ABSTRACT

Title of Dissertation:	THE IMPORTANCE OF FEMALE PHENOTYPE IN DETERMINING REPRODUCTIVE POTENTIAL AND RECRUITMENT IN ATLANTIC COAST STRIPED BASS (*MORONE SAXATILIS*)
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The influence of female phenotype on the reproductive potential of Atlantic coast striped bass is addressed in three key areas of research. The importance of the environment in shaping maternal phenotype was evaluated using a spawning stock time-series to evaluate possible environmental drivers of female migration timing in the Chesapeake Bay. Results showed that local and recent water temperature was the primary factor influencing timing of movement onto spawning grounds, with higher temperatures resulting in early movements. Next, two approaches were used to evaluate the influence of female energetic condition on reproductive potential. First, a field approach was used to test the hypothesis that relative total female condition (hereafter condition) has a positive influence on pre-fertilized indicators of reproductive potential (i.e., probability of spawning, relative fecundity, and relative oocyte volume). Results indicated that condition had a positive influence on residual fecundity, residual oocyte volume and indirectly on the probability of spawning. In

the second approach, a laboratory experiment was conducted to test the hypothesis that female condition has a positive effect on offspring size, growth and survival. The null hypothesis that the maternal influences on offspring phenotype did not differ in the Chesapeake Bay and Roanoke River populations also was tested. In contrast to the effects of female condition on pre-fertilized indicators of reproductive potential, condition had no influence on offspring phenotype in either population. Instead, post-spawn gutted weight alone had the greatest influence on offspring phenotype, although to a lesser and potentially insignificant degree in the Roanoke River.

Finally, a preliminary field evaluation was conducted in the Patuxent River, MD to determine whether maternal influences can lead to disproportionate numbers of mothers contributing to juvenile recruitment. Specifically, this study evaluated whether the variance in the distribution of half-sibling families was greater than expected by random reproductive success (i.e., Poisson process). If true, it was expected that the effective population size would be orders of magnitude smaller than the census size. Results provide preliminary evidence for higher than expected variance in reproductive success; however, methodological improvements will be necessary to confirm these results in the future.

THE IMPORTANCE OF FEMALE PHENOTYPE IN DETERMINING REPRODUCTIVE POTENTIAL AND RECRUITMENT IN ATLANTIC COAST STRIPED BASS (*MORONE SAXATILIS*)

by

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Advisory Committee:

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DEDICATION

This work is dedicated to several key individuals in my life. To Deborah for all of her love and support during this long and sometimes difficult road. To my mom and dad and brother and sister, for always believing in me and supporting all of my aspirations. To the memory of my faithful canine companion Sela, who kept me leveled headed throughout my graduate career. Finally, to the memories of my grandfathers Chester DiBari and Roy Peer, from whom I certainly inherited my curiosity for nature.

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CHAPTER 1

INTRODUCTION

Understanding the relationship between abundance and characteristics of spawners, and the number of new recruits they produce is central to ensuring the sustainability of fish populations. Traditional approaches to understanding patterns in stock and recruitment have principally focused on understanding recruitment variability in relation to a single factor, spawning stock biomass. Implicit in this approach is the assumption that the aggregate biomass of spawners is an effective index of spawning potential. However, because both the size and age structure of populations change in response to both natural sources of mortality and fishing, and because mass-specific fecundity is often lower for smaller individuals, a population's reproductive potential may not be directly proportional to spawning-stock biomass (Berkeley et al. 2004). Compounding this allometric impact on the number of eggs – the size, age and condition of mature females are known to directly influence survival of eggs and offspring (Trippel et al. 1997, Berkeley et al. 2004). If not accounted for in fisheries management, these effects could have negative consequences for the sustainability of fish populations.

With a goal of long-term sustainability, fisheries biologists estimate and attempt to maintain the ability of a population to replace itself through reproduction (Sissenwine and Shepherd 1987, Myers and Mertz 1998). To do this, quantitative models are used to provide management recommendations on suitable levels of exploitation, or harvest strategies. These recommendations are presented as biological reference points and are expressed as either rates of fishing mortality or a

level of spawner biomass. Often these reference points are based on models that rely on data relating recruitment to spawning stock biomass. However, female demographic structure (i.e., size, age, and condition) and its effects on reproductive potential usually are ignored. When this occurs, and instead spawning stock biomass is assumed proportional to reproductive potential, estimates of recruitment are often inaccurate and overly optimistic (Marshall and Frank 1999, Scott et al. 1999, Murawski et al. 2001), thereby risking the sustainability of fish populations. Thus, understanding the links between maternal characteristics, reproductive potential, and recruitment is critical to conserving and sustaining viable fish populations (Berkeley et al. 2004).

The idea that maternal characteristics (i.e., phenotype) might influence reproductive potential at the individual and population level is at least a century old. In fact, early studies showed that larger females are usually more fecund (Earll 1880) and faster growing iteroparous females may mature at younger ages (Alm 1959). Early studies also showed that older females might arrive on the spawning grounds earlier than younger females (Sund et al. 1938 cited in Chambers and Waiwood 1996) and these younger/smaller females may produce smaller eggs (Earll 1880). Since this early research, similar results have been observed in numerous species (Lambert 1987, Ware and Tanasichuk 1989, Schultz et al. 1991, Danylchuk and Fox 1994, Wright and Gibb 2005, Sogard et al. 2008). Thus, female size and age can influence reproductive potential directly, and can influence the spawning time of females. In fact, spawning time itself may directly affect reproductive potential by dictating which females escape a fishery before spawning (Quinn et al. 2007), and which

females spawn at a time that is optimal for offspring survival (Brannon 1987, Webb and McLay 1996).

Although a large majority of studies on reproductive potential focus on the importance of age and/or size, a growing body of evidence indicates that female energetic condition can influence both fecundity and skipped spawning behavior (i.e., non-annual spawning of mature fish) (Marteinsdottir and Begg 2002, Morgan 2004, Rideout and Rose 2006, Rideout et al. 2006, Kennedy et al. 2010). Fish condition represents the general well-being or fitness of individuals and is often assessed by the amount of energy or nutrient reserves (i.e. protein and lipid) within individual fish (Marshall et al. 2004). High body condition (i.e., high energy or nutrient reserves) is thought to be a direct consequence of an animal's success in acquiring resources (Baker 1989), which can then be used to increase fitness (Jakob et al. 1996).

In mature females, vitellogenesis will proceed and females will spawn when the various storage tissues are replete with energy. However, when sufficient energy reserves are not available, fish may respond in several ways. First, resource allocation to ovaries could be maintained at the expense of somatic energy reserves (Lambert and Dutil 2000). Alternatively, allocation to ovaries could be reduced in order to limit somatic energy losses. In fact, several species have been shown to recruit more ovarian follicles than are taken to full oocyte development (e.g., Atlantic herring [*Clupea harengus*] [Kurita et al. 2003], turbot [*Scophthalmus maximus*] [Bromley et al. 2000], Atlantic cod [*Gadus morhua*] [Kjesbu et al. 1991, Armstrong et al. 2001], sole [*Solea solea*] [Armstrong et al. 2001). In such cases, fecundity is down-regulated by atresia in relation to available energy reserves (Kurita et al. 2003).

In addition, as observed in numerous species some mature females may exhibit skipped spawning behavior and delay reproduction altogether when energy is limiting (reviewed by Rideout and Tomkiewicz 2011). Finally, some females also may be less likely to mature at a given size or age, compared to fish in better condition (e.g., Marteinsdottir and Begg 2002). Thus, reduced energetic condition can have important consequences for the reproductive potential of many species. Consequently, understanding the condition demographics of a stock could improve recruitment predictions (Marshall et al. 2000).

In addition to the effects of female phenotype on spawning phenology and gamete production, female phenotype can also influence reproductive potential via effects on offspring phenotype such as size, growth and survival. The idea that female phenotype might influence offspring phenotype is certainly not new (Earll 1880, Falconer 1965, Roach and Wulff 1987, Bernardo 1996). In teleosts, the effects of a female on her offspring's phenotype, which may be genetic or phenotypic (i.e., no separation of genetic and non-genetic effects), are evident across a wide range of marine and freshwater species. These effects are known as maternal influences and contrast with the less frequently examined maternal effects, which are the exclusive effects of a mother's phenotype (i.e., excluding offspring genotype) on her offspring's phenotype (Green 2008). Positive correlations between egg size and maternal age or length exist for a diverse array of marine and freshwater species (Hempel and Blaxter 1967, Chambers et al. 1989, Chambers and Waiwood 1996, Johnston 1997, Heyer et al. 2001). Additionally, maternal effects have been demonstrated on egg and larval viability, larval size and growth in freshwater (i.e., Heyer et al. 2001) and marine fish

species (i.e.,Marteinsdottir and Steinarsson 1998, Trippel 1998, Berkeley et al. 2004). Behaviorally, the timing of spawning may also influence progeny growth and survival by influencing subsequent hatch dates, which can determine the temporal coherence of larvae with optimal physical and feeding conditions (Secor and Houde 1995, Sirois and Dodson 2000, Lapolla and Buckley 2005). Maternal size and age have been the focus of most of these studies, but influences of maternal energetic condition on progeny size, growth, or survival may also exist (Kerrigan 1997, McCormick 2003, Gagliano and McCormick 2007).

To date, most research on maternal influences in fishes has been conducted at the laboratory or mesocosm scale. These laboratory studies may not have fully characterized environmental factors (but see Bengtson et al. 1987, Benoit and Pepin 1999, Einum and Fleming 2000). Moreover, the level of selective mortality is often much higher in the field than levels obtained in either laboratory or mesocosm studies (Miller 1997). Because small changes in early survival and growth can have significant and counterintuitive influences on the probability of successful recruitment (Houde 1987, Rice et al. 1987, 1993), it is important that the influence of maternal effects under more natural conditions be assessed. Thus, these laboratory and mesocosm studies may shed little light on the consequences of egg and larval size and growth at the different temperatures and salinities present in the field, and in the face of highly selective sources of mortality.

Here I explore the potential influence of female spawning phenology, size, age and energetic condition on reproductive potential of Atlantic coast striped bass, *Morone saxatilis*. Striped bass is an anadromous species whose native populations

spawn along the Atlantic and Gulf coasts in tidal-freshwater areas of estuaries where they release pelagic eggs during spring months. Striped bass also is a long-lived (> 30 years) iteroparous species that may begin spawning as early as age-4 (Setzler-Hamilton et al. 1980, Mihursky and Milsaps 1987). This life-history strategy has provided opportunity to study how female size and age influence reproductive potential through fecundity and maturity. This size diversity enabled Houde and colleagues (Zastrow et al. 1989, Monteleone and Houde 1990) to provide insight into how striped bass maternal size influences offspring phenotype. In the late 1980s, they showed that maternal characteristics in striped bass influence egg size and viability, as well as larval size and growth in the laboratory. Despite the existing knowledge on factors influencing striped bass reproductive potential, there are three key areas of research that still remain unexplored regarding the importance of female phenotype: (1) the importance of the environment in shaping maternal phenotype; (2) the influence of female energetic condition on reproductive potential at pre- and post-gametic stages of progeny and (3) the relevance of maternal influences in nature. Here, I summarize approaches I used to improve our understanding of female influences on reproductive potential in striped bass.

Environmental influences on female phenotype

In many species, the timing of spawning occurs in a size- or age-dependent fashion, with larger and older females generally spawning before smaller and younger females (Lambert 1987, Danylchuk and Fox 1994, Wright and Gibb 2005, Sogard et al. 2008). Given that spawning time will dictate when progeny emerge into their

environment, timing can have important implications for their survival and thus the reproductive potential of individuals and potentially the population that is realized. However, for anadromous species spawning time also corresponds to spawning migration timing. Consequently, when fishing occurs on fixed temporal schedules and during migration runs, the fishery may select disproportionately for either larger or smaller females and could also truncate the temporal range of spawning events (Quinn et al. 2007). Thus, with or without fishing, the reproductive potential of individuals and populations can be affected by the nature of spawning and migration timing.

The timing of life-cycle events (i.e., phenology) such as spawning may also be influenced by environmental factors. In most anadromous species, water temperature generally serves as the dominant cue for migration and spawning time (Smith et al. 1994, Quinn and Adams 1996, Robards and Quinn 2002, Erickson et al. 2002, Papoulias et al. 2011, Paragamian and Kruse 2001), although river flow may play a secondary modulating role in some species (Ali 1992). Large-scale climate patterns such as the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO), however, can influence the local environment experienced by plants and animals. Consequently, large-scale drivers of regional climate also have the capacity to effect populations through changes in the timing of reproduction (reviewed by Ottersen et al. 2001).

In Chapter 2, I present the results of an analysis to determine the potential influence of both local/regional environmental and large-scale climatic variables on the timing of the spawning migration in Chesapeake Bay striped bass. Due to the

overwhelming importance of water temperature as a cue for spawning time in other species and as a regulator of the reproductive cycle in striped bass (Clark et al. 2005), I specifically tested two key hypotheses: (1) water temperature during the spring spawning season will be the dominant factor explaining variation in migratory timing of striped bass onto their spawning grounds; and (2) females will migrate earlier during warmer years. Migration timing was estimated from the annual distribution of females caught in the Maryland Department of Natural Resources gill net survey conducted on the Upper Bay and Potomac River spawning grounds during spawning seasons from 1985-2010. Specifically, migration timing was quantified as the day when 25, 50 and 75% of the cumulative number of migrating females were collected. The influence of local environmental and large-scale climatic variables on migration timing was then determined using linear models. Additionally, environmentally driven shifts in migration timing were explored in the context of a temporally fixed "trophy" fishing season in Maryland waters of Chesapeake Bay and its possible effects on mortality prior to spawning and selectivity for larger females. I anticipate this work will be submitted as a manuscript to Global Change Biology with myself and Thomas J. Miller as co-authors.

The importance of energetic condition on striped bass reproductive potential

Although the reproductive biology of striped bass has been studied extensively in the laboratory (i.e., Specker et al. 1987, Berlinsky and Specker 1991, Mylonas et al. 1997, Clark et al. 2005), little is known about the reproductive ecology of wild populations beyond general spawning behavior, and fecundity and maturity

relationships. Furthermore, estimates of fecundity have been parameterized exclusively as functions of size and age (e.g., Jackson and Tiller 1952, Hollis 1967, Mihursky and Milsaps 1987), and often with substantial unexplained residual variance in the relationships. Whether female energetic condition is able to explain the large residual variance that remains in the relationship between female size and fecundity remains unexplored. In addition, Secor and Piccoli (2007) recently presented evidence for skipped spawning behavior in striped bass. However, to date there is unknown whether the energetic links to skipped spawning observed in other species (reviewed by Rideout and Tomkiewicz (2011)) also occurs in striped bass. Consequently, the potential importance of energetic condition to the production of pre-fertilized stages of offspring remains unexplored in striped bass.

In Chapter 3 I use relative female mass as a proxy for relative total energetic condition to test the hypothesis that relative total condition has a positive influence on reproductive potential. For this study I evaluated reproductive potential using three measures: (1) the probability of a mature female spawning, (2) relative fecundity and (3) relative oocyte volume. My approach to test this hypothesis was two-fold. First, I quantified the size, age, and condition demographics of female striped bass during two spawning seasons. Second, because relative total condition should represent the relative total energy of a female, I then tested whether relative total condition was positively related to reproductive potential and compared those results to tissue-specific measures of energetic condition. I anticipate this work will be submitted as a manuscript to Transactions of the American Fisheries Society with myself and Thomas J. Miller as co-authors.

In addition to the effects on pre-fertilized stages of offspring, the effects of female energetic condition on post-fertilized stages (i.e., fertilized eggs and larvae) also remain unexplored in striped bass. Specifically, what influence does female energetic condition have on offspring size, growth and survival? For striped bass, environmental factors are believed to be the primary determinants of growth and survival of early-life stages in the wild (Rutherford and Houde 1995, Secor and Houde 1995, Martino and Houde 2010). Selection appears to favor individuals maintained in low salinity waters up- estuary of the salt front (Secor et al. 1995) and within the estuarine turbidity maximum (ETM) (North and Houde 2001), where prey are abundant and turbidity may reduce predation on early life stages. However, maternal size does influence egg viability and larval growth in the laboratory (Zastrow et al. 1989, Monteleone and Houde 1990) and may contribute to recruitment variability (Cowan et al. 1993). Less understood is the importance of striped bass maternal energetic condition on offspring size, growth and survival. As shown in other species, however, the influence of energetic condition may not be limited to the number of gametes produced, but may also extend to egg quality and larval vital rates (Kerrigan 1997, McCormick 2003, Gagliano and McCormick 2007).

For striped bass, the effects of energetic condition beyond the unfertilized gamete have yet to be determined. In Chapter 4 I conducted a randomized complete block experiment (two female lines [Chesapeake Bay and Roanoke River, NC], nine females per line) to explore the role of maternal energetic condition on post-fertilized offspring. Specifically, I tested the hypothesis that pre-spawn relative total condition (i.e., as in Chapter 3, a measure of total weight relative to length) has a positive effect

on offspring size, growth and survival either alone or in combination with other female variables. Also like Chapter 3, I evaluated whether the relative total condition of a female had a greater influence on offspring than tissue-specific measures of relative condition – specifically liver and muscle indices. Because maternal influences have been shown to vary between populations of the same species (Marteinsdottir and Able 1988), I also tested the null hypothesis that the maternal influences on offspring phenotype were equal in two genetically distinct populations – specifically, the Chesapeake Bay and Roanoke River, North Carolina, populations. I anticipate this work will be submitted as a manuscript to the Journal of Experimental Marine Biology and Ecology with myself and Thomas J. Miller as co-authors.

Importance of maternal influences in nature

To date, most research on maternal effects in fishes has been conducted at the laboratory or mesocosm scale. Unfortunately, laboratory studies are not capable of fully characterizing the suite of environmental factors that affect the survival of offspring from fertilization to juvenile stages. Furthermore, mortality rates acting on these early-life stages are extremely high and selective (Cowan et al. 1993). Under such circumstances, it is likely that those larvae that survive are not a random sample of the original distribution of larval traits (Crowder and Rice 1992, Miller 1997). Rather, mortality is most likely selective. Still, in many cases it is unclear whether selective mortality emerges from density effects upon competitive interactions (Webster 2004), food and environmental effects on larval growth (Meekan et al.

2003), genotypes that influence physiological performance (Planes and Romans 2004), maternal effects such as egg size and provisioning (Jones and McCormick 2002), or a combination of such factors. Identifying selective sources, however, can help to understand recruitment variability and predict future recruitment. Furthermore, there is growing evidence demonstrating selection for maternal characteristics in wild populations of benthic spawning salmonids (Seamons et al. 2004, 2007, Williamson et al. 2010).

To provide a first test of whether maternal influences affect the distribution of juvenile survivors in a natural population of a pelagic spawning teleost, I conducted a case study on striped bass in the Patuxent River. The Patuxent River is an ideal natural system for exploring the role of maternal influences for two primary reasons. First, it is a relatively small system, which makes representative sampling of the striped bass population feasible in terms of both the likely size of the spawning stock (i.e., 4,882 – 10,000; 4,882 based on a 3-fold increase in spawning stock abundance since 1991 [ASMFC 2011]; a probable minimal spawner abundance in 1991 estimated from egg production in Secor and Houde (1995); and an approximate two-fold greater abundance, 10,000, presuming that egg mortality and inefficient sampling minimized the Secor and Houde (1995) egg abundance estimate). Specifically, by selecting the egg and early juvenile stage as the focus of my study, striped bass juveniles are unlikely to have become so broadly distributed that they could have left the Patuxent River system. Thus, from the viewpoint of this project, the Patuxent River represents a closed system.

Due to the genetic (i.e., no maternal markers due to heteroplasmy) and biological (i.e., polygynous male behavior), a specific test of maternal selection in wild striped bass populations is not currently possible using the microsatellites currently available. However, it is still possible to provide a first test for evidence that maternal influences might affect the distribution of survivors. Specifically, I tested the hypothesis first suggested by Myers and Mertz 1998Chapman 1990) that a disproportionate number of offspring are produced by a few females. Because I was limited to using nuclear markers, I specifically tested the hypothesis that the variance in the distribution of half-sibling families is greater than expected by random reproductive success (i.e., a Poisson process). One female and many males, or one male and many females may produce half-sibling families, thus a specific test of maternal influences is not my goal. However, evidence of greater than expected variance in reproductive success could provide preliminary evidence for the possibility of maternal influences in striped bass. I tested this hypothesis by evaluating whether the distribution of half-sibling group sizes in juveniles collected during two years deviates from the null expected Poisson distribution. If true, I further hypothesized that effective population size (N_e) would be orders of magnitude smaller than the estimated census population size of breeding males and females, since increased variance in reproductive success causes reductions in N_e. In the process of testing these hypotheses, I also evaluated the utility of the sampling design and genetic markers used to test my hypotheses. I anticipate this work will provide a foundation for the development of an NSF proposal with myself, Thomas J. Miller and Allen R. Place as principal investigators.

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CHAPTER 2:

LOCAL WATER TEMPERATURE AS A DRIVER OF CHANGES IN THE MIGRATION PHENOLOGY OF CHESAPEAKE STRIPED BASS: IMPLICATIONS FOR SUSTAINABLE MANAGEMENT

Abstract

Reproductive phenologies of a many species are strongly influenced by temperature. As global temperatures have risen, accumulating evidence indicates that reproductive behaviors, including migrations, are occurring earlier across a range of taxa. Alone, these changes bear important ecological importance – particularly regarding possible changes in reproductive success. However, in species such as striped bass (*Morone saxatilis*) that are harvested during the spawning season under a fixed schedule, changes in migration timing can also lead to unexpected changes in fishing mortality. Striped bass is an anadromous species that spawns in spring in tributaries along the eastern US, including Chesapeake Bay. In this region there is strong evidence for climate change, as well as changes in large-scale climatic factors that can influence temperature trends and other local environmental variables. Here, I used a time-series of gill-net catch data to test the hypothesis that water temperature, rather than other local or large-scale climatic factors, was the dominant factor explaining variation in migratory timing of Chesapeake Bay striped bass onto their primary spawning grounds. I further hypothesized that females migrate earlier during warmer years. Results indicated that local and recent water temperature was the primary factor influencing the timing of movement onto spawning grounds, with higher temperatures resulting in early migratory movements. Temperature also exhibited consistent effects on all female size classes, although over the entire time-series, there

was a clear tendency for larger females to annually move onto the spawning grounds earlier. My results also indicated that in cool years when females moved onto the spawning grounds later, more females were caught in the fishery before they could spawn. Although this situation provides some impetus for adjusting the fishery according to temperature, there are also some possible evolutionary consequences that may occur if the fishery continues under the current regulations. Together, my results indicate that climate warming could have important implications for fishing mortality, reproductive potential and recruitment.

Introduction

The timing of life-cycle events in plants and animals (i.e., phenology) is critical to the successful closure of life cycles. Recently, changes in the phenologies of a range of taxa have been reported in response to climate change (Parmesan 2006). Common shifts include earlier flowering, budding, egg-laying, and migrations, with most tied closely to corresponding increases in temperature (Menzel and Fabian 1999, Totland and Alatalo 2002, Cotton 2003, Visser and Both 2005). A large majority of these shifts among all taxa involve changes in the timing of reproduction – and with good reason. Timing of reproduction is a life-history trait with substantial importance for offspring survival, and therefore fitness (Clutton-Brock 1988, Varpe et al. 2007). Furthermore, there is only a limited time period during the year when conditions are favorable for successful reproduction (Visser et al. 2004). To match reproduction with these favorable conditions, reproductive events are frequently triggered by environmental cues perceived by mature individuals. Consequently, when environmental conditions exhibit temporal shifts in response to climate change,

reproductive events often display corresponding shifts (Beebee 1995, Crick and Sparks 1999, Juanes et al. 2004).

Spawning migration is a common process in the reproductive phenologies of many fishes. Natural selection favors traits that increase the likelihood that migration will lead to successful reproduction (Bernatchez and Dodson 1987, Gross 1987, Dodson 1997). One trait believed to be under selection in anadromous fishes is the timing of adult migration and spawning (Leggett and Whitney 1972, Beacham and Murray 1987, Brannon 1987, Gilhousen 1990). The timing of migration should coincide with suitable environmental conditions, and avoid predictable periods of especially stressful, energetically demanding, or dangerous conditions (Hodgson and Quinn 2002). However, for anadromous species, the timing of migration and spawning primarily reflect the needs of the offspring, so migration takes place at a time when a large fraction of the progeny will survive and emerge to benefit from favorable feeding conditions in spring (Brannon 1987, Webb and McLay 1996). Quinn and Adams (1996) hypothesized and demonstrated that for species with large spatial and/or temporal separation between the environmental conditions experienced by migrating adults and their offspring, females should return at the long-term average optimal date, with little inter-annual variation in response to environmental changes. However, in species with little spatial and/or temporal separation between the environments experienced by returning adults and their progeny, adults should respond to inter-annual environmental variability and behaviorally adjust the timing of migration and spawning to optimize conditions for their young.

Striped bass (*Morone saxatilis*) is an anadromous species found along the

Atlantic coast of North America from Florida (U.S.) to Nova Scotia (Canada). Migratory adults generally occur in the coastal ocean from summer through winter and enter estuaries along the Atlantic coast in spring to spawn. Males and females stage down-estuary of spawning grounds for a brief period before undertaking spawning movements (i.e., runs) onto the spawning grounds in and above the salt front (salinity 1 isohaline). Striped bass are total, capital spawners, releasing all of their eggs in a short period of time. Once fertilized, eggs hatch within 29 to 80 hours (Hardy 1978). According to the Quinn and Adams (1996) conceptual model, given the short delay between adult migration and larval production, female striped bass should adjust the timing of their final run and spawning in response to environmental variability to optimize the environments experienced by their young.

Although physical accounts of striped bass spawning behavior in relation to environmental variables are limited, several studies have shown that egg abundance generally increases as temperature rises (Grant and Olney 1991, Rutherford and Houde 1995, Secor and Houde 1995, Jahn 2010). Spawning generally corresponds to temperatures favorable for early-life stages (Morgan and Rasin 1973, Secor and Houde 1995), beginning when temperatures reach 12 to 14°C during the spring and continuing until temperatures reach 23°C (Setzler-Hamilton et al. 1980). Often spawning peaks after temperature increases of 2-3°C over a several day period (Rutherford and Houde 1995). Although these temperature increases often occur after peaks in freshwater flow, it appears that temperature increases rather than changes in flow are more associated with spawning events (Jahn 2010). Furthermore, it has been shown experimentally that temperature plays a dominant role in the

initiation, maintenance and termination of the female striped bass reproductive cycle when compared to photoperiod (Clark et al. 2005). Consequently, temperature appears to act as a dominant cue for striped bass spawning behavior.

Long-term environmental records show considerable evidence of climate change during the 20th Century along the North American Atlantic coast. Long-term analyses of the heat content and sea surface temperature (SST) time series in the North Atlantic show statistically consistent warming over the last 30-50 years (Levitus 2000, Barnett et al. 2001). Surface and subsurface water temperature in Chesapeake Bay also increased approximately 0.16°C and 0.21°C, per decade, respectively, from 1949 to 2002 (Preston 2004), with slightly higher rates during the 1980s and 1990s. Broad scale climate indices such as the North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO) also indicate environmental changes over this period. The NAO is a large-scale atmospheric climatic index representing the strength of the pressure gradient between the Icelandic low and Azores high pressure. Positive phases, such as those that occurred during the 1980s and 1990s, are associated with warmer and wetter conditions over the North Atlantic (Hurrell 1995), but NAO can also influence wind speed and direction (Alheit and Hagen 1997, Drinkwater et al. 2003). Furthermore, NAO is correlated to the low-frequency decadal scale patterns of water temperature in the Chesapeake Bay (Austin 2002). The AMO represents a large-scale oceanic climate index, thought to be driven by thermohaline ocean circulation, that has a period of 65-80 years (Sutton and Hodson 2005). Like the NAO, the AMO can influence regional temperatures and precipitation; however its effects are strongest in the summer (Enfield et al. 2001,

Sutton and Hodson 2005). Due to their influence on local environmental variables, both indices can change the characteristics of the physical (and indirectly biological) environment experienced by plants and animals. Consequently, these large-scale drivers of regional climate can alter entire populations through changes in the timing of reproduction, abundance and spatial distribution (reviewed by Ottersen et al. 2001, Hatun et al. 2005, Nye et al. 2009).

There is strong evidence for climate change in the eastern US and Chesapeake Bay, as well as changes in large-scale climatic factors that also can influence temperature trends and other local environmental variables. These large-scale climatic and/ or local environmental factors may in turn influence the timing of the striped bass spawning migration. Striped bass spawning migration involves two phases, which together likely influence timing onto the spawning grounds: 1) late-winter/early-spring movement from offshore wintering grounds off the North Carolina coast to staging grounds located in brackish water, and 2) springtime (April-May) movement from staging grounds to tidal freshwater spawning grounds (i.e., spawning runs). Here, I test the hypothesis that changes in water temperature during the spring spawning season are the dominant factor explaining variation in migratory timing of striped bass onto their spawning grounds. I also hypothesize that females migrate earlier during warmer years. Because anecdotal evidence suggests that spawning time may be size- or age-dependent, the water temperature hypothesis was tested while controlling for female size effects. This further enabled a test of whether size-dependent migrations were occurring during the spawning season. Finally, the potential population effects of the striped bass "trophy" fishing season were explored

in the context of migration timing. The "trophy" season opens during the spawning season to target large migratory females as they move to and from their spawning grounds. Currently the season opens on a fixed schedule; however, if female striped bass migration timing varies with inter-annual fluctuations in temperature or other environmental variables as hypothesized, then later peak migrations during cooler than average years could lead to higher fishing mortality for mature, egg-bearing females.

Methods

Striped bass spawning phenology datasets

Female striped bass were collected in a spawning survey on the Potomac River (PR) and Upper Bay (UB) spawning grounds. Maryland Department of Natural Resources (MD-DNR) conducted the survey from 1985-2010 using multi-panel experimental drift gill nets. Due to logistical constraints, gill nets were not set in the PR in 1994. Gill nets were fished 4-6 days per week from late March or early April until striped bass catches dropped to 0 over several days, usually in late May. Gill nets were first set when weekly temperatures were at or below 12°C (striped bass usually begin spawning at temperatures between 12-14°C [Setzler-Hamilton et al. 1980]). Individual mesh panels were 45.7 m long and ranged from 2.44 to 3.5 m deep depending on mesh size. The panels were constructed of multifilament nylon webbing in 7.6, 9.5, 11.4, 13.3, 15.2, 16.5, 17.8, 20.3, 22.9, and 25.4 cm stretch-mesh. In the UB, all 10 panels were tied together, end to end, to comprise a single gang of nets. In the PR, due to the design of the fishing boat, the 10 panels were fished as two

gangs of 5 panels. In both systems, all 10 meshes were fished twice daily unless the weather prohibited a second set. Whether the gill nets were fished in suites of 10 or 5 panels, the order of meshes within the suite was randomized with gaps of 0.91 to 3.04 m between each mesh. Overall soak times for each mesh panel ranged from 15 to 65 min. Sampling locations were assigned using a stratified random survey design. The PR and UB spawning areas were each considered a stratum. One randomly chosen site per day was fished in each spawning area. Sites were chosen from a grid superimposed on a map of each system. The PR grid consisted of 40, 0.8-square km quadrants, and the UB grid consisted of 31, 1.6-square km 32 quadrants. Upon arrival at each site, nets were deployed and soaked for the desired time. All striped bass captured were then removed and measured for total length (mm), sexed by expression of gonadal products, and released.

Local environmental and large-scale climatic data

Data for several local and regional environmental variables were retrieved from multiple sources that maintained consistent data over the entire time-series (1985-2010) of the gill net survey. Temperature data from three sources were used in the analyses. One source was local surface water temperature recorded on the spawning grounds during each day of the gill net survey. Regional surface water temperature data also was obtained from the NOAA Marine Environmental Buoy Database. The specific buoys included were the Thomas Point buoy (station id: TPLM2) located in the Chesapeake Bay and an offshore buoy located southeast of Cape May, New Jersey (station id: 44009). Each of these sites contained the most complete dataset of

water temperature in the Chesapeake Bay (i.e., TPLM2) and for locations offshore closest to wintering grounds (i.e., 44009).

Daily mean freshwater discharge data were obtained from the United States Geological Survey (USGS). Since the source of most freshwater in the UB is the Susquehanna River (Schubel and Pritchard 1986), daily mean discharge data (USGS 01578310) for the Susquehanna River at Conowingo, Maryland was used as a measure of freshwater input. In the PR, daily mean discharge data (USGS 01646500) at Little Falls pump station near Washington, DC was used.

Local daily weather data (i.e., air temperature, wind speed, wind direction) was obtained from the National Climatic Data Center. Data representing the UB and PR local atmosphere was obtained from the Baltimore-Washington International Airport, Maryland (WBANID: 93721) and from the Washington, D. C. National Airport, Washington, D. C., (WBANID: 13743) respectively. Wind directions from these data represent the direction from which wind was blowing, and was measured to the nearest degree based on a 360 degree compass, with 360 degrees being from the North and 180 degrees being from the South.

Data representing the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO) were included to evaluate the importance of large-scale climate patterns on migratory phenology. NAO is a large-scale atmospheric climatic index representing the strength of the pressure gradient between the Icelandic low and Azores high pressure. Daily NAO index data were obtained from the National Center for Atmospheric Research, Climate and Global Dynamic's Climate Analysis Section. A detailed description of the methodology used to calculate the

NAO daily index can be found at the NOAA National Weather Service Climate Prediction Center website (CPC 2005). AMO is a time-series of changes in the sea surface temperature of the North Atlantic Ocean. Monthly unsmoothed AMO time series data were obtained from NOAA's Earth System Research Laboratory (ESRL 2011).

For all environmental and climatic variables, the data were separated into seasonal time periods to determine which had the greatest influence on spawning phenology. The time periods evaluated included seasons prior to the spawning season (i.e., winter [January-March]), fall [October-December], summer [July-Sep]), the individual months just preceding and during the spawning season (i.e., March, April, May), and the spawning season (April-May). In addition the period from October-March was evaluated because these months encompass the period of vitellogenic activity in striped bass prior to the spawning season (Sullivan et al. 1997). Means for each environmental and climatic variable were obtained during each of these periods and used in subsequent analyses to determine which factors influenced spawning phenology. Because effects of the NAO are most pronounced during the winter, and because winter is usually defined by the mean NAO from December-March (Hurrell and Van Loon 1997), this NAO period also was included as a variable. Mean NAO and AMO also were determined during the entire year preceding and including the spawning season (i.e., June 1 of previous year – May 31 of spawning season). In addition, to further evaluate the importance of freshwater discharge, the days of maximum and minimum discharge were determined in the UB and PR for March, April and May, as well as the spawning season (April-May).

Analyses

Prior to using the gill net survey data, size-selectivity corrections were conducted to adjust catches for the differential selectivities of the various meshes used in the survey. Size-selectivity corrections were obtained for each mesh size using the SELECT model (Millar and Fryer 1999). Parameter estimates were obtained using Millar 2010) code from the Next Generation R functions for trawl and net selectivity. Attempts were made to fit the data to multiple types of models (i.e., normal scale shift, normal location shift, bimodal log normal, bimodal normal scale and bimodal normal location). However, it was determined that none of the models fit well if they included mesh sizes 7.6, 16.5, or 25.4 cm. Thus, these mesh sizes were eliminated from the analysis. Although these mesh sizes accounted for 30% of the collection gear, only 18 and 24% of all recorded striped bass were caught in the excluded mesh sizes in the PR and UB, respectively. Because the eliminated mesh sizes did not include female sizes not already observed in the remaining mesh sizes used, size bias was not believed to be an issue in the final analysis of spawning phenology. Without those mesh sizes, the best fitting model was determined to be the bimodal normal scale model. Selectivity corrected catches for each size-class were then standardized as the number of fish $\cdot$ 4,000 $m^{-2} \cdot hour^{-1}$. The selectivity corrected data were then separated into four size categories to account for size-specific spawning time behavior: females < 700 mm, females 700-799 mm, females 800-899 mm and females 900-999 mm. Although females larger than 999 mm were caught, their abundance was too low to be included in this analysis.

The spawning stock survey sought to sample every 6 days during the entire spawning season; however, this was not always achieved. Consequently, in some years more dates were sampled than in others. Thus dates selected for analyses were taken as a random sample of survey dates at each site. Random sampling was conducted without replacement of all potential sampling dates in a given year so that the total number of sampling dates equaled the minimum number of actual days of field sampling at each site (i.e., 28 days in the PR and 24 days in the UB). Due to changes in the size/age distribution of the stock during the time-series included in this study, some years included very few catches of some size classes of females. Consequently, when catches of a particular size class occurred on fewer than 6 days in a given year, that year of data was not included in the analysis for the pertinent size-classes. Years included in the analysis are shown in Table 1. Resampling was conducted on the final dataset 100 times for each year, site and size-class combination. For each resampling event, the day when 25 (d_{25}), 50 (d_{50}) and 75% (d_{75}) of the cumulative number of migrating females was collected was determined. These three quantiles served metrics for migration timing, and were used to determine whether the effects of environmental variables on migratory timing were consistent over the majority of the catch distribution. In addition to estimating the three quantiles, the interquartile range of catches (IQRC) also was estimated for each site, year and size-class combination to determine whether the range of spawning times was related to environmental variables.

To determine the potential influence of both local/regional environmental and large-scale climatic variables on d_{25}, d_{50}, d_{75} and IQRC, Pearson correlations were

determined for each catch index and environmental variable combination at each site separately. The correlations were then used to determine which environmental and climatic variables showed significant relationships with d_{25}, d_{50}, d_{75} and IQRC, and whether recent or past environmental or climatic conditions were more important.

To determine whether multiple environmental factors acted together to cue migration timing, the environmental and climatic variables that showed significant correlations with d_{25}, d_{50} and d_{75} were included in a principal component analysis (PCA) for each site separately. The PCA was primarily used to account for possible collinearity among environmental variables; however, it also allowed the variables to be reduced down to a set of linear combinations (principal components [PC]) that could then be used as independent variables in general linear models (GLM). Separate GLMs were then conducted using each PC as an independent variable. In each GLM, one PC was evaluated separately to determine its effect on d_{25}, d_{50} and d_{75}. Size class and size class × environmental variable also were included in each GLM to account for size effects. To determine which PC explained the most variance in d_{25}, d_{50} and d_{75}, the eta-squared coefficient (η^2: $SS_{\text{environmental effect}}/SS_{\text{total}}$) was calculated.

To determine whether a linear combination of environmental variables (i.e., PCs) or individual variables explained more variation in d_{25}, d_{50} and d_{75}, GLMs were also conducted using the individual variables included in the respective PCAs for each location. For these GLMs the models were identical to those described above with the exception that single PCs were replaced by single environmental variables. The proportion of variance in d_{25}, d_{50} and d_{75} explained by each environmental

variable was then estimated by η^2 to determine which environmental variable explained most of the variance in d_{25}, d_{50} and d_{75}. The η^2 were then compared among all environmental variables and PCs to determine if water temperature on the spawning grounds explained most of the variance in d_{25}, d_{50} and d_{75}. The GLM that included the environmental variable or PC that explained most of the variance in d_{25}, d_{50} and d_{75} (and thus removed most of the systematic variance from the error term) was used to determine if d_{25}, d_{50} and d_{75} differed among size class. When the effect of size was significant in the absence of an interaction, Tukey's honestly significant difference (HSD) test was conducted to determine which size classes exhibited differences in d_{25}, d_{50} and d_{75}. The same PCA and GLM analyses described above were also conducted using IQRC as an independent variable. All analyses were conducted in R (R Development Core Team 2011).

Finally, to determine if the environmental variables and PCs that influenced migration phenology could also affect the proportion of egg-bearing females caught during the "trophy" fishing season, Pearson correlations were used. Since 2002, Maryland Department of Natural Resource has conducted a creel survey to estimate the proportion of mature, egg-bearing females caught during the "trophy" striped bass fishing season. Here, Pearson correlations were used to determine the relationship between the proportion of mature, egg-bearing females caught and the environmental variables and PCs determined to be important to d_{25}, d_{50} and d_{75}.

Results

Temporal trends

In the UB and PR, indices of spawning phenology (i.e., d_{25}, d_{50} and d_{75}) generally showed negative trends for the female size classes with the longest time-series (Figure 2.1). The trends in the UB were based on the 800-899 mm female size-class and showed pronounced decreases of 5, 6, and 14 days in the estimates of d_{25}, d_{50} and $d_{75,}$ respectively, during the period from 1991-2010 (Figure 2.1). In contrast, the trends in the PR were based on the 900-999 mm female size-class and showed less pronounced decreases over a slightly shorter time-series (i.e., 1992-2009) (Figure 2.1). Nevertheless, even for PR females, estimates of d_{25}, and d_{50} declined by 12, and 4 days respectively. The d_{75} index did not decline in the PR

In the UB, water temperatures appear to have been relatively stable from 1985-1995, but since then have increased rapidly (Figure 2.2). In contrast, April-May air temperatures have demonstrated an increasing trend in the UB since the mid 1980s (Figure 2.2). Only May mean wind speed showed a consistent decreasing linear trend from 1985-2010 (Figure 2.2). Mean winter freshwater flow and April-May NAO both showed strong fluctuations and neither showed a consistent increasing or decreasing trend (Figure 2.2).

Unlike the UB, in the PR none of the environmental variables that showed significant correlations with d_{25}, d_{50} and d_{75} showed consistent trends over the entire time series. However, PR water temperature and April air temperature did show increasing trends since the late 1980s (Figure 2.3). The increasing water temperature trend in the PR, however, was less pronounced than that in the UB, particularly prior

to 2010 (Figure 2.3). April wind direction and March freshwater flow both showed increasing trends toward the early- to mid-1990s, followed by decreasing trends through 2010, while March NAO appeared to show a pattern opposite to water temperature (Figure 2.3).

Environmental and climatological correlations with d_{25}, d_{50} and d_{75} and IQRC

In the UB, the d_{25}, d_{50} and d_{75} were negatively correlated with mean air and water temperature during the spring (April-May), indicating that the migratory movements onto the spawning grounds occurred early during warmer springs (Table 2.2a). Although correlations were strong and significant for the larger size classes, few significant correlations existed for the smaller size classes, but these size classes also had fewer years of data available. However, even for the smaller size classes the correlations were negative, indicating consistency with larger size classes. Other local environmental variables that showed some correlation with day of catch were May wind speed and winter flow rates. In all cases, May wind speed and winter flow rates were positively related to day of catch, indicating that the day of catch occurred early during years when May wind speed and winter flow rates were lower (Table 2.2a). Among the large-scale climatic variables evaluated, only April-May NAO showed a significant correlation with day of catch, and only for the largest size class (Table 2.2a). Other than winter flow, no local environmental or large-scale climatic variables prior to spring exhibited significant correlations with the UB d_{25}, d_{50} and d_{75} indices.

Estimates of d_{25}, d_{50} and d_{75} in the PR exhibited the strongest overall correlations with mean air and water temperature, also indicative that movements onto the spawning grounds occurred earlier during warmer years (Table 2.2b). Other local environmental variables that showed some correlation with d_{25}, d_{50} and $d_{75,}$ were April wind direction, as well as March flow rates (Table 2.2b). April wind direction showed positive correlations where present and indicated that when April winds were blowing more from the northwest, d_{25}, d_{50} and d_{75} tended to occur later. Much like the UB, flow showed largely positive correlations with day of catch, indicating that the d_{25}, d_{50} and d_{75} generally occurred later when flow was higher (Table 2.2b). Large-scale climatic factors, particularly NAO, appeared to show slightly greater correlations with the day of catch in the PR than UB. March NAO showed relatively strong and positive correlations with d_{25}, d_{50} and d_{75} for the larger size classes (Table 2.2b). Much like the UB, local environmental factors during spring – specifically temperature, were the primary variables significantly correlated with d_{25}, d_{50} and d_{75}.

In contrast to observed relationships between environmental variables and the d_{25}, d_{50} and d_{75}, no local or large-scale climatic variables showed consistent and significant correlations with the IQRC in either the UB or PR (all $P > 0.05$).

Separate PCAs for each spawning ground accounted for collinearity and reduced the environmental variables shown in Table 2.2 and Figures 2.2 and 2.3 to the dominant linear combinations of variables to explain the trends in d_{25}, d_{50} and d_{75}. In the UB, the first principal component (PC) explained 41% of the variability in the data. This axis was mostly explained by mean winter flow and April-May mean NAO, with flow oriented negatively and NAO positively on the axis (Table 2.3a,

Figure 2.4a). The second PC, which explained 27% of the variability, was strongly, positively correlated with mean water temperature during the spawning season (Table 2.3a, Figure 2.4a). Finally, the third PC was strongly, positively correlated with May mean wind speed, and explained 20% of the variability in the data (Table 2.3a, Figure 2.4a).

In the PR PCA, the first PC explained 40% of the variability in the data. This axis was strongly, negatively correlated with mean water temperature and positively correlated with March mean NAO (Table 2.3b, Figure 2.4b). The second PC explained 26% of the variation in the data and was strongly, negatively correlated with April wind direction (Table 2.3b, Figure 2.4b). Finally, the third PC explained 24% of the variation in the data and was positively correlated with March mean flow (Table 2.3b, Figure 2.4b).

Environmental and climatological effects on d_{25}, d_{50} and d_{75}

For the UB, the first two dominant PCs were included in separate general linear models (GLM) to determine the effect of each PC on d_{25}, d_{50} and d_{75} and whether the d_{25}, d_{50} and d_{75} varied by size-class. GLM results indicated that only PC2 exhibited a significant effect on d_{25}, d_{50} and d_{75} and the effect was negative (Table 2.4, Figure 2.5). Because PC2 was dominated by UB mean water temperature, these results indicated that water temperature during the spring was important in determining the arrival of female striped bass on the UB spawning grounds and that higher water temperatures result in earlier presence of female striped bass on the spawning grounds. Furthermore, the significant effect of size-class indicated that the

mean d_{25}, d_{50} and d_{75} for each size-class was not always equal (Table 2.4). Further analysis using Tukey HSD revealed that in cases where significant contrasts between size-classes were present, larger females were arriving on the spawning grounds earlier than smaller females under similar environmental conditions and at each percentile day of catch examined (Table 2.6a). In addition, differences in mean arrival dates on the spawning grounds were as much as 8 days between the largest size-class and the two smallest size classes (Table 2.6a).

In the PR only PC1 exhibited a significant effect on d_{25}, d_{50} and d_{75} in the GLMs and the effect was positive (Table 2.5, Figure 2.6). These results indicated that the female striped bass arrived on the PR spawning grounds earlier when water temperature was warmer, as was the case for the UB. Yet, these results also indicated that females tended to arrive earlier when March NAO was lower. Much like the UB, size effects on d_{25} and d_{50} were evident; however, unlike the UB, there was no significant size effect on d_{75} (Table 2.5). Still, like the UB, where mean differences in d_{25} and d_{50} were evident between size-classes, the larger size-class did arrive significantly earlier, although the maximum difference in arrival time appeared to be slightly less in the PR (i.e., 5 days compared to 7 or 8 days) (Table 2.6b).

The GLMs that included the individual environmental variables as covariates indicated that the dominant variables in each PCA explained the most variation in d_{25}, d_{50} and d_{75}. The GLMs also indicated that water temperature was the most important single environmental variable and explained more variation in d_{25}, d_{50} and d_{75} than any other single variable (Table 2.3, 2.4). However, in both the PR and UB, the dominant linear combination of variables always explained more variation in d_{25}, d_{50}

and d_{75} than did water temperature, or any other single variable alone – although in both PCAs the dominant component included water temperature as a dominant variable (Table 2.3, 2.4).

Environmental influences on the proportion of egg-bearing females caught

Among the environmental variables showing significant influences on d_{25}, d_{50} and d_{75} in both the UB and PR, only water temperature on the spawning grounds exhibited a significant relationship with the proportion of egg-bearing females caught during the "trophy" fishing season (Figure 2.7). The relationship between water temperature and the proportion of egg-bearing females caught was negative, indicating that a larger proportion of egg-bearing females was caught in years when mean water temperatures were colder (Figure 2.7). All other variables and PCs showed non-significant correlations (all $p > 0.05$).

Discussion

This is the first study to evaluate the influence of both local environmental variables and large-scale climatic patterns on female striped bass spawning migration over a consistent time-series and in relation to female size. As hypothesized, my results show that local and recent water temperature was the primary factor influencing the timing of movement, with higher temperatures resulting in early movements onto the Chesapeake Bay spawning grounds. However, the results of the principal components analysis suggest that other variables such as freshwater flow, wind (speed and direction) and broad-scale climate may also influence migration

timing. Nevertheless, the dominance of temperature in these components confirms its primary role in determining spawning phenology in striped bass. Temperature also exhibited consistent effects on all female size classes, although considering the entire time-series, there was a clear tendency for larger females to move onto the spawning grounds earlier in the year.

The migration of striped bass in response to specific environmental signals suggests that like other anadromous species, they are adapted to respond to certain cues that promote successful reproduction. The reproductive cycle of most fishes is controlled by complex interactions of environmental factors, assuring that fish spawn at an optimal time for survival of their offspring (Munro et al. 1990). Quinn and Adams (1996) suggest that the extent to which fish are influenced by the inter-annual variability in environmental factors depends critically on the spatial and temporal separation between migration/spawning and emergence of offspring. For example, salmonids display large spatial and temporal separation between the environmental conditions experienced by migrating adults and their offspring. Due to this spatial and temporal separation, salmonids should return at the long-term average optimal date for reproductive success, which should be under genetic control (Quinn and Adams 1996). In fact, migration timing is heritable in Pacific salmonids and return dates appear to be dictated largely by innate genetic responses to photoperiod (Quinn and Adams 1996, Quinn et al. 2000, Dickerson et al. 2005). Conversely, in many clupeids, and also in striped bass and other anadromous species, which have very short egg incubation periods, there is small spatial and temporal separation between the environmental conditions experienced by migrating/spawning adults and their

offspring. In these species, migrating/spawning adults will experience very similar environmental conditions to their larval offspring. Thus, adults can respond to the environmental conditions they experience by behaviorally adjusting the timing of migration and spawning to optimize conditions for their young (Quinn and Adams 1996). Since the environmental conditions experienced by spawning and migrating adults are similar to the conditions experienced by offspring, environmental factors should be more important cues. In fact, many anadromous fishes are capable of adapting behaviorally to short-term environmental variation (Quinn and Adams 1996) that can be used as cues to reduce the effects of environmental variability on reproductive success (Leggett 1985).

