ARTICLE

Climate Change, Migration Phenology, and Fisheries Management Interact with Unanticipated Consequences

A. C. Peer^{*1} and T. J. Miller

Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Post Office Box 38, Solomons, Maryland 20688, USA

Abstract

Accumulating evidence indicates that as global temperatures rise, reproductive behaviors, including migrations, are occurring earlier across a range of taxa. Alone, these changes are ecologically important; however, for some fish populations, management practices may unknowingly interact with climate-induced changes in reproductive phenology, leading to unanticipated changes in fishing mortality. The potential for such an interaction exists for the Chesapeake Bay Striped Bass Morone saxatilis fishery, which opens on the same week each year during the spawning season. Earlier migrants spawn before the fishery opens; however, later migrants are vulnerable to fishing before they reach the spawning grounds. Consequently, if there are climate-induced changes in Striped Bass spawning phenology, unexpected levels of fishing mortality may occur for egg-bearing, prespawn females. To evaluate the potential consequences of this temporally fixed fishing season, we analyzed a time series of gill-net catch data using an inference-based modeling approach to identify the environmental cues driving variation in the migratory timing of Striped Bass onto their two primary spawning grounds. We hypothesized that factors driving migratory timing would also influence the proportion of egg-bearing, prespawn females caught in the fishery each year. Results indicated that spring water temperature was the primary factor influencing the timing of movement onto spawning grounds, with higher temperatures resulting in early migrations. Importantly, our results indicated that in cool years, when females moved onto the spawning grounds later, more egg-bearing females were caught in the fishery before they could spawn. This situation provides impetus for establishing management approaches that reduce potential climateinduced variability in fishing mortality in the Chesapeake Bay and fisheries around the globe.

The timing of life cycle events in plants and animals is critical to the successful completion of life cycles. Recently, changes in phenology in response to climate change have been reported for a range of taxa (Parmesan 2006). Many of these changes involve shifts in the timing of reproduction—and with good reason. Timing of reproduction is a life history trait with substantial fitness consequences (Clutton-Brock 1988; Varpe et al. 2007), and there is a limited window that is favorable for reproduction each year (Visser et al. 2004). To reproduce at optimal time periods, mature individuals frequently respond to environmental cues, which trigger reproductive events (Munro et al. 1990).

Spawning migrations are 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 (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; Gilhousen 1990). The timing of migration should coincide with environmental conditions that are suitable for offspring survival and should avoid predictable periods of especially stressful, energetically demanding, or dangerous conditions (Hodgson and Quinn 2002). 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 longterm average optimal date, with little interannual variation in

^{*}Corresponding author: adam.peer@ferc.gov

¹Present address: Federal Energy Regulatory Commission, 888 First Street Northeast, Washington, D.C. 20246, USA.

Received December 20, 2012; accepted September 5, 2013

response to environmental changes. However, in species with little spatial and/or temporal separation between the environments experienced by adults and their progeny, adults should respond to interannual environmental variability and should behaviorally adjust the timing of migration and spawning to optimize conditions for their young.

The Striped Bass Morone saxatilis is an anadromous fish that is found along the Atlantic coast of North America from Florida (USA) to Nova Scotia (Canada). Migratory adults generally occur in the coastal ocean during summer through winter and enter estuaries in the spring to spawn (Boreman and Lewis 1987). Striped Bass migration into Chesapeake Bay involves two phases, which together likely influence the time of arrival onto the spawning grounds. First, late-winter and early spring migrations occur from offshore wintering grounds off the Virginia and North Carolina coasts to staging grounds that are located in brackish-water areas of the Chesapeake Bay. Females then undertake springtime (April-May) spawning runs to spawning grounds that are located in and above the salt front in tidal freshwater. Females release all of their eggs within a short period of time. Once fertilized, eggs hatch within 29-80 h (Hardy 1978). Given the short delay between spawning migrations and larval production, Quinn and Adams' (1996) conceptual model suggests that female Striped Bass should adjust the timing of their final run and spawning in response to environmental variability so as to optimize the environments experienced by their young.

Striped Bass generally spawn at temperatures between 12°C and 23°C (Setzler-Hamilton et al. 1980). Peak spawning occurs after temperature increases of 2-3°C over a several-day period (Rutherford and Houde 1995). Several studies have shown that egg abundance generally increases as spring water temperature rises (Grant and Olney 1991; Secor and Houde 1995). Furthermore, it has been shown experimentally that temperature plays a dominant role in the termination of the female Striped Bass reproductive cycle (Clark et al. 2005). Although water temperature may be a dominant cue for Striped Bass spawning behavior. river flow pulses and wind events on the spawning grounds also may affect their reproductive success (North et al. 2005). These types of events can affect circulation patterns on Striped Bass nursery grounds, affect the trapping ability of the estuarine turbidity maximum (an important nursery area for larval Striped Bass; North and Houde 2001), and potentially reduce retention and survival of Striped Bass eggs and larvae (North et al. 2004). Modeling and field evidence suggest that storm events are associated with episodic mortalities of Striped Bass eggs and larvae (Rutherford and Houde 1995; North et al. 2005). Given the likely negative effects of wind and flow pulses on early life survival, these events could serve as negative cues that delay upriver spawning runs. Thus, the dominant influence of temperature on spawning behavior could be modulated by flow and/or wind pulses.

In addition to the possible migratory cues provided by the environment, temperature-dependent gonadal development may also determine the timing of spawning migrations. Specifically, warmer water temperature during vitellogenesis may result in earlier spawning time for spring-spawning teleosts. In the laboratory, Kjesbu et al. (2010) determined that oocyte growth in Atlantic Cod *Gadus morhua* was faster and spawning occurred earlier at warmer temperatures. In the field, Ware and Tanasichuk (1989) demonstrated that gonadal development in Pacific Herring *Clupea pallasii* was positively correlated with the average sea surface temperature during the 90-d period that preceded spawning. In Striped Bass, vitellogenesis generally begins in October and ends in April. Thus, winter water temperatures on overwintering grounds could influence spawning time by altering rates of vitellogenesis and gonadal development.

Alone, the potential effects of water temperature (spring or winter), river flow, and wind on spawning phenology are ecologically important. However, in some fish populations, management practices may unknowingly interact with climate-induced alterations in reproductive phenology, leading to unanticipated changes in fishing mortality. Temporal fishing closures are a traditional and still commonly used management approach to protect mature adults during the reproductive period (National Research Council 2001; Russell et al. 2012). In many cases, closure dates are established without firm knowledge of temporal patterns or drivers of reproductive activity (Pears et al. 2007; Loher 2011). Even for fisheries where spawning behavior is thought to be understood, closures that are designed to protect spawners often fail to encompass the entire spawning season (Greenley 2009). Such is the case for the Chesapeake Bay "trophy" Striped Bass fishery. The trophy fishery opens during the spawning season to target large migratory females as they move to and from their spawning grounds. Currently, the season opens each year on a fixed date (i.e., the third Saturday in April); however, if female Striped Bass migration timing varies with interannual fluctuations in temperature, flow, or wind, then conditions leading to later peak migrations could result in higher fishing mortality on mature, egg-bearing females.

We used a time series of gill-net catches from two Chesapeake Bay spawning grounds and an inference-based modeling approach to quantify the effect of water temperature, river flow pulses, and wind pulses on the timing of spawning migrations by female Striped Bass. Specifically, we evaluated whether spring water temperature on the spawning grounds, winter water temperature on the wintering grounds, or both had a positive effect on migration timing, either by cueing the spawning runs to occur at optimal times for offspring survival (i.e., spring water temperature) or by controlling gonadal development (winter water temperature). Additionally, we evaluated whether river flow pulses and/or wind pulses had a negative influence on spawning runs, as these types of events likely produce suboptimal conditions for offspring survival. Because each environmental variable could influence migration timing either in isolation or in combination with one or more other variables, our multiple hypotheses (and models) included all possible combinations of environmental variables. Furthermore, because anecdotal evidence (i.e., Hollis 1967) suggests that spawning time is size dependent, with larger females migrating earlier, we also included female size as an additional variable. Overall, we tested 31 hypotheses to determine the influence of environmental variables and female Striped Bass size on the timing of female migration onto the two dominant Chesapeake Bay spawning grounds. Finally, because the environmental factors driving migration timing could influence the proportion of egg-bearing females that are caught in the trophy fishery, we used a correlation analysis to test the hypothesis that the factors driving migratory timing are strongly associated with the proportion of egg-bearing, prespawn females caught in the fishery each year.

