

THE REPRODUCTIVE BIOLOGY OF STRIPED BASS (*MORONE SAXATILIS*)
IN CHESAPEAKE BAY

A Thesis

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In Partial Fulfillment

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Master of Science

By

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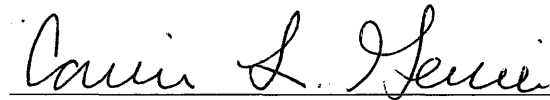
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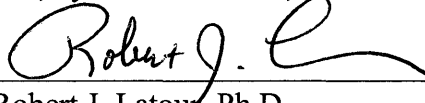
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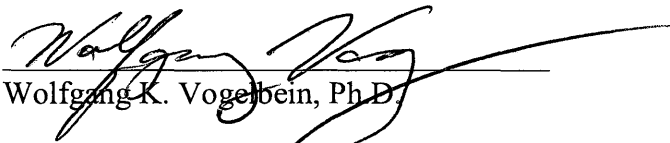


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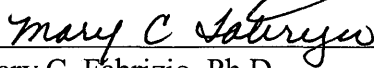
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DEDICATION

I dedicate this work to my parents, Daniel and Lynn Gervasi, who have always encouraged me to follow my dreams and have supported me my whole life. They are two of the most hardworking and dedicated people I know, and have taught me never to settle for anything. I owe my passion for marine science to them and would never be where I am now without their love and support.

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PREFACE

Chapters 1 and 2 of this thesis will be submitted for publication in *Marine and Coastal Fisheries*, and each are formatted under the journal guidelines. Sampling and laboratory methods were the same for both chapters, so are only presented in-depth in Chapter 1.

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ABSTRACT

The Striped Bass (*Morone saxatilis*) is an anadromous finfish that supports a lucrative fishery along the Atlantic coast of the United States and serves as a vital component of estuarine food webs. Once Striped Bass stocks were restored after crashing in the late 1980s, abundance skyrocketed to record levels. Over the past decade however, abundance has steadily declined, concurrent with an outbreak of mycobacteriosis. Disease prevalence is currently >50%, and previous research has demonstrated disease-positive fish exhibit slower growth and increased natural mortality compared to disease-negative fish. The purpose of this research was to provide a contemporary description of Chesapeake Bay Striped Bass reproductive metrics, which have not been thoroughly described since the stock crashed but before it rebounded. Additionally, the effects of mycobacteriosis on reproductive output were assessed via egg-per-recruit analysis. Female Striped Bass were collected from the York, James, and Rappahannock Rivers and the mainstem of the Chesapeake Bay from 2003-2013. Oocyte development, maturity, oocyte size, fecundity, the gonadosomatic index, and oocyte dry mass were fit to regression models against age, length, or weight in order to determine the influence of month, year, disease prevalence, and female pre-spawning condition. The best fitting models for maturity-at-age and fecundity-at-length were combined with a growth model and estimates of fishing mortality and disease progression to create egg-per-recruit models that simulated the effects of decreased growth and increased natural mortality due to disease on the lifetime reproductive output of Chesapeake Bay Striped Bass. Lower age-at-maturity was seen for disease-positive fish compared to disease-negative fish, but no other reproductive metrics were affected. The increased natural mortality caused by the disease was shown to appreciably reduce reproductive output. This study provides critical biological metrics that can be used to inform future studies and reveals the extent to which mycobacteriosis can influence Striped Bass population dynamics.

THE REPRODUCTIVE BIOLOGY OF STRIPED BASS (*MORONE SAXATILIS*) IN
THE CHESAPEAKE BAY

The Striped Bass

The Striped Bass (*Morone saxatilis*, Walbaum 1792) is an anadromous teleost native to the Atlantic coast of the United States from the St. Lawrence River, Canada to the St. Johns River, Florida and is also native to the Gulf of Mexico (Merriman 1937). This species was introduced to the Pacific U.S. coast in 1879 for recreational fishing (Forrester et al. 1972) and has since been established in many river and reservoir systems throughout the United States and across the globe (Hill et al. 1989). The Striped Bass is a top predator and a vital component of marine and estuarine food webs (Carpenter et al. 1985, 1987, Hartman and Brandt 1995). Age-0 fish feed primarily on invertebrates, predominantly polychaetes, gammarid, and mysid shrimp. By age 2, the Striped Bass diet shifts to primarily schooling fishes (i.e., clupeids), crustaceans, and polychaetes, though benthic fishes also contribute to the diet (Hartman and Brandt 1995).

Historical studies of Striped Bass life history have indicated that males typically mature at 2-4 years of age while females mature at 4-8 years, with a maximum reported age of 25-30 years (Merriman 1937). Spawning occurs in the fresh waters of major river systems from as early as mid-February in Florida to as late as June or July in the St. Lawrence River, Canada. Spawning peaks may occur several times during the spawning season with high variability, and are apparently triggered by notable temperature increases (Setzler et al. 1980). In the Chesapeake Bay, spawning occurs from late March to early June (Chapoton and Sykes 1961, Dovel 1971). Females are total spawners, broadcasting all eggs into the environment over a 3-5 day period following the onset of

egg release. Fertilized eggs remain pelagic until hatching which generally occurs 1-4 days from release, depending on temperature (Coutant 1985).

Striped Bass inhabit coastal waters typically within 6-8 km from shore but will move further offshore during migration. In the north, from Cape Hatteras, North Carolina to New England, substantial numbers of Striped Bass emigrate from bays and estuaries beginning at age-2-3 and engage in coastal migrations that move north in spring and south in fall (Merriman 1941). Southern populations (Florida to southern North Carolina and the Gulf of Mexico) are predominantly non-migratory (Gauthier et al. 2013). The extent of migration varies among populations or individuals and between sexes, with large females exhibiting the longest migrations (Bigelow et al. 1953). In the Chesapeake Bay, Striped Bass tagging studies have shown that some males may remain residents throughout their lives, while females are likely to migrate offshore beginning as early as age-3 with frequency of migration increasing with age (Mansueti 1961, Dorazio et al. 1994). Secor et al. (1995) and Secor and Piccoli (2007) used otolith Sr:Ca analysis to show that within the Hudson River and Chesapeake Bay stocks, resident, estuarine, and coastal migratory contingents exist.

Five distinct stocks have been shown to exist along the Atlantic coast of the United States (Hudson River, Delaware River, Chesapeake Bay, North Carolina, and South Carolina), with significant genetic differentiation among all regions (Gauthier et al. 2013). Each stock origin ecosystem provides critical foraging and refuge habitat for spawning and early life development (ASMFC 2013). The Hudson River, Delaware River, North Carolina, and South Carolina populations were not shown to migrate to and

remain in other systems, but the Chesapeake Bay population contributes to all other systems with the exception of South Carolina (Gauthier et al. 2013). Furthermore, the Chesapeake Bay's spawning community contributes to a large proportion of the Atlantic Coast population, though the contribution varies spatially and temporally. Fabrizio (1987) determined that 54% of the age-2-5 Striped Bass collected in Rhode Island coastal waters were from the Chesapeake Bay stock. The Striped Bass fishery is thus largely dependent upon spawning success and young-of-the-year survival of the Chesapeake Bay fish (Richards and Rago 1999).

The Striped Bass fishery

Morone saxatilis has been commercially and recreationally targeted for decades. Striped Bass served as a key food source to early settlers when New England was first colonized, and commercial fisheries of varying intensity have existed since the late 1800s along the South Atlantic coast (Hill et al. 1989). The most frequently used gear types include gill nets, haul seines, floating traps, pound nets, and rod and reel (Musick and Wiley 1972).

In the United States, several Striped Bass management strategies have been enacted at the state level since the 1600s, but abundance plummeted in the 1980s due to recruitment overfishing and possibly poor water quality (Richards and Rago 1999). In 1981, the Atlantic States Marine Fisheries Commission (ASMFC 2013) developed an Interstate Management Fisheries Plan for the Striped Bass, also known as the Plan, which recommended minimum size limits for specific areas and recommended that spawning

areas be closed to fishing during the spawning season. Over the next few years, the Plan was modified to further restrict harvest by setting targets for reduced fishing mortality, and it proposed the need to protect the Chesapeake Bay's relatively abundant 1982 year-class (Richards and Rago 1999). Protection of this year-class was accomplished by states either instituting a fishing moratorium or increasing minimum size limits. Maryland and Delaware declared moratoria on Striped Bass fishing in 1985 (Weaver et al. 1986) and although several other states chose to increase size limits, the limited abundance of harvestable sized fish implied that these actions were essentially closures (Richards and Rago 1999). Given that the Plan articulated management recommendations, states could ignore it without facing legal consequences. However, in 1984, Congress passed the Atlantic Striped Bass Conservation Act, which strengthened the Plan by threatening moratoria on any states that did not comply with the ASMFC's management guidelines (Conservation Act, Public Law [P.L.] 98-613 and its successors).

The Plan and the Conservation Act were essential in restoring the Striped Bass population. The Chesapeake Bay was stocked with millions of hatchery-reared fingerlings from 1985-1993, which was beneficial, but decreased fishing mortality and consecutive years of strong recruitment due to favorable environmental conditions ultimately allowed the stocks to rebound (Richards and Rago 1999). By 1994, juvenile Striped Bass recruitment had reached record highs and indices of adult population size had reached historical levels. Furthermore, coast wide recreational catch skyrocketed (Field 1997) and in January 1995, the Chesapeake Bay stock was officially declared restored (Richards and Rago 1999). Striped Bass abundance along the coast increased

steadily through 2006, then began to decline and has continued since. In the Chesapeake Bay, young-of-the-year (YOY) and age-1 indices have been variable but generally declining since 2004, and in 2012 the lowest YOY index value of the whole time series was observed. Currently, Atlantic coast Striped Bass are not overfished and overfishing is not occurring (ASMFC 2013).

The reproductive biology of fishes

Reproductive success is what allows a species to persist and is thus vital to any population (Lowerre-Barbieri 2009). To maximize the likelihood of success, reproductive strategies differ greatly among fishes due to varying environmental pressures and evolutionary history (Lowerre-Barbieri et al. 2011). Nearly all fishes reproduce sexually, though some may exhibit different strategies including hermaphroditism (sequential or simultaneous), parthenogenesis (unisexuality), or gonochorism (bisexuality), or even a combination of the three (Miller and Kendall 2009, Lowerre-Barbieri et al. 2011). Additionally, over 97% of the 18,000+ species of bony fishes are oviparous, meaning that eggs are fertilized and develop in the external environment (Scott 1987). Most oviparous fishes lay many small eggs, typically less than 1 mm in diameter. Parental care varies greatly among fish species, with some fishes exhibiting extreme parental care by brooding the egg mass in a pouch or in the mouth for protection (Miller and Kendall 2009), while others display no parental care. The majority of fishes are considered iteroparous, spawning many times during their life span. Few species spawn once and then die, termed semelparous (Scott 1987). Before ovulation, fish oocytes undergo

several stages of maturation, which is called oogenesis. There are several growth stages that result in formation of a haploid cell and a mature egg that will support the developing embryo (Miller and Kendall 2009).

Egg quality is defined as the overall health of an egg and its impact on fertility, hatching success, survival, and growth and survival of the larva (Bachan et al. 2012). Lipids are generally considered the main sources of energy for marine fish eggs (Almansa et al. 1999). Phospholipids and triglycerides are especially important components, as they impact hatching success, embryonic development, and survival (Mukhopadhyay and Ghosh 2007). Polyunsaturated fatty acids in fish eggs, specifically docosahexaenoic acid (DHA), eicosapentaenoic acid (EPA), and arachidonic acid (AA), are associated with fertilization, hatching success, and larval survival (Mukhopadhyay and Ghosh 2007). Egg quality is largely a factor of the diet and genetics of adult fishes as well as environmental conditions. Quality of fish eggs often contributes to recruitment variability in wild fish stocks (Almansa et al. 1999, Thorsen and Kjesbu 2001, Bachan et al. 2012).

The Striped Bass is oviparous and iteroparous. Spawning occurs once annually, with the entire clutch of eggs developing simultaneously (Wallace and Selman 1981) and oogenesis is group synchronous. Several studies have indicated that skipped spawning can occur, and some older fish may not spawn every year (Merriman 1941, Jackson and Tiller 1952, Raney 1952). Striped bass are polygamous and sexually dimorphic, with females growing larger than males (Fay et al. 1983). Hermaphroditism has been reported in *M. saxatilis*, although cases are typically uncommon (Schultz 1931, Morgan et al.

1950, Westin and Rogers 1978). Fecundity is largely correlated with female weight, age, and length and can range from approximately 15,000 eggs in a 1.8 kg fish (Mansueti and Hollis 1963) to 40,507,500 eggs in a 14.5 kg fish (Jackson and Tiller 1952).

Various studies have described the reproductive biology of Striped Bass throughout its range, including a synthetic review study published several decades ago (Setzler et al. 1980). The review compiled information on such characteristics as maturity, fecundity, oocyte size, mating, and spawning habits. However, the majority of the studies mentioned in the review had low sample sizes, and many of the methods used are now somewhat antiquated. For example, studies on maturation staged gonads based on gross examination since more accurate histological methods were not available. Since then, (Berlinsky and Specker 1991) examined ovarian lipid content, gonadosomatic indices, oocyte diameter, and oocyte stages for wild Striped Bass from several areas, including the Chesapeake Bay. However, fish were only collected in December and March, which does not encompass the entire spawning season. Berlinsky et al. (1995) was the first study to determine a maturity schedule for Striped Bass utilizing histological staging techniques. However, the data used in the study were from the 1980s. There have been no comprehensive publications on the reproduction of coastal Striped Bass since the stock crashed and rebounded.

The Chesapeake Bay

The Chesapeake Bay is a vital habitat for Atlantic Striped Bass. Over the past century, the bay has experienced substantial anthropogenic change (Jackson et al. 2001,

Kemp et al. 2005, Diaz and Rosenberg 2008). Technological advances in fishing practices have allowed for increased fishing pressure, leading to overfishing of many species (Jackson et al. 2001). Extreme nutrient enrichment from large-scale agricultural practices and waste water treatment plants has led to the propagation of harmful benthic macroalgae and phytoplankton, depletion of dissolved oxygen in bottom waters, and loss of seagrasses (Kemp et al. 2005, Orth et al. 2011). Ecosystem models of the Chesapeake Bay have revealed that hypoxia is causing diversion of energy into microbial pathways, which may negatively affect higher trophic levels (Baird and Ulanowicz 1989). In addition to increased nutrient enrichment, the Chesapeake Bay has recently experienced many effects of climate change (Najjar et al. 2010). Cronin et al. (2003) showed that water temperatures in the Chesapeake Bay have increased during North Atlantic Oscillation (NAO) events in the past. However, the late 20th and early 21st century temperature extremes associated with NAO exceeded those of the past 2000 years, suggesting the climate system is behaving anomalously, most likely due to anthropogenic global warming (Cronin et al. 2003). Warming may exacerbate hypoxic conditions and the occurrence of harmful algal blooms caused by nutrient enrichment, which may have adverse impacts on hatching success and adult fitness in fish populations (Najjar et al. 2010).

Habitat loss, eutrophication, and increased water temperatures have caused several disease outbreaks among animal populations in Chesapeake Bay. A parasitic dinoflagellate (*Hematodinium* sp.) has been causing high mortality in blue crab (*Callinectes sapidus*) particularly in high salinity regions of the bay (Messick et al. 2000).

Messick et al. (1999) showed that parasite infection intensity increases at warmer water temperatures and decreases at lower water temperatures. Decades of overfishing of the Eastern oyster (*Crassostrea virginica*) population in the bay coupled with major outbreaks of MSX and dermo disease in the 1990s have led to a dramatic decrease in the population, which has led to a decrease in water quality (Harvell et al. 1999). Research has shown that warmer winters decrease MSX parasite mortality and warming in general causes more favorable conditions for parasites (Harvell et al. 1999). The Striped Bass has also recently been subjected to disease outbreaks in the Chesapeake Bay. In 1988 Striped Bass from Maryland waters of the bay experienced high mortality attributed to Gram-positive bacteria of the genus *Streptococcus* (Baya et al. 1990). Additionally, Gram-negative bacteria of the genus *Edwardsiella* were reported to cause visceral and dermal lesions in Striped Bass in 1994 (Baya et al. 1997).

In the late 1990s, underweight Striped Bass were observed with external erosive skin lesions in the Chesapeake Bay. Vogelbein et al. (1999) isolated acid-fast bacteria of the genus *Mycobacterium*, which cause the disease mycobacteriosis, from the lesions and spleens of affected fish. Subsequent surveys have demonstrated extremely high prevalence (>50%) of the disease (Cardinal 2001, Overton et al. 2003, Gauthier et al. 2008). Skin lesions and granulomatous inflammation caused by bacterial disease have been observed in Striped Bass previously, attributed to *Aeromonas*, *Edwardsiella*, *Flexibacter*, *Pseudomonas*, and *Vibrio* spp., among others (Toranzo et al. 1983, Mitchell 1984, Plumb 1990, Baya et al. 1997). However, the presence of nonbranching acid-fast

bacteria within granulomas in the current epizootic distinguishes mycobacteria as the causative agent.

