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Distribution, Age, and Growth, and Feeding Ecology of Paddlefish (Polyodon spathula) In Unaltered Missouri River, South Dakota

Rudolph S. Rosen

DISTRIBUTION, AGE AND GROWTH, AND FEEDING ECOLOGY OF PADDLEFISH (*Polyodon spathula*) IN UNALTERED MISSOURI RIVER, SOUTH DAKOTA

BY

RUDOLPH A. ROSEN

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This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable as meeting the thesis requirements for this degree, but without implying that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Thesis Adviser Date

Head, Wildlife and Fisheries Science Department Date

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DISTRIBUTION, AGE AND GROWTH, AND FEEDING ECOLOGY OF PADDLEFISH (*Polyodon spathula*) IN UNALTERED MISSOURI RIVER, SOUTH DAKOTA

Abstract

RUDOLPH A. ROSEN

Four hundred eighty-four paddlefish (*Polyodon spathula*) were captured 26 June 1975 to 11 August 1976 from an unaltered stretch of Missouri River in South Dakota. Vital statistics were measured on all fish, 171 were sacrificed during the analysis of food habits, and 301 fish were tagged and released.

Paddlefish were located by observation, gill netting, and snagging. Paddlefish were primarily found downstream from submerged sandbars from late spring to early fall. The crests of the sandbars were 0.1 to 1.0 m deep and immediately downstream, the depth was 1.5 to 4.5 m, and the current velocity was 0 to 0.3 m/sec. Most paddlefish concentration areas were adjacent to channels with current velocities ranging from 0.7 to 1.3 m/sec. Paddlefish were located in slow or dead water areas which had depths of over 3 m during late fall to early spring. All paddlefish concentration areas from late fall to early spring were adjacent to channels. Paddlefish in channelized river appeared to inhabit slow or dead water areas adjacent to the river channel, oxbow lakes, and non-flowing tributaries.

Halo-like bands in dentary bone cross sections may be produced as a result of the food habits of paddlefish. The eye to fork length was a more valid index of paddlefish growth than total length or fork length. Factors to allow conversion of total length and fork length, to eye to fork length were calculated. The mean weight and mean length of paddlefish were 5,900 g and 730 mm, respectively. The length - weight formula was $W= -463.67 + 8.24\ L + 0.085\ L^2$ or in logarithmic terms, $\text{Log}\ W= -3.85 + (2.66)(\text{Log}\ L)$; where W=weight (g) and L=eye to fork length (mm). The average condition factor, K, was 1.47, and the average K for female paddlefish was 1.45 and for male paddlefish 1.48. Factors to allow conversion of K values calculated from total length and fork length to eye to fork length were given. K values increased as length of the fish increased until the fish were approximately 700 mm long, K values decreased with increased length thereafter. K values were highest during spring and fall. Females were significantly heavier and longer than males in any given age-class.

Four stages of ovary maturation were described, and few female paddlefish with mature ovaries were captured.

The sex ratio for the population was estimated to be 0.85 males to 1 female. The presence or absence of tubercles on the dorsal surface of paddlefish was not an indicator of sex.

Thirty-five and one-half percent of all fish examined had scars on their bodies, and 27.4% of these fish had lost part or all of their rostrum. Sixty-seven percent of the fish tagged which were recaptured traveled downstream, 26% upstream, and 7% stayed in the same area. Three fish ranged 680 to 780 km within 3 to 8 months after capture.

Food of paddlefish was nearly 100% zooplankton, and lack of selective feeding was strongly indicated. Vernal and autumnal feeding peaks were evident, and feeding nearly ceased from July to September Paddlefish appeared to feed continuously when food consumption levels were high and non-food items composed 37 to 78%, by volume, of the total stomach contents.

INTRODUCTION

Paddlefish, Polyodon spathula (Walbaum), range from Montana (Robinson 1966) to Louisiana (Douglas 1974) and are confined to the lakes, reservoirs, and larger streams of the Mississippi River drainage. Early accounts stated that paddlefish populations once extended into the Great Lakes region (Coker 1923; Trautman 1957). Paddlefish in South Dakota are restricted to the Missouri River, and their occurrence in tributaries more than a few kilometers from the confluence of the tributary with the Missouri River is rare.

The Missouri River in South Dakota, 880 km long in 1892, drained a total of 259,000 km^2 (Petsch 1946). Once known as the gorge of the Missouri and characterized by high bluffs and a narrow flood plane, the Missouri River, from the North Dakota border to Gavins Point, is now a series of reservoirs. At Gavins Point, the gorge opens into a wide flood plane 6 to 13 km across. The river in this area has historically changed course with every big flood (Petsch 1946). Dams constructed along the Missouri River in South Dakota have blocked upstream fish movement, eliminated lotic habitat, created a series of resident paddlefish populations in resultant reservoirs, and provided a means to modify the amount of water flowing through the system at any given time. A section of free-flowing river extends 93 km downstream from the lowermost dam, Gavins Point Dam, and except for decreased turbidity (Whitley and Campbell 1974), remains similar to habitat available to paddlefish in this region before the influence of man. Bank stabilization and channelization have altered the river channel downstream from this 93 km reach to the mouth of the Missouri River (Whitley and Campbell 1974). Free-flowing river exists elsewhere, but no stretch of river similar to that below Gavins Point Dam is accessible to paddlefish. Plans are presently underway to stabilize the banks of this last remnant of free-flowing Missouri River in this region. Bank stabilization will eventually eliminate the habitat in which paddlefish live. This study documents aspects of the life history of paddlefish; it presents what may be the last look at this primitive species as it inhabits habitat unique to this portion of the Missouri River.

The objectives of this study were: (1) evaluate vital statistics from paddlefish collected 26 June 1975 to 11 August 1976; (2) describe habitat preferences and distribution of paddlefish in unaltered Missouri River; (3) describe habitat available to paddlefish in channelized Missouri River; and (4) present a detailed analysis of food habits, food selectivity, and feeding periodicity of paddlefish over a one year period in unaltered Missouri River.

Paddlefish were primarily river fish, but extensive commercial utilization during the first decade of this century (Hussakop 1910; Alexander 1914; Stockard 1907) left little doubt that paddlefish frequented lakes and still water areas connected to rivers. Stockard (1907) reported paddlefish in lakes connected to major waterways by as much as 160 km of bayou. Recent information about paddlefish has been collected below obstructions to upstream movement of fish (Robinson 1966; Rehwinkel 1975) and from reservoirs in which large numbers of paddlefish were trapped (Sprague 1959; Houser 1965). Published work documenting the distribution and habitat of paddlefish in main river channels does not exist. A more complete review of literature prior to 1960 was given by Meyer (1960).

Early workers dispelled the misconception that paddlefish dug for food with their paddle (Alexander 1914; Jordan 1925) and established that paddlefish were planktivores (Stockard 1907; Eddy and Simer 1929; Forbes 1888). Hoopes (1960) found that 46% of the stomach contents, by volume, from 64 paddlefish collected from the Mississippi River in Iowa, was composed of mayfly naiads. Meyer (1960) reported that immature insects represented 95% of the stomach contents of paddlefish from the Mississippi

River while fish he examined from the Missouri River fed primarily on plankton. Rare occurrences of fish remains in paddlefish stomachs, such as those reported by Fitz (1966), Forbes (1888), and Meyer (1960), indicated that the fish was capable of piscivorous feeding. Unconfirmed reports, including two to this investigator, point to the fact that paddlefish may "bite" on baited hooks (Fitz 1966; Meyer 1960). Recent published studies documenting food habits of paddlefish (Sprague 1959; Hoopes 1960; Meyer 1960) did not evaluate either selectivity or periodicity of feeding.

STUDY AREA

The study area, a free-flowing section of the Missouri River without stabilized banks and channelization, began at the U.S. Highway 81 bridge at Yankton, South Dakota, and extended 84 km downstream to Ponca State Park, Nebraska (Fig. 1). This stretch of river forms the border between South Dakota and Nebraska. The study area was divided into zones to provide a location index.

The discharge of water from Gavins Point Dam determined the volume of water flowing through the study area except during spring when three intermittent waterways, entering the Missouri River along the study area, contributed to downstream discharge. The average daily discharge is normally about 1,000 m^3/sec from mid-March or April to November, the navigation season, and approximately 600 m^3/sec during winter months when ice may cover parts of the river and ice jams present the threat of flooding. Transition from high to low flow is usually abrupt, accomplished in a few days. An average daily discharge of 1,700 m^3/sec was maintained during the summer and fall of 1975 due to above normal amounts of water that entered the Missouri River upstream (Fig. 2).

The river substrate was fine sand with small amounts of silt accumulated in areas of dead water. The gradient

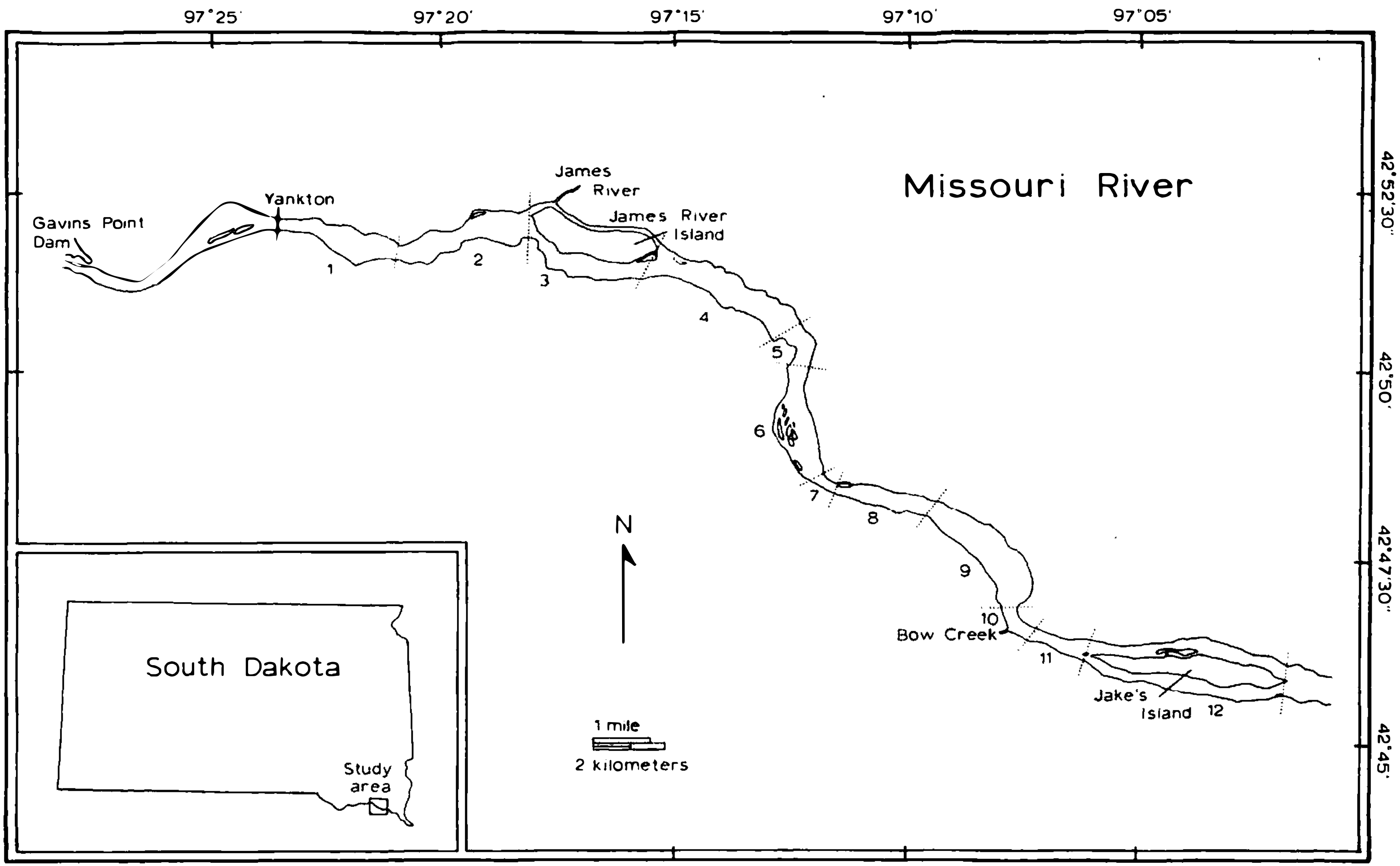

Figure 1. Missouri River study area.

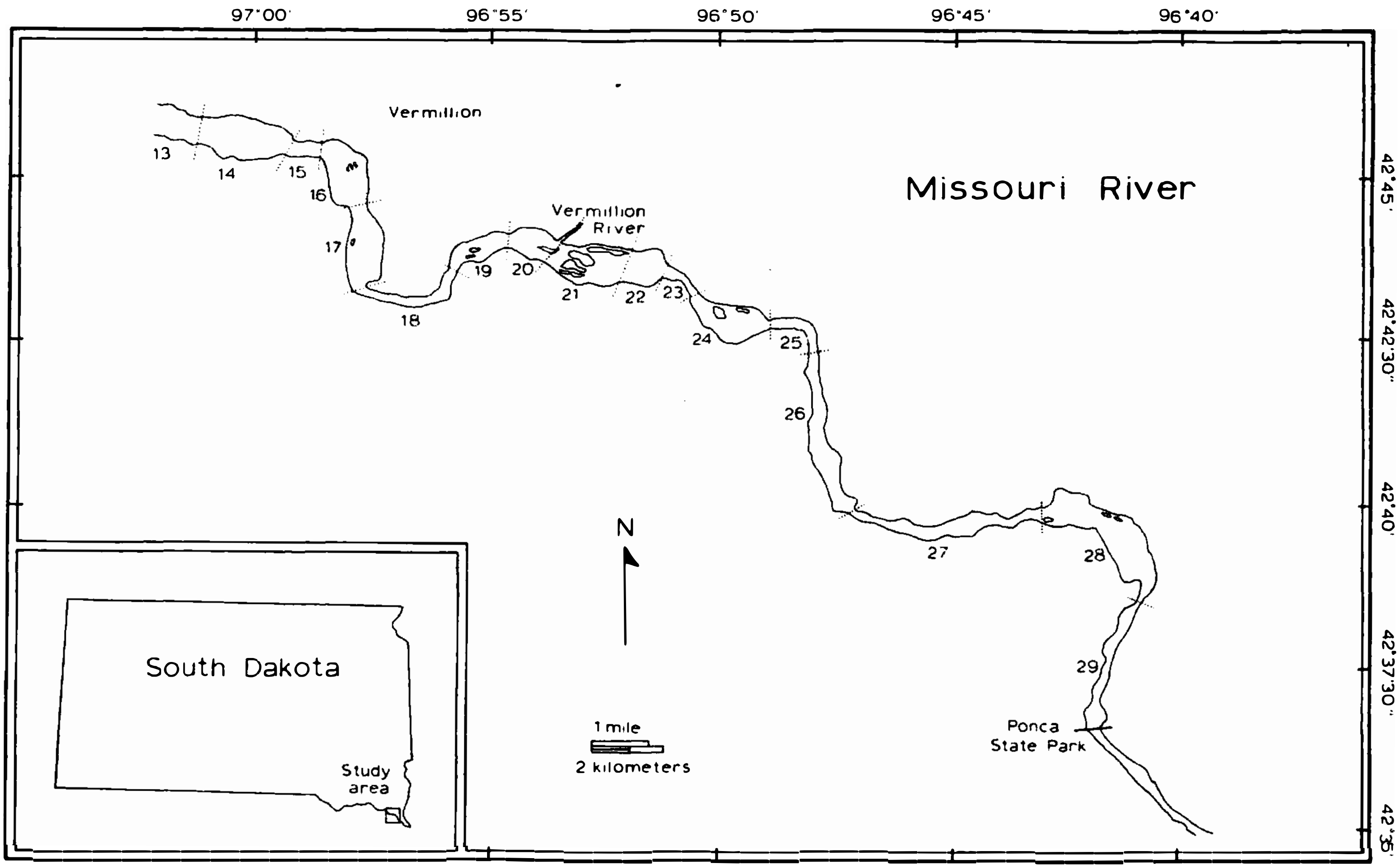

Figure 1. Continued. Missouri River study area.

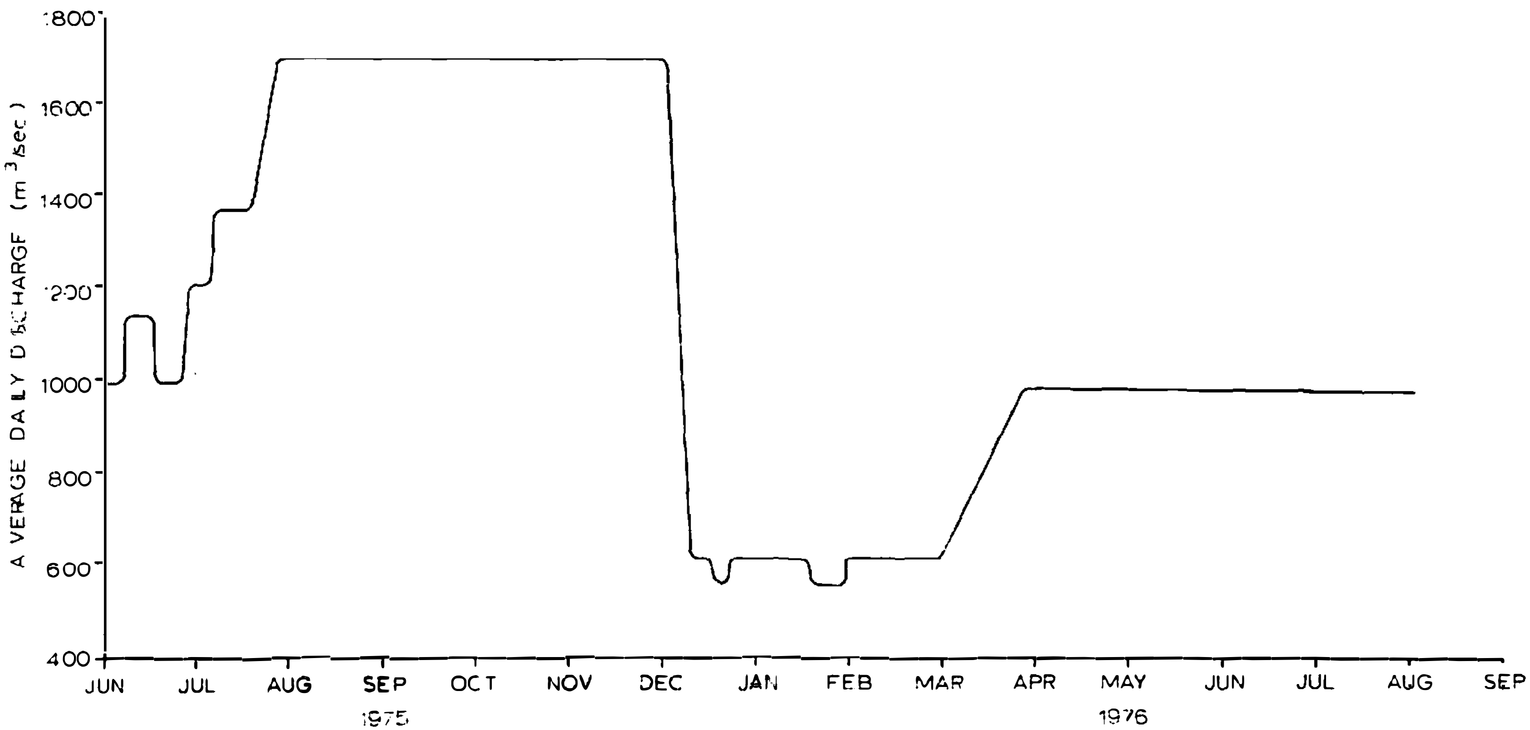

Figure 2 Average daily downstream discharge from Gavins Point Dam, 1 June 1975 to 31 July 1976.

was 0.18 m/km (Petsch 1946), and current velocity ranged from 1.3 m/sec in channel areas to dead water (0.0 m/sec) below sandbars. Water temperatures in channels ranged from slightly above 0 C to 24 C. The width, excluding islands, varied from 0.3 to 1.3 km and averaged 0.7 km. Depth was highly variable. Channels averaged approximately 4 to 6 m deep, and the rest of the river ranged from a few centimeters to 2 m in depth. The bottom profile was a maze of shallow and deep channels, flat shallow planes, and submerged and emergent sandbars. The entire topography was constantly shifting; masses of sand might be deposited or removed in a day, and extensive changes might occur during a year. Numerous backwater channels (chutes) bordering the main river channel ran through low lying marsh.