METHODS

Striped Bass spawning phenology data sets.-Female Striped Bass were collected during spawning surveys on the Potomac River and Upper Chesapeake Bay (hereafter, Upper Bay) spawning grounds (Figure 1). Each of these spawning grounds is located in and above the salt front (salinity = 1% isohaline) in tidal freshwater. The Maryland Department of Natural Resources (MDDNR) conducted the spawning surveys from 1985 to 2010 using multipanel experimental drift gill nets. Due to logistical constraints, gill nets were not set in the Potomac River during 1994. Gill nets were fished 4-6 d/week from late March or early April until no Striped Bass were caught 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°C and 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 using multifilament to form 10 stretchmesh sizes: 7.6, 9.5, 11.4, 13.3, 15.2, 16.5, 17.8, 20.3, 22.9, and 25.4 cm. In the Upper Bay, all 10 panels were tied together end to end to comprise a single gang of nets. In the Potomac River, due to the design of the fishing boat, the 10 panels were fished as two gangs of five panels. In both systems, all 10 mesh panels were fished twice daily unless the weather prohibited a second set. Whether the gill nets were fished in gangs of 10 or 5 panels, the order of mesh sizes within the suite was randomized, with gaps of 0.91-3.04 m between panels. Overall soak times for each mesh panel ranged from 15 to 65 min. Sampling locations were assigned by using a stratified random survey design in which each spawning area served as 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 Potomac River grid consisted of forty 0.8-km² quadrants, and the Upper Bay grid consisted of thirty-one 1.6-km² quadrants. Upon arrival at each site, nets were deployed and soaked for the desired time. All of the captured Striped Bass were removed and measured for TL (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). Temperature data from two sources were used in the analyses. One source was local surface water temperature recorded by MDDNR on the spawning grounds during each day of the gill-net survey; this source represented spring water temperature during the spawning season. None of the National Oceanic and Atmospheric Administration (NOAA) buoys provided a consistent time series of water temperature for the period 1985–2010. Accordingly, we used daily air temperature data collected from November to March of each year at Oceana Naval Air Station (ONAS; Virginia Beach, Virginia; Figure 1) to represent winter sea surface temperature at Striped Bass wintering grounds offshore of Virginia and North Carolina. Air temperature data at ONAS were positively correlated with existing sea surface temperature data at the NOAA Chesapeake Light, Virginia, station (CHLV2 station; r = 0.76, P < 0.0001; Figure 1) and NOAA moored buoy 44014 (r =0.64, P = 0.03; Figure 1); thus, we believed that the ONAS data were representative of winter sea surface temperatures at overwintering grounds.

Daily mean freshwater discharge data were obtained from the U.S. Geological Survey (USGS). Daily mean discharge data for the Susquehanna River at Conowingo, Maryland (USGS station 01578310), were used as a measure of freshwater input to the Upper Bay. Daily mean discharge data recorded at the Little Falls Pump station near Washington, D.C. (USGS station 01646500), were used as the measure for the Potomac River.

Local daily wind speed and wind direction data were obtained from the National Climatic Data Center. Data representing the local atmosphere for the Upper Bay were obtained from the Thomas Point moored buoy in Maryland, and atmospheric data for the Potomac River were obtained from the Marine Corps Base in Quantico, Virginia (Figure 1). Wind direction (i.e., representing the direction from which the wind was blowing) was measured to the nearest degree based on a 360° compass.

Analyses.-To create an index of migration timing, gill-net survey data were corrected for size selectivity to adjust catches for the differential selectivities of the various mesh sizes used in the survey. Size-selectivity corrections were obtained for each mesh size by using the SELECT model (Millar and Fryer 1999). Parameter estimates were obtained using Millar's (2010) code from the Next Generation R functions for trawl and net selectivity. Preliminary attempts were made to fit the data to multiple types of models (i.e., normal scale shift, normal location shift, bimodal lognormal, bimodal normal scale, and bimodal normal location), with the goal of determining which type would provide the best assessment of selectivity. However, when we attempted to fit each model type, the model deviance was unsatisfactory when the data included 7.6-, 16.5-, or 25.4-cm mesh (i.e., the smallest, midpoint, and largest mesh sizes fished). Therefore, these mesh sizes were eliminated from the data set. Although the three excluded mesh sizes accounted for 30% of the collection gear, only 18% and 24% of all recorded Striped Bass were caught in these mesh sizes in the Potomac River and Upper Bay, respectively. The data from the eliminated mesh sizes did



FIGURE 1. Map of the Chesapeake Bay and surrounding region; the Striped Bass spawning grounds in the Upper Bay and Potomac River are highlighted in white. Black circles represent stations from which environmental data used in the analyses were obtained (MCB = Marine Corps Base; NAS = Naval Air Station).

not include female sizes that were not already observed in the remaining mesh sizes, and thus size bias was not believed to be an issue in the final analysis of spawning phenology. After the 7.6-, 16.5-, and 25.4-cm mesh sizes were excluded, all of the models were reassessed and the best-fitting model was identi-

fied as the bimodal normal scale model. Selectivity-corrected catches for each size-class were then standardized (number of fish·4,000 m⁻²·h⁻¹). The selectivity-corrected data were separated into four length-classes of females (<700, 700–799, 800–899, and 900–999 mm TL) to allow for size-specific spawning

time behavior. Although females larger than 999 mm TL were caught, their abundance was too low to be included in this analysis.

The spawning stock gill-net survey attempted to sample spawning fish every 6 d during the entire spawning season. However, this was not always achieved, and some years had more sampling dates than others. Thus, dates selected for analvses 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 d in the Potomac River and 24 d in the Upper Bay). Due to changes in the size and age distributions of the stock during the time series included in this study, some size-classes of females were represented in catches only a few times during some years. Consequently, when catches of a particular size-class occurred on fewer than 6 d in a given year, that year of data for the pertinent size-class was removed from the analysis. Years that were included in the analysis are shown in Table 1. Resampling was conducted on the final data set 100 times for each combination of year, site, and size-class. For each resampling event, we determined the days when 25% (d_{25}), 50% (d_{50}), and 75% (d_{75}) of the cumulative number of migrating females was collected. These three quantiles served as indices of migration timing and were used as dependent variables in linear models to determine whether the effects of environmental variables on migratory timing were consistent over the majority of the catch distribution at each site separately.

The independent environmental variables included in our models were spring water temperature on the spawning grounds (hereafter, "spring water temperature"), winter air temperature near wintering grounds (hereafter, "winter air temperature"), and indices of flow and wind pulse timing and duration. Spring water temperature was calculated as the mean water temperature from April 9 to May 10 on the Potomac River spawning

TABLE 1. Specific years of data that were included in the analysis for determining the days when 25, 50, and 75% of the cumulative number of female Striped Bass spawners (four size-classes) were collected during a fisheryindependent survey on the Chesapeake Bay spawning grounds. The available time series was from 1985 to 2010.

Size-class (mm TL)	Years included in analysis				
Upper Bay					
<700	1985–1992, 1995–1996				
700–799	1988–1992, 1995–1999, 2001				
800-899	1991-2007, 2009-2010				
900–999	1995-2002, 2004-2010				
Po	otomac River				
<700	1985–1993, 1995–1997				
700–799	1989–1993, 1995–1997				
800-899	1992-1993, 1995-2007				
900–999	1992–1993, 1995–2009				

ground and the mean from April 14 to May 15 on the Upper Bay spawning ground. The dates included in our estimate of spring water temperature at each spawning ground represented the range of dates when temperature data were collected during each year of the time series. Winter air temperature was calculated as the mean air temperature at ONAS from November to March of each year.