Mycobacteriosis

Mycobacterium spp. are ubiquitous microorganisms. They are frequently isolated from water and soil in the environment and are common pathogens of humans (most notably the cause of leprosy, tuberculosis, and Buruli ulcer) as well as fishes (Jacobs et al. 2009). Over 120 species of mycobacteria are currently recognized, the majority of which are non-tuberculosis mycobacteria (NTM). *Mycobacterium* spp. are Gram-positive, aerobic, acid-fast, non-motile, and non-spore forming (Falkinham et al. 1980, Frerichs 1993). *Mycobacterium marinum*, *M. fortuitum*, and *M. chelonae* are the most commonly described species in literature on fish disease, and affect multiple species (Gauthier and Rhodes 2009).

Mycobacteriosis is a severe, subacute to chronic disease that targets the spleen, liver, and kidney. The disease causes scale loss, skin ulceration, pigmentation changes, emaciation, exophthalmia, and/or spinal defects (Nigrelli and Vogel 1963, Snieszko 1978). Granulomatous inflammation and often severe tissue damage are characteristic of the disease (Roberts 2012). The granulomas are described microscopically by a central area of necrosis surrounded by macrophages, fibrous connective tissue, and epithelioid cells (Talaat et al. 1997, Diamant et al. 2000). Mycobacteriosis has affected over 160 species of marine and freshwater fishes worldwide, in cultured and wild populations. It is the most common chronic disease affecting tropical aquarium fishes, but the impact on

wild populations and associated fisheries is not as well understood (Jacobs et al. 2009). Zoonotic transmission of the disease from fish to humans has been documented in some cases. Potentially pathogenic mycobacteria (PPM) can cause disease under certain circumstances such as skin lesions or immune dysfunctions. The most common causative agents are *Mycobacterium marinum*, *M. avium*, *M. abscessus*, *M. chelonae*, *M. aurum*, *M. poriferae*, *M. fortuitum*, *M. gordonae*, and *M. triplex* (Slany et al. 2011).

Several species of mycobacteria have been isolated from Striped Bass in the Chesapeake Bay, including *M. interjectum*, *M. marinum*, *M. scrofulaceum*, *M. szulgai* and *M. triplex* (Rhodes et al. 2004). However, the most commonly isolated species by far are *M. shottsii* (Rhodes et al. 2003) and *M. pseudoshottsii* (Rhodes et al. 2005), both relatively newly described species closely related to *M. marinum* and *M. ulcerans* which are common pathogens of fishes and humans, respectively. Rhodes et al. (2004) found that *M. shottsii* was present in the spleens of 57% of the Striped Bass analyzed from the Chesapeake Bay (n=192). *Mycobacterium pseudoshottsii* has been found in water samples and sediments from the mainstem and tributaries of the Chesapeake Bay, and has also been identified in menhaden and anchovy tissues. *Mycobacterium shottsii* has not been detected in water, sediment, or prey fish tissues, suggesting that the species may be an obligate pathogen of Striped Bass (Gauthier et al. 2010).

Mortality from mycobacteriosis is not often observed in wild fish populations. However, fisheries stock assessments have demonstrated a decrease in Striped Bass biomass in the Chesapeake Bay since the late 1990s (ASMFC 2013) and tag return modeling by Jiang et al. (2007) detected an increase in natural mortality in Maryland

waters of the bay since 1999. Furthermore, Gauthier et al. (2008) used epidemiological models to demonstrate that Striped Bass in the mainstem of the Chesapeake Bay are experiencing disease-associated mortality, and the authors suggested that mycobacteriosis may be responsible for the decreased biomass of the Chesapeake Bay Striped Bass. Additionally, Latour et al. (2012) modeled growth data and determined that disease-positive Striped Bass exhibit significantly lower growth trajectories when compared to disease-negative Striped Bass in the Chesapeake Bay. Research has shown that mycobacteriosis is not only extremely prevalent in Striped Bass of the Chesapeake Bay, but that it has also become detrimental to the population. However, many questions remain, specifically concerning population level effects of the disease such as impacts on reproduction, physiology, and behavior (Rhodes et al. 2004).

Reproduction and disease

Reproductive biology is a fundamental component of fisheries management since it plays a critical role in population regulation (Hixon et al. 2002). In addition, fecundity is a critical parameter of population dynamics and in estimating future stock biomass (Hunter et al. 1992). Previous research has demonstrated negative effects of disease on reproduction in fishes, specifically in aquaculture. Ramsay et al. (2009) showed that the parasitic disease *Pseudoloma neurophilia* (Microsporidia) was associated with reduced weight and fecundity of zebrafish (*Danio rerio*). Reduced fecundity and failure to spawn due to destruction of ovaries was observed in golden shiners (*Notemigonus crysoleucas*) infected with the microsporidian *Ovipleistophora ovariae* (Summerfelt and Warner

1970). Astrofsky et al. (2000) found that zebrafish infected with *Mycobacterium* spp. exhibited increased mortality and decreased reproductive rates. Effects that mycobacteriosis may have on reproductive success of Chesapeake Bay Striped Bass remain unknown, but could have significant impacts on future productivity of the species when combined with other stressors.

Objectives

The purpose of this research is to describe the reproductive biology of female Striped Bass based on fish collected from the primary tributaries of the Virginia portion of Chesapeake Bay (York, James, and Rappahannock Rivers) and the bay mainstem and to investigate potential disease-associated reproductive differences due to the prevalence of mycobacteriosis. In addition, egg-per-recruit models were constructed to quantify the population level impacts of disease on reproductive potential. This study provides an update on knowledge of the general reproductive biology of Chesapeake Bay Striped Bass, which has not been analyzed in detail since the stock decline and recovery. Additionally, this study contributes further insight into the extent that mycobacteriosis is impacting the Chesapeake Bay population, which will allow for more informed management of this important species.

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CHAPTER 1

THE REPRODUCTIVE BIOLOGY OF CHESAPEAKE BAY STRIPED BASS
(*MORONE SAXATILIS*) WITH CONSIDERATION OF THE EFFECTS OF
MYCOBACTERIOSIS

Abstract

The Striped Bass, *Morone saxatilis*, spawning community in the Chesapeake Bay contributes to over half the coastal population, and is economically and ecologically important. A thorough reproductive study on the Chesapeake Bay Striped Bass has not been conducted since the early 1990s, just after the stock had crashed but before it rebounded. Due to management efforts, the population has grown tremendously, necessitating an update to fecundity and maturity schedules. Additionally, mycobacteriosis is currently affecting over 50% of Chesapeake Bay Striped Bass, and there has been little research on population level effects of the disease. The objectives of this study were to update current knowledge on reproductive metrics of Striped Bass in the bay and examine disease-associated effects of mycobacteriosis. Reproductive and disease data were obtained from female Striped Bass collected during spring 2012-2013 in major tributaries of the Chesapeake Bay with supplemental data from the bay mainstem from 2003-2007 incorporated where possible. Major findings include much earlier Striped Bass maturation-at-age compared to previous studies and a dependency of oocyte diameter and gonadosomatic index on month and female pre-spawning condition. There was a significant difference between maturity rates for disease-positive and disease-negative fish, with disease-positive fish maturing earlier than disease-negative fish (age at 50% maturity = 2.52 and 2.95 years, respectively). Mycobacteriosis prevalence across rivers and years was 63.5%, but only 6.8% of disease positive fish were moderately to severely infected. The disease was not shown to significantly affect oocyte development, oocyte size, fecundity, the gonadosomatic index, or oocyte dry weight.

INTRODUCTION

Persistence of fish populations is highly dependent on reproductive success, which can be generally defined as reproductive output and the survival of offspring (Lowerre-Barbieri 2009). Fishes have developed a variety of reproductive trait adaptations in order to maximize success, largely based upon environmental conditions and evolutionary history. One fundamental goal of fisheries management is to conserve sufficient reproductive potential such that a given population can persist or rebuild. Several metrics can be used to determine reproductive potential, and therefore meet this goal.

Maturation rates and fecundity for example, dictate reproductive output, which is a common measure of reproductive potential and presumed to correlate with future population size (Lowerre-Barbieri 2009). Oocyte quality, which is defined as the overall health of an oocyte, is also of importance, as it can impact fertility, hatching success, offspring survival, and growth and survival of larvae (Bachan et al. 2012). Lipids are generally considered the main sources of energy for marine fish oocytes (Almansa et al. 1999) and phospholipids and triglycerides are especially important components because they impact hatching success, embryonic development, and survival (Mukhopadhyay and Ghosh 2007). Oocyte quality is largely a factor of the diet and genetics of adult fishes as well as environmental conditions, and quality of fish oocytes often contributes to recruitment variability in wild fish stocks (Almansa et al. 1999, Thorsen et al. 2003, Bachan et al. 2012). A common method for easily estimating fish oocyte quality is by determining the dry weight of a single oocyte (Alós et al. 2013). Oocytes with high lipid

content are denser and thus heavier than lower quality oocytes with low lipid content. The gonadosomatic index (GSI) is commonly used to measure development and spawning seasonality and is defined as the ratio of the gonad weight of a fish to its total body weight. Changes in maturation, fecundity, and oocyte quality are related to fish size and are considered density-dependent (Rose et al. 2001). Fluctuations in population size can therefore lead to changes in reproductive metrics. Because reproductive success is so vital to the persistence of fish populations, it is important to not only understand how fishes reproduce, but also to keep track of changes in reproductive metrics over time. Regular updates on the reproductive biology of fish species are therefore necessary.

The Striped Bass (*Morone saxatilis*) is an oviparous and iteroparous anadromous finfish with coastal populations spanning the Atlantic coast of the United States from Nova Scotia to Florida (Merriman 1937). Various studies have described the reproductive biology of Striped Bass throughout its range, including a synthetic review study published several decades ago (Setzler et al. 1980). The review compiled information on characteristics such as maturity, fecundity, oocyte size, mating, and spawning habits. However, the majority of the studies mentioned in the review had low sample sizes, and many of the methods used are now somewhat antiquated. For example, studies on maturation staged gonads based on gross examination since more accurate histological methods were not available. Since then, Berlinsky and Specker (1991) examined ovarian lipid content, gonadosomatic indices, oocyte diameter, and oocyte stages for wild Striped Bass from several areas, including the Chesapeake Bay. However, fish were only collected in December and March, which does not encompass the entire spawning season.

Berlinsky et al. (1995) was the first study to determine a maturity schedule for Striped Bass utilizing histological staging techniques. However, the data used in the study were from the 1980s.

The Chesapeake Bay Striped Bass population has experienced considerable change over the past 30 years. Moratoria were enacted in the mid-1980s in both Maryland and Virginia due to low population abundance and concerns about the effects of poor water quality on larval survival (Richards and Rago 1999). Decreased fishing pressure combined with favorable environmental conditions supported improved recruitment during the late 1980s and limited commercial and recreational fisheries resumed in the early 1990s. Population trends continued to increase such that the stock was declared recovered in 1995 (Field 1997, Richards and Rago 1999) and coastwide estimated abundances peaked at the highest levels on record in the mid-2000s (ASMFC 2013).

In 1997, histopathology of splenic tissue from Chesapeake Bay Striped Bass revealed granulomatous inflammation associated with acid-fast bacteria, consistent with infection by *Mycobacterium* spp. (Vogelbein et al. 1999, Gauthier and Rhodes 2009). Mycobacteriosis is a cosmopolitan disease of fishes, affecting a wide range of wild and aquacultured species. The most commonly recovered isolates from Chesapeake Bay Striped Bass are the relatively newly described species *M. shottsii* (Rhodes et al. 2003) and *M. pseudoshottsii* (Rhodes et al. 2005), followed by a diverse suite of slow growing isolates (Rhodes et al. 2004). Mycobacteriosis in Striped Bass commonly manifests as visceral disease with the spleen and anterior kidney as primary target organs.

Granulomatous dermatitis is also common and results in scale loss, formation of shallow ulcerations, and pigmentation changes (Vogelbein et al. 1999). Recent investigations of disease prevalence have shown that over half the Chesapeake Bay population is disease-positive and that fish are experiencing disease-associated mortality and reduced growth (Gauthier et al. 2008, Latour et al. 2012).

The purpose of this research was to provide a contemporary description of the reproductive biology of female Chesapeake Bay Striped Bass in light of the documented high abundance of the species coastwide and the considerable prevalence of mycobacteriosis in bay fish. The reproductive metrics examined were oocyte development, maturity, oocyte diameter, fecundity, gonadosomatic index, and oocyte quality (dry weight). Data for each metric were analyzed to develop relationships as a function of age and size and each model was parameterized to include a variety of temporal, spatial, and disease (prevalence) covariates. A model selection criterion was used to compare competing model parameterizations and to support conclusions drawn about factors potentially affecting Striped Bass reproduction. Our results provide insights into the current reproductive biology of Striped Bass which can be used to better understand the productivity of this species and to inform future management practices.

METHODS

Field collection

Female Striped Bass were collected from the York, James, and Rappahannock rivers of the Chesapeake Bay using staked gillnets from February to May, 2012 (n=369,

Figure 1). In the York and James rivers, the gillnets used for collection were 273 m long with 12.4 cm stretched mesh monofilament netting strung between poles set in the riverbed approximately 9.14 m apart. In the Rappahannock River, the gillnet used was 277 m long with 12.7 cm stretched mesh netting with poles spaced every 14.6 m. Additional fish were collected from February to May, 2013 by the aforementioned York River nets and also a cooperating commercial fisherman in the York River using anchored gillnets with 15.2, 21.6, and 22.9 cm stretched mesh netting (n=100). In the laboratory, each fish was examined for skin lesions, then fork length (FL, mm), weight (g), and eviscerated weight (EW, g) measurements were taken. Otoliths were removed for aging, spleens were collected for histology, and both ovaries were removed and weighed. Sections from the right ovaries of each fish were collected for detailed reproductive analyses. Spleens were fixed in Z-fix (Anatech, Battle Creek, Michigan, USA) for at least 72 hours. The ovarian sections were fixed in 10% buffered formalin for at least 72 hours and then transferred to 70% ethanol. In 2013, additional samples of oocytes from 47 fish that were deemed spawning capable, based on visual examination of the ovaries (Peer et al. 2012), were collected from the remaining ovary and stored in pre-cleaned 20 ml scintillation vials in a -80° C freezer for dry weight determination. Furthermore, for 79 out of the 100 fish collected in 2013, additional samples of oocytes from the remaining ovary were removed and analyzed immediately for fresh oocyte diameter using a Nikon SMZ 1500 stereomicroscope and NIS-Elements software program.

Since the gillnet mesh sizes did not permit frequent collection of small, likely immature fish, supplemental data on Striped Bass maturity were incorporated from the

Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP, Latour et al. 2003). ChesMMAP is a fisheries-independent survey that operates in the mainstem of Chesapeake Bay according to a random stratified sampling design (five regional strata and three depth strata: 3.0-9.1 m, 9.1-15.2 m, and >15.2 m). Each year, five cruises are conducted bi-monthly (Mar, May, Jul, Sep, and Nov), and during each cruise, approximately 80 sites are sampled using a 13.7 m, four seam bottom trawl towed for 20 min. Detailed biological data are obtained from either the total survey collection (small catches) or a random sub-sample (large catches). Striped Bass maturity was determined via gross examination of ovaries based on color and oocyte size and the supplemental data included collections from March of 2002 to 2007 (n=502). All protocols for sampling and euthanizing fish were approved by the College of William & Mary's Institutional Animal Care and Use Committee.

Laboratory analysis

For the river collections, a transverse section of the right sagittal otolith was used to age Striped Bass by three readers following the methods of Secor et al. (1995) (n=465). Final age assignments were achieved when at least two of the readers agreed on the age of a specimen. If all three readers disagreed, the otolith was re-read by all readers until a consensus was reached. For the ChesMMAP mainstem collections, otoliths were aged previously using the same method.

