. Fish placed in a small shallow pool were seen to swim slowly around the borders with the mouth slightly open, and at times to close it as if swallowing. The movement of swimming always involved the lateral movement of the bill accompanied by a similar rythmic body motion. This characteristic movement, considered by many investigators as being an adaptation to secure food while swimming in vegetation, occurs even when the fish is in water free from vegetation or plant debris of any kind, and it appears to be the natural type of movement in fish of this type, rather than any special modification for securing of food. Beach (1902) and Stockard (1907) call attention to the fact that paddlefish in their natural habitat are often seen to leap out of the water, making a loud splash as they fall back to the surface. Beach explains this action as an attempt on the part of the fish to free itself of the lampreys which are said to be common ectoparasites. At Lake McIntyre, especially during the warm afternoons of the summer months, the spoonbills were seen to jump from the water quite frequently, and because of the great number present in this lake, they kept up a constant splashing at regular intervals. Although no explanation can be given at the present time for this peculiar habit, is it likely that the conclusions of Stockard, who attributed the action to lack of an adequate oxygen supply in the warm water, are more nearly correct than those of Beach, for in no case in over three hundred examinations of this fish did we observe lampreys attached to the body surface.

Only in one collection from the gills was there any definite evidence of bottom feeding as is commonly believed by fishermen and many investigators. This was the collection from the gills made in March from McIntyre Lake, and contained insect eggs and ostracods which were either bottom or vegetation forms. The presence of a few ostracods and chironomid larvae in several of the stomachs from the Illinois River may be indicative of bottom feeding, but is not conclusive evidence, as bottom organisms are often stirred up by river conditions and found in the plankton. The absence of mud and bottom diatoms and also the scarcity of these bottom forms in the Illinois River specimens seem more to indicate that the latter possibility offers a more plausible explanation of the occurrence of such forms. Forbes and Richardson (1908) stated that they found no evidence of mud or bottom fauna in the stomachs of the paddlefish. Most of the stomach contents examined in this study consisted of the same organisms as the plankton collected from the same waters at the same time as the fish. The bulk of the stomach contents consisted only of the larger plankton organisms, while the smaller forms were almost entirely absent. The animals which were most abundant in the plankton were not necessarily the most abundant species in the stomach contents. This was due to the selective action of the gill rakers which only retained the larger species which did not always form the greater part of the plankton. The smaller forms which were eliminated were often the most abundant and characteristic forms of the plankton. Insect larvae and copepods which formed the bulk of the diet of the paddlefish were only fairly common in the plankton of McIntyre Lake. The smaller cladocerans, rotifers, protozoans, and algae which formed a prominent part of the plankton constituted only a very small portion of the food of the paddlefish. This elimination of the smaller organisms, which included practically all the algal portion of the plankton, enabled the paddlefish to secure an entirely animal diet.

It is uncertain as to the level at which the paddlefish normally feeds. According to Forbes and Richardson, fishermen at Alton, Illinois state that the paddlefish feeds at the upper levels of the water. Others believe that it feeds from the lower levels. Our plankton records were largely based on surface collections although several were made from the bottom to the surface. There was no evidence in any of the data collected to show where the paddlefish fed, for the same plankton organisms were found in both the surface and bottom collections. All organisms found in the stomachs likewise occurred in both the surface and bottom plankton collections.

The paddlefish, because of the selective gill apparatus previously described, consumes only a small part of the plankton passing through its mouth. The waters bearing a heavy micro- or nanno-plankton and only a slight macro-plankton would hardly form a profitable feeding area for the paddlefish because only a certain type of plankton is available. As this fish can utilize only part of the plankton it must pass a much larger volume of water through its gills than it would if all the plankton were available. Accordingly, the amount of water bearing plankton and passing through the gills of the paddlefish must be enormous. It is of interest to estimate the amount of water required to supply enough food to fill the stomach of a moderately large paddlefish. The largest stomach examined had a capacity of about 700 cubic centimeters. This was almost entirely filled with Entomostraca and insect larvae; and first it was necessary to determine the number of these forms present in the stomach and then find the number of the same organisms normally present in a given volume of water at the place where the fish had fed. Assuming that the gills strained out all these forms, it is comparatively easy to compute the volume of water that must pass over them in order that enough food may be secured to fill the stomach. The contents of a well filled stomach from McIntyre Lake contained 80 Corethra larvae and 300 *Cyclops leuckarti* per cubic centimeter. At this rate, a stomach with a capacity of 700 cc. would contain 56,000 Corethra larvae, and 210,000 *Cyclops leuckarti.* The largest numbers of Corethra larvae found in a collection of plankton was 900 per cubic meter and the greatest number of Cyclops *leuckarti,* found in a collection of another date, was 1035 per cubic meter. Thus, it would require 62 cubic meters of water to supply enough Corethra larvae and about 203 cubic meters of water to furnish enough Cyclops to fill a stomach with a capacity of 700 cc. These figures are merely a rough estimate but they serve to demonstrate that the paddlefish strains an enormous amount of water to satisfy its appetite. The variation in plankton distribution from day to day and within similar areas of the same locality is well within the limits of the variation in the computed amount of water required for the two organisms. The plankton net is far from being 100% efficient but there is reason to believe that it is more efficient than the gill rakers of the paddlefish which do not secure many of the smaller organisms found in the silk net collections. Although the plankton data may not have been acquired at the exact spot or level at which the fish had fed, it is close enough to the vicinity to make it possible to form some idea of the volume of water utilized by this fish. Furthermore, from the many plankton collections taken at different parts of the lake, there was no evidence that the plankton organisms were unusually abundant in any one area. There seems rather to be a general distribution with some variation in regard to levels but not enough to greatly influence these figures.