The banks of the river have been stabilized from Ponca State Park to Sioux City, Iowa; and from Sioux City downstream, the river has been channelized to permit barge traffic. Work was done along a 40 km stretch of river beginning about 15 km downstream from Sioux City to evaluate paddlefish populations in channelized river. The river profile was a deep "U"-shaped channel. The river banks were lined with wing dams and revetments and the width was approximately 300 m. Several oxbow lakes, openings in revetments, mouths of tributaries, and backwaters behind wing dams provided the only dead water. Sandbars, except those located behind and created by wing dams, did not exist. Work in this area will be referred to only in the evaluation of paddlefish habitat in channelized river. All references to study area in other sections of this report pertain to that stretch of Missouri River between Yankton and Ponca State Park.

METHODS

Paddlefish were captured at least once each month from 26 June 1975 to 11 August 1976. All fish, except 6, were captured during daylight. Sampling dates were dependent on weather or equipment condition, and sampling locations within the study area were variable.

The average daily downstream discharge from Gavins Point Dam and average daily water temperatures were obtained from records maintained by the U.S. Army Corps of Engineers, Gavins Point Dam, Yankton, South Dakota. The velocity of flow was measured with a Gurley Current Meter No. 622. Average weekly plankton flow into the study area was obtained from data collected at Gavins Point Dam by North Central Reservoir Investigations, Yankton, South Dakota. Depth was measured with a line weighted on one end and marked at 1 m intervals. A 4.3 m aluminum, V-hull boat equipped with a 20 horsepower outboard motor was used. The bow of the boat was equipped with a 1.2 by 1.2 m plywood platform from which nets were set.

Habitat preferences were documented throughout the year by determining the habitat in which paddlefish were found. Paddlefish were visually located during late spring to early fall. A boat driven near paddlefish produced immediate, characteristic reactions by the fish.

Paddlefish in the immediate vicinity behaved in one of the following ways: (1) dove deeply or remained deep in the water and swam away (in this case direct observation was impossible); (2) leapt from the water; (3) "ran" through the wake of the boat; (4) flicked the surface with their fins; and (5) sprinted, for a short distance, just below the surface of the water. A boat traveling 24-32 km/hr was most effective in producing the above reactions, but at these speeds fish were often hit by the boat or the lower unit of the motor. Fish could be seen to a depth of approximately 1.0 m under most light conditions. Large concentrations of paddlefish gave the surface of the water directly above the concentration a blackish appearance on a clear day with the sun high in the sky. Paddlefish concentrations were also located by watching for jumping fish. Previously described by Stockard (1907) and Meyer (1960), this behavior appeared to occur infrequently, therefore, if in a given spot several fish jumped during a short period of time, a large concentration was indicated. Paddlefish could not be visually located from late November to April, and fish concentrations had to be located by gill netting and snagging.

Fish were caught with snag fishing equipment or gill nets. A short stiff rod, equipped with a heavy open reel filled with 35 kg test line, to which a heavy sinker and one or two large treble hooks were attached, was used for snagging paddlefish. Gill nets were 3 m deep and 100 m long with a 7.6 or 10.2 cm bar mesh. Mesh size of 10.2 cm was used most often. A net equipped with large floats to keep the float line on the surface was preferred, except during winter months when a sinking net was used.

Effective capture of paddlefish required that paddlefish concentrations be located 12 to 24 hours prior to netting or snagging. Care was taken not to disturb the fish before setting nets by drifting or wading into the area from an upstream direction. Three types of capture situations were primarily encountered: (1) where a sandbar formed a lagoon or inlet in a manner that allowed a net to be set across the opening, thus trapping the fish; (2) where a net was set, with the current, from a submerged sandbar, through the center of density in the concentration area; and (3) where a small area, not adjacent to a sandbar and usually over 1 m deeper than the surrounding area, was known to contain fish, a net was set directly over the spot. In capture situations (2) and (3), once the net was in place, paddlefish were driven into the net with the boat, a procedure similar to corralling cattle. Fish were captured within 15 minutes after the net was set in all three cases. Paddlefish were usually captured by snagging during winter, as netting was difficult and fish were not so easily driven into nets. Gill nets which remained in place overnight and "drifting" gill nets were also used in attempts to capture fish.

Fish were weighed to the nearest 100 g on a calibrated spring scale. Total length, fork length, and eye to fork length (distance from the orbit of the eye to the fork in the tail) were measured to the nearest centimeter. The presence or absence of body scars, including partial loss of the rostrum (paddle), and the method of capture was noted for each fish. Sacrificed fish were sexed, state of gonads noted, left dentary bones removed, and on a sample of 56 fish the presence or absence of tubercles on their dorsal surface noted. Released fish were tagged with numbered jaw bands inserted around the lower left jaw or numbered dart tags inserted near the dorsal fin. The fish were released in the same location as capture and their general condition upon release was noted. A section of the right dentary bone, about 2 mm thick, was removed from a sample of 45 tagged fish using a coping saw with a fine blade.

One hundred fifty-three paddlefish were aged by examination of dentary bone sections (Adams 1942). A Dremel Moto-tool mounted on a slicing device (Moseley 1964) was used to section dentary bones. The sections, approximately 0.2 mm thick, were examined with transmitted light under a binocular dissecting microscope. Sections were found easiest to read when they were: (1) polished on a fine carboridium stone, (2) a drop of xylene placed on them, and (3) the direct beam of a high intensity light shined up through the section. The thin, more transparent bands were interpreted as winter growth and counted as annuli. Halo-like bands, which coalesced with other bands or bands which were not continuous around the section, were not counted as annuli. Annuli were counted in the measal arm of the dentary section, and when readable, confirmed by counts in other regions of the section. Paddlefish raised in a South Dakota pond that had completed their first growing season, exhibited only the central core evident in dentary sections of older fish as a dentary bone cross section; the central core was considered the first year of growth. A review of the use of dentary bones in aging paddlefish was given by Meyer (1960).

Statistical computations were performed by electronic computer. Conversion factors were formulated to allow conversion of total and fork length to eye to fork length and correlation coefficients between the three measurements were determined. The correlation coefficient between the rostrum to eye length (distance from the tip of the rostrum to the orbit of the eye) and the eye to fork length was calculated. The length-weight relationship was expressed as a curvilinear function and also in logarithmic terms. The homogeneity of regression coefficients obtained through curvilinear regression was determined by an F-test in an analysis of covariance following a modification of the procedures listed by Steel and Torrie (1960). The condition factor (K) was determined from length and weight data by the formula (Beckman 1948):

$$K= \frac{W \times 10^5}{L^3}$$

where W=weight (g), and L= length (mm); conversion factors were calculated from mean length and weight data to allow conversion of K factors calculated from total, and fork length to eye to fork length. All K values and mean lengths calculated in other studies were reported in terms of eye to fork length; conversion factors were applied where appropriate. Sex ratios were calculated for each age-class using fish sacrificed for food habit studies.

Zooplankton samples were obtained with a metered Miller Sampler fitted with No. 10 netting and with a Wisconsin Net fitted with No. 20 netting. Zooplankton samples were collected immediately after and in the same location as fish were caught. Samples were diluted to convenient volumes for analysis. Two ml aliquots were counted in a circular counting wheel (Ward 1955) under a binocular dissecting microscope; at least 4 aliquots per sample were counted. Organisms were identified to species with the aid of a key to zooplankton of the Missouri River reservoirs (Novotony 1975).

Volume for each species of zooplankton was measured by water displacement in a 0.2 ml pippette calibrated to enable measurements of 0.001 ml. Cyclops varicans and Mesocyclops edax were not abundant plankters, therefore, the average volume of Cyclops bicuspidatus, a similarly sized cyclopod copepodite, was used as an estimate of their average volumes.

Food habits were determined by examining the digestive tract contents from 3 to 6 fish arbitrarily selected from a sample of fish caught at the same time. The digestive tract was clamped shut at the esophagus, immediately anterior to the spiral intestine, and at the anus to prevent loss or movement of materials. The entire digestive tract was removed, placed in 75% formalin and later transferred to 10% formalin. The pyloric caeca and spiral intestine were examined for the presence or absence of food only; however, the contents of the entire stomach were removed, excess moisture drained, and weight and volume of the contents measured to the nearest 0.1 g and 0.1 ml, respectively. A random sample of food material, totaling 2 to 5 ml was removed from the anterior third of the stomach, diluted to a convenient volume, and food organisms were identified and counted in the same manner previously described for zooplankton. The entire contents of each stomach were examined for macroscopic food items under a magnifying glass.

Each stomach was analyzed separately and the percent by volume, percent by number, total volume, and electivity value for each food item was recorded. Electivity was determined by the following formula (Ivlev 1961):

$$E= \frac{r_i + P_i}{r_i + P_i}$$

where: E=electivity, r_i=% composition of species in the stomach, P_i=% composition of species in the plankton. E values range from -1.0 to +1.0, the former indicating total selection against species i, (i.e., absent in stomach but present in plankton), and approachment of the latter indicating total selection for species i, (i.e., abundant in stomach, but scarce in plankton). The percent weight of stomach contents per body weight of fish was determined to provide an index of fullness for each fish. The percent total stomach content composed of plankton was determined by calculating the total volume of plankton present in the stomach and comparing this value with the total volume of material present in the stomach.

Diel feeding activity was measured on 28 August, 4 September, and 2 October 1975 and 21 May 1976 by capturing fish in the same location at dusk and at dawn the following day, and on 16 June 1976 by capturing fish in the same location at dawn and dusk. Stomachs were removed from 3 fish at each sampling. The average percent weight of stomach contents per body weight of fish was determined for each sample and comparisons were made.

Paddlefish digestion rate was measured. Thirty-five fish were captured from the same area at the same time. Fish were immediately placed into a portable swimming pool 3 m in diameter and 1 m deep. Water was filtered through No. 0 netting and the oxygen level and water temperature were kept equal to that in the river by frequently pumping fresh river water into the pool. An initial sample of fish was sacrificed and their stomachs removed. Additional fish were sacrificed and treated as above, at intervals for 48 hours. The average percent weight of stomach contents per body weight of fish and the general state of digestion were determined for each sample and comparisons were made.

RESULTS AND DISCUSSION

Fish Sampling

Ninety-four and eight-tenths percent of the 484 fish captured were caught by gill net, 3.7% by snagging, and 1.5% were killed and recovered after being hit by the boat. Optimum catches were obtained when the area from which paddlefish were to be captured was not disturbed for at least 12 hours prior to gill netting. Disturbances included boats running through the area and high waves. Fish in deep areas appeared to be less affected by disturbances than fish in shallow water. At least one day had to elapse before netting the same area again for an optimum catch. Best results were obtained when nets were set no further than 25 m from the point of maximum fish concentration. Gill nets set and left untended one to several hours were not effective. Excellent results were obtained when fish were driven into the gill net immediately after it was set. Paddlefish were not highly vulnerable to gill nets and were more apt to become entangled when forced into the net. Other advantages of driving fish into nets were: (1) the whole operation took little time and allowed many such net sets per day, and (2) increased net visability due to the accumulation of waterborne material was not a problem.

Paddlefish were captured in gill nets when their caudal fin, pectoral fins, rostrum and mouth, or opercular flaps became entangled in the mesh. Gill nets were selective for certain size fish. Paddlefish captured in 10.2 cm (bar measure) mesh nets ranged from 1,100 to 14,300 g. Fish weighing less than 2,000 g appeared less likely to be caught than heavier fish. Fish over 14,300 g were not captured, but this was probably not entirely due to net selectivity against larger fish. Paddlefish heavier than 14,300 g have become entangled in gill nets of similar and even smaller mesh.

Gill nets with float lines that remained on the surface of the water were the most effective means to capture paddlefish during late spring, summer, and fall. Paddlefish were often caught at the surface of the water and frequently jumped over the net during this time. Fish were vigorous during summer and early fall and were often able to break free of the net once entangled. Thirty to sixty percent of the paddlefish seen hitting the net during summer and fall escaped. The actual percentage of fish lost was probably higher since not all fish that ran into the net were observed doing so.

Gill nets with float lines that allowed the net to rest on the bottom were used during winter. Paddlefish at this time were not observed near the surface of the water and nearly all fish which ran into nets remained entangled.

Paddlefish during winter lacked the vigor observed during summer and early fall, and difficulty was encountered when trying to move fish into nets. Snagging for them in proper habitat usually yielded 3 to 5 fish within 15 minutes.

Habitat of Paddlefish

Kendeigh (1961) defined the habitat of a species as the set of physical conditions which surround it. Paddlefish in the study area were subject to varied amounts of change in their physical environment. Fish traveled to another area where proper conditions existed when the area in which they were living became unfit. Paddlefish may traverse all types of accessible lotic and lentic waters when traveling to preferred areas. The determination of paddlefish habitat was based on the results of over 600 hours of observation and extensive sampling in all types of habitat available to paddlefish in the study area.

Late Spring, Summer, and Early Fall Under Conditions of Normal Stability

Paddlefish were primarily found immediately downstream from submerged sandbars during late spring, summer, and early fall. The most important modification attributable to sandbars, or reefs as they were called locally, was the reduction in current velocity in the area directly downstream. Current velocity increased as water passing over the crest of a sandbar was forced into a smaller space. The water dropped into an area of greater depth and the current velocity was reduced. The greater the differential between water depth at the crest of the sandbar and water depth below the sandbar, the greater was the decrease in current velocity. Paddlefish were found below sandbars when the crest was 0.1 to 1.0 m deep and the depth below the sandbar was 1.5 to 4.5 m. Most fish were noted in areas 2 to 3 m deep where the current velocity was 0 to 0.3 m/sec. Fish preferred areas with the least amount of current.

Nearly all large concentrations of paddlefish were found below sandbars or in slow or dead water areas adjacent to channels. The channels were located to one side or directly downstream from the paddlefish concentrations and had water velocities from 0.7 to 1.3 m/sec. Paddlefish were often observed below every sandbar where proper conditions existed after a period of several calm days.

Paddlefish had a tendency to concentrate in, or immediately downstream from, irregularities along the face of sandbars. It became apparent after many hours of observation, which notch or point along an extensive sandbar was most likely to contain a high concentration of paddlefish.

Paddlefish sometimes inhabited areas not directly associated with sandbars, but the same physical features found immediately downstream from sandbars were also apparent in these areas. Each was at least 1.5 m deep, had current velocities of 0 to 0.3 m/sec, and were usually adjacent to channels. These paddlefish concentration areas were deep holes protected from current by an island or deep areas protected from current by other shoreline irregularities. Paddlefish occasionally frequented back-water chute areas and entered non-flowing tributaries. Occurrence in these areas appeared to be transient and was usually restricted to single or small groups of fish.

Late Spring, Summer, and Early Fall Under Highly Unstable Conditions

Flow through the study area 25 July to 1 December 1975 was nearly double that normally encountered during this time (Fig. 2). Nearly all mid-river sandbars were washed away during the initial days of high flow. Several islands covered with dense vegetation became the only submerged river features near the surface. Massive shifts of sand occurred daily and the crests of most visible sandbars were from 0.7 to 1.5 m below the surface during the first few weeks of high flow. Sandbars built up to near normal depths and stability increased as time passed, but the total area of river composed of sandbar complex remained reduced.

Paddlefish were difficult to locate during the initial increase in flow and for a few days thereafter. The fish were found nearly anywhere reduced current was available, e.g., below remaining emergent islands or submerged ones, in slough areas adjacent to the river, below the few deep sandbars, and below any other obstruction to current. Fish in one section of river having no protected areas were observed to remain within a few meters of the shoreline. When sandbars of normal depth but of a highly unstable nature did appear about 2 weeks after the water rise, fish were found to immediately inhabit the area downstream. Sandbars became relatively stable after about 5 to 7 weeks of high flow and paddlefish appeared to resume normal habitation.

The control exerted by the complex of dams on the downstream discharge of the Missouri River is unnatural. High flows occurred during the late spring and early summer before the dams were built. Flow decreased during summer and fall until the low winter flow remained. The increased discharge beginning in late March or April that now occurs is probably equivalent to, if not less drastic than, the traditional spring and early summer flooding, but now high flows may be maintained, increased, or decreased throughout the year. Daily fluctuations in discharge, the result of varied power production at Gavins Point Dam, are highly unnatural, but have their greatest effect near the dam.

Late Fall, Winter, and Early Spring

The discharge of water from Gavins Point Dam is normally reduced in late November. Large numbers of paddlefish were observed in several dead or slow water areas over 3 m deep just before the discharge reduction, a decrease of over 1,000 m^3/sec, in 1975. Biweekly sampling in these areas several months prior to the flow reduction revealed that paddlefish density began increasing in October. The concentration areas were the most stable areas paddlefish had inhabited and were all adjacent to the main channel of the river. Large numbers of paddlefish remained in all these areas except one after the reduction in flow. A shift of the sandbar in this particular case during the reduction of flow left the area too shallow, about 1 m, for paddlefish.