To quantify wind and flow pulses, we first assumed that if wind and flow pulses influence spawning time, then the combined duration and timing of pulses should be more important than the separate effect of pulse timing or pulse duration. For example, a pulse that occurs early in the spawning season and is of short duration is likely to have less influence than a pulse that occurs early and is longer in duration. Additionally, a pulse that occurs late in the spawning season will likely have little influence on spawning time since most females have already spawned. Thus, we calculated a single variable (pulse duration timing [PDT]) that combined both duration and timing for flow or wind. To calculate wind PDT, we first identified wind pulses as those events that (1) had wind velocities (m/s) greater than the long-term average (1976-2010; based on the shortest time series; i.e., Thomas Point) at each spawning ground during April and May; (2) occurred between the earliest d_{25} and latest d_{75} at each site during the entire time series; (3) lasted at least 2 d (sensu North et al. 2004); (4) moved upstream or downstream within 45° of parallel with water flow (i.e., 192° SW in the Upper Bay and 142° SE in the Potomac River); and (5) occurred after water temperature reached 12°C (i.e., when spawning is usually initiated in the Chesapeake Bay; Setzler-Hamilton et al. 1980). Pulses occurring before the water temperature reached 12°C were deemed unlikely to affect spawning. Although North et al. (2004) used wind stress (dynes/cm²) rather than wind velocity to define pulses, we did not have the daily downstream river inflow data (i.e., m/s) that would be necessary to calculate wind stress. Instead, we simply used wind velocity. However, we did verify that the wind stress pulses identified by North et al. (2004) in the Upper Bay occurred when wind velocity was greater than the long-term average. Thus, we believe our definition was inclusive of the wind pulses identified by North et al. (2004). Flow pulses were identified as discharge events that were twice the average flow from April and May during each year at each site (sensu North et al. 2005) and that occurred after water temperature reached 12°C at the spawning ground. To quantify pulse duration (P_d) for both wind and flow, we calculated the cumulative number of days with pulses during each year at each site. To quantify pulse timing (P_t) , we calculated the number of days between the first day in which water temperature reached 12°C and the first day in which a pulse occurred for each year at each site. Wind PDT and flow PDT were then calculated as

$$PDT = |(P_t - P_d) - c|,$$

where *c* is a constant equal to the maximum number of days between the earliest d_{25} and latest d_{75} in the Upper Bay

(n = 48) and the Potomac River (n = 38). Using this equation, wind PDT and flow PDT were low when P_d was low and P_t occurred late, and PDT values were high when P_d was high and P_t occurred early. Based on our hypothesis, high wind PDT or flow PDT should result in later migration timing of Striped Bass.

We hypothesized that spring water temperature, winter air temperature, wind PDT, flow PDT, and female TL—alone or in combination—would influence the migration timing of female Striped Bass. This approach produced 31 alternative hypotheses (i.e., all possible combinations of variables), which we tested through model selection using an information-theoretic approach (i.e., Akaike's information criterion [AIC]). All 31 models were linear and of the form

$$d_t = X_0 + \sum_{i=1}^m \gamma_i X_{i,t} + \varepsilon_t,$$

where d is the response variable (i.e., d_{25} , d_{50} , or d_{75}) in year t, X_0 is the intercept, *i* represents the covariate (i.e., spring water temperature, winter air temperature, wind PDT, flow PDT, or female size), $X_{i,t}$ is the value of covariate *i* in year *t*, γ_i describes the effect of covariate *i*, and ε_t is an independently and normally distributed random variable with variance σ (~N[0, σ^{2}]). All variables were continuous except female size, which was included as a categorical variable with four levels (i.e., the length-classes described above). We used the second-order AIC approximation (AIC $_c$), which adjusts for sample size (Burnham and Anderson 2002), to compare among models. Multimodel inference was conducted by first ranking the fitted models from best to worst based on the delta AIC (Δ_i), which is a measure of the difference in AIC between a given model and the best model (i.e., the model with the lowest AIC value; Burnham and Anderson 2002). Inference was also based on Akaike weights (w_i) , which indicate the probability that a particular model is the best among the entire set of candidate models (Burnham and Anderson 2002). Because multiple models can compete for the top rank (i.e., $\Delta_i < 2$), we also computed the weighted averages of parameter estimates (Burnham and Anderson 2002). This approach uses all of the information available from the complete model set to compute model-averaged parameter estimates and unconditional SEs that can be used to assess the magnitude of an effect (Burnham and Anderson 2002). To evaluate parameter estimates for each female length-class relative to all other female length-classes, the ordering of length-classes (i.e., levels) was rearranged in the models to permit all possible comparisons in separate model runs. All analyses were conducted in R using the AICcmodavg package (R Development Core Team 2011).

RESULTS

Temporal Trends

In the Upper Bay and the Potomac River, the indices of migration timing (i.e., d_{25} , d_{50} , and d_{75}) generally occurred

earlier for the female size-classes with the longest time series (Figure 2). Because some years of data were excluded for certain female size-classes (Table 1), loess fits in Figure 2 were only applied to the size-classes with the longest time series for each spawning ground. The trends in the Upper Bay were based on the 800–899-mm size-class of females and showed that d_{25} , d_{50} , and d_{75} occurred 5, 6, and 14 d earlier, respectively, during the period from 1991 to 2010 (Figure 2). In contrast, the trends in the Potomac River were based on the 900–999-mm size-class of females and showed less-pronounced decreases over a slightly shorter time series (i.e., 1992–2009; Figure 2). Nevertheless, even for Potomac River females, the estimates of d_{25} and d_{50} were 12 and 4 d earlier, respectively. The d_{75} index did not decline in the Potomac River.

Among environmental variables, only spring water temperature in the Upper Bay exhibited an observable trend during the entire time series (Figure 3). Spring water temperature in the Upper Bay was relatively stable from 1985 to 1995 but increased thereafter (Figure 3). In the Potomac River, spring water temperature also was stable from 1985 to 1995 and exhibited a gradual and less-consistent increase after 1995 (Figure 3). All other environmental variables displayed little or no positive or negative trend during the entire time series.

Female Size and Environmental Effects on Migration Timing Indices

Female size, spring water temperature, and winter air temperature explained most of the variability in d_{25} , d_{50} , and d_{75} for female Striped Bass in the Chesapeake Bay. For both the Upper Bay and Potomac River spawning grounds, the best models (i.e., $\Delta_i < 2$) for explaining d_{25} , d_{50} , and d_{75} included female size and spring water temperature only (Tables 2, 3). Winter air temperature also was included in the second-ranked model for d_{25} in the Upper Bay and in all of the best models for the Potomac River (Tables 2, 3). Although all of the top-ranked models for the Upper Bay and Potomac River included some combination of female size, spring water temperature, and winter air temperature, all of these models had w_i values less than 0.90, indicating uncertainty that these models were in fact the best (Burnham and Anderson 2002). Given these conditions, we used model averaging (multimodel inference) to evaluate the importance of each parameter based on the entire set of models (Burnham and Anderson 2002).

