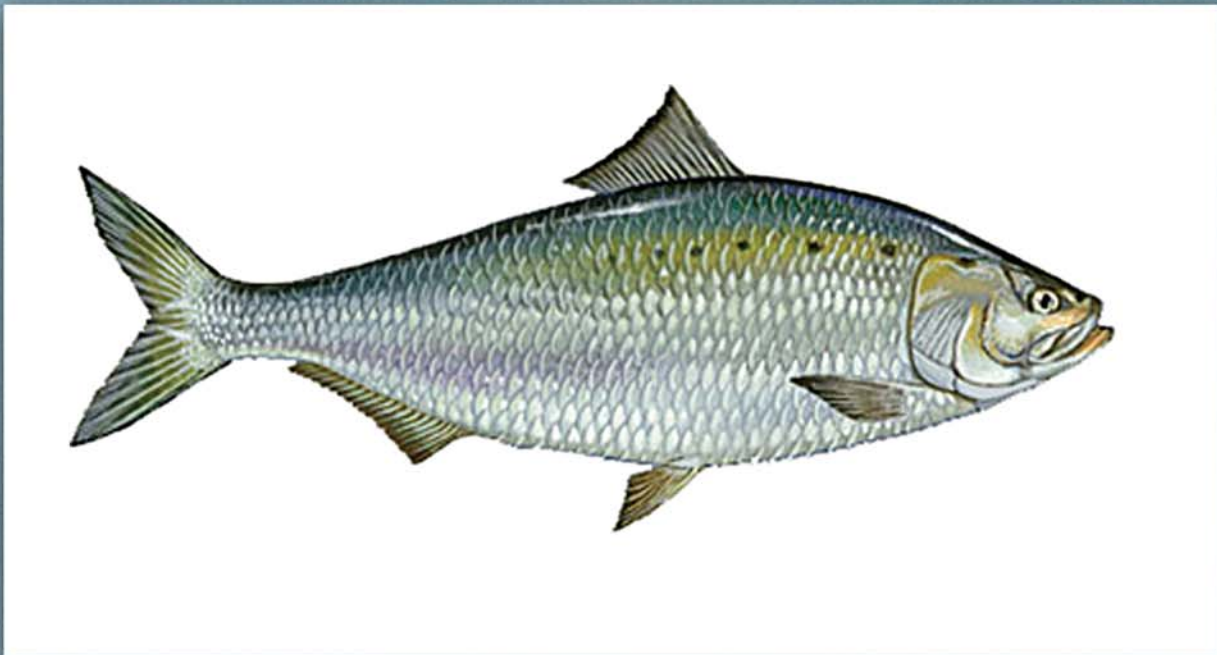


*Alosine Species Team
Background and Issue Briefs*



Alosine Species Team
Background and Issue Briefs

ECOSYSTEM BASED FISHERIES MANAGEMENT FOR CHESAPEAKE BAY
Alosine Species Team Background and Issues Briefs

Contents

Acknowledgements A-iii
Alosines Species Team A-v
Alosines Workplan A-vii

BACKGROUND

Ecological Valuation A/1-1
Richard McBride

Ecosystem Services A/1-3
Kate Taylor

Alosine Life History in Chesapeake Bay A/1-1
Troy Tuckey

The Historical Fishery and Management..... A/1-13
John Waldman and Bob Sadzinski

Traditional Management (Single Species, Multispecies, and Ecosystem Based) A/1-17
Kate Taylor

Restoration Versus Harvest A/1-21
Steve Gephard

Community-Based Stewardship: Protection and Restoration of
Habitats and Watersheds A/1-23
Jake Kritzer

References A/1-29

HABITAT

Migratory Barriers A/2-1
Steve Gephard and John Waldman

Flow and Water Quality A/2-5
Troy Tuckey and Bob Sadzinski

Land-Use Ecology A/2-11
John Waldman and Steve Gephard

Physical Alterations	A/2-13
<i>Steve Gephard</i>	
References	A/2-17
FOODWEB	
Forage, Competition, and Predation	A/3-1
<i>Julie Harris, Rich McBride, John Waldman, Jake Kritzer and Steve Gephard</i>	
Ecological Impact in Freshwater, Alosines as Vectors of Biological Materials	A/3-11
<i>Jake Kritzer, Julie Harris, Rich McBride, John Waldman, and Steve Gephard</i>	
References	A/3-15
STOCK DYNAMICS	
Alosine Stock Assessments History	A/4-1
<i>Andrew Kahnle</i>	
Anthropogenic Mortality	A/4-7
<i>Bob Sadzinski</i>	
Life History of Alosines: Growth, Condition and Reproduction	A/4-11
<i>Rich McBride, Mike Hendricks, Bill Duffy, and Jake Kritzer</i>	
Connectivity and Stock Structure	A/4-23
<i>Jake Kritzer</i>	
References	A/4-29
SOCIOECONOMICS	
Cultural, Economic and Environmental Considerations in the Management of Alosines in the Chesapeake Bay and Along the Atlantic Coast.....	A/5-1
<i>Kate Taylor</i>	
Restoration.....	A/5-11
<i>Steve Gephard</i>	
Management Guidelines (Socioeconomics, Management Considerations)	A/5-17
<i>Andy Kahnle</i>	
References	A/5-21

Acknowledgments

Support for this project was provided by the U.S. EPA Chesapeake Bay Program, the Maryland Department of Natural Resources, and the Maryland Sea Grant College Program.

Maryland Sea Grant would like to thank the Alosine Species Team members for their contributions. We also acknowledge and are grateful for the efforts of the many other contributors who provided insights and materials needed for completion of the Ecosystem Issue Briefs.

Alosine Species Team

CHAIR: Troy Tuckey, Virginia Institute of Marine Science

Steve Gephard, Connecticut Department of Environmental Protection

Julie Harris, North Carolina State University

Andy Kahnle, New York Department of Environmental Conservation

Jake Kritzer, Environmental Defense Fund

Wilson Laney, United States Fish and Wildlife Service

Richard McBride, Northeast Fisheries Science Center

Bob Sadzinski, Maryland Department of Natural Resources

Kate Taylor, Atlantic States Marine Fisheries Commission

John Waldman, The City University of New York

Maryland Sea Grant and the Alosines Species Team would also like to thank the following individuals for their contributions to the Issues Briefs:

William Duffy, National Marine Fisheries Service

Michael Hendricks, Pennsylvania Fish and Boat Commission

Marek Topolski, Maryland Department of Natural Resources

ALOSINE BACKGROUND AND ECOSYSTEM ISSUE BRIEF				
ALOSINE BACKGROUND BRIEFS				
Section	Authors	Issue Brief		
1. Valuation	McBride	Ecological		
	Taylor	Ecosystem Services		
2. Early and Late Life History	Tuckey	Early & Late (American shad, Hickory shad, Blueback herring, Alewife)		
3. Management	Waldman	The Historical Fishery and Management		
	Taylor	Traditional Management		
	Gephard	Restoration vs. Harvest		
	Kritzer	Community-based Management		
ALOSINE ECOSYSTEM ISSUE BRIEFS				
QET	Authors	Issue Brief	Metric/Indicator Needed	Reference Point Needed
Habitat Suitability	Gephard, Waldman	4. Migratory Barriers	Habitat connectivity	Hectares/km of blocked vs available habitat
				Number of dams/blockages removed
	Sadzinski, Tuckey	5. Flow and Water Quality	Thermal regime	Number of rivers/streams meeting temperature requirements, Impervious surface or Index of urbanization
			Hypoxia	Number of rivers/streams experiencing hypoxia, Nutrient loads, Incidence (or area) of invasive aquatic plants
	Waldman, Gephard	6. Land-Use Ecology	Competing Uses	% habitat coverage (agricultural, forest, etc.), quality and quantity of buffer areas
	Gephard	7. Physical Alterations	Habitat Structure/Morphology	Km of channelization, bulk heads, or dredging; Incidence (or area) of invasive aquatic plants
Foodweb	Harris, McBride, Waldman, Kritzer, Gephard	8. Forage	Trophic structure	Biomass changes through time
				Predator species composition
				Community metric that characterizes the predator field that may consume alosines
			Prey field	Forage availability
				Community metrics that characterize prey composition and availability for alosines
		9. Competition	Competition	Abundance indices or ratios
		10. Predation	Predator field	Alosine predator to alosine abundance ratios
				Predator species composition (e.g., invasive species)
	Kritzer, Harris, McBride, Waldman, Gephard	11. Vectors	Nutrient cycling	Release of nutrients from spawning activities, associated mortalities, impact on freshwater ecosystem
				Measure of the marine isotopic signatures in freshwater foodwebs
Stock Dynamics	Kahnle	12. Stock Assessments History	Stock recruitment variability	Juvenile recruitment indices
			Abundance	Spawning run sizes
	Sadzinski	13. Anthropogenic Mortality	Development	Construction of fishways (# of fishways or \$ spent), Watershed development plans including alosines
	McBride, Hendricks, Duffy, Kritzer	14. Growth, Condition, Reproduction	Disease	Type and prevalence of disease
	Kritzer	15. Connectivity & Stock Structure	Demographic structure	Spawning run age distributions
			Population connectivity	Number of spawning runs
Socioeconomics	Taylor	16. Cultural, Economic and Environmental Considerations	Demographics and trends	License sales
			Institutions and governance	Federal, state, local government involvement; NGO involvement (e.g., River Keeper, watershed associations)
			Community culture and lifestyle	Number of festivals and heritage-based activities
			Globalization	Market demand for alosine products
		Community	Number of recreational fishery participants	
	Gephard	17. Restoration	Land use and development	Construction of fishways (# of fishways or \$ spent), Watershed development plans including alosines
	Taylor, Sadzinski, Kahnle, Gephard	18. Management Guidelines & Considerations	Income and Livelihoods	Income generated from alosine fisheries, Number of fishers

BACKGROUND

Ecological Valuation

Richard McBride

Alosines are fishes of the subfamily Alosinae, commonly called “shads,” of the herring family (Clupeidae). This document reviews the biology and ecology of the four anadromous alosines in the Chesapeake Bay ecosystem. The anadromous alosines of the Chesapeake Bay are American shad *Alosa sapidissima*, hickory shad *Alosa mediocris*, blueback herring *Alosa aestivalis*, and alewife *Alosa pseudoharengus* (Murdy et al. 1997). As anadromous fish, they live most of their life at sea, where they mature, and return to freshwater habitats to spawn.

The value of a species can be measured both by what is gained by its presence and lost by its absence. Historically, these alosines were among the most abundant and economically valuable fishes of the Chesapeake Bay (Loesch and Atran 1994; Hildebrand and Schroeder 1928); however, today they are largely regulated by a moratorium on directed fishing (Markham and Weinrich 1994; Olney and Hoenig 2001). Their serial decline in abundance, for more than a century, has left their fisheries in dismal shape and has threatened their prominent contribution to American heritage (Limburg and Waldman 2009).

Imagine, in 1920, over 32 million pounds of alosines were extracted from Chesapeake Bay (Hildebrand and Schroeder 1928). At the time, the fishing industry was still a pioneering enterprise and marine populations were largely believed to be limitless. However, alosine landings in the bay had already been declining for over a decade (Hildebrand and Schroeder 1928). These harvests meant millions of fish were not feeding in the bay for several months of every year or migrating back out into the ocean after spawning to enter the coastal food web. The ecological consequence of such massive extractions are difficult to evaluate, but clearly the flow of biomass and energy through marine and freshwater systems has been interrupted for a sustained period of decades, and has not recovered.

Our failure to rehabilitate such fisheries underscores our incomplete knowledge about the ecological value of alosines. There has, at any rate, been no recognized benefit to such declining populations. This introductory section outlines the lost value of these declining fisheries and what sociological and cultural value would be gained if they could be successfully restored. Additionally, a brief description of the current state of knowledge concerning the life history of each species in Chesapeake Bay is provided. Subsequent sections (i.e., Habitat, Foodweb, Stock Dynamics, and Socioeconomics) focus on issues that affect Chesapeake Bay alosines and must be considered and evaluated in an ecosystem-based fishery management plan.

Ecosystem Services

Kate Taylor

Ecosystem services are the benefits that humans derive from natural resources and processes. Fish populations, for example, can provide a number of ecosystem services, such as the regulation of food web dynamics, providing biodiversity and acting as indicators in monitoring programs (Holmlund 2004). Four main categories of ecosystem services were identified by the Millennium Ecosystem Assessment (2005): provisioning (e.g. food, water and timber), regulating, (e.g. climate regulation and water purification), supporting services (e.g. photosynthesis and nutrient cycling) and cultural services (e.g. recreational opportunities or aesthetic value). Alosine populations contribute in many ways to three categories of services (provisioning, supporting and cultural) within marine and freshwater ecosystems in the Chesapeake Bay and along the Atlantic coast.

Provisioning

American shad were considered one of the most valuable food fish of the U.S. Atlantic coast before World War II (Rulifson et al. 1982) and the river herring fishery is considered one of the oldest documented fisheries in North America (CRASC 2004). Commercial and recreational in-river fisheries for all four alosine species occurred during the spring migration, as alosines move into freshwater to spawn. Prior to the closure of the commercial ocean fishery in 2005, American shad were also harvested at-sea during their migration from their feeding grounds to their spawning rivers along the East Coast. River herring are an easy fish to catch and were traditionally harvested locally for food or sold smoked, salted, or pickled (Collette and Klein-McPhee 2002; ASMFC 2009), while American shad were prized for the delicious meat and roe. The scientific name for American shad, *Alosa sapidissima*, translates as “most delicious herring”. American shad has been an important food source of the Mattaponi and Pamunkey tribes of Virginia. Although the directed harvest of American shad is prohibited in Virginia, both tribes have been granted the right to maintain a spring roe fishery. Since 1950, the Chesapeake Bay region has seen the largest declines in commercial landings of American shad and river herring along the East Coast (NMFS, personal communication 2010).

Supporting

As environmental management shifts from a traditional single species approach to an ecosystem based approach it becomes essential to have an understanding of the connections and interactions that occur within ecosystems. Examples of supporting services provided by alosine species include: serving as prey or bait for commercially important species; as forage for birds, mammals and other predatory fish; nutrient cycling; and increased biodiversity. As a result of the

migration from marine to freshwater, alosines fall prey to wide range of predators, including spiny dogfish, American eel, cod, hake, perch, salmon, pollock, weakfish, whales, seals, otters, cormorants, herons, bald eagles, foxes, raccoons, and turtles (Collette and Klein-McPhee 2002; ASMFC 2009). River herring are also a preferred bait in the striped bass recreational fishery in the Chesapeake Bay. Retail prices of \$3 - \$5 for individual live river herring have been reported at bait shops in the Mid-Atlantic (ASMFC 2009). The alosines that elude predators and fishing hooks eventually enter freshwater streams to spawn and release important marine-derived nutrients into the ecosystem through egg deposition, excretion, and mortality.

Cultural

Native American legends describe that the notoriously boney American shad was created from a complaining porcupine that was turned inside out and cast into the water. Today the influence of American shad is reflected in the names of towns such as Shadwell, VA and Shad Landing, MD. Cultural services that stem from alosines help foster social relations, increase awareness of a common cultural heritage, provide a sense of place to community members (MEA 2005), increase environmental awareness and stimulate local economies. Examples of cultural services provided by alosine species include: recreational fisheries, ecotourism, seasonal festivals, and volunteer monitoring programs.

American shad provide a fierce fight for recreational fishermen and it is estimated that American shad recreational fishermen in the Delaware River collectively spent \$3 million in 2007 (MDNR 2009). Additionally, there are at least 32 shad and river herring festivals that occur coastwide to celebrate the return of alosines in the spring (ASMFC 2010), which can help fund local environmental organizations, businesses and in some cases provide scholarships to local students. Within the Chesapeake Bay there are multiple fishways that have been built which allow for public viewing opportunities of alosines during their migration into freshwater to spawn. Such facilities can also be utilized by state and local agencies to engage volunteers in fish monitoring programs that collect data on the health of local alosine stocks and encourage conservation and restoration of essential habitat.

Alosine Life History in Chesapeake Bay

Troy Tuckey

Multiple issues influence growth, mortality, feeding, and reproduction of alosines in Chesapeake Bay. These issues can range from affects of water flow on larval and juvenile growth within tributaries to processes that may affect adult oceanic and spawning migrations. Understanding the diverse array of issues requires a familiarity with the species involved. What follows is a brief summary for each species to describe what is known about life history characteristics of Chesapeake Bay alosines. This overview provides the context to examine the subsequent issue briefs and relevance to alosine ecosystem-based fisheries management. Generally, adult American shad, blueback herring, and alewife migrate from overwintering grounds on the continental shelf to spawn in rivers, streams, and creeks in late winter and early spring. While hickory shad also spawn in late winter and early spring, little is known about the distribution of adults. Larval and early juvenile development occurs in non-tidal and tidal freshwater areas although residency within rivers during the first year of life varies by species with juvenile hickory shad likely the first to move downstream into estuarine waters.

American Shad

Eggs and Larvae

Eggs of American shad are the largest of the alosine species found in Chesapeake Bay with egg diameters after hydration ranging from 2.3 - 3.5 mm (Lippson and Moran 1974). Eggs are released into the water column in tidal freshwater areas of major tributaries and are buoyant and semi-demersal. In Chesapeake Bay, American shad eggs have been observed as early as March and may extend into June in some years, however peak egg abundance is typically observed during April and May when water temperatures range between 13 – 19 °C (Bilkovic et al. 2002; Hoffman and Olney 2005; Tuckey 2009). Time to hatch is temperature dependent and may take as few as two days at warm water temperatures (26 °C) to as long as 12 days at cool temperatures (13 °C; Limburg 1996). Larvae hatch at approximately 5.7 mm notochord length and typically absorb the yolk within the first 3-5 d, after which the onset of feeding must begin (Marcy 1972; Jones et al. 1978). Larval American shad feed visually and consume small zooplankton during early developmental stages. Early growth is typically sigmoidal with a reduction in growth at approximately 25 – 30 mm total length corresponding with the onset of metamorphosis to the juvenile stage. Larvae in Chesapeake Bay tributaries are susceptible to high mortality rates (0.21/d; Houde and Zastrow 1993) and are consumed by predators such as smallmouth bass, sunfishes, and shiners (Johnson and Dropkin 1992; Johnson and Ringler 1995). Water temperature, prey level, and pH control survival and growth of American shad larvae with optimum conditions at temperatures > 20 °C, pH > 7.0, and prey levels > 50 /l (Leach and Houde 1999). In other systems, year class strength is believed to be established during the larval stage,

which is influenced by a number of biotic and abiotic factors also likely to occur in Chesapeake Bay tributaries (Savoy and Crecco 1988).

Juveniles (Age 0)

American shad typically complete metamorphosis and are considered juveniles at approximately 25 – 30 mm TL. While American shad remain immature until age 3 or older, it is only during the first few months that juveniles reside in Chesapeake Bay tributaries. Distribution of juvenile American shad within rivers is largely size-based with larger individuals moving downstream towards the salt water-freshwater interface as they grow. Food items of juvenile American shad include zooplankton, aquatic insect larvae, and flying insects (Walburg 1957; Massmann 1963; Hoffman et al. 2007). Growth rates of American shad juveniles vary among rivers and among cohorts (a group of fish hatched within a 5-d interval) within rivers (Hoffman and Olney 2005; Tuckey 2009). Instantaneous growth among cohorts of Pamunkey River American shad was relatively constant between cohorts and years and ranged between 0.037 to 0.066 mm/d (Hoffman and Olney 2005). Growth rates decrease as juveniles age between 40 and 100 d with instantaneous growth rates that range between 0.77 to 1.15 mm/d at 40 days old to 0.17 to 0.48 mm/d at 100 days old (Tuckey 2009). Growth of American shad juveniles from different rivers within a single year varied by up to 50% and show evidence of density-dependent growth (Tuckey 2009; Figure 1).

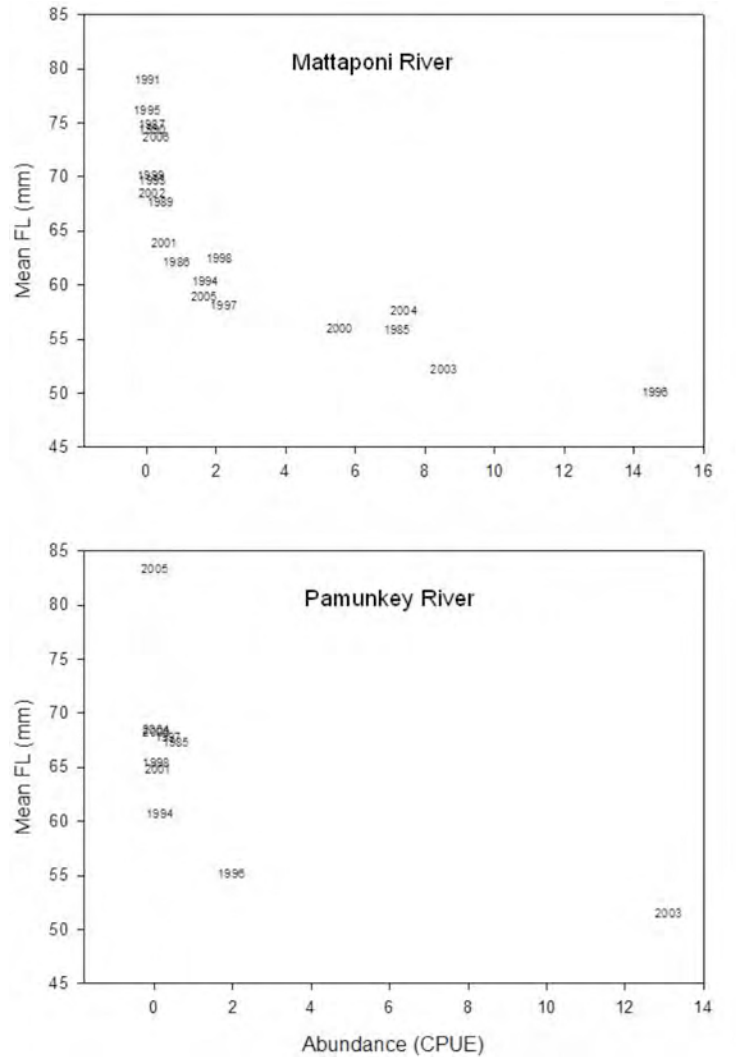


Figure 1. Evidence of density-dependent growth for American shad juveniles in the Mattaponi and Pamunkey rivers, VA. Shown is the geometric mean catch per unit effort and mean fork length in September from the Virginia Institute of Marine Science striped bass seine survey from 1985-2007. Missing years in the figures are years no American shad were collected in September (Tuckey 2009).

Mortality rates of juveniles decrease with age and size and can vary greatly among years. Hoffman and Olney (2005) found that cohort-specific mortality rates had more variability than cohort-specific growth rates for American shad in the Pamunkey River. Mortality rates for

juvenile American shad cohorts in the Pamunkey River were higher than reported elsewhere and ranged from 0.044 to 0.093/d (Hoffman and Olney 2005). In a comparison among rivers and years, total mortality rates ranged from 0.04 to 0.07 /d in the Mattaponi and Pamunkey rivers from 2005 to 2007 (Tuckey 2009). Within cohorts, total mortality estimates ranged from 0.01 /d to 0.21 /d or 1% to 18.9% /d.

Juvenile American shad move downstream throughout summer and early fall and accumulate in the lower freshwater portion of the estuary (Limburg 1996; Hoffman et al. 2007). Migrants remain in tidal freshwater until late fall when emigration to higher salinity, overwintering estuarine habitats occurs (Hoffman and Olney 2005). Diets of migrating juveniles shift in the estuarine portion of the bay to calanoid copepods, mysid shrimp, and larval fishes. Residency within Chesapeake Bay lasts until February or March when juveniles leave the estuary and enter the coastal ocean (Hoffman et al. 2008). Juveniles have been captured during the Cooperative Winter Tagging Cruises in the nearshore Atlantic Ocean off NC and VA during January and early February (USFWS and East Carolina University, unpublished data). American shad that began life in Chesapeake Bay are not observed again in the Chesapeake watershed until sexual maturity three to seven (and in a few instances eight) years later (Maki et al. 2001, 2002; Tuckey and Olney 2010).

Adults

Adult American shad reside in the coastal ocean and migrate along North America following water temperature cues (Leggett and Whitney 1972). During summer months American shad are found off the coast of Newfoundland and during winter they are located off the Mid-Atlantic Bight near North Carolina and further south off the coast of Florida (Limburg et al. 2003). In late winter, adults begin to migrate north and enter natal rivers to begin the spawning run, which occurs during February and March in Chesapeake Bay. Adults spend approximately 30 days on the spawning grounds within tidal and non-tidal freshwater reaches of major tributaries (Hyle 2004; Olney et al. 2006; Aunins and Olney 2009). Bilkovic et al. (2002) found that preferred spawning habitats include shallow depths (<5 m), high dissolved oxygen levels (> 8 mg/l), and current velocities in the range of 0.3 – 1.0 m/s.

Age composition of spawning females is between three and nine years with most females reaching maturity at age five (Maki et al. 2001 and 2002; Tuckey and Olney 2010). Maturity schedules among Virginia tributaries (i.e., among stocks) vary with a delay occurring in the James and Rappahannock rivers relative to the York River (Tuckey and Olney 2010). American shad are iteroparous in Chesapeake Bay and evidence indicates that not all of the reproductive potential is expended each year, perhaps allowing resorbed eggs to help offset the cost of spawning (Olney et al. 2001; Hyle 2004). American shad are batch spawners and have indeterminate fecundity making it difficult to estimate total annual fecundity (Olney et al. 2001; Olney and McBride 2003; Hyle 2004). Batch size estimates from the York River, range from 11,295 to 79,147 eggs per female and there is a significant relationship between female body size and the number of hydrated eggs produced (Olney and McBride 2003). Seasonal fecundity of an “average” virgin American shad was estimated to be between 380,000 and 550,000 eggs (Hyle 2004). American shad females leave the spawning grounds once spawning ceases and return to the coastal ocean (Hyle 2004).

Hickory Shad

Eggs and Larvae

Hickory shad eggs range in diameter from 0.98 and 1.64 mm and under laboratory conditions hatch between 48 and 70 hours after fertilization (Mansueti 1962). Yolk-sac larvae range between 5.2 and 6.5 mm TL (Lippson and Moran 1974). Yolk is absorbed after three days at water temperatures between 18.3 – 21.1 °C when larvae reach approximately 6.5 mm TL. Metamorphosis of larvae from brackish waters below a spawning site has been observed at lengths between 9 to 20 mm TL (Mansueti 1962). Collections of larval hickory shad in Chesapeake Bay are rare most likely due to sampling issues, but in the neighboring Roanoke River, NC larval hickory shad accounted for 40% and 59% of the alosines captured in a two-year study of alosine early life history demonstrating that densities of hickory shad can be high (Walsh et al. 2005).

Juveniles (Age 0)

Juvenile hickory shad can attain adult meristic characters at very small sizes (17 – 49 mm TL; Mansueti 1962). Hickory shad are easily separated from other alosines by the projecting lower jaw that enters the dorsal profile (Hildebrand and Schroeder 1928). A thorough understanding of juvenile population dynamics throughout their range remains largely unknown. The distribution of hickory shad juveniles does not coincide with that of the other alosines for the most part and catches of juveniles suggest that estuarine or coastal waters serve as primary nursery habitat. Batsavage and Rulifson (1998) found that juvenile hickory shad may move directly into marine waters, bypassing the estuarine nursery used by other alosines.

Adults

Hickory shad are found from Massachusetts to Florida. The spawning range of Hickory shad is thought to range from Maryland to Florida and spawning occurs during April and May in the Patuxent River, MD (Mansueti 1962; Richkus and DiNardo 1984). Maximum size for adult hickory shad is approximately 600 mm TL (Waldman and Limburg 2003). Hickory shad spawn between March and May at water temperatures between 10 and 23 °C, with peak egg collections at water temperatures between 12 and 16 °C in the Neuse River, NC (Burdick and Hightower 2006; Harris 2010). Hickory shad spawn in a variety of habitats from backwaters to mainstem portions of rivers and tributaries in tidal and non-tidal freshwaters (ASMFC 1999). Spawning habitats selected by hickory shad include cobble and boulder substrates with adequate water velocity (> 0.1 m/s; Harris 2010).

Adult hickory shad were captured in the estuarine portion of Little Egg Harbor, NJ throughout summer and fall demonstrating a different life history strategy for this species compared with American shad, blueback herring, and alewife, where adults of these species spend summer and fall in the coastal ocean (Rountree and Able 1997; Murauskas 2006; Murauskas and Rulifson 2009). Hickory shad are piscivorous and readily take bait supporting a hook and line fishery in the Chesapeake Bay. Adults will also feed on fishes, squid, small crabs and other crustaceans (Hildebrand and Schroeder 1928; Harris et al. 2007). Little is known about stock dynamics of hickory shad in Chesapeake Bay.

Blueback Herring

Eggs and Larvae

Eggs of blueback herring are between 0.87 and 1.11 mm in diameter when fertilized and larvae hatch at lengths between 3.1 and 4.2 mm TL (Lippson and Moran 1974). Absorption of the yolk occurs by about 6.0 mm TL and 2 to 3 d of age when the onset of external feeding commences (Mansueti 1962). Early stages of blueback herring larvae can be difficult to discern from other alosines because the characteristic black peritoneum (lining of the abdominal cavity) has not yet developed. However, external pigment patterns and other morphological characteristics can aid in the identification of blueback herring larvae (Walsh et al. 2005). Hatching of blueback herring occurs from April through June in Chesapeake Bay tributaries (Hildebrand and Schroeder 1928; O'Connell and Angermeier 1999; Dixon 1996; Tuckey 2009). Larval blueback herring feed on small zooplankton, such as rotifers and cladocerans (Crecco and Blake 1983), and metamorphosis to the juvenile stage occurs at approximately 20 mm TL (Lippson and Moran 1974). The larval distribution of blueback herring, alewife and American shad overlap in time and space, so larvae of all three species are likely susceptible to the same suite of predators.

Juveniles (Age 0)

Juvenile blueback herring can tolerate a wide range of salinity (Chittenden 1972), but tidal freshwater portions of rivers and small streams and creeks serve as primary nursery habitats, similar to American shad and alewife juveniles. At this stage juvenile blueback herring can be distinguished from the other alosines by the presence of a dusky to black colored peritoneum, as well as jaw shape and eye diameter (Lippson and Moran 1974).

Juvenile alosines have overlapping distributions that may result in competition for resources. However, studies have shown that spatial separation in the water column exists as well as the selection of different prey items in the diet, perhaps reducing competition introduced by overlapping distributions (Crecco and Blake 1983; Loesch 1987). The diet of juvenile blueback herring consists primarily of adult copepods, cladocerans, and crustacean eggs and some aquatic insect larvae (Davis and Cheek 1966; Burbidge 1974).

Growth of blueback herring juveniles in Virginia tributaries is sigmoidal with faster growth at younger ages and a gradual slowing of growth towards fall (Tuckey 2009; Fig 2). Maximum length reached at the end of residence in the tidal-freshwater nursery is between 63.0 and 90.2 mm TL and an age range of 72 to 179 d (Tuckey 2009). Instantaneous growth rates at 40 d range from 0.43 to 1.05 mm/d and at age 100 d slow to 0.08 to 0.48 mm/d. Burbidge (1974) examined growth of blueback herring in the James River, VA, and found that growth rates were highest at up-stream sites. Mean monthly lengths increased from 36.8 to 72.4 mm fork length from June to November, or approximately 0.3 mm/d. Dixon (1996) found average growth rates for blueback herring in the Rappahannock River at ages 30 to 60 d old ranged from 1.2 to 0.80 mm/day. Estimated total mortality rates ranged from 0.012 to 0.15 /d (Dixon 1996; Tuckey 2009).

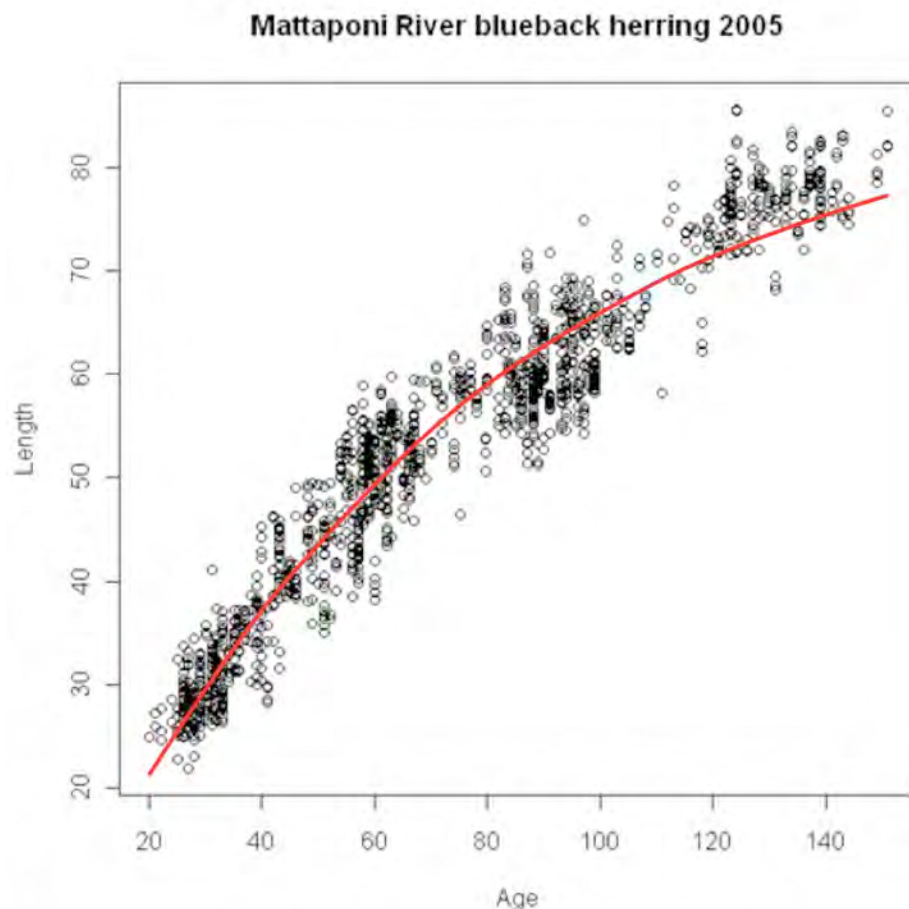


Figure 2. Growth of juvenile blueback herring in the Mattaponi River, 2005. Individual lengths (mm) at age (days) are shown (circles, $n = 1,625$) and the von Bertalanffy model fit (red line).

Emigration of juvenile blueback herring out of nursery habitats and into coastal waters varies with latitude. Yako et al (2002) found that blueback herring and alewife migrated during midday from July through early November with peaks (>96%) occurring in early July and early September during periods associated with the new moon, low prey (*Bosmina*) density, and low rainfall. Kosa and Mather (2001) examined blueback herring and alewife migration in small coastal systems in Massachusetts and found that migration occurred in peaks during July and again in September primarily between 1200 and 1600 h. Conversely, Davis and Cheek (1966) found that migration of juvenile blueback herring and alewife began during the first significant decrease in water temperature and increase in water level during October or November in the Cape Fear River System, North Carolina. In Chesapeake Bay, blueback herring leave tidal nurseries and enter the estuarine portions of the bay and rivers in fall (Dixon 1996; Tuckey 2009). After emigrating from nursery habitats, juvenile blueback herring overwinter in nearshore coastal waters or high salinity portions of estuaries before entering the coastal ocean the following spring (Hildebrand and Schroeder 1928; Milstein 1981). Blueback herring have been captured in coastal trawl surveys during summer, fall, and winter north of latitude 40° N, and during spring have been captured throughout the continental shelf between Cape Hatteras, N.C. and Nova Scotia (Neves 1981).

