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MOVEMENT AND REPRODUCTION OF SHOVELNOSE STURGEON, SCAPHIRHYNCHUS PLATORYNCHUS (RAFINESQUE), IN THE MISSOURI RIVER SOUTH DAKOTA

by

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INTRODUCTION

The shovelnose sturgeon, Scaphirhynchus platorynchus, is one of the least known fishes in North America. The majority of North American freshwater fishes are annual spawners that mature in 2-5 years with a maximum longevity of 15 years. In contrast, most sturgeon do not mature until they are 10-20 years old and then spawn at intervals of two or more years. Life spans range from 20-30 years for the smaller sturgeon to over 100 years for the larger species.

Sturgeon are characterized by a long tapering snout, subconical in many but extremely depressed, broad and shovel-like in others. The body is long and subcylindrical and the flat ventral surface is usually white. The darker lateral and dorsal surfaces are armored with five longitudinal rows of large bony shields or scutes. The carinate scutes are strongly spined in young sturgeon but dull with age and may become completely embedded within the skin in the older fish of some larger species. Small dermal plates cover the body between the scutes. The head is protected by bony plates joined by sutures and the skeleton is mainly cartilaginous with a persistent notochord. A traverse row of four barbels is located anterior to the subterminal protractile mouth. The anal and dorsal fins are placed far back on the body, posterior to the abdominal pelvic fins. The pectoral fins are relatively large and situated near the ventro-lateral

border just behind the gill opening. The upper lobe of the heterocercal caudal fin terminates in a filament in some species.

Prior to 1950 there were only a few definitive studies on North American sturgeon, including the notable works of Ryder (1890), Harkness (1923) and Greeley (1937). Fisheries biologists therefore were forced to rely upon information on related species in the Russian and European literature. Research by Canadian scientists, especially Jean-Paul Cuerrier, Etienne Magnin, and George Roussow, spurred renewed interest in North American sturgeon in the early 1950's. The introduction of the fin ray technique for aging sturgeon by Roussow was a significant contribution (Cuerrier, 1951).

The 25 known species of sturgeon are distributed among four genera: Acipenser, Scaphirhynchus, Huso, and Pseudoscaphirhynchus (Harkness and Dymond, 1961). Both species of Scaphirhynchus and five species of Acipenser are indiginous to North America. Four of these seven are anadromous, two on each coast, while Scaphirhynchus and the lake sturgeon, Acipenser fulvescens, are restricted to fresh water. All three fresh-water species are found in the Mississippi basin. The shovelnose and pallid sturgeon, S. album, are confined to the Mississippi River and its larger tributaries, especially the Missouri River. The wide ranging lake sturgeon is found in three major North American drainage basins; the Mississippi, the Great Lakes and the

Hudson Bay.

The lake sturgeon is the best known North American sturgeon and references to this species were heavily utilized during this study. A monograph by Harkness and Dymond (1961) summarized the data on lake sturgeon and contained an extensive literature review. Age and growth studies on this species were reported by Cuerrier (1951), Cuerrier and Roussow (1951), Probst and Cooper (1955), Magnin (1966a), Royer et al. (1968), and Haugen (1969). Reproduction was studied by Barney (1924), Roussow (1957), Cuerrier (1966), and Magnin (1966b and c). The Wisconsin Department of Natural Resources has studied age, growth, and reproduction as they relate to managing the sturgeon sport fishery (Wirth, 1956; Priegel and Wirth, 1971). Information on food habits is included in some previously cited studies and an investigation on movement was published by Magnin and Beaulieu (1960).

The shovelnose sturgeon, also called the sand sturgeon, hackleback, or switchtail, has been found in every state along the Mississippi-Missouri-Ohio river drainage. At one time its distribution included the Ohio River eastward into Pennsylvania, the Rio Grande in New Mexico, the Platte westward into Wyoming, the Missouri into Montana, and several tributaries east of the Mississippi (Bailey and Cross (1954). A shovelnose was captured in the Tombigbee River in Alabama and was the first for that river but not for the state (Chermock, 1955). The shovelnose range is now

generally restricted to the Mississippi and Missouri rivers and the lower stretches of their larger tributaries. According to Trautman (1957) its distribution in Ohio is now restricted to the extreme western part of the state. All records from the Rio Grande and Platte rivers are very old. Reports, however, confirm its continued existence in tributaries of the Missouri River in Montana and the Red River basin in Texas and Oklahoma (Bonn and Kemp, 1952; Bailey and Cross, 1954).

The shovelnose sturgeon is one of the smaller sturgeon species. Rafinesque (1820, as cited by Bailey and Cross, 1954) reported weights up to 9 kg, but these were seriously questioned. Eddy and Surber (1943) stated that it rarely exceeds a length of 91 cm or 2.7 kg. The largest Ohio River shovelnose taken by Everman (1902) was a female, 74.9 cm long weighing 2.1 kg. The average length (method of measurement not given) and weight of the females was 64.5 cm and 1.5 kg; for the males 55.1 cm and 0.9 kg.

In the Mississippi River bordering Iowa and Illinois, Monson and Greenbank (1947) reported their four largest shovelnose were females between 78.7-81.3 cm fork length and averaging 2.7 kg. The mean weight of shovelnose collected from the Mississippi River was 600 g (Barnickol and Starrett, (1951). This included nearly 600 fish ranging in total length (tip of snout to base of caudal filament) from 35.6 to 86.4 cm. More recent Mississippi River collections included fish up to 12 years old and 73.7 cm fork length (Helms, 1973;

1974). In the Red Cedar-Chippewa River system (a tributary of the upper Mississippi) shovelnose ranged between 50.8 and 82.3 cm fork length and the largest sturgeon weighed 2.6 kg; about 50% of the fish collected were between 62 and 70 cm (Christenson, 1975).

In the late 1800's shovelnose sturgeon were considered a nuisance by commercial fishermen and many were intentionally destroyed. By 1900, however, they became commercially important. The roe, made into caviar, was highly prized and the "hog-dressed" fish made one of the most esteemed smoked fish products from the Mississippi River (Coker, 1930). Barnickol and Starrett (1951) reported a marked decrease in commercial catches between 1899 and 1946 (from about 84,825 to 13,600 kg - for Illinois, Missouri and Iowa) but recent catches reported from Iowa (Helms, 1972) have been as high as 27,200 kg.

Trautman (1957) and Harkness and Dymond (1961) indicated that sturgeon may be susceptible to overfishing because they mature late in life and grow slowly. In the Missouri River, Funk and Robinson (1974) suggested that overfishing contributed to the decline in shovelnose abundance, but they apparently believed that habitat changes associated with channelization had a greater impact. Barnickol and Starrett (1951) also cited habitat reduction and deterioration as a major factor causing the decline of shovelnose.

Shovelnose have a marked preference for lotic environments. Commercial fishermen usually fish main channel or

near-channel habitats and their larger catches of shovelnose are usually in areas with sand or gravel bottoms and substantial current. Schmulbach et al. (1975) and Kallemeyn and Novotny (1977) also found shovelnose abundance was highest in main channel and sand bar habitats in the Missouri River where current was substantial. Coker (1930) noted that a specimen captured in a slough of the Mississippi River near Keokuk caused excitement because few shovelnose were caught in habitats other than the main channel. The reduction of lotic environment in the Mississippi River by the lock and dam system for navigation, and the large main stem reservoirs on the Missouri River, has apparently impacted shovelnose abundance. Coker (1930) stated that shovelnose were virtually eliminated from Lake Keokuk on the Mississippi River because of their preference for current, while Barnickol and Starrett (1951) and Held (1969) suggested that siltation caused by channelization and damming has reduced both the quantity and availability of food used by shovelnose.

Declining catches of shovelnose were reported in the large main stem storage reservoirs on the Missouri River by Nelson (1961), Gasaway (1970), and Walburg (1964; 1977). The author, while working for NCRI* in the late 1960's, captured very few shovelnose within Lake Francis Case (Fort Randall Reservoir in South Dakota), but collected large numbers at the upper end of the reservoir near Chamberlain,

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*North Central Reservoir Investigations, Bureau of Sport Fisheries and Wildlife, Yankton, South Dakota.

South Dakota where the current increased. Construction of Missouri River dams has also prevented shovelnose from reaching traditional riverine spawning areas in at least one location (Walburg, 1977). The main stem reservoir system on the Missouri, completed in the late 1960's, now impounds over 1400 km of river, at full pool, leaving only 510 km of free-flowing river between Fort Peck Dam in Montana and Gavins Point Dam in southeastern South Dakota. Furthermore, only a relatively short 83 km section of unchannelized river exists downstream of Gavins Point Dam (the site for this study), since the Missouri River has stabilized banks or is channelized from Ponca, Nebraska downstream to its confluence with the Mississippi River near St. Louis, Missouri. This severe reduction in riverine habitat has been detrimental to the shovelnose and will continue to influence the abundance of this species in the future.

Sturgeon are usually aged using cross sections of the primary or marginal ray of the pectoral fin. Cuerrier (1951) described the technique and discussed the validity of the observed annuli. The fin-ray procedure has been successfully used for lake sturgeon (Cuerrier and Roussow, 1951; Probst and Cooper, 1955; Royer et al., 1968), white sturgeon (Pycha, 1956; Semakula and Larkin, 1968), and several other species (Cuerrier, 1951; Magnin, 1964).

In fin-ray sections from sexually mature sturgeon, there are several single annuli between periodic "belts" of closely

spaced annuli. The belts form during the several-year period prior to spawning when much of the available energy is diverted into the maturing gonads, and the widely spaced annuli are laid down for a few years after spawning as more energy is used for growth (Roussow, 1957). Therefore, in addition to ages a fin-ray section also provides information about the age at maturity (first annulus of the first belt), the age at first spawning (last annulus of the first belt), and the interval between spawning attempts.

The only age and growth data available for shovelnose sturgeon were reported by Fogle (1963), Zweiacker (1967), and Helms (1973;1974). Helms (1974) aged 110 shovelnose collected from the Mississippi River near Bellevue, Iowa; these fish ranged from 18.8 to 60.2 cm fork length and were assigned to age groups 0 through III. The assessed ages compared favorably with lengths determined by length-frequency distribution and age groups 0 and I could be identified using only length during most of the year. Mean fork lengths at time of capture were 22.6, 34.8, 48.0, and 55.9 cm for ages 0, I, II, and III, respectively. In additional collections Helms (1973) reported shovelnose up to 12 years old and more than 71 cm in fork length. Average calculated fork lengths at annulus formation ranged from 21 cm to 70.9 cm for shovelnose at 1 and 11 years of life, respectively. Growth rates decreased after the fourth year of life, apparently as fish attained sexual maturity.

Zweiacker (1967) and Fogle (1963) worked with shovelnose

in the Missouri River bordering South Dakota. Young fish were not collected in either study and length ranges were relatively narrow. Fogle (1963) aged 35 fish ranging from 45.7 to 58.4 cm total length. He assessed their age from 3 to 10 years old. Zweiacker (1967) aged 288 shovelnose that ranged from 8 to 27 years old and 48 to 55 cm fork length. Body length did not increase consistently with age for the Missouri River fish and neither Fogle nor Zweiacker were able to validate the marks interpreted as annuli. Unsuccessful attempts to age shovelnose sturgeon from the Chippewa River in Wisconsin (Christenson, 1975) were attributed to very slow growth of fish in the size ranges collected, and evidence suggests that slow growth also occurs in the Missouri River populations (Zweiacker, 1967).

Even though the literature on shovelnose sturgeon is conflicting or deficient in several respects, all previous investigations indicate that shovelnose spawn in the spring as do other sturgeon. Forbes and Richardson (1920) reported shovelnose spawning between April and June in the Mississippi River bordering Illinois. They thought that shovelnose ascended tributaries to spawn. In the Mississippi River near Keokuk, Iowa, Coker (1930) reported large numbers of shovelnose with eggs and milt flowing during mid-May. He noted that the end of the spawning season, or at least the declining phases, were demarked by the last shipments of caviar from local processors. In 1916, the last shipments were made around mid-June. Coker (1930) suggested that spawning occurs

on rocky bottoms in swift water. Commercial fishermen south of Dubuque, Iowa, reported shovelnose spawning during April and May (Barnickol and Starrett,1951). During this period males predominated in drift-net catches from the channel. The fishermen thought that females sought "cover" during this time and returned to the channel in June. These observations suggest that spawning may not occur in the main channel, or at least not in the stretch used by commercial fishermen.

More recent work in the Mississippi River bordering Iowa has confirmed spring spawning (Helms, 1972; 1973). Ripe males were collected during late May and gravid females were present in catches through mid-June. The first spent female, a positive sign of spawning activity, was observed in late May. Although Helms did not locate spawning areas he noted that shovelnose were seasonally abundant in tailwater areas of the lock and dams during May and June.

Further north in Minnesota and Wisconsin, spawning occurs in May and June (Eddy and Surber, 1943; Christenson, 1975). Eddy and Surber thought that shovelnose spawned in areas of rapid current and they observed large numbers of sturgeon during the spawning season at a dam on the St. Croix River near Taylor Falls, Minnesota. Christenson (1975) reported recently spent female shovelnose in late May and early June catches from the Red Cedar-Chippewa River System, but was unable to locate spawning areas. June (1977) was also unable to locate spawning grounds in the middle Missouri River but he suggested that, based on catches of ripe

individuals, spawning occurred over rock, rubble, and gravel bottoms. He reported peak spawning in mid-July.

Monson and Greenbank (1947) published the first information on the size of shovelnose at maturity. They determined that most females did not mature until they reached a fork length greater than 63.5 cm while 32% of the males less than 63.5 cm were mature. They conceded, however, that male maturity was difficult to determine. Barnickol and Starrett (1951) examined shovelnose from the same area (the Iowa-Illinois section of the Mississippi River). The smallest mature female was 63.5 cm while males reached maturity at 49.5-55.9 cm. Total lengths in this study were taken from the tip of the snout to the base of the caudal filament. Christenson (1975) reported similar results in the Chippewa River, Wisconsin, a tributary of the Mississippi River. The smallest mature male and female he collected was 56.1 cm and 62.7 cm in fork length, respectively. Helms (1972; 1973) concurred that males and females mature at about 55.9 and 63.5 cm, respectively, and provided the only age at maturity data known for shovelnose sturgeon. Males matured earlier than females; about 40% of age IV males were mature or developing while females spawned for the first time at age VII or older.

There is some evidence indicating that shovelnose sturgeon in the Missouri River mature at a smaller size than Mississippi River shovelnose. Zweiacker (1967) thought that all or most of the shovelnose he captured were mature, even

though several were only 43.2-48.3 cm in fork length. These Missouri River shovelnose were reported to be 8 to 27 years old, but the lack of known age fish and the narrow size range of fish in Zweiacker's collections prevented him from validating the ages. He found that shovelnose grew slowly but steadily up to about 50 cm fork length and then growth in length was very slow.

Shovelnose sturgeon are apparently opportunistic feeders, utilizing macroinvertebrates found in the benthos and drift. Shovelnose locate food with the sensory organs on the snout and barbels and the food items are sucked from the bottom with the protrusible mouth. Shovelnose reportedly use the rostrum to disturb the bottom when feeding (Forbes and Richardson, 1920).

Immature aquatic insects, including mayflies, dragonflies, caddis flies, and midge larvae form the bulk of their diet (Eddy and Surber, 1943; Barnickol and Starrett, 1951; Hoopes, 1960; Held, 1969; and Modde and Schmulbach, 1977). Held (1969) found immature aquatic insects in over 97% of the 75 Missouri River fish he collected in mid-June. Chironomidae larvae, primarily Tendipedidae and Heleidae, and mayfly naiads, primarily Baetidae, were the most important food items. Modde and Schmulbach (1977) examined Missouri River shovelnose collected throughout the year and reported the annual diet was dominated by Trichoptera (dragonfly), Diptera (chironomid), and Ephemeroptera (mayfly) immatures. They found that changes in water discharge rates at Gavins Point

Dam about 50 km upstream affected the availability and vulnerability of prey and suggested that seasonal feeding patterns were related to changing discharge rates from the main-stem reservoir. During October-January when discharges were decreasing, shovelnose utilized drift organisms. During this period 69% of the drift biomass consisted of caddis fly larvae. Through the winter when discharges were consistently low shovelnose preyed on a large variety of organisms, including the three major food items and odonate naiads, crustaceans, and terrestrial insects. During late spring and summer (May-September) discharges from the dam were high and shovelnose preyed on benthos, primarily chironomids. Shovelnose sturgeon in the Mississippi River also utilize aquatic insect larvae such as caddis fly larvae (Hoopes, 1960), dragonfly naiads (Eddy and Surber, 1943), and mayfly naiads (Barnickol and Starrett, 1951).

There is evidence that the shovelnose is an opportunist when the occasion arises. Both Held (1969) and Modde and Schmulbach (1977) observed utilization of terrestrial insects, and Held found a few stomachs containing large numbers of microcrustaceans, particularily cladocerans, indicating that these fish had apparently utilized zooplankton occasionally. During the present study I examined specimens in early summer and found a few stomachs full of isopods. Walburg et al. (1971) reported that shovelnose at Gavins Point Dam tailwaters about 50 km upstream of the study area also utilized isopods (Ascellus) heavily, apparently due to their availability.

The primary objective of this study was to provide additional life history information on the shovelnose sturgeon. The shovelnose, earlier in this century, was an important commercial species in the Mississippi River and it could regain much of its former importance if sufficient information becomes available for its proper management. Proper management is also a necessity to maintain shovelnose populations despite continuing encroachment by man on the large-river ecosystems vital to the shovelnose. The present research, therefore, was designed to furnish additional information on reproduction and movement of the shovelnose sturgeon.

METHODS AND MATERIALS

I. DESCRIPTION OF THE STUDY AREA

This study was conducted along 20 km of the Missouri River bordering Clay County in southeastern South Dakota (Figure 1). The study area is near the center of an 83 km segment of unchannelized river between Yankton, South Dakota and Ponca, Nebraska. The most downstream of six main stem Missouri River reservoirs (Lewis and Clark Lake behind Gavins Point Dam) is at Yankton, about 47 km upstream of the study area. From Ponca downstream to Sioux City, Iowa (42 km), the Missouri River has stabilized banks, and from Sioux City to St. Louis, Missouri, (1182 km) it is channelized.

The study area was arbitrarily divided into five sampling zones with the upstream boundry about 0.8 km upstream of Wildlife Landing (R53W, T92N, Sec. 18). The Wildlife Landing sampling zone (Section 1, Figure 1) extended downstream to Bow Creek and the Highline Landing zone (Section 2) encompassed the river from Bow Creek downstream to the tip of Goat Island. The Goat Island zone (Section 3) included the river on both sides of the large permanent island at the center of the study area. The Boat Club and Clay County Park Landings marked the upstream boundries of those two zones. Fishing success was usually better in the Wildlife, Boat Club, and Clay County Park zones than in the other two, so the former zones were used more heavily. Field work was conducted from mid-June to early November in 1968 and from mid-April to early

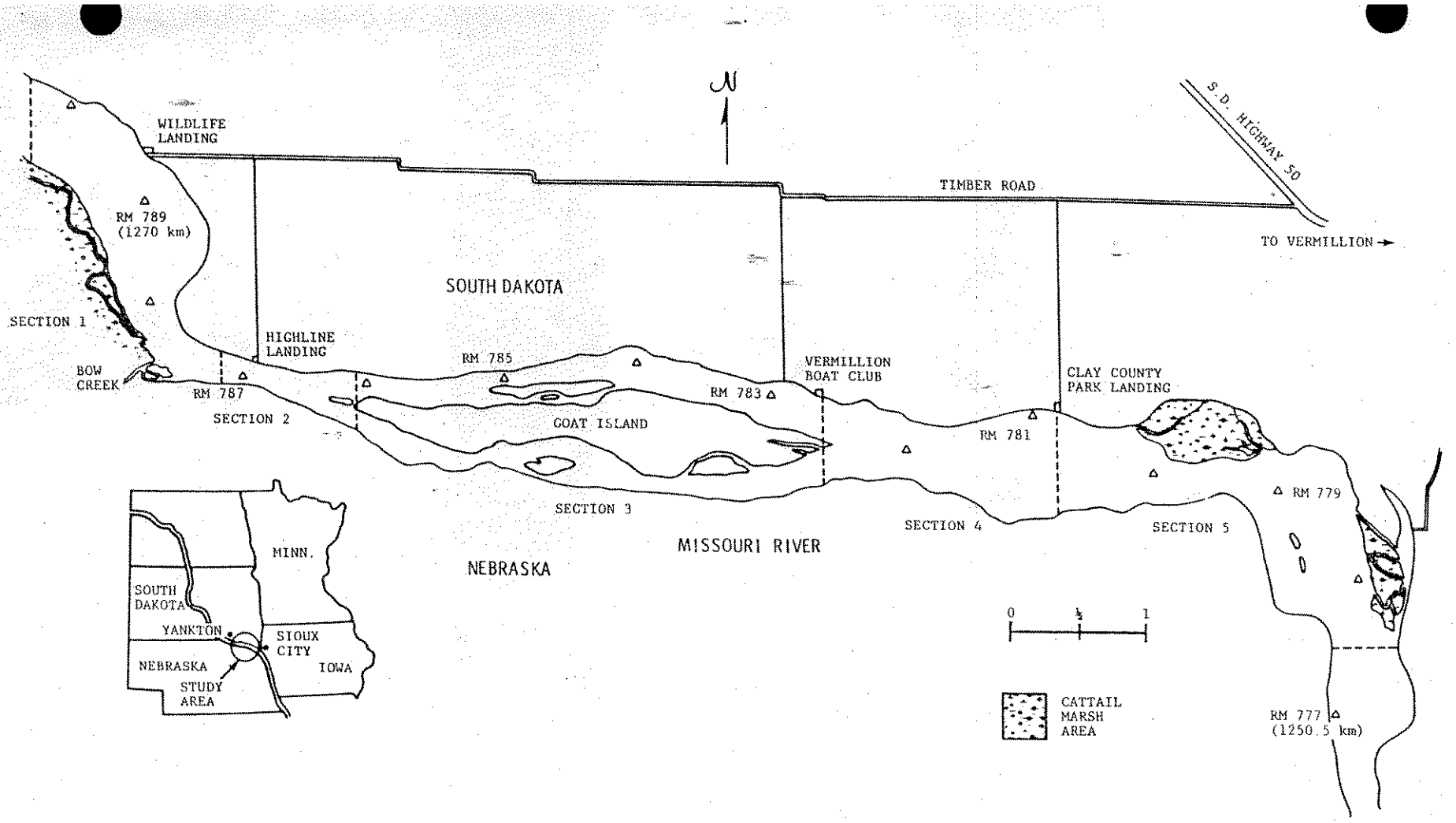

Figure 1. Map of the unchannelized Missouri River study area showing locations of boat landings, islands and marsh areas, and the five sampling sections.

December in 1969. Field work continued in 1970 under a separate grant but results from 1970, except for recapture data, were not used in this dissertation.

The unchannelized river between Yankton and Sioux City has an average width of 720 m and average flow velocity of 5.5 km/hr (Morris et al., 1968). During 1977, Kallemeyn and Novotny (1977) found widths in the unchannelized river below Gavins Point Dam ranged between 300 and 1500 m, and the stream gradient was approximately 0.2 m/km. Within the study area, width between normal high water levels rarely exceeded 1000 m and water more than 3 m deep was usually limited to narrow channels 3 to 10 m wide, immediately adjacent to each shore. An extensive series of sand bars impeded boat traffic in the central part of the river in most areas. The widest continuous expanse of open water (700-1000 m) was at Wildlife Landing. Unlike other wide sections, the channel here was near the center of the river with bar areas on each side. At Highline Landing, the narrowest portion within the study area, the river was 300 to 400 m wide.

Water depth throughout the study area rarely exceeded 7 m and was generally less than 2 m. Large backwater areas with marshes and shallow channels or chutes were present on the Nebraska shore opposite Wildlife Landing and on the South Dakota shore below Clay County Park (Figure 1). Main chutes in the backwater areas were 0.5 to 1 m deep; marsh areas were usually covered by 100 cm of water or less. Small backwater

areas were scattered along both shores. Backwater habitat formed 16% of the total aquatic habitat within the unchannelized river while the river proper (main channels and sand bars) accounted for 81% (Morris et al., 1968). The physical and chemical limnology has been described by Morris et al. (1968).

II. FIELD COLLECTING EQUIPMENT

A variety of fishing gear was used in order to adequately sample the various habitats and reduce problems associated with gear selectivity; gear included gill nets, trammel nets, set lines, one-half meter fry nets, a 220-volt AC electroshocker, a bag seine, and a 4.9 m otter trawl. During 1968 the more efficient gear, primarily gill nets, were heavily utilized to catch adult shovelnose for tagging. More emphasis was placed on locating young-of-the-year and immature sturgeon in 1969 and less efficient gear, such as the trawl and electroshocker, were used more frequently than in 1968. Even with this switch in emphasis, overall catch success per unit of effort was better in 1969. This was due mainly to experience with respect to where and when to set gill and trammel nets and which mesh sizes to use.

Nylon gill nets were 91.4 m long by 1.8 m deep. In 1968, three different mesh sizes were used (2.5 cm, 3.8 cm, and 6.4 cm bar measure), but each gill net had a single mesh size. In 1969, experimental gill nets donated by the South Dakota Department of Game, Fish and Parks were used. Each net had

six panels, and each panel was 15.2 m long; mesh sizes ranged from 1.9 cm to 6.4 cm (all mesh sizes are expressed as bar measure). In addition, a gill net with two 45.7 m long panels of 2.5 and 3.8 cm mesh was used in 1969. It was very difficult to maintain the condition of the nets since they were frequently snagged or sanded in. To compensate for this, records were kept when sections were torn and the recorded length of the net was decreased accordingly. Nylon trammel nets were also 91.4 m by 1.8 m, with an inner mesh of 5.1 cm and outer walls of 35.6 cm. Trammel nets were used only periodically because they were difficult to clean and less efficient for shovelnose than gill nets. Gill and trammel nets were set parallel with the current and anchored with cement blocks, when set in open channel areas, or a metal stake driven into the sand bar, when set in a hole downstream of a bar. Data obtained with each set included date, location, depth, duration of set, water temperature, type of net (including mesh size), and weather condition. Gill and trammel net catches were expressed on a catch-per-unit-effort (CPUE) basis. Since the average gill net set was about 20 hours, one unit of effort was defined as 91.4 m of net fished 20 hours.

Set lines were used for a short period in 1968 to sample deep fast-water areas inaccessable to the other gear. Each set line included 25 to 50 hooks at 30 to 60 cm intervals along the main line. These caught channel catfish more frequently than sturgeon. Considerable time was needed to procure bait and bait the hooks so use of this gear was

discontinued after a short trial period.

A 220-volt AC boat-mounted boom shocker was used to sample backwater channels in marsh areas, shallow sand bar areas in the river proper, and margins of the main channel. Electrofishing with uninterrupted AC current was generally conducted between sunset and midnight. The 4.9 m semi-ballon otter trawl was constructed from 3.8 cm mesh with a 0.6 cm mesh cod-end liner. Trawling was confined to back-water channels and main river channels. The trawl was pulled upstream, into the current, to keep the net open and maintain control in the fast current. A 9.1 by 1.8 m nylon bag seine, with a 0.6 cm mesh bag, was used to sample shoreline and backwater areas. Areas suitable for seining were limited since the shoreline usually dropped abruptly and backwater areas contained dense stands of cattails. This net consistently captured cyprinids and smaller individuals of some 20 different species, but no sturgeon.

During the 1968 field season, Namminga (1969) sampled macroscopic drift within the study area. Since his sampling techniques were suitable for collecting fish fry I analyzed his samples to monitor fish larvae. In 1969 I used the same gear and sampling technique, exclusively for fish fry. Namminga (1969) described the 0.5 m fry nets, the technique, and the locations sampled in 1968. Since no sturgeon fry were collected in the 110 surface and mid-water samples taken during August and September 1968, fry nets were used only intermittently during July and August in 1969. Sampling

dates and locations were selected so that areas which could potentially contain young sturgeon were sampled with drift nets while other gear was being used in the same area to collect mature sturgeon.

III. FIELD AND LABORATORY METHODS

Fish were placed in live tanks as they were removed from the nets. Live tanks consisted of 95 liter rectangular polyethylene containers (Regal Plastics, Model RT-31-20) fitted with overflow drains. River water was pumped into the tanks by a 12-volt DC submersible pump, mounted off the side of the boat. The two tanks, with lids on, also served as tables for tagging operations and as containers for transporting fish. Fish other than shovelnose were identified, counted and returned to the river after each net was fished. Recaptured shovelnose with secure tags were also released immediately after they were measured and weighed. Tagging was frequently conducted after each net was fished, or after all nets were fished if catches were small. However, if the weather was unsuitable for tagging or catches were very large, some or all sturgeon were transferred to a live box in the river or to the lab at Vermillion, South Dakota. In this case, shovelnose were usually tagged and released within a 24 hour period.

Total and fork lengths to the nearest millimeter, weight to the nearest quarter ounce (7 grams), general physical condition, tag number and type, date and location of capture, and date and location of release were recorded for each tagged fish. Since the sexes are similar, sex was determined only

for ripe males or gravid females. Fork length was considered as the distance from the tip of the snout to the posterior end of the shortest rays of the caudal fin, and was the principal length used for this study. Total length was measured from the tip of the snout to the end of the dorsal lobe of the caudal fin, excluding the caudal filament. Weights in the field were taken with a 1500 g capacity spring scale fitted with a scoop. This was suspended in front of the operator at eye level during use. Weights in the lab were taken with a 10.9 kg capacity Toledo commercial scale.

Shovelnose were tagged with monel metal strap tags (National Band and Tag Co., Newport, Kt.; size 1, 3, or 4) or plastic dart tags (Floy Model FT-6). During most of 1968, size 4 monel bands were clamped over the posterior edge of the operculum. Control fish tagged in this manner were held for three months in lab holding tanks and then released because tags were firmly in place and the sturgeon exhibited normal behavior. However, during October and November 1968 several recaptured shovelnose exhibited considerable tissue erosion around the tags and a few had obviously sloughed the tag. In October, I switched to plastic dart tags or size 1 monel tags. Time consuming precautions were necessary to get the small monel tags to crimp correctly over the opercle and they were difficult to see, so less than 100 shovelnose were tagged with size 1 bands.

After considerable experimentation, plastic dart tags were inserted by hand through a small incision made at the

lateral trailing edge of one of the overlapping dorsal scutes, about midway between the head and the dorsal fin. The barb was pushed between overlapping scutes into the epaxial muscles and then twisted so the barb would hook on the anterior edge of a scute. To reduce infection, scalpel and tags were soaked in a 2% Lysol solution prior to use. Plastic dart tags were used in the fall of 1968 and throughout spring and summer 1969. In summer 1969, however, some tags could be easily removed from recaptured shovelnose, suggesting that many tags did not remain hooked over the anterior edge of the scute. Then in October 1969, shovelnose which had lost the dart tag appeared among the recaptures.

In October 1969, I tried monel strap tags again, but this time clamped size 3 tags over the anterior margin of the pectoral fin about 1 cm from the juncture of the fin with the body. This technique required less time than tagging with dart tags or monel bands on the opercle, and produced a smaller wound. The pectoral fin tag was used throughout the rest of the study and proved to be the most enduring tag. Some of these tags remained on sturgeon for more than eight years.

Tagged fish were usually released in the vicinity where captured, or at the boat landing nearest the point of capture. Some, however, were transported to other areas to check on homing tendencies. Correspondence with state Fish and Game officials, conversations with local fishermen, and newspaper articles alerted the public to the tagging study. Recaptures reported by fishermen were limited but this was expected since

shovelnose were taken only incidentally by sport fishermen. Most recaptures were obtained by University of South Dakota personnel during normal field operations.

All shovelnose transferred to the lab were placed in outdoor holding tanks containing aerated tap water. The redwood or galvanized metal tanks had capacities ranging from 870 to 2,000 liters. Very few problems were encountered in holding shovelnose; they were hardy and withstood handling and temperature differentials very well. Some experimental fish were held for three months without feeding with no difficulty.

Subsamples of the catch, usually 25 to 50 shovelnose per month, were sacrificed for information on morphology and reproduction. These were selected randomly on an unscheduled basis depending on catch success. The total catch for the day or random samples were usually taken until the monthly quota was met. Unusually large and small shovelnose and those exhibiting injuries or abnormal morphology were frequently included. Shovelnose in good condition were sometimes held for a few days before being sacrificed, but injured or dead fish were processed immediately.

Earlier observations indicated that the length of the caudal filament was quite variable so, as previously noted, it was excluded from the total length. When the subsampled sturgeon were processed, caudal filament length was recorded separately, to the nearest millimeter, along with standard, fork and total lengths. Standard length and scute counts were made as suggested by Bailey and Cross (1954). Weight

was taken on a Toledo scale to the nearest quarter ounce (7 grams) and converted to grams. The length of the inner and outer barbels, to the nearest millimeter, was the distance from the posterior edge of their bases to the apex. Snout or rostrum measurements were taken with a caliper to the nearest 0.01 ml. Snout length was taken as the distance from the tip of the snout, along the midline, to the anterior cartilaginous edge of the buccal depression. Snout width was taken along the plane of greatest width. The marginal ray of the left pectoral fin was removed, and placed in a numbered coin envelope and saved for future age and growth studies. Some stomachs, including the esophageal portion (Held, 1969), were also removed and preserved in 10% formalin for future research.

Internal organs were exposed by making a mid-ventral incision from the anus forward through the pectoral girdle. Sex and maturity, determined by visual examination, were recorded according to Zweiacker's (1967) descriptions. Both gonads were removed and weighed to the nearest 0.01 g on an Ohaus Dial-O-Gram (Model 310) balance, prior to fixation. In 1968, gonads were fixed and stored in 10% bufferred formalin while in 1969 they were fixed in cold Bouin's solution and later transferred to 70% ethanol for storage. Gonads from all sturgeon processed during 1968 and 1969 were retained, and in spring 1970 stages of maturity were reassigned based on histological studies and original sex designations were checked.

One or three segments were taken from each gonad for embedding. Single segments were removed from the middle of the gonad, but when three segments were removed they came from the anterior, posterior, and middle regions. The gonad material was dehydrated using 70%, 90%, and absolute ethanol (formalin preserved tissue was first rinsed in cold tap water and then dehydrated in 30 and 50% ethanol) and cleared in xylene or benzene. Paraffin embedding was conducted under partial vacuum. Serial sections, both cross and transverse, were cut at 8-10 u and stained with Delafield's hemotoxylin and eosin or Mallory's triple stain. Larger mature ova were difficult to section and good serial series were rarely obtained. A Russian technique for dehydrating and embedding mature ova, discovered after the present histological studies were completed, is recommended for future work (Lemanova and Nusenbaum, 1968).

The diameter of spermatocytes, oogonia, nuclei, etc. and the thickness of egg membranes were measured from material fixed in Bouin's and stained with haematoxylin and eosin, using a calibrated micrometer eyepiece. Measurements of oocytes and egg membranes were taken from the largest section of that particular structure in the series. When the oocyte or nucleus was oval in outline the diameter recorded was the average of the shortest and longest diameters. All photomicrographs were taken with a Bausch and Lomb Dynazoom Photobinocular microscope.

Diameters of oocytes were also determined from whole

oocytes teased from preserved ovaries. Eggs were removed from a small section of the ovary and placed in a petri dish, then measurements were made with a micrometer eyepiece mounted in a binocular dissecting microscope. Prior to measuring, the oocytes were scanned under low power and 5 to 10 of the largest oocytes from each ovary were selected because the objective, in this case, was to determine the size of the largest eggs in each reproductive stage.

Seasonal variation in gonad size was estimated by calculating the gonosomatic index (GSI = gonad weight X 100/body weight).

Abundance of shovelnose sturgeon at different sampling locations and between seasons was compared by quantifying gill net catches on the basis of equal effort. Catch-per-unit-effort (CPUE) for gill nets was defined as the number of fish collected in 91.4 m (300 ft) of net set for 20 hours (average duration of all sets was about 20 hours).

An important aspect of growth is the relationship between length and weight. If form and specific gravity remain constant, this relationship may be expressed by the equation (Ricker, 1958):

$$W = \alpha L^{\beta}$$

where W is weight in grams
L is fork length in centimeters
α and β are empirically derived constants

A regression analysis was performed on the logarithms of the lengths and weights to estimate the parameters α and β, and illustrate similarities between sexes, reproductive stages,

and seasons, with respect to length-weight relationships. Length-weight regressions were also used to compare shovelnose sturgeon from the Missouri, Mississippi, and Ohio rivers. The relative well-being or plumpness of shovelnose sturgeon collected during different seasons or from different localities was compared by calculating the condition factor using the formula (Lagler, 1956):

$$K_{FL} = W \times 10^3 / L^3$$

A preliminary estimate of the number of shovelnose sturgeon within the study area was obtained from tagging and recapture data, using the formula:

$$P = \sum m\ (u + r) / \sum r$$

where P is the population estimate
m is the number of marked fish in the population
r is the number of marked fish recaptured from the population
u is the number of unmarked fish collected along with the marked fish

A Monroe Epic 3000 desk calculator and IBM 1120 computer were used for most computations and programs for CPUE, length-weight relationships, and condition factors were written by the author.

RESULTS AND DISCUSSION

I. DESCRIPTION OF MISSOURI RIVER SHOVELNOSE STURGEON

Between June 1968 and December 1969 over 4800 shovelnose sturgeon were captured by gill and trammel netting, trawling, trot lining, and electrofishing. Stationary gill and trammel nets were more effective than other capture techniques and were used extensively. Shovelnose numerically accounted for 67% of the fish captured in gill and trammel nets and some samples contained only sturgeon, especially when nets were set in pools just downstream of sand bars adjacent to the main channel (Table 1). Goldeye, sauger, redhorse, channel catfish, and carpsuckers were the species most frequently captured with sturgeon. Only one pallid sturgeon and one paddlefish were caught during the study, primarily because my nets were not suitable for catching these large fish. Pallid sturgeon are far less abundant than shovelnose in the Missouri River (Bailey and Cross, 1954) while paddlefish are considered relatively abundant in the unchannelized Missouri River (Rosen, 1976). Channel catfish and blue suckers were common associates of shovelnose in mid-channel areas and pools adjacent to the channel, while carp, smallmouth and largemouth buffalo, shortnose gar, and gizzard shad were abundant in nets set in backwater areas. Schmulbach et al. (1975) and Kallemeyn and Novotny (1977) have described the relative abundance of fishes within different habitat types of both

Table 1. Classification, number, and percent composition of fish collected in 184 gill net and 38 trammel net samples from an unchannelized section of the Missouri River, southeastern South Dakota, June 1968-December 1969. Most samples were collected from the main channel or behind sand bars adjacent to the main channel.

Scientific Name	Common Name*	Number Caught	Percent Composition
ACIPENSERIDAE	STURGEON		
Scaphirhynchus platorynchus	Shovelnose sturgeon	4801	67.3
Scaphirhynchus albus	Pallid sturgeon	1	<0.1
POLYODONTIDAE	PADDLEFISH		
Polyodon spathula	Paddlefish	1	<0.1
LEPISOSTEIDAE	GAR		
Lepisosteus osseus	Longnose gar	17	0.2
Lepisosteus platostomus	Shortnose gar	87	1.2
CLUPEIDAE	HERRING		
Alosa chrysochloris	Skipjack herring	4	<0.1
Dorosoma cepedianum	Gizzard shad	34	0.5
HIODONTIDAE	MOONEYE		
Hiodon alosoides	Goldeye	1064	14.9
ESOCIDAE	PIKE		
Esox lucius	Northern pike	25	0.4
CYPRINIDAE	MINNOWS		
Cyprinus carpio	Carp	45	0.6
Hybopsis spp.	Chubs	5	<0.1
CATOSTOMIDAE	SUCKERS		
Carpiodes spp.	Carpsuckers	218	3.1
Cycleptus elongatus	Blue sucker	141	2.0
Ictiobus bubalus	Smallmouth buffalo	23	0.3
Ictiobus cyprinellus	Bigmouth buffalo	21	0.3
Moxostoma spp.	Redhorse	171	2.4
ICTALURIDAE	FRESHWATER CATFISH		
Ictalurus furcatus	Blue catfish	1	<0.1
Ictalurus nebulosus	Brown bullhead	3	<0.1
Ictalurus punctatus	Channel catfish	163	2.3
PERCICHTHYIDAE	TEMPERATE BASS		
Morone chrysops	White bass	3	<0.1
CENTRARCHIDAE	SUNFISH		
Lepomis macrochirus	Bluegill	1	<0.1
Pomoxis annularis	White crappie	2	<0.1
Pomoxis nigromaculatus	Black crappie	1	<0.1
PERCIDAE	PERCH		
Perca flavescens	Yellow perch	3	<0.1
Stizostedion canadense	Sauger	274	3.8
Stizostedion vitreum	Walleye	22	0.3
SCIAENIDAE	DRUM		
Aplodinotus grunniens	Freshwater drum	5	<0.1
TOTAL		7136	100 %

*Common names according to American Fisheries Society (Bailey et al., 1970).

unchannelized and channelized sections of the Missouri River.

A. SPATIAL AND SEASONAL DISTRIBUTION

The study area included a variety of habitats ranging from deep channels with velocities exceeding 1m/sec to shallow standing water in cattail marshes. The main channel usually coursed along one or both sides of the river flood plain and the central portion was festooned with exposed sand bars and sand flats covered with 10-150 cm of water. Sand bars were common wherever the channel curved and the morphometry of pools below sand bars frequently changed as sand bars shifted with changing discharge rates. Small side channels were common in areas separated from the main channel by sand bars and small islands, and 2-6 m wide chutes penetrated each cattail marsh. Habitat types have been described in more detail by Kallemeyn and Novotny (1977).

Considerable time was spent sampling diverse habitats for sturgeon. Shovelnose were never taken from shallow, quiet-water habitats by seining or electrofishing, and trawling in chutes within marshes was also unproductive. The only sturgeon caught in a marsh area was collected by electrofishing in an open-water chute about 1 km downstream of Clay County Park Landing (Figure 1). Coker (1930) noted that when a shovelnose was captured in a Mississippi River slough near Keokuk, Iowa, it generated excitement because sturgeon normally were caught only in the main river. Based on electroshocking catches during the present study, shovelnose are also rare in the broad, shallow sand flats that

covered a large portion of the lower Boat Club and Clay County Park sampling sections.

Trawling in the main channel was restricted to areas where current was slow enough to permit an effective tow speed (trawls were pulled upstream so gear could be drifted back off snags). During August and September 1969 when most trawling was done, only eight shovelnose were caught in 30 trawl samples. Deep (> 6 m) main channel areas with fast current velocities were never sampled effectively with a trawl. A few gill nets were set parallel with the current in deep fast water where large snags were available for anchoring the net, but these sets contained few fish of any species. The rapid current (mean velocity 1.5 m/sec; Morris et al., 1968) probably reduced the efficiency of the net. Trot lines baited with worms were tried in July 1968 and five sets (20 to 48 hooks per set) caught three shovelnose. Trot lines, however, were abandoned because of the time required to secure bait and set the lines, and the catch was mostly channel catfish.

