

W&M ScholarWorks

Reports

11-2017

A Brief Guide to Striped Bass Ecology & Management in Chesapeake Bay

Mary C. Fabrizio Virginia Institute of Marine Science

Troy D. Tuckey Virginia Institute of Marine Science

Susanna Musick Virginia Institute of Marine Science

Follow this and additional works at: https://scholarworks.wm.edu/reports

Part of the Aquaculture and Fisheries Commons, Laboratory and Basic Science Research Commons, Marine Biology Commons, and the Natural Resources and Conservation Commons

Recommended Citation

Fabrizio, M. C., Tuckey, T. D., & Musick, S. (2017) A Brief Guide to Striped Bass Ecology & Management in Chesapeake Bay. Virginia Institute of Marine Science, College of William and Mary. https://doi.org/10.21220/V5NQ9X

This Report is brought to you for free and open access by W&M ScholarWorks. It has been accepted for inclusion in Reports by an authorized administrator of W&M ScholarWorks. For more information, please contact scholarworks@wm.edu.

A BRIEF GUIDE TO STRIPED BASS ECOLOGY & MANAGEMENT IN CHESAPEAKE BAY



Mary C. Fabrizio Troy D. Tuckey Susanna Musick

Prepared for the Recreational Fishing Advisory Board Virginia Marine Resources Commission

December 2017



EXECUTIVE SUMMARY

Chesapeake Bay striped bass support important recreational fisheries along the US Atlantic coast; in the late 1970s, the population of striped bass collapsed as a result of overfishing and poor water quality in rivers used for spawning and rearing of young. Informed by stock assessments, strict management regulations were enacted in the mid-1980s and early 1990s; these highly effective regulations resulted in the recovery of the population in 1995. A key to the successful recovery of the Atlantic coast striped bass was the wide range of ages of spawning females and the associated differences in spawning behavior among ages. Age diversity among spawning females and the variation in timing of spawning within a year ensure that some eggs and larvae encounter favorable growing conditions in nursery areas. In addition, survival of young striped bass is affected by the amount of freshwater flow in the tributaries, the number and strength of pulsed freshwater discharges, and wind and temperature conditions during spring; these conditions affect feeding opportunities and growth of young fish through complex physical processes that occur in nursery habitats. The annual production of young striped bass (recruitment) partially reflects environmental conditions, which vary from year to year.

Environmental conditions, including temperature and dissolved oxygen levels, also affect habitat use and the distribution of juvenile and adult striped bass in Chesapeake Bay. Since recovery, the striped bass population in Chesapeake Bay has likely exerted high predatory demand on forage fish populations in the bay; menhaden, gizzard shad, bay anchovy, and herrings are the primary prey of large striped bass in the bay, whereas smaller fish consume a greater proportion of invertebrates such as crabs and worms. When striped bass consume other fish, their exposure to contaminants increases; thus, larger striped bass tend to exhibit higher concentrations of contaminants than smaller fish. Due to the high variability in feeding patterns and growth rates, contaminant concentrations in striped bass are difficult to predict from size or age alone.

Migratory behaviors in striped bass vary among individuals; some fish are resident in the bay year-round, whereas others participate in extensive migrations along the Atlantic coast. Groups of fish that share the same migratory behavior profile are termed contingents and members of a contingent may experience different growth and mortality rates. Regardless of their migratory behavior, mature striped bass return to the bay to spawn in the spring; although spawning occurs in multiple tributaries and in the upper bay, the striped bass population in Chesapeake Bay is considered a single stock. Since the late 1990s, the Chesapeake Bay stock of striped bass has experienced increases in natural mortality rates, and this increase is believed to be associated with disease (mycobacteriosis).

Currently, striped bass are not overfished and are not experiencing overfishing; however, abundance has declined since 2005. Although well-studied, future research on Chesapeake Bay striped bass should focus on the effects of disturbances that threaten the long-term sustainability of the stock. In particular, alterations and reductions in habitat quality and quantity, and long-term environmental changes associated with climate change present formidable challenges. We conclude this report with 29 recommendations for research to advance our understanding of the population biology and ecology of Chesapeake Bay striped bass.



Image courtesy of the Integration and Application Network (ian.umces.edu/symbols/)

INTRODUCTION – Chesapeake Bay striped bass support important recreational fisheries along the US Atlantic coast. Management of the fisheries is informed by stock assessments.

Striped bass (*Morone saxatilis*) have been an important fishery in the United States since the early 1600's, and the fishery was regulated as early as 1639. Today, striped bass are targeted by recreational anglers from ME to SC; commercial fisheries are permitted in states that produce large numbers of juveniles (NC, VA, MD, DE, NY) as well as MA and RI. In Virginia, striped bass support valuable recreational and commercial fisheries.

Most of the annual harvest of striped bass along the Atlantic coast is due to the recreational sector (Figure 1). This is also true of harvests in Virginia (Figure 2). However, since 2010, similar numbers of fish were harvested by recreational and commercial fishers from Virginia waters (Figure 2). Also, as a result of annual quotas, commercial harvests in Virginia have remained relatively steady since the mid-1990s.

Along the coast, more fish were harvested annually by the recreational fishery than the commercial fishery during the last decade (2006-2015; Figure 3). A similar result can be seen for harvests in Virginia (Figure 4). However, estimates of harvests do not include fish that die after capture and release (for example, fish that are released because they are smaller than the minimum size). Thus, the number of harvested fish represents only one type of removal or loss from the population; another type is the loss associated with postrelease mortality. Post-release mortality varies by sector, but is estimated to be 9% for the recreational fishery. Taking this post-release mortality into account, the recreational fishery along the coast was responsible for 85 to 90% of annual striped bass removals during the last decade (ASMFC 2016).

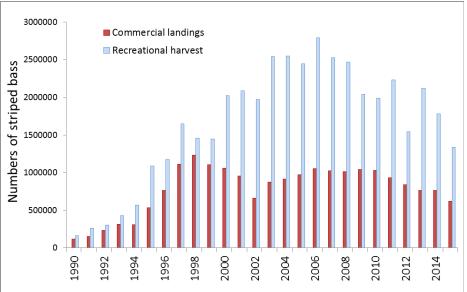


Figure 1. Annual harvest of striped bass (in numbers of fish) along the coast and by sector, 1990 to 2015. Adapted from ASMFC 2016.

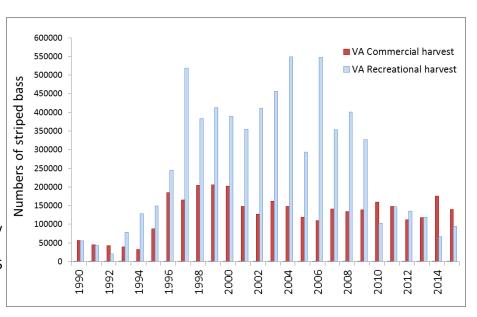


Figure 2. Annual harvest of striped bass (in numbers of fish) in Virginia by sector, 1990 to 2015. Adapted from ASMFC 2016.

In general, fisheries managers aim to maintain a population of fish large

enough to sustain commercial and recreational fisheries in the future. To do this, scientists collect information and data to assess the status of fish stocks by estimating the number of fish in the population. Stock

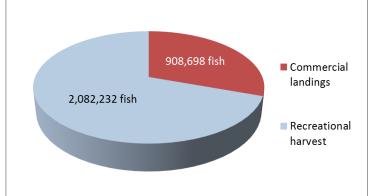
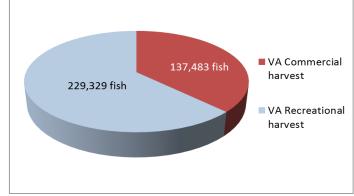
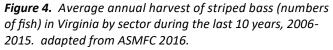


Figure 3. Average annual harvest of striped bass (numbers of fish) across all states and by sector during the last 10 years, 2006-2015. Adapted from ASMFC 2016.





assessments provide information for making decisions about bag limits, seasonal closures, minimum sizes, and other restrictions. Stock assessments are based on catch data collected through logbooks, observers, and recreational anglers including telephone interviews and dockside surveys (NOAA Fisheries 2017). Stock assessments also use abundance data from scientific surveys to help inform scientists about the number of adult and juvenile fish in the population; biological data from such surveys provide information about fish growth and mortality. To manage a fishery, managers need to understand how many fish are old enough to spawn (spawning stock biomass, or SSB), the growth rate of individual fish, the numbers of new fish expected to enter the population (juvenile abundance index), and the numbers of fish that leave the population through natural mortality (M) and fishing mortality (F; Figure 5).

Stock assessment models use observations of the catch, stock abundance (numbers of fish), mortality, growth, reproduction and movement to determine the condition of the fisheries resource. Fisheries managers then use these models to set catch targets and make regulations to help ensure that there are enough fish in the population to support recreational and commercial fisheries (NOAA Fisheries 2017).

