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To Stock or Not to Stock? Assessing the Restoration Potential of a Remnant American Shad Spawning Run with Hatchery Supplementation

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ARTICLE

To Stock or Not to Stock? Assessing the Restoration Potential of a Remnant American Shad Spawning Run with Hatchery Supplementation

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Abstract

Hatchery supplementation has been widely used as a restoration technique for American Shad *Alosa sapidissima* on the East Coast of the USA, but results have been equivocal. In the Penobscot River, Maine, dam removals and other improvements to fish passage will likely reestablish access to the majority of this species' historic spawning habitat. Additional efforts being considered include the stocking of larval American Shad. The decision about whether to stock a river system undergoing restoration should be made after evaluating the probability of natural recolonization and examining the costs and benefits of potentially accelerating recovery using a stocking program. However, appropriate evaluation can be confounded by a dearth of information about the starting population size and age structure of the remnant American Shad spawning run in the river. We used the Penobscot River as a case study to assess the theoretical sensitivity of recovery time to either scenario (stocking or not) by building a deterministic model of an American Shad population. This model is based on the best available estimates of size at age, fecundity, rate of iteroparity, and recruitment. Density dependence was imposed, such that the population reached a plateau at an arbitrary recovery goal of 633,000 spawning adults. Stocking had a strong accelerating effect on the time to modeled recovery (as measured by the time to reach 50% of the recovery goal) in the base model, but stocking had diminishing effects with larger population sizes. There is a diminishing return to stocking when the starting population is modestly increased. With a low starting population (a spawning run of 1,000), supplementation with 12 million larvae annually accelerated modeled recovery by 12 years. Only a 2-year acceleration was observed if the starting population was 15,000. Such a heuristic model may aid managers in assessing the costs and benefits of stocking by incorporating a structured decision framework.

Stocking is a commonly used tool in fisheries management (Molony et al. 2003), particularly for the restoration of anadromous fish stocks (Moring 1986). The decision to use hatchery products is often contentious. Stocking requires the allocation of resources, has uncertain benefits, and, in some cases, may have deleterious effects (Schramm and Piper 1995). Straying

into other populations, for example, can cause unintended consequences (Emlen 1991; Waples 1991) and may necessitate management to reduce the potential risks of unintended natural straying (Hayes and Carmichael 2002). Other risks and pitfalls of starting new hatchery rearing operations are reviewed in Molony et al. (2003). Common problems include (1) poorly

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defined objectives, (2) lack of a rigorous scientific approach, and (3) lack of clearly defined recovery indicators by which to cease stocking operations.

American Shad *Alosa sapidissima* is an anadromous clupeid native to the East Coast of North America that spawns in rivers from the St. Johns River, Florida, to the St. Lawrence River, Quebec (Liem 1966; Collette and Klein-MacPhee 2002). Since the late 1800s, a suite of anthropogenic factors has caused a decline in anadromous stocks in the genus *Alosa* along the East Coast (Bilkovic et al. 2002). Most notably, the construction of dams with inadequate fish passage has greatly reduced access to spawning and nursery grounds (Rulifson 1994). Although some fishways were constructed when the dams were built, most were recognized to be ineffective within a short time (Stevenson 1899). American Shad have become of increasing conservation concern in recent decades, as the number of spawning runs has declined to fewer than half their historic levels (Limburg et al. 2003).

Hatchery supplementation efforts for American Shad spawning runs date back more than a century, with the species first being reared and stocked in the Connecticut River in 1867. Hatchery rearing was common in many large coastal rivers by the turn of the century. By 1949, billions of American Shad larvae had been stocked by hatcheries, but spawning runs continued to decline rangewide. This was likely due to continued dam construction, deteriorating water quality, and unregulated fisheries. Due to a perceived lack of efficacy in these programs, most were halted. The Pennsylvania Fish and Boat Commission's Van Dyke Hatchery was the first modern shad hatchery, starting operations in the mid-1970s (M. Hendricks, Pennsylvania Fish and Boat Commission, personal communication). By the 1990s, other state and federal hatcheries had come online to produce shad larvae for restoration efforts from Maine to South Carolina. As with earlier efforts, these hatchery efforts have had equivocal success. Stocking often accompanies other restoration efforts, making assessment difficult or worse (Aunins 2010). Poor utilization of fishways, commercial in-river fisheries, and incidental bycatch in ocean-intercept fisheries, are now seen as the main culprits for diminished shad spawning runs, even when bolstered by hatchery supplementation (ASMFC 2007).

