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SPECIAL SECTION: AMERICAN SHAD AND RIVER HERRING

Alosine Restoration in the 21st Century: Challenging the Status Quo

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Abstract

Despite the expenditure of millions of dollars on restoration efforts for depleted North American stocks of alosine fishes, rangewide abundance levels for multiple species have declined to historic lows. Stocking practices aimed at rebuilding spawning runs are deemed successful when numerical abundance levels are shown to increase in response. However, these practices may only yield short-term gains in abundance at the ultimate expense of population genetic integrity and do not ensure the long-term persistence and evolutionary potential of a species. Although molecular methods are now widely employed in fisheries management and provide a suite of powerful management tools, these approaches have not been well integrated into alosine management strategies. We review the net effects of stocking practices on population genetic integrity and species' long-term persistence as it is currently understood and highlight what is known in this regard for alosines in North America, with particular focus on American shad *Alosa sapidissima*. We find that stocking practices carry a substantial risk to the persistence of genetically distinct alosine spawning populations and suggest that future restoration efforts proceed by providing access to historical spawning grounds, either through dam removal or through providing effective fish passage, followed by natural recolonization of reclaimed habitat. We also identify important areas of research relevant to future alosine restoration that require exploration and identify recent developments that may alter future restoration decisions in an adaptive management framework.

It is now broadly acknowledged among fisheries professionals that several anadromous alosine fishes in North America are in crisis. Several species are of increasing conservation concern and have experienced dramatic rangewide declines in abundance (Limburg and Waldman 2009; Figure 1) and extirpations of spawning populations (Limburg et al. 2003) in response to anthropogenic factors (i.e., overfishing and spawning habitat loss or degradation; Bilkovic et al. 2002). Despite closures of ocean-intercept and regional commercial and recreational fisheries (ASMFC 1999, 2008) and ongoing restoration efforts, rangewide abundance levels for some species (i.e., American

shad *Alosa sapidissima*, alewife *A. pseudoharengus*, and blueback herring *A. aestivalis*) have continued to decline to all-time lows and exhibit no signs of recovery (ASMFC 2007).

Actions to restore alosine spawning populations in the United States have consumed vast amounts of resources and have included stocking activities (supportive breeding and stock transfers) and the provision of access to historical spawning habitat (through the modification of fish passage facilities and dam removal). These restoration practices are deemed successful when numerical abundance levels are shown to increase in response (see Cooke and Leach 2003; Hendricks 2003; Olney et al. 2003;

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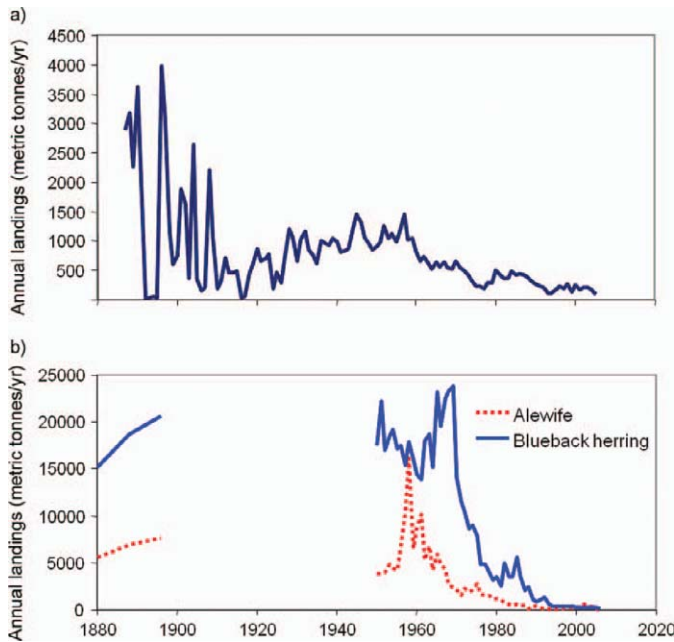


FIGURE 1. Temporal trends in historical landings of a) American shad (data source: ASMFC 2007) and b) river herrings (data source: Limburg and Waldman 2009) along the Atlantic coast of North America.

St. Pierre 2003; Weaver et al. 2003), but does increased abundance alone constitute successful restoration? Is it enough to provide recreational fishers with angling opportunities and to attain levels of spawning stock biomass that yield a “harvestable surplus” (ASMFC 2010), or should fisheries management focus on the long-term persistence of alosine stocks, with the aim of gradually reducing human intervention to sustain them? This is an important distinction, because how successful restoration is defined should determine the future direction of management decisions. If the attainment of “healthy, self-sustaining populations” (as expressed in the vision statement of the Atlantic States Marine Fisheries Commission) is indeed the goal, devising management strategies that ensure the long-term persistence of populations is the most appropriate way to achieve successful restoration of alosine stocks. However, this reveals an underlying contradiction, as some current restoration practices (i.e., stocking activities) may be inadvertently (and ironically) hindering restoration success. Specifically, stocking practices may yield only short-term gains in abundance at the ultimate expense of population fitness and may jeopardize the genetic integrity of distinct stocks (Lynch and O’Hely 2001). This may impede long-term persistence and negatively impact species’ evolutionary potential (i.e., quantitative trait heritability; Frankham 1995). Despite these concerns, the Atlantic States Marine Fisheries Commission maintains that “the risk of [stocking practices] has not been identified as a significant issue in [recovery planning]” and continues to advocate the use of stocking in alosine restoration (MDMR 2009).