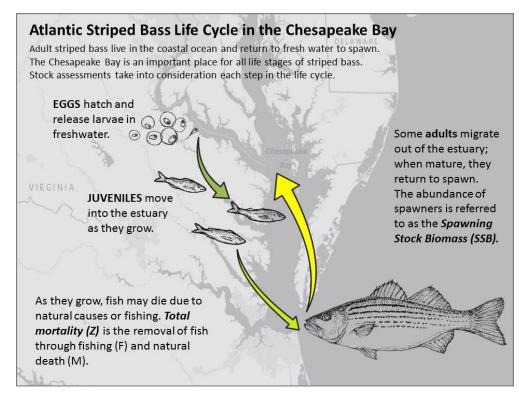


Figure 5. Life cycle of the Atlantic striped bass and key stock assessment concepts.

POPULATION DYNAMICS – The striped bass population in Chesapeake Bay collapsed in the late 1970s, but as a result of strict management regulations enacted in the mid-1980s and early 1990s, the population was recovered in 1995.

The striped bass population in Chesapeake Bay collapsed in the late 1970s due to a combination of factors including overfishing and poor water quality in some of the nursery areas (Richards and Rago 1999). Strategies to recover the population included fishery closures and harvest restrictions (quotas, gear restrictions, area and seasonal closures, length limits) that protected young female fish until they were able to grow to a size large enough to reproduce (Figure 6). Production of eggs and juveniles relies on the presence of sufficient numbers of mature female striped bass as well as favorable environmental conditions for survival and growth of eggs, larvae, and juveniles. The population of striped bass in Chesapeake Bay responded well to management measures, and recruitment - or the numbers of juveniles entering the population – began to increase in the late 1980s (Richards & Rago 1999). Protection of young females was critical during the period of recovery because most egg

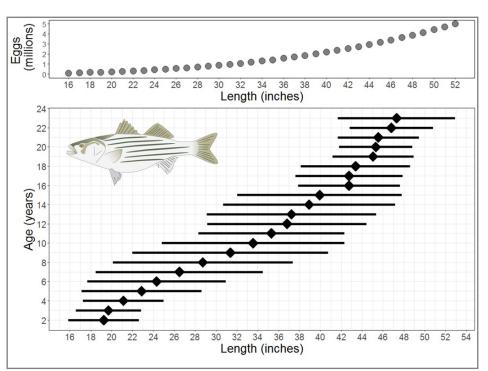


Figure 6. Average (filled diamonds) and range of lengths (thick black lines) of striped bass between 2 and 23 years old in Chesapeake Bay. Also shown is the average number of eggs (in millions) produced by female striped bass between 16 and 52 inches. For example, a 20-inch fish produces about 247,000 eggs; a 28-inch fish produces about 710,000 eggs; and a 36-inch fish produces about 1,568,000 eggs. Length at age data are from Liao et al. 2017. Average egg production was estimated from the egg-weight relationship in Lewis & Bonner (1966). Image of striped bass courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

production was associated with these young female fish (Secor 2000a). In addition, the striped bass population was able to persist during the period of poor recruitment because of their long reproductive lifespan (about 25 years), and their unique traits and habitat requirements; unlike other species with fishery closures or partial closures (American shad, shortnose sturgeon), the unique characteristics of striped bass (long reproductive lifespan, high survival rates, and fast growth) allowed the population to respond to management regulations (Secor 2000a). Also, because population numbers were low during the 1970s-1980s, competition was reduced and striped bass growth and potential recruitment were high (Rutherford et al. 2003).

In recent years, concerns about the recovered population in Chesapeake Bay have been raised because of disease (mycobacteriosis) and reduced prey availability in the Bay (Hartman & Margraf 2003; Uphoff 2003). Mycobacteriosis leads to cryptic mortality (i.e., mortality which is not observed) which explains the increase in non-fishing mortality observed in recent stock assessments (Gauthier et al. 2008). In addition, the sublethal effects of mycobacteriosis (i.e., effects that do not cause mortality but may alter growth and other processes) are thought to limit growth of striped bass in Chesapeake Bay (Latour et al. 2012; Lapointe et al. 2014). For example, fish with mycobacteriosis exhibit smaller maximum sizes (Latour et al. 2012), and in the presence of

high temperature (82°F), adult striped bass with mycobacteriosis are less able to cope with low dissolved oxygen conditions (Lapointe et al. 2014). Waters with dissolved oxygen levels below 2 mg of oxygen per liter (2 mg/L) are considered hypoxic and harmful to aquatic life. In warm (82°F), hypoxic waters, striped bass with mycobacteriosis have about one-third of the energetic capacity of healthy striped bass at 68°F (Lapointe et al. 2014), indicating that striped bass that occupy warm hypoxic waters have less energy available for locomotion, growth, and reproduction. Because fish with mycobacteriosis grow slower than healthy fish, a 3.3% loss of lifetime reproductive output could be expected (Gervasi 2015). However, the greatest effect of the disease is through mortality, particularly of older fish (6 years and older), and this can result in a 74.5% loss in reproductive output (Gervasi 2015).

REPRODUCTION – One key to the successful recovery of the striped bass along the Atlantic coast was the wide range of ages of spawning females and the associated differences in spawning behavior among ages. Resiliency of the stock depends on a diverse age structure of spawning fish.

Striped bass mature earlier now than they did in the 1970s and 1980s, with 50% of females mature at age 2.95 years compared with the ranges reported previously, 3-4 years and 6-7 years (Gervasi 2015). For species like striped bass, the timing of spawning in spring is a critical determinant of the number of young fish that are produced each year (Secor & Houde 1998), and a greater diversity of ages among spawning females is believed to contribute to the likelihood of dominant year classes (Secor 2000b). This is because smaller/younger females tend to spawn later in the spawning period, whereas larger/older females spawn earlier (Secor 2000b). This behavior is a type of bet-hedging against the highly variable environmental conditions that occur in nursery areas in the spring when striped bass spawn in the Chesapeake Bay region. The age diversity of spawners was a critical attribute of the population during the recovery period (1985-1995) and high age diversity was associated with greater juvenile abundance (Secor 2000b). Like other long-lived fishes, an individual mature striped bass may not spawn every year; when this 'skipped spawning' occurs later in life, the effect on reproduction is greater than when this occurs early in life (Secor 2008). The implications of these phenomena are that the age structure of the spawning fish should be protected and maintained in order to promote resiliency to environmental change and fishing pressure (Secor 2008).

Water temperature may be more important than number of daylight hours in initiating, maintaining, and terminating striped bass reproduction (Clark et al. 2005). Cool temperatures prior to spawning are necessary for female striped bass to initiate the reproductive cycle (Clark et al. 2005). Warm winter temperatures may negatively affect reproduction in striped bass by reducing the time available for egg development or by changing the time of spawning. Climate-related variations in annual spring-time temperatures may also affect the population by contributing to mortality of egg-bearing females (Peer & Miller 2014). For example, in cool years, egg -bearing females delay entry to the spawning grounds and are vulnerable to the fishery for a longer period of time compared with warm years (Peer & Miller 2014). Climate-induced changes in the timing of the spawning migration may thereby have indirect effects on the fishing mortality of adult striped bass (Peer & Miller 2014).

RECRUITMENT – Survival of early life stages of striped bass is affected by the amount of freshwater flow in the tributaries, the number and strength of pulsed freshwater discharges, and wind and temperature conditions during spring. Decadal variations in periods of high and low recruitment appear to be characteristic of fishes that use Chesapeake Bay as a nursery area.

Recruitment is highly variable in striped bass (Martino & Houde 2010). Environmental factors affect the survival of striped bass eggs and larvae, particularly mean springtime freshwater flow (North & Houde 2001; Kim-

merer et al. 2001; Martino & Houde 2010). For example, 1999 was a low-flow year in the Chesapeake Bay region and striped bass larvae were virtually absent in the nursery areas of the upper bay (North & Houde 2001). In estuaries like Chesapeake Bay, the mixing of fresh and saltwater creates conditions that are favorable for the growth of zooplankton, on which young striped bass feed. This area where freshwater and saltwater mix is characterized by reduced water clarity and is called the estuarine turbidity maximum (ETM) zone. In the upper Chesapeake Bay, the ETM is an important nursery area because striped bass larvae are retained within salinity conditions that are favorable to growth (North & Houde 2001; North et al. 2005). Feeding opportunities for larval striped bass within the ETM are enhanced in years of high freshwater flow because both larvae and their prey (zooplankton) are retained within the ETM (Martino & Houde 2010). Freshwater flow and temperatures in spring were important factors to explain variation in recruitment of striped bass in the upper bay between 1986 and 2006; strong year classes, like those observed in 1996 and 2003, were produced in years of high freshwater flow (Martino & Houde 2010). In the Patuxent River, low temperatures and high flows in winter were associated with high abundance of juvenile (age-0) striped bass in the following summer and fall (Wingate & Secor 2008). In another study, variation in juvenile abundance in the upper bay from 1986 to 2002 could be explained by mean spring freshwater flow and the number of pulsed freshwater events during the spawning season (North et al. 2005). Timing of striped bass spawning in relation to pulsed freshwater-discharge events may negatively affect egg transport if spawning occurs before or during these pulsed events (North et al. 2005). This is because strong wind events and pulsed discharges of freshwater to the bay reduce the likelihood of egg transport to the ETM (North et al. 2005).