In the Upper Bay, females migrated earlier during years when spring water temperature was warmer, and larger females tended to migrate earlier than smaller females. These trends were evident from model averaging, which indicated that female size and spring water temperature each had a significant negative effect on migration timing (i.e., 95% confidence limits were negative and did not include zero; Table 4; Figure 4). Thus, winter air temperature, flow PDT, and wind PDT had no effect on migration timing (Table 4; Figure 4). Parameter estimates for the effect of spring water temperature on d_{25} , d_{50} , and d_{75} were



FIGURE 2. Time series for the days when 25, 50, and 75% of the cumulative number of female Striped Bass spawners were collected during a fishery-independent survey on the Chesapeake Bay spawning grounds (left panels: Upper Bay; right panels: Potomac River). Four female size-classes are represented. The light-gray shaded region denotes the days when the fishing season is open in the Chesapeake Bay. In the shaded region between dotted lines, the fishery may be open or closed depending on when the third Saturday in April occurs. Data from the size-class with the longest time series for each spawning ground were fitted with a loess smoother (dashed line; span = 0.75) to show dominant trends for the entire time series.

consistent and indicated that for every 1°C increase in water temperature, migration timing occurred about 3 d earlier (Table 4). Parameter estimates for the effect of female size on d_{25} , d_{50} , and d_{75} also were consistent for each size-class comparison and generally indicated that larger females arrived on the spawning grounds earlier than smaller females (Table 4). The only female size-classes that did not display differences in migration timing were (1) the 700–799-mm versus <700-mm class and (2) the 900–999-mm versus 800–899-mm class (Table 4). Similar to the Upper Bay results, Striped Bass females also migrated to the Potomac River spawning ground earlier during years when spring water temperature was warmer, and larger females migrated earlier than smaller females. These trends were evident from model averaging, which indicated that female size and spring water temperature had negative effects on migration timing and that flow PDT and wind PDT had no effect; however, winter air temperature had a positive effect (Table 4; Figure 4). Parameter estimates for the



FIGURE 3. Trends in the environmental variables included as independent variables in linear models to evaluate factors influencing Striped Bass migration timing onto the Chesapeake Bay spawning grounds (left panels: Upper Bay; right panels: Potomac River). Pulse duration timing (PDT) refers to wind and flow variables that incorporated both the timing and duration of pulse events. The lower panel shows winter air temperature data for Oceana Naval Air Station (Virginia Beach, Virginia) near the overwintering grounds. Individual data points are shown as dots. Trend lines fitted to the data were derived using a loess smoother (span = 0.5); the gray region around each trend line represents the 95% confidence interval.

PEER AND MILLER

TABLE 2. Candidate subset of the 10 best linear models for determining the effect of environmental variables on Striped Bass migration timing (i.e., days when 25, 50, and 75% of the cumulative number of female spawners were collected) to the Upper Bay spawning ground (temp = temperature). Pulse duration timing (PDT) refers to wind and flow variables that incorporated both the timing and duration of pulse events. Shown are the number of parameters (*K*; includes intercept and variance), the second-order Akaike's information criterion (AIC_c), each model's AIC difference relative to the best model (Δ_i), and the Akaike weight (w_i). Gray shading indicates models with substantial evidence in support (i.e., $\Delta_i < 2$). The candidate subset of models shown only includes those with Δ_i less than 2 and the next two best models.

Model	Log-likelihood	K	AIC_c	Δ_i	w_i			
	Day of 25% catch							
Size, spring temp	-169.18	6	352.22	0.00	0.33			
Size, spring temp, winter temp	-168.32	7	353.19	0.97	0.20			
Size, spring temp, wind PDT	-168.86	7	354.26	2.03	0.12			
Size, spring temp, flow PDT	-169.04	7	354.63	2.40	0.10			
Size, spring temp, winter temp, flow PDT	-167.84	8	355.04	2.81	0.08			
Size, spring temp, winter temp, wind PDT	-168.07	8	355.48	3.26	0.06			
Size, spring temp, wind PDT, flow PDT	-168.70	8	356.74	4.52	0.03			
Size, spring temp, winter temp, wind PDT, flow PDT	-167.56	9	357.41	5.19	0.02			
Spring temp	-176.07	3	358.65	6.42	0.01			
Spring temp, wind PDT	-175.39	4	359.63	7.41	0.01			
	Day of 50% catch							
Size, spring temp	-168.46	6	350.70	0.00	0.49			
Size, spring temp, winter temp	-168.43	7	353.19	2.59	0.13			
Size, spring temp, wind PDT	-168.46	7	353.35	2.64	0.13			
Size, spring temp, flow PDT	-168.46	7	353.35	2.65	0.13			
Size, spring temp, winter temp, flow PDT	-168.43	8	356.06	5.35	0.03			
Size, spring temp, winter temp, wind PDT	-168.43	8	356.06	5.35	0.03			
Size, spring temp, wind PDT, flow PDT	-168.46	8	356.11	5.41	0.03			
Size, spring temp, winter temp, wind PDT, flow PDT	-168.43	9	358.94	8.24	0.01			
Spring temp	-178.00	3	362.48	11.78	0.00			
Spring temp, wind PDT	-177.70	4	364.36	13.66	0.00			
	Day of 75% catch							
Size, spring temp	-165.73	6	345.33	0.00	0.45			
Size, spring temp, wind PDT	-165.53	7	347.60	2.27	0.15			
Size, spring temp, flow PDT	-165.58	7	347.70	2.38	0.14			
Size, spring temp, winter temp	-165.66	7	347.86	2.53	0.13			
Size, spring temp, wind PDT, flow PDT	-165.39	8	350.13	4.80	0.04			
Size, spring temp, winter temp, wind PDT	-165.47	8	350.29	4.96	0.04			
Size, spring temp, winter temp, flow PDT	-165.55	8	350.46	5.13	0.03			
Size, spring temp, winter temp, wind PDT, flow PDT	-165.37	9	353.03	7.70	0.01			
Spring temp	-173.78	3	354.05	8.72	0.01			
Spring temp, wind PDT	-173.16	4	355.17	9.84	0.00			

effects of spring water temperature on d_{25} , d_{50} , and d_{75} in the Potomac River were consistent and, like the Upper Bay estimates, indicated that migration timing occurred approximately 3 d earlier for every 1°C increase in water temperature (Table 4). Parameter estimates for the effect of female size on d_{25} , d_{50} , and d_{75} in the Potomac River also were consistent for each size-class comparison. Although parameter estimates indicated that larger females were on the Potomac River spawning ground earlier than smaller females in two comparisons (i.e., 900–999-mm versus <700-mm class; 900–999-mm versus 800–899-mm class), no other comparisons indicated

differences in migration timing between female size-classes (Table 4).

Environmental Influences on the Proportion of Egg-Bearing Females Caught in the Fishery

Spring water temperature and wind PDT were the only variables to display significant correlations with the proportion of egg-bearing females caught during the trophy fishing season in the Chesapeake Bay (Figure 5). However, spring water temperature was the only variable from both spawning grounds to exhibit the same strong relationship with the proportion of egg-bearing

TABLE 3. Candidate subset of the 10 best linear models for determining the effect of environmental variables on Striped Bass migration timing (i.e., days when 25, 50, and 75% of the cumulative number of female spawners were collected) to the Potomac River spawning ground. Variables and model selection statistics are defined in Table 2. Gray shading indicates models with substantial evidence in support (i.e., $\Delta_i < 2$). The candidate subset of models shown only includes those with Δ_i less than 2 and the next two best models.

Model	Log-likelihood	K	AIC_c	Δ_i	w_i	
	Day of 25% catch					
Size, spring temp, winter temp	-152.29	7	321.13	0.00	0.40	
Size, spring temp, winter temp, wind PDT	-151.84	8	323.04	1.90	0.15	
Size, spring temp, winter temp, flow PDT	-152.19	8	323.72	2.59	0.11	
Spring temp, winter temp	-157.86	4	324.56	3.43	0.07	
Size, spring temp, wind PDT	-154.40	7	325.35	4.22	0.05	
Size, spring temp	-155.87	6	325.60	4.47	0.04	
Size, spring temp, winter temp, wind PDT, flow PDT	-151.74	9	325.76	4.63	0.04	
Spring temp, winter temp, wind PDT	-157.35	5	326.00	4.87	0.04	
Spring temp, winter temp, flow PDT	-157.78	5	326.87	5.73	0.02	
Size, spring temp, wind PDT, flow PDT	-154.20	8	327.76	6.62	0.01	
Day of 50% catch						
Size, spring temp, winter temp	-149.79	7	316.12	0.00	0.44	
Size, spring temp, winter temp, wind PDT	-149.43	8	318.21	2.09	0.15	
Size, spring temp, winter temp, flow PDT	-149.72	8	318.79	2.67	0.12	
Spring temp, winter temp	-155.29	4	319.44	3.31	0.08	
Size, spring temp, winter temp, wind PDT, flow PDT	-149.36	9	321.01	4.89	0.04	
Spring temp, winter temp, wind PDT	-154.88	5	321.06	4.94	0.04	
Size, spring temp, wind PDT	-152.52	7	321.58	5.46	0.03	
Size, spring temp	-153.92	6	321.71	5.59	0.03	
Spring temp, winter temp, flow PDT	-155.23	5	321.77	5.65	0.03	
Spring temp, winter temp, wind PDT, flow PDT	-154.82	6	323.50	7.38	0.01	
	Day of 75% catch					
Spring temp, winter temp	-165.15	4	339.14	0.00	0.27	
Size, spring temp, winter temp	-161.49	7	339.53	0.39	0.22	
Spring temp, winter temp, wind PDT	-165.02	5	341.34	2.20	0.09	
Spring temp, winter temp, flow PDT	-165.14	5	341.59	2.45	0.08	
Size, spring temp, winter temp, wind PDT	-161.41	8	342.17	3.03	0.06	
Size, spring temp, winter temp, flow PDT	-161.49	8	342.33	3.19	0.05	
Spring temp	-168.05	3	342.59	3.45	0.05	
Size, spring temp	-164.61	6	343.08	3.94	0.04	
Spring temp, wind PDT	-167.26	4	343.38	4.24	0.03	
Spring temp, winter temp, wind PDT, flow PDT	-165.02	6	343.90	4.76	0.02	

