STATUS AND HABITAT REQUIREMENTS OF THE WHITE STURGEON POPULATIONS IN THE COLUMBIA RIVER DOWNSTREAM FROM MCNARY DAM

Final Report of Research

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EXECUTIVE SUMMARY

Effects of dam construction and operation on white sturgeon populations in the Columbia River were examined in a cooperative study by two state and two federal agencies. Reproduction, population dynamics, and habitat were compared between the unimpounded river downstream from Bonneville Dam and three reservoirs between Bonneville and McNary dams from 1986-91.

We conclude that dams constrain movements of white sturgeon and have functionally isolated populations in Columbia River reservoirs. The status and productivity of each population of white sturgeon are unique, and productivity is less in reservoirs than in the unimpounded river downstream from Bonneville Dam. Recruitment and subsequent population size in impoundments are limited by the effects of river discharge in spring on spawning habitat, which is restricted to high-velocity areas in the tailwaters of each dam. Reservoirs provide large areas of suitable habitat for juvenile and adult white sturgeon, but compensatory population responses may reduce productivity as carrying capacity for a particular life stage is approached. Overexploitation of white sturgeon in recent years has collapsed fisheries in The Dalles and John Day reservoirs. Population collapse is likely if overexploitation continues.

Our conclusions suggest several alternatives for protecting and enhancing white sturgeon production to mitigate the detrimental effects of development and operation of the hydroelectric system. We recommend experimentally evaluating the feasibility of these alternatives. Yield of fisheries can be enhanced with more intensive management of harvest for impounded white sturgeon populations. Yield can be optimized by management strategies tailored to the unique attributes of each population, and by increased monitoring and regulation of fisheries to maintain optimum exploitation rates. Production might also be enhanced by augmenting river discharge during May and June during low flow years to improve spawning and recruitment. Transplants of juveniles from large populations in Bonneville Reservoir and downstream from Bonneville Dam should be evaluated for their potential to enhance recruitment-limited populations in The Dalles and John Day reservoirs.

We also recommend examining and developing several other promising strategies for protecting, enhancing, or mitigating for white sturgeon. Levels of contaminants in sturgeon tissue and associated risks to fish health should be evaluated to identify constraints on population productivity. Habitat requirements of subadult and adult life stages and amount of suitable habitat should be estimated to determine constraints on enhancement. Hatchery technology should be further refined and evaluated for enhancement of threatened populations of white sturgeon.

Finally, we suggest evaluating the need and identifying potential measures for protecting and enhancing populations and mitigating for the effects of the hydropower system on white sturgeon in the Columbia and Snake rivers upstream from McNary Dam where information is lacking.

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PREFACE

This is the final report for research on white sturgeon *Acipenser transmontanus* funded by the Bonneville Power Administration (BPA) from 1986-92 and conducted by the National Marine Fisheries Service (NMFS), Oregon Department of Fish and Wildlife (ODFW), U.S. Fish and Wildlife Service (USFWS), and Washington Department of Fisheries (WDF). Findings are presented as a series of papers, each detailing objectives, methods, results, and conclusions for a portion of this research. Volume I of this report includes papers which directly address objectives of the research program. Volume II includes supplemental papers which provide background information needed to support results of the primary investigations addressed in Volume I. Volume I also includes an introductory section which summarizes important results, conclusions, and recommendations.

Construction and operation of the hydropower system have affected the productivity of white sturgeon populations restricted to a series of reservoirs and river segments. We define productivity as the capacity of a population to elaborate biomass and equate production with the capacity to provide yield. Several impounded populations can sustain little or no harvest and others risk extinction. Dams have restricted movements of two principal food sources, eulachon *Thaleichthys pacificus* and lamprey *Lampetra* spp. Impoundment and dam operation have also altered spawning and rearing habitat. Finally, reservoir habitat has favored new communities of potential prey, predators, and competitors.

This study addresses measure 903(e)(l) of the Northwest Power Planning Council's 1987 Fish and Wildlife Program that calls for "research to determine the impact of development and operation of the hydropower system on sturgeon in the Columbia River Basin." Study objectives correspond to those of the "White Sturgeon Research Program Implementation Plan" developed by BPA and approved by the Northwest Power Planning Council in 1985. Work was conducted on the Columbia River from McNary Dam to the estuary.

Research objectives included:

1. Describe the reproduction and early life history of white sturgeon.

2. Describe the life history and population dynamics of subadult and adult white sturgeon.

3. Define habitat requirements and quantify habitat availability for white sturgeon.

4. Evaluate the need and identify potential methods for protecting, mitigating, and enhancing populations of white sturgeon.

To ascertain effects of the hydropower system on white sturgeon, we compared populations and habitat in the three lowermost reservoirs between Bonneville and McNary dams, with the population and habitat in the unimpounded reach between Bonneville Dam and the estuary. The unimpounded population has unrestricted access to the ocean, exhibits seasonal migrations, spawns successfully each year, includes all life history stages, and sustains productive fisheries. Dam construction likely had little effect on population characteristics and habitat use in the lower Columbia River.

Tasks were apportioned among cooperating agencies as follows:

NMFS - Describe reproduction and early life history and define habitat requirements for spawning and rearing downstream from Bonneville Dam. Quantify habitat from Bonneville Dam to the estuary.

ODFW - Describe life history and population dynamics of subadults and adults between Bonneville and McNary dams. Evaluate the need and identify potential methods for protecting, mitigating, and enhancing populations between Bonneville and McNary dams.

USFWS - Describe reproduction and early life history and define habitat requirements for spawning and rearing between Bonneville and McNary dams. Quantify habitat available from McNary to Bonneville dams.

WDF - Describe life history and population dynamics downstream from Bonneville Dam. Describe reproduction and early life history downstream from Bonneville Dam. Describe white sturgeon fisheries between Bonneville and McNary dams.

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CONCLUSIONS

A synthesis of research results presented in detail in appending papers (referenced with corresponding volume and letter) yields the following conclusions:

1. Dams limit movements of white sturgeon and have functionally isolated populations in mainstem Columbia River reservoirs. Individual white sturgeon regularly traveled long distances in the unimpounded river downstream from Bonneville Dam (1.D). Fish ranged into the ocean offshore of Oregon and Washington and into estuaries and rivers (1.D). Extensive seasonal movements between the Columbia River estuary and the

gorge downstream from Bonneville Dam were observed (I.D). Movements of white sturgeon in mainstem impoundments were restricted by dams which bound each reservoir (I.E). Tagged fish were seldom recovered in a reservoir other than where released (I.E). Existing fish passage facilities at dams are not extensively used by white sturgeon (I.F). Observed levels of movement among reservoirs may be sufficient to maintain genetic similarity of impounded populations (I.E). However, the productivity of each impounded population depends on resources available in that reservoir (I.E, I.H).

2. <u>The status and dynamics of each impounded or unimpounded population of white sturgeon are unique.</u> Densities ranged from 0.3 fish/hectare in John Day Reservoir to 14.6 fish/hectare in the unimpounded river (I.G, 1.H). Substantial variation was observed in annual recruitment, size distribution, growth rate, condition factor, and size at female maturation (I.G, I.H). The quantity and quality of the habitat suitable for white sturgeon varied for each population (I.J).

3. <u>Productivity of white sturgeon populations is less in reservoirs than in the unimoounded area downstream from Bonneville Dam.</u> Estimates of sustainable annual yield in reservoir populations ranged from 0.09 kg/hectare in John Day Reservoir to 1.27 kg/hectare in Bonneville Reservoir (I.H). Sustainable annual yield was estimated at 16.3 kg/hectare for the unimpounded river (I.G). Downstream from Bonneville Dam, white sturgeon can range widely among scattered and diverse habitats to take advantage of seasonally optimum conditions (I.G). Fish also have access to estuary and ocean food resources (I.G). The productivity of impounded populations is reduced by dam construction which restricts each population to river segments that do not include conditions optimal for all life cycle stages (I.H).

4. <u>Recruitment and subsequent oopulation size are limited by the effects of river discharge on spawning habitat which is restricted to high-velocity areas immediately downstream from each dam.</u> Much of the difference in productivity among white sturgeon populations was related to differences in the number of recruits (I.H). Large numbers of potential spawners were present in each impounded population (I.G, I.H) but each population did not have access to favorable spawning conditions during each year (I.C, I.J). Optimum spawning habitat is characterized by mean water column velocities exceeding 1 m/s and a substrate of cobble or boulder (I.A, I.B, I.J). Suitable conditions were once provided by rapids and falls throughout the lower Columbia River (I.J) but impoundment has restricted suitable habitat to the tailrace areas of each dam only if river discharge is high enough to produce suitable water velocities (I.A, I.B). The quantity of habitat suitable for spawning in impoundments is reduced when spring river discharge is low, and varies among dam tailraces at any given discharge (I.C, I.J).

5. <u>Reservoirs provide large areas of suitable habitat for juvenile and adult white sturgeon. but compensatory population responses mav reduce productivity if carrying capacity is exceeded.</u> Survival, growth rate, and condition factor of some size classes of white sturgeon in impoundments often approach or exceed levels seen in the unimpounded population (I.C, I.G, 1.H). Impoundment actually appears to have

increased the amount of suitable habitat (I.J) and growth rate (II .L) for juvenile white sturgeon, but low densities in The Dalles and John Day reservoirs suggest the available habitat is underseeded (I.H). Negative correlations of density with growth rate, condition factor, and size at female maturation in Bonneville Reservoir suggest compensation occurs when carrying capacity is approached (I.H).

6. Fisheries for white sturgeon have recently collapsed in The Dalles and John Dav impoundments and population collapse is likely if high exoloitation continues. Exploitation rates regularly exceeded optimums of 5-15% predicted by simulations based on observed characteristics of impounded populations (I.H). Recent expansion of fisheries in reservoirs reduced abundance and catch rates of white sturgeon, and was reflected in skewed shapes of catch curves (I.H). Substantial populations of large, mature fish remain in each reservoir, but exploitation rates observed in some years exceed rates at which any fish would survive to reproduce (I.H).

RECOMMENDATIONS

A synthesis of research results presented in detail in appending papers (referenced with corresponding volume and letter) yields the following recommendations for experimentally evaluating measures for protecting or enhancing white sturgeon, developing promising alternative strategies, or evaluating other populations in the Columbia and Snake rivers:

1. Intensify management of fisheries for impounded white sturgeon populations. Tailor manaqement strategies to the unique attributes of each population to optimize production and help offset the effects of hydroelectric system operation on yield. Closely monitor and regulate fisheries to maintain exploitation at optimum rates. Fisheries for white sturgeon in The Dalles and John Day reservoirs have collapsed in the last ten years because of overexploitation (I.H). These impounded populations cannot sustain exploitation rates comparable to those that can be sustained by the more productive population downstream from Bonneville Dam (I.G, I.H). Yield can be optimized in each reservoir with specific regulatory actions tailored to the unique characteristics of each population and river reach (I.H).

2. Experimentally evaluate whether augmented river discharqe in May and June improves spawning and recruitment, and enhances depressed white sturqeon populations in The Dalles and John Day reservoirs. Poor recruitment limits the size and subsequent productivity of white sturgeon populations in The Dalles and John Day reservoirs (I.H). Reproductive success has been positively correlated with river discharge which affects the amount of habitat suitable for spawning (I.B, I.C, I.J). Large numbers of mature spawners are present in each reservoir, habitat suitable for rearing of juveniles is abundant, and growth of juveniles is good (I.C, 1.3, II.L). Increased river discharge during spring spawning periods could improve spawning success and fully seed the available rearing habitat. Operations of projects within guidelines

that optimize physical conditions (water velocity, temperature, etc.) during periods of spawning and rearing may increase production.

3. Evaluate the feasibility of enhancing depleted populations in The Dalles and John Day reservoirs by transplanting juvenile white sturgeon from populations in Bonneville Reservoir and downstream from Bonneville Dam. A series of recent year-class failures in The Dalles and John Day reservoirs has depressed populations and reduced productivity of fisheries (I.H). Even if increased river discharge provided an immediate solution to spawning limitations, the late age of recruitment would result in an 8-15 year lag time until fish were recruited to fisheries (I.H). This delay could be reduced by transplanting juvenile white sturgeon from more productive populations. Relatively poor growth of juveniles downstream from The Dalles Dam suggests removal of some might be compensated by improved growth of the remainder, resulting in no net loss in production of the source population. This alternative would evaluate the potential for direct supplementation without incurring the expense and genetic or disease risks of a hatchery (I.H).

4. Investigate levels of contaminants in sturgeon tissue. assess risks to fish health, and evaluate constraints on population productivity. Changes in flow and sedimentation patterns related to development and operation of the hydropower system may have altered patterns of contaminant cycling through the system. Because of their longevity and benthic feeding habits, white sturgeon are particularly susceptible to bioaccumulation which could impair survival, growth, or reproduction. Dead eggs and deformed juveniles were observed in The Dalles Reservoir, but the correlation with contaminants is unknown (II.S). Identifying potentially harmful contaminants and determining their levels in white sturgeon may help define actions to protect and enhance populations.

5. Identify habitat requirements of subadult and adult white sturgeon guantify amounts of suitable habitat, and evaluate constraints on enhancement. Production of impounded white sturgeon populations will ultimately be constrained by the availability of suitable habitat. Habitat use and availability have been determined for juveniles but not for larger fish (I.J). Reduced population productivity is a likely response of populations that exceed the productive capacity of the habitat. For instance, higher density of juvenile fish in Bonneville Reservoir is accompanied by reduced growth rate, reduced condition factor, and delayed maturity (I.H). Assessing the quality and quantity of habitats used by subadult and adult white sturgeon will help identify appropriate enhancement and habitat protection measures.

6. Hatchery technology should be further refined and evaluated for enhancement of threatened populations of white sturgeon. Hatchery technology has recently been adapted for white sturgeon and might be used to supplement recruitment where natural reproduction is poor and alternatives for increasing natural reproduction are limited (I-H). However, conditions optimizing growth, feed utilization, health, and survival of juvenile white sturgeon in rearing facilities are not clearly defined. Other research now focuses on broodstock development and nutrition. Work to define optimum rearing densities, lighting

conditions, and water recycling/reclamation systems will facilitate use of aquaculture for enhancing sturgeon. Evaluations of cost-effectiveness and genetic and disease risks are a prerequisite for introductions of hatchery-reared fish into a wild population (I.H).

7. Investigate the need and ootential measures for protecting and enhancing populations and mitigating effects of the hydropower system in the Columbia and Snake rivers upstream from McNary Dam, where information is lacking. This research concluded that impoundment reduced the productivity of white sturgeon populations and that population status varied among impoundments. White sturgeon occur in sections of the Columbia and Snake rivers in addition to those examined by this study, but information needed to estimate the effects of the hydropower system is limited upstream from McNary Dam.

REPORT SUMMARY

Reproduction and Early Life History

A. Spawning Characteristics and Early Life History of White Sturgeon *Acipenser transmontanus* in the Lower Columbia River *(McCabe and Tracy)*

1. Spawning downstream from Bonneville Dam occurred in all 5 years of the study (1987-91). The duration of the spawning season was estimated for 1988 through 1991 to range from 38 to 47 days.

2. Newly-spawned eggs were collected near cobble and boulder substrates at temperatures of 10 to 18°C, depths of 3 to 23 m, mean water column velocities of 1.0 to 2.8 m/s, bottom velocities of 0.6 to 2.4 m/s, and turbidities of 2.2 to 11.5 NTU.

3. Larvae dispersed as far as 175 km downstream to freshwater portions of the upper estuary.

4. Young-of-the-year were most abundant in depths greater than 12 m and growth was rapid, with individuals reaching a minimum total length of 176 mm and a minimum weight of 30 g by the end of September.

B. Location and Timing of White Sturgeon Spawning in Three Columbia River Impoundments *(Anders and Beckman)*

1. Spawning between Bonneville and McNary dams occurred only in tailrace areas in the furthest upstream 3 km of each pool, where the water velocity was greatest.

2. Spawning success was positively related to river discharge. The number of white sturgeon eggs collected was ten to one hundred times greater in average water years (1990, 1991) than in low water years (1987, 1988).

3. Spawning occurred between 12 and 20°C. Optimal temperatures for spawning were 13 to 14°C.

4. Spawning usually began earliest in the season and lasted longest in The Dalles Dam tailrace, and started latest in the season and was shortest in McNary Dam tailrace.

5. The mean lengths of spawning periods were 44, 22, and 18 days in Bonneville, The Dalles, and John Day reservoirs.

C. Factors Affecting Spawning and Recruitment of White Sturgeon in the Columbia River Downstream from McNary Dam *(Parsley et al.)*

1. The number of eggs spawned and subsequent mortality among life stages determines population size for each year class. The factors influencing the number of eggs spawned and subsequent mortality vary among areas that support white sturgeon; white sturgeon populations can be enhanced by addressing factors limiting each life stage.

Life History and Population Dynamics

D. Migration and Distribution of White Sturgeon in the Columbia River Downstream From Bonneville Dam and in Adjacent Marine Areas *(DeVore* and Grimes)

1. Seasonal patterns of white sturgeon migration and distribution in the lower Columbia were described based on release of 40,221 marked fish and recapture of 5,049 from 1965-1991.

2. Fish generally migrated upstream in the fall, were quiescent during winter, moved downstream in spring (except for spawners), and congregated in the estuary in the summer.

3. Distribution was related to the seasonal abundance of important forage species: eulachon *(Thaleichthys pacificus)*, northern anchovy *(Engraulis mordax)*, and salmonids *(Oncorhynchus spp.)*.

4. A small proportion (4%) of the white sturgeon tagged in the lower Columbia River were later recaptured in rivers, estuaries, and marine areas between the Umpqua River in southern Oregon and Heron Island in Puget Sound, Washington.

E. Distribution and Movements of White Sturgeon in Three Lower Columbia River Reservoirs *(North et al.)*

1. Large juveniles and adults were most common in Bonneville Reservoir and least common in John Day Reservoir.

2. Fish were found at depths from 10 to 30 m throughout each reservoir. Density generally decreased as distance from the upstream dam increased.

3. Individual fish traveled widely within each reservoir but rarely passed a dam.

F. Fishway Use by White Sturgeon to Bypass Mainstem Columbia River Dams *(Warren and Beckman)*

1. Fish locks at Bonneville Dam were used periodically from 1938-56 to pass white sturgeon above the dam, with a peak annual passage of 1,526 fish in 1950.

2. Upstream passage of white sturgeon through fishways is limited: annual counts averaged 36, 530, and 11 fish at Bonneville, The Dalles, and John Day dams from 1986 to 1991. Number of white sturgeon using fishways was greatest from July through September.

G. Dynamics and Potential Production of White Sturgeon in the Columbia River Downstream from Bonneville Dam *(DeVore et al.)*

1. Abundance and density of white sturgeon in the lower Columbia River was greater than that reported for any population.

2. High population productivity results from good growth, high condition factor, and a low median age of maturation for females.

3. Abundant food, access to the ocean, and favorable hydrologic conditions during spawning contribute to the observed high population productivity.

4. Natural mortality averaged 15% and exploitation in recreational and commercial fisheries averaged 28% from 1985-91.

5. Average annual abundance of white sturgeon $\geq$ 54 cm fork length during the study years was 893,800 fish. Abundance of exploited age classes decreased during the study, which is consistent with increasing exploitation rates.

6. Simulations indicated that maximum sustained yield (MSY) of 1.4 kg per recruit occurred at a 32% exploitation rate assuming a constant number of recruits. Simulations that assume significant stock-dependent recruitment (Beaverton-Holt: A=0.5) predicted an MSY of 0.3 kg per recruit at a 4% exploitation rate.

H. Dynamics and Potential Production of White Sturgeon Populations in Three Columbia River Reservoirs *(Beamesderfer and Rien)*

1. Significant differences were observed among reservoirs in abundance, biomass, size composition, sex ratio, size at female maturity, growth rate, condition factor, and rate of exploitation.

2. Growth rate, condition factor, and size at female maturity were inversely correlated with recruitment rate and resulting density.

3. Sustainable yield varied 10-fold among reservoirs as a result of differences in population dynamics.

4. Yield per recruit was greatest at annual exploitation rates between 5 and 15% and potential egg production per recruit declined exponentially with increasing exploitation.

5. White sturgeon fisheries in reservoirs have collapsed with recent overexploitation. Reservoir populations cannot sustain harvest levels comparable to the unimpounded population.

Habitat Requirements and Availability

I. Habitat Use by Spawning and Rearing White Sturgeon in the Columbia River Downstream from McNarv Dam (Parsley *et al.)*

1. Habitat for spawning, egg incubation, yolk-sac larvae, young-of-the-year, and juvenile white sturgeon was determined.

2. Spawning occurred in high water velocities over coarse substrates.

3. Juveniles inhabited deep, low-velocity areas with fine substrates.

J. An Evaluation of Spawning and Rearinq Habitat for White Sturqeon in the Lower Columbia River (Parsley and Beckman)

1. Hydroelectric development has reduced spawning habitat in impoundments by reducing water velocity and by inundating several rapids and falls that provided suitable spawning conditions.

2. The lower river provides suitable spawning habitat at very low river discharges, whereas greater discharges are needed to provide even marginal spawning habitat in the impoundments.

3. Impoundment has increased rearing habitat.

REPORTS

Reproduction and Early Life History

REPORT A

Spawning Characteristics and Early life History of White Sturgeon *Acipenser transmontanus* in the Lower Columbia River

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ABSTRACT

Although white sturgeon Acipenser transmontanus experiences intense fishing pressure in the Columbia River (Oregon and Washington) and other rivers within its range, little is known about the spawning characteristics and early life history of this long-lived species. Spawning characteristics and early life history of white sturgeon were studied in the lower Columbia River downstream from Bonneville Dam from 1988 through 1991. Based on white sturgeon egg collections, we determined that successful spawning occurred in all four years; the estimated number of spawning days each year ranged from 38 to 47 days. The spawning period extended from late April or early May through late June or early July of each year. Spawning occurred primarily in the fast-flowing section of the river downstream from Bonneville Dam at water temperatures ranging from 10 to 19°C Freshly fertilized white sturgeon eggs were collected at turbidities ranging from 2.2 to 11.5 NTU, near-bottom velocities ranging from 0.6 to 2.4 m/s, mean water column velocities ranging from 1.0 to 2.8 m/s, and depths ranging from 3 to 23 m. Bottom substrate in the spawning area was primarily cobble and boulder. With the exception of 1989, there were no significant regression relationships between white sturgeon egg catches at an index site and water velocity or Bonneville Dam discharge during the spawning period. Apparently, adequate water velocities for white sturgeon spawning were generally present throughout the spring and early summer. White sturgeon larvae were dispersed over a wide area (in some instances over 175 km) after hatching; larvae were collected as far downstream as the upper end of the Columbia River estuary, which is a freshwater environment. Young-of-the-year (YOY) white sturgeon were first captured in late June, less than 2 months after spawning was estimated to have begun. Growth was rapid during the first summer, with YOY white sturgeon reaching a minimum mean total length of 176 mm and a minimum mean weight of 30 g by the end of September. YOY white sturgeon were more abundant in deeper water (mean minimum depth $\geq$ 12.5 m) of the lower Columbia River. This research indicated that a large area of the lower Columbia River is used by white sturgeon at different life history stages.

White sturgeon _Acipenser transmontanus_ is the largest of all sturgeon species endemic to North America and is found along the west coast of North America from the Aleutian Islands, Alaska, to Monterey, California (Scott and Crossman 1973). Although this species is considered to be anadromous (Scott and Crossman 1973), some populations in the Columbia River Basin are landlocked because of dam construction (Cochnauer et al. 1985, Beamesderfer et al. 1990).

Historically, white sturgeon was abundant in the Columbia River (Oregon and Washington) and in the late 1800s supported an intense commercial fishery. Commercial catches peaked in 1892, when more than 2.4 million kg were landed (Craig and Hacker 1940). After the record catch in 1892, catches declined, and by 1899 the annual catch was less than 33,250 kg. Annual catches during the early 1900s were less than 104,930 kg (Craig and Hacker 1940).

White sturgeon populations in the Columbia River, particularly the one downstream from Bonneville Dam (the lowermost dam), recovered sufficiently from the overfishing of the late 1800s to the point where they now support important recreational and commercial fisheries. The population of white sturgeon in the lower Columbia River, which extends from the mouth to Bonneville Dam, is one of the largest in the world. Estimated catches of white sturgeon in recreational and commercial fisheries in the lower Columbia River in 1990 were 17,300 and 5,200 fish, respectively (Oregon Department of Fish and Wildlife and Washington Department of Fisheries 1991). Presently, white sturgeon is the most popular recreational fish in the Columbia River from the mouth to McNary Dam (River Kilometer [RKm] 470) (Oregon Department of Fish and Wildlife and Washington Department of Fisheries 1991).

Although white sturgeon experiences intense fishing pressure in the Columbia River and other rivers within its range, little is known about the spawning characteristics and early life history of this long-lived species. Stevens and Miller (1970) described the distribution of white and/or green sturgeon _A. medirostris_ larvae in California's Sacramento-San Joaquin River system, and Kohlhorst (1976) described sturgeon (most were probably white sturgeon) spawning in the Sacramento River based on larval collections.

From 1988 through 1991, we studied spawning characteristics and early life history of white sturgeon in the lower Columbia River. Specific goals of the study were to define where and when spawning occurred and the environmental conditions at the time of spawning. Additional goals were to determine larval distribution and habitat use by young-of-the-year (YOY) white sturgeon. Results from our study will be useful to resource managers responsible for white sturgeon populations in the lower Columbia River and in other areas.

METHODS

Egg and Larval Sampling

From 1988 through 1991, sampling was conducted for white sturgeon eggs and larvae in the Columbia River downstream from Bonneville Dam (RKm

234). The sampling period varied among years; however, in all years, sampling was conducted from at least April through early July. Generally, sampling was conducted weekly during the spawning period. A D-shaped plankton net was used to collect white sturgeon eggs and larvae. This net was 0.8 m wide at the bottom of the mouth opening, 0.5 m high, and was constructed of 7.9-mesh/cm nylon marquisette netting. Depending upon the water velocity, two to six lead weights (4.5 or 9.1 kg each) were attached to the net frame to hold the net on the river bottom. A digital flow meter (General Oceanics Model 2030[1]) was suspended in the mouth of the net to estimate the water volume sampled. Typically, two plankton nets were fished simultaneously for about 30 min from an anchored 12.2-m research vessel. When water velocities were extremely high, only one plankton net was fished, often for one hour. Artificial substrates constructed of latex-coated animal hair were also used to collect white sturgeon eggs (McCabe and Beckman 1990).

In 1990 and 1991, a 3.0-m beam trawl was used in late June, July, and August to collect white sturgeon larvae and YOY. The overall width of the trawl was about 3.0 m and the height was 0.5 m; the estimated fishing width of the net was 2.7 m. A 1.59-n knotless nylon liner was inserted in the body of the net. The beam trawl was towed slowly along the bottom for time periods ranging from 2 to 20 min.

White sturgeon eggs and larvae were initially preserved in an approximately 4% buffered formaldehyde solution. Later, they were transferred to a 20% methanol solution.

White sturgeon egg or larval sampling was conducted at various sites in the lower Columbia River from RKm 29 to 234 (Table 1, Figure 1). We selected a site at RKm 230 for detailed monitoring of white sturgeon spawning in the lower Columbia River. The most frequent egg sampling was done at this site, henceforth referred to as the index site.

In 1988, a 12-h study using a plankton net was done at this index site to determine if catches of white sturgeon and larvae changed during different light conditions. The 12-h study began at 1843 hours on 25 May and ended at 0623 hours on 26 May. One plankton net was normally fished for 1 h during each sampling effort.

Young-of-the-Year Sampling

A 7.9-m (headrope length) semiballoon shrimp trawl was used from 1988 through 1991 to collect juvenile white sturgeon, including YOY. Mesh size in the trawl was 38 mn (stretched) in the body; a 10-mm mesh liner was inserted in the cod end. In 1990 and 1991, a 3.0-m beam trawl was also used to collect YOY white sturgeon (see Egg and Larval Sampling). Shrimp trawl efforts were normally 5 min in duration in an upstream direction. The trawling effort began when the trawl and the proper amount of cable were deployed, and the effort ended 5 min later. The beam trawl was fished for 2 to 20 min depending upon water velocity, bathymetry, and

1 Reference to trade names does not imply endorsement by NMFS or NOAA.

Table 1. Numbers of sampling efforts for white sturgeon eggs, larvae, and young-of-the-year in the lower Columbia River, 1988-1991. When two plankton nets were fished simultaneously, the data were combined and considered as one sampling effort. Location is shown in River Kilometers (RKm).

Year Location	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Total
				Plankton net					
1988									
RKm 172-228	0	0	8	17	1	0	0	0	26
RKm 229-230	1	2	16	5	2	1	0	0	27
RKm 231-233	1	3	6	1	0	0	0	0	11
1989									
RKm 153-171	0	0	2	0	0	0	0	0	2
RKm 172-228	0	0	18	16	5	0	0	0	39
RKm 229-230	1	2	4	5	3	1	0	0	16
RKm 231-233	0	0	1	0	0	0	0	0	1
1990									
RKm 112-171	0	0	0	1	0	0	0	0	1
RKm 172-228	0	0	29	10	3	0	0	0	42
RKm 229-230	0	5	5	4	3	0	0	0	17
RKm 231-233	0	1	2	2	0	0	0	0	5
1991									
RKm 193-228	0	1	13	8	5	0	0	0	27
RKm 229-230	0	4	4	7	6	0	0	0	21
RKm 231-233	0	0	0	0	0	0	0	0	0
				Artificial substrate					
1988									
RKm 197-228	0	0	3	1	0	0	0	0	4
RKm 229-230	0	0	5	1	2	0	0	0	8
RKm 231-234	0	0	5	6	0	0	0	0	11
1989									
RKm 220-228	0	0	2	3	0	0	0	0	5
RKm 229-230	0	1	0	0	0	0	0	0	1
RKm 231-234	0	0	12	6	0	0	0	0	18
1990									
RKm 229-230	0	3	5	0	0	0	0	0	8
RKm 231-234	0	0	9	4	2	0	0	0	15
1991									
RKm 229-230	0	2	3	3	3	0	0	0	11
RKm 231-234	0	0	6	4	0	0	0	0	10

Table 1. Continued.

Year Location	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Total
				Beam trawl					
1990									
RKm 29-120	0	0	0		11	5	0	0	31
RKm 121-212	0	0	0	15	12	2	0	0	16
1991									
RKm 44-120	0	0	1	9	19	4	0	0	33
RKm 121-218	0	0	1	12	9	4	0	0	26
				Shrimp trawl					
1988									
RKm 46-120	4	3	3	6	6	3	4	3	32
RKm 121-211	19	17	10	31	40	56	6	39	218
1989									
RKm 38-120	3	3	3	6	18	11	7	30[a]	81
RKm 121-218	17	24	34	40	50	67	25	49	306
1990									
RKm 45-120	0	42	29	24	27	37	13	32	204
RKm 121-212	0	18	21	0	19	5	4	23	90
1991									
RKm 45-120	0	33	29	16	15	30	31	0	154
RKm 121-212	0	24	2	20	21	1	25	0	93

[a] Includes eight sampling efforts conducted in November.

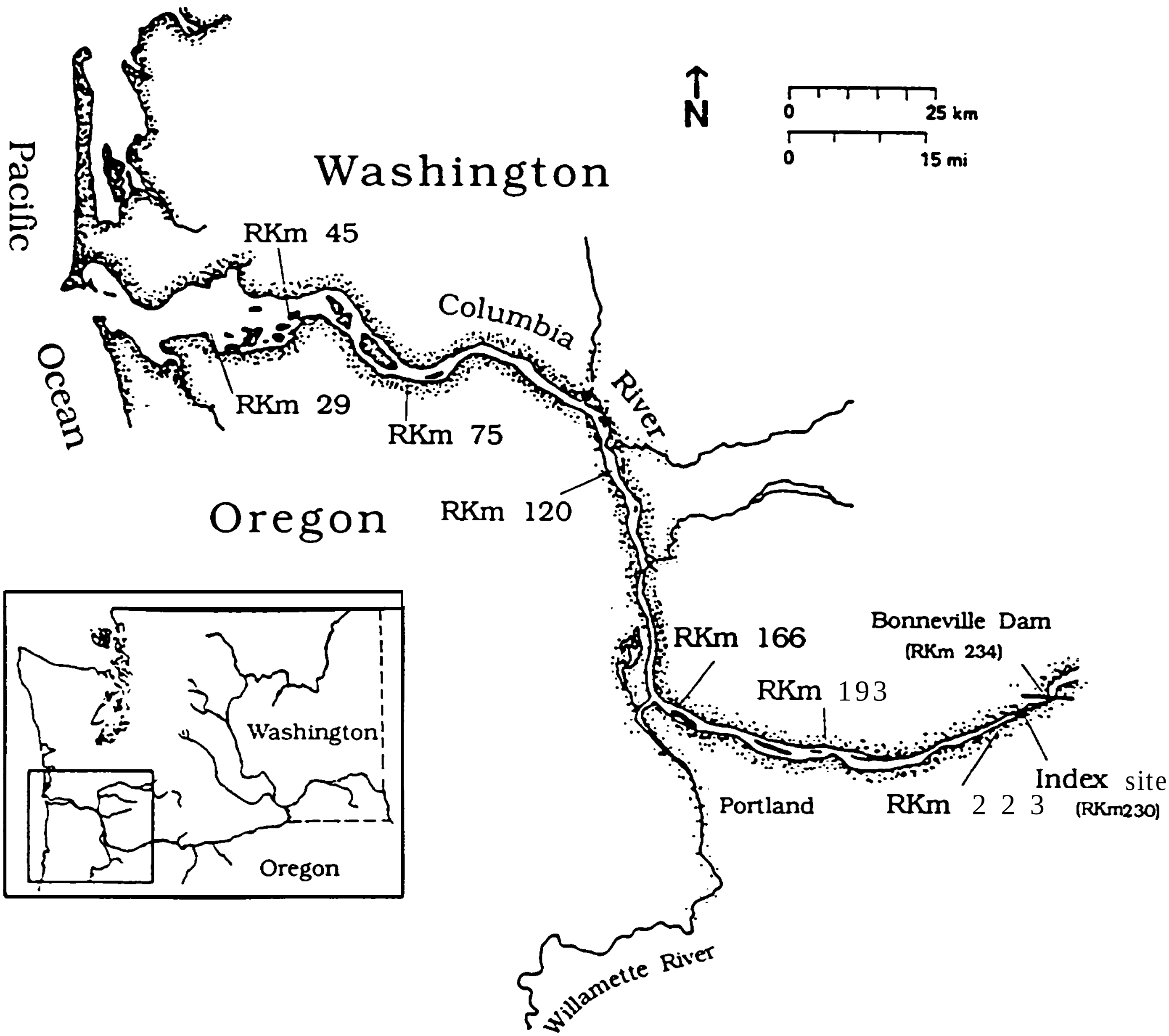

Figure 1. Location of white sturgeon study area in the lower Columbia River, 1988-1991.

bottom substrate. Using a radar range-finder, we estimated the distance fished during each sampling effort.

Trawling was conducted from late March or early April through September or October of each year. In 1989, a limited amount of sampling was conducted in early November. Trawling was done at selected sampling stations extending from RKm 29 to 218 (Table 1). Sampling stations were selected to determine the range of habitat used by juvenile white sturgeon; no attempt was made to randomly select the sites. Trawling effort and the geographic range of sampling varied among years (Table 1). In 1988 and 1989, more trawling effort was concentrated in the river upstream from RKm 120. However, in 1990 and 1991, much more trawling was done in the river between RKm 45 and 120 than in previous years. White sturgeon captured in the bottom trawls were measured (total length) and weighed (g).

In 1990, a 20-h study was conducted during part of the day and all of the night at RKm 75 to determine if catches of juvenile white sturgeon, particularly YOY, increased during hours of darkness. On 31 July and 1 August, 14 trawling efforts (7.9-m shrimp trawl) were done from 1155 through 0800 hours.

Physical Conditions

Selected physical parameters were measured in conjunction with biological sampling: minimum and maximum bottom depth (m); bottom water temperature ("C); bottom water turbidity (NTU); and water velocities at 0.2 of the total depth, 0.8 of the total depth, and about 0.6 m above the bottom. By averaging the water velocities measured at 0.2 and 0.8 of the total depth, we calculated a mean water column velocity (Buchanan and Somers 1969). Water velocities were measured only during egg and larval sampling. Depth was measured with electronic depth sounders, and velocity with a Gurley current meter attached to a 45.4-kg lead fish. Turbidity was determined in the laboratory using a Hach Model 2100A Turbidimeter.

Data Analyses

The developmental stages of white sturgeon eggs were determined based on descriptions developed by Beer (1981). Timing of egg deposition was estimated using developmental stages of eggs and temperature-egg developmental data from Wang et al. (1985); water temperature at the time of egg collection was used in making the estimates. A daily index of spawning activity was calculated based on back-calculated spawning dates.

Simple and multiple regressions were used to determine relationships between measured physical parameters (water temperature, turbidity, water velocity, and Bonneville Dam discharge) and abundance of freshly fertilized (stage 2) white sturgeon eggs collected in plankton nets at the index site (RKm 230). It was assumed that stage 2 eggs were approximately 3 h or less old (Beer 1981). Bonneville Dam discharge for these comparisons was determined by averaging hourly discharges at the time of sampling and during the 3 h prior to sampling. We assumed that white sturgeon egg abundance did not follow a normal distribution; consequently, we transformed egg abundance, which was expressed as number/1,000 m^3 of water, to log,, of (number + 1/1,000 m^3) prior to analysis. One was added to the catches because of some zero values (Sokal and Rohlf 1969). Data collected just prior to, during, and just after the spawning period were used for these comparisons.

Day and night catches of freshly fertilized white sturgeon eggs from the 12-h study (25-26 May 1988) at the index site (RKm 230) were compared using a two-sample t-test (Ryan et al. 1985). Day was defined as the period from 0.5 h before sunrise to 0.5 h after sunset. The data were standardized to number of eggs/1,000 m^3 of water and then transformed to log,, of (number of eggs + 1/1,000 m^3). White sturgeon larval catches were compared in a manner similar to freshly fertilized eggs, except it was not necessary to add one to the catches.

For data analysis, YOY white sturgeon were separated from older juvenile sturgeon using length frequencies. A YOY was defined as being less than 1 yr old and $\geq$ 25 mm total length.

Day and night catches of YOY white sturgeon from the 20-h study (31 July-1 August 1990) at RKm 75 were compared using a two-sample t-test. Prior to using the t-test, we calculated the area fished for each effort using the distance fished during a trawl effort and the estimated fishing width of the 7.9-m semiballoon shrimp trawl (5.3 m). Then the data were standardized to number of YOY/ha and transformed to log,, of (number of YOY + 1/ha); transformed values were used in the t-test.

RESULTS

Eggs

The number of white sturgeon eggs collected from 1988 through 1991 varied annually, ranging from 1,404 in 1988 to 2,785 in 1990 (Table 2); however, sampling effort was not equal each year. The percent of white sturgeon eggs collected in plankton nets (as opposed to artificial substrates) also varied annually, ranging from 37% in 1991 to 87% in 1989. Virtually all white sturgeon eggs were collected in a 11-km long section of the river extending from RKm 223 to 234. In both 1990 and 1991, four white sturgeon eggs were collected at RKm 193. In all years, 4% or less of white sturgeon eggs collected in plankton nets were fungus infected.

Based on the spawning index, which was derived from back calculations using the developmental stages of all eggs, we estimated that spawning occurred on 38 days in 1988 (beginning on 22 April and ending on 22 June), with 58% of the spawning days in May (Figure 2). In 1989, spawning occurred on an estimated 43 days (beginning on 22 April and ending on 2 July), with 53% of the spawning days in May. In 1990, spawning was estimated to have occurred on at least 47 days (beginning on 23 April and ending on 9 July), with 47% of the spawning days in May. It is likely that some spawning occurred after 9 July 1990 because post-hatch larvae were collected on 18 July. Considering the water temperature at this time, these post-hatch larvae probably developed from eggs spawned on about 14 July. Finally, for 1991, we estimated that spawning occurred on

Table 2. Numbers of white sturgeon eggs and larvae collected in the Columbia River downstream from Bonneville Dam, 1988-1991; plankton nets and artificial substrates were used to collect eggs, and plankton nets and a 3.0-m beam trawl (in 1990 and 1991) were used to collect larvae. Area refers to the geographic range (in River Kilometers [RKm]) over which eggs or larvae were collected. Fungus-infected eggs collected in plankton nets are shown in parentheses and are included in the numbers reported for the nets. A hyphen (-) indicates that no sampling was conducted.

Sampling period	Eggs			Larvae		
	Area (RKm)	Net	Substrate	Area (RKm)	Net	Trawl
			1988			
15-30 Apr	230-231	19	-		0	-
1-15 May	228-233	163 (1)	46	228-230	11	-
16-31 May	230-233	405 (10)	539	193-231	71	-
1-15 Jun	226-234	112 (5)	84	181-230	5	-
16-30 Jun	226-230	20 (1)	16	226	3	-
1-15 Jul		0	0		0	-
16-31 Jul		0	0		0	-
Total		719 (17)	685		90	-
			1989			
15-30 Apr	230	385	47		0	-
1-15 May	224-234	275 (1)	37	174-232	19	-
16-31 May	224-234	703 (6)	212	181-230	39	-
1-15 Jun	222-234	640 (23)	9	193-230	64	-
16-30 Jun	226-230	13 (3)	0	181-230	13	-
1-15 Jul	226	2 (1)	-		0	-
16-31 Jul		0	-		0	-
Total		2,018 (34)	305		135	
			1990			
15-30 Apr	230-231	386	258		0	-
1-15 May	223-234	904 (38)	153	223-232	34	-
16-31 May	193-234	187 (7)	275	181-230	34	-
1-15 Jun	224-234	210 (8)	260	112-230	33	-
16-30 Jun	224-230	109 (20)	0	45-230	41	12
1-15 Jul	226-234	8	35	67-226	1	25
16-31 Jul		0	0	127-230	9	1
Total		1,804 (73)	981		152	38

Table 2. Continued.

Sampling period	Eggs Area (RKm)	Net		Substrate	Larvae Area (RKm)	Net	Trawl
				1991			
15-30 Apr		0		0		0	-
1-15 May	224-234	129	(1)	589		0	-
16-31 May	193-234	303	(3)	265	193-230	28	0
1-15 Jun	226-234	46	(7)	205	193-230	17	-
16-30 Jun	224-234	227	(1)	164	45-230	45	33
1-15 Jul	193-230	30	(2)	50	98-230	37	18
16-31 Jul		0		0		0	0
Total		735	(14)	1,273		127	51

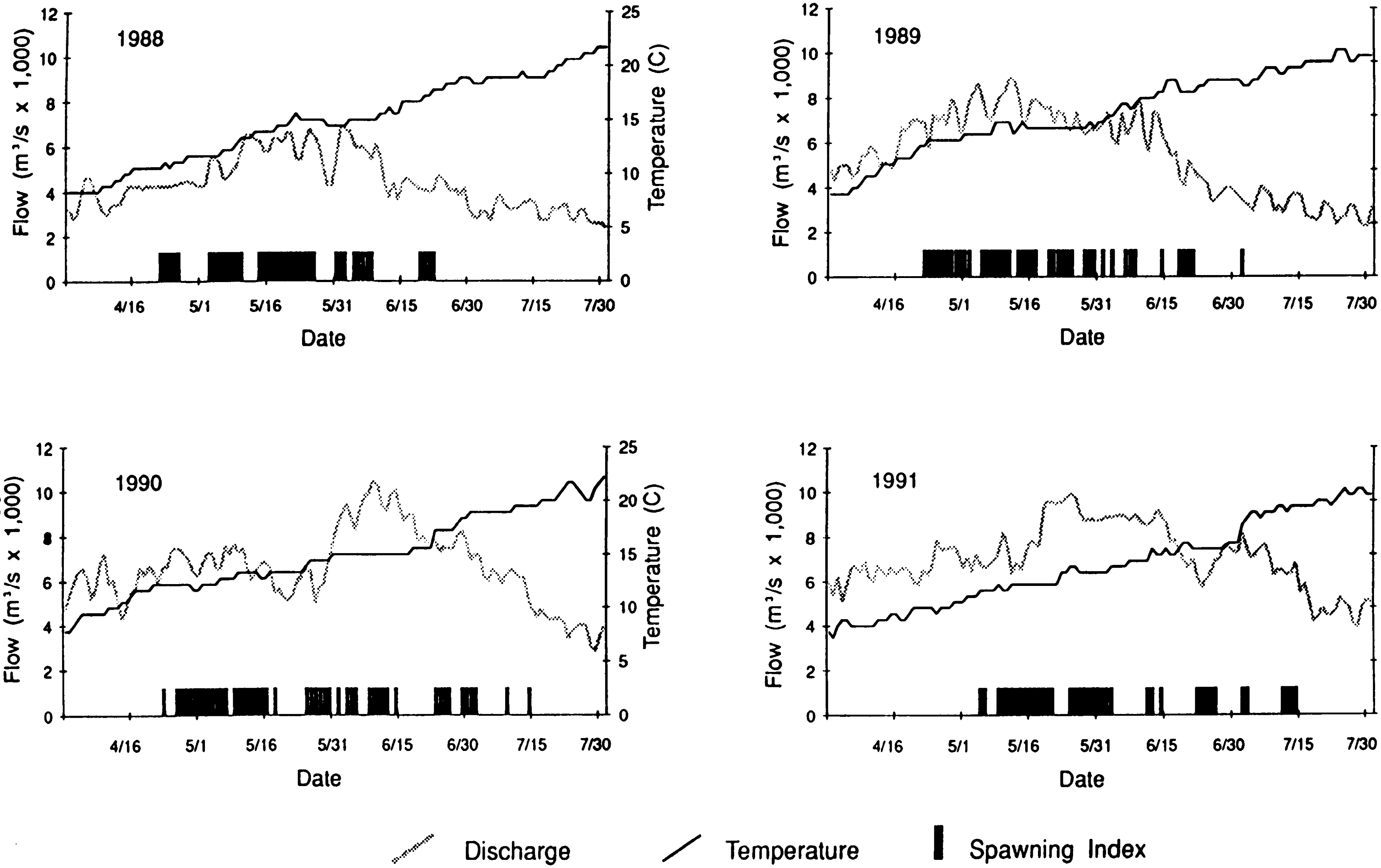

Figure 2. Water temperatures (°C) and Bonneville Dam discharges (mean hourly water discharges by day) from 1 April through 31 July (1988-1991); discharge is shown as $m^3/s \times 1,000$. Water temperatures were measured at Bonneville Dam. The spawning index shows the days on which we estimated that white sturgeon spawned.

39 days (beginning on 5 May and ending on 14 July), with 56% of the spawning days in May.

Water temperatures, measured at Bonneville Dam and at sampling sites during the spawning period, varied annually (Figure 2). Water temperatures at Bonneville Dam sometimes differed from those at egg collection sites. Combining data from 4 years, we observed that spawning occurred at water temperatures ranging from 10 to 19°C (Bonneville Dam or sampling site temperatures).

Bonneville Dam discharge (mean hourly discharge by day) also varied annually (Figure 2). The highest daily flows through Bonneville Dam occurred during spawning periods in 1990 and 1991. Combining data from all years, we found that spawning occurred at mean discharges ranging from 3,399 to 10,505 m^3/s; however, virtually all spawning occurred on days when mean discharge was greater than 4,000 m^3/s. Bonneville Dam discharges were less than 4,000 m^3/s for only 2 days during the 1988 spawning period and for only 6 days during the 1989 spawning period. The spawning index indicated that spawning occurred on one of these days in 1989. In 1990 and 1991, Bonneville Dam discharges were greater than 4,000 m^3/s throughout spawning periods.

During the 4-year study, freshly fertilized white sturgeon eggs were collected at temperatures ranging from 10 to 18°C turbidities ranging from 2.2 to 11.5 NTU, near-bottom velocities ranging from 0.6 to 2.4 m/s, mean water column velocities ranging from 1.0 to 2.8 m/s, and depths ranging from 3 to 23 m.

Spawning occurred primarily in the area near RKm 230 and upstream. Freshly fertilized white sturgeon eggs were collected from RKm 234, about 600 m downstream from the spillways at Bonneville Dam, to RKm 193. However, in each year, more than 70% of freshly fertilized eggs collected in plankton nets were taken at the index site (RKm 230) or upstream from the index site. In three of four years (1988-1990), 94% or more of the freshly fertilized eggs (plankton nets) were collected at the index site or upstream from the index site. Only small numbers of freshly fertilized eggs were collected at RKm 193--three in 1990 and one in 1991.

Substrate in the river section where freshly fertilized eggs were most abundant was primarily cobble and boulder. We are not sure of the composition of the substrate near RKm 193; however, there are small rocky islands in the area, and on occasion large amounts of sand were collected in the plankton net. In addition, there is a rocky reef several kilometers upstream from this sampling site.

At the index site, freshly fertilized white sturgeon eggs were collected over a range of environmental conditions from 1988 through 1991 (Table 3). Water temperatures ranged from 10 to 18°C, bottom water turbidities ranged from 2.2 to 11.5 NTU, near-bottom water velocities ranged from 1.0 to 2.1 m/s, and mean water column velocities ranged from 1.5 to 2.6 m/s. Estimated Bonneville Dam discharges at the index site during spawning ranged from 3,890 to 9,600 m^3/s. In all years, the highest catches occurred during late April or May.

Table 3. Uhite sturgeon egg (freshly fertilized) catches and accompanying physical measurements for the index site near RKm 230 in the lower Columbia River, 1988-1991. Water temperatures (on site), turbidities, and bottom velocities were measured just above the bottom; Bonneville Dam flow was the average of the hourly discharges at the time of sampling and during the 3 h prior to sampling.

Date	Temp. (°C)	Turb. (NTU)	Velocity (m/s) Bottom	Velocity (m/s) Mean column	Dam flow (m^3/s x 1,000)	No. eggs	Eggs/ 1,000 m^3
				1988			
25 Apr	10	4.5	1.0	1.5	3.89	3	0.9
5 May	11	6.4	1.4	1.8	5.14	24	10.3
10 May	13	6.0	1.0	1.6	5.95	80	28.4
18 May	13	6.0	1.2	1.6	6.24	4	1.1
23 May	14	5.4	1.2	2.1	5.59	10	3.4
2 Jun	14	6.0	1.4	2.3	6.51	18	5.4
8 Jun	14	3.5	1.4	2.0	5.43	19	6.5
16 Jun	16	3.5	1.1	1.8	4.50	0	0.0
20 Jun	16	3.2	1.1	1.5	4.17	9	3.6
29 Jun	17	3.1	1.0	1.6	3.90	0	0.0
				1989			
18 Apr	10	12.0	1.5	1.9	6.46	0	0.0
27 Apr	12	10.0	1.5	2.2	7.11	348	115.6
1 May	12	7.5	1.7	2.0	6.96	17	5.4
10 May	13	7.5	--	2.4	7.89	70	21.5
17 May	14	9.2	1.6	2.3	8.30	525	149.6
24 May	14	5.9	1.4	2.2	6.82	18	5.7
1 Jun	14	5.4	1.6	2.2	6.80	1	0.3
8 Jun	16	5.3	2.0	2.6	7.66	99	30.6
15 Jun	17	3.4	1.5	2.2	5.91	0	0.0
21 Jun	17	3.7	1.0	1.9	4.60	0	0.0
28 Jun	18	3.3	1.1	1.6	3.98	0	0.0
6 Jul	19	3.5	1.0	1.6	3.72	0	0.0
				1990			
23 Apr	11	3.0	1.1	1.5	6.61	0	0.0
30 Apr	11	3.5	1.1	2.2	7.20	225	70.07
7 May	12	3.9	1.7	2.6	7.57	32	7.8
14 May	12	3.7	1.8	2.3	7.03	292	87.8
22 May	13	3.0	1.1	1.7	4.69	0	0.0
29 May	14	3.0	1.4	2.3	5.90	39	13.5
5 Jun	15	3.4	1.7	2.5	8.32	19	5.2
11 Jun	15	6.5	1.5	2.4	9.07	23	6.8
18 Jun	15	5.6	2.1	2.7	9.01	0	0.0

Table 3. White sturgeon egg (freshly fertilized) catches and accompanying physical measurements for the index site near RKm 230 in the lower Columbia River, 1988-1991. Water temperatures (on site), turbidities, and bottom velocities were measured just above the bottom; Bonneville Dam flow was the average of the hourly discharges at the time of sampling and during the 3 h prior to sampling.

Date	Temp. (°C)	Turb. (NTU)	Velocity (m/s) Bottom	Velocity (m/s) Mean column	Dam flow ($m^3/s \times 1,000$)	No. eggs	Eggs/ 1,000 m^3
				1988			
25 Apr	10	4.5	1.0	1.5	3.89	3	0.9
5 May	11	6.4	1.4	1.8	5.14	24	10.3
10 May	13	6.0	1.0	1.6	5.95	80	28.4
18 May	13	6.0	1.2	1.6	6.24	4	1.1
23 May	14	5.4	1.2	2.1	5.59	10	3.4
2 Jun	14	6.0	1.4	2.3	6.51	18	5.4
8 Jun	14	3.5	1.4	2.0	5.43	19	6.5
16 Jun	16	3.5	1.1	1.8	4.50	0	0.0
20 Jun	16	3.2	1.1	1.5	4.17	9	3.6
29 Jun	17	3.1	1.0	1.6	3.90	0	0.0
				1989			
18 Apr	10	12.0	1.5	1.9	6.46	0	0.0
27 Apr	12	10.0	1.5	2.2	7.11	348	115.6
1 May	12	7.5	1.7	2.0	6.96	17	5.4
10 May	13	7.5	--	2.4	7.89	70	21.5
17 May	14	9.2	1.6	2.3	8.30	525	149.6
24 May	14	5.9	1.4	2.2	6.82	18	5.7
1 Jun	14	5.4	1.6	2.2	6.80	1	0.3
8 Jun	16	5.3	2.0	2.6	7.66	99	30.6
15 Jun	17	3.4	1.5	2.2	5.91	0	0.0
21 Jun	17	3.7	1.0	1.9	4.60	0	0.0
28 Jun	18	3.3	1.1	1.6	3.98	0	0.0
6 Jul	19	3.5	1.0	1.6	3.72	0	0.0
				1990			
23 Apr	11	3.0	1.1	1.5	6.61	0	0.0
30 Apr	11	3.5	1.1	2.2	7.20	225	70.07
7 May	12	3.9	1.7	2.6	7.57	32	7.8
14 May	12	3.7	1.8	2.3	7.03	292	87.8
22 May	13	3.0	1.1	1.7	4.69	0	0.0
29 May	14	3.0	1.4	2.3	5.90	39	13.5
5 Jun	15	3.4	1.7	2.5	8.32	19	5.2
11 Jun	15	6.5	1.5	2.4	9.07	23	6.8
18 Jun	15	5.6	2.1	2.7	9.01	0	0.0

Results of simple regressions between white sturgeon egg (freshly fertilized) abundance and five physical parameters (water temperature, turbidity, near-bottom velocity, mean water column velocity, and Bonneville Dam discharge) for the index site were not significant ($P > 0.05$), with the exceptions of mean water column velocity and discharge in 1989 and temperature in 1990 (Table 4). These analyses indicate that once spawning began near RKm 230, changes in discharges from Bonneville Dam and accompanying water velocity changes did not generally have a significant impact on spawning (as measured by egg collections). Apparently, adequate water velocities for white sturgeon spawning were generally present throughout the spring and early summer, at least near RKm 230. Results from multiple regressions between white sturgeon egg abundance and physical parameters were significant ($P < 0.05$) for the following combinations: 1) temperature and discharge in 1989; 2) temperature, turbidity, and discharge in 1989; and 3) temperature and mean water column velocity in 1990 (Table 4).

Results from the 12-h study at the index site are presented in Table 5. Catches of freshly fertilized white sturgeon eggs were not significantly different between night and day (two-sample t-test, $P > 0.05$). The plankton net was damaged during the effort that started at 1951 hours; data from this set were not used in the statistical analysis. Based on collections of freshly fertilized eggs during the 12-h study and daylight collections during the four years, it appears that adult white sturgeon spawn throughout the 24-h day.

Larvae

White sturgeon larvae were collected from RKm 45 to RKm 232 in the lower Columbia River from 1988 through 1991 (Table 2). River Kilometer 45 is located in the upper end of the Columbia River estuary (Figure 1); however, this section of the estuary is a freshwater environment. Assuming that most white sturgeon spawning and egg incubation occurred in the 11-km section (RKm 223-234) of the river downstream from Bonneville Dam, larvae collected at RKm 45 were transported over 175 km downstream after hatching.

White sturgeon larvae were collected from early May through late July, reflecting the protracted spawning period (Table 2). All white sturgeon larvae in 1988 and 1989 were collected in plankton nets, and in 1990 and 1991, 71% or more of the total catch occurred in plankton nets. In 1988 and 1989, white sturgeon larvae were not collected as far downstream as in 1990 and 1991. Undoubtedly, smaller areas of capture in 1988 and 1989 were due to lack of sampling with the 3.0-m beam trawl in these years. All white sturgeon larvae collected in the upper estuary in 1990 and 1991 were collected in the beam trawl. White sturgeon larvae were collected at depths ranging from 4 to 29 m. When white sturgeon larvae were collected in plankton nets, they were most likely being transported by water currents, since the nets were fished from an anchored boat.

Results from the 12-h study at the index site are presented in Table 5. Catches of white sturgeon larvae were not significantly different between night and day (two-sample t-test, $P > 0.05$). Larvae

Table 4. Regression analyses of white sturgeon egg abundance versus five physical parameters (water temperature, turbidity, near-bottom water velocity, mean water column velocity, and Bonneville Dam discharge) for the index site near RKm 230 in the lower Columbia River, 1988-1991. Only freshly fertilized white sturgeon eggs were used in these analyses. An asterisk indicates a significant regression ($P \leq 0.05$).

Independent variable(s)	r^2	df (total)	F	P
		1988		
Temperature	0.14	9	1.31	0.29
Turbidity	0.31	9	3.54	0.10
Near-bottom vel.	0.13	9	1.16	0.31
Column vel.	0.05	9	0.40	0.54
Discharge	0.30	9	3.42	0.10
Temp., col. vel.	0.20	9	0.88	0.46
Temp., dischg.	0.37	9	2.08	0.20
Temp.,turb., dischg.	0.37	9	1.19	0.39
		1989		
Temperature	0.15	11	1.80	0.21
Turbidity	0.26	11	3.58	0.09
Near-bottom vel.	0.30	10	3.91	0.08
Column vel.	0.44	11	8.00	0.02*
Discharge	0.59	11	14.20	<0.01*
Temp., col. vel.	0.47	11	4.02	0.06
Temp., dischg.	0.62	11	7.40	0.01*
Temp.,turb., dischg.	0.76	11	8.52	0.01*
		1990		
Temperature	0.32	12	5.29	0.04*
Turbidity	0.06	12	0.68	0.43
Near-bottom vel.	0.05	12	0.53	0.48
Column vel.	0.11	12	1.38	0.26
Discharge	0.08	12	0.94	0.35
Temp., col. vel.	0.45	12	4.14	0.05*
Temp., dischg.	0.34	12	2.58	0.12
Temp.,turb., dischg.	0.35	12	1.59	0.26

Table 4. Continued.

Independent variable(s)	r^2	df (total)	F	P
		1991		
Temperature	0.11	10	1.12	0.32
Turbidity	0.07	10	0.71	0.42
Near-bottom vel.	0.20	10	2.19	0.17
Column vel.	0.06	10	0.56	0.47
Discharge	0.13	10	1.30	0.28
Temp., col. vel.	0.13	10	0.60	0.57
Temp., dischg.	0.16	10	0.74	0.51
Temp.,turb., dischg.	0.17	10	0.47	0.71

Table 5. Summary of white sturgeon egg (freshly fertilized) and larval collections during a 12-h study at the index site near RKm 230 in the lower Columbia River. Sampling was done from 1843 hours on 25 May to 0623 hours on 26 May 1988 using a plankton net. Bonneville Dam flow was the average of hourly discharges at the time of sampling and during the 3 h prior to sampling.

Sampling times (hours)[a]	Bonneville Dam flow (m^3/s x 1,000)	Eggs		Larvae	
		No.	No./1,000	No.	No./1,000 m^3
1843-1943	7.24	4	1.5	9	3.4
1951-2051 [b]	7.40	3	1.2	0	0.0
2100-2200	7.00	0	0	5	1.8
2206-2306	6.74	108	37.9	7	2.5
2314-0014	6.50	7	2.5	9	3.2
0020-0120	6.51	27	9.6	9	3.2
0128-0228	6.58	34	11.6	3	1.0
0234-0334	6.66	3	1.1	7	2.5
0340-0440	6.72	1	0.4	8	2.8
0445-0545	6.77	32	10.8	1	0.3
0553-0623	6.76	18	11.9	7	4.6

[a] Sunset on 25 May was at 2030 hours; sunrise on 26 May was at 0515 hours.
[b] Questionable sampling effort, net was damaged.

were collected in all sampling efforts during the 12-h survey, with the exception of the effort that started at 1951 hours. The plankton net was damaged during this effort, and data from this set were not used in the statistical analysis.

Young-of-the-Year

Annual catches of YOY white sturgeon varied considerably, ranging from 11 in 1988 to 273 in 1990 (Table 6). Annual catches shown in Table 6 are not necessarily indicative of YOY abundance in respective years, since sampling gears and schemes were not the same in each year. In 1988 and 1989, the 3.0-m beam trawl was not used, whereas in 1990 and 1991 it was used. The beam trawl is more effective at capturing small YOY white sturgeon than the 7.9-m semiballoon shrimp trawl. Also, in 1990 and 1991, more sampling was conducted in the lower 120 km of the study area than in 1988 and 1989.

Based on sampling from 1988 through 1991, it appears that YOY white sturgeon are primarily using the section of river extending from RKm 45 to 166 (Table 6). Relatively few YOY white sturgeon were collected in the 68 km of river between Bonneville Dam (RKm 234) and RKm 166; small catches were made at RKm 211 in July 1990 and September 1991.

In 1990 and 1991, YOY white sturgeon were first captured in late June; less than 2 months after spawning was estimated to have begun. In all four years, YOY white sturgeon appeared to grow well during their first summer; however, monthly mean lengths and weights varied among the four years (Table 6). During all four years, YOY white sturgeon reached a minimum mean total length of 176 mm and a minimum mean weight of 30 g by the end of September. No statistical comparisons among years were done because of small sample sizes, the protracted spawning period of white sturgeon, and the fact that YOY white sturgeon were collected throughout the month.

The YOY white sturgeon were more abundant in deeper areas of the lower Columbia River, at least during daylight; mean minimum depths during trawling efforts in which YOY were captured were $\geq$ 12.5 m in all years. Mean maximum depths at which YOY white sturgeon were captured were $\geq$ 15.8 m in all years. The bottom substrates over which YOY white sturgeon were found were predominantly sand; however, much of the bottom in the lower Columbia River is composed of sand.

During the 31 July-1 August 1990 20-h sampling survey (sampled from 1155 through 0800 hours) at RKm 75, 52 YOY white sturgeon were collected (Table 7). Over 78% of YOY white sturgeon were collected during hours of darkness, indicating that they were more vulnerable to the trawl at night or moved into the sampling area at night. Catches of YOY white sturgeon (no./ha) were significantly higher during hours of darkness than during daylight (two-sample t-test, $P < 0.01$). The YOY were collected at depths that ranged from 11 to 15 m.

Table 6. Summary of young-of-the-year white sturgeon catches in the Columbia River downstream from Bonneville Dam, 1988-1991.

Month	Capture location (RKm)	Number	Total length (mm)		Weight (g)	
			Mean	SD	Mean	SD
			1988			
Jul	126	1	86.0	0.0	3.0	0.0
Aug	127-153	2	134.0	41.0	13.0	9.9
Sep	153	2	235.0	35.4	60.5	29:o
Oct	127-162	6	248.3	9.8	68.2	8.9
Total		11				
			1989			
Jul	49-153	17	93.4	25.8	5.0	3.1
Aug	49-153	15	176.7	29.9	31.6	13.5
Sep	46-153	12	224.4	30.4	59.7	18.7
Oct	49-162	56	269.4	23.5	87.4	18.5
Nov[a]	107-120	11	273.8	17.7	90.4	20.2
Total		111				
			1990[b]			
Jun	45-120	7	32.1	4.3	<1.0	<1.0
Jul	45-211	125	75.6	27.3	3.2	2.8
Aug	50-166	79	123.8	37.5	12.3	10.4
Sep	49-166	14	222.6	28.4	54.4	19.8
Oct	46-166	48	224.4	28.5	51.9	17.4
Total		273				
			1991[c]			
Jun	45-166	27	30.4	4.1	<1.0	<1.0
Jul	45-166	89	55.7	17.8	1.3	1.2
Aug	49-127	55	97.1	27.6	6.1	4.8
Sep	45-211	47	176.4	38.3	29.8	16.2
Total		218				

[a] Sampling for November was conducted on 1 November 1989.
[b] Includes samples collected at RKm 75 on 31 July-1 August 1990.
[c] No sampling was done in October 1991.

Table 7. Sumnary of young-of-the-year white sturgeon catches during a 20-h study at RKm 75 in the lower Columbia River, 31 July-l August 1990. Sampling was done from 1155 hours on 31 July to 0800 hours on 1 August using a 7.9-m semiballoon shrimp trawl.

Hour[a]	Depth range	No.	No./ha	Length range (mm)
1155	13-14 m	0	0	-
1357	13-14 m	0	0	-
1533	10-15 m	0	0	
1702	13-14 m	1	4	79
1830	12-14 m	1	4	108
1933	11-14 m	6	21	79-114
2029	12-14 m	1	4	79
2130	12-14 m	12	39	57-120
2230	13-15 m	12	38	54-122
0030	12-14 m	15	55	61-141
0218	12-14 m	2	10	82-86
0527	13 m	0	0	
0646	12-13 m	2	10	86-113
0800	12-13 m	0	0	

[a] Sunset on 31 July was at 2047 hours; sunrise on 1 August was at 0555 hours.

