HABITATS AND MOVEMENTS OF PALLID AND SHOVELNOSE STURGEON IN THE YELLOWSTONE AND MISSOURI RIVERS, MONTANA AND NORTH DAKOTA

by

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APPROVAL

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency and is ready for submission to the College of Graduate Studies.

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INTRODUCTION

Pallid sturgeon (*Scaphirhynchus albus* Forbes and Richardson) were listed as endangered in 1990 under the Endangered Species Act of 1973 (Dryer and Sandvol 1993). There is little quantitative information on movements and habitat use. This study was implemented to supplement research initiated by the Montana Department of Fish, Wildlife and Parks (MDFWP) and the U. S. Fish and Wildlife Service (USFWS) on pallid sturgeon and a closely related species, the shovelnose sturgeon (*Scaphirhynchus platorynchus* Rafinesque).

REVIEW OF PALLID AND SHOVELNOSE STURGEON BIOLOGY

Description and Taxonomy

The sturgeons (Family Acipenseridae) are large freshwater or anadromous fishes of the infraclass Chondrostei. Sturgeons have a holarctic distribution (Berra 1981). Infraclass Chondrostei have retained ancestral features including a cartilaginous skeleton, retention of the notochord as adults, heterocercal tail, spiracle, spiral valve, and five rows of boney scutes derived from ganoid scales (Moyle and Cech 1982; Birstein 1993). Both sexes of Acipenseridae are morphologically similar, except females are generally larger (Gilbraith et al. 1988). However, sexual dimorphism was reported for *Acipenser ruthenus*, as paired fins were slightly longer in the females (Breder and Rosen 1966).

Sturgeons are an ancient group, with fossils known from the Upper Cretaceous (Bailey and Cross 1954). There are about 24 living sturgeon species comprising 4 genera (*Acipenser*, *Huso*, *Psuedoscaphirhynchus*, and *Scaphirhynchus*; Rochard et al. 1990). The beluga sturgeon, an old world species, is the world's largest freshwater fish, reaching weights of 1,300 kg and lengths of up to 8 m (Berra 1981). The largest North American sturgeon is the white sturgeon (*Acipenser transmontanus*), which grows to about 4 m in length and up to 590 kg in weight. Chondrosteans are a highly endangered group as most species are endangered or threatened (Birstein 1993).

River sturgeons (Genus *Scaphirhynchus*) are characterized by a flattened shovel-shaped snout; a long, slender, and completely armored caudal peduncle; prolonged upper lobe of the caudal fin; and the absence of a spriacle (Smith 1979). This morphology and such features as small eyes, a tough leathery skin (Cross and Collins 1975), dorsoventrally flattened body, and sensitive barbels are adaptations to a life in large, swift, and turbid rivers. Three species of *Scaphirhynchus* are known: pallid sturgeon, shovelnose sturgeon, and Alabama sturgeon (*S. suttkusi*). Pallid and shovelnose sturgeon occur in the Mississippi river basin, while Alabama sturgeon, only recently described, are found in the Mobile Bay Basin (Williams and Clemmer 1991).

The pallid sturgeon was first described by Forbes and Richardson (1905) based on nine specimens collected from the Mississippi River near Grafton, Illinois in 1904. They considered pallid sturgeon to represent a new genus and named the species *Paraschaphirhynchus albus*. In a later review of *Scaphirhynchus*, Bailey and Cross (1954) considered *albus* and *platorynchus* to be congeners of the genus *Scaphirhynchus*. They resemble the old world genus *Psuedoscaphirhynchus*, and together the two genera comprise the subfamily Scaphirhychinae.

Carlson et al. (1985) described the occurrence of hybrids between *S. albus* and *S. platorynchus* in the Mississippi and Missouri Rivers in Missouri. Electrophoretic examination of pallids, shovelnose, and hybrids found them to be indistinguishable at all 37 loci examined (Phelps and Allendorf 1983). The authors attributed the genetic similarity of the two species to recent or incomplete reproductive isolation accompanied by rapid morphological differentiation.

Pallid sturgeon closely resemble shovelnose sturgeon but attain larger sizes. Pallids are generally lighter in color than shovelnose, although color is not consistently reliable for distinguishing the two species (Kallemeyn 1983). Important meristic and morphometric features used to separate pallids from shovelnose are the dorsal and anal fin ray counts, arrangement and length of the barbels, the height of the tenth lateral plate, and lesser degree of scutellation (Bailey and Cross 1954). Pallid sturgeon have 37 or more dorsal fin rays and 24 or more anal fin rays. The bases of the outer barbels are usually posterior to the bases of the inner barbels, so that the bases form a curve that is convex anteriorly. In contrast, the bases of the barbels of shovelnose sturgeon are even. In pallid sturgeon, the inner barbels are less than one sixth the head length, and shorter than the outer barbels (Pflieger 1975).

Distribution

The range of the pallid sturgeon is the mainstem of the Mississippi River from its mouth to the confluence of the Missouri River, and the Missouri River upstream to Fort Benton, Montana as well as the lower portions of a limited number of tributaries. These tributaries include the lower 56 km of the Big Sunflower River (Keenlyne 1989) and the St. Francis River, the lower 64 km of the Kansas River (Cross 1967), the lower 34 km of the Platte River (Keenlyne 1989), and the lower 322 km of the Yellowstone River

(Brown 1971). The total length of its habitat is about 5,725 kilometers of river. Bailey and Cross (1954) noted that the pallid sturgeon's habitat was mostly limited to turbid waters. Smaller rivers such as the Ohio River, or the Mississippi above the confluence with the Missouri, have none, or very few, records of pallid sturgeon occurrence. This is in contrast to the range of the shovelnose sturgeon, which in addition to these areas of sympatry also includes most large tributaries such as the Red, Arkansas, Ohio, and upper Mississippi Rivers, as well as the Rio Grande River (Bailey and Cross 1954; Lee et al. 1980).

Abundance

Despite being one of the largest North American freshwater fishes, the pallid sturgeon is a poorly known species; it was not described until 1905 (Forbes and Richardson 1905). Bailey and Cross (1954) stated that the species is "nowhere common". Although pallid sturgeon were probably never as abundant as shovelnose sturgeon (Forbes and Richardson 1905, Bailey and Cross 1954, Fisher 1962), in recent years a decline in pallid sturgeon abundance has been documented, particularly in the Missouri River from the Fort Peck dam in Montana downstream to the Gavin's Point dam near Yankton, South Dakota (Keenlyne 1989). Although poor sampling efficiencies in large rivers may contribute to its apparent rareness (Kallemeyn 1983), observations of pallid sturgeon over its entire range have declined from an average of 50 per year in the 1960's to just 6 per year in the 1980's (Keenlyne 1989). Shovelnose sturgeon have also been reduced in abundance (Bailey and Cross 1954) but apparently have not declined to the same extent as pallid sturgeon.

Causes of Decline

Most authors attribute the decline of pallid sturgeon to the massive habitat alterations that have taken place over virtually all of its range (Kallemeyn 1983; Gilbraith et. al. 1988; Keenlyne 1989; Dryer and Sandvol 1993). Starting with Fort Peck in 1938, a total of six mainstem dams have been built on the Missouri River. Approximately 51% of the total range of the pallid sturgeon has been channelized for barge navigation and 28% has been impounded. The remaining 21% of its range is below dams, and therefore has altered temperature, flow, and sediment dynamics (Keenlyne 1989).

Habitat modifications such as dams and channelization are thought to have impacted pallid and shovelnose sturgeon by blocking movements to spawning or feeding areas, destroying spawning areas, altering temperatures, turbidity, and flow regimes, and reducing food supply (Keenlyne 1989). Moreover, these alterations have led to a loss of sediment loads and flood pulses thereby disrupting the processes of meandering, erosion and accretion (Hesse 1987). This causes a loss of connection to the floodplain which reduces allocthonous carbon inputs, causing a decline in overall productivity (Hesse 1987; Junk et al. 1989). Also, reduction in habitat diversity and quantity may effectively remove habitat-related reproductive isolating mechanisms, thereby leading to hybridization between pallid and shovelnose sturgeon.

Commercial fishing is known to have severely reduced sturgeon stocks in the Missouri and Mississippi in the late 1800's (Keenlyne 1989). Although pallids were not usually distinguished from shovelnose or lake sturgeon in the catch records, it is likely that their stocks also suffered from overharvest. As long ago as 1951, declines in Mississippi and Missouri River stocks of sturgeon were noted (Barnickol and Starret 1951). The commercial catch of shovelnose sturgeon in parts of the Mississippi River declined up to 94% during the period from 1899 to 1946 (Barnickol and Starret 1951). Shovelnose and probably pallid sturgeon were considered a nuisance by some commercial fisherman and were intentionally destroyed (Carlander 1954; Moos 1978). Forbes and Richardson (1905) reported that pallid sturgeon represented only a small portion of the commercial sturgeon harvest in the Mississippi, but they were much more prevalent in the catch of the Lower Missouri River.

Pollution of the waters in the pallid and shovelnose sturgeon's range may also be a threat to their survival. High levels of pollutants in the Mississippi and Missouri River has precipitated fish consumption warnings and restricted commercial fishing in some areas (Keenlyne 1989). Because the pallid sturgeon has a long life span, and feeds on other fishes and insects (Carlson et al. 1985), it would tend to bioaccumulate pollutants. Concentrations of heavy metals and organic compounds found in pallid sturgeon from the Missouri River may be high enough to have an effect on reproduction (Ruelle and Keenlyne 1993).

Habitat

Habitat use by pallid sturgeon is poorly known. Pallid sturgeon distribution and general observations seem to indicate that they require large, turbid riverine habitat with a firm sandy or gravelly substrate (Bailey and Cross 1954). Bailey and Cross (1954) noted that pallid sturgeon were most closely associated in habitat and distribution with sicklefin chub (*Macrhybopsis meeki*), a species of large, turbid rivers (Lee et al. 1980). Notably, the sicklefin chub is another candidate species for endangered status. Cross and Collins (1975) state that the pallid sturgeon is restricted to large, muddy rivers with swift currents. Researchers in Missouri captured both pallid and shovelnose in gear-sets along sandbars on the inside of riverbends, and in deeply scoured pools behind wing dams, indicating overlap of habitat use by the two species. However, 4 of 11 pallids captured in the Missouri study were captured in gear-sets in swifter currents where shovelnose sturgeon were less numerous (Carlson et. al. 1985).

Quantitative data on habitat use by pallid sturgeon are limited. Several pallids have been observed by SCUBA diving and gillnetting in the tailwaters of Fort Peck dam on the Missouri River, particularly during the winter months. Depths in this tailpool range to 12.2 m (Clancy 1990). Prior to this study, habitat data gathered by use of radio telemetry from the fish captured below Fort Peck dam have yielded a total of five observations of habitat use on two pallid sturgeon. One of the pallid sturgeon moved about 272 km downstream, and the other moved about 72 km downstream from the Fort

Peck tailrace during the period from March to mid-June. Current velocity near the river bottom at relocation sites ranged from 0.46 to 0.96 m/s, turbidity ranged from 12 to >100 Jackson tubidity units, while depth ranged from 1.7 to 2.7 m. Both of these individual pallid sturgeon appeared to prefer turbid water, as relocations in the vicinity of the confluence with the Milk River were consistently in the plume of turbidity along the north bank where the Milk River entered the Missouri River.

Pallid sturgeon movements and habitat use were studied in Lake Sharpe, South Dakota using sonic telemetry (Erickson 1992). Lake Sharpe is a 137 km segment of the Missouri River below Oahe Dam and above Big Bend Dam; the upper segment is riverine. Pallid sturgeon were most often found at depths from 4 to 6 m, bottom current velocities from 0 to 0.73 m/s, and substrates ranging from mud to gravel and cobble. Pallid sturgeon movement was greater at night and was positively correlated with water temperatures and discharge, and larger fish moved more than smaller fish. However because Lake Sharpe is a highly altered habitat, it is possible that these data do not reflect true habitat preference.

The shovelnose sturgeon is a benthic, rheophilic species that occurs in large rivers, living primarily in the strong currents of the main channels over sand or gravel substrates (Bailey and Cross 1954). In Pool 13 of the upper Mississippi River, radio-tagged shovelnose sturgeon were found exclusively in the riverine portion of this habitat, which also has sections that are of a more lentic nature (Hurley et al. 1987). Habitat use differed between spring and summer. In the high water of spring shovelnose sturgeon used velocity refuges such as wing dams. In the summer when water levels were lower, shovelnose sturgeon were found in main channels more often. Depths at shovelnose sturgeon locations ranged from 1 to 10 m (mean, 4.4 ± 0.07 m). Bottom current velocities at shovelnose sturgeon locations ranged from 5 to 65 cm/s (mean, 33 ± 0.5 cm/s). Surface current velocities ranged from 10 to 105 cm/s (mean, 59 ± 0.9 cm/s). Most relocations were over sand substrate, but shovelnose sturgeon were also found associated with the large rock substrate that composed the wing dams.

Helms (1974) captured shovelnose sturgeon in the upper Mississippi River by drifting trammel nets. Catch per unit effort (CPUE) was highest in tailwater areas below dams (mean, 5.3 fish/drift; *N* = 32 drifts), where shovelnose sturgeon made up 80% of the catch. CPUE was lower in main channel, main channel border, and side channel habitats (means, 2.9; 2.5; 3.0; *N* = 240; 484; 33 drifts respectively). Low current velocity habitats could not be sampled by this method.

In the upper Mississippi River, shovelnose sturgeon were generally sedentary, but did exhibit movements of up to 11.7 km/d (Hurley et al. 1987). Helms (1974) also found modest movement of tagged shovelnose sturgeon; mean upstream and downstream distances from capture site were 2.6 and 0.8 km, respectively. However, individual shovelnose sturgeon were recaptured as far as 193 km from the original capture site. Schmulbach (1974) reports downstream movements of up to 534 km, while Moos (1978) documented movements of up to 250 km for shovelnose sturgeon in the Lower Missouri River.

Food Habits

As with other biological attributes, information on the diet of pallid sturgeon is limited. Carlson et al. (1985) examined nine pallid sturgeon stomachs. They found that fish (primarily cyprinids) and larval Trichoptera were the most prevalent food items by volume (38% for each) and frequency of occurrence (56% for each). The remainder of the stomach contents were comprised of other aquatic insects and invertebrates, as well as plant material and sand, which were probably taken incidentally. In the same study, the stomachs of shovelnose sturgeon (*N* = 234) contained fewer fish (2% by volume; 4% by frequency of occurrence) while pallid/shovelnose hybrids (*N* = 9) were intermediate in fish consumption (31% by volume; 22% by frequncy of occurrence). A pallid sturgeon from the Kansas River also had fish and larval aquatic insects in its stomach (Cross 1967).

Feeding behavior of pallid sturgeon has been observed in captivity. At Aksarben Aquarium in Nebraska, a single pallid sturgeon is fed goldfish and other small fish. A pallid sturgeon specimen and some presumed pallid/shovelnose hybrids held at Blind Pony hatchery in Missouri are fed small fish and crayfish. Pallid sturgeon broodstock held at the Gavin's Point National Fish Hatchery in South Dakota are fed live rainbow trout along with prepared broodstock diet.

Modde and Schmulbach (1977) studied food habits of shovelnose sturgeon in an unchannelized reach of Missouri River in South Dakota. Stomach contents consisted primarily of benthic insects. Trichoptera, Diptera and Ephemeroptera were the most important groups, although many other macroinvertebrate groups were represented. No fish were found in shovelnose sturgeon stomachs. The authors described the shovelnose sturgeon as an opportunistic macroinvertebrate feeder that does not exhibit specific preferences for any food items. Trichoptera, Diptera and Ephemeroptera were again found to be the most important food items in shovelnose sturgeon stomachs in the Mississippi and Missouri Rivers in Missouri (Carlson et al. 1985). However, in this study a few fish were found in shovelnose sturgeon stomachs. In a recent study in the Missouri River above Fort Peck reservoir in Montana, Trichoptera, Diptera and Ephemeroptera were the most prevalent invertebrate food items in shovelnose sturgeon stomachs. Larval fish were also found in the diet during late spring months (Douglas Megargle, Montana Cooperative Fishery Research Unit, Pers. Comm.). Other authors also report that benthic insects are the most important food items (Eddy and Surber 1947; Barnickol and Starret 1951, Hoopes 1960; Held 1969, Helms 1974; Elser et al. 1977, Berg 1981; Gardner and Berg 1982; Gardner and Stewart 1987).

Reproduction and Early Life History

Pallid sturgeon are long lived, slow growing and mature at advanced ages (Gilbraith et al. 1988). Fogle (1961) reported that males were sexually mature at 3 to 4 years old and lengths of 533 to 584 mm. However, Keenlyne and Jenkins (1993) estimated that males reach sexual maturity at age 5 to 7 years, and may not spawn every year. Females were estimated to begin egg development at age 9 to 12 years, and spawn for the first time at ages 15 to 20, with intervals of several years between spawning. Factors such as forage availability and other environmental conditions may influence age of sexual maturity and the length of intervals between spawning years (Dryer and Sandvol 1993).

Keenlyne et al. (1992) reported on the fecundity of a pallid sturgeon specimen captured in the Missouri River in North Dakota. The specimen weighed 17.1 kg, was 140.4 cm in fork length, and was estimated to be 41 years old, based on pectoral fin annuli. Ovary mass was 11.4% (1.925 kg) of total body weight. Oocytes averaged 87/g, yielding a fecundity estimate of 170,000 eggs. Oocytes were in late state of maturity as indicated by a uniformly light black color and ovoid shape. Oocytes ranged from 2.5 to 3.0 mm in length and 2.0 to 2.5 mm in diameter.

Time of spawning has not been well documented, but is believed to occur sometime from March through July depending on location (Forbes and Richardson 1905; Gilbraith et al. 1988; Keenlyne and Jenkins 1993). More recent observations include adults in spawning condition in late May and early June in the vicinity of the Missouri/Yellowstone River confluence (Allan Sandvol, USFWS, pers. comm.).

Little information on pallid sturgeon reproduction exists. Sampling for young of the year fishes below Gavin's Point Dam (Kozel 1974), in Lake Oahe (Beckman and Elrod 1971) and for larval fishes in the middle Missouri (Hergenrader et al. 1982) have yielded no pallid sturgeon. There is no information on the locations or physical parameters of pallid sturgeon spawning habitat. However, their spawning habitat must be similar to that of the shovelnose sturgeon as hybridization has been documented (Carlson et al. 1985). Introgression may be occurring because reproductive isolating mechanisms have been lost due to degradation of, or the blocking of access to, preferred pallid sturgeon spawning habitat.

Details of pallid sturgeon spawning are not known but may be similar to those reported for other sturgeon species. Breder and Rosen (1966) report that as a group, sturgeon exhibit uniform spawning behavior. All sturgeon species spawn in the spring or early summer, are multiple spawners, and release their eggs at intervals. The adhesive eggs are released in deep channels or rapids and are left unattended (Gilbraith et al. 1988). The larvae of Acipenserids are pelagic, becoming buoyant or active immediately after hatching (Moyle and Cech 1982). White sturgeon in the Columbia River spawned in the swiftest water velocities available (0.8 - 2.8 m/s mean column velocity) over cobble, boulder or bedrock substrates in depths of 4 to 23 m (Parsley et al. 1993).

Shovelnose sturgeon are reported to spawn over rocky or gravely substrates in main channel habitats of the Mississippi and Missouri Rivers and their major tributaries (Moos 1978; Helms 1974). In the Tongue River, Montana, shovelnose sturgeon spawned when water temperatures reached 17 ° C to 21.5 ° C in early June to mid-July (Elser et al. 1977). In the Missouri River near Vermillion, South Dakota, shovelnose sturgeon spawned when water temperatures reached 18 ° to 19 ° C (Moos 1978). In the Missouri

River above Fort Peck reservoir in Montana, shovelnose sturgeon spawned in June and early July (Berg 1981).

Larval pallid and shovelnose sturgeon are nearly identical (Carlson 1983). However, recent work (Snyder 1994) has provided some diagnostic characters to separate pallid and shovelnose sturgeon larvae, except for recently hatched specimens less than 10 mm (total length; TL). However, identification of certain larger specimens remains difficult due to overlap of characters. Also, it is suspected that the pallid sturgeon broodstock used to produce the specimens for the study by Snyder (1994) were actually pallid x shovelnose sturgeon hybrids.

Age and Growth

The age and growth of pallid sturgeon is not well documented. The largest specimen on record was 30.8 kg (Brown 1971). Six pallid sturgeon from Lake Oahe on the Missouri River in South Dakota were aged and lengths were back calculated by using pectoral fin ray cross sections (Fogle 1963). Estimated ages ranged from 5 to 10 years. Average lengths at ages were as follows: 1 = 279 mm; 2 = 378 mm; 3 = 470 mm; 4 = 574 mm; 5 = 638 mm; 6 = 672 mm; 7 = 732 mm; 8 = 790 mm; 9 = 838 mm; 10 = 881 mm.

Kallemyn (1983) presented length-weight relationships for fish from Lake Oahe and Lake Sharpe (two mainstem Missouri River reservoirs in South Dakota) based on the data of Fogle (1961; 1963) and June (1981), respectively. These relationships showed that from ages O to 6 or 7, and a length of 600 mm, pallid sturgeon increase their length relatively more than their body weight. After 600 mm is reached, weight increases more rapidly than length. Findings of a recent study supported this growth pattern (Keenlyne and Maxwell 1993).

Carlson et al. (1985) aged pallid, shovelnose and hybrid sturgeon from the Missouri and Mississippi Rivers in Missouri. Eight pallid sturgeon had estimated ages ranging from age 4 to age 9 and had slower growth than the Lake Oahe fish aged by Fogle (1963). Lengths of pallid sturgeon were significantly greater than lengths of shovelnose sturgeon of the same age, while hybrids were generally intermediate in length.

Keenlyne et al. (1992) aged a 1404 mm fork length pallid sturgeon taken from the Missouri River in North Dakota. The specimen weighed 17.1 kg, and age was estimated at 41 years based on pectoral fin ray annuli, the oldest pallid sturgeon on record. However, the authors note that if size is a reasonable indicator of age, this specimen was not unusually old, since larger specimens have been captured.

Helms (1974) aged shovelnose sturgeon from the Mississippi River. Ages ranged from 0 to 12 years and fork lengths ranged from 188 mm to 716 mm. However, other authors (Christiansen 1975; Berg 1981) have questioned these growth rates as being higher than those reported elsewhere (Schmulbach 1974). Berg (1981) aged 122 shovelnose sturgeon from the Missouri River above Fort Peck Reservoir in Montana. Ages ranged from 8 to 33 years and averaged 21.3 years. Fork lengths ranged from 533 to 945 mm; weights ranged from 0.8 to 3.9 kg. Similar sizes are reported from the Yellowstone River in Montana (Peterman and Haddix 1975; Elser et al. 1977, Backes et al. 1994). Reports from the upper portions of the Missouri and Yellowstone River systems in Montana and North Dakota indicate that both pallid and shovelnose sturgeon attain larger sizes in the upper basin than in the lower portions of the Missouri and Mississippi basins (Helms 1974; Haddix and Estes 1976; Elser et al. 1977; Rehwinkle 1978; Berg 1981; Keenlyne 1989; Backes et al. 1994; Keenlyne et al. 1994).

REVIEW OF UNDERWATER TELEMETRY

Both radio (Haynes et al. 1978; Buckley and Kynard 1985; Wooley and Crateau 1985; Hurley et al. 1987; Curtis 1990; Hall et al. 1991; Seibel and Kynard 1992) and ultrasonic (McCleave et al. 1977; Apperson and Anders 1990; Hall et al. 1991; Kieffer and Kynard 1992; Moser and Ross 1995) transmitters have been used in sturgeon telemetry studies. Because radio signals penetrate the water/air interface, rapid relocations by moving boats (Hall et al. 1991) or aircraft (Tyus 1990) are possible. However, radio signals cannot be received from tagged fish in deep water particularly in waters of high conductivity such as the Missouri (Clancy 1990) and Yellowstone rivers. Clancy (1991) found that radio signals of tagged pallid sturgeons were not detectable in water deeper than 4.6 m.

Ultrasonic telemetry is superior to radio telemetry in salt water or deep fresh water with high conductivity because unlike radio signals, sonic signal strength is not attenuated in these habitats. Disadvantages of ultrasonic telemetry are that signals are adversely affected by aquatic vegetation, thermoclines, turbulence, boat motors and raindrops (Strasko and Pincock 1977; Winter 1983). Also, because a hydrophone must be submerged in the water to receive sonic signals, locations over large areas are time consuming and range of detection is less than with radio signals.

Surgical implantation of radio and/or sonic transmitters has been used in sturgeon telemetry studies (Wooley and Crateau 1985; Hall et al. 1991; Kieffer and Kynard 1993; Moser and Ross 1995). Internal transmitters do not cause drag or abrasion and cannot be snagged, although the procedure takes longer to perform than external attachment, and the fish must undergo a longer recovery period (Winter 1983). This method is considered best for long-term attachment (Strasko and Pincock 1977; Winter 1983). Tyus (1988) documented long-term retention of surgically implanted radio transmitters in Colorado squawfish (*Ptychocheilus lucius*) and razorback sucker (*Xyrauchen texanus*) of up to 8 years. However, loss of surgically implanted transmitters has been documented for shortnose sturgeon (Kieffer and Kynard 1993), Atlantic sturgeon (Moser and Ross 1995), channel catfish (*Ictalurus punctatus*, Summerfelt and Mosier 1984; Marty and Summerfelt 1986), and rainbow trout (*Oncorhynchus mykiss*; Chisolm and Hubert 1985).

Other sturgeon researchers have used external attachment of transmitters (McCleave et al. 1977; Haynes et al. 1978; Buckley and Kynard 1985; Wooley and Crateau 1985; Hurley et al. 1987; Apperson and Anders 1989; Hall et al. 1991; Kieffer and Kynard 1993; Seibel and Kynard 1992; Moser and Ross 1995). External transmitter loss has been reported for pallid sturgeon (Clancy 1990; 1991), Atlantic sturgeon (Kieffer and Kynard 1993; Moser and Ross 1995), and shortnose sturgeon (Kieffer and Kynard 1993; Moser and Ross 1995).

STUDY OBJECTIVES

The overall objective of this study was to describe and compare habitat use and movements of pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota. Observations of habitat use and movements of pallid and shovelnose sturgeon were obtained through radio and sonic telemetry. Specific hypotheses tested considered differences in substrate use, depth, current velocities, channel width, locations, home range, movement patterns, movement rates, diel movement, grouping of sturgeon, and macrohabitats between pallid and shovelnose sturgeon. Differences in habitat use and movements between telemetered individuals of both species and among seasons were also examined.

STUDY AREA

The study area included about 375 km of the Missouri River from Fort Peck dam in Montana, downstream to the headwaters of Lake Sakakawea in North Dakota as well as the lower 113 km of the Yellowstone River from the Intake diversion dam at Intake, Montana to its confluence with the Missouri River in North Dakota (Figure 1). The Pallid Sturgeon Recovery Plan identifies the study area as a recovery-priority area based on recent records of pallid sturgeon occurrence and the probability that this area provides suitable habitat for pallid sturgeon recovery (Dryer and Sandvol 1993). Hereafter, the confluence of the Yellowstone River and Missouri River will be referred to as the confluence. The overall study area can be divided into three distinct reaches (Tews 1994):

1) The Yellowstone River (river km 0.0 - 113.0). The Yellowstone River is the longest undammed river in the contiguous United States, and its lower reaches represent what is probably the most pristine large prairie river in North America (White and Bramblett 1993), although 31% of its drainage basin area is behind dams (Koch et al. 1977). Discharge, temperature, sediment load and suspended sediment are all higher in the Yellowstone River than in the Missouri River. The mean annual discharge of the Yellowstone River at Sidney, Montana, located about 47 km above the confluence of the Missouri River for 78 years of record (1911 - 1931, 1934 - 1993) is 361 m^3/s (12,760

ft^3/s). The highest instantaneous peak flow on record was 4503 m^3/s (159,000 ft^3/s). The lowest instantaneous low flow on record was 13.3 m^3/s (470 ft^3/s). Water temperatures at this gage ranged from 0.0 °C to 29.0 °C (water years 1951 - 1985). Daily sediment load at this station ranged from 63 to 3,030,000 tons, while suspended sediment ranged from 8 to 26,800 mg/L (water years 1971 to 1981, 1983 - 1992; U. S. Geological Survey 1993).

The upper part of the study reach has numerous islands, bars, backwaters and chutes; a primarily cobble and gravel substrate; a sinuous to irregular (Kellerhals et al. 1976) channel pattern and an average slope in a representative reach of 0.046% (Koch 1977). At Sidney, Montana, located about 47 km above the confluence of the Missouri River, slope declines and sand replaces gravel as the predominant substrate while islands, bars and lateral channel habitats remain common.

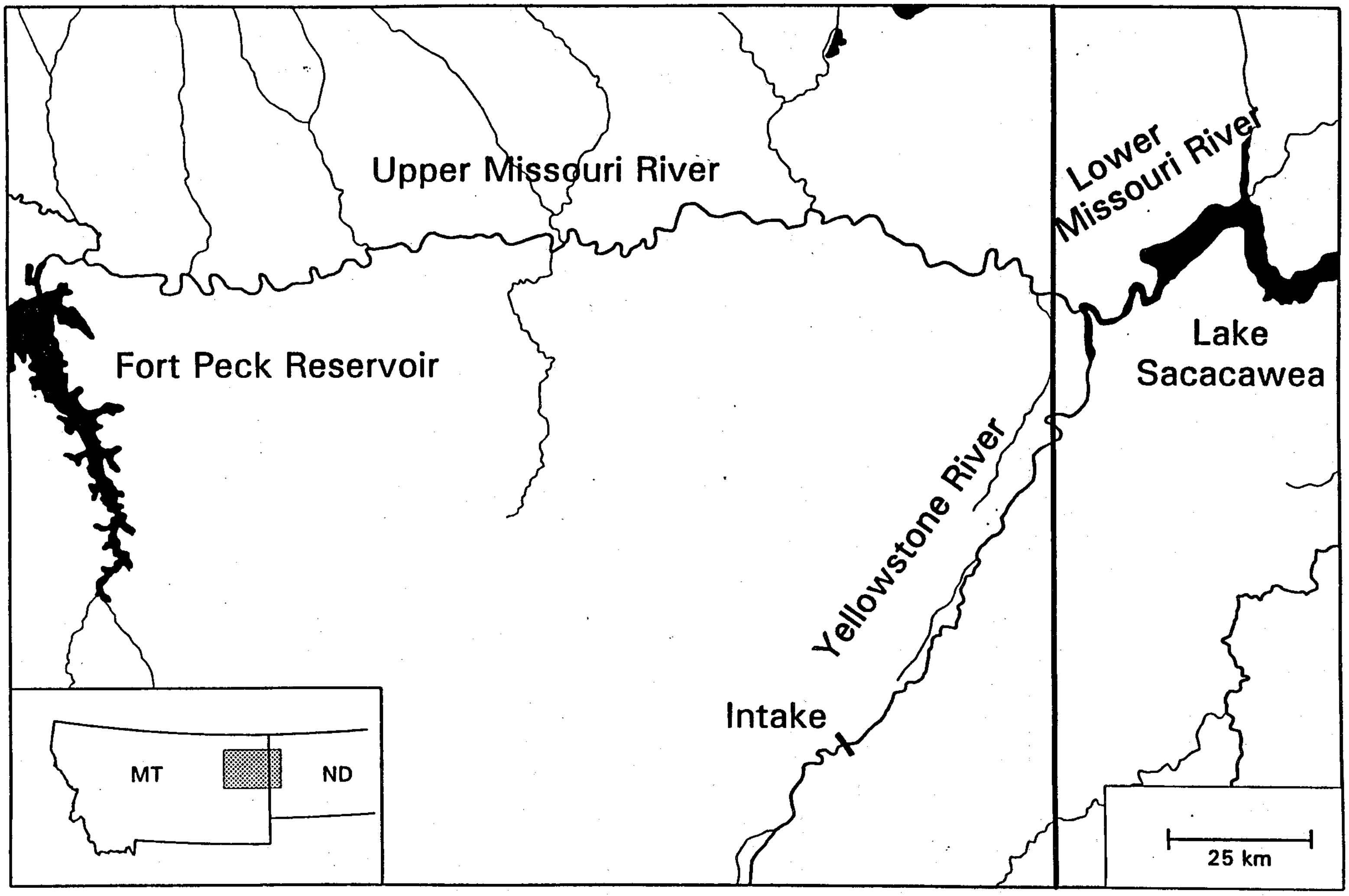

Figure 1. Map of the study area.

2) Upper Missouri River (river km 2545.4 - 2850.5). In contrast to the free-flowing Yellowstone River, the hydrograph, sediment dynamics and temperature regime of this reach of the Missouri River in the study area have been altered by the completion of Fort Peck Dam in 1937 (Gardner and Stewart 1987; Hesse 1987; Latka et al. 1993). Although the Milk and Poplar rivers, entering the Missouri River 17.2 and 140 km below Fort Peck dam, respectively, help restore some of the river's natural character, temperatures are affected for the entire 298 km length of the Missouri River below Fort Peck dam in Montana (Gardner and Stewart 1987).

This reach includes the Fort Peck dam tailrace and dredge cuts, located just below Fort Peck dam. The area is characterized by relatively cold, clear water from the hypolimnetic release, 56.5 m below the surface of the reservoir at full pool (Gardner and Stewart 1987). Because this water carries no suspended sediment, severe bank and bed degradation has occurred in this area. Substrates which were probably formerly primarily sand are now gravel and cobble, and the lack of turbidity allows abundant growth of periphyton. Located 2..6 and 10.0 km below the dam are areas known as the dredge cuts that were deepened by dredging during construction of Fort Peck dam. The dredge cuts are essentially lentic habitats whose level is controlled by the level of the river. Depths in the dredge cuts are generally greater than those found elsewhere in the study area, ranging to about 14 m, and velocities near zero are common (Tews 1994).

The river undergoes a transition from an erosional to a depositional character, although this is due to the impacts of Fort Peck dam rather than natural factors as on the Yellowstone River. Prior to the construction of Fort Peck dam, the entire reach was probably depositional. Substrate in the upper part of the reach is cobble and gravel, while the lower part of the reach is characterized by numerous shifting sand bars (Gardener and Stewart 1987). Gradient is generally lower than that in the Yellowstone River, ranging from 0.011% to 0.028% (Tews 1994).

The mean annual discharge of the Missouri River at Culbertson, Montana, located about 63 km above the confluence of the Yellowstone River for 44 years of record (1941 - 1952, 1958 - 1993; all post-Fort Peck dam) is 291 m^3/s (10,270 ft^3/s). The highest instantaneous peak flow on record was 2215 m^3/s (78,200 ft^3/s). The lowest instantaneous low flow on record was 16.3 m^3/s (575 ft^3/s). Water temperatures at this gage ranged from 0.0 °C to 24.5 °C (water years 1965 - 1979). Daily sediment load at this station ranged from 421 to 147,000 tons, while suspended sediment ranged from 30 to 2,940 mg/L (water years 1972 to 1976; USGS 1993).

3) Lower Missouri River (river km 2475.0 - 2545.4). This reach extends from the confluence of the Yellowstone and Missouri rivers located about 5 km east of the Montana - North Dakota border to the headwaters of Lake Sakakawea. The amount of riverine habitat in this reach varies with the elevation of water in Lake Sakakawea. At full pool (560 m), this reservoir inundates all but about 24 km of the Missouri River. However, because of below full pool water elevations in Lake Sakakawea during this

study, about 50 - 80 km of riverine habitat existed below the confluence of the Yellowstone River (Tews 1994). Due to the influence of the Yellowstone River, the Missouri River regains some of its natural character below the confluence of the two rivers. Sandbars and islands are common, and depths are greater than in the Yellowstone or Upper Missouri Rivers.

METHODS

Capture and Transmitter Attachment

Adult pallid and shovelnose sturgeon were captured by drifting sinking trammel or gill nets. Nets were set perpendicular to the current and drifted for 1 to 42 min, average drift time was about 7 min (Tews 1994). Nets were 1.8 m high by 15 - 37 m long and either mono- or multi-filament gill or trammel nets (Tews 1994; Krentz 1994). One pallid sturgeon was captured by hand by SCUBA divers in a semi-riverine area adjacent to the dredge cuts below Fort Peck dam. Most pallid and shovelnose sturgeon for this study were captured by MDFWP or USFWS biologists; although in 1992, five shovelnose sturgeon were obtained from anglers at the Intake diversion dam on the Yellowstone River. Following capture, sturgeon were weighed, measured, and fitted with transmitters.

A variety of sonic and radio transmitters, either surgically implanted or externally attached were used in this study. All fish received a radio transmitter, and some fish received both radio and sonic transmitters. Surgically implanted transmitters were implanted following the methods of Clancey (1992). The fish were suspended in 6.4 mm netting with their ventral surface up. River water was pumped over the gills with a small bilge pump. Two incisions were made in the ventral body wall: the primary incision about 64 mm long and located about midway along the longitudinal axis of the body; the secondary incision was about 25 mm long and located just anterior of the pelvic fins. The sonic transmitter was inserted first and positioned anterior to the primary incision. Next, the antenna of the radio transmitter was fed into a catheter which was then inserted into the primary incision and pushed posteriorly along the inner body wall until it appeared at the secondary incision. The catheter and antenna were then pulled through the secondary incision while simultaneously inserting the radio transmitter into the primary incision (Ross 1981). About 20 cm of antenna was left trailing from the secondary incision. Both incisions were closed with a series of individual inverted mattress sutures using Ethibond green braided polyester suture material attached to an OS-4 curved cutting needle. The transmitters and all surgical equipment were soaked in Novalsan disinfectant prior to implantation. Following surgery, the fish were held in a live car in quiet water for about 20 min and then released.

The external radio and sonic transmitters were attached to the dorsal fin, following methods used successfully for white sturgeon (Apperson and Anders 1989). Plastic-coated braided stainless steel wires attached to the transmitter were passed through the fleshy base of the dorsal fin. The wires were then passed through holes in a mounting plate cut from a piece of PVC tubing the same size as the transmitter, convex side towards the dorsal fin. The wires were then secured with crimps made from copper tubing. The plastic coating was stripped from the stainless steel wires at the crimps. This allowed the two dissimilar metals to contact each other, therefore the crimps and wires should degrade by electrolysis, allowing the transmitter to detach after an unknown length of time.

Telemetry

Each radio transmitter had a unique frequency between 48.00 and 49.99 Mhz, and each sonic transmitter had a unique pulsed code at 75 kHz. Radio transmitters allowed aerial surveys of the large study area, and sonic transmitters allowed the possibility of relocating fish in water too deep for radio signals to penetrate the water/air interface. An Advanced Telemetry Systems scanning radio receiver and a Sonotronics model USR-91 sonic receiver with a submersible directional hydrophone were used to locate fish.

Telemetered fish were located using a combination of boat and aircraft searches. During May through August 1992, May through November 1993 and May through September 1994, fish were located approximately bi-weekly during aerial surveys of the study area in a single-engine fixed-wing aircraft. Following aerial surveys, observations were made from a 5.3 m aluminum jet boat. During other time periods, fish were located approximately monthly, primarily by MDFWP biologists.

During aerial surveys, a whip-style antenna was attached to the wing strut of the aircraft, and when radio signals were loudest the fish's location was marked on 7.5 minute U. S. Geological Survey (USGS) topographic maps. The precision of aerial relocation was about ± 0.4 km.

Boat surveys proceeded in a downstream direction. This allowed a quiet approach by drifting over sturgeon rather than motoring up into radio range from downstream. Sturgeon relocations made from the boat were done by first detecting the radio signal with a whip-style antenna. Range of radio reception varied with depths of fish and conductivity of the water. The deeper the fish and the higher the conductivity, the shorter the range of reception. The radio signal was generally initially received with the whip antenna at a range of 400 to 600 m or more.

Once a radio signal was detected, one of two methods of determining the fish's location was used, depending on if the fish had both sonic and radio transmitters or just a radio transmitter. For those fish with radio transmitters only, locations were determined by triangulating the radio signal from shore with a directional loop antenna. Surveyor's pin flags were placed to define two intersecting lines that were then sighted from the river and the boat was maneuvered over the fish's location. Blind tests with dummy transmitters placed in the river showed this technique to be accurate to within about 3 m of the actual location, which is about the same as the boat's maneuvering error.

For those fish with both radio and sonic receivers, the directional loop antenna was used to determine the fish's position in the channel cross section while drifting downstream from above the fish. The boat was maneuvered to drift directly over the fish, and the motor was turned off. The loop antenna could generally receive the radio signal from distances less than about 400 m. The sonic signal was usually detectable at about 100 m and was quite directional. As the boat drifted over the fish, the signal became omnidirectional when within about a 10 m diameter area. When the location of the fish was determined, it was marked with a float. This location was then confirmed by triangulating the radio signal.

When a fish's location had been determined, it was monitored for 10 min to determine if it was moving or not by using the radio receiver and directional loop antenna. If the fish did not move for 10 min it was classified as non-moving. If the fish moved during the 10 min period, it was classified as moving.

Sampling Design

To avoid bias, and to provide good coverage of samples in time and space, a random sampling scheme was followed for gathering data. The study area was divided into six units, approximately centered on boat ramp facilities. The units were about 32 km in length.

Two types of sampling activities were conducted: 1) Daily sampling involved making relocations and habitat use observations on all fish in a selected unit. Two sampling periods were established; early morning to afternoon and midday to dusk, and two directions of travel (upstream or downstream) were possible. Following relocation flights, the units containing telemetered fish were listed. Then the unit, sampling period, and direction of initial travel were chosen randomly without replacement. All data collected during daily sampling were considered independent for subsequent analysis. 2) Diel sampling consisted of monitoring a single fish's movements and habitat use for a period of 10 to 12 or more hours during daylight hours or overnight. A sampling unit, direction of travel and time period were randomly selected, a fish was located, and this fish was relocated at least hourly during the diel sampling period. On some occasions, due to their proximity, observations were made on more than one fish during a diel sampling period. If a fish moved out of range at night, it was not relocated until the next morning due to the difficulty of navigating after dark.

Locations

Once a fish's location was determined, date and time of day was recorded, and habitat was characterized at the site. The latitude and longitude of the location was determined with a Magellan portable Global Positioning System (GPS) unit. The center of the river was digitized and geo-referenced using USGS 7.5 minute topographic maps. A computer program was used to place the latitude and longitude of fish locations on this line and to calculate the river km of fish locations.

Water Chemistry, Temperature and Discharge

Water chemistry variables were usually measured along the bank near the fish's location because strong current often prevented anchoring the boat in midchannel. These variables were found to be homogeneous with respect to channel cross section location. Water temperature was measured with a hand-held thermometer. Dissolved oxygen was measured with an Otterbine Sentry III meter, and conductivity was measured with a VWR automatic temperature compensated digital conductivity meter. Secchi disc transparency was measured with a Secchi disc attached to a calibrated rod.

Submersible miniature temperature recorders were used in three locations in the study area in May through November in 1993 and 1994. One temperature logger was placed in the Yellowstone River about 1 km above the confluence (this station will be referred to as the Lower Yellowstone River Station) and one temperature logger was placed in the Upper Missouri River (Upper Missouri River Station) about 2 km above the confluence. The third temperature logger was placed in the Lower Missouri River (Lower Missouri River Station) about 47 km below the confluence. Additional temperature data were obtained from a Montana Department of Fish, Wildlife, and Parks temperature chart recorder in the Yellowstone River about 112 km above the confluence (Upper Yellowstone River Station).

Discharge data were obtained from USGS streamflow gaging stations. Discharge on the Yellowstone River was obtained from a gaging station near Sidney, Montana. Discharge on the Upper Missouri River was obtained from a gaging station near Culbertson, Montana.

Substrate

The substrate at the fish's location was determined by feeling with probes made from 3 m-long steel conduits. Turbid water and/or depth usually prevented visual examination of substrates. Substrates were classed as fines and sand (0 - 4 mm); gravel (5 mm - 75 mm) and cobble (76 mm - 300 mm); boulder and bedrock (>300 mm). Blind tests with the probe over known substrates showed that pure cobble and cobble/gravel mixtures were not distinguishable, so these two classes were combined. Additionally, we discovered that much of the sand substrate in the study area existed as sand "dunes". Therefore, in 1993 and 1994, sand substrates with dunes at least 0.3 m high were classed as sand dunes.

The relative proportions of substrate classes available in the Yellowstone River and Lower Missouri River were estimated by taking substrate measurements at 1273 randomly selected points in 1993 and 1994. Location of substrate measurement points was determined by a random sampling scheme that involved randomly choosing X and Y coordinates with replacement on the plan view of the river channel during daily sampling activities. As the boat proceeded downstream, distance downstream (Y-coordinate) was determined by randomly choosing a time from 1-10 min travel time. A relative distance across the channel (X-coordinate) was determined by randomly choosing a number between 1-9 that indicated a position in the channel cross-section that corresponded to 0.10 of channel width at the chosen Y-coordinate (0 was left bank, 10 was right bank). The latitude and longitude of each random point was also recorded which allowed for estimates of substrate availability for specific river reaches.

