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Dynamics and Potential Production of White Sturgeon in the Unimpounded Lower Columbia River

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Abstract.—The unimpounded lower Columbia River downstream from Bonneville Dam (LCR) supports the greatest abundance and density of white sturgeon *Acipenser transmontanus* reported in the species' range. The high productivity of the population resulted from growth that was as good as or better than reported for other populations, the highest mean relative weight reported for any white sturgeon population, and a relatively low median age (24 years) of first maturity for females (95% of females matured between 16 and 35 years of age). Estimated instantaneous natural mortality was 10%. During 1986–1990, the estimated instantaneous fishing mortality for age-12–17 fish averaged 36% in LCR fisheries. Over the same period, the average annual abundance estimate of LCR white sturgeon 54 cm fork length (FL) or longer was 895,500 fish, and the average density was 14.6 fish per ha. Population simulations, under the assumption of constant recruitment, predicted a maximum sustainable yield (MSY) of 3.0 kg/recruit at an 18% exploitation rate (of the 82–166-cm FL population). Reproductive potential was 93,400 eggs/recruit for an unexploited population and 4,800 eggs/recruit at the predicted MSY exploitation rate. The 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 period.

The unimpounded lower reach of the Columbia River, which extends from Bonneville Dam to the sea, supports one of the most productive sturgeon fisheries in North America and perhaps the world. The annual harvest of white sturgeon *Acipenser transmontanus* in this reach has averaged 36,800 fish in the recreational fishery and 9,200 fish in the commercial fishery during the past 10 years (WDF and ODFW 1992), and the average yield of white sturgeon in the combined fisheries during the past 10 years has been approximately 350,000 kg annually. In terms of effort, the white sturgeon fishery ranks as the largest recreational fishery in the Columbia basin, with a 10-year annual average of 145,000 angler trips (Melcher and King 1991).

The longevity, slow growth, and delayed maturation of sturgeons make them susceptible to overexploitation (Rieman and Beamesderfer 1990; Rochard et al. 1990; Smith 1990; Birstein 1993). Excessive harvest in the 19th century brought about the collapse of the Columbia River white sturgeon stock. Intensive white sturgeon fishing on the Columbia River began in 1889 and peaked in 1892, when about 2,500,000 kg of white sturgeon were landed. The stock was depleted by 1899, after 10 years of unregulated exploitation (Craig and Hacker 1940; Figure 1). Subsequent restrictions on season, gear, and minimum size failed to bring about an increase in white sturgeon production, as evidenced by poor yields during the first half of this century. Only after a maximum-size regulation designed to protect sexually mature white sturgeons was enacted in 1950 did the population rebound. Annual harvests doubled by the 1970s and doubled again by the 1980s. However, current harvest restrictions may not be adequate to protect stocks from overexploitation.

Sturgeons have been severely affected by hydroelectric development and operation that has drastically altered the large river systems they inhabit. Many species of sturgeons and paddlefishes are now endangered, threatened, or extinct, largely because their habitats were destroyed (Rochard et al. 1990; Birstein 1993). Hydroelectric development of the Columbia River main stem since 1933 may have reduced the productivity of white sturgeon (Fickeisen 1985; Beamesderfer et al. 1995, this issue). Preimpoundment conditions can now be found only in the 234-km free-flowing reach downstream from Bonneville Dam. We believe the larger yields in lower Columbia River white sturgeon fisheries are evidence of a relatively high population productivity that is linked to the unaltered habitat in this reach of the Columbia River.

Productive populations and high-yield fisheries for white sturgeon can only be sustained through scientific management that is based on a thorough understanding of population dynamics and limit-

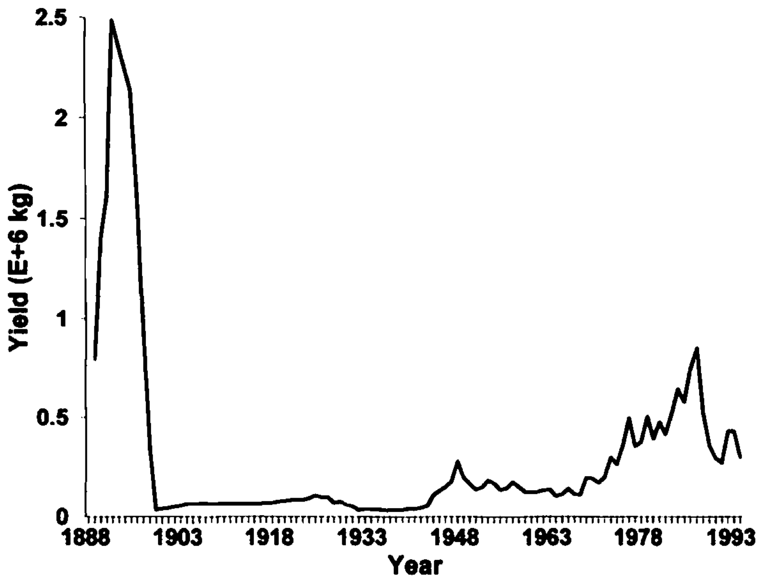

FIGURE 1.—Annual yields (millions of kilograms) of white sturgeon in the lower Columbia River, 1888–1991.

ing factors. In this paper, we examine the characteristics of the white sturgeon population in the free-flowing river between Bonneville Dam and the Pacific Ocean (Figure 2). We use this information to estimate maximum sustainable yield (MSY) and exploitation rate. Comparisons of populations in the free-flowing lowest reach of the river and in upstream impoundments may help identify factors limiting production. Beamesderfer et al. (1995) have made such comparisons.