The purpose of this paper is not to condemn alosine management for previous restoration decisions. It is easy to be critical of past fisheries management practices when armed with hindsight (McHugh 1970), but that approach would not constructively contribute to the future success of restoration activities. Rather, the goal here is to enlighten management by highlighting the potential consequences of stocking practices to the ultimate success of alosine restoration and to show that due diligence is required before embarking on future stocking programs for restoration purposes. This is particularly relevant because stocking efforts (including interbasin stock transfers) in support of river herring (alewife and blueback herring) restoration are increasing (MDMR 2009; CDEP 2009). To this end, we (1) highlight an important deficiency in current alosine stock assessments used to inform management, (2) examine the risks of stocking practices to population persistence, (3) discuss the effects of stocking activities on American shad spawning populations as currently understood, (4) examine recent findings for American shad that challenge established theory and may alter management strategies, and (5) identify gaps in our knowledge about alosines that require investigation for management to make well-informed decisions about future restoration activities. Through this effort we hope to raise awareness among the alosine management and scientific communities and show how the incorporation of a molecular component into an adaptive management framework (ASMFC 2010) will benefit future restoration efforts and help to ensure the long-term persistence of genetically distinct alosine stocks.

MANAGEMENT INFORMATION DEFICIENCIES

The long-term persistence of species is contingent on the ability of populations to mount variable responses to future perturbations; this ability, in turn, dependent on the amount of genetic variation present at the population level (Allendorf and Lundquist 2003). Intraspecific genetic variation is crucial for facilitating evolutionary processes and maintaining adaptive potential, and it has been shown to improve colonization success (Gamfeldt et al. 2005), increase resistance to pathogens (Pearman and Garner 2005), enhance population stability (Bjornstad and Hansen 1994; Doebeli and de Jong 1999; Agashe 2009), and ensure population persistence (Newman and Pilson 1997; Vilas et al. 2006). However, populations are not necessarily equivalent in their amounts of genetic variation or their responses to future environmental conditions (Petit et al. 1998). Therefore, understanding the magnitude and spatial distribution of intraspecific genetic variation across a species’ range is an integral component of resource management and is important for the prioritization of the use of limited conservation resources, the designation of management units, the protection of adaptive genetic variation, and the preservation of species’ evolutionary potential (Allendorf 1986).

Information about the amount and distribution of intraspecific genetic variation among alosines would benefit

conservation and restoration efforts, as knowledge of the relative contributions of populations to species-level genetic variation would aid the prioritization of populations for management, leading to an effective conservation strategy and the long-term persistence of alosine stocks. However, there is currently a greater understanding of the magnitude and distribution of intraspecific genetic variation for mummichog *Fundulus heteroclitus* (Duvernell et al. 2008) than for many alosine fishes (but see Hasselman 2010; Hasselman et al. 2010). Indeed, a search on Thomson Scientific's Web of Science for the subject terms "Alosa AND genetic" revealed only 34 publications, compared with 1,721 publications for "Salmo AND genetic" and 1,914 publications for "Oncorhynchus AND genetic." These values suggest 50–56 × greater effort to gathering genetic data for these salmonid genera than for *Alosa* spp. This is a somewhat depressing, and rather embarrassing, revelation given the historical (cultural and commercial) relevance of alosines in North America (McPhee 2002; Greene et al. 2009; ASMFC 2010). Such data are critical to fish management and are available for many species but are largely missing for alosines.

Although molecular methods are widely recognized as a necessary component of a comprehensive fisheries management strategy (Hallerman 2003), these approaches have not been well integrated into alosine management and restoration practices. The management of alosine fishes has been guided primarily by state-based stock assessments that rely on conventional fisheries management indices (e.g., mortality estimates, juvenile abundance indices, stock–recruitment, and yield per recruit) and assessments of critical habitat quantity and quality (ASMFC 1999, 2008). While these approaches provide valuable information, they only constitute parts of a more inclusive multidisciplinary management plan and provide an incomplete picture of how future restoration efforts should proceed. Molecular methods are now widely employed in fisheries management, and provide a suite of powerful tools for making well-informed decisions. Alosine management needs to begin incorporating molecular information into stock assessments if future restoration activities are to successfully "protect, enhance, and restore" spawning stocks that are "robust enough to withstand unforeseen threats" (ASMFC 2010).

The absence of a molecular component in most current alosine stock assessments probably reflects its omission from prior mandates (i.e., the alosine interstate fishery management plan [FMP] and subsequent amendments; ASMFC 1985, 1999, 2009, 2010), but it speaks to the larger issue of the need for integrating population genetic principles into fisheries science (Hallerman 2003). Those engaged in alosine management may be unaware of the inherent value of genetic monitoring and uncertain how to implement molecular information in future restoration decisions. Further, there may be a general lack of hands-on experience in molecular ecology (i.e., genotyping, data analyses, and synthesis of results) among individuals within the alosine management structure (ASMFC 1999). Specifically, those directly involved in stock assessments may be classically trained

in traditional fisheries science and management practices and have limited experience with molecular methods and the practical application of these tools in a restoration or management context. Thus, these fisheries professionals would not necessarily be in a position to advise management about the value of including genetic monitoring in the existing FMP. However, learning tools are now available for guiding resource managers in the practical application of genetic principles to conservation (e.g., http://alaska.fws.gov/gem/mainPage_1.htm). Fortunately, the need to understand the spatial distribution of alosine genetic variation has recently been acknowledged (ASMFC 2009, 2010), and this sounds a hopeful note for the incorporation of genetic monitoring in future stock assessments.

IMPACTS OF STOCKING

Although the objective of stocking activities is often to increase fish population abundance, stocking practices can have unintended negative consequences for population persistence (Lynch and O'Hely 2001; Halbisen and Wilson 2009). The negative effects of stocking practices on the genetic integrity and fitness of wild fish populations have been well documented (e.g., Hindar et al. 1991; Lynch and O'Hely 2001; Araki et al. 2007), and there is a rich literature with which to examine the potential risks to alosine fishes. Here, we distinguish between the effects of two types of stocking practices—supportive breeding and stock transfers—both of which can have deleterious consequences for fitness and both of which have been used extensively for alosine restoration (Hendricks 2003). Supportive breeding entails the reproduction of a segment of a wild population in captivity followed by the release of the captive progeny to supplement that same wild population (Ryman and Laikre 1991; Ford 2002). No exogenous genes are introduced into the population (Ryman and Laikre 1991). Stock transfers, on the other hand, involve the relocation of individuals between wild populations and can include the translocation of prespawn adults or the transfer of captive-bred progeny of wild-origin fish from one wild population to another. This can introduce genes that might otherwise not be observed in the population. Both strategies carry important risks to population persistence and can negatively impact a species' evolutionary potential (Frankham 1995). We discuss the potential consequences (generally) of these stocking practices in turn.