My results indicate that striped bass were responding primarily to inter-annual variation in temperature, and there are multiple lines of evidence supporting my observation that temperature was the dominant cue. For example, at several spawning grounds along the Atlantic coast, peaks in striped bass egg abundance were observed when water temperatures were increasing (Chesapeake Bay tributaries, Maryland and Virginia, USA: Grant and Olney 1991, Olney et al. 1991, Rutherford and Houde 1995, Secor and Houde 1995, Jahn 2010; Miramichi River, New Brunswick, Canada: Robichaud-LeBlanc et al. 1996; Savannah River, Georgia, USA: Van den Avyle and Maynard 1994). Douglas et al. 2009) observed that increases in temperature cued the movement of striped bass onto the spawning grounds in the Miramichi River, Canada. In addition, Clark et al. (2005) showed experimentally that temperature played a prominent role in the initiation, maintenance and termination of the female striped bass reproductive cycle when compared to photoperiod. Although

Jahn (2010) observed that egg abundances were higher after pulses in freshwater flow that were twice the average flow each season, such pulses were uncommon and probably did not provide the consistent cue that temperature can provide for striped bass spawning. Furthermore, my results indicate that water temperature was more important for spawning movements than mean or peak flows during the spawning season.

Temperature appears to be a critical environmental cue for spawning and migration timing in anadromous species (i.e., Atlantic salmon [*Salmo salar*] Smith et al. 1994, American shad [*Alosa sapidissima*] Quinn and Adams 1996, sockeye salmon [*Onchorhynchus nerka*], steelhead [*O. mykiss*] Robards and Quinn 2002, green sturgeon [*Acipenser medirostris*] Erickson et al. 2002, shovelnose sturgeon [*Schaphirhynchus platorynchus*] Papoulias et al. 2011 white sturgeon (*Acipenser transmontanus*) [Paragamian and Kruse 2001], and lake sturgeon (*Acipenser fulvescens*) [Bruch and Binkowski 2002], striped bass [Clark et al. 2005]). Temperature may be particularly important, not only because it can act as an environmental cue, but also because it can serve as a rate-limiting factor for reproductive development, by modifying the levels of hormones controlling the rate of vitellogenesis (Kjesbu 1994, Bromage et al. 2001). Furthermore, the relative uniformity and reliability of important environmental conditions during the spawning season will determine the types of spawning cues that are important (Wingfield et al. 1992). In this regard, the effects of freshwater flow are probably less reliable and predictable compared to temperature, although flow may be important for salmonids

entering rivers from estuaries or migrating up small tributaries (Smith et al. 1994, Erkinaro et al. 1999).

Spawning at the right time of the year, with respect to environmental variation can be critical to offspring survival (Heath 1992, Pope and Shepherd 1994). For example, temperature has been shown to be positively related to length-specific and cumulative growth rates in striped bass larvae collected in Chesapeake Bay tributaries (Rutherford and Houde 1995, Secor and Houde 1995). Slower growth at low spring temperatures results in longer stages durations (Rutherford and Houde 1995), potentially exposing larvae to increased risk of predation.

Temperature can also have direct effect on striped bass larval mortality. Storm fronts that pass over the Chesapeake Bay can cause water temperatures to drop near or below 12°C, resulting in episodic mortalities of eggs and newly hatched larvae (Rutherford and Houde 1995). Although cohort-specific mortality rates of striped bass larvae can be highly variable above 12°C, they have been shown to be strongly temperature-dependent, with both early (< 14° C) and later (> 21° C) cohorts experiencing higher mortality (Secor and Houde 1995). These results indicate that both high and low temperatures during the spring can have lethal effects on larvae, either directly or by limiting growth. Thus, for eggs and larvae to survive, they must be spawned within an appropriate temperature range. In fact, striped bass generally begin and end spawning at 12°C and 23°C, respectively – promoting the probability that eggs and larvae will be in water temperatures suitable for survival. Temperature-cued migration and spawning runs likely have been selected to minimize the

probability that offspring will emerge into suboptimal temperatures for growth and survival.

Temperature may also be the cue that best ensures larvae are produced at time when sufficient prey resources are available for developing larvae (i.e., the match-mismatch hypothesis; Cushing 1982, Cushing 1990). In the Chesapeake Bay, *Eurytemora affinis* is a dominant copepod and preferred prey resource for larval striped bass (Setzler-Hamilton et al. 1982, Bradley 1991, Martino and Houde 2010). Multiple environmental factors are known to influence *E. affinis* production, including freshwater flow, temperature and salinity. Freshwater flow appears to be the dominant controller of inter-annual variability in *E. affinis* abundance, with higher than average spring flows correlated with high *E. affinis* abundances (Kimmel and Roman 2004). However, within year production of *E. affinis* is temperature-dependent and generally increases as temperatures rise during the spring (Hirche 1992, White and Roman 1992, Devreker et al. 2006, Lloyd 2006). Striped bass spawning also occurs as temperatures rise during the spring, increasing the likelihood that larvae emerge into an environment with sufficient prey resources to grow and survive. Excellent or poor year-classes may result, depending on the temporal overlap between larval and zooplankton production (Martino and Houde 2010); however, selection for temperature cued spawning likely minimizes the probability of failed year-classes.

Despite the strong influence that temperature had on striped bass movements onto the spawning grounds, flow and wind variables in both systems also showed a slight influence on the timing of migration in both systems. However, the specific

flow and wind variables influencing migration timing were not consistent between spawning grounds, and explained less variation than water temperature. This indicates that these variables probably are not dominant cues for migration timing. However, the fact that in both systems, freshwater flow exhibited a positive relationship with migration timing suggests that during high-flowing winters to early springs there is a delay in movement onto the spawning grounds. This relationship may be due to the effects of flow on movements of females from offshore feeding grounds to their staging locations just below the spawning grounds. However, residual current velocities are low (e.g., upper Bay mean = 8 cm s^{-1} during spring; North 2001) observed in the Chesapeake Bay. Such flows are probably insufficient to increase energetic demands to any extent and thereby reduce up-Bay swimming speeds of mature females that are usually > 70 cm in length.

Another possible explanation for the negative relationship between spawning runs and flow is that flow was simply confounded by its relationship with spring water temperature. However, winter flow and March flow showed no significant relationship with spring water temperature in the UB and PR, respectively. Wingate and Secor (2008) observed an equally poor correlation between winter flow and spring water temperature in the Patuxent River, Chesapeake Bay. Thus, a confounding of flow and water temperature does not explain the negative relationship between the timing of spawning runs and flow. Furthermore, a satisfactory explanation for the negative effect of winter and March flow does not currently exist.

Although wind speed and direction also exhibited a moderate influence on migration timing, the potential mechanisms driving these trends also are unclear. In

the UB, May wind speed showed a positive effect on d_{25}, d_{50} and d_{75}, indicating that migration timing was later at higher wind velocities. This could be due to increased water turbulence or changes in circulation caused by higher winds, which may be perceived as a negative cue reflecting poor spawning opportunities. In fact, North et al. (2004) indicate that wind events in upper regions of the Chesapeake Bay can change the circulation and salt front structure of the estuarine turbidity maximum (ETM, an important nursery area for larval striped bass, characterized by elevated turbidity and high zooplankton concentrations (North and Houde 2001, North and Houde 2003)) and potentially affect down-Bay transport of eggs. Furthermore, coupled biophysical model simulations conducted by North et al. (2005) showed that wind events resulted in a 13.2% reduction in the number of egg-like particles transporting to optimum ETM nursery grounds compared to steady-state conditions. Their model also indicated that wind events result in the loss of eggs down-estuary of the ETM, where poorer survival may occur (Secor et al. 1995). Together, these results indicate that higher wind speeds could have negative impacts on striped bass early-life survival. Thus, higher wind speeds and/or its effects on water circulation could serve as a negative cue, delaying spawning runs up-river.

In the PR, wind direction was more important than wind speed, with later movements onto the spawning grounds generally occurring when winds were more northerly. One possible explanation is that more northerly winds were associated with colder water temperatures; however, spring water temperature on the spawning grounds and air temperature were not correlated with April wind direction. Perhaps a more likely explanation is the positive association between north and northwest winds

and storm fronts (Jackson 1995). Water turbulence (and changes in circulation as described above), pulsed flows, rapidly declining temperatures or perhaps even the low pressure associated with storm fronts could serve as negative cues, suppressing movements of striped bass onto the spawning grounds. In fact, decreased striped bass spawning activity in the Chesapeake Bay has been observed during cold fronts and storms (Secor and Houde 1995). This is consistent with my hypothesis, and suggests that more northerly winds, storm fronts or other correlated factors may act as a negative cue for female striped bass.

Like wind speed and direction, the effect of NAO was not consistent between the two spawning grounds and only March NAO had a significant effect on d_{25}, d_{50} and d_{75} in the PR. The nature of the effect or cause for the influence of March NAO is not understood; however, it was negatively correlated with water temperatures on the PR during the spawning season. This outcome is opposite to the expectation based on the effects of winter NAO, which is usually positively associated with temperature in the North Atlantic and surrounding regions (Hurrell and Van Loon 1997). However, monthly relationships and/or spring NAO may not show the same influences on local climate as those observed for winter NAO – the period when NAO is most pronounced. NAO is primarily a winter phenomenon, and its connection to wind, temperature and precipitation is strongest during winter (Ottersen et al. 2001). Furthermore, even within regions where the link between NAO and local climate is strongest, as along the Norwegian west coast, ecological responses to NAO fluctuation may vary greatly at small spatial scales (Ottersen et al. 2001). Austin (2002) also showed that cross correlations between winter water temperatures

in the Chesapeake Bay and NAO did not show significant coherence unless lowess fits (0.25 and 0.5) were cross correlated. This indicated that the inter-annual variability between NAO and water temperature was not correlated, despite the existence of consistent low frequency (i.e., decadal) trends between NAO and water temperature (Austin 2002). Drinkwater (1996) showed particularly high variability in the water temperatures off Cape Hatteras during the positive NAO phase during the 1980s and 1990s, and Lozier et al. 2008) indicated that changes in ocean heat content between 35 and 45°N did not necessarily coincide with changes in NAO phase. Thus, while NAO may be an important driver of the low frequency decadal patterns observed over the Chesapeake Bay region, its high frequency, interannual signals are not linked to the high frequency signals of water temperature (Austin 2002), which are likely the primary cues influencing striped bass spawning behavior.

Although water temperature was the dominant environmental factor influencing the migration timing of female striped bass, female size also influenced their migration behavior. In both the UB and PR, the largest size-classes of females consistently moved onto the spawning grounds earlier than the smallest size-classes. This is the first time size-dependent migration behavior has been shown in striped bass using fishery independent data, although Peer (2012) did show a similar pattern using fishery dependent data, and others have anecdotally suggested this type of behavior in the past (Hollis 1967). Size- or age-dependent migration behavior, however, is not unique to striped bass. In several species, older or larger females spawn eggs or release larvae earlier (Lambert 1987, Ware and Tanasichuk 1989, Schultz et al. 1991, Danylchuk and Fox 1994, Wright and Gibb 2005, Sogard et al.

2008) – although in some cases later (Gillet et al. 1995, Morgan 2003) in the spawning season.

Although the cause for these size-dependent migrations and spawning is not thoroughly understood, one possible explanation is that larger and older females are in better energetic condition and are able to begin and complete the annual reproductive cycle earlier than smaller or younger females. In fact, in Atlantic herring (*Clupea harengus*), females that are fed higher rations and/or are in better condition begin ovary development earlier (González-Vasallo 2006, Kennedy et al. 2010). Peer (2012) also showed female striped bass in better energetic condition were caught earlier in the Chesapeake Bay and those females also tended to be larger and older. Thus, the energetic state of female striped bass and its links to size and age may explain the size-dependent migration and spawning behavior. Still, Sogard et al. 2008), who conducted research on *Sebastes* spp. suggest that size or age-dependent spawning (or parturition) may be an adaptive strategy of long-lived species, in which a maternal lineage spreads reproduction temporally across a spawning season. Although neither explanation for size/age dependent migration or spawning behavior can be confirmed at this point for striped bass, it is possible that both mechanisms are important.

Long-term trends (1949-2002) in the Chesapeake Bay indicate significant warming of surface and subsurface waters at a rate between 0.16-0.20°C per decade, and slightly higher rates during the 1980s and 1990s (Preston 2004). Although the effects of progressively earlier spawning on striped bass recruitment are currently unexplored, recruitment indices indicate that inter-annual variability in age-0

recruitment (relative abundance in summer [July-September]) in the Chesapeake Bay is more influenced by flow than temperature (North and Houde 2001, Martino and Houde 2010). This suggests that temperature effects on migration and spawning time likely do not carry through to influence age-0 recruitment. In fact, no relationship between striped bass migration time and age-0 recruitment has been observed (personal observation). However, progressively earlier spawning of females with increasing spring temperatures could have an impact on age-1 recruits, by increasing the growing season for age-0 striped bass. In many species, early hatch dates can lead to a protracted growing season during the first year of life, leading to larger size and condition by fall and enhanced overwinter survival (Ludsin and DeVries 1997, Hurst and Conover 1998). Thus, if warmer springs lead to earlier spawning and hatch dates in striped bass, recruitment could in fact improve with increasing temperatures in the Chesapeake Bay. This of course assumes that larval and juvenile prey production is suitable and there are negligible bioenergetic effects of warming on juveniles and adults – both of which are uncertain at best.

Exploitation often leads to changes in abundance, size and age composition of fish spawning stocks. In the Chesapeake Bay, a recreational fishing season on adult striped bass (i.e., "trophy" season) has taken place in the mainstem of the Bay during the spawning season since 1991. In 1991 the trophy season took place from May 11-27; however, since that time the season has progressively advanced toward earlier dates, and since 2001 the season has begun on the third Saturday in April. Creel surveys have indicated that a high proportion of spawning capable and gravid females were caught (29-63%) in the fishery from 2002-2010 (MDDNR 2010). My results

indicated that the annual proportion of egg-bearing females caught before they spawned was negatively correlated with mean water temperature in the UB and PR. When these correlations are considered with the effects of temperature on migration timing, my results indicate that in cool years when females moved onto the spawning grounds later, more females were caught in the fishery before they could spawn. This result provides some basis for adjusting the dates of the fishery according to temperature.

There are also some possible evolutionary consequences that may occur if the striped bass fishery continues under current regulations. When exploitation is selective and occurs over long periods of time there can be evolutionary effects leading to changes in age and size maturation (Law 2000). As my results indicate, larger females move onto the spawning grounds earlier than smaller females. As the "trophy" fishery currently exists (i.e., fixed opening date), larger and older females are more likely than smaller females to escape the fishery in any year, but the effects may be even greater in warmer years when smaller pre-spawn females may be targeted relatively heavily. Over long periods of time, the effects of climate change could lead to selection for increased size at maturation, and thus increased reproductive potential by individual females (e.g., as shown in *Menidia menidia*, Conover 2002). However, selection for larger females may also result in selection for later maturation (Kronert et al. 1989), which could reduce population reproductive potential. Selection for larger females could also reduce the size and age diversity of active female spawners, which may lead to poor year-classes in striped bass and other species (e.g., Lambert 1990, Secor 2000, O'Brien et al. 2003).

Due to the size dependent nature of female spawning time (i.e., larger females spawn earlier), selection for later maturation could also lead to a truncation in the size and age distribution of spawners and the temporal distribution of spawning. Such truncation could reduce the probability of producing successfully recruiting juvenile cohorts by shortening the hatch-date distribution and the probability of eggs and larvae encountering optimal conditions (Lambert 1990, Secor 2000). In fact, theoretical attempts to consider the consequences of a mismatch in timing between reproduction and prey production in a single year indicate that protracted spawning might help to reduce the effect of short-term mortality episodes on year-class strength (Cushing 1990, Mertz and Myers 1994). Thus, although traditionally there has been concern over the removal of older and larger adults from a population, removal of smaller females may also influence the spawning times and a population's temporal range of spawning, which could have adverse effects on recruitment.

In addition to changing maturation schedules, selective fishing practices may also influence migration timing (Quinn et al. 2007). Because the "trophy" fishery in the Chesapeake Bay opens after some females are already on the spawning grounds, the probability of being caught before spawning is higher later in the spawning season. Similar escapement fisheries occur in Bristol Bay, Alaska, where the probability of a sockeye salmon being caught can increase significantly during the course of the season (Quinn et al. 2007). Quinn et al. (2007) observed that from 1969-2003 the fishery for sockeye salmon became progressively more directionally selective for earlier spawners. Furthermore, Quinn et al. (2007) documented that observed median dates of upstream migration became earlier and were not related to

sea surface temperatures. However, they were not able to completely disentangle the underlying effects of selection versus environment. Still, Quinn et al. (2007) believe that temporal biased selection on migrating species may be common. Although the temporal changes in migration timing in striped bass appear to be largely a response to temperature changes, long-term selection by the fishery could eventually lead to evolutionary changes in the population if migration timing is heritable in striped bass.

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Table 2.1. Specific years of data that were included in the analysis for determining day of 25, 50, and 75% catch of female striped bass. The time-series available was from 1985-2010.

Size-class	Upper Bay
< 700 mm	1985-1992, 1995-1996
700-799 mm	1988-1992, 1995-1999, 2001
800-899 mm	1991-2007, 2009-2010
900-999 mm	1995-2002, 2004-2010
	Potomac River
< 700 mm	1985-1993, 1995-1997
700-799 mm	1989-1993, 1995-1997
800-899 mm	1992-1993, 1995-2007
900-999 mm	1992-1993, 1995-2009

Table 2.2. Pearson correlations of local environmental and large-scale climatic variables that showed significant relationships with day of 25, 50 and 75% catch for at least one striped bass female size class in the Upper Bay (a) and Potomac River (b). Significant ($p < 0.05$) relationships are shown in bold and nearly significant ($0.08 > p > 0.05$) relationships are italicized.

	Day of 25% catch				Day of 50% catch				Day of 75% catch			
Environmental factor	< 700 mm	700-799 mm	800-899 mm	900-999 mm	< 700 mm	700-799 mm	800-899 mm	900-999 mm	< 700 mm	700-799 mm	800-899 mm	900-999 mm
a.												
Upper Bay mean water temperature	-0.11	-0.27	**-0.68**	-0.33	-0.29	-0.34	**-0.74**	*-0.49*	-0.45	-0.06	**-0.72**	**-0.61**
April-May mean air temperature	0.06	-0.24	-0.47	**-0.61**	-0.04	-0.34	**-0.54**	**-0.75**	-0.25	0.03	**-0.54**	**-0.57**
May mean wind speed	0.31	0.39	**0.56**	0.28	0.39	-0.05	**0.49**	0.37	0.02	-0.18	0.34	0.1
Winter mean flow	0.21	0.42	0.29	**0.53**	-0.03	**0.74**	0.27	0.37	0.09	**0.61**	0.26	0.36
April-May mean NAO	0.01	0.03	-0.31	**-0.64**	0.06	-0.31	-0.24	**-0.58**	0.25	-0.32	-0.13	-0.05
b.												
Potomac mean water temperature	-0.42	*-0.69*	*-0.46*	**-0.58**	-0.45	*-0.7*	-0.41	**-0.68**	-0.42	-0.43	-0.28	**-0.61**
April mean air temperature	-0.44	*-0.55*	*-0.49*	**-0.72**	-0.48	-0.42	-0.33	**-0.77**	-0.45	-0.1	-0.11	**-0.63**
April mean wind direction	0.18	0.29	0.32	0.03	0.19	0.16	0.48	0.23	0.2	-0.03	**0.55**	0.36
March mean flow	0.33	**0.72**	0.31	0.45	0.18	0.6	0.21	0.41	0.03	0.35	0.05	0.29
March mean NAO	0.14	-0.12	**0.69**	**0.66**	0.17	0.01	**0.67**	**0.77**	0.2	0	**0.52**	**0.7**

Table 2.3. Standard deviations and factor loadings for the first 3 principal components of principal component analyses conducted on the local environmental and large-scale climatic variables shown to exhibit significant correlations (Table 2.2) with day of 25, 50 and 75% catch in the Upper Bay (a) and Potomac River (b).

a.

	Importance of components		
	Standard deviation	Proportion	Cumulative Proportion
PC1	1.27	0.41	0.41
PC2	1.04	0.27	0.68
PC3	0.89	0.20	0.87
	Factor loadings		
	PC1	PC2	PC3
Upper Bay mean water temperature	-0.37	0.69	0.50
May mean wind speed	0.48	-0.43	0.68
Winter mean flow	-0.55	-0.48	-0.24
April-May mean NAO	0.57	0.34	-0.48

b.

	Importance of components		
	Standard deviation	Proportion	Cumulative Proportion
PC1	1.26	0.40	0.40
PC2	1.03	0.27	0.66
PC3	0.98	0.24	0.90
	Factor loadings		
	PC1	PC2	PC3
Potomac River mean water temperature	-0.62	-0.40	0.29
April wind direction	0.29	-0.82	0.31
March mean flow	0.18	0.40	0.90
March mean NAO	0.71	-0.11	-0.11

Table 2.4. General linear model results showing the effects of individual local environmental variables from the Upper Bay region, large-scale climatic variables, and principal components on day of 25, 50 and 75% catch of female striped bass collected on the Upper Bay spawning grounds. Principal components (PC) were derived from the principal components analysis that included the individual variables shown below (see Table 2.3). Eta-squared coefficients (η^2) are shown for PCs or environmental variables that explained a significant proportion of the variance in respective components of the catch distribution.

	Day of 25% catch			Day of 50% catch			Day of 75% catch		
	F	P	^{2}	F	P	^{2}	F	P	^{2}
PC1	$0.15_{1,46}$	0.7		$0.07_{1,46}$	0.79		$0.09_{1,46}$	0.77	
Size	$6.04_{3,46}$	0.0015		$8.18_{3,46}$	0.0002		$7.02_{3,46}$	0.0006	
PC1 × Size	$0.71_{3,46}$	0.55		$0.85_{3,46}$	0.48		$1.44_{3,46}$	0.24	
PC2	$42.30_{1,46}$	< 0.0001	0.38	$46.08_{1,46}$	< 0.0001	0.36	$24.17_{1,46}$	< 0.0001	0.26
Size	$6.90_{3,46}$	< 0.0001		$9.70_{3,46}$	< 0.0001		$6.73_{3,46}$	< 0.0001	
PC2 × Size	$1.81_{3,46}$	0.16		$1.94_{3,46}$	0.14		$1.37_{3,46}$	0.26	
Water temperature	$14.64_{1,46}$	0.0004	0.18	$21.40_{1,46}$	< 0.0001	0.22	$21.86_{1,46}$	< 0.0001	0.24
Size	$5.19_{3,46}$	0.003		$7.81_{3,46}$	0.0002		$6.16_{3,46}$	0.001	
Water temperature × Size	$1.78_{3,46}$	0.16		$2.46_{3,46}$	0.07		$1.92_{3,46}$	0.14	
May mean wind speed	$8.69_{1,46}$	0.005	0.14	$5.52_{1,46}$	0.02	0.08	$0.29_{1,46}$	0.59	
Size	$2.77_{3,46}$	0.052		$4.81_{3,46}$	0.005		$5.37_{3,46}$	0.003	
May mean wind speed × Size	$0.75_{3,46}$	0.53		$1.42_{3,46}$	0.25		$1.39_{3,46}$	0.26	
Winter mean flow	$7.29_{1,46}$	0.009	0.09	$6.35_{1,46}$	0.015	0.07	$6.97_{1,46}$	0.01	0.08
Size	$9.02_{3,46}$	< 0.0001		$11.86_{3,46}$	< 0.0001		$9.86_{3,46}$	< 0.0001	
Winter mean flow × Size	$0.14_{3,46}$	0.94		$0.69_{3,46}$	0.57		$0.66_{3,46}$	0.58	
April-May mean NAO	$3.72_{1,46}$	0.06		$3.65_{1,46}$	0.06		$0.56_{1,46}$	0.46	
Size	$8.49_{3,46}$	0.00015		$10.82_{3,46}$	< 0.0001		$7.57_{3,46}$	0.0003	
April-May mean NAO × Size	$1.37_{3,46}$	0.26		$0.78_{3,46}$	0.51		$0.50_{3,46}$	0.68	

Table 2.5. General linear model results showing the effects of individual local environmental variables from the Potomac River region, large-scale climatic variables, and principal components on day of 25, 50 and 75% catch of female striped bass collected on the Potomac River spawning grounds. Principal components were derived from the principal components analysis that included the individual variables shown below (see Table 2.3). Eta-squared coefficients (η^2) are shown for PCs or environmental variables that explained a significant proportion of the variance in respective components of the catch distribution.

	Day of 25% catch			Day of 50% catch			Day of 75% catch		
	F	P	^{2}	F	P	^{2}	F	P	^{2}
PC1	$21.36_{1,44}$	< 0.0001	0.28	$24.14_{1,44}$	< 0.0001	0.3	$14.65_{1,44}$	0.0004	0.22
Size	$3.62_{3,44}$	0.02		$3.54_{3,44}$	0.022		$2.25_{3,44}$	0.095	
PC1 × Size	$0.48_{3,44}$	0.7		$0.28_{3,44}$	0.84		$0.17_{3,44}$	0.92	
PC2	$0.60_{1,44}$	0.44		$0.0008_{1,44}$	0.98		$0.50_{1,44}$	0.48	
Size	$3.42_{3,44}$	0.025		$3.33_{3,44}$	0.03		$2.60_{3,44}$	0.06	
PC2 × Size	$0.15_{3,44}$	0.93		$0.35_{3,44}$	0.79		$0.57_{3,44}$	0.64	
Water temperature	$13.82_{1,44}$	0.0005	0.26	$14.51_{1,44}$	0.0004	0.21	$8.74_{1,44}$	0.005	0.15
Size	$3.26_{3,44}$	0.03		$3.12_{3,44}$	0.04		$2.09_{3,44}$	0.11	
Water temperature × Size	$0.06_{3,44}$	0.98		$0.07_{3,44}$	0.98		$0.11_{3,44}$	0.95	
April mean wind direction	$1.73_{1,44}$	0.19		$3.91_{1,44}$	0.054		$5.22_{1,44}$	0.027	0.08
Size	$3.82_{3,44}$	0.02		$3.94_{3,44}$	0.014		$3.14_{3,44}$	0.03	
April mean wind direction × Size	$0.38_{3,44}$	0.77		$0.67_{3,44}$	0.57		$0.99_{3,44}$	0.41	
March mean flow	$8.55_{1,44}$	0.005	0.13	$4.09_{1,44}$	0.049	0.07	$0.90_{1,44}$	0.35	
Size	$4.21_{3,44}$	0.01		$3.64_{3,44}$	0.019		$2.49_{3,44}$	0.07	
March mean flow × Size	$0.02_{3,44}$	0.99		$0.04_{3,44}$	0.98		$0.13_{3,44}$	0.94	
March mean NAO	$12.70_{1,44}$	0.0008	0.18	$14.96_{1,44}$	0.0003	0.2	$9.64_{1,44}$	0.003	0.16
Size	$3.46_{3,44}$	0.024		$3.31_{3,44}$	0.03		$2.14_{3,44}$	0.11	
March mean NAO × Size	$1.52_{3,44}$	0.22		$1.08_{3,44}$	0.37		$0.53_{3,44}$	0.66	

Table 2.6. Tukey honestly significant difference test for multiple comparisons of mean differences in the day of 25, 50 and 75% catch among different female size classes of striped bass collected in the Upper Bay (a) and Potomac River (b). Comparisons are post-hoc results derived from the general linear models shown in Tables 2.4 and 2.5, which included PC2 and PC1 as covariates in the Upper Bay and Potomac River GLMs, respectively.

	Day of catch					
	25%		50%		75%	
Size-class contrasts	Mean difference	*P*	Mean differenc	*P*	Mean difference	*P*
a.			Upper Bay - PC2			
< 700 mm vs 700-799 mm	1.19	0.96	2.56	0.62	1.83	0.92
< 700 mm vs 800-899 mm	-3.83	0.34	-4.66	0.08	-10.05	0.002
< 700 mm vs 900-999 mm	-7.33	0.016	-6.15	0.016	-9.41	0.0056
700-799 mm vs 800-899 mm	-5.02	0.08	-7.22	0.002	-11.88	< 0.0001
700-799 mm vs 900-999 mm	-8.52	0.001	-8.71	0.0002	-11.24	0.00019
800-899 mm vs 900-999 mm	-3.49	0.26	-1.48	0.81	0.64	0.99
b.			Potomac - PC1			
< 700 mm vs 700-799 mm	-2	0.81	-2.31	0.7		
< 700 mm vs 800-899 mm	-0.93	0.96	-0.84	0.97		
< 700 mm vs 900-999 mm	-5.41	0.026	-5.11	0.03		
700-799 mm vs 800-899 mm	1.08	0.96	1.47	0.89		
700-799 mm vs 900-999 mm	-3.41	0.38	-2.8	0.51		
800-899 mm vs 900-999 mm	-4.49	0.061	-4.26	0.062		

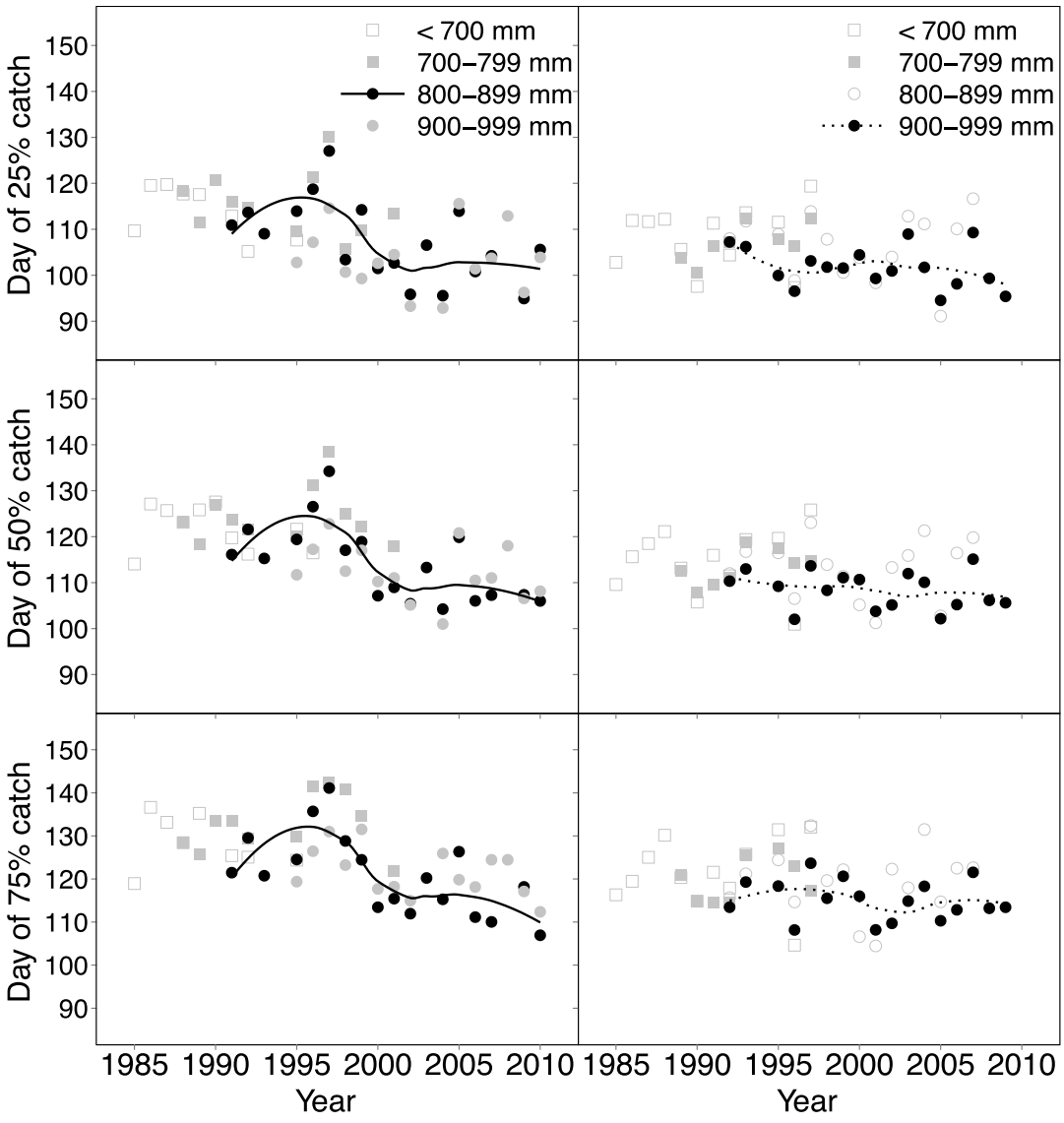

Figure 2.1. Day of 25, 50 and 75% catch for four size-classes of female striped bass collected from 1985-2010 in the Upper Bay (left panels) and Potomac River (right panels). Data from the size class with the longest time-series (solid circles) for each system were fitted with a loess smoother (span = 0.75) to show dominant trends for the entire time series. All dates providing acceptable data are shown in Table 2.1.

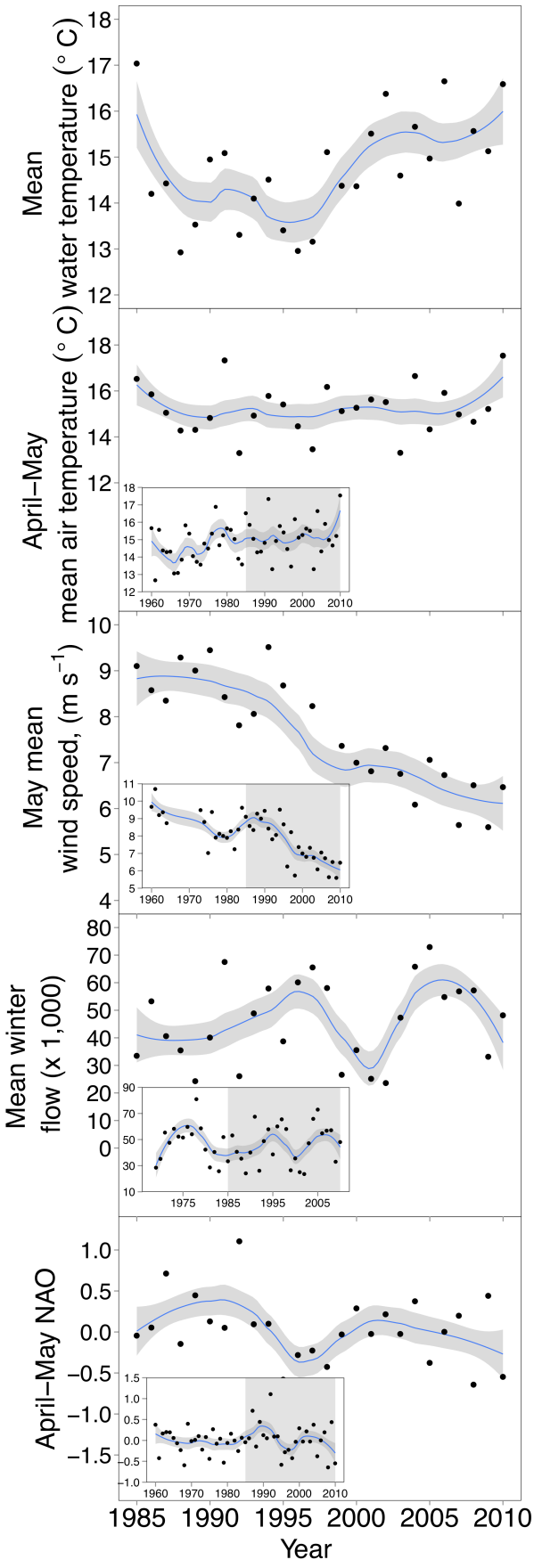

Figure 2.2. Local environmental and large-scale climate variables observed to show significant correlations with day of 25, 50 and/or 75% of female striped bass catch on the Upper Bay spawning grounds. Trend lines were derived using a loess smoother (span = 0.5). The gray region represents the 95% confidence interval.

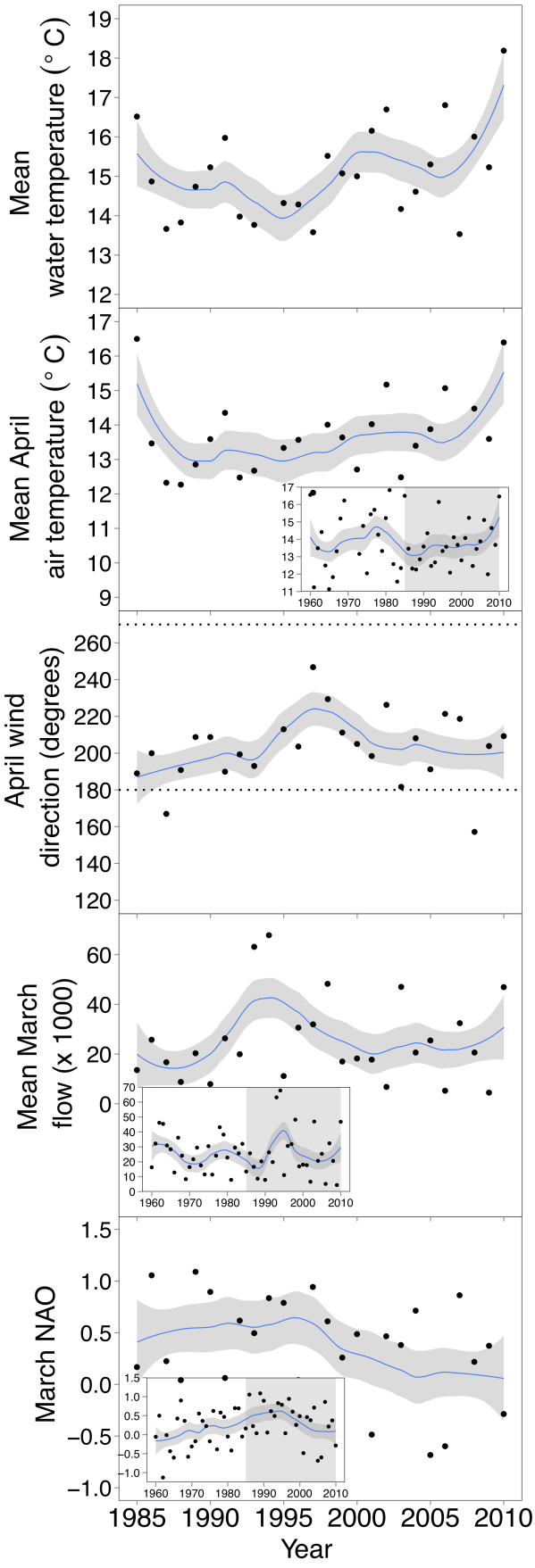

Figure 2.3. Local environmental and large-scale climate variables observed to show significant correlations with day of 25, 50 and/or 75% of female striped bass catch on the Potomac River spawning grounds. For April wind direction, upper and lower dashed lines represent direct west and south, respectively. Trend lines were derived using a loess smoother (span = 0.5). The gray region represents the 95% confidence interval.

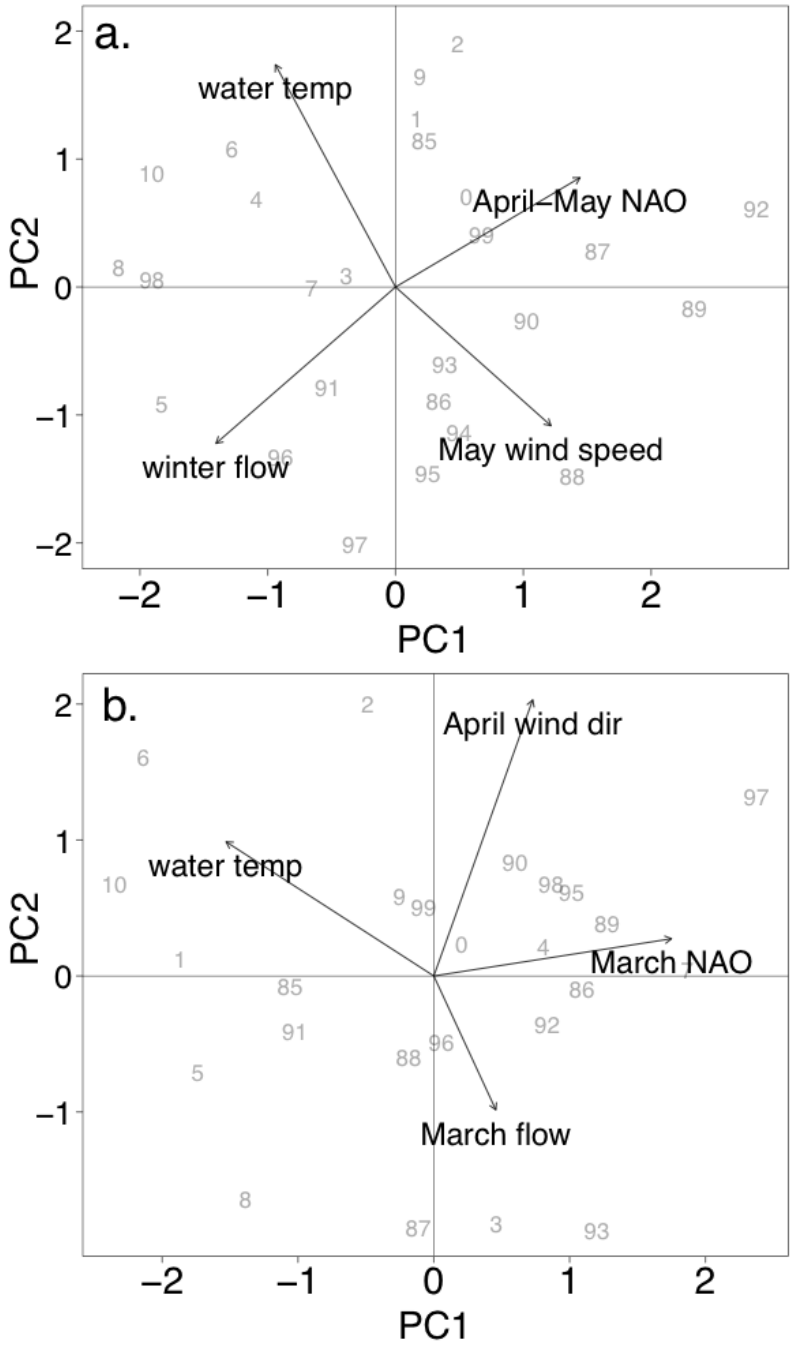

Figure 2.4. Biplots for principal components analyses that included the local environmental and large-scale climatic variables that showed significant correlations with day of 25, 50, and/or 75% catch of female striped bass on the Upper Bay (a) and Potomac River (b) spawning grounds.

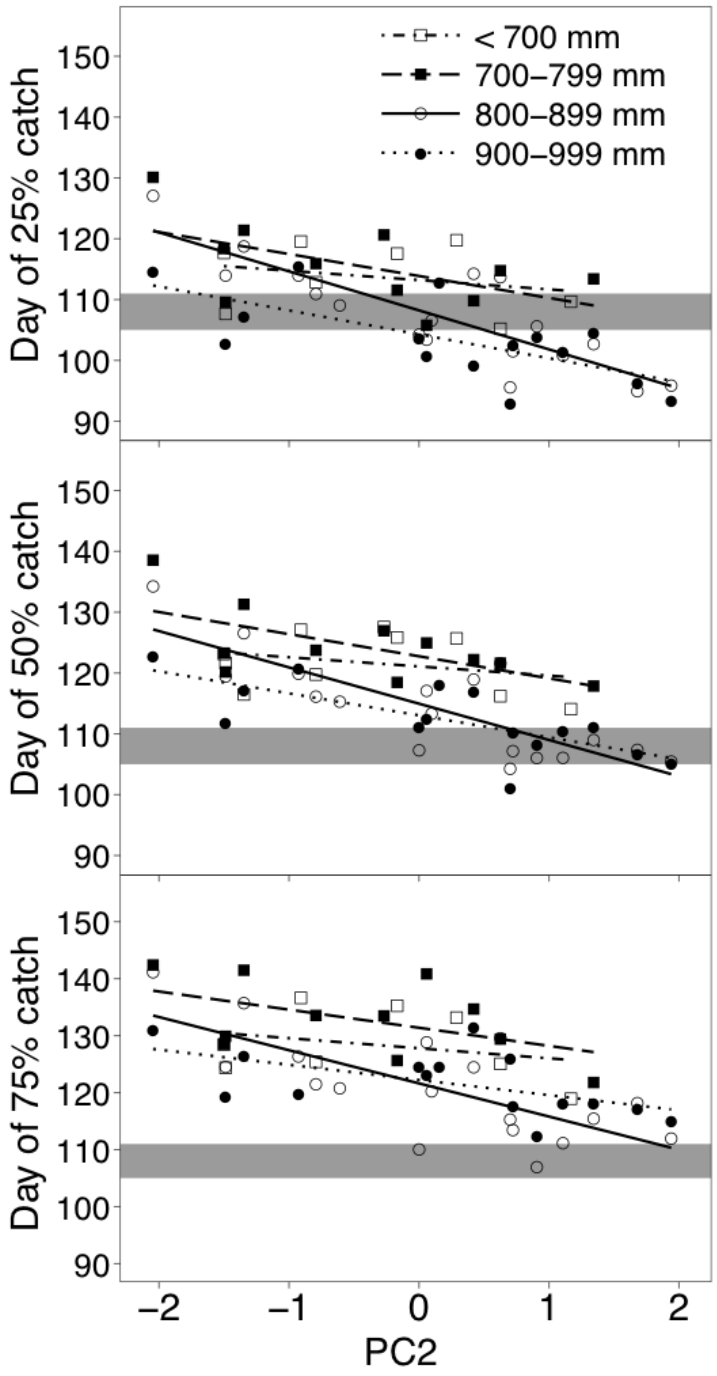

Figure 2.5. Illustration of the general linear model results (Table 2.4) showing the relationships between PC2 and day of 25, 50 and 75% catch of four size-classes of females striped bass caught by gill net on the Upper Bay spawning grounds. The shaded region shows the range of dates representing the third Saturday in April, which is the first day the "trophy" striped bass fishing season opens on adult striped bass migrating up the mainstem of the Chesapeake Bay. Linear relationships and shaded region thus show escapement potential as a function of the environmental variables in PC2.

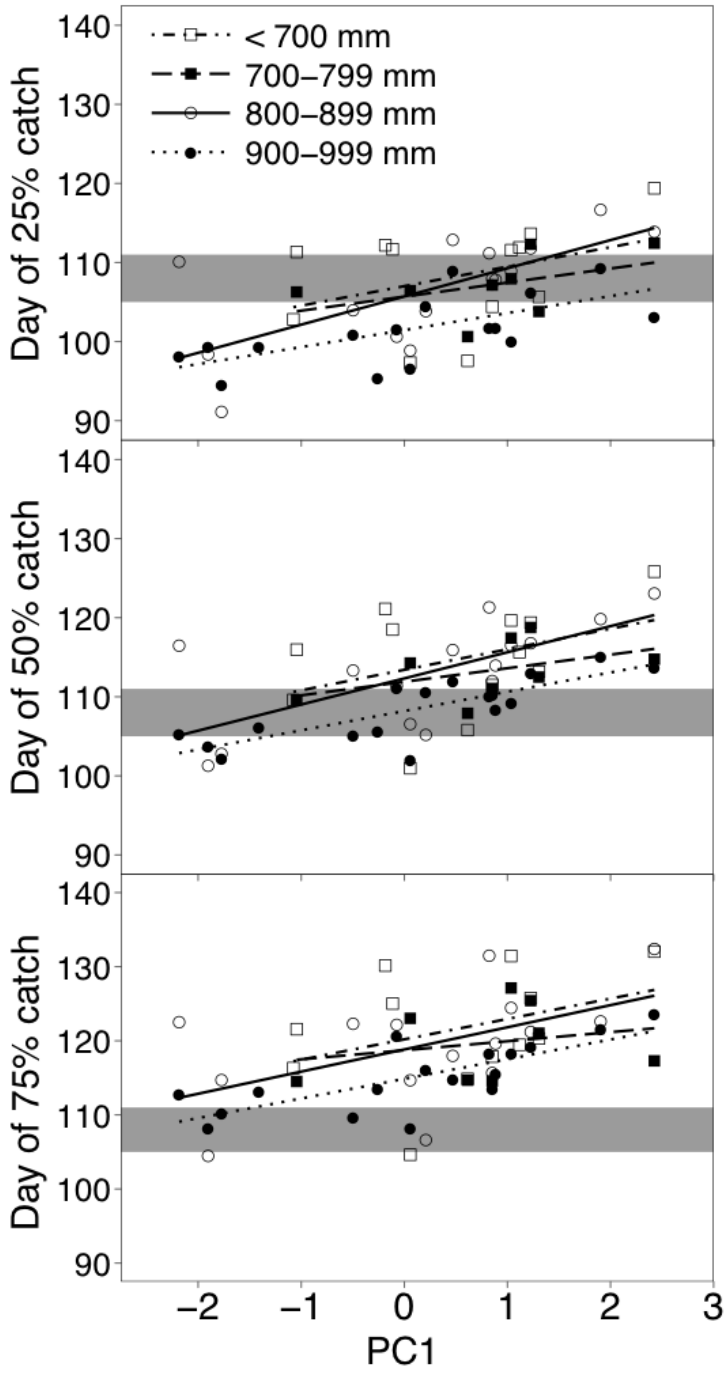

Figure 2.6. Illustration of the general linear model results (Table 2.5) showing the relationships between PC1 and day of 25, 50 and 75% catch of four size-classes of females striped bass caught by gill net on the Potomac River spawning grounds. The shaded region shows the range of dates representing the third Saturday in April, which is the first day the "trophy" striped bass fishing season opens on adult striped bass migrating up the mainstem of the Chesapeake Bay. Linear relationships and shaded region thus show escapement potential as a function of the environmental variables in PC1.