A long-term study of recruitment of juvenile fishes in Chesapeake Bay suggests that much of the variation observed in annual juvenile abundances occurs on decadal scales; a shift likely occurred in 1992 such that recruitment of river-spawning fishes such as striped bass was favored over that of shelf-spawning fishes such as summer flounder (Wood & Austin 2009). This synchrony in recruitment was observed during the period 1968-2004 and is thought to reflect changes in regional climate conditions (Wood & Austin 2009).

Juvenile striped bass in Chesapeake Bay exhibit density-dependent growth (that is, slower growth in the presence of more juvenile striped bass); this type of response suggests that prey availability limits growth in highabundance years (Martino & Houde 2012). Furthermore, density-dependent growth is believed to lead to sizeselective mortality in winter (Martino & Houde 2012). Local density of fish is also related to body condition of juvenile striped bass in Chesapeake Bay such that juvenile fish tend to exhibit low condition when densities are high; these density effects were more important for explaining spatial variation in condition than temperature, salinity, dissolved oxygen, or depth (Schloesser 2015). Feeding incidence and prey per gut of striped bass larvae from the upper bay were similar during high (2007) and low (2008) recruitment years (Shideler & Houde 2014), suggesting that factors other than larval feeding contributed to differences in recruitment for these two year classes. Indeed, recruitment success depends on the availability and quantity of nursery habitats (Kimmerer et al. 2009), as well as predation on young striped bass.

As the climate warms, increasing water temperature and precipitation will likely affect recruitment of striped bass in Chesapeake Bay in a number of ways (Kerr et al. 2009). First, high water temperatures (above 84°F) reduce growth rates of juvenile striped bass, potentially exposing them to higher rates of predation (Cox and Coutant 1981). Second, warmer water holds less oxygen, which may result in a loss of suitable habitat available to striped bass (Coutant 1990). Third, rising water temperatures may also affect the timing of spawning of striped bass and create a mismatch between the production of young striped bass and their food. Conversely, higher streamflow due to increased precipitation may enhance reproductive success of striped bass by stimulating the base of the food web and providing more food for young fish (North and Houde 2003; Martino and Houde 2004). Whereas increased water temperature appears to have negative effects on recruitment, increased precipitation events may flush larvae out of nursery habitats and reduce reproductive success.

HABITAT – Habitat use by juvenile and adult striped bass in Chesapeake Bay is shaped by environmental conditions, including temperature and dissolved oxygen levels.

As the climate warms, water temperatures will continue to rise and the extent and duration of low dissolved oxygen (hypoxia) events are predicted to increase. Hypoxia occurs when the level of dissolved oxygen in the water drops below the critical threshold for most aquatic organisms (2 mg/L); when this occurs, organisms cannot obtain sufficient oxygen from the water and may die if they cannot move to areas with more oxygenated waters. Currently, conditions in Chesapeake Bay may be limiting for striped bass in summer, when high temperatures combine with low dissolved oxygen. Fish can avoid hypoxic conditions, but may be forced to use habitats that exceed their temperature preference (Kraus et al. 2015). In response to elevated temperatures, fish metabolic rates increase and their need to consume prey also rises. Thus, as a result of hypoxia and the use of warmer-than-preferred areas, fish may need to locate and consume additional prey to be able to gain enough energy to cope with temperature stress.

Juvenile (age-0) striped bass from the Chesapeake Bay grow best at relatively warm temperatures (82°F) and intermediate salinity (7 psu – or about 23% of full-strength seawater; Secor et al. 2000). When dissolved oxygen declines to low levels (4 mg/L or lower), food consumption by juvenile fish declines and their growth is depressed (Brandt et al. 2009). Unlike other shallow-water, small-bodied fishes (e.g., killifishes and silversides) striped bass are incapable of obtaining oxygen by gulping air at the surface (Dixon et al. 2017). Instead, juvenile striped bass cope with oxygen stress by resting on the bottom (Dixon et al. 2017); juvenile striped bass are 5 times more tolerant of hypoxia (less than 2 mg/L) at rest than when swimming (Nelson & Lipkey 2015). Ultimately, however, when exposure to hypoxia is prolonged, fish will die (Dixon et al. 2017).

The concentration of dissolved oxygen in bottom waters is a good predictor of the presence of striped bass in tributaries of Chesapeake Bay; further, dissolved oxygen is associated with the percent of impervious surfaces (paved surfaces, buildings, and compacted soils) in the watershed (Uphoff et al. 2011). Aquatic environments in suburban watersheds (10% or more impervious surfaces) are highly impacted and exhibit dissolved oxygen concentrations that seldom exceed 3 mg/L. In these watersheds, striped bass occurred in only 10% of samples, whereas 50% of samples from aquatic habitats with dissolved oxygen levels exceeding 5 mg/L contained striped bass (Uphoff et al. 2011). Maintenance of healthy aquatic environments that support striped bass requires management of impervious surfaces in the watershed to avoid low dissolved oxygen concentrations in these waters.

Adult striped bass tagged in the Patuxent River avoided hypoxic areas in summer and occupied surface waters that were warmer than optimal temperatures (Kraus et al. 2015). These surface waters in summer may be areas with the highest growth rate potential for adult striped bass because of the high abundance of prey in these surface waters (Kraus et al. 2015). Indeed, the recovery of striped bass in the 1990s may have been aided by the concentration of striped bass and their prey in warm, surface waters (Costantini et al. 2008). Currently, however, surface water temperatures exceed the threshold (82°F) tolerated by striped bass and may be contributing to reduced growth of adult striped bass.

Little is known about habitat use by adult striped bass in winter. One tagging study found that striped bass 3.1 feet total length (TL) and larger spend more than 90% of their time in the upper 32.8 feet of the water column in temperatures of 43-48°F near the mouth of the Chesapeake Bay; these fish also moved a minimum of 23.3 to 108.5 km during the 30-day period in winter during which they were tracked (Graves et al. 2009). However, this study included information from only 8 fish, and should be repeated with more fish to better understand habitat use in winter.

Habitat degradation has negative consequences on striped bass populations, the fisheries that target striped bass, and the local economies supported by these fisheries. For example, angler catch rates decline when low dissolved oxygen conditions are present in the bay (Lipton & Hicks 2003). Furthermore, anglers are likely to

decrease their participation in the fishery if dissolved oxygen levels are allowed to deteriorate so that they never exceed 5 mg/L (Lipton & Hicks 2003). These changes in angler behaviors occur because expected catch rates and travel costs and time significantly influence the choice of fishing location by anglers (Lipton & Hicks 2003). In the presence of hypoxia, economic losses for the Patuxent River were estimated to be \$100,000 and almost \$300,000 if the river is allowed to become anoxic (no dissolved oxygen in the water); economic losses increase as the area impacted by low dissolved oxygen increases (Lipton & Hicks 2003).

Climate change can also impact striped bass fisheries in the mid-Atlantic region (Kerr et al. 2009), but the consequences of climate change on recreational fisheries depend on the magnitude of environmental change. For example, damage to infrastructure that supports recreational fisheries (such as marinas, docks, and boat launches) may be offset by the increased numbers of fishing days due to warmer temperatures (Kerr et al. 2009). The availability of striped bass and the catchability of legal-sized fish will be affected by climate change and will impact where and when fish are available for capture (Kerr et al. 2009). Finally, climate change effects will be manifested by changes in the productivity of the stock that will in turn affect stock size and resilience (Kerr et al. 2009). Effects of climate change on human communities that participate in recreational or commercial fishing can be assessed using newly developed indices to measure vulnerability to climate change (Colburn et al. 2016), although these indices have not yet been applied in the Chesapeake Bay region.

FEEDING ECOLOGY – After the striped bass population in Chesapeake Bay recovered, this species likely exerted high predatory demand on forage fish populations in the bay.

Feeding studies of striped bass focus on habits of either resident fish (fish that inhabit Chesapeake Bay) or coastal migrants (fish that leave the bay). Within the bay, young striped bass (7.8–15.7 inches fork length [FL]) successfully feed within oyster reefs: all striped bass collected from an oyster reef in the Piankatank River contained food in their stomachs, whereas striped bass feeding in nearby sand bar or oyster shell bar habitats did not (Harding & Mann 2003).

The recovery of the striped bass stock in Chesapeake Bay increased the predatory demand in the bay at the same time that Atlantic menhaden abundance declined (Uphoff 2003). After 1998, potential striped bass predation on menhaden may have exceeded the supply of menhaden (Uphoff 2003). Consistent with this hypothesis are observations of fish that were smaller than expected for a given age, and the appearance of mycobacteriosis in striped bass (Jacobs et al. 2009).

