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SPECIAL SECTION: AMERICAN SHAD AND RIVER HERRING

## Relative Sensitivity of New England American Shad to Fishing, Discard Mortality, and Dam Passage Failure or Mortality

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### Abstract

American shad *Alosa sapidissima* in Atlantic coastal rivers of the New England states are affected by anthropogenic sources of mortality, such as discards of immature fish (bycatch) in various fisheries, directed fishing on prespawning adults, and the passage failure or mortality of mature fish at migratory barriers. We evaluated the relative importance of these factors, independently and in combination, by modeling the predicted lifetime spawning stock biomass of an age-1 female recruit (SSBR) with an assumed constant rate of natural mortality. Discard losses had the greatest impact on the SSBR, followed by directed fishing and upstream passage mortality, upstream passage failure (the fish survived but did not pass the barrier or spawn), and downstream losses of postspawning adults. Fishery managers strive to keep mortality rates below those that reduce SSBR to less than 30% of that of a stock with no anthropogenic mortality. In our modeling, SSBR dropped below that benchmark when bycatch rates exceeded 0.21, directed fishing or upstream passage mortality exceeded 0.45, and upriver passage failure without mortality exceeded 0.70. Since the downriver passage mortality of adults occurred after spawning, SSBR did not decline below the benchmark even at 100% downriver loss. The impacts of upstream passage mortality always exceeded those from comparable downstream passage mortality. Fishing and discard losses seriously reduced any gain in SSBR from reduced fish passage mortality or failure. The results in this paper suggest that among the anthropogenic factors evaluated, American shad in New England are most sensitive to discard losses of immature shad in ocean fisheries and that fish passage improvements at dams are most effective when they are developed in combination with reductions in fishery-related losses.

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American shad *Alosa sapidissima* are anadromous fish that spawn in Atlantic coastal rivers of North America. Those in New England waters have been in decline since colonial times. Their demise started with the construction of mill dams in the late 1600s and accelerated dramatically during the 1800s' textile boom (ASMFC 2007). Early observers noted that the abundance of American shad in rivers declined following the construction of dams and concluded that fish passage was needed to save the stocks (Loesch and Atran 1994). Fish passage devices were constructed, but they were often ineffectual and the problems were exacerbated by water pollution and other habitat changes (ASMFC 2007).

Prespawning mature American shad were historically caught in directed recreational and commercial fisheries while in the rivers and in directed commercial fisheries while in the ocean. In-river commercial harvest has ended in all New England rivers except the Connecticut, and a limited recreational take is still allowed in a few New England states. Interstate fishery management plans coordinated by the Atlantic States Marine Fisheries Commission (ASMFC) led to closure of the directed ocean harvest of American shad in all coastal states in 2005 (ASMFC 2007). Immature and mature American shad were also taken incidentally (bycatch) in various commercial fisheries in oceans and estuaries along the Atlantic coast. Through the early 2000s,

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bycatch was generally landed (ASMFC 2007). Since the ocean closure in 2005, most of this bycatch has been discarded at sea.

Current populations of American shad in New England rivers are at historic lows (Kocik 2000; Boreman and Friedland 2003; ASMFC 2007), and recent management has focused on restoration activities, including the construction and refinement of fish passage devices at the many obstructions to migration and the augmentation of stock sizes with larval or adult stocking. These efforts led to many improvements in fish passage, and passage generally increased (ASMFC 2007). However, the number of fish passed at a given dam often reached a plateau several years after passage improvements. Passage numbers at most dams have declined in recent years. Savoy and Crecco (2004) attributed the decline in the passage of American shad in the Connecticut River to predation by large striped bass *Morone saxatilis* on mature American shad. Leggett et al. (2004) suggested that the decline in the Connecticut River stock was also caused by physiological stress from the increased migratory distance in fish moved above the dams. ASMFC (2007) hypothesized that directed ocean harvest and ocean bycatch have been factors in the decline in some rivers. It is also possible that dam passage success has been too low to reverse the decline in abundance of shad stocks.

