

The Elusive Minimum Viable Population Size for White Sturgeon

HENRIETTE I. JAGER*

Environmental Sciences Division, Oak Ridge National Laboratory, Post Office Box 2008, Oak Ridge, Tennessee 37831-6036, USA

KEN B. LEPLA

Environmental Affairs, Idaho Power Company, Boise, Idaho 83702, USA

WEBB VAN WINKLE

Van Winkle Environmental Consulting, Boise, Idaho 83714, USA

BRAD W. JAMES

Washington Department of Fish and Wildlife, 2108 Grand Boulevard, Vancouver, Washington 98661, USA

STEVEN O. MCADAM

British Columbia Ministry of Environment, 2202 Main Mall, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

Abstract.—Daming of large rivers in the U.S. Pacific Northwest and Canada has divided the historical population of white sturgeon *Acipenser transmontanus* into more than 36 fragmented populations, few of which are thriving. We now face the challenge of managing these populations to avoid extirpation. Two goals of this study were to identify extinction thresholds related to small size and inadequate habitat for this species. The minimum viable population size (MVP) is the threshold size above which populations support recruitment and grow and below which populations fail to support recruitment and decline. We estimated a single, cross-population MVP using data from multiple populations and quantile regression, which removed the effects of factors other than population size. Only two populations (those in the Bonneville and Dalles reservoirs on the Columbia River), both with significant increasing trends, were larger than our MVP estimate. We detected significant decreasing trends in two populations—those below Bonneville Dam and in the Kootenai River. To discover how site-specific differences in river habitat influence MVP, we used a population viability analysis (PVA) model that incorporated Allee mechanisms. The PVA model identified a river segment length below which extinction was certain regardless of initial population size. Above this threshold, simulated populations in river segments that were longer or that provided more frequent recruitment opportunities were able to persist with smaller initial sizes. Two priorities emerged for white sturgeon: monitoring age structure and understanding the circumstances preventing recruitment to age 1. Our results ultimately guided us toward thresholds in rearing habitat and age structure that promise to develop into more useful conservation tools than MVP for this and similar long-lived species.

The minimum viable population size (MVP) has been a “holy grail” for conservation biologists seeking to determine when habitat fragmentation has caused irrevocable harm. Because fragmentation of large rivers has created smaller isolated populations of sturgeon, the existence of a threshold size has been a concern for these species. Retrospective studies of actual extinctions suggest that MVP thresholds do actually exist for other vertebrate populations (e.g., Brook et al. 2006; Fagan and Holmes 2006).

Gilpin and Soulé (1987) envisioned declining

populations, upon reaching the MVP, falling into an “extinction vortex” created by positive feedbacks among forces leading toward extinction. These forces, collectively known as Allee effects (Allee 1938), include both deterministic and stochastic factors that cause population growth rates to decrease at small sizes (Dennis 2002; Courchamp et al. 2008). However, only deterministic, strong Allee effects produce a distinct threshold MVP below which populations decline, and above which they increase (Berec et al. 2006). Weak Allee effects slow the growth of smaller populations, but they do not create an extinction threshold (Lande 1998; Courchamp et al. 2008). Demographic stochasticity (individual variation in births, deaths, and mating opportunities), which is higher in small populations, is

* Corresponding author: jagerhi@ornl.gov

Received April 10, 2009; accepted May 3, 2010
Published online September 29, 2010

a weak Allee effect. Environmental stochasticity (temporal variation in vital rates) causes populations to fluctuate, which is particularly dangerous for small populations near the brink of an extinction vortex. In practice, the effects of demographic stochasticity and environmental stochasticity are difficult to distinguish (Kendall 1998; Fagan et al. 1999; Gregory et al. 2010), except in laboratory populations (e.g., *Tribolium* beetles, Melbourne and Hastings 2008).

The idea that a single threshold MVP exists clearly distinguishes viable from unviable populations naturally evokes skepticism. Part of this skepticism comes from distrust of population viability analysis (PVA) models typically used to estimate an MVP. Caughley (1994) suggested that the MVP is “a slippery notion” and that models used for PVA “are essentially games played with guesses.” Another source of skepticism is the notion that a single, canonical abundance threshold applies to populations in different habitats. To address these valid concerns, tools are needed to confirm MVP thresholds based on empirical data, and to tailor thresholds to site-specific habitat differences.

This study focuses on the white sturgeon *Acipenser transmontanus*, a semi-anadromous fish that inhabits large rivers draining to the Pacific coast of North America. Damming of large rivers has divided historical white sturgeon populations into more than 36 smaller fragmented populations, few of which are thriving. We now face the challenge of managing these populations to identify and avoid extinction thresholds related to small size and inadequate habitat. The largest populations are those with access to the ocean in the Sacramento River (not shown), lower Columbia River, and lower Fraser River (Figure 1). Those in the lower Columbia River continue to support a significant fishery (Rieman and Beamesderfer 1990). The population between Hells Canyon and Lower Granite Dam on the Snake River, a major tributary of the Columbia River, is the largest inland population with consistent annual recruitment (Figure 1). Numerous, short, inland segments (reservoirs) of the upper Columbia and Snake rivers have white sturgeon populations that are small or functionally extirpated (Figure 1). Declines of sturgeon in longer river segments are harder to explain. Poor survival of spawned eggs to age 1 is the bottleneck in both the Nechako River and the Kootenai River in Canada, possibly due to large-scale movement of sediment and the resulting loss of interstitial space in historical spawning areas (Paragamian and Wakkinen 2001; Paragamian et al. 2002; McAdam et al. 2005). The population (or populations) between Grand Coulee Dam, Washington, and H. L. Keenleyside Dam, British Columbia, is (or are) aging after more than 30 years of recruitment failure (Irvine et al. 2007). The small size

of the population above Brownlee Dam in the Snake River is attributed to severe water quality problems in the reservoir during summer (Lepla and Chandler 1997). Populations in the Hanford Reach, the four lower Snake River reservoirs, and C. J. Strike reservoir are intermediate in size and support intermittent spawning (Figure 1). The frequency of recruitment to age 1 has not yet been measured in these systems.

In this study, we evaluated extinction thresholds for white sturgeon. We addressed each of two concerns about MVP thresholds, namely, that they (1) are based on models and (2) do not consider site-specific habitat. To produce empirical estimates of MVP, we assembled data for white sturgeon populations spanning most of their geographic range. We used these data to determine the population size at which population trends go from positive to negative and the population size at which the size structure indicates healthy recruitment to younger age-classes. We demonstrated a new statistical approach for estimating a single cross-population MVP from empirical data. Recognizing that habitat-mediated recruitment frequency is an important property of white sturgeon populations, we developed a simple combinatorial model to estimate recruitment failure from spawner abundance, and we used a population viability analysis (PVA) model to quantify the effect of local habitat size and recruitment frequency on MVP. Our approach combined the strengths of PVA modeling and empirical data to evaluate extinction thresholds and their relevance for fragmented white sturgeon populations.

Methods

We assembled data from 36 populations of white sturgeon in the USA and Canada from agency reports and population assessments (Figure 1; see Appendix for data sources). This represents all populations north of California (we were unable to obtain data from the state of California). At least one population estimate was available for each of 28 populations. We treated the segment between Grand Coulee Dam, Lake Roosevelt, in the United States and the Canadian segments below H. L. Keenleyside Dam as distinct populations, as recommended by Hildebrand et al. (1999) and Golder Associates Ltd. (2004b). In the middle Snake River, separate surveys were conducted for Lower Granite Reservoir and the free-flowing reach below Hells Canyon Dam (Cochnauer 1983; Lepla 1994; Everett and Tuell 2003). We combined these segments for our analysis of recruitment, which does not rely on having data for the same years, but we treated them separately in our analysis of population trends.

In our search for an empirical estimate of MVP, we



FIGURE 1.—Locations and status codes for populations of white sturgeon in the Columbia and Fraser River basins.

looked for changes in population health along a continuum of population sizes. We identified quantile regression as an appropriate tool for developing relationships between indicators of population health (e.g., positive trend or good recruitment) and population size. Relationships for upper quantiles (e.g., 90th percentile) are robust to other factors that might limit populations besides the one of interest (i.e., population size) (see Cade et al. 1999). Points representing populations limited by other factors (e.g., habitat) do not have an undue influence on the relationship.