The Penobscot River Restoration Project (PRRP) is an ambitious cooperative effort (including Pennsylvania Power & Light Co., the Penobscot Indian Nation, six conservation groups, and state and federal agencies) to restore 11 diadromous fish species to the Penobscot River, while maintaining hydroelectric power production (Day 2006). Proposed restoration efforts include the removal of the two most seaward dams, Veazie and Great Works dams (river kilometers [rkm] 48 and 60, respectively), and modification of a third, Milford Dam (rkm 62), with improved fish passage. Further upstream, a "nature-type" bypass channel around a fourth dam, Howland Dam (rkm 100), will be installed. All fish passage improvements are planned to be complete by 2014. It is anticipated that American Shad will have access to 93% of their historic spawning habitat in the

Penobscot River watershed following project completion (Trinko Lake et al. 2012). In addition to its role in the PRRP, the Maine Department of Marine Resources (MDMR) has been proactive in developing an operational plan for the restoration of diadromous fishes to the Penobscot River. This long-term plan includes a conceptual framework for shad restoration (MDMR 2009).

Although the Penobscot River historically supported American Shad spawning runs that may have numbered as high as 2 million fish prior to the 1830s (Foster and Atkins 1869), the current spawning run is presumed to be nearly extirpated (ASMFC 2007). Habitat loss is likely a major factor behind shad declines in the Penobscot River. Currently shad are restricted to habitat below Veazie Dam, with virtually no upstream passage being available for more than 130 years. There is an extant spawning run below Veazie Dam, but it is poorly characterized, as there is no commercial fishery, targeted recreational fishing is minimal, and the fishway at Veazie Dam is not conducive to alosine passage (Haro et al. 1999). Only about 25 shad have been recorded to have passed the current fishway since its installation in 1970 (O. Cox, MDMR, unpublished data). Historically, shad accessed 145 km of main-stem habitat in the Penobscot system (Collette and Klein-MacPhee 2002). Beginning in 1771, dams excluded shad from historic spawning grounds, and by the time Bangor Dam (rkm 41; removed in 1995) was complete in 1877, the spawning run could no longer support a commercial fishery (ASMFC 2007).

While there have been no studies to obtain estimates of run size, the MDMR has conservatively estimated the spawning run to comprise as few as 1,000 adults. With the anticipated change in habitat accessibility in the Penobscot River, an area-based model predicts the potential for a sustained run size of over 633,300 fish (MDMR 2009). As with many restoration efforts coastwide, the uncertainty of the current spawning run size and the efficacy of the tools at hand confound the decision-making process. Restoration options include annually stocking 6–12 million larvae (reared from 500 to 1,200 adult American Shad from donor stock) into the Penobscot River until a restoration target of 633,300 spawners is realized for a period of five consecutive years. This option is being weighed against natural recolonization of newly accessible habitat, though a significant delay in the timeline of restoration is feared.

Until recently few tools were available with which to assess the theoretical potential for American Shad expansion into new habitat, and the available models may be unsuitable (but see Harris and Hightower 2012). Based on a simple matrix model, if the spawning run is indeed as low as 1,000, reaching the restoration goal through natural recolonization may take more than a century (MDMR 2009). This model, however, does not include life history complexity (i.e., iteroparity) and specific survival and fecundity parameters that are likely important to shad population dynamics. This management dilemma, while specific to the Penobscot River, is symptomatic of the quandary of shad restoration coastwide. To stock or not to stock? Managers must

balance risks and benefits to make informed decisions; however, a framework with which to assess sensitivity to assumptions (e.g., of starting spawning run size) and describe best-case projections of hatchery supplementation has been lacking. We sought to develop a model that would be instructive in assessing these questions. Such an approach is relevant not only to the decision of when (or if) to use hatchery supplementation but also when to cease stocking operations. We applied our shad population recovery model to the Penobscot River as a case study to probe the impacts of alternative management actions. Additionally, we assessed the relative sensitivity of a population to stocking, initial run size, and at-sea mortality.

METHODS

Model construction.—We reviewed the published literature and ASMFC publications for reproductive and survival estimates for American Shad. These data were then used in a population model designed to conduct sensitivity analyses of the effects of the parameters commonly measured in population recovery research, both with and without stocking. We used Stella (High Performance Systems, Inc., Hanover, New Hampshire) modeling software to construct a deterministic age-structured model. Data drawn primarily from ASMFC (2007) were used to define an age-structured population model with a maximum age of 9 years that was reflective of iteroparous spawning runs in the northern extent of the shad range (Figure 1). All of the processes modeled were based on annual time steps from the initiation of spawning. Age-0 individuals were recruited in a density-dependent fashion. Specific life history input variables included length at age, critical life stage recruitment relations, juvenile survival, adult survival, and the size–fecundity relationship. Our model had the following simplistic assumptions: (1) sex ratios were equal and (2) all shad return to their natal rivers and no straying from other rivers contributes to the Penobscot River spawning run. The stock–recruitment parameters of the model were adjusted such that the spawning run stabilized

