Investigation of Potential Methods by which to Determine and Monitor Reproductive Senescence in White Sturgeon

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2003

Abstract

As the Kootenai River white sturgeon population is substantially older than previously believed, it is essential for management decisions to known if reproductive senescence occurs in chondrosteans. Reproductive senescence, as seen by a decrease in fecundity and ovarian follicle size, has been described in few sturgeon species. Based on descriptions of the life history of other chondrosteans, Kootenai River white sturgeon should remain reproductive throughout their life spans. Females may experience a slight decrease in fecundity with age, though evidence suggests that fertility of the highly fecund, old females will not decline. The decrease in fecundity in some sturgeon species was not found to be significant and fecundity remained high, regardless of the decrease, as the individuals were large in size. Fecundity does remain to be the most reliable predictor of reproductive senescence, however accurate measures of fecundity changes with age are not possible in the Kootenai River white sturgeon as lethal sampling is required. Gonadal histology may allow for senescence to be identified and monitored through the examination of gonial mitosis, incidence of and stages of maturation affected by atresia, and infiltration of connective tissue. Proximate analysis of ovulated and anovulated egg samples will characterize the energy content of eggs which may change with age. It is unclear at this time whether the spawning frequency will change with age.

Introduction

Senescence is defined as "the persistent decline of viability caused by physiological deterioration as organisms age" (Blarer et al., 1995). The decline or loss of viability with age may be seen as an increase in mortality rate and/or a decrease in reproductive potential. The decrease in reproductive potential is referred to as reproductive senescence and has been described in mammals (e.g., Nozaki et al., 1995; Wolf et al., 2000; Armstrong, 2001) and fishes (e.g., Nikolskii, 1969; Woodhead, 1979; Wooton, 1979; Margolis-Nunno et al., 1986; Koslow et al., 1995; Reznick et al., 2002). An organism may reproduce throughout its life span or reproduction may cease at some stage during its life span (e.g., menopause in women). If an organism continues to reproduce throughout its life span, reproductive potential may decrease with age as fecundity, fertility, or reproductive frequency decreases.

In fishes, fecundity is the most common measure of reproductive potential (Moyle and Cech, 1996), and reproductive senescence is often recognized by a decrease in fecundity with age and body size. Ideally, fecundity should be measured as the number of eggs spawned. However, it is typically measured as the total number of mature ovarian follicles in the ovary just prior to spawning (absolute fecundity), which assumes that few mature follicles will be retained (Wooton, 1979), or the total number of ovarian follicles per gram of body weight (relative fecundity). In long-lived fishes, fecundity has been described to increase rapidly in early reproductive years, increase slowly to a steady level in mid-reproductive years, and may decrease or remain steady in the oldest fish (Nikolskii, 1969). In fishes, age and body size are closely related and indeterminant growth occurs, unlike in birds and mammals which stop growing once sexual maturation is reached (Wooton, 1979; Moyle and Cech, 1996; Billard and Lecointre, 2001). Hence, fecundity often may be more strongly correlated with body weight than age and length in fishes (Nikolskii, 1969; Raspopov, 1987). Because age and size are so closely related in fishes, the effect of age on fecundity may often be detected only if the effects of size are removed (Wooton, 1979). This addresses a complication in the use of phenotypic criteria, such as fecundity, as an indicator of senescence. As well, interpretation of fecundity data is often further complicated by the relationship between fecundity and frequency of spawning, egg size, fertility, population density, and environmental factors (Bagenal, 1978). Having recognized these complications, fecundity changes associated with body size and age remains to be one of the most reliable predictors of reproductive senescence.

The potential for reproductive senescence in the Kootenai River white sturgeon population is a critical issue managers are currently facing. With the proposed underaging of the Kootenai River white sturgeon (Paragamian et al., submitted), the adult population is substantially older than previously believed (10 to 30 years older). These new data have led to the need to investigate several questions essential to management decisions for this federally-listed endangered population: 1) does reproductive senescence occur in chondrosteans and 2) are there potential methods by which to determine and monitor reproductive senescence in the Kootenai River white sturgeon?

Review of Reproductive Senescence and Sex Ratios in Chondrosteans

Reproductive senescence, as seen by a decrease in fecundity and ovarian follicle size, has been described in few sturgeon species. In those species for which evidence of reproductive senescence exists, the decrease in fecundity did not appear significant and fecundity remained high, regardless of the decrease, as the individuals were large in size (body weight and length). It does appear that sturgeons remain reproductive throughout their life span. The following is a review of the available literature pertinent to fecundity, age, size, and reproductive senescence of sturgeon species worldwide.

