

Evaluating Risks for Threatened Aquatic Species: the Shortnose Sturgeon in the Connecticut River

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Abstract.—The shortnose sturgeon, *Acipenser brevirostrum*, is a long-lived species that grows slowly, matures at an advanced age, and spawns only intermittently. In the Connecticut River, there are two distinct subpopulations of shortnose sturgeon, which have been separated by the Holyoke Dam for 157 years. My research addressed the viability and persistence for these two separate populations and the effects of dispersal, variation in survival and reproduction, and catastrophes. My risk-based approach used a stage-based metapopulation model that I constructed in RAMAS[®] GIS incorporating the available data. Based on the existing data, this population model for the shortnose sturgeon metapopulation in the Connecticut River made several predictions. The observed stability of the two subpopulations was possible either: with reproduction in both upper and lower subpopulations and small to moderate rates of dispersal between them; or with no reproduction in the lower subpopulation, very high reproduction in the upper subpopulation and high rate of net downstream dispersal. My results provided estimates of extinction risk for the shortnose sturgeon metapopulation under various management options and highlighted three key areas for future research, demonstrating the value of a risk-based approach. This approach is particularly useful for management of long-lived aquatic species.

In the Connecticut River, there are two distinct subpopulations of shortnose sturgeon, *Acipenser brevirostrum*, which have been separated by the Holyoke Dam for 157 years (Taubert 1980a; Buckley 1982; Dadswell et al. 1984; Buckley and Kynard 1985). The upstream subpopulation from Holyoke Dam at river kilometer (rkm) 140 to Turners Falls Dam (rkm 200) is landlocked with access only to freshwater. The downstream subpopulation from Holyoke Dam south to Long Island Sound has access to rich estuarine feeding grounds, although another dam, Enfield Dam (rkm 110), must be crossed (Buckley and Kynard 1985). The Holyoke Dam might interfere with the successful dispersal upstream and spawning of the lower subpopulation (Kynard 1997), as well as block to a large extent the downstream dispersal of the upper subpopulation to the rich feeding grounds. There are fish lifts at the Holyoke Dam in operation to aid upstream movement for at least part of the year (April–October), although, only 81 shortnose sturgeon were lifted from 1975 to 1995 (Kynard 1998).

This research addresses the issue of viability and persistence for these two separate subpopulations using a stage-based population modeling approach. The stage-based approach provides an important tool to evaluate the long-term survival

of populations and the effects of various management strategies. In this case, I used population modeling to assess the impacts of rates of dispersal over the Holyoke Dam and catastrophes and the long-term survival of the upper and lower Connecticut River subpopulations.

The shortnose sturgeon is an endangered species that inhabits Atlantic coast rivers from Saint John River, New Brunswick, Canada to the St. Johns River, Florida, United States (Vladykov and Greeley 1963; Dadswell et al. 1984; Kynard 1997). It is a long-lived species that grows slowly, matures at an advanced age, and spawns only intermittently. Additionally, these fish show a general pattern of dispersal downstream in summer to feed and upstream in later winter or early spring to spawn (Kynard 1997). Once shortnose sturgeon attain adult size (45–55 cm or 3–10 years, depending on latitude), they begin seasonal migration downstream in fall and upstream in spring. In the late winter to mid-spring, a portion (30–40% of adults; Kynard 1997) of the population spawns “en masse” at a location upstream determined by a suitable temperature and flow rate and bottom type. Males first spawn at 3–5 years, while females first spawn from 6 to 12 years. Fecundity estimates range from 27,000–208,000 eggs/fish (Dadswell 1979; Dadswell et al. 1984). Eggs are released and

quickly sink to the bottom becoming adhesive; hatching of the feeding larvae occurs in approximately 8–12 d (Meehan 1910). Little is known about the survival rates of the larvae and juvenile but the early growth is rapid (e.g. 3 mm every 10 d; Taubert 1980a, 1980b).

These characteristics make the shortnose sturgeon vulnerable to extinction (Parent and Schriml 1995; Auer 1996; Boreman 1997; Gross et al. 2001, this volume). The interference with seasonal migrations and potential loss of spawning habitat, usually caused by dams or other obstructions, are thought to be a major factor in the reduced size of sturgeon populations (Parent and Schriml 1995; Auer 1996).

I investigated the consequences to long-term viability of the "metapopulation" (subpopulations linked by migration) under different scenarios of dispersal. Since there is little direct evidence that spawning is occurring below the dam but is well documented above the dam (although there is some indirect evidence, see Buckley 1982; Buckley and Kynard 1983), what effect would this have on the long-term viability on these two subpopulations? Additionally, how would varying levels of one-way and two-way dispersal affect the stability of the metapopulation?