Gill and trammel nets set in pools behind sand bars, and in relatively deep open-water areas adjacent to the main channel, were by far the most productive. Shovelnose were most abundant in pools 1.8 to 4.6 m deep and catches usually decreased as water depth and velocity increased. Pools behind sand bars were usually shallow (< 1.5 m) for 3 to 9 m downstream of the bar but then deepened rapidly to 3 m or more. Catch per unit effort (CPUE) for nets with the upstream

(shallow) end in 0-3 m of water and the downstream (deep) end at 1.8-4.6 m ranged between 18.1 and 19.8 (Table 2). Nets set in shallow water (< 1.8 m) and deep sets (upstream end of net at 3.3-4.6 m and downstream end at more than 6 m) caught very few sturgeon. Shovelnose apparently prefer intermediate currents found in pools or open water areas adjacent to the main channel. Kallemeyn and Novotny (1977) reported a mean current velocity of 0.5 m/sec for sand-bar pools and velocities between 0.3 and 1.2 m/sec in main channel border habitats. Barnickol and Starrett (1951) used trammel nets in the Mississippi River and indicated that shovelnose sturgeon were most common over a sand or gravel bottom in the presence of some current. Mississippi River commercial fishermen fish dam tailwaters heavily for sturgeon but also use stationary or drifting trammel-net sets in the main channel and adjacent habitats (Helms, 1972).

The mean CPUE for the Missouri River study area was 18.4 sturgeon per set (Table 3). The Vermillion Boat Club section had the highest mean CPUE (23.5) while the Highline Landing section had the lowest (13.6). One of the most reliable fishing locations within the study area, a pool behind a stable sand bar just downstream of Goat Island, was found in the Boat Club section and was fished whenever this section was sampled. Less frequent sampling of this section during August and September when sturgeon catches were small throughout the study area also contributed to the high mean CPUE for this section. The Highline Landing section was narrow

Table 2. Catch per unit effort (CPUE) of shovelnose sturgeon as a function of water depth in the unchannelized Missouri River, South Dakota, June 1968-December 1969.

	Water Depth (m)	Number Samples	Total Number Sturgeon	Average Sample Duration (h)	CPUE*
Shallow end of net	0 -1.5	154	2452	20.7	18.1
	1.8-3.0	125	2175	20.2	19.3
	3.3-4.6	5	2	20.4	0.6
	Total	284	4629	20.5	18.4
Deep end of net	0 -1.5	16	31	18.1	3.5
	1.8-3.0	199	3423	19.9	19.8
	3.3-4.6	58	1080	22.8	19.1
	4.9-6.0	7	85	21.9	14.2
	>6.0	4	10	21.0	2.2
	Total	284	4629	20.5	18.4

*CPUE = number of sturgeon caught in 91.4 m (300 ft) of net set for 20 h.

Table 3. Catch per unit effort (CPUE) of shovelnose sturgeon captured by gill nets at five sampling sections in the unchannelized Missouri River, June 1968-December 1969.

Sampling Zone	Number Samples	Total Number Sturgeon	Average Sample Duration (h)	CPUE*
Wildlife landing	94	1503	19.7	18.6
Highline landing	12	121	19.8	13.6
Goat Island	20	382	23.6	19.9
Vermillion Boat Club	57	1287	22.0	23.5
Clay County Park Landing	101	1336	19.8	15.4
Total	284	4629	20.5	18.4

*CPUE = number of sturgeon caught in 91.4 m of net set for 20 h.

(300-400 m) and the relatively deep (5-8 m) main channel occupied most of the flood plain. Very few sand bars and associated pools were present.

The Wildlife and Clay County Park sections contained the greatest variety of habitats. Sand bar pools and channel border areas suitable for gill netting were abundant, but many sand bars were unstable. Since the habitats were diverse and often transitory, more exploratory fishing occurred in these two sections. This probably contributed to the smaller average catches for these two sections in comparison to the Boat Club and Goat Island sections (Table 3). The smaller CPUE at Clay County Park in comparison with Wildlife Landing may have been a sampling artifact resulting from proportionally heavier sampling at Clay County Park during August and September 1968, when few sturgeon were captured anywhere in the study area.

Shovelnose sturgeon were readily captured by gill nets during April through June and again during October through early December (Table 4). Winter weather, ice cover, and low water levels precluded sampling during the winter. Shovelnose catches were high from April through June, then declined markedly in July. Very few sturgeon were captured during August and September. Decreasing catches were apparently related to increasing water temperatures. During both 1968 and 1969 water temperatures peaked at 24°C during the third week in July, remained above 20°C through August, and gradually decreased to approximately 16°C by the end of

Table 4. Catch per unit effort (CPUE) of shovelnose sturgeon captured by gill nets during seven sampling periods, from the unchannelized Missouri River, South Dakota, June 1968-December 1969.

Sampling Period	Number Samples	Total Number Sturgeon	Average Sample Duration (h)	CPUE*
April-May	21	422	23.9	20.1
June	38	816	18.5	27.2
July	47	421	14.6	13.2
August	39	193	19.5	6.2
September	38	218	21.9	6.1
October	53	1126	23.7	23.3
November-December	48	1432	22.9	29.8
Total	284	4629	20.5	18.4

*CPUE = number of sturgeon caught in 91.4 m of net set for 20 h.

September (Figure 2). During early October water temperatures began decreasing rapidly and sturgeon catches increased. Chi Square analysis indicated that something other than chance caused differences in the CPUE among months (X^2=30.52, df=6).

Increased movement during the spring spawning season probably contributed to high June catches. Mid-June samples during both years contained an unusually large percentage of male shovelnose. This probably indicated that spawning activity had commenced, because Cuerrier (1966) and Helms (1972) observed a predominance of male sturgeon in catches just

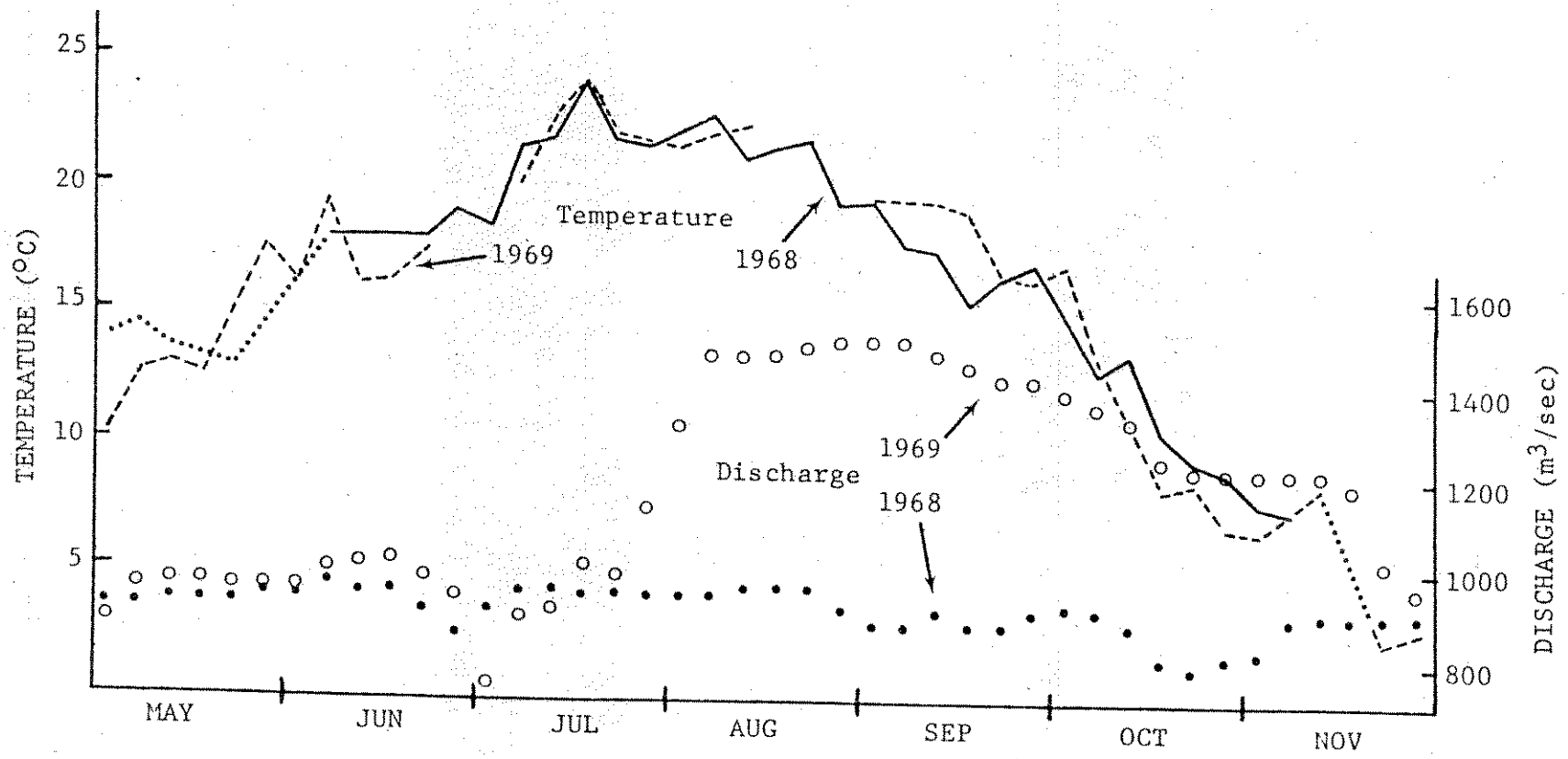

Figure 2. Water temperatures in the Missouri River study area during 1968 and 1969, and discharge rates from Gavins Point Dam 47 km upstream of the study area. Data points represent averages of 5-day time periods and dotted line sections indicate when water temperatures were estimated using data from Gavins Point Dam.

prior to and during the spawning season. High catches during the fall (October and November) were probably related to cooling water temperatures when sturgeon began concentrating in pools behind sand bars. Studies of seasonal movement patterns for several fish species have revealed distinct spring and fall peaks in movement similar to that observed for shovelnose. For example, Holt et al. (1977) found that mean daily movements of walleye in Lake Bemidji were longest in spring and fall and shortest in summer. They attributed these activity changes to water temperature and food availability. Largemouth and smallmouth bass, white sucker, and northern pike also exhibit spring and fall movement peaks (Cleary and Greenbank, 1954; Warden and Lorio, 1975).

During late November and early December, when water temperatures declined below 4°C, shovelnose were concentrated in pools behind sand bars and apparently exhibited little movement. Gill nets were lifted slowly and carefully because many shovelnose were caught only by one or two spiny projections on the scutes or rostrum, and were not "gilled" as they normally were in spring and fall.

Exploratory fishing during July, August, and September failed to locate any concentration of sturgeon. Trawling, electrofishing, and seining along shorelines, within marshes (in chutes), and on shallow sand flats during these months was unproductive. Low August and September catches may result from sturgeon moving into deep regions of the main channel in search of food or preferred temperatures. I was,

however, unable to effectively sample deeper sections of the main channel because of the abundant snags, fast current, and uneven bottom contours. Shovelnose in the Mississippi River are also seasonally scarce during mid-summer. Commercial fishing activity is highest during the May-June spawning season in dam tailwater areas bordering Iowa, then catches decline until late summer (Helms, 1972). The literature Harkness and Dymond (1961) reviewed suggested that lake sturgeon move into deep water during the summer.

Variations in discharge rates from Gavins Point Dam may also influence seasonal movements of shovelnose sturgeon. During 1969, discharge rates increased rapidly in late July and remained high through August and September (Figure 2), exhibiting a negative relationship with gill net CPUE (Table 4). Modde and Schmulbach (1977) also observed high summer discharge rates during 1971-72 and suggested that the increased velocity of the water mass may reduce accessibility of food items. Perhaps low summer catches were related to dispersal of sturgeon during this period when shovelnose are feeding primarily on benthic organisms. During 1968, discharge rates from Gavins Point Dam were fairly uniform through the year. Although summer catches of sturgeon were low in 1968, there was not as much difference between spring and summer catch rates in 1968 as there was in 1969.

B. LENGTH, WEIGHT, AND EXTERNAL MORPHOLOGY

Missouri River shovelnose sturgeon fell within a narrow range of lengths and weights (Figures 3 and 4). In 1969, fork lengths for 132 males ranged from 37.2 to 58.3 cm ($\bar{x}$ = 49.9 cm) while the range for 126 females was 40.8 to 60.2 cm ($\bar{x}$ = 51.2 cm). Weights ranged between 149 and 822 g for males ($\bar{x}$ = 436.3 g) and between 220 and 1021 g for females ($\bar{x}$ = 474.9). The larger mean length and weight of females could be due to a faster growth rate than males, but for other species of sturgeon most authors believe females are larger, on the average, because females live longer and thus grow bigger than males. Most studies have detected no significant growth rate differences between sexes in lake sturgeon or other North American species of sturgeon (Probst and Cooper, 1955; Magnin, 1962; Haugen, 1969). Conversely, Sunde (1959) found that female lake sturgeon in the Saskatchewan River Delta grew faster than males after age 20, about the age when females attain sexual maturity. A longer life span for females, however, is common for sturgeon. Harkness and Dymond (1961) reviewed the literature on this, citing several dramatic examples. In Lake Winnebago, Probst and Cooper (1955) found more lake sturgeon males than females in all total length classes up to 49 inches (approx. 20 years old) but more females than males as length increased beyond this. Females comprised 95.8% of the lake sturgeon between 152 and 200 cm. In three other lakes in the same area, females accounted for about 50% of the catch up to 150 cm

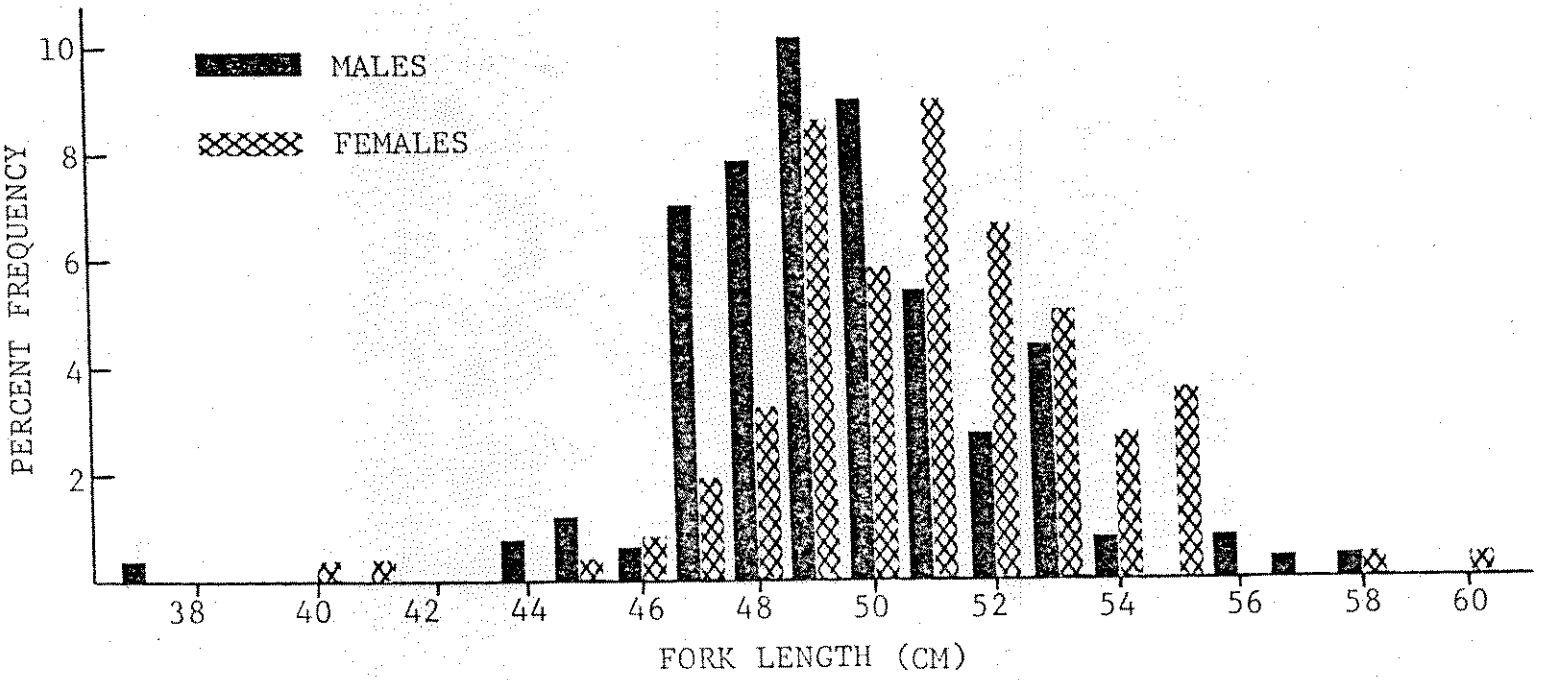

Figure 3. Fork length frequencies of 258 shovelnose sturgeon from the unchannelized Missouri River, 1969.

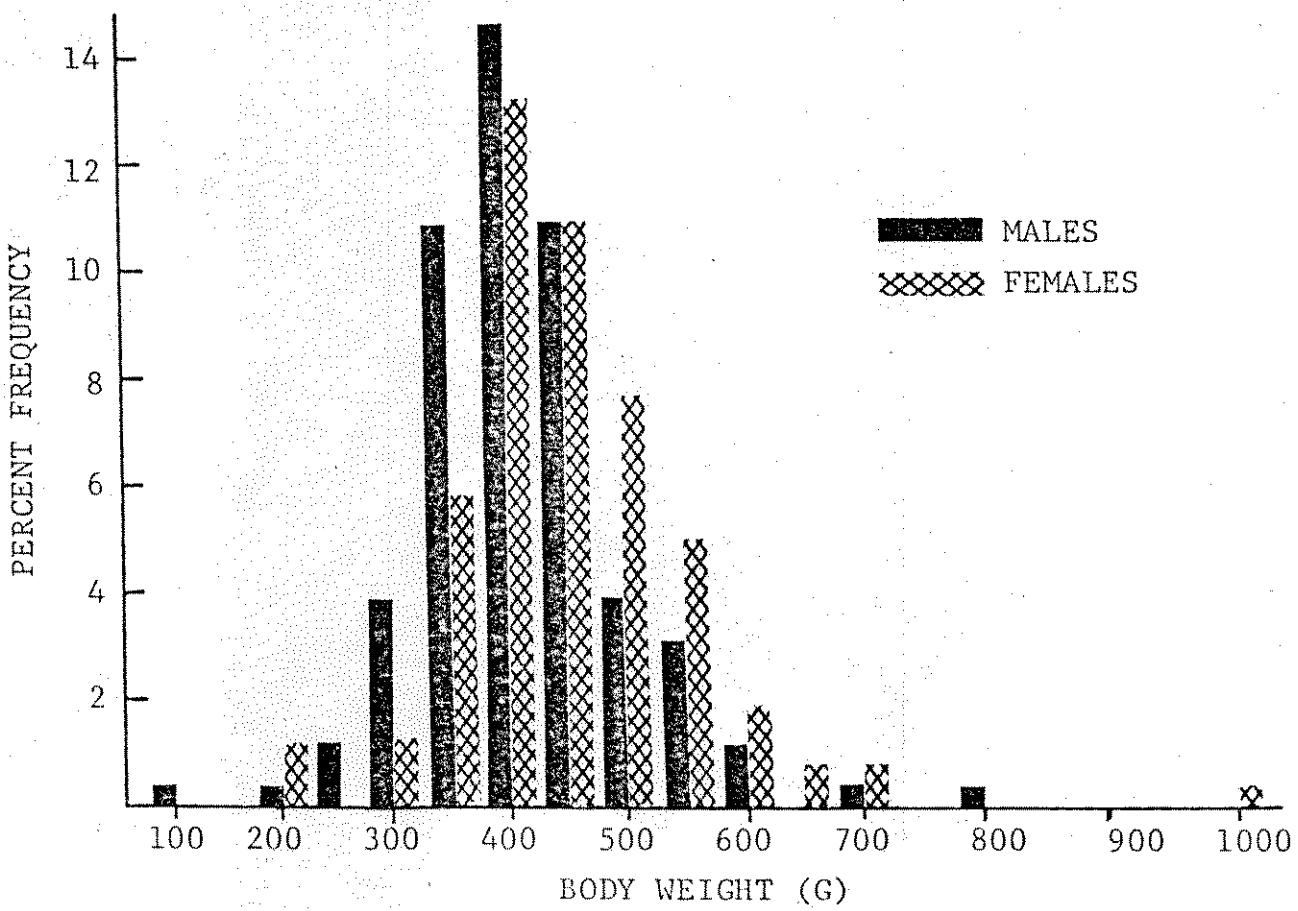

Figure 4. Body weight frequencies of 258 shovelnose sturgeon from the unchannelized Missouri River, 1969.

total length, but 95% of the sturgeon larger than 150 cm.

In the 1969 processed subsample (Figures 3 and 4), 76.8% of the shovelnose had fork lengths within a 6 cm range (47-53 cm) and 71.4% fell into a 200 g weight range (300-499 g). Since subsampling was not entirely random, this narrow size range might imply a biased sample. A few sturgeon were selected rather than randomly drawn for processing because of net damage, unusual size (both large and small), or external abnormalities. However, when the size distributions of the 1969 subsample were compared with length and weight frequencies for all shovelnose captured in 1968, the distributions were similar (Table 5). In 1968, 74.5% of the shovelnose were within the 47 to 53 cm fork length range and 75.4% weighed between 300 and 499 g. If the ranges are increased to 10 cm (47-57 cm) and 400 g (300-699 g) from 92 to 96% of the shovelnose were included. Only two shovelnose less than 40 cm were taken during the two years of field work. These were both immature males, 35.4 and 37.2 cm fork length weighing 191 and 148 g, respectively. Of 563 shovelnose processed in 1968 and 1969 there were only five shovelnose less than 44 cm. Large shovelnose were also poorly represented in 1968 and 1969 subsamples, with only six longer than 60 cm. The largest shovelnose taken during this study was a giant compared to the rest. Surprisingly this was a male, 73 cm fork length weighing 1786 g. The next largest fish was a female which weighed 1304 g and was 65 cm long.

This unusually narrow size range suggested gear

Table 5. Comparison of length and weight frequencies for the total catch of shovelnose sturgeon collected during 1968 with a subsample of the 1969 catch from the Missouri River, South Dakota. Numbers of fish are expressed as a percentage of the total in that group.

Fork Length Class (mm)	Percent Distribution 1968 (N=1554)	Percent Distribution 1969 (N=258)	Weight Class (g)	Percent Distribution 1968 (N=1554)	Percent Distribution 1969 (N=258)
≤449	0.6	1.9	100-199	0	0.4
450-469	4.7	2.8	200-299	2.6	2.7
470-489	20.9	19.8	300-399	30.6	21.8
490-509	31.1	33.4	400-499	44.8	49.6
510-529	22.5	23.6	500-599	16.9	19.7
530-549	12.5	12.8	600-699	3.7	3.9
550-569	4.8	4.2	700-799	0.9	1.1
570-589	1.7	1.1	800-899	0	0.4
590-609	0.7	0.4	900-999	0.3	0
≥610	0.5	0	≥1000	0.2	0.4

selectivity, or the possibility that small immature and larger mature sturgeon were distributed in habitats not sampled adequately during this study (e.g., tributary streams). However, a limited size range was anticipated because of previous research on shovelnose in the unchannelized Missouri River (Zweiacker, 1967), so a variety of gear was used to reduce selectivity and considerable effort was expended searching for large and small sturgeon. Moreover, the numerous spiny projections on the scutes and rostrum of sturgeon make them susceptible to gill and trammel nets and reduces the size selectivity of these gear (Cuerrier and Roussow, 1951).

Of the seven types of gear used, the gill and trammel nets were most efficient. Mesh sizes ranged from 1.9 to 6.4 cm bar measure and shovelnose beyond the size range of those captured are susceptible to these mesh sizes. The mean total length of shovelnose taken from the Mississippi River with 3.8 cm trammel nets was 64.8 cm (Starrett and Barnickol, 1955). More importantly, the size range was 21 to 79 cm. In contrast, the mean total length of shovelnose from 3.8 cm gill nets used during this study was 52.7 cm. A 5.1 cm bar mesh trammel net used by Starrett and Barnickol (1955) yielded a higher average length (68.1 cm) but did not increase the size range. The average total length of Missouri River shovelnose from the same gear (5.1 cm trammel net) was 53.8 cm. Gill nets with 6.4 cm mesh used during this study captured shovelnose sturgeon with mean total length of 53.6 cm, less than 1 cm longer than the mean length in 3.8 cm mesh gill nets. While the mean total length indicated that 6.4 cm gill nets did not catch appreciably larger shovelnose than 3.8 cm nets, a substantially lower catch rate for the 6.4 cm nets (CPUE of 2.6 for the 6.4 cm nets vs 21.9 for the 3.8 cm nets) indicated that the 6.4 cm mesh was too large to effectively sample the Missouri River shovelnose population. Upstream of the study area, experimental gill nets with panels ranging from 1.9 to 8.9 cm bar mesh were fished in the tailwaters of Gavins Point Dam by the U. S. Fish and Wildlife Service from February 1968 through January 1969 (Walburg et al., 1971). The shovelnose sturgeon was eight in relative

abundance among 29 species caught and the largest was 72 cm in total length. Although the mean total length from their catches was 59.1 cm,* they included the caudal filament in the total length measurement and this could inflate their average length by 3 cm or more. Collective evidence indicates that the mesh sizes used during the present study were adequate for collecting sturgeon over a wider size range than apparently occurs in the Missouri River. Certainly, comparable gear captures larger shovelnose in the Mississippi River.

The characteristics of the remaining gear used in this study were more suitable for capturing smaller shovelnose than gill and trammel nets. However, none of the shovelnose taken by other gear, with the exception of one fry captured in a 0.5 m plankton net, were smaller or larger than those captured in gill and trammel nets. In conclusion, length and weight frequency distributions presented in Figures 3 and 4 and Table 5 are presumably representative of the shovelnose population in this section of the Missouri River.

The two species of Scaphirhynchus, the shovelnose and pallid sturgeon, have a slender filament extending from the upper lobe of the caudal fin. Bailey and Cross (1954) included the filament in caudal fin measurements but indicated that it was commonly broken. Barnickol and Starrett (1951) excluded it from their total length measurements. Filament length was extremely variable for shovelnose captured during

*Length data supplied by Mr. Gerald L. Kaiser, North Central Reservoir Investigations. U. S. Fish and Wildlife Service, Yankton, South Dakota.

the present study and was excluded from total length measurements (Table 6). The longest caudal filament observed was 14.0 cm. It was more frequently broken on large than small shovelnose, but a fragment of varying length remained on many individuals. The author recommends that filament length be excluded from the total length and measured separately if desired. This is especially true when length-weight relationships and condition factors are calculated on a total length basis. Its inclusion in this case may add several centimeters to the length with no effect on weight.

The relationships between standard, fork, and total lengths of Missouri River shovelnose were constant throughout the size range and exhibited almost no difference with respect to sex (Figure 5). Conversion factors for these three lengths were calculated by regression analysis of 254 shovelnose processed in 1968. The conversion equations for lengths in millimeters are:

$$F.\ L. = 11.55 + 1.05\ (S.\ L.)$$
$$T.\ L. = 34.49 + 1.12\ (S.\ L.)$$
$$T.\ L. = 24.02 + 1.06\ (F.\ L.)$$

Standard length was the distance from the anterior tip of the rostrum to the posterior end of the last carinate scute of the lateral series (Bailey and Cross, 1954). Total length was the distance from the anterior tip of the rostrum to the tip of the dorsal lobe of the caudal fin, excluding the caudal filament. Fork length was the distance from the rostrum tip to the notch in the caudal fin.

Scute counts in the dorsal, lateral, and ventrolateral

Table 6. Lengths of caudal filaments for 253 shovelnose sturgeon collected from the unchannelized Missouri River, South Dakota, during 1968.

Fork Length Class (mm)	Number of Fish	Filament Length (mm)		
		Mean	Minimum	Maximum
410-419	1	39.0	—	—
440-449	2	16.5	8	25
450-459	3	21.7	18	29
460-469	6	34.8	10	64
470-479	21	33.2	0	64
480-489	30	22.1	0	88
490-499	27	24.8	0	104
500-509	42	29.4	0	115
510-519	39	22.3	0	72
520-529	27	22.2	0	60
530-539	17	32.1	13	71
540-549	16	15.4	0	34
550-559	10	20.5	0	32
560-569	5	7.0	0	19
570-579	3	29.0	12	40
600-609	1	5.0	—	—
610-619	2	1.0	0	2
650-659	1	12.0	—	—
Total	253	24.6	0	115

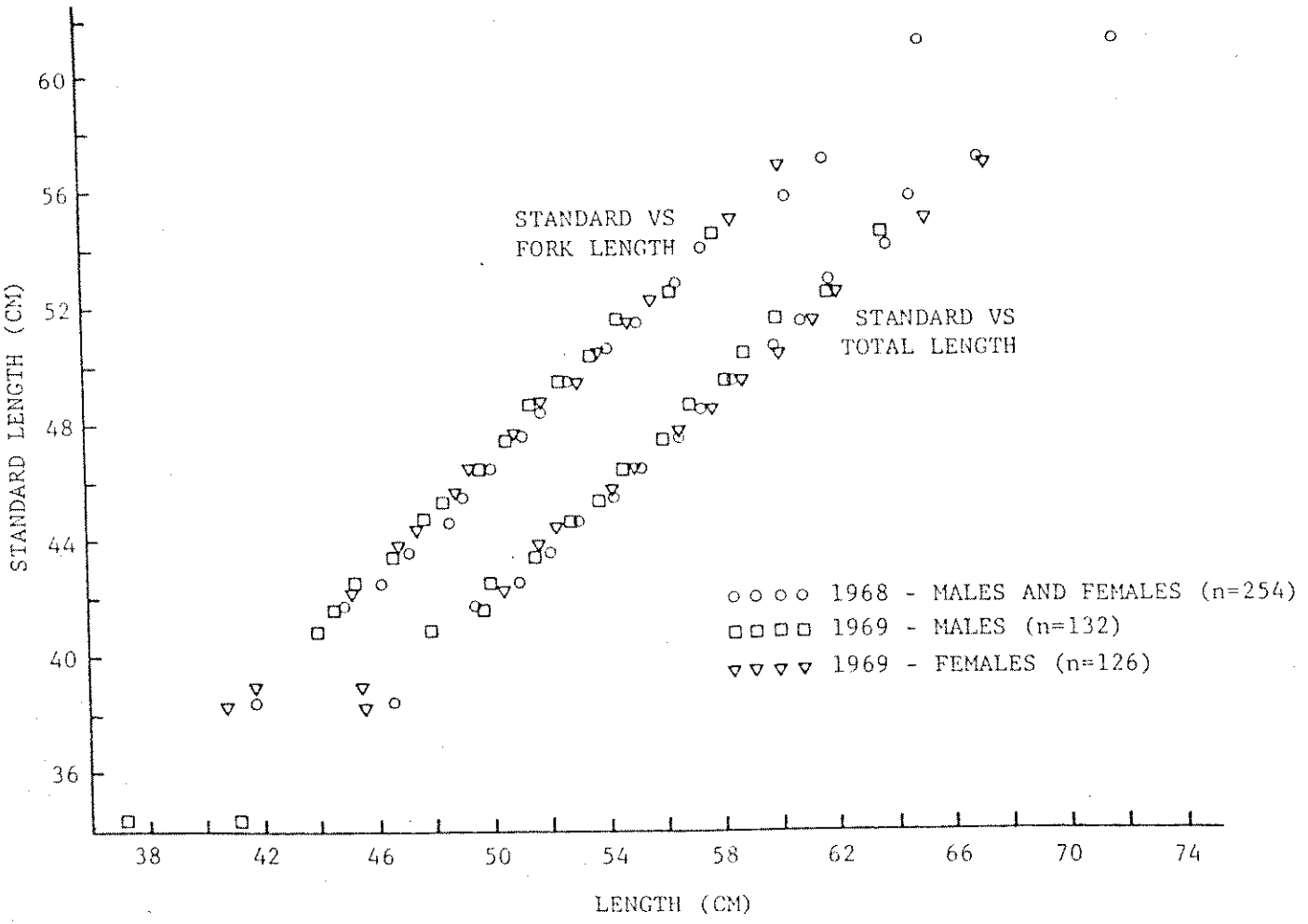

Figure 5. Relationships between standard, fork, and total lengths in shovelnose sturgeon collected in the unchannelized Missouri River. Data points represent means for 10 mm standard length groups.

rows obtained during the present study and those reported by Bailey and Cross (1954) indicated that scute counts cannot be used to distinguish between shovelnose and pallid sturgeon (Table 7). However, inner barbel length and the ratio of outer to inner barbel length are reliable characteristics for distinguishing shovelnose from pallid sturgeon. The mean rostrum width and length were both slightly larger in female than male shovelnose, but like other morphological characteristics, ranges in the two sexes overlapped extensively (Table 8).

Length-weight relationships were computed from the logarithmic transformation of the exponential function, $W = cL^n$, where W = weight in grams and L = fork length in centimeters. The equation $Log_{10}W = -3.243 + 3.458\ Log_{10}FL$ for 512 shovelnose collected during 1968 and 1969 adequately describes this relationship for the Missouri River population. Since length-weight relationships may be different for males and females, and may change temporally, separate length-weight relationships were computed for various subsamples (Table 9). Subsamples of males and females were selected from both the 1968 and 1969 processed fish. Subsamples, including both processed and tagged fish, were selected in May, July and November of 1969 to check seasonal variations. The fish in each seasonal subsample were caught within a four day period. The length-weight relationships were similar for all subsamples (Table 9). If weights for a hypothetical 50 cm sturgeon, which is near the mean fork length for Missouri River shovelnose, are

Table 7. Scute counts and proportional barbel lengths of shovelnose and pallid sturgeon. Barbel lengths are expressed as a percentage of standard length.

	Present Study		Bailey and Cross (1954)			
	Shovelnose Sturgeon (N=115)		Shovelnose Sturgeon (N=51)		Pallid Sturgeon (N=15)	
	Range	Mean	Range	Mean	Range	Mean
Scute Counts						
Dorsal	13-18	15.8	14-19	16.0	14-18	15.5
Lateral	38-49	43.4	38-47	43.1	40-48	44.3
Ventrolateral	9-14	11.5	10-14	11.6	9-13	11.2
Barbel Length						
Inner	4.9 -9.2	6.2	5.3 - 8.2	6.5	3.7 - 5.0	4.5
Outer	6.8 -9.9	8.2	6.2 -10.8	8.6	7.4 -11.4	8.7
Outer/Inner Ratio	0.74-1.61	1.32	1.17- 1.48	1.34	1.32- 2.41	1.98

Table 8. Comparison of rostrum measurements between male and female shovelnose sturgeon collected from the unchannelized Missouri River, South Dakota, during 1968-1969.

	Rostrum Width (mm)	Rostrum Length (mm)	Rostrum Ratio (W/L)
Males			
Number	76	76	76
Mean	6.13	7.17	0.86
Range	5.22-7.19	6.05-8.99	0.72-0.96
Females			
Number	61	61	61
Mean	6.43	7.28	0.88
Range	5.17-7.25	6.14-8.54	0.79-0.97

Table 9. Length-weight relationships and coefficients of condition (K_{FL}) for shovelnose captured in the unchannelized Missouri River in southeastern South Dakota, June 1968-December 1969.

Groups	Number of Fish	Mean Weight (g)	Mean Fork Length (cm)	Length-Weight Relationship	Condition Factor* (K_{FL})	Calculated Weight of 50 cm (FL) Shovelnose Sturgeon (g)
Processed shovelnose 1968-1969 combined	512	456.2	50.8	$\text{Log}_{10} W = -3.243 + 3.458 \text{ Log}_{10} FL$	3.48	429
Males-1968	63	446.9	50.3	$\text{Log}_{10} W = -2.863 + 3.238 \text{ Log}_{10} FL$	3.51	435
Females-1968	58	510.8	52.2	$\text{Log}_{10} W = -2.869 + 3.241 \text{ Log}_{10} FL$	3.59	434
Males-1969	116	456.9	50.2	$\text{Log}_{10} W = -2.987 + 3.313 \text{ Log}_{10} FL$	3.60	438
Females-1969	111	485.3	51.5	$\text{Log}_{10} W = -2.781 + 3.189 \text{ Log}_{10} FL$	3.55	434
May 1969	89	451.1	50.2	$\text{Log}_{10} W = -2.378 + 2.956 \text{ Log}_{10} FL$	3.57	441
July 1969	42	448.9	50.9	$\text{Log}_{10} W = -2.475 + 3.000 \text{ Log}_{10} FL$	3.40	419
November 1969	107	467.3	51.4	$\text{Log}_{10} W = -2.499 + 3.018 \text{ Log}_{10} FL$	3.45	425

*$K_{FL} = \frac{Wt. \cdot 10^3}{FL^3}$, where FL = fork length in cm and Wt. = body weight in g.

calculated using those equations, the calculated weights range from 419 to 441 g; less than a one ounce spread (Table 9).

Like length-weight relationships, the coefficients of condition, or relative plumpness, of Missouri River shovelnose were very similar for males and females (Table 9). There was a slight change in condition factors on a seasonal basis, probably reflecting changes in weight due to maturation of gonads and subsequent release of the sex products, and perhaps seasonal changes in feeding. Male shovelnose lose about 4% of their weight after spawning while most females lose 12-15%. Condition factors for the separate reproductive stages show these changes clearly (Table 10). Condition factors increased as shovelnose approached spawning condition (developers to pre-spawners to spawners) and then decreased abruptly after spawning occurred. Modde and Schmulbach (1977) indicated that shovelnose coefficients of condition were also affected by seasonal feeding patterns. They found lowest condition factors during late summer and early fall when shovelnose were foraging on benthic organisms. However, coefficients of condition increased during late fall and winter as decreasing flow rates apparently increased the vulnerability of drift organisms, and subsequently the sturgeon ration biomass.

During the study, abnormal external features were observed on several sturgeon. In many cases abnormalities were obviously caused by physical damage from which the

Table 10. Coefficients of condition for shovelnose sturgeon from the unchannelized Missouri River, South Dakota, showing changes in condition with respect to reproductive stages and sex.

Reproductive Stage	Number of Fish		Mean Fork Length (cm)		Mean Weight (g)		K_{FL}***	
	Male	Female	Male	Female	Male	Female	Male	Female
Developing*	24	79	49.2	51.5	403	471	3.38	3.45
Prespawning**	29	39	49.8	51.3	438	512	3.55	3.79
Spawning	52	29	50.3	52.1	464	543	3.65	3.84
Spent	14	38	50.8	51.1	450	440	3.43	3.30

*Mature shovelnose that will not spawn during the next spawning season. This stage contains new recruits to the mature population and adult sturgeon that have spawned previously but are now in a resting phase.

**Mature shovelnose captured in the fall that will spawn the following spring.

***K_{FL} = Weight x $10^3/FL^3$.

shovelnose had recuperated. For example, the anterior end of the rostrum was mutilated and subsequently healed on several shovelnose captured during 1968 and 1969. Four shovelnose were captured with no caudal fin. In each case the caudal peduncle terminated just posterior of the anal fin. Although this was assumed to result from accidental injury it could have been a developmental abnormality. The anal fin in these fish apparently was a functional substitute for the missing caudal fin; one of these fish was recaptured 26 km upstream 168 days after it was tagged and released at Wildlife Landing.

Missing dorsal scutes was another common abnormality. Although two or three scutes were absent on a few individuals the most common condition was a single missing scute, usually the seventh but sometimes the sixth or eighth. This condition might have resulted from a developmental abnormality, but the sixth, seventh, and eighth scutes are susceptible to damage because they are located dorsally at the place of greatest body depth.

The most unique abnormality observed was one-eyed sturgeon. Twelve of 5129 sturgeon collected between June 1968 and July 1970 had epidermal tissue covering one eye. In one individual the skin covering was incomplete and an apparently normal eye was visible through the small opening. The left eye was more commonly covered than the right eye (Figure 6). No histological sections were made but portions of the covered eye probably had atrophied. Pigmentation over the covered eye was generally lighter than normal pigmentation

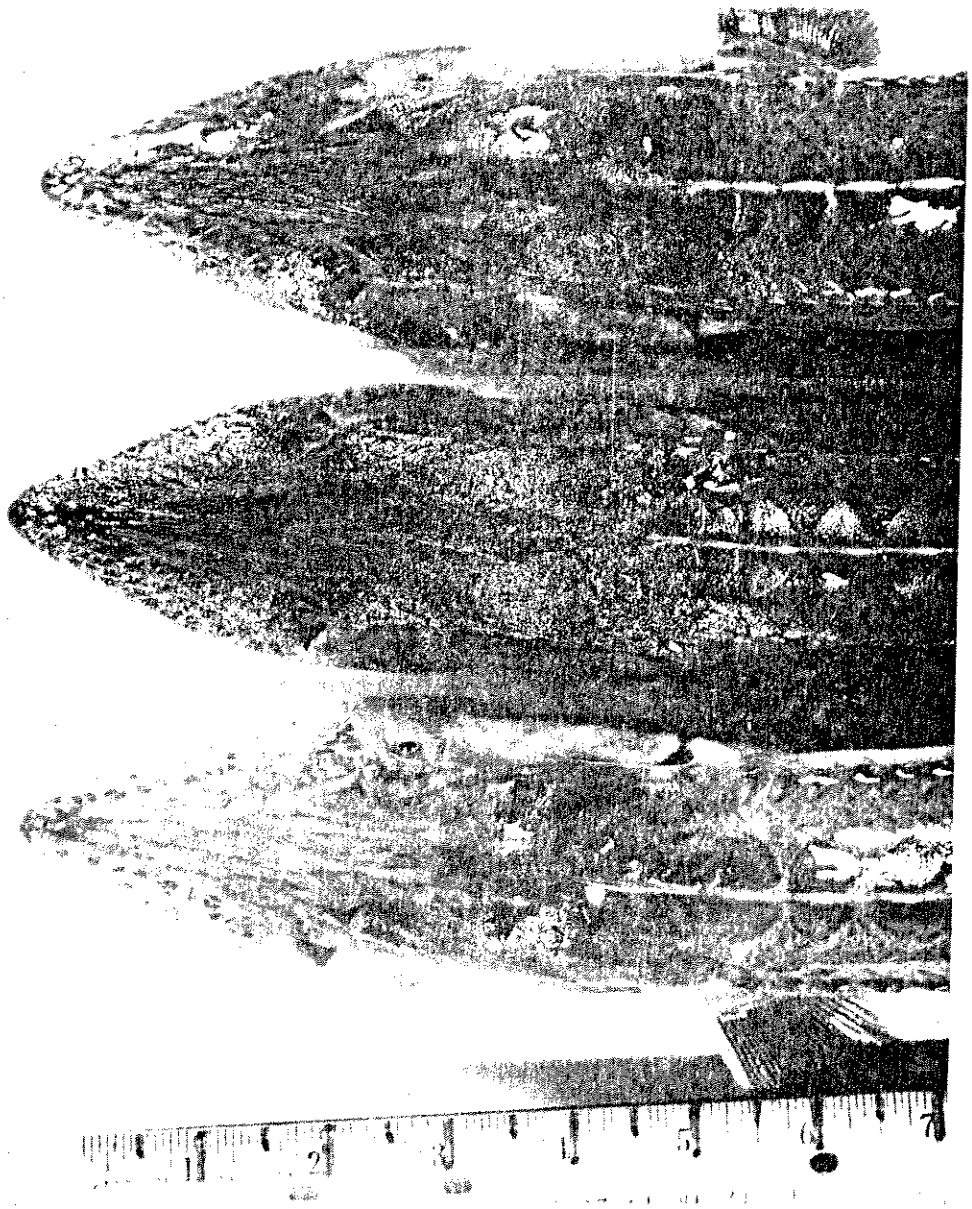

Figure 6. Photograph of three shovelnose sturgeon with "covered" left eyes, collected from the unchannelized Missouri River in southeastern South Dakota during 1969.

on the head. Although this condition was observed in fewer than 0.3% of the sturgeon collected, it is quite possible that a few one-eyed sturgeon were missed because the eyes are small.

