



Life History and the Costs of Reproduction in Northern Great Plains Paddlefish (*Polyodon spathula*) as a Potential Framework for Other Acipenseriform Fishes

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*A 14-year investigation of a North American Acipenseriform fish, the paddlefish *Polyodon spathula* in the Yellowstone River, Montana, and North Dakota, USA has provided a detailed empirical framework of the life history in relation to the costs of reproduction for that species and potentially for closely related sturgeons. Nearly all aspects of life histories of males and females differed from each other after the immature period. The five periods in the juvenile and adult life histories for males and females, which occur at different ages for each sex, were (1) immature, (2) maturing, (3) somatic growth and reproduction, (4) prime reproduction, and (5) senescence to death. During the first period (immature), fishes exhibit rapid somatic growth as well as accumulation of energy reserves in the form of gonadal fat bodies (GFBs) and other fat deposits. During the second period (maturing), somatic growth slows as production and stored energy reserves are diverted into reproduction. In the third period, fish are allocating energy to both somatic growth and reproduction. Reproductive periodicity is typically close to two years for males and three years for females; gonadal recrudescence is slower than in older fish. The gonadosomatic index (GSI) is increasing, and GFBs are depleted over 2–3 spawns in females and reduced more gradually in males. Fish make longer pre-spawning migrations upriver. In the fourth period (prime reproduction), somatic growth is slow or negative, as energy is routed more strongly into reproduction. GSI is at a maximum; GFBs are completely depleted in females. Reproductive periodicity is typically one year for males and two years for females; the rate of gonadal recrudescence is at its maximum. Fish make shorter pre-spawning migrations upriver. In the fifth period (senescence to death), GSI of some of the oldest females decreases; the oldest males have few energy reserves and are long and lean. Distinct male-female differences in life histories were consistent with theoretical models and with empirical observations of the lack of direct male competition for females. The framework outlined for this paddlefish stock may exist among other Acipenseriform fishes and is potentially useful for evaluating their life histories.*

Keywords paddlefish, sturgeon, life history, sexual dimorphism, cost of reproduction

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Introduction

Numerous papers and books have been written about the costs of reproduction in relation to the evolution of life histories of fishes and other organisms (Williams, 1966; Charlesworth, 1980; Emlen, 1984; Stearns, 1992). Bell (1980) reviewed the subject and posed the question: "How should animals . . . order their reproduction in time so as to achieve the greatest possible fitness?" (p. 45). A key underlying concept is that reproduction depletes the limited energy resources available to a fish, such that present reproduction reduces future reproductive capability and performance (Horn, 1978; Partridge, 1987; Roff, 1992). Costs of reproduction to an individual fish or a stock can be observed indirectly through a variety of measures of performance, including a reduced growth rate (Hirshfield, 1980), increased mortality rate (Tanasichuk, 2000), reduced future fecundity and a lengthened period of gonadal recrudescence (including omitted spawning (Holmgren, 2003; Engelhard and Heino, 2006)). The costs of reproduction in fishes are influenced by genetic, biological, physiological, and behavioral characteristics of the individual fish or stock as well as by external factors such as habitat quality and community interactions (Winemiller, 1992).

An adequate scientific assessment and understanding of the costs of reproduction in a fish stock requires information on the entire life history (Scarnecchia, 1983). Sex-specific information is needed on a number of life history characteristics, including fish size, growth rates, mortality rates, age at maturity, fecundity, reproductive periodicity (i.e., pattern of iteroparity or, alternatively, semelparity), behavior (especially pre-reproductive behaviors such as migrations), and senescence (Charlesworth, 1980; Roff, 1992; Stearns, 1992). An adequate assessment also requires knowledge of biological, physiological, and ecological energetics of the fish (Adams and Breck, 1990).

The North American paddlefish (*Polyodon spathula*) is an ancient (MacAlpin, 1947), migratory (Russell, 1986), zooplanktivorous (Fredericks and Scarnecchia, 1997), Acipenseriform fish closely related to sturgeons (Grande and Bemis, 1991) and native to the Mississippi and Missouri rivers and a few Gulf Coast drainages (Gengerke, 1986; Graham, 1997). The species has long supported commercial and recreational fisheries throughout the central United States (Coker, 1930; Pasch and Alexander, 1986; Graham, 1997). It is also an important source of high-priced caviar (Coker, 1930; Waldman and Secor, 1998; Williamson, 2003). Knowledge of paddlefish reproduction and its costs is of interest not only in the context of understanding the evolution of life histories, but also more practically in species conservation (Jennings and Zigler, 2000). Natural reproduction has been eliminated or reduced throughout large portions of the species' range (Sparrowe, 1986; Graham, 1997; Jennings and Zigler, 2000). Conservation of paddlefish and other Acipenseriform fishes requires an improved understanding of their reproduction, in that reproduction is widely regarded as a weak link in their prospects for long-term survival. Knowledge of paddlefish reproduction may be useful in the management of related Acipenseriform species as well as other long-lived, late-maturing species, which often present special challenges for fisheries scientists and managers (Boreman, 1997; Musick, 1999).

Investigations on a North American Acipenseriform fish, the Yellowstone-Sakakawea stock of paddlefish in eastern Montana and western North Dakota, USA (Scarnecchia et al., 1996b) conducted over the period 1991–2004 have provided sufficient sex-specific information on fish size, growth, age at maturity, reproductive periodicity, migration patterns, fecundity, energy reserves, and senescence to characterize the life history of both individual fish and the stock as a whole. Life history information can be viewed in relation to the costs of reproduction, resulting in a comprehensive depiction of the life history strategy of

this stock and a detailed empirical framework that can be evaluated in relation to the life history strategies of the other Acipenseriform and other fishes worldwide. Our objective is to characterize biological and energetic aspects of reproduction in relation to the overall life history of the Yellowstone-Sakakawea paddlefish stock.

Study Site

The Yellowstone-Sakakawea paddlefish stock inhabits the Lower Yellowstone River (YR) and Missouri River (MR) of eastern Montana and western North Dakota (Scarnecchia et al., 1995b). The two rivers dissect the Missouri Plateau area, which consists of exposed bedrock, generally of Late Cretaceous to Tertiary (Oligocene) origin (Leonard, 1911; Torrey and Kohout, 1956; Howard, 1960). Treeless uplands, which consist mostly of grasslands and scattered badlands, dominate the semi-arid region, except near rivers where the forested floodplains contain cottonwoods (*Populus* spp.). The Yellowstone River, one of the United States' last free-flowing large rivers, originates in Yellowstone Park and flows northward to Livingston, Montana, then predominantly northeastward for 1,091 river kilometers (Rkm) to its confluence with the Missouri River 33 km southwest of Williston, North Dakota. The average gradient in the lower Yellowstone River is 0.53 m/Rkm (Graham et al., 1979). The direct-runoff hydrograph is strongly influenced by snowmelt; elevated levels of discharge and sediment occur in spring, with the peak discharge typically occurring in June. Over the period 1910–2002, average discharge of the lower Yellowstone River at Sidney, Montana (YR km 47), during June was 1100 m³/s (U.S. Geological Survey, 2003). Firehammer (2004) described river reaches in the lower portion (YR km 114 to YR km 40) as containing “multiple islands and alluvial channel bars with swift current and substrate consisting of cobble and gravel” (p. 19). Sand replaces gravel as the predominant substrate in the lowermost 40 Rkm (Bramblett, 1996).

The Missouri River originates with the merging of the Gallatin, Jefferson, and Madison rivers in southwestern Montana, flows northward, then eastward to the North Dakota state line and its confluence with the Yellowstone River (a site hereafter called the Confluence). The portion of the river above the Confluence has been strongly influenced by Fort Peck Dam. Dam completion and consequent controlled water releases have resulted in a more stable discharge, a reduction in sediment load, and colder summer water temperatures than before impoundment (Welker and Scarnecchia, 2004).

Before the twentieth century, paddlefish inhabiting the study area had free access throughout the entire Mississippi and Missouri River basins; migrations of hundreds of kilometers have been documented in the lower Missouri River and Mississippi River (Russell, 1986). With the completion of two mainstem Missouri River dams and reservoirs, Fort Peck Dam and Reservoir, Montana in 1937 (Fort Peck Reunion Committee, 1977) and Garrison Dam and Lake Sakakawea, North Dakota, in 1953, paddlefish movements were impeded, and putative stocks became isolated physically from each other. Lake Sakakawea (area, 156,000 Ha), the primary rearing habitat for this stock (Fredericks and Scarnecchia, 1997), has exhibited wide fluctuations in water levels from its origin in December 1953 through 2004 (Scarnecchia et al., 1996b; U.S. Army Corps of Engineers, 2005). As of 2004, the Yellowstone-Sakakawea paddlefish stock's range extended from Garrison Dam up through Lake Sakakawea, and from the headwaters of the reservoir (the location of which can vary more than 50 Rkm depending on reservoir elevation) upriver to the Confluence, westward up the Missouri River 302 Rkm to the tailrace of Fort Peck Dam, and southwestward up the Yellowstone River 114 Rkm to Intake, the site of a low-head irrigation diversion dam

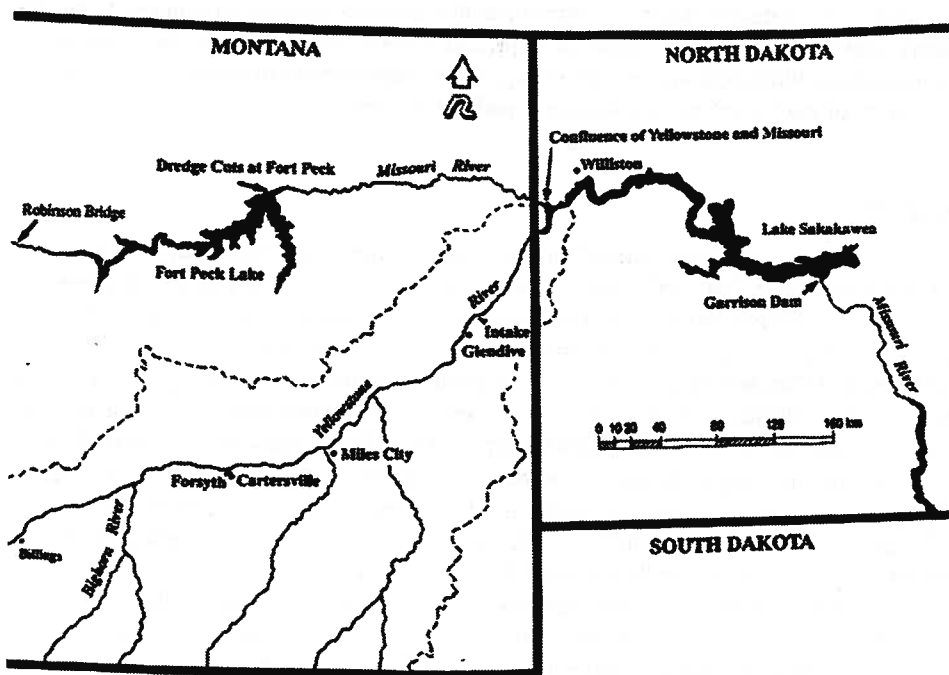


Figure 1. Map of Lower Yellowstone and Missouri Rivers and Missouri River mainstem reservoirs in eastern Montana and western North Dakota.

northeast of Glendive (Torrey and Kohout, 1956; Figure 1). In years of high runoff, some migratory paddlefish move either over or around the dam (via a flooded side-channel) past Intake and on upstream as far as the Cartersville Diversion Dam at Forsyth (YR Rkm 382).

Background on the Yellowstone-Sakakawea Paddlefish Stock and Fishery

The general life history and stock status of the Yellowstone-Sakakawea paddlefish have been described by Robinson (1966), Rehwinkel (1978), and most recently by Scarnecchia et al. (1996b). During the period 1953–1966, from the closure of Garrison Dam to the complete filling of Lake Sakakawea, the population size of Yellowstone-Sakakawea paddlefish increased greatly as a result of increased rearing habitat and trophic upsurge in the newly formed, slowly filling reservoir. The population has since declined in abundance as the reservoir has aged (Scarnecchia et al., 1996b).

Since the dam was closed, nearly all Yellowstone-Sakakawea paddlefish have reared in Lake Sakakawea as immature fish and as mature fish between spawning migrations. During their first summer, age 0 fish rear in the reservoir headwaters, where, by July and August, as 150- to 250-mm, fork-length (FL) fish, they feed selectively on invertebrates, chiefly the large, predaceous cladoceran *Leptodora kindtii* (Fredericks, 1994). Age 0 paddlefish have been documented to commonly be eaten by walleye *Sander vitreus* and sauger *Sander canadensis* (Mero et al., 1995; Parken and Scarnecchia, 2002). By late fall or the following summer, for the rest of their lives, they are filter-feeding with the aid of long, filamentous gill rakers (Kofoid, 1900; Imms, 1904) on a wide variety of zooplankton and other invertebrates (Michaletz et al., 1982; Fredericks, 1994; Scarnecchia et al., 1995a; Fredericks

and Scarnecchia, 1997). Available evidence from visual observations and netting indicates that adult fish are widely distributed throughout the reservoir in summer (Jeff Hendrickson, North Dakota Game and Fish Department, Personal Communication). A small percentage of fish is stranded or rears volitionally in the Dredge Cuts, large, clear, flooded borrow pits immediately below Fort Peck Dam. Some of these fish infrequently exit the Dredge Cuts and migrate downriver.

In spring (April–June), sexually mature fish ascend the Yellowstone River (and to a lesser extent the Missouri River) during rising discharge (Firehammer, 2004). Some fish also move from Lake Sakakawea into the Missouri River below the Confluence in the autumn prior to the spawning year. In the Yellowstone River, fish typically remain in the river in May and June until spawning is completed or until river discharge drops sharply, at which time fish descend into the reservoir (Firehammer, 2004; Firehammer and Scarnecchia, 2006). In the Missouri River above the Confluence, some fish linger well into the summer and fall, a possible response to regulated flows. Although exact spawning sites have not been identified and may vary from year to year, eggs have been recovered at several sites in the Yellowstone River in May and June (Firehammer et al., 2006). Larval fish have also been found in both rivers in summer (Gardner, 1995). Newly hatched larvae descend from the Yellowstone River into the turbid headwaters of Lake Sakakawea (Fredericks and Scarnecchia, 1997).

During the spring pre-spawning migration (May–June), a recreational fishery based on snagging adult fish occurs at several sites along the Missouri and Yellowstone Rivers in both Montana and North Dakota. Anglers use long, heavy spinning rods with 6/0 to 10/0 treble hooks and 13.6- to 22.7-kg test line to snag the fish as they congregate at known staging sites. Important fishing sites in North Dakota include (in order, progressively upriver) the Pumphouse (MR Rkm 2,503) near Williston, the Confluence (MR Rkm 2,542, YR Rkm 0), and Sundheim Park (YR Rkm 14.5). The most important fishing site in Montana is at Intake (YR Rkm 114). Other fishing sites in Montana include the Sidney Bridge (YR Rkm 46.6), Richland Park (YR Rkm 35.5), and at least two Fort Peck Tribal fishing sites on the Missouri River (Wolf Point, Rkm 2,744 and Frazer Rapids, Rkm 2,813). A small bow and arrow fishery also exists in the Dredge Cuts (MR Rkm 2,846; Needham and Gilge, 1986). Additional details about the snag fishery and the socio-economic characteristics of the anglers are documented elsewhere (Scarnecchia et al., 1996a; Scarnecchia and Stewart, 1997a, b).

The interstate fishery is managed cooperatively under a joint management plan developed by the states of North Dakota and Montana (Scarnecchia et al., 1995b). Both states monitor harvest with angler tag systems, in which successful anglers must attach an individually numbered, locking angler tag to the fleshy tissue at the front portion of the base of the paddlefish's dorsal fin. Retention of snagged paddlefish is also mandatory in both states, except during specified catch-and release periods, when release of fish is mandatory (Scarnecchia and Stewart, 1997a). The snag fishery in each state has been managed under progressively more restrictive regulations over the past decade. As of 2006, allowable harvest was limited to a maximum of 1,000 fish per year per state, with an annual creel limit of one fish per state per person. The North Dakota fishery extends from May 1 until May 31 or until the harvest cap is met; the Montana fishery extends from May 15 until June 30 or until the harvest cap is met. Harvest in North Dakota from 2000 to 2004 ranged from 1,041 fish in 2003 to 2,205 fish in 2000 (mean, 1,450 fish); harvest in Montana over the same period ranged from 329 fish in 2004 to 1,209 fish in 2003 (mean, 754 fish). Harvest in both states is strongly influenced by May–June discharges in the Missouri and Yellowstone rivers. Higher discharges result in extensive upstream migrations and higher harvests in

Montana whereas lower discharges result in fewer and less extensive upstream migrations and higher harvests in North Dakota.

Materials and Methods

The costs of reproduction were assessed through an analysis of twelve life history attributes: (1) size of mature fish, (2) population age structure, (3) age at maturity, (4) longevity, (5) growth, (6) reproductive periodicity, (7) fecundity, (8) weight and composition of gonadal fat bodies, (9) energetic tradeoffs between somatic growth and reproduction in extreme cases, (10) migration distance and location fidelity, (11) mortality rates, and (12) senescence.

Data Sources

Cleaning Stations

Life history information was obtained over a 14-year period (1991–2004) mainly from two cleaning stations, one in each state, at the Confluence and Intake. A high percentage of harvested fish (from 65 to 98% of the annual harvest, depending on the year) (North Dakota Game and Fish Department and Montana Department of Fish, Wildlife and Parks, Unpublished Data) were processed at one or the other of these stations. Under the community-based roe donation programs at each site, anglers receive free cleaning of their fish (male or female) for a donation of the roe, if present. From each fish, data collected included the date of harvest, harvest location (Rkm), body length (BL; anterior of eye to fork of caudal fin; Ruelle and Hudson, 1977) to the nearest 2.5 cm, weight to the nearest 0.5 kg, sex, maturation stage (Scarnecchia et al., 1996c; Bruch et al., 2001), gonad weight, gonadal fat weight, and dentaries (lower jaw bones) for age determination (Adams, 1942; Scarnecchia et al., 2006). With high grading and release of fish prohibited and enforced, the catch, which consists almost entirely of sexually mature, pre-spawning migratory fish (Scarnecchia et al., 1996b), is reliably indicative of the actual run composition. Although fishing methods in each state are the same, in most analyses, data from each state's fishery were analyzed separately to detect any upriver versus downriver differences in life history components and to provide a second, independently collected data set for the stock.

Adult Tagging

Over the period 1964–2004, more than 14,000 migratory fish, nearly all of which have been found to be adult pre-spawners (Scarnecchia et al., 1995b, 1996b) were captured with angling, gillnets, or seines and tagged with individually numbered metal (monel) or plastic poultry band tags around their dentaries. Tags were recovered from fish subsequently gillnetted and released by state fisheries agencies or harvested by recreational anglers and brought to the Confluence or Intake for cleaning. Beginning in 1991, dentaries were removed from most tagged fish brought into the cleaning stations. Other data available from mark-recapture tagging efforts included tag and recovery dates and locations, BL and weight, and sex (for harvested fish).

Life History Variables

Size of Mature Fish

Length- and weight-frequency distributions, as well as mean lengths and weights of harvested paddlefish by sex were summarized annually from 1991 to 2004.