females caught (Figure 5). The relationship between spring water temperature and the proportion of egg-bearing females caught was negative, indicating that a larger proportion of egg-bearing females was caught during years when mean spring water temperatures were colder (Figure 5). In contrast, wind PDT in the Upper Bay displayed no relationship with the proportion of egg-bearing females caught, whereas wind PDT in the Potomac River displayed a negative relationship (Figure 5).

DISCUSSION

Our inference-based modeling approach showed strong support for the hypothesis that spring water temperature on or near the spawning grounds is the dominant cue triggering the spawning migration for female Striped Bass. Our results show that females move onto Upper Bay and Potomac River spawning grounds approximately 3 d earlier for every 1°C increase in spring water temperature. In contrast, there was weak evidence that winter air temperature was important and no evidence that flow PDT or wind PDT influenced the timing of spawning migrations. Overall, the impacts of these temperature-dependent migrations will require additional investigation; however, our results indicate that an interaction with Maryland's temporally fixed opening of the trophy fishing season could have unexpected effects on fishing mortality of Striped Bass.

TABLE 4. Model-averaged parameter estimates for the effect on Striped Bass migration timing (i.e., days when 25% [d_{25}], 50% [d_{50}], and 75% [d_{75}] of the cumulative number of female spawners were collected). Pulse duration timing (PDT) refers to wind and flow variables that incorporated both the timing and duration of pulse events (temp = temperature). Model-averaged estimates and 95% confidence limits (in parentheses) are shown. Estimates with confidence limits that exclude zero are in bold italics. For size-classes, negative parameter values indicate earlier migration timing by the larger size-class.

	Parameter estimates					
Variable	<i>d</i> ₂₅	d_{50}	d_{75}			
	Upper Bay					
Spring temp	-3.14(-4.90, -1.37)	-3.12 (-4.56, -1.68)	-3.48 (-5.08, -1.88)			
Flow PDT	0.05 (-0.10, 0.20)	0.00 (-0.12, 0.12)	-0.03(-0.17, 0.10)			
Wind PDT	0.03 (-0.05, 0.12)	0.00(-0.07, 0.08)	0.02 (-0.05, 0.10)			
Winter temp	-1.13(-2.88, 0.62)	-0.17 (-1.66, 1.32)	-0.26(-1.91, 1.39)			
Size (900–999 versus <700 mm)	-8.14 (-13.95, -2.32)	-7.04(-11.81, -2.26)	-4.26 (-9.70, -1.18)			
Size (800–899 versus <700 mm)	-4.87(-10.45, 0.71)	-5.79 (-10.34, -1.24)	-5.75 (-10.97, -0.53)			
Size (700–799 versus <700 mm)	1.08 (-4.94, 7.10)	2.23 (-2.74, 7.19)	3.64 (-2.01, 9.29)			
Size (900–999 versus 700–799 mm)	-9.22 (-14.61, -3.83)	-9.27 (-13.97, -4.56)	-7.90 (-12.95, -2.85)			
Size (800–899 versus 700–799 mm)	-5.95 (-11.06, -0.84)	-8.02(-12.49, -3.54)	-9.39 (-14.19, -4.59)			
Size (900–999 versus 800–899 mm)	-3.27 (-7.80, 1.26)	-1.25(-5.23, 2.73)	1.49 (-2.76, 5.74)			
	Potoma	ac River				
Spring temp	-3.08 (-4.67, -1.50)	-3.09 (-4.58, -1.61)	-3.05 (-4.89, -1.22)			
Flow PDT	0.02 (-0.08, 0.12)	0.02 (-0.08, 0.11)	0.00 (-0.12, 0.11)			
Wind PDT	-0.05(-0.14, 0.04)	-0.04(-0.13, 0.05)	-0.04 (-0.15 , 0.08)			
Winter temp	1.70 (0.32, 3.09)	1.77 (0.45, 3.08)	1.94 (0.29, 3.59)			
Size (900–999 versus <700 mm)	-5.30 (-8.94, -1.66)	-4.99 (-8.45, -1.53)	-5.25 (-9.62, -0.88)			
Size (800–899 versus <700 mm)	-0.67 (-4.39, 3.06)	-0.57 (-4.11, 2.97)	-1.07 (-5.54, 3.40)			
Size (700–799 versus <700 mm)	-1.75 (-6.13, 2.64)	-2.09 (-6.26, 2.07)	-2.53(-7.78, 2.73)			
Size (900–999 versus 700–799 mm)	-3.55(-7.75, 0.65)	-2.90(-6.88, 1.09)	-2.72 (-7.76, 2.32)			
Size (800–899 versus 700–799 mm)	1.08 (-3.20, 5.35)	1.52 (-2.54, 5.58)	1.46 (-3.68, 6.59)			
Size (900–999 versus 800–899 mm)	-4.63 (-8.01, -1.25)	-4.42 (-7.63, -1.21)	-4.18 (-8.23, -0.13)			

Environmental factors have been identified as cues for spawning and migration timing in many anadromous species (Atlantic Salmon Salmo salar: Smith et al. 1994; Juanes et al. 2004; American Shad Alosa sapidissima: Quinn and Adams 1996; White Sturgeon Acipenser transmontanus: Paragamian and Kruse 2001; Lake Sturgeon Acipenser fulvescens: Bruch and Binkowski 2002; Green Sturgeon Acipenser medirostris: Erickson et al. 2002; Sockeye Salmon Oncorhynchus nerka and steelhead O. mykiss: Robards and Quinn 2002; Shovelnose Sturgeon Scaphirhynchus platorynchus: Papoulias et al. 2011). However, the importance of these factors relative to genetic control appears to vary among species, particularly between salmon and other anadromous fishes. For salmonids, the timing of migration and reproduction is under strong genetic control (Hodgson and Quinn 2002). Although some interannual variation in timing is correlated with temperature or other environmental conditions in the ocean and rivers (Hodgson et al. 2006), the timing of salmonid maturation and migration seems to be less flexible than that in other teleosts (Quinn et al. 2009). This low plasticity in timing for salmonids likely evolved because the long migrations and protracted developmental period of embryos separate the environmental conditions experienced by migrating adults

from conditions acting on juveniles (Hodgson et al. 2006). Thus, in general, the best strategy for salmonids is to spawn at a time corresponding to long-term average optimal conditions (Quinn et al. 2009).