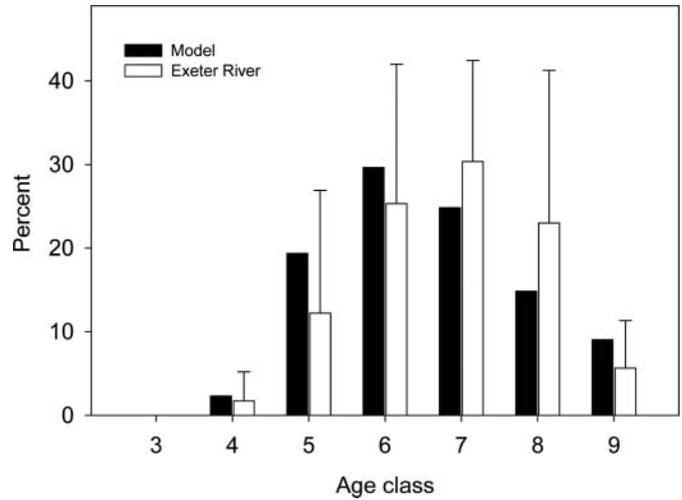


FIGURE 2. Spawning run age distribution of American Shad in the Exeter River, New Hampshire, and modeled Penobscot River population stabilized after 100 years averaged over 100 runs.

at 633,000. The specific inputs for this model are described below.

Size and fecundity.—As there has been virtually no monitoring of the remnant spawning run in the Penobscot River, we used size-at-age information for fish captured in the Exeter River in New Hampshire (New Hampshire Fish and Game Department, unpublished data; Figure 2) and the Merrimack River in Massachusetts (ASMFC 2007). The modeled lengths of fish (L) at age a were based on a normal curve with an increasing mean from age 4 to age 9 (47–62 cm; Table 1). Length affected the model only through fecundity. No data specific to the fecundity of American Shad in Maine are available. Therefore, we followed ASMFC (2007) in assuming that most Maine shad spawn between 20,000 and 150,000 eggs per female (Liem and Scott 1966), similar to Canadian stocks. Fecundity (F) was

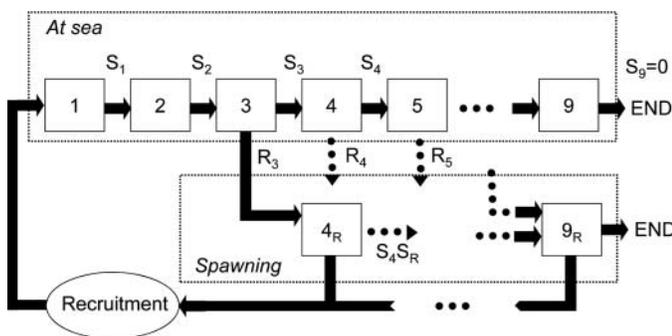


FIGURE 1. Schematic of the deterministic age-structured model of American Shad population recovery using the Penobscot River population as a case study. The letter S represents survival and the letter R represents recruitment to the spawning population. The components of recruitment to age 1, the mortality rate at sea, postspawn survival, and spawner recruitment are explained in the text. All fish are removed from the model at age 9.

TABLE 1. Values of recruitment, length, and fecundity used in the population model. Recruitment data are for New England recruitment of female American Shad and are from the ASMFC. Recruitment to first spawning is the year-class-specific probability of first spawning based on cumulative recruitment. Cumulative recruitment includes first and repeat spawners for the stability model. Length data were estimated from New England rivers and were used to determine the fecundity range (conservatively based on Canadian stocks, as described in Liem and Scott [1966] using the relationship described in Methods).

Age (years)	Recruit to first spawn	Cumulative recruitment	Fork length (cm)	Fecundity
4	0.02	0.2	47	20,654
5	0.23	0.25	52	34,674
6	0.48	0.61	57	58,210
7	0.64	0.86	60	79,433
8	0.71	0.96	61	88,480
9	1.00	1.00	62	97,724

calculated as

$$F = 10^{mL+b}, \quad (1)$$

where m (the slope) and b (the intercept) were determined so as to conservatively set the range up to about 100,000 (20,654–97,724). Using this relationship, egg production from wild fish was calculated as a function of individual fork lengths (Table 1). Fecundity was calculated under the assumptions that one-half of the spawning run was female (i.e., that there was a 1:1 sex ratio), that shad mature at age 4, and that older fish spawn every year after their initial spawning. The total number of wild-spawned eggs (E_w) was derived by summing over all of the age-classes that produced eggs:

$$E_w = \sum_{a=4}^9 [pN_a(eF_a) \cdot 0.5], \quad (2)$$

where e is the proportion of mature (spawning) adults (i.e., recruitment; ASMFC 2007; Table 1), F_a is the fecundity of an individual of length L_a at age a , N_a is the total number of age- a fish, and p is migratory success (the probability of successfully spawning once having entered the river). We arbitrarily set p to 0.9 to account for in-river mortality and other factors that might lead to failure to spawn.