C. MISSOURI, MISSISSIPPI, AND OHIO RIVER SHOVELNOSE

A comparison of the physical characteristics of shovelnose sturgeon from the Ohio, Mississippi, Chippewa (a tributary of the Mississippi), and Missouri rivers indicated that shovelnose collected from the Missouri River study area in South Dakota:

a) have a mean length and weight which is less than those from the Ohio, Mississippi, and Chippewa rivers.

b) have a lower condition factor than sturgeon in the Ohio and Mississippi rivers.

c) reach sexual maturity at smaller lengths than shovelnose in the Mississippi and Chippewa rivers.

d) apparently grow slower than shovelnose from the Ohio and Mississippi rivers.

Length-frequency distributions from three studies on the Mississippi River and similar data from the Ohio and Chippewa rivers were compared to the length-frequency distribution of 1554 shovelnose collected from the Missouri River during 1968 (Figure 7). The narrow length range of the Missouri River population contrasts sharply with the wider length ranges of the Ohio and Mississippi River sturgeon. It is also apparent that Missouri River shovelnose are smaller since the modal length was around 50 cm, compared to modal lengths of 53 to 66 cm for shovelnose from other rivers.

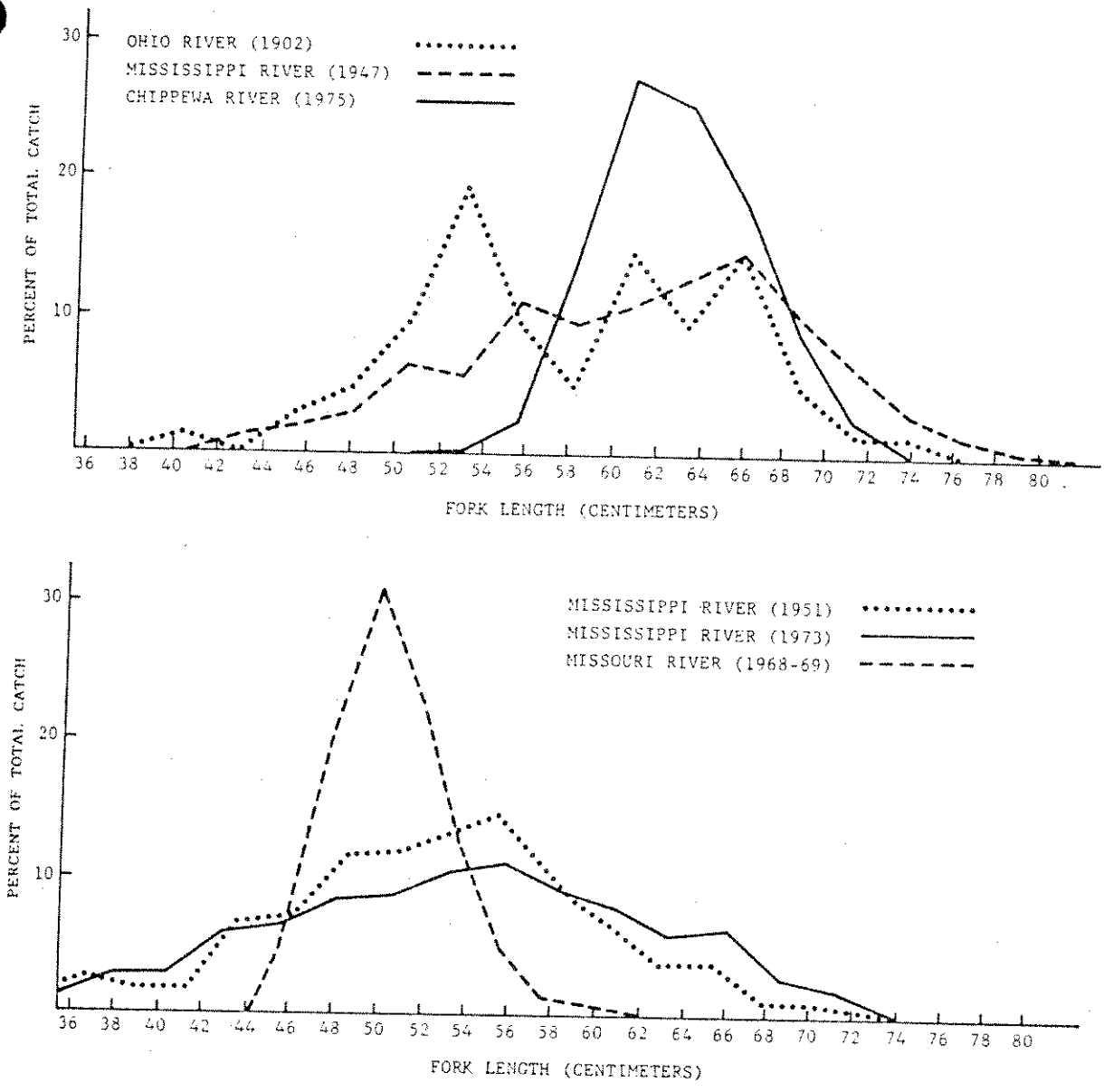

Figure 7. Length-frequency distributions of shovelnose sturgeon collected from the Ohio, Mississippi, Chippewa, and Missouri Rivers. Trace values not shown; data from Barnickol and Starrett (1951) was converted using FL = (TL - 2.402)/1.06.

Mississippi River - Monson and Greenbank (1947); n = 877.
- Barnickol and Starrett (1951); n = 310.
- Helms (1973); n = 635

Ohio River - Everman (1902); n = 62

Chippewa River - Christenson (1975); n = 952.

Missouri River - 1968 and 1969; n = 1554.

The largest shovelnose in the 1968 Missouri River catches had a fork length of 65 cm, and Figure 7 shows that fish longer than this are common in other rivers. Monson and Greenbank (1947) reported shovelnose up to 81 cm fork length and Barnickol and Starrett (1951) working in the same stretch of the Mississippi reported fork lengths up to 78.5 cm. Chippewa River shovelnose exhibited the longest mean fork length (64.2 cm), but this population had a relatively narrow length range similar to the Missouri River population.

Since older sturgeon grow more in weight than length (Harkness and Dymond, 1961; Helms, 1974), weights provide the best basis for comparing large shovelnose. The largest shovelnose reported for the Ohio and Mississippi rivers weighed 2155 and 2681 g, respectively while the largest sturgeon processed from the Missouri River during 1968 and 1969 was 1304 g (Table 11). Indeed, the mean weights reported by Everman (1902) and Monson and Greenbank (1947) were close to the maximum recorded during the current study.

To some extent, the lengths and weights reported for shovelnose from different rivers reflect a bias caused by capture methods. A sampling bias, however, cannot completely explain why the Missouri River catches contained sturgeon only within a relatively narrow length range and noticably smaller than sturgeon from the other rivers (Figure 7 and Table 11). For example, Everman (1902) examined fish from commercial seining operations and this technique would be expected to collect shovelnose comparable in length to

Missouri River fish, as well as sturgeon both bigger and smaller than those collected in the Missouri River. Although one peak in Everman's length data indicated that sturgeon around 53 cm fork length were common in the Mississippi River, most of his sturgeon were longer than Missouri River fish. Monson and Greenbank (1947) examined shovelnose at commercial markets so their data are probably biased towards larger fish. However, some gill nets I used in the Missouri River had mesh sizes which should have captured bigger sturgeon comparable to those collected by Monson and Greenbank. Apparently, Mississippi and Ohio River sturgeon populations do contain shovelnose appreciably larger than Missouri River sturgeon.

Barnickol and Starrett (1951) and Helms (1973) used gill and trammel nets similar to those used to collect Missouri River shovelnose, but they collected fish over a much wider length range and both reported a modal length 6 cm longer than the 50 cm reported for Missouri River shovelnose (Figure 7). Helms' (1973) catches also contained shovelnose over a wider weight range than observed for Missouri River fish (Table 11). Christenson (1975) collected his shovelnose with a boat shocker which would have limited size selectivity, but the Chippewa River shovelnose were much larger than Missouri River fish. In summary, I believe that nets used to collect shovelnose from the Missouri River would have captured larger and smaller fish if they were in the river. Therefore, data presented in Figure 7 and Table 11 definitely indicate that shovelnose in the Missouri River are smaller

than those in the Ohio, Mississippi, and Chippewa rivers.

I used data from Monson and Greenbank (1947) to derive a length-weight relationship for Mississippi River shovelnose. In order to compare their data with mine it was necessary to use their middle value of the fork length class as the average for that class. The length-weight relationships for the Mississippi and Missouri River shovelnose are graphically compared in Figure 8. The curves show that Missouri River shovelnose weigh less per unit length than Mississippi shovelnose except at the lower end of the length range where computed weights for the two populations are similar. At 30 cm fork length the computed weights are 73 g and 74 g for the two rivers. A striking feature of these curves is that Missouri River shovelnose are absent from that portion of the curves representing the major growth in weight. As length increases the Mississippi River shovelnose become progressively heavier. As expected, the greatest differences occur in the 60 to 80 cm range. At 60 cm, calculated weights for Missouri and Mississippi River shovelnose are 805 and 949 g, respectively. At 80 cm, the computed weight for a Mississippi River shovelnose is over 550 g heavier than for a Missouri River fish (2736 g vs 2177 g). The two largest shovelnose taken during this study were 65 and 73 cm fork length and weighed 1304 and 1786 g, respectively. Surprisingly, these two fish fit the curve produced by the logarithmic equation for Mississippi River sturgeon, rather than that produced for Missouri River sturgeon. This may be a circumstantial

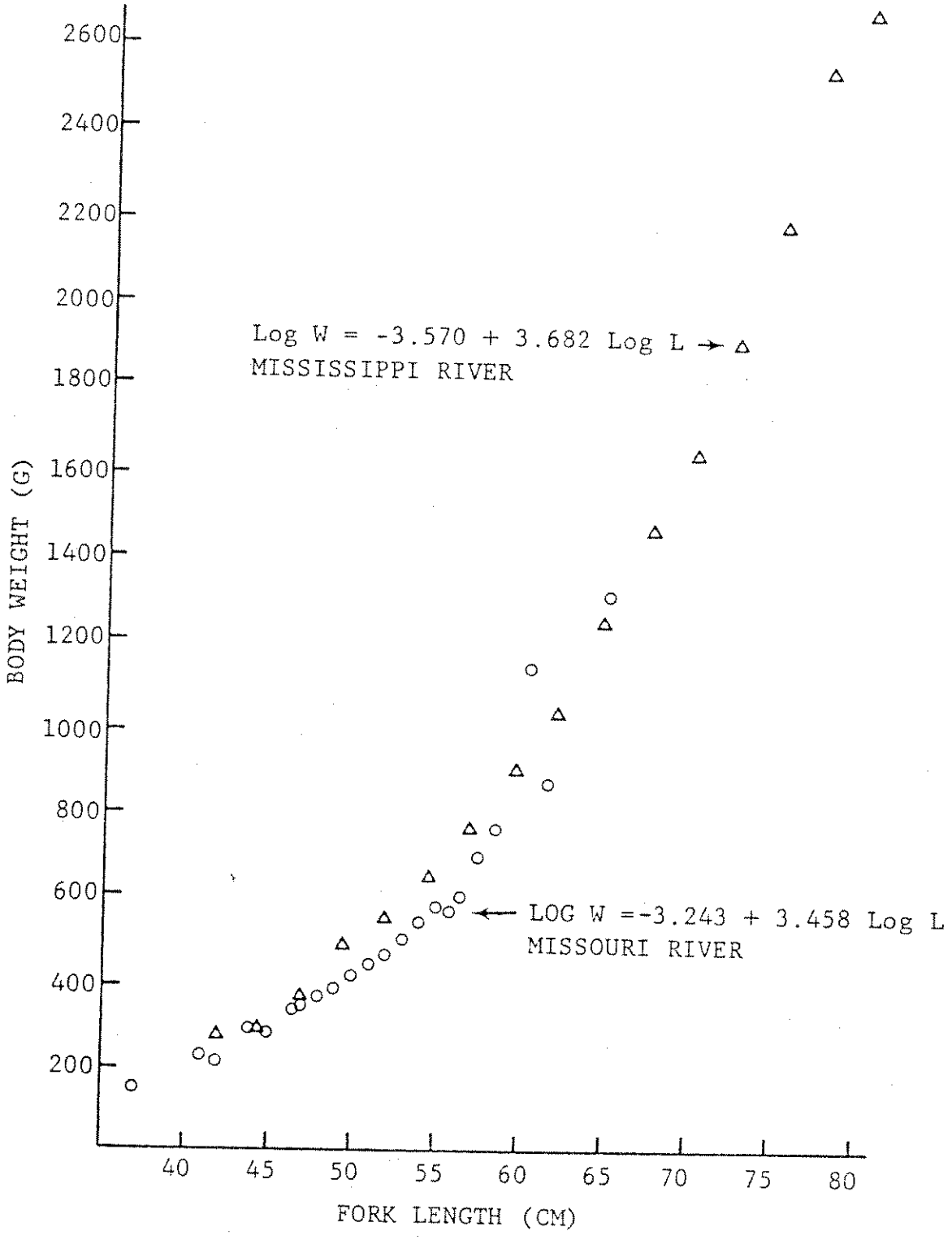

Figure 8. Relationships of fork length to weight for shovelnose sturgeon from the unchannelized Missouri River and from the Mississippi River (Monson and Greenbank, 1947). Points represent average for 10 mm length intervals (Missouri) and one inch intervals (Mississippi).

relationship and no conclusions should be drawn from just two specimens. Shovelnose between 60 and 74 cm fork length have been captured from Lewis and Clark Lake and Lake Francis Case, main-stem reservoirs on the Missouri upstream of the study area, (Shields, 1956, 1957, and 1958; Sprague, 1959; Nelson, 1961) and these fish fit the length-weight equation for Missouri River shovelnose quite well. For example, shovelnose ranging between 69.6 and 71.9 cm (mid-class value of 70.8 cm) averaged 1297 g, slightly lighter than the calculated weight of 1372 g for a 70 cm shovelnose using the Missouri River length-weight equation.

The condition factor or ponderal index expresses the relative well-being or plumpness of fish in numerical terms, and is commonly used as an indicator of the suitability of an environment for a particular species. Low condition factors indicate unsuitable environments or stress situations. Condition factors for shovelnose from the Ohio and Mississippi rivers, calculated from the mean fork lengths and weights reported by Everman (1902) and Monson and Greenbank (1947), were much higher than those for 512 Missouri River shovelnose (Table 11). Barnickol and Starrett's (1951) and Helms' (1973) data for Mississippi River shovelnose and Christenson's (1975) data on Chippewa River shovelnose yielded condition factors lower than the earlier Ohio and Mississippi River studies, but were still higher than for Missouri River fish. The lowest condition factor for Mississippi River fish, 3.98, was even higher than the factor of 3.84 for a subsample of

Missouri River spawning females (Table 8) that are expected to have a high condition factor. The low condition factors for shovelnose sturgeon in the Missouri suggests that the population is subject to some environmental stress which may depress growth.

Monson and Greenbank (1947) recommended that states along the Mississippi River adopt a minimum size limit of 63.5 cm (25 in.) fork length for the shovelnose commercial fishery to protect a portion of the breeding population. They found 55% of the male shovelnose and 92% of the females under 63.5 cm were immature. The smallest sexually mature female observed by Monson and Greenbank (1947) was in a fork length class of 50.8-53.1 cm while the smallest adult male was in a 48.3-50.5 cm class. Barnickol and Starrett (1951) presented supporting data, indicating that male shovelnose reach maturity at total lengths of 49.5 to 55.9 cm while the smallest mature female they examined was 63.5 cm. Helms (1972) reported immature males and females from the Mississippi River in Iowa longer than 63.5 cm fork length while the smallest mature male and female he observed were 55.9 and 61 cm, respectively. He reported that initial spawning for most females occurred at age VII and most males spawn first at age V (Helms, 1973).

By contrast, the smallest mature male and female shovelnose captured during the present study had fork lengths of 44.0 and 41.8 cm, respectively. Sexual maturity was determined by microscopic analysis of stained gonadal sections.

The shortest gravid male and female shovelnose observed during the spawning season were 44.2 and 47.6 cm fork length. Of 245 females analyzed for sexual maturity, only five were classified as immature; fork lengths ranged from 40.8 to 50.7 cm and weights from 227 to 482 g. Only two of 309 males were considered immature and microscopic examination of stained sections suggested that even these two might possibly have been recent recruits to the mature population (see Section III for further discussion). Fork lengths for the two males were 35.4 and 37.2 cm and weights were 191 and 149 g, respectively. The first stage in the reproductive cycle for mature shovelnose was referred to as the "developing" stage. Developing males averaged 49.2 cm fork length (range of 44.0-53.1 cm) and females 51.3 cm (range of 41.8-61.7 cm). The above evidence indicates that most male shovelnose in the Missouri River study area become mature at lengths around 40-50 cm while most females reach maturity when 45-55 cm.

Although female shovelnose in the unchannelized Missouri River apparently attain sexual maturity at a smaller size than Mississippi River fish, the number of eggs they produce per unit of body weight is comparable to egg production in Mississippi River shovelnose. Zweiacker (1967) found that gravid females in the Missouri River contained an average of 1909 eggs per 100 g body weight, while Helms (1973) reported an average of 1702 eggs per 100 g in Mississippi River sturgeon. However, since Missouri River shovelnose are smaller,

the total number of eggs per female is smaller than found in Mississippi River fish. Egg counts in females from the Missouri River ranged from 6709 to 15,637 (mean = 9210) in comparison to 13,908-51,217 eggs (mean = 24,325) in Mississippi River sturgeon.

The narrow size range of shovelnose sturgeon collected within the Missouri River study area, along with low conditioning factors, small size of mature individuals, and paucity of immature fish, suggest that the Missouri River population is environmentally stressed and probably exhibits a slow growth rate. This postulated slow growth is supported by data from 91 recaptured shovelnose. Changes in fork lengths and live weights between the time of tagging and recapture of these fish indicated that most recaptured shovelnose exhibited no growth (Table 12). Of those recaptured, only 45% were longer and only 37% heavier than when released. A shovelnose at large 3 years 250 days had the greatest gain in weight recorded for the 91 recaptures, but this fish gained only 99 g and grew only 7 mm. Two other shovelnose recaptured over 3 years after tagging had lost weight while fork lengths had increased by only 1 mm.

Only 13% of the 91 recaptured shovelnose exhibited a change in fork length greater than 5 mm. Christenson (1975) made repeated measurements on 20 shovelnose sturgeon over a one-month period to determine the degree of precision expected of field measurements, and found length measurements on individual specimens varied by ± 5 mm. If I assume that sturgeon

Table 12. Changes in fork length (mm) and body weight (g) between tagging and recapture dates, for 91 shovelnose from the unchannelized Missouri River, South Dakota.

Duration between Tagging and Recapture (months)	Number of Fish	Fork Length (mm)			Body Weight (g)		
		Mean Difference	Maximum Loss	Maximum Gain	Mean Difference	Maximum Loss	Maximum Gain
0 to 1	21	-0.5	- 9	+ 4	- 5.4	- 50	+64
>1 to 6	18	-0.7	- 7	+ 6	- 4.3	- 78	+43
> 6 to 12	23	-0.1	- 7	+ 6	+ 7.7	- 50	+71
>12 to 24	22	-0.3	- 6	+12	-15.4	-120	+85
>24 to 48	7	-0.9	-10	+ 7	-13.4	- 85	+99

in the Missouri River do not exhibit any measurable growth within 30 days, then recaptures within that time period serve as a control since measurements at tagging and recapture should be the same. Using this assumption, the precision of my length data was also near ± 5 mm (with one exception, fork length differences between tagging and recapture were ≤ 4 mm for fish at large ≤ 30 days). This same assumption indicates that repeated weight measurements would vary by about ± 64 g.

Growth, in terms of weight, was probably insignificant for sturgeon at large for ≤ one year since weight differences between tagging and recovery for these fish ranged only from +71 g to -78 g (Table 12). Sturgeon at large for 1 to 4 years, on the average, lost weight. Tagging has been reported to retard growth in several studies. For example, Priegel (1968) reported length increments of 102 walleyes recaptured after one growing season averaged only 53.7% of the mean annual growth increment of untagged fish in the population. Likewise, Muir (1960) reported a marked reduction in

the length increments of tagged fish from about 25% to about 80% (by age groups) of those attained by untagged fish. The stress of tagging, in addition to the environmental stress already imposed on shovelnose in this section of the Missouri River, could account for the apparent loss of weight by recaptured sturgeon.

Slow growth or no detectable growth has also been reported for shovelnose sturgeon from the Red Cedar - Chippewa River system, a tributary of the upper Mississippi River (Christenson, 1975). During 1967-73 he recaptured over 80 shovelnose that had been previously measured and tagged and the growth in length and weight was virtually zero. Thirteen of 19 fish that had been at large for 35 months or more showed a mean positive growth of 5 mm, no growth for one fish, and a mean loss of 5 mm in length for five fish. Since (Christenson (1975) indicated that his precision on length measurements was ± 5 mm, actual growth was not demonstratable. The Red Cedar-Chippewa River population also exhibited a narrow size range, similar to the Missouri River population (Figure 7).

Shovelnose collected from the Mississippi River bordering Iowa exhibited positive growth (Helms, 1973). Based on calculated fork lengths of 857 shovelnose, age I fish averaged 21.1 cm fork length but grew to 55.4 cm by age V and 70.1 cm by age X. Helms (1973) used growth data from 07 recaptured fish to calculate mean weekly growth increments for different sized fish. He excluded shovelnose

that were at large over the winter since growth during that time period was limited. Small fish (27.9 cm) grew almost 6 mm per week while larger shovelnose (53.3 cm) grew about 1 mm per week. Helms (1974) attributed reduced growth after the fourth year of life to attainment of sexual maturity.

A comparison of shovelnose age and growth studies from the Missouri and Mississippi rivers (Zweiacker, 1967; Helms, 1973 and 1974) provides additional evidence of slow growth by Missouri River sturgeon, and also some supporting data on age at maturity. In both studies fish were aged using cross-sections of the anterior pectoral fin ray. For many species of sturgeon, the ray section shows a number of single annuli representing years of growth prior to attainment of sexual maturity (Cuerrier, 1951; Roussow, 1957). However, when sturgeon reach sexual maturity the single annuli become narrowly spaced for several years, forming a belt. Following the first belt there are several widely spaced single annuli and then another belt. The belts apparently represent years of slow growth during which considerable energy is put into the developing gonads. The first belt documents age of sexual maturity and the last annulus in the first belt probably represents the year of first spawning (Roussow, 1957). The number of single annuli between belts represents the time period between spawnings.

Applying Roussow's interpretation, Zweiacker (1967) suggested that male shovelnose in the Missouri River usually reach sexual maturity at 3 to 4 years and females at 4 to 5

years. This agreed with age at maturity for shovelnose in the Mississippi River (Helms, 1972 and 1973). Zweiacker also proposed, based on belt patterns, that shovelnose spawn 2 to 3 years after reaching maturity, then probably every other year after that. Histological examination of gonads during the present study (see Section III) indicated that most male shovelnose spawn either every year or every other year while females usually spawn every 2 or 3 years, thus supporting Zweiacker's interpretation of belts on shovelnose fin ray sections. Additionally, few immature shovelnose were observed during the present study and Zweiacker suspected that all fish he aged were mature; that is, all ray sections exhibited belts.

Zweiacker (1967) determined ages of 228 shovelnose from the unchannelized Missouri River (collected from the study area) and suggested that ages ranged from 8 to 27 years, with a mean of 15.2 years. Approximately 79% of the sample population was considered to be 13 years or older, but their fork lengths only ranged from 48 to 55 cm. Shovelnose from the Mississippi River in their third and fourth growing seasons (age groups II and III) had fork lengths between 42 and 60 cm (Helms, 1974) overlapping the length range of Missouri River fish that were apparently much older. This indicates that growth of shovelnose in the Missouri River is much slower than Mississippi River shovelnose. In terms of weight, Missouri River shovelnose also exhibit slower growth. The length-weight relationship calculated by Helms for 110 aged

shovelnose indicated that a 50.8 cm (20 inch) shovelnose in the Mississippi River would weigh about 454 g (1 lb.) and would be 2 or 3 years old. In contrast, 512 shovelnose processed during the present study averaged 50.8 cm and 456.2 g, but were apparently four to seven times older according to Zweiacker's (1967) studies.

The present study was conducted in the unchannelized Missouri River in southeastern South Dakota, an area which is considered typical native habitat for shovelnose sturgeon. However, the flow regimen in this section of the Missouri River has been under stringent control since 1955 when the U. S. Army Corps of Engineers completed the most downstream of six main-stem Missouri River reservoirs by closure of Gavins Point Dam. This dam, about 47 km upstream of the study area, is used primarily to regulate water levels in the Missouri River for commercial navigation. Therefore, even this unchannelized section of the river has been impacted by man-made structures and resource management. Furthermore, shovelnose habitat has been degraded and eliminated downstream by channelization and reduced upstream by the main-stem reservoirs. The completed reservoir system now impounds 1444 km (74%) of the upper Missouri River between Gavins Point Dam and the headwaters of Fort Peck Dam in Montana, and the river is extensively channelized from Sioux City, Iowa (about 59 km downstream of the study area) to St. Louis, Missouri. These changes have removed good sturgeon habitat above and below the study area, impacted

channelized section (Schmulbach, et al., 1975). Morris, et al. (1968) found that channelization of the Missouri River bordering Nebraska had reduced both the benthic area and the average standing crop of drift organisms, and both benthic and drift organisms are important components of the shovelnose diet (Held, 1969; Modde and Schmulbach, 1977).

In conclusion, the author suggests that the narrow range in length and weight of shovelnose in the study area, low condition factors, slow growth, paucity of young fish, and only limited reproductive success (see Section III) are related to the extensive man-made modifications imposed on the Missouri River ecosystem. Zweiacker's (1967) age data, although unverified, supports this conclusion because his assigned ages indicate that most shovelnose within the study area were spawned prior to closure of Gavins Point Dam.

The unchannelized Missouri River in southeastern South Dakota may also be overpopulated with shovelnose. This might be expected if shovelnose have moved into the unchannelized area from less suitable reservoir and channelized river habitats. Although good population estimates of shovelnose within the study area were inhibited by low recapture percentages, tag loss, and immigration and emigration, some preliminary figures indicate that shovelnose may be very abundant within the study area.

For estimating populations, tag loss and dilution of marked fish within the study area by immigration and emigration were probably the most important sources of error during

this study. Therefore, only recapture data over short time periods were considered. During 1968 and 1969, there were three relatively short time periods when more than 500 shovelnose were marked and released, resulting in 8-20 recaptures (Table 13). In these three cases population estimates, based on the Schnabel formula (Lagler, 1956), ranged from 3,264 to 3,742 shovelnose per km of river length. Fewer than 2% of the marked shovelnose were recaptured during these three time periods and the estimates might also have been biased by non-random distribution of marked fish. However, even if these estimates are 20-30% too high (tag loss and emigration of tagged fish will bias the estimates upwards) there still would be nearly 2500 shovelnose per km within the study area.

Table 13. Estimated population size (number/km) of shovelnose sturgeon in the unchannelized Missouri River in southeastern South Dakota.

Time Period	Length of River Fished (km)	Number Marked	Number Recaptured	Estimated Population* No./km	95% Confidence Limits
1968					
Sep 19 to Nov 2	5.63**	638	11	3642	2003-7284
1969					
Apr 15 to Jun 26	6.44***	549	8	3264	1674-7460
Oct 9 to Dec 3	11.26#	1057	20	3742	2430-6084

*$P = \Sigma mc/\Sigma r$ (Lagler, 1956).

**Shovelnose released and recaptured between Vermillion Boat Club Landing and 2 km downstream of Clay County Park Landing (See Figure 1).

***Shovelnose released and recaptured from Wildlife Landing downstream to west end of Goat Island.

#Shovelnose released and recaptured between Highline Landing and 2 km downstream of Clay County Park Landing.

RESULTS AND DISCUSSION (cont'd)

II. MOVEMENT

Shovelnose sturgeon movement in the unchannelized Missouri River was investigated by conventional tagging and recovery. Tagging began in mid-June 1968 and continued through mid-July 1970. During that period, 3,543 sturgeon were tagged and released within the 20 km study area (Table 14). Only 22 of 1,258 (1.8%) sturgeon tagged during 1968 were recaptured during the first year. During 1969, an additional 2,084 sturgeon were tagged of which 120 were recaptured. When the tagging program was terminated in mid-July 1970, 158 shovelnose (4.5%) had been recaptured. Only nine of the fish recaptured by July 1970 were caught by sport fishermen (three outside the study area) while the remainder were caught by personnel of the University of South Dakota.

Although field operations for the movement study were terminated in July 1970, recaptures of sturgeon tagged during 1968-70 continue to be taken (Schmulbach, personal communications). Continuing fisheries work by the University of South Dakota through 1972 resulted in 31 additional recaptures while commercial and sport fishermen reported 10 recaptures from 1972 through 1974, 8 from outside the study area (Table 14).

A. EVALUATION OF TAGGING METHODS

Monel strap and plastic dart tags were used during the current study. Between mid-June and late September 1968,

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Table 14. Number of shovelnose sturgeon tagged, types of tags used, and number of sturgeon recaptured by tag type between June 1968 and November 1974.

	Number Tagged				Number Recaptured					
		Tag Type				Tag Type				
Season	Total Number	Monel on Opercle	Plastic Dart	Monel on Pectoral	Total Number	Monel on Opercle	Plastic Dart	Monel on Pectoral	Lost Monel**	Lost Dart
1968 (Jun-Nov)	1258	640*	618	0	22	11	9	0	2	0
1969 (Apr-Dec)	2084	96	1354	634	120	6	46	11	13***	44***
1970 (Mar-Jul)	201	0	0	201	16	2	6	3	2	3
Subtotal	3543	736*	1972	835	158	19	61	14	17	47
1970 (Fall)					3	0	0	3	— #	— #
1971					24	1	0	23	—	—
1972		No sturgeon tagged and released by author after mid-July 1970			10	2	0	8	—	—
1973					2	0	0	2	—	—
1974					2	0	0	2	—	—
Subtotal					41	3	0	38	—	—
Total	3543	736*	1972	835	199	22	61	52	17	47

*Eight shovelnose tagged with both monel opercle and plastic dart tags.

**Strap tags clamped on opercle.

***Includes one recapture with tag intact but insufficient data to identify original tagging date and location.

#Field personnel not necessarily trained to recognize scars representing lost tags, and many cases of lost tags assumed to be unrecognizable.

No. 4 monel strap tags (National Band and Tag Co., Newport, Ky.) were clamped over the posterior margin of the opercle. Six shovelnose tagged in this manner were held for 3.5 months in live tanks and showed no indication of shedding tags when released in early October. However, a shovelnose was recaptured on October 16 and another on November 2, that had obviously sloughed the opercle tag. Additionally, several shovelnose recaptured during October were in the process of sloughing the opercle tag. Apparently current and suspended sediments striking the tag caused the cartilaginous opercle to gradually erode. The notch (scar) on the opercle was easily recognized, and during 1969 and early 1970 fifteen sturgeon with lost opercle tags were captured (Table 14). Among the recaptures, 17 of 36 opercular-tagged sturgeon lost the tag (assuming that all sturgeon which lost tags were recognized through July 1970). However, some opercle tags persisted for several years. One sturgeon with a strap tag securely clamped on the opercle was recaptured in September 1971, 3 years 81 days after it was tagged. The last sturgeon recaptured with an opercle tag was caught in April 1972, 3 years 258 days after tagging.

A smaller strap tag (No. 1) that clamped much tighter to the opercle than the No. 4 tag was applied to 96 shovelnose in 1969. Although no evidence of sloughing was observed on the four shovelnose recaptured with the small tag, few small tags were used because they were difficult to see. One of these four recaptured sturgeon was at large for 3 years

17 days.

From October 1968 through October 1969 most shovelnose were tagged with a plastic dart tag (Floy, model FT-6) inserted between the overlapping scutes along the dorsal ridge, at about mid-length. Most of the dart tags on nine sturgeon recaptured in 1968 and 30 caught between April and September 1969 were firmly attached. However, they did not remain hooked over the imbedded anterior edge of the scute as intended. Moreover, on some individuals it appeared that the exposed flexible tubing was oscillating in the current and retarding healing of the tag wound. Tags and tagging equipment were kept in a Lysol bath before and after use and only a few sturgeon exhibited acute infection around the tag.

On October 3, 1969, the first shovelnose bearing a scar indicating a lost dart tag was caught, then several more were seen later in the month. During the last four weeks of the 1969 field season I recaptured 61 sturgeon, including 11 with intact dart tags and 32 which had lost the dart tag. During 1970, six intact dart tags were collected between March and July, but after mid-summer 1970 no shovelnose with dart tags were recaptured. Helms (1972) also observed tag shedding when he tagged shovelnose sturgeon with dart tags between scutes of the lateral row or on the side between the dorsal and lateral rows of scutes. Helms, however, experienced good results when dart tags were inserted dorsal to the pectoral fin and anchored in the pectoral girdle.

In October 1969 I returned to a monel strap tag, but clamped it over the anterior margin of the pectoral fin about 1 cm from the fins juncture with the body. Strap tag application consumed less time than that of the dart tag and produced only a minor wound on the fin. Furthermore, pectoral tags on recaptured shovelnose were tight and only slight tissue destruction was observed. For long term studies the pectoral tag proved to be superior to either the monel opercle or plastic dart tag. Of the 42 recaptures that had carried tags for one full year or more, 35 had pectoral tags compared to 6 opercle tags and one dart tag. Additional Missouri River studies (Schmulbach, personal communication) and Mississippi River studies (Helms, 1972) also noted that the pectoral tag was very reliable. Christenson (1975) had satisfactory results with strap tags placed around the caudal peduncle of shovelnose in the Red Cedar-Chippewa River system.

B. MOVEMENT

Although shovelnose sturgeon were caught at many locations within the 20 km study area most were caught within 0.4 km of nine release points (Figure 9). Similarly, tagged sturgeon were released at these points or boat landings immediately adjacent to release points 4, 5, 7, and 9. Therefore, in describing movement, all shovelnose were considered to have been caught, tagged and released, and recaptured within these nine defined areas (each approximately 0.8 km in diameter). With the exception of fish used for homing experiments, all

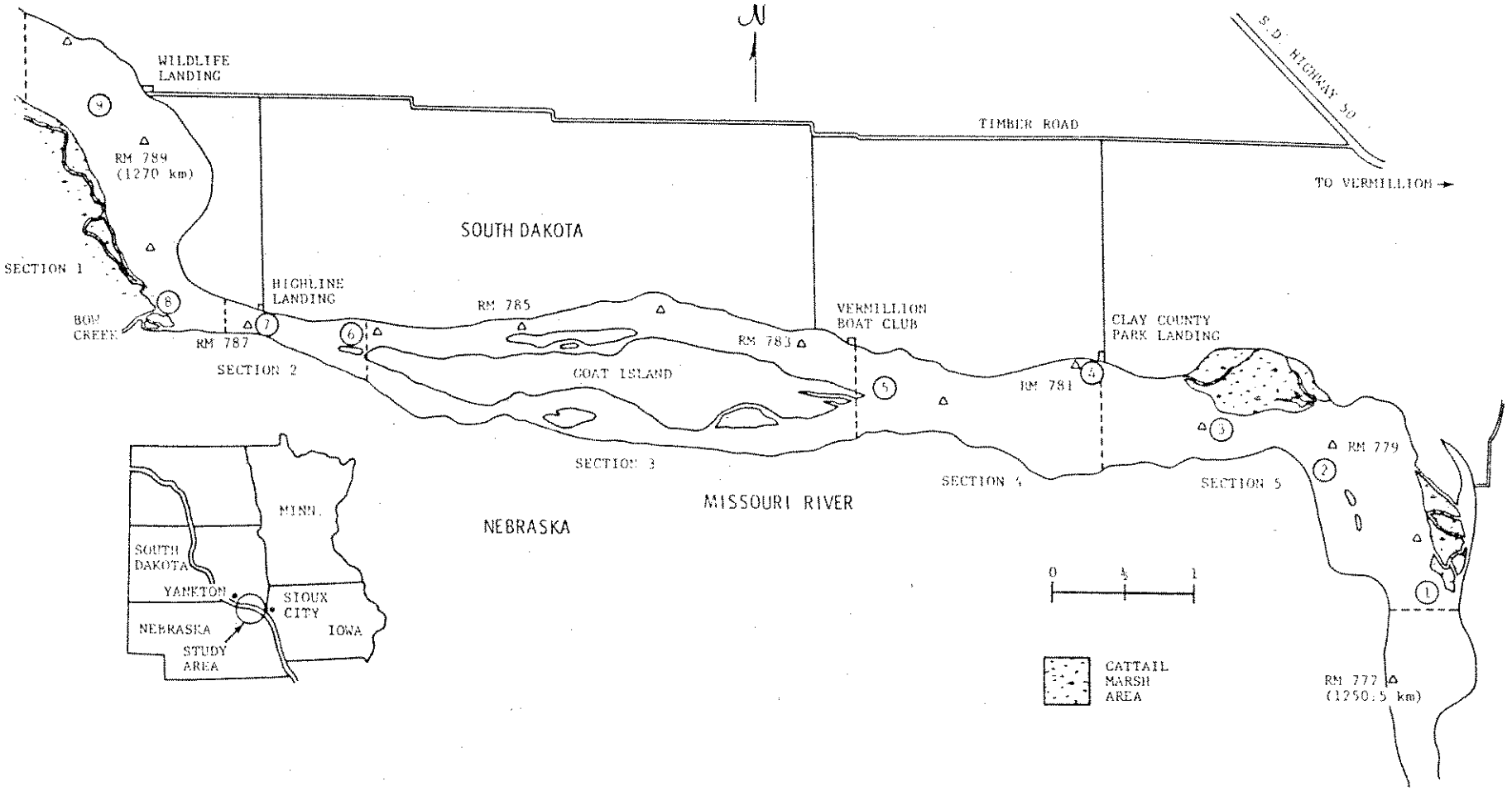


Figure 9. Location of the four boat landings and nine release points where tagged shovelnose sturgeon were released into the 20 km study area of the Missouri River in southeastern South Dakota. Most fish were captured within a 0.4 km radius of a release point.

tagged shovelnose were returned to the river at the release point or boat landing nearest its capture location.

1. Distance Moved and Time at Large

a. Single Recaptures. Between June 1968 and mid-July 1970 when field work was terminated, 94 shovelnose had been recaptured with intact numbered tags (Table 14). An additional 41 recaptures (of fish tagged during 1968-70) were reported between mid-July 1970 and October 1974 to University of South Dakota personnel. Approximately 69% of the recaptured sturgeon were caught within one year of their release date and during that period, 40 of 93 recaptures were caught either at their original release point or within 1.6 km of this point (Table 15). An additional 23 were caught between 1.6 and 3.2 km from the release point. The maximum distance traveled by a shovelnose at large for less than a year was 25.7 km. This fish was caught 168 days after its release. For the 93 shovelnose recaptured within one year, the average duration between tagging and recapture was 95.5 days and the average distance traveled was 3.1 km. Christenson (1975) reported shovelnose sturgeon in the Chippewa River, a tributary of the upper Mississippi River, that were at large up to 14 months and traveled an average of 1.9 km upstream or 1.8 km downstream. In the Mississippi River bordering Iowa, 82 tagged shovelnose sturgeon were recaptured during 1972 by experimental netting and commercial fishing (Helms, 1973). Two-thirds of these fish were at large for less than 128 days and had moved an average of 1.9 km.

Table 15. Time at large and distance moved between release and recapture points for 135 shovelnose sturgeon in the unchannelized Missouri River, South Dakota.

Distance Traveled (km)	Time between Tagging and Recapture in Years																			
	≤ 1 Year				> 1 Year ≤ 2 Years				> 2 Years ≤ 3 Years				> 3 Years ≤ 4 Years				> 4 Years ≤ 5 Years			
	1/4	1/2	3/4	1	1-1/4	1-1/2	1-3/4	2	2-1/4	2-1/2	2-3/4	3	3-1/4	3-1/2	3-3/4	4	4-1/4	4-1/2	4-3/4	5
0 < 1.6	29	2	6	3	1		2													
1.6 < 3.2	12	7	2	2		2	1		1	2	1				1					
3.2 < 4.8	1	1	5			2														
4.8 < 6.4	8	1	1																	
6.4 < 8.0	1		1				1	2												
8.0 < 9.7	2					2		4												
9.7 < 11.3	3		1			2		2			1									
11.3 < 12.7	1		2	1		1		3					2							
18 < 35		1														1				
35 < 100								1			1		1							2
100 < 150								1												
150 < 275										1							1			
Summary/Quarter																				
No. Recaptured	57	12	18	6	1	9	4	13	1	3	3	0	3	0	1	1	1	0	0	2
Distance moved (km)																				
Mean	2.4	4.2	4.5	3.9	1.3	6.3	1.8	23.7	2.9	84.7	33.5		35.7		2.1	19.3	239.8			41.0
Range	0 to 12.5	0 to 25.7	0 to 17.3	0 to 15.7		1.6 to 10.9	0 to 5.2	4.8 to 139.2		1.6 to 256.3	2.0 to 88.5		12.5 to 80.5							37.0 to 45.1
Mean Time Out (d)	20.6	144.7	222.0	330.0	365.0	488.4	611.8	694.5	742.0	858.0	932.7		1129.7		1353.0	1427.0	1465.0			1779.0
Summary/Year																				
No. Recaptured	93				27				7				5				3			
Distance moved (km)																				
Mean	3.1				13.7				51.0				25.7				107.3			
Range	0 to 25.7				0 to 139.2				1.6 to 256.3				2.1 to 80.5				37.0 to 239.8			
Mean Time Out (d)	95.5				601.3 (1 yr 236.3 days)				873.4 (2 yrs 143.4 days)				1233.8 (3 yrs 138.8 days)				1674.3 (4 yrs 214.3 days)			

Twenty-seven shovelnose were recaptured between one and two years after their release. All but three had moved at least 1.6 km from the point of release and 59% (16 of 27) were recaptured at least 7 km from the release point (Table 15). Two of these fish were recaptured outside the study area; one 77 km downstream near the mouth of the Floyd River at Sioux City, Iowa, and the other about 137 km downstream near the mouth of Blackbird Creek. The average time out for the 27 shovelnose at large between one and two years was 601.3 days, the average distance moved was 13.7 km.

