Life history and the costs of reproduction in the Yellowstone-Sakakawea paddlefish stock

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Abstract

Investigations on the Yellowstone-Sakakawea paddlefish *Polyodon spathula* stock of eastern Montana and western North Dakota conducted over the period 1991-2004 have provided information on fish size, growth, age-at-maturity, longevity, reproductive periodicity, migration patterns, fecundity, energy reserves, and senescence to characterize the life history in relation to the cost of reproduction. Immature fish and mature fish between spawning events rear in Lake Sakakawea, a Missouri River main stem reservoir. Life histories of males and females diverge between age-5 and age-10, as males divert some production away from somatic growth and into sexual maturation. Males mature as young as age-8 and are typically fully recruited by age-10. Females of the same brood years continue to grow more rapidly than their male counterparts until age-13 or age-14, when they begin to divert some production away from somatic growth and into sexual maturation. Females are fully recruited at age-17. By then, females typically weigh about 10 kg more than males, and this sexual size dimorphism is maintained throughout the lifespan. At the time of the males and females first upstream spawning migration, both sexes have mature gonads, to which are attached gonadal fat bodies of variable size, consisting mainly of lipids and water, that function in energy storage much like a capacitor. Among young spawners (ages 15-18), female gonadal weight per weight of fish is about 10 times that of males, and increases to about 13 times that of males by age-25. Increases in fecundity among young adult males and females are concurrent with decreases in the amount of gonadal fat. Males typically spawn every one or two years and deplete the gonadal fat gradually over several spawns. Females typically spawn every two or three years and deplete the fat more rapidly, over two to three spawns, so that it is largely exhausted by age-25. The lipid content of male

gonadal fat shows only a moderate relation to with the amount of gonadal fat, whereas female gonadal fat declines in lipid content (i.e., increases in water content) exponentially as the amount of gonadal fat decreases. After the females' depletion of the gonadal fat, fecundity (total green egg weight) remains steady for another decade, until age-35, when it begins to decrease. Results of this study are consistent with the idea that middle age and older paddlefish may be the most effective spawners. The younger recruits, not yet in their reproductive prime, are still developing their full reproductive capability, are growing more, traveling farther upriver, and spawning at longer intervals. The older, prime spawners are utilizing their full reproductive potential, growing less or not at all, traveling less far upriver, and spawning on average at shorter intervals. Catches of age-30 and older females outnumber those of males by more than three to one in North Dakota and more than four to one in Montana, a result of either higher natural mortality on males, greater harvest of males during their earlier and more frequent migrations, or both. By age-40, natural or fishing mortality has eliminated most fish of both sexes, although both male and female occasionally exceed age-50.   The distinct differences in most life history characteristics between males and females, as well as the larger size and higher age at maturity of females, are consistent with theoretical predictions of models of life history strategies as well as with empirical observations regarding the lack of direct male competition for females. The general life history pattern of growth and energy accumulation early in life followed by maturation, reproduction, energy depletion and senescence later in life outlined here appear to exist widely among Chondrostean fishes, and may exist in many other fishes as well. The energy accumulation and depletion may be less protracted and more difficult to observe in shorter-lived species and less extreme in less productive waters.

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 (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). The costs of reproduction in fishes are influenced by genetic, biological, physiological and behavioral characteristics of the individual fish or the stock as well as by external factors such as habitat quality and community interactions (Winemiller 1992).

Costs of reproduction to an individual fish or a stock can be observed indirectly through a variety of measures of performance, including a reduction in growth rate, increased mortality rate, reduction in future fecundity, and delays in future reproductive readiness. An adequate scientific assessment and understanding of the cost of reproduction in a fish stock requires information on the entire life history. Sex-specific information is needed on a number of life history characteristics of the species, 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). Interpretation of an individual aspect of a fish's life history in isolation rather than comprehensively considering the entire life history has resulted in much uncertainty and confusion about the adaptive value of particular life history characteristics and strategies (Scarnecchia 1983).

The North American paddlefish *Polyodon spathula*, is an ancient (MacAlpin 1947) , migratory (Russell 1986) zooplanktivorous (Fredericks and Scarnecchia 1997) Chondrostean fish closely related to sturgeons (Grande and Bemis 1991) and native to the Mississippi and Missouri rivers and selected Gulf Coast drainages (Gengerke 1986; Graham 1997) . In addition to its unique position in North America's fish fauna, the species has long supported commercial and recreational fisheries throughout the central United States (Coker 1930; Pasch and Alexander 1986; Graham 1997). It has also been an increasingly 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 will depend on a better understanding of reproduction, which is widely regarded as a weak link in the species' prospects for long-term survival. Knowledge gained from paddlefish may also be useful in the management of other long-lived, late-maturing species, which often present special challenges for fisheries scientists and managers (Boreman, 1997; Musick 1999).

Investigations on the Yellowstone-Sakakawea paddlefish stock of eastern Montana and western North Dakota (Scarnecchia et al. 1996a) 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 picture of the life history strategy of the stock. Our objective is to characterize biological and energetic aspects of reproduction in relation to the overall life history of the Yellowstone-Sakakawea paddlefish stock. Results presented for this stock have relevance to other stocks of paddlefish, other Chondrosteans, and other fishes worldwide.

Study Site

The Yellowstone-Sakakawea paddlefish stock inhabits the Lower Yellowstone (YR) and Missouri (MR) rivers of eastern Montana and western North Dakota (Scarnecchia et al. 1995b), an arid to semi-arid region described as continental in climate, with long severe winters (as low as -30° C), short hot summers (30-35° C), low rainfall (30 cm in the west to 40 cm in the east), low humidity and a growing season of about 115 days (Torrey and Kohout 1956; Howard 1960). The two rivers dissect the Missouri Plateau area, which consists of exposed bedrock, generally of Late Cretaceous to Tertiary (Oligocene) origin (Leonard 1911; Howard 1960). Treeless uplands, which consist mostly of grasslands and scattered badlands dominate the region, except near rivers, where the forested floodplains contain cottonwoods *Populus* spp. and ravines contain small cedars *Juniperus* spp.

The Yellowstone River, one of North America's 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. 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. Average discharge of the lower Yellowstone River at Sidney, Montana (YR km 47) during June over the period 1910-2002 was 1100 m^3/s (U.S. Geological Survey 2003). Firehammer (2004) described river reaches in the lower portion (YR km 71 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 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 basin (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 groups of putative stocks became isolated physically from each other. As of 2004, the Yellowstone-Sakakawea paddlefish stock's range extended from Garrison Dam up reservoir through Lake Sakakawea (reservoir area, 156,000 Ha). From the headwaters of the reservoir, the location of which can vary more than 50 Rkm depending on reservoir elevation, paddlefish distribution extends 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 northeast of Glendive (Torrey and Kohout 1956; Figure 1). In years of high spring discharge, some migratory paddlefish move either over or around the dam (via a flooded side-channel) past Intake as far as the Cartersville Diversion Dam at Forsyth (YR Rkm 382).

Lake Sakakawea, 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. After the initial filling of the reservoir over a 13-year period (1953-1966; Scarnecchia et al. 1996a), the reservoir water level reached its normal maximum elevation of 564.25 m in the summer (July) of 1969, dropped to 555.71 in August, 1990, rose to 564.58 by August, 1997, and dropped steadily over the period 1998-2004 to 553.72 in August 2004 (U.S. Army Corps of Engineers, 2005).

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. (1996a). 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. Since the time the dam was closed, nearly all Yellowstone-Sakakawea paddlefish have reared in Lake Sakakawea as immature fish and as mature fish between spawning migrations. A small percentage of fish is stranded or rears volitionally in the Dredge Cuts, large, clear, flooded borrow pits immediately below Fort Peck Dam. These fish periodically 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 preceding 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 into the summer and beyond, 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), where by July and August, as 150-250 mm fork length (FL) fish, they are feeding selectively on invertebrates, chiefly the large, predaceous cladoceran *Leptodora kindtii* (Fredericks 1994). Age-0 are commonly eaten by walleyes *Sander vitreum* and saugers *Sander canadense* (Mero et al. 1995; Parken and Scarnecchia 2002). By late fall or the following summer, they are filter-feeding on a wide variety of zooplankton and other invertebrates (Michaletz et al. 1982; Fredericks 1994; Scarnecchia et al. 1995a; Fredericks and Scarnecchia 1997), for the rest of their life, with the aid of long, filamentous gill rakers (Kofoid 1900; Imms 1904). 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, Riverdale, Personal Communication)

During the spring pre-spawning migration (May-June), a recreational fishery based on snagging adult fish occurs in both Montana and North Dakota at several sites along the Missouri and Yellowstone rivers. Anglers use long, heavy spinning rods with 8/0 to 10/0 treble hooks and 13.6-22.7 kg test line to snag the fish as they congregate at known holding sites. Important fishing sites in North Dakota include (in order, progressively upriver) the Pumphouse (MR Rkm 2503) near Williston, the Confluence (MR Rkm 2542, 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 2744; Frazer Rapids, Rkm 2813.3). A modest bow and arrow fishery also exists in the Dredge Cuts (MR Rkm 2846; Needhan and Gilge 1986). Additional details about the snag fishery as well as its socio-economic characteristics of the anglers are documented elsewhere (Scarnecchia et al. 1996b; Scarnecchia and Stewart 1997b).

The interstate fishery is managed cooperatively under a joint management plan developed by the states of North Dakota and Montana (Scarnecchia et al. 1995b). As of 2004, 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 this 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.

The fisheries are managed and monitored similarly in both states. 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 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). 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. 1996a), is generally indicative of the actual run composition.

Materials and methods

Data sources

Cleaning stations -- Life history information for Yellowstone-Sakakawea paddlefish was obtained over the 14-year period 1991-2004, mainly from two cleaning stations, one each 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 of these stations. Under the community-based roe-donation programs at each site, anglers receive free cleaning of their fish 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 increment, 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).

Adult tagging -- Over the period 1964-2004, more than 14,000 adult migratory fish 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, most tagged fish brought into the cleaning stations were also sampled for dentaries for age determination. Other data available from tagging 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 were summarized annually from 1991 to 2004.

Differences were assessed in mean weights between males and females each year.

Age structure - Age was estimated 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 Scarneccchia et al. (1996a) 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, each of 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 older), the final age was assigned by the primary reader. If the ages differed by more than these 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 based on recoveries of known-age coded-wire tagged fish and partially validated for old 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). To ascertain that the testes were from mature fish, in 2002, gonad samples were taken from 45 males 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 um sections of tissue that were floated into a glass slide and air-dried overnight. The tissue sections were later stained with an H and E (Harris’ Hematoxylin and Eosin) 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 maximum age of fish harvested each year. Sex-specific differences in longevity were evaluated by comparing with a Chi-square test the frequencies of male and female fish age-30 and older for each year from 1991 to 2004.

Growth rates -- Growth rates of male and female paddlefish was described with a von Bertalanffy growth function, expressed as

$$L=L_{\infty}e^{\mathbf{(1-K(t-t_{0}))}}$$

where L is length, L_∞ is the length of an infinitely old fish, K is the curvature parameter, and t_0 is the initial condition parameter (Moreau 1987). 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 size at age of pre-recruited males and females, and thereby to estimate the age when the males and females diverged in their growth rates. Weight-converted von Bertalanffy equations were also calculated, expressed in terms of L_∞ as:

$$\mathbf{W_\infty = a\, L_\infty{}^{b}}$$

where W_∞ is the weight of an infinitely old fish.

Post-maturation growth rates of all fish were 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 would occur. To test this hypothesis, lengths and weights were compared for individual fish tagged and recaptured at least eight years apart.

Reproductive periodicity -- Reproductive periodicity of males and females was determined from the minimum number of the years elapsed between jaw tagging and recovery of jaw tagging information for migratory fish. Fish tagged upriver 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. Downriver 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 acipenseriformes in general by Bemis and Kynard (1997). As a result, a fish with a reproductive cycle of two years might be caught in successive years as are result of being tagged in spring and recaptured the 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.

Fecundity -- Fecundity for both sexes was estimated from gonadal weights. Gonadal weight of females was estimated to the nearest 4.5 g from 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 estimated to the nearest gram from the testes, after it 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 (Crim and Glebe 1990; DeVlaming et al. 1982).

Gonadal fat weight -- Each gonad (i.e., testis for males, roe for females) had attached to it a clump of discrete, consolidated, easily identifiable fatty tissue, hereafter called gonadal fat. From 2001 through 2003, gonadal fat was weighed from nearly all (>90%) of fish brought into each cleaning station. The gonadal fat was separated manually from the gonads and weighed to the nearest gram. All samples were identified and matched to other life history data by the angler tag number.

Gonadal fat composition -- In 1997, sub-samples of the gonadal fat were collected from 29 fish, 13 males and 16 females, for proximate composition 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 Office 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 subjected to a Soxhlet extraction process with purified ether. The recovered solvent free residues collected were weighed and averaged. Results were expressed as percent lipids, percent moisture, and other. For the sexes separately, the ratio of gonadal fat to gonad weight, percent lipids, and the age of the fish were compared to investigate if any relationship existed among them.

Identifying costs of reproduction from examination of extreme cases -- The large sample sizes of data from harvested fish permitted us to separate out an adequate, non-random subsample of individual fish exhibiting major individual deviations in growth that might provide additional insight into the costs of reproduction. Especially long (at least 132.5 cm BL) and heavy (at least 46.5 kg) female fish were evaluated against 200 randomly chosen female fish for GSI and the amount of gonadal fat. 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 also be expected to have 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.

***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 <16, ages 16-25, ages >25; females:ages <25, ages >25) using Chi-square tests. In all comparisons, the null hypothesis was that there were no differences in migtion 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 and compared with catch curves (Ricker 1975), expressed as the negative slope of a plot between the natural logarithm of the numbers present versus age for all fully-recruited age classes. Because of documented variations in year class strength and spawning success, 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 would be the same.

To compare harvest rates between males and females, three tag groups from Montana (1984, 1986, and 1988) and five tag groups in North Dakota (combined spring and fall tag groups, 1993, 1994, 1996-1998) were compared. Sex at the time of tagging was not absolutely known. However, inasmuch as nearly all mature female fish in this stock were previously found to be heavier than nearly all mature male fish (Scarnecchia et al. 1996a), the sex of fish at the time of tagging was assigned by plotting the weight-frequency distributions from the harvested fish for the corresponding tag periods (1984, 1986, 1988 for Montana, 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.

Number of spawning events - The potential number of spawning events was estimated separately for males and females based on the age-at-maturity, reproductive periodicity, and the longevity.

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 of fish by age (for males and females), 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 old fish than for younger recruits. For condition, it was hypothesized that the oldest males (age-30 and older) would have lower condition (i.e., be leaner) than young recruits (age-15 and younger). It was also hypothesized that the oldest females (age-35 and older) would have lower condition than young recruits (age-22 and younger) 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). Comparisons between young and old fish were made with a Wilcoxon’s two-sample test. For fecundity, we hypothesized that the oldest females would have lower fecundity than middle-aged females.

Results

Size of mature fish -- More than 90% of mature fish could be correctly identified as male or female by length or weight alone; little overlap was observed in either body length or weight of male and female fish. At Intake in 1991, for example, only 22 of 1121 males (2%) reached a length in or above the interval of 107.5-112.5 cm BL, whereas only 114 of 1495 females (7.6%) were short enough to be in this interval. Weights also showed little overlap. Only one of 1452 males (<1%) that were weighed reached the 20-25 kg weight interval, whereas only 131 of 1868 females (7%) weighed little enough to be in this interval. In 1993, only 21 of 1075 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 1991-2004.

Age structure and age-at-maturity -- Mean ages of harvested females were greater than for males in all years 1991-2004 in both states, except for 1992 in North Dakota (Wilcoxon two-sample text, P<0.01; Tables 1, 2). The difference was in part associated with distinct differences between males and females in age-at-maturity and upstream migration; males entered the harvest at a younger age than females. Males began to enter the fishery at about age 8, and were fully recruited by about age-10, depending on the year. There was great consistency among years (1991-2004) and states in the first age-at-maturity; in nearly all years less than 1% of the harvested males were less than age-8 (Tables 1,2). Age-8 and age-9 migratory fish were observed to have fully-developed gonads. The observation of the sexual maturity of males of various ages was corroborated by histological analysis. Of 45 males evaluated histologically, ranging from age-6 (a 4.5 kg male) to age-35, all but two fish (ages 26 and 31) had at least some fully-developed spermatocytes, although 4 young fish (ages 6,10, 10,14) two middle-aged fish (ages 20, 22,26) and two older fish (ages 30,31) had some undeveloped spermatocytes present. Young, mature males age-15 or less constituted high fractions of the male fish harvested in Montana from 1991-2004, ranging from 34% (1991) to 86% (1997). (Table 2).

Females of the same brood year as males became sexually mature and entered the fishery several years later than their male counterparts. As with males, however, there was great consistency among years (1991-2004) and between states in age-at maturity. Females began to enter the fishery at about age-15, and were not fully recruited until about age-17 (Tables 1,2). The percentage of females age-15 and younger 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 younger 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 3 fish resulted in processed caviar exceeding 2.2 kg in weight. In contrast, nearly all of the 4,958 females age-16 and older had fully-developed stage-4 eggs.

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 1,2). 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 on females in North Dakota (27.8) was nearly three years greater than in Montana (25.0; Tables 1,2).