Supportive Breeding

The importance of maintaining a large genetically effective population size (N_e ; Wright 1931) for ensuring population persistence has been recognized for decades (e.g., Ryman and Ståhl 1980; Soulé et al. 1986; Allendorf and Ryman 1987). A population's N_e refers to the size of an ideal population experiencing the same rate of random genetic change over time as the real population under consideration (Crow and Kimura 1970). This is a crucial parameter in conservation biology because the rate of inbreeding (ΔF), and thereby the rate of loss of genetic variation per generation, is proportional to the inverse of the effective

population size ($\Delta F = 1/[2N_e]$; Crow and Kimura 1970). Supportive breeding favors the reproductive rate of one segment of the overall population and can lead to an increase in the total variance of family size (Ryman and Laikre 1991) and to reductions in N_e (Waples and Do 1994; Ryman et al. 1995). In fact, Brown et al. (2000) observed high reproductive variance in an American shad captive breeding program in Virginia and estimated a substantial (88%) reduction in the effective number of breeders (N_b) used in supplementation efforts. Further, when the absolute size of a wild population is small, supportive breeding may reduce N_e to a level below what it would have been had no supportive breeding occurred at all and can lead to serious depletion of genetic variation for the entire population (Ryman and Laikre 1991; Hedrick et al. 1994). Reduction in N_e and the loss of genetic variation can increase the risk of inbreeding and inbreeding depression (i.e., a reduction in fitness resulting from the mating of closely related individuals) and impede the ability of a population to mount a variable response to future stochastic processes (e.g., environmental and demographic factors), increasing the risk of population extinction (Saccheri et al. 1998). Serious reductions in genetic variation, and increases in the risks associated with these reductions, are more likely when a population is subjected to supportive breeding for multiple generations (Ryman and Laikre 1991).

Domestication selection is another unintended consequence of supportive breeding that may negatively influence population persistence. Traits that are advantageous in a captive environment are not necessarily beneficial in the wild (Halbisen and Wilson 2009), and selection in captivity may shift the distribution of traits away from its wild optimum. As a result, some hatchery-reared fish may exhibit reduced survival relative to their wild conspecifics (Hansen et al. 2000; Araki et al. 2007), negating the benefits of supportive breeding altogether. Moreover, releasing many individuals with a different trait distribution because of selection in captivity into a population can result in a reduction in the mean fitness of the entire wild population (Evans and Wilcox 1991; Ford 2002; Nickelson 2003). If supportive breeding proceeds for multiple generations, the trait distribution of the population may shift far from its wild optimum and negatively impact population persistence (Ford 2002). While the effect of inadvertent domestication selection may be reduced by regularly introducing wild broodstock into the captive environment, the effect cannot be completely eliminated (Lynch and O'Hely 2001; Ford 2002). In fact, it has been suggested that preventing fitness losses during supportive breeding is perhaps best achieved by conserving or restoring critical habitat (Ford 2002).

Stock Transfers

Stock transfers among divergent source populations may unintentionally reduce population fitness and jeopardize the persistence of genetically distinct populations. For anadromous fishes that exhibit philopatry, restricted levels of gene flow among genetically distinguishable spawning populations that are exposed

to differing selective forces provides the foundation for the establishment of local adaptations that may optimize population fitness in natal rivers. Although this is a simplistic depiction of an inherently complex process (e.g., the Dobzhansky-Muller model; see Edmands 2007), our purpose here is not to provide an overview of the relative roles of microevolutionary processes and the modes and strengths of natural selection required for the establishment or maintenance of local adaptations. Rather, we only wish to convey (to an audience that may not be well versed in molecular ecology and evolution) the general principle that, over time, restricted gene flow among populations that are exposed to differing selective pressures promotes the establishment of adaptations that may optimize population fitness. Stock transfers remove the reproductive barriers established through philopatry and create opportunities for nonnative genes or gene complexes to introgress into wild populations. This may inadvertently result in the loss of local adaptations and the breakdown of coadapted gene complexes (outbreeding; Edmands 2007; McClelland and Naish 2007), reducing population fitness (i.e., outbreeding depression; Lynch 1991; e.g., Neff 2004) and potentially increasing the risk of population extinction (Waples 1991), ultimately counteracting the desired effect of stocking efforts. Indeed, a growing body of literature on the impacts of outbreeding in fish has revealed changes in growth rate and behavior (McClelland et al. 2005; Tymchuk and Devlin 2005; Tymchuk et al. 2006) and increased susceptibility to disease (Goldberg et al. 2005) as well as decreased physiological performance (Foote et al. 1992; Cooke et al. 2001), homing ability (Bams 1976), marine survival (Gharrett et al. 1999; Gilk et al. 2004), and overall population fitness (McGinnity et al. 2003).

Stock transfers may also jeopardize the genetic integrity of divergent populations (Halbisen and Wilson 2009) and reduce native intraspecific genetic variation through interbreeding between genetically distinct populations (Hindar et al. 1991). Repeated stock transfers can result in the numerical replacement of the native population and erosion of that population's genetic composition, resulting in genetic homogenization and introgression (Evans and Wilcox 1991; Hansen et al. 2000). The genetic swamping (Bouzat et al. 2009) of indigenous gene pools through stock transfers is an important anthropogenic source of the loss of intraspecific genetic variation (Hansen et al. 2001). Stock transfers can have far-reaching spatial and temporal effects, as stocked fish can exhibit lower philopatry than wild fish (e.g., Bams 1976; Stabell 1984) and this may unintentionally lead to greater gene flow among other genetically distinct stocks.