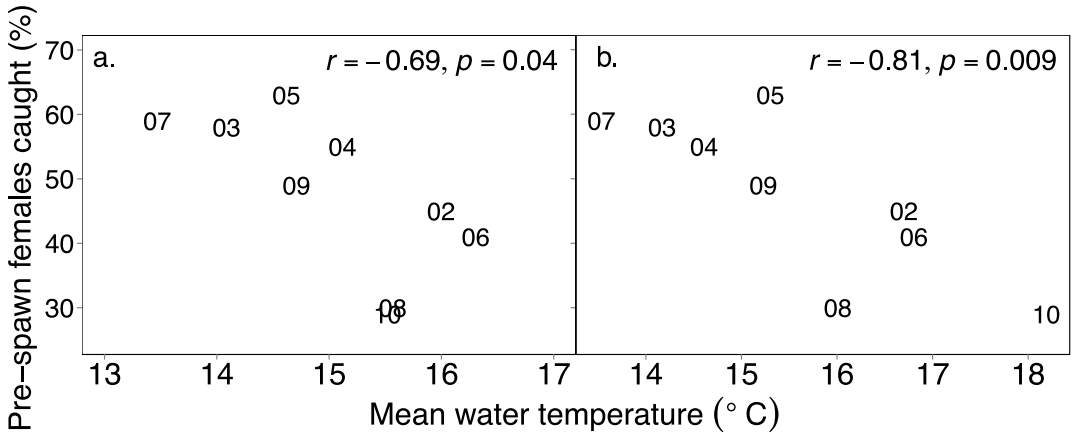

Figure 2.7. Relationship between mean water temperature during the spawning season on the Upper Bay (a) and Potomac River (b) spawning grounds and the proportion of mature, egg-bearing pre-spawn females caught. Percentages were based on the Maryland striped bass spring season creel survey. Data are shown as years.

CHAPTER 3:

SIZE, AGE, AND CONDITION DEMOGRAPHICS OF FEMALE STRIPED BASS DURING THE SPAWNING SEASON IN CHESAPEAKE BAY: TEMPORAL DYNAMICS AND INFLUENCES ON REPRODUCTIVE POTENTIAL

Abstract

Deriving quantitative information on factors that influence individual fish fecundity and the likelihood of skipped spawning is fundamental to reliable estimation of the reproductive potential of a given fish stock. Although numerous studies have focused on the importance of female age and/or size on reproductive potential, a growing body of evidence indicates that female energetic condition can have substantial influence on both fecundity and skipped spawning of teleosts. Striped bass (*Morone saxatilis*) reproductive biology as been studied extensively in the laboratory, yet little is known about the importance of female energetic condition to reproductive potential. To address this deficiency, I collected female striped bass in the Chesapeake Bay before and during the 2009 and 2010 spawning seasons to test the hypothesis that relative total condition (RTW) has a positive influence on reproductive potential measured as: (1) the probability of a mature female spawning, (2) relative fecundity and (3) relative oocyte volume. In line with my hypothesis, I observed that RTW had a positive influence on residual fecundity and residual oocyte volume. Furthermore, I was able to show that RTW explained a high degree of variation in my measures of reproductive potential, and was a more effective index of relative total energetic condition than tissue-specific measures. Contrary to my hypothesis, RTW did not exhibit an overall positive effect on the probability of spawning. However, females had a higher probability of spawning at smaller sizes

and nearly younger ages in 2010, when females were in better condition – suggesting an indirect effect of condition on spawning probability. Furthermore, the proportion of skip spawners was lower in 2010 (11%) compared to 2009 (18%). Together, my results show that female relative total condition during the spawning season is biologically significant and influences reproductive potential through egg production (number and size) and spawning frequency. These are important observations that require further exploration to identify the interannual variability in total condition and skipped spawning frequency, as well as the factors driving their variability. In doing so, we can begin to understand the true variation in population reproductive potential and attempt to develop better models that relate spawners to recruits.

Introduction

Understanding the relationship between characteristics of the spawning stock and the number of new recruits produced is central to understanding the dynamics of fish populations. Key to this process is reliable estimation of a population's reproductive potential, which represents its ability to produce viable offspring that may recruit to the adult population or fishery (Trippel 1999). Traditionally, spawning stock biomass (SSB) has been used in stock-recruitment models as a proxy for reproductive potential, which requires the implicit assumption of proportionality between total egg production (i.e., reproductive potential) and SSB (Trippel et al. 1997, Marshall et al. 1998). However, SSB and egg production may not be directly proportional because aggregate biomass ignores fundamental traits, such as age and energetic condition, which affect reproductive potential of fish stocks (i.e. proportion mature at age, fecundity, and offspring size and viability) (Stearns and Crandall 1984,

Kjesbu et al. 1991, Solemdal et al. 1995, Marshall et al. 1998, Marteinsdottir and Steinarsson 1998, Trippel 1998). Additionally, recent evidence indicates that some females in a population may not spawn each season (i.e., skipped spawning), and the frequency of this behavior may be related to nutritional condition (Rideout et al. 2006, Rideout and Rose 2006, Skjæraasen et al. 2009, reviewed by Rideout et al. 2005) – further uncoupling spawning stock biomass from reproductive potential. Overall, the misspecification of the functional relationship in the spawner-recuit relationship may be partly responsible for weak spawner-recruit relationships commonly reported (Goodyear and Christensen 1984, Cushing 1988, Walters and Collie 1988, Marshall et al. 1998). However, when SSB is replaced with measures that account for individual variation in reproductive potential within a stock, recruitment predictions can be enhanced (Marshall et al. 1998, Murawski et al. 2001). Thus, increasing awareness of factors that influence reproductive potential of individual fish within the spawning stock may improve recruitment predictions (Rothschild 1986, Rijnsdorp et al. 1991, Marshall et al. 1998, Ulltang 1996, Kjesbu et al. 1996, Trippel et al. 1997).

Deriving quantitative information on factors that influence individual fish fecundity and the likelihood of skipped spawning is fundamental to reliable estimation of the reproductive potential of a given stock (Oskarsson and Taggart 2006, Rideout et al. 2005). Various non-heritable maternal traits appear to influence both potential fecundity (i.e. number of vitellogenic oocytes in a prespawning ovary) and skipped spawning behavior. Numerous studies have focused on the importance of female age and/or size on fecundity (Kjesbu et al. 1998). A growing body of

evidence indicates that female energetic condition can have substantial influence on both fecundity and skipped spawning (Marteinsdottir and Begg 2002, Morgan 2004, Rideout et al. 2006, Rideout and Rose 2006, Kennedy et al. 2010).

Fish condition represents the general well-being or fitness of individuals and is often assessed by the amount of energy or nutrient reserves (i.e. protein and lipid) within individual fish (Marshall et al. 2004). High body condition (i.e., high energy or nutrient reserves) is thought to be a direct consequence of an animal's ability to acquire resources (Baker 1989), which can then be used to support increased fitness (Jakob et al. 1996). In fish, lipids are the primary energy storage material (Tocher 2003), and the lipid content of a fish represents the surplus energy available for future maintenance, growth, and reproduction (Kaufman et al. 2007). For females preparing to spawn, energy stores are critical for proper gonad development (Henderson et al. 1996, Berg and Finstad 2008), because reproduction typically involves the reallocation of energy previously stored in the body (Bagenal 1969). Usually, repletion of energy stores occurs when food supplies plentiful, so that reproductive growth can occur if food supplies become limited and rates of ingestion are insufficient to support gonadal growth and development (Jobling 1994). How energy reserves are stored depends on the species; lean fish such as gadoids tend to store energy in the liver, whereas fatty fish, such as clupeids and scombrids store most of their energy in the muscle or viscera (Jobling 1994, Nunes et al. 2011). Regardless of storage site, this stored energy is rerouted through the liver during vitellogenesis, packaged as vitellogenin (plasma precursor of yolk) and transported through blood plasma to the oocytes (Lubzens et al. 2010). When the various storage tissues are

replete with energy, vitellogenesis will proceed and females will spawn. However, if sufficient energy reserves are not available, fish may respond in several ways. First, resource allocation to ovaries could be maintained at the expense of somatic energy reserves (Lambert and Dutil 2000). Alternatively, allocation to ovaries could be reduced in order to limit somatic energy losses.

Fishes may initiate development of more ovarian follicles than are taken to full development (e.g., Atlantic herring [Kurita et al. 2003], turbot [*Scophthalmus maximus*] [Bromley et al. 2000], Atlantic cod [Kjesbu et al. 1991, Armstrong et al. 2001], sole [Armstrong et al. 2001). Fecundity is then down-regulated by atresia (oocyte resorption) in relation to available energy reserves (Kurita et al. 2003). In addition, as observed in numerous species, some mature females may skip spawning and delay reproduction altogether when energy is limiting (reviewed by Rideout and Tomkiewicz 2011). Finally, some females also may be less likely to mature at a given size or age, compared to fish in better condition (e.g., Marteinsdottir and Begg 2002). Thus, reduced energetic condition can have important consequences for the reproductive potential of many species. Consequently, understanding the condition demographics of a stock could improve recruitment predictions (Marshall et al. 2000).

Although the reproductive biology of striped bass has been studied extensively in the laboratory (i.e., Specker et al. 1987, Berlinsky and Specker 1991, Mylonas et al. 1997, Clark et al. 2005), little is known about the reproductive ecology of wild populations beyond general spawning behavior, and fecundity and maturity relationships. Mature adult females usually occur in the coastal ocean during most of

the year, but in the spring they enter estuaries along the Atlantic coast to spawn in tidal freshwater. Because striped bass are synchronous, total spawners, all eggs are released in a single event (Berlinsky and Specker 1991). This spawning strategy has enabled striped bass fecundity estimates to be easily determined. However, in all estimates, fecundity has been parameterized exclusively as functions of size and age (e.g., Jackson and Tiller 1952, Hollis 1967, Mihursky and Milsaps 1987), and often with substantial unexplained residual variance in the relationships. Whether female energetic condition is able to explain the large residual variance that remains in the relationship between female size and fecundity is currently unexplored. In addition, Secor and Piccoli (2007) recently showed evidence for skipped spawning behavior in striped bass. However, to date there is no understanding of whether the frequency of or energetic links to skipped spawning observed in other species also occurs in striped bass. Consequently, the potential importance of energetic condition to the reproductive potential of striped bass remains unknown.

Although energetic condition has been documented to influence reproductive potential in teleosts, there is little understanding of its importance to striped bass. To address this deficiency, I examined relative mass as a proxy for relative total energetic condition to test the hypothesis that relative total condition has a positive influence on reproductive potential. I evaluated reproductive potential using three measures: (1) the probability of a mature female spawning, (2) relative fecundity (i.e., residuals from the female length-fecundity relationship) and (3) relative oocyte volume (i.e., residuals from female length-oocyte volume relationship. My approach to test the hypothesis was two-fold. First, I quantified the size, age, and condition

demographics of female striped bass during two spawning seasons. Second, because a female's relative total condition is a measure of her relative total energy, I then tested whether relative total condition was positively related to reproductive potential. In addition, because the total condition of a female represents the sum of individual energy storage tissues, I determined whether relative total energy explained more variation than individual tissue-specific (i.e., liver, viscera, muscle) measures of relative condition.

Methods

Field sampling and ovary processing

Female striped bass in this study were collected by angling in the mainstem of the Chesapeake Bay, near the mouth of the Patuxent River, Maryland in 2009 and 2010. All handling of striped bass followed an approved University of Maryland's Institutional Animal Care and Use Committee protocol (Research Protocols: S-CBL-07-01 and S-CBL-10-02). Upon capture, each fish collected was euthanized with 500 $mg \cdot L^{-1}$ of tricaine methanesulfonate (MS-222) and then placed in an ice/water slurry to prevent atresia of oocytes. In the laboratory, the total wet weight (g) and total length (mm) of each fish were measured and their sagittal otoliths, liver, ovaries and the intact stomach/intestines and attached visceral fat (hereafter visceral tissue) were removed and weighed. Whole gutted bodies (i.e., entire fish minus all organs) of a subsample of females collected in 2010 (n = 38) were refrozen to determine the total energy in the gutted body.

For histological analyses, a small central section (~ 6 g) of one lobe of the ovary was immediately placed in a 4:1 solution of formaldehyde and glutaraldehyde

(4F:1G) and refrigerated at 4°C for 24 hours. Histological analyses were conducted to determine the reproductive stage of a subset of females (n = 140) and to develop models for predicting the reproductive stage of the remaining females using female characteristics, ovary color and energy density (kJ g^{-1}) (see Peer et al. 2012, [Appendix A]). Only the mature females (i.e., stages 2 [developing], 3 and 4 [both spawning capable]; See Peer et al. 2012 for full descriptions of the reproductive stages) were included in subsequent analyses (n_{2009} = 123, n_{2010} = 94). From the same lobe used for histological analyses, 2 small samples (~ 0.5 g) from the anterior and posterior portions of the ovaries were weighed and placed in 10% formalin for fecundity analysis.

To age each fish, transverse sections, approximately 1 mm thick, were cut through the otolith cores with a metallurgical wafering saw; otoliths were mounted on glass slides and polished. Annuli were enumerated based upon standard criteria under optical microscopy (Secor et al. 1995). A final age was determined based on two independent reads with no error between readers. When readers could not agree on an age, a second read was conducted. If agreement was not attained on the second read, the otolith was excluded from analyses.

To develop tissue-specific indices of energetic condition, energy densities of ovaries, livers, visceral tissue and gutted body tissue were determined. Developing these indices involved a two-step process, which required first determining the dry weight (g) of whole ovaries, livers and visceral tissue. Whole dry weights were then multiplied by the mean energy density (kJ g^{-1}) of dried samples from each tissue to estimate total energy (kJ). To estimate the mean energy density of the ovaries, the

wet-weight of the second ovary lobe was recorded and placed in a drying oven at 65°C until a consistent mass was obtained after two consecutive measurements separated by at least two days. To determine the mean energy density of the liver, the same drying procedure was used. Determining the mean energy density of the visceral tissue also followed the same drying procedure, but prior to drying, the stomach and intestines were cut open dorso-ventrally and washed with water to remove any digested food. To estimate the mean energy of the entire gutted body, frozen gutted bodies were cut into small (~ 25 g) pieces with a hand-held reciprocating saw and then ground three times in a meat grinder to homogenize the tissue. Two 200-gram subsamples for analyses were randomly selected and placed in an aluminum pan and dried to a constant weight.

To estimate the energy density of ovaries, livers, visceral tissue and gutted body tissue, samples of dried tissues were ground to a fine powder using either mortar and pestle, or a coffee grinder. Ground tissues were then pressed to form composite pellets (~ 0.5 g) and the energy density was estimated using an oxygen bomb calorimeter (Model 6200, Parr Instrument Company, Moline IL.) standardized with benzoic acid pellets (26.444 kJ/g). Replicate pellets of each tissue from each female were burned in the calorimeter. When the estimates differed by more than 400 kJ g^{-1} (~ 2%), a third pellet was ignited. Mean energy density of each tissue was equal to the mean of two composite tissue pellets that differed by less than 2%. Total energy (kJ) of the whole ovaries, liver and visceral tissue were then estimated by multiplying the mean energy density (kJ g^{-1}) by the total dry weight of the respective tissues.

The reproductive potential of all females was assessed by estimating potential

fecundity using the gravimetric method and by determining mean oocyte volume. Energy per oocyte also was estimated; however, because it was highly correlated with oocyte volume ($r = 0.88$, $P < 0.0001$), only oocyte volume was included in this analysis. Only stages 3 and 4 females (both spawning capable, based on model predictions (i.e., Peer et al. 2012 [Appendix A] and criteria developed by Brown-Peterson et al. 2011)) were included in the fecundity and oocyte volume analyses. To estimate fecundity, ooctyes from ovary tissue preserved in 10% formalin were either teased apart with probes, agitated with a stream of water while in a sieve (50 μm) with vacuum, or both to separate oocytes. An 8 cm wide × 20 cm long × 2 cm high plastic mold was then filled with a 3% agar solution to 1-cm depth and allowed to solidify. After the agar solidified in the mold, a continuous cut was then made at 1-cm within the periphery of the mold so that a 6 cm wide 18 cm long and 1-cm deep section of agar could be removed from the mold. All oocytes were then removed from the sieve and placed into the cavity left by the removed piece of agar. The 3% agar solution was then poured over the oocytes to fill in the cavity to 1-cm depth. Using a probe, oocytes were separated before the agar solidified. After the agar solidified a cut identical to that described above was again made at 1-cm within the periphery of the mold and the center section containing all ooctyes was removed and placed on a flatbed scanner (Canon CanoScan 8800F, Lake Success, NY). Klibansky and Juanes 2008) method was used to scan and count ooctyes for both subsamples of each spawning capable female using ImageJ (version 1.45h, Rasband 2011). The oocytes per gram of each subsample was determined and then multiplied by the mean oocytes per gram for each female, which was then multiplied by the ovary wet weight

to estimate potential fecundity. Using the unaltered images of the oocyte scans previously used for fecundity, diameters of 50 random oocytes from each female were measured using the ImageJ line selection tool. The mean oocyte diameter and volume were then calculated.

Statistical analyses

The demographics of the striped bass spawning stock were evaluated in each of two years. For these analyses, linear models were used to separately determine whether any of the female relative condition indices, size, or age differed between the years of this study, among female reproductive stages, or over the course of the spawning season. The reproductive characteristics of the stock were evaluated using an identical approach except that the dependent variables were residual fecundity and residual oocyte volume. All linear models included year and stage as class variables, calendar day of collection (i.e., day of year [doy]) as a covariate and all two-way interactions. If significant differences in stage means were detected, a post-hoc Tukey Honestly Significant Difference (HSD) multiple comparisons analysis was conducted on the means to determine which reproductive stages were significantly different. All analyses were conducted using the aov function in the R base package (R Development Core Team 2011).

In addition to the linear approach, a two-dimensional Kolmogorov-Smirnov (2DKS) test (reviewed in Garvey et al. 1998)) was applied to further evaluate the relationship between individual female variables and doy in situations where no significant doy effect was observed in the GLM, but a non-random threshold

relationship appeared to be present. In other words, 2DKS was used to determine whether the dependent variable showed constrained variance beyond a specific independent variable threshold. This test can be used to compare bivariate distributions by finding the maximum difference, D_{BKS} in the integrated probabilities for four quadrants around each point in the plane. When D_{BKS} between an observed and theoretical bivariate distribution or two observed bivariate distributions exceeds that expected from two random distributions, then the two tested distributions differ and a non-random relationship exists (Garvey et al. 1998). For this analysis, the original data were re-randomized 5000 times to determine if D_{BKS} deviated from that expected by chance. The 2DKS was run using the program written by Garvey 2005(2005).

To test the hypothesis that relative total condition positively influences reproductive potential, residual total weight, an index of relative total condition, was estimated as the residual from the nonlinear relationship between female total length and total body weight (i.e., weight = aTL^b, Appendix B). Alternative measures of relative condition were also developed using tissue specific measures of energy that represent the potential energy storage tissues used for reproduction. These relative condition indices were developed using similar nonlinear methodology (i.e., tissue energy = $a \times \exp^{(b \times TL)}$, Appendix B) used to determine residual total weight, except rather than use total body weight as a dependent variable, total energy in ovaries, liver and visceral tissue, as well as gutted body were included in separate regressions. The residuals from each relationship were then used as indices of relative condition and termed residual ovary energy, residual liver energy, residual visceral energy and

residual gutted weight (see Table 3.1 for acronyms of all measures of condition used in this study). Indices of relative reproductive output were also estimated as the residuals of nonlinear relationships between female total length and both individual female fecundity and oocyte volume data (Appendix B). These indices were termed residual fecundity and residual oocyte volume, respectively. Using the residual measures of condition, fecundity and oocyte volume permitted tests of relative condition effects on reproductive potential exclusive of the effects of female size.

Generalized linear models (GLM) were used to test the hypothesis that RTW was positively related to the probability of spawning (or skipped spawning behavior). GLMs also were used to determine whether the alternative tissue-specific measures of relative condition (i.e., RGW, ROE, RLE, or RVE), size (total weight, total length) or age explained more variation in the probability of spawning than RTW. Individuals that skip reproduction are those that have already undergone the physiological changes associated with maturation and are potentially capable of spawning (Jørgensen et al. 2006). Females in stage 2, as discussed above, were included as mature, but were in the developing phase during the spawning season and thus were incapable of spawning in the current season. Thus, stage 2 females were identified as non-reproductive (or skip spawners). Females in stages 3 and 4 were included as spawners, since they were capable of spawning in the current season. Consequently, in the GLM used to assess the influence of relative condition on the probability of spawning, skip spawners (0) and spawners (1) were included as binary dependent variables. To determine whether the probability of spawning differed between years, year was included as a class variable in all models, as well as a year × relative

condition variable interaction. All models had a logit link function and binomial error structure and were fitted using the glm function in the R base package. When analyses indicated no effect of year and no year × female variable interaction, models were fitted using female variables only to determine the proportion of deviation attributable to each variable by calculating the pseudo r^2 value (1 – (residual deviance/null deviance)) (Swartzman and Huang 1992).

Finally, linear models were used to test the hypotheses that RTW was positively related to residual fecundity and residual oocyte volume. In these analyses, the model included RTW, as well as doy, year, stage, doy × year, doy × stage, and year × stage interactions. Year, doy and stage were included as factors to account for their potential confounding effects in evaluating the importance of RTW on residual fecundity and oocyte volume. An identical GLM model structure also was used to determine whether the alternative indices of relative condition, size and age explained more or less variation in residual fecundity or residual ooctyte volume.

Results

Relative total weight as an index of relative total energy

Correlation analyses indicated that RTW was a good index of relative total body energy and not simply relative wet mass (Appendix C). Wet weights (g) of all individual tissues analyzed were all positively correlated with the total energy (kJ) of the respective tissues (gutted body [$r = 0.95$, $p < 0.0001$], liver [$r = 0.91$, $p < 0.0001$], viscera [$r = 0.73$, $p < 0.0001$], ovaries [$r = 0.99$, $p < 0.0001$]; Appendix C). Thus, RTW, which represents a length-specific composite mass of all individual tissues

analyzed, did reflect differences in relative total body energy and not differences in water mass.

Size, age and relative condition demographics

Assessment of demographic patterns in the population indicated that among all measures of relative condition evaluated in this study, overall annual differences were only evident in RVE, which was 570 kJ (28%) lower in 2010 (Table 3.2; Tukey, $p = 0.001$). For both RTW and RGW, a significant stage × year interaction prevented an overall annual effect from being observed. However, this interaction was due solely to skipped spawners (i.e., stage 2) exhibiting no annual differences ($p > 0.05$). To account for the effect of skipped spawners, a separate analysis was conducted without stage 2 females to determine whether there were annual differences in RTW and RGW. In this separate analysis, annual differences in RGW were evident, with RGW significantly greater in 2010 ($F_{1,146} = 103.85$, $p < 0.0001$, mean difference + 236 g (19%)). Likewise, RTW also was significantly greater in 2010 ($F_{1,146} = 52.08$, $p < 0.0001$, mean difference + 823 g (39%)).

In addition to the annual trends observed, within year temporal trends also were evident for RTW and ROE, RLE, RGW. There were significant decreases in each index during the course of the spawning season (Table 3.2, Figure 3.1).

Among the more traditional demographic measures of size and age, only total length of females showed significant annual differences (Table 3.2). Female striped bass were 28 mm shorter on average in 2010 than 2009 ($p = 0.006$). Within each year, female weight and age, but not length, showed nearly significant decreases over

the duration of the spawning season when data were analyzed using linear models (Table 3.2, Figure 3.1). Although significant linear temporal trends within a year were not detected for size and age, the female size and age did display nonlinear patterns suggesting possible threshold-like changes in the mean and variance over the course of a spawning season.

Trends in demographics, evaluated using the 2DKS analyses indicated that for stage 4 females, the null hypothesis of independence in the relationship between doy and female age could be rejected. D_{BKS} occurred when doy = 87 (D_{BKS} = 0.0878, p = 0.0004), indicating that the mean and variance of female age for stage 4 females were significantly lower after day 87. However, 2DKS test results indicated that for stages 2 and 3, the relationship between doy and age did not differ from one expected if the univariate distributions for both variables were generated independently (all $p >$ 0.05). 2DKS also indicated that for all female stages, the relationship between doy and gutted weight did not differ from one expected in the univariate distributions if both variables were generated independently (all $p > 0.05$). Weight, length and age differences were evident among stages, with females in stage 4 being significantly larger and older than those in stage 2 and 3 (Figure 3.1, Table 3.2, Tukey, all $p <$ 0.003), but with no differences between stages 2 and 3.

Probability of spawning

The probability of spawning showed no significant overall annual difference as a function of relative condition or weight (Table 3.3, Figure 3.2). However annual differences in the probability of spawning indicated significant effects as a function of

total length and nearly significant effects as function of age (Table 3.3, Figure 3.2). These results indicated that females in 2010 were spawning at a significantly smaller size (total length at 50% spawning probability: 853 mm in 2009; 802 mm in 2010) and nearly significant younger age (age at 50% spawning probability: 9 in 2009; 8 in 2010). The proportion of non-reproductive females collected in this study also was higher in 2009 (18%) compared to 2010 (11%).

Among all measures evaluated (i.e., relative condition, size and age), ROE, size and age clearly explained most of the variance in the probability of spawning (Table 3.3, Figure 3.2). The probability of spawning increased as females became larger, older and accumulated greater relative energy in their ovaries (Table 3.3, Figure 3.2). Furthermore, when both years were combined (i.e., because there were no year and interaction effects), pseudo-r^2 values indicated that length, gutted weight, age and ROE each explained approximately 13, 17, 18% and 19% of the variation in the probability of spawning. Although no overall between year effects of RTW or RGW were evident, significant interactions with year were present in each model, with the slopes being significantly greater in 2010 for each model (Table 3.3, Figure 3.2). When models were fit on each year separately, RTW and RGW had no effect on the probability of spawning in 2009 ($\chi^2_{1,117} = 0.05$, $P = 0.81$ and $\chi^2_{1,117} = 1.53$, $p = 0.22$, respectively); however, in 2010 both RTW and RGW had significant positive effects on the probability of spawning ($\chi^2_{1,88} = 14.10$, $p = 0.00017$ and $\chi^2_{1,88} = 21.72$, $p < 0.0001$, respectively), as is evident in Figure 3.3.

Factors influencing residual fecundity

Evaluation of the demographic trends in residual fecundity indicated that residual fecundity varied by year, over the course of the spawning season, and was influenced by reproductive stage. In this model, female relative condition variables were withheld due to the confounding effects of doy with relative condition (see *Size, age and relative condition demographics* section above). Results indicated that residual fecundity differed among stages and between years (Table 3.4). Evaluation of the intercepts showed that residual fecundity was on average 39,313 ($p = 0.003$) and 68,724 ($p = 0.002$) higher in stage 4 than stage 3 and higher in 2010 than 2009, respectively. Residual fecundity also showed a significant decline in both years as the spawning season progressed (Table 3.4, Figure 3.3).

As hypothesized, striped bass RTW exhibited a significant positive influence on residual fecundity (Table 3.5, Figure 3.4). Specifically, when stage and year were removed from the analysis, RTW explained 25% of the variation in residual fecundity. With the exception of RLE, all tissue-specific measures of relative condition also showed significant effects on residual fecundity. With the exception of RVE, all relationships between residual fecundity and condition metrics were positive. The effects of relative condition were consistent in both years and stages, as indicated by the absence of interactions with year and stage (Table 3.5, Figure 3.4). Relative condition of the gutted body (RGW) and ovaries (ROE) showed the strongest tissue-specific effects on residual fecundity (Table 3.5, Figure 3.4) and explained 13% and 27% of the variation in residual fecundity, respectively, when stage and year were removed from each analysis. RVE also had a significant

influence on residual fecundity, but the effect was negative (Table 3.5, Figure 3.4) and explained only 8% of the variation in residual fecundity when stage and year were removed from the analysis.

Factors influencing residual oocyte volume

Exploration of demographic patterns in oocyte volume indicated that unlike residual fecundity, no annual differences or within year temporal trends were evident, but residual oocyte volume was significantly greater in stage 4 females (Table 3.6, Figure 3.5). In addition, as hypothesized, RTW did have a significant positive influence on residual oocyte volume in the full model (Table 3.7, Figure 3.6). However, when year and stage were removed from the analysis, RTW only explained 5% of the variance. Further evaluation of tissue-specific measures of relative condition indicated that RGW and RLE had no influence on residual oocyte volume. However, similar to its influence on residual fecundity, RVE had a significant negative influence on residual ooctye volume (Table 3.7, Figure 3.6) and explained 22% of the variance when stage and year were removed. Much like the effects on residual fecundity, the index with the single largest effect on residual oocyte volume was ROE, which had a significant positive effect and explained 69% of the variance when year and stage were removed (Table 3.7, Figure 3.6).

Discussion

Despite a central tendency for recruitment to be positively correlated with spawning stock biomass (SSB) (Myers and Barrowman 1996), there is typically high

unexplained variability surrounding these relationships for most species. Although some of this variability may be due to measurement error or time-series effects (Walters and Ludwig 1981, Walters 1985), it is also possible that SSB is an imprecise and biased measure of reproductive potential (Marshall et al. 1998). Regarding the latter issue, more sensitive measures of the true reproductive potential of a stock may be necessary to provide more precise and less biased estimates of recruitment (Marshall et al. 1998). Here I showed that female energetic condition might provide a more sensitive measure of reproductive potential in striped bass. In line with my hypothesis, I observed that RTW had a positive influence on residual fecundity, residual oocyte volume and indirectly on the probability of spawning. Furthermore, I was able to show that RTW explained a high degree of variation in my measures of reproductive potential, and was a more effective index of relative total energetic condition than tissue-specific measures. Thus, increases in RTW were related to increases in striped bass reproductive potential.

Prior to my investigation, little was known about the condition and reproductive demographics of female striped bass during the course of the spawning season. Importantly, my results indicate that evaluating a striped bass stock based solely on size and age structure is insufficient to reliably forecast reproductive output during the spawning season. Although inter-annual differences were only evident for RGW (i.e., higher in 2010 for stage 3 and 4 females) and RTW (i.e., higher in 2010 for stage 4 females), within year temporal patterns were strong and indicated that the size, age and relative energetic condition of females was greater earlier in the season. In Chapter 2 I used a long-term fishery-independent spawning survey in the

Chesapeake Bay to show similar results indicating that larger striped bass females migrated onto their spawning grounds earlier. Larger and older females of other species have also been observed spawning eggs or releasing larvae earlier (Lambert 1987, Ware and Tanasichuk 1989, Schultz et al. 1991, Danylchuk and Fox 1994, Wright and Gibb 2005, Sogard et al. 2008) – although in rare cases later (Gillet et al. 1995, Morgan 2003) in the spawning season. Thus, the pattern I observed in striped bass is consistent with that observed in most other species.

Although the specific spawning pattern I observed has been anecdotally suggested for striped bass by other authors (Hollis 1967), I provide the first documentation of temporal trends in female relative condition during the spawning season. My data do not allow identification of the specific cause for this pattern. However, I suggest three possible explanations for the lower relative energetic condition found in all stages of females collected later in the season. First, females spawning later may have been exposed to a greater number of degree-days during maturation and thus lost more energy due to greater metabolic costs. Second, low energetic status, particularly lipid levels, can reduce the levels of hormones involved in gonadal development and thereby delay spawning time (Cerda et al. 1994, Matsuyama et al. 1994). Finally, it is also possible that females in poorer condition prior to the beginning of vitellogenesis, may begin vitellogenesis later than females in good condition. This may also explain why stage 4 females were collected, on average, 7 and 9 days earlier than stage 3 and 2 females, respectively. In fact, González-Vasallo 2006) observed that Atlantic herring (*Clupea harengus*; another total and capital spawner like striped bass) that fed on lower rations, began ovary

development much later in the year than those fed on higher rations. Danylchuk and Fox (1994) also showed that female pumpkinseed sunfish (*Lepomis gibbosus*) from populations that exhibited stunted growth and smaller adult size exhibited delayed maturation. Kennedy et al. (2010) observed a similar pattern in Atlantic herring, with fish in poor condition starting maturation later than those in better condition. However, Kennedy et al. (2010) also observed that some of the later maturing females were able to compensate by growing their oocytes quickly and thereby "catch-up" with the earlier maturing fish. My results suggest that striped bass may not possess the ability to "catch-up".

Contrary to my hypothesis, RTW did not exhibit an overall positive effect on the probability of spawning. Furthermore, with the exception of ROE, I observed no significant overall effects of any index of female relative condition on the probability of spawning. The observed effect of ROE, however, was expected and does not necessarily indicate that spawning females were in better condition. This is because by definition, skip spawners were either not allocating toward their ovaries, or were undergoing atresia and consequently would have less relative energy in their ovaries.

Although RTW did not show an overall influence on the probability of spawning, between year differences in the effect of RTW on the probability of spawning were evident by a significant RTW × year interaction. Further exploration showed that when models were fitted on each year separately, RTW and RGW had no effect on the probability of spawning in 2009, but in 2010 both RTW and RGW had significant positive effects on the probability of spawning. These results indicate that relative total energetic condition of female striped bass was important in explaining

spawning probability in 2010, but not 2009. Moreover, it appears that spawners can be in better condition than skippers in some years (i.e., 2010), although better condition is not a prerequisite for spawning.

Despite the absence of an overall effect of RTW on the probability of spawning, RTW does appear to influence the probability of spawning at smaller size and potentially younger ages. However, during years such as 2009, when condition was lower, younger and smaller females may be more likely to hedge their bets against spawning and favor saving energy for future survival and better reproductive opportunities. In fact, there appears to be evidence of this in my study, as the length at which 50% probability of spawning occurred was 51 mm shorter in 2010. In addition, I observed a nearly significant effect indicating that the age at which 50% probability of spawning occurred was 1 year younger in 2010. This observation in striped bass appears to be consistent with the modeling results of Jørgensen et al. 2006), who found that it was favorable for larger Atlantic cod to spawn even when their energy stores were not full. My results indicate that even in poor condition years like 2009, larger and older striped bass will still spawn. However, smaller and younger striped bass that spawn in good condition years like 2010 may forego spawning opportunities in poor condition years like 2009. Taken together, my results suggest that if relative total energetic condition does have an influence on the probability of spawning it may be expressed only in years of good overall condition and/or when condition variability in the population is high.

Although RTW did have an influence on spawning probability in 2010, size and age had the greatest overall influence on the probability of spawning. In both

years, larger and older females were more likely to spawn. My results for striped bass are consistent with results for Atlantic cod (Rideout and Rose 2006), Atlantic herring (Engelhard and Heino 2005, Kennedy et al. 2011), Greenland halibut (*Reinhardtius hippoglossoides*) (Walsh and Bowering 1981) and pumpkinseed sunfish (Danylchuk and Fox 1994), which all indicated that skipped spawning behavior was highest in the smallest size and age classes. As discussed earlier, energetic condition may play a role in influencing this size dependent pattern (i.e., smaller/younger females in poorer condition). However, other possible reasons for the size-dependent pattern may be that the ripening process in first time spawners may be more easily interrupted than for repeat-spawners (Rideout and Rose 2006). It is also possible that many skipped spawners were actually second-time spawners that were unable to recover from their first spawning (Jørgensen et al. 2006). Although these may provide proximate explanations for the size-dependent trends in skipped spawning behavior, size-specific metabolic and fecundity relationships may provide the ultimate reason. Specifically, it is known that small fish have higher weight-specific metabolic rates and swim less economically (Schmidt-Nielsen 1984). Furthermore, a 25% increase in fish length can double fecundity (Jørgensen et al. 2006). Thus, from a life-history perspective, there are certainly advantages to smaller and younger females exhibiting skipped spawning behavior, so that more energy can be allocated toward growth and future reproduction.

My results also indicated that the incidence of skipped spawning behavior might be more common in striped bass than previously estimated. In 2009 and 2010, the proportion of skip spawners represented 18 and 11% of all mature females

collected, respectively. These results also indicate that skipped spawning frequency was higher in 2009, when RTW was lower. This observation is consistent with the model results of Jørgensen et al. (2006), which supported the notion that skipping spawning frequency is higher in years when individual condition is poor. My observed frequency of skipped spawning in striped bass, however, is much higher than that detected by Secor and Piccoli (2007). They used otolith Sr:Ca to evaluate spawning frequency and observed that only 2% of females did not show evidence of an estuarine signature – which they believed was indicative of non-spawning behavior. Although it is likely that those females did not spawn, it is also likely that their method underestimates the proportion of skipped spawning. This is because they assumed that an estuarine signature (i.e., salinity < 30, Secor and Piccoli 2007) indicated that a female spawned in the respective year. However, this assumption is not supported by my data in which all females, including skipped spawning females, were collected in estuarine waters.

Despite the discrepancy between my results and Secor and Piccoli (2007), the proportion of skipped spawning behavior detected in my study is similar to that observed in other species. For example, Rideout and Rose (2006) observed that from 1978-2004, 18% of female Atlantic cod (*Gadus morhua*) skipped spawning, although in some years and in some regions of the Northwest Atlantic, skip spawning was > 40% (Walsh and Wells 1986). Engelhard and Heino (2005) also showed that between 29 and 55% of second-time Atlantic herring spawners exhibited skipped spawning behavior, while Rideout et al. (2000) showed that 33% of female cod from Smith Sound, Newfoundland skipped spawning in 1999. Thus, the incidence of skipped

spawning detected in striped bass during my study is certainly within the range observed in other species.

In fact, my estimates of skipped spawning are likely conservative given that the model used to predict reproductive stage in striped bass was not able to discriminate among immature, regenerating and early developing reproductive phases (i.e., Peer et al. 2012). Consequently, those phases were grouped into a single reproductive stage (i.e., stage 1) in the model. For my study, all females predicted to be in stage 1 were considered immature, and thus not included in the spawning probability analysis. Because early developing phase females are mature, but not capable of spawning in the current year, their exclusion from my spawning probability analysis likely leads to downward biased estimates of skipped spawning behavior.

Consistent with my hypothesis, I provided evidence that RTW was positively related to residual fecundity in striped bass. In addition, RTW explained more of the variance in residual fecundity (25%) than all tissue-specific indices of condition other than ROE, which explained 27% of the variation. It was expected that ROE would explain more variance in residual fecundity for two reasons. First, because ROE and residual fecundity were determined from the same tissue, they are highly dependent. ROE was based on the energy density of the ovaries. In contrast, RTW was based on weight, which is an index of energy, but may not explain as much variation as a direct measure of energy. Still, even though ROE should explain more variation in residual fecundity, this does not indicate it is a better index of female total relative condition during the spawning season. This is because energy frequently shifts between the

ovaries and other energy storage tissues (i.e., liver, visceral fat, muscle) during vitellogenesis and atresia. Thus, depending on the reproductive phase, ROE may not reflect the overall relative energetic status of the female. In contrast, because the wet weights of all tissues, including the gutted body, were positively correlated with total energy of each tissue, RTW did reflect the overall relative energetic status of individual females.

My observation of a positive effect of relative total condition (i.e., RTW) on residual fecundity is the first of its kind in striped bass. However, similar results have been observed in other species. Positive relationships between fecundity and condition have been observed multiple times in Atlantic cod (Kjesbu et al. 1991, Kjesbu et al. 1998, Marshall et al. 1998, Lambert and Dutil 2000, Marteinsdottir and Begg 2002), as well as other species (Pacific herring [*Clupea harengus pallasi*] Hay and Brett 1988; Atlantic herring Ma et al. 1998, Kennedy et al. 2010). However, in most of these examples, condition indices (i.e., Fulton's K, hepatsomatic index, liver weight) were shown to explain a significant amount of additional variation in the length-fecundity relationship. Koops et al. (2004) argued that because body weight (compared to length) generally explains a greater proportion of the variance in fish fecundity (Wootton 1998), the variance explained by weight-based condition indices may be due to body weight and not condition. As a result, condition indices rarely explain additional variance in fecundity-weight relationships (Koops et al. 2004), although it has been observed in some studies (Kennedy et al. 2010).

In this study I used residual fecundity and residual measures of energetic condition, both of which came from the relationship with total length. By using the

residuals for both fecundity and condition indices, I removed the effect of female size (both length and weight) from my analyses. This was verified when I observed that neither total weight, nor gutted weight explained any of the variation in residual fecundity. Furthermore, the wet weights of all individual tissues that made up the total wet weight of each female were positively correlated with the total energy density of those respective tissues. This indicates that RTW was a measure of energetic condition and not water weight. Consequently, my results do suggest that female total relative energetic condition (and not relative water weight) in striped bass did influence residual fecundity. Although RVE did exhibit a slight negative relationship with residual fecundity, this pattern did not breakdown the relationship between overall relative energetic condition (i.e., RTW) and residual fecundity – and possibly suggests that females in better condition were allocating relatively more stored energy in their visceral reserves toward reproduction.

Given the temporal trends observed for RTW and its positive effect on residual fecundity, it was not surprising to also detect intra- and inter-annual trends in residual fecundity. Residual fecundity was significantly higher in 2010, the same year that female RTW was higher. Residual fecundity also declined as the spawning season progressed, a pattern consistent in both years and stages. In other species, fecundity decreases as the spawning season progresses – a phenonmenon mostly evident in batch spawners (i.e., Hunter et al. 1992, Horwood 1993, Lowerre-Barbieri et al. 1996). For batch spawners, this temporal pattern may be more common due to frequent spawning, which requires a high amount of energy that must come from energy reserves or feeding. As energy reserves are utilized and not replenished

during the spawning season, less energy will be available at each successive ovulation. This intra-annual temporal pattern in relative fecundity also may occur in total spawners. One possible explanation for a progressive decline in residual fecundity in striped bass may be reduced energetic condition. As already discussed, RTW declined as the spawning season progressed and was positively related to residual fecundity. As noted above, reduced energetic condition as the spawning season progresses may be due to lower conditioned fish spawning later due to a delay in maturation. However, a reduction in condition may also be due to greater metabolic expenditures as spawning is delayed and water temperatures rise. Under both scenarios, the energetic condition of a female is low, either before or during the spawning season.

Reductions in fecundity during the spawning season may also be due to alterations in follicular development. For example, if condition is low prior to the initiation of vitellogenesis fewer follicles may be recruited, eventually leading to lower fecundity. However, some fishes recruit more follicles than are taken to full development (e.g., Atlantic herring [Kurita et al. 2003], turbot [*Scophthalmus maximus*] [Bromley et al. 2000], Atlantic cod [Kjesbu et al. 1991, Armstrong et al. 2001], sole [Armstrong et al. 2001]). Fecundity is subsequently down-regulated by atresia in relation to available energy (Kjesbu et al. 1991, Kurita et al. 2003, Kennedy et al. 2011). Thus, the lower conditioned females observed spawning later, may have had reduced fecundity due to low condition, or a progressive decline in condition during the spawning season, causing fewer follicles to be recruited for vitellogenesis.

Like the effect of RTW on residual fecundity, the effect of RTW on residual oocyte volume also was positive and consistent with my hypothesis. However, the variance in residual oocyte volume explained by RTW was low (5%). Still, the positive relationship I observed between RTW and residual oocyte volume is consistent with results on other fishes (Ouellet et al. 2001, Kjesbu and Holm 1994). This type of relationship may exist if sufficient energy reserves allow the more energy expensive process of increasing egg size (versus fecundity) to be regulated to maximum advantage (Kjesbu et al. 1991). However, my results indicate that this relationship was not strong in the striped bass population. This may be due to either low variation in the energetic condition of females and/or the low condition status of the current population (i.e., compared to historical populations [Jackson and Tiller 1952, Hollis 1967, Mihursky and Milsaps 1987]). Relative condition may not be the only factor influencing egg size. For example, water temperature may be important as a mechanism explaining the common pattern of decreasing egg size as the spawning season progresses – particularly in species that spawn between winter and summer (reviewed by Chambers 1997). For striped bass, my results suggest that temperature variation was not great enough, or does not have the same influence on production of striped bass oocytes.

My observation that residual oocyte volume did not exhibit significant changes over the duration of the spawning season contrasts with my results for residual fecundity. Although absolute oocyte size has been shown to decrease over the duration of the spawning season and spawning sequence (i.e., in the laboratory) in some batch spawners (e.g., Ware 1977, Daoulas and Economou 1986, Ouellet et al.

2001, Lowerre-Barbieri et al. 1996, Castro et al. 2009), this does not appear to be the case for total spawners such as striped bass. Oocyte size may be canalized as a result of the preferential resorption of smaller oocytes during down-regulation. Preferential resorption of smaller oocytes has been observed in sole (Witthames and Greer Walker 1995) and may occur due to less metabolic energy required to resorb smaller oocytes (Kurita et al. 2003). If this occurs in striped bass, it may select for larger vitellogenic oocytes in all size and condition phenotypes and may explain why RTW showed little to no influence on residual oocyte volume.

It has been suggested that condition must be quantified several months before spawning to detect a biologically meaningful and statistically defensible influence of female energetic condition on reproductive potential (Eliassen and Vahl 1982, Millner et al. 1991, Koops et al. 2004). My results for striped bass indicate this is not the case and I suggest two reasons. Indeed, in other capital spawners such as Atlantic cod, it has been shown that total female weight (interpreted to represent energy reserves by Skjæraasen and Nilsen 2006) several months before spawning explains most of the variation in fecundity. However, Skjæraasen and Nilsen (2006) also showed that total weight during the spawning season explained an equal amount of the variation in fecundity. Taken together, Skjæraasen and Nilsen (2006) results suggest that energy reserves at the time of vitellogenesis and during spawning were correlated. Furthermore, the relationships for cod observed by Skjæraasen and Nilsen (2006) occurred with feeding. Since striped bass do feed during the winter (Overton et al. 2008), the observations of Skjæraasen and Nilsen (2006) suggest that feeding may not preclude a correlation between the condition of females during spawning and

at the initiation of vitellogensis. Second, as shown in several studies (Kurita et al. 2003, Kennedy et al. 2007, Witthames et al. 2009), down-regulation of fecundity can occur and it appears to be related to energetic condition, either well before or close to the spawning period. My results indicate that down-regulation may be occurring in striped bass and this reduction in fecundity may be associated with energetic condition during the spawning season. Thus, condition measures evaluated during the spawning season may indeed have statistical and biological significance for fecundity. However, additional experimental research is needed to explore these alternatives in more detail.

Together, my results show that female relative total condition during the spawning season is biologically significant and influences reproductive potential through egg production (number and size) and spawning frequency. The significant influence of RTW suggests that the use of female residual total body weight during the spawning season does encompass the relative total energetic condition of the females and thus, serves as a good predictor of relative condition in striped bass. Although RTW did not directly influence the probability of spawning, it did appear to influence the frequency of skipped spawning through changes in the probability of spawning at size and age. By building upon this research and developing a better understanding of the factors causing or correlated with the total and/or age/size-specific frequency of skipped spawning in a given year, we can begin to understand important characteristics of the spawning stock. This will improve the current approach, which assumes that all sexually mature biomass spawns and contributes equally to the population's overall egg production. Drawing from my results that

provide a strong starting point, effectively refining the current SSB approach may require development of consistent relationships between female condition and the probability of spawning, fecundity and egg. It has yet to be determined whether female condition also influences offspring growth and survival in striped bass; however, I explore that possibility in Chapter 4. My research on the importance of energetic condition on reproduction may impart new knowledge that can help develop a better understanding of links between the spawning stock and recruits. The value of including striped bass female characteristics in stock-recruitment models has recently been demonstrated in a Ricker model that revealed the strong dependence of young-of-the-year recruitment on female age diversity (Houde 2008). Further refinements in these models may be possible by including metrics of female condition. By refining the links between spawners and recruits, improved stock-recruitment models will provide a more accurate understanding of the resiliency and sustainability of a stock.

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Table 3.1. Female measures of energetic condition and their respective acronyms. All residuals come from the relationship between female total length and the respective weight or total tissue energy measured.

Female condition variable	Acronym
residual total weight (kg)	RTW
residual gutted weight (kg)	RGW
residual total ovary energy (MJ)	ROE
residual total liver energy (MJ)	RLE
residual total visceral energy (MJ)	RVE

Table 3.2. General linear model results to evaluate if age (a), total length (b), gutted weight (c), residual total weight (d), residual gutted weight (e), residual ovary energy (f), residual liver energy (g), and residual visceral energy (h) vary by year, stage (i.e., reproductive stage) or calendar day of year (doy). Results for each model are shown in row format with *p*-value (italicized) shown below *F*-statistics. When interactions were significant in the analysis Type III SS were used and non-significant interactions were removed from the analysis (i.e., no results shown in table); otherwise, Type II SS were used and all interactions remained in the respective models.

	Year	Stage	Day of year (doy)	doy × Year	doy × Stage	Year × Stage
a.	3.7776	**18.9498**	2.7967	0.2993	0.7341	0.7209
	0.053	***< 0.0001***	*0.096*	*0.58*	*0.48*	*0.49*
b.	**7.6336**	**24.1042**	0.1422	0.098	0.3118	2.7165
	0.006	***< 0.0001***	*0.71*	*0.75*	*0.73*	*0.07*
c.	0.0266	**24.0889**	3.7354	0.573	0.2246	2.5844
	0.87	***< 0.0001***	*0.054*	*0.45*	*0.8*	*0.08*
d.	1.2308	0.1803	**45.6862**			**4.6152**
	0.27	*0.84*	***< 0.0001***			***0.01***
e.	**5.704**	0.9068	**31.0303**			**6.1323**
	0.02	*0.41*	***< 0.0001***			***0.003***
f.	0.9814	**32.868**	**7.3133**	0.7713	1.9962	2.2005
	0.32	***< 0.0001***	***0.007***	*0.38*	*0.14*	*0.11*
g.	**13.1721**	0.108	**71.4477**	**8.4173**		
	0.0004	*0.9*	***< 0.0001***	***0.004***		
h.	**11.0039**	0.8232	0.3187	0.0198	0.5363	0.3184
	0.001	*0.44*	*0.57*	*0.89*	*0.59*	*0.73*

Table 3.3. Generalized linear model (binomial error structure) results showing the influence of several condition indices, size and age on the probability of female striped bass spawning during 2009 and 2010 in the Chesapeake Bay. Likelihood ratio chi-square (LR χ^2) and degrees of freedom (df) are shown.