In this paper, we analyze the population characteristics of white sturgeon between Bonneville Dam and the sea. The term "lower Columbia River" generally refers to the stretch from the Snake River confluence to the Columbia River mouth. This stretch now has four impoundments—proceeding downstream, McNary, John Day, The Dalles, and Bonneville—as well as the final unimpounded reach. In our report, for simplicity, "LCR" means the reach of the lower Columbia River below Bonneville Dam.

Methods

Data collection.—Length intervals chosen for the following analyses were predicated on size slot intervals used in the management of LCR recreational and commercial fisheries. Management size limits, which were expressed as total length (TL) in inches, were converted to fork length (FL) in centimeters for analyses. Fork length was the preferred length measurement because it produced less variation in length assignments than total length. However, because total lengths were sometimes the only length measurement available, they were converted into fork lengths with the formula, $TL = 1.09 \cdot FL + 2.06$ ($N = 2{,}039$, $r^2 = 0.997$). Throughout the course of the study a maximum size limit of 166 cm FL was in place for all LCR white sturgeon fisheries. The recreational fishery was managed with a minimum size limit of 82 cm FL until April 1989, when the minimum size limit was increased to 92 cm FL to reduce harvest. The commercial minimum size limit remained at 110 cm FL throughout the course of this study.

Mark–recapture data were obtained from April–June Pacific salmon *Oncorhynchus* spp. and white sturgeon research fisheries conducted by the Washington Department of Fisheries (WDF) and the Oregon Department of Fish and Wildlife (ODFW) during 1983–1991 (Figure 2). White sturgeons 62 cm FL or longer were captured and tagged with sequentially numbered spaghetti tags, which were inserted at the base of the dorsal fin. All captured fish were checked for marks and measured for FL and TL. When possible, information on sex, stage of maturity, and age were collected. Commercial and recreational fisheries were sampled for recapture and biological data.

Age, growth, and condition.—White sturgeons were aged by counting periodic rings on cross sections of the anterior pectoral fin ray (Rien and Beamesderfer 1994; Tracy and Wall 1993). Samples were obtained from consumptive and research

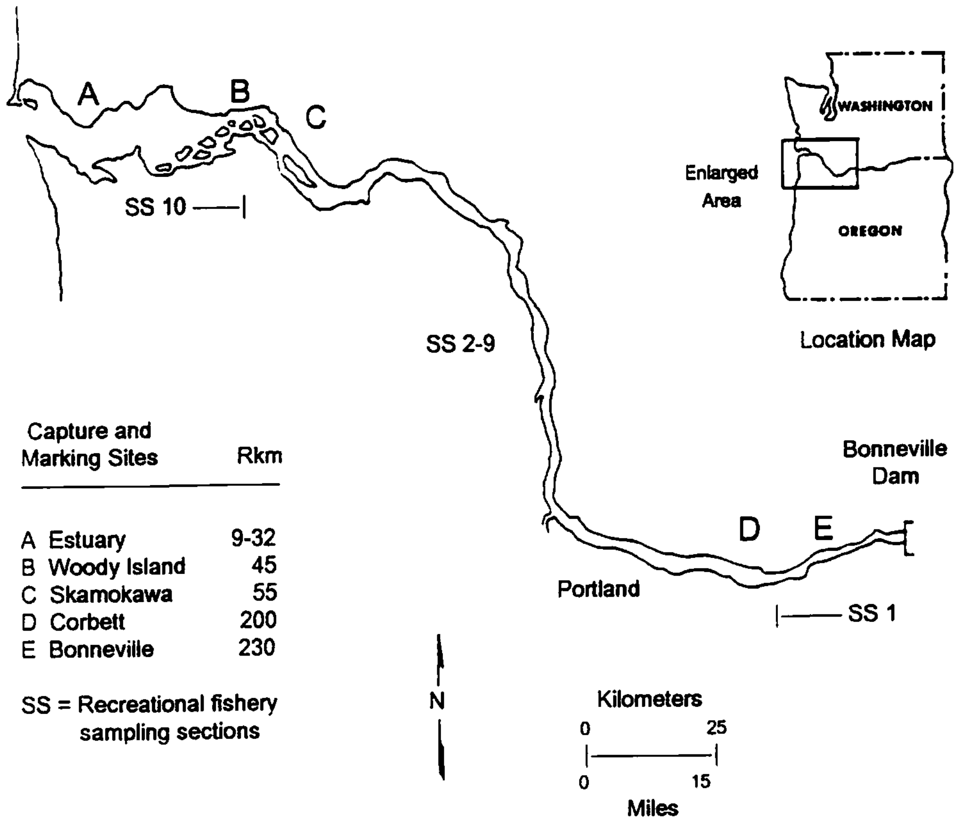

FIGURE 2.—The unimpounded lower Columbia River with locations where white sturgeons were captured and marked, 1985–1991.