Adults

Adult blueback herring are found in coastal waters, bays, and estuaries from Nova Scotia to northern Florida (Bigelow and Schroeder 1953). Blueback herring are widely distributed along the coast during spring, move north towards Georges Bank and the coastal Gulf of Maine in summer and early fall, and return to the mid-Atlantic coast in winter (Neves 1981). Adults feed on calanoid copepods, mysids, and other zooplankton, which is reflected in their distribution in the water column to depths <100 m (Neves 1981). During the spawning run, adults feed on zooplankton and benthic aquatic insects (Simonin et al. 2007). Maximum length of blueback herring is approximately 400 mm TL and maximum age is 13 years (Waldman and Limburg 2003).

Spawning runs of blueback herring in Chesapeake Bay typically begin in April and spawning occurs at water temperatures between 14 and 26 °C with the timing of spawning varying by 3 to 4 weeks annually (Pardue 1983; Loesch 1987). Spawning locations for blueback herring can vary depending on latitude and the overlapping distribution with alewife. Where the distributions of the two species overlap, spawning sites include fast flowing areas of rivers and streams. In systems where alewife are absent blueback herring spawn in seasonally flooded rice fields, oxbows, and swamps (Loesch 1987). Blueback herring reach maturity between 3 and 5 years in age and are capable of repeat spawning with 44 to 65% repeat spawners (Joseph and Davis 1965). Males mature earlier and dominate age-classes from 3 to 5, while females dominate older age-classes to age 8 (Joseph and Davis 1965; Loesch 1987).

Alewife

Eggs and Larvae

Alewife eggs are slightly larger than those of blueback herring (fertilized eggs: 0.95-1.25 mm diameter). Larvae hatch at about 3.5 mm TL and absorption of the yolk occurs by about 6.0 mm TL (Lippson and Moran 1974). External pigment patterns and other morphological characteristics aid in the separation of alewife larvae from other alosines (Chambers et al. 1976; Walsh et al. 2005). Hatching of alewife larvae occurs earlier than other alosines and extends from February through April in Chesapeake Bay tributaries (Hildebrand and Schroeder 1928; O'Connell and Angermeier 1999). Larvae feed on zooplankton consisting predominantly of copepods. Growth rates from Chesapeake Bay drainages are not available, but larval growth rates from the nearby Roanoke River, NC, were between 0.41 and 0.65 mm/d (Walsh et al. 2005). Metamorphosis to the juvenile stage occurs around 20 mm TL. Larvae in North Carolina had daily mortality rates of 91 and 98% per day (Walsh et al. 2005).

Water flow has been found to decrease larval alewife survival with both high discharge levels and drought conditions negatively affecting survival (Sismour 1994; O'Connell and Angermeier 1997).

Juveniles (Age 0)

Body shape and eye size are convenient characters used to distinguish alewife juveniles from other alosines. Juvenile alewives have a larger eye diameter and a deeper body than American

shad, hickory shad, and blueback herring (Lippson and Moran 1974). Juvenile alewives remain in tidal freshwater portions of rivers, streams, and ponds during the first summer and into fall prior to migration to the coastal ocean (Hildebrand and Schroeder 1928). The distribution of alewives and blueback herring in nursery habitats overlap, and diets consist of similar prey items, which creates the potential for competition (Davis and Cheek 1966; Grabe 1996). However, vertical distribution in the water column, as well as the temporal overlap of similar life history stages differs between species with alewife remaining deeper in the water column compared with blueback herring (Loesch et al. 1982). The spatial separation in the nursery habitat likely reduces interspecific competition among juveniles (Loesch 1987). Milstein (1981) found juvenile *Alosa*, including alewife, overwintering in coastal waters off New Jersey (out to 8 km) during late winter and early spring. Gahagan et al. (2010) found that low water temperature, elevated discharge and increased rainfall were significant factors responsible for alewife migration from a coastal lake in Connecticut. Whether these same triggers drive migration responses of alewife in riverine systems in Chesapeake Bay is unknown.

Adults

Alewives are found in coastal waters from Newfoundland to South Carolina (Hildebrand and Schroeder 1928). In Chesapeake Bay rivers, spawning runs of alewife occur as early as February and peak spawning occurs in Mid-March at water temperature between 12° and 16° C (Loesch 1987; O'Connell and Angermeier 1999). Migrations of alewife are strongly coupled to water temperature, and increasing water temperature associated with climate change may shift the timing of spawning migrations to an earlier period (Ellis and Vokoun 2009).

Alewives may spawn in areas with reduced flow compared with blueback herring and will readily enter ponds, lakes, and slow-flowing small streams (Hildebrand and Schroeder 1928; Loesch 1987). The age composition of spawning alewives ranges from 3 to 8 years and Virginia stocks are dominated by age-4 fish (Loesch 1987). After spawning, adults migrate to the coastal ocean and are found at depths < 100 m in northern latitudes around Georges Bank (Neves 1981). Joseph and Davis (1965) estimated that 61% of alewives were repeat spawners in the York River, VA. Adults feed on calanoid copepods, mysids, and other zooplankton (Neves 1981).

The Historical Fishery and Management

John Waldman and Bob Sadzinski

In pre-Colonial times, Native Americans used shad heavily as a food source. Many gear types were used by them, including hooks, harpoons, weirs, seines, gill nets, scoop nets, gigs, and hand nets. Another technique was to entrap migrating shad into blocked-off portions of rivers and streams. Gerstell (1998) relates a 1778 account of a Native American weir fishery in the Susquehanna basin. Angled stone weirs were laid to funnel water to a chute fitted with a collecting basket, then Indian men drove shad downstream towards the basket using a stream-wide rope made of vines to which tree boughs were fastened. This fishery could yield more than a thousand shad in half a day. Native Americans taught the earliest settlers fishing techniques and it is rumored they also passed on the art of “planking shad”, whereby they were nailed to boards and allowed to cook slowly by a fire, dissolving the bones.

In the Colonial era, alewives migrated up rivers and streams to spawn in such abundances that European observers were often incredulous. Bolster (2006) called alewives the “passenger pigeons of the sea.” Numerous quotations attesting to these spectacles include this early one from Massachusetts: “Experience hath taught them that at New Plymouth” “that in April there is a fish much like a herring that comes up into the small brooks to spawn, and where the water is not knee deep they will press up through your hands, yea, thow you beat at them with cudgels, and in such abundance as is incredible.” Likewise, American shad ran up almost 140 larger rivers in terrific numbers (Limburg et al. 2003).

These bounteous and valuable resources were subject to harvests for food, bait, and fertilizer. Spring fisheries focused effort prior to farming activities and was a significant source of food and income relative to the time of year. At the same time, the rivers they ascended were increasingly dammed for mills and industry, channelized, and used to carry away human and industrial wastes, all of which decreased alosine runs. Thus, there was a direct conflict between utilizing the benefits of the fishes themselves and the need to support the runs and the benefits of using the rivers for other societal needs, at a cost to the alosine populations. Moreover, there was a need to allow enough individuals to escape through the fishery to sustain yields.

Declines of anadromous fishes, including alosines were observed in the 1700s. Alewives, in particular, were integral to both market-based and subsistence economies. In discussing these depletions, Bolster (2006) noted that two months before the Revolutionary War began, a group of more than 30 men petitioned the New Hampshire General Assembly that all encumbrances and weir blocking Cohass Brook (a tributary of the Merrimack) be removed “So that said fish may have free Liberty to pass and re-pass in Said Brook for the Insuing year so they may increce their number.”

Earlier, the Province of Pennsylvania passed a law in 1700 barring the construction of fish weirs stretching across rivers and streams from shore to shore (Gerstell 1998). Although this regulation allowed passage to spawning grounds, it was enacted not for the protection of the fish but instead so that fish would be equally available to everyone who lived along the waterways. In 1731, a blocked run became an issue on the Susquehanna system and was brought to the Pennsylvania Assembly as a new dam prevented American shad from reaching Conestoga Creek, a tributary that had supplied residents with great quantities of fish. The mill dam owner agreed to leave a gap in the dam to allow fish to pass but before he opened it, the mill dam was destroyed by unknown people, launching what became known as the “shad wars” between fish harvesters and dam operators.

In Virginia, many of the early Colonial shad fisheries were operated by owners of large plantations. Notable among them were Thomas Jefferson, who brought shad to Monticello, and George Washington who ran a shad fishing business and leased fishing rights on his Potomac River holdings (Mansueti and Kolb 1953). In the early 1800s, commercial shad fishing on the Susquehanna River grew rapidly, with operations on most of the river’s 422-mile stem and tributary streams in New York, Pennsylvania, and Maryland (Gerstell 1998). Seine nets also became considerably lengthier at this time. Thousands of men prosecuted the fisheries in the spring, often leaving their primary jobs to do so. At times, shad were harvested in such large numbers that they could not be marketed; some were then sold for \$1.00 a wagonload to fertilize fields (Mansueti and Kolb 1953).

Shad gear practices expanded over time. In the early days of commercial shad fishing in Virginia haul seines were used almost exclusively but around 1835 gill nets were introduced and since became a major gear type. Pound nets were introduced to the area in 1858 and also became important contributors to total landings (Loesch and Atran 1994). Between 1973 and 1977, pound nets generated more than one-fifth of Virginia landings of American shad. In contrast, between 1983 and 1987, a period of low stock abundance, pound nets yielded only 5% of total landings. This discrepancy was attributed to more shad using shoal areas where pound nets fish when abundances are high (Loesch and Atran 1994). Other shad gear types used in the Chesapeake watershed included bow nets and lift nets (Gerstell 1998).

Shad landings reached their highest levels between 1850 and 1900. Demand grew from increasing populations and a faster distribution network that could reach distant locations. However, as total harvests grew from greater effort, river-specific yields fell. Shad culture and stocking were increased after 1880 but the higher catches were likely due to improvements in fishing methods more efficiently harvesting fish from declining stocks (Mansueti and Kolb 1953). The period of 1900 to 1950 was characterized by a spectacular decrease, then a gradual decline in the overall commercial production of shad, but some southern rivers still maintained productive fisheries.

During the 18th century, anglers could and did fish for shad and herring in the upper tributaries of the Chesapeake Bay using small haul seines or dip nets to supplement income, subsistence or trade. These artisanal fisheries generally fished on the spawning grounds and were opportunistic; harvesting proportional to available market after personal storage was maximized.

Background — The Historical Fishery and Management

Mansueti and Kolb (1953) characterized the management of shad as having been rationalized by various theories: (1) the “brood-stock” theory (in vogue from 1850 to their publication) in which shad were to be conserved by preserving the breeding individuals with laws and artificially propagating them in hatcheries, (2) the “optimum catch” theory (in vogue from about 1925 to 1940) in which shad fisheries were to be operated to produce the best catches, and (3) the “controlled-catch” theory (1930 to their publication) in which the fishing rate was stabilized by limiting the number of fishermen and gear by a licensing system. On a practical basis, Mansueti and Kolb (1953) recognized that among states, the total management toolkit included limitation of the number of fishermen and gear, setting fishing periods, stocking of fry and fingerlings, and manipulating environmental or artificial conditions in order to insure a greater production of fish. These remained the major management options till the present.

Traditional Management (Single Species, Multispecies, and Ecosystem Based)

Kate Taylor

The Atlantic States Marine Fisheries Commission (ASMFC) is currently responsible for the oversight and management of American shad, hickory shad, alewife and blueback herring in state waters (including 0 – 3 miles offshore) ranging from Maine through Florida. The Shad and River Herring Management Board (Board) directs management of these species and is comprised of members from each state or jurisdiction with a declared interest in the fishery, as well as representatives from National Marine Fisheries Service (NMFS) and the US Fish and Wildlife Service (USFWS). Member states and jurisdictions are required to implement regulations consistent with ASMFC plans approved by the Board, as required by the Atlantic Coastal Fisheries Cooperative Management Act of 1993.

The first Interstate Fishery Management Plan (FMP) for Shad and River Herring was developed in October 1985 (ASMFC 1985). Changes to the original FMP through multiple Amendments and Addendums have been implemented to address new challenges and needs:

- Amendment 1 to the Interstate FMP was adopted by the ASMFC in April 1999 (ASMFC 1999). The Amendment instituted a five-year phase-out of the American shad ocean intercept fishery, with the complete closure achieved by January 1, 2005, and required states to develop fisheries independent and dependent monitoring programs.
- Technical Addendum 1 to Amendment 1 and Addendum 1 to Amendment 1 were adopted in 2000 and 2002, respectively. These Addenda clarify fisheries independent and dependent monitoring requirements for ASMFC member states and jurisdictions.
- Amendment 2 to the Interstate FMP was adopted by the ASMFC in May 2009 (ASMFC 2009). The Amendment was initiated in response to recent declines in coastwide river herring populations, and growing concern over river herring bycatch in many small mesh fisheries. The Amendment requires states to develop sustainable fisheries management plans for any commercial or recreational fishery within their jurisdiction. Any state without an approved plan in place by January 1, 2012 will have their fishery closed. The Amendment also required states to develop fisheries independent and dependent monitoring programs.
- Amendment 3 to the Interstate FMP was adopted in February 2010 (ASMFC 2010). The Amendment was developed in response to the 2007 American shad stock assessment (ASMFC 2007), which found American shad stocks at all time lows. The Amendment requires states to develop American shad sustainable fisheries management plans for any commercial or recreational fishery within their jurisdiction. Any state without an approved plan in place by January 1, 2013 will have their fishery closed. All states are allowed to maintain a catch and release recreational fishery.

The agencies responsible for implementing the regulatory and monitoring requirements of the FMP within the Chesapeake Bay are Maryland Department of Natural Resources (MDNR), Virginia Marine Resources Commission (VMRC), Virginia Department of Game and Inland Fisheries, the Virginia Institute of Marine Science and DC Department of Environment (DDOE). Additional cooperative programs to promote interstate management of alosines within the Chesapeake Bay are accomplished through the Potomac River Fisheries Commission, established in 1962, the Chesapeake Bay Commission, established in 1980, and the Chesapeake Bay Program Executive Council. States and jurisdictions are allowed to put in place more conservative measures, for any alosine species, as they deem necessary.

	Recreational	Commercial
Maryland	Shad ¹ – No recreational harvest is permitted in Maryland; catch and release only. River Herring – Open season January 1 st through June 5 th .	Shad – No commercial fishery is permitted in Maryland. There is a two American shad per day allowance. River Herring – Open season January 1 st through June 5 th .
Potomac River	Shad – No recreational fishery is permitted in the Potomac River. River Herring – No restrictions.	Shad – No directed commercial fishery is permitted in the Potomac River. Commercial limit of one bushel per day for American shad. River Herring – No restrictions.
D.C.	Shad – No recreational fishery is permitted in DC. River Herring – Fishing is limited to dip-netting only.	No commercial shad or river herring fisheries exist in DC.
Virginia	American shad – No recreational fishery is permitted in VA. Hickory shad – 10 fish / day River Herring – No restrictions.	American shad – Bycatch allowed with permit only ² . Hickory shad – No restrictions. River Herring – No restrictions.

Table 1. Regulations for shad and river herring as of 2010. Regulations will change as states and jurisdictions implement the requirements of Amendments 2 and 3 to the ASMFC Shad and River Herring Fishery Management Plan.

¹ “Shad” refers to both American and hickory.

² Restriction apply to the permit, including harvest location and harvest composition

Monitoring

Within the Chesapeake Bay, the following fishery-independent monitoring is required by the ASMFC for American shad and river herring in the Chesapeake Bay through Amendments 2 and 3³: a juvenile abundance index survey in Maryland's Upper Chesapeake Bay by MDNR, a juvenile abundance index in the Potomac River by DDOE, a juvenile abundance index survey in the James, York and Rappahannock Rivers by VMRC, a spawning stock biomass survey in the Upper Chesapeake Bay by the MDNR, and a spawning stock biomass survey in the Rappahannock River, York River, and the James River by VMRC. Fishery-dependent monitoring is also required of MDNR, DC F&W and VMRC. Each jurisdiction must monitor and annually report commercial and recreational catch, effort, and catch composition.

³ Regulations may change as states and jurisdictions implement the requirements of Amendments 2 and 3 to the ASMFC Shad and River Herring Fishery Management Plan.

Restoration Versus Harvest

Steve Gephard

A species is perceived to be insufficiently abundant when it can no longer meet the demand for harvest (in the case of commercial species), access (in the case of recreational species), or observation (in the rare case of a charismatic species valued for its mere presence, e.g. alewife, in some communities). There can be three basic approaches to increasing abundance: reduce demand (harvest), increase supply (production), or both.

Reduction of harvest is generally done through traditional fishery management approaches: reduction of daily or seasonal catch limits, reduction of length of season, reduction of number of allowed participants, total or partial area closures, etc. Such measures are generally hoped to be temporary actions that allow fish stocks to recover. However, if the reason for the decline in abundance is over-fishing, it is unlikely that returning to past levels of harvest would be sustainable — the trend would just repeat itself. Therefore, increased production often accompanies reduction in harvest in hopes that when the benefits of increased production are realized, the population can support the past level of harvest.

Increase in production can be attempted in two ways. It is well established that alosines have been unable to access much of their historical spawning habitat due to the construction of barrier dams (Limburg and Waldman 2009). The first method of increasing production is to reconnect access of existing runs to some of the inaccessible habitat that is still in good condition. This is typically accomplished by removing dams (and other barriers) or building fishways to bypass them. With more of the watershed once again becoming active spawning and nursery habitat, more alosines are produced. The second way is to replace the reproductive output of natural habitat with hatchery production. A hatchery may be able to produce as many juvenile alosines as dozens of miles of natural stream habitat that are still inaccessible to anadromous runs. The risks of the first technique are (1) the upstream habitat is no longer suitable for the targeted alosines and (2) the methods of getting the fish upstream (e.g. a large pool-and-weir fishway) are not feasible or effective for that location. The risks of the second technique are those associated with most artificial fish culture programs: the inadvertent creation of deleterious genetic, physiological, and behavioral attributes that result in diminished performance and recruitment.

Management schemes designed to rebuild alosine runs must assess the opportunities and limitations of these approaches to develop effective restoration programs for targeted watersheds.

Community-Based Stewardship: Protection and Restoration of Habitats and Watersheds

Jake Kritzer

In addition to management of alosine fisheries by state and inter-state agencies, and broader environmental management by federal, state and municipal governments, there are numerous non-governmental organizations (NGOs) operating at the local level within the Chesapeake watershed. These NGOs, although typically not involved in fisheries management, are engaged in efforts to protect and restore habitats and water quality that are important to alosine populations, as well as education, outreach and advocacy. NGOs working at the local level include watershed associations, land trusts and land councils, fishermen's organization, and others. The Chesapeake Bay Program (CBP) has identified 615 organizations involved with watershed management activities. Of these, 303 focus on rivers that support alosine populations (Table 2).

The activities of these NGOs are many and varied, and difficult to summarize. The CBP conducted a survey in 1999 to gauge the primary concerns and activities of groups working on watershed conservation. The survey was published in CBP's *Bay Journal*, and sent to 290 organizations. A total of 84 organizations responded, including NGOs as well as a small number of state government entities. Of the top five issues of concern, management of alosines is connected to three: river and stream conservation, wildlife, and fisheries (CBP 2000)⁴.

The CBP survey also addressed the activities in which organizations were engaged. A total of 15 general categories of activities were identified. The six categories with the greatest level of activity were all aspects of public outreach and communications (CBP 2000). Active habitat restoration and improvement of water quality accounted for much less of the total activity reported (CBP 2000). These on-the-ground protection and restoration activities have very tangible, but also very discrete and site-specific, effects. In contrast, outreach and communications work can have more widespread effects (e.g., changes in citizens' behavior, policy changes by governments), but these are very difficult to track and evaluate. An effective strategy to optimize positive impact is likely to involve a combination of these approaches.

Whether the degree of activity of each type is in fact optimal, or whether the emphasis on outreach and communications is a result of restoration work being more expensive and involving greater logistical challenges (i.e., uncertain or imperfect techniques, regulatory hurdles), is unclear. Furthermore, with more than a decade having passed since the survey, the balance of different activities might have changed, although the priority issues are likely to have changed

⁴ The other two issues of concern were drinking water and flood control. Activities undertaken to address these concerns may have ancillary benefits for alosines, but are not done directly for conservation purposes. Conversely, some activities undertaken to meet address these concerns might have negative effects on alosines (e.g., damming).

less. Still, the CBP survey remains the best available summary of the interests and efforts of the broad array of community-based organizations within the Chesapeake watershed. The sheer number of active organizations (Table 2) and their diverse activities (CBP 2000) represents an important level of ecosystem-based management parallel to and interacting with management by governments. Whether increased coordination and support can elevate this community-based management potential to maximize overall effectiveness is worthy of investigation.

HABITAT

Migratory Barriers

Steve Gephard and John Waldman

Anadromous alosines need to ascend streams to varying degrees to access essential spawning habitat, with important variability in distance traveled upstream both among and within species (Greene et al. 2009). Dams and other artificial structures built in streams can create migratory barriers that prevent such access by these species and interrupt their life history (Figures 1 and 2). Not all barriers are physical objects. Plumes of elevated water temperature (Leggett and Whitney 1972), reduced water quality (Chittenden 1969), including reduced pH, and reduced water quantity, (Greene et al. 2009) can also inhibit upstream migration by these fishes. Other physical barriers include culverts (Clay 1995), other improperly designed road crossings, tide gates (Greene et al. 2009), perched utility services, and armored ‘aprons’ designed to combat progressive erosion of streambed elevations in artificially re-graded streams (Steve Gephard, CTDEP, Old Lyme, CT, pers. comm.). Such barriers are believed to represent one of the most important factors in the decline of anadromous alosine runs (Limburg and Waldman 2009).



Figure 1. Example of a Dam acting as a barrier to anadromous fish passage. Photo taken on 4/28/2008 of Derby Dam in Shelton, CT; photo credit CTDEP/Inland Fisheries Division.

Common types of dams in the Chesapeake Bay region include hydroelectric, flood control, water supply, agricultural, aesthetic/residential, former hydro-mechanical (mill), and former canal feeders. Most of the last two types are no longer used for their original purposes but have been orphaned (no designated purpose), adapted to new uses (e.g. residential), or preserved for historical purposes.

Dams are found in a variety of conditions, ranging from good working condition to partially breached. Even partially breached dams can

create migratory barriers due to rubble in the streambed, excessive velocities, or insufficient passage capacity. Dams range in height from over 100 ft high to less than 1 ft. Alosines cannot jump and even very low dams are capable of blocking migrations, depending upon the configuration of the dam and the nature of the stream. Generally, any dam that is higher than

two or three feet in height may block many alosine runs (Alex Haro, Conte Anadromous Fish Research Center, USGS, Turners Falls, MA, pers. comm.).



Figure 2. Example of migratory barrier, photo credit CTDEP/Inland Fisheries Division.

The Maryland stream blockage database shows approximately 800 blockages and it is conservatively estimated that 40% may have an impact on current or historical alosine runs (Jim Thompson, Maryland Dept. Natural Resources, Annapolis, MD, pers. comm.).

Upstream fish passage has been provided at some dams in the form of fishways. These allow adults to access upstream habitat to spawn. Afterwards, both the spent adults and the young-of-year need to migrate downstream to access essential marine habitat. One example is the installation in 1999 of a vertical slot fishway at the Boshers Dam on the James River in Richmond, VA, which provides access to over 221 km of upstream habitat to American shad and river herring (Weaver et al. 2003). Some dams and their associated impoundments are the source of migratory delays or direct mortality of migrants (Greene et al. 2009). Fish that are forced to swim through miles of long slack water rather than fast-flowing streams will take longer to reach the ocean. Some fish may become confused and trapped in the extensive canal systems of mill complexes while others may have to wait for weeks for water to spill over a dam or to find a relatively small passageway designed to allow fish pass downstream. Such delays may result in increased predation rates by predators attracted by schools of distressed alosines. Increased predation may occur in estuaries if the migrants experience osmoregulatory stress due to arrival late in the season due to upstream delays. Direct mortality can occur at dams if migrants pass through hydroelectric turbines or intakes for industrial or drinking water plants (Greene et al. 2009).

Upstream fish passage has also been provided at some sites in the form of dam removal. This action allows migrants to access upstream habitat, usually in a more efficient manner than fishways, and eliminates other concerns, such as habitat modification, migratory delays, and entrainment into water intake systems. One example is the removal of the Embury Dam on the Rappahannock River in Fredericton, VA (Alan Weaver, VA Dept. Game and Inland Fisheries, Richmond, VA, pers. comm.).

There are many different kinds of culverts and many can present migratory barriers. Headwater and residential culverts are often single or multiple round, corrugated, metal pipes set under roadways. These can have inadequate capacity, excessive slope, excessive velocity, and perched outlets. Highway and railroad culverts are often single or multiple pre-cast concrete box culverts. They also may present excessive velocities (with smooth concrete floors) and perched outlets but often have water levels that are too shallow to allow passage of alosines (Clay 1995). This occurs when engineers design them with capacity to pass 100 year floods and normal flows are spread out over multiple boxes and a very large total width.

Flow and Water Quality

Troy Tuckey and Bob Sadzinski

Natural Flow Regimes and Effects on Alosines

Water is the fundamental currency of aquatic life and changes involving water affect species survival, health, distribution, growth, and reproduction. The amount of water, timing of delivery, frequency of disturbances, and the amount of dissolved and particulate constituents that are carried by water are all part of natural ecosystems with which species have evolved. Through human alterations of watersheds, these conditions have shifted away from natural processes to new states that drive systems towards different, and perhaps unwanted, endpoints.

Under natural flow regimes there are a range of conditions (e.g., current velocity, dissolved oxygen, water temperature, pH; Table 1) that facilitate hatching of eggs and promote growth and survival of larval and juvenile alosines (Leach and Houde 1999; Bilkovic et al. 2002). For example, American shad spawning reaches in the Mattaponi and Pamunkey rivers, VA, were characterized by high dissolved oxygen (>8 mg/L) and relatively high current velocity (0.3 – 1.0 m/s), which may be salubrious conditions for hatching success (Bilkovic et al. 2002). Waters and Hightower (2007) found the hatch rate of blueback herring eggs was linearly related to dissolved oxygen levels ranging between 2.5 to 9.5 mg/L. In their study, lowest dissolved oxygen levels were observed in smaller tributaries to the Chowan River, North Carolina. If flow magnitude is too low, there may be insufficient velocity to keep developing eggs from becoming covered by silt and there may also be reduced nutrient loads derived from the neighboring watershed to fuel important phytoplankton blooms. Conversely, too much flow can wash eggs and poorly swimming larvae out of nursery habitats, increase mortality, and may also reduce residence time of nutrients in the nursery zone that support food web dynamics. While freshwater flow in Chesapeake Bay tributaries show no long-term trends, annual variations in flow are dramatic and affect salinity, stratification, suspended sediment loads, and nutrients (Kemp et al. 2005). Processes affecting production of alosines are complex, non-linear, and vary by river. Models developed in a study of growth of juvenile American shad and blueback herring in two Chesapeake Bay tributaries illustrated an exponential relationship between fish length at the end of summer and water flow during early development (i.e. egg and larval stages; Tuckey 2009).

Table 1. Habitat requirements for anadromous alosines, produced by MD DNR June 2009.

	Alewife		Blueback Herring		American Shad		Hickory Shad	
	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults
Temperature (°C)	10.0-28.0	4.2-16.7 (2)	10.0-30.0	13.0-22.0 (3)	15.6 - 23.90	10.0-30.0	15.6-23.9	10.0-30.0
Spawning Temperature (°C)	n/a	10.0-18.0	n/a	14.0-25.0	n/a	16.0-19.0	n/a	12.0-22.0 (peak 15.0-19.0)
Salinity (ppt)	0 - 5.0	0 - 30.0	0-2	0 - 35	0 - 30		0-30	
Dissolved Oxygen (mg/l)	>3.6	> 5.0 preferred	>3.6	>5	>5	>5	>5	>5
Spawning Substrate	n/a	from coarse gravel to organic detritus	n/a	gravel and clean sand if sympatric with bluebacks and when few alewife, spawn in areas with	n/a	sandy or rocky shallows dominated by extensive flats	n/a	mud, sand, gravel, and cobble (1)
Preferred Food	dipterans midges in July, cladocerans in august and September. Ostracods, insects eggs, and insect parts.	at sea, calanoid copepods, mysids, and other zooplankton. They also eat fish.	planktivorous (copepods, cladocerans, and larval dipterans, and in nova scotia, most importantly was microzooplankton such as calanoid copepods.)	February offshore was zooplankton. During spawning did not stop eating. In April, zooplankton, benthos, terrestrial insects and fish eggs.	Copepods, other crustaceans, zooplankton, chironimid larvae, terrestrial insects, and occasionally small fish such as bay anchovies.	Ostracods, amphipods, isopods, insects, and small fishes		Squid, fish eggs, small crabs, and pelagic crustaceans (adults on feed during freshwater spawning migrations)
Current Velocities	Avoid > 10 cm/s (1)	spawning in slow water, and movement upstream occurs over high flows	Avoid >10 cm/s (1)	relatively swift	0.06 - 75 m/s (1)	most frequent when 0.3 - 0.9 m/s (1) and spawn and egg		Spawning 0.20 - 0.39 m/s (1)

Sources

- 1- Atlantic Coast Diadromous Fish Habitat: A review of Utilization, Threats, Recommendations for Conservation, and Research Needs
- 2 - Development of Fishes of the Chesapeake Bay Region
- 3 - personal communication with James Mowrer (MD DNR Fisheries Service)

The timing of flow can also be important in determining production of larval and juvenile alosines. The spawning of anadromous alosines in late winter and early spring is an adaptation that allows developing larvae to feed on zooplankton blooms resulting from increased phytoplankton concentrations. Turbulent flows at larval emergence may reduce feeding success rates and decrease larval survival thereby effecting year class strength (Crecco et al. 1983; Savoy and Crecco 1988). For example, Dixon (1996) found that a high flow event during 1992 resulted in a bifurcated hatch date distribution of blueback herring juveniles and concluded that increased flow negatively impacted survival of eggs and larvae during the flow event. Whether the flow event flushed eggs and larvae out of the nursery or some other factors (i.e., increased turbidity, mortality, or a combination of factors) affected survival is unknown, but the bimodal distribution was not observed the previous year when flow was at the historic average (Dixon 1996). A

series of studies in the Connecticut River found that high flow and low water temperatures during June (when larvae hatch in the Connecticut River) adversely impacted year class strength of American shad larvae (for a summary see: Savoy et al. 2004). Conversely, increased flow during the juvenile stage may help stimulate secondary production of zooplankton prey, which can be utilized by juvenile alosines and actually contribute to the production of successful year classes (Hoffman et al. 2007). The timing and magnitude of flow can dramatically affect population dynamics of alosines.

Flow can also affect water quality through changes in water temperature, pH, turbidity, and nutrient cycling, that could drive episodes of hypoxia and either enhance or reduce feeding success. Leach and Houde (1999) found that sudden decreases in pH can negatively affect survival of larval American shad and such pH drops can be associated with rainfall events in Chesapeake tributaries. Similarly, increasing flow is usually associated with decreasing water temperatures, which can slow growth through a reduction in metabolic processes (Crecco and Savoy 1985; Leach and Houde 1999). Evidence from the Connecticut River suggests reduced feeding success due to increased turbidity. The geochemical processes that govern nutrient cycling are related to the spatiotemporal dynamics of water flow and storage. Klocker et al. (2009) found that N uptake and denitrification increased with hydrologic residence time for streams that were connected with the floodplain. Channelization of streams reduces connectivity with floodplains and decreases residence time for water and nutrients altering chemical processes in the watershed.

Unnatural Flow Regimes and Effects on Alosines

Alterations to freshwater flow due to water withdrawal or blockage by dams change the natural cycles that anadromous fishes have evolved to exploit. For example, the Susquehanna provides more than 50% of the flow to the Bay and Conowingo Dam generation cycles between 5,000 - 15,000 cfs and 85,000 cfs on a daily basis during shad spawning. This creates a highly altered flow regime and a highly perturbed environment for alosines. Additionally, this provides an ideal environment for striped bass predation on alosines (Mike Hendricks, personal communication). Aside from blocking spawning and rearing habitat above an obstruction, the altered flow regime downstream may not be suitable for the development of viable eggs and larvae of anadromous fishes. There may be changes to seasonal flow cycles, nutrient loads or timing, shifts in the location of suitable spawning habitat due to reduced water volume, or a combination of these factors that affect juvenile production. Additional stressors to alosines may involve municipal water usage facilities, including hydropower plants and water reservoirs, that may impinge eggs and poorly swimming larvae on intake pipes. Such facilities are considered detrimental to alosine production and have become an important part of management considerations (Olney et al. 2006).

Watershed development may also adversely impact natural flow regimes and water quality. Increased run-off due to impervious surfaces (Figure 3) changes flow patterns and duration and flushes additional nutrients and potential contaminants into streams and rivers. Impervious surfaces increased 41% (250,000 acres) between 1990 and 2000 in the Chesapeake Bay watershed and estimates suggest an additional increase to 1.1 million acres by 2010 (Chesapeake Bay Program 2010). Such rapid development will lead to increased runoff that carries nutrients, contaminants, sediments, and alters the natural flow regime of Chesapeake Bay.

Alteration of the landscape also affects ground water storage and recharge. Ground water can supply up to 50% of the total volume in streams and ranges from 16 – 92% for different systems in the Chesapeake watershed (Bachman et al. 1998). In addition to supplying water to streams, ground water also carries nitrogen in the form of nitrate. Depending on the age of the ground water and the geomorphology of the watershed, the amount of nitrate that is discharged can vary between 0.1 and 5 mg/L (Phillips 2007). Landscape changes that affect ground water recharge or storage need to be included in ecosystem studies targeting water quality and flow issues.

Climate change will likely affect flow regimes, sediment and nutrient loading, dissolved oxygen, water temperature and salinity in the Chesapeake Bay (Najjar et al. 2010). Increases in water temperature during winter and spring may shift the timing of spawning migrations (Quinn and Adams 1996), hatching and feeding success rates, and growth and mortality rates of Chesapeake Bay alosines. Further, alterations in flow regimes can be favorable or unfavorable depending on the timing and life stage that is affected. Watershed development and oversight will have to consider long-term climate trends coincidentally with water management issues.