DISCUSSION

Based on our collections of freshly fertilized eggs throughout the spawning period in each year, it appears that river conditions in the lower Columbia River were adequate for white sturgeon spawning. Generally, there was no relationship between spawning intensity (as measured by egg collections at the index site) and water velocities or dam discharge during the spawning period. The significant regressions for mean water column velocity and dam discharge in 1989 probably resulted from several zero egg abundance values. These correspond to lower discharges at the end of the spawning period and the paucity of zero egg abundance values for higher discharges. River flows during the spawning period in 1989 tended to be higher than those in 1988 and lower than 1990 and 1991. Kohlhorst (1976) could not demonstrate any effect of river flow on the intensity of white/green sturgeon spawning in the Sacramento River in 1973. Kohlhorst's estimates of spawning dates were based on back-calculations using collections of larval sturgeon. In a later study, Kohlhorst et al. (1991) found a significant ($P < 0.001$) positive correlation between white sturgeon year class strength and river outflow in the Sacramento-San Joaquin estuary. Khoroshko (1972) found that decreases in spring discharge (due to dam regulation) in the Volga River Basin (former Soviet Union) reduced the effectiveness of spawning by Russian sturgeon (A. quldenstadti Br.). During extremely low flow years in the lower Columbia River, spawning effectiveness could be lessened. Additional research should be done in the lower Columbia River, particularly during low flow years, to determine the lower threshold Bonneville Dam discharge for white sturgeon spawning.

All white sturgeon eggs collected downstream from Bonneville Dam were probably released by sturgeon spawning in this area, and not by sturgeon spawning in the impoundment created by Bonneville Dam. Although white sturgeon spawn in the impoundment upstream from Bonneville Dam (Miller et al. 1991), it is unlikely that any of these eggs are carried through Bonneville Dam. In 1990, Miller et al. (1991) collected white sturgeon eggs as far downstream as RKm 298, about 64 km upstream from Bonneville Dam.

We were unable to determine exactly where spawning occurred because we did not know how far white sturgeon eggs were carried by the river current immediately after spawning. Therefore, water velocities at actual spawning sites could have been different than those measured at collection sites of freshly fertilized eggs. The plankton nets and artificial substrates used to collect white sturgeon eggs were fished passively and relied on currents to carry eggs into the nets or onto the artificial substrates. Although white sturgeon eggs are adhesive and adhere to bottom substrate, at least some eggs are dislodged by water currents. In addition, if spawning occurred near the surface, eggs would be carried a greater distance before settling to the bottom than if spawning occurred near the bottom. It is not known exactly where white sturgeon spawn in the water column, although observations in the impoundment upstream from Bonneville Dam suggest that spawning can occur near the surface (Lance Beckman, U.S. Fish and Wildlife Service, Cook, Washington 98605, personal communication).

Spawning in the lower Columbia River in 1988-1991 occurred during good temperature regimes for successful incubation. Successful white sturgeon egg incubation occurs at temperatures between 10 and 18°C, with highest survival and uniform hatching between 14 and 16°C (Wang et al. 1985). In our study, we estimated that some spawning occurred at water temperatures of 18 or 19°C. The survival of these eggs was probably less than for eggs spawned at lower water temperatures. Wang et al. (1985) observed that substantial white sturgeon embryo mortalities occurred at water temperatures of 18 to 20°C; temperatures greater than 20°C are lethal. In the Sacramento River, Kohlhorst (1976) observed that water temperatures during the white/green sturgeon spawning period ranged from 7.8 to 17.8°C, with peak spawning occurring at about 14.4°C. It should be noted that Kohlhorst's estimates of the spawning period are based on back-calculations of larval ages, rather than on sturgeon eggs. Spawning dates can be more accurately estimated using eggs rather than larvae.

The protracted spawning period for white sturgeon in the lower Columbia River is advantageous for the survival and continued abundance of this species. Because spawning occurs over about a 2-month period, food demand by post-larval white sturgeon is distributed over a longer time, allowing more efficient use of food resources and ensuring that at least some larvae will encounter food and survive. In addition, the protracted spawning period lessens the possibility that a natural or man-made disaster would destroy an entire year-class.

Adequate water velocities are needed to disperse white sturgeon larvae out of spawning and egg incubation areas. Stevens and Miller (1970) noted a direct relationship between river flow and catches of white or green sturgeon larvae in the Sacramento-San Joaquin Delta. In a laboratory experiment, Brannon et al. (1985) observed that white sturgeon larvae swam up in the water column after hatching. In addition, Brannon et al. (1985) found that the behavior of white sturgeon larvae was affected by current velocity in laboratory experiments; there was an inverse relationship between water velocity and the amount of time larvae spent in the water column. If this adaptive behavior occurs in the lower Columbia River, white sturgeon larvae could still be dispersed over a wide area in low flow years.

All sampling for white sturgeon larvae was done using gear that sampled along or very near the bottom; therefore, we have no information regarding white sturgeon larvae higher in the water column. However, based on research by Stevens and Miller (1970) in the Sacramento-San Joaquin River System, it appears that white/green sturgeon larvae are primarily demersal. They caught 33 larvae in 16 bottom sampling efforts and only 1 larva in 8 surface and midwater efforts.

Dispersal of white sturgeon larvae over a wide area is probably very important in maintaining a stable population of white sturgeon in the lower Columbia River. Wide dispersal allows utilization of more feeding areas and rearing habitats by larval and post-larval white sturgeon and minimizes competition. However, it is also important that white sturgeon not be carried into saline portions of the Columbia River estuary. Brannon et al. (1985) found that salinities ≥ 16 ppt killed white sturgeon larvae and fry.

Food resources for YOY white sturgeon in many of the deeper areas (>12 m) of the lower Columbia River are probably not abundant. Little is known about the diet of YOY white sturgeon in the lower Columbia River; however, limited observations suggest that the amphipod Coroohium salmonis is the primary prey (Muir et al. 1988). Densities of C. salmonis in many of the deeper areas probably are low because of unstable substrates. Coroohium salmonis is a tube-builder and requires a more stable substrate to densely populate an area. In 1990, densities of C. salmonis at a deep area (19-21 m) at RKm 153 averaged less than 105 organisms/m^2 in June through September (McCabe and Hinton 1991). However, in a deep area at RKm 120 that had large numbers of YOY white sturgeon, the density of C. salmonis was relatively high in August 1990 (2,289/m^2), but dropped to 433 organisms/m^2 in September (McCabe and Hinton 1991). More research is needed to assess the abundance of benthic organisms in rearing areas of YOY white sturgeon.

Although prey abundance may be low in many of the deeper areas of the lower Columbia River, the substrate in these areas is probably ideal for efficient feeding by YOY white sturgeon. The white sturgeon has a protrusible mouth that is used to suck its prey from the bottom. In a laboratory experiment with juvenile Russian sturgeon ($\geq$ 130 mm long), Sbikin and Bibikov (1988) observed that juveniles preferred even, sandy bottoms to bottoms with stones or depressions. In addition, juveniles avoided vegetated areas.

Apparently the YOY white sturgeon are very effective and efficient predators on prey found in the rearing areas, as evidenced by their rapid growth during the summer and early fall. The YOY white sturgeon reached a mean total length of at least 176 mm by the end of September. Rapid growth during the first growing season reduces natural mortality; by the end of summer or fall, YOY white sturgeon in the lower Columbia River probably have few natural predators.

Sampling gears used to collect YOY white sturgeon in the lower Columbia River were limited to two types of bottom trawls which could not be used in shallow littoral areas. Observations made during other studies suggest that YOY white sturgeon do not use the shallow littoral areas. No YOY white sturgeon have been collected in intensive beach seining efforts at RKm 75 during the last 15 years (Richard D. Ledgerwood, National Marine Fisheries Service, P.O. Box 155, Hammond, Oregon 97121, personal communication). Most sampling was done during daylight, with limited sampling at night. The beach seining location was adjacent to the sampling site where 52 YOY white sturgeon were collected during a 20-h study in 1990. No YOY white sturgeon were collected in backwaters and shoreline areas during limited beach seining efforts in the lower Columbia River in August 1988 (McCabe et al. 1989).

We conclude that white sturgeon spawned successfully in the lower Columbia River during the period 1988 through 1991. A large geographic area of the lower Columbia River was used by white sturgeon at different life history stages, and maintenance of the quality and quantity of this habitat is essential for sustained production and fisheries.

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REPORT B

location and Timing of White Sturgeon Spawning in Three Columbia River Impoundments

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Abstract

Location and timing of white sturgeon *Acipenser transmontanus* spawning were documented in three Columbia River impoundments (Bonneville, The Dalles, and John Day pools) for up to five years (1987 through 1991). White sturgeon spawned every year of the study exclusively in tailrace areas in the furthest upstream 2.6 km of each pool, where the highest water velocities existed. White sturgeon spawning was positively related to river discharge. With similar annual effort, the number of white sturgeon eggs collected was one to two orders of magnitude greater in average water years (1990, 1991) than in low water years (1987, 1988).

White sturgeon spawned in 12°C to 18°C water, however, 65% of all newly spawned eggs (pre-cleavage fertilized eggs, spawned < 3 hours before collection) were collected in 13°C and 14°C water over cobble, rubble, and bedrock. Spawning generally began earliest in the season and lasted longest in the furthest downstream pool, and began latest and was shortest in the furthest upstream pool.

Introduction

With the exception of a few field studies (Miller 1972; Kohlhorst 1976), our understanding of natural spawning by white sturgeon until recently has been limited to information generated from culture and laboratory studies, due in part to the inherent difficulties of sampling large rivers. During the past five years, white sturgeon reproduction and recruitment (Miller and Beckman 1992), the environmental conditions associated with white sturgeon spawning (Parsley et al 1992; McCabe and Tracy 1992), and white sturgeon spawning cues (Anders and Beckman 1992), in the Columbia River downstream from McNary Dam have been studied. However, timing, specific location, and duration of white sturgeon spawning was not documented by these authors. Therefore, based on a need for this baseline data, our objective is to provide specific information regarding these parameters for white sturgeon spawning in the three impoundments of the Columbia River downstream from McNary Dam. This information will allow fisheries managers to effectively evaluate spawning success in these impoundments, and may also be used to manage white sturgeon populations. This work may also assist other researchers initiating studies involving white sturgeon or other sturgeon species in other aquatic systems.

Study Area

White sturgeon spawning was investigated in a 233 km section of the Columbia River between Bonneville Dam (RKm 237) and McNary Dam (RKm 470) in Bonneville, The Dalles, and John Day pools (Figure 1). Impoundment created lacustrine conditions in some areas of the river by increasing water depth and surface area compared to pre-impoundment conditions. Post-impoundment water management has also reduced water velocity in spring and early summer, and increased it during winter compared to pre-impoundment conditions.

Bonneville Pool (RKm 237-309) covers 7,600 ha of predominantly sand substrate. The Dalles Pool (RKm 309-348) covers 3,600 ha of predominantly sand, cobble, and bedrock substrates, and John Day Pool (RKm 348-470) covers 19,800 ha of mainly mud, sand, gravel, and cobble substrates. High water velocities (> 3 m/s) in the tailrace areas in the extreme upstream ends of each pool have exposed larger substrates, including cobble, rubble, boulder and bedrock, while transporting and depositing finer substrate materials in downstream portions of the impoundments. More detailed descriptions of the study area, including annual variation in spawning habitat availability, can be found in Parsley et al. (1992).

Methods

Timing and location of white sturgeon spawning was determined by collecting newly-spawned eggs from April or May through July, 1987 through 1991. Newly spawned white sturgeon eggs referred to eggs in the pre-cleavage, changing pigmentation stage (Beer 1981), which were spawned < 3 hours before collection. White sturgeon eggs were collected from the drift in plankton nets (0.78 m max. width, 0.54 m high, 1.59 mm knotless mesh) and in a beam trawl net (2.7 m x 0.5 m, 1.59 mm knotless mesh) following the techniques presented by Miller et. al 1991. Mean water

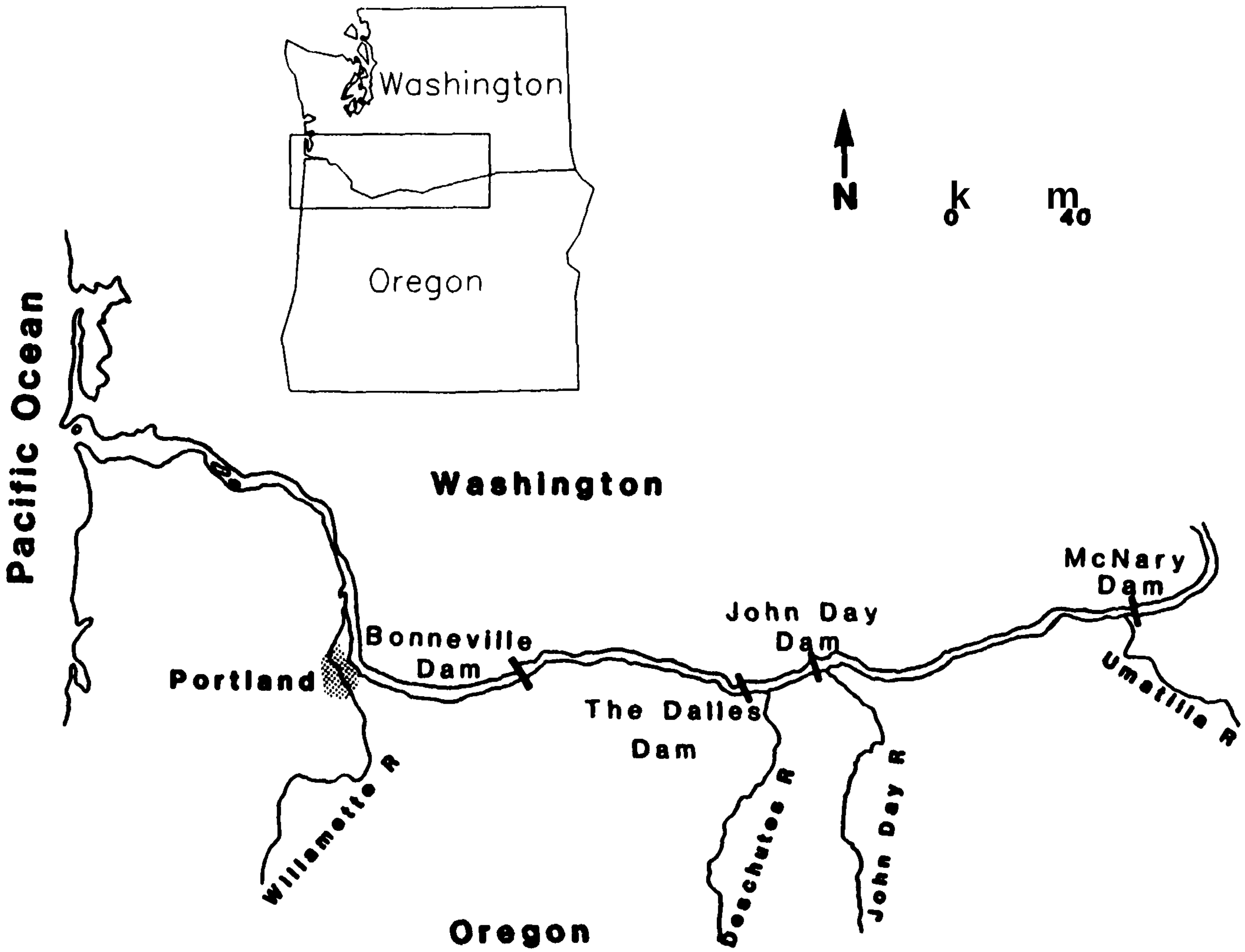

Figure 1. Columbia River showing study area between Bonneville and McNary Dams.

column velocity (sum of the velocity values measured at 20% and 80% of max. depth/2) was measured with a Price "AA" current velocity meter[1] wired to a Swoffer Instruments Model 2200 digital current velocity meter. Water temperature (°C) was measured with digital (YSI Model 58) or laboratory thermometers. River discharge data were provided by the U.S Army Corps of Engineers.

White sturgeon spawning dates were back-calculated from viable eggs using an exponential function involving water temperature and stage of embryonic development reported by Wang et al. (1985). Embryonic stages of white sturgeon eggs were determined using developmental criteria presented by Beer (1981), and a dissection microscope.

Since all white sturgeon eggs were collected only in tailrace areas from 1987 through 1991, Bonneville Pool is referred to as The Dalles Dam tailrace, The Dalles Pool is referred to as John Day Dam tailrace, and John Day Pool is referred to as McNary Dam tailrace when reporting or discussing egg collection results.

Results

Spawning location For safety reasons due to high water velocity, sampling was not possible in all spawning areas. However, collection locations of newly spawned white sturgeon eggs most accurately represented spawning locations, since newly spawned eggs were in the water column for less than 3 hours before collection. All but one newly spawned egg was collected from the drift less than 2.7 km downstream from each dam. Spawning may have occurred beyond the spawning areas determined by this study, however, up to five years of egg sampling in non-tailrace areas failed to collect white sturgeon eggs. Although we sampled up to 32 km downstream from these dams, no eggs of any embryonic stage were collected further than 10.1 km, 4.5 km, and 5.3 km downstream from The Dalles, John Day and McNary dams (Figure 2). During the five year study period, newly spawned eggs were collected at 6 to 10 sites in The Dalles Dam tailrace, 1 to 5 sites in John Day Dam tailrace, and 2 to 4 sites in McNary Dam tailrace.

During the study, two episodes of white sturgeon spawning were observed in The Dalles Dam tailrace, and verified by the collection of 45 newly spawned eggs at three locations slightly downstream from the observed activity. On 3 June, 1988, spawning activity was observed between 1200 and 1230 hours, and between 1300 and 1345 hours, and was characterized by numerous fish, perhaps as many as 25, breaching and rolling on the surface, concentrated in a small area. The majority of spawning activity was observed in a large turbulent eddy, just upstream from the Highway 197 bridge (Figure 2) near the rip-rap lined north bank. Eleven of the 45 newly spawned eggs were collected during a 30 minute stationary plankton net tow, while an additional 33 were collected in a second tow for 10 minutes in the same area, immediately after the first.

The percent composition of substrates over which white sturqeon

[1] Use of trade names does not imply endorsement by the USFWS

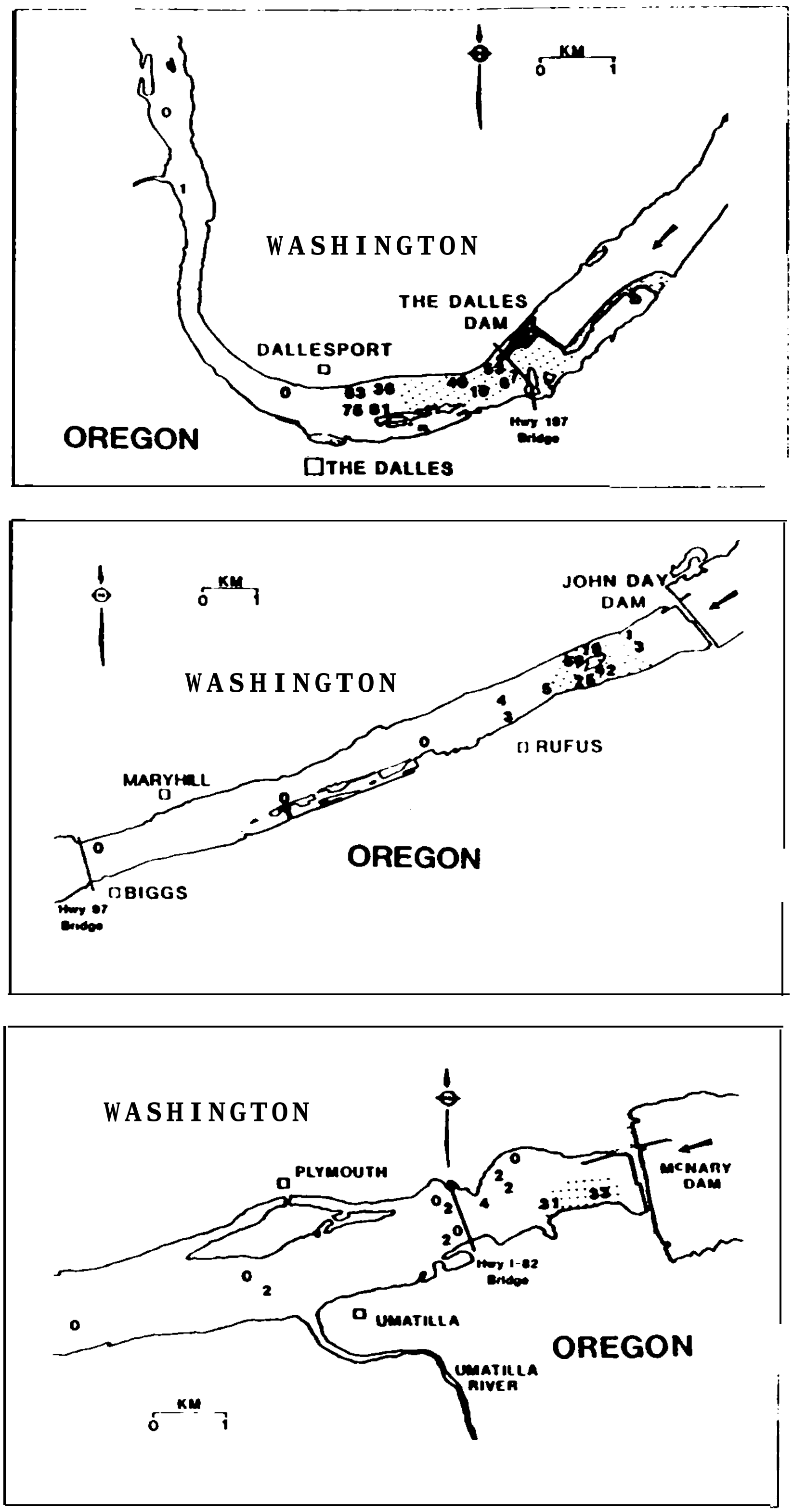

Figure 2. Location of white sturgeon spawning areas and numbers of eggs collected. Shaded areas indicate likely spawning areas.

spawned varied among tailraces, however, cobble, rubble, boulder, and bedrock existed in all the spawning areas, with gravel present in some areas to a lesser extent.

Egg collection We assumed that a positive relation existed between the number of white sturgeon eggs collected and the number of eggs spawned. Newly spawned eggs were collected in all tailraces every year they were sampled except in John Day Dam tailrace during 1988. During the study, 372 newly spawned white sturgeon eggs were collected in The Dalles Dam tailrace, compared to 159 and 28 in John Day and McNary dam tailraces (Figure 2).

Numbers of white sturgeon eggs of all embryonic stages collected were highly variable among years in each tailrace, and among pools each year. During the five years, more white sturgeon eggs were collected in The Dalles Dam tailrace (1440) than in John Day Dam tailrace (721), and McNary Dam tailrace (181). The number of white sturgeon eggs collected annually ranged from 104 to 772 ($\bar{X}$ = 360) in The Dalles Dam tailrace, 25 to 334 ($\bar{X}$ = 170) in John Day Dam tailrace, and 41 to 69 ($\bar{X}$=60) in McNary Dam tailrace.

Timing of spawning White sturgeon spawning in The Dalles Dam tailrace began approximately one week earlier than in John Day tailrace, and one to two weeks earlier than in McNary Dam tailrace during each year (Figure 3). White sturgeon spawning dates ranged from 19 May to 10 July in The Dalles Dam tailrace, from 1 June to 10 July in John Day Dam tailrace, and from 3 June to 15 July in McNary Dam tailrace.

The length of the spawning period (number of days) was always longest in the furthest downstream tailrace, and shortest in the furthest upstream tailrace (Figure 3). The mean length of white sturgeon spawning periods was 43.5 days in The Dalles Dam tailrace (4 yr mean), 21.5 days in John Day Dam tailrace (5 yr mean), and 18 days in McNary Dam tailrace (3 yr mean).

Spawning trends Three white sturgeon spawning trends were evident from this study. First, regardless of sample size, the number of eggs collected (and presumably the number of eggs spawned) was always greatest in The Dalles Dam tailrace, (furthest downstream) followed by collections from John Day Dam and McNary Dam tailraces.

Secondly, the number of white sturgeon eggs collected was markedly greater in years of average river discharge (1990, 1991) than in years of low river discharge (1987, 1988); no years of above average river discharge existed during this study. In The Dalles and John Day Dam tailraces, one to two orders of magnitude more eggs were collected in average water years than in low water years. Accompanying egg catch per unit effort (CPUE) values using the beam trawl were 7 to 8 times greater in The Dalles Dam tailrace, and an order of magnitude greater in John Day Dam tailrace; egg CPUE values using the plankton nets were at least twice as high in these tailraces during average water years compared to low water years.

Thirdly, spawning period duration was also greater in average water

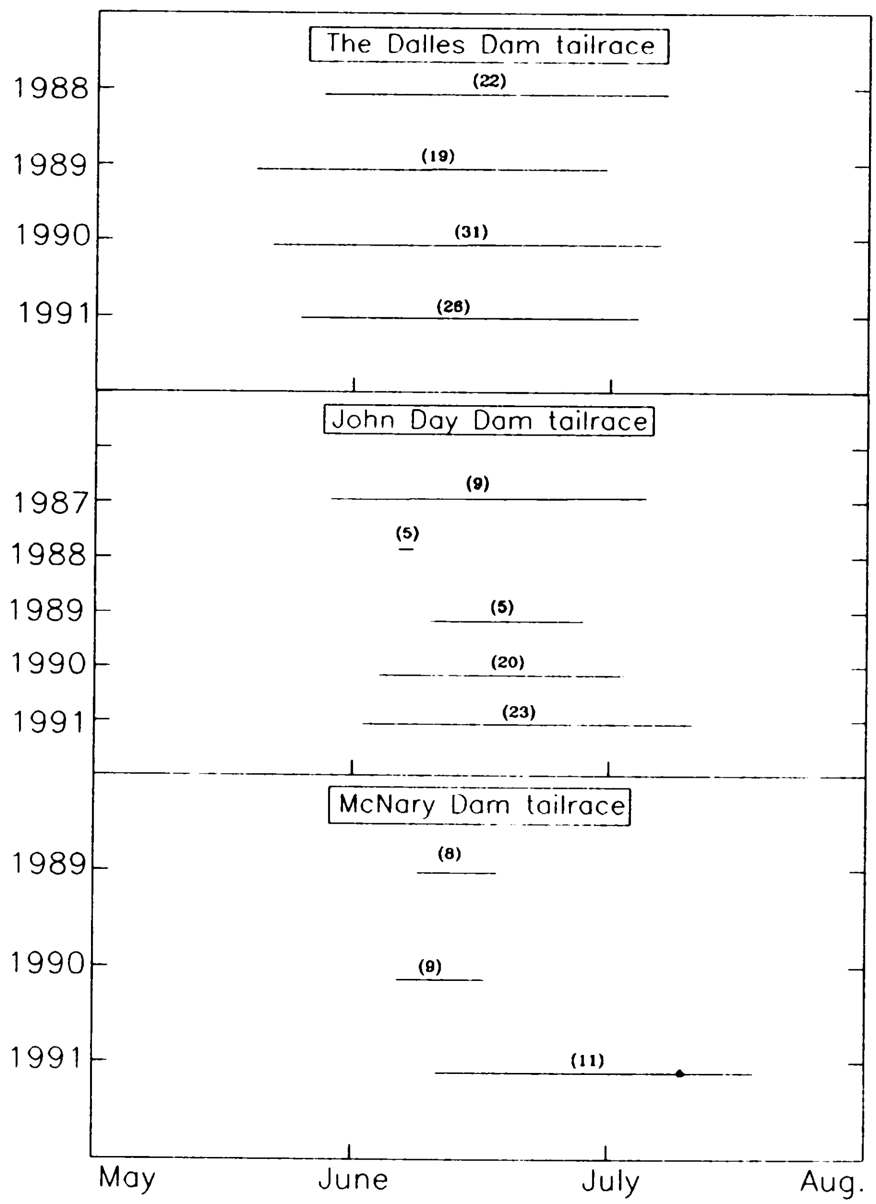

Figure 3. Timing and duration of white sturgeon spawning in three Columbia River impoundments. Estimated number of spawning days are indicated in parentheses.

years than in low water years. In the John Day Dam tailrace spawning occurred on 22 days in 1991 (average water year) compared to less than 10 spawning days in 1988 (low water year) (Figure 4).

Discussion

Spawning location White sturgeon spawned only in the furthest upstream several kilometers of each pool during each year of the study since these were the only areas available with adequate water velocities. The amount of spawning varied, often drastically, among years within each tailrace. Discharge was the only measured variable that also varied substantially among years in each spawning area. Depth, substrate, and water temperature in each spawning area remained relatively constant or unchanged among years, yet in low water years spawning in these areas appeared greatly reduced, indicating the importance of discharge (and subsequent water velocity) for spawning. In the same three impoundments from 1987 through 1991, newly spawned eggs were not collected in areas having water velocity less than 0.8 m/s (Parsley et al. 1992), while discharge and mean velocity were found to significantly effect white sturgeon spawning in The Dalles Dam tailrace (Anders and Beckman 1992). Depth, substrate, and water temperature similar to that found in spawning areas existed in non-tailrace areas of the pools, however, no white sturgeon spawning was detected in these areas from 1987 through 1991, presumably due to the lack of adequate water velocity.

In a cooperative white sturgeon study from 1987 through 1991, McCabe and Tracy (1992) studied white sturgeon spawning in the free-flowing Columbia River downstream from Bonneville Dam. The fact that white sturgeon successfully spawned every year in spawning areas in Bonneville Dam tailrace where mean water column velocity was always greater than 1.0 m/s suggests that suitable water velocity is extremely important to white sturgeon spawning. This conclusion is further supported by our estimates of reduced white sturgeon spawning in the three impoundment tailraces in years of low discharge.

Timing of spawning White sturgeon began spawning in the three impoundments every year they were sampled when water temperature exceeded 12°C. The timing of spawning initiation varied slightly among years due to annual climatic variation. In the free flowing river section downstream from Bonneville Dam, white sturgeon began spawning at 10°C (McCabe and Tracy 1992). In the impoundments, water temperature first reached 12°C in The Dalles Dam tailrace, followed sequentially by John Day and McNary Dam tailraces. This delayed initiation of spawning in each progressively upriver tailrace was most likely due to the timing of water warming in the impoundments.

Spawning periods were longest in the furthest downstream tailrace, and progressively shorter the two upstream tailraces. This may have been partly due to differences in white sturgeon broodstock abundance among pools. Abundance of adult white sturgeon was greatest downstream from Bonneville Dam (Devore at al. 1992), and decreased progressively in each upriver impoundment (Beamesderfer and Rein 1992). While the effect of increasing the number of spawning individuals in areas of currently

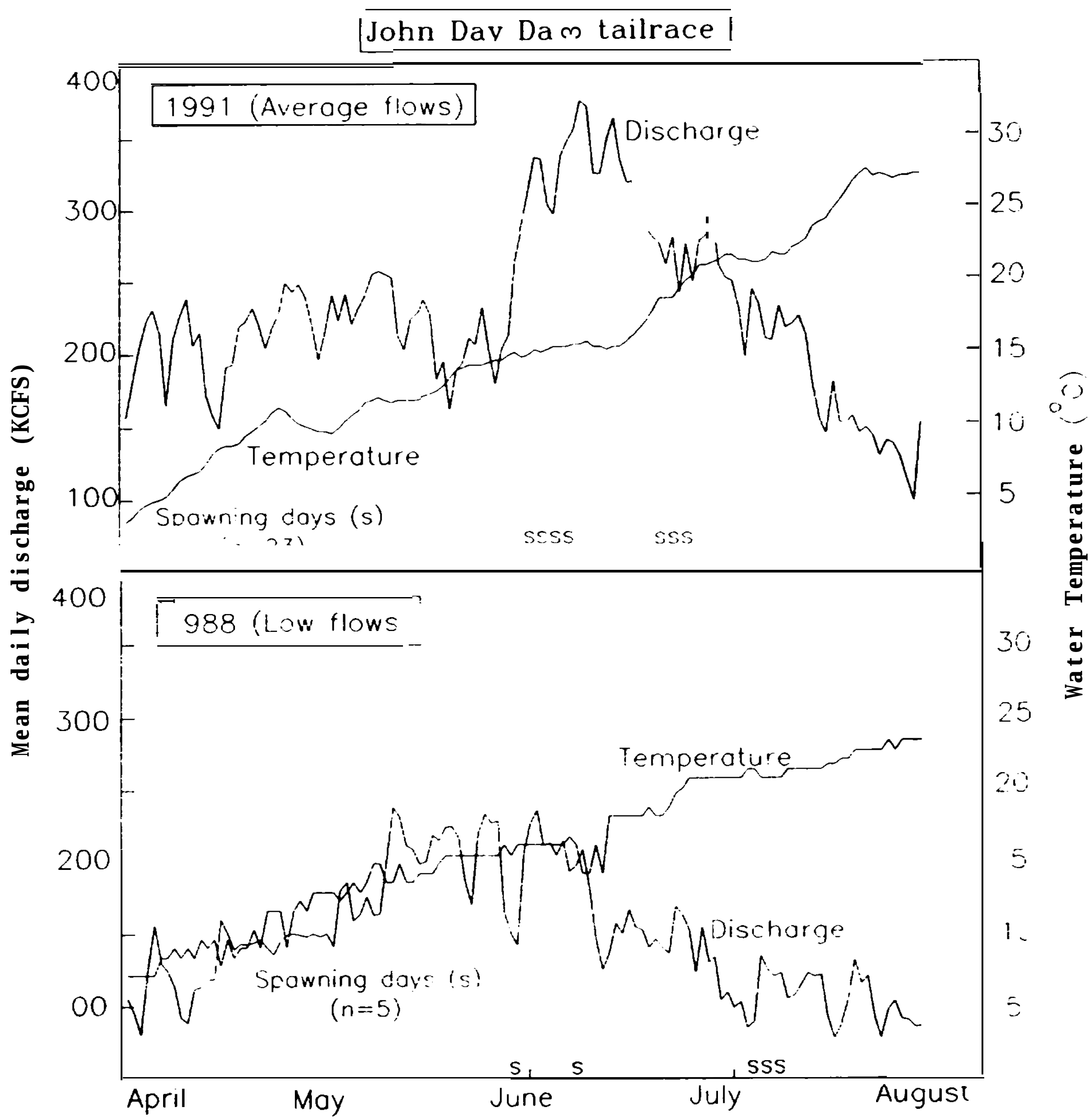

Figure 4. Mean daily discharge, water temperature and estimated number of days white sturgeon spawned in John Day Dam tailrace, 1988 and 1991. One letter (s) represents one spawning day.

depressed broodstock numbers is untested, spawning period duration appeared to be positively related to the abundance of spawning individuals (Figure 3).

Spawning duration may have also been influenced by spawning habitat availability. A given discharge provided a different amount and quality of spawning habitat in each tailrace because each tailrace had a unique channel morphology (Parsley et al. 1992). As a result, differing amounts of available spawning habitat in each tailrace may influence spawning duration. Parsley et al. (1992) discusses the effect of discharge on availability and quality of spawning habitat in detail.

Gear efficiency may also have increased in years with higher flows and dam discharges, allowing greater catches of white sturgeon eggs collected from the drift during years of higher discharge. However, higher egg and larvae CPUE values, and larger catches of YOY white sturgeon accompanied higher water years, which indicated an increased amount of white sturgeon spawning in years of higher discharge (Miller and Beckman 1992).

The trend of progressively less spawning, smaller egg sample sizes, and lower CPUE values in an upstream direction was best explained by the abundance of spawning white sturgeon in each of the pools. A larger number of reproducing white sturgeon existed in The Dalles Dam tailrace than in John Day Dam, and more reproducing white sturgeon existed in John Day Dam tailrace than in McNary Dam tailrace (Beamesderfer and Rien 1992).

In addition to enhancing our understanding of the timing, location, and duration of white sturgeon spawning, this research has provided fisheries managers with the necessary information to successfully monitor spawning of biologically and economically important white sturgeon populations in the three furthest downstream Columbia River impoundments. Only by understanding the reproductive biology of this unique species in an altered environment will we be able to assess the effects of changing water management on white sturgeon spawning, a skill necessary to ensure future reproduction and long-term survival of these white sturgeon populations.

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REPORT C

Factors Affecting White Sturgeon Spawning and Recruitment in the Columbia River Downstream from McNary Dam

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Abstract.-Recognition of the importance of biotic and abiotic factors which control production of white sturgeon *Acipenser transmontanus* is essential to properly manage the populations in the Columbia River downstream from McNary Dam, particularly in the three impoundments created by the construction of dams. Research conducted from 1987 through 1991 indicated that in years with low river discharge dam operations negatively affected white sturgeon spawning by reducing the amount and quality of spawning habitat, which contributed to year class failures or poor recruitment in the impoundments. Low river discharge had less of an adverse effect on white sturgeon spawning habitat in the free-flowing reach downstream from Bonneville Dam, with recruitment occurring in all years of the 5-year study. Dead white sturgeon eggs were more prevalent in the collections from the impoundments than from the free-flowing reach. Spawning began at lower temperatures in the free-flowing reach than in the impoundments, although water temperatures were similar among areas. Feeding conditions for post-yolk-sac larvae and juvenile white sturgeon were probably better in the impoundments than in the free-flowing reach, based on limited benthic invertebrate collections and estimates of the amount of habitat available for rearing; consequently, growth rates and mean length at age were greater for juvenile white sturgeon from the impoundments than from the free-flowing reach.

The ecology of North American sturgeons is poorly understood. These primitive long-lived fish reproduce only every 2-8 years; the seven different species require from 3 to 34 years to reach maturity with males maturing at a younger age than females (Conte et al. 1988). Thus they are susceptible to environmental perturbations and over-exploitation. As a result, sturgeon stocks have declined throughout their range. In North America green sturgeon Acipenser medirostris, Atlantic sturgeon A. oxvrhynchus, and white sturgeon A. transmontanus support limited commercial fisheries, and lake sturgeon A. fulvescens, green sturgeon, Atlantic sturgeon, and white sturgeon can be legally harvested by sport anglers. The other three species, shortnose sturgeon A. brevirostrum, pallid sturgeon Scaphirhynchus albus, and shovelnose sturgeon S. platorynchus are protected under the federal Endangered Species Act.

The Columbia River and its watershed have been drastically altered by human activities (Anonymous 1991; Ebel et al. 1989). Construction and operation of hydroelectric dams, agriculture, logging, mining, stream channelization, water pollution, and harvest have allowed some fish species to flourish, while others have declined. Fish adapted to riverine conditions have suffered most.

Historically, white sturgeon were abundant in the Columbia River, and supported an intense commercial fishery through the late 1800s. Commercial catches peaked in 1892, when more than 2.4 x 10^6 kg were landed (Craig and Hacker 1940). Overfishing soon decimated the population, and by 1899 the annual catch was less than 33,250 kg. Regulations on harvest during the mid 1900s allowed white sturgeon populations to recover sufficiently to support recreational and commercial fisheries. Presently, white sturgeon are the most popular recreational fish in the Columbia River from the mouth to McNary Dam (Oregon Department of Fish and Wildlife and Washington Department of Fisheries 1991). The four dams in this area (Figure 1) have divided the white sturgeon into essentially separate populations, although there is limited exchange among the areas through the fish ladders at each dam (Warren and Beckman 1992).

Fisheries management agencies are concerned about the future of white sturgeon populations in the Columbia River downstream from McNary Dam, particularly in the three impoundments. Rieman and Beamesderfer (1990) suggested that the white sturgeon fishery is on the verge of collapse. Typically, management agencies have responded to declines in populations by restricting harvest through minimum and maximum size limits, daily and annual harvest limits, and closed seasons and areas.

The prevailing philosophy of white sturgeon management relies on stock-recruitment relations and protects spawning stock to ensure future production. However, environmental effects on the stock-recruitment relations differ among areas and have changed over time because of changes to the environment caused by hydroelectric development. Year-to-year differences in environmental characteristics can cause fluctuations in reproduction at least as great as those associated with variation in stock density (Ricker 1975). Year-class failures have been observed in white sturgeon populations from impounded areas (Miller and Beckman 1992a) which implies that the environment affects white sturgeon reproduction more than stock-recruitment relations during some years and in some areas.

Biotic and abiotic factors ultimately control production (Karr and Dudley 1978) and recognizing the affect these have on stock-recruitment relations and how hydroelectric development and operation of the dams have affected the biotic and abiotic factors that influence white sturgeon populations will enable white sturgeon fisheries to be enhanced rather than maintained. Effective management of white sturgeon populations will only be achieved through an understanding of the factors affecting reproduction and early life history, as discussed by Le Cren (1962) 30 years ago;

> "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."

The size of an unexploited population at any given time has been set by preceding events. Effective management strategies to replenish depleted populations can be developed by identifying physical and biological bottlenecks that determine the population at each life history stage.

In this paper, we review factors known, or suspected, to influence white sturgeon populations in the lower 470 km of the Columbia River (Figure 1). Much of the review is drawn from the results of data collected in the Columbia River downstream from McNary Dam from 1987-1991. The goal is to identify factors that determine the numbers of fish in a cohort in each of the three impoundments and the unimpounded river reach that comprise this section of the river, and to determine how the construction and operation of hydroelectric dams have affected white sturgeon spawning and recruitment. Comparing factors among river reaches will provide insight into those that are limiting white sturgeon. We begin with factors controlling the numbers of eggs spawned, as a cohort in an unsupplemented population can be no larger than the number of eggs produced. Biological and physical processes cause mortality, which reduces the population over time. The causes and magnitude of mortality vary as ontogeny progresses (Figure 2).

Life Stages

Eggs

The number of white sturgeon eggs spawned annually in each river reach depends on the number of spawning females present, female fecundity, and a physical and chemical environment that permits vitellogenesis and cues spawning. In any one year only 10% to 20% of the adult female population is capable of spawning (Conte et al. 1988). The number of adult white sturgeon in the Columbia River downstream from McNary Dam differs among the four river reaches, and is greatest in the free-flowing reach downstream from Bonneville Dam, followed by Bonneville, The Dalles, and John Day pools (DeVore et al. 1992; Beamesderfer and Rien 1992).

Fecundity of white sturgeon increases with length (Beamesderfer and Rien 1992; DeVore et al. 1992), but sample sizes in those studies were too small to determine if differences in fecundity at length existed among the four areas. Size composition of white sturgeon populations varied among areas; smaller fish were more prevalent in the free-flowing reach and in

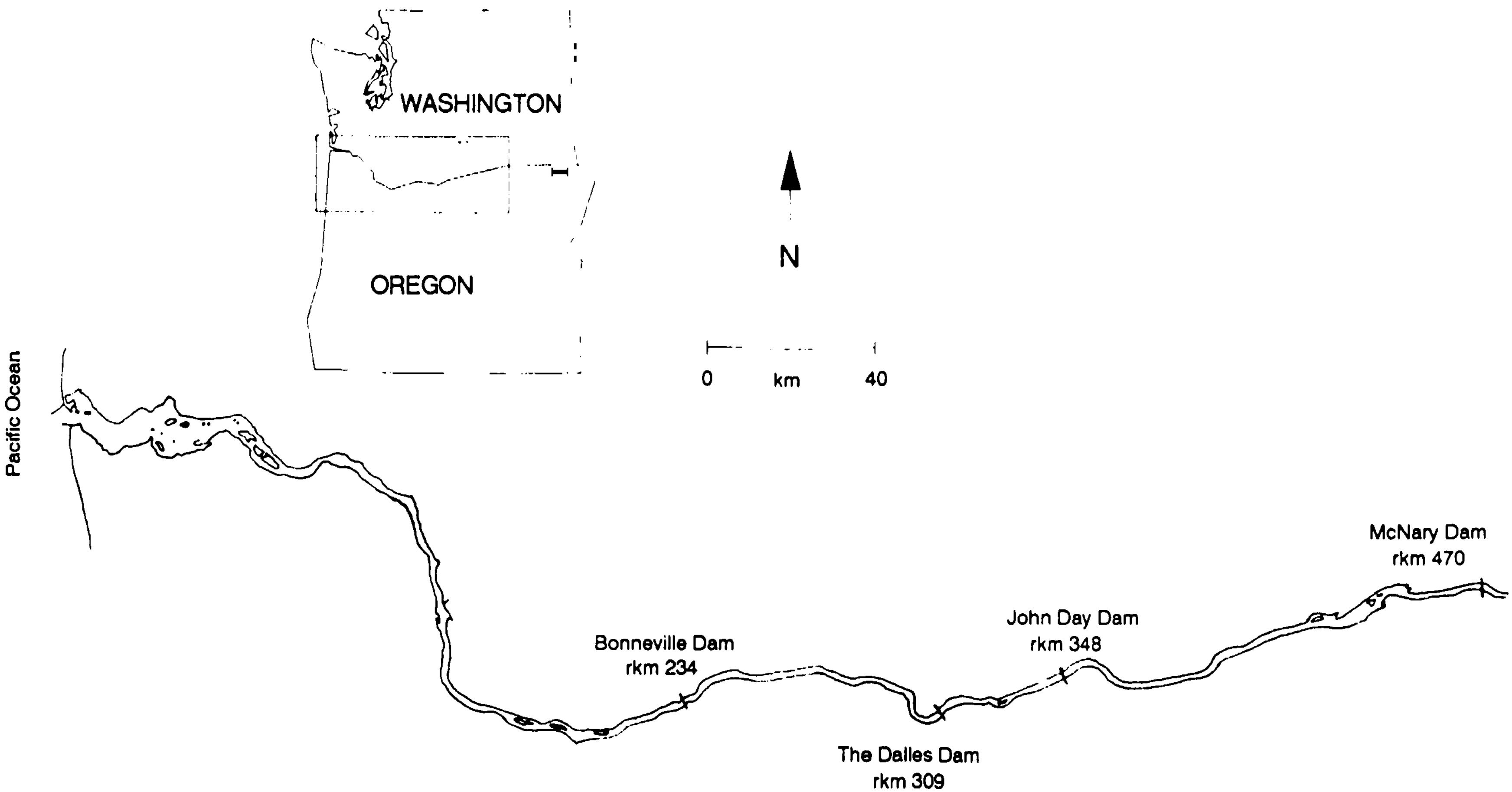

Figure 1. The Columbia River downstream from McNary Dam, showing the three impounded river reaches and the unimpounded lower river reach.

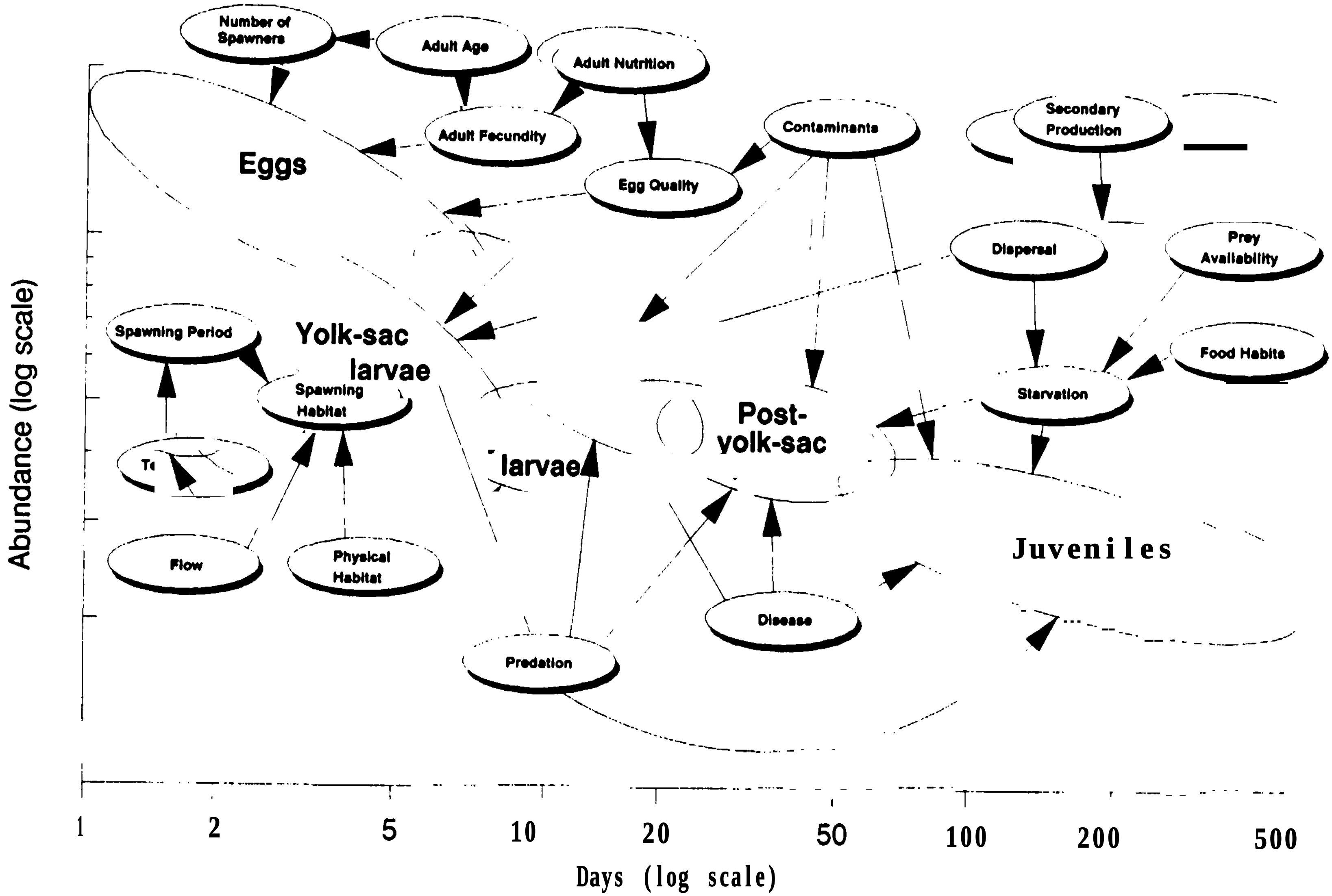

Figure 2. A conceptualization of the recruitment process in white sturgeon. Shown are biotic and abiotic factors that determine numbers of eggs spawned and subsequent causes of mortality that determine the number of white sturgeon in a cohort. Decreasing slopes are approximations, and are not based on calculated values of mortality or survival (figure adapted from Houde 1987).

Bonneville Pool than in The Dalles or John Day pools (Beamesderfer and Rien 1992; DeVore et al. 1992).

Because of the differences in numbers of adult fish and size composition of the four white sturgeon populations downstream from McNary Dam, wide variation in the number of eggs spawned in each river reach was expected. Estimates of the number of eggs spawned were never made, but egg deposition should have been greater in the free-flowing reach, followed by Bonneville, The Dalles, and John Day pools, based on population size. Estimates of the number of days that spawning occurred during each spawning period in each river reach and the catch per unit of effort of eggs during each year verified that more eggs were spawned in the free-flowing reach, followed by Bonneville, The Dalles and John Day pools (Anders and Beckman 1992; McCabe and Tracy 1992; Miller and Beckman 1992a).

Spawning occurs only if the physical environment permits vitellogenesis and cues ovulation. Vitellogenesis in white sturgeon requires two years in the San Francisco Bay estuary, with a reproductive cycle (time between spawnings) of 4-5 years (Chapman 1989). The reproductive cycle of the white sturgeon in the Columbia River downstream from McNary Dam is probably three years or more (Welch and Beamesderfer 1992).

Temperature and photoperiod have been suggested to be important environmental factors in fish maturation (de Vlaming 1972), and spermatogenesis in white sturgeon appears to be affected by temperature (Chapman 1989). No differences in mean daily water temperature among areas during 1990 and 1991 were detected (unpublished data, U.S. Fish and Wildlife Service), and because the four areas are at virtually the same latitude (45N-47'N), photoperiod does not differ among areas. Although water temperature and photoperiod were similar among reaches, spawning began earlier in the year and at lower water temperatures in the free-flowing reach than in the impoundments (McCabe and Tracy 1992; Anders and Beckman 1992).

Spawning should only occur when and where environmental factors are likely to be optimal for the survival and growth of progeny (Munro et al. 1990). White sturgeon spawning occurred in areas with high water velocities over coarse substrates (Parsley et al. 1992). Spawning in high water velocities may help separate and disperse the adhesive eggs. The coarse substrates provide a good surface for the eggs to attach.

The amount of spawning habitat in the study area differed among reaches because of the channel morphology in each reach, and among years because of changing river discharges (Parsley and Beckman 1992). Channel morphology and river discharge affect water velocities in a given reach. The impoundments have reduced the hydraulic slope of the river over vast reaches and inundated many rapids and falls that historically provided spawning habitat for white sturgeon. Differences in spawning habitat caused by channel morphology are evident during low river discharges because the discharge is essentially the same in each area; the free-flowing reach provides more spawning habitat than the impoundments at lower discharges (Parsley and Beckman 1992).

Mortality of eggs begins immediately following spawning, and can be divided into four categories: physiological mortality from abnormal egg development (including unfertilized eggs), losses from fungal infection, predation, and loss due to physical damage. Broadcasting large numbers of eggs is an adaptive strategy of many fishes, including white sturgeon, because of high mortality of spawned eggs.

The incidence of fungus-infected eggs in field collections was unusually high in The Dalles Pool, with 45% of the eggs collected over 5 years showing fungal infection, followed by Bonneville Pool with 21% (4-year average), John Day Pool with 17% (3-year average), and the free-flowing reach with 2% (5-year average)(Anders and Beckman 1992). Abnormally developing eggs quickly die and become covered with fungus, which can cause mortality of adjacent eggs and foster the spread of fungus. Abnormal development is induced by polyspermic fertilization, parthogenesis, mechanical disruption, and environmental perturbations including water temperature fluctuations, adverse water quality, and bio-accumulation of toxins (Beer 1981; Bosely and Gately 1981; Ginzburg 1968).

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, and agriculture. Water quality can be degraded more in some areas than 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 Oncorhvnchus mvkiss embryos. Tikhonova and Shekhanova (1982) determined that gastrulation in Russian sturgeon Acipenser queldenstaedti is the most sensitive stage to agricultural pesticides containing carbamates.

White sturgeon provide no parental care for their eggs, thus the eggs are vulnerable to predation. Miller and Beckman (1992c) found that white sturgeon eggs in Columbia River impoundments were eaten by largescale sucker Catostomus macrocheilus, common carp Cvorinus carpio, northern squawfish Ptvchocheilus oreqonensis, and prickly sculpin Cottus asper. Crayfish Pacifastacus leniusculus may also consume white sturgeon eggs. Estimates of the number of eggs consumed by predators are unavailable, but the effect of egg losses on recruitment in the impoundments is compounded by the low numbers of eggs spawned in these areas. Impoundment has favored predation on eggs by reducing water velocities over vast areas. High water velocities in the dam tailraces would reduce predation on white sturgeon eggs by excluding predators. However, water velocities are reduced during years of low river discharge (Parsley and Beckman 1992), and operation of McNary, John Day, and The Dalles dams to produce more power during peak energy needs and less power at other times reduces water velocities at night and allows predators access to white sturgeon eggs. Near-substrate water velocities measured at one location downstream from The Dalles Dam on 8 and 9 June 1988 ranqed from 0.43 to 1.83 m/s as discharge ranged from about 3,000 to 8,000 m/s (unpublished data, U.S. Fish and Wildlife Service). Generally, hourly discharge at Bonneville Dam was less variable than discharge at the upriver dams.

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 would kill some eggs. However, dislodged eggs have been hatched in aquaria (unpublished data, U.S Fish and Wildlife Service). Irregular substrates or those with interstitial spaces could provide protection from scouring and predation. Shifting substrates could crush eggs.

Egg mortality increases when incubation occurs at 18'C, and total mortality occurs at 20-C (Wang et al. 1985). Most white sturgeon spawning occurred at 14-C in the four reaches (Parsley et al. 1992), but some spawning occurred at temperatures greater than 18-C, particularly in the impoundments (Anders and Beckman 1992; McCabe and Tracy 1992). For unknown reasons, spawning in the free-flowing reach during 1987-1991 began on earlier dates and at lower temperatures than in the impoundments. Spawning in the free-flowing reach began at 10'C, but spawning did not begin in the impoundments until the temperature was 12-C, and often continued after temperatures reached 18'C. When this happened, dead eggs increased in the catch, and generally no yolk-sac larvae were collected from eggs spawned at the higher temperatures.

Yolk-sac Larvae

White sturgeon yolk-sac larvae have been described as "hardy" (Conte et al. 1988), referring to their ability to survive transport for artificial culture. Yolk-sac larvae must be tolerant of harsh physical conditions to survive in the turbulent environment in which hatching occurs. However, they are sensitive to poor water quality; Brannon et al. (1985b) reported that water quality parameters for chlorine and gas supersaturation may be more critical for white sturgeon than for salmonids. Maximum recommended nitrogen gas pressure for culture (and presumably in the wild) is 110% of saturation (Conte et al. 1988).

Losses of yolk-sac larvae in the Columbia River due to abnormal development or other factors have not been quantified and differences in mortality among the four river reaches could not be determined. Dead yolk-sac larvae were collected from the drift in the four river reaches, but the cause of death was unknown. Some mortality was caused by the collection process, but yolk-sac larvae that were probably dead prior to collection were found in the three impoundments. This 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 (one day or less old) collected from the John Day Pool were significantly longer than yolk sac larvae from the other two impoundments and the free-flowing reach (Student-Newman-Keuls test, $P \leq 0.05$). Yolk-sac larvae from the free-flowing reach were significantly shorter than those collected in each of the impoundments (unpublished data, U.S. Fish and Wildlife Service). Generally, larger size at hatch is advantageous for fish; predation is lessened and food is more available when exogenous feeding begins.

Size at hatch can be influenced egg size, dissolved oxygen concentrations, and water temperature during incubation (Viljanen and Koho 1991). Differences in size composition of mature female white sturgeon from the impoundments has been noted (Beamesderfer and Rien 1992) and larger female white sturgeon produce larger eggs (North et al. 1992). Because the majority of adult female white sturgeon in the John Day Pool were larger than those in the other areas, it is possible that the eggs spawned and thus the yolk-sac larvae would be larger in this pool.

Predation on yolk-sac larvae by fish probably occurs. Laboratory experiments by Brannon et al. (1986) showed that white sturgeon larvae were eaten by goldfish Carassius auratus, bluegill Lepomis macrochirus, juvenile chinook salmon Oncorhvnchus tshawvtscha, rainbow trout, and older white sturgeon. Yolk-sac larvae in the Columbia River are unlikely to encounter goldfish or bluegill, but are probably vulnerable to predation by the same fishes identified as egg predators. Yolk-sac larval white sturgeon have no defensive capabilities other than an ability to hide in the substrate after the swim-up phase and a limited ability to evade predator strikes.

Predation on yolk-sac larvae is related to predator abundance, dispersal of newly hatched larvae, and vulnerability of the larvae. White sturgeon larvae are most likely to be preyed upon by demersal fishes. Stevens and Miller (1970) observed that sturgeon larvae (white or green sturgeon) in California's Sacramento-San Joaquin River system were primarily demersal. They caught 33 larvae in 16 bottom sampling efforts and only 1 larva in 8 surface and midwater sampling efforts. Relative abundance of resident demersal fishes known to prey on white sturgeon eggs and suspected to prey on yolk-sac larvae was greatest in John Day Pool, followed by the free-flowing reach, Bonneville Pool and The Dalles Pool (unpublished data, National Marine Fisheries Service, Miller and Beckman 1992c).

If egg predators are attracted to spawning areas, rapid dispersal of newly hatched yolk-sac larvae would reduce encounters with potential predators. Upon hatching, white sturgeon larvae enter the water column, presumably to aid in downstream dispersal (Brannon et al. 1985a). Brannon et al. (1985a) found in laboratory studies that the duration of this swim-up phase was indirectly related to water velocity. However, the water velocities used in those experiments, 0.02 and 0.08 m/s, were considerably less than the 0-5-2.4 m/s water velocities measured near the substrate in white sturgeon spawning areas and the 0.3-2.4 m/s velocities measured near the substrate at sites where yolk-sac larvae were collected in the Columbia River (Parsley et al. 1992). Larval fish in water velocities this high could be transported downstream considerable distances in a short time. In the free-flowing reach, yolk-sac larvae have been collected over 175 km downstream from the known spawning area (McCabe and Tracy 1992).

White sturgeon yolk-sac larvae are probably most vulnerable to predators during the swim-up phase. The large opaque larvae drifting with the water currents may be quite obvious to visual predators. Turbidity and darkness may provide cover for the drifting larvae, but turbidities in the Columbia River have probably been reduced by construction of 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. A propensity to drift at night would reduce encounters with visual predators. Yolk-sac larvae of lake sturgeon are nocturnal drifters (Kempinger 1988). The majority of efforts to collect drifting white sturgeon yolk-sac larvae from the Columbia River were during daylight (unpublished data, U.S. Fish and Wildlife Service and National Marine Fisheries Service). However, in a 12-h study conducted downstream from Bonneville Dam, McCabe and Tracy (1992) found no significant difference between day and night catches of larval white sturgeon ($P > 0.05$).

Post-volk-sac Larvae

Mortality of larval fish is often greatest during the period of transition from endogenous to exogenous feeding (Hjort 1926). Post-yolk-sac larval white sturgeon require 25-30 days to metamorphose into juveniles with a full complement of fin rays and scutes. During this time, the fish actively feed on the substrate and are susceptible to predation, starvation, disease, and parasitism. Predation on post-yolk-sac larvae has been noted in laboratory experiments (Brannon et al. 1986), but has not been investigated in the Columbia River. Potential predators collected in association with post-yolk-sac larvae include bridgelip suckers Catostomus columbianus, largescale suckers, bullheads Ictal urus spp., common carp, peamouth ~~Mvlocheilus caurinus~~, chiselmouth Acrocheilus alutaceus, northern squawfish, prickly sculpin, larger white sturgeon, and starry flounder Platichthvs stellatus. Post-yolk-sac larvae develop defensive scutes as they grow, and their vulnerability to predation probably declines rapidly as they grow.

It is unknown if or when 'irreversible starvation' or the point-of-no-return' (May 1974) occurs for larval white sturgeon that are deprived of food. In a laboratory study, if food was not present post-yolk-sac white sturgeon re-entered the water column, presumably to be displaced farther downriver to a food source (Brannon et al. 1985a). White sturgeon raised in aquaria fed on common carp larvae, Daphnia spp., and benthic tubifex worms. Post-yolk-sac white sturgeon collected in the Columbia River fed primarily on amphipods (Corophium spp.; Sprague et al. 1992).

Post-yolk-sac white sturgeon are probably not food limited in the impounded areas. Limited studies on benthic invertebrates in the freshwater portion of the free-flowing reach and in The Dalles Pool showed that densities in The Dalles Pool were greater than densities of invertebrates in the free-flowing reach (McCabe et al. 1992; Sprague et al. 1992). Though benthic invertebrates have not been studied in Bonneville or John Day pools, impoundment and the corresponding reduction in water velocities have probably increased secondary production and benthic invertebrate densities.

Juveniles

Juvenile white sturgeon numbers are reduced by predation, starvation, disease, parasitism, and direct and indirect human actions. Losses of juveniles to predation are probably slight, due to the benthic habits, fast growth, and defensive scutes. Only one juvenile white sturgeon was consumed by a channel catfish Ictalurus ounctatus during a study that investigated gut contents of more than 4,780 northern squawfish, 1,050 walleye Stizostedion vitreum, 4,800 smallmouth bass Micropterus dolomieui, and 650 channel catfish (unpublished data, U.S. Fish and Wildlife Service). Other potential predators on white sturgeon listed previously were not examined in that study.

The impounded areas should be able to support densities of juvenile white sturgeon that are equal to or greater than densities in the free-flowing reach. Estimated juvenile white sturgeon densities in the four reaches, based on trawl catches, were highest in the free-flowing reach, followed by Bonneville, The Dalles, and John Day pools (unpublished data, National Marine Fisheries Service; Miller et al. 1991). Losses due to starvation are probably higher in the free-flowing reach than in the impoundments because juvenile white sturgeon feed primarily on benthic invertebrates, which are more abundant in the impounded areas than in the free-flowing reach. Generally, growth rates, mean length at age, and condition factors were greater for juvenile sturgeon captured in the impounded areas than for those collected in the free-flowing reach (Miller and Beckman 1992b), 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.

Hatchery reared white sturgeon are susceptible to many of the same diseases and parasites common to other fishes reared in culture facilities (Conte et al. 1988), but losses of white sturgeon to disease and parasites in the river are difficult to quantify. Fish weakened by disease or parasites are more vulnerable to predation. The degree of infestation by the nematode parasite Cvstooosis acipenseri varied spatially and temporally, and was greater in smaller white sturgeon (McCabe 1992). However, it is unknown if infestation causes mortality.

Human actions sometimes cause mortality of juvenile white sturgeon. Suction dredging in deep areas (20-26 m) in the lower 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. Suction dredging is rarely conducted in the impounded areas. Lost and abandoned gill nets kill substantial numbers of juvenile and adult white sturgeon in impounded areas (personal observations by the authors), and large numbers of fish are occasionally killed during maintenance activities at the dams (personal communication, John DeVore, Washington Department of Fisheries, Battle Ground, Washington). Hooking mortality of angler-caught sublegal-sized fish probably accounts for a minor loss of juvenile white sturgeon.

Conclusions

Construction and operation of dams in the Columbia River Basin have altered the historic river hydrograph by reducing discharges during the spring and summer, creating a more stable environment. Species adapted to an ever-changing riverine environment become more or less dependent on the annual cycles or fluxes (Nesler et al. 1988). Hubbs (1972) suggested that a steady-state environment is deleterious to most native stream fauna. Research since 1987 has revealed year-class failures and poor recruitment to young-of-the-year for white sturgeon in the three impoundments on the Columbia River downstream from McNary Dam, yet recruitment in the unimpounded river downstream from Bonneville Dam has occurred each year (McCabe and McConnell 1988; McCabe and Tracy 1992; Miller and Beckman 1992b). The combination of low broodstock numbers as a result of overexploitation (Rieman and Beamesderfer 1990) and poor spawning habitat as a result of hydroelectric development probably caused the lack of recruitment in the impoundments. For long-lived species like the white sturgeon, occasional year-class failures may not be detrimental to the population.