All shovelnose recaptured after two or more years were caught at least 1.6 km from their original release point, and 66% traveled at least 9.7 km (Table 15). Seven of 15 fish at large for 2 to 4 years were caught outside the study area; six downstream and one upstream. The fish recaptured upstream was at large for 3 years 332 days and had traveled 19 km, about one-half the distance to Gavins Point Dam which limits further upstream movement. The longest time between release and recapture was recorded for two sturgeon recaptured by sport fishermen near Ponca State Park, Nebraska. These two were at large for 4 years 300 days and 4 years 338 days and had moved 37 and 45 km downstream. Two shovelnose at large for 2-3/4 and 3-1/4 years were captured near Sioux City, Iowa about 80 km downstream. Maximum distances, however, were achieved by two shovelnose recaptured near Omaha, Nebraska. One was at

large for 4 years and 5 days and was caught at Desota Bend north of Omaha, nearly 240 km downstream. The other was recaptured at Dodge Park, about 250 km from the release point, after 2 years 124 days.

Although there was variation, distance traveled increased as time at large increased. For example, the average distance between release and recapture locations for shovelnose caught in one-year time blocks (Table 15) was 3.1 km for the first year, 13.7 km for the second year, 51.0 km for the third year (17.9 km average if the sturgeon caught at Dodge Park is excluded), 25.7 km for the fourth year, and 107.3 km for the fifth year.

University of South Dakota (USD) fisheries personnel continued to tag shovelnose sturgeon with monel tags on the pectoral fin after the present study ended. This effort provided an additional 39 recaptures through early 1975. Many of these sturgeon exhibited movements similar to those described above; 16 of 39 were recaptured within one year of their release and only 5 were at large for more than 2-1/2 years. Although 62% were caught within 16 km of their release points, a few traveled a considerable distance in a short time period. For example, a commercial fisherman recaptured one shovelnose almost 200 km downstream 80 days after its release, and another sturgeon was caught 530 km downstream of its tagging location only 264 days after being tagged (Schmulbach, personal communication). University of South Dakota personnel have recently reported 16 additional

recaptures during 1976, 1977, and 1978. Two of the most recent recaptures were caught near Omaha and had been at large for 7 years 14 days and 8 years 188 days (Schmulbach, personal communication).

Sport and commercial fishermen apparently became more aware of the tagging program during the 1970's while direct recapture efforts by USD personnel declined. As a result, 23 of the 39 recaptures from fish tagged between 1970 and 1975 were reported by fishermen and these reports revealed some relatively extensive movements. Two shovelnose were caught at Gavins Point Dam about 47 km upstream; one of these had been at large 4 years 29 days. Six shovelnose were recaptured between Omaha and Union, Nebraska, about 240 to 315 km downstream. These six had been in the river between 1 year 130 days and 2 years 126 days. Maximum distances traveled, however, were set by three shovelnose recaptured in the Missouri River between St. Joseph, Missouri and Atchinson, Kansas, 500-540 km from their point of release. One sturgeon caught north of the bridge at Atchinson, had been out for only 264 days; the sturgeon recaptured at St. Joseph was at large almost 2 years while the one caught south of Atchinson had been tagged 1 year 141 days.

b. Multiple Recaptures With conventional tag-recapture data, the distance a fish moves is assumed to be the length of a straight line between the release and recapture points. However, the fish may actually travel much farther if it moves both upstream and downstream before it

is recaptured. Multiple recaptures provide some evidence on this interim movement. Although nine shovelnose tagged during 1968 and 1969 were recaptured twice, six of these had lost the original tag and were released the second time with a new tag. One of the three double recaptures with tag intact had moved 4 km upstream in 94 days, then moved back downstream to the area where it was originally released after another 239 days. Another continued to move upstream; between September 27 and December 1, 1969 it had moved upstream about 3 km (from area 1 to 3) and on June 4, 1970 it was recaptured another 7 km upstream at area 5. The third double recapture had moved less than 0.5 km when it was recaptured the first time 18 days after its release; one year 330 days later it was recaptured about 6.5 km downstream. These limited data suggest that shovelnose move randomly back and forth within a segment of the river. This conclusion is supported by multiple recaptures of 26 shovelnose sturgeon in the Red Cedar and Chippewa rivers (Christenson, 1975). He reported random movement not disclosed by single recaptures. Twenty-two of the multiple recaptures involved Chippewa River shovelnose at large from 1 day to 13 months; 14 were initially recaptured upstream of the release point, 4 downstream, and 4 at the original release point. When recaptured the second time, 11 went upstream, 10 downstream, and 1 remained at the release point.

c. Summary. The Missouri River recapture data indicated that most shovelnose at large for a year or less

remain within a 8-16 km segment of the river, but they may move back and forth within this segment. This apparently random movement displaced shovelnose farther and farther from the original capture location as time increased. Many shovelnose at large for 2-4 years had moved 80-250 km from the original release points, and a few individuals had moved 500 km or more in that same time period. Helms (1972) and Christenson (1975) did not observe extensive movement for shovelnose in the Mississippi River and Red Cedar-Chippewa River System, but few of their recaptures were at large for more than one year. They reported maximum movement of 21 and 19 km, respectively. Their data were comparable to data for Missouri River shovelnose at large for less than one year.

A large-river ecosystem such as the Missouri River contains a diverse assemblage of habitat types and a large variety of fish species. This type of ecosystem probably contains a less uniformly distributed fish population than does either a lake or small stream, and considerable movement might be expected between habitat types and along the main axis of the river. Some fish species would be sedentary, others semi-mobile or mobile. Shovelnose sturgeon probably are best characterized as mobile, or as suggested by Funk (1957) might include both sedentary and mobile groups. Funk suggested that all fish species include both sedentary and mobile groups, and a species is best characterized according to the relative abundance of the two groups.

In addition to shovelnose sturgeon, several species

common in the Missouri River might be classified as mobile; including channel catfish, paddlefish, and walleye. In an unaltered area of the Little Sioux River, a tributary of the Missouri near Sioux City, Iowa, over 30% of the channel catfish recaptured by Welker (1967) had moved over 40 km. The maximum travel distance he reported was 191 km. In Missouri streams, Funk (1957) indicated that about 35% of the recaptured channel catfish moved 16 km or more. Paddlefish in the Missouri River are also reported to travel extensively. Adult paddlefish from Garrison Reservoir move 150-300 km up the Yellowstone River each spring prior to spawning (Rehwinkel, 1978). Although recaptures suggest that some paddlefish may remain in the Yellowstone over the winter many return to Garrison Reservoir, presumably each year. Long distant movement by walleye is apparently seasonal and associated with spawning, similar to paddlefish. Priegel (1968) reported maximum distances up to 156 km during walleye spawning runs in the Fox and Wolf Rivers; average distance traveled by recaptured walleye was 30 km.

2. Movement Within the Study Area

The intensive field effort along the 20 km study area produced a bias favoring recaptures within, rather than outside of the study area. These recaptures, however, provided valuable information concerning shovelnose movement. First, a large portion of the shovelnose were recaptured at or near the point where they were released (Table 16). For example, 17 of the 34 shovelnose recaptured at area 5 were released

Table 16. Release and recapture locations for 135 shovelnose sturgeon tagged and released in a 20 km section of the Missouri River, South Dakota.

Area of Release*	Area of Recapture*											Total Number Recaptured per Release Location
	Downstream	1	2	3	4	5	6	7	8	9	Upstream	
1	0	0	1	1	0	1	0	0	0	0	0	3
2	1	0	1	2	0	0	2	0	0	1	0	7
3	0	1	0	5	1	3	0	0	0	0	1	11
4	2	1	0	8	0	5	0	0	0	1	0	17
5	2	0	0	3	4	17	6	1	1	2	0	36
6	3	1	3	5	5	5	0	2	1	4	0	36
7	0	0	0	0	0	2	1	1	1	1	0	6
8	0	0	0	0	0	0	0	0	0	1	0	1
9	0	1	0	1	1	1	1	0	8	10	2	25
Total number	8	4	5	25	11	34	10	4	11	20	3	135

*Figure 9 shows location of sampling areas 1-9.

at that location, and 10 more were released at areas 4 and 6, immediately upstream and downstream of area 5. Thirty-four of the 135 recaptures (fish tagged from 1968 through mid-1970) were caught at the area where they were released and an additional 45 were caught in the area immediately upstream or downstream of the release point. However, it also appears that there is a mobile fraction of the shovelnose population because a few individuals were recaptured over 100 km from their original capture locations.

The distribution of recaptured shovelnose provided some evidence on preferred habitats. For example, none of the 17 shovelnose released at area 4 were recaptured there. But, this was expected since area 4 was primarily a release point and very little gill netting was attempted in the relatively straight and narrow channel at this location. Pools behind sand bars in area 6 were also characterized as shallow and unstable, and most shovelnose might move through this area rather than abide there for any period of time. This hypothesis is supported by the fact that sturgeon released from area 6 were not recaptured there, but had dispersed throughout the 20 km study area prior to recapture (Table 16).

Most recaptured shovelnose were caught at areas 3, 5, and 9 and pools behind sand bars were more numerous and stable in these three areas in comparison to the other six. However, my mark and recapture data indicated that the recapture location was also obviously dependent upon where fishing pressure and success were highest, and where tagged shovelnose were

released (Figure 10). Most shovelnose sturgeon were caught at areas 3, 5, and 9 (21, 28, and 24.5%, respectively). The recapture point appears to reflect the location of the largest catches more closely than the location where the largest number of tagged shovelnose were released. For example, relatively large numbers of tagged shovelnose sturgeon were released at the convenient boat landings at areas 4 and 7, but these two locations had few suitable netting locations and few shovelnose were recaptured there (Table 16 and Figure 10).

The temporal distribution of recaptures over the ten sampling months also closely paralleled fishing success (Figure 11). As field work began in early spring catches were frequently low, but the numbers of shovelnose caught, tagged, and recaptured increased through May and peaked in June. Catches were usually small through mid-summer and few sturgeon were recaptured. Catch, tagging, and recapture rates increased again in the fall, even exceeding the June peak. The highest percentage of recaptures, as well as the highest percentage of releases, occurred in October, but catch success peaked in November. The number of shovelnose tagged and released decreased between October and November because during late November 1969 several hundred sturgeon were released without tags as inclement weather hampered tagging. One reason for the smaller percentage of recaptures in November was that during November 1969, a large number of recaptures with lost Floy tags (not included

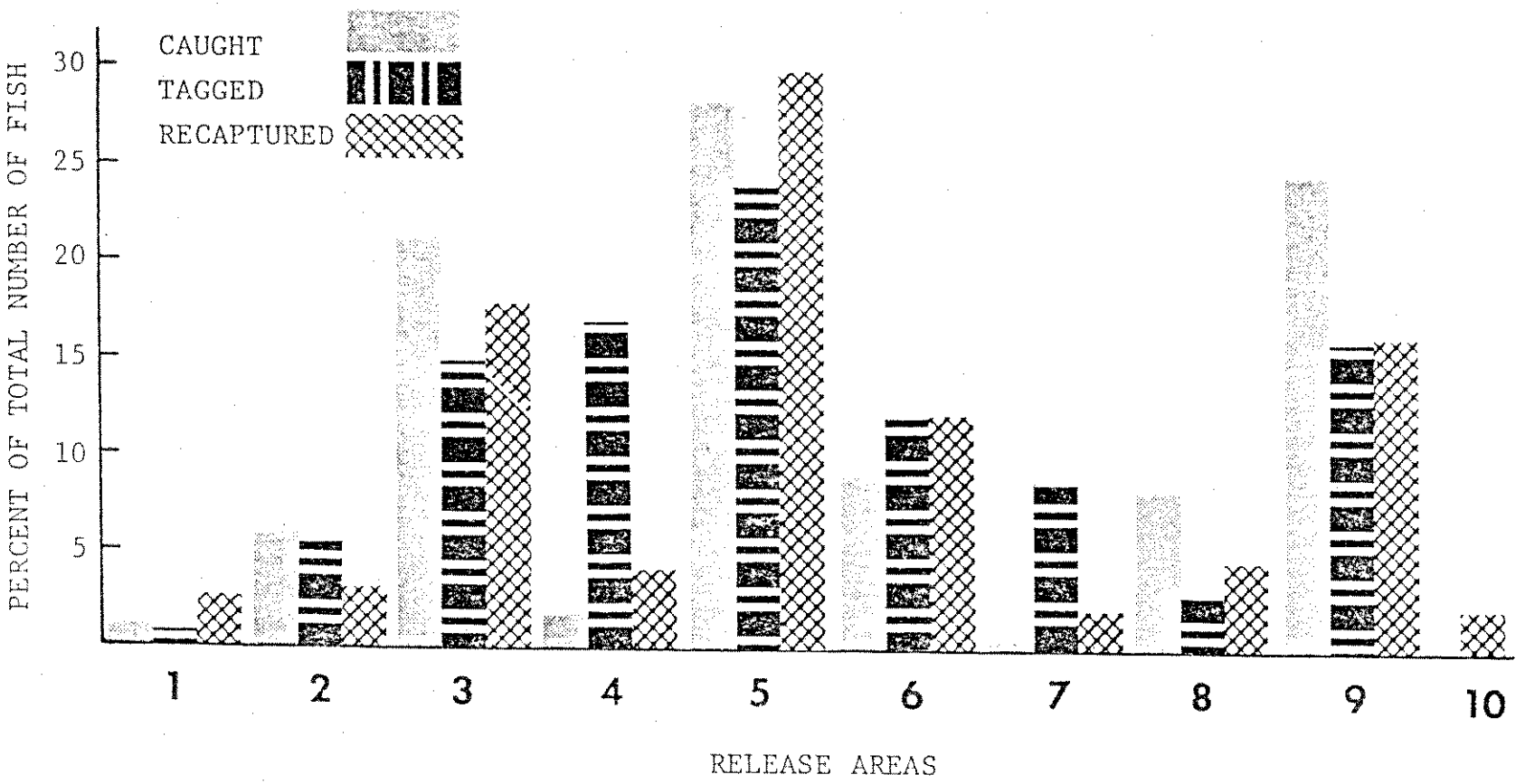


Figure 10. Percentage distribution illustrating where shovelnose sturgeon were caught, tagged and released, and recaptured within a 20 km Missouri River study area. Location of release points 1-9 are shown in Figure 9, and area 10 represents fish recaptured outside the study area.

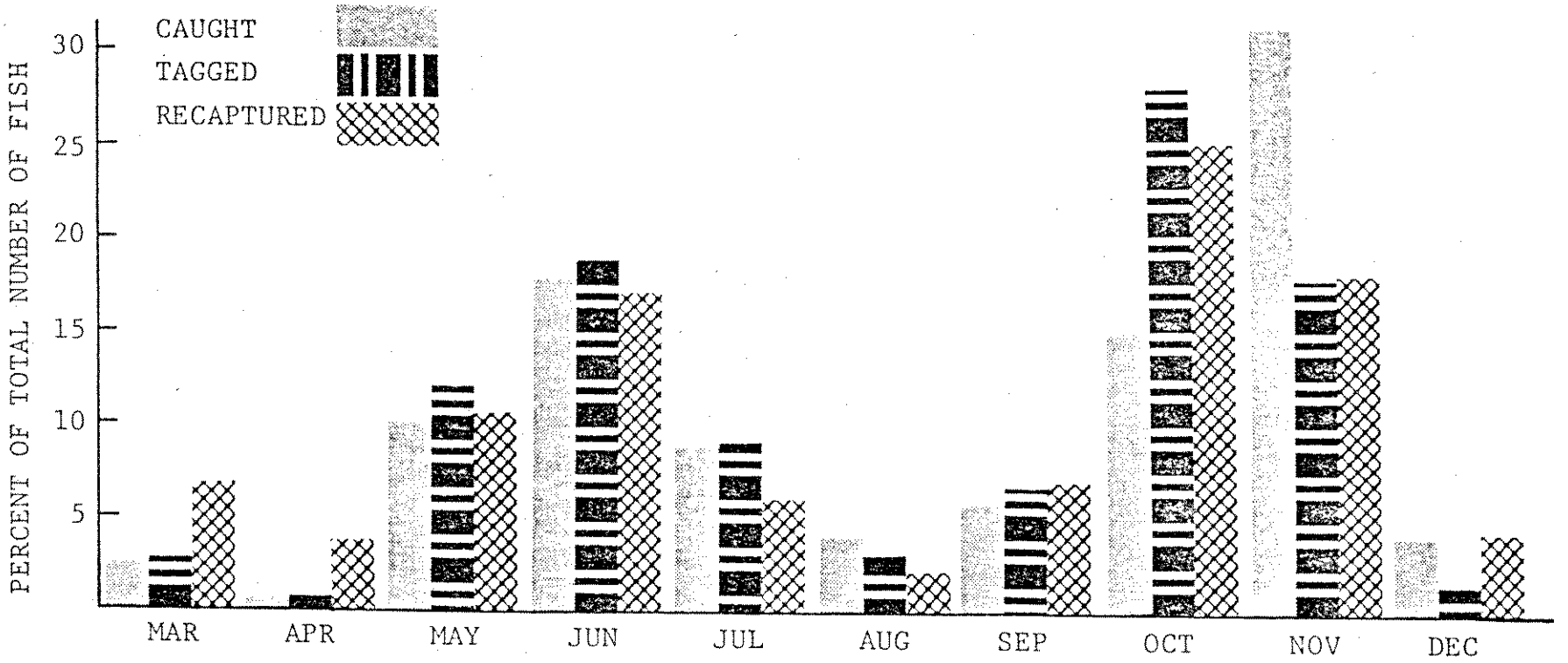


Figure 11. Percentage distribution showing which months shovelnose sturgeon were caught, and tagged and released within a 20 km Missouri River study area between June 1968 and July 1970, and which months the 135 recaptures were caught during 1968 through 1974.

in Figures 10 and 11) were caught.

Spring and fall catch rate peaks indicated that shovelnose sturgeon were either more abundant, active, or concentrated in the study area at these times (Figure 11 and Table 4). The tagging data suggested that shovelnose are more active during June and October-November. Based on date of release, recapture data were sorted into five time periods and the average distance traveled by shovelnose during these five periods was compared (Table 17). Only data for sturgeon at large for fewer than 66 days were used in these analyses since the longest of the time periods was 61 days.

Shovelnose sturgeon released in June, October, and November traveled longer distances, on the average, than shovelnose released in the early spring (April-May) or summer (July-September). The least movement occurred during the summer. Although the average distance moved by sturgeon released and recaptured in early spring was relatively high, the time at large was higher for this group than for any of the other groups. The percentage of mobile individuals was usually directly related to distance traveled (Table 17). For example, only 40% of the shovelnose recaptured in the summer moved and average movement was less than 0.8 km, while 71% moved during the spring and average movement was nearly 4.5 km. Increased activity during June could be a result of reproductive behavior. The high percentage of mobile fish in October also corresponded with relatively long travel distances, indicating that shovelnose are active in the fall.

Table 17. Average distance traveled by shovelnose sturgeon and percentage of the population exhibiting movement during five seasonal periods; for sturgeon tagged, released, and recaptured within 65 days.

Time Period of Release	Number of Recaptures	Average Time at Large (d)	Average Distance Traveled (km)	Gill Net CPUE*	Percentage Showing Movement
Apr-May	9	26.7	1.74	20.1	45
Jun	7	15.3	4.49	27.2	71
Jul-Sep	10	18.5	0.77	8.5	40
Oct	22	18.6	2.08	23.3	64
Nov	8	17.8	2.46	29.8	37

*Catch per unit effort = number of sturgeon caught in 91.4 m of net set for 20 h.

During November, 5 of 8 recaptures had not moved but the other three were recaptured 5.2 to 9.3 km from their release locations. This produced a high average distance for the group even though most of the individuals were sedentary.

Relatively high spring and fall activity interrupted by a sedentary summer season appears to be a behavior pattern common to many fish species. Using underwater telemetry, Holt et al. (1977) found that mean daily movement for walleye was shortest in the summer and higher in spring and fall, and radio-tagged largemouth bass displayed a similar seasonal pattern (Warden & Lorio, 1975). Rock bass, channel catfish, carp, and smallmouth bass in Missouri also exhibited high spring activity followed by a sedentary summer (Funk, 1957). The exact or primary cause of increased spring movement cannot always be determined, but it may be associated with spawning activities, feeding, water temperature, flow rates, or other physical or chemical characteristics of the water

body (Cleary and Greenbank, 1954; Funk, 1957; Priegel, 1968; Warden & Lorio, 1975; and Holt et al., 1977).

C. DISPLACEMENT EXPERIMENTS

Previous investigations of fish movement have shown that individuals of many species normally limit their movements to a specific area or home range for a considerable period of time (Gerking, 1953; Kudrna, 1965; McCleave, 1967; McCleave et al., 1977). Many species which maintain a home range also have the capability to return to the home range if they are displaced by natural or artificial phenomenon (Gerking, 1959); Jahn, 1969; Warden and Lorio, (1975). My recapture data for shovelnose sturgeon suggested that shovelnose do not establish a home range, and the following experiment indicated that they do not exhibit a tendency to return to the point of original capture (ie, home range).

During 1968 and 1969 about 1,000 tagged sturgeon were displaced either upstream or downstream from where they were captured. Although a few were displaced almost 13 km downstream (from area 9 to area 4), most were transferred between 1.6 and 3.2 km from the original capture area; about 19% upstream and 81% downstream. Twenty-three displaced fish were recaptured by early July 1970, but no evidence of homing was observed (Table 18).

Thirteen of the 23 recaptures moved back towards the original point of capture after being displaced (ie, they moved upstream if displaced downstream - or vice versa).

Table 18. Distance and direction of movement for shovelnose sturgeon displaced from their original capture location prior to their release back into the Missouri River, South Dakota.

Tag		Tagged and Released		Distance Displaced (km)	Time at Large (d)	Distance Moved After Release (km)	Homing Index***
No.	Type*	Date	Area**				
214	M.O.	Oct '69	7	2.9 D#	2	0	0
204	F	Oct '68	4	2.4 D	6	2.4 U#	+4
1953	F	Oct '69	4	12.1 D	7	2.4 U	+1
1157	F	Jun '69	4	1.3 U	10	4.8 D	-4
626	F	Apr '69	6	3.2 D	11	1.6 U	+2
603	M.P.	Oct '69	4	2.4 D	13	1.3 D	-2
878	M.P.	Nov '69	6	3.2 D	15	0.3 D	0
784	M.P.	Nov '69	6	0.8 U	18	0.3 D	+2
967	M.P.	Nov '69	6	3.2 D	21	8.5 D	-4
730	M.P.	Nov '69	6	0.8 U	27	4.8 D	-4
1690	F	Sep '69	8	1.6 D	33	1.6 U	+4
1901	F	Oct '69	4	12.1 D	38	1.3 D	-1
1930	F	Oct '69	4	12.1 D	38	1.3 D	-1
224	M.O.	Oct '69	7	2.9 D	42	6.4 D	-4
248	M.O.	Jul '68	4	1.3 U	108	2.4 U	-4
1327	F	Jun '69	7	2.9 D	150	2.9 D	-4
1153	F	Jun '69	4	1.3 U	159	1.6 D	+3
327	F	Nov '69	7	3.2 D	215	3.2 U	+4
217	F	Oct '69	4	2.4 D	220	2.4 U	+4
605	F	Nov '68	7	3.2 D	225	5.6 D	-4
221	M.O.	Oct '69	7	2.9 D	246	1.3 U	+2
248	F	Oct '68	4	2.4 D	356	2.4 U	+4
60	M.O.	Jun '68	4	1.3 U	464	4.5 D	-4

*M.O. = Monel tag on opercle, M.P. = Monel tag on pectoral fin, F = Floy dart tag.

**See Figure 9 for location of release areas.

***See text for explanation.

#D = downstream, U = upstream.

However, some individuals (Table 18, tag numbers 1157, 730, and 60) continued past the original capture location and then moved away from the original point of capture. Unfortunately, these tag recaptures did not monitor movement continuously between release and recapture. Therefore, some of these fish which were at large for long periods, such as fish No. 60 at large for 464 days, could have returned to a home range and remained there for some time before moving along. Movement of recaptured sturgeon which were at large for short time periods (for example, No. 1157 and 730), however, suggested that there was no tendency to return to a home range.

To measure the movement of displaced fish more objectively, each recapture was given a positive or negative score (the homing index) so that the sum of all scores would be positive if a tendency for homing occurred (Table 18). The grading scheme was:

+4	recaptured at the point of original capture after being displaced
+3	at recapture, had returned about 75% of the distance displaced
+2	at recapture, had returned about 50% the distance displaced
+1	at recapture, had returned about 25% the distance displaced
0	did not move after being displaced
-1	was recaptured about 125% of the distance it had been displaced
-2	was recaptured about 150% the distance it had been displaced
-3	was recaptured about 175% the distance it had been displaced
-4	was recaptured > 200% the distance it had been displaced

Five individuals received a grade of +4 while eight received a grade of -4. The sum of all grades was -6 (-36 and +30)

indicating that the displaced shovelnose did not exhibit a tendency to return to a home range. Displaced sturgeon were recaptured up to 464 days after release but no relationship was observed between time at large and tendency to move back to the original capture point.

Individual fish which establish a home range can apparently recognize their surroundings and retain impressions of the immediate environment for a considerable period of time (Gerking, 1959). Thus, they might have an advantage over individuals new to the area (for example, fish introduced by stocking). This line of reasoning suggests that a fish tagged and released back into its home range would be less likely to move, or move a shorter distance, than a fish which was displaced, and released into a new area. A comparison of displaced and non-displaced shovelnose revealed that about half (47%) of the non-displaced fish and 30% of the displaced shovelnose were recaptured within 1.6 km of their original point of capture (Table 19). Although this suggests that displaced shovelnose may move farther, the percentage of displaced and non-displaced shovelnose moving < 3 km was nearly equal; 69.5% compared to 67.1%. Overall, movement by these two groups was quite similar.

Although displaced shovelnose showed no homing tendency, recaptured shovelnose did exhibit an apparent group movement. On 30 occasions two or more shovelnose were recaptured on the same date, or within a 48-hour period of each other. In approximately two-thirds of these cases at least two

Table 19. Comparison of distances traveled by shovelnose sturgeon displaced prior to their release back into the Missouri River and by sturgeon released at their original capture location. Table includes only data for recaptures at large less than 465 days since the longest time at large for a displaced sturgeon was 464 days.

Distance Traveled (km)	Number of Recaptures Grouped by Time at Large (months)								All Recaptures			
	1-3		4-6		7-9		10-15		Number		Percentage	
	Org.*	Dis.*	Org.	Dis.	Org.	Dis.	Org.	Dis.	Org.	Dis.	Org.	Dis.
<1.6	23	6	2	0	5	1	4	0	34	7	46.6	30.4
1.6 < 3.2	8	4	4	3	1	1	2	1	15	9	20.5	39.1
3.2 < 4.8	1	0	1	0	4	1	0	1	6	2	8.2	8.7
4.8 < 6.4	6	2	1	0	0	1	0	0	7	3	9.6	13.0
6.4 < 8.0	0	1	0	0	1	0	0	0	1	1	1.4	4.4
8.0 < 9.7	1	1	0	0	0	0	0	0	1	1	1.4	4.4
9.7 < 11.3	3	0	0	0	1	0	0	0	4	0	5.5	0
≥11.3	1	0	1	0	2	0	1	0	5	0	6.8	0
Total	43	14	9	3	14	4	7	2	73	23	100.0	100.0

*Org. = number of sturgeon released at their original capture location.
Dis. = number of sturgeon displaced prior to their release.

recaptured fish had been tagged and released together (Table 20). The first pair of tagged shovelnose was caught at area 3 on July 1, 1968, but pairs like this were anticipated because both had been released only 5 days earlier, 1.6 km downstream. Recaptures that had been at large for longer time periods were more intriguing. For example, on May 25-26, 1969, four sturgeon were recaptured at area 5 that had been released 207 to 228 days earlier. Three were caught and released at area 5 just a few days apart while the fourth was caught at area 5 at the same time and displaced about 1.6 km downstream to area 4. About 2 weeks later on June 10, five of nine shovelnose recaptured at area 9 formed a group; these five were tagged and released at area 9 between 31 and 34 days earlier. Recaptures during 1970, 1971, and 1974 provided even stronger evidence of grouping because pairs or triplets were recaptured more than a year after release. For example, on October 5-6, 1971 two shovelnose caught at area 3 were fish released 699 and 700 days previously at area 6. On that same date three recaptures at area 2 just 1.6 km downstream, had also been released from area 6 between 697 and 698 days ago. Then about 2 weeks later, a pair of shovelnose was recaptured in area 4 that had also been released at area 6, 713 days previously. Although not captured on the same date, the source of two recaptures caught near river mile 758 about a week apart in the fall of 1974 was intriguing. These two fish had been released in late fall 1969 at release points 4 and 6 (river miles 781 and 786) and

Table 20. Area of release and number of days between release and recapture for shovelnose sturgeon caught on occasions when two or more sturgeon were recaptured on the same date.

Recapture Date	Number of Fish Recaptured	Recapture Area	Group Movement	Comments
1968				
Jul 1	2	5	Yes	Both fish released at area 2, 5 days earlier.
Oct 16	4	5	Yes	Three of the four recaptures were tagged and released at area 4, 6-7 days earlier.
Oct 24	2	5	No	
Oct 25-26	2	5	Yes	Both fish released at area 5, 16 days earlier.
Oct 30	2	5	No	
1969				
May 8	2	9	No	
May 11	2	9	No	
May 25-26	4	5	Yes	Two of the four sturgeon were released at area 5, 207 and 210 days prior to recapture. The other two sturgeon were released 220 and 228 days earlier, at areas 4 and 5 respectively.
Jun 5	2	3	No	Both fish released at area 5, but time out was 218 days for one and 239 days for the other.
Jun 10	9	9	Yes	Five of the recaptured sturgeon were released 31-34 days previously at area 9.
Jun 10	3	5	Yes	All three released at area 5 the day before.
Oct 30-31	3	5	No	
Nov 6	6	6	No	No group movement detected but recaptures included 3 lost tags.
Nov 7	6	6	No	No group movement detected but recaptures included 4 lost tags.
Nov 12-13	8	3	Yes	Two sturgeon released at area 4, 13-14 days prior to recapture. Recaptures included 5 lost tags.
Nov 23-24	6	6	Yes	Four of the six recaptures were released 15-18 days prior to recapture at area 6.
Nov 30	5	3	Yes	Two of the recaptured sturgeon were released at area 4, 38 days earlier.
Dec 1	2	3	No	
Dec 5	9	5	Yes	Two of the recaptured sturgeon were released at area 6, 26-27 days earlier. Recaptures included 5 lost tags.
1970				
Jun 25	3	8	Yes	Two of the three recaptures had been released at area 9, 110 days prior to their recapture.
Oct 30	2	3	Yes	Both sturgeon had been released at area 4, 364-365 days before recaptured.
1971				
Mar 8	2	4	No	
Mar 12	3	4	Yes	Two of the three recaptured sturgeon were released 1 yr 124-6 days earlier at area 5.
Mar 13	2	3	Maybe	The two recaptures were released 1 yr 126 days and 1 yr 134 days earlier, one at area 5 and the other at area 6.
Sep 21-22	3	9	Yes	Two of the three sturgeon were released at area 6 1 yr 317 and 1 yr 321 days earlier.
Oct 5-6	2	3	Yes	Both sturgeon were released at area 6 and were at large for 1 yr 334-5 days.
Oct 5-6	3	2	Yes	All three recaptures were at large for 1 yr 332-3 days and were released at area 6.
Oct 21	2	4	Yes	Both sturgeon were released at area 6, 1 yr 348 days prior to recapture.
Nov 19	3	8	No	
1974				
Sep 30 and Oct 8	2	Mile 758*	Maybe	These two fish, recaptured 9 days apart, were at large 4 yr 300 days and 4 yr 338 days; one was released at area 4 and one at area 6.

*Two shovelnose sturgeon recaptured downstream of the study area at river mile 758

were caught at river mile 758 by a local sportfisherman, Mr. L. Saboda, almost 5 years after they were tagged and released.

Although this phenomenon of grouped recaptures suggests that shovelnose might run in schools, no one has observed schooling behavior in the sturgeon family. The author believes that these grouped recaptures occur because shovelnose travel along the river by moving from pool to pool. Throughout the 1968 to mid-1970 field work, catches were consistently higher in pools behind sand bars. If the more suitable (i.e., preferred) pools are fairly limited - we located fewer than nine good pools within the 20 km study area - then most shovelnose would be concentrated within a finite number of locations along the river. Therefore, tagged shovelnose released together may actually travel together for a time by simply moving in the same direction and from pool to pool at about the same rate. This could explain group recaptures for shovelnose recaptured within a few months of their release. Group recaptures after longer time periods may occur simply because shovelnose frequently cross paths; that is, shovelnose released together do not necessarily travel together but could be found at the same pool fairly frequently if they are moving back and forth between a relatively limited number of preferred pools.

In conclusion, catch and recapture data indicate that shovelnose sturgeon exhibit random movement. Within the study area, the number moving upstream nearly equals the

number moving downstream. Multiple recaptures in this study and those by Christenson (1975) also suggest that shovelnose move randomly back and forth within the river although seasonal trends in activity were noted. Shovelnose were more abundant at the Wildlife Landing, Boat Club, and Clay County Park areas (release points 9, 5, and 3, respectively) than at the other six points of the study area, and this was apparently due to better habitat in these areas. Pools behind sand bars and slack-water areas adjacent to the main channel were more abundant (and more stable) at these three subsections of the study area. Shovelnose probably move along the river by moving from pool to pool, or to open areas with reduced-flow adjacent to the main channel.

Most shovelnose remain near the area where released for several months (51% recaptured within 3 months had moved less than 1.6 km), but distance between release and recapture points increased with time. The average distances moved by shovelnose at large for 1 to 5 years were 3.1, 13.7, 51.0, 25.7, and 107.3 km respectively. After several years at large, shovelnose were found 80 to 540 km downstream of the study area; upstream movement was limited to < 50 km by Gavins Point Dam.

Displacement of tagged fish indicated that shovelnose have no tendency to "home" back to the original capture location and displaced shovelnose were apparently no more active than the shovelnose released where they were captured.

Shovelnose sturgeon were more abundant, or at least more

susceptible to capture gear, during spring and fall and recapture data indicated that they were also more active during these two seasons. Neither catch data at Gavins Point Dam tailwaters (Walburg, et al., 1971) nor tag recaptures during the present Missouri River study indicated any noticeable upstream migration associated with the spawning season as observed by Eddy and Surber (1943) and Helms (1972) in the Mississippi River. Although recapture data suggested that shovelnose were sedentary during the hottest summer months, few sturgeon were caught in these months so their habitat preference during summer is unknown. They could move into deeper holes in the main channel which I was unable to fish effectively, or into tributaries, or just disperse into several of the available habitats. Shovelnose caught in early December and again in March were very lethargic, implying that they are probably sedentary during the winter, but Modde and Schmulbach (1977) reported that shovelnose actively feed during the winter period.

RESULTS AND DISCUSSION (cont'd)

III. REPRODUCTION

The shovelnose sturgeon reproductive cycle was interpreted after determining temporal changes in gonadal gross morphology, microscopic anatomy, and gonosomatic index (GSI = gonad weight x 100/body weight). Three criteria were used because one or two were insufficient to describe the reproductive cycle, which apparently was complicated by the existence of mature fish that did not spawn every year. The possibility that some mature shovelnose don't spawn annually was anticipated because gonads in several different stages of maturity were always present in the population, and research on other species of sturgeon has shown that they spawn at intervals of several years (Magnin, 1962; Cuerrier, 1966; Semakula and Larkin, 1968).

A. GROSS MORPHOLOGY OF GONADS

The paired elongated testes were situated dorsolateral and parallel to the alimentary tract and extended from the pericardial cavity posteriorly to a point midway between the posterior extension of the gas bladder and anus. The testes were supported along their dorsal surface by mesorchia which were continuous with the peritoneal lining of the gas bladder and dorsal body wall. Numerous efferent sperm ducts and blood vessels traversed the mesorchia.

The paired ovaries, similar in length to the testes, occupied the same relative position to the other body organs as the testes. The mesovaria, containing the major blood vessels supplying the ovaries, were comparable to the mesorchia in form and areas of attachment. Mature ovaries contained brown or black ova which completely filled the body cavity and distended the abdomen. This distention was externally obvious in females for several months prior to spawning. Ovaries with less developed ova were compressed much like the testes and similarily located.

The medial portion of the ovary was composed of a layer of connective tissue with associated vascular elements and some smooth muscle. Compact leafy folds of ovarian tissue extended laterally into the body cavity from this medial foundation to produce a lamellar structure. The lamellae were perpendicular to the longitudinal axis of the gonad and macroscopically visible in all ovaries containing developing light colored eggs. The transverse lamellae were clearly visible in the spent ovaries of shovelnose, a condition also noted in lake sturgeon, A. fulvescens, (Magnin, 1966a). This lamellar structure is also present in paddlefish, Polydon spathula, (Larimore, 1950), and Atlantic sturgeon, A. oxyrhynchus (Magnin, 1962).

Another structural feature common to shovelnose, paddlefish and several other sturgeon is the presence of adipose tissue associated with the gonads (Larimore, 1950; Magnin, 1962 and 1966c; Cuerrier, 1966). This fatty tissue is

intimately associated with the gonadal tissue and the peritoneal covering of the gonads also envelops the associated adipose tissue. Gonads in early stages of maturation were associated with extensive fat bodies, but the amount of fat decreased as the gonads developed and was almost completely absent in ripe and spent gonads. This relationship between gonadal maturation and decreasing fatty tissue has also been observed in paddlefish and several species of sturgeon (Larimore, 1950; Magnin, 1962; Cuerrier, 1966). In female shovelnose this relationship was very obvious since fat was estimated to comprise 70-90% of the total volume of immature ovaries or ovaries in early maturation stages.

The presence of fat created interpretation problems during gross examination of the gonads. In the male, the similarity in the gross appearance of adipose and testicular tissue frequently created the false impression of a larger testis. In the immature female, the ovary was a small band of ovarian tissue along the dorso-lateral face of the extensive fatty mass. Since fat under gross inspection resembles testicular tissue, the immature female could be mistaken for a male. However, closer inspection of the tissue under low power (100 X) of the microscope revealed the more translucent ovarian tissue and oocytes. The absence of fat helped distinguish spent from developing ovaries.

As the gonads mature the corresponding decrease in fatty tissue associated with the gonads suggests that fat serves as a source of energy and material for maturation of the sex

cells. Cuerrier (1966) and Magnin (1962) declared that the adipose tissue apparently contributed directly to the development of the gonads in the lake sturgeon.

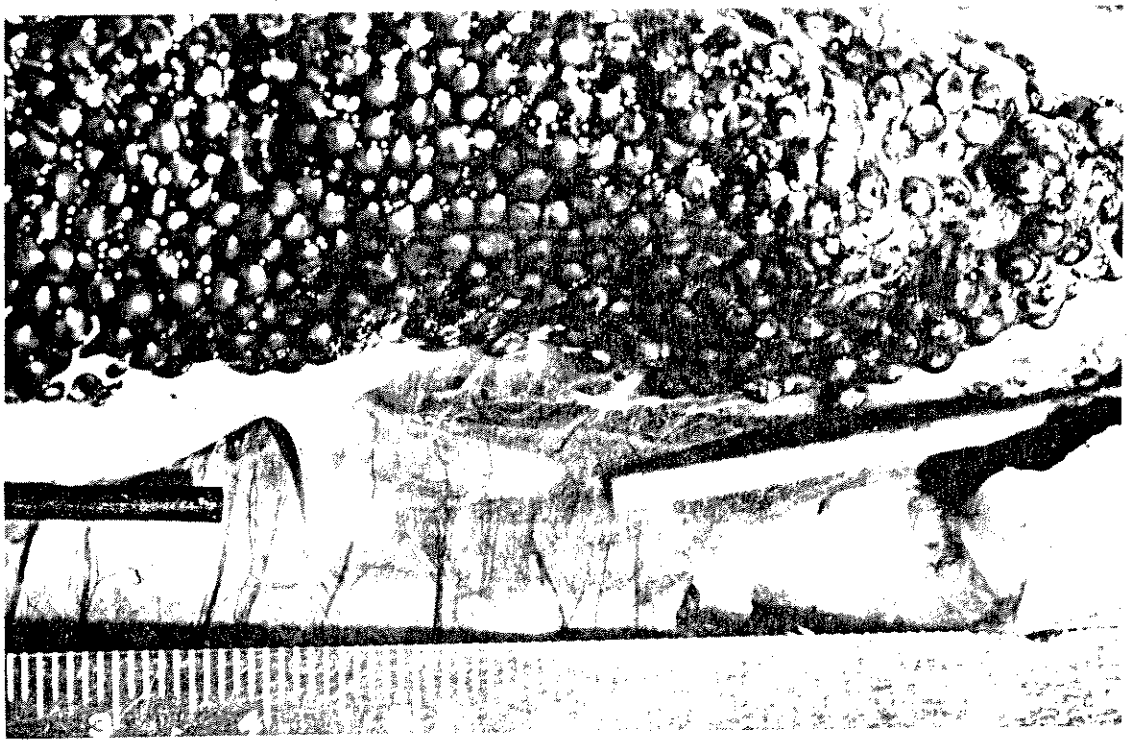
Ripe ova are released into the body cavity from the gymnovarian ovary and enter the paired oviducts through ostia. The oviducts fuse at the posterior end of the body cavity to form a short urogenital sinus and the eggs are shed through a single urogenital pore located immediately caudad to the anus. Externally this double oriface structure (the vent) measured 5-6 mm wide and 7-8 mm long. No external sexual dimorphism was detected in this structure.