Population Age Structure

Age was determined for a total of 22,800 fish over the period 1991–2004, 12,124 fish (6,215 males, 5,909 females) from the Montana harvest and 10,676 fish (5,688 males, 4,988 females) from the North Dakota harvest. Dentaries were removed, cleaned of excess flesh, and stored dry in individual envelopes. The dentaries were later cleaned and sectioned as described in Scarnecchia et al. (1996b) and ages assessed by counting annuli (Adams, 1942; Meyer, 1960; Scarnecchia et al., 2006) using a Biosonics Optical Pattern Recognition System. From 1999 to 2004, a two-reader double-blind protocol was used, along with a tolerance for minor disagreement. In this protocol, two persons (designated primary and secondary readers) aged the sections separately. If there was agreement (plus or minus 1 year for fish under age 20, plus or minus 2 years for ages 20 to 34, and plus or minus three for ages 35 and over), the final age was assigned by the primary reader. If the ages differed by more than the criteria, the sections were read independently again. If the age estimates still did not meet agreement criteria, the section was aged with both readers in consultation and a final age was assigned by the primary reader. The accuracy of age determination using dentaries was validated (Campana, 2001) for young recruits (age 10 and under) based on recoveries of known-age, coded-wire tagged fish and partially validated for older recruits based on jaw-tag recoveries (Scarnecchia et al., 2006). The precision of age determination was verified as being within acceptable boundaries (Campana, 2001) based on coefficients of variation between two readers (Scarnecchia et al., 2006). Mean ages of fish caught in Montana and North Dakota were compared with a Wilcoxon's two-sample test. The null hypothesis was that mean ages of fish caught in both states would be the same.

Age at Maturity

Age at maturity was assessed by visual inspection of testes and ovaries from harvested fish, using criteria outlined in Bruch et al. (2001). Mature females were clearly identifiable as having Stage 4, grey-black eggs. Mature males were identifiable by the presence of well-developed testes, described by Larimore (1950) as "two ribbon-like bands extending anteriorly along the lateral margins of the dorsal surface of the body cavity . . . , suspended . . . from the dorsal wall and . . . concealed ventrally by heavy layers of fat" (p. 119). In 2002, to ascertain that the testes were from mature fish, gonad samples were taken from 88 males (61 from the Confluence, 27 from Intake) and evaluated with histological methods. Formalin-fixed tissues were trimmed into pieces and embedded in paraffin blocks. A rotary microtome was used to make 8- μ m sections of tissue, which were floated onto a glass slide and air dried overnight. The tissue sections were later stained with Harris's hematoxylin and eosin (H and E) staining protocol. A glass cover slip was adhered to the tissue on the slide with mounting media and then air dried before examination under a microscope.

Longevity

Longevity was assessed by the number and percentage of fish reaching age 30, as well as by the maximum age of fish harvested each year. Sex-specific differences in longevity were

evaluated by comparing the frequencies of male and female fish age 30 and over for each year from 1991 to 2004 with a Chi-square test.

Growth

Growth of male and female paddlefish was described with a von Bertalanffy growth function, expressed as $L = L_{\infty} e^{(1-K(t-t_0))}$, where L is length, L_{∞} is the asymptotic length, K is the Brody growth coefficient, and t_0 is the initial condition parameter (Ricker, 1975; Moreau, 1987; Chen et al., 1992). Data from 2003 and 2004 were selected for analysis. In addition to fitting the three parameter model, a two parameter model (i.e., $t_0 = 0$) was fit to data from four years (1996, 1997, 2003, 2004) to force the data for both sexes through the origin ($L = 0, t = 0$). The latter approach enabled us to extrapolate the approximate age when males and females diverged in their growth trajectories. Weight-converted von Bertalanffy equations were also calculated, expressed in terms of L as $W = aL^b$, where W is the weight.

Post-maturation growth of all fish was also estimated by comparing lengths and weights of fish at the time of tagging and recapture. We hypothesized that once fish were mature, little or no growth in length or weight would occur. To test this hypothesis, growth (weight gain or loss) was compared among individual fish tagged and recaptured at least eight years apart. Growth for these fish was expressed as weight change per year, i.e., as the weight gain or loss divided by the number of years between tagging and recapture.

Reproductive Periodicity

Reproductive periodicity of males and females was determined from the number of years to the first peaks in returns of tagged migratory fish. Fish tagged in Montana were tagged and recovered only in the period May to early July, so that the elapsed years between tagging and recovery adequately represented reproductive periodicity. In North Dakota, however, fishes returning to spawn in a given year were sometimes found to enter the Missouri River downstream of the Confluence the previous fall, when they were sometimes captured during fall gill netting activities, a two-step spawning migration as described for other Acipenseriform fishes by Bemis and Kynard (1997). As a result, a fish with a reproductive cycle of two years might be caught in successive years by being tagged in spring and recaptured during fall of the next year. Similarly, a fish with a reproductive cycle of three years might be caught at a two-year interval. Whereas pre-spawning fish were found by Firehammer (2004) to linger in the Missouri River for long periods before the following year's upstream migration, post-spawning fish migrated rapidly downriver into the reservoir, and were seldom caught in the fall. As a result, sex-specific reproductive periodicity for fish tagged in North Dakota was evaluated using only those fish tagged and recovered before August. Reproductive periodicity of individual fish was also evaluated in relation to the age of the fish at the time of harvest. The null hypothesis, that mean ages of fish with different reproductive periodicities would be the same, was evaluated with a Kruskal-Wallis test separately for Montana-caught and North Dakota-caught fish.

Fecundity

Fecundity for both sexes was estimated from gonadal weights. Gonadal weight of females was determined by recording, to the nearest 4.54 g (0.01 lb.), the fresh weight of unprocessed roe (called hard roe by Ryder (1890), but hereafter called green egg weight), which included

all ovarian tissue and fat in the interstices between individual eggs. Gonadal weight of males was determined by weighing the testes to the nearest gram after they had been manually separated from any attached fat. Gonadal weight was expressed as a distinct variable, as well as converted into the gonadosomatic index (GSI), i.e., gonadal weight as a percentage of fish weight (DeVlaming et al., 1982; Crim and Glebe, 1990).

Weight and Composition of Gonadal Fat Bodies

Each testis and ovary had attached to it a clump of discrete, consolidated, easily identifiable fatty tissue, hereafter called a gonadal fat body (GFB). From 2001 through 2003, GFBs were weighed from nearly all (> 90%) of fish brought into each cleaning station. Each GFB was separated manually from the gonads and weighed to the nearest gram. Weights of the paired GFBs were combined for each fish and identified by the angler tag number.

In 1997, sub-samples of the GFBs were collected from 29 fish, 13 males and 16 females, for lipid analysis. Samples were identified by angler tag number, preserved in dry ice, and delivered within 48 h to the U. S. Fish and Wildlife Service Laboratory at Bozeman, Montana, for analysis. All samples were stored at -20°C from receipt until the day of processing. Each thawed sample was weighed and an equivalent (or multiple) mass of distilled water was added prior to grinding and homogenizing. After grinding, a 200-ml aliquot of the homogenate was collected and decanted to an evaporation dish and placed in a drying oven. Two small weighed aliquots were also collected and used for moisture determination. The dried material generated from the 200-ml aliquot was sub-sampled in duplicate and each sub-sample subjected to Soxhlet extraction with purified ether. The recovered solvent-free residues were weighed and averaged. Results were expressed as percent lipids, percent moisture, and all other substances combined. For each sex, the ratio of GFB weight to gonad weight, percent lipids, and the age of the fish were compared to investigate if any relationship existed among them. Ratios of GFB weight to gonad weight (Y) in relation to percent lipids (X) were fitted for each sex separately with an exponential (decay) model $Y = Ce^{-(100-X)/T}$ where e is the base of the natural logs, and C and T (the time constant of the decay curve) are parameters. The equations were also linearized ($\log_e Y$ versus X), linear regressions fit, and tested for significance at $p = 0.05$.

Energetic Tradeoffs between Somatic Growth and Reproductive Investment in Extreme Cases

Large sample sizes permitted us to separate out an adequate, non-random sub-sample of individual fish exhibiting major individual deviations in growth that might provide additional insight into the energetic tradeoffs between somatic growth and reproduction. Especially long (≥ 132.5 cm BL) and heavy (≥ 46.5 kg) female fish were evaluated against 200 randomly chosen female fish for GSI and the weights of GFBs. The few males greater than 25 kg were also identified and their reproductive status assessed according to established criteria (Scarnecchia et al., 1996c; Bruch et al., 2001). Our hypothesis was that the longest and the heaviest females would have significantly lower GSI values than random mature females, as a result of directing more of their energy into somatic tissue growth and less into reproduction. The hypothesis was evaluated with a Wilcoxon two-sample test. For both females and males, abnormally large fish might be associated with a high incidence of complete or partial failure in the reproductive system, in which more energy had been

diverted into somatic growth rather than into reproduction. This possibility was investigated by examination of abnormalities of gonads from fish observed at the cleaning stations.

Migration Location Fidelity in Relation to Tagging Location (State), Sex, and Age

It was hypothesized that if migration location (and possibly spawning site) fidelity occurred in this stock, North Dakota-tagged fish (i.e., fish tagged downriver) should be recaptured at a higher frequency in North Dakota (i.e., downriver) than in Montana (i.e., upriver) in subsequent years and Montana-tagged fish (i.e., fish tagged upriver) should be recaptured at a higher frequency in Montana (i.e., upriver) than in North Dakota (i.e., downriver) in subsequent years. Upriver and downriver migration location fidelity was also evaluated separately in relation to sex of fish as well as by age group (males: ages 15 and under, 16–25, 26 and over; females: ages 25 and under, 26 and over) using Chi-square tests. In all comparisons, the null hypothesis was that there were no differences in migration fidelity in relation to tagging location (Montana or North Dakota), sex, or age group.

Mortality Rates

Total mortality rates (Z) of fully-recruited male and female paddlefish were estimated with catch curves (Ricker, 1975), expressed as the negative slope of a plot between the natural logarithm of the numbers caught versus age for all fully-recruited age classes. Because of documented variations in year class strength and spawning success (North Dakota Game and Fish Department, Unpublished Data), the assumption of constant recruitment was not appropriate. To smooth out the annual variations in recruitment, a composite catch curve was calculated separately by sex for all years from 1991 to 2004 for the Montana-caught fish as a group and the North Dakota-caught fish as a group. The catch curves were fitted by regression methods and slopes of curves compared with a t -test. The null hypothesis was that mortality rates for males and females did not differ.

Three tag groups from Montana (i.e., all fish tagged in 1984, 1986, and 1988) and five tag groups from North Dakota (all fish tagged both spring and fall, 1993, 1994, 1996–1998) were used to compare harvest rates between males and females. Sex at the time of tagging was not absolutely known. However, inasmuch as nearly all mature female fish in this stock have previously been found to be heavier than nearly all mature male fish (Scarnecchia et al., 1996b), the sex of fish at the time of tagging was assigned by plotting the weight-frequency distributions from the harvested fish for the corresponding periods (1984, 1986, 1988 for Montana; 1993, 1994, 1996–1998 for North Dakota) and determining the weight at which the highest percentage of fish would be assigned the correct sex. Sex was then assigned accordingly for all fish jaw tagged that year. An absolute determination of the sex of harvested fish was made at the time of harvest, and errors in the assignment of sex were corrected. From this approach, harvest rates of putative male and female fish were calculated for the six tag groups and rates compared with Chi-square tests. The null hypothesis in each case was that harvest mortality rates for males and females would be the same.

Senescence

Senescence was defined by Partridge (1987) as “the innate deterioration in the body, leading to a decline in adult fitness components, such as life expectancy and fertility with increasing age” (p. 317). Senescence was evaluated in three ways: by investigating the total mortality

rate (Z), the condition (expressed as relative weight (Wege and Anderson, 1978), including gonadal weight, for males and females separately) by age, and the fecundity (for females) by age. If senescence was occurring, we hypothesized that mortality rates, as expressed by the catch curves, would be higher for older fish than for younger recruits. For condition, it was hypothesized that the oldest males (age 30 and over) would have lower condition (i.e., be leaner) than young recruits (age 15 and under) and middle-aged recruits (ages 16–29). It was also hypothesized that the oldest females (age 35 and over) would have lower condition than young recruits (age 22 and under) and middle-aged recruits (ages 23–34). Condition was expressed as relative weight $W_r = W/W_s$ (Anderson and Neumann, 1996), where W_s was sex-specific standard weights for paddlefish as calculated by Brown and Murphy (1993). For fecundity, we hypothesized that the oldest females in Montana and North Dakota (age 36 and over) would have a lower mean GSI, than middle-aged females (ages 28–35). Fecundity comparisons were conducted separately for Montana and North Dakota fish. All comparisons for condition and fecundity were made with Wilcoxon's two-sample test.

Results

Size of Mature Fish

More than 90% of mature fish were identifiable as male or female by length or weight alone since little overlap was observed in either BL or weight of male and female fish. At Intake in 1991, for example, only 22 of 1,121 males (2%) reached a length in or above the interval of 107.5–112.5 cm BL, whereas only 114 of 1,495 females (7.6%) were short enough to be in this interval. Weights also showed little overlap. Only one of 1,452 males (<1%) reached the 20–25 kg weight interval, whereas only 131 of 1,868 females (7%) weighed little enough to be in this interval. In 1993, only 21 of 1,075 males (2%) reached a length in or above the interval of 107.5–112.5 cm BL, whereas only 78 of 583 females (13.3%) were short enough to be in this interval. This overall pattern of sexual size dimorphism—distinctly larger females than males—held for all years from 1991 to 2004.

Population Age Structure

Mean ages of females harvested were significantly greater than for males in all years 1991–2004 in both states (Wilcoxon two-sample test, $p < 0.01$; Tables 1 and 2), except for 1992 in North Dakota, when no differences were found.

Distinct differences in mean age structure were identified between fish harvested downriver in North Dakota and fish harvested upriver in Montana over the period 1991–2004. Fish harvested downriver were significantly older than fish harvested upriver for all 14 years for males (Wilcoxon two-sample test, $p < 0.01$) and 11 of 14 years for females ($p < 0.01$; Tables 1 and 2). The three exceptions, where upriver age exceeded downriver age were 1991 ($p = 0.01$) 1992 ($p = 0.01$), and 1997 ($p < 0.01$). Annual mean age of males from North Dakota ranged from 17.7 (1997) to 23.1 (2003), whereas annual mean ages of males from Montana ranged from 12.4 (1996) to 18.4 (1991). In 2003, for example, mean age of males in North Dakota (23.1) was more than 8 years greater than in Montana (14.9); mean age of females in North Dakota (28.3) was more than 6 years greater than in Montana (21.7). In 2004, mean age of males in North Dakota (19.5) was more than three years greater than in Montana (16.3); mean age of females in North Dakota (27.8) was nearly three years greater than in Montana (25.0; Tables 1 and 2). Mature males age 15 and under constituted high

Table 1
Age (years) summary for paddlefish caught in North Dakota, 1991–2004

Year	Males							Females						
	No. of fish	Mean age (yr)	%fish <8 yr	%fish <16 yr	%fish ≥30 yr	No. fish ≥30 yr	Max. age (yr)	No. of fish	Mean age (yr)	%fish <16 yr	%fish ≥30 yr	No. fish ≥30 yr	Max. age (yr)	
1991*	74	20.7	0	10.8	4.1	3	37	54	24.1	0	7.4	4	33	
1992	19	22.1	0	5.2	10.5	2	33	22	24.3	0	4.5	1	34	
1993*	48	22.1	0	33.3	0	0	29	72	25.2	0	9.8	7	35	
1994*	368	18.4	<1	35.1	3.0	11	43	471	25.1	<1	13.2	62	39	
1995*	567	21.5	0	17.1	7.2	41	40	548	28.1	0	35.2	193	44	
1996*	297	22.9	0	24.9	15.2	45	45	325	29.8	<1	59.1	192	45	
1997*	315	17.7	0	36.8	<1	1	34	297	24.6	<1	16.5	49	37	
1998*	667	20.7	0	28.6	11.2	75	42	625	28.1	<1	38.2	239	48	
1999*	466	20.2	<1	23.4	2.8	13	35	413	26.3	<1	24.2	100	44	
2000*	454	19.3	<1	30.2	3.7	17	45	400	26.2	1	25.8	103	45	
2001*	726	22.3	<1	18.4	12.9	94	40	549	26.7	<1	34.4	189	45	
2002*	841	23.0	<1	17.7	20.2	170	53	454	27.9	1.7	47.8	217	50	
2003*	434	23.1	<1	20.1	24.9	108	49	356	28.3	<1	49.7	177	47	
2004*	412	19.5	<1	41.0	19.4	80	46	402	27.8	<1	43.3	174	47	
Total	5688					660		4988				1707		
Percent age ≥30						11.6						34.2		

Asterisk (*) denotes a significant difference ($p < 0.01$) in mean age between males and females.

Table 2
Age (years) summary for paddlefish caught in Montana, 1991–2004

Year	Males							Females						
	No. of fish	Mean age (yr)	%fish <8 yr	%fish <16 yr	%fish ≥30 yr	No. fish ≥30 yr	Max. age (yr)	No. of fish	Mean age (yr)	%fish <16 yr	%fish ≥30 yr	No. fish ≥30 yr	Max. age (yr)	
1991*	721	18.4	1.3	33.7	5.0	36	40	975	25.5	<1	14.8	144	42	
1992*	219	17.8	<1	39	2.3	5	33	471	26.2	<1	21.0	99	40	
1993*	1144	15.8	<1	47.2	<1	8	35	605	22.8	3.3	6.0	36	38	
1994*	1116	15.0	1.7	56.9	0	0	29	190	23.0	2.6	5.3	10	35	
1995*	769	14.7	<1	69.6	2.9	22	40	582	26.7	2.6	35.4	206	49	
1996*	630	12.4	0	86.0	<1	4	42	466	25.5	<1	23.8	111	41	
1997*	488	14.1	0	70.0	1.8	9	37	297	25.6	<1	24.9	74	41	
1998*	295	15.3	<1	68.8	3.1	9	34	276	25.1	1.8	22.8	63	43	
1999*	587	15.5	<1	62.4	1.7	10	42	703	22.3	5.3	10.2	72	43	
2000*	216	15.3	4.6	64.8	2.3	5	38	282	24.6	2.5	25.2	71	50	
2001*	149	18.1	<1	45.6	9.4	14	48	177	23.4	1.1	13.0	23	43	
2002*	394	18.5	5.84	45.4	17.3	68	45	316	23.5	3.8	26.0	82	56	
2003*	387	14.9	0	67.4	9.8	38	43	447	21.6	<1	12.3	55	47	
2004*	100	16.3	0	64.0	12.0	12	41	122	25.0	0	28.0	34	44	
Total	6215					240		5909				1080		
Percent age > 30						3.9						18.3		

Asterisk (*) denotes a significant difference ($p < 0.01$) in mean age between males and females.

fractions of the male fish harvested in Montana from 1991 to 2004, ranging from 34% (1991) to 86% (1997; Table 2). A much lower percentage of the North Dakota harvest of males consisted of fish age 15 and under (5–41%; Table 2).

Age at Maturity

The differences in age structure were in part a result of distinct differences between males and females in age at maturity. Males matured, migrated upriver, and entered the harvest several years younger than females. Males began to enter the fishery at about age 8, and most had recruited by age 10–12. There was great consistency among years (1991–2004) and states in the first age at maturity; in nearly all years fewer than 1% of the harvested males were less than age 8 (Tables 1 and 2). Age 8 and age 9 migratory males were observed to have fully developed gonads. The observation of the sexual maturity of males of various ages was corroborated by histological analysis. Of 88 males evaluated histologically, ranging from age 6 (a 4.5-kg male) to age 37, all but three fish (ages 26, 26, and 31) had at least some fully developed spermatocytes.

Females of the same brood year thus entered the fishery several years later than males of their cohort. As with males, however, there was great consistency among years (1991–2004) and between states in age at maturity. Females began to mature and enter the fishery at about age 15 (Tables 1 and 2), and most had recruited by ages 17–19. The percentage of females age 15 and under ranged from less than 1% to a maximum of 5.3% over the period 1991–2004. Evidence of immature status of the young fish came from a review of the maturation data from the 30 females age 15 and under caught in North Dakota. Twelve of the 30 fish were specifically identified as having immature eggs (stages 1–3, unsuitable for processing into caviar), and only three fish resulted in processed caviar exceeding 2.2 kg in weight. In contrast, nearly all of the 4,958 females age 16 and over had fully developed stage 4 eggs.