There is a need to identify the most critical anthropogenic factors inhibiting the restoration of American shad in New England rivers. Boreman and Friedland (2003) evaluated the sensitivity of American shad to fishing and concluded that the species was relatively insensitive to fishing compared with other managed fish stocks and that attempts to rebuild American shad stocks cannot rely on fishery restrictions alone. Moreover, the authors suggested that attempts to create more riverine habitat and enhance spawning biomass would be more constructive. The authors did not compare the sensitivity to fishing with the sensitivity to other anthropogenic factors, such as bycatch and dam passage mortalities. We feel that the focus of such sensitivity analyses should be on anthropogenic factors because we cannot control natural factors such as predation.

The objectives of our paper were to (1) identify the relative sensitivity of New England American shad to discard mortality, directed fishing, and passage failure or loss at migratory barriers and (2) identify the reductions in these mortalities that would be needed to achieve acceptable rates of total mortality in New England shad populations in dammed rivers.

**METHODS**

We evaluated the effects of various anthropogenic mortalities from estimates of the lifetime spawning stock biomass of an age-1 female recruit (spawning stock biomass per recruit, or SSBR). Such analyses are commonly used to evaluate the consequences of management strategies on fish stocks (Boreman 1997; Gabriel et al. 1989; Goodyear 1993). Estimates were obtained from the sum of weight at age (kg) times the probability of surviving to that age using a modification of a model provided by Boreman

(1997), namely,

$$SSBR = \sum_{i=1}^n \lambda_i \varphi_i \prod_{t=0}^{n-1} e^{-(F_t+FD_t+P_t+M_t)},$$

where  $\lambda_i$  is the proportion of females mature at age  $i$ ,  $\varphi_i$  is the mean weight of an age- $i$  female,  $F_t$  is the instantaneous rate of fishing mortality during period  $t$ ,  $FD_t$  is the instantaneous rate of discard mortality during period  $t$ ,  $P_t$  is the instantaneous rate of dam passage mortality or failure during period  $t$ ,  $M_t$  is the instantaneous rate of natural mortality during period  $t$ , and  $n$  is the oldest spawning age (11).

We used an age-invariant  $M = 0.38$  based on a maximum age of New England American shad (ASMFC 2007) and the formula by Hoenig (1983), that is,

$$\log_e(M) = 1.46 - 1.01 \cdot \log_e(T_{MAX}),$$

where  $T_{MAX}$  is the maximum age of the fished stock.

The variable  $SSBR_{MAX}$  was defined as the spawning stock biomass that results when only natural mortality acts on the population. Recruits were subjected to natural and discard mortality until they matured. The fraction mature at age was then subjected to age-invariant rates of directed fishing mortality and/or upriver passage mortality or failure and downriver passage mortality. We obtained data for maturity and weight at age from ASMFC (2007). The data were for female American shad from the Merrimack River (Table 1). Weight at age was modeled with the Gompertz growth curve (Ricker 1975). Maturity at age was developed from data on spawning marks at age, as described by Maki et al. (2001).

Our analyses assumed a type I fishery when modeling directed fishing and dam-related mortalities and a type II fishery when modeling discard mortality. A type I fishery is defined as one in which natural mortality occurs at times of the year other than the period of fishing, while a type II fishery is defined as one in which fishing and natural mortality occur concurrently

TABLE 1. Model inputs for New England American shad.

Age	Fraction mature	Weight at age (g)
1	0.00	22
2	0.00	164
3	0.00	492
4	0.02	901
5	0.25	1258
6	0.61	1510
7	0.86	1670
8	0.96	1766
9	1.00	1820
10	1.00	1851
11	1.00	1868

(Ricker 1975). Type I modeling is commonly applied to pulse fisheries that occur over a brief period of the year; it is appropriate for American shad fisheries and dam-related mortalities, which occur during the brief spawning migration. Type II modeling is more appropriate for the discard mortality of American shad, which presumably occurs throughout the year among prespawning fish in the ocean. Our model assumed that maturation and weight at age remained constant at various levels of mortality and abundance. Application of the model to the population level further assumes that recruitment remains constant.

To simplify the comparisons among various mortalities, our analyses assumed that

1. All spawning habitat and all spawning occurred upriver of the first and only barrier in the river system.
2. Directed fishing occurred on the spawning stock below the first barrier and thus before any passage mortality.
3. Discard mortality occurred on immature fish in ocean fisheries.
4. All fish that passed upriver participated in spawning. Fish that did not pass downriver after spawning died.