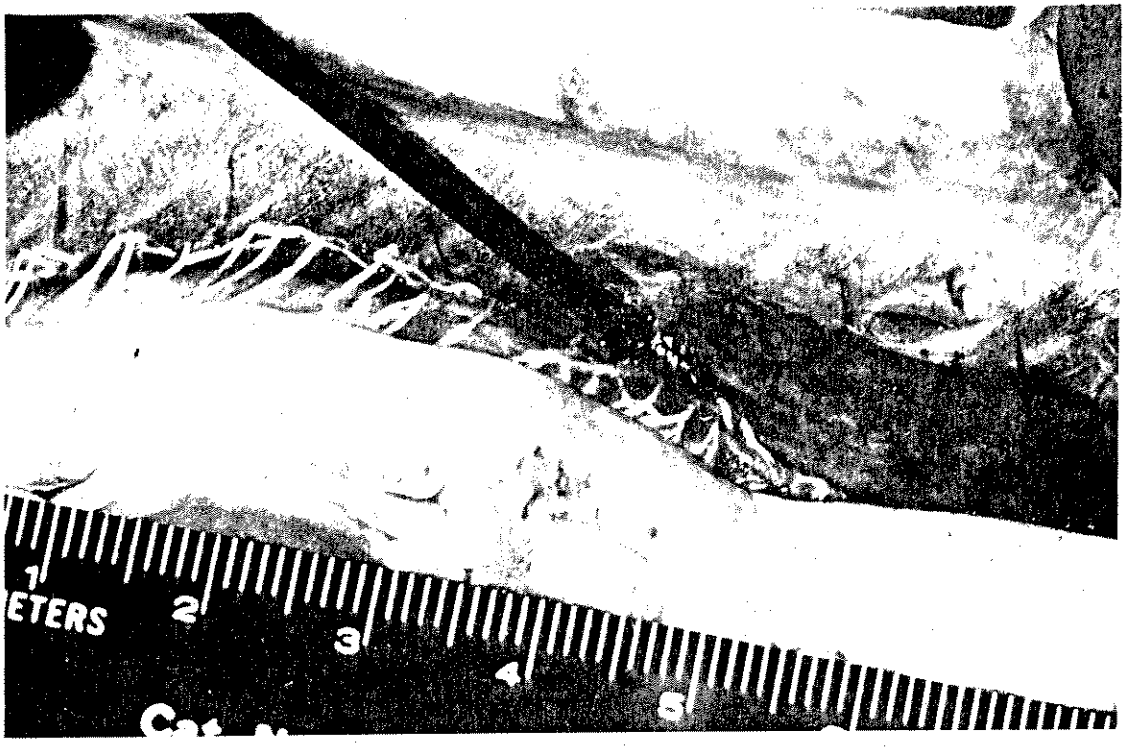
The structure of the shovelnose oviduct which is present in both sexes, was rather unique. The major portion of an oviduct consisted of a thin-walled sac located in the extreme dorsal portion of the body cavity just lateral to the mesentery supporting the gonads (Figure 12). The anterior one-third lay alongside the gas bladder while posteriorly the two ducts met at the dorsal midline but remained separate along most of their length. The dorsal and lateral walls of the oviduct adhered to, or may have been continuous with, the peritoneum covering the gas bladder and body cavity. The ventral wall consisted of a very thin transparent mesentery extending from the lateral body wall to the gas bladder, and more posteriorly, to the mesentery at the dorsal midline. The overall appearance was that of a thin-walled expansible sinus.

In shovelnose the ostia of both sexes were situated

Figure 12. Ostia and oviduct in gravid female shovelnose sturgeon (50.7 cm fork length) captured in the Missouri River study area on 4 June 1970. The fish is oriented ventral side up with head to the left and the right ovary displaced over the air bladder. The light colored wooden dowel is inside the oviduct. Numbered units are centimeters.

Figure 13. Ostia, oviduct, and vasa efferentia in ripe male shovelnose (50.5 cm fork length) captured in the Missouri River study area on 4 June 1970. The fish is oriented ventral side up with head to the left. The dark wooden dowel is inserted into the ostia pointing towards the oviduct. The numerous vasa efferentia are traversing from the left testis dorsally towards the kidney.

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lateral to the gas bladder at least two-thirds of the distance from the bladder's anterior end. The location of the ostia is similar to that in the Atlantic sturgeon (Ryder, 1890). The tissue forming the funnel was more substantial than tissue forming the ventral oviduct wall, and the funnel projected into the oviduct. The collapsible apex of the funnel evidently acts as a one-way valve since fluids or eggs within the oviduct could not be forced anteriorly into the coelom. The ostia in the male was less developed than in the female. The diameter of the funnel mouth in the female and male shown in Figures 12 and 13 was 15 mm and 7 mm, respectively. The funnel length from mouth to apex was 15 mm and 8 mm, respectively. Measurements from females in different stages of maturity were variable since the ostia are quite flexible. However, the ostia and oviducts in an immature female resembled those of the male shown in Figure 13 more closely than those of the spawning female. In four shovelnose (male spawner, female spawner, female developer and hermaphrodite) used for detailed analysis of the oviduct, the total length from the ostia to the urogenital pore averaged 85 mm (range 79-90 mm) or 16.4% of the total length of the fish.

The oviducts, clearly discernible in the males, don't have a reproductive function. Macroscopically the male gonoducts cannot be followed completely but numerous vasa efferentia were visible departing dorsally along the entire length of the testes (Figure 13). Near the dorsal body

wall they turned slightly caudad, probably connecting with the archinephric duct through conscripted kidney tubules. Although microscopic evidence was not available, the male ducts in shovelnose appeared to agree with those in lower actinopterygians described by Romer (1962) and Hoar (1969). Accordingly, the archinephric ducts conduct both sperm and urinary wastes, the testes connecting to these ducts via the kidneys. In the European and Atlantic sturgeon, tubules in the anterior three-fourths of the kidneys serve for both sperm and urine transfer whereas in the sterlet, A. ruthenus, only the anterior one-third serves this dual purpose (Magnin, 1962).

B. REPRODUCTION IN MALES

1. Microscopic Anatomy of the Testis

Internally the testis was composed of a compact mass of seminiferous lobules which were branched and convoluted with no obvious orientation. Therefore, the appearance of the lobules was very similar in both longitudinal and cross-sections of the testis. Elongate fibroblasts and small capillaries were found between the thin walls of adhering lobules. Connective tissue, interstitual cells, and numerous blood vessels formed the stroma in larger interlobular spaces.

The interstitual cells in shovelnose are apparently similar to interlobular interstitual cells reported for river lamprey, Lampetra fluviatilis, (Hardisty, Rothwell and Steele, 1967), paddlefish, (Larimore, 1950), and Clupea

sprattus and Latimeria (Marshall and Lofts, 1956). In some fish Leydig cell homologues are distributed in the lobule walls rather than in the interlobular spaces. These, referred to as "lobule boundry cells", are present in brook trout, Salvelinus fontinalis (Henderson, 1962), lake chub, Couesius plumbeus (Ahsan, 1966) and in Esox lucius, Salvelinus sp., and Labeo sp. (Lofts and Marshall, 1957; Marshall and Lofts, 1956).

In earlier stages of maturation the germinal epithelium consisted of primary and secondary spermatogonia which lined the lobules (Figure 14). Later the epithelium became less distinct as the lobules filled with nests of spermatogenic cells. Although these nests were distinct the very thin connective tissue enclosing each nest was obscure. Each nest arose from repeated divisions of a single cell and subsequent divisions within that nest were synchronous. Therefore, all cells within one nest belonged to one spermatogenic stage. Within a single lobule several nests were present, each maturing independently, so that several stages of spermatogensis were found in one lobule. The occurrence of lobules (or tubules) containing nests of synchronously dividing spermatogenic cells derived from a single gonial cell is typical of early spermatogenesis in other fish species.

Primary and secondary spermatogonia were easily distinguished. Primary spermatogonia measured 10 to 11 μ in diameter and usually occurred as single cells with an obscure cell membrane (Figure 15). The lightly staining nuclei were

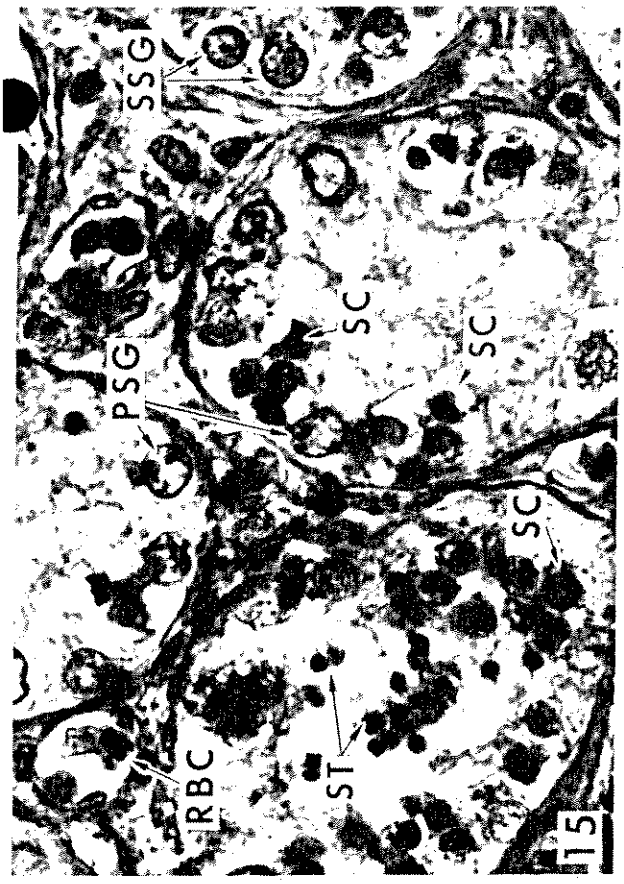
Figures 14-17. Photomicrographs of 10μ sections of testes of shovelnose sturgeon, stained with hematoxylin and eosin.

Figure 14. Section of mature developing testis (Stage II) filled with seminiferous lobules containing nests of spermatogonia (SG). 600X.

Figure 15. Early Stage III testis under oil (1000X) showing major portions of three lobules and interlobular stroma. Primary spermatogonia (PSG) and small nests of secondary spermatogonia (SSG) are visible and most of one lobule is filled with nests of spermatocytes (SC) and spermatids (ST). Blood vessel in stroma contains red blood cell (RBC).

Figure 16. Stage III testis exhibiting active spermatogenesis. Lobules are filled with nests containing spermatocytes (SC), meiotic prophase nuclei (MPN), maturing spermatids (ST), and early spermatozoa (SZ). A few nests of spermatogonia (SG) also are present. 400X.

Figure 17. Prespawning testis (Stage IV) collected in November 1969. The lobules are filled with maturing spermatozoa. A nest of spermatocytes (right center) and a few primary spermatogonia also are present. 400X.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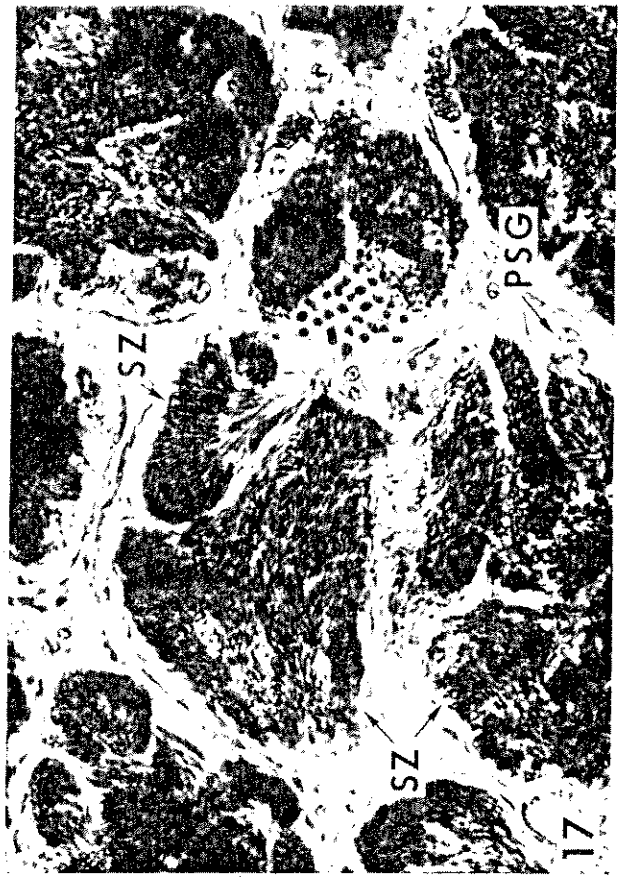
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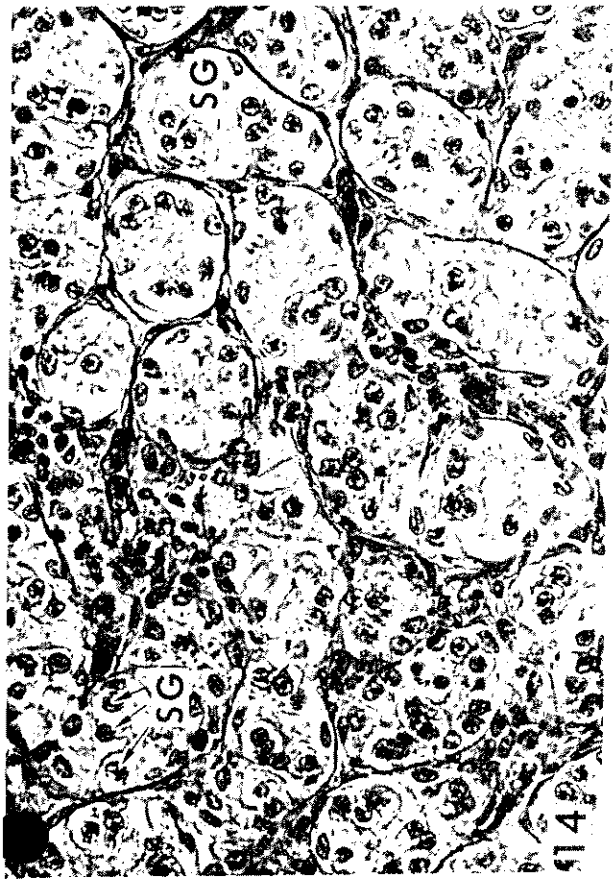
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SG
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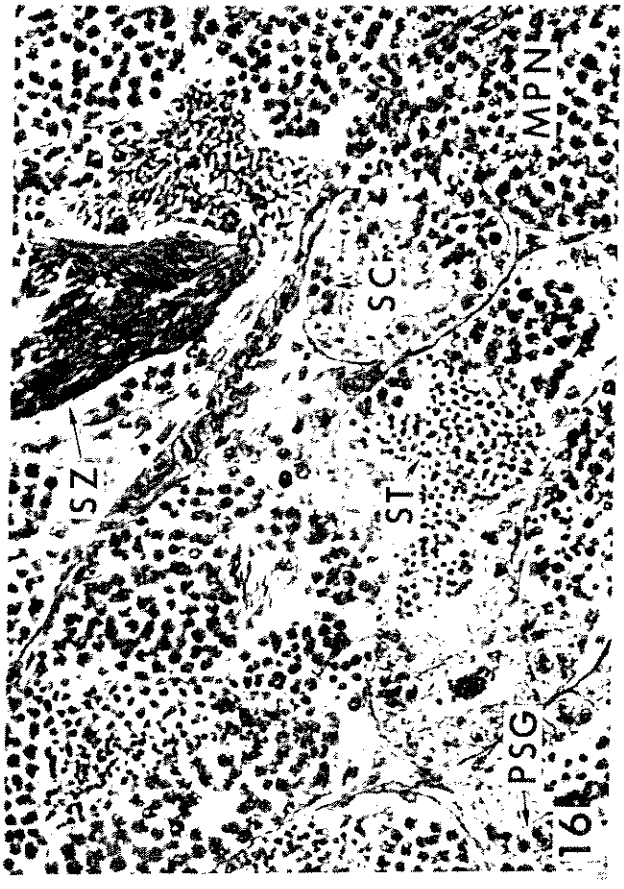

SZ
SC
ST
MPN
PSG
16

spherical (mean diameter of 6.0 μ) to elliptical (4.5 to 8.0 μ) and contained one nucleolus, typically found near the periphery. The scant nuclear chromatin was also peripherial in most cases. Secondary spermatogonia were usually spherical and smaller than primary spermatogonia, with an average diameter of 9.6 μ. Their spherical nuclei contained one or two centrally located nucleoli, averaged 5.75 μ in diameter, and had a reticulate arrangement of heavy chromatin strands. These cells divide mitotically to form primary spermatocytes.

Large numbers of spermatocytes were present in shovelnose testes only during a brief meiotic phase which occurred during August and September. The dramatic increase in cell division during this phase quickly filled the lobules with cells in many stages of spermatogenesis (Figure 16). Nests of spermatocytes decreased rapidly thereafter, and by November most nests contained spermatids and spermatozoa. Very few spermatocytes remained in the lobules by the following spring.

A few male shovelnose collected at the beginning of this meiotic phase had testes with only a few nests of spermatocytes. These early nests of primary spermatocytes contained nuclei averaging 4.45 μ in diameter. The lobules then quickly filled with nests of spermatocytes, usually with 30 or more cells, and numerous meiotic stages could be observed (Figure 16). No attempt was made to clearly differentiate between primary and secondary spermatocytes because of the numerous meiotic configurations and continuous size range of

the spermatocyte nuclei. In addition, the secondary spermatocyte is transient and rarely seen in its resting state (Weisel, 1943; Ahsan, 1966). The spermatocyte nuclei progressively became more basophilic and decreased in size as the spermatid stage was approached. The spermatocyte nuclei, had no nucleoli, were much more basophilic than in the spermatogonia, and filled most of the cell (Figure 16). Ahsan (1966) and Weisel (1943) described spermatogenic cells in the lake chub and sockeye salmon, respectively, and reported ample cytoplasm and nucleoli in the secondary spermatogonia but the primary spermatocytes had little cytoplasm and no nucleoli. This agrees with the interpretation of spermatogenic cell differentiation in shovelnose.

Larimore (1950) described paddlefish testicular cells which were similar to shovelnose secondary spermatogonia, but referred to them as primary spermatocytes. Otherwise, paddlefish and shovelnose testicular cells were very similar. The 14 male paddlefish examined by Larimore (1950) were all taken in April or May. At this time of the year the actively maturing shovelnose testes were filled primarily with spermatids and spermatozoa and few spermatocyte nests were present. If paddlefish have a brief but active meiotic phase in late summer as in the shovelnose, then there would have been few spermatocytes present in Larimore's collections. It is possible, therefore, that Larimore (1950) did not make the correct distinction between spermatogonia and spermatocytes.

In shovelnose, large clusters of spermatids were located centrally in the lobule. They initially appeared as cells with dense spherical nuclei 2 to 3 μ in diameter with little cytoplasm (Figure 16). As spermiogenesis proceeded the nest walls disintegrated and the nuclei became irregular to crescent shaped as the chromatin converged to one side. Mature spermatids appeared as short 1 μ diameter rods.

Spermatozoa occurred in compact groups staining deep blue to black with Delafield's hematoxylin. The early spermatozoa remained in dense arrays for several months but became more loosely organized as the spawning season approached. Within the clusters they were frequently oriented in the same direction with parallel flagella and the heads fanned out in a parachute-like cluster (Figure 17) similar to those described in perch (Turner, 1919) and bluegill (James, 1946). In a fresh milt smear from a spent shovelnose taken July 2, 1970, the length (head and mid-piece) of the spermatozoa averaged 7.7 μ with extremely long flagella of 40 to 45 μ. The head was tipped with a small round structure probably containing the acrosome. In stained material the body was of similar size, the 1 μ mid-piece less basophilic than the head, and the flagella appeared much shorter, probably because of incomplete staining.

2. Reproductive Stages

Based on macroscopic and microscopic examinations of 309 testes collected from May 1968 through November 1969, the reproductive cycle of male shovelnose was divided into six

testicular stages:

Stage I. Immature Testes
II. Developing Testes
III. Spermatogenic Testes
IV. Prespawning Testes
V. Spawning Testes
VI. Spent Testes

The testes used for microscopic analyses were taken from 100 males captured between April 15 and November 24, 1969.

a. Immature Testes: Stage I (Figure 18). Only two shovelnose were considered immature and their assignment to this stage was questionable because, microscopically, these Stage I testes were very similar to developing (Stage II) testes. They were considered immature primarily because the fish were small and a large amount of adipose tissue was associated with the testes. These males were the smallest shovelnose captured, and the only fish less than 40 cm fork length. They were 35.4 and 37.2 cm long and weighed 191 and 149 g, respectively. Only 10 of 563 processed shovelnose weighed less than 300 g. Eight of these were males and five of the eight were definitely mature since they were either captured in ripe condition (determined by macroscopic examination) or examined microscopically. A sixth male was assigned to Stage II on the basis of testicular gross morphology and the remaining two were assigned to Stage I. Macroscopically, the immature testes were narrow yellowish bands situated along the dorso-lateral surface of large,

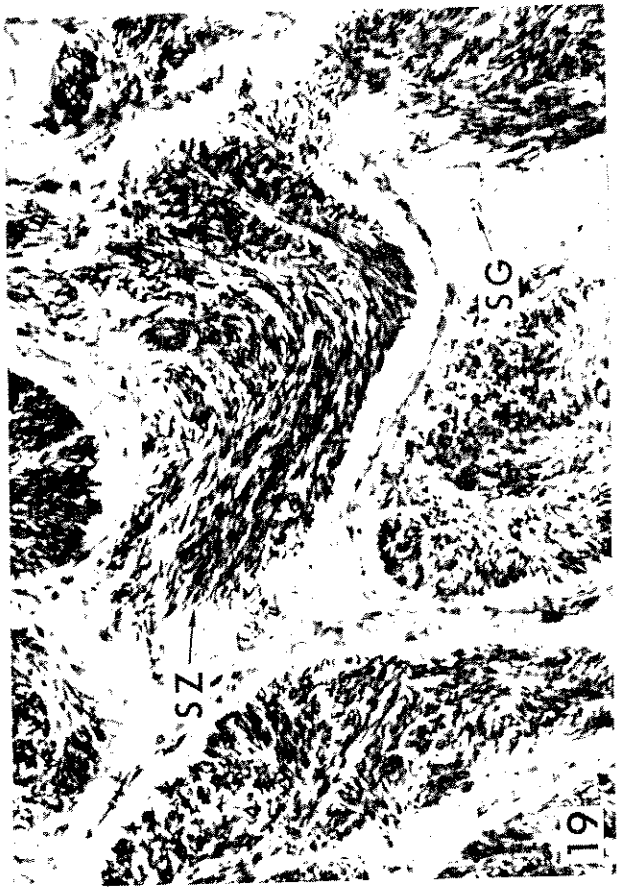
Figures 18-21. Photomicrographs of 10μ sections of testes of shovelnose sturgeon, stained with hematoxylin and eosin.

Figure 18. Section of testis from immature shovelnose showing testicular tissue along edge of adipose tissue mass. Testis filled with compact seminiferous lobules. 100X.

Figure 19. Spawning testis (Stage V) with all lobules filled with spermatozoa (SZ). Note lobule walls with a few spermatogonia (SG). 400X.

Figure 20. Spent testis (Stage VI) collected in July 1969. Lobules have empty lumina or contain residual spermatozoa. 40X.

Figure 21. Spent testis (Stage VI) collected in October 1969. Residual spermatozoa (RSZ) and phagocytes (P) remain but lobules are filled with primary and secondary spermatogonia (SG). 400X.



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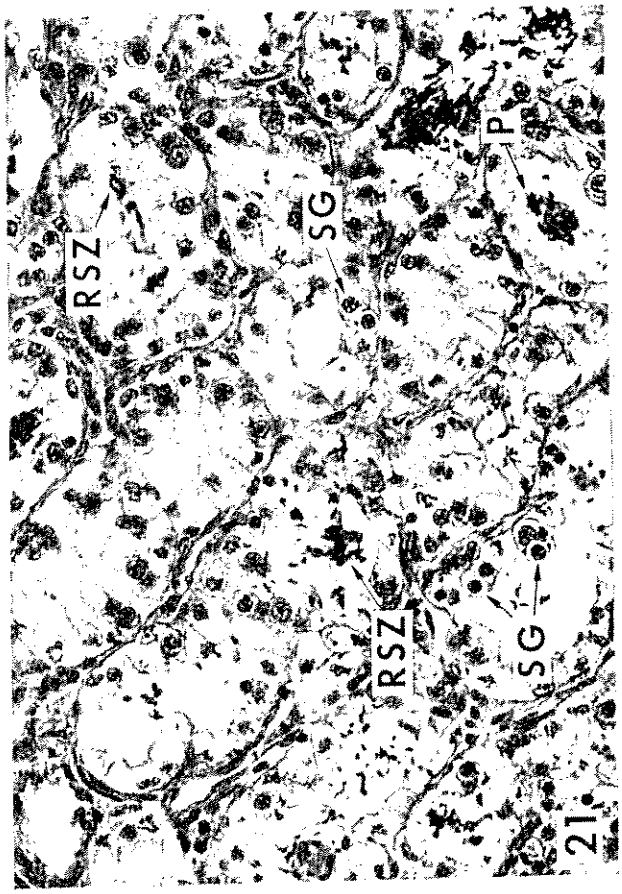

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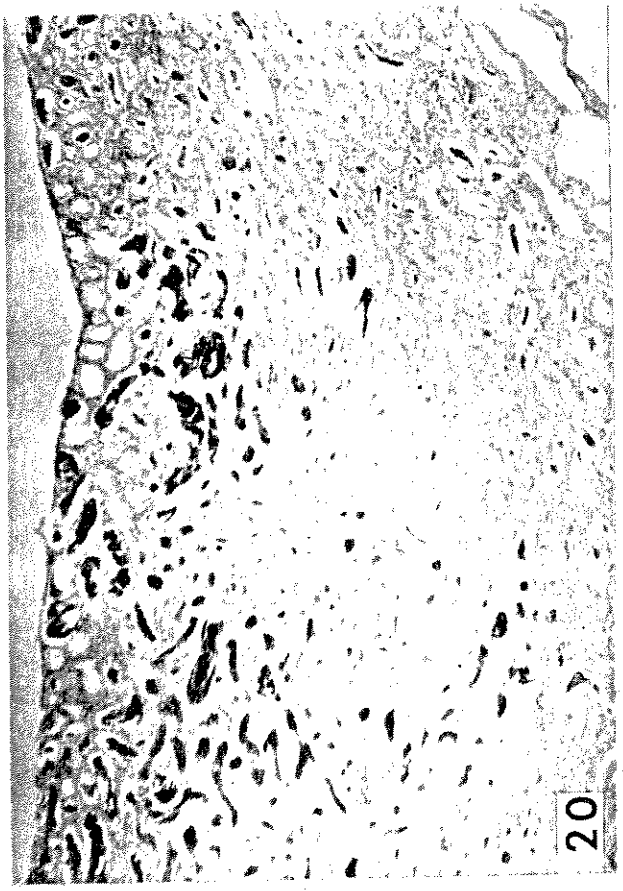

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lighter colored, fat bodies. The adipose tissue comprised 85-90% of the total cross-sectional area. Helms (1973) also described immature testes in shovelnose from the Mississippi River as narrow yellow bands, and found the testes formed less than 5% of the volume of the gonad-fat body complex. Microscopically, immature testicular tissue was composed of numerous compact lobules with no lumina. The peritoneal lining over the testicular tissue was continuous over the adipose tissue (Figure 18). The histological appearance of the two shovelnose testes regarded as immature did not resemble those of immature catfish and chinook salmon sent for comparison by Mr. Lafayette Eller from the Fish-Pesticide Research Lab in Columbia, Missouri. In the catfish and salmon, the lobules were widely spaced and they appeared as islands separated from each other by relatively wide expanses of stromal tissue. The lobules in the shovelnose, on the other hand, were compact and each lobule was in direct contact with at least three or four others. The lobules in shovelnose also appeared to be more developed and filled primarily with secondary spermatogonia.

Since the testes assigned as immature were very similar microscopically to developing testes, and no testes were available from sturgeon known to be immature, the assignment of testes to Stage I is questionable. The available evidence indicates that small males whose testes are associated with large amounts of adipose tissue are either immature or maturing fish which are being recruited into the breeding

population. Regardless of which interpretation is correct, it was apparent that few small shovelnose existed in this section of the Missouri River (at least my extensive sampling failed to capture small sturgeon). During 1968 and 1969 reliable length measurements were obtained from 3992 sturgeon and only 34 or 0.85% were less than 45 cm in fork length. The paucity of small shovelnose certainly was not entirely a result of sampling bias. Attempts were made to sample all available habitats within the study area with several types of gear. The only habitat which was not extensively sampled was the deep water zones within the main channel. However, shovelnose probably spend three or more years as immatures (Zweiacker, 1967; Helms, 1973) and it is doubtful that immature fish would spend this entire period within a restricted habitat such as the main channel.

b. Developing Testes: Stage II (Figure 14). Shovelnose with Stage II testes were collected from the river during every month of the year. Young males pass through Stage II as they mature and some spent males apparently revert to this developing phase before spawning again. Developing testes were narrow bands of yellowish-white to gray testicular tissue associated with fat bodies which usually comprised less than 50% of the gonad-adipose structure. Stage II testes, with rare exceptions, had a gonosomatic index (GSI) of less than 1.0 (Table 21). Shovelnose assigned to Stage II ranged from 44 to 53 cm in fork length with a mean weight of 403 g. The testes contained compact well defined lobules (Figure 14).

Table 21. Relationship of gonosomatic index, fork length, and body weight to reproductive stages in mature male shovelnose sturgeon processed in 1969. Males of uncertain reproductive stage were excluded.

Reproductive Stage	Number of Fish	Gonosomatic Index* Mean ± 1 SD**	Gonosomatic Index* Range	Fork Length (cm) Mean ± 1 SD	Fork Length (cm) Range	Body Weight (g) Mean ± 1 SD	Body Weight (g) Range
Developing	24	0.68 ± 0.25	0.25 - 1.22	49.2 ± 2.26	44.0 - 53.1	403.1 ± 67.8	227 - 546
Spermatogenesis	12	1.56 ± 1.43	0.29 - 4.92	50.5 ± 3.03	48.0 - 58.3	443.7 ± 137.2	326 - 822
Prespawning	29	2.61 ± 0.71	1.57 - 4.13	49.8 ± 1.60	47.0 - 53.5	437.4 ± 59.0	312 - 581
Spawning	52	1.83 ± 0.60	0.81 - 3.87	50.3 ± 2.89	44.2 - 59.3	464.1 ± 93.0	319 - 751
Spent	15	0.67 ± 0.41	0.25 - 1.93	52.4 ± 6.36	47.2 - 73.1	550.8 ± 359.8	376 - 1786

*GSI = (Gonad weight/body weight) x 100.

**SD = Standard deviation.

Most lobules had either no lumen or a small one. A relatively dense stroma of connective and vascular tissue filled the interlobular areas. During this stage the spermatogonia proliferate mitotically producing the cells which undergo spermatogensis in later stages. Mitotic nuclei were never abundant, suggesting a slow but continous increase in spermatogonia. In most Stage II testes the majority of the gonial cells were secondary spermatogonia located either in small nests or singly, but some primary spermatogonia and spermatocytes were always present. Spermatozoa and spermatids were seldom present, occurring only as residual entities from the proceeding spawning season.

c. Spermatogenic Testes: Stage III (Figures 15 and 16). This brief but prolific growth phase occurred from August through October. Nearly every lobule was filled with actively dividing spermatocytes undergoing meiosis, spermatids, and developing spermatozoa. Early Stage III testes resemble Stage II testes macroscopically, but they enlarged rapidly to form relatively large, light gray to white testes

characteristic of mature fish. Adipose tissue formed only a small portion (usually less than 15%) of the gonad in late Stage III males. The GSI of early Stage III testes was less than 1.0, but it increased dramatically as spermatogensis continued. Most Stage III males had GSI indices between 0.5 and 3.5. The largest GSI recorded for a Stage III male was 5.6, for a specimen collected in late August 1968. The largest GSI for 1969 males was 4.9 (Table 21).

Early Stage III testes contained a few active spermatogenic nests. However, lobules quickly increased in size as they became filled with active nests (Figures 15 and 16). The lobule walls were thin during this period and interlobular areas also decreased in size. The majority of the stromal tissue was located in spaces where three or more lobules abut each other. Spermatocytes with nuclei undergoing meiosis occurred in large nests and filled most of the testes. Nuclei in leptotene (MPN-meiotic prophase nuclei) and later meiotic configurations were common (Figure 16). As Stage III continued the number of spermatid nests increased rapidly. Although spermatids were more centrally located within the lobule there was no radial sequence of maturing nests within a lobule. The lumina increased in diameter as spermatids were liberated from the cyst walls. Spermiogenesis began shortly after the testes entered Stage III since a few nests of spermatids were observed early into Stage III. As maturation progressed dense clusters of spermatozoa increased in abundance while the peripherally located spermatogonia

apparently decreased.

d. Prespawning Testes: Stage IV (Figure 17). Since the preceeding Stage III was of short duration most actively maturing males were in Stage IV by early October. The GSI was greater than 1.0 (Table 21) and the testes were large, light gray to white organs.

After most lobules were filled with clusters of spermatozoa rather than active spermatogenic nests, the testes were assigned to Stage IV. Spermiogensis was now the principal activity. The lobules were larger than in the preceeding stages and the lumina diameter continually increased as spermatids and spermatozoa matured. The strongly basophilic clusters of spermatozoa remained relatively compact and the lobules walls appeared extended (Figure 17). A few spermatogonia were present. The remaining nests of spermatocytes and early spermatids interrupted the uniform masses of spermatozoa and became progressively less abundant as spermiogensis progressed. By late November the testes were almost completely filled with spermatozoa. Over the winter months (December to March) spermatogenesis was essentially arrested as the testes went into a dormant phase in December.

e. Spawning Testes: Stage V (Figure 19). From January until spawning occurred all testes packed with spermatozoa were assigned to Stage V. Since spermatogenesis was nearly completed by December and no discernable histological changes occurred during the inactive mid-winter period, Stage V was arbitrarily set to start with the calendar year.

Renewed spermatogenic activity was observed in the spring and as spawning time approached changes in testicular gross morphology were evident. The testes were large creamy white, soft organs. The vasa efferentia became distinct as white tubules in the mesorchia (Figure 13). Little adipose tissue was associated with these testes. Spawning activity peaked in June but commenced as early as late May and extended into early July. The GSI remained above 1.0 with rare exceptions and the mean for Stage V testes was 1.83 (Table 21).

A few spermatogenic nests remained in spring testes, but as the spawning season approached clusters of spermatozoa became less compact and the already uncommon nests of spermatids and spermatocytes decreased even more. The lobule walls thickened slightly as spermatogonia, mainly primary spermatogonia, began to increase (Figure 19). As males became ripe some lobules increased in size as they conducted spermatozoa towards the efferent ducts, and in limited areas adjacent to the efferent ducts the lumina began to empty. When this occurred the tension on the lobule walls was reduced, the epithelium thickened, and the spermatogonia became more obvious.

f. Spent Testes: Stage VI (Figures 20 and 21).

Spent testes of shovelnose retained the creamy white color of the ripe testes and did not exhibit much hemorrhagic tissue, i.e. appear "bloodshot". However, they became flaccid and much smaller than the turgid Stage V testes. A comparison of spawning and spent testes volumes indicated a

reduction usually exceeding 50%. Spent testes were the same size as Stage II testes and mean GSI values were similar for both stages; 0.68 and 0.67 (Table 21). Freshly spent testes, however, had little adipose tissue, were lighter colored, and much softer than developing testes. The GSI of spent testes was usually less than 1.0.

The largest portion of spent testes was occupied by lobules which were collapsed and elongated, either empty or partially filled with residual spermatozoa (Figure 20). The germinal epithelium thickened rapidly forming a complete lining within the lobule wall (Figure 21). While primary spermatogonia were numerous, secondary spermatogonia very rapidly became the most abundant cell type. In most spent testes residual spermatozoa disappeared within a couple of months. Testes taken in October and November with residual spermatozoa, but otherwise very similar to Stage II, were classified as spent. Phagocytic cells were not as numerous as expected but were obvious within the lumina in some fish (Figure 21). Apparently most spermatozoa were expelled during spawning and this may account for the low number of phagocytes observed. Residual spermatogenic nests were rare in spent testes.

3. The Reproductive Cycle

During any month of the year two distinct groups of mature male shovelnose were present. One group will spawn during the next spawning season while the other contained mature

males that will not spawn in the next season but require an additional year or more to produce spermatozoa. This either indicates that males recently recruited into the breeding population require two or more years before spawning for the first time, or that some mature males do not spawn annually, or that both of the above occur. The paucity of small shovelnose in Missouri River collections prevented me from determining the length of the maturation process in recently recruited males. However, since my sample consisted almost entirely of sexually mature fish, it appeared that male shovelnose don't necessarily spawn every year.

During January through May all mature males in the population were assigned to either Stage II or V (Figure 22). Stage II males represented recently mature fish that have not yet spawned for the first time, and/or mature males that probably spawned last year but did not undergo spermatogensis in preparation for spawning during the current year. Stage II, as previously noted, is a period of slow but sustained proliferation of gonial cells in preparation for the active meiotic phase that occurs in August.

During the first five months of the year Stage II and V males could be identified by visible characteristics and the GSI. Stage V testes were large, light gray to white, and had little if any adipose tissue. As the spawning season approached the creamy white color and soft texture made them even more distinctive, and the vasa efferentia were conspicously filled with sperm. With rare exceptions, Stage V

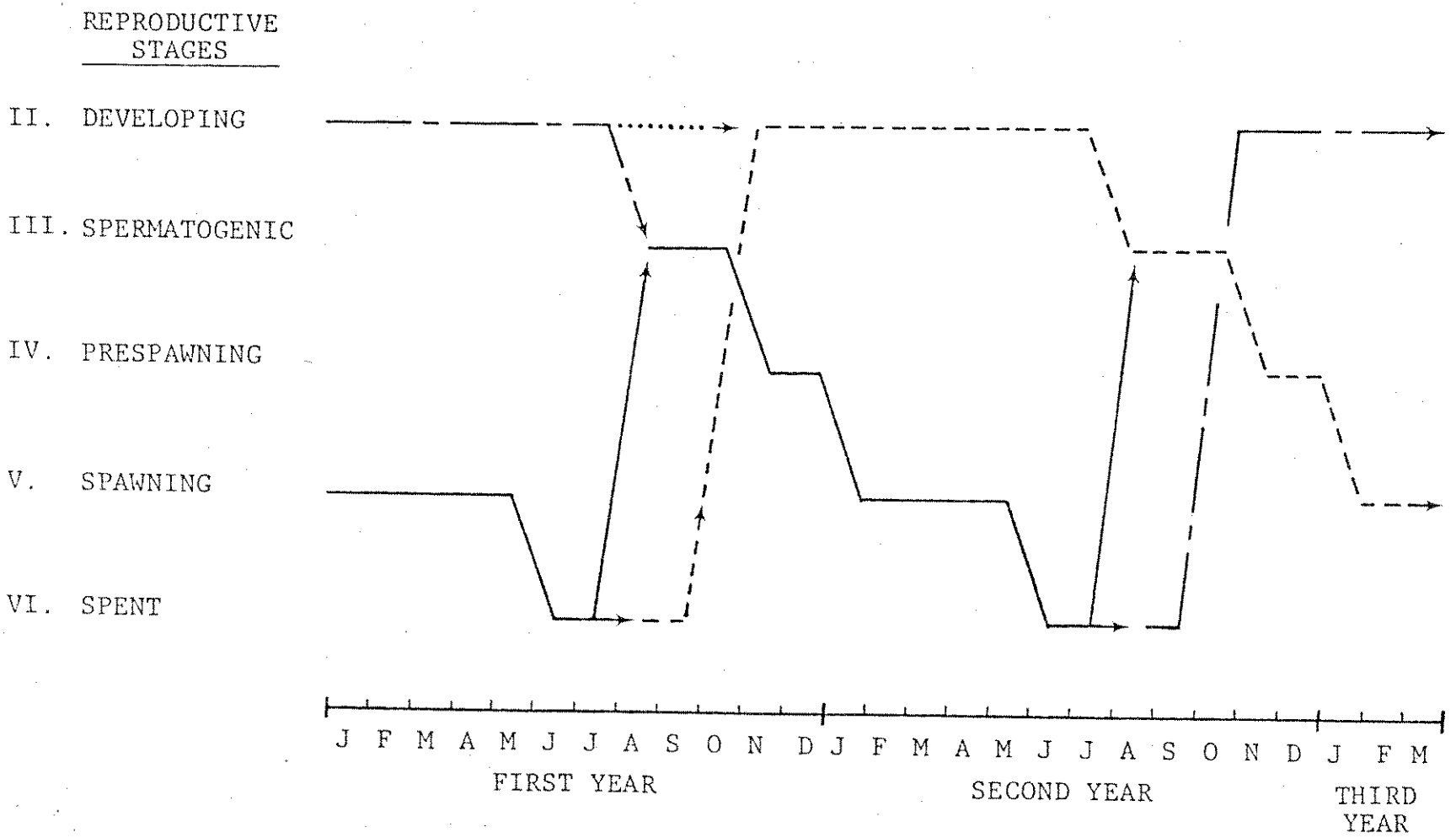


Figure 22. Diagramatic representation of reproductive stages of mature male shovelnose showing duration and potential sequence of reproductive stages.

testes had a GSI > 1.0. The smaller, yellowish to gray, Stage II testes usually had considerable adipose tissue and, with rare exceptions, GSI indices < 1.0.

During the June-July spawning season Stage II males remained in the developing phase and there was no change in morphology or GSI. Stage V testes, however, changed dramatically as spawning occurred. The volume of the testes decreased rapidly and the GSI declined below 1.0. Recently spent testes could be distinguished from Stage II because they remain creamy white and were softer. However, spent testes in shovelnose don't assume the flaccid, "bloodshot" or transparent appearance characteristic of many other fish species, and spent testes soon became difficult to separate from developing testes without microscopic analysis. If large fat bodies accompanied the testes, they were assigned to Stage II, but testes with small amounts of adipose tissue could be either Stage II or VI. Within a month after spawning most spent testes were similar to developing testes in gross morphology and GSI.

By late July and early August all males were either Stage II or VI, and proper identification required stained sections. At this time the reproductive cycle became complicated because both developing and spent fish can remain in their respective stages or proceed to the active spermatogenic Stage III (Figure 22). The dual fate of spent testes was obvious in microscopic sections. Many of the testes containing residual spermatozoa became filled with nests of

active spermatocytes exhibiting meiotic prophase nuclei. These spent males were entering Stage III. At the same time several spent males (containing residual spermatozoa) were collected that had dormant testes, that is, the testes contained mostly spermatogonia. These males apparently recovered more slowly and eventually progressed to Stage II during the fall (Figure 22). A few dormant spent males were observed as late as November. The males that spawned in June or July and then progressed into Stage III in August will spawn during the next season and, therefore, are on an annual cycle. Spent males that proceeded into Stage II during the fall will remain in Stage II during the winter and spring, and then progress into Stage III the next summer (broken line, Figure 22).

The possible dual destiny of Stage II males during late summer was not as evident as the dual pathway followed by Stage VI males. Stage III testes which did not contain residual spermatozoa or phagocytes were assumed to represent Stage II testes proceeding into the active spermatogenic phase. In addition, a decline in relative abundance of Stage II males between spring and fall suggested that many Stage II males progressed into Stage III in August and September. It was possible that all males assigned to Stage II during the summer proceeded into Stage III in August and September. If this is the case, then all Stage II males observed during the fall and winter must represent spent and immature males progressing into Stage II. The scarcity of immature males,

and the occurrence of early fall Stage II testes with no sign of residual spermatozoa, however, suggested that a few late summer developing males might remain in Stage II in the fall (dotted line, Figure 22).

The Stage II males that proceeded into Stage III in August did not spawn during the preceeding June-July season but will apparently spawn next year. They, therefore, represent males that are probably spawning every other year, or they are new mature males that will spawn for the first time next year. If a few late summer developing males remain in Stage II during the fall and winter they apparently represent males that spawn every third year.