Diets of large (>18 inches TL) striped bass from Chesapeake Bay in spring and fall 1997 showed that only a few species of prey fish were dominant across seasons and size ranges (Walter & Austin 2003). Although menhaden were the primary prey of striped bass from most areas of the bay, gizzard shad were a key prey item for striped bass captured from low salinity areas (Walter & Austin 2003). Other important prey included spot, croaker, and herrings; thus, bottom fishes contributed a greater percentage of the diet than was previously observed (Walter & Austin 2003). The diet of striped bass collected between 1998 and 2001 varied with size of the fish, such that small (5.9 -11.8 inches TL) striped bass consumed primarily invertebrates (such as worms and crabs) in spring; by fall, bay anchovy were the dominant prey particularly in the lower and middle bay (Overton et al. 2009). Larger striped bass preyed on pelagic schooling fishes (bay anchovy, menhaden); in the upper bay, gizzard shad and menhaden were important prey for larger striped bass (Overton et al. 2009). Large striped bass (> 27.6 inches TL) exhibited a greater reliance on small pelagic prey (bay anchovy) during spring and summer than had been observed previously (Overton et al. 2009). A modeling study of Chesapeake Bay striped bass for the period 1955 to 2001 indicates that in the 1990s, striped bass consumed less menhaden and more bay anchovy than during the 1950s (Overton et al. 2015). Most of the difference in estimated consumption was associated with consumption patterns of the younger fish (Overton et al. 2015). For example, in the 1990s, 2-year-old striped bass consumed about 8 times more blue crabs than during the 1950s (Overton et

al. 2015). Furthermore, the diets of striped bass reflected the decline in menhaden abundance observed during the 1990s (Overton et al. 2015).

Outside of Chesapeake Bay, coastal striped bass greater than one-year old rely on menhaden, anchovies, alewife, blueback herring, and Atlantic herring regardless of season or size (Walter et al. 2003). Diets of striped bass in Delaware Bay and north were dominated by invertebrates; in the absence of large schools of menhaden, coastal striped bass may feed on organisms found on the bottom such as invertebrates (Walter et al. 2003).

Along the coast, striped bass compete for menhaden, bay anchovy, and other pelagic prey with other fisheating species such as spiny dogfish (Bangley & Rulifson 2014), summer flounder, bluefish, and weakfish (Wuenschel et al. 2013). Diets of striped bass (16.6 – 36.2 inches FL) collected in NJ coastal waters between June and October 2005 varied with fish size, and diet overlap with other species increased several fold in the fall (Wuenschel et al. 2013). During winter, striped bass (>15.7 inches TL) off the coast of VA and NC fed primarily on menhaden and bay anchovy, but also on croaker and spot (Overton et al. 2008). In more recent years (2002-03, 2005-07), a greater proportion of the diet of coastal striped bass was comprised of menhaden compared with earlier years (1994-96; Overton et al. 2008).

Condition, defined as the health or nutritional status, of adult striped bass can be assessed by measuring the moisture content of muscle tissue, and fish with greater than 80% moisture content are considered to be in poor condition (Jacobs et al. 2013). Further, this condition indicator could be used to set targets for management: for example, in fall, a healthy population in Chesapeake Bay would be indicated by 75% of the population having moisture values below the threshold (Jacobs et al. 2013). Alternatively, an index of body fat, which requires less time to determine than moisture content, could be used to evaluate striped bass condition in the bay (Jacobs et al. 2013). More recently, tools such as the fatmeter can be used to determine fish condition without having to sacrifice the fish (Schloesser and Fabrizio 2017).

CONTAMINANTS – Concentration of mercury in Chesapeake Bay striped bass increases with fish size and is higher among striped bass that consume other fish.

In recent years, mercury levels have been the focus of contaminant studies in Chesapeake Bay striped bass. The degree to which striped bass consume other fish is a dominant determinant of mercury concentrations in striped bass (Xu et al. 2013), and total mercury and methylmercury concentrations increase with size of individual striped bass from the Chesapeake Bay (Mason et al. 2006); methylmercury is the organic form of mercury that is readily available for uptake by aquatic animals and humans. In addition, striped bass that remain in the bay have higher methylmercury burdens than migratory fish of the same size (Mason et al. 2006). However, none of the striped bass (20 – 22.8 inches FL) from the lower Chesapeake Bay had total mercury levels that exceeded the EPA human health screening value (300 ug/kg wet weight; Xu et al. 2013). None of the striped bass from the middle and upper Chesapeake Bay or the Potomac River exceeded the 1.0 mg/kg mercury threshold used by the FDA, although three fish exceeded the 0.5 mg/kg threshold used by some states for mercury advisories (Gilmour & Riedel 2000).

STOCK STRUCTURE – The striped bass population in Chesapeake Bay is considered a single stock, although spawning occurs in multiple tributaries and in the upper bay.

Striped bass in Chesapeake Bay spawn where fresh and estuarine waters mix, in a zone known as the estuarine turbidity maximum (North & Houde 2001). In Virginia, striped bass spawn in the James, Chickahominy, Pamunkey, Mattaponi, and Rappahannock rivers; these areas serve as primary nursery areas for striped bass. Similarly, striped bass use multiple tributaries in Maryland for spawning and rearing of young, including the Potomac, Patuxent, Nanticoke, Choptank, Chester, Blackwater, Wicomico, Manokin, Transquaking, and Pocomoke rivers; the upper bay is a significant spawning and primary nursery area for striped bass (Speir et al. 1999). In any given year, the number of fish spawning in a particular river varies; for example, more eggs and larvae were found in the Pamunkey River compared with the Mattaponi River in 1997 (Bilkovic et al. 2002). Although juvenile production varies from river to river, the group of striped bass spawning in Maryland and Virginia waters encompasses a single Chesapeake Bay stock (Brown et al. 2005; Gauthier et al. 2013). Further, some individuals from the Chesapeake Bay stock have been shown to contribute to spawning in other areas (Delaware River, Hudson River, and North Carolina, Gauthier et al. 2013; Kneebone et al. 2014). Although the Chesapeake Bay stock is considered a single well-mixed genetic population, differences in growth (up to age were observed among fish from the Choptank River, Nanticoke River, and C&D Canal (Woods et al. 1999). Growth differences were also observed among and within offspring of the same parents (Woods et al. 1999), suggesting that local conditions, prey availability, and habitat use may contribute to differences among juvenile fish.

MIGRATORY BEHAVIORS – Striped bass exhibit a variety of migratory behaviors; some fish are resident in the bay year-round, whereas others participate in extensive migrations along the Atlantic coast. Groups of fish that share the same migratory behavior are termed contingents.

Juvenile striped bass in the Patuxent River exhibit variation in migratory behavior related to growth: juveniles that moved into brackish waters exhibited slower growth as larvae compared with juveniles that remained in freshwater (Conroy et al. 2015). Juvenile striped bass that moved into brackish waters were not in better condition than juveniles that remained resident in freshwater habitats (Conroy et al. 2015). This flexibility in migratory behavior is termed 'contingent behavior' (Secor 2007) and has been observed in juvenile striped bass from the St. Lawrence estuary as well (Morisette et al. 2016). Variability in migratory behavior is thought to promote colonization of new environments (Morisette et al. 2016) and resiliency of populations to fluctuating environments (Secor 2007).

Small striped bass (<7.9 inches TL) from Chesapeake Bay, Delaware Bay, and the Hudson River have been found in New Jersey estuaries, where they may reside for several months to years (Able et al. 2012). The presence of these small fish suggests that striped bass may use estuaries along the coast as nursery areas; these nurseries are termed secondary nurseries because they occur in estuaries that are not used by adult striped bass as spawning areas (Able et al. 2012). Eventually, striped bass from secondary nurseries move into the coastal ocean and join the migrating population at similar sizes and ages as those from primary nurseries (Able et al. 2012).

As adults, Chesapeake Bay striped bass undertake coastal feeding migrations, but the portion of the stock that participates in coastal movements varies (contingent behavior), with some adult striped bass remaining resident in the bay for several years. Such contingent behavior has been observed in other species including white perch (Kerr & Secor 2009). Because individuals belonging to the resident contingent remain within the upper estuary, this behavior may result in differential mortality due to variations in local harvest restrictions

(Gahagan et al. 2015). Adult fish that migrate from the upper bay exhibit either estuarine or oceanic migrations; as fish increase in age, they are more likely to undertake oceanic migrations (Secor & Piccoli 2007). By age 13, about 75% of females leave the bay, and about 50% of males leave the bay (Secor & Piccoli 2007). Thus, substantial numbers of males undertake oceanic migrations – a finding that is in contrast to what was previously reported. Further, young females (ages 3-4) generally do not undergo mass emigration from (movement out of) the bay, however, some yearling fish were shown to move into coastal habitats (Secor & Piccoli 2007). During spring, adult striped bass move upriver for spawning, feeding, or both (Wingate et al. 2011). During summer, about 40% of the fish that were tagged in the Patuxent River were present within the river; most tagged fish spent 5-7 months in the river suggesting that such systems are important habitats during a major portion of the year (Wingate et al. 2011).