First, we specified a threshold for each measure of population health (i.e., trend ≥ 0 or a measure of age structure that indicates successful reproduction). Next,

we developed a quantile-regression relationship between the index of population health and population size. We estimated parameters (intercept, β_0 , and slope, β_1) for quantile θ , by minimizing equation (1), which assigns weight θ to individual observations, i , with positive residuals, $r_i > 0$, and $1 - \theta$ to observations with negative residuals, $r_i < 0$ (Cade et al. 1999; Koenker 2005):

$$r_i = y_i - [\hat{\beta}_0 + \hat{\beta}_1 \log_e(N_i)]$$

$$\left\{ \begin{matrix} \hat{\beta}_0 \\ \hat{\beta}_1 \end{matrix} \right\} = \min_{\beta} \sum_{i=1}^n \begin{cases} \theta r_i, r_i > 0 \\ (1 - \theta)r_i, r_i < 0 \end{cases} \quad (1)$$

In equation (1), y_i is the index of health (of which we consider two alternatives) for each i where $i = 1$ to n populations. We present two tests, a Wald test and a likelihood-ratio test, that measure whether the coefficient of log population size differs from zero. The likelihood-ratio test is generally preferred, but the two tests are asymptotically equivalent, converging to a chi-square distribution. We present P -values based on the chi-square tests, leaving it to readers to set their tolerance for type I error. We give additional details specific to each measure of population health in two sections below (on population trend analysis and recruitment analysis).

We propose as an MVP estimate the population size at which an upper quantile curve crosses a specified threshold of population health. As a first step toward suggesting confidence intervals on the proposed MVP (“Every serious estimate deserves a reliable assessment of precision” Koenker and Hallock 2001), we demonstrate the ability to produce confidence intervals on quantile relationships as $\hat{y}_i \pm \phi^{-1}(1 - \alpha/2) \cdot \hat{y}_{SE_i}$ (Zhou and Portnoy 1996; Chapter 3 in Koenker 2005). This interval covers probability $(1 - \alpha)$ at any given population size. The standard error, \hat{y}_{SE_i} , is determined from the parameter SE values calculated via the asymptotic-sparsity method (SAS 2008). This method relies on asymptotic (large sample) properties, but does not require identical, independently distributed errors (Cade et al. 2005; Koenker 2005; SAS 2008).

We provide the equations needed to estimate upper and lower 95% confidence limits on the quantile relationships. These provide candidate lower and upper limits on the MVP estimate by crossing the threshold of population health below the intersection for 90th quantile curve, giving us some confidence that the true MVP lies between these value (although further research is needed to evaluate whether any specific probability statement about the MVP is possible).

The choice of an upper quantile is somewhat arbitrary, but requires compromise between removing effects of limiting factors other than population size and avoiding extremely high quantiles that have undesirable properties (e.g., quantile crossing; Koenker 2005:55–56). We evaluated the sensitivity of our recruitment-based MVP estimate to the choice of an upper quantile by comparing estimates over a range of values. The number of distinct quantile relationships available is discrete and depends on sample size; intermediate quantiles are interpolated from these (SAS 2008).

Population trend analysis.—Theoretically, the best estimate of a strong Allee threshold is the population size below which per-capita population growth changes from positive (above MVP) to negative (below MVP).

However, because a growing population can still go extinct due to stochastic fluctuations in population size, variation in population size is also important.

Estimates of population size and 95% confidence limits were available for 10 white sturgeon populations from surveys conducted during three or more years using Schnabel estimates for closed populations based on multiple mark–recapture methods. Although details varied slightly among populations depending on gear type, estimates typically applied to white sturgeon larger than a minimum catchable fork length (FL), which varied among sites from 34 to 54 cm for sturgeon caught with setlines. Full recruitment to setline and gill-net gear with typical hook or mesh sizes, respectively, occurs for sturgeon larger than 60 cm, but sturgeon smaller than 10 cm have been captured.

Our goal was to determine whether one could classify a population as having a significant positive or negative trend, λ , based on its initial population size. Two steps in this analysis were to estimate the population trend, λ , and develop an empirical relationship between trend and population size. To estimate population trends, we used weighted Poisson regression (equation 2). To account for differences in uncertainty among population estimates, N_t , we weighted each year t 's estimate by $w_t = N_t/V_t$, where $V_t = 1/4(U_{95} - L_{95})^2$ for the lower, L_{95} , and upper, U_{95} , 95% confidence bounds on N_t (equation 2). The variance–covariance matrix, Σ , of errors, ϵ , is described in equation (2). We modeled first-order autocorrelation, ρ (equation 2).

$$N_t = N_0 e^{\lambda t} + \epsilon_t, \quad \epsilon_t \sim N(\mathbf{0}, \Sigma)$$

$$\Sigma_{t,t+i} = \begin{cases} \frac{\mu_t}{w_t}, & i = 0; \mu_t = \log_e(N_0 e^{\lambda t}) \\ \rho, & i = 1 \\ 0, & i > 1 \end{cases} \quad (2)$$

We estimated population trends (coefficient λ) and reported the SE associated with each trend and the probability of nonzero trend based on a chi-square test (Table 1).

For the second step, we used quantile regression to fit the upper 90 percentile of λ with respect to log-transformed population size. We propose using the population size at which the quantile relationship intersects zero growth (i.e., the population size required for population increase) as an estimator of MVP.

Recruitment analysis.—We evaluated a second definition of MVP based on recruitment status by examining the sizes of white sturgeon populations currently having a large proportion of smaller fish

TABLE 1.—Summary of white sturgeon population data for 36 populations, including empirical trend estimates for 10 populations and the proportion smaller than 83 cm for 29 populations. Rivers are the lower Columbia (LC), upper Columbia (UC), Fraser–Nechako (FR), and Snake (SN). We use the following index of harvest: 0 = none, 1 = catch and release (<10/year), 2 = tribal fishery/low-level harvest (<50/year), 3 = mid-level (<1,000/year), 4 = high-level (<10,000/year), and 5 = very high (>100,000/year).

Population, river	Distance inland (km)	Reach length (km)	Survey years	Population estimates			Trend \pm SE Pr ($\lambda \neq 0$)	Percent \leq 83 cm	Harvest index
				Initial	Arithmetic mean	Geometric mean			
Below Bonneville Dam, LC	0	235	17	222,100	236,629	211,017	-0.0590 ± 0.0125 ($P < 0.0001$)		5
Bliss Reservoir, SN	1,420	21	1	83	83	83		6.0	1
Bonneville Reservoir, LC	235	74.4	5	32,000	73,757	65,039	0.0557 ± 0.0043 ($P < 0.0001$)	65.0	4
Brownlee Reservoir, SN	977	279	2	155	155	155		4.0	0
Chief Joseph Reservoir, UC	877.1	83.7	0					0.0	1
C. J. Strike Reservoir, SN	1,314	106.7	3	2,192	2,622	2,600	0.0120 ± 0.03 ($P = 0.6887$)	3.8	1
Duncan Reservoir, UC	1,311	300	0					0.0	0
Grand Coulee–Lake Roosevelt, UC	1,170	235	1	2,295	2,295	2,295		0.0	2
Hells Canyon Reservoir, SN	917	41	0					18.0	0
Hells Canyon Dam to Salmon River, SN	754.76	162.2	3	10,000	6,042	5,484	-0.0156 ± 0.0120 ($P = 0.1931$)	69.0	2
Ice Harbor Reservoir, LC	538	51.5	1	4,832	4,832	4,832		3.5	2
John Day Reservoir, LC	347	25	4	19,300	30,807	29,587	0.0434 ± 0.0231 ($P = 0.0603$)	15.6	3
Keenleyside–Arrow Lake, UC	1,251	5	4	52	60	58	-0.0001 ± 0.0827 ($P = 0.9991$)	0.0	0
Kootenai River and Lake, UC	1,300	270	4	1,194	905	890	-0.0379 ± 0.0041 ($P < 0.0001$)	0.0	0
Little Goose Reservoir, LC	632	59.6	1	6,492	6,492	6,492		15.7	2
Lower Fraser River, FR	78	211	7	47,431	52,883	52,607	-0.0145 ± 0.0094 ($P = 0.1232$)	24.8	3
Lower Granite Reservoir, SN	692	62.8	2	1,372	1,588	1,573		56.0	2
Lower Monumental Reservoir, SN	589	46.7	1	4,262	4,262	4,262		6.4	3
Lower Salmon Reservoir, SN	1,441	12	1	21	21	21			0
Hanford Reach (Mc Nary–Priest Rapid Dams), LC and SN	372	282.7	1	8,250	8,250	8,250		11.0	3
Mica Reservoir–Kinbasket, UC	1,610	330	0						0
Middle Fraser River, FR	211	459	1	3,745	3,745	3,745		33.0	2
Nechako River, FR	790	516	1	571	571	571		5.4	1
Oxbow Reservoir, SN	958	19.3	0						0
Priest Rapids Reservoir, UC	639.1	29.0	1	551	551	551		0.0	1
Revelstoke Reservoir, UC	1,481	129	0						0
Rock Island Reservoir, UC	729.5	33.8	0						1
Rocky Reach Reservoir, UC	762.2	67.6	2	29	40	38		14.0	1
Brownlee Reservoir, SN	1,256	58	1	726	726	726		4.0	0
The Dalles Reservoir, LC	308	39	5	27,700	46,160	32,212	0.1565 ± 0.0185 ($P < 0.0001$)	45.0	4
U.S.–Canada border to Keenleyside Dam, UC	959.9	56	5	1,050	1,179	1,172	0.0267 ± 0.1878 ($P = 0.1546$)	1.0	1
Upper Fraser River, FR	790	310	1	815	815	815		63.2	0
Upper Salmon Reservoir, SN	1,453	55	1	777	777	777		19.0	1
Wanapum, UC	669	61.2	1	134	134	134		13.0	1
Wells Reservoir, UC	829.6	47.5	1	31	31	31		15.4	1