Factor	LR ^{2}	df	*p*
Total body weight residuals	1.5313	1	0.22
Year	0.5044	1	0.48
Total body weight residuals × Year	10.508	1	0.001
Gutted body weight residuals	0.0549	1	0.81
Year	1.0959	1	0.3
Gutted body weight residuals × Year	9.5848	1	0.002
Ovary energy residuals	46.748	1	< 0.0001
Year	0.131	1	0.72
Ovary energy residuals × Year	1.989	1	0.16
Liver energy residuals	3.2361	1	0.07
Year	0.8682	1	0.35
Liver energy residuals × Year	0.0902	1	0.76
Visceral energy residuals	1.8635	1	0.1722
Year	1.0378	1	0.308
Visceral energy residuals × Year	0.1079	1	0.74
Age	64.761	1	< 0.0001
Year	2.728	1	0.098
Age × Year	0.589	1	0.44
Total length	53.058	1	< 0.0001
Year	4.473	1	0.03
Total length × Year	0.129	1	0.72
Gutted weight	42.923	1	< 0.0001
Year	0.317	1	0.57
Gutted weight × Year	0.141	1	0.7

Table 3.4. General linear model results for evaluating whether residual fecundity varies between 2009 and 2010 (year), between reproductive stage 3 and 4 (stage) and by calendar day of year (doy).

Source	df	*F*	*p*
Day of year (doy)	1	8.3602	0.004
Year	2	10.8372	0.001
Stage	1	9.2465	0.003
doy × Year	2	0.0037	0.95
doy × Stage	1	2.0921	0.15
Year × Stage	2	1.6614	0.2
Residual	143		

Table 3.5. Linear model results for the effect of seven separate relative condition indices on striped bass residual fecundity. Each separate model is shown in row format, with the relative condition main effect designating the row for each separate model. Significant effects are shown in bold and all *p*-values are italicized.

Condition Main Effects			Covariate, Main Effects & Interactions							
			Year	Stage	Day of year (doy)	Main effect ! Year	Main effect ! Stage	doy ! Year	doy ! Stage	Year ! Stage
Residual total weight	*F*	**23.825**	0.2694	**7.5077**	0.5075	0.5295	0.1344	0.3621	1.1135	1.1089
	p	***< 0.0001***	*0.6*	***0.007***	*0.48*	*0.47*	*0.71*	*0.55*	*0.29*	*0.29*
Residual gutted weight	*F*	**8.3802**	0.4435	**10.2213**	2.8822	2.057	0.0603	0.2579	1.3079	1.1226
	p	***0.004***	*0.51*	***0.002***	*0.09*	*0.15*	*0.81*	*0.61*	*0.25*	*0.29*
Residual ovary energy	*F*	**32.5095**	**8.9596**	1.7489	3.6203	0.2773	0.0294	0.2951	0.7671	0.7334
	p	***< 0.0001***	***0.003***	*0.19*	*0.059*	*0.6*	*0.86*	*0.59*	*0.38*	*0.39*
Residual liver energy	*F*	1.9026	**13.698**	**8.2218**	2.4592	0.762	0.0061	0.1688	1.2478	1.2649
	p	*0.17*	***0.0003***	***0.005***	*0.12*	*0.38*	*0.94*	*0.68*	*0.27*	*0.26*
Residual visceral energy	*F*	**4.9062**	**6.3541**	**6.5223**	**5.2521**	0.7831	0.1009	0.0658	0.5583	1.7275
	p	***0.028***	***0.013***	***0.012***	***0.02***	*0.38*	*0.75*	*0.8*	*0.46*	*0.19*

Table 3.6. General linear model results for evaluating whether residual oocyte volume varies between 2009 and 2010 (year), between reproductive stage 3 and 4 (stage) and by calendar day of year (doy).

Source	df	*F*	*p*
Day of year (doy)	1	0.5144	0.47
Year	1	0.7406	0.39
Stage	1	20.1501	< 0.0001
doy ! Year	1	0.0125	0.91
doy ! Stage	1	0.1932	0.66
Year ! Stage	1	0.2698	0.6
Residual	142		

Table 3.7. Linear model results for the effect of seven separate relative condition indices on striped bass on residual oocyte volume. Each separate model is shown in row format, with the condition/feeding history main effect designating the row for each separate model. Significant effects are shown in bold and all *p*-values are italicized.

Condition Main Effects			Covariate, Main Effects & Interactions							
			Year	Stage	Day of year (doy)	Main effect ! Year	Main effect ! Stage	doy ! Year	doy ! Stage	Year ! Stage
Residual total weight	*F*	**8.3103**	3.0181	**20.7644**	0.2525	0.3061	0.0055	0.6142	0.0327	0.5197
	p	***0.0045***	*0.052*	***< 0.0001***	*0.62*	*0.74*	*0.94*	*0.54*	*0.86*	*0.6*
Residual gutted weight	*F*	0.0131	1.6075	**23.9305**	0.4596	1.7268	0.5016	0.8239	0.001	0.4093
	p	*0.91*	*0.2038*	***< 0.0001***	*0.49*	*0.18*	*0.48*	*0.44*	*0.97*	*0.66*
Residual ovary energy	*F*	**275.0884**	5.4256	0.2935	0.1591	1.2361	0.7056	1.1262	0.0038	1.0889
	p	***< 0.0001***	*0.02*	*0.59*	*0.69*	*0.27*	*0.4*	*0.29*	*0.95*	*0.3*
Residual liver energy	*F*	3.6231	0.2647	**5.2724**	0.722	0.2841	**6.7942**	0.2197	3.0149	0.1169
	p	*0.06*	*0.61*	***0.02***	*0.4*	*0.59*	***0.01***	*0.64*	*0.08*	*0.73*
Residual visceral energy	*F*	**42.091**	**4.1474**	**22.6861**	0.0801	1.5086	0.1156	0.7972	0.0848	0.0014
	p	***< 0.0001***	***0.04***	***< 0.0001***	*0.78*	*0.22*	*0.73*	*0.37*	*0.77*	*0.97*

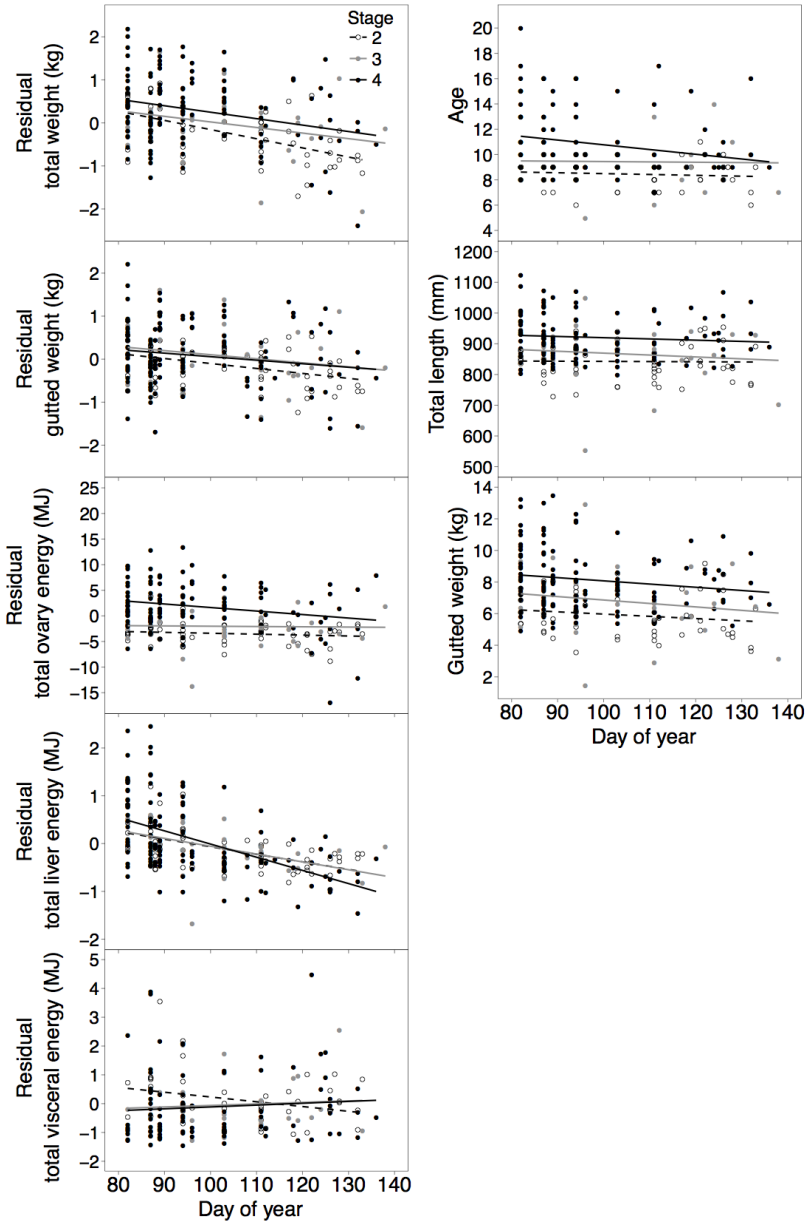

Figure 3.1. Indices of female striped bass relative condition (left-side panels), and size and age (right-side panels) as a function of calendar day of year (doy) during the spawning seasons of 2009 and 2010 in the Chesapeake Bay for females of different reproductive stage. Lines represent the main effect of reproductive stage in the general linear models used to determine how condition, size and age vary among reproductive stage, year and doy. Tissue-specific indices are reported in megajoules (MJ).

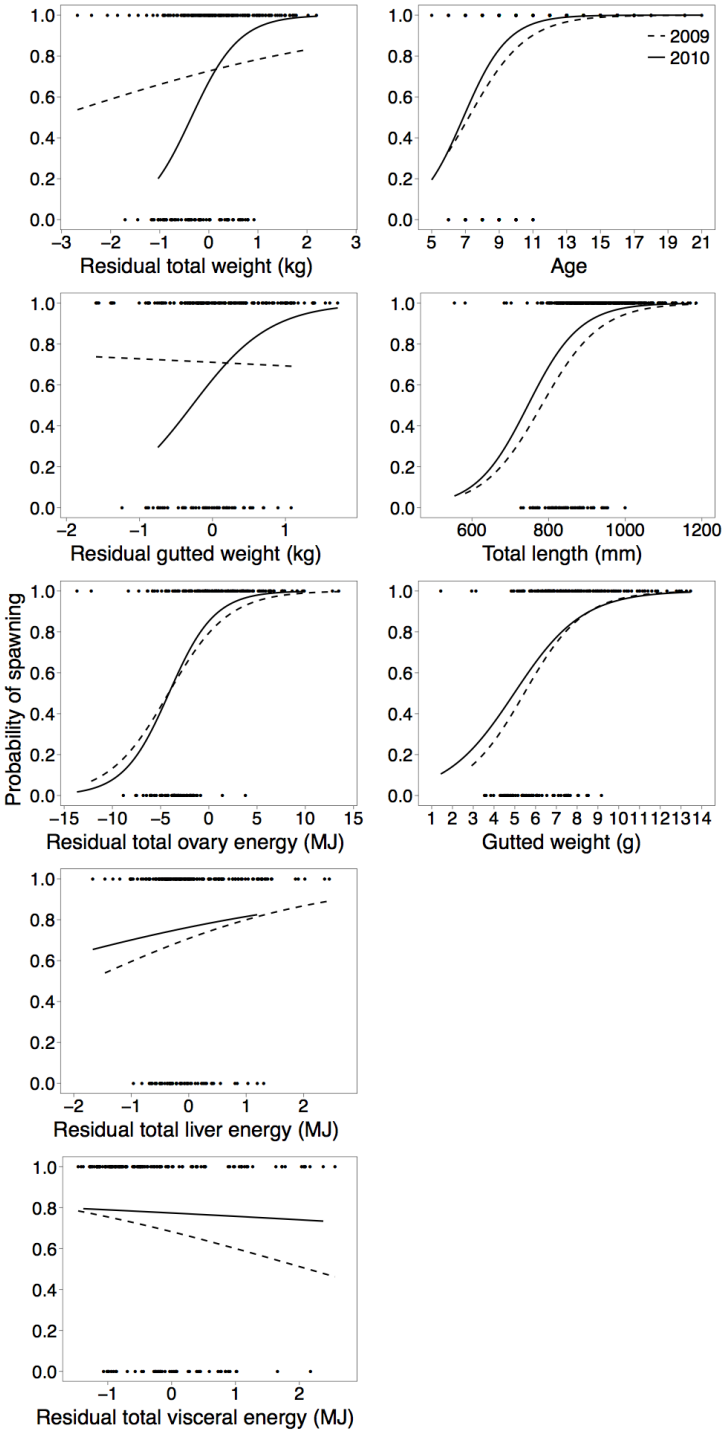

Figure 3.2. Probability of spawning as a function of female striped bass relative condition indices (left-side panels) and size and age (right-side panels) during 2009 and 2010 in the Chesapeake Bay. Tissue-specific indices are reported in megajoules (MJ).

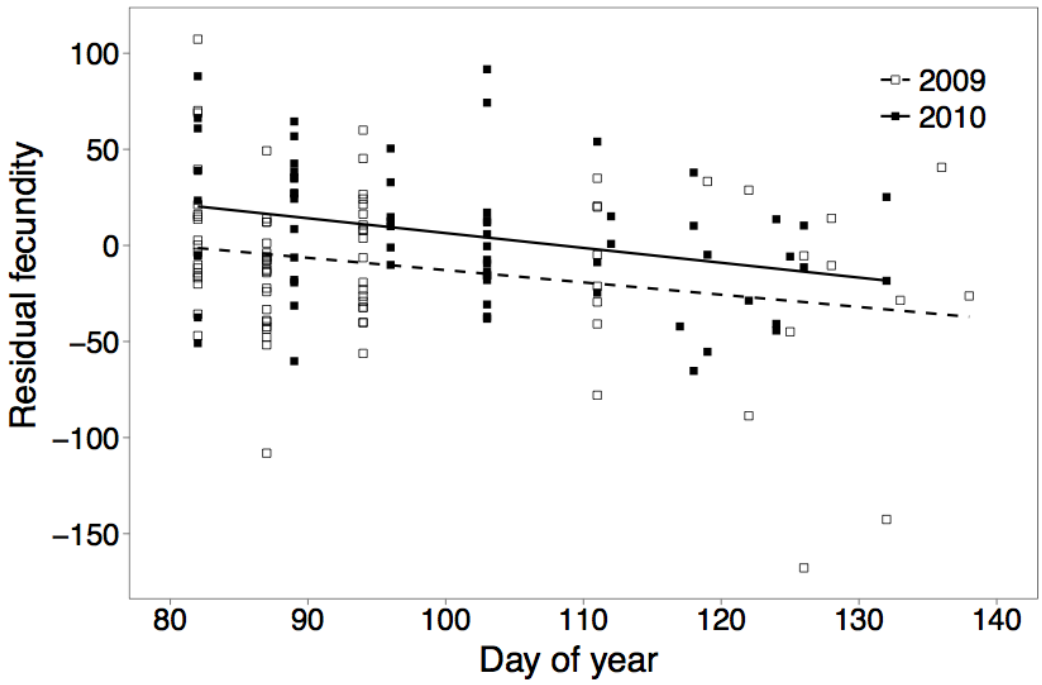

Figure 3.3. Residual fecundity as a function of calendar day of year (doy) for female striped bass collected in the mainstem of the Chesapeake Bay during 2009 and 2010. Lines show the main effect of year in the general linear model used to determine whether residual fecundity varies by reproductive stage, year or doy.

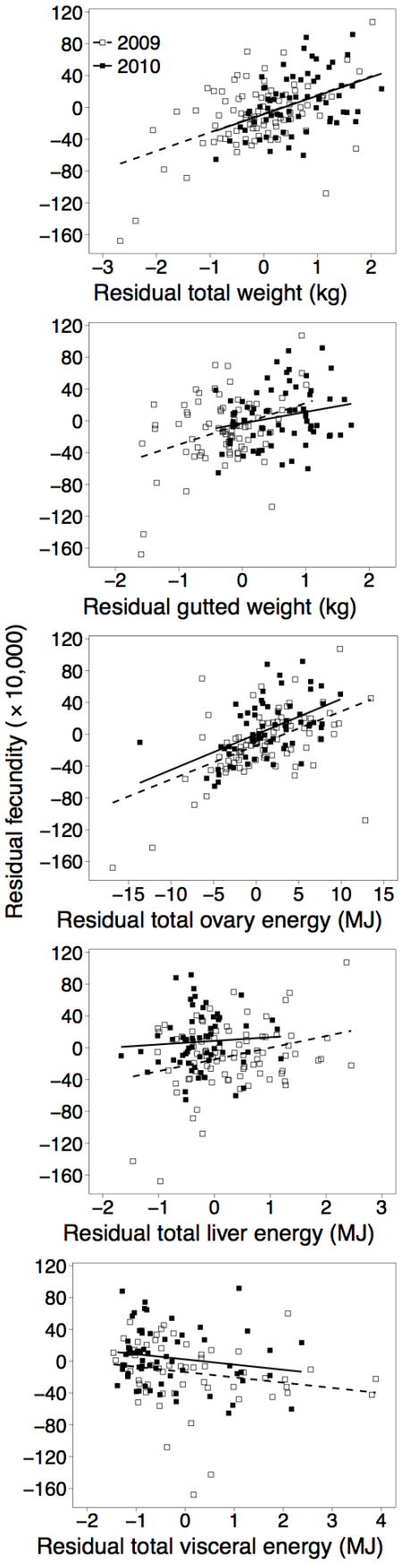

Figure 3.4. Residual fecundity as a function of several condition indices for female striped bass collected in the Chesapeake Bay in 2009 and 2010. Lines show the main effect of year in the general linear models used to determine how condition influences residual fecundity. Tissue-specific indices are reported in megajoules (MJ).

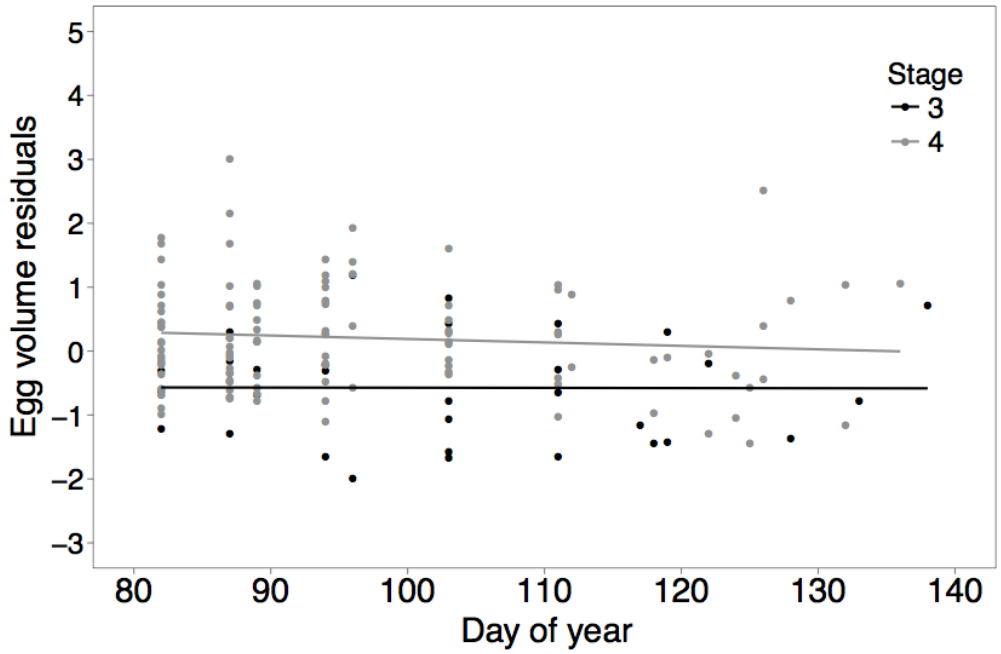

Figure 3.5. Residual oocyte volume as a function of calendar day of year (doy) for female striped bass collected in the mainstem of the Chesapeake Bay during 2009 and 2010. Lines show the main effect of reproductive stage in the general linear model used to determine whether residual oocyte volume varies by reproductive stage, year or doy.

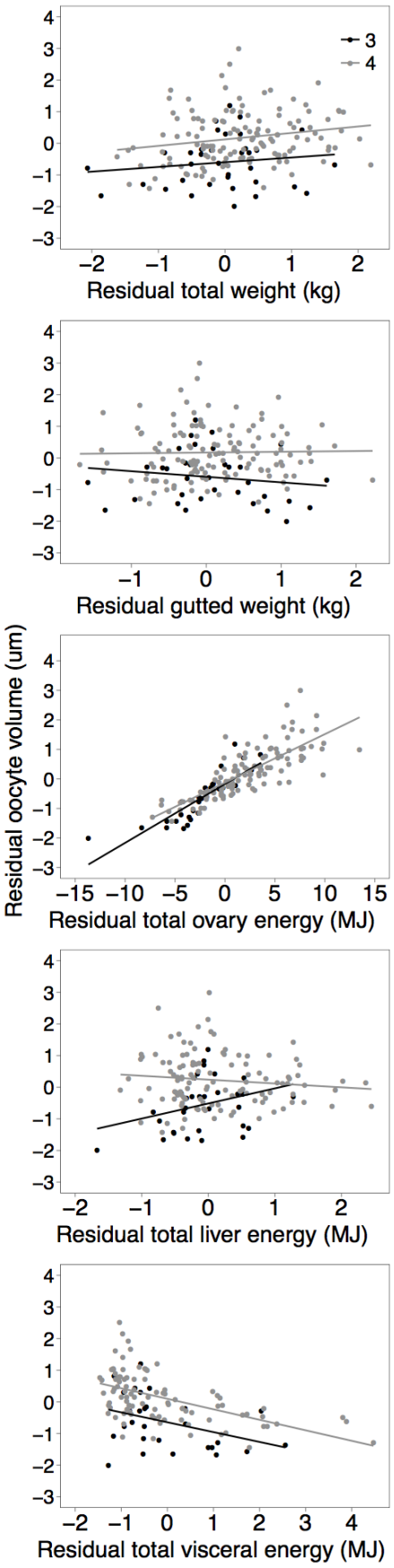

Figure 3.6. Residual oocyte volume as a function of several condition indices for female striped bass collected in the Chesapeake Bay in 2009 and 2010. Lines show the main effect of year in the general linear models used to determine how condition influences residual fecundity. Tissue-specific indices are reported in megajoules (MJ).

CHAPTER 4:

THE ROLE OF MATERNAL SIZE AND ENERGETIC CONDITION ON PROGENY SIZE, GROWTH AND SURVIVAL IN TWO POPULATIONS OF ATLANTIC COAST STRIPED BASS (*MORONE SAXATILIS*)

Abstract

Evidence suggests that early-life survival in teleosts is not completely random, but depends on the characteristics of individual larvae. Larval characteristics result from parentally-derived traits and genetics that may be modified by environmental processes, but together influence larval size, growth and survival. Regarding parental contributions, maternal influences have received the greatest attention due to nutritional provisioning of the embryo. In Chesapeake Bay striped bass (*Morone saxatilis*), maternal size does influence egg size, larval size and larval growth. However, it is unknown whether other maternal characteristics may be more important, and whether maternal influences vary between distinct striped bass populations. Here, I tested the hypothesis that relative gutted weight (RTW; a measure of energetic condition) has a positive effect on offspring size, growth and survival, either alone or in combination with other female variables. Because maternal influences can vary between populations adapted to different environments, I also tested whether maternal influences were equal in two striped bass populations. Females collected from the Chesapeake Bay (CB) and Roanoke River, NC (RR) were spawned in hatcheries and offspring were included in a randomized complete block experiment to test my hypotheses. Results indicated that RTW had no influence on egg or larval phenotype in either CB or RR populations. In fact, no single index of energetic condition had a strong influence on larval phenotype in either population.

Instead, maternal post-spawn gutted weight (post-GW) alone had the greatest influence on egg and larval phenotype in striped bass, although to a lesser and potentially insignificant degree in RR compared to the CB population. Dynamic patterns in the maternal size effect on larval survival also were observed in the CB population, providing new insight into the potential role of both maternal phenotype and the unique composition and size of the oil globule in striped bass eggs. Furthermore, my test of population differences in maternal influences indicated that the relationship between post-GW and egg and larval size characteristics differed between populations and suggested that maternal influences on egg and larval size may not be evident in the RR population. My results indicate that there is still much to be understood about maternal influences in striped bass, particularly with regard to their influence on growth and survival. Distinct maternal influences in the CB and RR population also bring attention to the possible adaptive significance of maternal influences in the context of habitat variability. Together, my results provide further support for preserving female size, age and genetic diversity as management strategies to promote potential growth and survival advantages their larvae may have under different environmental conditions.

Introduction

High rates of mortality during the larval stage of marine fishes typically result in the survival to recruitment of less than 1% from each cohort (Houde 2008). Individuals that survive early-life stages are rare exceptions (Crowder et al. 1997). Furthermore, evidence suggests that mortality is not completely random, but depends

on the characteristics of individual larvae (Rosenberg and Haugen 1982, Methot 1983, Rice et al. 1987, Pepin 1991, reviewed by Houde 2009). From the moment of conception, individuals vary in development and growth rates that will predispose some individuals to a higher probability of surviving to later developmental stages (McCormick and Hoey 2004). These characteristics of early larvae are a result of parentally-derived traits that may be modified by environmental processes (McCormick 2003, Chambers and Leggett 1996), but that together set the stage for larval and juvenile growth and survival.

With the exception of catastrophic environmental events, factors affecting survival of larval and juvenile fishes are believed to be related by what Cushing (1975) called the "single process." Under this process, as the length of time that larvae spend in a stage vulnerable to high mortality increases, the time over which mortality operates also increases, thereby increasing cumulative mortality (Dahlberg 1979, McGurk 1986, Houde 1987). Moreover, it is clear that small changes in growth and mortality rates of larvae can generate order-of-magnitude or greater differences in annual recruitments (Shepherd and Cushing 1980, Davis et al. 1991, Houde 2002).

Growth and survival of early life stages are strongly influenced by abiotic factors such as temperature, salinity, oxygen or wind forcing (Peterman and Bradford 1987, Blaxter 1991, Sponaugle and Pinkard 2004). Temperature plays a central role due to its importance in controlling physiological processes (Blaxter 1991, Fuiman 2002), and is the environmental variable most frequently linked to the recruitment variability of temperate marine fishes (Sissenwine 1984). Beginning at the egg stage, low temperatures can extend the hatch period and early hatching fish larvae exposed

to lower temperatures may be smaller than late hatching counterparts (Methven and Brown 1991). During the larval stage, numerous studies have shown a relation between temperature and growth, indicating slower growth at low temperatures (e.g., Uphoff 1989, Rutherford and Houde 1995, Betsill and Van den Avyle 1997). Due to the effects of temperature on growth and development rates of eggs and larvae, it is clear that the length of time that eggs and larvae remain at vulnerable stages can be influenced by temperature.

As soon as endogenous reserves have been consumed and morphological changes, such as development of a functional visual system and jaw musculature allow successful foraging, prey availability becomes essential for larval growth and survival. However, poor nutritional condition of larvae not only contributes to an increase in mortality rates through starvation, but can lead to an increase in predation mortality rates through diminished escape responses or increased duration of the larval stage due to reduced growth (Houde 1977, Buckley 1984, Rice et al. 1987, 1993). Thus, cohorts exhibiting poor synchrony between hatching and food resources may exhibit increased vulnerability to starvation or predation mortality. Despite these observations, in natural populations, environmental factors such as temperature and prey availability may explain less than 40% of variation in larval growth (Wilson and Meekan 2002, Caldarone et al. 2003), and may have effects of a similar magnitude on mortality – suggesting that other processes, such as parental effects, must account for a substantial amount of variability in vital rates during early life.

The idea that parents might influence offspring size, growth, or viability is not new, and has been explored in a wide range of taxa (Falconer 1965, Roach and Wulff

1987, Bernardo 1996). Maternal contributions are generally considered more important than paternal contributions, because females provide nutritional provisioning to the embryo (Bernardo 1996). In fact, the effects of a female on her offspring's phenotype, which may be genetic or phenotypic (i.e., no separation of genetic and non-genetic effects), are evident across a wide range of marine and freshwater fishes. These effects are known as maternal influences and are in contrast to the less frequently examined maternal effects, which are the exclusive effects of a mother's phenotype (i.e., excluding offspring genotype) on her offspring's phenotype (Green 2008). Positive correlations between egg size and maternal age or length exist for a diverse array of marine and freshwater fishes (Hempel and Blaxter 1967, Chambers et al. 1989, Chambers and Waiwood 1996, Johnston 1997, Heyer et al. 2001). Additionally, maternal influences have been demonstrated on egg and larval viability, larval size and growth in many freshwater (i.e., Heyer et al. 2001) and marine fish species (i.e., Marteinsdottir and Steinarsson 1998, Trippel 1998, Secor and Houde 1995Berkeley et al. 2004). Maternal size and age have been the focus of most of these studies, but there may be effects of maternal energetic condition on progeny size, growth, or survival.

From fertilization of the egg to the onset of feeding, larvae are dependent on the energy reserves within the yolk and oil (Love 1980). These yolk and oil reserves are derived directly from reserves the female mobilizes during maturation and oogenesis (Mommsen and Korsgaard 2008). Thus, maternal history can significantly influence the size and provisioning of larvae through both nutritive products and developmental and metabolic hormones that are sequestered into the egg during

gametogenesis (Ojanguren et al. 1996, Kerrigan 1997, McCormick 1998, 1999). Feeding conditions experienced by females prior to and during spawning can modify energetic investment in ovaries, the level of yolk and oil reserves in eggs, as well as somatic development in larvae at hatching (Kerrigan 1997, McCormick 2003, Bunnell et al. 2007). Furthermore, females in better energetic condition can produce offspring with larger energy reserves (e.g. Kerrigan 1997, McCormick 2003, Gagliano and McCormick 2007) and enhanced embryonic and larval survival (Gagliano and McCormick 2007). Thus, maternal effects on offspring may be significantly modulated by conditions experienced by females before reproduction (Chambers and Leggett 1996). Consequently, energy-driven mechanisms may partially determine offspring viability, particularly in stressful maternal environments (i.e. low food levels and high population density) (Gagliano and McCormick 2007).

Although there is little doubt that an offspring's phenotype integrates information derived from maternal influences, offspring themselves are also directly affected by local environmental conditions, which can shift the optimal value of a trait or combination of traits (Einum and Fleming 2000, Benoit and Pepin 1999, Gagliano et al. 2007). In young fishes, environmental effects have the potential to modulate maternal effects, causing variation in growth and performance traits not predicted under optimal conditions (Chambers and Leggett 1996, Heath and Blouw 1998). Evidence shows that variation in the environmental or biotic conditions (e.g. temperature and food availability) experienced by progeny leads to alterations in maternal contributions that may not always be additive, and can be more pronounced under non-ideal conditions for progeny (Hutchings 1991, Benoit and Pepin 1999,

Einum and Fleming 2000). Thus, the strength of maternally-derived differences in size, growth, and subsequent survival of progeny will be highly dependent on the environment encountered, and likely most prominent under non-ideal conditions (Hutchings 1991, Blom et al. 1994, Einum and Fleming 2000).

For striped bass (*Morone saxatilis*), environmental factors are believed to be the primary determinants of growth and survival of early-life stages (Rutherford and Houde 1995, Secor and Houde 1995, Martino 2008). Selection appears to favor individuals maintained in low salinity waters up- estuary of the salt front (Secor et al. 1995) and within the estuarine turbidity maximum (ETM) (North and Houde 2001, North and Houde 2006), where prey are abundant and turbidity may protect them from predation. However, maternal size does influence egg viability and larval growth in the laboratory (Zastrow et al. 1989, Monteleone and Houde 1990) and may contribute to recruitment variability (Cowan et al. 1993). Less understood is the importance of striped bass maternal energetic condition on offspring size, growth and survival. In Chapter 3 I showed that relative total energetic condition of female striped bass had a positive effect on relative fecundity. I also showed that when the spawning population was in better energetic condition, females spawned at a smaller size and younger age. Thus, the energetic condition of individual females and the population can influence the initial number of gametes spawned in a given year. As shown in other species, however, the influence of energetic condition may not be limited to the number of gametes produced, but may extend to egg quality and larval vital rates. For striped bass, the effects of energetic condition beyond the unfertilized gamete have yet to be determined.

Here I explore the role of maternal energetic condition on post-fertilized offspring by testing the hypothesis that pre-spawn relative total condition (i.e., a measure of total weight relative to length, *sensu* Chapter 3) has a positive effect on offspring size, growth and survival either alone or in combination with other female variables. Also, I evaluated whether the relative total condition of a female had a greater influence on offspring than tissue-specific measures of relative condition – specifically liver and muscle indices. In addition, because maternal influences may be more evident under sub-optimal conditions, I tested the hypothesis under both high and low food availability to larvae in an attempt to provide a range of opportunities to induce a maternal condition response. Because maternal energy allocated for reproduction must pass through eggs to influence larval phenotype, I also explored the role of egg size and energetics on larval phenotype. No specific hypotheses were tested with regard to egg influences on larval phenotype. Rather, the goal was to provide context for the observed maternal influences on larval phenotype. Finally, because maternal influences can vary between populations of the same species (Marteinsdottir and Able 1988), I also tested the null hypothesis that the maternal influences on offspring phenotype were equal in two genetically distinct populations – specifically, the Chesapeake Bay and Roanoke River populations. Mixed stock analyses indicated morphometric and genetic differences between the Chesapeake Bay and Roanoke River populations (Wirgin et al. 1997, Waldman et al. 1997) and genetic studies using randomly amplified polymorphic DNA (RAPD) analysis, suggest that the Chesapeake Bay and Roanoke River populations are genetically subdivided, with limited gene flow (Bielawski and Pumo 1997). Behaviorally, these

populations also exhibit distinct spawning and feeding migrations. A large proportion of mature females (50-75%) from the Chesapeake Bay initiate a coastal feeding migration along the Atlantic coast around the timing of maturation (ages 5-8) (Secor and Piccoli 2007), whereas a much smaller proportion of adults from Roanoke River display oceanic migration (Haeseker et al. 1996) and thus feed mostly within Albemarle Sound during summer and fall. Because food-webs, water temperature and other environmental factors differ between the Atlantic coast and Albemarle Sound, females from different populations could have different lipid profiles and thus energetic condition. Thus, if maternal energetic condition does have an influence on offspring size, growth and survival, the effects could vary between the Chesapeake Bay and Roanoke River populations.

Methods

Adult females

Mature females were collected via electrofishing in Spring 2008 from the Chesapeake Bay (CB) and the lower Roanoke River (RR), North Carolina. Chesapeake Bay females were collected on the spawning grounds in the Patuxent and the Nanticoke Rivers, Maryland and from the Mattaponi River, Virginia. Roanoke River females were collected on the spawning grounds below Roanoke Rapids Lake dam. Females estimated to be within 12 hours of natural spawning during field examination were brought back to one of three hatcheries (Manning Fish Hatchery, Maryland Department of Natural Resources [Patuxent River and Nanticoke River], King and Queen Hatchery, Virginia Department of Game and Inland Fisheries

[Mattaponi River], Watha State Fish Hatchery, North Carolina Wildlife Resources Commission [Roanoke River]), weighed (i.e., pre-spawn total weight, [pre-TW], kg), measured (total length [TL], mm), injected with human chorionic gonadotropin and allowed to spawn in large tanks in the presence of 3-4 males, randomly assigned to each spawning tank. Progeny from 18 females (n=9 Chesapeake Bay [n= 4 Mattaponi R., n=3 Nanticoke R., n=2 Paxtuxent R.], n = 8 Roanoke River) were selected for the experiment. These females and their eggs represented an unbiased sample when included with a larger sample of females and eggs not included in this experiment (Figure 4.1). After spawning, a sub-sample of fertilized eggs was removed at 4 hours post-fertilization (hpf) and preserved in 4% formalin for analysis of egg characteristics (see below). Live, fertilized eggs (12-36 hpf) were then transported in insulated coolers from each hatchery to the Chesapeake Biological Laboratory (CBL) and placed in 60-liter, flow-through tanks maintained at 19°C and salinity 1. Photoperiod was set at 13:11 L:D to approximate the ambient spring photoperiod. Embryos and hatched larvae were allowed to acclimate at 19°C and salinity 1 until 4 days post hatch (dph).

Female characteristics

After spawning, females were removed from each tank, weighed (i.e., post-spawn total weight [post-TW], kg), measured (TL), euthanized with 500 $mg \cdot L^{-1}$ of tricaine methanesulfonate (MS-222), and immediately placed on ice or frozen prior to transport to CBL. Once at CBL, each fish was thawed to allow removal of all internal organs. The gutted body of each female was then weighed to determine the gutted

weight (i.e., post-spawn gutted weight [post-GW], kg). The whole liver and sagittal otoliths were removed and kept for indices of energetic condition and aging, respectively.

To test the hypothesis that relative total condition positively influences reproductive potential, residual total weight (RTW), an index of relative total condition, was estimated as the residual from the nonlinear relationship between female TL and total body weight. Because only 17 females were used in my experiment, the model used to produce residuals included the females in my experiment, as well as those females collected for Chapter 2. As discussed in Chapter 3, RTW was believed to be the best index of pre-spawn relative total energy given that the relative total weight of a female should provide an index of the relative total energy available for reproduction. Alternative measures of energetic condition were also included in this study to determine if other condition indices were more important than RTW. These alternatives included a measure of post-spawn RTW (PRTW), which was identical to RTW, except that total pre-spawn weight was replaced by total post-spawn weight. Estimation of PRTW also included the post-spawn females used in Chapter 2. In addition, tissue-specific measures of condition were included as alternatives to RTW. These tissue-specific measures included the hepatosomatic index (HSI):

$$HSI = [W_L/(W_S - W_L)] \cdot 100$$

where, W_L is total liver wet weight (g) in the post-spawn female. Energetic measures of liver condition were also determined using the same tissue drying and bomb calorimetry methods described in Chapter 3. Using bomb calorimetry, the total liver

energy (TLE, kJ) for each female was determined by multiplying the energy per gram of dry liver (kJ g^{-1}) by the liver dry weight (g). The relative liver energy (RLE, kJ g^{-1} female weight) was then determined by dividing TLE by the female gutted-weight. TLE and RLE were then used as alternative measures of energetic condition in subsequent analyses.

Egg characteristics

To assess whether maternal RTW or other maternal phenotypes influenced egg phenotype in the CB and RR female lines, several egg characteristics were measured. Egg, yolk and oil volumes were calculated from diameter measurements taken on 30, 4-hpf eggs from each female using the Optimas imaging system (Media Cybernetics, Bethesda, MD). Egg diameters were calculated from three digitized points on the circumference of each egg using the formula below adapted from Miller et al. (1995):

$$Diameter = \frac{abc}{2\sqrt{s(s-a)(s-b)(s-c)}}$$

$$s = \frac{a+b+c}{2}$$

where *a*, *b*, and *c* are the lengths (mm) of the chords connecting the three points. Egg volume (i.e., including perivitelline space, mm^3) was then calculated using the formula for a sphere ($4/3\pi \times radius^3$). Oil volume (mm^3) in the egg was estimated based on two measurements (polar and equatorial lengths [mm]) using the formula for volume of an oblate spheroid ($1/6\pi \times length^2 \times height$), which closely approximates

the shape of the oil droplet. Determination of yolk volume in the egg requires two steps. First, the volume for the whole yolk oil complex was calculated based on the formula for volume of a prolate spheroid ($4/3\pi \times \text{length} \times \text{height}^2$), because the shape approximates an elongated sphere. Then the volume of the oil globule was subtracted from the volume of the yolk and oil complex to obtain the yolk volume.

To calculate egg dry weight, a random sample of frozen preserved eggs was rinsed in deionized, distilled water and dried overnight at 40°C in a drying oven. Dried eggs were removed from the oven and placed in a desiccator while they cooled to room temperature. Eggs were weighed in four groups of ten eggs each (40 eggs per female) to ± 1 μg on a micro-balance (Sartorius ME 36S, Elk Grove, IL).

To determine the energy density (kJ) of spawned eggs, three replicates of 30, 4-hpf eggs per female were dried overnight at 40°C. Two pellets (~ 0.04 g) per replicate were formed and ignited in the calorimeter described above using a Parr 1109 semi-micro oxygen bomb (Parr Instruments, Moline, IL).

The lipid and protein content of eggs were determined by proximate analysis using 20 eggs from each female that were dried to a constant weight in a freeze dryer (Labconco FreeZone 2.5, Kansas City, MO). CHN analysis was conducted using an elemental analyzer (CE440 Exeter Analytical, Chelmsford, MA) to provide estimates of the total mass of nitrogen (N, mg) per egg for each female. The total mass of protein per egg (mg) was then estimated by multiplying N × 6.25. The total mass of lipid per egg was estimated as: mean egg dry weight - protein – ash

where protein is protein per egg (mg) and ash is the mass of ash per egg (mg) determined by combusting 3.0 mg dry weight of eggs in a muffle furnace at 500°C for 6 hours. Calculations assumed carbohydrate weights were negligible.

Larval growth and survival

To test the hypothesis that maternal RTW influenced larval size, growth, survival and oil resorption in the CB and RR female lines, a randomized complete block experiment was conducted with 9 CB and 8 RR female lines. The design also included two feeding treatments (high and low), with three replicates per treatment. Some studies have indicated that maternal influences may be more evident under sub-optimal offspring conditions, thus a low feeding treatment was included to represent sub-optimal conditions and to maximize the potential for inducing maternal influences in this experiment. For each female line, 4 dph larvae were randomly placed into six, 8-L black tanks, with 320 larvae per tank. Three of the six tanks were randomly designated as high ration tanks, and the remaining three were low ration tanks. One high and one low ration tank from each population was then randomly placed into one of 3 water baths (blocks), such that each maternal line was represented in each bath twice: one high ration tank and one low ration tank. Each water bath was maintained at 19°C and each 8 L tank was maintained at 19°C and salinity 1 via a flow through system. Photoperiod was 13 L:11 D. The experiment terminated at 27 dph.

Feeding began at 5 dph. Live nauplii of San Francisco strain *Artemia franciscana* were cultured daily and used as live food. Larvae in the high and low

ration tanks initially were provided with prey concentrations of 520 *Artemia* · L^{-1} and 80 *Artemia* · L^{-1}, respectively, which provides a range of high and low prey concentrations within the range of zooplankton concentrations (< 50 to > 1000 L^{-1}) observed in tidal freshwater of the Chesapeake Bay during spring months (Heinle and Flemer 1975, Lippson et al. 1979). This feeding ration was equivalent to 13 *Artemia* · $larva^{-1}$ and 2 *Artemia* · $larva^{-1}$, respectively, twice per day. To account for increased consumption, feedings increased to 4 and 6 times per day at 15 and 24-dph, respectively.

Ten larvae were removed from each tank at 4, 7, 12, 17, 22, and 27 dph and fixed in 4% formalin. Larvae were removed before the first feeding each day to eliminate effects of food weight on larval weight. Each larva was measured for total length (TL) and standard length (SL) using the Optimas imaging system. Larvae were then rinsed in distilled water to remove formalin and any residual solutes and dried to a constant weight at 65°C. The mean length and weight of larvae for each tank and day combination were then determined and used to estimate growth in length and weight over consecutive sampling periods using an exponential model:

$$G = \frac{\ln S_2 - \ln S_1}{t_2 - t_1}$$

where G is the instantaneous growth rate (d^{-1}) in mm or μg, S is either mean length (mm) or weight (μg) and t is time (dph). G was estimated because growth in length and weight was exponential over the duration of the experiment and G provided a better fit to the actual size increase over an exponential growing period. Furthermore, this allowed growth to be included in the repeated measures analysis described below.

To estimate survival, dead larvae were counted and removed from each tank every two days beginning at 6 dph. The survival rate expected if no larvae had been preserved was determined for each day dead larvae were removed using the following set of equations adapted from Monteleone and Houde 1990):

$$z = m + r - mr \quad \text{or} \quad m = \frac{z - r}{1 - r}$$

where z is the total observed mortality (%), r is the mortality (%) due to removals, and m is the estimated natural mortality (%). Additionally, the instantaneous daily mortality rate also was determined, by first estimating the expected percentage survivorship at time t (N_t) as $1 - m$. The instantaneous daily mortality rate was then calculated as:

$$Z = \frac{\ln N_t - \ln N_0}{t}$$

where Z is the instantaneous daily mortality rate, N_0 is 100 (%), N_t is the expected survival (%) and t is the experimental interval of interest.

Larval oil resorption estimates

In addition to larval size, growth, and survival, larval oil volume and oil volume resorbed were also calculated. Larval oil volume was measured for all larvae sampled for larval size and growth estimates. Larval oil volume was determined using the same methods described for eggs. Oil volume was calculated at each age that larvae were sampled; however, oil volume also was estimated on days corresponding to mortality estimates from the exponential model:

$$V_t = ae^{-b \cdot t}$$

where V_t is the estimated oil volume at each larval age (t). Oil volume resorbed at each age was calculated as the volume of oil at 4 days post fertilization minus the oil volume present at each age.

Statistical analyses

Female, egg and larval characteristics

Prior to testing the key hypotheses, the characteristics of the females, eggs and 4-dph larvae were evaluated and compared between the CB and RR populations. These analyses provided appropriate perspective for interpreting maternal influences. This first analysis involved characterizing each female population based on the maternal phenotypes measured. T-tests were conducted on each maternal variable to determine if maternal phenotype was different between the two populations. Because variances were not equal between populations for most maternal variables, unequal variances t-tests were conducted (Ruxton 2006). If maternal variables also exhibited non-normality those variables were ranked prior to conducting the unequal variances t-test. Next, egg phenotype was characterized for each population. To determine if egg phenotype varied between the populations, separate analyses of covariance (ANCOVA) were conducted with the egg variable included as the dependent variable and female weight included as a covariate. To facilitate interpretation of coefficients in the ANCOVA, female weight was centered. Centering enabled population effects to be interpreted as the estimated average difference in egg characteristics between populations at an average female weight (i.e., 9,952 g.).

Maternal and egg influences on early life

To initially explore the hypothesis that maternal RTW would have a positive influence on offspring phenotype, Pearson correlations were conducted for each population to determine the relationships between maternal RTW and all egg variables. In addition, the correlations between all other maternal variables and all egg variables were evaluated to determine if other maternal phenotypes had similar or greater maternal influences. Correlations were also conducted between all maternal variables and larval standard length, dry weight and oil globule size at 4-dph.

Following the correlation analyses, separate general linear models were conducted to test the hypothesis that maternal RTW would have a positive influence on larval TL, weight, instantaneous growth in length and weight, oil globule resorbed, oil globule volume and percent mortality in both the CB and RR populations. In each model the full temporal range of larval measurements estimated over the entire 27-day experiment was included. To find the optimal model for each larval dependent variable, I used the top-down strategy as recommended by Verbeke and Molenberghs (2009) and Diggle (2002). The full statistical model can be written as:

$$\left.\begin{aligned} larval_{tij} = \beta_0 &+ \beta_1 \times age_t + \beta_2 \times maternal_{ij} + \beta_3 \times ration_j \\ &+ \beta_4 \times age_t \times maternal_{ij} + \beta_5 \times age_t \times ration_j \\ &+ \beta_6 \times maternal_{ij} \times ration_j \end{aligned}\right\} \quad \text{Fixed}$$

$$+ u_{0j} + u_{1j} \times age_t + u_{0i|j} + \varepsilon_{tij} \quad \} \quad \text{Random}$$

where $larval_{tij}$ represents an individual larval variable quantified at larval age *t* for ration *i* nested within female *j*. The parameters β_0 through β_6 represent the fixed effects coefficients associated with the intercept, larval age (*age*), the female identity

level and ration-level covariates, and their two-way interactions. Although all female variables were initially included in the full model, I only show one maternal variable (i.e., *maternal*) in the equation, with all corresponding interactions. Also shown are the random female identity effects associated with the intercept (u_{0j}) and slope (u_{1j}), the random effect associated with ration nested within a female ($u_{0i|j}$) and the residual error (ε_{tij}). An identical model was used for each population to evaluate the influence of egg phenotype on larval phenotype, except that $maternal_{ij}$ was replaced by egg variables (i.e., egg_{ij}).

Although the experiment was designed and conducted as a blocked experiment, preliminary results indicated that block was not significant in any analyses and thus was not included in the final mixed models. Evaluation of significant maternal variables began with the "beyond optimal" model that included all maternal variables (fixed factors), larval age (fixed factor with repeated measures) and ration nested within female (random factor, $u_{0i|j}$) to account for the dependence among feeding treatments within each population. The statistical model also included key interactions such as the interaction of each maternal variable × larval age to determine whether maternal influences vary with larval age. Also included were ration, ration × larval age, and the interaction of each maternal variable × ration as fixed covariates. The maternal variable × ration was evaluated to determine whether maternal influences varied with prey availability. A random intercept and slope (larval age as a continuous variable) also were included to allow correlations between larval measurements to change with time.

Because denominator degrees of freedom are often substantially affected by more complex covariance structures, such as those typical of repeated measures analysis, the Kenward-Roger correction was used to prevent inflation of Type I error rates (Littell et al. 2006). To determine the best model, five alternative covariance structures (autoregressive of order one, autoregressive of order one with heterogeneous variance, first-order ante-dependence, compound symmetry, and unstructured [Littell et al. 2006]) were evaluated using restricted maximum likelihood estimation (REML). The model with the covariance structure that produced the lowest AIC was chosen as the best structure. After the best random structure was identified, the best fixed structure was determined using maximum likelihood estimation. Models with different fixed structures (but same random structure) were compared using maximum likelihood estimation, by manually removing non-significant fixed terms in sequential order from highest to lowest *p*-value, and testing whether they were significant using the likelihood ratio test. In situations where the remaining significant maternal factors showed variance inflation (VIF)> 5.0, maternal variables explaining the least variance were removed until the remaining variables showed low VIF (< 5.0) and the model showed the lowest Akaike information criterion (AIC) of all possible remaining variable combinations. The model that met the above criterion and showed homogeneity of conditional residual variance was chosen as the best-fitted and most parsimonious model.