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%) of North Dakota-caught fish were greater than age-30. For females, in contrast, 1080 of 5,909 (18.3%) Montana-caught fish and 1,707 of 4,988 (34.2%) North Dakota-caught fish were age-30 or older. 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 past 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 1,2).

Growth rates --Paddlefish growth curves differed markedly between males and females, a pattern consistent every year from 1991 to 2004. Mature females reached a significantly greater maximum length and weight than mature males, and were both longer and heavier than mature males at all ages. In 2003 for example, L_∞ values for males in Montana and North Dakota were 99 cm BL and 101.1 cm BL, respectively, whereas L_∞ values for females were 118 cm BL and 125 BL, respectively (Figures 2a,b). W_∞ values for males were about 14 kg and 14.5 kg, respectively, compared to about 30 and 34.5 kg for females, respectively (Figures 3a,b). In 2004, L_∞ values for males in Montana and North Dakota were 101.3 cm BL and 101.3 cm BL, respectively. W_∞ values for males were about 14.8 and 15.1 kg respectively, compared to about 32.4 and 35.5 kg for females, respectively. In both years, considerable variation existed in growth rates among individual paddlefish, however, as indicated by the scatter of points around the fitted line (Figures 2a,b; 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 crossed differed between 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 females thus grew at similar rates until somewhere between ages 5 and 10, but diverged thereafter as males of a give brood-year slowed their growth and began sexual maturation. Females of that brood year, in contrast, continued growing more rapidly than the males and would not begin maturation for several years.

Once sexual maturity had been 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 of male and female fishes, and from recaptured mature fish tagged at least 8 years earlier. Noticeable growth of fish continued until about age-20 in males and age-25 in females, when growth curves closely approached the asymptote (Figures 2a,b; 3a,b). As seen from dentaries, the males grew rapidly until about age 5-7, and then slowed growth as maturation began. Late in life, annuli on dentaries were tightly packed (Plate 1), consistent with the asymptotic portion of the von Bertalanffy curves. Females grew more rapidly than males from after males began maturing until the females reached about age 13-14, when their growth also slowed markedly associated with their maturation. In later years, their 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. 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). Many fish also lost weight.

Reproductive periodicity -- The reproductive periodicity was of a shorter interval 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, with a secondary peak in returns occurring six years after tagging, indicating that the most common reproductive periodicity was three years (Figure 5b). Unlike males, few females made spawning migrations in successive years; only 3 females from Montana were recaptured one year after tagging, whereas 57 fish were recaptured two years after tagging and 99 fish were recaptured three years after tagging (Figures 5a,b).

The reproductive periodicity for fish tagged before August in North Dakota was on average shorter than for Montana. For males, the frequency of recaptures after one and two years was similar, indicating that reproductive periodicity was equally likely to be one or two years (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 the greater mean age of the North Dakota fish (Tables 1,2), there was no evidence that *within* either group of fish, older age was associated with a shorter reproductive periodicity. For Montana-caught fish, the mean age of females 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 males, mean age of fish with a two-year periodicity (16.6; n = 53) was not significantly different than for males 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 (n = 28.3; n = 27; T-test, P= 0.45). For males, no significant differences were found between males with a two-year periodicity (23.3; n = 49) and those with a one-year periodicity (23.3, n = 49; T-test, P = 0.84).

Fecundity -- Males and females exhibited distinctly different strategies of fecundity and investment in reproduction. Females channeled a much higher fraction of their total weight into gonads than did males. GSI (gonad weight/fish weight) in sexually mature females was less than 10% for very young or precocious spawners (ages 15-18), increased rapidly to 20% for young spawners (ages 19-24), remained steady at 20% for middle age spawners (ages 25-35), and dropped slightly older and senescent spawners (age-35 and older; 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), in contrast, was a tiny fraction of that for females, ranging from 1% at ages 8-10 to about 1.5% at age-15 and older (Figure 8a,b). A typical female at age-30 thus had a GSI of about 13 times higher than for a male of comparable age.

Gonadal fat weight -- The amount of fat attached to the gonads of an individual paddlefish varied greatly; in some fish of both sexes fat weight constituted as much as as 15% of fish weight and several times the gonadal weight, whereas in others fat weight was less than 1% of total fish weight and a small fraction of the gonadal weight (Plates 3-6).

The role of gonadal fat was clarified when the weight of fat per fish weight was plotted against fish age. As with most other life history traits, females and males differed markedly in the relation of gonadal fat to age. For Montana females, the ratio of gonadal fat weights to fish weights averaged over 5% for young and precocious 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), gonadal fat had been almost completely depleted (<1%), and it remained so throughout the rest of the lifespan (Figure 9a). Fishes caught in North Dakota showed the same pattern, with slightly higher ratios of gonadal fat to fish weight at most ages (Figure 9b). The depletion of gonadal fat from age-15 to age-25 coincided with the steady rise in in GSI over the same period (Figures 7a,7b). This depletion of fat by age-25, as well as the wide range in amounts of gonadal fat for fish of different ages, was also apparent in a plot of (gonadal fat)/(gonadal fat plus green egg weight) against age (Figure 10)

For Montana males, gonadal fat weight per fish weight was highest at first maturity (ages 9-13), reaching an average of 6-7% of the body weight, and decreased gradually thereafter, dropping to 3% of body weight after age 25 (Figure 11a). For North Dakota males, the pattern of depletion was similar as for the Montana fish, with slightly higher fat levels at comparable ages (Figure 11b). The amount of gonadal fat continued to decrease into old age. Despite the well-defined patterns of depletion of the fat (rapidly in the females, gradually in the males), not all young spawners had similar concentrations of gonadal fat; some had large amounts and others had little. Old fish of both sexes, however, almost always had little or no gonadal fat.

Gonadal fat composition -- Lipid content of gonadal fat also differed markedly between males and females. Males, which had lower GSI values than females, had higher lipid content of fat, commonly exceeding 50%. Considerable variation was found in lipid content in relation to the ratio of gonadal fat to testes weight (Figure 12a). In contrast, only those females with the highest amounts of gonadal fat in relation to fecundity (which were also the youngest fish) had fat consisting of >50% lipids. Females with less gonadal fat also had exponentially lower percentages of lipids in the fat (Figure 12b). This exponential pattern was much more pronounced for females than for males (Figures 12a,b).

Identifying costs of reproduction from examination of extreme cases -- Evidence was found that especially long and heavy fish may have put less energy, on a percentage of weight basis, into reproduction than a typical fish. For especially long female fish at least 132.5 cm long, GSI was significantly lower (mean, 0.186; n = 60) than for 200 randonly selected fish (mean, 0.199, n = 200; Wilcoxon two-sample test; P=0.02). Differences in GWT (green egg weight plus attached fat 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 fish at least 46.5 kg in weight, mean GSI was sigificantly 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 GWT (green egg weight plus fat 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). Extremely large males also provided evidence of the cost of reproduction. Over the entire period 1991-2004, only two males were found to weigh more than 27.2 kg; upon being cleaned, both fish were found to have undeveloped, non-functional testes, a characteristic rarely seen in this stock.

Migration location fidelity in relation to tagging location (state), sex and age – 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 more significantly more likely to be recaptured in subsequent years in North Dakota (Chi-square test; $P<0.0001$; N =1033)). For males as a group, the pattern of fidelity 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). 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) 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 females as a group, the pattern of fidelity held for females age-25 and under (P=0.0055) and for females age-26 and over ($P<0.0001$). For younger females (age-25 and under), however, 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 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).

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 and 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 8 tag groups analyzed, the five earliest tag groups all had significantly (Chi-square test, P <0.05) or highly significantly (P<0.01) higher rates for females (F) than for males (M):(MT1984: F52% vs M32%; MT1986: F38% vs M20%; MT1988: F52% vs M 25%; ND1993: F49% vs M 29%; ND1994: F53% vs M19%) . Sex specific harvest rates for the three most recent tag groups (ND1996, ND1997 and ND1998) were not significantly different from each other (P>0.05) and were all between 14% and 22%.

Senescence -- Senescence was observed differently in males and females. In females, senesence was manifested most obviously as a decline in gonadal weight (GSI). From age-25 to age-35, females had maintained their fecundity, even with the depletion of most of the gonadal fat a decade earlier. For fishes over age-35, however, a decline in fecundity was apparent (Figure 14). In males, senesence manifested itself as a slight but steady decline in condition factor with age (Figures 15). Relative weights for males for the combined years 1996, 1997, 2003, and 2004 remained within the narrow range of 0.82-0.89 from age-9 to age-38, when sample sizes became too small for a reliable assessment. Mean W_r for males age-30 and older (mean, 0.849; n = 296) were significantly lower than for males age-15 and younger (mean, 0.866; n = 1729; Wilcoxon two-sample test; p=0.0003). This decline was associated with a progressive loss of gonadal fat and became particularly obvious for fishes older than age-35.

No such loss in condition was found for females, however. Relative weights for females for the four years combined also 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. Also in contrast to males, mean W_r for females increased gradually with fish age. Mean W_r for females age-35 and older (mean, 1.043, n = 294) was significantly higher than for females age-22 and younger (mean, 0.989, n = 1091; Wilcoxon two-sample test, $P<0.0001$). Whereas males became measurably thinner with advancing age, females tended to become plumper. Even the oldest females showed no detectable loss in condition, despite detectable declines in fecundity as measured by gonadal weight (Figure 14). Neither sex showed any noticeable increase in mortality rate at advanced ages (Figure 13a,b).

Discussion

Summary of the life history -- The foregoing investigations of Yellowstone-Sakakawea paddlefish have permitted us to interpret the life history of the stock in terms of the costs of reproduction. Newly-hatched paddlefish move into in Lake Sakakawea, North Dakota, where they selectively feed on the large predaceous cladoceran *Leptodora kindtii*. By no later than their second year, they have begun to filter feed (Fredericks 1994). 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 between 5 to 10, depending on the year, indicating that males and females grow at similar rates to at least age-5. Over the ensuing decade, life histories of males and females diverge greatly (Figures 2, 3; Stamps 1993) as males begin diverting production away from somatic growth into sexual maturation (Plate 1). Males become sexually mature starting at about age-8, and are fully recruited by about age-10 (Tables 1,2). Females of the same brood years are not yet burdened with the costs of reproduction and continue to grow more rapidly than their male counterparts, channeling energy predominantly into somatic growth until about age-13 or age-14, when they begin diverting energy into sexual maturation (Plate 2) . By age-15, females weigh on average about 10 kg more than males, and this sexual size dimorphism is maintained throughout the rest of the lifespan (Figures 2,3). Females are fully recruited at about age-17. At the time of the males and females first upstream spawning migration, both sexes have mature gonads, to which are attached gonadal fat bodies consisting mainly of lipids and water that have been amassed during their immature growth period in the reservoir. Some first-time migrants have amassed large amounts of gonadal fat, most have amassed some fat, and a few have amassed little or no fat (Figure 10). Among young spawners, female gonadal weight per weight of fish is about 10 times that of males, and increases to about 13 times that of males by age-25. Increases in fecundity among young adult males and females, as indicated by the GSI (Figures 7,8) are concurrent with decreases in the amount of gonadal fat (Figures 9,10). Males typically spawn every one or two years (Figures 2a,3a) and deplete the lipid reserves gradually over several spawns (Figure 10a,b). Females typically spawn every two or three years (Figures 2b, 3b) and deplete the lipid reserves more rapidly, over two or three spawns, so that it is largely depleted by age-25 (Figure 9a,b) . The lipid content of male gonadal fat shows only a moderate relation to the amount of gonadal fat present (Figure 12a), whereas females gonadal fat declines exponentially in lipid content (i.e., increases in water content) as the amount of fat decreases (Figure 13b). After the females’ depletion of the gonadal fat, fecundity remains steady and reproductive effort is maximized for another decade, until about age-35, when on average it begins to decrease, an indication of senescence (Figure 14). Younger fish, both male and female, are more likely to migrate upriver to Montana whereas older fish, both male and female, are more likely to remain downriver in North Dakota. Fish migrating upriver to Montana that are tagged there are more likely to be recaptured in Montana in subsequent years, whereas fish tagged in North Dakota are more likely to be recaptured in North Dakota in future years. Tagged young (<age-15), middle-aged (ages 16-25), and old (>age-25) males show no significant difference in their comparative likelihood of being recaptured upriver in Montana rather than in North Dakota. Among young females (up to age-25), 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-25), 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. Despite higher fishing mortality rates on females tagged as migratory adults, the number of age-30 and older females exceeds that of males (Tables 1,2) as a result of an earlier harvest and higher natural mortality on younger mature males (at a time when females are not yet vulnerable to harvest) and the more frequent spawning migrations of males. Total mortality rates are comparable for males and females over age-25 (Figure 13a,b). By age-40, mortality (natural or fishing) has removed most fish of both sexes, although both male and females occasionally exceed age-50 (Tables 1, 2).

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. 1996a). Other investigators, however, have found little difference in size at age for mature 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. 1996a; Bowersox 2004), in localities where growing seasons are shorter, age-at-maturity later, reproductive periodicity of a longer interval, and lifespans longer (Paukert and Fisher 2001). In Montana stocks, Scarnecchia et al. (1996a) and Bowersox (2004) found differences in age-at-maturity between males and females of 8-9 years. 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 gates 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, provides 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 paddlefish sexual size dimorphism -- The pronounced sexual size dimorphism and differential age-at-maturity in Yellowstone-Sakakawea paddlefish are best understood in the context of the entire life history and the cost 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 in the vast majority of North American freshwater fish species, males mature earlier than females. Our results indicate that Yellowstone-Sakakawea paddlefish are an extreme case, where males are much smaller than females and mature at a much younger age. This pattern is pervasive in other Acipenseriformes as well (e.g., shovelnose sturgeon, *Scaphirhynchus platorynchus*; 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 *Semotilis atromaculatus,* bluntnose minnow *Pimephales notatus,* central stoneroller *Campostoma 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 were smaller than females, neither territorial behavior nor parental care occurs (Roff 1992). The few observations available on paddlefish pre-spawning behavior and spawning in their turbid habitats provide no evidence that large 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 (perhaps several) male fish (Russell 1986). Pairing at spawning is thus highly unlikely. In addition, the high turbidity commonly associated with undammed 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 instead 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). The may 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 external visual differences and resulting cues in paddlefish do not exist. But it is consistent with a lack of direct competition by males for exclusive access to females.   It is also consistent with the overall similarities in appearance between males and females. Humans have yet to be able to reliably distinguish mature male and female paddlefish of the same size without internal examination of the gonads, ultrasonography (Moghim et al. 2002), or genetic analysis.

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 terms of their reproductive units (eggs) than do males, whose reproductive units (sperm) in even small individuals are many times more numerous than needed to fertilize all available eggs. The higher GSI for females than for males observed in this study is similar to results from other Chondrosteans. For example, Van Eenennaam et al. (2006) reported that GSI in green sturgeon was 7-17% whereas that for males was 2-8%. Zweiacker (1967) reported that shovelnose sturgeon gonads from mature fish constituted 7-22% of body weight in 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 from rapid growth in the first few years (Figures 2,3; Plate 1) renders them sufficiently large to escape predation from most other piscivorous species. The early 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). In later years, 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 1997).

Third, the extreme male-female differences observed in Yellowstone-Sakakawea paddlefish are accentuated by 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-Sakakaewea stock contrasts with results from hatchery-rearing 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 interannual differences in habitat conditions in Lake Sakakawea, the constant 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.

The role of gonadal fat -- The relations between gonadal fat, maturation state (GSI), and fish age found for the Yellowstone-Sakakawea stock clarify observations and speculations about the gonadal fat made for more than a century. Stockard (1907) reported the presence of large amounts of gonadal fat in plump male paddlefish fish from the Lower Mississippi River. Larimore (1950) described it in both male and female fish, and it has since been observed in paddlefish at other locations (Pool 13, Upper Mississippi River: Gengerke 1978; Lake Cumberland, Kentucky: Hageman et al. 1986; Russell 1986). Similar fat deposits have also been noted in other Chondrosteans: 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 (1993), who described it 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 testes has projections extending into the edge of the gonad and between the marginal tubules. The connective tissue covering of the testes also extends over the mass of fat.” (p. 119). For female fish, Larimore (1950) reported that “Immature females are covered on the under side with large masses of fat, such as were described for the males... . The interesting fact that undeveloped ovaries have excessive fat, whereas ripe ovaries do not, was brought to my attention by Mr. P. B. Barnickol, who examined many paddlefish during his work on the Mississippi River.” (p.121). Our results, along with observations of a few thousand female fish, differ somewhat from Barnickol’s observation in that ripe ovaries from mature Yellowstone River females ages 15-20 that have not spawned more than once or twice may have considerable fat associated with them. It is depleted during these years as GSI rises gradually, a pattern described by Roff (1992) as asymptotic. By age-25, however, when GSI has reached its maximum levels, nearly all gonadal fat in females has been depleted.

Our results for gonadal fat are also supported by other studies elsewhere. Hageman et al.

(1986) reported, but presented no data, that the amount of gonadal fat in paddlefish from Lake Cumberland, Kentucky was inversely related to the GSI. They speculated that the gonadal fat might provide an important energy source for the gonadal development. For Chinese sturgeon *Acipenser sinensis* 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 to 3.5 mm). In contrast, for 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 x 4.2 - 4.5 x 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, similar to what has been described here.