(<83 cm FL). We adopted the population size at which recruitment reached levels considered by sturgeon biologists to be healthy as an estimate of MVP. Three lines of evidence support the claim that healthy populations not influenced by harvest or dams have age distributions dominated by smaller fish. The Pacific States Marine Fisheries Commission (PSMFC

1992) proposed a threshold of greater than 60% of fish less than 83 cm FL (~92 cm total length [TL]) as a management target. In part, this is based on the fact that the minimally harvested population below Hells Canyon Dam historically exhibited an age distribution dominated by fish smaller than 83 cm (over 80%, Coon et al. 1977; Lukens 1985), and this proportion has

decreased to around 60% (Lepla et al. 2001; Everett and Tuell 2003). In the upper Columbia River, 65–70% of white sturgeon captured before dams were constructed (1981–1983) were smaller than 1 m TL (RL&L Environmental Services 1996; Hildebrand et al. 1999). Finally, modeling exercises suggest that this is a reasonable estimate of the unharvested stable age distribution (Golder Associates 2004a).

We described the relationship between recruitment and population size using a logit model (equation 3) for the proportion of smaller sturgeon, p_{83} , in each population (y_i in equation 1 = p_{83}), that is,

$$\log_e \left(\frac{p_{83}}{1 - p_{83}} \right) = a + b \log_e(N)$$

$$p_{83} = \frac{1}{1 + e^{-\{a + b \log_e(N)\}}} \quad (3)$$

We used quantile regression to examine relationships between upper quantiles of p_{83} and log-transformed population size (equation 3, thereby removing the effect of other limiting factors). We estimated MVP based on the 90th quantile. For the recruitment-based estimate, we demonstrated a way to quantify uncertainty in the MVP estimate: we produced a lower bound on MVP from the upper 95% confidence limit on the quantile relationship. Finally, we examined sensitivity of the recruitment-based MVP estimate to the choice of quantile by comparing estimates across a range of upper quantiles (75% to 95%).

PVA modeling.—We used an individual-based population viability analysis (PVA) model for white sturgeon (Jager et al. 2002) to examine minimum viable population size and the minimum river-segment length required for population persistence. Because our model is individual based, we define persistence, P_{500} , simply as having at least one individual by the end of the 500-year period. We estimated the MVP as the initial size above which an isolated population of white sturgeon has an estimated 90% chance of persistence to 500 years. We note that the MVP estimated using the PVA method is not necessarily a threshold. Simulated river segments starting with larger populations may simply take longer to reach local extinction, rather than experiencing a density-related shift from population decline to growth.

Simulating Allee effects.—Because Allee effects are the basis for the presence of a MVP threshold, we added one strong Allee mechanism to the weak Allee effects (demographic and environmental stochasticity) already represented in the white sturgeon PVA model described by Jager et al. (2002). How sturgeon populations respond to density is poorly understood,

but life history traits can help to identify species that are more vulnerable to Allee effects (Courchamp et al. 2008, p. 187). Sturgeons are broadcast spawners that form spawning aggregations and release demersal (sinking) eggs into a turbulent water column or near the river bottom (Paragamian and Wakkinen 2001). Bruch and Binkowski (2002) observed that male lake sturgeons *A. fulvescens* “make concerted efforts to be one of the two primary males on either side of the female during the spawning bout.” Those investigators observed that most of the eggs deposited by female lake sturgeon were fertilized by the two closest males on either side, with lesser contributions from three to five satellite males. Fertilization success decreases as the number of broadcast spawners declines over a broad set of assumptions (Pennington 1985; Domeier and Colin 1997; Lundquist and Botsford 2004). Consequently, we simulated an increase in the fertilization success for the eggs of a given female as the number of males per female increased. Literature values suggest that fertilization starts at a minimum percentage of 60% of eggs with one male present (Cherr and Clark 1985; Levitan 2005), and increases to 75% with two males (Levitan 2005) and 85% with three males. We postulate a maximum of 90–95% fertilization with four or more males present, which corresponds to the percentages reported for white sturgeon in a laboratory setting (Deng et al. 2002; Yesaki et al. 2002). A Michaelis–Menton–Monod model to describe the proportion of eggs fertilized, p_{fert} , with an asymptote, $k = 1$, and half-saturation constant, $h = 0.7$ males per female, fit these literature values reasonably well (equation 4), where N_m is the number of males per female.

$$p_{fert} = \frac{kN_m}{N_m + h} \quad (4)$$

We used a negative binomial model to describe the distribution of white sturgeons ready to spawn because field data in the Snake River suggest that sturgeon counts are clumped (e.g., the variance in sturgeon numbers was 100 times larger than the mean number caught using setlines in 2005 in the Bliss–C. J. Strike reach, Lepla and Chandler 1997). We assumed that the distance within which a male sturgeon can find ripe females is x km and the length of the river segment is L . A negative binomial distribution of breeding adults was generated as a compound gamma-Poisson distribution (i.e., by first drawing a gamma variate, m , and then using this as the mean number of local males in the Poisson process). The gamma distribution’s shape and scale parameters were derived from the expected number of local spawners, $\mu_1 = N_i x/L$ and variance = $100 \mu_1$, where N_i is total number of spawners. The

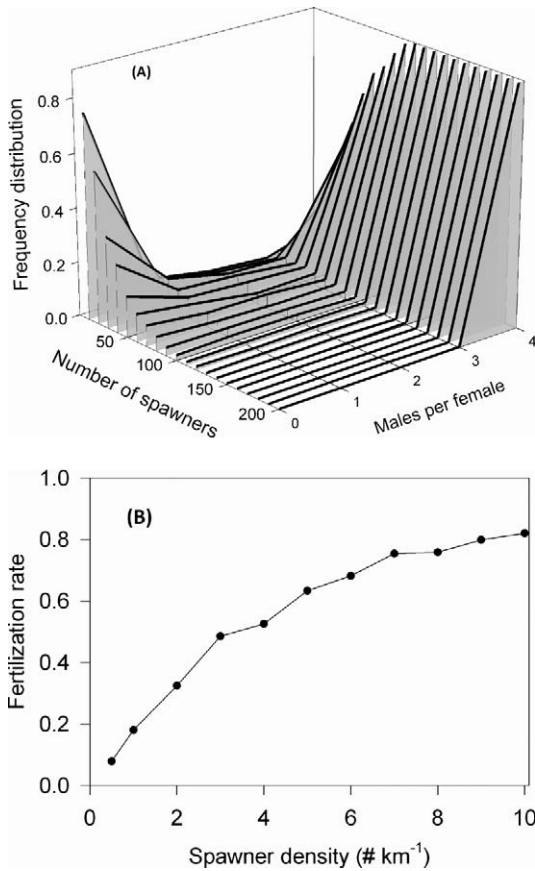


FIGURE 2.—Proposed relationship for fertilization Allee effect among white sturgeon. Panel (A) shows the frequency distribution of the number of males at different spawner densities (note that “4” includes ≥ 4 males per spawning female). When the proposed relationship between the number of male sturgeons and the fraction of eggs fertilized is integrated over this distribution, a near-linear relationship between fertilization rate and spawner density results, as shown in panel (B).

number of males, N_m , for each breeding female is drawn from a Poisson distribution with mean $\mu_2 = 0.5m$ (i.e., half the realized number of local spawners). The frequency distribution of N_m values shifts to the right (more males per female) as the number of spawners increases (Figure 2A).