Methods

To assess the probability of extinction for the Connecticut River shortnose sturgeon subpopulations, I constructed a stage-based population model in RAMAS[®] GIS (Akçakaya 1997). As a simplification, a stage-based approach was used rather than represent every year of life up to the maximum life span of 60 years individually. Only females were included in this model, although the annual survival rates for adults used were based on males and females. General assumptions in the model were that: sturgeon begin maturing at age five; all adults (5 years old and older) had the same annual survival probabilities; the annual growth rate of the population was near 1.0 (i.e., on average the population did not have a tendency to grow or decline); and annual survival rates and fecundities fluctuated from year to year and these fluctuations were fully correlated between the upper and lower subpopulations (i.e., environmental conditions similarly affected the two subpopulations). The two subpopulations upper (upstream of Holyoke Dam) and lower (downstream of Holyoke Dam) were considered indi-

vidual subpopulations, that comprised a larger metapopulation connected loosely by occasional dispersal over the Holyoke Dam. For each set of conditions, I ran a minimum of 10,000 replications, each for 100 years.

Each population consisted of ten stages, one stage for each of the first nine age-classes and all older individuals were lumped together as stage 10. Each stage included individuals from that age up to the age of the next stage (e.g., stage 1 contained individuals from 1 to 2 years of age). Whenever possible, empirical data were used in the model. Where data were scarce, a detailed description of the values chosen is provided. A summary of the parameters used for the model is shown in Table 1.

Annual Survival

Annual survival of sturgeon adults is estimated at 0.88 (Taubert 1980a). This estimate is based on mark-recapture studies that predominantly included fish ≥ 45 cm in fork length. Survival probabilities for life history stages other than adults, i.e., fish < 45 cm, are unknown. I assumed the probability of surviving: from age one to two as 10%, from two to three as 22%, from three to four as 51%, from four to five as 62%, and > 5 years of age as 88% annually. These values were selected for two reasons. First, it is likely that survival of adults is greater than that of juveniles. Second, field observations suggest that the subpopulations have been stable since the 1970s (Taubert 1980a, 1980b; Savoy and Shake 1992). Thus, the survival rates were selected to produce a population growth rate near 1.00.

Table 1. The parameters used in the shortnose population model; the values represent the annual means and standard deviations (S.D.).

Parameter	Mean	S.D.
Survival to age		
1 year	0.0066	
2	0.10	0.010
3	0.22	0.022
4	0.51	0.051
5	0.62	0.062
>5	0.88	0.088
Reproduction ^a	32.92	6.584
Dispersal		
Upstream	0.005	
Downstream	0.001 to 0.100	

^a number of female eggs produced which survive to age 1 year

Initial Abundance

Initial abundance based on population estimates from the literature (Dadswell et al. 1984; Savoy and Shake 1994; Kynard 1997), was 800 adults (≥ 45 cm FL) for the lower subpopulation from Holyoke Dam to Long Island Sound and an upstream subpopulation with 400 adults. I assumed an initial stable age distribution since field data suggest that abundance has been stable for the last 30 years. The total female population size and abundance in each stage were extrapolated from the estimate of adults (assumed ≥ 5 years), a 1:1 sex ratio, and the assumption of a stable age distribution.

Reproduction

Fecundity, based on captured individual females, is extremely variable. One estimate (Dadswell 1979; Dadswell et al. 1984) found 49,000–208,000 eggs per fish in the Saint John River, New Brunswick, Canada. In this population model, though, stage 1 represents fish that begin the time step of simulation at age one year. Reproduction in the model includes both the reproductive process of production of eggs and the survival of daughters to 1 year of age.

The shortnose sturgeon reaches maturity throughout its range at a fork length of 45–55 cm for males and females (Dadswell et al. 1984); in the model, reproduction began at stage 10. Individual fish, though, do not reproduce every year; spawning generally occurs every two to four years in the late winter or spring (Dadswell et al. 1984; Bain 1997). Based on these data and the described assumptions, the reproductive output for mature females was based on a series of estimations (Boreman 1997). First, I estimated the fork length for each age-class from the equation derived by Buckley (Dadswell et al. 1984) for the lower Connecticut River. Second, using the weight-length relationship for the lower Connecticut River (Dadswell et al. 1984), the average weight was determined for each age-class. Third, the number of eggs potentially produced for each age-class was based on an average of 11,568 eggs/kg of body weight (Dadswell et al. 1984). This value for the average number of eggs produced per each age-class was multiplied by the fraction of females mature at each age based on measurements made by Dovel (1981), and the frequency of spawning. This multiplication yielded the total number of eggs produced by each age-class. Fourth, only the daughters were included in the model.

The reproduction value used in the stage matrix, therefore, was the number of daughter eggs (half of the total number of eggs assuming a sex ratio of 1:1) produced, multiplied by the probability of hatching of 0.066 estimated by Meehan (1910), and by the probability of surviving from egg to 1 year (assumed since unknown empirically) of 0.10. The assumption that survival to age one is 0.10 is not crucial because the survival parameters in the model (see Table 1) were fit to give a growth rate near 1.00.