To facilitate the comparison of impacts among mortality sources, we modeled the effects of each anthropogenic mortality factor separately by holding the other factors at zero. We also modeled various dam-related mortalities in conjunction with directed fishing or discard mortality. For upriver passage, we modeled two scenarios: (1) fish that did not successfully pass upriver died (upstream failure with mortality) and (2) fish that did not pass upriver did not spawn but survived to participate in future spawning runs (upstream failure with survival). Although the percentage that move beyond a barrier is usually envisioned when discussing fish passage, we used the inverse ( $1 -$  the passage rate), termed passage failure, for purposes of comparison with other mortality sources. All instantaneous rates were transformed to annual fractions of loss or failure ( $u$  for fishing and discard mortality and  $p$  for dam-related mortality or failure), as described by Ricker (1975) when discussing results, because it is a more intuitive metric.

For added perspective on the relative impacts of the various anthropogenic mortalities on American shad populations, we compared SSBR trajectories with SSBR predicted at a benchmark of  $Z_{30}$ . This benchmark was suggested for American shad by ASMFC (2007); it is defined as the rate of total mortality (anthropogenic and natural) that results in an SSBR that is 30% of that obtained from a stock affected only by natural mortality. ASMFC (2007) selected this relative level of spawning stock biomass based on experience with other fish species with similar life spans. The author assumed that mortality rates at or below these values would maintain a stable spawning stock biomass. We considered mortality rates to be excessive if they resulted in SSBR values below that at  $Z_{30}$ .

## RESULTS

In all cases, SSBR declined as the rates of the various anthropogenic mortalities or upriver passage failure increased (Table 2). Discard losses of immature fish had the greatest impact on SSBR at a given exploitation or loss rate, followed by directed fishing and upstream passage failure with mortality, upstream passage failure with survival, and downstream passage mortality (Figure 1). The effects of directed fishing and upriver passage failure with mortality were identical because both operate on the spawning population as it migrates into the spawning river. The SSBR dropped below that at  $Z_{30}$  when discard mortality rates exceeded 0.21, directed fishing or upstream passage mortality exceeded 0.45, or upstream passage failure with survival exceeded 0.70. Since downriver mortality occurred after spawning in our model, even 100% downriver passage mortality did not reduce SSBR below  $Z_{30}$ . The impacts of upstream passage failure with or without mortality generally exceeded those from comparable downstream passage mortalities.

Directed fishing exacerbated the impacts of fish passage mortality or failure (Figure 2A, B, C). As the exploitation rate from fishing increased at a given level of passage mortality or failure, SSBR declined. Moreover, as exploitation increased, SSBR dropped below that at  $Z_{30}$  at lower and lower passage mortality or failure. In fact, at an exploitation rate of  $u > 0.45$ , SSBR remained below that at  $Z_{30}$  even at zero passage mortality or failure (Figure 2A, B, C). As fishing is added to the mix of mortalities, dam passage loss or failure must decrease (passage success must increase) to maintain a given level of SSBR. For example, increasing the exploitation rate from zero to  $u = 0.1$  at an upstream passage mortality of  $p = 0.40$  lowered the SSBR from 0.232 to 0.194, a decrease of about 16% (Figure 2A). Upstream passage mortality would have to decrease to  $p = 0.33$  to restore SSBR to 0.232. The impacts of adding an exploitation rate of 0.10 to upstream passage failure with survival and to downstream passage mortality decreased SSBR in both cases by approximately 23% (Figure 2B, C). The decrease in these failure and mortality rates needed to restore the former SSBR was much greater than that for upstream mortality.

The effects of directed fishing on the gains from improved fish passage appeared to be worse at the lower levels of upstream fish passage mortality or failure. For example, increasing the exploitation rate from zero to  $u = 0.1$  at upstream and downstream passage mortalities of  $p = 0.80$ , 0.50, and 0.20 lowered the SSBR 12, 16, and 20%, respectively (Figure 2A, C). A similar change was not noted when adding directed fishing mortality to upstream passage failure without mortality (Figure 2B).