In the Russian sturgeon (*Acipenser gueldenstaedti*), the quality of eggs and egg weight and content (dry matter, lipid, total nitrogen) were found to change with age and fish size (Krivobok and Storozhuk, 1970). The eggs of Russian sturgeon females spawning for the first time were found to be less viable (smaller larvae with higher mortality) compared to iteroparous females (Krivobok and Storozhuk, 1970). Egg weight was smallest in the youngest females (19 to 25 years), increased with age and size (maximum egg weight reached between 25 and 32 years), and decreased in the oldest and largest females (32 to 39 years). Egg weight was reduced in older and larger Russian sturgeon as the moisture content decreased and the fat content increased. This change in egg weight was attributed to aging. The mean age of the females in this study was 28 years and ranged from 19 to 37 years (Krivobok and Storozhuk, 1970). The maximum historical age described for Russian sturgeon is greater than 50 years, whereas maximum present age of Russian sturgeon was reported to be 38 (Billard and Lecointre, 2001).

In sevryuga or stellate sturgeon (*Acipenser stellatus*), absolute fecundity increased with fish weight (Veshchev and Novikova, 1986). A decrease in fecundity was not observed in the largest fish. Age data were not available for fecundity comparisons, however Veshchev and Novikova (1986) stated that the range of absolute fecundity varied the greatest in older fish. The younger age class of spawners in the lower Volga River was predominately males, whereas older age classes of spawners were females. Females on the spawning grounds ranged in age from 9 to 27 years (Veshchev and Novikova, 1986). The maximum historical age of stellate sturgeon is 41 years, compared to the current maximum age of 30 years (Billard and Lecointre, 2001).

Absolute fecundity of Amur sturgeon (*Acipenser schrencki*) increased with fish length, body weight, and age (Krykhtin and Gorbach, 1996). The highest fecundity was reported in the largest and oldest individual. Variation in fecundity was highest in the youngest females and more stable in the middle- and older-aged fish in contrast to the stellate sturgeon (Veshchev and Novikova, 1986). The relative fecundity in the Amur sturgeon did not change with an increase in length, body weight, or age and decreased in the smallest and largest individuals. The age of females in this study ranged from 8 to 45 years, and the maximum reported age of this species is 60 years (http://www.fishbase.org).

Absolute fecundity of beluga sturgeon (*Huso huso*) in the Caspian Sea increased with fish length, age, and body weight (Raspopov, 1987). Unlike stellate sturgeon (Veshchev and Novikova, 1986) but similar to Amur sturgeon (Krykhtin and Gorbach, 1996), the coefficient of variation of absolute fecundity decreased with increasing age, body weight, and length in beluga. Comparison of fecundity of females of equal length and weight revealed that fecundity in beluga did not increase with age and, in some cases, decreased with age. The age of female beluga on the spawning grounds from 1970-1985 was determined to be 16 to 51 years (Raspopov, 1987). The maximum historical age of beluga is 118 years, while the present maximum age is 60 years (Billard and Lecointre, 2001).

In the kaluga (*Huso dauricus*), absolute fecundity was found to increase with increasing fish length, body weight, and age, and less variation in fecundity occurred in larger fish (length) as was seen in the Amur sturgeon (Krykhtin and Gorbach, 1996) and beluga (Raspopov, 1987). Absolute fecundity of the kaluga increased almost proportionally to the age of the female, and the female with the oldest age and greatest body weight did have the highest absolute fecundity. However, the relative fecundity did not change with increasing length, body weight, or age and decreased in the smallest and largest individuals, similar to the Amur sturgeon. The age of females ranged from 11 to 57 years (Krykhtin and Gorbach, 1996). The maximum reported age of kaluga is 55 years (Billard and Lecointre, 2001; http://www.fishbase.org).

In the North American Atlantic sturgeon (*Acipenser oxyrinchus*), a significant positive relationship between fecundity and body size (length), as well as ovarian follicle size and body size, was found (Van Eenennaam et al., 1996). Fecundity and ovarian follicle size increased significantly from 15 to 30 years of age. Females spawning for the first time had smaller eggs and lower fecundity compared to iteroparous females, similar to Russian sturgeon (Krivobok and Storozhuk, 1970). Peak egg production and oocyte size was reached at age 23 to 30 years, followed by a decrease in fecundity in females older than 30 years of age (Van Eenennaam and Doroshov, 1998). Oocyte diameter did not decrease in females older than 30 years of age. The decrease in fecundity with age was not significant (~2.2×10^6 ovarian follicles in 27 to 30 year old females to ~2.0×10^6 ovarian follicles in older than 30 year old females; Van Eenennaam and Doroshov, 1998). Age of females on the spawning grounds in the Hudson River ranged from 14 to 43 years (Van Eenennaam and Doroshov, 1998). The maximum age reported for Atlantic sturgeon is 60 years (Billard and Lecointre, 2001; http://www.fishbase.org).