Total number of larvae.—The total number of larvae was derived from three components: (1) the number of eggs from natural reproduction based on the fecundity of wild individuals (E_w from equation 2), (2) the hatchability rate of eggs from natural reproduction (h ; our starting assumption was that egg-to-larval survival was 10%), and (3) the number of larvae produced from hatchery eggs (E_H ; included in stock recruitment without an additional hatchability or mortality factor). In this model, the number of hatchery larvae is equal to the number of hatchery eggs, as stocking numbers are based on live larvae released.

Stock-recruitment.—A density-dependent curve for alosines has not been well documented. In the absence of a more appropriate relationship, we used a Ricker stock-recruitment relationship from spawned eggs to age-1 subadults. Recruitment from total number of larvae to age-0 juveniles was modeled by using a Ricker (1975) stock-recruitment relationship,

$$R = \alpha(hE_w + E_H)e^{-\beta(hE_w + E_H)}, \quad (3)$$

where R is the recruitment of age-0 fish, α and β are parameters determining the shape of the stock-recruitment relationship, and $hE_w + E_H$ is the total number of larvae. In this relation, the value of α determines the rate of increase in recruitment while that of β (the capacity parameter) determines the strength of density dependence resulting in a leveling off of the population with increased abundance. While recruitment is poorly characterized for American Shad, there are data with which to describe the rate of spawning run increases in recovering stocks. The values

of the exponential growth constant (r), which range from 0.15 to 0.45 for the spawning run (*not* the population), were based on estimates from stock assessments presented in ASMFC (2007). We used a conservative value of $r = 0.15$ for spawning run growth to set the base model α value. This was done by removing density dependence (setting β equal to 0) and running the model for 100 years at a range of α values. The natural log-transformed spawning run values were regressed against year, and the slope of the linear regression (r) was recorded. This was repeated for 10 α values from 0.002 to 0.011 and the resulting relation ($R^2 = 0.997$) was used to solve for α when r was set to 0.15 ($\alpha = 3.232 \times 10^{-3}$):

$$r = 0.148 \log e(\alpha) + 0.992. \quad (4)$$

β was parameterized and selected by running the model with a series of values (from 1 to 10×10^{-10}), averaging the run size from year 75 to year 100, and fitting the following curve ($R^2 = 0.9998$):

$$\text{Run Avg} = (3.464 \times 10^{-4})^{\beta-1.000}. \quad (5)$$

The base-model value of β value was selected such that run size stabilized at the management target of 633,000 spawning shad. This resulted in $\beta = 5.4737 \times 10^{-10}$.

Mortality.—The mortality associated with the model includes “at-sea” natural mortality and “acute postspawn” mortality. At each step of the model, all nonreproductive fish (ages 1–8) incur a constant natural mortality (M) of 0.38, as determined by Hoenig’s methods (ASMFC 2007), such that survival was calculated as

$$N_{(t+1)} = N_t e^{-Mt}, \quad (6)$$

where N is population size and t is time. The maximum age in the model is 9 (i.e., all fish attaining age 9 die). Iteroparity was included in this model by allowing spawning fish to spawn and, for those that survived acute postspawning mortality, to return to the ocean. For northern rivers the species is increasingly iteroparous with latitude (Chittenden 1976), though this is poorly quantified in many rivers, including the Penobscot River. Iteroparity has been described in the synthesis paper of Leggett and Carscadden (1978), which reported clinal variation in spawning among populations. We used the reported data to regress the incidence of repeat spawning (I) against latitude, providing the relationship ($R^2 = 0.76$)

$$I = 5.08(\text{Latitude}) - 165. \quad (7)$$

Given the latitude of the Penobscot River (44.5°N), this relationship predicts a 61% rate of iteroparity. Because the model was not individual based, iteroparity was calculated as a summation

of probabilities of repeat spawning, i.e.,

$$I = \frac{\sum_{i=4}^9 (\text{spawning at age } i + n | \text{spawned at age } i)}{\sum_{i=4}^9 (\text{spawning at age } i)}. \quad (8)$$

We forced all spawners to spawn in all successive years. The degree of iteroparity was therefore controlled by survival in the year after spawning. Acute postspawn survival (S_s) was set at 70%. Survival to age $i+1$ from spawning at age i is represented by the product of acute postspawn survival and at-sea survival for 9 months, namely,

$$S_{i \text{ to } i+1} = S_s e^{(-M \cdot 0.75)}. \quad (9)$$

The result is a calculated iteroparity rate of 48%. This is about 80% of what was predicted by Leggett and Carscadden (1978).