The impact of bycatch mortality on the gain in SSBR from fish passage improvements was similar to, but much greater than, that from directed fishing (Figure 3A, B, C). As the exploitation rate from discards increased, SSBR dropped below that at  $Z_{30}$  at lower and lower passage mortality or failure, and it remained below the  $Z_{30}$  benchmark at  $u > 0.21$  even at zero dam related mortality or failure (100% passage success). Adding a discard mortality of  $u = 0.10$  to an existing upstream mortality of

TABLE 2. Predicted spawning stock biomass per recruit (SSBR; kg) resulting from various sources of anthropogenic mortality. The predicted SSBR at the ASMFC benchmark of  $Z_{30} = 0.198$  (see text).

Fraction passage failure or mortality	SSBR				
	Discards of immature fish	Directed fishing	Upstream failure with mortality	Upstream failure with survival <sup>a</sup>	Downstream mortality
0.00	0.666	0.666	0.666	0.666	0.666
0.05	0.516	0.586	0.586	0.632	0.617
0.10	0.395	0.516	0.516	0.599	0.573
0.15	0.299	0.454	0.454	0.566	0.534
0.20	0.223	0.399	0.399	0.533	0.498
0.25	0.163	0.349	0.349	0.499	0.466
0.30	0.117	0.306	0.306	0.466	0.437
0.35	0.082	0.267	0.267	0.433	0.411
0.40	0.057	0.232	0.232	0.399	0.387
0.45	0.038	0.201	0.201	0.366	0.365
0.50	0.024	0.173	0.173	0.333	0.346
0.55	0.015	0.148	0.148	0.300	0.328
0.60	0.009	0.125	0.125	0.266	0.312
0.65	0.005	0.104	0.104	0.233	0.297
0.70	0.003	0.085	0.085	0.200	0.283
0.75	0.001	0.068	0.068	0.166	0.271
0.80	0.000	0.052	0.052	0.133	0.260
0.85	0.000	0.037	0.037	0.100	0.249
0.90	0.000	0.024	0.024	0.067	0.240
0.95	0.000	0.012	0.012	0.033	0.231
1.00	0.000	0.000	0.000	0.000	0.222

<sup>a</sup>Fish that do not pass upriver but survive to spawn in subsequent years.

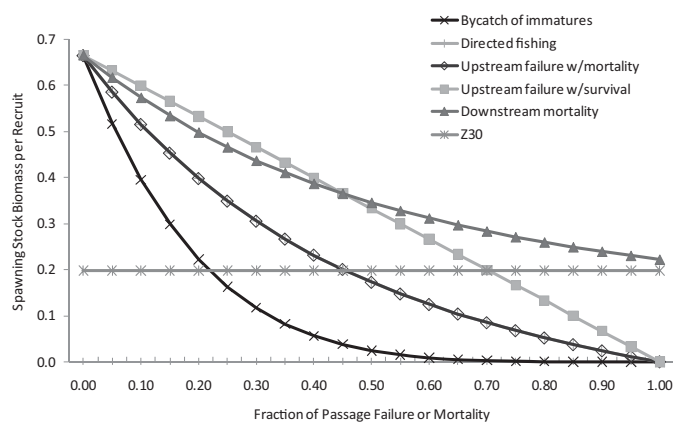


FIGURE 1. Predicted spawning stock biomass per recruit (SSBR) resulting from various anthropogenic mortalities expressed as fraction lost or passage failure. Upstream failure with mortality represents upstream passage in which unsuccessful fish die. Upstream failure with survival represents upstream passage in which unsuccessful fish survive. Downstream mortality represents downriver passage mortality. The bycatch of immatures represents the exploitation rate from the bycatch of immature fish, and  $Z_{30}$  is the benchmark SSBR. Directed fishing represents the exploitation rate from fishing that targets mature fish. The results of directed fishing and upstream failure with mortality were identical.

$p = 0.40$  lowered the SSBR from 0.232 to 0.138, a drop of 40% (Figure 3A). Upstream mortality would have to be lowered to  $p = 0.21$  to restore SSBR to 0.232. The impacts of adding discard mortality to upstream passage failure with survival and downstream passage mortality were identical to those for upstream mortality; however, the trade-offs needed to restore SSBR were greater (Figure 3B, C).