Year-class strength is determined by the number of eggs spawned and the survival rates over several independent life stages, all of which must be high to produce a strong year-class (Walters and Collie 1988). Increasing the number of white sturgeon eggs spawned or decreasing mortality at any life stage should increase the white sturgeon populations in the impounded reaches. Increasing the number of eggs spawned could be achieved by increasing adult numbers and providing better spawning habitat. Survival of eggs and larvae could be enhanced by providing higher water velocities in the impounded areas by increasing river discharge during the spawning, incubation, and yolk-sac larvae periods. Simulating natural flow patterns containing spring runoff spikes that are near the magnitude of historic flows may be necessary to improve white sturgeon spawning in the impoundments. Nesler et al. (1988) suggested restoring spring runoff spikes to stimulate spawning by Colorado squawfish (Ptychocheilus lucius) in areas downstream from dams.

Measures being considered to increase water velocities in impoundments to aid in the outmigration of threatened and endangered salmonids in the Columbia River Basin should benefit white sturgeon spawning if they coincide with white sturgeon spawning. Juvenile salmonid outmigrations generally occur during the white sturgeon spawning period. Potential actions include lowering water elevations in impoundments and augmenting spring and summer flows; both will increase water velocities. The increased water velocities will improve spawning habitat, aid the dispersal of white sturgeon larvae, and could reduce predation on white sturgeon eggs and larvae. Parsley and Beckman (1992) showed that lower water elevations in John Day Pool provided more spawning habitat for white sturgeon in the McNary Dam tailrace.

White sturgeon populations in the impoundments could be increased directly through supplementation. Broodstock numbers in the impoundments could be increased by providing better passage at the dams. Fish elevators at Bonneville Dam were once effective in passing white sturgeon from the free-flowing reach into Bonneville Pool (Warren and Beckman

1992). A similar elevator existed at The Dalles Dam. These could be reactivated to allow white sturgeon passage into lower density areas or existing ladders could be modified to increase white sturgeon passage.

Juvenile white sturgeon could be stocked into low density reaches from hatchery operations, or by transplanting fish from the free-flowing reach into the impoundments. Bottom trawling at certain locations during spring and fall was very effective at capturing large numbers (i.e. > 100 fish/5 min tow) of juvenile white sturgeon. These fish could be transported upriver, perhaps using existing juvenile salmonid transportation barges or trucks, into impoundments with low densities of white sturgeon. Collection and transportation of wild fish would alleviate concerns about the genetic integrity of hatchery reared fish. Removing several thousand juvenile white sturgeon from the free-flowing reach would probably have a minimal effect on the white sturgeon fishery in that reach.

Without successful reproduction or supplementation of fish in the impoundments, the probable consequence of current white sturgeon management strategies will at best be the further curtailing of recreational and commercial harvest opportunities, and at worst the extirpation of white sturgeon from vast reaches of the Columbia River Basin as existing fish die. Past reliance on harvest management only as a means of maintaining white sturgeon populations was due to the paucity of information on white sturgeon ecology. Hydroelectric development has affected white sturgeon populations, with this new information, additional management strategies can be developed to enhance white sturgeon populations.

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Life History and Population Dynamics

REPORT D

Higration and Distribution of White Sturgeon in the Columbia River Downstream from Bonneville Dam and in Adjacent Harine Areas

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Abstract.- White sturgeon *(Acipenser transmontanus)* migrations within and outside the lower Columbia River downstream from Bonneville Dam (LCR) were documented based on tag data. This study, the most extensive white sturgeon tagging study reported, was based on 26 years of mark and recapture data where 40,221 white sturgeon were captured, marked, and released and 5,049 marked fish were recaptured and removed from the marked population. Results of this research effort confirmed a general pattern of seasonal distribution within the LCR described by past researchers. A consistent annual migration pattern of upstream migration in the fall, a quiescent winter period, downstream migration in the spring, and a large congregation of sturgeon in the estuary in the summer were described for subadult white sturgeon in the LCR. Seasonal availability of adult salmonids *(Oncorhynchus sp.)*, eulachon *(Thaleichthys pacificus)*, and northern anchovies *(Engraulis mordax)* were thought to influence white sturgeon seasonal distribution within the LCR. Seasonal spawning migrations by adult white sturgeon could not be identified from this tagging study, although other data supported this phenomenon. Tag recoveries outside the LCR described out-of-system migrations ranging from the southern Oregon coast to Puget Sound, Washington.

White sturgeon *(Acipenser transmontanus)* range along the Pacific coast of North America from the Aleutian Island chain in Alaska to Monterey, California (Scott and Crossman 1973). Major white sturgeon production areas have been identified in the Sacramento/San Joaquin, Columbia, and Fraser river basins. White sturgeon are diadromous but many populations have survived isolation by dams.

Columbia River white sturgeon are most abundant in the lower Columbia River downstream from Bonneville Dam (LCR) (DeVore et al. 1992). The LCR white sturgeon population has a greater potential productivity relative to impounded populations in the basin. This is partly attributed to the ability of LCR sturgeon to utilize ocean-based food resources and escape in-river exploitation (DeVore et al. 1992).

White sturgeon migrations are primarily associated with feeding, reproduction, and water temperature (Bajkov 1949, 1951; Miller 1972; Scott and Crossman 1973; Haynes 1978; Haynes and Gray 1981)) although changes in distribution have been associated with catastrophic events such as the Mt. St. Helens eruption in 1980 (Stockley 1981; Galbreath 1985). Seasonal migrations of the LCR population were documented by past researchers. Bajkov (1951) described a general pattern of "small and medium sized individuals" migrating upstream in the fall and early winter and downstream in late winter and early spring. Bajkov concluded that these patterns of movement were migrations by immature sturgeon feeding on salmon and lamprey carcasses in the fall and smelt in the spring. Similar patterns of seasonal movement have been documented for other populations, including those isolated by dams (Coon et al. 1977; Haynes 1978; Haynes and Gray 1981; Dixon 1986; North et al. 1992), indicating a possible genetic propensity for seasonal migrations.

Miller (1972) and Haynes (1978) observed larger fish moving upstream in the winter and early spring in the Sacramento and Columbia rivers, respectively. They hypothesized that these fish were reproductively mature and migrating to spawning areas. In the LCR, spawning takes place in the 5 km reach downstream from Bonneville Dam each spring (McCabe and Hinton 1990; Grimes 1991; McCabe and Tracy 1992). Upstream spawning migrations by mature adults would be expected each year prior to the spawning season.

White sturgeon are capable of making extensive migrations outside their natal river basins (Chadwick 1959; Scott and Crossman 1973; Kohlhorst et al. 1991). The degree of mixing and genetic transfer between populations in the Sacramento/San Joaquin, Columbia, and Fraser river basins is currently unknown, although there is genetic evidence that the Columbia Basin provided founders for the Fraser system following the last ice age (Brown et al. 1992).

The LCR white sturgeon tagging study is the most extensive white sturgeon tagging program reported in the literature. For the 26 year period since 1965, a total of 40,221 white sturgeon have been tagged with 5,049 marked white sturgeon recovered and removed from the tagged population. The duration and magnitude of the study have given managers a long time series of critical data to refine harvest management strategies for the LCR population.

Understanding migration and distribution patterns is necessary for accurate population dynamics modeling and effective fisheries management strategies; critical components for optimizing the production potential of a population. This report documents the distribution and seasonal migrations of LCR white sturgeon based on tagging and catch sampling data. Seasonal abundance of forage species are compared with distribution of white sturgeon. Aspects of the life history of LCR white sturgeon pertaining to seasonal distribution are discussed.

Methods

Lower Columbia River research fisheries conducted by the Washington Department of Fisheries (WDF) and the Oregon Department of Fish and Wildlife (ODFW) from 1983-1991 were used to capture and mark white sturgeon. Sturgeon were marked using sequentially numbered spaghetti tie tags inserted at the base of the dorsal fin. Research fisheries were located at: Columbia River estuary (rkm 9-32), Woody Island (rkm 45), Skamokawa (rkm 55), Mayger (rkm 87), Kalama (rkm 127), Corbett (rkm 200), and Bonneville (rkm 230) (Figure 1). Drift and set gillnets with stretch mesh sizes ranging from 15.9 to 30.5 cm (6¼ to 12 in) were used to capture sturgeon (Appendix Table 1).

Mark recoveries were primarily obtained from commercial and recreational fishery sampling conducted by WDF and ODFW. These recoveries were referred to as "in-sample". Voluntary tag recoveries were also solicited from commercial fishermen and recreational anglers. Recoveries from marine and other areas outside the LCR were primarily obtained from voluntary returns. Additional recoveries from tagging efforts in 1965-1982 were used to document distribution of marked fish outside the LCR.

Seasonal distribution patterns within the LCR *were* compared using mark recovery frequency distributions by recovery month and recovery area. Tag recoveries were adjusted by the sampling rate calculated for each recovery area stratification. Area stratifications were recreational fishery sampling sections 1, 2-9, and 10 (Figure 1). Catch per unit effort (CPUE) data from the recreational fishery (Melcher and King 1991) were also used to determine seasonal distribution patterns. The CPUE in recreational fisheries was assumed to reflect relative abundance of sturgeon. Recreational CPUE comparisons were made by month and area. Multiple recaptures of marked sturgeon were also reviewed to ascertain seasonal migration patterns.

Seasonal distributions of sturgeon were compared to seasonal abundance of known forage species. Commercial landings of Columbia River smelt *(Thaleichthys pacificus)*, commercial landings of northern anchovies *(Engraulis mordax)* in ocean areas 1 and 2 (Cape Falcon, Oregon to the Queets River mouth in Washington) (Figure 2), Bonneville Dam counts of shad *(Alosa sapidissima)*, and Bonneville Dam counts of adult and jack salmonids *(Oncorhynchus sp.)* were used as indices of forage abundance.

Out-of-system migration analysis used tag and recovery information from white sturgeon tagged between 1965 and 1991, and recovered outside the LCR. Tag recoveries were enumerated by recovery location and month

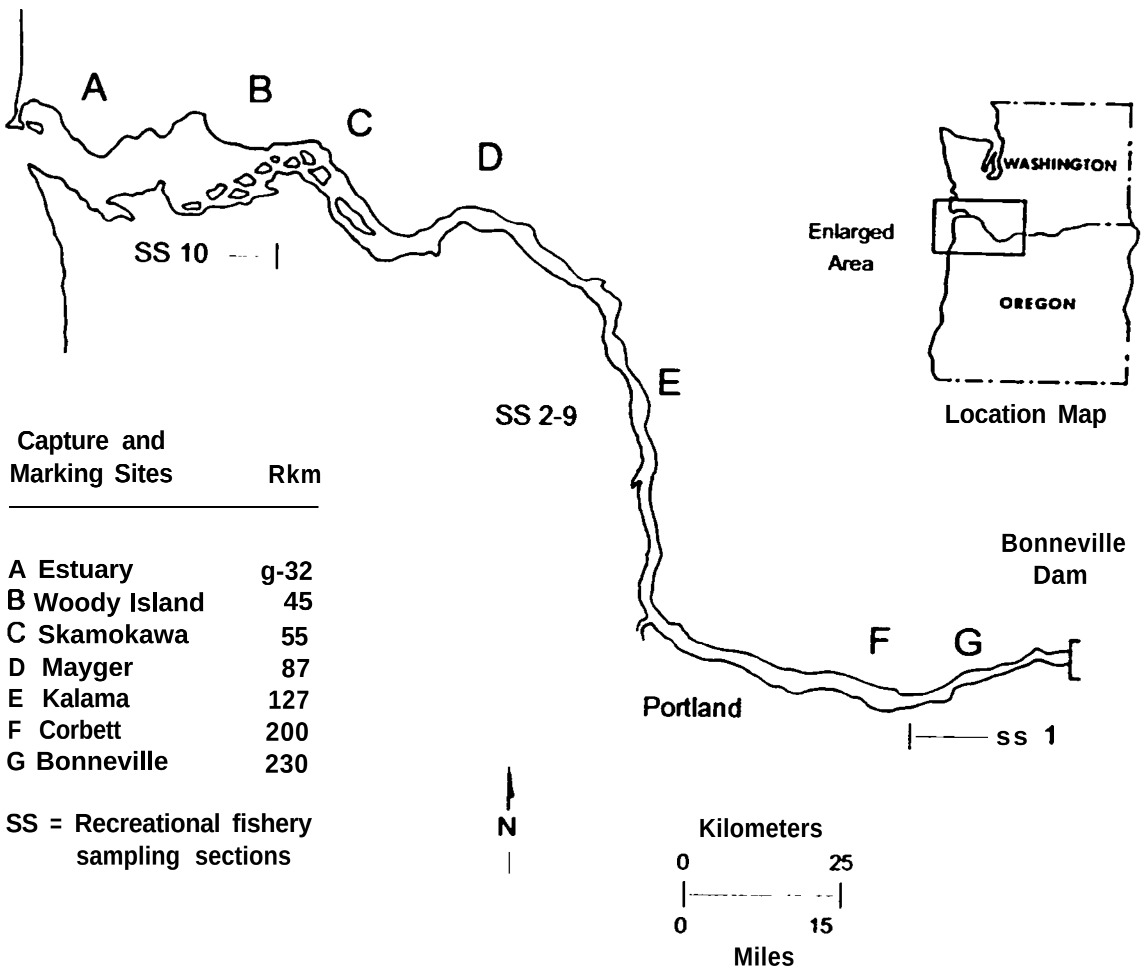

Figure 1. Locations white sturgeon were captured and marked on the Columbia River downstream from Bonneville Dam, 1983-1991.

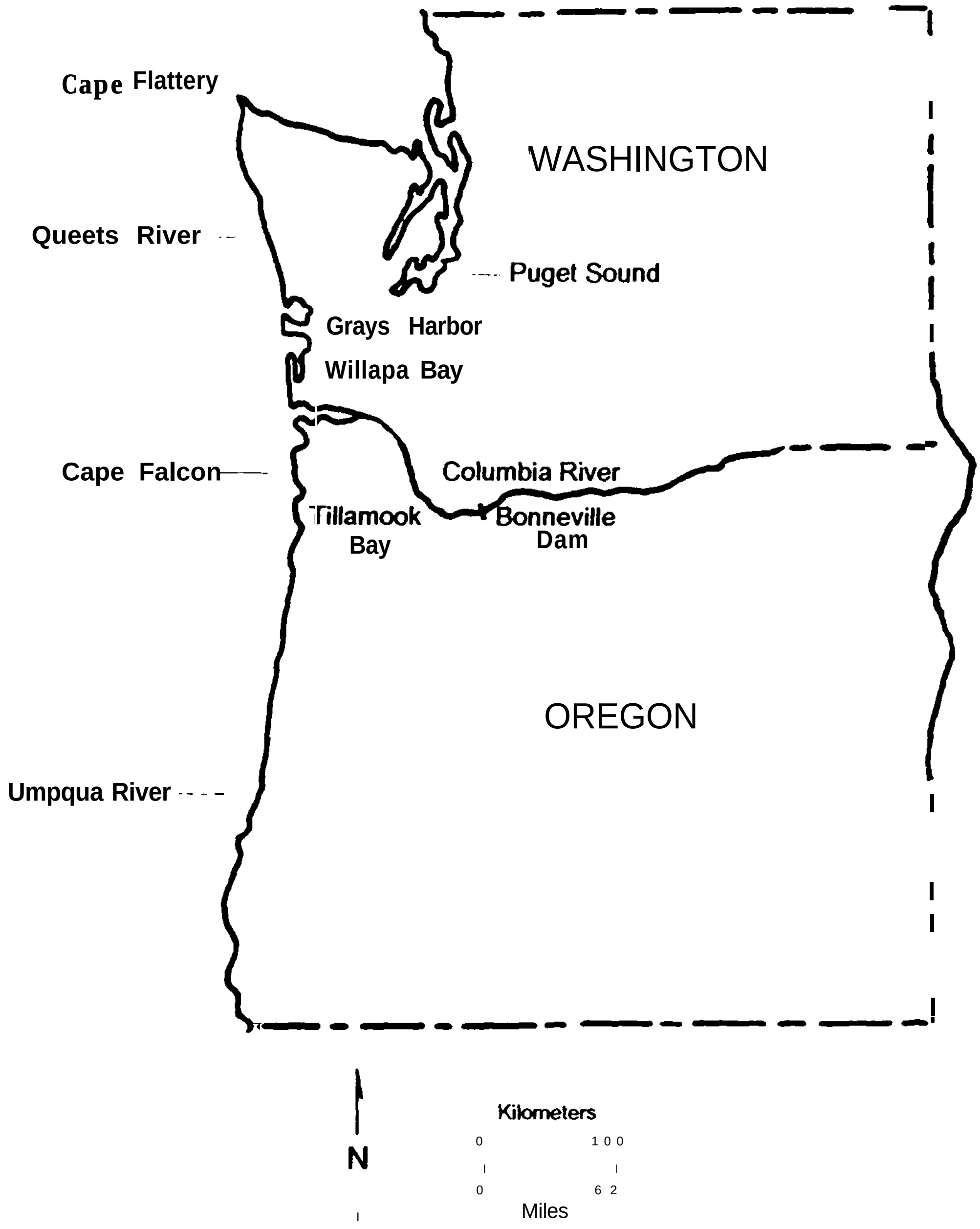

Figure 2. Map of Washington and Oregon coastal areas showing extent of out-of-system tag recoveries from white sturgeon tagged in the Columbia River downstream from Bonneville Dam, 1970-1991.

for all years combined. Recovery location and month were compared to document seasonal patterns.

Results

Consistent seasonal patterns of LCR white sturgeon distribution were identified using mark recovery frequency distributions by month and area. The frequency of white sturgeon mark recoveries in upstream areas of the LCR (recreational fishery sampling section 1) was greatest in the spring and fall (Figure 3). Middle reaches of the LCR (recreational fishery sampling sections 2-9) had the greatest frequency of mark recoveries in the fall and winter/early spring months. The estuary (recreational fishery sampling section 10) eclipsed all other LCR areas for summer mark recoveries. In fact, estuary mark recoveries in summer months outnumbered all other recoveries combined, indicating the highest annual concentration of white sturgeon in the LCR. Seasonal distribution patterns were similar regardless of the area sturgeon were tagged (Figure 4). This result indicates that there was little bias resulting from tagging location and/or there is not a significant nonmigratory "resident" population in the LCR. Recreational CPUE data showed the same seasonal trends of white sturgeon distribution within the LCR (Figure 5). Multiple recoveries of marked LCR white sturgeon supported the general trend of high summer abundance in the estuary, upstream migration in the fall, higher abundance in upstream areas in the fall, winter, and early spring, and downstream migration in the spring.

Comparison of white sturgeon distribution within the LCR with that of important forage species did not indicate a strong correlation between abundance of northern anchovies in ocean areas 1 and 2 and abundance of white sturgeon in the estuary in the summer (Figure 6). The increased abundance of white sturgeon in the middle reaches of the LCR was associated with abundance of smelt in the winter and early spring months. Increased numbers of sturgeon in recreational fishery sampling sections 2-9 in the fall and early winter was not associated with abundance of an identified forage species but may represent a general upstream migration from the estuary in the fall and/or increased abundance of salmonids during that time. Similarly, increased abundance of immature white sturgeon upstream in the fall, winter, and early spring may be associated with the presence of salmonid carcasses. There was no apparent association between sturgeon distribution in the LCR and high shad abundance in May and June.

There were 211 out-of-system mark recoveries of LCR white sturgeon from 1970-1991 (Table 1). The majority of out-of-system recoveries occurred in adjacent marine areas from Neah Bay to the north of the Columbia River to Tillamook Bay, Oregon to the south (Figure 2). The most distant recoveries were from Heron Island, Washington in Puget Sound to the north and from the Umpqua River, Oregon to the south. These migrations represented minimum movements of 528 km to the north of the Columbia River mouth and 298 km to the south. The average time at large for out-of-system recoveries was 620 days, ranging from 32 to 2,391 days. An insufficient number of recoveries prevented analysis for seasonal patterns of out-of-system mark recoveries.

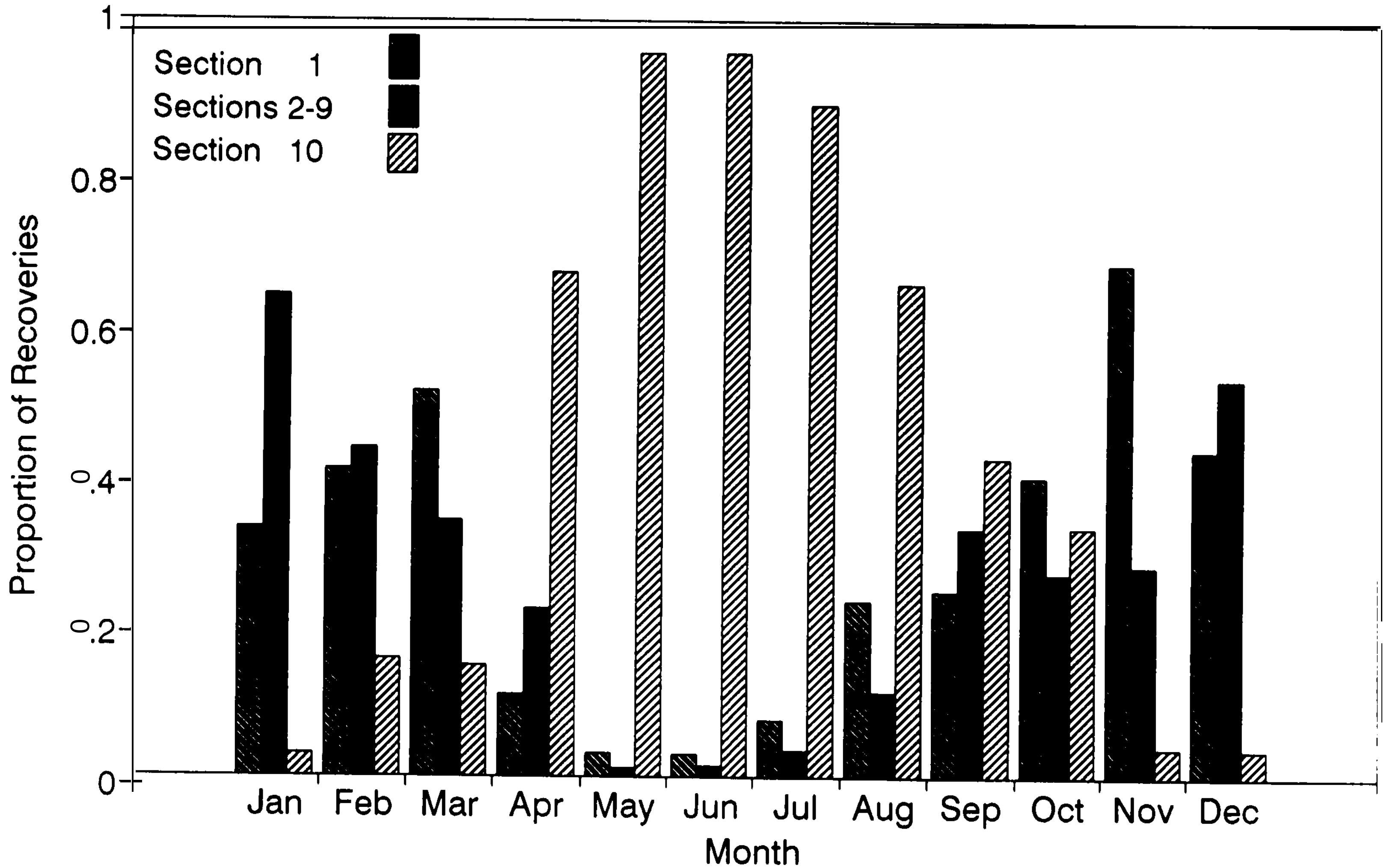

Figure 3 Proportion of in-system recoveries by month and area for white sturgeon marked in the lower Columbia River, 1983-1991.

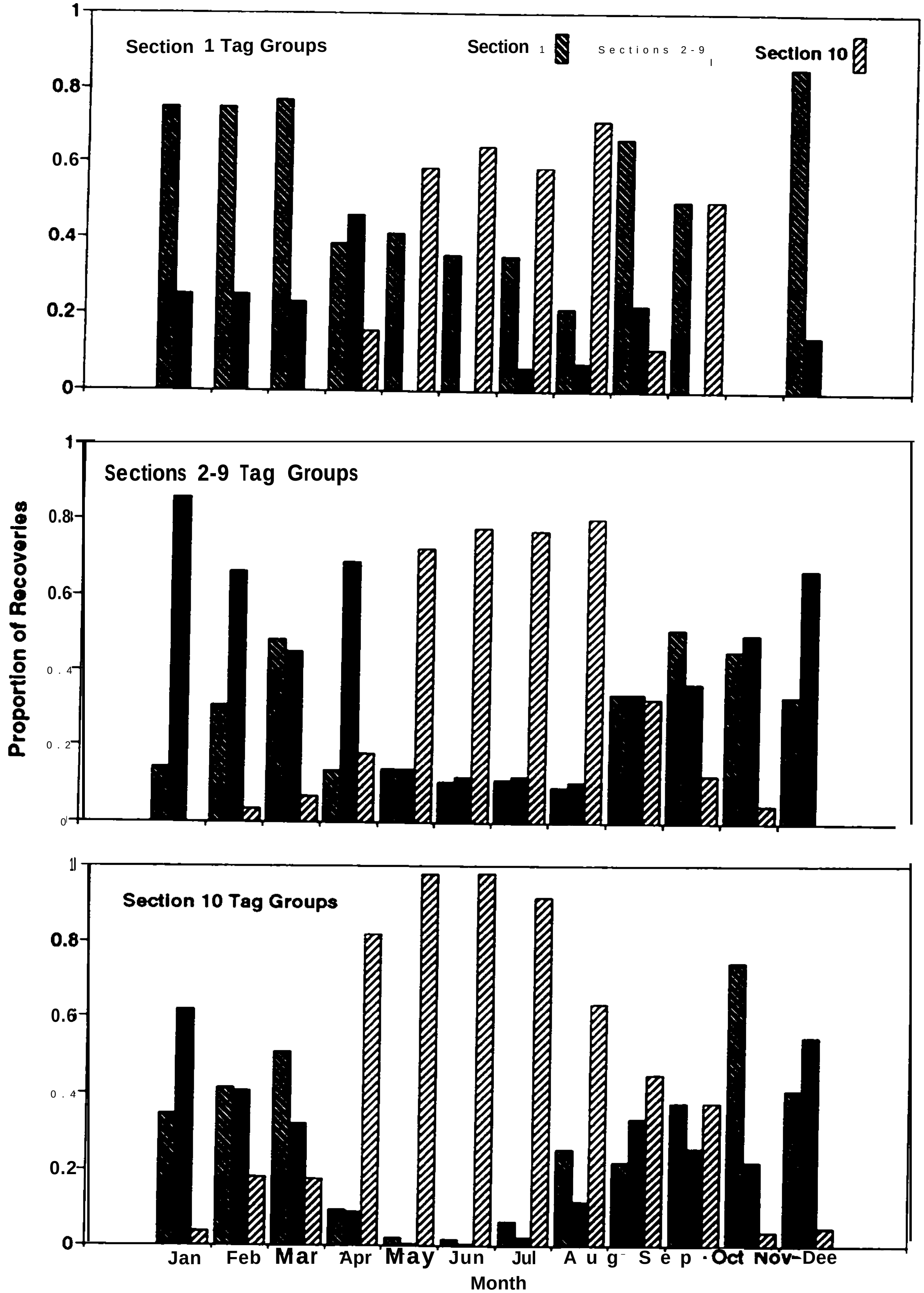

Figure 4. Proportion of in-system recoveries by month and area for white sturgeon marked in three areas of the lower Columbia River, 1983-1991.

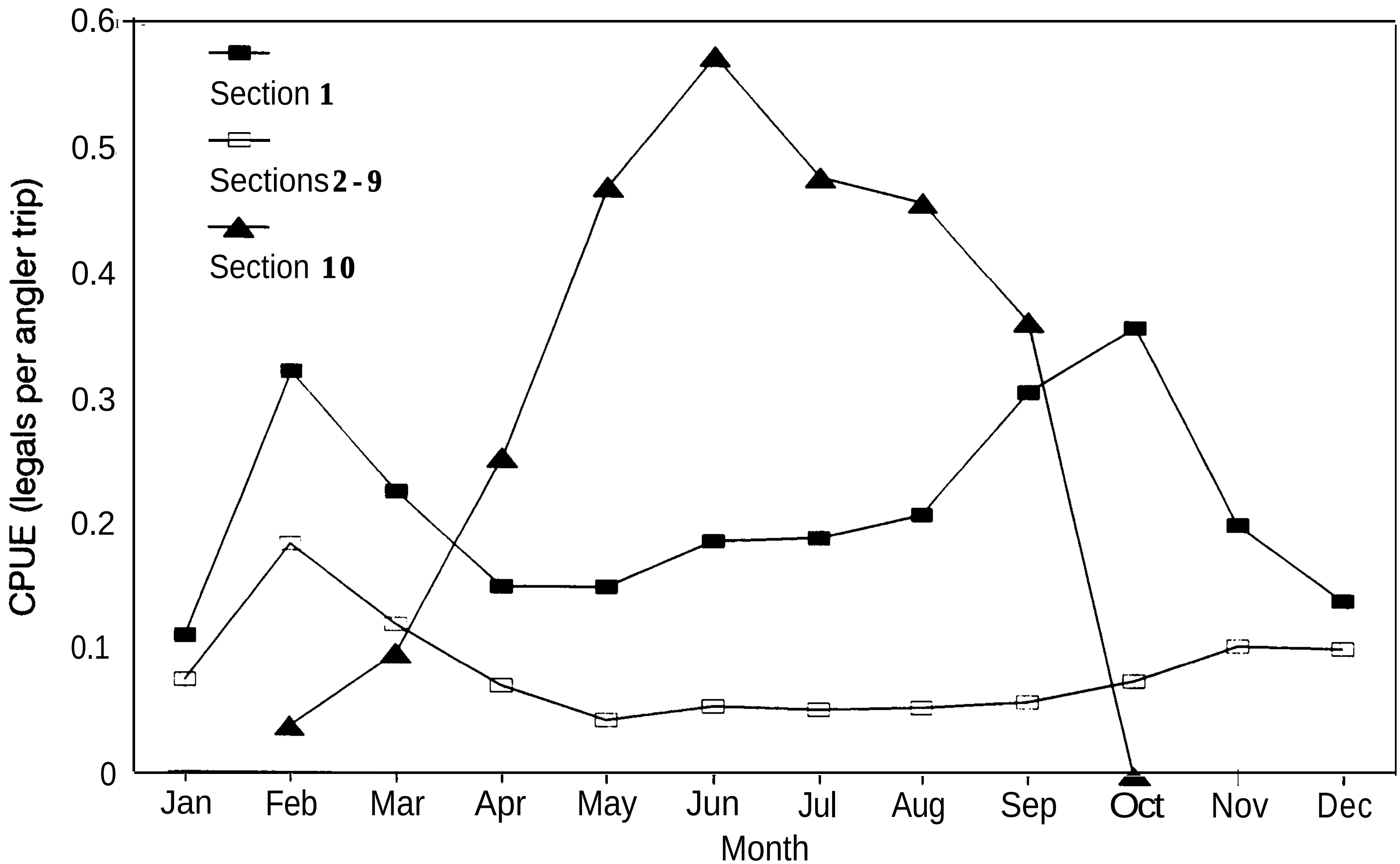

Figure 5. Average catch per unit effort (CPUE) by month for lower Columbia River recreational sturgeon fisheries, 1983-1991. CPUE is defined as the number of legal sized white sturgeon retained per angler trip.

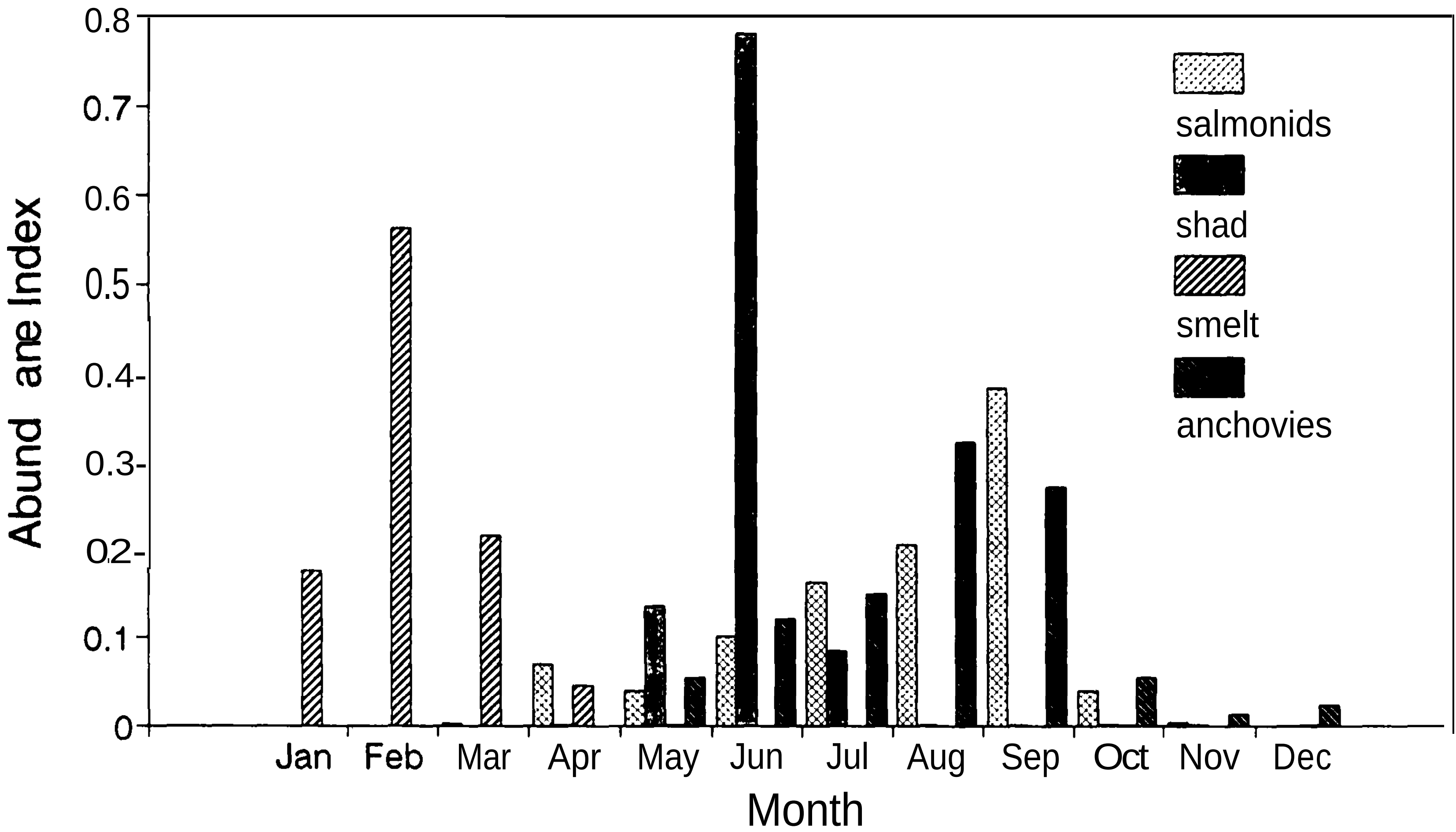

Figure 6. Abundance indices of lower Columbia River white sturgeon forage species. Indices are 1983-1991 **average monthly proportions of Bonneville Dam passage of adult salmonids and shad, and commercial landings of smelt and anchovies.**

Table 1. Out-of-system tag recoveries of marked lower Columbia white sturgeon, 1970-1991.

Recovery Location	Description	Number of Recoveries	Approximate distance from mouth of the Columbia River (km)
Heron Island	Case Inlet, south Puget Sound, WA	1	528
Clallum Bay	Straight of Juan De Fuca, east of Sekiu, WA	1	279
Neah Bay	Cape Flattery, WA	20	250
Makah Bay	West of Neah Bay, WA	1	233
Hoh River	North WA coast	1	161
Quinault River	North WA coast	11	113
Chehalis River	East Grays Harbor tributary	70	108
Humptulips River	North Grays Harbor tributary	2	89
John's River	Southeast Grays Harbor tributary	2	87
Grays Harbor	Central WA coast	22	74
Willapa River	East Willapa Bay tributary	10	71
Naselle River	South Willapa Bay tributary	30	68
Nemah River	South Willapa Bay tributary	1	58
Palix River	Southeast Willapa Bay tributary	1	50
Willapa Bay	South WA coast	17	37
Columbia River	Mouth of Columbia River	6	0
Oregon Coast	Seaside, OR, north OR coast	1	29
Nehalem Bay	North OR coast	1	64
Oregon Coast	Rockaway Beach, north OR coast	1	72
Tillamook Bay	North OR coast	6	81
Tillamook River	Tillamook Bay tributary	1	89
Oregon Coast	Nestucca Bay, OR, north OR coast	1	130
Yaquina Bay	Central OR coast	2	219
Umpqua River	Winchester Bay tributary, south OR coast	2	298
Total Recoveries		211	

Observations made during estuary sturgeon tagging indicated that fish captured and tagged in the estuary were composed of immigrants from the ocean as well as migrants from upstream areas. The two groups were differentiated by lighter skin color, sharper scutes, and superior condition factor of the ocean fish. Presence of algae and barnacles on the tag of some of the recaptured marked fish was additional evidence of ocean residence.

Discussion

Seasonal distribution patterns of LCR white sturgeon documented in our analysis were similar to that reported by Bajkov (1951). In both studies there was evidence of a general pattern of upstream migration in the fall, a quiescent winter period, downstream migration in the spring, and a large congregation of sturgeon in the estuary in the summer. Ephemeral food availability appeared to be the primary motivation for white sturgeon concentrations and migrations.

Forage species such as Columbia River smelt and salmonids seemed to influence the seasonal distribution of LCR white sturgeon. Likewise, high abundance of northern anchovies in the estuary in summer probably influences the high summer concentration of sturgeon in the estuary. Our abundance index of commercial anchovy landings from ocean areas 1 and 2 did not support this conclusion. A better index of anchovy abundance in the Columbia River would be monthly landings of anchovies caught in the Columbia River estuary. Unfortunately, that data was unavailable. Peak landings of anchovies caught in the Columbia River estuary are thought to coincide with peak catches of white sturgeon in the estuary.

Out-of-system migrations documented in our study ranged 826 km from Puget Sound to the southern Oregon coast (Figure 2). The most distant recovery represented a migration that was less than the 1,062 km documented by Chadwick (1959) or the 1,170 km reported by Kohlhorst et al. (1991). One unsubstantiated recovery of a marked LCR white sturgeon caught off Naknek, Alaska (>3,200 km from the Columbia River mouth) was reported by a Columbia River fisherman. The location was within the extreme northern range for white sturgeon (Scott and Crossman 1973), however, we could not verify the report. No marked fish from the LCR were recovered in other production basins, although white sturgeon are capable of migrating the distance to reach either the Sacramento/San Joaquin or Fraser basins. Several white sturgeon tagged in San Pablo Bay, California have been recaptured in Oregon and Washington coastal rivers and estuaries, including the LCR (Chadwick 1959; Kohlhorst et al. 1991). There is probably some interchange between populations based on the distribution of out-of-system recoveries and the genetic relatedness of white sturgeon populations (Brown et al. 1992). More intensive sampling of sturgeon outside the Columbia River would probably yield recoveries of LCR sturgeon in more distant areas including other white sturgeon production areas.

The extent of out-of-system migration could not be adequately determined due to the lack of sampling outside the Columbia River, however it appeared limited and variable. In contrast to Bajkov (1951), who assumed few LCR sturgeon migrated into marine waters, our data indicated LCR sturgeon do readily utilize ocean areas. The proportion of reported out-of-system recoveries to total recoveries in our study was .04. The proportion of out-of-system recoveries increased 100 to 500 percent during the year of the Mt. St. Helens eruption and for the next two years. Bajkov (1951) and Kohlhorst et al. (1991) reported out-of-system recovery proportions of .004 and .009 for LCR and Sacramento/San Joaquin white sturgeon, respectively. Although comparative data suggest a more extensive marine migration of LCR white sturgeon than previously assumed or reported, there does not seem to be a significant proportion of the LCR standing stock residing in the ocean. Factors influencing the frequency of out-of-system recoveries include the proportion of the LCR population with tags, the occurrence and scope of commercial and recreational fisheries outside the LCR, and catastrophic events affecting LCR water quality (Stockley 1981; Galbreath 1985). More analysis is needed to understand the frequency, timing, and environmental cues associated with out-of-system migrations.

Many authors report a distinct upstream migration in the winter and spring into known spawning areas by large, presumably reproductively mature individuals (Miller 1972; Scott and Crossman 1973; Haynes 1978). We were unable to document size specific spawning migrations due to a paucity of recoveries of large marked fish. However, Melcher and King (1991) present data relating the incidence of handling of sturgeon >6 ft. total length by month and area in the LCR recreational fishery which indicates that the highest hooking rates of large fish occurs in the upper LCR in the spring. Coupled with broodstock monitoring catches of mature sturgeon in the spring, as well as larval sampling data, there is clear evidence that large mature white sturgeon do congregate in the upper LCR in the spring. We believe that a more extensive tagging and recovery effort of large LCR white sturgeon would confirm a distinct upstream spawning migration in winter and early spring months.

There are unanswered questions pertaining to movements and distribution of LCR white sturgeon: What proportion of the LCR population migrates to marine areas? What is the duration of marine residence? What factors are responsible for marine migrations, especially in light of an abundant forage base in the LCR? What are the movements and distribution of large mature sturgeon? Further research is needed to fully understand these migration patterns. We recommend that radio and/or sonic tracking studies be conducted in the LCR. Better comprehension of migration patterns will help refine our understanding of population dynamics. Conservative harvest management strategies, such as the creation of sanctuaries to protect spawning fish, may be identified pending conclusive results.

Acknowledgements

We thank Chuck Tracy and Brad James for providing helpful comments during the writing of this report. Technical staff from the Washington Department of Fisheries and Oregon Department of Fish and Wildlife assisted in data collection and analysis of supporting data. This research was funded by the Federal Aid to Fish Restoration Act, Dingell-Johnson project F-77-R.

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Appendix Table 1. White sturgeon tagging summary by research fishery and year, 1983-1991.

Year/ Fishery	No. Drifts	No. Captured	No. Tagged	No. Recaptured
1983				
Corbett	60	749	691	27
Mayger	49	743	457	4
Woody Island	24	583	483	14
Estuary	5	9	9	0
Total	138	2,084	1,640	45
1984				
Corbett	29	341	292	16
Mayger	4	88	37	0
Skamokawa	20	431	350	5
Woody Island	12	303	268	4
Estuary	2	2	2	0
Total	67	1,165	949	25
1985				
Corbett	30	256	177	7
Kalama	5	204	88	2
Mayger	13	117	109	3
Skamokawa	15	613	360	11
Estuary	23	635	624	5
Total	86	1,825	1,358	28
1986				
Corbett	35	504	231	17
Mayger	7	105	96	2
Skamokawa	22	2,392	1,076	54
Woody Island	20	1,028	777	59
Estuary	38	2,451	2,155	39
Total	122	6,480	4,335	171
1987				
Corbett	30	261	201	4
Mayger	13	37	33	1
Skamokawa	9	497	251	9
Woody Island	21	406	296	10
Estuary	74	3,164	2,948	116
Total	147	4,365	3,729	140

(Continued)

Appendix Table 1. White sturgeon tagging summary by research fishery and year, 1983-1991. (Continued).

Year/ Fishery	No. Drifts	No. Captured	No. Tagged	No. Recaptured
1988				
Bonneville	NA	88	17	0
Corbett	31	631	481	17
Mayger	6	161	76	2
Skamokawa	9	35	26	1
Woody Island	20	763	601	11
Estuary	55	1,532	1,409	100
Total	121	3,210	2,610	131
1989				
Bonneville	NA	30	24	0
Corbett	27	275	174	0
Mayger	10	45	39	1
Skamokawa	2	165	85	0
Woody Island	21	1,569	812	50
Estuary	55	4,921	4,249	225
Total	115	7,005	5,383	276
1990				
Bonneville	NA	54	50	0
Corbett	30	389	214	14
Mayger	14	32	25	1
Woody Island	30	763	369	21
Estuary	52	5,320	2,756	432
Total	126	6,558	3,414	468
1991				
Bonneville	NA	84	65	2
Corbett	30	217	83	9
Coho[1]	74	252	51	3
Skamokawa	3	40	36	0
Woody Island	20	1,237	749	43
Estuary	71	7,530	3,967	643
Total	198	9,360	4,951	700
Grand Ave.	124	4,672	3,152	220

[1] *Data are combined for a77 coho test fisheries occurring in September. Catch areas were Chinook, Skamokawa, and Eagle cliff, WA and Astoria, OR.*

REPORT E

Distribution and Movements of White Sturgeon in Three lower Columbia River Reservoirs

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Oregon Department of Fish and Wildlife

In press: <u>Northwest Science</u>

Abstract

We determined the distribution and movement of white sturgeon (Acipenser transmontanus) in Bonneville, The Dalles, and John Day reservoirs on the Columbia River from April through August, 1989-1991. The study also evaluated effects of hydroelectric dams on white sturgeon populations. Differences in catch per setline-day indicated that white sturgeon densities were greatest in Bonneville Reservoir and least in John Day Reservoir. White sturgeon concentrated in tailraces of dams and density generally declined downstream through each reservoir. Distribution within each reservoir varied with sampling month and related, in part, to temperature. Most fish were caught at depths from 10 to 30 m. Tagged fish were often recaptured in locations other than those where originally marked. Some fish were recaptured as far as 152 km from where released. Individual fish frequently traveled the length of a reservoir, but were seldom recaptured in another reservoir. Dams restrict white sturgeon movements, may limit populations in some reservoirs, and concentrate fish innnediately downstream, potentially increasing their vulnerability to exploitation. To optimize these fisheries, resource managers must recognize differences among reservoirs and employ regulatory schemes specific to each.

Introduction

The white sturgeon *Acipenser transmontanus* is a unique and ancient species endemic to large, cool rivers along the Pacific coast of North America. White sturgeon are among the largest freshwater fish in North America, exceeding 6 m and 800 kg (Scott and Crossman 1973). In the Columbia River basin, white sturgeon historically ranged from the ocean as far as 1300 km upstream into Idaho, Montana, and Canada. Individual fish were thought to have moved freely throughout the area (Scott and Crossman 1973). Sturgeon regularly undertook long-distance movements, apparently to take advantage of seasonal changes in food and habitat in this dynamic river environment (Bajkov 1951).

Dams, constructed on the mainstem Columbia since 1933, limit the distribution and constrain movements of sturgeon which, unlike salmon, do not normally use fish ladders. Cochnauer et al. (1985) suggested that white sturgeon populations in some landlocked portions of the river were isolated with respect to reproduction. Productivity appeared to vary among populations as some supported fertile fisheries while others could sustain no exploitation (Cochnauer et al. 1985). Also, dams may have led to genetic divergence of impounded populations due to reproductive isolation (Brown et al. 1992).

Understanding the distribution and movement of white sturgeon in landlocked populations may help determine why some populations thrive while others appear to be in danger of extirpation. Size-specific seasonal movements have been observed for landlocked white sturgeon in the unimpounded Hanford Reach of the mid-Columbia River (Haynes et al. 1978, Haynes and Gray 1981), but no information exists for impounded populations. This paper investigates white sturgeon distribution and movement within and among the lower Columbia River reservoirs.

Study Area

The study area included the three lowest mainstem reservoirs of the Columbia River: Bonneville (Lake Bonneville), The Dalles (Lake Celilo), and John Day (Lake Umatilla). Bonneville Reservoir (74 km; 8400 ha) is relatively shallow (average depth 6.7 m) with mostly sand substrate supporting large beds of rooted aquatic macrophytes during the summer. The Dalles Reservoir is the smallest (38 km; 4500 Ha; average depth 7.5 m), and the most riverine, with cobble, gravel, and sand substrates distributed throughout most of its length. John Day Reservoir is the largest (123 km; 21,000 Ha; average depth 8.0 km) and the most diverse. The reservoir grades from a riverine upper section with gravel and cobble substrates to a shallow transition section with sand substrate, and finally to a lentic lower section with steep cliff and boulder banks. Average daily river discgarge through the study area ranges seasonally from 3000 to over 12,000 m^3/s.

Methods

To estimate population statistics, we collected white sturgeon during 1988-1989, and 1991 in Bonneville Reservoir; 1987-1989 and 1991 in The Dalles Reservoir; and 1990-1991 in John Day Reservoir.

Stratified sampling was conducted from April through September in 1987 and 1990, May through August in 1988, and April through August in 1989 and 1991. We divided Bonneville Reservoir into eight 10-km segments, The Dalles Reservoir into six 7-km segments, and John Day Reservoir into ten 12.5-km segments (Figure 1). We also sampled the boat-restricted zones (BRZ's) which are less than 0.3 km long, and immediately downstream from The Dalles, John Day, and McNary dams. The BRZ's are unlike the remainder of the reservoir because water velocities are typically higher and potential prey fishes are concentrated or injured by the adjacent dam. Because BRZ's are unique habitats, their results are reported separately.

Sampling was distributed equally among segments and river kilometer sampling sites in each reservoir to obtain representative population samples. Each segment was normally sampled every 4 weeks in Bonneville Reservoir, every 3 weeks in The Dalles Reservoir, and every 5 weeks in John Day Reservoir. In 1991, we concentrated our sampling locations where we caught most sturgeon in previous years.

White sturgeon were collected using setlines which provide the greatest catch rate and are less size-selective than other types of gear (Elliott and Beamesderfer 1990). Each line had 40 hooks (sizes 12/0, 14/0, and 16/0) baited with pieces of Pacific lamprey <u>Lampetra tridentata</u>. We fished lines for an average 24.8 hr per set. Sets were concentrated in main-channel habitats outside navigational lanes at depths from 3 to 51 m.

We measured sturgeon fork length (FL) to the nearest cm and examined each fish for tags, tag scars, fin marks, barbel clips, and scute marks. Untagged sturgeon longer than 64 cm were spaghetti tagged at the anterior base of the dorsal fin. Sturgeon longer than 84 cm were tagged with a second spaghetti or Petersen disc dangler tag at the base of the posterior end of the dorsal fin (Smith 1978). A total of 7351 fish were tagged with individually numbered spaghetti and disc tags. The Washington Department of Fisheries (WDF) also provided tag recoveries from the recreational and commercial fisheries in the three reservoirs and in the free-flowing river between Bonneville Dam and the ocean.

We examined white sturgeon distribution by comparing setline catch rate among areas. Statistical differences ($p < 0.05$) in catch rates were evaluated on transformed catch per set data [ln(catch+l)] with programs of the Statistical Analysis System (Anonymous 1988a, Anonymous 1988b). To examine seasonal changes in distribution within each reservoir, we used an index (I) where :

$$I = \frac{S - L}{T}$$

and S is river km where fish were captured, L is river km of the lower reservoir boundary, and T is reservoir length in km. The values were averaged for all fish captured during a sampling cycle. A high river kilometer index indicates upstream distribution; a low index indicates

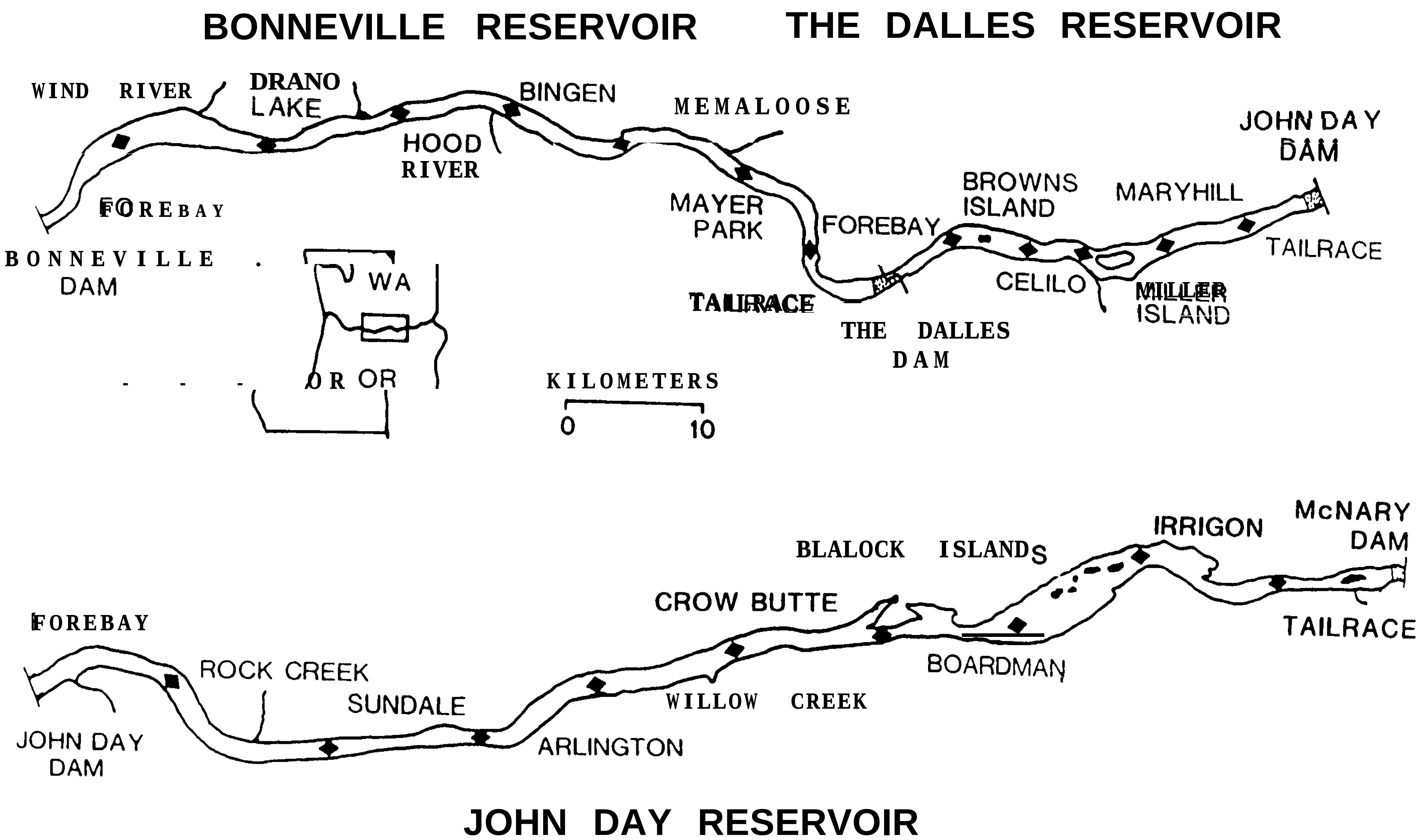

Figure 1. Columbia River from Bonneville to McNary Dams. Sampling area boundaries are indicated by ♦'s. Boat-restricted zones in dam tailraces are shaded.

downstream distribution. We assumed that seasonal changes in average catch rates implied changes in movement rates. The relationship between catch and water temperature was evaluated using linear regression.

We compared numbers of fish released and recaptured at each site to estimate the extent of movement within each reservoir and to determine whether individuals moved among reservoirs. Recaptures included all fish caught with setlines, and sport and commercial fisheries, where the kilometer of capture could be determined.

Results

Distribution

White sturgeon were not evenly distributed among study reservoirs. Average setline catch per day in Bonneville Reservoir (4.10 fish/set in 942 sets) was 1.5 times greater than in The Dalles Reservoir (2.70 fish/set in 978 sets), and 7.5 times greater than in John Day Reservoir (0.55 fish/set in 1194 sets). Catch rate differences among reservoirs were statistically significant (Table 1).

Densities (catch per day, 1987-1990) of white sturgeon were greater in the BRZ downstream of each dam than in the rest of the reservoir by 3 times in Bonneville Reservoir, 6 times in The Dalles Reservoir, and over 20 times in John Day Reservoir. Densities outside BRZ's generally decreased with distance from the dam (Figure 2). Catch rates outside BRZ's approached those near dams only at the mouth of the Klickitat River (Memaloose segment) in Bonneville Reservoir. Catch rate differences among segments were significant in all three reservoirs (Table 1).

Seasonal changes in distribution were noted in The Dalles and John Day reservoirs. Relative numbers of white sturgeon collected in midreservoir increased from April through June and declined by August and September, implying downstream and then upstream redistribution of fish (Figure 3). Differences in catch proportions in lower, middle, and upper thirds of each reservoir were related to month (Bonneville: X^2 = 186.75; df = 8; $p < 0.001$; The Dalles: X^2 = 1,197.19; df = 10; $p < 0.001$; John Day: X^2 = 334.78; df = 10; $p < 0.001$).

Catch rates in all three reservoirs peaked in June or July. Monthly differences in catch rates were significant (Table 1). Mean monthly catch rate generally increased with increasing temperature up to about 18°C and declined at greater temperatures (Figure 4). Linear regressions show that about 10-30% of the catch rate variation is related to water temperature (Bonneville: df = 3; r^2 = 0.32; p = 0.32; The Dalles: df = 3; r^2 = 0.09; p = 0.62; John Day: df = 4; r^2 = 0.17; p = 0.41).

Catch rates at different depths were significantly different, except in John Day Reservoir where sampling success was poor (Table 1). Few white sturgeon were captured at depths less than 10 m (Figure 5). No meaningful size-depth relationship in catch rate was evident

TABLE 1. Log-transformed catch [ln(catch+l)] of white sturgeon per setline day in Bonneville, The Dalles, and John Day reservoirs, 1987-1990. The Analyses of Variance (ANOVA) are one-way comparisons except Catch vs. depth*size which evaluates interaction in a two way ANOVA.

Comparison	Reservoir	df_1*	df_2*	F*	p*
Catch vs. reservoir	--	2	3,111	774.60	0.0001
Catch vs. area	Bonneville	8	933	12.00	0.0001
	The Dalles	6	971	43.62	0.0001
	John Day	10	1,183	75.06	0.0001
Catch vs. month	Bonneville	4	922	39.48	0.0001
	The Dalles	4	930	12.40	0.0001
	John Day	5	1,144	6.78	0.0001
Catch vs. depth	Bonneville	6	916	2.89	0.0086
	The Dalles	6	927	2.37	0.0282
	John Day	6	1,142	1.49	0.1783
Catch vs. depth*size	Bonneville	12	2,748	1.38	0.1676
	The Dalles	12	2,781	2.08	0.0153
	John Day	12	3,426	1.48	0.1237

* Degrees of freedom (df), test stastistic (F), and observed probability level (p) in ANOVA.

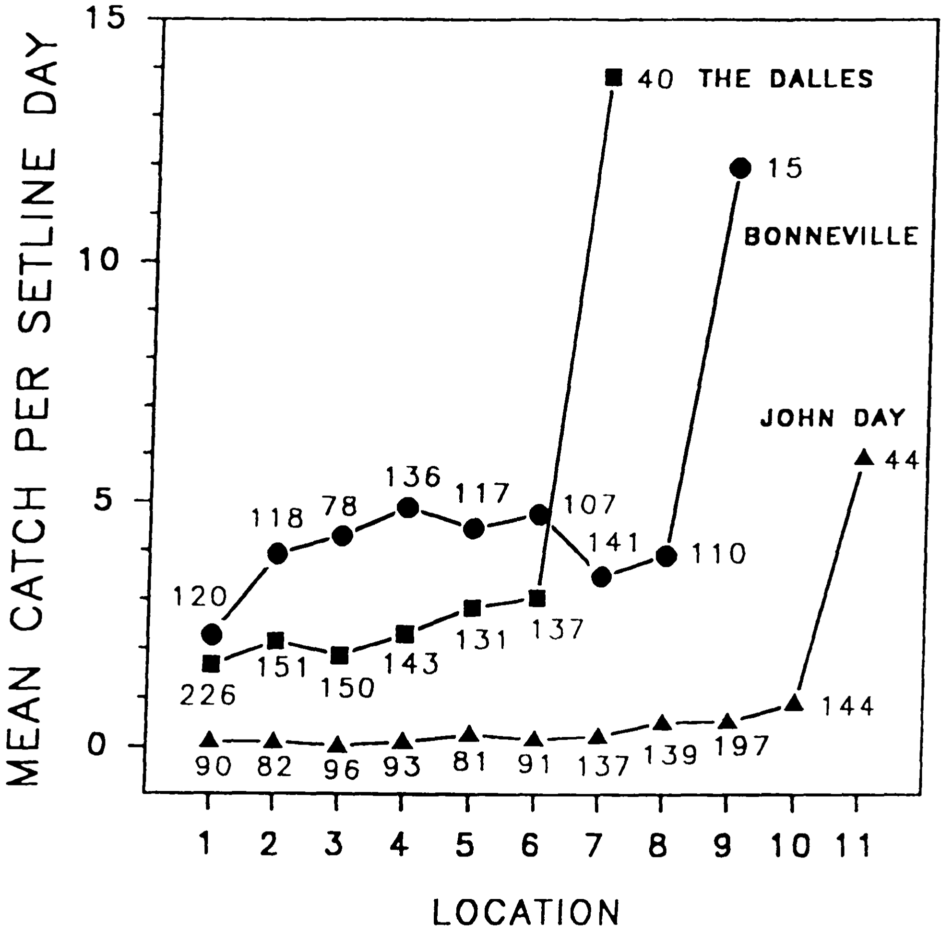

Figure 2. Mean catch per setline day of white sturgeon in Bonneville, The Dalles, and John Day reservoirs, 1987-1990. Number of sets indicated for each reservoir segment. Locations are: Bonneville Reservoir; 1 = Forebay, 2 = Wind River, 3 = Drano Lake, 4 = Hood River, 5 = Bingen, 6 = Memaloose, 7 = Mayer Park, 8 = Tailrace, 9 = The Dalles Dam Boat Restricted Zone (BRZ). The Dalles Reservoir; 1 = Forebay, 2 = Browns Island, 3 = Celilo, 4 = Miller Island, 5 = Maryhill, 6 = Tailrace, 7 = John Day Dam BRZ. John Day Reservoir; 1 = Forebay, 2 = Rock Creek, 3 = Sundale, 4 = Arlington, 5 = Willow Creek, 6 = Crow Butte, 7 = Boardman, 8 = Blalock Islands, 9 = Irrigon, 10 = Tailrace, 11 = McNary Dam BRZ.

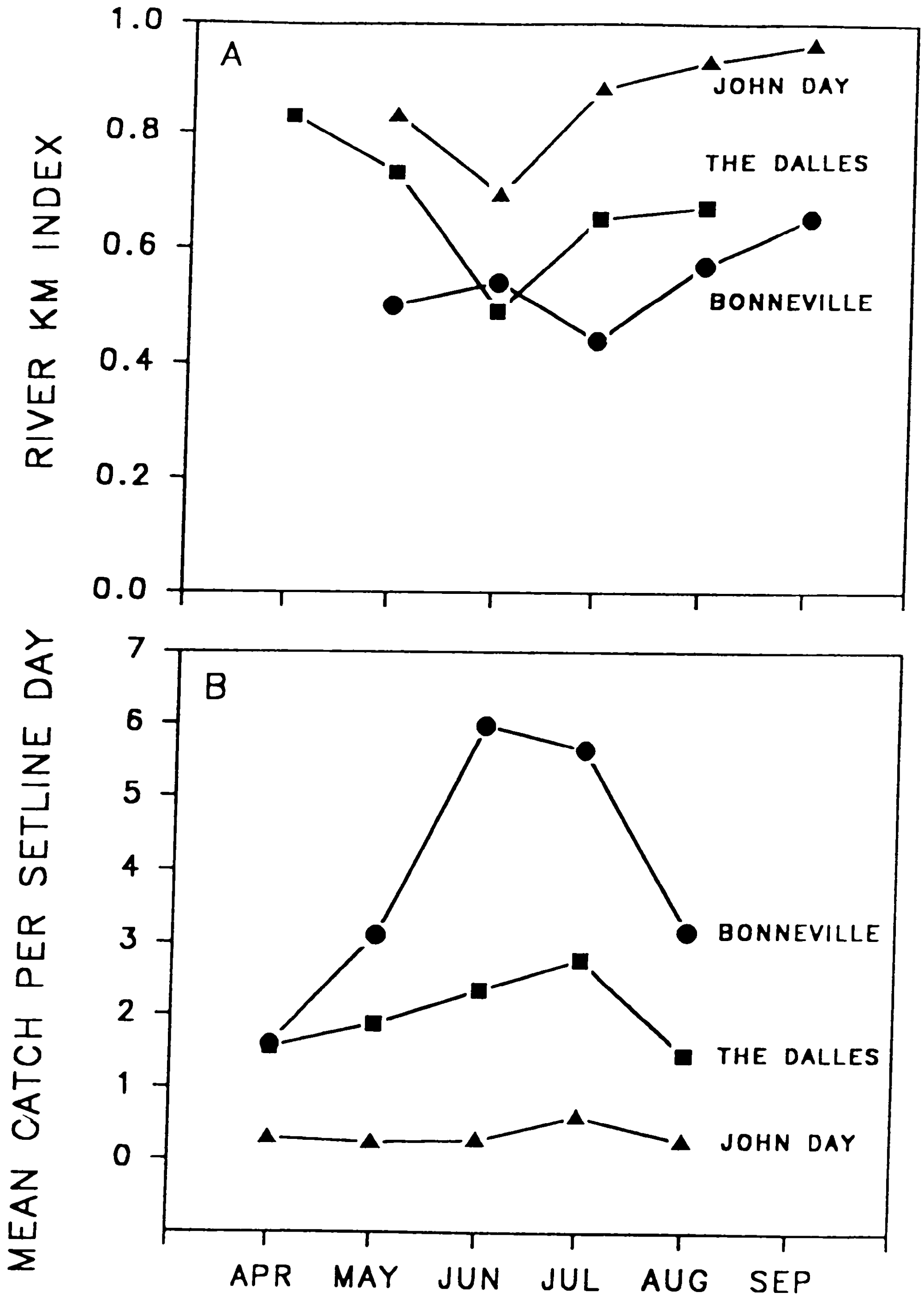

Figure 3. Index of white sturgeon distribution (A) and mean catch per setline day (B) in Bonneville, The Dalles, and John Day Reservoirs, 1987-1990. The index is the mean distance from release (km) of all white sturgeon caught during a month. The index is standardized for reservoir size by subtracting the lower reservoir bound and dividing by reservoir size. Sturgeon collected in tailrace Boat Restricted Zones are excluded.