A protracted reproductive cycle with several years between spawnings is a common feature for other sturgeon species (Magnin, 1962; Cuerrier, 1966; Semakula and Larkin, 1968). Some species not only exhibit several years between spawnings, but all members of the population are not necessarily on the same cycle. For example, tagging of lake sturgeon in Lake Winnebago, Wisconsin, has shown that some males spawn annually while others spawn every 2 or 3 years (Wirth and Cline, 1955; Wirth, 1958). Magnin (1966a) obtained similar results for lake sturgeon in the Nottaway River, Canada. Literature on lake sturgeon also suggests that the spawning cycle varies with geographic location. Sunde (1959), working on the Nelson River, Manitoba, indicated that males spawned every 4 or 5 years. Males in the Lake St. Pierre Region, Quebec, spawned every 2 years (Cuerrier, 1966) while Roussow (1957) found the

average interval between spawning for male lake sturgeon in the Ottawa River area was 7 years. Many European and Asian sturgeon also exhibit an extended reproductive cycle and females typically have a more extended cycle than males (Cuerrier, 1966).

In the Missouri River shovelnose population during August and early September it was impossible to distinguish between testes in Stage II, early Stage III, and Stage VI without histological analysis. The GSI was < 1.0 for all three stages and gross morphology was similar. However, spermatogenesis progressed rapidly and by mid-September most Stage III testes had a GSI > 1.0. High GSI values occurred earlier in 1968 than 1969, some ranging from 2.0 to 5.6 in August 1968, indicating that Stage III probably started earlier in 1968. As Stage III progressed the testes became larger and lighter gray in color. Size and coloration were variable, however, and may introduce some error if used without the GSI. Spent testes could not be distinguished by gross examination from developing testes in late September and October, but spent males became developing males sometime in the fall so these fish had the same destiny (Figure 22).

From October through December male shovelnose could again be divided into two groups, based upon their spawning potential. Males with relatively large, light colored testes and a GSI > 1.0 were in Stage III or IV and represented that portion of the male population that would spawn during the next season. Males with smaller yellowish to gray testes, varying

amounts of adipose tissue associated with the testes, and a GSI < 1.0 were in Stage II or VI. These fish represented the non-spawning portion of the population (Figure 22).

Spermatogenesis in shovelnose testes was arrested during the winter as the gonads became quiescent. This resting phase contrasted sharply with the active production of spermatids and spermatozoa from August through October. In this respect, maturation in shovelnose was very similar to maturation in yellow perch, Perca flavescens, threespine stickleback, Gasterosteus aculeatus, and northern pike, Esox lucius (Turner, 1919; Craig-Bennett, 1931; Lofts and Marshal, 1957). All species exhibited active spermatogenesis in late summer, an inactive winter period, and spring spawning. This cycle is also similar to that observed in other sturgeon, especially the Russian sturgeon, Acipenser guldenstaedti (Lemanova and Nusenbaum, 1968). Russian sturgeon spawn in late May and early June in the Volga River, and during these months males in Stages II, V, and VI are collected in the Volograd fish-lift. By the end of June spawning males (Stage V) are no longer present but some Stage III males appear. Russian sturgeon, therefore, enter the active spermatogenic phase a little earlier than shovelnose. In the Volga River, 90% of the breeding males complete spermatogenesis in September and progress into Stage IV. By March all breeding males were in the "completed" Stage IV, comparable to Stage V in this study (Lemanova and Nusenbaum, 1968).

Since the Missouri River population contains a mixture of males on 1, 2, and perhaps 3-year spawning cycles, only a fraction of the population spawns during one season. The percentage of the sexually mature population that spawns each year was estimated by comparing the relative abundance of spawning and non-spawning males. As previously stated, from October through May it was possible to separate breeding and non-breeding males by calculating the GSI (< 1.0 = non-breeding; > 1.0 = breeding) and observing testicular gross morphology. Sufficient Missouri River sturgeon with known GSI were available during May, October, and November to provide adequate estimates (Table 22). Spawning males comprised over 65% of the processed males in May, 69% in October, and 80% in November. The mean of these months indicated that about 71% of the mature males in the Missouri River study area spawn during a given season.

Although 71% of the mature males spawn in a given year, only a portion of these spawn annually while the others are on a 2 or 3-year cycle. Spent males that enter Stage III in August-September represent males on an annual cycle (solid line, Figure 22) while spent males not entering Stage III in August-September plus the Stage II males entering Stage III at the same time, represent the males on 2 or 3-year cycles. A few males entering Stage III in August-September probably were entering the breeding population for the first time but I believe that fraction is quite small so I assumed that recruitment was insignificant. Unfortunately, detailed

Table 22. Number of male shovelnose sturgeon processed during 1968 and 1969 showing proportion of males with a gonosomatic index greater than 1.0. Males with a GSI greater than 1.0 during April-May and October-November represent the spawning portion of the population.

Gonosomatic Index* (GSI)	Number per Month							
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
≤1.0	0	11	32	19	19	4	13	6
>1.0	4	21	77	12	22	11	29	24
Total	4	32	109	31	41	15	42	30
Percentage with GSI >1.0	100	65.6	— **	—	—	—	69.0	80.0

*GSI = (Gonad weight/body weight) x 100.

**Spawning and non-spawning males cannot be separated on basis of GSI during June-September.

microscopic examination of testes during August and September is required to determine the percentage of males on an annual cycle, and sample sizes were small at this time since fishing success was poor. Only 12 Stage III testes were examined microscopically, but 5 of these contained residual spermatozoa. Assuming that all spent males entering Stage III were recognized, 42% (5/12) of the Stage III males were on an annual cycle. The remaining Stage III males and the spent males remaining in Stage VI were on a 2 or 3-year cycle. Therefore, considerably fewer than 42% of the entire male population was spawning annually. If we assume that about 30% of the males spawn annually and that the rest spawn biennially and are distributed randomly so that half (35%) spawn each year, then this indicates that about 65% of the males

spawn in any one year. This latter estimate of 65% is close to the 71% estimated previously.

The annual variation in the GSI for male shovelnose from the Missouri River is shown in Figure 23. One plot (the solid line) was based on the GSI values for all males processed in 1968 and 1969 (Table 22), including breeding and non-breeding mature fish. This curve, therefore, is not directly comparable to plots seen in the literature for fish species that spawn annually. In order to obtain a curve more representative of a true annual cycle (Figure 23, the dash line), non-breeding males were excluded during April-June and in October-November by excluding fish with a GSI less than 1.0 during these months. By using June, some error was introduced because spent males (breeding fish) might have been excluded. However, the 1969 June samples examined microscopically contained few spent males with a GSI below 1.0 so the error was minor.

Gonosomatic indices for male shovelnose ranged from 0.25 to 5.64. Lowest indices were observed during the summer after spawning while highest indices were recorded during August-October, at the completion of the active spermatogenic Stage III. The small decrease in the GSI between May and June for breeding fish (dash line, Figure 23) suggested that a few male shovelnose may discharge spermatozoa during May. The occurrence of ripe males in the field by early June in both 1968 and 1969 supports the possibility that a few fish could spawn in May. The sharp decline in

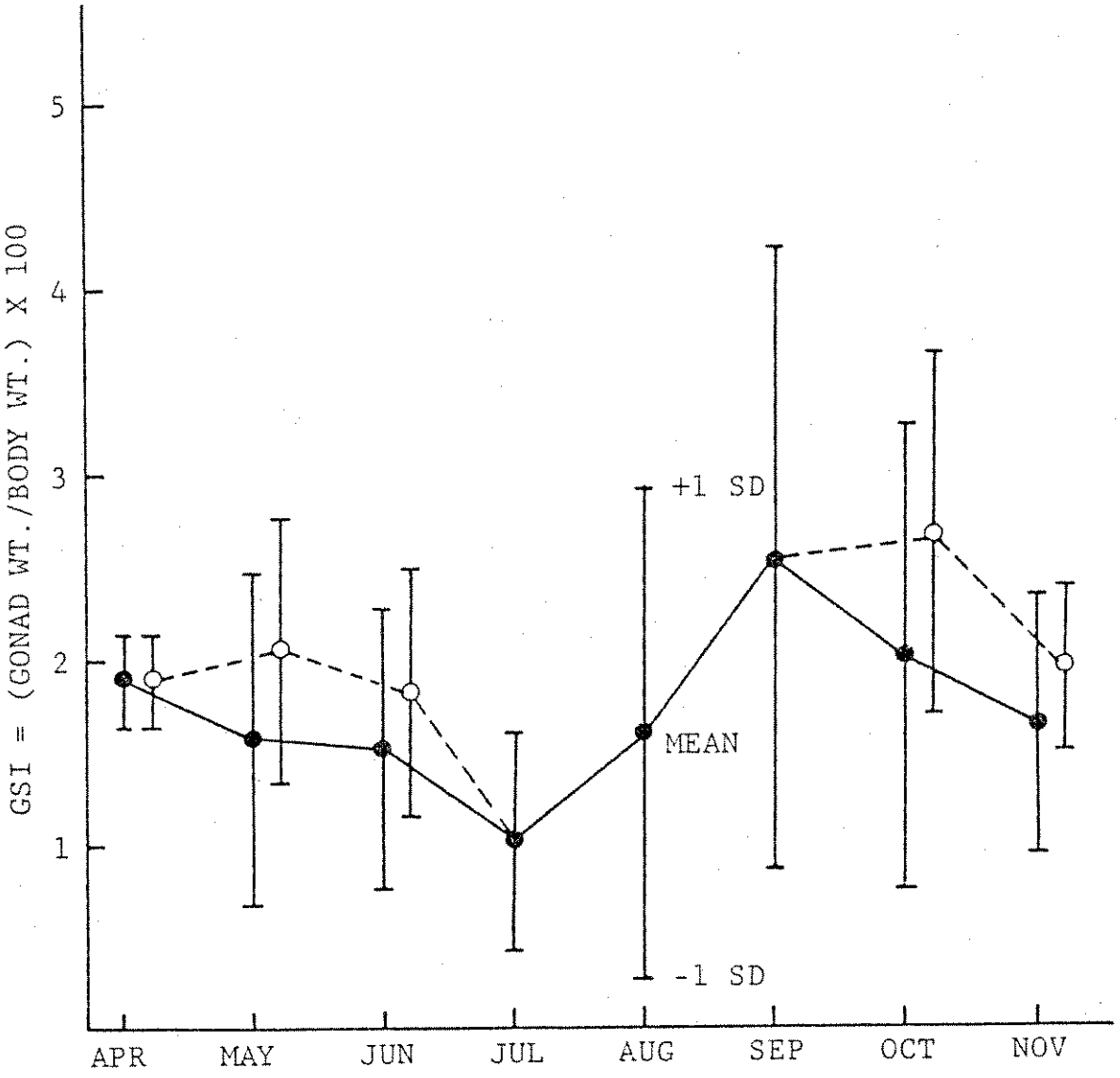


Figure 23. Seasonal variation in gonosomatic index of male shovelnose sturgeon collected from the Missouri River, South Dakota in 1968-1969. Solid line represents GSI for all male shovelnose, including both breeding and non-breeding fish. Dash line represents GSI of the breeding portion of the male population. Vertical line shows $\pm$ 1 standard deviation.

GSI between June and July correlated with the high occurrence of ripe males in June field samples and the appearance of spent males in July collections.

July and August GSI values were markedly lower than September and October values. The increase, especially between August and September, reflects the rapid increase in the volume of the testis during active spermatogensis. The steep slope emphasizes the rapidity of this phase. GSI values in excess of 4.0 were observed only during the August-October period. The decrease in the average GSI between October and November could not be explained by microscopic analysis. Spermiogenesis occurred during this period, but this would not account for the observed drop in the GSI. Adipose tissue associated with the testes could be an important factor here. If fat is utilized heavily in the early winter for maturation of spermatozoa or some other physiological function, it could account for some of this decrease. Cuerrier (1966) implied that adipose tissue was utilized for maturation of spermatozoa, but he did not indicate when utilization was highest. However, Cuerrier (1966) reported that the greatest amount of fat was found on the Stage III testes and decreased thereafter.

Male shovelnose were not collected during the winter, but late November testes were essentially identical to April testes based on stained sections. Average GSI values for breeding males in November and April were 1.93 ± 0.42 and 1.87 ± 0.26, supporting the theory that winter was a quiescent period.

C. REPRODUCTION IN FEMALES

The reproductive cycle of female shovelnose was divided into six stages corresponding closely to those used for males. In both sexes Stage I represented the immature individuals and Stage VI spent fish. Stage II, the developing stage, was regarded as the initial step in the cycle for mature fish. Stage III, the spermatogenic phase in males, was the yolk deposition phase in females while Stages IV and V represented shovelnose in the fall and spring, respectively, that were approaching spawning condition. The maturation cycle for females was based upon the microscopic analysis of ovaries from 111 females processed in 1969 and macroscopic comparisons between these ovaries and an additional 134 ovaries collected during 1968 and 1969. This comparison technique provided a reliable method for determining female reproductive stages without requiring stained sections and was based primarily on gross morphology and the size of the largest eggs within the ovary.

The six reproductive stages used in this study coincided closely with those established by Loukine (1941) and Moltchanova (1941) for the Russian sterlet, A. ruthenus. Loukine (1941) also included a Stage 0 which he considered to be indistinguishable ovaries and testes since both gonads appeared as narrow semitransparent bands. Stage 0 gonads were never seen during this study and only a few Stage I females (immature) were collected.

1. Microscopic Anatomy of the Ovary

Oogonia and oocytes are located within transverse lamellae (Figure 24) which extend into the body cavity from a medial foundation of dense connective, vascular, and smooth muscle tissue. The peritoneum covering the medial foundation is continuous over the entire organ, including any adipose tissue associated with the ovary.

Oogonia usually occurred in clusters within a germinal epithelium, frequently interspersed among oocytes adjacent to the lamellar border (Figures 25 and 26). These clusters varied in size from a few oogonia to 50 or more and were present during all stages of the reproductive cycle. They were common in immature, developing, and spent ovaries. Although oogonia became less obvious as the ovaries approached spawning condition it was difficult to tell if they actually decreased in number. The apparent decrease could have been an illusion created by the marked decrease in the relative volume of the germinal epithelium and stromal tissue as the ovary filled with mature oocytes.

Most oogonia were between 8 to 12 μ in diameter (mean diameter = 9.7 μ). They were grouped in clusters but remained nearly spherical (Figure 26). The cytoplasm, which stained lightly in hematoxylin and eosin, was surrounded by a delicate cell membrane. The spherical, centrally located nucleus (mean diameter = 5.9 μ) contained chromatin granules surrounding a single prominent nucleoli. Investing cells, similar to those described in the sea lamprey, Petromyzon marinus,

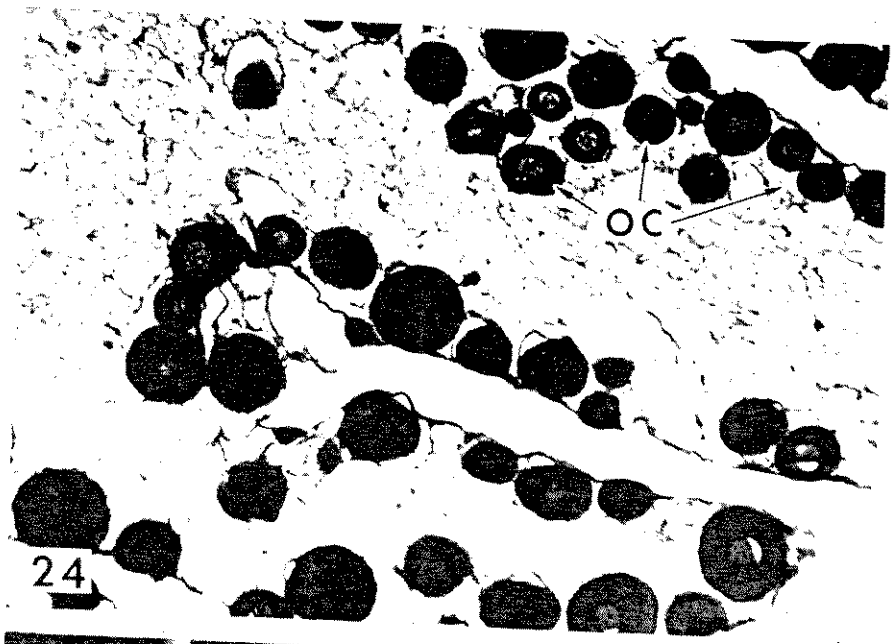
Figures 24-27. Photomicrographs of 10 μ sections of shovelnose sturgeon ovaries, stained with hematoxylin and eosin.

Figure 24. Immature ovary with developing oocytes (OC) along the edge of adipose tissue. Note the basophilic cytoplasm and numerous nucleoli. 60 X.

Figure 25. Mature developing ovary (Stage II) with numerous oocytes and well developed stroma. The largest oocytes are near 500 μ diameter. 60 X.

Figure 26. Cluster of oogonia (OG) and investing cells. Cell with prominent nucleus near center of cluster is transforming into an oocyte (TOC). 1000 X.

Figure 27. Early oocyte with granular cytoplasm and two prominent nucleoli (N). Follicle cells completely surround the oocyte. 1000 X.



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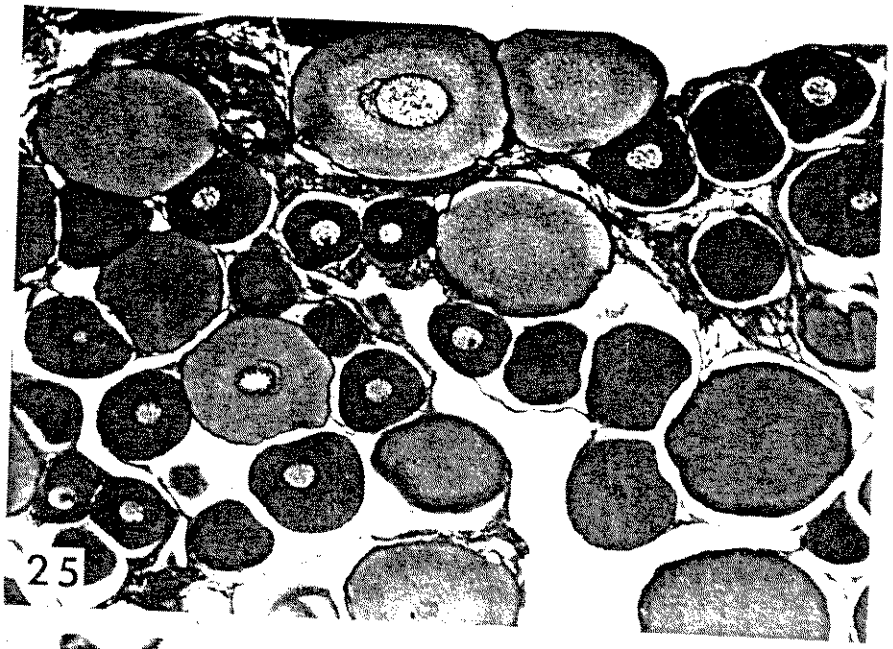

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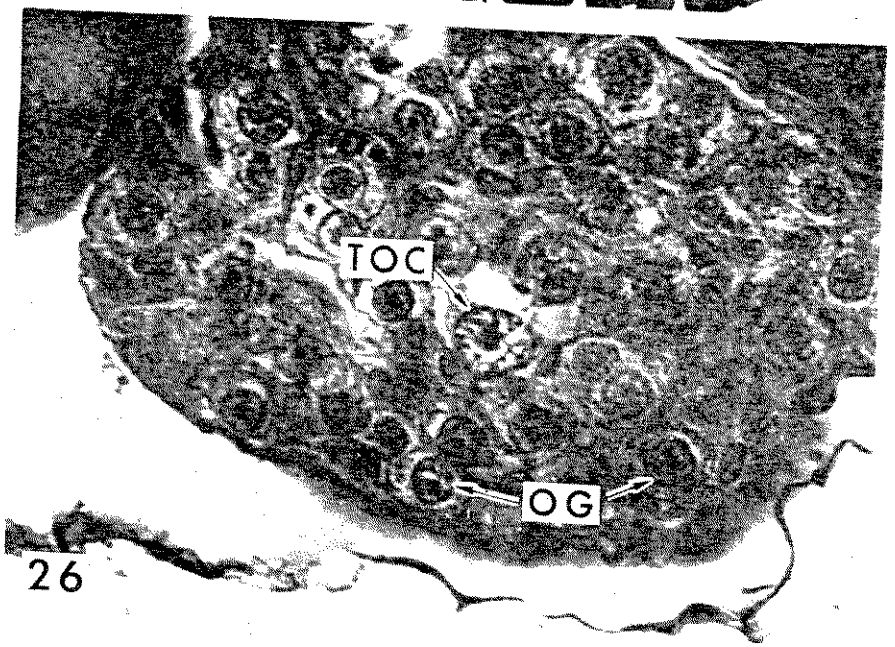

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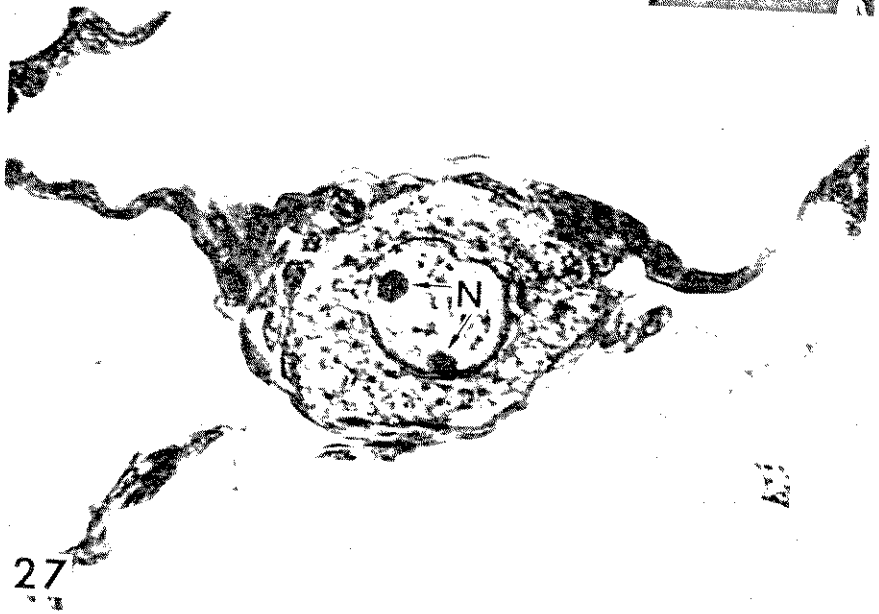

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(Lewis and McMillan, 1965), were found within the oogonial clusters. Their irregularly shaped nuclei contain a slightly denser chromatin than oogonial nuclei. The investing cells are dispersed among the oogonia, and larger ones are frequently curved to follow the circumference of the oogonia.

In sea lamprey and a few teleost species, the mitotic proliferation of oogonia is completed prior to sexual maturity (Zuckerman, 1962). More commonly however, mitosis continues during sexual maturity to produce new oogonia, as for example in crappies, Pomoxis spp. (Cooper, 1952); brook stickleback, Eucalia inconstans (Braekevelt and McMillan, 1967); Mummichog, Fundulus heteroclitus (Matthews, 1938); and paddlefish (Larimore, 1950). Shovelnose apparently belong in the latter group. Mitotic figures were observed in the oogonia but were relatively infrequent.

The transition from oogonia to oocyte was initiated by an increase in size of the germ cell. Within a cluster only a few oogonia underwent this transition at any given time (Figure 26). Primary oocytes were about twice the size of oogonia when meiotic figures first became obvious. Various stages of prophase were recognized in the early primary oocytes but none of the later stages of prophase were seen. These oocytes evidently entered the arrested diplotene stage characteristic of yolky vertebrate eggs (Zuckerman, 1962). When this occurs, the nucleus returns to a condition resembling interphase and meiosis is not completed until shortly before ovulation.

After the initial transition oocytes grew rapidly. Oocytes less than 150 μ in diameter usually contained a few prominent basophilic nucleoli and a granular basophilic cytoplasm (Figure 27). The cytoplasm became less granular and more basophilic as the oocyte matured and many additional nucleoli appeared along the periphery of the nuclear membrane, (Figure 25). Oocytes in an immature ovary were frequently located near the peritoneum covering the ovary and adipose tissue formed a major portion of the gonad (Figure 24). As the ovaries matured the oocytes enlarged, became more numerous, and filled the bulk of the ovary (Figure 25). Concurrently, the gross appearance of the ovary assumed a lamellar structure with compact leafy folds. These folds were obvious during Stage II and Stage III (vitellogenesis) and again in the spent ovary, but in a gravid ovary the lamellae were obliterated by the abundant large oocytes.

2. Reproductive Stages

The ovarian external morphology exhibited more obvious changes than the testes as they matured. Therefore, after the reproductive stages were defined using microscopic analysis I was able to develop a technique for identifying the reproductive stages without using stained sections. Identification was based on gross morphology and the size of the largest oocytes. Although the female GSI had a wider range (0.3-21.2) than males (0.3-5.6), it was not a good distinguishing character since females in Stages I, II, and III had overlapping GSI values, and all three stages were present

in collections throughout the year.

The size distribution of oocytes within stained sections from ovaries in the six maturation stages indicated that all ovaries contained oocytes in the 100-400 μ diameter size category (Figure 28). However, most ovaries also had a distinct group of larger oocytes and the oocyte size distribution was bimodal for Stages III, IV, and V. Measurements of the largest oocytes on stained sections indicated that the largest oocyte size was a good indicator of ovarian reproductive stages. There was overlap in the sizes of the largest eggs between some stages, especially between Stages II and VI, but in these cases differences in ovarian gross morphology permitted positive identification of the reproductive stage.

The potential of identifying reproductive stages utilizing sizes of the largest oocytes prompted an examination of preserved ovaries. Eggs were teased from preserved ovaries and then measured with a binocular dissecting scope fitted with an ocular micrometer. This procedure was easier than preparing histological sections and produced comparable results (Table 23). Oocyte diameters from preserved ovaries were larger than those determined from stained material because:

a) Diameter measurements of preserved oocytes included the membranes adhering to the oocyte, while measurements from stained sections excluded the follicle and conjunctive tissue.

b) Absolute maximum diameter was not measured in stained material unless the section contained a mid-plane section of the oocyte.

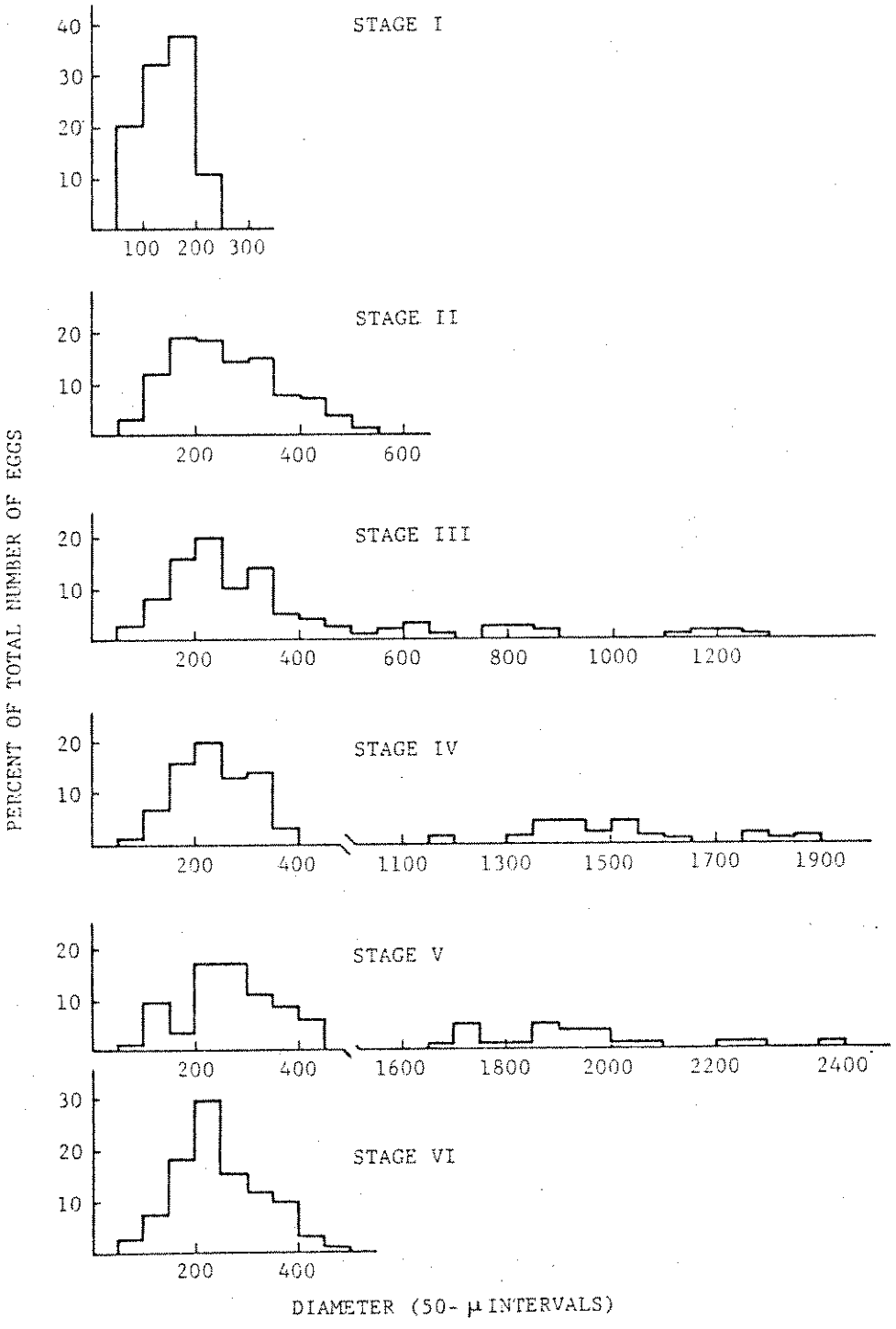


Figure 28. Histograms of oocyte diameter frequencies within the six reproductive stages of shovelnose sturgeon. Measurements were taken from 10 μ sections of ovaries imbedded in paraffin. Sturgeon were collected from the unchannelized Missouri River, South Dakota. Oocytes less than 50 μ were excluded.

c) Some shrinkage, in addition to that caused by preserving, occurred during imbedding and sectioning.

d) Stage IV and V ovaries were difficult to section and mid-plane sections were limited.

Table 23. Diameter (μ) of the largest oocytes in shovelnose sturgeon ovaries at the six reproductive stages. Sturgeon were collected from the unchannelized Missouri River, South Dakota, and ovaries were preserved in 10% buffered formalin or Bouin's solution.

		Microscopic Sections		Whole Preserved Oocytes	
Reproductive Stage	Sample Size	Mean (μ)	Range (μ)	Mean (μ)	Range (μ)
Immature	25	209	185- 230	306	250- 425
Developer	50	410	300- 525	522	400- 675
Yolk deposition	50	761	380-1330	958	450-1500
Prespawning	25	1525	1350-2218	1893	1609-2252
Spawner	25	2045	1688-2550	2608	2359-2824
Spent	50	359	255- 435	500	375- 625

a. Immature Ovary: Stage I (Figure 24). Although identification of immature male shovelnose was tentative, immature females were identified with confidence. Oocytes between 100-200 μ in diameter accounted for over 60% of the eggs in immature ovaries (Figure 28). The diameter of the largest oocytes averaged about 210 μ (in stained sections) in contrast to a mean diameter of around 410 and 360 μ in stages of mature shovelnose (Stages II and VI) that also have small eggs (Table 23). The external morphology was also distinctive since the lamellar structure did not become obvious until females attained maturity.

The immature ovary was intimately associated with a relatively large fat body that looked superficially similar

to an early mature testis. Indeed, the whole structure looked like a testis and, as mentioned earlier, could be misidentified. The ovary proper was represented by a thin ridge of ovarian tissue, situated along the dorso-lateral surface of the fat body. Some eggs could be detected with a dissecting scope but were not discernible to the unaided eye. The GSI of immature ovaries (which included the fat tissue) averaged 1.8 (range of 0.5-3.1).

Oocytes and clusters of oogonia in immature ovaries were frequently located along the periphery of the gonad (Figure 24), but in some cases filled much of the ovary. The larger oocytes (around 200 μ diameter) had a central nucleus containing numerous, deeply basophilic, nucleoli located around the periphery of the nucleus. Adipose tissue formed a major portion of the gonad in some immature females.

Three thin membranes or cell layers could be distinguished around the largest oocytes. Immediately adjacent to the oocyte membrane were small elongated nuclei of follicle cells, each separated by a distance about equal to their length. External to the follicle layer was a thin (≤ 1 μ) homogeneous layer that stained clear blue in Mallory's Triple Stain. This layer adhered to the follicle layer so closely that the follicular nuclei seemed to be partially imbedded within it. The outer third layer consisted of loose connective tissue which was continuous with the stromal tissue of the ovary. This outer stratum, referred to as the conjunctive tissue by Moltchanova (1941) could also be termed the theca.

Only 5 of 245 processed females were identified as

immatures. This supports the hypothesis, made earlier in the male discussion section, that few small shovelnose are present within this section of the Missouri River.

b. Developing Ovary: Stage II (Figure 25). The light gray to white Stage II ovaries were always associated with yellow adipose tissue. The amount of fat varied but it usually formed 25-50% of the ovarian volume. Lamellae were evident as compact leafy folds along the lateral surface of the ovary and some oocytes, exceeding 0.5 mm diameter also were visible. The GSI ranged from 0.75-4.46 and averaged 1.78 (Table 24).

Stage II ovaries were collected during every month of field sampling and accounted for 33% of the females processed during 1968 and 1969. This developing phase represents a period of oocyte proliferation and growth prior to yolk deposition. The ovaries of both immature and spent sturgeon apparently progress through Stage II prior to spawning. Ovaries with gross morphology typical of Stage II, except with less fat, are collected in the fall and probably represent spent ovaries entering Stage II.

Most of the oocytes in Stage II ovaries were between 100-400 μ in diameter (Figure 28), but the largest measured 400-500 μ (Table 23). Many Stage II ovaries had densely packed oocytes and well developed stromal tissue, especially fibrous connective tissue (Figure 25). In some ovaries, however, oocytes were sparse and adipose rather than stromal tissue was common. Clusters of oogonia were common. The

Table 24. Relationship of gonosomatic index, fork length, and body weight to reproductive stages in mature female shovelnose sturgeon processed in 1968 and 1969.

Reproductive Stage	Number of Fish	Gonosomatic Index* Mean ± 1 SD**	Gonosomatic Index* Range	Fork Length (cm) Mean ± 1 SD	Fork Length (cm) Range	Body Weight (g) Mean ± 1 SD	Body Weight (g) Range
Developing	79	1.78 ± 0.83	0.75 - 4.40	51.5 ± 3.00	41.8 - 61.7	470.6 ± 104.75	219.7 - 1020.6
Yolk deposition	48	2.79 ± 1.27	0.85 - 5.65	51.5 ± 2.65	47.0 - 58.6	475.7 ± 89.16	318.9 - 779.6
Prespawning	39	9.40 ± 2.64	5.50 - 15.07	51.3 ± 3.02	46.9 - 65.1	512.0 ± 148.36	347.3 - 1304.1
Spawning	29	15.42 ± 3.57	7.97 - 22.34	52.1 ± 3.06	47.6 - 60.4	542.9 ± 160.57	389.8 - 1268.7
Spent	38	1.54 ± 0.81	0.69 - 3.70	51.1 ± 2.20	47.2 - 56.3	440.3 ± 66.59	326.0 - 645.0

*GSI = (Gonad weight/body weight) x 100.

**SD = Standard deviation.

basophilic stain in the cytoplasm reached a maximum intensity in oocytes around 300 μ. The acidophilic nucleoplasm contained many small nucleoli located at the periphery (Figure 25).

Membranes and cell layers of larger Stage II oocytes were thicker than those in the immature ovary. The follicle remained as a single layer of cells, but the cells were thicker and shorter so the nuclei were closer together. The homogeneous layer between the follicle and conjunctive cells attained its maximum thickness of 3-4 μ during this stage. This layer appeared glossy and stained pink in hematoxylin and eosin, or a clear medium blue in Mallory's Triple Stain. Moltchanova (1941) and Magnin (1966a) called this layer the "membrane anhiste", but they did not describe its structure. A homogeneous layer, perhaps comparable to the "membrane anhiste" occupied the same relative position around brook trout oocytes (Hurley and Fisher, 1966), and they referred to it as the membrana propria folliculi. This layer disappears as the eggs mature in shovelnose, lake, and Russian

sturgeon (Moltchanova, 1941; Magnin, 1966a). Hurley and Fisher (1966) made no definite statement on the fate of the membrana propria folliculi but gave the impression that it did not persist. The outer layer around the shovelnose oocytes, the conjunctive layer, was similar to that seen in immature ovaries. It was frequently a single layer of squamous cells but became stratified where it joined stromal tissue.

c. Yolk Deposition: Stage III (Figures 29 and 30). This stage was characterized by oocyte growth and yolk deposition. The lamellae projecting from the medial core of connective tissue were obvious and the larger oocytes (1.0 - 1.5 mm) became pale yellow. Adipose tissue contributed less than 25% to the total ovarian volume and was frequently limited to medial surfaces. Two groups of oocytes were present in State III ovaries; those typical of Stage II ovaries and a group of larger oocytes exhibiting vitellogenesis. These two groups can be distinguished in formalin preserved ovaries. When observed under a dissecting microscope, the nucleus of the smaller oocytes appeared as a dark sphere within the translucent cytoplasm. The yolk filled cytoplasm of the larger eggs, on the other hand, was opaque and the whole cell was uniformly dark. The GSI of Stage III ovaries ranged between 0.85 and 5.65 (Table 24). Females in Stage III were collected throughout the year but were most abundant in early summer.

Although many eggs in Stage III ovaries enlarged to exceed the maximum size seen in Stage II (about 675 μ), new oocytes were being recruited so that a reserve stock was maintained. Size-frequency histograms indicated that all mature ovaries, regardless of reproductive stage, retained this stock of oocytes with diameters between 100 and 500 μ. About 18% of the oocytes in Stage III ovaries I examined exceeded 500 μ, suggesting that the reserve stock accounted for about 80% of the oocytes in the mature ovary (Table 25). However, several Stage III ovaries were in early Stage III. Counts of small vs large eggs in Stage IV and V ovaries indicated that the reserve stock was closer to 75% (Table 25).

Vitellogenesis began when oocytes were approximately 600-700 μ in diameter. The yolk appeared initially as a narrow band of deeply stained eosinophilic granules within the basophilic cytoplasm (Figure 29). The granules became more numerous, changed shape from spherical to elliptical as they increased in size, and dispersed into the cytoplasm. After most of the cytoplasm was filled, a zonation of granule sizes existed. Near the cell membrane and nucleus there was a dense array of small spherical granules. Centrally the granules were larger, elliptical, and more dispersed. The bulk of the cytoplasm finally filled with these large elliptical granules, the largest about 8 μ by 12 μ (Figure 30).

Yolk deposition, including the zonation of granule sizes, is apparently identical in several species of sturgeon (Moltchanova, 1941; Magnin, 1962 and 1966a; Lemanova and Nusenbaum,

Table 25. Distribution of oocyte sizes in female shovelnose sturgeon ovaries at different reproductive stages. Oocytes less than 50 μ in diameter were not included in these data.

Reproductive Stage	Number of Eggs Measured	Percentage of Eggs by Size Groups (Diameter in μ)				
		50 < 200	50 < 300	50 < 400	50 < 500	≥ 500
Immature	85	89.4	100	0	0	0
Developing	410	34.2	66.3	88.1	99.0	1.0
Yolk deposition	285	27.4	56.8	75.8	82.1	17.9
Prespawning	133	24.1	57.1	74.4	74.4	25.6
Spawning	83	14.5	48.2	67.5	73.5	26.5
Spent	123	28.5	74.0	95.9	95.9	4.1

1968), and parallels, to some degree, yolk deposition in amphibians (Balinsky, 1965). Elasmobranchs, cyclostomes, and ganoids also have a yolk distribution similar to amphibians (Balinsky, 1965; Lewis and McMillan, 1965). Yolk deposition in teleost fishes, however, is quite different. In teleosts, yolk first occurs as oil droplets and produces a "frothy" cytoplasm. Secondary yolk forms after these primary yolk vacuoles fill the cytoplasm, first within the primary vacuoles and later between the vacuoles. This intravesicular and extravesicular secondary yolk eventually merges to form a solid yolk globule filling the mature egg. This process has been described in brook stickleback by Braekevelt and McMillan (1967), in goldfish by Beach (1959), in crappies by Cooper (1952), and largemouth bass and bluegill by James (1946).

The number of chromatin granules within the nucleus decreased during Stage III, but the number of nucleoli remained

Figures 29-34. Photomicrographs of oocytes and their associated membranes of shovelnose sturgeon from the Missouri River. The 10 μ sections were stained with Delafields hematoxylin and eosin.

Figure 29. Oocytes in Stage III ovary exhibiting beginning of yolk deposition. Yolk granules (Y) formed in the cytoplasm near the cell membrane. Note numerous nucleoli (N) along periphery of nucleus. 150X.

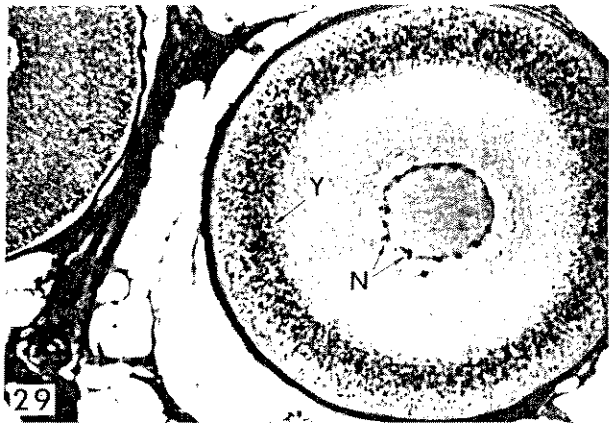
Figure 30. Membranes in Stage III oocyte include a zona radiata (ZR) adjacent to the cell membrane; then progressing outward a gelatinous membrane (GM), follicle cells (FC), the membrane anhiste (MA), and conjunctive tissue (CT). 1000X.

Figure 31. Stage IV oocyte with central nucleus and cytoplasm full of yolk granules; zona radiata and gelatinous membrane are well developed. Note sparse stroma and early oocyte. 100X.

Figure 32. Membranes of the Stage IV oocyte at 400X. The zona radiata (ZR) has two strata and is about twice as wide as the gelatinous membrane (GM). Small pigment granules are present just under the cell membrane and follicle cells (FC) and the conjunctive layer are thin.

Figure 33. Oocyte in Stage V ovary collected June 10, 1969. Nucleus has migrated into dense yolk at animal pole and a few nucleoli are present along the nuclear membrane. 60X.