Careful investigations would probably indicate that the relationships observed in Yellowstone-Sakakawea paddlefish with regard to gonadal fat, i.e., of energy accumulation and storage during favorable feeding conditions for use in reproduction later in life, applies to a variety of Chondrosteans as well as other fish species. However, to evaluate the applicability of our results elsewhere, other factors must be accounted for. First, to avoid confusion, the age and the approximate number of probable spawning events should be estimated for the fish from which maturation is assessed and gonadal fat is weighed. For example, in results of Wei et al. (1997) the absence of gonadal fat in fish with Stage 3 eggs might occur because of environmental stressors, as they suggest, or it might occur from selectively sampling older, repeat spawners between spawning years. Secondly, our results indicate that although large amounts of gonadal fat are associated with young fish typically in their first or second spawning event, not all young, first-time spawners have large amounts of gonadal fat (Figure 11). The wide individual variation observed in the amounts of gonadal fat 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 Sakakwea may vary widely, with significant impacts on the growth rates and gonadal fat accumulation of individual fish. In addition, the characteristic large size and plumpness of reservoir-reared Yellowstone-Sakakawea paddlefish contrasts markedly with the historical leanness of fish from this stock prior to reservoir construction (Scarnecchia et al. 1995a) . For stocks of paddlefish restricted to less suitable, strictly riverine feeding habitats, or for riverine sturgeon stocks, gonadal fat accumulation at all ages may be minimal. At the other extreme, for some diets in production-oriented aquaculture situations, the fat accumulation in Chondrosteans has been considerable (S. Doroshov, University of California, Personal Communication).

Although high amounts of gonadal fat have been shown to be associated with young fish of both sexes, our observational approach (i.e., seeing the inside of each fish only once, at harvest) has not allowed us to specify exactly when throughout the life cycle the gonadal fat accumulated. It is not known if any accumulation occurs, for example, between the first and second spawns, or between the second and third, or if depletion is inexorable after sexual maturation begins. It is also not known if under better environmental conditions, fat accumulation in older fish would occur. Results from first-time spawners, however (Figure 10), indicate that most gonadal fat is accumulated from reservoir feeding before the first spawn. Among older females from Lake Sakakawea, (age-25 and older), no measurable consolidated gonadal fat is found, so accumulation in later years is minimal. This result, combined with the mimimal growth or even loss of weight among older tagged fish indicates that nearly all production, i.e., elaboration of fish tissue (Chapman 1968) in older Yellowstone-Sakakaewea paddlefish fish is routed into reproduction (gonadogenesis; Gessner et al. 2002), maintenance, or both.

Accumulation and depletion of fat occurs at other locations besides the gonads, including the muscle, liver and other organs, the gut, along body walls, and in the interstices between eggs, as in 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 in the body walls and musculature. 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. Such 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 locations in the fish.

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 (Fredericks and Scarnecchia 1997) dipnetted in August , as well 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 significant zooplankton food supply available during the brief summer. In this situation, the storage of gonadal fat during times of plenty may function much as a capacitor, providing the paddlefish with a predictable energy supply to be discharged as needed for off-season maintenance as well as the high energy demands of sexual maturation. Similar conclusions have been reached by Sulak and Randall (2002) for Gulf sturgeon *Acipenser oxyrynchus desotoi.* They hypothesized that the long period of fasting in that species was associated with the times (e.g., extreme cold or warm water) and locations (freshwater) when poorer feeding opportunities rendered food acquisition efforts energetically ineffective. Seasonal storage of energy reserves was reported by MacKinnon (1972), who 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 have been shown to use fat stores as a reliable energy supply for spawning (Greene 1913; Lisovskaya 1977; Pond 1978).

Sex differences in reproduction and energy depletion - In our study, females typically depleted their gonadal fat rapidly in two to three spawning events on a three-year cycle, so that older females not only had much less gonadal fat than young females, and what they had was also lower in lipids. 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 overwintering, whereas males lost only 50-55% of their lipids over the same period. Idler and Bitners (1960) reported that female sockeye salmon *Oncorhynchus nerka* ovaries consumed 8% of the energy expended from a standard female during the spawning migration, whereas testes consumed only 0.5% in a male. Love (1970) noted that in the cod *Gadus mordua*, 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). Along with depletion of the amount by weight of the gonadal fat mass, female paddlefish also deplete the lipid content more rapidly. Our conclusion is that because of the females' large investment in eggs, their energy demands for migration and spawning are greater than for males, and their depletion of gonadal fat more rapid as measured by weight and lipid content. Males, in contrast, typically deplete their gonadal fat by weight and lipid content much more gradually in a series of spawning events on a typical one- or two- year cycle.

Sex-specific mortality rates and the cost of reproduction - Although the relations between natural mortality and reproduction are complicated by the effects of harvest, results indicate that the males, which mature 8-10 years before females (Tables 1,2), suffer both a higher natural mortality as well as harvest mortality associated with maturation and upriver migration at an earlier age. The one- or two-year periodicity for males and the two- or three-year periodicity for females (Figures 5, 6) corroborate results of Firehammer (2004), who found the same sex-specific differences in periodicity of radio-tagged males and females in this stock. By the time a typical female make 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 the higher natural mortality rate later in life as well. This conclusion is consistent with the idea that the entire process of reproduction, including migration to spawning areas and the spawning itself, has a cost (Bell 1980; Roff 1992). These costs 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 river fishery is reflected in the much higher incidence of females than males age-30 and older (Tables 1,2).

Although full recruitment for the stock was tentatively estimated at ages-10 for males and age-17 for females based on age-frequency distributions, the low numbers of recruits past these ages (up to about age-25 for males, age-15 for females; Figure 13) indicates that either 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 ages 10 and 17, respectively. 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 if significant delays in maturation are occurring in some individuals.

Number of spawning events --The age-at-maturity in combination with the average reproductive periodicity (Figures 5,6) and maximum age (Tables 1,2) indicate that males will spawn more often than females both with 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. Similarly, the longest period between tagging and recovery in Montana for a male fish was 26 years for males and 24 years for females. 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. For them to spawn the same number of times, the female would have to live to age-56, which occurs rarely at present rates of total mortality (a combination of natural mortality and harvest). The number of spawns would be correspondingly higher for both male and female fish, with a still greater discrepancy between males and females, with 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 6,a,b). Although females live on average longer than males (Tables 1,2), they spawn fewer times in their lifetime because they spawn at greater intervals (Figures 5,6) and invest more per spawn (Figures 7,8). This combination of attributes has been used to explain the differences in life histories between males and females, as well as to explain iteroparity versus semelparity among stocks within a species (Leggett and Carscadden 1978; Bell 1980)

Older fish are less migratory -- The tendency for more older fish to be caught downriver in North Dakota and more younger fish to be caught upriver in Montana was consistent with the greater gonadal fat reserves available to younger fish. In contrast to older fish, where energy is more strongly routed to reproduction, activities of younger fish include more somatic growth, more pronounced movements 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. The greater movements of young recruits than older fish are consistent with results of Yellowstone-Sakakawea paddlefish movements and spawning. Firehammer and Scarnecchia (2006) found that despite yearly migrations of some adult paddlefish to Intake (YR Rkm 114), most fish did not migrate that far upriver in most years. 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 with the larger and older fish. Estimated spawning areas (Rkm) 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: genetics or energetics? Although the tendency for Montana-tagged fish to be captured in Montana and North Dakota-tagged fish to be recaptured in north Dakota is superficially consistent with the idea of homing and some degree of stock separation (Ricker 1972), evidence from several other sources supports the idea that migration location fidelity is at least partially a result of energetics. First, the younger fish of both sexes, which have higher gonadal fat reserves, tend to migrate farther upriver. Second, age-specific differences in fidelity were found between Montana-tagged fish and North-Dakota-tagged fish.

Third, higher annual catches of paddlefish upriver in Montana are strongly positively related to higher annual discharge in the Yellowstone River during the harvest season, indicating that migrations are strongly influenced by discharge (Unpublished Data, University of Idaho). Fourth, 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). Unlike some fishes which home repeatedly to specific locations for spawning, paddlefish are highly variable in their annual migrations, which are strongly influenced by annual variations in river discharge, turbidity, and other factors (Russell 1986; Firehammer 2004). Although genetic differences have been demonstrated among paddlefish from different regions (Epifanio et al. 1996), and cannot be ruled out as contributor to migration location fidelity in the Yellowstone-Sakakawea stock, within a restricted region such as between Fort Peck and Garrison Dams, fidelity may be more a result of energetics than genetics. This conclusion is supported by genetics studies, which show low overall genetic variation among paddlefish populations (Carlson et al., 1982; Epifanio et al. 1996).

Older fish as prime spawners – The tendency for the predominantly older North Dakota-tagged fish to migrate and presumably 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 2,3) a lower GSI for young recruits than for older fish (Figure 7a,b) , and a higher amount of gonadal fat in young recruits than older fish. (Figure 9a,b). 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 or both), 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 1,2, accompanying inserts).

A long reproductive periodicity and a short spawning season - The long reproductive periodicity for females, especially for young fish (Figures 5,6) coupled with the short migration and spawning season for this stock (typically mid-April-mid-July; Firehammer and Scarnecchia 2006) results 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 caviar-quality eggs late in the spawning season, often weeks after peak river discharge; evidently not all mature females with Stage 4 eggs migrating upriver in a given year actually spawn. This spawning mismatch would be more likely to occur for fish with a three-year periodicity than a two-year periodicity, further supporting 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 to provide 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, not spawn the next year (Figure 5). 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 relations between 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 fish is only viewed once, in the river, at harvest. Although hatchery-reader broodstock may be used to clarify the reproductive state in successive years, the natural spawning cues identified by wild fish will be absent.

Applicability to other fishes – The overall life history strategy of Yellowstone-Sakakawea paddlefish in relation to the cost of reproduction, including their sexual size dimorphism, their energy storage early in life followed by maturation, their reproductive periodicity, and their energy depletion later in life, appear to apply more widely to other Chondrosteans and may apply to many other fishes as well. The pattern may simply be more easily detected and quantified in a long-lived species or stock than in a short-lived stock; in the latter case an entire life history as outlined here may be compressed into less than 10 years. Other Chondrosteans and other fishes inhabiting less productive habitats 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 are explainable as adaptive (Wootton 1984) and are consistent with models of life history strategies (Bell 1980; Roff 1992). The distinct differences in life history strategies between the sexes identified in this study must be considered when implementing sound harvest management strategies for this species. 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, or discriminant analysis from fish of known sex should be used. Harvest regulations should be adopted that reduce the tendency to overharvest the larger mature fish, which are typically females (Scarnecchia et al. 1989). Inasmuch as most fishing methods and angler preferences are size selective (Walters and Martell 2004), care should be taken to insure that a range of ages of mature fish, including middle-aged and older individuals, persist and are allowed to spawn. Such a harvest management strategy will help to maintain adequate recruitment and reduce harvest impacts on the various life history strategies that have evolved in the species.

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Figure 14. Age-specific gonad weight (GSI) for female paddlefish, 2003.

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

List of Plates

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 when the fish was 1) immature, 2) maturating, 3) exhibiting both somatic growth and reproductive activity and 4) in its prime period of reproduction. Insert shows approximate ages associated with these four 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 when the fish was 1) immature, 2) maturating, 3) exhibiting both somatic growth and reproductive activity and 4) in its prime period of reproduction. Insert shows approximate ages associated with these four 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 3. Testes and large gonadal fat accumulation in a male paddlefish.

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

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

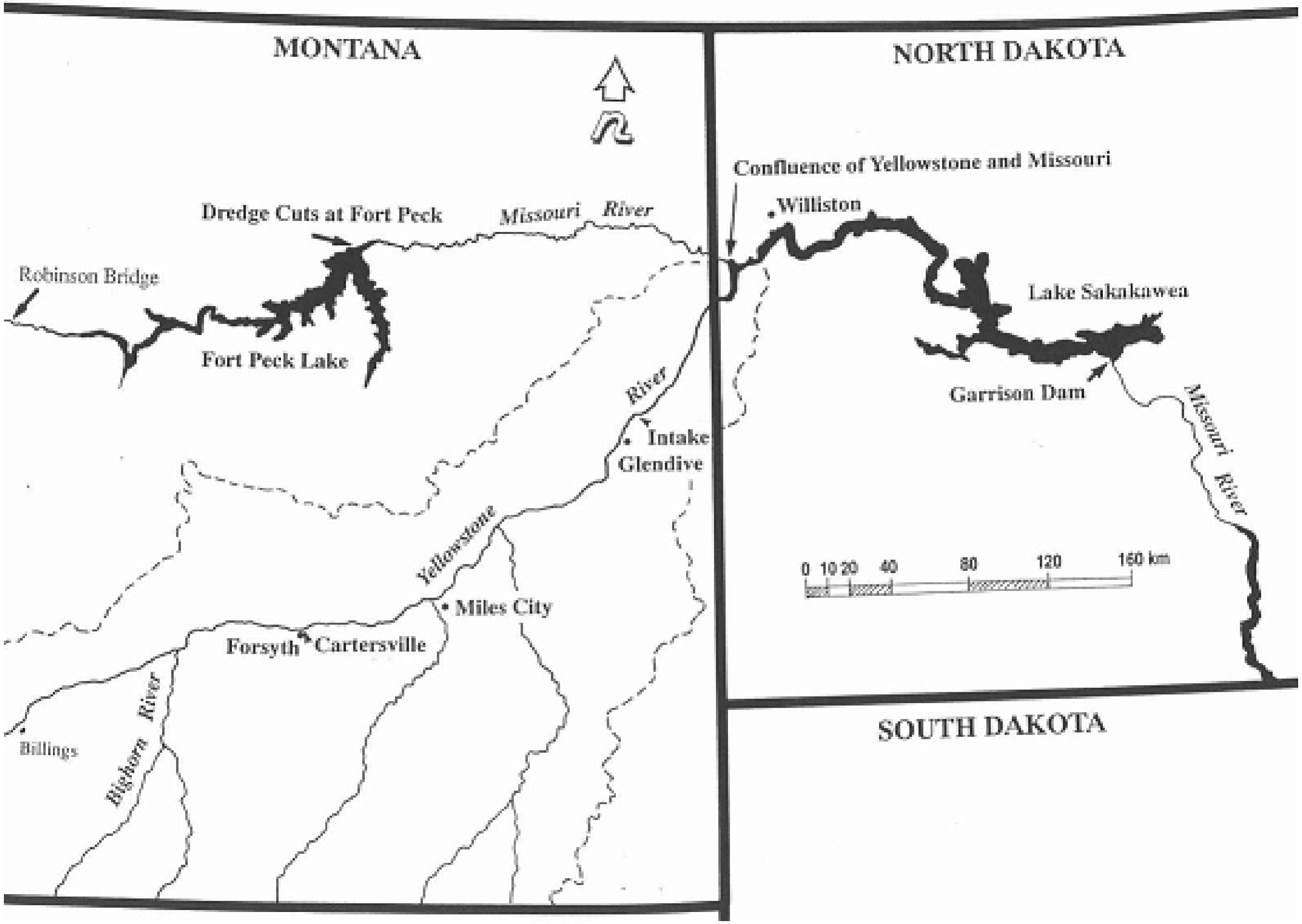
Plate 6. Fully developed ovary with egg mass filling much of body cavity. The little gonadal fat that is present is such fish is on the underside of the egg mass and hidden from view.