Dispersal

Based on fish lift data (Kynard 1998), a total of 81 shortnose sturgeon have been lifted over Holyoke Dam in the 21 years that the fish lift has been operated, resulting in an annual average of 3.6 (± 2.75) fish per year. Assuming this average in a downstream subpopulation of 800 adults, approximately 0.5% of the adult females were lifted each year over the dam, assuming a sex ratio of 1:1 and that only adults migrated. Downstream dispersal (C. Tomichuk, Northeast Utilities, personal communication), based on observations, has been estimated as 100 fish in 100 years, which is approximately 0.1% of the adult females of the upstream subpopulation. I examined a number of upstream and downstream dispersal rates in the model, ranging from 0.001 to 0.500. Dispersal in the model represents the percentage of a population that moves permanently from one population to another in a single year, e.g., 0.001 means 0.1% of the population moves from one population to another each year.

Annual Variation

An important aspect of population modeling is the incorporation of stochasticity. A stochastic population model, one that includes variability (especially environmental), more accurately reflects population growth in a dynamic world than a model that utilizes static parameters. In this shortnose sturgeon model, environmental stochasticity was modeled as variation around the annual mean demographic parameters with 10% and 20% coefficients of variation (standard deviation/mean) for the survival probabilities and fecundities, respectively. The values chosen were similar to those estimated for other species such as cod (Ginzburg et al. 1990).

Results

The metapopulation model performed realistically. Both the upper and lower shortnose subpopulations, independently, were stationary (neither increased nor decreased) in the absence of density dependence under the assumed growth rate of 1.004. The probability of extinction in 100 years was 0.0%. In contrast, if there was no reproduction in the lower subpopulation, the median time to extinction predicted under the model was 16.8 years and the probability of extinction was 100%, despite an initial abundance of 3810 females.

Extinction risks declined dramatically as the reproduction in the lower subpopulation was increased from 0% to 100% of baseline (values in Table 1 are assumed to be "baseline"). If reproduction in the lower subpopulation was at least 75% of baseline, the probability of extinction was 1% or less and the median time to extinction was greater than 100 years. In general, population abundance is just slightly increasing over time with baseline levels of reproduction but sharply drops to zero in less than 20 years if there is no reproduction (Figure 1a). The probability of a decline in abundance in 100 years decreases as the size of the decline increases (Figure 1b); the probability of a 10% decline is near 45% whereas the probability of a 70% decline is less than 5% with normal reproduction levels. The probability of a large decline (>50%) is quite low (less than 10% probability in 100 years) with normal reproduction levels but is 100% if there is no reproduction.

Under exponential growth, if fish only migrated downstream and the lower subpopulation had no reproduction, the metapopulation (upper and lower together) showed a decline as the lower subpopulation siphoned individuals from the upper subpopulation. With this one-way dispersal, the higher rates of dispersal resulted in lower final mean abundances. Under downstream dispersal rates of 0.1–1% annually, the metapopulation had a zero probability of going extinct (Figure 2b), but the final abundance of the combined subpopulations decreased to 16–35% of the initial abundance (Figure 2a).

When the downstream dispersal rate increased to 10–30%, there was an even larger decline in the final abundance of the metapopulation to one individual or zero, and the probability of extinction of the metapopulation reached 100% in 60 years. Median time to extinction for the metapopulation under these dispersal rates of

10%, 20% and 30% were 43.0, 26.0, and 22.1 years, respectively. For the lower subpopulation, dispersal rates of 0.1–30% did not mitigate its severe decline in abundance under no reproduction.

With inclusion of baseline levels of reproduction (as defined in Table 1) for both the upper and lower subpopulations, the effects of one-way (downstream) dispersal on the extinction risk were undetectable even at rates of 50%. The number of fish in the upper subpopulation, though, decreased 2–100% as the downstream dispersal rate increased. Normal reproduction levels, though, were insufficient to maintain both subpopulations at their initial abundance under any of these one-way dispersal rates. Overall the probability of extinction was zero for the metapopulation with reproduction in both subpopulations and downstream dispersal.

What level of compensation would be required to offset the loss from the upper subpopulation when the lower subpopulation has no reproduction? If the downstream dispersal rate was only 0.1% annually, increasing reproduction of the upper subpopulation to 125%, 150%, and 200% of the baseline value reduced the extinction probabilities to 0% for the whole metapopulation, but the mean final abundance for the lower subpopulation was 0, 17, and 100 females, respectively. Even with 200% of baseline reproduction in the upper subpopulation, the lower subpopulation went extinct, whereas the upper subpopulation and the whole metapopulation persisted for the next 100 years. An increasing level of reproduction was required as the dispersal rate was increased to maintain both subpopulations at a stable level over the course of 100 years. Increasing reproduction in the upper subpopulation 3, 8, and 19 times the baseline were necessary for stability under dispersal rates of 10%, 20%, and 30%, respectively.