Spleens from the river samples were processed for routine paraffin histology (n=466, Prophet 1992). Six approximately equal cross sections were cut from each spleen

leaving a 1-2 mm section between each of the six sections to avoid duplicating results by reading contiguous sections. This allowed simultaneous histologic evaluation of spleens at six levels. Following cutting, tissue slices were placed into cassettes and stored in 70% ethanol until they were dehydrated, cleared, and infiltrated with embedding medium (paraffin wax). They were then sectioned on a rotary microtome at 5 μm , and stained with hematoxylin and eosin. Stained slides were examined under a light microscope for the presence and quantity of granulomas. Disease prevalence was determined by categorizing fish as disease-positive if at least one granuloma was present in the splenic sections and disease-negative if no granulomas were present. Total area (mm^2) of the splenic sections was measured using NIS-Elements, and a disease severity index was calculated as $\log_{10} ([\text{total number of granulomas in six splenic sections} * \text{total splenic area} + 1])$ (Latour et al. 2012). Fish were then assigned to one of four mycobacterial visceral disease categories based on the severity index: 'disease-negative' for $\text{SI}=0$, 'mild' for $0 < \text{SI} \leq 0.1$, 'moderate' for $0.1 < \text{SI} \leq 0.5$, and 'severe' for $\text{SI} > 0.5$ (Lapointe et al. 2014). Disease prevalence and severity for the ChesMMAAP mainstem collections were previously determined in the same fashion.

Routine paraffin histology was also employed on ovarian subsections collected from the rivers following the same methods utilized for the spleens. The stained ovarian slides were examined for oocyte stage and categorized based on the histologic stage determinations established by Brown-Peterson et al. (2011). Fish were labelled as either immature, developing, early-stage vitellogenic, late-stage vitellogenic, or regressing / regenerating based on the histologic appearance of the oocytes. Detailed descriptions of

these phases are provided in Brown-Peterson et al. (2011). Fish in the early and late-stage vitellogenic phases were categorized as spawning capable. To examine maturity schedules, immature fish were assigned a “0” and all mature fish (developing, spawning capable, or regressing / regenerating) were given a “1”. To examine oocyte development, spawning capable fish were assigned a “1” and all other fish were assigned a “0”.

Fecundity was measured from the collected ovarian sections by counting the total number of spawning capable oocytes from an approximately 0.5 g subsample of one ovary using a Nikon SMZ 1500 stereomicroscope and NIS-Elements software program. Samples were taken from the center of the ovarian section since previous research has determined that oocyte distribution is homogeneous throughout the ovary (Scofield 1931, Merriman 1941, Lewis and Bonner 1966). Fecundity was not determined for fish in the immature, developing, regressing, or regenerating stages of gonad development. Total ovarian oocyte counts were calculated by scaling the subsample counts up by the total weight of both ovaries.

To determine oocyte diameter, a clump of oocytes was placed under a microscope and teased apart, and the largest oocyte diameters were measured using NIS-Elements. At least 5 oocytes were measured so that an average could be determined. Average diameters were determined for all ovarian subsamples after preservation and for 79 of the fish from 2013, fresh diameters were also determined immediately after dissection. For the samples where both fresh and preserved oocyte diameters were determined, a regression was created to determine the relationship between preserved and fresh diameters and correct for shrinkage due to preservation, where fresh diameter = 0.194 *

$e^{(2.060 * \text{preserved diameter})}$. Oocyte dry weight was determined by counting out 100 spawning capable oocytes in triplicate from each of the 47 frozen samples collected in 2013, then weighing and drying them in an oven at 60° C for 48 hours. The oocytes were then re-weighed and the dry weight of a single oocyte was calculated by dividing the total dry weight by 100. The gonadosomatic index was determined for each fish from the rivers and mainstem by dividing the weight of both gonads by the total body weight.

Statistical analysis

A variety of model types were considered for each of the following response variables: oocyte development, maturity, average oocyte diameter (mm), fecundity (10^6 oocytes), gonadosomatic index (gonad weight/body weight*100), and oocyte dry weight (g) (Table 1). Linear, logarithmic, and/or nonlinear power models were fitted using regression techniques to establish relationships of each response variable with age (years), FL (mm), and/or fish weight (g). Binomial generalized linear models (GLM; logit link) were used to analyze the development and maturity data. Once suitable model forms were identified for each response variable, multiple model parameterizations that reflected different combinations of hypothesized predictor variables were examined to identify the parameterization with the most empirical support. The predictor variables considered were disease prevalence, month, year, and condition (Fulton's K). Fulton's K was defined as $100,000 * EW / FL^3$, where EW = eviscerated weight (g) and FL = fork length (mm). Samples were pooled across rivers since York, James, and Rappahannock river fish exhibit no genetic differentiation (Gauthier et al. 2013). Disease severity was

not included as a covariate because the vast majority (93.2%) of disease-positive fish were only mildly infected. Since the power model is nonlinear, covariates were incorporated using a general fixed-effects nonlinear modeling framework (Kimura 2008). This method considers the relationship between a response variable and an independent variable on an individual fish basis. The response for the i^{th} individual is modeled as follows:

$$(1) \quad y_i = a_i * t^{b_i} + \varepsilon_i$$

where for the i^{th} fish, y_i is the dependent variable, t is the independent variable, a_i and b_i are the parameters to be estimated, and ε_i is the additive error term, which is assumed to be independent and normally distributed. The parameters a_i and b_i can vary for each fish due to the influence of covariates and are modeled as:

$$(2) \quad \begin{pmatrix} a_i \\ b_i \end{pmatrix} = \begin{pmatrix} \beta_{0a} + x_{i1}\beta_{1a} + \dots + x_{ij}\beta_{ja} \\ \beta_{0b} + x_{i1}\beta_{1b} + \dots + x_{ij}\beta_{jb} \end{pmatrix}$$

where x_{ij} is the j^{th} covariate with coefficients β_{ja} and β_{jb} .

Diagnostics (QQ and residuals plots) were examined for each model to check for violation of distributional and variance assumptions. Unless otherwise stated, diagnostics for each of the models presented revealed that model assumptions were met. In cases where log transformations were applied to account for multiplicative error, a correction factor was applied to the model predictions to counteract bias (Sprugel 1983). Variance

inflation factors were calculated, if necessary, to check for collinearity among covariates. All analyses were performed using the statistical software package R (version 3.1.2; R Core Development Team 2014). Model comparisons were conducted separately using bias corrected Akaike's Information Criterion (AICc) (Akaike 1973, Burnham and Anderson 2002), and statistical inference was based on estimated AICc model weights.

Development. – In order to determine whether or not spawning seasonality was captured each year (2012 and 2013), the percent of fish in the spawning capable phase of oocyte development was analyzed by month for each year. Three binomial GLM parameterizations were fit to development-at-length to examine the effects of size on the proportion of fish in the spawning capable phase (Table 1).

Maturity. – Maturity data collected in February, March, and April of 2012 and 2013 were combined with data from the March collections from ChesMMAAP for 2003 to 2007. Due to relatively low sample sizes in some years, data were pooled over years. A total of four binomial GLM parameterizations were fitted to both Striped Bass maturity-at-age and -at-length data (Table 1). Following model selection, age and length at 50% maturity were estimated from the model configurations with the most empirical support.

Oocyte size. – Fresh oocyte diameters were estimated for each fish using the previously determined regression between fresh and preserved oocyte diameters. Scatter plots of estimated fresh oocyte diameter-at-age and -at-length generally each showed a linear relationship. Thus, linear and logarithmic models were considered. A total of twelve parameterizations were fitted to data associated with each independent variable (Table 1).

Fecundity. – Only oocytes that were early-stage vitellogenic or late-stage vitellogenic according to histological determination were considered for fecundity analysis. Fecundity-at-age and -at-length data were modeled using linear and logarithmic models, again following from the trends observed in plots of the raw data. Although estimation assumptions of least squares were met for the fecundity-at-age data, diagnostic plots revealed that the residuals of models fitted to the fecundity-at-length data were normally distributed but non-constant across the length range. Therefore, the variance was explicitly modeled using a power-of-the-mean variance model:

$$(3) \quad \text{var}(\varepsilon_i) = \sigma^2(f(x_i, \beta))^{2\theta}$$

where the exponent 2θ explains the dependence of the variance (σ^2) of each observation on the corresponding mean value ($f(x_i, \beta)$) (Ritz and Streibig 2008). Fourteen model parameterizations were fitted to data associated with the respective age and length variables (Table 1).

GSI. – Linear and power models were fitted to the GSI-at-age and -at-length data. Twelve covariate combinations were considered for the data (Table 1). The average gonadosomatic index for fish in each of the five developmental stages (immature, developing, early-stage vitellogenic, late-stage vitellogenic, and regressing / regenerating) was also determined.

Dry weight. – Linear models were fit to the oocyte dry weight data and were log transformed since the error structures were multiplicative. A total of six model parameterizations were considered (Table 1).

RESULTS

The total count of female Striped Bass collected in 2012 was 369, with 249 of the fish from the York River (67%), 68 from the James River (18%), and 52 from the Rappahannock River (14%). A total of 100 female Striped Bass were collected in 2013, all from the York River. From the bay mainstem, 502 fish were collected from 2003 to 2007 for inclusion in the maturity analyses. Overall, fish ranged in age from 1-18 years. Histological examination of spleens showed that 296 fish (63.5%) from the rivers and 204 fish (41%) from the mainstem were disease-positive, a combined total of 500 fish (52%). In 2012, disease prevalence in the James River was 64.7%, prevalence in the Rappahannock River was 67.3%, and prevalence in the York River was 62.9%. In 2013, prevalence was 63.0% with all fish from the York River. Of the disease positive fish from the rivers combined, 93.2% were mildly infected, 4.7% were moderately infected, and 2.0% were severely infected. Of the disease-positive mainstem fish, 70.1% were mildly infected, 19.6% were moderately infected, and 10.3% were severely infected. In the rivers, prevalence increased with age until age-8 and then dropped off in the older fish. Similarly, prevalence in the mainstem increased with age to age-6 and then dropped off. Overall, severity appeared to follow the prevalence trend (Figure 2).

Development

The percent of fish from 2012 with oocytes in the spawning capable phase increased from February to March (42.9% and 45.8%, respectively) and then decreased in April (36.1%). The peak in spawning capable over time suggests that the spawning seasonality is encompassed in the data. In 2013, the percent of spawning capable fish increased over time, from 44.4% in February to 68.7% in March, and 81.8% in April. Sample size in 2013 was relatively small compared to 2012, and there were only 11 fish captured in April of 2013. Since seasonality was captured in 2012, development-at-length was assessed. The binomial GLMs with no covariates, with a year covariate, and with a prevalence covariate were all approximately equally supported according to AIC ($\Delta\text{AIC} = 0.0, 1.5, \text{ and } 1.1$, respectively), so the model with no covariates was chosen for the sake of parsimony (Table 2, 3, Figure 3). Model results revealed the proportion of fish in the spawning capable phase increased significantly with fish length.

Maturity

Histological stage determinations from 448 fish collected in 2012 and 2013 revealed that 43 fish were immature (9.6%), 184 were developing (41.1%), 201 were early-stage vitellogenic (44.9%), 16 were late-stage vitellogenic (3.6%), and 4 were regressing/regenerating (0.89%). Pooling across all of the maturity designations implies that 405 fish were mature at the time of sampling (90.4%). A binomial GLM model that included prevalence as a covariate received the most empirical support for maturity-at-age, but the model without covariates also received marginal support ($\Delta\text{AICc} = 1.76$).

The prevalence model also received the most support for maturity-at-length, but prevalence was not a significant predictor ($p = 0.13$) and the model with no covariates was roughly equally supported ($\Delta AICc = 0.33$) (Table 2, 4, Figure 4). For the sake of parsimony, the simpler model with no covariates was chosen. Age at 50% maturity was 2.95 years for disease-negative fish and 2.58 years for disease-positive fish. Length at 50% maturity was 311.08 mm.

Oocyte Size

Average preserved oocyte diameter ranged from 0.14mm to 1.17 mm with an average of 0.60 mm ($n=432$). When the regression curve was used to assign fresh diameters to the remainder of the data set, fresh oocyte diameter ranged from 0.26 mm to 2.16 mm with an average of 0.77 mm, suggesting rather substantial shrinkage ranging from 0.12 mm to 0.99 mm due to preservation. According to AICc, the logarithmic model applied to the diameter-at-age data received more empirical support than the linear model (Figure 5a), and diagnostic plots revealed that the assumptions of normality and homogeneity of variance were met. A linear model was fit to diameter-at-length (Figure 5b). The models that received the most empirical support included either age or fork length as independent variables and month and condition factor as covariates (Table 2, 5). The covariates were significant categorical predictors in the best fitting models but were not collinear according to model diagnostics.

Fecundity

Fish used to determine fecundity ranged in age from 4-18 years ($n=163$). Fecundity ranged from 33,378 oocytes in a 532 mm FL, age-5 fish to 3,149,106 oocytes in a 930 mm FL, age-9 fish with an average of 1,182,443 oocytes across all samples. Average fecundity of fish captured in March (1,298,659) was greater than that of fish captured in February (1,090,414), and much greater than average fecundity of fish captured in April (585,177), likely because all of the oldest fish were captured in February and March and the majority of fish captured in April were age-5. The best fitting model for fecundity-at-age was a logarithmic model with no covariates included, though all of the other models considered received marginal support, with ΔAIC_c values ranging from 1 to 3.2 (Table 2, 6, Figure 6a). A generalized least squares model where the error was modelled as the power-of-the-mean variance was fitted to the fecundity-at-length data (Table 2, 6, Figure 6b). The variance parameter estimate (θ) was 0.5773, which suggests that the variance structure resembles that of a Poisson distribution (Huet et al. 2004). The ΔAIC_c value for the model including month and year was 0.00 compared to 0.97 for the model with no covariates, meaning the two models were roughly equally supported. The year + month + prevalence and year + month + prevalence + condition models also received considerable support, where ΔAIC_c was 0.14 and 0.31, respectively. Examination of the model outputs revealed that the standard errors for all of the covariates were quite high, indicating imprecise estimation of the covariate coefficients. Therefore, for the sake of parsimony, the simpler model with no covariates was chosen.

Gonadosomatic Index

GSI essentially doubles as immature oocytes reach the developing stage (average GSI = 0.723 and 1.799, respectively, standard error (SE) = 0.034 and 0.062). From developing to early-stage vitellogenic GSI almost triples in size (average = 5.419, SE = 0.179), and then doubles again as the oocytes transition to late-stage vitellogenic (average = 11.328, SE = 0.556). After spawning is complete and oocytes are in the regressing/regenerating stage, GSI decreases to approximately the same level as for immature/developing fish (average = 1.199, SE = 0.382) (Figure 7). There is a significant difference in average GSI between consecutive oocyte stages. The best fitting model for GSI-at-age was a linear model with month and condition as the covariates (Table 2, 7, Figure 8a). A logarithmic model with month and condition gained the most empirical support for GSI-at-length (Table 2, 7, Figure 8b).

Dry Weight

The dry weight of one oocyte ranged from 0.077 g to 0.511 g with a mean of 0.238 g. Age was not a significant predictor of oocyte dry weight, so fork length and fish weight were used as the independent variables. The best fitting models for the dry weight of one oocyte were log-transformed linear models with no covariates included, though the prevalence and condition models received some support, with ΔAICc values around 2 (Table 2, 8, Figure 9).

DISCUSSION

The Chesapeake Bay Striped Bass spawning population contributes to a significant proportion of the coast-wide stock (Gauthier et al. 2013), and is therefore an extremely important source of the Atlantic coastal population. In addition to understanding the effects of harvest impacts, it is also important to understand Striped Bass biology and monitor changes in key biological metrics. Reproductive biology is especially important, since it plays a critical role in population regulation and is therefore a fundamental component of fisheries management (Hixon et al. 2002). Several studies have previously documented the reproductive biology of Chesapeake Bay Striped Bass (Setzler et al. 1980, Berlinsky and Specker 1991, Berlinsky et al. 1995) but those studies occurred prior to the decline and subsequent recovery of the stock, and before the outbreak of mycobacteriosis. Due to the lack of information available following the rebound of the population, an update to reproductive metrics was warranted.

Reproductive metrics then and now

All of the models fit to Chesapeake Bay Striped Bass development, maturity, oocyte size and quality, fecundity, and GSI data revealed significant positive relationships between the reproductive metrics and fish size or age, suggesting that larger, older females have a significantly greater contribution to reproductive success than smaller, younger fish, which has been demonstrated for many fish species in past studies (Field et al. 2008, Hixon et al. 2014).

One major change in Striped Bass reproduction compared to previous literature was the maturity schedule. The age at 50% maturity for disease-negative fish determined in this study (2.95 years) is much lower than what was determined in previous studies. According to Jackson and Tiller (1952), female Striped Bass in the Chesapeake Bay did not begin spawning until age-4 or 5. In the Potomac River, MD between 1974 and 1976, only 44.4% of females collected at age-3 were mature, suggesting age at 50% maturity was somewhere between age-3 and 4 (Wilson et al. 1975). Merriman (1941) examined maturity-at-age for mixed stock coastal fish, and determined an age at 50% maturity between 4 and 5 years. Berlinsky et al (1995) also examined coastal fish, and half maturity wasn't reached until after age-5. The most recent Striped Bass stock assessment report uses maturity estimates from Maryland, which show a much later age at 50% maturity, between ages 6 and 7 (ASMFC 2013). So there are significant differences in the literature among maturity estimates, and maturity-at-age was higher in all previous studies compared to the current study. Decreased age-at-maturity often indicates a stock's response to fishing pressure, environmental stress, or reduction in size (Trippel 1995). The intense fishing pressure exerted on the population in the 1980s and the subsequent dramatic decline in population size could have selected for earlier maturation, which has been observed in other fishes (Heino and Godø 2002, Marty et al. 2014). Regardless of the reason, it is clear that the stock assessment is not using the most up to date values for maturity. Fisheries stock assessments rely upon maturation rates to estimate spawning stock biomass (SSB), and fishing regulations are set based upon the estimates of SSB. It

is therefore of utmost importance to ensure maturation estimates are accurate, so that regulations will achieve maximum sustainable yield.