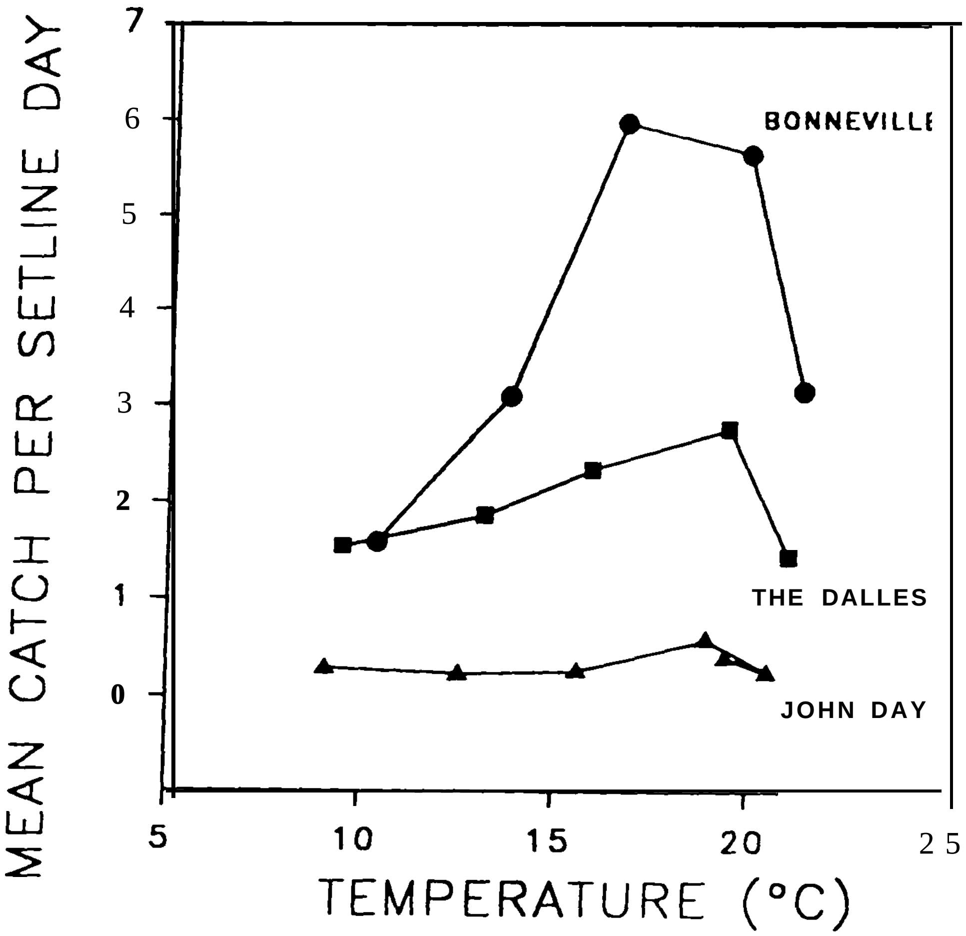

Figure 4. **Mean catch of white sturgeon per setline day versus mean monthly temperature for Bonneville, The Dalles, and John Day Reservoirs,** 1987-1990. **Sturgeon collected in the tailrace Boat Restricted Zones are excluded.**

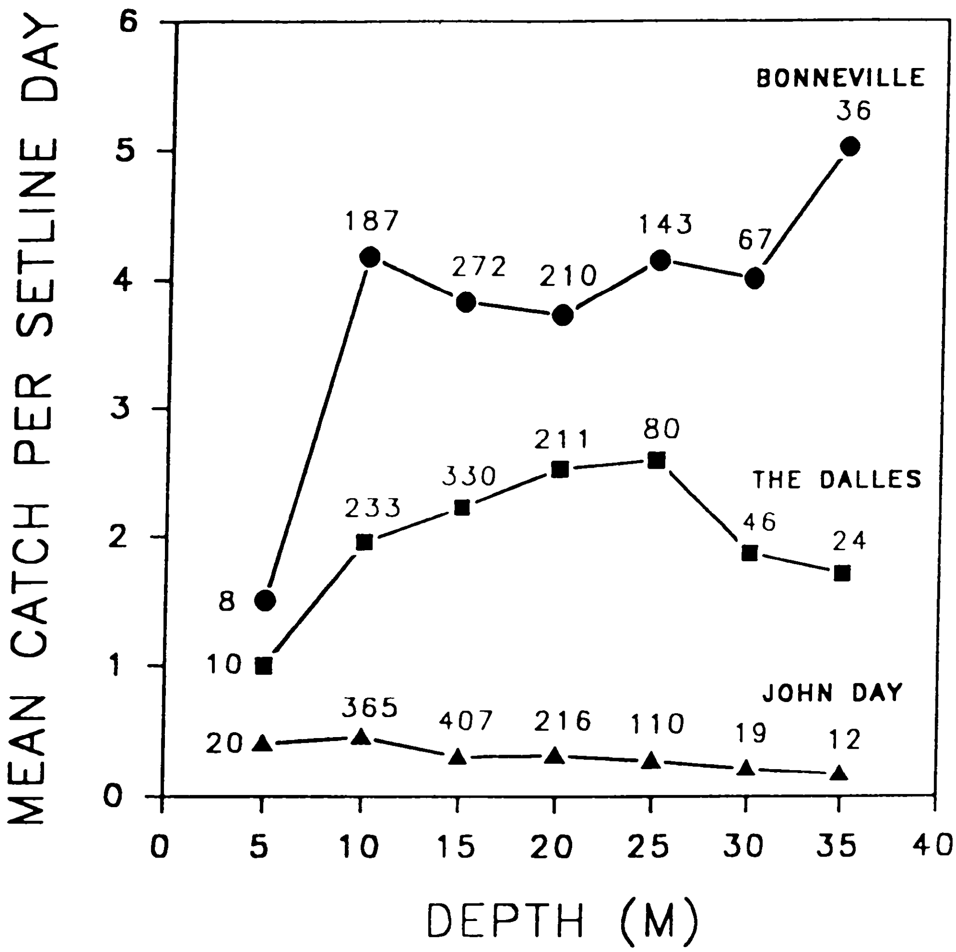

Figure 5. Mean catch of white sturgeon per setline day by 5-m depth intervals for Bonneville, The Dalles, and John Day Reservoirs, 1987-1990. Number of sets is indicated for each depth interval. Sturgeon collected in the tailrace Boat Restricted Zones are excluded.

(Figure 6), although a statistically significant size-depth interaction was noted for The Dalles Reservoir (Table 1).

Movements

Movements up to 152 km were observed among tagged sturgeon. Of 635 tagged individuals, 59% moved at least 1 km and many moved 10-30 km (Figure 7). Average distance traveled between release and recapture was 8.1 km. Of sturgeon that moved between tagging and recapture, 49.9% moved upriver and 50.1% moved downriver. Differences in fish size did not appear to affect distance or direction of fish travel.

Most movement was restricted to the collection reservoir and the extent of movement was related to reservoir length (Figure 7). Only 4% of 635 recaptured white sturgeon moved past a dam in the study area (Table 2). Of these, 26 moved downstream, and 1 moved upstream.

Discussion

The large differences observed in white sturgeon densities in the three study reservoirs may reflect differences in reproductive success, exploitation rate, and habitat availability. Regular year-class failures in John Day Reservoir, and to a lesser degree in The Dalles Reservoir (personal communication, L. Beckman, U.S. Fish and Wildlife Service, Willard, Washington) may have reduced white sturgeon numbers in these reservoirs. Recently, commercial fisheries have increased their exploitation of white sturgeon. John Day and The Dalles reservoirs were fished more than Bonneville Reservoir from 1980 to 1990 (personal communication, S. King, Oregon Department of Fish and Wildlife, Clackamas, Oregon). Finally, each reservoir has different physical conditions that may furnish critical resources in varying amounts. Although past fishery management has treated the three reservoirs as a homogenous unit, our data imply that unique regulatory schemes may be necessary to optimize the fishery in each.

The small, unique areas in the tailraces immediately downstream of each dam (BRZ's) yielded high catch rates throughout the study. Beamesderfer and Rieman (1991) reported similar concentrations near dams for another resident predator, the northern squawfish (Ptvchocheilus oreqonensis). Increased food availability may explain these concentrations as these predators eat migrating salmonids (Oncorhvnchus spp.), shad (Alosa saoidissima), and Pacific lamprey that have been injured and also concentrated during dam passage. Merrell (1961) observed a white sturgeon eating steelhead (0. mykiss) and chinook salmon (0. tshawvtscha) which, he thought, were injured as they passed through an industrial plant on the Willamette River in Oregon. Concentrations of white sturgeon in dam tailraces increase their vulnerability to exploitation by bank anglers. Existing sanctuaries in dam tailraces provide significant conservation benefits to white sturgeon populations.

Downstream from each dam, white sturgeon densities generally decreased as conditions became less riverine. The pattern in which white sturgeon moved downstream in summer and upstream in fall was

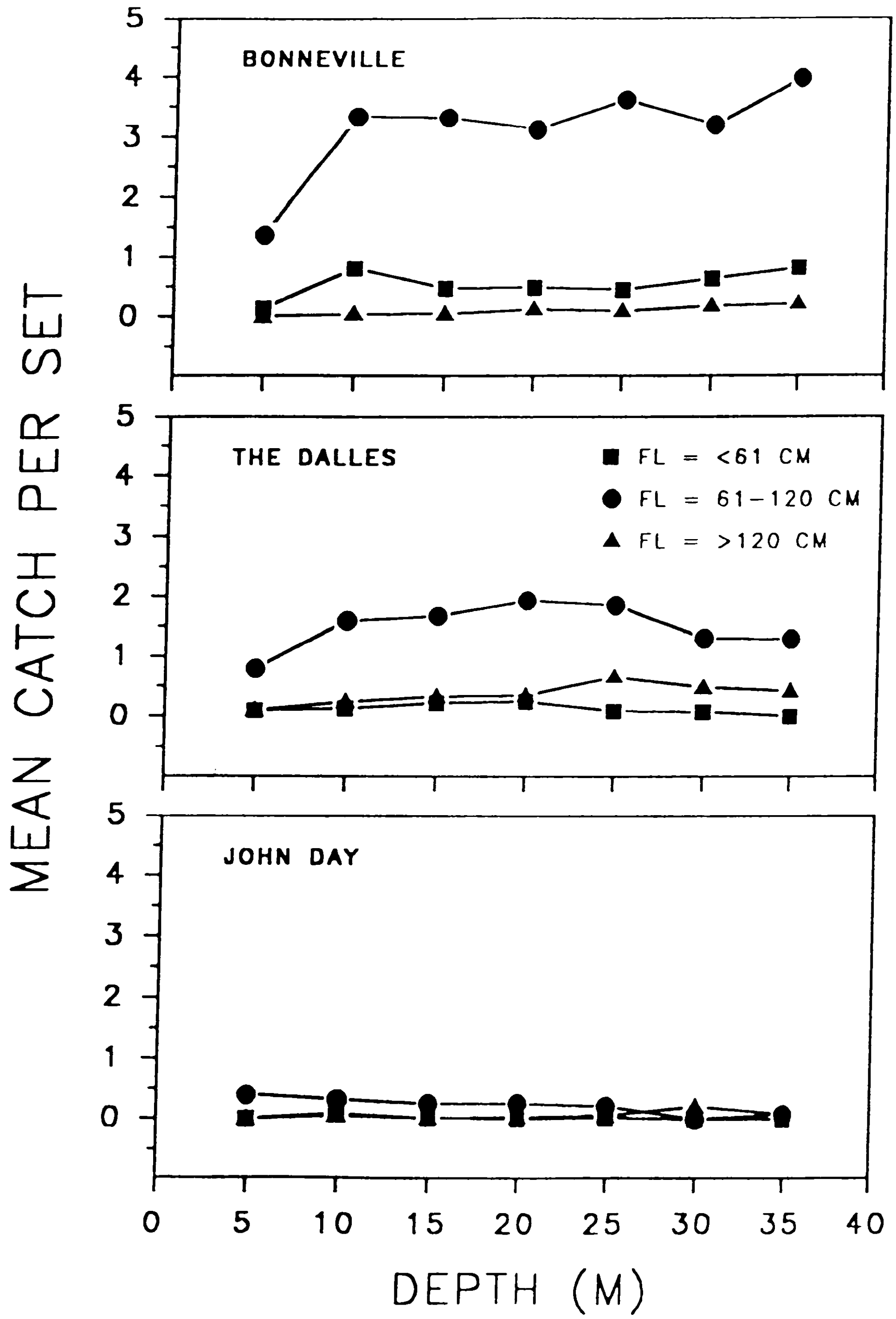

Figure 6. Mean catch of three size-classes of white sturgeon per setline day by 5-m depth intervals for Bonneville, The Dalles, and John Day Reservoirs, 1987-1990. Number of sets is indicated for each depth interval. Samples collected in the tailrace BRZ's are excluded.

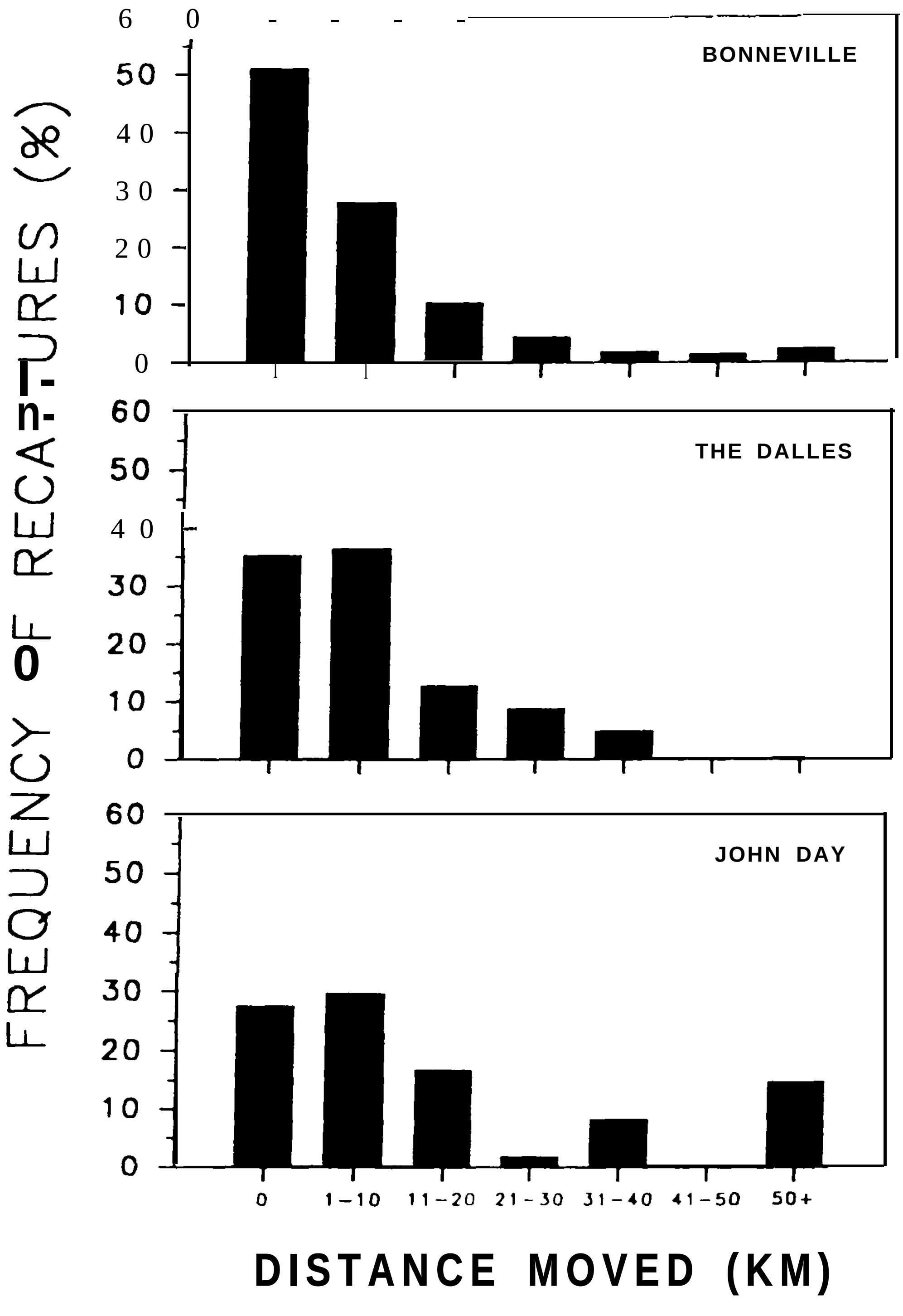

Figure 7. Frequency of white sturgeon recaptures by distance traveled between release and recapture in Bonneville, The Dalles, and John Day reservoirs, 1987-1991.

TABLE 2. Number of tagged white sturgeon released in Bonneville, The Dalles, or John Day reservoirs and recaptured in another reservoir or outside the study area, 1987-1991.

Release location	Recapture location	Recapture year					
		1987	1988	1989	1990	1991	Total
Bonneville	Below Bonneville	-	-	3	4	1	8
The Dalles	Bonneville			3	3	10	16
John Day	Bonneville					1	1
John Day	The Dalles					1	1
The Dalles	John Day	1	-	-	-	-	1

reported by Haynes et al. (1978) in a study on the unimpounded Columbia River upstream of the McNary Dam reservoir (Lake Wallulla), and by Bajkov (1951) downstream of study reservoirs.

We caught white sturgeon at all depths, but observed little difference in catch rates at depths greater than 10 m. Although the low catch rates at depths less than 10 m in all reservoirs imply that white sturgeon prefer deep water, we took too few shallow water samples to confirm this preference. Fishers report good seasonal catches from shallow water flats with mussel beds. Additional work is needed to evaluate depth preferences and their interactions with current velocity and substrate preferences.

White sturgeon moved long distances over relatively short time periods in each reservoir. Frequent movements of marked fish indicate they were well mixed in each reservoir, minimizing the chance for biases due to marking and recapture (Ricker 1975). Dams constrain movements of most white sturgeon, although a few passed a dam. Most dam passage was downstream rather than upstream. Although distribution of our sampling efforts made observations of downstream movements more likely than upstream movements, we saw virtually no upstream passage of dams by white sturgeon we tagged or of any of the thousands of fish tagged annually by fishery managers monitoring sturgeon populations downstream of Bonneville Dam. Avenues for downstream passage include fish ladders, spillways, turbines, or navigation locks. Opportunities for upstream movements are limited to navigation locks or fish ladders which were designed for salmonids and rarely permit sturgeon to pass.

The minimal downstream movement from one reservoir to another is likely to have little effect on population size or productivity, either up or downstream of the dam passed. However, this movement may prevent genetically different populations from developing in each pool. Even minimal immigration is sufficient to prevent genetic differentiation unless there is strong differential selection in different areas (Nei 1987). Divergence depends on the number of migrants entering a population, not their proportion (Allendorf and Phelps 1981). Relatively few migrants are needed to counteract the effects of genetic drift in large populations. The white sturgeon movements we observed are inconsistent with observations of genetic diversity among white sturgeon populations in Bonneville, The Dalles, and John Day reservoirs based on differences in mitochondrial DNA (Brown et al. 1992).

White sturgeon evolved in a river environment characterized by diverse habitats corresponding to the surrounding topography and dynamic seasonal changes in prey abundance. The species appears to have adopted a nomadic life history strategy, in response to these conditions. This behavior persists in white sturgeon populations in the free-flowing section of the river downstream of Bonneville Dam (Bajkov 1951).

Dams are barriers to sturgeon movements and have created a series of populations which are functionally, if not genetically, discrete. Fish restricted to a reservoir cannot range among widely scattered habitats nor take advantage of seasonal concentrations of prey. Each population must depend on conditions within a specific reservoir to sustain production. Dams appear to provide optimal conditions only in small areas (BRZ's) and result in a net reduction in habitat quality. Impoundment has reduced habitat diversity by creating a homogenous slack-water habitat which may not furnish optimal conditions for the white sturgeon life cycle in all years. The combination of reduced habitat diversity and constraints on movement may reduce white sturgeon productivity in the impounded portions of the river.

Acknowledgments

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REPORT F

Fishway Use by White Sturgeon to Bypass Mainstem Columbia River Dams

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Fishway Use by White Sturgeon on the Columbia River

White sturgeon (Acipenser transmontanus) is one of seven sturgeon species found in North America. It is also the largest freshwater fish in North America exceeding 1,000 pounds in weight and sometimes reaching nearly 20 feet in length. Modern relics of an ancient group of fishes, white sturgeon inhabit the larger rivers and bays of the Pacific coast from Ensenada, Mexico to the Aleution Islands of Alaska. The sturgeon are distinguished from typical bony fish (such as a salmon) by a skeleton that is mostly cartilaginous, a notochord instead of a backbone, primitive fin and jaw structures and a unique digestive system. When allowed access to the ocean the white sturgeon are semianadramous--that is, they are capable of migrating regularly between fresh water and salt, spending different parts of their lives in one or both environments. Some populations of white sturgeon may spend their entire lives in freshwater. White sturgeon can spawn several times in a lifetime, and females spawn at intervals ranging from 2 to 8 years. White sturgeon may spawn in areas of deep gravel riffles, in deep holes, and over rocky bottoms where swift current exists.

Sturgeon stocks have been depressed throughout the world because of demand for their highly valued flesh and caviar produced from their eggs. Human activities in watersheds where sturgeon live have affected sturgeon habitat. Historically, sturgeon products have been considered valuable in Europe, Asia, and North America. The largest white sturgeon resource in North America is in the Columbia River, and yet historically, it has never been a high priority of concern because of declining salmon stocks. During the late 1800's white sturgeon were nearly wiped out by commercial fishing but populations have been slowly recovering and they are now an important resource for both commercial and recreational fishermen. Angling for white sturgeon has become the most popular sport fishery below Bonneville Dam of the Columbia River.

Much of the research literature on white sturgeon in the Columbia River has stated that the dams are migration barriers to white sturgeon, causing isolated or landlocked populations (that are unable to migrate up or down the river or to the ocean but rather are confined to reservoirs). It is suggested that fish ladders at the dams are inadequate for sturgeon use and that passage is minimal at best. However, biologists have seemed unaware that annual reports from the U.S. Army Corps of Engineers indicate that white sturgeon passage does occur at Bonneville, The Dalles, John Day, McNary, and Priest Rapids dams. On the Columbia River, dams from Bonneville Dam all the way upstream to Wells Dam were constructed with fishways (fish ladders) to allow salmon and steelhead passage upriver to their spawning grounds (Figure 1). These fish ladders were not designed with white sturgeon in mind, and yet they have been observed moving past the fish counting stations. Use of fishways by white sturgeon is highly variable among the dams.

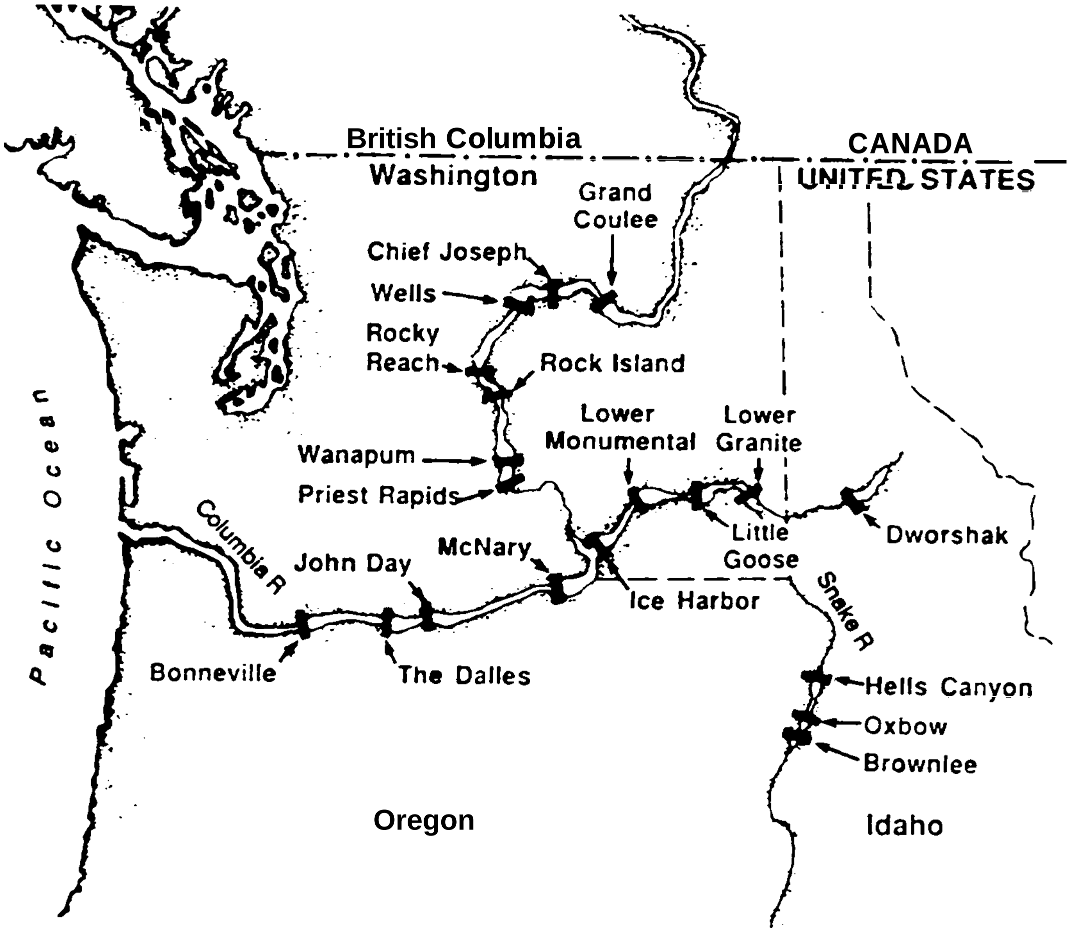


Figure 1. Columbia and Snake River Dams

Fish Ladder Design

The purpose of fish ladders, is to enable fish to migrate past natural or man-made barriers. First introduced in Europe over 300 years ago, with the aim of passing water around or through an obstruction, fish ladders are engineered as to dissipate the energy in the water sufficiently to permit fish to ascend without undue stress.

Since the construction of Bonneville Dam, fish ladders have undergone many design improvements as new biological knowledge has become available. Because of the complexity of fish ladder design, this publication describes only the general characteristics of the fish ladders at Bonneville, The Dalles, and John Day dams, where white sturgeon passage has been observed most frequently.

Fish ladders on the lower Columbia River dams are primarily overflow weir-type that gradually ascend from downstream (the tailrace) to upstream (the forebay) of the dam. The weirs act as barriers in the ladder to control water flow and to form a series of steps and pools. Typical weirs range from 24 to 30 feet in width and 6 feet in height. They are spaced 10 to 16 feet apart and have a minimum one foot vertical drop between each pool. Weirs can be either "full width" which allow water to flow evenly over the entire width or "restricted" which allows water to flow over only a portion of the weir. Water flows through a fish ladder at a rate of approximately 8 feet per second.

It was initially assumed that salmon and steelhead, for whom the fish ladders were designed, prefered to jump from one pool to the next. However, when it was discovered that fish prefer to stay under water while moving upstream, the ladder weirs were constructed with orifices at the bottom that range from 18 to 24 inches square. The orifice is the most critical component that allows white sturgeon to use the fish ladders since white sturgeon are bottom dwellers. The size of the weir orifices could limit very large white sturgeon from using the fish ladders.

HISTORICAL PASSAGE OF WHITE STURGEON THROUGH FISH LOCKS AND LADDERS

Bonneville Dam, completed in 1938, was the second dam built on the Columbia River. A second powerhouse on the Washington shore was completed in 1981. The dam is located 145 miles from the mouth of the river, where tidal exchange has its farthest upstream influence. The dam was constructed with fish locks (an elevator-like structure) and overflow weir-type fish ladders to enable migrating salmon and steelhead to bypass this man-made barrier. The fish passage facilities proved effective for these fish but left much to be desired for the bottom-dwelling white sturgeon, which lacked the ability to negotiate waterfalls and other barriers. The white sturgeon was no longer able to journey up or down the Columbia and Snake rivers; many were trapped above Bonneville Dam and it was not known how this would affect their survival without access to the ocean.

Use of Fish Locks

Bonneville Dam was constructed with three pairs of fish locks-- one pair on the south end of the Oregon powerhouse (Figure 2) and one pair on each end of the spillway. The locks measured 20 feet square and had a lift height of about 90 feet. Cables activated a grated rack to direct fish to the top. The basic operation was similar to that of a navigation lock. Fish entering the lock were trapped; water filled the lock to a level equal to that of the forebay; and then a grated floor was raised to the top of the lock, where fish could exit into the forebay. A single lock cycle took about 30 minutes to an hour, and the operator periodically conducted a lift even though there was no way of knowing exactly how many fish, if any, were trapped. Biologists the from U.S. Army Corps of Engineers would generally operate the locks to coincide with the peak timing of salmon and steelhead runs.

It was discovered that at certain times of the year many white sturgeon congregated at the base of Bonneville Dam. White sturgeon less than 4 feet in length were often found in the powerhouse draft tubes (the area below the turbine blades) during repair or maintenance work. More importantly, white sturgeon were able to enter the fish locks and be elevated into the Bonneville Dam forebay. Ivan J. Donaldson, resident fish biologist for the Corps of Engineers at Bonneville Dam from 1940 to 1973, was largely responsible for operating the fish locks. He wrote in a 1946 Annual Report on the Passage of Fish:

> "Few have done so, but rarely does a sturgeon ascend the ladders. The men who are most familiar with their habits are convinced that the sturgeon have a yearly period of migration in the summer months when the water is warm. In 1939, 1942, and 1946, it was demonstrated that these fish will move into the fish elevators but the migration ceases about the first of October."

The fish lock was so successful, in fact, that in 1951 a record 119 white sturgeon were lifted to the forebay in one day. However, a former fish lock operator (name unknown) informed Ivan Donaldson that several hundred white sturgeon had been lifted at one time in 1938 or 1939. On the other hand, not all lifts resulted in high catches; sometimes no white sturgeon were trapped. Donaldson recorded that unsuccessful fish hauls in locks seemed to be related to water conditions at the entrance of the fish collection system; when swifter than normal flows from the fish lock collection system occurred, the catch of white sturgeon was poor.

During a 31 year period (1938-1969), 4,711 white sturgeon were lifted by fish locks or ascended ladders over Bonneville Dam (Figure 3). The fish locks were operated in 12 of the 31 years only, yet they accounted for 97% of the total white sturgeon that reached the forebay. White sturgeon entering the fish locks were limited to 4.5 feet or less, because of the design of the fish collection system.

The last recorded use of a Bonneville Dam fish lock was in 1971 when the fish ladder on the Oregon shore was drained for repair. The original intent of the fish locks, as we have said, was to pass salmon and steelhead upriver and to serve as a backup when fish ladders were drained

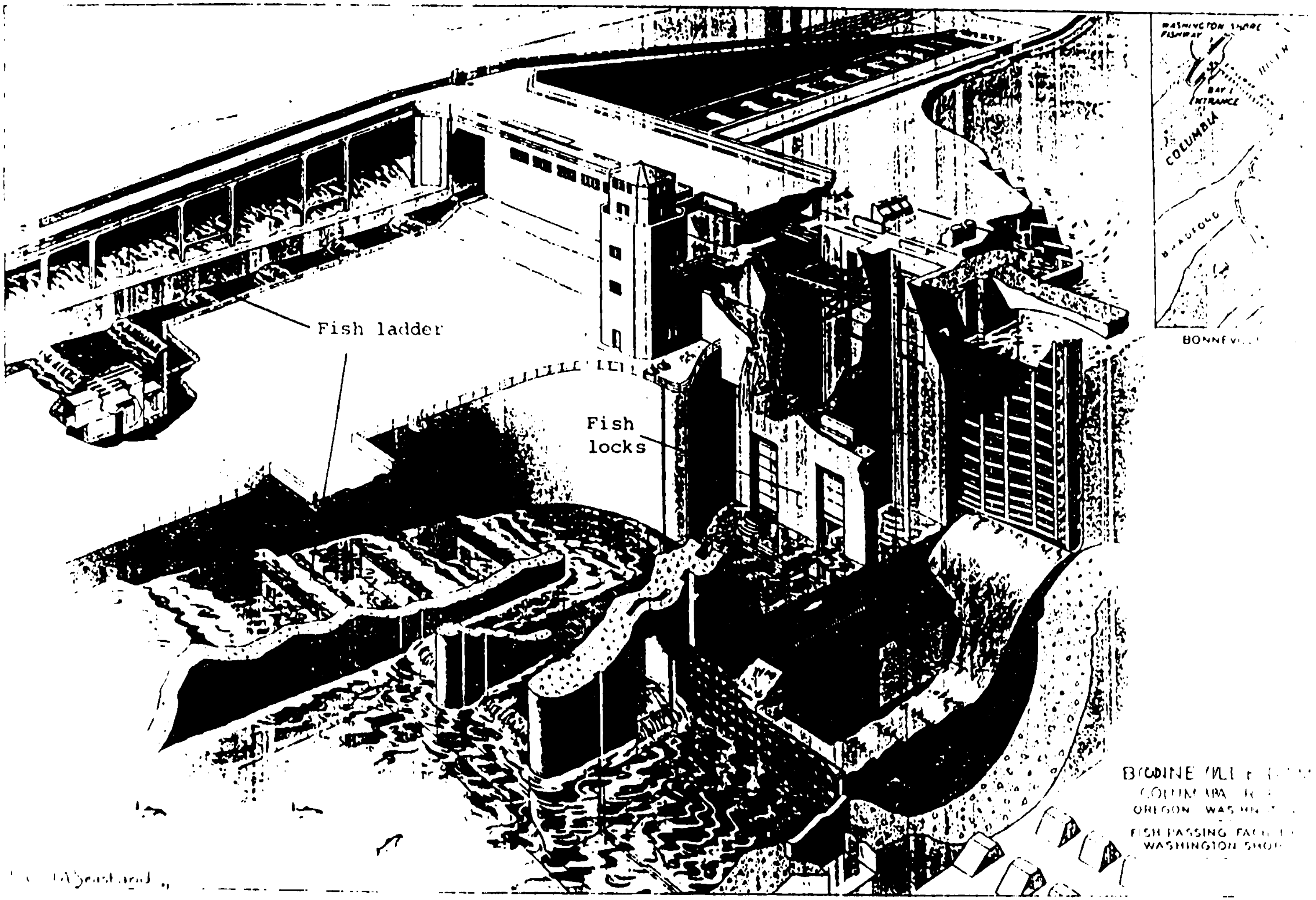
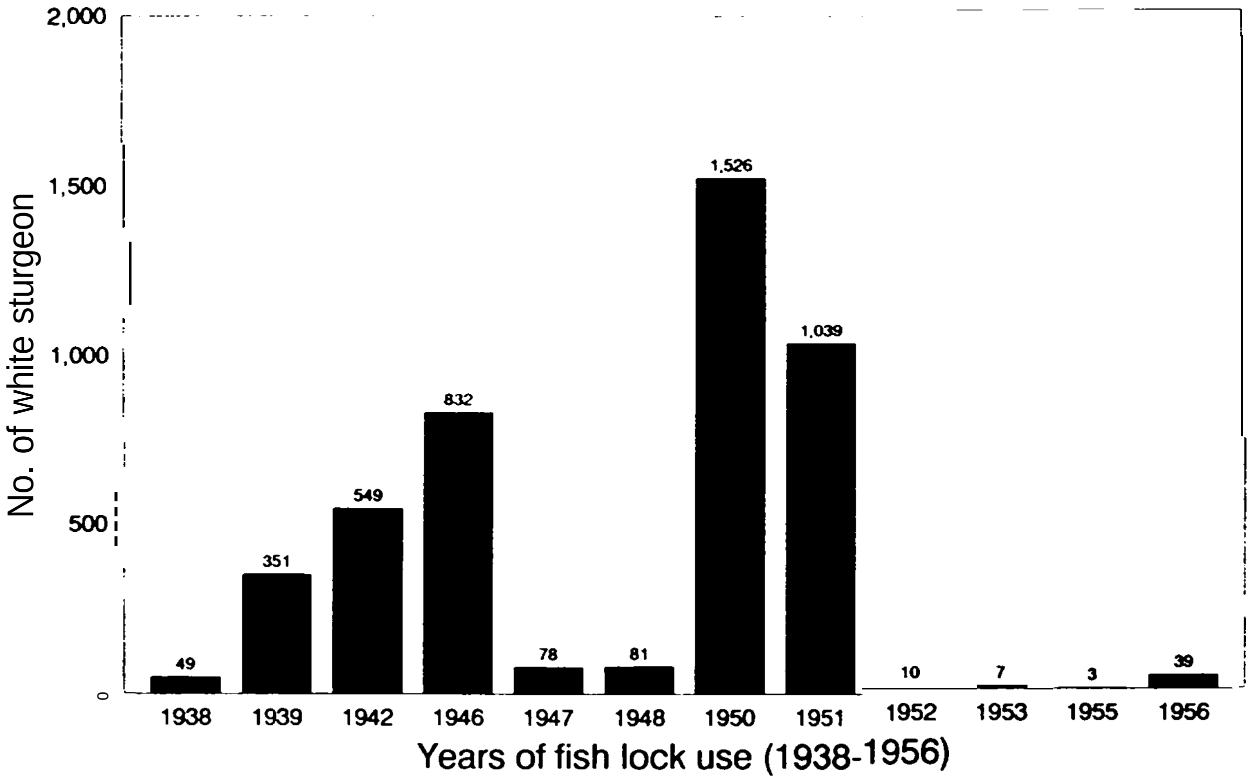


Figure 2.

Bonneville Dam - Fish Passing Facilities
Corps of Engineers, Portland District



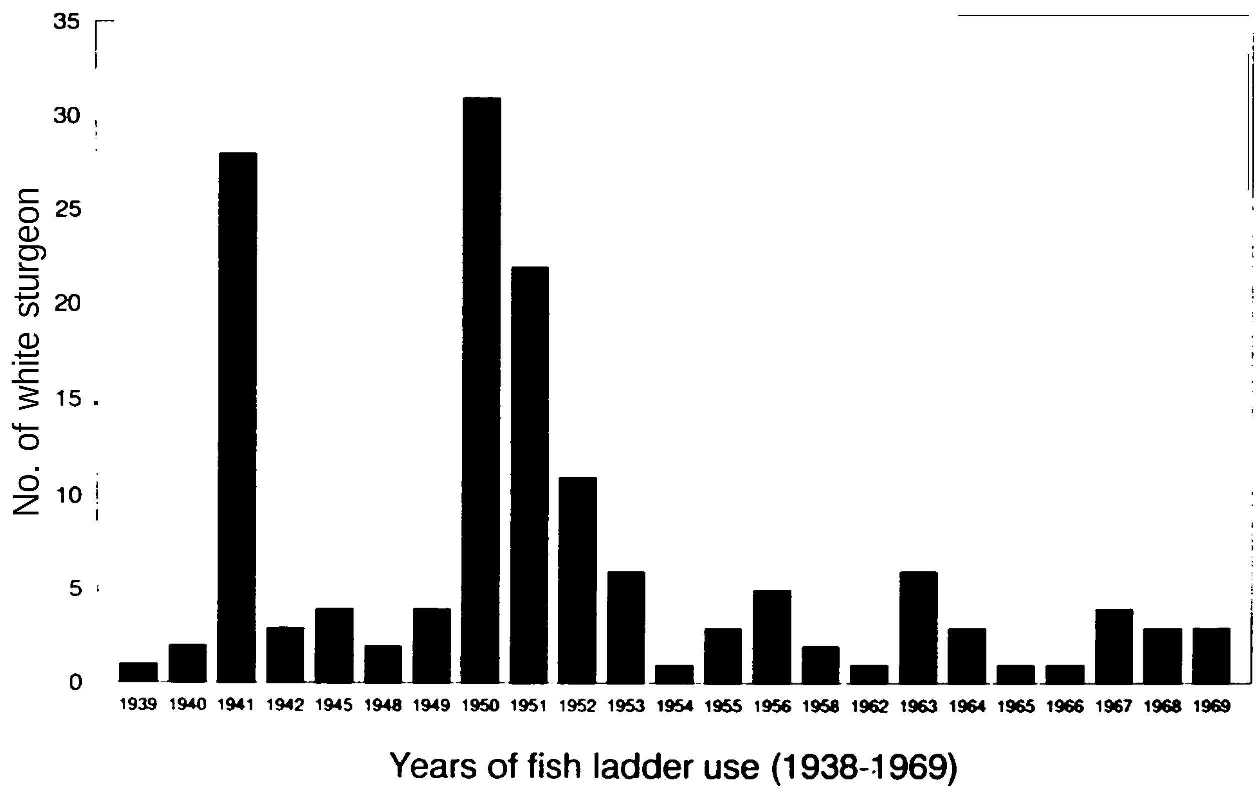


Figure 3. Historical Use of Fish Locks and Fish Ladders by White Sturgeon at Bonneville Dam

for maintenance or repair. However, the fish locks were not suitable for salmon and steelhead passage, were very time consuming, and were labor-intensive. They were discontinued for white sturgeon use because of lack of the time and money involved and because few people were really interested in providing passage for white sturgeon.

It is interesting to note that the fish locks at Bonneville Dam gained attention from other parts of the world. In 1946, a Russian fisheries scientist visited the dam seeking information on how to lift sturgeon above the dams being built in Russia. In 1960, French engineers planning a dam on the Sefid Ruud River, a tributary of the Caspian Sea in Iran, requested information on how to pass sturgeon over dams.

Use of Fish Ladders

Initially, it was believed that the Bonneville Dam fish ladders represented the white sturgeon's limit of physical ability and only a small percentage (3% of the total passage count) from 1938 to 1969 had used the ladders. However, white sturgeon passage over the dam improved after 1950 when all the ladder weirs were modified to provide passage by orifices at the ladder floors. This allowed white sturgeon to swim through rather than over the weirs.

White sturgeon using the fish locks and ladders to bypass Bonneville Dam led early fishery biologists to believe that a summer migration occurred in August. Although they could not explain why this seasonal migration took place it was observed annually from 1938 to 1969 (Figure 4).

WHITE STURGEON PASSAGE SINCE 1986

At Bonneville, The Dalles, and John Day dams from 1986 to 1991, fish ladder use by white sturgeon was greatest from Hay through November each year (Figure 4) with most sturgeon being observed during July and August. This peak of fish ladder use by white sturgeon is similar to historical passage at Bonneville Dam. The typical length of white sturgeon using the fish ladder was two to four feet.

Fishery biologist Alexander D. Bajkov noted in 1951 during a white sturgeon tagging experiment that many small sturgeon were located in the tailrace area of Bonneville Dam from mid-August through November. He commented:

> "... a strong possibility that a general upstream migration of sturgeon was underway in the late summer and fall. Simultaneously the absence of sturgeon had been noticed immediately above Bonneville Dam when an experimental set line of 60 hooks failed to catch a single sturgeon during 12 consecutive days. This unusual experience strongly indicates the possibility that the entire sturgeon population moved upstream from the Bonneville lake forebay area into the upper part of the river. This theory seems to be logical because the absence of fish immediately above the dam coincided with the tremendous concentration of small sturgeon just below the dam."

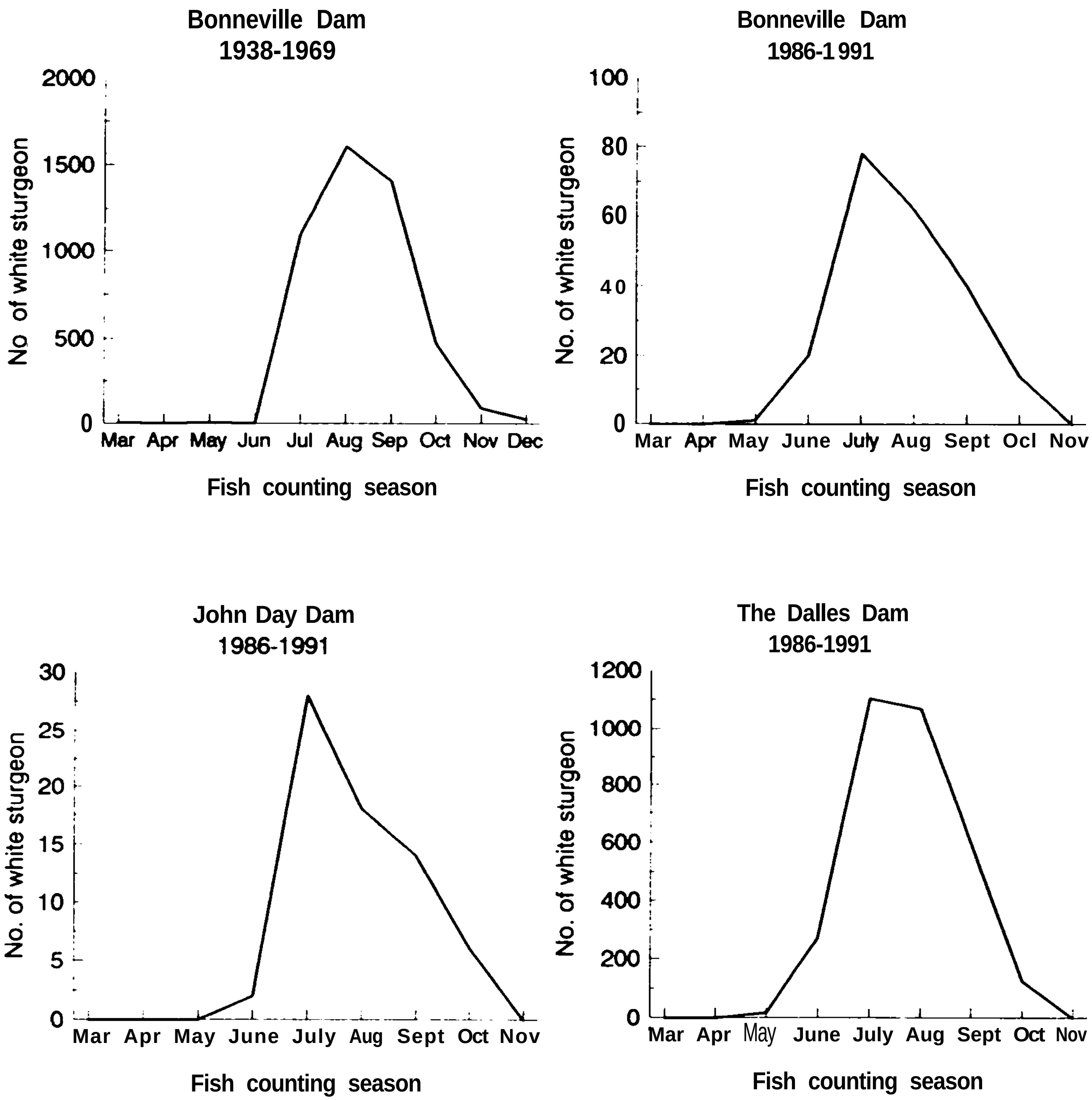


Figure 4. Peak Migration of White Sturgeon through Fishways

Perhaps this timing of migration of white sturgeon is associated with locating a suitable food supply or appropriate overwintering areas.

There is speculation also that white sturgeon enter and exit reservoirs through the navigation locks, but there has been no study to confirm the extent of movement through these locks. However, in 1961 when The Dalles navigation lock was drained for maintenance, several white sturgeon were found. Further evidence of white sturgeon movement between Columbia River reservoirs has been found in tagging studies done by the Oregon Department of Fish & Wildlife. From 1987 to 1991, 26 recaptures of tagged white sturgeon showed downstream movement between reservoirs, and one fish moved upstream.

Documentation of White Sturgeon Passage

Because of Donaldson's interest in white sturgeon at Bonneville Dam, the annual fish passage reports from 1938 to 1969 contained detailed information about this fish. He learned much about white sturgeon biology from using fish locks to lift white sturgeon over the dam and conducting his own studies.

From 1969 to 1980, white sturgeon passage was reported from only Bonneville Dam; but since 1985, white sturgeon passage has been recorded and entered into annual fish passage reports from Bonneville, The Dalles, and John Day dams. It should be noted that white sturgeon counts are only recorded at the convenience of the fish counter when not preoccupied by the official counts of salmonids and shad. Hence, the counts do not represent net upstream passage, nor are they adjusted for nonobservation periods. There are two fish-counting stations at each dam, one on each side of the river, and they are located on the upper end of the fish ladder near the exit into the forebay. Fish counters are in an isolated viewing room and observe fish passage through a window 5 feet wide. The fish-counting schedule at each dam ranges from March through November, and fish counters record from 5 a.m. to 9 p.m., with a lo-minute break each hour.

Bonneville Dam

Bonneville Dam is the first hydroelectric facility up the Columbia River. Its fish ladders are the second most used by white sturgeon to traverse over a dam (Figure 4). The dam has four fish ladders and there are no discernable differences in white sturgeon counts between the two counting stations on the Washington shore and the two on Bradford Island (Figure 5). During the 1986 to 1991 period, white sturgeon ranged from 1 to 7 feet in length, with most being about 3 feet. Only 13 white sturgeon were observed passing downstream, and 58 percent of the white sturgeon total were recorded during morning hours (5 to 11 a.m.).

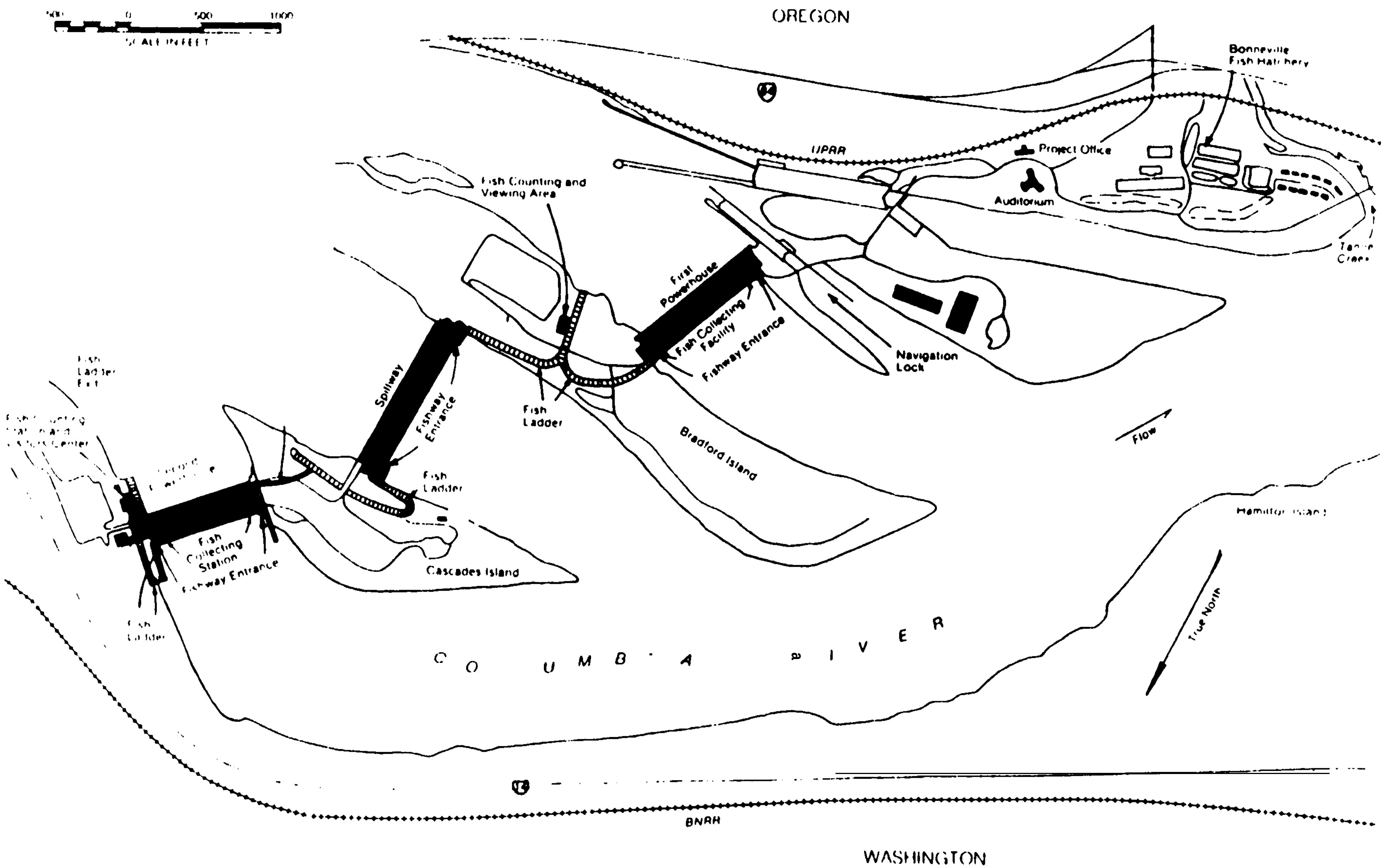


Figure 5. Bonneville Dam and Fish Passage Facilities

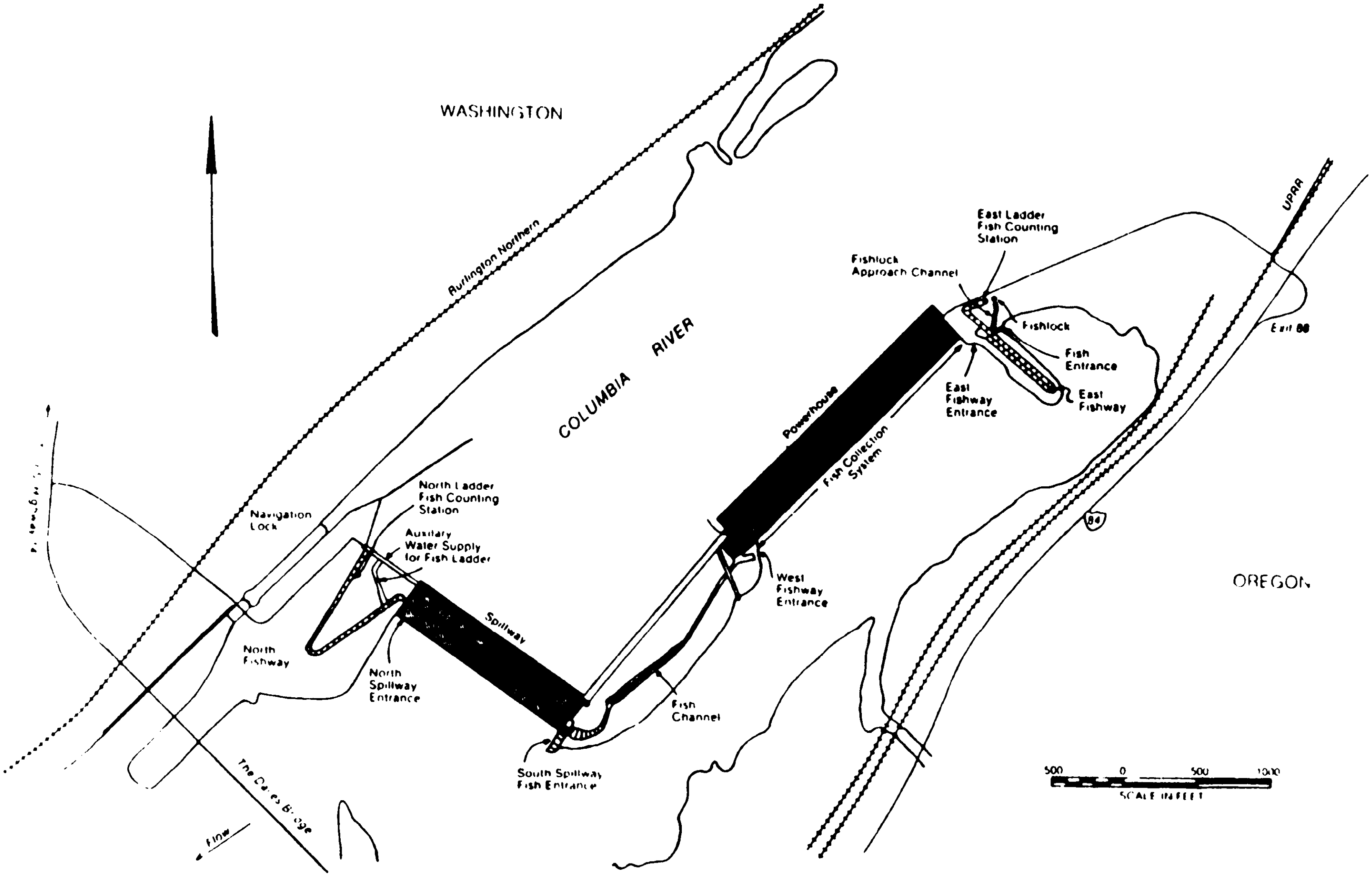


Figure 6. The Dalles Dam and Fish Passage Facilities

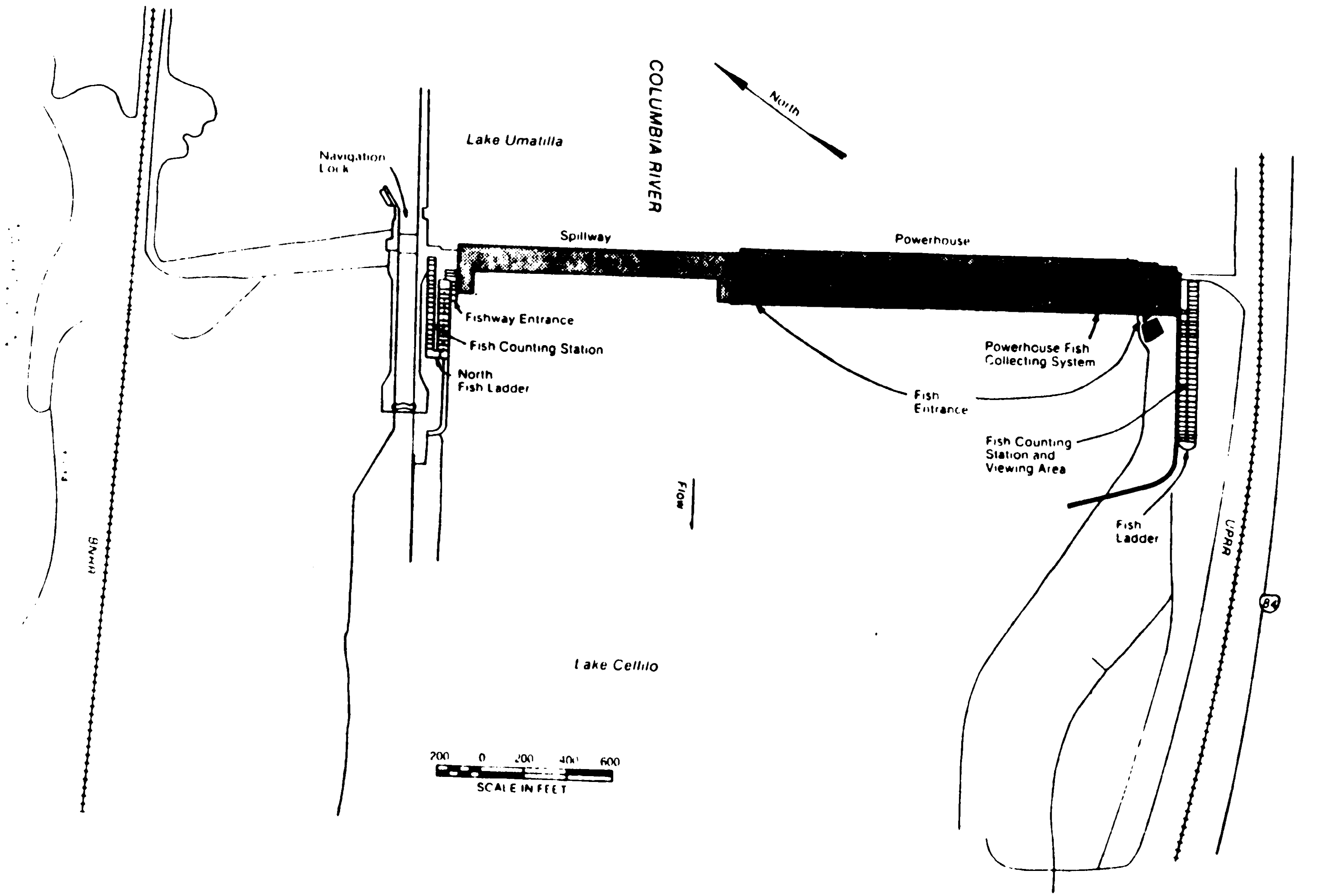


Figure 7. John Day Dam and Fish Passage Facilities

The Dalles Dam

The Dalles Dam, completed in 1957, is the second dam up the Columbia River and is located 191 miles from the mouth. Fish passage facilities include a north and east fish ladder (Figure 6). the east fish ladder includes a fish channel connecting the west fishway entrance and south spillway entrance. and a second channel connecting with the fish collection system along the powerhouse. There is a fish lock also located near the east fish ladder that is inoperable and there are no records of its use to lift white sturgeon over the dam.

The Dalles Dam has the highest recorded fishway use by white sturgeon, and from 1986 to 1991, the east fishway accounted for the vast majority of sturgeon passage in the Columbia River (Figure 4).

White sturgeon as long as 11 feet have ascended or descended the east ladder and an individual fish counter noted that an extremely large white sturgeon tilted sideways to squeeze by the viewing window. In the 1986 to 1991 period, the most frequent size class observed was about 3 feet. Observations at The Dalles Dam, unlike those at Bonneville Dam, showed little difference in the timing (a.m. vs p.m.) of white sturgeon passage. Only 8 percent of the white sturgeon were noted to have descended past the viewing window.

It is interesting to note that counts for other species such as walleye and northern squawfish are also consistently higher here than at other dams. Why white sturgeon and other species use the east fish ladder so much more than others is unknown, since the design of the east fish ladder is similar to that of other Columbia River fish ladders.

John Day Dam

Located at river mile 215, John Day Dam became operational in 1969 and has two fish ladders, one each on the Oregon and Washington sides (Figure 7). No fish locks were included in the fish passage facilities. The total white sturgeon passage from 1986 to 1991 was 68 fish, the lowest number observed of the dams under consideration, with the Washington side accounting for 59 of the total. The size of white sturgeon ranged from 2 to 5 feet in length, with 3 feet again being the most common size. Nine white sturgeon were observed passing downstream and 43 white sturgeon were recorded during the p.m. counting hours (12 noon to 9 p.m.).

STURGEON IN RUSSIA

American Rivers are not the only ones faced with man-made obstructions causing sturgeon migration problems. In Russia, where sturgeon are also highly valued, hydroelectric facilities inhibit sturgeon migration as well. Although the power dams are constructed with traditional fish ladders they are impractical for large adult sturgeon to use. Therefore, fish elevators much like the once-used fish locks at Bonneville Dam were specially built for them. Two fish elevators were installed at the Volgograd power dam on the Volga River, a tributary to the Caspian Sea. These elevators lift sturgeon during the main spawning migration of three species--beluga sturgeon, <u>Huso huso</u> (twice the size of white sturgeon), Russian sturgeon, Acipenser queldenstaedti, and stellate sturgeon, A. stellatus. The results have been highly successful, allowing approximately 23,000 sturgeon a year to bypass the dam.

BENEFITS OF STURGEON PASSAGE

In September of 1942, Ivan Donaldson wrote to Captain R.B. Cochrane, Area Engineer at Bonneville Dam, this one of many recommendations concerning the fisheries problem at Bonneville Dam:

> "Look ahead to the building of Umatilla and be willing to build a pair of locks for salmon and for sturgeon. I suggest that they also be designed for bottom travelling fish which do not like to rise over any wall. The design should be such that sturgeon can enter from a level with the bottom of the deepest hole at the dam. I would like to think that we have demonstrated by cutting holes in the bottom stoplogs, which regulate the fish entranceway elevation to the ladder collection bays, that sturgeon will then enter the collection bays (some will anyway) and be lifted over the dam. . . . . We may find in the future that sturgeon must migrate to some extent."

Even though the use of fish locks has ceased, fish ladders continue to allow limited passage of white sturgeon at some of the Columbia River dams. Fishway use by white sturgeon at The Dalles Dam east fish ladder has ranged from 187 to 791 white sturgeon per year since 1985. If it was known why more white sturgeon use the east fish ladder then maybe other fishways could be changed to improve white sturgeon passage.

If passage facilities for white sturgeon on the Columbia River were to be improved, several benefits might accrue:

- Recruitment of white sturgeon to upper reservoirs where populations are sparse (resulting in more spawning adults and larger populations).
- Migration of white sturgeon to more suitable habitat for feeding and/or spawning.
- Improved opportunity to maintain the health and survival of this unique fish.
- Improved genetic diversity

In the meantime, white sturgeon are still making efforts to maintain their migratory instincts with limited use of fish ladders to bypass Columbia River dams. How much we are willing to help them by improving passage possibilities remains to be seen.

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REPORT G

Dynamics and Potential Production of White Sturgeon in the Columbia River Downstream from Bonneville Dam

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Washington Department of Fisheries

For submission to: North American Journal of Fisheries Management

Abstract.- The lower Columbia River downstream from Bonneville Dam (LCR) supports the greatest abundance and density of white sturgeon *(Acipenser transmontanus)* reported in the species' range. High productivity of the population resulted from growth that was as good or better than reported for other populations, the highest mean relative weight or condition factor reported for any white sturgeon population, and a relatively low median age of first maturity for females of 24 years (95% of females matured between 16 and 35 years of age). Estimated annual total mortality was comprised of 15% annual natural mortality and an average annual exploitation rate of 28% in LCR fisheries. The 1986-1990 average annual abundance estimate of LCR white sturgeon ≥54 cm fork length (≥ 2 ft. total length) was 893,800 fish at an average density of 14.6 fish per hectare. Population simulations, assuming constant recruitment, predicted a maximum sustainable yield (MSY) of 1.4 kg per recruit at a 32% exploitation rate (of the 3-6 ft. population). In terms of reproductive potential, this translated to 11,890 eggs per recruit for an unexploited population, declining to 90 eggs per recruit at the predicted MSY exploitation rate. Simulations that assumed significant stock dependent recruitment (Beaverton-Holt: A=0.5) predicted an MSY of 0.3 kg per recruit at an exploitation rate of 4%. Actual MSY for the LCR white sturgeon population would be within this range. Factors most responsible for the favorable production potential of the population were access to marine areas, abundant food resources, and consistently favorable hydrologic conditions during the spawning timeframe which enhanced recruitment.