EFFECTS OF STOCKING ON AMERICAN SHAD

Stocking efforts to restore depleted American shad spawning runs in the United States have been extensive. Cumulatively, hundreds of millions of American shad eggs, larvae, juveniles, and prespawn adults have been used for supportive breeding and stock transfers among several rivers within their native range

since 1870 (New York Times 1874; reviewed in Hendricks 2003). Although a thorough review of American shad stocking history is beyond the scope of this synthesis, prior summaries (Leach 1925; Hendricks 2003) and ongoing research (D. J. Hasselman and M. L. Hendricks, Pennsylvania Fish and Boat Commission, unpublished) reveal that stock transfers have not occurred among semelparous spawning runs south of the Cape Fear River, North Carolina, but have historically focused on iteroparous spawning runs in the Chesapeake Bay, the Delaware, Hudson, Connecticut rivers, and other rivers in New England.

The specific impacts of past stocking practices on American shad population fitness and genetic variation remain largely unknown (but see Aunins 2010), but they should be of great concern. American shad spawning populations have been shown to comprise genetically distinguishable groups (Bentzen et al. 1989; Hasselman 2010; Hasselman et al. 2010), and the broad distribution of reproductively isolated spawning runs (~30–50°N; Walburg and Nichols 1967) and the presence of intraspecific life history variation (e.g., semelparity versus iteroparity; Leggett and Carscadden 1978) may have led to the spatial segregation of neutral and adaptive genetic variation and the establishment of local adaptations. Previous stocking practices may have inadvertently decreased population fitness (via domestication selection or the loss of local adaptations) and/or intraspecific genetic variation (via reduced N_e , interpopulation homogenization, and introgression), placing the long-term persistence of some spawning populations at risk.

The spawning population in the Susquehanna River provides an excellent case study of the effects of stocking practices on genetic variation among American shad. No spawning run has been subjected to more extensive stocking pressure than the Susquehanna River. Since 1971, this population has been supplemented with over 449 million American shad eggs or larvae from several East Coast rivers, including the Hudson and Delaware rivers (Brown and St. Pierre 2001; Hendricks 2003). Additionally, 33,000 prespawners from the Hudson and Connecticut rivers were transplanted to the Susquehanna River between 1980 and 1987 (Hendricks 2003). These efforts were deemed “successful,” as hatchery fish constituted 46% of the 163,000 adult American shad returning to the Susquehanna River in 2000 (Hendricks 2003). However, a recent genetic assessment of the Susquehanna River spawning population suggests that the proportional contributions of the stocking sources has had a great influence on the gene frequencies and genetic structure of the stock and that out-of-basin stock transfers have limited the long-term adaptive potential of this spawning population (Julian and Bartron 2006). In short, stocking practices have probably jeopardized the genetic integrity of the original Susquehanna River spawning stock and may have negatively impacted the evolutionary potential and long-term viability of the remnant wild population.

It is unlikely that the negative effects of previous American shad stocking practices are limited to the Susquehanna River. Indeed, the James River has been the recipient of mil-

lions of American shad larvae of Pamunkey River origin since 1994 (Brown et al. 2000), and the lack of significant genetic differentiation among these spawning runs now (compared with the subtle but significant differentiation prior to stocking) suggests that this has led to the replacement of the original James River lineage with the Pamunkey River lineage (Aunins 2010). Moreover, in a rangewide survey of American shad neutral genetic variation, Hasselman (2010) found that the degree of standardized genetic differentiation among U.S. American shad spawning populations was significantly ($P < 0.001$; sequential Bonferroni correction) weaker (mean $F'_{ST} = 0.044 \pm 0.031$) than that detected among Canadian spawning runs (mean $F'_{ST} = 0.157 \pm 0.067$). In fact, nonsignificant ($P > 0.05$; sequential Bonferroni correction) genetic differentiation was observed among most pairwise comparisons of neighboring drainages in the United States (17/20), as well as among most rivers tributary to the Chesapeake Bay (18/21). This offers a stark contrast to the levels of genetic differentiation and patterns of population structure observed among Canadian spawning populations (Figure 2; Hasselman et al. 2010), which have never been subjected to stocking practices. Hasselman (2010) also examined historical stocking records from 1871 to the present and observed that the degree of genetic differentiation between spawning populations subject to stock transfers was lower than would have been predicted based on geographic distance alone; this effect increased with distance between the stocking source and recipient spawning population. These results suggest that stock transfers among American shad spawning populations have served to homogenize gene pools via genetic swamping (Bouzat et al. 2009) and to diminish the degree of population structure among iteroparous spawning populations in the United States.

ADAPTIVE ALOSINE MANAGEMENT

As we indicated in the introduction, the purpose of this paper is not to lay blame on alosine management for past restoration decisions; a management strategy is only as effective as the accuracy of the information on which it is based. However, recent findings challenge established views about the spatial distribution of intra-specific neutral genetic variation for American shad and should alter restoration practices within an adaptive management framework. Previous synoptic surveys of neutral genetic variation among American shad largely employed mitochondrial DNA (mtDNA) to resolve population structure (Bentzen et al. 1989; Nolan et al. 1991; Epifanio et al. 1995; Waldman et al. 1996). However, mtDNA is a single, nonrecombining molecular marker that cannot generate independently replicated data (Ballard and Whitlock 2004) for the examination of spatial genetic patterns. Multiple unlinked microsatellite loci are now sought to inform conservation and management decisions (Crandall et al. 2000; Allendorf et al. 2004) and can provide independent data for assessing the magnitude and spatial distribution of neutral genetic variation.