For a particular spawner density, we obtained the average proportion fertilized (Figure 2B) by integrating fertilization rates (equation 4) over the distribution of N_m values (Figure 2A).

At low densities, sturgeon may also experience two Allee mechanisms not represented here: social disruption (Allen et al. 2009) and higher egg predation (Bruch and Binkowski 2002; Gascoigne and Lipcius

2004). On the other hand, sturgeon are protected from Allee effects by the fact that one individual female sturgeon can produce many eggs (Jerde et al. 2009).

A simple combinatorial model describes the relationship between spawning frequency and the minimum number of females needed to avoid years with spawning failure under ideal environmental conditions. Consider an iteroparous species with interval k years between reproductive events. Let N denote the number of mature females in the population. To begin with, we wish to determine the probability of at least 1 year in a sequence of k years with no recruitment. Because each individual female can choose 1 year to reproduce (she is unable to reproduce again within the interval), the sample space consists of all possible combinations of individual spawning females distributed among k years. We choose a spawning year between 1 and k for each of N spawning females (trials). The total number of ways to partition N female spawners across k years is k^N . The number of ways to partition N female spawners across k years such that no year lacks a female spawner (i.e., no spawning failures), is given by

$$S(N, k) = \frac{1}{k!} \sum_{t=0}^{k-1} (-1)^t \binom{k}{t} (k-t)^N.$$

For a specified interval of k years, the ratio $S(N, k) : k^N$ gives the proportion of combinations that have no years with spawning failures and the annual risk of spawning failure,

$$p_a = \sqrt[k]{1 - \frac{S(N, k)}{k^N}}.$$

This result also applies to longer sequences of years if we assume that females continue in a deterministic schedule after choosing the first year of spawning. The preceding equation predicts that the frequency of year-class failures decreases as the number of mature females increases and the interval between spawning events decreases, as illustrated in Figure 3.

Simulation experiments.—The PVA model for white sturgeon populations has been described fully elsewhere (Jager et al. 2002). Because we simulated individual sturgeon, demographic stochasticity (i.e., females that fail to mate because no males are ready to breed during the same year) occurs more often in small, rather than in large, populations. We simulated the previously described fertilization Allee mechanism, but we did not restrict the ability of males to find females because distances traveled in these river segments, which are isolated between dams, are generally much shorter than historical spawning migration distances.

Hydrologic year type was the source of environmental stochasticity in the PVA model. The prevailing

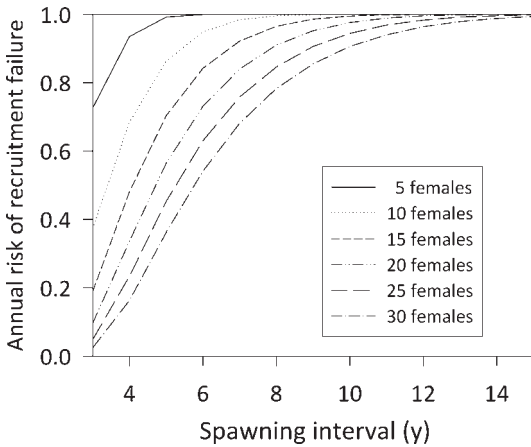


FIGURE 3.—Combinatorial model showing that the frequency of year-class failures decreases as the number of mature females increases and the interval between spawning events decreases.

paradigm for sturgeon is that hydrologic year type (wet versus dry years) drives year-to-year variation in the availability of hydraulically complex spawning habitat required for spawning (Parsley and Beckman 1994). In regulated rivers, a threshold in suitable habitat size (river length) exists beyond which the habitat provided by impounded reservoirs is supplemented by free-flowing river habitat (Jager et al. 2001). In two scenarios, we simulated habitat that permitted spawning in (1) all years and (2) only in wet years. In the Snake River, wet years occur about 25% of the time.

Simulations compared MVP estimates for river segments ranging from 10 to 290 km in length and initial population sizes ranging from 50 to 10,000 individuals age 1 and older. We simulated 200 replicate populations over 500 years for each initial population size and river-length scenario. Our operational definition for MVP based on PVA modeling is the initial population size needed to attain 90% chance of persistence to 500 years, or P_{500} . One important point about PVA-based estimates of MVP is that they do not imply the existence of, or correspond to, thresholds in per-capita population growth (recall the distinction between weak and strong Allee effects). In other words, if we have a population whose vital rates cause decline regardless of initial size, increasing the number of initial individuals will increase the fraction that persist and eventually reach 0.9.

Results

With the amount and type of data available to us, we were more successful in obtaining empirical estimates

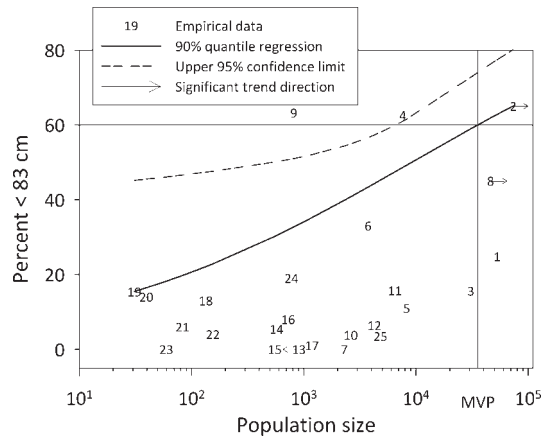


FIGURE 4.—Logistic quantile relationships between an index of current recruitment (percent less than 83 cm) and average population size for 25 white sturgeon populations. Above and to the left of the 90% quantile model (solid curve) is an upper 95% confidence limit on the quantile relationship (dashed curve). The threshold of recruitment associated with healthy populations at 60% is indicated by a horizontal line, and the vertical line to the x-axis indicates the proposed MVP estimate. Arrows show the direction of trends for three of four populations deemed significant. Populations shown are as follows: 1 = lower Fraser River, 2 = Bonneville Reservoir, 3 = John Day Reservoir, 4 = Lower Granite–Hells Canyon, 5 = McNary–Hanford Reach, 6 = middle Fraser River, 7 = Lake Roosevelt, 8 = the Dalles Reservoir, 9 = upper Fraser River, 10 = C. J. Strike Reservoir, 11 = Little Goose Reservoir, 12 = Lower Monumental Reservoir, 13 = Kootenai River, 14 = Nechako River, 15 = Priest Rapids Dam, 16 = C. J. Strike Reservoir to Swan Falls, 17 = U.S.–Canada border below Keenleyside Dam, 18 = Wanapum, 19 = Wells Reservoir, 20 = Rocky Reach, 21 = lower Salmon River to Bliss Dam, 22 = Brownlee Reservoir, 23 = Arrow Lake, 24 = Shoshone Falls to Upper Salmon Dam, and 25 = Ice Harbor.

for MVP by using recruitment status as a measure of population health than by using population trends. We summarize population estimates, habitat attributes, and trend analysis results for the populations used in our analyses in Table 1.

Population Trend Analysis

We evaluated trends in 10 populations by fitting equation (2) (Table 1). Setting the type I error at 0.05, we found evidence for a significant negative trend in two populations and for a significant positive trend in two populations (Figure 4; Table 1). In the remaining six populations, we were unable to detect a significant nonzero trend over time (Table 1).

Increasing trends were detected in two lower Columbia reservoirs connected to the ocean with large populations (>25,000 individuals; Figure 4). The Kootenai population, which is federally endangered

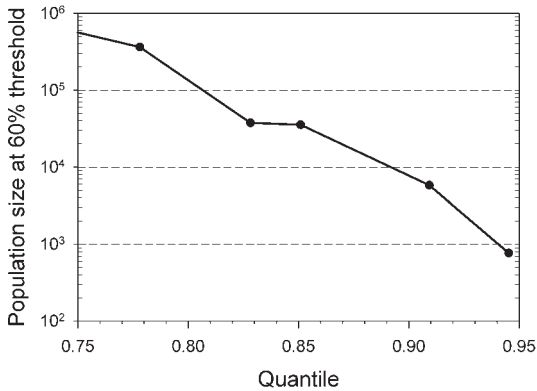


FIGURE 5.—Estimated population sizes corresponding with healthy recruitment (60% less than 83 cm) for a range of upper quantiles.

in Canada, showed a negative trend (Figure 4). This population declined from 1,194 white sturgeon in 1982 (Duke et al. 1999) to 760 individuals in 2000 (McAdam et al. 2005). Population surveys for 17 years gave us high power to detect a decline in the second population, below Bonneville Dam (Table 1). This population has access to the estuary and ocean, but may have declined due to overharvest in the large commercial fishery that it supports or due to density-dependent factors.