The lower Columbia River downstream from Bonneville Dam (LCR) supports one of the most productive sturgeon fisheries in North America and perhaps the world. Annual harvest of white sturgeon (*Acipenser transmontanus)* in the LCR has averaged 46,000 fish in recreational fisheries and 9,200 fish in commercial fisheries during the past ten years (WDF and ODFW 1992). Average yield of white sturgeon in combined LCR fisheries during the past ten years has been approximately 350,000 kg annually. The sturgeon fishery ranks as the largest recreational fishery in the Columbia Basin in terms of effort with a ten year annual average of 145,000 angler trips (Melcher and King 1991).

The high productivity and stability of fisheries in the LCR may be unique among sturgeon production areas. Most sturgeon populations have suffered decreased productivity or depletion from overexploitation and habitat changes (Rochard et al. 1990). The longevity, slow growth, and delayed maturation of sturgeon makes them susceptible to overexploitation. The large river systems they inhabit have been drastically altered by hydroelectric development and operation.

Long term overexploitation reduces yield and fishery quality and risks stock collapse (Rieman and Beamesderfer 1990). Excessive harvest in the 19th century collapsed Columbia River sturgeon stocks. Intensive sturgeon fishing on the Columbia River began in 1889 and peaked in 1892 with about 2,700,000 kg of sturgeon landed. The stock was depleted by 1899 after a ten year period of unregulated exploitation (Craig and Hacker 1940). Season, gear, and minimum size restrictions failed to bring about an increase in sturgeon production. Only after a maximum size regulation, designed to protect sexually mature sturgeon, was enacted in 1950 did the sturgeon population rebound. Annual harvests doubled by the 1970's and doubled again by the 1980's. Current harvest restrictions may be inadequate to protect stocks from overexploitation.

Hydroelectric development of the Columbia River mainstem since 1933 may have reduced the productivity of white sturgeon (Fickeisen 1985). Mainstem dams have effectively isolated subpopulations of white sturgeon and denied access to a variety of habitats that may have enhanced production of sturgeon historically. Pre-impoundment conditions can now be found only in the 234 km free flowing reach downstream from Bonneville Dam. Factors that may favorably affect survival and productivity of sturgeon that are unavailable to impounded populations include access to marine environments, consistently better flows during spawning, and greater availability of anadromous prey species.

The beneficial use of the LCR white sturgeon population can only be sustained through scientific management based on a thorough understanding of limiting factors and population dynamics. Comparisons of the characteristics of populations in the free-flowing LCR and impoundments may help identify factors limiting production.

In this paper, we examine the characteristics of the white sturgeon population in the free-flowing LCR between the ocean and Bonneville Dam located at river kilometer (rkm) 234. We use this information to project sustainable yield and exploitation rate.

Methods

Data Collection.- Mark-recapture data were obtained from salmon and sturgeon research fisheries conducted by the Washington Department of Fisheries (WDF) and the Oregon Department of Fish and Wildlife (ODFW) during 1983-1991 (Figure 1, Appendix 1). Sturgeon $\geq$62 cm fork length (FL) were captured and tagged with sequentially numbered spaghetti tags inserted at the base of the dorsal fin. All fish captured were sampled for marks, fork length, and total length (TL). Additional information collected when possible included sex, stage of maturity, and age. Commercial and recreational fisheries were sampled to supplement mark-recapture and biological data.

Age and Growth.- White sturgeon were aged by counting periodic rings on cross sections of the anterior pectoral fin ray (Rien and Beamesderfer 1992; Tracy and Wall 1992). Samples were obtained from consumptive and research fisheries during 1987-1992. Aging techniques were validated using oxy-tetracycline (OTC) marking (Leaman and Nagtegaal 1987; Tracy and Wall 1992; Rien and Beamesderfer 1992).

Length measurements were made for each fish that had a fin ray sample removed. Fork length was the preferred length measurement since there was less variation in length assignments than the total length measurement. Total lengths were sometimes the only length measurement available and were converted into fork lengths using TL=1.09*FL+2.06 (Tracy and Wall 1992).

Length at age relationships for white sturgeon were quantified by fitting length (cm FL) and age (years) data to a von Bertalanffy growth function (VBGF) (Tracy and Wall 1992).

Length and weight (kg) measurements were taken during research fisheries, commercial and recreational fishery sampling, and from natural mortalities. Data were fitted to a standard allometric function. Data were transformed to ln(FL) and ln(W) then fitted to a linear regression.

Reproductive Potential.- White sturgeon sampled in the commercial catch (110-166 cm FL) were measured to the nearest cm FL and sexed by visual examination of gonads. Sturgeon >166 cm FL examined during broodstock monitoring activities were sexed by first trying to express sperm from ripe males. Females and males not fully mature were sexed by surgical biopsy and the use of an otoscope according to the procedures outlined in Conte et al. (1988). Ovarian samples were removed from females and preserved in 10% formalin.

Fecundity was determined by weighing an ovary subsample, counting the eggs in the subsample, and expanding the egg count by the proportional difference in weight of the subsample and the total weight of ovarian tissue. Subsample weights were measured to the nearest 0.01 grams prior to formalin preservation. A fecundity/FL relationship was developed by fitting the data to an allometric equation. Sex ratios were determined for 122-183 cm TL and over 183 cm TL size classes.

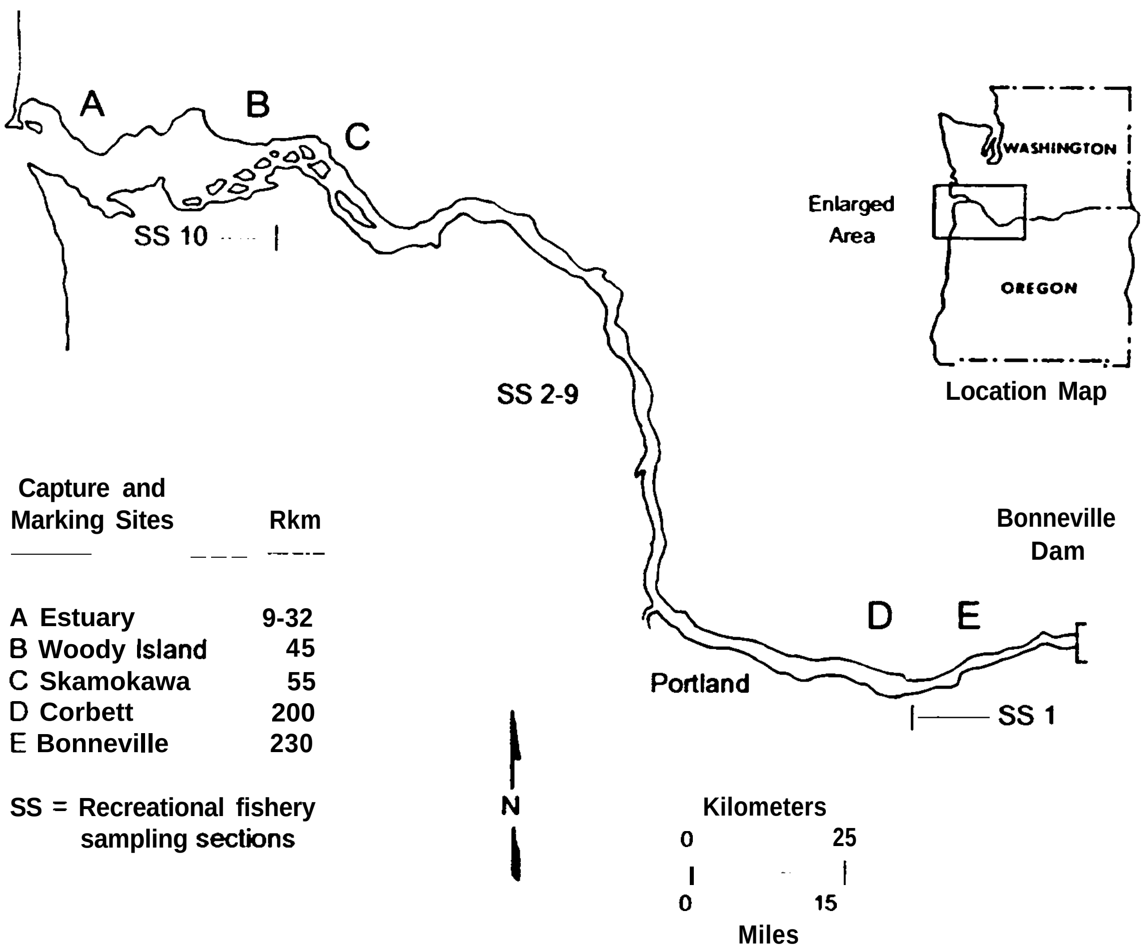

Figure 1. Locations white sturgeon were captured and marked on the Columbia River downstream from Bonneville Dam, 1985-1991.

Stage of maturity for females was categorized according to a qualitative histological classification modified from Chapman (1989). Egg diameter was measured to the nearest 0.1 mm using a micrometer and dissecting scope. Mean egg diameter was calculated from measurements of 10 eggs. Maturity samples were stratified into the following stages: pre-vitellogenic (eggs translucent, <0.6 mm diameter), early vitellogenic (eggs opaque, 0.6-2.1 mm diameter), late vitellogenic (eggs pigmented, 2.2-2.9 mm average diameter), ripe (eggs fully pigmented and detached from ovarian tissue, $\geq$3.0 mm average diameter), and spent (gonads flaccid with some residual fully pigmented eggs). Attritic oocytes were noted when disintegrating black eggs encompassed the majority of the gonad. Occasionally, samples exhibited a stage of maturity that was intermediate from the listed criteria. Staging the maturity of these samples was made subjectively.

Ovarian maturity was classified into three general categories to generate the length-at-maturity dataset: immature/resting (all pre-vitellogenic fish, and early vitellogenic fish recovered from July to December), maturing (early vitellogenic fish recovered from January to June and late vitellogenic fish recovered from April to December), and mature (ripe fish, spent fish, and late vitellogenic fish recovered from January to March). These classifications correspond to the estimated year of spawning: immature/resting fish would spawn $\geq$ 2 years from the recovery year, maturing fish would spawn the following year, and mature fish would spawn that year. The proportion of maturing females relative to the total sample of immature and maturing fish was estimated for each size class.

A relationship describing size specific maturity was developed using a maximum likelihood estimation procedure using a cumulative normal probability curve as a functional model of the maturation process (Welch and Beamesderfer 1992). A binomial probability distribution for the uncertainty in maturation estimates was assumed. The cumulative normal probability model was fitted to the length-at-maturity dataset to describe the change in maturity as a function of two parameters: μ, the length (or age) at which 50% of females were maturing, and the variance σ^2, a measure of the length range over which the change from an immature to a mature state occurred. Assuming the cumulative normal model appropriately described sturgeon maturation, 95% of females matured over a length interval of $\pm 2\sigma$ about the mean length of maturation. A third parameter, c (the asymptote of the size-at-maturity function), predicted the maximum percentage of maturing females in any given year. The duration of the maturation cycle was calculated as $1 + 1/c$. The reciprocal of the maximum likelihood estimate of c described the duration of the maturation and resting phases and 1 year was added to account for the fact that mature samples were omitted in the analysis.

Exploitation and Mortality.- Annual size specific exploitation rates (u) for lower Columbia River white sturgeon fisheries were calculated as the ratio of marks harvested to marks-at-large (Ricker 1975). Instantaneous exploitation rates (F) were calculated using $F=Zu/A$ (Ricker 1975).

Mark recoveries obtained within one year of release were expanded by the sample rate to estimate total mark harvest. Recreational fishery sample rates were calculated for recreational fishery sampling sections 1, 2-9, and 10 (Figure 1). Commercial sample rates were stratified by season. Mark recoveries in recreational fisheries were expanded by a cumulative tag retention rate to correct for tag loss (Appendix 2). Commercial mark recoveries were corrected by expanding observed tag scars by the sample rate. Tag scars were proportioned to all tag groups observed in the fishery.

Mark recoveries obtained primarily from random fishery sampling (in-sample) were used in estimating LCR exploitation although voluntary recoveries were used when no in-sample recoveries were obtained and for areas that were not sampled. Voluntary recoveries were expanded by a voluntary reporting rate calculated as the ratio of voluntary recoveries to estimated mark harvest for each area. Exploitation in LCR tributaries, and ocean and estuarial areas outside the LCR was estimated using voluntary mark recovery information. Tag recoveries were expanded by voluntary reporting rates calculated for Columbia River fisheries.

Exploitation estimates for tag groups marked exclusively in the estuary (rkm 9-32) and those for tag groups marked in other areas (rkm 45-206) were compared using a paired t-test (Sokal and Rohlf 1981).

Mortality was estimated using catch curves (Ricker 1975) derived from two separate sources: 1) an age frequency distribution of catches from research fisheries and, 2) recaptures in successive years of marked fish cohorts.

The catch of white sturgeon during 1990 and 1991 research fisheries at Corbett, Woody Island, and the estuary were pooled to create a composite length frequency distribution. Corrections for gear vulnerability (size selectivity) were made using mark-recapture data from these same fisheries (Hamley 1975; Lagler 1978; Beamesderfer and Rieman 1988). Vulnerability was estimated using the ratio of recaptures to marks-at-large by 10 cm FL intervals, and was based on data collected from 1983-1991 research fisheries employing nets with similar specifications. Only recaptures within three months of marking were used to reduce growth related bias. Vulnerability curves describing the relationship between recapture rate and fork length were fit with non-linear least squares regressions (SAS 1988). The combined length frequency distribution was corrected by dividing the observed frequency in each size class by the relative vulnerability (Beamesderfer and Rieman 1988).

The adjusted length frequency was converted to age frequency using pooled age at length data collected during 1987-1992 (Tracy and Wall 1992). Instantaneous total mortality rate (Z) and annual total mortality rate (A) estimates were made from the slope of the descending limb of the log transformed catch curve (Ricker 1975). These estimates correspond to age 10-16 fish representing age classes recruited to the recreational fishery. Confidence limits (95%) about Z were calculated from the regression as ± 2 SE.

Mortality estimates were also made by regressing log catch per angler trip on recapture year of a cohort of marked fish (Ricker 1975). The cohort was comprised of 82-91 cm FL (36-40 in. TL) fish marked during

1985-1987 research fisheries. Recaptures were expanded by a cumulative monthly tag retention rate to correct for tag loss (Appendix 2). Recaptures of 1986 and 1987 mark groups were weighted relative to recaptures of the 1985 mark group to derive a 1985-1987 composite recapture frequency.

Instantaneous natural mortality rate (M) for fish of harvestable size was calculated as M=Z-F. Conditional natural mortality rate (n) was calculated from the instantaneous natural mortality rate estimate ($n=1-e^{-M}$) (Ricker 1975). Estimates of n were averaged to determine the natural mortality rate for the population.

Abundance.- The Chapman (1951) modification of the Peterson mark-recapture model for closed populations was used to estimate annual abundance of harvestable size white sturgeon each year from 1987-1990. Fish were marked during April-June research fisheries and recaptured by sampling July-March consumptive fisheries.

Recruitment to harvestable size was accounted for by marking fish <82 cm FL in 1987 and 1988, and <92 cm FL in 1989 and 1990. It was assumed marked and unmarked fish recruited at the same rate. Separate abundance estimates for two length intervals (82-91 cm FL and 92-166 cm FL) were calculated to reduce size selectivity bias and to account for the change in the minimum allowable length in recreational fisheries from 82 cm FL to 92 cm FL in 1989. Confidence limits (95%) were calculated assuming recaptures approximated a Poisson distribution (Ricker 1975).

Abundance of sturgeon >54 cm FL but <82 cm FL in 1987 and 1988, and <92 cm FL in 1989 and 1990 was estimated by extrapolating from mark-recapture estimates using length frequency distributions of annual research fishery catches corrected for gear vulnerability. Annual abundance estimates of sturgeon >166 cm FL (>72 in TL) were made by expanding the number of sturgeon >166 cm FL reported handled in the recreational fishery each year (Melcher and King 1991) by the estimated exploitation rate of sturgeon in the 110-166 cm FL length interval.

Annual abundance estimates were made for sturgeon at age 10 and age 25 using population specific age-at-length data (Tracy and Wall 1992). Population density estimates were calculated from abundance estimates and surface area estimates for the LCR (Parsley and Beckman 1992).

The effect of applying a closed population estimator to an open population was evaluated by simulating various immigration, emigration, and recapture scenarios over a nine month period. Immigration and emigration values of 10% and 30% of initial abundance (at the start of the recovery period) were used. The estimator was considered satisfactory for scenarios resulting in estimates between initial abundance and initial abundance plus immigration.

Productivity.- The production potential of the population was described using relationships between exploitation and yield (kg) per recruit and reproductive potential (egg production) per recruit. An age-structured population simulation model, MOCPOP 2.0 (Beamesderfer 1991), was used to calculate yield and reproductive potential for a range of exploitation rates. Both constant recruitment to age 1 and a Beaverton-Holt stock dependent recruitment relationship with A=0.5 (Beaverton and Holt 1957) were modeled.

Results

Age and Growth

Ages were assigned to 783 fish ranging in age from 1 to 65 years and in size from 17 to 262 cm FL. The relationship that best described the length-at-age data was the following VBGF: $L_t=276.3(1-e^{(-0.0346(t+1.125)})$ (Tracy and Wall 1992). Oxytetracycline validation results indicated that one annulus was deposited each year, and that ageing techniques used to age LCR white sturgeon were valid.

Paired length and weight measurements were obtained from 5,336 LCR white sturgeon with lengths ranging from 37 to 262 cm FL and weight from 0.59 to 187.8 kg. The length-weight relationship was fitted to the following allometric function ($r^2=0.97$): $W=1.043E\text{-}5*L^{2.958}$ (Figure 2).

Reproductive Potential

The sex ratio for the 110-166 cm FL size class was 44.7% female and 55.3% male (n=5,729). Fish >166 cm FL had a sex ratio of 46.5% female and 53.5% male (n=71).

The fecundity/FL relationship ($F=0.0736*L^{2.937}$,n=38),as described by linear regression of log transformed variables, was a poor fit with an r^2 of 0.59. Fork lengths ranged from 115 to 215 cm while estimated fecundities ranged from 98,200 to 699,000 eggs (Figure 3).

There were 1,271 ovaries examined for stage of maturity, with 1,174 (92%) categorized as pre-vitellogenic, 58 (5%) as early vitellogenic, 15 (1%) as late vitellogenic, 22 (2%) as ripe or spent, and 2 (<1%) classified as unknown. Early and late vitellogenic females were collected throughout the year (Figure 4). This is consistent for a species with a maturation cycle longer than one year (Chapman 1989; Kroll 1990; Doroshov et al. 1991; North et al. 1992). The lack of maturation data for the months of January, April, July, and December reflect the absence of commercial fisheries or broodstock monitoring activities during these months. Mature females were present prior to and during the spawning timeframe and rare during other timeframes (Figure 4). A time series of egg diameters from vitellogenic females shows a delineation between early vitellogenic, late vitellogenic, and ripe maturation stages consistent with the above patterns (Figure 5).

Maximum likelihood estimates for μ and σ^2 were 160 cm and 18 cm, respectively (Figure 6). Therefore, 160 cm FL was the median length at first maturity with 95% of the females maturing between 124 and 196 cm FL ($\pm 2\sigma^2$). These lengths correspond to ages 24, 16, and 35 years, respectively. The estimate of c, the maximum proportion of maturing females, was 0.50, corresponding to lengths $\geq$ 230 cm FL (Figure 6).

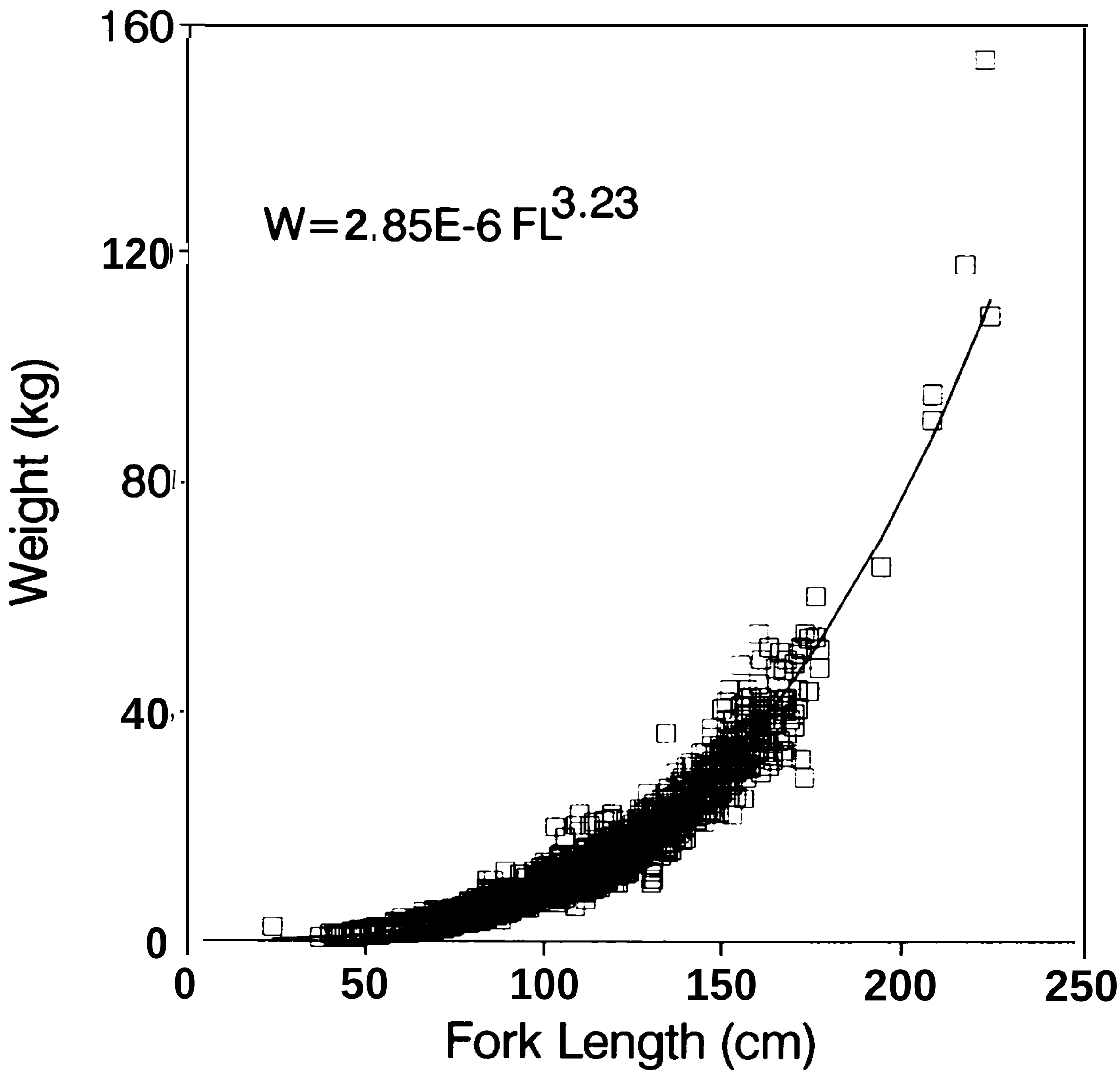

Figure 2. Weight at length relationship for white sturgeon in the Columbia River downstream from Bonneville Dam, 1987-1992.

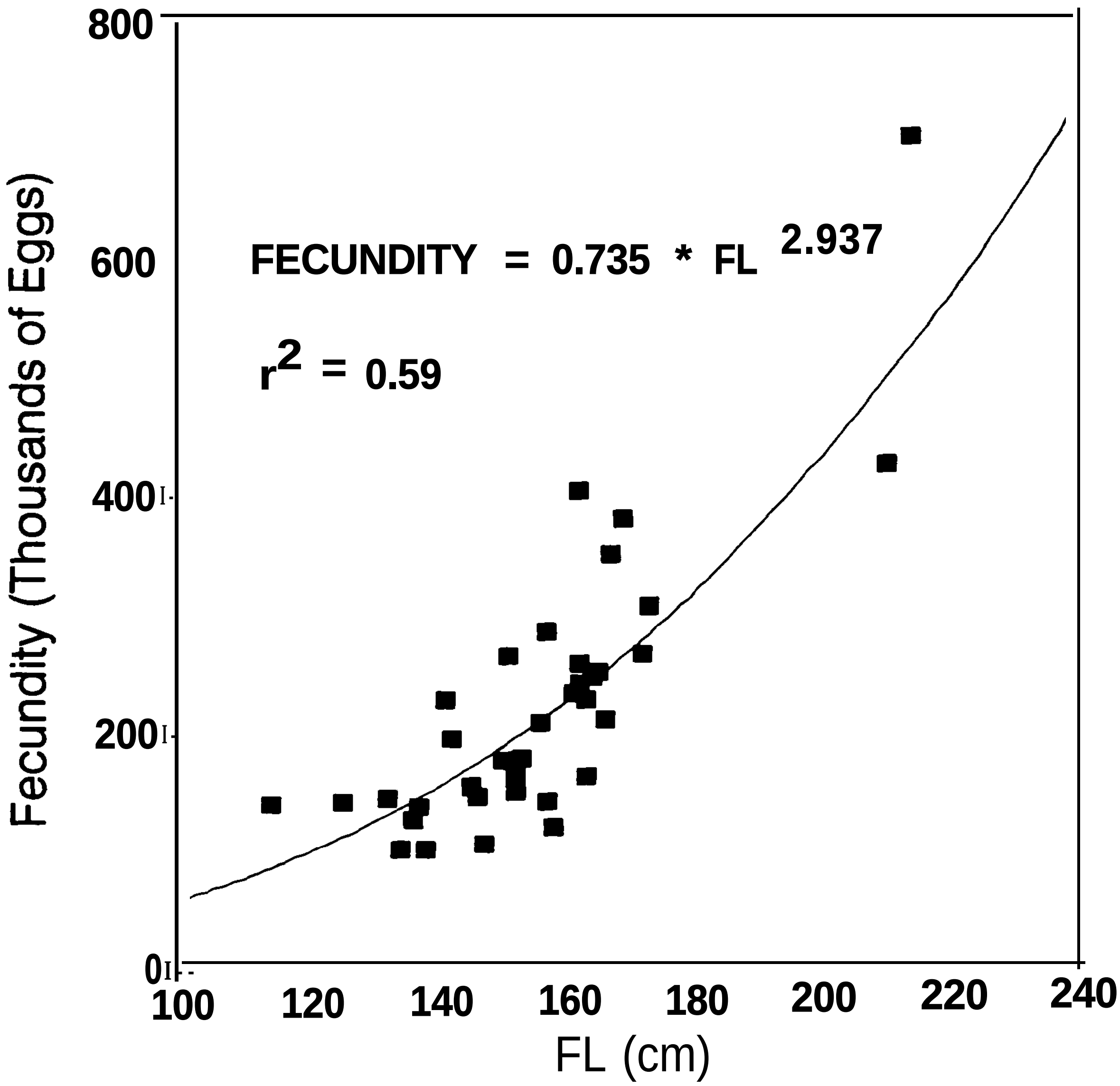

Figure 3. Fecundity by fork length of female white sturgeon in the Columbia River downstream from Bonneville Dam.

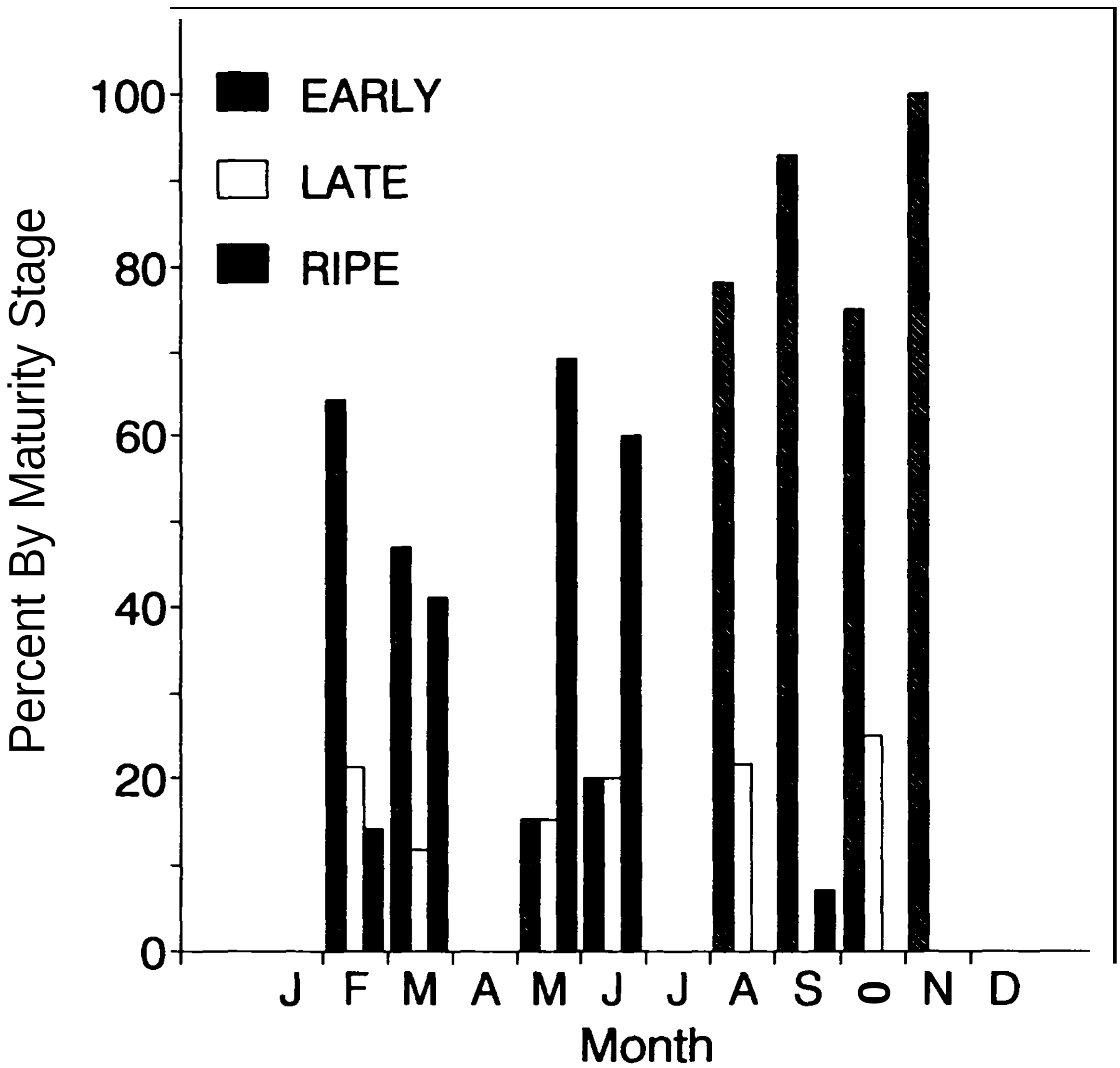

Figure 4. Maturity of vitellogenic ovary samples by month for white sturgeon in the Columbia River downstream from Bonneville Dam, 1987-1991.

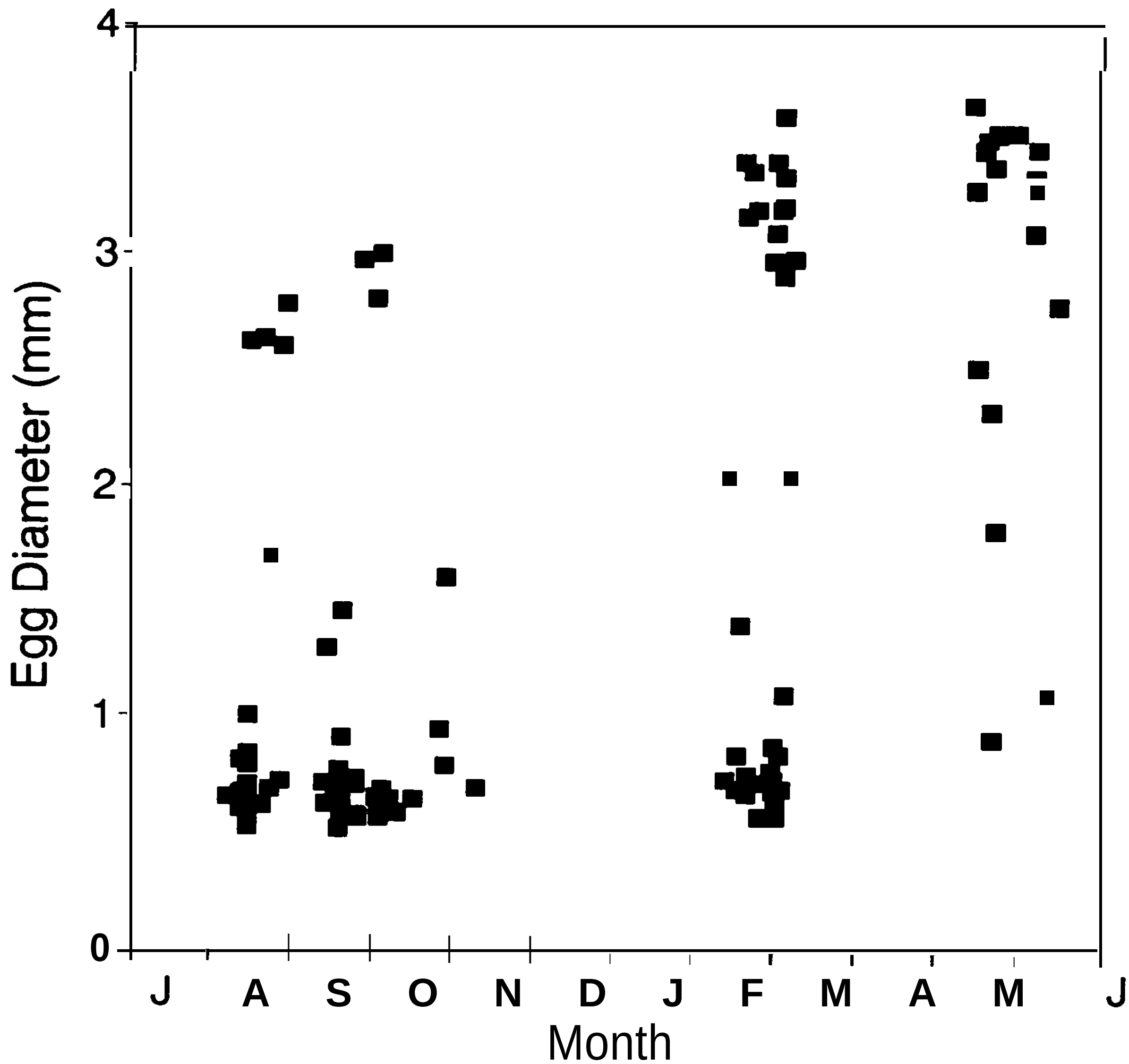

Figure 5. Mean egg diameter by sample date (July-June) of white sturgeon in the Columbia River downstream from Bonneville Dam, 1987-1991.

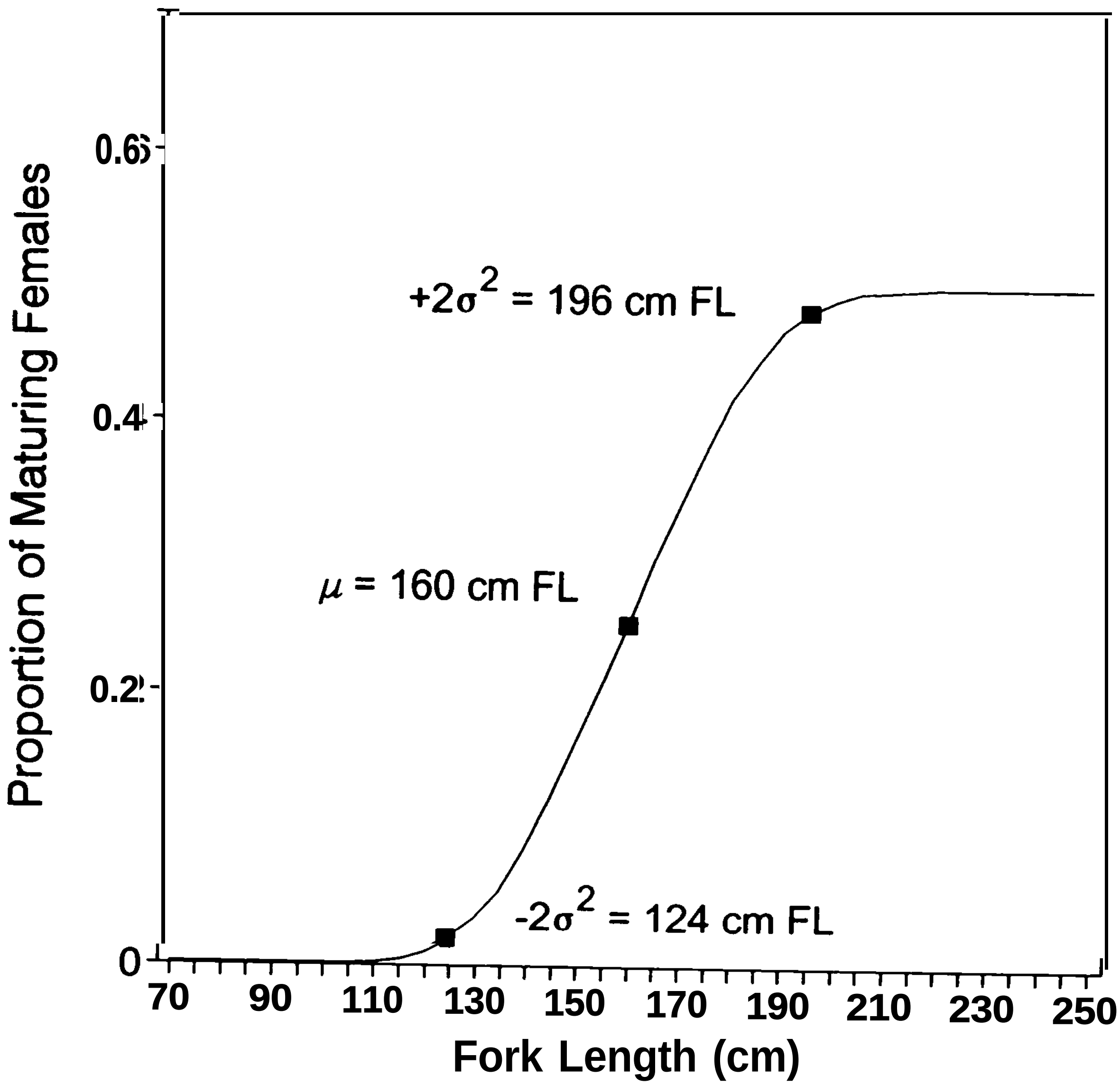

Figure 6. Proportion of maturing female white sturgeon by fork length (cm) with maximum likelihood estimates of μ and σ^2 in the Columbia River downstream from Bonneville Dam, 1987-1991.

Exploitation and Mortality

Estimated exploitation rates (u) in Columbia River fisheries were highest in the 122-152 cm TL interval where fish were vulnerable to both recreational and commercial fisheries (Table 1). Geometric means of exploitation estimates corresponding to periods and length intervals specific to the total mortality estimates were 0.28-0.29. Exploitation of marked fish outside the LCR ranged from <1%-2%. These estimates were based on voluntary mark recaptures expanded by reporting rates of 22% and 43% for LCR commercial and recreational fisheries, respectively. Exploitation estimates derived using estuary tag groups compared to estimates derived from non-estuary tag groups showed no significant difference ($P > 0.8502$).

Gear vulnerability curves generated from research fishery gillnet catches were:

$$Y = 0.064 * e^{\frac{(X-94.1)^2}{-413}} \tag{1}$$

for the 65-105 cm FL interval, and:

$$Y = 0.017 * e^{\frac{(x-135)^2}{825}} \tag{2}$$

for the 105-165 cm FL interval (Figure 7).

Total instantaneous mortality rate (Z) and annual mortality rate (A) derived from the 1990-1991 catch curve for 10-16 year old fish were 0.53 and 0.41, respectively (Figure 8). Total mortality estimates from the marked cohort regression were similar with values of 0.51 and 0.40 for Z and A, respectively (Table 2). Instantaneous and conditional natural mortality estimates (M and n) averaged 0.16 and 0.15, respectively (Table 3).

Abundance

Annual abundance estimates for white sturgeon $\geq$ 54 cm FL ($\geq$ 2 ft. TL) ranged from 678,000 to 1,058,300 fish in 1986-1990 (Table 4). Average abundance for 1986-1990 was 895,500 sturgeon $\geq$ 54 cm FL. There was a decline in the exploited age classes (92-166 cm FL) between 1986 and 1990, consistent with the high exploitation estimates (Tables 1 and 4). Abundance of oversized sturgeon ($\geq$ 167 cm FL) ranged between 6,900 and 10,900 (Table 4). The estimated abundance of age 10 fish ranged from 124,800 to 189,000 fish while abundance of age 25 fish ranged between 600 and 1,000 (Table 4). The average density of white sturgeon $\geq$ 54 cm FL in the LCR was 14.6 fish per hectare and ranged from 11.1 to 17.3 fish per hectare (Table 4).

Simulations indicated that the recapture sampling strategy as well as the magnitude and timing of immigration and emigration influenced the accuracy of the modified Peterson estimator. The estimator was satisfactory when recapture sampling was spread throughout the nine month

Table 1. Estimated exploitation of marked white sturgeon from the Columbia River downstream from Bonneville Dam, 1985-1991. Year groupings and length intervals correspond to length and time intervals used in calculating total mortality.

Period[a]	Total length interval	Marks-at-large	Marked fish harvest: Observed	Marked fish harvest: Expanded[b]	Exploitation
1985-1986	91-101cm	227	13	66	0.29
1986-1987	91-121cm	2,099	146	614	0.29
1987-1988	91-121cm	1,834	130	487	0.27
		1985-1988 Geometric mean[c]			0.28
1988-1989	91-152cm	1,280	54	243	0.19
1989-1990	122-152cm	165	11	61	0.37
1990-1991	122-152cm	105	7	40	0.38
		1985-1991 Geometric mean[d]			0.29

[a] *The 12 month period following capture and marking. Marking took place from April-June of each year.*

[b] *Observed marked fish harvest expanded for fishery sub-sampling, harvest outside* the *Columbia River, and corrected for tag loss.*

[c] *An estimate of the 1985-1988 average composite exploitation experienced by 91-101 cm TL white sturgeon marked in 1985, 1986 and 1987.*

[d] *An estimate of the previous 5-6 year average composite exploitation experienced by 15-16 year old white sturgeon sampled in 1990-1991.*

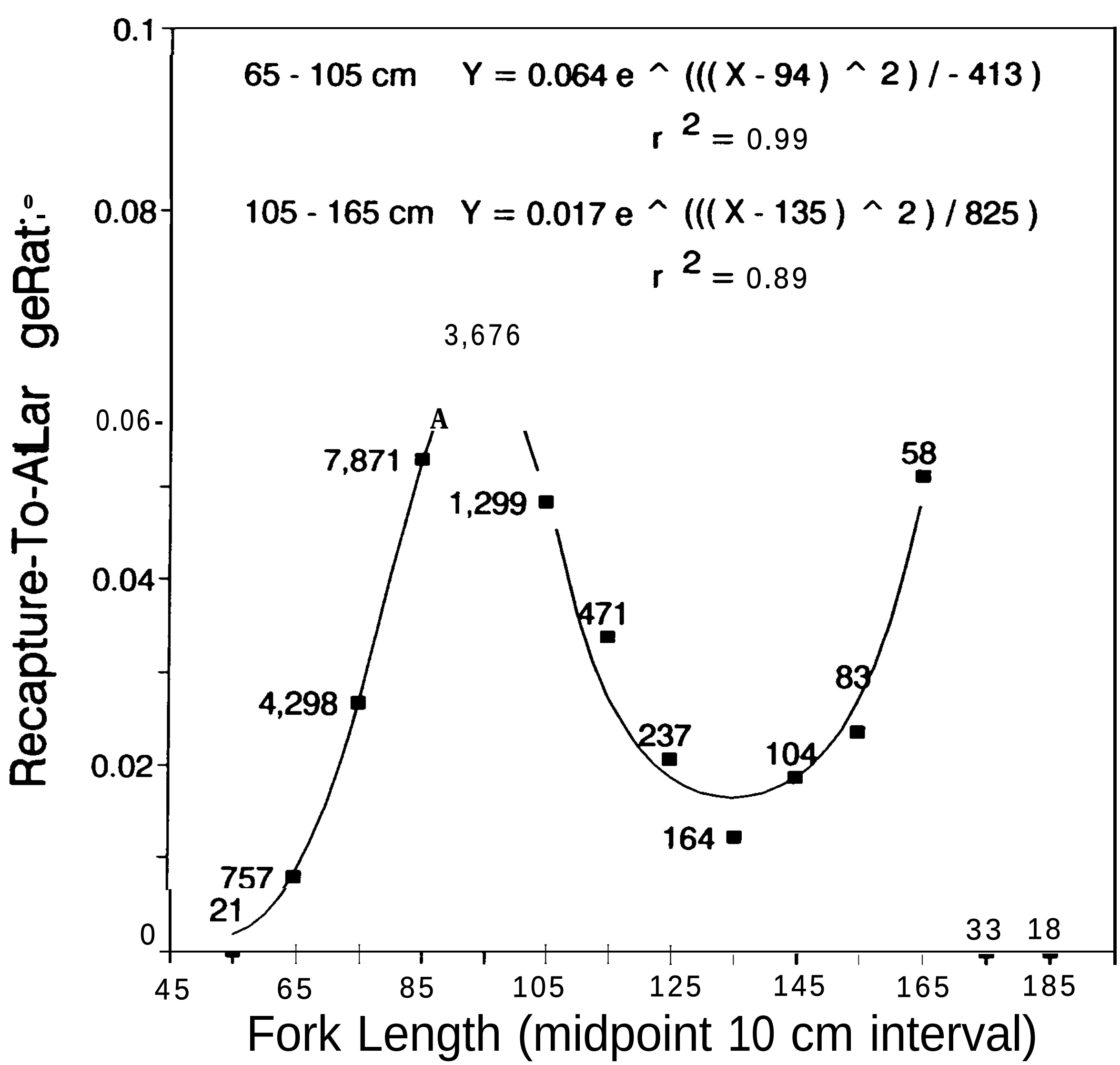

Figure 7. Ratio of recaptures to marks-at-large by 10 cm fork length interval for white sturgeon captured using 6¼ - 74 inch mesh gillnets on the Columbia River downstream from Bonneville Dam, 1983-1991. Only recaptures during the April-June marking period were included. Curves representing the 65-105 cm and 105-165 cm relationships were fit to the ratios using non-linear least squares regression. The number of marks-at-large are presented for each point.

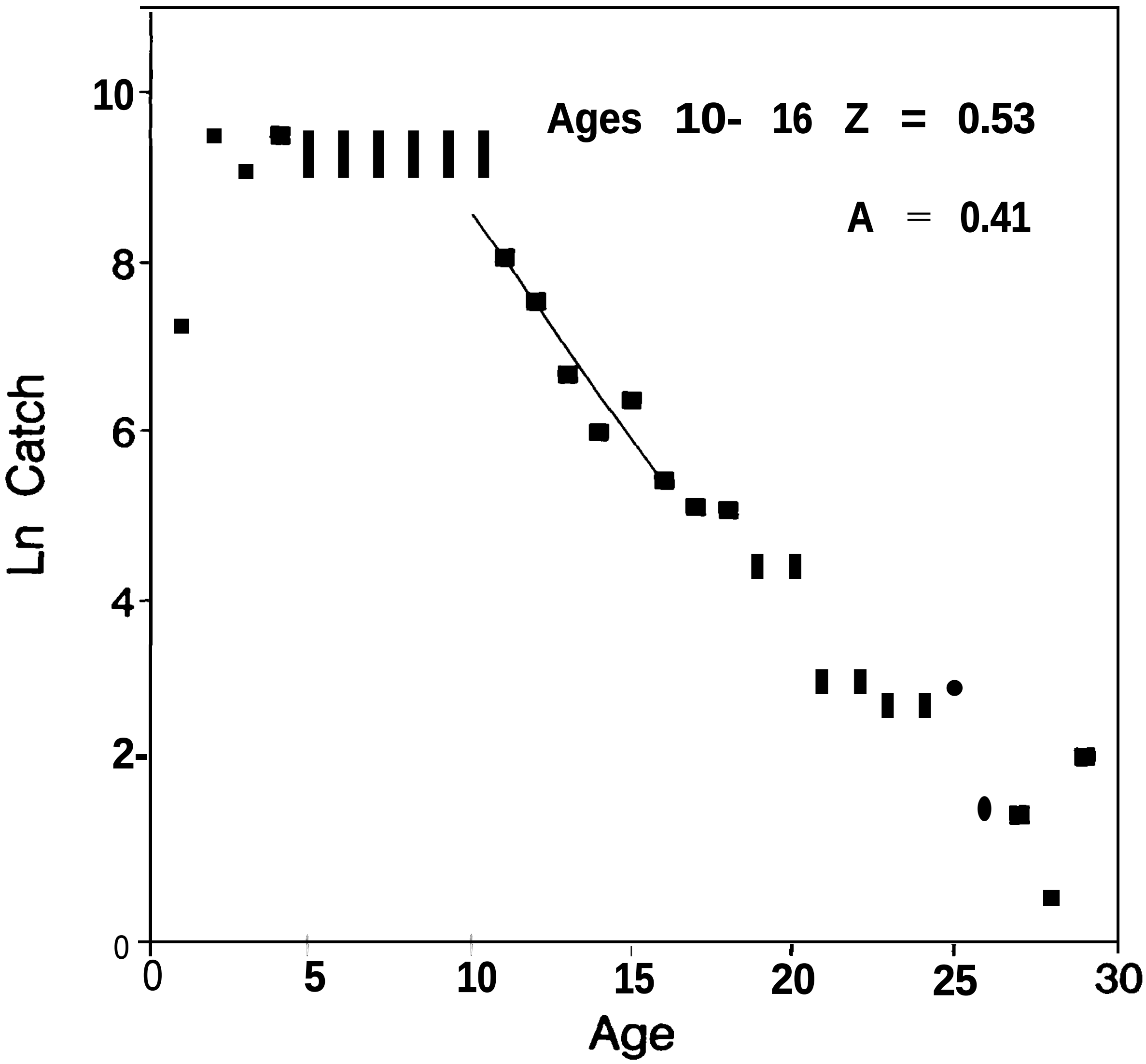

Figure 8. Catch curve for white sturgeon captured during research gillnet fisheries on the Columbia River downstream from Bonneville Dam. April-June 1990 and 1991 catches were combined and corrected for gillnet size selectivity. Instantaneous (Z) and annual (A) total mortality rates corresponding to the regression line equalled 0.53 ± 0.13 (Z) and 0.41 ± 0.07 (A) for ages 10-16.

Table 2. Recreational fishery recapture data and corresponding mortality estimates for white sturgeon marked in the Columbia River downstream from Bonneville Dam, 1985-1989.

Recapture period[a]	Recaptures by mark group[a] 1985	1986	1987	Weighted average	Angler trips	Recaptures per angler trip
	47					
1985-1986 / 1986-1987	14	162				
1987-1988	11	137	148			
1988-1989		89	78			
Weighted recapture frequency[b]						
1985-1986	47			47	135,100	0.0003
1986-1987	34	34		34	145,600	0.0002
1987-1988	14	28	14	19	175,300	0.0001
1988-1989	11	19	7	12	149,800	0.0001
			Instantaneous total mortality (Z)			0.51 ± 0.13[c]
			Annual total mortality (A)			0.40 ± 0.12

[a] *Combined insample and volunteered mark recaptures by 12 month period following initial capture and release. Mark groups consisted of 91-101 cm TL fish tagged during April-June, 1985-1987 research fisheries. Recaptures were expanded to account for tag loss.*

[b] *Recaptures of 1986 and 1987 mark groups were weighted relative to the 1985 mark group to derive a combined 1985-1987 mark group average recapture frequency .*

[c] *Instantaneous total mortality (± 2 SE) was estimated from a linear least squares regression of log-transformed recaptures per angler trip.*

Table 3. Mortality estimates for white sturgeon sampled from the Columbia River downstream from Bonneville Dam.

Category	1985-1988	1990-1991
Total mortality		
Marked cohort (91-101 cm TL)		
Instantaneous (Z)	0.51	
Annual (A)	0.40	
Research fishery catch curve (ages 10-16)		
Instantaneous (Z)		0.53
Annual (A)		0.41
Fishing mortality		
Instantaneous (F)	0.36	0.37
Conditional (m)	0.30	0.31
Exploitation (u)	0.28	0.29
Natural mortality		
Instantaneous (M): M = Z - F	0.15	0.16
Conditional (n): n = I-e^(-M)	0.14	0.15
Average (methods and years combined)		
Instantaneous (M)	0.16	
Conditional (n)	0.15	

Table 4. Abundance of white sturgeon in the Columbia River downstream from Bonneville Dam, 1986-1990, based on mark-recapture estimates and research and recreational fishery length frequency distributions.

Fork length interval (cm)[a]	Abundance				
	1986	1987	1988	1989	1990
54-81[b]	755,200	788,300	740,500	496,200	593,500
82-91	66,400[c]	115,500[c]	95,600[c]	84,900b	125,500[b]
95% CI	(48,700) (99,300)	(82,000) (183,200)	(65,600) (161,600)		
92-166[c]	148,100	146,300	111,100	90,000	77,900
95% CI	(110,500) (215,300)	(111,700) (205,000)	(74,900) (192,800)	(66,800) (132,500)	(59,400) (109,400)
≥ 167[d]	7,600	8,200	8,900	6,900	10,900
Total (254 cm)	977,300	1,058,300	956,100	678,000	807,800
Number per Ha (254 cm)	16.0	17.3	15.6	11.1	13.2
Number Age 10	188,900	189,000	160,700	124,800	161,300
Age 25	600	1,000	900	600	700

[a] *Intervals correspond to total lengths of 24-35, 36-39, 40-72, and >72 inches.*

[b] *Abundance for these length intervals was extrapolated from the mark-recapture estimates using research fishery length frequencies.*

[c] *Mark-recapture abundance estimates were made for 82-166 cm FL fish in 1986-1988 and for 92-166 cm FL fish in 1989-1990.*

[d] *Abundance of fish ≥ 167 cm FL was calculated by dividing the handle of ≥ 167 cm FL fish in the recreational fishery by the 110-166 cm FL recreational fishery exploitation rate.*

recapture period and a portion of the immigration and emigration occurred after month five (at 30% of initial abundance) or month three (at 10% of initial abundance).

Productivity

Population simulation using constant recruitment predicted maximum sustainable yield (MSY) was 1.4 kg per recruit at an exploitation rate of 0.32 (Figure 9A). Estimated sustainable annual yield, based on the number of age 1 recruits, was 997,000 kg (16.3 kg/Ha), assuming constant recruitment. Maximum sustainable yield dropped to 0.3 kg per recruit at an exploitation rate of 0.04 when a stock-dependent recruitment function (Beaverton-Holt: A=0.5) was applied.

Egg production per recruit ranged from 11,890 for an unexploited population and decreased exponentially to 90 (assuming constant recruitment) or 3,500 (assuming stock dependent recruitment: A=0.5) at MSY exploitation rates (Figure 9B).

Discussion

The LCR supports the largest abundance and highest density of white sturgeon in the three identified production areas (Sacramento/San Joaquin, Columbia, and Fraser basins). Pycha (1956) estimated 11,154 white sturgeon ≥102 cm TL in the Sacramento/San Joaquin estuary in 1954. Kohlhorst (1980) estimated the abundance of the same population to be 40,000 in 1968 and 74,500 in 1979. Recent abundance estimates show a marked increase: 128,300 in 1984, 96,200 in 1985, and 84,000 in 1987 (Kohlhorst et al. 1991), although average stock size was less than estimated for the LCR population. The 1986-1990 average abundance for the same size classes of LCR white sturgeon was 123,200. Estimated abundance of Columbia Basin populations upstream from Bonneville Dam were also lower than LCR estimates, ranging from 870 fish in the Kootenai system to 51,400 fish (≥70 cm FL) in Bonneville Reservoir (Cochnauer 1983; Cochnauer et al. 1985; Lukens 1985; Apperson and Anders 1990; Beamesderfer and Rien 1992). There are no reported estimates of white sturgeon abundance or density from the Fraser Basin. However, annual harvest estimates of Fraser River sturgeon (Semakula and Larkin 1968; Parks 1978) indicated that abundance and density may be significantly lower than for the LCR population.

White sturgeon from the LCR appear to have better growth than other populations. Tracy and Wall (1992) reported higher average length at age for the LCR population compared to populations from Bonneville Reservoir (Malm 1981), the Snake River (Coon et al. 1977; Lukens 1982, 1984), and the Fraser River (Semakula 1963). A comparison of VBGFs from Sacramento River and LCR populations indicate that LCR sturgeon grew slower at young ages, but attained a larger ultimate length (Tracy and Wall 1992). Mean relative weights are higher for LCR sturgeon than for any other white sturgeon population reported (Beamesderfer 1992). The superior growth rates and condition factor of the LCR population is probably due to abundant food resources associated with marine-based prey species. White sturgeon in the LCR make seasonal migrations to feed on eulachon

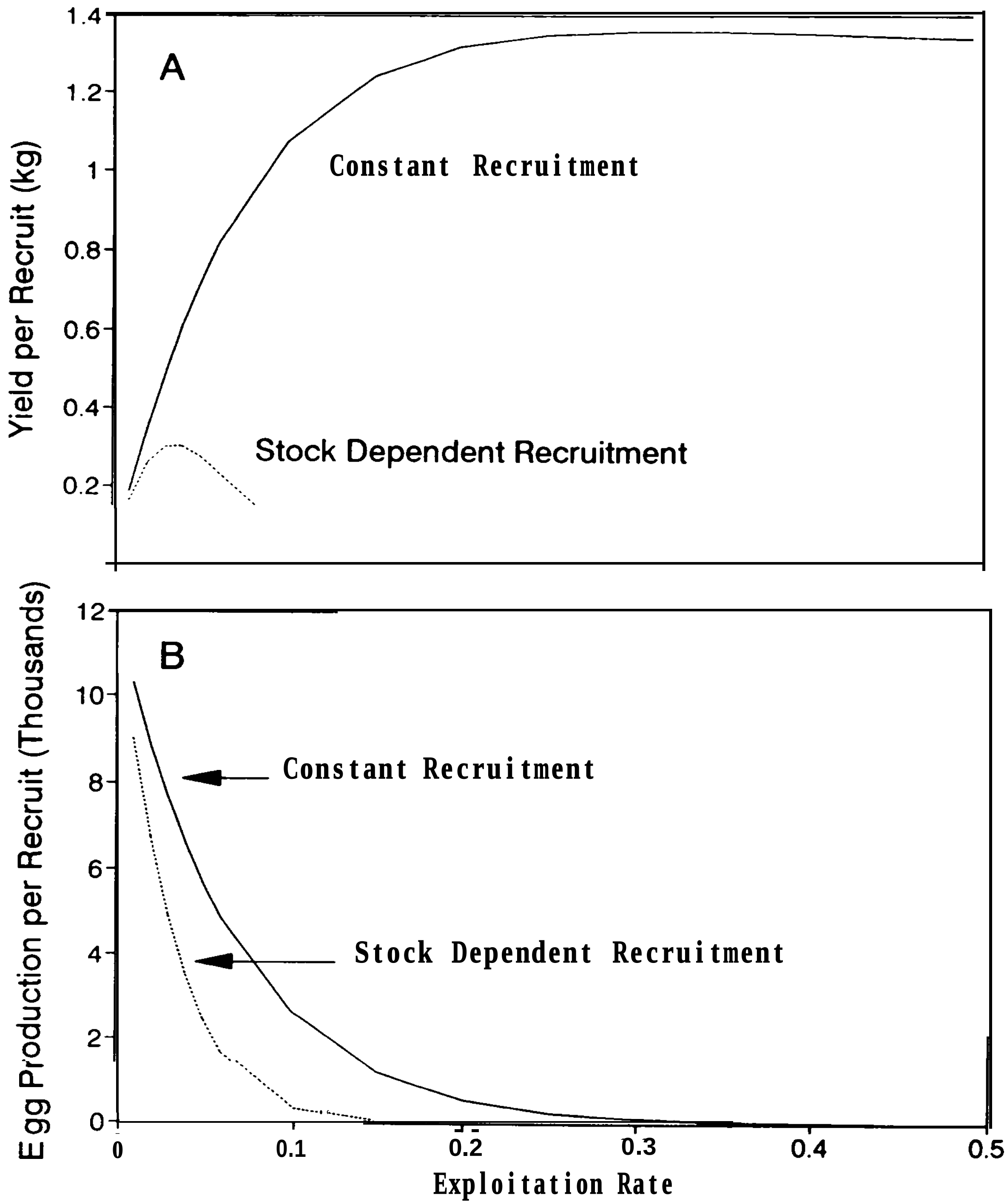

Figure 9. Simulated yield (A) and reproduction (B) per recruit relative to 92-183 cm TL exploitation using constant and stock dependent (Beverton-Holt A = 0.5) recruitment for the Columbia River white sturgeon population downstream from Bonneville Dam.

(Thaleichthys pacificus), northern anchovy *(Engraulis mordax)*, American shad *(Alosa sapidissima)* and moribund salmonids (Bajkov 1951; DeVore and Grimes 1992). The biomass of prey species is high and well distributed seasonally. Therefore, LCR sturgeon can subsist on alternative resources in the event of declines in usual prey species.

A problem in this study, as in most sturgeon studies, was the lack of samples from large fish. The age structure of the LCR population, managed with a slot limit, had proportionally more older and larger fish than most populations and was therefore more difficult to model without adequate samples from those fish. Age composition and mark recoveries obtained from recreational and commercial fisheries were biased due to minimum and maximum size limits. Sturgeon captured in the Bonneville broodstock monitoring program provided valuable aging and maturity samples but sampling was not representative of that segment of the population because reproductively mature fish were more prevalent than in a random sample. Representative sampling of the over 6 ft. TL segment of the population would have resulted in more accurate modeling of age, growth, and reproductive potential.

Our estimate of natural mortality (M=0.15) was higher than the 0.07 we estimated from a generalized relationship Pauly (1980) developed using multiple regression of mean water temperature and VBGF parameters K and L_∞. However, the similarity of total mortality estimates using two different methods suggested reasonable accuracy. In comparison, Semakula (1963) calculated a natural mortality rate of 0.089 for Fraser River white sturgeon, and Lukens (1985) determined a natural mortality rate of 0.13 for Snake River white sturgeon (Hells Canyon population). Kohlhorst et al. (1991) report estimates of survival and exploitation for the Sacramento/San Joaquin white sturgeon population, from which we calculated estimates of M ranging from 0.05 to 0.20. High natural mortality estimates may in part result from undocumented illegal harvest. Considering the popularity of LCR sturgeon fisheries, significant illegal harvest probably occurred. The high effort and catch could also be responsible for a relatively high incidental fishing mortality (e.g. hooking mortality) which would result in overestimating natural mortality.

Parameter estimates that relied on mark-recapture data would have been biased if survival of marked fish was affected by handling stress and marking techniques (Wydoski and Emery 1983). We were unable to estimate survival differences between marked and unmarked fish in this study, but assumed any differential survival was minor. Multiple recaptures of marked fish in commercial and recreational fisheries support this assumption. Lower survival of marked fish would have produced overestimation of marks-at-large which would have resulted in underestimates of exploitation and overestimates of abundance and natural mortality.

We used a closed system population estimator because of tag shed and recruitment problems inherent with a long time series model. Abundance of open system populations is typically estimated using a multiple mark-recapture estimator such as the Jolly-Seber model (Ricker 1975). The multiple mark and recapture periods (≥ 5) in Jolly-Seber methodology would have required a five year mark and recapture study resulting in bias from tag shed and recruitment. Also, migration studies suggest that only a small portion of the LCR white sturgeon population reside in marine areas for a significant duration (DeVore and Grimes 1992). The modified Peterson model we used, when applied to a population open to both immigration and emigration, may overestimate abundance (Robson and Regier 1968). However, our simulations indicated that, as long as immigration, emigration, and recoveries were not limited to the first five months of the recapture period (for levels of immigration/emigration at 30% of initial abundance), abundance estimates would fall between initial abundance (at the start of the recovery period), and initial abundance plus immigration. We concluded that we overestimated initial abundance but underestimated the annual abundance of fish that utilize the LCR.

Population simulation, assuming constant recruitment, indicates that the LCR population can withstand relatively high exploitation (MSY at 32% annual exploitation of the 3-6 ft. population). An historical collapse in stocks due to overexploitation is compelling evidence that the assumption of constant recruitment is unrealistic. The recovery of the population after protection of broodstock with a 6 ft. maximum size limit also suggests a relationship between stock size and recruitment, although the data does not indicate the appropriate degree of density dependence. Kimura et al. (1984) suggest that the Beaverton-Holt recruitment function with A=0.5 is a reasonable low bound for most fish populations. Therefore, the actual stock recruitment relationship for LCR white sturgeon, as well as MSY, probably occurs within the ranges modeled.

Managers should be aware that although LCR white sturgeon may be able to withstand relatively high harvest rates there is a danger of overexploitation leading to a decline in productivity. Sturgeon throughout their range have a common history of decline or depletion due to overexploitation and habitat changes (Rochard et al. 1990). Optimal sustainable yields can only be achieved for the LCR population with conservative management schemes, especially in light of recent increases in recreational catch and effort. Since 1988, Columbia River managers have reduced harvest rates to half the rates of 1985-1987 in the LCR by eliminating target commercial seasons in 1989, increasing the recreational minimum size limit by four inches in 1989, and reducing the daily bag limit in recreational fisheries to one fish <48 in. plus one fish ≥48 in. in 1991. In 1992 Washington adopted further restrictions by establishing a spring spawning sanctuary in the 6.5 km reach downstream from Bonneville Dam (on the Washington side of the river) and reducing the maximum size limit in recreational and commercial fisheries to 60 in. TL.