Looking at the problem another way, I allowed two-way dispersal and the reproduction of the lower subpopulation was increased from zero to 25%, 50%, or 75% of baseline. With no reproduction in the lower subpopulation, a decline in abundance was likely with downstream dispersal rates between 0.1% and 10% and an upstream dispersal rate of 0.5% (Figure 3a). Under a dispersal rate of 0.5% in both directions, the probability of quasiextinction was zero but the lower subpopulation did not persist near its initial abundance unless it had baseline reproduction. If normal reproduction occurred in both the upper and lower subpopulations, the probability of a decline

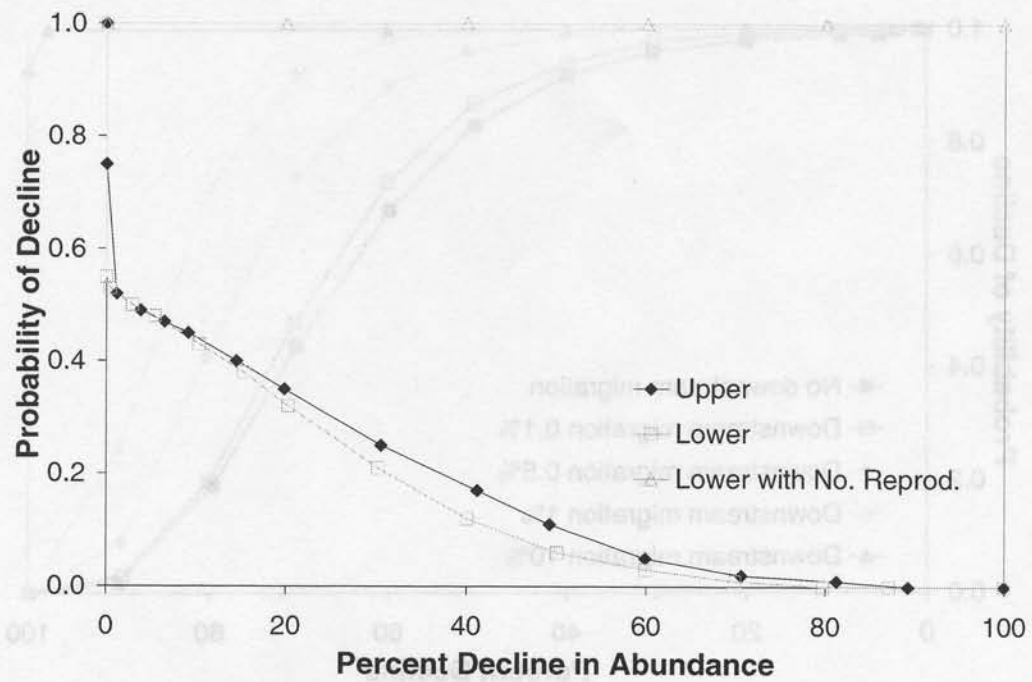
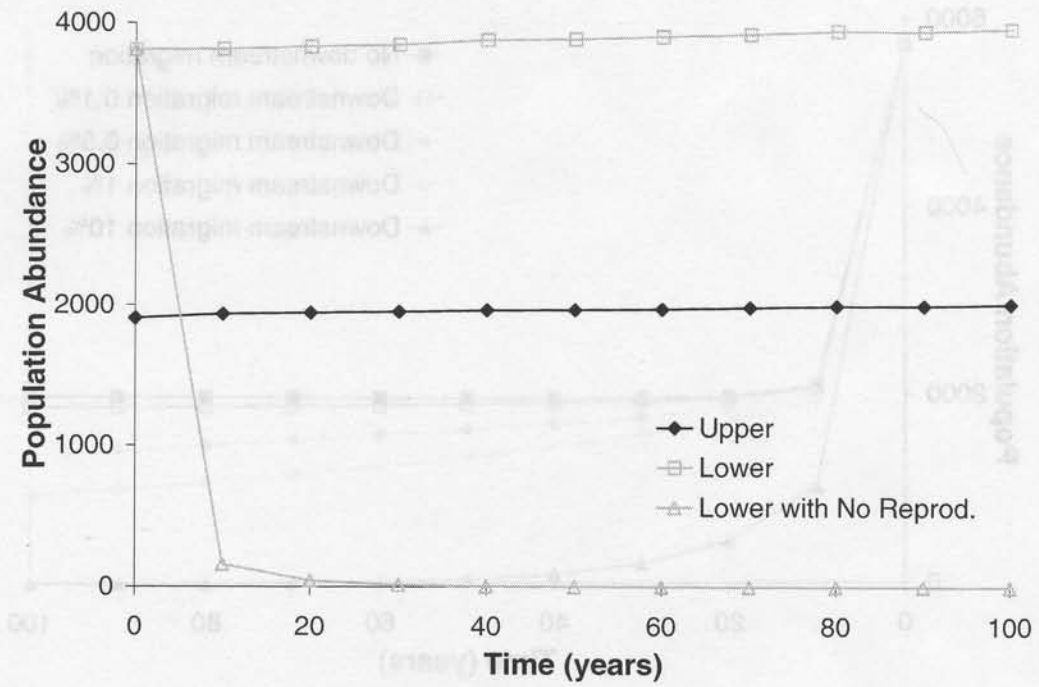


Figure 1. Shown are the (a) mean population abundance over time and (b) risk of decline in mean female abundance, in 100 years, as a percentage of the initial abundance, for the upper, lower, and lower with no reproduction shortnose populations.