Trends in populations tended to increase with population size, but the number of populations for which we had trends was too low to lend much confidence to the results. To demonstrate the method, we fitted the equation $\lambda = -0.0963 + 0.0235 \log_e(N)$ to the upper 90th percentile of λ for all 10 populations, where N is the average population size and λ is the trend (equation 2) estimated over the years surveyed. The Wald test ($\chi^2 = 2.21$, $P > = 0.1371$) and the likelihood-ratio test ($\chi^2 = 7.22$, $P > = 0.0072$) measured the degree to which adding $\log_e(N)$ to equation (2) improved predictions, as indicated by lower P -values. We did not use the quantile regression to estimate a cross-system MVP because too few populations were included to extrapolate to all white sturgeon populations.

Recruitment Analysis

We estimated the upper 90th quantile relationship, $\text{logit}(p_{83}) = -2.7204 + 0.2983 \log_e(N)$, where N is the average population size and p_{83} is the percentage of white sturgeon smaller than 83 cm FL. The Wald test ($\chi^2 = 3.62$, $P > = 0.057$) and likelihood-ratio test ($\chi^2 = 2.64$, $P > = 0.104$) measured the degree to which adding $\log_e(N)$ to equation (3) improved predictions, where lower P -values imply greater improvement.

The choice of an upper quantile represents a trade-off between eliminating other factors that limit recruitment and avoiding extreme quantiles because statistical problems emerge as values approach one (and zero). The estimated MVP was constant over the range of quantiles between 82.8% and 91% (Figure 5). The 90 percentile quantile-logistic curve crossed the 60% recruitment threshold for p_{83} near 35,500 individuals (vertical line in Figure 4). The intersection between the upper 95% confidence interval and threshold $p_{83} = 60\%$ for the 90th quantile relationship occurred at approximately 5,580 individuals (Figure 4). The intersection between the lower 95% confidence interval and 60% was beyond the range of the data.

PVA Modeling

Two scenarios for environmental stochasticity bounded our model-based MVP estimates. Simulated populations in longer river segments achieved persistence to 500 years, $P_{500} = 0.9$, with smaller initial populations than those inhabiting shorter river segments. In simulations that allowed spawning in all years (no environmental stochasticity), persistence to 500 years was predicted for greater than 98% of populations beginning with at least 50 individuals and 10 km of free-flowing habitat (results not shown). To achieve these odds in river segments with adequate conditions for spawning only in wet years (25% of years: high environmental stochasticity; see Jager et al. 2001), it was necessary to be in a longer river segment (>70 km) with a larger initial population (>6,000 individuals) (Figure 6).

Discussion

Allee effects are not usually the initial cause of population decline, but rather a consortium of positive feedbacks that kick in beyond the point of no return defined by the MVP threshold. In this study, we combined empirical and PVA modeling methods to better understand MVP thresholds for white sturgeon. Although we ultimately concluded that the MVP was not a holy grail worthy of pursuit for this species, we swept a path toward defining more meaningful extinction thresholds related to habitat and recruitment frequency.

Suspicious of model-based estimates, we set out to discover a single, robust MVP threshold for white sturgeon based on empirical data. Empirical methods for estimating MVP are important because they provide a “reality check” for model-based estimates. We developed a new method for estimating MVP from synoptic (“snapshot” in time) data spanning multiple populations. We recognized that a single abundance threshold would be unlikely to apply to all populations

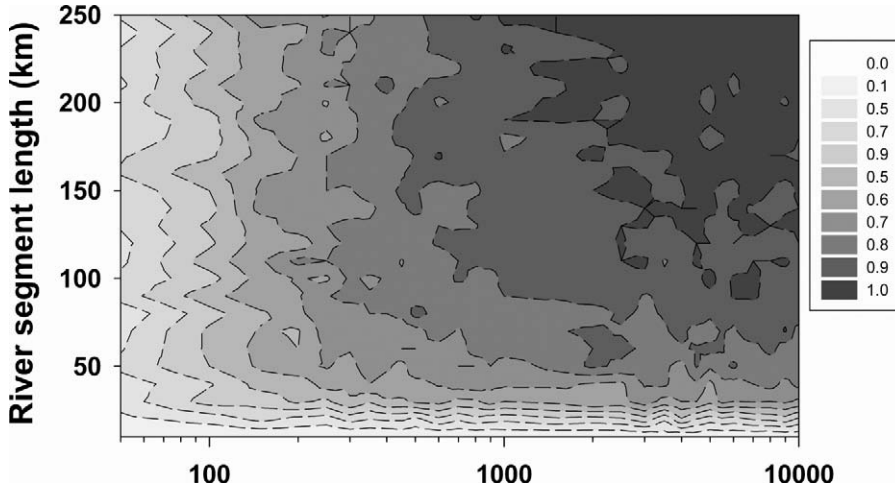


FIGURE 6.—Simulated probability of persistence to 500 years as a function of initial population size (*x*-axis) and river segment length with spawning possible only in wet years (roughly 25% of years) and no restrictions on the distance to find mates. Note the shift in the location of the 90% (0.9) contour toward the upper right corner with increasing initial population size and river segment length.

of this species, which now exists in fragmented river segments, many of which lack the full complement of required habitat. We therefore used PVA modeling to discover (1) habitat-related extinction thresholds and (2) habitat influences that might alter the MVP threshold locally. We discuss these two complementary approaches as follows.

Cross-Population MVP

Quantile regression enabled us to model risk associated with small population size, while removing the effects of other factors contributing to differences among white sturgeon populations in rivers of the U.S. Pacific Northwest and western Canada. Recruitment status provided a better measure of population health than population trends in our efforts to estimate a single cross-population MVP for white sturgeon because we had information on the recent recruitment status for many of these populations. By adopting a recruitment index as our measure of population health, we hypothesize that a sufficiently large adult population is required to support an age structure consistent with good recruitment, and that an age structure that includes younger fish is consistent with population growth. The MVP based on empirical recruitment data were 35,500, with a lower bound based on a 95% confidence interval on the quantile relationship of 5,580 individuals. This MVP estimate seems high, although both populations with significant increasing trends also exceeded this size. We showed that this MVP estimate was relatively insensitive to choice of

upper quantile and to populations with low recruitment, but we found it to be sensitive to the population size of a population with a high recruitment index: our MVP estimate increased substantially when we combined the adjacent Hells Canyon and Lower Granite Reservoir populations.

We see two areas for future research. First, simulation studies with known model-based MVP thresholds are needed to add statistical rigor to the confidence intervals associated with quantile-based MVP estimates. Second, alternative methods for defining an MVP can be applied, depending on the types of data available. A threshold based on population trends would be closer to the theoretical definition of an Allee effect, but too few white sturgeon populations had historical data to estimate trends, and the number of years supporting most trend estimates was small. If long historical time series were available to characterize population dynamics over a wide range of sizes, time-series methods (see Dennis and Otten 2000; Traill et al. 2007; Gregory et al. 2010) would provide another alternative for detecting Allee effects and estimating MVP.

Habitat Influences

Other factors are usually responsible for driving populations to small sizes where the MVP becomes relevant. Our PVA results highlighted the importance of habitat influences on recruitment. Simulated MVP thresholds varied among (or were irrelevant for) populations that experienced different local habitat

conditions. We used PVA modeling to understand interactions between extinction thresholds related to population size (i.e., MVP) and habitat. We varied the length of free-flowing habitat and recruitment frequency and found that persistence was not possible for river segments below a threshold length, regardless of initial population size. For simulated populations that did have sufficient rearing habitat and different vital rates, the local PVA-based MVP threshold increased with increased habitat size. These results suggest classifying white sturgeon populations into three groups: (1) healthy populations with annual recruitment, (2) demographic sink populations lacking a threshold amount of habitat required to persist, and (3) populations with local habitat conditions that permit intermittent recruitment.

Group 1.—Consistent annual recruitment is a distinguishing characteristic of white sturgeon populations with “healthy” age structure (Figures 1, 4). Based on our PVA model results, populations with annual recruitment have very low MVP thresholds, around 50 individuals. The simple combinatorial equation illustrated by Figure 3, which relates the risk of recruitment failure to spawner abundance, gives similar estimates. These low values are consistent with the idea that high fecundity can protect populations from Allee effects (Jerde et al. 2009) and suggests that we need not be concerned about Allee effects in populations with ocean access and consistent annual recruitment.