Depth and Channel Width

Depth at the fish's location was measured with an Eagle Mach 2 recording depth finder. A cross section of the channel at the fish's location was produced by running a transect perpendicular to the direction of the current while recording the bottom profile with the depth finder. Channel width was estimated with a Ranging MK5 rangefinder. The fish's location along the cross section was marked on the chart paper by pressing the recorder's mark button. The depth of the river at the fish's location as well as the maximum depth of the channel in the cross section was recorded. Relative depth was then calculated by dividing the depth at the fish's location by the maximum depth of the channel in the cross-section. Because both pallid sturgeon and shovelnose sturgeon have morphological adaptations for a benthic existence, fish were assumed to be on the bottom of the river.

Current Velocity

Surface, mean column, and bottom current velocity was measured at the fish's location. Mean column velocity was calculated as the mean of current velocities measured at 0.2 and 0.6 total depth. Triplicate measures were taken at each level, and the mean of these three measures used for comparisons. Current velocities were measured with a Marsh-McBirney Model 201 portable meter with the velocity probe and a 6.8 kg lead weight mounted to a cable suspension system, or a General Oceanics Model 2030R velocity meter. Although sturgeon were assumed to be on the bottom of the river, surface and mean column velocities were also measured and are presented here for ease of comparison to other studies that lack bottom velocity data.

Channel Pattern and Islands and Bars

Locations used by pallid and shovelnose sturgeon were characterized by classifying the channel pattern of the reach within about 0.5 km upstream and downstream of the fish's location according to categories described by Kellerhals et al. (1976). Channel patterns were defined as: 1) straight - very little curvature within reach; 2) sinuous - slight curvature with a total lateral extent of meandering of less than about two channel widths; 3) irregular - occasional curves with a belt width of less than about two channel widths; and 4) irregular meanders - increased curves with a vaguely repeated pattern present.

The presence of islands and alluvial bars within two channel widths of the fish's location was also recorded. Alluvial bars are less stable than islands, are frequently located along sides of the channel, are at elevations lower than the valley floor, and are often not vegetated or have vegetation characteristic of an earlier sere than islands. In contrast, islands are relatively stable, usually vegetated features at or near the same elevation as the valley floor.

The type of alluvial bar was classified according the scheme of Kellerhals et al. (1976). Categories of bars were: 1) channel side bars; 2) channel junction bars; 3) point bars; and 4) midchannel bars. At locations with an island or alluvial bar, the successional stage was classed as: 1) bare or pioneer (grass, forbs, seedling willows or cottonwoods); 2) willow/cottonwood thicket; 3) young cottonwood forest; or 4) mature cottonwood gallery forest or later sere. A location was classified as both island and alluvial bar if both were present.

Finally, the river geomorphic condition within two channel widths of the fish's position was characterized as: 1) run - a straight reach; or 2) curve - a reach within two channel widths of the curve's maximum bend.

Island Density Use and Availability

Aerial photos and USGS 7.5 minute topographic maps were used to characterize the Lower Missouri River and the Yellowstone River in terms of island density (Kellerhals et al. 1976). Because islands cause more than one flow channel and create a diversity of depths and current velocities, island density was used as a measure of habitat complexity. Islands were defined as relatively stable, usually vegetated features at or near the same elevation as the valley floor (Kellerhals et al. 1976). Reaches were classified using the following categories: 1) none - no islands; 2) single - a single island, no overlapping of islands; 3) frequent - occasional overlapping of islands, with average spacing between islands less than 10 river widths; and 4) split channel - islands overlap other islands frequently or continuously, the number of flow channels is usually two or three.

Reaches $\geq$ 0.5 km from an island were classified as island density category 1. Reaches with islands (categories 2 - 4) were defined as lengths of river $\leq$ 0.5 km from an island. If islands in a reach overlapped or were spaced $\leq$ 0.5 apart, the reach was classed according to island density as listed above.

The center of the river was digitized and geo-referenced using USGS 7.5 minute topographic maps. The Universal Transverse Mercator (UTM) coordinates for the beginning and ending of each reach were recorded. A computer program was used to calculate the river km from the UTM's. The length of each reach was then calculated from the river km data.

Aerial photographs of the river taken in August, 1993 were used to verify and adjust the locations of reaches shown on the USGS maps. The Lower Missouri River from the US Highway 85 bridge near Williston, North Dakota, and the Yellowstone River from the confluence to the diversion structure on the Yellowstone River at Intake, Montana was classified. The Missouri River below the Highway 85 bridge did not fit this classification because it is a delta-like area mostly inundated by Lake Sakakawea at full pool. Also, only two fish were located in this area over the course of the study. The Missouri River above the confluence of the Yellowstone River was also rarely used and so was not included. Alluvial bars were not estimated because their number and magnitude varied with discharge which differed between when the fish were located and when the photographs were taken.

Only those locations made on the river with latitude and longitude recorded from the GPS unit were used in calculating use of island density categories. Since the accuracy of GPS locations is about 90 m, no location within 90 m of an island density category reach edge was used. Aerial locations were not used because the unknown accuracy of the location generates an unknown potential for misclassification with respect to island density category.

DATA ANALYSIS

In telemetry studies, individual animals are sampled over time. Because the sample size is a function of the frequency of sampling, sample sizes can be artificially inflated by increasing the frequency of sampling. This is a concern particularly when data are collected intensively, as occurs when monitoring diel activity, movements and habitat use (White and Garrott 1992), and bring into question independence of such data. In this study, data collected during daily sampling are considered independent. However, because diel sampling consisted of repeated observations of an individual fish over a relatively short period of time, data collected in this manner were not considered independent. Therefore, for analysis, daily sampling data were combined with one randomly selected data point per diel sampling period per fish. These data are referred to in the text as independent observations and are used for depth, velocity, substrate, macrohabitat and overall movement analyses. In contrast, all observations, including those from diel sampling, were used for analyses of diel activity patterns, for hourly movement rates, and for reporting overall ranges of depth and velocities used by pallid and shovelnose sturgeon.

In the dynamic environment of a large river, microhabitat features such as depth and velocity are expected to vary with discharge. Selection of these habitat variables by pallid and shovelnose sturgeon involved choosing among the range of depths and velocities available over the individual fish's home range. In order to demonstrate preference or choice by an individual sturgeon, the use of certain depths or velocities must be compared to the availability of those depths or velocities at the same time that the use is documented (Seibel and Kynard MS). Since the home range of pallid and shovelnose sturgeon may be in excess of 200 km of river, it is not feasible to measure use and availability of depth and velocity at the same time over such a large area. Moreover, to adequately describe the relative frequencies of depth and velocity over such a large area, even given stable flow conditions, would require an effort beyond the scope of this study. Therefore, only use and not preference for these microhabitat variables will be described.

When comparing depths, channel widths and current velocities at pallid and shovelnose sturgeon locations, first the normality of the data set was tested using the Komolgorov-Smirnov Test (Neter et al. 1993). If the Komolgorov-Smirnov test failed to reject the hypothesis that the data were normal, the t-test was used to test if means were significant different. In contrast, if the Komolgorov-Smirnov test rejected the hypothesis that the data were normal, the Mann-Whitney U test was used to test if the medians were significantly different.

Water Temperatures

Minimum, maximum and median daily temperatures for the four thermograph stations were tabulated. The sign test (Neter et al. 1993) was used to compare daily temperatures from all combinations of stations within each year to determine which stations had warmer or cooler water temperatures. The sign test computes the percentage of times that the value of the first variable is larger than the value of second variable, and compares this percentage to 50% under the null hypothesis. Because the different stations differed in coverage of temperatures through time, only temperatures measured on the same day were compared between stations.

Substrate

The hypothesis that substrate use by pallid and shovelnose sturgeon did not differ was tested with Pearson's χ^2 test. Because individual sturgeon had widely varying numbers of substrate observations, three separate random samples of substrate use consisting of one observation per individual fish were drawn without replacement for both species. Although this resulted in a smaller sample size and consequent reduction of power, by using only one observation per individual potential bias from individual fish with different substrate preferences and/or larger numbers of observations was eliminated.

The hypothesis that pallid and shovelnose sturgeon use substrate types in proportion to their availability was tested by using a χ^2 technique for availability estimates generated by random points (Marcum and Loftsgaarden 1977). This technique first tests the hypothesis that overall use is proportional to availability. If a significant result is obtained, confidence intervals are constructed for each resource category. If a confidence interval contains zero, the resource is used in proportion to its availability. If a confidence interval is positive, the resource class is preferred, and if it is negative the resource class is avoided. A necessary assumption is that the relative proportions of substrate available is constant. This assumption was checked by comparing estimates of substrate relative proportions from 1993 and 1994.

Substrate use by pallid and shovelnose sturgeon was compared to the estimated availability of substrates in that species' home range. The assumption that all individuals of each species has the same substrate preferences is necessary when grouping all observations for that species together for statistical testing. For example, an individual fish with a large number of observations coupled with a strict substrate preference may alter the results of the test. This assumption was checked by comparing the results of the χ^2 test from the grouped sample to the results of χ^2 tests using three random sub-samples with equal contribution from each fish. If the results from the grouped and χ^2 tests are different, the assumption that all individuals of the species have the same substrate preferences is not founded.

Depth and Channel Width

Two approaches were used in comparing depths, maximum depths, and relative depths used by pallid and shovelnose sturgeon. The first approach involved comparing overall depths used by pallid and shovelnose sturgeon.

The second approach used an analysis of variance (ANOVA) to simultaneously test the following a priori hypotheses: 1) mean depths, maximum depths, and relative depths used by pallid sturgeon and shovelnose sturgeon were not different; 2) mean depths, maximum depths, and relative depths used by pallid and shovelnose sturgeon in the Yellowstone River were not different from those used in the Lower Missouri River; 3) the difference in mean depths, maximum depths, and relative depths between shovelnose and pallid sturgeon is the same in the Lower Missouri River and the Yellowstone River (no interaction between species and rivers); 4) Variance of mean depths, maximum depths, and relative depths used by individual fish of each species in each river is equal to zero. The linear statistical model for depth, maximum depth, and relative depth was:

$$Y_{l(ijk)} = \mu + S_i + R_j + (SR)_{ij} + I(SR)_{k(ij)} + E_{l(ijk)} \qquad (1)$$

$$i = 2$$

$$j = 2$$

$$\sum k(ij) = 62$$

$$1 \leq (ijk) \leq 18$$

where Si is the effect of the ith species, Rj is the effect of the jth river, (SR)ij is the effect of the species by river interaction, $I(SR)_{k(ij)}$ is the effect of the individual fish within the species by river combination, and $E_{l(ijk)}$ is the residual error term. The species (pallid or shovelnose sturgeon) and the rivers (Yellowstone or Lower Missouri Rivers) were treated as fixed effects. The individual fish was treated as a random effect, nested within one of the four species and river combinations. The residuals were tested for normality using the Wilks-Shapiro test and checked for outliers by producing boxplots.

The utility of including other variables in the linear model was checked by plotting residuals versus the values of the variables. If a pattern was apparent in the plot, the variable was included in the model. Variables checked in this manner were discharge, month and year, water temperature, hours before and after sunrise and sunset, diel category, substrate type, river kilometer (location), and Secchi disk reading. Because of small sample size, data for the Upper Missouri River were not included in the model.

Current velocity

As with depth, two approaches were used in comparing means of surface, mean column, and bottom current velocities used by pallid and shovelnose sturgeon. The first approach compared overall current velocities use by the two species.

The second approach used an ANOVA to simultaneously test the following a priori hypotheses: 1) means of surface, mean column, and bottom velocities used by pallid sturgeon and shovelnose sturgeon were not different; 2) means of surface, mean column, and bottom velocities used by pallid and shovelnose sturgeon in the Lower Missouri River and the Yellowstone River were not different; 3) the difference in means of surface, mean column, and bottom velocities between shovelnose and pallid sturgeon is the same in the Lower Missouri River and the Yellowstone River (no interaction between species and rivers) 4) Variance of means of surface, mean column, and bottom velocities used by individual fish of each species in each river is equal to zero. The linear statistical model for surface, mean column and bottom velocities was:

$$Y_{l(ijk)} = \mu + S_i + R_j + (SR)_{ij} + I(SR)_{k(ij)} + E_{l(ijk)} \tag{2}$$

$$i = 2$$

$$j = 2$$

$$\Sigma k(ij) = 62$$

$$1 \leq (ijk) \leq 18$$

where S_i is the effect of the ith species, R_j is the effect of the jth river, $(SR)_{ij}$ is the effect of the species by river interaction, $I(SR)_{k(ij)}$ is the effect of the individual fish within the species by river combination, and $E_{l(ijk)}$ is the residual error term. The species (pallid or shovelnose sturgeon) and the rivers (Yellowstone or Lower Missouri Rivers) were treated as fixed effects. The individual fish was treated as a random effect, nested within one of the four species and river combinations. The residuals were tested for normality using the Wilks-Shapiro test and checked for outliers by producing boxplots. As with depth, the utility of including other variables in the linear model was checked by plotting residuals versus the values of the variables and looking for patterns. If patterns were apparent the variable was included in the model. Because of small sample size, data for the Upper Missouri River were not included in the model.

General Distribution, Home range, Diel Activity, and Movement

River kilometer of fish locations in the Yellowstone and Lower Missouri rivers were sorted into 2 km reaches and separated by season and species. Histograms were made from these data and general distributions and seasonal use were identified from the histograms. This allows identification of areas used with high frequency by pallid and shovelnose sturgeon regardless of capture location and the year in which observations were made.

To identify areas of high use temporally and spatially, aggregations of telemetered pallid and shovelnose sturgeon were identified. Aggregations were defined as more than 3 telemetered pallid or shovelnose sturgeon occupying the same 1 km reach of river on the same day. By identifying aggregations temporally, periods when pallid and shovelnose sturgeon tend to aggregate can be identified. By identifying aggregations during the presumed spawning season for pallid and shovelnose sturgeon, potential spawning locations can be identified. Aggregations are presented graphically and in tabular form.

Overall home range in kilometers was calculated by subtracting the fish's uppermost location from the fish's lowermost location. In cases where individual fish were found in the Upper Missouri River, in addition to the Lower Missouri River and/or the Yellowstone River, this segment was added to the range. Home range was also calculated for each species by season, i.e. summer = June 21 - September 22; fall =

September 23 - December 20; winter = December 21 - March 19; spring = March 20 - June 20. A Kruskal-Wallis ANOVA was used to test for differences among median seasonal ranges within species. Dunn's nonparametric multiple comparison test was used to test which seasonal home ranges were significantly different from each other. Mann-Whitney U tests were used to test for differences between median seasonal ranges between species.

Days at large was the length of time between the capture of the fish and the last relocation or until I determined that the fish had lost its transmitter. Relocations were usually attained by telemetry; however, in two cases, pallid sturgeon were captured and not radio-tagged but were later recaptured and radio-tagged at that time. Also, on one occasion a pallid sturgeon was recaptured after losing its radio transmitter. In these three cases, location and date from the captures was added to the telemetry data.

Diel activity patterns were assessed by tabulating the times when fish were observed and whether the fish was moving or not moving. This information was obtained from both daily and diel sampling activities. Sunset and sunrise tables for Williston, North Dakota were used to place the time of observation relative to sunrise and sunset. Four diel categories were established: 1) Day = ≥1 h after sunrise until ≤ 1 h before sunset; 2) Dusk = < 1 h before sunset until < one h after sunset; 3) Dark = ≥ 1 h after sunset until ≥ 1 h before sunrise; 4) Dawn = < 1 h before sunrise until < 1 h after sunrise.

The proportion of observations that were from moving fish was calculated for each diel category for pallid and shovelnose sturgeon. In addition, to examine individual variability of diel movements, the proportion of observations that were from moving fish was calculated for the three individual fish of each species with the most observations.

Direction and rate of fish movements were calculated by subtracting the river kilometer of a location from the previous location and dividing by the time between the locations. When the time elapsed between locations was greater than 24 h, movement rate was calculated as km/d. When the time elapsed between locations was less than 24 h, movement rate was calculated as km/h. Because additional movement may have occurred between locations, calculated movement rates represent the minimum movement for the time period between locations.

The Mann-Whitney U test was used to test hypotheses that the median movement rates were the same between species and between upstream and downstream movements within species. Kruskal-Wallis ANOVA was used to test the hypotheses that movement rates were the same for each season within species, followed by Dunn's multiple comparison test.

Clustering

An analysis of the degree of "clustering" or use of common reaches of river during the different seasons was performed to determine if pallid and shovelnose sturgeon were more closely associated in some seasons relative to others. First, individual fish were separated into "batches", i.e. groups of fish of the same species that were captured in the same general area (a reach of river from 1 km to about 30 km long) at about the same time (up to 21 d from first to the last capture). By forming batches, the effect of widely separated capture locations is controlled. Three batches of pallid sturgeon with five to seven individuals each were formed. Six batches of shovelnose sturgeon with two to seven individuals each were formed.

Locations (river km) of individual fish were then separated by season and batch. The mean river km location of each individual for each season was calculated. Locations from the Upper Missouri River were not used in this calculation because this would introduce a third dimension to the data. If fish in a batch are widely dispersed during a season, the variance of mean river location will be relatively large. Conversely, if fish in a batch are clustered during a season, the variance of mean river location will be relatively small. The hypothesis that fish in each batch had the same degree of clustering in each season was tested by testing for homogeneity of variance among batches using Bartlett's χ^2 Test.

Movement into the Yellowstone River and the Lower Missouri River

The number of observations of fish passing upstream from the Lower Missouri River into the Yellowstone River or Upper Missouri River were tabulated. Preference for entering the Yellowstone River or the Upper Missouri River was tested by Pearson's χ^2 observed versus expected analysis. Median discharges on the Yellowstone River and the

Upper Missouri River during periods when telemetered pallid and shovelnose sturgeon passed the confluence were compared with the Mann-Whitney U test.

Movement Regression Models

Linear regression models were constructed for movements of 24 individual pallid sturgeon and 22 individual shovelnose sturgeon. River kilometer was the response variable and predictor variables were discharge and photoperiod.

Discharge data from the USGS gaging station on the Yellowstone River near Sidney, Montana were used for locations on the Yellowstone River. Discharge data from the USGS gaging station on the Missouri River near Culbertson, Montana were used for locations on the Upper Missouri River. Since no large tributaries enter the Missouri or Yellowstone rivers below these gages, discharge in the Lower Missouri River is essentially equal to the discharge at Sidney plus the discharge at Culbertson. However, the Sidney and Culbertson gages are 47 km and 62 km above the confluence, respectively. Therefore, discharge in the Lower Missouri River was calculated as discharge at Sidney the previous day plus discharge at Culbertson the previous day. Photoperiod was calculated from a table with sunrise and sunset times for Williston, North Dakota (U. S. Navy 1977).

Models were constructed for river kilometers of each fish using discharge alone, photoperiod alone, and both discharge and photoperiod. Since discharge was different in the three river segments (Yellowstone River, upper and Lower Missouri River) separate parameter coefficients were calculated for each segment that an individual fish was located in. Photoperiod models had only one parameter estimate. Sign (positive or negative) of parameter coefficients indicate if locations predicted from the model are farther upstream or downstream as the magnitude of dependent variables increase. Sign and magnitude of parameter coefficients and coefficients of simple determination (r^2) were compared between individual fish, species and model. Because a complete data set of river temperatures was not available, models using water temperature as the predictor variable were not constructed.

These linear regression models were constructed as an exploratory data analysis tool to identify potential environmental cues for movements of pallid and shovelnose sturgeon. Hypothesis testing and confidence intervals based on these models are statistically invalid because the assumptions of independence with respect to responses and errors are clearly violated.

Island Density Use Versus Availability

Preference of island density categories was examined by using Pearson's χ^2 analysis (Nue et al. 1974). Two general hypotheses were tested: 1) use of island density categories occurs in proportion to availability, considering all categories simultaneously, and 2) use of island density categories occurs in proportion to availability, considering each category separately.

Use of island density categories by pallid and shovelnose sturgeon was estimated by calculating the proportion of independent observations in each island density category. Use was calculated for each species with all observations pooled, as well as separated by season (spring and summer only).

Availability was calculated according to the hypothesis being tested. For example when testing for preference for all pallid sturgeon pooled together, availability of island density categories for the entire pallid sturgeon range was used. When testing preference for an individual fish, only the reaches in that individual's home range were used for availability.

Individual variation in preference of island density categories was examined by testing preference of individual fish. Thirteen individual pallid sturgeon with $N \geq 10$ observations and 9 shovelnose sturgeon with $N \geq 8$ observations were tested. In addition, random samples of one and two observations from each individual fish were taken to examine the effects of many observations from few individuals on the pooled results. If the results of testing the random samples agree with results from the pooled samples, there is little individual variation.

RESULTS

Twenty four pallid sturgeon and 27 shovelnose sturgeon were captured and equipped with radio or radio and sonic transmitters (Tables 1 and 2). Fork length range was from 1151 to 1600 mm and from 581 to 947 mm for pallid and shovelnose sturgeon, respectively (Figure 2). Pallid sturgeon weight range was from 10.7 to 28.2 kg, while shovelnose sturgeon weight ranged from 0.8 to 4.2 kg.

Because the sex of pallid and shovelnose sturgeon cannot be determined externally, the sex of most of the telemetered fish was unknown. However, the presence of eggs was observed in seven shovelnose sturgeon that had transmitters surgically implanted (Table 2). Also, one telemetered pallid sturgeon was observed to be extruding eggs when it was snagged by a paddlefish (*Polyodon spathula*) angler (Table 1).

Table 1. Statistics of pallid sturgeon captured and radio tagged in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Radio frequency	Date of capture	Capture location (river km)[a]	Radio transmitter weight (g) type[b]	Sonic transmitter weight (g) type[b]	Weight (kg)	TL	FL
48.520	9/30/92	2531.3	14.0 A		10.70	1349	1242
48.540	9/15/92	2523.2	14.0 A		24.50	1702	1600
48.562	5/21/94	108.0	12.7 A		18.8	1489[c]	1384
48.570	5/21/93	114.2	14.0 A			1245	1151[d]
48.580	4/15/93	2520.0	14.0 A	28.0 A	13.85	1470	1385
49.020	10/19/92	2531.3	14.0 A		16.10	1453	1366
49.030[e]	4/23/93	2.7	56.0 A		28.15	1650	1566
49.050	9/30/92	2531.3	56.0 A	88.0 A	22.20	1646	1524
49.070	10/19/92	2531.3	14.0 A		16.60	1529	1402
49.100	6/17/92	9.1	56.0 A	88.0 A	12.70	1435	1336
49.130	10/19/92	2531.3	14.0 A		10.80	1384	1308
49.170	10/21/92	2520.0	14.0 A		19.30	1585	1486
49.240	9/16/93	2542.5	32.5 A		10.80	1400	1292
49.350	4/30/94	21.2	35.0 A		17.24	1511[c]	1405
49.370	9/28/93	2531.3	33.7 A		15.90	1428	1325
49.630	9/29/93	2531.3	34.4 A		14.50	1519	1400
49.650	9/28/93	2531.3	34.1 A		16.80	1545	1430
49.670	4/24/93	3.2	35.0 C	28.0 C	14.53	1570	1365
49.680	4/10/92	2523.2	128.0 B	56.0 C	22.20	1021	945
49.712	9/28/93	2531.3	36.8 A		20.60	1635	1525
49.810	4/22/93	2.7	19.0 A		14.98	1470	1373
49.830	4/15/93	2520.0	19.0 A	28.0 A	20.20	1620	1514
49.850	9/14/93	2532.9	19.0 A		17.50	1540	1410
49.870	3/20/93	2847.9	19.0 A	28.0 A	17.68	1631	1524

[a] River kilometers 0 - 114.2 are on the Yellowstone River; 2520 - 2545.4 are on the Lower Missouri River; and 2545.4 - 2850.5 are on the Upper Missouri River.

[b] Type A transmitter: External attached to base of dorsal fin; Type B transmitter: Internal with protruding antenna; Type C transmitter: Internal.

[c] Total length calculated from TL = (FL + 47.59)/1.04 (Keenlyne and Maxwell 1993).

[d] Fork length calculated from FL = (TL - 47.59)/1.04 (Keenlyne and Maxwell 1993).

[e] This individual was known to be female because it was observed to be running eggs after being captured by an angler (Steve Krentz; USFWS Personal Communication).

Table 2. Statistics of shovelnose sturgeon captured and radio or sonic tagged in the Yellowstone and Missouri rivers in Montana and North Dakota, 1991-1994.

Radio frequency	Date of capture	Capture location (river km)	Radio transmitter weight (g) type[a]	Sonic transmitter weight (g) type[a]	Weight (kg)	TL	FL
3335	7/30/91	2847.9		28.0 C	0.77	640	581[b]
48.280	5/20/94	24.9	16.0 A		1.33	744	678
48.300	5/20/94	24.9	16.0 A		1.56	799	730
48.320	5/20/94	24.9	16 A		1.76	828	749
338	7/31/91	2847.9		28.0 C	0.95		
48.340	5/20/94	24.9	16.0 A		1.53	776	699
48.360	5/20/94	24.9	16.0 A		2.44	888	806
48.380	5/20/94	24.9	16.0 A		2.07	862	781
48.550	5/27/93	12.3	14.0		2.36	851	777
48.560	8/6/91	111.0	14.0	28.0	2.91	869	797[b]
48.590	6/9/93	7.0	12.7			940	833
48.600	8/6/91	111.0	34.0	28.0	3.09	919	844[b]
48.620	8/7/91	111.0	34.0	28.0	3.40	927	852[b]
48.640	8/7/91	111.0	34.0	28.0	3.09	914	840[b]
48.660	8/8/91	2532.9	34.0	28.0	3.09	917	842[b]
48.680	10/9/91	2536.1	34.0	28.0		919	823
48.740	8/8/91	2534.5	12.0	28.0	1.77	856	785[b]
48.760	9/4/91	2540.1	12.0	28.0	2.63	940	861
48.820[c]	6/2/92	114.2	40.0	28.0	3.04	894	825
48.840[c]	6/1/92	114.2	40.0	28.0	3.49	1021	945
48.860[c]	6/2/92	107.8	40.0	28.0	3.20	860	823
48.880[c]	6/3/92	114.2	40.0	28.0	3.78	910	878
48.900[c]	6/3/92	114.2	40.0	28.0	3.46	940	873
48.920[c]	6/1/92	114.2	40.0	28.0	4.20	1039	947
48.940[c]	6/8/92	114.2	40.0	28.0	2.90	868	803
49.710	9/28/92	2544.1	36.8		2.30	894	820
49.790	9/28/92	2544.1	36.8		2.70	856	787

[a] Type A transmitter: External attached to base of dorsal fin; Type B transmitter: Internal with protruding antenna; Type C transmitter: Internal.

[b] Fork length calculated from FL = (TL - 24.02)/1.06 (Moos 1978).

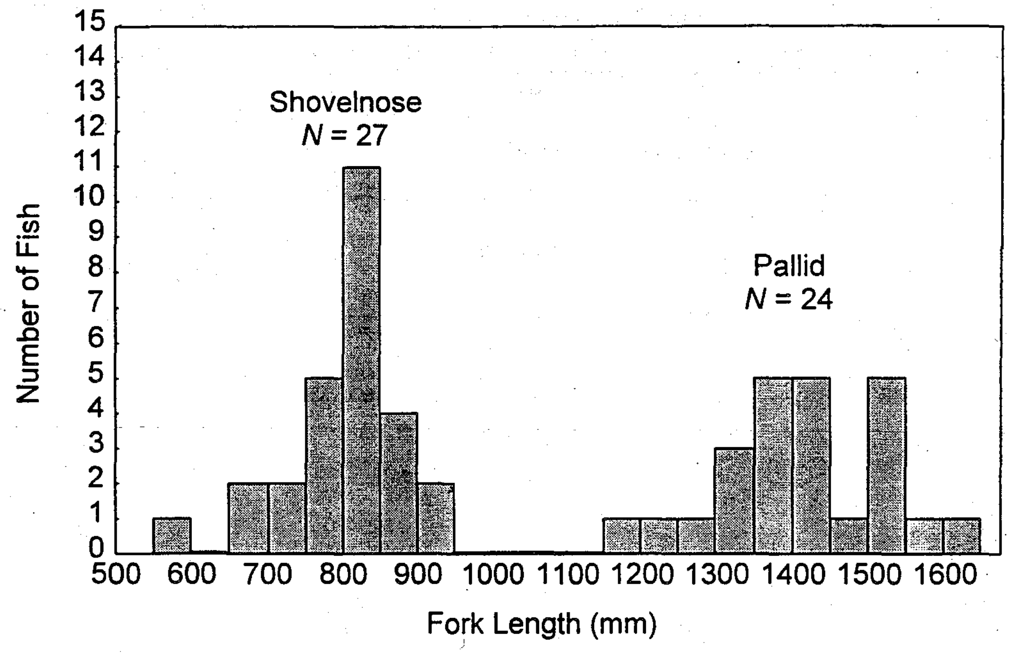

Figure 2. Fork lengths of pallid and shovelnose sturgeon telemetered in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Water Chemistry and Temperature

Water chemistry was similar at locations of both species (Table 3). Water temperature at pallid sturgeon locations ranged from 3.0 to 26.0 ° C compared to 3.0 to 27.0 ° C at shovelnose sturgeon locations. Dissolved oxygen was similar at locations of both species; the mean at pallid sturgeon locations was 8.7 mg/L while the mean at shovelnose sturgeon locations was 9.0 mg/L. Mean conductivity was also similar; 526 umhos at pallid sturgeon locations and 536 umhos at shovelnose sturgeon locations. Secchi disk transparency was likewise similar; the mean at pallid sturgeon locations was 20 cm and the mean at shovelnose sturgeon locations was 27 cm.

Table 3. Water chemistry parameters and temperatures measured at locations of pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

	Water temperature (°C)	Dissolved oxygen (mg/L)	Conductivity (micromhos)	Secchi disk transparency (cm)
Pallid sturgeon				
Mean	15.8	8.7	526	20
Median	18.0	8.5	550	9
Minimum	3.0	7.0	67	1
Maximum	26.0	12.0	880	204
N	159	72	119	115
Shovelnose sturgeon				
Mean	18.5	9.0	536	27
Median	20.0	8.6	545	22
Minimum	3.0	7.4	287	1
Maximum	27.0	11.1	903	>100
N	144	47	81	65

Although ranks of daily water temperatures varied among thermograph stations (Figure 3), the sign test found significant differences among the four stations (Table 4, Figure 4). Temperatures in the Yellowstone River were generally higher than in the Missouri River. The Lower Yellowstone River Station had significantly higher maximum, minimum and median temperatures than the Lower Missouri River Station in both 1993 and 1994. The Lower Yellowstone River Station also had significantly higher maximum, minimum, and median temperatures than the Lower Missouri River Station in 1994. In 1994, all temperatures at the Lower Yellowstone River Station were higher than those at the Lower Missouri River Station, except for 3.18% of minimum temperatures. The Upper Missouri River Station thermograph was lost in 1994.

Table 4. Results of Sign Test for temperatures at four thermograph stations in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. V1 and V2 are the first variable and second variables listed in the Test column, respectively. Percent V1 < V2 is the percent of non-ties in which V1 is less than V2. UY = Upper Yellowstone River Station; LY = Lower Yellowstone River Station; UM = Upper Missouri River Station; LM = Lower Missouri River Station.

Year	Test (V1 vs. V2)	Non-ties (*N*)	Percent (V1 < V2)	*P* Level
1993	LY maximum vs. UM maximum	159	38.36	0.004304
1993	LY median vs. UM median	160	33.12	0.000028
1993	LY minimum vs. UM minimum	160	35.00	0.000203
1993	LY maximum vs. LM maximum	160	31.25	0.000003
1993	LY median vs. LM median	160	33.75	0.000055
1993	LY minimum vs. LM minimum	161	40.99	0.027334
1993	UY maximum vs. LY maximum	135	49.63	1.000000
1993	UY median vs. LY median	135	62.96	0.003431
1993	UY minimum vs. LY minimum	135	77.78	0.000000
1993	UM maximum vs. LM maximum	171	28.07	0.000000
1993	UM median vs. LM median	170	57.65	0.055186
1993	UM minimum vs. LM minimum	171	68.42	0.000002
1993	UY maximum vs. LM maximum	143	36.36	0.001484
1993	UY median vs. LM median	143	58.04	0.065808
1993	UY minimum vs. LM minimum	143	96.50	0.000000
1993	UY maximum vs. UM maximum	142	38.03	0.005618
1993	UY median vs. UM median	142	42.96	0.118037
1993	UY minimum vs. UM minimum	142	78.17	0.000000
1994	LY maximum vs. LM maximum	158	0	0.000000
1994	LY median vs. LM median	157	0	0.000000
1994	LY minimum vs. LM minimum	157	3.18	0.000000
1994	UY maximum vs. LM maximum	35	11.43	0.000011
1994	UY median vs. LM median	35	51.43	1.000000
1994	UY minimum vs. LM minimum	35	88.57	0.000011
1994	UY maximum vs. LY maximum	35	45.71	0.735317
1994	UY median vs. LY median	35	82.86	0.000200
1994	UY minimum vs. LY minimum	35	100.00	0.000000

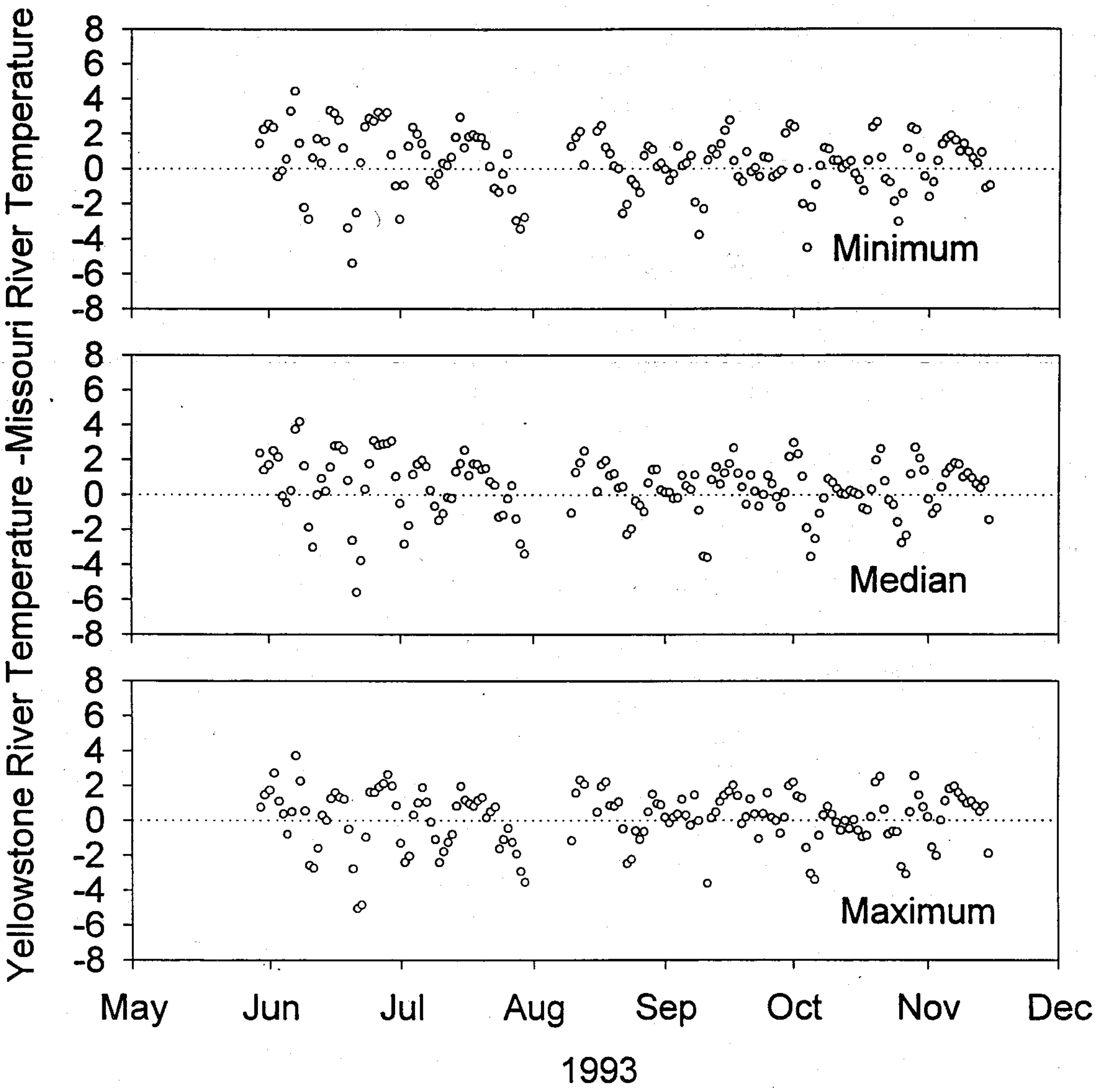

Figure 4. Minimum, median and maximum daily temperatures from the Lower Yellowstone River minus minimum, median and maximum daily temperatures from the Upper Missouri River Station, 1993. Points above zero represent temperatures that are higher at the Lower Yellowstone River Station than at the Upper Missouri River Station, and vice-versa.

Within the Yellowstone River, daily maximum, minimum and median temperatures were either significantly higher at the Lower Yellowstone River Station than at the Upper Yellowstone River Station, or not significantly different. This same pattern existed for the Missouri River; Lower Missouri River Station temperatures were either significantly higher or not significantly different than Upper Missouri River Station temperatures.

Discharge

Discharge regimes in the Yellowstone and Missouri rivers differed markedly (Table 5, Figure 5). The hydrograph of the Upper Missouri River is typical of a river regulated by a dam while the Yellowstone River's hydrograph is more typical of an

Table 5. Summary statistics for discharge data at gaging stations on the Yellowstone River near Sidney, Montana and on the Missouri River near Culbertson, Montana for water years 1992-1994.

Parameter	Yellowstone River			Missouri River		
	1992	1993	1994	1992	1993	1994
Annual mean flow (m^3/s)	284.9	366.7	264.9	204.2	193.8	228.9
Highest daily mean flow (m^3/s, date)	1,113.0 (6/20)	1,404.7 (7/29)	945.9 (5/17)	260.5 (4/20)	458.8 (7/24)	416.3 (4/23)
Lowest daily mean flow (m^3/s, date)	122.1 (8/20)	65.1 (1/4)	57.8 (8/28)	90.9 (9/26)	91.2 (10/4)	79.3 (11/23)
Annual runoff (acre-ft)	7,303	9,379	6,772	5,234	4,954	5,852

undammed river. Annual mean flow, highest daily mean flow, and annual runoff were all higher in the Yellowstone River than in the Missouri River (Table 5).

Mean annual flow, annual runoff, and highest daily mean flow in the Yellowstone River were highest in water year 1993, and lowest in water year 1994. In contrast, Missouri River mean annual flow and annual runoff were highest in water year 1994, and lowest in water year 1993.

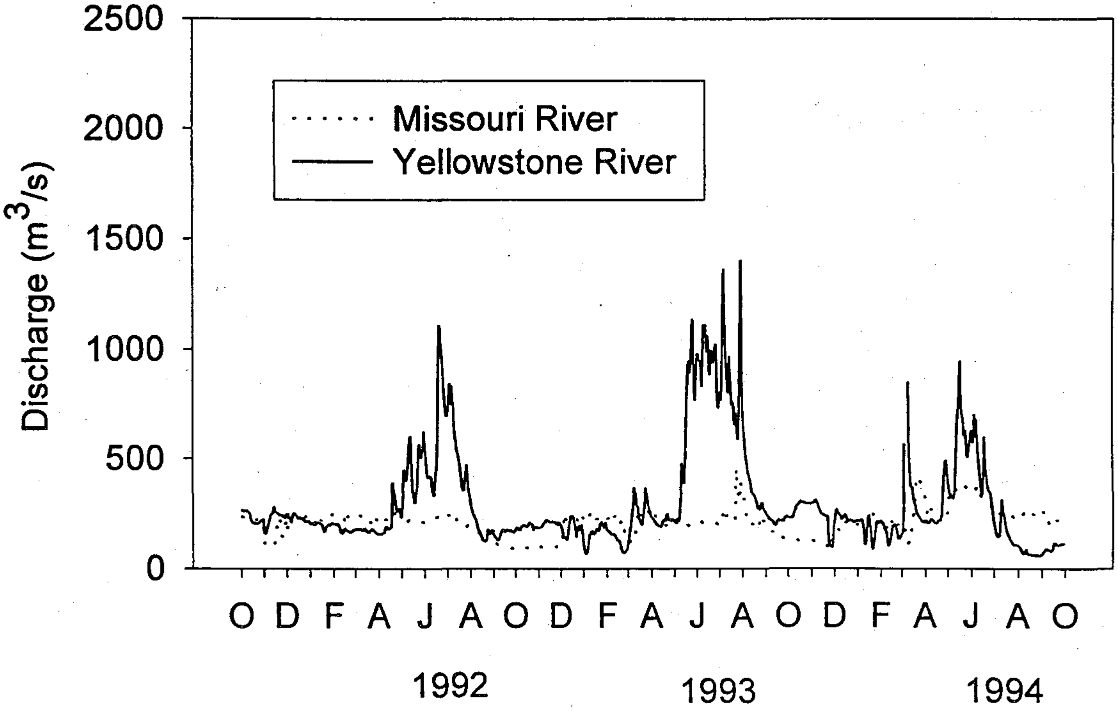

Figure 5. Discharge in the Yellowstone River at Sidney, Montana and the Missouri River at Culbertson, Montana, water years 1992-1994.

Substrate

Substrate availability showed the same pattern in both 1993 and 1994. Substrate in the Lower Missouri River was predominantly sand. In the Yellowstone River, the lower reaches of the study area were predominantly sand and the upper reaches were predominantly gravel and cobble. The transition occurred about 50 km above the confluence. Boulder and bedrock were rare throughout the study area (Figure 6). Observations of substrate use were made on 23 pallid sturgeon (*N* = 181) and 21 shovelnose sturgeon (*N* = 169). The number of observations per individual ranged from 1 to 36 for pallid sturgeon and 1 to 27 for shovelnose sturgeon (Tables 6 and 7). Pallid sturgeon were found most often (92.8%) over fines and sand (Table 6). Gravel and cobble were used less (4.4%), and use of boulder and bedrock substrates was rare (2.7%). In contrast, shovelnose sturgeon were found most often (69.2%) over gravel and cobble (Table 7). Fines and sand were used less (26.6%), and use of boulder and bedrock substrates was rare for shovelnose sturgeon (3.1%).

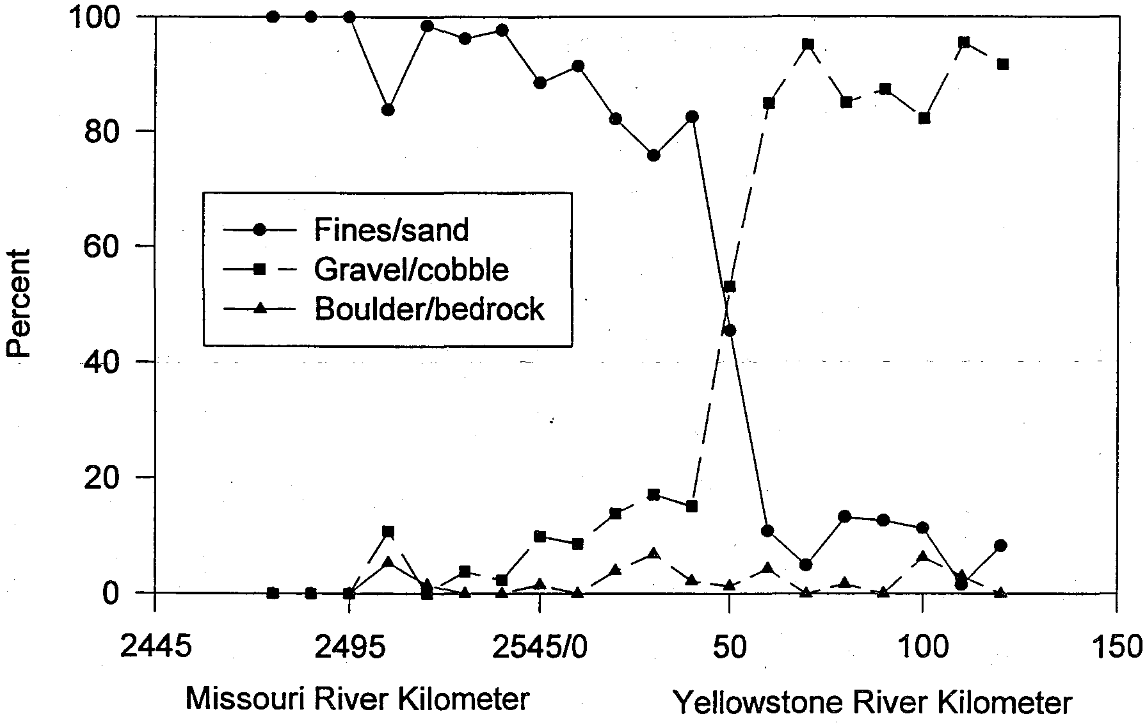

Figure 6. Estimate of distribution of substrate types in the Yellowstone and Missouri rivers in Montana and North Dakota, 1993-1994 by river kilometer from $N = 1273$ random points. River kilometer 0 is the confluence of the Yellowstone and Missouri rivers, river kilometers 0 to 150 are in the Yellowstone River, river kilometers 2445 to 2545 are in the Lower Missouri River.

The null hypothesis that substrate use by pallid and shovelnose sturgeon was the same was rejected for three random samples of substrate use (Pearson's χ^2 test: $P = 0.00012$; $P = 0.00003$; $P = 0.00017$; Table 8). Pallid sturgeon use of fines and sand was significantly greater than shovelnose sturgeon use, while shovelnose sturgeon use of gravel and cobble was significantly greater than pallid sturgeon use. Use of boulder and bedrock substrate was not significantly different for the two species.