Figure 34. Membranes surrounding a Stage V oocyte just prior to spawning. Inner and outer zona radiata were obvious (IZR and OZR) and the gelatinous membrane (GM) was amorphous. Note nucleus, micropyle (M) and thin follicle cell layer (FC). 400X.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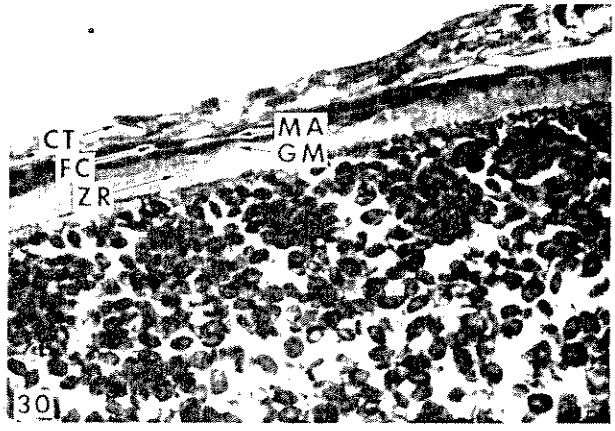
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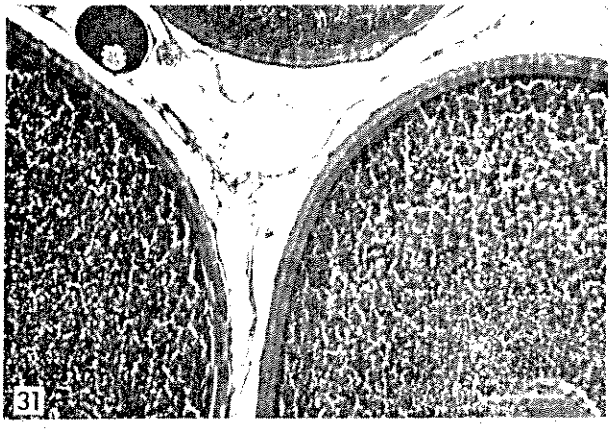
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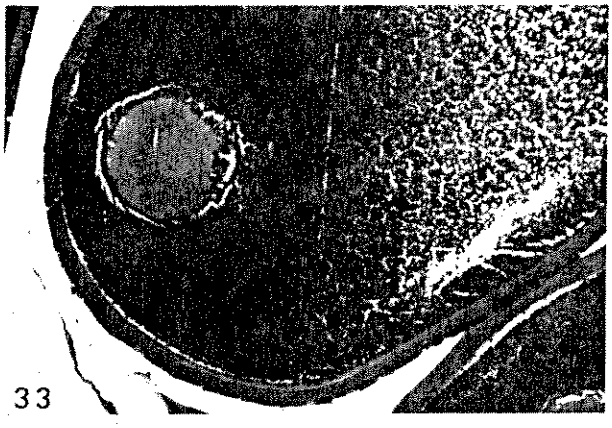
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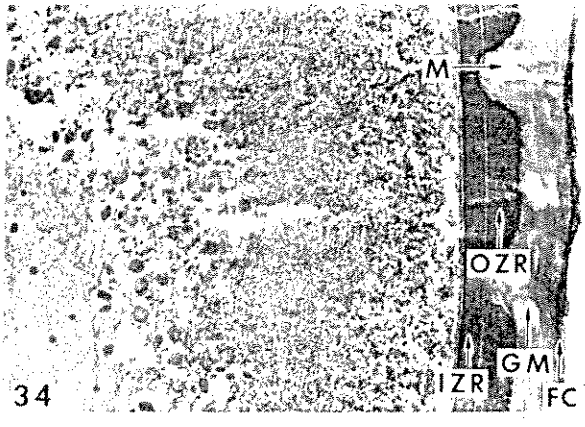
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high. Approximately 30 to 60 nucleoli were seen at the periphery of the nucleus (section 10 μ thick) and many smaller ones were scattered throughout the nucleus. The stromal tissue appeared less capacious but was still well developed. Adipose tissue was reduced but still present in some sections.

Concurrent with the beginning of vitellogenesis the zona radiata appeared. This hyaline acidophilic membrane was devoid of radial striations initially, but after it reached a thickness of a few microns striations became visible and a new layer appeared between the zona radiata and the follicle cells (Figure 30). This membrane in sturgeon has several names. Moltchanova (1941) called it the alveolar layer which she believed was produced by follicle cells. Ryder (1890) used the term colloidal membrane. Magnin (1962) described it as a homogenous gelatinous envelope and stated that Russian authors called it the gelatinous membrane.

In late Stage III the zona radiata had two distinct but seemingly identical strata which frequently separated during sectioning. The inner strata was slightly thinner and the thickness of the two strata was about 10 μ. The gelatinous membrane peripheral to the zona radiata was about 5 μ thick by late Stage III. Initially, fine wavy lines were seen in the gelatinous membrane, but by late Stage III the gelatinous matrix had a fine columnar-like configuration. The chemicals used in preparing histological sections apparently

shrank the matrix (or expanded the canals) so that the columnar structure was manifested (Figure 32).

In Stage III the three outermost envelopes, the follicle, membrane anhiste, and conjunctive layer were all thin, obviously stretched by the rapid growth of the oocyte during yolk deposition. The membrane anhiste had diminished considerably by this time. The conjunctive tissue, however, was several layers thick where it encountered the stroma or another oocyte.

Different authors have used different terms for the same membrane, especially if they were working on different taxa. In this paper the actual egg membrane, merely a boundary line under the light microscope, was referred to as the cell or vitelline membrane. The membrane just external to the cell membrane, which exhibited the obvious radial striations of the microvilli, was called the zona radiata. These two terms, as used here, correspond to the classification proposed by Ludwig (1874; cited by Hurley and Fisher, 1966). Many authors refer to the zona radiata as the vitelline membrane, or zona pellucida if it has no striations. The zona radiata is also frequently called the chorion by fisheries biologists (Hoar and Randall, 1969). More specifically, fisheries biologists use the term chorion for the outermost membrane of the ovulated egg which becomes "hardened" on contact with water and persists as the protective case around the embryo. According to Ludwig's scheme the term chorion

is not used for a primary membrane, that is, one formed by the oocytes, but is limited to secondary membranes formed by the follicle cells. While some authors believe that the zona radiata is produced by the follicle cells the majority say that it is formed by the oocyte (Hurley and Fisher, 1966). The origin of the zona radiata in sturgeon is evidently still unsettled but the gelatinous membrane is a secondary membrane according to Moltchanova (1941). Since the zona radiata is present in shovelnose before the gelatinous membrane, and continues to expand while the latter separates it from the follicle cells, it is probably formed by the oocyte. In sturgeon, the term chorion is acceptable for the gelatinous membrane since it is a secondary membrane and is also the outermost covering on the mature ovum. The sturgeon chorion is probably the gelatinous coat described by Ginsburg (1961) and Ryder (1890), who have shown that it provides the adhesive substance which attaches fertilized eggs to the substrate.

d. Prespawning Ovary: Stage IV (Figures 31 and 32). Most females with Stage IV ovaries were collected during August through December. During this period the ovaries filled most of the body cavity and the largest eggs were pigmented, going from brown in summer to black in fall. The largest eggs in preserved ovaries were 1.6 to 2.2 mm in diameter and filled the entire ovary (Table 23). During the summer and early fall different colored ovaries were taken on

the same date, indicating that maturation began earlier or progressed faster in some females. By late fall most of the Stage IV ovaries were identical, uniformly dark brown to black. On each dark egg a germinal disk representing the animal pole appeared as a lighter spot surrounded by a dark ring. Adipose tissue was rare or absent and the lamellar structure was obliterated as large eggs filled the ovaries. The GSI increased as these large eggs matured and ranged from 5.5 to 15.1 with a mean of 9.4 (Table 24).

There were two distinct oocyte groups in Stage IV ovaries. The smaller oocytes (100-500 μ) accounted for about 74% of all eggs (Figure 28 and Table 25) and represented the reserve stock for future spawning seasons. The remaining 26% provided the eggs for the next spawning season.

Increasing pigmentation of the large oocytes marked the beginning of Stage IV. Microscopically, this began as minute black pigment granules appeared in the cortical zone just below the cell membrane. These early Stage IV oocytes had a central nucleus with yolk granules distributed through the cytoplasm in a manner similar to late Stage III oocytes (Figure 31). At about mid-Stage IV the nucleus migrated toward the presumptive animal pole, identified at that time by an accumulation of small yolk granules. By late fall the nucleus had moved into dense yolk at the animal pole and most of these dark eggs had a noticeable bulge at the animal pole.

The nuclear membrane in late Stage IV was marked by a ring of nucleoli but the membrane itself was not evident. The nucleoplasm was finely granular and contained only a few centrally located nucleoli. These large yolk-filled eggs were difficult to section and open spaces along boundaries were commonly produced during sectioning.

The 'membrane anhiste' apparently disappeared early in Stage IV. The follicle and conjunctive layers were very thin and stressed by the growth of the large oocytes. The stroma was likewise reduced (Figure 31). In early Stage IV oocytes, the double zona radiata was 21 μ wide and the gelatinous membrane was 11 μ. The inner stratum of the zona radiata was half as thick as the outer stratum (Figure 32). In mid-Stage IV oocytes, the zona radiata and gelatinous layers were 29.5 μ and 15 μ thick, respectively. The relative thickness of these membranes was the same in ripe eggs during the spring spawning season.

e. Spawning Ovary: Stage V (Figures 33 and 34). All females with dark eggs collected during the first 6 months of the year (January-June) were assigned to Stage V. Like the testes, the ovaries changed little over the winter and the separation of Stages IV and V was based primarily on temporal rather than morphological criteria. However, the mean diameter of Stage V oocytes was about 500 μ larger than that in Stage IV. Most Stage V females could be recognized by external inspection because the large mass of black eggs

inflated the abdomen and produced an externally visible dark color.

Mature eggs in preserved Stage V ovaries were 2.3-2.8 mm in diameter ($\bar{x}$ = 2.6 mm) and capped by a germinal disk on the animal pole (Table 23). Although the ovaries appeared to be a solid mass of large oocytes, the smaller white oocytes of the reserve stock were visible under a dissecting scope. As in Stage IV, the reserve stock accounted for about 75% of all oocytes in the Stage V ovary (Figure 28 and Table 25). Fatty tissue was absent on Stage V ovaries.

The GSI of Stage V females ranged from 8.0 to 22.3. Although spawning activity peaked in June, a few Stage V females were observed during July and these could be confused with early Stage IV females which will not spawn until the following year. However, prespawning females had a GSI less than 10% in July through mid-August while all Stage V females caught in July, with one exception, had a GSI of 10% or more.

The migration of the nucleus into the animal pole was completed during Stage V and the nucleus of late Stage V oocytes was embedded entirely within the dense, finely granular yolk at the animal pole (Figure 33). The convex bulge at the animal pole was obvious. The large dark eggs dominated stained sections and the stroma was distended. In Russian sturgeon the nucleoli reportedly disappeared prior to ovulation (Lemanova and Nusenbaum, 1968). In shovelnose, there

were fewer nucleoli in late Stage V oocytes than in previous stages, but a few peripherally located nucleoli were always present. The zona radiata and gelatinous membrane increased slightly during Stage V and the division of the zona radiata into two strata was obvious (Figure 34). The follicle and conjunctive layers were stretched very thin. In a few late Stage V ova the gelatinous layer had lost its columnar pattern and became amorphous (Figure 34). Micropyles were observed at the animal pole; these appeared as narrow canals extending through the inner zona radiata which opened into depressions of the outer strata. Ginsburg (1961) observed an average of 10 micropyles grouped over the animal pole in Russian sturgeon, but observed that numerous micropyles did not result in polyspermic fertilization.

f. Spent Ovary: Stage VI (Figures 35 and 36). Spent ovaries were collected from June through November and exhibited a mean GSI of 1.54 (range 0.7 to 3.7; Table 23). They were flaccid, translucent, contained no adipose tissue, and did not acquire the hemorrhagic tissue commonly reported in many other fish species. The leaf-like lamellae were obvious and ruptured follicles were identified with a dissecting scope.

Few mature eggs remained trapped in spent ovaries. Spawning females collected during the spawning season were either full of eggs or completely spent, indicating that female shovelnose probably void their eggs over a short time

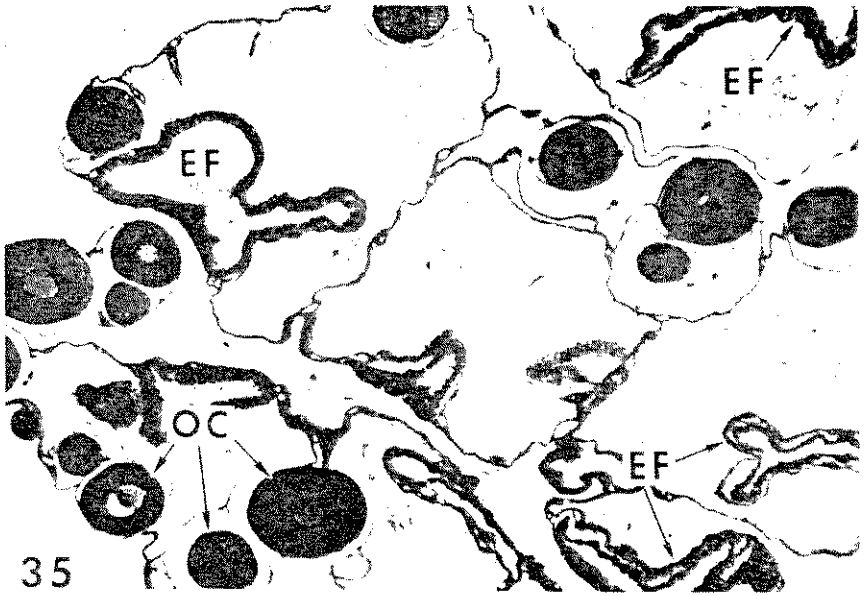
Figures 35-38. Photomicrographs of spent ovaries of shovelnose sturgeon and ovaries with atretic oocytes. The 10 μ sections were stained with Delafields hematoxylin and eosin.

Figure 35. Ovary from recently spent shovelnose sturgeon showing empty follicles (EF) and the reserve stock of developing oocytes (OC). 40X.

Figure 36. Hypertrophied wall of empty follicle showing columnar follicle cells (FC), a thin band of elastic fibers, and conjunctive tissue (CT). 1000X.

Figure 37. Mature Stage V oocytes exhibiting atresia. Numerous vacuoles (V) and angular chunks of yolk (AY) are dispersed in the cytoplasm. The zona radiata (ZR) and gelatinous membrane have degenerated. 100X.

Figure 38. Stage III ovary collected October 22, 1969 containing numerous atretic oocytes (AO). Egg membranes and almost all yolk have been reabsorbed from atretic eggs which are densly pigmented. Black atretic eggs and the white oocytes beginning yolk deposition produce a coloration referred to as the 'salt and pepper' condition. 40X.



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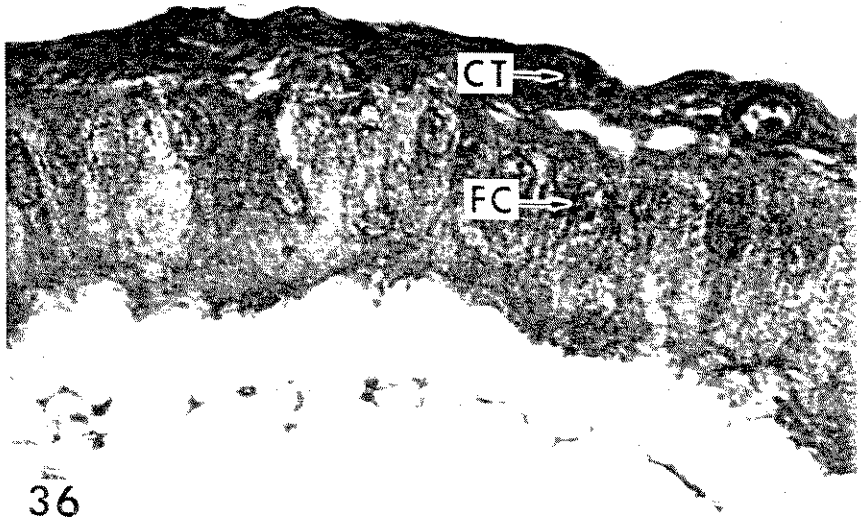

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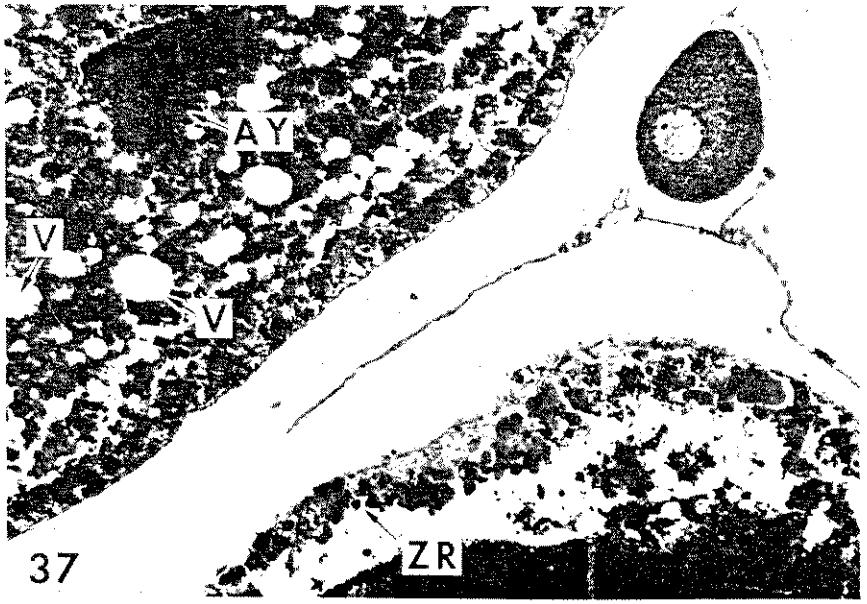

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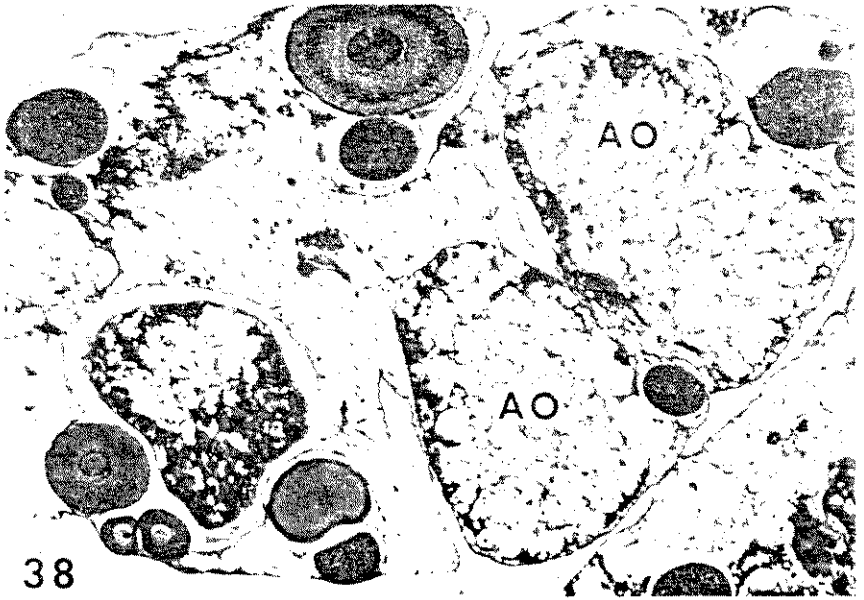

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period. Harkness and Dymond (1961) found that the eggs of ripe lake sturgeon flowed so readily that it was difficult to handle them during the stripping operation. Conversely, ripe males exuding milt were collected from the unchannelized Missouri River over an extended period (late May through June), and testicular histological sections confirmed the presence of numerous ripe males during this period. Each male might have spawned with several females during the season.

The mean size of the largest oocytes in spent ovaries was 359 μ (Table 23), and the diameter measurements of all oocytes indicated that an oocyte stock, similar in abundance to those in Stage II ovaries, was retained after spawning (Figure 28). Microscopically, oocytes in recently spent ovaries were scattered with intervening open areas occupied by empty follicles (Figure 35). Oocyte structure was identical to that described for oocytes in Stage II ovaries.

Immediately after spawning the ruptured follicle wall consisted of three layers (Figure 36). The most ectad layer was composed of low cuboidal to squamous cells of conjunctive tissue. Next was a wavy band of collaginous or elastic fibers which resembled the membrane anhiste in appearance and staining properties. In ruptured follicles this membrane was slightly wider (5-6 μ) than its counterpart in late Stage II oocytes. If the membrane anhiste is composed of elastic fibers, a structure compatible with its suspected supportive function, then it would stretch and become thinner as the

oocyte grows. It might even persist througout oogenesis even though too narrow to be evident under the light microscope, and reappear after ovulation. The third layer was composed of columnar follicle cells with nuclei located just inside the membrane anhiste. As the follicle began to collapse the conjunctive layer became several layers deep and seemingly disorganized, the follicle cells became cuboidal, and the fibrous band (membrane anhiste?) became more convoluted. In four of five spent ovaries collected in August 1969, most post ovulatory follicles had collapsed completely. They appeared as deflated spheres containing the sinuous fibrous band and randomly distributed ovoid cells with deeply staining basophilic nuclei. The eosinophilic fibrous band was persistent and remained in many Stage II ovaries as a small compact bundle surrounded by a few stromal cells.

The diffuse appearance of spent ovaries changed rapidly and by early fall a well developed stroma surrounded a compact array of oocytes. By late fall the spent ovaries resembled Stage II ovaries, except for the presence of collapsed follicles. The gross morphology of these two stages was also similar and separation of Stage II and VI ovaries by external morphology alone was tentative.

Since ripe females apparently retained very few mature ova after spawning, atresia of large yolk-filled ova was uncommon. However, structures that were assumed to represent late stages of atretic oocytes were present in all mature

ovaries. In other fish species two slightly different atretic processes have been described, depending primarily upon the amount of yolk contained in the oocyte (Beach, 1959; Braekevelt and McMillan, 1967; Lewis and McMillan, 1965). Atresia of large black yolk-filled ova and the occurrence of structures interpreted as a late phase of atresia of none-pigmented oocytes, suggested that two processes also occurred in shovelnose.

Atretic mature ova containing yolk exhibited several characteristic features. The zona radiata and chorion were ruptured as atresia began. The zonation of yolk granules seen in normal eggs was completely disrupted. The dense yolk at the animal pole was initially separated into several angular particles but soon became an amorphous mass while numerous vacuoles formed throughout the cytoplasm (Figure 37). Black pigment granules and parts of the zona radiata were present at the periphery, along with follicle cells. As atresia continued vacuolation increased and a reticulum began to form. A few yolk granules or particles remained for some time but the reticulum, resembling adipose tissue, soon filled the atretic oocyte (Figure 38). There was little structural change as the atretic oocyte became smaller, eventually forming a small sphere of condensed pigment and connective tissue.

Pigmentation increased during atresia of mature ova, due at least partly to condensation of pigment granules as the ova

shrank. Most black particles in later stages of atresia were slightly larger than the original pigment granules and measured 1-2 μ in diameter. This suggested that the primary granules either enlarged or coalesced, or were derived from a separate source. Regardless of its source, the pigment was persistent and remained even after most traces of the atretic oocyte disappeared. Approximately 20% of the Stage II and Stage III ovaries contained a mixture of white eggs and black pigment producing a condition that I referred to as the 'salt and pepper' ovary. The 'salt and pepper' ovary resulted when developing white eggs were mixed with black pigmented atretic oocytes in many cases (Figure 38). In some ovaries there was very little 'pepper' while in others, white eggs appeared to be embedded in a dark matrix. I assumed these various degrees of 'salt and pepper' also represented ovaries with atretic oocytes. Microscopic analysis revealed that 72% of the Stage II ovaries and 59% of those in Stage III contained some black granules, but most of these did not produce a visible salt and pepper condition.

The morphology of atretic oocytes suggested that much yolk was dissolved by enzymes rather than engulfed by phagocytes. Beach (1959) implied that enzymatic digestion was also more important than phagocytosis in goldfish, the enzymes being produced by follicle cells. Follicle cells in sturgeon were distributed primarily along the periphery of the atretic oocyte. Phagocytes were seen within the yolky

cytoplasm but apparently there was no mass invasion of phagocytes. This would agree with the atretic processes observed in sea lamprey and brook stickleback. In these fish, mass phagocytosis occurred during atresia of younger oocytes but not during reabsorption of mature ova (Braekevelt and McMillan, 1967; Lewis and McMillan, 1965).

Oocytes in all maturity stages are subject to atresia, but the process is usually more noticeable in mature oocytes. Although early atretic stages involving unpigmented oocytes were not observed in sturgeon, there were structures assumed to represent later stages of atresia that were different from those previously described. The main characteristics of these structures were the absence of pigment and the presence of an acidophilic band at the periphery. The homogeneous wavy band appeared to be identical with the fibrous band in post-ovulatory follicles. A thin boundary of connective tissue surrounded the undulating fibrous band while the bulk of the follicle was a fine reticulum containing small spherical basophilic nuclei. I assumed that these follicles probably diminished in size, eventually forming small compact bundles containing only the fibrous band and stromal cells, identical to the end product of the post-ovulatory follicle. This may account for the relatively high frequency of acidophilic follicular bundles seen in shovelnose ovaries.

3. Reproductive Cycle

The female shovelnose reproductive cycle was more complex than the male cycle. Whereas many males spawn annually, it appeared that few or none of the females do. The difference between the sexes occurred mainly during Stages II and III which are more protracted in females. This might be expected since ovaries are heavier than testes, and therefore require more raw materials and presumably more time to develop. Mature ovaries comprised over 22% of the total body weight in some shovelnose (mean GSI = 15.4), while testes seldom accounted for more than 5% (Tables 21 and 24).

Most female shovelnose were apparently on a 2 or 3-year reproductive cycle, and the relative abundance of females within the five mature reproductive stages indicated that a 3-year cycle might be more common. Mature females were partitioned into three groups; those that spawned in the current year, those that will spawn next year, and the third group which did not spawn in the current year and probably will not spawn next season. First, there was no evidence that spent females progressed into Stage III in the same year that they had spawned, as was observed in some males. Therefore, females that spawned in the current year were represented by spawning (Stage V) and spent (Stage VI) females. This group comprised 29.4% of the females processed in 1968 and 1969 (Table 26). Secondly, since females in Stage III were common in collections from June through November it was apparent

Table 26. Monthly distribution of female shovelnose sturgeon among the six reproductive stages. The data were derived from processed females selected from the 1968 and 1969 Missouri River samples.

Reproductive Stage	Months								All Months Combined	
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Number	Percentage
Immature	0	2	0	0	1	1	1	0	5	2.0
Developing	1	15	5	14	14	4	18	9	80	32.7
Yolk deposition	0	2	14	9	9	2	8	4	48	19.6
Prespawning	0	0	1	4	18	2	12	3	40	16.3
Spawning	4	5	15	7	1	0	2*	0	34	13.9
Spent	0	0	9	8	12	6	0	3	38	15.5
All stages	5	24	44	42	55	15	41	19	245	100.0

*Two females that would have normally spawned in June or July were used as experimental fish and sacrificed in October. At that time, all Stage V ova were atretic.

that yolk deposition required more time than the spermatogenic Stage III in males. Therefore, females in Stages III and IV represent fish that will spawn next season. This group accounted for 36% of the processed females (Table 26). Finally, Stage II females were common during all months of field sampling, implying that this stage has a long duration. These females did not spawn during the current year, and must progress through Stages III, IV, and V before spawning, so they won't spawn next season. This group comprised almost 33% of the processed females. In summary, female shovelnose spend about a year in Stage II, then progress through Stage III and IV during the following year, and spawn the third year.

Selection of females for processing was not strictly random, and thus the percentages shown in the tabular data may be biased. Since most shovelnose were the same size (see Section 1), there was a preference for unusually small and large fish. Selectivity for small fish would have inflated the relative abundance of immature fish, but only 5 of 245 females were immature. The paucity of immature females was additional evidence that recruitment into the spawning population was low. Preferential selection of large fish probably had little effect because large females could belong to any of the five mature stages. There also was some selection for females full of dark eggs, both in the spring and fall. This may have increased the percentage

of Stage IV and V females, but I felt the impact was small because the relative abundance of Stage V and VI females was about equal, as would be expected.

Another possible source of bias was incorrectly identifying spent ovaries as Stage II ovaries in the fall. Spent ovaries "recuperated" during the summer so that by October it was difficult to distinguish Stage VI and II ovaries. This error, if it occurred, would cause the percentage of spawners to be too low, and indeed this group of females was a little below the expected abundance of fish on a 3-year cycle.

Close examination of oocyte growth rates in Stages II, III, and VI provided additional information on the possible duration of these stages, and also indicated that some females spawn every other year. This 2-year cycle is shown in Figure 39 as a solid line and the sequence of stages is best explained starting with spent females in 1968 (the first year).

Spent females were collected from June through November. When the average diameter of the largest oocytes in each female was plotted against time of collection, an estimate of oocyte growth rate was obtained (Figure 40). In June, the average diameter of the largest oocytes in spent females was 420-520 μ. This size corresponded with the size of the largest reserve oocytes found in spawning females (Figure 28). Spent females taken later in the summer and fall had progressively larger oocytes and a regression line indicated that the average oocyte growth rate was 30 μ per month (Figure 40).

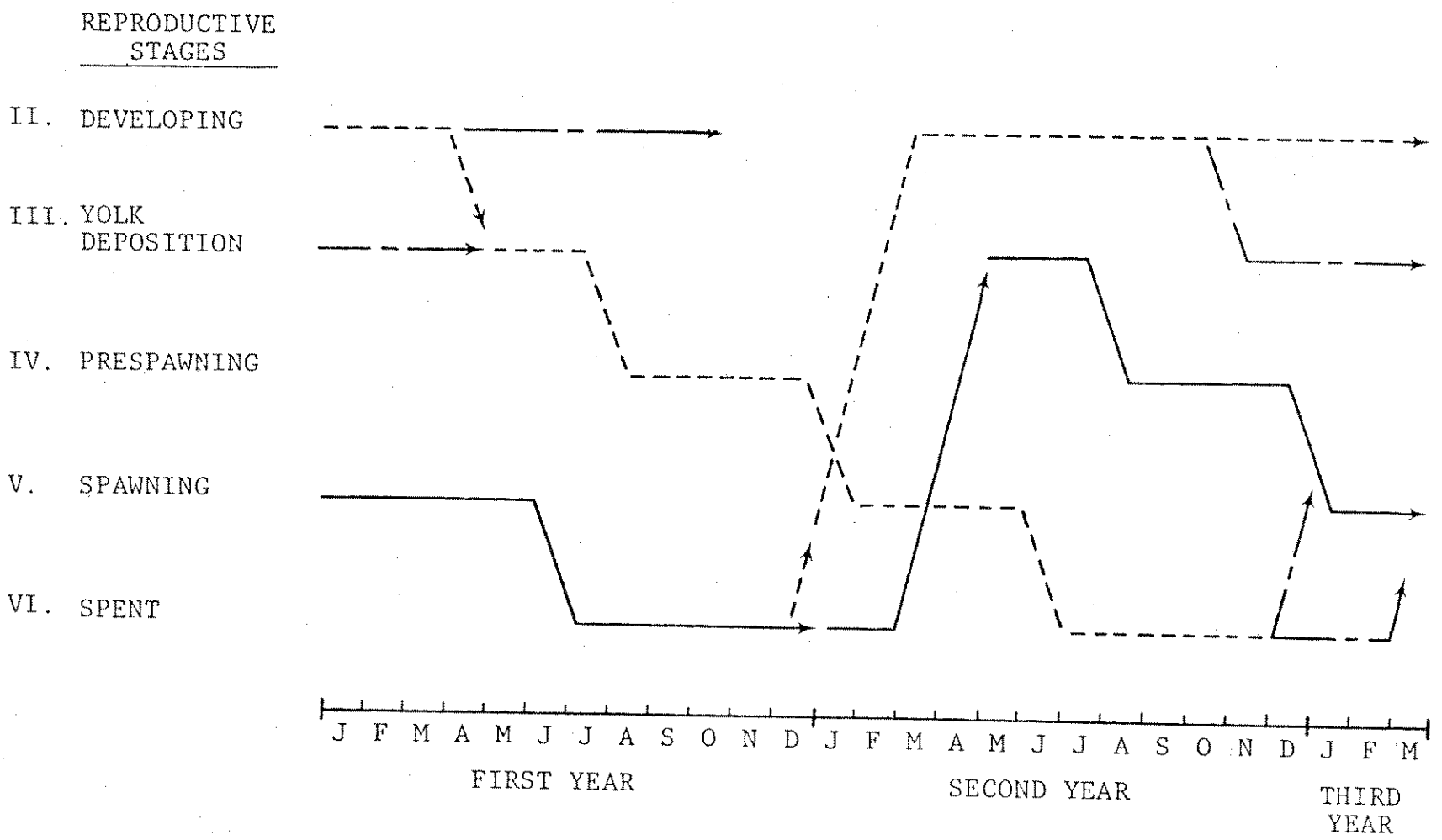


Figure 39. Diagramatic representation of 2- and 3-year reproductive cycles in female shovelnose sturgeon collected from the unchannelized Missouri River, South Dakota. Females on a 2-year cycle (solid line) progressed into the yolk deposition stage during the winter or spring following the spawning season. Females on a 3-year cycle (dash line) progressed into Stage II after spawning and remained in that developing stage for nearly a year before beginning yolk-deposition.

By November, the largest oocytes were around 625 μ, near the maximum size for oocytes in Stage VI ovaries.

Most Stage VI females probably remained in that stage through the 1968-69 winter (Figure 39), and progressed into early Stage III during the following spring. Even if Stage VI females progressed into Stage III in the fall, they probably remained inactive over the winter and were still in early Stage III in the spring.

Within Stage III ovaries, oocyte measurements indicated that early Stage III ovaries with relatively small oocytes were present during much of the year (Figure 41). The largest Stage III oocytes were present in June through August, indicating that yolk deposition was completed during the summer. Moreover, early Stage IV ovaries with light brown eggs appeared in the June through August period, reaffirming that yolk deposition was completed during the summer. These observations suggested that the females that spawned in 1968 spent the following winter in either late Stage VI or early Stage III, then completed yolk deposition during the summer of 1969. These females progressed into Stage IV during late summer 1969 (most of the early Stage IV females were collected in August) and spent the second winter in late Stage IV (Figure 39). In spring 1970 these females were in Stage V, ready to spawn in June or July, i.e., a 2-year cycle.

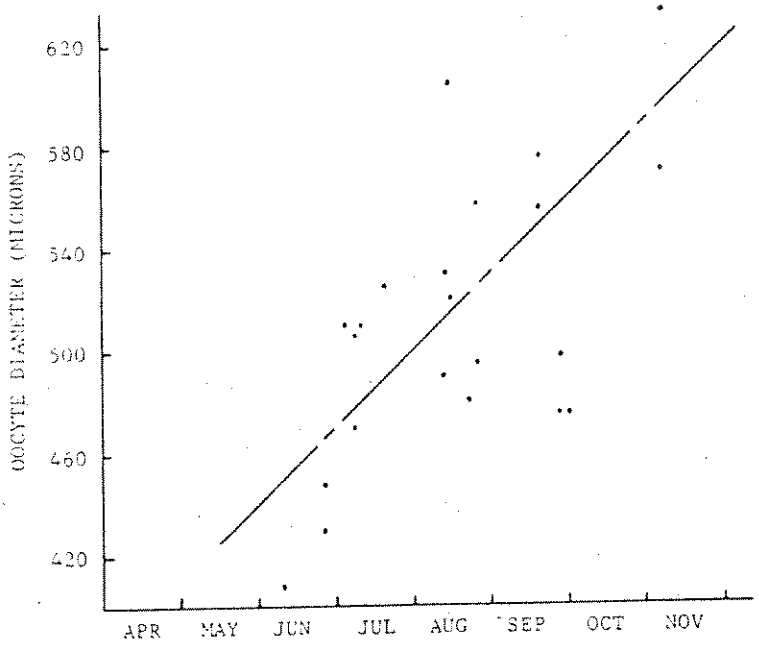


Figure 40. Relationship between collection date and the size of the largest oocytes (mean diameter in μ) in shovelnose ovaries from spent females collected from the unchannelized Missouri River, South Dakota.

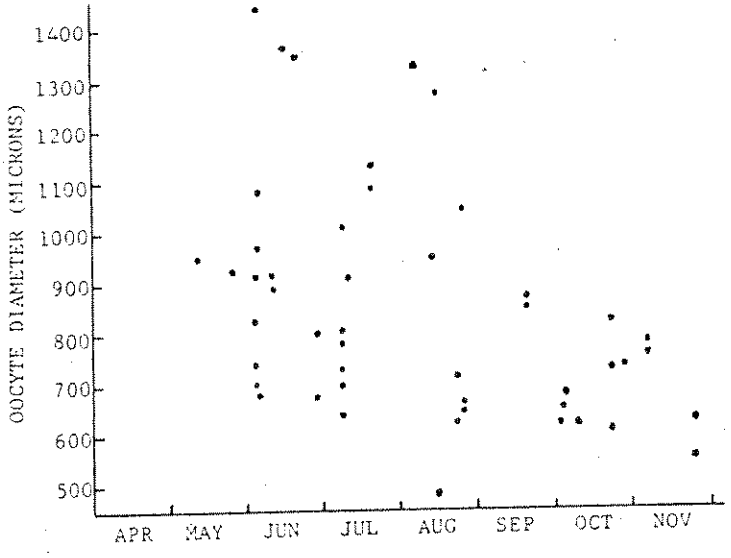


Figure 41. Relationship between collection date and size of the largest oocytes (mean diameter in μ) in shovelnose ovaries during the yolk depostion phase (Stage III).

The two-year cycle described above requires that females are in Stage VI through one summer and Stage III during the next summer. But, all spent females don't follow this sequence because Stage II females were also collected during the summer. Some Stage II females represent immatures recently recruited into the mature population, but many of the Stage II ovaries collected in the summer contained atretic pigmented eggs and/or remains of post-ovulatory follicles, indicating that these females had spawned before. Also, the relative abundance of Stage II females indicated that many of the mature females go through Stage II prior to Stage III. Based on this evidence, I believe that a portion of the Stage VI females progressed into Stage II in late fall (see dash line-Figure 39). The females going into Stage II develop slowly and probably remain in Stage II during 1969 (assuming they spawned in 1968), then progress into Stage III in late fall 1969 or spring 1970, and finally spawn in 1971 (a 3-year cycle).

The temporal size distribution of oocytes in Stage II ovaries appeared to be random (Figure 42), indicating that females in both early and late Stage II were present in the population during most of the year. Several Stage II ovaries with relatively large eggs (580-620 μ) was observed in October and November, and these apparently match the October-November cluster of early Stage III ovaries with relatively small eggs (550-750 μ, Figure 41), indicating some Stage II females progress into Stage III in the fall. Females that

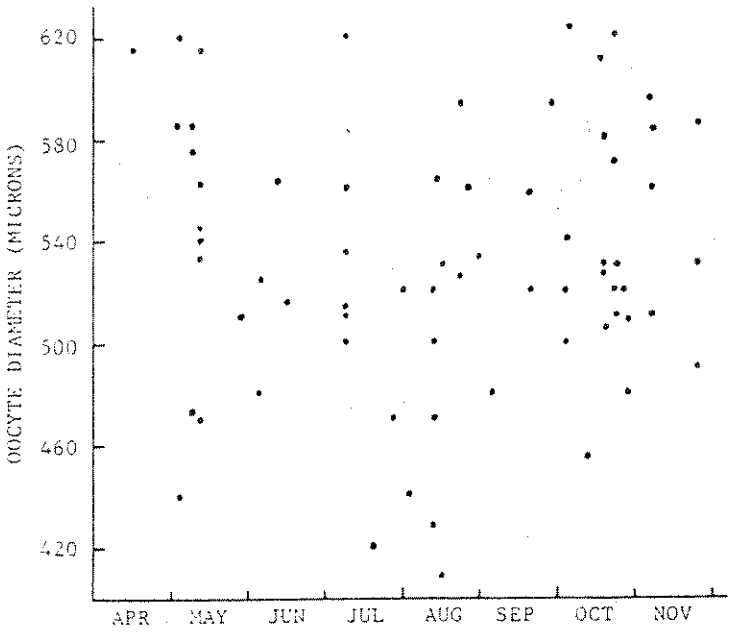


Figure 42. Relationship between collection date and size of the largest oocytes (mean diameter in μ) in developing ovaries (Stage II) from females collected from the unchannelized Missouri River, South Dakota.

enter Stage III in the fall might complete yolk deposition in late spring (a few Stage III females taken in June had oocytes larger than expected-Figure 41) and progress into Stage IV in the summer. Indeed, a few early Stage IV females were observed in June and July.

Female shovelnose are apparently spawning every two or three years. A four-year cycle is possible if some females remain in Stage II for two years rather than one, but there was no evidence to indicate that this occurred. About one-third of the population spawns every year but there is no method to determine the percentage of two-year and three-year spawners. In fact, these unknown percentages may not be constant since biennially spawning females could switch

to a three-year cycle or vice versa. This does occur in some sturgeon. Jankovic (1958) found that female sterlet up to seven years old spawn annually while most of the older females spawn biennially. In lake sturgeon Sunde (1959) noted the opposite; females between 20 and 35 pounds spawned, on the average, every five years and heavier females averaged four years.

An extended reproductive cycle is the rule rather than the exception in female sturgeon. In North America, lake sturgeon females spawn every four to seven years (Roussow, 1957). Barney (1924) stated that female lake sturgeon in Minnesota spawned every four years. His conclusions were based on the existence of four different oocyte size classes in the ovaries. Cuerrier (1966), Sunde (1959) and Priegel (1964) concluded that spawning occurred at four and five year intervals after analyzing factors such as spawning frequency, gross morphology of the ovaries, and GSI. Magnin (1966a) studied histological sections and the frequency of reproductive stages and concluded that the cycle was six years long. Several investigators indicated that the duration of the sturgeon reproductive cycle may vary within a single population as well as between geographic localities.

D. SPAWNING SEASON

1. Time and Duration

Most of the literature reported that shovelnose spawn in May and June (Eddy and Surber, 1943; Barnickol and

Starrett, 1951; Shields, 1958; Helms, 1972; Christenson, 1975). However, spawning may begin in April in Kansas (Minckley, 1959) and extend well into July at Lake Oahe in northern South Dakota (June, 1977). Many European and Asian sturgeon species, and probably all North American species spawn in the late spring or early summer (Harkness and Dymond, 1961; Magnin, 1962 and 1966a; Cuerrier, 1966; Lemanova and Nusenbaum, 1968).

Within the Missouri River study area the shovelnose spawning season was established by documenting the dates when ripe males and gravid females occurred, the initial appearance of spent females, and the last observation of females with large dark eggs. Gravid females were most commonly encountered during the third week in June in 1968 and from June 4 through 19 in 1969. The highest incidence of ripe males (milt could be extruded by hand) occurred on June 28 in 1968 and on June 10 in 1969. The relative temporal abundance of gravid females and ripe males indicated that spawning began earlier in 1969 than 1968. However, spent females were collected earlier in 1968 than 1969. Spent females were first observed on June 10 in 1968 and on June 26 in 1969. Although spawning activity apparently peaked in June, a few gravid females were collected during July and the last females with large dark eggs were caught on July 30 during both years.