Large, migratory striped bass use estuaries along the Atlantic coast for foraging as far north as New England (Mather et al. 2009; Pautzke et al. 2010; Baker et al. 2016; Hollema et al. 2017), and fish may remain in these estuaries for a large portion of the year. For example, striped bass were present off Massachusetts from May to November and were subsequently observed at known spawning areas in Chesapeake Bay, Delaware River, and the Hudson River the following spring (Kneebone et al. 2014). In 2008 to 2010, the Chesapeake Bay stock was the largest contributor to the population of fish in Massachusetts (Kneebone et al. 2014). These fish often returned to the same feeding grounds in subsequent years, and typically used nearshore areas within 3 miles of the shore as migratory corridors between Massachusetts and their spawning grounds (Kneebone et al. 2014).

During winter, adult striped bass in the Patuxent River move downriver and into the bay and beyond (Wingate et al. 2011). Winter aggregations of striped bass occur in the Atlantic Ocean from just south of Cape Hatteras to as far north as Sandy Hook, NJ, although the northern extent varies greatly from year to year (Waldman et al. 2012). Interestingly, the stock composition of the group of striped bass that winters near the Delaware Bay and Cape Hatteras was similar and included fish from Chesapeake Bay as well as other stocks (Waldman et al. 2012). In one year, a large proportion of the fish off New Jersey during winter were fish from the Hudson River stock (Waldman et al. 2012).

STOCK ASSESSMENT – Natural mortality rates in striped bass increased since the late

1990s and this increase is believed to be associated with disease.

As with many other species, age estimates for striped bass determined from otoliths (fish ear bones) are more accurate and precise than those from scales (Liao et al. 2013). When scale-based ages are used in stock assessments, abundance is underestimated by 15%, biomass of spawning females is underestimated by 19%, and fishing mortality in recent years is overestimated by 19% (Liao et al. 2013).

Estimation of natural and fishing mortality rates remains a topic of interest among stock assessment scientists. A modeling simulation indicated that tagging studies should aim to include five or more age groups, rather than tagging only the youngest ages (Jiang et al. 2007a). More importantly, information about the tag-reporting rate (the proportion of tags that are turned in compared with the total number of tags actually caught) was needed to accurately assess mortality, particularly in the presence of age-dependent natural mortality (Jiang et al. 2007a). In a subsequent study, an increase in natural mortality was shown to occur in the late 1990s and the increase was associated with the appearance of mycobacteriosis in Chesapeake Bay striped bass (Jiang et al. 2007b).

Finally, striped bass were included in an extended multispecies stock assessment focused on menhaden and other prey species; predation mortality on menhaden (as well as prey fishes in general) must be quantified in order to produce effective assessments of prey fish, their predators, and the fisheries that target these species (Garrison et al. 2010). This research is currently underway in the Chesapeake Bay region (for example, Wood-land et al. 2017).

RECREATIONAL & COMMERCIAL FISHERIES – Currently, striped bass are not

overfished and are not experiencing overfishing; however, abundance has declined since 2005.

In 1981, the Atlantic States Marine Fisheries Commission (ASMFC) drafted a fisheries management plan for striped bass. Since the time of the original fishery management plan, there have been six Amendments and several Addendums; these documents can be viewed at http://www.asmfc.org/species/atlantic-striped-bass. In 1984, in response to a collapsed population, two amendments were passed to reduce fishing mortality and to recommend management measures. The Atlantic Striped Bass Conservation Act (Public Law 98-613) was also passed in 1984 (ASMFC 2016). This Act mandated the implementation of striped bass regulations and authorized the ASMFC to hold states responsible for complying with management recommendations. Amendment 3 was approved in 1984 and required states to adopt size regulations that would protect the group of striped bass that hatched in 1982, so that 95% of females hatched in that year could spawn at least once before reaching a size available to the fishery. Amendment 3 also took into consideration the juvenile abundance index, setting a target for the number of juvenile striped bass in the population. After decades of exploitation, and record declines in catch, Maryland closed their striped bass fishery in 1985; Virginia followed with a closure in 1989. That same year, Amendment 4 was implemented to focus on rebuilding the resource and a

new target fishing mortality rate (number of fish removed from the population through fishing) was set. In 1990, to further protect migrating striped bass and help rebuild stocks, all fishing for striped bass was banned in the Exclusive Economic Zone, that is, in waters from 3 to 200 nautical miles off the coast.

Fishing moratoria in Chesapeake Bay were lifted in 1990, and studies have shown that the 1981 moratorium in Maryland stimulated recovery in later years (Secor 2000a; Richards & Rago, 1999). During the next 5 years, recreational landings grew to 6.8 million pounds in 1994 under Amendment 4. In 1995, the Chesapeake Bay stock was declared restored and recreational landings grew to 12.5 million pounds (ASMFC 2016). Amendment 6 was adopted in 2003 to address several concerns including a perceived decrease in the abundance of large striped bass in the coastal migratory population, and to prevent the Amendment 5 exploitation target from being exceeded. New fishing mortality targets and thresholds were established through Amendment 6, and minimum size limits and new bag limits were set, with the Chesapeake Bay having more conservative measures. A bycatch monitoring and research program was started in 2007 through Addendum I to improve estimates of striped bass discards. In addition, a Presidential Executive Order encouraged states to designate striped bass a gamefish (implying the closure of all commercial fisheries). Addendum II was approved in 2010 to establish a new value for recruitment failure. Next, in 2012, Addendum III was approved to implement a commercial harvest tagging program to limit illegal harvest. Finally, Addendum IV was approved in 2014 to establish new fishing mortality reference points in response to a decline in spawning stock biomass.

Currently, Amendment 6 manages the Chesapeake Bay stock separately because of the size availability of striped bass in the bay. The Chesapeake Bay quota allocates shares to Maryland, the Potomac River Fisheries Commission, and Virginia. Each of these jurisdictions allocates their portion of the quota to its recreational and commercial fisheries. Virginia's regulations further divide their catches into Bay and Coastal areas (Figure 7). Virginia also regu-

Striped Bass Management Timeline

Fishery Management Plan – 1981
Amendment 1 – 1984
Amendment 2 – 1984
Amendment 3 – 1985
Amendment 4 – 1989
Addendum I – 1991
Addendum II – 1992
Addendum III – 1993
Addendum IV – 1994
Amendment 5 – 1995
Addendum I – 1997
Addendum II – 1997
Addendum III – 1998
Addendum IV – 1999
Addendum V – 2000
Amendment 6 – 2003
Addendum I – 2007
Addendum II – 2010
Addendum III – 2012
Addendum IV—2014

lates its recreational striped bass through seasonal restrictions. The most recent regulations allow an open season in the bay and coastal areas for the spring and summer from May 16 through June 15 with a minimum size of 20 inches TL and a maximum size of 28 inches, a possession limit of two fish per person, with one trophy-sized striped bass 36 inches or greater. The coastal trophy-size fishery in VA applies from May 1 to May 15 and excludes the upper spawning tributaries of the James, Pamunkey, Mattaponi, and Rappahannock rivers. The bay and tributary trophy fishery applies from May 1 to June 15. Anglers may keep only one trophy fish per day, and those who want to keep a trophy striped bass must have a trophy permit and must report the catch. In the fall, the bay fishery runs from October 4 to December 31 and requires a minimum size of 20 inches, with a maximum size of 28 inches (TL). Only one fish may be 28 inches, and only two fish per person may be kept per day. The coastal striped bass fishery is open from January 1 to March 31, and from May 16 to December 31. One fish per person per day may be kept with a minimum size of 28 inches TL (VAC 20-252-10 ET SEQ).

Historically, the recreational fishery has been the predominant source of fishery removals since the early 1990s (Figure 1). Further, since Amendment 6 was implemented in 2003, the majority of recreationally-caught striped bass have been released.

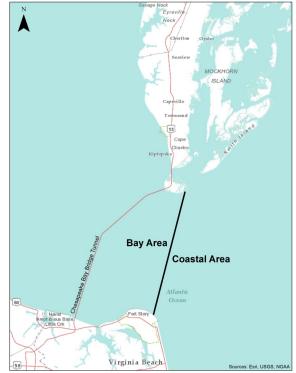


Figure 7. Virginia's Bay and Coastal fishery areas for striped bass based on VMRC Regulation 4 VAC 20-252-20.

The most recent stock assessment found that Atlantic coast striped bass are not overfished and are not experiencing overfishing (ASMFC 2016). Overfished refers to a population whose abundance is below the desired threshold abundance; overfishing refers to a fishing mortality rate (F) that exceeds the desired threshold. Both thresholds are determined from the stock assessment.