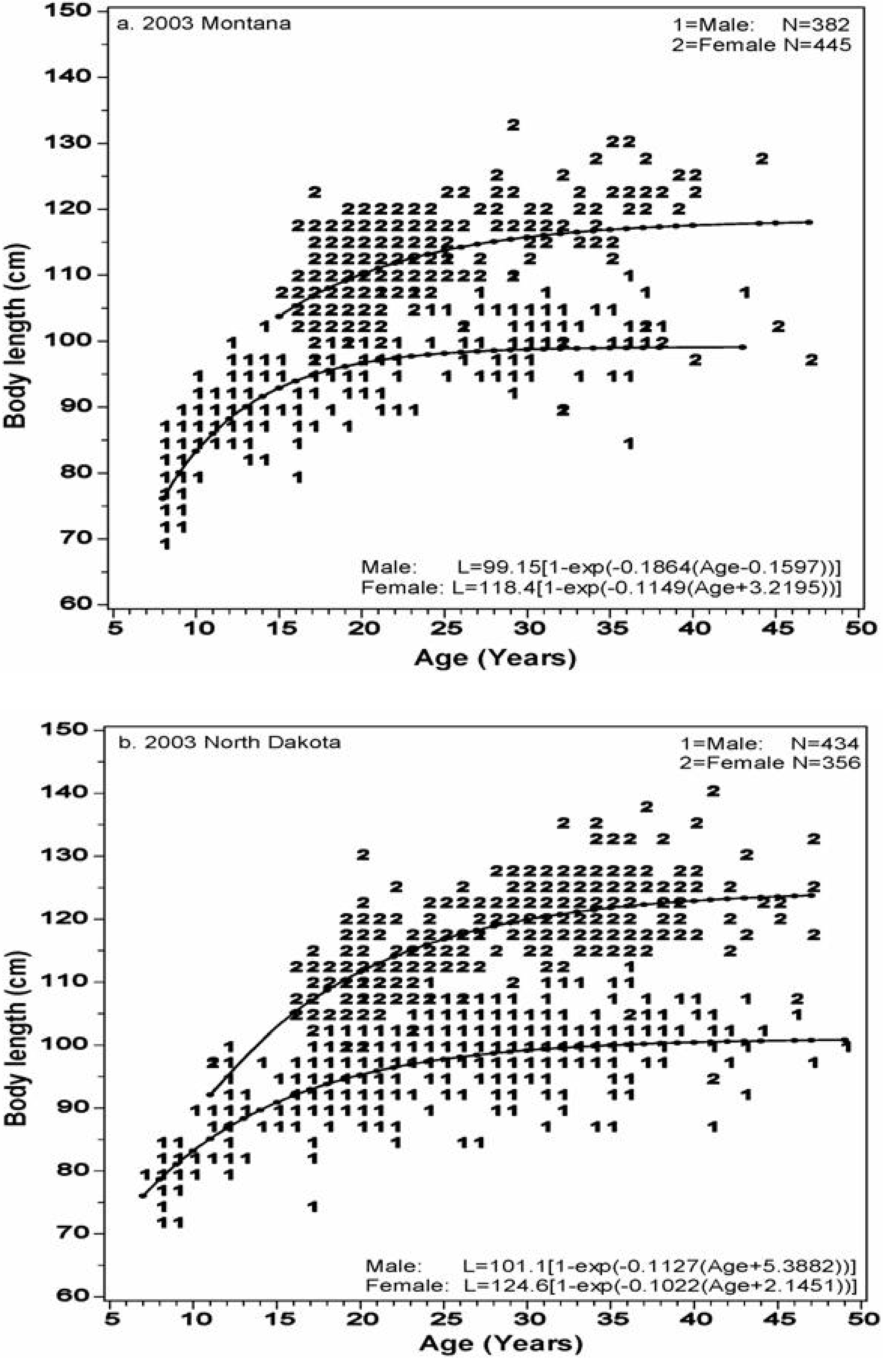
Table 1. Age summary for paddlefish caught in North Dakota, 1991-2004.

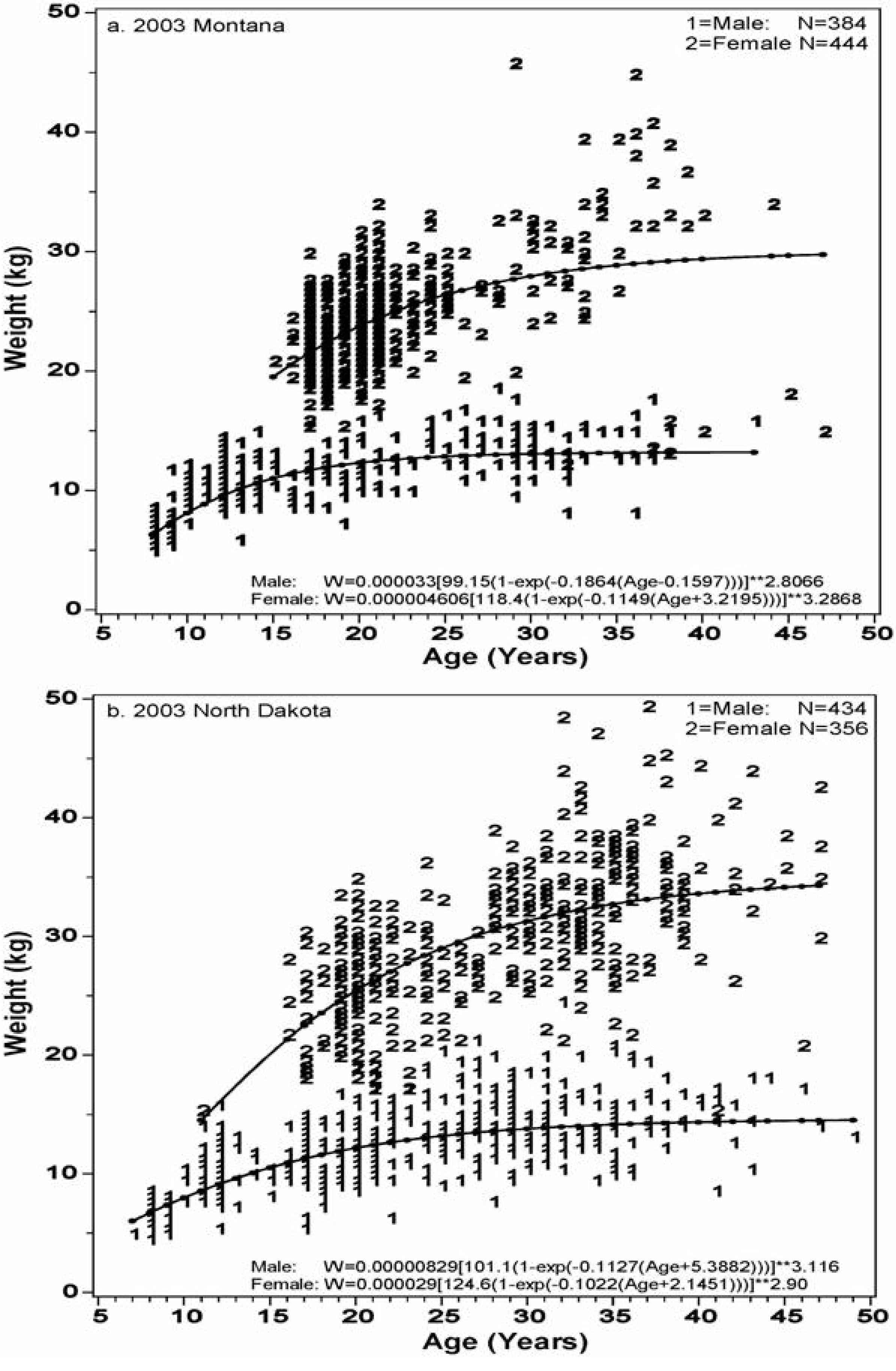
	Males							Females					
Year	N	Mean Age	% < 8	% < 16	% >=30	No. >=30	Oldest Fish	N	Mean Age	% < 16	% >=30	No. >=30	Oldest Fish
1991	74	20.7	0	10.8	4.1	3	37	54	24.1	0	7.4	4	33
1992	19	22.1	0	5.2	10.5	2	33	22	24.3	0	4.5	1	34
1993	48	22.1	0	33.3	0	0	29	72	25.2	0	9.8	7	35
1994	368	18.4	<1	35.1	3.0	11	43	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 older than age>=30						**11.6**						**34.2**	

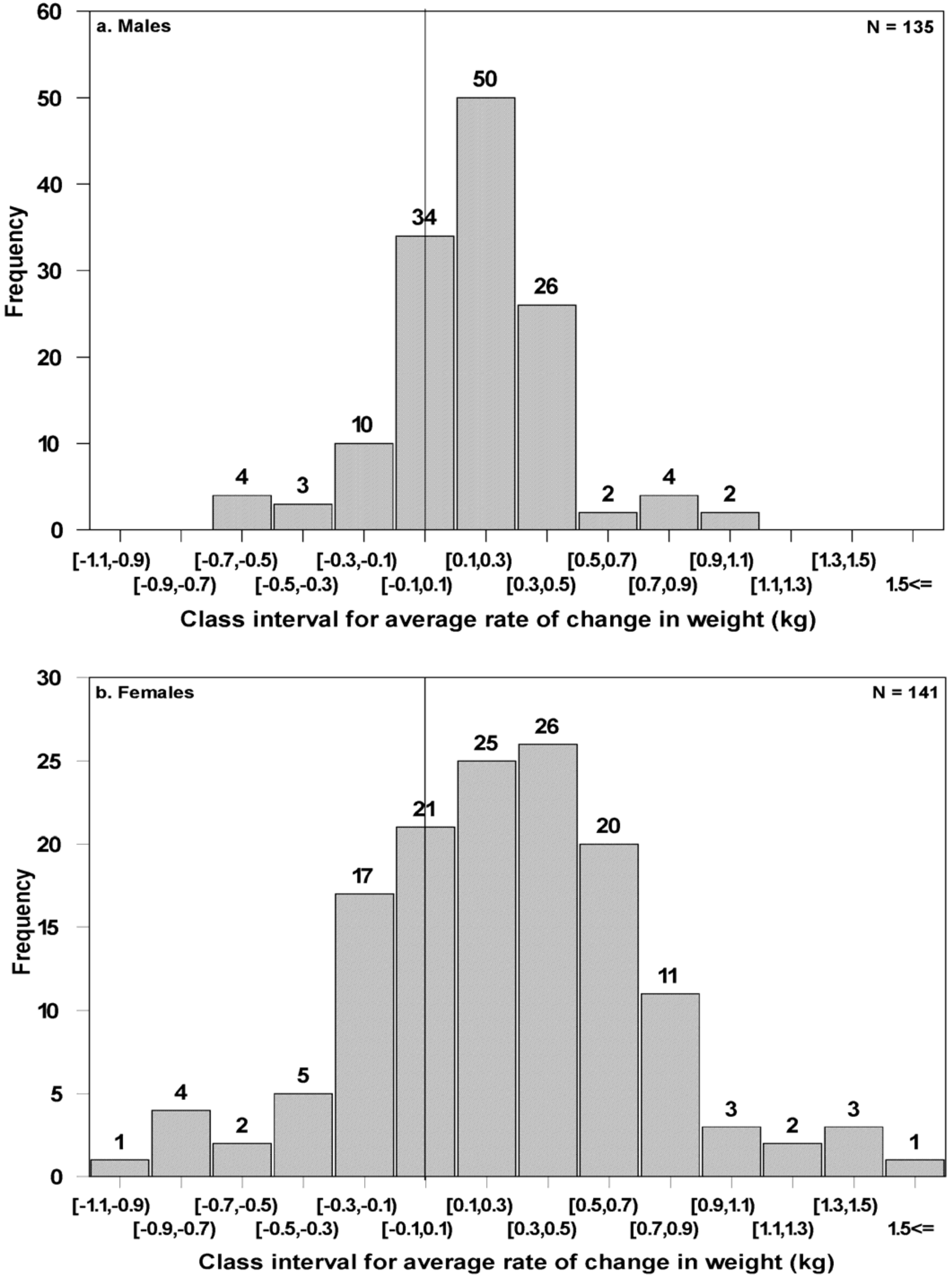
Table 2. Age summary for paddlefish caught in Montana, 1991-2004.

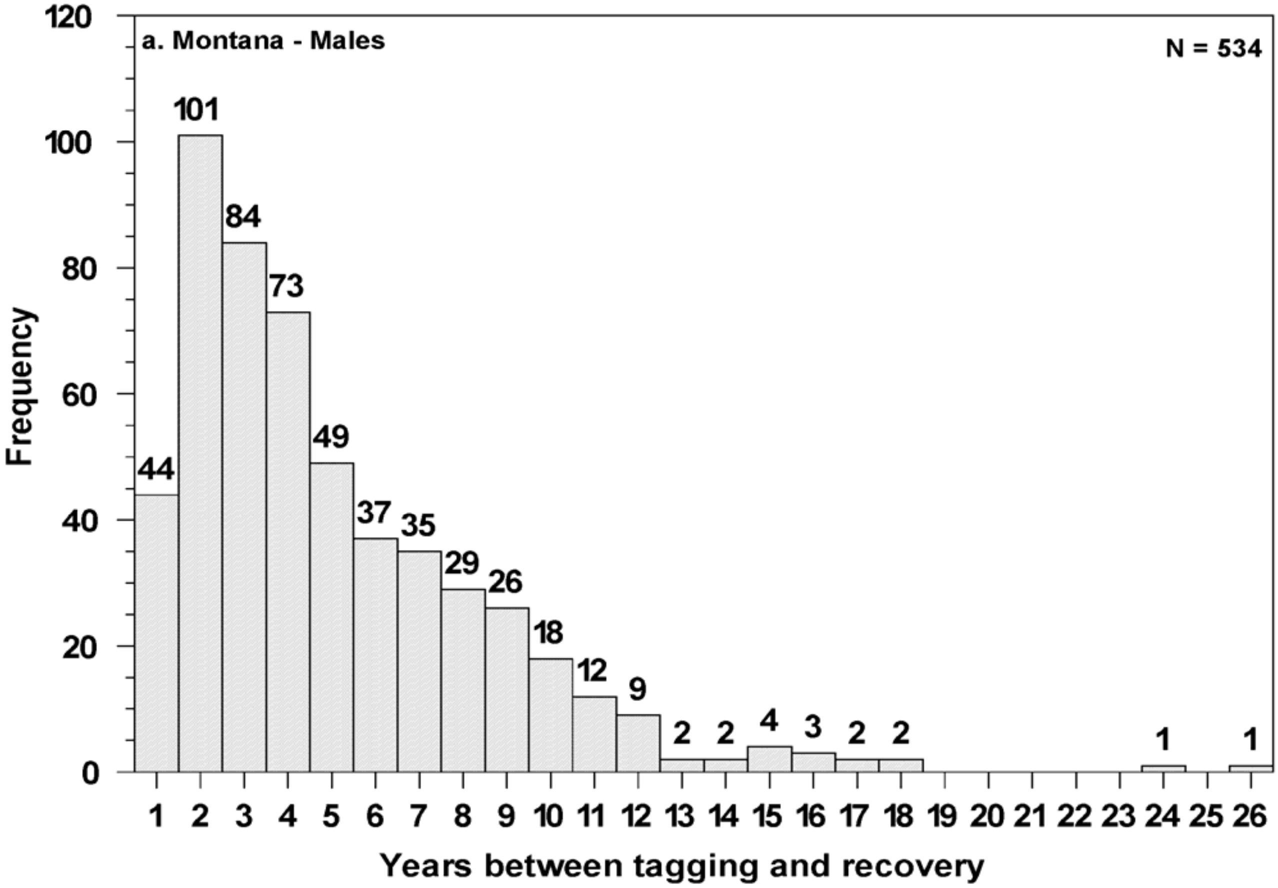
	Males							Females					
Year	N	Mean Age	% < 8	% <16	%>=30	No.>= 30	Oldest Fish	N	Mean Age	%< 16	%>=30	No. >= 30	Oldest Fish
1991	721	18.4	1.3	33.7	5.0	36	40	975	25.5	<1	14.8	144	42
1992	219	17.8	<1	39	2.3	5	33	471	26.2	<1	21.0	99	40
1993	1144	15.8	<1	47.2	<1	8	35	605	22.8	3.3	6.0	36	38
1994	116	15.0	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 older than age>=30						**3.9**						**18.3**	

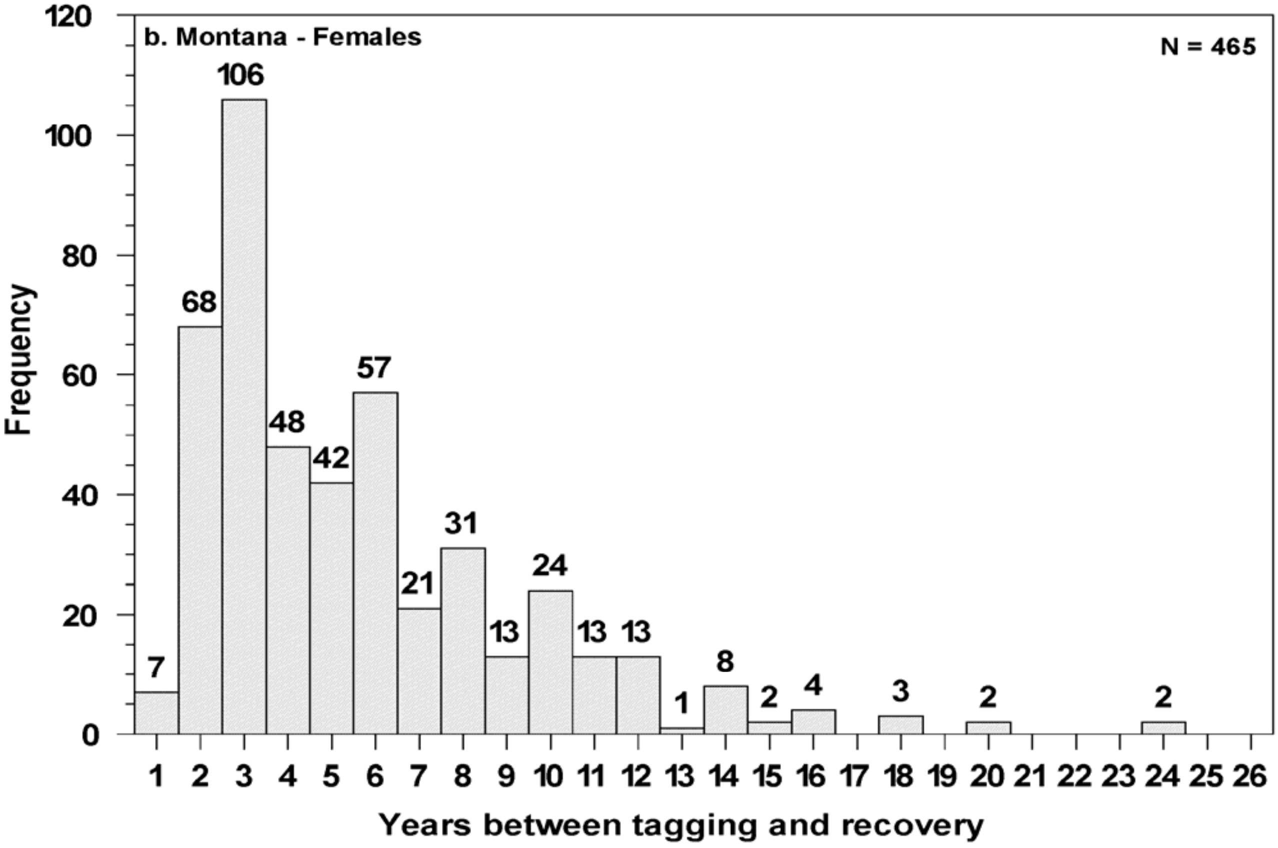

MONTANA
NORTH DAKOTA
Confluence of Yellowstone and Missouri
Williston
Dredge Cuts at Fort Peck
Missouri River
Robinson Bridge
Fort Peck Lake
Lake Sakakawea
Garrison Dam
Missouri River
River
Intake
Glendive
Yellowstone
Miles City
Forsyth
Cartersville
Bighorn River
Billings
0 10 20 40 80 120 160 km
SOUTH DAKOTA