Longevity

Based on the harvested fish, female longevity was on average greater than for males. For males, only 240 of 6,215 (3.9%) Montana-caught fish and 660 of 5,688 (11.6%) North Dakota-caught fish were age 30 and over (Tables 1 and 2). For females, in contrast, 1,080 of 5,909 (18.3%) Montana-caught fish and 1,707 of 4,988 (34.2%) North Dakota-caught fish were age 30 and over (Tables 1 and 2). A fish reaching age 30 was significantly more likely to be a female than a male for every year over the period 1991–2004 (Chi-square test, $p < 0.0001$). Overall, a fish reaching age 30 was more than four times more likely to be a female than a male in Montana and more than three times more likely to be a female than a male in North Dakota. Although longevity beyond age 30 was on average less common for males than for females, the oldest individual males were often as old as the oldest females. A few males and females exceeded age 40 in most years; only two fish exceeded age 50, one male and one female (Tables 1 and 2).

Growth

Paddlefish growth curves also differed markedly between males and females (Figures 2 and 3), a pattern consistent every year from 1991 to 2004. Mature females reached a greater maximum length and weight than mature males, and were both longer and heavier than

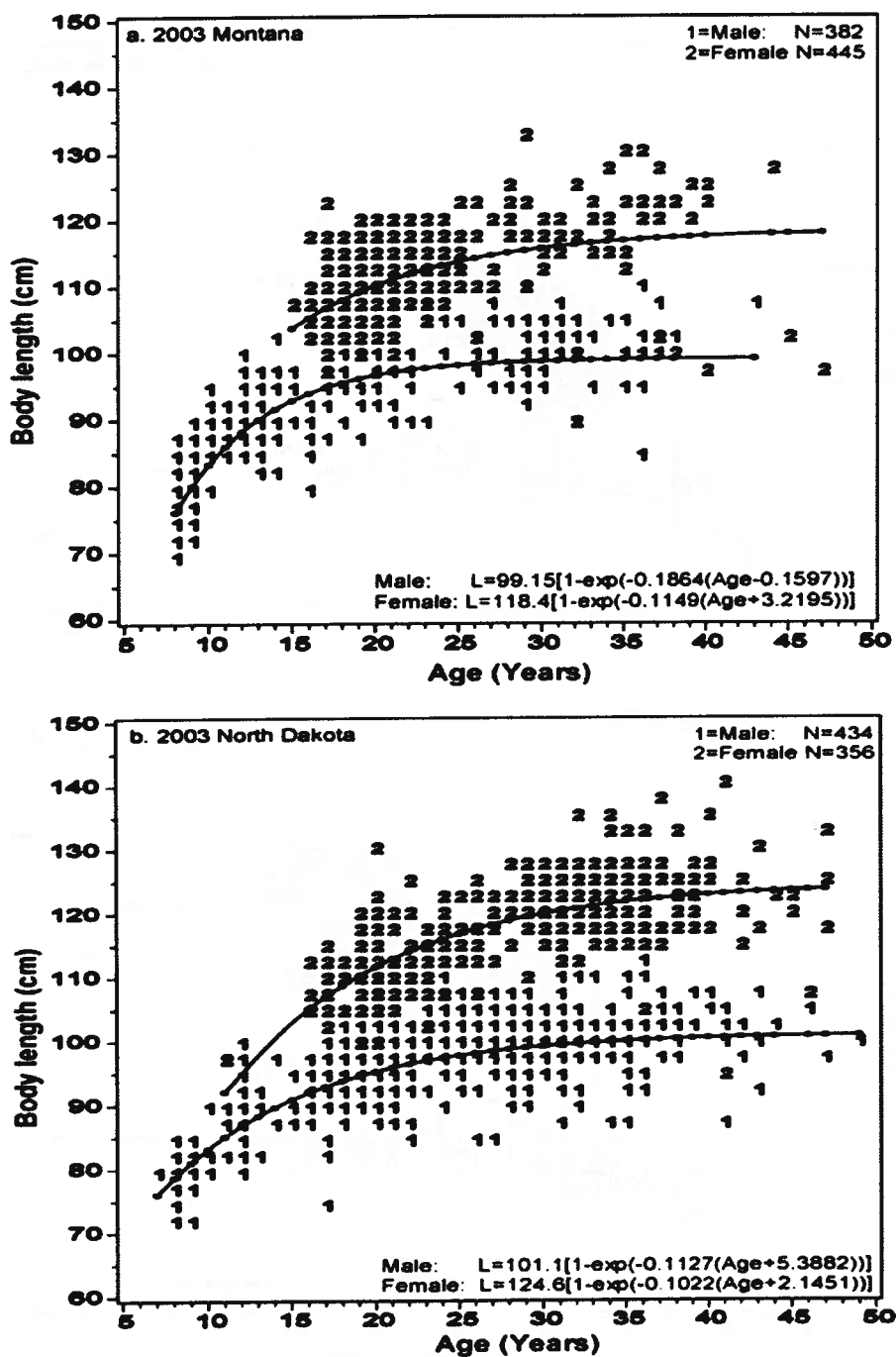


Figure 2. von Bertalanffy growth curves for (a) Montana paddlefish and (b) North Dakota paddlefish, 2003.

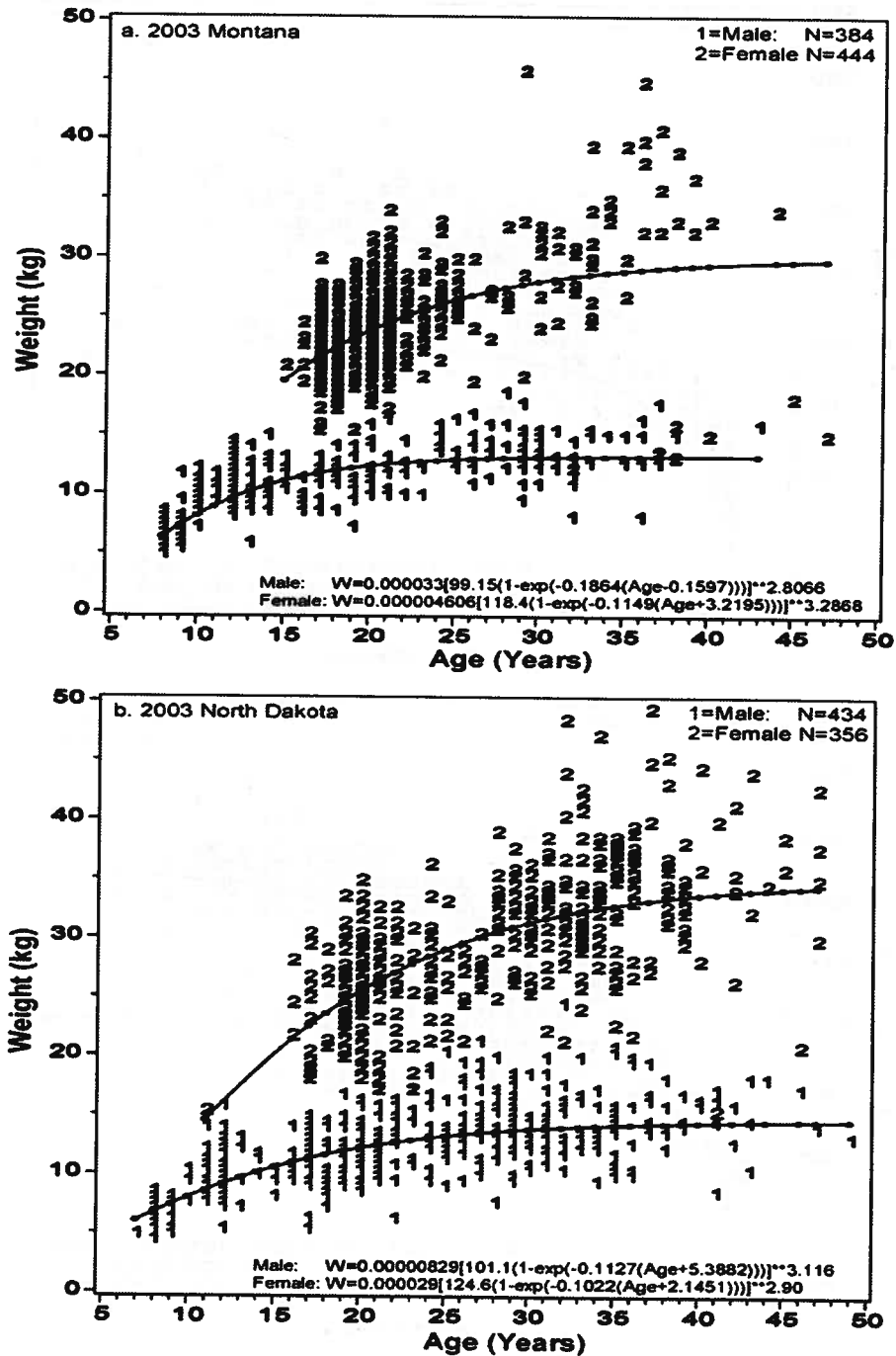


Figure 3. Weight-converted von Bertalanffy growth curves for (a) Montana paddlefish and (b) North Dakota paddlefish, 2003.

mature males at all ages. In 2003, the L_{∞} value was higher for females (118.4 cm BL) than for males (99.1 cm BL) in Montana and higher for females (124.6 cm BL) than for males (101.1 cm BL) in North Dakota (Figures 2a,b). Estimated W_{∞} values were also higher for females (30 kg and 34.5 kg) than for males (14 kg and 14.5 kg) for Montana and North Dakota, respectively (Figures 3a,b). Similar differences were found in 2004. For example, L_{∞} values were 121.0 cm BL and 124.8 cm BL for females and 101.3 cm BL and 101.3 cm BL for males in Montana and North Dakota, respectively. W_{∞} values were 32.4 kg and 35.5 kg for females and 14.8 kg and 15.1 kg for males in Montana and North Dakota, respectively. Considerable variation existed in growth of individual fish, as indicated by the scatter of points around the fitted lines for 2003 (Figures 2a,b and 3a,b).

The use of the two-parameter von Bertalanffy model, which produced a slightly worse fit than the three-parameter model but forced the curves through the origin, permitted extrapolations of growth when fish were in the reservoir and not available for sampling. The exact age at which curves for the two sexes merged differed among the four years investigated (1996, 1997, 2003, and 2004) and between the states, ranging from age 5.5 in 2003 for Montana to age 10.2 for 2004 in North Dakota. Males and female size at age was similar until somewhere between ages 5 and 10, but diverged thereafter as males of a given brood-year slowed their growth and began sexual maturation. Females of that brood year, in contrast, continued growing more rapidly than males and would not begin maturation for several years.

Once sexual maturity was reached, subsequent growth in length and weight slowed, as readily seen from three sources: from the von Bertalanffy growth curves, from the annulus spacing on dentaries, and from changes in weight and length of recaptured mature fish tagged at least 8 years earlier. Growth continued until about age 20 in males and age 25 in females, when growth curves closely approached the asymptote (Figures 2a,b and 3a,b). As seen from dentaries (Plate 1), growth of males was rapid until about age 5–7 and then slowed as maturation began. Late in life, annuli on dentaries were tightly packed, consistent with the asymptotic portion of the von Bertalanffy curves. In contrast, dentaries from females indicated that growth was rapid until about age 13–14 and then slowed as maturation began. In later years, their dentary annuli were also tightly packed (Plate 2). Based on recaptures of fish tagged at least 8 years previously (which are typically older fish), male fish in their middle and later years grew little, generally less than 7.5 mm per year, and not more than 16.5 mm per year expressed over these periods of eight or more years. A typical male gained only from 0.1 to 0.3 kg per year (Figure 4a), a typical female 0.1–0.5 kg per year (Figure 4b) expressed over these periods of eight or more years. Many fish also lost weight. Thirteen percent of males and 29% of females lost weight at a rate of at least 0.1 kg per year (expressed over the 8 or more year period) between tagging and recapture (Figure 4).

Reproductive Periodicity

The reproductive periodicity interval (i.e., period of gonadal recrudescence) was shorter for males than for females. For male fish tagged in Montana, most recoveries occurred in the second year after tagging, indicating that the most common reproductive periodicity was two years (Figure 5a). In contrast, most recoveries of females occurred three years after tagging, indicating that the most common reproductive periodicity was three years (Figure 5b). A secondary peak in returns occurred six years after tagging. Unlike males, few females made spawning migrations in successive years; only seven females from Montana were recaptured

Male

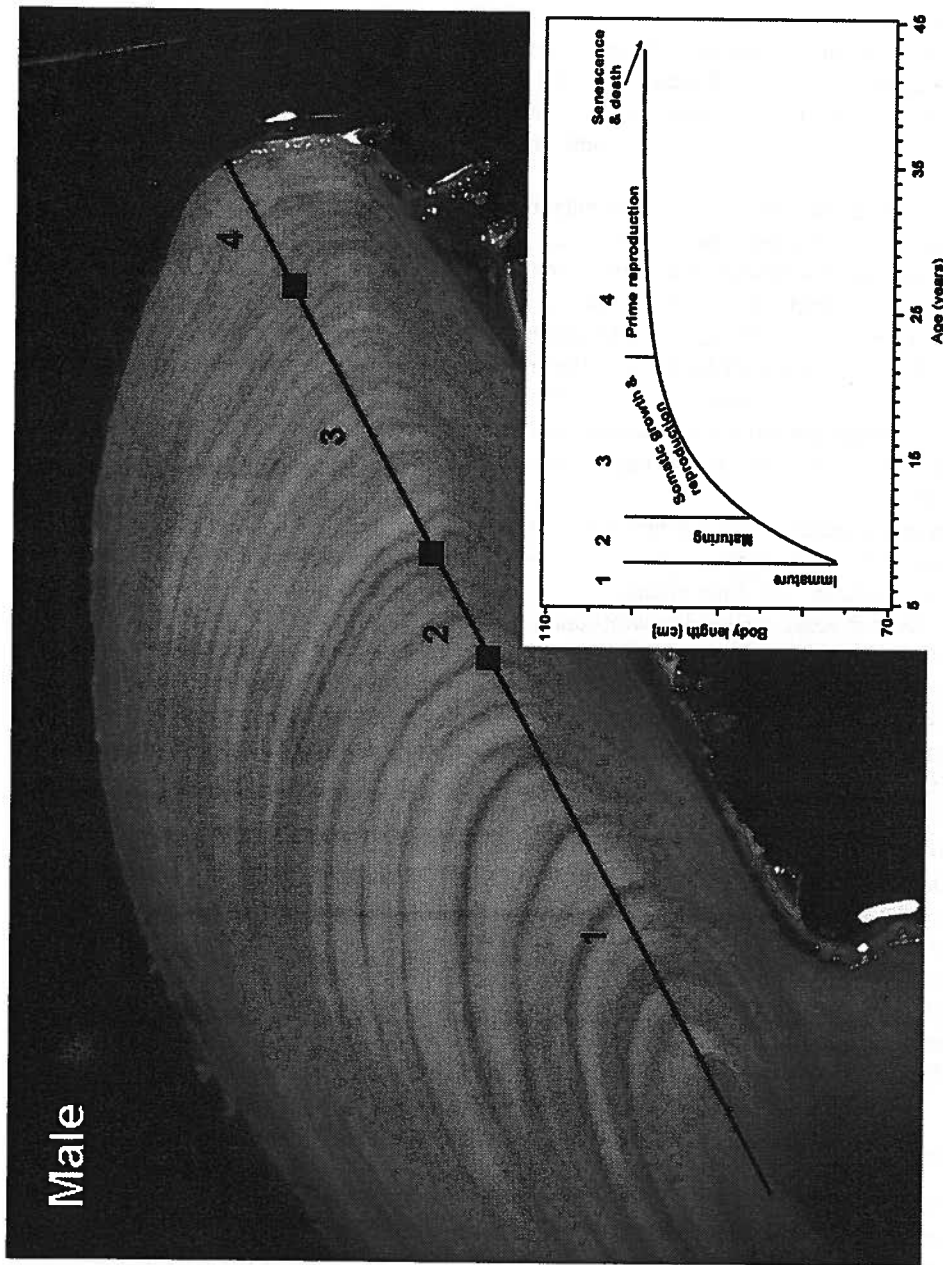


Plate 1. Cross-section of paddlefish dentary from a male paddlefish (BL 107 cm, 15.9 kg in weight; estimated age 40 years) showing approximate periods identified as (1) immature, (2) maturing, (3) somatic growth and reproduction, (4) prime reproduction, and (5) senescence and death. Insert shows approximate ages associated with these five periods. Correspondence between annuli spacing on dentary and growth as depicted in the insert is only approximate because each fish has a unique growth and maturation history and trajectory.

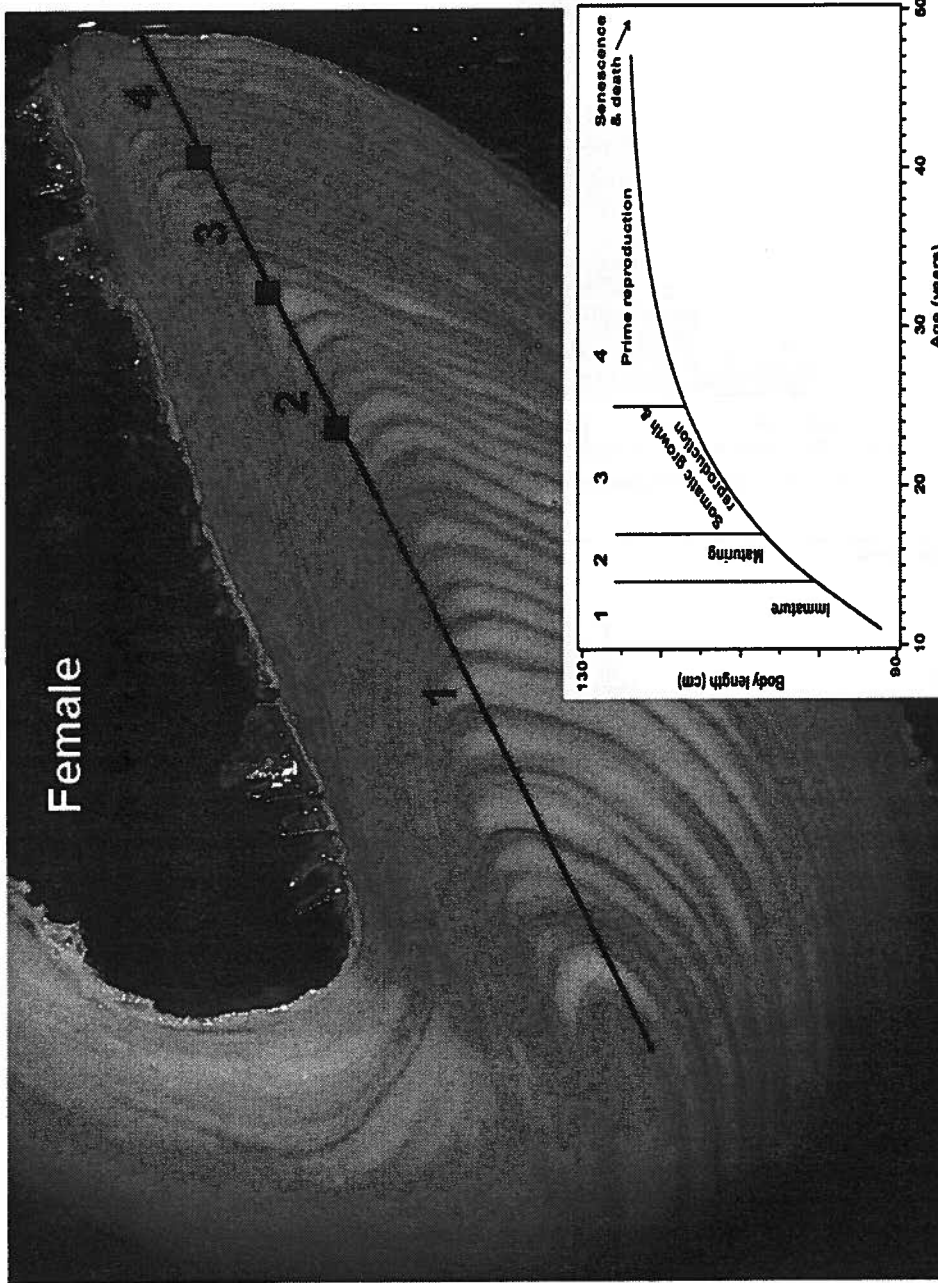


Plate 2. Cross-section of paddlefish dentary from a female paddlefish (BL 127 cm, 34.1 kg in weight; estimated age 39 years) showing approximate periods identified as (1) immature, (2) maturing, (3) somatic growth and reproduction, (4) prime reproduction, and (5) senescence and death. Insert shows approximate ages associated with these five periods. Correspondence between annuli spacing on dentary and growth as depicted in the insert is only approximate because each fish has a unique growth and maturation history and trajectory.