**DISCUSSION**

Our analyses were designed to provide perspective on the most important anthropogenic factors affecting American shad restoration in New England rivers and on the reductions in mortalities that might be needed to restore populations in dammed rivers. Admittedly, our analyses were simplistic in that they considered passage at a single dam and only a few mortality factors operate concurrently (Leggett et al. 2004). Moreover, many stocks spawn below as well as above the first dam (ASMFC 2007). Had we assumed multiple dams in our analyses and spawning above the most upriver dam, the results could have elevated the importance of upriver passage mortality or failure above that of fishing and discard mortality, depending on

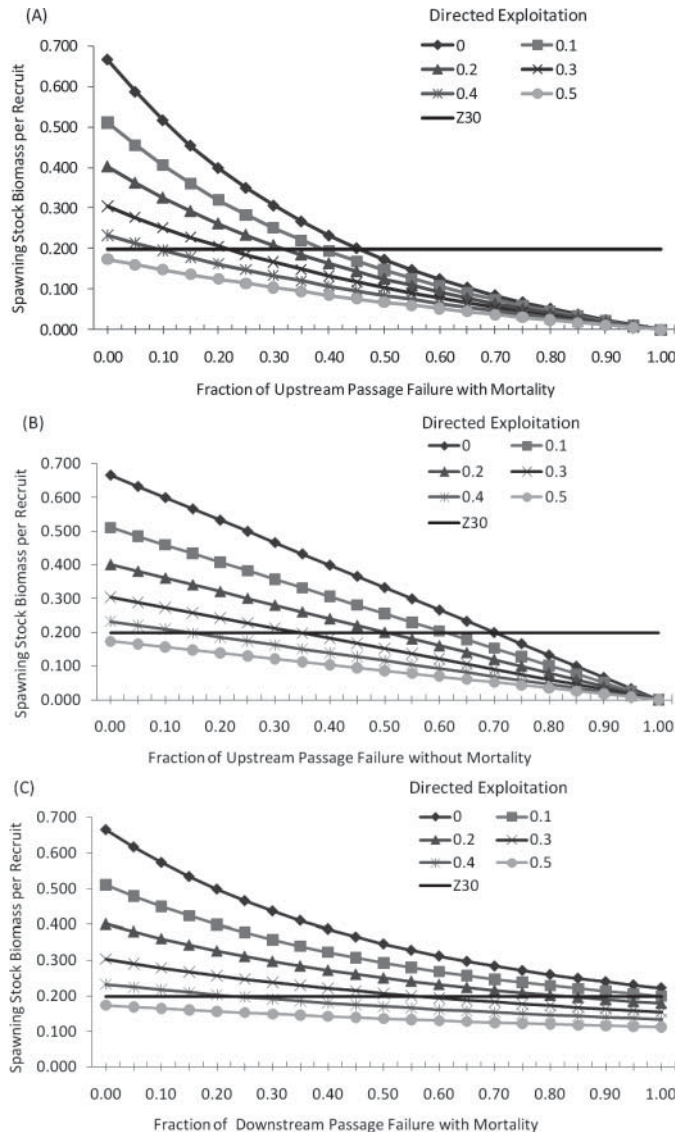


FIGURE 2. Predicted spawning stock biomass per recruit resulting from fish passage loss or failure and concurrent directed-fishing mortality. Panel (A) depicts the results for upstream failure with mortality, panel (B) the results for upstream failure with survival, and panel (C) the results for downstream mortality. See Figure 1 for additional information.

the level of passage mortality and the number of dams involved. This is because the impact of multiple passage mortalities is multiplicative while fishing and discard mortality is not, at least within a year. An assumption of spawning below the first impassible barrier would have lowered the relative impact of dam passage mortalities because they would only act on that portion of each mature year-class that attempted to move above the barrier. All fish that did not attempt passage would be allowed to spawn.