In contrast to salmonids, species like Striped Bass exhibit very short temporal delays between migration timing and the hatching of offspring. Consequently, environmental conditions experienced by female Striped Bass moving toward the spawning grounds (especially during the final run) and the conditions experienced by their newly hatched offspring are more strongly correlated than in salmonids. As a result, female Striped Bass should exhibit less genetic control and rely more on proximate environmental factors to advance or delay migration and spawning so as to match the optimal conditions for offspring (sensu American Shad: Quinn and Adams 1996). Our analyses indicate that migration timing in female Striped Bass is strongly related to interannual variability in spring water temperature-an observation that is consistent with the use of water temperature as a proximate cue. Others have drawn similar conclusions for American Shad and Alewives Alosa pseudoharengus, which also exhibit short temporal delays between spawning and the hatching of offspring (Leggett and Whitney 1972; Quinn and



FIGURE 4. Relationships between mean spring water temperature and the days when 25, 50, and 75% of the cumulative number of female Striped Bass spawners were collected during a fishery-independent survey on the Chesapeake Bay spawning grounds (left panels: Upper Bay; right panels: Potomac River). Four female size-classes are represented. The light-gray shaded region denotes the days when the fishing season is open in the Chesapeake Bay. In the shaded region between dotted lines, the fishery may be open or closed depending on when the third Saturday in April occurs.

Adams 1996; Ellis and Vokoun 2009). Environmental variables such as water temperature are likely important cues for spawning and migration in species that exhibit short delays between spawning and hatch.

Although our study is the first to use a long time series of field data to evaluate Striped Bass spawning migration cues, it is not the first to indicate a primary role for water temperature. Douglas et al. (2009) observed that increases in temperature cued the movement of Striped Bass onto the spawning grounds in the Miramichi River, New Brunswick, Canada. Clark et al. (2005) showed experimentally that temperature played a prominent role in the initiation, maintenance, and termination of the reproductive cycle in female Striped Bass. Moreover, across the latitudinal gradient of Striped Bass spawning grounds along the Atlantic coast, peaks in egg abundance have been observed when water temperatures were increasing (Chesapeake Bay tributaries, Maryland and Virginia: Olney et al. 1991, Secor and Houde 1995, and Jahn 2010; Savannah River, Georgia: Van den Avyle and Maynard 1994; Miramichi River: Robichaud-LeBlanc et al. 1996). Thus, spring water temperature appears to be a primary cue for the spawning migration.



FIGURE 5. Relationships between environmental variables and the proportion of mature, egg-bearing, prespawn female Striped Bass caught in the Chesapeake Bay "trophy" fishery from 2002 to 2010 (left panels: Upper Bay; right panels: Potomac River). Pulse duration timing (PDT) refers to wind and flow variables that incorporated both the timing and duration of pulse events. The lower panel shows winter air temperature data for Oceana Naval Air Station (Virginia Beach, Virginia) near the overwintering grounds. Data points are represented by two-digit codes for year (02 = 2002; etc.).

Spawning at the right time of the year with respect to environmental variation is often critical to offspring survival (Heath 1992; Pope and Shepherd 1994). Temperature can have a direct effect on Striped Bass early life stage mortality. Episodic mortalities of eggs and newly hatched larvae occur when temperatures fall below 12°C (Rutherford and Houde 1995). Cohort-specific mortality rates of Striped Bass are strongly temperature dependent, with both early (<14°C) and late (>21°C) cohorts experiencing higher mortality (Secor and Houde 1995). Thus, 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 cues may also ensure that larvae are produced at a time when sufficient prey resources are available (i.e., the match–mismatch hypothesis; Cushing 1982). In the Chesapeake Bay, the copepod *Eurytemora affinis* is a preferred prey resource for larval Striped Bass (Setzler-Hamilton et al. 1982; Bradley 1991; Martino and Houde 2010). Production of *E. affinis* is temperature dependent intra-annually and generally increases as temperatures rise during the spring (Hirche 1992; Lloyd 2006), although flow may be the dominant interannual factor affecting *E. affinis* production (Kimmel and Roman 2004). Because year-class strength probably varies in response to the temporal overlap between larval Striped Bass production and zooplankton production (Martino and Houde 2010), selection for temperature-cued migration and spawning likely minimizes the probability of failed year-classes.

Temperature may also serve as a rate-limiting factor for reproductive development by modifying the levels of hormones that control the rate of vitellogenesis (Kjesbu 1994; Bromage et al. 2001). Thus, migration timing could also be influenced by the temperatures experienced by female Striped Bass during vitellogenesis, which generally begins in October and ends in April. We hypothesized that if temperature-dependent rates of gonadal development are important to migration timing, then winter air temperature should emerge as an important variable in our models. However, no effect of winter air temperature was observed for the Upper Bay, and the weak (i.e., 95% confidence limits barely outside of zero) positive effect observed for the Potomac River was opposite our expectation. Winter air temperature may therefore have little or no effect on migration timing in female Striped Bass.

Our analysis indicated that flow PDT had no influence on migration timing for females migrating to either of the two spawning grounds, a result that is largely consistent with Jahn's (2010) investigation. Jahn (2010) observed that Striped Bass egg abundances were generally higher during the days after highmagnitude pulses in freshwater flow (i.e., twice the average flow each season). However, these flow pulses were often followed by increases in water temperature, suggesting that flow pulses could be correlated with temperature-mediated cues. Our results also indicated that wind PDT, like flow PDT, did not influence the timing of migration onto the spawning grounds. We suggest that wind and flow pulses are either too infrequent to have been selected as a cue or simply do not exhibit substantial positive or negative effects on Striped Bass reproductive success.

Although spring water temperature was the dominant environmental factor influencing the migration timing of female Striped Bass, female size also influenced migration behavior. In both the Upper Bay and the Potomac River, the largest sizeclasses of females moved onto the spawning grounds consistently earlier than the smallest size-classes. This is the first time that size-dependent migration behavior in Striped Bass has been demonstrated using fishery-independent data, although Hollis (1967) anecdotally suggested this type of behavior. 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 in the spawning season (Atlantic Herring Clupea harengus: Lambert 1987; Pacific rockfishes Sebastes spp.: Sogard et al. 2008; Atlantic Mackerel Scomber scombrus: Jansen and Gislason 2011), although in some cases the older or larger females spawn later in the season (Roach Rutilus rutilus: Gillet et al. 1995: American Plaice Hippoglossoides platessoides: Morgan 2003).

The reasons for these size-dependent migrations and spawning are not thoroughly understood. It may be 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 (e.g., Atlantic Herring: González-Vasallo 2006; Kennedy et al. 2010). Sogard et al. (2008) suggested also that size- or age-dependent spawning (or parturition) may be an adaptive strategy of long-lived species such as Pacific rockfishes, in which a maternal lineage spreads reproduction temporally across a spawning season. Although neither explanation for size- or age-dependent migration or spawning behavior can be confirmed at this point for Striped Bass, it is possible that both mechanisms are important.

Exploitation often leads to changes in abundance, size, and age composition of spawning stocks. A recreational fishing season on adult Striped Bass (i.e., trophy season) has taken place in the main stem of the Chesapeake Bay during the spawning season since 1991. In 1991, the trophy season took place from May 11 to May 27; however, the season has progressively advanced toward earlier dates, and since 2001 the season has begun on the third Saturday in April. Creel surveys indicated that a high proportion (29-63%) of spawning-capable and gravid females was caught in the fishery from 2002 to 2010 (MDDNR 2010). Our results indicate that the annual proportion of egg-bearing females that were caught before they spawned was negatively correlated with spring water temperature in the Upper Bay and the Potomac River. When these correlations are considered in the context of temperature-dependent spawning migrations, our results indicate that in cool years, when female Striped Bass 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 trophy fishery to reduce the temperature-dependent effects of fishing mortality.

Our results and those of others indicate that phenological changes in spawning behavior are occurring in response to rising global temperatures. Our investigation indicates that female Striped Bass are migrating-and likely spawningapproximately 3 d earlier for each 1°C increase in spring water temperature. Based on model-averaged projections for the Chesapeake Bay region, water temperature could increase by 2-5°C over the next 60 years (Pyke et al. 2008). This could lead to 1-2-week earlier spawning of female Striped Bass by the end of the 21st century. Alone, climate-induced phenological changes have the potential to negatively influence reproduction and recruitment (e.g., Both et al. 2006; Mackas et al. 2007; Watanuki et al. 2009). However, our results demonstrate that management practices may unknowingly interact with climate-induced changes in reproductive phenology, leading to unanticipated changes in fishing mortality.