If the analyses conducted above showed a significant maternal variable × larval age interaction, a second series of linear mixed models was conducted to determine which maternal phenotypes influenced larval size, growth and mortality at

each age separately. Although model selection procedure was identical to that described above, the structure was different. The primary differences were that initial full models did not include larval age, and a random slope and intercept were only included if they reduced the AIC. In addition, the covariance structure options were limited to unstructured and compound symmetry.

Population differences in early life characteristics

To test the null hypothesis that maternal influences on larval phenotype were similar between the CB and RR populations, another series of linear mixed models was conducted. The model selection procedure was identical to that described in the *Maternal and egg influences on early life* section above; however, the statistical model was different. The statistical model was:

$$\left.\begin{aligned} larval_{tij} = {} & \beta_0 + \beta_1 \times age_t + \beta_2 \times maternal_{ij} + \beta_3 \times ration_j \\ & + \beta_4 \times pop_j + \beta_5 \times age_t \times maternal_{ij} + \beta_6 \times age_t \times ration_j \\ & + \beta_7 \times age_t \times pop_j + \beta_8 \times maternal_{ij} \times ration_j \\ & + \beta_9 \times pop_j \times ration_j + \beta_{10} \times maternal_{ij} \times pop_j \end{aligned}\right\} \text{Fixed}$$

$$\left.\begin{aligned} & + u_{0j} + u_{1j} \times age_t + u_{0i|j} + \varepsilon_{tij} \end{aligned}\right\} \text{Random}$$

where $larval_{tij}$ represents a larval phenotype (i.e., either length, dry weight, growth in length, growth in weight, or mortality) at larval age *t* for tank *i* nested within female *j*. The parameters β_0 through β_{10} represent the fixed effects associated with the intercept, larval age (*age*), the female identity level and tank-level covariates, and their two-way interactions. All other terms are identical to the previous model; however, instead of ration being nested within a female, the dependence among tanks

within each population was accounted for by nesting tank within female. In addition, because an objective of this analysis was to determine whether differences existed in progeny phenotypes between the two populations, the initial full model structure also included population (*pop*), as well as population × age to determine whether differences between populations varied by larval age. In addition, population × ration was included as a covariate to determine whether the effect of ration varied by population. In addition, a maternal phenotype × population interaction was included to determine whether maternal influences were different between the populations.

Results

Female, egg and 4-dph larval characteristics

The females from the two different populations used in this experiment had similar length-weight relationships and similar mean values for all characters measured, except HSI and residual PRTW, which were significantly higher in the Chesapeake Bay (CB) and Roanoke River (RR) females, respectively (Figures 4.2 and 4.3). Roanoke females did exhibit lower variance in age, TL and all weight categories; however, variances were relatively similar for all other female variables (Figure 4.3).

In contrast to the maternal characteristics, eggs and 4-dph larvae were significantly different for several of the characteristics measured. Analysis of covariance indicated that egg surface area:volume and total energy were significantly higher (0.74 mm^{-1} [28%] and 0.0012 kJ [15%], respectively, Figure 4.4), in the CB population and egg volume and total protein were significantly higher (3.43 mm^3

[102%] and 38.6 μg [54%], respectively, Figure 4.4) in the RR population compared to CB (Figure 4.4). No significant population differences were observed for egg dry weight, yolk volume, 1-dph larval dry weight, 1-dph SL and 4-dph larval dry weight (Figure 4.4). Due to a significant population × post-GW interaction, overall significant differences between populations could not be determined for oil globule volume or egg total lipid weight (Figure 4.4). However, for both oil globule volume and egg total lipid weight, the slopes of the relationship between female weight and egg characteristic were significantly greater than zero in the CB population (both $p < 0.0002$), but not in the RR population ($p = 0.98$ and $p = 0.80$, respectively). Furthermore, the effect of population was significant (both $p < 0.00012$), and parameter estimates indicated that the estimated difference in the average oil globule volume and egg total lipid weight was 0.12 mm^3 (100%) and 59.5 μg (41%) greater in the CB population for an average weight female. For the initial larval characteristics measured, only 4-dph SL showed an overall significant difference, with larvae from RR 0.33 mm (6%) larger (Figure 4.4).

Maternal influences on early-life characteristics

Initial correlation analyses between maternal variables and egg and 4-dph variables indicated that RTW and other measures of female energetic condition had little influence on initial offspring phenotype in either population (Table 4.1). In contrast, maternal size, specifically post-GW, pre-TW and TL exhibited strong positive correlations with multiple egg variables in the CB population (Table 4.1). The RR population showed fewer significant maternal – egg correlations and no

significant maternal – 4-dph larval correlations (Table 4.1). In the RR population, there were no overall, or dominant relationships between maternal phenotype and either egg or 4-dph larval phenotype.

Similar to the correlation analyses, the hypothesis that RTW positively influences larval phenotype could not be supported by mixed models analyses. In fact, RTW showed no significant influence – positive or negative on larval phenotype. Furthermore, alternative tissue-specific measures of energetic condition also exhibited no significant influence on larval phenotype. In contrast, in both populations, maternal post-GW explained most of the variance in all larval phenotypes measured (Table 4.2, 4.3).

For the CB population, repeated measures mixed models analyses indicated that maternal post-GW had a significant effect on all larval variables measured (Table 4.2). Post-GW had a significant negative effect on larval instantaneous growth in length and weight over the duration of the experiment (Table 4.2). In contrast, the effect of post-GW on oil globule resorbed and oil globule volume was positive over the duration of the experiment. Likewise, post-GW had a positive effect on larval TL and weight; however, significant post-GW × larval age interactions in both models indicated that the effect of post-GW was not consistent over the duration of the experiment (Table 4.2). When the post-GW × larval age interaction was evaluated further using mixed models at each separate age, results showed that the effect of post-GW on larval TL and weight remained positive over the duration of the experiment. However, the slopes decreased during the course of the experiment, indicating that the effect of post-GW on larval TL and weight decreased over time.

The effect of post-GW on larval percent mortality also was not consistent over the duration of the experiment as indicated by a significant post-GW × larval age interactions (Table 4.2). When the CB maternal weight × larval age interaction was evaluated further using mixed models analysis at each age separately, results showed that at 6, 8, and 10 dph, maternal weight showed a significant negative relationship (all $p < 0.05$) with percent larval mortality, indicating that larger females produced larvae with lower mortality. However, by 12 dph the effect shifted and maternal weight showed a significant positive effect on mortality ($p < 0.05$), indicating that mortality was now greater in larvae from larger females. Furthermore, this effect continued through the remainder of the experiment (all $p < 0.05$).

Similar to the CB population, post-GW of RR females exhibited the greatest overall influence on larval phenotype compared to other maternal phenotypes analyzed. However, unlike the CB population, no female characteristic in the RR population influenced larval oil globule volume, oil globule resorbed or percent mortality (Table 4.3). Like the CB population, post-GW had a negative effect on larval instantaneous growth in length and weight over the duration of the experiment (Table 4.3). Unlike the CB population, post-GW did not have an overall effect on larval TL or weight, but there was a post-GW × larval age interaction indicating that the effect of post-GW was not consistent over the duration of the experiment (Table 4.3). When the post-GW × larval age interaction was evaluated further using mixed models at each separate age, results showed an initial positive effect of post-GW on larval TL at 5 and 7-dph (all $p < 0.05$), no effect of post-GW from 12-17-dph, and a negative effect from 22-27-dph (all $p < 0.05$). Models also indicated that there was

no effect of post-GW on larval weight until 22-dph, when post-GW exhibited a negative effect through 27-dph (all $p < 0.05$). The absence of an overall effect of post-GW on larval TL and weight, and the absence of any significant maternal influence on oil globule resorbed, oil globule volume and percent mortality indicated much weaker maternal influences in the RR population (Table 4.3).

Finally, no maternal phenotype × ration interaction was evident in any model for the CB or RR population, indicating that maternal influences did not vary with ration (Table 4.2, 4.3).

Egg influences on early-life characteristics

In the CB population, larval size, growth, oil characteristics, and mortality were each significantly influenced by egg quality characteristics (Table 4.4). Egg lipid weight and egg total energy had significant negative effects on larval instantaneous growth in length and weight, respectively, over the duration of the experiment (Table 4.4). Egg dry weight and egg total energy had significant positive effects on larval oil globule resorbed and oil globule volume, respectively, over the duration of the experiment (Table 4.4). Egg dry weight also had significant positive effects on larval TL and weight; however, significant egg dry weight × larval age interactions indicated that these effects were not consistent over the duration of the experiment (Table 4.4). When the egg dry weight × larval age interaction was evaluated further using mixed models at each separate age, results showed that like the effect of female post-GW, the effect of egg dry weight on larval TL and weight remained positive over the duraction of the experiment. Furthermore, like the post-

GW models, the slopes decreased during the course of the experiment, indicating that the effect of egg dry weight on larval TL and weight decreased over time.

Egg lipid, and to a minor degree egg protein, significantly influenced mortality in CB larvae (Table 4.4). Over the duration of the experiment, egg lipid showed a positive effect on larval mortality, indicating that eggs with more lipids produced larvae with lower survival (Table 4.4). However, there was a significant egg lipid × larval age and egg protein × larval age interaction, indicating that the effect of egg lipid and protein was not consistent across all larval ages (Table 4.4). When this interaction was evaluated further using mixed models at each age separately, results showed that by 6 – 10 dph, egg protein was negatively related to mortality (all $p < 0.001$) with egg lipid showing no effect. This indicated that eggs with higher protein initially produced larvae that had lower mortality through 10 dph. At 12 dph egg protein no longer showed a significant effect; however, egg lipid showed a significant positive effect ($t = 3.95_{13.3}$, $p = 0.0016$) on larval mortality. This indicated that by 12 dph, larvae hatched from eggs with greater lipids were exhibiting greater mortality. Furthermore, the significant positive effect of egg lipids was maintained through the end of the experiment (all $p < 0.05$).

Unlike the relatively weak effects of female characteristics on larval characteristics in the RR population, egg characteristics exhibited relatively strong effects on larval growth, size and oil characteristics (Table 4.5). Furthermore, in each case, either egg dry weight or egg total lipid weight had a significant positive effect on larval size, growth or oil characteristics (Table 4.5). Egg total lipid weight had significant positive effects on larval instantaneous growth in length and weight over

the duration of the experiment (Table 4.5). Egg dry weight and total lipid weight also had significant positive effects on larval oil globule resorbed and oil globule volume, respectively (Table 4.5). In addition, egg dry weight had a significant positive effect on larval TL and weight; however, a significant egg dry weight × larval age interaction suggested this effect might not be consistent over the duration of the experiment. However, when the egg dry weight × larval age interaction was evaluated further using mixed models at each separate age, results showed that like the effect of female post-GW, the effect of egg dry weight on larval TL and weight remained positive over the duration of the experiment. Slopes did however decrease during the course of the experiment, indicating that the effect of egg dry weight on larval TL and weight decreased over time.

Similar to the CB population, egg lipid showed the strongest effect on larval mortality. However, in the RR population the effect was negative, indicating that larvae hatched from eggs with more lipids exhibited higher survival (Table 4.5). However, like the CB population, a significant egg lipid × larval age interaction indicated that this effect was not consistent over the duration of the experiment (Table 4.5). Furthermore, a significant egg total energy × larval age interaction also was observed in the RR population (Table 4.5). When these interactions were evaluated further using mixed models at each age separately, model results indicated that egg total energy had a significant negative effect on larval mortality by 6 – 10-dph (all $p <$ 0.05), indicating that larvae hatched from eggs with higher energy had greater survival through 10-dph. By 12-dph, no egg effect on mortality was observed. However, from 14 to 18-dph, egg lipid exhibited a significant negative effect (all $p <$

0.05) on mortality, here indicating that at this point, egg lipids were the primary egg constituent leading to lower mortality. From 20-dph to the end of the experiment, no egg variables showed significant effects on mortality.

Population differences in maternal influences

The null hypothesis that maternal influences on larval phenotype did not differ between the CB and RR populations was not supported by mixed models analyses. Mixed models analyses also indicated a lack of strong overall population differences in larval size, growth, oil resorbed and mortality (Table 4.6). The absence of an overall population difference for larval TL, weight, growth in length, growth in weight and oil resorbed was largely due to the presence of post-GW × population interactions (Table 4.6). Although this interaction prevented an overall population effect from being detected for larval TL, weight, growth in length, growth in weight and oil resorbed, it also indicated that maternal influences on these larval traits differed between populations. For models with larval TL, weight and oil resorbed, as independent variable, the slopes for the relationship between post-GW and each respective larval trait were significantly greater than zero in the CB population. However, these same models indicated that the slopes for the relationship between post-GW and each larval trait were not significantly different from zero in the RR population (Table 4.6). Thus, the effect of post-GW on larval TL, weight and oil resorbed did differ between populations. In the case of larval instantaneous growth in length and weight, post-GW × population interactions were also evident (Table 4.6). In both populations the slopes for the relationship between post-GW and larval

growth were negative and significantly different than zero, but in both growth models the slopes were more negative in the RR population (Table 4.6).

Although a significant population difference was present for larval mortality, a significant population × larval age interaction also was evident, indicating that the effect of population was not constant over the duration of the experiment (Table 4.6). When this interaction was explored further using mixed models at each age separately, results indicated that a significant effect of population was not evident until 16-dph, at which point larval mortality was significantly lower in the CB population ($p < 0.0001$). This effect persisted through the end of the experiment, indicating that after 14-dph, larval mortality was significantly lower in the CB population. Finally, no population × ration interactions were evident in any of the mixed models (Table 4.6), indicating that the effect of ration was similar between both populations.

Discussion

Results of this experiment indicated that pre-spawning energetic condition of females (RTW) had no influence on egg or larval phenotype in either Chesapeake Bay (CB) or Roanoke River (RR) populations. My null hypothesis could not be rejected. In fact, no single index of energetic condition had a strong influence on larval phenotype in either population. Instead, maternal size (post-GW) alone had the greatest influence on egg and larval phenotype in striped bass, although to a lesser and potentially insignificant degree in RR compared to the CB population. Although no previous studies on maternal influences have been conducted using females from

the Roanoke River, the significant influence of maternal size on progeny size and growth variables observed in the CB population was consistent with previous studies conducted using Chesapeake Bay females (Zastrow et al. 1989, Monteleone and Houde 1990). The dynamic patterns in the maternal size effect on larval survival, however, provide new insight into the potential role of both maternal phenotype and the unique composition and size of the oil globule in striped bass eggs. Furthermore, my test of population differences in maternal influences indicated that the relationship between post-GW and egg and larval size characteristics differed between populations and suggested that maternal influences on egg and larval size may not be evident in the RR population.

I explored the relationship between several maternal phenotypes and the characteristics of early-stage offspring (i.e., egg and 4-dph larvae) as a preliminary test of the hypothesis that RTW had a positive influence on offspring phenotype. These correlations revealed that in the CB population, maternal size showed strong positive correlations with all measures of egg and larval phenotype except yolk volume and larval oil globule volume, which showed positive, but non-significant and nearly significant correlations, respectively. In contrast, neither maternal size nor condition influenced egg or 4-dph larval characteristics in the RR population. The maternal size influences on eggs in the CB population were consistent with Zastrow et al. (1989), who showed similar positive correlations between female weight and egg lipid, protein, oil volume, and yolk volume in Chesapeake Bay populations from the Patuxent and Nanticoke Rivers and C&D Canal. However, the maternal weight – egg phenotype correlations in my study were stronger, and possibly resulted from

Zastrow et al. (1989) using pre-spawn female weight, which included the ripe ovaries, rather than the post-spawn weight used in my study.

Maternal size influences on the physical and chemical characteristics of eggs are ubiquitous in marine and freshwater fishes. In most species, positive relationships have been observed between female size and egg size, oil globule size, lipid and protein composition (Blaxter and Hempel 1963, Chambers et al. 1989, Berkeley et al. 2004), although in some cases female size had no influence on egg characteristics (Marsh 1984, Hinckley 1990, Chambers and Waiwood 1996). In at least one of these studies, the absence of a maternal size influence on egg characteristics was likely due to small female size variation (i.e., Chambers and Waiwood 1996). Likewise, the lower female size variation in the RR females compared to the CB females may have led to my observation of no maternal size or energetic condition influence on egg characteristics in the RR population. However, the absence of a maternal size effect on egg dry weight and oil globule volume was still evident when females included in my experiment were pooled with RR and CB females spawned in 2007 and 2009. These pooled results provide additional evidence that maternal influences on offspring size may not exist in the RR population.

Although no other maternal influence studies have been conducted with RR striped bass, Secor (1990) also found no maternal – egg correlations in land-locked striped bass populations from two heavily impounded spawning grounds on the Santee and Cooper Rivers, South Carolina. Like the Santee and Cooper Rivers, the Roanoke River also is heavily impounded, and is managed to provide moderate sustained flow during the spawning season to promote year-class strength (Hassler et

al. 1981, Rulifson and Manooch 1990, Carmichael et al. 1998). These impoundments likely reduce the variability in flow experienced by eggs in these systems, compared to those in the less impounded Chesapeake Bay tributaries. Because flow and egg phenotype likely play a role in how eggs are positioned in the water column and because position may influence egg survival (Bergey et al. 2003), the lower flow variability in impounded systems may select for a single optimum egg phenotype. If maternal influences are adaptive, the variation among egg phenotype may have become canalized in systems with low environmental variability. Marteinsdottir and Able (1988) provided similar reasoning for their observation of maternal size effects on egg diameter in one population of *Fundulus heteroclitus*, but not another. They indicated that the eggs from the population exhibiting maternal influences had a higher probability of being exposed to different environmental conditions and thus the maternal influences were probably an adaptive response. Thus, my observation of no maternal influences on egg phenotype in the RR population may be an evolved response to low flow variability.

Like the correlation results described above for offspring 4-dph and younger, detailed statistical analyses also revealed that post-GW and not RTW (or other indices of condition) had the strongest influence on larval growth beyond 4-dph. In the RR population smaller females (lower post-GW) produced larvae that grew faster in length and weight. This is in contrast to what Monteleone and Houde (1990) observed from smaller Chesapeake Bay females, which produced larvae that grew slower in length, but not weight. However, smaller females from Monteleone and Houde (1990) experiment produced eggs that were lower in dry weight, whereas

smaller RR females in my study produced eggs slightly heavier in dry weight and total lipids. Thus, both studies indicate that larger and more lipid-rich eggs produced larvae that grow faster. Studies on other fish species show similar trends and indicate that larger eggs may provide greater energy reserves, which can support high metabolic requirements and enable faster larval growth (([*Oncorhynchus mykiss*], Escaffre and Bergot 1984), (Atlantic cod [*Gadus morhua*] [Marteinsdottir and Steinarsson 1998, Browman et al. 2003], ([*Amphiprion melanopus*], Green and McCormick 2005)). However, in striped bass and other teleosts, smaller eggs can produce larvae that grow faster (i.e., Eldridge and Whipple 1982, Donelson and Munday 2009, Segers et al. 2012) – and this appears to be evident in the CB population as I discuss below.

Similar to the RR population, in the CB population, maternal post-GW showed an overall negative relationship with larval growth in length and weight. However, in contrast to the RR population, larger CB females produced heavier eggs with larger oil globules and greater lipid reserves. Furthermore, in the CB population, larger eggs with larger oil globules and more lipids produced larvae that grew slower. These results differ from the RR population and from Monteleone and Houde (1990) experiment, where the opposite trend was observed, as discussed above. However, as demonstrated in previous striped bass experiments, and experiments on other fish species, smaller eggs can produce larvae that grow faster (Eldridge and Whipple 1982, Secor 1990, Donelson and Munday 2009, Segers et al. 2012).

Several explanations have been proposed to explain faster growth in larvae produced by smaller eggs. First, Secor (1990) speculated that slower early growth of

larvae from larger eggs might be due to greater metabolic demands required for activity and routine metabolism. Larger eggs, yolk and oil size will increase mass and swimming profile area and thus negatively affect the hydrodynamics of larval swimming (Secor 1990). Because routine metabolism is proportional to tissue weight, larvae from larger eggs will convert yolk less efficiently into growth and development (Secor 1990). If oil globule size alone is the primary metabolic constraint however, it does not appear to be a factor in other species, which show a positive relationship between oil globule or yolk size and larval growth (Escaffre and Bergot 1984, Berkeley et al. 2004).

A second possible explanation is provided by Segers et al. (2012), who demonstrated in a mouthbrooding cichlid (*Simochromis pleuropilus*) that small larvae from smaller eggs exhibited higher gene expression of growth hormone receptor (GHR) – a key gene involved in the early growth of vertebrates. They speculated that elevated GHR might enhance utilization of yolk and/or serve to increase appetite and foraging activity. In either case, greater gene expression in smaller offspring appears to enable growth compensation for lower maternal investment in small *Simochromis pleuropilus* eggs (Segers et al. 2012) – a mechanism that may be at work in other species as well.

A third and final explanation for the negative relationship between egg size and larval growth in the CB population and the Eldridge and Whipple (1982) and Secor (1990) studies may derive from unique maternal provisioning. Eggs of striped bass are quite distinct in comparison to other teleosts that exhibit a positive relationship between maternal size/age and larval growth – particularly with regard to

the lipid composition. Specifically, striped bass eggs are very high in lipids, with most of the egg lipids being WE and nearly 90% of the oil globule being composed of WE (Eldridge et al. 1983). In contrast, the eggs of Atlantic cod and many Pleuronectiformes do not contain an oil globule and have a higher percentage of triacylglycerols (TAG) (8.9 - 14.2 %) compared to WE (2 - 4.3%) (reviewed in Wiegand 1996). Furthermore, although *Sebastes* spp. are live-bearing, their larvae do contain oil globules, and the larvae at birth contain higher percentages of TAG (10.5%) compared to steryl and WE (1.9%) (MacFarlane and Norton 1999).

One possible reason for the difference in lipid composition between striped bass eggs and those of the other species described above may lie in their common pelagic nature, but distinct external environments. For all species that spawn pelagic eggs, a mechanism is required to reduce specific gravity below that of the external medium to maintain buoyancy. Species like striped bass require molecules less dense than freshwater to decrease egg density and give the egg positive hydrostatic lift (Mangor-Jensen and Waiwood 1993). This comes in the form of a large, WE-rich oil globule (Eldridge et al. 1983), which enables the egg to be nearly neutrally buoyant and only slightly heavier than freshwater (Mangor-Jensen and Waiwood 1993). A large periviteline space likely reduces sinking velocity even further by increasing egg size without increasing specific weight – an apparent adaptation to low salinity (Mangor-Jensen and Waiwood 1993, Bergey et al. 2003).

Although squalene, WE, alkyldiacylglycerols, and triacylglycerols (TAG) are commonly used for buoyancy purposes by marine fish (Phleger 1998), WE and TAG appear to be the dominant lipid components contributing to buoyancy in eggs

containing oil globules. Wax esters have lower density and greater positive buoyancy than TAG (Phleger 1998) and this may be why many species that spawn pelagic eggs in freshwater produce eggs with over 80% WE and < 21% TAG (e.g., Sand et al. 1969, Kaitaranta and Ackman 1981, Anderson and Arthington 1990). Interestingly, this is even true in burbot (*Lota lota*) (81.8% WE, 4.1% TAG) – the only freshwater species of the marine-dominated Gadidae family (Kaitaranta and Ackman 1981). Thus, WE clearly play an important role in egg buoyancy.

In addition to buoyancy, WE in the striped bass oil globule also serves as an energy source (Chu and Ozkizilcik 1995). However, there is evidence to suggest that the WE-rich oil globule in striped bass may be mostly used for buoyancy, and at a slight cost to larval metabolic efficiency. In striped bass and other teleosts, WE are used for metabolism at lower rates than TAG (Patton et al. 1975, Ozkizilcik et al. 1996, MacFarlane and Norton 1999). Fish also convert WE to TAG for utilization, but require dietary protein for this conversion (Sargent and Gatten 1977). Thus, the overall impression is that WE are difficult to digest (Sargent and Gatten 1977). This may explain why oil globule utilization is faster in striped bass larvae that are fed a higher ration and conserved in starved larvae (Eldridge et al. 1977, Dergaleva 1977). It may also explain why WE are retained until metamorphosis, instead of being utilized for early energetic demands (Chu and Ozkizilcik 1995). Furthermore, the retention of the oil globule, especially in slow growing striped bass, is inconsistent with species that possess TAG-rich oil globules. For example, in species such as walleye (*Sander vitreus*), which havea TAG-rich oil globule, smaller and slower growing larvae do not delay utilization of the oil globule. Together, these results

suggest that there are potential metabolic costs to having a large, WE-rich oil globule and this may be responsible for the reduced growth in CB larvae produced by eggs with a larger oil globule. If these metabolic costs are true and evident in nature, it is likely that the reduced specific gravity provided by the WE produces a selective advantage to eggs and larvae by preventing them from sinking to the bottom and potentially enabling them to maintain position in resource rich regions of the nursery.

The role of WE still does not explain why RR eggs with more lipids produce larvae that grow faster. There are two possible reasons that derive from the distinct characteristics between CB and RR eggs. First, CB eggs have an oil globule that is twice as large as RR eggs. Assuming RR oil globules are mostly WE (i.e., as observed in other striped bass genetic strains), then RR eggs likely contain half the amount of WE observed in CB eggs. If this is true, and if WE have metabolic costs associated with them, then smaller amounts of WE may have little or no negative effects on RR larval growth. Second, RR eggs also have more protein than CB eggs. Since growth is primarily an increase in body muscle mass by protein synthesis (Rønnestad and Thorsen 1999), then the higher protein levels in RR larvae may enable them to overcome any possible negative effects of the already small amount of WE. Although these explanations are plausible, additional research is necessary to determine the repeatability of my results, and possible mechanisms for the contrasting egg influences on larval growth in the RR and CB population.

RTW and all other measures of energetic condition had no influence on larval size in either population. Instead, female post-GW again had the strongest influence on larval size in both populations, although the effects were stronger in the CB

population. In the CB population, post-GW maintained a positive influence on larval size throughout the experiment, despite the negative relationship observed between female size and larval growth in length and weight. These results seem to indicate that the faster growth in smaller larvae, from smaller females, was not sufficient to overcome the initial size disadvantage present at 4-dph. Monteleone and Houde (1990) also showed that maternal size exhibited a significant positive influence on larval length and weight through 25 dph, although they did not observe a convergence in size – as my results suggest. However, like my study, Eldridge and Whipple (1982) and Secor (1990) did observe a convergence in weight and length between small and large larvae that came from small and large eggs, respectively.

In contrast to the CB population, no maternal characteristic had an overall effect on larval length or weight in the RR population. Although there was a significant post-GW × larval age interaction, the effect of post-GW on larval size was not consistent over the duration of the experiment. Thus, unlike the CB population, post-GW and other maternal characteristics appeared to have little influence on larval size. However, like the CB population, egg dry weight had a positive influence on larval length and weight over the duration of the experiment, indicating that larger eggs in both populations produced larger larvae that maintained their size advantage during the 27-day experiment.

Much like the maternal influences on larval growth and size, my results indicated no effect of RTW on larval mortality. However, my study did provide the first evidence for significant maternal influences on larval mortality in striped bass, but only in the CB population. Neither female nor egg phenotype influenced larval

mortality in the RR population. However, similar to the influences on larval growth and size, post-GW did influence larval mortality in the CB population. Although there was no overall influence of any maternal phenotype on larval mortality, a post-GW × larval age interaction was evident. Further exploration indicated that the post-GW influence on larval mortality shifted with larval age. From 4 to 10-dph, survival was greater in larvae from larger females; however, by 12-dph the relationship shifted and survival became lower in larvae from larger females. This shift did not coincide with either yolk or oil globule depletion, which occurred at 7 and 22 to 27-dph, respectively. However, the shift did occur shortly after the oil globule begins to decline in striped bass (i.e., 5-7 dph, Chu and Ozkizilcik 1995). Thus, one possible explanation for this trend could be a delayed response to contaminants transferred maternally to the eggs and processed by larvae as they utilized the oil globule. Recently, it has been shown that PCBs are still relatively high in migratory striped bass, when compared to other marine species (Frohmberg 2008). Furthermore, PCBs can reduce initial size and growth of striped bass larvae (Ostrach et al. 2008), and adverse effects on survival are certainly possible (i.e., Olsson et al. 1999).

Another possible explanation for the negative relationship between post-GW and larval survival may be due to the composition of the oil globule, which as discussed earlier, is dominated by WE. Because WE are difficult to digest (Sargent and Gatten 1977), increased metabolic costs may be involved when utilizing WE as an energy source – which may in turn result in decreased survival if proper development is inhibited. Furthermore, because oil globule and WE utilization increases after feeding commences (Chu and Ozkizilcik 1995) at around 5-dph (Rees

and Harrell 1990), the mortality effects may not be observed until feeding is well established. The only other study to report a negative relationship between maternal size/provisioning and larval survival was for the damselfish (*Pomacentrus amboinensis*) (Gagliano and McCormick 2007); however, the egg composition of this species is unknown. Indeed, all other studies that have evaluated the influence of maternal or egg/oil globule size on larval survival showed either no effect (Chambers et al. 1989, Fuiman and Ojanguren 2011), a positive influence (Blaxter and Hempel 1963, Marsh 1984, Chambers et al. 1989, Berkeley et al. 2004) or a positive influence only at low prey densities for larvae (Hutchings 1991, Gisbert et al. 2000, Jónsson and Svavarsson 2000). Furthermore, in those species that exhibited a positive influence of egg size/oil globule size on larval survival, the dominant neutral lipid constituent was TAG, not WE and/or WE were lower than TAG (Tocher and Sargent 1984, Moodie et al. 1989, MacFarlane and Norton 1999). These results are consistent with my hypothesis that WE may have metabolic costs that may reduce survival in larvae emerging from eggs that have higher concentrations of WE. Still, further research will be necessary to determine the true influence of WE on larval survival in striped bass and other species.

Above I showed using separate mixed models analyses on each population, that maternal influences on larval phenotype – specifically the effect of post-GW – were stronger in the CB population. However, to formally test the null hypothesis that maternal influences on larval phenotype were equal in both populations, I conducted mixed models analyses with both populations combined. My results from these analyses indicated significant differences in the maternal influences on larval

size and oil characteristics, but no difference in the maternal influence on larval growth or mortality. The differences in maternal influences on larval size and oil characteristics was evident through significant post-GW × population interactions. Although one other study has tested for inter-population differences in maternal influences on larval traits (Green and Chambers 2007), ours is the first study to show a significant difference in maternal size influences between populations. In the CB population, maternal post-GW had a clear positive influence on larval size and oil characteristics; however, in the RR population post-GW and other maternal characteristics had no convincing effect on larval size and oil globule characteristics. Although the absence of a maternal influence in the RR population could be due to a small sample size, post-GW still exhibited no relationship with egg dry weight and oil globule volume in the pooled data set of 25 RR females. Together, these results suggest that maternal influences on eggs, and potentially larvae, may not exist in Roanoke River striped bass.

My experimental results indicate that maternal size, but not energetic condition, had a dominant effect on larval phenotype – particularly in the CB population. The absence of a relative condition effect is consistent with my observation of a very small effect of relative condition on oocyte volume in Chapter 3. Together, these two chapters suggest that relative condition significantly influences gamete number and skipped spawning behavior, but may have little effect on pre- and post-fertilized offspring size and offspring vital rates. Despite evidence for female size influences on CB offspring, they were largely absent from the RR population. This may be due to selection for a single optimum egg size in the

Roanoke River, where flow variability is lower and energy is higher compared to Chesapeake Bay tributaries. The lower energy Chesapeake Bay tributaries also appear to select for larger eggs with larger oil globules (*sensu* Bergey et al. 2003). The larger oil globule, however, may carry with it some negative consequences in the form of reduced larval growth and survival – at least in a controlled laboratory environment. In nature these results may translate differently in Chesapeake Bay tributaries, especially if eggs with larger oil globules stay closer to the surface and are transported more quickly to the salt front, where zooplankton are more abundant. Furthermore, larvae with larger oil globules may exhibit enhanced survival at the lower temperatures they may be exposed to in nature – especially if larger females are spawning earlier, as my results from Chapters 2 and 3 show. Overall, these results indicate that there is still much to be understood about maternal influences in striped bass, particularly with regard to their influence on survival, both in the laboratory and in nature. At present, however, my results provide further support for preserving female size and age diversity as management strategies to promote potential larval growth and survival advantages under different environmental conditions.

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Table 4.1. Pearson correlations among female (all capital letters), egg and initial larval characteristics (all lower-case letters) from the Chesapeake Bay (white) and Roanoke River (gray) populations. Significant ($p < 0.05$) and nearly significant ($0.05 \geq p \geq 0.07$) correlations are indicated by enlarged and bold font and enlarged italicized font respectively.

PRE-TW	**0.95**	**0.89**	0.44	0.46	0.62	0.30	0.53	0.07	-0.18	-0.06	-0.09	0.09	-0.05	-0.12	-0.13	-0.12	0.42	0.08	0.52
0.93	POST-GW	**0.86**	0.45	0.35	**0.68**	0.35	0.46	0.22	-0.21	-0.07	-0.09	0.07	0.01	-0.03	-0.19	-0.11	0.41	0.09	0.32
0.92	**0.98**	TL	0.20	0.39	0.62	0.35	0.08	-0.30	0.10	-0.08	0.01	0.28	0.33	0.25	-0.03	0.11	0.65	0.38	0.50
0.43	**0.70**	**0.67**	AGE	0.33	0.56	0.54	0.57	0.46	-0.60	-0.13	-0.13	-0.48	-0.41	-0.29	-0.77	-0.22	-0.08	-0.46	0.07
-0.38	-0.44	-0.41	-0.54	HSI	**0.77**	**0.78**	0.23	-0.12	-0.32	0.24	-0.34	-0.45	-0.03	-0.20	-0.07	-0.28	-0.16	-0.34	0.64
0.81	**0.83**	**0.82**	0.38	0.04	TLE	**0.92**	0.15	0.07	-0.37	0.08	-0.24	-0.40	0.14	0.07	-0.36	-0.19	0.07	-0.21	0.36
-0.54	-0.53	-0.53	-0.42	**0.88**	-0.03	RLE	-0.04	-0.02	-0.37	0.16	-0.29	-0.51	0.13	0.12	-0.39	-0.18	-0.07	-0.29	0.24
0.79	0.60	0.53	0.06	-0.30	0.46	-0.47	RTW	**0.70**	-0.54	0.02	-0.20	-0.26	**-0.72**	**-0.72**	-0.22	-0.43	-0.23	-0.49	0.19
0.53	**0.65**	0.49	0.54	-0.37	0.43	-0.33	0.61	PRTW	-0.56	0.02	-0.17	-0.38	*-0.60*	*-0.58*	-0.31	-0.41	-0.44	*-0.54*	-0.39
0.80	**0.88**	**0.91**	0.63	-0.08	**0.82**	-0.28	0.43	0.45	egg weight	-0.32	0.49	0.59	**0.70**	**0.83**	0.23	**0.88**	*0.63*	**0.90**	-0.17
0.43	0.26	0.24	-0.01	-0.26	-0.04	-0.51	**0.75**	0.32	0.20	egg volume	**-0.96**	0.29	-0.51	-0.46	0.67	-0.64	-0.04	-0.14	-0.18
-0.47	-0.37	-0.32	-0.12	0.40	0.04	**0.69**	**-0.71**	-0.44	-0.27	**-0.92**	egg s:v	-0.16	0.63	0.48	-0.47	**0.71**	0.06	0.27	0.15
0.36	0.57	0.52	0.05	-0.04	0.58	-0.34	0.52	0.37	**0.70**	0.56	*-0.66*	yolk	0.12	0.47	0.60	0.30	**0.79**	**0.81**	-0.31
0.76	**0.87**	**0.87**	0.60	-0.06	**0.85**	-0.23	0.37	0.52	**0.96**	0.01	-0.15	0.62	oil globule	**0.81**	-0.09	**0.74**	0.39	0.62	0.13
0.72	**0.83**	**0.84**	0.61	-0.02	**0.82**	-0.20	0.29	0.41	**0.97**	-0.01	-0.11	*0.64*	**0.98**	egg total energy	-0.35	**0.86**	*0.70*	**0.86**	-0.30
0.77	**0.84**	**0.88**	0.64	-0.09	**0.74**	-0.30	0.40	0.37	**0.99**	0.25	-0.31	**0.69**	**0.91**	**0.94**	egg lipid	-0.26	0.12	0.27	-0.01
0.80	**0.89**	**0.87**	0.54	-0.07	**0.91**	-0.21	0.14	0.59	**0.91**	0.02	-0.13	0.56	**0.97**	**0.92**	**0.83**	egg protein	-0.50	-0.62	0.12
0.64	**0.75**	**0.78**	*0.62*	0.03	**0.73**	-0.12	0.31	0.41	**0.94**	0.11	-0.12	0.54	**0.83**	**0.90**	**0.93**	**0.85**	SL (4dph)	**0.88**	-0.12
0.79	**0.93**	**0.94**	**0.72**	-0.20	**0.89**	-0.28	0.32	0.48	**0.94**	**0.94**	-0.08	0.44	**0.91**	**0.89**	**0.89**	**0.94**	**0.86**	weight (4dph)	-0.23
0.38	*0.60*	*0.65*	**0.72**	0.05	0.57	-0.03	-0.10	0.20	**0.83**	*0.66*	0.12	0.11	*0.66*	**0.75**	**0.84**	**0.71**	**0.90**	**0.81**	oil (4dph)

Table 4.2. Repeated measures mixed model results for the Chesapeake Bay population, with larval characteristics as dependent variables and maternal characteristics as independent variables. Numerator and denominator (Kenward-Roger correction for repeated measures) degrees of freedom are shown as subcripts to *t* and *F* values.

	Multiple regression solution Type III test of fixed effects			ANOVA Type III test of fixed effects	
Effect	Estimate	*t*	*P*	*F*	*P*
			Larval total length		
Intercept	6.7233	24.28_{53}	< 0.0001		
Post-GW	0.000098	3.95_{53}	0.0002	$57.69_{1,45.9}$	< 0.0001
Ration (high)	1.7131	11.32_{53}	< 0.0001	$118.71_{1,45.9}$	< 0.0001
Post-GW ! Larval age				$4.53_{5,88}$	0.001
Larval age				$58.73_{5,88}$	< 0.0001
Larval age ! Ration				$73.16_{5,88}$	< 0.0001
			Larval weight		
Intercept	-1.8127	$-18.38_{55.1}$	< 0.0001		
Post-GW	0.000042	$4.89_{53.1}$	< 0.0001	$175.57_{1,35.9}$	< 0.0001
Ration (high)	0.9411	$17.41_{58.4}$	< 0.0001	$694.95_{1,38.1}$	< 0.0001
Post-GW ! Larval age				$5.39_{5,80.7}$	0.0003
Larval age				$36.82_{5,89.7}$	< 0.0001
Larval age ! Ration				$29.08_{5,125}$	< 0.0001
			Instantaneous growth in length		
Intercept	1.8106	$9.43_{44.1}$	< 0.0001		
Post-GW	-0.00005	$-3.02_{41.7}$	0.0043	$9.13_{1,41.7}$	0.0043
Ration (high)	0.9068	$8.39_{43.7}$	< 0.0001	$49.80_{1,74.4}$	< 0.0001
Larval age				$22.97_{4,66.1}$	< 0.0001
Larval age ! Ration				$2.63_{4,66.1}$	0.0419
			Instantaneous growth in weight		
Intercept	8.1449	$13.80_{58.2}$	< 0.0001		
Post-GW	-0.00028	$-5.81_{58.9}$	< 0.0001	$33.76_{1,58.9}$	< 0.0001
Ration (high)	3.2685	$8.10_{44.1}$	< 0.0001	$114.58_{1,84.8}$	< 0.0001
Larval age				$28.78_{4,83.4}$	< 0.0001
Larval age ! Ration				$7.03_{4,83.4}$	< 0.0001
			Oil globule resorbed		
Intercept	0.1771	$11.02_{66.8}$	< 0.0001		
Post-GW	0.00001	8.121_{46}	< 0.0001	$65.95_{1,46}$	< 0.0001
Ration (high)	0.01697	$2.14_{44.1}$	0.0377	$4.58_{1,46}$	< 0.0001
Larval age				$203.47_{4,141}$	0.0377
			Oil globule volume		
Intercept	-4.3068	$17.29_{82.2}$	< 0.0001		
Post-GW	0.000089	4.72_{47}	< 0.0001	$22.31_{1,47}$	< 0.0001
Larval age				$43.51_{4,141}$	< 0.0001
			Percent mortality		
Intercept	0.3984	$6.72_{49.5}$	< 0.0001		
Ration (high)	-0.1685	$-5.15_{49.6}$	< 0.0001	$35.73_{1,45.1}$	< 0.0001
Larval age				$13.01_{11,232}$	< 0.0001
Post-GW ! larval age				$16.12_{12,357}$	< 0.0001
Larval age ! Ration				$18.41_{11,357}$	< 0.0001

Table 4.3. Repeated measures mixed model results for the Roanoke River population, with larval characteristics as dependent variables and maternal characteristics as independent variables. Numerator and denominator (Kenward-Roger correction for repeated measures) degrees of freedom are shown as subscripts to *t* and *F* values.

	Multiple regression solution Type III test of fixed effects			ANOVA Type III test of fixed effects	
Effect	Estimate	*t*	*P*	*F*	*P*
Larval total length					
Intercept	2.3352	$31.47_{40.2}$	< 0.0001		
Ration (high)	0.1866	$10.24_{38.5}$	< 0.0001	$161.87_{1,20.6}$	< 0.0001
Post-GW ! Larval age				$4.86_{5,88}$	0.0007
Larval age				$16.36_{5,58.9}$	< 0.0001
Larval age ! Ration				$22.69_{5,108}$	< 0.0001
Larval weight					
Intercept	0.06649	$0.19_{38.9}$	0.8474		
Ration (high)	0.8637	$10.24_{37.1}$	< 0.0001	$202.92_{1,23.4}$	< 0.0001
Post-GW ! Larval age				$4.82_{5,45.7}$	0.0007
Larval age				$13.20_{5,65}$	< 0.0001
Larval age ! Ration				$19.01_{5,104}$	< 0.0001
Instantaneous growth in length					
Intercept	2.5507	$7.97_{35.9}$	< 0.0001		
Post-GW	-0.00014	$-4.56_{34.6}$	< 0.0001	$20.84_{1,34.6}$	< 0.0001
Ration (high)	0.7947	$8.08_{42.3}$	< 0.0001	$77.88_{1,72.3}$	< 0.0001
Larval age				$10.20_{4,64.4}$	< 0.0001
Larval age ! Ration				$4.28_{4,64.4}$	0.0039
Instantaneous growth in weight					
Intercept	8.1449	$13.80_{58.2}$	< 0.0001		
Post-GW	-0.00028	$-5.81_{58.9}$	< 0.0001	$16.59_{1,35}$	0.0003
Ration (high)	3.2685	$8.10_{44.1}$	< 0.0001	$71.33_{1,51.4}$	< 0.0001
Larval age				$10.90_{4,54.3}$	< 0.0001
Larval age ! Ration				$4.52_{4,35}$	0.0032
Oil globule resorbed					
Intercept	0.1183	30.89_{41}	< 0.0001		
Larval age				$78.25_{1,62.6}$	< 0.0001
Oil globule volume					
Intercept	0.01068	$2.21_{44.2}$	0.0321		
Larval age				$46.40_{2,73.3}$	< 0.0001
Percent mortality					
Intercept	-0.1581	$-1.42_{41.5}$	0.1642		
Ration (high)	-0.4465	$-3.17_{38.3}$	0.003	$25.91_{1,33}$	< 0.0001
Larval age				$207.27_{11,66.9}$	< 0.0001
Larval age ! Ration				$15.31_{11,66.9}$	< 0.0001

Table 4.4. Repeated measures mixed model results for the Chesapeake Bay population, with larval characteristics as dependent variables and egg characteristics as independent variables. Numerator and denominator (Kenward-Roger correcation for repeated measures) degrees of freedom are shown as subscripts to *t* and *F* values.

	Multiple regression solution Type III test of fixed effects			ANOVA Type III test of fixed effects	
Effect	Estimate	*t*	*P*	*F*	*P*
Larval total length					
Intercept	6.6251	$23.30_{48.7}$	< 0.0001		
Egg dry weight	3.8795	$4.10_{48.7}$	0.0002	$193.97_{1,40.9}$	< 0.0001
Ration (high)	1.7054	$13.06_{48.7}$	< 0.0001	$299.34_{1,40.9}$	< 0.0001
Larval age				$39.46_{5,76.4}$	< 0.0001
Egg dry weight × Larval age				$5.92_{5,76.4}$	0.0001
Larval age × Ration				$54.63_{5,76.4}$	< 0.0001
Larval weight					
Intercept	-1.8127	$-14.41_{70.1}$	< 0.0001		
Egg dry weight	1.6757	$4.00_{68.2}$	< 0.0001	$163.18_{1,48.3}$	< 0.0001
Ration (high)	0.9411	$17.41_{58.4}$	0.0002	$610.30_{1,45.3}$	< 0.0001
Larval age				$32.85_{5,111}$	< 0.0001
Egg dry weight × Larval age				$5.27_{5,97.3}$	0.0003
Larval age × Ration				$30.78_{5,140}$	< 0.0001
Instantaneous growth in length					
Intercept	2.214	$12.03_{44.2}$	< 0.0001		
Egg lipids	-4.8748	$-5.90_{42.4}$	< 0.0001	$34.82_{1,42.4}$	< 0.0001
Ration (high)	1.0436	$12.29_{42.4}$	< 0.0001	$150.98_{1,42.4}$	< 0.0001
Larval age				$22.97_{4,66.1}$	< 0.0001
Instantaneous growth in weight					
Intercept	7.8355	$7.06_{38.5}$	< 0.0001		
Egg total energy	-320.77	$-2.87_{36.3}$	0.0068	$8.23_{1,36.3}$	0.0068
Ration (high)	3.5861	$8.86_{37.6}$	< 0.0001	$92.32_{1,70.5}$	< 0.0001
Larval age				$28.30_{4,58.7}$	< 0.0001
Larval age × Ration				$3.11_{4,58.7}$	0.0217
Oil globule resorbed					
Intercept	0.2076	$8.64_{57.8}$	< 0.0001		
Egg dry weight	0.2978	3.80_{46}	0.0004	$14.47_{1,47}$	0.0004
Larval age				$204.28_{4,143}$	< 0.0001
Oil globule volume					
Intercept	-4.2113	-18.97_{58}	< 0.0001		
Egg total energy	106.92	10.52_{39}	< 0.0001	$110.66_{1,39}$	< 0.0001
Larval age				$39.50_{4,112}$	< 0.0001
Larval age × Ration				$7.45_{5,101}$	< 0.0001
Percent mortality					
Intercept	0.3345	$3.87_{29.1}$	0.0006		
Egg lipid	1.5571	$2.21_{24.2}$	0.0372	$10.39_{1,21.9}$	0.0039
Egg lipid × ration (high)	-0.4056	-5.58_{184}	< 0.0001	$27.92_{1,184}$	< 0.0001
Larval age				$8.03_{11,215}$	< 0.0001
Egg lipid × larval age				$9.53_{11,96.4}$	< 0.0001
Egg protein × larval age				$3.10_{12,128}$	0.0007
Ration × larval age				$54.72_{12,261}$	< 0.0001

Table 4.5. Repeated measures mixed model results for the Roanoke River population, with larval characteristics as dependent variables and egg characteristics as independent variables. Numerator and denominator (Kenward-Roger correction for repeated measures) degrees of freedom are shown as subscripts to *t* and *F* values.

	Multiple regression solution Type III test of fixed effects			ANOVA Type III test of fixed effects	
Effect	Estimate	*t*	*P*	*F*	*P*
Larval total length					
Intercept	4.5343	$4.50_{50.3}$	< 0.0001		
Egg dry weight	13.4083	$3.33_{50.3}$	0.0016	$25.70_{1,37.3}$	< 0.0001
Ration (high)	1.466	$7.91_{50.3}$	< 0.0001	$145.96_{1,37.3}$	< 0.0001
Larval age				$3.51_{5,65.3}$	0.0072
Egg dry weight × Larval age				$3.96_{5,65.3}$	0.0034
Larval age × Ration				$20.78_{5,65.3}$	< 0.0001
Larval weight					
Intercept	-3.1546	$-5.91_{45.4}$	< 0.0001		
Egg dry weight	7.3407	$3.44_{45.4}$	0.0013	$32.44_{1,37.4}$	< 0.0001
Ration (high)	0.7751	$7.89_{45.4}$	< 0.0001	$196.51_{1,37.4}$	< 0.0001
Larval age				$3.79_{5,78}$	0.004
Egg dry weight × Larval age				$2.61_{5,78}$	0.0307
Larval age × Ration				$32.52_{5,78}$	< 0.0001
Instantaneous growth in length					
Intercept	-0.4989	$-0.85_{35.1}$	0.401		
Egg lipids	11.0399	$2.80_{34.9}$	0.0082	$7.86_{1,34.9}$	0.0082
Ration (high)	0.8627	$8.71_{36.4}$	< 0.0001	$62.01_{1,52.8}$	< 0.0001
Larval age				$11.99_{4,55}$	< 0.0001
Larval age × Ration				$3.48_{4,55}$	0.0132
Instantaneous growth in weight					
Intercept	0.1675	$0.42_{40.8}$	0.6743		
Egg lipids	8.3471	$3.31_{29.1}$	0.0025	$10.98_{1,29.1}$	0.0025
Ration (high)	0.7520	$6.20_{55.6}$	< 0.0001	$98.97_{1,30.5}$	< 0.0001
Larval age				$19.21_{4,71}$	< 0.0001
Larval age × Ration				$5.64_{4,70.9}$	0.0005
Oil globule resorbed					
Intercept	-0.08658	$-6.55_{43.6}$	< 0.0001		
Egg dry weight	0.8077	$15.61_{43.5}$	< 0.0001	$243.63_{1,43.5}$	< 0.0001
Larval age				$176.95_{1,44.5}$	< 0.0001
Oil globule volume					
Intercept	-6.3030	$-9.98_{72.2}$	< 0.0001		
Egg lipids	19.1420	$4.44_{71.8}$	< 0.0001	$19.70_{1,71.8}$	< 0.0001
Larval age				$41.18_{1,71.9}$	< 0.0001
Percent mortality					
Intercept	0.9417	$32.06_{56.3}$	< 0.0001		
Ration (high)	-0.3695	-18.60_{30}	< 0.0001	$1028.51_{1,208}$	< 0.0001
Larval age				$142.77_{12,151}$	< 0.0001
Larval age × Ration				$167.77_{12,141}$	< 0.0001

Table 4.6. Repeated measures mixed model results with larval total length, weight, instantaneous growth in length and weight, and percent mortality as dependent variables and genetic population as the primary independent variable. Population and ration were binary variables with CB and high equal to 1, respectively. Numerator and denominator (Kenward-Roger correction for repeated measures) degrees of freedom are shown as subscripts to *t* and *F* values.