Few areas of river remained that exhibited a slow or dead current coupled with a depth of over 3 m once the flow had been reduced; paddlefish may have concentrated in all such areas throughout the winter. Areas in which paddlefish concentrate must necessarily be adjacent to the main river channel as all isolated parts of the river quickly freeze. The main river channel is subject to ice jams and ice cover; but of all water adjacent to the main channel, dead water areas freeze first. One sample was taken during a warm spell which was preceded by several days of very cold weather. The paddlefish concentration area from which the sample was desired was still covered by a thin sheet of ice. It was possible to proceed into the center of the concentration area by breaking loose pieces of ice. A sample of fish was quickly taken indicating that paddlefish remained in deep still water areas when ice cover was present.

Paddlefish were occasionally found in channel areas with relatively swift currents during winter. It was not known to what extent paddlefish utilized these areas since large concentrations of fish were not noted in them. Five fish were caught in a channel area where the current velocity reached 0.7 m/sec. It was located directly downstream from a deep still water area.

Paddlefish redistributed themselves to areas downstream from shallow sandbars when ice disappeared from the river and the discharge from Gavins Point Dam was increased during March. The fish may have been highly dispersed as large concentrations were not noted. Evidence of a spawning run as reported from other locations (Russell 1972; Robinson 1966; Friberg 1973) was not noticed.

Channelized River

Conclusions concerning paddlefish in the channelized portion of the Missouri River located downstream from Sioux City, Iowa, must be viewed as tentative since only 23 hours of observation and 7 gill net sets constituted the basis for evaluation. Oxbow lakes or other lake-like areas which were accessible to the river comprised the most important habitat available to paddlefish in channelized river. One gill net placed near the entrance to the Missouri River in Snyder Bend, an oxbow lake near Salix, Iowa, yielded 24 paddlefish. Paddlefish are known to remain in Snyder Bend during winter, as they have been caught under the ice by commercial fishermen. Paddlefish were observed in small inlets and behind wing dams which provided areas of reduced current. Fish were also seen in the mouth of a small, non-flowing tributary. Openings in revetments allowed low areas behind them to flood during high water. Paddlefish may have utilized these areas although no fish were observed in them.

The channelized section of the Missouri River was evaluated only during the period of high water in 1975. Areas in which fish were found may not always be accessible. The total area adjacent to the main river channel composed of still water fluctuated with the downstream discharge from Gavins Point Dam, but very little still water ever existed beyond the wing dams and revetments. Strong current and massive upwelling in the main river channel may preclude long term habitation of paddlefish in the main channel. It is suspected that paddlefish only use the channel as a highway from one still water area to another.

Age and Growth

Aging

Ability to determine the age of paddlefish was directly related to the clarity and creditability of growth rings (annuli) in dentary bone cross sections. Rings were evident in most cross sections and counting was simple. Interpreting the halo-like bands, or false annuli, caused the most problems with aging. Halo-like bands were especially numerous in the central portion of the dentary section, the portion of the cross section corresponding to rapid growth during initial years of life. Halo-like bands appeared as an additional ring of growth between each consecutive annulus in many cross sections (Fig. 3). Halo-like bands may intergrade or become indiscernible from annuli in the outer edges of dentary sections from fish older than 10 years. These rings or halo-like bands were therefore considered annuli, and because of this, ages of some fish may have been biased upward.

Halo-like bands may be formed as a result of feeding habits. Paddlefish fed extensively during spring, ceased feeding during summer, and resumed feeding in fall. The growth patterns of paddlefish were suspected to have been affected by the period of feeding inactivity which occurred between two feeding peaks, thus, producing the halo-like

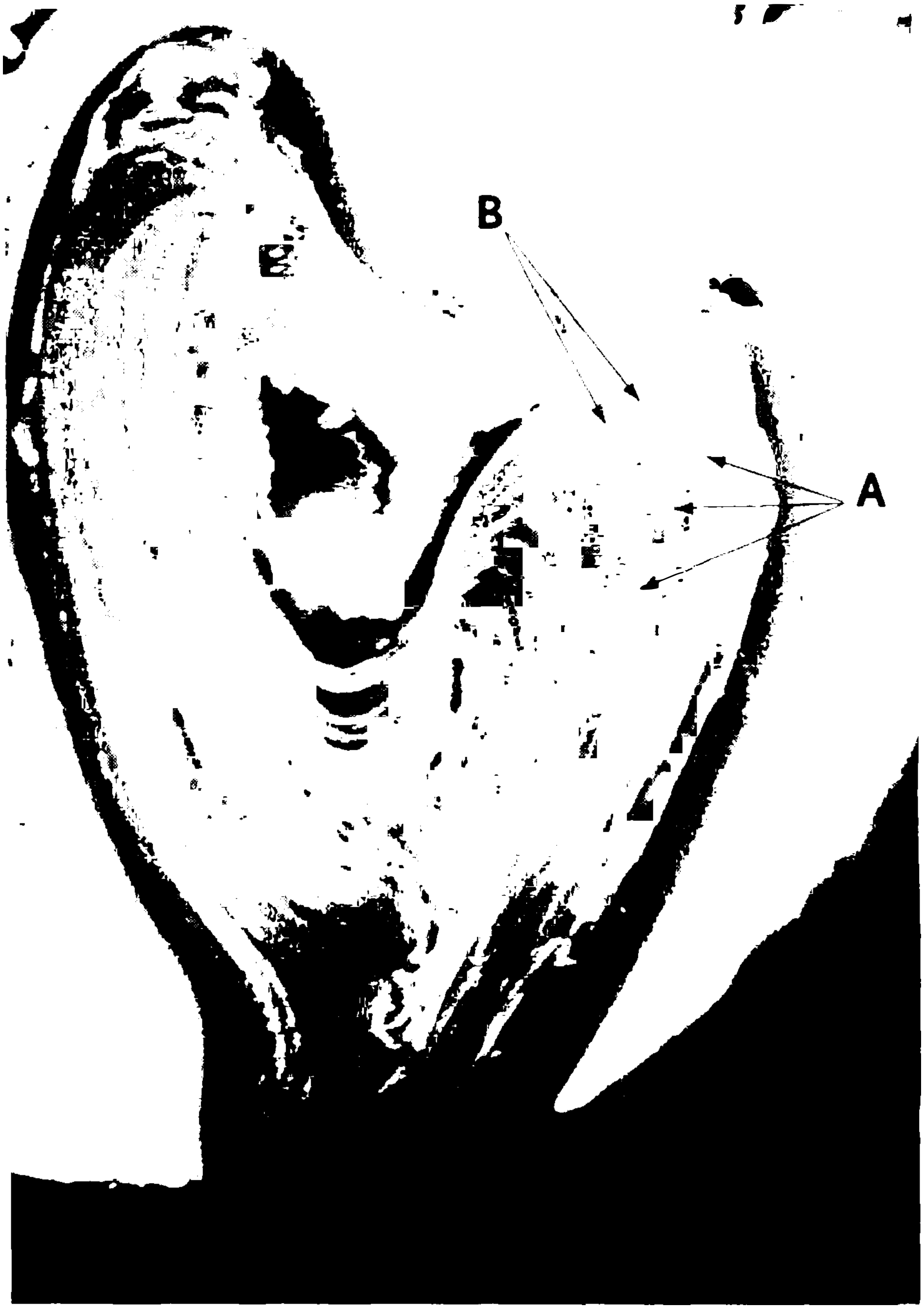

Figure 3. Dentary bone cross section from a paddlefish, age-class 9. A, annuli; B, halo-like bands.

band in addition to the normal annular mark. Numerous halo-like bands between the first few annuli may be a result of other factors in addition to feeding.

Meyer (1960) mentioned that halo-like markings occurred outside certain annuli, but no reports have mentioned a conspicuous pattern of halo-like band, annulus, halo-like band, annulus, etc., as was evident in many cross sections from this study. Summer feeding lulls have not been noted in previous studies, many of which were conducted during summer. The phenomenon may be somewhat local; therefore, since the study area was an open system, with downstream movement of fish evident and movement into the area from downstream strongly suspect, immigrant or migrant fish may not reflect the halo-like bands between annuli formed while in other areas, and fish living in other areas may not exhibit halo-like bands at all.

There was no conspicuous periodic crowding of annuli in dentary bone cross sections. Sprague (1959) and Meyer (1960) noted that annuli became crowded at intervals of 4 to 7 years in fish beyond about 5 years of age. Meyer explained this phenomenon, at least for females, as the possible interruption of growth during development of the large egg masses characteristic of paddlefish.

A method to determine the accuracy of aging techniques was developed. A small section of dentary bone, removed from a subsequently tagged and released fish, may be compared to dentary bone cross sections upon recapture of the fish. Additional growth will be apparent and discrepancies, such as halo-like bands, may be explained. Results concerning effects the removal of the dentary bone cross section has upon the health of the fish are encouraging but inconclusive. Mr. Virgil Gosch, Nebraska Game and Parks Commission, in a personal communication, noted the condition of the jaws from 2 paddlefish which had a section of dentary bone removed. The fish were caught by sport fishermen 6 months after being tagged during the present study. He stated that the tag itself produced a more severe and unhealing sore than was left as a result of removal of the dentary bone section. A tagged fish recaptured in the present study had a section of dentary bone removed 2 weeks prior. Healing had begun, but the wound was still quite raw.

Problems were encountered with the method used to cut the dentary bone. The saw blade was not fine enough to remove a small section of bone without damaging the outer edges of the section. Annuli became crowded in this region of the section in older fish and any damage to the region made the section useless. A high speed, battery operated saw, similar to that used in laboratory preparation of dentary bone cross sections, would have been ideal for field use. A tool of this type would have allowed the removal of a thin, readable section directly from the fish.

Length Relationships

Eye to fork length was a more valid index of paddlefish growth than total length or fork length. Growth in length of the rostrum was not proportional to growth in length of the body. The coefficient of determination (r^2) between the rostrum to eye length and the eye to fork length was 0.22 (Fig. 4) indicating that only 22% of the variation in eye to fork length was explained by variation in rostrum to eye length. The correlation coefficient (r) was 0.68 between both the total length and rostrum to eye length and between the fork length and rostrum to eye length. Eye to fork length of fish included in this analysis ranged from 460 to 1,020 mm. Use of eye to fork length allowed accurate measurement of fish which had lost part or all of their rostrum.

Thompson (1934) concluded that paddlefish showed an increase in the proportion of the rostrum length to the length of the rest of the body until the fish reached a total length of approximately 250 mm, after which the proportion of the rostrum decreased. Thompson (1934) also stated that the heterogonic growth occurred in the part of the rostrum distal to the barbels. Meyer (1960) calculated an r value of 0.988 between the total length and distance from the tip of the rostrum to the medial edge of

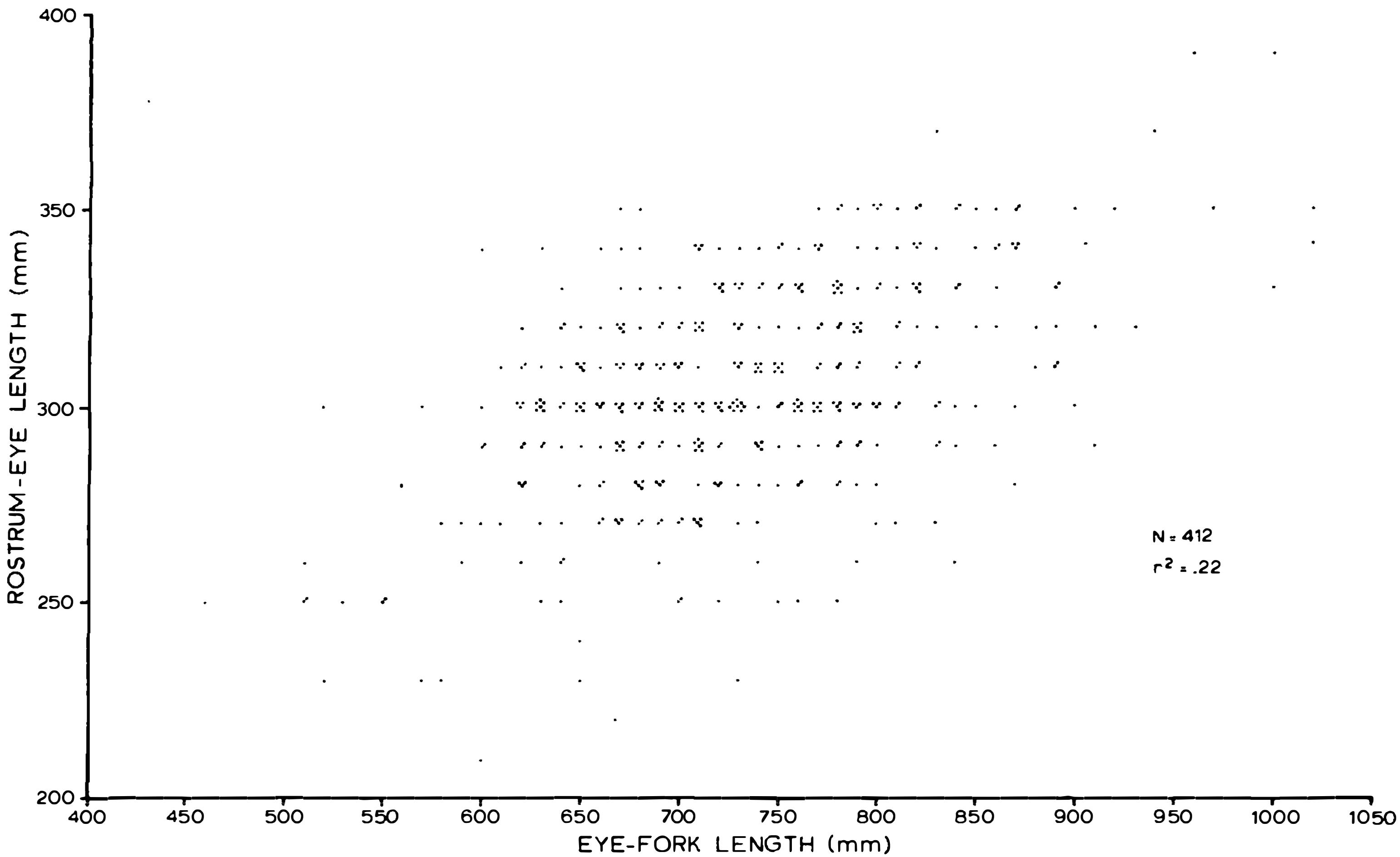

Figure 4. Relationship between eye-fork length and rostrum-eye length.

the upper jaw from fish ranging 17 to 2,160 mm. The present study indicated little relationship between growth of the rostrum and growth of the rest of the body; the study by Meyer (1960) showed opposite trends.

Correlation coefficients between the three lengths measured were (n = 410): (1) total length and fork length, r = 0.97; (2) total length and eye to fork length, r = 0.93; (3) fork length and eye to fork length, r = 0.97. Factors that allowed conversion of total length and fork length to eye to fork length were:

$$(0.63)\ (TL) = EFL$$

$$(0.71)\ (FL) = EFL$$

where TL = total length, EFL = eye to fork length, and FL = fork length.

Mean Weight and Mean Length

The mean weight and mean length of paddlefish were 5,900 g and 730 mm, respectively. Results from studies conducted in the same area during consecutive years showed close agreement (Table 1). The mean weight of paddlefish captured in the present study was similar to the mean weight of fish sampled by Friberg (1974) from Zone 4 (Fig. 1) A creel census conducted by Kallemeyn (1975) during the 1972-73 and 1973-74 legal snagging seasons for paddlefish at the tailwaters of Gavins Point Dam, 9 km upstream from the present study area, yielded

Table [illegible]. Mean weight and mean length of paddlefish from different studies.

Number of Fish	Year	Mean Weight (g)	Range	Mean Length (mm)	Range	Location	Reference
484	1975, 76	5,900	1,100-14,300	730	460-1,020	Missouri River 5 to 89 km downstream from Gavins Point Dam Yankton, South Dakota	Present study
325	1972, 73	4,900	1,500-16,400	---	---------	Missouri River 11 km downstream from Gavins Point Dam Yankton, South Dakota	Friberg (1974)
51	1972-73[2]	10,600	1,600-26,300	852	597-1,168	Missouri River Gavins Point Dam tailwaters Yankton, South Dakota	Boehmer (1973)[1]
----	1972-73[2]	7,800	------------	---	---------	Missouri River Gavins Point Dam tailwaters	
----	1973-74[2]	5,600	------------	---	---------	Yankton, South Dakota	Kallemeyn (1975)
243	1956, 58, 59	3,600	500-18,600	620	290- 870	Mississippi River Pool 19, Burlington, Iowa	Meyer (1960)[1]
----	1964	9,970	2,490-19,050	---	---------	Yellowstone River Intake irrigation dam	
----	1965	9,920	2,270-20,870	---	---------	Glendive, Montana	Robinson (1966)
1,696	1973	14,860	3,630-35,150	867	640-1,104	Yellowstone River Intake irrigation dam	
1,910	1974	16,160	3,630-35,380	882	664-1,103	Glendive, Montana	Rehwinkel (1975)
----	1970	24,900	------------	---	---------	Missouri River Big Bend Dam tailwaters Fort Thompson, South Dakota	
----	1971	26,300	------------	---	---------		
----	1972	28,100	------------	---	---------		
----	1973	28,100	------------	---	---------		Friberg (1974)
----	1974	23,100	------------	---	---------	Missouri River Big Bend Dam tailwaters Fort Thompson, South Dakota	Kallemeyn (1975)
155	1958	4,700	500-18,300	630	340- 910	Missouri River Fort Randall Dam tailwaters Pickstown, South Dakota	Sprague (1959)[1]
30	1974	------	------------	956	813-1,118	Missouri River Fort Randall Dam tailwaters Pickstown, South Dakota	Kallemeyn (1974)

[1] Means calculated from data presented in the study.
[2] Fish caught during legal fishing season.

mean weights of paddlefish similar to the mean weight of fish sampled in the present study; but the mean weight of fish was found to be much higher in a creel census conducted by Boehmer (1973) during the 1972-73 season at the same tailwater area. Mean weights of paddlefish caught below the Intake irrigation dam during consecutive years were similar, but mean weights of fish captured in 1964 and 1965 were over 4,800 g less than mean weights of fish caught in 1973 and 1974 (Robinson 1966; Rehwinkel 1975). A creel census conducted at the tailwaters of Big Bend Dam from 1970 through 1974 revealed that the mean weight of harvested paddlefish was similar from year to year (Friberg 1974; Kallemeyn 1975).