Model execution.—The model censuses the existing population in each age-class and calculates the required summary statistics, including run size, population size, contributions of each age-class, total fecundity, and total larval production. At the next iteration, annual at-sea mortality and postspawning mortalities are incurred. All surviving individuals of each year-class graduate to the next year-class as reproductive or nonreproductive individuals based on age and the probability of previous spawning. Starting numbers for each age-class at sea and as spawners were determined by running the base model using the values to generate proportional representation within the population. The base model was run using the parameters described above and a starting run size of 1,000 spawning American Shad.

Exeter River data.—Data from the Exeter River, New Hampshire, were used to compare the age structure of the stabilized model with data from a New England river with a small run of American Shad captured at a fish trapping facility (18–163 annual run from 1995 to 2004, for a total of 529 fish aged; New Hampshire Fish and Game, unpublished data). The age distribution generated by the model and the age distribution (average) from the Exeter River were compared using a Kolmogorov–Smirnov two-sample test.

Local sensitivity.—The local sensitivity of two variables—the modeled spawning run size and the estimated time to attainment of 50% of the maximum population level in the base model—to the estimated life history parameters was evaluated. The parameters included stock–recruitment parameters, fecundity parameters, and survival values. Changes in run size and time to 50% recovery were evaluated after a 1% increase in life history parameters. Sensitivity (S) was defined as

$$S = \frac{(R_a - R_n)/R_n}{(P_a - P_n)/P_n}, \quad (10)$$

where R_a is the model result for the altered parameter, R_n is the model result for the unaltered parameter, P_a is the altered

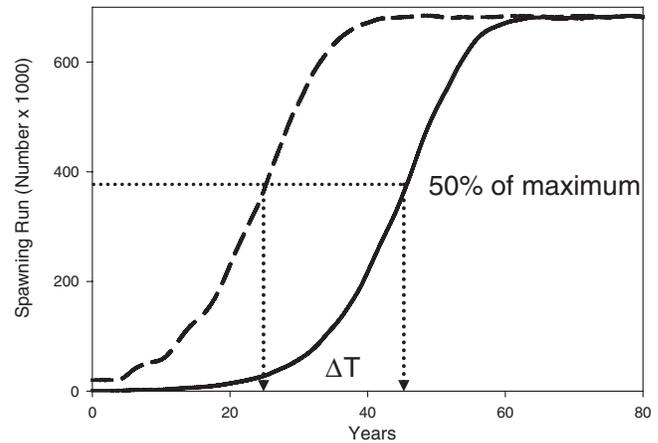


FIGURE 3. Example of modeled American Shad spawning run size increase over time assuming instantaneous access to habitat made available through planned restoration on the Penobscot River. The plots represent 100 averaged runs of the base model (solid line; e.g., a starting run size of 1,000) and the model with a shifted parameter (dashed line; e.g., a starting run size of 20,000). The calculated shift in reaching 50% of the maximum spawning run size is indicated by the dotted lines.

parameter, and P_n is the nominal parameter (Haefner 2005). Parameters were considered “highly sensitive” if $|S| > 1.00$.

Effects of starting population and stocking.—In our model, neither the starting population size nor hatchery stocking influenced the stabilized population level. In order to assess the sensitivity of modeled American Shad recovery to changes, in both initial run populations and hatchery stocking we used the change in the time to attain 50% of the maximum value as a metric. As above, the model stabilized at an average spawning run of 633,000. Therefore, we used the year in which the model surpassed 316,500 spawning shad (Figure 3). The precise value (fraction of year) was calculated via linear regression of the points that bracketed this value.

To assess the impact of hatchery supplementation, we modeled the annual stocking of between 0 and 48 million American Shad larvae annually. This was done using the base model with 1,000 shad in the spawning run. To assess the impact of starting run size, we modeled the time to 50% recovery over a range of starting run sizes (1,000–300,000) without stocking. Similarly, the model was run using a stocking rate of 12 million larvae annually over the same range of starting populations.

RESULTS

Base Model Run

Using the inputs from the base model, the adult spawning distribution in this system was dominated by fish of ages 5–7, with very few above age 7 (Table 1; Figure 2). The age distribution generated by the model and the age distribution (average) from the Exeter River were not significantly different (Kolmogorov–Smirnov two sample test; $P = 0.078$).