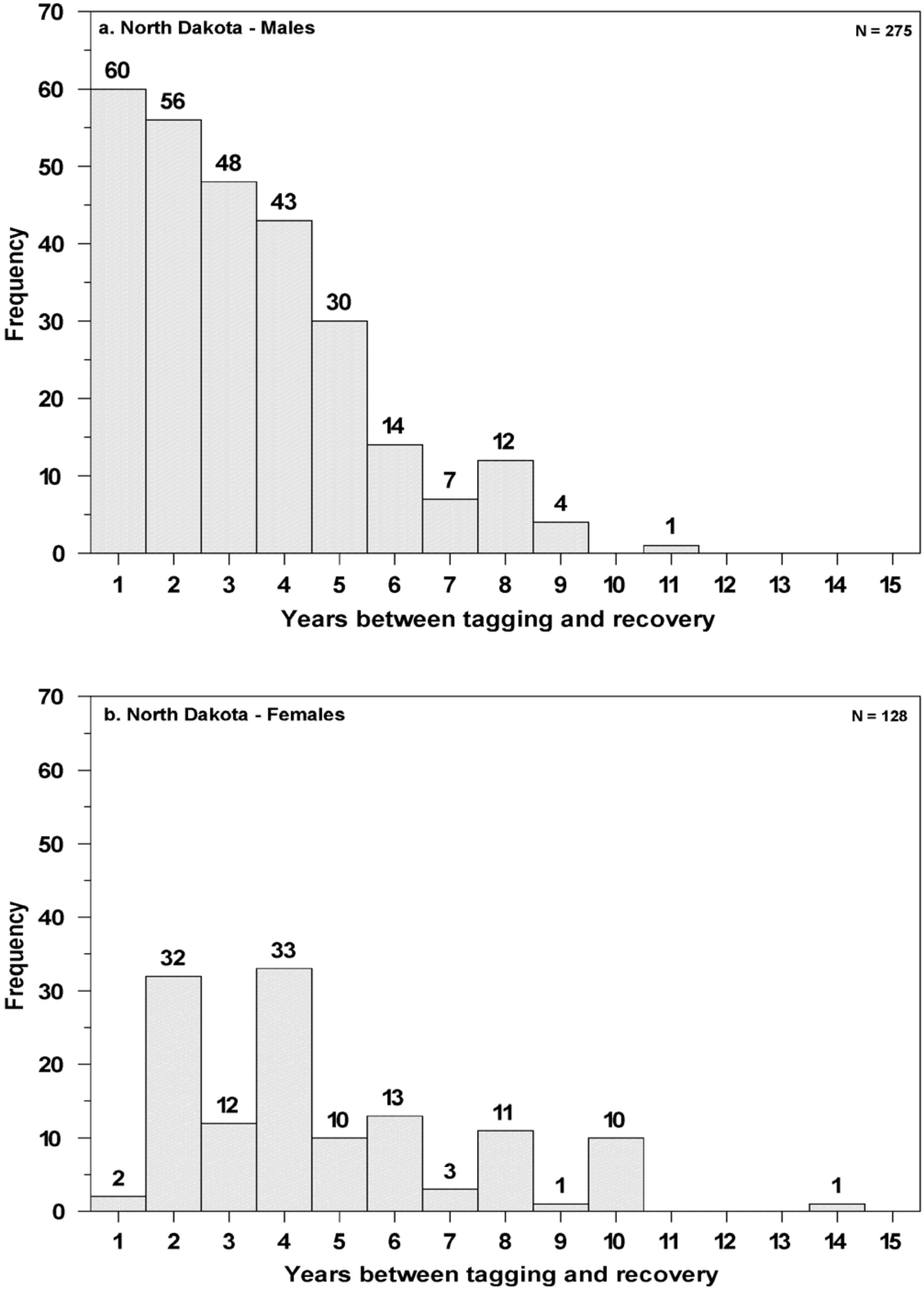

a. 2003 Montana
1=Male: N=382
2=Female N=445
Male: L=99.15[1-exp(-0.1864(Age-0.1597))]
Female: L=118.4[1-exp(-0.1149(Age+3.2195))]
Body length (cm)
Age (Years)
150
140
130
120
110
100
90
80
70
60
5
10
15
20
25
30
35
40
45
50
b. 2003 North Dakota
1=Male: N=434
2=Female N=356
Male: L=101.1[1-exp(-0.1127(Age+5.3882))]
Female: L=124.6[1-exp(-0.1022(Age+2.1451))]
Body length (cm)
Age (Years)

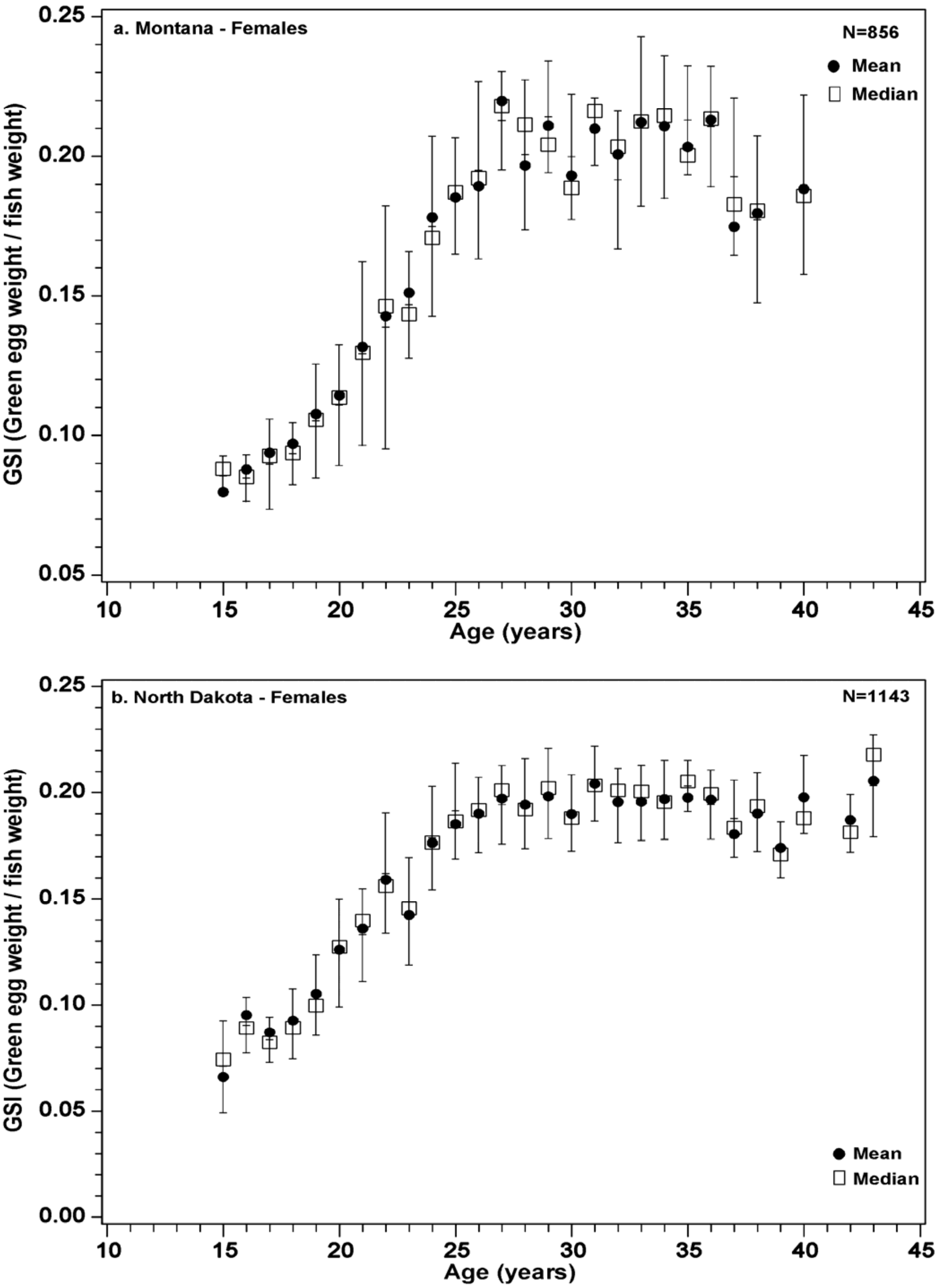

a. 2003 Montana
1=Male: N=384
2=Female N=444
Weight (kg)
Age (Years)
0
10
20
30
40
50
5
10
15
20
25
30
35
40
45
50
Male: W=0.000033[99.15(1-exp(-0.1864(Age-0.1597)))]**2.8066
Female: W=0.000004606[118.4(1-exp(-0.1149(Age+3.2195)))]**3.2868
b. 2003 North Dakota
1=Male: N=434
2=Female N=356
Weight (kg)
Age (Years)
0
10
20
30
40
50
5
10
15
20
25
30
35
40
45
50
Male: W=0.00000829[101.1(1-exp(-0.1127(Age+5.3882)))]**3.116
Female: W=0.000029[124.6(1-exp(-0.1022(Age+2.1451)))]**2.90

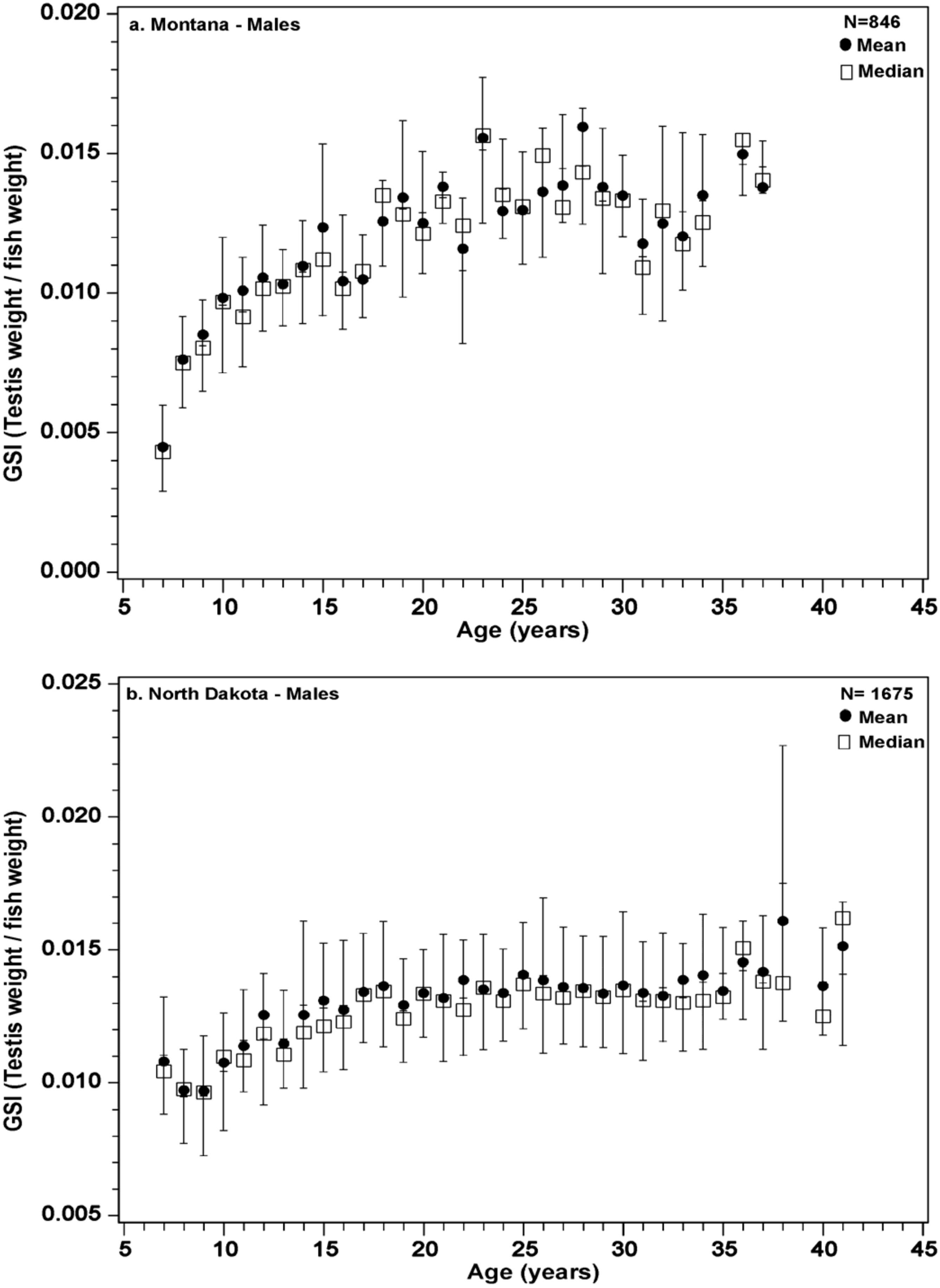

a. Males
N = 135
Frequency
0
10
20
30
40
50
60
4
3
10
34
50
26
2
4
2
[-1.1,-0.9)
[-0.9,-0.7)
[-0.7,-0.5)
[-0.5,-0.3)
[-0.3,-0.1)
[-0.1,0.1)
[0.1,0.3)
[0.3,0.5)
[0.5,0.7)
[0.7,0.9)
[0.9,1.1)
[1.1,1.3)
[1.3,1.5)
1.5<=
Class interval for average rate of change in weight (kg)
b. Females
N = 141
Frequency
0
5
10
15
20
25
30
1
4
2
5
17
21
25
26
20
11
3
2
3
1
[-1.1,-0.9)
[-0.9,-0.7)
[-0.7,-0.5)
[-0.5,-0.3)
[-0.3,-0.1)
[-0.1,0.1)
[0.1,0.3)
[0.3,0.5)
[0.5,0.7)
[0.7,0.9)
[0.9,1.1)
[1.1,1.3)
[1.3,1.5)
1.5<=
Class interval for average rate of change in weight (kg)

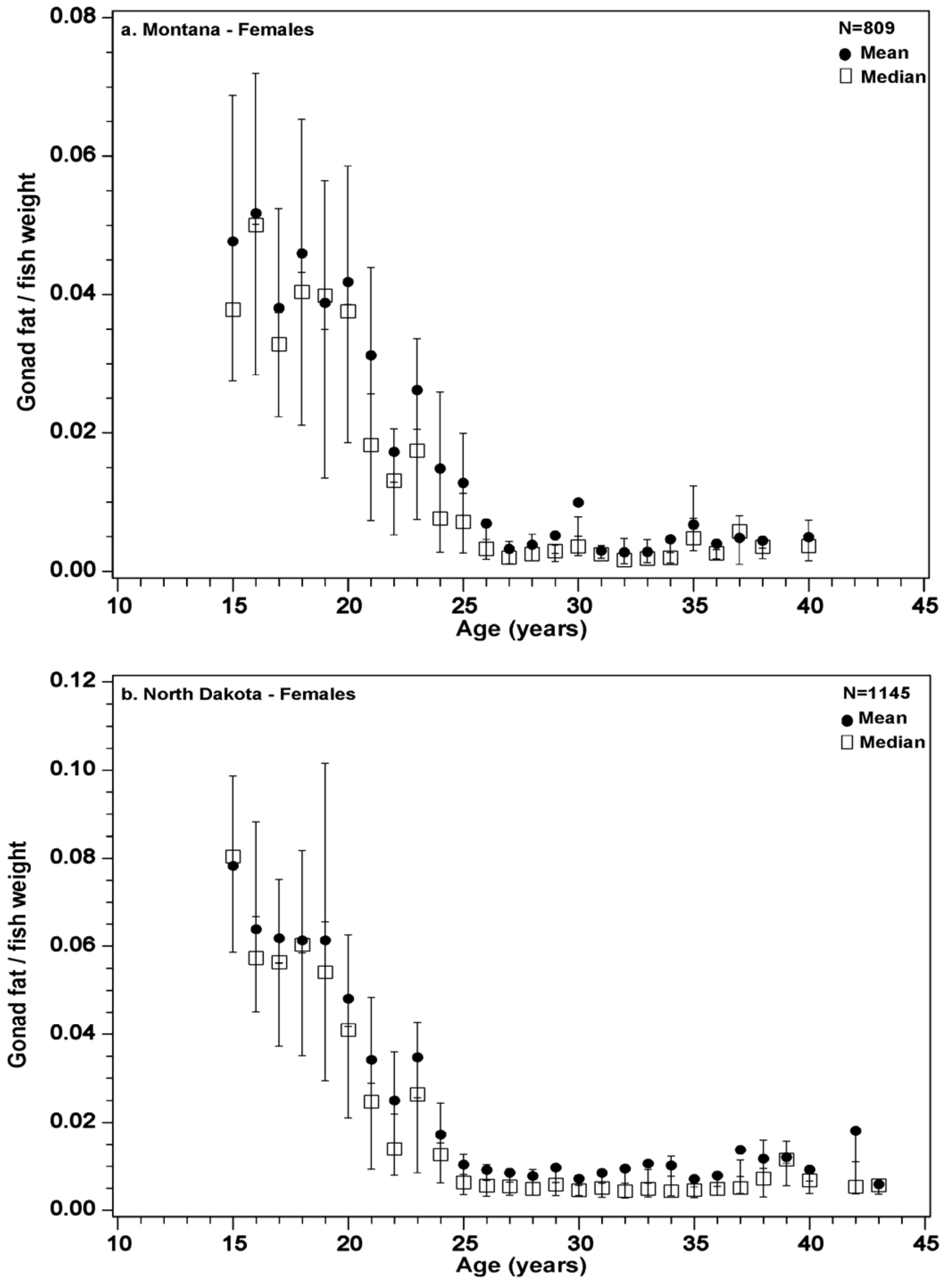

a. Montana - Males
N = 534
Frequency
Years between tagging and recovery
0
20
40
60
80
100
120
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26
44
101
84
73
49
37
35
29
26
18
12
9
2
2
4
3
2
2
1
1