Group 2.—Many white sturgeon populations with poor recruitment (Figure 1) appear to fall below a threshold amount of required spawning and rearing habitat. Such populations inhabit the Kootenai River, Lake Roosevelt, below H. L. Keenleyside Dam, and short reservoir segments of the lower Snake, middle Snake, and upper Columbia rivers. Poor water quality is another habitat-related problem (Brownlee Reservoir). We surmise that efforts to revive populations by adding individuals to achieve an MVP in river segments with poor habitat are not likely to succeed because they are demographic sinks. Before deciding to add individuals to a population in this group by whatever means (passage, translocation, supplementation), it should be determined that the segment is not a demographic sink (see Jager 2006).

Group 3.—In river segments with sufficient (or intermittently sufficient) habitat, the PVA-based MVP threshold depends on the frequency of successful recruitment. Recruitment occurs annually in only four river segments (i.e., two lower Columbia River reservoirs [Bonneville and the Dalles], below Hells Canyon Dam on the Snake River, and in the Fraser River; Figure 1). For other river segments that show any evidence of recruitment, success is sporadic and

seems to be associated with years wetter than normal (e.g., John Day Reservoir on the lower Columbia River and C. J. Strike Reservoir on the Snake River). From a population modeling perspective, different river segments support white sturgeon populations with different vital rates. In this study, we found that recruitment frequency had a significant effect on PVA-based MVP predictions, with fewer adults required for persistence (i.e., lower MVP) in river segments that supported annual recruitment than in river segments that only permitted recruitment in years wetter than normal.

Historical changes in habitat have been linked with both persistent and intermittent recruitment failures. Korman and Walters (2001) used a population model to infer from a shift toward older age-classes that recruitment failure in the Nechako River began around 1967, at a population size of approximately 4,500 individuals. Similar shifts in size structure of aging populations have been observed elsewhere (e.g., McNary Reservoir [Rien and Beiningger 1997], Lake Roosevelt [Irvine et al. 2007], and Kootenai River [Paragamian et al. 2002]).

Conclusions

Our study leads us to suspect that extinction thresholds related to habitat and recruitment frequency are more important than thresholds related to population size for white sturgeon. Clearly, a strategy of detecting and addressing primary causes of decline as early as possible is more likely to succeed than managing to the point of no return or MVP. Perhaps we should examine a new extinction threshold minimum viable recruitment (MVR), as indicated by age structure. Age structure provides a temporally integrated index of historical recruitment status that can be measured at a single point in time. Holmes and York (2003) suggested that shifts in age structure are an important early warning sign for long-lived species, and this seems to be the case for white sturgeon. We propose that thresholds related to recruitment frequency and habitat may be a more relevant alternative for long-lived riverine fishes, particularly if the goal is to detect problems early.

Acknowledgments

This research grew out of an earlier informal comparison that was presented by Webb Van Winkle at the 2004 American Fisheries Society meeting in Madison, Wisconsin. Other coauthors included Paul Anders, Larry Hildebrand, Tom Rien, and Ken Lepla. White sturgeon population data for upper Columbia River in Canada and Canadian rivers was kindly provided to us by Larry Hildebrand and Robyn Irvine (Golder Associates Ltd., Castlegar, British Columbia),

and Troy Nelson (Fraser River Sturgeon Conservation Society). We thank Brian Cade (U.S. Geological Survey) for his advice regarding construction of quantile regression confidence intervals. We appreciate three thorough reviews that greatly improved the manuscript. This research was sponsored in part by Idaho Power Company under U.S. Department of Energy (DOE) contract no. ERD-99-1813. Oak Ridge National Laboratory is managed by UT-Battelle, LLC, for the DOE under contract DE-AC05-00OR22725. The U.S. Government retains, and the publisher, by accepting the article for publication, acknowledges that the U.S. Government retains, a nonexclusive, paid-up, irrevocable, worldwide license to publish or reproduce the published form of this manuscript, or allow others to do so, for U.S. Government purposes.

References

- Allee, W. C. 1938. The social life of animals. Norton, New York.
- Allen, P. J., C. C. Barth, S. J. Peake, M. V. Abrahams, and W. G. Anderson. 2009. Cohesive social behaviour shortens the stress response: the effects of conspecifics on the stress response in lake sturgeon *Acipenser fulvescens* (Rafinesque). *Journal of Fish Biology* 90:104.
- Berec, L., E. Angulo, and F. Courchamp. 2006. Multiple Allee effects and population management. *Trends in Ecology and Evolution* 22:185-191.
- Brook, B. W., L. W. Traill, and C. J. A. Correy. 2006. Minimum viable population sizes and global extinction risk. *Ecology Letters* 9:375-382.
- Bruch, R. M., and F. P. Binkowski. 2002. Spawning behavior of lake sturgeon (*Acipenser fulvescens*). *Journal of Applied Ichthyology* 18:570-579.
- Cade, B. S., B. R. Noon, and C. H. Flather. 2005. Quantile regression reveals hidden bias and uncertainty in habitat models. *Ecology* 86:786-800.
- Cade, B. S., J. W. Terrell, and R. L. Schroeder. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology* 80:311-323.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Biology* 63:215-244.
- Cherr, G. N., and W. H. Clark. 1985. Gamete interaction in the white sturgeon *Acipenser transmontanus*: a morphological and physiological review. *Environmental Biology of Fishes* 14:11-22.
- Cochner, T. G. 1983. Abundance, distribution, growth, and management of white sturgeon (*Acipenser transmontanus*) in the Middle Snake River, Idaho. Report to Idaho Power Company, Boise.
- Coon, J. C., R. R. Ringe, and T. C. Bjornn. 1977. Abundance, growth, and movements of white sturgeon in the mid-Snake River. University of Idaho, Idaho Water Resources Research Institute, Research Technical Completion Report, Project B-026-IDA, Moscow.
- Courchamp, F., L. Berec, and J. Gascoigne. 2008. Allee effects in ecology and conservation. Oxford University Press, Oxford, UK.
- Deng, X., J. P. Van Eenennaam, and S. I. Doroshov. 2002. Comparison of early life stages and growth of green and white sturgeon. Pages 237-248 in W. Van Winkle, P. J. Anders, D. H. Secor, and D. A. Dixon, editors. *Biology, management, and protection of North American sturgeon*. American Fisheries Society, Symposium 28, Bethesda, Maryland.
- Dennis, B. 2002. Allee effects in stochastic populations. *Oikos* 96:386-401.
- Dennis, B., and M. R. M. Otten. 2000. Joint effects of density dependence and rainfall on abundance of San Joaquin kit fox. *Journal of Wildlife Management* 64:388-400.
- Domeier, M. L., and P. L. Colin. 1997. Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science* 60:698-726.
- Duke, S., P. Anders, G. Ennis, R. Hallock, J. Hammond, S. Ireland, V. Paragamian, and R. Westerhof. 1999. Recovery plan for Kootenai River white sturgeon (*Acipenser transmontanus*). *Journal of Applied Ichthyology* 15:157-163.
- Everett, S., and M. Tuell. 2003. Evaluate potential means of rebuilding sturgeon populations in the Snake River between Lower Granite and Hells Canyon dams: 2001 annual report. Bonneville Power Administration, DOE/BP-00004046-1, Portland, Oregon.
- Fagan, W. F., and E. E. Holmes. 2006. Quantifying the extinction vortex. *Ecology Letters* 9:51-60.
- Fagan, W. F., E. Meier, and J. L. Moore. 1999. Variation thresholds for extinction and their implication for conservation strategies. *American Naturalist* 154:510-520.
- Gascoigne, J. C., and R. N. Lipcius. 2004. Allee effects driven by predation. *Journal of Applied Ecology* 41:801-810.
- Gilpin, M. E., and M. E. Soulé. 1987. Minimum viable populations: processes of extinction. Pages 19-34 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Cambridge University Press, Cambridge, Massachusetts.
- Golder Associates. 2004a. Proposed methodology for white sturgeon enhancement in Rocky Reach Reservoir. Report prepared for Public Utility District No. 1 of Chelan County, Wenatchee, Washington.
- Golder Associates. 2004b. Upper Columbia white sturgeon stock monitoring and data management program. British Columbia Ministry of Water, Land and Air Protection, Nelson.
- Gregory, S. D., C. J. A. Bradshaw, B. W. Brook, and F. Courchamp. 2010. Limited evidence for the demographic Allee effect from numerous species across taxa. *Ecology* 91:2151-2161.
- Hildebrand, L., C. McLeod, and S. McKenzie. 1999. Status and management of white sturgeon in the Columbia River in British Columbia, Canada: an overview. *Journal of Applied Ichthyology* 15:164-172.
- Holmes, E. E., and A. E. York. 2003. Using age structure to detect impacts on threatened populations: a case study with Steller sea lions. *Conservation Biology* 17:1794-1806.
- Irvine, R. L., D. C. Schmidt, and L. R. Hildebrand. 2007. Population status of white sturgeon in the lower Columbia River within Canada. *Transactions of the American Fisheries Society* 136:1472-1479.
- Jager, H. I. 2006. Chutes and ladders and other games we play