fisheries during 1987–1992. Aging techniques were validated by oxytetracycline (OTC) marking (Leaman and Nagtegaal 1987; Tracy and Wall 1993; Rien and Beamesderfer 1994). Recoveries of OTC-injected fish indicated that one annulus was deposited each year and that techniques used to age LCR white sturgeons were valid (Tracy and Wall 1993).

Length measurements were made for each fish that had a fin ray sample removed. Length-at-age relationships for white sturgeon were quantified by fitting data for length (cm FL) and age (years) to a von Bertalanffy growth equation.

Length and weight (kg) measurements were taken during sampling of research, commercial, and recreational fisheries, and from natural mortalities. Data were fitted to an exponential function by using nonlinear least-squares regression. Relative condition was determined by estimating mean relative weight (W_s based on the standard weight determined for white sturgeon: W_s = 2.735 E − 6·FL$^{3.232}$ (Beamesderfer 1993). This analysis was restricted to fish measuring 54 cm FL or more to minimize effects of errors in weighing small fish and of developmental changes in body form from juveniles to adults (Beamesderfer 1993).

Reproductive potential.—White sturgeons sampled in the commercial harvest (110–166 cm FL) were measured to the nearest centimeter FL and sexed by visual examination of gonads. White sturgeons longer than 166 cm FL that were examined during broodstock monitoring activities were sexed by first trying to express sperm from ripe males. Females and males that were 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 multiplying egg density by ovary weight. Egg density was determined by counting ova in a weighed subsample of ovarian tissue. Subsample and most whole ovary weights were measured to the nearest 0.01 g prior to preservation in formalin. A fecundity–FL relationship was developed by fitting the data to an allometric equation. Sex ratios were determined for two size-classes (110–166 cm FL and >166 cm FL).

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 with a micrometer and dissecting microscope. Mean egg diameter was calculated from measurements of 10 eggs. Maturity samples were stratified into the following stages: previtellogenic (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 diameter), ripe (eggs fully pigmented and detached from ovarian tissue, ≥3.0 mm diameter), and spent (gonads flaccid with some residual fully pigmented eggs). Degenerative oocytes were noted when disintegrating black eggs encompassed the majority of the gonad. Occasionally, samples exhibited a stage of maturity that was intermediate relative to the listed criteria. Staging the maturity of these samples was subjective.

Ovarian maturity was classified into three general categories to generate the length-at-maturity data set: immature–resting (all previtellogenic 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 2 years or more 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 with a maximum-likelihood estimation procedure that used a cumulative normal probability curve as a functional model of the maturation process (Welch and Beamesderfer 1993).

Exploitation and mortality.—Annual size-specific exploitation rates (u) for LCR white sturgeon fisheries were calculated as the ratio of marked fish harvested to marked fish at large (Ricker 1975). Instantaneous exploitation rates (F) were calculated with $F = Zu/A$ (Ricker 1975), Z being instantaneous total mortality and A being annual mortality.

Groups of tagged fish were released each year between April and June. Marked fish recovered within 1 year of release were expanded by the fishery sample rate to estimate total harvest of marked fish. Recreational fishery sample rates were estimated by applying the number of fish seen during random fishery sampling (in-sample) to annual harvest estimates (Melcher and King 1991). Recreational harvest of marked fish was calculated for recreational fishery sampling sections 1, 2–9, and 10 (Figure 2). Commercial fishery sample rates were estimated by applying the number of fish randomly sampled at various LCR landing sites and fish buying stations to annual commercial harvest recorded on Washington and Oregon commercial fish-receiving tickets. Estimates of the commercial harvest of marked fish were calculated for all river sections and stratified by season. Recoveries of marked fish in recreational fisheries were expanded by a cumulative tag retention rate to correct for tag loss (DeVore et al. 1993). Recoveries of marked fish in the commercial fishery were corrected for tag loss by expanding observed tag scars by the sample rate. Tag scars were proportioned to all tag groups (tag application year) observed in the fishery.

Recoveries of marked fish obtained primarily from random fishery sampling were used in estimating LCR exploitation; voluntary recoveries were used when no in-sample recoveries of a tag group 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 harvest of marked fish for all tag groups in each area. Exploitation in LCR tributaries and areas outside the LCR was estimated with voluntary mark–recovery information. Non-LCR tag recoveries were expanded by voluntary reporting rates calculated for LCR fisheries.