It is important to note that in all of these studies, the number of spawning females in the oldest age class was low (n=1-6) compared to the youngest and middle age classes of spawning females (n=3-58). This has several implications. First, these observations of changes in absolute or relative fecundity with age should be verified by collecting additional data from these species. Second, these data suggest that the number of individuals reaching the maximum age for the species is low. Mortality rates in long-lived species appear to be linear throughout their life span, with an increase in mortality at older ages seen in some species (see Woodhead, 1979). The metabolic requirements for reproduction in large, old fish with high fecundity are significant. It has been suggested that the energy required for gonadal development in old fish in resource-limited environments or under adverse environmental conditions may be an important factor in mortality (Woodhead, 1979). It is unknown whether spawning periodicity changes with age as the energy requirements increase with increasing fecundity in old, large sturgeon. The spawning interval has been described in the Kootenai River white sturgeon population as 3 to 5 years (Paragamian et al., submitted). This was recently determined in the aging population, and therefore suggests that spawning periodicity does not change with age in sturgeon. This should be further examined as it does have serious implications for the successful collection and spawning of broodstock and sustainability of the Kootenai River sturgeon population.

Evidence for testicular changes associated with aging have been described in several species of fish (see Woodhead, 1979) and black-footed ferret (Wolf et al., 2000). In fish, the loss of spermatogenic tissue and infiltration of connective and adipose tissue into testes was found with increasing age (Woodhead, 1979). In the black-footed ferret, decreased testes volume and sperm motility were described to occur with age (Wolf et al., 2000). No literature addressing the potential for reproductive senescence in male chondrosteans was found.

A skewed sex ratio toward females has been described in several populations of older sturgeon (stellate sturgeon, Veshchev and Novikova, 1986; impounded population of white sturgeon in the Columbia River, Beamesderfer et al., 1995; Atlantic sturgeon, Van Eenennaam et al., 1996). The sex ratio in the Kootenai River white sturgeon population has been assumed to be equal because reliable data were not available (Paragamian et al., submitted). If the sex ratio in the Kootenai River sturgeon population is skewed toward females, this may be beneficial to the sustainability of the population: Recruitment of hatchery fish into the adult population is expected to begin in 2020 (Paragamian et al., submitted), and as males reach first sexual maturity earlier than females, young, ripe males may spawn with highly fecund females with good egg quality.

Potential Methods to Determine/Monitor Reproductive Senescence

Based on review of mammalian and fish literature, several methods may be employed to determine if reproductive senescence is occurring in the Kootenai River population. They include: 1) changes in fecundity; 2) an increase in connective tissue in the ovary; 3) an increase in follicular atresia; 4) a decline or cessation of gonial mitosis; 5) a change in lipid, dry matter, and nitrogen content of eggs; 6) a change in pituitary activity; and 7) a decrease in fertility. The following is a more detailed discussion of each and the potential feasibility of the use of these methods to determine and monitor the occurrence of reproductive senescence in the Kootenai white sturgeon population.

Fecundity. Fecundity changes associated with length, body weight, and age in several sturgeon species have been described above. However, the use of fecundity changes to monitor or determine if reproductive senescence in the Kootenai River white sturgeon population is occurring is not feasible. Absolute fecundity determination requires sacrificing females from different age and size classes which is not an option for this federally-listed endangered population. Relative fecundity determination would require several large ovarian subsamples (at least 4 to 6 one-g samples) and information on ovary weight. Theoretically, the subsamples could be collected from ovulating females in the conservation propagation program, and the total ovary weight may be estimated based on information gathered for cultured white sturgeon. However, the accuracy of the fecundity calculation would be unknown as the ovarian weight in wild populations compared to cultured white sturgeon is not well understood.

Connective Tissue in Ovary. The connective tissue of an organ is its stroma, and the stroma is responsible for transmitting blood and lymph vessels and nerve fibers essential to nutritional and regulatory support (Banks, 1993). An increase in the infiltration and proliferation of stroma throughout the ovary was seen in aging guppies and Siamese fighting fish (Woodhead, 1979). The degree of connective tissue infiltration may be assessed in the Kootenai River white sturgeon population through histological comparison of past (archived) and present individual gonad samples. This will provide the baseline required to determine if an increase in connective tissue is occurring. Continual collection and analysis of gonadal tissue from fish sampled during broodstock collection will be beneficial in determining if connective tissue infiltration is associated with age in sturgeon.