Oocyte diameter was dependent upon month and condition. The observation that oocyte diameter-at-age and -at-length increases from February to April agrees with findings from previous research (Setzler et al. 1980), and is mainly due to an increase in oocyte size as spawning approaches. Previous research has demonstrated a positive correlation between pre-spawning condition of females and oocyte diameter in cod (Ouellet et al. 2001). The exponential relationship between fresh and preserved oocyte diameters suggests that larger oocytes exhibit substantially greater shrinkage when preserved than smaller oocytes. During final maturation, the content of free amino acids in oocytes increases, leading to osmotic water influx and a swelling of the yolk compartment (Selman et al. 1994, Cerda et al. 1996). The higher water content in advanced oocytes compared to immature or developing oocytes explains the increase in shrinkage since preservation causes dehydration.

Fecundity-at-length relationships for Striped Bass have been determined several times in the literature (Figure 10, Holland and Yelverton 1973, Goodyear 1984, Olsen and Rulifson 1992, Sadler et al. 2001, Richards et al. 2002). Data were fit to linear models in each of the studies with the exception of Sadler et al. (2001), who fit a power model to fecundity-at-length of Striped Bass from the Rappahannock and James Rivers of the Chesapeake Bay. The equations used are highly variable, especially for smaller fish. Several factors including differences in methodology, sample size, age composition of samples, environmental conditions, biomass, prey availability, and fishing pressure could

account for the differences and require further examination. The variability among studies highlights the need to regularly analyze fecundity patterns and ensure standardization of laboratory techniques.

Average gonadosomatic index at each stage was comparable to previous literature (Berlinsky and Specker 1991), suggesting that female reproductive condition has not changed significantly in the past couple decades. In the previous study, histologic examination of ovaries was used to stage oocytes as primary growth (immature), secondary growth (developing), vitellogenic (early vitellogenic), or atretic (post-spawning). Average GSI for immature fish was 0.72% in the current study and approximately 0.5% in the previous study. For developing fish, average GSI was 1.8% and ~1%, respectively. The historical averages are a bit lower, but that is likely because all of the fish captured at those stages were captured in the fall or winter, not during the spawning season. Early vitellogenic stage fish had an average GSI of 5.42% in the current study, compared to ~5.5% in the previous study. Berlinsky and Specker (1991) did not determine GSI values for any fish in the late vitellogenic stage, but the post spawn averages are very similar (1.2% in the current study and ~1% in the previous study). For late-stage vitellogenic fish in the current study, the average GSI was 11.33%. Weakfish have been shown to exhibit similar maximum GSI values between approximately 10 and 15% for gravid females (Shepherd and Grimes 1984). Additionally, month and condition significantly affected GSI. Since oocyte size and mass increase as spawning approaches, the ratio of gonad weight to total body weight would

also increase. Similarly, fish in good pre-spawning condition generally produce larger oocytes than fish in poor condition.

The oocyte dry weight models with no covariates received the most support according to AICc. Dry weight increased linearly with fish weight and length, though the independent variables were only weakly significant and age was not used since it was not a significant predictor. Hempel and Blaxter (1967) reviewed several studies on oocyte dry weight of Atlantic Herring, and found significant positive relationships between dry weight and fork length in 10 out of the 27 studies. There was no significant relationship in the other studies. The authors suggest that oocyte weight is far less dependent on the size and age of the mother than is fecundity. The current models suggest that this may also be the case for Striped Bass, but larger fish are able to produce somewhat higher quality eggs than smaller fish. Ouellet et al. (2001) found a significant relationship between oocyte dry weight and female pre-spawning condition in Atlantic cod. In Striped Bass, oocyte dry weight significantly impacted fertilization rate but did not affect hatching rate, overall survival of embryos, or estimated total number of hatched prolarvae in a study of a South Carolina hatchery (Secor et al. 1992). In the current study, there was no significant relationship between oocyte dry weight and female condition (Fulton's K). It is possible that oocyte lipid content, which makes oocytes denser and heavier, is not as variable or as vital to spawning success in the Striped Bass as in other fish species. However, the sample size of oocytes measured for dry weight was rather low (n=47) so a larger sample size could possibly reveal a relationship between dry weight and condition.

Mycobacteriosis

Previous research has demonstrated negative effects of disease on reproduction in fishes, specifically in aquaculture. Ramsay et al. (2009) showed that the parasitic disease microsporidiosis caused by *Pseudoloma neurophilia* (Microsporidia) was associated with reduced weight and fecundity of zebrafish (*Danio rerio*). Additionally, reduced fecundity and failure to spawn due to destruction of ovaries was observed in golden shiners (*Notemigonus crysoleucas*) infected with the microsporidian *Ovipleistophora ovariae* (Summerfelt and Warner 1970). Astrofsky et al. (2000) found that zebrafish infected with *Mycobacterium* spp. exhibited increased mortality and decreased reproductive rates. The maturity-at-age model including disease prevalence received marginally more support than the model with only age ($\Delta AICc=1.76$) and prevalence was a significant covariate according to the p-value (0.05). Age at 50% maturity was quite different between disease-positive and -negative fish, with disease-positive fish maturing at an earlier age than disease-negative fish (2.58 years and 2.95 years, respectively). The process of maturation can be stressful, and therefore increase the risk of disease. It is possible that fish that mature earlier in life are more susceptible to infection than fish that mature later on.

The lack of significance of disease prevalence in any of the other models is likely seen because the majority of fish collected that were disease-positive were only mildly infected even though prevalence was extremely high. Since the disease is progressive with no evidence of regression or resolution (Gauthier et al. 2008), it is possible that the mortality of severely diseased fish is so high that they simply die before they are

captured. However, the dominant mycobacteria species are the newly described *M. shottsii* and *M. pseudoshottsii*, both of which are relatively slow-growing (Gauthier et al. 2008). Since the disease has only been impacting the population for approximately 15 years (i.e.: about the life span of a Striped Bass) and it develops slowly, there may have not been enough time at the present date for the population to have developed prominent severe infection.

The present study provides a much needed update of the reproductive biology of Chesapeake Bay Striped Bass. Several changes to the population have occurred over the past several decades, including a dramatic fluctuation in biomass, as well as the emergence of an enzootic disease, necessitating an update of biological metrics. The results of this study provide estimates of Striped Bass oocyte development, maturity, fecundity, oocyte size and quality, and female condition, which can be used in future studies to answer questions about how reproductive metrics play a role in the health and sustainability of this economically and ecologically vital fish species.

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TABLE 1. Types of models used for each response variable, the general model forms and the combinations of covariates considered. P=disease prevalence, M=month, Y=year, C=condition.

Response	General Model Form(s)	Covariate Combinations
Development	FL: binomial	none
		Y
		P
Maturity	Age: binomial, FL: binomial	none
		P
Egg Diameter	Age: logarithmic, FL: linear	none
		P
		M
		M, Y
		M, P
Fecundity	Age: logarithmic, FL: linear, modeled variance	M, C
		none
		Y
		P
		Y, P
		Y, M
		Y, M, P
Y, M, P, C		
GSI	Age: linear, FL: logarithmic	none
		P
		M
		M, Y
Dry Weight	Weight: linear, multiplicative error, FL: linear, multiplicative error	M, P
		M, C
		none
Dry Weight	Weight: linear, multiplicative error, FL: linear, multiplicative error	P
		C

TABLE 2. Residual sum-of-squares (RSS) / residual deviance (RD), R^2 , Akaike's information criterion (AIC), and ΔAIC_c for all models fitted to Striped Bass data. P=disease prevalence, M=month, Y=year, C=condition.

Response Var.	Independent Var.	Covariates	RSS/RD	R^2	AIC _c	ΔAIC_c	
Development	FL	None	435.04	-	439.07	0.00	
		Y	434.52	-	440.58	1.51	
		P	434.14	-	440.20	1.13	
Maturity	Age	None	704.12	-	708.12	1.70	
		P	700.42	-	706.42	0.00	
	FL	None	701.62	-	705.62	0.33	
		P	699.29	-	705.29	0.00	
Egg Diameter	Age	None	39.100	0.404	194.23	43.21	
		P	39.059	0.405	195.80	44.79	
		M	37.668	0.426	182.19	31.18	
		M, Y	37.501	0.429	182.32	31.31	
		M, P	37.608	0.427	183.56	32.55	
		M, C	34.879	0.468	151.02	0.00	
	FL	None	35.479	0.459	152.24	70.32	
		P	35.476	0.459	154.25	72.33	
		M	33.782	0.485	135.15	53.23	
		M, Y	33.652	0.487	135.55	53.63	
		M, P	33.782	0.485	137.20	55.29	
		M, C	29.723	0.547	81.91	0.00	
		Age	None	39.961	0.440	237.80	0.00
			Y	39.704	0.444	238.88	1.08
P	39.955		0.440	239.88	2.08		
Y, P	39.703		0.444	241.01	3.21		
Y, M	38.628		0.459	238.80	1.00		
Y, M, P	38.620		0.459	240.96	3.16		
Y, M, P, C	37.820		0.470	239.85	2.05		
Fecundity	Age	None	182.12	-	915.36	0.97	
		Y	184.88	-	916.32	1.93	
		P	177.11	-	916.14	1.74	
	FL	Y, P	178.37	-	917.00	2.60	
		Y, M	159.57	-	914.40	0.00	
		Y, M, P	148.84	-	914.54	0.14	
		Y, M, P, C	157.31	-	914.70	0.31	
		Age	None	3448.1	0.346	2156.70	43.22
			P	3446.9	0.346	2158.58	45.10
M	3270.9		0.380	2137.62	24.14		
M, Y	3270.4		0.380	2139.61	26.13		
M, P	3270.5		0.380	2139.62	26.14		
M, C	3081.4		0.416	2113.48	0.00		
GSI	Age	None	3142.3	0.404	2115.92	71.48	
		P	3140.7	0.405	2117.75	73.30	
		M	2955.5	0.440	2093.10	48.66	
	FL	M, Y	2947.6	0.441	2093.98	49.54	
		M, P	2954.8	0.440	2095.06	50.62	
		M, C	2633.0	0.501	2044.44	0.00	
		Dry Weight	Weight	None	0.452	0.099	-78.38
P	0.447			0.101	-76.50	1.88	
C	0.450			0.103	-76.18	2.20	
FL	None		0.462	0.078	-77.27	0.00	
	P		0.459	0.084	-75.19	2.07	
	C		0.462	0.078	-74.87	2.39	

TABLE 3. Estimates, standard errors, z-values, and p-values for each coefficient of the best fitting development model.

Coefficient	Estimate	Std. Error	t-value	p-value
Intercept	-5.758	0.501	-11.48	<0.0001
FL	0.009	0.001	11.43	<0.0001

TABLE 4. Estimates, standard errors, z-values, and p-values for each coefficient of the best fitting maturity models.

Coefficient	Estimate	Std. Error	t-value	p-value
Intercept	-2.620	0.280	-9.369	<0.0001
Disease-pos	0.369	0.191	1.928	0.054
Age	0.892	0.084	10.591	<0.0001
Intercept	-3.603	0.331	-10.87	<0.0001
FL	0.011	0.001	12.59	<0.0001

TABLE 5. Estimates, standard errors, t-values, and p-values for each coefficient of the best fitting oocyte diameter models.

Coefficient	Estimate	Std. Error	t-value	p-value
Intercept	-1.597	0.202	-7.923	<0.0001
ln(Age)	0.710	0.038	18.706	<0.0001
Month (Mar)	0.090	0.030	2.959	<0.01
Month (Apr)	0.161	0.051	3.152	<0.01
Fulton's K	0.799	0.137	5.843	<0.0001
Intercept	-1.650	0.181	-9.095	<0.0001
FL	0.002	7.95e ⁻⁵	22.016	<0.0001
Month (Mar)	0.082	0.028	2.925	<0.01
Month (Apr)	0.196	0.047	4.152	<0.0001
Fulton's K	0.976	0.128	7.636	<0.0001

TABLE 6. Estimates, standard errors, t-values, and p-values for each coefficient of the best fitting fecundity models.

Coefficient	Estimate	Std. Error	t-value	p-value
Intercept	-1.565	0.250	-6.258	<0.0001
log(Age)	1.268	0.114	11.114	<0.0001
Intercept	-1.462	0.101	-14.503	<0.0001
FL	0.003	0.000	21.586	<0.0001

TABLE 7. Estimates, standard errors, t-values, and p-values for each coefficient of the best fitting GSI models.

Coefficient	Estimate	Std. Error	t-value	p-value
Intercept	-9.413	1.587	-5.932	<0.0001
Age	0.806	0.047	16.965	<0.0001
Month (Mar)	0.577	0.284	2.034	<0.05
Month (Apr)	2.017	0.450	4.481	<0.0001
Fulton's K	6.173	1.195	5.166	<0.0001
Intercept	-71.638	3.978	-18.011	<0.0001
ln(FL)	10.112	0.499	20.267	<0.0001
Month (Mar)	0.574	0.262	2.189	<0.05
Month (Apr)	2.020	0.416	4.856	<0.0001
Fulton's K	8.233	1.129	7.290	<0.0001

TABLE 8. Estimates, standard errors, t-values, and p-values for each coefficient of the best fitting oocyte dry weight models.

Coefficient	Estimate	Std. Error	t-value	p-value
Intercept	$1.207e^{-1}$	$3.993e^{-2}$	3.023	<0.01
Weight	$1.074e^{-5}$	$4.530e^{-6}$	2.370	<0.05
Intercept	$-6.580e^{-3}$	$1.021e^{-1}$	-0.064	0.949
FL	$2.637e^{-4}$	$1.225e^{-4}$	2.153	<0.05

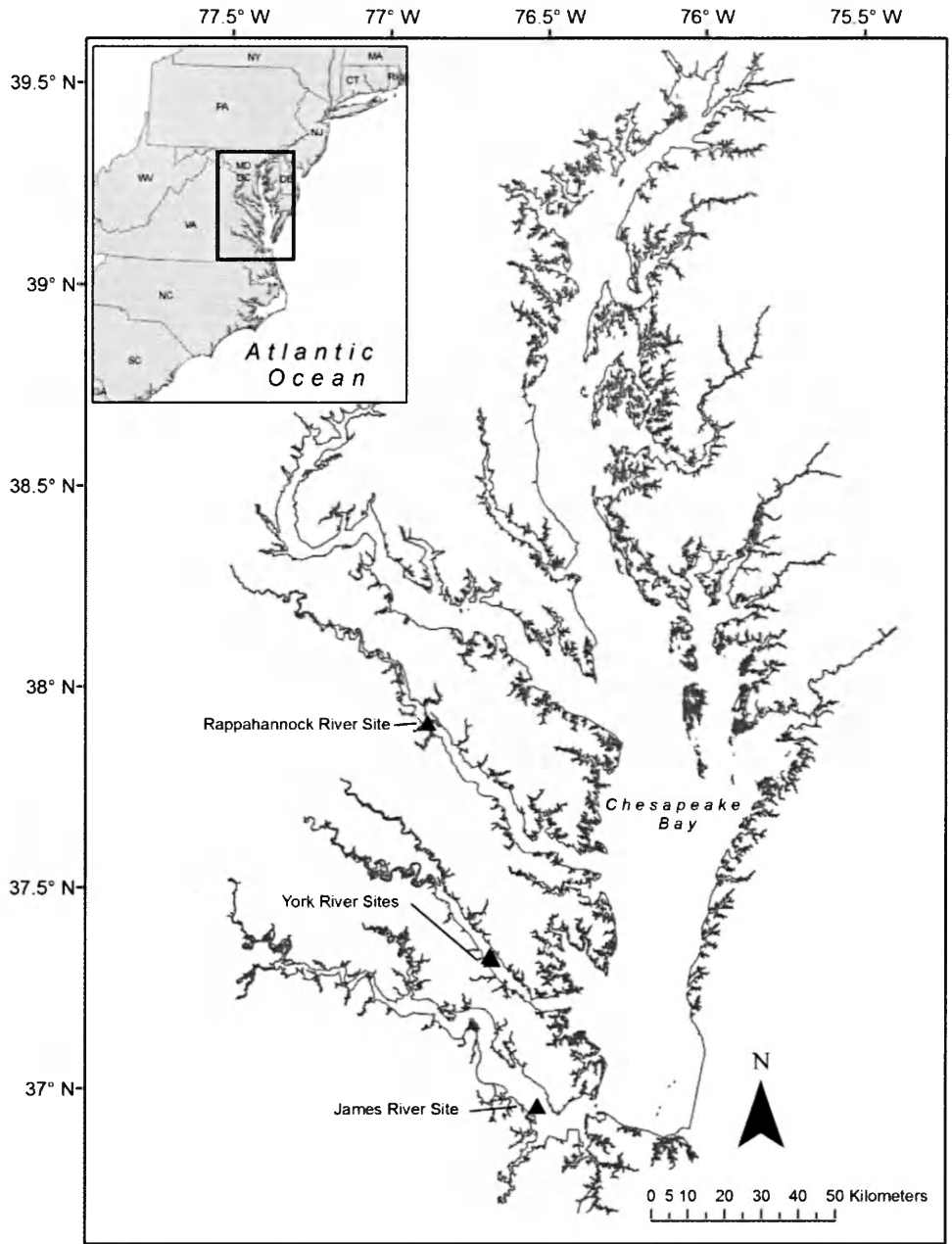


FIGURE 1. Map of Striped Bass sampling locations in tributaries of the Chesapeake Bay.