Table 6. Summary of observations of substrate use by telemetered pallid sturgeon in the Yellowstone and Missouri rivers, Montana and North Dakota, 1992-1994.

Transmitter frequency	Fines and sand		Gravel and cobble		Boulder and bedrock		
	N	%	*N*	%	*N*	%	Total *N*
49.680	36	100.0	0	0.0	0	0.0	36
49.100	26	100.0	0	0.0	0	0.0	26
49.650	16	100.0	0	0.0	0	0.0	16
49.630	9	75.0	3	25.0	0	0.0	12
49.050	9	90.0	1	10.0	0	0.0	10
49.712	9	100.0	0	0.0	0	0.0	9
49.850	5	55.6	3	33.3	1	11.1	9
49.030	7	100.0	0	0.0	0	0.0	7
49.810	6	85.7	1	14.3	0	0.0	7
49.370	6	100.0	0	0.0	0	0.0	6
49.130	5	100.0	0	0.0	0	0.0	5
49.350	5	100.0	0	0.0	0	0.0	5
49.830	5	100.0	0	0.0	0	0.0	5
48.540	4	100.0	0	0.0	0	0.0	4
49.070	4	100.0	0	0.0	0	0.0	4
48.580	3	75.0	0	0.0	1	25.0	4
49.240	2	50.0	0	0.0	2	50.0	4
49.020	3	100.0	0	0.0	0	0.0	3
49.670	3	100.0	0	0.0	0	0.0	3
48.520	2	100.0	0	0.0	0	0.0	2
49.170	2	100.0	0	0.0	0	0.0	2
49.870	1	100.0	0	0.0	0	0.0	1
48.570	0	0.0	0	0.0	1	0.0	1
Totals	168	92.8	8	4.4	5	2.8	181

The hypothesis that pallid sturgeon used substrate classes in proportion to their availability was rejected (χ^2, $P < 0.05$) for the grouped sample (Table 9). Pallid sturgeon preferred fines and sand, avoided gravel and cobble, and used boulder and bedrock in proportion to their availability. Also, all three random samples for pallid sturgeon yielded the same results as the grouped sample. Because these results agree, it is reasonable to assume that all radio-tagged pallid sturgeon had similar substrate preferences.

Table 7. Summary of observations of substrate use by telemetered shovelnose sturgeon in the Yellowstone and Missouri rivers, Montana and North Dakota, 1992-1994.

Transmitter frequency	Fines and sand		Gravel and cobble		Boulder and bedrock		
	N	%	*N*	%	*N*	%	Total *N*
48.940	15	55.6	9	33.3	1	11.1	25
48.900	1	5.6	17	94.4	0	0.0	18
48.860	3	17.6	13	76.5	1	5.9	17
48.640	0	0.0	13	100.0	0	0.0	13
48.880	1	8.3	10	83.3	1	8.3	12
48.840	0	0.0	9	100.0	0	0.0	9
48.920	0	0.0	9	100.0	0	0.0	9
48.660	2	22.2	7	77.8	0	0.0	9
48.620	3	37.5	5	62.5	0	0.0	8
48.680	1	16.7	5	83.3	0	0.0	6
48.300	2	33.3	4	66.7	0	0.0	6
48.590	2	40.0	3	60.0	0	0.0	5
48.820	2	40.0	3	60.0	0	0.0	5
48.380	2	40.0	2	40.0	1	20.0	5
48.340	3	60.0	1	20.0	1	20.0	5
48.550	1	25.0	3	75.0	0	0.0	4
48.280	2	50.0	2	50.0	0	0.0	4
48.360	0	0.0	2	100.0	0	0.0	2
49.790	2	50.0	0	50.0	0	0.0	2
48.320	2	100.0	0	0.0	0	0.0	2
49.710	1	100.0	0	0.0	0	0.0	1
Totals	45	26.6	117	69.2	5	3.0	169

In 1993 and 1994 I added sand dunes as a substrate category. The χ^2 test with this additional category indicate that pallid sturgeon prefer sand dunes and avoid gravel and cobble ($P < 0.05$; Table 9; Figure 7). Sand and fines and boulder and bedrock were used in proportion to their availability.

The hypothesis that all observations of substrate use for shovelnose sturgeon were in proportion to their availability was also rejected ($P < 0.005$; Table 9). In contrast to pallid sturgeon, shovelnose sturgeon avoided sand, preferred gravel and cobble, and used boulder and bedrock in proportion to their availability. However, individual shovelnose sturgeon were more variable in their substrate use. In contrast to the grouped χ^2 test, the χ^2 tests for the three random sub-samples were not significant (Table 8). This indicates that individual shovelnose sturgeon substrate preferences are variable. Therefore, because the assumption that all telemetered shovelnose sturgeon had the same substrate preferences was not supported, the results of the overall test are not valid.

Table 8. Three random samples of one observation of substrate use per individual fish for telemetered pallid ($N = 23$) and shovelnose ($N = 21$) sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. An asterisk indicate substrate use that is significantly different for the two species ($P < 0.05$, Pearson's χ^2 test). Letters in parentheses indicate results of Marcum-Loftsgaarden χ^2 analysis. P = preference, A = avoidance, and NS = substrate was not significantly preferred or avoided.

	Pallid sturgeon			Shovelnose sturgeon		
Substrate class	Sample 1	Sample 2	Sample 3	Sample 1	Sample 2	Sample 3
Fines and sand	20*(P)	21*(P)	20*(P)	8*(NS)	8*(NS)	8*(NS)
Gravel and cobble	0*(A)	0*(A)	1*(A)	12*(NS)	13*(NS)	13*(NS)
Boulder and bedrock	3(NS)	2(NS)	2(NS)	1(NS)	0(NS)	0(NS)
Totals	23	23	23	21	21	21

Table 9. Substrate use versus availability for telemetered pallid and shovelnose sturgeon as determined by Marcum-Loftsgaarden (1980) χ^2 analysis in the Yellowstone and Missouri rivers, Montana and North Dakota, 1993-1994.

		Substrate class			
Test	Result	Sand	Sand dunes	Gravel-cobble	Boulder and bedrock
all pallids 1992-1994	reject Ho[a]	preferred	not tested	avoided	ns[b]
all pallids, 1993-1994	reject Ho	ns[b]	preferred	avoided	ns[b]
all shovelnose 1992-1994	reject Ho	avoid	not tested	preferred	ns[b]
all shovelnose, 1993-1994	reject Ho	ns[b]	ns[b]	not significant	ns[b]

[a] Reject null hypothesis that use of substrate classes occurred in proportion to their availability.

[b] Not significant ($P < 0.05$)

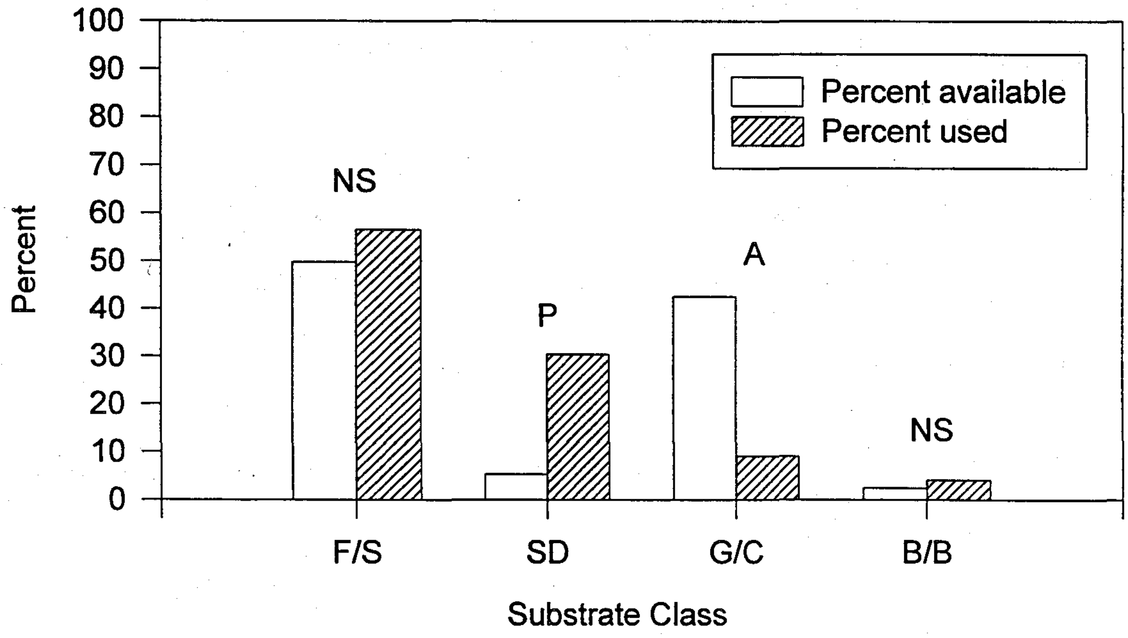

Figure 7. Substrate use and availability for telemetered pallid sturgeon in the Yellowstone and Missouri rivers, Montana and North Dakota, 1993-1994. P indicates that the substrate class was significantly preferred, A indicates that the substrate class was significantly avoided, and NS indicates that use of the substrate class was not significantly different from its availability as determined by Marcum-Loftsgaarden chi-square analysis ($P < 0.05$, see methods). Abbreviations for substrate classes are: F/S = fines and sand; SD = sand dunes; G/C = gravel and cobble; B/B = boulder and bedrock.

Depth

Independent observations of depths used were made on 24 pallid sturgeon (*N* = 164; Table 10) and 24 shovelnose sturgeon (*N* = 147; Table 11). The number of observations per individual ranged from 1 to 29 for pallid sturgeon and 1 to 23 for shovelnose sturgeon. Median depths, relative depths, and maximum depths at locations of moving

Table 10. Summary of observations of depths used by telemetered pallid sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Location	Minimum (m)	Maximum (m)	N^a observations	*N* fish	Mean (m)	SD (m)	N^b observations
			Depth				
Yellowstone	0.6	7.0	124	21	2.93	1.46	83
Upper Missouri	2.0	14.5	12	2	7.74	4.34	10
Lower Missouri	0.8	8.2	174	16	3.11	1.47	71
Overall	0.6	14.5	310	24	3.30	2.08	164
			Maximum depth				
Yellowstone	1.2	7.8	112	20	4.18	1.27	73
Upper Missouri	2.1	5.5	4	1	3.8	2.4	2
Lower Missouri	2.2	8.2	164	17	4.74	1.35	62
Overall	1.2	8.2	280	22	4.43	1.34	137
			Relative depth (depth/maximum depth)				
Yellowstone	0.22	1.0	112	20	0.71	0.22	73
Upper Missouri	0.50	0.93	4	1	0.72	0.30	2
Lower Missouri	0.13	1.0	161	16	0.68	0.22	59
Overall	0.13	1.0	277	22	0.70	0.22	134

[a] = All observations are used for reporting ranges.

[b] = Only "independent" observations are used for reporting means and standard deviations.

and non-moving pallid sturgeon and shovelnose sturgeon were not significantly different ($P \geq 0.05$) so observations from moving and non-moving fish were combined for further analysis.

Table 11. Summary of observations of depths used by telemetered shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Location	Minimum (m)	Maximum (m)	N^a obser-vations	N fish	Mean (m)	SD (m)	N^b obser-vations
			Depth				
Yellowstone	0.9	8.8	215	19	2.2	1.00	129
Upper Missouri	4.3	10.1	7	2	7.6	3.61	2
Lower Missouri	1.2	5.8	23	6	2.4	1.35	16
Overall	0.9	10.1	245	24	2.3	1.24	147
			Maximum depth				
Yellowstone	1.4	8.8	175	19	3.0	1.19	112
Upper Missouri	--	--	0	0	--	--	--
Lower Missouri	2.3	7.0	12	2	4.7	1.79	5
Overall	1.4	8.8	187	20	3.1	1.26	117
			Relative depth (depth/maximum depth)				
Yellowstone	0.33	1.0	175	19	0.78	0.18	112
Upper Missouri	--	--	0	0	--	--	--
Lower Missouri	0.71	0.93	12	2	0.83	0.09	5
Overall	0.33	1.0	187	20	0.78	0.18	117

[a] = All observations are used for reporting ranges.

[b] = Only "independent" observations are used for reporting means and standard deviations.

Depths at pallid and shovelnose sturgeon locations were similar, but pallids used greater depths more often (Figure 8). Pallid sturgeon were found in depths ranging from 0.6 to 7.0 m (*N* = 124) in the Yellowstone River, 2.0 to 14.5 m (*N* = 12) in the Upper Missouri River, and 0.8 to 8.2 m (*N* = 174) in the Lower Missouri River. Shovelnose sturgeon were found in depths ranging from 0.9 to 8.8 m (*N* = 215) in the Yellowstone River, 4.3 to 10.1 m (*N* = 7) in the Upper Missouri River, and 1.2 to 5.8 m (*N* = 23) in the Lower Missouri River.

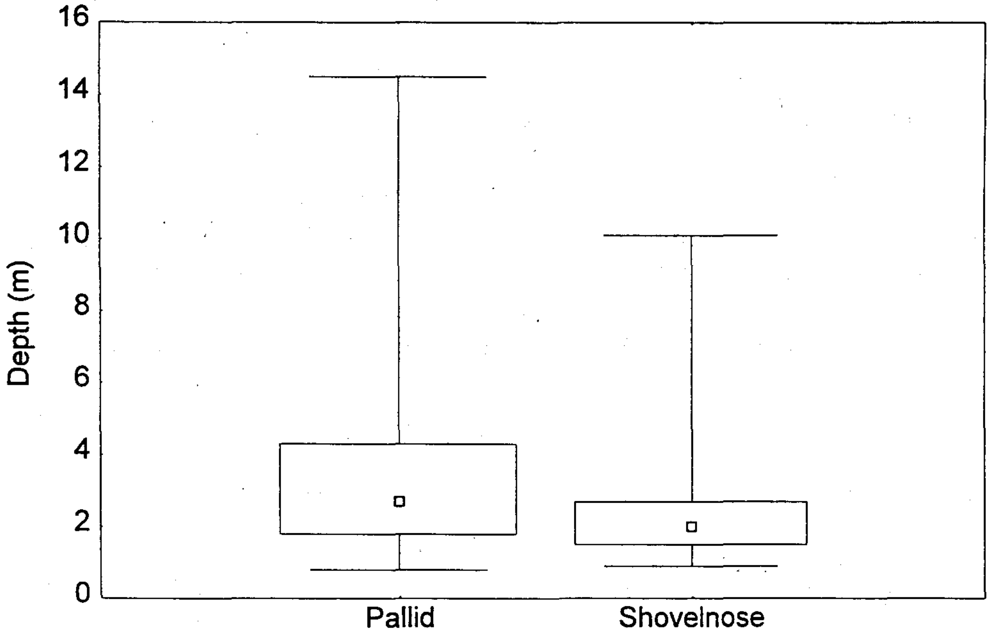

Figure 8. Depths at telemetered pallid (*N* = 164) and shovelnose sturgeon (*N* = 147) locations in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Small box is median, large box is 25% and 75% percentiles, and whiskers are minimum and maximum values.

The overall mean depth for pallid sturgeon was 3.30 m (*N* = 164, SD = 2.08), compared to an overall mean depth of 2.29 m (*N* =147, SD = 1.24) for shovelnose sturgeon. These means include seven observations for pallid sturgeon and two observations for shovelnose sturgeon in the Missouri River just below Fort Peck Reservoir where depths are greater than elsewhere in the study area. The greatest depth measured outside of this area was 8.8 m, in the Yellowstone River in an area scoured by a wing deflector. Excluding the observations from the Fort Peck tailrace, the overall mean depth for pallid sturgeon was 2.98 m (N =158, SD = 1.47), and the overall mean depth for shovelnose sturgeon was 2.21 m (N =145, SD = 1.04). The overall median of depths used by pallid and shovelnose sturgeon were significantly different (Mann-Whitney U test; P = 0.0000001).

Overall mean maximum depth at pallid sturgeon locations was 4.4 m and 3.1 m at shovelnose sturgeon locations (Figure 9). Overall means of maximum depths at pallid and shovelnose sturgeon locations were significantly different (t-test; $P < 0.000001$; following Levene's test for equal variance; $P = 0.241$). Mean relative depths were greater at shovelnose sturgeon locations than at pallid sturgeon locations (Figure 10). The overall mean relative depth for pallid sturgeon was 0.70 and was 0.78 for shovelnose sturgeon. These means were significantly different (Mann-Whitney U test; $P = 0.0054$). Depth and relative depth data were not normally distributed (Kolmogorov-Smirnov test; depth $P < 0.01$; relative depth $P < 0.05$), while the maximum depth data were normally distributed ($P > 0.05$).

The ANOVA based on model (1) gave the following results for depths (Table 12): 1) mean depths used by pallid sturgeon and shovelnose sturgeon were significantly different ($P = 0.0170$); 2) mean depths used by pallid and shovelnose sturgeon in the Yellowstone River were not significantly different from those in the Lower Missouri River ($P = 0.5855$); 3) the difference in mean depths between shovelnose and pallid sturgeon were not significantly different between the Lower Missouri River and the Yellowstone River (i.e. no interaction between species and rivers; $P = 0.3753$); 4) the variance among mean depths of individual fish of each species is significantly different than zero ($P = 0.0355$), after considering variation due to location in either the lower Missouri or Yellowstone river.

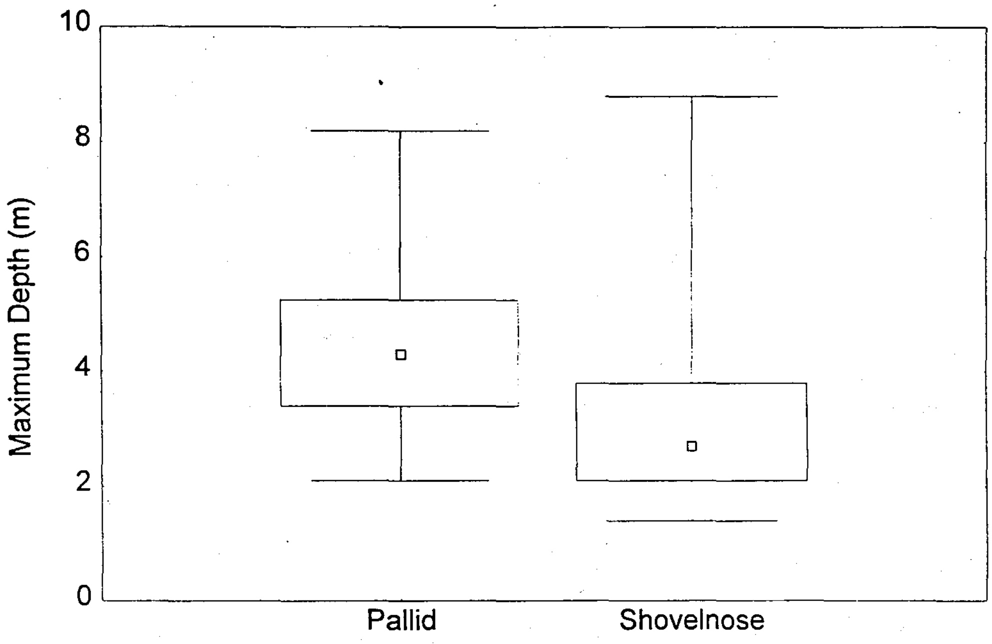

Figure 9. Maximum depths at telemetered pallid ($N = 137$) and shovelnose sturgeon ($N = 117$) locations in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Small box is median, large box is 25% and 75% percentiles, and whiskers are minimum and maximum values.

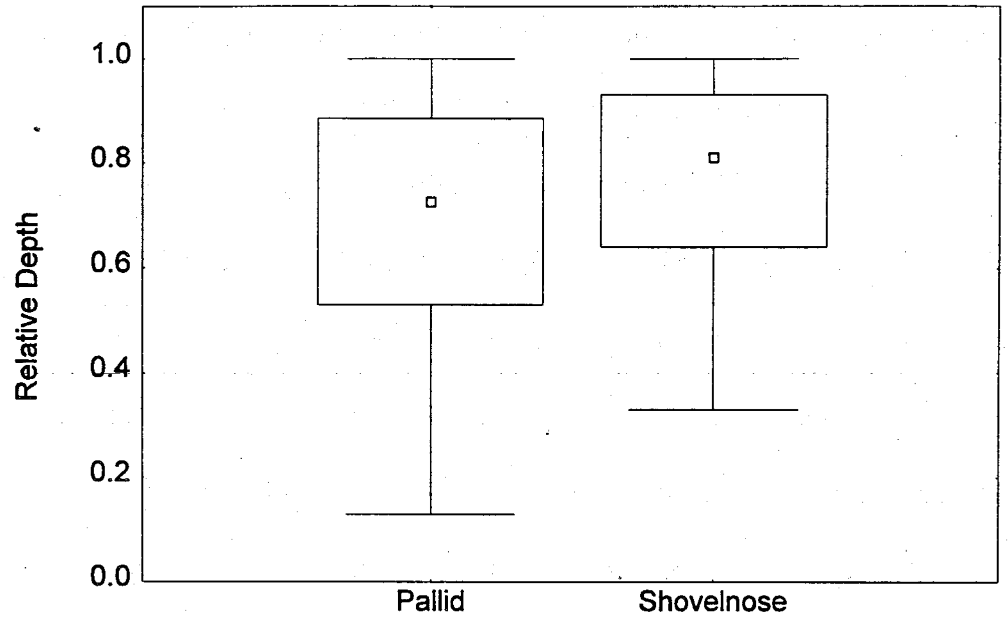

Figure 10. Relative depths at telemetered pallid (*N* = 134) and shovelnose sturgeon (*N* = 117) locations in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Small box is median, large box is 25% and 75% percentiles, and whiskers are minimum and maximum values.

The ANOVA based on model (1) gave the following results for depths (Table 12): 1) mean depths used by pallid sturgeon and shovelnose sturgeon were significantly different ($P = 0.0170$); 2) mean depths used by pallid and shovelnose sturgeon in the Yellowstone River were not significantly different from those in the Lower Missouri River ($P = 0.5855$); 3) the difference in mean depths between shovelnose and pallid sturgeon were not significantly different between the Lower Missouri River and the Yellowstone River (i.e. no interaction between species and rivers; $P = 0.3753$); 4) the variance among mean depths of individual fish of each species is significantly different than zero ($P = 0.0355$), after considering variation due to location in either the lower Missouri or Yellowstone river.

Table 12. Results of ANOVA Model (1) and tests of overall means of depth, maximum depths, and relative depths for telemetered pallid sturgeon and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Variable	Source of Variation	*P*	Degrees of Freedom
Depth	Overall	0.000001[a]	[b]
	Species	0.0170	181.55
	River	0.5855	183.22
	River x Species	0.3753	184.55
	Individual(River x Species)	0.0355	237
Maximum Depth	Overall	<0.000000[c]	250
	Species	0.0213	147.56
	River	0.0479	149.50
	River x Species	0.9423	151.24
	Individual(River x Species)	0.0036	194
Relative Depth	Overall	0.0054[a]	[b]
	Species	0.0966	179.43
	River	0.9860	181.57
	River x Species	0.7512	183.45
	Individual(River x Species)	0.1844	192

[a] Mann-Whitney U test.

[b] Degrees of freedom not defined for Mann-Whitney U test.

[c] t-test.

ANOVA results for maximum depths were as follows (Table 12): 1) mean maximum depths at pallid sturgeon and shovelnose sturgeon locations were significantly different ($P = 0.0213$); 2) mean maximum depths at pallid and shovelnose sturgeon locations in the Yellowstone River were significantly different than in the Lower Missouri River ($P = 0.0479$); 3) the difference in mean maximum depths for shovelnose and pallid sturgeon were not significantly different between the Missouri River and the

Yellowstone River (i.e. no interaction between species and rivers; $P = 0.9423$); and 4) the variance among mean maximum depths of individual fish of each species is significantly different than zero ($P = 0.0036$), after considering variation due to location in either the lower Missouri or Yellowstone river.

Results pertaining to relative depths from the ANOVA based on model (1) were as follows (Table 12): 1) mean relative depths at pallid sturgeon and shovelnose sturgeon locations were nearly significantly different ($P = 0.0966$); 2) mean relative depths at pallid and shovelnose sturgeon locations in the Yellowstone River were not significantly different from those in the Lower Missouri River ($P = 0.9860$); 3) the difference in mean depths for shovelnose and pallid sturgeon were not significantly different between the Missouri River and the Yellowstone River (i.e. no interaction between species and rivers; $P = 0.7512$); and 4) the variance among mean depths of individual fish of each species is significantly different from zero ($P = 0.1844$), after considering variation due to location in either the lower Missouri or Yellowstone river.

The Wilks-Shapiro test rejected the hypothesis that the residuals were normal ($P = 0.0001$). The boxplot indicated two outliers among the residuals. However, hypothesis testing results were robust to outliers since decisions of hypothesis tests made at the $\alpha = 0.05$ level were the same with and without the two outliers in the data set.

The slope of the relationship of predicted depth relative to hours following sunrise for pallid sturgeon was positive (slope = 0.77, Figure 11) but was not significantly

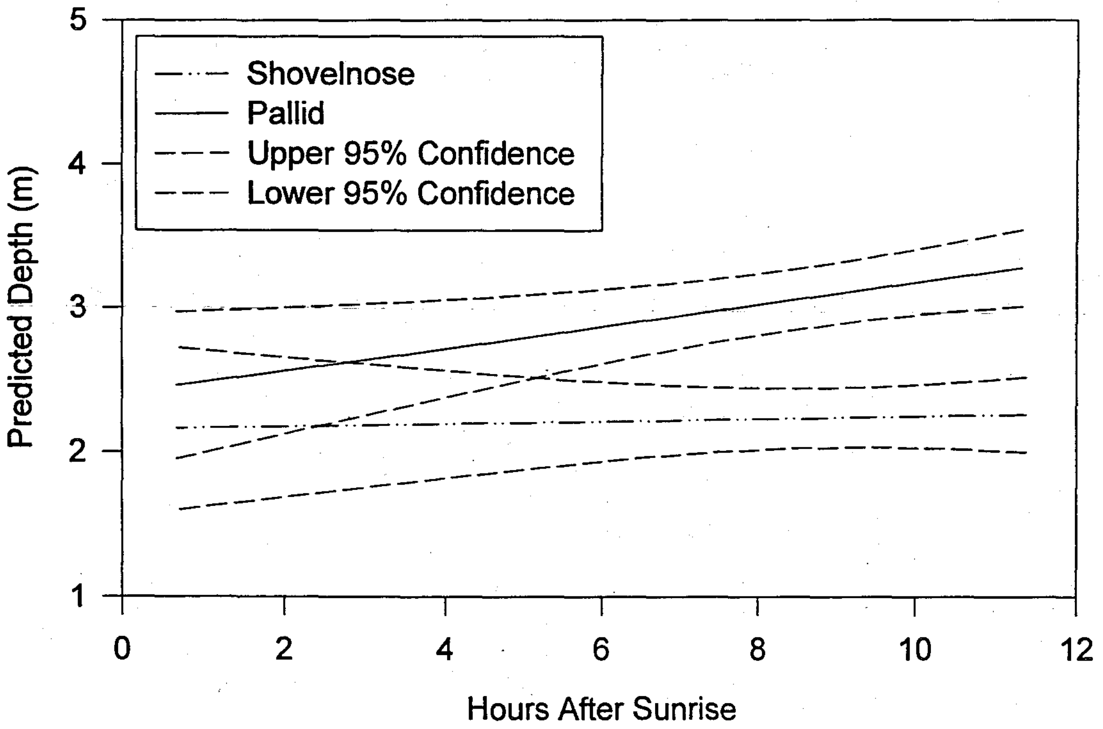

Figure 11. Predicted depths and 95% confidence intervals for telemetered pallid and shovelnose sturgeon, versus hours after sunrise.

different than 0 slope (*P* = 0.1268). The slope of the relationship of predicted depth relative to hours following sunrise for shovelnose sturgeon was only slightly positive (slope = 0.009), and also not significantly different than zero slope (*P* = 0.7817). Therefore, although not statistically significant, the data suggest that pallid sturgeon showed a greater increase in their predicted depth during the hours following sunrise than did shovelnose sturgeon.

Current velocity

Independent observations of bottom velocities used by 24 pallid sturgeon (*N* = 173; Table 13) and 24 shovelnose sturgeon (*N* = 119; Table 14) were made. The number of observations per individual ranged from 1 to 36 for pallid sturgeon and 1 to 21 for shovelnose sturgeon.

Pallid sturgeon were found using bottom velocities ranging from 0.13 to 1.32 m/s (*N* = 159) in the Yellowstone River, 0.0 to 0.70 (*N* = 12) in the Upper Missouri River, and 0 to 1.37 m/s (*N* = 244) in the Lower Missouri River (Table 13). Shovelnose sturgeon used bottom velocities ranging from 0.03 to 1.51 m/s (*N* = 172) in the Yellowstone River, 0.02 to 0.20 m/s (*N* = 2) in the Upper Missouri River, and 0.40 to 0.82 m/s (*N* = 23) in the Lower Missouri River (Table 14).

Current velocities at pallid and shovelnose sturgeon locations overlapped (Figures 12 and 13). The overall mean bottom velocity for pallid sturgeon was 0.65 m/s (*N* = 173, SD = 0.28, Table 13), and for shovelnose sturgeon was 0.78 m/s (*N* = 119, SD = 0.33, Table 14). These means include seven observations for pallid sturgeon and two observations for shovelnose sturgeon in the dredge cuts below Fort Peck Reservoir where areas of low and zero velocity are found. Excluding these observations, the overall mean bottom velocity for pallid sturgeon was 0.68 m/s (*N* =166, SD = 0.26) and for shovelnose sturgeon was 0.79 m/s (*N* =117, SD = 0.32).

Table 13. Summary of observations of current velocities used by telemetered pallid sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Location	Minimum (m/s)	Maximum (m/s)	N^a observations	N fish	Mean (m/s)	SD (m/s)	N^b observations
			Surface				
Yellowstone	0.27	1.82	156	21	1.06	0.33	86
Upper Missouri	0.00	0.91	12	2	0.20	0.33	10
Lower Missouri	0.49	1.58	223	12	0.99	0.34	54
Overall	0.00	1.55	391	22	0.98	0.39	150
			Mean Column				
Yellowstone	0.14	1.55	156	21	0.90	0.28	86
Upper Missouri	0.00	0.82	12	2	0.17	0.29	10
Lower Missouri	0.18	1.40	223	12	0.82	0.24	54
Overall	0.00	1.55	391	22	0.82	0.32	150
			Bottom				
Yellowstone	0.13	1.32	159	21	0.72	0.26	88
Upper Missouri	0.00	0.70	12	2	0.13	0.23	10
Lower Missouri	0.00	1.37	244	17	0.63	0.21	75
Overall	0.00	1.37	415	24	0.65	0.28	173

[a] = All observations are used for reporting ranges.

[b] = Only "independent" observations are used for reporting means and standard deviations.

Overall means of surface, mean column, and bottom velocities used by pallid and shovelnose sturgeon were significantly different (surface $P = 0.000180$; mean column $P = 0.000197$; bottom $P = 0.000613$; t-test with separate estimates of variance). Surface, column and bottom velocity data were normally distributed (Kolmogorov-Smirnov test; surface velocity $P > 0.20$; mean column velocity $P > 0.20$; bottom velocity $P > 0.05$).

Table 14. Summary of observations of current velocities used by telemetered shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Location	Minimum (m/s)	Maximum (m/s)	*N*[a] observations	*N* fish	Mean (m/s)	SD (m/s)	*N*[b] observations
			Surface				
Yellowstone	0.04	2.16	166	18	1.20	0.46	95
Upper Missouri	--	--	0	0	--	--	0
Lower Missouri	0.78	0.99	11	1	0.88	0.11	4
Overall	0.04	2.16	177	18	1.19	0.45	99
			Mean Column				
Yellowstone	0.03	1.81	166	18	1.02	0.39	95
Upper Missouri	--	--	0	0	--	--	0
Lower Missouri	0.23	0.88	11	1	0.66	0.29	4
Overall	0.03	1.81	177	18	1.00	0.40	99
			Bottom				
Yellowstone	0.03	1.51	172	19	0.82	0.33	101
Upper Missouri	0.02	0.20	2	2	0.11	0.13	2
Lower Missouri	0.40	0.82	23	6	0.61	0.11	16
Overall	0.02	1.51	197	24	0.78	0.33	119

[a] = All observations are used for reporting ranges.

[b] = Only “independent” observations are used for reporting means and standard deviations.

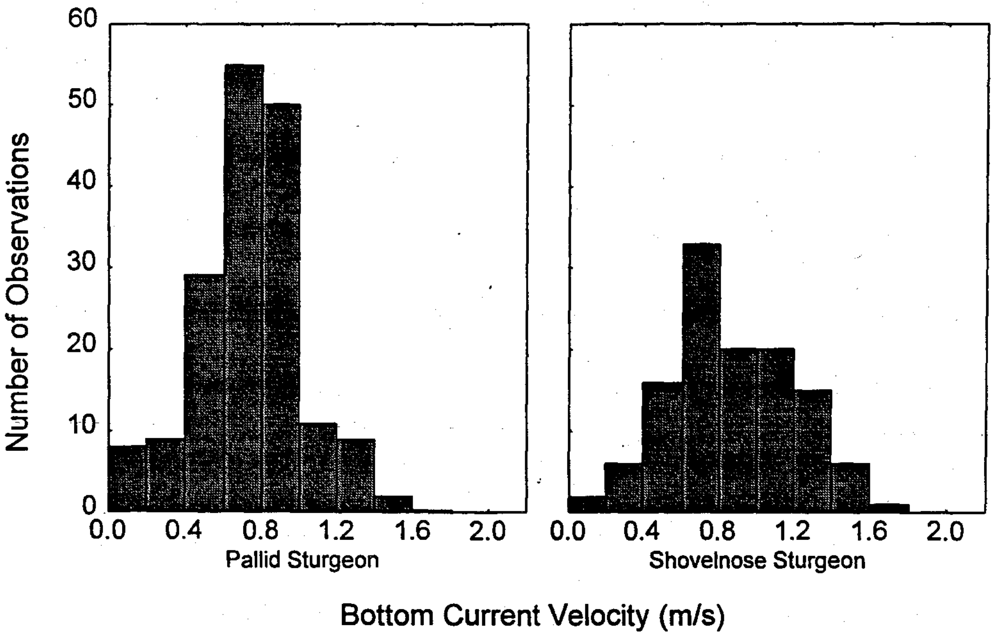

Figure 12. Bottom current velocities at telemetered pallid and shovelnose sturgeon locations, Yellowstone and Missouri rivers, Montana and North Dakota, 1992 - 1994.

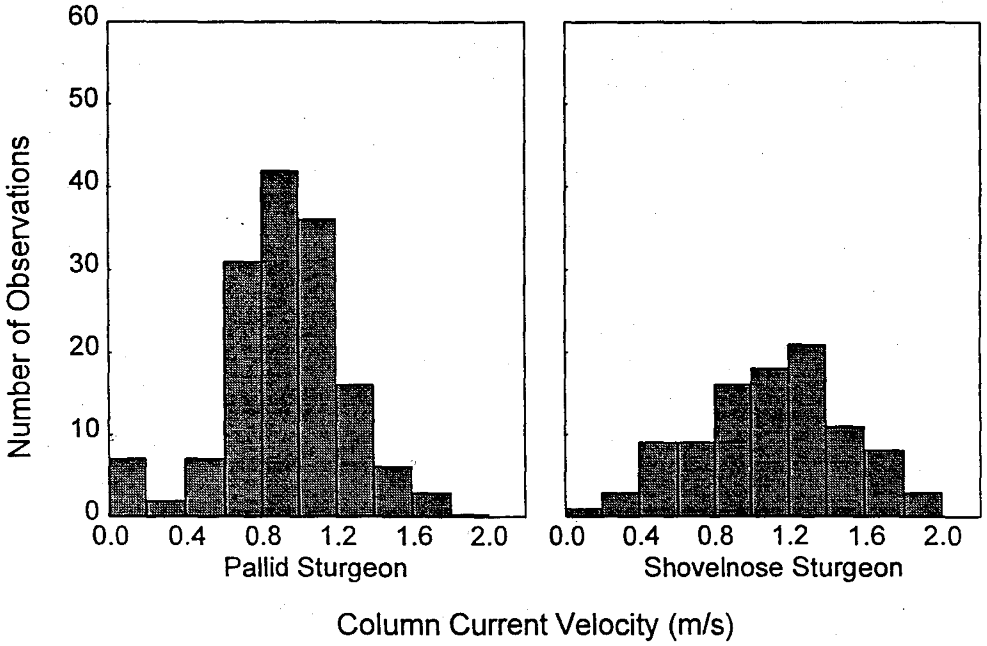

Figure 13. Column current velocities at telemetered pallid and shovelnose sturgeon locations, Yellowstone and Missouri rivers, Montana and North Dakota, 1992 - 1994.

Based on the ANOVA (model 2, Table 15): 1) mean bottom velocities used by pallid sturgeon and shovelnose sturgeon were not significantly different ($P = 0.1414$); 2) mean bottom velocities used by pallid and shovelnose sturgeon in the Missouri River and the Yellowstone River were significantly different ($P = 0.0079$); 3) the difference in mean bottom velocities between shovelnose and pallid sturgeon was not significantly different between the Missouri River and the Yellowstone River (i.e. no interaction between species and rivers; $P = 0.1432$); and 4) variance among mean bottom velocities used by individual fish of each species is not significantly different than zero ($P = 0.7782$), after considering variation due to location in either the lower Missouri or Yellowstone river. ANOVA results for surface and mean column velocities were similar (Table 15).

Table 15. Results of ANOVA Model (2) and tests of overall means of surface, mean column, and bottom current velocities for telemetered pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Variable	Source of variation	*P*	Degrees of freedom
Surface velocity	Overall	0.0038[a]	170.50
	Species	0.5309	63.33
	River	0.1345	66.59
	River x Species	0.3159	61.14
	Individual(River x Species)	0.0251	187
Mean column velocity	Overall	0.0038[a]	159.67
	Species	0.5060	67.38
	River	0.0308	71.52
	River x Species	0.1314	64.59
	Individual(River x Species)	0.1783	187
Bottom velocity	Overall	0.0026[a]	208.04
	Species	0.1414	228.29
	River	0.0079	229.58
	River x Species	0.1432	230.37
	Individual(River x Species)	0.7782	217

[a] t-test with separate variance estimates.

The residuals were normal (Wilks-Shapiro test; $P = 0.09$) and the boxplot indicated no outliers among the residuals. The plots of residuals versus the variables discharge, month and year, water temperature, daylight, darkness, dawn, and dusk categorical variables, substrate type, river kilometer (location), and Secchi disk reading showed no pattern and so were not included in ANOVA model (2).

Channel Width

Channel widths at pallid sturgeon locations ranged from 110 to 1100 m with a mean of 324 m and a median of 300 m ($N = 144$). Channel widths at shovelnose sturgeon locations ranged from 25 to 800 m with a mean of 208 m and a median of 160 m ($N = 161$). Channel widths at pallid and shovelnose sturgeon locations were not normally distributed ($P < 0.01$; Komolgorov-Smirnov Test). Median channel width at pallid sturgeon locations was significantly greater than at shovelnose sturgeon locations ($P < 0.000001$; Mann-Whitney U).

General Distribution

General distribution of pallid sturgeon included portions of the Yellowstone River and Upper and Lower Missouri rivers (Figure 14). All observations of telemetered pallid sturgeon occurred in riverine portions of the study area, except for one pallid sturgeon that was captured and subsequently relocated adjacent to the dredge cuts below Fort Peck dam. Although pallid sturgeon were relocated in areas that would be inundated by Lake Sakakawea at full pool, no pallid sturgeon were relocated in non-riverine areas of Lake Sakakawea.

In spring, pallid sturgeon ranged from river km 2476 in the Missouri River to river km 114 in the Yellowstone River, just below the Intake diversion dam (Figure 14). However, most locations (75%) were in the lower 28 km of the Yellowstone River or the 28 km of the Lower Missouri River below the confluence (15%). The area of highest use was the Yellowstone River from the confluence to river kilometer 12, where 60% of observations occurred. The 2 km reach with the most locations was river km 6 - 8 on the Yellowstone River, where 20% of observations occurred. Only the one pallid sturgeon that was captured below Fort Peck dam was relocated in the Upper Missouri River.

The distribution of summer observations of pallid sturgeon was similar to that of spring, but more observations (39%) occurred in the Lower Missouri River. However, 25% of these observations were from a single individual (frequency 49.110). As in spring, the 2 km reach with the most locations was river km 6 - 8 on the Yellowstone River, where 13% of observations occurred. Pallid sturgeon ranged from river km 2468 in the Lower Missouri River to river km 110 in the Yellowstone River. Only four summer observations of pallid sturgeon were made in the Upper Missouri River. Except for the one pallid sturgeon that was captured below Fort Peck dam, the uppermost location on the Upper Missouri River was at river km 2764, 219 km above the confluence.

Fall distribution of pallid sturgeon was different than spring and summer. Most (96%) fall observations were in the Lower Missouri River. Only three observations were in the Yellowstone River, where they ranged to 6 km above the confluence. Excluding the one pallid sturgeon that was captured below Fort Peck dam, just one observation was made in the Upper Missouri River, at river kilometer 2676, 131 km above the confluence.

Winter distribution of pallid sturgeon was similar to fall. All winter observations of pallid sturgeon were in the Lower Missouri River. Pallid sturgeon were found from the confluence area to about 50 km below the confluence. The 2 km reach with the most observations was river km 2523 - 2525, which is about 20 km below the confluence.

General distribution of shovelnose sturgeon included portions of the Yellowstone River and Upper and Lower Missouri rivers (Figure 15). As with pallid sturgeon, all observations of telemetered shovelnose sturgeon occurred in riverine portions of the study area, except for two individual shovelnose sturgeon that were captured and subsequently relocated adjacent to the dredge cuts below Fort Peck dam. No shovelnose sturgeon were located in Lake Sakakawea.

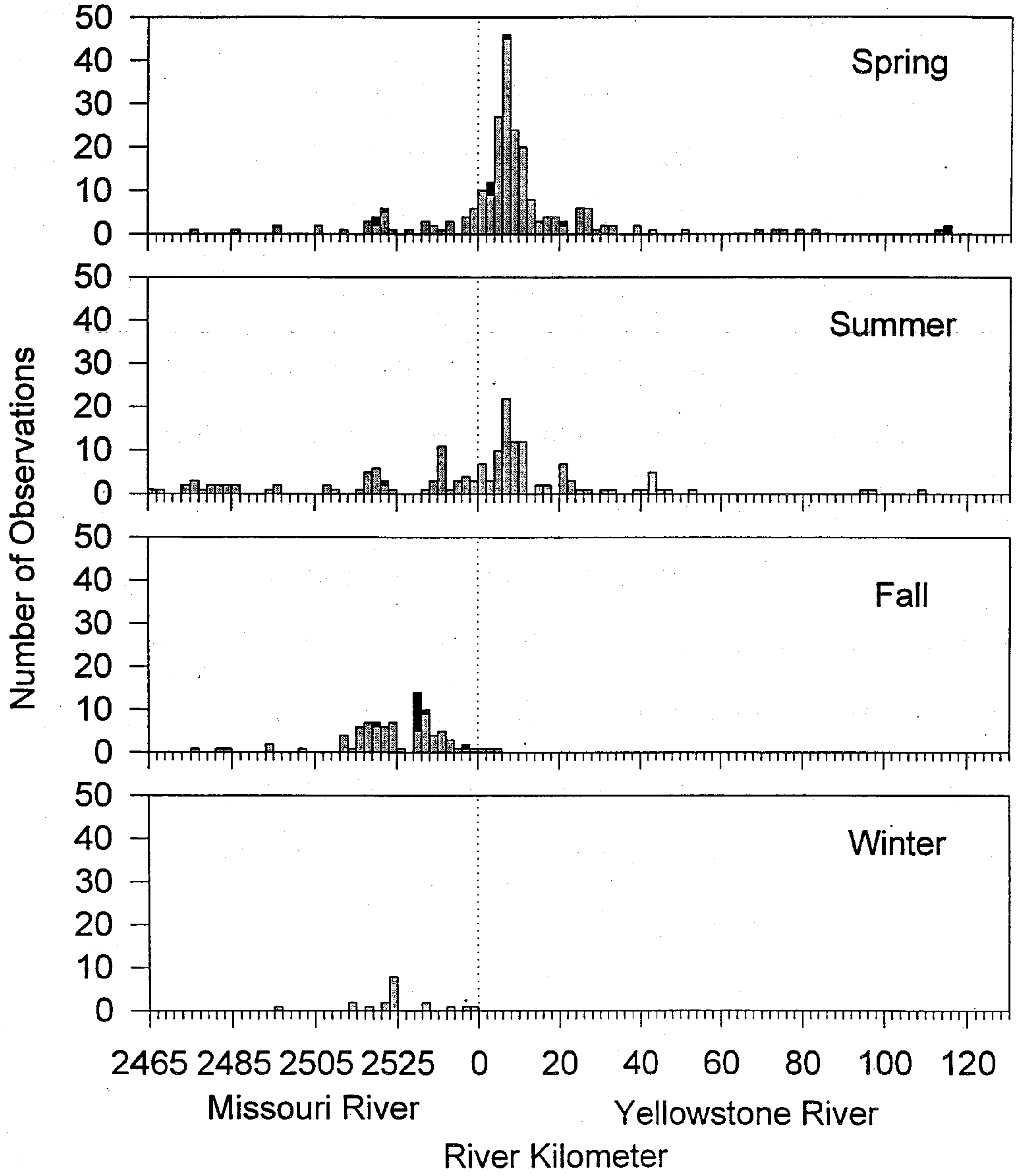

Figure 14. Locations of pallid sturgeon by river kilometer in the Yellowstone and Lower Missouri rivers in Montana and North Dakota, 1992-1994. Black bars are capture locations, gray bars are telemetry relocations.