Mortality was estimated from a catch curve derived from an age frequency distribution of research fishery catches (Ricker 1975). The catches 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 with mark–recapture data collected from 1983–1991 research fisheries that used nets with similar specifications. Vulnerability correction factors were estimated with the ratio of recaptures to marked fish at large by 10-

cm FL intervals (Hamley 1975; Lagler 1978; Beamesderfer and Rieman 1988). Only recaptures within 3 months of marking were used to reduce growth-related bias. Vulnerability curves describing the relationship between recapture rate and fork length were fit with nonlinear least-squares regression (SAS Institute 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 by using pooled age-at-length data collected during 1987–1992.

Estimates of instantaneous total mortality rate (Z) were made from the slopes of the descending limb of the log-transformed catch curve (Ricker 1975). These estimates correspond to age-12–17 fish, representing age-classes recruited to the recreational fishery during 1986–1991 (the period during which exploitation was measured) and age-23–29 fish, representing age-classes that had escaped exploitation. Total mortality of age-18–22 fish was not calculated because these age-classes were subject to most of their exploitation prior to 1986. Confidence limits (95%) about Z were calculated from the regression as ± 2 SE.

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).

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

Recruitment to harvestable size was accounted for by including recaptures of marked fish less than 82 cm FL in 1987 and 1988, and fish less than 92 cm FL in 1989 and 1990. We assumed that marked and unmarked fish recruited at the same rate and that any differential survival was minor. Separate abundance estimates for two length intervals (82–91 cm FL and 92–166 cm FL) were calculated to account for the increase in the minimum allowable length in recreational fisheries from 82 cm FL to 92 cm FL in 1989. Confidence limits (95%) were calculated under the assumption that recaptures approximated a Poisson distribution (Ricker 1975).

Abundances of white sturgeons longer than 54 cm FL but shorter than 82 cm FL in 1987 and 1988, and shorter than 92 cm FL in 1989 and 1990 were estimated by extrapolating mark–recapture estimates by using length frequency distributions of annual research fishery catches corrected for gear vulnerability. Annual abundance estimates of white sturgeons longer than 166 cm FL were made by expanding the number of fish longer than 166 cm FL handled in the recreational fishery each year (Melcher and King 1991) by the estimated exploitation rate of fish 110–166 cm FL. Although multiple handling of individual white sturgeons longer than 166 cm FL in the recreational fishery could lead to overestimates of abundance, this was somewhat offset by a decreased catchability of the larger mature fish. We were uncertain how this methodology biased abundance estimates of fish longer than 166 cm FL.

Annual abundance estimates were made for white sturgeons at age 10 and age 25 with age-at-length data. Mean annual abundance of age-1 fish was estimated by back-calculating age-10 abundance with estimated instantaneous natural mortality rate. Population density was estimated from abundance and surface area estimates for the LCR (Parsley and Beckman 1993).

The effect of applying a closed population estimator to an open population was evaluated by simulating monthly changes in population parameters when migration was varied over a 9-month period. Immigration and emigration values of 10% and 30% of initial in-river abundance (at the start of the recovery period) were used. The number marked, number captured, and number recaptured were from 1990 data and held constant for all migration scenarios. Initial abundance, proportion marked, sample rate, and migration timing were varied. Sensitivity of the estimator to all migration occurring in the first 3 months of the 9-month recapture period was evaluated in relation to scenarios in which the migration was spread out throughout the recapture period. We considered the estimator satisfactory for scenarios that resulted in estimates between initial abundance and initial abundance plus immigration.

Productivity.—The production potential of the population was described by 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 for fish 82–166 cm FL. Constant recruitment to age 1 was assumed.

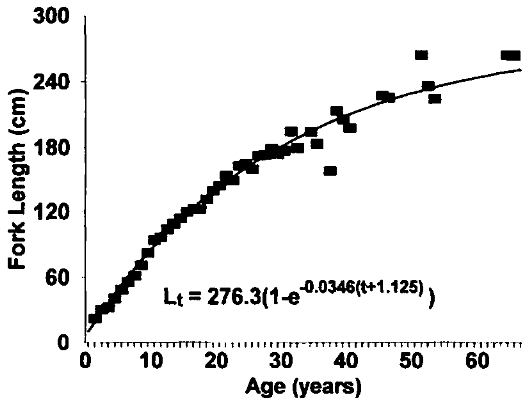

FIGURE 3.—Mean length at age and von Bertalanffy growth curve for white sturgeons in the unimpounded lower Columbia River.