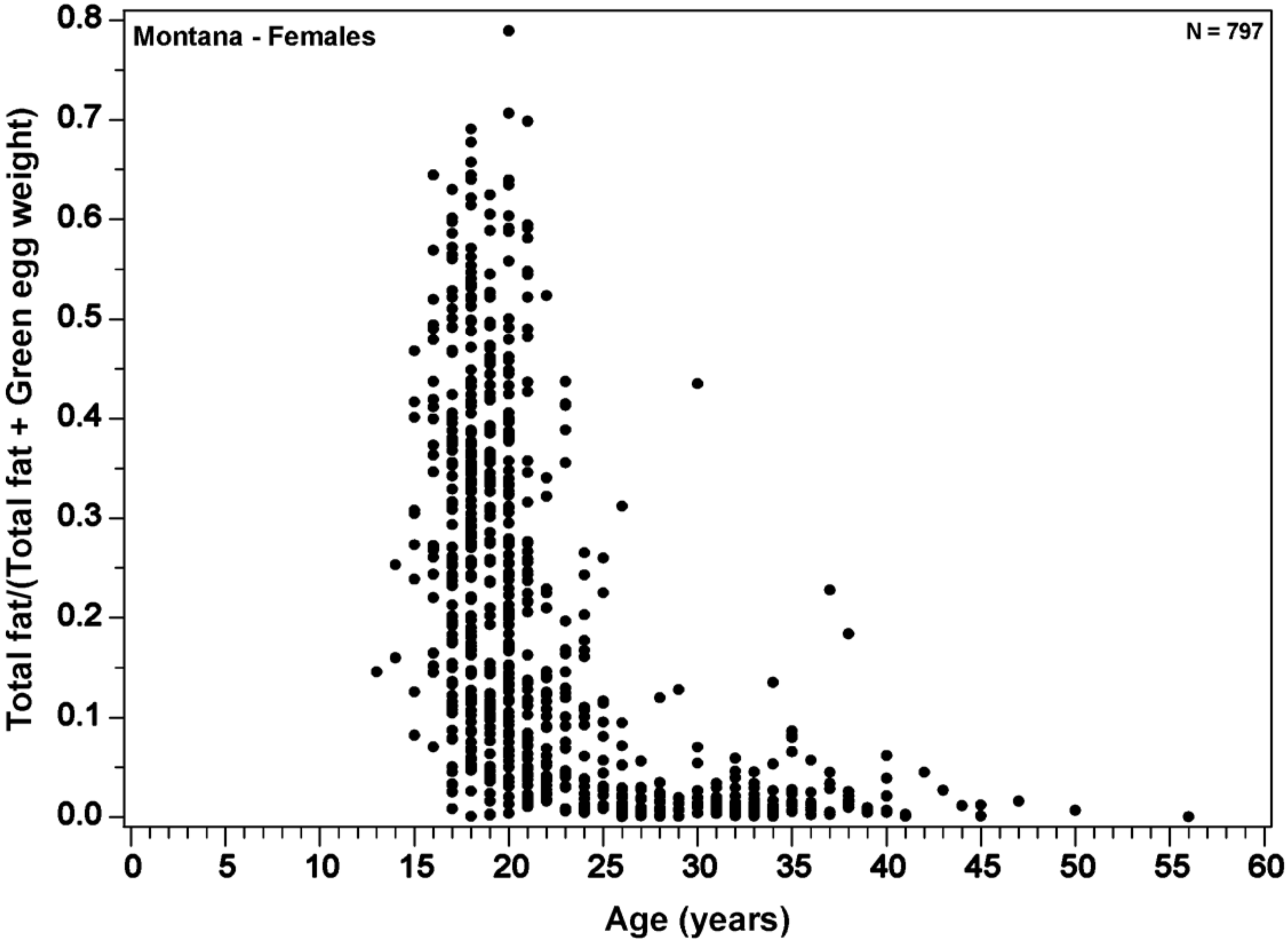

b. Montana - Females
N = 465
Frequency
Years between tagging and recovery
0
20
40
60
80
100
120
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26
7
68
106
48
42
57
21
31
13
24
13
13
1
8
2
4
3
2
2

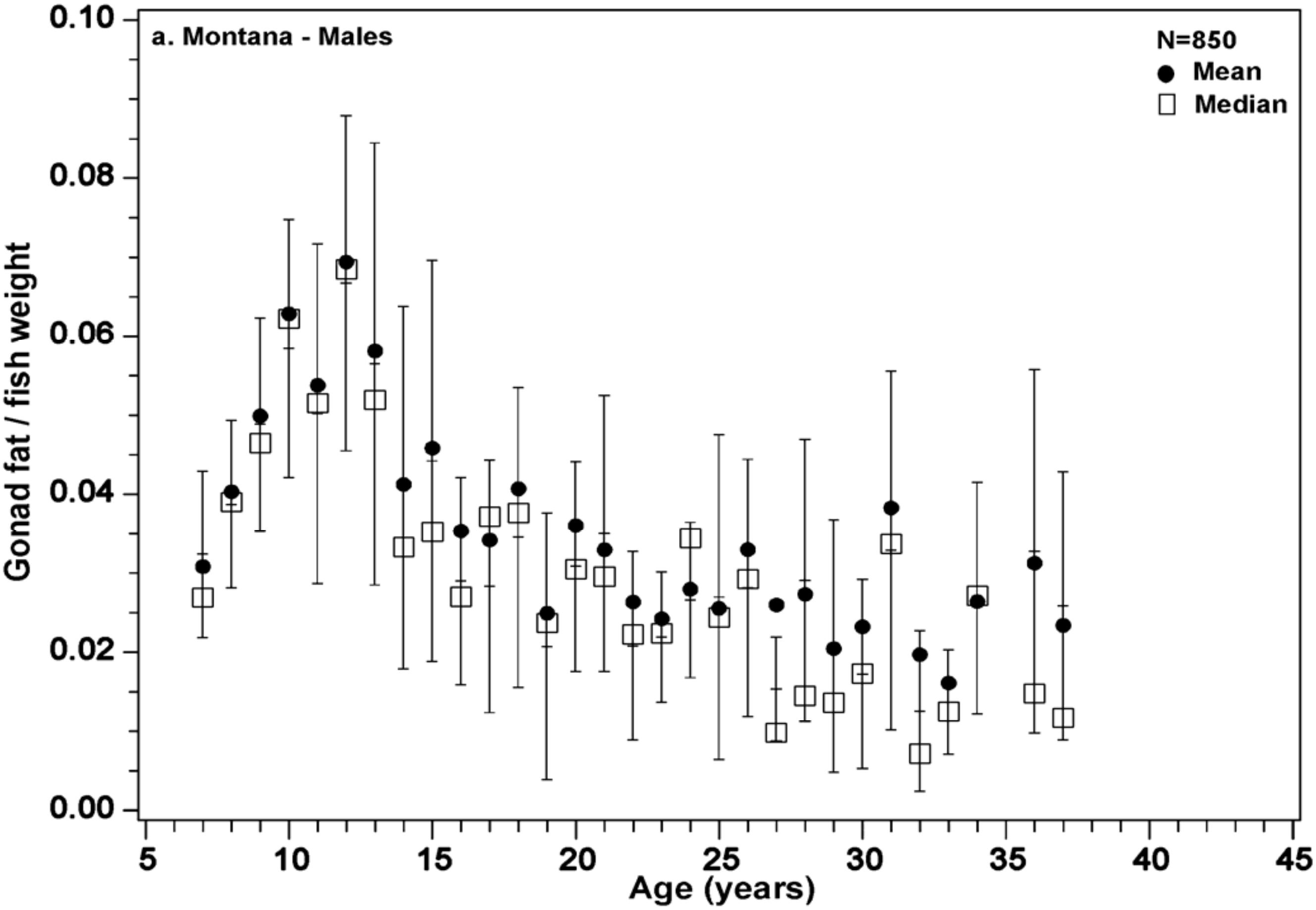

a. North Dakota - Males
N = 275
Frequency
Years between tagging and recovery
0
10
20
30
40
50
60
70
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
60
56
48
43
30
14
7
12
4
1
b. North Dakota - Females
N = 128
Frequency
Years between tagging and recovery
0
10
20
30
40
50
60
70
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
2
32
12
33
10
13
3
11
1
10
1

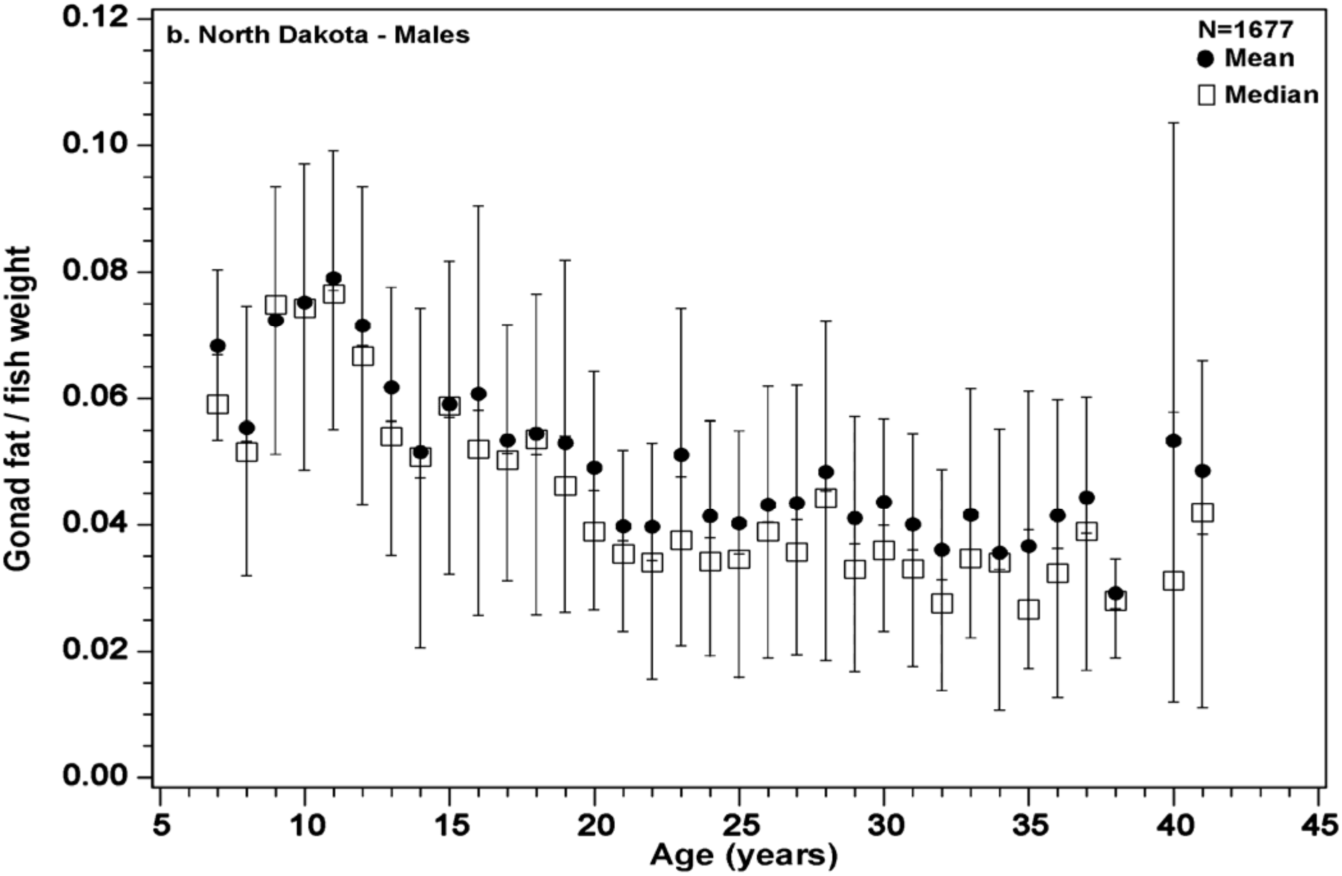

a. Montana - Females
N=856
● Mean
□ Median
GSI (Green egg weight / fish weight)
0.25
0.20
0.15
0.10
0.05
10
15
20
25
30
35
40
45
Age (years)
b. North Dakota - Females
N=1143
● Mean
□ Median
GSI (Green egg weight / fish weight)
0.25
0.20
0.15
0.10
0.05
0.00
10
15
20
25
30
35
40
45
Age (years)

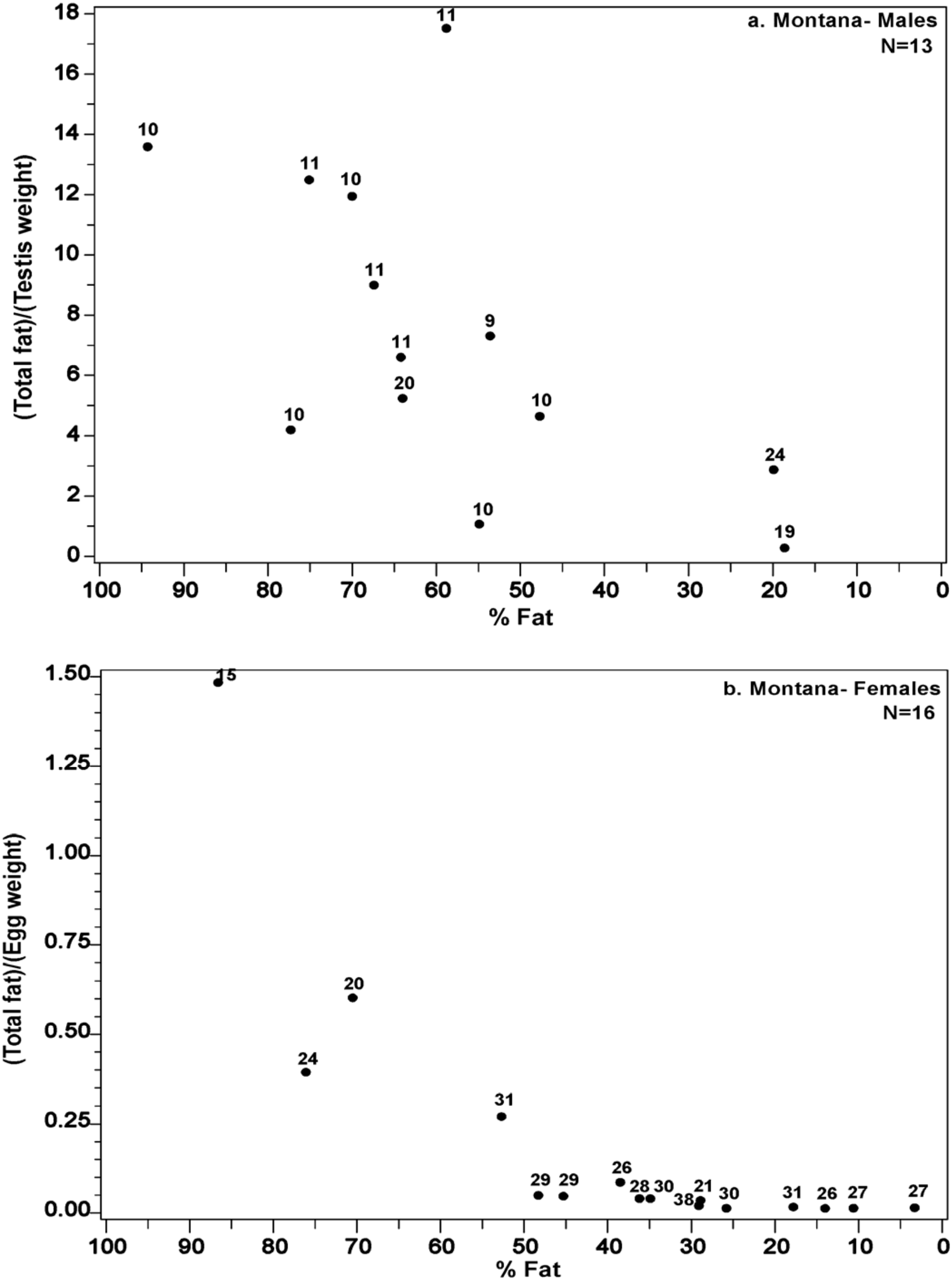

a. Montana - Males
N=846
● Mean
☐ Median
GSI (Testis weight / fish weight)
0.000
0.005
0.010
0.015
0.020
Age (years)
5
10
15
20
25
30
35
40
45
b. North Dakota - Males
N= 1675
● Mean
☐ Median
GSI (Testis weight / fish weight)
0.005
0.010
0.015
0.020
0.025
Age (years)
5
10
15
20
25
30
35
40
45