The modeling used in our analyses makes many assumptions about the characteristics and dynamics of the population being modeled. Specifically, it assumes that natural mortality,

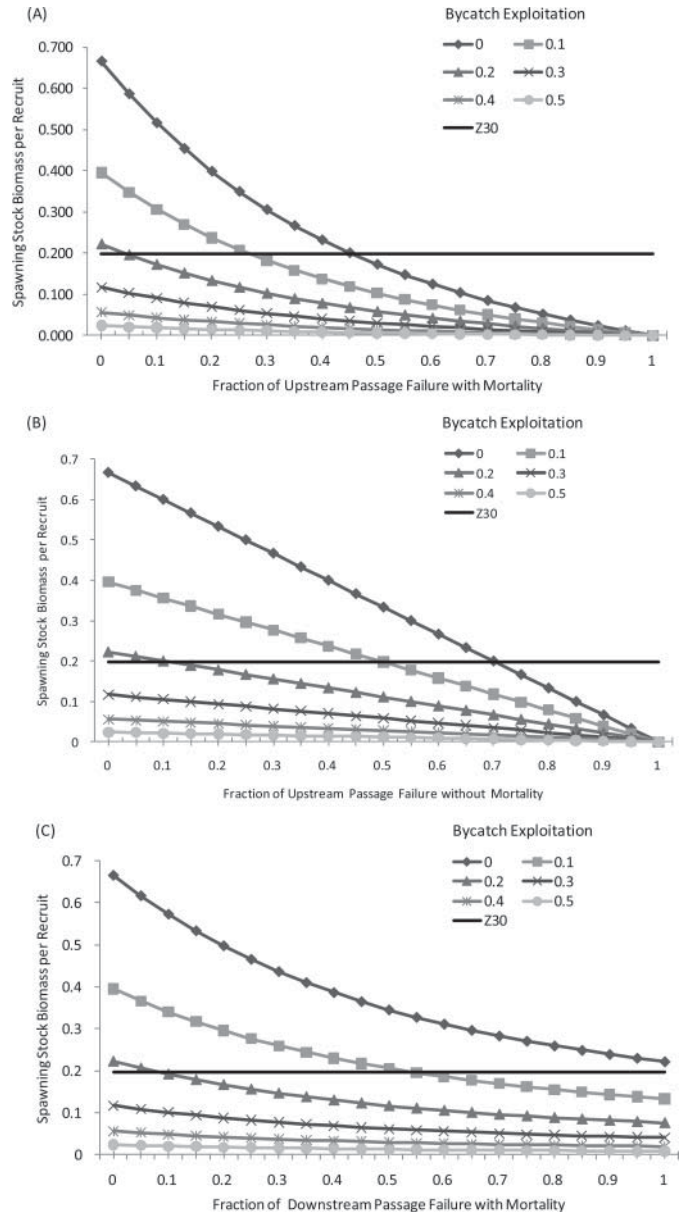


FIGURE 3. Predicted spawning stock biomass per recruit resulting from fish passage loss or failure and concurrent discard fishing mortality of immature fish. Panel (A) depicts the results for upstream failure with mortality, panel (B) the results for upstream failure with survival, and panel (C) the results for downstream mortality. See Figure 1 for additional information.

$F$ ,  $FD$ , and  $P$  are age invariant and that maturity at age and weight at age remain constant at the various levels of mortality evaluated. Application of model results at the population level also assumes a population at equilibrium with a stable recruitment. The assumptions of age-invariant natural mortality may not be realistic for any fish population, including New England American shad. Given that the young of this species often serve as prey for other fish, it is logical that rates of natural mortality would be greater on the youngest, smallest fish and decrease as fish grow (Boudreau and Dickie 1989;

Lorenzen 1996). Age-invariant  $F$  and  $P$  may be realistic with the exception that bycatch-related discard mortality may be age dependent if different ages move differently in the ocean relative to fisheries. Constant maturity at age or mean weight at age at different  $F$  and  $P$  are not likely to be realistic for fished stocks because fishing has been shown to erode the fastest-growing and earliest-maturing fish in a population, thus changing both parameters (Conover and Munch 2002; Goodyear 2002; Conover et al. 2005; Williams and Shertzer 2005). Likewise, age structure has changed in several New England American shad populations in recent years (Leggett et al. 2004; ASMFC 2007).

The impacts of different age-invariant values of  $M$  and the use of age-variable values of  $M$  on the model used in our analyses were evaluated in recent coastwide status assessments of American shad populations (ASMFC 1998, 2007). Both studies found that SSBR decreased at a given level of human-induced mortality as  $M$  increased. However, the SSBR values from age-variable  $M$  inputs were similar to those obtained using the age-invariant  $M$  developed from the maximum age and the approach of Hoenig (1983). The use of different  $M$  values and the resulting differences in SSBR estimates would have changed the point at which SSBR dropped below the ASMFC benchmark in our analyses. However, it would not have changed the relative impacts of various mortalities that we evaluated.