Some recreational anglers in Virginia are engaged in the trophy fishery for striped bass; although this component of the recreational fishery is small, the trophy fishery provides information on large fish. As of 1995, when the striped bass population was declared recovered, the number of citations (fish greater than 40 lbs or approximately 44 inches TL) for Virginia striped bass increased (Figure 8). However, since 2012, citations have declined. The reasons for this decline are uncertain, but likely include a reduced number of large fish in the population, a change in the availability of large fish within state waters, and a decline in angler fishing effort. Unfortunately, infor-

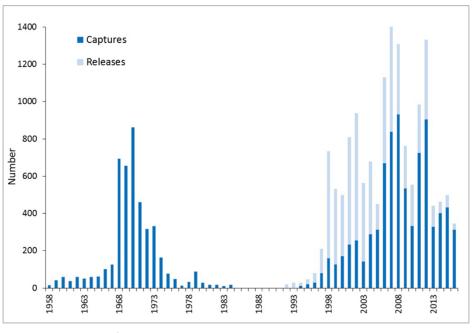


Figure 8. Number of citations issued by the Virginia Saltwater Fishing Tournament, 1958-2016.

mation on effort specifically targeting striped bass in the Virginia recreational sector is not available, nor do we know if and how availability may have changed.

Since 2009, total removals (including discards) of striped bass from the Chesapeake Bay by the recreational and commercial fisheries show a decrease in the proportion of fish aged 11 years and older, indicating that older, larger fish are captured less often in recent years compared with 2004 to 2009 (except for 2012; Figure 9). A decline in the proportional catch strongly indicates a decline in the abundance of fish 11 years and older in the population (in the absence of age-specific regulatory measures).

In contrast to what was observed in the bay, the proportion of fish 11 years old and older that comprises fishery removals from the ocean (Figure 10) has been stable since 2004. In 2014, an increase in the proportion of these older fish was observed. Together, these figures indicate that fewer older (> 11 years) striped bass have been removed from Chesapeake Bay since 2009, but the proportion of older fish removed from the ocean has remained stable since 2004. Thus, older fish are more likely to be encountered in the ocean than in the bay.

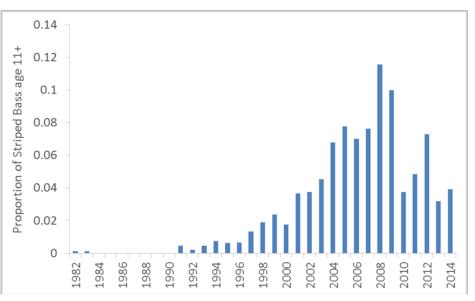


Figure 9. Proportion of Striped Bass 11 years old and older removed from Chesapeake Bay by commercial and recreational fisheries, 1982-2014.

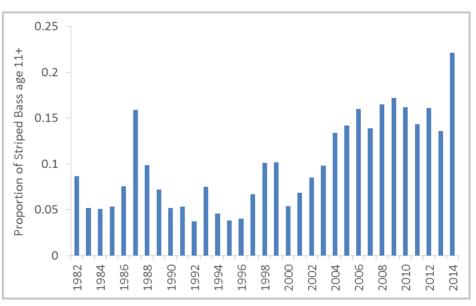


Figure 10. Proportion of Striped Bass 11 years old and older removed from the coastal ocean by commercial and recreational fisheries, 1982-2014.

RECOMMENDATIONS FOR RESEARCH – Although well-studied, future research on

Chesapeake Bay striped bass should focus on gaining a better understanding of habitat use of adult striped bass (particularly in winter), the ability of the stock to adapt to broad-scale environmental changes such as those anticipated under climate change, assessing the effects of habitat modifications (such as water with-drawals) on recruitment, and filling the needs of the stock assessment model.

Striped bass research continues to provide insights on the behavior and population biology of this species, yet the population continues to face disturbances that threaten its long-term sustainability. In particular, alterations and reductions in habitat quality and quantity and long-term environmental changes associated with global warming present formidable challenges. We recommend the following research (in no particular order) to advance our understanding of striped bass ecology and management: (1) examine the effect of a warming climate on the timing of spawning in Chesapeake Bay tributaries; (2) assess the ability of the Chesapeake Bay stock to adapt to broad-scale environmental changes such as those anticipated under climate change; (3) reevaluate the synchrony in recruitment of river-spawning fish like striped bass and shelf-spawning fish like summer flounder; (4) assess the quantity and quality of nursery habitats for striped bass in Virginia; (5) determine the impact of invasive blue catfish on larval and juvenile striped bass survival; (6) examine the relationship between condition of adult fish in fall to the production of young fish in the spring; (7) identify the location and design of all intake pipes (permitted commercial intakes and non-permitted agriculture intakes) located in striped bass nursery habitats in Chesapeake Bay, quantify water withdrawals, and assess effects on recruitment; (8) investigate the use of Virginia's coastal bays by small striped bass as a secondary nursery; (9) characterize the age and size composition of fish harvested by recreational anglers from Virginia coastal waters; (10) describe the distribution of large striped bass during winter, particularly in coastal waters; (11) determine contaminant levels other than mercury from harvestable striped bass; (12) examine the effects of recreational fishery regulations (e.g., slot limits) on the size and age structure of harvested and discarded striped bass; (13) evaluate angler preferences for size limits, bag limits, and fishing season in Chesapeake Bay; and (14) apply community social vulnerability indices to measure the effects of climate change on recreational and commercial fishers in Chesapeake Bay.

In addition to our recommendations above, the Atlantic States Marine Fisheries Commission recommended the following research to improve the accuracy and precision of stock assessments (Appleman, et al. 2016). Here, we provide a simplified description of those recommendations: (15) continue collection of paired scale and otolith samples from the fishery to permit estimation of ages from historical samples that used only scales; (16) determine gear-specific discard mortality rates and the magnitude of bycatch mortality in the fishery; (17) improve estimates of striped bass harvest removals in coastal areas during wave 1 and in inland waters of all jurisdictions year round; (18) evaluate the percentage of anglers that use circle hooks; (19) develop a refined and cost-efficient coastal population index for striped bass; (20) improve estimates of fishing mortality rates by integrating tagging models into the stock assessment (21) use tagging data to develop a movement model that can be used in the stock assessment; (22) use state-of-the-art modeling approaches to estimate fishing mortality rates from tagging data; (23) develop methods for combining results from tagging programs that release fish in different areas on different dates; (24) evaluate reliability of estimates of gear-specific mortality (trawls, pound nets, gill nets, and electrofishing), tag-induced mortality, and tag loss; (25) develop field or modeling studies to estimate natural mortality and other factors affecting the tag-return rate; (26) re-evaluate estimates of maturity at age for coastal striped bass; (27) examine methods to estimate annual variation in natural mortality; (28) develop reliable estimates of poaching loss from striped bass fisheries; and (29) improve methods for determining the sex ratio of the population particularly during spawning.

ACKNOWLEDGMENTS

We thank Charles Southall (MRFAB) and Ken Schultz (formerly, MRFAB) for informative discussions that helped us frame this report and for their thoughtful reviews of a previous draft. Olivia Phillips (VIMS) and Brian Gallagher (VIMS) also reviewed the draft and provided many suggestions to improve the presentation. This project was funded by the Marine Recreational Fishing Advisory Board and the Virginia Marine Resources Commission.

References

- Able, K. W., T. M. Grothues, J. T. Turnure, D. M. Byrne, & P. Clerkin. (2012). Distribution, movements, and habitat use of small striped bass (*Morone saxatilis*) across multiple spatial scales. *Fishery Bulletin*, 110: 176–192.
- Appleman, M., C. Godwin, W. Laney, G. Shepherd, & D. Orner. (2016). 2016 Revew of the Atlantic States Marine Fisheries Commission Fishery Management Plan for Atlantic Striped Bass.
- Atlantic States Marine Fisheries Commission (ASMFC). (2016). 2016 Review of the Atlantic State Marine Fisheries Commission Fishery Management Plan for Atlantic Striped Bass (*Morone saxatilis*): 2015 Fishing Season. A report prepared by the Atlantic Striped Bass Plan Review Team. 37 pp. Arlington, VA.
- Baker, H. K., J. A. Nelson, & H. M. Leslie. (2016). Quantifying striped bass (Morone saxatilis) dependence on saltmarshderived productivity using stable isotope analysis. Estuaries and Coasts, 39: 1537–1542.
- Bangley, C. W., & R. A. Rulifson. (2014). Feeding habits, daily ration, and potential predatory impact of mature female spiny dogfish in North Carolina coastal waters. *North American Journal of Fisheries Management*, 34: 668–677.
- Bilkovic, D. M., J. E.Olney, & C. H. Hershner. (2002). Spawning of American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) in the Mattaponi and Pamunkey rivers, Virginia. *Fishery Bulletin*, 100: 632–640.
- Brandt, S. B., M. Gerken, K. J. Hartman, & E. Demers. (2009). Effects of hypoxia on food consumption and growth of juvenile striped bass (*Morone saxatilis*). Journal of Experimental Marine Biology and Ecology, 381(SUPPL.) S143–S149.
- Brown, K. M., G. A. Baltazar, & M. B. Hamilton. (2005). Reconciling nuclear microsatellite and mitochondrial marker estimates of population structure: breeding population structure of Chesapeake Bay striped bass (*Morone saxatilis*). *Heredity*, 94: 606–615.
- Clark, R. W., A. Henderson-Arzapalo, & C. V. Sullivan. (2005). Disparate effects of constant and annually-cycling daylength and water temperature on reproductive maturation of striped bass (*Morone saxatilis*). Aquaculture, 249: 497–513.
- Colburn, L. L., M. Jepson, C. Weng, T. Seara, J. Weiss, & J. A. Hare. (2016). Indicators of climate change and social vulnerability in fishing dependent communities along the Eastern and Gulf Coasts of the United States. *Marine Policy*, 74: 323–333.
- Conroy, C. W., P. M. Piccoli, & D. H. Secor. (2015). Carryover effects of early growth and river flow on partial migration in striped bass *Morone saxatilis*. *Marine Ecology Progress Series*, *541*: 179–194.
- Costantini, M., S. A. Ludsin, D. M. Mason, X. Zhang, W. C. Boicourt, & S. B. Brandt. (2008). Effect of hypoxia on habitat quality of striped bass (*Morone saxatilis*) in Chesapeake Bay. *Canadian Journal of Fisheries and Aquatic Sciences*, 65: 989-1002.
- Coutant, C. C. (1990). Temperature-oxygen habitat for freshwater and coastal striped bass in a changing climate. *Transactions of the American Fisheries Society* 119: 240–253.
- Cox, D. K. & C. C. Coutant. (1981). Growth dynamics of juvenile striped bass as functions of temperature and ration. *Transactions of the American Fisheries Society* 110: 226-238.