All paddlefish populations in areas associated with reservoirs had greater mean weights than fish restricted primarily to lotic water, with the exception of the low mean weight recorded by Sprague (1959) at Fort Randall Dam and the high mean weight reported by Boehmer (1973) at Gavins Point Dam (Table 1). Fish captured from the tailwaters of Big Bend Dam, Fort Randall Dam, and Intake Dam may have spent lengthy periods of time in reservoirs. The population Meyer (1960) studied from the Mississippi River had access to tailwaters, river channels, slough areas, and lake-like areas. Paddlefish live year-round in the river below Gavins Point Dam; they may frequent lake-like areas during part of their life as they are capable of reaching all accessible water areas connected to the Missouri-Mississippi River drainage.

<u>Length - Weight Relationship</u>

The length - weight formula was (Fig. 5):

$$W = -469.67 + 8.24\ L + 0.085\ L^2$$

or in logarithmic terms:

$$\text{Log } W = -3.86 + (2.66)\ (\text{Log } L)$$

where W = weight (g) and L = eye to fork length (mm). There was no significant difference between the length - weight regression of female paddlefish (n = 87) and the length - weight regression of male paddlefish (n = 75) at $p \leq .01$. There was no significant difference between the length - weight regression of fish which had lost part of their rostrum (n = 41) and the length - weight regression of normal fish (n = 417) at $p \leq .01$.

<u>Coefficient of Condition</u>

The average condition factor, K, (n = 462) was 1.47, and the average K for female paddlefish (n = 86) was 1.45 and for male paddlefish (n = 79) 1.48. Factors allowing conversion of K values calculated from total length and fork length to eye to fork length were:

$$3.93\ K(TL) = K(EFL)$$

$$2.84\ K(FL) = K(EFL)$$

where TL = total length, FL = fork length, and EFL = eye to fork length.

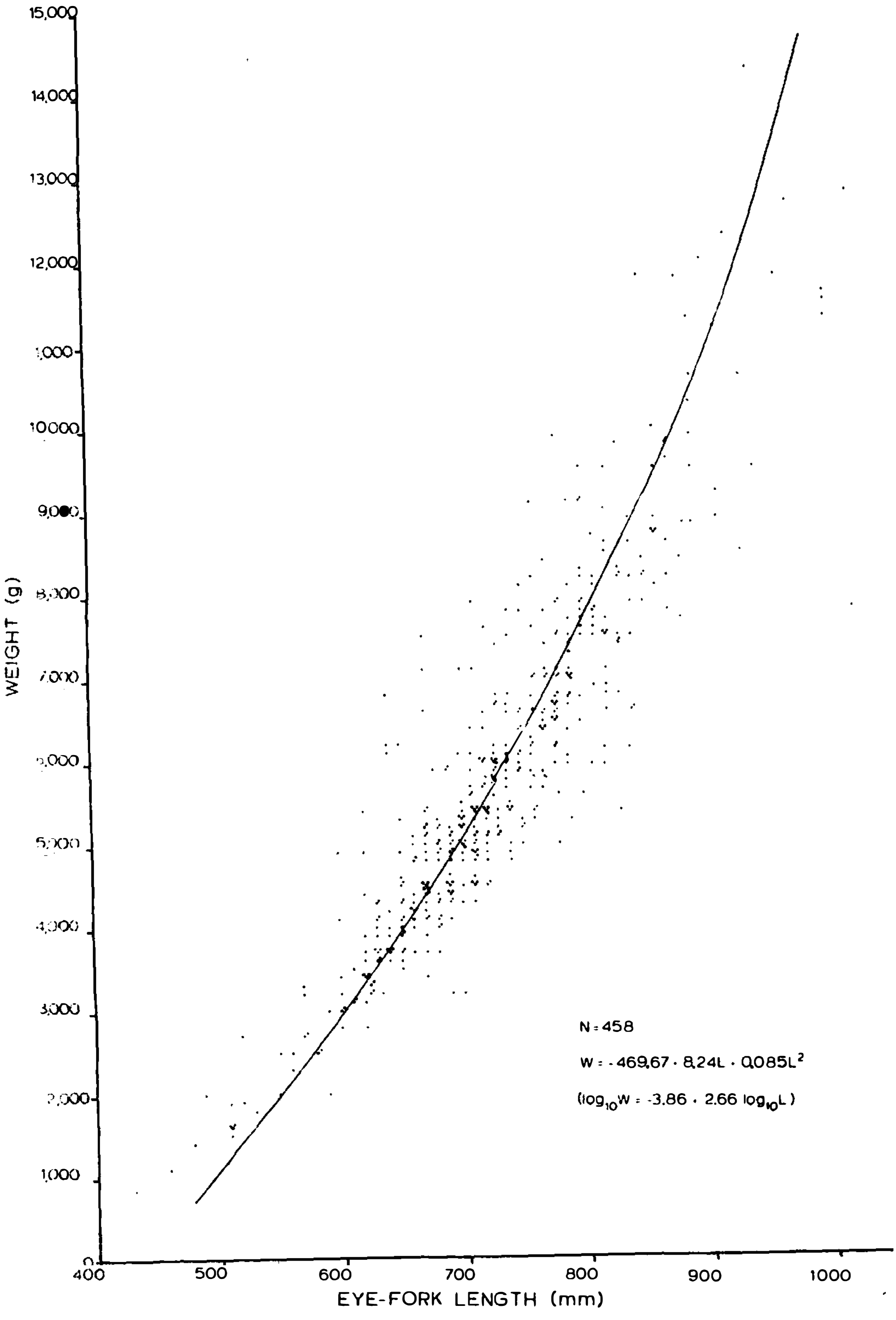

Figure 5. Relationship between eye-fork length and weight.

Average K values indicated: (1) fish in the present study were slightly heavier for their length than in most other studies, and (2) consistent trends were not apparent with regard to differences in coefficients of condition between males and females from the same population. Meyer (1960) and Shields (1956) calculated average K values of 1.45 and 1.26, respectively from paddlefish captured in the tailwaters of Fort Randall Dam in South Dakota. Shields (1956) determined that males had higher K values than similarly sized females. Male and female paddlefish from the Osage River in Missouri had K values of 1.75 and 2.14, respectively (Russell 1972). The high K value reported for female paddlefish by Russell (1975) was a result of heavy egg masses. Fish collected from the Mississippi River near Burlington, Iowa, had an average K of 1.34 (Meyer 1960).

K values increased as length of the fish increased until fish were about 70 cm long, K values decreased with increased length thereafter (Table 2). Therefore, short fish and long fish, from the size range of paddlefish sampled, weighed less for their length than fish of medium size. Meyer (1960) found that K values increased as length increased in fish from the tailwaters of Fort Randall Dam. Shields (1956) came to similar conclusions with male paddlefish from the same tailwaters, but found no

Table 2. Mean coefficients of condition, range, and standard deviation for paddlefish of similar length.

Length (cm)	Number of Fish	Mean K	Range	SD
45 - 49	3	1.36	1.13 - 1.70	0.29
50 - 54	8	1.33	1.13 - 1.92	0.25
55 - 59	15	1.34	0.97 - 1.78	0.20
60 - 64	45	1.52	1.17 - 2.59	0.29
65 - 69	94	1.53	0.97 - 2.49	0.24
70 - 74	107	1.50	0.93 - 2.20	0.20
75 - 79	91	1.45	1.05 - 2.09	0.18
80 - 84	55	1.40	1.05 - 1.86	0.19
85 - 89	27	1.42	1.13 - 1.92	0.16
90 - 94	11	1.37	1.06 - 1.65	0.22
95 - 99	2	1.36	1.33 - 1.39	0.04
100 -104	5	1.05	0.74 - 1.21	0.21
Totals	463	1.47	0.74 - 2 59	0.24

consistent trends in female paddlefish. Fish from the Osage River and the Mississippi River showed no consistent trends in K with regard to length. The low condition factor of large fish in the present study as opposed to studies conducted at the tailwaters of Fort Randall Dam may have been the result of decreased concentrations of food available to paddlefish in open river; a larger fish therefore unable to maintain plumpness as readily as smaller fish.

Seasonal trends in the coefficient of condition (Table 3) corresponded to seasonal trends in feeding; K values were highest during spring and fall, the periods of peak feeding activity. Seasonal differences were not evident in fish from the Mississippi River (Meyer 1960).

Sexual Dimorphism

Sexual dimorphism was demonstrated in terms of differential growth between sexes in any given age-class. Females were significantly heavier than males at $p \leq .01$ (Fig. 6). Females were significantly longer than males at $p \leq .01$ (Fig. 7). Russell (1972) reported similar findings from paddlefish in Missouri. He also determined that significant differences in growth between most age-classes did not exist.

Table 3. Mean coefficients of condition, range, and standard deviation for paddlefish sampled during different months.

Date	Number of Fish	Mean K	Range	SD
1975				
June	4	1.51	1.39 - 1.66	0.13
July	6	1.36	0.94 - 1.72	0.27
August	65	1.33	0.93 - 2.10	0.19
September	117	1.45	1.05 - 2.49	0.25
October	106	1.44	0.74 - 2.59	0.23
November	43	1.52	1.13 - 2.21	0.19
December	8	1.38	0.97 - 1.70	0.23
1976				
January	3	1.27	1.22 - 1.33	0.05
February	5	1.44	1.30 - 1.64	0.13
March	5	1.53	1.28 - 1.73	0.17
April	10	1.51	1.35 - 1.73	0.13
May	42	1.70	1.37 - 2.09	0.19
June	37	1.59	1.16 - 1.87	0.16
July	12	1.38	1.21 - 1.57	0.13
Totals	463	1.47	0.74 - 2.59	0.24

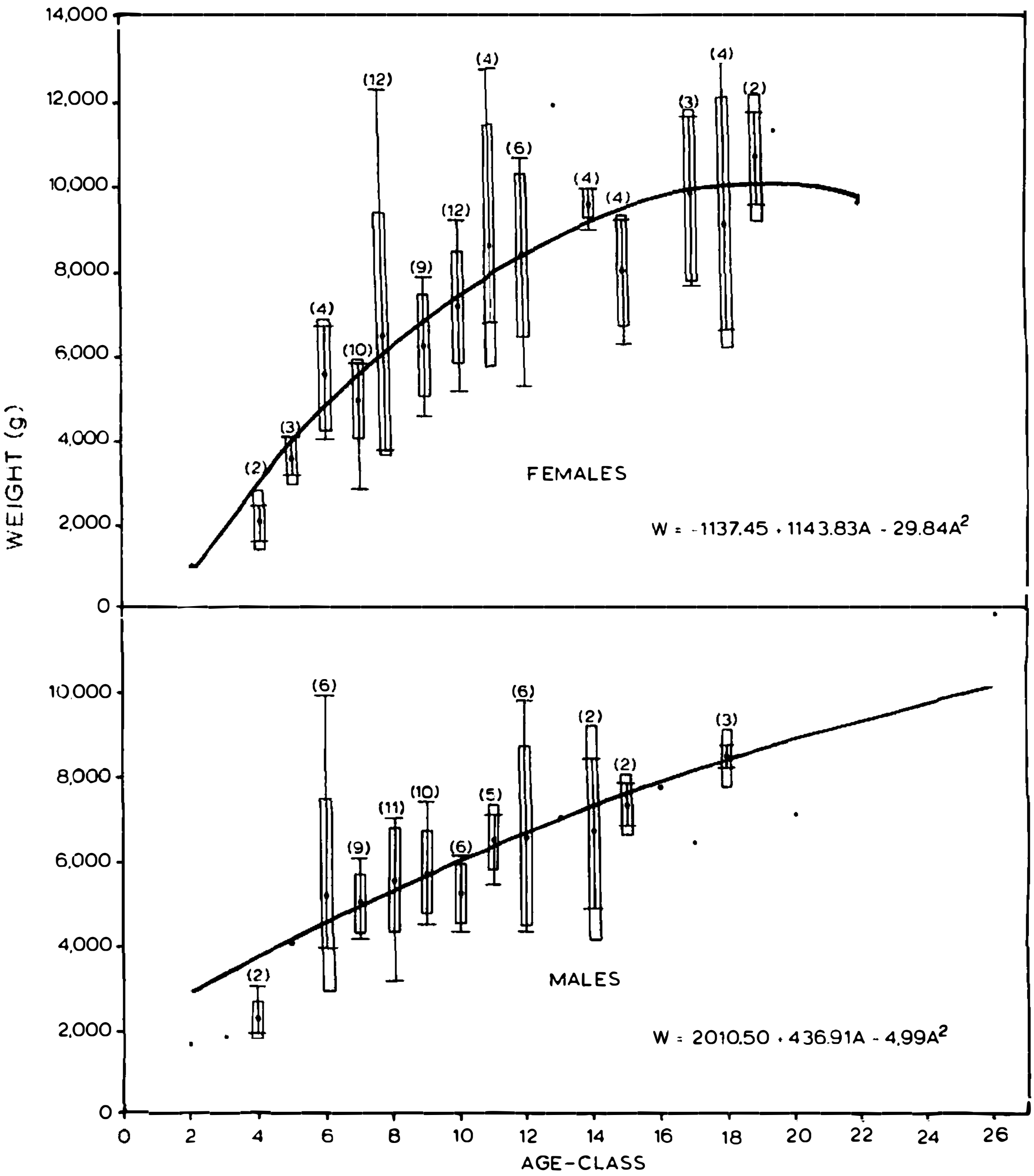

Figure 6. Differential growth in terms of weight between male and female paddlefish from different age-classes as expressed by curvilinear regression. Point, mean; hollow bar, standard deviation on either side of mean; vertical line, range. Sample size in parentheses, points without standard deviation or range represent single fish.

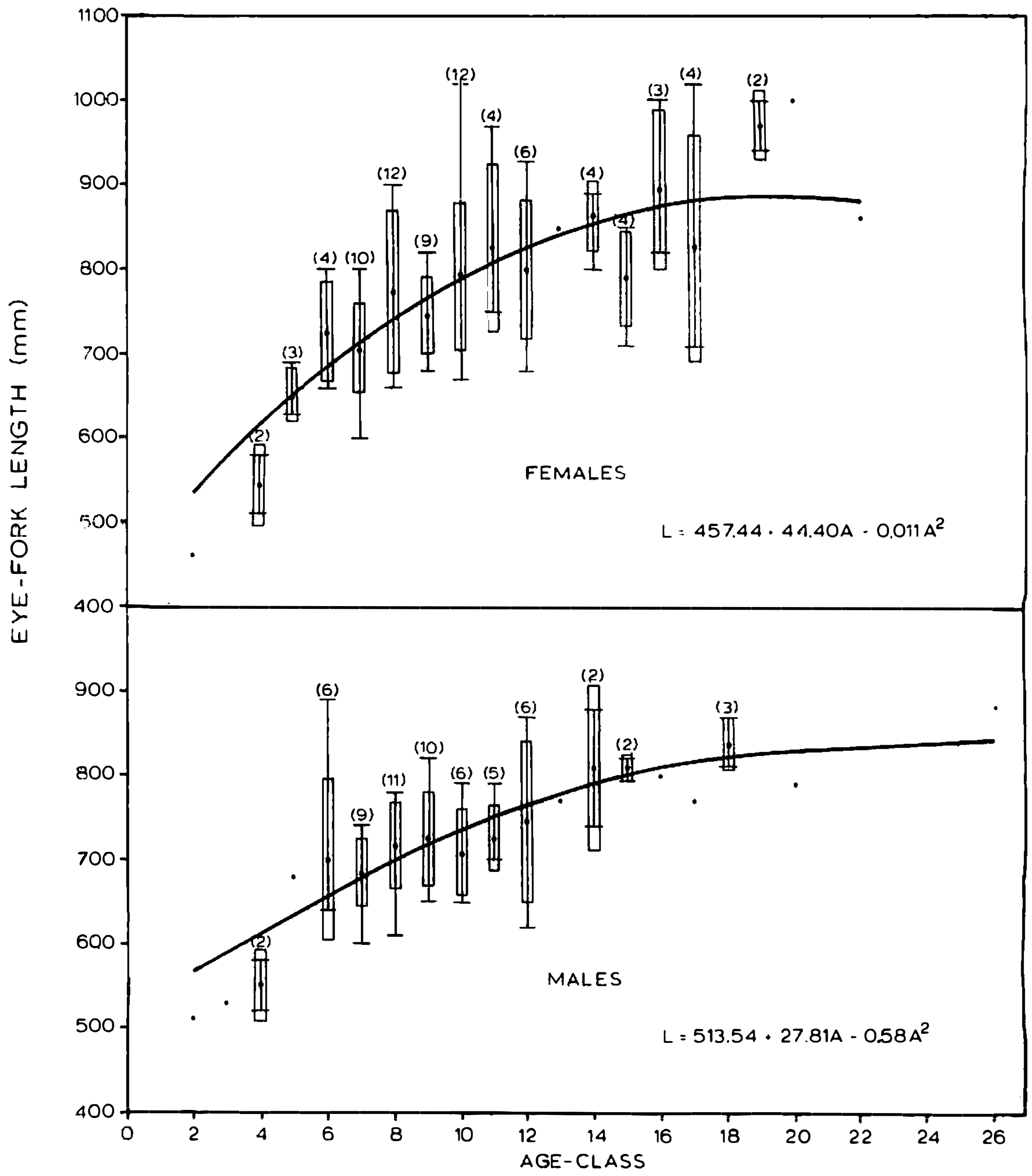

Figure 7. Differential growth in terms of length between male and female paddlefish from different age-classes as expressed by curvilinear regression. Point, mean; hollow bar, standard deviation on either side of mean; vertical line, range. Sample sizes in parentheses, points without standard deviation or range represent single fish.

State of Gonads, Sex Ratios, and Tubercles

State of Gonads, Males

Testes in paddlefish were located along the lateral margins of the dorsal surface of the body cavity. They appeared as thin bands, 2-4 mm wide, and laid flush along the dorsal surface of a fat deposit. In some specimens, usually larger fish, the testes appeared expanded, 10-20 mm wide and 1-2 mm thick. Microscopic examination for motile sperm was not performed, therefore, it is not known whether expanded testes were an indicator of maturity. Larimore (1950) discussed spermatogenesis in paddlefish but offered no macroscopic means to determine maturity.

State of Gonads, Females

The ovaries of female paddlefish were highly convoluted structures located in a position similar to that of the testes. Mature female paddlefish do not appear to develop mature eggs every year. All females possessed ovaries in one of the following stages of maturation: (1) Immature, white granular. - Ovaries were white to slightly pink and highly granular in appearance. Various amounts of fat were evident on the underside of the ovaries. The amount of fat did not seem to be dependent upon the size of the fish. (2) Immature, white and black granular. - Ovaries exhibited a continuum in color from white with a few minute black spots (developing eggs),

to a blackish appearance with many large black spots and many minute white spots. The developing eggs increased to about 1 mm in diameter during this stage. Little fat was noted under the ovaries. (3) Immature, eggs. - Individual eggs, grey in color, were clearly evident and ranged from 1 to 2 mm in diameter. Minute white spots were scattered throughout the ovary and no fat was in evidence.
(4) Mature, eggs. - Eggs were grey to black in color and from 2.0 to 2.5 mm in diameter. Ovaries were very large and filled the body cavity of the fish. Developing oocytes were described by Larimore (1950).