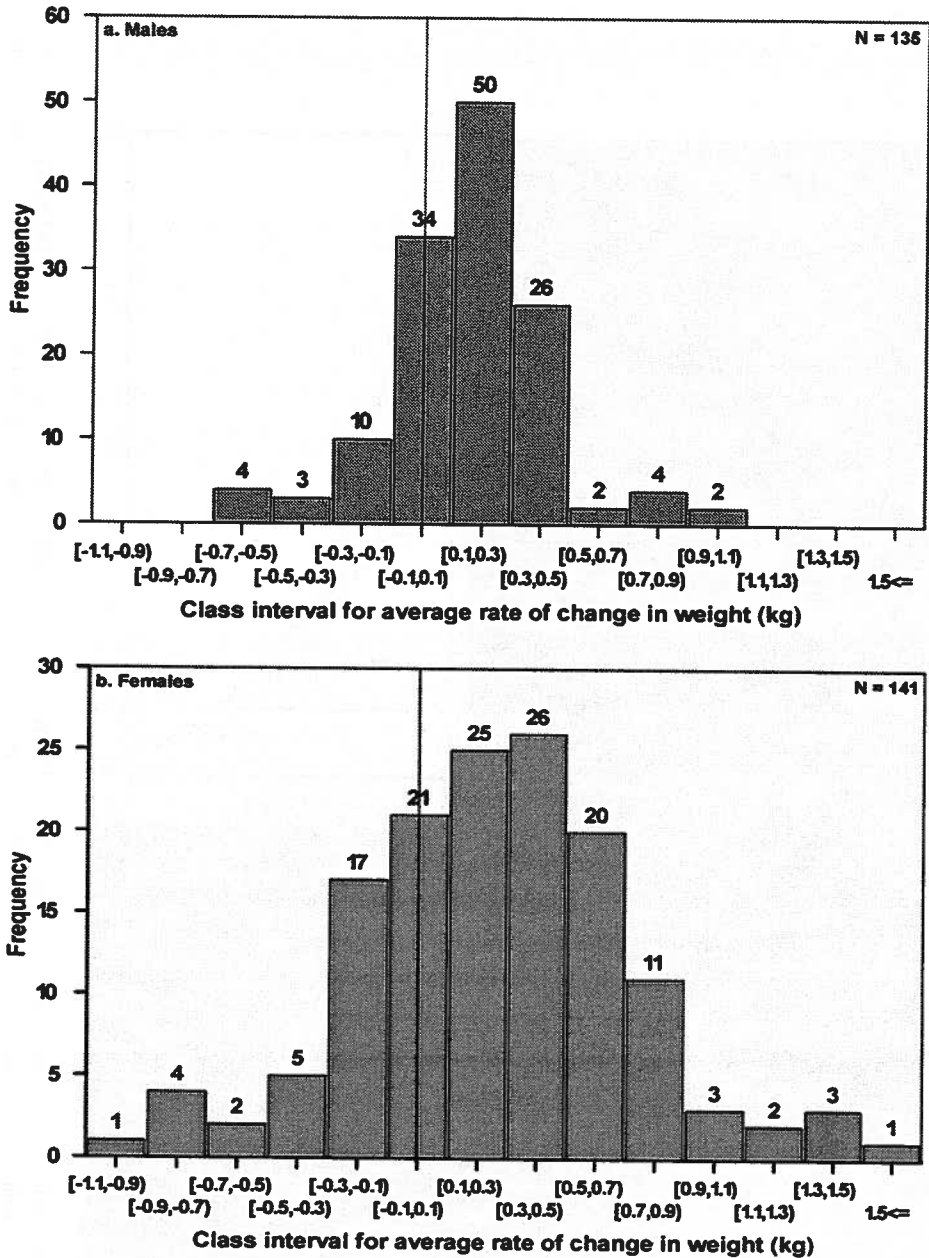


Figure 4. Change in weight per year for male and female paddlefish tagged and recaptured at least 8 years apart, Montana and North Dakota-caught fish combined. Change was calculated as the difference in initial and final weights divided by the number of years between tagging and recapture.

one year after tagging, whereas 68 were recaptured two years after tagging and 106 were recaptured three years after tagging (Figure 5a,b).

The reproductive periodicity for fish tagged before August in North Dakota was on average shorter than for Montana. For males, the frequencies of recapture after one and two years were comparable, indicating that reproductive periodicity was one or two years,

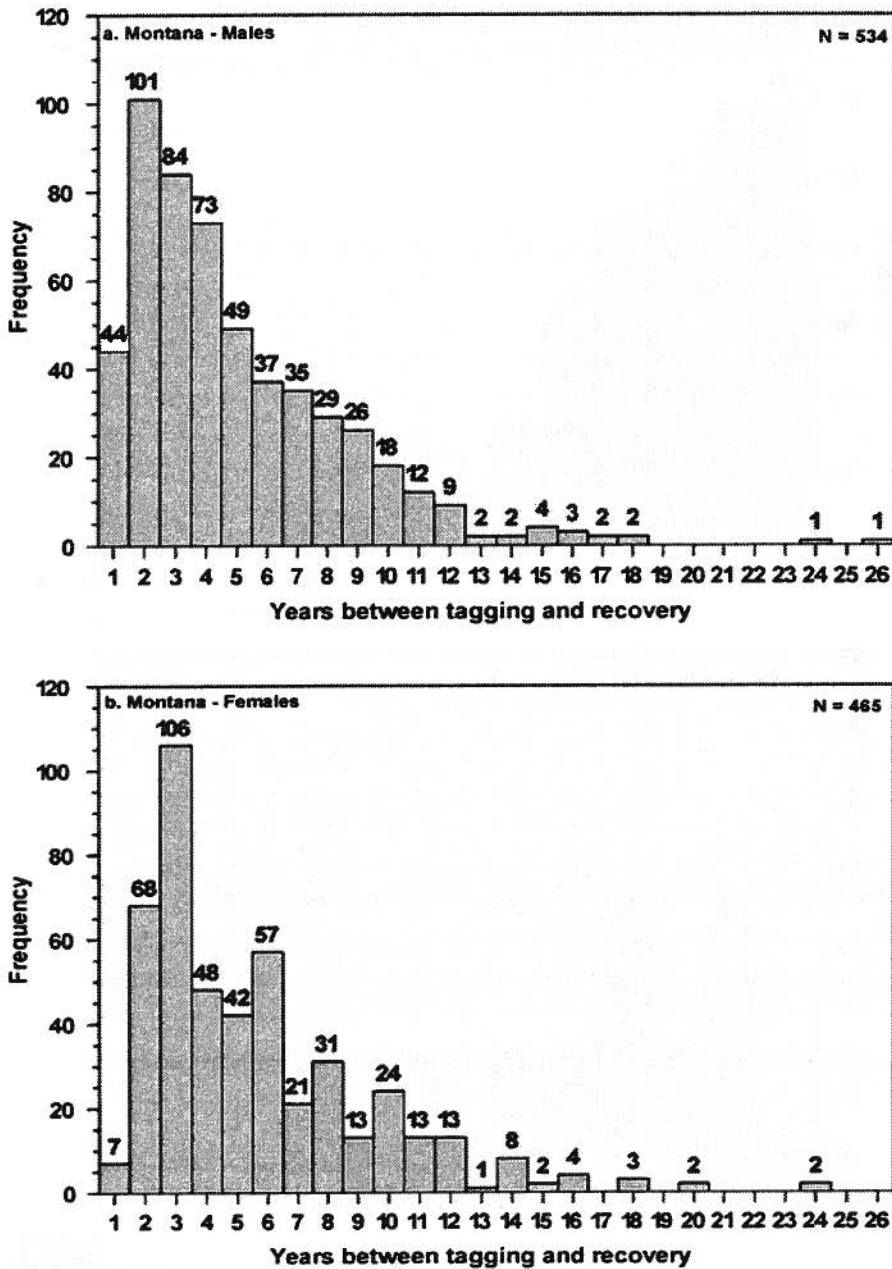


Figure 5. Frequency distribution of the number of years between tagging and recovery for Montana-caught fish (a) males and (b) females, 1964–2004. Peak recoveries are reported two years after tagging for males and three (and six) years after tagging for females.

with similar probabilities (Figure 6a). For females, peak recaptures occurred not three years later, as for Montana-tagged fish, but two years and four years later, indicating a typical reproductive periodicity of about two years (Figure 6b). Although the shorter reproductive periodicity for North Dakota-caught fish than for Montana-caught fish was associated with

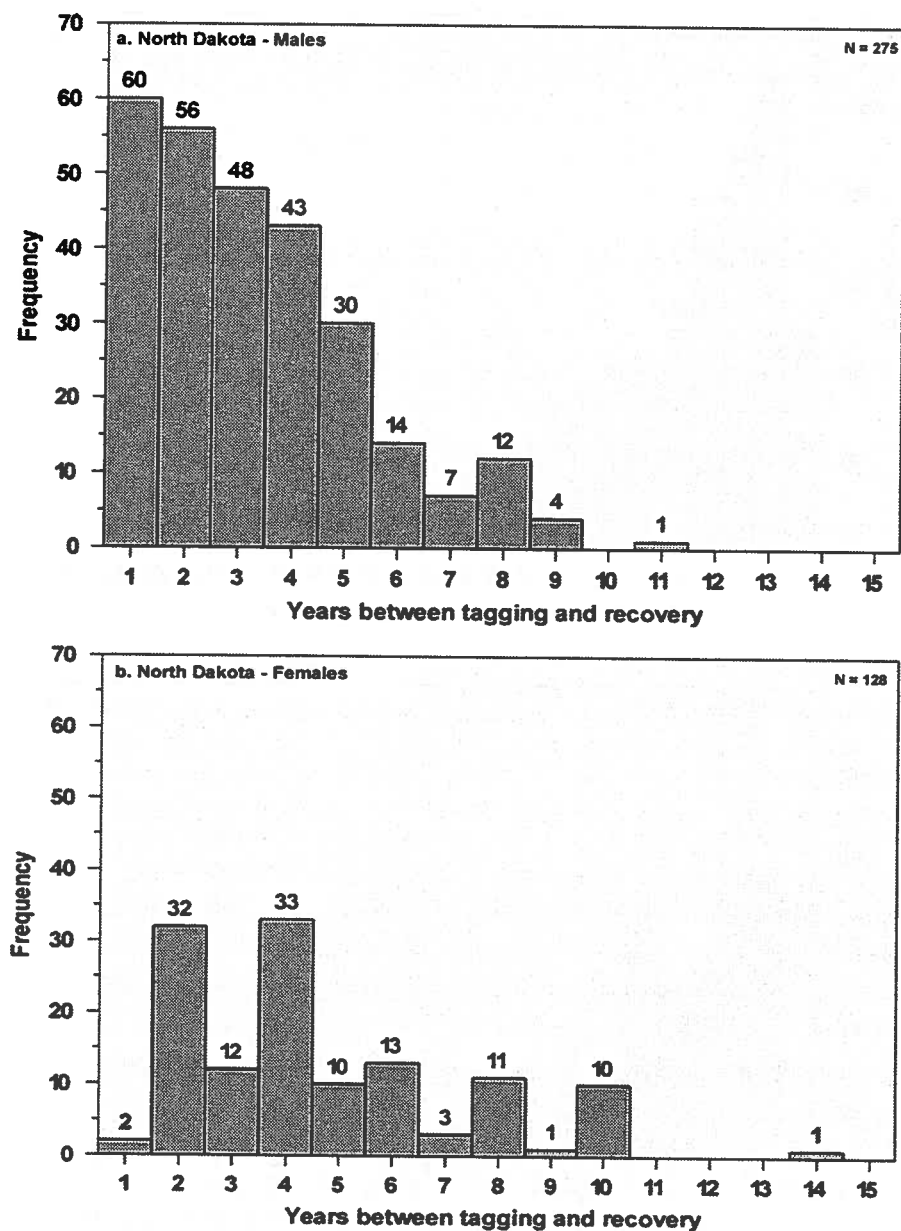


Figure 6. Frequency distribution of the number of years between tagging and recovery for North Dakota-caught fish (a) males and (b) females, 1993–2004. All fish were tagged and recaptured before August. Peak recoveries are reported one or two years after tagging for males and two (and four) years after tagging for females.

the greater mean age of the North Dakota fish (Tables 1 and 2), there was no evidence that *within* either group of fish, older age was associated with a shorter reproductive periodicity. For Montana-caught females, the mean age of fish with a two-year periodicity (25.1; $n = 35$) was not significantly different than for those with a three-year periodicity (25.1; $n = 37$; Kruskal-Wallis Test, $p = 0.91$) For Montana-caught males, mean age of fish with

a two-year periodicity (16.6; $n = 53$) was not significantly different than for those with a one-year periodicity (15.3; $n = 26$; Kruskal-Wallis test, $p = 0.45$). Similar results were found for the North Dakota-caught fish. No significant differences were found in mean age for females with a three-year periodicity (26.6, $n = 11$) and those with a two-year periodicity (28.3; $n = 27$; t-test, $p = 0.45$). For males, no significant differences were found in mean age between fish with a two-year periodicity (23.1; $n = 53$) and those with a one-year periodicity (23.1, $n = 53$; t-test, $p = 0.84$).

Fecundity

Large differences in GSI (gonad weight/fish weight) were found between male and female paddlefish. GSI in sexually mature females was less than 10% for very young spawners (ages 15–18), increased rapidly to 10–18% for young spawners (ages 19–24), remained steady at 20% for middle-aged spawners (ages 25–35), and decreased slightly for older and senescent spawners (age 36 and over; Figures 7a,b). In extreme individual cases, the egg weight exceeded 25% of total body weight. GSI in sexually mature males (testes weight/fish weight) was, in contrast, a fraction of that for females, ranging from about 1% of body weight at ages 9–10 to about 1.3–1.4% at age 15 and over (Figure 8a,b). By age 25, a typical female had a GSI about 15 times higher than a male of comparable age.

Weight and Composition of Gonadal Fat Bodies

GFB weight of an individual fish varied greatly; in some fish of both sexes it constituted as much as 15% of fish weight and several times the gonadal weight, whereas in others it was less than 1% of total fish weight and a small fraction of the gonadal weight (Plates 3–6).

The role of the GFB was clarified when GFB weight per fish weight was plotted against fish age. As with most other life history traits, females and males differed markedly in the relation of GFB weight to age. For Montana females, the ratio of GFB weight to fish weight averaged over 5% for very young spawners (ages 15–18) but dropped sharply in the next few years (1–4%; ages 19–24). By the time females were middle-aged spawners (age 25), GFBs had been almost completely depleted (<1%) and remained so thereafter (Figure 9a). Fish caught in North Dakota showed the same pattern, with slightly higher ratios of GFB weight to fish weight at most ages (Figure 9b). The depletion of GFBs from age 15 to age 25, as indicated by the rapidly declining ratio, coincided with the steady rise in GSI over the same period (Figures 7a,b). This depletion of fat by age 25, as well as the wide range in weights of GFBs for fish of different ages, was also apparent in a plot of (GFB weight)/(GFB weight plus green egg weight) against age (Figure 10), indicating that it was a major shift in the relative proportions of green egg weights and GFB weights, rather than major changes in fish weights that occurred with age.

For Montana males, GFB weight per fish weight was highest at first maturity (ages 9–13), reaching an average of 6–7% of the fish weight, and decreased gradually thereafter, decreasing to 3% of fish weight after age 25 (Figure 11a). For North Dakota males, the pattern of depletion was similar as for the Montana fish, with slightly higher ratios of GFB weight to fish weight at comparable ages (Figure 11b). GFB weights and ratios of GFB weight to fish weight continued to decrease into old age. Despite the well-defined patterns of GFB depletion (rapidly in females, gradually in males), not all young spawners had GFBs of similar weights; some had large GFBs per fish weight and others had small

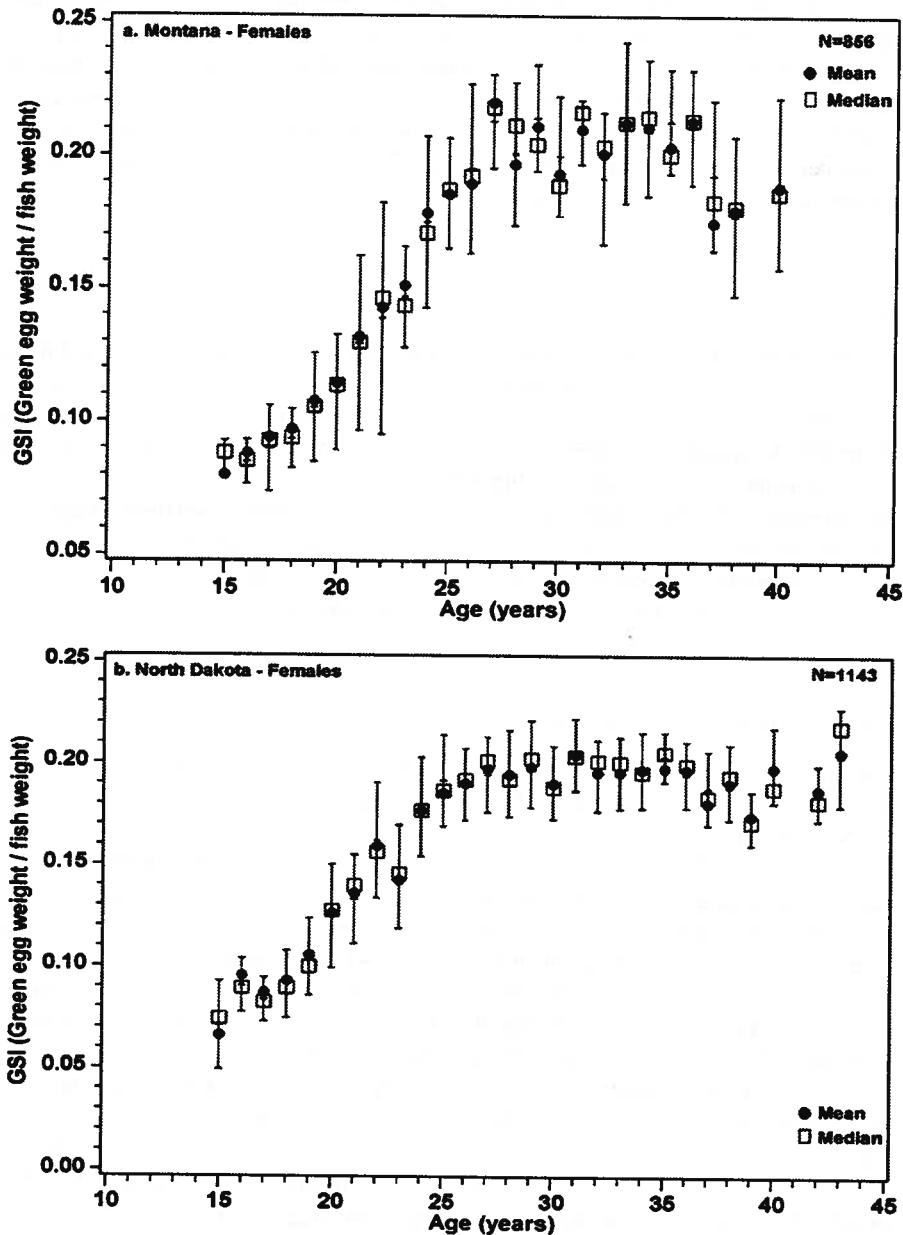


Figure 7. Gonadosomatic index (mean, median, and inter-quartile range) for female paddlefish caught in 2001–2003 in (a) Montana and (b) North Dakota.

ones. Old females always had little or no gonadal fat and GFBs in old males were much reduced.