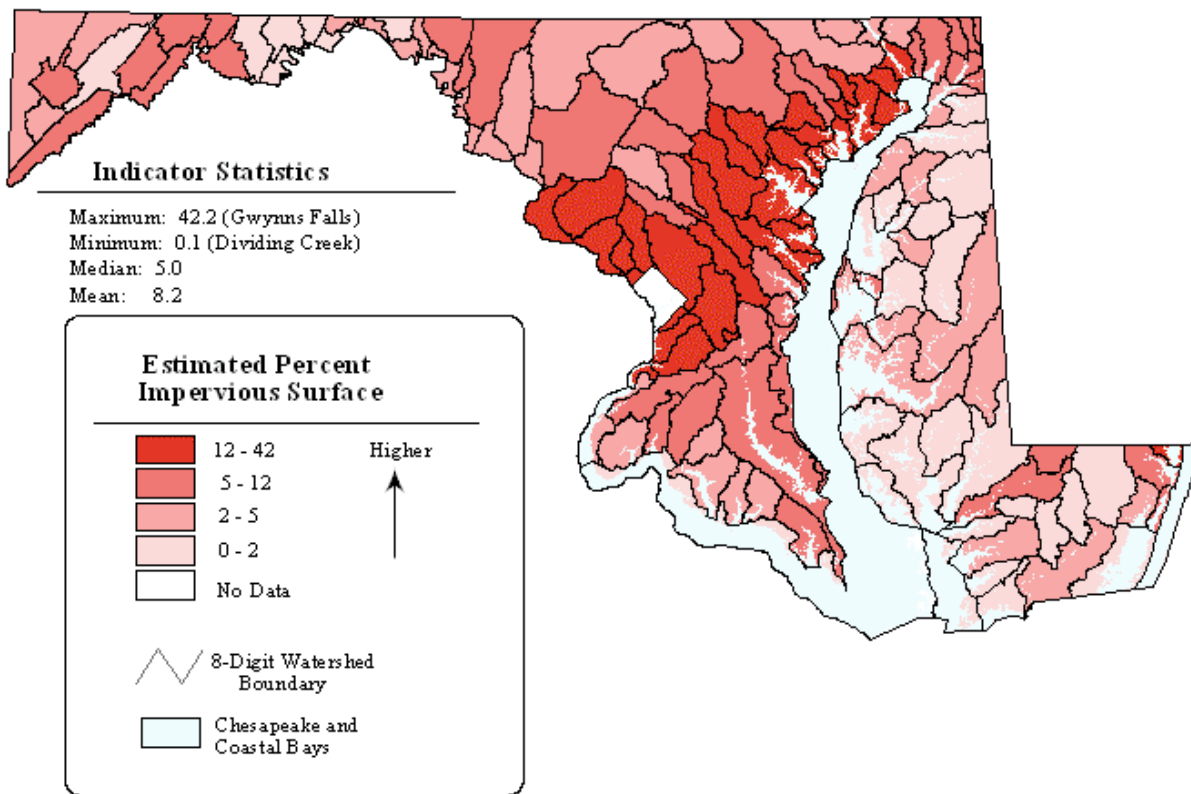


Figure 3: Figure showing the percent impervious surfaces in the Chesapeake and Coastal Bays, prepared in March 2000 by: Maryland Department of Natural Resources and Chesapeake & Coastal Watershed Service; Note: The legend classification is a quartile ranking of the watersheds in Maryland.

Ecosystem Restoration

Watersheds that no longer support desirable functions (i.e., lost fish habitat due to low DO) are often targeted for restoration. How restoration is undertaken has been the subject of recent debate (Poole et al. 2004; Palmer 2009). Historically, ecosystem restoration has focused on returning a single disturbed system to a previous state or some similar condition based on a reference site (Palmer 2009). One problem with this approach is realized in the concept of multiple stable states, which suggests that changing the shape of a streambed, for example, may not restore the functionality of the streambed because the system may have adapted to a different equilibrium. More than one aspect of the streambed has changed, and it may take much more to return the system to its desired condition than adding bends to the previously channelized system (Palmer 2009). Furthermore, the scale of restoration efforts tends to be too small relative to the level of degradation within a watershed. What is in need of restoration is the functionality of the system including biodiversity, flow regimes, nutrient cycling and the spatial and temporal dynamics within which these functions operate. Process oriented targets that consider a distribution of conditions provide greater benefit than threshold values that have no time, frequency, or spatial aspect (Poole et al. 2004).

Land-Use Ecology

John Waldman and Steve Gephard

Land use has large effects on the ecology of watersheds because the terrestrial matrices of drainages contribute most of the organic and inorganic materials that either drive or compromise food webs. That is, undisturbed watersheds leak appropriate quantities of nutrients and sediments into drainages that are essential to normal physical and biological processes. But radical transformations of land use may substantially increase or decrease material fluxes to drainages, which may dramatically alter their ecosystems and, thus, their suitability for alosines and other fishes.

Land use changes in Atlantic coast watersheds since European colonization have been profound. For Chesapeake Bay, the principal causes of impairment occurred on its surrounding basin, not directly in the Bay (Goetz et al. 2004). The scale of sediment and nutrient loading to the Bay is enormous; the Susquehanna River alone carries 100 million metric tons of sediments and 50 thousand tons of nitrogen annually (Goetz et al. 2004). But such inputs to the Bay have not been constant over time. Using the stratigraphic record, Cooper (1995) found that since Colonial times sedimentation, eutrophication, turbidity, and anoxia have increased.

It is generally accepted that the detrimental land use changes offset many of the improvements made to Chesapeake Bay since monitoring of environmental indicators began in the mid-1980s. Jantz et al. (2005) quantified changes in land usage between 1990 and 2000. They found a 61% increase in developed land, of which 64% was derived from agricultural and grasslands and 33% from forest. Empirical analyses of Chesapeake Bay subwatersheds showed high sensitivity of water quality to land use. Goetz et al. (2004) found that for a rating of excellent stream health, watershed impervious surfaces should not exceed 6% of total area and at least 65% of riparian zones should be vegetated. For a rating of good stream health, those values should have thresholds of 10% and 60%, respectively.

While there have been no studies conducted on changes in land use and subsequent effects on alosine populations within the Chesapeake Bay, these issues have been examined in other regions. Swaney et al. (2006) analyzed the history of land use in the Hudson River watershed. This terrain was almost entirely forested in 1609. By 1880, 68% of the watershed was farmland, but as soil productivity declined and industry provided other jobs, much cleared land reverted to secondary forest. Modeling suggests that fully forested primeval landscape would have suffered only one-eighth of the erosive losses of today, and that at the peak of farming in the 1880s, erosion was double that of current rates (Swaney et al. 2006). Deforestation also likely released soil nutrients to runoff and altered hydrology due to increased evapotranspiration. This process and the resultant impacts likely occurred in the Chesapeake Bay region, as well.

Contemporary land use effects on an alosine were studied by Limburg and Schmidt (1990) within the Hudson River drainage. They estimated an urban-rural gradient metric among four regional groupings of tributaries, with each group consisting of four streams. Seven land-use types were used to characterize watersheds, with industrial, residential, and transportation uses being combined to define urbanization. Although eggs and larvae of 23 fish species were captured, 93% were alewives. When they contrasted the abundances of these collections with environmental parameters, the strongest relationship ($r_2 = 0.73$, $P < 0.0001$) found was with their index of urbanization.

It is clear that landscape changes occur in many fashions and over broad regions and that there is little that can be done directly in managing landscapes to assist alosine stocks. However, the sustainability of alosine runs may be used as one more reason to encourage good fundamental riparian corridor management, such as creating and protecting buffers from development and minimizing erosion and nutrient runoff from disturbed lands.

Physical Alterations

Steve Gephard

Alosines utilize a variety of river and estuarine habitats during their life cycles. For these fishes, the erection of dams that block their migrations and thus deny access to spawning habitat may be the most significant physical alteration of rivers (Figures 4 and 5). However, other habitat modifications may also harm alosine populations in less obvious ways. Unfortunately, there has been little direct study of the effects of physical alterations of habitats on shads and river herrings, requiring that such analysis be extrapolated from other species and general principles.

Channelization for shipping or flood control can have multiple detrimental effects. Dredging to deepen channels—sometimes substantially—causes at least short term increases in turbidity, which could impede fish movements and also primary productivity. Sedimentation from smaller dredging or construction projects near spawning ponds or reaches may cover preferred spawning sites. Channelization may also alter river current patterns and velocities and the position of estuarine salt fronts. Dredging deeper channels often requires concomitant widening of channels, which may eliminate shallows or bottom structures useful to various life stages of these species.



Figure 4. Example of stream alteration, photo credit CTDEP/Inland Fisheries Division.

Dredging for navigation or other purposes may also eliminate the braided channels that exist naturally in some estuarine systems. These variegated areas may include quiet backwaters and sunken timber habitats that are valuable for young fishes (Sukhodolov et al. 2009) and for the general ecological productivity of the entire river.



Figure 5. Example of stream alteration, photo credit CTDEP/Inland Fisheries Division.

Many other physical alterations likely affect alosines in rivers. These include the construction of bulkheads or of landfilling, resulting in the loss of natural shorelines, the building of piers, platforms, and jetties, which may dissuade fish movements, provide cover for predators, and offer lower quality habitat (Able et al. 1998), and the placement of wing dams that change flow patterns. Moreover, both development and sea level rise are resulting in less total wetlands acreage, which may have broader biodiversity and trophic consequences (Gibbs 2000).

Potential Indicators, Reference Points, or Metrics

- Migratory barriers - A comprehensive survey of alosine habitats in the Chesapeake Bay watershed is needed. Primary focus should be on identifying migratory barriers that blocks or reduces habitat availability for alosines, but should also identify available habitat that may be threatened or altered in the future as land development changes. A comprehensive survey would provide managers a tool to evaluate trade-offs or mitigation activities as development continues in the watershed. This activity could also include studies to determine actual spawning within the creeks, streams, tributaries to supplement restoration activities, but would be much more costly.
 - *Reference point*: hectares/km of open versus blocked habitat.
- Flow and water quality –
 - *Reference points*: water quality metrics, temperature, DO, nitrogen, establish reference rivers
- Impervious surfaces in watershed
 - *Reference points*: Index of urbanization (given Limburg and Schmidt findings cited in “Land Use Ecology”)
- Habitat structure/morphology (channel and substrate)
 - *Reference points*: miles of channelization, bulk-heading and/or dredging in waterways; incidence of invasive aquatic plants and/or contaminated sediments.

References

- Able, K.W., J.P. Manderson, and A.L. Studholme. 1998. The distribution of shallow water juvenile fishes in an urban estuary: the effects of manmade structures in the lower Hudson River. *Estuaries and Coasts* 21:731-744.
- Bachman, L.J., Lindsey, B.D., Brakebill, J.W., and Powars, D.S., 1998, Ground-water discharge and base-flow nitrate loads of nontidal streams, and their relation to a hydrogeomorphic classification of the Chesapeake Bay watershed: U.S. Geological Survey Water-Resources Investigations Report 98-4059, 71 p.
- Bilkovic, D. M., C. H. Hershner, and J. E. Olney. 2002. Macroscale assessment of American shad spawning and nursery habitat in the Mattaponi and Pamunkey Rivers, Virginia. *North American Journal of Fisheries Management* 22:1176-1192.
- Chittenden, M.E., Jr. 1969. Life history and ecology of the American shad, *Alosa sapidissima*, in the Delaware River. Doctoral dissertation. Rutgers University, New Brunswick, New Jersey.
- Chesapeake Bay Program. 2010. Impervious surfaces. Accessed January 7, 2010 from <http://www.chesapeakebay.net/Impervioussurfaces.htm>.
- Clay, Charles H. 1995. Design of fishways and other fish facilities. CRC Press. Boca Raton, Florida.
- Cooper, S.R. 1995. Chesapeake Bay watershed historical land use: impact on water quality and diatom communities. *Ecological Applications* 5:703-723.
- Crecco, V. A., T. Savoy, and L. Gunn. 1983. Daily mortality rates of larval and juvenile American shad (*Alosa sapidissima*) in the Connecticut River with changes in year-class strength. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1719-1728.
- Crecco, V. A. and T. Savoy. 1985. Effects of biotic and abiotic factors on growth and relative survival of young American shad, *Alosa sapidissima*, in the Connecticut River. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1640-1648.
- Dixon, D. A. 1996. Contributions to the life history of juvenile blueback herring (*Alosa aestivalis*): phototactic behavior and population dynamics. Doctoral Dissertation. Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point. 288 p.
- Greene, K.E., J.L. Zimmerman, R.W. Laney, and J.C. Thomas-Blate. 2009. Atlantic coast diadromous fish habitat: a review of utilization, threats, recommendations for conservation, and research needs. Atlantic States Marine Fisheries Commission Habitat Management Series No. 9, Washington, D.C.
- Gibbs, J.P. 2000. Wetland loss and biodiversity conservation. *Conservation Biology* 14:314-317.

- Goetz, S.J., C.A. Jantz, S.D. Prince, A.J. Smith, D. Varlyguin, and R.K. Wright. 2004. Integrated analysis of ecosystem interactions with land use change: the Chesapeake Bay watershed. *Ecosystems and Land Use Change, Geophysical Monograph Series 153*:263-275.
- Hoffman, J. C., D. A. Bronk, and J. E. Olney. 2007. Contribution of allochthonous carbon to American shad production in the Mattaponi River, Virginia, using stable isotopes. *Estuaries and Coasts* 30:1034-1048.
- Jantz, P., S. Goetz, and C. Jantz. 2005. Urbanization and the loss of resource lands in the Chesapeake Bay watershed. *Environmental Management* 36: 808-825.
- Kemp, W. M., W. R. Boynton, J. E. Adolf, D. F. Boesch, W. C. Boicourt, G. Brush, J. C. Cornwell, T. R. Fisher, P. M. Gilbert, J. D. Hagy, L. W. Harding, E. D Houde, D. G. Kimmel, W. D. Miller, R. I. E. Newell, M. R. Roman, E. M. Smith, and J. C. Stevenson. 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Marine Ecology Progress Series* 303:1-29.
- Klocker, C. A., S. S. Kaushal, P. M. Groffman, P. M. Mayer, R. P. Morgan. 2009. Nitrogen uptake and denitrification in restored and unrestored streams in urban Maryland, USA. *Aquatic Sciences* 71:411-424.
- Leach, S. D. and E. D. Houde. 1999. Effects of environmental factors on survival, growth, and production of American shad larvae. *Journal of Fish Biology* 54:767-786.
- Leggett, W.C. and R.R. Whitney. 1972. Water temperature and the migration of American shad. *Fisheries Bulletin* 70: 659-670.
- Limburg, K.E., and R.E. Schmidt. 1990. Patterns of fish spawning in Hudson River tributaries: response to an urban gradient? *Ecology* 71:1238-1245.
- Limburg, Karin E. and John R. Waldman. 2009. Dramatic declines in North Atlantic diadromous fishes. *BioScience* 59: 955-965.
- Najjar, R. G., C. R. Pyke, M. B. Adams, D. Breitburg, C. Hershner, M. Kemp, R. Hogwarth, M. R. Mulholland, M. Paolisso, D. Secor, K. Sellner, D. Wardrop, and R. Wood. 2010. Potential climate-change impacts on the Chesapeake Bay. *Estuarine, Coastal and Shelf Science* 86:1-20.
- Olney, J. E., D. M. Bilkovic, C. H. Hershner, L. M. Varnell, H. wang, and R. L. Mann. 2006. Six fish and 600,000 thirsty folks – A fishing moratorium on American shad thwarts a controversial municipal reservoir project in Virginia, USA. *American Fisheries Society Symposium*, 2006. 587-597.
- Palmer, M. A. 2009. Reforming watershed restoration: Science in need of application and applications in need of science. *Estuaries and Coasts* 32:1-17.
- Phillips, S.W. 2007. Chapter 4. Transport of Nitrogen in Ground Water. *In: Synthesis of U.S. Geological Survey science for the Chesapeake Bay ecosystem and implications for environmental management: U.S. Geological Survey Circular 1316*. 63 p.
- Poole, G. C., J. B. Dunahm, D. M. Keenan, S. T. Sauter, D. A. McCullough, C. Mebane, J. C. Lockwood, D. A. Essig, M. P. Hicks, D. J. Sturdevant, E. J. Materna, S. A. Spalding, J. Risley, and M. Deppman. 2004. The case for regime-based water quality standards. *BioScience* 54:155 – 161.

- Quinn, T. P. and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. *Ecology* 77:1151-1162.
- Savoy, T. and V. A. Crecco. 1988. The timing and significance of density-dependent and density-independent mortality of American shad, *Alosa sapidissima*. *Fishery Bulletin* 86:467-481.
- Savoy, T., V. A. Crecco, and B. C. Marcy, Jr. 2004. American shad early life history and recruitment in the Connecticut River: A 40-year summary. *American Fisheries Society Monograph* 9:407-417.
- Sukhodolov, A., W. Bertoldi, C. Walter, N. Surian, and M. Tubino. 2009. Implications of channel processes for juvenile fish habitats in Alpine rivers. *Aquatic Sciences – Research Across Boundaries* 71:338-349.
- Swaney, D.P., K.E. Limburg, and K. Stainbrook. 2006. Some historical changes in the patterns of population and land use in the Hudson River watershed. *American Fisheries Society Symposium* 51:75-112.
- Tuckey, T. D. 2009. Variability in juvenile growth, mortality, maturity, and abundance of American shad and blueback herring in Virginia. Doctoral Dissertation. Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point. 195 p.
- Waters, C. T. and J. E. Hightower. 2007. Effect of water quality on hatching success of bluebackherring eggs in the Chowan River Basin, North Carolina. *Proceedings of the Annual Conference Southeast Association of Fish and Wildlife Agencies* 61:23-28.
- Weaver, L. A., M. T. Fisher, B. T. Boshers, M. L. Claud, and L. J. Koth. 2003. Boshers Dam vertical slot fishway: a useful tool to evaluate American shad recovery efforts in the upper James River. *Biodiversity, Status, and Conservation of the World's Shads. American Fisheries Society Symposium* 35:339-347.

FOODWEB

Forage, Competition, and Predation

*Julie Harris, Rich McBride, John Waldman,
Jake Kritzer and Steve Gephard*

Introduction

Alosines mostly feed on secondary production, such as zooplankton, and are eaten by a wide variety of finfish, avian, and mammalian predators, including humans. They feed throughout their life cycle, in freshwater, brackish, and saltwater habitats, although feeding intensity may vary greatly by habitat and life stage. Alosines are important components of food webs (Figure 1), most notably because they are capable of shaping zooplankton communities and because they serve as prey for numerous species. Moreover, their predators live in both aquatic and terrestrial biomes, and alosines migrate between marine and freshwater biomes, so alosines are important vectors of nutrients within and between watershed and coastal marine ecosystems. This section begins with some general statements about alosine feeding patterns and then details feeding habits for different species by major life history stage. It continues by reviewing known alosine predators: native fishes, non-native fishes, and other predators. It ends by outlining even more general ecological interactions between alosines and freshwater communities. Specific examples focus on the Chesapeake Bay and its tributary rivers, when possible.

Forage

General Overview

The specific food items and modes of feeding for alosines vary by species, life stage, diel time period, and habitat type (Crecco and Blake 1983; Grabe 1996; Walter and Olney 2003; Simonin et al. 2007; Murauskas 2006). Alosines generally begin life as opportunistic feeders—primarily as planktivores (Munroe 2002). However, diet changes with growth and development, specifically with shifts in gill-raker morphology. MacNeill and Brandt (1990) found that as alewives grew, they increased the length, number, and spacing of their gill rakers, enabling them to catch larger prey. A total account of the diet over the life cycle often includes diatoms, crustaceans (including cladocerans, copepods, ostracods, shrimps, and amphipods), insects (both aquatic and terrestrial stages), fish eggs, and, at larger sizes, fish and squid (Murdy et al. 1997).

Diet is affected by the repertoire of feeding behaviors available to the species and environmental conditions (Janssen 1976, 1978; Janssen and Brandt 1980; Stone and Daborn 1987; Stone and Jessop 1994). For example, alewives feed on macrozooplankton using a ‘particulate-feeding’ mode when prey visibility is high, but they feed on microzooplankton using a ‘filter-feeding’ mode when prey visibility is low. In Atlantic Ocean coastal waters and in the Great Lakes, alosines migrate vertically, apparently to follow prey (Neves and Depres 1979; Janssen and Brandt 1980; Neves 1981; Stone and Jessop 1994). Alosines appear to be primarily visual feeders and,

for most species, feeding intensity appears lowest during the night (Grabe 1996; Johnson and Dropkin 1996). Peak feeding typically occurs in the late afternoon or early evening, especially for American shad (Massman 1963; Levesque and Reed 1972; Burbidge 1974; Grabe 1996; Jessop 1990; Stone and Jessop 1994; Johnson and Dropkin 1996; Harris and McBride 2009); however, some species appear capable of feeding at night (Janssen et al. 1995).

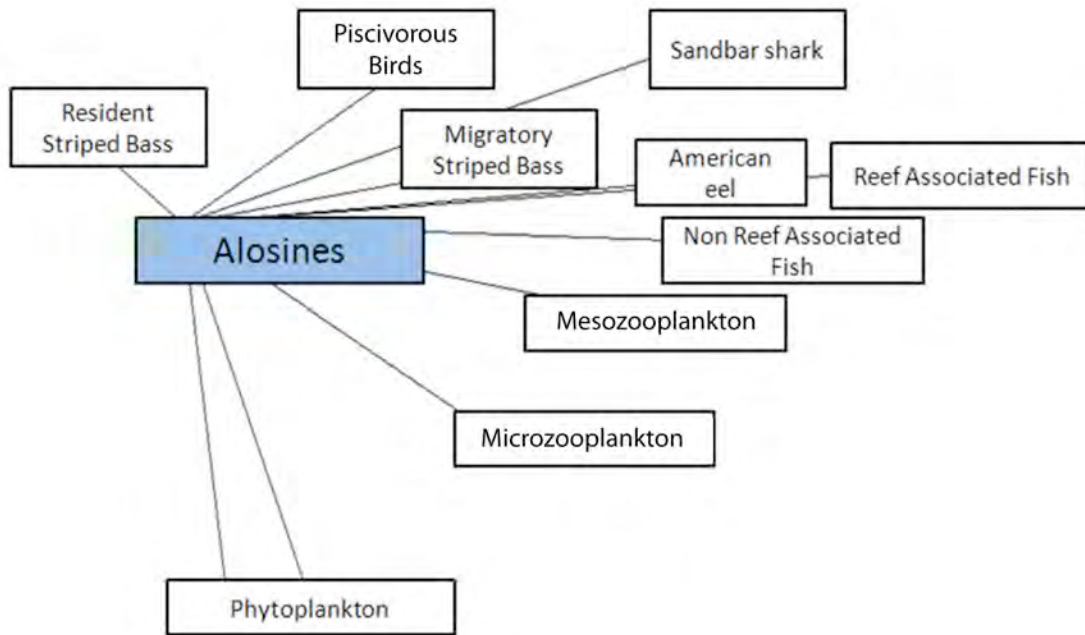


Figure 1. Foodweb of alosines: schematic depicts current representation of alosines in the Chesapeake Bay Fisheries Ecosystem Model (Christensen et al. 2009).

Feeding intensity and growth vary with environmental conditions, habitat, and life stage. As an example, feeding by American shad juveniles appears to slow or cease, and growth declines, when water temperatures decrease to between 6 °C and 13 °C (Chittenden 1972; Limburg 1996; Zydlewski and McCormick 1997). Growth rates are higher at higher temperatures, higher pH, and higher prey densities (Leach and Houde 1999), although, there are upper temperature limits as well (Limburg 1996). While larval and juvenile American shad feed and grow in the freshwater rivers of Chesapeake Bay, adults appear to drastically reduce feeding while on their spawning migration in freshwater, often losing considerable weight (Walburg 1956; Massman 1963; Walter and Olney 2003). It has been suggested that this reduction in feeding could be the result of limited availability of appropriate-sized prey (Atkinson 1951), but it could also be a behavioral change.

Riverine: Larvae, Juveniles, and Adults

Larvae

Larval alosines consume various types of zooplankton (Crecco and Blake 1983; Johnson and Dropkin 1996, 1997). Research on the Connecticut and Susquehanna rivers suggest that larval American shad mainly feed on chironomid pupae and larvae, trichopteran larvae, copepods, and

cladocerans, notably *Bosmina* spp. (Levesque and Reed 1972; Crecco and Blake 1983; Johnson and Dropkin 1995). Larval blueback herring in the Connecticut River were observed to consume rotifers, including *Keratella* spp., and cladocerans, mainly *Bosmina* spp, and once they increased in size, they consumed more copepods and chironomids (Crecco and Blake 1983). Species with overlapping larval stages, such as American shad and blueback herring in the Connecticut River, appear to feed selectively on different zooplankton (species and/or size) which reduces interspecific competition (Crecco and Blake 1983).

Forage behaviors and prey sizes selected vary by the size and age of the alosine larvae. Larger and older American shad larvae attack prey more frequently and more successfully than younger stages, although successful predation attempts were still low (8%) for older larvae (Ross and Backman 1992). Crecco and Blake (1983) observed that prey size increased with an increase in the gape size of larval American shad and blueback herring.

Survival and growth rates of larval American shad have been linked to prey density. Under experimental conditions, American shad larvae grew faster and had higher survival at higher prey densities of *Artemia*. Food deprivation for as little as two days had significant effects on survival, but changes in growth rates were not detectable until after four days of starvation (Johnson and Dropkin 1995). Leach and Houde (1999) similarly found that production of larvae was best when both temperature and prey densities were high (>20 °C and >50 *Artemia* nauplii l⁻¹, respectively).

Juveniles

Numerous studies on feeding habits of juvenile alosines have occurred, some in rivers of Chesapeake Bay. While in freshwaters, juvenile American shad appear to feed opportunistically on a variety of prey types, from both aquatic and terrestrial origins (Ross et al. 1997). In general, riverine foods include various terrestrial and aquatic insects (mainly chironomids), and small crustaceans (mainly cladocerans; Walburg 1956; Massman 1963; Davis and Cheek 1966; Domermuth and Reed 1980; Grabe 1996; Ross et al. 1997). Ostracods, amphipods, other dipteran larvae and pupae, and copepods have also been observed in stomach contents, sometimes in high abundances (Massman 1963; Domermuth and Reed 1980; Grabe 1996). In the Pamunkey River, age-0 American shad had 14 different taxa in their diet, but consumed mostly ostracods, *Ephemera* and other insects, and nematodes (Walburg 1956). During late summer in the Pamunkey and Mattaponi Rivers, juvenile American shad fed on insects (Massman 1963).

Blueback herring juveniles are collected along with American shad in riverine habitats, but are usually smaller and consume different types or sizes of prey. Compared to American shad juveniles, blueback herring often appear to prefer copepods and smaller species of cladocerans (Burbridge 1974; Domermuth and Reed 1980; Grabe 1996). In the James River, age-0 blueback herring consumed primarily copepods, appearing to select adult copepods over nauplii. Consumption and growth rates were highest when zooplankton densities were highest. Feeding can be intense enough that less preferred prey, such as smaller cladocerans, become dominant in the remaining plankton assemblage (Burbidge 1974).

Although most research on feeding by alewife has been completed in reservoirs, some work on feeding by juveniles in riverine environments has occurred. In the lower Hudson River, alewives

consume amphipods, chironomids, and other insects (Grabe 1996). Foraging by both landlocked and anadromous juvenile alewives appears to structure freshwater zooplankton communities (Post et al. 2008).

Adults

Adult alosines feed on a variety of types of prey. Evidence suggests that some species reduce food intake during the spawning migration in freshwater (Walter and Olney 2003; Murauskas 2006), although it is not known whether this is a result of reduced prey availability, reduced feeding intensity, or both. American shad eat little in freshwater rivers, often consuming items that appear low in caloric value, and lose considerable weight during the spawning migration (Leggett 1972; Chittenden 1976; Walter and Olney 2003; Harris and McBride 2009). Walter and Olney (2003) found that American shad in the York River, Virginia, consumed almost entirely green and woody plant material. It has been suggested that adult American shad may not feed in rivers because freshwater zooplankton are too small (Atkinson 1951); however, consumption may vary within a river (Harris and McBride 2009), possibly due to differences in prey compositions at different sites.

Hickory shad similarly appear to reduce consumption during the spawning migration in freshwater (Murauskas 2006). However, hickory shad with fish in their stomachs (*Dorosoma*, *Anchoa*, and *Notropis*) have been collected during the spawning migration in freshwater portions of the St. Johns River, Florida (Harris et al. 2007).

For both blueback herring and alewife, natural and stocked landlocked populations have been established (Simonin et al. 2007; Post et al. 2008). Much study has focused on the feeding habitats of these landlocked populations (Janssen and Brandt 1980; Davis and Foltz 1991; Guest and Drenner 1991; Janssen et al. 1995); however, there is evidence that anadromous and landlocked alewives may be morphologically different and play different roles in the food web (Post et al. 2008). In freshwater rivers, the foods consumed by blueback herring may be system-specific. In the Chowan River, North Carolina, adult blueback herring feed on a varied diet dominated by fish eggs and cladocerans (Creed 1985). In the St. Johns River, Florida, blueback herring consumed mainly calanoid copepods, fish eggs, and plant material, but also consumed some fish (McBride et al. 2010). In the upper Hudson River, blueback herring fed on zooplankton, while individuals in the Mohawk River consumed benthic aquatic insects in large quantities, including Baetidae, Ephemeridae, and Chironomidae (Simonin et al. 2007). Simonin et al. (2007) determined that freshwater food sources were being incorporated into tissues and were thus important for the energetic budget. In contrast, Post et al. (2008) suggested that anadromous alewives may not eat while in spawning lakes.

Estuarine: Juveniles and Adults

Foods of juvenile and adult alosines in estuaries have been examined only to a limited extent. In Minas Basin, Nova Scotia, alewives fed mostly on larger, more benthic prey (e.g. amphipods, mysids, and crangonids), whereas blueback herring fed mostly on microzooplankton (e.g., calanoid copepods, larval cyprids, and larval mollusks; Stone and Daborn 1987). In Chesapeake Bay, overwintering juvenile American shad ate a variety of prey types, depending on their location in the estuary, including crustaceans (calanoid copepods, ostracods, and mysids) and fish (*Micropo-*

gonias, *Anchoa*, *Brevoortia*; Hoffman et al. 2008). At the mouth of the York River, Virginia, Walter and Olney (2003) found that mysids dominated American shad diets, followed by calanoid copepods. Murauskas (2006) found that fish dominated the diet of hickory shad in the Pamlico Sound, North Carolina.

Offshore: Sub-adults and Adults

Alosines are found offshore of Chesapeake Bay during spring (Neves and Depres 1979; Neves 1981). They migrate vertically in the water column, which authors suggest is to follow the diel movements of zooplankton (Neves and Depres 1979; Neves 1981; Stone and Jessop 1994). American shad collected in oceanic waters often have full stomachs (Walter and Olney 2003). In coastal and oceanic waters near Chesapeake Bay, American shad consumed mostly crustaceans, including calanoid copepods and mysid shrimp. Near Oregon Inlet in North Carolina, Holland and Yelverton (1973) collected American shad with various types of crustaceans and fish (*Anchoa*) in their stomachs. Hickory shad found in the ocean outside Pamlico Sound contained fish, mainly *Anchoa*, in their stomachs (Murauskas 2006).

Blueback herring and alewife collected offshore consumed a variety of organisms. Holland and Yelverton (1973) collected blueback herring off the coast of North Carolina with zooplankton in their stomachs, including various amphipods, copepods, isopods, cumaceans, mysids and decapod larvae. They collected alewife with similar zooplankton prey as well as fish remains. Offshore of Nova Scotia, alewives feed primarily on euphausiids, but also consume hyperiid amphipods, calanoid copepods, crustacean larvae, polychaetes, chaetognaths, mysids, pteropods, and fish larvae. Daily ration was 1.2% of body weight during winter and 1.9% during summer (Stone and Jessop 1994). Netzel and Stanek (1966) reported low feeding rates by blueback herring and alewives offshore.

Interspecific Competition for Food

Interspecific competition for food among alosines likely occurs, but may not greatly affect populations. Spawning areas and juvenile nurseries are generally located in association with high productivity in both space and time. High densities of fish in localized areas may create a venue for food limitation, but behavioral (i.e., diel feeding period and specific location) and morphometric (i.e., stage and gape size) differences between species are believed to reduce interspecific competition (Dommermuth and Reed 1980; Crecco and Blake 1983; Loesch 1987; Stone and Daborn 1987; Grabe 1996).

Feeding Intensity and Year-class Strength

Multiple studies focused on understanding how year-class strength may be affected by biotic and abiotic factors have been completed in the Connecticut River. Juvenile indices of year class strength from 1966 to 1973 were positively correlated with recruitment levels of adult females 4-6 years later, which suggests that year-class strength is established prior to the juvenile stage (Crecco et al. 1983). Mortality rates were highest among young larvae, ranging from 19.8-25.6%/d for the first feeding larvae, 4.3-8.7%/d for larvae approaching metamorphosis, and 1.8-2.0%/d for juveniles (Crecco et al. 1983). Survival and growth of American shad larvae appear linked to high prey densities and other, abiotic factors that affect feeding success, such as flow

and temperature (Crecco et al. 1983; Crecco and Savoy 1984; Crecco and Savoy 1985; Crecco et al. 1986; Johnson and Dropkin 1995). Specifically, highly turbulent waters may produce unfavorable conditions for first feeding larvae (Crecco et al. 1986). However, Hoffman et al. (2007) found that production of juvenile American shad increased with higher flows in the Mattaponi River, Virginia. Higher flows in this river system increased terrestrially derived organic matter that stimulated zooplankton abundance. Thus, environmental conditions that favor increased food abundance and successful feeding likely improve year-class strength.

Predation on Alosines

General Statement

There are many alosine predators. Recently, particular attention has focused on predation by striped bass, whose populations have increased in abundance in recent decades. Savoy and Crecco (2004) postulated that increased predation rates related to increased striped bass abundance could be partially responsible for the recent dramatic drop in both adult American shad and blueback herring in the Connecticut River. There is also a suite of introduced finfish piscivores that could potentially affect alosine populations. If so, then consumption rates of predators could confound efforts to restore alosine populations. Far less attention has been given to other predators, but there are many other fish, avian, reptilian and mammal piscivores, that feed on alosines. Below we discuss some alosine predators—there are likely others that we have not identified. In general, the suite of native and non-native predators, as well as the effects of predation on alosine populations, are still unclear and require further study.

Native Fish Predators

Eggs

In a landlocked population, alewife eggs were consumed by spottail shiners *Notropis hudsonius*, emerald shiners *Notropis atherinoides*, and adult alewives (Edsall 1964). In rivers, the distribution of alewife spawning habitats overlaps with the distribution of *Notropis*, so egg consumption is possible. American eels have also been observed to consume alewife eggs.

Larvae

American shad larvae released into the Susquehanna River to enhance the stock were vulnerable to predation by juvenile smallmouth bass *Micropterus dolomieu*, spotfin shiners *Cyprinella spiloptera*, and mimic shiners *Notropis volucellus* (Johnson and Ringler 1995, 1998).

Juveniles and Adults

Striped Bass

Alosines, especially blueback herring and alewife, are seasonally common prey of striped bass when they are spatially and temporally located together in estuarine and riverine habitats, including parts of Chesapeake Bay (Trent and Hassler 1966; Walter and Austin 2003; Walter et al. 2003; Tuomikoski et al. 2008). Similarly, age-1 striped bass have been observed to prey on age-0 alosines when the two are located together in the Albemarle Sound during the alosine outmigration (Rudershausen et al 2005; Tuomikoski et al. 2008). The recent coast-wide

recovery of striped bass, particularly in Chesapeake Bay, has led to concern regarding possible increases in their predatory rates on common prey species, including alosines (Hartman and Margraf 2003; Savoy and Crecco 2004; Heimbuch 2008; Davis and Schultz 2009). However, Overton et al. (2009) found that alosines were only common prey for small (150-300 mm) striped bass and some studies in Chesapeake Bay do not cite alosines as a major prey type for striped bass (Walter et al. 2003). Kahnle and Hattala (2007) examined correlations between striped bass abundances and adult American shad abundances over time in a variety of river systems and did not find a consistent pattern, suggesting that the effect of striped bass predation on an American shad population is still unknown. Offshore, alosines were rarely observed in the stomachs of striped bass taken by hook and line in the recreational fishery (Overton et al. 2008). Additional research on predation by different sizes of striped bass in all habitats would help better evaluate the population-level effects of their predation.

Other Fishes

Predation on alosines has been observed by other piscivorous fishes. Age-0 bluefish *Pomatomus saltatrix* feed on age-0 alosines in the Hudson River (Juanes et al. 1993; Buckel et al. 1999), but not in the lower Chesapeake Bay, where they do not appear to overlap spatially (Gartland et al. 2006). Juvenile alewives were also observed in the stomach of one older bluefish in the Long Island Sound (Richards 1976).

Sea lampreys *Petromyzon marinus* are known to feed on alewife and American shad in oceanic waters and often feed on these anadromous prey species even as they travel long distances and enter fish water habitats (Warner and Katkanshy 1970; Potter and Beamish 1977; Beamish et al. 1979).