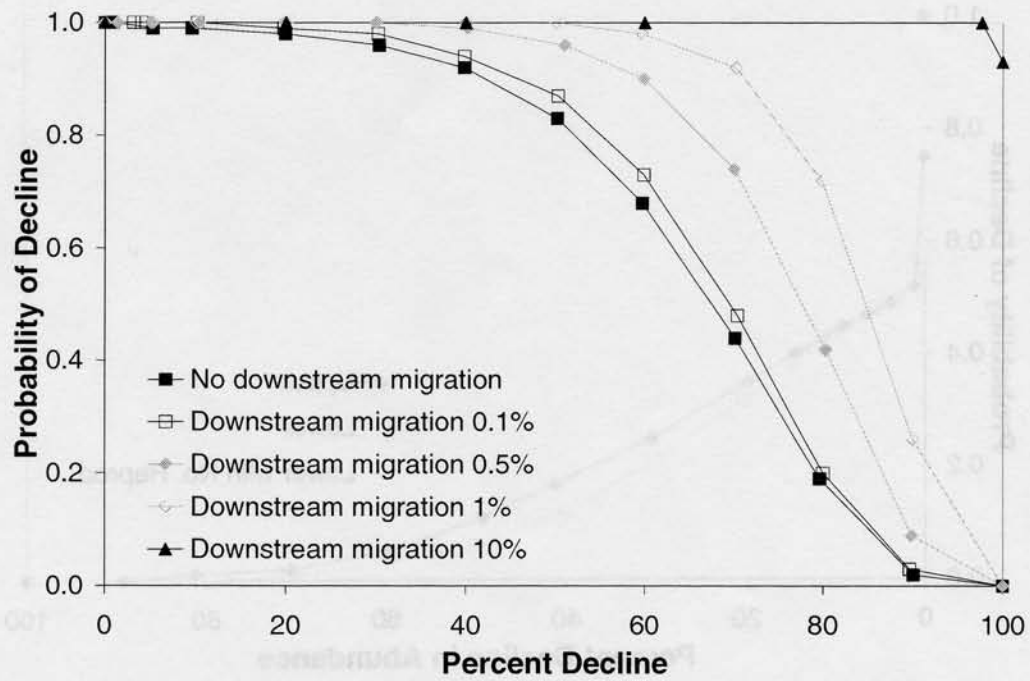
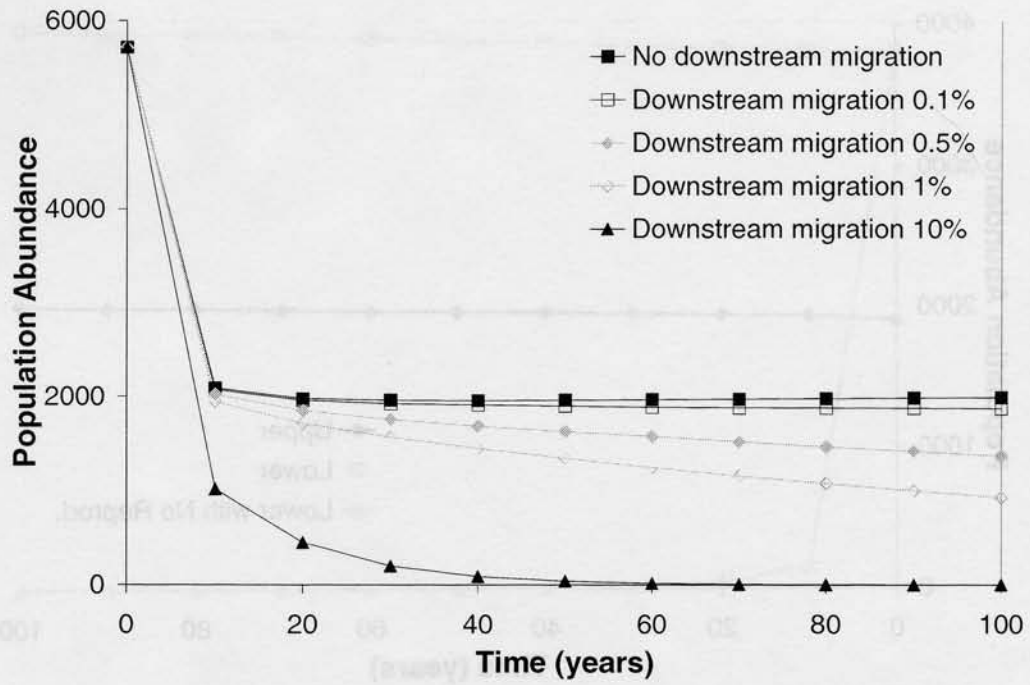


Figure 2. The mean population abundance over time (a) and the risk of a decline in 100 years in abundance (b) for the whole shortnose metapopulation (both upper and lower populations) with 0, 0.1, 0.5, 1.0 or 10.0% downstream dispersal annually.