Lipid content of GFBs also differed markedly between males and females. Males, which had lower GSI values than females, had higher lipid content of GFBs, commonly exceeding 50%. A significant relation was found between the lipid content and the $\log_e$ (GFB weight/testes weight) ($r^2 = 0.49$; $p = 0.0072$; Figure 12a). The relation for females was

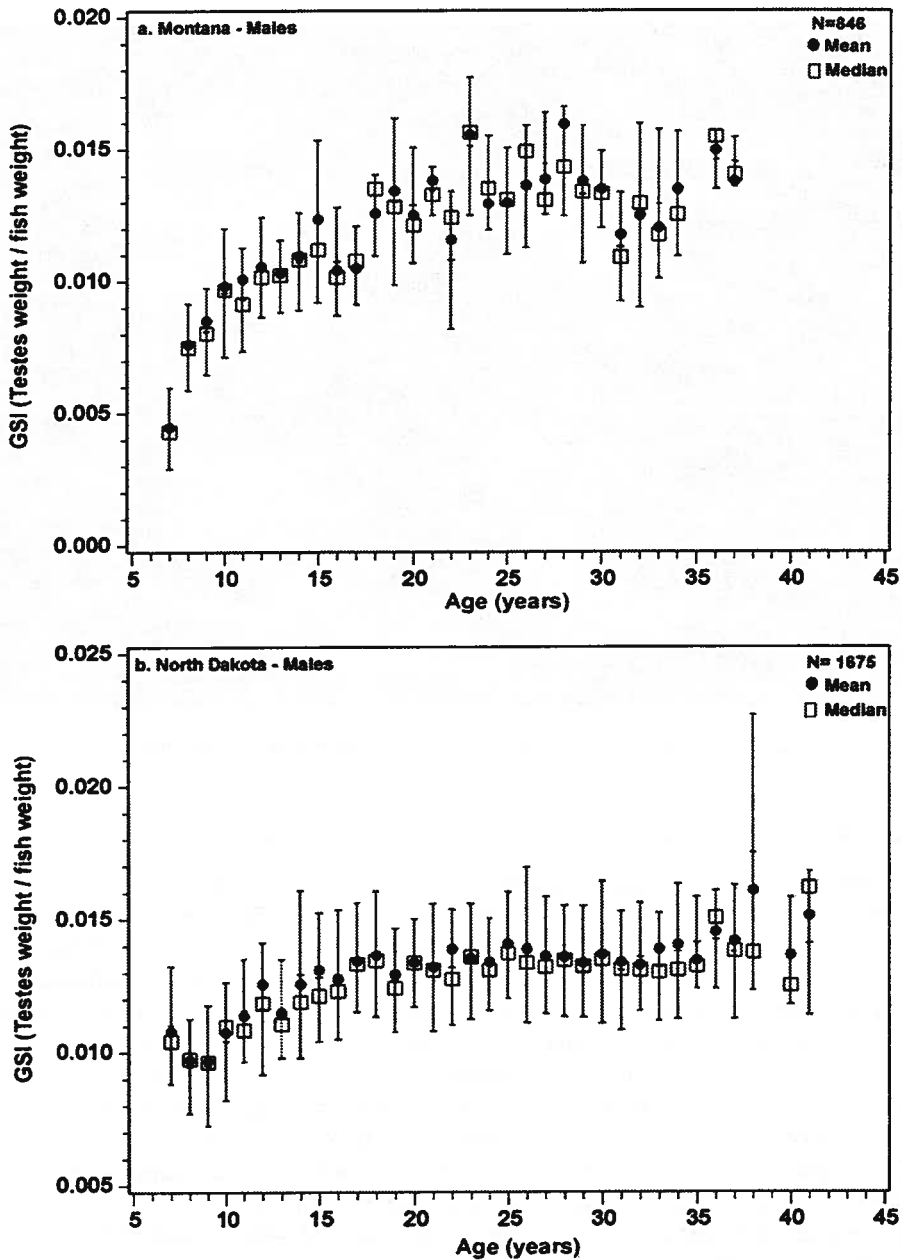


Figure 8. Gonadosomatic index (mean, median, and inter-quartile range) for male paddlefish caught in 2001–2003 in (a) Montana and (b) North Dakota.

much stronger than for males ($r^2 = 0.90$; $p < 0.0001$; Figures 12 a,b); only those females with heavier GFBs in relation to fecundity (which were also the youngest fish) had GFBs consisting of $> 50\%$ lipids. Females with smaller (i.e., lighter) GFBs had exponentially lower percentages of lipids in their GFBs (Figure 12b).

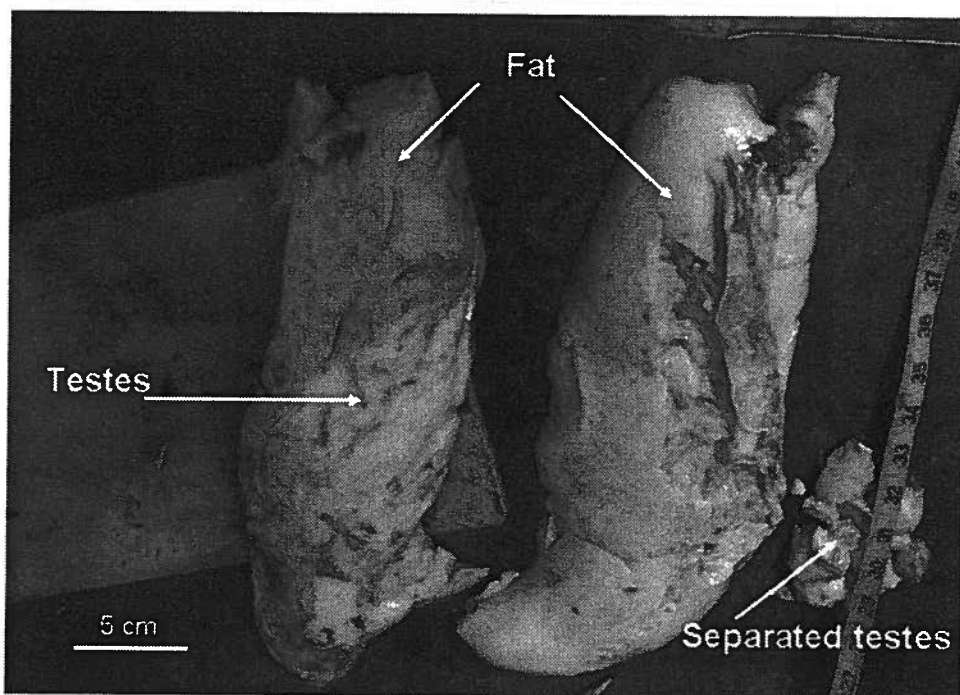


Plate 3. Testes and large gonadal fat accumulation in a male paddlefish.

Energetic Tradeoffs between Somatic Growth and Reproduction in Extreme Cases

Evidence was found that especially long and heavy fish may have put less energy, as a percentage of total weight, into reproduction than a typical fish. For especially long females (≥ 132.5 cm), GSI was significantly lower (mean, 0.186; $n = 60$) than for 200 randomly selected fish (mean, 0.199, $n = 200$; Wilcoxon two-sample test; $p = 0.02$). Differences in the ratio of green egg weight plus GFB weight divided by fish weight were not significantly different between especially long fish and the random fish, however (Wilcoxon two-sample test, $p = 0.28$). For especially heavy females (≥ 46.5 kg), mean GSI was significantly lower (mean, 0.173, $n = 28$) than for 200 randomly selected fish (mean, 0.196, $n = 200$, Wilcoxon two-sample test, $p = 0.004$). Differences in the ratio of green egg weight plus GFB weight divided by fish weight were not significantly different between especially heavy fish and the random fish, however (Wilcoxon two-sample test, $p = 0.42$). The two heaviest males sampled (> 27.2 kg) over the entire period 1991–2004 also provided evidence of energetic tradeoffs between somatic growth and investment in reproduction. Both fish were found to have undeveloped, non-functional testes, a characteristic rarely seen in this stock.

Migration Distance and Location Fidelity

Fish tagged in Montana (i.e., upriver) were significantly more likely to be recaptured in subsequent years in Montana, and fish tagged in North Dakota (i.e., downriver) were significantly more likely to be recaptured in subsequent years in North Dakota (Chi-square test; $p < 0.0001$; $n = 1033$). For all males (both states) as a group, the pattern of fidelity

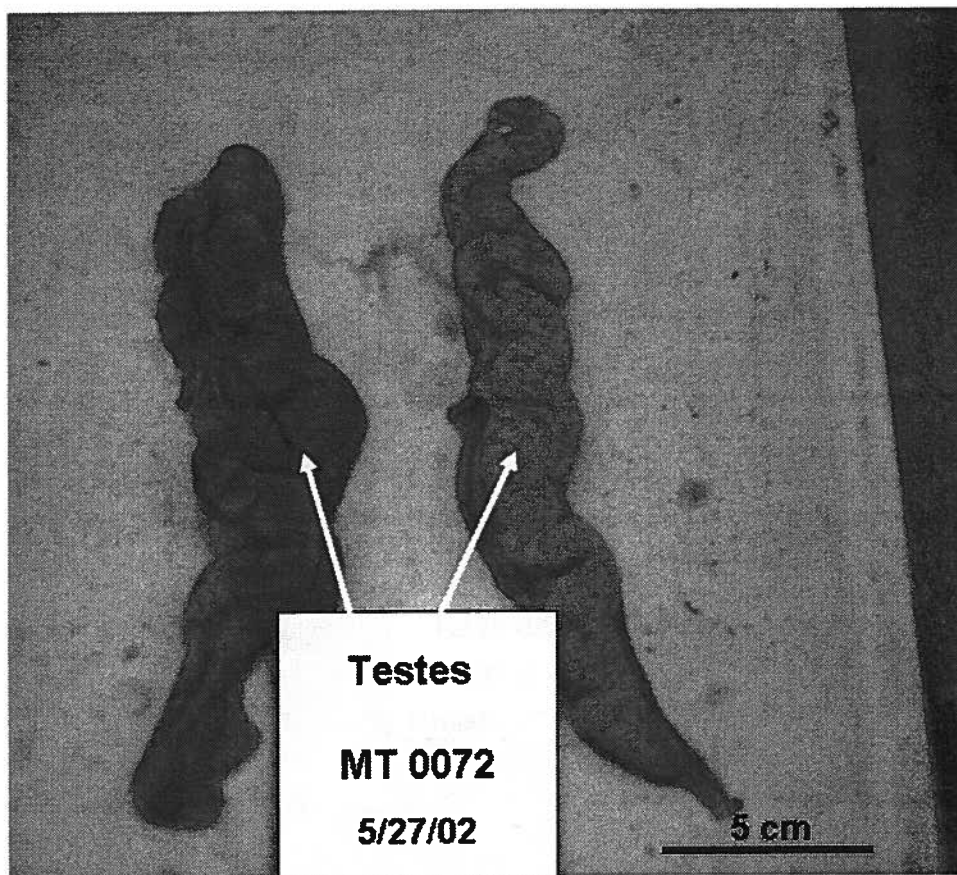


Plate 4. Testes with almost no gonadal fat present. Estimated fish age 27 years.

to site (state) of tagging and recapture held for fish age 15 and under ($p < 0.0001$; $n = 177$), ages 16–25 ($p < 0.0001$; $n = 252$) and ages 26 and over ($p < 0.0001$; $n = 161$). In comparisons within states, for young males (age 15 and under) no difference in site fidelity was detected between Montana-tagged and North Dakota-tagged fish ($p = 0.72$). Similarly, for middle-aged males (ages 16–25), no difference in site fidelity was detected between Montana-tagged and North Dakota-tagged fish ($p = 0.18$; $n = 252$). For older males (ages 26 and over), no difference in site fidelity was detected between Montana-tagged and North Dakota-tagged fish ($p = 0.23$; $n = 161$). For Montana-tagged male fish, no significant difference was found in fidelity among the three age groups ($p = 0.76$). For North Dakota-tagged male fish, no significant difference was found in fidelity among the three age groups ($p = 0.89$; $n = 183$).

For all females (both states) as a group, the pattern of fidelity to state of tagging and recapture held for females age 25 and under ($p = 0.0055$) and for females age 26 and over ($p < 0.0001$). In comparisons within states, for younger females (age 25 and under), Montana-tagged fish were more likely to show site fidelity to Montana than were North Dakota-tagged fish likely to show fidelity to North Dakota ($p = 0.047$; $n = 115$). Among older females (age 26 and over) North Dakota-tagged fish and Montana-tagged fish showed

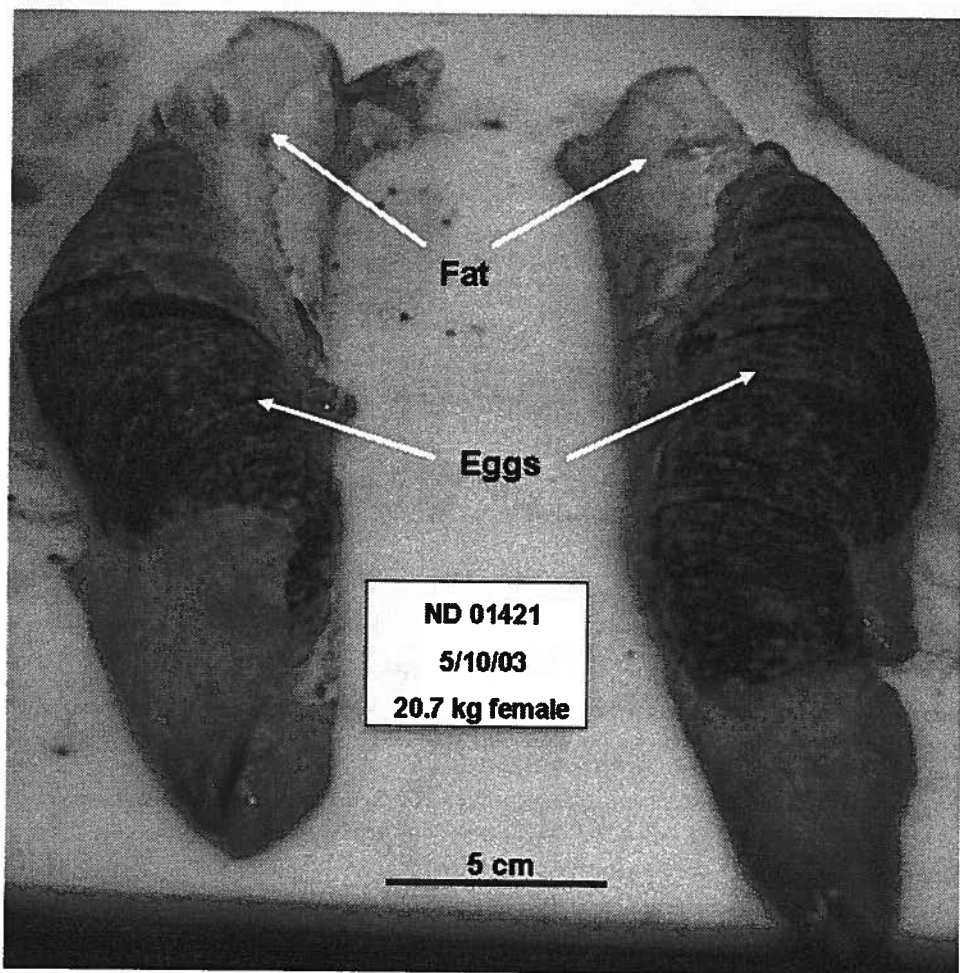


Plate 5. Ovaries and large accumulation of gonadal fat in a female paddlefish. Estimated fish age 19 years.

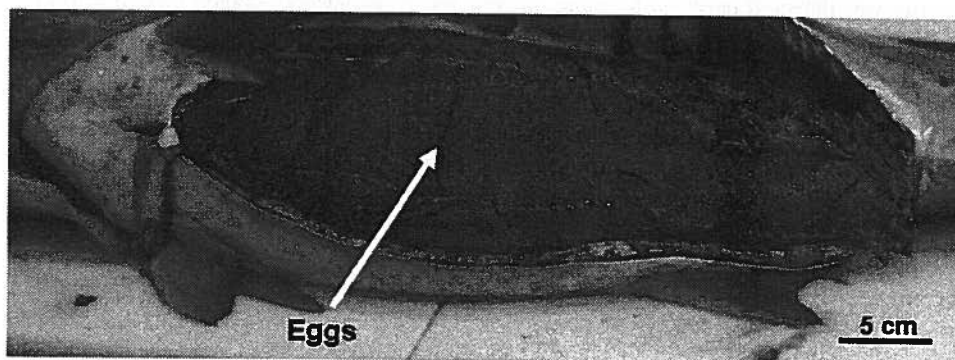


Plate 6. Fully developed ovary with egg mass filling much of body cavity. The little gonadal fat that is present in such fish is on the underside of the egg mass and hidden from view.

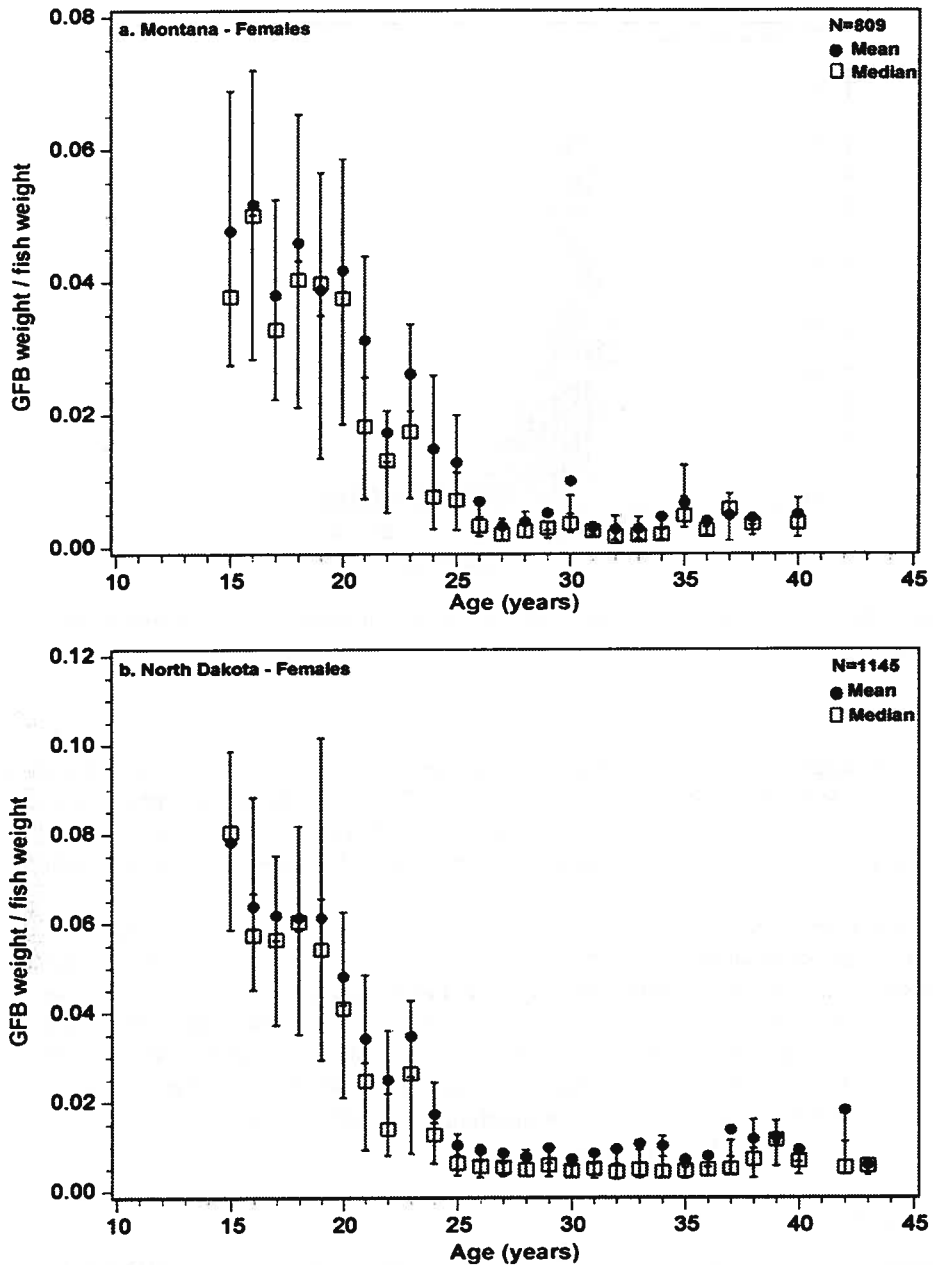


Figure 9. Ratio of gonadal fat body (GFB) weight to total fish weight (mean, median, and inter-quartile range) versus age for female paddlefish 2001–2003 from (a) Montana and (b) North Dakota. A minimum of 5 observations per age were required.

no significant differences in site fidelity ($p = 0.09$; $n = 172$). For Montana-tagged females, no significant difference was found in site fidelity between the two age groups ($p = 0.23$; $n = 120$). Conversely, for North Dakota-tagged females, a significantly higher rate of site fidelity was detected for older fish than for younger fish ($p = 0.0089$; $n = 167$).