Paddlefish age and weight at the initiation of each stage of ovary maturation was difficult to determine. Paddlefish completed at least 8 growing seasons and weighed at least 7,500 g before the initial stage of ovary maturation ended (Table 4). The small number of fish found to possess ovaries containing immature or mature eggs precluded determination of the age or weight at which these stages of maturation were completed. Maturation may not have been dependent on age, but on the amount of energy available to the fish for expenditure in development of the large egg mass. The appearance of the ovaries at stage 3 indicated that full maturation of the eggs would have occurred within 1 to 2 years. The range in age and weight of fish during the initial two stages of ovary maturation was very large; individuals which had spawned within a few

Table 4. Mean age and mean weight, range, and standard deviation of female paddlefish at different stages of ovary maturation.

Stage of Maturity	Mean Age	SD	Range	Mean Weight	SD	Range	Number of Fish
(1) Immature, white granular	9	3.1	2-17	6,300	2,227	1,600-12,300	66
(2) Immature, white and black granular	14	4.2	8-22	9,740	1,799	7,500-12,800	12
(3) Immature, eggs (1-2 mm)	13.5	2.1	12-15	8,600	566	8,200- 9,000	2
(4) Mature, eggs	16	0	0	10,750	1,060	10,000-11,500	2

years previous to sampling would have ovaries in early developmental stages, as would paddlefish which possessed mature ovaries for the first time.

Eggs may have begun developing and proceeded accordingly at certain ages but it is likely that size of the fish was a more important factor in ovary development. The smallest paddlefish reported by a recent worker to possess mature ovaries weighed 7,500, 9,600, and 10,000 g and had ages of 15, 16, and 18, respectively (Robinson 1966). Russell (1972) conducted work on a spawning run, therefore only mature fish were examined. He concluded that most females with mature ovaries weighed at least 13,600 g, an occasional fish weighed as little as 10,900 g, and the age at maturity was between 10 and 12 years. Results from the present study and other recent studies indicated that female paddlefish may mature beyond a weight and age of about 10,000 g and 10 years, respectively.

Few female paddlefish were found to possess mature or nearly mature ovaries. There are several possible explanations for the apparent lack of fish with mature ovaries in the population: (1) Fish matured, traveled downstream to spawning grounds, and then returned. Spawning habitat similar to that described by Purkett (1961) did not exist in the study area. Four paddlefish fry were, however, captured in the study area by personnel of North Central Reservoir Investigations, Yankton, South Dakota, during June, 1976. The fry apparently came from eggs deposited in the study area. Therefore, if a downstream spawning migration did exist, not all mature fish participated. All conditions required for paddlefish spawning may not be fully understood. (2) The sampling method excluded larger, more mature fish. Boehmer (1973) found that creeled paddlefish from the tailwaters of Gavins Point Dam ranged from 1,600 to 26,300 g, but fish larger than 14,300 g were not captured in the present study. Fish larger than 14,300 g apparently did not make up a large proportion of the population in the study area because nets of the size used during the study would have retained at least a few of the larger specimens. (3) Sufficient food was not available for growth and development of the large egg masses. (4) Most fish in the population spawned previous to sampling and therefore had ovaries in an immature developmental stage, e.g., conditions during 1974 may have been excellent in regard to the initiation of paddlefish spawning. Meyer (1960) reported an incident in April 1959 when thousands of paddlefish caught by commercial fishermen were all found to be immature. The catch was composed of all ages and sizes and a nearly equal sex ratio was noted.

Sex Ratios

The sex ratio for the entire population was estimated to be 0.85 males to 1 female, and the sex ratio for each age-class varied (Table 5). These results may be slightly biased since no method was used to ensure random selection of fish to be sacrificed. Paddlefish harvested in the tailwaters of Big Bend Dam, South Dakota, consisted of 82, 76, and 71% females during the years 1973, 1972, and 1971, respectively (Friberg 1974). Other studies have reported higher percentages of males than females. Paddlefish sampled by Shields (1956) from the tailwaters of Fort Randall Dam consisted of 70% males. A sex ratio of 3.3 males to 1 female was reported by Robinson (1966) from a rotenoned area. Other areas sampled by Robinson (1966) yielded sex ratios ranging from 1.8: 1.0 (n = 37) to 36.8: 1.0 (n = 832). Rehwinkel (1975) observed high male to female ratios.

Tubercles

No satisfactory method to determine the sex of paddlefish without gonadal examination has been found. Friberg (1974) stated that prominent tubercles over the dorsal surface of the fish always indicated a male, but not all males had this characteristic. He also noted that some females had tubercles, but the tubercles were not prominent. Results from the present study were inconclusive (Table 6).

Table 5. Sex ratios of paddlefish with calculated ages.

Age-Class	Number of Fish	Males (%)	Females (%)	Sex Ratio
2	2	50	50	1.00:1.00
3	1	100	0	---
4	4	50	50	1.00:1.00
5	4	25	75	0.33:1.00
6	10	60	40	1.50:1.00
7	19	47	53	0.89:1.00
8	23	48	52	0.92:1.00
9	19	52	47	1.13:1.00
10	18	33	67	0.49:1.00
11	9	56	44	1.27:1.00
12	12	50	50	1.00:1.00
13	2	50	50	1.00:1.00
14	6	33	67	0.49:1.00
15	6	33	67	0.49:1.00
16	4	25	75	0.33:1.00
17	5	20	80	0.25:1.00
18	3	100	0	---
19	2	0	100	---
20	2	50	50	1.00:1.00
22	1	0	100	---
26	1	100	0	---
Totals	153	46	54	0.85:1.00

Table 6. Mean age, mean weight, range, and percentage of male and female paddlefish with and without tubercles from a sample of 32 males and 24 females.

With Tubercles					
	%	Mean Age Class	Range	Mean Weight (g)	Range
Males	53	12.8	7-26	6,060	4,300-11,800
Females	21	12.0	6-22	7,900	6,700- 8,100

Without Tubercles					
	%	Mean Age Class	Range	Mean Weight (g)	Range
Males	47	8.4	6-11	5,520	4,000- 7,100
Females	79	12.3	8-19	7,980	4,600-12,000

Females appeared less likely to have tubercles but no determination of sex could be made on the basis of the presence or absence of tubercles. Age and weight of females did not seem to be factors in the development of tubercles, but old males appeared to be more likely to have tubercles than young males. The presence or absence of tubercles did not appear to be influenced by the maturity of fish, as paddlefish thought too small to be mature were observed with or without tubercles.

Occurrence of Injuries to Paddlefish

Thirty-five and one-half percent of all fish examined in this study had obvious scars on their bodies and 27.4% of these fish had lost part or all of their rostrum. Paddlefish may have received injuries as reflected by scars in three major ways: (1) Paddlefish were hit by boats, or the lower unit of motors. Fish were extremely susceptible to injury in this manner during late spring, summer, and early fall. It was not unusual to hit at least one paddlefish a day while working in areas paddlefish concentrated. Boaters often made sport of "looking for paddlefish", during the course of which, many fish were hit. These collisions may instantly kill or eventually lead to the death of the fish. Many damaged rostrums probably resulted from collision with boats since many of the fish which I hit, had among their injuries severed or chipped rostrums.

(2) Paddlefish often tore free of the large treble hooks used to snag paddlefish. Often the gash was superficial, but when the hook removed a large piece of flesh or the fish was severely cut by the line, death may have resulted. Several fish were observed with recent, obvious hook injuries. (3) Paddlefish may have passed over or through dams. The frequency with which this event has occurred is not known, but one fish is known to have passed through two dams (Friberg 1973). Some paddlefish may have been injured during passage over or through dams.

Tagging Studies

One hundred ninety-one and 58 paddlefish were tagged with jaw bands and dart tags from 26 June to 14 November 1975, respectively. Fifteen jaw tags (8%) were returned by September 1976. No dart tags were returned. Return of tags was on a volunteer basis. Friberg (1974) stated that anglers below Gavins Point Dam were not very cooperative with regard to returning tags from paddlefish marked during 1972 and 1973. Elser (1975) reported that the return of jaw tags was much higher than return of dart tags from paddlefish in Montana.

Sixty-seven percent of the tagged fish which were recaptured traveled downstream, 26% upstream, and 7% stayed in the same area (Fig. 8). Three fish ranged from 680 to 780 km downstream within 3 to 8 months after capture.

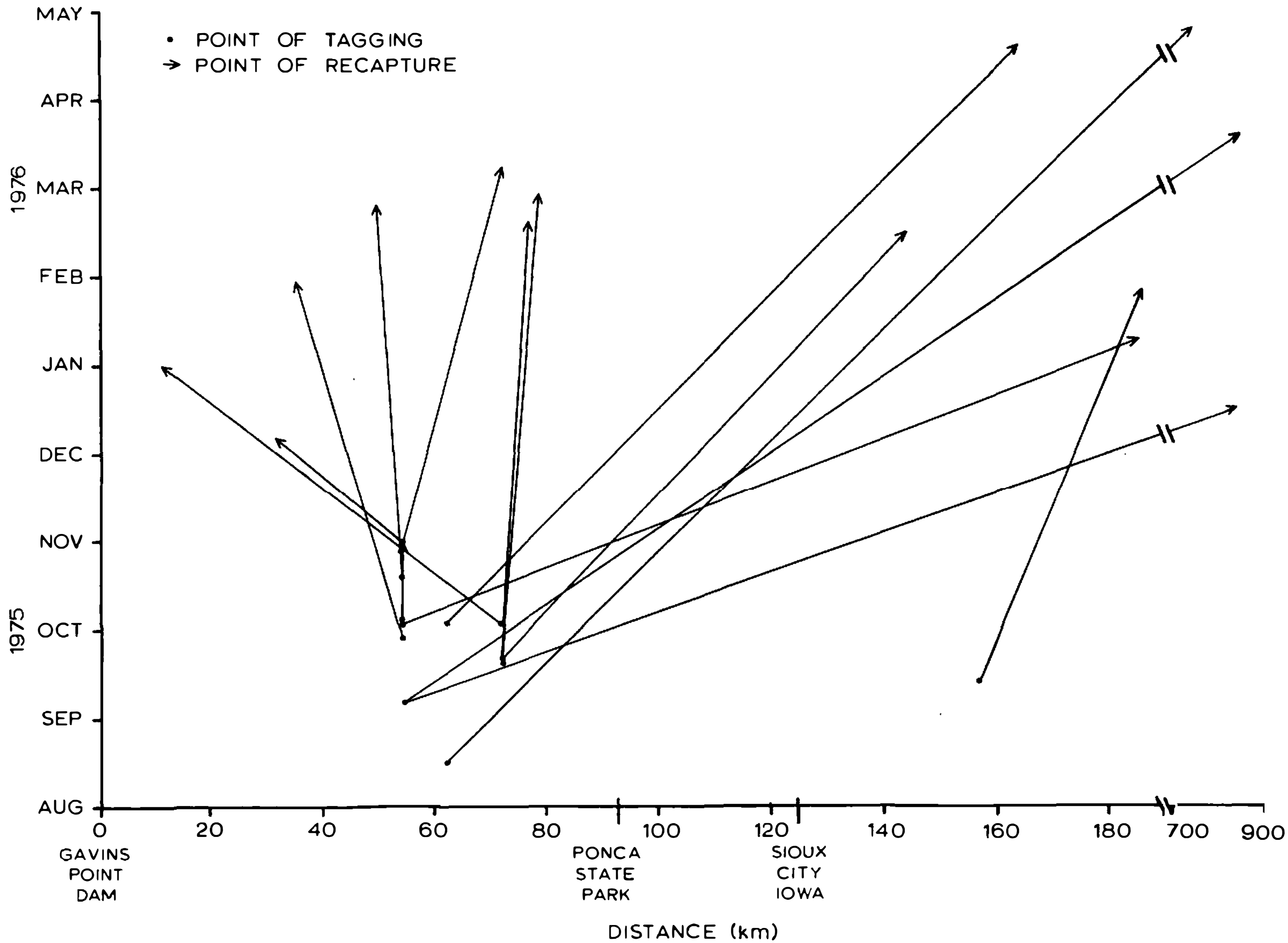

Figure 8. Movement of paddlefish tagged in 1975 and recaptured.

Experiments whereby a small block of styrofoam was attached by a length of string to the dorsal fin of a tagged paddlefish established the fact that once tagged, paddlefish initially traveled downstream. Thomas Russell (personal communication) stated that fish which have had sonar tags placed on them during their upstream spawning migration initially traveled downstream, and 2 to 3 days later, resumed upstream movement. Fish in the present study were under no pressure to move back upstream.

Most tagged fish traveled downstream, below the study area, and did not return at least until late spring 1976. Little fishing pressure occurred below the study area, and in some stretches of river there was no snagging for paddlefish, yet 43% of all returns from fish tagged in the study area were captured from 50 to 750 km downstream from the study area. Conversely, 57% of all returns from fish tagged in the study area remained within the study area and only 50% of these were found to have traveled upstream.

Intense fishing pressure occurred upstream from the study area. A creel census at the tailwaters of Gavins Point Dam from 1 October 1972 to 30 April 1973, estimated that 13,890 angler hours yielded 4,293 paddlefish (Friberg 1974). No fish tagged in the present study were caught in the tailwater area. A lower, yet substantial amount of fishing took place down to approximately 11 km below Gavins

Point Dam. Higher than usual fishing pressure was evident during the study period due to a mild winter which left most of the river free of ice cover. An estimated 600-1,000 paddlefish were removed from one area approximately 75 km downstream from Gavins Point Dam (Virgil Gosch, personal communication). It follows that if a substantial portion of the tagged fish remained within the study area or moved upstream into the tailwaters of Gavins Point Dam, a higher percentage of fish would have been recovered from these areas.

Two possible explanations for the high percentage of fish recaptured downstream from the study area were:
(1) Paddlefish traveled downstream when the discharge from Gavins Point Dam was reduced in late November. A slight decrease in water level resulted in a downstream paddlefish movement during their upstream spawning run in Missouri (Thomas Russell, personal communication), but thousands of paddlefish caught each winter in the study area precluded this occurring on a large scale below Gavins Point Dam.
(2) Paddlefish subjected to physically traumatic experiences, gill netting and tagging, moved downstream and remained for some time. The large number of fish which were hit by boats, passed through the dam, or broke free of snag hooks, must have left the area if this assumption were true. The percentage of population reported scarred

in the present study would have been underestimated and immigration of large fish into the study area must have been occurring. The concept of an open river, the upper boundary necessarily originating at Gavins Point Dam, by which paddlefish travel great distances upstream and down over a lifetime, must be considered.

Paddlefish may have been a highly mobile species before construction of dams which now block their movement; they may not have been segregated into separate populations but were freely integrated over their entire range. Results from tagging studies in Montana indicated that paddlefish annually migrated up the Yellowstone River from Garrison Reservoir during spring (Rehwinkel 1975; Robinson 1966). Elser (1975) reported extensive interchange of paddlefish between the Missouri River and Yellowstone River.

Paddlefish were tagged in 1972 and 1973 by Friberg (1974) to estimate the number of paddlefish below Gavins Point Dam. Six percent of the tags were returned and the population was estimated at 70,270 fish. The study implied that all tags returned were from fish caught in the tailwaters of Gavins Point Dam. The present study indicated that a large proportion of the fish tagged traveled downstream from the area of capture, if this occurred in 1972 and 1973, then the population was overestimated by Friberg (1974).

A compilation of tagging and recapture data, 26 June

1975 to 10 August 1976, is presented in Appendix A.

Food Habits

Food of Paddlefish

Food of paddlefish was nearly 100% zooplankton. Aquatic insects and amphipods made up the remainder of food items in paddlefish stomachs (Table 7). Large amounts of detritus and some algae were also ingested. Over 75% of the stomach contents by volume was composed of *Daphnia pulex*, calanoid copepodites, *Diaptomus siciloides*, and *Diaptomus forbesi* when these organisms were present in stomachs *Daphnia pulex* was the most important food organism; when present it represented an average of over 37% of the stomach contents by volume. Mean volumes for individual food items ranged from 2.0×10^{-5} to 2.4×10^{-4} ml for cyclopoid copepodites and *Daphnia pulex*, respectively (Table 8). Calanoid copepodites, cyclopoid copepodites, and *Diaptomus siciloides* made up 29, 20, and 18% of the average stomach contents by number, respectively, when present in stomachs. No food was consumed by paddlefish from 12 August to 5 September 1975 and from 18 March to 30 March 1976. Traces of food items were found in stomachs from 29 June to 11 August 1976.