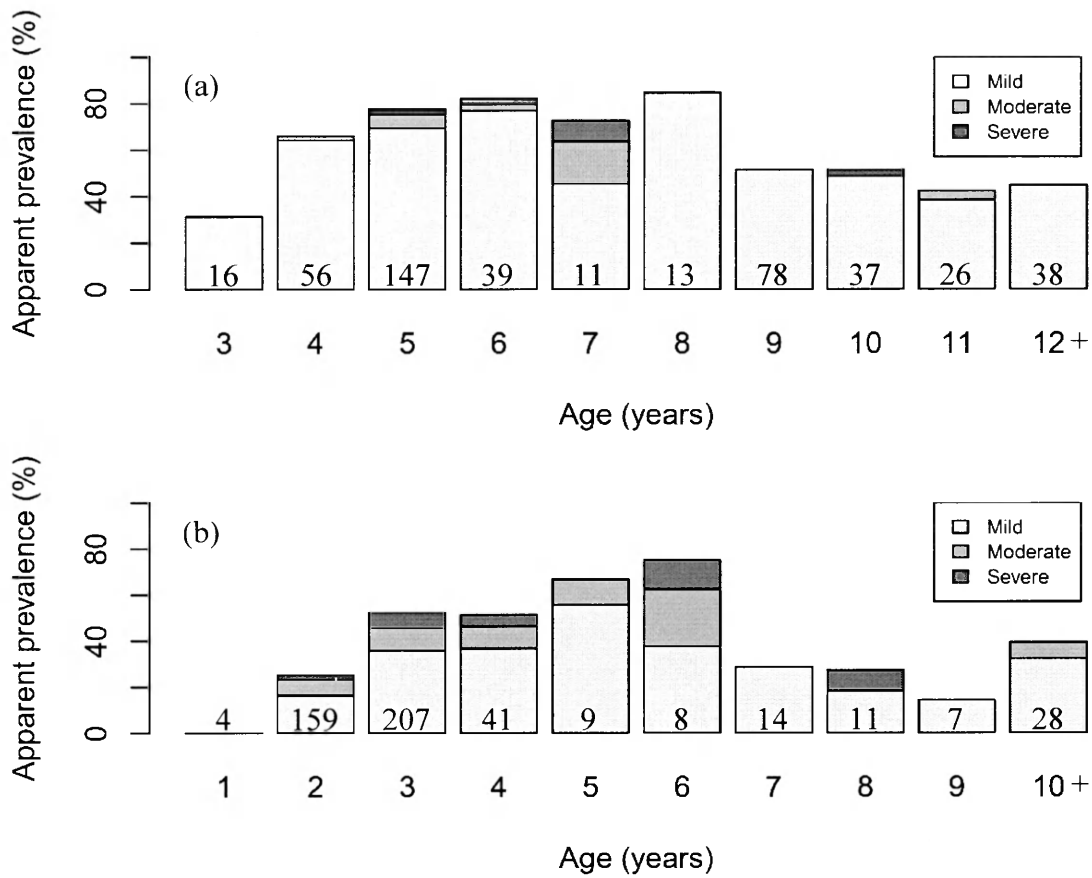


FIGURE 2. Apparent prevalence of mycobacteriosis in Chesapeake Bay Striped Bass from the York, James, and Rappahannock Rivers (a, current data) and from the mainstem (b, historic data). Shading denotes percent of fish in each severity category. Numbers inside bars denote total sample size (disease-positive and -negative) at each age.

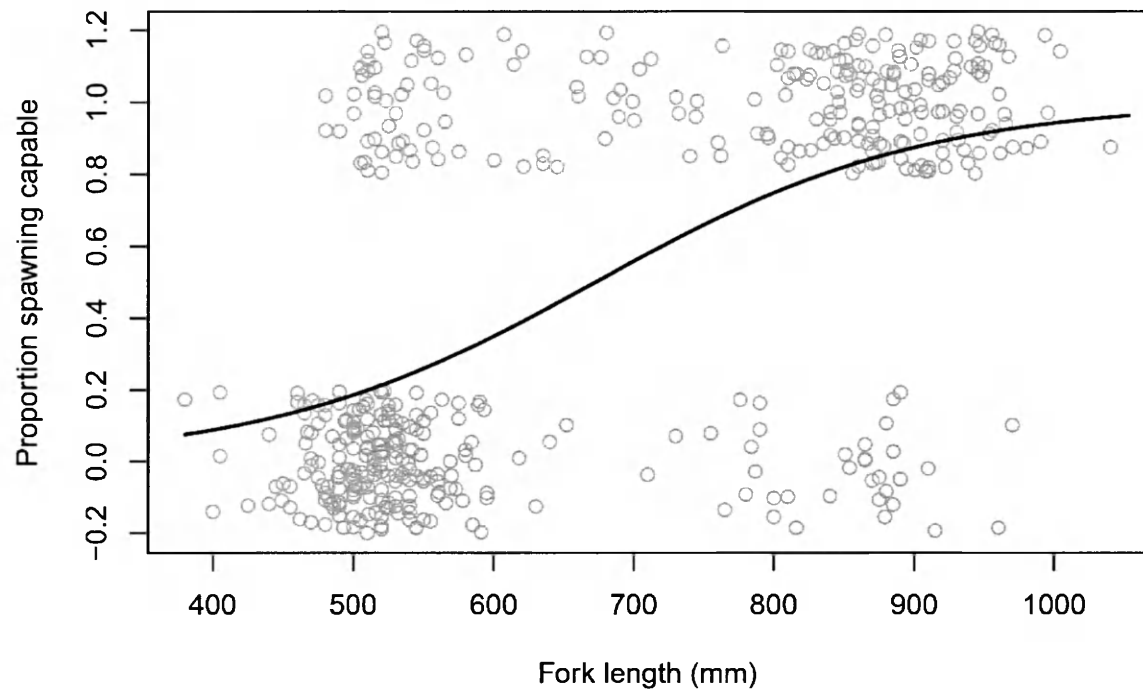


FIGURE 3. Chesapeake Bay Striped Bass development in terms of proportion of spawning capable fish at length and model predictions. Raw data are jittered along the y-axis for visualization.

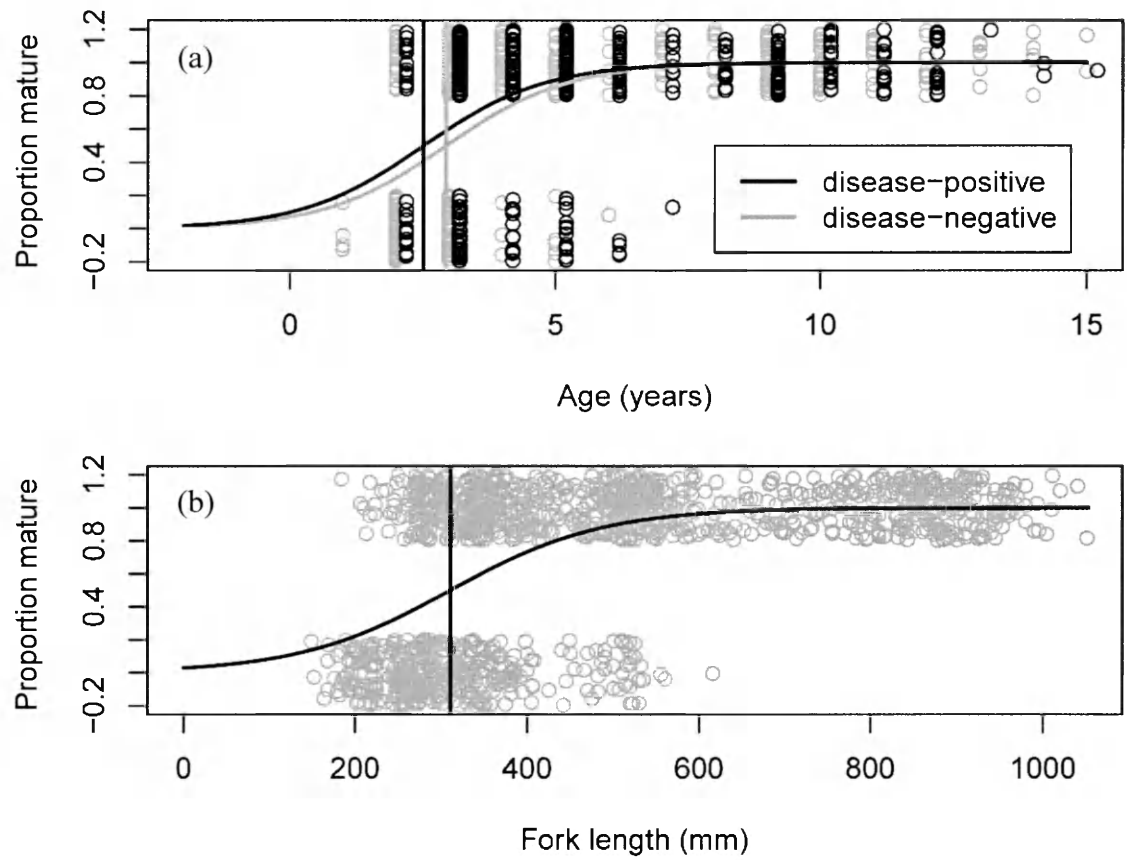


FIGURE 4. Chesapeake Bay Striped Bass proportion mature-at-age (a) and -at-length (b) and model predictions. Raw data are jittered along the y-axis for visualization. In panel (a), 0.2 is added to the raw age data for disease-positive fish for visualization. Vertical lines denote age at 50% maturity for disease-positive (2.52) and disease-negative fish (2.94) and length at 50% maturity (311.08 mm).

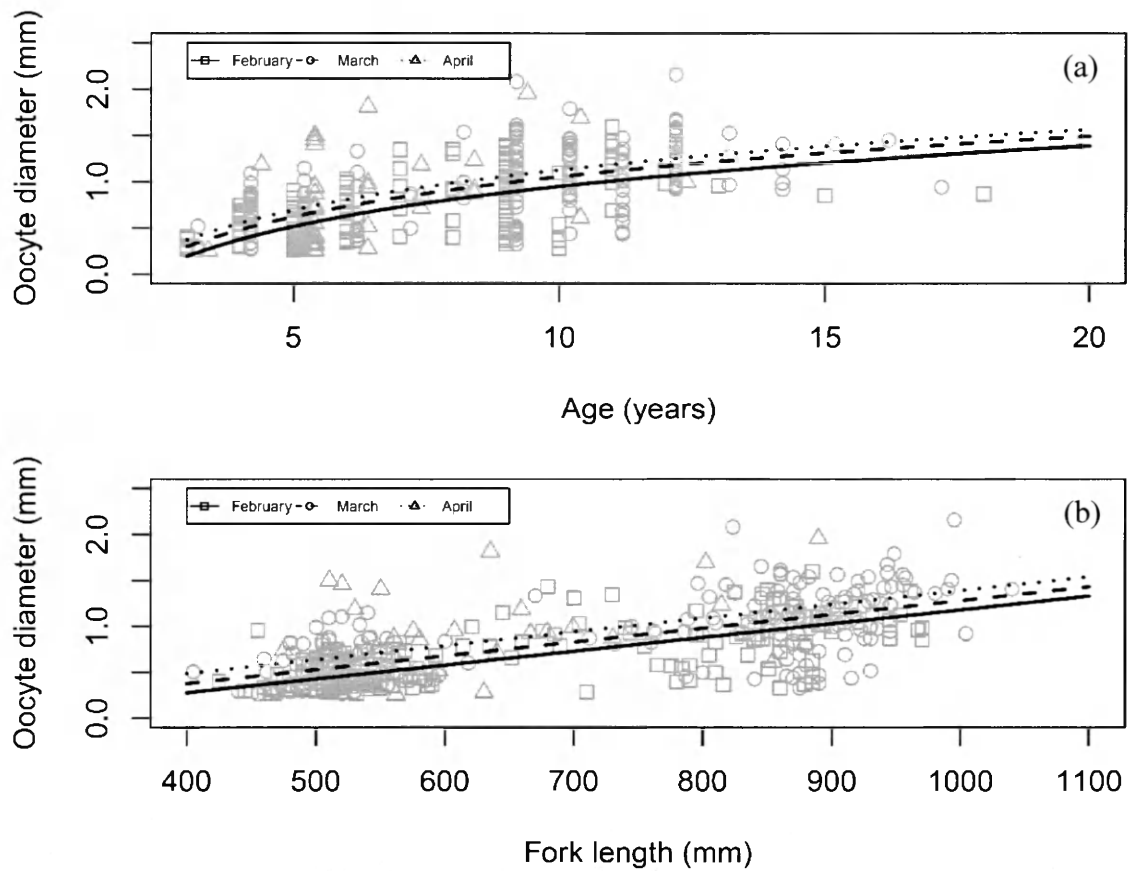


FIGURE 5. Chesapeake Bay Striped Bass fresh oocyte diameters-at-age (a) and -at-length (b) and model predictions for each month. Condition is set to the mean value. To the raw age/length data for March and April, 0.2 and 0.4, respectively are added for visual purposes.

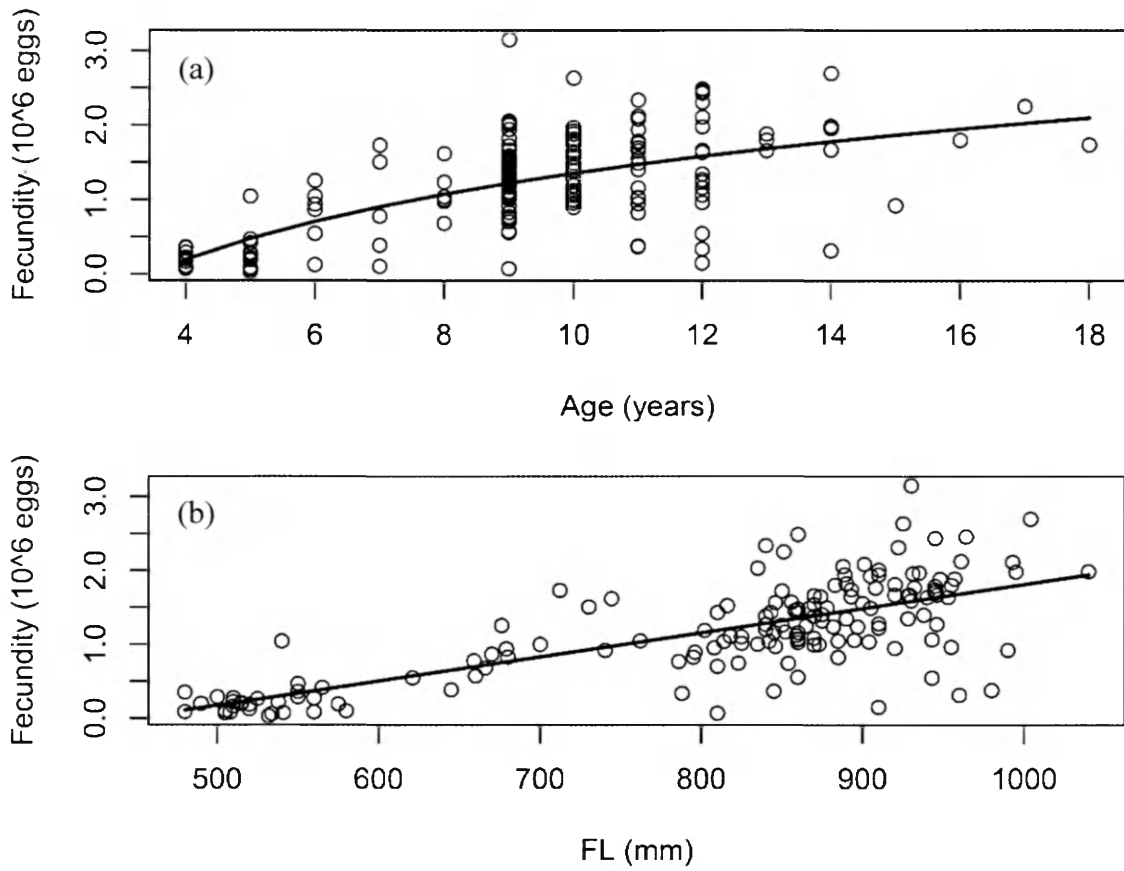


FIGURE 6. Chesapeake Bay Striped Bass total fecundity-at-age (a) and -at-length (b) and model predictions.