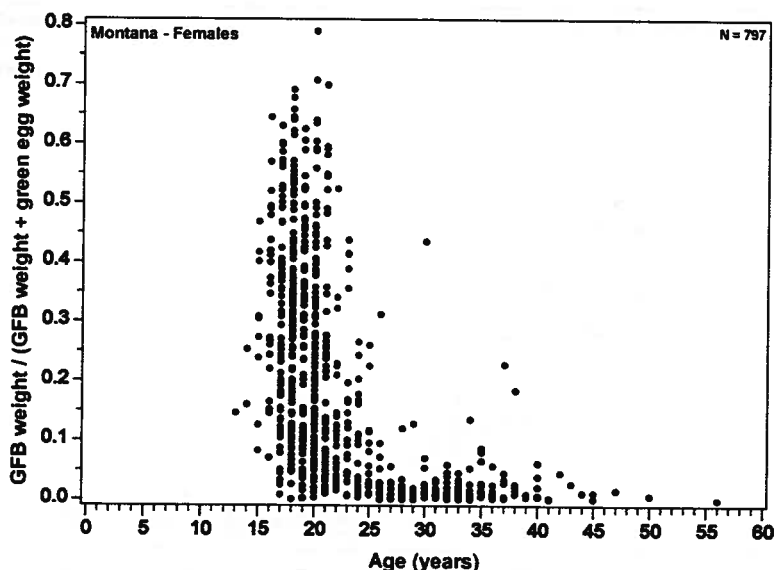


Figure 10. Ratio of total GFB weight to GFB weight plus green egg weight in relation to the age of female paddlefish, Montana-caught fish, 2001–2003.

Mortality Rates

For fish caught in each state, average total mortality rates (Z) over the period 1991–2004 were similar for males and females (Figure 13a,b). The exact slope of the curves depended on which years were included, but overall, slopes of catch curves for males and females were nearly parallel, ranged narrowly from 0.247 to 0.262, and were not significantly different in either state (t -test, $p > 0.05$).

For harvest mortality, both Montana and North Dakota tag groups tended to have higher rates for females than for males. Of the eight tag groups analyzed, the five earliest tag groups all had rates significantly higher (Chi-square test, $p < 0.05$) or highly significantly higher ($p < 0.01$) rates for females (F) than for males (M): (MT1984: F52% vs. M32%; MT1986: F38% vs. M20%; MT1988: F52% vs. M25%; ND1993: F49% vs. M29%; ND1994: F53% vs. M19%). Sex-specific harvest rates for the three most recent tag groups (ND1996, ND1997, and ND1998) were not significantly different between sexes ($p > 0.05$) and were all between 14% and 22%.

Senescence

Neither sex showed any detectable increase in mortality rate at advanced ages (Figure 13a,b). In females, senescence was only seen as a decline in gonadal weight (GSI). From age 25 to age 35, females maintained their GSI, even with the depletion of most of the gonadal fat a decade earlier. For fishes over age 35, however, a slight decline in GSI was apparent (Figure 7a,b; Figure 14). For Montana fish, the decline in mean GSI for fish over age 35 from fish ages 28–35 did not achieve statistical significance (Wilcoxon's test, $p = 0.10$). For the older North Dakota fish, however, the decline in GSI in the older fish was highly significant ($p = 0.004$). No loss in condition was found for females with age. Relative weights for females for the four years fluctuated within the range of 0.96 to 1.07 from age 17 to age 41, when sample sizes became too small for a reliable assessment. W_r for females increased

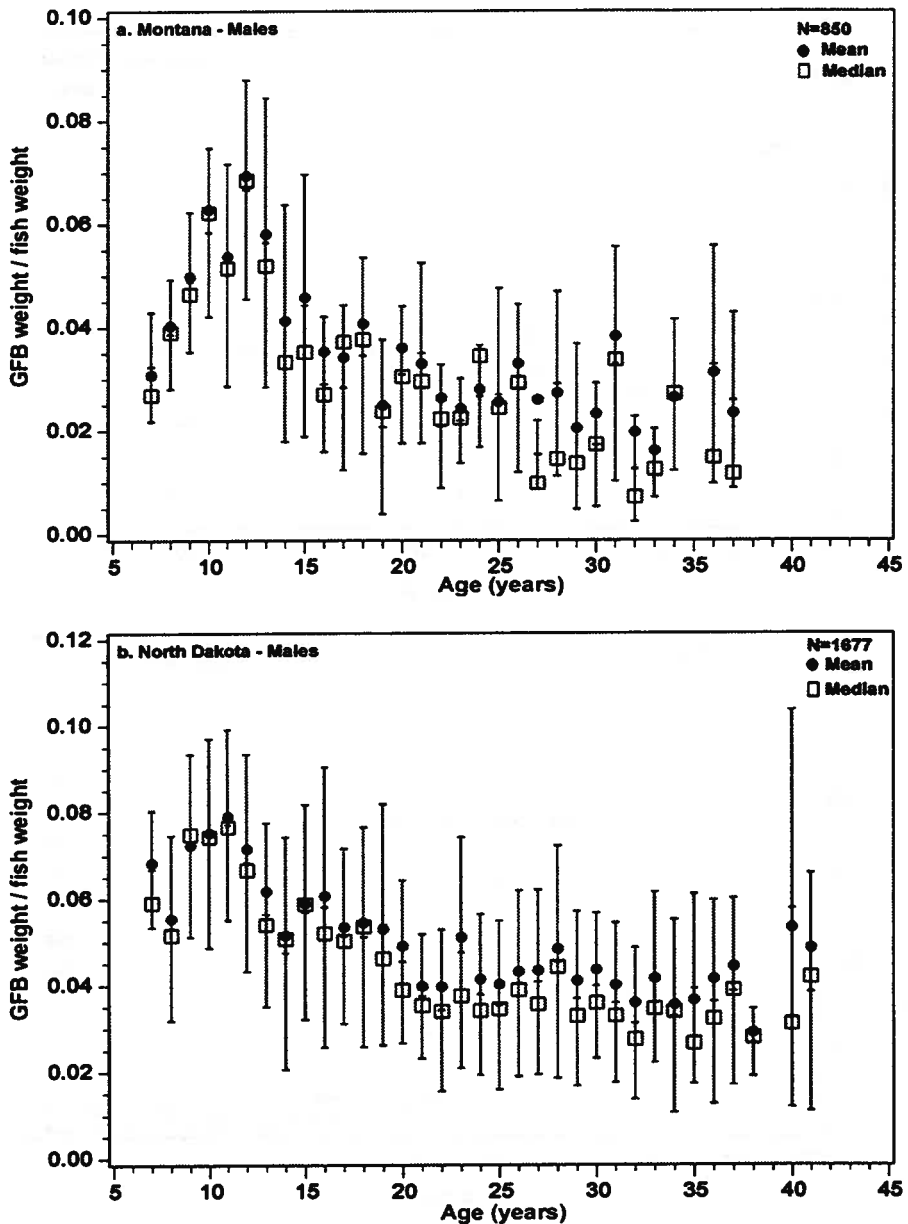


Figure 11. Ratio of GFB weight to fish weight (mean, median, and inter-quartile range) versus age for male paddlefish, 2001–2003 from (a) Montana and (b) North Dakota. A minimum of 5 observations per age were required.

gradually with fish age. Mean W_r for females age 35 and over (mean, 1.043, $n = 294$) was significantly higher than for both females age 22 and under (mean, 0.989, $n = 1091$) and females age 23 to 34 (mean, 1.006, $n = 1374$; Wilcoxon two-sample test, $p < 0.0001$). Even the oldest females showed no detectable loss in condition, despite detectable declines in GSI (Figure 14). In males, senescence was not clearly detectable. Relative weights for males for the combined years 1996, 1997, 2003, and 2004 remained within the narrow range

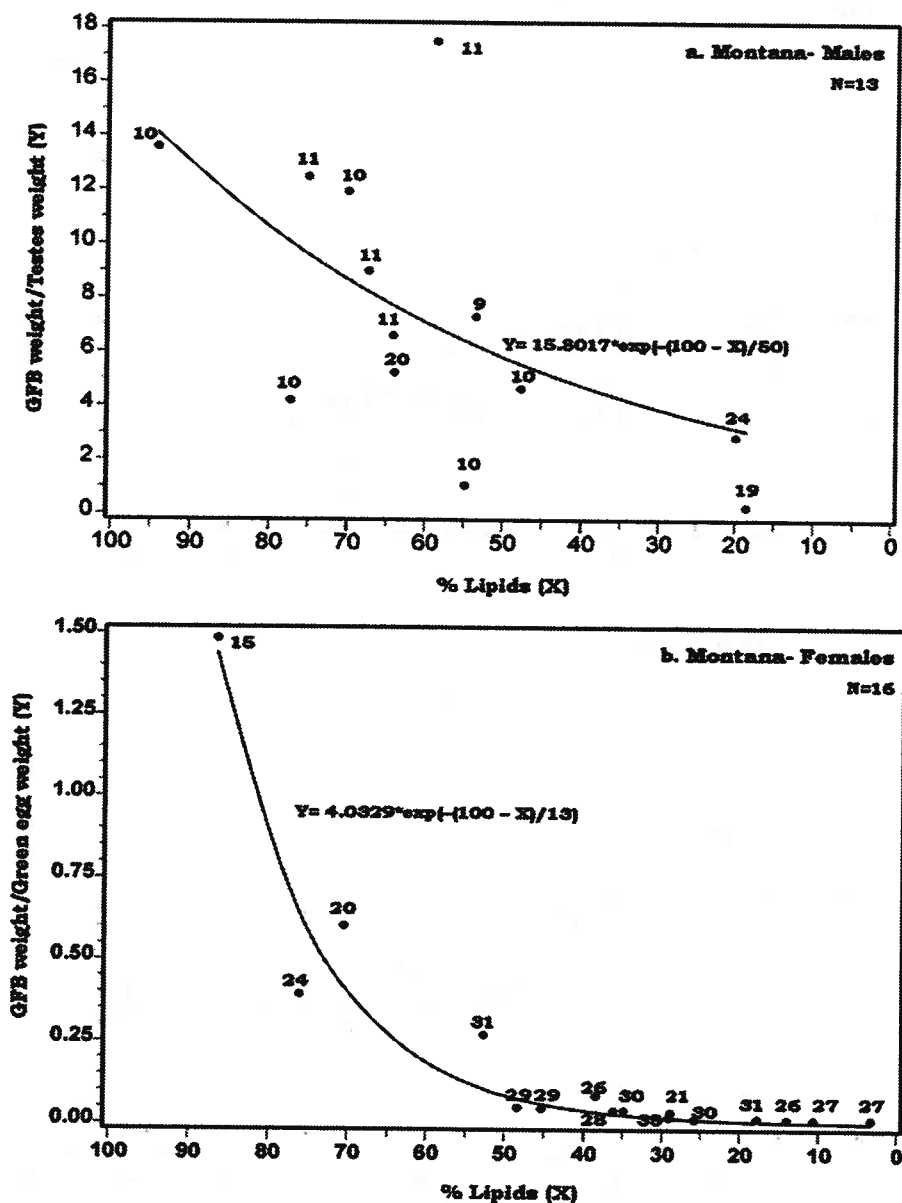


Figure 12. Percent lipids of GFBs in relation to the ratios of GFB weight to testis weight for Montana-caught paddlefish (a) males and (b) females. Numbers next to data points are estimated ages of the fish based on annuli on dentaries.

of 0.82–0.89 from age 9 to 38 (Figure 15). Although mean W_r for males ages 16–29 (0.849; $n = 1105$) and age 30 and over (0.849; $n = 296$) were both significantly lower than for males age 15 and under (0.866; $n = 1729$; Wilcoxon two-sample test; $p = 0.0003$), they were not significantly different from each other ($p = 0.26$). Occasional very thin, old male fish were recognizable and noted by us at the cleaning stations, however, and their advanced age was later confirmed. These fish were too few, however, to be statistically detectable.

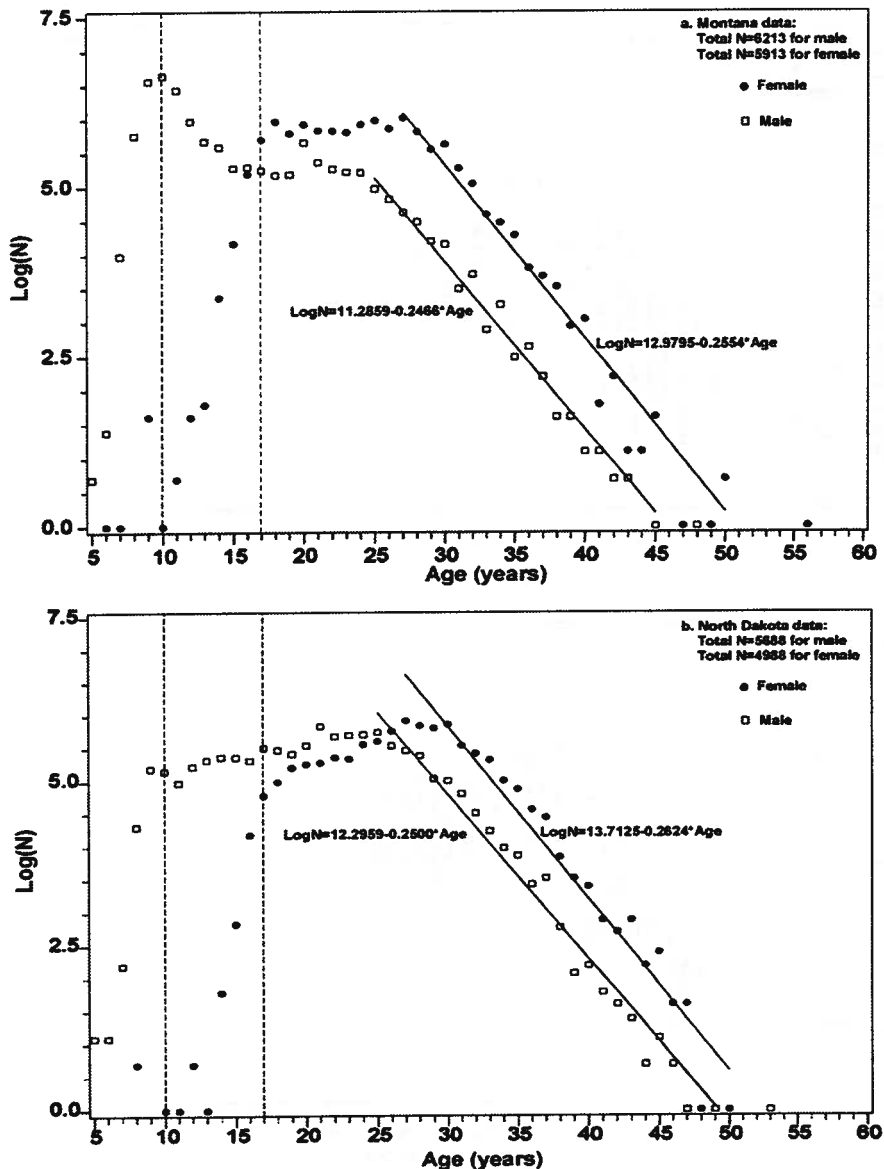


Figure 13. Catch curves and instantaneous rates of total mortality for male and female paddlefish (a) Montana-caught fish and (b) North Dakota-caught fish, 1991–2004.

Discussion

Life History Summary

The life history pattern of the Yellowstone-Sakakawea paddlefish stock can be summarized as follows. Newly hatched fish move into Lake Sakakawea, North Dakota, where by late summer they selectively feed primarily on the large predaceous cladoceran *Leptodora kindtii*. By no later than their second year, they have begun to filter feed (Fredericks, 1994;

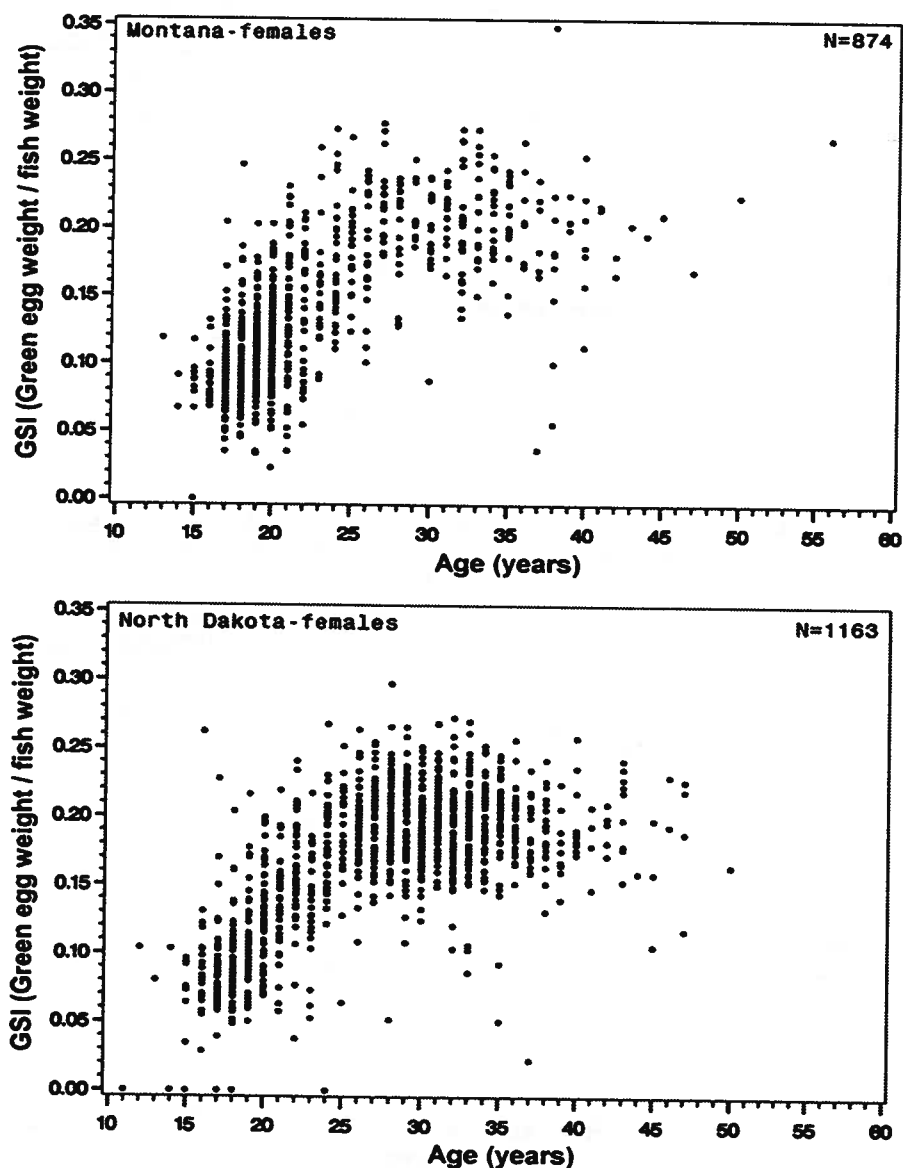


Figure 14. Age-specific gonadosomatic index (GSI) for female paddlefish for (a) Montana and (b) North Dakota, 2001–2003. The few fish with GSI = 0 represent the only fish sampled in early stages of egg development (stages 1 and 2). All other ovaries were weighed.