The ages of American shad lost to landed or discarded bycatch are known for only a few fisheries. We modeled discard impacts at the immature life stage because data on the bycatch of the Atlantic herring *Clupea harengus* and Atlantic mackerel *Scomber scombrus* fisheries of the Atlantic Ocean off of the northeastern states indicated that most of the shad catch consisted of immature fish (Becker 2011).

Our analyses indicated that the discard mortality of immature American shad has the greatest impact on SSBR among the mortalities evaluated. This observation agrees with a large body of literature suggesting that the impact of a given level of mortality increases as age at harvest or other loss decreases (Gabriel et al. 1989; Goodyear 1993; Prager et al. 1987). Even modest levels of discard mortality can essentially eliminate the potential population benefit from improved fish passage. American shad bycatch can no longer be legally landed in any New England state, but the extent of bycatch that is discarded at sea from ocean fisheries is essentially unknown. American shad appear to be a rare or poorly reported event in the fisheries observer data obtained by the National Marine Fisheries Service Observer Program. For example, NFSC (2009) reported that only 2,918 kg of American shad were observed during 10,108 observer-days on a range of commercial fishing trips in northeastern ocean waters from July 2007 through June 2008. However, 405,881 kg of unidentified herring were landed during this time period that were tentatively identified as American shad by the author. Becker (2010a, 2010b) reported on the monitoring of landings from the commercial Atlantic herring fishery at processing facilities from Cape May, New Jersey, through Prospect Harbor, Maine. From January through December 2010, he examined

46 samples and observed 171 kg of American shad in 58,783 kg of landed bycatch. Few data are available from onboard observers on the bycatch of shad in the nearshore and estuarine commercial fisheries of New England. Based on reports by fishermen, few American shad have been taken by these fisheries in recent years (ASMFC 2007, 2008, 2009). However, differentiating among alosines in commercial catches is difficult. Given the potential importance of bycatch to shad recovery, studies of bycatch and related mortality should be a priority.

Directed harvest of American shad continues from several northeastern rivers. However, losses to this source have been relatively low in recent years. Fewer than 400 shad were harvested from Maine rivers in 2008 (Brown 2009) and none from New Hampshire rivers for the past several years (ASMFC 2007; NHFG 2009). The Technical Committee for Anadromous Fishery Management of the Merrimack River Basin reported that a mean of 627 American shad were harvested annually from the Merrimack River below the first dam in 1984–1988 (TCAFMMRB 1997). The Connecticut Department of Environmental Protection estimated that means of 12,251 and 3,052 shad were taken annually in the Connecticut River commercial and recreational fisheries in 2004–2008 (CTDEP 2009). Exploitation rates from shad losses to directed fishing in New England rivers have been estimated only for the Connecticut River, for which Savoy and Crecco (2004) reported that the annual exploitation rate from the combined commercial and recreational fisheries has remained at 0.05 or less since the mid-1990s. One can infer maximum exploitation rates for the recreational fishery on the Merrimack River in 1984–1988 when data on passage and harvest are available (ASMFC 2007) if one assumes that passage at the first dam plus harvest below the dam represent a minimum population estimate and that harvest divided by this minimum population estimate provides a maximum estimate of  $u$ . Given this assumption, the mean exploitation rate in 1984–1988 was 0.05. Exploitation rates from directed harvest of American shad in other New England rivers remain unknown because concurrent estimates of harvest and population size or passage are not available for these rivers. However, the low levels of loss suggest relatively low exploitation rates.

Our analyses suggest that at a given rate of loss or passage failure, directed fishing on an American shad population per se is less significant than bycatch but more significant than upstream passage failure or downstream passage mortality. However, the current rates of directed fishing summarized above appear to be low relative to the passage sources of mortality and thus less important a factor in regulating the population. Since fishing on New England shad stocks usually occurs on populations that inhabit dammed rivers, the more important impact of fishing is probably the resulting erosion of the benefits from improved fish passage. This is especially the case where most or all of the spawning habitat occurs above the dam or dams.

