Abstract

Phenology in a Changing Environment: Assessing and Forecasting the Timing of the Spawning

Migration of the Albemarle Sound and Roanoke River Stock of Striped Bass

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The seasonal timing of key biological events (phenology), such as migrations, can vary greatly

and have strong impacts on fisheries and their management. The Striped Bass (*Morone saxatilis*)

population of the Roanoke River undergoes a yearly upstream spawning migration and

subsequently becomes susceptible to an estuarine and freshwater fishery that has a seasonal

closure set on May 1st each year. This seasonal closure is static each year yet tagging studies of

Albemarle Sound/Roanoke River (A/R) Striped Bass stock indicate their migration timing can be

highly variable. The objective of this study is to create an ecological forecast of the A/R stock of

Striped Bass migration timing. The forecast revealed the overwhelming importance of Roanoke

River discharge on A/R stock migration timing, with a consistent indication that late February to

early March is when discharge becomes a key factor. This may be of interest to stakeholders

involved in the management of the Roanoke River flow regime, especially as impacts of flows

on Striped Bass recruitment have been highlighted as an area of future research in the most

recent stock assessment. Another implication of this research for management is that the

migration timing of Striped Based has shifted earlier in the year in relation to the current

seasonal fishery closure. Temperatures in the Roanoke River and overwintering grounds of coastal Virginia have increased over the study period, which could be driving this shift to earlier migration phenology. Nonetheless, despite a high amount of variance explained, the forecast proved to have low predictive skill up until right before the typical spawning timing and was only able to skillfully predict Striped Bass spawning during years with normally timed phenology. Thus, an operational nowcast of Striped Bass spawning phenology would be possible to develop, but additional research would be needed if stakeholders require longer lead times to act on a forecast. A separate analysis using historical egg survey data analyzed the effect of different sampling frequencies on phenology metrics. These metrics were computed based on a hypothetical sampling schedules of between one and five days per week. Accuracy of calculated phenology metrics compared to observed phenology gradually increased with increasing sampling effort. Eggs have not been collected on the Roanoke River since 1993, yet migration phenology has shifted earlier in recent years. Additional efforts to survey Striped Bass eggs on the Roanoke River should be considered to assess if spawning has also shifted earlier and to support development of a potential phenology nowcast, which could be useful for anglers, fisheries managers, and water managers.

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Migration of the Albemarle Sound and Roanoke River Stock of Striped Bass

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CHAPTER 1: Literature Review

1.1 Striped Bass Ecology and Management in North Carolina

Striped Bass (*Morone saxatilis)* are a highly valuable recreational and commercial species and are a popular sportfish for anglers along the East Coast (ASMFC 2017). Understanding how Striped Bass will be affected by climate change is an important issue for US East Coast stakeholders. North Carolina holds the southernmost major spawning population of anadromous Striped Bass (A/R stock). There is a separate North Carolina stock south of the A/R stock in the Tar-Pamlico and Neuse Rivers. However, this stock supports very little natural spawning and is heavily dependent on stocking (Knight et al. 2015). The A/R stock is a specific management unit that describes the Striped Bass population that spawns in the Roanoke River (Figure 1.1) that then spend their early years primarily in the Albemarle Sound (Figure 1.1). Hughes et al. (2015) used otolith microchemistry to show that a significant proportion of adult Striped Bass sampled in their study used the Perquimans River in the northern Albemarle Sound as nursery habitat. This stock is considered a facultative anadromous stock since anadromy is size dependent (Callihan et al. 2014). Small, but sexually mature, fish, which are between 450-600 mm total length (TL) for females and 350-600 mm TL for males, remain in Albemarle Sound when not spawning in riverine habitat (Callihan et al. 2015). 96.8% of female A/R Striped Bass are mature at age four with a mean TL of 475 mm (Boyd et al. 2011). Female Striped Bass tend to be longer and heavier than males, with the larger size classes mostly females (Callihan et al. 2015; Secor et al. 2020a). During years of low abundance, Striped Bass tag returns from the Roanoke River Management Area (RRMA) and the Albemarle Sound Management Area (ASMA) show a preference towards the western ASMA, with greater expansion into the eastern

ASMA and Pamlico Sound during high abundance periods (Hassler et al. 1981; Callihan et al. 2014; Zurlo et al. 2014). The RRMA extends from the mouth of the Roanoke River to the Roanoke Rapids Dam (Figure 1.1) and the ASMA is comprised of four main water bodies: the Croatan Sound, Albemarle Sound, Currituck Sound, and Chowan River. Intermediate-sized fish (700-850 mm TL) emigrate into oceanic waters during summer but generally stay close to the coast of North Carolina (Callihan et al. 2015). Chesapeake Bay Striped Bass typically begin overwintering in Southern New England ocean waters at about 800 mm TL and ages 10-12, with a high degree of year-round residency in the Chesapeake Bay at smaller sizes (Secor et al. 2020b). Striped Bass exhibit a high degree of natal homing in the RRMA, Chesapeake Bay, and Hudson Bay (Callihan et al. 2015, Secor et al. 2020a, 2020b).

Similar to the aforementioned pattern seen in Chesapeake Bay, A/R Striped Bass larger than 900 mm TL show consistent migratory patterns where they leave the Roanoke River in the late spring (May-June) after spawning and migrate to coastal waters as far north as Massachusetts in the summertime (Callihan et al. 2015; ASFMC 2017). This group of Striped Bass joins the Atlantic Ocean Striped Bass Migratory Stock (AOSBMS), which is comprised of all anadromous Striped Bass on the East Coast that leave their respective natal rivers at the end of the spring and migrate poleward to cooler coastal waters (Zurlo et al. 2014; Callihan et al. 2015; ASFMC 2017; Essig et al. 2019). The AOSBMS is primarily made of four stocks including the RRMA, Delaware Bay, Hudson River, and the Chesapeake Bay, comprising 70-90% of the overall coastal stock (Essig et al. 2019). Large anadromous individuals of these stocks overwinter off the coasts of Virginia and North Carolina in the winter after feeding in southern New England during summer and early fall months (Callihan et al. 2014, 2015; Secor et al. 2020a, 2020b). Large highly migratory Striped Bass move away from Southern New England

in the fall (September-October) to coastal Virginia and North Carolina waters, with this southward migration occurring in January for Hudson River fish and March for the A/R stock (Callihan et al. 2015; Secor et al. 2020a). Striped Bass from the A/R stock enter the Roanoke River once temperatures consistently remain above 9-10° C, while Hudson Bay fish initiate marine exit at a similar temperature of 10-12° C (Callihan et al. 2015; Secor et al. 2020b). Striped Bass from the A/R stock then start migrating upriver when river temperatures reach 17-18° C, which typically occurs in March-April (Carmichael et al. 1998; Callihan et al. 2015). Spawning onset is associated with temperatures rising above 18° C in the RRMA and occurs primarily in Weldon, NC (Figure 1.1) at river mile 131 (Hassler et al. 1981; Rulifson 1990).

The A/R stock is managed based on distinct management areas that the fish travel through, with the present boundaries between management areas established in 1991 (Gambill & Bianchi 2019). RRMA covers the lower Roanoke River (Figure 1.1), which makes up 130 miles of brown-water river below the Roanoke Rapids Dam (Figure 1.1; LeGrand & Hall 2014). The lower Roanoke River officially begins at the fall line, which divides the Piedmont, north and west of the Roanoke Rapids just below the nearby dam, and the Coastal Plain that begins around Weldon, NC (Figure 1.1) (LeGrand & Hall 2014). The Roanoke River has the widest floodplain of any North Carolina river. Flow is heavily regulated by the three dams in the lower river, with the headwaters beginning in the mountains of Virginia (LeGrand & Hall 2014). The multiple dams affect the sediment and average river flows, creating a more consistent release of sediment and water compared to a natural flow regime (LeGrand & Hall 2014). Flow regimes in spring are regulated to meet Striped Bass spawning criteria with a three-tiered flow regime that began in 1988 (Zincone & Rulifson 1991). The negotiated flow regime, which is based on pre-impoundment conditions begins with an initial high flood flow from March 1 – April 16, a

gradually diminishing flow from April 17 – May 12, and a level plateau from May 13 – June 30 (Zincone & Rulifson 1991). In 2016 a flow regime was implemented where weekly outflows from the Roanoke Rapids Dam (Figure 1.1) roughly equal the previous week's intake into the Kerr Reservoir to mimic a quasi-run of river operation (Army Corp of Engineers 2016). The new flow regime allows for discharges to reach 35,000 cubic feet per second (cfs), with the previous flow regime limiting flows from 9,500-13,700 cfs during the anadromous fish migration period (i.e., April 1-June 15) (Army Corp of Engineers 2016).

The influence of dams on this river system makes the management of flow regimes very important to this fishery. Water resource managers are a stakeholder that could benefit from improved understanding of changes and variations in the Striped Bass migration timing as this could allow them to optimize flows to maximize fish passage and spawning success. The optimal flow regime for fish migration may depend on the size distribution of Striped Bass each year. Highly migratory A/R Striped Bass showed faster upriver migration speeds in larger individuals than small individuals (Callihan et al. 2015). The ability of Striped Bass to move against artificial velocity barriers greatly improves with increasing size (Haro et al. 2004).

As of 2022, the Striped Bass fishery in the RRMA has an open season from March 1-April 30, with the May 1st closure intended to protect large spawning females. Male Striped Bass typically arrive on the spawning grounds about two weeks before females, causing most fish found in the Roanoke River before May to be males (Callihan et al. 2015). The seasonal closure is designed to limit catch of female Striped Bass so they can spawn that season. Striped Bass migration timing in North Carolina rivers varies interannually by about ~1 month (Callihan et al. 2015; Smith & Rulifson 2015). For example, in 2013 ocean temperatures off Virginia reached 9-10° C a month later than it did in 2012, causing tagged Striped Bass to migrate 19 days later than

in 2012 (Callihan et al. 2015). During some years, females arrive at their spawning grounds well in advance of the fishery closure intended to protect them (Peer & Miller 2014). This occurrence will likely become more frequent under climate change since many spring-spawning fishes are reproducing earlier in the year in response to warming temperatures (Poloczanska et al. 2013; Asch 2015). This is likely to occur for Striped Bass since throughout the range of this species the migration and spawning activities are cued by rising spring temperatures (Rulifson 1990; Van den Avyle & Maynard 1994; Secor et al. 1995; Douglas et al. 2009; Callihan et al. 2015).

The NC Wildlife Resources Commission (NC WRC) is responsible for inland fisheries and manages the RRMA as a recreational fishery only. The commercial RRMA fishery ended in 1991 (Gambill & Bianchi 2019). Since 1991, the total allowable catch (TAC) of the A/R stock has been divided with half going to the commercial ASMA fishery and to the other half split evenly between the RRMA and ASMA recreational fisheries (NCMDF & NCWRC 2014). NC Department of Marine Fisheries (NC DMF) manages the ASMA as a joint coastal water system with commercial and recreational fishing (Gambill & Bianchi 2019). The Albemarle Sound is shallow, relatively fresh estuary with salinities usually below 11 psu in the eastern extremity close to the Croatan Sound (Hassler et al. 1981). The ASMA is connected to the ocean through the Oregon Inlet and is the final drainage for eight rivers in NC (Figure 1.1; Hassler et al. 1981). The AOSBMS is subject to authority of the Atlantic States Marine Fisheries Commission (ASMFC) when fish are residing in the Atlantic Ocean. The Atlantic Ocean management area covers waters less than three miles from shore, with catch in the U.S. exclusive economic zone (3-200 miles) prohibited since 1990.

Records of Striped Bass landings in NC go back to 1887, yet the data available are sparse and difficult to draw any concrete conclusions from until data collection improved in the 1950s

(Hassler et al. 1981; Gambill & Bianchi 2019). Historically, catch of Striped Bass on the East Coast was high from the 1950s and peaked in 1973 at 14.7 million pounds (Essig et al. 2019). In 1983 East Coast landings saw a 90% decline from the peak observed in the 1970s, and the population was classified as having experienced a crash (Essig et al. 2019). With commercial ASMA landings displaying a distinct decline starting in 1988, landings in this fishery reached an all-time low in 1997 (Gambill & Bianchi 2019). Strong declines were also seen in the juvenile abundance indices in multiple Striped Bass spawning systems. High fishing mortality was attributed as the primary cause for the overall decline (Essig et al. 2019). Management measures were put in place and the four east coast stocks were declared recovered between 1995-1998 (Essig et al. 2019; ASFMC 2019). In 1997 the A/R stock was officially declared recovered by the ASMFC, with an estimated two million fish in the RRMA in 1999 (NCDMF & NCWRC 2004). After the recovery, TAC for the A/R stock slowly increased to a recent maximum of 505,000 pounds from 2003-2014 (NCMDF & NCWRC 2014; Gambill & Bianchi 2019). The TAC was then lowered after the 2014 benchmark stock assessment and reduced to 275,000 pounds (NCMDF & NCWRC 2014; Gambill & Bianchi 2019). Commercial landings are split evenly between beach seine, trawl, and gill net gear as mandated by state fishing regulations (Gambill & Bianchi 2019). The commercial fishery extends from October through April with the primary catch occurring in March during the years 1994 – 2018 (Gambill & Bianchi 2019).