In the coastal waters of the Gulf of Maine, Atlantic cod migrated inshore during spring in association with alewives and blueback herring (*Alosa aestivalis*). It has been speculated that the decline in these forage stocks may have triggered the collapse of the coastal cod fishery (Ames 2004).

In coastal waters of the south Atlantic, king mackerel preyed on alosines, but to a very small extent (Saloman and Naughton 1983). *Alosa* sp. composed less than 0.5 percent of the stomach contents of king mackerel collected off North Carolina and South Carolina.

Bell and Nichols (1921) found “shad” in the stomachs of cub sharks, *Charcharhinus comersonii*, and tiger sharks, *Galeocerdo tigrinus*, in marine waters off the coast of North Carolina in August.

Longnose gar, *Lepisosteus osseus*, have been observed to consume alosines in rivers in Virginia (McGrath 2010). Most of the alosine consumption was of blueback herring.

Non-native Fish Predators

Alosines evolved and flourished in the presence of a natural suite of predators and competitors. As a result of anthropogenic actions, such as purposeful and accidental introductions and the creation of physical connections among waters that allowed movements of fishes, most rivers on

the east coast of North America host predators and competitors not present before European colonization. As an example, Snyder (2005) reported 33 alien species (28% of total) in the Susquehanna River watershed. Some of these were localized, but others include well-established predatory fishes such as flathead catfish, northern pike, largemouth bass, smallmouth bass, and a number of sunfishes. The Chesapeake Bay watershed has experienced substantial ichthyofaunal changes, as well. Populations of piscivorous catfishes (flathead, blue, and channel catfishes) have been introduced and expanded in population size in the Chesapeake Bay concurrent with declines in some smaller native catfish species (white and brown bullhead catfishes; Viverette et al. 2007). Northern snakehead has also recently become established in portions of the Chesapeake watershed, and it is known as a voracious predator (Odenkirk and Owens 2005).

The effects of most introduced fishes on anadromous alosine populations have not been well studied. Blue catfish *Ictalurus furcatus* introduced into rivers in Virginia prey on American shad, blueback herring, and alewife (MacAvoy et al. 2000; MacAvoy et al. 2001). Flathead catfish *Pylodictis olivaris* have been observed to feed on juvenile and adult alosines in North Carolina rivers (Guier et al. 1981; Ashley and Buff 1987; Pine et al. 2005). It has been speculated that flathead catfish may be an impediment to American shad restoration efforts in the Delaware and Susquehanna river drainages (Brown et al. 2005). In coastal lakes of Massachusetts, where largemouth bass *Micropterus salmoides* are introduced, resident largemouth bass eat juvenile blueback herring and alewife during the seasonal period when the two overlap (Yako et al. 2000); however, population level effects of predation by largemouth bass on river herring may not be substantial.

Other Natural Predators

General Statement

Comparatively little work was identified to document predation by avian and mammalian predators, and no information on reptilian predation was found, although likely some predation by this group (e.g., snapping turtles and water snakes in freshwater habitats) does occur. Additional research focused on piscivory of alosines would help better understand their importance in food-web dynamics.

Avian Predators

In New England rivers, alewives and blueback herring are preyed on by double-crested cormorants, a piscivorous bird that has recently been increasing in abundance in some areas (Blackwell et al. 1995; Blackwell et al. 1997; Dalton et al. 2009; Davis and Schultz 2009). Davis and Schultz (2009) suggest that increased predation, from striped bass or double-crested cormorants, could potentially be leading to a decline in alewife populations in Bride Brook, Connecticut; however, research by Dalton et al. (2009) suggests that recent alewife mortality rates are not much higher than they were when double-crested cormorants were largely absent, suggesting that this predator may not have a notable impact on alewife mortality or population size.

Bald eagles (*Haliaeetus leucocephalus*) and ospreys (*Pandion haliaetus*) feed on alosines and their recovery in Chesapeake Bay following the ban of DDT in the 1970s may be influenced by the ecology of anadromous clupeids (Viverette et al. 2007). Bald eagles in the Hudson River have also been observed to prey on river herring (Thompson et al. 2005). In Nova Scotia,

Canada, the seasonal run of adult alewives was among the top four species contributing to the diet of ospreys (Green et al. 1981).

Mammalian Predators

There is inferential evidence that alewives are prey of bottlenose dolphins *Tursiops truncatus* and harbour porpoises *Phocoena phocoena*, although American shad can detect the echolocation of these predators and possibly avoid them (Mann et al. 1998; Plachta and Popper 2003). Harbour seals *Phoca vitulina* in Atlantic Canada consume American shad (Leim and Scott 1966; Scott and Crossman 1973) and river herring, especially alewife (Bowen and Harrison 1996).

Ecological Impact in Freshwater: Alosines as Vectors of Biological Materials

*Jake Kritzer, Julie Harris, Rich McBride,
John Waldman, and Steve Gephard*

One important ecological function served by anadromous alosines is the transportation of energy, carbon, and nutrients between freshwater and saltwater ecosystems. Considerable research has focused on the importation of marine derived nutrients (MDN) into freshwater systems by Pacific salmon (Donaldson 1969, Naiman et al. 2002, Moore and Schindler 2004, Schindler et al. 2005, Cederholm et al. 1999). Relatively little research has focused on such a mechanism for Atlantic anadromous alosines. Durbin et al. (1979) first suggested that the input of nitrogen and phosphorus by alewife into a coastal pond could be comparable to that of a Pacific salmon run. Inputs of alewife carcasses, gametes, and excretion are potentially significant inputs to freshwater systems (Post and Walters 2009; Walters et al. 2009). The run of alewife into Bride Brook, Connecticut delivers more than 1000g of marine-derived nitrogen, a quantity sufficient to enable detection of marine-derived nitrogen at all stream trophic levels (Walters et al. 2009).

West et al. (2010) studied the nutrient loading of alewife in Connecticut waters and concluded that runs do not always result in a net import of nutrients into freshwater systems. At some population sizes, alewife runs may actually result in a net export of nutrients into the ocean. The dynamics of this import/export mechanism is complex and the direction of nutrient flow is very site specific and dependent upon the nutrient budget of the pond and the population size of the fish (West et al. 2010). A run of alewives may be a net nutrient exporter from a specific lake at low population levels but as restoration progresses and the population level increases, the run could switch to a net nutrient importer (West et al. 2010). In lakes and ponds in which cultural eutrophication is occurring, stakeholders may oppose alewife restoration because of concerns that the importation of MDN by alewives will exacerbate water quality problems (West et al. 2010). Anthropogenic causes of eutrophication of lakes and ponds are well-known and the role alewife restoration plays in the process will likely vary by lake. In some lakes, alewives may not contribute to eutrophication at all and in other lakes, the contribution by alewives may be negligible in comparison to the anthropogenic causes.

The rate of importation of MND may be affected by the rates of iteroparity by alosines in the system. The rate of iteroparity in Chesapeake Bay alosines (excluding hickory shad) is less than that of alosines in New England (Greene et al. 2009), where much of the research on transportation of nutrients has been conducted. However, the total volume of marine-derived carbon in predators of alosines in Ward's Creek, Virginia was 36% (Garman and Macko 1998). Similarly, marine-derived carbon and sulfur account for more than 40% of the total amount of either element in the tissues of the predatory catfish *Ictalurus furcatus* in the Rappahannock River (MacAvoy et al. 2000). Alosines represent the major source of those isotopes. In addition, these

studies might actually underestimate the contribution of marine-derived isotopes due to the slow turnover rate of isotopes in the tissues of predators, resulting in delayed ability to detect a signal (MacAvoy et al. 2001). With population changes, reduced access to some historic spawning areas, and differences in the percentages that spawn in multiple years, there could be spatial differences in nutrient pathways in Chesapeake Bay rivers and more general differences in the impacts of anadromous alosines on food web dynamics.

Alosines as Plankton Grazers

Most adult alosines are generally believed to cease feeding in freshwater, but juveniles feed on zooplankton during their freshwater phase (Leim 1924, Batsavage and Rulifson 1998, Gregory et al. 1983, Crecco and Blake 1983). In New England, landlocked alewife populations have become established in lakes and where these populations exist in less productive lakes with less abundant populations of copepods etc., the fish have been shown to ‘over graze’ the copepods. This may result in a paucity of phytoplankton grazers and nuisance algal blooms have resulted (Post et al. 2008). This has given rise to public concerns in New England about alewives in lakes and created some resistance to restoration of anadromous alewives. Post et al. (2008) concluded that the morphology and the feeding habits of landlocked and anadromous alewives are sufficiently different to suggest that over grazing of copepods in most lakes by anadromous alewife is unlikely and that this would be even less likely in the more productive lakes and ponds south of New England, such as in Maryland.

Alewives as Mussel Transport

Freshwater mussels use fish to transport their larval stages (glochidia) to suitable nursery habitat (Nadeau 2009; McCann 2009). Glochidia attach to the gills of fish, feed on the fish’s blood, and grow in a generally benign manner before dropping off and settling into the substrate to grow to adults. If the host species is migratory, wide dispersal of the mussel is likely. Many species of mussels have very specific host preferences and anadromous species, including alosines, are targeted to realize extensive upstream transport throughout a watershed. Examples of mussel species that are known to use alosines as hosts include the alewife floater (*Anodonta implicata*) and the eastern pearlshell (*Margaritifera margaritifera*) (Nadeau 2009).

There are 16 species of native mussels in Maryland and most are in decline (McCann 2009). Of these species, nine are rare, four are State endangered, one is federally endangered, and two are species of Special Concern (McCann 2009). In Virginia, there are 19 federally endangered mussel species, 9 are state endangered (only), and 8 are state threatened (only) (Anon. 2008). Restoration of anadromous alosine species both in terms of numbers and geographical distribution will benefit some of these mussels.

Potential Indicators, Reference Points, or Metrics

- Predator field – How are predator populations changing through time in relation to alosine populations? Are alosines exposed to the same suite of predators or has the community composition changing (i.e., potential effects of invasive or introduced species)?
 - *Reference point:* Community metric that characterizes the predator field that may consume alosines.
- Prey field – Is there sufficient food available and is it of the proper type?
 - *Reference point:* Community metrics that characterize prey composition and availability for alosines.
- Nutrient cycling – Release of nutrients from spawning activities and associated mortalities and impact on freshwater ecosystem.
 - *Reference point:* Measure of the marine isotopic signatures in freshwater foodwebs.

Table 1. Federal and State Listed Mussel Species in Virginia.

SCIENTIFIC NAME	COMMON NAME	STATUS
<i>Alasmidonta heterodon</i>	dwarf wedgemussel	FE SE
<i>Alasmidonta varicose</i>	brook floater	SE
<i>Alasmidonta viridis</i>	slippershell mussel	SE
<i>Cumberlandia monodonta</i>	spectaclecase	FC SE
<i>Cyprogenia stegaria</i>	fanshell	FE SE
<i>Dromus dromas</i>	dromedary pearlymussel	FE SE
<i>Elliptio crassidens</i>	elephantear	SE
<i>Epioblasma brevidens</i>	Cumberlandian combshell	FE SE
<i>Epioblasma capsaeformis</i>	oyster mussel	FE SE
<i>Epioblasma florentina walkeri</i>	tan riffleshell	FE SE
<i>Epioblasma torulosa gubernaculum</i>	green blossom	FE SE EX
<i>Epioblasma triquetra</i>	snuffbox	SE
<i>Fusconaia cor</i>	shiny pigtoe	FE SE
<i>Fusconaia cuneolus</i>	finerayed pigtoe	FE SE
<i>Fusconaia masoni</i>	Atlantic pigtoe	ST
<i>Hemistena lata</i>	cracking pearlymussel	FE SE
<i>Lampsilis abrupta</i>	pink mucket	FE SE EX
<i>Lasmigona holstonia</i>	Tennessee heelsplitter	SE
<i>Lasmigona subviridis</i>	green floater	ST
<i>Lemiox rimosus</i>	birdwing pearlymussel	FE SE
<i>Leptodea fragilis</i>	fragile papershell	ST
<i>Lexingtonia dolabelloides</i>	slabside pearlymussel	FC ST
<i>Ligumia recta</i>	black sandshell	
<i>Pegias fabula</i>	littlewing pearlymussel	FE SE
<i>Plethobasus cyphus</i>	sheepnose	FC ST
<i>Pleurobema collina</i>	James spinymussel	FE SE
<i>Pleurobema cordatum</i>	Ohio pigtoe	ST
<i>Pleurobema plenum</i>	rough pigtoe	FE SE
<i>Pleurobema rubrum</i>	pyramid pigtoe	SE
<i>Ptychobranthus subtentum</i>	fluted kidneyshell	FC
<i>Quadrula cylindrica strigillata</i>	rough rabbitsfoot	FE SE
<i>Quadrula intermedia</i>	Cumberland monkeyface	FE SE
<i>Quadrula pustulosa pustulosa</i>	pimpleback	ST
<i>Quadrula sparsa</i>	Appalachian monkeyface	FE SE
<i>Toxolasma lividus</i>	purple lilliput	SE
<i>Tritogonia verrucosa</i>	pistolgrip	ST
<i>Truncilla truncata</i>	deertoe	SE
<i>Villosa fabalis</i>	rayed bean	FC EX
<i>Villosa perpurpurea</i>	purple bean	FE SE
<i>Villosa trabalis</i>	Cumberland bean	FE SE EX

KEY

FE - Federally Endangered SE - State Endangered

FT - Federally Threatened ST - State Threatened

FC – Candidate: FWS has enough information to list the species as threatened or endangered, but this action is precluded by other listing activities

EX - Believed to be extirpated in Virginia

References

- Ames, E. P. 2004. Atlantic cod stock structure in the Gulf of Maine. *Fisheries* 29(1):10-28.
- Anon. 2008. Freshwater mussel guidelines for Virginia. Joint White Paper: USFWS, Gloucester, VA and VDGIF, Richmond, VA. Last update: March 7, 2008. 13 pp.
- Ashley, K. W., and B. Buff. 1987. Food habits of flathead catfish in the Cape Fear River, North Carolina. *Proceeding of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 41:93-99.
- Atkinson, C. E. 1951. Feeding habits of adult shad (*Alosa sapidissima*) in fresh water. *Ecology* 32:556-557.
- Batsavage, C.F. and R.A. Rulifson. 1998. Life history aspects of the hickory shad (*Alosa mediocris*) in the Albemarle Sounds/Roanoke River watershed, North Carolina. Report to the North Carolina Marine Fisheries Commission, Fishery Resource Grant No. M6057, ICMR Contribution Series No. ICMR-98-02, Morehead City, North Carolina.
- Beamish, F. W. H., I. C. Potter, and E. Thomas. 1979. Proximate composition of the adult anadromous sea lamprey, *Petromyzon marinus*, in relation to feeding, migration and reproduction. *Journal of Animal Ecology* 48:1-19.
- Bell, J.C. and J.T. Nichols. 1921. Notes on the food of Carolina sharks. *Copeia* 1921 (92): 17-20.
- Blackwell, B. F., W. B. Krohn, and R. B. Allen. 1995. Foods of nestling double-crested cormorants in Penobscot Bay, Maine, USA: Temporal and Spatial Comparisons. *Colonial Waterbirds* 18(2):199-208.
- Blackwell, B. F., W. B. Krohn, N. R. Dube, and A. J. Godwin. 1997. Spring prey use by double-crested cormorants on the Penobscot River, Maine, USA. *Colonial Waterbirds* 20(1):77-86.
- Bowen, W. D., and G. D. Harrison. 1996. Comparison of harbor seal diets in two inshore habitats of Atlantic Canada. *Canadian Journal of Zoology* 74:125-135.
- Brown, J.J., J. Perillo, T.J. Kwak and R.J. Horwitz. 2005. Implications of *Pylodictis olivaris* (flathead catfish) introduction into the Delaware and Susquehanna drainages. *Northeastern Naturalist* 12(4):473-484.
- Buckel, J. A., D. O. Conover, N. D. Steinberg, and K. A. McKown. 1999. Impact of age-0 bluefish (*Poatomus saltatrix*) predation on age-0 fishes in the Hudson River estuary: evidence for density-dependent loss of juveniles striped bass (*Morone saxatilis*). *Canadian Journal of Fisheries and Aquatic Sciences* 56:275-287.

- Burbidge, R. G. 1974. Distribution, growth, selective feeding, and energy transformations of young-of-the-year blueback herring, *Alosa aestivalis* (Mitchill), in the James River, Virginia. Transactions of the American Fisheries Society 103:297-311.
- Cederholm, C. J., M. D. Kunze, T. Murota, and A. Sibatani. 1999. Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. Fisheries 24(10):6-15.
- Chittenden, M. E. 1972. Responses of young American shad, *Alosa sapidissima*, to low temperatures. Transactions of the American Fisheries Society 101:680-685.
- Chittenden, M. E. 1976. Weight loss, mortality, feeding, and duration of residence of adult American shad, *Alosa sapidissima*, in fresh water. Fishery Bulletin 74:151-157.
- Christensen, V., A. Beattie, C. Buchanan, H. Ma, S. J. D. Martell, R. J. Latour, D. Preikshot, M. B. Sigrist, J. H. Uphoff, C. J. Walters, R. J. Wood, and H. Townsend. 2009. Fisheries Ecosystem Model of the Chesapeake Bay: Methodology, Parameterization, and Model Explanation. U.S. Dep. Commerce, NOAA Tech. Memo. NMFS-F/SPO-106 (2009) 146 pp.
- Crecco, V. T., and M. M. Blake. 1983. Feeding ecology of coexisting larvae of American shad and blueback herring in the Connecticut River. Transactions of the American Fisheries Society 112:498-507.
- Crecco, V., T. Savoy, and L. Gunn. 1983. Daily mortality rate of larval and juvenile American shad (*Alosa sapidissima*) in the Connecticut River with changes in year-class strength. Canadian Journal of Fisheries and Aquatic Sciences 40:1719-1728.
- Crecco, V. A., and T. F. Savoy. 1984. Effects of fluctuations in hydrographic conditions on year-class strength of American shad (*Alosa sapidissima*) in the Connecticut River. Canadian Journal of Fisheries and Aquatic Sciences 41:1216-1223.
- Crecco, V. T., and T. F. Savoy. 1985. Effects of biotic and abiotic factors on growth and relative survival of young American shad, *Alosa sapidissima*, in the Connecticut River. Canadian Journal of Fisheries and Aquatic Sciences 42:1640-1648.
- Crecco, V., T. Savoy, and W. Whitworth. 1986. Effects of density-dependent and climatic factors on American shad, *Alosa sapidissima*, recruitment: a predictive approach. Canadian Journal of Fisheries and Aquatic Sciences 43:457-463.
- Creed, R. P. Jr. 1985. Feeding, diet, and repeat spawning of blueback herring, *Alosa aestivalis*, from the Chowan River, North Carolina. Fishery Bulletin, U.S. 83: 711-716.
- Dalton, C. M., D. Ellis, and D. M. Post. 2009. The impact of double-crested cormorant (*Phalacrocorax auritus*) predation on anadromous alewife (*Alosa pseudoharengus*) in south-central Connecticut, USA. Canadian Journal of Fisheries and Aquatic Sciences 66:177-186.
- Daniels, R. A., K. E. Limburg, R. E. Schmidt, D. L. Strayer, and R. C. Chambers. 2005. Changes in fish assemblages in the tidal Hudson River, New York. American Fisheries Society Symposium 45:471-503.

- Davis, J. R., and R. P. Cheek. 1966. Distribution, food habits, and growth of young clupeids, Cape Fear River System, North Carolina. D. J. Report F-16-R, North Carolina.
- Davis, B. M., and J. W. Foltz. 1991. Food of blueback herring and threadfin shad in Jocassee Reservoir, South Carolina. *Transactions of the American Fisheries Society* 120:605-613.
- Davis, J. P., and E. T. Schultz. 2009. Temporal shifts in demography and life history of an anadromous alewife population in Connecticut. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 1:90-106.
- Domermuth, R. B., and R. J. Reed. 1980. Food of juvenile American shad, *Alosa sapidissima*, juvenile blueback herring, *Alosa aestivalis*, and Pumpkinseed, *Lepomis gibbosus*, in the Connecticut River below Holyoke Dam, Massachusetts. *Estuaries* 3:65-68.
- Donaldson, J.R. 1969. Phosphorus budget of Iliama Lake, Alsask, as related to the cyclic abundance of sockeye salmon. Doctoral dissertation. University of Washington, Seattle, Washington.
- Durbin, A.G., S.W. Nixon, and C.A. Oviatt. 1979. Effects of the spawning migration of the alewife, *Alosa pseudoharengus*, on freshwater ecosystems. *Ecology* 60: 8-17.
- Edsall, T. A. 1964. Feeding by three species of fishes on the eggs of spawning alewives. *Copeia*. 1964:226-227.
- Garman G. C., and Macko S. A. 1998. Contribution of marine-derived organic matter to an Atlantic coast, freshwater, tidal stream by anadromous clupeid fishes. *Journal of the North American Benthological Society* 17: 277-285.
- Gartland, J., R. J. Latour, A. D. Halvorson, and H. M. Austin. 2006. Diet composition of young-of-year bluefish in the lower Chesapeake Bay and the coastal ocean of Virginia. *Transactions of the American Fisheries Society* 135:371-378.
- Grabe, S. A. 1996. Feeding chronology and habits of *Alosa spp.* (Clupeidae) juveniles from the lower Hudson River estuary, New York. *Environmental Biology of Fishes* 47:321-326.
- Greene, E. P., A. E. Greene, B. Freedman. 1981. Foraging behavior and prey selection by ospreys in coastal habitats in Nova Scotia, Canada. *In* *Biology and Management of Bald Eagles and Ospreys: Proceedings of the 1st International Symposium on Bald Eagles and Ospreys*, Montreal, 28-29 October 1981.
- Greene, K.E., J.L. Zimmerman, R.W. Laney, and J.C. Thomas-Blate. 2009. Atlantic coast diadromous fish habitat: A review of utilization, threats, recommendations for conservation, and research needs. *Atlantic States Marine Fisheries Commission Habitat Management Series No. 9*, Washington, D.C.
- Gregory, R. S., G. S. Brown, and G. R. Daborn. 1983. Food habits of young anadromous alewife, *Alosa pseudoharengus*, in Lake Ainslie, Nova Scotia. *Canadian Field-Naturalist* 97: 423-426.
- Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries* 25:15-21.

Alosine Species Team Background and Issues Briefs

- Guest, W. C., and R. W. Drenner. 1991. Relationship between feeding of blueback herring and the zooplankton community of a Texas reservoir. *Hydrobiologia* 209:1-6.
- Guier, C.R., L.E. Nichols, and R.T. Rachels. 1981. Biological investigation of flathead catfish in the Cape Fear River. Proceedings of the Annual Conference. Southeastern Association of Fish and Wildlife Agencies 35:607-621.
- Harris, J. E., R. S. McBride, and R. O. Williams. 2007. Life history of hickory shad in the St. Johns River, Florida. *Transactions of the American Fisheries Society* 136:1463-1471.
- Harris, J. E., and R. S. McBride. 2009. American shad feeding on spawning grounds in the St. Johns River, Florida. *Transactions of the American Fisheries Society* 138:888-898.
- Hartman, K. J., and F. J. Margraf. 2003. US Atlantic coast striped bass: issues with a recovered population. *Fisheries Management and Ecology* 10:309-312.
- Heimbuch, D. G. 2008. Potential effects of striped bass predation on juvenile fish in the Hudson River. *Transactions of the American Fisheries Society* 137:1591-1605.
- Hoffman, J. C., K. E. Limburg, D. A. Bronk, and J. E. Olney. 2008. Overwintering habitats of migratory juvenile American shad in Chesapeake Bay. *Environmental Biology of Fishes* 81:329-345.
- Hoffman, J.C., D.A. Bronk, and J.E. Olney. 2007. Contribution of allochthonous carbon to American shad production in the Mattaponi River, Virginia using stable isotopes. *Estuaries and Coasts* 30(6):1034-1048.
- Holland, B. F., and G. F. Yelverton. 1973. Distribution and biological studies of anadromous fishes offshore North Carolina. North Carolina Department of Natural and Economic Resources, Division of Commercial and Sport Fisheries, Special Scientific Report Number 24, Morehead City, North Carolina.
- Janssen, J. 1976. Feeding modes and prey size selection in alewife (*Alosa pseudoharengus*). *Journal of the Fisheries Research Board of Canada* 33:1972-1975.
- Janssen, J. 1978. Feeding-behavior repertoire of alewife, *Alosa pseudoharengus*, and ciscoes *Coregonus hoyi* and *Ciscoes artedii*. *Journal of the Fisheries Research Board of Canada* 35:249-253.
- Janssen, J., and S. B. Brandt. 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 37:177-184.
- Janssen, J., W. R. Jones, A. Whang, and P. E. Oshel. 1995. Use of the lateral line in particulate feeding in the dark by juvenile alewife (*Alosa pseudoharengus*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:358-363.
- Johnson, J. H., and D. S. Dropkin. 1995. Effects of prey density and short term food deprivation on the growth and survival of American shad larvae. *Journal of Fish Biology* 46:872-879.
- Johnson, J. H., and D. S. Dropkin. 1996. Feeding ecology of larval and juvenile American shad (*Alosa sapidissima*) in a small pond. *Journal of Applied Ichthyology* 12:9-13.

- Johnson, J. H., and D. S. Dropkin. 1997. Food and prey selection of recently released American shad (*Alosa sapidissima*) larvae. *Journal of Freshwater Ecology* 12:355-358.
- Johnson, J. H., and N. H. Ringler. 1995. Estimating losses to predation of recently released American shad larvae in the Juniata River, Pennsylvania. *North American Journal of Fisheries Management* 15:854-861.
- Johnson, J. H., and N. H. Ringler. 1998. Predator response to releases of American shad larvae in the Susquehanna River basin. *Ecology of Freshwater Fish* 7:192-199.
- Jessop, B. M. 1990. Diel variation in density, length composition, and feeding activity of juvenile alewife, *Alosa pseudoharengus* Wilson, and blueback herring, *A. aestivalis* Mitchell, at near-surface depths in a hydroelectric dam impoundment. *Journal of Fish Biology* 37:813-822.
- Juanes, F., R. E. Marks, K. A. McKown, and D. O. Conover. 1993. Predation by age-0 bluefish on age-0 anadromous fishes in the Hudson River Estuary. *Transactions of the American Fisheries Society* 122:348-356.
- Kahnle, A. W., and K. A. Hattala. 2007. Striped bass predation on adult American shad: occurrence and observed effects on American shad abundance in Atlantic coastal rivers and estuaries. American Shad Stock Assessment, Stock Assessment Report Number 07-01 (Supplement), VI, Section 5: 182-194. National Oceanic and Atmospheric Administration Award NA05NMF4741025.
- Leach, S. D., and E. D. Houde. 1999. Effects of environmental factors on survival, growth, and production of American shad larvae. *Journal of Fish Biology* 54:767-786.
- Leim, A.H. 1924. The life history of the shad (*Alosa sapidissima*) (Wilson) with special reference to the factors limiting its abundance. *Biological Board of Canada, Contributions to Canadian Biology* 2:163-284.
- Leim, A.H. and W.B. Scott. 1966. Fishes of the Atlantic coast of Canada. Fisheries Research Board of Canada, Ottawa. Bulletin No. 155:1-485.
- Leggett, W. C. 1972. Weight loss in American shad (*Alosa sapidissima*, Wilson) during the freshwater migration. *Transactions of the American Fisheries Society* 101:549-551.
- Levesque, R. C., and R. J. Reed. 1972. Food availability and consumption by young Connecticut River shad *Alosa sapidissima*. *Journal of the Fisheries Research Board of Canada* 29:1495-1499.
- Limburg, K. E. 1996. Growth and migration of 0-year American shad (*Alosa sapidissima*) in the Hudson River estuary: otolith microstructural analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 53:220-238.
- Loesch, J. G. 1987. Overview of life history aspects of anadromous alewife and blueback herring in freshwater habitat. *American Fisheries Society Symposium* 1:89-103.
- MacAvoy S. E., Macko S. A., McIninch S. P., Garman G. C. 2000. Marine nutrient contributions to freshwater apex predators. *Oecologia* 122: 568-573.

- MacAvoy, S. E., S. A. Macko, and G. C. Garman. 2001. Isotopic turnover in aquatic predators: quantifying the exploitation of migratory prey. *Canadian Journal of Fisheries and Aquatic Sciences* 58:923-932.
- MacNeill, D. B., and S. B. Brandt. 1990. Ontogenic shifts in gill-raker morphology and predicted prey capture efficiency of the alewife, *Alosa pseudoharengus*. *Copeia* 1:164-171.
- Mann, D. A., Z. M. Lu, M. C. Hastings, and A. N. Popper. 1998. Detection of ultrasonic tones and simulated dolphin echolocation clicks by a teleost fish, the American shad (*Alosa sapidissima*). *Journal of the Acoustical Society of America* 104:562-568.
- Massmann, W. H. 1963. Summer food of juvenile American shad in Virginia waters. *Chesapeake Science* 4:167-171.
- McBride, R. S., J. E. Harris, A. R. Hyle, and J. A. Holder. 2010. The spawning run of blueback herring in the St. Johns River, Florida. *Transactions of the American Fisheries Society* 139:598-609.
- McGrath, P.E. 2010. The life history of longnose gar, *Lepisosteum osseus*, an apex predator in the tidal waters of Virginia. PhD Thesis, College of William and Mary, Williamsburg, VA
- McCann, J. M. 2009. Maryland's freshwater mussels: a declining resource. *The Maryland Natural Resource*. 12(2): 7 – 9. Spring. Annapolis, MD.
- Moore, J.W., and D.E. Schindler. 2004. Nutrient export from freshwater ecosystems by anadromous sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal Fisheries and Aquatic Sciences* 61: 1582-1589.
- Moring J.R., and Mink L.H. (2002) Anadromous alewives, *Alosa pseudoharengus*, as prey for white perch, *Morone americana*. *Hydrobiologia* 479:125-130.
- Murauskas, J. G. 2006. Investigating the reproductive migration of adult hickory shad, *Alosa mediocris*. Master's Thesis. East Carolina University, Greenville, North Carolina.
- Murdy, E. O., R. S. Birdsong, and J. A. Musick. 1997. *Fishes of Chesapeake Bay*. Smithsonian Institution Press, Washington, D.C.
- Munroe, T. A. 2002. Herrings. Family Clupeidae. Pages 111-160 in B. B. Collette and G. Klein-MacPhee, editors. *Bigelow and Schroeder's Fishes of the Gulf of Maine* (3rd Ed.). Smithsonian Institution Press. Washington, D.C.
- Naiman, R.J., R.E. Bilby, D.E. Schindler, and J.M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* 5: 399-417.
- Nadeau, E. 2009. *Freshwater mussels and the Connecticut River Watershed*. Connecticut River Watershed Council, Greenfield, MA. Xvii+132 pp.
- Netzel, J., and E. Stanek. 1966. Some biological characteristics of blueback and alewife from Georges Bank, July and October, 1964. *International Commission for the North Atlantic Fisheries, Research Bulletin* 3:106-110.

- Neves, R. J. 1981. Offshore distribution of alewife, *Alosa pseudoharengus*, and blueback herring, *Alosa aestivalis*, along the Atlantic coast. *Fishery Bulletin, U.S.* 79 (3):473-485.
- Neves, R. J., and L. Depres. 1979. The oceanic migration of American shad, *Alosa sapidissima*, along the Atlantic coast. *Fishery Bulletin, U.S.* 77 (1):199-211.
- Odenkirk, J., and S. Owens. 2005. Northern snakeheads in the tidal Potomac River system. *Transactions of the American Fisheries Society* 134:1605-1609.
- Overton, A. S., C. S. Manooch III, J. W. Smith, and K. Brennan. 2008. Interactions between adult migratory striped bass (*Morone saxatilis*) and their prey during winter off the Virginia and North Carolina Atlantic coast from 1994 through 2007. *Fishery Bulletin* 106:174-182.
- Overton, A. S., F. J. Margraf, and E. B. May. 2009. Spatial and temporal patterns in the diet of striped bass in the Chesapeake Bay. *Transactions of the American Fisheries Society* 138:915-926.
- Pine, W. E. III., T. J. Kwak, D. S. Waters, and J. A. Rice. 2005. Diet selectivity of introduced flathead catfish in coastal rivers. *Transactions of the American Fisheries Society* 134:901-909.
- Plachta, D. T. T., and A. N. Popper. 2003. Evasive responses of American shad (*Alosa sapidissima*) to ultrasound stimuli. *Acoustic Research Letters Online* 4(2):25-30.
- Post, D. M., E. P. Palkovacs, E. G. Schielke, S. I. Dodson. 2008. Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology* 89:2019-2032.
- Post, D.M., and A.W. Walters. 2009. Nutrient excretion rates of anadromous alewives during their spawning migration. *Transactions American Fisheries Society*. 138: 264-268.
- Potter, I. C., and F. W. H. Beamish. 1977. Freshwater biology of adult anadromous sea lampreys *Petromyzon marinus*. *Journal of Zoology* 181:113-130.
- Richards, S. W. 1976. Age, growth, and food of bluefish (*Pomatomus saltatrix*) from east-central Long Island Sound from July through November 1975. *Transactions of the American Fisheries Society* 105:523-525.
- Ross, R. M., and T. W. H. Backman. 1992. Larval American shad: Effects of age and group size on swimming and feeding behavior. *Transactions of the American Fisheries Society* 121:508-516.
- Ross, R. M., R. M. Bennett, and J. H. Johnson. 1997. Habitat use and feeding ecology of riverine juvenile American shad. *North American Journal of Fisheries Management* 17:964-974.
- Rudershausen, P. J., J. E. Tuomikoski, J. A. Buckel, and J. E. Hightower. 2005. Prey selectivity and diet of striped bass in western Albemarle Sound, North Carolina. *Transactions of the American Fisheries Society* 134:1059-1074.
- Saloman, C. H. and S. P. Naughton. 1983. Food of king mackerel, *Scomberomorous cavalla*, from the southeastern United States including the Gulf of Mexico. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, Florida. NOAA Technical Memorandum NMFS-SEFC-126:1-25.

Alosine Species Team Background and Issues Briefs

- Savoy, T. F., and V. A. Crecco. 2004. Factors affecting the recent decline of blueback herring and American shad in the Connecticut River. *American Fisheries Society Monograph* 9:361-377.
- Scott, W.B. and E.J. Crossman. 1973. *Freshwater fishes of Canada*. Fisheries Research Board of Canada, Ottawa. Bulletin 184:1-966.
- Schindler, D. E., P. R. Leavitte, C. S. Brock, S. P. Johnson, and P. D. Quay. 2005. Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. *Ecology* 86:3225-3231.
- Simonin, P. W., K. E. Limburg, and L. S. Machut. 2007. Bridging the energy gap: anadromous blueback herring feeding in the Hudson and Mohawk Rivers, New York. *Transactions of the American Fisheries Society* 136:1614-1621.
- Snyder, B.D. 2005. The Susquehanna River fish assemblage: surveys, composition, and changes. *American Fisheries Society Symposium* 45:451-470.
- Stone, H. H., and G. R. Daborn. 1987. Diet of alewives, *Alosa pseudoharengus* and blueback herring, *A. aestivalis* (Pisces: Clupeidae) in Minas Basin, Nova Scotia, a turbid, macrotidal estuary. *Environmental Biology of Fishes* 19:55-67.
- Stone, H. H., and B. M. Jessop. 1994. Feeding habits of anadromous alewives, *Alosa pseudoharengus*, off the Atlantic Coast of Nova Scotia. *Fishery Bulletin* 92:157-170.
- Thompson, C. M., P. E. Nye, G. A. Schmidt, and D. K. Garcelon. 2005. Foraging ecology of bald eagles in a freshwater tidal system. *Journal of Wildlife Management* 69(2):609-617.
- Trent, L. and W.W. Hassler. 1966. Feeding behavior of adult striped bass, *Roccus saxatilis*, in relation to stage of sexual maturity. *Chesapeake Sci.* 7: 189-192.
- Tuomikoski, J. E., P. J. Rudershausen, J. A. Buckel, J. E. Hightower. 2008. Effects of age-1 striped bass predation on juvenile fish in western Albemarle Sound. *Transactions of the American Fisheries Society* 137:324-339.
- Viverette, C. B., G. C. Garman, S. P. McIninch, A. C. Makham, B. D. Watts, and S. A. Macko. 2007. Finfish-waterbird trophic interactions in tidal freshwater tributaries of the Chesapeake Bay. *Waterbirds* 30:50-62.
- Walburg, C. H. 1956. Observations on the food and growth of juvenile American shad, *Alosa sapidissima*. *Transactions of the American Fisheries Society* 86:302-306.
- Walter, J. F.III., and H. M. Austin. 2003. Diet composition of large striped bass (*Morone saxatilis*) in Chesapeake Bay. *Fishery Bulletin* 101:414-423.
- Walter, J. F. III., A. S. Overton, K. H. Ferry, and M. E. Mather. 2003. Atlantic coast feeding habits of striped bass: a synthesis supporting a coast-wide understanding of trophic biology. *Fisheries Management* 10:349-360.
- Walter, J. F., III, and J. E. Olney. 2003. Feeding behavior of American shad during spawning migration in the York River, Virginia. Pages 201-209 in K. E. Limburg and J. R. Waldman, editors.