- with rivers. II. Translocation. *Canadian Journal of Fisheries and Aquatic Sciences* 63:176–184.
- Jager, H. I., J. A. Chandler, K. B. Lepla, and W. Van Winkle. 2001. A theoretical study of river fragmentation by dams and its effects on white sturgeon populations. *Environmental Biology of Fishes* 60:347–361.
- Jager, H. I., W. Van Winkle, K. B. Lepla, J. A. Chandler, and P. Bates. 2002. Factors controlling white sturgeon recruitment in the Snake River. Pages 127–150 in W. Van Winkle, P. J. Anders, D. H. Secor, and D. A. Dixon, editors. *Biology, management, and protection of North American sturgeon*. American Fisheries Society, Symposium 28, Bethesda, Maryland.
- Jerde, C. L., C. J. Bampfyde, and M. A. Lewis. 2009. Chance establishment for sexual, semelparous species: overcoming the Allee effect. *American Naturalist* 173:734–746.
- Kendall, B. E. 1998. Estimating the magnitude of environmental stochasticity in survivorship data. *Ecological Applications* 8:184–193.
- Koenker, R., and K. F. Hallock. 2001. Quantile regression. *Journal of Economic Perspectives* 15:143–156.
- Koenker, R. 2005. *Quantile regression*. Cambridge University Press, Cambridge, UK.
- Korman, J., and C. Walters. 2001. Nechako River white sturgeon recovery planning: summary of stock assessment and October 2–3, 2000 workshop. Prepared by Ecometric Research for British Columbia Fisheries, Victoria.
- Lande, R. 1998. Demographic stochasticity and Allee effect on a scale with isotropic noise. *Oikos* 83:353–358.
- Lepla, K. B. 1994. White sturgeon abundance and associated habitat in Lower Granite Reservoir, Washington. Master's thesis. University of Idaho, Moscow.
- Lepla, K. B., and J. A. Chandler. 1997. Status of white sturgeon in the C. J. Strike reach of the middle Snake River, Idaho. Idaho Power Company, Technical Report 3.1-B, Boise.
- Lepla, K. B., J. A. Chandler, and P. Bates. 2001. Status of Snake River white sturgeon associated with the Hells Canyon Complex. Chapter 1 in K. Lepla, editor. *Status and habitat use of Snake River white sturgeon associated with the Hells Canyon Complex*. Idaho Power Company, Technical Report, Appendix E.3.1-6, Boise.
- Levitán, D. R. 2005. Sex-specific spawning behavior and its consequences in an external fertilizer. *American Naturalist* 165:682–694.
- Lukens, J. R. 1985. Hells Canyon fishery investigations. Idaho Department of Fish and Game, Job Performance Report, Project F-73-R-7, Boise.
- Lundquist, C. J., and L. W. Botsford. 2004. Model projections of the fishery implications of the Allee effect in broadcast spawners. *Ecological Applications* 14:929–941.
- McAdam, S. O., C. J. Walters, and C. Nistor. 2005. Linkages between white sturgeon recruitment and altered bed substrates in the Nechako River, Canada. *Transactions of the American Fisheries Society* 134:1448–1456.
- Melbourne, B. A., and A. Hastings. 2008. Extinction risk depends strongly on factors related to stochasticity. *Nature* (London) 454:100–103.
- Paragamian, V. L., and V. D. Wakkinen. 2001. Temporal distribution of Kootenai River white sturgeon spawning events and the effect of flow and temperature. *Journal of Applied Ichthyology* 18:542–549.
- Paragamian, V. L., V. D. Wakkinen, and G. Kruse. 2002. Spawning locations and movement of Kootenai River white sturgeon. *Journal of Applied Ichthyology* 18:608–616.
- Parsley, M. J., and L. G. Beckman. 1994. White sturgeon spawning and rearing habitat in the lower Columbia River. *North American Journal of Fisheries Management* 14:812–827.
- Pennington, J. T. 1985. The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. *Biological Bulletin* 169:417–430.
- PSMFC (Pacific States Marine Fisheries Commission). 1992. *White sturgeon management framework plan*. PSMFC, Portland, Oregon.
- Rieman, B. E., and R. C. Beamesderfer. 1990. White sturgeon in the lower Columbia River: is the stock overexploited? *North American Journal of Fisheries Management* 10:388–396.
- Rien, T. A., and K. T. Beiningen. 1997. Effects of mitigative measures on productivity of white sturgeon populations in the Columbia River downstream from McNary Dam, and determine the status and habitat requirements of white sturgeon populations in the Columbia and Snake rivers upstream from McNary Dam. Bonneville Power Administration, Portland, Oregon.
- RL&L Environmental Services. 1996. *The distribution and status of white sturgeon in isolated water bodies within the Columbia River basin in B.C.: 1995 study results*. British Columbia Ministry of Environment, Lands and Parks, Castlegar.
- SAS (SAS Institute). 2008. *The QuantReg procedure*. SAS/STAT 9.2 user's guide. SAS Institute, Cary, North Carolina.
- Traill, L. W., C. J. A. Bradshaw, and B. W. Brook. 2007. Minimum viable population size: a meta-analysis of 30 years of published estimates. *Biological Conservation* 139:159–166.
- Wood, C., D. Sneep, S. McAdam, J. Korman, and T. Hatfield. 2007. *Recovery potential assessment for white sturgeon*. Department of Fisheries and Oceans, Research Document 2007/003, Nanaimo, British Columbia.
- Yesaki, T. Y., R. Ek, J. Siple, J. P. Van Eenennaam, and S. I. Doroshov. 2002. The effects of iodophor disinfection and transportation on the survival to hatch of fertilized white sturgeon (*Acipenser transmontanus*) eggs. *Journal of Applied Ichthyology* 18:639–641.
- Zhou, K. Q., and S. L. Portnoy. 1996. Direct use of regression quantiles to construct confidence sets in linear models. *Annals of Statistics* 24:287–306.