	Multiple regression solution Type III test of fixed effects			ANOVA Type III test of fixed effects	
Effect	Estimate	*t*	*P*	*F*	*P*
Larval total length					
Intercept	2.1441	42.60_{112}	< 0.0001		
population (CB)	-0.1908	$-3.94_{83.5}$	0.0002	$23.86_{1,76.7}$	< 0.0001
Post-GW	-0.0000087	-1.86_{108}	0.066	$4.17_{1,76.6}$	0.0447
Post-GW × population (CB)	0.000018	$3.92_{83.8}$	< 0.001	$15.38_{1,76.6}$	0.0002
Ration (high)	0.1935	15.45_{97}	< 0.0001	$195.83_{1,79}$	< 0.0001
Larval age				$50.57_{5,146}$	< 0.0001
Larval age × Ration				$51.23_{5,146}$	< 0.0001
Post-GW × Larval age				$7.54_{5,146}$	< 0.0001
Larval weight					
Intercept	-0.9039	-4.96_{148}	< 0.0001		
population (CB)	-0.7580	$-5.02_{77.8}$	< 0.0001	$25.23_{1,77.8}$	< 0.0001
Ration (high)	0.8768	15.58_{101}	< 0.0001	$542.73_{1,78.1}$	< 0.0001
Post-GW	-0.00004	-2.36_{145}	0.02	$3.91_{1,80.6}$	0.0515
Post-GW × population (CB)	0.000069	$4.78_{77.7}$	<0.0001	$22.82_{1,77.7}$	< 0.0001
Larval age				$61.32_{5,143}$	< 0.0001
Larval age × Ration				$63.93_{5,143}$	< 0.0001
Post-GW × Larval age				$8.25_{5,143}$	< 0.0001
Instantaneous growth in length					
Intercept	2.5865	$6.65_{76.5}$	< 0.0001		
population (CB)	-0.7711	$-1.87_{75.8}$	0.0657	$3.49_{1,75.8}$	0.0657
Post-GW	-0.00014	$-3.77_{75.8}$	0.0003	$23.11_{1,75.8}$	< 0.0001
Post-GW × population (CB)	0.000088	$2.23_{75.8}$	0.0286	$4.98_{1,75.8}$	0.0286
Ration (high)	0.8549	$12.14_{78.3}$	< 0.0001	$105.29_{1,123}$	< 0.0001
Larval age				$27.24_{4,123}$	< 0.0001
Larval age × Ration				$4.38_{4,123}$	0.0024
Instantaneous growth in weight					
Intercept	11.1832	$7.98_{79.2}$	< 0.0001		
population (CB)	-3.4934	$-2.35_{77.6}$	0.0211	$5.54_{1,77.6}$	0.0211
Post-GW	-0.00057	$-4.29_{77.6}$	< 0.0001	$33.45_{1,77.6}$	< 0.0001
Post-GW × population (CB)	0.000317	$2.22_{77.6}$	0.0292	$4.93_{,77.6}$	0.0292
Ration (high)	3.1966	$10.98_{74.2}$	< 0.0001	$182.52_{1,123}$	< 0.0001
Larval age				$29.43_{4,128}$	< 0.0001
Larval age × Ration				$7.68_{4,128}$	< 0.0001
Oil resorbed					
Intercept	-1.7586	$-8.42_{84.3}$	< 0.0001		
population (CB)	-0.1422	$-0.64_{85.1}$	0.527	$3.51_{1,83}$	0.0645
Post-GW	-0.00003	-1.69_{83}	0.0951	$1.83_{1,83}$	0.1797
Post-GW × population (CB)	0.000097	4.52_{83}	< 0.0001	$20.42_{1,83}$	< 0.0001
Larval age				$407.20_{4,340}$	< 0.0001
Larval age × population				$137.81_{4,340}$	< 0.0001
Percent mortality					
Intercept	-0.6509	$-7.01_{82.1}$	< 0.0001		
population (CB)	-0.1723	$-4.28_{82.1}$	< 0.0001	$16.30_{1,103}$	0.0001
Ration (high)	-0.3736	$-9.25_{82.1}$	< 0.0001	$22.71_{1,103}$	< 0.0001
Larval age				$12.48_{11,307}$	< 0.0001
Larval age × population				$10.47_{11,308}$	< 0.0001
Post-GW × larval age				$20.96_{12,311}$	< 0.0001
Larval age × ration				$14.12_{11,308}$	< 0.0001

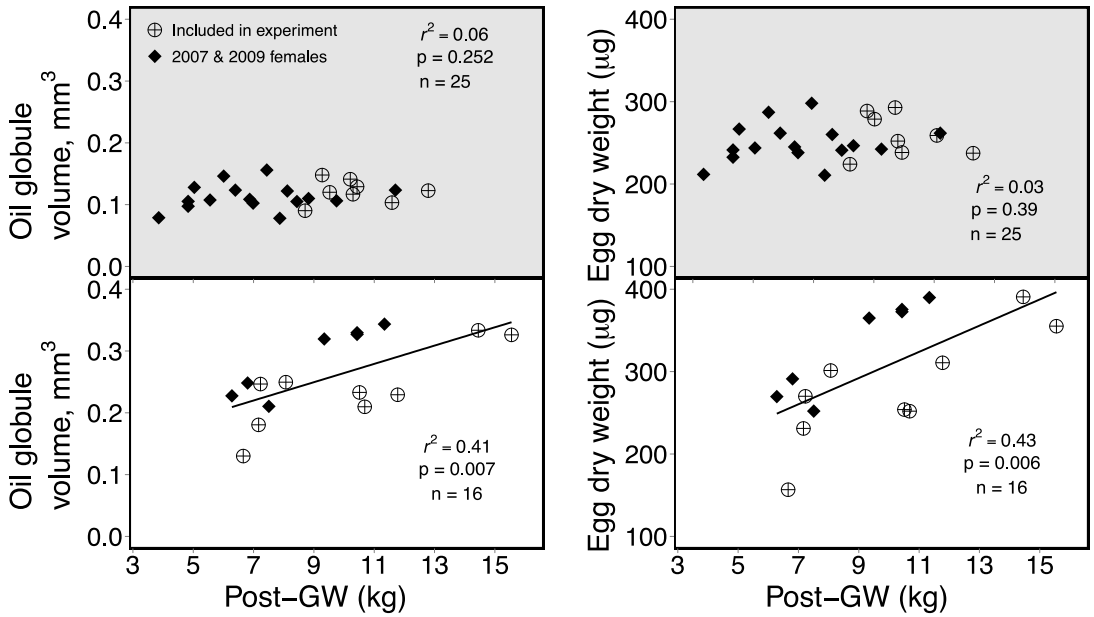

Figure 4.1. Relationships between the gutted weight of post-spawn (Post-GW) females and the oil globule volume and dry weight of their eggs. Females were collected in the Chesapeake Bay (white background) and Roanoke River (gray background).

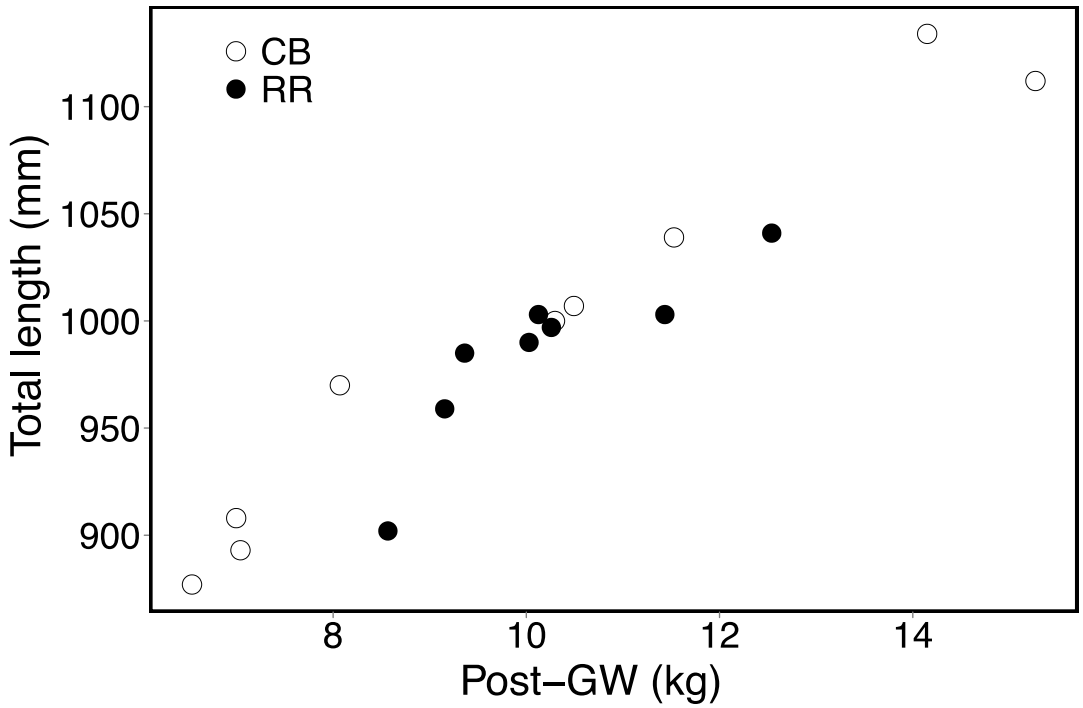

Figure 4.2. Relationship between post-GW and total length of females from the Chesapeake Bay (CB) and Roanoke River (RR).

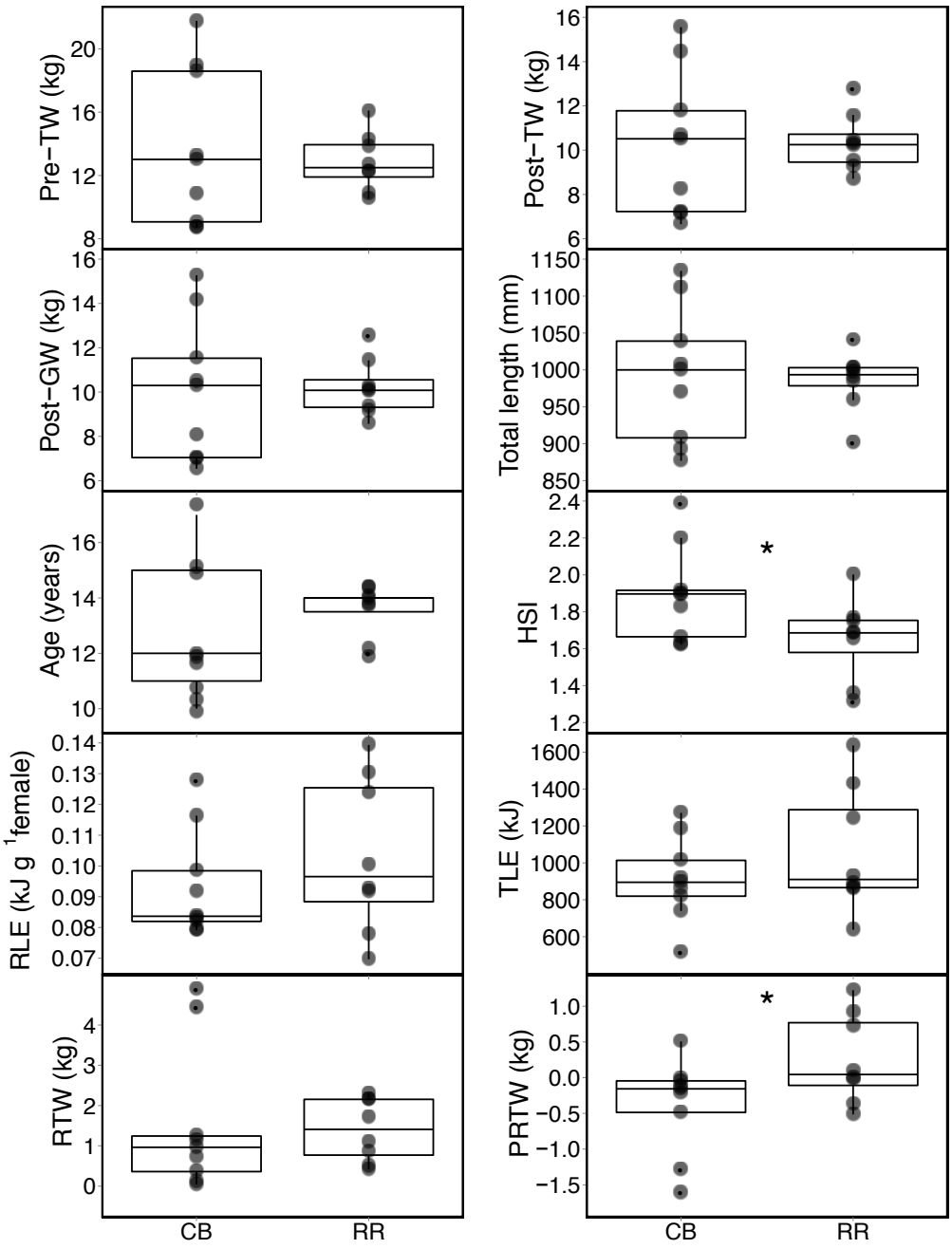

Figure 4.3. Boxplots and raw data (closed circles) for Chesapeake Bay (CB) and Roanoke River (RR) female variables. Asterisks (*) indicate significant differences 0.05) between populations based on unequal variances t-test.

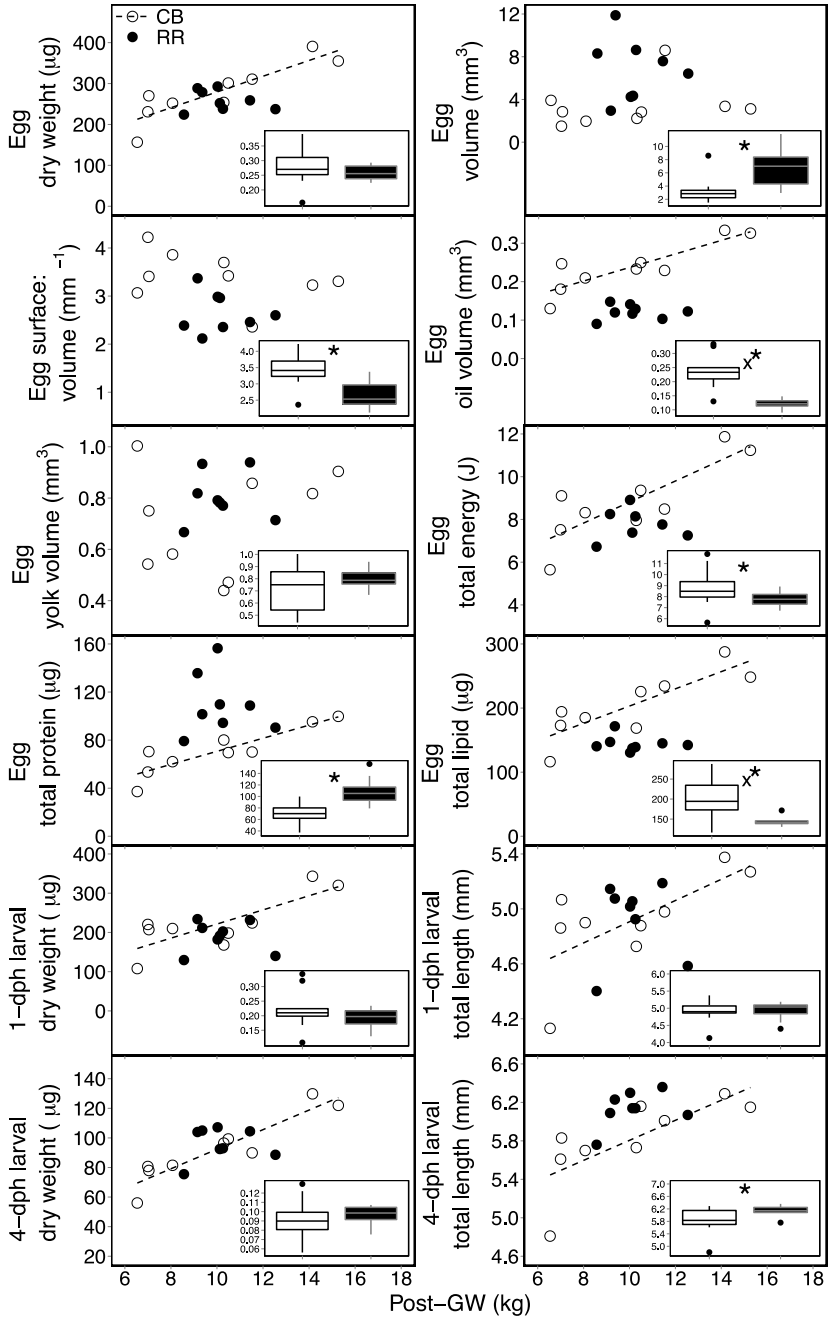

Figure 4.4 Illustrated results of analysis of covariance showing the effects of female post-GW on egg and 4-dph larval traits (scatter plots) and population differences in those respective traits (inset box plots). Regression lines are shown if slopes were significantly different than zero ($p < 0.05$). For box plots, significant population differences are indicated by an asterisk (*) and significant population effects in the presence of an interaction are indicated by ×* ($p < 0.05$).

CHAPTER 5:

TESTING FOR EVIDENCE OF MATERNAL INFLUENCES IN A NATURAL STRIPED BASS POPULATION: LESSONS LEARNED AND CHALLENGES AHEAD

Abstract

Understanding the cause of recruitment variability remains a fundamental challenge for fishery scientists. This is due in part to uncertainties in the characteristics of juvenile survivors, which prevents a full understanding of the factors governing recruitment through the first year of life. In stochastic environments, survivors may simply be those produced during chance matching of reproductive activity to optimal environmental conditions. However, survivors may also be those that possess exceptional phenotypes. Furthermore, as shown in many laboratory studies, exceptional phenotypes may be produced by specific maternal phenotypes. In pelagic spawning species such as striped bass (*Morone saxatilis*) it is currently unknown whether maternal influences on offspring affect fitness in nature. Here, I use the Patuxent River, Chesapeake Bay as a model system during 2007 and 2009 to test the hypothesis that a few parents produce a disproportionate number of juvenile offspring. This hypothesis was tested by determining if the distribution of half-sibling family sizes at the juvenile stage deviated from a null distribution generated by random mating and survival (i.e., Poisson). I further hypothesized that the effective population size, N_e, would be orders of magnitude smaller than the estimated census population size, since increased variance in reproductive success causes reductions in N_e. Results indicated that observed half-sibling family size distributions deviated significantly from both Poisson and overdispersed Poisson (i.e.

negative binomial) distributions. However, the observed data did show a greater tendency to fit the negative binomial distribution better, suggesting that some parents may contribute disproportionately more offspring than expected by random survival. Although N_e estimates were unreliable for 2009 samples, N_e estimates for 2007 were as much as two orders of magnitude lower than the estimated census population size. Results provide preliminary evidence for higher than expected variance in reproductive success, although, increased juvenile sample sizes and additional genotypic loci are necessary to confirm these results in the future.

Introduction

Fish abundance fluctuates because of high variability in recruitment. However, accurately predicting recruitment success and the cause of recruitment variability remains a fundamental challenge for fishery scientists. This is largely due to complexities and uncertainties in the sources that govern successful survival during the first year of life. Before reaching the juvenile stage, high rates of mortality result in less than 1% of larvae surviving (Houde 1987). In stochastic environments, survivors may simply be those produced during chance matching of reproductive activity to optimal environmental conditions (Hedgecock 1994). Under this scenario, the timing of spawning and subsequent hatch dates can determine the temporal coherence of larvae with optimal physical and feeding conditions, thereby influencing growth and survival (Sirois and Dodson 2000, Lapolla and Buckley 2005). Ultimately, however, early-life stages must overcome multiple challenges requiring individuals to evade predators, avoid competitors, locate and capture prey, and

counter unfavorable physical conditions – suggesting that survivors may be exceptional individuals (Crowder and Rice 1992, Rice et al. 1993, Crowder et al. 1997, Fuiman and Cowan 2003). Thus, survival may depend on the characteristics of individual larvae (Rosenberg and Haugen 1982, Methot 1983, Rice et al. 1987, Fuiman et al. 2006).

From the moment of conception, individuals vary in development and growth rates that may predispose some individuals to a higher probability of surviving later developmental stages (McCormick and Hoey 2004). Selection on larval characteristics such as growth rate (Rosenberg and Haugen 1982, Meekan and Fortier 1996), size (Miller et al. 1988, Pepin 1991) and condition (McCormick and Hoey 2004) can occur. Yet, in many cases it is unclear whether selective mortality emerges from density effects upon competitive interactions (Webster 2004), or food and environmental effects on larval growth (Meekan et al. 2003), or genotypic influences on physiological performance (Planes and Romans 2004), or maternal influences such as egg size and provisioning (Jones and McCormick 2002), or a combination of such factors. Identifying which of these selective sources are important could ultimately help explain recruitment variability.

For striped bass (*Morone saxatilis*), food and environmental effects on larval growth and survival have been the most common selective mechanisms used to explain patterns of individual and cohort survival. Evidence suggests that rates of embryo and larval mortality are most influenced by day of spawning, with each daily cohort of larvae experiencing differing fates determined largely by local conditions at spawning and in the following days (Secor and Houde 1995, Rutherford and Houde

1995). In particular, spring temperature and freshwater river flow are recognized as important determinants of survival in Chesapeake Bay (Secor and Houde 1995, McGovern and Olney 1996, Rutherford et al. 1997, Martino and Houde 2010) and in the Sacramento-San Francisco Bay estuary (Turner and Chadwick 1972, Kimmerer 2002).

Selection also appears to favor individual larvae maintained in low salinity waters up-estuary of the salt front (Secor and Houde 1995) and within the estuarine turbidity maximum (ETM) near the salt front (North and Houde 2001, North and Houde 2003, North and Houde 2006). Individuals in the ETM region grow faster (Secor and Houde 1995, Martino 2008) and in high flow years, striped bass larvae and zooplankton prey exhibit greater spatial coherence within the ETM (Martino and Houde 2010). This coherence leads to enhanced feeding opportunities and is subsequently associated with strong year-classes (Martino and Houde 2010).

In addition to the selective pressures induced by abiotic and biotic environmental conditions, laboratory studies indicate that maternal influences may also serve as a selective mechanism on striped bass early-life survival. Maternal influences represent an effect on offspring derived from the maternal parent that may be genetic or phenotypic (Green 2008). In striped bass, maternal influences experiments indicate that striped bass egg hatchability (Zastrow et al. 1989) and early larval survival (Chapter 4) are positively related to female size. However, in Chapter 4 I demonstrated that survival after 12 dph is lower in larvae from larger females – possibly owing to the unique lipid composition of striped bass eggs compared to other species. Still, experimental results indicated that larger females produce larger eggs

and larvae, that remain larger through at least 27-dph (Chapter 4, Zastrow et al. 1989, Monteleone and Houde 1990).

In addition to striped bass, maternal influences on offspring size, growth, or viability is well documented across taxa (Falconer 1965, Roach and Wulff 1987, Bernardo 1996) and in a wide range of marine and freshwater teleosts (see review in Green 2008). Much of this evidence comes from laboratory experiments. Despite the important information laboratory studies provide, most are conducted under optimal or controlled environmental conditions (e.g., Trippel et al. 1997, but see Bengtson et al. 1987, Hutchings 1991, Benoit and Pepin 1999, Einum and Fleming 2000). Consequently, evidence is generally lacking for the role of maternal influences under more natural conditions where selective pressures can be particularly strong and maternal influences may be more significant (Benoit and Pepin 1999).

The value of understanding maternal influences under natural conditions, and the implications of such effects on recruitment (i.e., Marshall and Frank 1999, Scott et al. 1999, Murawski et al. 2001) have recently led to both larger and more natural experiments. The first such experiment was conducted in mesocosms under semi-natural conditions (Clemmesen et al. 2003) and recent experiments have gradually moved into completely natural environments (i.e., Seamons et al. 2004, 2007, Sekino et al. 2005, Williamson et al. 2010). By and large, this transition to natural systems has been aided by development of high resolution genetic markers (e.g., microsatellites) that permit the identification of individuals and discrimination of parental and sibling relationships. Although some studies utilizing genetic markers in natural environments have successfully demonstrated selection for maternal

characteristics (i.e., size) (Seamons et al. 2004, 2007, Williamson et al. 2010), others have produced equivocal results (Sekino et al. 2005).

Most studies evaluating selection for maternal phenotype in nature collect mature adults and utilize nuclear markers to determine parentage of offspring (e.g., Seamons et al. 2004, Seamons et al. 2007, Williamson et al. 2010). However, when parental DNA is not available, researchers must rely on egg-derived characteristics as a surrogate for the maternal phenotype and genotype. This approach requires two key assumptions. First, one must assume that females spawn once and males only spawn with one female to uniquely identify the number and abundance of half-sibling groups (i.e., maternal families). Second, to track the relative changes in abundance of each half-sibling group, one must be able to definitively age individuals in the population to assign individuals to cohorts. Unfortunately, in striped bass, males likely spawn throughout the spawning season and potentially with more than one female per day (Dr. Curry Woods, personal communication). Thus, testing for evidence of maternal selection in wild-spawning striped bass requires the use of a resolute maternal marker (i.e., mtDNA) that can segregate half-sibling paternal families into appropriate maternal families. Recently, however, it was shown that heteroplasmy (i.e., multiple haplotypes) is frequently observed in the striped bass mtDNA genome (Williams et al. 2012). On it own, heteroplasmy is not problematic; however, due to local thermodynamic optima within a PCR reaction, different haplotypes can be preferentially amplified creating one to three groups of haplotypes per individual (unpublished results). As a result, mothers often display sequences that are unique compared to their offspring (unpublished results).

Due to the genetic and biological limitations described above, a specific test of maternal selection in wild striped bass populations is not currently possible. However, it is still possible to provide a preliminary evaluation of whether maternal influences might affect the distribution of survivors. Specifically, I test the hypothesis first suggested by Chapman (1990) that a disproportionate number of offspring are produced by a few females. Because I was limited to using nuclear markers, I specifically tested the hypothesis that the variance in the distribution of half-sibling families is greater than expected by random reproductive success (i.e., a Poisson process). One female and many males, or one male and many females may produce half-sibling families, thus a specific test of maternal influences was not my goal. However, evidence of greater than expected variance in reproductive success could provide preliminary evidence for the possibility of maternal influences in striped bass.

I used a Poisson distribution as my null expectation, based on the theory that if each breeding individual is thought of as producing a large number of potential members of the next generation by producing seeds or eggs, and if the probability of each of these actually becoming a mature member of the next generation is small, independent of the fate of the others, and equal for all of them, then the distribution of the number of offspring of each parent will be Poisson (Holgate and Lakhani 1967). It is well accepted that there may be nonrandom (non-Poisson) distributions of progeny per parent in populations due to genetic, environmental (Hedrick 2005) and possibly maternal influences. If few parents are contributing to age-0 recruitment each year, it was expected that there would be larger variance in reproductive success

than expected under the random survival Poisson model.

If large variance in reproductive success is evident, I further hypothesized that the effective population size, N_e, would be orders of magnitude smaller than the estimated census population size of breeding males and females, since increased variance in reproductive success causes reductions in N_e. Nunney (1996) showed theoretically that the N_e/N ratio within a generation for many organisms should usually be within 0.25 to 0.75. However, in some organisms such as shellfish and fishes there may be very high fecundities and very high mortalities of the early-life stages (i.e., Type III survivorship curves). This combination of high fecundities and selective (or chance) success of the progeny of a few parents can result in quite high variance in progeny number and consequently the N_e/N ratio can be much less than 0.25 (Hedrick 2005). Thus, I specifically hypothesized that the N_e/N ratio would be less than 0.25 in striped bass. In the process of testing these hypotheses, I also evaluated the utility of the sampling design and genetic markers used to test my hypotheses.

Methods

Field sampling

To test for genetic evidence of maternal selection in the field, eggs and juveniles were collected in the Patuxent River (tributary of Chesapeake Bay; Figure 5.1), Maryland during 2007 and 2009. The Patuxent River is a relatively small system (~ 68 river km from mouth to upper spawning grounds) which makes representative sampling of the striped bass population over the region where offspring

may become distributed, feasible in terms of both the likely size of the census spawning (males and females) population (i.e., 4,882 – 10,000; 4,882 based on a 3-fold increase in spawning stock abundance since 1991 [ASMFC 2011]; a probable minimal spawner abundance in 1991 estimated from egg production in Secor and Houde 1995]; and an approximate two-fold greater abundance, 10,000, presuming that egg mortality and inefficient sampling minimized the Secor and Houde (1995) egg abundance estimate. Eggs were sampled in low salinity regions of the river every 3-5 days from the first week of April through mid-May (Table 5.1). On each daily excursion nine to twelve fixed stations were sampled. To represent the entire range of likely egg and larval distributions of striped bass, sampling began at the most downstream station where eggs were absent and continued upstream until no eggs were observed. At each station, a 60-cm paired bongo net (280 μm mesh) was deployed in stepped oblique increments for replicate, five minute-duration tows. A mechanical flow meter (General Oceanics, model 2030R, Miami, FL) was attached to the net to estimate tow distance (d) and volume filtered ($V = [(3.14 \times \text{net diameter}^2)/4] \times d$). Collections were screened on board and eggs were removed and separated into two subsamples (i.e., one from each net). One subsample was placed in cryovials, filled with ambient water and flash frozen in liquid nitrogen. The second subsample was preserved in 4% formaldehyde for egg abundance estimates.

Young-of-the-year juveniles were sampled at 13 fixed beach sites stratified within four subareas of the entire Patuxent River estuary. Sampling was conducted bimonthly in 2007 and weekly in 2009 from the last week in June through the end of July. At each site on each date, 1-3 samples were collected using a 30.5 m long, 1.6

m high, 64 mm mesh, bag-less beach seine. For each sample, the seine was pulled parallel to shore over a measured distance to estimate area swept. In 2007 and 2009, 757 and 899 juveniles were sampled, respectively. Each striped bass juvenile collected was measured (TL) and weighed in the field and placed in 95% ethanol for genetic analyses and otolith-aging analysis.

Aging and cohort selection

To determine the ages and hatch date distributions of surviving juveniles, sagittal otoliths were removed from a subsample of at least 300 juveniles collected each year. For each year, the subsample included juveniles selected randomly in proportion to their relative abundance at each site on each collection date. Prior to aging, otoliths were embedded in epoxy, sectioned in a transverse plane with an Isomet saw and mounted on a glass slide. Otoliths were polished to the core with 3-μm alumina to create an even plane and eliminate surface pits and cracks (Secor et al. 1991). A light microscope (Olympus BX51, Center Valley, PA, USA) fitted with a digital camera (Lumenera Infinity 1, Ottawa, ON, Canada) was used to capture color images of otoliths that were used to count the number of daily increments of each juvenile. Daily increments have been verified in striped bass and can be accurately read in well fed juveniles for the first 68 days (Jones and Brothers 1987). Each otolith was read once by two readers. If the difference in increment counts between two readers was ≥ 10%, otoliths were re-read by each reader. If increment count differences remained ≥ 10% those juveniles were not included in the analyses. Final increment count equaled the mean of the counts for two readers. Final ages were

calculated as the number of increments plus a temperature-adjusted correction factor for first increment deposition (Houde and Morin 1990).

These ages were used to determine a preliminary hatch date frequency distribution for each year. For each year, the final hatch date distribution was estimated from individuals collected during the second week of July, because this was the only week when all sizes had recruited to the seine. These hatch date distributions were then adjusted for cumulative mortality differences in daily cohorts by applying a constant daily mortality rate of 0.01 d^{-1} (i.e., juvenile mortality rate estimated by Martino 2008]). Back-calculated hatch dates were then used to determine the window(s) when the surviving cohorts were produced during 2007 and 2009. Juvenile survivors of the dominant cohorts from this window were used in subsequent molecular and statistical genetic analyses.

Egg abundance and phenotype

To estimate egg abundance and determine the genotypes of eggs corresponding to the surviving juvenile cohorts, hatch dates of the dominant juvenile cohorts were used to determine the egg sampling dates to include in all subsequent analyses. Thus, although eggs were observed in collections outside of the juvenile hatch date frequency distribution, those eggs were not counted or genotyped for this study. By excluding non-surviving cohorts, I provide the best means of testing for evidence of maternal based non-random survival by: 1) reducing the number of family lines to track, 2) and eliminating family lines that likely died from mass mortality events, such as storms and temperature declines.

Using formalin preserved eggs from bongo net collections, eggs from one tow, per site, per date were sorted and counted to determine the number of eggs collected at each site on each date. Egg densities (D; number m^{-3}) at each site on each day were estimated from egg counts and volume filtered based on flowmeter readings. The abundance of eggs (A) expressed as the numbers of eggs under 1.0 m^2 of river surface was derived from the density estimates: $A = dD$, where d = mean river depth (meters) at each station (*sensu* Secor and Houde 1995). The estimated river-segment egg abundances were calculated by multiplying the abundance at each station by the area of the river segment that each station represented. River segment boundaries were defined as the mid-distances between adjacent stations. Riverwide abundances for each collection day were estimated by summing all station abundances. Areas and volumes represented by stations were obtained from Cronin (1971). Frozen eggs from those sampling dates were slowly thawed under refrigeration (4°C) and individual eggs were then placed in vials filled with 95% ethanol for subsequent genetic analyses.

Molecular techniques

DNA was extracted, amplified and genotyped from preserved eggs and juveniles. DNA from juvenile white muscle or gill tissue was extracted using the Qiagen DNeasy Blood and Tissue Kit (Valencia, CA). Due to the high lipid content of striped bass eggs, DNA from individual eggs was extracted by placing each whole egg into beaded columns within a solution of 83 µl each of TE (1% Tris [1M, pH 8.0], 0.2% EDTA [0.5M, pH 8.0], 98.8% DI water), 10% Chelex, 2% Sarcosyl, and

20 µl proteinase K. Columns were boiled at 97°C for 5 min and subjected to a series of cooling and mixing in a FastPrep Cell Disrupter (Carlsbad, CA). Vials were then centrifuged, and the aqueous solution placed in Zymo columns (Zymo DNA Clean and Concentrator kit, Irvine, CA) to elute purified DNA for amplification. DNA from both eggs and juveniles was then amplified using PCR with 5 microsatellite loci (MSM1558, MSM1559, MSM1592, MSM1602, MSM1626) identified by Rexroad et al. 2006).

Each microsatellite locus was amplified and labeled using 5' dye labeled oligonucleotide primers as follows: 10µl reactions consisting of 3µl DEPC treated water, 5µl Promega 2X master mix (M7505, Madison, WI), 1µl forward and reverse primer at 5µM each and 1µl 10ng/µl DNA template were cycled in an MJ Research PTC-200 thermal cycler (St. Bruno, Quebec, Canada) using a 384 well aluminum block. Cycling conditions consisted of an initial denaturation at 95°C for 2 minutes, 35 cycles of denaturation at 95°C for 15 seconds, primer annealing at 56°C for 30 seconds, and elongation at 72°C for 1 minute, followed by a 15 minute polishing step at 72°C and a final temperature of 4°C. 2.5µl of the reactions for each of the four dye types (FAM, NED, VIC, and PET) were combined and precipitated with 1µl of 3M sodium acetate pH 5.6 and 25µl of 95% ethanol for 20 minutes at -20°C. Samples were spun at 3000 × g for 20 minutes and the supernatant was decanted. The pellets were washed with 50µl of 70% ethanol, centrifuged at 3000 × g for 5 minutes, and the supernatant was decanted. The plates were inverted and spun at 50 × g for 2 minutes to remove residual ethanol and air-dried for 5 minutes. Labeled products were resuspended in 10µl HIDI formamide (4311320, Applied Biosystems, Carlsbad,

CA) and 0.5μl LIZ 500 size standard (4322682). Samples were heat denatured at 95°C for 3 minutes and snap cooled on ice before loading onto a 3130XL genetic analyzer (Applied Biosystems) for electrophoresis. Alleles were scored and sized using Genemapper 3.0 (Applied Biosystems) and binned using TANDEM (Matschiner 2009).

Data analysis

All loci were first characterized for each year and life-stage combination. Observed heterozygosity, expected heterozygosity and allele number were calculated using Arlequin version 3.11 (Laurent Excoffier 2005). Deviations from Hardy-Weinberg equilibrium (HWE) and heterozygote deficiencies were examined in GENEPOP 4.0.10 using an exact test based on a Markov Chain method (Rousset 2008). Null allele frequencies were also estimated using maximum likelihood and the EM algorithm of Dempster and Laird (1977). The presence of genotypic disequilibrium between all pairs of loci in each year and life-stage was tested using the log-likelihood ratio *G*-statistic implemented in GENEPOP. Significance levels for deviations from HWE, heterozygote deficiencies and genotypic disequilibrium were adjusted for multiple simultaneous comparisons according to the sequential Bonferroni procedure using a global significance level of 0.05 (Rice 1989). Allelic richness was estimated using rarefaction to compensate for sample size disparities (Kalinowski 2005).

To estimate the number and size of half-sibling groups for each year and life-stage combination, kinship reconstruction analyses were conducted using a pairwise

score method implemented in the online software PEDIGREE 2.2 (http:// herbinger.biology.dal.ca:5080/Pedigree). Because females are likely to spawn with multiple males on a given day, half-sibling groups were reconstructed rather than full-sibling groups. However, because males are also likely to spawn more than once per season and possibly multiple times per week or day (Dr. Curry Woods, personal communication), a half-sibling group may also be composed of multiple females. To reduce the possible number of females associated with a juvenile half-sibling group, the half-sibling groups estimated in PEDIGREE were further broken down into 7-day cohorts using the otolith based hatch date estimates. A 7-day cohort was used because Secor et al. (1995) showed that mean aging error was ± 3 d in fish aged up to 40 d. Although the mean age of juveniles collected in both years was 65 d, the results of Jones and Brothers (1987) suggests little difference in the aging error between 40 and 65 d in juvenile striped bass.

To determine whether the distribution of half-sibling family sizes in each year represented a random process, the observed distributions were compared to the null expected Poisson distribution:

$$\frac{e^{-x}\mu^{x}}{x!}$$

where x is the half-sibling group size and μ is the ratio of the true juvenile sample size to the observed total number of half-sibling groups estimated by PEDIGREE. Alternatively, if the observed distribution signified higher variance in reproductive success than expected with random family survival, then the distribution should fit better to an overdispersed Poisson distribution (i.e., variance > mean). To test this

hypothesis, the observed distribution was compared to a negative binomial distribution:

$$\frac{x+k-1}{x}\frac{\mu}{k+\mu}$$

where x and μ have the same definition as the Poisson distribution and k is the overdispersion parameter. The observed distributions were also compared to the expected Poisson and negative binomial distributions under scenarios of increasing half-sibling group sizes until half-sibling group sizes equaled the true juvenile sample size. Assuming the observed half-sibling distributions (i.e. by proportion) in each year were accurate, these additional comparisons permitted an assessment of whether the number of half-sibling groups observed was underestimated. In other words, if the observed data fit better to the expected distributions with larger half-sibling group sizes, there would be support for the conclusion that the number of half-sibling groups observed was underestimated. To determine whether the observed distributions were significantly different from a Poisson or negative binomial distribution, chi-squared analysis was conducted.

Poisson and negative binomial distributions were also examined in a simulation to determine the possible combination of juvenile sample size and total number of half-sibling groups that would permit distinguishing one distribution from the other. The analysis was conducted as a 5 × 5 factorial design that included five levels for the number of total half-sibling groups (100, 125, 250, 500, 1000) and five levels of juvenile sample sizes (100, 125, 250, 500, 1000). This design enabled determination of the possible juvenile sample sizes required to distinguish the null Poisson distribution against the alternative negative binomial distribution.

To evaluate whether the half-sibling reconstructions and half-sibling family size distributions were accurate, the likely resolution of the five microsatellites used in this study was evaluated. To evaluate the resolution of five microsatellites, the number of half-sibling groups was estimated separately using two, three, four and five loci. The working assumption was that sufficient resolution should be achieved if there was an asymptotic relationship between the number of loci and the number of half-sibling groups. To account for the possibility of large sibling groups artificially resulting in an asymptotic relationship when all individuals were included, analyses were also conducted using random sub-samples of 50 and 150 individuals.

Finally, two genetic methods were used to estimate the effective population size (N_e). The online program ONeSAMP was used to estimate short-term effective population size estimates as inferred from single time samples. This method enabled separate estimates of N_e for the 2007 and 2009 juveniles collected. ONeSAMP is a recently developed method, estimating N_e and 95% credible limits (CL) using approximate Bayesian computation (Tallmon et al. 2008). ONeSAMP uses eight summary statistics for which population genetics theory or simulations have established a relationship with N_e (Tallmon et al. 2008). This method generates 50,000 simulated populations with N_e between an upper and a lower limit specified by the prior. For this analysis, the upper and lower limits were set at 2-400, 4-1000 and 6-2000 to test the robustness of the estimates to changes in the prior. The second method used to estimate N_e considers linkage disequilibrium, the nonrandom association of alleles at different loci (LDNE; Waples 2008). In this analysis, only alleles with frequency ≥ 0.05 were included. Using LDNE confidence intervals were

estimated using jackknife methods, because parametric methods tend to produce confidence intervals that are too narrow (Waples 2008). N_e estimates were obtained for juveniles from both years and eggs from 2009. Estimates could not be obtained from 2007 eggs due to too many missing data.

Results

In both years, striped bass egg abundance peaked after water temperatures first began to rise above 12°C and declined thereafter (Figure 5.2). In 2007, this peak might have occurred a few days prior to April 23; however, due to logistical constraints sampling was not conducted between April 14 and April 22, 2007. Without those sampling dates in 2007, it appears that peak egg abundance was higher in 2009, but this cannot be confirmed (Figure 5.2). Still, eggs were present on all sampling dates in 2009, but in 2007 eggs were not evident in samples collected after May 8 (Table 5.1). By design, eggs were not counted on dates that fell outside of the juvenile hatch date frequency; however, in both years eggs were present prior to the hatch dates of the first observed surviving juvenile cohorts (Figure 5.2).

The juvenile hatch date frequency distribution indicated that the egg sampling design used in this study did cover the dominant range of hatch dates for the surviving juveniles. The hatch date frequency also indicated that the first survivors appeared after water temperatures on the nursery grounds were > 12°C, but the largest proportion of survivors hatched when water temperatures were > 15°C (Figure 5.2).

Genetic results from egg and juvenile tissues showed that all five microsatellite loci were polymorphic for each year and life-stage combination analyzed (Table 5.2). Observed and expected heterozygosities were high for each locus and ranged from 0.821 to 0.984 (Table 2). Allelic richness (A_R) varied across loci, but was consistently highest at MSM1592 and MSM1626 (Table 5.2). In general A_R was higher at each locus in the juvenile samples compared to the egg samples collected each year (Table 5.2). A_R was similar for juveniles in 2007 and 2009 at all loci except at MSM1558 and MSM1602, which were higher in 2007 (Table 5.2). A_R was similar for eggs in 2007 and 2009 at all loci (Table 5.2).

For each year and life-stage combination, the majority of loci were not in Hardy-Weinberg equilibrium (HWE) after correction for multiple tests (Table 5.2). In juveniles, null alleles did not appear to be the cause for the significant departures from HWE expectations since there was only one indication of significant heterozygote deficit (2007: MSM1559) and there were no high estimated frequencies of null alleles (Table 5.2). However, in the eggs, MSM1592 and MSM1626 showed significant heterozygote deficit in both years and null allele frequency estimates were higher than those in juveniles, indicating that null alleles may be responsible for the departures from HWE in eggs.

Tests among pairs of loci indicated that linkage disequlibrium was rarely significant (Table 5.3). With the exception of eggs in 2007, which had two loci pairs exhibiting significant linkage disequilibrium, all other year and life-stage combinations had only one pair of loci exhibiting significant linkage disequilibrium (Table 5.3). Furthermore, none of the pairs showed consistent linkage disequilibrium

across all year and life-stage combinations, although the significant linkage of MSM1559 × MSM1602 was consistent for eggs in both years (Table 5.3).

Sibship reconstructions of juveniles during both years indicated that most (2007: 75%, 2009: 62%) half-sibling partitions were composed of one or two siblings in a 7-day cohort (Figure 5.3). Although half-sibling groups were as large as 13 individuals in 2009, the relationships between the number of loci and the number of half-sibling groups discussed below indicate that these group sizes may be inflated.

In both years, observed half-sibling group size distributions were statistically different from the expected Poisson and negative binomial frequencies produced when the juvenile sample size and total number of half-siblings were set equal to those in the observed distribution (Figure 5.4). Visual inspection, however, clearly indicates that the observed distributions in both years demonstrated a better fit to the overdispersed negative binomial distribution. Furthermore, the more overdispersed observed distribution in 2009 exhibited a better fit to the negative binomial distribution (Figure 5.4). The observed distributions in both years also displayed better fits to Poisson (i.e., based on visual inspection) and negative binomial (i.e., no statistical difference) expected frequencies when the number of half-sibling groups was increased above the number of half-sibling groups observed in the true sample size (Figure 5.4).

To evaluate the possible juvenile sample sizes required to test the null hypothesis of a Poisson distributed half-sibling group number against the alternative negative binomial distribution, a factorial designed simulation was conducted. Results from this analysis indicated that to detect a difference between a Poisson and

negative binomial distribution, the juvenile sample size likely needs to be greater than four times the number of half-sibling groups present in the population (Figure 5.5).

To evaluate the reliability of the sibling reconstructions conducted, the relationship between the number of microsatellite loci and the number of partitioned half-sib groups was evaluated using random subsamples of 50 and 150 individual juveniles and eggs and juveniles combined. Under each subsampling scheme except one (i.e., subsample of 50 eggs and juveniles from 2009), the relationship between the number of loci and number of half-sibling groups showed no tendency to reach an asymptote (Figure 5.6).

Effective population size (N_e) estimates were variable during both years. When using 2007 juveniles and the ONeSAMP procedure, results were relatively robust to changes in the prior, producing mean N_e of 276.88 (95% CL = 236.98 – 329.35), 323.15 (95% CL = 265.11 – 382.42), and 291.47 (95% CL = 243.55 – 339.82), when priors were set at 2-400, 4-1000 and 6-2000, respectively. ONeSAMP estimates of N_e were not robust to changes in the prior when using 2009 juveniles. These mean N_e estimates were 491.21 (95% CL = 427.74 – 573.49), 688.32 (95% CL = 580.63 – 827.13) and 961.36 (95% CL = 742.56 – 1123.62), when priors were set at 2-400, 4-1000 and 6-2000, respectively. LDNE calculated slightly lower estimates for the 2007 juveniles (mean = 97.5, 95% CI = 63.7 – 157.6) and the large confidence intervals produced when evaluating the 2009 juveniles (mean = 528.3, 95% CI = 250.6 – 5009.4) suggested that the 2009 estimates were not reliable.

N_e estimates for eggs in 2009 appeared to be more reliable than for juveniles. When using ONeSAMP, mean N_e was estimated at 431.2 (95% CL = 369.7 – 512.8),

402.53 (95% CL = 351.63 – 498.77) and 443.21 (95% CL = 351.23 – 525.69). As for the juveniles, slightly lower estimates for N_e were obtained using the LDNE procedure (mean = 263.7, 95% CI = 188.5 – 393.0). However, the N_e for eggs in 2009 was surprisingly similar if not lower than the juvenile N_e. Regardless of the estimation method or life-stage, the N_e/N ratio ranged from 0.01 to > 1 with 95% confidence intervals and limits considered, but for the most reliable juvenile data in 2007 the ratio was between 0.01 and 0.08. Although the robustness of these methods to loci number has not been fully evaluated in in published estimates from literature, N_e were similar when either four or five loci were used with the data in 2007 (Table 5.4). However, when the juvenile data in 2009 were evaluated at 2, 3, 4, and 5 loci the results again indicated unreliable results (Table 5.4). Overall, these results indicate that the juvenile N_e estimates and N_e/N ratios in 2007 were the most reliable.

Discussion

Based on low observed levels of genetic variability in Chesapeake Bay striped bass, Chapman (1990) suggested that "inordinately successful spawning by a few females could produce dominant year classes in which a few genotypes are over-represented." I set out to test this hypothesis in the Patuxent River, Maryland by evaluating whether the variance in the distribution of juvenile half-sibling families was greater than expected by random reproductive success (i.e., a Poisson process). If few parents are in fact contributing disproportionately to age-0 recruitment, I also hypothesized that N_e would be orders of magnitude smaller than the estimated census population size, since increased variance in reproductive success causes reductions in

N_e. My results indicated that the observed half-sibling family distributions of juveniles collected in 2007 and 2009 were statistically different from either a Poisson or overdispersed (i.e., negative binomial) distribution. However, the fits were clearly closer to a negative binomial distribution. In addition, the 2007 juvenile data indicated that the ratio of N_e/N (i.e., estimated as low as 0.02) was nearly two orders of magnitude smaller than the estimated census size. Together these results suggest that if the observed half-sibling distributions and N_e estimates are accurate, then some parents, and potentially some females may be contributing disproportionately to the Patuxent River striped bass population.