- Biodiversity, Status, and Conservation of the World's Shads. American Fisheries Society Symposium 35, Bethesda, Maryland.
- Walters, A.W., R.T. Barnes, and D.M. Post. 2009. Anadromous alewives (*Alosa pseudoharengus*) contribute marine-derived nutrients to coastal stream food webs. *Canadian Journal Fisheries and Aquatic Sciences* 66:439-448.
- Warner, R. W., and S. C. Katkansky. 1970. An inflammatory lesion in an American shad, *Alosa sapidissima*. *Journal of the Fisheries Research Board of Canada* 27:191-193.
- West, D.C., A.W. Walters, S.R. Gephard, and D.M. Post. 2010. Nutrient loading by anadromous alewife (*Alosa pseudoharengus*): contemporary patterns and predictions for restoration efforts. *Canadian Journal of Fisheries and Aquatic Sciences* 67(8): 1211-1220
- Yako, L. A., M. E. Mather, and F. Juanes. 2000. Assessing the contribution of anadromous herring to largemouth bass growth. *Transactions of the American Fisheries Society* 129:77-88.
- Zydlewski, J., and S. D. McCormick. 1997. The loss of hyperosmoregulatory ability in migrating juvenile American shad, *Alosa sapidissima*. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2377-2387.

STOCK DYNAMICS

Alosine Stock Assessments History

Andrew Kahnle

Chesapeake Bay alosines have a long history of stock status investigations. Initial attempts to characterize stock status in the late 1800s and early 1900s focused on summary and evaluation of landings data. As data quality improved and fisheries theory and assessment science matured, assessments became increasingly sophisticated with the use of complex computer generated population models. Assessments have been conducted by biologists working for federal and state fisheries agencies, universities, and most recently the Atlantic States Marine Fisheries Commission (ASMFC). Most of the status assessments were made on stocks of American shad. A few assessments have been made on river herring and hickory shad. Most assessments have been made at the species and stock (river specific) level.

First records of periodic catch and effort data for alosines were collected by the US Fish Commission and the US Fishery Laboratory in Beaufort, NC and date back to the late 1800s and early 1900s (Manooch and Manooch 1988, Wolfe 2000). In Chesapeake Bay, weekly catch and effort data in commercial fisheries have been collected in Maryland waters by the state of Maryland since 1944 (Walburg 1955, Walburg and Sykes 1957) and by logbook in Virginia waters by the Virginia Institute of Marine Science since 1953 (Nichols and Massmann 1963). The Potomac River Fisheries Commission has recorded commercial landings by state since 1964 and by month, area, gear, and effort since 1976 (ASMFC 2007).

Hickory Shad

Kriete and Loesch (1976) reported that landings of hickory shad declined 56% between 1975 and 1976 in the York River and 93% between 1975 and 1976 in the Rappahannock River.

River Herring

Kriete and Loesch (1976) used catch-per-unit effort (CPUE) in various commercial gears to evaluate relative abundance of river herring in Virginia tributaries of Chesapeake Bay. Between 1967 and 1976, CPUE of river herring declined 91 % in the Rappahannock River and 87% in the Potomac River. CPUE of alewife and blueback herring in the Rappahannock River declined 92% and 97% during the same time period.

Crecco and Gibson (1990) evaluated the status of several blueback herring and alewife stocks between New Brunswick, Canada and North Carolina, USA using long term commercial catch and effort, age composition, and relative abundance data for juveniles and adults. The assessment developed stock specific estimates of maximum sustained yield (MSY) and exploitation rates (u) at MSY (u_{msy}) and at stock collapse (u_{coll}). These rates, termed benchmark exploitation rates, were then compared to recent estimates of u . Stocks were considered overfished if the observed u

exceeded u_{msy} and severely overfished if u exceeded u_{coll} . Stocks were considered fully exploited if u was within 75% of u_{msy} and partially exploited if u was less than 75% of u_{msy} .

Data were not available to directly estimate benchmark exploitation rates for Chesapeake Bay stocks and so these values were derived from the following analyses. In the first step, the assessment combined biomass per recruit (B/R) and yield per recruit (Y/R) from species specific (stocks combined) Thompson-Bell yield per recruit models with species and stock specific Shepherd stock recruitment relationships (S-R) for several stocks outside of the Chesapeake. Modeling identified MSY, F (instantaneous rates of fishing) at MSY, and F at stock collapse and determined species specific relationships between the slope of the S-R curve at the origin or alpha (α) and F at MSY and stock collapse. In the second step, estimates of alpha were developed for Chesapeake Bay blueback herring and alewife from life history based models. These alpha estimates were then used in the alpha- benchmark relationships to predict F at MSY and collapse. Benchmark F estimates were converted to estimates of u_{msy} and u_{coll} assuming a Type I fishery and an instantaneous rate of natural mortality of $M = 1.0$. A Type I fishery is one in which fishing mortality is assumed to occur at the start of the biological year and natural mortality occurs after fishing mortality ends. Results were $u_{msy} = 0.62$ and $u_{coll} = 0.75$ for alewife and $u_{msy} = 0.67$ and $u_{coll} = 0.81$ for blueback herring.

Crecco and Gibson (1990) developed estimates of recent instantaneous total mortality (Z) by catch curve analyses of age for alewife and blueback herring of the Nanticoke, Potomac, and Rappahannock Rivers. Since $Z = F + M$, estimates of current F were developed by subtracting $M = 1.0$ from Z . Estimates of F were then converted to u . Results for the Nanticoke, Potomac, and Rappahannock Rivers were $u = 0.49, 0.80,$ and 0.37 for alewife and $u = 0.24, 0.67,$ and 0.42 for blueback herring. Fishing rates for alewife stocks in the Potomac River exceeded u_{coll} , and this stock was considered severely overfished to the point of recruitment failure. Concurrent abundance indices for the stock had also declined. Fishing rates for Nanticoke River alewife and blueback herring of the Potomac River were within 75% of u_{msy} and the stocks were considered fully exploited. All of these stocks had also declined. Fishing rates for the Rappahannock River alewife and blueback herring and the Nanticoke River blueback herring were less than u_{msy} and these stocks were considered lightly exploited. Even so, alewife of the Rappahannock River were considered severely depleted because the alewife stock in this river had declined precipitously.

American Shad

During the 1950s, a series of studies were conducted by biologists working for the US Fish and Wildlife Service to determine status of shad populations in Chesapeake Bay. Walburg and Nichols (1967) reported on Bay-wide trends in harvest, Walburg (1955) reported on analyses of shad stocks in Maryland waters, Walburg and Sykes (1957) reported on stocks in the James and Potomac Rivers, and Nichols and Massmann (1963) reported on stocks in the York River. In general, these studies used tag release recapture methods combined with catch and effort data to estimate exploitation rate in various commercial fisheries, location specific population size, escapement, and the fraction of each population caught by defined units of effort (q). Where historical catch and effort data were available, they estimated historical population size and escapement. The authors also examined scales for descriptions of spawning history.

Walburg (1955) reported that commercial harvest of American shad from Chesapeake Bay declined from 19 million lbs in 1897 to less than 3 million lbs in 1941. Walburg (1955) estimated that exploitation rate in the Maryland part of Chesapeake Bay was $u = 0.52$ in 1952. Population estimates in 1944-1952 ranged from 1,800,539 lbs to 3,274,149 lbs. Walburg and Sykes (1957) estimated that in 1952 in the James River the exploitation rate was $u = 0.73$, the population size was 1,363,149 lbs, escapement was 369,186 lbs and the proportion of repeat spawning was 0.27. The authors further reported that exploitation rate and fraction repeat spawn in the Potomac River in 1952 were $u = 0.58$ and 0.17. Population estimates for the period of 1944 – 1952 ranged from 824,347 – 2364,908 lbs. Nichols and Massmann (1963) reported that in the York River (1953-1959), exploitation rates ranged from $u = 0.44$ to $u = 0.58$, population estimates ranged from 0.8 million pounds to 1.4 million pounds, and escapement varied from 0.4 million pounds to 0.7 million pounds. Fraction repeat spawn in York River shad (1957 – 1959) ranged from 0.23 to 0.45 in males and from 0.12 to 0.21 in females.

Gibson et al. (1988) combined stock specific Thompson-Bell biomass per recruit (B/R) and yield per recruit (Y/R) models with stock specific Shepherd stock-recruitment models for twelve Atlantic coastal stocks of American shad, including that in the Susquehanna River, to estimate maximum sustainable yield (MSY) and maximum sustainable fishing rate (Fmsy). Modeling used an assumed rate of natural mortality of $M = 0.8$. The authors also evaluated the relationship between these values and various life history and river characteristics. The authors found that MSY was correlated to river drainage area and Fmsy was correlated to latitude and flow variation. These relationships were then used to predict Fmsy for stocks from rivers without adequate data for a stock recruitment curve. Estimates of historical and current F were obtained from data on catchability (fraction of a fish stock caught by a unit of effort) and effort. Stock recruitment modeling of the Susquehanna River stock estimated that $MSY = 1,342,000$ lbs and $Fmsy = 0.7$. Estimates of mean F and harvest during the mid 1970s were $F = 0.942$ and 2,500,000 lbs suggesting that overfishing was occurring during that time. Predicted Fmsy for stocks in the Potomac, Nanticoke, Choptank, York, and James Rivers were 1.158, 0.985, 0.907, 1.231, and 1.280, respectively. Estimates of recent fishing rates were below these benchmarks for all of the rivers.

ASMFC (1998) examined catch and harvest data, exploitation rates, fish-lift counts, and current and historic in-river and coastal fishing rates, to evaluate stock status for selected rivers. The authors used a Thompson-Bell Y/R model to develop an overfishing definition of F30 for stocks of the Upper Bay in Maryland. F30 was defined as that rate of fishing that reduced the spawning stock biomass to 30% of that present with no fishing. Modeling assumed $M = 1.50$. The authors also examined trends in abundance and total mortality (Z) in the Upper Bay stock and trends in relative stock abundance using CPUE in the commercial fishery of the James, York, and Rappahannock Rivers. Effects of river and directed ocean harvest on stocks of Maryland and Virginia were evaluated by dividing in-river harvest and estimated stock specific losses to the ocean fishery by stock size for the stocks in the Upper Bay and by in-river commercial CPUE for Virginia Rivers. In the latter analyses, in-river CPUE were considered to reflect relative stock size.

ASMFC (1998) concluded that the mean fishing mortality (river and ocean) for stocks of the Upper Bay in the mid 1990s was $F = 0.12$. This was well under the overfishing definition of F30 = 0.43. Relative abundance of juvenile fish and estimates of adult abundance for the Upper Bay

stocks increased from 1980 through 1995. The authors concluded that the increased abundance resulted from factors in addition to increased introductions of hatchery produced larvae. Commercial CPUE declined in the York River, increased in the mid 1980s and then declined in the Rappahannock River, and varied without trend in the James River. The assessment concluded that there was no evidence that the fishing rates caused by ocean landings had increased and thus ocean landings did not appear to be the cause for the recent stock declines in the York or Rappahannock Rivers. Moreover, based on juvenile production, there was no evidence for recent recruitment failure in the Pamunkey or Mattaponi Rivers which are tributaries of the York River in Virginia.

ASMFC (2007) evaluated selected indices of abundance for age zero and mature American shad from various fishery-dependent and independent sample programs, passage at dams, age and size data, and estimates of total mortality (Z). The assessment also developed restoration targets for CPUE in fishery independent pound net sampling in the York, Rappahannock, and James Rivers and fishery dependent CPUE estimates for the existing pound net fishery of the Potomac River. CPUE targets were developed from historic landings and effort data. The assessment also developed a benchmark value for total mortality of $Z_{30} = 0.85$ using a Thompson-Bell yield-per-recruit model for the York River in Virginia. Z_{30} was defined as that rate of total mortality that reduced the spawning stock biomass to 30% of that present with no man-induced mortality. Modeling assumed that $M = 0.35$. Sensitivity analyses of the BPR modeling revealed that Z_{30} was influenced by M . Age variable inputs of M generally resulted in lower estimates of Z_{30} while Z_{30} increased with increasing M when using age invariant inputs of M .

The ASMFC (2007) assessment reported that access to American shad spawning habitat in the Susquehanna River was restricted by the construction of hydroelectric dams in the early 1900s. Overfishing likely impacted the stock as well. Fish lifts or ladders were added to the lowermost four mainstem dams starting in 1972. However, upstream passage efficiency has been low and downstream passage is through turbines or spill. The lowermost dam (Conowingo Dam) is at river mile 10. The current restoration goal for the Susquehanna stock of American shad is achievement of a spawning population of 2 million fish. Fish lift counts at Conowingo Dam and CPUE in the Conowingo dam tailrace recreational fishery increased from 1972 through 2002. Lift counts peaked at almost 200,000 fish, but have since declined. Millions of larvae are stocked annually to the Susquehanna River and tributaries. The high percent of adults from these stockings in fish lifted above Conowingo Dam suggest that the recent increase was a result of these introductions. Relative abundance of age zero American shad above the lower four dams generally correlated with stock abundance. Estimates of total mortality or Z have been generally higher than the Z_{30} benchmark and the cause needs to be determined.

The only tributary in the Maryland portion of Chesapeake Bay outside of the Susquehanna River with an abundance index for American shad was the Nanticoke River. The CPUE data from the Nanticoke River pound net fishery has trended up in the last few years, but may have been driven by stocking of hatchery produced larvae. Estimates of total mortality (Z) generally exceeded the benchmark level. Limited data suggests that stocks are very low in other Chesapeake Bay tributaries in Maryland. Baywide indices of age zero abundance in Maryland waters increased from the 1990s through about 2005. Indices have since declined.

Fishery-dependent CPUE in commercial pound nets, fishery-independent CPUE in gill net samples, and indices of age zero abundance in the Potomac River all increased strongly from the early 1980s through 2005. Estimates of total mortality (Z) have declined since 2002 and estimates have bracketed the benchmark Z_{30} estimates. CPUE estimates in the pound net fishery remain well under the benchmark (target) value of 13.6 pounds per net day.

Abundance and mortality data in Virginia were available for the York, Rappahannock, and James Rivers. Relative abundance of mature fish was measured by CPUE in fishery independent sampling by staked gill nets. Sampling was designed to mimic methodology of commercial fisheries and the indices were calculated using the area under the curve method (Olney and Hoenig 2001). Indices trended downward in the York River, but upward in the James and Rappahannock Rivers. Recent CPUE were below target for the James and York Rivers and above target for the Rappahannock River. Recent estimates of total mortality have generally exceeded the benchmark rates. All systems appear to have shown periodic recruitment failure. The James River stock appears to have been sustained by stocking of larval hatchery fish.

Anthropogenic Mortality

Bob Sadzinski

Human populations are increasing rapidly in the Chesapeake Bay watershed, and are estimated to increase by sixteen percent by 2030 (http://planning.maryland.gov/msdc/s3_projection.shtml accessed 14 October 2010). As the human population increases, so does its potential to negatively impact streams and rivers because new development occurs generally near freshwater streams.

There are presently only four significant stocks (Potomac, Susquehanna, Nanticoke, and Patuxent rivers) of American shad and likely hickory shad in Maryland's portion of the Chesapeake Bay, while river herring are found in all major river systems and in most tertiary streams with suitable water quality and flow. Based on commercial landings, empirical data and juvenile indices, the Nanticoke, Susquehanna, Choptank, Chester, Northeast and Potomac rivers, presently have spawning populations of river herring. These rivers are characterized by good water quality and suitable spawning habitat including no lower stream blockages. In contrast, western shore Maryland tributaries including the Bush, Patapsco and South rivers have poor water quality, the one exception being the Patuxent River which has marginal water quality.

In Virginia waters, three major rivers (Rappahannock, York and James) dominate the American shad runs, while little is known about hickory shad populations. River herring inhabit most streams but in-river juvenile production estimates have not been conducted.

One of the most significant sources of anthropogenic mortality for alosines is non-directed or ancillary mortality and includes dams with inadequate passage, turbine mortality and bycatch mortality. Dams also impact water flow and hydrodynamics (Richter and Thomas 2007), which can change migratory behavior as well as larval and juvenile development.

Delays due to inefficient passage is difficult to quantify because the sources of mortality from this include increased predation, bioenergetics costs resulting in possible losses of eggs or their viability and spawning delay resulting in absorbed eggs.

Quantifying losses due to fish passage is possible if baseline data is collected including number lifted, operation changes and stock size. However, the key to lifting alosines above structures is timely introduction to suitable spawning habitat and then allow timely outmigration with minimum lethal effects.

Sadzinski and Uphoff (2002, unpublished) have noted that Susquehanna River populations of American shad are significantly impacted by turbine mortality such that restoration cannot occur under current conditions. These authors have concluded that a significant change in upstream

efficiency occurred in the late 1990s whereby increased attractive flows resulted in a higher percentage of the stock relocated above dams and then to lethal downstream outmigration either through turbines or over dams during spill.

Table 1. Prioritized Listing of Dam Projects Considered For Removal or Fish Passage During 2004 – 2010 to Meet the New Fish Passage Goal

Jurisdiction	Name	Location	Watershed	Type	Miles Opened
Virginia	Brassfield Dam	Petersburg	Appomattox	Fish Lift	120
	Embrey Dam	Fredricksburg	Rappahannock	Removal	71
	Ashland Water Supply	Ashland	South Anna	Notch	28
	Ashland Mills	Ashland	South Anna	Fishway	9
	Woolen Mills	Charlottesville	Rivanna	Removal	22
	Ruffins Dam	Massaponax	Rappahannock	Removal	8
	Charles Lake Dam	Charles City	James	Fishway	3
				VA TOTALS	261 miles
Maryland	Octoraro	Octoraro	Susquehanna	Removal	19
	Barren Creek	Mardela Springs	Nanticoke	Fw-culvert	12
	Dorsey Run	Howard Co.	L. Patuxent	Removal	10
	Johnsons Pond	Salisbury	Wicomico	Fishway	8
	Chicowicomico	Vienna	Nanticoke	Fishway	8
	Mill Lane Dam	Elkton	Bohemia	Fishway	6
	CSX – Dorsey Run	Howard Co.	L. Patuxent	Fishway	1
				MD TOTALS	64 miles
Pennsylvania	Ironstone Mill	Lancaster Co.	Conestoga R.	Fw/remove?	24
	Unnamed Dam	Lancaster Co.	Conestoga R.	Removal	7
	Hershey Foods	Hershey	Swatara Cr.	Fishway	12
	City of Lebanon	Lebanon	Swatara Cr.	Notch	21
Pennsylvania	Black Dam	Newville	Conodoguinet	Removal	23
	Heishmans Mill	Newville	Conodoguinet	Fishway	6
	Catawissa Boro	Catawissa	Catawissa Cr.	Fishway	21
	Detters Mill	York Co.	W. Conewago	Removal	3
	Carson Long	Perry Co.	Shermans Cr.	Fishway	12
	Boy Scout Dam	Perry Co.	Shermans Cr.	Removal	5
	Chester Water	Chester	Octoraro Cr.	Fishway	14
	Int'l Paper Dam	Clinton Co.	Bald Eagle Cr.	Removal	14
	Marietta Water Co.	Marietta	Chickies Cr.	Removal	2
	Krieder Dam	Lancaster Co.	Chickies Cr.	Removal	3 (resident only)
	Trindle Spg.	Cumberland	Yellow Breeches	Removal	2 (resident only)
	S. Middletown	Cumberland	Yellow Breeches	Removal	4 (resident only)
	PADOT Dam	Columbia Co.	Fishing Cr.	Removal	27 (resident only)
	McCoys Dam	Centre Co.	Spring Cr.	Removal	2 (resident only)
	Siloam Dam	Adams Co.	Conococheague	Removal	12 (resident)
	University Dam	Adams Co.	Conococheague	Removal	3 (resident)
	Milesburg Dam	Centre Co.	Wallace Run	Removal	4 (resident)
	Picric Dam	Cameron Co.	Sinnemahoning	Removal	10 (resident)
	Yeagertown Mill	Mifflin Co.	Tea Creek	Removal	7 (resident)
				PA TOTALS	164 miles (migratory); 74 miles (resident)

Life History of Alosines Growth, Condition, and Reproduction

Rich McBride, Mike Hendricks, Bill Duffy, and Jake Kritzer

This chapter reviews and synthesizes information on the life history of alosines, emphasizing investigations of Chesapeake Bay populations, for use in ecosystem management. The three main elements of life history are growth, mortality, and reproduction. First, we review the overall process of growth, and then focus in more detail on its constituent elements of size and age, as well as the related characteristic of condition. Estimates of mortality rates and predation-induced mortality are reviewed in more detail elsewhere in this volume (see Assessment History, and Anthropogenic Mortality sections), but we briefly review stage-dependent sources of mortality to complement reviews of the other life history traits. Next, we examine the different dimensions of reproduction, including spawning grounds, spawning seasonality, sex ratio, spawning frequency, and egg production. Dispersal of early life stages and migration of the juveniles and adults are important traits affecting life history, but since these topics are treated elsewhere, we do not review them here. Finally, this chapter concludes with a synthesis of how growth, mortality, and reproduction interact synergistically to affect success of restoration efforts, recruitment dynamics, fishery policies, and other aspects of ecosystem-based management.

Growth

Somatic growth is the change in size of an individual over time. It begins at hatching, when alosine yolk-sac larvae are as small as 5 mm, and is especially rapid in the first year. After about 6 months, by the end of November, American shad grow to 60-119 mm total length (TL), blueback herring grow to 50-74 mm TL, and alewife grow to 60-84 mm TL (Hildebrand and Schroeder 1928). Data for juvenile hickory shad are scarce but they appear to grow faster and most individuals leave the estuary earlier (summer) than observed for the other alosines (Massmann 1953; Mansueti 1962). Most juvenile alosines spend their first winter outside estuaries, in nearshore continental shelf habitats (Milstein 1981; Fay et al. 1983), but at least some individuals overwinter in Chesapeake Bay at sizes > 60 mm and may even be found in the Bay the next winter at sizes > 140 mm (Hildebrand and Schroeder 1928; Mansueti 1962; Hoffman et al. 2008).

Growth may be habitat-specific. Hatchery-reared and wild American shad in the Susquehanna River grow considerably faster above dams than those found downstream in Chesapeake Bay (Fig. 1). The mean total length of American shad collected above Conowingo Dam in November and December, 1995-2000, was 129 mm with a maximum of 178 mm (N=1,339). Prior to this period, the largest juvenile American shad ever collected above Conowingo Dam was 211 mm, collected on 12/2/1986, a year when more than a dozen specimens over 200 mm were collected. These high growth rates above the dam may arise from lower densities and reduced intraspecific

competition (M. Hendricks, unpublished data). Density-dependent effects on growth have been suggested for juvenile American shad in the Connecticut River as well (Marcy 1976). Growth rates can vary between years and rivers in North Carolina (Fay et al. 1983), and, in the laboratory, temperature, pH, and prey levels influenced growth of American shad larvae (Johnson and Dropkin 1995; Leach and Houde 1999).

Despite these sources of growth variation, the sizes of overwintering juveniles are remarkably similar across a wide latitudinal range (29-45°N), at least for American shad (Walburg 1957; Conover 1990). Juveniles measured at the end of the growing season were generally 70-120 mm from Florida to Canada (Conover 1990). Conover (1990) pointed out that spawning begins much earlier in the south, often by 3-4 months. Therefore, fish at southern latitudes grow slower than fish at northern latitudes. Juvenile American shad of the Chesapeake Bay (~38°N) grow at a relatively slow rate, similar to that observed for Delaware Bay and more southern systems (Limburg et al. 2003). It has been proposed that this compensatory growth process – whereby fish are not growing at a physiological maximum at southern latitudes – is adaptive (Conover 1990). This can occur when there are mortality costs from fast growth, such as observed when silversides (*Menidia menidia*) that feed at higher rates are more vulnerable to predation because of the energetic demands of digestion (Lankford et al. 2001).

Age-1 or age-2 American shad are not typically found in bays because they have left for coastal waters (e.g., Nichols and Massman 1963, but see Hoffman et al. 2008), so sizes at these ages are rarely measured directly. Also, size estimates from fish collected in bays may not be representative of the migratory component of the stock. Nonetheless, it is apparent that growth in length slows in association with maturation, beginning at age-2. After maturation in the ocean, males and females return to spawn in freshwater rivers (Nichols and Massmann 1963; Fig. 2) and surplus energy is diverted from somatic to reproductive growth. Mature American shad are sexually dimorphic: females grow faster and attain larger sizes in the Susquehanna River (Fig. 2) and elsewhere (see [Size](#) below).

Growth data and model parameters are less available for other alosines. A preliminary growth curve of Chesapeake Bay hickory shad can be found in Mansueti (1962), and growth of hickory shad in Florida was reported by Harris et al. (2007). Unpublished growth data of Chesapeake Bay river herrings can be found in Lipton (1979), Travelstead (1980), and Fay et al. (1983). Published data exists from studies by Walsh et al. (2005) working in North Carolina, Marcy (1969) and Gahagan et al. (2010) working in Connecticut, and Messieh (1977) working in Canada.

Size

Size changes with growth over the life of an individual, but after accounting for this, there are well known differences in size between populations, sexes, and species. Hildebrand (1963, p. 296) reported historic size data across Chesapeake Bay: the average size of female American shad was under six pounds (about 57.5 cm; 22.75 in.), whereas the average size of males was about 3.5 pounds (about 50 cm; 20 in.). Nichols and Massmann (1963) reported similar, if slightly smaller, sizes of American shad in the York River during the 1957-59 seasons (mean female weight 3.2 lbs [1.45 kg], male weight 2.3 lbs [1.05 kg]). Size of American shad in the

Susquehanna River during 1995-2010 was also similar to these earlier reports but varied substantially among years (Fig. 3A, B).

All four Chesapeake Bay alosines vary considerably in maximum size (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953). American shad is the largest herring in the western North Atlantic Ocean (Waldman and Limburg 2003), growing as large as 30 inches (76 cm) and 12 pounds (5.4 kg). There is, however, a distinct latitudinal trend in adult sizes of American shad. Average sizes are approximately 50 cm in New England and Canada, whereas they are only approximately 40 cm in the Chesapeake Bay region and further south (Leggett and Carscadden 1978; McBride and Holder 2008).

Hickory shad are intermediate in size relative to American shad and the river herrings (Waldman and Limburg 2003). It grows to 18 inches (46 cm) and 2 pounds (0.9 Kg), although Hildebrand (1963; p. 321) notes that commercial catches in the Chesapeake Bay and at Beaufort, North Carolina, consisted mostly of fish between 12 and 15 inches (30-38 cm) in length. Hickory shad are also dimorphic, again with females larger than males (Harris et al. 2007; McBride and Holder 2008). In the Patuxent River during April and May, Mansueti (1962) reported a mean male size of 358 mm total length (range: 287-414) and a mean female size of 376 mm total length (range: 320-452).

Blueback herring and alewife are smaller still (Waldman and Limburg 2003). They grow to 15 in (38 cm) and 13 ounces (0.37 kg), but Hildebrand (1963) notes that the usual size of these river herrings is under 12 in (30 cm) and 0.5 pound (0.25 kg). Although some authors have noted a trend for larger river herring at higher latitudes, Loesch (1987) cautions that at least some of this trend is due to different methods for estimating size and age.

Age

Age composition of American shad in the York River system ranged from 2 to 8 years during 1957-1959 ($n = 1,555$) (Nichols and Massmann 1963). Tuckey and Olney (2010) report American shad ages up to 10 in the York ($n = 2,730$), James ($n = 1,911$), and Rappahannock ($n = 1,263$) rivers during 1998-2006, but the appearance of greater longevity in these recent years is likely an artifact of much larger sample sizes than aged by Nichols and Massmann (1963). Age composition of known-age (e.g., marked as larvae, recaptured as adults) American shad in the Lehigh River, Delaware Bay system, range from 3 to 9 years (Fig. 2).

As noted for growth data, age data is less available for other alosines. Published estimates from outside of the Chesapeake region indicate that hickory shad in Florida and river herrings in Connecticut live 7-8 years (Harris et al. 2007; Marcy 1969). However, unpublished studies of Chesapeake Bay populations show that alewife may live to 11 years and blueback herring live to 13 years (Lipton 1979; Travelstead 1980; Fay et al. 1983; Waldman and Limburg 2003).

Age is the basis for estimating growth rates, maturation, longevity, and demographic structure, but it has proven difficult to measure for alosines. Early work dates back to the 1920s (Borodin 1924), when scale ageing methods were widely being developed by fishery scientists (Lee 1920). Scale ageing methods are still widely used to age alosines (e.g., Baglinière et al. 2001), but more

and more studies are finding that otolith-based age estimates are more reliable (Lipton 1979; Travelstead 1980; McBride et al. 2005; LaBay and Lauer 2006; Harris et al. 2007; Duffy 2010).

Mixed results arose when the accuracy of a scale ageing method was measured for two populations of American shad. Cating (1953) developed a scale ageing method, which was validated by Judy (1961) using marked fish recaptured from the Connecticut River stock. However, successful validation of Cating's method did not occur using known-age fish from the Delaware River system (McBride et al. 2005). To explain these conflicting results, Duffy (2010) reported that the transverse grooves, which are key morphological landmarks used in Cating's method, are not consistently nor discretely aligned with each annulus, at least as first reported by Cating (1953; his Table 1). Duffy (2010) demonstrated this by using specimens from a wide latitudinal range: Merrimack River (MA) to St. Johns River (FL). He proposed instead an otolith ageing method that proved to be more accurate and precise than scale ageing results. These problems with ageing imply that estimates of growth rates, longevity, and demographic structure are, at the very least, less precise when using scales compared to what is possible with otoliths. More problematic, scales tend to underestimate the age of older fish and this can introduce a bias that precludes formulation of age-based stock assessments.

Condition

In addition to length- or weight-at-age metrics, the related characteristic of condition accounts for the bioenergetic status of a fish. Condition can be measured in several ways. Fulton's K , where $K = W \times L^{-3}$ (W = body weight, L = body length), can change dramatically for American shad during the spawning run. Fulton's K increases at the beginning of the spawning run, as the gonad develops fully during the migration to brackish and freshwater habitats, but then declines later in the spawning run as the fish spawns sequential batches of eggs. This is most dramatic for American shad, which do not feed adequately during the spawning run to replenish energy reserves (Walter and Olney 2003; Harris and McBride 2009). Harris and McBride (2009) estimated that American shad in the St. Johns River, Florida, lose 40-50% of their somatic weight, independent of gonad weight changes during the spawning run. Other alosines feed on the spawning grounds so their weight loss is not as significant (Harris et al. 2007; Simonin et al. 2007; McBride et al. 2010). This weight loss translates into significant energy loss. York River American shad consume about 30% of their energy reserves to migrate to the spawning grounds, spawn, and return to the sea (Glebe and Leggett 1981).

Condition can also be measured as the deviation from predicted mass. First, length (L) and weight (W) data are fitted to a population-specific allometric model, $\hat{W} = \alpha \times L^\beta$, and then relative condition (K_n) is calculated as $K_n = W / \hat{W}$ for each fish (Le Cren 1951). Using this condition estimator, significant deviations from unity occurred in some years, and were specifically lower than average during the years 1998-2001 for American shad caught at Conowingo Dam on the Susquehanna River (Fig. 3C). Fish with low K_n values are in poor condition, all other things being equal. The benefits for survival or egg production when fish are fatter or thinner are unknown, but presumably reflect the amount of energy in the ecosystem that can be assimilated by the fish and used as surplus energy (i.e., above that required for basic metabolism).

Mortality

Mortality rates affect demographic structure and longevity. Comprehensive reviews of sources and methods to calculate mortality are treated elsewhere in this volume (see Predation and Stock Assessment sections). Here, the source and effects of mortality in relation to specific life history stages are outlined briefly.

Among the early life stages (i.e., eggs, larvae, and young of the year), there are many environmental sources of mortality. For example, cold temperatures (< 16 C) were postulated to double American shad egg mortality in 1968 vs. 1967 in the Connecticut River (Marcy 1972, 1976). Spring rainstorms that produce dramatic, episodic high river discharge (i.e., spates) are associated with rapid drops in pH that can increase alosine egg mortality (Hendrey 1987; Klauda and Palmer 1987). Fishing mortality, which mostly affects mature fish, is an obvious anthropogenic source of mortality (Maki et al. 2002). There are also concerns about bycatch mortality or fishing on mixed-stocks of alosines in Chesapeake Bay or the Atlantic Ocean, and both will confound estimation of mortality by stock (Limburg et al. 2003; Hoenig et al. 2008; McBride and Holder 2008). Other anthropogenic sources of mortality that can operate at all life stages include entrainment by power plant cooling systems (Schubel et al. 1977), turbine mortality associated with hydropower facilities (Gibson and Myers 2003), and declining water quality (Chittenden 1976; Summers and Rose 1987).

Reproduction

Spawning Grounds

All four alosine species spawn in rivers and creeks of Chesapeake Bay (Mansueti 1962; Bilkovic et al. 2002a; Loesch 1987; O'Connell and Angermeier 1997). Details of spawning habitat suitability and preferences are found elsewhere (see Habitat Brief).

Spawning Seasonality

American shad populations spawn earliest in the south (Florida, December-March) and latest in the north (Canada, May-July) (Hildebrand and Schoeder 1928; Limburg et al. 2003). A similar pattern is evident for hickory shad (Harris et al. 2007). Latitudinal differences in spawning seasonality are driven by temperature. American shad spawning runs generally peak at 18 C, regardless of latitude (Leggett and Whitney 1972). Offshore concentrations of American shad follow similar isotherms (Dadswell et al. 1987).

In Chesapeake Bay, alosines spawn in aggregate throughout spring and early summer. Spawning by American shad occurs in March-May (Hildebrand 1963; Olney et al. 2001; Bilkovic et al. 2002b). Mansueti (1962) reported spawning by hickory shad in May and June; however, recent evidence indicates that hickory shad spawn in the Susquehanna River in April (M. Hendricks, Pennsylvania Fish and Boat Commission, unpublished data). Spawning by alewife occurs early, in February-April, compared to spawning by blueback herring, which occurs in April and May (Hildebrand and Schoeder 1928; O'Connell and Angermeier 1997).

Sex Ratio

For American shad, the relative proportion of males and females within a river is skewed during most of the spawning migration. Males dominate the early run and females can dominate the later part of the run (Chittenden 1975; McBride and Holder 2008). Males can dominate (53-58%) river herring runs (Fay et al. 1983).