As of 2018, the AOSBMS was overfished and experiencing overfishing, with the spawning stock biomass (SSB) below target levels and fishing mortality above target levels (Gambill & Bianchi 2019; ASFMC 2019). The Atlantic Striped Bass Management Board concluded that fishing mortality needed to be reduced by 18% to meet target mortality levels (ASFMC 2019). To meet this goal, most states employed catch reduction efforts with increased

regulations, such as a slot limit of 28 – 35 inches (ASFMC 2019). The 2017 stock assessment of the A/R stock shows that the population is also overfished and experiencing overfishing (Lee et al. 2020). The A/R stock SSB for 2017 was estimated at 35.6 metric tons, well below the 121 metric ton threshold (Lee et al. 2020). Similarly, the A/R stock fishing mortality for 2017 was 0.27, well above the threshold level of 0.18 (Lee et al. 2020). The overfished stock is also estimated to have a severely truncated age structure, with age 8+ fish almost nonexistent in recent years (Lee et al. 2020). In the ASMA and RRMA, the combined commercial and recreational harvests of this species was approximately 240,000 pounds in 2017, which was the last year of data covered in the A/R stock 2020 stock assessment (ASMFC 2017). In 2022 the combined harvest quota for commercial and recreational fisheries in the ASMA and RRMA was reduced to about 50,000 pounds, the lowest TAC since the 1990s.

1.2 Forecasting Fish Phenology

Climate change and climate variability lead to shifts in the seasonal timing of fish migration and reproduction (i.e., fish phenology) across many ecosystems and species (Asch et al. 2015), with changes especially common among anadromous fishes, such as Striped Bass (Peer & Miller 2014; Nack et al. 2019). Phenology is the study of the timing of biological events and the factors that drive that timing (Asch 2019). Warming temperatures can lead to faster gonadal development in poikilothermic fishes (Pankhurst & Porter 2003). Many marine species are highly susceptible to changing environmental conditions and can alter behavior to adapt (Tommasi et al. 2017a). Changes in river flow and oceanic currents under climate change can alter fish migration phenology (Peer & Miller 2014; Asch 2015). For instance, Striped Bass migration timing has been shown to be variable as a response to changing temperatures in the

Roanoke River, Chesapeake Bay, and Hudson River (Rulifson et al. 1993; Peer & Miller 2014; Nack et al. 2019; Secor et al. 2020a). Similarly, river herring in the Albemarle Sound watershed and Gulf of Maine have also shifted toward earlier phenology as a response to rising temperatures (Lombardo et al. 2019; Staudinger et al. 2019). These changes in fish phenology can have ecosystem consequences leading to mismatches between trophic levels if prey items favored by fishes do not also show a synchronous response to climate change (Cushing et al. 1990). Variability in phenology can also affect reproductive success of species, which can have negative impacts on fisheries (Cushing et al. 1990; Payne et al. 2017). Mismatches in phenology are a key point in studying how marine species can or will adapt to climate change and climate variability.

The recent progress made in developing earth system and biogeochemical models makes skillful seasonal and decadal scale forecasts now possible (Payne et al. 2017; Fennel et al. 2019; Jacox et al. 2020). Biogeochemical models can generate hindcasts, short-term forecasts, and long-term projections involving different climate scenarios. These forecasts make it possible to anticipate regional changes to important environmental and biological factors relevant to fisheries (Park et al. 2019; Fennel et al. 2019). Forecasts can be utilized to inform fisheries management and avoid future fisheries collapse (Hobday et al. 2016; Park et al. 2019). Forecasts can be generated for both aquaculture of fish and shellfish in stationary pens and large open-water fisheries for migratory species (Hobday et al. 2016). Global marine biogeochemical predictions developed using coupled ocean climate models can skillfully predict chlorophyll concentration a season to a full year in advance (Park et al. 2019; Fennel et al. 2019). Currently there are only a few operational forecasting systems for aquatic living resources run by a natural resources management agency due to constraints related to the large manpower commitment,

access to data at a meaningful spatial scale, computational resources, poor understanding of all relevant environmental variables, and adequacy of data assimilation methods (Fennel et al. 2019). Forecasts can be used at a variety of spatiotemporal scales and by multiple types of stakeholders who may not necessarily rely on the forecast heavily each year or use the forecast on its own without additional management considerations (Hobday et al. 2016). However, forecasts can be especially helpful when they can predict drastic shifts in environmental conditions, which can prepare fisheries and management for those changes (Hobday et al. 2016, 2019; Mills et al. 2017).

Ecological forecasts can predict biological productivity, spatial distribution, and phenology, with forecasts of spatial distribution among the most common type of forecast developed for living marine resources (LMR). Seasonal forecasts of fish phenology, abundance, and distribution have been developed for several US fisheries, including Maine lobster (*Homarus americanus*) (Mills et al. 2017), Pacific sardine (*Sardinops sagax)* (Tommasi et al. 2017b), and Chinook Salmon (*Oncorhynchus tshawytscha*) (Anderson & Beer 2009). However, no such forecasting system has been developed for the LMR of the Southeast US. Phenological forecasts require high-temporal-resolution datasets (i.e., daily to weekly resolution) to accurately address key fisheries issues, such as the opening/closure of a fishery (Payne et al. 2017). There are multiple decades of sub-daily data on the A/R Striped Bass migration making it an ideal species to study the effects of climate change on fish phenology in the Southeast US.

The goal of this project was to create a model that can forecast the Striped Bass migration timing based on the environmental conditions encountered in the months and weeks leading up to spawning. The timing of spawning in Striped Bass has been linked to seasonal changes in temperature both locally and throughout the species range. Warming spring temperatures cue

movement of Striped Bass to spawning grounds in New Brunswick, Canada (Douglas et al. 2009), Chesapeake Bay and its tributaries (Secor & Houde 1995), the Roanoke River and Albemarle Sound (Rulifson 1990; Callihan et al. 2015), and the Hudson River in New York (Nack et al. 2019). Interannual variations in the onset and end of the spawning season in the Roanoke and Tar Rivers in North Carolina have been linked to temperature anomalies (Callihan et al. 2015; Smith & Rulifson 2015).

Skillful forecasts of LMR can be developed based on either accurate forecasts of future climate conditions, persistence of current climate anomalies, or the continued influence of past climate anomalies on marine organisms as they age, grow, and reproduce (Payne et al. 2017). The model developed herein focuses on the latter two processes that can lead to forecast skill. The current generation of seasonal climate forecasts, such as the National Center for Environmental Prediction Climate Forecast System v2 (Saha et al. 2014) and North American Multi-Model Ensemble (Kirtman et al. 2014), have not been tested over the full period of the available biological data that were used to generate an ecological forecast for Striped Bass. Forecasts for Gulf of Maine lobster and Pacific salmon migrations use lags based on observed data rather than coupled climate models to create seasonal forecasts (Payne et al. 2017). A similar approach was used for this forecast where biological and environmental data from early in the season informed a forecast for later in the season. Over 1,000 pages of data tables on historical A/R Striped Bass egg and creel surveys going back to 1960 were digitized for the model developed herein. The sub-daily fisheries independent egg survey and the fisheries dependent creel survey at Weldon, NC make it possible to have accurate estimates of the daily phenology of the A/R stock Striped Bass migration and spawning events.

Figure 1.2 displays the hypothesized relationships that could lead to early migration of Striped Bass in the proposed forecast. Rising temperatures in the ASMA and RRMA are hypothesized to have the strongest effect on A/R Striped Bass migration as a similar effect has been demonstrated for spring water temperature on Chesapeake Bay Striped Bass phenology (Peer & Miller 2014). Overwintering temperatures will also likely have a strong impact on migration timing as these temperatures will directly affect the rate of gonadal development (Clark et al. 2005; Genner et al. 2010). In a controlled environment, Chesapeake Bay Striped Bass showed large increases in spawning-related hormones starting in January when temperatures at the time of the study began to rapidly increase (Woods & Sullivan 1993).

Pulse duration timing (PDT) metrics are used in this analysis as they capture the timing and occurrence of high flow and wind events that can create barriers to fish migration (Haro et al. 2004; Peer & Miller 2014). Peer & Miller (2014) showed river flow PDT and wind PDT were not key factors in migration timing among Chesapeake Bay Striped Bass, but they could have a different relationship to the A/R stock Striped Bass phenology. Since the RRMA is highly influenced by three main stem dams in the river, high flow events are unlikely and don't occur as often as they would under natural conditions (LeGrand & Hall 2014). It is unlikely that river PDT will have a strong influence on the migration timing, but it is important to consider in case of unusually high flows. River discharge prior to marine exit may play a role in anadromous fish migration timing due to the changes in potential salinity and olfactory cues to fish waiting to migrate in staging areas (Mundy et al. 2011). To account for these additional potential effects, average daily discharge from the Roanoke Rapids Dam will also be included in the forecast.

Stock composition and variation in the percentage of the stock that is highly migratory (i.e., that uses ocean habitat) could have a substantial influence on migration timing as different

sizes of spawning individuals may migrate from very different regions and environments

(Callihan et al. 2015). Larger individuals may be better suited for surpassing velocity barriers

and be less impacted by high flow periods (Haro et al. 2004).

Regional climate indices may affect migration timing due to their influence on a variety

of climate and weather patterns in a region. Also, large Striped Bass spend a significant amount

of time in ocean waters, which are influenced by regional climate indices. El Niño Southern

Oscillation (ENSO), North Atlantic Oscillation (NAO), and Atlantic Multidecadal Oscillation

(AMO) are the principal regional climate indices that impact temperature and precipitation in the

Roanoke River basin (McCulloch 2017). These climate indices can influence precipitation and

river flow patterns and consequently Striped Bass phenology. NAO measures the sea surface

pressure differences between the subtropical high near the Azores Islands and the subpolar low

located near Iceland (Hurrell 1995; Roberts et al. 2019). Decadal climate variability affects air

temperatures within the lower Roanoke River watershed, such that the NAO is positively

correlated with winter temperatures whereas the AMO is more closely associated with annual

mean temperature (McCulloch 2017; Roberts et al. 2019). The AMO describes a 65-80-year

cycle in temperature anomalies, which is based on variations in sea surface temperatures from

the North Atlantic basin (0ºN-70ºN) (Enfield et al. 2001). The AMO has distinct warm and cool

phases affecting the whole North Atlantic basin, with a cool phase in the 1970-1990s and warms

phases occurred in the 1960s and from the mid-1990s to present (McCulloch 2017). ENSO is a

naturally occurring anomalous state in the tropical Pacific Ocean where positive values of this

index indicate an El Niño phase and negative values indicate La Niña phases (Wolter & Timlin

1998). Teleconnections associated with ENSO-related climate variations in the tropical Pacific

lead to changes in precipitation in North Carolina, such that El Niño years are characterized by

greater rainfall and La Niña years by drier conditions during winter (Roswintiarti et al. 1998).

Changes in precipitation may affect flow rates or water levels in the Roanoke River; however,

for the lower Roanoke River, these conditions are controlled by releases from the main stem

dams (Legrand et al. 2014).

In terms of the influence of climate indices on fishes, the AMO is negatively correlated

with the larval abundance of freshwater fishes in the Roanoke River, whereas the NAO is

hypothesized to modulate the abundance of anadromous fish larvae via its effect on winter

temperature (McCulloch 2017). More specifically, the AMO is positively correlated to Striped

Bass larval abundance in Chesapeake Bay (Nye et al. 2014). In the Hudson River estuary,

Striped Bass abundances increased during the positive AMO phase (Buchsbaum & Powell 2008;

O'Connor 2012; Nye et al. 2014). McCulloch (2017) showed that minimum winter air

temperatures, spring flows and spring precipitation had an impact on Striped Bass larval

abundance in the lower RRMA. Neither NAO nor AMO had a strong impact on Striped Bass

larval abundance; however, NAO may indirectly impact larval abundance since the NAO is

positively correlated with winter RRMA air temperatures (McCulloch 2017). NAO is an

important factor influencing the presence of several coastal NC species in the fall but had a less

important influence on fish presence in the spring (Roberts et al. 2019). Given the regulation of

spring flows in the Roanoke River, precipitation changes and wet vs. dry seasons affected by

NAO and ENSO may have muted effects on conditions that A/R Striped Bass experience. NAO

was not strongly associated with precipitation in RRMA (McCulloch 2017). With the shift

toward a quasi-run of river dam release schedule in 2016, variability in climate indices may be

more important in the lower Roanoke River in recent years and have a stronger impact on Striped

Bass phenology. Since local climate rather than regional climate is more likely to directly impact

adult Striped Bass, regional climate indices are not hypothesized to have a strong effect on yearly forecasts but are potentially more important for future decadal projections, especially since these indices exhibit strong fluctuations at this time scale. However, there are some exceptions to this pattern. For example, Auth et al. (2011) found that climate indices explained more variation in larval concentration and diversity than local environmental variables.

1.3 Research Objectives

The primary objective of my thesis was to establish an ecological forecast of Striped Bass migration timing that emulates a potential operational forecast that could be used by managers. Ecological forecasts have been developed for several LMR in the US but not for any in the Southeast US. This forecast should identify key environmental and biological variables that affect the migration timing of A/R Striped Bass. Factors affecting the phenology of Chesapeake Bay Striped Bass have been established by Peer and Miller (2014); however, this has not been done for the A/R stock. This research has been made possible by digitizing historical surveys of Striped Bass eggs and recreational catch (Hassler et al. 1981).

