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# Recovery of White Sturgeon Populations through Natural Production: Understanding the Influence of Abiotic and Biotic Factors on Spawning and Subsequent Recruitment

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*Abstract.*—Recovery or maintenance of sturgeon populations through natural production in perturbed rivers requires adequate knowledge of the abiotic and biotic factors that influence spawning and cause mortality of embryonic, larval, and juvenile life stages. Although it is known that year-class strength of white sturgeon *Acipenser transmontanus* is determined within 2–3 months after spawning, little is known about specific causes of mortality to early life stages during this period. Initial spawning success is critical in the development of a strong year-class, and maximized recruitment may be dependent upon water temperature and the availability of optimal in-river habitat. Analyses have shown that increased river discharge combined with suitable water temperatures during spawning, egg incubation, yolk sac larvae dispersal, and first exogenous feeding result in greater recruitment. However, little is known about the importance of other variables, such as food availability or losses due to predation that influence year-class strength.

The Columbia River and its watershed have been drastically altered by human activities (Ebel et al. 1989; Anonymous 1991; National Research Council 1996) that undoubtedly have influenced population size and recruitment success of many fish species including white sturgeon *Acipenser transmontanus*. Construction and operation of hydroelectric dams, agriculture, logging, mining, stream channelization, flood control operations, water pollution, and harvest histories have allowed some native and introduced fish species to flourish, while other native species have declined. Fish adapted to riverine conditions, such as white sturgeon, have suffered most.

Historically, white sturgeon were abundant in the Columbia River Basin and briefly supported an intense commercial fishery through the late 1800s. Commercial catches peaked in 1892, when more than 2.4 million kg were landed (Craig and Hacker 1940). Overfishing soon decimated the population, and by 1899 the annual catch was less than 33,250 kg. Harvest regulations implemented

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during the mid 1900s allowed some white sturgeon populations to recover sufficiently to support recreational and commercial fisheries. Miller et al. (1995) reviewed the current status of this long-lived fish in the Columbia Basin. They report that population status and recruitment success vary widely throughout the Columbia River Basin. In general, current population trends and sizes can be characterized as stable at a relatively high population size in the lower Columbia River, stable or variable at low to moderate population sizes in middle reaches, and stable at extremely low to negligible population sizes in upper reaches of the basin.

Fishery managers are now faced with several dilemmas regarding management of white sturgeon populations in the Columbia River Basin. Mainstem hydroelectric dams are barriers to upstream movements by white sturgeon because fishways at the dams were constructed to pass anadromous salmonids (Warren and Beckman 1992). Thus, upstream immigration by fish into lower density areas or to make use of historically productive spawning or rearing environments no longer occurs. While some areas where population productivity is high experience interannual variations in recruitment, other areas have low recruitment that precludes harvest opportunities, and some areas have had a virtual lack of recruitment for several decades. The latter case led to listing the Kootenai River population of white sturgeon as an endangered species by the U.S. Fish and Wildlife Service in 1994 under the Endangered Species Act (USFWS 1994). Fishery management responses to declines in white sturgeon populations have generally been to protect spawning stocks by restricting harvest through minimum and maximum size limits, imposing daily and annual harvest limits, and closing seasons and areas. This management approach of protecting spawning stock to maintain production has been relatively successful in the lower Columbia River as evidenced by the maintenance of harvest opportunities. However, populations are still declining in other areas of the Columbia River Basin despite decades of restrictions on harvest that have included catch-and-release fishing only or complete elimination of fishing for white sturgeon. Thus, environmental effects on stock–recruitment relations for white sturgeon differ among areas and among years within areas, further confounding management efforts.

Effective management of self-sustaining white sturgeon populations or recovery of declining populations through natural production will be achieved only through an understanding of the factors affecting reproduction and early life history, as stated by Le Cren (1962) "An understanding of the dynamics of the whole reproductive and recruitment process is urgently needed, and is probably the largest gap in our knowledge of fish population dynamics." Sissenwine (1984) also noted that a major source of uncertainty in fisheries management and a central problem of fishery science is a lack of understanding of recruitment variability. Houde (1987) reiterated, "Recruitment variability remains the single least understood problem in fishery science."

A review of factors known or speculated to influence stage-specific mortality during the early life history of white sturgeon is appropriate because the causes of variability or failure in recruitment of white sturgeon to age-0 among areas or among years within an area are largely unknown. Through this review of published articles and gray literature reports, knowledge gaps and information needs will become apparent. Once the dynamics of the recruitment process are better known, defensible decisions can be made to implement a variety of alternatives ranging from regulating harvest to altering hydropower system operations or constructing artificial spawning areas to benefit natural production in white sturgeon populations.

Houde (1987) provided a conceptualization of the recruitment process that has been adapted to facilitate this review (Figure 1). This conceptualization shows probable sources of mortality, sources of nutrition, and mechanisms of control for four early life stages. Some readers will disagree with Houde's (1987) terminology, particularly the use of the terms eggs and yolk sac larvae. Balon (1984) would prefer that these two stages be referred to as embryos and free embryos. Because this review is based on an adaptation of Houde's (1987) conceptualization, the original terminology has been retained. Thus, eggs are defined as embryos that are still within egg envelopes, regardless of developmental stage. Yolk sac larvae (a misnomer according to Balon (1984), who states that the correct term is free embryos) are defined as embryos that have hatched and are relying on endogenous food resources. Larvae are white sturgeon that have begun exogenous feeding yet do not have a full complement of fins and scutes. That is, larvae are fish that are actively feeding but do not yet physically resemble mature sturgeon. Juveniles have their full