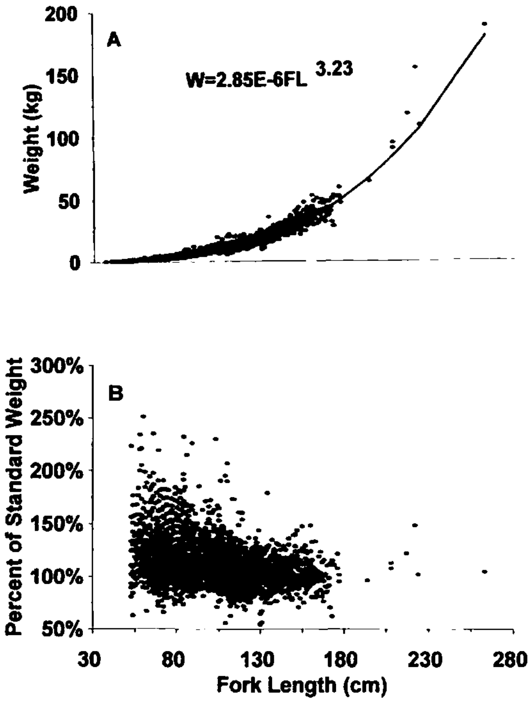

FIGURE 4.—(A) Weight at length relationship and (B) relative weights of white sturgeons in the unimpounded lower Columbia River.

Results

Age, Growth, and Condition

Ages were assigned to 783 fish that ranged 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 von Bertalanffy growth equation: $L_t = 276.3[1 - e^{-0.0346(t+1.125)}]$ (Figure 3), L being fork length in centimeters and t being age in years.

Paired length and weight measurements were obtained from 5,222 LCR white sturgeons that ranged in length from 54 to 263 cm FL and in weight from 0.7 to 187.8 kg (Figure 4A). Relative weight for LCR white sturgeon averaged 112% (Figure 4B).

Sex and Maturity

The sex ratio for the 110–166-cm FL size-class was 44.7% female to 55.3% male (N = 5,729). Fish longer than 166 cm FL had a sex ratio of 46.5% female to 53.5% male (N = 71). Fork lengths in the fecundity–FL relationship ranged from 115 to 215 cm, and estimated fecundities ranged from 98,200 to 699,000 eggs (N = 38, r^2 = 0.59; Figure 5).

In all, 1,271 ovaries were examined for stage of maturity; 1,174 (92%) were categorized as previtellogenic, 58 (5%) as early vitellogenic, 15 (1%) as late vitellogenic, 22 (2%) as ripe or spent, and 2 (<1%) as unknown. Early and late vitellogenic females were collected throughout the year. This is consistent with a maturation cycle longer than 1 year (Chapman 1989; Kroll 1990; Doroshov et al. 1991; North et al. 1993). Mature females were present prior to and during the spawning period and rare at other times. Mature females provided 54% of vitellogenic ovary samples collected in February–June, but only 2% in August–November. The lack of maturation data for January, April, July, and December reflects the absence of commercial fisheries or broodstock monitoring activities during these months.

The median length at first maturity was 160 cm

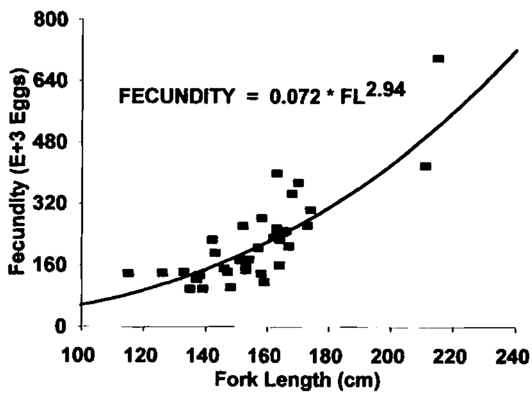

FIGURE 5.—Fecundity (thousands of eggs) of female white sturgeons in relation to fork length in the unimpounded lower Columbia River.

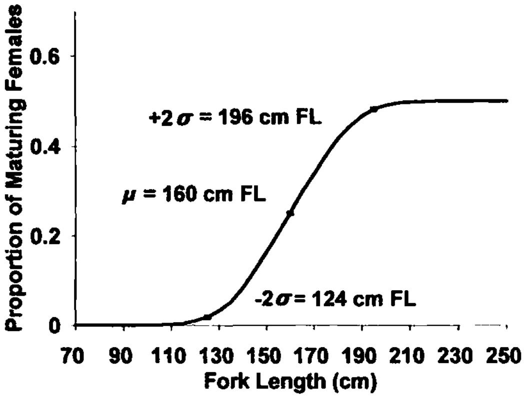

FIGURE 6.—Maturity of female white sturgeons in relation to fork length in the unimpounded lower Columbia River. Maturity was calculated with equations of Welch and Beamesderfer (1993); μ is the median length at maturity and σ is the standard deviation.

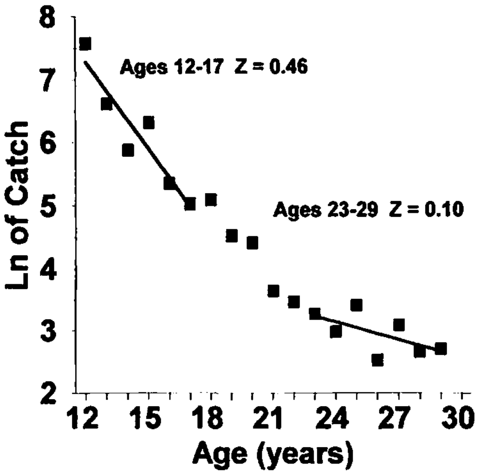

FIGURE 7.—Catch curve for white sturgeons captured during research gill-net fisheries on the unimpounded lower Columbia River (ln = $\log_e$).