- Dixon, R. L., P. A. Grecay, & T. E. Targett. (2017). Responses of juvenile Atlantic silverside, striped killifish, mummichog, and striped bass to acute hypoxia and acidification: Aquatic surface respiration and survival. *Journal of Experimental Marine Biology and Ecology*, 493: 20–30.
- Gahagan, B. I., D. A. Fox, & D. H. Secor. (2015). Partial migration of striped bass: Revisiting the contingent hypothesis. *Marine Ecology Progress Series*, 525: 185–197.
- Garrison, L. P., J. S. Link, D. P. Kilduff, M. D. Cieri, B. Muffley, D. S. Vaughan, A. Sharov, B. Mahmoudi, & R. J. Latour. (2010). An expansion of the MSVPA approach for quantifying predator – prey interactions in exploited fish communities. *ICES Journal of Marine Science*, *67*: 856–870.
- Gauthier, D. T., R. J. Latour, D. M. Heisey, C. F. Bonzek, J. Gartland, E. J. Burge, & W. K. Vogelbein. (2008). Mycobacteriosis -associated mortality in wild striped bass (*Morone saxatilis*) from Chesapeake Bay, USA. *Ecological Applications* 18: 1718-1727.
- Gauthier, D. T., C. A. Audemard, J. E. L. Carlsson, T. L. Darden, M. R. Denson, K. S. Reece, & J. Carlsson. (2013). Genetic population structure of US Atlantic coastal striped bass (*Morone saxatilis*). Journal of Heredity 104: 510-520.
- Gervasi, C. L. (2015). The reproductive biology of striped bass (*Morone saxatilis*) in Chesapeake Bay. M. S. Thesis, Virginia Institute of Marine Science, The College of William & Mary.
- Gilmour, C. C., & G. S. Riedel. (2000). A survey of size-specific mercury concentrations in game fish from Maryland fresh and estuarine waters. *Archives of Environmental Contamination and Toxicology*, *39*: 53–59.
- Graves, J. E., A. Z. Horodysky, & R. J. Latour. (2009). Use of pop-up satellite archival tag technology to study postrelease survival of and habitat use by estuarine and coastal fishes: an application to striped bass (*Morone saxatilis*). *Fishery Bulletin* 107: 373–383.
- Harding, J. M., & R. Mann. (2003). Influence of habitat on diet and distribution of striped bass (*Morone saxatilis*) in a temperate estuary. *Bulletin of Marine Science*, 72: 841–851.
- Hartman, K. J., & F. J. Margraf. (2003). US Atlantic coast striped bass: issues with a recovered population. *Fisheries Management and Ecology 10: 309-312*.
- Hollema, H. M., J. Kneebone, S. D. McCormick, G. B. Skomal, & A. J. Danylchuk. (2017). Movement patterns of striped bass (*Morone saxatilis*) in a tidal coastal embayment in New England. *Fisheries Research* 187: 168-177.
- Jacobs, J. M., R. M. Harrell, J. Uphoff, H. Townsend, & K. Hartman. (2013). Biological Reference Points for the Nutritional Status of Chesapeake Bay Striped Bass. *North American Journal of Fisheries Management*, 33: 468–481.
- Jacobs, J. M., M. R. Rhodes, A. Baya, R. Reimschuessel, H. Townsend, & R. M. Harrell. (2009). Influence of nutritional state on the progression and severity of mycobacteriosis in striped bass *Morone saxatilis*. *Diseases of Aquatic Organisms*, *87*: 183–197.
- Jiang, H., C. Brownie, J. E. Hightower, & K. H. Pollock. (2007a). Estimating fishing mortality, natural mortality, and selectivity using recoveries from tagging young fish. *North American Journal of Fisheries Management*, 27: 773–781.
- Jiang, H., K. H. Pollock, C. Brownie, J. M. Hoenig, R. J. Latour, B. K. Wells, & J. E. Hightower. (2007b). Tag return models allowing for harvest and catch and release: Evidence of environmental and management impacts on striped bass fishing and natural mortality rates. *North American Journal of Fisheries Management*, *27*: 387–396.
- Kerr, L. A., W. J. Connelly, E. J. Martino, A. C. Peer, R. J. Woodland, & D. H. Secor. (2009). Climate change in the U.S. Atlantic affecting recreational fisheries. *Reviews in Fisheries Science*, 17: 267–289.
- Kerr, L. A. & D. H. Secor. (2009). Bioenergetic trajectories underlying partial migration in Patuxent River (Chesapeake Bay) white perch (*Morone americana*). Canadian Journal of Fisheries and Aquatic Sciences 66: 602-612.
- Kimmerer, W. J., J. H. Cowan, L. W. Miller, & K. A. Rose. (2001). Analysis of an estuarine striped bass population: effects of environmental conditions during early life. *Estuaries* 24: 557-575.
- Kimmerer, W. J., E. S. Gross, & M. MacWilliams. (2009). Is the response of estuarine nekton to freshwater flow in the San Francisco estuary explained by variation in habitat volume? *Estuaries and Coasts* 32: 375-389.
- Kneebone, J., W. S. Hoffman, M. J. Dean, D. A. Fox, & M. P. Armstrong. (2014). Movement patterns and stock composition of adult striped bass tagged in Massachusetts coastal waters. *Transactions of the American Fisheries Society*, 143: 1115–1129.

- Kraus, R. T., D. H. Secor, & R. L. Wingate. (2015). Testing the thermal-niche oxygen-squeeze hypothesis for estuarine striped bass. *Environmental Biology of Fishes*, *98*: 2083–2092.
- Lapointe, D., W. K. Vogelbein, M. C. Fabrizio, D. T. Gauthier, & R. W. Brill. (2014). Temperature, hypoxia, and mycobacteriosis: Effects on adult striped bass *Morone saxatilis* metabolic performance. *Diseases of Aquatic Organisms*, 108: 113 –127.
- Latour, R. J., D. T. Gauthier, J. Gartland, C. F. Bonzek, K. A. McNamee, W. K. Vogelbein, & D. MacLatchey. (2012). Impacts of mycobacteriosis on the growth of striped bass (*Morone saxatilis*) in Chesapeake Bay. *Canadian Journal of Fisheries and Aquatic Sciences*, 69: 247–258.
- Lewis, R. M., & R. R. Bonner, Jr. (1966). Fecundity of the striped bass, *Roccus saxatilis* (Walbaum). *Transactions of the American Fisheries Society 95: 328-331.*
- Liao, H., C. M. Jones, & J. L. Gilmore. (2017). Virginia and Chesapeake Bay finfish ageing and population analysis. 2016 Final Report to the Virginia Marine Resources Commission. Old Dominion University.
- Liao, H., A. F. Sharov, C. M. Jones, & G. A. Nelson. (2013). Quantifying the effects of aging bias in Atlantic striped bass stock assessment. *Transactions of the American Fisheries Society* 142: 193-207.
- Lipton, D., & R. Hicks. (2003). The cost of stress: low dissolved oxygen and economic benefits of recreational striped bass (*Morone saxatilis*) fishing in the Patuxent River. *Estuaries* 26: 310-315.
- Martino, E. M., & E. D. Houde. (2004). Environmental controls and density dependent constraints in the recruitment process of striped bass *Morone saxatilis* in the estuarine transition zone of Chesapeake Bay. *ICES CM* J05: 1–24.
- Martino, E. M., & E. D. Houde. (2010). Recruitment of striped bass in Chesapeake Bay: spatial and temporal environmental variability and availability of zooplankton prey. *Marine Ecology Progress Series* 409: 213-228.
- Martino, E. M., & E. D. Houde. (2012). Density-dependent regulation of year-class strength in age-0 juvenile striped bass (*Morone saxatilis*). Canadian Journal of Fisheries and Aquatic Sciences 69: 430-446.
- Mather, M. E., J. T. Finn, K. H. Ferry, L. A. Deegan, & G. A Nelson. (2009). Use of non-natal estuaries by migratory striped bass (*Morone saxatilis*) in summer. *Fishery Bulletin* 107: 329-338.
- Mason, R. P., D. Heyes, & A. Sveinsdottir. (2006). Methylmercury concentrations in fish from tidal waters of the Chesapeake. Archives of Environmental Contamination and Toxicology 51: 425-437.
- Morissette, O., F. Lecomte, G. Verreault, M. Legault, & P. Sirois. (2016). Fully equipped to succeed: migratory contingents seen as an instrinsic potential for striped bass to exploit a heterogeneous environment early in life. *Estuaries and Coasts* 39: 571-582.
- Nelson, J. A. & G. K. Lipkey. (2015). Hypoxia tolerance variance between swimming and resting striped bass *Morone saxatilis. Journal of Fish Biology* 87: 510-518.
- NOAA Fisheries Fish Stock Assessment 101 Series. Retrieved 29 September 2017 from: <u>http://www.nmfs.noaa.gov/</u> stories/2012/05/05 23 12stock assessment 101 part1.html
- North, E. W., & E. D. Houde. (2001). Retention of white perch and striped bass larvae: Biological-physical interactions in Chesapeake Bay estuarine turbidity maximum. *Estuaries* 24: 756-769.
- North, E. W., & E. D. Houde. (2003). Linking ETM physics, zooplankton prey, and fish early-life histories to white perch (*Morone americana*) and striped bass (*M. saxatilis*) recruitment success. *Marine Ecology Progress Series*, 260: 219–236.
- North, e. W., R. R. Hood, S.-Y. Chao, & L. Sanford. (2005). The influence of episodic events on transport of striped bass eggs to the estuarine turbidity maximum nursery area. *Estuaries* 28: 108-123.