Maturation

Before migrating to estuaries to run upriver to spawn, maturation of alosines occurs at sea. American shad first enter the Chesapeake Bay with maturing gonads, containing yolked oocytes, about a month before spawning begins (Olney et al. 2001). Very few mature females are < 4 years old (5-9%, Nichols and Massmann 1963; 0-4%, Tuckey and Olney 2010). Males, however, mature at a younger age so more young males (< 4 years) enter Virginia rivers (32-37%, Nichols and Massmann 1963). American shad age at first spawning (mode) was age 4 for both sexes when an active fishery was operating in the 1950s (Nichols and Massmann 1963). Age at first spawning (mode) has recently been higher, age 5, for females measured in Virginia rivers since a fishing moratorium was imposed in 1994 (Maki et al. 2001; Tuckey and Olney 2010).

Spawning Frequency

The number of lifetime spawning events can vary by latitude for American shad, which are iteroparous (spawn in multiple years) north of approximately Cape Hatteras and semelparous (spawn one year and die) in the south. Iteroparity has been demonstrated in the York River, with fish marked and later recaptured on the spawning grounds (Nichols 1960). Both male and female American shad can spawn up to four times in a lifetime in the York River (Nichols and Massmann 1963).

Spawning frequency can also vary within a season because American shad are batch spawners (Olney et al. 2001; Olney and McBride 2003). Hyle (2004) measured the length of the spawning season and the spawning rate (every 2-3 days) of American shad, estimating that the average female spawned 11-17 batches per season in the Mattaponi River. Harris et al. (2007) also observed batch spawning by hickory shad in Florida.

Annual Egg Production

Annual egg production has been incorrectly measured in many previous studies by counting the number of yolked oocytes in females caught below the spawning grounds (e.g., Nichols and Massmann 1963). American shad have asynchronous oocyte development, which means that the sizes of vitellogenic (yolked) oocytes do not form a discrete clutch, and new recruitment from previtellogenic stages can occur during the spawning season (Mylonas et al 1995; Olney et al. 2001). Thus, a single count of yolked oocytes prior to spawning (e.g., the determinate method of fecundity calculation) is likely to underestimate the number of eggs spawned during the spawning season. Furthermore, some American shad may migrate downstream after spawning with significant numbers of yolked oocytes still in the gonad, which become atretic and may be important as an energy source during the outmigration (Olney et al. 2001). For these reasons, annual egg production of American shad is best calculated as the product of batch fecundity and spawning frequency during the spawning period (e.g., the indeterminate method of calculating

annual fecundity; Murua et al. 2003). Using the indeterminate method to estimate annual fecundity, an average American shad can produce about 800,000 eggs annually (Hyle 2004; unpublished data), which is more than twice the previous estimate (~300,000; Leggett and Carscadden 1978) developed using the determinate method for estimating fecundity.

Synthesis

Life history traits of alosines have been well studied in some cases but poorly studied in others. American shad populations in several Virginia rivers have been repeatedly studied, often with complementary methods, over several decades. Nonetheless, recent investigations suggest the need to improve methods to age American shad or estimate its annual egg production (examples above). Studies of hickory shad have been so uncommon that questions about whether it was even anadromous persisted into the 1960s (Mansueti 1962). Despite these gaps in our knowledge, the aggregate knowledge about alosines is generally good compared to many fish groups because they are economically important, culturally valuable, and at least when they are in the river, fairly amenable to routine monitoring or even detailed research investigations.

One important message that emerges from this body of work is that life history traits are not invariant. Leggett and Carscadden's (1978) seminal work on life history adaptation of American shad across its latitudinal range demonstrates the plasticity of traits such as age, size, and egg production. They interpreted these results as evidence for the adaptive significance of homing by American shad, such that American shad return to spawn at a latitude at which their life history traits are adjusted to achieve peak lifetime fecundity. While this plasticity may be adaptive, allowing American shad to colonize rivers from Canada to Florida, it also means that life history traits are dynamic over evolutionary – and presumably ecological – time scales. Therefore, historic practices to enhance stock levels that involved moving spawning adults or fertilized eggs from one river to another are confounded by this inherent life history variation. If fish are adapted to a certain latitude, then moving them to another river, particularly outside of their natal estuarine system may introduce life history traits that are not adapted to the new habitat. For example, by successfully moving fish from southern rivers, where growth rates are slower, the outcome could be reduced yield of the enhanced stock (Conover 1998). Improvement of local spawning habitat, especially mitigation or restoration of the effects of dams, and reducing direct sources of mortality (i.e., targeted fishing, bycatch, lethal pollutants, invasive predators) are the most direct way to maintain genetic integrity of alosine stocks while increasing reproductive potential (Hendricks 2003; Weaver et al. 2003).

Although more research on specific life history traits is still needed, it appears that the most urgent need is to integrate life history information with respect to environmental or anthropogenic drivers. For example, modeling by Tuckey and Olney (2010) show that relatively minor differences in size, age, and maturity that exist between Virginia rivers can lead to significantly different population levels in those rivers (see also Tuckey 2009). They also observed that the dominant age at maturity (mode = age 5) is the age at full recruitment to the fishery, so they postulated that heavy fishing pressure on virgin females contributed to overfishing and the eventual moratorium on fishing in Chesapeake Bay in 1994.

Maki et al. (2002) looked at the same population of American shad and concluded that that maturation occurs earlier today than it did in the 1950s. Although maturing earlier is an

appropriate response for an individual fish – because it will increase the likelihood of successfully spawning before dying – this is not a good outcome for most fisheries. When size and age of maturity declines, it is typically associated with shorter and younger fish in the population, but such a restructured population has a lower reproductive potential than the original population (Beamish et al. 2006) and yields are lower (Law 2000). Declining trends in maximum size of several populations is evident for several populations of American shad and hickory shad (McBride and Holder 2008) as well as the river herrings (Schmidt et al. 2003; Davis and Schultz 2009; McBride et al. 2010). Most concerning is the possibility that the fastest-growing individuals may be removed from the population, leading to fishery-induced evolution of growth rates or maturation rates (ICES 2007; Brown et al. 2008). Another important area of integrative life history research is to understand how natural mortality during the first year can restructure alosine demographics and affect year class strength (Limburg 2001; Hoffman and Olney 2005).

A life history trait as simple as sex ratio could have significant implications on estimates of spawning stock biomass. Sex ratio is often assumed to be 1:1 in stock assessments, although this condition is difficult to verify with alosines and may not be true. It is evident that males spawn at smaller sizes and younger ages, but it is less clear if sperm limitation occurs or if spawning ratios can be behaviorally adjusted to optimize fertilization success. Extremely low number of females have been documented throughout alosine spawning runs which has raised concerns that some fishing gears, particularly gill nets, may select females and reduce their numbers on the spawning grounds (e.g., Williams and Bruger 1972; McBride and Holder 2008). Sex ratios that deviate from unity can lower estimates of stock productivity (Morgan 2008).

In sum, life history traits act in concert as populations decline or rebuild. Furthermore, the effects of life history traits, whether working individually or in combination, on the abundance, biomass, recruitment, size structure, age structure and sex ratio of alosine populations not only have important implications for single-species productivity, recovery and sustainability, but also for ecosystem processes as well. For example, fish of different sizes feed on different sizes and types of prey, and serve as prey to different sizes and types of predators. Also, there might be age-, size-, or sex-dependent difference in the timing of migration, duration of time spent in the spawning stream, and frequency of spawning. These differences can affect the function of alosines as vectors of carbon, nutrients and energy to freshwater systems (see Vectors chapter). Single life history traits may be simple proxies for status of some stocks, but a mechanistic understanding of how life history processes are affected by fishing and the environment, and in turn affect ecosystem dynamics, requires an integrated approach, which, in the long run, can better predict population responses within a context of ecosystem-based management of Chesapeake Bay.

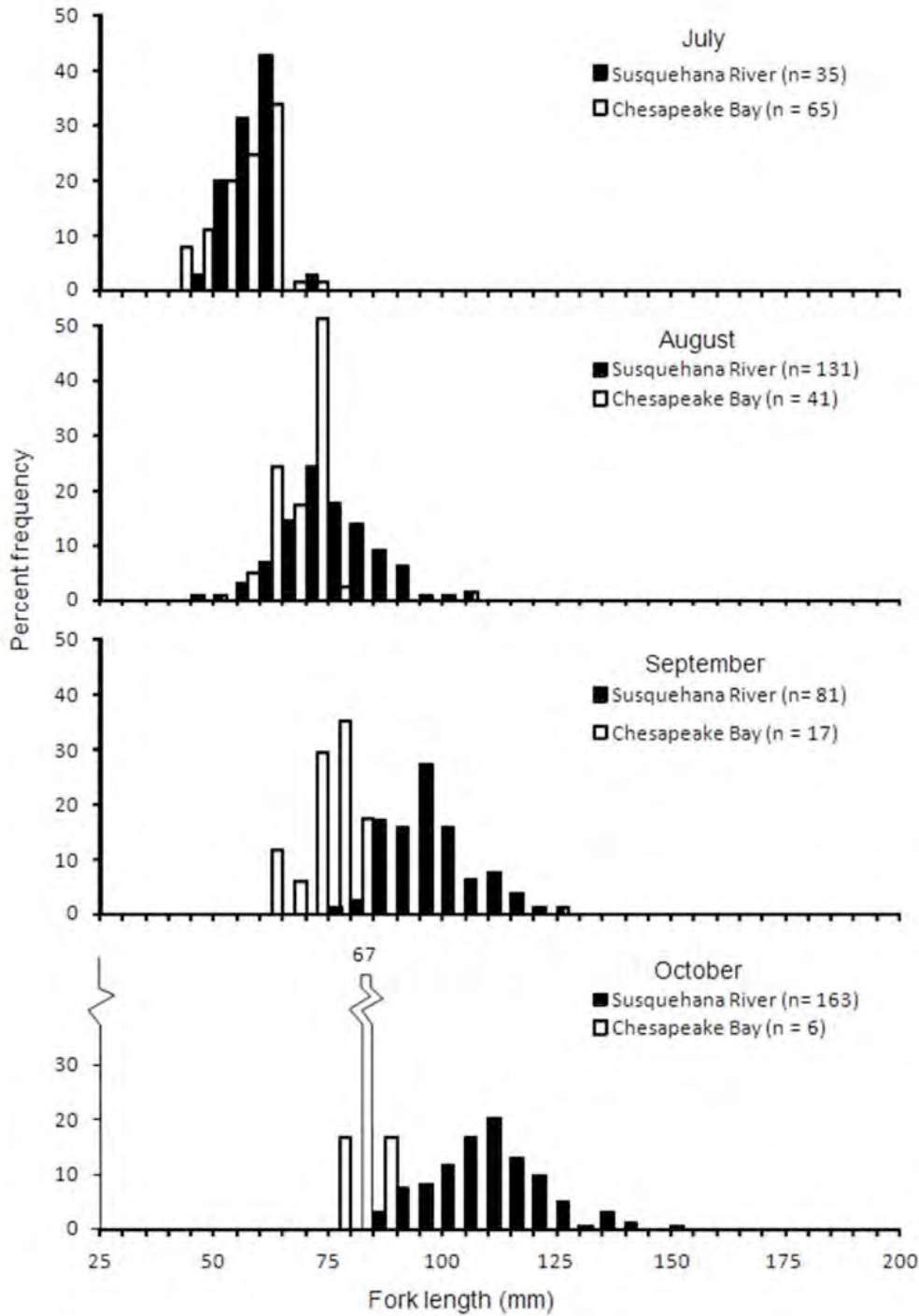


Figure 1. Percent length frequencies for juvenile American shad collected in the the Susquehanna River and Chesapeake Bay during July, August, September, and October, 1996. Number of fish = n. (Data source: M. Hendricks, Pennsylvania Fish and Boat Commission, unpublished data)

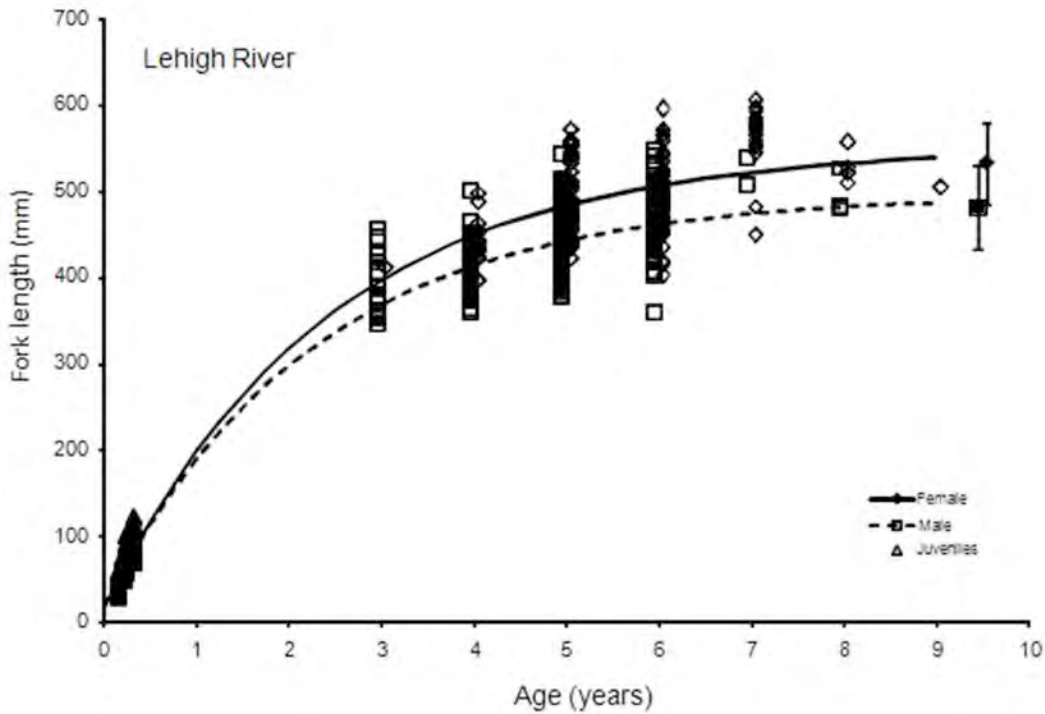


Figure 2. Size at age for known-age American shad from the Delaware Bay - Lehigh River system, Pennsylvania. Fish were marked as larvae and recaptured either as juveniles by seining in the autumn or as adults by electrofishing or with gill nets (see Hendricks et al. 1991, 2002; McBride et al. 2005). Individual fish were marked during the period 1995-2001. Size at capture (open symbols) and predicted size at age 8 (closed symbols \pm 95% confidence limits) are plotted together with predicted curves fitted using the von Bertalanffy growth equation (Data source: M. Hendricks, Pennsylvania Fish and Boat Commission, unpublished data).

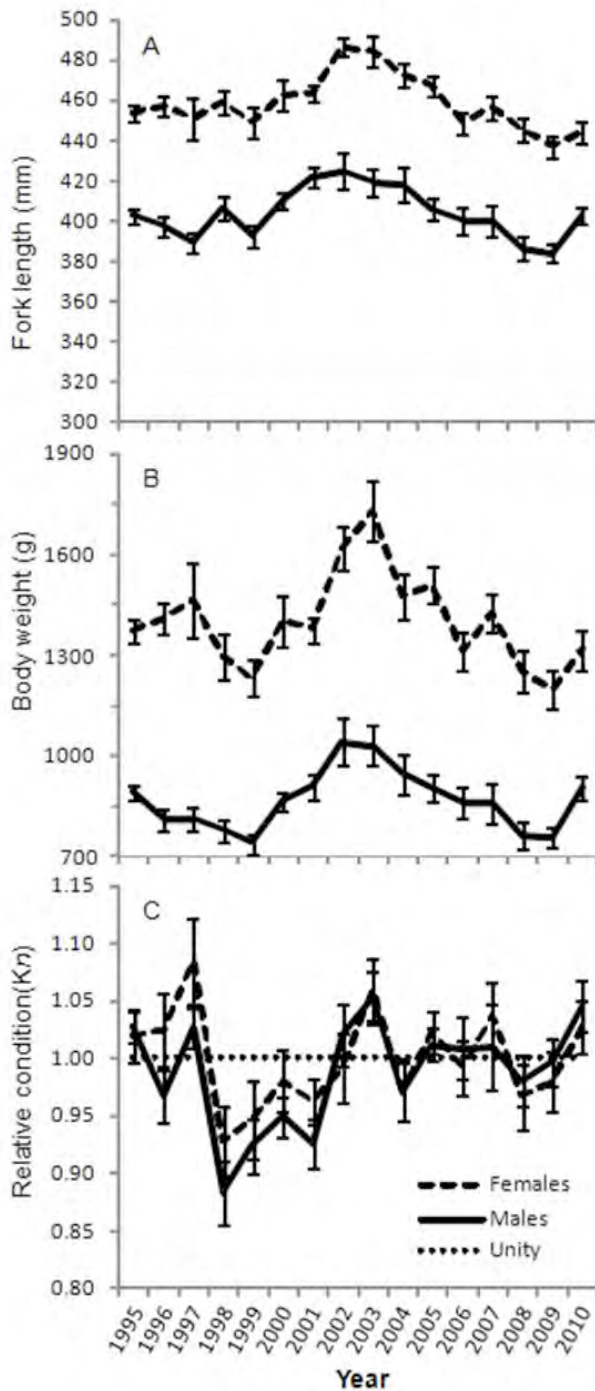


Figure 3. Annual mean (\pm 95% c.l.) size and condition of 1847 male and 1670 female American shad collected in the Susquehanna River, at the Conowingo Dam West Fish Lift, from 1995 to 2010. (A) Fork length in mm (males: 402 ± 31 [mean \pm s.d. for all years combined]; females: 459 ± 32). (B) Weight in g (males: 863 ± 221 ; females: 1406 ± 329). (C) Condition (K_n , males: 0.992 ± 0.126 ; K_n , females: 1.00 ± 0.147 see text for calculation of K_n) (Data source: M. Hendricks, Pennsylvania Fish and Boat Commission, unpublished data).

Connectivity and Stock Structure

Jake Kritzer

Alosine populations are defined by groups of inter-breeding spawners using the same freshwater habitat. Depending upon species and location, these spawning habitats can be large mainstem rivers, tributaries to those rivers, lower order coastal streams, headwater ponds or lakes, dammed impoundments along the course of a river, and even brackish tidal waters below impassable barriers. These spawning populations are actually sub-populations within larger metapopulations defined by riverine or estuarine watersheds, given that fish can and do stray among neighboring sub-populations (e.g., Paklovacs et al. 2008). Less frequent exchange among major watershed metapopulations must also occur to maintain minimal genetic homogeneity and prevent speciation (e.g., Walther et al. 2008). Therefore, multiple ecologically and demographically relevant metapopulations likely exist along the coast, nested within a larger evolutionarily significant coast-wide metapopulation (Jones 2006). The extent of interconnectedness varies between these scales, with important implications for conservation and management (Kritzer and Sale 2004).

There is limited information on alosines during their first winter after leaving freshwater systems. However, Brown et al. (2000), report that young-of-year alewives migrate from freshwater to overwintering grounds in the shallow nearshore areas of mid to high salinity levels, where fish from different sub-populations are likely to co-occur. Subsequently, fish migrate further offshore as they enter the second year of life where fish from along the entire coast share a common ocean environment (Neves 1981; Cournane and Correja 2010). During either of these life stages occurring outside of spawning grounds, fish will experience more similar environmental conditions and anthropogenic impacts, which can induce synchrony in population fluctuations that is less than those experienced by purely marine fish but greater than those experienced by purely freshwater fish (Myers et al. 1997).

Sharing estuarine and oceanic areas also allows the possibility of fish from different spawning populations schooling together, perhaps leading to some fish leaving their natal run and joining another. Social transmission of migratory behavior has been hypothesized as a mechanism for connectivity among Atlantic herring populations (McQuinn 1997). Little is known about the nature of oceanic migrations in alosines. However, tagging (Dadswell et al. 1987), distribution data (Neves 1981; Figure 1), and catch records (Klauda et al. 1991) all indicate that fish do not remain directly offshore of their natal rivers. Therefore, it is likely that some interactions do occur among spawning populations at sea, but the spatial scale over which populations form aggregations and exhibit common migratory behaviors is unknown. In the absence of oceanic interactions, straying might simply occur by accident, perhaps when chemical or other cues from a nearby river approximate those from a fish's natal river.

Regardless of the mechanism, the key attribute for conservation and management is the level of straying that results in significant ecological and demographic effects (e.g., substantial increase in local forage base for predators). Jones (2006) has argued that latitudinal variation in life history traits is the best indication of metapopulation structure among alosines. Life history variation is a product of inherent genetic differences developed over time through adaptation to local conditions, as well as plastic responses to environmental conditions and harvest, and indicates evolutionarily significant metapopulation structure. However, on smaller scales that are ecologically and demographically significant, life history traits are unlikely to provide sufficient resolution to distinguish fish from different natal origins since inter-populations variation will not be much greater than between-population variation over small scales. Instead, direct examination of genetic structure, independent of its expression as life history variation, coupled with approaches such as tagging and microchemical analysis, lends stronger insights into connectivity on an intra-watershed scale. Following is an overview of these types of data for the alosine species.

American Shad

Historically, American shad populations were estimated to occur in approximately 138 rivers across their native range. Today, only about half of these populations are extant (Limburg et al. 2003). Genetic and tagging evidence, in addition to independent fluctuations in abundance, all indicate that American shad form discrete populations that display the high homing fidelity typical of nearly all anadromous fishes (e.g., Leggett and Whitney 1972, Melvin et al. 1986).

Differences among American shad populations indicative of connectivity in the form of gene flow may be studied indirectly via phenotypic analysis or mark-recapture, or directly via genetic analysis. Much of what is known about large-scale migratory circuits, the annual timing of these movements, and the locations of wintering regions is the product of the ambitious mark-recapture program of Dadswell et al. (1987). In this study, American shad tagged in the Hudson River and New York Bight were mainly recaptured in the Hudson itself, but recoveries stretched from slightly south of Cape Hatteras, NC, to Halifax, NS, and in the Cumberland Basin in the upper Bay of Fundy. Melvin et al. (1986) tagged 5,074 adults in the Annapolis River, Nova Scotia, during the 1981 and 1982 spawning runs. They estimated a homing fidelity rate of 97%, based on 56 of 58 recaptures in fresh waters in subsequent years. Morphological differences as discriminators among American shad populations have received scant study. Some differences were seen in five meristic characters among four major northern populations (Carscadden and Leggett 1975). Although limited in scope, the low degree of overlap in population values was viewed as evidence that American shad show high homing behavior and, thus, occur as discrete stocks.

With the advent of mitochondrial DNA (mtDNA) analysis in the 1980s, two laboratories proceeded to characterize genetic variability among populations of American shad, those of P. Bentzen at McGill and Dalhousie University, and I. Wirgin at City College of New York and the New York University Medical Center. Although neither group included all possible extant populations, most of the major ones were included. In summary, significant ($P < 0.05$) differences among populations were found throughout the species' range (Bentzen et al. 1988, 1989; Nolan et al. 1991, Waldman et al. 1996).

Later, as analysis of nuclear DNA microsatellites emerged as a powerful alternative to mtDNA analysis, Waters et al. (2000) compared the results of both approaches to the same populations. Gene flow rates ($N_e m$) were estimated among three American shad populations (Hudson, James, Pamunkey) using several quantitative approaches. Values for $N_e m$ ranged between 3.9 and 71.2. Although these values are high for anadromous fishes, the authors concluded that American shad show significant but subtle differentiation and that straying among rivers is sufficient to permit only marginal population differentiation.

Along with other latitudinal differences in various life history characteristics that have been seen for American shad, Bentzen et al. (1989) found less heterogeneity among mtDNA haplotypes among southern than in northern populations. To explain this, they noted that the temperature window for spawning in northern rivers (~ 3 weeks) is considerably shorter than that in southern rivers (2-3 months). This abbreviated spawning season may result in less opportunity for straying among northern populations, which would result in genetic differences being maintained.

A non-genetic, phenotypic approach was recently used to estimate homing in American shad. Using geochemical signatures in shad otoliths, Walther et al. (2008) found that although most American shad spawning in Virginia's York River were homing to their natal river, there was much less fidelity to individual tributaries. They estimated that approximately 6% of the spawning adults in the York were strays from other rivers.

River Herring

One or both of alewives and blueback herring occur in the larger Atlantic rivers that support American shad. However, across their broad ranges they also occur in countless smaller systems. Nonetheless, these many populations have received little research that allows inferences on population connectivity.

Palkovacs et al. (2008) examined genetic variation among five populations of alewife in Connecticut coastal streams. Sequence analysis of the mitochondrial DNA control region and analysis of nuclear DNA microsatellites showed that these populations were generally not significantly differentiated from each other. Mean gene flow across these anadromous populations based on private alleles was $N_m = 3.11$. However, Chilakamarri (2005), using microsatellite analysis, showed moderate differentiation between an alewife population in a stream entering Long Island Sound in eastern Connecticut and another in a tributary to the Connecticut River.

Hickory Shad

There does not appear to be any information on the connectivity and stock structure of hickory shad populations. Though hickory shad distributions are similar to that of American shad in Chesapeake Bay, unit stocks have not been defined.

Potential Indicators, Reference Points, or Metrics

- *Reference points:*
 - Spawning run sizes
 - number of runs (in terms of creeks, streams, and rivers that are occupied)
 - demographics structure of spawners
 - juvenile recruitment indices
 - population connectivity

References

- ASMFC (Atlantic States Marine Fisheries Commission). 1998. American shad stock assessment peer review report. Atlantic States Marine Fisheries Commission, Washington, D.C.
- ASMFC. 2007. American shad stock assessment report for peer review. Stock Assessment Report No. 07-01 of the Atlantic States Marine Fisheries Commission, Washington, D.C.
- Baglinière, J. L., and 11 coauthors. 2001. Guide pour l'interprétation des écailles et l'estimation de l'âge chez les aloses (*Alosa* spp.) de la façade Atlantique-est et de la Méditerranée-ouest. Bulletin Français de la Pêche et de la Pisciculture 357/360:485-530.
- Beamish, R. J., G. A. McFarlane, and A. Benson. 2006. Longevity overfishing. Progress in Oceanography 68(2-4):289-302.
- Bentzen, P., W.C. Leggett, and G.G. Brown. 1988. Length and restriction site heteroplasmy in the mitochondrial DNA of American shad (*Alosa sapidissima*). Genetics 118:509-518.
- Bentzen, P., G.G. Brown, and W.C. Leggett. 1989. Mitochondrial DNA polymorphism, population structure, and life history variation in American shad (*Alosa sapidissima*). Canadian Journal of Fisheries and Aquatic Sciences 46:1446-1454.
- Bigelow, H. B. and W. C. Schroeder. 1953, Fishes of the Gulf of Maine. U. S. Fish and Wildlife Service Fishery Bulletin 74(53), 577 p.
- Bilkovic, D. M., C. H. Hershner, and J. E. Olney. 2002a. Macroscale assessment of American shad spawning and nursery habitat in the Mattaponi and Pamunkey Rivers, Virginia. North American Journal of Fisheries Management 22:1176-1192.
- Bilkovic, D. M., J. E. Olney, and C. H. Hershner. 2002b. Spawning of American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) in the Mattaponi and Pamunkey Rivers, Virginia. Fishery Bulletin, U. S. 100:632-40.
- Borodin, N. 1924. Age of shad (*Alosa sapidissima* Wilson) as determined by the scales. Transactions of the American Fisheries Society 54(1):178-184.
- Breder, C. M., Jr., and D. E. Rosen. 1966. Modes of Reproduction in Fishes. The Natural History Press, Garden City, NY.
- Brown, C. J., A. J. Hobday, P. E. Ziegler, and D. C. Welsford. 2008. Darwinian fisheries science needs to consider realistic fishing pressures over evolutionary time scales. Marine Ecology Progress Series 369:257-266.

Alosine Species Team Background and Issues Briefs

- Brown, S.K. K.R. Buja, S.H. Jury, M.E. Monaco and A Banner. 2000. Habitat Suitability Index Models for Eight Fish and Invertebrate Species in Casco and Sheepscot Bays, Maine. *North American Journal of Fisheries Management* 20: 408-435.
- Cating, J. P. 1953. Determining age of Atlantic shad from their scales. *Fishery Bulletin, U. S.* 54(85):187-199.
- Carscadden, J.E., and W.C. Leggett. 1975. Meristic differences in spawning populations of American shad, *Alosa sapidissima*: evidence for homing to tributaries in the St. John River, New Brunswick. *Journal of the Fisheries Research Board of Canada* 32:653-660.
- Chilakamarri, S. R. 2005. Genetic differentiation in alewife populations using microsatellite loci. Master's Thesis, Worcester Polytechnic Institute.
- Chittenden, M. E., Jr. 1975. Dynamics of American shad, *Alosa sapidissima*, runs in the Delaware River. *Fishery Bulletin, U.S.* 73(3):487-494.
- Chittenden, M. E., Jr. 1976. Present and historical spawning grounds and nurseries of American shad, *Alosa sapidissima*, in the Delaware River. *Fishery Bulletin, U. S.* 74(2):343-352.
- Conover, D. O. 1990. The relation between capacity for growth and length of growing season: evidence for the implications of countergradient variation. *Transactions of the American Fisheries Society* 119(3):416-430.
- Conover, D. O. 1998. Local adaptation in marine fishes: Evidence and implications for stock enhancement. *Bulletin of Marine Science* 62(2):477-493.
- Cournane, J. and S. Correia. 2010. Identification of river herring hotspots at sea using multiple fishery dependent and independent datasets. Report to the New England Fishery Management Council Atlantic Herring Plan Development Team. available at: http://www.mafmc.org/fmp/msb_files/Cournane__Correia_NEFMC_Herring_PDT_identification_RH_hotspots_08_2010.pdf
- Crecco, V. A. and M. Gibson. 1990. Stock Assessment of river herring from selected Atlantic coast rivers. Special Report No. 19 of the Atlantic States Marine Fisheries Commission.
- Dadswell, M. J., G. D. Melvin, P. J. Williams, and D. E. Themelis. 1987. Influences of origin, life history, and chance on the Atlantic coast migration of American shad. *American Fisheries Society Symposium* 1:313-330.
- Davis, J. P., and E. T. Schultz. 2009. Temporal shifts in demography and life history of an anadromous alewife population in Connecticut. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 1(1):90-106.
- Duffy, W. 2010. An analysis of the current method of ageing American shad *Alosa sapidissima* with a new validated method using otoliths. Master of Science Thesis. University of Massachusetts, Dartmouth, Massachusetts.
- Fay, C. W., R. J. Neves, and G. Pardue. 1983. Alewife/blueback herring. *Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Mid-Atlantic)*. United States Fish & Wildlife Service, Division of Biological Services, FWS/OBS-82/11.9. U.S. Army

- Corps of Engineers, TR EL-82-4:25 pp (<http://www.nwrc.usgs.gov/wdb/pub/species_profiles/82_11-009.pdf>, Accessed: October 26, 2010).
- Gahagan, B. I., K. E. Gherard, and E. T. Schultz. 2010. Environmental and endogenous factors influencing emigration in juvenile anadromous alewives. *Transactions of the American Fisheries Society* 139(4):1069-1082.
- Gibson, A. J. F., and R. A. Myers. 2003. A statistical, age-structured, life-history-based stock assessment model for anadromous *Alosa*. *Biodiversity, Status, and Conservation of the World's Shads. American Fisheries Society Symposium* 35:275-283.
- Gibson, M. R., V. A. Crecco, and D. L. Stang. 1988. Stock assessment of American shad from selected Atlantic coast rivers. Atlantic States Marine Fisheries Commission. Special Report No. 15.
- Glebe, B. D., and W. C. Leggett. 1981. Latitudinal differences in energy allocation and use during the freshwater migrations of American shad (*Alosa sapidissima*) and their life history consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 38:806-820.
- Harris, J. E., and R. S. McBride. 2009. American shad feeding on spawning grounds in the St. Johns River, Florida. *Transactions of the American Fisheries Society* 138:888-898.
- Harris, J. E., R. S. McBride, and R. O. Williams. 2007. Life history of hickory shad in the St. Johns River, Florida. *Transactions of the American Fisheries Society* 136:1463–1471.
- Hendrey, G. R. 1987. Acidification and anadromous fish of Atlantic estuaries. *Water, Air, & Soil Pollution* 35(1):1-6.
- Hendricks, M. L., T. R. Bender, and V. A. Mudrak. 1991. Multiple marking of American shad otoliths with tetracycline antibiotics. *North American Journal of Fisheries Management* 11(2):212-219.
- Hendricks, M. L., R. L. Hoopes, D. A. Arnold, and M. L. Kaufmann. 2002. Homing of Hatchery-Reared American Shad to the Lehigh River, a Tributary to the Delaware River. *North American Journal of Fisheries Management* 22(1):243-248.
- Hendricks, M. L. 2003. Culture and transplant of Alosines in North America. *Biodiversity, Status, and Conservation of the World's Shads. American Fisheries Society Symposium* 35:303-312
- Hildebrand, S. F. 1963. Family Clupeidae. Pages 257-454 *in* *Fishes of the Western North Atlantic. Part Three. Number 1.* Sears Foundation for Marine Research, Yale University, New Haven.
- Hildebrand, S. F., and W. C. Schroeder. 1928. *Fishes of Chesapeake Bay.* Bulletin of the United States Bureau of Fisheries XLIII(Part 1):1-388.
- Hildebrand, S.F. 1963. Family Engraulidae. Pages 152-249 *in* Y. H. Olsen, ed. *Fishes of the Western North Atlantic, Part 3.* Memoir Sears Foundation for Marine Research.
- Hoenig, J. M., R. J. Latour, and J. E. Olney. 2008. Estimating stock composition of anadromous fishes from mark-recovery data: Possible application to American shad. *North American Journal of Fisheries Management* 28:507–515.

Alosine Species Team Background and Issues Briefs

- Hoffman, J. C., K. E. Limburg, D. A. Bronk, and J. E. Olney. 2008. Overwintering habitats of migratory juvenile American shad in Chesapeake Bay. *Environmental Biology of Fishes* 81(3):329-345.
- Hoffman, J. C., and J. E. Olney. 2005. Cohort-specific growth and mortality of juvenile American shad in the Pamunkey River, Virginia. *Transactions of the American Fisheries Society* 134(1):1-18.
- Hyle, A. R. 2004. Reproductive biology of American shad, *Alosa sapidissima*, in the Mattaponi River. Master of Science Thesis. College of William and Mary:vii, 88 leaves.
- ICES. 2007. Report of the study group on fisheries induced adaptive change (SGFIAC). ICES CM 2007/RMC:03:19 pp (<<http://www.ices.dk/reports/SSGSUE/2009/SGFIAC09.pdf>>, Accessed: October 26, 2010).
- Johnson, J. H., and D. S. Dropkin. 1995. Effects of prey density and short term food deprivation on the growth and survival of American shad larvae. *Journal of Fish Biology* 46:872-879.
- Jones, C.M. 2006. Estuarine and diadromous fish metapopulations. Page 119-154 in J.P. Kritzer and P.F. Sale, editors. *Marine Metapopulations*. Academic Press, San Diego, California.
- Judy, M. H. 1961. Validity of age determination from scales of marked American shad. *Fishery Bulletin*, U. S. 61:161-170.
- Klauda, R. J., and R. E. Palmer. 1987. Responses of blueback herring eggs and larvae to pulses of acid and aluminum. *Transactions of the American Fisheries Society* 116(4):561-569.
- Klauda, R. J., S. A. Fischer, L. W. Hall, Jr., and J. A. Sullivan. 1991. American shad and hickory shad. Pages 9.1-9.27 in S. L. Funderburk, J. A. Mihursky, S. J. Jordan, and D. Riley, editors. *Habitat requirements for Chesapeake Bay living resources*, 2nd edition. Chesapeake Bay Program, Living Resources Subcommittee, Annapolis, Maryland.
- Kriete, W. H., Jr. and J. G. Loesch. 1976. Status and distribution of Alosine stocks in Chesapeake Bay. Pp 47 – 104. IN. *Proceedings of a workshop on American shad*, 14-16 Dec, 1976, Amherst, MA.
- Kritzer, J.P. and P.F. Sale. 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish and Fisheries* 5: 131-140.
- LaBay, S. R., and T. E. Lauer. 2006. An evaluation of the accuracy of age estimation methods for southern Lake Michigan alewives. *North American Journal of Fisheries Management* 26:571-579.
- Lankford, T. E., J. M. Billerbeck, and D. O. Conover. 2001. Evolution of intrinsic growth and energy acquisition rates. II. Trade-offs with vulnerability to predation in *Menidia menidia*. *Evolution* 55(9):1873-1881.
- LaPointe, D. F. 1957. Age and growth of the American shad, from three Atlantic coast rivers. *Transactions of the American Fisheries Society* 87:139-150.
- Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* 57:659-668.
- Leach, S. D., and E. D. Houde. 1999. Effects of environmental factors on survival, growth, and production of American shad larvae. *Journal of Fish Biology* 54:767-786.