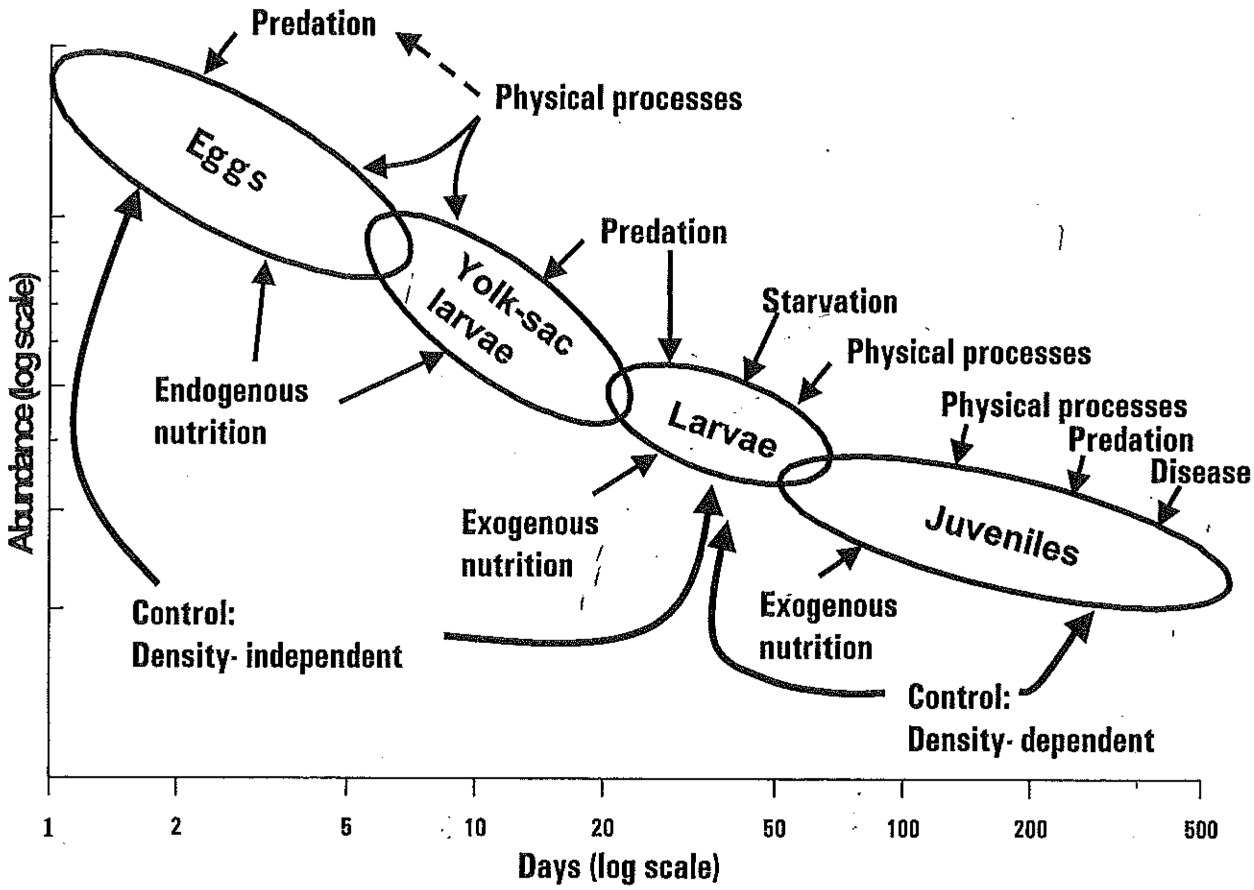


Figure 1. Conceptualization of the recruitment process adapted from Houde (1987) for white sturgeon showing probable sources of death, nutrition, and mechanism of control for the early life history stages. Negative slopes in abundance throughout each life stage are an approximation not a measurement of the degree of mortality that could be expected.

complement of fins and scutes and resemble mature sturgeon but are not sexually mature. Several additions to Houde's (1987) initial conceptualization were made to accommodate the differences between pelagic marine fishes, which Houde's (1987) paper reported on, and recruitment of freshwater riverine white sturgeon. Houde (1987) provided a speculative analysis of stage-specific growth and mortality rates of marine fishes to provide insight into the factors affecting the recruitment process. Currently there is little available information on these stage-specific rates for white sturgeon. Thus, this review is limited to identification and discussion of factors that influence recruitment of white sturgeon, albeit generally at unknown stage-specific mortality rates.

## Initial Abundance of Eggs

Natural production of a year-class of white sturgeon *Acipenser transmontanus* can only occur with successful spawning. Houde (1987) implies, but doesn't actually state, that the one caveat to successful natural recruitment in any population is that gametogenesis, spawning, and egg fertilization must occur. The number of white sturgeon eggs spawned and successfully fertilized annually in each population depends on the number of spawning adults present, female fecundity, and a physical and chemical environment that permits vitellogenesis, cues spawning, and promotes mixing and fertilization of eggs (Figure 2). This sets an initial abundance of eggs from which the subsequent year-class is established.

Spawning occurs only if the physical environment permits vitellogenesis and cues ovulation, and should only occur when and where environmental factors are likely to be optimal for the survival and growth of progeny (Munro et al. 1990). In the pelagic marine environments that concerned Houde (1987), physical and environmental conditions among years may not be as variable as riverine environments and thus the