TABLE 2. Sensitivity (S) to model parameters of the modeled American Shad stabilized population level and the rate of attainment of 50% of the target population level. Parameters include α (which determines the rate of increase in recruitment), β (which determines the strength of density dependence), h (hatch success), m (the slope of the fecundity relationship), b (the intercept of the fecundity relationship), the at-sea mortality rate, and acute postspawn survival. Values of $|S| > 1.00$ are indicated by bold italics.

Parameter	Nominal value	S of stabilized run size	S of time to 50%
α	0.003232	0.97	-0.99
β	5.2043×10^{-10}	-0.99	0.11
h	0.1	-0.03	-0.88
m	0.0045	-0.34	-5.26
b	2.2	-0.26	-4.42
At-sea mortality rate	0.38	-1.98	2.35
Acute postspawn survival	0.7	0.75	-0.93

The stabilized run size and time to 50% recovery from this model were predictably sensitive to the stock-recruitment parameters α and β (Table 2). Run size was highly sensitive to changes in β , while this parameter had little influence on recovery time. Recovery time had a greater sensitivity to α and stabilized run size a comparable sensitivity. Recovery time was sensitive to the parameters influencing survival (hatch success, at-sea mortality, and postspawn mortality) though except for at-sea mortality these parameters had little effect on stabilized run size. Fecundity estimators understandably influence some outputs. Time to recovery was sensitive to both fecundity estimators, but stabilized run size was not.

Effect of Stocking and Population Size

Stocking had a strong effect on the time to recovery in the base model. Predictably, stocking more fish resulted in a

more rapid recovery, with diminishing effects at higher levels of supplementation. With a starting spawning run of 1,000, the annual supplementation of 3 million larvae accelerated the time to recovery by 4 years. An additional 9 million larvae (12 million total annually) accelerated recovery by only 8 additional years. The effect of stocking was greatly dependent upon run size. The effect of stocking 12 million larvae annually with a starting run size of 1,000 fish was to advance recovery by 12 years (Figure 4). However, when 5,000 fish were present in the spawning run, the additional gain in recovery time was less than half that—only 4 years (Figure 5). In the same vein, when the starting run size was 15,000, the additional gain was a mere 2 years. The salient point here is that in even without stocking, the time to recovery is very sensitive to starting run size. Time to recovery approximated a linear relationship with the \log_{10} transformed value of run size, so that small differences in run size at low levels of stocking had great effects on time to recovery. Conversely,

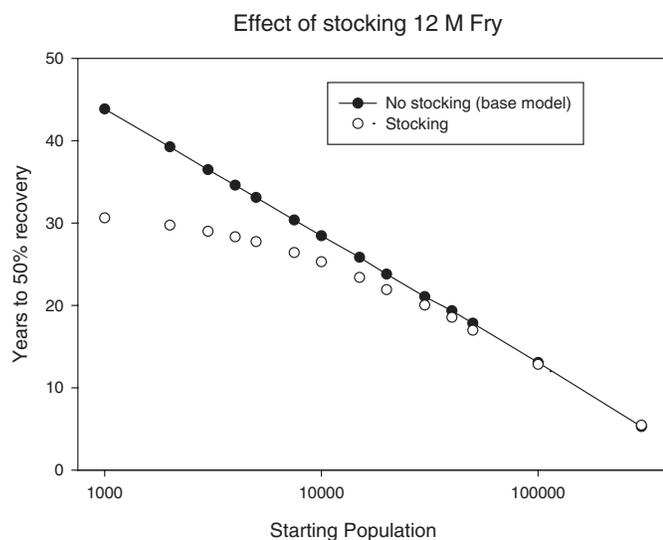


FIGURE 4. Effects of the starting size of the American Shad spawning run on the modeled number of years needed to reach 50% recovery with and without supplemental stocking of 12 million larvae assuming instantaneous access to habitat made available through planned restoration on the Penobscot River.

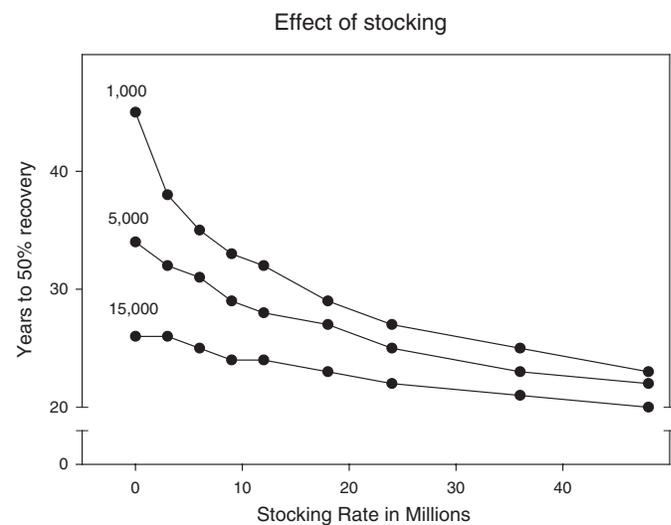


FIGURE 5. Years to 50% recovery with variable supplemental stocking rates and initial starting populations of 1,000, 5,000, and 15,000, assuming instantaneous access to habitat made available through planned restoration of American Shad on the Penobscot River.

at higher run sizes, differences had a diminishing influence on recovery time.