Hydroelectric development has impacted LCR white sturgeon to some degree, although probably less than the impounded populations. Parsley and Beckman (1992) demonstrated that suitable spawning habitat exists in the Bonneville Dam tailrace at lower discharges than in upstream spawning areas, although the amount of suitable spawning habitat has been affected by hydropower development. Spring flows in the LCR prior to hydroelectric development were much higher and, if spawning habitats were fully seeded, decreased spring flows would result in reduced recruitment. Low spring flows in the Sacramento/San Joaquin Basin were correlated to low recruitment (Kohlhorst 1980). Nevertheless, Parsley et al. (1992) found recruitment was higher with less annual variation in the LCR than in impounded areas upstream from Bonneville Dam.

The LCR supports the most productive population of white sturgeon based on perennially good recruitment, superior growth and condition factor, the highest abundance and densities reported in the species range, and relatively high sustainable yields. Access to marine environments, abundant food resources, and suitable spring flows for spawning every year are the primary reasons for this high productivity. Despite the great production potential of this population, history has taught us that this resource is vulnerable to collapse from overexploitation. Therefore, our challenge is to manage the resource for long term sustainable exploitation and protect critical habitats needed to maintain a highly productive population.

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Appendix 1. Numbers of white sturgeon captured and marked during research fisheries on the Columbia River downstream from Bonneville Dam, 1985-1991.

Year Fishery	Location (Km)	Period	Mesh size (in)	Number drifts	Number captured	Number tagged
1985						
Corbett	200	Apr	6¼-7½	30	256	177
Skamokawa	55	Apr-May	6½-7¼	15	613	360
Estuary	9-32	May-Jun	7¼-9	23	635	624
Total				78	1,504	1,161
1986						
Corbett	200-214	Mar-May	6¼-7½	41	733	315
Skamokawa	55	Mar-May	6½-7¼	22	2,392	1,076
Woody Island	45	Apr	6½-7¼	20	1,028	777
Estuary	9-32	Mar-Jun	7½-9	38	2,451	2,155
Total				121	6,604	4,323
1987						
Corbett	200	Apr	6¼-7½	30	261	201
Skamokawa	55	Mar-Jun	64	9	497	251
Woody Island	45	Apr	6½-7¼	21	406	296
Estuary	9-32	Apr-Jun	7¼-8	74	3,164	2,948
Total				134	4,328	3,696
1988						
Corbett	200	Apr	6¼-7½	31	631	481
Skamokawa	55	May	6½	9	35	26
Woody Island	45	Apr	6½-7¼	20	763	601
Estuary	9-32	May-Jun	74	55	1,532	1,409
Total				115	2,961	2,517
1989						
Corbett	200	Apr	6¼-7½	27	275	174
Skamokawa	55	Apr-May	6¾	2	165	85
Woody Island	45	Apr	6½-7¼	21	1,569	812
Estuary	9-32	Apr-Jun	6¼-7½	55	4,921	4,249
Total				105	6,930	5,320

Continued

Appendix 1. Continued.

Year Fishery	Location (Rkm)	Period	Mesh size (in)	Number drifts	Number captured	Number tagged
1990						
Bonneville[a]	230	May-Jun	9½-11	11	54	50
Corbett	200	Apr	6¼-7½	30	389	214
Woody Island	45	Apr	6⅝-7	30	763	369
Estuary	9-32	Apr-Jun	7¼	52	5,320	2,756
Total				123	6,526	3,389
1991						
Bonneville[a]	230	May-Jun	9½-11	21	83	65
Corbett	200	Apr	6¼-7½	30	217	83
Skamokawa	55	May	7¾	3	40	36
Woody Island	45	Apr	6⅝-7	20	1,237	749
Estuary	9-32	Apr-Jun	7¼	71	7,530	3,967
Total				134	7,110	5,344

[a] *Monitoring of Oregon private hatchery broodstock collection activities. Effort was number of nights fished instead of number of drifts.*

Appendix 2: Tag Retention Rates

Tag retention rates were derived from recaptures of fish that were initially double tagged (anterior and posterior insertion sites at the base of the dorsal fin). Recaptures were summarized by retention (anterior only, posterior only, or both tags present) and by months-at-large (Appendix 2 Table 1). Tag retention data were pooled for 1-3 and 4-6 months-at-large, then for subsequent six month periods. Retention rates were estimated from pooled retention ratios using an iterative model incorporating probability formulas described in Ricker (1975).

Appendix 2 Table 1. Retention of spaghetti tags applied to white sturgeon in the Columbia River downstream from Bonneville Dam, 1986-1991.

Months at large	Anterior				Posterior			
	Recaptures[a]		Retention rate		Recaptures[a]		Retention rate	
	Retained	Lost	Monthly	Cumulative	Retained	Lost	Monthly	Cumulative
1- 3	1,222	44	0.978		1,222	44	0.978	
4- 6	274	25	0.990		276	23	0.994	
7-12	594	65	0.999	0.90	586	73	0.994	0.88
13-18	759	99	0.993		717	141	0.977	
19-24	266	42	0.999	0.86	219	89	0.983	0.69
25-30	335	69	0.986		270	134	0.986	
31-36	102	30	0.995	0.77	65	67	0.940	0.44
37-42	86	29	0.992		48	67	0.980	
43-48	32	13	0.995	0.71	14	31	0.950	0.29

[a] *The number lost was expanded by the predicted number of recaptures with both tags missing.*

Appendix 3. Equations and definitions of variables and parameters used in a model of the population dynamics of white sturgeon. Included are variable and parameter values estimated for the white sturgeon population residing in the Columbia River downstream of Bonneville Dam.

Variable or parameter	Definition	Equation	Length interval FL (cm)	Value
$N_{x,t}$	Age-specific number of fish in the population in any year	$= (N_{x-1,t-1}) (S_x)$		
x	Age			
t	Year			
x_{max}	Maximum age			80
S_x	Age-specific annual rate of survival	$= 1 - [m_x + n_x - (m_x) (n_x)]$		
m_x	Conditional harvest mortality rate			
n_x	Conditional natural mortality rate			0.15
L_x	Length at age (von Bertalanffy equation)	$= L_\infty \{1 - Exp[-k(x - t_0)]\}$		
L_∞	von Bertalanffy equation length at infinity			276.313
k	von Bertalanffy equation parameter			0.0346021
t_0	von Bertalanffy equation parameter			-1.1249161
W_x	Weight at age	$= (a_w) (L_x)$ ^ b_w		
a_w	Length-weight equation coefficient			2.85 E-6
b_w	Length-weight equation exponent			3.23

Continued

Appendix 3. Continued.

Variable or parameter	Definition	Equation	Length interval FL (cm)	Value
P_t	Net reproductive potential of all ages in any given year	$= \Sigma P_{x,t}$		
$P_{x,t}$	Reproductive potential of each age class at or above the age of female maturity	$= (N_{x,t})(pf)(ps_x)(F_x)$		
pf	Proportion of the population that is female		82-166 ≥ 167	0.447 0.465
ps_x	Proportion of the population of females of each age class that spawn in any year	$= C_\infty \Phi$ for $L_x \leq \mu$ $= C_\infty (1-Q)$ for $L_x > \mu$		
C_∞	Maximum proportion of spawning females			0.50
Φ	Cumulative normal distribution function dependent variable $= \frac{1}{\sqrt{2\pi}} EXP[-(L_x - \mu)^2\sigma^2] \sum_{i=1}^{5} b_i \{1 + p\left\lvert \frac{L_x - \mu}{\sigma} \right\rvert \}^{1-i}$			
μ	Mean length of female sexual maturity			160
σ	Variance about mean length of female sexual maturity			18
$b_1,..,b_5$	Constants (0.31938153, -0.356563782, 1.781477937, -1.821255978, 1.330274429)			
p	Constant (0.2316419)			
F_x	Age-specific fecundity of females	$= (a_f)(L_x)^\wedge b_f$		
a_f	Length-fecundity equation coefficient			0.0735

Continued

Appendix 3. Continued.

Variable or parameter	Definition	Equation	Length interval FL (cm)	Value
b_f	Length-fecundity equation exponent			2.937159
R_t	Number of age 1 recruits to the population (corresponds to $N_{1,t}$)	$= (P_t)/\{1-(A_b)[1-(P_t/P_r)]\}$		
P_r	Replacement reproductive potential at equilibrium			
A_b	Beverton-Holt recruitment parameter describing shape of curve			0.50

REPORT H

Dynamics and Potential Production of White Sturgeon Populations in Three Columbia River Reservoirs

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Abstract.- White sturgeon Acipenser transmontanus were sampled in three lower Columbia River reservoirs from 1987-91 to describe population dynamics and to evaluate the ability of these stocks to sustain harvest. Significant differences were observed among reservoirs in abundance, biomass, size composition, sex ratio, size of females at maturity, growth rate, condition factor, and rate of exploitation. No differences were detected in fecundity, natural mortality rate, or longevity, in part because of sampling difficulties. Recruitment rates and densities were inversely correlated with growth rate, condition factor, and size of females at maturity. Differences in population dynamics among reservoirs resulted in 10-fold differences in sustainable yields. Differences were even larger if relative reservoir sizes were considered. Maximum yields per recruit were predicted at annual exploitation rates between 5 and 15%, although potential egg production per recruit declined exponentially with increasing exploitation. Potential yield from these impounded populations appears to have been reduced by dam construction, which restricts populations to river segments which may not include conditions optimal for all life stages.

Introduction

Despite the value or potential value of sturgeon fisheries worldwide, the population dynamics and factors regulating production in this ancient family are poorly understood. This lack of knowledge is likely a contributor to, and a result of the depressed or endangered status of sturgeons almost everywhere (Rochard et al. 1990). The longevity and delayed maturation of sturgeons appear to render populations incapable of sustaining even moderate exploitation without collapse (Smith 1914, Smith et al. 1984, Threader and Brousseau 1986, Young et al. 1988, Rieman and Beamesderfer 1990, Smith 1990). Populations have also been severely affected by changes in their large-river habitats, especially those related to dam construction (Artyukhin et al. 1979, Votinov and Kas'yanov 1979, Assis 1990, Lane 1991).

Construction of hydroelectric dams across the Columbia River has segregated white sturgeon Acipenser transmontanus stock into a series of functionally discrete populations (North et al. 1992b) which have access to different habitats (Parsley and Beckman 1992). Habitat varies in the mainstem Columbia River in a largescale pattern related to the surrounding topography, which includes interior mountains, a semi-desert plain, a gorge through the Cascade Range, a drowned coastal valley, and estuary. Where white sturgeon historically ranged freely undertaking extensive seasonal migrations among habitats (Bajkov 1951)' dam construction now constrains movement to river segments, each containing a subset of the conditions previously available. Impoundment has also reduced habitat diversity, replacing the free-flowing river with a more lentic environment.

Habitat differences probably have a complex effect on white sturgeon populations, potentially affecting each life history stage differently. Comparisons of available habitat will not estimate this net effect on white sturgeon because it is unknown where in the life cycle the population is regulated and what combination of habitats optimizes conditions throughout the life cycle. Effects may be difficult to detect with simple comparisons of density or harvest, which are confounded if rates of exploitation vary among populations or years. However, the net effect of habitat differences should be reflected in the potential production or sustainable yield of the population. We define potential production as the capacity of a population to elaborate biomass and equate production with the capacity to provide yield. Potential yield is a useful measure of the benefits we might obtain by exploiting populations under existing environmental conditions. Potential yield can be predicted with rates of reproduction, growth, and mortality by using systems analysis and simulation methods which allow differences in exploitation rates to be factored out.

We assess the abundance, dynamics, and sustainability of fisheries for white sturgeon populations in three lower Columbia River reservoirs. We estimate and compare numbers, recruitment, sex ratio, maturity, fecundity, growth, condition, mortality, and longevity for each population. We then use these statistics to model populations and to estimate the potential yield of each.

Study Area

John Day, The Dalles, and Bonneville reservoirs are a series of impoundments operated for hydroelectric power generation, navigation, and flood control on the mainstem Columbia River (Figure 1). In all three reservoirs, littoral zones are limited, hydrologic retention times are short (average l-5 d), and current is measurable most of the year.

The three reservoirs differ in other respects. John Day Reservoir is the largest (123 km long; 21,000 ha; average depth 8.0 m) and most diverse of the three. This reservoir grades from a riverine upper third with gravel and cobble substrate to a shallow transition zone with sand substrate to a more lentic lower section with steep cliff and boulder sides. The Dalles Reservoir is the smallest (38 km long; 4,500 ha; average depth 7.5 m) and the most riverine, with cobble, gravel, and sand substrates distributed throughout most of its length. Bonneville Reservoir (74 km long; 8,400 ha) is shallow (average depth 6.7 m) with a mostly sand substrate, which supports large beds of rooted aquatic macrophytes during summer.

Methods

Data collection.- White sturgeon were sampled in the three reservoirs from April through August, 1987-91 with setlines and gill nets (Elliott and Beamesderfer 1990, North et al. 1992b), and by inspecting catches in sport and commercial fisheries (Hale and James 1992). Upper and lower size limits on catches in sport and commercial fisheries were 82-166 cm and 110-166 cm fork length (FL), although larger fish were occasionally examined from illegal sizes confiscated by authorities. Setline effort was evenly distributed within each reservoir, which was completely sampled in sequential periods of 3 weeks for The Dalles Reservoir in 1987 and 1988, 4 weeks for Bonneville Reservoir in 1989, and 5 weeks for John Day Reservoir in 1990 (North et al. 1992b). All reservoirs were sampled during 1991. Gill nets were used in The Dalles Reservoir in 1987 and all reservoirs in 1991.

Sex and maturity were determined by examining the gonads of fish harvested in fisheries and by surgical biopsy of live fish longer than 170 cm FL (North et al. 1992a). Gonads of ripe females collected in fisheries and subsamples removed for egg counts were weighed. Pectoral fin sections were removed for age estimation from a subsample of the catch (30 fish per 20 cm FL interval in each reservoir and year if available). All fish were measured (FL to the nearest cm) and weighed (to the nearest 0.1 kg). Fish collected alive and in good condition with setlines were released after tagging with individually-numbered spaghetti or disk tags and removing a barbel or a lateral scute specific to year of capture (Rien et al. 1992). The minimum size tagged was 70 cm. Tags and marks were noted upon recapture in setlines and sport and commercial fisheries.

Population Statistics.- Abundance was estimated for fish in the 70-166 cm size range using a Schnabel multiple mark-recapture method modified by Overton (1965) to account for removals. Mark-recapture

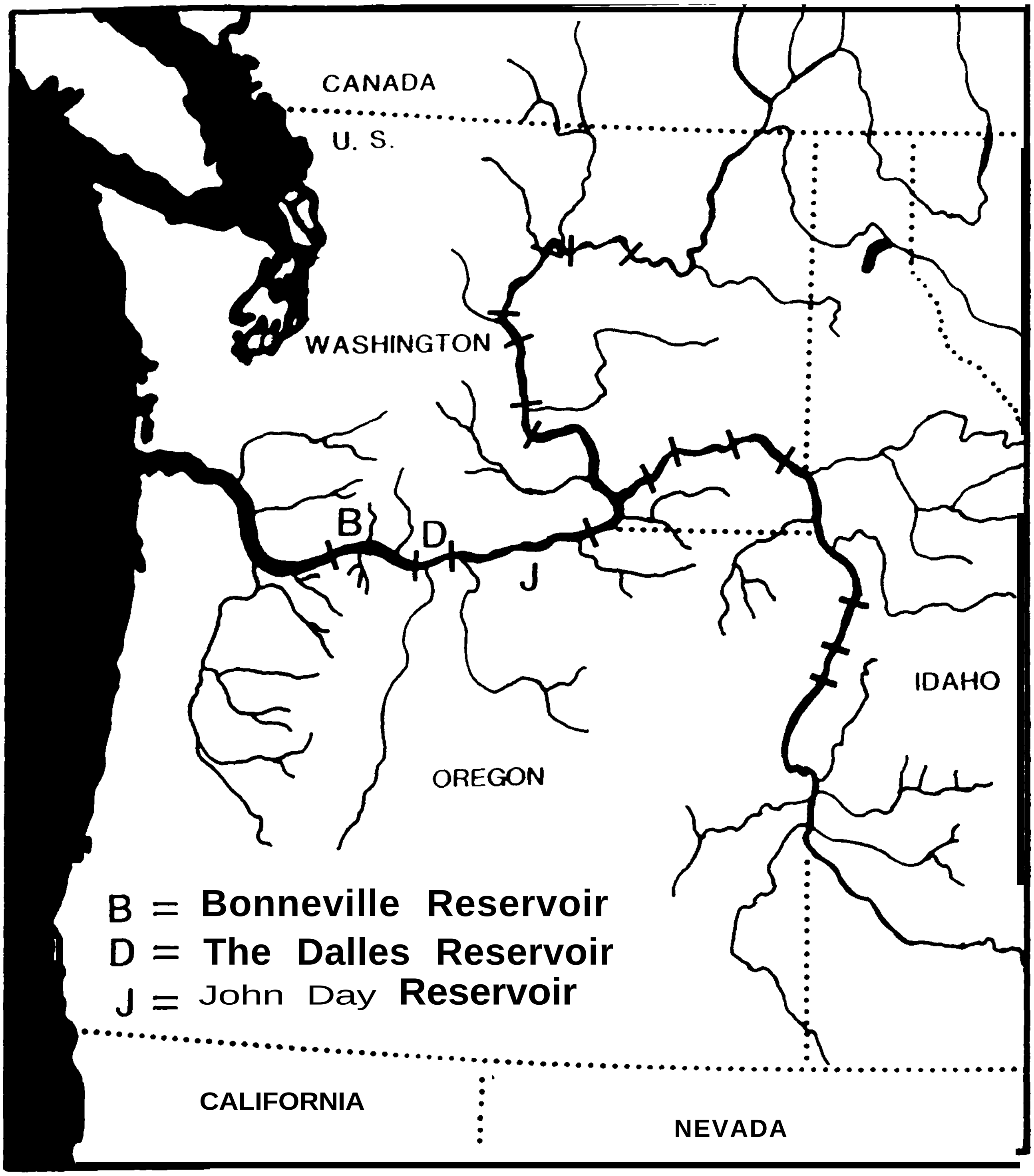

Figure 1. The lower Columbia River basin and reservoirs between Washington and Oregon.

samples were grouped by 3-5 week sampling period and fish recaptured in the same period in which they were marked were not treated as recaptures in population estimation. Removals included mortalities during sampling and harvest estimated in sport and commercial fisheries (Hale and James 1992). Fish that lost their tags were identified from secondary marks. Numbers of fish in various size classes were estimated from catch rate in setlines. Catch was adjusted for size selectivity of the gear by dividing by the recapture rate of marked fish of similar sizes (Beamesderfer and Rieman 1988). Recapture rates were estimated for fish in 54-81, 82-109, 110-166, and > 166 cm size classes for each year with the same approach used to estimate abundance. Recapture rates for years and reservoirs were averaged after dividing the recapture rate in each size class by rate for the most vulnerable size class in that year. Relative vulnerabilities were 0.90 (70-81 cm FL), 0.93 (82-109 cm), 1.00 (110-166 cm), and 0.65 ($\geq$ 167 cm).

Recruitment to the population, the fishery, and the protected oversized group were approximately represented as number of fish at ages 1, 10, and 25, respectively. Numbers of 10 and 25-year old fish were calculated from mark-recapture estimates of abundance using age distribution in the setline catch. Number of age 1 fish was estimated from number of age 10 fish by assuming an annual total mortality rate equal to the average for unexploited ages 5-10 from Bonneville and The Dalles reservoir gillnet catches (0.24).

Sex ratio, the proportion of females spawning each year, and fecundity were estimated from gonad inspections. Sex ratio was estimated for two size classes in each reservoir corresponding to fish within the fishery slot limit (82-166 cm) and fish larger -than the maximum size limit (166 cm). Chi-square contingency tables were used to test for independence in sex ratio between size classes in each reservoir (SAS Institute 1988). Similar tests were used to compare sex ratio among reservoirs for each size class. The relationship between size and female maturity was described in each reservoir with a cumulative normal probability curve fit with maximum likelihood methods recognizing the binomial nature of the data (Welch and Beamesderfer 1992). Comparisons of maturity curves were based on 95% joint confidence regions about paired estimates of equation parameters (Welch and Beamesderfer 1992). Comparisons were also made among size classes and reservoirs with chi-square tests like those used to test for sex differences in numbers. Egg counts in subsamples of female gonads were expanded by the difference in subsample and total gonad weights, and individual fish from all reservoirs were pooled for a single estimate of the fecundity-size relationship.

Age was estimated by counting marks in thin cross sections of the anterior pectoral fin ray (Rien and Beamesderfer 1992). Von Bertalanffy equations describing mean size at age in each reservoir were fit with a nonlinear regression based on observations for individual fish (SAS Institute 1988). Statistical comparisons among reservoirs were based on joint 95% confidence regions for the von Bertalanffy parameters L_∞ and k estimated for each population (Kimura 1980, Moreau 1987). To facilitate comparisons, the von Bertalanffy parameter t_0 was standardized at a value estimated with pooled data from all three reservoirs (-2.6).

Length (L)-weight (W) equation parameters were estimated for each reservoir with linear regressions on log-transformed observations of length and weight. Relationships were compared among reservoirs with joint 95% confidence regions for estimates of parameter pairs (Neter et al. 1985). Condition factor was also compared among reservoirs with estimates of mean relative weight (Wr) based on the standard weight equation

$$W = 2.735E\text{-}6\ L^{3.232}$$

from Beamesderfer (1992). Statistical comparisons of relative weight among reservoirs were based on an Analysis of Variance including Tukey's pairwise comparisons (SAS Institute 1988).

Total annual rate of mortality was estimated using three methods (Ricker 1975). Estimates of instantaneous rates were made from the slope of the descending limb of catch curves from gill nets for ages 5-10, and from setlines for ages 10-15 and 15-25. These age groups correspond to unexploited sizes, sizes vulnerable only to sport fisheries, and sizes vulnerable to sport and commercial fisheries, respectively. Catch curves were derived from age frequencies based on age-length keys developed for a subsample of the catch in each year and length distributions for that same year. Setline catches were adjusted for size differences in catchability, but comparable data were not available for gill nets.

Total mortality rate was also estimated by comparing catch rate in setlines of an aged cohort of fish in successive years with the same information used in catch curves. Finally, estimates were made by comparing catch rate in setlines of a cohort of tagged fish in successive years. Rates were estimated as the quotient of observations when only two observations were available (Ricker 1975). Rates were estimated with a linear least squares regression of log-transformed catch when three or more observations were available. Approximate 95% confidence limits about rate estimates were estimated from regressions as $\pm$ 2 SE.

Exploitation rate was estimated as the number of tagged fish observed in the catch of sport and commercial anglers divided by the number of tagged fish at large. Number of tagged fish in the commercial catch was estimated from a known-proportion subsample examined at commercial fish buyers. Number of tagged fish in the sport catch was estimated from tags returned by anglers corrected for a nonresponse rate based on selected subsamples in interviews of anglers (Hale and James 1992).

Natural mortality rate was estimated with a regression based on growth rate and temperature:

$$M = 10^{[-0.0066\ -\ 0.279\ \log_{10}(L_\infty)\ +\ 0.6543\ \log_{10}(k)\ +\ 0.4634\ \log_{10}(T)]}$$

M= instantaneous rate of annual mortality, k and $L\infty$ are parameters from the von Bertalanffy equation, and T = mean annual water temperature in °C (Pauly 1980).

Maximum age in all reservoirs was based on the maximum age observed in any reservoir. Observed maximum ages were compared with ages predicted by growth curve parameters (t_0 + 3 / k: Pauly 1980):

Potential Production.- We substituted population statistics into an age-structured model (Beamesderfer 1991) to estimate the potential yield and reproduction for each white sturgeon population (Table 1). An equilibrium population was structured for each reservoir population based on constant recruitment (age 1) in each year for the number of years equal to the life span of white sturgeon. Weight of fish harvested and population fecundity in the final year of the simulation were estimated for a range of exploitation rates to identify maxima and corresponding exploitation rates. Yield and reproductive potential were expressed relative to number of recruits because we lack information on survival between the egg stage and age 1. Reservoir-specific inputs were used except where no difference was detected among reservoirs (Table 2).

Results

Population Statistics

White sturgeon numbers (>54 cm) varied from 6,300 fish in John Day Reservoir to 51,400 in Bonneville Reservoir (Table 3). Densities ranged from 0.30 fish/ha in John Day Reservoir in 1990 to 6.16 fish/ha in The Dalles Reservoir in 1987. Biomass of white sturgeon ranged from 3.6 kg/ha in John Day Reservoir in 1990 to 81.4 kg/ha in The Dalles Reservoir in 1987. Small fish (54-81 cm) composed a greater proportion of the population in Bonneville Reservoir than in the other two reservoirs (Table 3). Numbers of large fish (>167 cm) ranged from 500 to 1,000 among reservoirs (Table 3).

Recruitment of age 1 fish varied among reservoirs from a minimum average of 1,200 in The Dalles Reservoir in 1988 to a maximum average of 25,700 in Bonneville Reservoir (Table 3). Numbers surviving to the approximate average age of recruitment to fisheries in all reservoirs ranged from 140 to 3,020 (Table 3).

Sex ratio of all fish collected was near 50:50, although larger fish were predominantly female (Table 4). Differences in sex ratio between fish less than and greater than 167 cm were significant in a pooled reservoir sample and in individual reservoir samples (Table 4). Significant differences were also observed in sex ratio among reservoirs for fish in the small (82-166 cm) size group (df = 2, X^2= 23.43, P < 0.001) but not the large ($\geq$ 167 cm) size group (df = 2, X^2 = 3.29, P = 0.193).

Maturity and fecundity of females also varied with size (Figure 2). More females matured at small sizes in Bonneville Reservoir than in

Table 1. Equations and definitions of variables and parameters used in a model of the population dynamics of white sturgeon.

Variable or parameter	Definition	Equation number
$N_{x,t}$	Age-specific number of fish in population in any year $= (N_{x-1,t-1})(S_x)$	1
x	Age	
t	Year	
x_{max}	Maximum age	
S_x	Age-specific annual rate of survival $= 1 - [m_x + n_x - (m_x)(n_x)]$	2
m_x	Exploitation (harvest mortality rate)	
n_x	Conditional natural mortality rate	
L_x	Length at age $= L_\infty \{1 - EXP[-k(x - t_0)]\}$	3
L_∞	Von Bertalanffy equation length at infinity	
k	Von Bertalanffy equation parameter	
t_0	Von Bertalanffy equation parameter	
W_x	Weight at age $= (a_w)(L_x)^{b_w}$	4
a_w	Length-weight equation coefficient	
b_w	Length-weight equation exponent	
$P_{x,t}$	Reproductive potential of each age class at or above the age of female maturity $= (N_{x,t})(pf)(ps)(F_x)$	5
pf	Proportion of the population that is female	
ps_x	Proportion of the population of females of each age class that spawn in any year $= C_\infty \Phi$ for $L_x \leq \mu$ $= C_\infty (1 - \Phi)$ for $L_x > \mu$	6 7
C_∞	Maximum proportion of spawning females	

Table 1 (continued).

Φ	Cumulative normal distribution function dependent variable $= \frac{1}{\sqrt{2\pi}} EXP[-(Lx - \mu)^2/2\sigma^2] \sum_{i=1}^{5} b_i \{1 + p \left\lvert \frac{L_x - \mu}{\sigma} \right\rvert \}^{1-i}$	8
μ	Mean length of female sexual maturity	
σ	Variance about mean length of female sexual maturity	
$b_1,..,b_5$	Constants (0.31938153, -0.356563782, 1.781477937, -1.821255978, 1.330274429)	
p	Constant (0.2316419)	
F_x	Age-specific fecundity of females $= (a_f)(L_x)^{b_f}$	
a_f	Length-fecundity equation coefficient	
bf	Length-fecundity equation exponent	
P_t	Net reproductive potential of all ages in any given year $= \Sigma P_{x,t}$	10
R_t	Number of age 1 recruits to the population (corresponds to $N_{1,t}$) $= (P_t)/\{1 - (A_b)[1 - (P_t/P_r)]\}$	11
P_r	Replacement reproductive potential at equilibrium	
Ab	Beverton-Holt recruitment equation parameter describing shape of curve	

Table 2. Estimates of population statistics used in simulations of white sturgeon populations in three lower Columbia River reservoirs.

Statistica	Ages	Reservoir		
		Bonneville	The Dalles	John Day
n	1-10	0.24	0.24	0.24
	>10	0.049	0.047	0.043
L_∞	>0	316	359	396
k	>0	0.021	0.021	0.019
t_0	>0	-2.6	-2.6	-2.6
x_{max}	>0	100	100	100
a_w	>0	3.11E-6	1.35E-6	2.40E-6
b_w	>0	3.19	3.38	3.26
pf	>0	0.50	0.50	0.50
μ	>0	168	164	194
σ^2	>0	53	26	40
c	>0	0.5	0.5	0.5
a_f	>0	3.39E-4	3.39E-4	3.39E-4
b_f	>0	4.05	4.05	4.05
R	1	10,000	10,000	10,000

Table 3. Abundance of white sturgeon based on mark-recapture estimates (Ñ for fish 70-166 cm FL) in three lower Columbia River reservoirs, 1987-1990. Confidence intervals (95%) are in parentheses.

Year	Ñ	Fork Lengths[a] (cm)					Age			No. per Ha	Kg per Ha
		54-81	82-109	110-166	≥167	Σ	1	10	25		
					Bonneville Reservoir						
1989	35,400 (27,500 - 45,400)	32,900	16,700	1,200	600	51,400	25,700	3,020	340	6.12	30.0
					The Dalles Reservoir						
1987	23,600 (15,700 - 33,600)	7,800	11,000	7,900	1,000	27,700	13,600	1,600	160	6.16	81.4
1988	9,000 (7,300 - 11,000)	4,200	4,300	2,000	800	11,300	1,200	140	40	2.51	35.5
					John Day Reservoir						
1990	3,900 (2,300 - 6,100)	3,600	1,700	500	500	6,300	3,200	380	60	0.30	3.6

[a]Correspond to total lengths of 24-35, 36-47, 48-72, and ≥73 inches.

Table 4. Sex of white sturgeon collected in three lower Columbia River reservoirs, 1987-91. Results of chi-square tests for independence of length and sex are reported for each reservoir.

Reservoir	Length (cm)	Female	Male	df	x^2	P^a
Bonneville	82-166	823	711			
	≥ 167	54	24	1	7.26	0.007
The Dalles	82-166	717	854			
	≥ 167	37	25	1	4.73	0.030
John Day	82-166	233	283			
	≥ 167	32	10	1	15.00	to.001
Combined	82-166	1,773	1,848			
	≥ 167	123	59	1	24.03	to.001

[a]Considered significant if $P < 0.05$.

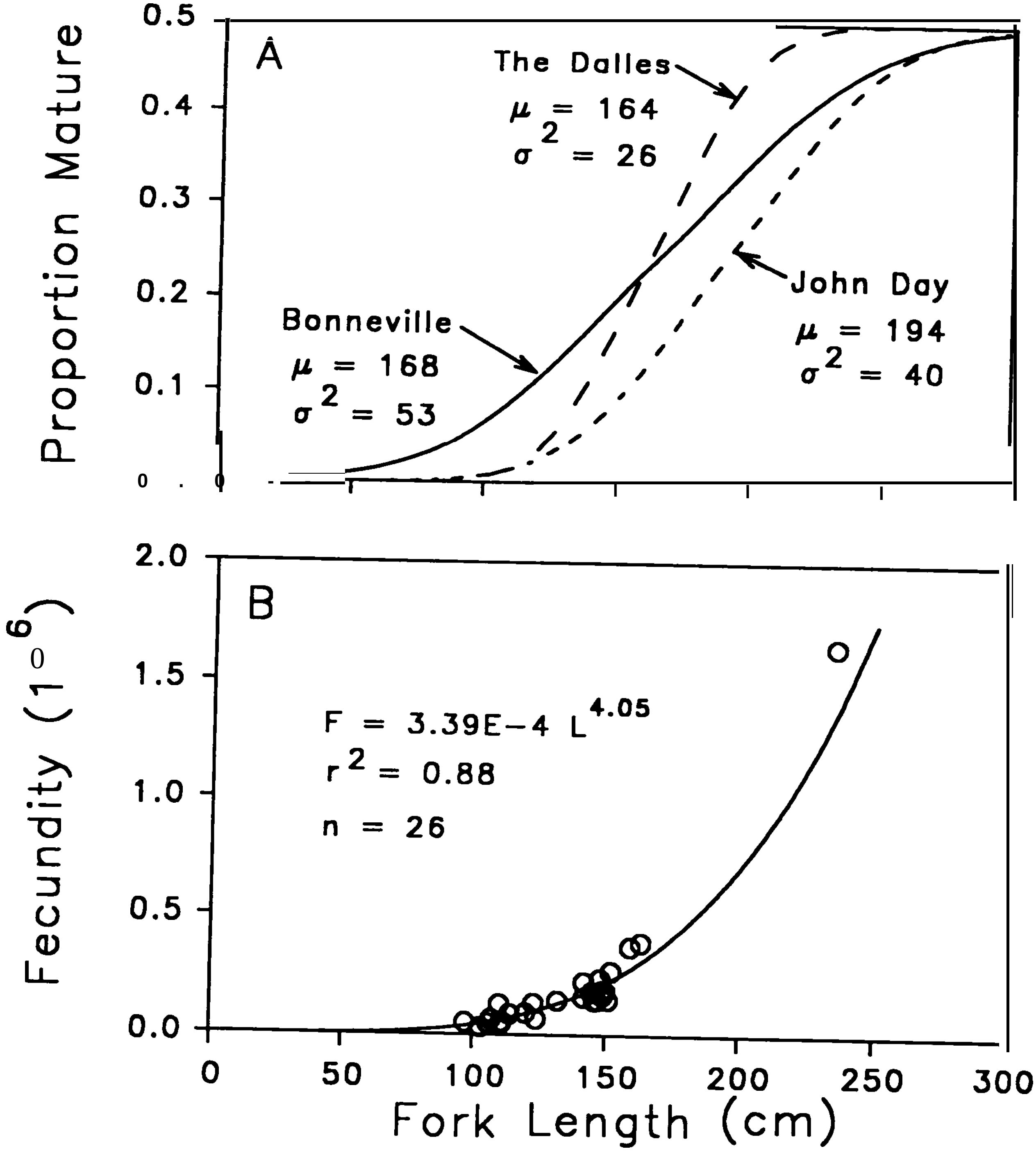

Figure 2. Maturity (A) and fecundity (B) versus size of female white sturgeon in three lower Columbia River reservoirs. Maturity equations are from Welch and Beamesderfer (1992).

The Dalles or John Day reservoirs (Figure 2A). Reservoir differences in proportion of maturing f males were significant for fish in the 82-166 cm size group (df = 2, X^2 - 6.10, P= 0.047) but not for fish $\geq$167 cm (df = 2, X = 4.60, P=0.101). Comparisons of joint confidence regions about paired parameter estimates likewise detected significant differences among reservoirs (Welch and Beamesderfer 1992). The difference between size groups in proportion of matu ing females was significant in a pooled-reservoir sample (df = 1, X^2 - 237.92, P < 0.001).

Fish in Bonneville Reservoir were smaller than similar-aged fish in the other two reservoirs (Figure 3). Mean size at age differed between John Day and The Dalles Reservoirs slightly among old fish. Joint 95% confidence regions for the von Bertalanffy parameters L_∞ and k indicated differences in equations describing mean length at age were significant between Bonneville and the other two reservoirs (Figure 4).

Comparisons of the relative weight index (Wr) indicate fish condition was slightly poorer in Bonneville Reservoir (97%) than in The Dalles Reservoir (99%) or John Day Reservoir (100%). Relative weight in Bonneville Reservoir was significantly different from relative weight in the other two reservoirs (Analysis of Variance with pairwise multiple comparisons: df = 2, 6061; F = 26.72; P < 0.001). Comparisons of confidence regions for joint estimates of parameters in length-weight equations confirm each reservoir is unique (Figure 5).

Instantaneous total mortality rates estimated for ages 5-10 from gill net catch curves were 0.20 ± 0.33 for The Dalles Reservoir in 1987 and 0.28 ± 0.12 for Bonneville Reservoir in 1991 (Figure 6). Estimates of total mortality rates for larger sizes were uncertain. Estimates based on catch curves varied widely among years (Figure 7) and were often less than estimates of fishing mortality for the same periods (Table 5). Estimates based on catch rates of cohorts in successive years also varied and several were less than or near zero (Table 6).

Annual exploitation rate in combined fisheries was 9-21% in Bonneville Reservoir, 23-42% in The Dalles Reservoir, and less than 10% in John Day Reservoir. Commercial fisheries harvested a majority of the catch in most years when both sport and commercial fisheries were surveyed (Table 5). Harvest and exploitation varied annually (Table 5).

Instantaneous natural mortality rates estimated with the regression of growth parameters and mean annual water temperature were 0.049 for Bonneville Reservoir, 0.047 for The Dalles Reservoir, and 0.043 for John Day Reservoir.

A white sturgeon estimated to be 104 years old was collected in this study and six other fish were estimated to be between 50 and 80 years old. Observed maxima were less than the 147 years predicted from von Bertalanffy curve parameters.

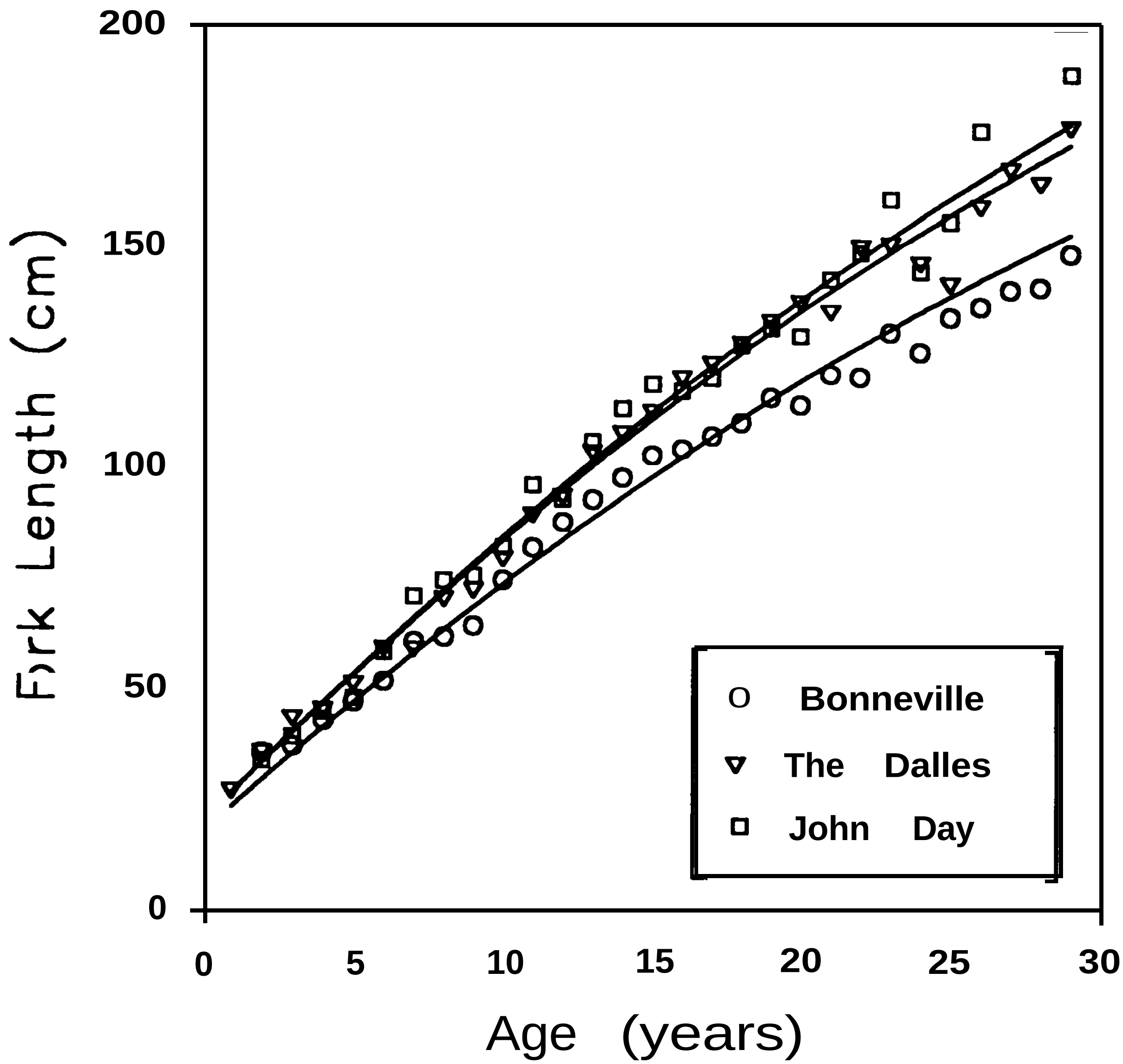

Figure 3. Mean length at age and von Bertalanffy lines for white sturgeon in three lower Columbia River reservoirs. Equation parameters (L_∞, k, t_0) are 316, 0.021, and -2.6 for Bonneville Reservoir, 359, 0.021, and -2.6 for The Dalles Reservoir, and 396, 0.019, and -2.6 for John Day Reservoir.

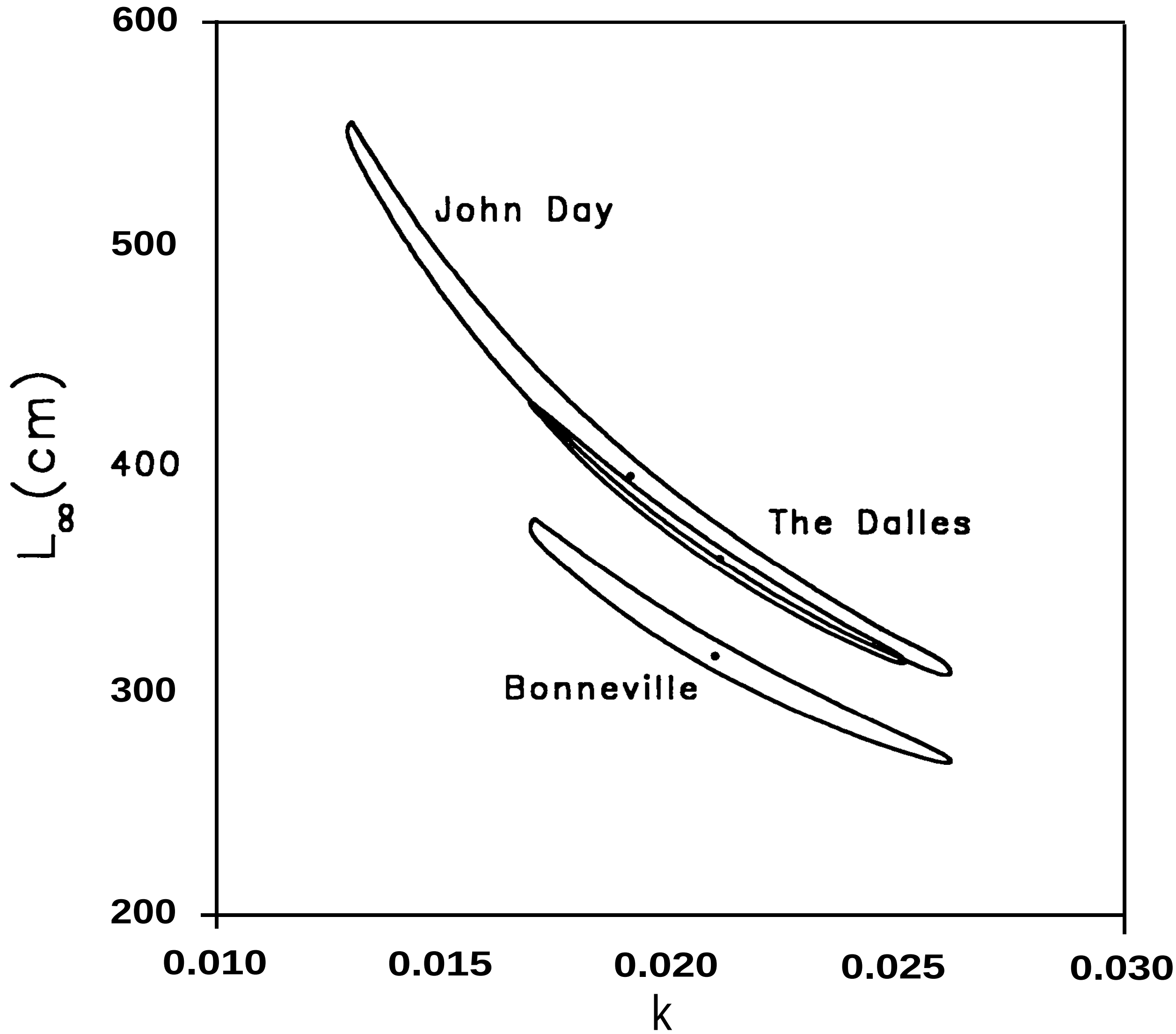

Figure 4. Joint 95% confidence regions for von Bertalanffy parameters L_∞ and k estimated with t_0 fixed at -2.6 for white sturgeon in three lower Columbia River reservoirs. Parameter pairs are considered. significantly different if point estimates are not within the confidence region for another reservoir.

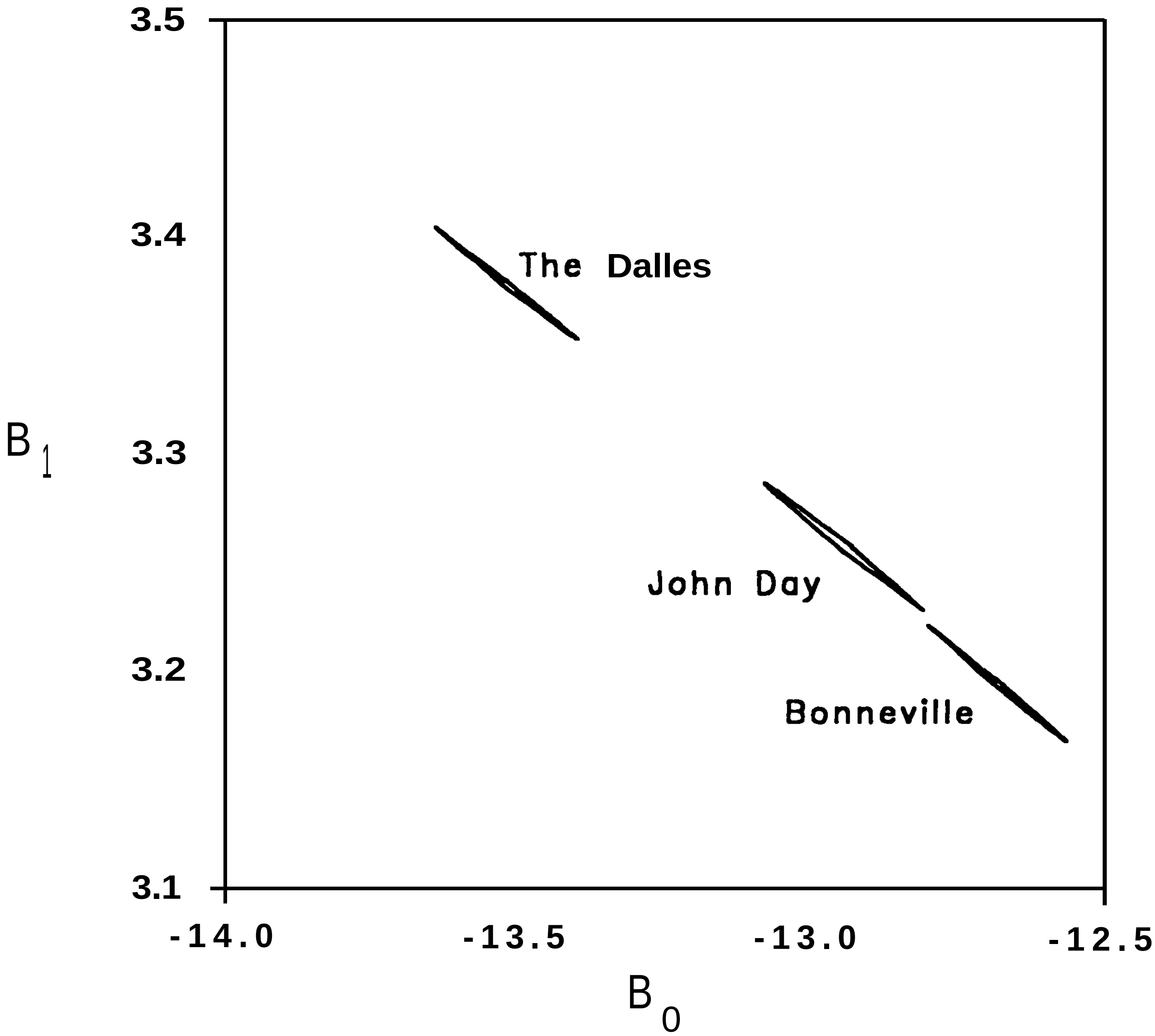

Figure 5. Joint 95% confidence regions for estimates of length-weight equation parameters for white sturgeon in three lower Columbia River reservoirs. Parameter pairs are considered significantly different if point estimates are not within the confidence region for another reservoir.

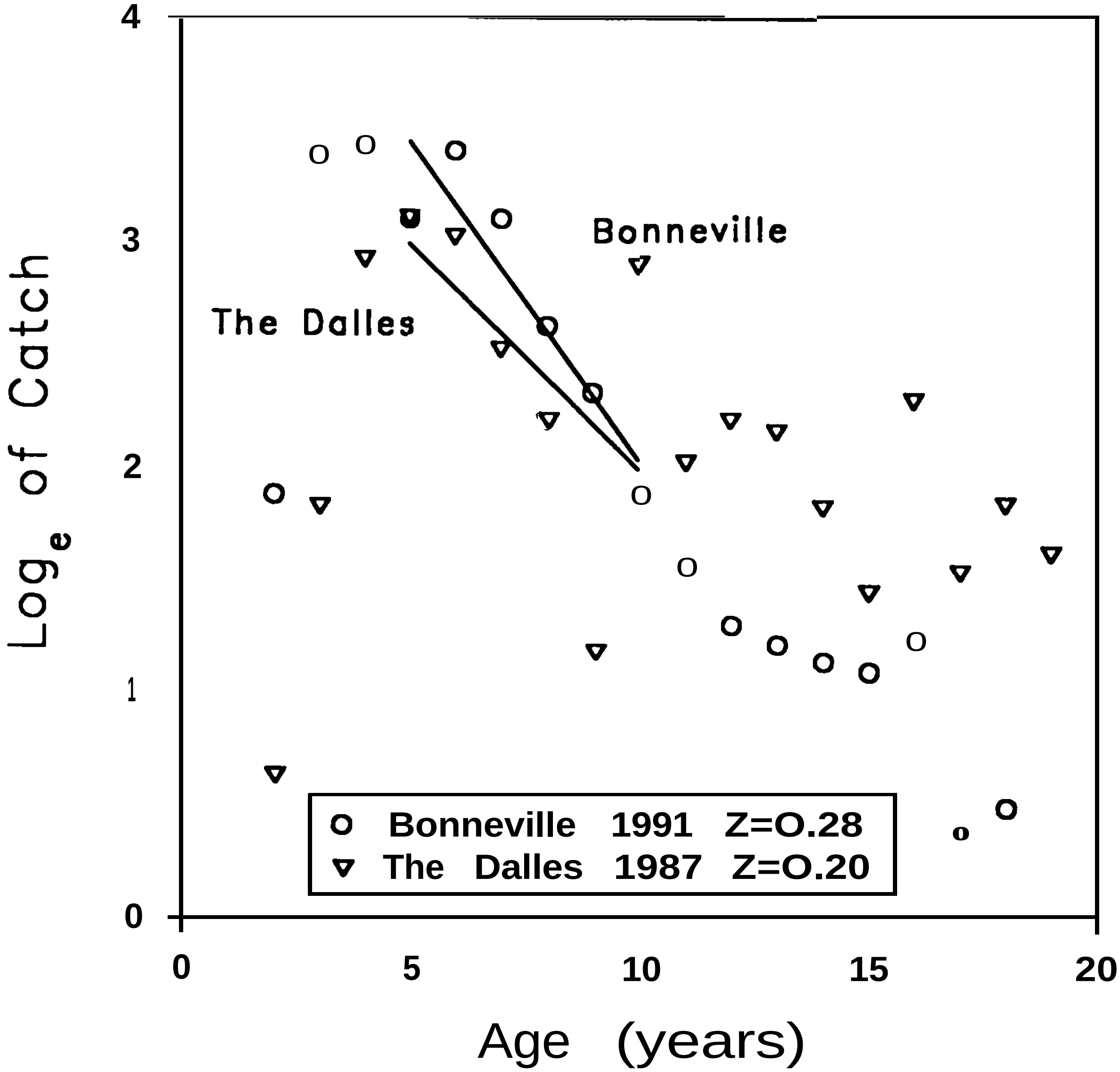

Figure 6. Catch curves for white sturgeon captured in gill nets in Bonneville and The Dalles reservoirs. Instantaneous rates of total mortality (Z) are indicated for each regression line.

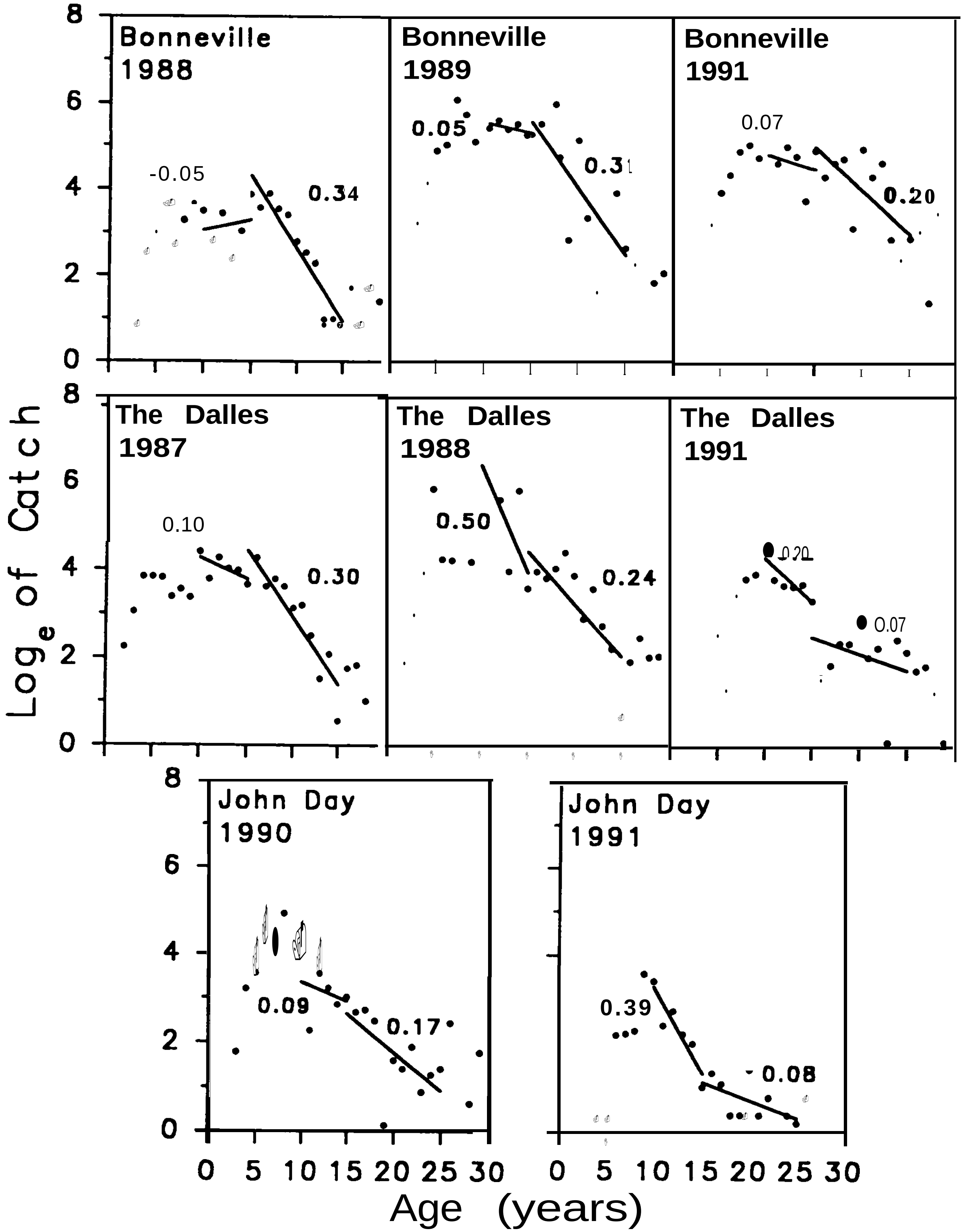

Figure 7. Catch curves for white sturgeon captured in setlines in three Columbia River reservoirs, 1987-91. Instantaneous rates of total mortality (Z) are indicated for each regression line.

Table 5. Numbers (with percent exploitation in parentheses) of white sturgeon caught by sport and commercial fisheries in three lower Co1 umbia River reservoirs, 1987-91.

Fishery	1987	1988	1989	1990	1991
			Bonneville Reservoir		
Sport	--	1,530 (3)	2,800 (5)	2,110 (--)	--
Commercial	--	2,030 (6)	1,410 (15)	1,890 (--)	1,160 (--)
			The Dalles Reservoir		
Sport	1,990 (11)	910 (5)	500 (--)	--	--
Commercial	3,800 (31)	1,010 (18)	1,930 (--)	1,210 (--)	340 (--)
			John Day Reservoir		
Sport	--		280 (--)	320 (5)	140 (8)
Commercial	--	1,1& (--)	170 (--)	410 (--)	40 (--)

Table 6. Cohort analyses for estimating total annual mortality rate of white sturgeon in three lower Columbia River reservoirs.

Reservoir	Year	Ages	Setline Days	Sturgeon/day	Z[a]
			Total Catch Cohort		
Bonneville	1988	10-24	170	2.0588	
	1989	11-25	775	2.8026	
	1991	13-28	168	3.3810	-0.155
The Dalles	1987	10-24	233	2.6137	
	1988	11-25	675	1.5733	
	1991	14-29	138	0.6957	0.317
John Day	1990	10-24	327	0.3945	
	1991	11-25	96	0.6250	-0.460
			Tagged Fish Cohorts		
Bonneville[b]	1989	>9	775	0.0477	
	1991	>10	168	0.0476	0.001
The Dalles[c]	1988	>8	675	0.0904	
	1989	>9	70	0.0571	0.459

[a]Estimated $-\text{Log}_e$(catch rate in year b / catch rate in year a}^[l/(b-a)] for samples from 2 years and with a regression on Ln[catch rate] for samples from 3 years.
[b]Fish tagged in 1988.
[c]Fish tagged in 1987.

Potential Production

Maximum yield per recruit was approximately 25% greater in John Day and The Dalles reservoirs than in Bonneville Reservoir (Figure 8A). Yield per recruit was greatest at annual exploitation rates between 5 and 15%. Estimates of sustainable annual yield (kg) based on number of age 1 recruits observed in each reservoir were 10,700 (1.27/ha) in Bonneville Reservoir, 4,000 (0.88/ha) in The Dalles Reservoir, and 1,800 (0.09/ha) in John Day Reservoir.

Differences in reproductive potential among reservoirs were also substantial (Figure 8B). Reproductive potential per recruit declined exponentially with increasing exploitation and approached zero at rates exceeding 20%.

Discussion

Characteristics of white sturgeon populations varied significantly among reservoirs. In Bonneville Reservoir greater numbers of recruits resulted in greater densities but were accompanied by a smaller average size, growth rate, condition factor, and size of female maturity. Recruitment was less in The Dalles Reservoir but average size, growth rate, condition factor, and size of female maturity were greater than in Bonneville Reservoir. Population statistics in John Day Reservoir were similar to those in The Dalles Reservoir, but recruitment and density were much lower than in the other two reservoirs and the size composition was skewed to larger, older fish.

No differences were detected among reservoirs in fecundity, longevity, or natural mortality rate, in part because of sampling difficulties. Our sample size for fecundity was very small. Fecundity could only be estimated from dead fish. Most mature females were larger than those legally harvested in fisheries, catchability of these large fish in our setline sampling was poor, and the rarity and value of these mature fish precluded sacrifice. Many of these large, old fish were also difficult to age (Rien and Beamesderfer 1992). Natural mortality rate was very low and small differences were impossible to detect from the difference between uncertain estimates of total and fishing mortality rate. Rates estimated with Pauly's regressions are consistent with observed maximum ages. For instance, an instantaneous annual mortality rate of 0.05 after age 10 would result in only 1% survival to age 100. At greater mortality rates, chances of observing 100 year-old fish approach zero.

Our attempts to characterize white sturgeon populations were also confounded by differences in exploitation rate among reservoirs and years. Differences among reservoirs affected standing stock and size composition, and precluded direct comparisons to evaluate habitat differences. For instance, commercial fisheries were most intense in John Day Reservoir during the 1980's (S. King, Oregon Department of Fish and Wildlife, personal communication) and could help account for the current low abundance of white sturgeon in that reservoir. Harvest rate of white sturgeon by anglers in John Day Reservoir declined from 0.11

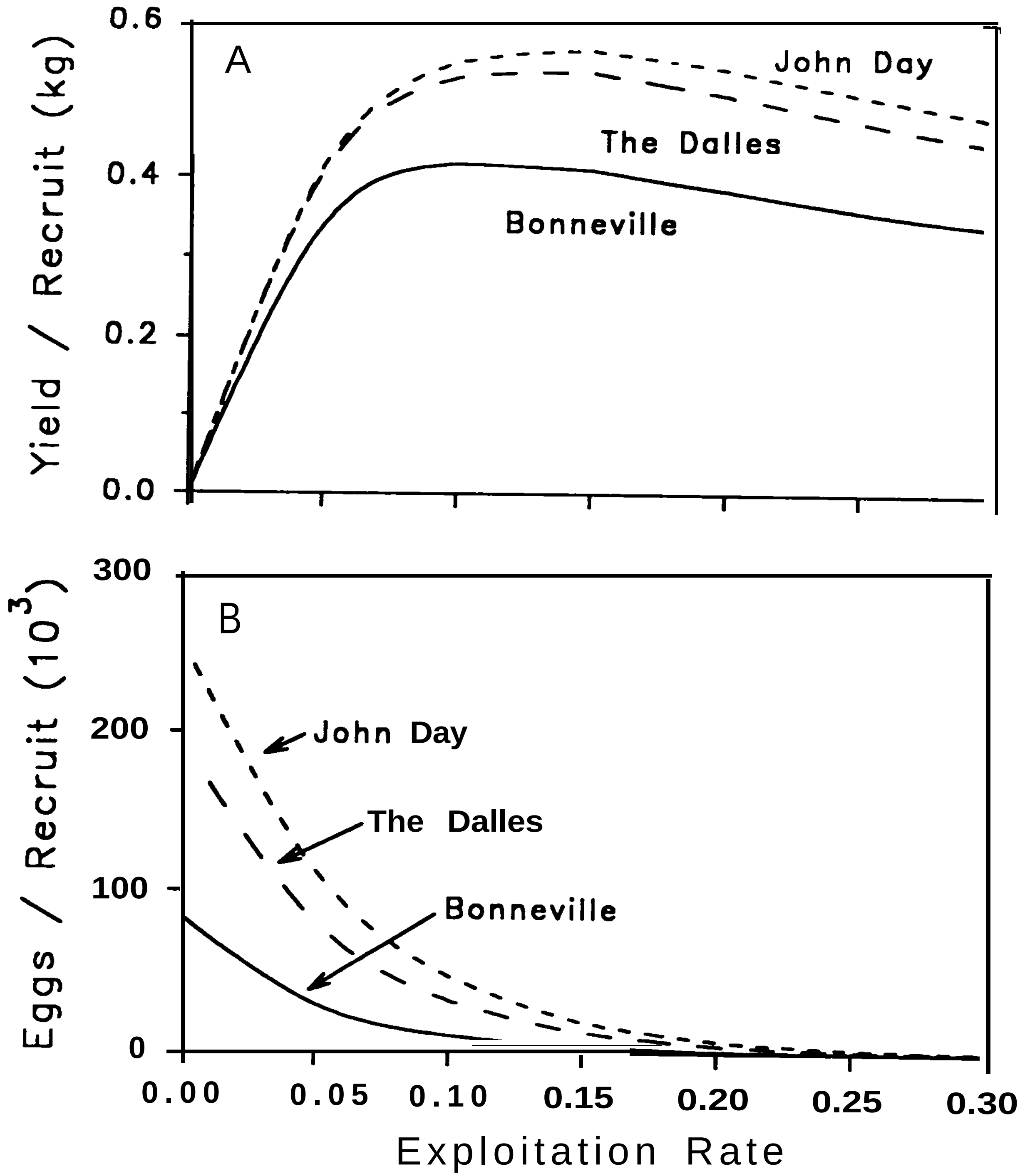

Figure 8. Simulated yield (A) and reproduction (B) per recruit in relation to exploitation rates under a 82-166-cm size window for white sturgeon populations from three lower Columbia River reservoirs.

fish per trip in 1983-86 (Beamesderfer et al. 1990) to 0.04 fish per trip in 1989-91 (Hale and James 1992). A trend in increasing harvest from 1979 to 1987 by commercial fisheries in all three reservoirs (ODFW and WDF 1991) would violate stable age structure assumptions of catch curve estimates of total mortality rate (Ricker 1975) and would explain total mortality rate estimates which were less than zero or observed exploitation rates.

The net effect of differences that we could distinguish in population characteristics among reservoirs was substantial variation in potential yield among the three reservoirs. Differences as great as 25% were seen in yield per recruit. Differences in net yield were much larger as a result of observed differences in recruitment among the reservoirs. Differences were further magnified when yield was calculated relative to reservoir area. With current recruitment levels, Bonneville Reservoir can sustain the largest net yield and John Day the least despite the opposite pattern in yield per recruit.

Productivity of white sturgeon populations in reservoirs was much less than in the unimpounded area between Bonneville Dam and the estuary. We estimated no reservoir supported more than 6.2 white sturgeon/hectare or could sustain yield greater than 1.3 kg/hectare. The unimpounded river supported 14.6 white sturgeon/hectare and could sustain yields of 16.3 kg/hectare at current levels of recruitment (Devore et al. 1992). Parsley and Beckman (1992) suggest that large amounts of habitat suitable for white sturgeon occur in all areas.