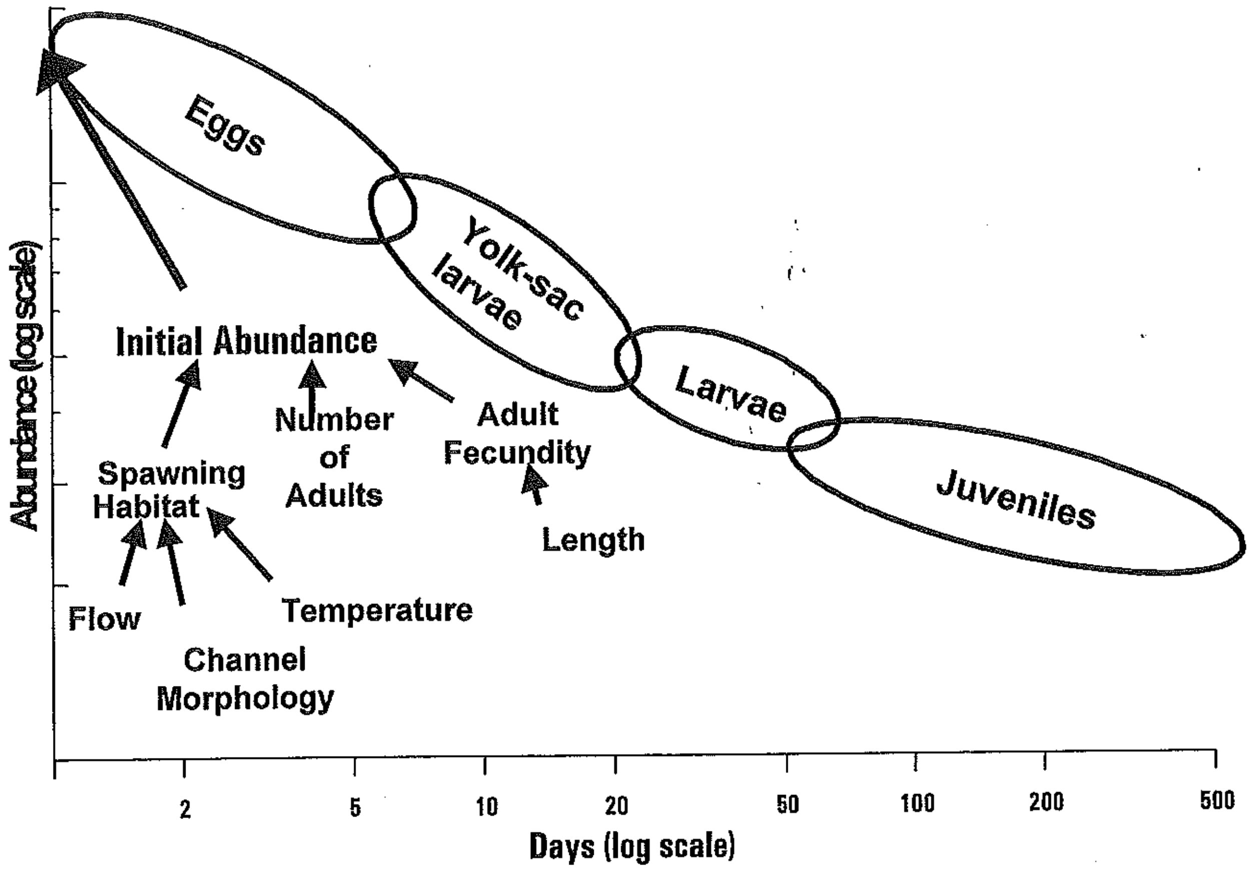


Figure 2. Conceptualization of the recruitment process for white sturgeon showing factors influencing the initial abundance of spawned eggs in a population.

actual occurrence of spawning may rarely be questioned. However, riverine environments where white sturgeon spawn, particularly those altered by human development, can be quite variable, and the influence of physical and environmental conditions on gametogenesis, vitellogenesis, spawning and egg fertilization cannot be discounted. Temperature and photoperiod have been suggested as important environmental factors in fish maturation (de Vlaming 1972), and gametogenesis in white sturgeon is affected by temperature (Chapman 1989; Webb et al. 1999).

The maternal contribution to recruitment variability in white sturgeon populations in the Columbia River Basin is also important. White sturgeon are relatively unique among iteroparous fishes in that individual females do not spawn every year. Conte et al. (1988) reports that in any year only 10% to 20% of the white sturgeon adult female population is capable of spawning. Vitellogenesis in white sturgeon requires two years in the San Francisco Bay estuary, with a reproductive cycle (time between spawning) of 4–5 years (Chapman 1989). The reproductive cycle of white sturgeon in the Columbia River downstream from McNary Dam is probably three years or more (Welch and Beamesderfer 1992). The size and age composition of spawning stocks as well as overall population numbers will influence the number of eggs spawned. The fecundity of white sturgeon has been shown to increase with length (Beamesderfer et al. 1995; DeVore et al. 1995).

Physical factors and environmental conditions influence spawning and thus contribute to recruitment variability. The amount and quality of spawning habitat available to individual populations of white sturgeon differs among reaches because of channel morphology and among years because of variation in river discharge (Parsley and Beckman 1994). White sturgeon spawning in the Columbia and Snake rivers generally occurs in areas with fast water velocities, coarse substrates and water depths of 3 m or more (Parsley et al. 1993; R. L. & L. Environmental Services Ltd. 1994; Parsley and Kappenman 2000). Spawning in fast water velocities would separate and disperse the adhesive eggs, and the coarse substrates would provide a good surface for the adhesive eggs to attach. Impoundments have reduced the hydraulic slope of the river over vast reaches and inundated many areas that historically may have provided spawning habitat for white sturgeon. Because of differences in channel morphology and a greater hydraulic slope, the free-flowing reaches provide more spawning habitat than the impoundments at reduced discharges (Parsley and Beckman 1994) causing variability in spawning habitat quantity and quality among areas within years.

Interannual variation in spawning is also caused by the thermal regime of rivers within the Columbia River Basin. Developments within the Columbia River Basin for hydroelectric power generation and operations at dams that are used to store water for flood control and power generation have resulted in temperature variations from the historic thermal regime. The timing and duration of the spawning season for white sturgeon in any given year vary with water temperature. White sturgeon spawning in the Columbia River Basin generally occurs when water temperatures are between 10 and 18 C (Parsley et al. 1993; R. L. & L. Environmental Services; Ltd. 1994) with the peak of spawning occurring when temperatures are generally between 13 and 15 C. These temperatures can occur for variable periods during the months of April, May, June, or July. Kootenai River white sturgeon also spawn during May and June but at water temperatures that are much cooler. Typically, spawning by white sturgeon in the Kootenai River begins when temperatures are 8–9 C and ceases when temperatures approach 12 C (Paragamian et al. 1995; Paragamian et al. 1997). Although the primary force behind the thermal regime is regional climatic conditions, the hydropower system is often manipulated to provide cooler water temperatures during the summer to benefit outmigrating juvenile anadromous salmonids. These manipulations can lower river water temperature by several degrees and often occur during times when white sturgeon are spawning. It is unknown, but probable, that these temperature variations disrupt spawning activities by white sturgeon.

## Eggs

Mortality of viable white sturgeon eggs begins immediately after spawning and can be divided into three categories: physiological mortality from abnormal egg development and subsequent fungal infection, predation, and mortality due to physical processes. Broadcast spawning large numbers of eggs is an adaptive strategy of many fishes including white sturgeon, and high mortality of spawned eggs is expected. Mortality of fish eggs is typically considered to be density independent. However, abnormally developing eggs can become covered with fungus that can cause mortality of adjacent eggs and foster the spread of the fungus. Abnormal development can be induced by polyspermic fertilization, parthenogenesis, mechanical disruption, and environmental perturbations including water temperature fluctuations, adverse water quality, and bioaccumulation of toxins (Cherr and Clark 1985; Beer 1981; Bosely and Gately 1981; Ginzburg 1968).