The Hassler (1981) egg survey was also used to assess the effect of reduced egg sampling effort on phenology metric accuracy. Few fisheries independent surveys sample populations daily; instead, monthly, seasonal, or annual surveys are much more commonplace (Mackas et al. 2012). However, less frequent sampling may reduce the ability of researchers to accurately estimate long-term phenological changes. Since Striped Bass spawning has been assessed historically at a sub-daily scale, I estimated how the accuracy of estimating phenological metrics changes with reduced sampling by modeling subsets of this historical dataset. This may help

determine the ideal design of fisheries independent surveys that aim to study phenological change. Striped Bass eggs have not been collected on the Roanoke River since 1993 and resuming this survey may be important for assessing if Striped Bass spawning has shifted earlier in the year, which would in turn impact the effectiveness of the static seasonal fishing closure.

This thesis is broken up into four chapters with an appendix section. Chapter I is a literature review of topics influencing the creation of an ecological forecast on Striped Bass phenology. The chapter is made to be broad and provide background information on the ecology and management of Striped Bass, as well as background on ecological forecasting. Chapter II and Chapter III are written to be independent chapters, so they may be easily submitted as publications in the near future. Both chapters repeat some information from Chapter I, since they are all written to be read independently of each other. Chapter II covers the development and results of the ecological forecast on A/R Striped migration and spawning. Chapter III focuses on creating hypothetical sampling schedules of the Striped Bass egg survey to assess the efficacy of sampling at intervals of less than once a day. Information in Chapter III may inform future survey design. Chapter IV focuses on summarizing conclusions from previous chapters, management recommendations, and future modeling considerations.
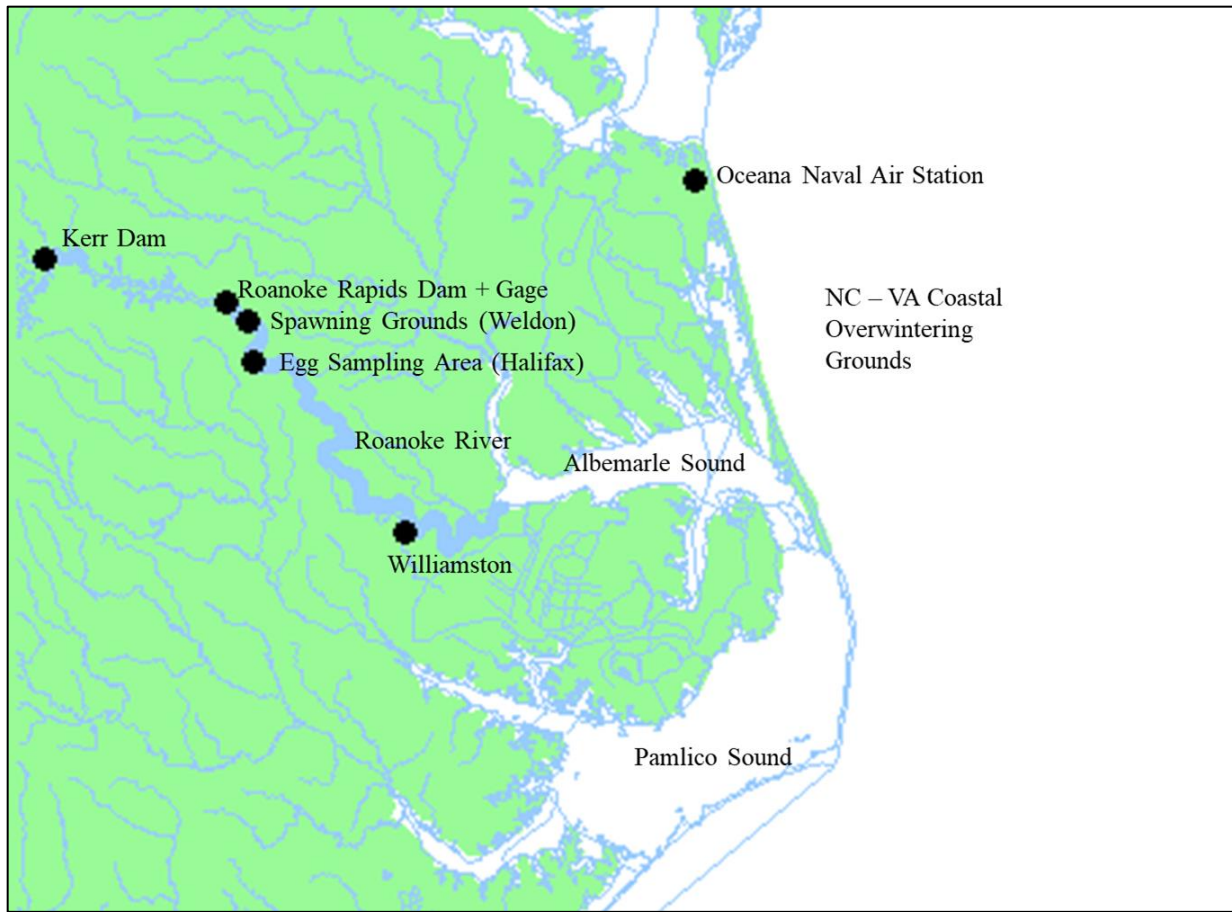
Figure 1.1. Map of Striped Bass spawning grounds in the Roanoke River and data collection sites.
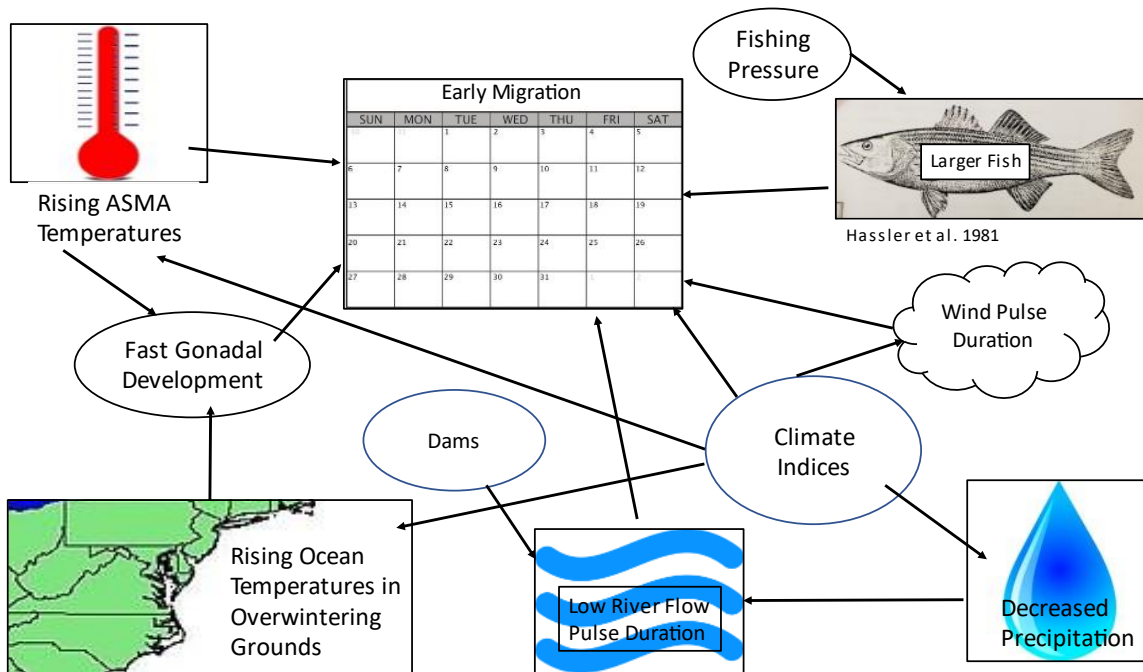
Figure 1.2. This conceptual diagram represents the environmental and biological variables that are used in the ecological forecast. The arrows represent relationships that would lead to an early spawning event.

CHAPTER 2: Phenology in a Changing Environment: An Ecological Forecast of Albemarle Sound/Roanoke River Striped Bass Stock Migration

2.1 Introduction:

Environmental variability can cause the seasonal timing of key biological events (phenology), such as migrations and spawning, to be altered relative to the typical seasonal cycle (Asch et al. 2015). Anadromous fishes, such as Striped Bass (*Morone saxatilis*), exhibit variable phenology, due to a sensitivity to environmental conditions regardless of whether those conditions reflect interannual variation or longer-term changes in climate (Peer & Miller 2014; Nack et al. 2019). Warming temperatures can lead to faster gonadal development in poikilothermic fishes, which may impact the timing of migrations to spawning grounds (Pankhurst & Porter 2003). Changes in river flow, temperature, oceanic currents, genetic diversity, population dynamics, and other abiotic and biotic factors can alter fish migration phenology (Anderson & Beer 2009; Peer & Miller 2014; Asch 2015). Variability in phenology can affect reproductive success of a population or lead to mismatches with other trophic levels, which can have negative impacts on fisheries (Cushing et al. 1990; Payne et al. 2017).

Multiple researchers around the world have developed ecological forecasts for living marine resources (LMR) to help stakeholders prepare for changes in fish phenology, abundance, habitat, or distribution (Hobday et al. 2019). Seasonal forecasts of LMR have been developed for several US fisheries, including Maine lobster (Tommasi et al. 2017a; Mills et al. 2017), Pacific sardine (Tommasi et al. 2017b), and chinook salmon (Anderson & Beer, 2009). However, to the best of my knowledge, no such forecasting system has been developed for the LMR of the Southeast US. The migration timing of anadromous fishes may offer opportunities for ecological forecasting in this region. In particular, Striped Bass migration timing has shown variability in

response to changing temperatures in the Roanoke River, Chesapeake Bay, and Hudson River (Rulifson et al. 1993; Peer & Miller 2014; Nack et al. 2019). Phenological forecasts require high temporal resolution datasets (i.e., daily to weekly resolution) to accurately address key fisheries issues, such as optimizing the seasonal opening and closure of a fishery (Payne et al. 2017). The Albemarle Sound / Roanoke River (A/R) stock of Striped Bass is a well-studied population with an abundance of environmental and biological data going back to the 1960s, thus making them a good candidate species for development of a phenological forecast (Hassler et al. 1981; Essig et al. 2018).

North Carolina holds the southernmost spawning population of anadromous Striped Bass on the east coast of the US (i.e., the A/R stock). Spawning onset is associated with temperatures rising above 18º C. Spawning primarily occurs in Weldon, NC at river mile 131 (Figure 1.1; Hassler et al. 1981; Rulifson 1990). Small, but sexually mature, fish below 600 mm TL remain in Albemarle Sound year round when not spawning in riverine habitat (Figure 1.1; Callihan et al. 2015). Intermediate sized fish (700-850 mm TL) emigrate into oceanic waters during summer but generally stay close to the coast of North Carolina and Virginia as they overwinter (Callihan et al. 2015). Highly migratory fish are those larger than 900 mm, showing consistent migratory patterns where they leave the Roanoke River in the late spring after spawning and migrate to coastal waters as far north as Massachusetts in the summertime (Zurlo et al. 2014; Callihan et al. 2015; ASFMC 2017). Abundance is related to the size structure of the stock and consequently changes the proportion of fish migrating from different areas to spawn in the Roanoke River (Lee et al. 2020). For example, a less abundant stock will have fewer large individuals that are migrating from ocean overwintering habitats. These larger and older individuals may have different phenologies than the younger spawners. Similarly, larger Striped Bass have also been

shown to migrate upriver faster and more easily surpass river velocity barriers (Haro et al. 2004; Callihan et al. 2015).

There are multiple hypothesized environmental variables that could affect Striped Bass phenology, with the following relationships describing the environmental variables used in this study. The Roanoke River is heavily regulated by the three dams extending north to its headwaters in the mountains of Virginia, with the Kerr Dam actively regulating discharges that flow through the other two dams (Figure 1.1; LeGrand & Hall 2014). Beginning in the early 1990s, flow regimes in spring were regulated to meet Striped Bass spawning criteria with a three-tiered flow regime that starts with a high initial water release that diminishes into a level plateau over the season (Zincone & Rulifson 1991). Rising temperatures in the Albemarle Sound Management Area (ASMA) and Roanoke River Management Area (RRMA) are hypothesized to have a strong effect on the Striped Bass migration timing since spring water temperature has a substantial influence on Chesapeake Bay Striped Bass phenology (Peer & Miller 2014; Callihan 2015). Wind and river pulse duration timing (PDT) metrics are a second factor that are hypothesized to influence A/R stock phenology as they capture the timing and occurrence of high river flow and high wind events that can create barriers to fish migration (Haro et al. 2004; Peer & Miller 2014). River discharge prior to marine exit may play a role in anadromous fish migration timing due to the changes in potential salinity and olfactory cues to fish waiting to migrate in staging areas (Mundy et al. 2011).

Regional climate indices may affect migration timing due to their connections to regional environmental state. El Niño Southern Oscillation (ENSO), North Atlantic Oscillation (NAO), and Atlantic Multidecadal Oscillation (AMO) are the principal regional climate indices that impact temperature and precipitation in the Roanoke River basin (McCulloch et al. 2017).