Around the globe, temporal fishing closures are a commonly used management approach to protect mature adults during the reproductive period (National Research Council 2001; Russell et al. 2012). In many cases, closure dates are established without firm knowledge of temporal patterns or drivers of reproductive activity (Pears et al. 2007; Loher 2011). Furthermore, many fisheries, including the Striped Bass trophy fishery in the Chesapeake Bay, utilize temporally fixed fishing seasons. These approaches fail to consider how changes in climate can alter spawning phenology and thus the effectiveness of fishing regulations. Our results indicate that the interaction among climate change, spawning phenology, and fisheries management could have important yet unanticipated consequences for fishing mortality as well as for reproductive potential and recruitment of fishery species around the globe.

ACKNOWLEDGMENTS

We thank the MDDNR, especially B. A. Versak, for providing the spawning stock survey data used in this study. Interpretation of these data and any conclusions drawn are those of the authors and do not necessarily represent the views of the MDDNR. We acknowledge E. D. Houde, P. Pepin, R. M. Harrell, T. P. Quinn, and an anonymous reviewer for helpful comments on previous versions of this manuscript. This research was supported in part by an award from the Maryland Sea Grant College Program (SA7528085-EE) to T.J.M. This is Contribution Number 4815 from the University of Maryland Center for Environmental Science.

REFERENCES

- Boreman, J., and R. R. Lewis. 1987. Atlantic coastal migration of Striped Bass. Pages 331–339 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper, editors. Common strategies of anadromous and catadromous fishes. American Fisheries Society, Symposium 1, Bethesda, Maryland.
- Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441:81–83.

- Bradley, B. P. 1991. Distribution of copepods in coastal zone waters: seasonal succession in Chesapeake Bay. Bulletin of the Plankton Society of Japan Special Volume:129–131.
- Bromage, N., M. Porter, and C. Randall. 2001. The environmental regulation of maturation in farmed finfish with special reference to the role of photoperiod and melatonin. Aquaculture 197:63–98.
- Bruch, R. M., and F. P. Binkowski. 2002. Spawning behavior of Lake Sturgeon (Acipenser fulvescens). Journal of Applied Ichthyology 18:570–579.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Springer Science, New York.
- Clark, R., A. Henderson-Arzapalo, and C. Sullivan. 2005. Disparate effects of constant and annually-cycling day length and water temperature on reproductive maturation of Striped Bass (*Morone saxatilis*). Aquaculture 249:497– 513.
- Clutton-Brock, T. H. 1988. Reproductive success. University of Chicago Press, Chicago.
- Cushing, D. H. 1982. Climate and fisheries. Academic Press, London.
- Dodson, J. J. 1997. Fish migration: an evolutionary perspective. Pages 10–36 in J. G. J. Godin, editor. Behavioural ecology of teleost fishes. Oxford University Press, Oxford, UK.
- Douglas, S. G., G. Chaput, J. Hayward, and J. Sheasgreen. 2009. Prespawning, spawning, and postspawning behavior of Striped Bass in the Miramichi River. Transactions of the American Fisheries Society 138:121–134.
- Ellis, D., and J. C. Vokoun. 2009. Earlier spring warming of coastal streams and implications for Alewife migration timing. North American Journal of Fisheries Management 29:1584–1589.
- Erickson, D. L., J. A. North, J. E. Hightower, J. Weber, and L. Lauck. 2002. Movement and habitat use of Green Sturgeon *Acipenser medirostris* in the Rogue River, Oregon, USA. Journal of Applied Ichthyology 18:565– 569.
- Gilhousen, P. 1990. Prespawning mortalities of Sockeye Salmon in the Fraser River system and possible causal factors. International Pacific Salmon Fisheries Commission Bulletin 26:1–58.
- Gillet, C., J. P. Dubois, and S. P. Bonnet. 1995. Influence of temperature and size of females on the timing of spawning of Perch, *Perca fluviatilis*, in Lake Geneva from 1984 to 1993. Environmental Biology of Fishes 42:355– 363.
- González-Vasallo, B. D. 2006. Regulatory reproductive mechanisms and somatic growth in Atlantic Herring (*Clupea harengus* L.). Master's thesis. University of Bergen, Bergen, Norway.
- Grant, G. C., and J. E. Olney. 1991. Distribution of Striped Bass Morone saxatilis (Walbaum) eggs and larvae in major Virginia rivers. Fishery Bulletin 89:187– 193.
- Greenley, A. P. 2009. Movements of Lingcod (*Ophiodon elongatus*) tagged in Carmel Bay, California. Master's thesis. San Jose State University, San Jose, California.
- Gross, M. R. 1987. Evolution of diadromy in fishes. Pages 14–25 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper, editors. Common strategies of anadromous and catadromous fishes. American Fisheries Society, Symposium 1, Bethesda, Maryland.
- Hardy, J. D. J. 1978. Development of fishes of the Mid-Atlantic Bight: an atlas of egg, larval and juvenile stages, volume 3. Aphredoderidae through Rachycentridae. U.S. Fish and Wildlife Service, FWS/OBS-78/12, Washington, D.C.
- Heath, M. R. 1992. Field investigations of the early-life stages of marine fish. Advances in Marine Biology 28:1–174.
- Hirche, H. J. 1992. Egg production of *Eurytemora affinis*—effect of *k*-strategy. Estuarine Coastal and Shelf Science 35:395–407.
- Hodgson, S., and T. P. Quinn. 2002. The timing of adult Sockeye Salmon migration into fresh water: adaptations by populations to prevailing thermal regimes. Canadian Journal of Fisheries and Aquatic Sciences 80:542– 555.
- Hodgson, S., T. P. Quinn, R. Hilborn, R. C. Francis, and D. E. Rogers. 2006. Marine and freshwater climatic factors affecting interannual variation in the

timing of return migration to fresh water of Sockeye Salmon (*Oncorhynchus nerka*). Fisheries Oceanography 15:1–24.

- Hollis, E. H. 1967. An investigation of Striped Bass in Maryland. Maryland Department of Chesapeake Bay Affairs, Final Report F-3-R, Annapolis.
- Jahn, G. L. 2010. The influence of episodic river flow events on Striped Bass (*Morone saxatilis*) spawning in Chesapeake Bay, USA. Master's thesis. University of Maryland, College Park.
- Jansen, T., and H. Gislason. 2011. Temperature affects the timing of spawning and migration of North Sea mackerel. Continental Shelf Research 31:64–72.
- Juanes, F., S. Gephard, and K. Beland. 2004. Long-term changes in migration timing of adult Atlantic Salmon (*Salmo salar*) at the southern edge of the species distribution. Canadian Journal of Fisheries and Aquatic Sciences 61:2392–2400.
- Kennedy, J., J. E. Skjæraasen, R. D. M. Nash, A. Thorsen, A. Slotte, T. Hansen, and O. S. Kjesbu. 2010. Do capital breeders like Atlantic Herring (*Clupea harengus*) exhibit sensitive periods of nutritional control on ovary development and fecundity regulation? Canadian Journal of Fisheries and Aquatic Sciences 67:16–27.
- Kimmel, D., and M. Roman. 2004. Long-term trends in mesozooplankton abundance in Chesapeake Bay, USA: influence of freshwater input. Marine Ecology Progress Series 267:71–83.
- Kjesbu, O. S. 1994. Time of start of spawning in Atlantic Cod (*Gadus morhua*) females in relation to vitellogenic oocyte diameter, temperature, fish length and condition. Journal of Fish Biology 45:719–735.
- Kjesbu, O. S., D. Righton, M. Krüger-Johnsen, A. Thorsen, K. Michalsen, M. Fonn, and P. R. Witthames. 2010. Thermal dynamics of ovarian maturation in Atlantic Cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 67:605–625.
- Lambert, T. C. 1987. Duration and intensity of spawning in herring *Clupea harengus* as related to the age structure of the mature population. Marine Ecology-Progress Series 39:209–220.
- Leggett, W. C., and R. R. Whitney. 1972. Water temperature and the migrations of American Shad. U.S. Marine Fisheries Service Bulletin 70:659–670.
- Lloyd, S. S. 2006. Zooplankton ecology in the Chesapeake Bay estuarine turbidity maximum, with emphasis on the calanoid copepod *Eurytemora affinis*. Doctoral dissertation. University of Maryland, College Park.
- Loher, T. 2011. Analysis of match-mismatch between commercial fishing periods and spawning ecology of Pacific Halibut (*Hippoglossus stenolepis*), based on winter surveys and behavioural data from electronic archival tags. ICES Journal of Marine Science 68:2240–2251.
- Mackas, D. L., S. Batten, and M. Trudel. 2007. Effects on zooplankton of a warmer ocean: recent evidence from the Northeast Pacific. Progress in Oceanography 75:223–252.
- Martino, E. J., and E. D. Houde. 2010. Recruitment of Striped Bass in Chesapeake Bay: spatial and temporal environmental variability and availability of zooplankton prey. Marine Ecology Progress Series 409:213–228.
- MDDNR (Maryland Department of Natural Resources). 2010. Chesapeake Bay finfish/habitat investigations. Maryland Department of Natural Resources, U.S. Fish and Wildlife Service Federal Aid Project, F-61-R-3, Annapolis.
- Millar, R. B. 2010. Software for selectivity analysis of covered cod-end and alternate haul data using SELECT. Available: http://www.stat.auckland. ac.nz/~millar/selectware/code.html. (August 2013).
- Millar, R. B., and R. J. Fryer. 1999. Estimating the size-selection curves of towed gears, traps, nets and hooks. Reviews in Fish Biology and Fisheries 9:89–116.
- Morgan, M. J. 2003. Variation with age in the timing and duration of spawning in American Plaice. Journal of Fish Biology 62:464–473.
- Munro, A. D., A. P. Scott, and T. J. Lam. 1990. Reproductive seasonality in teleosts: environmental influences. CRC Press, Boca Raton, Florida.
- National Research Council. 2001. Marine protected areas: tools for sustaining ocean ecosystems. National Academy Press, Washington, D.C.
- North, E., S. Y. Chao, Sanford, L. P., and R. R. Hood. 2004. The influence of wind and river pulses on an estuarine turbidity maximum: numerical studies and field observations in Chesapeake Bay. Estuaries 27:132–146.