The incidence of fungus-infected eggs in field collections of white sturgeon eggs varies considerably. In egg collections made by the U.S. Fish and Wildlife Service and the National Marine Fisheries Service from lower Columbia River impoundments and the free-flowing river downstream from Bonneville Dam, the proportion of fungus-infected eggs was unusually high in The Dalles Pool; 45% of the eggs collected over 5 years had a fungal infection. Bonneville Pool had a 21% incidence of infected eggs (4-year average), John Day Pool had 17% (3-year average), and the free-flowing reach had 2% (5-year average; Anders and Beckman 1992). High egg mortalities in the impoundments but not in the free-flowing reach, as evidenced by fungal infection, indicate that impoundment has adversely affected either the physical or physiological environment for vitellogenesis, ovulation, spawning, or egg incubation. It is not known specifically what causes the high egg mortality, but water quality in the Columbia River has been degraded by industrial wastes (Damkaer and Dey 1989), mining, agriculture, and urbanization. Water quality can be degraded more in some areas than in others (Damkaer and Dey 1989) and the impoundments may serve as settling basins for pollutants. Bosely and Gately (1981) reported levels of polychlorinated biphenyls in white sturgeon ova from Bonneville Pool that are known to cause mortality of developing rainbow trout *Oncorhynchus mykiss* embryos. Tikhonova and Shekhanova (1982) determined that gastrulation in Russian sturgeon *A. gueldenstaedti* is the most sensitive stage to agricultural pesticides containing carbamates.

The fate of eggs dislodged from the substrate and those that do not adhere to a surface is unknown. Many dislodged eggs could settle in areas favorable to egg predators, or the trauma of dislocation could kill some eggs. However, dislodged eggs have been hatched in aquaria (M. J. Parsley, U.S. Geological Survey, unpublished data). Irregular substrates or those with interstitial spaces could provide protection from scouring and predation, and shifting substrates could crush eggs.

Incubating white sturgeon eggs are vulnerable to predation by fish. Miller and Beckman (1996) found that largescale sucker *Catostomus macrocheilus*, common carp *Cyprinus carpio*, northern pikeminnow *Ptychocheilus oregonensis*, and prickly sculpin *Cottus asper* ate white sturgeon eggs in Columbia River impoundments. It is probable that some invertebrates (e.g., decapods) also consume white sturgeon eggs. Estimates of the number of eggs consumed by predators are unavailable, but the low numbers of eggs spawned in some areas could compound the effect of egg losses on recruitment. Impoundment and power-peaking dam operations have favored predation on eggs by reducing water velocities over vast areas. High-water velocities in white sturgeon spawning areas could reduce predation on white sturgeon eggs by excluding predators. However, in the regulated Columbia River, water velocities in spawning areas are generally reduced during years of low river discharge (Parsley and Beckman 1994). Diel fluctuations in river discharge at the dams to produce more power during peak energy needs and less power at other times also reduce water velocities (generally during nighttime), which could increase predator access to white sturgeon eggs. Near-substrate water velocities measured at one location downstream from The Dalles Dam on 8 and 9 June 1988 ranged from 0.43 to 1.83 m/s as discharge ranged from about 3,000–8,000 $m^3/s$ during one power-peaking cycle (M. J. Parsley, U. S. Geological Survey, unpublished data).

Water temperature strongly influences egg survival as well as timing of spawning. Most white sturgeon spawning in the Columbia and Snake rivers occurs at optimal temperatures for egg development (Parsley et al. 1993; R. L. & L. Environmental Services, Ltd. 1994), but some spawning has occurred at temperatures greater than 18°C, particularly in the impoundments (Anders and Beckman 1992; McCabe and Tracy 1994) and some spawning occurs at water temperatures considerably less than optimal (McCabe and Tracy 1994; Paragamian et al. 1997). Egg mortality increases when incubation occurs at 18°C, and total mortality occurs at 20°C (Wang et al. 1985). During some years, spawned eggs may be lost because hydrosystem operations, hydrologic, or climatic conditions cause sudden increases in water temperatures. Eggs that are spawned at cooler-than-optimal temperatures generally develop normally and hatch after a prolonged period of time (Wang et al. 1985).

## Yolk Sac Larvae

Upon hatching, white sturgeon yolk sac larvae enter a "swim-up" phase (Brannon et al. 1985a) presumably to be dispersed downriver into habitats that will be favorable for feeding when the yolk sac is exhausted. According to laboratory experiments conducted by Brannon et al. (1985a) the duration of the swim-up phase was negatively correlated with water velocity. White sturgeon yolk sac larvae have been described as "hardy" (Conte et al. 1988), which refers to their ability to survive transport for artificial culture. Wild yolk sac larvae must be tolerant of harsh physical conditions to survive in the turbulent riverine environment in which hatching occurs. Density-independent mortality at this life stage could be caused by several factors including poor water quality, physical processes that cause either physical or physiological trauma leading to death, poor maternal contribution to embryo quality leading to reduced fitness, and predation. Losses of yolk sac larvae in the Columbia River from abnormal development or other factors have not been quantified and studies to investigate differences in mortality among reaches have not been done. Dead yolk sac larvae have been collected from the drift in at least four river reaches, but the cause of death was unknown (M. J. Parsley, U. S. Geological Survey, unpublished data). The collection process may have caused some mortality, but natural mortality could have been caused by poor water quality, nutrient imbalance in the yolk sac, or physical trauma associated with hatching in the turbulent environment.

Yolk sac larvae are sensitive to poor water quality and pollutants. Brannon et al. (1985b) reported that water quality parameters for chlorine and gas supersaturation might be more critical for white sturgeon than for salmonids. The anti-sapstain wood preservative Bardac 2280 (principal active ingredient 80% didecyldimethylammonium chloride, DDAC) a common wood preservative, has been found to be particularly toxic to white sturgeon yolk sac larvae with a 24-h 50% lethal concentration (LC50) value between 1 and 10 ppb (Farrell et al. 1998). Spill at dams can cause supersaturation of atmospheric gases in waters during yolk sac larval dispersal. Counihan et al. (1998) conducted laboratory experiments investigating the effects of dissolved gas supersaturation on white sturgeon yolk sac larvae and found that signs of gas bubble trauma were evident in 1–2-d old fish after only 15 min of exposure at 118% supersaturation. Yolk sac larvae exposed to total dissolved gas levels of 118% experienced no mortality, though their behavior was different from control groups. Because of the development of a bubble in the buccal cavity, these fish were unable to descend from the surface. Yolk sac larvae exposed to total dissolved gas levels of 131% experienced 50% mortality after 13 d of exposure.