ENSO-related climate variations in the tropical Pacific lead to changes in precipitation in North

Carolina, such that El Niño years are characterized by greater rainfall and La Niña years by drier

conditions during winter (Roswintiarti et al. 1998). Precipitation changes may affect Roanoke

River flows, including pulses in river flow. The AMO describes a 65-80-year cycle in

temperature anomalies, which is based on variations sea surface temperatures from the North

Atlantic basin (0ºN-70ºN) (Enfield et al. 2001). The NAO measures the sea surface pressure

differences between the subtropical high near the Azores Islands and the subpolar low located

near Iceland (Hurrell 1995). Decadal climate variability affects air temperatures within the lower

Roanoke River watershed, such that the NAO is positively correlated with winter temperatures

whereas the AMO is more closely associated with annual mean temperature (McCulloch 2017;

Roberts et al. 2019). These three indices are all calculated using variables from the ocean basins

they represent and will have a stronger hypothesized impact on the larger Striped Bass that

overwinter in the ocean.

Striped Bass are a valuable recreational and commercial species across the East Coast,

and many stocks have experienced periods of overfishing and recovery (ASMFC 2017). For

instance, commercial A/R stock landings displayed a distinct decline in the 1980s due to

overfishing, with large declines in landings in 1990s reflecting changing regulations in part

(Gambill & Bianchi 2019). Following the implementation of fishing effort controls, in 1997 the

A/R stock was officially declared recovered by the Atlantic States Marine Fisheries Commission

(ASMFC), with an estimated population size of two million fish in 1999 (NCDMF & NCWRC

2004). Following an increase over time in fishing effort, the 2017 stock assessment of the A/R

stock showed that the population is once again overfished and experiencing overfishing (Lee et

al. 2020). Currently the A/R stock fishery has an open season from March 1-April 30, with the

May 1st closure intended to protect large spawning females (Lee et al. 2020). Male Striped Bass typically arrive on the spawning grounds about two weeks before females, making most fish in the Roanoke River before May likely to be males (Callihan et al. 2015). The seasonal closure is designed to limit catch of female Striped Bass so they can spawn that season, which occurs typically in May. A forecast of A/R stock phenology could help better inform the timing and effectiveness of this seasonal closure. A similar seasonal closure exists in the Chesapeake Bay for Striped Bass, which can have variable effectiveness given changing phenology (Peer & Miller 2014). A forecast of Striped Bass migration timing may be of interest to fisheries and dam management agencies who actively control the Roanoke River flow regime and set the yearly fishing season.

With multiple decades of sub-daily data on the A/R Striped Bass migration and spawning activity, they make an ideal population to study the effects of climate change on fish phenology in the Southeast US. The historical and more recent phenology of this stock has been described, including trends over time using recently analyzed historic data. The goal of this research was to create a model that can forecast the Striped Bass migration and spawning timing based on the environmental and biotic conditions encountered in the months and weeks leading up to spawning (Figure 1.1). This forecast was based on the continued influence of past and current climate anomalies on marine organisms as they age, grow, and reproduce (Payne et al. 2017). The primary forecast described herein was designed to emulate an operational forecast and took weekly averages of explanatory variables to forecast the day of the year of key phenology metrics (Figure 1.1). A retrospective forecast was generated to create confidence intervals of predicted values and assess model skill. By iteratively leaving out data from different years, an ensemble of models was generated with slightly different data used for model fitting in each

iteration. These modeling methods were used to identifying key variables that influence A/R migration and spawning phenology.

2.2 Methods:

2.2.1 Environmental data:

Based on previous research on Striped Bass spawning habitat, phenology, and migration patterns, eight independent environmental variables were chosen to include in the forecast models: spring river temperature anomalies, winter ocean temperature anomalies, river pulse duration timing (PDT), wind PDT, river discharge, and three regional climate indices ENSO, NAO, and AMO. The abiotic independent variables will be described in greater depth below.

2.2.1.1 Temperature in oceanic and river habitats:

River and ocean temperature have been shown to be linked to the onset of spawning in A/R Striped Bass (Callihan et al. 2015; Smith & Rulifson 2015). Daily data on air and water temperature in Halifax, NC for April-June are included in reports on historical egg production surveys (Figure 1.1; Hassler et al. 1981; Rulifson 1993). However, my model required temperature data from months prior to egg production surveys since the goal of this project was to produce a forecast that could be disseminated in advance of the spawning season. As a result, I utilized daily air temperature data (Table 1.1) from a time series that integrates observations from Weldon, NC and Roanoke Rapids, NC spanning between 1904 and the present (Figure 1.1; McCulloch 2017; State Climate Office of North Carolina 2017).

In-situ water temperatures were not available from January – June in each year of the historical period; however, daily air temperatures are available for the entire period. Air temperatures were converted to river temperature via a bias correction to account for the fact that releases of water from the Kerr Reservoir upstream of the Striped Bass spawning grounds can impact river temperature, potentially causing discrepancies between the air temperatures and in situ temperatures experienced by fish (Figure 1.1; Rulifson & Manooch 1990). Regression models (Table 2.2) were created using the entirety of each water temperature data source, as well as two additional models of the US Geological Survey (USGS) temperature data that modeled data before and after day of the year 81 (first day of spring) separately to create a winter and spring model. The regression model with the highest adjusted R^2 (0.80) was the USGS temperature-based model that included data from the entire modeling period (Jan 1-June 30) rather than the alternative models divided by season (Table 2.2). The bias correction was applied to the raw Roanoke Rapids air temperatures that was then smoothed using a three-day moving average (Mills et al. 2017). These river temperature data were then converted to daily anomalies using combined means from both periods including the years 1960-1993 and 2005-2016. This was done since using absolute values can lead to overinflated skill estimates in forecasts (Hobday et al. 2019).

The overwintering grounds of the migratory component of the A/R Striped Bass stock are important since the temperatures in this area can affect the rate of gonadal development, which could influence spawning timing (Laney et al. 2017). Air temperature data from overwintering grounds were obtained from the weather station at the Oceana Naval Air Station in Virginia Beach, VA (Table 2.1; State Climate Office of North Carolina 2017). This site was selected due to its spatial overlap with A/R Striped Bass overwintering grounds identified based on acoustic

telemetry (Callihan et al. 2015), the availability of air temperature data that have been collected daily since March 1945 (State Climate Office of North Carolina 2017), and the fact that air and sea surface temperature at this site have been shown to be closely correlated (Peer & Miller 2014).

2.2.1.2 Wind speed and river flow pulse duration timing (PDT):

Daily pulses of fast-moving water can be created in the Roanoke River through wind events, rain events, or large dam releases. River and wind pulse events have been shown to affect egg and larvae abundances, overall reproductive success, and recreational catches of pre-spawning female Striped Bass (North et al. 2005; O'Connor et al. 2012; Peer & Miller 2014). Similarly, in the Roanoke River, spring river discharge is negatively correlated with interannual variations in juvenile abundance of estuarine fishes, including Striped Bass (Rulifson & Manooch 1990; McCulloch 2017; Lee et al. 2020). Intermediate flow levels (5,000-11,000 cfs) in this river are associated with heightened egg viability and greater recruitment in the A/R Striped Bass stock (Rulifson & Manooch 1990). Flow levels that are too low can cause eggs to get buried in the sediment and high flow levels (> 20,000 cfs) can cause eggs to become stranded on flooded riverbanks, both leading to poor recruitment (Rulifson & Manooch 1990). In addition to effects on early life stages, it has also been hypothesized that strong winds and river flow may inhibit spawning migrations, thus, delaying spawning phenology (Anderson & Beer 2009; Peer & Miller 2014).

Pulse Duration Timing (PDT) was calculated as follows using methods outlined in Peer & Miller (2014):

1. The direction of wind flow was analyzed when the wind was parallel to water flow in the Roanoke River below the Roanoke Rapids Dam (Figure 1.1). In other words, wind direction was southeast or blowing in directions between 90-180°.

2. Pulses were calculated as the number of days when these conditions were met:

    a. Mean wind velocity on a given day exceeded the climatological mean for 1960-1993.

    b. River velocity on a given day was over 2 m s^{-1}. This is a modification from the PDT calculation methodology from Peer & Miller (2014). The justification for this modification is explained below.

3. The pulse event in question occurred between the earliest historically observed migration start date from either the creel or egg surveys and the latest observed spawning date (t_{start} and t_{end}, respectively). This is important because pulses occurring at other times of the year would not likely affect fish migration.

4. Pulse duration (Pd) for week y was calculated as the cumulative number of days with pulses between t_{start} and week y. Pulse timing (Pt) was computed as the difference between the first day when water temperatures estimated for the Roanoke River reached 10º C consistently and the first day of a wind or river flow pulse in a year. The day when the temperature threshold reached 10º C consistently was defined as when the temperature remained above that point for the rest of the season. The 10º C temperature was used in this calculation because Callihan et al. (2015) showed that tagged Striped Bass consistently started entering the Roanoke River when temperatures were 9-10º C. Since potential delays in spawning due to pulses are influenced by both the event's timing and duration, these two metrics were combined into a single quantity, such that:

$$PDT(y) = |[Pt(y) - Pd(y)] - c|$$

where c is a constant equal to the difference between t_{start} and t_{end}.

5. Years where no pulses occurred were listed as 0 for the entire year.

To evaluate the possibility that river flow and wind velocity may affect A/R Striped Bass spawning migrations, I used flow data from the US Geological Survey (USGS) river discharge gauge in Roanoke Rapids, NC and wind data from Climate Retrieval and Observations Network of the Southeast (CRONOS) database (Figure 1.1; Table 2.1; State Climate Office of North Carolina 2017). Daily data from this gauge were available for the years 1911-present (Table 2.1). The nearest weather station in CRONOS that has wind observations encompassing the full period of the egg production surveys is located at Raleigh-Durham Airport, which is ~90 miles from the A/R Striped Bass spawning grounds (Figure 1.1). A bias correction was developed comparing this data source with wind data from the Halifax-Northampton Regional Airport (KIXA) station in Roanoke Rapids, which had data from a shorter period (2009- 2020) that did not encompass the full duration of this study (Table 2.2). The KIXA station was chosen due to its proximity to the spawning grounds and relatively greater temporal coverage when compared to other nearby CRONOS wind stations (Figure 1.1).

Peer and Miller (2014) used a PDT method for determining the effect of river flow on Striped Bass migration timing. I improved upon this previous work by using an alternative method of calculating river flow PDT that incorporated Striped Bass physiological thresholds. Haro et al. (2004) ran Striped Bass through a flume in which only 65% of the Striped Bass could swim to the top of the flume when the flume had a flow velocity of 2 m s^{-1}. This indicated that at 2 m s^{-1} water velocity, a sizable portion of Striped Bass were hindered from moving passed this velocity barrier. For my model, river pulses were described as any day in which the daily

velocity exceeds 2 m s^{-1}. To calculate velocity of the Roanoke River, I used the equation

Velocity = Discharge / Cross Sectional Area. Daily discharge was available across the entire

modeling period through the USGS gauge at Roanoke Rapids (Table 2.1; State Climate Office of

North Carolina 2017). D. Walters (USGS, 2020) provided multiple cross sectional area

measurements a year taken at the Roanoke Rapids gauge site. A regression model was developed

to generate daily cross sectional area estimates based on daily gauge height values regressed

against available cross sectional area values:

Equation 1: *Cross Sectional Area (ft²) = Gauge Height (ft) * 826.53 + 239.89*

Gauge height was only readily available from 1974-present. Doug Walters from USGS

provided a relationship between gauge height and discharge to estimate the gauge heights from

1960-1973 when direct measurements of gauge height were missing (D. Walters, USGS,

personal communication). Then daily velocity was calculated as described above and used to

identify pulses over 2 m s^{-1}. Raw river discharge values were also considered in the forecast

models to account for the direct effects of discharge on migration rather than the effects of

occurrence and timing of large pulses. River discharge prior to marine exit may play a role in

anadromous fish migration timing due to the changes in potential salinity and olfactory cues to

fish waiting to migrate in staging areas (Mundy et al. 2011).

Peer and Miller (2014) used a different method to calculate flow PDT that was updated

for this study. In Peer and Miller (2014), a pulse was counted when the daily average river flow

was greater than twice the yearly average. Peer and Miller (2014) found many years with zero

values of PDT in their study of Striped Bass phenology in Chesapeake Bay. Using the original

Peer and Miller (2014) PDT calculation method, I also had zero-inflated data for flow PDT

(Figure 2.1). When using that calculation method, a day with relatively high discharge across the

time series could be a relatively average discharge in a high discharge year. This created more

pulses in low discharge years and less pulses in years with high flow. To make the pulse

threshold more relevant to Striped Bass biology, the pulse threshold was changed when the daily

average velocity was above a specific velocity threshold. Originally the velocity threshold used

velocities of 3 m s^{-1} to define a pulse. This velocity had a strong effect on the ability of Striped

Bass to climb an experimental flume (Haro et al. 2004). The 3 m s^{-1} velocity only had about 5%

of Striped Bass fully passing the velocity barrier, indicating that it was a hard barrier to

migration for most Striped Bass. In contrast, the 2 m s^{-1} threshold indicated a hindrance to

Striped Bass migration timing (Haro et al. 2004). The 3 m s^{-1} pulse threshold also yielded many

years with zero pulses, so a 2 m s^{-1} threshold was adopted in my ecological forecast to minimize

zero inflation.