Scarnecchia et al., 1996b). Although the immature fish are not actively sampled beyond age 1 in the reservoir, extrapolated von Bertalanffy growth curves (two parameter; $t_0 = 0$) for males and females merge at ages 5 to 10, indicating that males and females grow at similar rates to at least age 5. Over the ensuing decade, most important aspects of male and female life histories diverge greatly (Figures 2 and 3; Stamps, 1993). Males begin diverting energy and production away from somatic growth into sexual maturation (Plate 1) starting at about age 8, and most are recruited by ages 10–12 (Tables 1 and 2). Females of the same brood years, not yet burdened with the costs of reproduction, grow more rapidly than males of

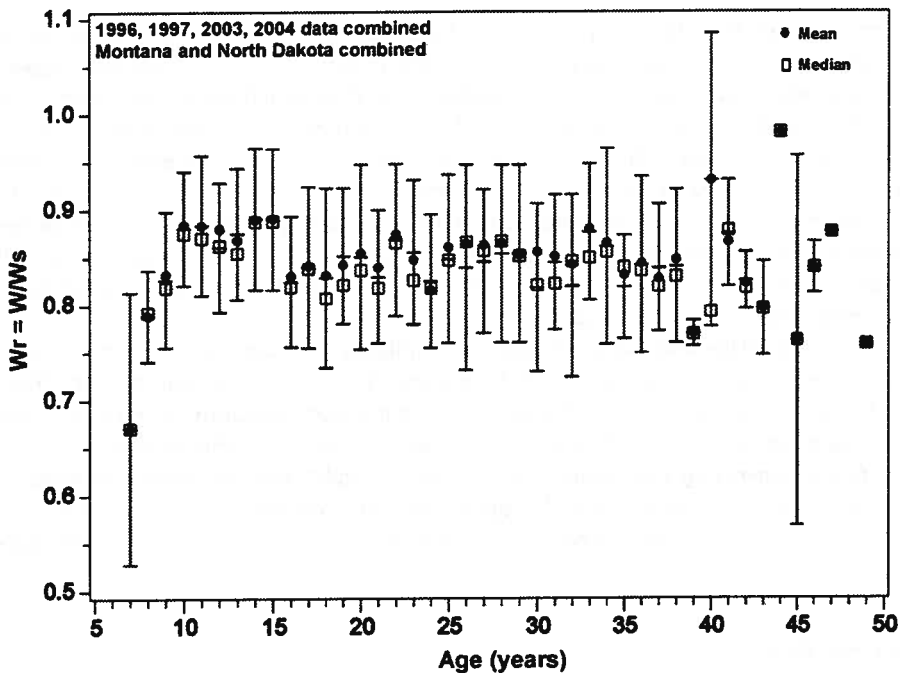


Figure 15. Relative weight W_r (ratio of actual weight to standard weight, mean, median, and inter-quartile range) in relation to age for male paddlefish, Montana-caught and North-Dakota-caught fish combined, 1996, 1997, 2003, and 2004 data combined.

their cohort until about ages 13–14, when they begin diverting energy into sexual maturation (Plate 2). Most females are recruited by ages 17–19. By age 15, females weigh on average about 10 kg more than males, and this sexual size dimorphism is maintained thereafter (Figures 2 and 3). At the time of the first upstream spawning migration, both sexes have mature gonads, to which are attached GFBs containing lipids that have been amassed during the immature growth period in the reservoir. Most first-time migrants have amassed GFBs; some of them large and some small or nearly absent (Figure 10). Among young spawners, female GSI is about nine times that of males and increases to about 15 times that of males by age 25. Increases in fecundity among young adult males and females, as indicated by the GSI (Figures 7 and 8), are concurrent with decreases in GFB weight (Figures 9 and 11). Males typically spawn every one or two years (Figures 5a and 6a) and their GFBs decline gradually over several spawns (Figure 11). Females typically spawn every two or three years (Figures 5b and 6b), and their GFBs decline more rapidly so that they are largely depleted after two or three spawns by age 25 (Figure 9a,b). The lipid content of GFBs of both males and females declines with decreases in GFB weight/gonal weight (Figure 12a,b); females show an especially well-defined exponential decline. After the females deplete their GFBs, GSI remains steady and reproductive effort is maximized for another decade, until about age 35, when on average it begins to decrease, an indication of reproductive senescence (Figures 7a,b and 14).

Energetic tradeoffs may also influence migratory activity. Younger fish, both male and female, are more likely to migrate farther upriver (into Montana) whereas older fish, both male and female, are more likely to remain downriver (in North Dakota). Some individual

fidelity exists in this migration pattern. Fish migrating upriver to Montana that are tagged there are more likely to be recaptured in Montana in future years, whereas fish tagged in North Dakota are more likely to be recaptured in North Dakota in future years. Tagged young (age 15 and under), middle-aged (ages 16–25), and old (age 26 and over) males are equally likely (compared to each other) to be recaptured upriver in Montana rather than in North Dakota. Among young females (age 25 and under), Montana-tagged fish are more likely to be recaptured upriver in Montana than North Dakota-tagged fish are to be recaptured downriver in North Dakota. For older females (age 26 and over), North Dakota-tagged fish are more likely to be recaptured downriver in North Dakota than Montana-tagged fish are to be recaptured upriver in Montana.

Females tend to outlive males. Despite higher fishing mortality rates on females tagged as migratory adults, the number of age 30 and over females exceeds that of males (Tables 1 and 2) as a result of an earlier harvest and higher natural mortality on younger mature males (at a period of their life when females are not yet vulnerable to harvest) and the more frequent spawning migrations of males. Total mortality rates are similar for males and females over age 25 (Figure 13a,b). By age 40, mortality (natural or fishing) has eliminated most fish of both sexes, although both males and females occasionally exceed age 50 (Tables 1 and 2).

The Costs of Reproduction

The distinct life history aspects of the Yellowstone-Sakakawea paddlefish (i.e., size and age at maturity, longevity, growth rates, reproductive periodicity, fecundity (GSI), migration distance, mortality rates, and senescence), the role of GFBs in energy storage and spawning, the change in period of gonadal recrudescence with age, and the distinct sex-specific differences in all of these attributes provide us with a detailed empirical framework for understanding the stock. We also suggest that the framework outlined in this paper should be considered in evaluating the life histories of other paddlefish and sturgeon stocks. Many of the life history attributes are associated with or explained by the costs of reproduction within the species as a whole or by the relative costs between males and females. The costs of reproduction are manifested as (1) allocation of energy between somatic growth and investment in reproduction, (2) depletion of GFBs, (3) mortality rates associated with age at maturity, reproductive periodicity, and differential investment in each reproduction event, and (4) migratory activity.

Allocation of Energy between Somatic Growth and Investment in Reproduction

Sexual Size Dimorphism. The distinct sexual size dimorphism reported in this study, where mature females are much larger than males at a particular age has been reported in numerous other localities (e.g., Pool 13, Upper Mississippi River, Iowa: Gengerke, 1978; Table Rock Reservoir and Lake of the Ozarks, Missouri: Russell, 1986; Fort Peck Lake, Montana: Bowersox, 2004). The difference has been associated with faster growth of females of a brood year after males of that brood year have undergone sexual maturation (Rosen et al., 1982; Alexander et al., 1985; reviewed by Stamps, 1993; his Figure 4) and later age at maturity for females (Russell, 1986; Scarnecchia et al., 1996b). Other investigators, however, have found little difference in size at age between mature male and female paddlefish (e.g., Lake Cumberland, Kentucky: Hageman et al., 1986; Lower Tennessee and Cumberland Rivers, Kentucky: Timmons and Hughbanks, 2000; several Louisiana waters: Reed, 1989). The greatest amount of sexual size dimorphism has been

reported in the more northerly and northwesterly stocks (e.g., South Dakota: Friberg, 1972, 1974; Iowa: Gengerke, 1978; Scarnecchia et al., 1989; Montana: Scarnecchia et al., 1996b; Bowersox, 2004), in localities where growing seasons are shorter, age at maturity is later, reproductive periodicity is of a longer interval, and life spans are longer (Paukert and Fisher, 2001). In Montana stocks, Scarnecchia et al. (1996b) and Bowersox (2004) found eight to nine year differences in age at maturity between males and females. In Louisiana, by contrast, Reed (1989) found that male and female paddlefish typically differed in age at maturity by two or three years: males began maturing as early as age 4 and were all mature by age 9; females began maturing as early as age 7 and were all mature by age 10. Fish in Louisiana also had a much shorter lifespan (maximum estimated age 14 years). Reproductive periodicity was not reported but, in view of the short lifespan, would also probably be at more frequent intervals than in Montana. The differences among stocks in the extent of sex-specific differences in growth rates and age at maturity are thus strongly influenced by the ecological factors affecting productivity (Carlson and Bonislawsky, 1981; Russell, 1986). Growing season, expressed as latitude, provide one coarse measure of those factors. Within a climatic zone, factors such as reservoir productivity (Houser and Bross, 1959) can also be important in influencing growth rates and age at maturity.

Evolutionary Basis of Sexual Size Dimorphism. The pronounced sexual size dimorphism and differential age at maturity in Yellowstone-Sakakawea paddlefish are best understood in terms of the costs of reproduction. Bell (1980) discussed differential age at maturity (which he called *bimaturism*) in fishes, reviewed species-specific age-at-maturity information in Carlander (1969), and noted that males mature earlier than females in the vast majority of North American freshwater fish species. The Yellowstone-Sakakawea paddlefish stock is an extreme case, where males are much smaller than females and mature at a much younger age. This pattern is pervasive in other Acipenseriform species as well (e.g., shovelnose sturgeon, *Scaphirhynchus platyrhynchus*; Keenlyne, 1997; Chinese sturgeon, *Acipenser sinensis*; Wei et al., 1997; Dabry's sturgeon *Acipenser dabryanus*, Zhuang et al., 1997; Green sturgeon *Acipenser medirostris*, Van Eenennaam et al., 2006).

Several aspects of paddlefish life history and behavior probably contribute to the size dimorphism and differential age at maturity. First, the few North American freshwater fish species where males are larger than females (e.g., creek chub *Semotilus atromaculatus*, bluntnose minnow *Pimephales notatus*, central stoneroller *Camptostoma anomalum*) have life histories where nest building, defense of breeding opportunity from other males (e.g., territorial guarding; Pyron, 1996), or direct competition for exclusive breeding opportunities (e.g., pairing) favor larger size in males. In contrast, in nearly all cases where males are smaller than females, neither territorial behavior nor parental care occur (Roff, 1992). The few observations available on paddlefish pre-spawning behavior and spawning in their turbid habitats provide no evidence that larger size in males would confer a significant competitive advantage. Pre-spawning pairing has not been observed; paddlefish have instead been found to congregate in groups with fish of different sizes prior to spawning, in locations such as below dams (Southall and Hubert, 1984; Moen et al., 1992) and in deep pools of rivers (Firehammer, 2004). The only documented observation of spawning (Osage River, Missouri; Purkett, 1961) was described as a "rush" by a female fish for some distance along with rapid agitation of the caudal peduncle. Such a rush would most likely be conducted in the presence of more than one male fish (Russell, 1986). Pairing at spawning is thus highly unlikely. In addition, the high turbidity commonly associated with un-dammed paddlefish spawning habitat in spring (Purkett, 1961; Firehammer, 2004)

would minimize the advantage of visual cues, even if the species relied heavily on sight, which it does not. The species has reduced eyes and uses electrosensory capability for food acquisition (Freund et al., 2002; Wilkins et al., 2002). We have observed on several occasions that completely blind paddlefish with their eye sockets grown over with integument can feed and migrate to spawning areas (Rosen and Hales, 1982; our unpublished data). They also utilize spawning tubercles for tactile cues: males, and to a much lesser extent, females often have tubercles on the dorsal surface (Russell, 1986; Stastny, 1994). The lack of primary importance of paddlefish vision for survival is not proof that paddlefish do not cue on external visual differences in reproduction, but it is consistent with a lack of direct competition by males (e.g., combative behavior) for exclusive access to females.

Second, the higher GSI for females than for males is consistent with the greater size of females, indicating that the females gain more in fitness from large size in gamete production than do males, whose gamete production is, even in small individuals, more than adequate to fertilize all available eggs. The higher GSI for females than for males observed in this study is similar to results from other *Acipenseriform* species. For example, Van Eenennaam et al. (2006) reported that GSI in green sturgeon was 7–17% for females and 2–8% for males. Zweigacker (1967) reported that shovelnose sturgeon gonads constituted 7–22% of body weight in mature females but only 1–6% in males. Although the males evidently gain little from attaining as large a size as females, the size attained by them in the first few years of life (Figures 2 and 3; Plate 1) renders them sufficiently large to escape predation from most other piscivorous species. The rapid growth may be critical to paddlefish survival, because studies indicate that age 0 and age 1 fish are easily captured (Scarnecchia et al., 1997) and highly vulnerable to predation (Mero et al., 1995; Parken and Scarnecchia, 2002). From their middle years until old age, when fish of both sexes have reached lengths and weights near their maxima, natural mortality rates from all causes, including predation, are very low, and harvest and damage from motorboat propellers (Rosen and Hales, 1980) are primary causes of mortality (Scarnecchia and Stewart, 1997a).

Third, the extreme male-female differences in size observed in Yellowstone-Sakakawea paddlefish may be in part due to the longer lifespan in more northerly stocks than in more southerly stocks (Reed, 1989). A 10-year difference in age at maturity for a fish that can live to 50 years may thus be comparable to a two-year difference for a fish that lives 10 years.

Size Versus Age at Maturity. The overall consistency among years in age at maturity within both males and females in the Yellowstone-Sakakawea stock contrasts with results from hatchery-reared fish reported by Mims and Knaub (1993), who suggested that age may be a less critical factor in maturity than size. These different conclusions may not be incompatible. Despite inter-annual differences in habitat conditions in Lake Sakakawea, the consistently short growing season may not provide as great a scope for variation in annual production and feeding opportunities as can be induced through intensive aquaculture. It may thus be possible to accelerate paddlefish growth and age at maturity in culture situations much more than would be typically observed in the wild (Mims et al., 1999). Great acceleration in growth rates has been achieved in culture situations for white sturgeon *Acipenser transmontanus* and other sturgeons (Conte et al., 1988). Growth in culture facilities may be especially accelerated over those of wild fish for stocks in northern latitudes, which have a brief growing season. In this case, age at maturity may be less subject to variation (and manipulation) in the wild stock in its habitat than in the more rapidly growing hatchery-reared fish.

Depletion of GFBs

The Role of Gonadal Fat Bodies. The relations among GFB weight, maturation state (GSI), and fish age found for the Yellowstone-Sakakawea stock clarify observations and speculations about the GFBs in Acipenseriform species made for nearly a century. Stockard (1907) reported the presence of large GFBs in plump male paddlefish from the Lower Mississippi River. Larimore (1950) described them in both male and female fish, and they have since been observed in paddlefish at other locations (Pool 13, Upper Mississippi River: Gengerke, 1978; Lake Cumberland, Kentucky: Hageman et al., 1986; Russell, 1986). GFBs have also been noted in other Acipenseriformes: in the shortnose sturgeon *Acipenser brevirostrum* by Ryder (1890), in the Chinese paddlefish *Psephurus gladius* by Chenhan et al. (1995), in *Acipenser naccarii* by Garcia-Gallego et al. (1999), and in the hybrid bester (Beluga *Huso huso* x sterlet *Acipenser ruthensis*) by Steffens and Jahnichen (1995), who described them as "lipid deposition in the gonads" (p. 346). Ryder (1890) reported that for both sexes of young (46–61 cm in length) shortnose sturgeon, "the reproductive organs, both ovary and testis, are found embedded in depressions on the inner face of a rich, creamy-yellow body . . . considerably more voluminous than the reproductive tissue itself . . . composed in great part of fatty tissue. . . . The latter history of this fatty body shows that it does not keep pace with the growth of the proper reproductive tract, which becomes more and more voluminous as sexual maturity is reached until the ovary becomes the bulkiest organ in the body-cavity" (p. 251). Larimore (1950) described male paddlefish testes from fish caught on the Upper Mississippi River as "concealed ventrally by heavy layers of fat. . . . Microscopic examination shows that the fat adjacent to the testis has projections extending into the edge of the gonad and between the marginal tubules. The connective tissue covering of the testis extends also over the mass of fat." (p. 119). For female fish, Larimore (1950) reported that "Immature ovaries are covered on the under side by large masses of fat, such as were described for the testes. . . . The interesting fact that undeveloped ovaries have excessive fat, whereas ripe ovaries do not, was brought to my attention by Mr. P. G. Barnickol, who examined many paddlefish during his work on the Mississippi River." (p. 121). Our results differ somewhat from Barnickol's observations in that ripe ovaries from mature Yellowstone River females ages 15–20 that have not spawned more than once or twice may have GFBs of considerable weight associated with them.

Our observations of an inverse relationship between GFB weight and GSI are supported by other studies. Hageman et al. (1986) reported, but presented no data, that the size of fat "storage bodies" (GFBs) in paddlefish from Lake Cumberland, Kentucky, was inversely related to the GSI. They speculated that the storage bodies might provide an important energy source for gonadal development. For Chinese sturgeon in the Yangtze River, Wei et al. (1997) reported that females with stage 3 eggs in September and October had gonadal fat of 60–70%, GSI 2.8–7.1% (mean 4.8%) and egg diameter 2.0–2.5 mm. By November and December, gonadal fat was lower (20–60%), GSI higher (2.4–9.0%, mean 7.3%), and egg diameter larger (2.5–3.5 mm). In contrast, for a sample of 54 females with stage 4 (i.e., caviar-sized) eggs, the fish had no gonadal fat, a much higher GSI (11.77–25.95%, mean, 19.11%); and a greater egg diameter (4.0×4.2 – 4.5×5.0 mm). The lower weight of gonadal fat associated with an increasing GSI and egg maturation is similar to what we observed. Craig (1977) reported that perch *Perca fluviatilis* depleted stored energy reserves as they reproduced and aged.