Absent the likely deficiencies of my data (discussed below), my results are largely consistent with Chapman (1990) suggestion that a disproportionate number of offspring are produced by a few females – or in my specific case, a few maternal or paternal families. This of course assumes that my juvenile collections represent the majority of surviving families and my census population sizes are relatively accurate. Chapman (1990) based his suggestion of high variability in reproductive success on the observation of low mtDNA variability and the dominance of specific haplotypes. Although Chapman (1990) did not specifically implicate maternal influences as a cause for his observation, this certainly could be a factor driving my observation of high variance in the half-sibling distributions. In fact, in salmonids, female size has often been observed to provide a fitness advantage, resulting in as much as 23-fold higher reproductive success in large compared to small females (van den Berghe and Gross 1989, Ford et al. 2008). Often, however, salmonid males exhibit higher variance in reproductive success than females, with larger males showing greater

fitness (Dickerson et al. 2005, Ford et al. 2008). More recently, Rowe et al. (2008) showed that pelagic spawners (i.e., Atlantic cod [*Gadus morhua*]) can also exhibit high variance in male reproductive success that is positively correlated with male size. Thus, both maternal and paternal influences could be responsible for the reproductive variance observed in my study.

Despite the potential for maternal and paternal influences to affect reproductive variance, the sweepstakes reproductive success (SRS) hypothesis (Hedgecock 1994) is the most common explanation for the high variance in reproductive success. This is particularly true for broadcast spawning species like striped bass, which are characterized by high fecundities and high early-life mortality (i.e., Planes and Lenfant 2002, Osborne et al. 2005, Gomez-Uchida and Banks 2006, Hedgecock et al. 2007, Liu and Ely 2009). This hypothesis suggests that for species with type III survivorship, the majority of recruited offspring in a given spawning season may be from a small number of parents because of the necessity of matching reproductive activity with environmental conditions condusive to spawning, fertilization, larval development and recruitment. In fact, in striped bass, SRS was the proposed explanation for the high variance in reproductive success observed in three age-0 annual cohorts produced in the Santee-Cooper system, South Carolina (Liu and Ely 2009). As in my study, Liu and Ely (2009) used microsatellites and sibship reconstruction to show that the variance in sibling family size was high. Specifically, they showed that full-sib families made up 31-60% of the juveniles collected each year. They also observed full-sib families as large as 27 individuals – a size much larger than the largest half-sib family (i.e., 13 individuals) observed in

my study. It is possible, however, that the Liu and Ely (2009) results are atypical of natural spawning, open populations along the Atlantic coast. The Santee-Cooper system is land-locked and annually stocked with large numbers of hatchery-produced progeny from a low number of contributing parents (Liu and Ely 2009). Thus, it is likely that the large, full-sib families they observed were a function of artificial breeding and stocking practices. My results might be more typical of natural spawning populations; however, this assumes my results are accurate.

A test of my second hypothesis could only be assessed on the 2007 juvenile data due to unreliable N_e estimates from 2009 juveniles. N_e estimates from 2009 juveniles had very large confidence intervals (LDNE estimate) or were not robust to changes in the prior (ONeSAMP). In contrast, the N_e estimate based on 2007 juveniles was quite low when using both N_e estimation procedures and was robust to changes in the prior. Furthermore, as hypothesized, the N_e/N ratio in 2007 was less than 0.25 when using both methods and including confidence intervals. N_e/N ratios can be much less than 0.25 when species exhibit a combination of high fecundities and selective (or chance) survival of offspring from a few parents (Hedrick 2005). The result is high variance in reproductive success, which appeared to be evident in the half-sibling group size distributions as well. The low N_e/N observed in 2007 is certainly consistent with my half-sibling distributions fitting closer to a negative binomial distribution and higher than expected variance in reproductive success.

In theory, the low N_e I observed in 2007 could be due to fluctuating population sizes or unequal sex ratios. In fact, striped bass males may outnumber females on the spawning grounds by more than 10:1 (Chapman 1990). However,

population abundance has been relatively stable since 1996 (ASMFC 2011). Furthermore, sex ratios likely do not vary substantially from year to year. Thus, the low N_e observed in 2007 may be due to high variance in reproductive success, which in turn could be due to maternal selection.

Although sexual selection, including maternal selection, may explain the low N_e/N observed in the 2007 Patuxent River striped bass population, SRS is the most common explanation for high variance in reproductive success. In fact, low N_e/N is a key element of the SRS hypothesis, which suggests that N_e should be orders of magnitude smaller than N if the number of winners of the sweepstakes reproductive lottery is small (Hedgecock 1994, Hedgecock et al. 2007). Tests of the SRS hypothesis are numerous in a broad range of marine animal taxa. Furthermore, most studies that evaluate N_e/N ratios in broadcast spawning species show strong support for the hypothesis, with N_e/N ratios often five orders of magnitude lower than census adult population sizes (Hauser et al. 2002, Turner and Wares 2002, Hutchinson et al. 2003, Hoarau et al. 2005, Gomez-Uchida and Banks 2006). In 2007 I observed N_e estimates (ONeSAMP: 95% confidence limits = 243.6-339.8; LDNE: 95% confidence interval = 63.7-157.6) that could be up to two orders of magnitude smaller than my estimated N (4,882-10,000) – a value much larger than that observed in pelagic marine spawners such as Atlantic cod, dark-blotched rockfish (*Sebastes crameri*), New Zealand snapper (*Pagrus auratus*), red drum (*Scianops ocelletus*) and plaice (*Pleuronectes platessa*) (Hauser et al. 2002, Turner and Wares 2002, Hutchinson et al. 2003, Hoarau et al. 2005, Gomez-Uchida and Banks 2006).

The N_e/N ratio observed in 2007 also was higher than that observed in the Santee-Cooper population, which had a ratio of 0.00025 (Liu and Ely 2009). However, as noted above, stocking practices may have affected the N_e/N ratio in the Santee-Cooper system. In fact, the Ne/N ratio observed in 2007 was closer to the lower end of Ne/N ratios observed in Pacific salmonids, which can range from 0.02 – 0.73 (Ardren and Kapuscinski 2003, Shrimpton and Heath 2003). The lower N_e/N in salmonid populations are likely attributed to reductions in returning spawners as a result of anthropogenic disturbances (Shrimpton and Heath 2003). Thus, it appears that my N_e/N ratio for striped bass in 2007 is generally less than that observed in benthic spawning salmonids, but greater than that observed in marine pelagic spawners.

Although my observation of a low N_e/N in 2007 appears to be sound based on the two methods used to estimate N_e and the consistent results with four and five loci, my observation of a deviation in the half-sibling family distribution from a Poisson model is far from conclusive. This is due to low resolution of my analysis, which included only five microsatellite loci. The low resolution was evident when I evaluated the relationship between the number of loci and the number of half-sibling families estimated at those loci. When I took random samples of 50 and 150 individuals, or included all individuals genotyped, linear to exponential trends were observed in these relationships. If resolution had been sufficient, the number of half-sibling groups should have reached an asymptote with an increasing number of loci. The absence of an asymptotic relationship indicates that the sibling group sizes reported in this study are maximum estimates. This conclusion was also supported by

the fact that my observed half-sibling group size distributions fit better to both Poisson and negative binomial distributions when the total number of half-sibling groups modeled was greater than the total number of half-sibling groups observed. Together, these results indicate that additional loci are necessary to produce reliable half-sibling reconstructions.

The influence of additional loci on the half-sibling distribution is unknown, but it would likely decrease the numbers of larger sibling groups and change the shape of the observed distributions. It is certainly possible that the sibling family distributions would still deviate from a Poisson distribution, but only future studies can confirm my findings. Thus, future field studies that aim to test hypotheses regarding maternal influences in striped bass will need to further evaluate the required number of microsatellite (or other nuclear markers) loci needed to conduct sibling or parental reconstructions with sufficient resolution. My results clearly indicate that five loci are insufficient.

In addition to the low resolution of using five microsatellite loci to conduct sibling reconstructions, the markers themselves also showed a tendency to exhibit deviations from Hardy-Weinberg expectations. The primary concern with these deviations was the possible presence of null alleles. In my study, null alleles could potentially explain the deviations from Hardy-Weinberg expectations; however, if this were true heterozygote deficits should be apparent. Although heterozygote deficits were consistent at MSM1592 and MSM1626 in eggs from both years, juvenile data only showed a significant deficit at MSM1559 in 2007. For problematic loci in eggs, a large number of samples were removed from the analysis due to poor

expression of PCR product. Poor expression also may have accounted for the higher frequency of null alleles in eggs compared to juveniles. Thus, the potential issue with null alleles appears to be limited to egg DNA and two loci. If future research endeavors include egg DNA in their analyses different loci may need to be utilized. Given the low concentration of DNA in eggs, this will likely require further optimization of PCR conditions so that less DNA template is utilized in experiments to select ideal loci.

Interestingly, Liu and Ely (2009) also observed significant deviations from Hardy-Weinberg expectations in juvenile striped bass collected in the Santee-Cooper system. They suspected this might be due to a low number of contributing parents, which may also be the case in the Patuxent River. It is also possible that highly polygynous behavior in males could lead to deviations from Hardy-Weinberg expectations, especially if a small number of males are contributing more to the juvenile population.

Although future research to test hypotheses regarding maternal selection may not need to rectify the observed deviation from Hardy-Weinberg expectations in juveniles, future studies must reliably estimate the number juveniles needed to test the null hypothesis that the observed distribution of sibling groups is Poisson distributed. I conducted a factorial designed simulation to determine the juvenile sample size necessary to distinguish between a Poisson random process and an overdispersed process (i.e., negative binomial) indicative of high reproductive variance. My results indicated that regardless of the true number of half-siblings present in the juvenile population, the sample size necessary to detect a difference between a Poisson and

negative binomial distribution would need to be approximately four times larger than the number of half-sibling groups. Of course, these results are based on the use of five microsatellite loci. Since more microsatellite loci are clearly needed to accurately partition individuals into sibling groups, it is possible that the distributions and sample size requirements will change. Thus, future simulations will be necessary to effectively determine the necessary samples sizes needed to test my hypotheses.

If eggs are used in future research to test hypotheses regarding reproductive variance, samples sizes will likely need to be much higher than those collected for juveniles. Although I genotyped nearly twice the number of eggs in 2009 compared to juveniles, rarefied allelic diversity was lower in eggs and N_e appeared to be lower in eggs. Theoretically, allelic diversity and N_e in eggs should be equal to or greater than values observed in juveniles. My different result suggests that the number of eggs genotyped and possibly the frequency of sampling in the field were insufficient. This certainly indicates that a much larger number of eggs must be sampled for genetics and possibly at greater frequency than every three days.

Regardless of the egg sample size requirements, without a maternal marker eggs will not be good surrogates of maternal genotype given the ability and likelihood that male striped bass spawn multiple times with multiple females in a season (Dr. Curry Woods, personal communication). Although microsatellites are capable of partitioning individuals into full and half-sibling groups, a full-sibling group could underestimate the family size of a female given that she could and likely does spawn with multiple males (i.e., based on laboratory behavior [Hocutt et al. 1990]). Additionally, half-sibling groups observed could represent one female mating with

multiple males, or one male mating with multiple females. Otolith based daily aging of juveniles could help to partition the half-sibling families down to smaller sizes, however, daily aging is only accurate to within ± 3 days at best. Thus a half-sibling family could only confidently be partitioned into one-week periods, which could represent many females spawning with one male. Consequently, without a maternal marker, eggs will never be successful surrogates of maternal genotype in striped bass. Any future studies that hope to test for evidence of female reproductive variance or maternal influences in striped bass will need to develop a maternal marker or capture adults and reconstruct family relationships using nuclear markers and parentage analysis. Given that molecular technology is currently available to to proceed with the latter option, collection of adults should be the next step in testing for evidence of maternal influences in natural striped bass populations.

Together, my results suggest that variance in reproductive success in striped bass may be greater than expected for a random Poisson process. This evidence leaves open the possibility that a small proportion of females contribute to recruitment. Thus, maternal influences could affect the distribution of juvenile survivors in a population. However, due to the deficiencies in my data and restrictions on using nuclear DNA markers, a full and adequate test of my hypotheses cannot be conducted at this time. To ensure successful future tests of my hypotheses, simulations to determine appropriate sample sizes must precede research efforts. Furthermore, if eggs are to be used as surrogates of maternal phenotype and genotype, then resolute maternal markers must be developed. In lieu of maternal markers, parentage analysis can be conducted using nuclear markers, but this will

require adequate sampling of adult striped bass. However, often fewer than 100 females are caught annually during the Maryland Department of Natural Resource's annual spawning stock survey (personal observation), suggesting that catching a large proportion of spawning females may be prohibitively difficult. The challenges of testing my hypotheses on a pelagic spawning species are evident from this study; however, with adequate funding and strategic methodologies a better understanding of maternal influences in wild striped bass populations can be achieved.

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Table 5.1. Dates when striped bass eggs were collected by bongo net in the Patuxent River.

2007		2009	
Date	Eggs Present?	Date	Eggs Present?
April 3	yes	April 2	yes
April 7	no	April 7	yes
April 10	yes	April 10	yes
April 13	no	April 13	yes
April 23	yes	April 16	yes
April 27	yes	April 20	yes
April 30	yes	April 23	yes
May 2	yes	April 27	yes
May 4	yes	April 30	yes
May 8	yes	May 4	yes
May 10	no	May 7	yes
May 12	no	May 11	yes
May 18	no		

Table 5.2. Summary of microsatellite diversity and statistics for 5 loci evaluated in egg and juvenile striped bass collected in the Patuxent River. Shown are the number of alleles (n), rarefied estimates of allelic richness (A_R), observed heterozygosity (H_o), expected heterozygosity (H_e), *P*-values for Hardy-Weinberg equilibrium (HWE) tests (Arlequin 3.1), heterozygote deficit and null allele frequencies (Genepop 4.0.10). Significant deviations from HWE and significant heterozygote deficit after sequential Bonferroni correction are indicated by an asterisk (*).

Locus	n	A_R	H_o	H_e	Hardy-Weinberg equilibrium *P*-value	Heterozygote deficit *P*-value	Null allele frequency
2007 Juveniles (N = 298)							
MSM1558	19	17.95	0.885	0.886	< 0.0001*	0.04	0.0088
MSM1559	19	18.75	0.899	0.926	< 0.0001*	0.0028*	0.0201
MSM1592	29	25.53	0.952	0.935	0.0296	0.13	0.0028
MSM1602	18	17.07	0.891	0.903	< 0.0001*	< 0.0001	0.0016
MSM1626	26	24.16	0.930	0.941	0.0004*	0.18	0.0067
2007 Eggs (N = 259)							
MSM1558	14	13.77	0.841	0.837	< 0.0001*	0.0035	0.0197
MSM1559	14	13.84	0.821	0.866	0.0015*	0.115	0.0119
MSM1592	28	27.28	0.865	0.919	< 0.0001*	0.0068*	0.0557
MSM1602	14	13.98	0.859	0.880	< 0.0001*	< 0.0001*	0.0287
MSM1626	21	21.00	0.868	0.917	0.03	0.0008*	0.0245
2009 Juveniles (N = 341)							
MSM1558	15	14.62	0.984	0.889	0.0007*	1	0
MSM1559	20	17.68	0.895	0.921	< 0.00001*	0.032	0.0128
MSM1592	29	26.96	0.971	0.938	0.099	0.09	0.0014
MSM1602	14	13.63	0.958	0.901	0.00003*	1	0
MSM1626	28	26.15	0.974	0.952	0.08	0.99	0
2009 Eggs (N = 616)							
MSM1558	15	13.85	0.859	0.831	< 0.0001*	0.008	0.0085
MSM1559	15	13.52	0.868	0.798	< 0.0001*	0.0011	0.0133
MSM1592	31	25.54	0.927	0.929	0.1	< 0.0001*	0.0117
MSM1602	15	13.35	0.889	0.877	< 0.0001*	0.041	0.0087
MSM1626	26	21.72	0.855	0.929	< 0.0001*	< 0.0001*	0.0427

Table 5.3. *P*-values for genotypic disequilibrium between all pairs of loci for eggs and juveniles collected in 2007 and 2009. Significant genotypic disequilibrium after sequential Bonferroni correction for multiple tests is shown by an asterisk (*).

	2007		2009	
Locus pair	Eggs	Juveniles	Eggs	Juveniles
MSM1558 ! MSM1559	0.00454*	0.03806	NA	0.11349
MSM1558 ! MSM1592	0.01661	0.26892	0.01053	0.00246*
MSM1559 ! MSM1592	0.40286	0.71026	0.18333	0.45406
MSM1558 ! MSM1602	0.03289	0.15927	0.02104	0.00699
MSM1559 ! MSM1602	< 0.00001*	0.01001	0.0015*	0.67149
MSM1592 ! MSM1602	0.03037	0.62515	0.32964	0.31524
MSM1558 ! MSM1626	0.01308	0.03112	0.0663	0.19829
MSM1559 ! MSM1626	0.81259	0.46215	0.01255	0.77569
MSM1592 ! MSM1626	0.21544	0.0315	0.23525	0.25454
MSM1602 ! MSM1626	0.42671	0.00129*	0.38111	0.32688

Table 5.4. Effective population size estimates when using between 2 and 5 microsatellite loci. The asterisk indicates that uninformative (i.e., negative) values were produced.

Number of loci used	Method	Mean N_e	95% CI
	2007 Juveniles		
2	LDNE	152.6	60.1 - 800.8
3	LDNE	61.7	42.2 - 91.0
4	LDNE	102.1	75.6 - 141.6
5	LDNE	97.5	63.7 - 157.6
2	ONeSAMP	385.1	106.1 - 1105.3
3	ONeSAMP	362.5	304.2 - 397.5
4	ONeSAMP	323.4	281.2 - 368.1
5	ONeSAMP	291.5	243.6 - 339.8
	2009 Juveniles		
2	LDNE	*	
3	LDNE	1901.4	361.5 - infinity
4	LDNE	1917.3	488.5 - infinity
5	LDNE	528.3	299.9 - 1528.4
2	ONeSAMP	2014.3	501.5 - 4116.9
3	ONeSAMP	1322.2	752.2 - 1768.6
4	ONeSAMP	1254.3	841.1 - 1565.5
5	ONeSAMP	961.4	742.6 - 1123.6

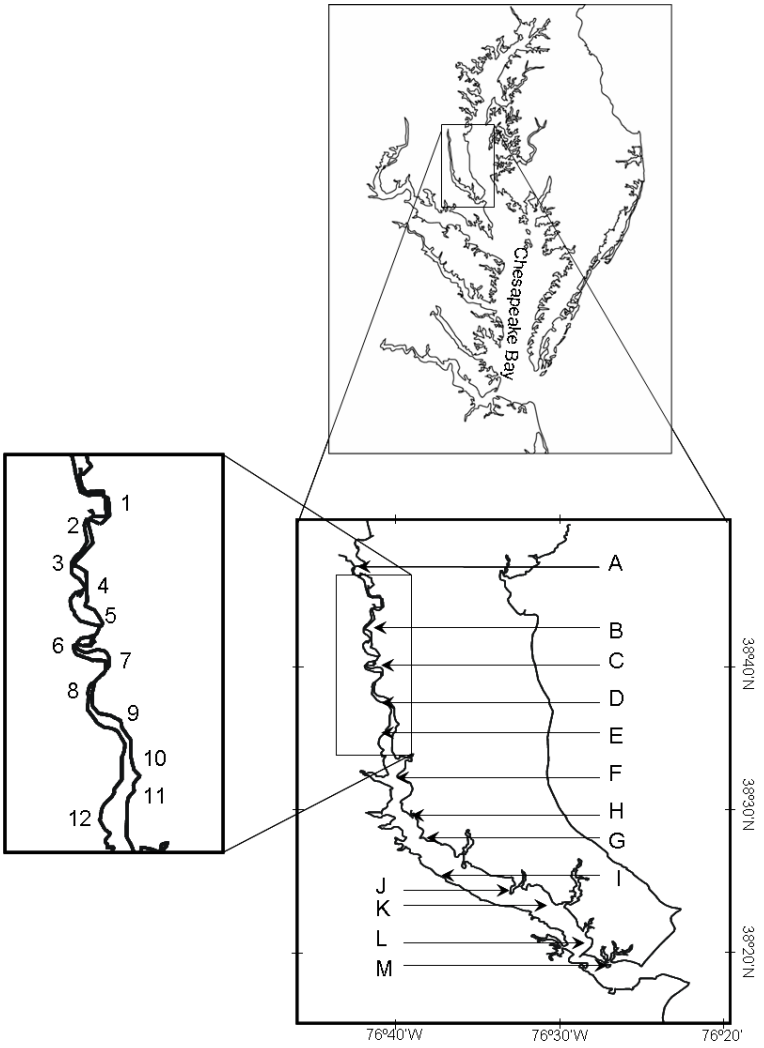

Figure 5.1. Map of the Patuxent River showing the stations where striped bass eggs were collected using a bongo-net (Arabic numerals) and the stations where striped bass juveniles were collected by seine (capital letters).

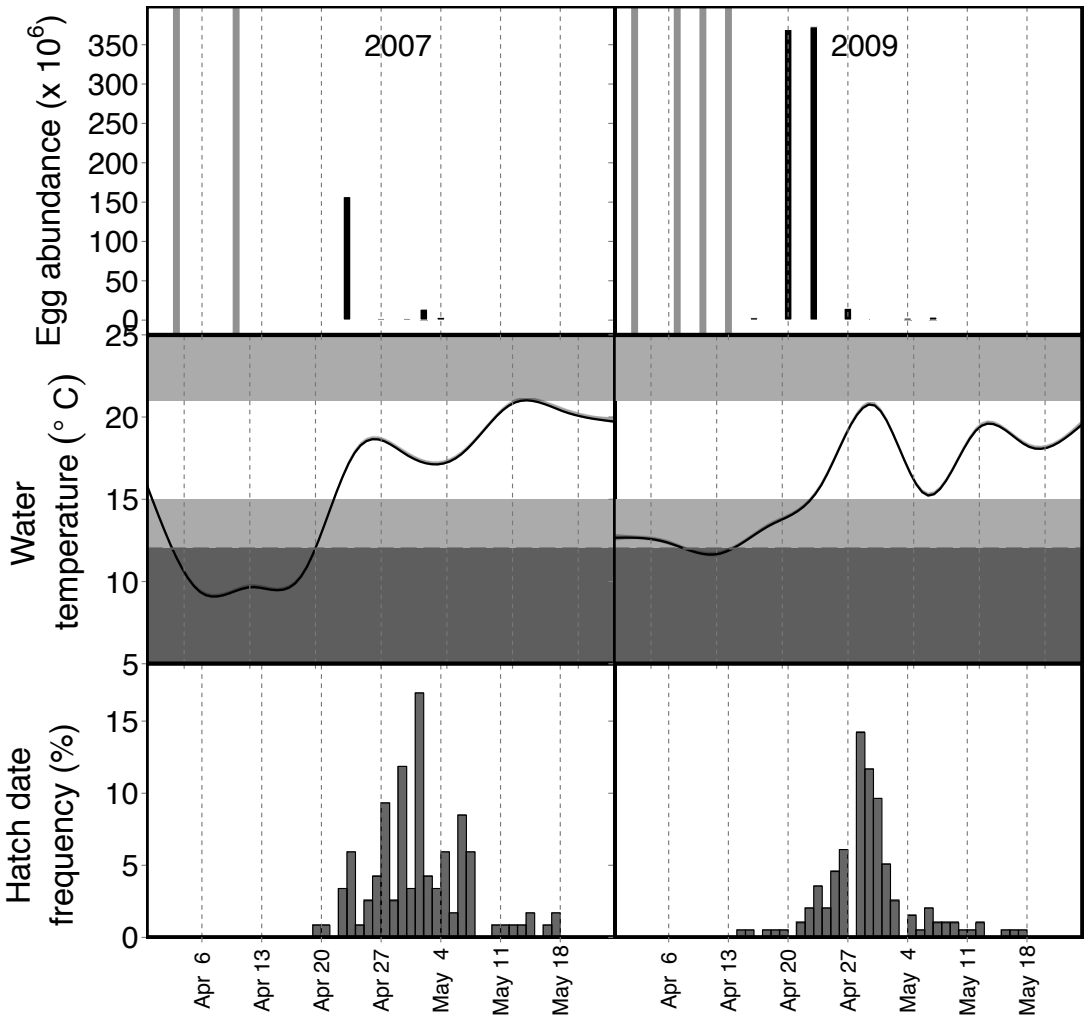

Figure 5.2. Egg abundance and juvenile otolith derived hatch date frequencies for striped bass collected in the Patuxent River in 2007 (left panels) and 2009 (right panels). Vertical gray bars in top panels represent dates when eggs were observed in bongo nets, but not counted. Center panels represent mean daily water temperature measured at Jug Bay (just upstream of bongo station 1 [Figure 1]). Dark gray and light gray regions of water temperature panels represent lethal (< 12°C) and suboptimal (< 15°C and > 21°C) temperatures, respectively, for larval striped bass.

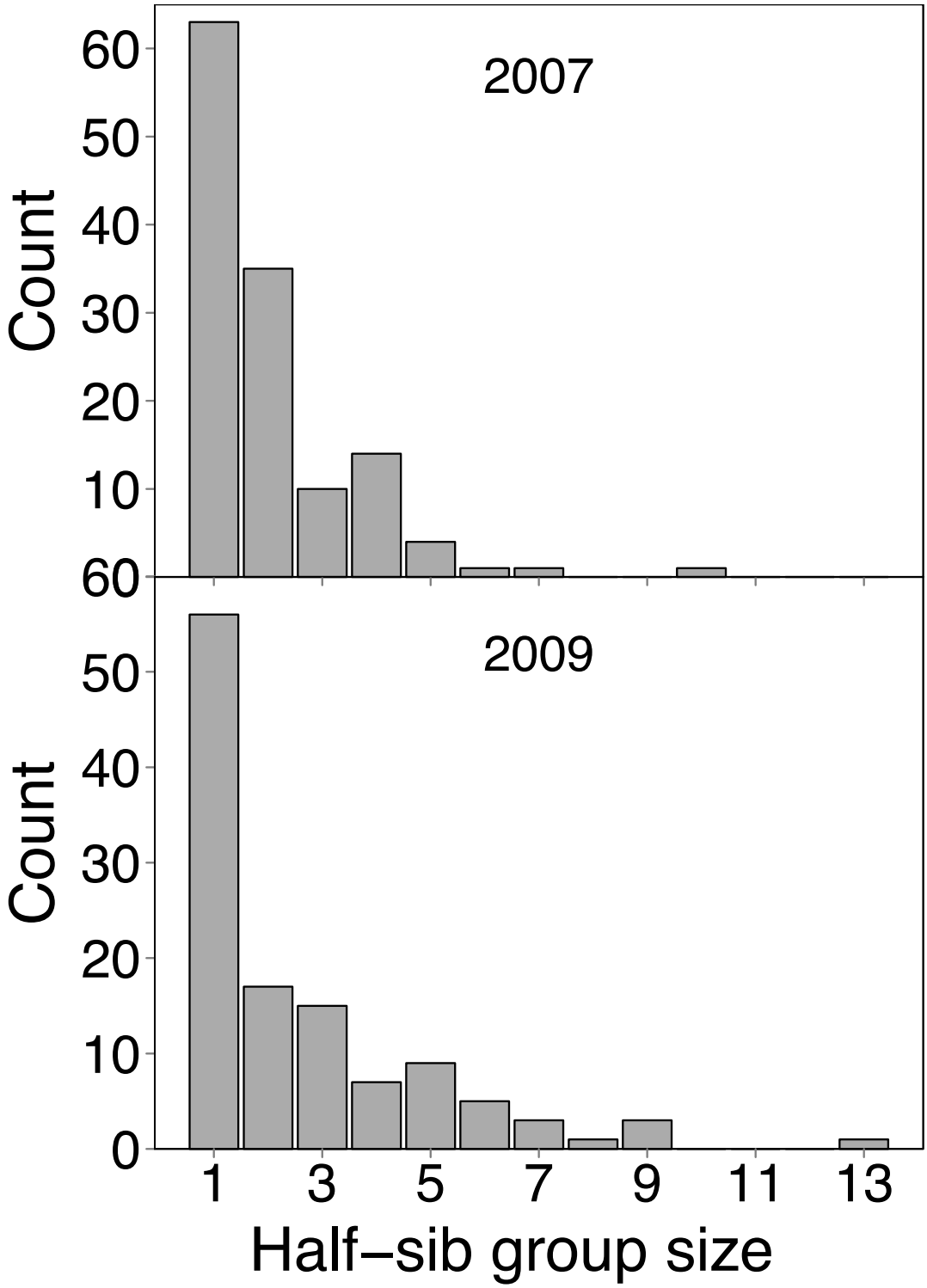

Figure 5.3. Size distributions of half-sib families for juvenile striped bass collected in 2007 and 2009.

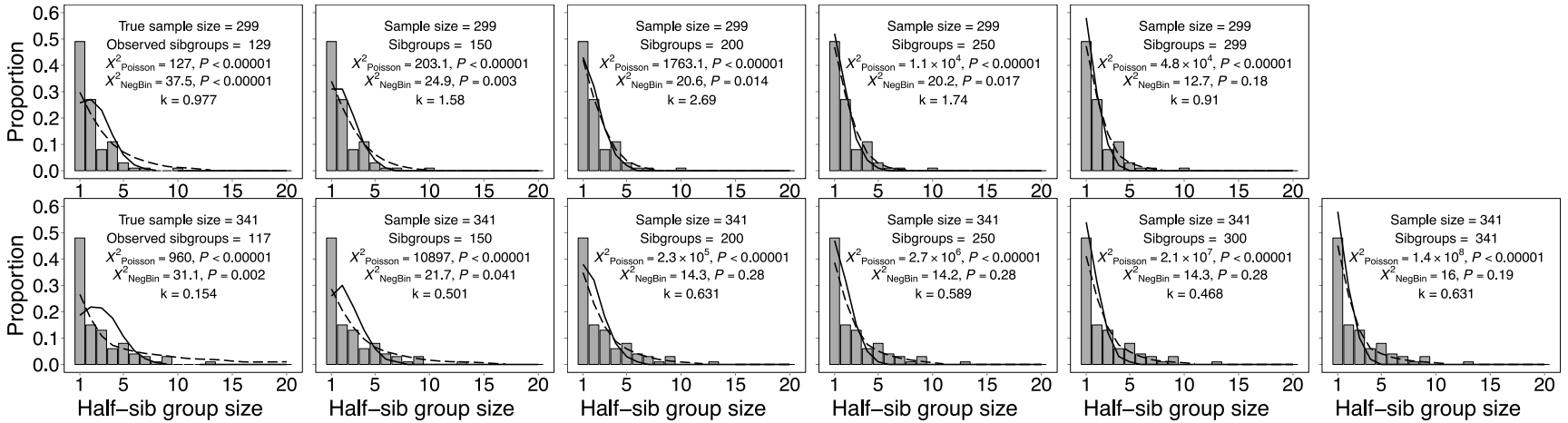

Figure 5.4. Observed frequency distributions of half-sibling group size based on sibling reconstructions conducted on juvenile striped bass collected in 2007 (top panels) and 2009 (bottom panels). Expected frequencies of half-siblings based on Poisson (solid lines) and negative binomial distributions (dashed lines) are shown for scenarios including half-sibling group sizes ranging from the observed to a maximum equal to the true juvenile sample size collected each year. Results from chi-square analyses are shown, as well as the dispersion parameter (k) for the negative binomial distribution.

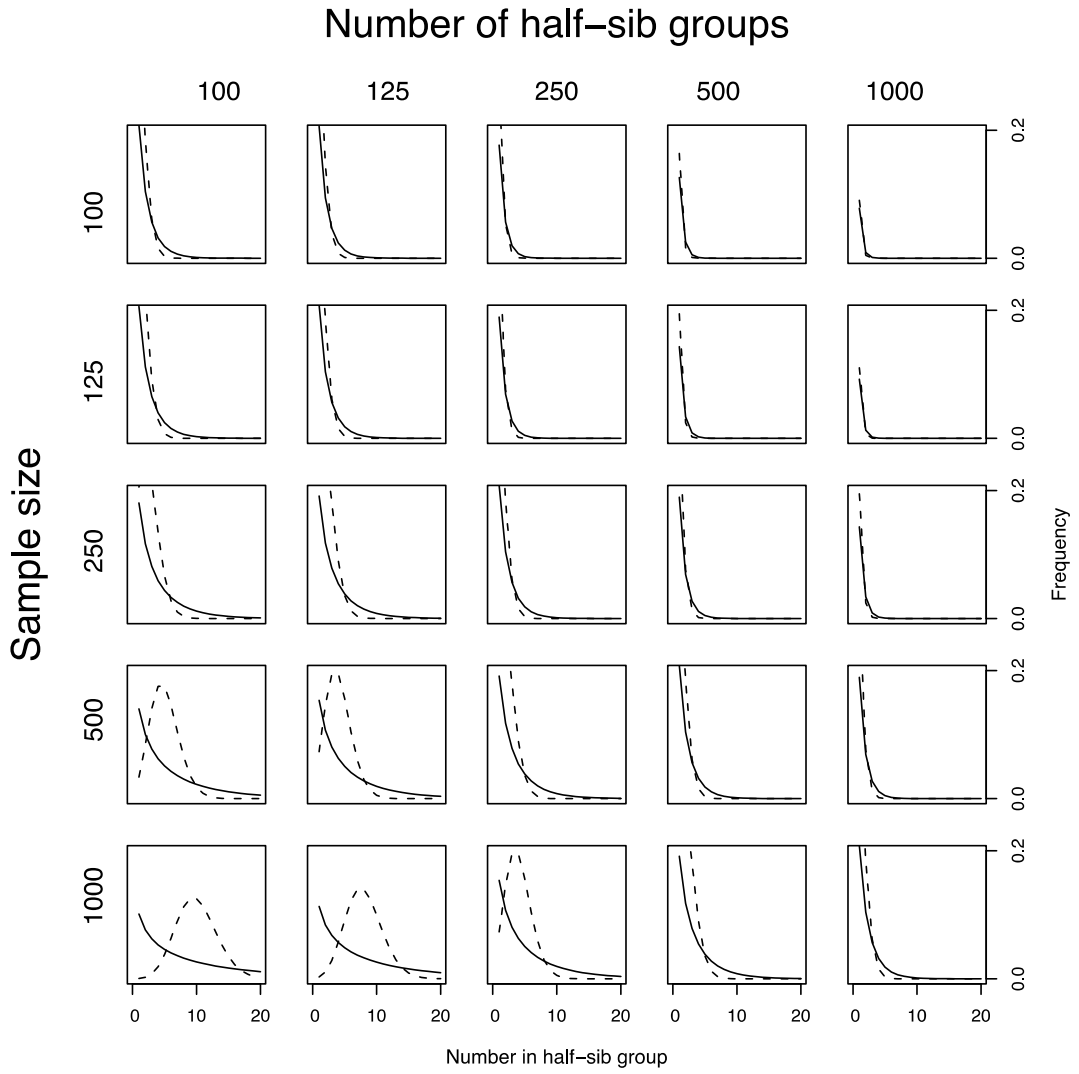

Figure 5.5. Results of factorial simulation designed to evaluate the necessary juvenile sample size requirements for determining differences in Poisson (dashed line) and negative binomial (solid line) distributions for the number in a half-sibling group.

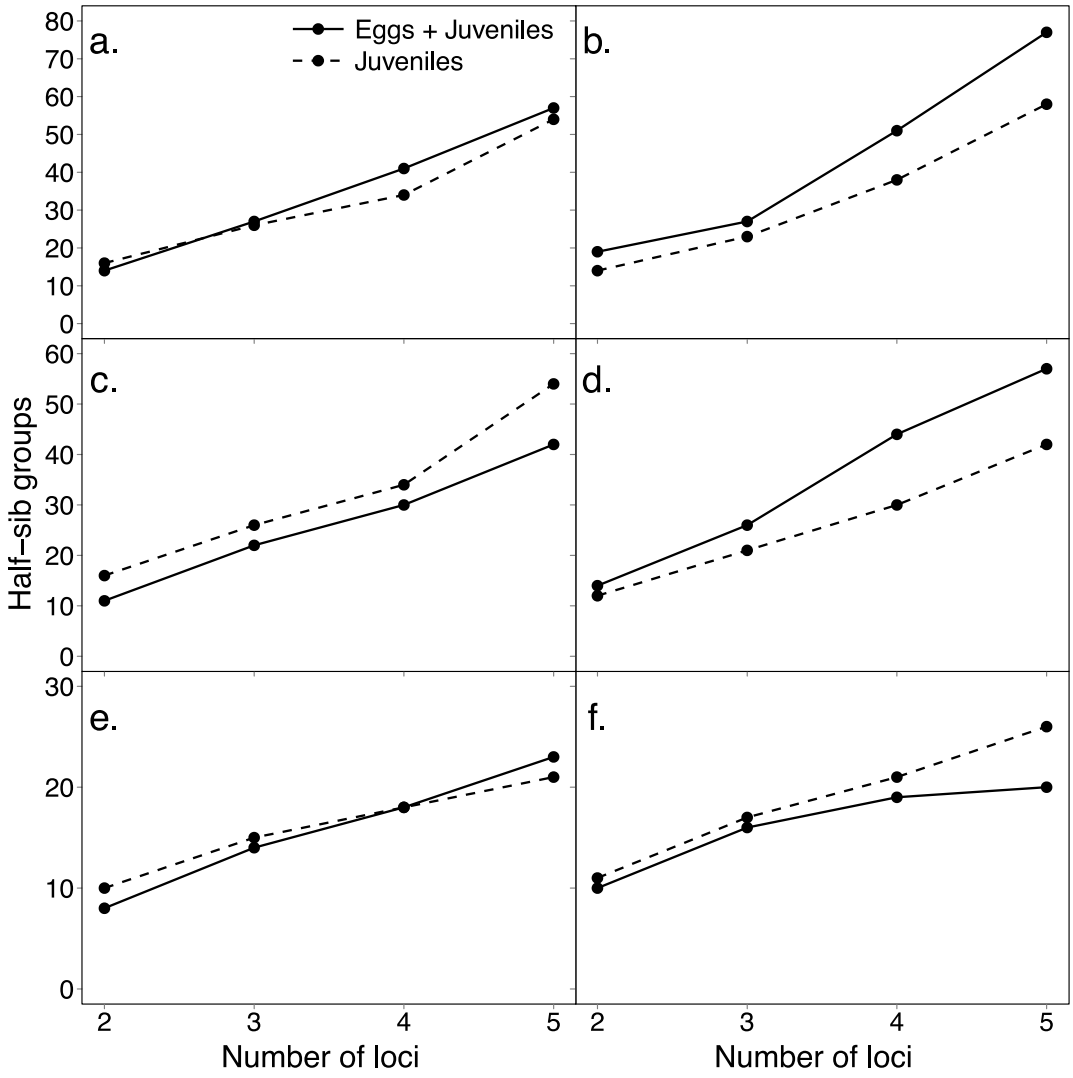

Figure 5.6. Relationship between the number of microsatellite loci and the number of half-sibling groups using data from juveniles (dashed line) and eggs and juveniles combined (solid line). Left and right panels represent samples collected in 2007 and 2009, respectively. Estimates of half-sibling group number was estimated using all data (a, b) and random subsamples of 150 (c, d) and 50 (e, f) individuals.

CHAPTER 6:

SUMMARY

Understanding the reproductive potential of individual females and populations is essential for accurate determination of a population's resiliency to fishing. Accurately predicting the resiliency of a stock to fishing requires knowledge of a population's reproductive potential and how that relates to the number of new recruits produced. In many stock assessments the reproductive capacity of a population is addressed through spawner-recruit models, where spawning stock biomass is used as a proxy for population reproductive potential (Murawski et al. 2001). However, often there is high unexplained variability in spawner-recruit data, leading some scientists to question the ability of spawning stock biomass to track true variation in stock reproductive potential (Marshall et al. 1998). Furthermore, spawner-recuit models inherently assume that spawner biomass is directly proportional to reproductive potential (i.e., total egg production; Marshall 2009). However, because both the size and age structure of populations change in response to both natural sources of mortality and fishing, and because mass-specific fecundity is often lower for smaller individuals, a population's reproductive potential may not be directly proportional to spawning stock biomass (Berkeley et al. 2004). Compounding this allometric effect on the number of eggs – the size, age and condition of mature females are known to directly influence survival of eggs and offspring (Trippel et al. 1997, Berkeley et al. 2004). If not accounted for in fisheries management, these effects could have consequences for sustainability of fish populations.

The goal of my dissertation was to evaluate environmental and demographic factors influencing the reproductive potential of Atlantic coast striped bass. I began by evaluating how the environment can influence a maternal phenotype and potentially control reproductive potential. Specifically, in chapter 2, " Local water temperature as a driver of changes in the migration phenology of Chesapeake Bay striped bass: Implications for sustainable management" I assessed how local environmental and large-scale climatic variables influence the spawning phenology of striped bass. In chapters 3 and 4, I evaluated the importance of energetic condition on striped bass reproductive potential. I determined the importance of female total relative energetic condition on the probability of spawning, fecundity and oocyte size in chapter 3, " Size, age and condition demographics of female striped bass during the spawning season in Chesapeake Bay: Temporal dynamics and influences on reproductive potential." Subsequently, in chapter 4, "The role of maternal size and energetic condition on progeny size, growth and survival in two populations of Atlantic coast striped bass (*Morone saxatilis*)," I conducted laboratory experiments on two distinct striped bass populations to determine the importance of female total relative energetic condition on progeny size, growth and mortality. Finally, I conducted a field experiment, reported in chapter 5, "Testing for evidence of maternal influences in a natural striped bass population: Lessons learned and future challenges" to provide a first test of whether the maternal influences observed in the laboratory are evident in natural striped bass populations.

In chapter 2, I analyzed spawning stock survey data to test the hypothesis that changes in water temperature during the spring spawning season would be the

dominant factor explaining variability in migratory timing of striped bass onto their spawning grounds. As hypothesized, results indicated that local and recent water temperature was the primary factor influencing the timing of movement, with higher temperatures resulting in early movements onto the Chesapeake Bay spawning grounds. However, results of a principal components analysis suggested that other variables such as flow, wind (speed and direction) and broad scale climate might also influence migration timing. Nevertheless, the dominance of temperature in these components reaffirms its primary role in determining the migration phenology in striped bass. Temperature exhibited consistent effects on all female size classes, although over the entire time-series, there was a clear tendency for larger females to annually move onto the spawning grounds earlier.

In evaluating the striped bass "trophy" fishing season in the Chesapeake Bay, three possible consequences of temperature and size-dependent spawning behavior emerged. First, during cool years when females moved onto the spawning grounds later, more females were caught in the fishery before they could spawn. Second, larger females move onto the spawning grounds earlier than smaller females. As earlier spawners, larger females may have greater potential for escaping the fishery and these effects may be greater during warmer years. If larger females consistently have a higher probability of escaping the fishery, over long periods of time, the effects of the fishery and climate change could lead to selection for increased size at maturation. This could lead to a truncation of the temporal distribution of spawners in future populations if later spawning, smaller size-classes in the current population become immature size-classes in future populations. If this occurs, the probability of

spawning during optimal environmental conditions could decrease, leading to a higher frequency of failed year-classes. Finally, because spawning generally occurs before the "trophy" fishery opens on the third Saturday in April, there is increased probability of females being caught later in the spawning season and before reaching the spawning grounds. Under long-term selection by the fishery, this could eventually lead to evolutionary changes (i.e., progressively earlier spawning independent of climate effects) in the population if migration timing is heritable in striped bass. If these changes do not occur in step with climate effects on larval prey production, evolutionary changes in migration timing could lead to mismatches between larval striped bass and zooplankton production.

In chapter 3 I evaluated the importance of female energetic condition on reproductive potential, by testing the hypothesis that relative total condition has a positive influence on reproductive potential (i.e., probability of a mature female spawning, relative fecundity and relative oocyte volume). My results showed that improving spawner-recruit relationships and the traditional spawning stock biomass approach to estimating reproductive potential might require inclusion of an index of individual energetic condition. In support of my hypothesis, I observed that relative total condition had a positive influence on residual fecundity, residual oocyte volume and indirectly on the probability of spawning. Furthermore, I was able to show that relative total condition explained a high degree of variation in my measures of reproductive potential, and was a more reliable index of relative total energetic condition than tissue-specific measures. Thus, increases in relative total condition were related to increases in striped bass reproductive potential.

Together, my results show that female relative total condition observed during the spawning season is biologically significant and does have an influence on reproductive potential through egg production (number and size) and spawning frequency. Although relative total condition did not directly influence the probability of spawning, it did appear to have an influence on the frequency of skipped spawning behavior through changes in the probability of spawning at size and age. Specifically, in 2009, when females were in better condition, spawning occurred at a significantly smaller size and nearly younger age. These are important observations that require further exploration to identify the interannual variability in total condition and skipped spawning frequency, as well as the factors driving their variability. In doing so, we can begin to understand the true variation in population reproductive potential and attempt to develop better models that relate spawners to recruits. The value of including striped bass female characteristics in stock-recruitment models has recently been demonstrated in a Ricker model that revealed the strong dependence of young-of-the-year recruitment on female age diversity (Houde 2008). Further refinements in these models may be possible by including metrics of female condition. By refining the links between spawners and recruits, improved stock-recruitment models will provide a more accurate understanding of the resiliency and sustainability of a stock.

In chapter 4 I conducted an experiment to evaluate whether the female relative total condition also had a positive influence on reproductive potential beyond the unfertilized egg stage. In the laboratory, I conducted a randomized complete block experiment (two female lines [Chesapeake Bay (n = 9 females) and Roanoke River,

NC (n = 8 females)]) to test the hypothesis that pre-spawn relative total condition has a positive effect on offspring size, growth and survival, either alone or in combination with other female variables. Counter to my hypothesis, results of this experiment indicated that relative total condition had no influence on egg or larval phenotype in either Chesapeake Bay (CB) or Roanoke River (RR) female lines. Instead, post-spawn gutted weight alone had the greatest influence on egg and larval phenotype in striped bass, although to a lesser and potentially insignificant degree in RR compared to the CB female line. Although no previous studies on maternal influences have been conducted using females from the Roanoke River, the significant influence of maternal size on progeny size and growth variables observed in the CB line was consistent with previous studies conducted using Cheasapeake Bay females (Zastrow et al. 1989, Monteleone and Houde 1990). The dynamic patterns in the maternal size effect on larval survival, however, provide new insight into the potential role of both maternal phenotype and the unique composition and size of the oil globule in striped bass eggs. Specifically, the results on survival and growth bring to question the role of the wax ester rich oil globule as a valuable energy source for developing striped bass embryos and larvae. The negative effects of female size and oil globule lipid mass on larval survival and growth suggest that a larger oil globule may not have energetic benefits. Rather than an efficient energetic source (which wax esters are not), the oil globule may have evolved more specifically for buoyancy, and thus the maintenance of eggs and larvae within ideal environments. In addition, my test of female line differences on maternal influences indicated that the post-GW effect on larval size characteristics were not equal in the CB and RR female lines and

suggested that maternal influences on larval size may not be evident in RR female lines.

These results indicate that there is still much to be understood about maternal influences in striped bass, particularly with regard to their influence on survival, both in the laboratory and in nature. At present, however, my results provide further support for the notion of preserving female size and age diversity due to the potential growth and survival advantages their larvae may have under different environmental conditions.

Finally, in chapter 5 I provided a first test of whether the maternal influences observed in the laboratory can influence the distribution of juvenile survivors in natural populations. Using the Patuxent River, Maryland as a model system, striped bass eggs and juveniles were collected during two years and microsatellites were used to reconstruct half-sibling relationships. Using these data, I tested the hypothesis that the variability in the distribution of half-sibling families is greater than expected by random reproductive success (i.e., a Poisson process). If true, I further hypothesized that the effective population size (N_e) would be orders of magnitude smaller than the estimated census population size of breeding males and females, since increased variability in reproductive success causes reductions in N_e. My results indicated that the observed half-sibling family distributions of juveniles collected in 2007 and 2009 were statistically differed from either a Poisson or overdispersed (i.e., negative binomial) distribution. However, the fits were clearly closer to a negative binomial distribution, providing some evidence for greater than expected variance in reproductive success in the Patuxent River population. The 2007 juvenile data also

indicated that the ratio of N_e/N (i.e., estimated as low as 0.02) was nearly two orders of magnitude smaller than the estimated census size – again indicating high variance in reproductive success. Unfortunately, the 2009 N_e estimates were not reliable, preventing any evaluation of the variance in reproductive success during this year.

Results of this study leave open the possibility that maternal influences could affect the family size distribution of juvenile survivors in Patuxent River striped bass. However, due to deficiencies in the data (i.e., low resolution markers) and restrictions to using nuclear DNA markers, a full and adequate test of my hypotheses could not be conducted. To ensure successful future tests of the hypotheses, simulations to determine appropriate sample sizes must precede research efforts. Furthermore, if eggs are to be used as surrogates of maternal phenotype and genotype, then resolute maternal markers must be developed. In lieu of maternal markers, parentage analysis can be conducted using nuclear markers; however this will require adequate sampling of adult striped bass – which may be prohibitively difficult. The challenges of testing hypotheses on a pelagic spawning species are evident from this study; however, with adequate funding and strategic methodologies, a better understanding of maternal influences in striped bass populations can be achieved.

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A standardized method and analytical approach for predicting female reproductive stage in teleosts by using ovary color and female characteristics

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Abstract

Determining and understanding patterns in the reproductive status of fishes is essential for assessing individual and population reproductive potential. The least biased method for determining reproductive stage is through the use of ovarian histology; however, this method can be time consuming and expensive. To overcome these restrictions, we developed models to predict female striped bass reproductive stage using ovary color and other female characteristics. In my approach we develop a standardized and calibrated method for quantifying ovary color and outline an analytical approach that utilizes binary and ordinal logistic regression. My results indicate high accuracy (< 6 % error) in the ability of binary models to predict between regressing (i.e, recently spawned) and non-regressing (i.e., all other phases) reproductive phases, and even better accuracy (4% error) in the ability of ordinal models to predict among four non-regressing reproductive phases. All best fitting models required the inclusion of an ovary color variable and ovary energy density; however, good predictive accuracy also was obtained when we replaced ovary energy density with ovary percent water to produce models requiring minimal time and cost. Although tested on striped bass, my method could be used to develop similar models for other species.

Introduction

Standardized determination of the reproductive status of individual fish is key to accurately quantifying reproductive and stock dynamics (Brown-Peterson et al. 2011). Reproductive characterization provides an understanding of species- and population-specific reproductive cycles and characteristics, such as spawning stock size, temporal and spatial spawning patterns, the size and age of sexually maturity, and distinction between reproductive and non-reproductive (i.e., skipped spawning) individuals. Consequently, determining and understanding patterns in reproductive status is essential for assessing individual and population reproductive potential.