The pattern of differences among populations implies environmental rather than genetic causes. Genetic differences are unlikely because many individuals predate dam construction and existing movement among reservoirs may be adequate to prevent genetic divergence (North et al. 1992b). Relatively poorer condition, lower growth rate, and an earlier size of female maturity in Bonneville Reservoir may represent a compensatory response to intraspecific competition. Strong recruitment of young fish in Bonneville resulted in densities greater than in The Dalles or John Day Reservoirs although less than the unimpounded river.

Production of white sturgeon populations above Bonneville Dam would likely be greater if dams did not constrain white sturgeon movements. Unused habitat in The Dalles and John Day reservoirs could be fully seeded with white sturgeon spawned in favorable habitat concentrated in Bonneville Reservoir and downstream from Bonneville Dam. White sturgeon spawned in Bonneville Reservoir could have dispersed into rearing habitat upstream or downstream where increased growth and a larger size of female maturity would increase the potential yield and reproductive potential per recruit.

These results suggest several possibilities for improving production of impounded populations of white sturgeon. Improved fish passage at dams is one alternative. Fish ladders might be redesigned to provide upstream access to white sturgeon. White sturgeon occasionally pass ladders and some ladders are used more frequently than others (Warren and Beckman 1992). Fish lifts were examined with some promise at Bonneville Dam from 1938-56 (Warren and Beckman 1992). However, fish passage may not be as effective for the iteroparous sturgeon as it is for semelparous salmonids which die after spawning and do not require a return avenue downstream. Physically collecting and transporting juveniles to underseeded reservoirs could provide harvest benefits similar to improved passage without the confounding problem of downstream passage after spawning.

Supplementation of underseeded reservoirs with hatchery-reared fish could be another alternative for enhancement. Hatchery technology has recently been adapted for white sturgeon using wild broodstock (Conte et al. 1988). However, release of large numbers of offspring from a few parents could pose substantial genetic risk to wild fish. Technology has not yet been applied in a production-level conservation hatchery and many problems (disease, feeding, size and time of release) need investigation. Finally, carrying capacity limitations and resulting stunting is far more likely for the long-lived, iteroparous and resident sturgeon than for anadromous and semelparous salmon. Similar problems with salmon have led to a reevaluation of salmon hatcheries and a call for rigorous scrutiny of potential new programs (Hilborn 1992). Transplants of fish would allow investigation of the potential for supplementation without incurring the expense and genetic and disease risks of a hatchery.

More intensive regulation of fisheries is another alternative for mitigating effects of dams on white sturgeon productivity. Observed rates of exploitation generally exceeded optimum rates predicted by simulations and in several cases exceeded rates where any fish would survive to reproduce and sustain the population. This intensive harvest appears to have collapsed fisheries in The Dalles and John Day reservoirs and risks collapse of populations if continued. Substantial populations of large, mature fish remain in each reservoir and could, if protected, replenish depleted populations within 10-15 years if managed on a sustainable basis.

Optimum rates of exploitation also vary among populations dependent on the characteristics of each. For instance, maximum yield per recruit would occur at lesser rates of exploitation in Bonneville Reservoir than in the other two reservoirs (unless population characteristics compensated for differences in exploitation) Management strategies which recognize these differences with regulations unique to each population would maximize yield. Different size restrictions may also be appropriate for each population and could be identified with a more detailed series of population simulations.

We conclude impounded populations of white sturgeon in the lower Columbia River can sustain exploitation, but yield is less than would be expected if populations were not segregated by a series of dams. Several alternatives for mitigating dam effects to enhance production of impounded stocks were identified, but an effective program will require further investigation of habitat constraints and potential compensation in population parameters.

Acknowledgments

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Habitat Requirements and Availability

REPORT I

Habitat Use by Spawning and Rearing White Sturgeon in the Columbia River Downstream from McNary Dam

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Abstract

Habitats used by spawning and rearing white sturgeon *Acipenser transmontanus* were determined by measuring water temperature, depth, mean water column and near-substrate velocities, and substrate type at sites where eggs, larvae, young-of-the-year, and juveniles (ages 1-7) were collected. Spawning and egg incubation occurred in the swiftest water available (0.8 to >2.8 m/s, mean column velocity), which was downstream from the four mainstem Columbia River dams in our study area. Substrates where spawning occurred were predominately cobble, boulder, and bedrock. Yolk-sac larvae were transported by the river currents from spawning areas into deeper, slower-velocity areas with finer substrates. Young-of-the-year white sturgeon were found at depths of 9-57 m, at mean column velocities $\geq$0.6 m/s, and over substrates of hard clay, mud and silt, sand, gravel, and cobble. Juvenile fish were found at depths of 2-58 m, at mean column velocities $\geq$1.2 m/s, and over substrates of hard clay, mud and silt, sand, gravel, cobble, boulder, and bedrock.

Introduction

White sturgeon *Acipenser transmontanus* are an important recreational and commercial resource of the Pacific Northwest. This ancient fish from the Lower Jurassic is the largest freshwater fish in North America; it is restricted to Pacific coastal waters and river systems from central California to southern Alaska. White sturgeon have been reported to attain lengths of over 6 m and weights in excess of 580 kg, and they may live 100 years or more (Scott and Crossman 1973).

Since the late 1930's, extensive hydroelectric development has occurred in the mainstem Columbia River and its tributaries. This development isolated the once diadromous white sturgeon in impoundments created by dams, and it altered the natural hydrograph of the river by reducing peak discharges in spring and increasing discharges in winter. Hydroelectric dams and other developments have adversely affected sturgeons in other river systems (Khoroshko 1972; Votinov and Kas'yanov 1978; Deacon et al. 1979; Rochard et al. 1990).

Existing knowledge about the habitat used or preferred by white sturgeon is limited, and thus the effects of hydroelectric development and operations on them are largely unknown. Participants in a workshop to identify white sturgeon research priorities (Fickeisen et al. 1984) ranked the need for habitat information as the highest priority. Two bibliographies on white sturgeon (Fickeisen 1985; Lane 1985) listed over 200 publications and reports, none of which addressed the water temperatures, water depths, water velocities, or substrates used by white sturgeon. Most field investigations of white sturgeon have addressed issues such as relative abundance and distribution in various areas (Stevens and Miller 1970; Kohlhorst 1976; Gray and Dauble 1977; Coon 1978; Malm 1981; Cochnauer 1983), age and growth (Coon 1978; Kohlhorst et al. 1980; Hess 1984), or movements (Bajkov 1951; Miller 1972; Haynes et al. 1978; Haynes and Gray 1981). These investigators included incidental comments on the habitat used by adult and larval white sturgeon, but none presented specific data to support their statements.

White sturgeon spawning in the wild has rarely been documented. Kohlhorst (1976) collected naturally spawned white sturgeon eggs from the Sacramento River, and spawning downstream from each of the four dams on the lower 470 km of the Columbia River has been confirmed (Duke et al. 1990; McCabe and McConnel 1988). Naturally spawned eggs have also been collected from the Kootenai River in northern Idaho (K. Apperson, Idaho Department of Fish and Game, personal communication).

We present specific information on the habitat used by spawning and rearing white sturgeon in the Columbia River. This information can be used to evaluate the effects of hydroelectric development and operations on the availability of habitat for white sturgeon.

Study Area

The Columbia River downstream from McNary Dam [river km (rkm) 0-470] is divided into three impoundments and an unimpounded river reach (Figure

1). The unimpounded reach (rkm 0-234), henceforth referred to as the lower river, has a surface area of 61,300 hectares and is considered estuarine to rkm 74. The lower river has an extensive, nonvegetated littoral zone; 55% of the total area is less than 4 m deep and has a predominantly sand substrate. The impoundments vary in size, depth, and substrate composition. Their littoral zones are generally vegetated with submergent plants. Bonneville Pool (rkm 234-309) has a surface area of 7,600 hectares; 20% of the total area is less than 4 m deep and has a predominantly sand substrate. The Dalles Pool (rkm 309-348) has a surface area of 3,600 hectares; 9% of the total area is less than 4 m deep and has a bedrock, cobble, and sand substrate. John Day Pool (rkm 348-470) has a surface area of 19,800 hectares; 25% of the total area is less than 5 m deep and has extensive areas of mud, sand, gravel, and cobble substrate. Water velocities are highest in the tailrace of each dam. Additional information on the study area can be found in Ebel et al. (1989).

Flows in the Columbia River are dependent on snowmelt and rainfall in headwater areas and are regulated by an extensive network of storage, diversion, and run-of-the-river dams throughout the watershed. Flows at Bonneville Dam during our study (1987-1991) varied seasonally and annually (Figure 2); the May-July average flow was lowest in 1988 (4,520 m^3/s) and highest in 1991 (7,240 m^3/s).

Methods

We determined physical habitat used by white sturgeon by measuring water depth, mean water column and near-substrate water velocities, substrate, and water temperature at locations where newly spawned eggs, yolk-sac larvae, young-of-the-year (YOY), and juveniles (ages 1-7) were collected with various fishing gears during 5 years of study. An observation of habitat use consisted of an effort with a passively or actively fished gear that resulted in the collection of any life stage of white sturgeon, regardless of the number captured (Bovee 1986). Observations were pooled among years, and those observations from the impounded areas were pooled. Results of habitat use from the impounded areas and the free-flowing lower river are presented separately.

Observations were obtained from the lower river and The Dalles Pool from 1987 through 1991, Bonneville Pool from 1988 through 1991, and John Day Pool from 1989 through 1991. We sampled for eggs and larvae from April through July. We sampled for older fish primarily from April through September, with some effort made during all months of the year. Most sampling was done during daylight hours. Some habitat descriptors were not measured at every sampling site.

Water depth was measured to the nearest 0.3 m with a recording fathometer. When depth varied during a sampling effort, we recorded the maximum depth.

Water velocities were measured with cable-suspended Gurley current meters or Price "AA" current velocity sensors connected with Swoffer

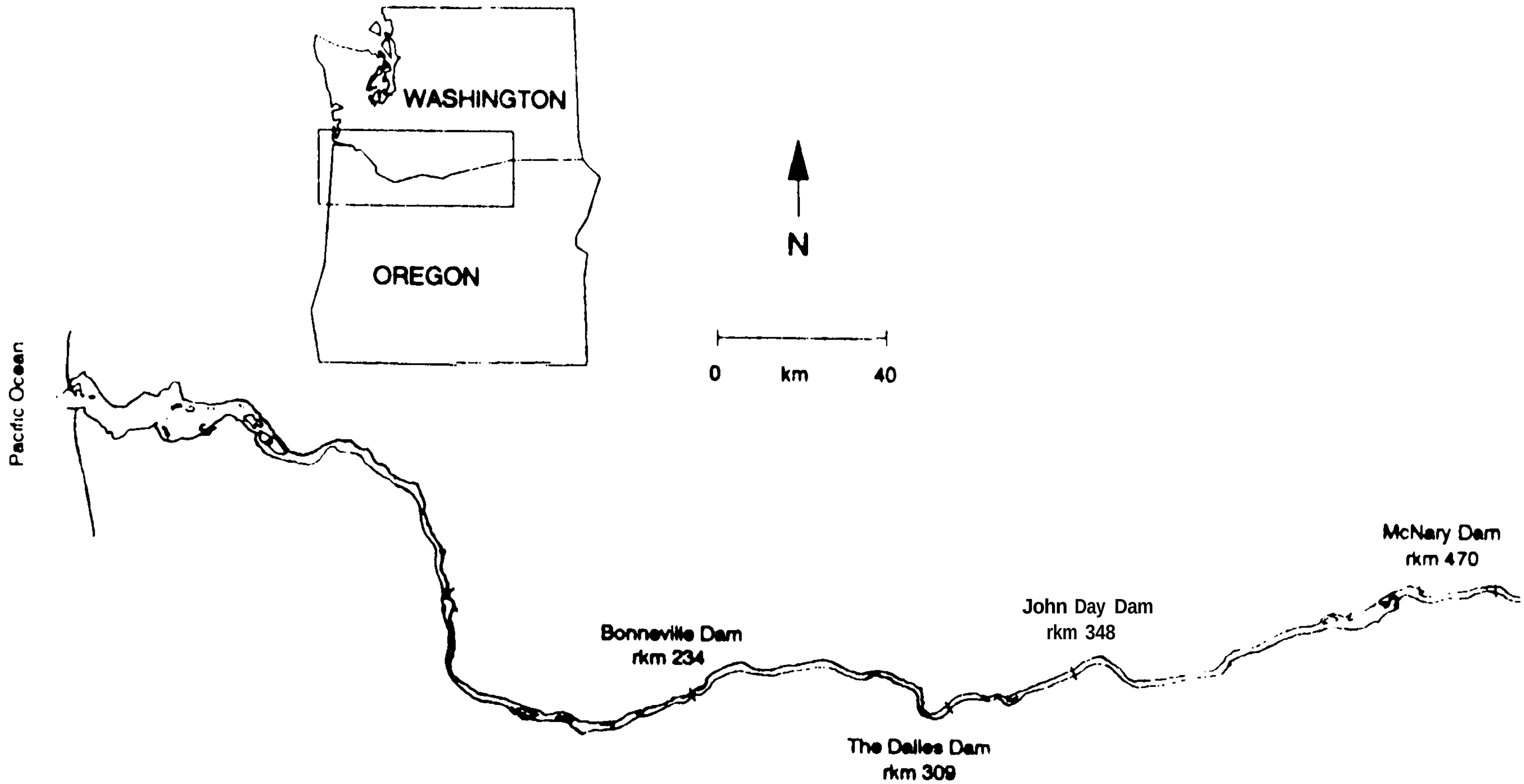

Figure 1. The study area on the Columbia River showing locations of the four mainstem dams.

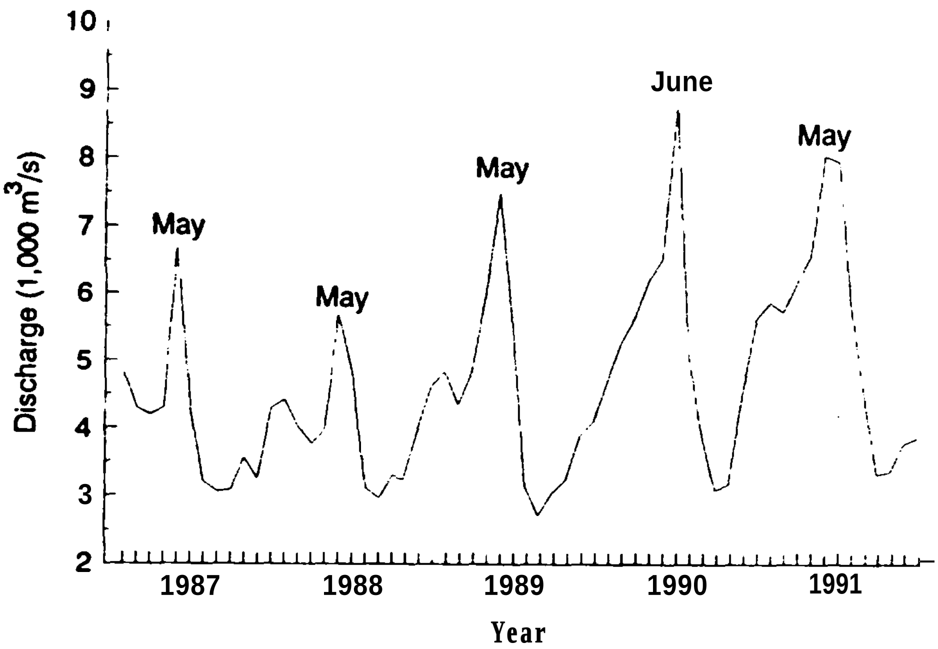

Figure 2. Mean monthly discharge (1,000 m^3/s) at Bonneville Dam, 1987-1991.

Instruments Model 2200 direct-reading current velocity meters[1]. Sounding weights used to deploy the sensors ranged from 13.6 to 45 kg. Measurements were taken at 0.2 and 0.8 of the water depth and within 1 m of the substrate. Mean water column velocity was calculated by averaging the velocities measured at 0.2 and 0.8 of the water depth (Buchanan and Somers 1969).

Substrate type was determined by visual observation, from samples with a 0.1-m Van Veen grab, from "incidental catch" of substrate in our fish sampling gears, from commercially available navigation charts and preimpoundment air photos, and data collected in other studies. Substrates were categorized by particle size (Table 1).

Water temperatures were measured with digital or laboratory thermometers or obtained from digital recording thermographs that were placed on the substrate in the dam tailraces.

Eggs and yolk-sac larvae were collected from the drift in plankton nets and 3-m-wide beam trawl nets fished on the substrate (McCabe and McConnell 1988; Palmer et al. 1988). Eggs were also collected on artificial substrates placed in spawning areas (McCabe and Beckman 1990). The plankton nets were constructed of 1.59-mm knotless nylon mesh attached to an inverted U-shaped frame (1.3-cm-diameter stainless steel rod) 0.76 m across the bottom and 0.54 m high. Two to six lead weights (4.5 or 9.1 kg each) attached to the net frame held the net on the substrate. Single or paired nets were fished from an anchored boat for 5-60 min. An effort with a single net or paired nets was considered one observation. The 3-m-wide by 0.5-m-high beam trawl was also constructed of 1.59-mm knotless nylon mesh and was attached to an aluminum alloy frame that had weighted skids. This gear was either fished passively on the substrate or was towed slowly upriver; tows were 5-30 min in duration.

All white sturgeon eggs collected were assigned a developmental stage based on the criteria established by Beer (1981). We used observations of newly spawned eggs (eggs that were changing pigmentation and had not undergone first cleavage) to define habitat use by spawning white sturgeon. We used observations of all eggs (including newly spawned eggs) to define habitat for incubating eggs.

Larval, YOY, and juvenile white sturgeon were captured with towed bottom trawls of various designs, including the 3-m beam trawl described above. The trawls most frequently used included a 7.9-m semiballoon shrimp trawl (McCabe and McConnell 1988) and a 6.2-m high-rise trawl (Palmer et al. 1988; Parsley et al. 1989). Tows were 5-15 min in duration in an upstream direction.

Sampling sites were chosen to encompass a broad range of habitats. Most sites were repetitively sampled (we usually allowed at least 24 h between efforts) during three or more sampling seasons regardless of whether white sturgeon were ever collected at the site.

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[1]The use of trade names does not imply endorsement by the U.S. Fish and Wildlife Service or the National Marine Fisheries Service.

TABLE 1. Size categories for substrate particles.

Category	Particle size (mm)
Organic debris[a]	
Hard clay	0.00024 - <0.004
Mud and silt	0.004 - <0.062
Sand	0.062 - <2
Gravel	2 - <64
Cobble	64 - <250
Boulder	250 - 4,000
Bedrock[a]	

[a]These categories were not classified by particle size.

Results

Soawninq and Egg Incubation

White sturgeon spawned from April through July, when water temperatures were 10-18°C (Figure 3), as determined by the collection of newly spawned eggs. White sturgeon spawned in the impoundments at water temperatures greater than 12°C, but spawning in the lower river was comnon at water temperatures of 10-12°C. Most spawning occurred at 14°C (Table 2). Estimated spawning dates from back-calculated ages of later-stage eggs (i.e., more developed) indicated that limited spawning also occurred during some years in all four areas at water temperatures between 18 and 20°c.

Newly spawned eggs were collected from the drift near the substrate at depths of 4-24 m (Figure 4), and spawning activity of adult fish was observed on a few occasions at one location where the depth was about 7 m. Eggs of all developmental stages (i.e., newly spawned and incubating eggs) were collected at depths of 4-27 m (Figure 4).

White sturgeon spawned in extremely fast-flowing water. Mean column velocities measured at sites where newly spawned eggs were collected ranged from 0.8 to 2.8 m/s, and velocities near the substrate ranged from 0.5 to 2.4 m/s (Figure 5). Incubating eggs were collected from sites with mean column and near-substrate velocities of 0.5 to 2.8 m/s and 0.2 to 2.4 m/s (Figure 5). Unfortunately, water velocities were not measured during the few occasions when spawning activity was observed directly. The mean column velocity measured at a location few days after we observed spawning and at a river discharge similar to when the spawning occurred was 2.1 m/s.

Newly spawned eggs and incubating eggs were collected primarily over cobble and boulder substrates, but were also collected over sand, gravel, and bedrock (Table 2; Figure 6).

Larvae

Yolk-sac larvae of white sturgeon were collected from sites where eggs were taken and from sites further downstream, where they apparently were dispersed by the river currents after hatching. Larvae were collected at depths of 4-58 m, at mean column and near-substrate velocities of 0.4-2.7 and 0-3-2.4 m/s, and over substrates of sand, gravel, cobble, boulder, and bedrock (Table 2; Figure 7).

Young-of-the-year

White sturgeon YOY were captured downstream from spawning areas from June through November. Because of the protracted spawning season and short incubation period, YOY were often captured while spawning was still in progress. As a result, the lengths of YOY captured during the study were variable, ranging from 20 to 321 mm total length.

The YOY were captured from deep, slow-velocity areas with substrates generally finer than those in the spawning areas. The YOY were collected

TABLE 2. Range and median values for habitat descriptors measured at sites where various life stages of white sturgeon were collected in the Columbia River, 1987-1991.

Life stage	Lower river		Impounded areas	
	Range	Median	Range	Median
Spawning				
Water temperature (°C)[a]	10-18	14	12-18	14
Depth (m)	4-23	6	4-24	11
Mean column velocity (m/s)	1.00-2.80	2.10	0.81-2.10	1.46
Velocity near the substrate (m/s)	0.60-2.40	1.40	0.52-1.62	1.04
Substrate		Boulder[b]		Cobble[b]
Incubating eggs				
Depth (m)	4-23	14	4-27	11
Mean column velocity (m/s)	0.80-2.80	2.00	0.50-2.10	1.39
Velocity near the substrate (m/s)	0.50-2.40	1.20	0.18-1.77	1.04
Substrate		Boulder[b]		Cobble[b]
Yolk-sac larvae				
Depth (m)	4-29	16	5-58	12
Mean column velocity (m/s)	0.70-2.70	1.60	0.41-2.10	1.10
Velocity near the substrate (m/s)	0.40-2.40	1.00	0.27-1.68	0.84
Substrate		Sand[b]		Cobble[b]
Young-of-the-year				
Depth (m)	9-38	19	9-57	30
Mean column velocity (m/s)	no data		0.18-0.63	0.38
Velocity near the substrate (m/s)	no data		0.12-0.55	0.31
Substrate		Sand[b]		Sand[b]
Juvenile				
Depth (m)	2-40	16	6-58	19
Mean column velocity (m/s)	0.40-1.10	0.65	0.09-1.20	0.61
Velocity near the substrate (m/s)	0.20-0.80	0.60	0.06-0.64	0.37
Substrate		Sand[b]		Sand[b]

[a] Water temperature on days that newly spawned eggs were collected.
[b] Mode

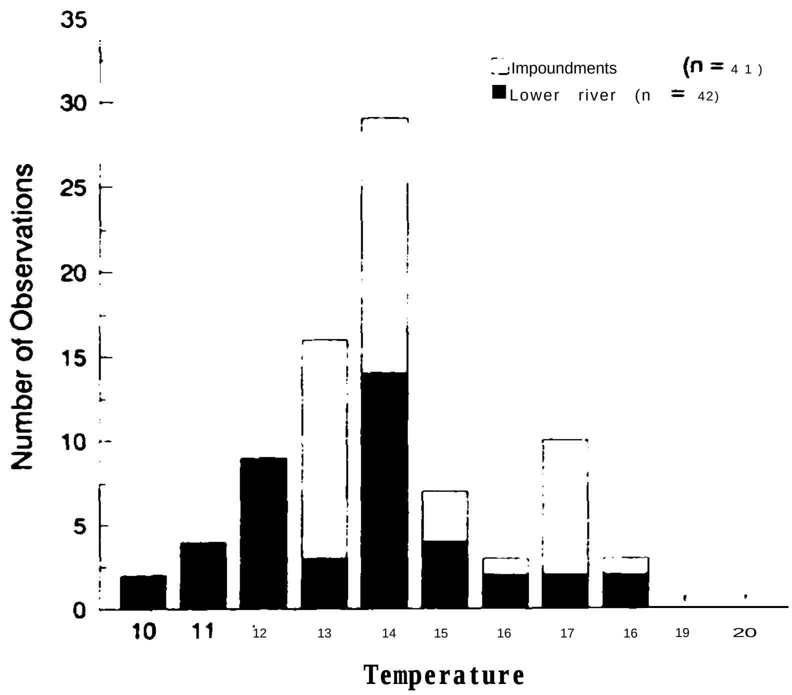

Figure 3. Water temperatures (°C) on days during which newly spawned white sturgeon eggs were collected in the Columbia River, 1987-1991.

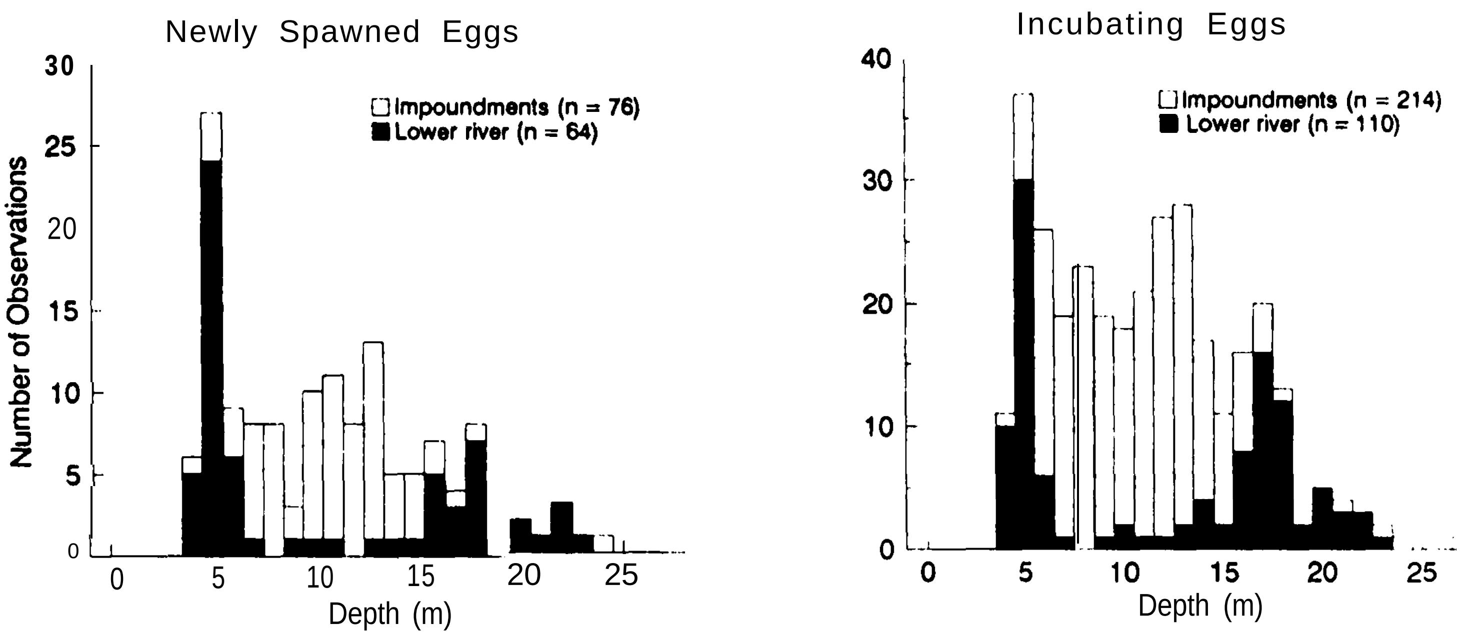

Figure 4. Water depths at which newly spawned and incubating white sturgeon eggs were collected in the Columbia River, 1987-1991.

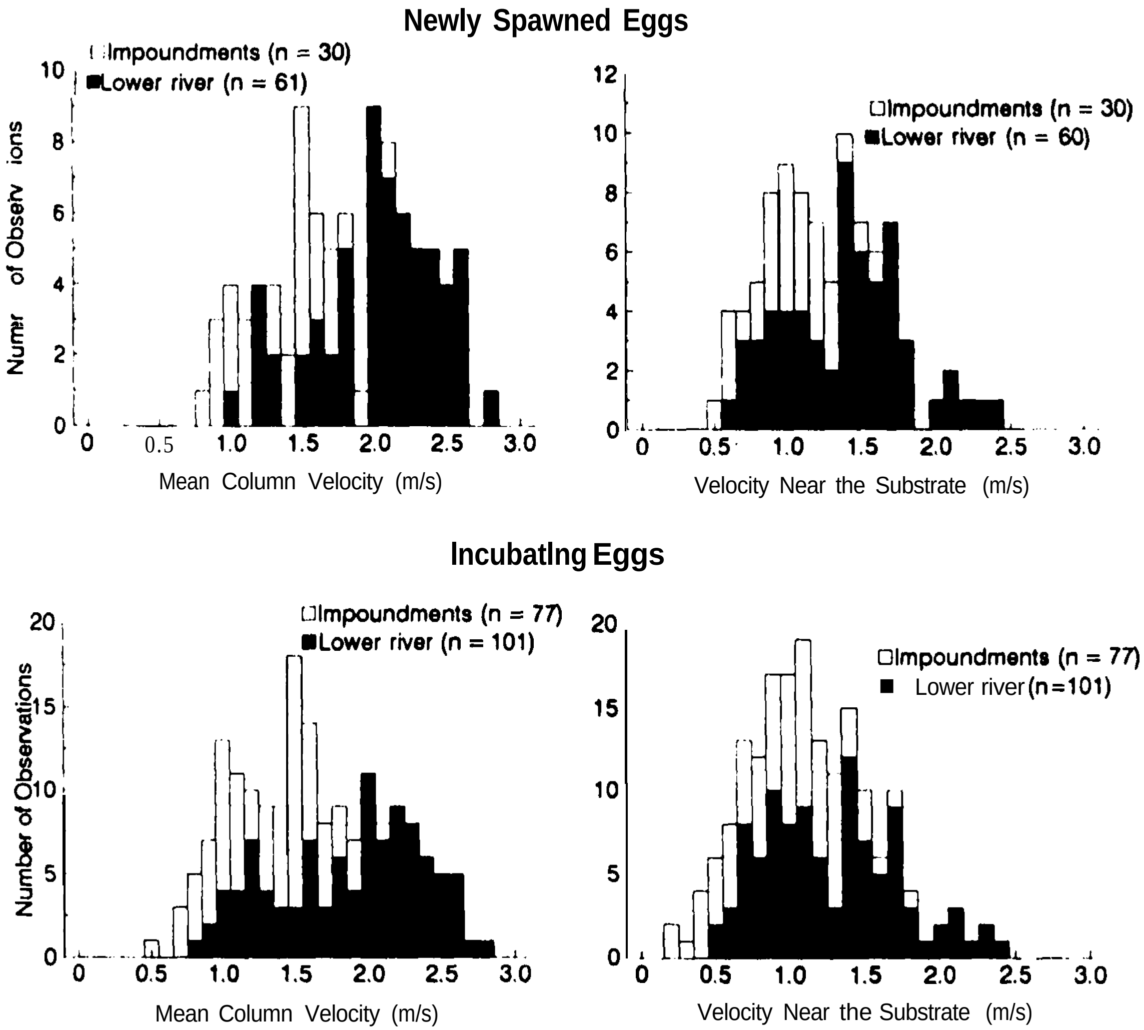

Figure 5. Water velocities at sites where newly spawned and incubating white sturgeon eggs were collected in the Columbia River, 1987-1991.

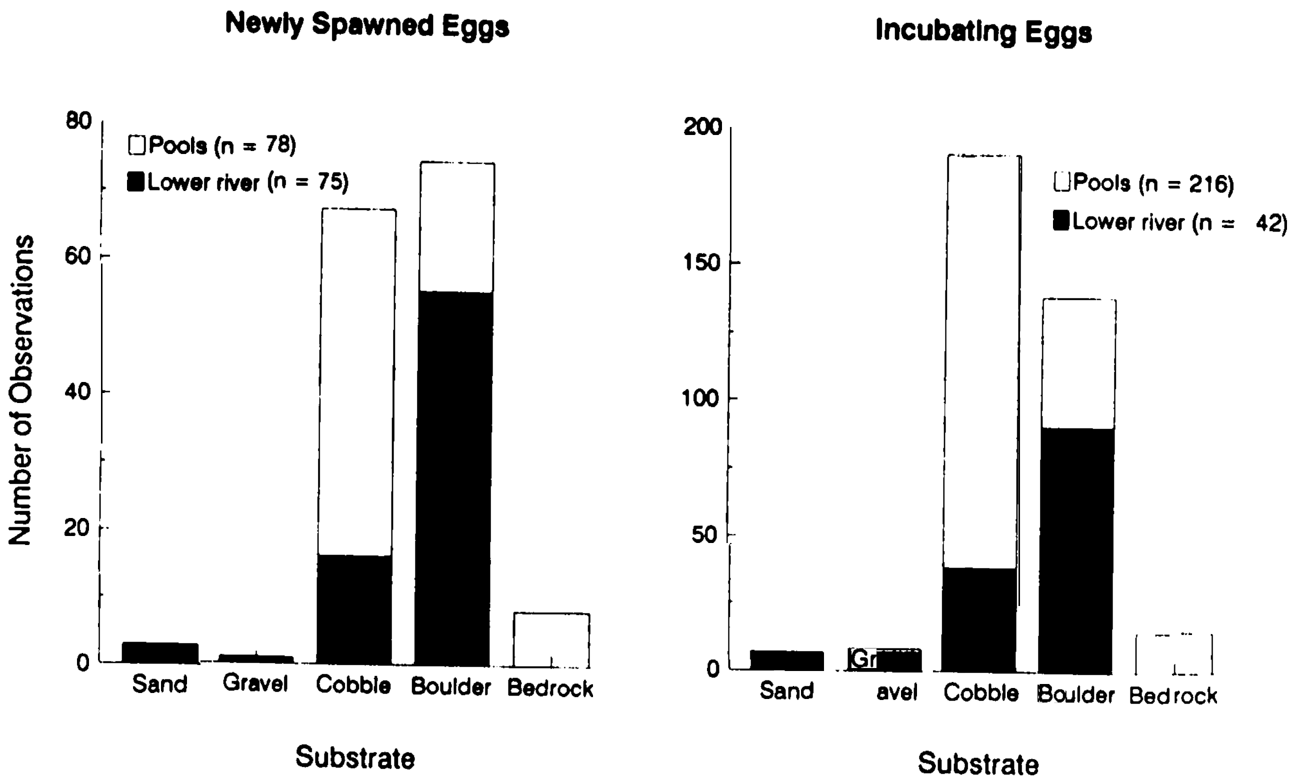

Figure 6. Substrates over which newly spawned and incubating white sturgeon eggs were collected in the Columbia River, 1987-1991.

Larvae

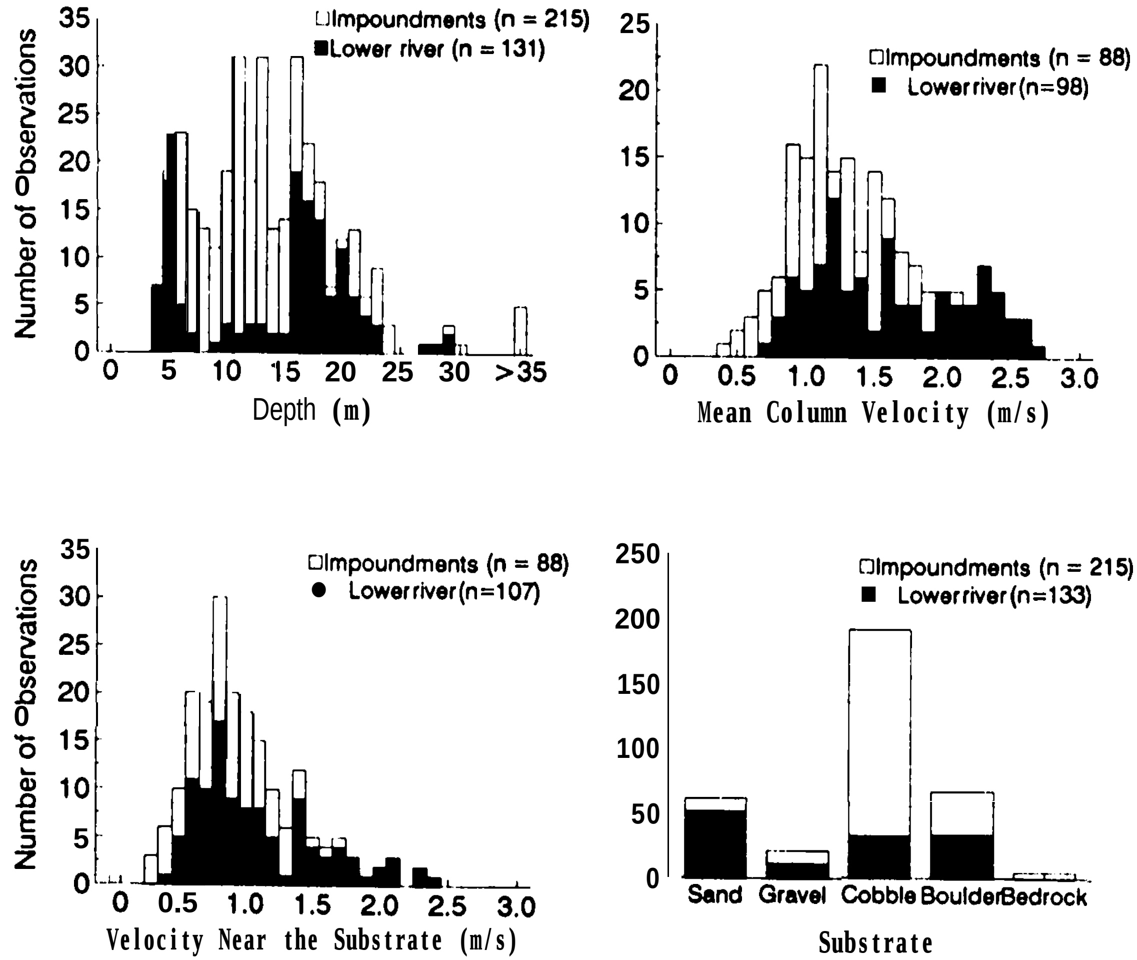

Figure 7. Water depths, mean water column and near-substrate velocities and substrates at sites where white sturgeon larvae were collected in the Columbia River, 1987-1991.

at depths of 9-57 m, at mean column and near-substrate velocities of 0.2-0.6 and 0.1-0.6 m/s, and over substrates of mud and silt, sand, gravel, cobble, and hard clay (Table 2; Figure 8). The YOY were captured primarily in areas with sand substrates, particularly in the lower river.

Juveniles

Juvenile white sturgeon were captured at depths of 2-58 m, at mean column and near-substrate velocities of 0-1-1.2 and 0.1-0.8 m/s, and over substrates of mud and silt, sand, gravel, cobble, boulder, and hard clay (Table 2; Figure 9). In the lower river, nearly all (99.7%) of the observations of juveniles were over sand, which was the predominant substrate in this reach. Juveniles ranged from 150 to 1,030 mm fork length.

Discussion

Spawning adults and rearing white sturgeon used a variety of water depths, velocities, and substrates, as evidenced by the ranges presented. White sturgeon spawning coincided with the peak of the hydrograph, which may have aided downriver dispersal of newly hatched larvae to habitat favorable for growth. The median water temperature at which spawning occurred in our study area (14°C) is equivalent to the temperature identified as optimal for white sturgeon egg development (Wang et al. 1985). Limited spawning occurred at water temperatures between 18 and 20°C, but Wang et al. (1985) reported that elevated mortality occurred in developing white sturgeon embryos incubated at water temperatures of 18°C, and complete mortality occurred when embryos were incubated at 20°C.

Spawning and egg incubation were observed at a range of water depths and velocities. White sturgeon are believed to be broadcast spawners; therefore, water depth per se may not be important in the selection of a spawning site. All newly spawned eggs were collected in areas of high water velocities, which would displace eggs downriver from the actual location (depth) where spawning occurred. We do not know where in the water column white sturgeon eggs and sperm are expelled. However, on a few occasions we observed adult fish breaching and rolling at the surface in turbulent water, and we collected newly spawned eggs within 1 m of the water surface immediately downstream from the site.

Spawning may have occurred in nearby areas of higher water velocity than where newly spawned eggs were collected. However, safety concerns, difficulty in retrieving our nets, and the potential for loss of gear precluded sampling those areas. Generally, we did not attempt to collect eggs from areas where mean column velocities were faster than 2.1 m/s in the impoundments and 2.7 m/s in the lower river. Hydraulic simulations of water velocities in the tailraces within 8 km of the dams (U.S. Fish and Wildlife Service, unpublished data) showed that areas with mean column velocities faster than 2.0 m/s exist at commonly occurring discharges, though the area of high velocity in each tailrace differed at each discharge because of the channel morphology.

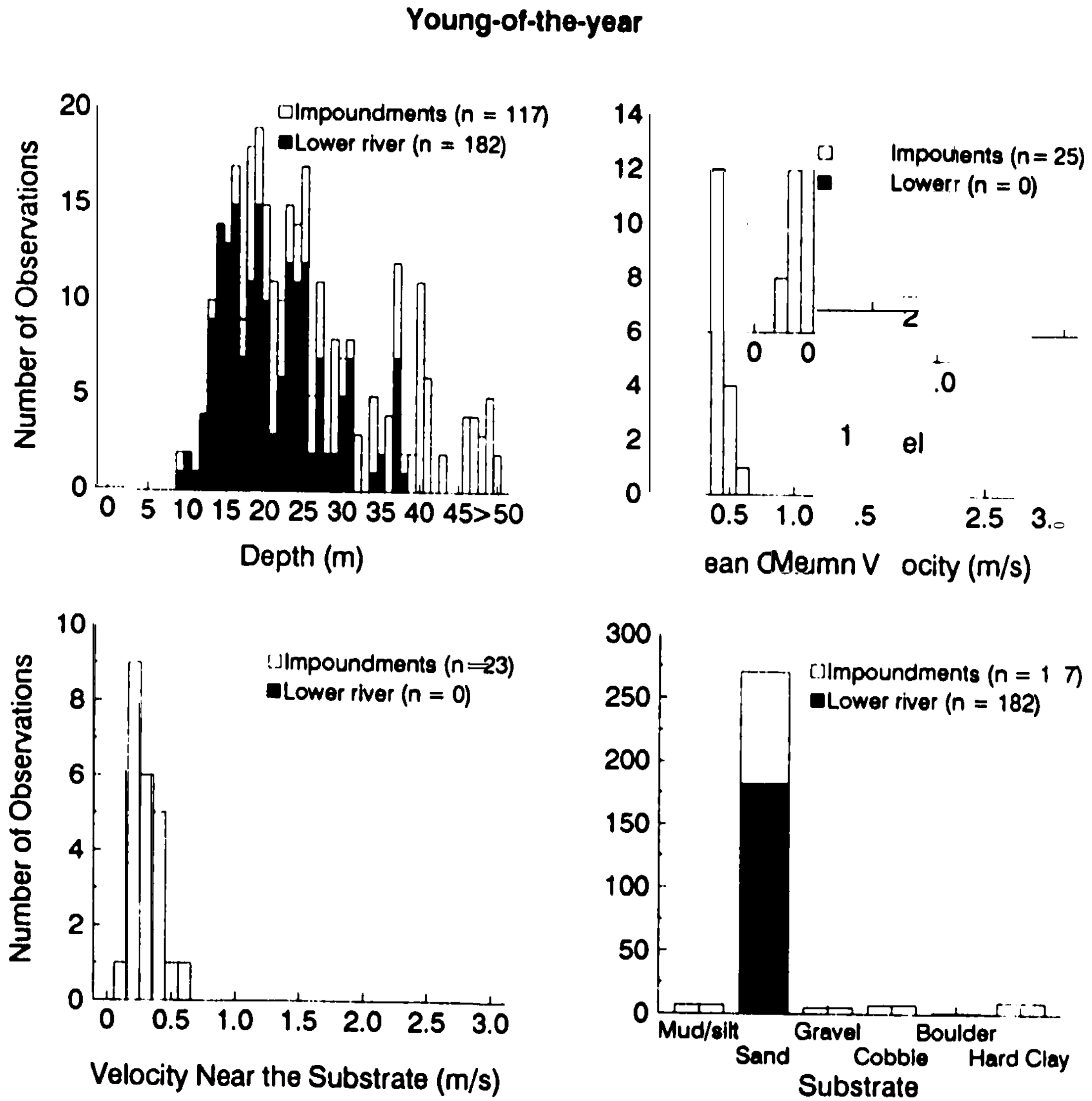

Figure 8. Water depths, mean water column and near-substrate velocities, and substrates at sites where young-of-the-year white sturgeon were captured in the Columbia River, 1987-1991.

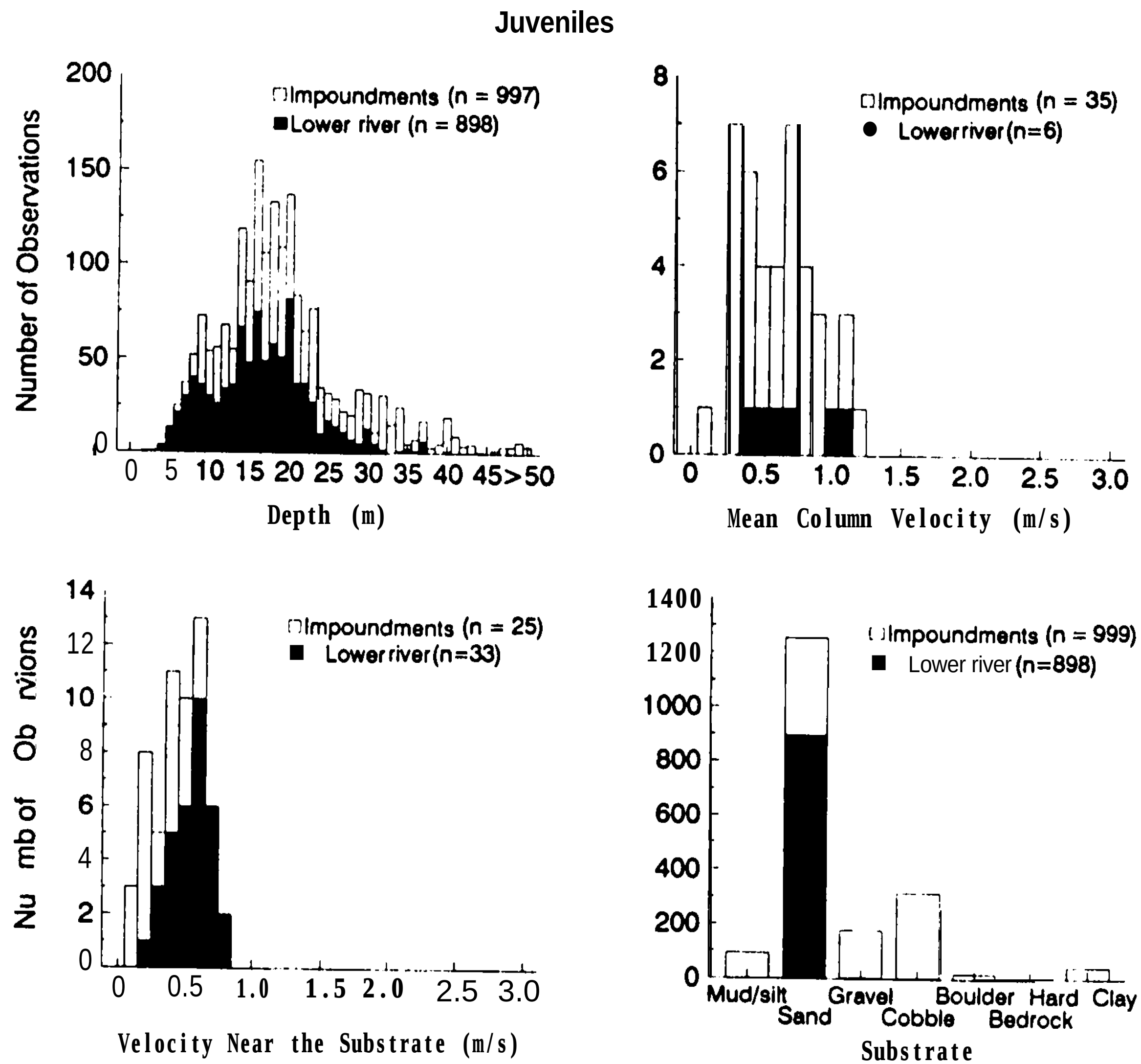

Figure 9. Water depths, mean water column and near-substrate velocities and substrates at sites where juvenile white sturgeon were captured in the Columbia River, 1987-1991.

Water velocities at sites used for spawning may have been higher than the lowest velocities we measured where newly spawned eggs were collected. Six of the nine observations with mean column velocities of less than 1.2 m/s were from one location (rkm 307), on the outer edge of an eddy formed by a slight bend in the northern shoreline downstream from The Dalles Dam. The velocity of adjacent water was much higher. Also, eggs were collected from the drift; thus, spawning occurred at or upstream from our sampling sites, where water velocities often were higher.

We do not know if an upper threshold exists for water velocities used by spawning white sturgeon. Velocities in excess of 3.7 m/s were measured adjacent to and upstream from several sites where eggs were collected. Spawning adults may exceed 2 m in length, and they probably can negotiate water velocities that are within two to three times their body length (4-6 m/s). Swiming performance studies have shown that Acipenser sp. of the Volga River can sustain swimming at velocities that were 1.2-4.5 body lengths per second (Malinin et al. 1971). Eggs spawned in these velocities could be dispersed widely downstream.

Most newly spawned and incubating eggs were collected over substrates of cobble or boulder. Those that were collected over sand were probably spawned upstream over a larger substrate and transported downstream by the river currents. Gravel substrates were not prevalent within our study area, but gravel did occur in combination with cobble and boulders in many places. Each of these substrates would provide a solid base for adhesive eggs to attach, although some are dislodged and transported downstream. We do not know if substrate imbeddedness, angularity, or interstitial spaces between particles are important. Substrate irregularities would provide protection for the eggs from scouring but may also provide refuge for egg predators.

The substrates used by spawning white sturgeon are probably a function of the water velocities present in the spawning areas. Finer substrates are displaced from areas of high water velocities. Sturgeon spawning has been reported to occur over gravel or rock (Dees 1961; Nikolskii 1961; Magnin 1966; Buckley and Kynard 1985; Crance 1986)) and Kohlhorst (1976) reported that white sturgeon in the Sacramento River may spawn over a mud, sand, or gravel bottom. However, this conclusion was based mostly on catches of larvae, not newly spawned eggs, thus limiting the ability to pinpoint spawning sites.

Larval white sturgeon are dependent on currents to transport them from incubation areas into rearing areas. Therefore, those that we captured from the drift were probably in transport between areas. Brannon et al. (1984, 1985) investigated the behavior of yolk-sac white sturgeon raised in aquaria. They identified a "swim up" phase that may be a mechanism for downstream dispersal from spawning areas. Upon hatching, larvae swam towards the surface and remained in the water column for a period that was inversely related to water velocity. The larvae then sought cover in or on the substrate and entered a "hiding" phase that lasted until the yolk was absorbed (about 12 d posthatch), at which time they began feeding on the substrate and within the water column. If food was not present, the fish reentered the water column and were again transported downstream. Feeding fish showed a slight preference for sand substrates but also used detritus and gravel substrates if food was present. The deep, slow-moving water in which we observed larvae would provide cover from light for the photophobic larvae, and food may be more available for the newly feeding fish.

The habitats in which we captured YOY and juvenile white sturgeon indicate a tolerance (but not necessarily a preference) for a wide range of environmental conditions. Most of the observations of YOY and juveniles were from the unimpounded lower Columbia River and Bonneville Pool, where sand was the predominant substrate. Other substrates were available in John Day and The Dalles pools, but poor recruitment to the YOY stage in these pools during our study limited the potential for observations of YOY and juveniles over other substrates.

Young-of-the-year and juvenile white sturgeon were most often captured within the thalweg. Efforts adjacent to the thalweg in shallower water rarely collected white sturgeon. Other investigators have suggested that white sturgeon make feeding forays into shallow water during hours of darkness (Haynes and Gray 1981). Most of our observations were made during the day; those made at night showed no apparent movement of YOY or juvenile fish into shallow areas. However, we have collected white sturgeon juveniles and adults in shallow water (<7 m deep) with gill nets set for 24 h (U.S. Fish and Wildlife Service, unpublished data). A preference for the thalweg may have prevented fish from becoming stranded in isolated pools as river levels rose and fell with the changing hydrograph that was characteristic of the river prior to impoundment.

We provide the most thorough description to date of the habitat used by white sturgeon. Our study provides measurements in time and space from a range of conditions. However, we were limited to sampling habitats suitable for our fishing gear. For example, we were unable to sample with our bottom trawls in areas with rugged bottom topography. Telemetry studies should be conducted to augment and verify observations from this study. Additional information on larval and YOY habitat preferences for velocities and substrates may be best obtained through laboratory studies.

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REPORT J

An Evaluation of Spawning and Rearing Habitat for White Sturgeon in the Lower Columbia River

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Abstract.- Estimates of spawning habitat for white sturgeon *Acipenser transmontanus* in the tailraces of the four dams on the lower 470 km of the Columbia River were obtained by using the Physical Habitat Simulation System of the U.S. Fish and Wildlife Service's Instream Flow Incremental Methodology to identify areas with suitable water depths, water velocities, and substrates. Rearing habitat throughout the lower Columbia River was assessed by using a geographic information system to identify areas with suitable water depths and substrates. The construction of the dams reduced the availability of spawning habitat for white sturgeon, but increased the amount of rearing habitat for young-of-the-year (YOY) and juvenile white sturgeon. Areas with water velocities required for spawning are present only in the dam tailraces. The Bonneville Dam tailrace provides high quality spawning habitat at river discharges lower than those needed to provide low to medium quality spawning habitat in the tailraces of The Dalles, John Day, and McNary dams. The lack of high quality spawning habitat in The Dalles, John Day, and McNary dam tailraces during years of low river discharge may limit successful reproduction and recruitment during these years. The three impoundments and the free-flowing Columbia River downstream from Bonneville Dam provide extensive areas that are suitable for rearing YOY and juvenile white sturgeon.

The productivity of lotic environments is controlled by four factors: flow regime (river hydrograph), physical habitat structure (channel morphology and substrate), water quality (including temperature), and energy inputs from the watershed (nutrients and organic matter)(Karr and Dudley 1978). The interaction of these factors determines primary and secondary production, which ultimately affect the status of fish populations. Restriction or limitation of any one of these factors during any life stage sets the adult population size (Orth 1987). If the riverine environment and thus the interaction of these factors is altered, changes to fish populations and how they respond to management strategies can be expected.

White sturgeon Acipenser transmontanus management in the Columbia River basin currently relies on moderating fishing mortality through slot length limits (Oregon and Washington), daily and annual catch restrictions (Oregon and Washington), and catch and release fishing (Idaho). Le Cren (1962) disclosed the management philosophy that has prevailed for white sturgeon:

"It is true that legal restrictions on fishing have often aimed at sharing the catch more equitably or preventing fishing by unauthorized persons; but in the background all the time has been the idea that conservation of adult stock is of fundamental importance, and sometimes this idea has become a sacred obligation".

This management strategy allowed white sturgeon to recover from overexploitation that decimated the fishery during the late 1800's, but development of the Columbia River basin for hydroelectric power generation during the mid 1900's profoundly altered the riverine environment. Construction and operation of dams in the Columbia River basin altered the flow regime, increased water depths, and reduced water velocities over extensive areas. Dams on other river systems have adversely affected sturgeon populations (Khoroshko 1972; Votinov and Kas'yanov 1978; Deacon et al. 1979; Rochard et al. 1990).

Recent research has documented spawning and identified the habitat used by various life stages of white sturgeon in the lower Columbia River (McCabe and Tracy 1992; Anders and Beckman 1992; Parsley et al. 1992). Successive year-class failures and poor recruitment to young-of-the-year (YOY) have been noted in the three impoundments downstream from McNary Dam (Miller and Beckman 1992), yet spawning and recruitment in the unimpounded river downstream from Bonneville Dam occurred during the same years (McCabe and Tracy 1992). In this paper we estimate the amount of habitat available for spawning and rearing (YOY and juvenile) white sturgeon in the three impoundments and free-flowing river that comprise the lower 470 km of the Columbia River. The goal is to determine if habitat for spawning and rearing of YOY or juvenile white sturgeon has been altered by hydroelectric development and if habitat is limiting the white sturgeon population at these life stages. Fishery managers may need to adopt new strategies if habitat alterations caused by development have changed the role that the external environmental controls identified by Karr and Dudley (1978) have on the white sturgeon populations.

Study Area

This study was conducted in the Columbia River from the mouth (river km 0) to McNary Dam (river km 470). The four dams within the study area are operated primarily for hydroelectric power generation and divide the river into three impoundments--Bonneville Pool, The Dalles Pool, and John Day Pool--and a free-flowing river reach (Figure 1). The four river reaches differ in length, surface area, and other physical characteristics (Table 1). Ebel et al. (1989) and Anonymous (1991) provide a background on the biotic and abiotic environment and the alterations to the environment caused by development and operation of the numerous hydroelectric and water diversion dams in the Columbia River basin.

River discharges through the study area are regulated by storage reservoirs located upriver in the Columbia and Snake river basins. The reservoirs in the study area have little storage capacity, and discharges through the dams are run-of-the-river. Therefore, mean daily discharge at each dam is similar, though hourly hydrographs of discharge among dams can be variable. Typically, hourly discharge at Bonneville Dam is relatively stable, whereas discharges at McNary, John Day, and The Dalles dams peak in the morning and are lower at night.

Two types of spill may occur at each dam during spring and summer: forced spill, when discharge is greater than the hydraulic capacity of the turbines (Table l), and planned spill, to aid in passing outmigrating juvenile salmonids. Usually, planned spill is during the evening, when total discharge is lowest.

Water elevations within each river reach are affected by river discharge, pondage in the three impoundments, and tides in the lower river reach. Pondage is regulated by the rule curves in effect at each dam. Water elevations fluctuate more in the dam tailraces than in the forebays. The greatest fluctuations occur in the Bonneville Dam tailrace and in the John Day Dam forebay (Table 1).

Methods

Two methodologies were used to quantify the physical habitat for spawning and rearing white sturgeon. We used the Physical Habitat Simulation System (PHABSIM; Bovee 1982) to evaluate habitat available for spawning white sturgeon by determining the relation between river discharge and spawning habitat downstream from each dam within the study area, and we used a geographic information system (GIS) to identify and quantify habitat for rearing (YOY and juvenile) white sturgeon throughout the study area. Both methods determine the overall quality as habitat of a particular unit of area of the river. Summing those areas gives an estimate of the quantity of habitat for each river reach. Temporal comparisons of habitat were made with the PHABSIM, but not with the GIS. The study area was spatially too extensive to permit using PHABSIM throughout the length of the river.

Paramount to quantifying spawning and rearing habitat was the establishment of criteria that defined habitat quality for these life

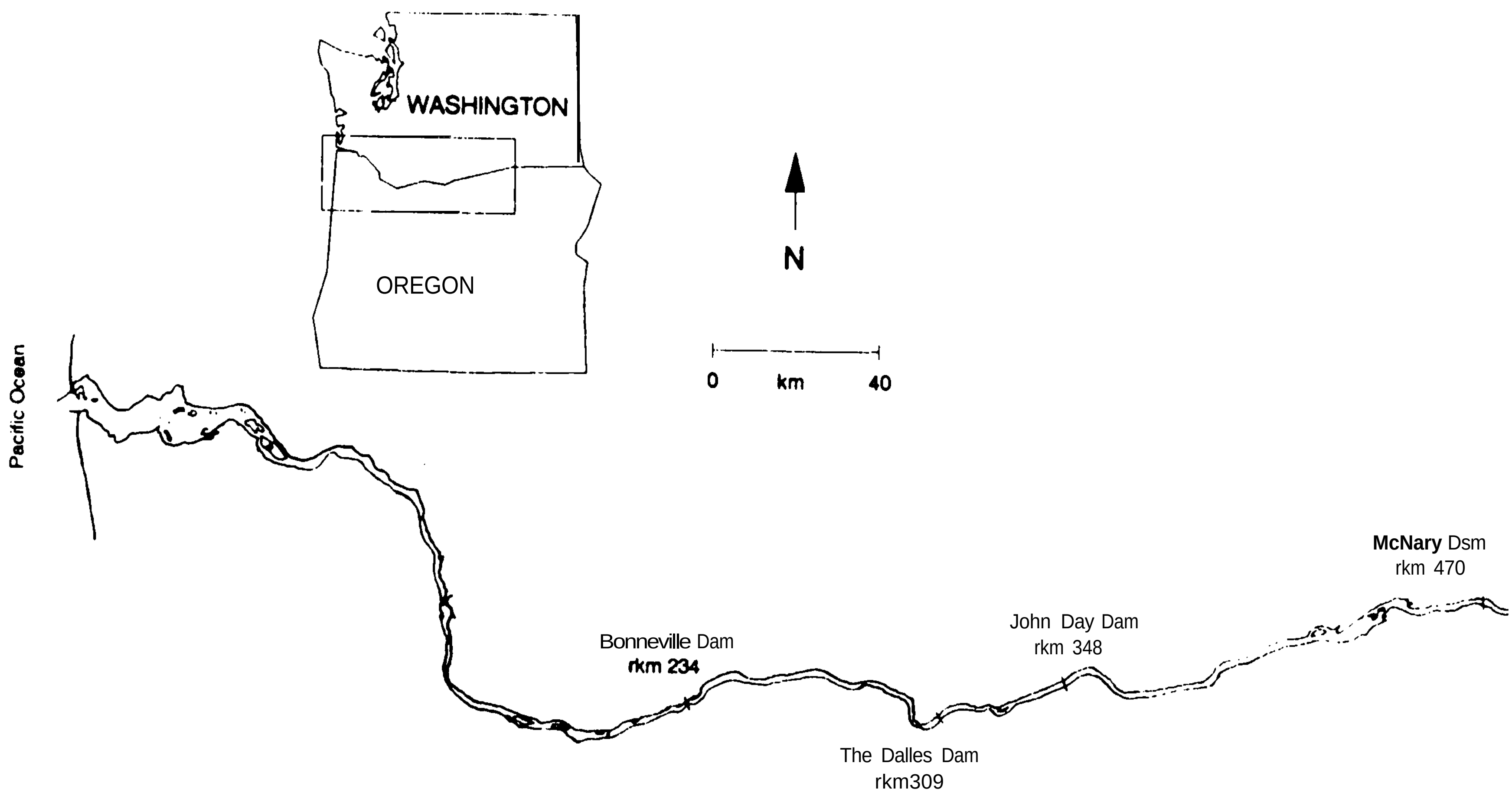


Figure 1. The Columbia River downstream from McNary Dam, with locations of the four mainstem dams and river reaches. Flow is from right to left-

Table 1. Characteristics of the four river reaches in the lower 470 km of the Columbia River. Bathymetry and substrate areas were derived during this study.

		River reach			
		Lower river	Bonneville Pool	The Dalles Pool	John Day Pool
Length (km)		234	75	39	122
Surface area (hectares)		61,148	7,632	3,639	19,781
Range in water surface elevations' (m)					
Tailrace		2.6-8.6	22.3-25.9	48.3-50.4	80.5-82.4
Forebay		Sea level	21.5-23.2	47.5-48.6	77.2-81.6
Hydraulic capacity of the upstream dam (m/s)		8,550	10,645	10,022	13,533
Bathymetry contours (m)b		Area (hectares)			
1.82	1.52	25,172	1,036	195	2,500
3.66	4.57	8,289	499	139	2,504
5.49	7.62	6,787	1,010	336	2,228
9.14	10.67	8,076	1,748	896	1,936
18.29	13.72	12,024	2,993	1,485	1,589
>18.29	>19.81	710	346	587	9,025
Substrates (hectares)					
Hard clay		4	0	0	0
Mud/silt		0	0	286	7,793
Sand		60,397	6,729	573	6,793
Gravel		142	357	175	3,645
Cobble		236	195	1,743	1,399
Boulder		369	103	198	69
Bedrock		0	248	663	83

[a]From mean daily minimums and maximums recorded at each dam during 1986 & 1988.

[b]First column is depth contours from nautical charts of the lower river, Bonneville, and The Dalles pools. Second column is depth contours from nautical charts of John Day Pool.

stages to be used as standards for comparison of habitat among the areas. Parsley et al. (1992) described the habitat used by various life stages of white sturgeon within the study area. We used the data from their paper to construct microhabitat criteria curves that depict the suitability of depths, mean water column velocities, and substrates for white sturgeon spawning (Figure 2), YOY, and juveniles (Figure 3), and the suitability of water temperatures for white sturgeon spawning. The criteria curves define the suitability of each habitat descriptor on a scale of 0 to 1 (0 = unsuitable and 1 = most suitable). The curves were fit by eye to the habitat use data presented in Parsley et al. (1992), and the resulting curves were scrutinized by us and other white sturgeon researchers for soundness. Microhabitat criteria curves are often developed in this manner (Bovee and Zuboy 1988).

Spawning Habitat

The relation between river discharge and white sturgeon spawning habitat downstream from each dam was assessed through the computer models of the PHABSIM. The PHABSIM has been described extensively in the literature (Stalnaker 1979; Bovee 1982; Milhous et al. 1989) and the following discussion is drawn largely from Bovee (1986). Measurements of water depth, velocities, and substrates along transects placed in the study area divide the river into a large number of rectangular cells (plane view). Each cell has a unique combination of depth, velocity, and substrate. Depth and velocities will vary with discharge, while substrate is fixed. Cells on the edge of the river will vary in surface area as water elevations rise and fall, while those always inundated have a fixed surface area. Changes in depth and velocity at points along each transect at unmeasured discharges are predicted by hydraulic simulation models described by Bovee and Milhous (1978) and Milhous et al. (1989). Habitat is estimated when the predicted water depth, velocity, and substrate for each cell is evaluated against the microhabitat criteria used to define habitat. The depth, velocity, and substrate for each cell are compared with the criteria to determine an overall habitat quality for each cell. This value is then multiplied by the surface area of the cell to obtain an index of microhabitat, called weighted usable area (WUA). Summing the WUA for all cells gives the WUA for the study site for a given discharge. We simulated spawning habitat for discharges ranging from 1,415.6 to 14,156 m^3/s at 707.8 m^3/s intervals (50,000 to 500,000 ft^3/s at 25,000 ft^3/s intervals).