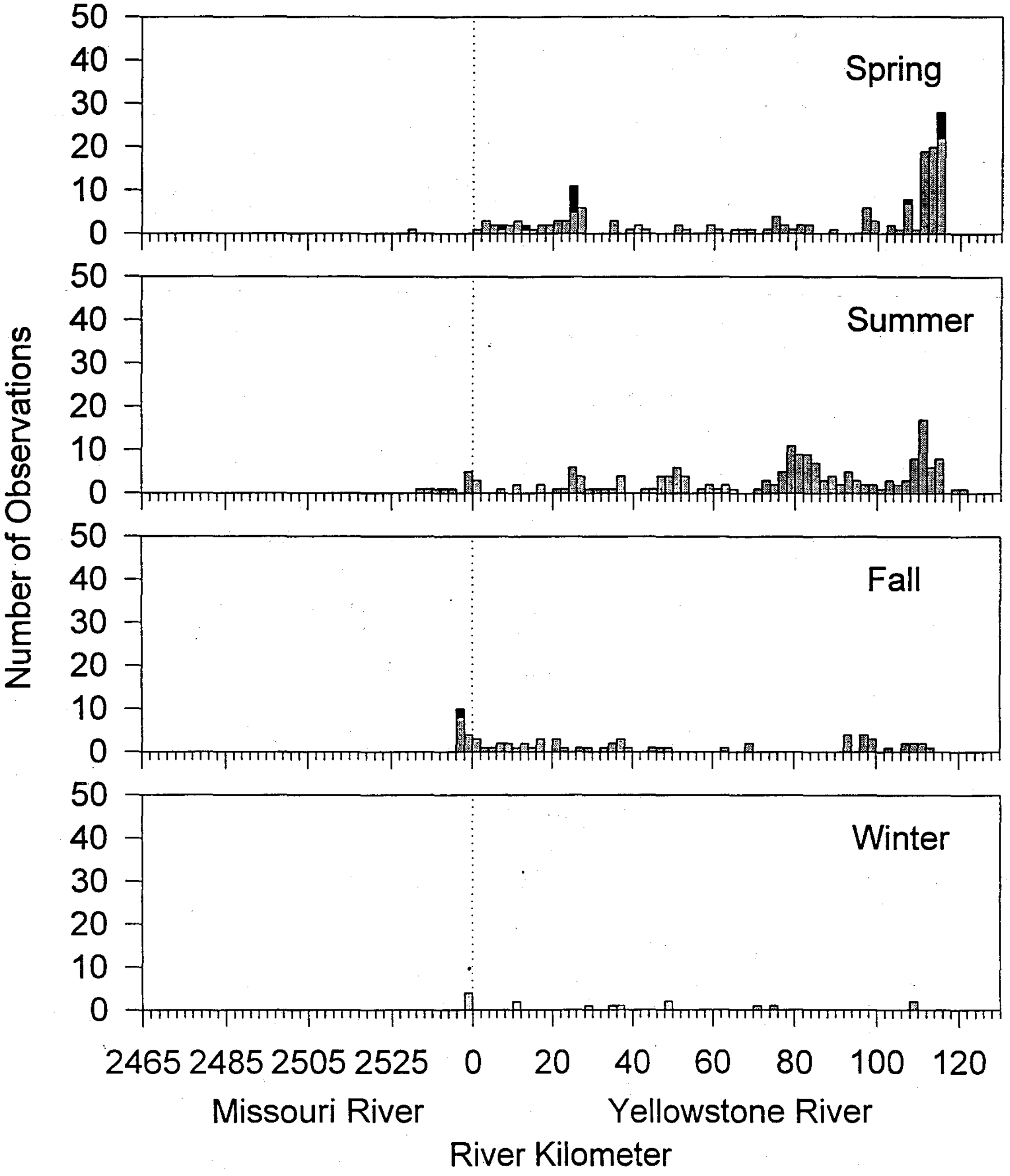

Figure 15. Locations of shovelnose sturgeon by river kilometer in the Yellowstone and Lower Missouri rivers in Montana and North Dakota, 1992-1994. Black bars are capture locations, gray bars are telemetry relocations.

In spring, shovelnose sturgeon ranged from river km 2,531 in the Missouri River to river km 114 in the Yellowstone River (Figure 15). Overall, 99% of observations were in the Yellowstone River. Most locations were in two general areas, located at river km 0 - 28 (27%) and river kilometer 106 - 114 (51%). The 2 km reach with the most locations (17%) was river km 114 - 116 on the Yellowstone River which includes the area just below the Intake diversion dam. One observation was from the Upper Missouri River at river km 2562, 17 km above the confluence.

As with pallid sturgeon, the distribution of summer observations of shovelnose sturgeon was similar to that of spring. Most (94%) observations were in the Yellowstone River. The 2 km reach with the most locations (9%)was river km 110 - 112 on the Yellowstone River. Two shovelnose sturgeon were relocated upstream of Intake diversion dam. Shovelnose sturgeon ranged from river km 2748 in the Lower Missouri River to river km 122 in the Yellowstone River. One observation was from the Upper Missouri River at river kilometer 2748, 203 km above the confluence.

In contrast to pallid sturgeon, the general distribution of shovelnose sturgeon in fall and winter was not markedly different from their distribution in spring and summer. Telemetered shovelnose sturgeon ranged from river km 2542 in the Lower Missouri River to river km 113 in the Yellowstone River. The 2 km reach with the most locations (14%) was river km 2541 - 2543 on the Lower Missouri River, about 4 km below the confluence. Excluding one shovelnose sturgeon that was captured below Fort Peck dam, just one observation was from the Upper Missouri River at river kilometer 2747, 202 km above the confluence.

Winter distribution of shovelnose sturgeon ranged from river km 2545 on the Missouri River to river km 108 on the Yellowstone River. The 2 km reach with the largest number of locations (14%) was river km 2541 - 2543 on the Lower Missouri River, about 4 km below the confluence. One observation was from the Upper Missouri River at river kilometer 2747, 202 km above the confluence.

In general, pallid sturgeon locations in all seasons were less dispersed than were seasonal locations of shovelnose sturgeon (Figures 14 and 15). Pallid sturgeon used fairly discrete areas of the river during each season while shovelnose sturgeon were generally located in the entire 113 km length of the Yellowstone River below Intake diversion dam in each season.

Aggregations

Twenty nine aggregations (defined as groups of 3 or more telemetered sturgeon in a 1 km reach on the same day) of pallid sturgeon, and 20 aggregations of shovelnose sturgeon were identified (Tables 16 and 17; Figure 16). Most (90%) pallid sturgeon aggregations were in the lower 13 km of the Yellowstone River in spring or summer, 3 fall/winter aggregations were in the Lower Missouri River. All shovelnose sturgeon aggregations were in the Yellowstone River, and most of these (65%) were in the

Yellowstone River from river km 111.0 to river km 114.2. Two aggregations of shovelnose sturgeon were observed in fall in the Lower Missouri River.

Aggregations in spring and early summer may indicate potential pallid sturgeon spawning areas. A telemetered pallid sturgeon (frequency 49.030), snagged by a paddlefish angler on the night of 29 May 1993 at river km 14.2 on the Yellowstone River, was a gravid female with ripe eggs. A non-telemetered male pallid sturgeon with running milt was also snagged that night at that same location (Steve Krentz, US Fish and Wildlife Service, Pers. Comm.). Additional indications of potential spawning areas for pallid sturgeon were obtained by plotting locations of frequency 49.030 and aggregations of pallid sturgeon during April-August 1993 (Figure 17). These locations indicate that potential pallid sturgeon spawning areas were in the Yellowstone River from about river km 6 to river km 14.

Table 16. Aggregations of pallid sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Aggregations are defined as river reaches ≤1 km with ≥ 3 telemetered pallid sturgeon present on the same day. River kilometer is location of center of reach; river kilometers 0-11 are on the Yellowstone River; river kilometers 2524-2545 are on the Lower Missouri River.

Date	River kilometer	Length of reach	Number of fish in aggregation
10/19/92	2531.0	0.1	3
4/23/93	2.9	0.6	3
5/12/93	0.5	0.1	3
5/23/93	5.7	0.9	5
5/25/93	5.4	0.5	3
5/25/93	9.3	0.1	3
5/27/93	8.8	0.1	3
5/29/93	9.7	0.1	3
5/31/93	6.8	0.6	3
6/3/93	1.7	0.6	3
6/4/93	4.8	0.1	3
6/4/93	7.0	0.1	3
6/5/93	3.5	0.1	3
6/5/93	7.7	0.1	4
6/5/93	12.1	0.8	3
6/8/93	7.0	0.1	5
6/17/93	10.3	0.7	4
6/21/93	10.6	0.7	3
6/23/93	11.0	0.1	3
7/15/93	8.2	0.9	4
9/28/93	2531.0	0.1	4
11/12/93	2525.4	0.1	3
2/12/94	2524.8	0.1	4
5/18/94	7.4	0.3	3
5/18/94	9.1	1.0	3
5/19/94	4.4	0.1	3
5/24/94	10.3	0.1	4
6/12/94	7.1	0.1	4
6/14/94	3.8	0.1	4

Table 17. Aggregations of shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Aggregations are defined as river reaches ≤1 km with ≥ 3 telemetered pallid sturgeon present on the same day. River kilometer is location of center of reach; river kilometers 0-114 are on the Yellowstone River; river kilometers 2542-2545 are on the Lower Missouri River.

Date	River kilometer	Length of reach	Number of fish in aggregation
6/2/92	114.2	0.1	3
6/5/92	114.3	0.1	3
6/8/92	114.2	0.2	3
6/9/92	113.7	1.0	5
6/10/92	111.6	0.2	5
6/10/92	114.0	0.5	3
6/11/92	111.7	0.1	3
6/12/92	111.4	0.6	3
6/15/92	112.9	0.9	3
6/15/92	114.0	0.1	3
6/16/92	113.6	0.9	3
6/26/92	111.7	0.7	6
7/7/92	111.5	0.3	3
9/28/92	2543.9	0.6	3
10/7/92	2542.6	0.8	4
8/11/93	78.6	0.1	4
5/20/94	24.9	0.1	3
6/12/94	25.4	0.5	6
6/23/94	25.6	0.1	3
7/7/94	47.4	0.5	3

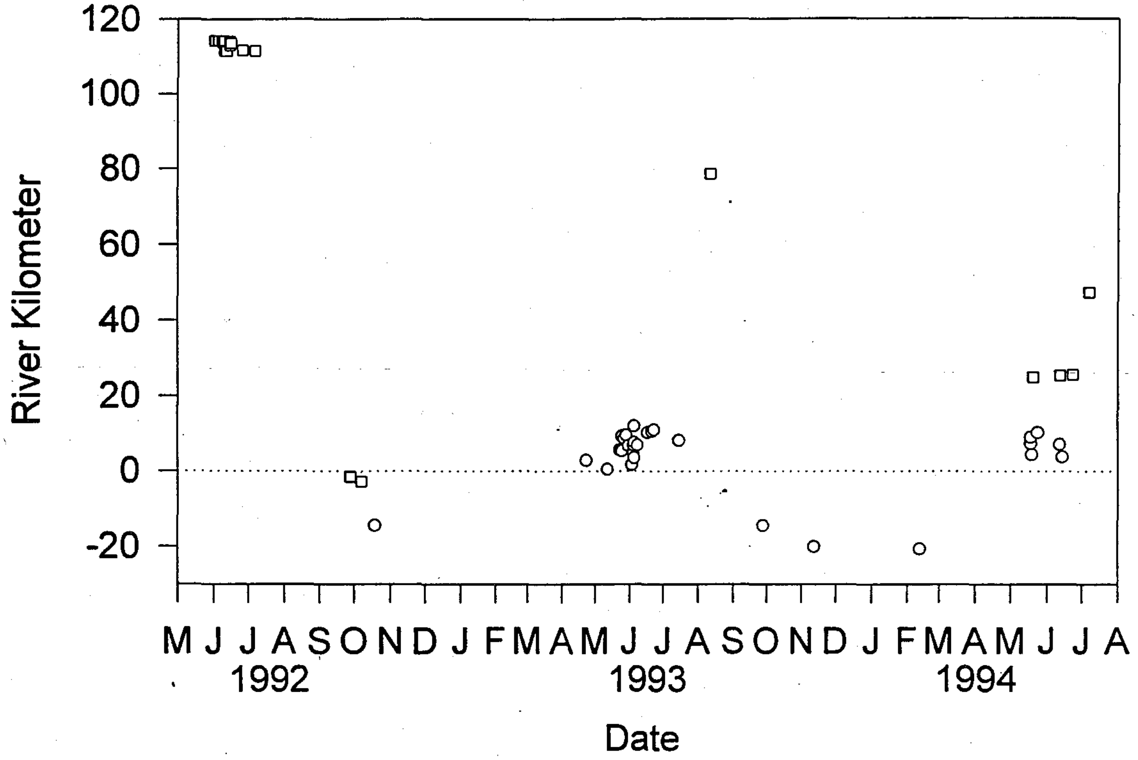

Figure 16. Aggregations of telemetered pallid sturgeon (open circles) and shovelnose sturgeon (open squares) in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Aggregations were defined as groups of three or more individuals in a reach of river one km long.

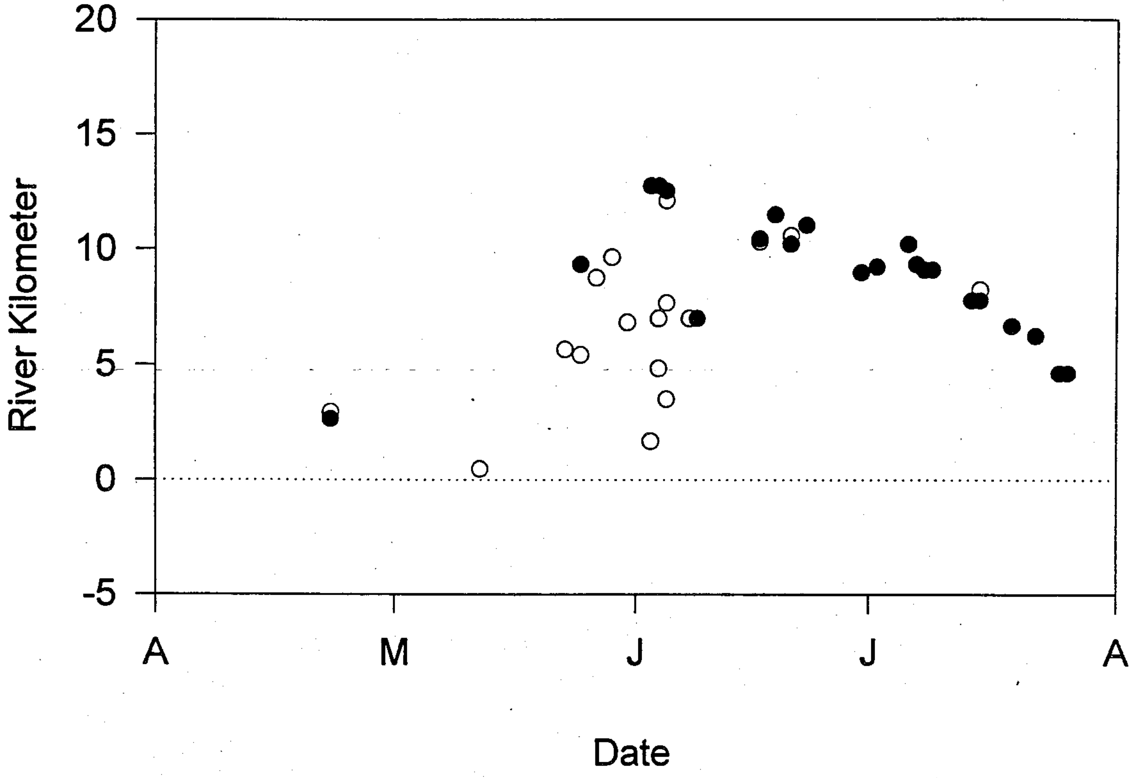

Figure 17. Aggregations of telemetered pallid sturgeon (open circles) and locations of a gravid female pallid sturgeon (radio frequency 49.030; solid circles) during April-July 1993, illustrating potential pallid sturgeon spawning locations. Aggregations were defined as groups of three or more individuals in a reach of river one km long.

Home Range

Home range was measured for 24 pallid sturgeon and 26 shovelnose sturgeon (Tables 18 and 19). The home range for pallid sturgeon was from 12.4 to 331.2 km. The home range for shovelnose sturgeon was from 0 to 254.1 km. Days at large ranged from 27.2 to 1334 for pallid sturgeon and 14.1 to 594 for shovelnose sturgeon.

Home range of pallid and shovelnose sturgeon was different between seasons (Table 20; Figures 18 and 19). Mean, median, and maximum home ranges were highest in spring or summer, and lowest in winter for both pallid and shovelnose sturgeon. The hypothesis that median home ranges were equal for each season was rejected for both pallid ($P = 0.0004$) and shovelnose ($P = 0.0005$) sturgeon (Kruskal-Wallis ANOVA).

Table 18. Days at large, number of locations and home range for telemetered pallid sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Transmitter frequency	Days at large	*N* locations	Home range (km)
48.520	175.00	9	12.4
48.540	151.00	13	17.2
49.830[a]	166.00	10	35.4
49.170	274.18	30	35.4
49.030	427.14	38	36.6
49.650	358.00	46	41.2
49.050	295.13	46	42.1
49.670	73.10	26	43.3
48.580	101.14	32	43.7
49.350	191.00	24	45.2
49.370	405.00	38	50.6
49.680	801.00	247	51.5
49.810	296.10	28	52.7
49.020	289.12	18	61.2
49.070	236.14	11	68.0
49.870	215.00	10	71.6
49.130	337.15	43	79.8
49.712	351.14	30	84.0
49.100	700.00	272	94.7
48.562	30.00	6	111.0
49.630[b]	631.12	56	134.8
48.570	27.17	8	149.4
49.850	419.00	32	231.8
49.240[b]	1334.00	13	331.2

[a] Includes data from recapture, after transmitter was lost.

[b] Includes data from initial capture, before transmitter was attached

Pallid sturgeon winter home ranges were significantly smaller than all other seasonal home ranges. Pallid sturgeon spring home ranges were significantly larger than fall and winter home ranges, but not significantly different than summer home ranges ($P < 0.15$; Dunn's multiple comparison test; Table 20). Shovelnose sturgeon winter home ranges were significantly smaller than spring and summer home ranges ($P < 0.15$; Dunn's multiple comparison test; Table 20).

Table 19. Days at large, number of locations and home range for telemetered shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Transmitter frequency	Days at large	*N* locations	Home range (km)
338	453.00	4	0.0
3335	454.00	5	1.6
48.360	67.00	8	3.9
48.880	73.00	34	3.9
49.710	138.00	7	3.9
49.790	177.00	9	4.2
48.820	14.14	10	6.8
48.600	300.00	8	11.6
48.640	440.00	45	24.2
48.840	63.10	16	25.6
48.740	74.00	4	28.2
48.300	112.14	16	30.3
48.760	252.00	5	31.4
48.920	75.00	17	35.6
48.860	534.10	65	36.6
48.320	31.00	18	41.0
48.380	67.00	36	59.1
48.900	443.15	56	72.4
48.590	72.10	34	88.8
48.340	67.00	24	89.1
48.550	337.00	15	91.1
48.620	556.00	34	97.3
48.660	594.00	43	97.7
48.940	526.00	57	119.1
48.680	517.00	26	123.9
48.280	171.00	26	254.1

Home range during summer ($P = 0.34$), fall ($P = 0.76$), and winter ($P = 0.63$) were not significantly different (Mann-Whitney U) between pallid and shovelnose sturgeon. Spring ranges were less similar and nearly statistically significant ($P = 0.10$).

Table 20. Seasonal home ranges (km) for telemetered pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Seasonal home ranges with the same letter are significantly different from each other.

Species	Season	*N* fish	Mean	Median	Maximum	Significant?[a]
Pallid	Summer	20	38.4	18.0	224.2	a
Pallid	Fall	16	23.0	14.1	146.7	b,c
Pallid	Winter	5	0.9	0	4.3	a,b,d
Pallid	Spring	22	46.6	34.8	149.4	c,d
Shovelnose	Summer	22	52.7	33.8	254.3	e
Shovelnose	Fall	14	14.4	13.6	40.5	
Shovelnose	Winter	7	1.0	0	3.9	e,f
Shovelnose	Spring	19	29.1	21.4	95.6	f

[a] Statistical significance determined by using Dunn's multiple comparison test, $P < 0.15$

The maximum distances moved between successive relocations for pallid and shovelnose sturgeon during the winter was only 5.9 and 3.9 km, respectively. Despite the relatively small number of relocations made during winter, linear regression of sample size versus range was not significant for pallid ($P = 0.20$) or shovelnose ($P = 0.43$) sturgeon.

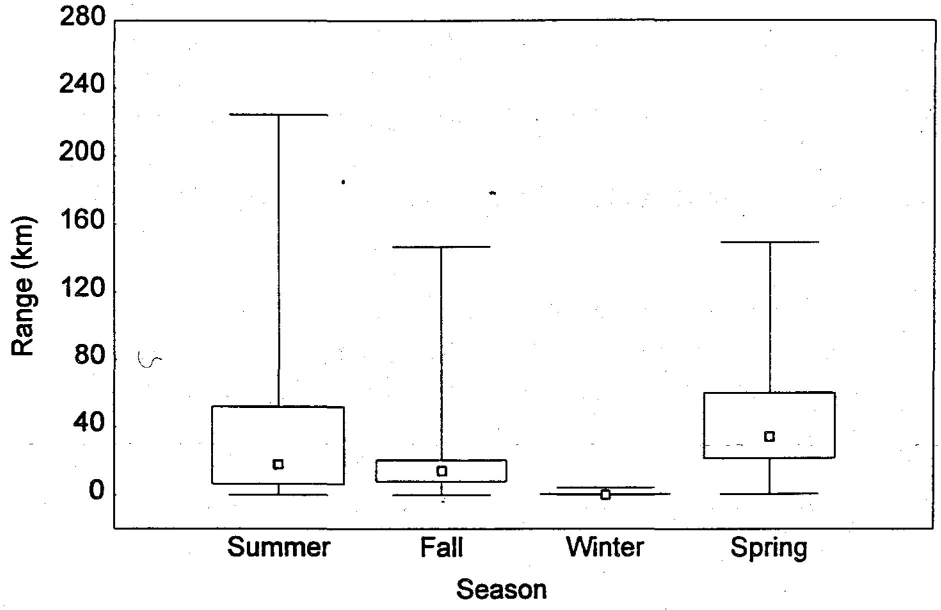

Figure 18. Range by season for telemetered pallid sturgeon (summer $N = 20$; fall $N = 16$; winter $N = 5$; spring $N = 22$) in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Small box is median, large box is 25% and 75% percentiles, and whiskers are minimum and maximum values.

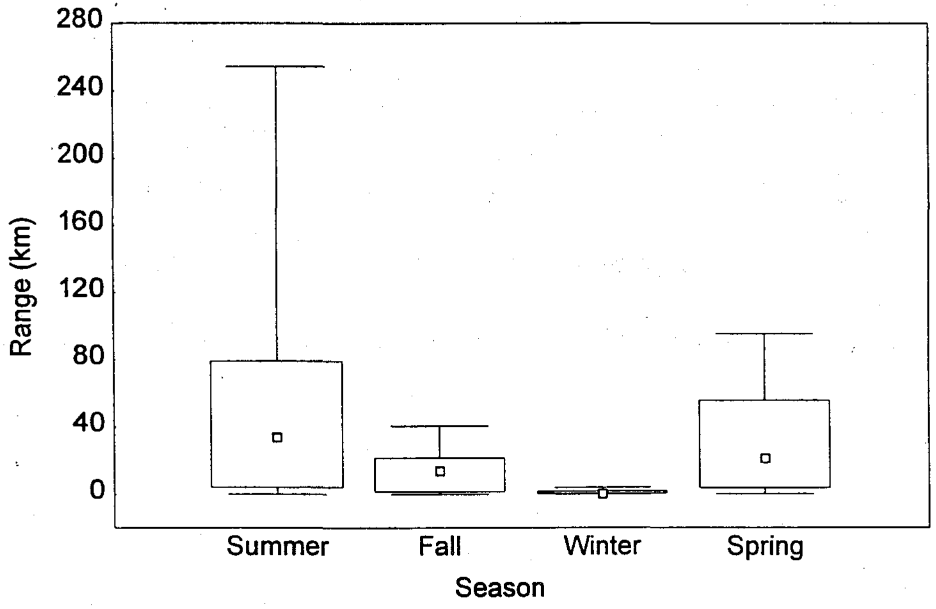

Figure 19. Range by season for telemetered shovelnose sturgeon (summer $N = 22$; fall $N = 14$; winter $N = 7$; spring $N = 19$) in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Small box is median, large box is 25% and 75% percentiles, and whiskers are minimum and maximum values.

Diel Movement

Both pallid and shovelnose sturgeon were observed moving during all four diel categories (Tables 21 and 22; Figure 20). Diel activity differed between pallid and shovelnose sturgeon. The highest proportion of pallid sturgeon observed moving was

Table 21. Summary of information on diel activity for telemetered pallid sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Diel category	*N* observations	Proportion of observations on moving fish
	All pallid sturgeon	
Day	452	0.53
Dusk	32	0.34
Night	57	0.37
Dawn	18	0.33
Total all diel periods	559	0.49
	Pallid sturgeon 49.680	
Day	117	0.68
Dusk	2	1.00
Night	8	0.75
Dawn	2	0.00
Total all diel periods	129	0.67
	Pallid sturgeon 49.100	
Day	84	0.87
Dusk	8	0.50
Night	13	0.46
Dawn	4	0.75
Total all diel periods	109	0.79
	Pallid sturgeon 49.630	
Day	36	0.17
Dusk	5	0.20
Night	4	0.75
Dawn	1	0.00
Total all diel periods	46	0.22

during day (0.53) while the highest proportion of shovelnose sturgeon observed moving was during night (0.52). Diel activity also differed between individual fish of both species. For example, three individual pallid sturgeon had daytime movement proportions of 0.17, 0.68. and 0.87 (Table 21). Three individual shovelnose sturgeon had daytime movement proportions of 0.23, 0.29 and 0.76 (Table 22).

Table 22. Summary of information on diel activity for telemetered shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Diel category[a]	*N* observations	Proportion of observations on moving fish
	All shovelnose sturgeon	
Day	152	0.34
Dusk	19	0.47
Night	31	0.52
Dawn	10	0.30
Total all diel periods	212	0.38
	Shovelnose sturgeon 48.590	
Day	31	0.23
Dusk	1	0.00
Night	0	--
Dawn	0	--
Total all diel periods	32	0.22
	Shovelnose sturgeon 48.860	
Day	21	0.29
Dusk	3	0.00
Night	6	0.00
Dawn	2	0.00
Total all diel periods	32	0.19
	Shovelnose sturgeon 48.380	
Day	17	0.76
Dusk	2	1.00
Night	8	0.50
Dawn	2	0.00
Total all diel periods	29	0.66

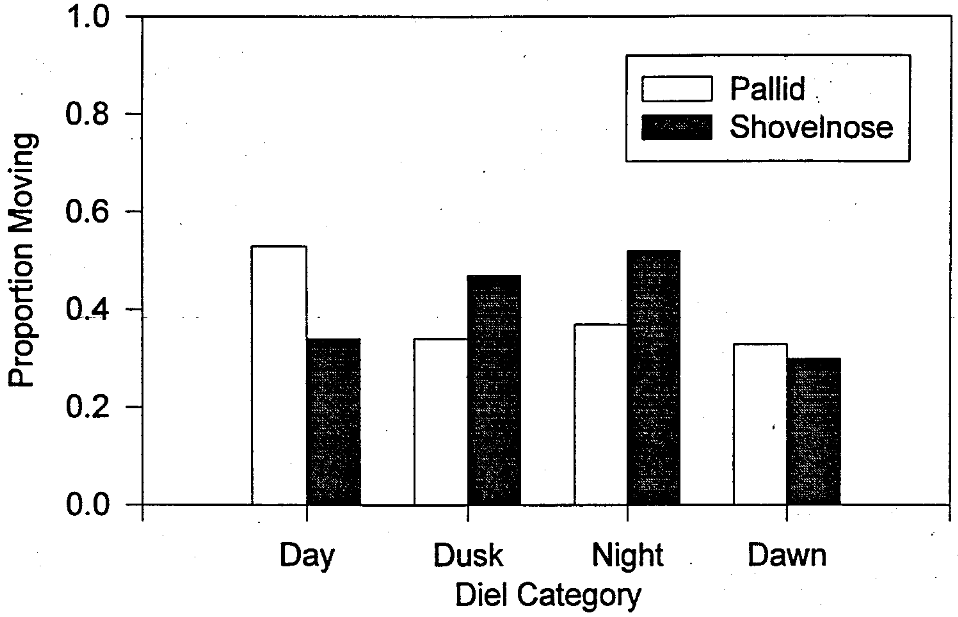

Figure 20. Proportions of observations on moving pallid and shovelnose sturgeon during four diel periods in Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Diel categories are: 1) Day - ≥1 h after sunrise until ≤ 1 h before sunset; 2) Dusk - < 1 h before sunset until < 1 h after sunset; 3) Dark - ≥ 1 h after sunset until ≥ 1 h before sunrise; 4) Dawn - < 1 h before sunrise until < 1 h after sunrise.

Movement Rates

Both pallid and shovelnose sturgeon were capable of substantial movement rates (Table 23 and Figures 21-24). Pallid sturgeon moved up to 21.4 km/d and shovelnose sturgeon moved up to 15.0 km/d. Hourly movements ranged to 9.5 km/h for pallid sturgeon and to 6.6 km/h for shovelnose sturgeon. Pallid sturgeon were observed to be not moving during 46% of relocations compared to 32% for shovelnose sturgeon.

Movement rate data were not normally distributed (Komolgorov-Smirnov test; $P < 0.01$). Upstream and downstream movement rates measured as km/d and km/h for pallid and shovelnose sturgeon were significantly different (Mann-Whitney U test; Table 23). Pallid sturgeon had significantly greater median movement rates than shovelnose sturgeon for both upstream and downstream movements measured as km/d and km/h.

Table 23. Movement rates for telemetered pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. P = pallid sturgeon; S = shovelnose sturgeon, DS = downstream movements; US = upstream movements. Mann-Whitney *P* levels are for the results of the hypothesis tests between numbered variables.

Variable	*N*	Mean	Median	Minimum	Maximum	Mann-Whitney *P*-level
(1) P DS (km/d)	197	1.9	0.69	0.003	21.4	
(2) S DS (km/d)	165	1.0	0.33	0.009	15.0	
(3) P US (km/d)	206	1.7	0.65	0.0005	21.0	
(4) S US (km/d)	174	1.0	0.48	0.008	12.6	
P no move	443					
S no move	174					
(5) P DS (km/h)	53	1.7	0.42	0.003	9.2	
(6) S DS (km/h)	16	0.22	0.04	0.006	1.8	
(7) P US (km/h)	57	2.1	0.83	0.005	9.5	
(8) S US (km/h)	20	0.99	0.20	0.005	6.6	
Hypotheses tested						
(1) vs. (2)						< 0.000001
(3) vs. (4)						0.000001
(5) vs. (6)						0.001
(7) vs. (8)						0.005
(1) vs. (3)						0.49
(2) vs. (4)						0.41
(5) vs. (7)						0.30
(6) vs. (8)						0.08

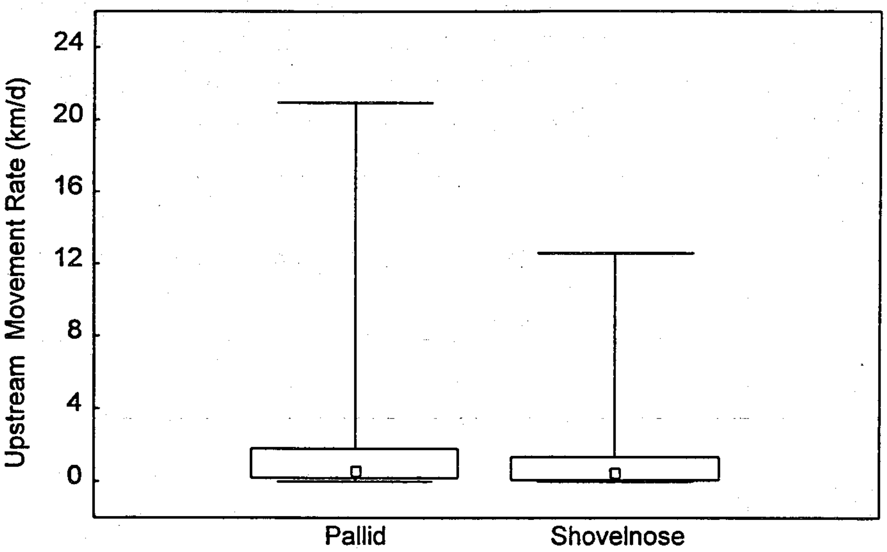

Figure 21. Upstream movement rates measured at intervals greater than 24 h for telemetered pallid ($N = 206$) and shovelnose sturgeon ($N = 174$) in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Small box is median, large box is 25% and 75% percentiles, and whiskers are minimum and maximum values.

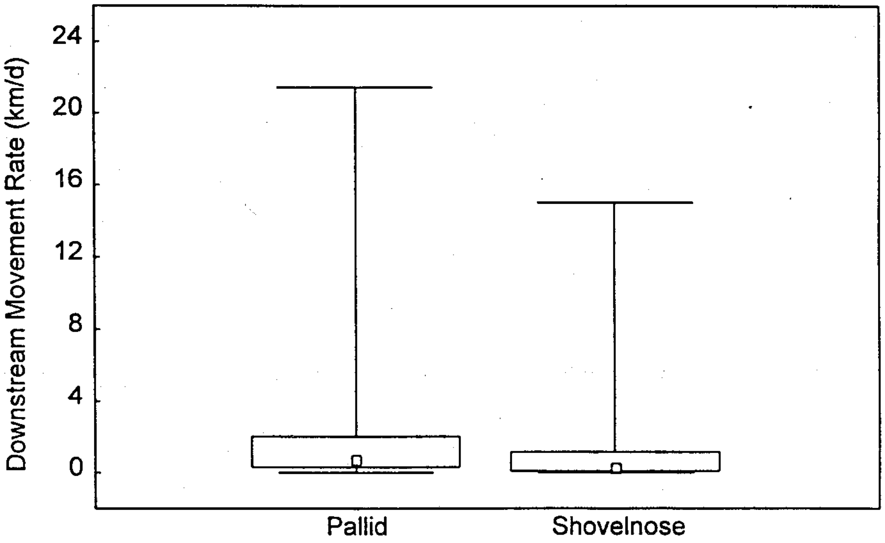

Figure 22. Downstream movement rates measured at intervals greater than 24 h for telemetered pallid ($N = 197$) and shovelnose sturgeon ($N = 165$) in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Small box is median, large box is 25% and 75% percentiles, and whiskers are minimum and maximum values.

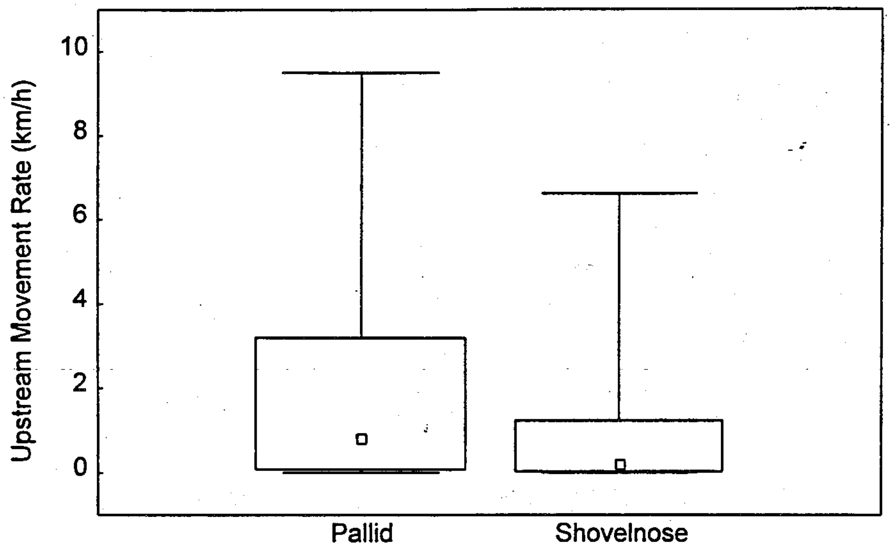

Figure 23. Upstream movement rates measured at intervals less than 24 h for telemetered pallid ($N = 57$) and shovelnose sturgeon ($N = 20$) in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Small box is median, large box is 25% and 75% percentiles, and whiskers are minimum and maximum values.

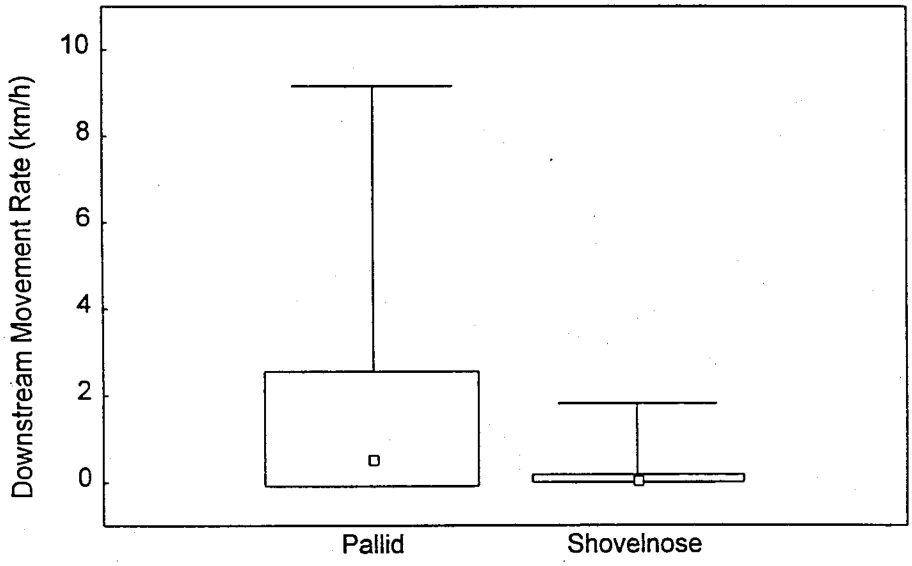

Figure 24. Downstream movement rates measured at intervals less than 24 h for telemetered pallid ($N = 54$) and shovelnose sturgeon ($N = 16$) in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Small box is median, large box is 25% and 75% percentiles, and whiskers are minimum and maximum values.

Pallid and shovelnose sturgeon were capable of rapid upstream and downstream movements. Upstream and downstream movement rates for each species were not significantly different (Mann-Whitney U; Table 23). Shovelnose sturgeon upstream and downstream movement rates (km/h) were close to being significantly different (*P* = 0.08).

Movement rates varied by season for both pallid and shovelnose sturgeon (Table 24). Mean, median, and maximum movement rates from highest to lowest were in spring, summer, fall, and winter, respectively, for both species.

Since downstream and upstream movement rates were not significantly different, they were combined for each species and categorized by season (Figures 25 and 26). Median seasonal movement rates were significantly different for both pallid and shovelnose sturgeon (Kruskal-Wallis ANOVA; *P* < 0.0001; Table 25). Because hourly movement rates were not documented for winter, and only rarely in fall, these rates were not tested.

Table 24. Movement rates for telemetered pallid and shovelnose sturgeon by season in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. P = pallid sturgeon; S = shovelnose sturgeon; DS = downstream movements; US = upstream movements.

Variable	*N*	Mean	Median	Minimum	Maximum
Summer					
P DS (km/d)	81	1.6	0.6	0.02	11.2
P US (km/d)	51	1.6	0.4	0.02	10.5
P DS (km/h)	28	2.2	1.1	0.003	9.2
P US (km/h)	26	1.9	1.0	0.01	8.8
P no move	311				
S DS (km/d)	74	0.9	0.4	0.01	6.3
S US (km/d)	83	1.3	0.8	0.01	12.6
S DS (km/h)	8	0.10	0.07	0.01	0.31
S US (km/h)	13	1.4	0.2	0.005	6.6
S no move	116				
Fall					
P DS (km/d)	35	1.2	0.4	0.02	10.6
P US (km/d)	36	1.1	0.8	0.02	5.5
P DS (km/h)	1	0.01	--	0.01	0.01
P US (km/h)	0	--	--	--	--
P no move	32				
S DS (km/d)	27	0.2	0.1	0.01	1.1
S US (km/d)	34	0.5	0.3	0.01	1.7
S DS (km/h)	0	--	--	--	--
S US (km/h)	0	--	--	--	--
S no move	9				
Winter					
P DS (km/d)	5	0.01	0.01	0.003	0.01
P US (km/d)	9	0.04	0.04	0.01	0.06
P DS (km/h)	0	--	--	--	--
P US (km/h)	0	--	--	--	--
P no move	5	--	--	--	--
S DS (km/d)	4	0.03	0.03	0.03	0.05
S US (km/d)	6	0.07	0.07	0.01	0.1
S DS (km/h)	0	--	--	--	--
S US (km/h)	0	--	--	--	--
S no move	5				

Table 24. Continued...

Variable	*N*	Mean	Median	Minimum	Maximum
Spring					
P DS (km/d)	76	2.7	1.1	0.01	21.4
P US (km/d)	110	2.2	1.0	0.01	21.0
P DS (km/h)	24	1.2	0.3	0.01	8.2
P US (km/h)	31	2.3	0.8	0.01	9.5
P no move	95				
S DS (km/d)	60	1.7	0.9	0.02	15.0
S US (km/d)	51	1.0	0.3	0.01	4.5
S DS (km/h)	8	0.3	0.03	0.01	1.8
S US (km/h)	7	0.3	0.05	0.01	1.6
S no move	44				

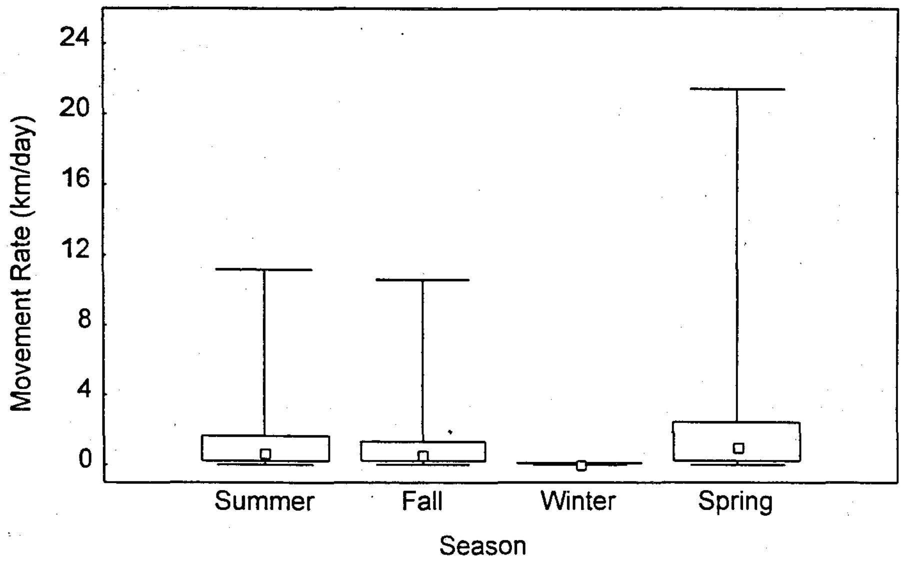

Figure 25. Movement rates by season measured at intervals greater than 24 h for telemetered pallid sturgeon (summer *N* = 132; fall *N* = 71; winter *N* = 14; spring *N* = 186) in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Small box is median, large box is 25% and 75% percentiles, and whiskers are minimum and maximum values.