Appendix: Sources of Data

- Beamesderfer, R. C. P., T. A. Rien, and A. A. Nigro. 1995. Differences in the dynamics and potential production of impounded and unimpounded white sturgeon populations in the lower Columbia River. *Transactions of the American Fisheries Society* 124:857–872.
- Cochnauer, T. G. 1983. Abundance, distribution, growth, and management of white sturgeon (*Acipenser transmontanus*) in the middle Snake River, Idaho. Report to Idaho Power Company, Boise.
- Coon, J. C., R. R. Ringe, and T. C. Bjornn. 1977. Abundance, growth, and movements of white sturgeon in the mid-Snake River. University of Idaho, Idaho Water Resources Research Institute, Research Technical Completion Report, Project B-026-IDA, Moscow.
- DeVore, J. D., B. W. James, C. A. Tracy, and D. A. Hale. 1995. Dynamics and potential production of white sturgeon in the unimpounded lower Columbia River. *Transactions of the American Fisheries Society* 124:845–856.
- Everett, S., and M. Tuell. 2003. Evaluate potential means of rebuilding sturgeon populations in the Snake River between Lower Granite and Hells Canyon dams: 2001 annual report. Bonneville Power Administration, DOE/BP-00004046-1, Portland, Oregon.
- Golder Associates. 2003. White sturgeon investigations in Priest Rapids and Wanapum reservoirs on the middle Columbia River, Washington, U.S.A. Report prepared for Public Utility District No. 2 of Grant County, Ephrata, Washington.
- Golder Associates. 2004a. Proposed methodology for white sturgeon enhancement in Rocky Reach Reservoir. Report prepared for Public Utility District No. 1 of Chelan County, Wenatchee, Washington.
- Golder Associates. 2004b. Upper Columbia white sturgeon stock monitoring and data management program. British Columbia Ministry of Water, Land and Air Protection, Nelson.
- Golder Associates. 2005a. Upper Columbia white sturgeon stock monitoring and data management program. British Columbia Ministry of Water, Land and Air Protection, Nelson.
- Golder Associates. 2005b. A synthesis of white sturgeon investigations in Arrow Reservoir, B.C., 1995–2003. British Columbia Hydropower, Castlegar, British Columbia.
- Golder Associates. 2006. Nechako River white sturgeon tagging project: 2005 data report. British Columbia Ministry of Environment, Prince George.
- Hildebrand, L., C. McLeod, and S. McKenzie. 1999. Status and management of white sturgeon in the Columbia River in British Columbia, Canada: an overview. *Journal of Applied Ichthyology* 15:164–172.
- Irvine, R. L., D. C. Schmidt, and L. R. Hildebrand. 2007. Population status of white sturgeon in the lower Columbia River within Canada. *Transactions of the American Fisheries Society* 136:1472–1479.
- Jerald, T. 2007. White sturgeon (*Acipenser transmontanus*) population assessment and preferred habitats in Wells Dam Reservoir. Central Washington University, Ellensburg.
- Korman, J., and C. Walters. 2001. Nechako River white sturgeon recovery planning: summary of stock assessment and October 2–3, 2000, workshop. Prepared by Ecometric Research for British Columbia Fisheries, Victoria.
- Lane, D. E. 1991. Status of the white sturgeon, *Acipenser transmontanus*, in Canada. *Canadian Field Naturalist* 105:161–168.
- Leibe, R., G. Sykes, and R. Manson. 2007. Adult white sturgeon monitoring: Nechako River, 2006. Prepared by Triton Environmental for Alcan Primary Metal, Vanderhoof, British Columbia.
- Lepla, K. B. 1994. White sturgeon abundance and associated habitat in Lower Granite Reservoir, Washington. Master's thesis. University of Idaho, Moscow.
- Lepla, K. B., J. Anderson, and P. Bates. 2002. An assessment of white sturgeon in the Shoshone Falls–Upper Salmon Falls reach of the Snake River. Idaho Power Company, Boise.
- Lepla, K., P. Bates, and B. Bentz. 2004. Stock assessments of Snake River white sturgeon below upper and lower Salmon Falls dams. Idaho Power Company, Boise.
- Lepla, K. B., and J. A. Chandler. 1995. A survey of white sturgeon in the Bliss Reach of the middle Snake River, Idaho. Idaho Power Company, Technical Report E.3.1-E, Boise.
- Lepla, K. B., and J. A. Chandler. 1995. A survey of white sturgeon in the lower Salmon Falls reach of the middle Snake River, Idaho. Idaho Power Company, Technical Report E.3.1-B, Boise.
- Lepla, K. B., and J. A. Chandler. 1997. Status of white sturgeon in the C. J. Strike reach of the middle Snake River, Idaho. Idaho Power Company, Technical Report E.3.1-B, Boise.
- Lepla, K. B., J. A. Chandler, and P. Bates. 2001. Status of Snake River white sturgeon associated with the Hells Canyon Complex. Chapter 1 in K. Lepla, editor. Status and habitat use of Snake River white sturgeon associated with the Hells Canyon Complex. Idaho Power Company, Technical Report, Appendix E.3.1-6, Boise.
- Lukens, J. R. 1981. Status of white sturgeon populations in the Snake River, lower Salmon to Shoshone Falls and Bliss Dam to Givens Hot Spring. Idaho Department of Fish and Game, Report to Idaho Power Company, Boise.
- Lukens, J. R. 1985. Hells Canyon fishery investigations. Idaho Department of Fish and Game, Job Performance Report, Project F-73-R-7, Boise.
- Nelson, T. C., W. J. Gazey, and K. K. English. 2007. Status of white sturgeon in the lower Fraser River: report on the findings of the lower Fraser River white sturgeon monitoring and assessment program, 2006. Report prepared for the Fraser River Sturgeon Conservation Society, Vancouver.
- Nelson, T. C., W. J. Gazey, K. K. English, and M. L. Rosenau. 2004. Status of white sturgeon in the lower Fraser River. Fraser River Sturgeon Conservation Society, Vancouver.
- Pacific States Marine Fisheries Commission. 1992. White sturgeon management framework plan. Pacific States Marine Fisheries Commission, Portland, Oregon.
- Paragamian, V. L., R. C. P. Beamesderfer, and S. C. Ireland. 2005. Status, population dynamics, and future prospects of the endangered Kootenai River white sturgeon

- population with and without hatchery intervention. *Transactions of the American Fisheries Society* 134:518–532.
- Perrin, C. J., L. L. Rempel, and M. L. Rosenau. 2003. White sturgeon spawning habitat in an unregulated river: Fraser River, Canada. *Transactions of the American Fisheries Society* 132:154–165.
- Ptolemy, J., and R. Vennesland. 2003. Update COSEWIC status report on the white sturgeon *Acipenser transmontanus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa. Available: lbc.leg.bc.ca/public/pubdocs/bcdocs/362040/. (August 2010).
- Rien, T. A., and K. T. Beiningen. 1997. Effects of mitigative measures on productivity of white sturgeon populations in the Columbia River downstream from McNary Dam, and determine the status and habitat requirements of white sturgeon populations in the Columbia and Snake rivers upstream from McNary Dam. Bonneville Power Administration, Portland, Oregon.
- Rien, T., M. Hughes, J. Kern, O. Langness, D. Gilliland, B. Cady, B. James, M. Parsley, D. Gadowski, P. Kofoot, K. Kappenman, B. Parker, M. Webb, C. Anthony, C. Schreck, and M. Fitzpatrick. 2005. White sturgeon mitigation and restoration in the Columbia and Snake rivers upstream from Bonneville Dam. Bonneville Power Administration, Portland, Oregon.
- Rien, T., M. Hughes, J. Kern, O. Langness, D. Gilliland, B. Cady, B. James, M. Parsley, D. Gadowski, P. Kofoot, K. Kappenman, B. Parker, M. Webb, C. Anthony, C. Schreck, and M. Fitzpatrick. 2006. White sturgeon mitigation and restoration in the Columbia and Snake rivers upstream from Bonneville Dam. Bonneville Power Administration, Portland, Oregon.
- RL&L Environmental Services. 1996. The distribution and status of white sturgeon in isolated water bodies within the Columbia River basin in B.C.: 1995 study results. British Columbia Ministry of Environment, Lands and Parks, Castlegar.
- RL&L Environmental Services. 1997. Columbia River white sturgeon investigations: 1996 study results. British Columbia Ministry of Environment, Lands and Parks, Castlegar.
- RL&L Environmental Services. 1999. White sturgeon investigations in Arrow Reservoir, B.C. British Columbia Ministry of Environment, Lands and Parks, Castlegar.
- RL&L Environmental Services. 2000. Fraser River white sturgeon monitoring program: comprehensive report (1995 to 1999). British Columbia Fisheries, Castlegar.
- Upper Columbia River Recovery Team. 2002. Draft upper Columbia River white sturgeon recovery and management plan. Upper Columbia River Recovery Team, Prince George, British Columbia. Available: lbc.leg.bc.ca/public/pubdocs/bcdocs/362040/. (August 2010).
- Ward, D. L. 1998. Effects of mitigative measures on productivity of white sturgeon populations in the Columbia River downstream from McNary Dam, and determine the status and habitat requirements of white sturgeon populations in the Columbia and Snake rivers upstream from McNary Dam. Bonneville Power Administration, Portland, Oregon.
- Ward, D. L. 1999. Effects of mitigative measures on productivity of white sturgeon populations in the Columbia River downstream from McNary Dam, and determine the status and habitat requirements of white sturgeon populations in the Columbia and Snake rivers upstream from McNary Dam. Bonneville Power Administration, Portland, Oregon.
- Ward, D. L. 2000. White sturgeon mitigation and restoration in the Columbia and Snake rivers upstream from Bonneville Dam. Bonneville Power Administration, Portland, Oregon.
- Ward, D., J. Holmes, J. Kern, M. Hughes, T. Rien, O. Langness, D. Gilliland, B. Cady, B. James, J. DeVore, D. Gadowski, M. Parsley, P. Kofoot, K. Kappenman, B. Parker, M. Webb, C. Anthony, C. Schreck, and M. Fitzpatrick. 2003. White sturgeon mitigation and restoration in the Columbia and Snake rivers upstream from Bonneville Dam. Bonneville Power Administration, Portland, Oregon.
- Wood, C., D. Sneep, S. McAdam, J. Korman, and T. Hatfield. 2007. Recovery potential assessment for white sturgeon. Department of Fisheries and Oceans, Research Document 2007/003, Nanaimo, British Columbia.
- Yarmish, J. A., and B. M. Toth. 2002. 2001/2002 assessment of upper Fraser River white sturgeon. Report produced by Lheidli T'enneh First Nation for the Upper Fraser River Nechako Fisheries Council and Fisheries Renewal BC, Prince George, British Columbia.