The diet of paddlefish collected from the tailwaters of Fort Randall Dam, South Dakota, was composed almost entirely of zooplankton (Sprague 1959; Meyer 1960). Mayfly

Table 7 Stomach contents of 112 paddlefish from 12 August 1975 to 11 August 1976, expressed as percent number per stomach, and percent volume per stomach (in parentheses); averages are the average of values where the food item is present in the stomach

Food Item	1975 8-12 to 9-5	9-19	9-27	10-3	10-17	10-31	11-14	12-30	1976 1-24	2-19	3-18 to 3-30	4-22	5-20	6-16	6-29 to 8-11	Average
Cladocera																
Diaphanosoma brachyurum		5.1 (8.1)	6.9 (11.2)	9.5 (13.2)	5.1 (6.7)	T										6.7 (9.8)
Bosmina longirostris														T		T
Daphnia pulex		4.7 (22.8)	0.6 (3.0)	T	2.0 (4.3)	12.6 (3[illegible])	7.6 (34.4)	17.3 (42.5)	16.1 (44.1)	7.2 (26.3)	33.9 (65.5)	33.9 (65.5)	30.1 (69.3)	12.1 (54.8)		13.2 (37.3)
Cyclopoida copepodites		10.8 (4.6)	9.6 (4.2)	7.7 (2.9)	8.2 (2.8)	19.1 (5.0)	36.5 (14.2)	18.1 (4.0)	23.2 (5.5)	30.3 (9.2)	14.6 (2.4)	14.6 (2.4)	4.0 (0.8)	57.7 (21.8)		20.0 (6.4)
Mesocyclops edax		1.8 (2.0)	1.6 (2.1)	1.5 (1.0)	T								1.1 (0.6)	T		1.5 (1.6)
Cyclops bicuspidatus thomasi		2.3 (2.4)	2.0 (2.5)	4.3 (3.1)	4.6 (4.5)	5.9 (4.4)	5.3 (5.9)	13.0 (7.7)	16.[illegible] (11.0)	15.7 (13.6)	15.4 (7.1)	15.4 (7.1)	1.9 (1.0)	1.0 (1.0)		7.3 (5.3)
Cyclops vernalis							T	T						T		T
Cyclops varicans rubellus		1.3 (1.6)	T	3.0 (2.0)			T						T			2.1 (1.8)
Calanoida copepodites		64.6 (42.3)	61.4 (41.9)	41.7 (23.9)	13.7 (7.3)	14.2 (5.7)	29.7 (17.9)	10.5 (3.4)	9.8 (3.6)	16.2 (7.3)	6.9 (1.7)	6.9 (1.7)	53.0 (17.2)	25.9 (15.1)		29.0 (15.6)
Diaptomus ashlandi		0.5 (0.9)	0.5 (0.8)	1.8 (2.7)	1.2 (1.6)	6.8 (6.5)	0.7 (0.8)	0.9 (0.4)	4.0 (3.5)		10.0 (6.1)	10.0 (6.1)	4.1 (2.7)	1.2 (1.7)		2.8 (2.9)
Diaptomus siciloides		7.1 (8.1)	11.7 (13.5)	19.5 (20.1)	59.1 (53.5)	29.4 (14.3)	14.1 (18.5)	20.6 (15.7)	21.0 (16.3)	17.9 (15.4)	9.2 (4.0)	9.2 (4.0)	1.4 (0.7)	0.7 (0.7)		18.0 (15.1)
Diaptomus sicilis		T	0.7 (1.3)	6.1 (8.8)	1.8 (2.7)	6.3 (12.5)				2.4 (7.7)		1.5 (1.0)				3.1 (5.6)
Diaptomus forbesi		1.8 (6.0)	5.0 (19.6)	6.7 (22.3)	4.0 (12.3)	5.6 (12.9)		19.4 (26.2)	9.0 (16.1)	10.2 (20.5		8.5 (12.3)	4.4 (7.8)	1.4 (4.8)		6.5 (14.1)
Amphipoda		T														T
Hydracarina		.														T
Insecta																
Plecoptera																T
Ephemeroptera			T				T									T
Acari					T	T										T
Trichoptera			T	T	T	T						T				T
Diptera																
Chironomid larvae		T		T								T		T		T
Other Diptera														T		T
No. of paddlefish examined	44	4	3	4	4	4	4	4	3	3	5	3	6	6	15	Totals 112
No. of paddlefish with food	0	4	3	4	4	4	4	4	3	3	0	3	6	6	0	48
Percent total average stomach content composed of zooplankton	0	35.5	43.9	22.2	34.7	55.4	40.4	30.3	63.2	51.7	0	60.4	60.3	31.0	0	44.1

Table 8. Mean length and mean displacement volume of major food items of paddlefish.

Organism	Mean Length (mm)	Range (mm)	Mean Volume (ml)
Cladocera			
Diaphanosoma brachyurum	1.2	0.5 - 1.4	7.4×10^{-5}
Daphnia pulex	1.4	0.7 - 1.9	2.4×10^{-4}
Cyclopoida			
copepodites	0.6	0.3 - 1.0	2.0×10^{-5}
Cyclops bicuspidatus thomasi	0.9	0.7 - 1.2	5.7×10^{-5}
Calanoida			
copepodites	0.8	0.3 - 1.5	3.1×10^{-5}
Diaptomus ashlandi	1.1	0.9 - 1.4	7.5×10^{-5}
Diaptomus siciloides	1.0	0.9 - 1.2	5.3×10^{-5}
Diaptomus sicilis	1.1	1.0 - 1.2	8.0×10^{-5}
Diaptomus forbesi	1.8	1.2 - 2.1	1.8×10^{-4}

naiads made up 95% (Meyer 1960) and 46% (Hoopes 1960) of the stomach contents of paddlefish from the Mississippi River, Iowa.

The average stomach content composed of plankton on each sample date ranged from 22.2% to 63.2% and the average from 12 August 1975 to 11 August 1976 was 44.1% (Table 7). The range of values from each sample was small and direct observation of stomach contents confirmed the presence of large amounts of detritus and some sand in addition to plankton. Non-food materials passed through the digestive tract and were evident in the feces. Plant material, in the form of detritus, passed largely unchanged through the digestive system. Algae, primarily *Asterionella*, was often conspicuous in the feces when large amounts of detritus and food material was not being consumed. The amount of detritus and sand in the stomach would have been dependent upon the amount of waterborne detritus and sand passing through the area in which feeding had occurred.

Food Selectivity

Paddlefish were not selective feeders (fish used in this analysis ranged from 1,600 g to 12,800 g). The relative proportion of zooplankton available to paddlefish was reflected by the relative proportion of food items in the stomach (Fig. 9). Seasonal food habits of paddlefish were strictly governed by the presence and relative

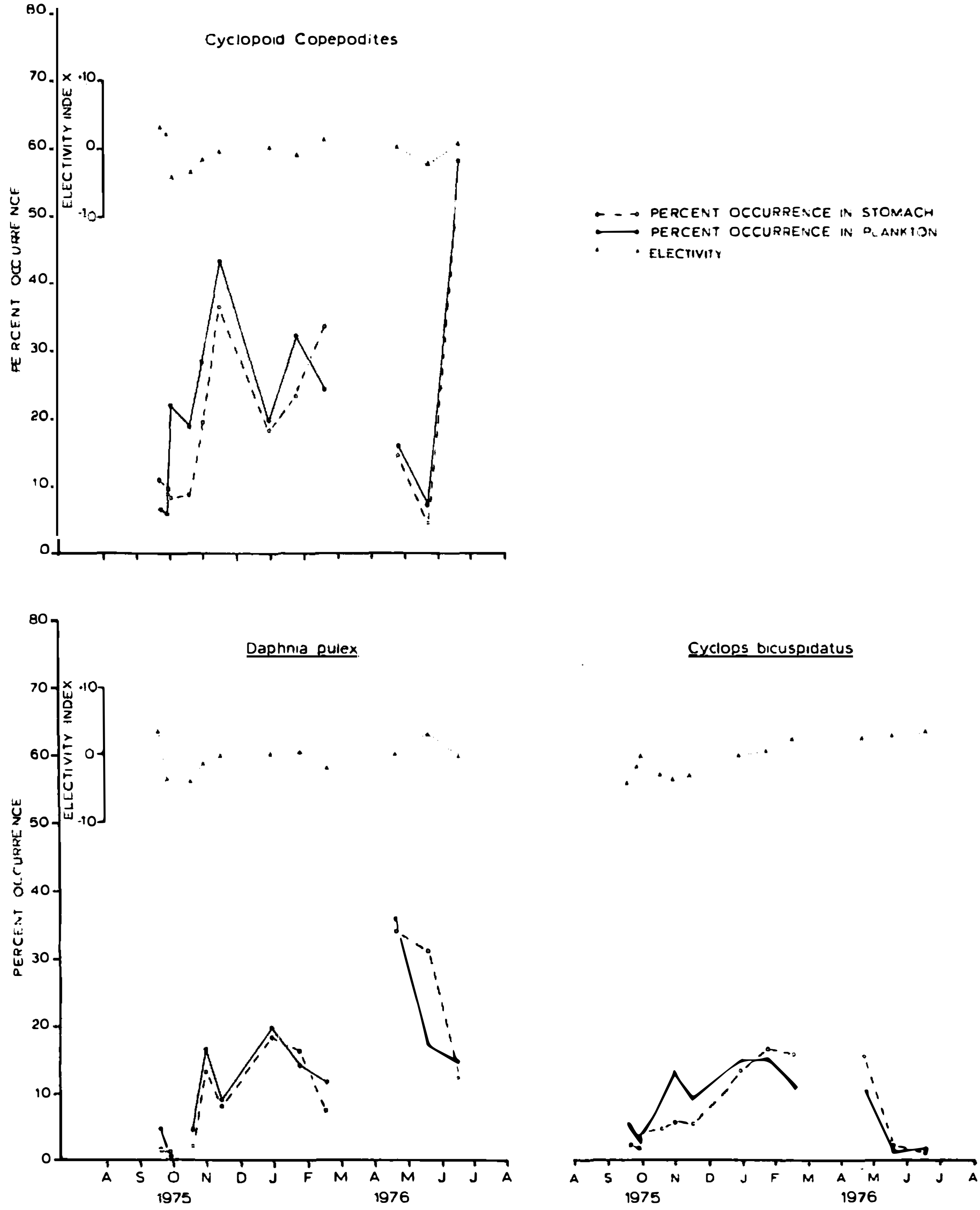

Figure 9. Mean percentage composition in the plankton and stomach, and electivity index of major food items on each sample date.

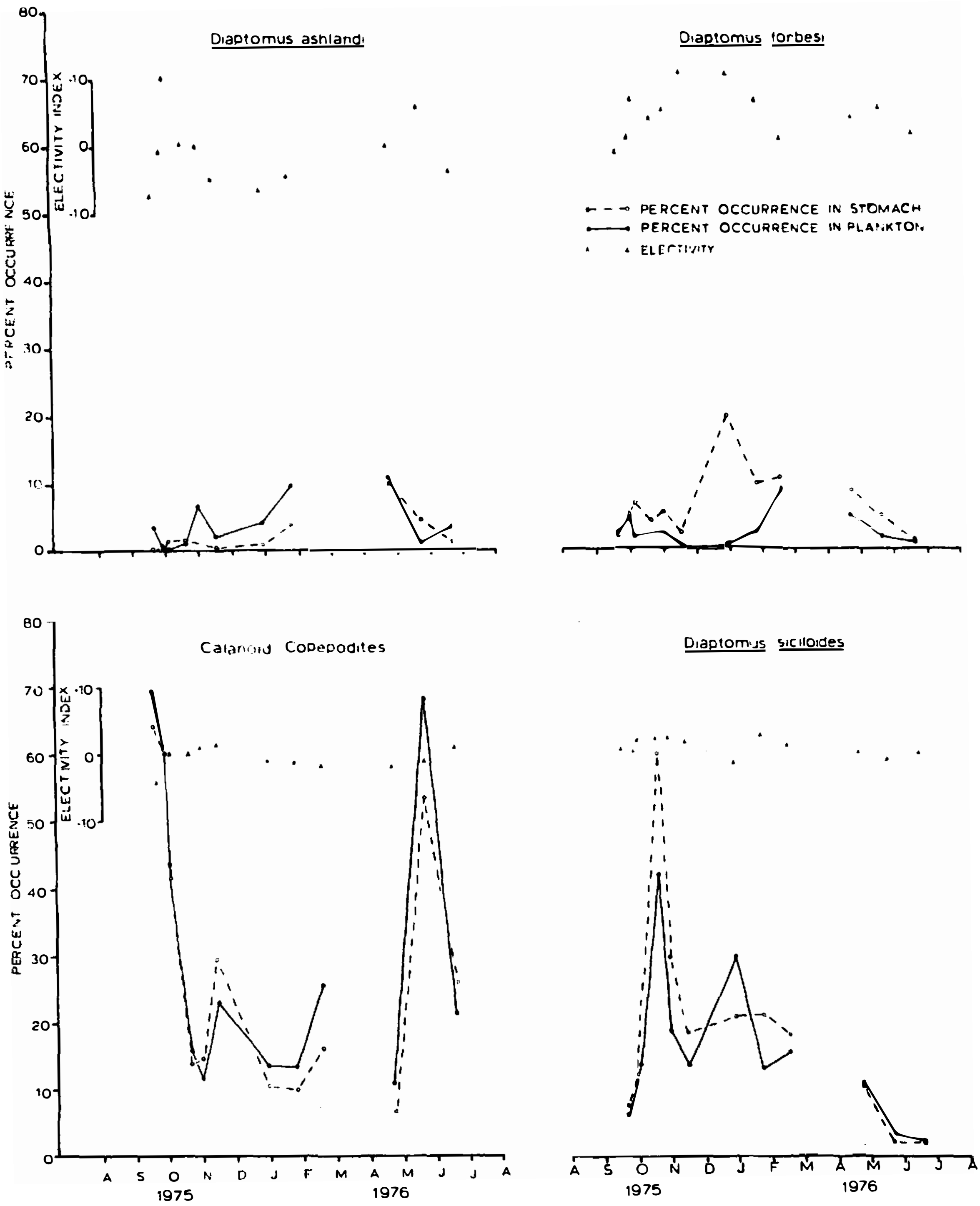

Figure 9. Continued. Mean percentage composition in the plankton and stomach, and electivity index of major food items on each sample date.

abundance of potential food items. Calanoid copepodites constituted a large percentage of the plankton and stomach contents during early fall and late spring. Cyclopoid copepodites were abundant in both plankton and stomachs during winter and early summer. Diaptomus siciloides was an important food item during late fall. Diaphanosoma brachyurum was an important food of paddlefish during autumn; D. brachyurum was nearly absent from the plankton during the rest of the year.

All food items except Cyclops varicans rubellus and Diaptomus forbesi had E values nearly equal to 0, indicating a lack of selection by paddlefish for or against a food item (Fig. 10). D. forbesi was a large and highly mobile copepod. The positive selection for this species was possibly due to its ability to evade capture by nets and not the active pursuit of it by paddlefish. Cyclops varicans rubellus was an insignificant species in both plankton and stomachs. The species was observed in measurable numbers on two sampling dates (Table 7) and had E values equal to +0.669 and -0.007. Small sample size and number coupled to yield the misleading mean E value calculated for this species.

Naupuli were not included as a food item in the analysis of food habits. Naupuli were often abundant in plankton but were rarely observed in paddlefish stomachs; when observed, the naupuli were usually large. Organisms

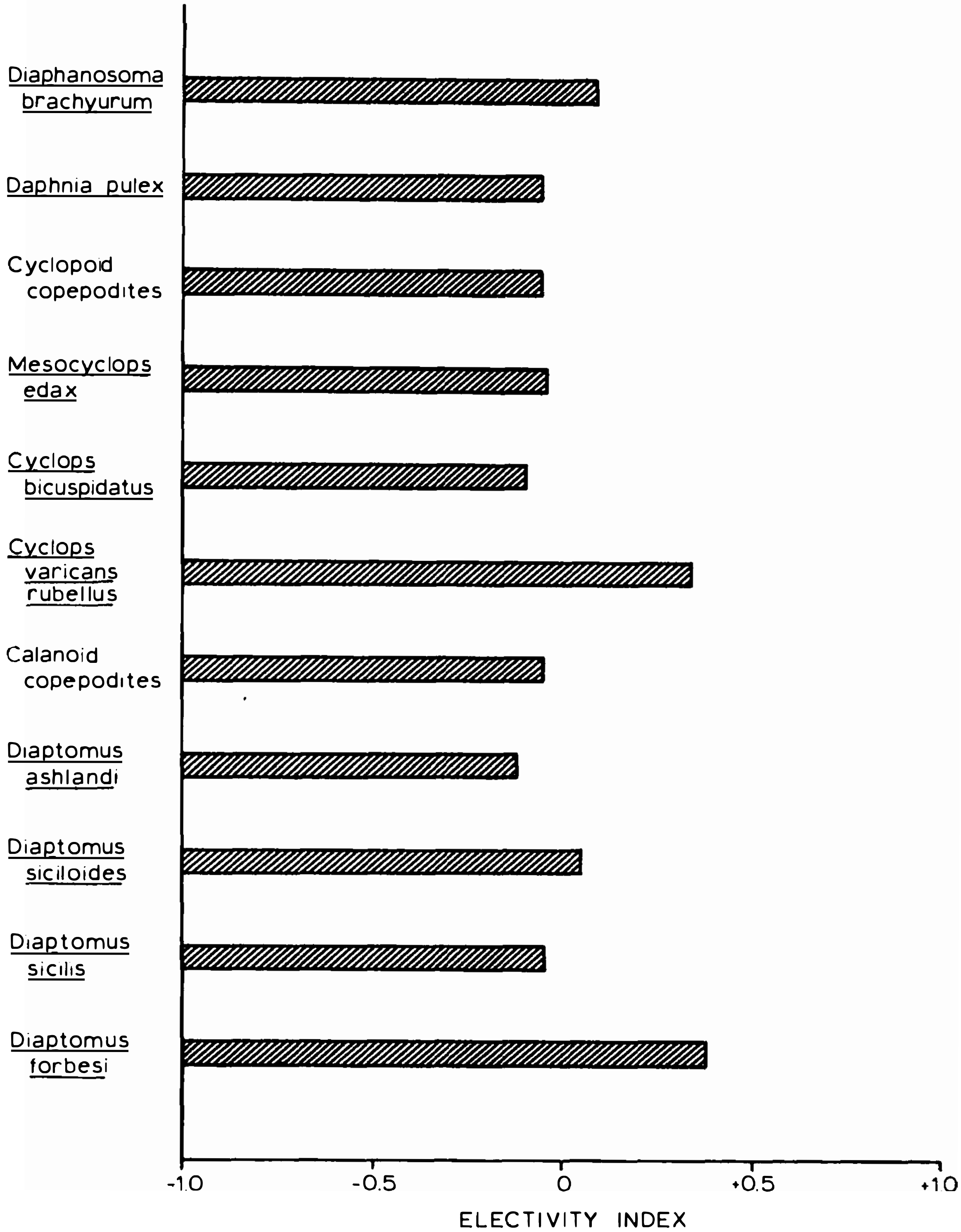

Figure 10. Mean electivity of food items when present in the stomach.

below a certain size were, for the most part, excluded from the stomach by the food straining mechanism (gill rakers) of paddlefish. Small cyclopod copepodites were also absent from stomach contents. More cyclopod copepodites were found in plankton than in stomachs except from two samples (Fig. 9). Cyclopod copepodites below a certain size were not retained by the gill rakers and were therefore not ingested.

Direct measurement of the distance between gill rakers was not effective in determining the minimum particle size retained by paddlefish (Table 8). The measured distance between gill rakers was from 0.04 to 0.08 mm; the average minimum size organism retained was 0.25 mm long. Gill rakers must have been forced out from the gill arches and separated somewhat as food was being strained. Organisms as small as 0.12 mm were observed in stomachs, but any small particle abundant in the water would occasionally be ingested in conjunction with normal feeding activity.

Seasonal Trends

The weight of the stomach contents in proportion to the body weight of fish was similar for paddlefish captured in the same area at the same time and from fish captured within a few days of each other from different areas within the study area. When one fish was found to have an empty stomach, all fish sampled had empty stomachs; when one fish was filled with food, all fish were found similarly full. Examination of the pyloric caeca and the spiral valve intestine lent credence to the feeding status of fish as determined by the amount of material in the stomach. Paddlefish that were feeding or had recently fed intensively had highly expanded, thin walled, and flaccid pyloric caeca and spiral valve intestines. The pyloric caeca contained a network of large and small passageways and the opening through the intestine was large. Paddlefish which had not fed recently or had fed very little exhibited tightly contracted and thick walled pyloric caeca and spiral valve intestines. The openings in the pyloric caeca and intestines were minute (Fig. 11).