2.2.1.3 Regional climate indices:

ENSO, NAO, and AMO are the principal regional climate indices that impact

temperature and precipitation in the Roanoke River basin (McCulloch et al. 2017). Given the

influence of these climate indices on the early life history of Striped Bass and other anadromous

fishes, I hypothesize that they may also modulate interannual variations in the timing of

spawning migrations. Consequently, I incorporated monthly data on the Multivariate ENSO

Index (MEI) (Wolter & Timlin 1998), AMO (Enfield et al., 2001), and daily NAO (Hurrell,

1995) into my forecast model using data available from the NOAA Climate Prediction Center

and NOAA Earth System Research Laboratory. As with winter ocean temperatures, climate

indices values inputted into the models were cumulative values to reflect impact of persisting

conditions. Climate indices were entered into models as the cumulative value of the climate indices data during each initialization week.

2.2.2 Biological data:

My model development takes advantage of a historical dataset that includes 34 years of Striped Bass egg production surveys conducted in the Roanoke River (Hassler et al. 1981; Rulifson 1993). These surveys were initiated in 1959 by Dr. William W. Hassler from North Carolina State University and were continued up until 1987 (Hassler et al. 1981). Dr. Roger Rulifson from East Carolina University then assumed responsibility for egg production surveys during 1988-1993. Yearly summaries of daily data generated by these surveys are hereafter referred to as the Hassler and Rulifson reports, respectively (Rulifson et al. 1995). Collectively, the Hassler and Rulifson reports document an egg survey that sampled Striped Bass eggs throughout the spawning season from 1960-1993 creating a rich long-term dataset that was able to effectively capture the timing of the Striped Bass spawning in that period. Striped Bass eggs hatch within 48 hours of fertilization making them effective indicators of recent spawning activity (Hassler et al. 1981). Prior to my initial work on this research project, these surveys had not been converted to a spreadsheet format and some have never been digitized. The initial phase of data processing included digitizing all relevant data sources from the historical surveys using Able2Extract conversion software (investintech.com/prod_a2e.htm#convert).

These surveys collected fish eggs from late April through mid-June below the Striped Bass spawning ground at Barnhill Landing, NC and Halifax, NC (Figure 1.1). The Rulifson surveys spanned between approximately April 15 through June 14. The Hassler reports

documenting these surveys generally did not begin their full sampling effort until after April 29, with only the occasional once a day sample taken before late April to assess the presence of any Striped Bass eggs. During the Hassler surveys, eggs were sampled with 5-minute tows every three hours, whereas Rulifson collected samples at 4-hour intervals for five minutes (Rulifson 1993). Sampling occurred 24 hours a day for the duration of the spawning season (Hassler et al. 1981; Rulifson 1993). Samples were collected at the surface for all years and oblique tows were also collected in the years of the Rulifson reports (Hassler et al. 1981; Rulifson 1993). Surface tow results were used in my model to remain consistent between the Rulifson and Hassler surveys. The egg survey used a 10-inch diameter, 6:1 mouth-to-tail ratio bongo net with a 500-µm mesh. The nets used solid sample cups and a low-speed flow meter to calculate water filtered.

The Hassler and Rulifson reports both used standardized daily estimated egg concentrations that accounted for the cross-sectional area of the river where the samples were collected. Using standardized data from these egg production surveys, my forecast made predictions of three indicators of Striped Bass spawning phenology: start of season (date of 15th cumulative percentile of egg concentration each year), season midpoint (date of the 50th percentile), and season end (date of the 85th percentile). These cumulative percentiles are well-established indicators of interannual phenological variability and have been used to study phenology of marine organisms, particularly zooplankton and larval fishes, across many ecosystems (Greve et al. 2005; Chiba et al. 2012; Mackas et al. 2012). Research on Striped Bass in Chesapeake Bay has already established that these metrics are useful for assessing interannual phenological variability in this species (Peer & Miller 2014).

The Hassler reports also listed daily estimates of Striped Bass catch and effort from a creel survey in Weldon, NC, which I used to calculate a second phenology metric in the same way that they were calculated for the egg survey. Full-time creel clerks were employed at Weldon, NC boat ramp day and night to conduct full interviews of anglers and obtain data on the amount of time fishing and number of fish caught (Hassler et al. 1981). The creel survey is a fisheries-dependent data source with very different collection methods than the egg survey, but with the same level of temporal and spatial resolution. This allowed for a key comparison into the performance of fisheries independent and dependent data sets.

Years in which the egg or creel survey start of season metric occurred in the first week of the survey were excluded from analyses since the survey may not have started sampling close enough to the true beginning of the spawning run to accurately assess phenological metrics. There should be multiple days with zero catch early in an annual dataset to indicate the spawning migration had not yet begun (Staudinger et al. 2019). In these years when the survey began late relative to the spawning run, a substantial portion of the eggs or catch was observed before the occurrence of days with zero catches. Years removed for this reason from the spawning phenology metrics were 1967, 1972, 1974, 1975, 1979, 1985, and 1986. The years removed from the creel survey on adult migration beginning and midpoint were 1964-1967, 1969, 1975, and 1982-1987.

Initial results showed key differences in the phenology of the two surveys indicating that the egg survey-based phenology was measuring spawning activity whereas the creel survey measures migration phenology (Figure 2.2). Key differences were especially noticeable in the beginning metrics with the creel survey-based phenology occurring much earlier in the year (Figure 2.2). Therefore, hereafter I refer to the egg survey when referencing spawning phenology

and the creel survey when referencing migration phenology. In many years of the egg survey, a distinct and large burst of egg abundance was observed, with sometimes a few small peaks following later (Rulifson 1995). Therefore, a peak egg concentration metric was also forecasted that represented the highest daily abundance of eggs estimated in a single day to try to predict this important feature of the Striped Bass spawning run. A peak metric was not considered for the creel survey as large single daily spikes in abundance were not observed.

The following biological variables were included as independent variables in all modeling approaches. Stock abundance was accounted for in modeling because Callihan et al. (2014) reported that, in years with high abundance, Striped Bass utilize the adjacent Pamlico Sound estuary system as habitat and overwintering grounds, whereas the western Albemarle Sound is the preferred habitat used by juveniles. Stock abundance was also used as a forecast covariate since years with higher or lower stock abundance can coincide with robust or reduced size structure, respectively, which can influence habitat use. The Hassler reports list a yearly catch per unit effort (CPUE) estimate based on a creel survey conducted throughout the lower Roanoke River (Hassler et al. 1981). Here CPUE was used as a proxy for stock size. To calculate CPUE, creel census observers use a stratified design to record boat counts, angler effort, and catch data (Hassler et al. 1981). From 1988-1993 and 2005-2016, CPUE (fish/trip) estimates were obtained from NCWRC that were derived from their creel survey also measured by fish caught per trip (J. McCargo, NCWRC, pers. comm.). The Hassler creel survey focused most of its effort in Weldon, NC where the Striped Bass spawning grounds are centered. CPUE annual anomalies was inputted into the models to account for slight differences in collection methods between the Hassler derived estimates and the more recent NCWRC estimates.

Correlation coefficients were assessed using the exact data that was entered in the generalized additive models (GAMs) with Bonferroni corrected p-values. Many environmental variables were correlated with at least one other variable, and all biological variables were correlated with at least one other variable (Table 2.3). Furthermore, all three biological independent variables used were significantly correlated with each another (Table 2.3). The largest significant correlation coefficient was between cumulative ocean temperature anomalies and cumulative NAO values ($r = 0.54$), with most correlation coefficients being less than ± 0.4 (Table 2.3). Variance inflation factors were also generated to test for multicollinearity. Multicollinearity was not an issue across all models as no variance inflation factor was above ten (Tommasi et al. 2015). Many variables considered in the modeling were significantly correlated. However, most were weak to moderate correlations ($r = 0.3$-0.5) (Mundy et al. 2011; Muhling et al. 2018). Collinearity could be a potential issue in the models. To assess this possibility, a principal component analysis among environmental variables was generated for the spawning beginning metric. The first three principal components, which are orthogonal to each other, were used as independent variables to create weekly GAM forecasts. The results of the principal component-based GAMs were very similar to the weekly forecast GAMs based on the original environmental variables. As a result, the weekly forecast was kept as the primary modeling method for ease in interpreting the results.

Univariate regression models were run using all dependent variables to obtain the rate of phenological change per unit of change in each dependent variable. Environmental variables were averaged yearly and compared to the phenology response variables using univariate regression models to obtain rates of change in phenology per unit of each variable (Table 2.4).

2.2.3 Ecological forecasting:

2.2.3.1 Weekly forecasts:

Three different modeling approaches were utilized to forecast Striped Bass migration and spawning phenology. The primary approach was a series of models that generated sequential weekly forecasts of spawning and migration timing during each year using a GAM approach. GAMs have been shown to be an effective tool for modeling phenology data (Ciannelli et al. 2007; Lombardo et al. 2019). This approach was used to simulate operational forecasting and will be referred to as weekly models. The second modeling approach was a retrospective forecast performed on a monthly basis with the goal of generating confidence intervals of predicted phenology that can be used to assess whether intervals based on multiple predicted values per year encompass observed phenology values. The third modeling approach was a comparison of three different models: a base, a reduced, and a biological model with the aim of estimating the impact of excluding or including biological variables to predictive models (e.g., yearly sex ratio and average length of spawning fishes). Goodness of model fit was assessed using generalized cross validation (GCV) scores. All weekly GAMs were also compared using an information-theoretic approach based on the corrected Akaike Information Criterion (AICc) and Akaike weights (Burnham & Anderson 2011). F scores of all model variables were compared to assess importance of the environmental variables to migration and spawning phenology. The GAM output plots describing the partial effects of each independent variable were also characterized and summarized in terms of statistical significance, linearity, and positive or negative relationships to show the relationship between explanatory and response variables (Appendix Figure 1).

All modeling was conducted with R version 4.0.5 (R Core Team, 2021) using the mgcv package for GAMs (Marra & Wood 2011). Knots were limited to three for all variables in models since all modeling had less than thirty data points (Tommasi et al. 2015). A double penalty shrinkage approach was applied to models to improve performance and automatically remove or limit the effect of non-significant variables (Marra & Wood 2011). The forecasts were initialized using the Hassler daily eggs survey data from 1960-1987 and the Hassler daily creel survey data from 1963-1987. Initialization in this context refers to the time period when data were directly inputted into a model prior to making a forecast of conditions during a subsequent time period. For this forecast, models were initialized on a weekly basis each year during the season between January 1st to June 30th. The Chesapeake Bay stock of Striped Bass showed large increases in spawning related hormones starting in January when temperatures at the time began to rapidly increase, so only data after January 1st were used for model initialization (Woods & Sullivan 1993).

Each weekly forecast of migration and spawning timing incorporated weekly mean data from that particular initialization week on river and ocean temperature anomalies, weekly cumulative river and wind PDT, annual A/R stock CPUE estimates, and monthly data on the three regional climate indices. All biological variables used in modeling were lagged by one year, meaning CPUE estimates entered into a model for 1965 were observed CPUE estimates from 1964. This reflects the fact that much of this biological context for the current year would be unknown at the time of forecast initialization. Note that the yearly estimates of average length and average sex ratio were not available for as many years as the other variables, allowing for fewer years of data to be entered into the models. A model with few years of data and many variables can lead to over-parameterization, which can lead to poor forecast performance

(Burnham & Anderson 2002). Therefore, a separate biological model was generated using a reduced set variables to compare to base models.

Variables that focus primarily on the ocean component of the Striped Bass migration are most likely to have a strong impact on the rate of gonadal development and affect migration and spawning timing in a different way than more direct impacts of other variables. The cumulative effect of ocean conditions is likely more aligned with earlier phenology than a snapshot from one particular week (Wolkovich et al. 2012). To account for this distinction, the ocean temperature anomalies and the three climate indices were inputted into the model as cumulative values where each new anomaly value was added to the total of all previous values that year. For each initialization period the maximum value from the yearly cumulative total was then selected as the input value for that weekly model. However, instantaneous values of river variables may provide a more direct cue for migration or spawning. Therefore, river variables (i.e., discharge, river temperature anomalies, river and wind PDT) were averaged by week during model initialization. Since ocean conditions are unlikely to affect Striped Bass once they reach the Roanoke River, models switch from examining mostly ocean-based variables to examining mostly river-based variables. This switch occurs after day of the year 87 (March 13 in non-leap years), which is the earliest observed data of migration based on the creel survey. Another justification for this aspect of my modeling approach is that there are many covariates considered for these models and a limited number of years of data making it difficult to use all the variables in a single model without resulting in issues with lack of convergence when fitting the model. In GAM model equations, k is the number of splines used for a given variable, DOY is Day of Year, and s denotes use of a smoother. The equations for the ocean and river models are:

Equation 2. Ocean Model (DOY < 87): *DOY of Phenology Metric ~ s(Cumulative Ocean*

   Temperature Anomalies, k=3) + s(River Discharge, k =3) + s(Cumulative NAO,

   k=3) + s(Cumulative ENSO, k=3) + s(Cumulative AMO, k=3) + s(Lagged CPUE

   Anomalies, k=3)

Equation 3. River Model (DOY >= 87): *DOY of Phenology Metric ~ s(River Temperature*

   Anomalies, k=3) + s(River Discharge, k=3) + s(River Velocity PDT, k=3) +

   s(Wind PDT, k=3) + s(Lagged CPUE Anomalies, k=3)

Multiple model checks were implemented to test key assumptions of GAMs, such as lack

of autocorrelation, normal residuals, and the absence of multicollinearity. The acf plot function

in R was used to assess autocorrelation with none of the models exhibiting high correlations

across lags in the data. QQ plots were examined to assess whether residuals were normally

distributed using the qq.gam function, with no models showing non-normal residuals.