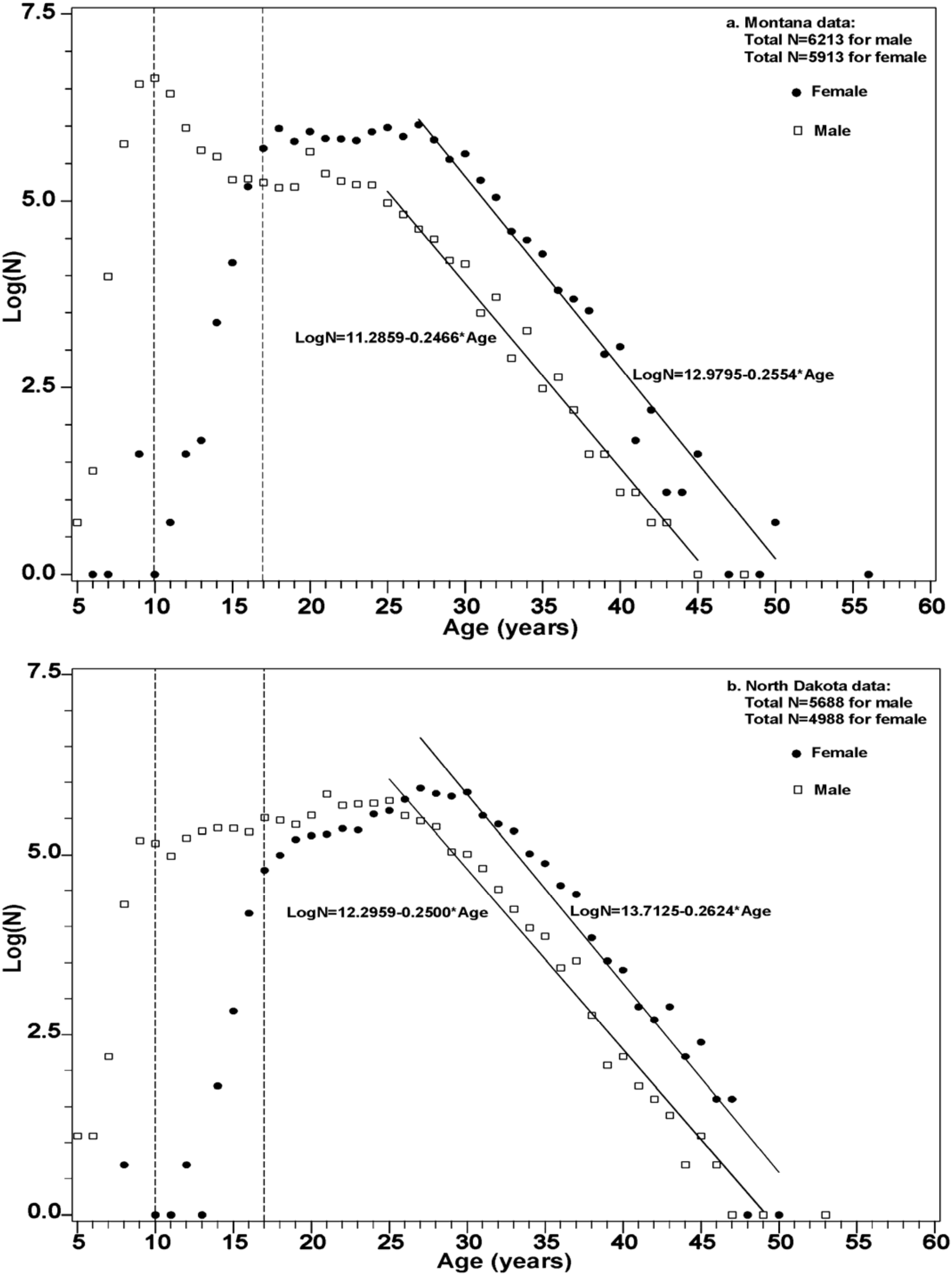

a. Montana - Females
N=809
● Mean
□ Median
Gonad fat / fish weight
0.08
0.06
0.04
0.02
0.00
10
15
20
25
30
35
40
45
Age (years)
b. North Dakota - Females
N=1145
● Mean
□ Median
Gonad fat / fish weight
0.12
0.10
0.08
0.06
0.04
0.02
0.00
10
15
20
25
30
35
40
45
Age (years)

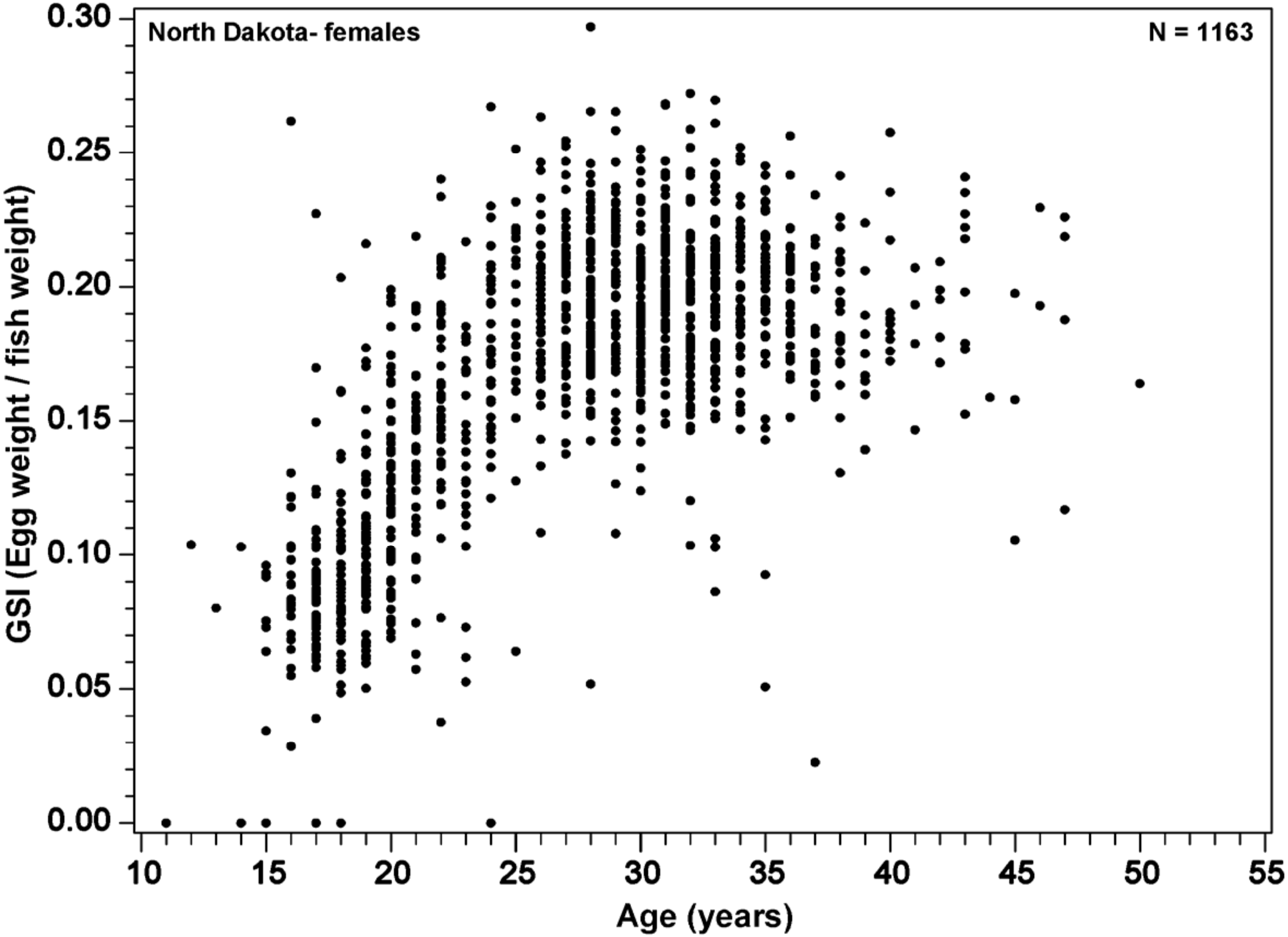

Montana - Females
N = 797
Total fat/(Total fat + Green egg weight)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Age (years)
0
5
10
15
20
25
30
35
40
45
50
55
60

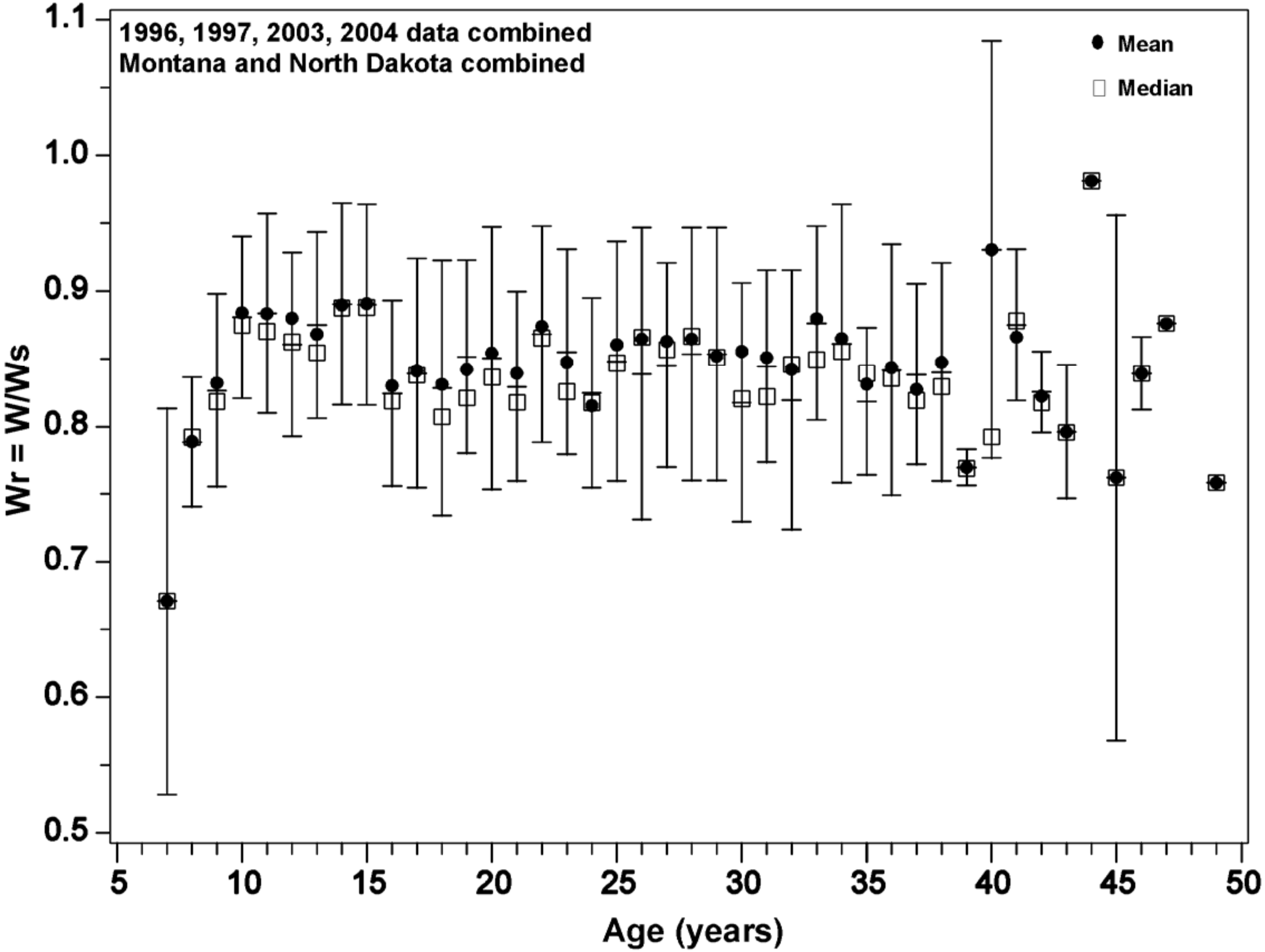

a. Montana - Males
N=850
● Mean
☐ Median
Gonad fat / fish weight
0.00
0.02
0.04
0.06
0.08
0.10
Age (years)
5
10
15
20
25
30
35
40
45

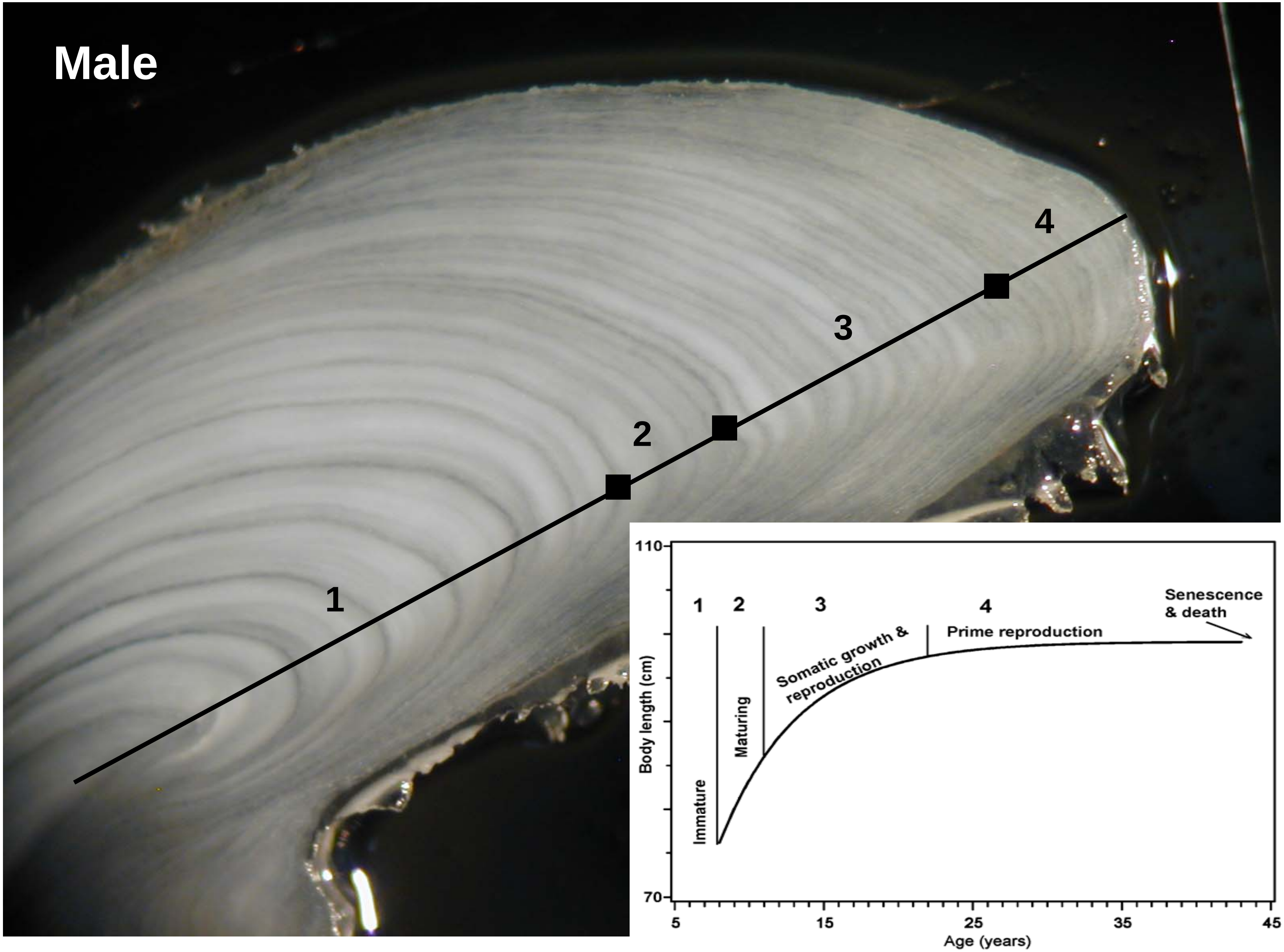

b. North Dakota - Males
N=1677
● Mean
☐ Median
Gonad fat / fish weight
0.00
0.02
0.04
0.06
0.08
0.10
0.12
Age (years)
5
10
15
20
25
30
35
40
45