Vernal and autumnal feeding peaks were evident (Fig. 12). Feeding continued throughout winter at a low level until early spring. The cessation of feeding in late March coincided with the increase in discharge from Gavins Point Dam, about 600 m^3/sec to 1,000 m^3/sec in 1976; feeding may have ceased for two reasons: (1) Paddlefish took advantage of the expanded water area and redistributed themselves when the water level increased; the activity precluded feeding. (2) The increase in flow was followed by a short period of high instability as extensive sandbars, laid bare by the receding water months before, were inundated. High waterborne sand load and a rapidly changing river profile

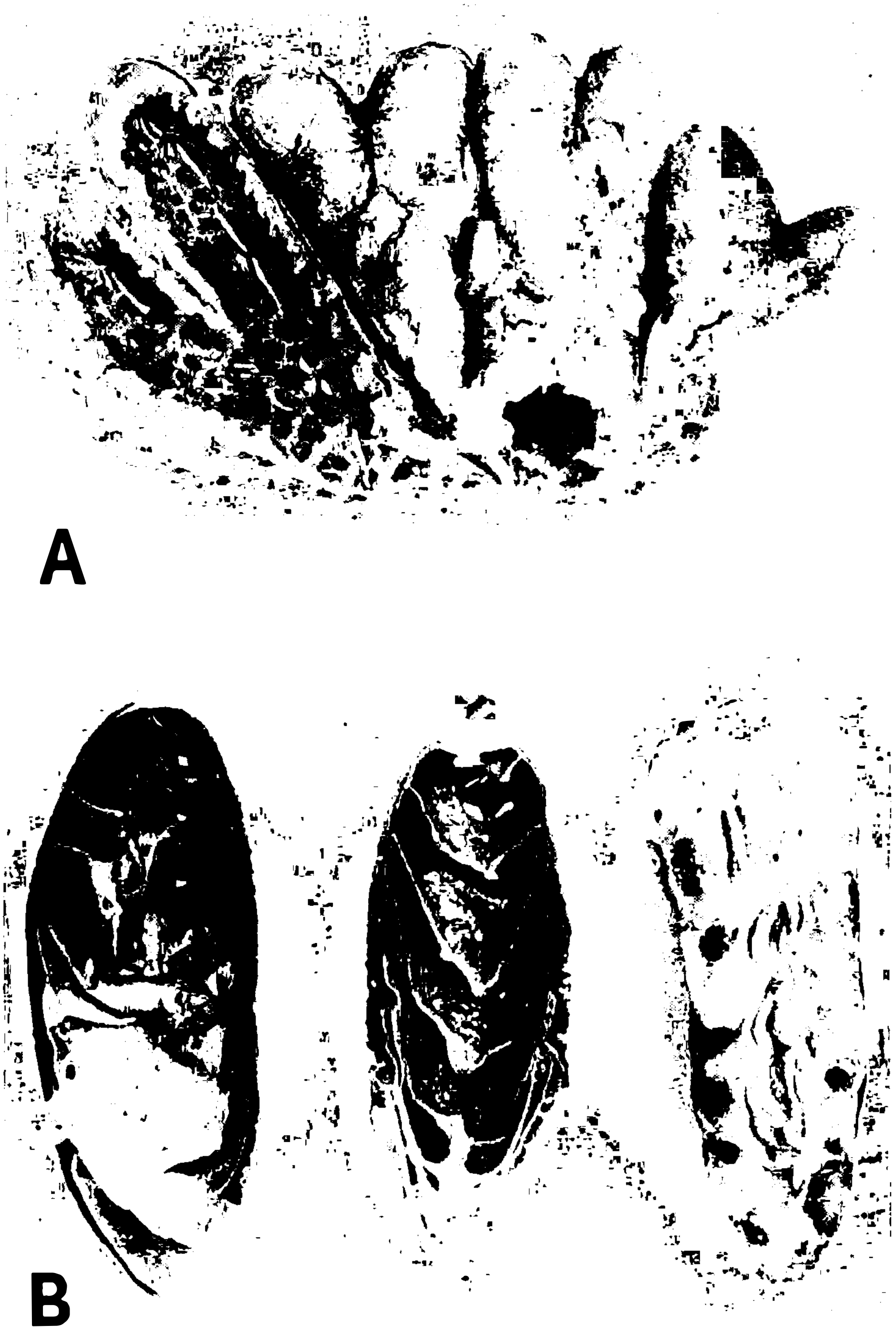

Figure 11. A. Pyloric caeca from feeding paddlefish.
B. Spiral valve intestines from paddlefish of similar weight. Left to right, during peak feeding, moderate feeding, and no feeding.

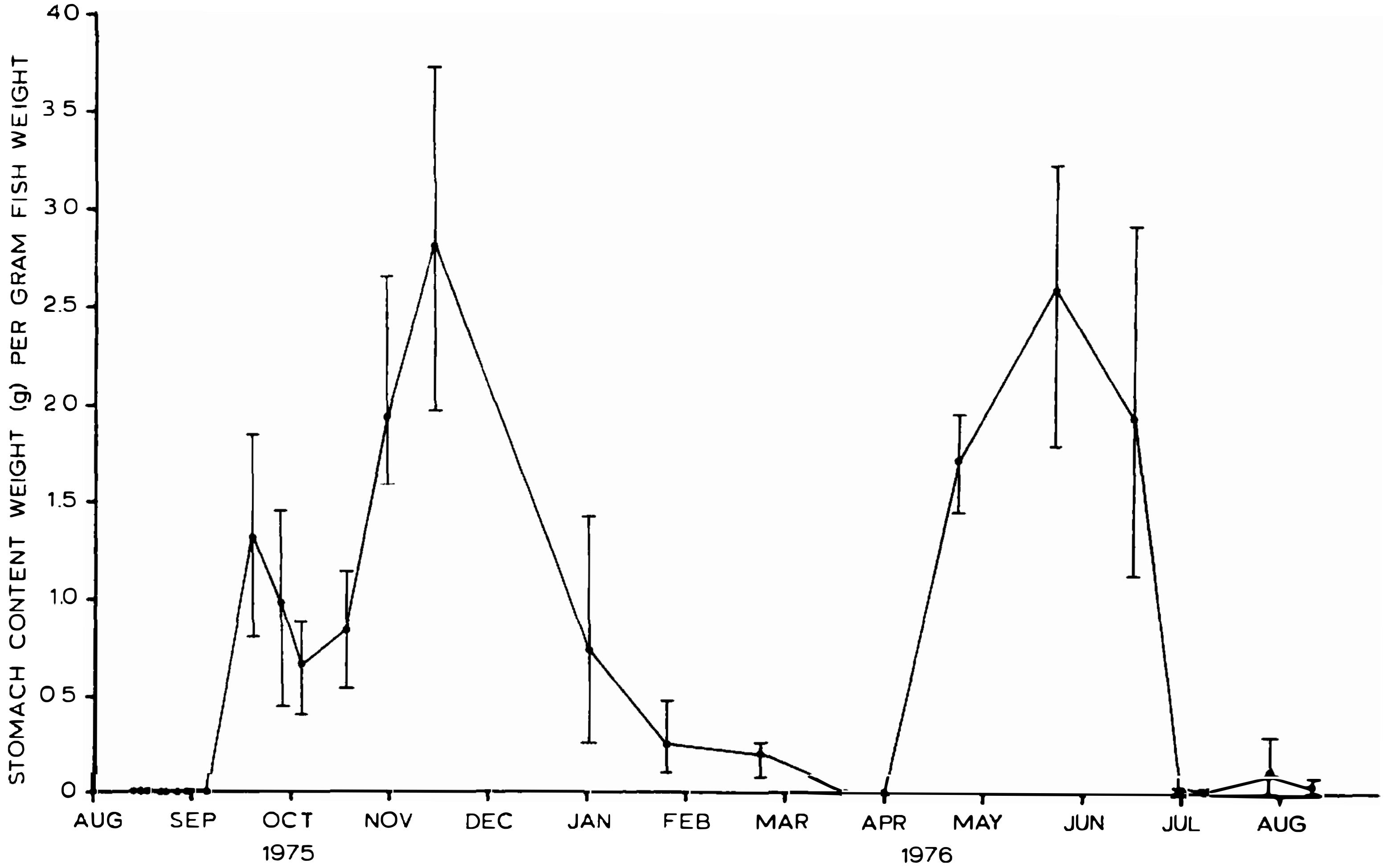

Figure 12. Seasonal feeding 12 August 1975 to 11 August 1976, expressed as the mean ratio of stomach content weight to fish weight. Point, mean; vertical line, range.

may have consequently hindered feeding activity.

Paddlefish ceased feeding or fed very little from July to early September (Fig. 12). Forty-four and 15 paddlefish were sacrificed and their digestive tracts examined during this period in 1975 and 1976, respectively. No food was found in 1975 and only small highly digested traces of food, usually less than 2 g/fish, were present in stomachs during 1976. The pyloric caeca and spiral valve intestines from fish captured in the summer of 1975 were totally contracted; during the summer of 1976, pyloric caeca and intestines contained small amounts of food, were slightly expanded, and small passageways were evident. Three explanations may be plausible for lack of feeding during summer: (1) Paddlefish feeding was optimum within a certain temperature range. Reduced feeding at low temperatures has been noted from species of fish in natural habitat (Mathur 1973), and was evident in paddlefish collected during winter. Low food consumption due to high water temperature was not unusual (Mathur 1973; Barber and Minckley 1971); but paddlefish may have ceased feeding altogether, as was evident in 1975. Assuming this explanation was correct would place the optimum temperature range for feeding between approximately 7 and 20 C; temperatures above 20 C depressed feeding. (2) Highly unstable conditions and excessive waterborne sand loads hampered feeding. The river was in constant turmoil from the high flow during the summer of 1975. Flow was normal and the river was fairly stable during the summer of 1976. Paddlefish stopped feeding during the summer of 1975, and feeding was nil during the summer of 1976. Although high instability in itself may have hindered feeding, it was probably not the entire cause of the summer feeding lull. (3) Food during the summer was at a very low level or was not available to paddlefish. Zooplankton samples taken in paddlefish concentration areas during the summer always revealed that large numbers of zooplankters were present. Williams (1971) stated that the general nature of the zooplankton in the Missouri River below Gavins Point Dam was established in Lewis and Clark Reservoir, and the abundance of zooplankton declined somewhat as distance from the dam increased. Williams (1971) also concluded that production in backwater areas contributed to plankton flow. Spring and fall peaks in the abundance of zooplankton entering the study area were evident (Fig. 13) and substantiated by the studies of Cowell (1967) and Williams (1971). Zooplankton did not drop to exceptionally low levels during the summer. Biweekly zooplankton samples taken 12 April to 16 August 1976 by personnel of North Central Reservoir Investigations, Yankton, South Dakota, in a channel area of the Missouri River, Zone 15, (Fig. 1), revealed that zooplankton decreased from spring to mid-summer but did remain available (Fig. 14).

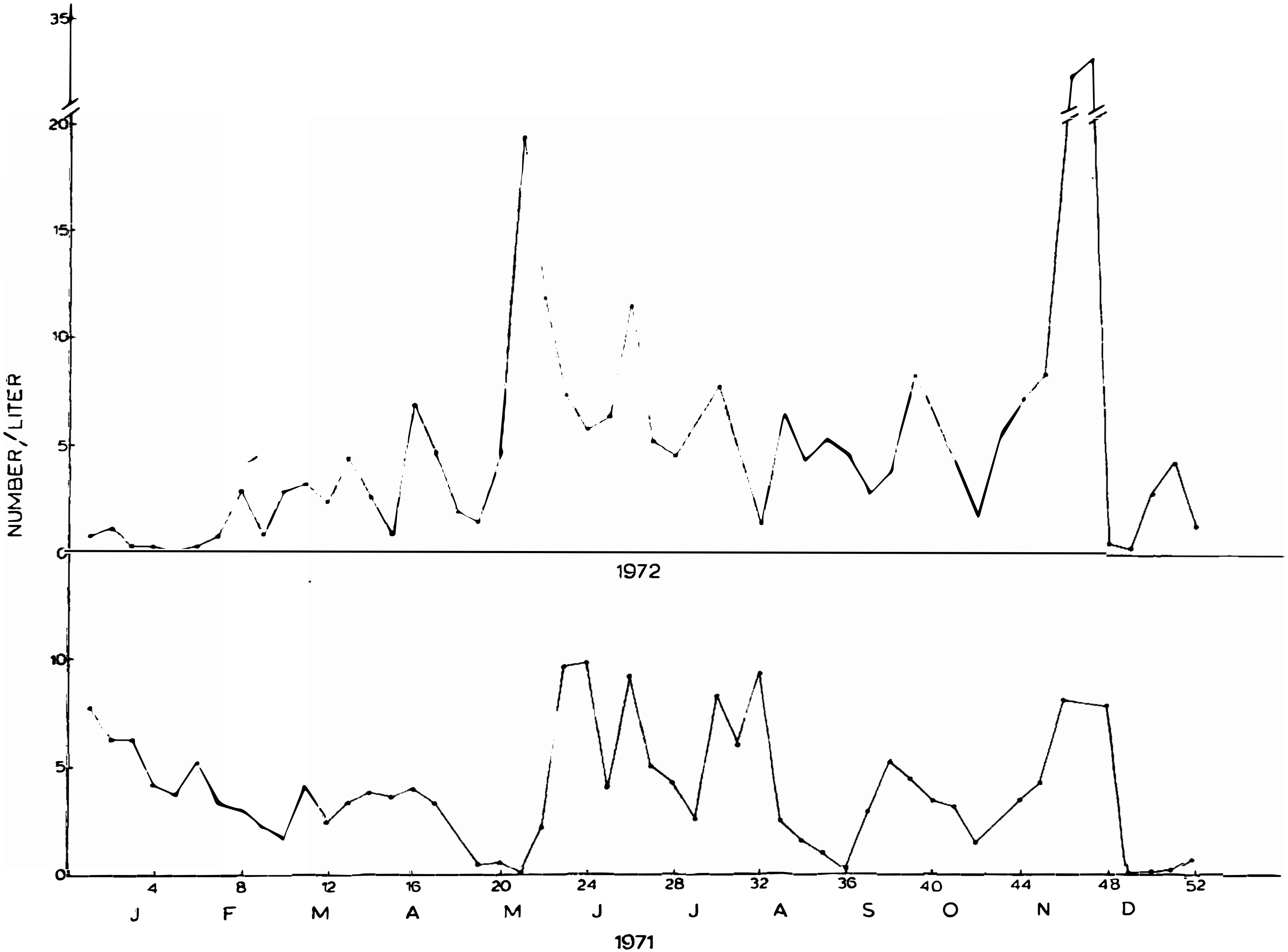

Figure 13. Mean weekly zooplankton flow, excluding naupuli, into study area from Gavins Point Dam, 1971 through 1972. (Unpublished data, North Central Reservoir Investigations, Yankton, South Dakota.)

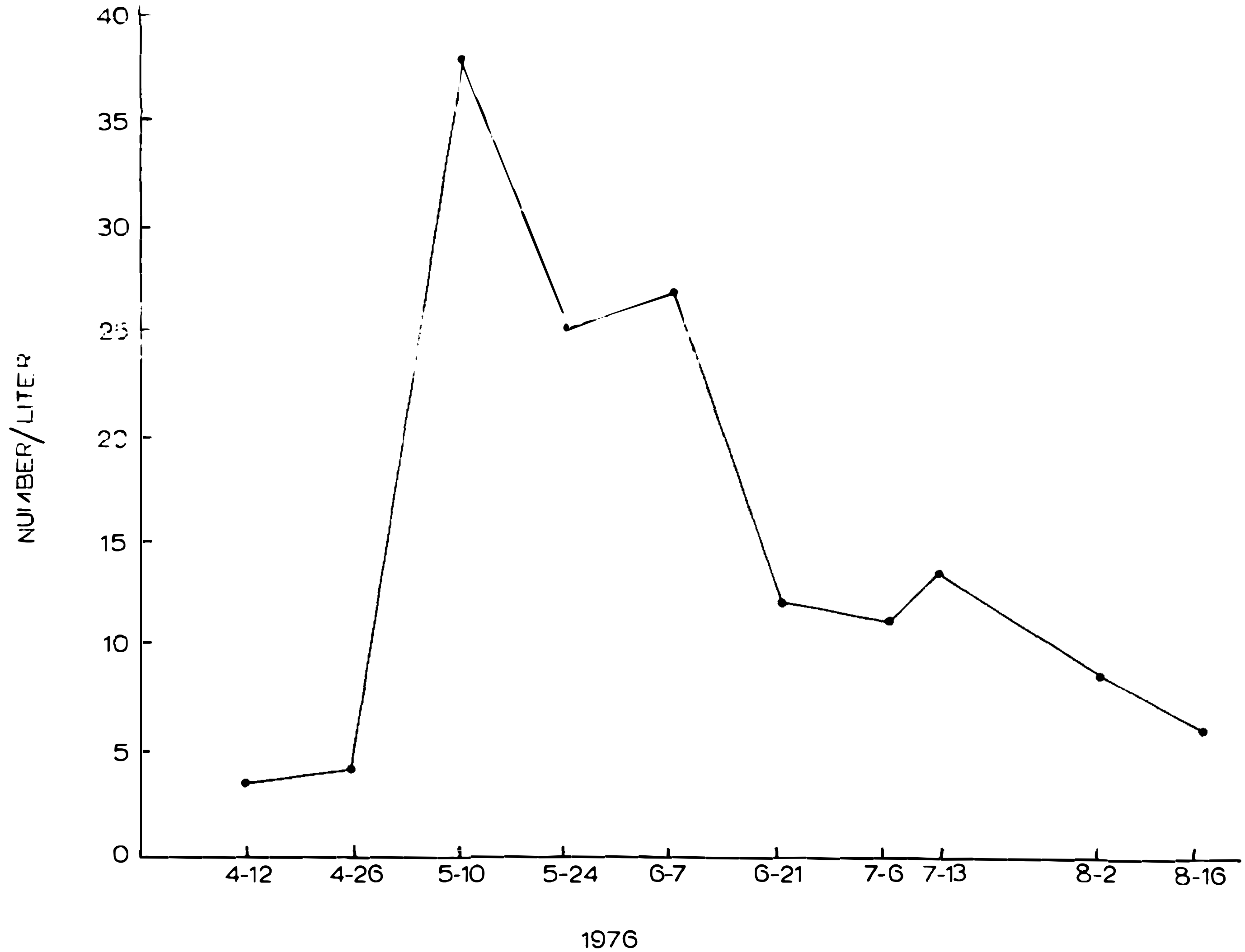

Figure 14. Mean zooplankton flow, excluding naupuli, through a channel area in Zone 15, 12 April to 16 August 1976. (Unpublished data, North Central Reservoir Investigations, Yankton, South Dakota.)