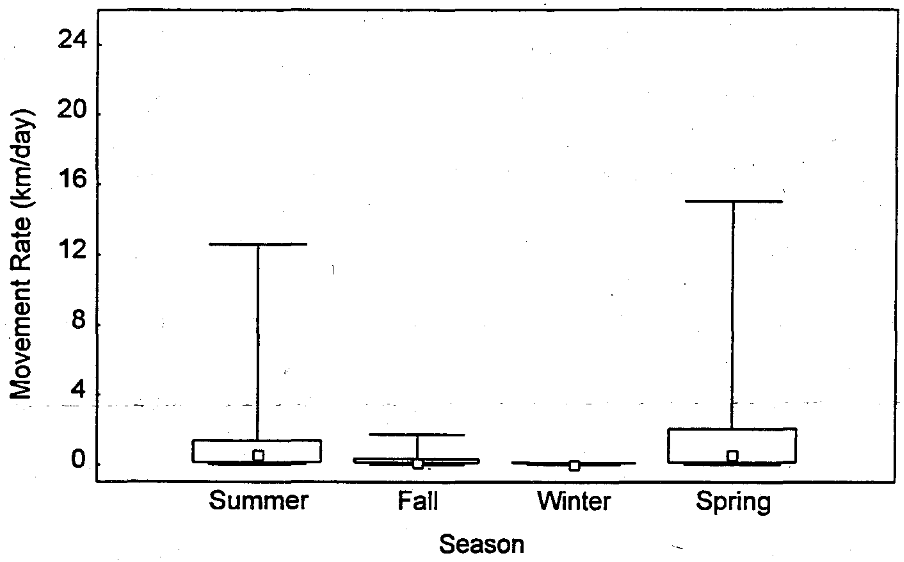

Figure 26. Movement rates by season measured at intervals greater than 24 h for telemetered shovelnose sturgeon (summer $N = 157$; fall $N = 61$; winter $N = 10$; spring $N = 111$) in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Small box is median, large box is 25% and 75% percentiles, and whiskers are minimum and maximum values.

Table 25. Results of testing for differences in seasonal movement rates measured as km/d for telemetered pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Seasonal movement rates with the same letter are significantly different from each other ($P \leq 0.05$).

Species	Season	Significant?[a]
Pallid	Summer	a
Pallid	Fall	b,c
Pallid	Winter	a,b,d
Pallid	Spring	c,d
Shovelnose	Summer	e,f
Shovelnose	Fall	e,g,h
Shovelnose	Winter	f,g,i
Shovelnose	Spring	h,i

[a] Statistical significance determined by using Kruskal-Wallis ANOVA followed by Dunn's multiple comparison test, $P < 0.15$.

Movement Patterns

Figure 27 depicts movements of a pallid sturgeon captured in the Lower Missouri River in April, 1992. This individual displays four characteristics of movement patterns typical of pallid sturgeon captured near the confluence (Tews 1994): 1) movement upstream from the Lower Missouri River into the Yellowstone River in April, May or June; 2) a period of residency in the Yellowstone River during May, June or July; 3) movement downstream from the Yellowstone River to the Lower Missouri River during July, August or September; and 4) a period of residency and limited movements in the Lower Missouri River during winter months.

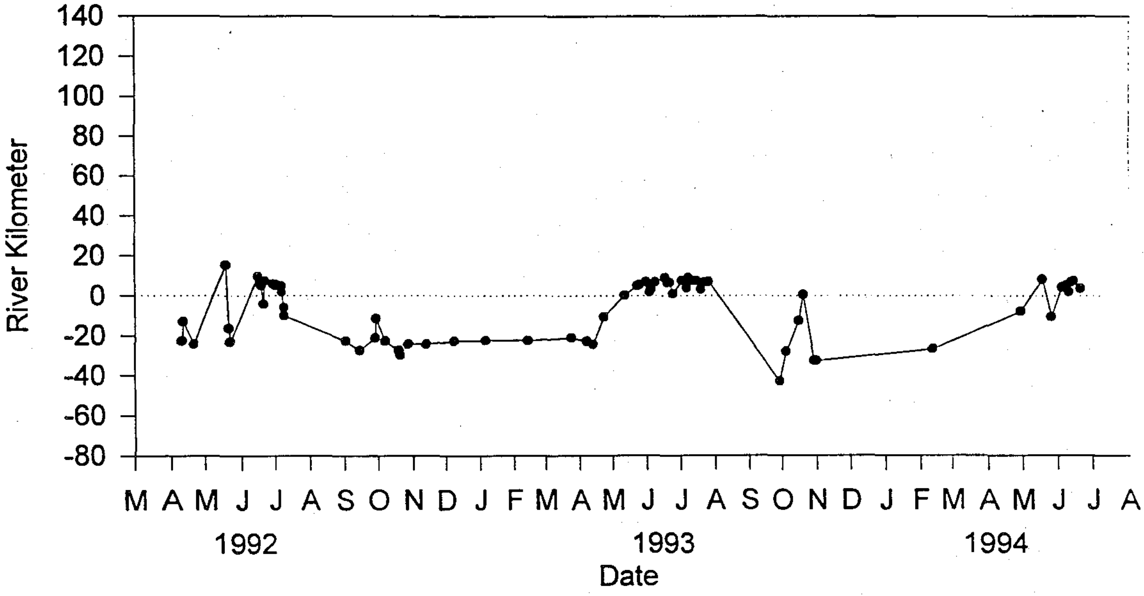

Figure 27. Movements of pallid sturgeon 49.680 in the Yellowstone and Lower Missouri rivers in Montana and North Dakota, 1992-1994. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

Fifteen of 15 (100%) pallid sturgeon captured near the confluence displayed movement upstream from the Lower Missouri River into the Yellowstone River in April, May or June. Nineteen of 19 (100%) displayed a period of residency in the Yellowstone River during May, June or July. Ten of 14 (71%) displayed movement downstream from the Yellowstone River to the Lower Missouri River during July, August or September. Thirteen of 14 (93%) displayed a period of residency and limited movements in the Lower Missouri River during winter months.

Exceptions to these general movement patterns were displayed by two pallid sturgeon captured in the Upper Missouri River and two pallid sturgeon captured in the Yellowstone River near the Intake diversion dam. One individual pallid sturgeon (radio frequency 49.240) was initially captured by MDFWP biologists in January 1991 in the Fort Peck dam tailrace (river km 2846). No transmitter was attached at this time, but the same individual was captured in September 1993 in the Lower Missouri River, 3 km below the confluence, where a transmitter was attached. The fish was next located in April, 1994 in the Yellowstone River at river km 24. It moved to the confluence in July and then moved 219 km upstream the Upper Missouri River by September 1994.

The second pallid sturgeon (radio frequency 49.870) captured in the Upper Missouri River in the Fort Peck tailrace was captured in March 1993. It remained in the tailrace area until late May, and it was relocated 65 km downstream in July. By September, it was back in the Fort Peck tailrace area.

Shovelnose sturgeon differed from pallid sturgeon with respect to movement patterns. Figure 28 depicts the movements of a shovelnose sturgeon captured in the Yellowstone River in June, 1992. While most pallid sturgeon had summer locations upstream of winter locations, shifting seasonally from the Lower Missouri River to the Yellowstone River, most shovelnose sturgeon were found almost exclusively in the Yellowstone River, and some had winter locations upstream of summer locations. Six of 15 (40%) shovelnose sturgeon with a discernible movement pattern had summer locations higher upstream than fall or winter locations, while 9 of the 15 (60%) had winter or fall locations upstream of summer locations.

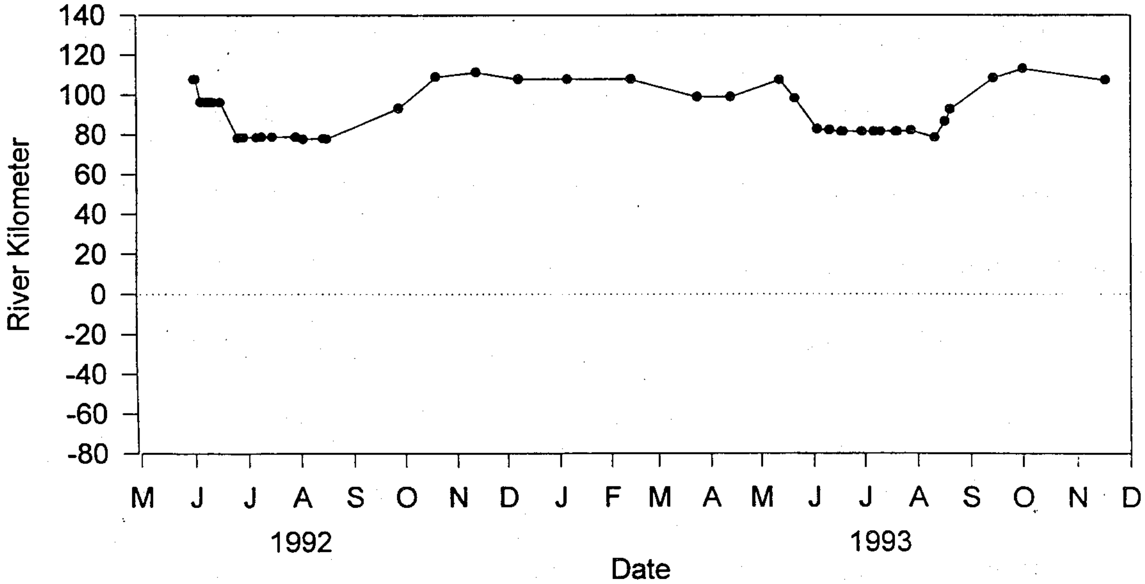

Figure 28. Movements of shovelnose sturgeon 48.860 during 1992-1993 in the Yellowstone River, Montana. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

Two pallid sturgeon were captured near the Intake diversion dam. The first was captured in May, 1993 (radio frequency 48.570). Thirteen days later, it was relocated 154 km downstream in the Lower Missouri River. Fourteen days after that relocation, it had returned to the Intake diversion dam, a total roundtrip of 308 km in 27 d. This individual shed its transmitter shortly thereafter. The second pallid sturgeon (radio frequency 48.562) captured near Intake diversion dam displayed a similar movement pattern. It was captured in May 1994, was relocated 15 days later, 105 km downstream in the Yellowstone River, about 9 km above the confluence. Contact with this fish was lost shortly afterwards.

One individual (radio frequency 48.900) had summer locations upstream of fall and winter locations in 1992 and early summer locations downstream of late summer locations in 1993. Contact with this individual was lost in late August 1993, after it had passed upstream of the Intake diversion dam. At least one other individual shovelnose sturgeon 1992 when the maximum flow was 181.53 m^3/s. Figures depicting movements for all telemetered pallid and shovelnose sturgeon are presented in the Appendix (Figures 35-82).

Clustering

Barlett's test indicated significant heterogeneity of variance of seasonal mean river km ($P < 0.0000001$) for two of three pallid sturgeon batches (groups of fish captured in the same general area and time, see Data Analysis) and nearly significant for the third

(*P* = 0.06; Table 26). A significant result was obtained for all three shovelnose sturgeon batches (*P* = 0.01; *P* = 0.00001; *P* = 0.0003). Therefore, it appears that both pallid and shovelnose sturgeon differed in the amount of clustering on a seasonal basis.

Ranks of clustering (variance) for all three batches of pallid sturgeon from least clustered to most clustered were: summer, spring, fall, and winter. Shovelnose sturgeon batches were more variable in their clustering ranks. Two shovelnose sturgeon batches were least clustered in spring and most clustered in winter. This pattern is similar to that seen in the pallid sturgeon batches, except that the season of least clustering was spring rather than summer. The third shovelnose sturgeon batch clustered differently. This batch was less clustered in fall and winter and more clustered in spring and summer.

Table 26. Summary of information on analysis of clustering by season for telemetered pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Species (batch)	Season	N fish	N observations	Variance	Variance rank	Bartlett's *P* level
pallid (1)	summer	5	46	365.7	1	< 0.000000
pallid (1)	fall	6	30	58.4	3	
pallid (1)	winter	4	8	21.4	4	
pallid (1)	spring	6	79	125.4	2	
pallid (2)	summer	4	53	125.1	1	0.06
pallid (2)	fall	3	5	9.2	3	
pallid (2)	winter	2	2	0	4	
pallid (2)	spring	4	33	99.0	2	
pallid (3)	summer	7	52	895.4	1	< 0.000000
pallid (3)	fall	6	38	41.8	3	
pallid (3)	winter	5	5	34.4	4	
pallid (3)	spring	7	103	472.1	2	
shovelnose (4)	summer	3	47	536.3	3	0.01
shovelnose (4)	fall	3	18	1127.7	2	
shovelnose (4)	winter	1	2	1.6	4	
shovelnose (4)	spring	3	17	1373.1	1	
shovelnose (5)	summer	4	36	1013.4	2	0.00001
shovelnose (5)	fall	4	19	138.7	3	
shovelnose (5)	winter	2	3	34.5	4	
shovelnose (5)	spring	3	16	1738.8	1	
shovelnose (6)	summer	6	116	1050.4	3	0.0003
shovelnose (6)	fall	3	20	2313.3	1	
shovelnose (6)	winter	3	6	2068.4	2	
shovelnose (6)	spring	7	96	640.1	4	

Movement into the Yellowstone and Lower Missouri rivers

On 31 occasions, pallid sturgeon were located below the confluence and subsequently located upstream, having entered either the Yellowstone River or the Upper Missouri River. These locations were made on 18 individual pallid sturgeon. On 28 occasions during 1992-1994, the subsequent location was in the Yellowstone River, and on 3 occasions, all during 1994, the subsequent location was in the Upper Missouri River. Pallid sturgeon entered the Yellowstone River significantly more than expected by chance (Pearson's χ^2 analysis; $P = 0.000007$).

Median discharge was significantly higher in the Yellowstone River (median = 251.3 m^3/s; mean = 368.6 m^3/s; SD = 283.2) than in the Upper Missouri River (median = 214.1 m^3/s; mean = 215.4 m^3/s; SD = 70.9) for the periods when pallid sturgeon passed upstream from the Lower Missouri River to the Yellowstone River (Mann-Whitney U test; $P < 0.0000001$). Median discharge was significantly higher in the Upper Missouri River (median = 239.6 m^3/s; mean = 237.5 m^3/s; SD = 26.8) than in the Yellowstone River (median = 116.4 m^3/s; mean = 157.8 m^3/s; SD = 96.7) when pallid sturgeon entered the Upper Missouri River (Mann-Whitney U test; $P = 0.000005$).

Ten observations of 6 individual shovelnose sturgeon passing the confluence were made during 1992-1994, and 8 of the 10 subsequent observations were in the Yellowstone River. Both times that telemetered shovelnose sturgeon entered the Upper Missouri River were during 1994. Shovelnose sturgeon entering the Yellowstone River was nearly significantly more than expected by chance (Pearson's χ^2 analysis; $P = 0.058$). Median discharges in the Yellowstone River (median = 166.2 m^3/s; mean = 175.2 m^3/s SD = 80.4) and Upper Missouri River (median = 214.1 m^3/s; mean = 172.1 m^3/s; SD = 61.9) were not significantly different during periods when shovelnose sturgeon entered the Yellowstone River. However, median discharge in the Upper Missouri River (median

= 243.3 m^3/s; mean = 248.0 m^3/s; SD = 47.4) was significantly higher than in the Yellowstone River during periods when shovelnose sturgeon entered the Upper Missouri River. Because the thermograph from the Upper Missouri River Station was lost during 1994, I was unable to compare water temperatures between the two rivers when pallid and shovelnose sturgeon entered the Upper Missouri River.

Movement Regression Models

Models of locations (river km) with discharge as the predictor variable that appeared to fit well were created for 18 of 24 (75%) pallid sturgeon. Coefficients of simple determination (r^2) ranged from 0.3275 to 0.9655. Because discharge was different in the three river segments (Yellowstone River, Upper and Lower Missouri River), separate parameter estimates were calculated for each river segment.

Sign (positive or negative) and magnitude of parameter estimates varied among the three river segments and among individuals. In the Yellowstone River, 10 of 13 (77%) significant parameter estimates were positive, indicating that these pallid sturgeon were found higher upstream during higher discharges. In the Lower Missouri River, 15 of 15 (100%) parameter estimates were negative, indicating that within the Lower Missouri River, these pallid sturgeon were found at lower river kilometers during higher discharges. The one significant parameter estimate for a pallid sturgeon in the Upper Missouri River was negative.

Models of locations (river km) with discharge as the predictor variable that appeared to fit well were created for 12 of 22 (54%) shovelnose sturgeon. Coefficients of simple determination (r^2) ranged from 0.2793 to 0.9046. As with pallid sturgeon, sign and magnitude of parameter estimates varied among the three river segments and among individuals. However, in contrast to pallid sturgeon, the majority of parameter estimates in the Yellowstone River were negative (9 of 12; 75%). In the Lower Missouri River, 3 of 3 (100%) parameter estimates were negative. The one estimate for a pallid sturgeon in the Upper Missouri River was positive.

Models of locations (river km) with photoperiod as the predictor variable that appeared to fit well were created for 16 of 24 (67%) pallid sturgeon. Coefficients of simple determination (r^2) ranged from 0.1468 to 0.8696.

As with discharge models, sign and magnitude of parameter estimates varied among individuals. Fourteen of the 16 (88%) parameter estimates for pallid sturgeon were positive, indicating higher predicted river kilometer locations with increased photoperiod.

In a like manner, models of locations (river km) with photoperiod as the predictor variable that appeared to fit well were created for 11 of 22 (50%) shovelnose sturgeon. Coefficients of simple determination (r^2) ranged from 0.1298 to 0.8884.

Sign and magnitude of parameter estimates varied among individual shovelnose sturgeon. Seven of the 11 (64%) parameter estimates for shovelnose sturgeon were positive.

Models with both photoperiod and discharge appeared to fit well for 18 of 24 (75%) of pallid sturgeon and 16 of 22 (73%) of shovelnose sturgeon. Coefficients of simple determination ranged from 0.5991 to 0.9705 for pallid sturgeon and 0.3110 to 0.9566. Summaries of all movement regression models are presented in the Appendix (Tables 32-37).

Channel Pattern, Islands, and Bars

Channel pattern at pallid sturgeon locations was primarily sinuous (76.9% of locations) or irregular (15.1%; Table 27; Figure 29). Pallid sturgeon were rarely found in straight channels (7.5%) or channel patterns with irregular meanders (0.5%). Channel pattern at shovelnose sturgeon locations was more evenly distributed (Figure 29); 46.3% of observations were in sinuous channels, and 25.2% and 23.8% of observations were in straight and irregular channels, respectively (Table 27). Only 4.8% of observations were in channels with irregular meanders.

Use of reaches with islands and bars was similar for pallid and shovelnose sturgeon (Table 27; Figure 30). Most locations were near islands; 73.1% and 68.0% of locations for pallid and shovelnose sturgeon, respectively. Reaches with alluvial bars were used less than reaches with islands by both species (22.2% for pallid sturgeon and

32.7% for shovelnose sturgeon). Reaches without bars or islands were used least by both species (14.6% for pallid sturgeon and 24.5% for shovelnose sturgeon).

Table 27. Summary of observations of macrohabitat use for telemetered pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

	Pallid sturgeon		Shovelnose sturgeon	
Macrohabitat variable	Number of observations	Percent of observations	Number of observations	Percent of observations
Channel pattern				
Straight	16	7.5	37	25.2
Sinuous	163	76.9	68	46.3
Irregular	32	15.1	35	23.8
Irregular meanders	1	0.5	7	4.8
Bar or island[a]				
Bar	46	22.2	48	32.7
Island	155	73.1	100	68.0
No bars or islands	31	14.6	36	24.5
Sere[b]				
Bare or pioneer	47	26.0	48	43.2
Willow/cottonwood thicket	71	39.2	25	22.5
Young cottonwood	78	43.1	54	48.6
Mature cottonwood	6	3.3	23	20.7
Alluvial bar type[c]				
Channel side	15	32.6	30	62.5
Channel junction	5	10.9	4	8.3
Point bar	2	4.3	9	18.8
Mid-channel	28	60.9	17	35.4
Geomorphic condition				
Run or straight reach	197	93.8	137	92.6
Curve	13	6.2	11	7.4

[a] Locations were classified as both island and bar if both were present.

[b] Locations were classified with two seres if both island and bar if both were present.

[c] Locations were classified with more than one bar type if more than one bar was present.

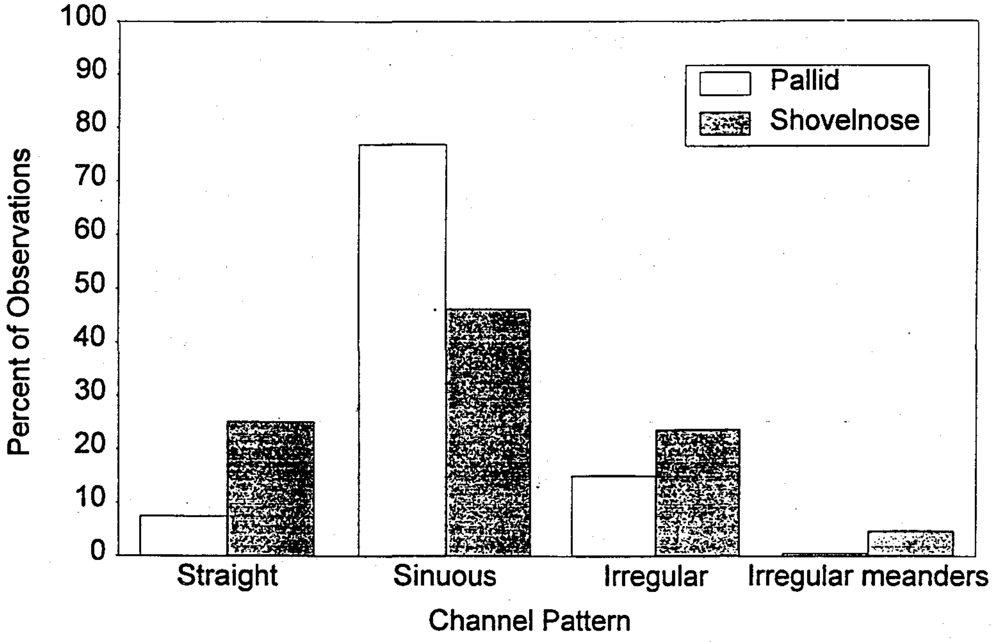

Figure 29. Percent of observations in four categories of channel pattern for telemetered pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

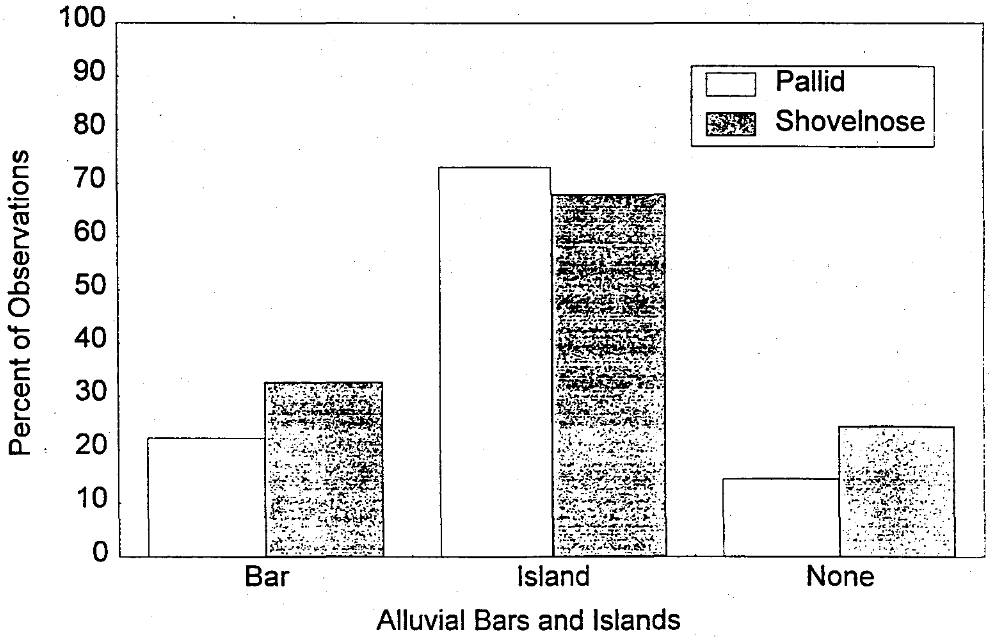

Figure 30. Percent of observations in reaches with and without islands and alluvial bars for telemetered pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Seral stage of islands and bars in reaches where pallid sturgeon were observed was most often a stage preceding mature cottonwood (Figure 31; Table 27). Shovelnose sturgeon had a similar pattern of use, but were found near islands with mature cottonwood forest more often (20.7% of observations) than pallid sturgeon (3.3% of observations).

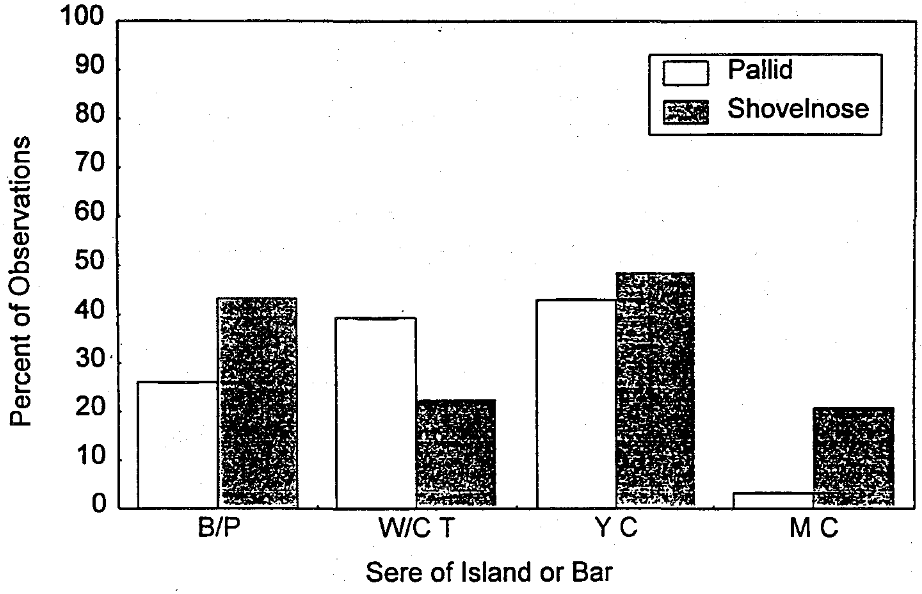

Figure 31. Percent of observations in four categories of seral stage of island or bar for telemetered pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. B/P = bare or pioneer; W/C T = willow/cottonwood thicket; Y C = young cottonwood forest; M C = mature cottonwood gallery forest.

When pallid sturgeon were found near an alluvial bar, the type of bar was most often a midchannel bar (60.9% of observations; Table 27; Figure 32). Channel side bars were also fairly common near pallid sturgeon locations (32.6% of observations). In contrast, shovelnose sturgeon were found near channel side bars most often (62.5% of observations), followed by midchannel bars (35.4%).

Most pallid and shovelnose sturgeon locations were in straight reaches; 93.8% and 92.6% of locations, respectively (Table 27). Areas near the apex of curves were only rarely used.

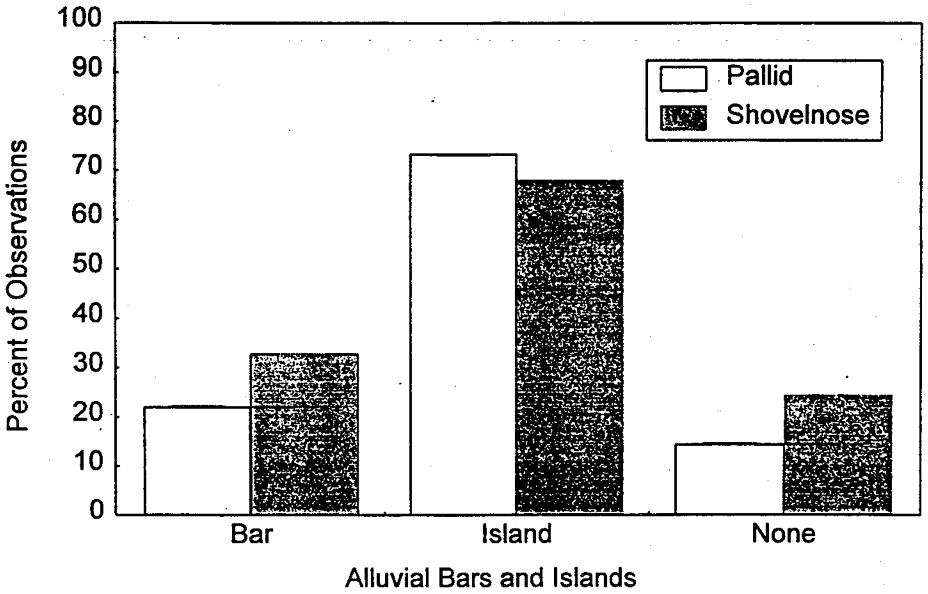

Figure 32. Percent of observations in four categories of alluvial bar for telemetered pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Island Density Use Versus Availability

Reaches without islands (island density category 1) were found from river km 2502.1 to river km 11.8 (Table 28; Figure 33), and comprised 31.1% of the Lower Missouri and Yellowstone rivers (Table 29). Single island reaches (island density category2) were found from river km 2532.9 to river km 111.8, and comprised only 7.7

of the Lower Missouri and Yellowstone rivers. Reaches with frequent islands (island density category 3) occurred primarily from river km 2511.7 to river km 59.1, and comprised 31.6% of the Lower Missouri and Yellowstone rivers. Split channel reaches (island density category 4) were found mostly in the Yellowstone River upstream of river km 61.4, and comprised 29.6% of the Lower Missouri and Yellowstone rivers.

Table 28. Island density category, locations, and lengths of reaches in the Lower Missouri and Yellowstone rivers, in Montana and North Dakota, 1992-1994. Island density categories are 1 = none - no islands; 2 = single - a single island, no overlapping of islands; 3 = frequent - occasional overlapping of islands, with average spacing between islands less than 10 river widths; and 4 = split channel - islands overlap other islands frequently or continuously, the number of flow channels is usually two ~~or~~ three.

Island density category	River kilometer downstream end	River kilometer upstream end	Length (km)	Percent of total
1	2502.1	2503.1	1.0	0.6
4	2503.1	2507.6	4.5	2.8
4	2507.6	2510.7	3.1	2.0
1	2510.7	2511.7	1.0	0.6
2	2511.7	2514.5	2.8	1.8
1	2514.5	2519.7	5.2	3.3
4	2519.7	2522.3	2.7	1.7
1	2522.3	2532.9	10.5	6.7
2	2523.9	2534.3	1.4	0.9
1	2534.3	2535.5	1.2	0.8
3	2535.5	2539.5	4.0	2.6
1	2539.5	2542.6	3.1	2.0
3	2542.6	17.2	20.0	12.7
1	17.2	18.1	1.0	0.6
3	18.1	20.0	1.9	1.2
1	20.0	24.5	4.5	2.8
3	24.5	31.5	7.0	4.4
1	31.5	33.2	1.7	1.1
2	33.2	35.0	1.8	1.1
1	35.0	35.5	0.6	0.4
2	35.5	36.9	1.3	0.8
1	36.9	41.2	4.4	2.8
3	41.2	45.1	3.8	2.4
1	45.1	50.4	5.3	3.4
3	50.4	59.1	8.7	5.5
1	59.1	61.4	2.3	1.5
4	61.4	71.5	10.2	6.4
1	71.5	72.1	0.6	0.4
4	72.1	86.5	14.4	9.1
3	86.5	88.5	2.0	1.3
4	88.5	91.5	3.0	1.9
1	91.5	92.7	1.2	0.7
4	92.7	96.6	4.0	2.5
3	96.6	99.0	2.4	1.5
4	99.0	103.9	4.9	3.1
2	103.9	107.2	3.2	2.1
1	107.2	110.2	3.1	1.9
2	110.2	111.8	1.6	1.0
1	111.8	114.3	2.4	1.5

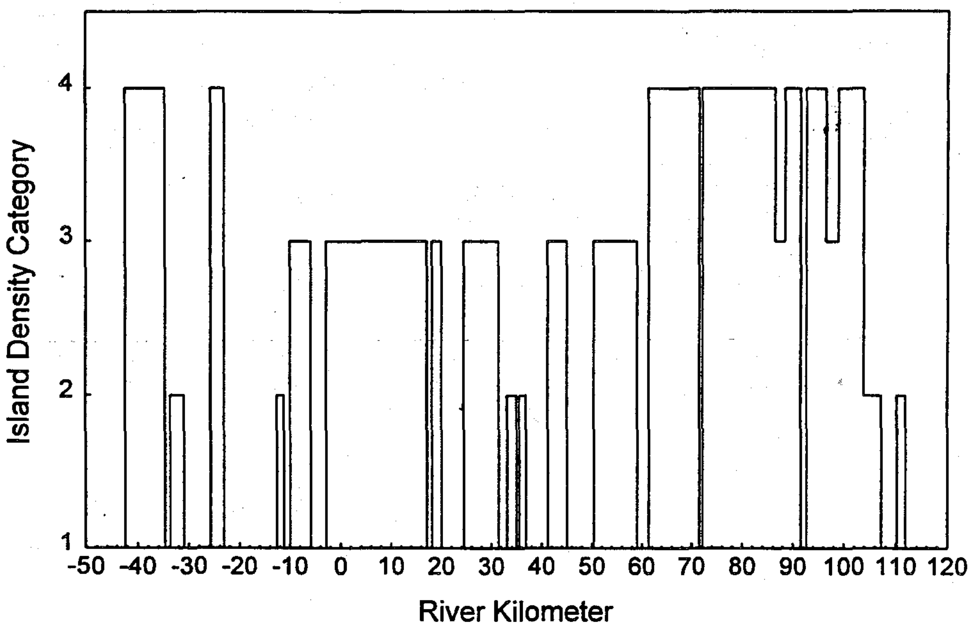

Figure 33. Distribution of available island density categories in the Lower Missouri River and Yellowstone River in Montana and North Dakota, 1992-1994. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River. Island density categories are 1 = none - no islands; 2 = single - a single island, no overlapping of islands; 3 = frequent - occasional overlapping of islands, with average spacing between islands less than 10 river widths; and 4 = split channel - islands overlap other islands frequently or continuously, the number of flow channels is usually two or three.

Table 29. Total lengths and percentages of reaches in island categories 1-4 in the Lower Missouri and Yellowstone rivers in Montana and North Dakota, 1992-1994. Island density categories are 1 = none - no islands; 2 = single - a single island, no overlapping of islands; 3 = frequent - occasional overlapping of islands, with average spacing between islands less than 10 river widths; and 4 = split channel - islands overlap other islands frequently or continuously, the number of flow channels is usually two or three.

Island density category	Total length (km)	Percent of total
1	49.0	31.1
2	12.2	7.7
3	49.8	31.6
4	46.7	29.6
totals	157.6	100.0

Use of reaches classified by island density categories by pallid sturgeon was significantly different than availability (Pearson's χ^2 analysis; $P < 0.00001$; Table 30). Pallid sturgeon preferred reaches with frequent islands and avoided reaches with no islands, single island reaches, and split channel reaches. Pallid sturgeon preferences in spring and summer were similar; reaches with frequent island were preferred and split channel reaches were avoided in both seasons. However, reaches with no islands were not significantly preferred or avoided in summer but avoided in spring. Single island reaches were not significantly preferred or avoided in spring or summer. Eight of 13 pallid sturgeon with $N \geq 10$ observations had significant ($P \geq 0.10$) island density category preferences (Table 30). All eight of these individuals preferred reaches with frequent islands, six individuals avoided reaches with no islands and two individuals avoided split channel reaches.

The effect of unequal sample sizes from individual fish contributing to the pooled result was examined. All six random samples showed significant preference for reaches with frequent islands, four samples showed avoidance of split channel reaches and one sample showed avoidance of reaches with no islands (Table 30).

Use of island density categories was significantly different than availability for the sample of all shovelnose sturgeon pooled ($P < 0.0379$); single island reaches were avoided (Table 31). In contrast to pallid sturgeon, spring and summer subsamples differed. Reaches with frequent islands were preferred in spring but avoided in summer.

Table 30. Summary of χ^2 analysis and conclusions on preference and/or avoidance of the four macrohabitat types for telemetered pallid sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Island density categories are 1 = none - no islands; 2 = single - a single island, no overlapping of islands; 3 = frequent - occasional overlapping of islands, with average spacing between islands less than 10 river widths; and 4 = split channel - islands overlap other islands frequently or continuously, the number of flow channels is usually two or three.

				Island density category			
Fish/category	N	χ^2	*P*	1	2	3	4
All pallids	246	207.94	<0.0000	avoid	avoid	prefer	avoid
Pallids spring	119	193.06	<0.0000	avoid		prefer	avoid
Pallids summer	102	70.17	<0.0000			prefer	avoid
49.680	36	44.46	<0.0000	avoid		prefer	avoid
49.030	20	11.40	0.0098	avoid		prefer	
49.650	19	2.16	0.5399				
49.630	18	13.03	0.0046	avoid		prefer	avoid
49.050	15	13.86	0.0031	avoid		prefer	
49.810	14	6.97	0.0730	avoid		prefer	
49.100	14	2.84	0.4170				
49.712	12	11.23	0.0106			prefer	
49.130	11	12.91	0.0048			prefer	
49.170	11	8.74	0.0330	avoid		prefer	
49.850	10	3.50	0.3208				
49.670	10	5.02	0.1704				
49.350	10	0.86	0.8351				
random 1	21	17.36	0.0006			prefer	
random 2	21	24.56	<0.0000			prefer	
random 3	21	10.67	0.0137			prefer	avoid
random 4	42	40.40	<0.0000			prefer	avoid
random 5	42	31.77	<0.0000		avoid	prefer	avoid
random 6	42	35.18	<0.0000			prefer	avoid

Only one of nine shovelnose sturgeon with $N \geq 8$ observations had significant ($P = 0.0052$) island density category preferences. This individual preferred split channel reaches.

As with pallid sturgeon, the effect of unequal sample sizes from individual fish contributing to the pooled result was examined by testing three random samples of one observation and three random samples of two observations per individual fish. Two random samples had significant results (Table 31). Both samples showed avoidance for reaches with frequent islands.

Table 31. Summary of Pearson's χ^2 analysis and conclusions on preference and/or avoidance of the four macrohabitat types for telemetered shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Island density categories are 1 = none - no islands; 2 = single - a single island, no overlapping of islands; 3 = frequent - occasional overlapping of islands, with average spacing between islands less than 10 river widths; and 4 = split channel - islands overlap other islands frequently or continuously, the number of flow channels is usually two or three.

				Island category			
Fish/category	*N*	χ^2	P	1	2	3	4
All shovelnose	139	8.43	0.0379		avoid		
shovelnose spring	42	12.53	0.0058			prefer	
shovelnose summer	91	16.90	0.0007			avoid	
48.940	15	12.74	0.0052				prefer
48.860	13	2.71	0.4385				
48.900	13	9.69	0.0214				
48.340	11	1.89	0.5956				
48.380	10	0.95	0.8133				
48.300	10	1.25	0.7434				
48.590	8	3.98	0.2637				
48.550	8	0.44	0.9319				
48.280	8	3.89	0.2747				
random 1	18	9.26	0.0261			avoid	
random 2	18	2.32	0.5087				
random 3	18	2.21	0.5300				
random 4	35	1.96	0.5797				
random 5	35	1.29	0.7316				
random 6	35	7.98	0.0465			avoid	

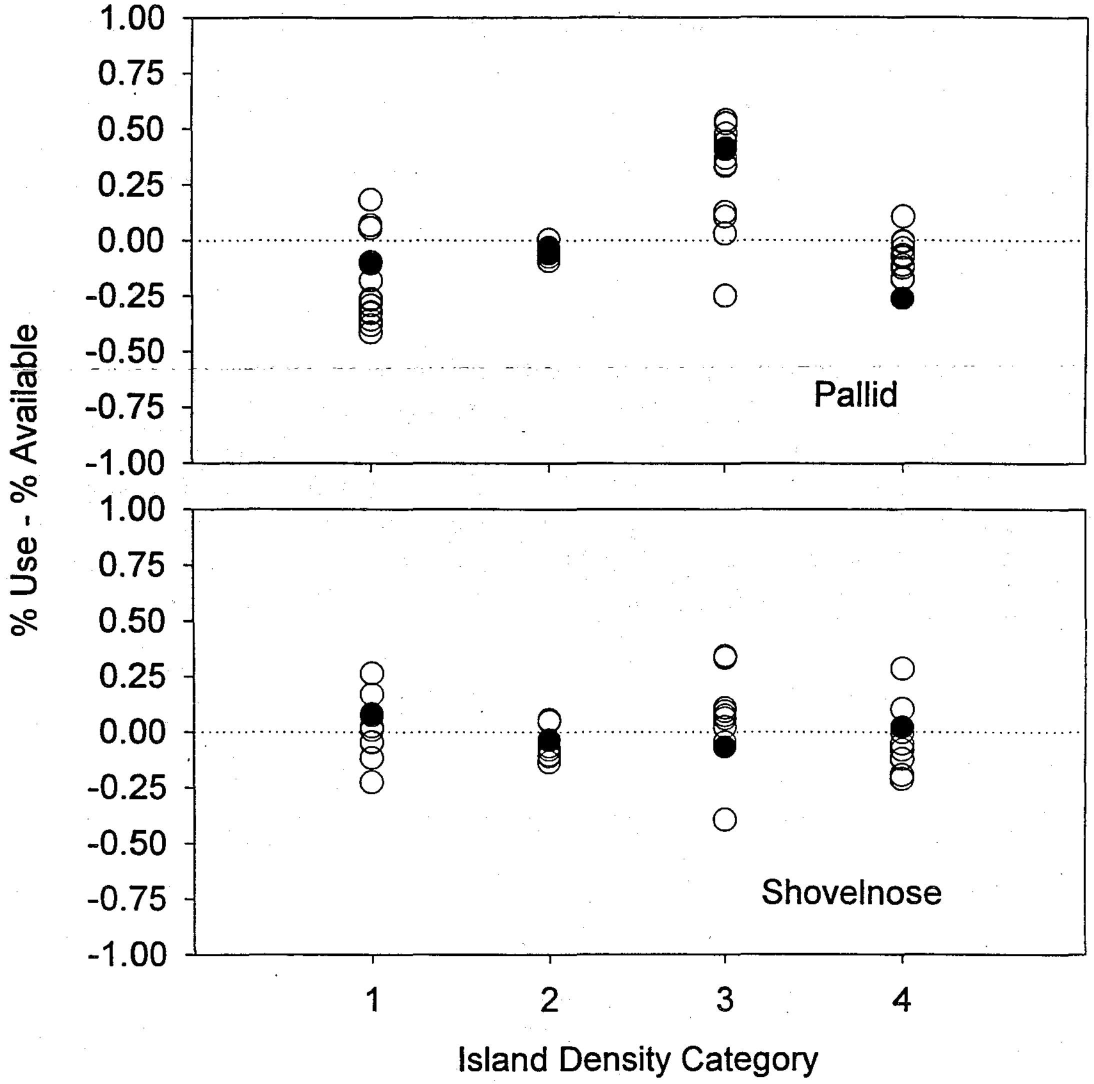

Figure 34. Percent use minus percent availability for 13 individual pallid sturgeon with *N* ≥ 10 observations and 9 individual shovelnose sturgeon with *N* ≥ 8 observations (open circles) for four macrohabitat categories in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. Solid circles are pooled value for all pallid sturgeon (*N* = 21 fish, *N* = 246 observations) and all shovelnose sturgeon (*N* = 18 fish, *N* = 139 observations). The range between the uppermost and lowermost open circles indicates the extent of variation among individual fish. Island density categories are 1 = none - no islands; 2 = single - a single island, no overlapping of islands; 3 = frequent - occasional overlapping of islands, with average spacing between islands less than 10 river widths; and 4 = split channel - islands overlap other islands frequently or continuously, the number of flow channels is usually two or three.

Use of reaches with no islands, single island reaches, and split channel reaches varied among individual pallid sturgeon. Use of reaches with frequent islands among individual pallid sturgeon was less variable and about the same as availability. Use of reaches with no islands and split channel reaches was generally less than available, and use of reaches with frequent islands was generally greater than available (Figure 34).

Individual shovelnose sturgeon also showed more variation in use of reaches with no islands, single island reaches, and split channel reaches than they did for reaches with frequent islands. In contrast to pallid sturgeon, no trends are evident in use of reaches with no islands, reaches with frequent islands, or split channel reaches (Figure 34).

DISCUSSION

As an endangered species, the pallid sturgeon is rare by definition and much basic life history and habitat data are lacking. Because of the pallid sturgeon's rarity, these data are difficult to obtain. In addition, habitat preference is difficult to determine since virtually the entire range of pallid sturgeon has been impacted by human activities such as dam construction and channelization (Dryer and Sandvol 1993). In these altered habitats, observed habitat use and behavior could be different from those under pre-impact conditions. However, within this study area, the undammed Yellowstone River and the Missouri River below the confluence probably represent the closest approximation to pre-impact habitat and thus behavior of pallid and shovelnose sturgeon that exists today.

Shovelnose sturgeon have been proposed as a surrogate species to obtain inference relative to the pallid sturgeon. Shovelnose sturgeon are sympatric over the entire range of pallid sturgeon and are often captured in the same gear sets (Carlson et al. 1985, Tews 1994), indicating periods of similar habitat use. The existence of pallid x shovelnose sturgeon hybrids further indicates that spawning habitat is similar, at least occasionally in altered habitats. In this study, I found that habitat use and movements of pallid sturgeon and shovelnose sturgeon were similar in certain aspects. Nonetheless, in part due to the large number of observations afforded by telemetry, important differences in habitat use and movements between the two species, as well as among individuals, were found.

However, because telemetered pallid sturgeon were larger than telemetered shovelnose sturgeon, the differences I observered between the two species are confounded with the size difference between pallid and shovelnose sturgeon. However, despite the size difference, telemetered individuals of both species were of adult size, and hence inference regarding differences between adult pallid and shovelnose sturgeon are valid. In conclusion, it appears that adult shovelnose sturgeon are of limited utility as adult pallid sturgeon surrogates, although as members of the same ecosystem, they are an indicator of ecosystem impacts that may be relevant to pallid sturgeon.