The relationships among age, GSI, and GFBs observed in this study should be evaluated in other Acipenseriform species and other fishes, but with caution. First, the age and the approximate number of probable spawning events should be estimated for the fish from

which maturation is assessed and GFBs or other fat is weighed. In results of Wei et al. (1997), for example, the absence of gonadal fat in fish with stage 3 eggs might have occurred because of environmental stressors, as they suggested, or it might have occurred from selectively sampling older, repeat spawners between spawning years. In addition, our results indicate that although large GFBs are associated with young fish typically in their first or second spawning event, not all young, first-time spawners have large GFBs (Figure 10). The wide individual variation in GFBs in first time spawners as well as the large annual variations in male weight at age 10 (Figure 3) indicates that feeding conditions and efficiency for immature paddlefish in Lake Sakakawea, and probably other *Acipenseriformes*, may vary widely, with significant impacts on the growth rates and gonadal fat accumulation of individual fish. The characteristic large, plump, reservoir-reared Yellowstone-Sakakawea paddlefish contrasts markedly with the historically lean fish from this stock prior to reservoir construction (Carufel, 1954; Scarnecchia et al., 1995a). For stocks of paddlefish restricted to less suitable, strictly riverine feeding habitats, or for riverine sturgeon stocks, GFBs and other body fat accumulation at all ages may be minimal. At the other extreme, GFB accumulation has been considerable in *Acipenseriform* species reared on particular diets in production-oriented aquaculture situations (S. Doroshov, University of California, personal communication).

Although we found large GFBs to be associated with young fish of both sexes, our observational approach (i.e., weighing GFBs only once, at harvest) did not allow us to specify exactly when throughout the life cycle the GFBs accumulated. It is not known if any accumulation occurs between the first and second spawns, between the second and third, or if depletion is inexorable after sexual maturation begins. It is also not known if fat accumulation in older fish would occur under better environmental conditions. Results from first-time spawners, however (Figure 10), indicate that most gonadal fat is accumulated during reservoir feeding before the first spawn; among older females from Lake Sakakawea, (age 25 and older), no large GFBs were found. This result, combined with the minimal growth (or weight loss) among older tagged fish indicates that nearly all production, i.e., elaboration of fish tissue (Chapman, 1968) in older Yellowstone-Sakakawea paddlefish is routed into reproduction (gonadogenesis; Gessner et al., 2002) or maintenance.

Accumulation and depletion of fat occurs at other locations besides the gonads, including the muscle, liver and other organs, within the walls of the body cavity, and in the interstices between eggs, as has been reported for other species (Jobling et al., 1998; Garcia-Gallego et al., 1999). Our field observations and unpublished data indicate that under conditions of high reservoir levels and productivity in 1996–1998, young male and female recruits were larger at age and were observed to have more fat within the musculature and ventral walls of the body cavity. Caviar processors at Intake and the Confluence frequently complained in those years about “fatty” eggs, i.e., eggs with significant accumulations of fat in the interstices between the eggs, because fatty roe is difficult to process into caviar. The relationship between fat accumulation and depletion under variable habitat conditions deserves further study and is the subject of a current investigation. More research is also needed regarding fat accumulation at different sites on the body.

The ability of paddlefish to accumulate gonadal fat when food supplies are abundant may be an important energy storage mechanism in habitats such as Lake Sakakawea, a Great Plains reservoir with a continental climate, a short growing season (Thornthwaite, 1941), a brief period of invertebrate food production, and resulting extreme seasonal variations in habitat conditions and feeding opportunities (Becker and Gorton, 1995). Rosen and Hales (1981) reported that paddlefish below Gavins Point Dam fed little in the winter. Although detailed seasonal studies have not been done, available evidence indicates that the period for

active feeding of Yellowstone-Sakakawea paddlefish is short. Spawning fish may ascend the river as early as the autumn before spawning or by April of the spawning year and remain in the river as late as July (Firehammer, 2004). In our 14 years of observations at the Confluence and Intake, we have not observed any food in the stomachs of adult paddlefish caught in May and June. In contrast, the age 0 and age 1 fish caught with dipnets in August (Fredericks and Scarnecchia, 1997), as well as the few fish of adult age we have sampled in Lake Sakakawea in August, had recently consumed large quantities of zooplankton. In addition to cessation of feeding during spawning migrations, Lake Sakakawea paddlefish spend much of the long winter in cold water without access to the abundant zooplankton food supply available during the brief summer. In this situation, the storage of gonadal fat during times of plenty may function as a capacitor, providing the paddlefish with a predictable energy supply to be discharged as needed for off-season maintenance and energy demands of sexual maturation. Other fish species, including *Acipenseriformes*, also have strongly seasonal feeding opportunities. Sulak and Randall (2002) hypothesized that long periods of fasting in Gulf sturgeon *Acipenser oxyrinchus desotoi* were associated with locations and thermal conditions that rendered food acquisition efforts energetically ineffective. MacKinnon (1972) found that plaice *Hippoglossoides platessoides* stored energy during the summer months for use in the winter for maintenance and gonad development. Numerous other species of fish undergoing fasting in the months prior to spawning have been shown to use fat stores as a reliable energy supply for maintenance and spawning (Greene, 1913; Idler and Clemens, 1959; Lisovskaya, 1977; Pond, 1978; Gilhousen, 1980; Brett, 1995).

Sex-Specific Differences in Reproduction and Energy Depletion. In our study, females typically depleted their GFBs rapidly in two to three spawning events; males depleted their GFBs more slowly. This result is also consistent with results of lipid depletion from other organs in other species. Jobling et al. (1998) reported that female Arctic charr *Salvelinus alpinus* lost 80% of their body lipids during spawning and over-wintering, whereas males lost only 50–55%. Idler and Bitners (1960) reported that sockeye salmon *Oncorhynchus nerka* ovarian development consumed 8% of the energy expended during the spawning migration, whereas testicular development consumed only 0.5%. Idler and Clemens (1959) reported that pre-spawning, migratory female sockeye salmon from Stuart Lake and Chilko Lake used more fat and protein reserves than did the males. This pattern is consistent with the higher GSI for females than for males and the higher energy costs associated with producing eggs than sperm. Idler and Clemens (1959), for example, found that the greater depletion of energy reserves in female sockeye salmon than in males was associated with the greater pre-spawning increase in GSI in females (3.6% to 15.7%) than in males (2.4% to 3.1%). For Yellowstone-Sakakawea paddlefish reaching age 25, GFBs are nearly all depleted in females but not necessarily in males, indicating that energy demands and constraints for females may be greater than for males.

The pattern of lipid depletion associated with spawning and maintenance is also similar to what has been reported elsewhere. Love (1970) noted that in the cod *Gadus morhua*, fish first depleted lipids and increased the percentage of water in the liver, after which, in extreme depletion, they switched to proteins. A similar pattern occurs in other organs in pink salmon *Oncorhynchus gorbuscha* (Parker and Vanstone, 1966). In Yellowstone-Sakakawea paddlefish, decline in lipids in females with age and declining size of GFBs was more closely exponential than for males (Figure 12), further suggesting tighter energy demands and constraints on females than on males.

Mortality Rates

Sex-Specific Mortality Rates and the Costs of Reproduction. Although the relationship between natural mortality and reproduction is complicated by the effects of harvest, results indicate that males, which mature 8–10 years before females (Tables 1 and 2) suffer both higher natural mortality and harvest mortality due to maturation and upriver migration at an earlier age. The one- to two-year periodicity for males and the two- to three-year periodicity for females (Figures 5 and 6) corroborate results of Firehammer (2004), who found the same sex-specific differences in spawning periodicity of radio-tagged males and females in this stock. By the time a typical female makes her first spawning migration, a typical male of her cohort may have migrated and spawned five or more times. After full recruitment of both sexes, overall total mortality rates between the sexes are not significantly different (Figure 13), even though females had higher harvest rates in five of the eight tag-groups investigated. This result indirectly indicates that males, which migrate to spawn at a younger age and return to spawn at more frequent intervals, have a higher natural mortality rate later in life as well. This conclusion is consistent with the idea that the costs of reproduction, including migration to spawning areas and spawning itself, are imposed on males much earlier in life and more frequently than in females. The combination of the males' higher natural mortality rate and more years of vulnerability to the snag fishery is reflected in the much higher incidence of females than males age 30 and older (Tables 1 and 2).

Although age at recruitment for the stock based on age-frequency distributions typically occurred from age 10 to age 12 for males and from age 17 to age 19 for females, low numbers of recruits past those ages (Figure 13) may indicate low recruitment; it may also indicate that young recruits are not as vulnerable to the fishery as older recruits, or that some fraction of the male and female fish delay maturation and recruitment beyond these ages. Some females, for example, have large GFBs at ages 20 and 21; these fish may also be first-time spawners that had more years to reach a larger size and to accumulate larger GFBs. Doroshov et al. (1997) reported a wide range of ages at maturity in white sturgeon (15–32 years) and suggested that such a wide range might be common in wild stocks. More research is needed to ascertain the range of ages at maturation occurring in paddlefish and other Acipenseriform species. In addition, the relationship between fat stores earlier in life and the physiological decision to mature deserves further investigation. The fat accumulation in Acipenseriform species may have significance in influencing the year of onset of the maturation process, as has been found for Atlantic salmon (e.g., Thorpe, 1986; Rowe et al., 1991; Thorpe, 1999).

Number of Spawning Events. The age at maturity in combination with the average reproductive periodicity (Figures 5 and 6) and maximum age (Tables 1 and 2) indicate that males will spawn more often than females both within a specified period of years and over their entire lifespan. A male maturing at age 9 and spawning every other year would spawn 11 times by age 30. A female maturing at age 17 and spawning every three years would spawn only five times by age 30. The longest period between tagging and recovery in Montana was 26 years for a male and 24 years for a female. Assuming that the fish were tagged on their first upstream migration as age 10 and age 17 fish, respectively, the fish would be at least 36 and 41 years old, which is consistent with the maximum ages estimated from dentaries. For such old fish, a male with a two-year average spawning periodicity thus could have spawned 14 times, whereas a female with a three-year average periodicity could have spawned nine times. The number of spawns would be correspondingly higher for both

male and female fish, with a still greater discrepancy between males and females and a more rapid reproductive periodicity (i.e., every year for males and every two years for females, as typically found in North Dakota-tagged fish; Figure 6a, b). Although females live on average longer than males (Tables 1 and 2), they spawn fewer times in their lifetime because they spawn at greater intervals (Figures 5 and 6) and invest more per spawn (Figures 7 and 8). This combination of attributes has been used to explain the differences in life histories between males and females of numerous species, as well as to explain iteroparity versus semelparity among stocks within a species (Leggett and Carscadden, 1978; Bell, 1980).

Migratory Activity

Older Fish are Less Migratory. The tendency for older fish to remain downriver in North Dakota and younger fish to move farther upriver into Montana was consistent with the greater energy reserves available to younger fish. In contrast to older fish, where energy is more strongly routed to reproduction, the energy of younger fish is routed more into somatic growth and longer upriver migrations prior to spawning. This conclusion is further supported by the high downriver site fidelity of the older fish previously tagged downriver in North Dakota. Exploratory movements (beneficial or not) of younger fish, such as more extensive upriver pre-spawning movements, may thus be more tolerable or less costly in terms of fitness for males than for females and less costly for younger females than for older ones. Older fish tend to explore less, remaining nearer spawning sites. Firehammer and Scarnecchia (2006) radio-tagged fish downriver in North Dakota and found that despite yearly migrations of some adult paddlefish to Intake (YR Rkm 114), most fish did not migrate that far upriver. Of 69 sexually mature paddlefish radio-tagged, only four were contacted within 15 km of Intake during a four-year study. Spawning also appeared to be concentrated downriver. Estimated spawning areas based on larval fish captures and drift rates have indicated that sites downriver (below YR Rkm 48), where most of the older fish typically remain, are more likely than sites upriver (such as Intake) to be the primary paddlefish spawning locations (Gardner, 1995; 1996).

Migration Location Fidelity. Evidence from several sources supports the idea that the migration location fidelity observed in this study and elsewhere (Stancill et al., 2002) is not as strongly genetic as in some salmon species (Ricker, 1972), but is also strongly influenced by energetics and inter-annual variations in river conditions such as discharge and turbidity (Russell, 1986; Firehammer, 2004). Younger fish of both sexes tend to migrate farther upriver; age-specific differences in fidelity were found between Montana-tagged fish and North Dakota-tagged fish. Higher annual catches of paddlefish up the Yellowstone River in Montana are strongly positively related to higher annual discharge in that river during the harvest season (Unpublished Data, University of Idaho). Adult paddlefish tagged in the Missouri River above the Confluence have been frequently recaptured in subsequent migrations in the Yellowstone River and vice versa (Scarnecchia et al., 1995b). Thus, unlike some fishes which home repeatedly to specific locations for spawning, paddlefish exhibit highly variable annual migrations influenced by their energetic situation and by annual variations in river discharge, turbidity, and other factors (Russell, 1986; Firehammer, 2004). This conclusion is supported by genetics studies which show low overall genetic variation among paddlefish populations (Carlson et al., 1982; Epifanio et al., 1996).

Implications for Recruitment Patterns in Paddlefish

Older Fish as Prime Spawners

The tendency for the predominantly older North Dakota-tagged fish to migrate and spawn at more frequent intervals (on average) than the younger Montana fish suggests that the middle age to older fish, which also migrate on average less distance upriver, are the prime spawners. This interpretation is supported by the higher growth rate of both young male and female recruits than in older fish (Figures 2 and 3), a lower GSI for young recruits than for older fish (Figures 7 and 8), and a higher amount of gonadal fat in young recruits than older fish. (Figures 9 and 11). The younger recruits, not yet in their reproductive prime, are still developing their full reproductive capability, are growing more, migrating farther (either for spawning or exploration), and spawning less often. The older, prime spawners are utilizing their full reproductive potential under the existing ecological and physiological conditions (Roff, 1992), growing less or not at all, not migrating as far (either for spawning or exploration or both), and spawning on average at shorter intervals (Plates 1 and 2, accompanying inserts).

Spawning Failure and Egg Reabsorption

The long gonadal development period for females, especially for young fish (Figures 5 and 6) coupled with the brief migration and spawning season for this stock (typically mid April to mid July; Firehammer and Scarnecchia, 2006) results in a short period of time each year in which sexual maturity and spawning cues must match for successful reproduction. Each year, we observe female paddlefish with apparently mature, stage 4 eggs late in the spawning season, sometimes weeks after peak runoff. Evidently not all such females migrating upriver in a given year actually spawn. This spawning failure would be more likely to occur for fish with a three-year periodicity than a two-year periodicity because of the longer, slower maturation process involved and the same narrow window for spawning for both two-year and three-year spawners. This idea further supports the interpretation that the older females are the most effective spawners. Although detailed sampling in the reservoir has not been done (and there is no fishery from which to obtain samples), these results suggest that those females whose egg development is slightly out of phase with spawning cues will not spawn, but will move down river into the reservoir (Firehammer and Scarnecchia, 2006), perhaps reabsorb their eggs and not spawn the next year. In some years, a few unspawned females caught in the river are found reabsorbing their eggs. We do not know how many years (if any) reabsorption will delay the reproductive cycle. Krykhtin and Svirskii (1997) suggested that maturation in the kaluga *Huso dauricus* may be delayed two years following reabsorption. More research is needed on the relationships among spawning periodicity, length of spawning season, and egg reabsorption in paddlefish. The main difficulty is that in nearly all cases, the reproductive status of a wild fish is only viewed once, at harvest. Although hatchery-confined broodstock may be used to clarify the reproductive state in successive years, the natural spawning cues identified by wild fish will be absent.

Life History Framework for Yellowstone-Sakakawea Paddlefish

The five periods of juvenile and adult life history for male and female Yellowstone-Sakakawea paddlefish, which occur at different ages for each sex, can be categorized as (1) immature, (2) maturing, (3) somatic growth and reproduction, (4) prime reproduction and (5) senescence to death (Plates 1 and 2; Figure 16). During the first period (immature), fish exhibit rapid somatic growth as well as accumulation of energy reserves in the form of

Paddlefish juvenile and adult life stages

	<u>Somatic growth</u>	<u>GSI</u>	<u>GFB</u>	<u>Spawning interval</u>	<u>Movements</u>
1. Immature	highest	low	increasing	---	reservoir
2. Maturing	moderate	increasing	near maximum	---	reservoir
3. Somatic growth and reproduction	moderate to low	increasing	decreasing	longer	longer upriver migration
4. Prime Reproduction	low to negative	high/stable	decreasing(?) depleted(?)	shorter and minimized	shorter upriver migration
5. Senescence to death	negative	decreasing	decreasing(?) depleted(?)	unknown or dysfunctional	shorter upriver migration

Figure 16. Juvenile and adult life stages of Yellowstone-Sakakawea paddlefish and corresponding status of somatic growth rates, GSI, GFB, spawning interval, and pre-spawning migration distance.

GFBs and other fat deposits. GFBs are near their maximum at the end of this period (Figures 9–11). During the second period (maturing), somatic growth slows (Figures 2 and 3) as production and stored energy reserves are diverted into reproduction. Total mortality rates are low during the latter portion of the immature period and the maturing period as the fish are large enough to avoid predation and no fishery acts on them. In the third period (somatic growth and reproduction), fish are allocating energy to both somatic growth (Figures 2 and 3) and reproduction (Figures 7 and 8). Reproductive periodicity is typically close to two years for males and three years for females; gonadal recrudescence is slower than in the fourth period. GSI is increasing (Figures 7 and 8) and GFBs are depleted over 2–3 spawns in females (Figure 9) and reduced more gradually in males (Figure 11). Fish are often migrating longer distances upriver. River fisheries on migratory fish deplete males more rapidly than females. In the fourth period (prime reproduction), somatic growth is slow or negative (Figure 4), as energy is strongly routed into reproduction. GSI is at a maximum (Figure 7 and 8); GFBs are completely depleted in females and are still being gradually reduced in males. Reproductive periodicity is typically one year for males and two years for females; the rate of gonadal recrudescence is at its maximum and faster than in the third period. Fish do not tend to migrate as far upriver prior to spawning. In the fifth period, indications of senescence are not strongly detectable, in part because of harvest having eliminated some of the oldest fish. GSI of some of the oldest females decreases, however, (Figures 7 and 14); the oldest males have few energy reserves (Figure 11) and are observed to be typically long and lean.

A Life History Framework for Other Paddlefish Stocks and Other Acipenseriform Species?

The life history framework of Yellowstone-Sakakawea paddlefish in relation to the cost of reproduction depicted in this paper, such as the sexual dimorphism in size and other life history characteristics, the development and depletion of GFBs with age and number of spawns, the more rapid gonadal recrudescence and shorter migrations among older fish, may occur in whole or in part in other paddlefish and sturgeon stocks. The pattern for

Yellowstone-Sakakawea paddlefish may be more easily detected and quantified for long-lived Acipenseriform stocks than for short-lived stocks; in the latter case an entire life history may be compressed into less than 10–15 years rather than the 40–50 years in our stock. Other Acipenseriform species and other fishes inhabiting less productive habitats (e.g., our resident Dredge Cuts fishes or strictly riverine populations) may also exhibit much less extreme and less easily measurable energy accumulation and depletion than the Yellowstone-Sakakawea paddlefish.

Management Significance

The distinct differences in life history strategies of male and female paddlefish in relation to the costs of reproduction identified in this study must be considered when implementing sound harvest management strategies for this species as well as for other Acipenseriform species exhibiting similar life histories. Stock assessment data collection should include information on gender of fish whenever possible. In situations where harvest does not permit internal examination of the fish, the use of genetic methods, laparoscopy, and ultrasonography (Moghim et al., 2002) may be useful. Discriminant analysis of morphometric or other potentially useful distinguishing aspects of males and females should be applied to fish of known sex for application to those of unknown sex. Since most fishing methods and angler preferences are size selective (Walters and Martell, 2004), harvest should be regulated to insure that a range of ages of mature fish, including middle-aged and older individuals that are the prime spawners, persist and are allowed to spawn. Harvest regulations should be adopted that reduce the tendency to over-harvest the larger mature fish, which are typically females (Scarnecchia et al., 1989). Since snag hooks generally harvest all sizes of fish, low harvest rates and prohibition of high-grading will discourage size-selective harvest (Scarnecchia et al., 1995b). Such harvest management strategies will help to maintain adequate recruitment and reduce harvest impacts on the various life histories that have evolved in paddlefish and other Acipenseriform species.

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