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PLANKTON FROM McINTYRE LAKE, AUGUST, 1927.

| Per cubic meter | Surface 8/17 | Surface 8/18 | Surface 8/19 | Surface 8/24 | Surface 8/24 | Bottom, 25 ft. 8/24 |
|---|---|---|---|---|---|---|
| Anabaena sp. | | 37000 | 9000 | | 24000 | rare |
| **Lysigonium (Melosira) granulata (Ehr.)** | 42500 | 36000 | | 36000 | 150000 | common |
| Fragilaria virescens Ralfs. | | | | | 200 | |
| Pediastrum duplex Meyen* | | | | 90 | | |
| **Difflugia globulosa Duj.** | | | | | 50 | |
| **Pleodorina californica Shaw*** | 6800 | 190 | | 1800 | 3150 | common |
| Euglena sp. | | | 180 | 90 | 200 | |
| Eudorina elegans Ehr.* | | 360 | | | 2070 | |
| Pandorina morum Bory de Saint Vincent* | 30 | | | | 100 | |
| Platydorina caudatum Kofoid* | 3400 | | | | 50 | |
| Peridinium tabulatum Ehr. | | | | | 50 | |
| Strombidium sp. | | | | | 500 | |
| Halteria grandinella O. F. M. | | 220 | | | | |
| Codonella cratera (Leidy) | | | | | 100 | |
| Synchaeta stylata Wierz. | 850 | | 1800 | 180 | 200 | |
| Polyarthra trigla Ehr. | 175 | | 180 | 3600 | 4000 | rare |
| **Diurella stylata Eyferth** | | | | | 100 | |
| Rattulus sp. | 170 | | | | | rare |
| Notholca longispina (Kellicott) | | | | | 50 | |
| Brachionus angularis Gosse | 1700 | 5400 | 5400 | 1350 | 950 | occasional |
| Brachionus budapestinensis Daday | 75 | 360 | | | | |
| Brachionus patulus O. F. M. | | 1800 | | | | |
| Schizocerca diversicornis Daday | 400 | 650 | | 45 | 400 | |
| Asplanchna priodonta | 170 | | 180 | | | |
| **Conochiloides dossuaris (Hudson)** | 13600 | 720 | 1800 | 90 | 1035 | |
| Filina (Triarthra) longiseta (Ehr.) | | | | 40 | 1000 | rare |
| Pedalia mira (Hudson) | | | 900 | | 1050 | occasional |
| **Keratella (Anuraea) cochlearis (Gosse)** | 1800 | 900 | 360 | 13500 | 9000 | occasional |
| Pleosoma sp. | 6800 | 3600 | 3600 | 7200 | 40000 | common |
| Monostyla quadridentata Ehr. | | | | | 100 | |
| Diaphanosoma brachyurum (Liéven) | | | | 5400 | 10300 | common |
| Daphnia longispina O. F. M. | | | | | 100 | |
| **Moina micrura Kurz** | | | 180 | 8100 | 41000 | abundant |
| **Cyclops bicuspidatus Claus** | | 180 | | 5000 | 6210 | abundant |
| **Cyclops leuckarti Claus** | | | | 450 | 1035 | |
| **Young Copepods** | | 200 | | 9000 | 25000 | |
| Ergasilus sp. | | | | | 207 | |
| **Corethra Larvae** | 40 | | 360 | 900 | 575 | common |

* Per colony.
Organisms shown in bold face type occurred also in the stomach contents.