Predation on white sturgeon yolk sac larvae is a probable source of mortality and is likely greatest during the swim-up phase. The large opaque larvae drifting with the water currents could be quite obvious to visual predators. Turbidity and darkness may provide cover for the drifting larvae, but turbidities in the Columbia River have been reduced by the impoundments. Brannon et al. (1985a) determined that laboratory reared yolk sac larvae were more apt to enter the water column during darkness than during daylight. However, in a 12-h study downstream from Bonneville Dam, McCabe and Tracy (1994) found no significant difference between day and night catches of larval white sturgeon ($P > 0.05$). A propensity to drift at night as lake sturgeon yolk sac larvae do (Kempinger 1988) would reduce encounters with visual predators. Yolk sac larval white sturgeon have no defensive capabilities other than a propensity to hide in the substrate after the swim-up phase and possibly a limited ability to evade predator strikes. Laboratory experiments by Brannon et al. (1986) showed that white sturgeon larvae were eaten by goldfish *Carassius auratus*, bluegill *Lepomis macrochirus*, juvenile chinook salmon *Oncorhynchus tshawytscha*, rainbow trout, and older white sturgeon. Yolk sac larvae in their natural environments are unlikely to encounter goldfish or bluegill, but are probably vulnerable to predation by the same fishes identified as egg predators.

Vulnerability of yolk sac larvae would be related to predator abundance and dispersal of newly hatched larvae. If egg predators were attracted to spawning areas, rapid dispersal of newly hatched yolk sac larvae would reduce encounters with these potential predators. Parsley et al. (1993) measured water velocities of 0.5–2.4 m/s near the substrate in white sturgeon spawning areas and 0.3–2.4 m/s near the substrate at sites where yolk sac larvae were collected in the Columbia River. Larval fish in water velocities this high would be transported downstream considerable distances in a short time. In the free-flowing Columbia River downstream from Bonneville Dam, yolk sac larvae have been collected over 175 km downstream from the known spawning area (McCabe and Tracy 1994). Stevens and Miller (1970) observed that sturgeon yolk sac larvae (white sturgeon or green sturgeon *A. medirostris*) in California's Sacramento–San Joaquin River system were primarily demersal. They caught 33 yolk sac larvae in 16 bottom-sampling efforts and only 1 in 8 surface and midwater sampling efforts.

## Larvae

The larval stage for white sturgeon generally lasts 25–30 d. Once the yolk sac is absorbed, the fish end their hiding phase and move out onto the substrate to begin feeding. Mortality of larval fishes is often greatest during the period of transition from endogenous to exogenous feeding (Hjort 1926). It is not known if white sturgeon larvae experience high mortality rates at this juncture in natural populations, but it is probable that some of the variation in year-class strength observed in white sturgeon populations is due to mortality at the larval stage.

Starvation is one biotic factor thought to regulate juvenile fish abundance in some freshwater and marine fish populations (Rice et al. 1987; Sinclair 1988). It is unknown if or when irreversible starvation (May 1974) occurs for larval white sturgeon deprived of food. Muir et al. (2000) found no evidence of larval starvation in the Columbia River downstream from Bonneville Dam and in the two lowermost impoundments. In a laboratory study, if food was not present, white sturgeon larvae reentered the water column, presumably to be displaced farther downriver to a food source (Brannon et al. 1985a). White sturgeon larvae collected in the Columbia River fed primarily on amphipods of the genus *Corophium* (Muir et al. 2000), a food that historically was found in the Columbia River estuary but not upriver in free-flowing environments. Other food items consumed that would have been historically available to larvae upstream of the upper extent of *Corophium* included copepods, Ceratopogonidae larvae and Diptera pupae and larvae.

Another source of mortality at the larval stage that can have significant affects on year-class strength is predation. Predation on white sturgeon larvae has been noted in laboratory experiments (Brannon et al. 1986) but has not been investigated under natural conditions. Larvae develop sharp scutes as they grow, possibly reducing their vulnerability to predation. Potential predators collected in association with larvae included bridgelip sucker *Catostomus columbianus*, largescale suckers, bullheads *Ameiurus* spp., common carp, peamouth *Mylocheilus caurinus*, chiselmouth *Acrocheilus alutaceus*, northern pikeminnow, prickly sculpin, larger white sturgeon, and starry flounder *Platichthys stellatus*.

## Juveniles

White sturgeon larvae metamorphose into juveniles within 3–4 months after egg fertilization. Predation, starvation, disease, parasitism, and physical processes caused by direct and indirect human actions reduce juvenile white sturgeon numbers. For many fish species, relative year-class strength is set prior to this life stage (Bradford 1992). Losses of juvenile white sturgeon to predation are probably slight because of the protective scutes, benthic habits, and fast growth. Only one juvenile white sturgeon was consumed by a channel catfish *Ictalurus punctatus*, during a study of the gut contents of more than 4,780 northern pikeminnow, 1,050 walleye *Stizostedion vitreum*, 4,800 smallmouth bass *Micropterus dolomieui*, and 650 channel catfish (M. J. Parsley, U. S. Geological Survey, unpublished data). Other previously listed predators on young white sturgeon were not examined in that study.

Juvenile white sturgeon feed primarily on benthic invertebrates (McCabe et al. 1993; Muir et al. 2000). Studies investigating productivity of benthic invertebrates that juvenile white sturgeon prey on between free flowing and impounded areas are lacking. Generally, growth rates, mean length at age, and condition factors of juvenile white sturgeon (1–8 years of age) were greater for those captured in the impounded areas than of those collected in the free-flowing reach (Miller and Beckman 1992), suggesting that food resources for juvenile white sturgeon were more limiting in the free-flowing reach than in the impounded areas at existing white sturgeon densities.

Losses of fish to disease and parasites in the wild are difficult to quantify. Hatchery reared white sturgeon are susceptible to many of the same diseases and parasites common to other fishes reared in culture facilities (LaPatra et al. 1995; Conte et al. 1988) and the white sturgeon iridovirus can cause significant mortality in cultured fish (LaPatra et al. 1994). This size-specific and stress-mediated virus has been found in white sturgeon throughout the Columbia River Basin (LaPatra et al. 1994). Fish weakened by disease or parasites could be more vulnerable to predation (Mesa et al. 1998) but this has not been investigated in white sturgeon. The nematode parasite *Cystoopsis acipenseri* is common to smaller white sturgeon and creates blister-like cysts located just under the skin of affected fish (McCabe 1993). The degree of infestation of white sturgeon by the nematode parasite varied spatially and temporally in the lower Columbia River and was greater in smaller white sturgeon (McCabe 1993). However, it is unknown if infestation increases mortality.