Substrate

Pallid sturgeon showed statistically significant preference for sandy substrates, and individual pallid sturgeon were less variable in substrate use than were individual shovelnose sturgeon. When sand dunes were distinguished from general sand substrates which included both dunes and flat sand, sand dunes were significantly preferred. Gravel and cobble substrates were significantly avoided. As a species, shovelnose sturgeon significantly preferred gravel and cobble substrates and avoided sand. However, individual shovelnose sturgeon were more variable in substrate use than were pallid sturgeon.

The substrate use observed in this study corresponds to the distribution of the two species. Pallid sturgeon are found only in the Mississippi and Missouri rivers, and their largest tributaries (Cross 1967, Lee et al. 1980, Keenlyne 1989) where sand is the predominant substrate (Dryer and Sandvol 1993). A data base of nation-wide pallid sturgeon captures is maintained by the U. S. Fish and Wildlife Service Office of Ecological Services in Bismarck, North Dakota. In this database, 166 of 173 (96%) pallid sturgeon captures with substrate data were over substrates composed at least partially of sand or fines. Erickson (1992) reports that in Lake Sharpe on the Missouri River in South Dakota about 73% of locations of pallid sturgeon ≥ 5 kg were over sand or fines. However, substrate use by small pallid sturgeon was different: 62% of locations of telemetered pallid sturgeon ≤ 5 kg were over substrates larger than sand.

In Montana, the Yellowstone and Missouri rivers change from sand-dominated substrate in their lower reaches to gravel and cobble-dominated substrate in the upper reaches. Although occasional records of pallid sturgeon from the gravel and cobble areas of these rivers exist (Brown 1955, Brown 1971, Watson and Stewart 1991, Gardner 1995), the majority of captures are from the lower, sand-dominated reaches (Krentz 1994, Tews 1994, Gardner 1995).

In contrast to pallid sturgeon, shovelnose sturgeon occur in smaller rivers (Christenson 1975) and farther upstream in large rivers such as the Missouri and Mississippi (Lee et al. 1980). In Montana, catch-per-unit-effort for shovelnose sturgeon is generally higher in the gravel/cobble-dominated reaches than in the sand dominated reaches of the Yellowstone and Missouri Rivers (Tews 1994, Bakes et al. 1994). In telemetry studies from the upper Mississippi River, researchers report that shovelnose sturgeon were most often relocated over sandy substrates (Curtis 1990), and also regularly associated with the large rock substrate that composed the wing dams (Hurley et al. 1987). However, gravel and cobble substrates in the upper Mississippi River are apparently quite rare (Curtis 1990).

Differences in substrate use may be related to the food habits of the two species. Small fish, such as cyprinids, may be easier to glean from a sand substrate than from a cobble substrate where interstices may offer a refuge from predation. Sand dunes may also offer a velocity refuge for pallid sturgeon or their prey. In contrast, shovelnose sturgeon consume primarily aquatic insects. Cobble and gravel substrates generally have higher benthic production than shifting, sandy substrates (Hynes 1970, Junk et al. 1989, Allan 1995). Perhaps smaller pallid sturgeon include more insects in their diet, which could explain the greater use of larger substrates for smaller pallid sturgeon reported by Erickson (1992).

Depth

Pallid and shovelnose sturgeon used a wide range of depths, and although I found much overlap of depth use, median depth at pallid sturgeon locations was significantly greater than median depth at shovelnose sturgeon locations. There was also significant variability in use of depths by individuals of both species. Although I observed radio-tagged pallid and shovelnose sturgeon in depths as great as 8.2 m and 10.1 m, respectively, there was probably a bias against locations in deep water because of the attenuation of radio signals by deep water with high conductivity.

Mean maximum depth in channel cross-sections occupied by pallid and shovelnose sturgeon were significantly different, with pallid sturgeon in deeper channels. Both species generally used the deeper parts of the channel cross-section they were located in, but median relative depth at shovelnose sturgeon locations were significantly greater than pallid sturgeon. Therefore, although shovelnose sturgeon used lesser absolute depths than pallid sturgeon, the depths they used relative to what was available in the channel cross-section were greater than those used by pallid sturgeon. This can be explained by considering the maximum depth of the channels where the observations occurred, coupled with the idea that both species have some minimum depth limit. For example, only 6 of 164 (3.7%) and 5 of 147 (3.4%) observations of pallid and shovelnose sturgeon, respectively, were in depths less than 1 m. A depth of 1 m in a channel with a 4 m maximum depth is a relative depth of 0.25. The same 1 m depth in a channel with a 3 m maximum depth is a relative depth of 0.33.

Mean depth at pallid sturgeon locations in the Missouri River above Fort Peck dam in Montana (MRFP; Gardner 1995) were about 1 m less than mean depth at pallid sturgeon locations in my study area. In the Missouri River between Oahe and Big Bend dams in South Dakota (MRSD), mean depth at pallid sturgeon locations was about 1.4 m deeper than in my study area (Erickson 1992). Since the pattern of mean depths at pallid sturgeon locations in the three study sites was the same as expected for the relative availability of depths (i.e. shallowest at the farthest upstream study site, and deepest at the farthest downstream study site; Ryder and Pesendorfer 1989), the difference in mean depths at pallid sturgeon locations between the three study areas are likely due to the distribution of available depths in the three sites. Similarly, mean depths at shovelnose sturgeon locations from my study are shallower than those reported from other shovelnose sturgeon telemetry studies farther downstream in the upper Mississippi River (Hurley et al. 1987, Curtis 1990).

Current Velocity

While the overall means of bottom current velocities used by the two species were significantly different, differences can be attributed to differences in current velocities in the Yellowstone River and the Lower Missouri River. When comparing current velocities used by both species in the same river, velocities were not significantly different. Mean bottom current velocities used by both species were higher in the Yellowstone River than in the Lower Missouri River. However, since most shovelnose sturgeon locations were in the Yellowstone River, and pallid sturgeon locations were more evenly divided between the Yellowstone River and the Lower Missouri River, the overall mean bottom current velocity for shovelnose sturgeon was significantly higher than for pallid sturgeon. This finding suggests two alternative hypotheses: 1) greater current velocities were available in Yellowstone River and pallid and shovelnose sturgeon were simply using velocities in proportion to velocity distribution, or, 2) current velocities available in the two rivers are the same, but pallid and shovelnose sturgeon use greater current velocities in the Yellowstone River. I have no data to suggest which hypothesis is more appropriate.

Mean bottom current velocities at pallid sturgeon locations in the MRFP were about 0.28 m/s faster than I found (Gardner 1995). Erickson (1992) reported mean bottom current velocities at pallid sturgeon locations in the MRSD which were 0.25 m/s slower for pallid sturgeon < 5 kg and 0.47 m/s slower for pallid sturgeon ≥ 5 kg than for pallid sturgeon in my study. Use of lower velocities in the MRSD may be a result of sturgeon locations in areas of reduced current in the headwaters of Lake Oahe or to overall current velocities available within his study area.

General Distribution

Pallid sturgeon were most often relocated in the Lower Missouri River and the lower 28 km of the Yellowstone River, although they were rarely located as far upstream as the Intake diversion dam on the Yellowstone River (river km 114.4). Pallid sturgeon were not located above Intake diversion dam, which may be a partial barrier to upstream movement. In contrast, telemetered shovelnose sturgeon were found principally in the Yellowstone River, from the Intake diversion dam (river km 114) to the confluence, and only rarely in the Lower Missouri River. Pallid sturgeon showed a pronounced seasonal shift in locations from the lower 28 km of the Yellowstone River in spring and summer to the 28 km of the Lower Missouri River below the confluence in fall and winter. Although individual shovelnose sturgeon changed locations seasonally, the seasonal distribution of all shovelnose sturgeon observations was not markedly different from season to season. Most locations of pallid sturgeon were grouped seasonally, while locations of shovelnose sturgeon during all seasons were less grouped.

Batches of pallid sturgeon that were initially captured at the same general time and location were most clustered in winter, indicating that pallid sturgeon may have specific wintering areas. In contrast, batches of shovelnose sturgeon that were captured at the same general time and location varied with respect to ranks of seasonal clustering, indicating more generalized seasonal habitat use. However, since fewer observations on fewer fish were obtained during fall and winter, these results may be biased toward greater clustering in these seasons. Because of this potential bias, these results should be considered as suggestive only.

All locations of telemetered pallid and shovelnose sturgeon were in riverine habitat, with the exception of one pallid and two shovelnose sturgeon that were observed in altered semi-riverine habitat below Fort Peck dam. No locations of either species were made in non-riverine portions of Lake Sakakawea. However, because radio signals were difficult to receive in deeper water, it is possible that telemetered fish may have used Lake Sakakawea without being detected. However, this is unlikely because pallid and shovelnose sturgeon were rarely located in the vincinity of the headwaters of Lake

Sakakawea. For example, only one individual pallid sturgeon and no shovelnose sturgeon were observed within 10 km of the headwaters of Lake Sakakawea.

Although about 305 km of riverine habitat on the Upper Missouri River from Fort Peck dam to the confluence of the Yellowstone River were available, both species were only rarely located in this reach. Because most fish in the study were initially captured in the Yellowstone River or the Lower Missouri River, this sample of fish may be biased against obtaining locations in the Upper Missouri River. However, since the home range for pallid sturgeon and shovelnose sturgeon was as high as 331 km and 254 km respectively, lack of use of the Upper Missouri River was not likely due to distance from capture location. Also, pallid sturgeon passed the confluence many times, but entered the Yellowstone River rather than the Lower Missouri River significantly more than expected by chance. Biologists also report lower capture rates of pallid and shovelnose sturgeon in the Upper Missouri River than in the Yellowstone River and the Lower Missouri River (Gardner and Stewart 1987; Tews 1994; Liebelt 1995).

Although alternative explanations such as genetically intrinsic homing may explain this preference for the Yellowstone River over the Upper Missouri River, it is likely that it is the result of altered ecological conditions on the Upper Missouri River created by Fort Peck dam. The effects of dams on ecological conditions of large rivers are well known, and a combination of the effects discussed below may account for lack of use of the Upper Missouri River. Dams on the Missouri River have had profound impacts on the ecosystem of the Missouri River which have led to declines in native aquatic and terrestrial communities (Hesse et al. 1989; Hesse et al. 1993; Hesse and Mestl 1993; Hesse and Sheets 1993). For example, declines in 2 species of birds and at least 32 species of fish are partially attributed to the operation of the seven mainstem dams on the Missouri River (Hesse and Mestl 1993; Hesse and Sheets 1993).

Fort Peck dam has affected the amplitude and timing of discharge and thermal regimes and interrupted sediment and organic matter transport. Altered discharge and thermal regimes on the Upper Missouri River may interrupt important environmental cues for timing of pallid and shovelnose sturgeon movements. Discharge and sediment load, together with physiographic setting and history are primary factors controlling the morphology of large alluvial rivers (Kellerhals 1989). Altered river hydrology and sediment dynamics are unstable processes, resulting in a state of flux until these destabilizing processes equilibrate (Hesse and Sheets 1993). Thus, the altered hydrograph and loss of sediment loads below Fort Peck dam will inevitably affect morphology, and therefore habitat for pallid and shovelnose sturgeon in the Lower Missouri River. Dams disrupt the connections of organic matter transport and concomitant faunal assemblages between upstream and downstream reaches emphasized in the river continuum concept (Vannote et al. 1980), thus Fort Peck dam may have impacted food webs in the Upper Missouri River.

The serial discontinuity concept (Ward and Stanford 1983) predicts changes in riverine ecological conditions relative to placement of dams along the river's longitudinal profile and position on the river continuum (Vannote et al. 1980). When a dam is placed on the lower reaches of a river, the water clarity, substrate stability, nutrient levels and nutrient availability, and maximum temperatures shift to values that are more typical of conditions farther upstream in the river (Ward and Stanford 1989). Thus, placement of Fort Peck dam on the lower reaches of the Missouri River in Montana has shifted conditions below the dam towards conditions more typical of river reaches upstream of the pallid sturgeon's native range. Turbidity is important in this system because Missouri River fish species have evolved under conditions of high natural turbidity (Pflieger and Grace 1985). Reduction of turbidity may reduce the ability of pallid sturgeon to feed on other fishes, while enhancing foraging ability of visually oriented non-native predators such as northern pike (*Esox lucius*) and walleye (*Stizostedion vitreum*).

Dams on the Missouri River have lessened floodplain connectivity through reduction of flooding (Hesse and Mestl 1993) The flood pulse concept (Junk et al. 1989) emphasizes the importance of lateral river-floodplain interactions that occur during the "flood pulse", when the floodplain is inundated. The flood pulse concept expounds the idea that flood pulses are the driving force responsible for the existence, productivity, and interactions of the major biota in river-floodplain ecosystems. Hence, reduction of river-floodplain connectivity may reduce productivity of the Lower Missouri River, thereby reducing food supplies for pallid and shovelnose sturgeon.

Damming of the Missouri River has reduced erosion and accretion processes adjacent to the river channel, thereby disrupting the succession of riparian plant communities (Johnson 1993), and reducing the recruitment of snags to the river channel

(Hesse and Mestl 1993). Altered riparian vegetation may affect energy dynamics and morphology of the Lower Missouri River. Large woody debris is important for production of aquatic invertebrates in sand bottomed rivers (Benke et al. 1984).

Aggregations

Pallid and shovelnose sturgeon aggregated most often in spring and early summer in both 1993 and 1994. Because these aggregations occurred during the suspected spawning season, they may be spawning aggregations. Pallid sturgeon aggregations during these periods were in the lower 12 km of the Yellowstone River, as were the relocations of a female pallid sturgeon known to be gravid. Therefore, it is likely that this part of the Yellowstone River is used by pallid sturgeon for spawning.

Potential shovelnose sturgeon spawning aggregations occurred in the Yellowstone River from river km 111.0 to 114.3, which is the reach directly below the Intake diversion dam. Shovelnose sturgeon may use this area for spawning, but also may be concentrated in this area because Intake diversion dam may be a partial barrier to upstream movements (Stewart 1995). Another potential spawning location for shovelnose sturgeon was from river km 24.9 to 25.6 on the Yellowstone River.

Occasional aggregations of pallid and shovelnose sturgeon occurred in fall, but probably because fewer relocations were made in fall, fewer aggregations were identified. However, Tews (1994) using locations of telemetered pallid sturgeon from this study as a guide, captured 39 pallid sturgeon in September and October of 1992 and 1993, in the

Lower Missouri River from river km 2520 to 2533, using trammel and gill nets. For example, in 1992 she captured 20 pallid sturgeon at river km 2531 during 4 d of netting. This included seven pallid sturgeon captured in the same net (Ann Tews, Montana Department of Fish, Wildlife, and Parks, Pers. Comm.).

Home Range, Movement Rates, and Diel Activity

Pallid and shovelnose sturgeon exhibited high vagility, with home ranges of over 300 and 250 linear km of river, respectively, for the two species. Both species were capable of rapid, long-range upstream and downstream movements. Pallid sturgeon moved up to 21 km/d; shovelnose sturgeon moved up to 15 km/d. Most long distance movements occurred in spring and summer. Because pallid and shovelnose sturgeon spawn in late spring to early summer (Forbes and Richardson 1905; Elser et al. 1977; Moos 1978; Berg 1981; Gilbraith et al. 1988; Keenlyne and Jenkins 1993), these movements may be associated with spawning activities. However, because both male and female pallid sturgeon (Keenlyne and Jenkins 1993) and shovelnose sturgeon (Moos 1978) probably do not spawn every year, some of these movements may be related to other factors such as seasonal shifts between overwintering and summer feeding areas.

Pallid sturgeon winter movement rates and ranges of activity were significantly smaller than all other seasonal ranges and movement rates. Shovelnose sturgeon displayed a similar pattern. Because relatively few observations were obtained during the winter seasons, lower movement rates and ranges may have been an artifact of reduced sampling frequency. However, if longer or faster movements actually occurred during winter, sturgeon must have returned to the same areas following movements. It seems more likely that little movement actually occurred.

Reduced activity in cold water months is likely due to temperature-related lowered metabolic states and a concurrent reduction in energy requirements. Water temperatures in the study area reached as low as 0.3 ° C as early as November. Many temperate fish species exhibit reduced activity in cold water temperatures.

The highest proportion of observations on moving pallid sturgeon was during the day, while the highest proportion of observations on moving shovelnose sturgeon was at night. However, because both pallid and shovelnose sturgeon also exhibited movement during other diel periods they cannot be classified as strictly diurnal, nocturnal, or crepuscular. I also observered substanial individual variation in diel movement patterns.

In contrast to the findings of my study, Erickson (1992) found that pallid sturgeon in the MRSD moved more at night than during the day. Increased movement at night in the MRSD may be related to reduced turbidity. Secchi disk depths in the MRSD ranged as high as 400 cm, while in the present study Secchi disk depths at pallid sturgeon locations averaged 20 cm and only rarely exceeded 100 cm. Since the MRSD study area begins directly below a dam and proceeds downstream into a reservoir, presumably sediment load and turbidity is much reduced from natural conditions. Therefore, in the absence of light attenuation by natural turbidity, pallid sturgeon may shift to a nocturnal activity pattern. In my study, a model was constructed that indicated that the predicted depth of pallid sturgeon was greater with hours following sunrise, when brighter conditions would prevail. Although this model was not statistically significant (*P* = 0.1268), it is suggestive that pallid sturgeon may be photophobic.

Movement Patterns

Regression models suggest that discharge and photoperiod may be important environmental cues for timing of movements by pallid and shovelnose sturgeon. Large amounts of variability (up to 97%) in river km location were explained by regression models using discharge and photoperiod as predictor variables.

Movement patterns varied between pallid and shovelnose sturgeon. For example, most pallid sturgeon were located farther upstream in the Yellowstone River with increasing discharge but the majority of shovelnose sturgeon were located farther downstream with increasing discharge. Differences between species were also evident in regression models using photoperiod as the predictor variable. In addition to differences between species, regression models indicated that response (movement up or downstream) varied among individuals within species.

As discussed above, because pallid sturgeon and shovelnose sturgeon probably do not spawn every year, this diversity of movement patterns within species may be related to the spawning condition of the individual fish. Thus, movement patterns may be different in spawning and non-spawning years. However, one individual pallid sturgeon (frequency 49.680) that was observed over 3 years had similar movement patterns each year. Therefore, if one of these years was a spawning year, its spawning year moment patterns were similar to non-spawning years.

Direction of movement for pallid sturgeon predicted by regression models relative to discharge varied among river segments (Yellowstone, Upper and Lower Missouri rivers). For example, while the majority of models for individual pallid sturgeon predicted upstream movement in the Yellowstone River relative to increasing discharge, all models predicted downstream movement relative to increasing discharge for pallid sturgeon in the Lower Missouri River. However, most models for individual pallid sturgeon predicted upstream movement relative to increasing photoperiod, regardless of river segment.

These results are congruous with the seasonal shifts exhibited by most pallid sturgeon. A typical pattern of movement for pallid sturgeon is movement upstream out of the Lower Missouri River in early spring, a period of increasing photoperiod and generally low discharge. At the time that most pallid sturgeon enter and move upstream in the Yellowstone River, discharge is increasing from the annual snowmelt, and photoperiod continues to increase. A period of residency in the Yellowstone River ensues, which includes the summer solstice (June 21), and relatively high discharge. Following this period of residency in the Yellowstone River, most pallid sturgeon moved downstream into the Lower Missouri River, during a period of decreasing photoperiod. By the time that pallid sturgeon reach their most downstream point in the Lower Missouri River in late summer, discharge is higher than it was when they entered the Yellowstone

River. Hence, movement in the Lower Missouri River is downstream relative to discharge, and upstream relative to photoperiod. Movement in the Yellowstone River is upstream with increasing discharge, and upstream with increasing photoperiod. The potential influence of temperature and tubidity on movements are not known.

Pallid sturgeon movements in the MRFP have been studied by radio telemetry (Gardner 1994). Movement patterns in this area are similar in that summer locations are the highest upstream locations and movement rates were highest in summer. Gardner (1995) also reports that pallid sturgeon moved farther upstream during years with higher discharge.

Ranges of activity for pallid sturgeon in the MRFP were fairly large. Average distance moved was 63 river km and the maximum home range was 98 river km. These ranges are smaller than I observed, which averaged 80 river km and were as large as 331 river km. The substrate of the MRFP in the downstream reaches is primarily sand and small gravel. Substrates change to predominately cobble by about 79 km upstream of the Fort Peck Reservoir headwaters (Gardner 1994). Pallid sturgeon are typically associated with sand substrates and strong current (Bailey and Cross 1954; Carlson et al 1985; this study). Thus, ranges of activity in the MRFP may be smaller than those observed in the present study because reduction of current velocities in the headwaters of Fort Peck Reservoir mark the usual downstream limit of pallid sturgeon distribution while the usual upstream limit is marked by the transition from sand-dominated to cobble-dominated substrates.

A telemetry study of pallid sturgeon in the MRSD found similar movement characteristics to those I found, as well as some differences (Erickson 1992). Pallid sturgeon in the MRSD had smaller ranges of activity, ranging to about 66 river km. However, the length of the reach in the South Dakota study area is only about 137 km between dams, and the lower portion of this reach is essentially lentic. Therefore, smaller ranges of activity for pallid sturgeon in the MRSD may be a function of a reduction of suitable riverine habitat.

As found in the current study, pallid sturgeon movements in the MRSD were related to discharge and pallid sturgeon also exhibited individual variation in direction of movement relative to discharge. Also concordant with my findings, Erickson (1992) observed that moment rates of pallid sturgeon were lowest in winter months and a significant positive correlation between water temperatures and movement rate of pallid sturgeon existed.

Researchers in the upper Mississippi River (Helms 1974; Hurley et al. 1987; Curtis 1990) report ranges of activity that averaged up to 18.5 for shovelnose sturgeon, which is smaller than the overall mean of 53.1 km that I observed. However these observations were primarily in the navigation pools of the Mississippi River, a series of essentially lentic pools with upstream riverine reaches, separated by locks and dams (Fremling et al. 1989) which may at least seasonally restrict movement of shovelnose sturgeon. As in the present study, the longest movements observed in studies from the upper Mississippi River (Helms 1974; Hurley et al. 1987; Curtis 1990), and a study in the

Missouri River (Moos 1978) were in spring. Modest movement was also reported for shovelnose sturgeon in the Red Cedar/Chippewa River system in Wisconsin (Christenson 1975). However, some reports in the literature for the Missouri River indicate long-range movements for shovelnose sturgeon of up to 250 km (Moos 1978) and 534 km (Schmulbach 1974).

Tews (1994) recaptured a shovelnose sturgeon in the Lower Missouri River 12 years after it was tagged in the Tongue River, 300 km upstream. Gardner and Stewart (1987) report that two shovelnose sturgeon tagged in the Yellowstone River were recaptured in the Upper Missouri River, over 400 km away from the tagging site. Hence, my findings and the reports from the Yellowstone River and Missouri River indicate that when large reaches of unobstructed river are available, shovelnose sturgeon are capable of very long range movements.

Macrohabitat

Pallid sturgeon were more specific and restrictive in use of macrohabitat categories than were shovelnose sturgeon. Pallid sturgeon were found most often in sinuous channels with islands or alluvial bars present. Straight channels, and channels with irregular patterns or irregular meanders were only rarely used by pallid sturgeon. Seral stage of islands or bars near pallid sturgeon was most often subclimax.

Like pallid sturgeon, shovelnose sturgeon were found most often in sinuous channels. However, in contrast to pallid sturgeon, shovelnose sturgeon were also frequently located in straight and irregular channels. Shovelnose sturgeon were also found more often in reaches without islands or alluvial bars than were pallid sturgeon. Also in contrast to pallid sturgeon, the distribution of seral stage of islands or bars near shovelnose sturgeon locations was more evenly spread across seral stages, including cottonwood gallery forest.

For locations in spring and summer, pallid sturgeon as a species, as well as the majority of individual pallid sturgeon, had a statistically significant preference for reaches with frequent islands, and avoided one or more categories of lesser or greater island density. The reaches with frequent islands that were used most often by pallid sturgeon were located primarily in the lower 20 km of the Yellowstone River. Although reaches with frequent islands were found farther upstream, they may not have been used by pallid sturgeon because sand substrate is diminished in these reaches. In contrast, shovelnose sturgeon were less specific with respect to use of island density categories. Because few statistically significant results were obtained for the island density use versus availability analysis less of a trend was evident for shovelnose sturgeon.

Because use of macrohabitats by pallid sturgeon was more specific and restrictive than shovelnose sturgeon, features in these macrohabitats may be more important to pallid sturgeon than to shovelnose sturgeon. Macrohabitats used by pallid sturgeon were diverse and dynamic. For example, river reaches with sinuous channel patterns and islands and alluvial bars generally have more diversity of depths, current velocities, and substrates than do relatively straight channels without islands or alluvial bars. Diversity of channel features such as backwaters and side channels is also higher. Subclimax riparian vegetational seres are indicative of a dynamic river channel and riparian zone (Johnson 1993). Because pallid sturgeon did not prefer the highest island density categories or channel patterns with the highest sinuosity, factors such as substrates or depths may limit pallid sturgeon use of these reaches.

Differences in macrohabitat use between pallid and shovelnose sturgeon may be related to differences in spawning requirements of the two species. Hybrids have not been documented in my study area, but they have been found in areas more impacted by loss of habitat diversity (Carlson et al. 1985; Dryer and Sandvol 1993; Keenlyne et al. 1993). Therefore, loss of a diversity of macrohabitats may lead to hybridization via a loss of habitat-related isolating mechanisms (Carlson et al. 1985).

Alternatively, or in addition to factors related to reproductive isolation, these macrohabitats may provide a better food base for pallid sturgeon. Although the data are limited, Carlson et al. (1985) report that the diet of pallid sturgeon includes more fish (primarily cyprinids) than the diet of shovelnose sturgeon. Therefore, pallid sturgeon are on a higher trophic level than the more insectivorous shovelnose sturgeon.

Ecological theory predicts that spatially heterogeneous habitats will support more species than homogeneous habitats (Pianka 1988; Allan 1995), which has been demonstrated for stream fish (Gorman and Karr 1978). Thus, more diverse river macrohabitats may support a more diverse fish community that in turn provides more food for pallid sturgeon. Cyprinids such as flathead chub (*Platygobio gracilis*), sturgeon chub (*Macrhybopsis gelida*), and sicklefin chub (*M. meeki*) are benthic fish that occur in the study area that are among the potential prey species for pallid sturgeon. Although little information on their life histories exists, it is likely that a diversity of habitat features such as backwaters and side channels are beneficial to production of these cyprinid species (Werdon 1993a; 1993b). Backwaters are particularly important habitats for fish production; although backwaters may comprise only 10% of the habitat, they may contain as much as 90% of the fish in a large river (Stalnaker et al. 1993).

Since pallid sturgeon feed at a higher trophic level than shovelnose sturgeon, they are part of a more complex food web, and may require more diverse habitats. Piscivorous fish are generally more susceptible to habitat degradation and homogenization than fish at lower trophic levels (Karr 1991). In contrast, the largely insectivorous shovelnose sturgeon may find adequate food supplies in a variety of macrohabitat types, including relatively simple habitats. Thus, severed links between trophic levels via loss of diverse riverine habitats may partially explain why pallid sturgeon have declined more than shovelnose sturgeon.

Water chemistry

Water chemistry and temperatures at locations of the two species were similar. Large rivers are chemically homogenous over moderate spatial scales, and are also not thermally stratified due to turbulent mixing of the water column (Hynes 1970, Ryder and Pesendorfer 1989). Therefore, over moderate spatial scales, it is not expected that pallid and shovelnose sturgeon select areas of widely divergent water chemistry and temperature. However, diel and seasonal temperature fluctuations occur, as well as seasonal changes in water physicochemical parameters such as turbidity and conductivity. Therefore, any differences in water chemistry and temperatures measured at locations of the two species are more likely a result of the temporal distribution of samples rather than spatial segregation. Further, the large latitudinal range of these two species indicates that they are eurythermal.

Daily water temperatures were lower significantly more than 50% of the time from late May though late November, 1993 in the Upper Missouri River than in the Yellowstone River. Flow regulation at Fort Peck dam flattens the hydrograph and removes peak flows associated with spring runoff. Sediment load and suspended sediment are higher in the Yellowstone River than in the Upper Missouri River, probably because releases from Fort Peck dam are free of sediment.

Summary of Findings

The most conspicuous feature of habitat use by pallid and shovelnose sturgeon in this study area was the lack of use of the Upper Missouri River. Altered ecological conditions on the Upper Missouri River resulting from the construction of Fort Peck dam may explain the lack of use of this habitat and emphasize the importance of natural river dynamic processes for these two species.

Habitat use and movements of pallid and shovelnose sturgeon were similar in some respects but important differences were found. Variation among individuals with respect to habitat use and movements of both species was also observed. Differences between habitat use and movements of pallid and shovelnose sturgeon in this study area and as reported in other studies may be related to local conditions. Pallid sturgeon preferred moderately diverse macrohabitat, sandy substrates and used greater depths and reaches with greater channel widths than shovelnose sturgeon. Shovelnose sturgeon used a wider variety of macrohabitats, gravel and cobble substrates and lesser depths than pallid sturgeon. Use of current velocities and water chemistry parameters were similar for the two species. Movement patterns for pallid and shovelnose sturgeon were different, but ranges of activity and movement rates were similar. Discharge and photoperiod may be important environmental cues for the timing of movements for both species. Because of the differences in habitat use and movements between the two species, adult shovelnose sturgeon appear to be of limited utility as an adult pallid sturgeon surrogate.

Implications for Recovery

Large, free flowing, sandy, diverse and dynamic riverine habitats were most used by pallid sturgeon. These habitats are provided for and maintained in a dynamic equilibrium by physical processes in large, undammed rivers. The Yellowstone/Lower Missouri River is the only river of this type remaining in the original range of the pallid sturgeon, and the lower 12 km of the Yellowstone River may provide spawning habitat for pallid sturgeon. Hence, the Yellowstone/Lower Missouri River represents critical habitat for pallid sturgeon and must be maintained in its present state. However, the apparent lack of recruitment to this population suggests that this habitat alone may not be sufficient for production of all life stages of pallid sturgeon.

The Upper Missouri River and Lake Sakakawea currently appear to be largely unsuitable as habitat for pallid sturgeon. To recover the Upper Missouri River to conditions capable of producing and sustaining pallid sturgeon it will be necessary to restore the physical conditions and processes such as hydrology, thermal regime and sediment dynamics that have been disrupted by Fort Peck dam. Also, because pallid sturgeon showed a distinct preference for riverine over reservoir habitats, it is important to maintain as much riverine habitat as possible. During this study, about 25 km of riverine habitat was present downstream of the US Highway 85 bridge, which would be innundated if Lake Sakakawea was at full pool. Maintaining the level of Lake Sakakawea at a lower elevation would preserve this area as potential pallid sturgeon habitat.

The long-range movements pallid sturgeon I observed coupled with the insularization of their habitat lead to concerns within the framework of metapopulation dynamics. Pallid sturgeon habitat along the entire length of the Missouri and Mississippi rivers has been fragmented by dams and perhaps by other habitat alterations such as channelization. For example, the Pallid sturgeon Recovery Plan (Dryer and Sandvol

1993) identifies six areas besides this study area where pallid sturgeon are frequently found. All six of these areas are separated from each other by dams, locks or channelized reaches. Although it is not known if the historical population structure of pallid sturgeon along the Mississippi and Missouri rivers was continuous, it is certain that the population has now been fragmented, particularly on the Missouri River. Thus, my findings of long-range movements lend support to the idea that connectivity between pallid sturgeon sub-populations may need to be restored (Dryer and Sandvol 1993).

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APPENDIX

Table 32. Summary of models of individual pallid sturgeon locations (river km) with discharge as the dependent variable in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. YS = Yellowstone River; UM = Upper Missouri River; LM = Lower Missouri River.

Frequency	Parameter	Estimate	*P* Parameter[a]	r^2	*P* Model
49.830	Intercept	6.3395		0.9655	0.0001
	Flow YS	0.0001	0.0008		
	Flow UM				
	Flow LM	-0.0761	0.0001		
49.030	Intercept	-11.1352		0.9174	0.0001
	Flow YS	0.0184	0.0001		
	Flow UM				
	Flow LM	-0.0334	0.0001		
49.070	Intercept	12.9879		0.8784	0.0002
	Flow YS	0.0102	0.0001		
	Flow UM				
	Flow LM	-0.1228	0.0082		
49.370	Intercept	-14.4350		0.8219	0.0001
	Flow YS	0.0501	0.0012		
	Flow UM				
	Flow LM	-0.0452	0.0001		
49.020	Intercept	35.9649		0.8136	0.0001
	Flow YS	-0.0241	0.0008		
	Flow UM				
	Flow LM	-0.1663	0.0001		
49.810	Intercept	13.0259		0.8127	0.0001
	Flow YS	-0.0071	0.0004		
	Flow UM				
	Flow LM	-0.0778	0.0001		
49.870	Intercept	340.0482		0.7383	0.0014
	Flow YS				
	Flow UM	-0.3146	0.0014		
	Flow LM				

Table 32. Continued...

Frequency	Parameter	Estimate	*P* Parameter[a]	r^2	*P* Model
49.050	Intercept	-6.6757		0.6963	0.0001
	Flow YS	0.0131	0.0001		
	Flow UM				
	Flow LM	-0.0278	0.0001		
49.680	Intercept	-15.9511		0.6855	0.0001
	Flow YS	0.0222	0.0001		
	Flow UM				
	Flow LM	-0.0257	0.0001		
49.130	Intercept	40.8722		0.6738	0.0001
	Flow YS	-0.0278	0.3829		
	Flow UM				
	Flow LM	-0.1106	0.0001		
49.350	Intercept	19.8321		0.6528	0.0018
	Flow YS	-0.0141	0.6624		
	Flow UM				
	Flow LM	-0.0636	0.0005		
49.650	Intercept	-17.3635		0.6453	0.0001
	Flow YS	0.0382	0.001		
	Flow UM	0.02309	0.1096		
	Flow LM	-0.0304	0.0001		
49.630	Intercept	84.5726		0.6293	0.0001
	Flow YS	-0.1250	0.0015		
	Flow UM				
	Flow LM	-0.1291	0.0001		
49.100	Intercept	-66.7469		0.6078	0.0001
	Flow YS	0.0818	0.0001		
	Flow UM				
	Flow LM	-0.0552	0.0001		
49.712	Intercept	-24.6091		0.5925	0.0005
	Flow YS	0.0533	0.0011		
	Flow UM				
	Flow LM	-0.0379	0.0071		

Table 32. Continued...

Frequency	Parameter	Estimate	*P* Parameter[a]	r^2	*P* Model
48.580	Intercept	-24.8312		0.5243	0.0116
	Flow YS	0.04169			
	Flow UM				
	Flow LM	-0.0440	0.2582		
49.850	Intercept	44.6641		0.4167	0.0396
	Flow YS	-0.0040	0.3872		
	Flow UM	0.0778	0.2802		
	Flow LM	-0.1009	0.0101		
49.170	Intercept	-7.6672		0.3275	0.0281
	Flow YS	0.0089	0.0294		
	Flow UM				
	Flow LM	-0.0096	0.0921		

[a] *P*-values are included as descriptive measures of apparent importance of predictors of river km location.

Table 33. Summary of models of individual shovelnose sturgeon locations (river km) with discharge as the dependent variable in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994. YS = Yellowstone River; UM = Upper Missouri River; LM = Lower Missouri River.

Frequency	Parameter	Estimate	*P* Parameter[a]	r^2	*P* Model
48.280	Intercept	57.6741		0.9046	0.0001
	Flow YS	-0.0598	0.0014		
	Flow UM	0.8409	0.0001		
	Flow LM				
48.550	Intercept	115.6034		0.8518	0.0001
	Flow YS	-0.1024	0.0001		
	Flow UM				
	Flow LM				
48.340	Intercept	87.4615		0.8470	0.0001
	Flow YS	-0.1202	0.0001		
	Flow UM				
	Flow LM				
48.300	Intercept	53.9876		0.8100	0.0001
	Flow YS	-0.0545	0.0001		
	Flow UM				
	Flow LM				
48.380	Intercept	67.9794		0.7460	0.0001
	Flow YS	-0.0758	0.0001		
	Flow UM				
	Flow LM				
48.590	Intercept	109.6311		0.7260	0.0001
	Flow YS	-0.0851	0.0001		
	Flow UM				
	Flow LM				
48.680	Intercept	-19.0288		0.6530	0.0001
	Flow YS	0.2765	0.0001		
	Flow UM				
	Flow LM	-0.2112	0.0722		

Table 33. Continued...

Frequency	Parameter	Estimate	*P* Parameter[a]	r^2	*P* Model
48.580	Intercept	-24.8312		0.5243	0.001
	Flow YS	0.0417	0.0049		
	Flow UM				
	Flow LM	-0.0440	0.2582		
48.940	Intercept	49.9168		0.4941	0.0001
	Flow YS	0.0414	0.0002		
	Flow UM				
	Flow LM	-0.2033	0.0001		
48.660	Intercept	38.7259		0.3810	0.0065
	Flow YS	0.0420	0.1269		
	Flow UM				
	Flow LM	-0.2007	0.0041		
48.880	Intercept	115.2167		0.3629	0.0049
	Flow YS	-0.0043	0.0049		
	Flow UM				
	Flow LM				
48.860	Intercept	102.0889		0.2793	0.0003
	Flow YS	-0.0212	0.0003		
	Flow UM				
	Flow LM				

[a] *P*-values are included as descriptive measures of apparent importance of predictors of river km location.

Table 34. Summary of models of individual pallid sturgeon locations (river km) with photoperiod as the dependent variable in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Frequency	Parameter	Estimate	*P* model[a]	r^2
48.562	Intercept	2620.5714		0.8696
	Photoperiod	-162.9328	0.0067	
48.580	Intercept	-245.3105		0.7704
	Photoperiod	16.3709	0.0001	
49.810	Intercept	-60.9048		0.7301
	Photoperiod	4.2983	0.0001	
49.070	Intercept	-104.7537		0.7162
	Photoperiod	7.8461	0.0010	
49.020	Intercept	-85.4487		0.6811
	Photoperiod	6.4347	0.0001	
49.170	Intercept	-62.9181		0.6345
	Photoperiod	4.0661	0.0001	
49.680	Intercept	-67.7128		0.6122
	Photoperiod	4.3081	0.0001	
49.830	Intercept	-140.3068		0.5591
	Photoperiod	9.3348	0.0129	
49.050	Intercept	-42.8311		0.5526
	Photoperiod	2.9789	0.0001	
49.870	Intercept	430.4658		0.4812
	Photoperiod	-10.8220	0.0261	
49.712	Intercept	-67.9483		0.4395
	Photoperiod	4.5872	0.0014	
49.030	Intercept	-81.1614		0.3911
	Photoperiod	5.2258	0.0001	
49.650	Intercept	-52.5973		0.3887
	Photoperiod	3.3023	0.0002	

Table 34. Continued...

Frequency	Parameter	Estimate	P model[a]	r^2
49.630	Intercept	-86.3660		0.2892
	Photoperiod	7.2503	0.0056	
49.130	Intercept	-63.9968		0.2194
	Photoperiod	5.3939	0.0158	
49.100	Intercept	-128.2188		0.1468
	Photoperiod	6.2393	0.0066	

[a] *P*-values are included as descriptive measures of apparent importance of predictors of river km location.

Table 35. Summary of models of individual shovelnose sturgeon locations (river km) with photoperiod as the dependent variable in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992-1994.

Frequency	Parameter	Estimate	*P* model[a]	r^2
48.590	Intercept	676.6348		0.8884
	Photoperiod	-41.0708	0.0001	
48.640	Intercept	70.3922		0.7838
	Photoperiod	2.6916	0.0001	
48.280	Intercept	489.9956		0.7754
	Photoperiod	-28.9324	0.0001	
48.940	Intercept	-158.6374		0.7224
	Photoperiod	15.5886	0.0001	
48.550	Intercept	261.5455		0.6625
	Photoperiod	-15.0191	0.0002	
48.600	Intercept	89.5538		0.5925
	Photoperiod	1.4793	0.0430	
48.840	Intercept	-237.4842		0.4968
	Photoperiod	21.6594	0.0023	
48.660	Intercept	-62.3809		0.4766
	Photoperiod	8.4612	0.0002	
48.860	Intercept	140.3791		0.4017
	Photoperiod	-3.4246	0.0001	
48.620	Intercept	-21.5770		0.3068
	Photoperiod	6.1979	0.0041	
48.900	Intercept	31.7595		0.1298
	Photoperiod	4.0594	0.0224	

[a] *P*-values are included as descriptive measures of apparent importance of predictors of river km location.

Table 36. Summary of models of individual pallid sturgeon locations (river km) with discharge and photoperiod as the dependent variables in the Yellowstone and Missouri rivers in Montana and North Dakota ,992-1994. YS = Yellowstone River; UM = Upper Missouri River; LM = Lower Missouri River.

Frequency	Parameter	Estimate	*P* Parameter[a]	r^2	*P* Model
49.830	Intercept	-26.2175		0.9705	0.0001
	Photoperiod	2.2859	0.0001		
	Flow YS	-0.0036	0.0023		
	Flow LM	-0.0692	0.0003		
	Flow UM				
49.030	Intercept	-31.1872		0.9346	0.0001
	Photoperiod	1.6626	0.0001		
	Flow YS	0.0119	0.0164		
	Flow LM	-0.0319	0.0001		
	Flow UM				
48.562	Intercept	3149.3078		0.9078	0.0280
	Photoperiod	-193.6969	0.0130		
	Flow YS	-0.0747	0.3462		
	Flow LM				
	Flow UM				
49.130	Intercept	-70.8851		0.8856	0.0001
	Photoperiod	9.8036	0.0001		
	Flow YS	-0.0740	0.0001		
	Flow LM	-0.0680	0.0001		
	Flow UM				
49.070	Intercept	-3.1234		0.8827	0.0012
	Photoperiod	1.4278	0.0003		
	Flow YS	0.0032	0.2087		
	Flow LM	-0.1146	0.0254		
	Flow UM				
49.370	Intercept	-23.9987		0.8438	0.0001
	Photoperiod	0.9033	0.0004		
	Flow YS	0.0435	0.0902		
	Flow LM	-0.0442	0.0001		
	Flow UM				

Table 36. Continued...

Frequency	Parameter	Estimate	*P* Parameter[a]	r^2	*P* Model
48.580	Intercept	-351.2286		0.8327	0.0001
	Photoperiod	25.2752	0.0001		
	Flow YS	-0.0399	0.0715		
	Flow LM	-0.0084	0.7349		
	Flow UM				
49.810	Intercept	-40.8029		0.8261	0.0001
	Photoperiod	3.7886	0.0001		
	Flow YS	-0.0132	0.0065		
	Flow LM	-0.0292	0.5014		
	Flow UM				
49.020	Intercept	19.8259		0.8139	0.0001
	Photoperiod	1.0987	0.0001		
	Flow YS	-0.0253	0.0121		
	Flow LM	-0.1487	0.2131		
	Flow UM				
49.680	Intercept	-45.2498		0.7821	0.0001
	Photoperiod	2.5878	0.0001		
	Flow YS	0.0090	0.1145		
	Flow LM	-0.0120	0.0001		
	Flow UM				
49.870	Intercept	274.7077		0.7734	0.0055
	Photoperiod	6.7662	0.0062		
	Flow YS				
	Flow LM				
	Flow UM	-0.4578	0.0198		
49.050	Intercept	-26.8210		0.7660	0.0001
	Photoperiod	1.9655	0.0001		
	Flow YS	0.0017	0.8867		
	Flow LM	-0.0235	0.0001		
	Flow UM				

Table 36. Continued...

Frequency	Parameter	Estimate	*P* Parameter[a]	r^2	*P* Model
49.170	Intercept	-75.1469		0.7313	0.0001
	Photoperiod	5.4154	0.0001		
	Flow YS	-0.0093	0.0485		
	Flow LM	-0.0046	0.2218		
	Flow UM				
49.350	Intercept	-8.0533		0.7026	0.0031
	Photoperiod	1.9872	0.0222		
	Flow YS	-0.0191	0.5623		
	Flow LM	-0.0584	0.0012		
	Flow UM				
49.650	Intercept	-31.9931		0.6799	0.0001
	Photoperiod	1.2531	0.0001		
	Flow YS	0.0296	0.1044		
	Flow LM	-0.0262	0.0002		
	Flow UM	0.0127	0.5760		
49.630	Intercept	-4.8591		0.6420	0.0001
	Photoperiod	5.7454	0.0005		
	Flow YS	-0.1263	0.0002		
	Flow LM	-0.0479	0.6289		
	Flow UM				
49.100	Intercept	-63.6713		0.6080	0.0001
	Photoperiod	-0.2605	0.0002		
	Flow YS	0.0830	0.0181		
	Flow LM	-0.0554	0.0001		
	Flow UM				
49.712	Intercept	-37.2640		0.5991	0.0018
	Photoperiod	1.0080	0.0007		
	Flow YS	0.0480	0.0632		
	Flow LM	0.0302	0.1419		
	Flow UM				

[a] *P*-values are included as descriptive measures of apparent importance of predictors of river km location.