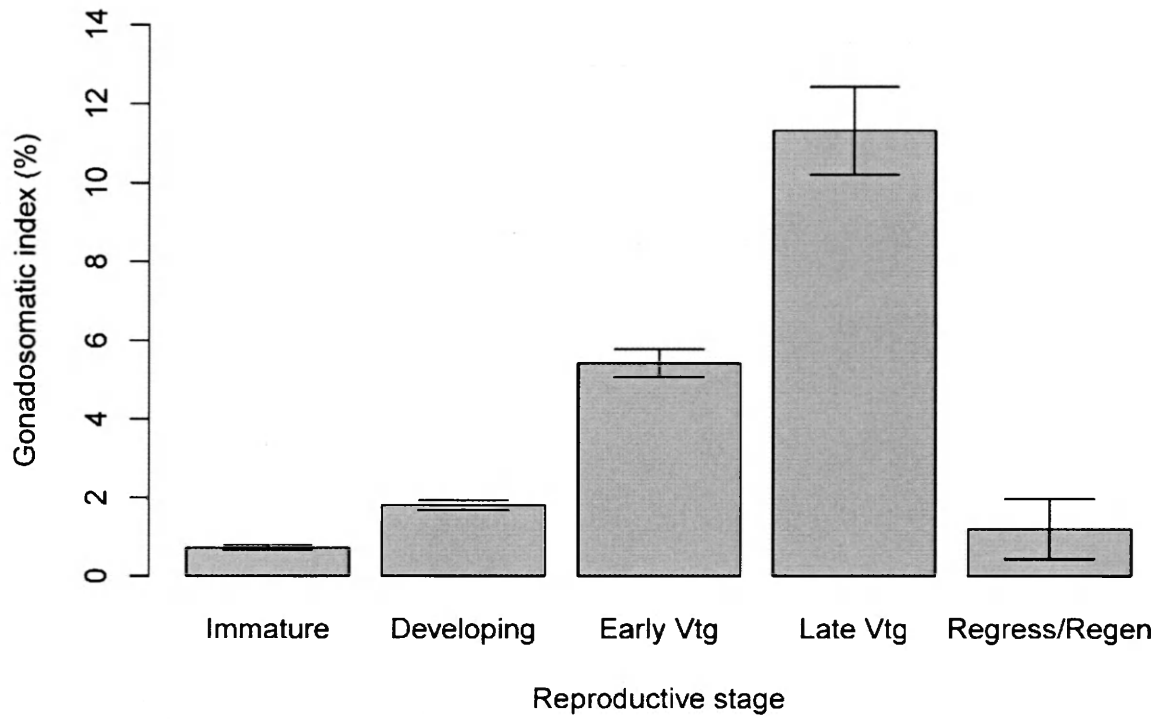


FIGURE 7. Average gonadosomatic index for each developmental stage of Chesapeake Bay Striped Bass eggs: immature, developing, early-stage vitellogenic, late-stage vitellogenic, and regressing/regenerating. Error bars denote standard error.

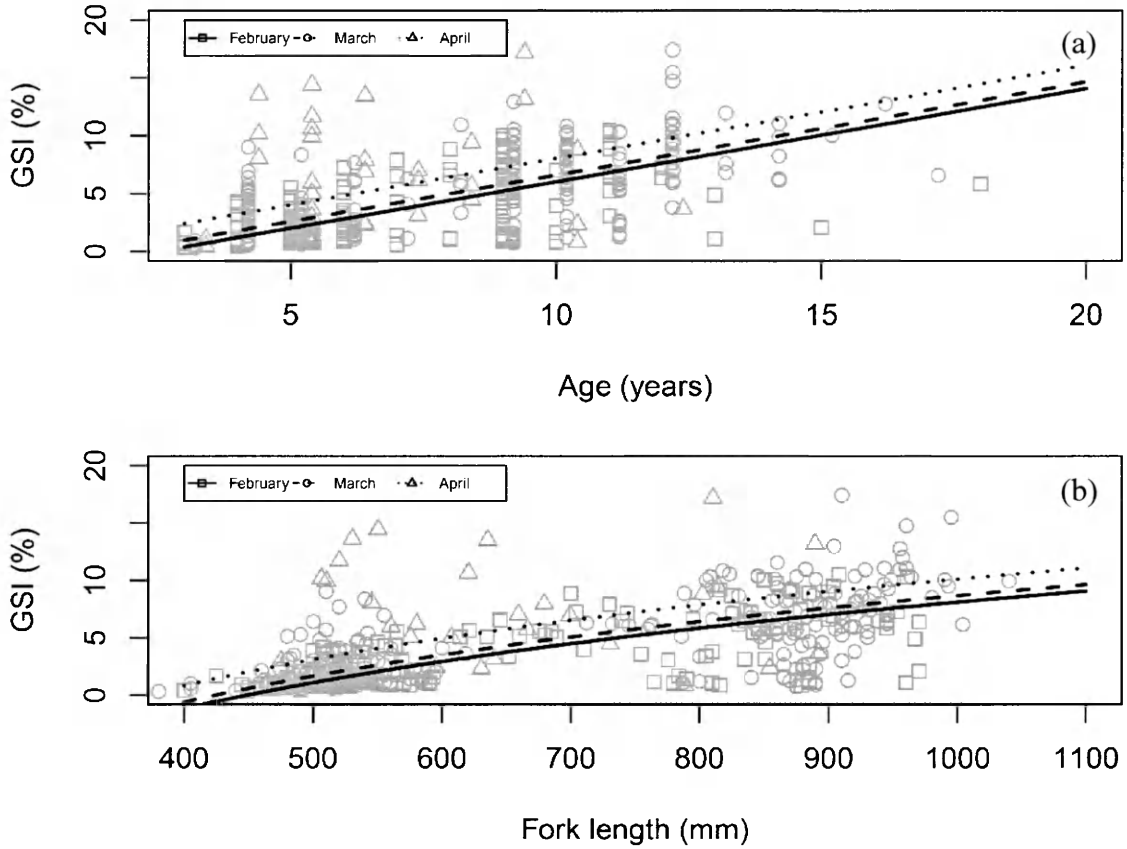


FIGURE 8. Chesapeake Bay Striped Bass GSI-at-age (a) and -at-length (b) and model predictions for each month. Condition is set to the mean condition. To the raw age/length data for March and April, 0.2 and 0.4, respectively are added for visual purposes.

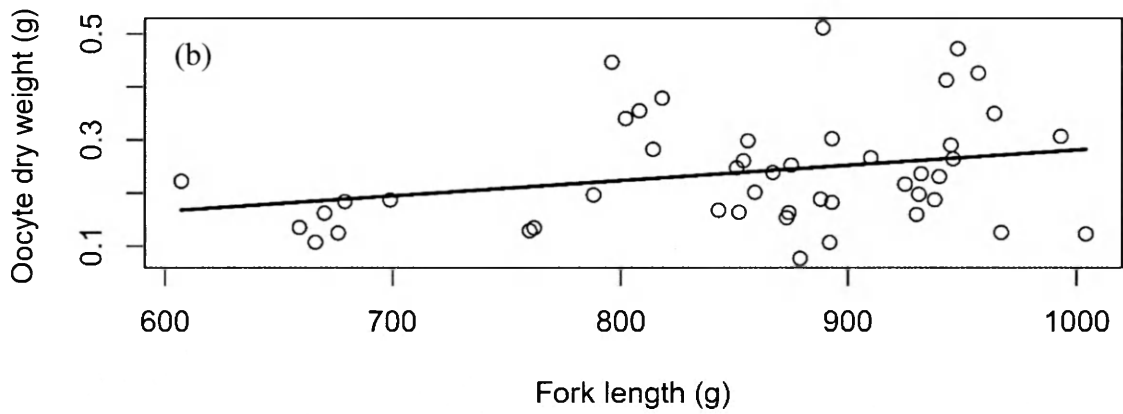
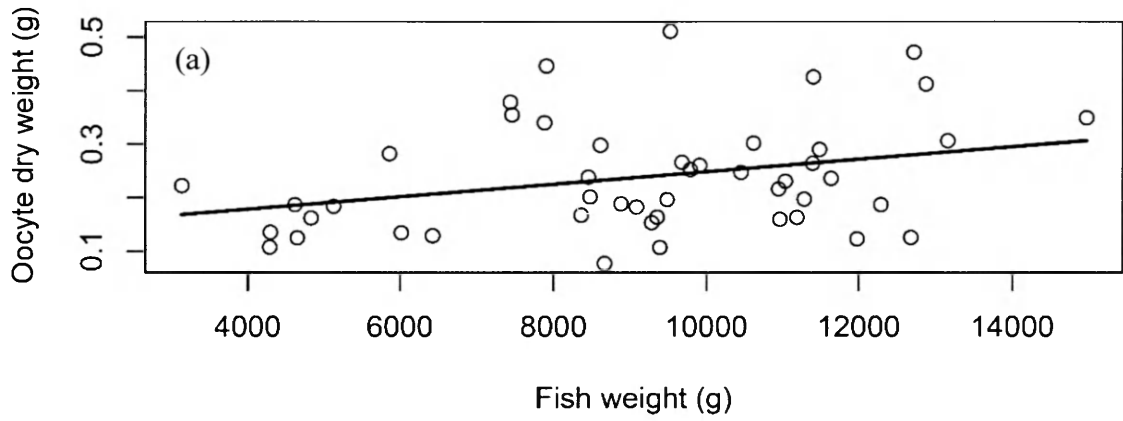


FIGURE 9. Chesapeake Bay Striped Bass oocyte dry weight as a function of fish weight (a) and as a function of fork length (b) and model predictions.

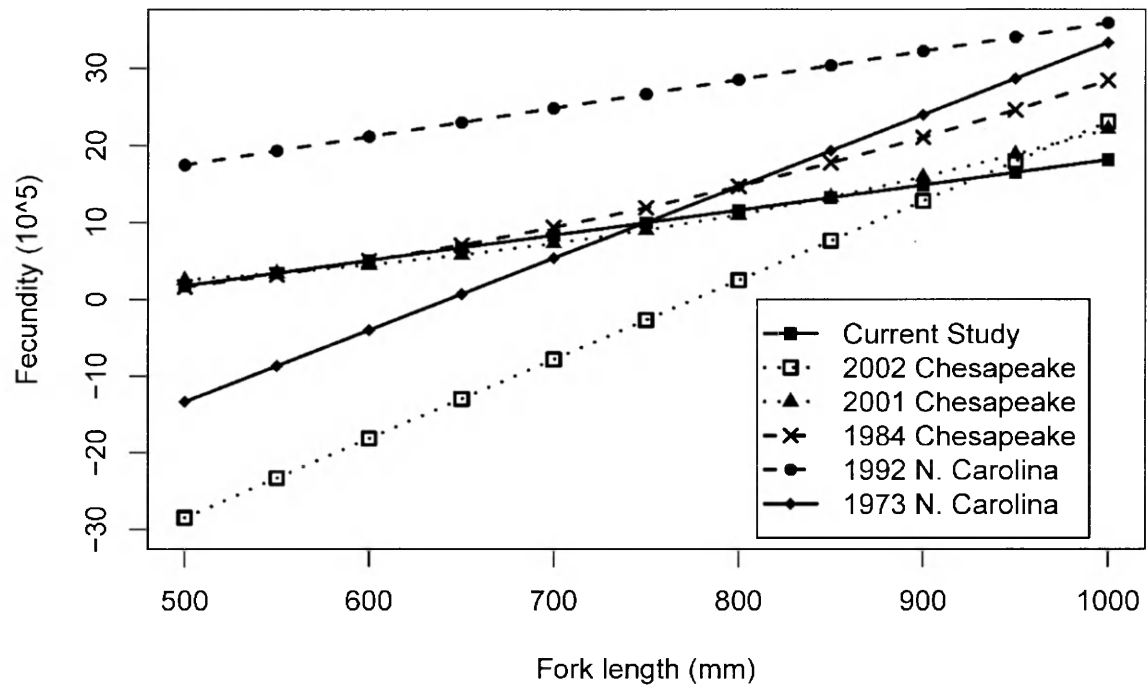


FIGURE 10. Predicted Striped Bass fecundity-at-length based on equations determined by the current study, Richards et al. (2002), Sadler et al. (2001), Goodyear (1984), Olsen and Rulifson (1992), and Holland and Yelverton (1973).

CHAPTER 2

DISEASE-ASSOCIATED EFFECTS ON EGG-PER-RECRUIT OF CHESAPEAKE

BAY STRIPED BASS (*MORONE SAXATILIS*)

Abstract

The emergence of mycobacteriosis in the Chesapeake Bay Striped Bass population in the late 1990s has prompted much research, and the current prevalence of greater than 50% raises questions about population level effects of the disease. The objectives of this study were to examine disease-associated effects of mycobacteriosis on reproductive output of Chesapeake Bay Striped Bass by creating an egg-per-recruit model. Disease and growth data obtained from female Striped Bass collected during spring 2012-2013 in the York, James, and Rappahannock Rivers of the Chesapeake Bay (n=469) were combined with data collected throughout the year from 2003-2007 from the bay mainstem (n=792). Fish ranged in age from 1-18 years and disease prevalence throughout the bay and across years was 50%, with prevalence increasing with age to age-6 and then decreasing in the older fish. Previous research has demonstrated that disease-positive fish have slower growth and increased natural mortality compared to disease-negative fish. Three model scenarios were developed to examine the effects of reduced growth, increased natural mortality, and combined effects on lifetime reproductive output. Results showed that disease-associated growth differences caused a 3.3% loss in lifetime reproductive potential, disease-associated natural mortality led to a 74.5% loss in reproductive output, and the combined effects caused a 75.1% loss. The results of this study indicate that mortality due to mycobacteriosis is significantly reducing the lifetime reproductive potential of Chesapeake Bay Striped Bass, which could lead to a significant decline in recruitment in future years.

INTRODUCTION

Successful management of fish populations requires an understanding of how factors such as fishing, disease, and climate change influence survival, distribution, and abundance (Pitcher et al. 1999). However, understanding such mechanisms is often difficult since fish live in a three-dimensional environment that can change rapidly. Forecasting human impact and ecosystem resilience is therefore challenging and perceived changes often cannot be distinguished from natural changes (De Leo and Levin 1997). Mathematical models are increasingly used to assess fish stocks and to predict how populations might respond to agents of change. Such mathematical approximations of fish population dynamics are important to the formation of informed and robust management policies.

Fisheries stock assessments integrate population processes, such as growth, recruitment, and survival with harvest impacts. These models use biological data, including fish length, age, and maturity along with catch data to estimate desired metrics such as annual population size and rates of fishing mortality. One metric that is of particular concern to fisheries managers is the reproductive capacity of a stock (Goodyear 1993). Reproductive capacity must exceed total mortality for populations to maintain high productivity.

Egg-per-recruit (EPR) models represent one method for estimating reproductive potential given information on growth, mortality, fecundity, and maturity. EPR models are commonly used to examine egg production responses under different assumptions about stock dynamics and to explore effects of different management scenarios. For

example, Prager et al. (1987) created an EPR model to evaluate different regulatory schemes for restoring Striped Bass stocks in Rhode Island and to better understand population responses to potential harvest policies. The Striped Bass is an economically and ecologically important anadromous teleost with native populations spanning the Atlantic coast of the United States. (Merriman 1937, Carpenter et al. 1985, 1987, Hartman and Brandt 1995, Buchheister and Latour 2015). Population abundance along the Atlantic coast plummeted in the 1980s due to recruitment overfishing and possibly poor water quality (Richards and Rago 1999), but timely management efforts and favorable environmental conditions supported strong recruitment in the early 1990s that allowed the stock to rebound (ASMFC 2013).