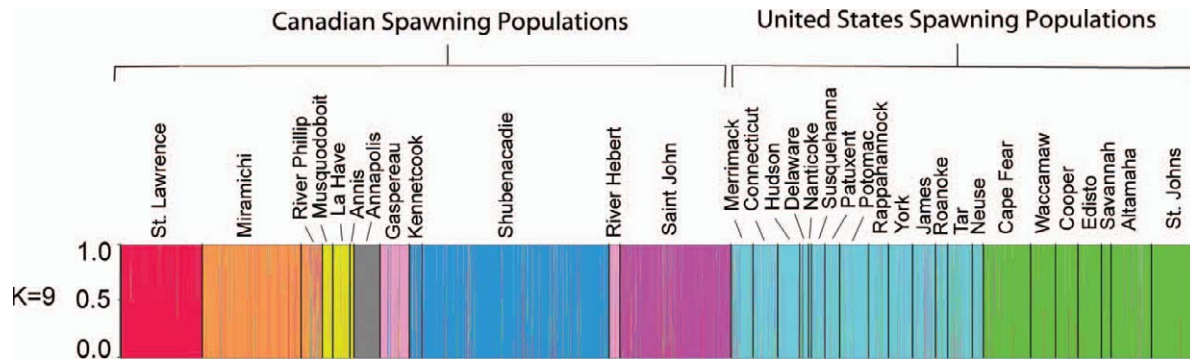


FIGURE 2. Analysis of American shad population structure using the Bayesian clustering algorithm implemented in the program STRUCTURE v. 2.1 (Pritchard et al. 2000) identified nine genetically distinguishable clusters (K) among 33 spawning runs from across the species' range; seven in Canada, and two in the United States. Individuals are represented by a thin vertical line which is partitioned into $K = 9$ coloured segments representing an individual's estimated membership fraction from each of the identified clusters. Black lines separate individuals from different spawning runs (labeled above). See Hasselman (2010) and Hasselman et al. (2010) for details.

Previous surveys of American shad microsatellite variation were restricted in geographic scope and revealed weak (although statistically significant) population structure among U.S. spawning populations (Brown et al. 2000); they failed, however, to detect a significant pattern of isolation by distance (IBD), suggesting that there is little geographic variation in genetic diversity across the species' range (Waters et al. 2000). Thus, alosine management may have been confident that stocking practices would have little consequence for a species already exhibiting weak genetic structure and that such practices could continue without causing irrevocable harm to the long-term persistence of American shad populations. However, those studies were limited in scope to a few loci and a few spawning populations within close (<500-km) geographic proximity to the centre of the species' range. Thus, some of those findings might not be valid within a broader geographic context (i.e., a reflection of spatial scale), which would have important management implications.

Using 13 polymorphic microsatellites, Hasselman (2010) examined the spatial distribution of American shad neutral genetic variation among 33 spawning populations from across the species' entire range (>5,000 km). Contrary to previous microsatellite studies, this investigation revealed important geographic variation in the distribution of American shad genetic diversity and detected a highly significant ($P < 0.001$) pattern of IBD across the species' range as well as among U.S. spawning populations. These observations highlight the importance of adequately sampling across a species' distribution before making inferences about rangewide patterns of genetic variation. However, it is worth noting that Hasselman (2010) may have reached the same general conclusions as Brown et al. (2000) and Waters et al. (2000) had that study been restricted to the same populations and geographic scale. Similarly, although Palkovacs et al. (2008) found minimal population structure among alewife spawning runs in Connecticut, this should not be taken as evidence that alewives do not exhibit genetic structure at larger spatial scales.

Although Hasselman (2010) confirmed that genetic differentiation was generally weak among U.S. American shad spawning populations, significant ($P < 0.05$; sequential Bonferroni correction) allelic heterogeneity was detected among the vast majority of spawning populations (514 of 528 pairwise comparisons), confirming that many spawning populations constitute genetically distinguishable groups (Bentzen et al. 1989). However, instances of allelic homogeneity were observed among rivers within the Chesapeake Bay and within the semelparous portion of the species' range, and it is uncertain to what extent this is due to human-mediated or natural levels of gene flow. Even so, these observations suggest that many American shad spawning populations across the species' range retain their unique multilocus genetic signatures and that it is not yet too late to preserve much of the existing genetic variation present among spawning stocks. This sounds a hopeful note for future management and restoration actions and for the long-term persistence of genetically distinguishable American shad spawning populations.

There are other recent (nonmolecular) findings for American shad that may have implications for future restoration efforts. The reproductive success of American shad has been associated with upstream spawning migration distance and the greater availability of suitable prey and optimal water temperatures for larval and juvenile growth (Limburg 1996). Indeed, various studies have reported alosine population expansion following improved access or transport of spawning stock upstream of migration barriers (reviewed in Cooke and Leach 2003). Thus, efforts to provide access to historical spawning habitat have largely focused on the removal of low-head dams or the provision of effective upstream fish passage where dam removal is not a viable option (St. Pierre 2003; Weaver et al. 2003). However, Castro-Santos and Letcher (2010) suggest that providing effective downstream passage for adult American shad may also be an important component of restoration success. High rates of adult mortality stemming from ineffective downstream fish

passage facilities may incur a selective pressure for reduced repeat spawning among iteroparous populations (Castro-Santos and Letcher 2010). Reduced iteroparity may ultimately hinder restoration efforts through a reduction in effective population size and decreased reproductive rate and by removing the buffer that iteroparity provides against the environmental stochasticity of northern rivers (Leggett and Carscadden 1978; Castro-Santos and Letcher 2010). This is particularly poignant given the projections for environmental variability under future climate change scenarios (Ficke et al. 2007). There is already some evidence that the Connecticut River American shad spawning population has experienced a decline in the rate of iteroparity (Leggett et al. 2004; Savoy and Crecco 2004; ASMFC 2007), and management needs to carefully consider this information in future restoration decisions about other iteroparous spawning populations.

RESEARCH NEEDS

There are a number of substantial gaps in our collective knowledge about alosines that require careful examination if recovery goals are to be met. The Atlantic States Marine Fisheries Commission (ASMFC; 2009, 2010) has identified several research areas that need attention and that largely focus on stock assessments and population dynamics, habitat, and life history. Although the ASMFC (2009, 2010) has recognized the need to understand alosine intraspecific genetic variation, this goal remains relatively obscure, as specific objectives have not been identified. We help elucidate this goal by identifying specific research objectives within the framework of “understanding intraspecific alosine genetic variation” that require immediate investigation if management is to make well-informed decisions about future restoration actions.