Human actions sometimes cause mortality of juvenile white sturgeon. Suction dredging in deep areas (20–26 m) in the lower Columbia River is known to seriously injure and kill juvenile white sturgeon (Buell 1992), and there is speculation that the dredging operations may attract feeding white sturgeon, compounding the losses. Lost and abandoned gill nets from commercial and subsistence fisheries can kill substantial numbers of juvenile and adult white sturgeon in impounded areas (authors personal observations), and large numbers of fish are occasionally killed during maintenance activities at the dams (J. DeVore, Washington Department of Fish and Wildlife, personal communication). Hooking mortality of angler-caught sublegal-sized fish probably results in a loss of juvenile white sturgeon, but has not been investigated.

## Summary

Year-class strength in any fishery is determined by the number of eggs spawned and the subsequent survival rates over several independent life stages, all of which must be high to produce a strong year-class (Walters and Collie 1988). Thus, preceding events have set the size of the unexploited juvenile white sturgeon population at any given time. Houde (1987) showed that variability in life stage duration resulting from variations in growth or development rates caused by environmental conditions could lead to drastic fluctuations in recruitment. The mortality associated with a prolonged period of time spent at one developmental stage caused by minor differences in water temperature or food availability (endogenous or exogenous) can have profound effects on year-class strength. Interannual variability in white sturgeon recruitment as shown by Counihan et al. (1999) and Counihan et al. (unpublished data) could result from any one or a combination of the factors listed above. Counihan et al. (in press) showed that year-class strength was apparently set within the first few months of spawning and that it was positively related to river discharge and negatively related to water temperature during the period when spawning and egg incubation were occurring.

White sturgeon, like many broadcast-spawning teleosts, probably experience very high mortality through the larval period and it is unknown if they experience significant mortality due to predation in the juvenile period, which is a common source of mortality among many juvenile fish. However, high mortality alone will not cause variability in recruitment. It must be coupled with high interannual variability as well (Bradford 1992). But high mortality alone, either occurring at a single life stage or cumulative over several stages, could cause very low levels of recruitment or recruitment failure. In areas with high interannual variability in white sturgeon recruitment, such as in some impoundments on the lower Columbia River, the causes of the variability may differ among years or even among areas within years. In areas where recruitment is virtually nonexistent, such as in the Kootenai River in Idaho and British Columbia or Lake Roosevelt, Washington, spawning by white sturgeon is known to occur annually, but few if any of the spawned eggs produce juvenile fish. Thus mortality in these areas must be exceptionally high somewhere in the recruitment process.

Considerable information has become available on the physiology, ecology, and biology of white sturgeon in the past decade. Though recent studies have identified many actual or potential causes of mortality, acceptable or "normal" rates by stage, which would typically be represented by the decreasing slopes through the four life stages in Figures 1 and 2, are not known. Research needs vary among populations according to the level of recruitment that occurs. In populations characterized by interannual variability in recruitment, prerecruit monitoring to provide managers with advance warning of reduced or missing year classes so that harvest regulations could be adjusted accordingly may be economically more viable than research on causes of the variability. While an understanding of the physiological, behavioral, and ecological linkages through which environmental factors influence recruitment rates and distribution patterns is helpful in explaining the need for regulation changes, long term monitoring of recruitment trends may prove more valuable to fisheries managers than short-term studies seeking potentially spurious environmental correlations of dubious management value (Walters and Collie 1988). Further research in these populations should focus on management of extremely long-lived species. Where recruitment is occurring and populations cannot sustain harvest, or where adult fish are present and recruitment is negligible, research needs are more specific to identifying population bottlenecks and recovery of depleted populations. Here, a better understanding of the causes of mortality or causes of a lack of spawning and knowledge of fish emigration are needed. Concurrent to these are the needs for better sampling methodologies, knowledge of the physiology and metabolic needs of different stages of fish, and the potential ramifications of population fragmentation caused by dams.

White sturgeon fishery managers confront three recruitment problems: variable annual recruitment, low recruit- ment (e.g. too low to provide recreational or harvest opportunities), and no recruitment. Highly variable annual recruitment occurs in some impoundments and management of these fisheries has traditionally been done by quota bag limits and size limits (Rieman and Beamesderfer 1990). Recruitment at levels too low to provide harvest opportunities, as occurs in the middle Snake River (Cochnauer et al. 1985), is generally not desirable from a fishery management perspective, though populations will persist and continue to provide recreational fishing opportunities with little danger of extinction. Areas of great concern to fishery managers are those with aging adult populations and a virtual lack of recruitment that will shortly lead to extirpation or extinction of individual populations. In severely depressed populations, as most sturgeon populations are (Rochard et al. 1990; Birstein 1993), depensatory population growth can occur when numbers of individuals fall below critical levels, further complicating recovery efforts. Biotic (e.g. deterministic) and abiotic (e.g. stochastic) processes acting in concert ultimately control production (Karr and Dudley 1978; Schlosser 1985). Recognizing the influence these processes have on stock–recruitment relations and how human development has affected the biotic and abiotic factors that influence white sturgeon populations could enable the white sturgeon fisheries in the Columbia River Basin and elsewhere to be enhanced.

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## References

Anders, P. J., and L. G. Beckman. 1992. Comparison of white sturgeon egg mortality and juvenile deformity among four areas of the Columbia River. In R. C. Beamesderfer and A. A. Nigro, editors. Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam, Volume II. Final report (Contract DE-AI79-86BP63584) to Bonneville Power Administration, Portland, Oregon.

Anonymous. 1991. The Columbia River system: the inside story. System Operation Review, Interagency Team, U.S. Bureau of Reclamation, U.S. Army Corps of Engineers, and Bonneville Power Administration. Box 2988, Portland, Oregon.

Balon, E. K. 1984. Reflections on some decisive events in the early life history of fishes. Transactions of the American Fisheries Society 113:178–185.