Although coastal Striped Bass are currently not overfished and overfishing is not occurring, estimates of female spawning stock biomass have been steadily declining since 2003 (ASMFC 2013), which is shortly after the emergence of mycobacteriosis in the Chesapeake Bay population (Vogelbein et al. 1999). Several studies have consistently demonstrated prevalence of over 50% (Overton et al. 2003, Gauthier et al. 2008, Latour et al. 2012). *Mycobacterium* spp. are ubiquitous microorganisms that are frequently isolated from water and soil in the environment and are common pathogens of humans (most notably the cause of leprosy, tuberculosis, and Buruli ulcer) as well as fishes (Jacobs et al. 2009, Gauthier et al. 2010). Visceral mycobacteriosis is a severe, subacute to chronic disease that targets the spleen, liver, and kidney. Dermal disease includes scale loss, skin ulceration, pigmentation changes, emaciation, exophthalmia, and/or spinal defects (Nigrelli and Vogel 1963, Snieszko 1978). Granulomatous inflammation and

often severe tissue damage are characteristic of the disease (Vogelbein et al. 1999). Mycobacteriosis has affected over 160 species of marine and freshwater fishes worldwide, in cultured and wild populations. It is the most common chronic disease affecting tropical aquarium fishes, but the impact on wild populations and associated fisheries is often not as well understood (Jacobs et al. 2009).

In general, mortality from mycobacteriosis is difficult to observe and quantify in wild fish populations. However, tag-return modeling by Jiang et al. (2007) detected an increase in natural mortality for Maryland Striped Bass since 1999 and Gauthier et al. (2008) used epidemiological models to demonstrate that Striped Bass collected in the mainstem of the Chesapeake Bay experience disease-associated mortality. Additionally, Latour et al. (2012) determined that disease positive Striped Bass exhibit significantly lower growth trajectories when compared to disease-negative Striped Bass in the Chesapeake Bay. Despite these advancements, disease impacts on other population level processes such as reproductive output remain largely unknown.

The purpose of this research was to quantify the extent to which mycobacteriosis impacts the lifetime reproductive potential of female Striped Bass in Chesapeake Bay by utilizing egg-per-recruit models. As a base model, we developed an EPR model under the assumption of no disease impacts. We then modified the model to account for the force-of-infection of mycobacteriosis, which is defined as the rate disease-negative animals become disease-positive, along with the effects of disease-associated mortality and growth. Inferences regarding disease impacts on reproductive output for Chesapeake Bay Striped Bass were based on relative comparisons of total lifetime egg production in the

absence of disease to lifetime egg production resulting from disease. This study contributes to ongoing investigations aimed at quantifying the population level impacts of mycobacteriosis on Striped Bass, which will allow for more informed management of this valuable species.

METHODS

Field collection and laboratory analysis

Female Striped Bass were collected from the York, James, and Rappahannock rivers of the Chesapeake Bay using gillnets from February to May, 2012-2013 (n=469, referred herein as current data). From these fish, fork length (FL) was measured, otoliths were removed for aging, spleens were histologically processed for disease prevalence and severity, and ovaries were processed for total fecundity and histologically assessed for maturity (see Gervasi et al., Chapter 1, for specific field and laboratory details). To increase the sample size of Striped Bass used to infer maturity, apparent prevalence of mycobacteriosis, and growth among disease-negative and -positive fish, additional data from 2003-2007 were utilized from the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP, n=792, referred herein as historic data, Latour et al. 2003). ChesMMAP is a bottom trawl survey that operates annually in the bay mainstem bimonthly (Mar, May, Jul, Sep, and Nov) according to a regional and depth random stratified sampling design. Striped Bass collected by ChesMMAP were categorized as mature or immature based on gross examination of ovaries, otoliths were removed for aging, and spleens were processed histologically for bacterial histology (n=792). All

protocols for sampling and euthanizing fish were approved by the College of William & Mary's Institution Animal Care and Use Committee.

Modeling

Base EPR model. – Egg-per-recruit models utilize the life history characteristics of maturity, mortality, growth, and fecundity to calculate lifetime reproductive potential. A base EPR model was constructed using current and historic data for disease-negative Striped Bass and, when appropriate, literature information. The purpose of the base model was to provide a reference level to which simulated disease-related impacts on reproductive potential could ultimately be compared. The general EPR model equation is as follows:

$$(1) \quad EPR = \sum_{t=1}^{t_{max}} N_t k_t m_t$$

where t indexes age which ranges from one, since age-0 fish are assumed to be immature, to the maximum age in the population (t_{max}), N_t is the number of females at age t , and k_t is the mean fecundity at age t adjusted by proportion mature-at-age (m_t).

Maturity-at-age was determined by Gervasi et al. (Chapter 1) using a binomial generalized linear model applied to current and historical data (the latter data source was restricted to females collected in March given the timing of Striped Bass spawning). Comparisons of model parameterizations with and without a disease prevalence covariate indicated a significant difference in the maturity schedules of healthy versus diseased

fish. Therefore, separate maturity ogives were used for the base and disease EPR models (Figure 1a).

The base model was initialized using a single individual age-1 female, and subsequent numbers-at-age were calculated as:

$$(2) \quad N_t = N_{(t-1)}e^{(-Z_t)}$$

where Z_t represents total age-specific mortality defined as the sum of age-specific fishing (F_t) and age-specific natural mortality (M_t); $Z_t = F_t + M_t$. Natural mortality-at-age was estimated using the mortality-weight equation for ocean ecosystems developed by Lorenzen (1996) and historic and current mean weight-at-age data. Age-specific fishing mortality rates, $F_t = sel_t * F$ were based on estimates from the most recent age-structured stock assessment for Striped Bass, with the fishing mortality value set at the current target value of 0.175 and multiplied by selectivity to the fishing gear at age (Figure 1b, ASMFC 2013).

Base model EPR was first calculated using direct estimates of fecundity-at-age (Gervasi et al. Chapter 1). However, to simulate the effects of disease-associated growth (more on this below), a composite relationship was also used to estimate k_t , where fecundity-at-age was estimated by determining predicted length at each age from the length-at-age model and then determining predicted fecundity at each of those lengths and consequently ages using the fecundity-at-length model. Gervasi et al. (Chapter 1) investigated disease-associated effects on total fecundity-at-age and found no significant

differences between disease-negative and -positive fish. Therefore, a single fecundity-at-age/length relationship was used for all EPR model configurations (Figure 1c, 1d).

Latour et al. (2012) demonstrated that disease-positive Striped Bass grow more slowly than disease-negative fish in Chesapeake Bay, which provides some guidance on the growth trajectories of each disease group. However, the primary goal of that study was to examine disease-associated impacts on growth rather than estimate “true” growth model parameters. Using a similar methodology, current and historical length-at-age data combined (n=1261) were analyzed to obtain more realistic growth parameters (particularly maximum FL, L_{∞}). Several model forms were considered (Table 1) and a Richards growth model (Richards 1959) parameterized with a disease prevalence covariate (Kimura 2008) received the most empirical support (Table 2, Figure 2). Accordingly, the growth trajectory for disease-negative fish from that analysis was incorporated into the base EPR model.

Disease EPR model. – To quantify the effects of mycobacteriosis on total lifetime reproductive output, the base EPR model was modified to incorporate force-of-infection, the aforementioned disease-associated growth differences, disease severity and progression, and stage-specific disease-associated mortality. Gauthier et al. (2008) showed that force-of-infection of mycobacteriosis in Chesapeake Bay Striped Bass is age-dependent ($\lambda(t)$) and best described by a log-logistic function of the form:

$$(3) \quad \lambda(t) = \frac{\alpha\beta(\alpha t)^{\beta-1}}{[1+(\alpha t)^{\beta}]}$$

where t indicates age and α and β are scale and shape parameters that control the age-dependency. Current and historic age-specific prevalence data combined were analyzed according to the methods of Gauthier et al. (2008) to evaluate the significance of a year covariate (2003-2007 and 2012-2013) on $\lambda(t)$ and to derive updated estimates of the α and β . Akaike's Information Criterion (AIC; Akaike 1973, Burnham and Anderson 2002) was used to compare force-of-infection parameterizations.

Efforts to assess disease severity both histologically (Gervasi et al., Chapter 1) and via inspection of external skin lesions (Sadler et al. 2014) have generally yielded three categorical designations (light, moderate, and heavy). Therefore, disease-positive fish were further classified according to severity categories within the EPR model, and transitions among disease stages were based on progression rates estimated from a tagging study recently conducted for Striped Bass in the Rappahannock River, VA (Sadler et al. 2014). In that study, fish were assigned a severity category (apparently disease-free, light, moderate, or heavy) based on the presence and severity of external skin lesions prior to receiving a tag and being released. Subsequent recoveries and re-examination of the external lesions of tagged fish led to the following estimates of disease progression: 100% of lightly infected fish became moderately infected after 386 days and 100% of moderately infected fish became severely infected after 753 days. For the disease EPR model, disease progression timelines were rescaled to represent annual transition probabilities (0.95 and 0.48, respectively). Sadler et al. (2014) also reported estimates of stage-specific differences in natural mortality rates based on ratios of tag-recoveries among apparently disease-negative and disease-positive fish across the

severity categories (Table 3). These differences were applied additively to the age-specific base natural mortality values to determine natural mortality values for each severity category within the EPR model.

The model began with one fish at age-1. As the model progressed to age-2, a proportion of fish would survive based on the disease-negative natural mortality rate. Of those fish that survived, a percentage would stay healthy and a percentage would become mildly diseased based on the force of infection at age-1. Healthy fish that survived to age-3 would again remain healthy or become mildly diseased, and based on the disease progression probability, a proportion of fish that were mildly diseased at age-2 would become moderately diseased at age-3 if they survived the disease-positive natural mortality rate. The remainder of the fish that survived would remain mildly diseased. This sequence continued, with fish staying healthy, or becoming mildly, moderately, or severely diseased at age-4, and again at age-5, with severely diseased fish remaining severely diseased if they survived. The model was run through 16 ages, so that the numbers of fish remaining would be split into four categories: healthy, mild, moderate, and severely diseased (Figure 3).

Three EPR scenarios were considered to quantify disease-associated impacts on lifetime reproductive output relative to the base EPR model: I disease-associated growth differences, II disease-associated mortality differences, and III disease-associated growth and mortality differences combined. For each scenario, total lifetime egg production was compared to that of the base model. The effects of uncertainty in growth, force-of-infection, and baseline and disease-associated natural mortality parameters within the

disease EPR model configurations were evaluated by running 1000 Monte Carlo simulations (Metropolis and Ulam 1949) assuming each parameter followed a normal distribution with a mean equal to the estimated value and a standard deviation of 10% of the mean. Naïve confidence intervals of total lifetime reproductive output for the base model and each disease scenario were calculated from the Monte Carlo simulation results.

RESULTS

The total count of female Striped Bass collected by both data sources, the mainstem from 2003-2007 (historic data) and the rivers from 2012-2013 (current data), was 1261, with 249 of the fish from the York River (20%), 68 from the James River (5%), 52 from the Rappahannock River (4%), and 792 from the bay mainstem (63%). Fish ranged in age from 1-18 years. Histological examination of spleens revealed that 630 fish (50%) were disease-positive, with prevalence increasing with age to age-6 and then dropping off in the older fish (Figure 4).

Based on AIC, the log-logistic function for force-of-infection with the year covariate was strongly supported over the time-invariant parameterization ($\Delta\text{AIC} = 19.4$). All disease EPR models were based on the log-logistic parameters (α and β) and force-of-infection at age was averaged over years and months (Figure 5). The total lifetime reproductive output for a disease-negative fish from the base model using the direct estimates of fecundity-at-age was 174502 (167603, 181721). When the composite relationship of length-at-age and fecundity-at-length was used to inform the model, the

output was 127440 (112173, 142862) eggs. Using the direct estimates of fecundity-at-age likely produce a more accurate output, but in order to analyze growth differences the composite relationship was needed. Relative to the number of eggs produced according to the baseline model with the composite fecundity-at-age relationship, the total lifetime egg production under scenario I was 0.967 with a naïve confidence interval of (0.867, 1.071). This estimate corresponds to a 3.3% decrease in reproductive output due to disease-associated growth differences that is indistinguishable from zero given the naïve confidence interval. For scenario II, the ratio of the disease EPR reproductive output to that from the baseline EPR model was 0.255 (0.183, 0.357), which corresponds to a 74.5% decrease that is significantly different from zero. The combined effects of disease-associated growth and mortality simulated in scenario III yielded a ratio of 0.249 (0.169, 0.358) or a 75.1% decline in lifetime reproductive potential.

DISCUSSION

Mycobacteriosis remains highly prevalent in female Chesapeake Bay Striped Bass. Differing growth trajectories among disease-positive and -negative fish had a negligible impact on lifetime reproductive potential of Chesapeake Bay Striped Bass (Scenario I). Although the growth model that included disease-prevalence as a covariate received the most empirical support, none of the disease model parameters were statistically significant, suggesting that mycobacteriosis does not have as great an impact on growth as was previously thought. However, the simulated effects of disease progression and associated natural mortality significantly reduced reproductive output

(Scenario II). The coast-wide Striped Bass population has greatly fluctuated in size over the past several decades, but has been steadily declining since 2004. In only 6 years the population halved, and the decline in abundance continues presently (ASMFC 2013). Female spawning stock biomass (SSB) has tracked the trends in overall abundance, and current levels are well below the target value and only barely above the threshold limit. Therefore, Striped Bass are not in a state of being overfished yet, but are on the borderline of transitioning to such a stock status. The results of this study show that lifetime reproductive potential of disease-positive Chesapeake Bay Striped Bass is appreciably reduced, which suggests that the increase in natural mortality attributed to mycobacteriosis may be at least partially responsible for the recently documented declines in abundance and spawning stock biomass. Since the Chesapeake Bay spawning stock contributes to a significant proportion of the Atlantic coast population, we recommend taking into account the effects of mycobacteriosis when making future management decisions for this socio-economically important species.

Several assumptions are inherent in the EPR model: (a) constant annual fishing mortality; (b) growth that follows the Richards growth model; (c) a closed population with no immigration or emigration; and (d) the fecundity-length relationship determined in Gervasi et al. (Chapter 1). Since these assumptions are applied to each model scenario, violation of any of the assumptions should not affect the comparisons among the model outputs. There are, however, several limitations to this study that require acknowledgement. Most notably, the egg-per-recruit models assumed equilibrium conditions in both the Striped Bass population and the force-of-infection of

mycobacteriosis. Fishing pressure and baseline natural mortality levels were held constant throughout the model simulation. However, over the course of 16 years (the assumed Striped Bass life cycle), fishing pressure can fluctuate in response to changes in management regulations and changes in predator/prey dynamics, other diseases, environmental conditions, etc. would likely impact natural mortality. Growth, maturity, and annual reproductive output can also vary temporally, as they are strongly linked to environmental conditions. As far as we know, mycobacteriosis has only been present in the Chesapeake Bay for approximately 15 years, or about one life cycle of the Striped Bass. Therefore, the host-pathogen relationship is not likely to have stabilized, and disease prevalence and severity will likely change, possibly continuing to fluctuate in future years. Future work utilizing a transitional egg-per-recruit model, which does not assume equilibrium, in addition to research on understanding the modes of disease acquisition/transition could prove to be fruitful.

Additionally, prevalence of mycobacteriosis decreases in older female Striped Bass, which could either be due to death or recovery. No evidence of regression or resolution of the disease has been observed to date (Gauthier et al. 2008), but it cannot be discounted since it is well known that many mycobacteria seen in human and veterinary cases can enter latency (Flynn and Chan 2001). If fish can recover from the disease, disease-associated mortality estimates are likely less than what was determined in previous studies. The mortality term is very important here since it is the major factor driving the results. Overestimation or underestimation of the mortality term would undoubtedly bias the results. This study utilized the results of a previous tagging study to

determine natural mortality rates for fish at each stage of disease severity (Sadler et al. 2014). The authors determined disease stage based on the presence and severity of external skin lesions, which does not necessarily represent the extent of visceral disease. It is likely that disease prevalence and severity determined using external signs were underestimated by Sadler et al. (2014), which means the disease-associated mortality estimates may be overestimated and represent inflated values. Alternatively, sampling may have presented a prevalence bias if diseased animals are more likely to be captured. Sampling bias could then have led to an overestimation of prevalence and thus a conservative estimation of disease-associated mortality.

It is also important to recognize that this study was based on data obtained from Chesapeake Bay fish. However, the Striped Bass population is coast-wide, so the model is limited spatially and does not necessarily apply to the entire coast-wide stock. Life history characteristics (e.g., growth, fecundity) as well as disease dynamics for the Delaware Bay, Hudson River, and North and South Carolina stocks likely differ significantly from those of Chesapeake Bay fish, and these differences could affect the base EPR estimate and any subsequent comparisons. Nevertheless, since the Chesapeake Bay spawning community contributes a majority of fish to the Atlantic Coast population (Fabrizio 1987), changes in the productivity of bay fish greatly affect the stock as a whole.