Table 37. Summary of models of individual shovelnose sturgeon locations (river km) with discharge and photoperiod as the dependent variables in the Yellowstone and Missouri rivers in Montana and North Dakota , 1992-1994. YS = Yellowstone River; UM = Upper Missouri River; LM = Lower Missouri River.

Frequency	Parameter	Estimate	*P* Parameter[a]	r^2	*P* Model
48.280	Intercept	233.4420		0.9566	0.0001
	Photoperiod	-11.8690	0.0001		
	Flow YS	-0.0380	0.2218		
	Flow LM				
	Flow UM	0.5990	0.0001		
48.340	Intercept	567.9087		0.9228	0.0001
	Photoperiod	-30.4603	0.0275		
	Flow YS	-0.1231	0.0001		
	Flow LM				
	Flow UM				
48.940	Intercept	-141.5530		0.9071	0.0001
	Photoperiod	16.3615	0.0001		
	Flow YS	-0.0394	0.0003		
	Flow LM	-0.1469	0.0001		
	Flow UM				
48.590	Intercept	615.5848		0.8918	0.0001
	Photoperiod	-36.4979	0.0001		
	Flow YS	-0.0120	0.5979		
	Flow LM				
	Flow UM				
48.550	Intercept	151.3812		0.8621	0.0001
	Photoperiod	-3.2582	0.0001		
	Flow YS	-0.0863	0.0013		
	Flow LM				
	Flow UM				
48.380	Intercept	425.3623		0.8529	0.0001
	Photoperiod	-22.5683	0.1970		
	Flow YS	-0.0810	0.0001		
	Flow LM				
	Flow UM				

Table 37. Continued...

Frequency	Parameter	Estimate	*P* Parameter[a]	r^2	*P* Model
48.300	Intercept	68.2170		0.8138	0.0001
	Photoperiod	-0.9560	0.0034		
	Flow YS	-0.0530	0.0001		
	Flow LM				
	Flow UM				
48.680	Intercept	-96.3097		0.7913	0.0001
	Photoperiod	8.4570	0.0001		
	Flow YS	0.1553	0.0085		
	Flow LM	-0.2003	0.0361		
	Flow UM				
48.640	Intercept	70.1502		0.7842	0.0001
	Photoperiod	2.7323	0.0001		
	Flow YS	-0.0009	0.8377		
	Flow LM				
	Flow UM				
48.660	Intercept	-60.1263		0.7798	0.0001
	Photoperiod	10.0010	0.0001		
	Flow YS	-0.0510	0.0581		
	Flow LM	-0.1848	0.0001		
	Flow UM				
48.820	Intercept	-353.2371		0.7559	0.0294
	Photoperiod	26.8367	0.8544		
	Flow YS	0.0818	0.0111		
	Flow LM				
	Flow UM				
48.840	Intercept	-308.7204		0.6698	0.0007
	Photoperiod	27.0151	0.0007		
	Flow YS	-0.0280	0.0216		
	Flow LM				
	Flow UM				

Table 37. Continued...

Frequency	Parameter	Estimate	*P* Parameter[a]	r^2	*P* Model
48.880	Intercept	94.6273		0.5709	0.0008
	Photoperiod	1.3982	0.7163		
	Flow YS	-0.0072	0.0002		
	Flow LM				
	Flow UM				
48.860	Intercept	134.3010		0.4273	0.0001
	Photoperiod	-2.7049	0.0001		
	Flow YS	-0.0083	0.1891		
	Flow LM				
	Flow UM				
48.900	Intercept	-2.4809		0.4062	0.0001
	Photoperiod	8.0979	0.0072		
	Flow YS	-0.0463	0.0002		
	Flow LM				
	Flow UM				
48.620	Intercept	-25.7874		0.3110	0.0166
	Photoperiod	6.8506	0.0049		
	Flow YS	-0.0135	0.7178		
	Flow LM				
	Flow UM				

[a] *P*-values are included as descriptive measures of apparent importance of predictors of river km location.

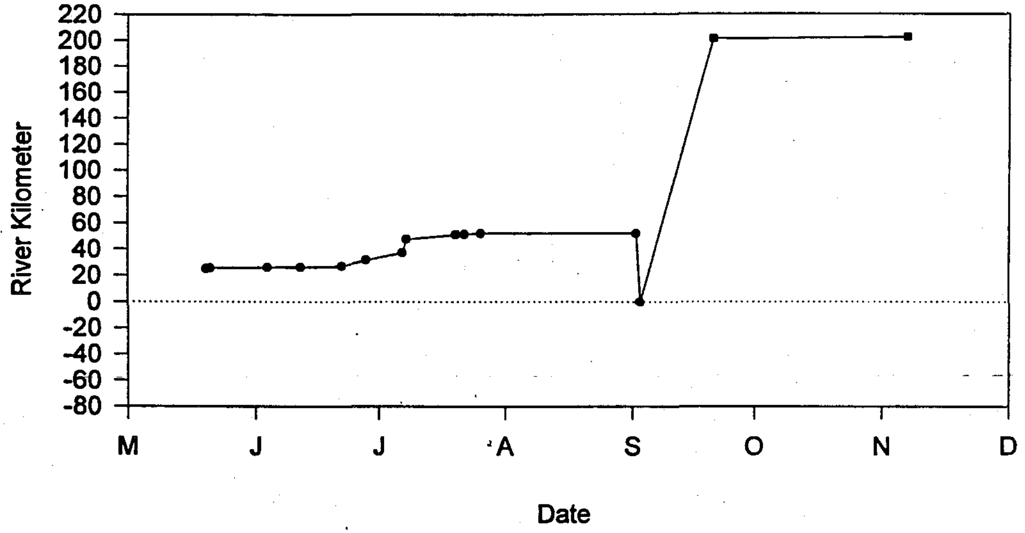

Figure 35. Movements of shovelnose sturgeon 48.280 in the Yellowstone and Missouri rivers in Montana and North Dakota during 1992-1994. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River. Square symbols indicate locations in the Upper Missouri River.

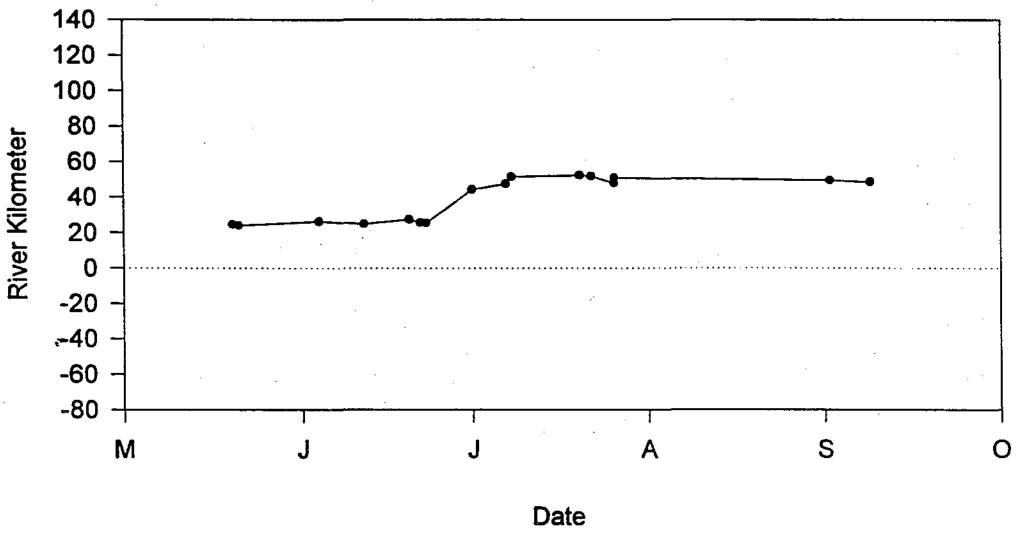

Figure 36. Movements of shovelnose sturgeon 48.300 during 1994 in the Yellowstone River, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

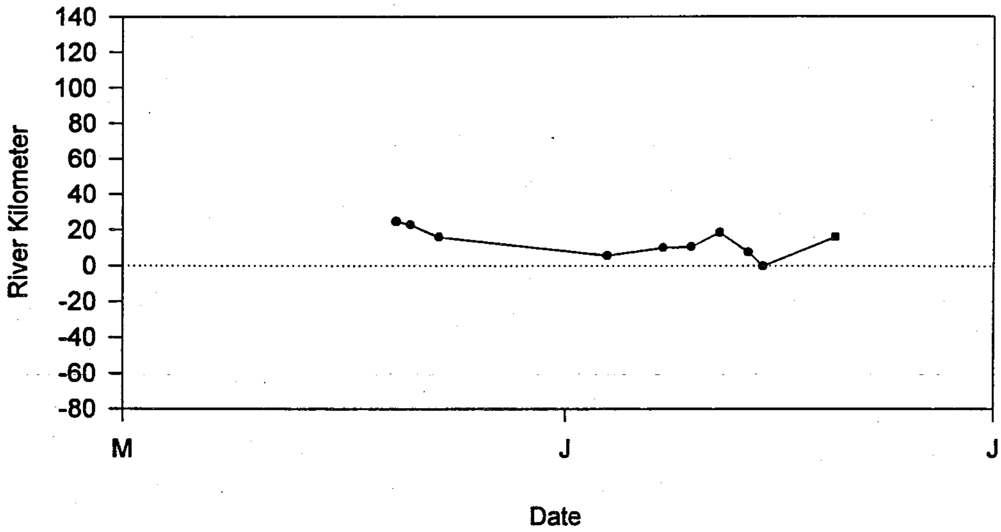

Figure 37. Movements of shovelnose sturgeon 48.320 during 1994 in the Yellowstone and Missouri Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River. Square symbols indicate locations in the Upper Missouri River.

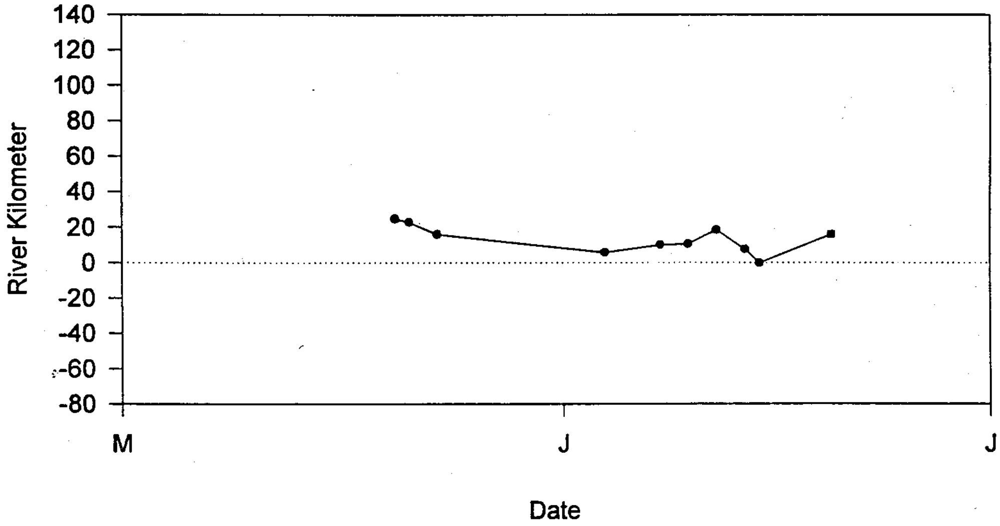

Figure 38. Movements of shovelnose sturgeon 48.340 during 1994 in the Yellowstone River, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

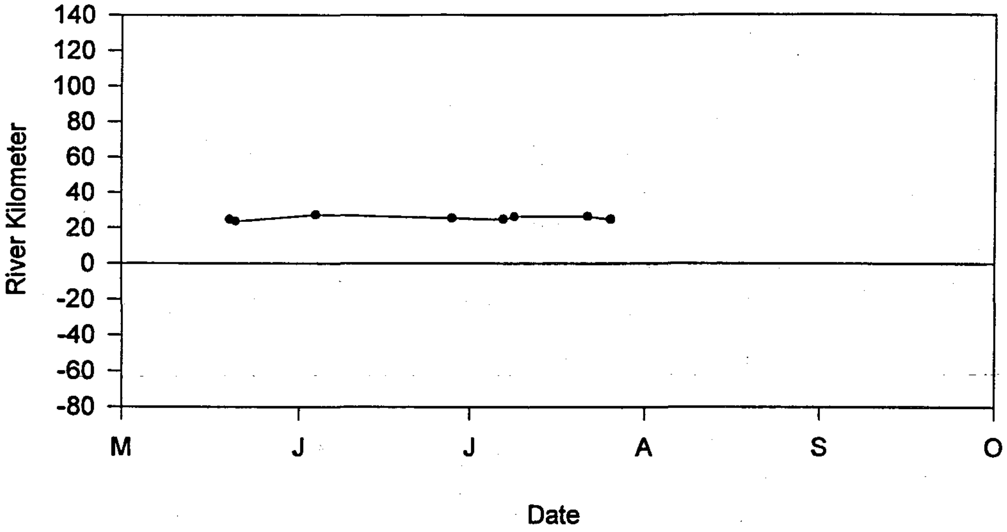

Figure 39. Movements of shovelnose sturgeon 48.360 during 1994 in the Yellowstone River, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

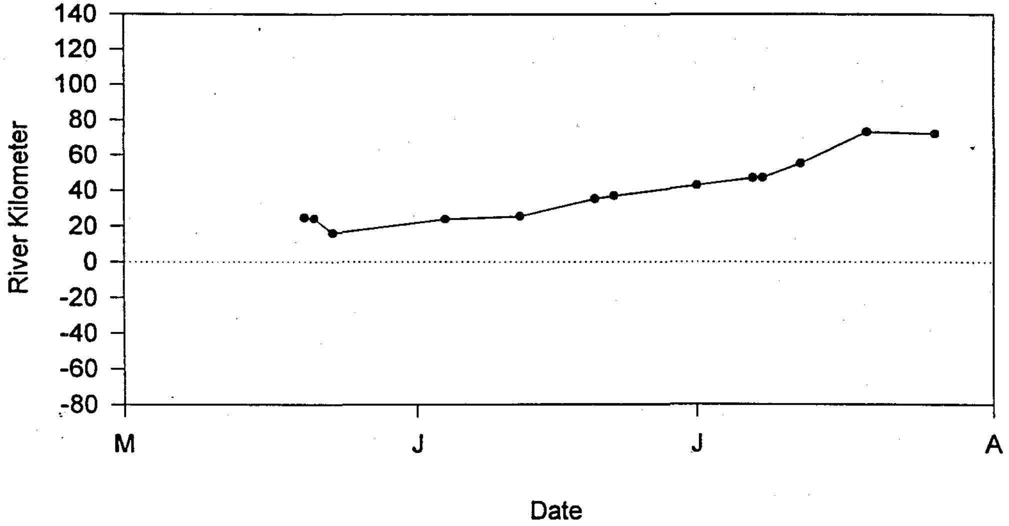

Figure 40. Movements of shovelnose sturgeon 48.380 during 1994 in the Yellowstone River, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

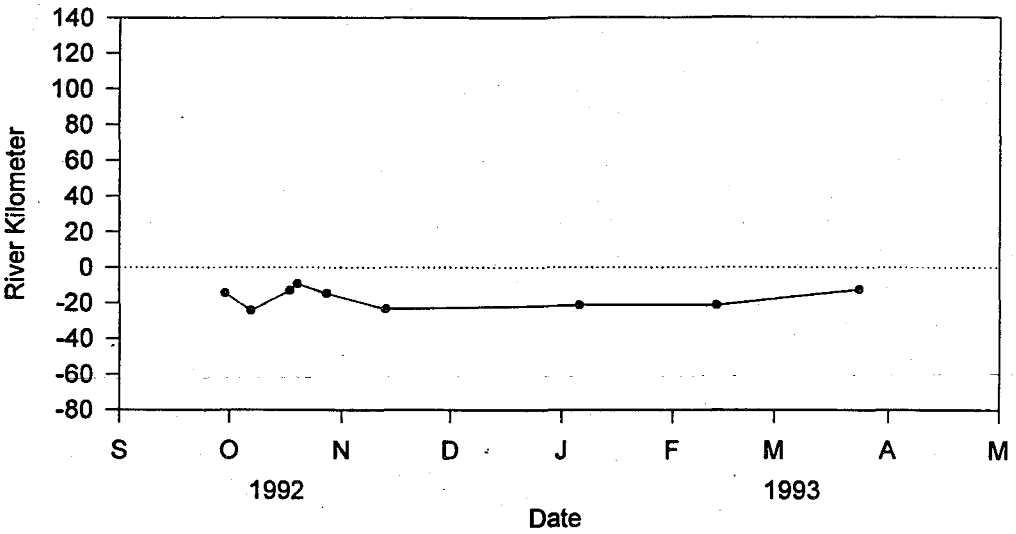

Figure 41. Movements of pallid sturgeon 48.520 during 1992-1993 in the Missouri River, North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

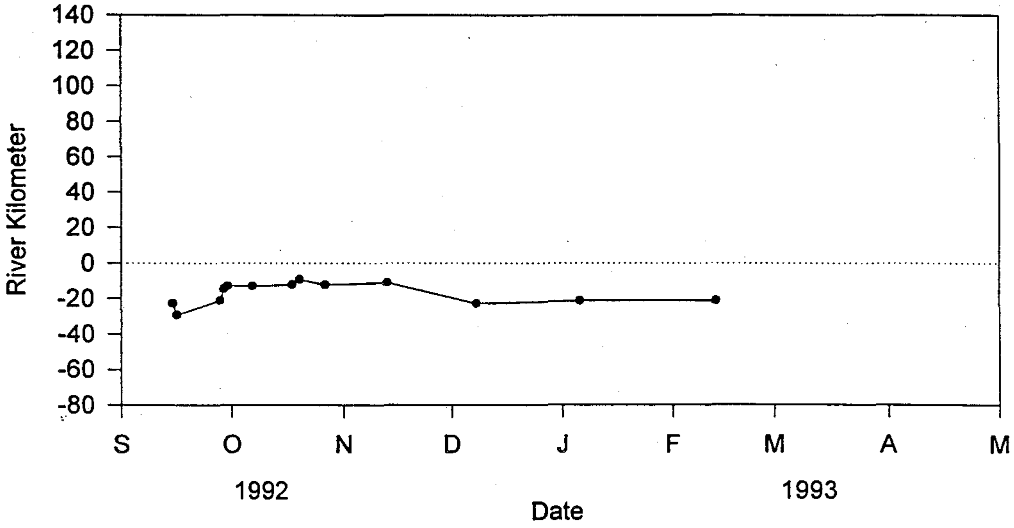

Figure 42. Movements of pallid sturgeon 48.540 during 1992-1993 in the Missouri River, North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

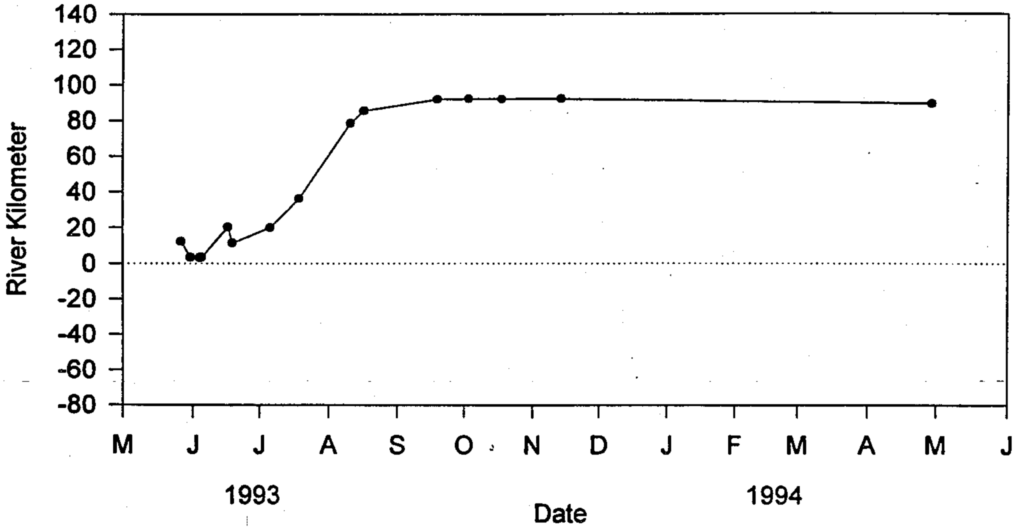

Figure 43. Movements of shovelnose sturgeon 48.550 during 1993-1994 in the Yellowstone River, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

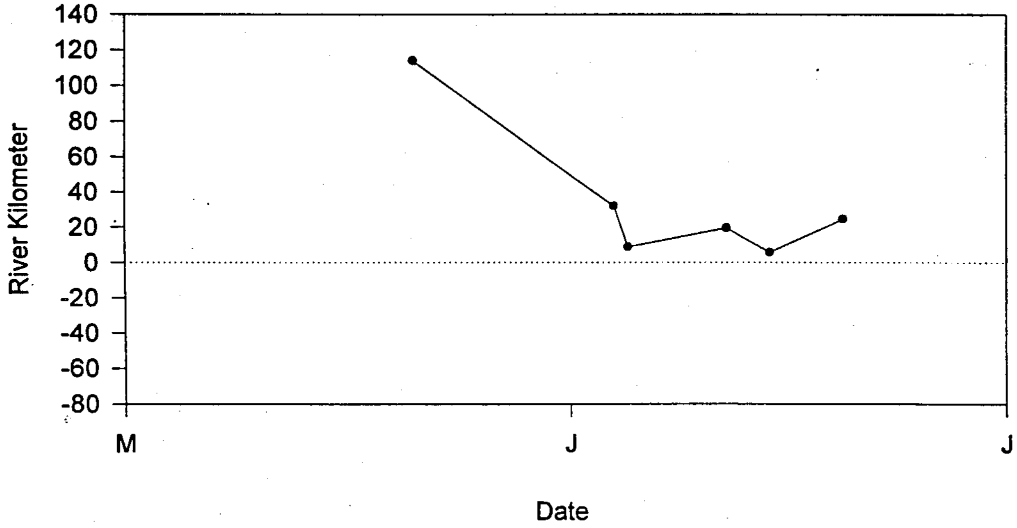

Figure 44. Movements of pallid sturgeon 48.562 during 1994 in the Yellowstone River, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

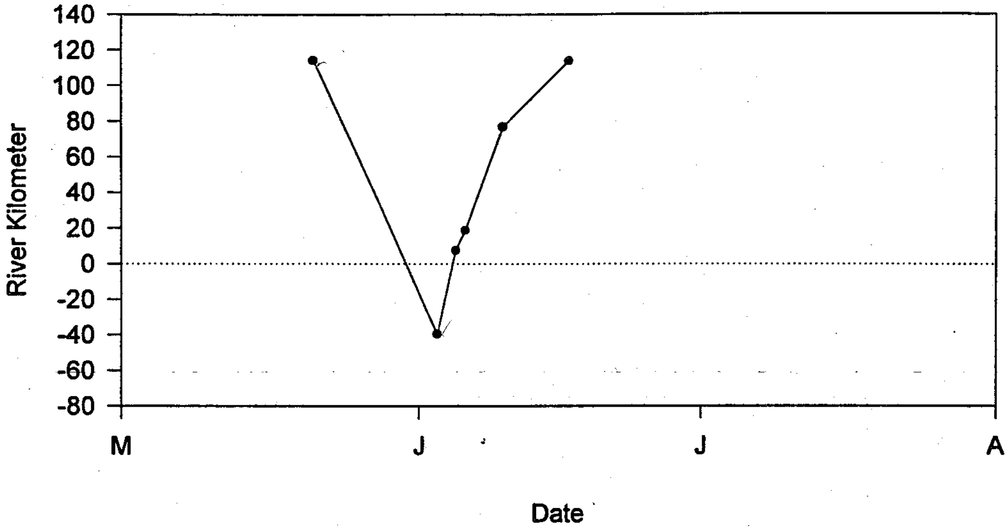

Figure 45. Movements of pallid sturgeon 48.570 during 1993 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

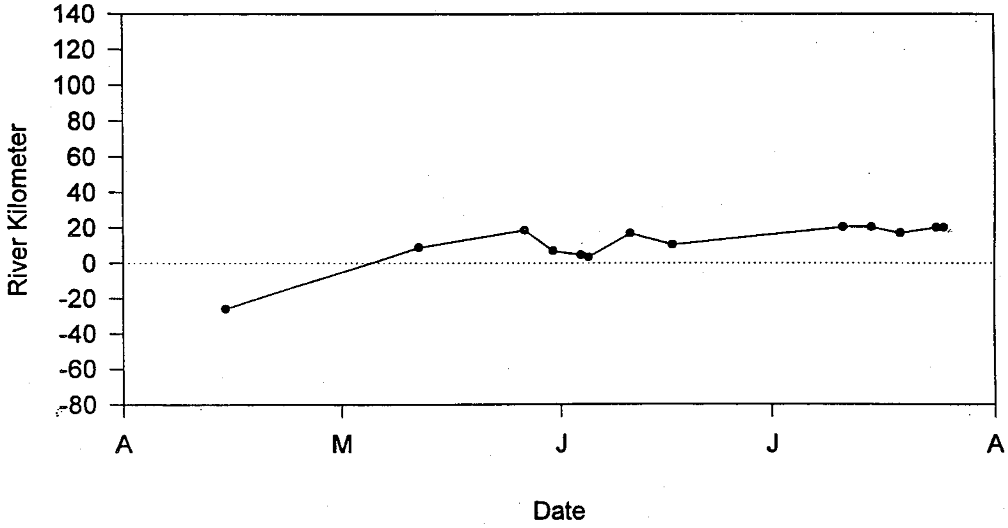

Figure 46. Movements of pallid sturgeon 48.580 during 1993 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

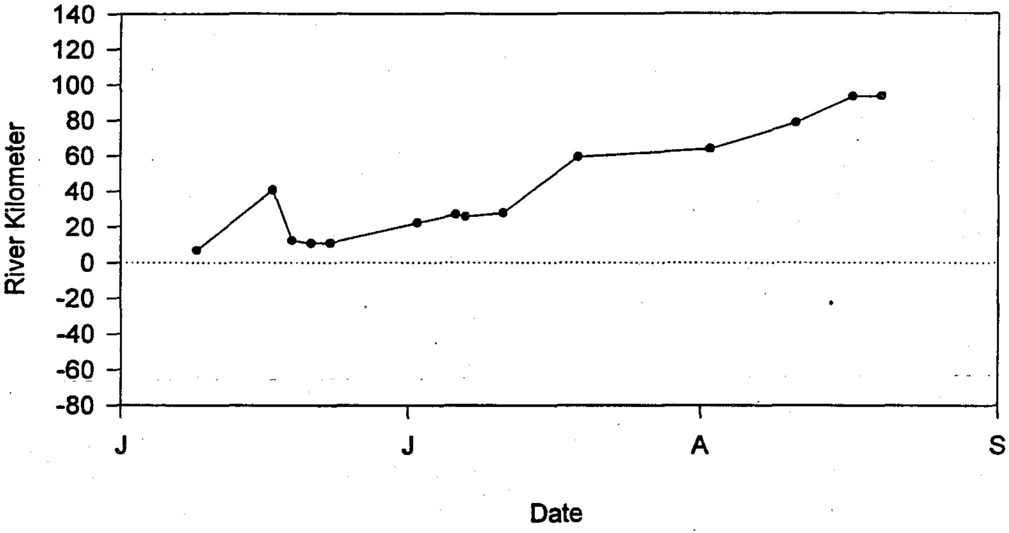

Figure 47. Movements of shovelnose sturgeon 48.590 during 1993 in the Yellowstone River, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

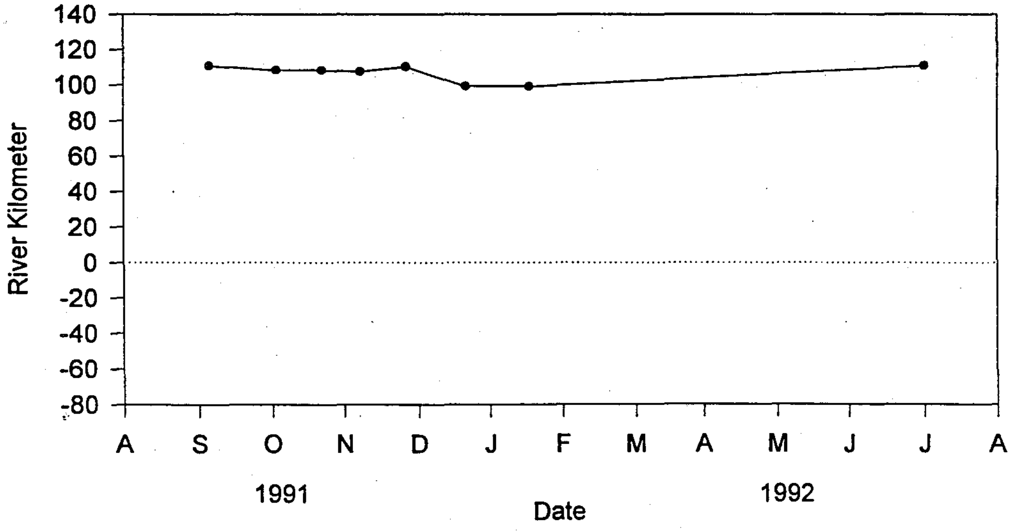

Figure 48. Movements of shovelnose sturgeon 48.600 during 1991-1992 in the Yellowstone River, Montana. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

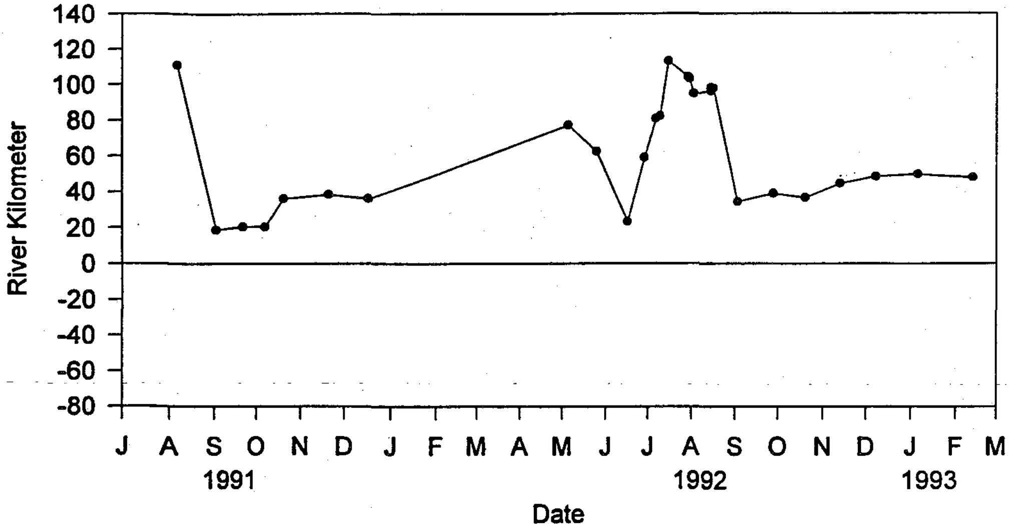

Figure 49. Movements of shovelnose sturgeon 48.620 during 1991-1993 in the Yellowstone River, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

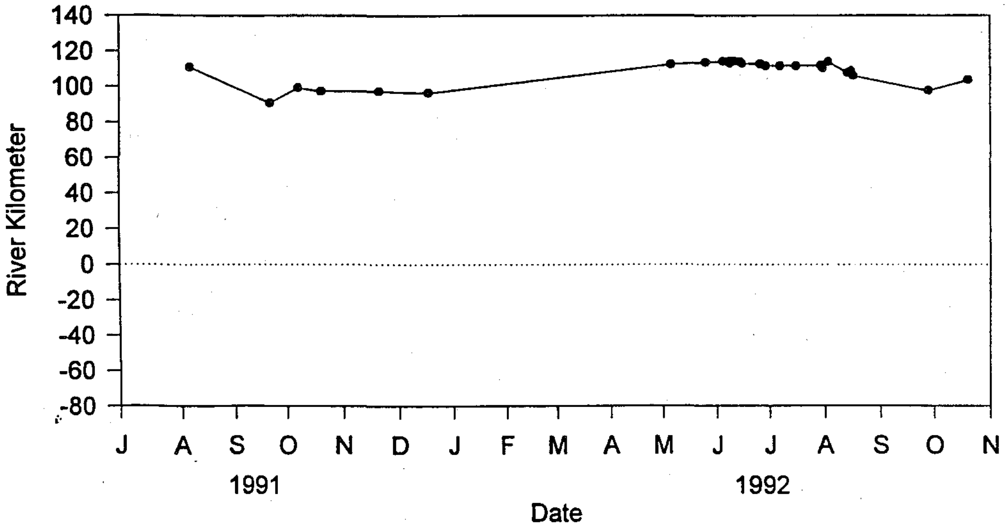

Figure 50. Movements of shovelnose sturgeon 48.640 during 1991-1992 in the Yellowstone River, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

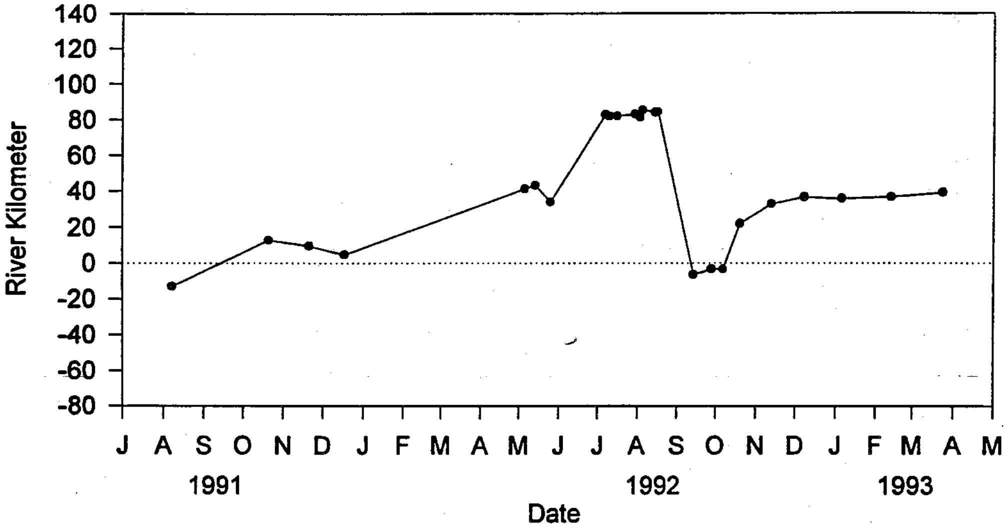

Figure 51. Movements of shovelnose sturgeon 48.660 during 1991-1993 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

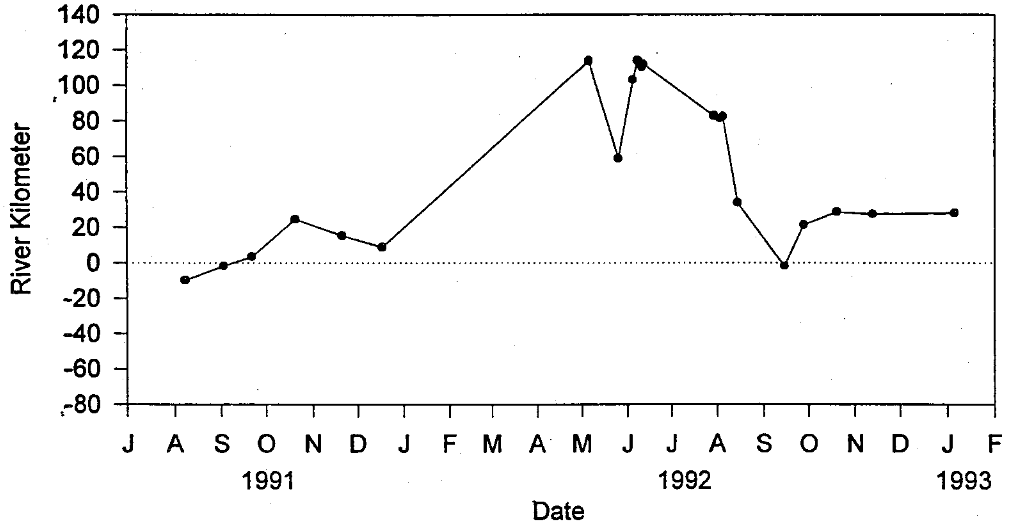

Figure 52. Movements of shovelnose sturgeon 48.680 during 1991-1993 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

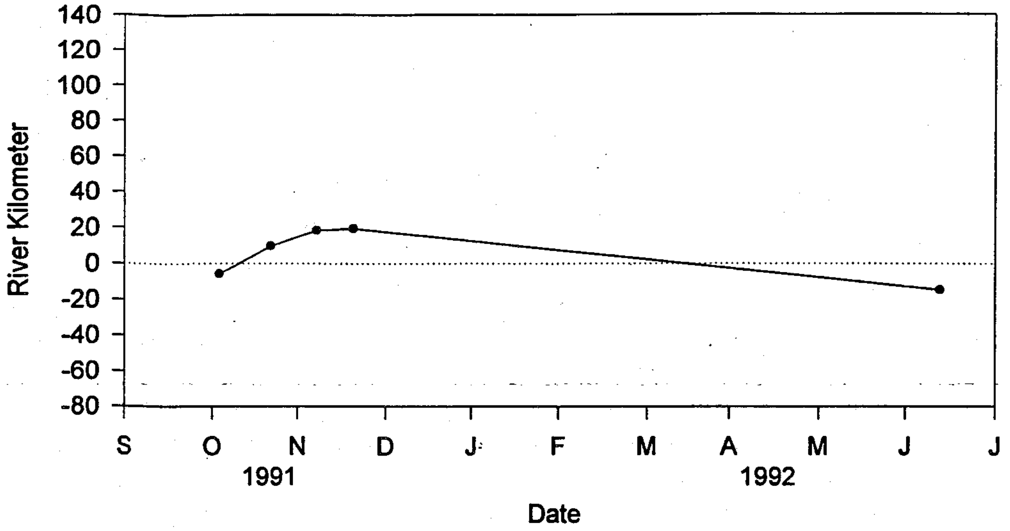

Figure 53. Movements of shovelnose sturgeon 48.760 during 1991-1993 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

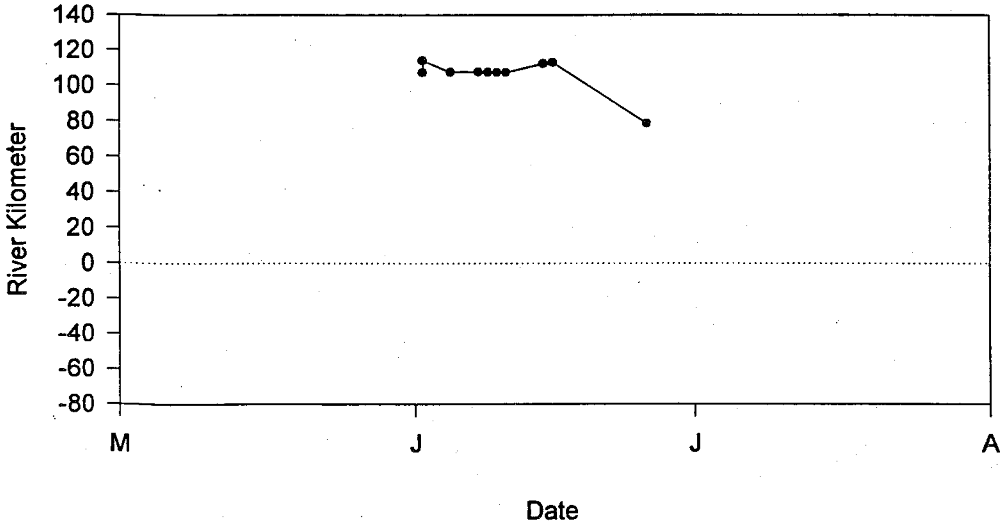

Figure 54. Movements of shovelnose sturgeon 48.820 during 1992 Yellowstone River, Montana. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

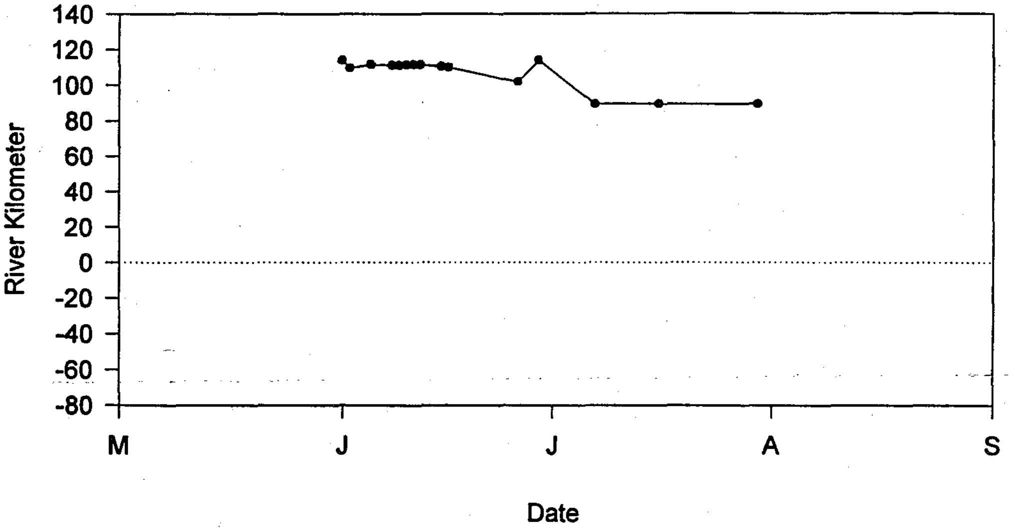

Figure 55. Movements of shovelnose sturgeon 48.840 during 1992 in the Yellowstone River, Montana. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

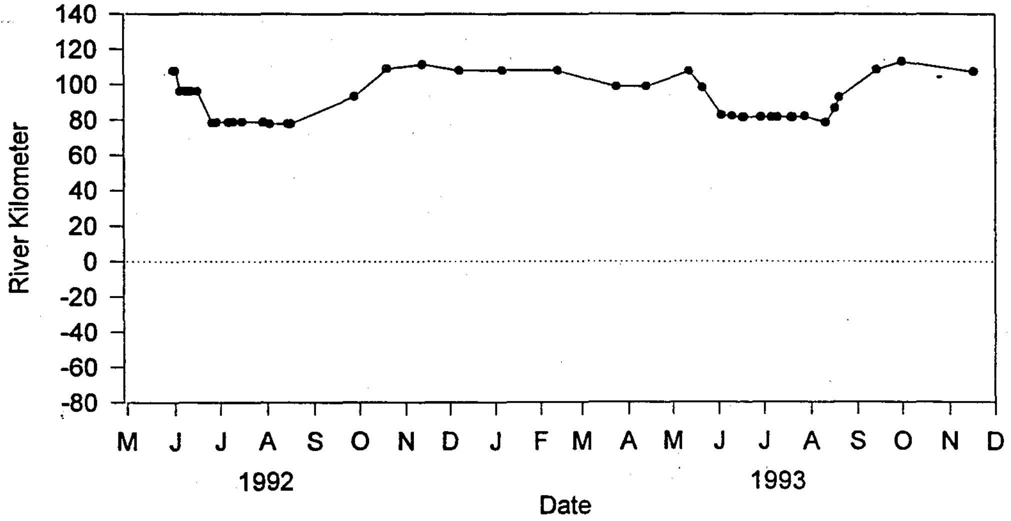

Figure 56. Movements of shovelnose sturgeon 48.860 during 1992-1993 in the Yellowstone River, Montana. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

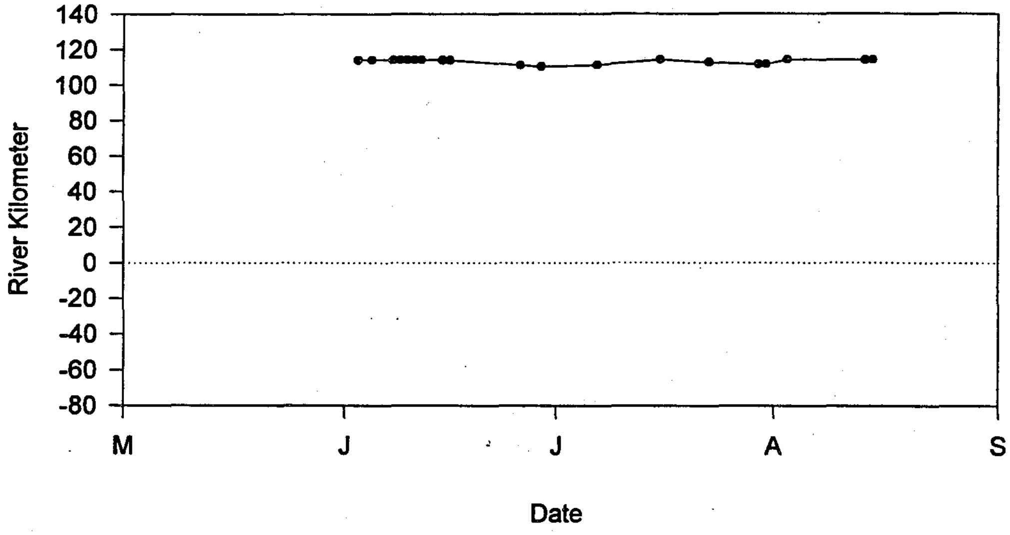

Figure 57. Movements of shovelnose sturgeon 48.880 during 1992 in the Yellowstone River, Montana. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