- Le Cren, E. D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *Journal of Animal Ecology* 20(2):201-219.
- Lee, R. M. 1920. A review of the methods of age and growth determination in fishes by means of scales. *Fish. Inv. Ser. II* 4(2):1-32.
- Leggett, W. C., and J. E. Carscadden. 1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): Evidence for population specific life history strategies in fish. *Journal of the Fisheries Research Board of Canada* 35:1469-1478.
- Leggett, W. C., and R. R. Whitney. 1972. Water temperature and the migrations of American shad. *Fishery Bulletin, U. S.* 70(3):659-670.
- Limburg, K. E. 2001. Through the gauntlet again: demographic restructuring of American shad by migration. *Ecology* 82(6):1584-1596.
- Limburg, K. E., K. A. Hattala, and A. Kahnle. 2003. American shad in its native range. Biodiversity, Status, and Conservation of the World's Shads. *American Fisheries Society Symposium* 35:125-140.
- Lipton, D. W. 1979. Comparison of scales and otoliths for determining age and growth of the alewife (*Alosa pseudoharengus*, *Wilson*). Master of Science Thesis. College of William and Mary, Williamsburg, Virginia, USA.
- Loesch, J. G. 1987. Overview of life history aspects of anadromous alewife and blueback herring in freshwater habitats. *American Fisheries Society Symposium* 1:89-103.
- Maki, K. L., J. M. Hoenig, and J. E. Olney. 2001. Estimating proportion mature at age when immature fish are unavailable for study, with application to American shad in the York River, Virginia. *North American Journal of Fisheries Management* 21:703-716.
- Maki, K. L., J. M. Hoenig, and J. E. Olney. 2002. Interpreting maturation data for American shad in the presence of fishing mortality: a look at historical data from the York River, Virginia. *North American Journal of Fisheries Management* 22:1209-1217.
- Manooch, C.M., III and A. Manooch. 1988. History of the Federal Fisheries Laboratory at Beaufort, NC. *Marine Fisheries Review* 50(4):72-76.
- Mansueti, R. J. 1962. Eggs, larvae, and young of the hickory shad, *Alosa mediocris*, with comments on its ecology in the estuary. *Chesapeake Science* 3(3):173-205.
- Marcy, B. C., Jr. 1969. Age determinations from scales of *Alosa pseudoharengus* (Wilson) and *Alosa aestivalis* (Mitchill) in Connecticut waters. *Transactions of the American Fisheries Society* 98(4):622-630.
- Marcy, B. C., Jr. 1972. Spawning of American shad, *Alosa sapidissima*, in the lower Connecticut River. *Chesapeake Science* 13(2):116-119.

- Marcy, B. C., Jr. 1976. Early life history studies of American shad in the lower Connecticut River and the effects of the Connecticut Yankee Plant. The Connecticut River ecological study: the impact of a nuclear power plant. American Fisheries Society Monograph No. 1:141-168.
- Massmann, W. H. 1953. Relative abundance of young fishes in Virginia estuaries. Transactions of the Eighteenth North American Wildlife Conference 18:439-449.
- McBride, R. S., J. E. Harris, A. R. Hyle, and J. C. Holder. 2010. The spawning run of blueback herring in the St. Johns River, Florida. Transactions of the American Fisheries Society 139(2):598-609.
- McBride, R. S., M. L. Hendricks, and J. E. Olney. 2005. Testing the validity of Cating's (1953) method for age determination of American shad using scales. Fisheries 30(10):10-18.
- McBride, R. S., and J. C. Holder. 2008. A review and updated assessment of Florida's anadromous shads: American shad and hickory shad. North American Journal of Fisheries Management 28(6):1668-1686.
- McQuinn, I.H. 1997. Metapopulations and the Atlantic herring. Reviews in Fish Biology and Fisheries 7: 297-329.
- Melvin, G.D., M.J. Dadswell, and J.D. Martin. 1986. Fidelity of American shad, *Alosa sapidissima* (Clupeidae), to its river of previous spawning. Canadian Journal of Fisheries and Aquatic Sciences 43:640-646.
- Messieh, S. N. 1977. Population structure and biology of alewives (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) in the Saint John River, New Brunswick. Environmental Biology of Fishes 2(3):195-210.
- Milstein, C. B. 1981. Abundance and distribution of juvenile *Alosa* species off southern New Jersey. Transactions of the American Fisheries Society 110:306-309.
- Morgan, M. J. 2008. Integrating reproductive biology into scientific advice for fisheries management. Journal of Northwest Atlantic Fishery Science 41:37-51.
- Murua, H., and 5 coauthors. 2003. Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. Journal of Northwest Atlantic Fishery Science 33:33-54.
- Myers, R.A., G. Mertz, and J. Bridson. 1997. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. Canadian Journal of Fisheries and Aquatic Sciences 54: 1400-1407.
- Mylonas, C. C., Y. Zohar, B. M. Richardson, and S. P. Minkinen. 1995. Induced spawning of wild American shad *Alosa sapidissima* using sustained administration of gonadotropin-releasing hormone analog (GnRH_a). Journal of the World Aquaculture Society 26(3):240-251.
- Neves, R.J. 1981. Offshore distribution of alewife, *Alosa pseudoharengus*, and blueback herring, *Alosa aestivalis*, along the Atlantic coast. Fishery Bulletin 79: 471-485.
- Nichols, P. R. 1960. Homing tendency of American shad, *Alosa sapidissima*, in the York River, Virginia. Chesapeake Science 1:200-201.

- Nichols, P. R., and W. H. Massmann. 1963. Abundance, age, and fecundity of shad, York River, Virginia, 1953-59. *Fishery Bulletin, U. S.* 63(1):179-187.
- Nolan, K., J. Grossfield, and I. Wirgin. 1991. Discrimination among Atlantic coast populations of American shad (*Alosa sapidissima*) using mitochondrial DNA. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1724-1734.
- O'Connell, A. M., and P. L. Angermeier. 1997. Spawning location and distribution of early life stages of alewife and blueback herring in a Virginia stream. *Estuaries* 20(4):779-791.
- Olney, J. E., S. C. Denny, and J. M. Hoenig. 2001. Criteria for determining maturity stage in female American shad, *Alosa sapidissima*, and a proposed reproductive cycle. *Bulletin Francais de la Peche et de la Pisciculture* 362/363:881-901.
- Olney, J. E., and J. M. Hoenig. 2001. Managing a fishery under moratorium: Assessment opportunities for Virginia's stocks of American shad. *Fisheries* 26:6-12.
- Olney, J. E., and R. S. McBride. 2003. Intraspecific variation in batch fecundity of American shad: revisiting the paradigm of reciprocal latitudinal trends in reproductive traits. *Biodiversity, Status, and Conservation of the World's Shads. American Fisheries Society Symposium* 35:185-192.
- Palkovacs, E.P., K.B. Dion, D. M. Post, and A. Caccone. 2008. Independent evolutionary origins of landlocked alewife populations and rapid parallel evolution of phenotypic traits. *Molecular Ecology* 17:582-597.
- Richter, B. D., and Thomas, G. A. 2007. Restoring environmental flows by modifying dam operations. *Ecology and Society* 12(1):12
- Schmidt, R. E., B. M. Jessop, and J. E. Hightower. 2003. Status of river herring stocks in large rivers. *Biodiversity, Status, and Conservation of the World's Shads. American Fisheries Society Symposium* 35:171-184.
- Schubel, J. R., C. F. Smith, and T. S. Y. Koo. 1977. Thermal effects of power plant entrainment on survival of larval fishes: a laboratory assessment. *Chesapeake Science* 18(3):290-298.
- Simonin, P. W., K. E. Limburg, and L. S. Machut. 2007. Bridging the energy gap: Anadromous blueback herring feeding in the Hudson and Mohawk Rivers, New York. *Transactions of the American Fisheries Society* 136(6):1614-1621.
- Summers, J. K., and K. A. Rose. 1987. The role of interactions among environmental conditions in controlling historical fisheries variability. *Estuaries* 10(3):255-266.
- Travelstead, J. G. 1980. Age determination and growth of the blueback herring, *Alosa aestivalis*. Master of Science Thesis. College of William and Mary, Williamsburg, Virginia. USA.
- Tuckey, T. D. 2009. Variability in juvenile growth, mortality, maturity, and abundance of American shad and blueback herring in Virginia. Ph. D. Dissertation. The College of William and Mary:202.
- Tuckey, T. D., and J. E. Olney. 2010. Maturity schedules of female American shad vary at small spatial scales in Chesapeake Bay. *North American Journal of Fisheries Management* 30:1020-1031.

- Walburg, C. H. 1955. Relative abundance of Maryland shad 1944-1952. U. S. Fish and Wildlife Service. Research Report 38. 17 pp.
- Walburg, C. H. and J. E. Sykes. 1957. Shad fishery of Chesapeake Bay with special emphasis on the fishery of Virginia. US Fish and Wildlife Research Report 48, 26 pp.
- Walburg, C. H. 1957. Observations on the food and growth of juvenile American shad, *Alosa sapidissima*. Transactions of the American Fisheries Society 86:302-306.
- Walburg, C. H. and P. R. Nichols. 1967. Biology and management of the American shad and status of the fisheries, Atlantic Coast of the United States, 1960. U. S. Fish and Wildlife Service, Special Scientific Report – Fisheries No. 550, Washington, DC
- Waldman, J.R., K. Nolan, J. Hart, I.I. Wirgin. 1996. Genetic differentiation of three key anadromous fish populations of the Hudson River. Estuaries 19:759-768.
- Waldman, J. R., and K. E. Limburg. 2003. The world's shads: summary of their status, conservation, and research needs. Biodiversity, Status, and Conservation of the World's Shads. American Fisheries Society Symposium 35:363-369.
- Walsh, H. J., L. R. Settle, and D. S. Peters. 2005. Early life history of blueback herring and alewife in the lower Roanoke River, North Carolina. Transactions of the American Fisheries Society 134:910–926.
- Walther, B.D., S.R. Thorrold, and J.E. Olney. 2008. Geochemical signatures in otoliths record natal origins of American shad. Transactions of the American Fisheries Society 137:57-69.
- Walter, J. F., III, and J. E. Olney. 2003. Feeding behavior of American shad during spawning migration in the York River, Virginia. Biodiversity, Status, and Conservation of the World's Shads. American Fisheries Society Symposium 35:201-209.
- Waters, J.M., J.M. Epifanio, T. Gunter, and B.L. Brown. 2000. Homing behaviour facilitates subtle genetic differentiation among river populations of *Alosa sapidissima*: microsatellites and mtDNA. Journal of Fish Biology 56:622-636.
- Weaver, L. A., M. T. Fisher, B. T. Boshers, M. L. Claud, and L. J. Koth. 2003. Boshers Dam vertical slot fishway: a useful tool to evaluate American shad recovery efforts in the upper James River. Biodiversity, Status, and Conservation of the World's Shads. American Fisheries Society Symposium 35:339-347.
- Williams, R. O., and G. E. Bruger. 1972. Investigations on American shad in the St. Johns River. Florida Department of Natural Resources, Marine Research Laboratory, Technical Series 66:1-49 (<<http://research.myfwc.com/publications/default.asp>>, Accessed: October 26, 2010).
- Wolfe, D. A. 2000. A history of the Federal Biological Laboratory at the Beaufort, North Carolina 1899-1999. US National Oceanic and Atmospheric Administration.

SOCIOECONOMICS

Cultural, Economic, and Environmental Considerations in the Management of Alosines in the Chesapeake Bay and Along the Atlantic Coast

Kate Taylor

Fish are an important nutritional source for human and wildlife populations, but they provide other services as well. Anadromous fish add to the biodiversity and transfer of energy of freshwater, brackish, and marine environments, and as predators and prey they can regulate the community structure in these systems. Therefore, their presence and abundance is a measure of not only their own population status but the status of the ecosystem as well. This section examines the contributing role of alosines within marine and freshwater ecosystems with a focus on the Chesapeake Bay region. In many instances coastwide data or data from other regions was supplemented when none existed for the Chesapeake Bay.

Provisioning

Food Source

Alosine fisheries have historically occurred in tidal and freshwater rivers and streams, but within the last 50 years landings from the ocean fisheries have increased dramatically. The in-river fisheries for all four species occur during the spring spawning migration as the fish move into freshwater to spawn. During the late 1800's and early 1900's large catches from the in-river fisheries were made along the coast each spring and the majority of the harvest was used for human consumption (ASMFC 1985). The ocean fisheries occurred for a longer duration of the year and often by foreign fleets from Russia (then the U.S.S.R.), Poland and Germany (then East Germany) (ASMFC 1985). The in-river fisheries tend to be traditional fisheries with long time local participants and known seasonal markets (ASMFC 1985). Prior to the closure of the directed commercial ocean fishery in 2003 American shad were also harvested during the migration from their feeding grounds to their natal spawning rivers along the East Coast. Currently, shad and river herring are caught as bycatch in many small mesh fisheries along mid-Atlantic and New England coast.

Tribal fisheries have been known to exist for alosines for centuries. Native American tribes would feast on the fish during the spring and smoke them for future use. In Massachusetts, herring served as a dual food source. The local tradition was to place a herring on every mound where corn was planted in the spring as both a sacrifice to the spirits and as a source of nutrients to provide a bountiful harvest (Puriton 2003). While active tribal fisheries still exist in at least Massachusetts (Wampanoag Tribes) and Virginia (Mattaponi and Pamunkey Tribes), little is known about these fisheries or where other such fisheries may be occurring.

The historic commercial harvest of American shad is significantly larger and more thoroughly documented than hickory shad. This potentially could be because of the preferred taste of American shad over hickory shad, which is reflected in the Latin name for American shad, *Alosa sapidissima*, meaning “most delicious herring” while the name of hickory shad, *Alosa mediocris*, translates into “mediocre herring”. The American shad fishery in the Chesapeake Bay was the most important fishery in the late 1800’s (ASMFC 2007). American shad was still considered one of the most valuable food fish of the U.S. Atlantic coast before World War II (Rulifson et al. 1982), with the meat referred to as the "poor man's salmon" (Bryant 1989). The fish provides a rich source of Omega-3, nearly twice as much per unit weight as wild salmon (EDF), while accumulating very low levels of toxins, such as PCBs and mercury (ASMFC 1999). The female shad are targeted for their roe, or eggs, as they are considered a delicacy.

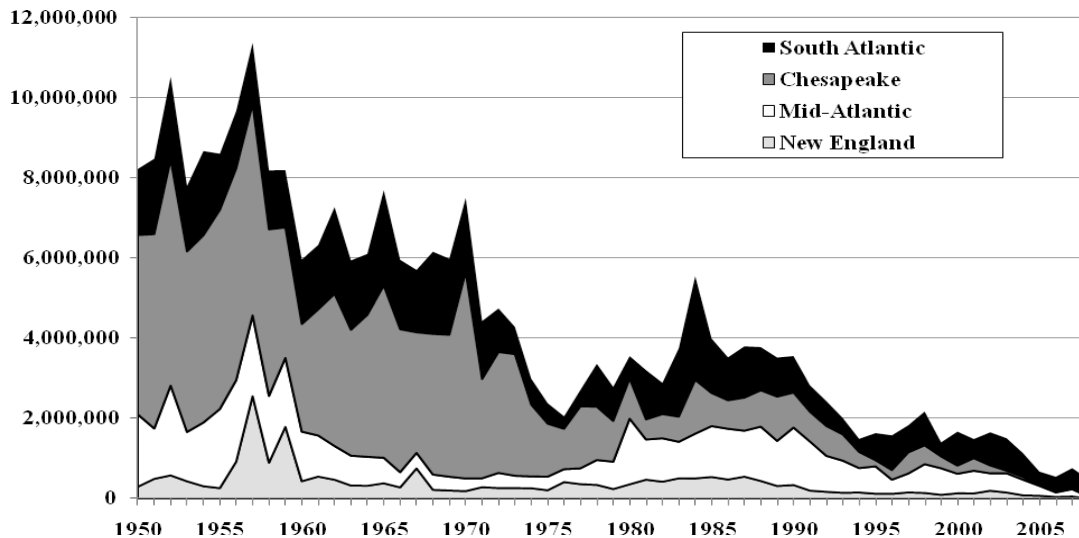


Figure 1. American shad coastwide landings by region in pounds from 1950 – 2009. Source: NMFS, personal communication (2010).

Landings for American shad show the historic abundance of the species and the decline of the fishery as the population and interest diminished (Walburg and Nichols 1967). American shad coastwide landings estimates from 1880-1900 ranged from 18 to 50 million pounds, but by the mid-1900’s the commercial landings had dropped to approximately 8-10 million pounds annually (Figure 1). Coastwide landings decreased further, to less than 2 million pounds in 1993 and to a low of 471,000 in 2008. Much of the coastwide decline of the fishery throughout the mid-twentieth century occurred in the Chesapeake region, which had accounted for more than 40% of all coastwide landings from 1950-1978, including a high of 69% of the coastwide landings in 1970. The targeted commercial fishery for American shad within the Chesapeake Bay has been closed since 1980 in Maryland waters and since 1994 in Virginia waters. Limited bycatch fisheries still exist in both states, and as recently as 2009 as much as 7,500 pounds of American shad were harvested from Maryland and Virginia waters (Figure 2).

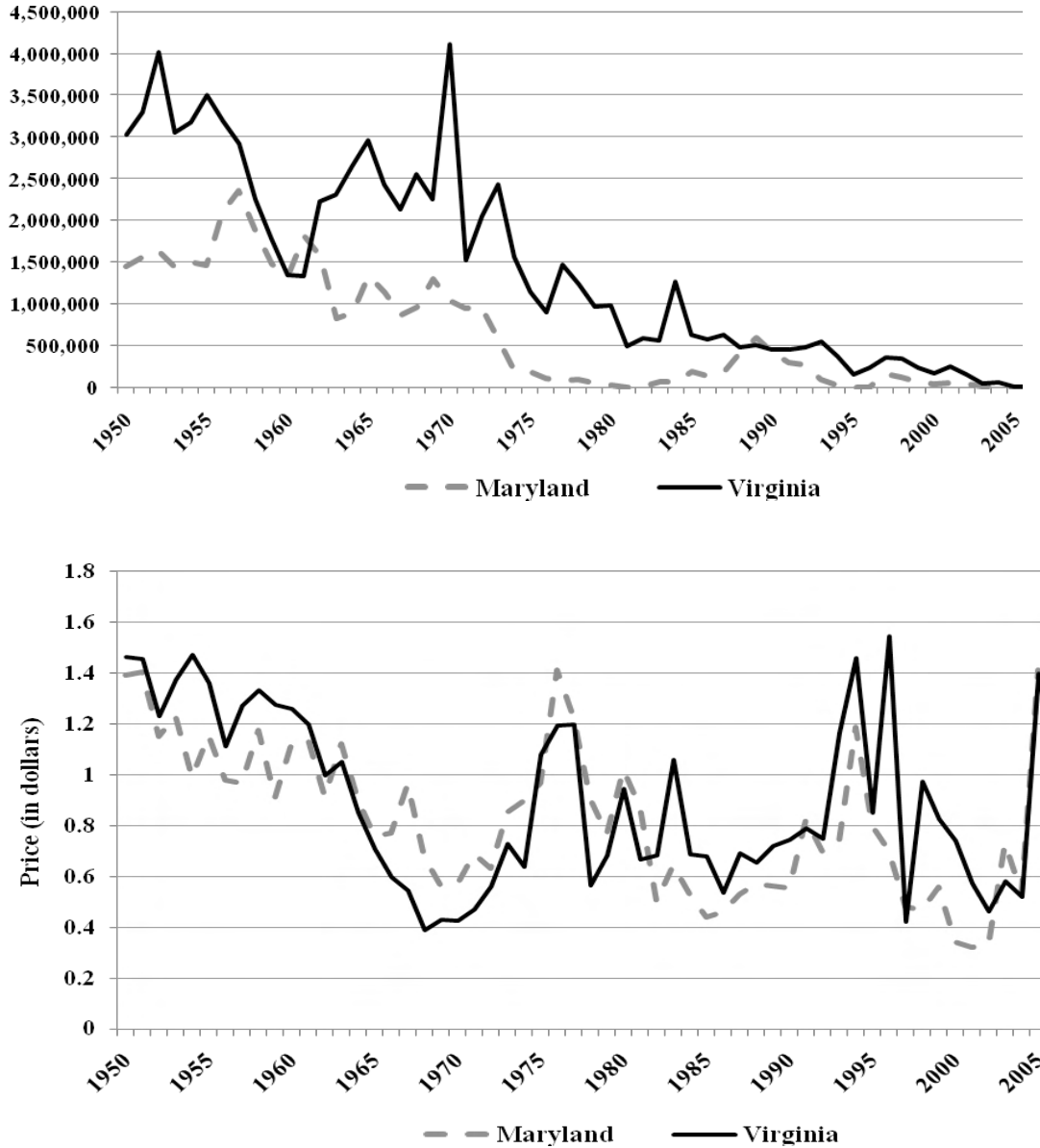


Figure 2. American shad landings (in pounds) in Maryland and Virginia from 1950 - 2009 (top) and the adjusted ex-vessel price per pound (in dollars) for American shad in Maryland and Virginia from 1950 - 2009 (bottom). Source: NMFS, personal communication.

Recreational fishermen are typically motivated by the experience of fishing and being outdoors rather than the ability to retain and consume their catch (Schramm and Gerard 2004). Nonetheless, recreational fishing can provide food for the communities that fish in areas where regulations allow for harvest. In 2008, Maryland Department of Natural Resources interviewed recreational anglers through a roving creel survey on the Susquehanna River, when the American shad fishery in Maryland waters was catch and release only. The majority of these interviewed anglers were targeting American shad during the spring. Nineteen percent of the recreational anglers interviewed said they would retain American shad if allowed (MDNR 2009). Although the intent behind retaining American shad was not ascertained (e.g. for bait or food),

given the small number of shad that fishermen wanted to keep it can be concluded that, if allowed, a majority of American shad harvested would be for personal consumption (MDNR 2009).

The river herring fishery is considered one of the oldest documented fisheries in North America (CRASC 1992). River herring are one of the easiest fish to catch and were locally harvested in great numbers for food or they were sold fresh, smoked, salted, or pickled (Collette and Klein-MacPhee 2002; ASMFC 1985). The historic catch may have exceeded 80 million pounds at the beginning of the twentieth century but fluctuated between 10 and 40 million during the first half of that century. Landings increased to over 75 million pounds by the mid-1950s, when the Chesapeake region accounted for over three-quarters of these landings (Figure 3). From 1966 - 1976 there was a significant increase in foreign vessels fishing for river herring off of the coast of the United States. In some years the foreign landings were more than double the Atlantic Coast landings for that time period (Figure 4). After the creation of the Exclusive Economic Zone (EEZ), which prohibited foreign fishing vessels within 200 miles of the US coast, coastwide landings declined to approximately 10 million pounds during the 1990's and decreased to a low of 725,000 pounds in 2005. The demand for alewives as a food source declined with the widespread use of refrigeration in the 20th century, which allowed other fish species to be widely distributed (MDMR 2008). Currently river herring are used primarily for bait, fertilizer, fish meal and oil (Collette and Klein-MacPhee 2002; ASMFC 2009).

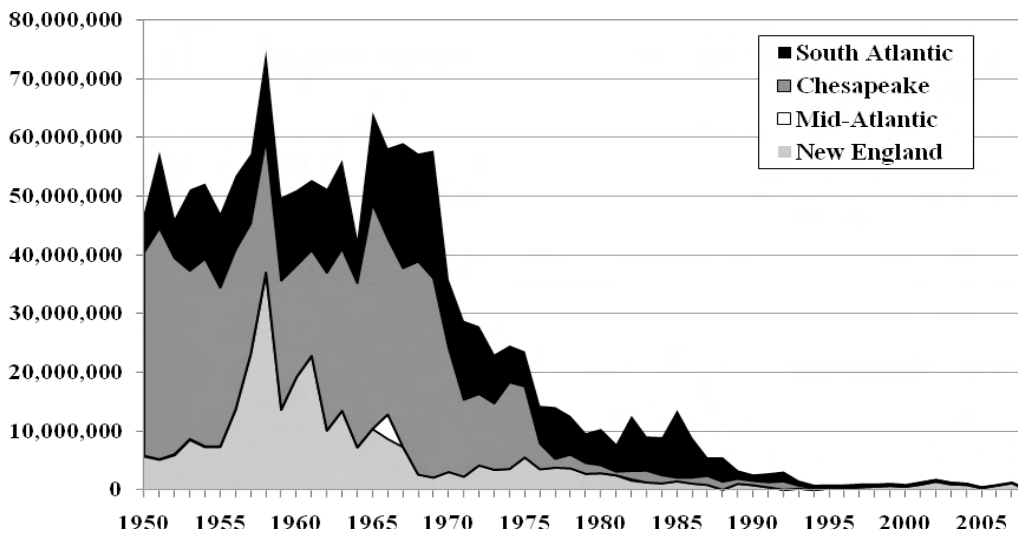


Figure 3. River herring coastwide landings by region in pounds from 1950 – 2009. Prior to 1998 NMFS did not differentiate between alewife and blueback herring. Since 2000 coastwide blueback herring landing have averaged 2% of coastwide alewife landings. Source, NMFS personal communication (2010).

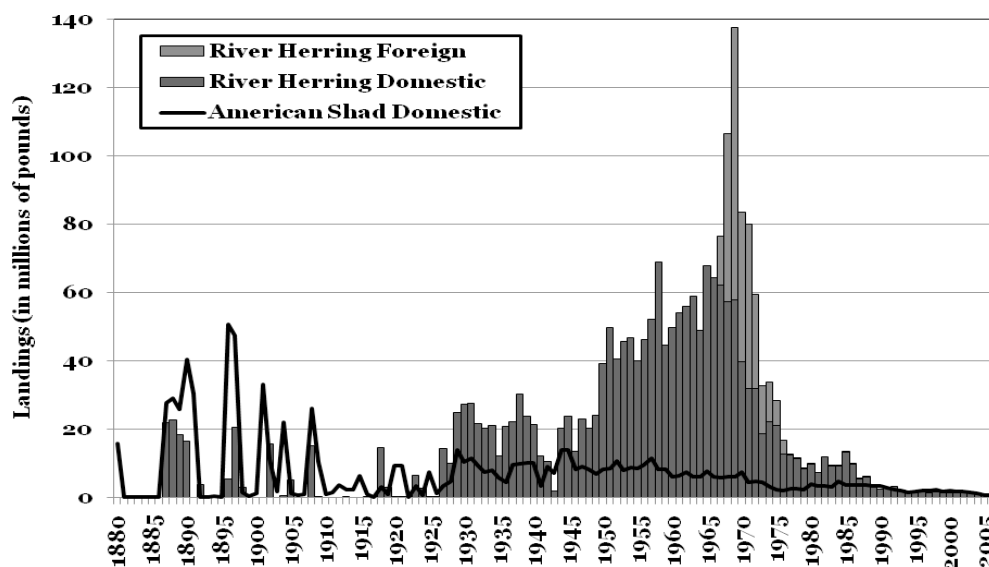


Figure 4. American shad (domestic) and river herring (domestic and foreign) commercial landings (in pounds) from 1880 - 2009.

Supporting Services

Alosine as Prey

As a forage fish, alosines are subject to predation by a wide variety of species while at sea and in coastal rivers and estuaries throughout their life (see Foodweb Brief for further details). Major predators include, but are not limited to, striped bass, spiny dogfish, bluefish, American eel, cod, white and silver hake, white and yellow perch, goosefish, salmon, pollack, weakfish, marine mammals and seabirds (Collette and Klein-MacPhee 2002, ASMFC 2009). No other species on this list is as emblematic and economically valuable to the Chesapeake Bay than striped bass. The Chesapeake Bay has historically had high striped bass abundance and serves as one of the largest sources of juvenile production for the Atlantic coast (Walter and Austin 2003). In 2008 the combined nominal ex-vessel value for the commercial fishery was nearly eight million dollars, and it was listed as the highest and second highest grossing finfish fishery in Maryland and Virginia, respectively (NMFS, personal communication 2010). The combined recreational catch for both states (including harvested and released fish) totaled approximately 2.5 million fish (NMFS, personal communication 2010).

The importance of river herring and shad as prey for striped bass has been documented in many regional and coastwide studies (Hartman and Brandt 1995; Walter et al. 2003; Walter and Austin 2003; Hartman 2003; Griffin and Margraf 2003; Ruderhausen et al. 2005; ASMFC 2007; Overton et al. 2008). Changes in prey availability have an important influence on the localized health of striped bass (Walter et al. 2003). For example, in the Chesapeake Bay in May the seasonal diet percent composition of alosines was over 70% for striped bass (sizes 458 – 1151 mm) (Walter and Austin 2003).

Seasonal Importance of Shad and River Herring as Bait

Additionally river herring is significantly important as seasonal bait in many economically important species coastwide. When available, river herring are a significant bait source for com-

mercial fisheries such as the American lobster fishery (ASMFC 2009). During alewife spawning season it is estimated that 30-50% of bait used in the lobster fishery is alewife (Collette and Klein-MacPhee 2002), as adult alewives are preferred bait for the spring lobster fishery (MDMR 2008). Since alosines are an important prey for striped bass, they are also a highly sought after bait for recreational fishermen targeting striped bass. The greatest recreational efforts for river herring occur in the mid-Atlantic region where they are harvested for bait (Collette and Klein-MacPhee 2002). For example, retail prices of \$3 and \$2 for individual live and dead river herring, respectively, have recently been reported for New Jersey bait shops and as high as \$5 per fish elsewhere (PFBC 2008).

Nutrient Cycling

Alosines play a role in cycling nutrients within foodwebs and between ecosystems (see Foodweb Brief for greater detail). As has been discussed, alosines are a forage fish. As a prey for numerous species, alosines contribute in transferring energy up the foodweb to larger predators. Alosines also provide an important link between freshwater and marine ecosystems as they migrate during the spring to spawn. Marine-derived nutrients are transferred by alosines to freshwater ecosystems through excretion and, in populations that are semelparous, mortality. For example, in Bride Brook, CT alosine contribute both nitrogen and phosphorus to the ecosystem which are rapidly incorporated into the foodweb (Davis and Shultz 2009).

Cultural Services

Cultural services can foster social relations, increase awareness of a common cultural heritage and provide a sense of place to community members (MEA 2005). In this regard, shad and river herring provide a number of cultural services, from supporting recreational fisheries to engaging the public through festivals and monitoring programs.

Recreational Fishery and Ecotourism

American shad are considered by some as one of the best game fish to catch. In his book “The Founding Fish” John McPhee describes the excitement surrounding the shad catch:

Shad don't exactly strike. First there's a fixed moment – a second or two in which you feel what appears to be a snag; then the bottom of the river appears to move and you start thinking five, six pounds. She stays low and holds. Now, straight across the river and away, deep, she strips line, your reel drag clicking. She turns and moves back. When, rising, she rolls near the surface; she looks even larger than she is.

For those river systems that still allow recreational fishing for alosines the recreational fishing season runs for six to ten weeks each spring. In Virginia a significant river herring fishery exists in the York, Rappahannock and especially in the James River. In Maryland there is a significant catch and release recreational fishery for shad in the Lower Susquehanna River and Deer and Octoraro creeks. A catch and release fishery also exists in the Potomac River.

A 1986 study of shad anglers fishing on the Delaware River indicated that they collectively spent about \$1.6 million during a nine week angling season (PFBC 2008), equivalent to approximately \$3 million in 2007. The willingness to pay by these shad anglers for the opportunity to fish was approximately \$3.2 million, or an equivalent \$6 million in 2007 (PFBC 2008). It is estimated that

a restored population of American shad on the Schuylkill River, the largest tributary of the Delaware River, would provide 60,000 – 170,000 angler trips every year (PFBC 2011). This would provide an economic benefit to local bait and tackle shops, hotels, restaurants, other shops and fishing guides.

Ecotourism

One of the biggest threats to shad and river herring is the construction of dams which cut off access to spawning habitat. However, dams built with effective fish passage not only provide a means for migrating fish to complete their journey, but also provide the public an opportunity to see these fish as they migrate upstream. Within the Chesapeake Bay, Boshers Dam on the James River was constructed in 1832 and prevented migrating fish from accessing more than 300 miles of habitat until a fishway was constructed in 1999. Inside the fishway a camera records video of the fish swimming through the dam. This video is used by state biologists to estimate the population of shad in the river and the video is also streamed online so that the public can view the fish migration (The streaming video can be viewed at: www.dgif.virginia.gov/fishing/shadcam/).

Along the Connecticut River there are two visitor centers located at Turners Falls Dam and Holyoke Dam in Massachusetts which provide tours to the public and school groups during the spring. Additionally, over 10,000 visitors annually come to the Amoskeag Fishways Learning Center along the Merrimack River in New Hampshire to watch and learn about the migrating fish. These visitor and learning centers not only conduct educational programs for community groups, but also provide local jobs.

For those dams that do not currently have adequate fish passage, installing fish passage would provide community benefits. Based on estimates from the Economic Policy Institute and the U.S. Fish and Wildlife Service, each \$1 million of fish passage improvement projects creates between 20 to 54 new jobs in the areas which the barriers exist. In 1987, the Chesapeake Bay Agreement committed member states “to provide for fish passage at dams, and remove stream blockages wherever necessary to restore passage for migratory fish” and set up a goal of opening up more than 1,300 miles of fish habitat. Since that time, Maryland has worked with local and federal partners, as well as concerned citizens, to re-open over 400 miles of stream habitats in Maryland. After the original goal was met by 2004 member states committed to the completion of 100 additional fish passage/dam removal projects and opening up an additional 1,500 miles of habitat or fish passage and watershed restoration by 2014. These projects can help to provide jobs in the communities that restoration work is being conducted.

Shad and River Herring Festivals

Festivals celebrating the return of shad and river herring each spring occur annually along the East Coast. There are 32 known festivals, including some which have run for over 60 years. Within the Chesapeake Bay the three major festivals are the Nanticoke River Shad Festival (Vienna, MD), the National Casting Call (Washington, DC) and the Annual Shad Planking (Wakefield, VA). Events at these festivals can include boat rides, fishing instruction and tournaments, arts and crafts vendors, educational exhibits, cooking demonstrations, and live music and dance.