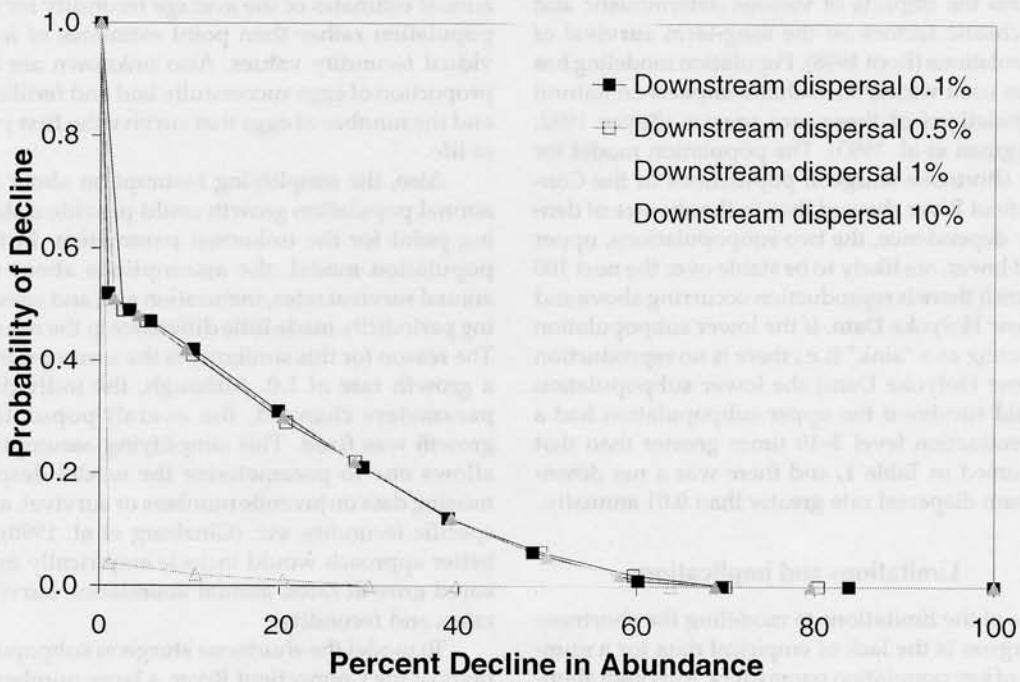
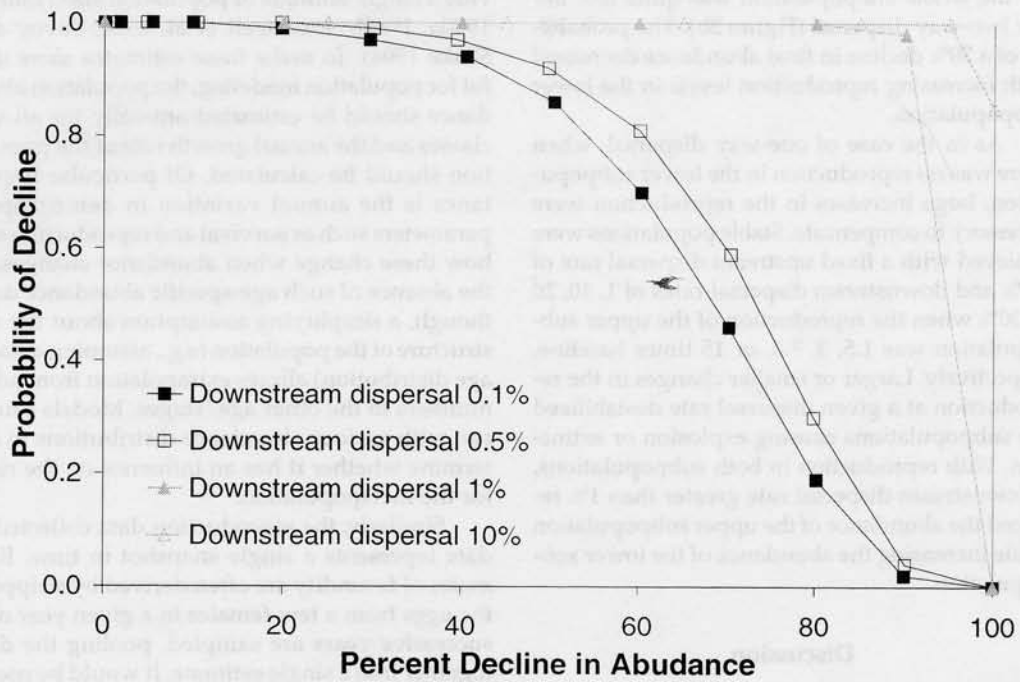


Figure 3. The risk of a decline in 100 years in abundance, as a percentage of the initial abundance, for the shortnose sturgeon metapopulation with 0.5% upstream dispersal and downstream dispersal of 0.1, 0.5, 1.0, or 10.0% annually when (a) the lower population has no reproduction and (b) when both populations have reproduction.

for the whole subpopulation was quite low under two-way dispersal (Figure 3b). The probability of a 50% decline in final abundance decreased with increasing reproduction levels in the lower subpopulation.