Beamesderfer, R. C. P., T. A. Rien, and A. A. Nigro. 1995. Differences in the dynamics and potential production impounded and unimpounded white sturgeon populations in the lower Columbia River. Transactions of the American Fisheries Society 124:857–872.

Beer, K. E. 1981. Embryonic and larval development of white sturgeon (*Acipenser transmontanus*). Masters thesis. University of California, Davis, California.

Birstein, V. J. 1993. Sturgeons and paddlefishes: threatened fishes in need of conservation. Conservation Biology 7:773–787.

Bosely, C. E., and G. F. Gately. 1981. Polychlorinated biphenyls and chlorinated pesticides in Columbia River white sturgeon *Acipenser transmontanus*. U.S. Fish and Wildlife Service, Marrowstone Field Station, Nordland, Washington. Unpublished report.

Bradford, M. J. 1992. Precision of recruitment predictions from early life stages of marine fishes. Fishery Bulletin 90:439–453.

Brannon, E., S. Brewer, A. Setter, M. Miller, F. Utter, and W. Hershberger. 1985a. Columbia River white sturgeon early life history and genetics study. Final report (Project Number 83-316) to Bonneville Power Administration. Portland, Oregon.

Brannon, E. L., C. L. Melby, and S. D. Brewer. 1985b. Columbia River white sturgeon enhancement. Final report (Project Number 83-316) to Bonneville Power Administration. Portland, Oregon.

Brannon, E., A. Setter, M. Miller, S. Brewer, G. Winans, F. Utter, L. Carpenter, and W. Hershberger. 1986. Columbia River white sturgeon population genetics and early life history study. Final report (Project 83-316) to Bonneville Power Administration. Portland, Oregon.

Buell, J. W. 1992. Fish entrainment monitoring of the Western-Pacific dredge RW Lofgren during operations outside the preferred work period. Buell and Associates, Inc. Portland, Oregon.

Chapman, F. A. 1989. Sexual maturation and reproductive parameters of wild and domestic stocks of white sturgeon, *Acipenser transmontanus*. Doctoral dissertation. University of California, Davis, California.

Cherr, G. N., and W. H. Clark. 1985. Gamete interaction in the white sturgeon *Acipenser transmontanus*: a morphological and physiological review. Pages 11–22 *in* F. P. Binkowski and S. I. Doroshov, editors. North American sturgeons: biology and aquaculture potential. Dr. W. Junk, Dordrecht, The Netherlands.

Cochnauer, T. G., J. R. Lukens, and F. E. Partridge. 1985. Status of the white sturgeon, *Acipenser transmontanus* in Idaho. Pages 127–133 *in* F. P. Binkowski and S. I. Doroshov, editors. North American sturgeons: biology and aquaculture potential. Dr. W. Junk, Dordrecht, The Netherlands.

Conte, F. S., S. I. Doroshov, P. B. Lutes, and E. M. Strange. 1988. Hatchery manual for the white sturgeon *Acipenser transmontanus*. Publication 3322. University of California, Oakland, California.

Counihan, T. C., A. I. Miller, M. G. Mesa, and M. J. Parsley. 1998. The effects of dissolved gas supersaturation on white sturgeon larvae. Transactions of the American Fisheries Society 127:316–322.

Counihan, T. C., A. I. Miller, and M. J. Parsley. 1999. Indexing the relative abundance of Age-0 white sturgeons in an impoundment of the lower Columbia River from highly skewed trawling data. North American Journal of Fisheries Management 19:520–529.

Craig, J. A., and R. L. Hacker. 1940. The history and development of the fisheries of the Columbia River. U.S. Department of the Interior, Bureau of Fisheries, Bulletin 32.

Damkaer, D. M., and D. B. Dey. 1989. Evidence for fluoride effects on salmon passage at John Day Dam, Columbia River, 1982-1986. North American Journal of Fisheries Management 9:154–162.

de Vlaming, V. L. 1972. Environmental control of teleost reproductive cycles: a brief review. Journal of Fish Biology 4:131–140.

DeVore, J. D., B. W. James, C. A. Tracy, and D. Hale. 1995. Dynamics and potential production of white sturgeon in the unimpounded lower Columbia River. Transactions of the American Fisheries Society 124:845–856.

Ebel, W. J., C. D. Becker, J. W. Mullan, and H. L. Raymond. 1989. The Columbia River - toward a holistic understanding. Pages 205–219 *in* D. P. Dodge, editor. Proceedings of the International Large River Symposium. Canadian Special Publication of Fisheries and Aquatic Sciences 106:205–219.

Farrell, A. P., C. J. Kennedy, A. Wood, B. D. Johnston, and W. R. Bennett. 1998. Acute toxicity of a didecyldimethylammonium chloride-based wood preservative, Bardac 2280, to aquatic species. Environmental Toxicology and Chemistry 17:1552–1557.

Ginzburg, A. S. 1968. Fertilization in fishes and the problem of polyspermy. Nauka Press. Moskva. 175 pp. Israel Program for Scientific Translations 1972.

Hjort, J. 1926. Fluctuations in the year class of important food fishes. Journal du Conseil 1:5–39.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. Pages 17–29 *in* R. D. Hoyt, editor. 10th annual larval fish conference. American Fisheries Society, Symposium 2, Bethesda, Maryland.

Karr, J. R., and D. R. Dudley. 1978. Biological integrity of a headwater stream: evidence of degradation, prospects for recovery. Pages 3–25 *in* J. Lake and J. Morrison, editors. Environmental impact of land use on water quality: final report on the Black Creek project. U.S. Environmental Protection Agency, EPA-905/9–77–007-D, Chicago.

Kempinger, J. J. 1988. Spawning and early life history of lake sturgeon in the Lake Winnebago System. Pages 110–122 in R. D. Hoyt, editor. 11th annual larval fish conference. American Fisheries Society, Symposium 5, Bethesda, Maryland.

LaPatra, S. E., J. M Groff, G. R. Jones, B. Munn, T. L. Patterson, R. A. Holt, A. K. Hauck, and R. P. Hedrick. 1994. Occurrence of white sturgeon iridovirus infections among cultured white sturgeon in the Pacific Northwest. Aquaculture 126:201–210.

LaPatra, S. E., G. R. Jones, K. A. Lauda, T. S. McDowell, R. Schneider, R. P. Hedrick. 1995. White sturgeon as a potential vector of infectious hematopoietic necrosis virus. Journal of Aquatic Animal Health 7:225–230.