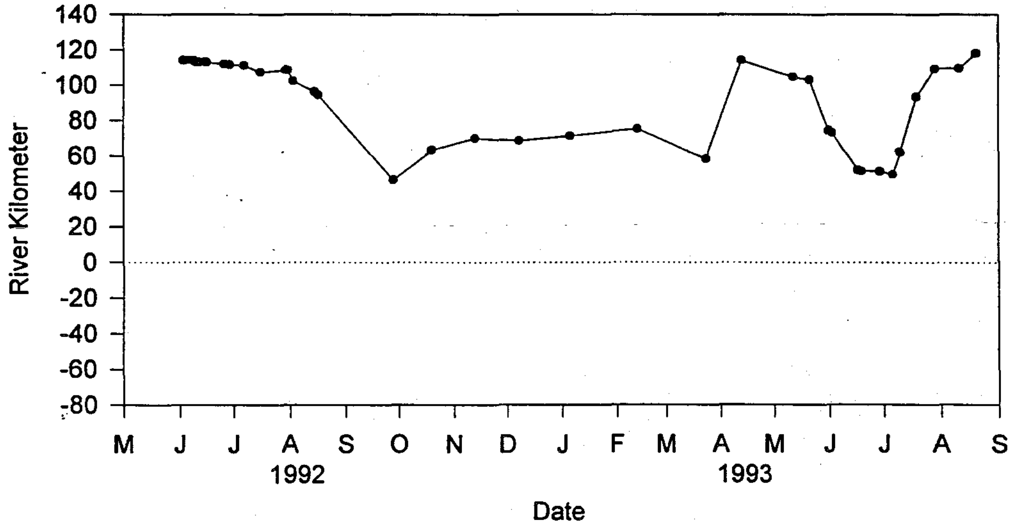

Figure 58. Movements of shovelnose sturgeon 48.900 during 1992-1993 in the Yellowstone River, Montana. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

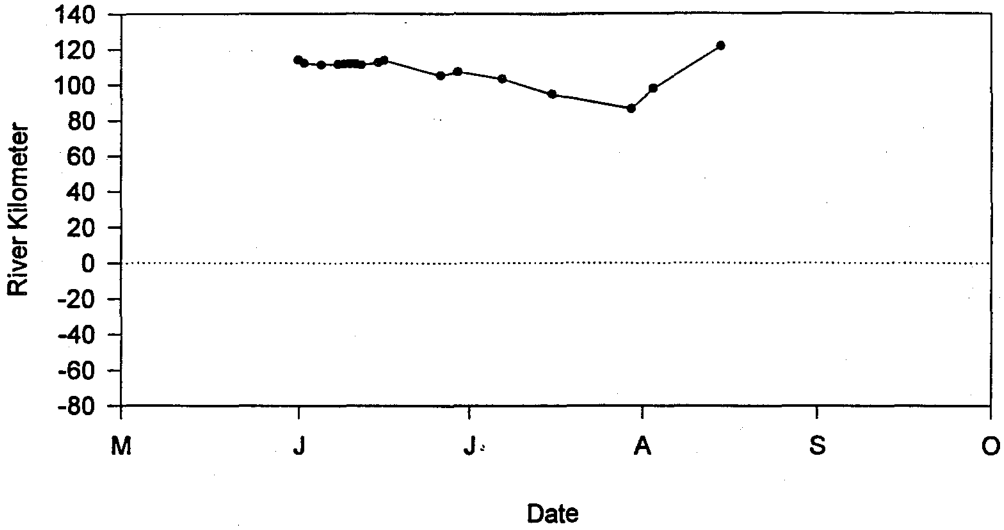

Figure 59. Movements of shovelnose sturgeon 48.920 during 1992 in the Yellowstone River, Montana. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

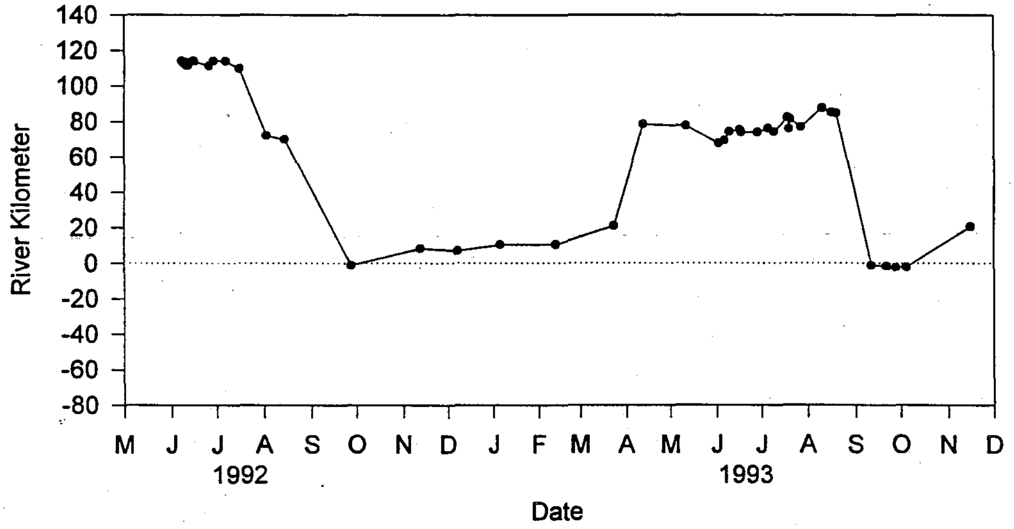

Figure 60. Movements of shovelnose sturgeon 940 during 1992 in the Yellowstone River, Montana. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

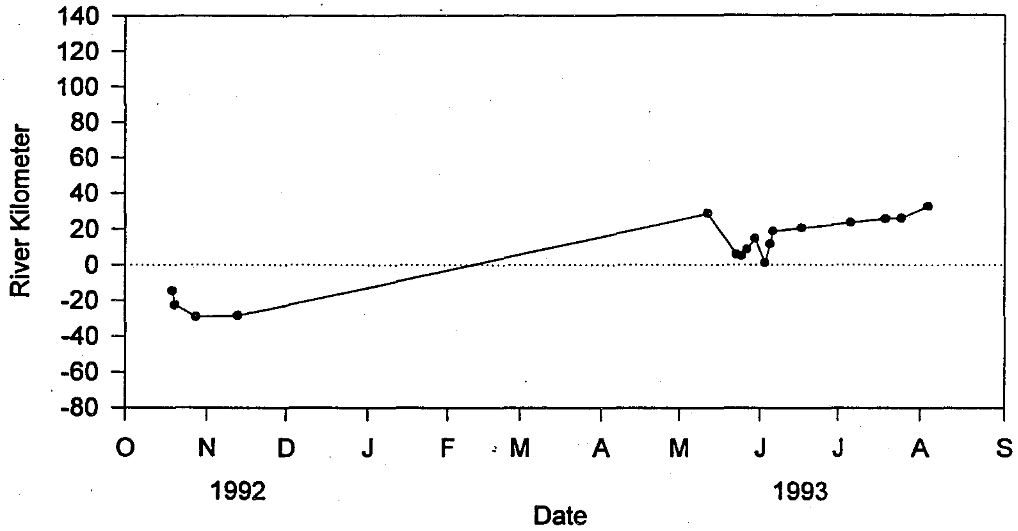

Figure 61. Movements of pallid sturgeon 49.020 during 1992-1993 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

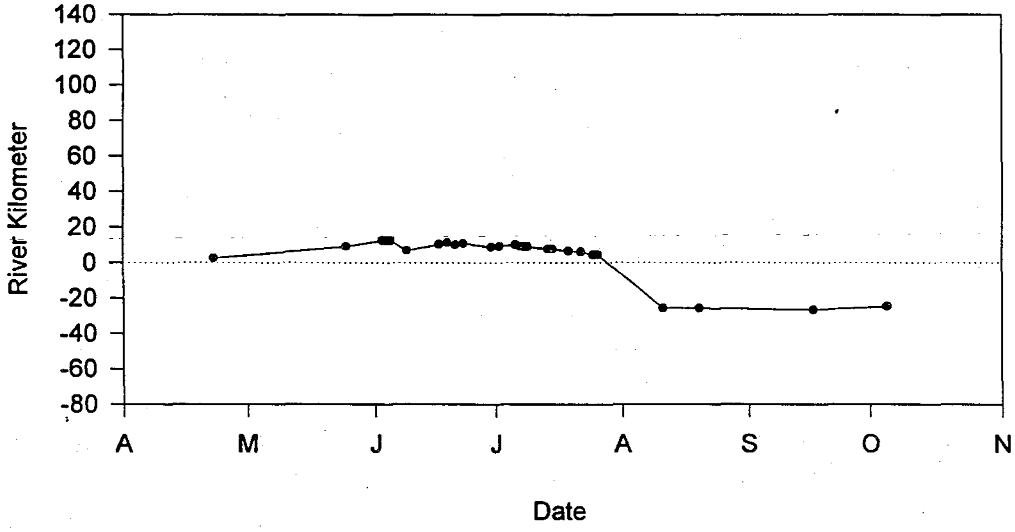

Figure 62. Movements of pallid sturgeon 49.030 during 1993-1994 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

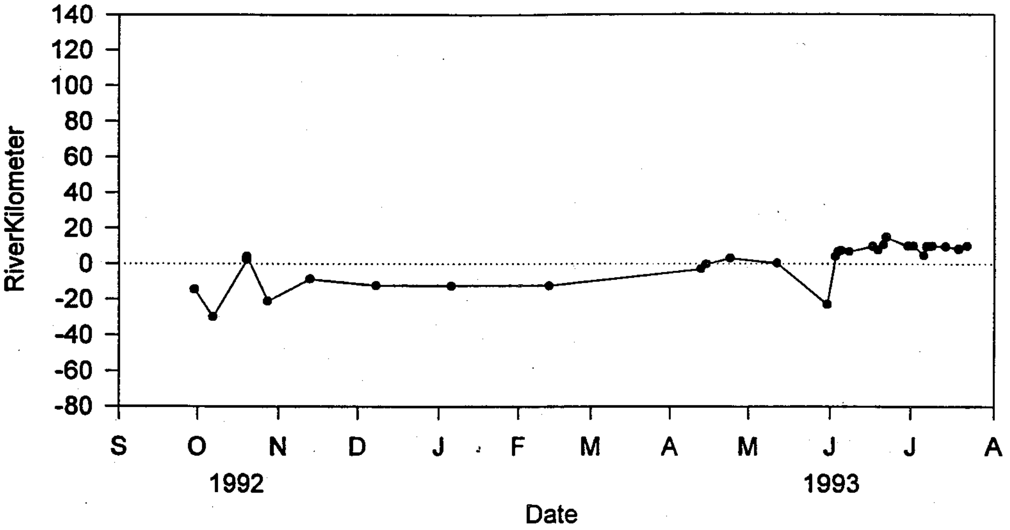

Figure 63. Movements of pallid sturgeon 49.050 during 1992-1993 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

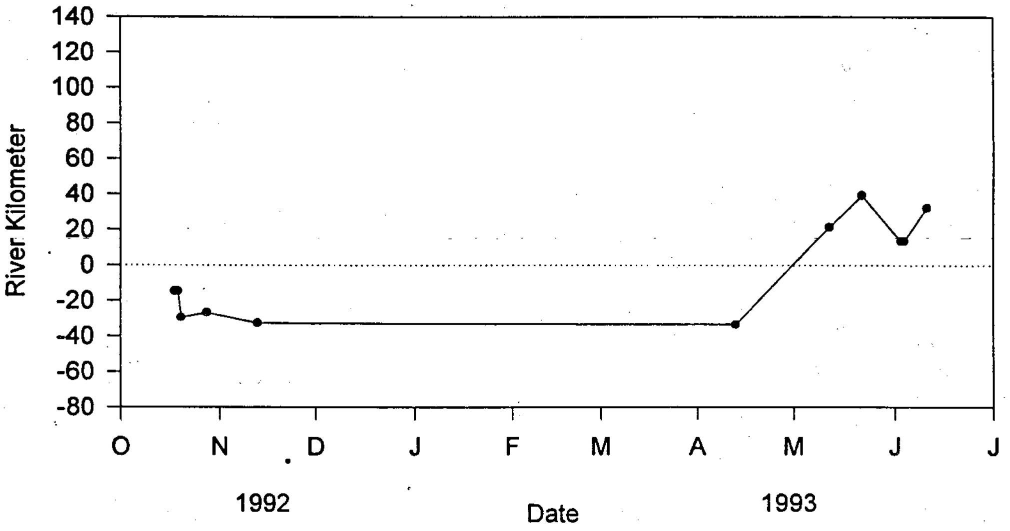

Figure 64. Movements of pallid sturgeon 49.070 during 1992-1993 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

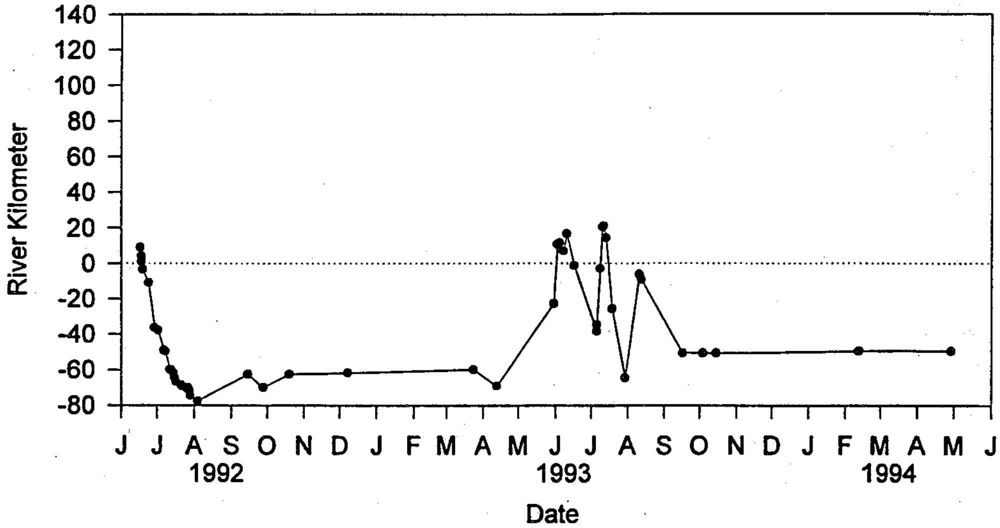

Figure 65. Movements of pallid sturgeon 49.100 during 1992-1994 in the Missouri and Yellowstone Rivers, North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

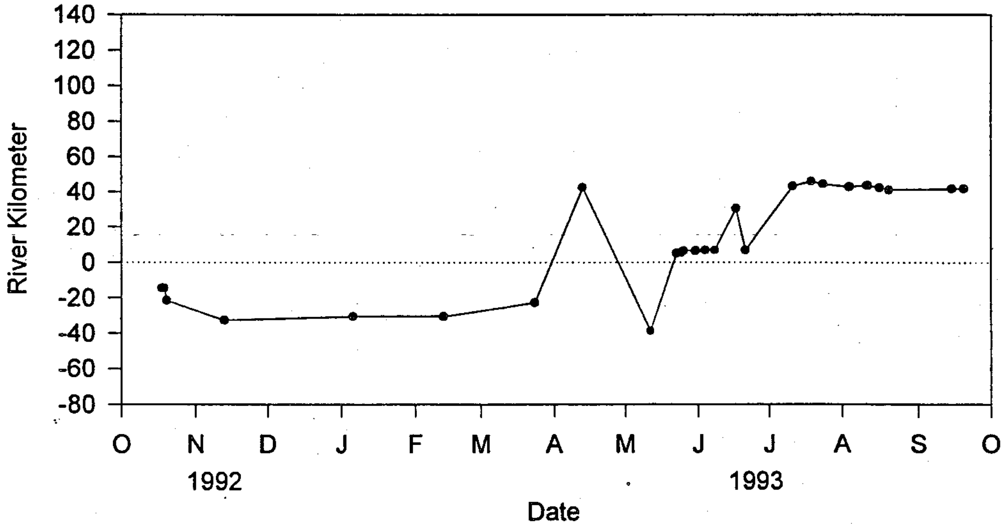

Figure 66. Movements of pallid sturgeon 49.130 during 1992-1993 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

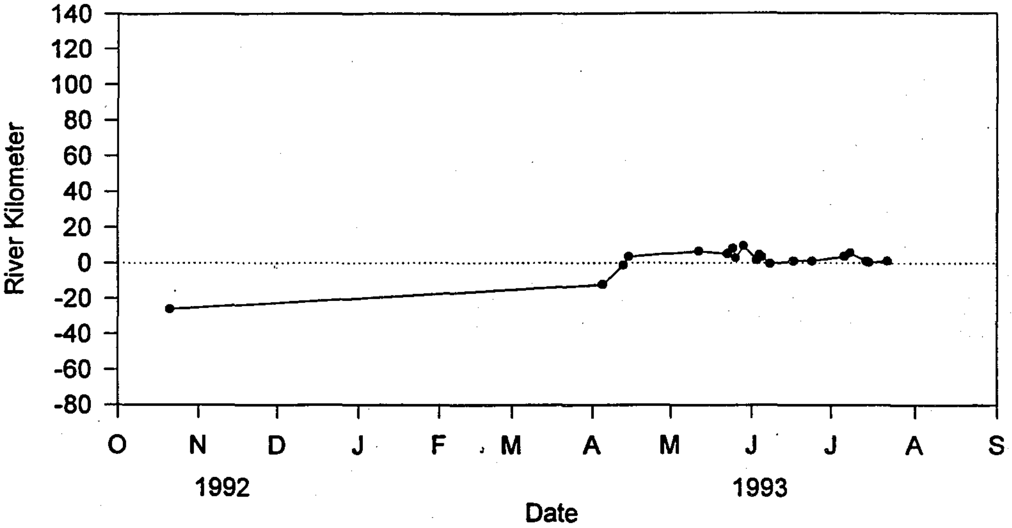

Figure 67. Movements of pallid sturgeon 49.170 during 1992-1993 in the Missouri and Yellowstone Rivers, North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

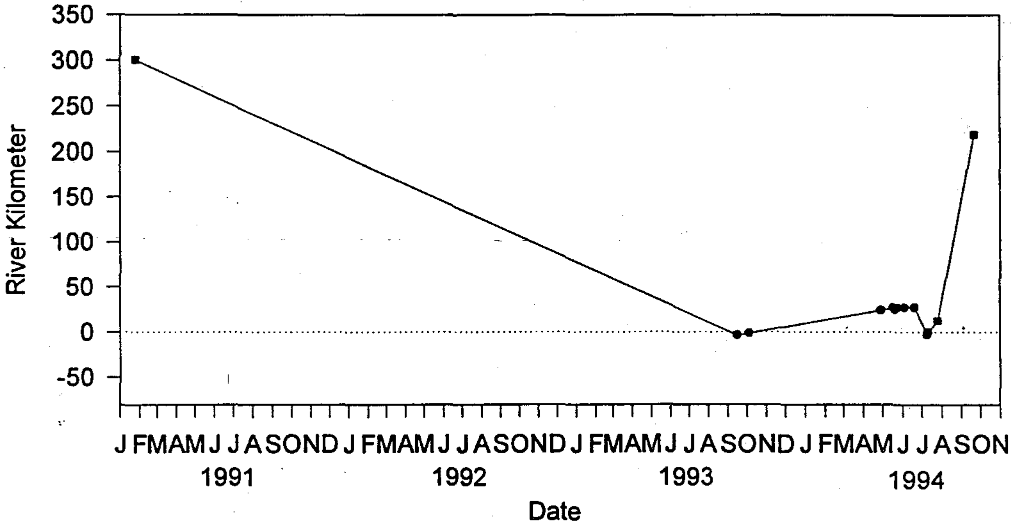

Figure 68. Movements of pallid sturgeon 49.240 during 1991-1993 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone or Upper Missouri River. Square symbols indicate locations in the Upper Missouri River.

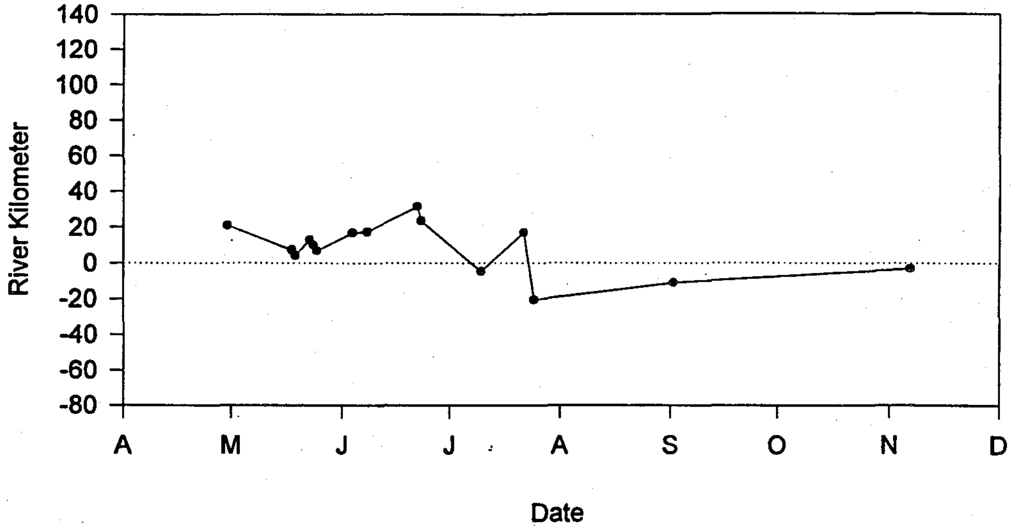

Figure 69. Movements of pallid sturgeon 49.350 during 1994 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

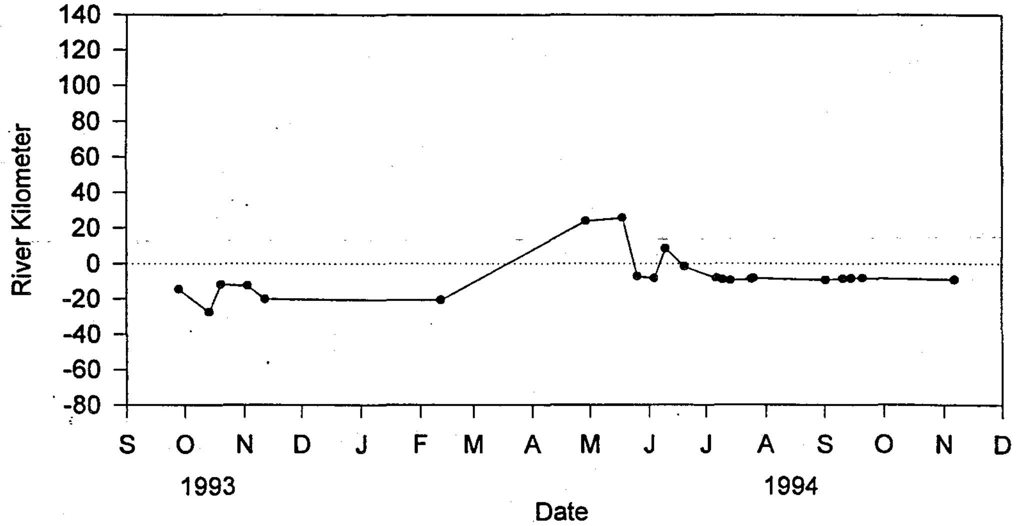

Figure 70. Movements of pallid sturgeon 49.370 during 1993-1994 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

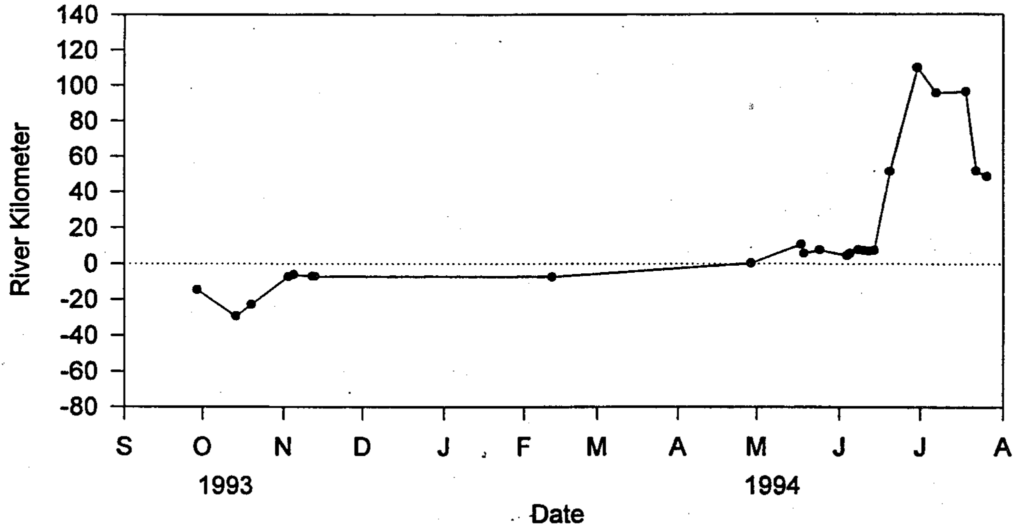

Figure 71. Movements of pallid sturgeon 49.630 during 1993-1994 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

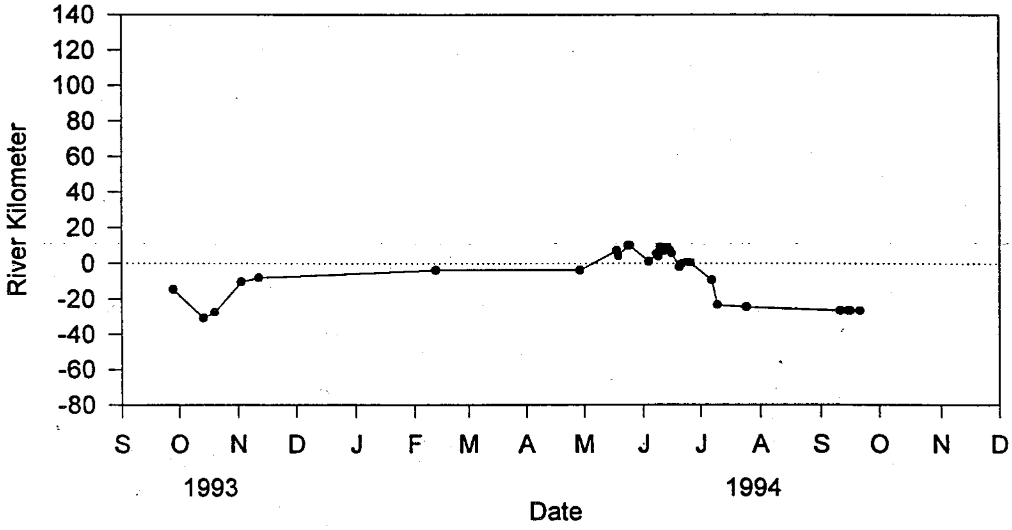

Figure 72. Movements of pallid sturgeon 49.650 during 1993-1994 in the Missouri and Yellowstone Rivers, North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone or Upper Missouri River. Square symbols indicate locations in the Upper Missouri River.

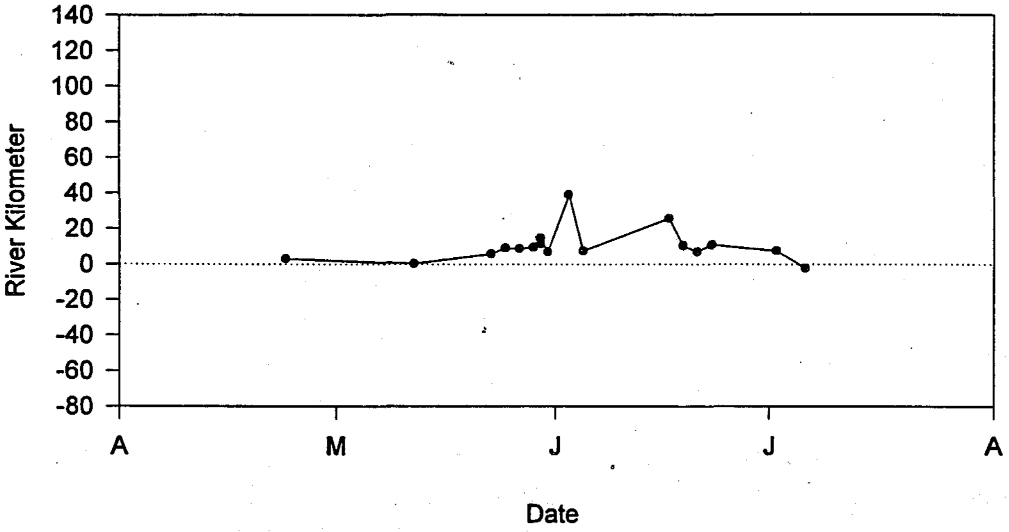

Figure 73. Movements of pallid sturgeon 49.670 during 1993 in the Missouri and Yellowstone Rivers, North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

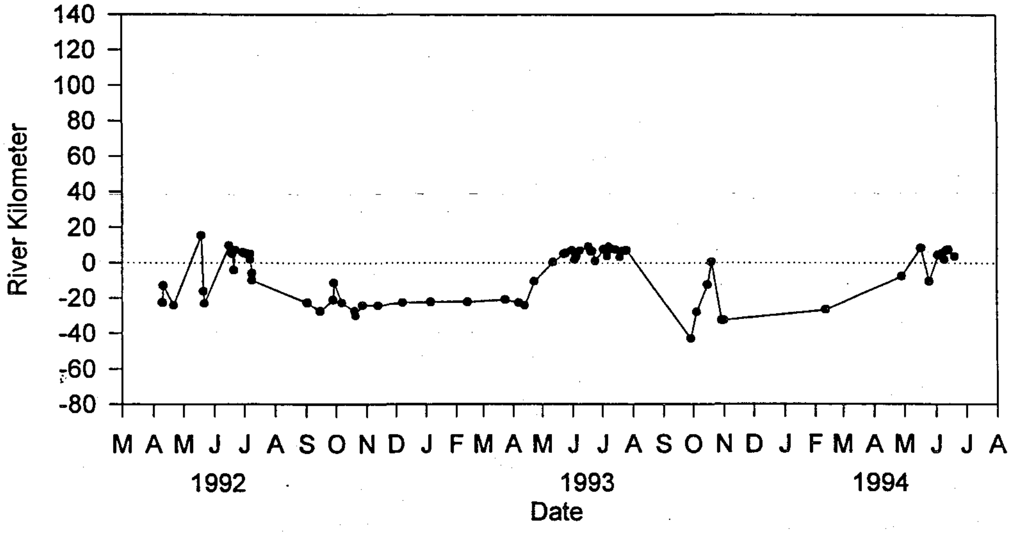

Figure 74. Movements of pallid sturgeon 49.680 in the Yellowstone and Lower Missouri rivers in Montana and North Dakota, 1992-1994. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

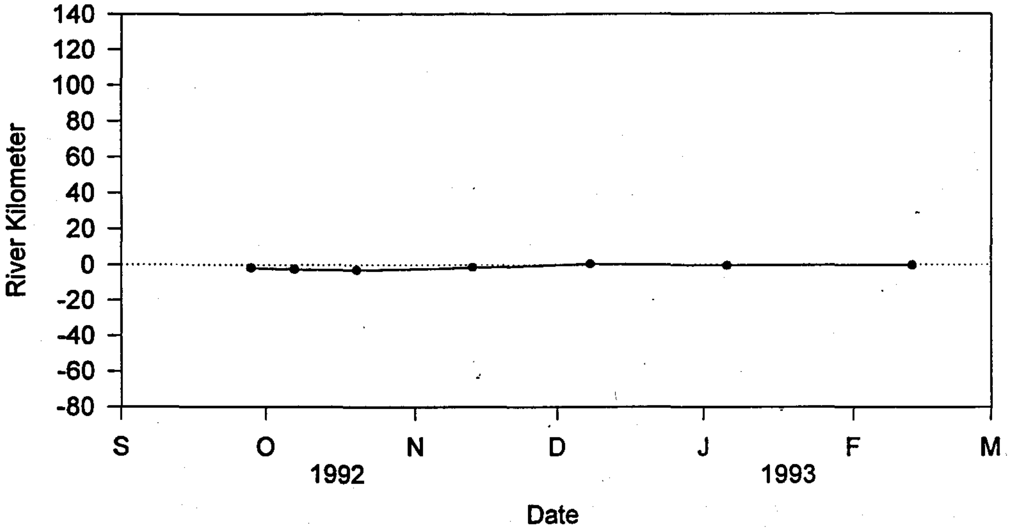

Figure 75. Movements of shovelnose sturgeon 49.710 during 1993-1994 in the Missouri and Yellowstone Rivers, North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

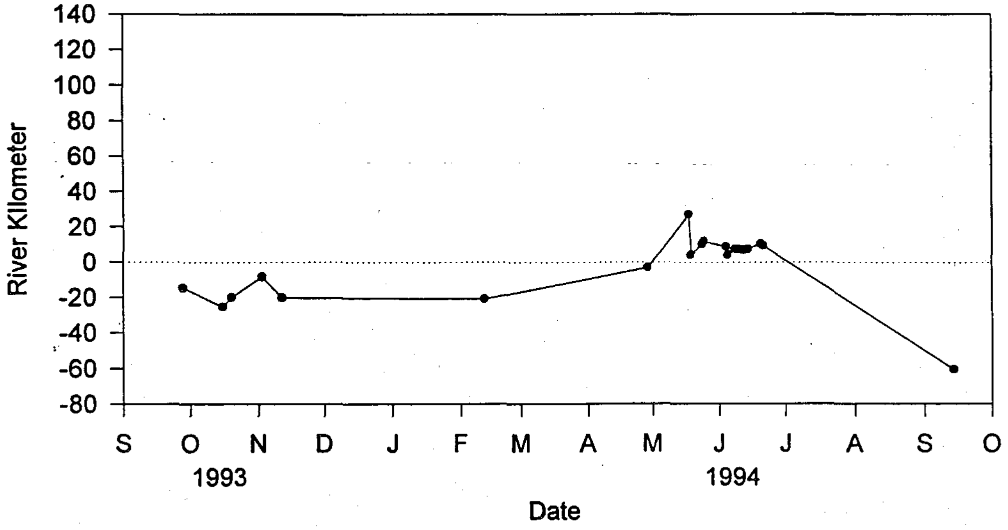

Figure 76. Movements of pallid sturgeon 49.712 during 1993-1994 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

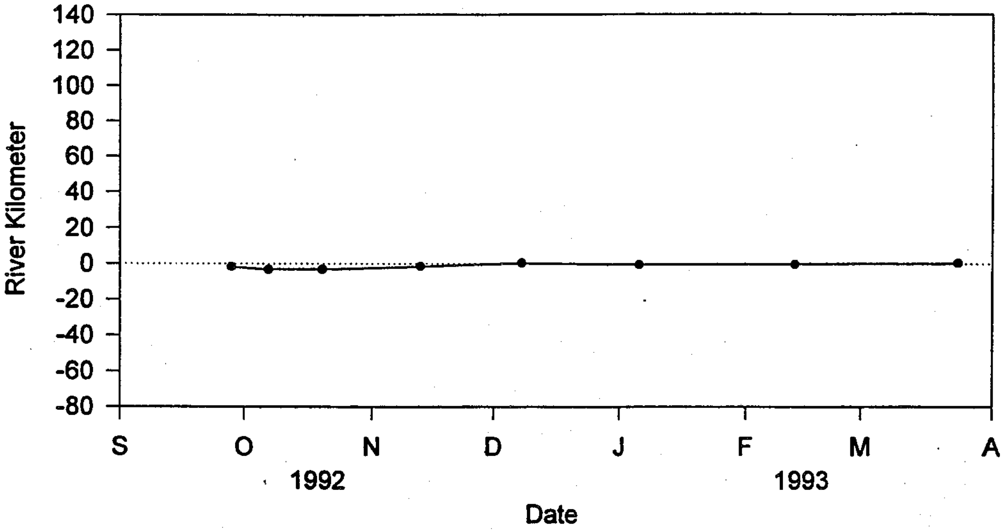

Figure 77. Movements of shovelnose sturgeon 49.790 during 1993-1994 in the Missouri River, North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

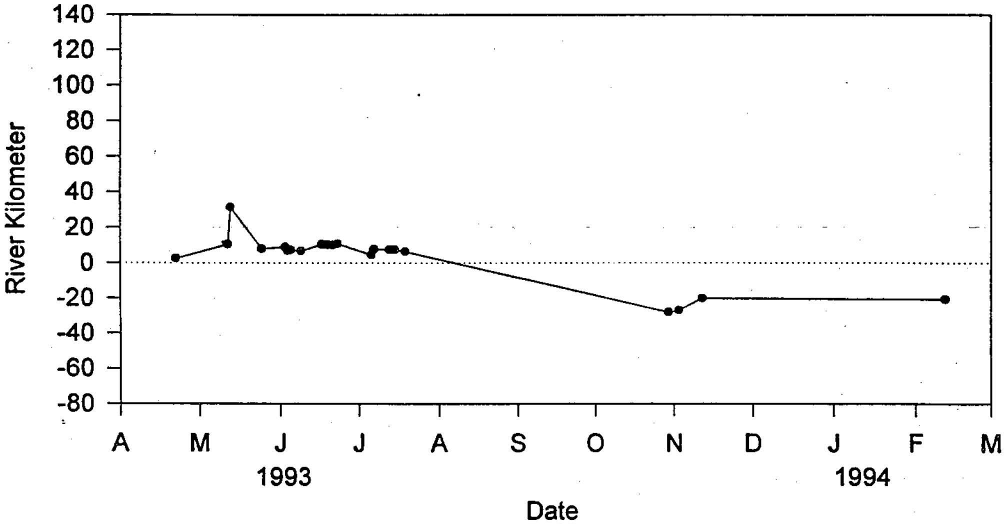

Figure 78. Movements of pallid sturgeon 49.810 during 1993-1994 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

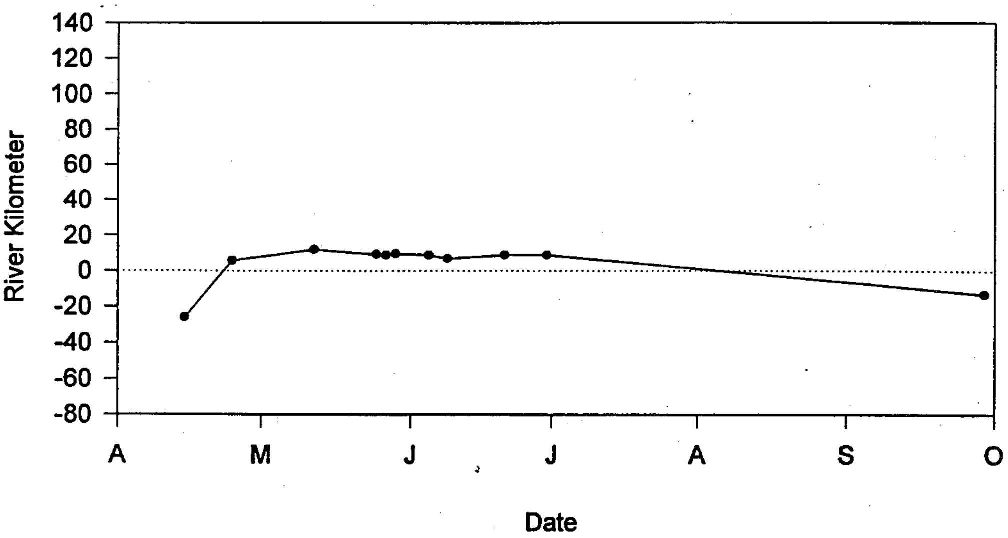

Figure 79. Movements of pallid sturgeon 49.830 during 1993 in the Missouri and Yellowstone Rivers, North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone River.

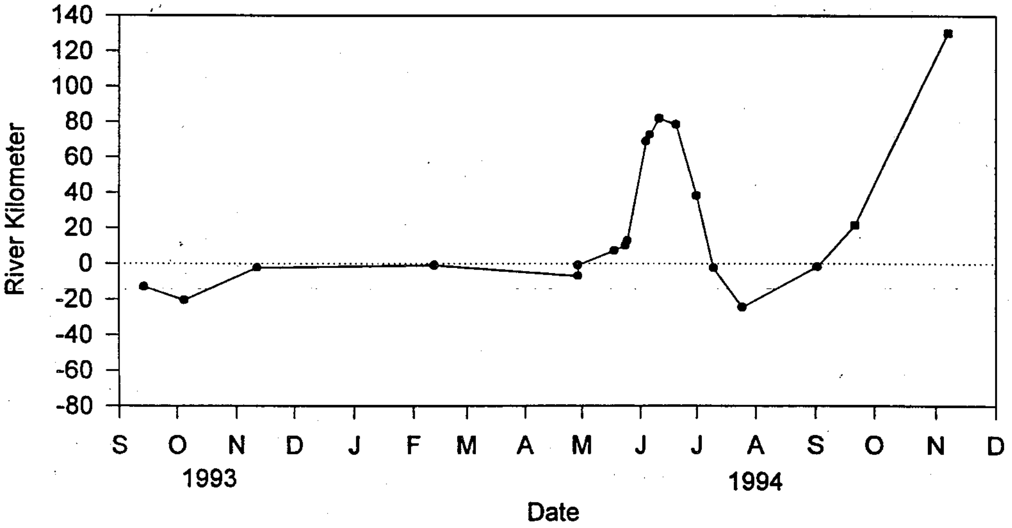

Figure 80. Movements of pallid sturgeon 49.850 during 1993-1994 in the Missouri and Yellowstone Rivers, Montana and North Dakota. Negative river kilometers are in the Lower Missouri River, positive river kilometers are in the Yellowstone or Upper Missouri River. Square symbols indicate locations in the Upper Missouri River.

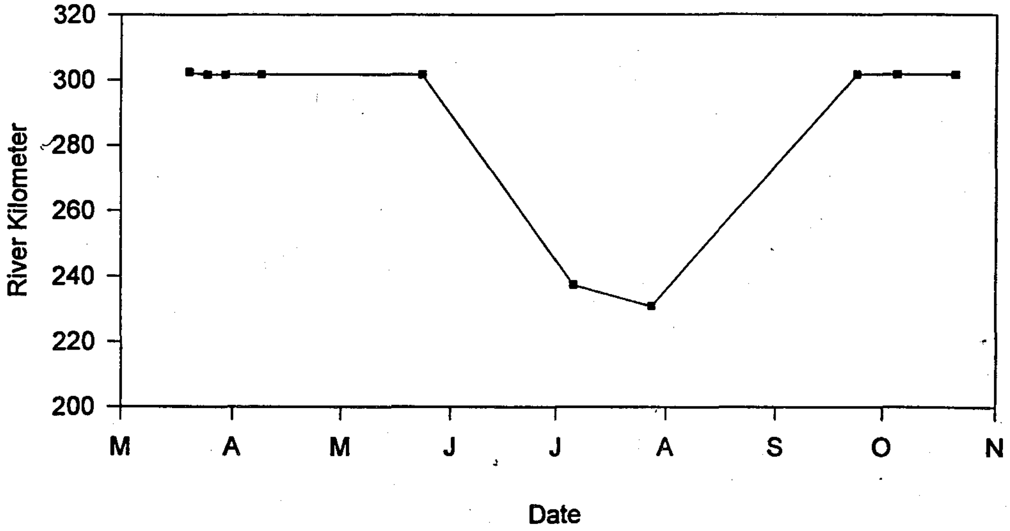

Figure 81. Movements of pallid sturgeon 49.870 during 1993 in the Upper Missouri River, Montana.

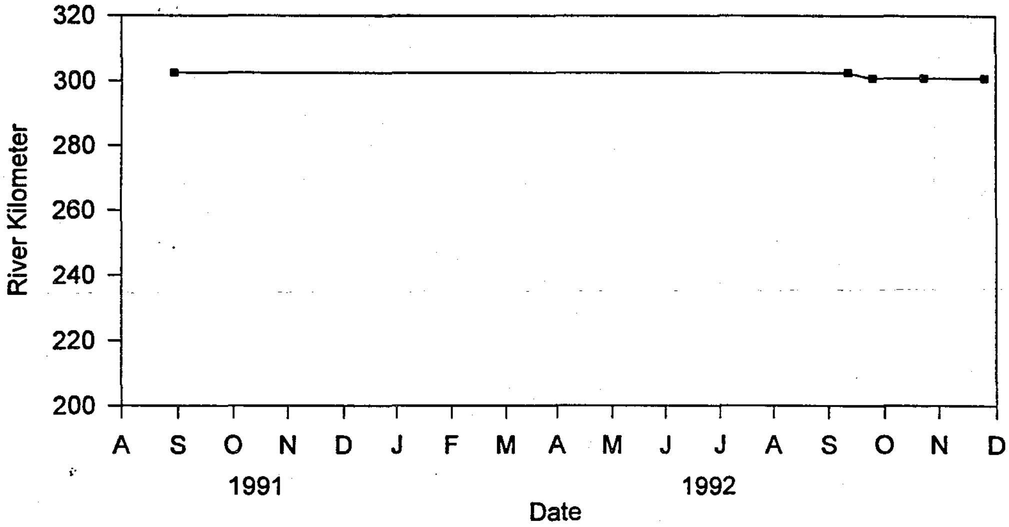

Figure 82. Movements of shovelnose sturgeon 3335 during 1991-1992 in the Upper Missouri River, Montana.