Sturgeon catches are sometimes dominated by males just prior to or during the spawning season (Loukine, 1941; Cuerrier, 1966). Mississippi River commercial fishermen have

observed that the predominance of male shovelnose in their trammel-net catches marked the spawning season (Barnickol and Starrett, 1951), and I noted a similar predominance of males in the Missouri River. In 1968, early June shovelnose catches in the study area contained more females than males, but on June 18 males comprised 85% of the catch (or at least that portion subsampled for processing). Males dominated gill net samples for the next 10 days and comprised 73% of the sturgeon processed on June 28. In 1969, males dominated gill net samples on June 10 when 17 of 18 processed fish were males; 16 of these males were ready for spawning.

Missouri River water temperatures in the study area revealed that in 1968, water temperatures (means for 5-day periods) increased steadily during the latter part of May and early June, then remained around 18° to 19°C from June 8 until July 3 (Figure 2). It then increased steadily to the summer maximum of 24°C on July 18. In 1969, temperatures during the same interval were more variable. After a steady increase in late May to 17.5°C (on May 28), the 5-day mean fluctuated up and down several degrees. After a low of 16°C on June 13, the temperature gradually increased to the summer maximum of 24°C which was reached at the same time as in 1968. The average maximum June air temperature in 1968 was 30.9°C and rainfall totaled 6.6 cm. June 1969 was wetter and colder; the average maximum temperature was 25.3°C and rainfall totaled 18.0 cm (U. S. Dept. Commerce, 1973).

If the criteria I used were good indicators of spawning

activity (i.e., relative abundance of ripe males and gravid females and the predominance of males) then spawning began earlier and lasted longer in 1969. These observations correlate with the faster increase in water temperatures, subsequent flucuations in temperature, and higher flow rates in 1969 (Figure 2). It is also possible that spawning was less successful in 1969. Although ripe males were taken over a longer period in 1969, the number of spent females was lower. In the subsamples of processed sturgeon only 11 spent females were taken in 1969 while 27 were observed in 1968. Although temperature changes of just a few degrees seem minor, lake sturgeon left the spawning beds in Gull River when the temperature dropped two degrees, from 14°C to 12°C, but returned after the water reached 13.5°C (Harkness and Dymond, 1961).

Helms (1972; 1973) and Christensen (1975), also keying on the first occurrence of spent females and last collections of gravid females, found that shovelnose in the Mississippi and Red Cedar rivers spawned during late May and June. Christensen (1975) observed spent females first on May 23 but continued to collect gravid females through late May at water temperatures between 19 and 20°C. Helms (1972; 1973) reported spent females were first collected in late May (May 29 one year and May 24 the next) and females with large dark eggs were caught through mid-June.

Over 40% of the commercial shovelnose harvest in the Mississippi River is taken during the spring run in May and June as fishermen exploit shovelnose concentrated in tailwater

areas below the lock and dams (Helms, 1972). Shovelnose spawning runs were also reported on the Ohio and St. Croix rivers (Jordan and Everman, 1902; Eddy and Surber, 1943). Although substantial numbers of spawning shovelnose were present in the unchannelized Missouri River during the spring, tag and recapture studies (Section II) did not reveal unusual upstream or downstream movement during the spawning season. In addition, no seasonal concentration of shovelnose was observed during a 1968-69 survey of the Gavins Point Dam tailwaters about 47 km upstream of the study area (Walburg et al., 1971).

Only one sturgeon fry was collected during this study. This specimen, taken in a 0.5 m plankton net on July 18, 1969 had obviously hatched sometime in June or late May. Positive identification was not possible due to lack of literature for sturgeon fry. However, this fry was probably a shovelnose since the only other sturgeon present in this area is the Pallid, S. albus, and it is relatively rare (Bailey and Cross, 1954). Only one pallid sturgeon was taken during this study as compared to over 4700 shovelnose.

Female shovelnose with running eggs (capable of being stripped) were never taken during this study. However, the scarity of females in this condition is apparently a universal situation in sturgeon and has been one of the difficulties encountered in attempts to artificially propagate these fish. In most sturgeon species ripe females are sacrificed to obtain viable eggs (Harkness and Dymond, 1961). Attempts to artificially propagate various North American sturgeon have

been largely unsuccessful, due primarily to:

a) the paucity of spawning females among fish captured at spawning time
b) the inability to manually strip most females
c) the difficulty of getting ripe eggs and milt at the same time
d) the susceptibility of sturgeon eggs to fungus infections

Similar difficulties were encountered in June 1969, during an attempt to artificially spawn shovelnose sturgeon. The brood fish, 8 mature females with dark distended abdomens and 13 males which expelled some milt when captured, were placed in a raceway at the federal fish hatchery in Yankon, South Dakota. A gravel bottom was prepared in the upper half of the raceway and water was supplied from Lewis and Clark Lake. Chorionic gonadotropin (PMS), in amounts suggested by hatchery personnel, was injected into five females on June 20. One female received a second dose on June 27 when 10 males were injected. None of these fish yielded eggs or milt during several attempts to strip them, even those males which were emitting milt when first caught. The project was terminated on July 23. Histological examination showed that 3 of the 5 injected females, sacrificed July 2, contained late Stage V ova. The remaining two, processed July 23, had atretic mature ova. All of these females would probably have spawned successfully if left in the river.

2. Spawning Location

No investigator has ever reported locating the spawning beds or observing the spawning act of shovelnose sturgeon.

The spawning habits and habitats of this species are therefore still open to conjecture. Forbes and Richardson (1920) thought that shovelnose must ascend smaller tributaries of the Mississippi River to spawn. Others, also working on the Mississippi River stated that shovelnose spawn in the swift water of the river proper, or larger tributaries, probably on a rocky bottom (Coker, 1930; Eddy and Surber, 1943). In the Missouri River, June (1977) stated that catches of ripe shovelnose in upstream areas of Lake Oahe suggested that shovelnose spawned over rock, rubble, and gravel bottoms of the main river, and in major tributaries.

Attempts made during this study to locate the spawning grounds were unsuccessful. However, on the basis of circumstantial evidence, I believe that spawning occurs in the swift water in or near the main channel. During both the 1968 and

cent to the main channel. At the same time, very few shovelnose were caught in backwater areas. Only one or two shovelnose were captured within the backwaters and none were taken by nets set to block the main entrances to these areas during the spawning season. There is no firm evidence that shovelnose sturgeon spawn in tributaries of the unchannelized Missouri River. Shovelnose apparently do not move into tributaries in large numbers, and Zweiacker (1967) collected only two shovelnose in the lower 8-10 km of the James River, a tributary of the Missouri about 20 km upstream of the

study area, when he sampled it in spring 1967. However, shovelnose have been collected in Missouri River tributaries (Schmulbach, personal communications) and more intensive sampling would be required to see if they utilize tributaries for spawning.

In conclusion, the occurrence of gravid and spent shovelnose sturgeon in the unchannelized Missouri River indicated that some sturgeon were spawning in the area, but the paucity of young-of-the year and immature sturgeon suggests that annual recruitment to the population is probably low.

E. HERMAPHRODITIC SHOVELNOSE

Hermaphroditic shovelnose sturgeon were recognized among the normal gonochoristic males and females collected during 1968 and 1969 (Table 27). Several suspected hermaphrodites proved to be females whose ovaries were associated with considerable adipose tissue, but 9 of 563 (1.6%) processed shovelnose were confirmed hermaphrodites. This relatively high incidence of hermaphroditism exceeded that found by Atz and Smith (1976) in Atlantic and shortnose sturgeon populations from the Hudson River, where only a single hermaphrodite of each species was identified. Atz (1964) also noted that only two cases of hermaphroditism in sturgeon had been reported previously, and one of these resulted from hybridization experiments. Since many sturgeon species are commercially processed for caviar, both in the United States and overseas, thousands of gonads are examined yearly. Despite this fact,

Table 27. Summary of hermaphroditic shovelnose collected in the unchannelized Missouri River, indicating gonadal maturity and relative extent of ovarian and testicular tissue.

Date Captured	Gonosomatic Index* (GSI)	Reproductive Stage**		Comments
		Testicular	Ovarian	
Apr	1.56	II	II	Ovotestis. Testicular and ovarian tissue intermingled. Several larger oocytes in late phase of atresia.
Jun	2.96	V	II	Spawning male. Few small oocytes (≈300 μ) within testicular tissue.
Jun	3.18	V	V	Ripe male with ovarian tissue along surface of testis. Spermatozoa in ducts adjacent to oocytes. Oocytes within normal connective tissue capsule. Mature ova less than 2 mm.
Jul	3.52	V	I	Ripe male. Small ovarian areas resemble immature ovary.
Jul	6.10	V-VI	V	Ovotestis. Milt extruded from testicular portion. Numerous large dark eggs, apparently ripe. No histological sections.
Aug	0.34	VI	II	Spent testis, residual spermatozoa. Small areas of ovarian tissue adjacent to testis. Oocytes around 400 μ.
Sep***	12.33	—	V	Left gonal-Testis (2.4 g); probably Stage II or VI. Right gonad-Ovary (98.1 g); ova appear to be fully mature. No histological sections.
Oct	4.20	III	IV	Spermatogenic Testis. Ovarian tissue primarily on surface. Follicular membrane of cuboidal cells, unusually thick (7-8 μ) for Stage IV oocytes. Late atretic eggs.
Nov***	1.88	—	IV	Ovotestis, but primarily testicular tissue. No histological sections.

*GSI = (gonad weight/body weight) x 100.

**I = immature, II = developing, III = spermatogenesis, IV = prespawning, V = spawning, VI = spent.

***Specimens captured during 1968. All other fish collected during 1969.

few cases of hermaphroditism have been reported. However, the Missouri River shovelnose sturgeon population appears to be different since June (1977) also found hermaphroditic shovelnose in his samples from Missouri River reservoirs.

Most reports on abnormal hermaphrodites consist of descriptions of individual fish that were discovered by chance. Therefore, data on the frequency of this phenomenon within a local population or a particular species are rare. However, June's (1977) data from Lake Oahe, a main-stem Missouri River reservoir in South and North Dakota, also documented the frequency of hermaphroditic shovelnose sturgeon. In Lake Oahe, 2.1% of the shovelnose (8 of 378) examined were hermaphroditic.

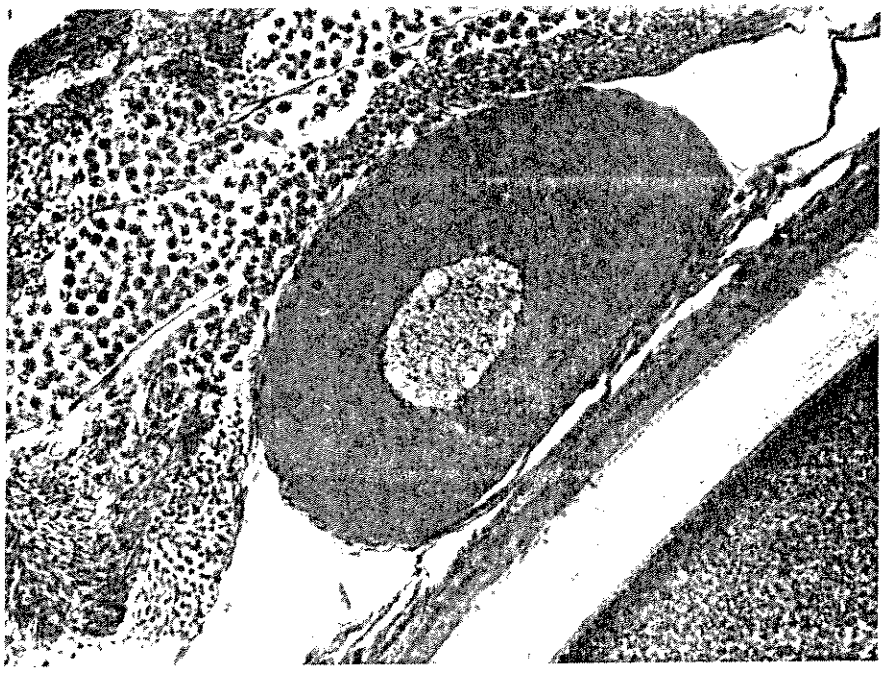
All hermaphroditic shovelnose examined by June (1977) had one ovary and one ovotestis, and the anterior part of the ovotestis was usually testicular tissue. In my study hermaphroditic shovelnose gonads were more variable, but all hermaphrodites had at least one ovotestis except for one (Table 27). In that exception the left gonad was a testis and the right one an ovary. The morphology of the ovotestes varied but two generalizations could be made. First, the ovarian and testicular portions were randomly distributed throughout the gonad with no consistent anterior-posterior orientation such as noted by June (1977). Secondly, most ovotestes were predominately testicular, usually with peripherally located ovarian tissue. In the single hermaphroditic Atlantic sturgeon described by Atz and Smith (1976), one ovotestis was predominantly testicular while the other was

predominantly ovarian, and the demarcation between ovarian and testicular tissue was definite. In contrast, the ovotestes of the single shortnose sturgeon consisted of eggs intermingled in a matrix of testicular tissue (Atz and Smith, 1976).

Stained gonadal sections were prepared for six of the nine hermaphrodites and the testicular tissue in these ovotestes was apparently normal and functional. Two specimens collected during the spawning season had ripe testicular portions which extruded milt and two others collected in July and August had spent testicular tissue. The testicular tissue in a hermaphrodite collected in October exhibited active spermatogenesis; typical of normal testes in the fall (Figure 43). Within the ovarian tissue of the ovotestes examined microscopically, the small reserve oocytes (maximum diameter of 500-600 μ) were apparently developing normally. In some ovotestes the larger oocytes typical of Stages IV and V appeared normal, while other ovotestes may not have produced viable eggs. For example, the hermaphrodite collected in September 1963 had mature eggs and a GSI typical of a spawning female, but had not spawned during the normal June-July season (Table 27). Atresia probably had begun but no histological sections were made of this specimen. The hermaphrodite collected in April contained several large pigmented oocytes, all in late stages of atresia, along with apparently normal Stage II (developing) oocytes. Both the male and female portions of the ovotestes of a hermaphrodite collected in June 1970 were apparently mature (Figure 44).

Figure 43. Photomicrograph of ovotestis from hermaphroditic shovelnose sturgeon collected during October 1969 from the unchannelized Missouri River, South Dakota. Testicular tissue at upper left exhibited active spermatogenesis. A portion of a large pigmented egg typical of a Stage IV ovary is at lower right. Both testicular and ovarian tissue were maturing simultaneously.

Figure 44. Ventral view of ovotestes in hermaphroditic shovelnose sturgeon collected in June 1970. Both right and left gonads are ovotestes, with the intestine in between.

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However, the ostia were small, characteristic of males, and several eggs were degenerating. Conversely, one hermaphrodite collected in June had mature eggs and ripe testicular tissue. The eggs apparently had normal zona radiata and gelatinous membranes, and well developed follicular and thecal membranes. This fish may have produced both viable sperm and eggs.

In at least three hermaphrodites, the testicular and ovarian tissues were maturing simultaneously. One of these sturgeon was collected in October and the ovarian tissue contained Stage IV oocytes which would have been ready to spawn the following spring. The testicular tissue exhibited active spermatogenesis and also would have been ripe the following spring. Two shovelnose had ovotestes with both testicular and ovarian tissues in spawning condition. One was captured June 5, 1969, and obviously had not yet spawned while in the other fish, taken July 30, 1968, the testicular tissue was ripe or partly spent and the ovarian portion still retained mature ova.

Synchronous maturation within a hermaphrodite produces the possibility of self-fertilization. Although no conclusions could be made concerning self-fertilization in the hermaphroditic sturgeon, Atz (1964) stated that self-fertilization is a rare event limited to a small number of teleosts. The three shovelnose containing both ripe sperm and eggs were, however, synchronous hermaphrodites since the term does not imply self-fertilization (Yamamoto, 1969).

The relatively high incidence of hermaphroditism in

Missouri River shovelnose suggests a high degree of abnormal development due to some unknown cause(s). Recent environmental changes in the Missouri River caused by channelization and reservoir construction make prime targets. However, there is no evidence that environmental conditions can produce hermaphrodites, even though it has been established that the environment can influence the sex ratio in some fish populations (Atz, 1964).

SUMMARY AND CONCLUSIONS

Between June 1968 and July 1970 over 5000 shovelnose sturgeon were collected from the unchannelized Missouri River in southeastern South Dakota. About 3540 shovelnose were tagged and released within a 20 km study area to study movement. Over 560 shovelnose were subsampled from 1968 and 1969 catches for analyses of external morphology and examination of gonads. Length-frequencies, length-weight relationships, and condition factors were calculated for Missouri River shovelnose and compared with the same data for shovelnose sturgeon populations in the Mississippi, Ohio, and Chippewa rivers. Reproductive cycles for both males and females were determined from microscopic analyses of stained gonad sections and temporal changes in gross morphology of the gonads. The results of these investigations are summarized as follows:

1. Gill and trammel netting, trawling, seining, and electrofishing catches indicated that shovelnose sturgeon prefer intermediate currents found in pools behind sand bars or open water areas adjacent to the main channel.

2. Gill net catches (CPUE) were highest in pools that were between 1.8 and 4.6 m deep, in those sections of the study area where sand bar pools were most abundant and stable, and during the spring (April-June) and fall (October-November).

3. Missouri River shovelnose sturgeon fell within a

narrow range of lengths and weights. Almost 75% of the shovelnose collected during 1968 had fork lengths within 47-53 cm and live weights between 300 and 499 g. Of 563 shovelnose processed in 1968 and 1969 only 5 were shorter than 44 cm and 6 longer than 60 cm.

4. A comparison of the physical characteristics of shovelnose sturgeon from the Ohio, Mississippi, Chippewa, and Missouri rivers indicated that Missouri River shovelnose had a lower condition factor and a mean length and weight less than those from the other three rivers, reached sexual maturity at smaller lengths than shovelnose in the Mississippi and Chippewa, and apparently grew slower than shovelnose from the Ohio and Mississippi rivers.

5. Most male and female shovelnose in the unchannelized Missouri River became mature at 40-50 cm and 45-55 cm fork length, respectively.

6. The narrow size range of shovelnose sturgeon collected within the Missouri River study area, along with low condition factors, small size of mature individuals, and paucity of immature fish, suggest that the Missouri River population is environmentally stressed and exhibits a slow growth rate.

7. Man-made modifications imposed on the Missouri River ecosystem, primarily the extensive damming and channelization, are probably detrimental to shovelnose sturgeon.

8. For tagging studies, a No. 3 monel strap tag clamped over the anterior ray of the pectoral fin proved to be superior to either a No. 4 strap tag on the opercle or a Floy dart tag inserted between overlapping dorsal scutes. Of 42 recaptures that had carried tags for one or more years, 35 had pectoral tags compared to 6 opercle tags and 1 dart tag.

9. Ninety-three of 135 recaptured shovelnose were caught within one year of their release and during that period 63 were caught within 3.2 km of the release location.

10. Although there was variation, distance traveled increased with time at large. Average distances moved by shovelnose recaptured in one-year time blocks over 5 years were 3.1, 13.7, 51.0, 25.7, and 107.3 km, respectively.

11. Some shovelnose sturgeon exhibited extensive movements. A few shovelnose tagged and released in the study area were recaptured near St. Joseph, Missouri and Atchinson, Kansas, 500-540 km downstream and several were recaptured near Omaha, Nebraska, 240-250 km downstream. Upstream movement was limited by Gavins Point Dam 47 km from the study area.

12. Several tagged shovelnose were at large four or more years, but the maximum time at large was 8 years 188 days.

13. During 1968 and 1969 about 1000 tagged sturgeon

were displaced either upstream or downstream from the original capture location. By early July 1970, 23 of these had been recaptured and no evidence of homing was observed.

14. Although no homing tendency was observed, recaptured shovelnose did exhibit an apparent group movement. In approximately two-thirds of the instances when two or more sturgeon were recaptured on the same date (and at one location) I found that two or more of the recaptures had been tagged and released together. These grouped recaptures probably resulted from fish traveling along the river by moving from pool to pool and frequently crossing paths as they move among a relatively limited number of preferred pools.

15. Temporal changes in gonadal gross morphology, microscopic anatomy, and GSI were described for male and female shovelnose sturgeon and six reproductive stages were defined; immature, developing (mature), spermatogenic (males) or yolk deposition (females), prespawning, spawning, and spent.

16. Only two males and five females among the 563 shovelnose processed during 1968 and 1969 were considered as immature.

17. Fatty tissue was intimately associated with the gonads, especially in immature and developing stages. This adipose tissue made small testes look bigger and could make some females look like males.

18. Apparently, all mature male shovelnose do not spawn annually. This produced two distinct groups within the male population; one group that will spawn during the next spawning season and a second group that required an additional year or more to produce spermatozoa.

19. The testes of annual spawners enter the active spermatogenic stage 2-3 months after spawning and contain mostly spermatozoa during the winter. The testes of males that are not spawning annually apparently enter the developing stage several months after spawning and may remain in the developing stage for a year or more before progressing to the spermatogenic stage.

20. The spawning portion of the male population can be distinguished from the non-spawners during October through May because the GSI of spawners exceeds 1.0 and the testes are large and light gray to white.

21. About 65-70% of the mature males spawned in a given year and an estimated 30% were spawning annually.

22. All six reproductive stages in females could be distinguished by gross examination of the ovaries and measuring the diameter of the largest oocytes.

23. Most female shovelnose were apparently on a 2- or 3-year reproductive cycle. Females on a 3-year cycle spent about one year in Stage II (the developing stage), then progressed through yolk deposition and the pre-spawning stage during the following year, and spawned

the third year. Females on a 2-year cycle spent very little time in Stage II, progressed into the yolk deposition stage during the late fall or winter following the May-June spawning season, and spawned every other year.

24. The spawning season began in late May and continued through June, as determined by the first occurrence of ripe males and gravid females, the initial appearance of spent females, and the last observations of females with large dark eggs.

25. Attempts to locate spawning grounds were unsuccessful, but on the basis of catches by several gear types I believe that spawning occurs in relatively swift water in or near the main channel.

26. Nine of 563 shovelnose (1.6%) processed during 1968 and 1969 were hermaphrodites. Microscopic analysis of stained gonad sections indicated that at least three individuals were synchronous hermaphrodites since both ripe sperm and mature eggs were present within the ovotestes.

LITERATURE CITED

Ahsan, Syed Nasar. 1966. Cyclical changes in the testicular activity of the lake chub, Couesius plumbeus (Agassiz). Can. J. Zool. 44(2):149-159.

Atz, J.W. 1964. Intersexuality in fishes. Pages 145-232 in C.N. Armstrong and A.J. Marshall, eds., Intersexuality in vertebrates including man. Academic Press. New York.

--------, and C.L. Smith. 1976. Hermaphroditism and gonadal Teratoma-like growths in sturgeon (Acipenser). Bull. South. Calif. Acad. Sci. 75(2):119-126.

Bailey, R.M., chairman. 1970. A list of common and scientific names of fishes from the United States and Canada. Am. Fish. Soc. Spec. Publ. No. 6. Washington, D.C.

----------, and F.B. Cross. 1954. River sturgeons of the American genus Scaphirhynchus: Characters, distribution and synonymy. Papers Mich. Acad. Sci. 39:169-208.

Balinsky, B.I. 1965. An introduction to embryology. W.B. Saunders Co., Philadelphia. 673 pp.

Barney, R.L. 1924. An extended reproductive cycle in Acipenser rubicundus. Manuscript, 15 pp., cited by Harkness and Dymond (1961).

Barnickol, P.G. and W.C. Starrett. 1951. Commercial and sport fishes of the Mississippi River between Caruthersville, Missouri and Dubuque, Iowa. Bull. Ill. Nat. Hist. Survey. 25(5):267-350.

Beach, A.W. 1959. Seasonal changes in the cytology of the ovary and of the pituitary gland of the goldfish. Can. J. Zool. 37:615-625.

Bonn, E.W. and R.J. Kemp. 1952. Additional records of freshwater fishes from Texas. Copeia. 1952(3):204-205.

Braekevelt, C.R. and D.B. McMillan. 1967. Cyclic changes in the ovary of the brook stickleback, Eucalia inconstans (Kirkland). J. Morph. 123(4):373-396.

Chermock, Ralph L. 1955. First record of a shovelnose sturgeon, Scaphirhynchus platorynchus, from the Tombigbee River, Alabama. Copeia. 1955(2):154.

Christenson, Lyle M. 1975. The shovelnose sturgeon, Scaphirynchus platorynchus (Rafinesque) in the Red Cedar-Chippewa River System, Wisc. Wisc. Dept. Nat. Resources Research Rept. 82, 23 pp.

Cleary, R.E. and J. Greenbank. 1954. An analysis of techniques used in estimating fish populations in streams, with particular reference to large non-trout streams. J. Wildl. Mgmt. 18(4):461-476.

Coker, Robert E. 1930. Studies of common fishes of the Mississippi River at Keokuk. U.S. Bureau Fish. Bull. 45(1072):141-225.

Cooper, L.J. 1952. A histological study of the reproductive organs of crappies (Pomotis nigromaculatus and P. annularis). Trans. Am. Microscop. Soc. 71:393-404.

Craig-Bennett, A. 1931. The reproductive cycle of the three-spined stickleback, Gasterosteus aculeatus L. Phil. Trans. Roy. Soc. B219:197-279.

Cuerrier, Jean-Paul. 1951. The use of pectoral fin rays for determining age of sturgeon and other species of fish. Can. Fish Cult. No. 11:10-18.

----------. 1966. L'esturgeon de lac, Acipenser fulvescens Raf. de la region du Lac St.-Pierre au cours de la periode du frai. Le Naturaliste Canadien. 93(4): 279-334.

----------, and G. Roussow. 1951. Age and growth of lake sturgeon from Lake St. Francis, St. Lawrence River. Report on material collected in 1947. Can. Fish Cult. No. 10:17-29.

Eddy, Samuel and Thaddeus Surber. 1943. Northern Fishes, with special reference to the Upper Mississippi Valley. Univ. of Minnesota Press, Minneapolis. 276 pp.

Evermann, B.W. 1902. Description of a new species of shad (Alosa ohiensis) with notes on other food-fishes of the Ohio River. Rep. U.S. Comm. Fish Fish. 27(1901):275-288.

Fogle, N.E. 1963. Report of fisheries investigations during the fourth year of impoundment of Oahe Reservoir, South Dakota, 1962. S.D. Dept. Game Fish Parks, Dingell-Johnson Proj. F-1-R-12 (Jobs 10-12):43 pp.

Forbes, S.A. and R.E. Richardson. 1920. The fishes of Illinois. Ill. Nat. Hist. Survey. Vol. 136, 357 pp; plus Atlas of 103 pp.

Funk, John L. 1957. Movement of stream fishes in Missouri. Trans. Am. Fish. Soc. 85(1):39-57.

----------, and J.W. Robinson. 1974. Changes in the channel of the lower Missouri River and its effects on fish and wildlife. Missouri Dept. Conservation, Aquatic Series 11. 52 pp.

Gasaway, C.R. 1970. Changes in the fish population in Lake Francis Case in South Dakota in the first 16 years of impoundment. Bur. Sport Fish. and Wildl. Tech. Paper No. 56, 1-30.

Gerking, Shelby D. 1953. Evidence for the concepts of home range and territory in stream fishes. Ecology. 34(2): 347-365.

----------. 1959. The restricted movement of fish populations. Trans. Am. Fish. Soc. 34:221-242.

Ginsburg, A.A. 1961. The block to polyspermy in sturgeon and trout with special reference to the role of cortical granules (alveoli). J. Embryol. Exptl. Morph. 9:173-190.

Greeley, J.R. 1937. A biological survey of the Lower Hudson Watershed. II. Fishes of the area with annotated list. N.Y. State Conservation Dept., Suppl. to 26th Ann. Rept., pp. 45-103.

Hardisty, M.W., B. Rothwell and K. Steele. 1967. The interstitial tissue of the testis of the river lamprey, Lampetra fluviatilis. J. Zool. Proc. Zool. Soc. London. 152(1):9-19.

Harkness, W.J.K. 1923. The rate of growth and the food of the lake sturgeon (Acipenser rubicundus LeSueur). Univ. of Toronto Studies, Biol. Ser. No. 18, 13-42.

----------, and J.R. Dymond. 1961. The Lake Sturgeon. The history of its fishery and problems of conservation. Ontario Dept. Lands and Forests, Fish and Wildl. Branch. 121 pp.

Haugen, Gordon N. 1969. Life history, habitat, and distribution of the lake sturgeon, Acipenser fulvescens, in the South Saskatchewan River, Alberta. Alberta Fish and Wildl. Div., Fish. Section, Res. Rept. No. 4, 27 pp.

Held, J.W. 1969. Some early summer foods of the shovelnose sturgeon in the Missouri River. Trans. Am. Fish. Soc. 98(3):514-517.

Helms, Don R. 1972. Progress report on the first year study of shovelnose sturgeon in the Mississippi River. Iowa Conservation Comm., Annual Prog. Rept. for Proj. 2-156-R-1, 22 pp.

----------. 1973. Progress report on the second year of study of shovelnose sturgeon in the Mississippi River. Iowa Conservation Comm., Annual Prog. Rept. for Proj. 2-156-R-2, 33 pp.

----------. 1974. Age and growth of shovelnose sturgeon, Scaphirynchus platorynchus (Rafinesque) in the Mississippi River. Proc. Iowa Acad. Sci. 81(2):73-75.

----------, and T.L. Boland. 1972. Upper Mississippi River natural resources bibliography. Upper Mississippi River Conserv. Committee Fish Tech. Section. June 1972, 62 pp.

Henderson, N.E. 1962. The annual cycle in the testes of the eastern brook trout, Salvelinus fontinalis (Mitchill). Can. J. Zool. 40:631-641.

Hoar, W.S. 1969. Reproduction. Pages 1-65 in W.S. Hoar and D.J. Randall eds., Fish Physiology, Volume III. Academic Press, New York.

---------, and D.J. Randall. 1969. Fish Physiology. Academic Press, New York.

Holt, C.S., G. Grant, G. Oberstar, C. Oakes, and D. Bradt. 1977. Movement of walleye, Stizostedion vitreum, in Lake Bemidji, Minnesota as determined by Radio-biotelemetry. Trans. Am. Fish. Soc. 106(2):163-169.

Hoopes, D.T. 1960. Utilization of mayflies and caddisflies by some Mississippi River fishes. Trans. Am. Fish. Soc. 89(1):32-34.

Hurley, D.A. and K.C. Fisher. 1966. The structure and development of the external membrane in young eggs of the brook trout, Salvelinus fontinalis (Mitchill). Can. J. Zool. 44(2):173-190.

Jahn, L.A. 1969. Movements and homing of cutthroat trout (Salmo clarki) from open-water areas of Yellowstone Lake. J. Fish. Res. Board Can. 26(5):1243-1261.

James, Marian F. 1946. Histology of gonadal changes in the bluegill, Lepomis macrochirus (Raf.) and the largemouth bass, Huro salmoides (Lécèpede). J. Morph. 79(1):63-91.

Jankovic, Draga. 1958. Ecological Research on Danubian Sterlet (Acipenser ruthenus L.). Institute Biologique, Beograd. Yugoslavia Monographies, 2:145.

Jordan, D.S. and B.W. Evermann. 1902. American food and game fishes. Doubleday, Page, and Co., New York.

June, Fred C. 1977. Reproductive patterns in seventeen species of warmwater fishes in a Missouri River reservoir. Env. Biol. Fish. 2(3):285-296.

Kallemeyn, L.W. and J.F. Novotny. 1977. Fish and fish food organisms in various habitats of the Missouri River in South Dakota, Nebraska, and Iowa. Fish and Wildl. Serv., Biol. Serv. Prog. FWS/OBS-77/25, August 1977. 100 pp.

Kudrna, Joel J. 1965. Movement and homing of sunfishes in Clear Lake. Iowa Acad. Sci. Vol. 72, 263-271.

Lagler, Karl F. 1956. Freshwater fishery biology. Wm. C. Brown Company, Dubuque, Iowa. 421 pp.

Larimore, R.W. 1950. Gametogenesis of Polyodon spathula (Walbaum): a basis for regulation of the fishery. Copeia. 1950(2):116-124.

Lemanova, N.A. and L.M. Nusebaum. 1968. An investigation of the sex organs of the Russian sturgeon (Acipenser güldenstädtii, Brandt) passed through the Volgograd fish-lift. (Transl. from Russian). Problems of Ichthyology, 9(5):619-626.

Lewis, J.C. and D.B. McMillan. 1965. The development of the ovary of the sea lamprey (Petromyzon marinus L.). J. Morph. 117(3):425-466.

Lofts, B. and A.J. Marshall. 1957. Cyclical changes of the testis lipids of a teleost fish, Esox lucius. Quart. J. Micr. Sci. 98:79-88.

Loukine, A.V. 1941. Les stades de maturité sexuelle du sterlet. Comp. Rend. Acad. Sci., U.S.S.R. 32(5):364-376.

Magnin, Etienne. 1962. Research concerning systematics and biology of the sturgeons Acipenser sturio, A. oxyrhynchus and A. fulvescens. Ann. Sta. Ctr. Hydrobiol. Appl. 9: 7-242.

----------. 1964. Croissance en longueur de trois esturgeons d 'Amerique du Nord: Acipenser oxyrhynchus Mitchell, Acipenser fulvescens Rafinesque et Acipenser brevirostris LeSueur. Verh. Intermat. Verein. Limnol. 15:968-974.

----------. 1966a. Croissance de l'esturgeon Acipenser fulvescens RAF. vivant dans le bassin hydrographique de la riviere Nottaway, tributaire de la Baie James. Trovaux sur les pecheries du Quebec, No. 11. Naturaliste Can. 92 (8-9):193-204.

----------. 1966b. Quelques donnees biologiques sur la reproduction des esturgeons Acipenser fulvescens RAF. de la riviere Nottaway, tributaire de la Baie James. Trovaux sur les pecheries du Quebec, No. 13. Can. J. Zool. 44: 257-263.

----------. 1966c. Recherches sur les cycles de reproduction des esturgeons Acipenser fulvescens RAF. de la riviere Nottaway, tributaire de la Baie James. Verh. Intermat. Verein. Limnol. 16:1018-1024.

----------, and G.Beaulieu. 1960. Deplacements des esturgeons (Acipenser fulvescens et A. oxyrhynchus) du fleuve St. Laurent d'apres les donnes du marguage. Naturaliste Can. 87(11):237-252.

Marshall, A.J. and B. Lofts. 1956. The Leydig-cell homologue in certain teleost fishes. Nature. 177(4511): 704-705.

Matthews, S.A. 1938. The seasonal cycle in the gonads of Fundulus. Biol. Bull. 75(1):66-74.

McCleave, J.D. 1967. Homing and orientation of cutthroat trout (Salmo clarki) in Yellowstone Lake, with special reference to olfaction and vision. J. Fish. Res. Board Can. 24(10):2011-2044.

McCleave, J.D., G. LaBar, and F. Kircheis. 1977. Within-season homing movements of displaced mature Sunapee trout (Salvelinus alpinus) in Floods Pond, Maine. Trans. Am. Fish. Soc. 106(2):156-162.

Minckley, W.L. 1959. Fishes of the Big Blue River Basin, Kansas. Univ. Kans. Publ. Mus. Nat. Hist. 11(7):401-442.

Modde, T. and J.C. Schmulbach. 1977. Food and feeding behavior of the shovelnose sturgeon, Scaphirhynchus platorynchus, in the unchannelized Missouri River, South Dakota. Trans. Am. Fish. Soc. 106(6):602-608.

Moltchanova, I. 1941. La structure histologique que des oeufs des sterlets aux stades differeuts de maturité sexuelle. Comp. Rend. Acad. Sci., U.S.S.R. 32(2): 163-165.

Monson, M.A. and J.Greenbank. 1947. Size and maturity of hackle-back sturgeon. Upper Mississippi River Conserv. Comm. Tech. Commit. Fish. Prog. Rept. 3:42-45.

Morris, L.A., R.N. Langemeier, T.R. Russell, and A. Witt, Jr. 1968. Effects of main stem impoundments and channelization upon the limnology of the Missouri River, Nebraska. Trans. Am. Fish. Soc. 97(4):380-388.

Muir, B.S. 1960. Comparison of growth rates for native and hatchery-stocked populations of Esox masquinongy in Nogies Creek, Ontario. J. Fish. Res. Bd. Canada. 17(6): 919-927.

Namminga, H.E. 1969. An investigation of the macroscopic drift fauna of the Missouri River. M.S. Thesis. Univ. S. Dak., Vermillion. 75 pp.

Nelson, W.R. 1961. Report of fisheries investigations during the sixth year of impoundment of Gavins Point Reservoir, South Dakota, 1960. S.D. Dept. Game Fish Parks, Dingell-Johnson Proj., F-1-R-10 (Jobs 2-4): 59 pp.

Priegel, G. 1964. Review of Lake Poygan sturgeon management problems. Wisc. Conserv. Dept. Mimeo. 12 page Mimeo Report of Jan. 1964.

Priegel, G.R. 1968. The movement, rate of exploitation and homing behavior of walleyes in Lake Winnebago and connecting waters, Wisconsin, as determined by tagging. Wisc. Acad. Science, Arts, and Letters. Vol. 56, 207-223.

Priegel, G.R. and T.L. Wirth. 1971. The Lake sturgeon. Its life history, ecology, and management. Wisc. Dept. Nat. Resources. Publ. No. 240-70: 20 pp.

Probst, R.T. and E.L. Cooper. 1955. Age, growth, and reproduction of the lake sturgeon, Acipenser fulvescens, in the Lake Winnebago Region, Wisc. Trans. Am. Fish. Soc. 84:207-227.

Pycha, Richard L. 1956. Progress report on white sturgeon studies. Calif. Fish and Game. 42(1):23-35.

Rehwinkel, Bruce J. 1978. The fishery for paddlefish at Intake, Montana during 1973 and 1974. Trans. Am. Fish. Soc. 107(2):263-268.

Ricker, W.E. 1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can., Bull. No. 119. 300 pp.

Romer, A.S. 1962. The Vertebrate Body. W.B. Saunders Co., Philadelphia.

Rosen, R.A. 1976. Distribution, age and growth, and feeding ecology of paddlefish, Polyodon spathula, in unaltered Missouri River, South Dakota. M.S. Thesis, S.D. State Univ., Brookings, S.D. 95 pp.

Roussow, G. 1957. Some considerations concerning sturgeon spawning periodicity. J. Fish. Res. Board Can. 14(4): 553-572.

Royer, L.M., F.M. Atton, and J.-P. Cuerrier. 1968. Age and growth of lake sturgeon in the Saskatchewan River Delta. J. Fish. Res. Board Can. 25(7):1511-1516.

Ryder, J.A. 1890. The sturgeons and sturgeon industries of the Eastern Coast of the United States with an account of experiments bearing upon sturgeon culture. Bull. U.S. Fish. Comm. for 1888. 8(8):213-328.

Schmulbach, J.; G. Gould, and C. Groen. 1975. Relative abundance and distribution of fishes in the Missouri River, Gavins Point Dam to Rulo, Nebraska. Proc. S. Dak. Acad. Sci. 54(1975):194-222.

Semakula, S.N. and P.A. Larkin. 1968. Age, growth, food, and yield of the white sturgeon (Acipenser transmontanus) of the Fraser River, British Columbia. J. Fish. Res. Board Can. 25(12):2589-2602.

Shields, J.T. 1956. Report of fisheries investigations during the third year of impoundment of Fort Randall Reservoir, South Dakota, 1955. S.D. Dept. Game Fish Parks, Dingell-Johnson Proj. F-1-R-5:91 pp.

----------. 1957. Report of fisheries investigations during the fourth year of impoundment of Fort Randall Reservoir, South Dakota, 1956. S.D. Dept. Game Fish Parks, Dingell-Johnson Proj., F-1-R-6:1-60.

----------. 1958. Report of fisheries investigations during the third year of impoundment of Gavins Point Reservoir, South Dakota, 1957. S.D. Dept. Game Fish Parks. Dingell-Johnson Proj., F-1-R-7:1-48.

Sprague, J.W. 1959. Report of fisheries investigations during the fourth year of impoundment of Gavins Point Reservoir, South Dakota, 1958. S.D. Dept. Game Fish Parks. 42 p. mimeo.

Starrett, Wm. C. and P. Barnickol. 1955. Efficiency and selectivity of commercial fishing devices used on the Mississippi River. Bull. Ill. Nat. Hist. Survey. 26 (4):325-366.

Sunde, L. 1959. The sturgeon fishery in Manitoba with recommendations for management (analysis of Nelson R. data: 1953-56). Fish Branch, Dept. Mines Resources Manitoba. Manuscript Rept.

Trautman, M.B. 1957. Fishes of Ohio. Ohio State Univ. Press, Columbus.

Turner, C.L. 1919. The seasonal cycle in the spermary of the perch. J. Morph. 32(3):681-711.

U.S. Dept. Commerce. 1973. Climatography of the United States No. 93-34. Climatic Summary of the United States - Supplement for 1961 through 1970, South Dakota.

Walburg, C.H. 1964. Fish population studies, Lewis & Clark Lake, Missouri River, 1956 to 1962. U.S. Fish Wildl. Serv., Spec. Sci. Rept. 482:1-27.

----------. 1977. Lake Francis Case, a Missouri River reservoir: changes in the fish population in 1954-75, and suggestions for management. U.S. Fish Wildl. Serv., Tech. Paper No. 95. 12 pp.

Walburg, C.H., G.L. Kaiser, and P.L. Hudson. 1971. Lewis and Clark Lake tailwater biota and some relations of the tailwater and reservoir fish populations. Pages 449-467 in G.E. Hall ed., Reservoir Fisheries and Limnology. Am. Fish. Soc. Spec. Publ. S. 449-467.

Warden, R.L., Jr., and W.L. Lorio. 1975. Movements of largemouth bass (Micropterus salmoides) in impounded waters as determined by underwater telemetry. Trans. Am. Fish. Soc. 104(4):696-702.

Weisel, G.F. 1943. A histological study of the testes of the sockeye salmon, Oncorhynchus nerka. J. Morph. 73 (2):207-230.

Welker, Bill. 1967. Movements of marked channel catfish in the Little Sioux River, Iowa. Trans. Am. Fish. Soc. 96 (3):351-353.

Wirth, T.L. 1956. The lake sturgeon management report for 1956. Wisc. Conserv. Dept., Fish Mgmt. Div. 5 page mimeo report of June 12, 1956.

----------. 1958. Winnebago studies. Annual progress report for the period July, 1957-June 1958. Wisc. Conserv. Dept., Fish Mgmt. Div. 13 page report of Aug. 11, 1958.

----------, and C. Cline. 1955. The harvest of lake sturgeon (Acipenser fulvescens) by spearers in Lake Winnebago and connecting waters, Wisc. Wisc. Conserv. Dept., Fish Mgmt. Div. 6 page mimeo report.

Yamamoto, Toki-o. 1969. Sex Differentiation. Pages 117-165 in W.S. Hoar and D.J. Randall eds., Fish Physiology, Vol. 3. Academic Press, New York.

Zuckerman, Sir Solly. 1962. The Ovary. Vol. 1. Academic Press, New York. 619 pp.

Zweiacker, Paul L. 1967. Aspects of the life history of the shovelnose sturgeon, Scaphirhynchus platorynchus (Rafinesque) in the Missouri River. M.S. Thesis, Univ. of S. Dak., Vermillion. 46 pp.