Reproductive classification of fishes by macroscopic external and internal appearance (i.e., ovary/oocyte color and shape) of the gonads has been conducted and developed for at least a century (i.e., Hjort 1914, Graham 1924, Hickling 1935, Vladykov 1956, Powles 1958, , Kynard and Kieffer 2002). Although these methods are fast and simple, they have the potential to produce biased and subjective classification (Kjesbu 2009). This has led to the recent increase in reproductive classification by histological techniques – which provide the most detailed information about reproductive status and the least-biased classification (Hunter and Macewicz 1985). Specifically, histological analyses provide detailed information about cellular substructures and their prevalence during the entire reproductive cycle (Tomkiewicz et al. 2003). Unfortunately, histological methods are also time consuming and more expensive than simple macroscopic observation, making it difficult to evaluate large sample sizes.

Here we ask whether histological and macroscopic methods could be combined to develop a model that can be used to predict reproductive status based on macroscopic and other easily attainable female characteristics. By combining the detailed accuracy of histology with the rapid and low-cost macroscopic methods, one may be able to develop a predictive model that can accurately determine the entire scope of reproductive plasticity by only using macroscopic methods and other easily attainable female characteristics. This approach has been attempted once before by Bryan et al. (2007), who used non-lethal endoscopic methods to determine the color of oocytes, which were then used to predict histologically determined reproductive stages of shovelnose sturgeon (*Scaphirhynchus platorynchus*). Although their model proved successful at predicting between reproductive and non-reproductive females, it was unable to decipher greater detail, and did not provide (or aim to provide) a standardized and calibrated macroscopic method that could be used in future studies for other species.

Here, we develop a model to predict female striped bass reproductive stage using ovary color and other female characteristics (i.e., gutted weight, age, ovary energy density, liver energy density, ovary percent water and liver percent water). In doing so, we develop a standardized and calibrated method for quantifying ovary color and outline an analytical approach that utilizes binary and ordinal logistic regression, which could be used to develop similar models for other species.

Methods

Field sampling and ovary processing

The female striped bass used in this study were collected in the mainstem of the Chesapeake Bay, outside of the mouth of the Patuxent River, Maryland in 2009 (n = 31) and 2010 (n = 109). Upon capture, each fish collected was euthanized with 500 $mg \cdot L^{-1}$ of tricaine methanesulfonate (MS-222) and then placed in an ice/water slurry to prevent atresia of oocytes. In the laboratory gutted weight (g) was measured and otoliths, liver and ovaries were removed. For histological analyses, a small section (~ 6 g) of one lobe of the ovary was then immediately placed in a 4:1 chilled (4°C) solution of formaldehyde and glutaraldehyde (4F:1G) and refrigerated at 4°C for 24 hours. The remaining portion of the lobe was then frozen in water for later color analysis. To determine the energy density and percent water of the ovaries, we then measured the wet-weight of the second lobe and placed it in a drying oven at 65°C until a consistent mass was obtained after two consecutive measurements separated by at least two days. To determine the energy density and percent water of the liver, the same drying procedure was used.

Prior to estimating the energy density of ovaries and livers, dried tissues were ground to a fine powder using either mortar and pestle, or a coffee grinder. Ground tissues were then formed into at least two composite pellets (~ 0.5 g) and the energy density was estimated using an oxygen bomb calorimeter (Model 6200, Parr Instrument Company, Moline IL.) standardized with benzoic acid pellets (26.444 kJ g^{-1}). Replicate pellets of each tissue from each female were ignited in the calorimeter, but when the estimates differed by more than 400 kJ g^{-1} (~ 2%) a third pellet was ignited. Energy density of each tissue was equal the mean of two composite tissue pellets that differed by less than 2%.

Histology

For histological analyses, samples fixed in 4F:1G were rinsed in 0.1M Sorenson's sodium phosphate buffer (pH 7.2-7.4) twice for 10 min each and placed in cassettes. Sequential dehydration was accomplished in a graded ethanol series of 70% (1×), 80% (2×), 95% (2×) and 100% (3×) ethanol for 20 min at each grade. This was followed by 20 min changes in xylene (2×), 30 min changes in low temperature paraffin (3×) and embedding in a final change of paraffin. Embedded samples were desiccated overnight, and thin sections (3.5 μm) cut with glass knives at 5 . Sections were placed onto drops of distilled water on glass slides and heated at approximately 60°C on a hotplate to adhere the sections to the slides. Sections were then stained with periodic acid-Schiff's (PAS) reagent.

Histologically-prepared ovary sections were viewed under a light microscope and categorized into one of six reproductive phases (Figure 1): 1) immature, 2) early developing, 3) developing, 4) spawning capable, 5) regressing, 6) regenerating. Detailed descriptions of these phases can be found in Table 2 of Brown-Peterson et al. (2011).

Ovary color analysis

Ovary color was quantified using image analysis. To determine red, green and blue color values of each ovary, the frozen ovary lobe was thawed to allow removal of the outer membrane. A composite sample of oocytes (~ 5 g) was then removed and immediately homogenized with a mortar and pestle while the sample was still cold. A 60 mm diameter, 15 mm deep petri dish was then filled to overflowing with the homogenized sample, ensuring no air pockets were present.

The petri dish was placed on flat-bed scanner (Canon CanoScan 8800F, Lake Success, NY) with the lid closed. Prior to taking images, the scanner was calibrated with an IT8 calibration target and calibration software (MonacoEZcolor). Images of the filled petri dish were then taken at 300 dpi with all advanced image settings turned off, and saved in tagged image file format (TIFF).

Image files were analyzed using ImageJ (version 1.45h, Rasband 2011). The color histogram plugin was used to determine the mean red, green and blue color values for the imaged sample. Using the mean color values, we also determined the proportion of each color and the ratio of red:green, red:blue, and blue:green.

Statistical analyses

To predict the reproductive stage of female striped bass we used both binary and ordinal logistic regression. All models were fitted in R (R Development Core Team 2011) using the rms package (Harrell 2011). My preliminary model development indicated that we would not be able to adequately fit an ordinal logistic regression model that included all 6 reproductive phases described above. This preliminary evaluation indicated that the regressing, immature and regenerating phases would need to be pooled, given that these adjacent phases were not distinguished by the means of the predictors. However, given my desire to predict which females were in the regressing phase, we decided to split my statistical analyses into two stages. First, we used a binary logistic regression model to determine my ability to correctly classify females as either regressing (i.e., recently spawned) or non-regressing (i.e., all other phases) using ovary color and other female characteristics. To determine the overall best model, we began with a full model that included mean ovary energy density (kJ g^{-1}), ovary percent water, gutted female

weight (g), female age, mean red ovary color, mean green ovary color, mean blue ovary color, red:green ovary color ratio, red:blue ovary color ratio, and green:blue ovary color ratio. We also included mean liver energy density (kJ g^{-1}) and liver percent water in the full model due to the important role of the liver in packaging and transporting vitellogenin (plasma precursor of yolk) to oocytes (Lubzens et al. 2010). Subsequently, we used a backward step-down variable deletion approach based on Akaike information criterion (AIC) to find the model that yielded the greatest reduction in deviance. We then performed an enhanced bootstrap using backward step-down variable deletion to both validate the best fitting model and to determine the predictive reliability of the model (Harrell 2001). A simple bootstrap estimates an accuracy index directly from averaging indexes computed on the original sample; however, the enhanced bootstrap uses a more indirect approach by estimating the bias due to overfitting or the "optimism" in the final model fit (Harrell 2001). Using re-sampling with replacement (set to 2,500 resamples), bootstrapping allowed the derivation of bias-corrected estimates of predictive accuracy without holding back data – which can have severe drawbacks (Harrell and Lee 1996, Harrell et al. 1998). After the best fitting binary model was determined and validated, we evaluated the predictive ability of the model using Nagelkerke's R_N^2 index and the discrimination index *D*, ([model likelihood ratio $\chi^2 - 1$] / n), which assess the ability of the model to make unbiased estimates of outcome (i.e., goodness of fit or calibration) and the model's ability to separate subjects outcomes (i.e., discrimination), respectively (Harrell 2001).

In addition to determining the best model, we used the same selection strategy described above to develop a predictive binary logistic model that would require the least amount of laboratory processing time and could be conducted on a small budget. For this model we excluded mean ovary energy and mean liver energy from the initial full model, and termed the resultant best model my 'least-effort' model.

In the second stage of my analyses, we determined the ability of ovary color and other female characteristics to predict the reproductive stages of non-regressing females only. For this analysis we used ordinal logistic regression with a continuation ratio model (CR) rather than a proportional odds model, because preliminary analyses indicated the CR model provided better fit to my data. The CR model is based on conditional probabilities and is suitable when subjects have to pass through one category to reach the next (Harrell et al. 1998), which is the case for reproductive stage. Like the binary models, we then used a backward step-down variable deletion approach based on AIC to find the model that yielded the greatest reduction in deviance to determine the best and least effort ordinal models. After the best fitting CR models were determined, we quantified the predictive ability of the model using the same strategy described above for the binary models, however, bootstrap resampling for ordinal models was stratified by the response variable to have all ordinal classes at least once represented in every bootstrap sample.

Results

The mean and standard deviation of all independent variables included in the full binary and ordinal regression models are shown in Table A.1.

Binary classification into regressing or other reproductive phases

The overall best binary logistic model for predicting whether females were in the regressing or non-regressing reproductive phase included ovary energy density, gutted body weight and the proportion of ovary color that was green (Table A.2). This model showed that for an average weight female, the probability of being in the regressing phase increased with decreasing ovary energy density and decreasing proportion of ovary color being green. Differences between observed reproductive stage and the predicted probability of being in the regressing stage showed that the best model incorrectly predicted a small and equal proportion (~ 3%) of females into the regressing and non-regressing phases (Figure A.2). Exploration of the characteristics of the incorrectly classified females indicated that those regressing females predicted to be non-regressing, had a high proportion (23-43%,) of atretic oocytes (Figure A.1). In addition, the four non-regressing females incorrectly classified as regressing were either regenerating (n = 2), or early developing with primary vitellogenic oocytes only (n = 2). Bias-corrected indices of predictive accuracy also indicated strong calibration ($R_N^2 = 0.87$) and discrimination ($D = 1.09$) ability (Table A.2). In addition, bias due to overfitting (i.e., optimism) was quite low for all indices and model parameters (Table A.3), indicating good performance of the model on future data.

The best, 'least-effort' binary logistic model included ovary percent water, gutted body weight and the green:blue ovary color ratio (Table A.2). Although this model showed less deviance reduction than the overall best model, much like the

overall best model, it incorrectly predicted a small, but nearly equal proportion of females into the regressing (4%) and non-regressing phases (3%) (Figure A.2). Furthermore, the characteristics of the incorrectly classified females were identical to those in the best overall model. Also, with the exception of the two additional females incorrectly classified as regressing, the same individuals were misclassified in both models. Although bias-corrected indices of predictive accuracy did indicate a slightly reduced calibration ($R_N^2 = 0.79$) and discrimination ($D = 0.85$) ability compared to the overall best model, optimism was similar, again indicating good predictive performance of the model on future data.

Ordinal classification of non-regenerating reproductive phases

Initial ordinal model development indicated that ordinal predictions were unable to distinguish between immature, regenerating, and some developing phases (i.e., those with mostly primary growth and cortical alveolar oocytes and some primary vitellogenic oocytes). Because females in each of these phases are not capable of spawning in the current year, we decided to group these phases together for my ordinal models and called it stage 1 (Figure A.1). Because females in the later developing phase (i.e., ovaries also included secondary vitellogenic oocytes) could be distinguished from those in stage 1, we grouped these females into a separate category called stage 2 (Figure A.1). In addition, my early model development indicated that we could separate the spawning capable phase into early and later subphases. The early and later developing subphases were called stages 3 and 4 in my ordinal model.

The overall best CR model included mean ovary energy, mean blue ovary color and mean red ovary color (Table A.2). Plots of predicted probabilities indicated very good fit to the observed reproductive stages (Figure A.3). There were 3 incorrect predictions (4% error) with one stage 1 female incorrectly classified as stage 2, one stage 3 female incorrectly classified as stage 4, and one stage 4 female incorrectly classified as stage 3 (Figure A.3). Bias-corrected indices of predictive accuracy also indicated excellent calibration ($R_N^2 = 0.95$) and discrimination ($D = 0.94$) ability, and optimism was low for all parameters and indices, indicating good predictive performance of the model on future data. Finally, the best 'least-effort' CR model included ovary percent water and the proportion of ovary color that was red (Table A.2). Plots of predicted probabilities for the least-effort CR model indicated poorer fit to the observed reproductive stages compared to the overall best CR model, with a total of 11 incorrect classifications (15% error) (Figure A.4). The greatest error for this model appeared to be in predicting stage 3, with the model predicting 4 females to be in stage 4 and 2 female to be in stage 2 (Figure A.4). In addition, one female in stage 1 was predicted to be in stage 2, one female in stage 2 was predicted to be in stage 4, and 3 females in stage 4 were predicted to be in stage 3 (Figure A.4). Furthermore, bias-corrected indices of predictive accuracy indicated weaker calibration ($R_N^2 = 0.69$) and discrimination ($D = 0.67$) ability than the best overall CR model; however, optimism for all indices and model parameters was low, indicating overall that the 'least-effort' model would have lower predictive accuracy than the overall best model, but similar unbiased performance on future data (Table A.3).

Discussion

We were able to use logistic models to predict the reproductive stages of female striped bass with high accuracy and without the need for histological analysis, by using a standardized and repeatable measure of ovary color in combination with other easily obtainable female characteristics. Although many have used color and other macroscopic (Hjort 1914, Graham 1924, Hickling 1935, Vladykov 1956, Powles 1958, Burnett et al. 1989, Kynard and Kieffer 2002) and biochemical (i.e., Heppell and Sullivan 1999) measures to estimate the reproductive stage of female teleosts, and some have tried to use color to predict the reproductive stage of females (i.e., Bryan et al. 2007), no one has provided a calibrated, standardized and repeatable procedure to predict the reproductive stage of female teleosts using ovary color and/or other female attributes in the absence of histology. My results indicate that for striped bass, predictive accuracy is highest (i.e., overall best models) when models include ovary energy density and one or two ovary color variables. My overall best binary model showed an ability to discriminate between regressing and non-regressing females very well, with less than 6% of the females incorrectly classified. Of the 8 incorrectly classified females, the non-regressing females predicted to be regressing (only 3%) would not have spawned – suggesting that we might overpredict the number of spawners in a given year. However, the regressing females predicted to be non-regressing were predicted by my overall best ordinal model to be in phases that would not have spawned (i.e., immature, regenerating or developing). Thus, the existing error in the binary logistic model likely would lead to little error in predicting

the numbers of spawners (i.e., spawning capable and regressing) and non-spawners (i.e., immature, regenerating and developing) in a given year.

My overall best ordinal regression model showed an even greater ability to discriminate striped bass females among the 4 non-regressing reproductive stages we established. Although we were forced to group immature, regenerating and early developing phase females into one reproductive stage (stage 1) to fit my data well, the overall best ordinal model accurately discriminated among stage 1, stage 2 (developing), stage 3 (early spawning capable) and stage 4 (spawning capable) females, with only 4% total error. Thus ovary color (specifically, mean blue and red) and ovary energy density were very strong predictors of whether striped bass females were in the developing, early spawning capable or spawning capable phases, however, discrimination among immature, regenerating and early developing phases was not possible.

Although ovary energy density did produce the best predictive models, my 'least-effort' models did indicate that if bomb calorimetry of ovaries is too expensive or time consuming, ovary energy density could be replaced by ovary percent water with a slight reduction in model fit and discrimination ability, but similarly unbiased performance on future data. For example, when we used binary logistic regression to discriminate between regressing and non-regressing females, model fit was slightly reduced in the 'least-effort' model, with 7% incorrectly classified females. However, like the overall best binary model, we observed that despite this error, there would be little error in predicting the numbers of spawners and non-spawners.

Although my 'least-effort' ordinal model did show reduced fit relative to the overall best ordinal regression model, only 5% of the total error would be problematic for discriminating between non-reproductive (i.e., stage 2) and reproductive (i.e., stages 3 and 4) females. This is because most of the total error (10%) was due to incorrect classification between stages 3 and 4, which would not be problematic for most studies, since both are spawning capable groups. Still, the greater error evident in the least-effort binary and ordinal models was likely due to the poorer resolving power of percent ovary water compared to ovary energy density. It is possible that some of this error might have been resolved by increasing the sample size. Thus, others that attempt to use this predictive approach to determine reproductive stages without using energetic densities of tissues need to consider that more robust sample sizes may be necessary for initial model development.

Despite the accuracy of my predictive models and the potential for similar models to be developed for other species, my analysis was not without shortcomings. Specifically, we were unable to distinguish between immature, regenerating and early developing reproductive phases. The inability of my ordinal models to discriminate among these phases may be due to the small sample size of females in these phases. Based on my catches, the females in these phases are smaller and younger and do not appear to migrate with the spawning stock while in the Chesapeake Bay. Consequently, in the future, additional sampling locations may be needed to target smaller striped bass females. Such constraints may not preclude development of more inclusive models in other species. It is also possible, however, that my inability to discriminate among immature, regenerating and early developing phases was due

to the very low ovary energy density at each of these stages and the similarity in ovary color. If this is true, my results may also be typical of other species. However, this should not deter others from using my methods to develop their own species-specific models that are capable of discriminating among these reproductive phases. Although discrimination among these phases is not always imperative, these phases would need to be identified for accurate quantification of skipped spawners in a population. Discrimination of early developing females will also be necessary to determine the beginning of the reproductive season and age/size at maturity. In cases such as these, and in situations where discrimination of immature, regenerating and early developing phases is not possible, my methods are still useful for identifying the regressing, developing, and spawning capable females. However, females classified in the immature, regenerating or early developing group (i.e., stage 1 in my analysis) would need to undergo further discrimination using histology and microscopic examination. Although not ideal, use of these predictive models in combination with histology can still substantially reduce time and costs.

The inability of my striped bass ordinal models to discriminate among immature, regenerating and early developing phases is a problem also associated with macroscopic methods. However, macroscopic methods also suffer from additional deficiencies that my methods do not. For example, unlike macroscopic methods that use descriptive terminology that can be highly subjective and ambiguous (e.g., subjective ovary color, flaccidity, texture and oocyte clarity) and lead to inter-reader error, my method is less biased because it is an objective, calibrated and standardized procedure. Consequently, my method essentially eliminates inter-reader error as long

as the instruments used to quantify ovary color and energy, and female size characteristics are appropriately calibrated. This may be especially beneficial in long-term studies in which several individuals could be involved in determining the reproductive phases of females. Another advantage of my method is that it is validated for accuracy with histological techniques. Macroscopic methods have rarely validated other than for commercially important Gadidae species, and when they are they often show strong tendency for misclassification at many stages (Tomkiewicz et al. 2003, Vitale et al. 2006, Ferreri et al. 2009). After initial model development, my method also requires very little training, since the predictor variables included in my modeling approach are easy to obtain using relatively simple instruments. This is especially true if future models can be developed without the need for ovary energy density. In contrast, due to the subjectivity and ambiguity of macroscopic techniques there can be a steep learning curve before individuals can efficiently and "confidently" evaluate the reproductive phases. Finally, my approach has the potential to be able to accurately discriminate among all reproductive phases if models are provided with appropriate predictor variables and sample sizes at each phase. Evidence from the few validation studies that do exist indicates that other macroscopic methods do not hold that potential (i.e., Vitale et al. 2006, Ferreri et al. 2009).

Despite the shortcomings of the ordinal model developed for striped bass, minimum estimates of skipped spawning still may be possible for female striped bass collected during the spawning season, given that developing phase females could be discriminated using my models. Although developing phase females collected in late

fall or winter would be considered as mature and reproductive, those collected during the spawning season (April through May) are not likely able to spawn in the current season, given that vitellogenesis can take several months to complete in striped bass (Sullivan et al. 1997). In addition, it has been suggested that some striped bass may require more than one year from initiation of secondary growth until spawning (Merriman 1941, Chadwick 1965, Specker et al. 1987). Furthermore, evaluation of the length frequency distributions of females collected on the two major Chesapeake Bay spawning grounds (i.e., Upper Bay and Potomac River) indicate that the developing phase females, which were all < 900 mm, are underrepresented on the spawning grounds (personal observation). Consequently, for striped bass, we feel confident that we could use the developing phase females to get minimum estimates of skipped spawning using my protocol and models. This might also be feasible in other species in which it can be determined that developing phase females will not spawn in the current season. This approach may be sufficient for detecting trends in a time series or for determining what factors may be influencing the proportion of skipped spawners, but for determining accurate measures of skipped spawning for any species, histology would likely be needed either alone or in combination with a model such as ours.

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TABLE A.1. The mean and standard deviation (in parentheses) for all female variables included in the initial full binary logistic and continuation ratio models used to predict the reproductive stages of striped bass.

Stage	Phase	n	Gutted body weight (kg)	Age	Ovary energy density (kJ g^{-1})	Liver energy density (kJ g^{-1})	Ovary percent water	Liver percent water	Red ovary color	Green ovary color	Blue ovary color	Red:green ovary color	Red:blue ovary color	Green:blue ovary color
0	Regressing	68	9.14 (2.31)	12.3 (2.64)	24.54 (2.28)	24.42 (1.27)	80.6 (8.4)	77.8 (3.3)	170.75 (19.91)	93.26 (28.84)	79.31 (19.16)	1.97 (0.51)	2.23 (0.40)	1.16 (0.17)
1	Immature Regenerating Early developing	8	4.95 (1.17)	7.6 (1.40)	25.07 (2.55)	27.58 (2.41)	83.3 (3.8)	76.3 (4.1)	185.80 (13.81)	105.09 (28.39)	76.88 (14.17)	1.87 (0.46)	2.47 (0.37)	1.36 (0.23)
2	Developing	19	5.95 (1.52)	8.3 (1.17)	30.85 (1.69)	26.62 (2.72)	71.4 (5.5)	72.9 (5.7)	198.02 (9.66)	124.61 (16.99)	73.38 (11.34)	1.61 (0.17)	2.69 (0.46)	1.68 (0.27)
3	Spawning capable (early)	13	7.34 (2.78)	8.7 (1.62)	34.76 (0.69)	27.43 (3.45)	59.9 (3.7)	72.3 (6.6)	194.10 (10.94)	127.99 (21.06)	67.27 (14.56)	1.55 (0.25)	2.98 (0.52)	1.94 (0.30)
4	Spawning capable	32	8.41 (2.17)	10.1 (2.00)	34.67 (0.58)	25.53 (2.56)	53.9 (5.1)	74.6 (4.9)	166.82 (10.51)	133.44 (14.05)	80.20 (16.92)	1.26 (0.13)	2.18 (0.49)	1.72 (0.29)

TABLE A.2. Binary logistic regression model results for predicting whether female striped bass are in the regressing or non-regressing phase, and ordinal continuation ratio model results for predicting reproductive stages among non-regressing females. The overall best models (Best Model) and models that require the least amount of time and money (Least Effort Model) are shown.

Variables & intercepts	n	df	LR $!^2$	AIC	Coefficient	S.E.	Wald *Z*	*P*
Binary - Best Model								
Overall model	140	3	154.5	44.3				< 0.0001
Intercept					24.5816	5.58	4.41	< 0.0001
Ovary energy density		1			-0.7277	0.17	-4.2	< 0.0001
Gutted body weight		1			0.0011	0	3.59	0.0003
Proportion ovary color = green		1			-41.8396	13.4	-3.13	0.0018
Binary - Least Effort Model								
Overall model	140	3	137.2	66.7				< 0.0001
Intercept					-3.6009	5.01	-0.72	0.47
Ovary percent water		1			11.0692	3.67	3.01	0.0026
Gutted body weight		1			0.0006	0	3.46	0.0005
Ratio green:blue ovary color		1			-6.677	1.89	-3.53	0.0004
Ordinal - Best Model								
Overall model	72	3	170.9	30.9				< 0.0001
Mean ovary energy		1			-5.6416	1.85	-3.05	0.0023
Mean blue ovary color		1			-0.2672	0.1	-2.64	0.0083
Mean red ovary color		1			0.3486	0.11	3.19	0.0014
Ordinal - Least Effort Model								
Overall model	72	2	135.1	65.1				< 0.0001
Ovary percent water		1			50.0961	10.4	4.84	< 0.0001
Proportion ovary color = red		1			43.0311	12.4	3.46	0.0005

TABLE A.3. Bootstrap evaluation of R_N^2, discrimination index (D) and parameter estimates obtained from the binary logistic (discrimination of regressing vs non-regressing females), and ordinal continuation ratio models (discrimination of non-regressing females) for the best-fitted overall models (Best Model) and best-fitted models that included predictor variables requiring the least time and money to analyze (Least Effort Model). Original values of statistics/estimates, optimism (i.e., bias due to overfitting) and bootstrap corrected statistics are shown.

	Original value	Optimism	Corrected value
Binary - Best Model			
R_N^2	0.8878	0.015	0.8728
D	1.1263	0.0407	1.0856
Intercept	0	0.0326	-0.0326
Slope	1	0.0735	0.9265
Binary - Least Effort Model			
R_N^2	0.8248	0.0355	0.7893
D	0.9485	0.0967	0.8518
Intercept	0	-0.0242	0.0242
Slope	1	0.1018	0.8982
Ordinal - Best Model			
R_N^2	0.9527	0.0001	0.9511
D	0.9588	0.018	0.9408
Intercept	0	0.0706	-0.0706
Slope	1	0.07	0.93
Ordinal - Least Effort Model			
R_N^2	0.8059	0.025	0.78
D	0.6905	0.0204	0.6701
Intercept	0	0.0532	-0.0532
Slope	1	0.1063	0.8937

FIGURE A.1. Reproductive phases (described by Brown-Peterson et al. 2011), reproductive stages (i.e., used for predictive models) and corresponding histological images and colors for female striped bass. Histological images show post-ovulatory follicles (POF) and atretic (A), primary growth (PG), cortical alveolar (CA), primary vitellogenic (Vtg1), secondary vitellogenic (Vtg2), and tertiary vitellogenic oocytes (Vtg3). My binary logistic models tended to incorrectly classify regressing* females (i.e., stage 0 with a high proportion of atretic oocytes) as stage 1 females. All histology images were captured at the same magnification (reference scale shown in spawning capable image).

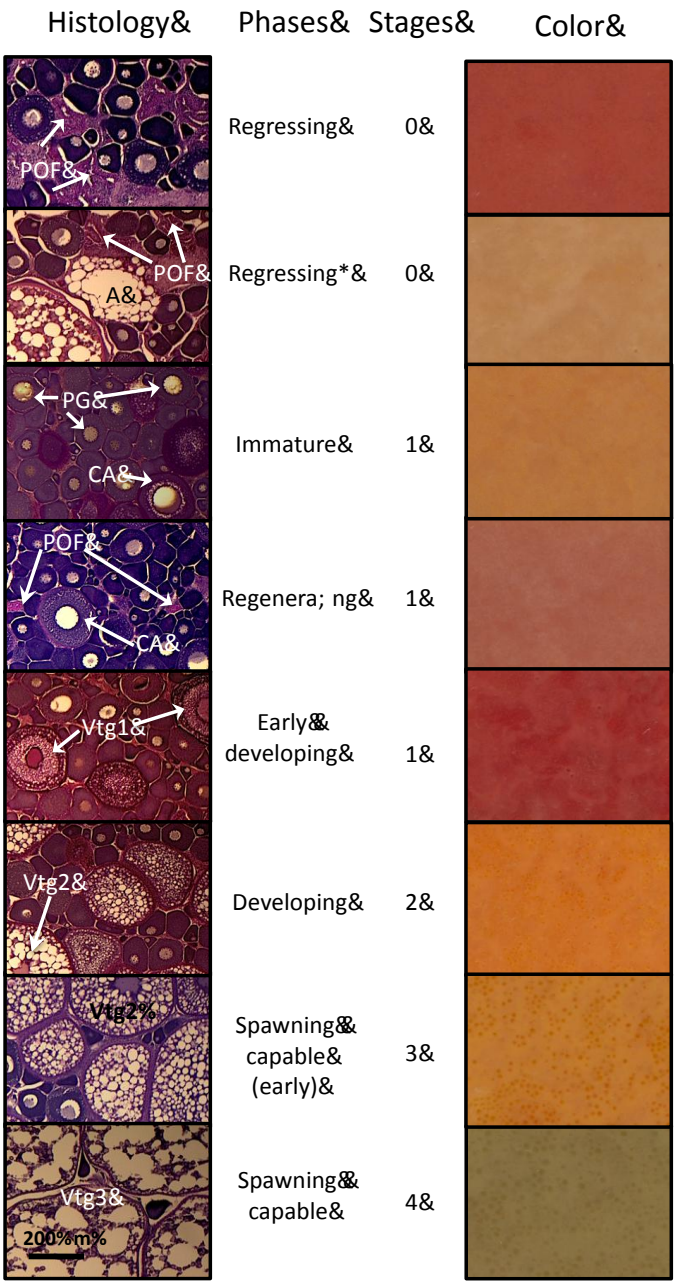


FIGURE A.2. Results showing observed reproductive phase of female striped bass and the predicted probability of females being in the regressing phase based on the (a) best overall binary logistic model and (b) least effort binary logistic model.

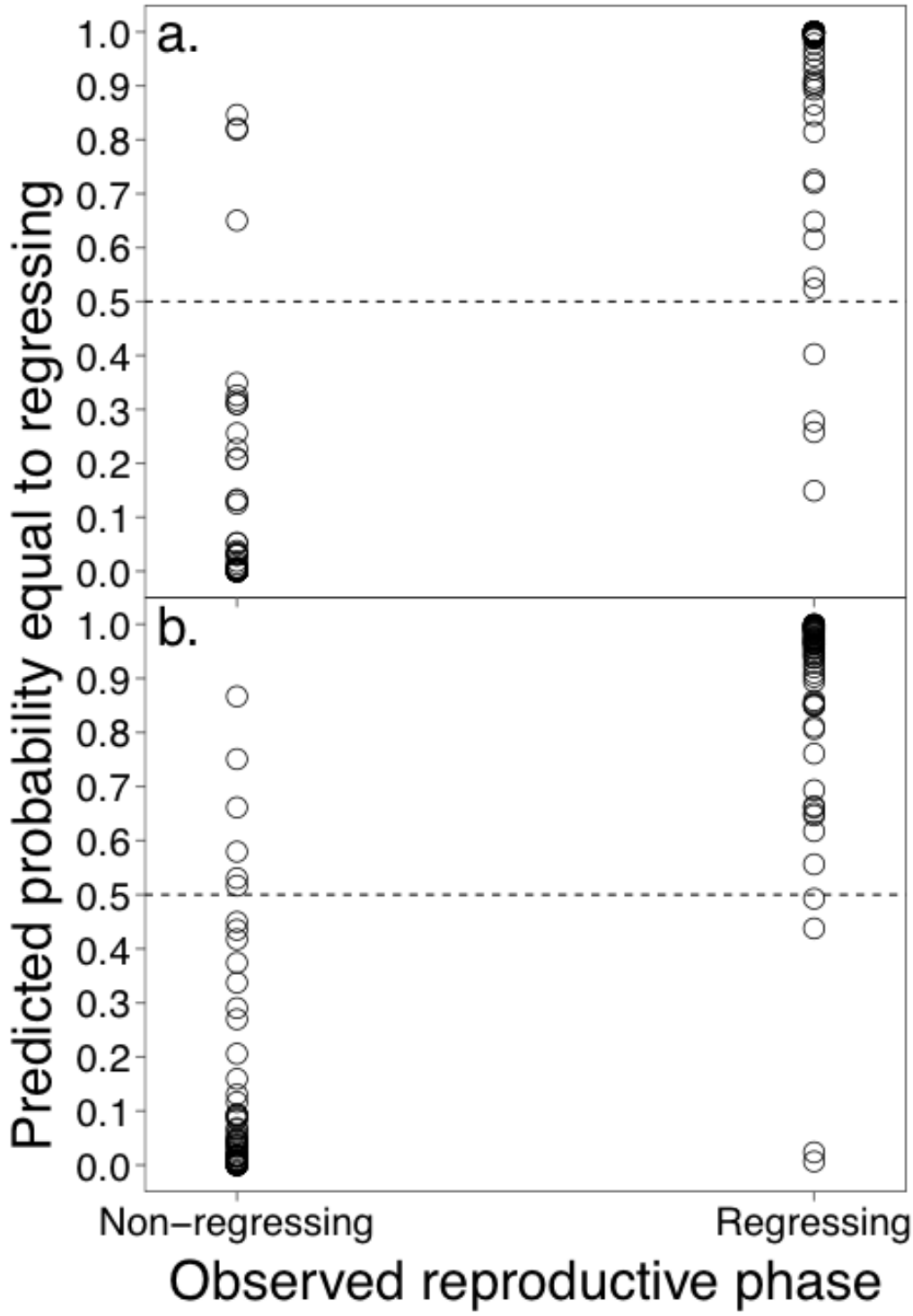


FIGURE A.3. The best overall ordinal model predictions showing observed reproductive stage of female striped bass and the predicted probability of females being in stage 1 (a), 2 (b), 3 (c) and 4 (d).

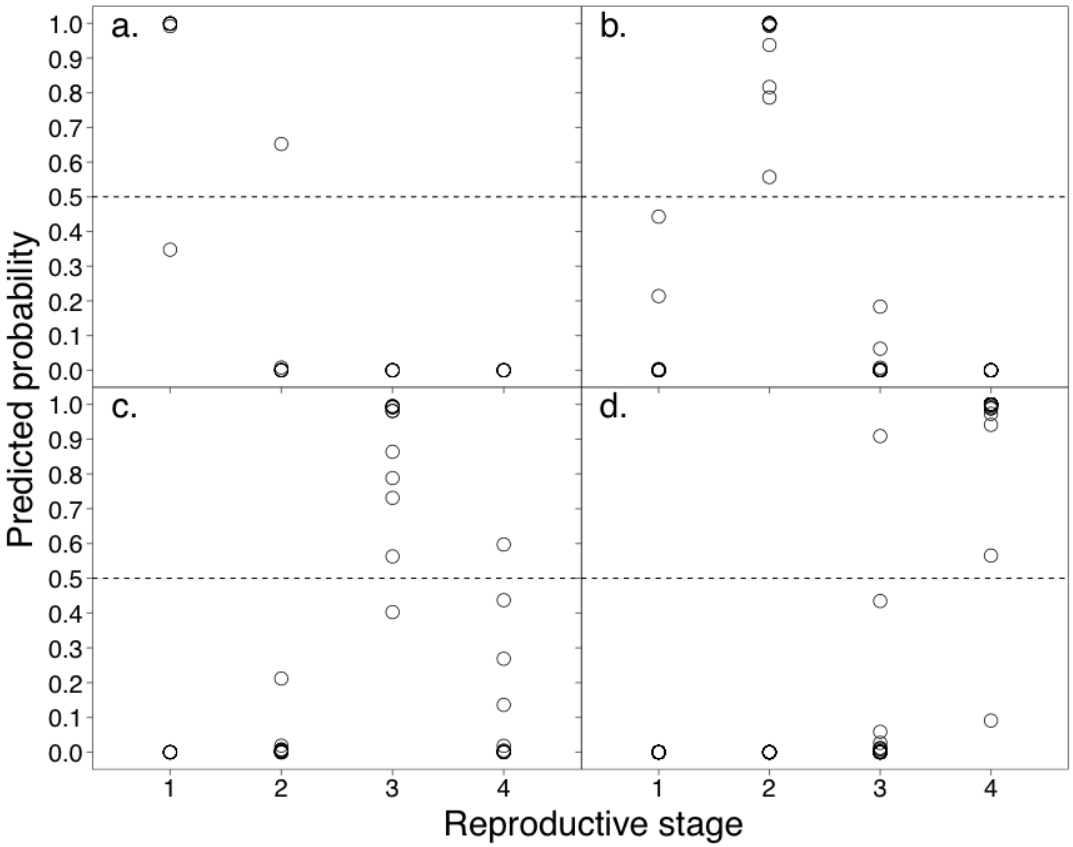
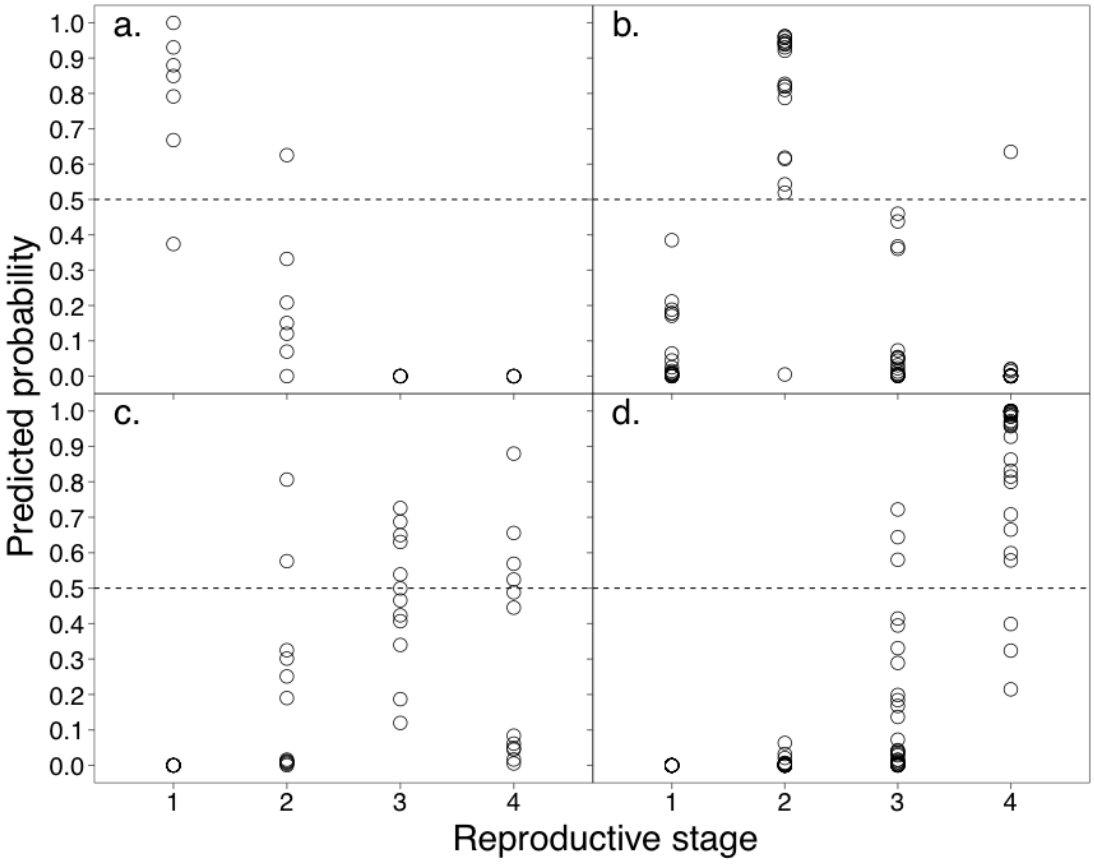
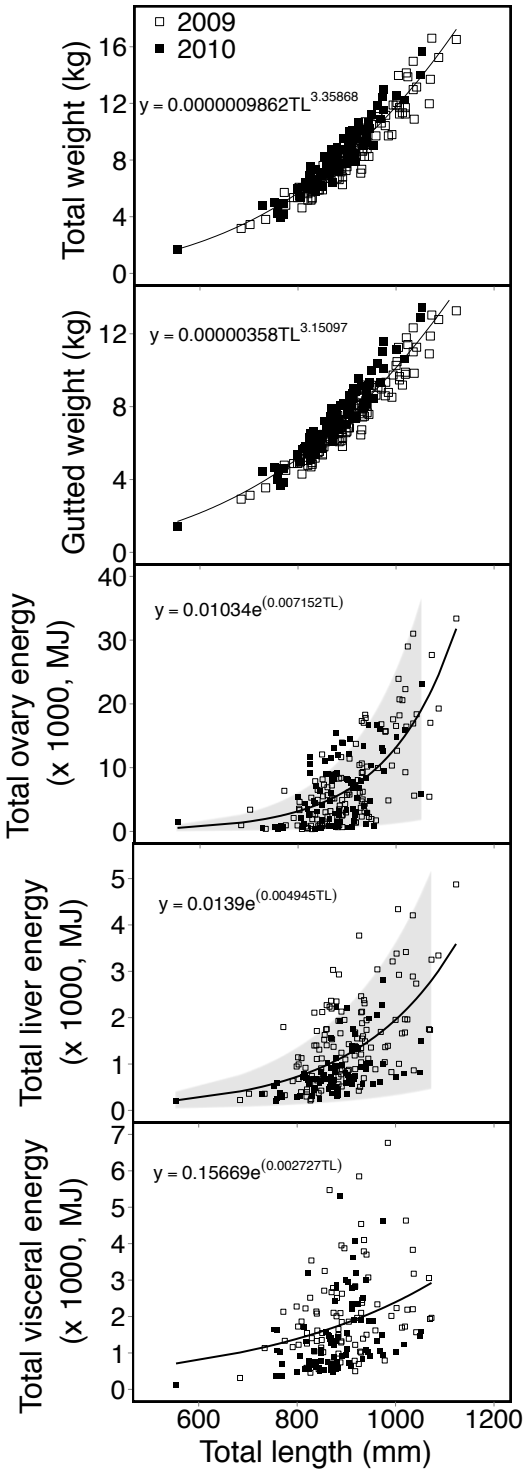


FIGURE A.4. The least effort ordinal model predictions showing observed reproductive stage of female striped bass and the predicted probability of females being in stage 1 (a), 2 (b), 3 (c) and 4 (d).

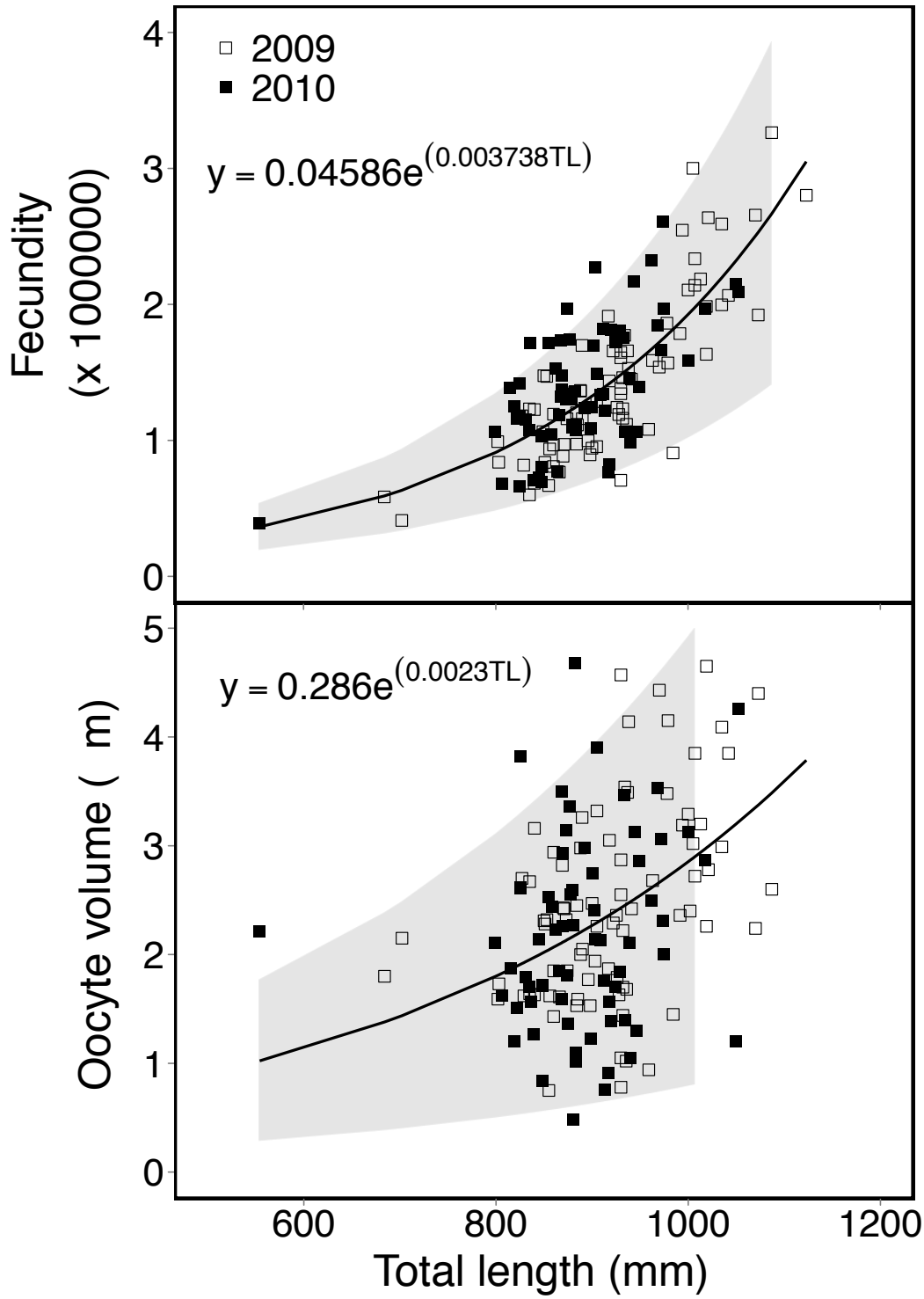


Appendix B. Nonlinear relationships between striped bass female total length and several female weight and tissue energy measures (A), as well as fecundity and oocyte volume (B). Relationships were produced from females collected in the mainstem of the Chesapeake Bay during March-May, 2009 and 2010.

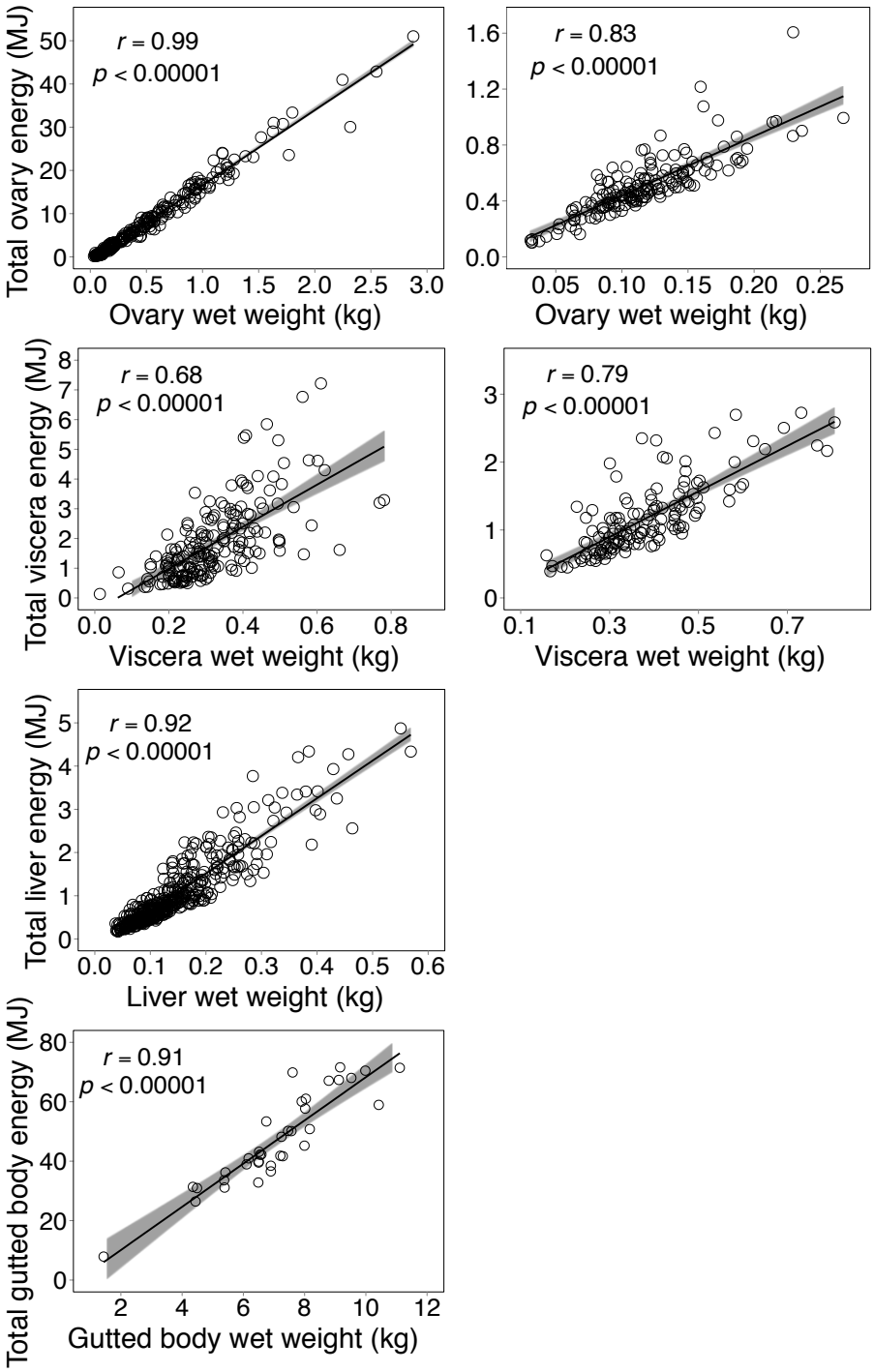
A. Nonlinear relationships between striped bass female total length and several female weight and tissue energy measures. Residuals from these relationships were used as measures of relative condition in Chapter 3.



B. Nonlinear relationships between striped bass female total length and fecundity and oocyte volume. Residuals from these relationships were used as measures of relative reproductive potential in Chapter 3.



Appendix C. Correlations between the total wet weights (kg) and total energy (MJ) of female striped bass tissues and gutted bodies. Female striped bass were collected in the mainstem of the Chesapeake Bay from March-May during 2009 and 2010. For total ovary energy and total visceral energy, panels on the left include only pre-spawn females (i.e., stages 2, 3, 4; see Appendix A) and panels on the right include only post-spawn females (i.e., stage 0; see Appendix A). Separate correlations for pre- and post-spawn females were not necessary for liver and gutted body.



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