Finally, there is no clear relationship between egg production and the number of subsequent recruits since recruitment is stochastic and highly dependent upon environmental conditions (Hilborn and Walters 1992). Even though this study suggests

that mycobacteriosis appreciably reduces the number of eggs produced in a population, it does not necessarily translate to a reduction in new recruits. Nevertheless, this study demonstrates the potential for mycobacteriosis to dramatically impact Striped Bass population dynamics, which highlights the need to consider the effects of disease in stock assessments and when making management decisions.

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TABLE 1. Growth models fit to Chesapeake Bay Striped Bass length-at-age data, model equations, references, and Δ AIC values.

Covariates	Model	Reference	ΔAIC
	von Bertalanffy	(von Bertalanffy 1938)	229.61
no covariates	Gompertz	(Gompertz 1825)	104.50
	Richards	(Porch et al. 2002)	23.437
	von Bertalanffy	(von Bertalanffy 1938)	228.53
disease prevalence	Gompertz	(Gompertz 1825)	96.14
	Richards	(Porch et al. 2002)	0.00

TABLE 2. Estimates, standard errors, t-values, and p-values for each coefficient of the best fitting growth model.

Status	Coefficient	Estimate	Std. Error	t-value	p-value
Disease-negative	L_{∞}	930.787	13.821	67.345	<0.0001
	d	-2.515	0.474	-5.307	<0.0001
	k	0.582	0.073	8.016	<0.0001
	t_o	5.457	0.231	23.632	<0.0001
Disease-positive	L_{∞}	0.843	23.098	0.036	0.971
	d	-0.445	0.789	-0.565	0.572
	k	-0.017	0.112	-0.151	0.880
	t_o	0.311	0.339	0.918	0.359

TABLE 3. Estimates of mortality and relative survival rates for Striped Bass in each disease category compared to non-diseased (clean) fish. The slope estimates the difference in natural mortality rate ($M_{\text{clean}} - M_{\text{diseased}}$) and is the slope of the regression line of $\log(\text{ratio of recaptures})$ versus time. The exponential slope is an estimate of the ratio of annual survival rates. Adapted from Sadler et al. (2014).

Comparison	slope	S.E.	p-value	exp(slope)
Light vs. clean	-0.09	0.08	0.341	0.91
Moderate vs. clean	-0.39	0.13	0.002	0.68
Heavy vs. clean	-0.59	0.16	< 0.001	0.55

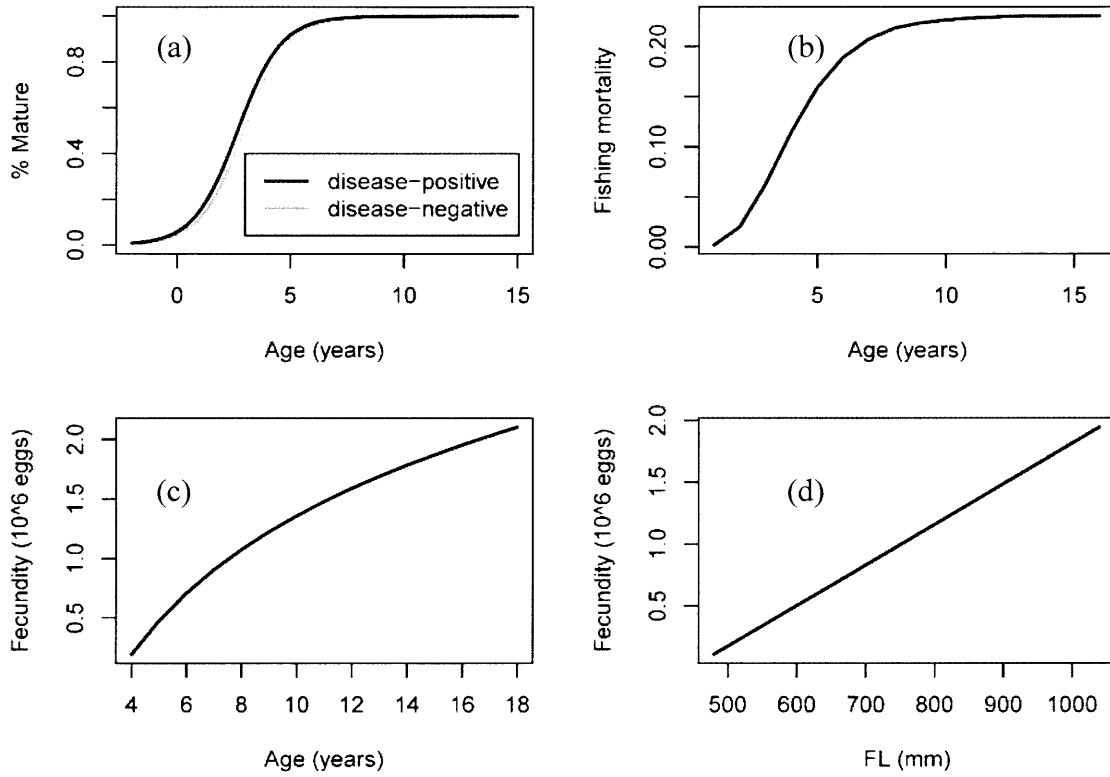


FIGURE 1. Chesapeake Bay Striped Bass predicted maturity-at-age (a), fishing mortality-at-age based on an annual fishing mortality value of 0.23 and selectivity to fishing gear at age (b), ASMFC 2013), and predicted fecundity-at-age (c) and -at-length (d).

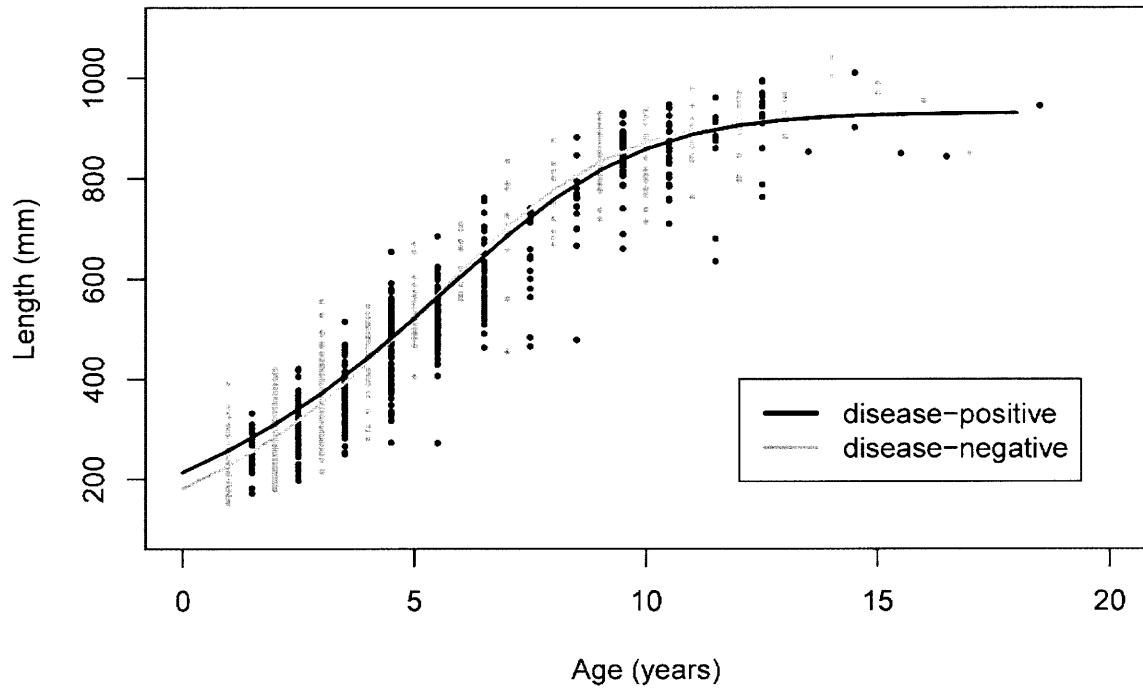


FIGURE 2. Chesapeake Bay Striped Bass length-at-age for disease-positive and disease-negative fish and corresponding Richards growth models.

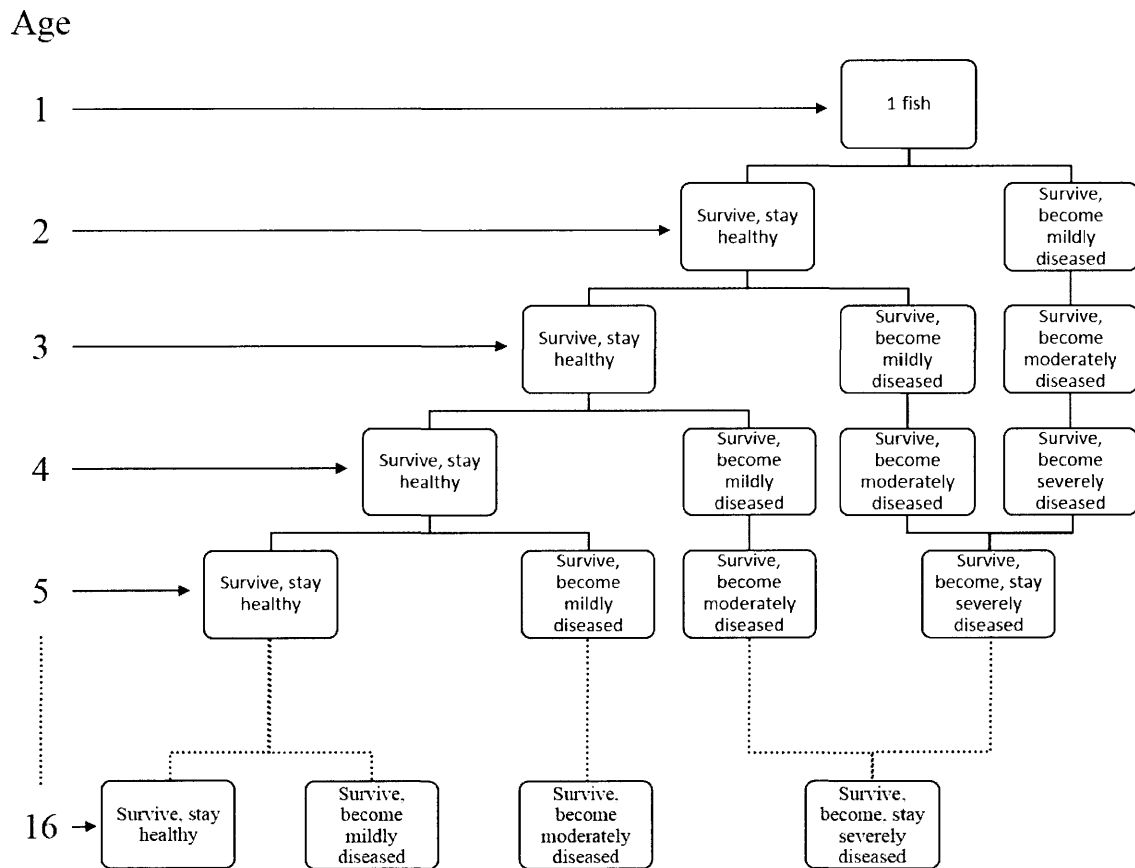


FIGURE 3. Simplified flow chart of the disease EPR model. Model begins with one fish at age-1 and fish that survive to the next year are moved into disease categories based on force-of-infection and disease progression.

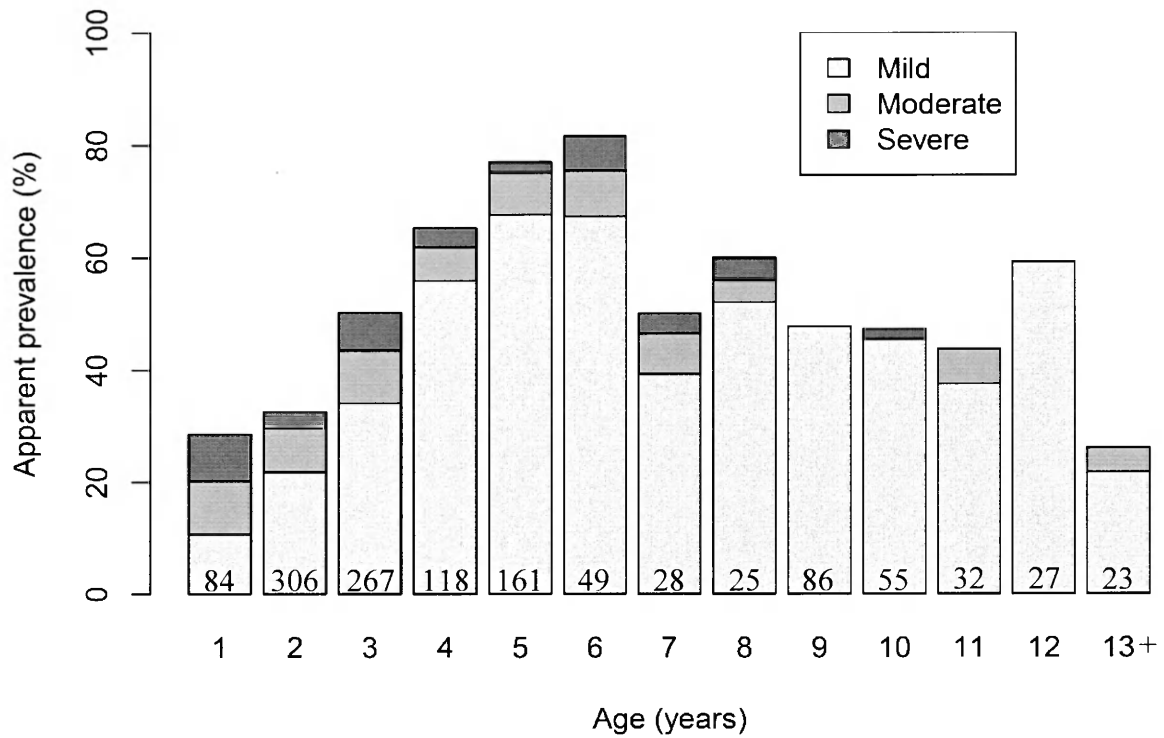


FIGURE 4. Apparent prevalence of mycobacteriosis in Chesapeake Bay Striped Bass, current and historic data combined (n=1261). Shading denotes percent of fish in each severity category. Numbers inside bars denote total sample size (disease-positive and -negative) at each age.

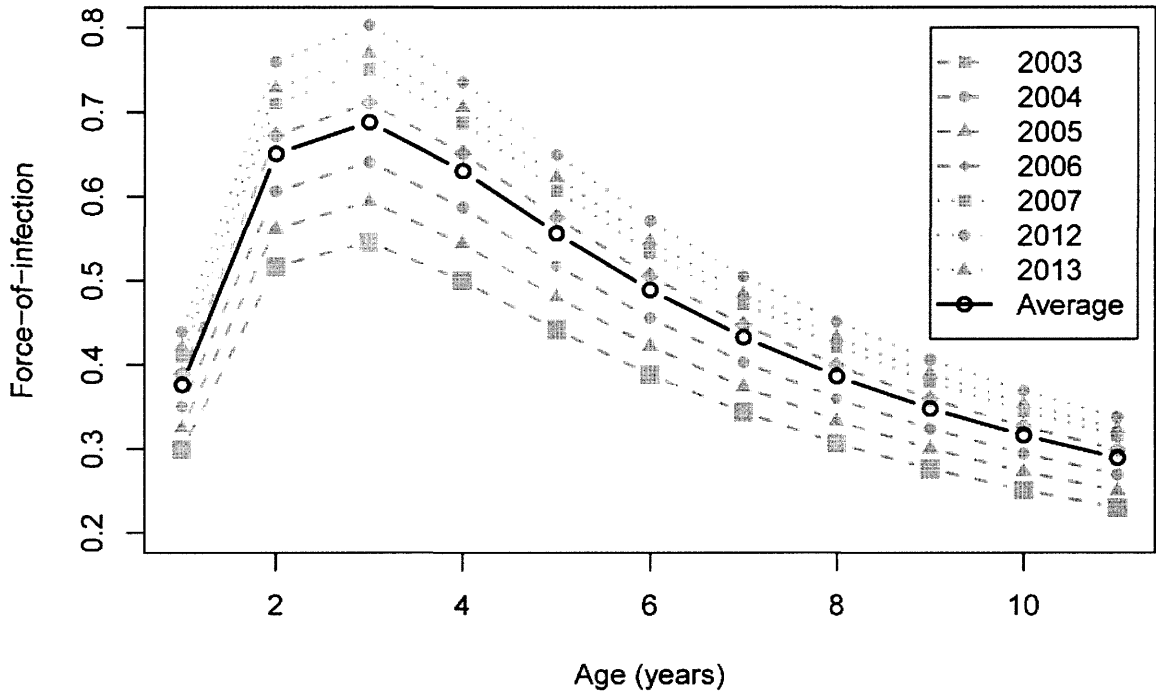


FIGURE 5. Force-of-infection of mycobacteriosis for ages 1-11+ Chesapeake Bay Striped Bass for 2003 to 2013 and the average over years.

VITA

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