Overton, A. S., C. S. Manooch, III, J. W. Smith, & 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 - 2007. *Fishery Bulletin* 106: 174-182.

- Overton, A. S, F. J. Margraff, & E. B. May. (2009). Spatial and temporal patterns in the diet of striped bass in Chesapeake Bay. *Transactions of the American Fisheries Society* 138: 915-926.
- Overton, A. S., J. C. Griffin, F. J. Margraf, E. B. May, & K. J. Hartman. (2015). Chronicling long-term predator responses to a shifting forage base in Chesapeake Bay: An energetics approach. *Transactions of the American Fisheries Society* 144: 956-966.
- Pautzke, S. M., M. E. Mather, J. T. Finn, L. A. Deegan, & R. M. Muth. (2010). Seasonal use of a New England estuary by foraging contingents of migratory striped bass. *Transactions of the American Fisheries Society* 139: 257-269.
- Peer, A. C. & T. J. Miller. (2014). Climate change, migration phenology, and fisheries management interact with unanticipated consequences. *North American Journal of Fisheries Management* 34: 94-110.
- Richards, R. A., & P. J. Rago. 1999. A case history of effective fishery management: Chesapeake Bay striped bass. North American Journal of Fisheries Management 19: 356-375.
- Rutherford, E. S., K. A. Rose, & J. H. Cowan, Jr. (2003). Evaluation of the Shepherd and Cushing (1980) model of densitydependent survival: a case study using striped bass (*Morone saxatilis*) larvae in the Potomac River, Maryland, USA. *ICES Journal of Marine Science* 60: 1275-1287.
- Schloesser, R. W. 2015. Condition of juvenile fishes in estuarine nursery areas: measuring performance and assessing temporal and spatial dynamics with multiple indices. Ph.D. Dissertation, Virginia Institute of Marine Science, The College of William & Mary.
- Schloesser, R. W., & M. C. Fabrizio. 2017. Condition indices as surrogates of energy density and lipid content in juveniles of three fish species. *Transactions of the American Fisheries Society* 146: 1058-1069.
- Secor, D.H. 2000a. Longevity and resilience of Chesapeake Bay striped bass. *ICES Journal of Marine Science*, Volume 57: 808–815.
- Secor, D. H. 2000b. Spawning in the nick of time? Effect of adult demographics on spawning behavior and recruitment in Chesapeake Bay striped bass. *ICES Journal of Marine Science* 57: 403-411.
- Secor, D. H. 2007. The year-class phenomenon and the storage effect in marine fishes. *Journal of Sea Research* 57: 91-103.
- Secor, D. H. 2008. Influence of skipped spawning and misspecified reproductive schedules on biological reference points in sustainable fisheries. *Transactions of the American Fisheries Society* 137: 782-789.
- Secor, D. H. & E. D. Houde. (1998). Use of larval stocking in restoration of Chesapeake Bay striped bass. *ICES Journal of Marine Science* 55: 228-239.
- Secor, D. H., & P. M. Piccoli. (2007). Oceanic migration rates of upper Chesapeake Bay striped bass *Morone saxatilis*, determined by otolith microchemical analysis. *Fishery Bulletin* 105: 62-73.
- Secor, D. H., T. E. Gunderson, & K. Karlsson. (2000). Effect of temperature and salinity on growth performance in anadromous (Chesapeake Bay) and non-anadromous (Santee-Cooper) strains of striped bass *Morone saxatilis*. *Copeia* 2000: 291-296.
- Shideler, A. C. & E. D. Houde. (2014). Spatio-temporal variability in larval-stage feeding and nutritional sources as factors influencing striped bass (*Morone saxatilis*) recruitment success. *Estuaries and Coasts* 37: 561-575.
- Speir, H., J. H. Uphoff, Jr., and E. Durell. (1999). A review of management of large striped bass and striped bass spawning grounds in Maryland. Fisheries Technical Memo No. 15, Maryland Department of Natural Resources, Annapolis, MD.
- Uphoff, J. H., Jr. (2003). Predator-prey analysis of striped bass and Atlantic menhaden in upper Chesapeake Bay. *Fisheries Management and Ecology* 10: 313-322.

- Uphoff, J. H., Jr., M. McGinty, R. Lukacovic, J. Mowrer, & B. Pyle. (2011). Impervious surface, summer dissolved oxygen, and fish distribution in Chesapeake Bay subestuaries: Linking watershed development, habitat conditions, and fisheries management. *North American Journal of Fisheries Management* 31: 554-566
- Virginia Marine Resources Commission. "Pertaining to the Taking of Striped Bass". Chapter 4 VAC 20-252-10 ET SEQ. April 2017. <u>http://www.mrc.state.va.us/regulations/fr252.shtm</u>
- Virginia Marine Resources Commission. Regulation: Striped Bass Map. http://www.mrc.virginia.gov/regulations/striperregmap.shtm
- Waldman, J., L. Maceda, & I. Wirgin. (2012). Mixed-stock analysis of wintertime aggregations of striped bass along the mid -Atlantic coast. *Journal of Applied Ichthyology* 28: 1-6.
- Walter, J. F., III, & 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, & M. E. Mather. (2003). Atlantic coast feeding habits of striped bass: a synthesis supporting a coast-wide understanding of trophic biology. *Fisheries Management and Ecology* 10: 349-360.
- Wingate, R. L. & D. H. Secor. (2008). Effects of winter temperature and flow on the summer-fall nursery fish assemblage in the Chesapeake Bay, Maryland. *Transactions of the American Fisheries Society* 137: 1147-1156.
- Wingate, R. L., D. H. Secor, & R. T. Kraus. (2011). Seasonal patterns of movement and residency by striped bass within a subestuary of the Chesapeake Bay. *Transactions of the American Fisheries Society* 140: 1441-1450.
- Wood, R. J. & H. M. Austin. (2009). Synchronous multidecadal fish recruitment patterns in Chesapeake Bay, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 66: 496-508.
- Woods, L. C., III, E. M. Hallerman, L. Douglass, & R. M. Harrell. (1999). Variation in growth rate within and among stocks and families of striped bass. *North American Journal of Aquaculture* 61: 8-12.
- Woodland, R., E. Houde, A. Buchheister, R. Latour, C. Lozano, C. Sweetman, M. Fabrizio, & T. Tuckey. (2017). Environmental, spatial and temporal patterns in Chesapeake Bay forage population distributions and predator consumption. Final Report to the Chesapeake Bay Trust, University of Maryland, Center for Environmental Science, Solomons, MD.
- Wuenschel, M. J., K. W. Able, J. M. Vasslides, & D. M. Byrne. (2013). Habitat and diet overlap of 4 piscivorous fishes: variation on the inner continental shelf off New Jersey. *Fishery Bulletin* 111: 352-369.
- Xu, X., M. C. Newman, M. C. Fabrizio, & L. Liang. (2013). An ecologically framed mercury survey of finfish of the lower Chesapeake Bay. *Archives of Environmental Contamination and Toxicology* 65: 510-520.