Although the magnitude and rangewide spatial distribution of neutral genetic variation has been explored for American shad using microsatellites (Hasselman 2010), this basic information is still needed for alewives, blueback herring, and hickory shad *A. mediocris*. These data are needed to resolve the spatial scale(s) of population structure so as to identify genetically distinct populations (Waples and Gaggiotti 2006) and estimate their relative abundance in mixed-stock fisheries, resolve intraspecific levels of neutral variation among populations, identify the relative contributions of populations to species-level genetic diversity, and designate conservation units.

Several population-genetic parameters stemming from the examination of neutral genetic markers are also required for effective management but have yet to be explored for any alosine spawning stock. Estimates of alosine migration rates (m) and quantification of the amount (i.e., the effective number of migrants [$N_e m$]) and directionality of gene flow among spawning populations are currently unavailable but will provide valuable information for resolving the spatial and temporal patterns of genetic variation (including the stability of metapopulation structure; Hasselman et al. 2010). Although estimates of N_e are not available for any alosine spawning population, this informa-

tion is urgently needed given the relevance of this parameter to conservation and the consequences of reductions of genetic variation for long-term population persistence. While several alosine spawning populations have been substantially reduced in abundance, no studies have been undertaken to examine whether they suffer from the deleterious effects of inbreeding and inbreeding depression.

While examinations of neutral genetic markers are valuable for resolving the spatial distribution of genetic diversity, they cannot attest to the presence of local adaptations. The wide geographic range of alosines and the philopatric nature of at least some species (Hendricks et al. 2002; Willis 2006) provide the opportunity for differential selective pressures in natal habitats to establish adaptations that optimize population fitness. However, there has been no study aiming at the detection of adaptive genetic variation for any alosine stock. This is an area that requires immediate investigation, and it could proceed through the detection and examination of quantitative trait loci (e.g., Gardner and Latta 2007; Boulding et al. 2008) and the genes of the major histocompatibility complex (e.g., Dionne et al. 2007; Thob et al. 2011).

Determining which spawning stocks are impacted by mixed-stock fisheries is an important research area for future alosine management. The ASMFC (2009, 2010) has recently advocated the use of otolith microchemistry, oxytetracycline otolith marking, and/or tagging to resolve the relative contributions of spawning populations to mixed-stock harvests. Although previous mixed-stock analyses of American shad using mtDNA (Nolan et al. 1991; Epifanio et al. 1995; Brown et al. 1999) provided only coarse resolution, microsatellites and single-nucleotide polymorphisms provide greater power for mixed-stock analysis and genetic stock identification (Kalinowski 2004; Winans et al. 2004), have provided demonstrable benefits elsewhere (Ruzzante et al. 2000; Hess et al. 2011), and should be considered for alosines.

Studies of allis shad *A. alosa* (also known as allice shad) and twaite shad *A. fallax* suggest that hybridization and introgression is an important consideration for management (Alexandrino et al. 2006; Coscia et al. 2010; Jolly et al. 2011) and may be of relevance for some North American alosines as well (i.e., American shad \times Alabama shad *A. alabamae* and alewife \times blueback herring; Bowen et al. 2008). The creation of dams, stocking activities, and other management actions could impact the incidence of hybridization and thus present a considerable threat to population persistence and parental species integrity. Unfortunately, data to address the degree of hybridization among closely related alosines in North America are lacking; obtaining them should be a top research priority, particularly for alewives and blueback herring.

RECOMMENDATIONS

Examination of neutral genetic variation among American shad (Bentzen et al. 1989; Julian and Bartron 2006; Hasselman

2010; Hasselman et al. 2010) suggests that current stocking practices are not consistent with the long-term persistence of wild, naturally reproducing, and genetically distinct alosine stocks and therefore conflict with the ASMFC vision statement calling for the attainment of “healthy, self-sustaining populations.” While modern alosine stocking programs aim to restore severely depleted populations to levels at which natural reproduction can replace hatchery production (Hendricks 2003), past stocking practices may have jeopardized the genetic integrity and long-term adaptive potential of several American shad spawning populations. Interbreeding and introgression may have led to reduced genetic differentiation and weakened population structure, declines in the level of intraspecific genetic variation, and reductions in population fitness, putting the long-term persistence of some spawning populations at risk. Future alosine restoration efforts should avoid stock transfers, which may result in unintended consequences that are ultimately counterproductive to restoration goals.

Despite the millions of American shad stocked in various rivers along the Atlantic coast of the United States, spawning populations continue to decline in abundance, prompting some researchers to question the value of American shad culture (Hendricks 2003). This is not a new assertion. Mansueti and Kolb (1953) opined over a half century ago that “no competent fishery biologist has advocated the stocking of [American] shad fry as a successful [rehabilitation] measure.” Indeed, it has been suggested for an equally lengthy period of time that the most promising restoration measures are proper conservation and the improvement of spawning habitat (Moss 1950). Much of the supportive breeding for American shad has involved inefficient strip spawning of females (Talbot 1954), which entails unnecessary mortality (particularly for iteroparous stocks) and yields only one clutch of eggs for a species that has recently been shown to exhibit batch spawning (Olney and McBride 2003). Greater recovery potential would exist if American shad were allowed to reproduce naturally over the duration of the spawning run. For this reason, we advocate a gradual phasing out of supportive breeding as a restoration measure for American shad and suggest greater effort toward providing access to historical spawning habitat. In particular, main-stem dam removals should be a high priority for providing access to historical spawning habitat; where this is impossible, upstream and downstream passage for adults should be made more effective. Likewise, restoration efforts can be directed toward improving and recreating spawning and rearing habitats. Further, given that interbasin stock transfers for river herrings have only recently commenced, now is the time to formally evaluate the effects of stocking practices on alosines, before river herrings irrevocably follow the same restoration and management trajectory as American shad.