Ivlev (1961) stated that evenly distributed food was consumed at a low rate while patchy distributed food, of the same amount in the same area, was consumed at a higher rate. Zooplankton was not distributed evenly horizontally or vertically within the river (Williams 1971); but during times of high instability a more even distribution would be suspect due to the extreme upwelling of water and the reduction of slow and dead water area. Normal conditions tended to be more tranquil and zooplankton may have accumulated in pockets of dead or slow water, especially if there was a steady influx of water or an adjacent channel discharging plankton into the area. Such situations, provided they were at least 1.5 m deep, were determined to be habitat of paddlefish in a previous section of this study.

Feeding Periodicity and Daily Ration

Change in feeding activity over the 24 hour period was not evident as stomach content weight to body weight ratios of fish taken at dawn and at dusk were not significantly different at $p \leq .05$. Paddlefish appeared to feed continuously when food consumption levels were high; but a few hours of feeding inactivity during the day may not have been measurable if paddlefish had a slow digestive rate. Attempts were made to sample fish from the same area at 4 hour intervals throughout a 24 hour period, but since prior disturbance in an area precluded further paddlefish capture, no results were obtained. Fish were captured on one occasion at 1800 hours and 200, 400, and 600 hours the following day from areas in Zones 17, 17, 20, and 25, respectively. No differences in stomach content weight to fish weight were observed.

An experiment to determine the digestive rate of paddlefish and thereby calculate daily ration and feeding intensity yielded inconclusive results. Water temperature remained near 18° C throughout the study and no evidence of feeding on the small amount of plankton which spilled over or passed through the filter was noted. Fish from the initial group (0 hour) had an average stomach content weight to body weight ratio of 2.7. Fish after 6 hours without food had an average ratio of 1.7. Fish in the 12, 24, 36, and 48 hour groups had average stomach content weight to body weight ratios of 1.1, 1.3, 1.0 and 1.2, respectively. No apparent reduction in stomach content was therefore evident after 12 hours. No regurgitation was observed, but it may have occurred.

Darnell and Meirotto (1962) reviewed the analysis of digestion rate in fish and stated that the rate of digestion in fish varied and was dependent on many factors. The digestion rate of paddlefish appeared to be slow; but when comparison was made with digestion rates of other fish, it was suspected that the experimental method in the present study may have altered normal digestion since total evacuation of the stomach within 24 hours was normal.

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APPENDIX A

Tagging and recapture data (tag number, date and location of capture or recapture, length, weight, and release upon recapture), Missouri River, 26 June 1975 to 10 August 1976.

APPENDIX A

Table 1 Tagging data

Tag Number	Date	Eye-Fork Length (cm)	Weight (kg)	Location or Zone
P2401	9-18-75	72	5.4	25
P2402	9-18-75	63	3.9	25
P2403	9-18-75	67	7.1	25
P2404	9-18-75	51	1.5	25
P2405	9-18-75	89	10.6	25
P2406	9-18-75	70	5.4	25
P2407	9-18-75	74	5.8	25
P2408	9-18-75	60	4.9	25
P2409	9-19-75	72	5.0	25
P2410	9-19-75	73	5.6	25
P2411	9-19-75	74	4.8	25
P2412	9-19-75	66	4.2	25
P2413	9-26-75	63	3.7	25
P2414	9-26-75	67	3.7	20
P2415	10-31-75	77	7.0	20
P2417	10-31-75	59	3.0	20
P2418	9-27-75	72	4.9	17
P2419	9-27-75	77	6.5	17
P2420	9-27-75	81	7.8	17
P2421	9-27-75	62	5.4	17
P2422	9-27-75	82	6.2	17
P2423	9-27-75	76	6.2	17
P2424	9-27-75	64	6.1	17
P2425	9-27-75	75	6.0	17
P2426	9-27-75	81	7.8	17
P2427	9-27-75	67	3.4	17
P2428	9-27-75	78	7.0	17
P2429	9-27-75	84	6.2	17

APPENDIX A
Table 1. continued

Tag Number	Date	Eye-Fork Length (cm)	Weight (kg)	Location or Zone
P2430	9-27-75	73	5.4	17
P2431	10- 2-75	73	7.4	17
P2432	10- 2-75	67	4.4	17
P2433	10- 2-75	74	5.4	17
P2434	10- 2-75	76	5.3	17
P2435	10- 2-75	67	6.6	17
P2436	10- 2-75	100	11.5	17
P2437	10- 2-75	83	7 4	20
P2438	10- 2-75	91	9.2	20
P2439	10- 2-75	65	4.1	20
P2440	10- 2-75	62	3.4	20
P2441	10- 2-75	69	4.5	20
P2442	10- 2-75	73	5.1	20
P2443	10- 2-75	64	6.2	20
P2444	10- 2-75	65	3.9	20
P2445	10- 2-75	64	3 6	20
P2446	10- 2-75	78	6.6	25
P2447	10- 2-75	72	5.8	25
P2448	10- 2-75	72	5.1	25
P2449	10- 2-75	63	4.1	25
P2450	10- 2-75	79	6.8	25
P2451	10- 2-75	87	9.6	25
P2452	10- 2-75	69	4.5	25
P2453	10- 2-75	73	5.1	25
P2454	10- 2-75	65	3.7	25
P2455	10- 2-75	70	5.2	25
P2456	10- 2-75	80	7.9	25
P2457	10- 2-75	64	3.7	25
P2458	10- 3-75	78	6.0	17
P2459	10- 3-75	85	8.2	17

APPENDIX A
Table 1 continued

Tag Number	Date	Eye-Fork Length (cm)	Weight (kg)	Location or Zone
P2460	10- 3-75	76	5.7	17
P2461	10- 3-75	79	7.7	17
P2462	10- 3-75	75	5.9	17
P2463	10- 3-75	75	6.6	17
P2464	10- 3-75	65	4.1	17
P2465	10- 3-75	71	4.8	17
P2466	10- 3-75	65	3.9	17
P2467	10- 3-75	75	5,2	17
P2468	10- 3-75	70	4,5	9
P2469	10- 3-75	81	7.6	9
P2470	10-17-75	79	7.0	17
P2471	10-17-75	71	5.0	17
P2472	10-17-75	82	6.6	17
P2473	10-17-75	72	5,3	17
P2474	10-17-75	81	7.7	17
P2475	10-17-75	65	6.2	17
P2476	10-17-75	70	4.3	17
P2477	10-17-75	64	6.8	17
P2478	10-17-75	87	8.6	17
P2479	10-31-75	67	4.2	17
P2480	10-31-75	71	4.9	17
P2481	10-31-75	67	4.5	17
P2482	10-31-75	73	5.8	17
P2483	10-31-75	69	4.5	17
P2484	10-31-75	74	6.6	17
P2485	10-31-75	73	5.9	17
P2486	10-31-75	73	6.0	17
P2487	10-31-75	73	5.8	17
P2488	10-31-75	82	7.5	17
P2489	10-31-75	86	8.9	17

APPENDIX A
Table 1. continued

Tag Number	Date	Eye-Fork Length (cm)	Weight (kg)	Location or Zone
P2490	10-31-75	82	8.6	17
P2491	10-31-75	73	5.3	17
P2492	10-31-75	62	3.7	17
P2493	10-31-75	73	6.2	17
P2494	10-31-75	86	8.7	17
P2495	10-31-75	78	7.0	17
P2496	10-31-75	72	6.0	17
P2497	10-31-75	68	3.7	20
P2498	10-31-75	78	6.2	20
P2499	10-31-75	69	5.2	20
P2500	10-31-75	79	6.7	25
P2501	6-26-75	78	6.7	10
P2502	6-26-75	89	11.3	10
P2503	6-26-75	78	7.9	9
P2504	7- 3-75	83	5.4	10
P2505	7- 5-75	94	14.3	17
P2506	7- 5-75	82	7.7	17
P2507	8-29-75	63	3.3	8
P2508	8- 5-75	64	3.7	20
P2509	8-13-75	63	4.3	20
P2510	8- 8-75	51	1.6	20
P2511	8-13-75	73	6.1	20
P2512	8-14-75	56	2.3	20
P2513	8-14-75	70	3.2	20
P2514	8-14-75	78	5.0	20
P2515	8-14-75	76	5.4	20
P2516	8-14-75	66	4.2	20
P2517	8-15-75	68	4.3	17
P2518	8-15-75	79	6.8	17
P2519	8-16-75	81	8.2	7

APPENDIX A
Table 1. continued

Tag Number	Date	Eye-Fork Length (cm)	Weight (kg)	Location or Zone
P2520	8-16-75	75	5.0	7
P2521	8-16-75	75	5.9	7
P2522	8-16-75	76	5.8	7
P2523	8-16-75	59	2.0	7
P2524	8-29-75	74	6.0	8
P2525	8-29-75	87	7.8	8
P2526	8-29-75	71	4.3	8
P2527	8-29-75	91	11.2	17
P2528	8-29-75	77	5.8	6
P2529	8-29-75	96	11.8	6
P2530	8-29-75	93	8.5	6
P2531	9- 4-75	83	9.8	16
P2532	9- 4-75	85	8.4	16
P2533	9- 4-75	71	4.9	16
P2534	9- 4-75	67	4.1	16
P2535	9- 4-75	68	4.1	16
P2536	9- 4-75	68	4.0	16
P2537	9- 4-75	75	6.1	16
P2538	9- 4-75	51	1.9	25
P2539	9- 4-75	65	4.0	25
P2540	9- 4-75	56	2.5	25
P2541	9- 4-75	71	4.5	25
P2542	9- 4-75	71	5.4	25
P2543	9- 4-75	61	3.1	25
P2544	9- 4-75	61	3.5	25
P2545	9- 4-75	62	3.1	25
P2546	9- 4-75	78	6.5	25
P2547	9- 4-75	79	7.0	25
P2548	9- 4-75	71	4.5	25
P2549	9- 4-75	64	3.9	25

APPENDIX A
Table 1. continued

Tag Number	Date	Eye-Fork Length (cm)	Weight (kg)	Location or Zone
P2550	9- 4-75	75	5.2	25
P2551	9- 4-75	71	4.9	25
P2552	9- 4-75	70	4.8	25
P2553	9- 4-75	81	6.0	25
P2554	9- 5-75	69	4.9	17
P2556	9- 5-75	74	6.1	17
P2557	9- 5-75	76	6.1	17
P2558	9- 5-75	77	5.8	17
P2559	9- 5-75	76	5.4	17
P2560	9- 5-75	86	8.7	9
P2561	9- 5-75	78	5.6	9
P2562	9- 5-75	74	6.2	9
P2563	9- 5-75	76	5.9	9
P2564	9- 5-75	62	3.6	9
P2565	9- 5-75	91	8.9	9
P2566	9- 5-75	81	7.5	9
P2567	9- 5-75	84	6.6	9
P2568	9- 5-75	69	4.3	7
P2569	9- 5-75	81	6.9	7
P2570	9- 5-75	86	8.7	7
P2571	9- 5-75	67	4.1	7
P2572	9- 5-75	79	6.4	7
P2573	9- 5-75	65	3.6	7
P2574	9- 5-75	73	5.4	7
P2575	9- 5-75	62	2.8	7
P2576	9- 5-75	65	3.5	7
P2577	9- 5-75	83	7.4	6
P2578	9- 5-75	72	7.6	6
P2579	9-12-75	74	6.7	Snyders Bend Lake, Iowa

APPENDIX A
Table 1. continued

Tag Number	Date	Eye-Fork Length (cm)	Weight (kg)	Location or Zone
P2580	9-12-75	80	9.1	Snyders Bend Lake, Iowa
P2581	9-12-75	66	4.8	Snyders Bend Lake, Iowa
P2582	9-12-75	78	7.5	Snyders Bend Lake, Iowa
P2583	9-12-75	65	4.5	Snyders Bend Lake, Iowa
P2584	9-12-75	72	6.0	Snyders Bend Lake, Iowa
P2585	9-12-75	81	8.1	Snyders Bend Lake, Iowa
P2586	9-12-75	67	7.5	Snyders Bend Lake, Iowa
P2587	9-12-75	75	6.4	Snyders Bend Lake, Iowa
P2588	9-12-75	71	5.4	Snyders Bend Lake, Iowa
P2589	9-12-75	83	8.3	Snyders Bend Lake, Iowa
P2590	9-12-75	74	7.5	Snyders Bend Lake, Iowa
P2591	9-12-75	67	5.4	Snyders Bend Lake, Iowa
P2593	9-12-75	71	5.6	Snyders Bend Lake, Iowa
P2600	9-18-75	89	10.3	25
P3001	5-21-76	73	6.7	17
P3002	5-21-76	65	4.5	17
P3003	5-21-76	69	5.9	17

APPENDIX A
Table 1. continued

Tag Number	Date	Eye-Fork Length (cm)	Weight (kg)	Location or Zone
P3004	5-21-76	79	9.1	17
P3005	5-22-76	74	6.8	17
P3006	4-22-76	67	5.2	20
P3007	4-22-76	77	6.4	20
P3008	4-22-76	67	5.2	20
P3009	4-22-76	62	3.9	20
P3010	4-22-76	69	4.8	20
P3011	4-22-76	70	4.9	20
P3012	4-22-76	65	3.7	20
P3013	6-16-76	66	5.0	17
P3014	6-16-76	71	5.9	17
P3015	6-16-76	76	7.6	9
P3016	6-16-76	76	6.8	9
P3017	6-16-76	83	8.2	9
P3018	6-16-76	78	6.5	9
P3019	6-16-76	57	3.2	9
P3020	6-16-76	66	5.1	9
P3021	6-16-76	65	4.5	9
P3022	6-16-76	83	8.2	14
P3023	6-16-76	76	8.2	14
P3024	6-16-76	79	8.1	14
P3025	6-16-76	67	5.0	14
P3026	6-16-76	72	6.6	14
P3027	6-16-76	78	7.9	14
P3028	6-16-76	72	6.0	14
P3029	6-16-76	62	4.4	14
P3030	6-16-76	77	7.1	14
P3031	6-16-76	78	6.8	14
P3032	6-16-76	55	2.5	14
P3033	6-16-76	78	7.2	14

APPENDIX A
Table 1. continued

Tag Number	Date	Eye-Fork Length (cm)	Weight (kg)	Location or Zone
P3034	6-16-76	74	5.9	14
P3035	6-16-76	68	5.0	14
P3036	6-16-76	57	3.3	17
P3037	6-16-76	63	3.7	17
P3038	6-16-76	75	7.8	17
P3039	6-16-76	78	8.4	17
P3040	6-30-76	69	5.0	17
P3041	6-30-76	73	5.9	17
P3042	6-30-76	63	3.2	17
P3043	6-30-76	76	6.2	17
P3044	8-10-76	76	5.7	16
P3045	8-10-76	71	4.8	16
P3046	8-10-76	73	5.7	16
P3047	8-10-76	73	5.2	16
P3048	8-10-76	87	7.4	16
P3049	8-10-76	66	4.1	16
P3050	8-10-76	83	7.0	16
P3051	8-10-76	83	6.8	16
P3052	8-10-76	87	9.1	16
03401	10-31-75	48	1.4	25
03402	10-31-75	69	4.9	25
03404	10-31-75	65	4.3	25
03405	10-31-75	73	6.0	25
03406	10-31-75	63	4.0	25
03407	10-31-75	64	3.7	25
03408	10-31-75	63	3.3	25
03409	10-31-75	68	5.2	25
03410	10-31-75	67	4.8	25
03411	10-31-75	71	5.6	25
03413	10-31-75	69	4.4	25

APPENDIX A
Table 1. Continued

Tag Number	Date	Eye-Fork Length (cm)	Weight (kg)	Location or Zone
03414	10-31-75	73	5.2	25
03416	10-31-75	72	5.4	25
03417	10-31-75	63	3.2	25
03418	10-31-75	84	8.9	25
03419	10-31-75	74	5.7	25
03420	10-31-75	77	5.9	25
03421	10-31-75	69	5.1	25
03422	10-31-75	60	3.0	25
03423	10-31-75	70	5.0	25
03424	10-31-75	62	3.4	25
03425	10-31-75	67	4.5	25
03426	11-13-75	70	5.0	25
03427	11-13-75	67	4.5	25
03428	11-13-75	65	5.3	25
03429	11-13-75	75	5.4	25
03431	11-13-75	70	5.3	25
03435	11-13-75	63	3.6	25
03443	11-13-75	71	5.3	25
03445	11-13-75	67	4.9	25
03447	11-13-75	71	5.1	25
03448	11-13-75	52	2.7	25
03449	11-13-75	66	4.7	25
03459	11-14-75	63	3.6	17
03476	11-13-75	63	4.3	25
03477	11-13-75	79	7.5	25
03478	11-13-75	68	4.1	25
03479	11-13-75	77	6.6	25
03480	11-13-75	49	2.0	25
03481	11-13-75	73	6.8	25
03482	11-13-75	78	7.5	25

APPENDIX A
Table 1. continued

Tag Number	Date	Eye-Fork Length (cm)	Weight (kg)	Location or Zone
03483	11-13-75	71	5.2	25
03484	11-13-75	67	4.5	25
03485	11-13-75	55	2.0	25
03487	11-13-75	57	2.7	25
03488	11-13-75	80	8.2	25
03489	11-13-75	60	3.2	25
03490	11-13-75	71	7.9	25
03491	11-13-75	76	6.2	25
03492	11-13-75	60	3.4	25
03493	11-13-75	83	7.5	25
03494	11-13-75	57	2.7	25
03495	11-13-75	66	4.1	25
03496	11-13-75	70	5.0	25
03497	11-13-75	67	4.4	25
03498	11-13-75	75	6.6	25
03500	11-13-75	80	7.9	25

APPENDIX A

Table 2. Recapture Data

Tag Number	Date Recaptured	Released Upon Recapture	Location or Zone
P2463	10-31-75	Yes	17
P2557	12- ?-75	?	Near Lexington, Missouri
P2493	12- 4-75	No	8
P2455	12-29-75	No	2
P2436	1-18-76	No	Near Whiting, Iowa
P2589	1-25-76	No	Near Onawa, Iowa
P2423	1-28-76	No	8
P2401	2- ?-76	No	Missouri River, Mile Marker 721
P2600	2-18-76	No	27
P2472	2-26-76	No	14
P2411	2-29-76	No	27
P2494	3- 7-76	No	25
P2556	3-17-76	?	80 km downstream from Kansas City, Missouri
P2445	4- 8-76	No	Missouri River, Mile Marker 709
P2513	4-25-76	No	Near Kansas City, Missouri
P3038	8-10-76	Yes	16