FL (μ); 95% of the females matured between 124 and 196 cm FL (±2σ) (Figure 6; Welsh and Beamesderfer 1993). These lengths correspond to ages 24, 16, and 35 years, respectively. The maximum proportion of maturing females was 0.50, corresponding to lengths of 230 cm FL and longer (Figure 6).

Exploitation and Mortality

Estimated exploitation rates (u) in Columbia River fisheries were highest for fish 110–138 cm FL, which were vulnerable to both the recreational and commercial fisheries (Table 1). The geometric mean of estimated exploitation of cohorts used in the catch curve analysis was 0.29. Exploitation of marked fish outside the LCR ranged from less than 1% to 2%. These estimates were based on voluntary recaptures of marked fish expanded by reporting rates of 22% and 43% for LCR commercial and recreational fisheries, respectively.

Total instantaneous mortality rate (Z) estimates derived from the 1990–1991 catch curve were 0.46 for fish 94–123 cm FL (ages 12–17) and 0.10 for fish 152–175 cm FL (ages 23–29) (Figure 7; Table 2). Instantaneous and conditional natural mortality estimates (M and n) were 0.10 and 0.09, respectively, for fish 94–123 cm FL and 0.10 and 0.09, respectively, for fish 152–175 cm FL (Table 2).

Abundance

Average annual abundance of white sturgeons 54 cm FL and longer in 1986–1990 was 895,500 fish and ranged from 678,000 to 1,058,300 fish (Table 3). There was a decline in the abundance of the exploited size-classes (92–166 cm FL) between 1986 and 1990, which was consistent with the high estimated exploitation (Tables 1, 3). A significant increase in the abundance of white sturgeons in the 82–91 cm size-class in 1990 was primarily caused by a change in management regulations that raised the minimum allowable size lim-

TABLE 1.—Estimated exploitation of marked white sturgeon from the Columbia River downstream from Bonneville Dam, 1986–1991. Periods and length intervals correspond to time and length intervals used in calculating total mortality.

Period[a]	Fork length interval	Number of marked fish	Number of marked fish harvested		Exploitation
			Observed	Expanded[b]	
1986–1987	82–110 cm	2,099	146	614	0.29
1987–1988	82–110 cm	1,834	130	487	0.27
1988–1989	82–138 cm	1,280	54	243	0.19
1989–1990	110–138 cm	165	11	61	0.37
1990–1991	110–138 cm	105	7	40	0.38
1986–1991 geometric mean					0.29

[a] The 12-month period following capture and marking, which occurred from April to June of each year.
[b] Observed marked fish harvest expanded for fishery subsampling and harvest outside the Columbia River and corrected for tag loss.

TABLE 2.—Mortality estimates for white sturgeons sampled from the Columbia River downstream from Bonneville Dam.

Parameter	Age-group 12–17	Age-group 23–29
Instantaneous total mortality (Z)	0.46	0.10
Instantaneous fishing mortality (F)	0.36	
Instantaneous natural mortality (M)	0.10	0.10
Conditional natural mortality (n)	0.09	0.09

it by 10 cm in 1989. Abundance of oversized white sturgeons (>166 cm FL) ranged between 6,900 and 10,900 (Table 3). The estimated mean annual abundance of age-1 fish was 399,500, abundance of age-10 fish ranged from 124,800 to 189,000, and abundance of age-25 fish ranged between 600 and 1,000 (Table 3). The average numerical density of white sturgeons 54 cm FL and longer in the LCR was 14.6 fish/ha (range, 11.1–17.3 fish/ha; Table 3). The average biomass of the population 54 cm FL and longer during the study was 5.3 million kilograms, and the average weight density was 87.5 kg/ha.

Sensitivity analyses indicated that the recapture sampling strategy, as well as the magnitude and timing of immigration and emigration, influenced the accuracy of the modified Petersen estimator. The estimator was satisfactory (i.e., estimates were within the range between initial abundance and initial abundance plus immigration) for low-migration scenarios (10% of the population immigrated or emigrated) and for high-migration scenarios (30% of the population migrated) when the migration was spread over the 9-month recapture period (Table 4). There was a slight bias—the estimator overestimated initial abundance plus immigration—for high-migration scenarios in which all the migration occurred in the first 3 months of the recapture period. The estimator generally predicted the combined population (initial abundance plus immigration) better than initial abundance. Estimates, with all migration scenarios modeled, were within ±9% of the combined population.

Productivity

Under an assumption of constant recruitment, population simulation predicted an MSY at 3.0 kg per recruit with an exploitation rate of 0.18 for the 82–166-cm FL population (Figure 8). Estimated sustainable annual yield, based on the number of age-1 recruits, was 1,198,400 kg (19.6 kg/ha). Egg production per recruit was 93,400 for an unexploited population and decreased exponentially to 4,800 at MSY exploitation (Figure 8).