2.2.3.2 Retrospective forecast:

A series of retrospective forecast GAMs was also created to test model skill. The

purpose of the retrospective forecasts was to create confidence intervals by rerunning a model

with one year of data missing and changing the missing year in each iteration. For example, one

model will aim to predict the phenology of 1972 and was missing data from 1960 (and 1972),

with the next iteration of the model missing data from 1961. By iteratively leaving out data from

different years, an ensemble of models is generated with slightly different data used for model

fitting in each iteration (Figure 2.3). Confidence intervals can then be generated by looking at the

range of predictions across these iterations. This process was repeated for each prediction year (Figure 2.3).

The same datasets from the weekly forecast approach were used in this analysis. Four versions of this approach were conducted for each prediction year using initialization periods split up by the months January, February, March, and April. These were also the four months that lead up to the average beginning of the spawning phenology where an accurate forecast during this time would be more useful. Since this approach was not developed to parallel an operational forecast, but instead to generate confidence intervals to evaluate model skill, fewer initialization periods were run for simplicity (i.e., monthly rather than weekly resolution). Each version only included data from a given month to generate forecasts. Retrospective forecasts for the first three months used the ocean model (Equation 2), while April used the river model (Equation 3). Violin plots with the overlayed observed phenology were used in comparisons with predicted values generated. Initial predictive skill was analyzed by examining the percentage of predicted violin distributions that contained the observed phenological event. The predictive skill was also analyzed on a broader basis by comparing predicted values in years that exhibited early, normal, or late observed phenology. Early, normal, and late phenology was determined by sorting observed phenology metrics from smallest to largest and then evenly splitting up the years into thirds.

The previous two modeling methods were also applied to the migration phenology end metric based on the creel survey. Many of the Hassler creel survey years have late survey start dates, with only thirteen years having adequate start dates where the beginning metric does not occur in the first week of the survey. The creel survey end metric is likely not affected much by late survey start dates. Thus, forecasts were generated for the end metric only, as opposed to the

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beginning, midpoint, and end metrics, which were used for the egg survey. The end metric may still be useful to managers as the fishery typically closes on a specific date, which could be informed by migration or spawning end timing.

2.2.3.3 Biological model comparison:

Given the limited number of years in the timeseries and large number of covariates, a full model with all theoretically important variables would likely be overparameterized or may not converge due to insufficient degrees of freedom. This is further complicated by a lack of data available on average length and sex ratio between 1960-1987, with only 16 years of available data (Table 2.1). The sex ratios and average length data have biases. Most of the available sex ratio and length data come from a tagging survey done in the lower Roanoke River commercial gillnet fishery during 1960-1977. Little information on gillnet mesh sizes used was available to assess whether all size classes of Striped Bass were represented in the catch. Only smaller fish were chosen to be tagged as fishermen were compensated by the pound of the released fish (R.A. Rulifson, pers. comm.). Despite this bias, there is still variation in these data and Peer and Miller (2014) have shown the strong influence of length on Striped Bass migration timing. More accurately collected biological data from the NCWRC occurred between 1988-1994 when the stock was severely overfished and larger individuals were likely not well represented in the population. However, the 1988-1994 period is needed for forecast validation. To assess the potential importance of these variables, a separate model considering these biological variables was created to run with a reduced dataset for the seventeen years that have available yearly sex ratio and average Striped Bass length (1960-1974, 1976-1977, 1985). Spawning beginning was

the only phenological metric used in this analysis for simplicity and because this metric would be of high interest to managers to have forecasts.

To properly isolate the impacts of the additional biological variables, three different models were compared to one another. A base model from the full weekly forecasting results was compared with a reduced model and a biological model. The reduced model contained less variables to avoid overparameterization and the biological model consisted of the reduced model plus yearly average Striped Bass length and sex ratio. The reduced set of variables was selected based on importance of the F scores from the full model for each phenological metric and data visualization in GAM partial effect plots. The following are the reduced equations used in the biological model comparison:

Equation 4. Reduced Ocean Model (DOY < 87): *DOY of Phenology Metric ~ s(Cumulative Ocean Temperature Anomalies, k=3) + s(River Discharge, k=3) + s(Lagged CPUE Anomalies, k=3)*

Equation 5. Reduced River Model (DOY >= 87): *DOY of Phenology Metric ~ s(River Discharge, k=3) + s(River Temperature Anomalies, k=3) + s(Lagged CPUE Anomalies, k=3)*

2.2.4 Forecast validation:

When creating ecological forecasts, the skill to which the response variable can be forecasted and the amount of lead time that can be accurately forecasted needs to be assessed

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with one method involving use of historical data (Hobday et al. 2016). Forecast skill should be evaluated with historical data that are distinct from those used for model development because otherwise the assessment of forecast accuracy can be overly optimistic, especially if a model is overfit (Brun et al. 2016; Muhling et al. 2020). Initial results examining the spawning and migration phenology revealed key differences in phenology patterns such that using the creel survey to validate the egg survey-based forecasts wasn't possible. Therefore, for validation purposes, forecasts for the egg survey-based models were validated using data from the Rulifson period (1988-1993). The Rulifson period has almost identical methods to the Hassler period but was carried out by a different research group and was considered a different dataset for the purposes of forecast validation. For the creel survey-based models, I used creel data from 2005-2016 for model validation. Data between 1994-2004 were not available and after 2016 the management of water releases from the Kerr Reservoir changed, which may affect phenology (US Army Corp of Engineers 2016; Riggs 2021). The models generated predictions based on environmental and biological data from the validation periods, but used the models developed during the original time period. These predictions were then compared to observed phenology metrics from the Rulifson egg survey and the 2005-2016 NCWRC creel survey, respectively.

Forecast skill was evaluated across each forecast week using three model performance indicators: root mean square error (RMSE), anomaly correlation coefficients (ACC), and absolute error (Tommasi et al. 2017b). Forecast skill was evaluated in a similar manner to Stock et al. (2015) and Tommasi et al. (2017b) to determine how far in advance the timing of Striped Bass spawning and migration can be forecasted. This was accomplished by using the ACC to compare forecasted and observed phenology:

Equation 6:
$$ACC(p, y) = \frac{\sum_{x=1}^{N}(F_x'(p, y) \times O_x'(p, y))}{\sqrt{\sum_{x=1}^{N} F_x'(p, y)^2 \sum_{x=1}^{N} O_x'(p, y)^2}}$$

where x is the year for which a forecast is developed; N is the number of years with forecasts; y is the week when a forecast is made; p is the phenological metric (i.e., start of season, season midpoint, end of season, and spawning peak); F' is the forecasted anomaly in spawning time and O' is the observed anomaly in spawning time. In meteorology, forecasts are considered useful when skill exceeds 60% (ACC > 0.6) and are classified as highly accurate if skill > 80% (ACC > 0.8) (Bauer et al., 2015; Payne et al. 2017).

2.3 Results:

<u>2.3.1 Striped Bass migration and spawning phenology and their trends:</u>

The start of the spawning phenology began as early as May 2nd (DOY 123) and the spawning season ended as late as May 31st (DOY 154), with an average beginning date of May 7th (DOY 131.4 ± 5.3 S.D.) (Figure 2.2). Over the historical period (1960-1993), the four spawning metrics varied between 20 and 25 days. The spawning season length (difference between the beginning and end metrics) was 10.4 ± 4.0 days on average, with the shortest season being 4 days and the longest 21 days. The mean spawning peak occurred on May 14th (DOY 135.8 ± 6.9 S.D.), with the earliest occurrence on May 4th (DOY 125) and the latest on May 29th (DOY 150). Similarly, the spawning midpoint occurred as early as May 4th (DOY 125) and as late as May 26th (DOY 147), with an average date of DOY 135.0 ± 6.1 S.D. The spawning metrics did not display significant changes over the historical period, with the exception of the spawning beginning that became slightly later over time. The other three spawning metrics also displayed later phenology over the historical period, albeit with a non-significant trend (Figure 2.2).

Migration season length lasted longer than the spawning season, with an average duration of 38.3 ± 7.8 S.D. days (Figure 2.2). The shortest migration season was 25 days, while the longest was 60 days. The historical migration beginning came as early as March 28th (DOY 87) and ended as late as June 12th (DOY 163), with an average beginning date of April 11th (DOY 102.3 ± 7.6 S.D.). The more recent migration period (2005-2016) beginning started as early as March 11th (DOY 70) and ended as late as May 22nd (DOY 142), with an average of beginning date of April 3rd (DOY 94.5 ± 13.5 S.D.). The migration midpoint occurred as early as

April 18th (DOY 109) and as late as May 27th (DOY 147), with an average date of May 6th (DOY 127.4 ± 11.1). Between 1960 and 1993 spawning and migration phenology metrics became gradually later in the year (Figure 2.2). When jointly examining the historical and more recent migration periods, the end metric varied by 47 days. The migration end metric showed significantly earlier phenology over time at a rate of change of 0.19 days earlier per year. This pattern of earlier migration was consistent for the two migration phenology metrics although these relationships were statistically insignificant (Figure 2.2).

My results showed large differences in phenological metrics and season length between the egg and creel surveys, suggesting that they are measuring different ecological processes (Figure 2.2). Migration season length was 28 days longer on average or almost four times as long as the average spawning season. Migration and spawning phenology beginning showed stark differences with the migration season occurring earlier in the year (Figure 2.2). In the RRMA, the fishing season typically closes on May 1st with the entire spawning season occurring after this date in all years (Figure 2.2). The migration beginning always occurred before this date in all years and the migration midpoint occurred before this date 38% of the time overall and 48% of the time in recent years (Figure 2.2).

2.3.2 Summary of trends in environmental variables:

Both ocean and river temperatures showed a small but significant increase over the course of the combined historical (1960-1993) and validation (2005-2016) periods (Table 2.5, Figure 2.4). When looking at the historical period only, there was no significant increase in either river or ocean temperature over time. Flow PDT calculation methods varied greatly with the velocity-based method that defines pulses as flows greater than 2 m s^{-1} having the most years

with non-zero flow PDT values (Figure 2.1). Velocities greater than 3 m s^{-1} only occurred in 6 of

the 34 years during the historical period creating a variable with mostly zeroes, which also

occurred with the Peer and Miller (2014) flow PDT calculation method (Figure 2.1). Wind PDT

had no zero value years and exhibited minimal variation over time (Figure 2.5). The AMO had a

cool phase occurring in the 1970-1990s and warms phases in the 1960s and from the mid-1990s

to present. NAO varied greatly over the study period with mostly positive phases in the mid-

1970s and early 1980s – mid 1990s. NAO also had some mostly negative phases in the late

1960s, late 1970s, and late 2000s. ENSO also varied greatly over the historical period with nine

El Niño events and seven La Niña events occurring over the entire study period.

2.3.3 Weekly GAMs:

To assess environmental variable significance and their relationship to the phenology

metrics, GAM output plots were characterized based on the prevailing shape (i.e., linear vs.

nonlinear) and direction of the relationship if linear (Appendix Figure 1). F statistics from the

weekly GAMs were also extracted to compare environmental variable importance across all

weekly models (Figure 2.6). Most variables when examined across phenology metrics had less

than 50% of the GAM output plots produce a relationship that did not include zero across its

range or where the variable was not removed by the double penalty approach applied during the

modeling (Figure 2.7). Discharge was the notable exception, which was frequently significant.

Discharge also exhibited a mostly positive linear relationship with phenology metrics (Figure

2.7). Across metrics, most significant, non-linear discharge plots showed minimal effects at low

discharges, but increased impact of discharge on phenology at high discharges (Appendix Figure

2). These positive linear and non-linear trends can be interpreted as indicating later migration

and spawning phenology occurred with increase discharge. Both the migration midpoint and end

dates both occurred one day later per 1,000 cfs increase in discharge and all spawning metrics

occurred about a half day later in the season per 1,000 cfs increase in discharge (Table 2.4).

Between late February and early March (initialization weeks 7-9), the discharge relationships of

all spawning metrics switched from a mixture of relationships (e.g., linear, non-linear,

unsignificant) to a clear trend of positive, linear output plots (Appendix Figure 2). A similar

pattern is also exhibited in the F scores, with higher F scores observed at that time of the year.

This pattern persisted through the rest of the migration season indicating that at this time of the

year discharge becomes a key factor for Striped Bass spawning phenology and continues to be

important (Figure 2.6).

Flow-based PDT exhibited low F scores and mostly non-significant GAM output plots

for the spawning beginning and the migration and spawning end metrics (Figures 2.6, 2.7). Wind

PDT also did not have a strong impact on Striped Bass phenology, except for the spawning

midpoint and peak. This trend in wind PDT indicated that the timing and occurrence of large

flow pulses did not significantly impact Striped Bass phenology, especially in the beginning and

end of the migration and spawning run.