Transects were surveyed in each tailrace to obtain river cross section profiles detailing river bed elevations, mean water column velocities, and substrates at verticals along each transect for input into the hydraulic simulation program IFG4 of the PHABSIM (Milhous et al. 1989). Five transects were surveyed downstream from Bonneville Dam, eight downstream from The Dalles Dam, five downstream from John Day Dam, and seven downstream from McNary Dam (Figure 4). Distances (nearest 0.3 m) between individual transects were measured with an electronic distance meter (EDM), and elevations (height above mean sea level, nearest 0.3 cm) were determined through standard surveying techniques. We used the EDM to measure the distance to a boat positioned along each transect describe bed elevations and to obtain water velocities for model calibration. Water

Spawning

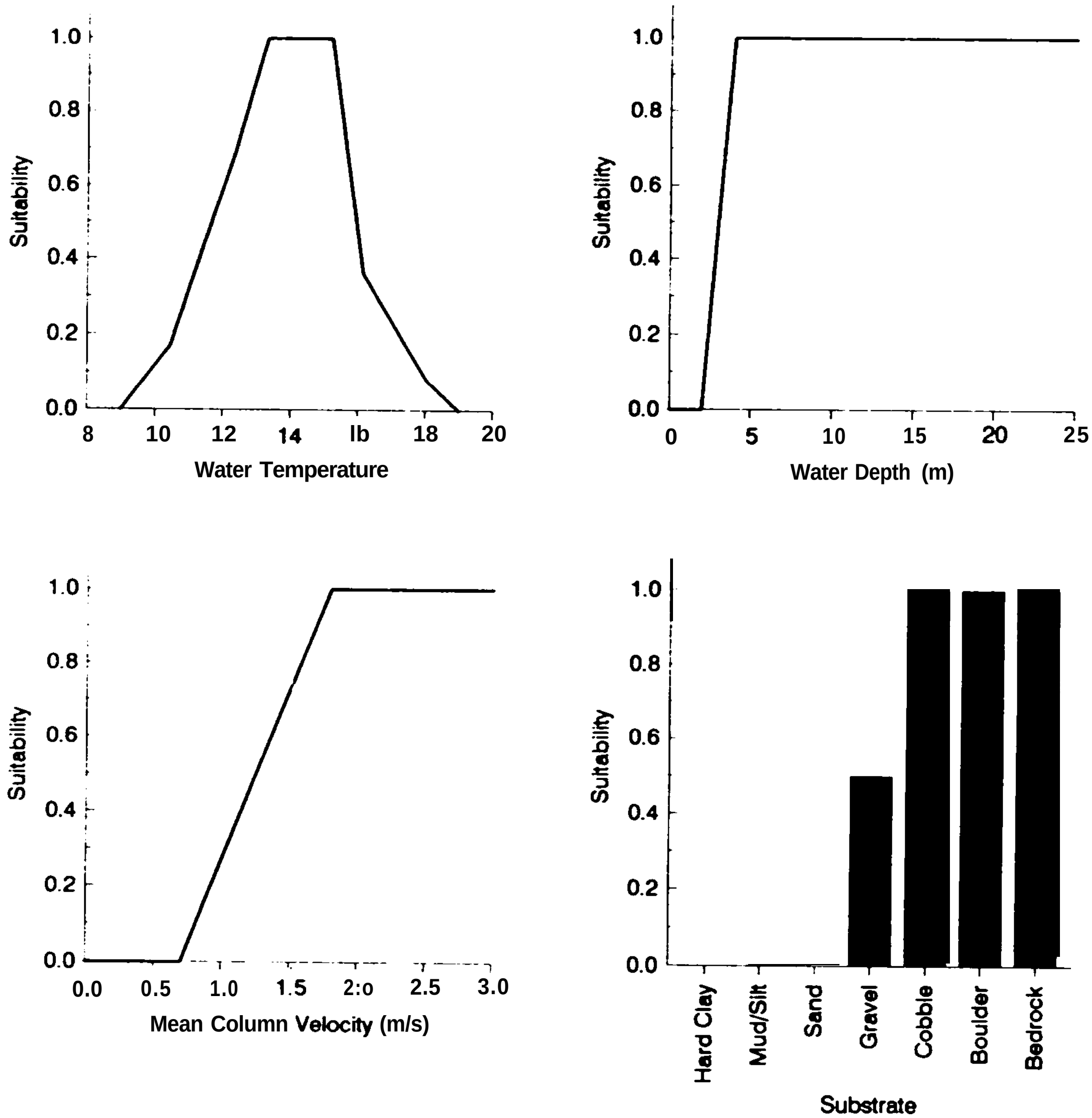


Figure 2. Microhabitat criteria curves depicting the suitability of water temperatures, depths, mean column velocities, and substrates for spawning white sturgeon.

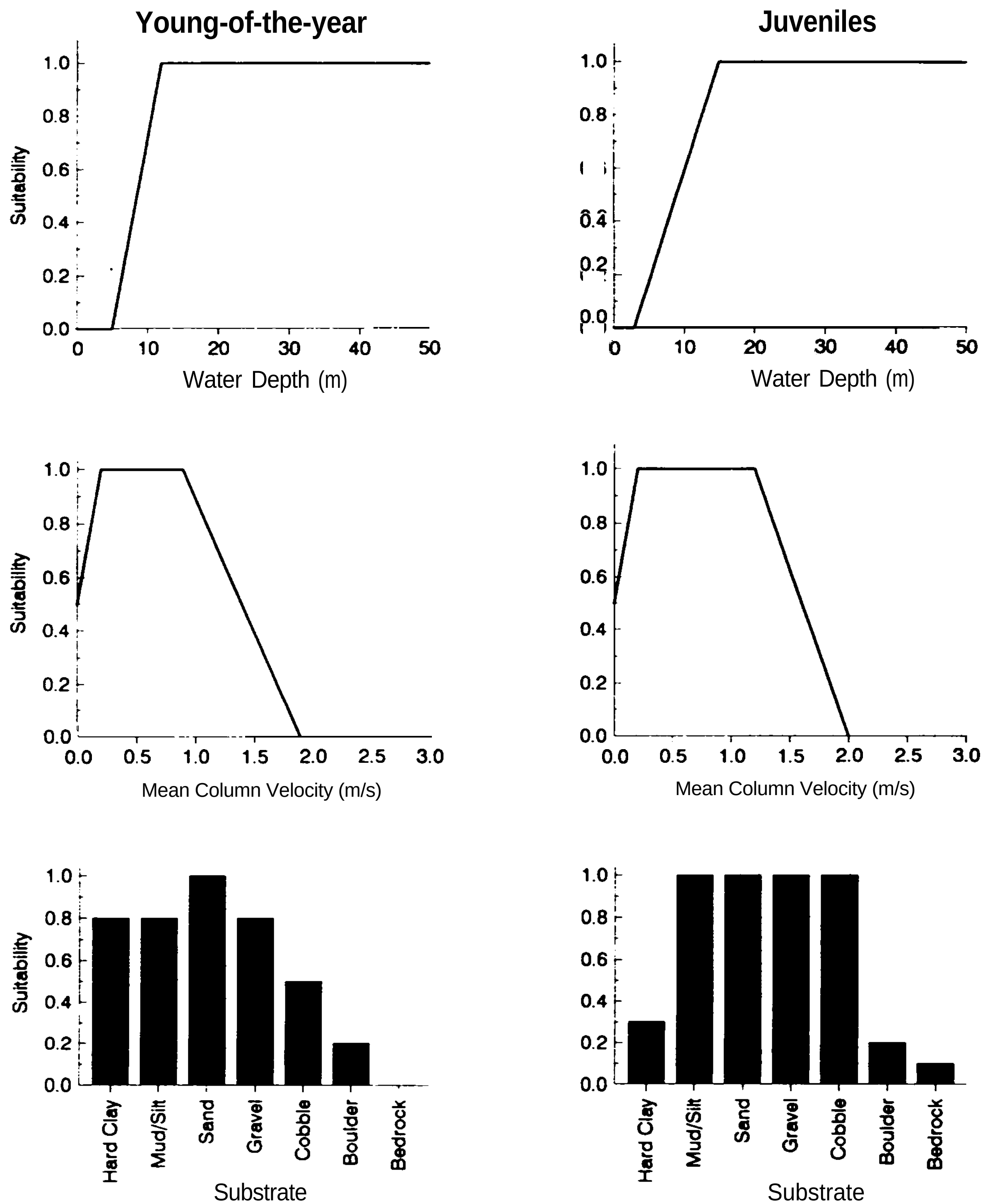


Figure 3. Microhabitat criteria curves depicting the suitability of water depths, mean column velocities, and substrates for young-of-the-year and juvenile white sturgeon.

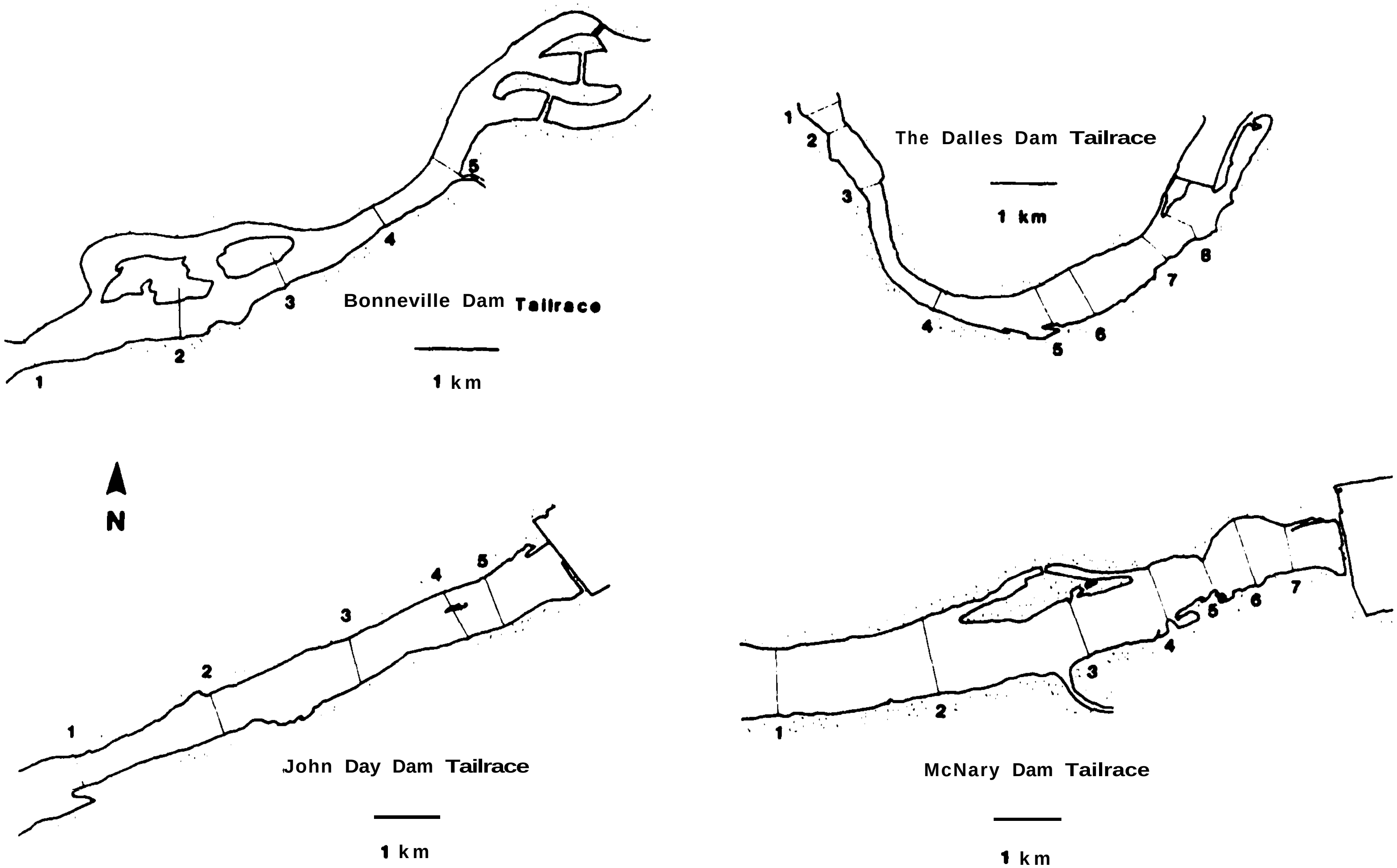


Figure 4. Locations of transects placed for hydraulic and spawning habitat simulations in Bonneville, The Dalles, John Day, and McNary dam tailraces.

surface elevations (nearest 0.3 cm) were measured at each transect at several discharges.

We used least-squares regression to determine the relation between tailwater elevation at the dam and water elevation at each transect. Each dam is an upstream hydraulic control, and hourly records of tailwater elevation and river discharge are kept by the U.S. Army Corps of Engineers. Regressions were based on hourly data for the months of April-July from one or more years. This relation predicted the tailwater elevation at each dam for the discharges to be simulated. These predicted tailwater elevations were then used to predict the water surface elevation at each transect for each discharge to be simulated.

The relation between discharge and white sturgeon spawning habitat within the area described by the transects was established with the HABTAE program of the PHABSIM (Milhous et al. 1989). This program integrated the output from the hydraulic simulation model (predicted depths, water velocities, and substrates at selected discharges) with the microhabitat criteria curves that defined habitat used by spawning white sturgeon. The lowest suitability for depth, mean column velocity, and substrate present for each cell (lowest limiting parameter approach, Bovee 1982) was used as the composite suitability index (CS) of spawning habitat for each cell. Model output (amount of spawning habitat versus discharge) allows comparisons of usable habitat and WUA. Usable habitat is the sum of the surface areas of all cells with a CS > 0. Weighted usable area is the sum of the products of the surface area of a cell and the CS of that cell. We multiplied model output by individual reach lengths to obtain surface areas to allow comparisons of spawning habitat within different reaches.

Daily spawning habitat from 1985 through 1991 was determined by integrating mean daily discharge and water temperature from April through July with the spawning habitat versus discharge relation for each tailrace. Mean daily discharge and water temperature for each dam were obtained from records maintained by the U.S. Geological Survey (Water Resources Division, Portland, Oregon), the U.S. Army Corps of Engineers (North Pacific Division, Portland, Oregon), the Fish Passage Center (Portland, Oregon), and the U.S. Fish and Wildlife Service (Cook, Washington). Daily spawning habitat (WUA) was averaged monthly and annually. Variation in spawning habitat for each tailrace and year was assessed by calculating the coefficient of variation in monthly habitat during 1985-1991.

Rearinq Habitat

The geographic information system EPPL7[1] was used to identify areas in each river reach that have suitable water depths and substrates for YOY and juvenile white sturgeon. A GIS is an assemblage of computer hardware and software tools that unites computerized mapping and data bases to

[1]The mention of commercial trade names does not imply endorsement by the U.S. Fish and Wildlife Service.

provide analysis and display of geographically oriented data. Star and Estes (1990) and Meaden and Kapetsky (1991) provided a background and applications of GIS.

Habitat for YOY and juvenile white sturgeon was quantified by using the GIS to identify areas in each river reach as suitable or unsuitable for these life stages. Mean column water velocities for the entire study area were not available; hence, analyses were limited to depth and substrate. The criteria curves for water velocities reveal that YOY and juvenile white sturgeon will use a wide range of water velocities (Figure 3). Water depth and substrate contours were digitized from maps and rasterized to either 9.29 m^2 or 37.16 m^2 cell sizes. Water depth contours were obtained from nautical charts produced by the National Oceanic and Atmospheric Administration (Distribution Branch, National Ocean Service, Riverdale, Maryland 20737-1199). Substrate contours were drawn from an assimilation of field measurements from this and other studies, pre-impoundment aerial photographs, and the nautical charts. Depths were depicted as discrete contours; therefore, we assigned a suitability to each depth contour by averaging, at 0.3-m intervals, suitabilities from the microhabitat criteria (Table 2). Substrate categories were also assigned suitabilities from the microhabitat criteria depicted in Figures 2 and 3.

High salinity in the estuary precludes the use of extensive areas of the unimpounded lower river reach by YOY and juvenile white sturgeon. The extent of saltwater intrusion is dynamic and depends on river discharge and tides. For this analysis, we used river km 45 as the downstream boundary for YOY and river km 30 as the downstream boundary for juveniles because the ability of white sturgeon to tolerate salinity increases with size.

For YOY and juvenile white sturgeon, a composite suitability index for each cell representing the river was derived by calculating the geometric mean of the suitabilities for the depth contour and substrate of that cell. The product of CS and the area of each cell gave a WUA for each cell. Summing all cells gave a WUA for each river reach, and identified areas within each river reach that were usable (CS = 0.001 to 1.00) or unusable (CS = 0). Quality rankings of low (CS = 0.001 to 0.40), medium (CS = 0.41 to 0.80), or high (CS = 0.81 to 1.00) were assigned to each cell in each river reach. Summing the areas of the cells with these classifications gave comparisons of the relative quality of the usable habitat among the river reaches.

Results

Spawning Habitat

The amount of spawning habitat for white sturgeon increased in each tailrace as discharge increased, however, the rate of increase among tailraces and discharges varied due to differences in channel morphology among areas (Figures 5 and 6). Spawning habitat increased because water velocities increased with discharge. The Bonneville Dam tailrace provides more high quality spawning habitat for white sturgeon at discharges that

Table 2. Microhabitat criteria values assigned to each depth contour depicted on nautical charts of the study area. Values were obtained by averaging criteria values at 0.3 m intervals within each contour.

River reach	Depth Contour (m)	Average criteria value: Young-of-the-year	Average criteria value: Juvenile
lower river reach,	0-1.82	0.00	0.00
Bonneville Pool, and	1.83-3.66	0.00	0.01
The Dalles Pool	3.67-5.49	0.02	0.14
	5.50-9.14	0.37	0.37
	9.15-18.29	0.95	0.85
	>18.29	1.00	1.00
John Day Pool	0-1.52	0.00	0.00
	1.53-4.57	0.00	0.04
	4.58-7.62	0.20	0.27
	7.63-10.67	0.63	0.52
	10.68-13.72	0.97	0.78
	13.72-19.81	1.00	0.99
	>19.81	1.00	1.00

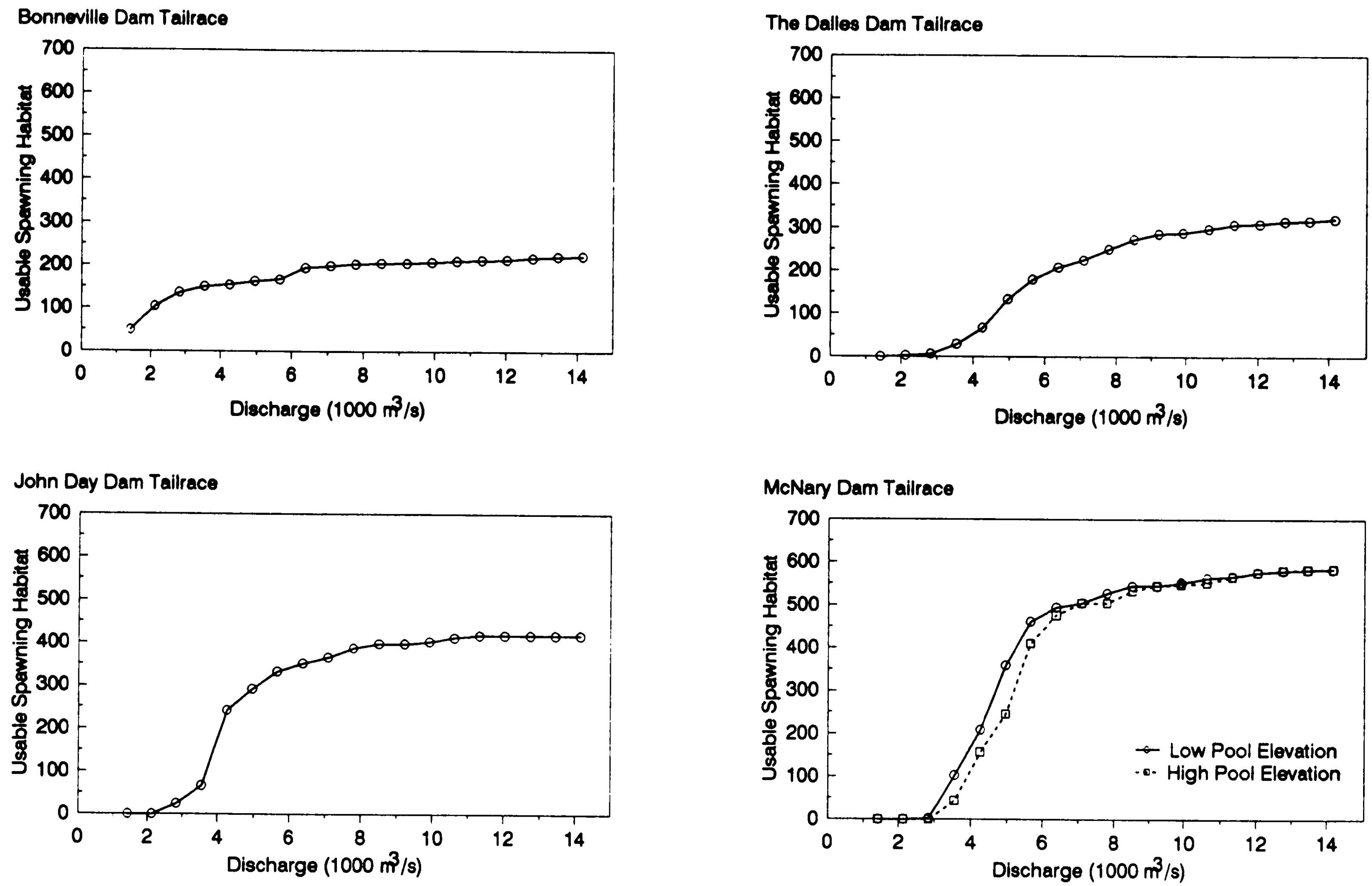


Figure 5. Total area (hectares) of usable spawning habitat for white sturgeon at river discharges ranging from 1,415.6 - 14,156 m^3/s in the tailraces of the four dams on the Columbia River downstream from McNary Dam.

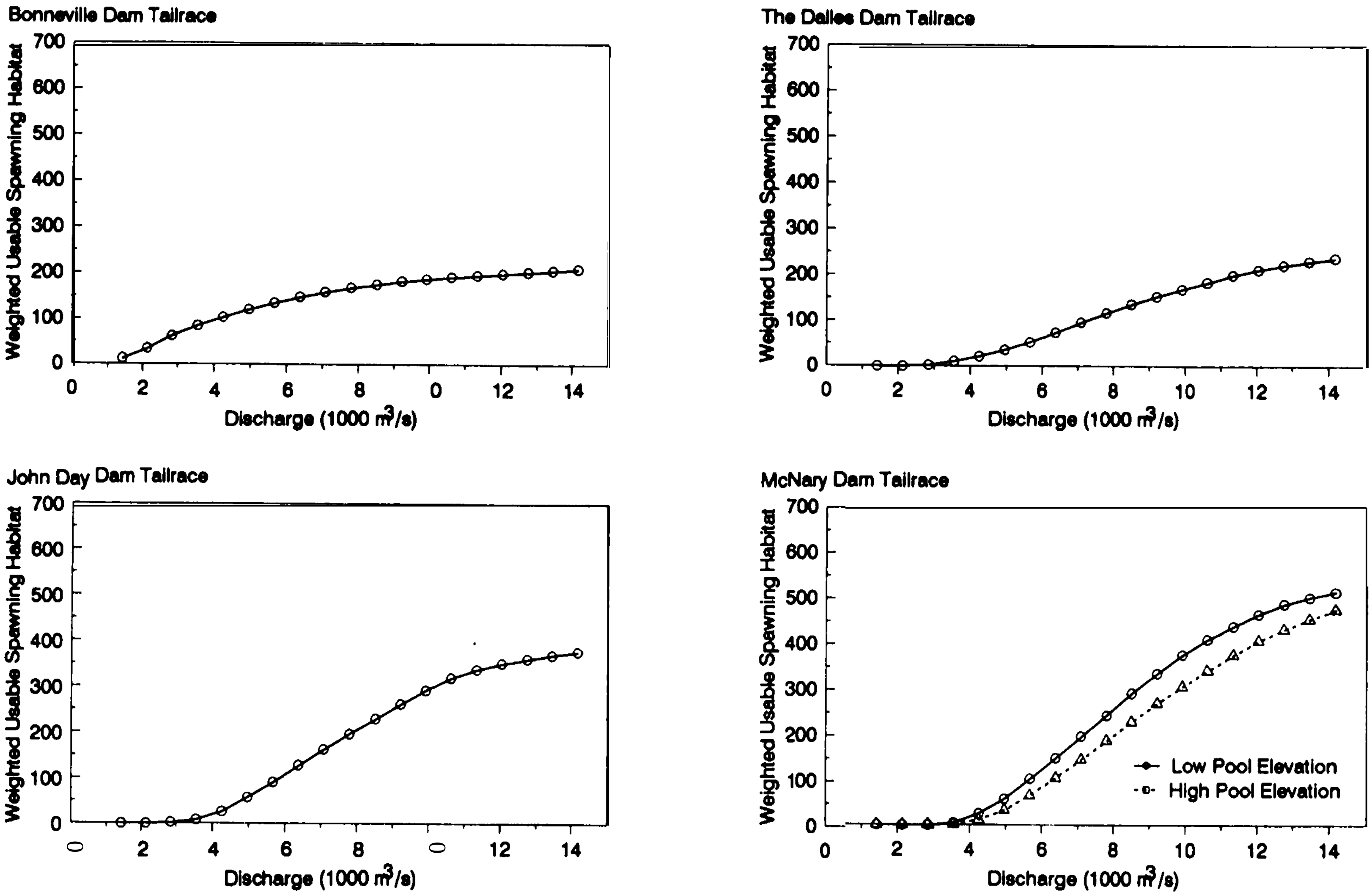


Figure 6. Total weighted usable area (hectares) of spawning habitat for white sturgeon at river discharges ranging from 1,415.6-14,156 m^3/s in the tailraces of the four dams on the Columbia River downstream from McNary Dam.

are lower than discharges needed to provide even low to moderate quality spawning habitat in the other tailraces.

Usable habitat (CS = 0.001 to 1.00), when expressed as the proportion of the total area of each tailrace, is nearly maximized in Bonneville, John Day, McNary, and The Dalles dam tailraces at about 6,370, 7,790, 8,500, and 9,200 m/s (225,000, 275,000, 300,000, and 325,000 ft^3/s) (Figure 7). Usable area increases only slightly at greater discharges. Weighted usable area (usable area with a quality component), when expressed as the proportion of the total area of each tailrace, is maximized at 6,370 m^3/s (225,000 ft^3/s) in the Bonneville tailrace, but continues to increase with increasing discharge in the other tailraces, indicating that the quality of the usable habitat present in these tailraces improves with increasing discharge (Figure 7).

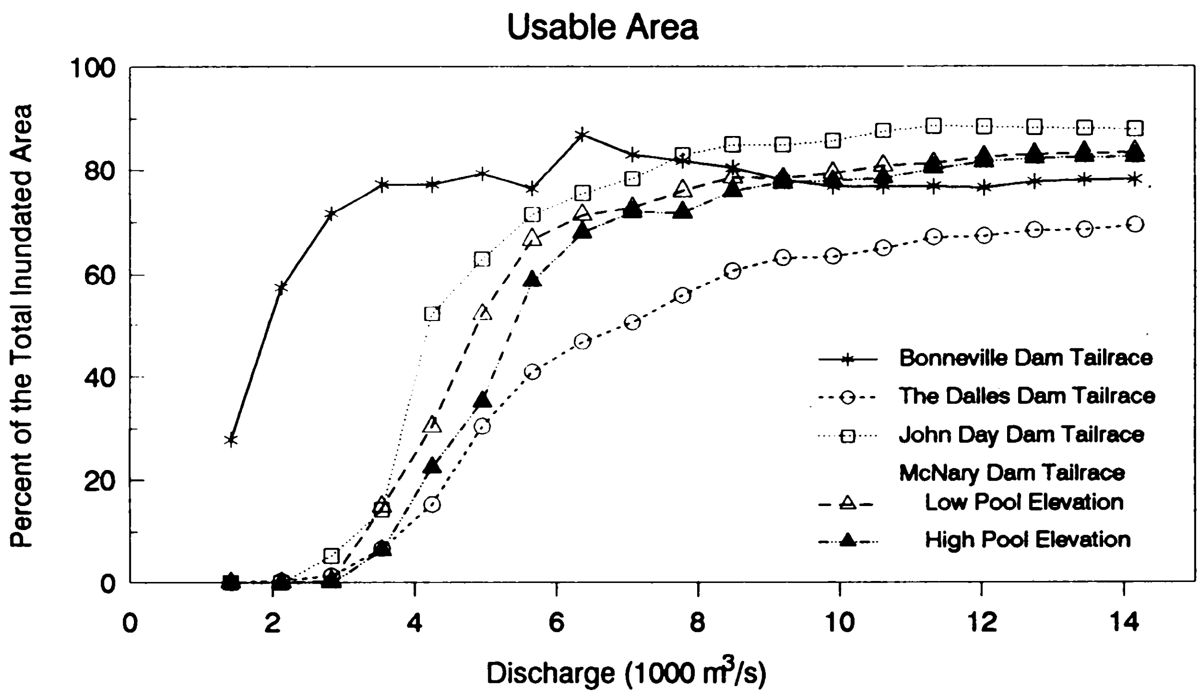
Incremental gains in habitat with increasing discharge in each tailrace were examined by plotting cumulative percent gain in total habitat as discharges range from 1,420 to 14,160 m^3/s (50,000 to 500,000 ft^3/s). Slopes of the plotted lines reveal the relative benefit of increases in discharge to habitat; steeper slopes indicate a greater gain. Cumulative gains in usable habitat are greatest in the Bonneville, John Day, and McNary dam tailraces at discharges less than 7,790 m/s (275,000 ft^3/s), and gains in usable habitat in The Dalles Dam tailrace are greatest at discharges less than 9,200 m/s (325,000 ft^3/s)(Figure 8).

Cumulative gains in WUA in the Bonneville Dam tailrace are greater at lower discharges than cumulative gains in WUA in the tailraces of the impounded reaches (Figure 8). Cumulative gains in WUA in the impounded reaches are nearly identical as discharge increases.

<u>Bonneville</u> Dam <u>Tailrace.</u> -- Habitat suitable for white sturgeon spawning is present at all simulated river discharges in the Bonneville Dam tailrace (Figures 5 and 6). The amount of habitat increases as discharge increases, and high quality habitat is present at discharges greater than 2,120 m^3/s (75,000 ft^3/s). River discharge during the white sturgeon spawning period is seldom less than 2,120 m^3/s (75,000 ft^3/s) at Bonneville Dam. Usable habitat in the main channel downstream from Bonneville Dam increases the most between discharges of 1,420 and 3,540 m^3/s (50,000 and 125,000 ft^3/s) and between 5,660 and 6,370 m/s (200,000 and 225,000 ft^3/s)(Figure 5). Weighted usable area increases as discharge increases (Figure 6). Approximately 90% of the usable habitat present at 14,160 m^3/s (500,000 ft^3/s) is achieved at 6,370 m^3/s (225,000 ft^3/s)(Figure 8), and about 70% of the WUA present at 14,160 m/s (500,000 ft^3/s) is attained at the same discharge (Figure 8).

Model output of white sturgeon spawning habitat in the Bonneville Dam tailrace reveals that spawning habitat first appears in the segment represented by transect 3 (Figure 4) and extended upriver and downriver as discharge increased. Cells with CS's of 0.81 or greater (high quality habitat) first appeared along this transect at a discharge of 2,124 m^3/s (75,000 ft^3/s).

Hydraulic simulations of water depths and velocities at different discharges in the river channels downstream from the two powerhouses and



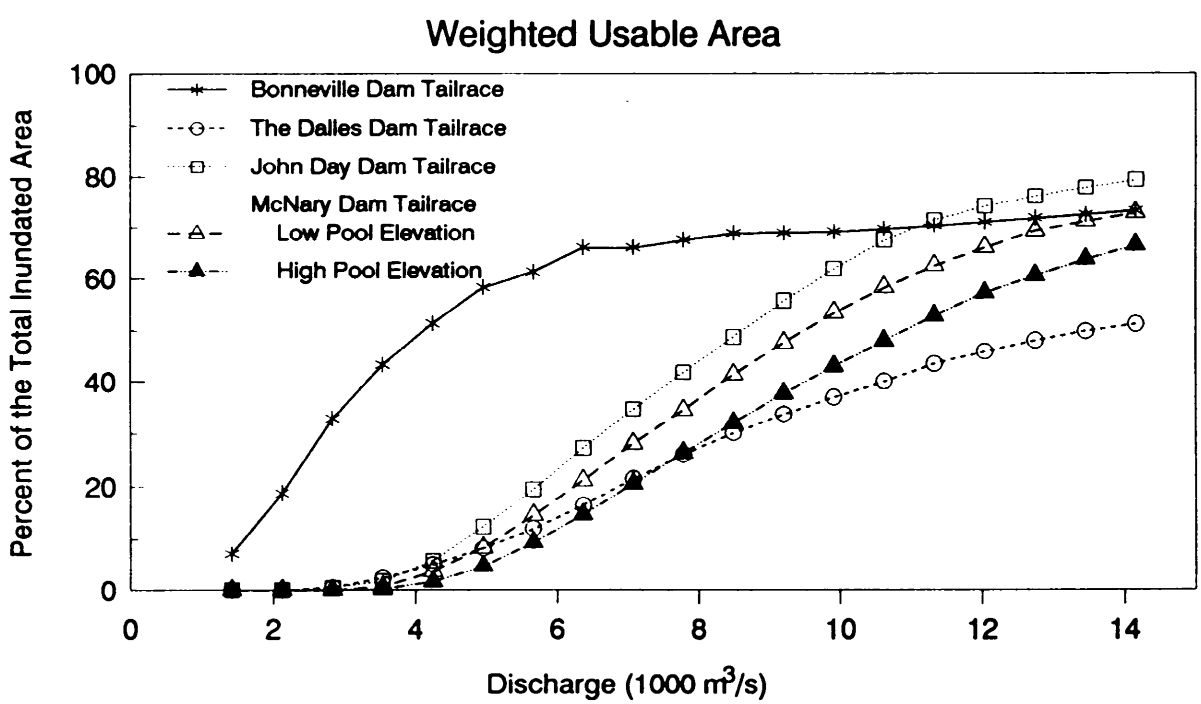
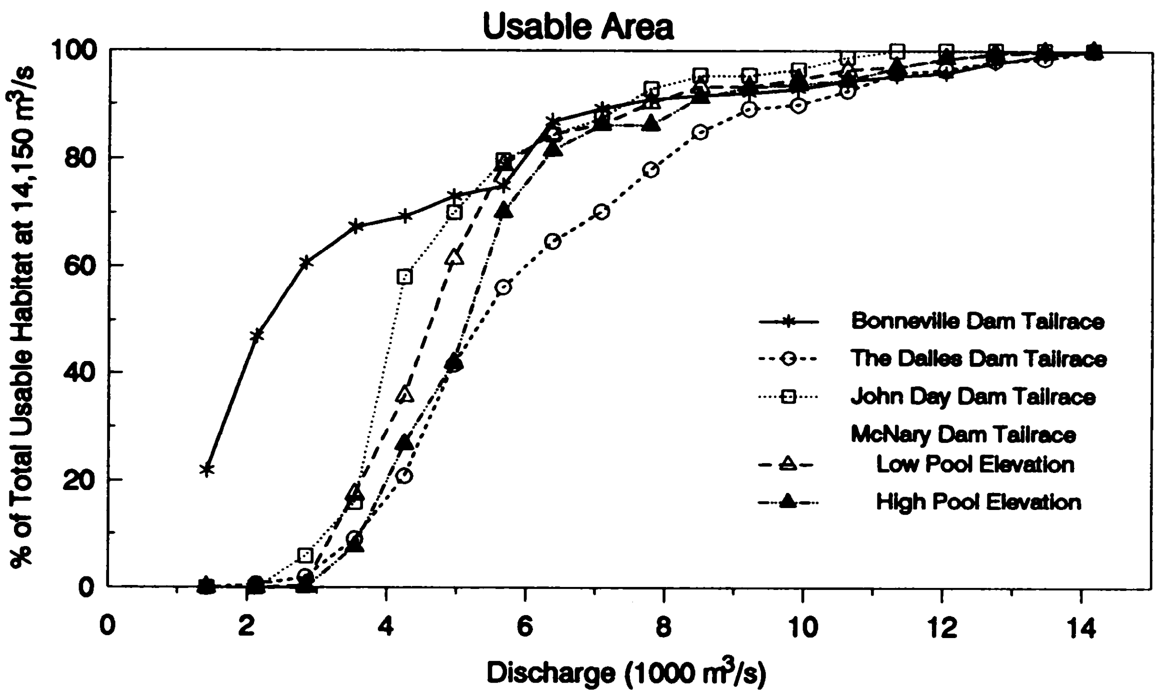


Figure 7. Usable spawning area (hectares) and weighted usable spawning area for white sturgeon at discharges through each river reach expressed as the percentage of the total inundated area of each reach at each discharge.



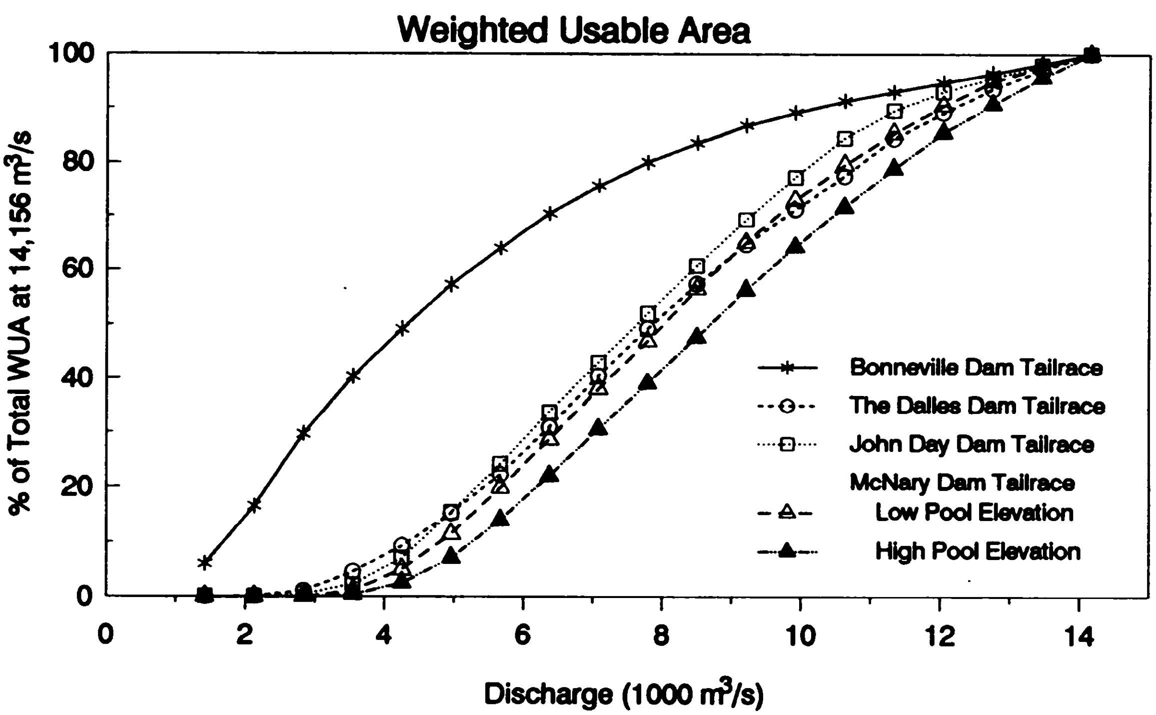


Figure 8. Incremental gains in percent usable spawning area and weighted usable spawning area as discharge increases to 14,156 m^3/s.

the spill basin were not possible as water elevations and discharges in each channel are unrelated. The total river discharge can pass through the channels in any combination, thus precluding valid simulations because different discharges may occur at the same water elevation. However, each channel is similar in physical morphometry to the main channel described by transects 1-5, and suitable spawning habitat is probably present in each channel when discharge is substantially greater than zero.

The Dalles Dam Tailrace. -- Spawning habitat is present, although low in quantity and quality, in this tailrace when river discharge is 2,120 m^3/s (75,000 ft^3/s). Appreciable increases in habitat are not evident until discharges exceed 3,540 m^3/s (125,000 ft^3/s)(Figures 5 and 6). Approximately 90% of the usable habitat present at 14,160 m^3/s (500,000 ft^3/s) is attained when discharge approaches 9,200 m^3/s (325 000 ft^3/s)(Figure 8), and 60% of the WUA present at 14,160 m^3/s (500,000 ft^3/s) is attained at the same discharge (Figure 8).

Model output of white sturgeon spawning habitat and discharge in The Dalles Dam tailrace shows that usable habitat first appears at transect 8 (Figure 4) and extended upriver and downriver as discharge increased. Cells with CS's of 0.81 or greater (high quality habitat) first occurred along transect 8 at a discharge of 4,250 m^3/s (150,000 ft^3/s).

John Dav Dam Tailrace. -- Spawning habitat was present in minimal area and quality in this tailrace when discharge was 2,830 m^3/s (100,000 ft^3/s)(Figures 5 and 6). Usable spawning habitat increased greatly as discharge increased from 2,830 through 6,370 m^3/s (100,000 through225,800 ft^3/s), and WUA increased most between discharges of 3,540 and 10,620 m/s (125,000 and 375,000 ft^3/s). Approximately 90% of the usable habitat present at a discharge of $4,160 m/s (509,000 ft^3/s) is realized as discharge approaches 7,080 m^3/s (250,000 ft^3/s)(Figure 8), whereas only about 50% of the WUA present at 14,160 m^3/s (500,000 ft^3/s) is achieved at the same discharge (Figure 8).

Model output of white sturgeon spawning habitat and discharge in the John Day Dam tailrace showed that spawning habitat first appeared along transects 4 and 5 (Figure 4) and extended downriver as discharge increased. Cells with CS's of 0.81 or greater (high quality habitat) first occurred along these transects at a discharge of 6,660 m^3/s (200,000 ft^3/s).

McNarv Dam Tailrace. -- It was necessary to derive two relations describing the amount of white sturgeon spawning habitat in the McNary Dam tailrace. The U.S. Army Corps of Engineers has maintained reservoir elevations in John Day Pool (measured at John Day Dam) at two levels, approximately 80.5 m and 81.4 m above mean sea level. Typically, the pool is kept at the lower elevation during winter and spring, and the higher elevation is maintained starting in mid to late June through the summer for irrigation withdrawals. During 1988, however, the reservoir elevation was maintained at the higher level throughout the year.

Habitat suitable for spawning was present in this tailrace when river discharge was 2,830 m^3/s (100,000 ft^3/s) or greater at either pool elevation (Figures 5 and 6). Usable spawning habitat increased greatly as discharge increased; the greatest gains were when discharge increased from 2,830 m/s to 8,490 m^3/s (100,000 to 300,000 ft^3/s)(Figure 5). Higher discharges were needed to achieve the same usable habitat when the pool elevation was maintained at the 81.4-m elevation than when it was at 80.5 m. Weighted usable area at both pool elevations increased progressively with discharge (Figure 6), with greater WUA at lower pool elevations. Approximately 90% of the usable area present at 14,160 m^3/s (500,000 ft^3/s) is attained at 7,790 m/s (275,000 ft^3/s) at either pool elevation (Figure 8), whereas only about 50% of the WUA present at a discharge of 14,160 m/s (500,000 ft^3/s) is realized at the same discharge and a pool elevation of 80.5 m. Only about 40% of the WUA present at 14,160 m/s (500,000 ft^3/s) is present at 7,790 m^3/s (275,000 ft^3/s) and a pool elevation of 81.4 m (Figure 8).

Model output of spawning habitat in the McNary Dam tailrace showed spawning habitat first appeared along transect 7 (Figure 4) at lower discharges, and extended downriver as discharge increased. Cells with CS's of 0.81 or greater (high quality habitat) first occurred along this transect at a discharge of 7,080 m^3/s (250,000 ft^3/s).

Time Series Analvsis of Spawninq Habitat

The amount of habitat suitable for white sturgeon spawning varied in all areas during 1985-1991 (Figure 9) and was controlled by discharge and water temperature. John Day and McNary Dam tailraces had the greatest variation in monthly spawning habitat. The effect of reduced discharge on spawning habitat during low-water years (1985, 1987-1989) is evident in the graphs depicting monthly spawning habitat in The Dalles, John Day, and McNary Dam tailraces (Figure 9). The reduced discharges in these years had less of an effect on spawning habitat in the Bonneville Dam tailrace because the physical morphology of this tailrace provides conditions that create habitat suitable for spawning at discharges lower than discharges needed in the other tailraces. The role of temperature in defining the spawning period and its effect on total spawning habitat is evident in each year, particularly 1986, and all tailraces.

Creation of an annual time series using temperature-conditioned annual average spawning habitat reveals that Bonneville Dam tailrace provided more spawning habitat during the low-water years (1985, 1987-1989) than the other three tailraces (Figure 10). More spawning habitat was present each year in Bonneville and John Day dam tailraces, and in McNary Dam tailrace in 1988, than in The Dalles Dam tailrace. The coefficient of variation in annual spawning habitat was generally lowest in Bonneville Dam tailrace (Figure ll), denoting that the amount of spawning habitat didn't fluctuate as much in this tailrace as it did in the other tailraces.

Rearing Habitat

The impounded river reaches have proportionately more rearing habitat than the unimpounded lower river reach (Table 3). Ranking the usable area of each river reach into high, medium, and low quality

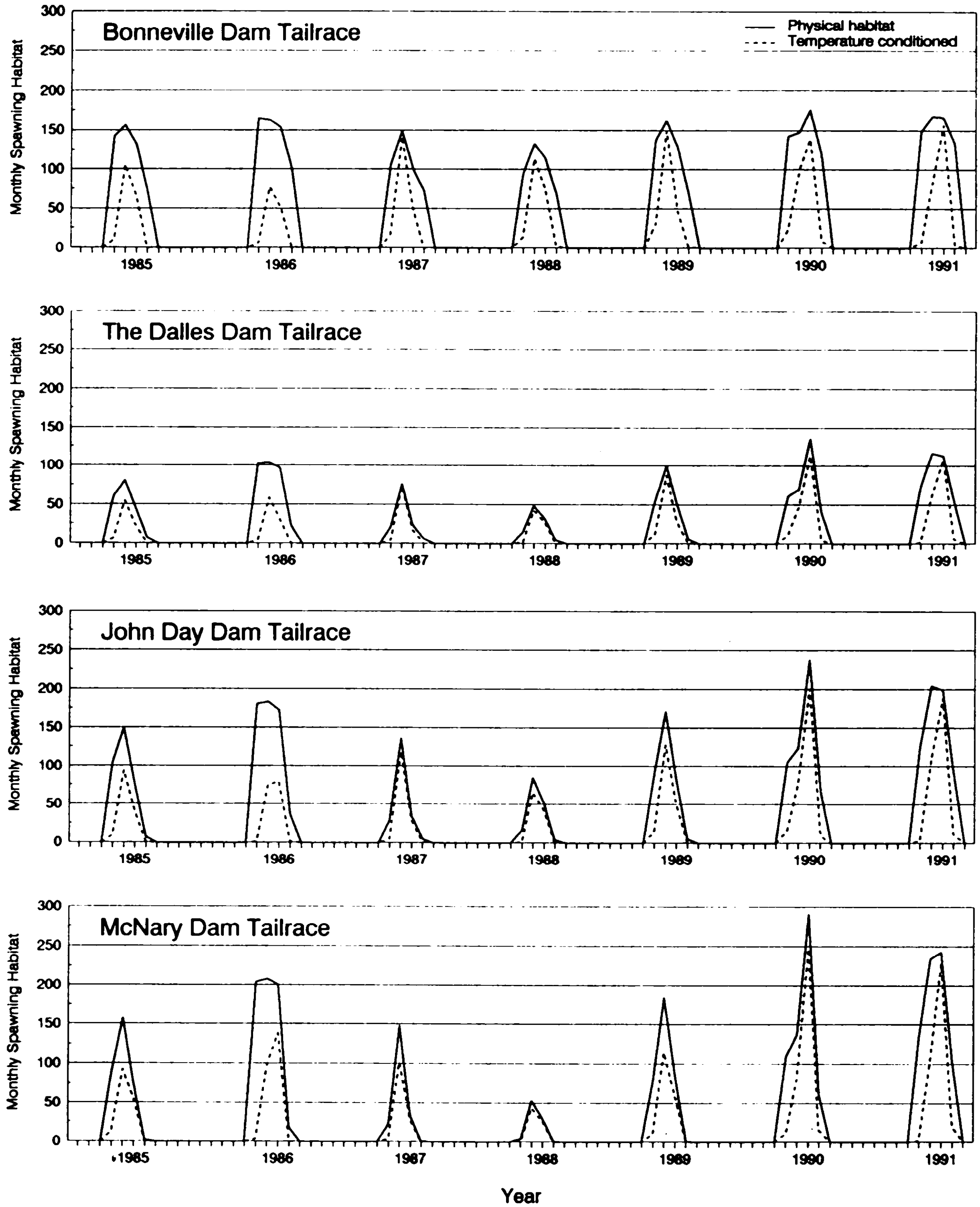


Figure 9. Monthly weighted usable area (hectares) present in Bonneville, The Dalles, John Day, and McNary dam tailraces during 1985-1991. Solid lines portray suitable microhabitat, dashed lines incorporate the suitability of daily water temperature in each tailrace, and therefore represent total habitat. Ascending limbs of the microhabitat (solid lines) are in April of each year, descending limbs are in July.

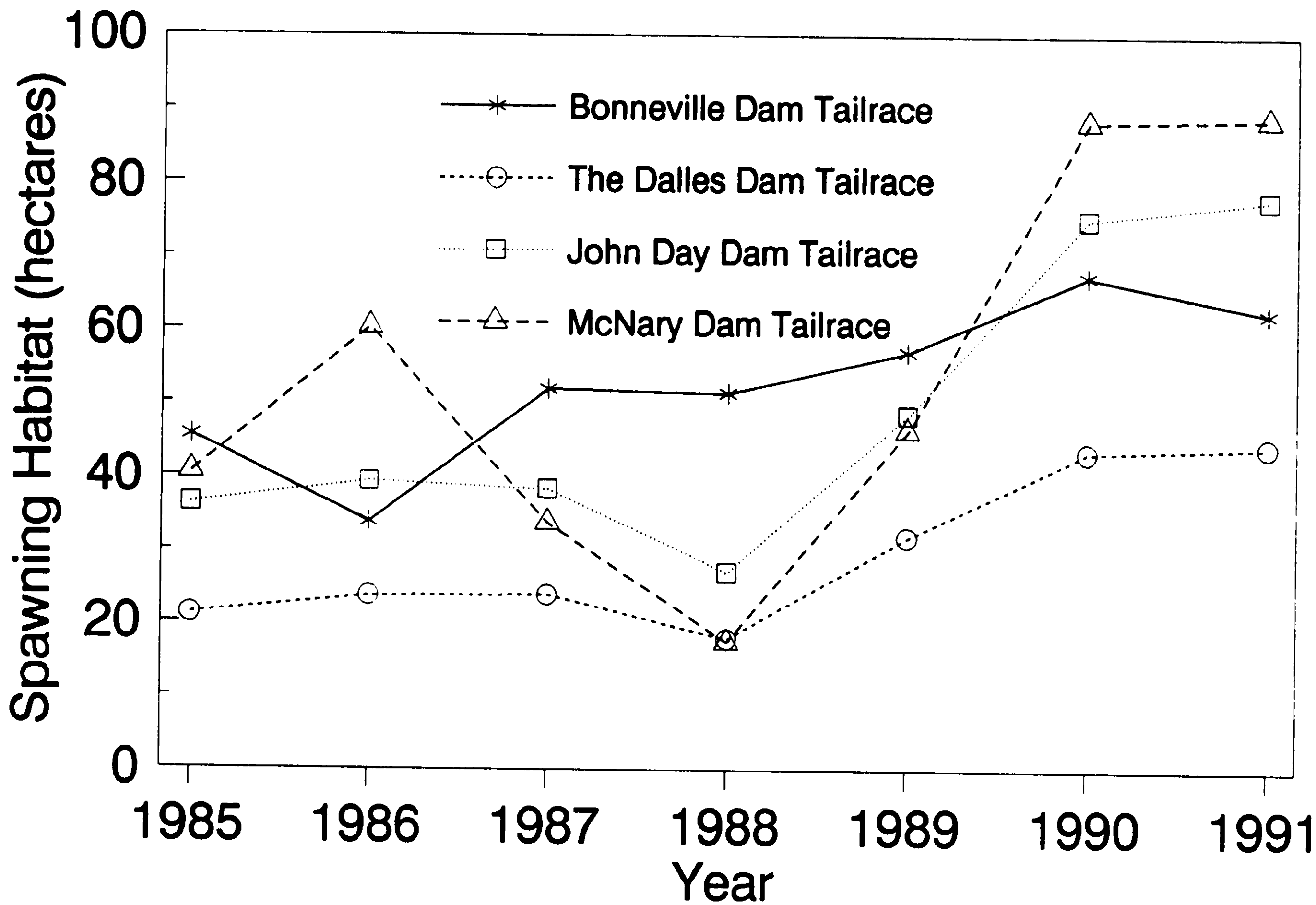


Figure 10. Composite index of annual weighted usable spawning habitat present in Bonneville, The Dalles, John Day, and McNary dam tailraces. The composite index was calculated by multiplying average monthly values of total habitat by the number of days in the month, summing those, and dividing the sum by the number of days during April, May, June, and July.

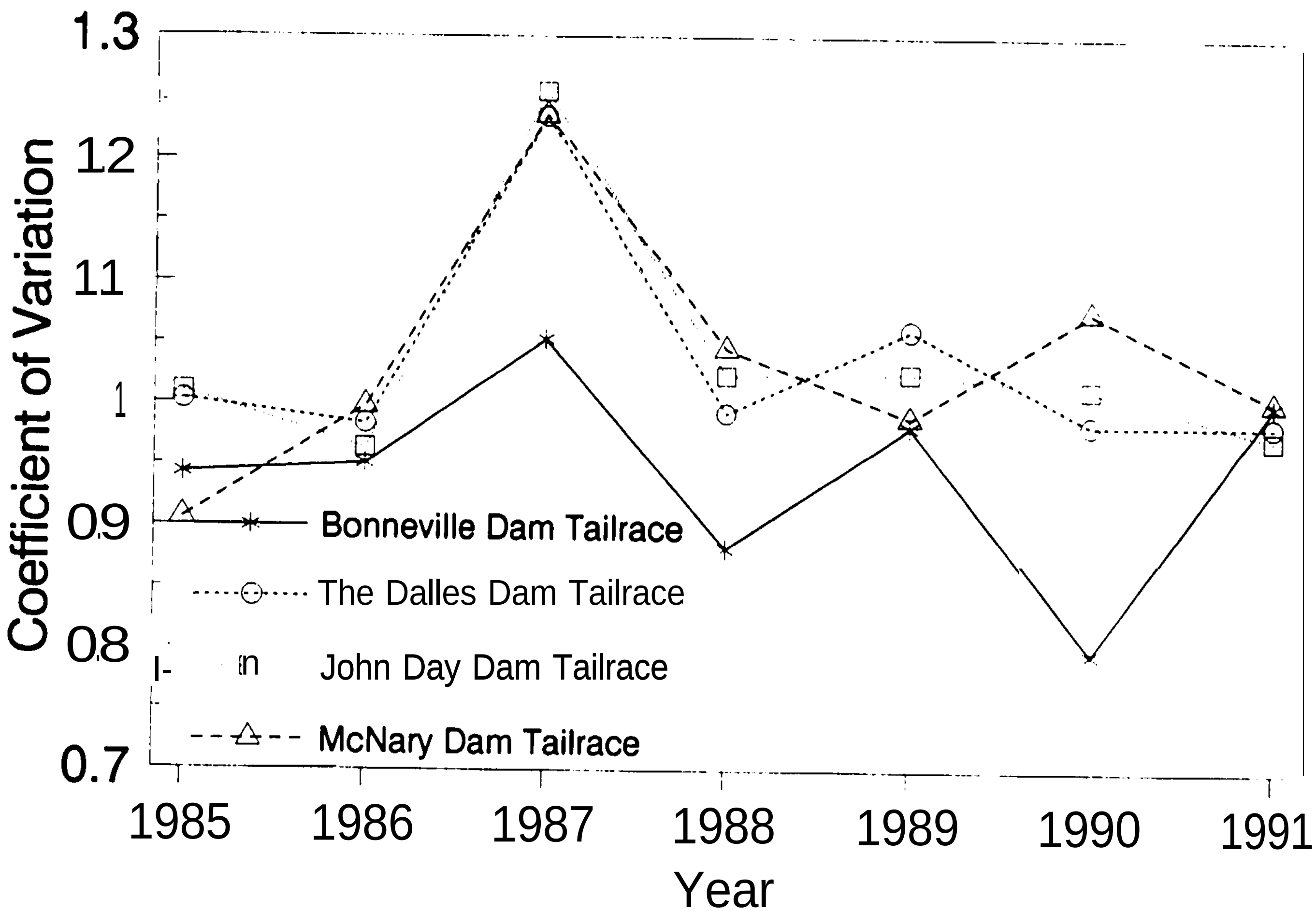


Figure 11. Coefficient of variation in seasonal weighted usable spawning area (total habitat) in Bonneville, The Dalles, John Day, and McNary dam tailraces.

Table 3. Amount of habitat for young-of-the-year and juvenile white sturgeon in the four river reaches downstream from McNary Dam. All areas are expressed in hectares; percentages are in parenthesis.

Habitat	River reach			
	Lower River	Bonneville Pool	The Dalles Pool	John Day Pool
	Young-of-the-year			
Total surface area	25,629	7,632	3,639	19,781
Usable area	13,744 (54)	5,935 (78)	2,700 (74)	14,727 (74)
High quality	6,477 (25)	3,100 (41)	633 (17)	10,206 (52)
Medium quality	3,779 (15)	1,870 (25)	1,759 (48)	3,422 (17)
Low quality	3,488 (14)	965 (13)	309 (8)	1,099 (6)
Weighted usable area	9,132	4,257	1,667	11,752
	Juveniles			
Total surface area	41,223	7,632	3,639	19,781
Usable area	23,090 (56)	6,618 (87)	3,442 (95)	17,277 (87)
High quality	7,791 (19)	3,218 (42)	1,542 (42)	10,586 (54)
Medium quality	5,219 (13)	1,752 (23)	850 (23)	4,077 (21)
Low quality	10,080 (21)	1,648 (22)	1,050 (29)	2,614 (13)
Weighted usable area	12,699	4,487	2,223	13,413

categories showed that differences exist in the amount and quality of the habitat for YOY and juvenile white sturgeon among the four reaches. The John Day Pool generally has more habitat for YOY and juveniles than the other reaches, including the unimpounded lower river.

Discussion

Hydroelectric development has reduced the availability of habitat for spawning white sturgeon and has increased the area suitable for YOY and juvenile white sturgeon in the impounded reaches. The four dams in the study area transformed the river from free-flowing to a series of pools, which inundated several rapids and falls that probably provided conditions suitable for spawning white sturgeon. In the present study area the dam tailraces provided the only habitat that approximates pre-impoundment rapids. During years of reduced river runoff, the lack of high quality spawning habitat in the impounded reaches may preclude successful reproduction by white sturgeon. Recruitment to YOY in the three impounded areas was poor during 1987-1989, when river discharges were low, and improved with the increased discharges during 1990 and 1991 (Miller and Beckman 1992a). Model output predicted lower amounts of spawning habitat during 1987-1989 relative to that predicted during 1990 and 1991. Restoring the historic natural hydrograph during the white sturgeon spawning period would improve the reproductive success of the impounded populations. Spawning areas might also be improved by physically altering the river channels to increase water velocities at low discharges (Khoroshko and Vlasenko 1970).

Rearing habitat is probably under-used in the impounded river reaches, though we investigated the physical, not the biological, ability of the river to support rearing white sturgeon. Successive year-class failures and low numbers of recruits to YOY during years of successful spawning have resulted in fewer fish to occupy the available habitat in these reaches. Impoundment has increased water depths upstream from the dams, and YOY and juvenile white sturgeon use the deeper water; thus the physical rearing habitat has increased. Rearing white sturgeon feed primarily on benthic invertebrates obtained from the substrate and drifting in the currents (Muir et al. 1988; Schreiber 1962), but they can also capture and feed on young fish (Brannon et al. 1986). Densities of benthic invertebrates were higher in The Dalles Pool than densities in the unimpounded lower river reach (Parsley et al. 1989; McCabe et al. 1992), and mean length at age for younger fish (1-5 years) is greater in the impounded areas than in the unimpounded lower river (Miller and Beckman 1992b). These findings indicate that stocking or transplanting young fish into the impounded areas has potential for increasing the populations that have had poor reproductive success.

Bonneville Dam tailrace provides high quality habitat for spawning white sturgeon at discharges lower than those needed to provide even low to medium quality habitat in the other three tailraces. Tidal fluctuations in the Pacific Ocean affect water levels to Bonneville Dam and cause backwater effects that are similar to an impoundment. However, the hydraulic slope of the river in the Bonneville Dam tailrace is much greater than the hydraulic slope of the other tailraces, resulting in higher water velocities at low discharges.

The estimates of spawning and rearing habitat we derived were contingent on several factors: the criteria curves that defined habitat the functions used to obtain a composite suitability index, the area encompassed by transects, the accuracy of the hydraulic simulations (spawning habitat), and the accuracy of the base maps used in the GIS (rearing habitat). The criteria curves we used were developed from data collected within the study area, and represent the best information on habitat use by white sturgeon. The data depict habitat use under current environmental conditions caused by hydroelectric operations, not pre-development conditions, and the effects on the analysis are unknown. Curves detailing habitat use in free-flowing rivers are needed; however, little free-flowing habitat with viable white sturgeon populations remains in the Columbia River basin.

The function used to derive CS for each cell and life stage could affect calculated habitat areas. We used the lowest value of the three habitat descriptors (lowest limiting parameter) as the composite suitability index for spawning habitat because the area of suitable water depths and substrates within the known spawning areas of each river reach is not appreciably affected by varying river discharges, while water velocities are greatly affected. Calculation of spawning WUA with a multiplicative function slightly lowered the estimates of spawning habitat (U.S. Fish and Wildlife Service, unpublished data).

White sturgeon YOY and juveniles use a wide range of water depths velocities, and substrate types, and any one physical habitat variable is probably no more important than another for these life stages. Therefore, we used the geometric mean of the suitabilities for water depth and substrate to derive a CS for YOY and juvenile white sturgeon. Water velocities at different river discharges throughout the study area were not estimated and were assumed suitable for these life stages in all areas at all discharges. This assumption was reasonable, considering the velocities used by both life stages and the known physical characteristics of the river reaches in the study area. The criteria curves depicting the suitability of water velocities for YOY and juveniles indicate that mean column velocities of 0.0 m/s are used by both life stages, and the upper limit is near 2.0 m/s. Except for the relatively small areas immediately downstream from the dams, where water velocities may exceed 2.0 m/s, the entire study area has velocities within this range.

Our estimates of spawning habitat are only for the areas encompassed by the transects placed across the river in each dam tailrace. The computer programs within PHABSIM use channel shape, reach length, and changes in water depth associated with discharge to simulate habitat. We have under-estimated the amount of spawning habitat in the Bonneville Dam tailrace, as we were unable to estimate habitat in the three short channels downstream from the two powerhouses and the spill gates and the short channel downstream from where the discharges from the second powerhouse and the spill gates meet. These areas probably provide suitable spawning habitat with sufficient discharge.

The hydraulic simulation model used to predict water velocities is generally accepted as adequate for use on smaller rivers and streams, but to our knowledge has never been applied to a river as large as the Columbia. The model outputs obtained are within acceptable ranges, and in theory the model is suitable for use on rivers this size (Robert Milhous, U.S. Fish and Wildlife Service, personal communication).

The analysis of spawning habitat at various discharges was based on total river discharge. Most calibration velocities were measured when the total river discharge was through the turbines; changes in the combinations of spill gates and turbines used to pass the water through each dam probably alter the velocity distribution along the transects closest to the dams. Estimates of usable spawning area should not be affected greatly, but estimates of WUA for spawning may differ with different combinations of spill and turbine discharge.

Young-of-the-year and juvenile habitat was assessed directly from maps detailing water depths and substrates. Physical habitat for these life stages does not seem to be limiting, though the biological capacity of the habitat to support these life stages was not addressed. Young white sturgeon feed primarily on benthic invertebrates, and the physical environment must produce an ample food source, either from secondary production or from allochthonous items.

Our estimates of rearing habitat are satisfactory for comparative purposes when the size of the study area is considered. We used the best available maps, but recent changes due to dredging, filling, and sediment deposition were not included. The maps also depict water depths at fixed river elevations. Water elevations fluctuate markedly in the upper end of the lower river reach, and the amount of habitat available for YOY and juvenile white sturgeon changes as river elevations rise and fall, but the areas are small compared with the total area of the lower river reach.

White sturgeon evolved in the Columbia River basin, which historically had a hydrograph characterized by discharges that were higher during summer and lower during winter relative to the hydrographs of recent years. Development of the water resources of the basin has not only altered the hydrograph, but has also lowered the hydraulic slope of vast river reaches. Both actions have reduced water velocities throughout much of the study area during the white sturgeon spawning period, resulting in poor recruitment in the impounded areas during years of low river discharge. This analysis revealed the importance of river discharge to white sturgeon spawning habitat, particularly in the impounded reaches upstream from Bonneville Dam. It also revealed that abundant rearing habitat exists in the impoundments. If recruitment can be bolstered, or the populations supplemented with young fish, the white sturgeon fishery in the lower 470 km of the Columbia River should continue and possibly improve.

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