The use of upstream regions by alosines following the provision of suitable passage facilities (or dam removal, e.g. Embrey Dam, Rappahannock River, Virginia) may not be immediately apparent and may lead some to question the value of such restoration actions in the future. However, this view

does not take into account the natural variation inherent in biological systems, the time required to observe the effects on stock abundance, or the long-term benefits of providing access to additional spawning habitat. Indeed, there are multiple examples of alosines expanding into and successfully spawning in reclaimed habitat following dam removal (Walburg and Nichols 1967; O'Donnell et al. 2000; Hart et al. 2002; Burdick and Hightower 2006). Following the provision of access to historical spawning grounds, some individuals are likely to use newly available habitat simply as a matter of chance. Those individuals may experience increased reproductive success because of the availability of suitable prey and optimal water temperatures for larval and juvenile growth (Limburg 1996), increasing the number of individuals eventually recruited to the spawning stock. As the stock begins to grow in abundance, an increasing number of individuals would use upstream spawning habitat and reap the fitness benefits of greater reproductive success. In this way, the propensity for alosines to use historical spawning grounds would increase, generating a positive feedback loop and gradually increasing the abundance of the entire spawning population.

The removal of dams in Maine provides an opportunity to empirically examine the potential for alosines to naturally recolonize formerly inaccessible habitat and will yield incredibly valuable insights into the colonization process for alosines (i.e., modes of dispersal), an opportunity that should not be wasted. Natural recolonizations by American shad have occurred on the Saco and Narraguagas rivers in Maine and have yielded sustained (albeit small) spawning runs (MDMR 2009). Proposals to stock alosines in the Penobscot River, Maine, immediately after dam removal and before natural recolonization can occur are misguided and not based on the results of scientific inquiry. Such proposals have little to do with science-based management and arguably more to do with providing the public with visual evidence of “successful fish restoration” following dam removal as justification for the cost of providing access to habitat.

One needs only consider nonnative American shad in the Columbia River to see the impact of providing access to additional spawning habitat. Historically, the limit of American shad upstream migration on the Columbia River was Celilo Falls (rkm 323, measuring from the mouth of the river). However, with the completion of the Dalles Dam (rkm 309) in 1957, the resulting reservoir inundated Celilo Falls and provided American shad with access to previously unavailable spawning habitat, precipitating the “Celilo invasion” (Hasselman et al. 2012). This prompted a sudden and dramatic increase in the number of adult American shad observed passing Bonneville Dam (rkm 235) in 1960, relative to the numbers seen in the previous 22 years (Figure 3). Although this is a rather ironic example, the salient point is that American shad will utilize upstream spawning habitats if suitable passage is provided, and the abundance of the spawning stock can increase dramatically in response. This sounds a hopeful note for East Coast managers and suggests that a reevaluation of current fish passage designs and modifications to meet the specifications of the Columbia River dams may be warranted.

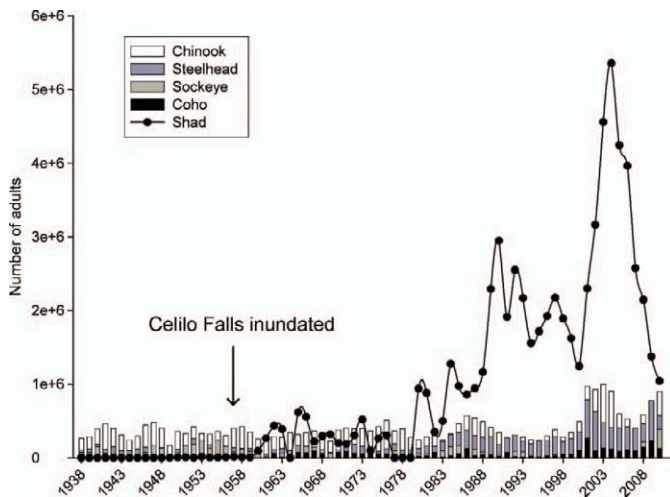


FIGURE 3. Adult anadromous fish counts at Bonneville Dam fish ladder. Data from Data Access in Real Time (DART: <http://www.cbr.washington.edu/dart/adultpass.html>)

Although stocking has probably had negative effects on American shad, whether these practices are consistent with the long-term sustainability of other alosine stocks remains uncertain. To some extent this reflects the absence of even the most basic information about the magnitude and spatial distribution of neutral genetic variation for this taxon. In this regard, and relative to other fishes of economic value and/or conservation concern, the alosine scientific and management community is well behind the curve with respect to what is now considered a standard component of comprehensive fisheries management strategies. This gap continues to widen as whole genomic approaches are increasingly applied in fisheries management (e.g., Boulding et al. 2008; Tymchuk et al. 2010), and the alosine scientific community needs to begin proactively incorporating genetic monitoring into state-based stock assessments as a first step toward closing this gap.

Although anadromous alosines exhibit philopatry (Hendricks et al. 2002; Willis 2006; Walther et al. 2008) and spawning site fidelity (Melvin et al. 1986), the degree of homing is not 100% accurate. Straying rates may vary spatially and temporally by species and may manifest themselves as gene flow among spawning stocks. Recent studies of European alosines (e.g., allis shad and twaite shad; Alexandrino et al. 2006; Coscia et al. 2010; Jolly et al. 2011) and alewives (Palkovacs et al. 2008) suggest that alosine straying rates are generally higher than those for anadromous salmonids, leading to lower levels of population structure on smaller spatial scales. This emerging generality suggests that although stock transfers between geographically proximal spawning runs are not always inappropriate, they nonetheless require careful scrutiny on a case-by-case basis and demand better understanding of each species' propensity to stray.