The ecological forecasts indicate that ocean and river temperature anomalies did not have

a strong impact on phenology when analyzed on a weekly basis. However, yearly regression

models indicated that increasing river temperatures lead toward earlier phenology for the

midpoint, end, and peak spawning and migration metrics (Table 2.4). This difference in model

results could be due to the use of anomalies vs. raw temperatures, the inclusion of additional

variables beyond temperature in the GAMs, or differences in the time scales used (weekly vs.

yearly). River temperature did lead toward earlier phenology at a rate of -4.4 days per degree

Celsius in the migration midpoint and end metrics when examined as annual averages, but not the migration beginning (Table 2.4). Spawning metrics had a similar trend with slightly smaller slope estimates (Table 2.4). Cumulative ocean temperature anomalies produced several positive linear relationships indicating that warmer winters can lead to later spawning phenology (Figure 2.7). This trend was the opposite of the hypothesized impact as warmer ocean temperatures should lead to faster gonadal development and earlier migratory phenology for spring-spawning fishes (Woods & Sullivan 1993). Both river and ocean temperature anomalies also produced many non-linear and non-significant GAM plots across all metrics (Figure 2.7). Ocean temperature anomalies had high F scores in some egg models initialized early in the year but were near zero in most other models (Figure 2.7). River temperature anomalies had relatively low F scores across most weekly models, with very little impact on the spawning beginning and end at the weekly forecast scale (Figure 2.7). Spawning midpoint, peak, and migration end showed some relatively higher river temperature F scores and few significant GAM output plots, with mostly non-linear relationships (Figures 2.6, 2.7).

The three climate indices produced few significant GAM output plots across the phenology metrics, with only NAO having at least some significant effect on most metrics (Figure 2.7). NAO had the most significant GAM output plots for the spawning end phenology, with a partially positive linear effect (Figure 2.7). The three climate indices showed low F scores across the spawning metrics, except for the migration and spawning end metrics (Figure 2.6).

The only biological variable in the weekly forecast, lagged CPUE anomalies, had low F scores and mostly insignificant GAM output plots for all metrics, except spawning beginning. The effect was largely non-linear, but otherwise had a negative, linear effect indicating earlier phenology at higher abundances. When abundance is lower, there tends to be a less diversified

stock structure leading to fewer individuals coming from different overwintering grounds and results in delayed migrations. Increases in lagged CPUE anomalies leads to earlier phenology for all migration metrics and spawning beginning at a rate of -0.8-2.2 days per increase in CPUE anomalies (Table 2.4).

Weekly forecasts were assessed for goodness of fit and prediction performance (Figure 2.8). Good model fit is indicated by low GCV and RMSE scores and high deviance explained. High ACC scores and low absolute errors show good predictive skill. Generally, GCV gradually declined as the weekly models progress towards later in the season, with the later models having lower GCV scores. However, note the spike in GCV scores during week 15 (early April) (Figure 2.8). AIC scores can be compared across weeks, but not across response variables. AIC scores across all metrics did not vary much across initialization weeks. However, the AIC showed a slight decline in most models between initialization weeks 9-18. (Figure 2.8). Across all weeks, the spawning beginning and end metrics had a consistently lower GCV scores, indicating better model fit than the models of spawning midpoint, peak, and migration end metrics (Figure 2.8). The migration end models exhibited much higher GCV scores and lower percentage of deviance explained than all the other spawning phenology models (Figure 2.8). Percentage of deviance explained fluctuates in similar patterns across metrics, with the first few weeks of January and March through early April for egg beginning and end having over 70% deviance explained (Figure 2.8). For migration survey end models, RMSE remained higher across most weekly models (Figure 2.8).

Absolute errors across models and metrics were relatively high relative to the short duration of the spawning season (Figure 2.8). Few models had average absolute errors less than five days (Figure 2.8). With an average spawning season length of ten days for the egg survey

and some spawning seasons estimated as short as four days, a small forecast error could potentially miss the spawning season. Most models across spawning metrics have average absolute errors between five to ten days, with the migration end metric typically greater than ten days (Figure 2.8). Spawning beginning had some of the lowest absolute errors across models and phenology metrics, with the migration end metric having one of the highest sets of absolute errors. ACC scores across the models and metrics were almost entirely below the 0.6 threshold associated with good forecasting skill, except for the late season models (Figure 2.8). Migration end was the only metric producing a good forecast occurring more than two weeks before spawning typically occurs (Figure 2.8). Low ACC scores indicate that the current suite of variables and modeling approach is unable to accurately forecast Striped Bass phenology, although a rise in the ACC at the end of the forecast period suggests an accurate nowcast may be possible.

Using an information theoretic approach, the top weekly GAMs with delta AIC scores under 10 were compared (Appendix Table 1). This comparison only used full weekly GAM models and assessed which week had the best forecasts for each phenology metric from an information theoretic approach. Weekly GAMs using data from weeks 16-19 (mid-April to early May) appeared in at least three of the five metric's top ΔAIC scores (Appendix Table 1). This covers the period right before the average spawning beginning date. Few models across the metrics had top ΔAIC scores from earlier in the spawning season using mostly ocean variables (Appendix Table 1).

2.3.4 Retrospective forecast GAMs:

GAMs were created using monthly averaged data to predict spawning metrics one year at a time where in each iteration a year of data was left out (Figure 2.9). The goal of this modeling method was to create confidence intervals using a leave-one-out approach. Predicted value distributions varied greatly across years, with some being highly clustered around short periods and others having ranges expanding across multiple weeks (Figure 2.9). To initially analyze model skill, the number of years in which the distribution of the predicted values contained the observed phenology metric date was calculated (Table 2.6). Spawning forecasts contained the observed phenology date 34-57% of the time, with the migration forecasts ranging from 41-66% (Table 2.6). The migration end forecasts had the highest average percentage (54.2%), while the spawning peak had the lowest (37.5%) (Table 2.6). Looking across the spawning metrics, the month of March had the highest average percentage (51.8%) with the month of February displaying the lowest (44.8%) (Table 2.6). Absolute mean error was calculated to further assess model skill (Table 2.6). The spawning peak metric had the highest absolute prediction errors, with the highest value of 7.5 days from the January models (Table 2.6). The spawning beginning had the lowest average absolute errors, with the lowest value of 3.9 days in the March models (Table 2.6). Standard deviations across the spawning metrics remained low, with the migration errors having much higher standard deviations (Table 2.6). The larger predicted distributions for the migration end could be driving the higher percentages of distributions that contain the observed phenology.

To further assess model prediction skill, the average predicted spawning metric date across the four months analyzed was compared to general historical spawning timing (Figure 2.10). Across the spawning metrics, the models generally were able to better predict years with normal phenology dates (Figure 2.10). For most of the metrics, the later months of March and

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April had higher prediction skill; however, the opposite was typically true for phenology metrics with normal timing (Figure 2.10). The migration end metric did not exhibit as distinct differences in ability to predict different seasonal timings as the spawning metrics (Figure 2.10). The migration end metric showed consistently low prediction accuracy across initialization months and seasonal timings (Figure 2.10).

2.3.5 Biological model comparison:

A series of three weekly forecasts were generated to compare the effectiveness of including the yearly average length of Striped Bass and sex ratio in the models. A base model used in the full ecological modeling approach was compared to a reduced model for the spawning beginning metric. Across model performance metrics and ACC scores, the base and reduced models had very similar results (Figure 2.11). However, the biological model showed far lower GCV scores indicating better model fit (Figure 2.11). The biological model's deviance explained varied greatly across weekly models and was both greater and lower than the base and reduced models at times (Figure 2.11). ACC scores of all three model methods were well below the 'good' threshold of 0.6 for all weeks except at the end of April (Figure 2.11). Average length and sex ratio had several models with high F scores, but for most of the modeling period produced near-zero F scores (Appendix Figure 3).

2.4 Discussion:

A/R and Chesapeake Bay Striped Bass stocks are subject to important seasonal management decisions whose efficacy could be affected by trends and changes in Striped Bass

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phenology. The goal of this project was to create an ecological forecast of A/R stock phenology; however, the forecast created was not skillful. The weekly forecast method aimed to simulate a potential operational forecast, such as the Maine Lobster forecast of migration and spawning phenology that would be produced each week (Mills et al. 2017). Despite high deviance explained in my models, predictive skill was poor across the metrics and initialization periods. The ACC scores across almost all initialization weeks and metrics were unable to yield many 'very good' (0.8) scores and only a few 'good' (0.6) scores (Figure 2.8). ACC statistics removes the average value from phenological events. The low ACC scores from the base model are similar to the retrospective analysis since both show that the models are only capable of forecasting close to normal phenology and not early or late phenology (Figure 2.10). Predicting early or late phenology is likely of most use to many user groups as large shifts could greatly impact preparations for fisherman or efficacy of management measures. Skillful forecasts of all spawning metrics occurred in late April, which is very close to the average spawning start time of May 7th. This small lead time would likely not be far enough in advance to make management or fishing decisions, although appropriate lead times could be established by surveying stakeholders. Average absolute errors remained high across all models, especially considering that the average length of the spawning season was ten days. Mills et al. (2017) was able to forecast lobster phenology within one week, whereas most initialization weeks in my model had absolute errors at or above one week. The A/R stock is the southernmost major spawning population of Striped Bass on the east coast, which may make predicting its phenology more difficult; Brun et al. (2016) showed that model prediction often declines close the edge of a species range. However, deviance explained remained high across most metrics and initialization weeks. Thus, the weekly forecast was able to explain a high amount of variability,

but unable to accurately predict future phenology with new conditions, which could be indicative of overparameterization or perhaps not including the most relevant variables. Week 13 showed an increase in deviance explained in most metrics. This point is when the models switch from being parameterized with winter variables based on oceanic conditions to river variables, pointing to possible discontinuity issues. The deviance explained rises after this point and this trend is not seen in other skill metrics.

These results prompted the biological variable comparison. This comparison was done to assess if additional biological data would help predictive skill. Given the similar performance of modeling methods in the biological model comparison with the fully parameterized model, it is unlikely that overparameterization is reducing predictive skill. The deviance explained in the biological model was higher than many of the base and reduced models indicating that the additional biological variables, such as size and sex composition of Striped Bass, helped to explain more variation in phenology. Sex ratio and average length only showed high F scores in a few weeks across the modeling period (Appendix Figure 3). The biological model also exhibited lower GCV scores. Together these factors indicate that length and sex ratio play an important role in the phenology of the A/R stock, but with the current data limitations, such as biases and limited degrees of freedom due to fewer years of available data, are unable to boost predictive skill. The importance of length is consistent with the Chesapeake stock. A potential explanation is that stock structure, such as the number of larger individuals coming from farther overwintering grounds, is an important driver of phenology (Callihan et al. 2015). Larger Striped Bass overwintering off the coast of the Mid-Atlantic Bight may be arriving later in the migration run, so when they are not present in the population, the phenology is pushed earlier by more smaller individuals coming from the Albemarle Sound. However, regression models indicate that

increasing CPUE anomalies leads toward earlier phenology (Table 2.4). Larger individuals could exhibit earlier phenology due to increased swimming capabilities; however, it is not possible to assess this for the A/R stock due to limited size data (Haro et al. 2004; Callihan et al. 2015). Many of the historical years come when the A/R stock was either overfished or experiencing overfishing and likely had few larger individuals. This could result in the phenology of larger individuals playing a small role in the forecast and the current effect of lagged CPUE in the models. This could also be driven by the practice of males typically arriving earlier in the spawning run (Carmichael et al. 1998; Callihan et al. 2015). A more male dominated migration run would have a large portion of the overall run arriving earlier in season and would push phenology metrics earlier. Given the biases described in Table 2.1 in collection of most of the available length and sex data, these results cannot be interpreted as the true impact of these biological variables on A/R Striped Bass phenology. Most of the length data are from fish below 600 mm TL, which is when Striped Bass start overwintering outside of the ASMA. Larger individuals that overwinter in coastal NC and those that overwinter in the Northern Mid-Atlantic Bight coastal waters will not be well represented by the available data used in this comparison analysis. Any future efforts to forecast A/R stock phenology should aim to utilize a different dataset or estimates size and age structure.

Even though the ecological forecasts may not have high predictive skill, they revealed variables that are important to Striped Bass phenology in the A/R stock. For example, key variables were compared to important factors that drive the phenology of Chesapeake Bay Striped Bass stock (Peer & Miller 2014). The Chesapeake Bay Striped Bass phenology was primarily driven by fish size and spring temperatures (Peer & Miller 2014). Temperature plays a much smaller role than other variables in the A/R stock, which could be due to the use of

anomalies in this study versus raw temperature values (Figures 2.8, 2.9). Temperature was also not an important variable for Colombia River Chinook Salmon run timing (Anderson & Beer 2009). Phenology of both Striped Bass stocks are not strongly driven by winter ocean temperatures in coastal VA. The A/R stock was in decline for many years of the historical time series, with low abundance years likely resulting in few larger individuals that are overwintering in the ocean. This potential loss of stock structure could be driving the weak influence of ocean variables on the phenology of the A/R stock. GAM outputs from all spawning metrics showed positive, linear relations with ocean temperatures indicating warm winters lead to later phenology, which is contrary to the hypothesized effect. Coupled with the weak importance of the three climates indices, this could indicate that ocean factors are not important to Striped Bass spawning and migration phenology. NAO was the only climate index of importance with a mostly positive, linear effect on spawning end (Figure 2.7). Thaxton et al. (2020) also observed similar reduced importance of NAO and AMO in the timing of ichthyoplankton ingress into the nearby Newport River, NC estuary.