Le Cren, E. D. 1962. The efficiency of reproduction and recruitment in freshwater fish. British Ecological Society Symposium 2:283–296.

May, R. C. 1974. Larval mortality in marine fishes and the critical period concept. In J. H. S. Blaxter, editor. The early life history of fish. Springer-Verlag, New York.

McCabe, G. T., Jr. 1993. Prevalence of the parasite *Cystoopsis acipenseri* (Nematoda) in juvenile white sturgeons in the lower Columbia River. Journal of Aquatic Animal Health 5:313–316.

McCabe, G. T., Jr., R. L. Emmett, and S. A. Hinton. 1993. Feeding ecology of juvenile white sturgeon (*Acipenser transmontanus*) in the lower Columbia River. Northwest Science 63:170–180.

McCabe, G. T., Jr., and C. Tracy. 1994. Spawning and early life history of white sturgeon *Acipenser transmontanus* in the lower Columbia River. Fisheries Bulletin 92:760–774.

Mesa, M. G., T. P. Poe, A. G. Maule, and C. B. Schreck. 1998. Vulnerability to predation and physiological stress response in juvenile chinook salmon (*Oncorhynchus tshawytscha*) experimentally infected with *Renibacterium salmoninarum*. Canadian Journal of Fisheries and Aquatic Sciences 55:1599–1606.

Miller, A. I., and L. G. Beckman. 1992. Age and growth of juvenile white sturgeon in the Columbia River downstream from McNary Dam. In R. C. Beamesderfer and A. A. Nigro, editors. Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam, Volume II. Final report (Contract DE-AI79-86BP63584) to Bonneville Power Administration, Portland, Oregon.

Miller, A. I., T. D. Counihan, M. J. Parsley, and L. G. Beckman. 1995. Columbia River Basin white sturgeon. Pages 154–157 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service. Washington, D.C.

Miller, A. I., and L. G. Beckman. 1996. First record of predation on white sturgeon eggs by sympatric fishes. Transactions of the American Fisheries Society 125:338–340.

Muir, W. D., G. T. McCabe, Jr., M. J. Parsley, and S. A. Hinton. 2000. Diet of first feeding larval, and young-of-the-year white sturgeon in the lower Columbia River. Northwest Science 74:25–33.

Munro, A. D., A. P. Scott, and T. J. Lam. 1990. Reproductive seasonality in teleosts: environmental influences. CRC Press, Boca Raton, Florida.

National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington D.C.

Paragamian, V. L., G. Kruse, and V. Wakkinen. 1995. Kootenai River white sturgeon spawning and recruitment evaluation. Annual Progress Report to the Bonneville Power Administration, Portland, Oregon.

Paragamian, V. L., G. Kruse, and V. Wakkinen. 1997. Kootenai River white sturgeon spawning and recruitment evaluation. Annual Progress Report to the Bonneville Power Administration, Portland, Oregon.

Parsley, M. J., and L. G. Beckman. 1994. White sturgeon spawning and rearing habitat in the lower Columbia River. North American Journal of Fisheries Management 14:812–827.

Parsley, M. J., and K. M. Kappenman. 2000. White sturgeon spawning areas in the lower Snake River. Northwest Science 74:192–201.

Parsley, M. J., L. G. Beckman, and G. T. McCabe, Jr. 1993. Habitat use by spawning and rearing white sturgeon in the Columbia River downstream from McNary Dam. Transactions of the American Fisheries Society 122:217–227.

R. L, and L. Environmental Services, Ltd. 1994. Status of white sturgeon in the Columbia River, B. C. Final Report prepared for B.C. Hydro, Vancouver, British Columbia, Canada.

Rice, J. A., L. B. Crowder, and F. P. Binkowski. 1987. Evaluating potential sources of mortality for larval bloater: starvation and vulnerability to predation. Canadian Journal of Fisheries and Aquatic Sciences 44:467–472.

Rieman, B. E., and R. C. Beamesderfer. 1990. White sturgeon in the lower Columbia River: Is the stock overexploited? North American Journal of Fisheries Management 10:388–396.

Rochard, E., G. Castelnaud, and M. LePage. 1990. Sturgeons (Pisces: Acipenseridae); threats and prospects. Journal of Fish Biology 37:123–132.

Schlosser, I. J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. Ecology 66:1484–1490.

Sinclair, M. 1988. Marine Populations: an essay on population regulation and speciation. University of Washington Press, Seattle and London.

Sissenwine, M. P. 1984. Why do fish populations vary? In R. May, editor. Exploitation of marine communities. Springer-Verlag, Berlin.

Stevens, D. E., and L. W. Miller. 1970. Distribution of sturgeon larvae in the Sacramento-San Joaquin River system. California Fish and Game 56:80–86.

Tikhonova, L. S., and I. A. Shekhanova. 1982. Effect of pesticides on Russian sturgeon, *Acipenser gueldenstaedti* (Acipenseridae), in the embryonic-larval period. Journal of Ichthyology 22:172–175.

USFWS (U.S. Department of Interior, Fish and Wildlife Service). 1994. Determination of endangered status for the Kootenai River white sturgeon population. Federal Register 59(171):45989.

Walters, C. J., and J. S. Collie. 1988. Is research on environmental factors useful to fisheries management? Canadian Journal of Fisheries and Aquatic Sciences 45:1848–1854.

Wang, Y. L., F. P. Binkowski, and S. I. Doroshov. 1985. Effect of temperature on early development of white and lake sturgeon, *Acipenser transmontanus* and *A. fulvescens*. Environmental Biology of Fishes 14:43–50.

Warren, J. J., and L. G. Beckman. 1992. Fishway use by white sturgeon on the Columbia River. Washington Sea Grant Program WSG-AS 93-02. Seattle, Washington.

Webb, M. A. H., J. P. Van Eenennaam, S. I. Doroshov, and G. P. Moberg. 1999. Preliminary observations on the effects of holding temperature on reproductive performance of female white sturgeon, *Acipenser transmontanus* Richardson. Aquaculture 176:315–329.

Welch, D. W., and R. C. Beamesderfer. 1992. Maturation of female white sturgeon in lower Columbia River impoundments. In R. C. Beamesderfer and A. A. Nigro, editors. Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam, Volume II. Final report (Contract DE-AI79-86BP63584) to Bonneville Power Administration, Portland, Oregon.