As in the case of one-way dispersal, when there was no reproduction in the lower subpopulation, large increases in the reproduction were necessary to compensate. Stable populations were achieved with a fixed upstream dispersal rate of 0.5% and downstream dispersal rates of 1, 10, 20 or 30% when the reproduction of the upper subpopulation was 1.5, 3, 7.5, or 15 times baseline, respectively. Larger or smaller changes in the reproduction at a given dispersal rate destabilized the subpopulations causing explosion or extinction. With reproduction in both subpopulations, a downstream dispersal rate greater than 1% reduced the abundance of the upper subpopulation while increasing the abundance of the lower subpopulation.

Discussion

To conserve rare species, there is a critical need to assess the impacts of various deterministic and stochastic factors on the long-term survival of populations (Root 1998). Population modeling has been used widely to evaluate impacts on natural populations of these rare species (Boyce 1992; Burgman et al. 1993). The population model for the shortnose sturgeon populations in the Connecticut River showed that, in the absence of density dependence, the two subpopulations, upper and lower, are likely to be stable over the next 100 years if there is reproduction occurring above and below Holyoke Dam. If the lower subpopulation is acting as a "sink" (i.e., there is no reproduction below Holyoke Dam) the lower subpopulation could survive if the upper subpopulation had a reproduction level 3–19 times greater than that assumed in Table 1, and there was a net downstream dispersal rate greater than 0.01 annually.

Limitations and implications

One of the limitations to modeling the shortnose sturgeon is the lack of empirical data for a number of key population parameters. Although abundance estimates exist for the Connecticut subpopulations of shortnose, these estimates are based on mark-recapture studies with a limited number of individuals and only adults included. Successive years of sampling are pooled to pro-

vide a single estimate of population size (Taubert 1980a, 1980b; Dadswell et al. 1984; Savoy and Shake 1994). To make these estimates more useful for population modeling, the population abundance should be estimated annually for all size classes and the annual growth rate of the population should be calculated. Of particular importance is the annual variation in demographic parameters such as survival and reproduction and how these change when abundance changes. In the absence of such age-specific abundance data, though, a simplifying assumption about the age structure of the population (e.g., assuming a stable age distribution) allows extrapolation from adult numbers to the other age/stages. Models can be run with various abundance distributions to determine whether it has an influence on the risks for the metapopulation.

Similarly, the reproduction data collected to date represents a single snapshot in time. Estimates of fecundity are often derived by stripping the eggs from a few females in a given year or if successive years are sampled, pooling the data together into a single estimate. It would be useful from a population modeling perspective to have annual estimates of the average fecundity for the population rather than point estimates of individual fecundity values. Also unknown are the proportion of eggs successfully laid and fertilized and the number of eggs that survive the first year of life.

Also, the simplifying assumption about the annual population growth could provide a starting point for the unknown parameters. In this population model, the assumptions about the annual survival rates, maturation age, and spawning periodicity made little difference in the results. The reason for this similarity is the assumption of a growth rate of 1.0. Although, the individual parameters changed, the overall population growth was fixed. This simplifying assumption allows one to parameterize the model despite missing data on juvenile numbers or survival, age-specific fecundity, etc. (Ginzburg et al. 1990). A better approach would include empirically measured growth rates, annual abundance, survival rates, and fecundity.

To model the shortnose sturgeon subpopulations of the Connecticut River, a large number of assumptions were made, that could have an impact of the predictions. This research, therefore, highlights three key areas for future research: (1) better estimates of the annual reproduction and its temporal variation in both the upper and lower

subpopulation; (2) more accurate measurement of the rate of downstream movement; (3) annual survival rates, and their temporal variation, for ages less than 5 years.

The model suggests that increasing the dispersal may have a large negative impact on the metapopulation abundance, especially if there is no increase in the downstream dispersal and/or there is no reproduction in the lower subpopulation. This fits with a source-sink model of population dynamics where one population siphons individuals from another population to the source's detriment (Pulliam 1988, 1996). Therefore, the model suggests that supplementation, habitat improvement or other management strategies that increase the reproduction in the upper and lower subpopulations would be better for the long-term survival of the shortnose metapopulation than increasing dispersal among the subpopulations (assuming little or no reproduction occurs in the lower subpopulation).

Acknowledgments

Funding for this research was provided by Electric Power Research Institute (EPRI) and Northeast Utilities (NU). I would especially like to thank Doug Dixon (EPRI), Christine Tomichek (NU), Cori Rose (National Marine Fisheries Service), Tom Savoy (Marine Fisheries Office), John Boreman (Woods Hole Oceanographic Institute), Saul Salia (University of Rhode Island), Resit Akçakaya (Applied Biomathematics), Christopher Grogan (University of Massachusetts, Amherst), Lev Ginzburg (Applied Biomathematics), David Secor (Chesapeake Biological Laboratory), and two anonymous reviewers for their valuable assistance and input.