Discussion

The LCR supports the greatest number and density of white sturgeons among the species' three identified production areas (Sacramento–San Joaquin, Columbia, and Fraser basins). Kohlhorst (1980) estimated the Sacramento–San Joaquin estuary population (≥92 cm FL) to be 40,000 fish in 1968 and 74,500 fish in 1979; more recent estimates are 128,300 fish in 1984, 96,200 in 1985, and 84,000 in 1987 (Kohlhorst et al. 1991). The 1986–1990 average abundance for the same size-classes of LCR white sturgeon was 123,200 fish. Estimated

TABLE 3.—Abundance estimates 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; CL = 95% confidence limits.

Category	Abundance in: 1986	1987	1988	1989	1990
Fork length (cm)					
54–81	755,200	788,300	740,500	496,200	593,500
82–91	66,400	115,500	95,600	84,900	125,500
CL (lower)	48,700	82,000	65,600		
CL (upper)	99,300	183,200	161,600		
92–166	148,100	146,300	111,100	90,000	77,900
CL (lower)	110,500	111,700	74,900	66,800	59,400
CL (upper)	215,300	205,000	192,800	132,500	109,400
>166	7,600	8,200	8,900	6,900	10,900
Total (≥54 cm)	977,300	1,058,300	956,100	678,000	807,800
Per hectare (≥54 cm)	16.0	17.3	15.6	11.1	13.2
Age (years)					
10	188,900	189,000	160,700	124,800	161,300
25	600	1,000	900	600	700

TABLE 4.—Sensitivity analysis of the Petersen abundance estimator to various rates of immigration and emigration (migration) during the 9-month recapture period.

Parameter	10% migration		30% migration	
	3 months	9 months	3 months	9 months
Number marked	913	913	913	913
Marked emigrants	91	91	274	274
Number examined				
Initial population	3,493	3,615	2,824	3,176
Immigrants	343	221	1,012	660
Combined	3,836	3,836	3,836	3,836
Recaptures	44	44	44	44
Population abundance				
Initial population	72,450	74,980	58,570	65,870
Immigrants	7,245	7,498	17,571	19,761
Combined population	79,695	82,478	76,141	85,631
Chapman estimate	77,900	77,900	77,900	77,900
Bias compared to:				
Initial population	0.08	0.04	0.33	0.18
Combined population	−0.02	−0.06	0.02	−0.09

abundance of Columbia basin populations upstream from Bonneville Dam were also lower than LCR estimates (Cochnauer 1983; Cochnauer et al. 1985; J. R. Lukens, Idaho Department of Fish and Game, unpublished) and ranged from 870 fish in the Kootenai system (K. Apperson and P. J. Anders, Idaho Department of Fish and Game, unpublished) to 51,400 fish (≥70 cm FL) in Bonneville Reservoir (Beamesderfer et al. 1995). There are no reported estimates of white sturgeon abundance or density in the Fraser basin. However, annual harvest and catch rate estimates of Fraser River white sturgeon (Semakula and Larkin 1968; Parks 1978) indicate that abundance and density may be substantially lower than for the LCR population. It is not clear if this difference is the result of overexploitation or relative production potential.

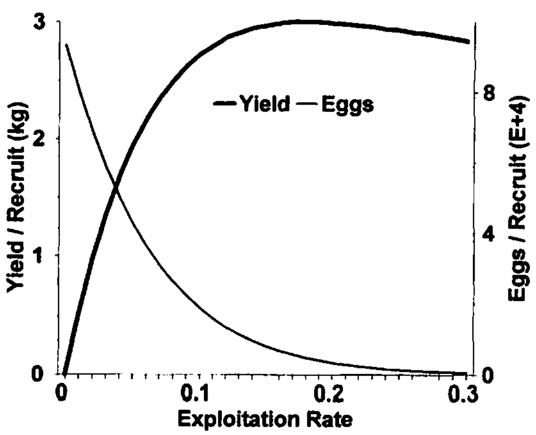

FIGURE 8.—Simulated yield and reproduction (10^4 eggs) per recruit in relation to exploitation rate under an 82–166-cm fork length size slot regulation for the white sturgeon population in the unimpounded lower Columbia River.

White sturgeons in the LCR appear to grow better than other populations. Tracy and Wall (1993) reported higher average length at age for the LCR population compared with populations from Bonneville Reservoir (Malm 1981), the Snake River (Coon et al. 1977; Lukens, unpublished), and the Fraser River (Semakula 1963). A comparison of von Bertalanffy growth equations for Sacramento River and LCR populations indicates that LCR white sturgeons grew slower at young ages but attained a larger ultimate length (Tracy and Wall 1993). Mean relative weights are higher for LCR white sturgeons than for any other white sturgeon population reported (Beamesderfer 1993). The superior growth rate and condition of LCR white sturgeons are probably a result of the abundant food resources associated with marine-based prey species. White sturgeons in the LCR make seasonal migrations to feed on eulachon *Thaleichthys pacificus*, northern anchovy *Engraulis mordax*, American shad *Alosa sapidissima*, moribund salmonids *Oncorhynchus* spp., amphipods *Corophium* spp., and other invertebrates (Bajkov 1951; DeVore and Grimes 1993; McCabe et al., 1993). The biomass of prey species is high and seasonally well distributed. Therefore, LCR white sturgeons can subsist on alternative resources in the event of declines in the usual prey species.