Follicular Atresia. Follicular atresia is the resorption of ovarian follicles and has been associated with stress, starvation, unfavorable temperature and photoperiod regimes, and sub-optimal water quality (Hinton et al., 1992; Linares-Casenave et al., 2002). In guppies, Siamese fighting fish, and dace, an increase in follicular atresia was seen with age (Wilkinson and Jones, 1977; Woodhead, 1979). Full reproductive capacity of guppies was reached between the ages of 10 and 12 months. By 30 months, few ripe ovarian follicles were found in the ovary, and the ripe follicles that were present were resorbed. At ages greater than 30 months, oocytes in all stages of development underwent atresia (Woodhead, 1979). A similar pattern of atresia was evident in the Siamese fighting fish, a species that can live up to a year after reproduction ceases. By 16 months of age, resorption of ripe ovarian follicles was seen in this species. After 20 months, atresia was evident in vitellogenic follicles, and in fish older than 30 months, no ripe follicles were found and oocytes in all developmental stages showed evidence of atresia (Woodhead, 1979). In the dace, first sexual maturity was reached in 3 years (Wilkinson and Jones, 1977). The occurrence of follicular atresia increased with age such that by 9 years of age, 100% of the females examined showed extensive follicular resorption. Histological analysis of gonadal tissue of the Kootenai River white sturgeon population will allow for the incidence of follicular atresia to be assessed (the occurrence of and stage of development in which atresia may occur). Because poor environmental conditions may induce atresia in fishes, including sturgeon (Webb et al., 1999; Linares-Casenave et al., 2002), and contaminant exposure has been shown to lead to an increase in the incidence of atresia (Hinton et al., 1992), factors other than age must be considered in the analysis of atresia in gonadal tissue. Hence, a comparison of gonadal tissue collected from individuals over time as well as individuals within a spawning season will be beneficial in identifying atretic changes associated with age not environmental conditions.

Gonial Mitosis. Based on histological examination, gonial mitosis does not appear to occur in older North American Atlantic sturgeon females (Van Eenennaam and Doroshov, 1998). This would suggest that old sturgeon become non-reproductive potentially due to a finite number of oocytes. However, there is no evidence of the lack of ovarian follicles in exceptionally large and old sturgeon females (e.g., Vladykov and Greeley, 1963; Tsepkin and Sokolov, 1971;

Veshchev and Novikova, 1986; Krykhtin and Gorbach, 1996; B. Goncharov, pers. comm.). The lack of primordial germ cells was also noted in several Atlantic cod and was attributed to reproductive senescence, however these fish were not in the oldest age class (Rideout and Burton, 2000). The occurrence of gonial mitosis in Kootenai River white sturgeon females and males could be easily characterized through histological analysis of ovarian and testicular tissue.

Lipid, Dry Matter, and Total Nitrogen Content of Eggs. As the size of wild Russian sturgeon increased, the lipid, dry matter, and total nitrogen content of ovulated eggs increased, while the proportion of extractable nitrogen relative to total nitrogen in the eggs decreased (Krivobok and Storozhuk, 1970). The moisture content of the eggs decreased and the fat content increased in large fish, hence a reduction in egg weight was found in large fish. These changes were attributed to the phenomena of aging. Specifically, the egg weight was lowest in 18 to 25 year old fish, highest in 25 to 32 year old fish, and decreased in fish greater than 32 years of age (Krivobok and Storozhuk, 1970). In orange roughy, another long-lived group-synchronous spawner, fecundity decreased after 60 years of age (Koslow et al., 1995). Fecundity was significantly correlated with the amount of lipid per gram of ovary. The predominant lipid was triacylglycerol (Koslow et al, 1995), which is the common lipid found in ovaries of fish that accumulate yolk or yolk platelets rather than oil globules, similar to sturgeon. Measurement of lipid, dry matter, and total nitrogen content of ovulated eggs of Kootenai River white sturgeon is feasible. Proximate analysis of ovulated and anovulated egg samples in females spawned in the conservation propagation program will reveal the protein (nitrogen content), lipid, ash, fiber, moisture, and carbohydrate levels. However, there are no reference points available with regard these parameters in the Kootenai River white sturgeon population. Comparison of these parameters to other populations of white sturgeon of known ages would not be helpful as the food source and environmental conditions differ. Therefore, this will not be useful as a "quick" tool to assess reproductive senescence but may provide information regarding potential senescence in individual females over time.