DISCUSSION

In regions where American Shad restoration is the goal, the decision to stock or not is made on the basis of the best available information. Our population model draws on data from diverse sources with unknown accuracy and precision in order to serve as a platform for assessing the sensitivities of population recovery. Given these limitations, it is important to point out that these parameters generated an age structure that was not different than what was observed in the Exeter River, a system that usually has fewer than 100 returns of shad annually (Figure 2). This lends support for the model's ability to evaluate potential population outcomes under different stocking levels and starting population sizes.

It is not surprising that the starting population size has a strong effect on the rate of (and years to) recovery (Figure 4), as this model is assuming newly opened habitat, but this effect is biologically noteworthy. An increase in starting run size from 1,000 to 5,000 fish is predicted to reduce the time to recovery by 11 years. The strong sensitivity of this model to starting run size highlights the importance of characterizing the extant population size prior to restoration. In our case study, the starting run size of the Penobscot River remains a critical unknown. Only recently have biologists recognized that there appears to be a self-sustaining population (A. Grote, University of Maine, personal communication) with juveniles in the estuary (C. Lipsky, NOAA–Fisheries, personal communication).

If hatchery supplementation is chosen as a recovery tool, it is also important to understand the predicted interaction between starting population and stocking effectiveness. This model shows the efficacy of stocking to be greatest at the lowest population levels. For example, at an assumed level of 1,000 fish in the spawning run, stocking 12 million larvae annually is predicted to accelerate anticipated recovery by 12 years. With 5,000 fish in the spawning run, the same aggressive stocking program would result in greatly diminished returns and advance recovery by fewer than 4 years. Note also that a difference in run size of only 4,000 fish has a comparable result in recovery. The diminishing effectiveness of stocking as natural or hatchery-aided recovery takes place is an important consideration before investing limited resources in hatchery-based supplementation. In our case study, the current plan for the Penobscot River (MDMR 2009) calls for stocking hatchery-reared individuals until carrying capacity is reached for five consecutive years. These data indicate that even at low run sizes supplementation may be ineffectual, and that at run sizes near the carrying capacity supplementation may be futile. Only at the lowest run sizes (less than 10% of the carrying capacity) did hatchery supplementation have the potential to noticeably increase run size. This indicates that stocking American Shad is a better tool for reintroduction than for supplementation.

In general, the efficacy of hatchery supplementation is by no means a known quantity. There are known risks with stocking out-of-basin fish, including outbreeding depression (Lynch 1991), low effective population size (Waples and Do 1994), and swamping of adaptive genetic variation (Hansen et al. 2001). Other restoration stocking projects with American Shad have considered these risks in designing a conservation plan. An initial goal for the James River, Virginia, hatchery program was to restrict the collection of broodstock to fish from within the river to minimize the potential risks associated with transfers (Brown et al. 2000). This goal could not be met, so next-best alternatives were considered, including using fish from rivers that (1) support large and viable stocks, (2) are nearest neighbors, and (3) are genetically less divergent from other stocks (Epifanio et al. 1995). For our case study, managers in Maine would face similar challenges in collecting broodstock. A Penobscot River shad stocking program would likely use out-of-basin source stock, as Penobscot River shad will be “not easily captured” until the Milford Dam fish lift is complete and operational (MDMR 2009). The nearest reliable source for shad broodstock is the Merrimack River, which is approximately 201 km from the mouth of Penobscot Bay and entails a more than 3-h transfer via stocking truck. There are at least three other river systems known to have shad runs that are closer, but all have small or unknown population sizes (MDMR 2009).

Our model is limited in that it does not take into account genetic stock structure or the potential for hatchery restoration to disrupt the genetic structure of a remnant population or compromise any undetected adaptive potential that is currently present. However, genetic structure must be carefully considered before a stocking program progresses, as effective restoration should attempt to recover representative diversity as far as is practical (Hasselman and Limburg 2012). Previous studies have found that American Shad have a shallow but significant stock structure (Bentzen et al. 1989; Brown et al. 2000). However, these results were obtained with a less than ideal power to differentiate stocks; the study used relatively few microsatellite loci (five) and spawning populations within close geographic proximity. A recent study in Canada with a broader geographic range and more statistical power (13 polymorphic microsatellite loci) found more substantial population structure between rivers (Hasselman et al. 2010). Even shallow stock structure is notable, as early shad restoration programs (1800s–1950) stocked over 1 billion larvae and often with mixed-river stocks (Hasselman and Limburg 2012). In the James River, the reproductive contribution of individual broodstock was clearly nonrandom and is cause for close hatchery management and evaluation. Although there did not appear to be a significant decline in microsatellite variation, one male fathered more than half the progeny and nearly half the progeny represented only three families (Brown et al. 2000).