- North, E., R. Hood, S. Chao, and L. Sanford. 2005. The influence of episodic events on transport of Striped Bass eggs to the estuarine turbidity maximum nursery area. Estuaries 28:108–123.
- North, E., and E. D. Houde. 2001. Retention of white perch and Striped Bass larvae: biological-physical interactions in Chesapeake Bay estuarine turbidity maximum. Estuaries 24:756–769.
- Olney, J. E., J. D. Field, and J. C. McGovern. 1991. Striped Bass egg mortality, production, and female biomass in Virginia rivers, 1980–1989. Transactions of the American Fisheries Society 120:354–367.
- Papoulias, D. M., A. J. DeLonay, M. L. Annis, M. L. Wildhaber, and D. E. Tillitt. 2011. Characterization of environmental cues for initiation of reproductive cycling and spawning in Shovelnose Sturgeon *Scaphirhynchus platorynchus* in the lower Missouri River, USA. Journal of Applied Ichthyology 27:335– 342.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37:637– 669.
- Pears, R. J., J. H. Choat, B. D. Mapstone, and G. A. Begg. 2007. Reproductive biology of a large, aggregation-spawning serranid, *Epinephelus fuscoguttatus* (Forsskal): management implications. Journal of Fish Biology 71:795– 817.
- Pope, J. G., and J. G. Shepherd. 1994. Successful surf-riding on size spectra: the secret of survival in the sea [and discussion]. Philosophical Transactions of the Royal Society of London Series B 343:41–49.
- Pyke, C. R., R. Najjar, M. B. Adams, D. Breitburg, M. Kemp, C. Hershner, R. Howarth, M. Mulholland, M. Paolisso, D. H. Secor, K. Sellner, D. Wardrop, and R. J. Wood. 2008. Climate change and the Chesapeake Bay: state-of-thescience review and recommendations. Chesapeake Bay Program Science and Technical Advisory Committee, Annapolis, Maryland.
- Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American Shad and Sockeye Salmon. Ecology 77:1151– 1162.
- Quinn, T. P., K. Doctor, N. Kendall, and H. B. Rich, Jr. 2009. Diadromy and the life history of Sockeye Salmon: nature, nurture, and the hand of man. Pages 23–42 *in* A. J. Haro, K. L. Smith, R. A. Rulifson, C. M. Moffitt, R. J. Klauda, M. J. Dadswell, R. A. Cunjak, J. E. Cooper, K. L. Beal, and T. S. Avery, editors. Challenges for diadromous fishes in a dynamic global environment. American Fisheries Society, Symposium 69, Bethesda, Maryland.
- R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Robards, M. D., and T. P. Quinn. 2002. The migratory timing of adult summerrun steelhead in the Columbia River over six decades of environmental change. Transactions of the American Fisheries Society 131:523–536.
- Robichaud-LeBlanc, K. A., S. C. Courtenay, and A. Locke. 1996. Spawning and early life history of a northern population of Striped Bass (*Morone saxatilis*) in the Miramichi River estuary, Gulf of St. Lawrence. Canadian Journal of Zoology 74:1645–1655.
- Russell, M. W., B. E. Luckhurst, and K. C. Lindeman. 2012. Management of spawning aggregations. Pages 371–404 in Y. Sadovy de Mitcheson and P. L. Colin, editors. Reef fish spawning aggregations: biology, research and management. Springer, Dordrecht, The Netherlands.
- Rutherford, E. S., and E. D. Houde. 1995. The influence of temperature on cohort-specific growth, survival, and recruitment of Striped Bass, *Morone saxatilis*, larvae in Chesapeake Bay. Fishery Bulletin 93:315–332.
- Secor, D. H., and E. D. Houde. 1995. Temperature effects on the timing of Striped Bass egg production, larval viability, and recruitment potential in the Patuxent River (Chesapeake Bay). Estuaries 18:527–544.
- Setzler-Hamilton, E. M., W. R. Boynton, K. V. Wood, H. H. Zion, L. Lubbers, N. K. Mountford, P. Frere, and J. A. Mihursky. 1980. Synopsis of biological data on Striped Bass, *Morone saxatilis* (Walbaum). NOAA Technical Report NMFS Circular 443.
- Setzler-Hamilton, E. M., P. W. Jones, G. E. Drewry, and F. D. Martin. 1982. A comparison of larval feeding habits among Striped Bass, White Perch and Clupeidae in the Potomac estuary. Final Report to Maryland Department of

Natural Resources, University of Maryland Center for Environmental Science, Reference Number (UMCES) CBL 81-87, Solomons.

- Smith, G. W., I. P. Smith, and S. M. Armstrong. 1994. The relationship between river flow and entry to the Aberdeenshire Dee by returning adult Atlantic Salmon. Journal of Fish Biology 45:953–960.
- Sogard, S. M., S. A. Berkeley, and R. Fisher. 2008. Maternal effects in rockfishes Sebastes spp.: a comparison among species. Marine Ecology Progress Series 360:227–236.
- Van den Avyle, M. J., and M. A. Maynard. 1994. Effects of saltwater intrusion and flow diversion on reproductive success of Striped Bass in the Savannah River estuary. Transactions of the American Fisheries Society 123:886– 903.
- Varpe, Ø., C. Jørgensen, G. A. Tarling, and Ø. Fiksen. 2007. Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model. Oikos 116:1331–1342.
- Visser, M. E., C. Both, and M. M. Lambrechts. 2004. Global climate change leads to mistimed avian reproduction. Advances in Ecological Research 35: 1–22.
- Ware, D. M., and R. W. Tanasichuk. 1989. Biological basis of maturation and spawning waves in Pacific Herring (*Clupea harengus pallasi*). Canadian Journal of Fisheries and Aquatic Sciences 46:1776–1784.
- Watanuki, Y., M. Ito, T. Deguchi, and S. Minobe. 2009. Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of anchovy. Marine Ecology Progress Series 393:259–271.