References

- Akçakaya, H. R. 1997. RAMAS GIS: Linking landscape data with population viability analysis. Applied Biomathematics, Setauket, New York.
- Auer, N. A. 1996. Importance of habitat and migration to sturgeons with emphasis on lake sturgeon. *Canadian Journal of Fisheries and Aquatic Sciences* 53(Supplement 1):152-160.
- Bain, M. B. 1997. Atlantic and shortnose sturgeons of the Hudson River: common and divergent life history attributes. *Environmental Biology of Fishes* 48:347-358.
- Boreman, J. 1997. Sensitivity of North American sturgeon and paddlefish to fishing mortality. *Environmental Biology of Fishes* 48:399-406.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23:481-506.
- Buckley, J. L. 1982. Seasonal movement, reproduction, and artificial spawning of shortnose sturgeon (*Acipenser brevirostrum*) from the Connecticut River. Master's thesis. University of Massachusetts, Amherst.
- Buckley, J., and B. Kynard. 1983. Spawning area habitat characteristics, population estimate and age structure of shortnose sturgeon (*Acipenser brevirostrum*) in the Connecticut River below Holyoke Dam, Holyoke, Massachusetts. Final report of Massachusetts Cooperative Fishery Research Unit to Northeast Utilities, University of Massachusetts.
- Buckley, J., and B. Kynard. 1985. Yearly movements of shortnose sturgeon in the Connecticut River. *Transactions of the American Fisheries Society* 114:813-820.
- Burgman, M. A., S. Ferson, and H. R. Akçakaya. 1993. *Risk Assessment in Conservation Biology*. Chapman and Hall, London.
- Dadswell, M. J. 1979. Biology and population characteristics of the shortnose sturgeon, *Acipenser brevirostrum* LeSueur 1818 (Osteichtheys: Acipenseridae), in the Saint John River estuary, New Brunswick, Canada. *Canadian Journal of Zoology* 57:2186-2210.
- Dadswell, M. J., B. D. Taubert, T. S. Squiers, D. Marchette, and J. Buckley. 1984. Synopsis of biological data on shortnose sturgeon, *Acipenser brevirostrum* LeSueur 1818. *FAO Fisheries Synopsis* 140:1-45.
- Dovel, W. L. 1981. The endangered shortnose sturgeon of the Hudson estuary: Its life history and vulnerability to the activities of man. The Oceanic Society. FERC Contract No. DE-AC 39-79 RC-10074.
- Ginzburg, L. R., S. Ferson, and H. R. Akçakaya. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. *Conservation Biology* 4:63-70.
- Kynard, B. 1997. Life history, latitudinal patterns, and status of shortnose sturgeon, *Acipenser brevirostrum*. *Environmental Biology of Fishes* 48:319-334.
- Kynard, B. 1998. Twenty-two years of passing shortnose sturgeon in fish lifts on the Connecticut River: What has been learned? Pages 255-264 in M. Jungwirth, S. Schmutz, and S. Weiss, editors. *Fish migration and fish bypasses*. Fishing News Books, London.
- Meehan, W. E. 1910. Experiments in sturgeon culture. *Transactions of the American Fisheries Society* 39:85-91.
- Parent, S., and L. M. Schriml. 1995. A model for the determination of fish species at risk based upon life-history traits and ecological data. *Canadian*

- Journal of Fisheries and Aquatic Sciences 52:1768-1781.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- Pulliam, H. R. 1996. Sources and sinks. Empirical evidence and population consequences. Pages 45-69 in O. E. Rhodes, R. K. Chesser, and M. H. Smith, editors. *Population Dynamics in Ecological Space and Time*. University of Chicago Press, Chicago.
- Root, K. V. 1998. Evaluating the effects of habitat quality, connectivity and catastrophes on a threatened species. *Ecological Applications* 8(3):854-865.
- Savoy, T., and Shake, D. 1992. Sturgeon status in Connecticut waters. Report of Connecticut Department of Environmental Protection to U.S. Fish and Wildlife Service, Newton Corner, Massachusetts.
- Savoy, T., and Shake, D. 1994. Anadromous fish studies in Connecticut waters. Report of Connecticut Department of Environmental Protection to U.S. Fish and Wildlife Service, Newton Corner, Massachusetts.
- Taubert, B. D. 1980a. Biology of the shortnose sturgeon, *Acipenser brevirostrum*, in the Holyoke Pool, Connecticut River, Massachusetts. Doctoral dissertation, University of Massachusetts, Amherst.
- Taubert, B. D. 1980b. Reproduction of the shortnose sturgeon (*Acipenser brevirostrum*) in Holyoke Pool, Connecticut River, Massachusetts. *Copeia* 1980:114-117.
- Vladykov, V. D.; Greeley, J. R. 1963. Order *Acipenseroidi*. Pages 24-60 in *Fishes of the western North Atlantic, volume I (III)*. Memoirs of the Sears Foundation for Marine Research, New Haven, Connecticut.