Pituitary Activity. The hormones produced along the hypothalamo-pitituary-gondadal axis are involved in gamete development and maturation in vertebrates. Abnormalities or changes in pituitary function with age have been described in humans (Marcus et al., 1993; Armstrong, 2001), monkeys (Nozaki et al., 1995; Shideler et al., 2001), and Siamese fighting fish (Woodhead, 1974). In mammals, an increase in follicle-stimulating hormone (FSH; Marcus et al., 1993; Shideler et al., 2001) and luteinizing hormone (LH; Nozaki et al., 1995) production from the pituitary has been described in anovulatory individuals and is associated with the aging process. The increase in these pituitary hormones is a result of decreased negative feedback of gonadal steroids on the pituitary. The aging changes seen in the ovaries of post-reproductive Siamese fighting fish (individuals of this species live well beyond the end of their reproductive life) parallel the changes associated with pituitary removal in teleosts (Woodhead, 1974). Removal of the pituitary gland in teleosts results in gonadal regression and inhibition of gonadal steroidogenesis (Redding and Patiño, 1993). The lack of gonadal steroidogenesis would result in a decrease in negative feedback on the pituitary similar to what has been described in mammals. Plasma profiles of the pituitary hormones, gonadotropin I (FSH-like activity) and II (LH-like activity), in white sturgeon have been described (Moberg et al., 1995). However, the antibodies required for the radioimmunoassays to measure these hormones are currently not available, and therefore the use of pituitary function as in indication of reproductive senescence in the Kootenai

River white sturgeon population is currently not possible. Collection and archival of blood plasma should be considered as analyses may be conducted once antibodies are available.

Decrease in fertility. In humans and other mammals, a decrease in fertility and oocyte number is seen with increasing age. In most mammalian species, the decline in fertility is seen well before the oocyte supply is depleted (Armstrong, 2001). There are no indications of decreased fertility in any species of old sturgeon to date, however, this may be easily confirmed or refuted given the nature of the Kootenai River white sturgeon conservation propagation program. Because the population is small and females are repeatedly spawned in the hatchery over time, documentation of egg size, fertility, hatchability of eggs, and newly hatched larval size as female's age is possible and would be scientifically interesting.

Conclusions and Recommendations

Reproductive senescence does occur in sturgeon (e.g., Veshchev and Novikova, 1986; Raspopov, 1987; Krykhtin and Gorbach, 1996; Van Eenennaam and Doroshov, 1998). Fecundity remains to be the most reliable predictor of reproductive senescence, however accurate measures of fecundity changes with age are not possible in the federally-listed population of white sturgeon in the Kootenai River as lethal sampling is required. It appears that the Kootenai River white sturgeon population will remain reproductive throughout their life span. Females may experience a slight decrease in fecundity with age as this relationship has been described to date in all long-lived species, including sturgeon, as curvilinear. Evidence also suggests that fertility of the highly fecund, old females will not decline as the population ages. It is unclear at this time whether the spawning frequency will change with age.

To monitor the potential reproductive senescence of this population, I recommend histological examination of gonadal tissue from both females and males sampled during the broodstock collection effort. Gonadal tissue collected by biopsy will provide only a "snapshot" of gonadal function, however tissue may be examined for the occurrence of gonial mitosis, incidence of and stages affected by atresia, and connective tissue infiltration. Females that are hormonally induced to ovulate in the conservation propagation program (ovulatory and anovulatory) should be monitored over time for changes in egg size, fertility, and hatchability of eggs, and newly hatched larval size. Proximate analysis of ovulated and anovulated eggs should be monitored to assess changes in protein, lipid, ash, fiber, moisture, and carbohydrate levels in females over time. As fish are recaptured and/or spawned over time, comparisons of the histological slides, fertility and hatchability of eggs, and energy content of eggs may allow for reproductive senescence to be documented and the prevalence of senescence within the population to be determined.

Acknowledgements

I would like to thank Sue Ireland, Bob Hallock, Scott Bettin, and the Kootenai Tribe of Idaho for providing me with the opportunity to research and write this report on reproductive senescence in sturgeon; Serge Doroshov, Joel Van Eenennaam, Frank Chapman, and Boris Goncharov for discussions about reproductive senescence in various sturgeon species; and Kevin Kappenman and Paul Anders for comments on an earlier draft of this report. Carisska Anthony assisted with the literature review. This report was funded by Bonneville Power Administration, Project 198806400, *Kootenai River White Sturgeon Studies and Conservation Aquaculture*.

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