Even without discards or directed fishing, our analyses suggest that the levels of upstream passage reported for American shad at migration barriers in New England rivers generally do

not achieve the levels needed to maintain SSBR at or above those at  $Z_{30}$ . Our analyses predicted that upstream passage survival must exceed 55% ( $\leq 45\%$  mortality) before the spawning stock biomass exceeds that at the  $Z_{30}$  level. Even if unsuccessful fish survive, passage levels must exceed 30% ( $\leq 70\%$  passage failure) before the population biomass exceeds the SSBR benchmark. Few dams in New England have even these minimal passage efficiencies. For example, on the Connecticut River, American shad must pass three dams to reach historic spawning habitat. Leggett et al. (2004) reported that since 1985 40% or more of the American shad in the lower estuary routinely pass above the first dam (Holyoke) in the system. In 1995–2007, the mean annual passage (measured as the percentage of fish that passed the preceding dam) at the next two dams was 2% (Turner's Falls) and 57% (Vernon) (Michael Hendricks, Pennsylvania Fish and Boat Commission, personal communication). Of the fish that make it past the first dam, only 0.1% makes it past the Vernon dam (99.9% passage failure or mortality). On the Merrimack River, a mean of 17% of the American shad that passed the first dam made it above the next dam (1989–2004; Michael Hendricks, personal communication). Passage over the Brunswick Dam on the Androscoggin River in Maine is thought to be low based on telemetry studies (ASMFC 2007).

Data on upriver passage at a given dam relative to passage at the preceding dam do not allow one to differentiate between the mortality between dams and poor passage at the upstream dam. However, the consequences to the stock are similar. Clearly, based on the results of our analyses, upstream passage to spawning habitat at most New England dams is low and by itself likely to be low enough to inhibit stock restoration. The addition of discard or fishing mortalities to these low passage values makes restoration problematic. The American shad populations in many of these river systems appear to persist at low levels from spawning below the first dam on the system and possible spawning between dams.

The American shad of the Connecticut River have not responded to the increased percentage of fish that pass the first dam (Leggett et al. 2004). Moreover, the authors noted a reduction in their mean size and age and a reduction in frequency of repeat spawning. All of these changes suggest excessive mortality on adults. The authors hypothesized that the problems with this stock were caused by increased physiological stress from extended migration and increased predation by striped bass. We suggest that poor upstream and downstream passage success or survival at Holyoke, Turners Falls, and Vernon dams are also factors in the decline of the stock. Since spawning is known to occur below the first dam, it might be helpful if the upriver passage of prespawning fish was reduced for this population to reduce mortality and increase population size until the passage or mortality problems have been rectified. Leggett et al. (2004) suggested this approach as well. This might be a helpful strategy at other New England dams with poor upriver passage rates, such as those on the Merrimack River. The risk to this approach is that any inheritable traits that predispose fish to move upriver

past the dam might be lost. However, once passage problems have been resolved, prespawning shad could be moved above the dam to recreate homing traits to the upriver reaches.

Our analysis suggests that the successful downstream passage of mature fish after spawning at barriers is not as important as upriver passage. This is surprising, in that New England American shad commonly spawn several times over their life span (ASMFC 2007). It is possible that some of the resilience shown by shad to downriver mortality is explained by the fact that first-time spawning is spread over several ages and that postspawning mortality only affects the mature component of a given age. It does not affect the entire cohort in a given year. Even without mortality, the late-maturing portion of the cohort only gets to spawn a couple of times in its life. Also, postspawning mortality means that the mature component at a given age does get to spawn before dying.

Even though downriver passage mortality was the least damaging in our analyses, losses from downriver passage exacerbate the effects of other anthropogenic problems and should be addressed eventually. Downstream passage facilities for postspawning mature fish are rare and success is usually undocumented. There are no downstream passage facilities on the Saco River in Maine, two dams on the Exeter River, or the lowermost dam on the Lamprey River in New Hampshire (ASMFC 2007). Limited downstream passage is provided at the lowermost dam on the Cochecho River, New Hampshire. Downstream passage facilities have been constructed at Vernon, Turners Falls, and Holyoke dams on the Connecticut River, but they are used by very few adult fish (Leggett et al. 2004).

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