The highlight of shad festivals centers around shad planking, which is a method of laying shad on oak planks and roasting the fish over hot coals for many hours. The method, which was adapted from Native Americans, helps to break down the approximately 769 tiny bones inside the small fish (Reynolds 2000). The reason behind the bones in the American shad is described in a legend of the Micmac Nation, a tribe located in northern New England and the Canadian Maritimes where American shad no longer exist. The legend says that an unhappy porcupine asked the Great Spirit to turn it into a better animal and the Great Spirit responded by turning the porcupine inside out and casting him into the river (Reynolds 2000). Historically the festivals relied on the catch of local shad and river herring fishermen to provide the food for the festival. As shad and river herring fisheries have diminished or have been shut down, communities have had to import fish from other states.

These festivals can provide many benefits to local communities. They help to promote community relations, increase awareness of cultural traditions, and educate the community about their local fisheries and ways to promote the health of these resources. Additionally, many of these festivals act as fundraisers for local recreational and environmental organizations. These organizations can use this money to develop monitoring and restoration programs which benefit countless other local species. Other organizations use the money as scholarships for local residents. In Lambertville, NJ the local shad festival has raised over \$330,000 in scholarship funds for students pursuing a career in the arts through higher education.

Table 1. Volunteer Shad and/or River Herring Monitoring Programs on the Atlantic Coast .

State	River System(s) / Location(s)	Agency	Current	Approx. # Participants
MA	3 rivers that run into Buzzards Bay	Coalition for Buzzards Bay	Y	U
MA	4-6 rivers on the North Shore	Eight Towns and Bay	Y	30
MA	North and South Rivers	North and South River Watershed Association	Y	40-50
MA	6 towns on Cape Cod	The Association to Preserve Cape Cod	Y	80+
MA	Concord River	Lowell Parks & Conservation Trust	N	-
MA	Marston Mills River	Marston Mills River Watershed Association	Y	10-15
MA	Neponset River	Neponset River Watershed Association	U	U
MA	Parker River	Parker River Clean Water Association	Y	35
MA	Ipswich River	Ipswich River Watershed association	Y	30 – 40*
MA	Coonamessett River	Coonamessett River Trust	U	U
MA	Charles River	Charles River Watershed Association	U	U
MA	Jones River	Jones River Watershed Association	Y	50
RI	Warwick Pond/Buckeye Brook	Buckeye Brook Coalition	Y	15-20
NY	11 Rivers on Long Island	Long Island South Shore Estuary Reserve (SSER) Council and the Seatuck Environmental Association	Y	25+*
NY	13 streams that drain into the Hudson River	NYSDEC	Y	70+

* Includes participation by local schools; u=unknown

Volunteer Fish Counts

Many recreational, state and environmental organizations conduct volunteer monitoring programs to count river herring and shad as they return to freshwater to spawn each spring. These programs are predominately found in the northeast, where there is a higher number of dams with fishways. Volunteers typically go to a fishway and count the number of fish swimming past during a timed interval. They can also keep track of weather conditions, any other wildlife they observe and ensure the proper maintenance and operation of the fishway during the spawning run. These volunteer programs provide many benefits including educating local community members about the resources in the rivers, providing meaningful assistance to conservation efforts and promote community involvement and relations. Another example of an innovative program to enhance community stewardship is the Adopt-a-Herring Program, which Frank et al. (2009) describe as a valuable conservation tool.

Traditional Importance in the Chesapeake Bay

Within the Chesapeake Bay, alosines have traditionally provided a significant cultural link and environmental connection. This is reflected in the town names, such as Shad Landing, Maryland and Shadwell, Virginia, which is the birthplace of Thomas Jefferson who was an avid shad fisherman. In 1936 Rachel Carson wrote in the Baltimore Sun that “just as the sacred cod of Massachusetts is the accepted emblem of the Bay State, so the shad may rightly be considered the piscatorial representative of the states bordering the Chesapeake.”

Restoration

Steve Gephard

For this discussion, ‘restoration’ is defined as the re-establishment of a run in a stream that historically supported a run that was subsequently lost. This can be contrasted with the term ‘enhancement,’ which commonly refers to increasing the size of a run that has previously been diminished in size, typically by anthropogenic activities. There are two aspects of restoration. One aspect is the geographic extent of the run. Each historic run had a range within the watershed or specific stream. The run usually ended at a point where the stream gradient became too steep to allow passage (including waterfalls) or above which no additional appropriate critical habitat was found. Often, construction of dams in the lower portion of a watershed resulted in the extirpation of the run throughout most of the watershed. In subsequent years, other anthropogenic activities further degraded alosine habitat within the portion of the watershed that was then inaccessible to the species. If a fish passage project is initiated at a lower dam to allow fish to return to upstream areas, that is restoration. However, due to other dams and habitat degradations, the run may not be fully restored to its historic range. It is possible that a run may only be partially restored to the watershed or that restoration is an incremental process that may take decades before fish passage is achieved at all artificial barriers.

The other aspect of restoration is run size. A historic run to a watershed may have averaged one million river herring a year. A lower dam may have extirpated the run that becomes the subject of a restoration program many years later. All dams could be removed so that the species have access to all historical habitat but the runs may only number half of a million fish a year. The run has been restored geographically, but not to its full historical size. There are many factors that could cause this, including factors at sea that impact marine survival and factors in the watershed that have reduced the productivity of the freshwater habitat. Genetic bottlenecks caused by large declines in run sizes or disruption of the native genome due to the introduction of non-native strains of fish could also affect run traits such as timing. Such changes in traits could be maladaptive and result in the diminishment of run size. Changes in the environment (including climate change) could also affect the run timing and temporal duration of the run.

Restoration programs can establish target population levels and these can operate at various scales. Local managers may wish to restore a run of 10,000 alewives to a stream, while at a national level, agencies could agree to achieve either landings or population estimates equal to some past year when the stocks were considered stable or self-sustaining. Alosine run sizes have been dwindling from the earliest days of European Contact, therefore restoration goals aiming to achieve landings commensurate with run sizes of the 1970s would not approach ‘true’ historical restoration. Programs with such goals may more accurately be referred to as a ‘recovery,’ particularly if the run becomes self-sustaining.

While federal agencies or fishery management institutions (i.e., interstate Fisheries Management Commissions or Fishery Management Councils) may aspire for stock recoveries at a coast-wide scale, most restoration programs operate at a local scale. Runs of alosines are restored one stream at a time. Sometimes the trends of river herring populations seem to conflict between local and national scales. A local fishway can be built, resulting in dramatically increasing number of river herring returning to that upper section of stream while indicators for runs throughout the state or country continue to drop. The increase in numbers returning to the stream is significant in the context of that stream but in the context of the entire coast, the increase could be swamped by the trends in other rivers. It may be necessary to restore hundreds of miles of many streams with the concomitant increase of juveniles going to sea before such local increases are reflected in national monitoring data. Furthermore, if the factors in the ocean that are driving down marine survival are significant, they may preclude the freshwater restoration projects from demonstrating clear or significant benefits. A new fishway that resulted in an increase in the annual run to that river of 10,000 could have resulted in an increase of 100,000 fish had not the marine factors depressed sea survival. Skeptics may question the value of a dam removal project in the face of decreasing river herring survival at sea, but it is possible that without the beneficial work within the freshwater habitat, the species could disappear entirely from the watershed. Keeping small runs alive may be important from a long-term regional genetic perspective as well as respecting the wishes of local communities.

Small restoration projects for alosines have been common but they have often been either tangential to the restoration of other anadromous species or not well-studied and documented. In the case of alewife, it has been typical to build a fishway to allow the fish to circumvent a dam and rebuild their numbers without a lot of monitoring, data collection, and analysis. American shad restoration has received a bit more attention but this species does not efficiently use many types of fishways (Larinier and Travade 1992; Sullivan 2004). Although some restoration projects have been successful, other similar ones have not and it is difficult to make definitive conclusions about what constitutes an effective restoration strategy.

Upstream fish passage, as well as safe and effective downstream passage are essential to restoration strategies if fish are to regain access to historic habitat, where little spawning habitat is typically available in the lower reaches of rivers. In most cases, dam removal is the most effective means to get alosines upstream. Alewife does not seem to have difficulty using well-designed fishways, particularly close to tidewater. American shad and blueback herring are less proficient at using fishways, particularly at dams taller than 25 feet (Haro et al. 1999). Hickory shad are known to use some Denil fishways in the Chesapeake Bay region but there are not much data on this usage. Furthermore, it appears that hickory shad spawn in tidewaters and often do not ascend upstream to where dams are located (Batsavage and Rulifson 1998). In Maryland, hickory shad spawning is documented in Deer Creek (a tributary to the Susquehanna River) and few fish have passed the fishway at Wilson Mill, using a Denil fishway.

Factors affecting the efficiency of alosines using fishways to move upstream include: dam height, distance from the sea, design, and the number of fishways downstream. At this time, the recommended design for fish passage of American shad and blueback herring above dams greater than 25 feet in height by the U.S. Fish & Wildlife Service engineering unit is a fish elevator [lift] (Curt Orvis, USFWS, Region 5, Hadley, MA; pers.com.). Some poorly designed fishways actually kill shad due to fishway induced injuries—either immediately (they never

reach the top of the fishway) or delayed prior to spawning (they ascend but are so badly injured they cannot spawn). It appears that the operation of the Rainbow Dam Fishway on the Farmington River in Connecticut has caused a decline in the run of shad to that river by moving all of the fish that were spawning below into the fishway that kills many (Steve Gephard, CTDEP, Old Lyme, CT; pers. comm.).

Downstream passage is also a concern where entrapment, delays in emigration, or mortality may occur. If juveniles do not reach the ocean, the upstream reproductive effort facilitated by the fishway has not only gone to waste, it may be counterproductive since many of the fish would have spawned downstream of the dam (and safely returned to sea) had the fishway not been built. Studies of turbine-induced mortality of young-of-year alosines have reported highly varied rates (Taylor and Kynard 1983; Mathur and Heisey 1992; RMC 1992) and the rate appears to be very site specific and influenced by the type of turbine and its operation. Shad runs north of Cape Fear, NC have evolved to be iteroparous (Leggett and Whitney 1972). If dams prevent post-spawned shad from reaching the ocean, these fish become “involuntarily semelparous,” which could greatly affect their population dynamics and long-term viability (Leggett et al. 2004). While some have argued that fishways do more harm than good for American shad runs by lengthening the migration length and concomitantly reducing iteroparity (Leggett et al. 2004), many believe that is an oversimplification that ignores the huge benefit gained by opening up large amounts of unused spawning and nursery habitat and simply underscores the need for effective downstream passage at dams (Castro-Santos and Letcher 2010). A case-by-case analysis would be needed to make such conclusions since the mortality rate per dam and the habitat benefit per dam will vary from river to river.

In the Susquehanna River, there are four major dams inhibiting migration and all have been equipped with fish elevators. Adult American shad have 25% mortality through the downstream dam but above this dam it is considered 100% mortality of adults. For juveniles, downstream mortality has been estimated to be 68% for fish passing through all four dams (Kahn and Weinrich 1994). In contrast, numerous balloon-tag studies of juvenile turbine mortality have estimated higher rates of survival. One-hour survival of juvenile American shad passing through a Kaplan turbine, operated at 55 to 56-wicket gate opening, at Conowingo Dam was 94.9% (RMC Environmental Services, Inc. 1993). Forty-eight hour survival was 92.9 percent. One-hour survival of juvenile American shad passing through Francis turbines at Holtwood Dam was 89 percent (Mathur and Heisey 1993). Twenty-four hour survival was 78 percent. One-hour survival of juvenile American shad passing through turbines at Safe Harbor Dam was 98%, 97.8% and 98.9% for Kaplan, mixed flow (unvented) and mixed flow (vented) turbines, respectively (Heisey et al. 1992). Forty-eight hour survival was 98%, 100%, and 67% (adjusted for controls) for Kaplan, mixed flow (un-vented) and mixed flow (vented) turbines, respectively. One-hour survival of juvenile American shad passing through turbines at York Haven Dam was 92.7% and 77.1% for a vertical shaft Kaplan (Unit 3) and a dual vertical shaft Francis turbine, respectively (Normandeau Associates 2002). Adjusted forty-eight hour survival exceeded the one-hour survival and was not utilized.

In the Susquehanna River, optimal spawning habitat is above the fourth major dam while sufficient spawning habitat exists above the third (B. Sadzinski personal communication). With the poor lift efficiencies (catchability) at each of the dams, most adult American shad never

arrive above the third dam, resulting in undetectable juvenile production during most years (Hendricks and Myers 2008)

It is possible that some dam removals may actually reduce the number of alewives in a system (whether observed or potential). Alewives spawn in ponded water and their larvae and young-of-year utilize ponded habitats. A fish passage project using a fishway allows the pond to continue to exist and be utilized by alewife. If the dam is removed, it is possible that the stream will not support as many juvenile alewife as could be expected with the pond still intact. Dam removals are initiated for many good reasons, in addition to fish restoration, and removing a dam still may be the best choice, but fish managers many need to realize that this could cause a decline in the run size of alewife.

Fish passage allows natural reproduction in formerly unavailable habitat. There are other ways of supporting upstream production as part of restoration strategies in the absence of providing upstream passage. A common method has been the capture of pre-spawn adults, placing them in specially-equipped transport tanks, and trucking them to upstream locations where they are released (Hendricks 2003). Such 'transplantation' has been done extensively for both American shad and/or alewife in Maine (Anon. 2005), New Hampshire (Patterson et al. 2009), Massachusetts (Anon. 1979), Connecticut (Steve Gephard, CTDEP, Old Lyme, CT, per.com.), and Pennsylvania (Hendricks 2003). Blueback herring has been transplanted in Massachusetts and Connecticut (Ken Sprankle, USFWS Sunderland, MA, pers. com.). Often, the effectiveness of this method has not been critically evaluated but visual surveys conducted for surface 'popping' behavior by young-of-year above dams in Connecticut where adult spawners have been transplanted, have documented successful reproduction in almost all cases (Steve Gephard, CTDEP, Old Lyme, CT, per.com.). It is not known how many of the fish spawned or how many young-of-year were produced, emigrated to sea and contributed to subsequent adult spawning runs, but the evidence of successful spawning is irrefutable. For example, alewives were absent in Latimer Brook (CT) prior to transplantation of adults from nearby Brides Brook and within five years of the multi-year transplantation project, a small run appeared and has now grown and become self-sufficient (Steve Gephard, CTDEP, Old Lyme, CT, per.com.). There are, however, many cases where the transplantation of American shad and alewives did not appear to result in success. Most of these involved high loading densities in the truck and long, interstate journeys. Much experience has been gained in the transplantation of these species and it is clear that great care must be taken to minimize the stress of the fish if this technique is to be successfully employed.

Another method for providing upstream production in the absence of fish passage has been the use of hatchery production. The culture of American shad and river herring has been used on the Susquehanna River, the Kennebec and other rivers in Maine, the Lehigh and other rivers in Pennsylvania, the Patapsco and Patuxent and other rivers in Maryland, the James and Potomac and other rivers in Virginia, and the Roanoke River in North Carolina (Hendricks 2003). Wild broodstock were obtained from various sources, spawned in the hatchery, and the progeny released into targeted watersheds at either the larval or feeding juvenile stage. Such stockings are known to have contributed to subsequent adult spawning runs (Hendricks 2003). An extreme case of hatchery releases of American shad involves the transcontinental railroad and the introduction of American shad larvae to the Sacramento River, California, in 1871. As a result, American shad were introduced to the U. S. west coast and are now established from southern California to Alaska (Petersen et al. 2003).

Both of these restoration methods carry risks. The problems with using genetically inappropriate stocks of salmon in West Coast hatcheries to mitigate or enhance native runs are well-documented. Similar problems could arise with East Coast alosines. A first step when considering such actions must be to ascertain the status of existing runs. If there is an existing (native) run of fish, both of these actions may be unwarranted. The reconnection of the run with upstream habitat (fish passage projects) should be the first priority. If either of these steps is to be undertaken, the use of existing, native broodstock should be used. Palkovacs et al. (2008) determined that sea-run alewives from all sampled streams in eastern Connecticut were indistinguishable using mtDNA and microsatellite analysis. They concluded that the relatively high straying rate in this species has resulted in a homogenization of Long Island Sound alewives into a single stock. In this case, using any one of these streams as a donor source for transplanting alewives into nearby streams without alewife runs appears to be an acceptable practice. It seems likely that similar widely-distributed distinct stocks occur in other portions of the East Coast, but genetic characterization of all runs is needed to develop a clear picture of stock structure and provide guidance on what stocks may be used to restore runs to which rivers.

Of the two techniques, priority should first be given to transplantation if the opportunity exists due to these facts: (1) transplantation supports natural spawning and feeding which is more likely to result in successful production and emigration to the sea; (2) transplantation reduces the chances for artificial selection; (3) traps and trucks are much less expensive to operate and maintain than a hatchery.

Fisheries are closed (or will be closed) in many rivers where restoration is needed, therefore fisheries-independent methods are necessary to document and monitor the results of restoration efforts. Viewing windows in fishways that are monitored directly by workers or indirectly through electronic fish counters or videography (analog or digital) are being used increasingly in New England as well as at Boshers' dam on the James River. If fishways are inefficient in passing alosines or are too far upstream to be used by all species, this method of monitoring may be either unsuccessful or only partially effective. Traps or nets can document presence/absence of species but rarely can be used to quantify abundance. There can be a substantial level of handling mortality associated with netting, which can be worrisome on small, threatened runs.

Restoration programs are best guided by well-considered plans. Elaborate plans may be needed to support fishway prescriptions by the Federal Energy Regulatory Commission (FERC) or other regulatory bodies. Restoration plans typically articulate the targeted species, targeted portions of watersheds, fish passage needs, and roles and responsibilities of partners. Projecting the potential number of adult returns possible under full restoration has been particularly challenging due to the lack of data. American shad production rates of 50 – 60 adults per acre of upstream habitat have been used in the Northeast (Wildman and Gephard 2009). This range has been supported by data from the Connecticut River and has been accepted by FERC, utility companies, and many stakeholders. Production rates of 90 adults per acre have been used for blueback herring based upon an average shad : blueback ratio observed at the Holyoke Dam on the Connecticut River (Wildman and Gephard 2009). Ranges of 900 – 1,000 adult alewives per acre have been used based on studies of coastal ponds in Rhode Island and Massachusetts (Richkus 1974). It is recognized that actual productive rates will vary by habitat type (large river, coastal pond, small brook), water quality, and likely latitude. More research is needed at both the local

and coastal level to expand our understanding of alosine freshwater production rates but the aforementioned rates may be used in the absence of more appropriate figures.

Management Guidelines (Socioeconomics, Management Considerations)

Andy Kahnle

Management of Chesapeake Bay Alosines is guided by various measures of stock condition in conjunction with societal visions of desirable future conditions. Where possible, stocks are managed at the species level and separately for spawning tributary or for groups of nearby and geographically related tributaries. At the most basic level, managers consider if the stock is present and spawning or if it has been extirpated from a given tributary. If absent, the goal is often to simply re-establish a self-sustaining spawning population or population of alosines. If anthropogenic barriers to spawning habitat are involved, then the restoration goal is likely to achieve spawning within all or part of a previously unavailable section of historical spawning habitat. If stocks are already spawning in a given tributary, but are at low abundance, then the restoration goal is likely to increase run size.

Restoration and enhancement can be guided by a target stock size, measured either as population size or as passage numbers where barriers occur. These targets are often developed from historical data or from information on surface area of historical spawning habitat. For example, the goal of American shad restoration activities on the Susquehanna River was based on historical spawning habitat and is to achieve self-sustaining populations of 2 million American shad and 5 million river herring (ASMFC 2007). Stock enhancement and restoration programs that involve the stocking of marked larvae, often define their goal as obtaining a population in which the contribution of hatchery fish in the juvenile or adult population becomes negligible (Richardson et al. 2006). Restoration and enhancement plans usually include analyses of cause of extirpation or reduced stock abundance and planned actions to rectify the problem.

Alosine stocks that have been fished often have a history of harvest related data as well as data from fishery independent monitoring. Fished stocks that have declined in abundance are often managed with a goal of restoring stock levels such that harvest or CPUE from fishery independent sampling rebound to a selected historic level deemed desirable. For example, goals of American shad enhancement efforts in the James, York, and Rappahannock Rivers consist of achieving selected historical levels of CPUE as measured by a fishery-independent sampling design that mimics commercial sampling during a period of relatively high abundance (ASMFC 2007). The comparable goal for Potomac River American shad involves achieving a historical CPUE in the ongoing pound net fishery. Index based restoration goals (CPUE) have not been developed for other alosines of Chesapeake Bay. A restoration goal commonly used for a recreational fishery involves obtaining a stock size that supports a certain level of fishing effort. For example, a goal of the Susquehanna River restoration plan is to provide 500,000 angler days for American shad and river herring throughout the basin.

Fished stocks can also be managed to maintain an exploitation rate (u) or a rate of instantaneous fishing (F) for mature fish at or below a benchmark rate which is estimated through various population modeling. Early assessments of American shad used this approach. ASMFC (1988) set a benchmark for the Susquehanna River at $F = 0.70$. ASMFC (1998) set a benchmark for Upper Chesapeake Bay in Maryland at $F = 0.43$. The most recent assessment of American shad stock status set an upper limit for total instantaneous mortality or Z (ASMFC 2007). The logic for this approach was that American shad experience mortality from a variety of anthropogenic sources that cannot be separated within the stock assessment: unintended bycatch at sea and from upriver and downriver passage over barriers as well as directed fishing, so these elements are combined with natural mortality as the target threshold rate. A benchmark of $Z = 0.62$ was developed for the York River in Virginia by ASMFC (2007). Mortality based benchmarks have not been determined for other alosine species of the Chesapeake Bay. The difficulty in using mortality based benchmarks is that existing mortality rates are difficult to measure in alosines and so it is often difficult to determine if rates exceed a given benchmark. Management response related to mortality benchmarks generally involves reducing anthropogenic related mortality when rates are excessive and making no change or relaxing restrictions when rates are at acceptable levels.

The above is a good description of goal-setting for restoration efforts when there is no spawning run, or at least one that is severely depleted, as well as for managing existing commercial and recreational fisheries. However, more detail could be provided on the social and economic *value* of these fisheries. For examples of this detail, see bulleted list below and the section that follows:

- overall participation in sport fisheries
- dollar value of commercial fisheries
- number, value and employment of support business for commercial and recreational fishing
- similar figures for industries that use harvested alosines (bait; reduction?)
- Relationship to community interest? Measured by attendance at shad festivals or volunteer monitoring activities?
- Angler participation by age group? Can you rebuild interest in fishing with younger groups, encourage continued fishing in senior groups, because shad fishing does not require extensive capital costs to participate?
- Create a wildlife metric in terms of the value of alosines value as prey to other species
- Create a water resource metric, in terms of setting minimum river flow rates and levels in accordance with maintaining alosine spawning habitat.

Potential Indicators, Reference Points, or Metrics

- Fishing – Commercial and recreational contributions to economy.
 - *Reference points*: Dollars derived from alosine fisheries.
- Cultural – Festivals and heritage-based activities.
 - *Reference points*: Measure of community involvement in alosine issues and activities.
- Restoration - Increased hatchery operations for restoration, construction of fishways, mitigation activities related to watershed development plans.
 - *Reference points*: Dollars spent on restoration; metrics characterizing alosine considerations in watershed development plans
 - overall participation in sport fisheries
 - dollar value of commercial fisheries
 - number, value and employment of support business for commercial and recreational fishing
 - similar figures for industries that use harvested alosines (bait; reduction?)

References

- Anon. 1979. Anadromous fish of Massachusetts. A summary of the regulation, management, and utilization of alewife, shad, and smelt. Dept of Fisheries, Wildlife and Recreational Vehicles, Division of Marine Fisheries. Commonwealth of Massachusetts. New Bedford, MA. 20 pp.
- Anon. 2005. Kennebec River Anadromous Fish Restoration: annual progress report- 2005. Maine Department of Marine Resources. Bureau of Sea-run Fisheries and Habitat, Augusta, ME. 28 pp.
- ASMFC (Atlantic States Marine Fisheries Commission), 1985. Fisheries Management Plan for Shad and River Herring. Report No. 6.
- ASMFC (Atlantic States Marine Fisheries Commission). 1988. Stock Assessment of American shad from selected Atlantic Coast rivers. Special Report Number 15. ASMFC, Washington, DC, USA.
- ASMFC (Atlantic States Marine Fisheries Commission). 1998. American shad stock assessment peer review report. ASMFC, Washington, DC, USA.
- ASMFC (Atlantic States Marine Fisheries Commission), 1999. Amendment 1 to the Fisheries Management Plan for Shad and River Herring. Report No. 35. Bryant, N. "Poor Man's Salmon Arrives in April". NY Times. Published March 19, 1989.
- ASMFC (Atlantic States Marine Fisheries Commission), 2007. American Shad Stock Assessment. Stock Assessment Report No. 07-01. Vol. I-III.
- ASMFC (Atlantic States Marine Fisheries Commission), 2009 . Amendment 2 to the Fisheries Management Plan for Shad and River Herring.
- Batsavage, C.F. and R.A. Rulifson. 1998. Life history aspects of the hickory shad (*Alosa mediocris*) in the Albemarle Sound/Roanoke River watershed, North Carolina. Report to the North Carolina Marine Fisheries Commission, Fishery Resource Grant No. M6057, ICMR Contribution Series No. ICMR-98-02, Morehead City, North Carolina.
- Bryant, N. (1989, March 19). OUTDOORS; 'Poor Man's Salmon' Arrives in April. *New York Times*.
- Carson, R.L., 1936. It'll Be Shad Time Soon. Baltimore Sunday Sun. Published March 1, 1936.
- Castro-Santos, Theodore and Benjamin H. Letcher. 2010. Modeling migratory energetics of Connecticut River American shad (*Alosa sapidissima*): implications for the conservation of an iteroparous anadromous fish. *Can.J.Fish.Aquat.Sci.* **67**: 806-830.
- Collette and Klein-MacPhee, 2002. Fishes of the Gulf of Maine. Smithsonian Institution Press. Washington. 3rd Edition. pp. 111-118.

- Constanze, R. et al. 1997. The value of the world's ecosystem services and natural capital. *Nature* Vol. 387. pp 253 – 260.
- CRASC (Connecticut River Atlantic Salmon Commission), 1992. A Management Plan for American shad in the Connecticut River Basin.
- Davis, J.P. and E.T. Schultz, 2009. Temporal Shifts in Demography and Life History of an Anadromous Alewife Population in Connecticut. *Marine and Coastal Fisheries: Dynamics, Management and Ecosystem Science*. pp 90-106.
- EDF (Environmental Defense Fund) Seafood Selector. American shad.
www.edf.org/page.cfm?tagID=15735
- Holmlund, C. M. and M. Hammer, 1999. Ecosystem services generated by fish populations. *Ecological Economics* 29. pp 253 – 268.
- E.P.I (Economic Policy Institute) and USFWS (U.S. Fish and Wildlife Service). National Fish Passage Program. www.fws.gov/fisheries/fwco/fishpassage
- Frank, Holly J., M.E. Mather, R.M. Muth, S.M. Pautzke, J.M. Smith, and J. T. Finn. 2009. The Adopt-a-Herring Program as a Fisheries Conservation Tool. *Fisheries*. 34(10): 496-507.
- Griffin, J.C. and F.J. Margraf, 2003. The diet of Chesapeake Bay striped bass in the late 1950's. *Fisheries Management and Ecology*, 10. 323 – 328.
- Haro, A., M. Odeh, T. Castro-Santos, and J. Noreika. 1999. Effect of slope and headpond on passage of American shad and blueback herring through simple Denil and deepened Alaska steep pass fishways. *North American Journal of Fisheries Management* 19: 51-58.
- Hartman, K.J. and S.B. Brandt, 1995. Estimating Energy Density of Fish. *Transaction of the American Fisheries Society*, 124. pp 347-355.
- Hartman, K.J., 2003. Population level consumption by Atlantic coastal striped bass and the influence of population recovery upon prey communities. *Fisheries Management and Ecology*, 10. pp 281 – 288.
- Heisey, P.G., D. Mathur and T. Rineer. 1992. A reliable tag-recapture technique for estimating turbine passage survival: application to young-of-the-year American shad (*Alosa sapidissima*). *Canadian Journal of Fisheries and Aquatic Sciences* 49(9): 1826-1834.
- Hendricks, M.L. 2003. Culture and transplant of alosines in North America. Pages 303-312 in K.E. Limburg and J.R. Waldman, editors. *Biodiversity, status, and conservation of the world's shads*. American Fisheries Society, Symposium 35, Bethesda, Maryland.
- Hendricks, M.L. and E. M. Myers. 2008. Abundance and distribution of American shad in the Susquehanna River. Job IV. *In: Restoration of American shad to the Susquehanna River*. Annual Progress Report. 2006. Susquehanna River Anadromous Fish Restoration Committee.
- Kahn, D. M., and D. Weinrich. 1994. Effects of stocking and natural reproduction on recovery of American shad in the upper Chesapeake Bay. Pages 86-96 in J. E. Cooper et al., editors. *Anadromous Alosa Symposium, Tidewater Chapter*, American Fisheries Society, Bethesda, Maryland.

- Larinier, M. and F. Travade. 1992. Fishways for shad. *Bulletin Francais de la Peche et de Pisciculture* 326-327: 125-133.
- Leggett, W.C. and R.R. Whitney. 1972. Water temperature and the migrations of American shad. *U.S. Fish and Wildlife Service Fisheries Bulletin* 70(3):659-670.
- Leggett, W.C., T.F. Savoy, and C.A. Tomichuk. 2004. The impact of enhancement initiatives on the structure and dynamics of the Connecticut River population of American shad. Pages 391 – 405 *in* P.M. Jacobson, D.A. Dixon, W.C. Leggett, B.C. Marcy, Jr., and R.R. Massengill, editors. *The Connecticut River Ecological Study (1965-1973) revisited: ecology of the lower Connecticut River 1973-2003*. American Fisheries Society, Monograph 9, Bethesda, Maryland.
- Mathur, D. and P.G. Heisey. 1992. Debunking the myths about fish mortality at hydro plants. *Hydro Review* 11:54-60.
- Mathur, D. and P.G. Heisey. 1993. Ask young clupeids if Kaplan turbines are revolving doors or blenders. *Hydraulic Engineering '93*. Proceedings of the 1993 conference sponsored by the Hydraulics Division/ASCE. July 25-30. 1993, San Francisco, California: 1332-1337
- McPhee, John, 2002. *The Founding Fish*. Farrar, Straus and Giroux. New York.
- MDMR (Maine Division of Marine Resources), 2008. River Herring Fact Sheet. www.maine.gov/dmr/searunfish/alewife/index.htm
- MDNR (Maryland Division of Natural Resources), 2009. Maryland Shad and River Herring Annual Compliance Report to ASMFC.
- Millennium Ecosystem Assessment, 2005. *Ecosystem and Human Well-Being – Synthesis*. Island Press, Washington, D.C.
- Normandeau Associates. 2002. Passage survival and condition of juvenile American shad through the York Haven Hydroelectric Station, York Haven, Pennsylvania. Report to York Haven Power Company. 31p.
- Overton, A. S., C.S. Manooch III, J.W. Smith and K. Brennan, 2008. Interactions between adult migratory striped bass (*Morone saxatilis*) and their prey during winter off the Virginia and North Carolina Atlantic coast from 1994 through 2007. *Fishery Bulletin*, 106: 2. pp. 174-182.
- Palkovacs, E.P., K.B. Dion, D.M. Post and A. Caccone. 2008. Independent evolutionary origins of landlocked alewife populations and rapid parallel evolution of phenotypic traits. *Molecular Ecology* 17, 582–597.
- Patterson, Cheri, M. Dionne, K. Sullivan, R. Heuss, R. Zobel, J. Fischer, K. Trull, R. Eckhart, and C. Warner. 2009. *New Hampshire's Marine Fisheries Investigation: Project 1: Anadromous Fish Investigations*. Federal-aid F-61-R (NH). Final Report. Concord, NH. 23 pp.
- Petersen, J. H., R. A. Hinrichsen, D. M. Gadomski, D. H. Feil, and D. W. Rondorf. 2003. American shad in the Columbia River. Pages 141-155 *in* K.E. Limburg and J.R. Waldman, editors. *Biodiversity, status, and conservation of the world's shads*. American Fisheries Society, Symposium 35, Bethesda, Maryland.

- PFBC (Pennsylvania Fish and Boat Commission), 2011. Schuylkill River American Shad. http://fishandboat.com/shad_schu.htm
- PFBC (Pennsylvania Fish and Boat Commission), 2008. PA Bulletin, Doc. No. 03-392, Rules and regulations [58 PA. Code Chs. 61 and 65], E. Summary of Changes. Filed for public inspection March 7, 2003. www.pabulletin.com.
- Puriton, T., F. Doyle and R. Stevenson, 2003. Status of River Herring on the North Shore of Massachusetts. Eight Towns & Bay.
- Reynolds, J., Food – Sister Act. NY Times Magazine. Published May 14, 2000.
- Richardson, B. R., P. Morin, M. W. Baldwin, and C. P. Stence. 2006. Restoration of American shad and hickory shad in Maryland's Chesapeake Bay. 2005 Final Progress Report. Maryland Department of Natural Resources, Technical Memorandum, Annapolis.
- Richkus, W. A. 1974. Factors influencing the seasonal and daily patterns of alewife (*Alosa pseudoharengus*) migration in a Rhode Island river. J. Fish. Res. Bd. Canada 31: 1485-1497.
- RMC (Research, Management, and Conservation Environmental Services Ltd.). 1992. Turbine passage survival of juvenile American shad (*Alosa sapidissima*) at the Holtwood Hydroelectric Station, Pennsylvania. Report prepared for Pennsylvania Power and Light Company, Allentown, Pennsylvania.
- RMC Environmental Services. 1993. Job V. Turbine passage survival of juvenile American shad at Conowingo Hydroelectric Station. In: Restoration of American shad to the Susquehanna River, Annual Progress Report, 1992. Susquehanna River Anadromous Fish Restoration Committee.
- Rudershausen P.J., J.E. Tuomikoski, J.A. Buckel, J.E. Hightower, 2005. Prey selectivity and diet of striped bass in western Albemarle Sound, North Carolina. Transactions of the American Fisheries Society, 134. pp 1059-1074.
- Rulifson, R.A., M.T. Huish and R.W. Thoesen, 1982. Anadromous fish in the southeastern United States and recommendations for development of a management plan. U.S. Fish and Wildlife Service, Atlanta, Georgia.
- Schramm Jr., H.L., P.D. Gerard. 2004. Temporal changes in fishing motivation among fishing club anglers in the United States. Fisheries Management and Ecology 11:313-321.
- Sullivan, T.J. 2004. Evaluation of the Turner's Falls Fishway complex and potential improvements for passing adult American shad. M.Sc. Thesis, Department of Natural Resource Conservation, University of Massachusetts, Amherst, MA. 105 pp.
- Taylor, R. and B. Kynard. 1983. Holyoke Dam fishery studies—1983. Report to Northeast Utilities Service Company, Berlin, Connecticut, USA.
- Walburg, C.H. and PR Nichols, Biology and management of the American shad and status of the fisheries, Atlantic Coast of the United States 1960, US Fish Wildl. Serv. Spec. Sci. Rep. Fish. 550 (1967), p. 105

- Walter, J.F. and H.M. Austin, 2003. Diet composition of large striped bass in Chesapeake Bay. *Fishery Bulletin – NOAA*. Vol 101, part 2. pp 414 – 423.
- Walter, J.F. III, A.S. Overton, K.H. Ferry and M.E. Mather, 2003. Atlantic coast feeding habitats of striped bass: a synthesis supporting a coastwide understanding of trophic biology. *Fisheries Management and Ecology*, 10. pp. 349-360.
- Wildman, Timothy and Steve Gephard. 2009. The plan to restore diadromous fishes to the Shetucket River Watershed. State of Connecticut- DEP/Inland Fisheries Division. Old Lyme, CT. 47 pp.