Hatchery restoration efforts have been deemed successful in a number of rivers where a large percentage of the individuals returning to spawn are of hatchery origin, reflecting population

increases comprised of donor stocks rather than native river stock (Aunins 2010). In the Potomac River, however, the increase in adult returns is thought to be driven largely by a reduction in the at-sea fishery (Aunins 2010), and not supplementation with hatchery fish. Increasing adult escapement and accessibility to spawning grounds via adequate fish passage may be a more powerful driver of population recovery than hatchery stocking (Aunins 2010) at all but the lowest run sizes.

In using the restoration of the Penobscot River as a case study, we reiterate that the study was not meant to predict the time course of recovery in the river once the anticipated dam removals are accomplished. A key assumption of this model is that the removal of the dams and the greater connectivity afforded by improvements to passage will allow for recolonization that will be dominated by fecundity, survival, and the theoretical carrying capacity of the system. The model does not attempt to quantify the quality of the habitat at the newly accessible historical spawning grounds. There are simply too many unknowns associated with the anticipated passage to base a recovery model on increased habitat accessibility. Such assumptions of access and utilization of habitat after restoration represent important goals of the PRRP assessment.

In constructing this model, we used the best available data, though we identified several key components for which the only data available are unsatisfactory. As a result, the specific values of many of the parameters could—and should—be critically evaluated. Specifically, there appear to have been no attempts to estimate the batch fecundity of Maine American Shad and few attempts for shad in their northern range as a whole (Collette and Klein-MacPhee 2002). Even if the fecundity estimates were precise and accurate, recent research has suggested that shad are not likely to spawn all available eggs (Olney and McBride 2003). It is also unknown what the average fertilization rate is for shad eggs released during a natural spawning event. Our model is also based on the best local data on maturity schedules, but maturity schedules vary spatially (Tuckey and Olney 2010) and aging shad via scales is imprecise at best (McBride et al. 2005; Duffy et al. 2011).

Our model is based on a Ricker-type recruitment curve. This type of curve has not been described for American Shad, and there have been few successful attempts to apply any type of stock–recruitment curve to alosines (Crecco et al. 1986). Early survival rates of wild shad larvae are difficult to assess and rarely studied (see Crecco et al. 1983 for one of the few exceptions). However, these rates are needed to assess the advantage of hatchery-produced larvae in shad recovery programs across the species' native range. The results of this model rely heavily on the density-dependent effects afforded by this recruitment model. Additionally, our assumption of a 10-fold increase in survival from eggs to larvae is based on what limited data are available and is likely an oversimplification. Survival rates among hatchery-raised shad can be known until stocking, but poststocking survival to juvenile stages or seaward migration is difficult to assess. Another recent model (Harris and High-

tower 2012) showed that increased access to habitat is not a panacea for population recovery and may not increase American Shad populations without increases in other factors in the newly available habitat, such as juvenile survival and spawning success.

Due to the high variability inherent in natural biological systems, many of the assumptions we used to construct our model were conservative in order to prevent overestimation of population trends. Reality may thus exceed the trends seen in this model. Our rate of iteroparity is low because it is based on the predictions of Leggett and Carscadden (1978). The calculated rate of run size increase ($r = 0.15$) is low compared with that of other recoveries involving American Shad due to increased habitat accessibility and natural population fluctuations. In northern systems, the degree of iteroparity may increase the rate at which new habitat is filled. In the context of this model, the degree to which hatchery supplementation might be effective is dependent upon the intrinsic growth rate.

It is not our intent to recommend stocking or not stocking in the Penobscot River or any other river; such decision would be value judgments. Rather, our intent is to highlight the sensitivities of this model in order to fill gaps in our knowledge so that management decisions can be based on the best science available. In practice, active restoration is an integration of both values and science (Hart et al. 2002). As such, the decision to stock or not to stock could be informed by the use of a structured decision-making approach. This process allows stakeholders to fully explore their fundamental objectives, ultimately focusing on the potential trade-offs of management action (Holling 1978). Irwin et al. (2011) suggest that linking management options to expected outcomes is most effectively accomplished through the use of quantitative systems models as decision-support tools. Such a decision-making framework would be instructive not only for the decision when or if to stock but also for the decision of when to stop.

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