A problem in this study, as in most sturgeon studies, was the lack of samples of large fish. The LCR population, which is managed with a size slot limit, had proportionally more older and larger fish than most populations. Parameter estimation for large fish was difficult without an adequate number of samples from those age-classes. Age composition and mark–recovery data, obtained from recreational and commercial fisheries, underrepresented large fish because of the maximum size limits. White sturgeons captured in the Bonneville broodstock monitoring program provided valuable aging and maturity samples. However, the broodstock capture strategy targeted large, mature fish during the spawning season and was probably not representative of the entire large fish population. Representative sampling of the white sturgeon population over 166 cm FL would have resulted in more accurate estimates of age, growth, and reproductive potential.

Abundance of open-system populations is typically estimated with a multiple mark–recapture estimator such as the Jolly–Seber model (Ricker 1975) or other maximum-likelihood estimation procedures (White et al. 1982). These estimation methods require multiple sample periods of equal interval and a relatively large number of recaptures to minimize variance. We restricted our recapture period to 9 months because excessive tag shedding (up to 71% after 48 months; DeVore et al. 1993) precluded a multiple-year analysis. The relatively low number of recaptures per sampling period also influenced our choice of the modified Petersen estimator.

The standard Petersen abundance estimator, incorporating a single instantaneous recapture event, overestimates abundance of populations open to both immigration and emigration (Robson and Regier 1968). However, our sensitivity analysis of the modified Petersen estimator, which incorporated continuous recapture sampling, resulted in estimates between initial abundance (in-river abundance at the start of the recapture period) and initial abundance plus immigration when migration extended beyond the first 3 months of the recapture period. Our tagging studies indicate that migration does occur throughout the year and is not confined to the first 3 months of our recapture period (DeVore and Grimes 1993).

Estimation bias due to violation of the closed-system assumption in the Petersen model would also be minimized if the fraction of the entire population using the ocean was small. Beamesderfer et al. (1995) theorize that the rapid stock depletion due to overfishing at the end of the 19th century would not have been possible if a significant portion of the population used the ocean as refuge. Migration studies suggest that only a small portion of the LCR white sturgeon population resides in marine areas for a significant period (DeVore and Grimes 1993). Therefore, we conclude that the modified Petersen estimator was fairly robust in the face of small violations of the closure assumption and that we overestimated initial abundance but underestimated the annual abundance of fish that use the LCR.

Population simulation indicated that the LCR population can withstand high exploitation relative to other sturgeon populations (MSY at 18% annual exploitation of the 82–166 cm FL population) if recruitment is unaffected by parental stock size. Rieman and Beamesderfer (1990) stated that, in an unaltered environment, white sturgeon recruitment may be independent of parental stock at high abundance. However, the recovery of the population after broodstock were protected with a maximum-size limit demonstrates a relationship between stock size and recruitment. The uncertainty of the degree of dependence of recruitment on parental stock indicates that current assumptions regarding sustainable yield may be optimistic.

Managers should be aware that, although LCR white sturgeon may be able to withstand relatively high harvest rates compared with other white sturgeon populations, there is a danger of overexploitation that might lead to a decline in productivity. Throughout their range, sturgeon species have a common history of decline or depletion caused by overexploitation and habitat changes (Rochard et al. 1990). Optimal sustainable yields (OSY) can only be achieved for the LCR population under conservative management schemes. The effects of recent harvest rates above OSY and hydroelectric development of the Columbia basin will not become fully evident for 20 or more years, as declining recruitment to broodstock reduces production.

Hydroelectric development has affected Columbia River white sturgeon production by altering the river's natural hydrograph and reducing spring flows in order to benefit power production (Beamesderfer et al. 1995). Kohlhorst et al. (1991) correlated low spring flows in the Sacramento–San Joaquin basin with low recruitment. Parsley and Beckman (1993) demonstrated that hydroelectric development reduced the amount of suitable spawning habitat downstream from Bonneville Dam, although more suitable habitat exists in the Bonneville Dam tailrace at lower discharges than in upstream spawning areas.

The LCR supports the most productive population of white sturgeon reported in the species' range. Access to marine environments, abundant food resources, and annual spring flows suitable for spawning are primarily responsible for this high productivity. Despite the great production potential of this population, history has taught us that this population is vulnerable to collapse from overexploitation. Therefore, our challenge is to manage the population for long-term sustainable exploitation and protect critical habitats needed to maintain high productivity.

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