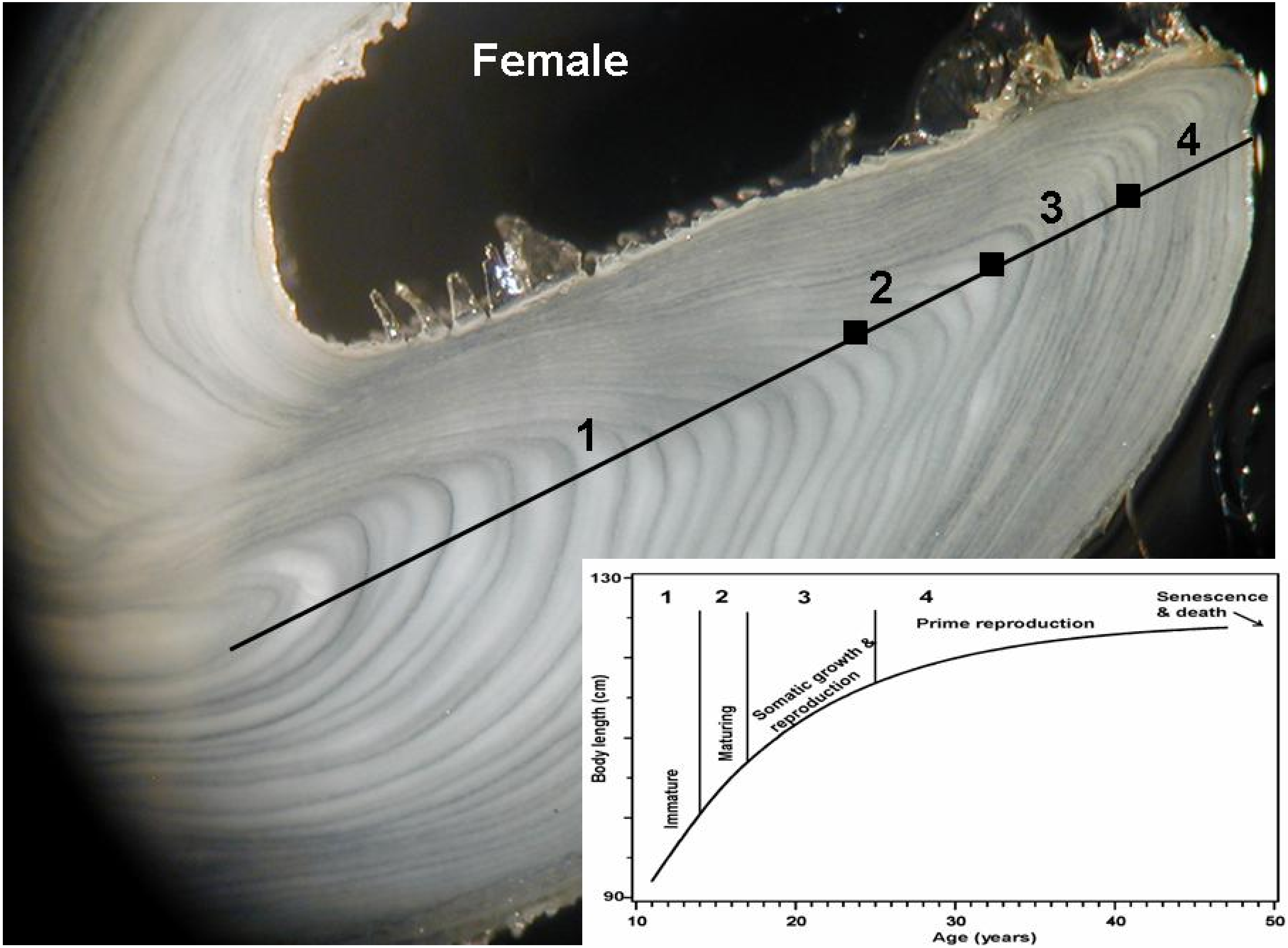
a. Montana- Males
N=13
(Total fat)/(Testis weight)
18
16
14
12
10
8
6
4
2
0
100
90
80
70
60
50
40
30
20
10
0
% Fat
11
10
11
10
11
9
11
20
10
10
24
10
19
b. Montana- Females
N=16
(Total fat)/(Egg weight)
1.50
1.25
1.00
0.75
0.50
0.25
0.00
100
90
80
70
60
50
40
30
20
10
0
% Fat
15
20
24
31
26
29
29
28
30
38
21
30
31
26
27
27

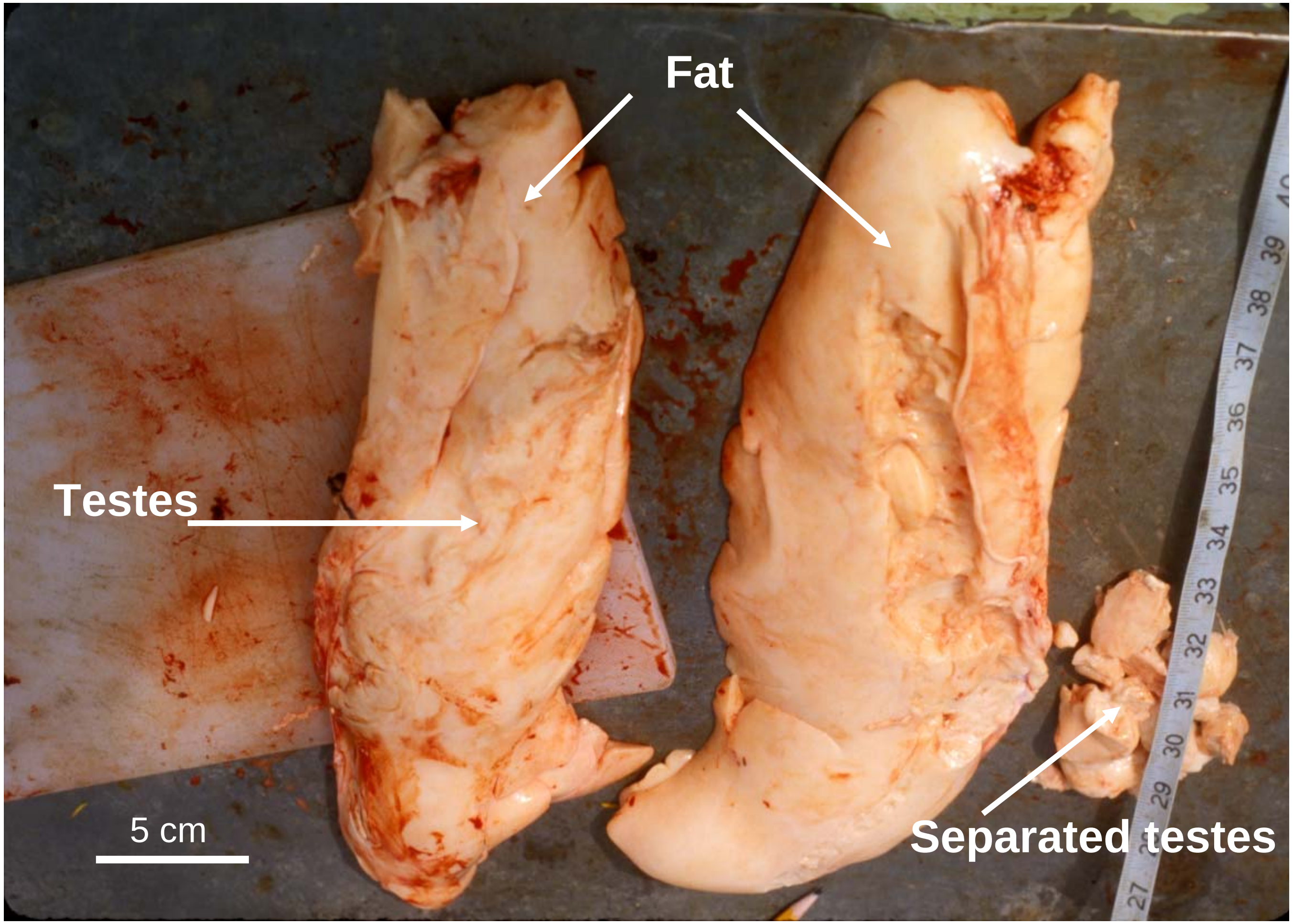

a. Montana data:
Total N=6213 for male
Total N=5913 for female
Female
Male
LogN=11.2859-0.2466*Age
LogN=12.9795-0.2554*Age
Log(N)
7.5
5.0
2.5
0.0
5
10
15
20
25
30
35
40
45
50
55
60
Age (years)
b. North Dakota data:
Total N=5688 for male
Total N=4988 for female
Female
Male
LogN=12.2959-0.2500*Age
LogN=13.7125-0.2624*Age
Log(N)
7.5
5.0
2.5
0.0
5
10
15
20
25
30
35
40
45
50
55
60
Age (years)

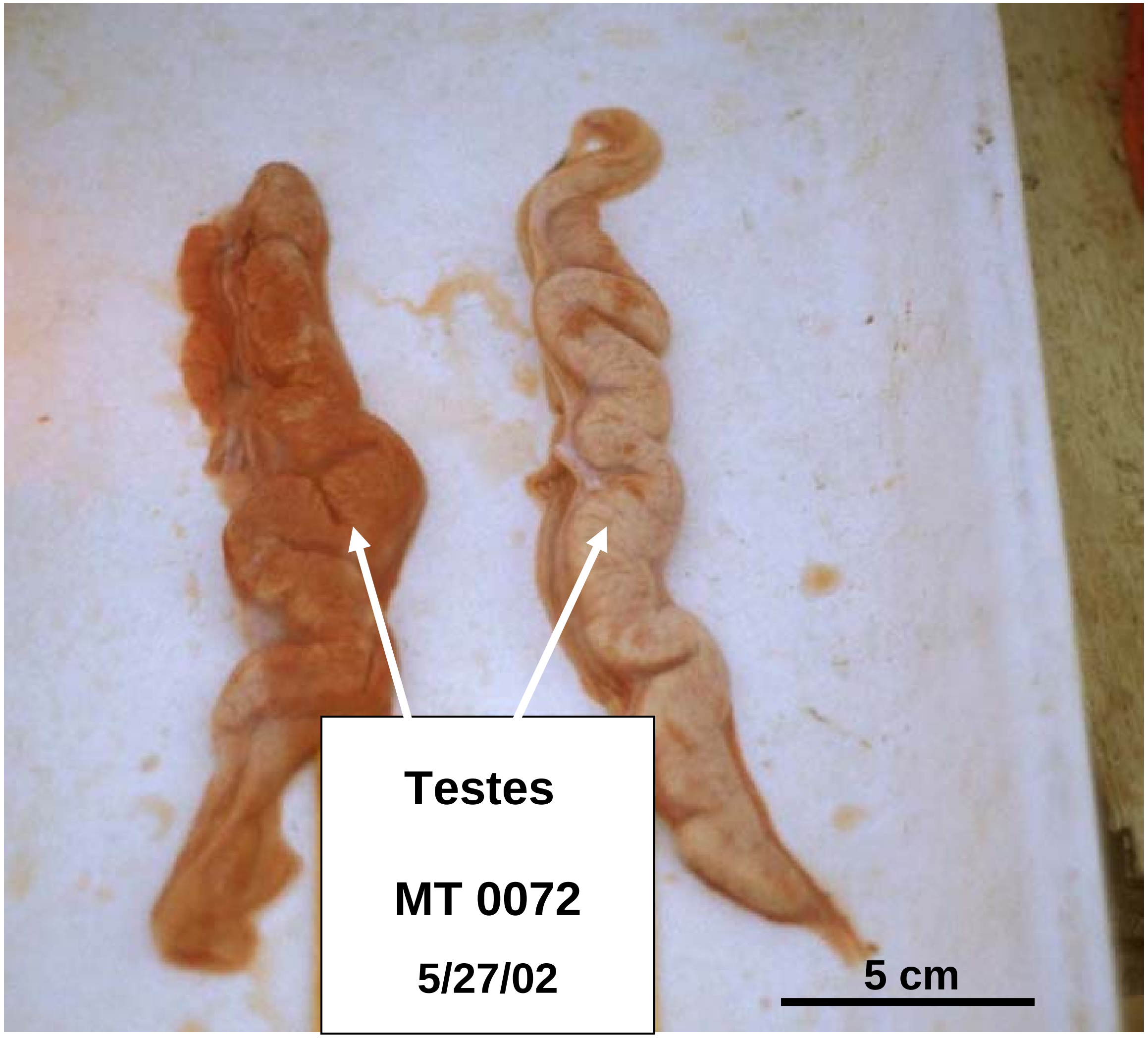

North Dakota- females
N = 1163
GSI (Egg weight / fish weight)
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Age (years)
10
15
20
25
30
35
40
45
50
55


1996, 1997, 2003, 2004 data combined
Montana and North Dakota combined
● Mean
☐ Median
Wr = W/Ws
1.1
1.0
0.9
0.8
0.7
0.6
0.5
5
10
15
20
25
30
35
40
45
50
Age (years)

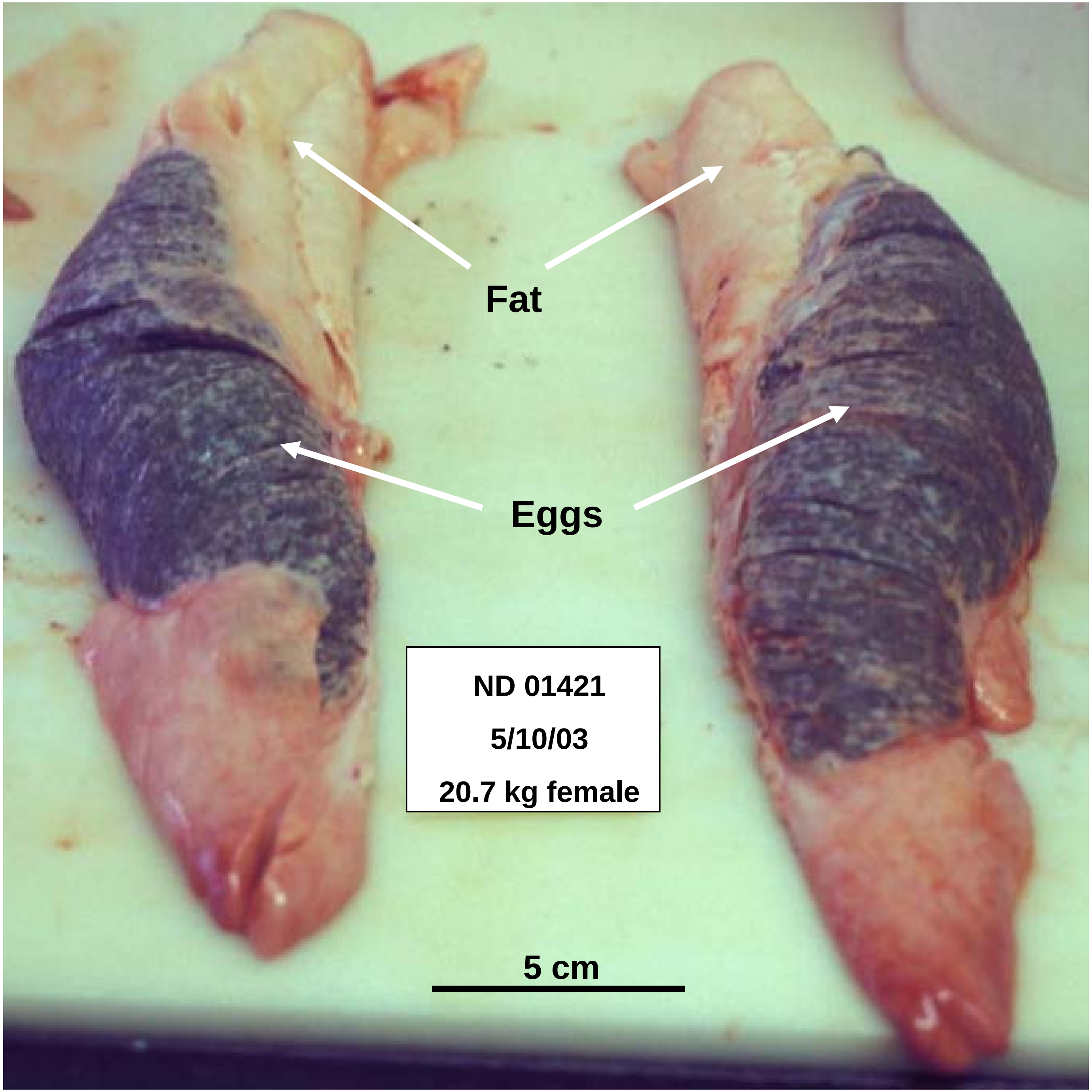

Male
4
3
2
1
110
70
Body length (cm)
5
15
25
35
45
Age (years)
1
2
3
4
Senescence
& death
Immature
Maturing
Somatic growth &
reproduction
Prime reproduction


Female
1
2
3
4
130
90
Body length (cm)
10
20
30
40
50
Age (years)
1
2
3
4
Immature
Maturing
Somatic growth & reproduction
Prime reproduction
Senescence & death


Fat
Testes
5 cm
Separated testes
27
29
30
31
32
33
34
35
36
37
38
39



Testes
MT 0072
5/27/02
5 cm



ND 01421

5/10/03

20.7 kg female


Eggs
5 cm