While some jurisdictions may already be involved in genetic monitoring for American shad, a coordinated effort needs

to take place on a rangewide scale for each alosine species. Because anadromous fishes do not heed political boundaries, alosine spawning populations in one state or province should not be considered in complete isolation from those in another region. A rangewide approach to genetic monitoring is not as daunting as it may seem and is readily accomplished through preparation, coordination, and cooperation. Field crews already conducting annual monitoring activities can be easily equipped with simple sampling protocols and the materials necessary to nonlethally obtain tissue (fin clips) for genetic analyses. Tissue samples from the various regions can then be sent to a single laboratory for processing to reduce the sources of genotyping error and ensure that the patterns detected among spawning populations are directly comparable. This approach has been successful in examining the rangewide distribution of neutral genetic variation for American shad (Hasselmann 2010) and could easily be extended to other alosines. Characterizing the rangewide distribution of neutral genetic variation and the spatial scale(s) of alosine population structure is a crucial first step toward effective management and provides the foundation for future examinations of adaptive genetic variation.

Although we have highlighted the negative consequences of stock transfers for long-term population persistence, there are circumstances under which the introduction of novel genes to a population may actually be beneficial. Several studies have shown how the introduction of a few migrant individuals into small and inbred populations can reverse the effects of inbreeding and inbreeding depression (i.e., genetic rescue; Westermeier et al. 1998; Ingvarsson 2001; Vilà et al. 2002; Tallmon et al. 2005; Bouzat et al. 2009). For alosine spawning stocks that are perceived to be very small (i.e., <1,000 spawners annually, as in remnant American shad spawning runs in Maine rivers [MDMR 2009]), assessments to determine whether these remnant populations suffer from the deleterious effects of inbreeding and inbreeding depression are needed. If this is found to be the case, then meaningful discussion about how to strategically recover levels of genetic variation through the introduction of novel genes can commence. However, because of the risk to the persistence of the remnant population, this decision is not one to be made lightly or in the absence of direct evidence of inbreeding that has been subjected to rigorous peer review in the primary literature to ensure scientific quality and integrity. While a very limited degree of introgression may provide new alleles without destroying local adaptation (Allendorf 1983), the loss of genotypic variance resulting from extensive hybridization of two populations is as irreversible as the loss of alleles from a population (Nelson and Soulé 1987). Furthermore, it is not likely that cultured stocks possess advantageous alleles that are unavailable to a local population through straying from other wild fish populations (Reisenbichler 1984). Interpopulation hybridization sometimes results in an initial increase in fitness, termed heterosis or hybrid vigor (Edmands 2007). Often the fitness reductions from hybridization are not observed until the F_2 or later generations, when deleterious interactions between

homozygous loci are exposed (Edmands 2007). Therefore, the detection of heterosis or hybrid vigor in the F_1 generation may be an unreliable predictor of the outcome of hybridization over successive generations (Lynch and Walsh 1998), and examples of heterosis followed by outbreeding depression have been observed across species (Edmands 1999; Marr et al. 2002).

CONCLUDING REMARKS

The management of anadromous alosine fishes in North America has reached a pivotal point. Do we continue to rely solely on traditional fisheries practices to guide restoration decisions, or do we begin to proactively incorporate powerful molecular approaches in an adaptive, ecosystem-based management framework? Continued rangewide declines of alosines despite extensive efforts to restore dwindling stocks reveal that we do not fully understand all the factors responsible for variations in stock abundance. It is doubtful that any one factor (e.g., habitat loss or degradation, overharvesting, an unknown component of marine mortality, striped bass predation [Savoy and Crecco 1995], etc.) is solely responsible for the persistent declines. Multiple sources of mortality probably contribute in varying degrees to the absence of alosine recovery. The incorporation of molecular information in future management decisions does not promise to resolve these issues and will not serve as a substitute for valuable information from critical habitat and standard fisheries indices (e.g., recruitment and mortality). Rather, molecular methods provide a suite of powerful tools to be used concurrently with information about habitat and population dynamics for making well-informed recommendations to fisheries management. This fact is sometimes ignored and can lead to the abuse of genetic information when it is considered in isolation.

With regards to future restoration actions, we echo the general sentiments of Edmands (2007) that alosine management should strive to do no harm. Although studies of the impacts of stocking practices have largely focused on salmonid populations, alosines are not immune to the negative consequences of stock transfers and supportive breeding. Indeed, data from the examination of neutral markers suggest that stocking activities have had harmful effects on American shad. For this reason, we believe that alosine management should immediately cease stock transfers, begin phasing out supportive breeding, and focus restoration resources on providing alosines with access to historical spawning habitat. Such a shift in restoration focus would not necessarily jeopardize the infrastructure (i.e., hatcheries and personnel) already invested in alosine restoration activities; rather, that infrastructure would provide valuable experimental research facilities and highly qualified staff to address the knowledge gaps outlined above in a controlled setting. The hatcheries would remain a valuable asset to alosine restoration, but in an experimental and research capacity (e.g., Oregon Hatchery Research Center; www.dfw.state.or.us/OHRC/).

The decline of anadromous alosines across their range was not an instantaneous event but one that occurred gradually over

a period of decades to centuries. Fisheries managers (and the public) need to recognize that the recovery of populations by providing access to historical spawning grounds will similarly be a gradual process. Dam removal and fish passage modification should not be presumed to yield immediate dividends in alosine abundance levels. No restoration measure will constitute a “quick fix,” and those anticipating such a solution are setting unrealistic recovery expectations. This does not mean that such actions are not worth pursuing for the benefit of future generations, but the changes necessary for the long-term persistence of alosines are required now. Indeed, the ultimate success or failure of future alosine restoration will depend on our ability to demonstrate the courage required to make the tough choices that lay before us. The scenario we leave behind as our legacy and as a testament of our commitment to alosine restoration awaits these difficult decisions. If we do not take the steps that are required now, it may not be long before discussions of restoration turn to consideration of legal protection under the provisions of the U.S. Endangered Species Act and the Canadian Species at Risk Act.

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