Peer and Miller (2014) did not include raw river discharge in their model and used a different calculation method for flow PDT that could be driving the differences in importance of flow related variables for these stocks. Chesapeake Bay Striped Bass spawning occurs closer to the salt front than the A/R stock, which could make the A/R stock phenology more dependent on Roanoke River flows since they spawn far up the Roanoke River (Peer & Miller 2014). These differences could warrant stock-by-stock considerations for seasonal management decisions, such as fisheries opening and closures. There could be genetic stock structure effects, such as those observed among Colombia River Chinook Salmon populations, that could be driving some

of these differences in phenology (Anderson & Beer 2009); however, more data are needed to assess this as a potential effect.

Changes in flow patterns in the Roanoke River may be the primary environmental driver of phenology and should be considered by fishery and dam managers. Roanoke River discharge was the most important variable for A/R Striped Bass phenology across all metrics, with a mostly positive, linear trend indicating high flows lead to later phenology at a rate of one day later phenology per 1,000 f s^{-1} (Figures 2.8, 2.9). This trend was also consistent with that of Colombia River Chinook Salmon (Anderson & Beer 2009). Given the importance of discharge in the phenology models of the A/R stock, the recent 2016 change in Kerr Dam discharges could affect migration and spawning phenology. Throughout the historical period, discharges have remained below 20,000 cfs in most years (Appendix Figure 4). Discharges above 22,900 cfs coincide with velocities above 3 m s^{-1} and represent strong barriers to Striped Bass migration up the Roanoke River (Appendix Figure 5). After 2016, there were multiple days of flows greater than 20,000 cfs during the migration of Striped Bass in every year, showing a sharp increase in velocity barriers (Riggs 2021). Discharge of 10,000 cfs coincides with velocities of 2 m s^{-1} and represent a less severe velocity barrier to Striped Bass migration (Appendix Figure 5). Previously established discharge release limits, with a maximum of 13,700 cfs, during the migration season are similar to the 2 m s^{-1}, a moderate velocity barrier, and should be considered when managing Striped Bass migration phenology. Rising F scores (Figure 2.6) and significant GAM output plots (Appendix Figure 2) between mid-February and early March indicate that this is when flow conditions begin to affect Striped Bass spawning and migration phenology. This also indicated that river conditions affect Striped Bass before DOY 87 when the PDT metrics begin to be calculated. Previous flow considerations for anadromous fish migrations began on April 1st,

which is well behind when flow conditions are affecting Striped Bass in the Roanoke River (Army Corp of Engineers 2016). Water resource managers should consider this impact of flows on the Striped Bass when establishing flow regimes in the Roanoke River.

Given the low importance of PDT metrics on phenology and the importance of discharge, pulses may not be a strong driver of phenology. Wind and river velocity PDT metrics only had a strong impact on spawning midpoint metrics indicating that high frequency of pulses or early pulses led to later spawning midpoint dates. While Striped Bass remain on the spawning grounds a pulse could delay the actual spawning event but does not impact fish that are more actively moving toward the spawning grounds. Given the effect of higher discharges leading to later phenology but pulses having a minimal effect, Striped Bass may prefer to not spawn in high flow conditions. There may be specific flow rates or water quality conditions associated with those flow rates that Striped Bass prefer to spawn in. Discharges above 20,000 cfs can lead to Striped Bass eggs spilling into newly flooded riverbanks away from the main stem of the river and preventing them from reaching suitable habitat for early life history stages (Rulifson & Manooch 1990; Zincone & Rulifson 1991). This may be a potential factor for Striped Bass choosing when to spawn as they may wait for high flow conditions to subside towards slightly lower, more favorable flow levels. The most recent stock assessment has also cited the importance of appropriate flow rates for transporting eggs and larvae to the nursery habitat of the Western Albemarle Sound that yields high recruitment (Lee et al. 2020). Onset of spawning may also be influenced by some social dynamic that is not currently captured in modeling. When spawning, as many as fifty male Striped Bass will follow a single female to the water surface in a 'rock fight' to fertilize the eggs that the female releases (Hassler et al. 1981; Lee et al. 2020). Male

Striped Bass have been observed spending more time on the spawning grounds than females, so there may be sex specific dynamics affecting phenology (Carmichael et al. 1998).

The ocean temperatures of the overwintering grounds and river temperatures are significantly increasing over time (Table 2.5, Figure 2.4). Increasing temperature and salinity trends have also been observed in the Pamlico Sound during the same period of increase in temperatures in the AMSA (Bangley et al. 2018). Increasing temperatures have led to earlier observed migration timing in tagged A/R Striped Bass and the Chesapeake Bay stock (Peer & Miller 2014; Callihan et al. 2015). Lombardo et al. (2019) also found shifts toward earlier phenology in River Herring in the Albemarle Sound that coincided with rising temperatures. The forecasts indicate that the A/R stock migration timing is not strongly driven by ocean or river temperatures; however, this may indicate that temperatures are simply not important for predicting phenology. Specific temperatures thresholds that relate to physiological tolerances or spawning preferences may be more impactful to Striped Bass than anomalies. Regression models between river temperatures and migration phenology indicated earlier phenology with increasing temperatures (Table 2.4). The migration end metric does show a significant shift toward earlier phenology in more recent years (Figure 2.2). During the recent period of migration (2005-2016), beginning phenology has a minimum DOY of 70, with the historical migration beginning having a minimum DOY of 87. The trend of earlier phenology in the recent survey period could make a larger portion of the stock susceptible to exploitation during the window when the fishing season is open. These shifts toward earlier phenology could be driven by the increases in river and ocean temperature (Figure 2.4). As climate change continues to warm the planet, the migration timing of the A/R stock may also continue to shift along with the changing climate. This shift could also be present in the spawning phenology; however, it is difficult to assess this possibility

without additional egg sampling in more recent years. Shifts toward earlier phenology could make current seasonal closures mismatched with current management objectives to maintain a high level of Striped Bass escapement.

Another potential cue for initiating migrations could be day-light progression (Asch 2019). As days become longer, this could initiate spawning or migration phases. With the current weekly modeling approach, day light hours or DOY is not possible to include as a variable as the amount of change in day light hours for a given DOY will remain consistent each year across the time series. This yields a variable with zero variation from year to year and is not possible to include in the models as it has no degrees of freedom. If this variable was to be included in modeling, it would help reinforce the predictive skill of normally timed phenology as daylight hours will not change from year to year. Another potentially important environmental factor is dissolved oxygen since tagged Striped Bass in the Chesapeake Bay actively avoided hypoxic areas (Kraus et al. 2015). To the best of my knowledge, there is no daily dataset on dissolved oxygen that covers the full historical period used in this study.

It should be noted that climate indices in the Pacific have recently been shown to have non-stationary correlations with regional climate patterns and ecosystem characteristics since the early 1980s in the Northern Pacific (Litzow et al. 2020). Similar non-stationarity patterns are also evident with NAO in the eastern United States (Joyce et al. 2002). Furthermore, climate change could negatively affect the ability of climate indices to predict changes in ecosystems and fisheries. As a result, regional-scale climate indices could improve model skill at an interannual or decadal scale but are unlikely to improve forecasts at a multidecadal or centennial scale, which could be driving the low importance of climate indices in the forecasts. Climate indices are often proxies for more localized conditions and, when the most appropriate local

environmental factors are included in models, climate indices may not provide additional benefits to modeling.

This analysis included phenology metrics from both fisheries dependent and fisheries independent sources. The creel survey-based migration phenology was consistently outperformed by the spawning metrics in predictive skill and model fit. The average migration season length is much longer making it a less discrete event and could be more difficult to predict than the more condensed spawning season. However, larger forecast errors are less of a concern with this less discrete event. Also, fisher behavior and fisheries regulations may add additional sources of process error to forecasts reliant on fisheries-dependent data. Dennis et al. (2015) found a similar pattern in the Torres Strait tropical lobster fishery, with skill level of total allowable catch model predictions significantly improving with the inclusion of fisheries-independent data. The poor predictive ability in the migration end models may also be attributed to shifting baselines, as the river and ocean temperatures didn't significantly increase in the historical period but did increase in recent years. Brun et al. (2016) found that, in predicting distribution of several plankton species in the North Atlantic, model skill decreased as temporal distance between predictions and the training dataset period increased. The gap between 1993 and 2005 in the migration initialization period and validation period could be driving some of the model's poor performance. The historical data may be limiting the model's ability to predict under novel conditions. Having an adequate source of fisheries-independent data will be an important consideration for future operational forecasts.

In conclusion, this study aimed to create an ecological forecast of the A/R stock of Striped Bass migration timing. The forecast proved to have low prediction skill up until right before the typical spawning period and was only able to skillfully predict years with normally

timed phenology. The full potential of the forecast predictability is likely not yet realized as sufficient data on variables hypothesized to be important, such as average length, are not currently available. The forecasts did reveal the overwhelming importance of raw river discharge on A/R stock migration timing, with a consistent indication that late February to early March is when discharge becomes a key factor influencing migration. This result may be of interest to stakeholders involved in the management of the Roanoke River flow regime, especially as impacts of flows on Striped Bass recruitment have been highlighted as an area of interest in the most recent stock assessment (Lee et al. 2020). Fisheries managers may also have to consider the implications of the migration timing shifting earlier in the year in regard to current seasonal fishery closures.

Table 2.1. Summary of data sources and variables considered

Summary of Environmental and Biological Variables		
Variables	**Source**	**Location and Notes**
Striped Bass Size and Sex Composition (Sex Ratio, Average Length)	Hassler reports (yearly, 1960-1977), NCWRC Creel Survey (yearly, 1989-1993), NCDMF (yearly, 1981-85)	Hassler tagging data was primarily collected at Williamston, NC. However, only small fish were collected purposely since the researchers paid commercial fishermen by the pound for tagged fish. NCWRC and NCDMF data come from several locations throughout the Roanoke River.
Spawning Stock Abundance (CPUE Anomalies)	Hassler Creel Survey (yearly, 1963-1988), NCWRC Creel Survey (yearly, 1989-1993, 2005-Present)	Generated from creel survey data from throughout the Roanoke River Measured in fish/trip
Spawning and Migration Activity (Phenology Markers)	Hassler (daily, 1960-1988) and Rulifson (daily, 1989-1993) Egg Survey Reports	Eggs collected in Halifax, NC and daily creel data used was from Weldon, NC
River Water and Air Temperature (River Temperature Anomalies)	Hassler and Rulifson reports (daily, water temperature, 1960-1977), NC State Climate Office (daily, air temperature, 1960-Present), USGS water temperature (daily, 1999-2016)	River air temperature from Roanoke Rapids, NC. River water temperature used for bias correction from Halifax, NC. NC State Climate Office temperatures switch from collection at Weldon to Roanoke Rapids in 1972.
Albemarle Sound Water Temperature	Albemarle Sound Water Quality Monitoring Program (daily, 2009-2016)	Only data source close to Albemarle Sound is at the mouth of the Scuppernong River
Overwintering Grounds Ocean Water Temperature	State Climate Office of North Carolina (daily, 1945-present)	Oceana Naval Air Station in Virginia Beach, VA

Roanoke River Discharge and Gauge Height (Discharge, PDT)	USGS gauge 02080500 discharge (daily, 1911-present), gauge height (daily, 1974-present)	Roanoke Rapids, NC
Wind Speed (PDT)	CRONOS (daily, 1960-present)	Primary dataset from Raleigh-Durham Airport, NC (KRDU station) and bias correction data from Roanoke Rapids (2009-2020, KIXA Station)
Climate Indices (ENSO, NAO, AMO)	NOAA Climate Prediction Center and NOAA, Earth System Research Laboratory (daily and monthly, 1960-present)	AMO (North Atlantic Ocean, 0º-70ºN) and NOA (North Atlantic Ocean, 20ºN-90ºN) and ENSO (east-central tropical Pacific between 120°-170°W)

Table 2.2. Regression models generated for bias correction of: (1) air temperatures in the Roanoke River relative to water temperatures, and; (2) wind velocity from Raleigh-Durham Airport relative to Roanoke Rapids, NC

Equation	R^2	Slope p-value	d.f.
Spawning Grounds Air Temps ~ 0.466 * (Hassler Water Temps) + 9.121 ; Slope CI: 0.441 - 0.491, Intercept CI: 8.665 - 9.577	0.49	<2e-16	1367
Spawning Grounds Air Temps ~ 0.734 * (USGS Water Temps) + 4.349 ; Slope CI: 0.721 - 0.747, Intercept CI: 4.144 - 4.554	0.80	<2e-16	3133
Spawning Grounds Air Temps ~ 0.273 * (Winter USGS Water Temps) + 5.732 ; Slope CI: 0.647 - 0.690, Intercept CI: 6.180 - 7.032	0.41	<2e-16	1353
Spawning Grounds Air Temps ~ 0.668 * (Spring USGS Water Temps) + 6.606 : Slope CI: 0.256 - 0.291, Intercept CI: 5.591 - 5.873	0.68	<2e-16	1778
Roanoke Rapids Wind Data ~ 0.607 * (Raleigh-Durham Airport) + 1.192 ; Slope CI: 0.547 - 0.667, Intercept CI: 0.842 - 1.543	0.50	<2e-16	399

Table 2.2. Correlation matrix of variables used in ocean model (Equation 2; upper table) and river model (Equation 3; lower table). Bold values are correlation coefficients that have Bonferroni corrected p-values below 0.05. The CPUE anomalies (fish/trip), sex ratio, and average length are all values lagged by one year. Cum stands for cumulative. All other abbreviations are described in the thesis text.

	Discharge	Cum Ocean Anomaly	Cum NAO	Cum AMO	Cum ENSO	CPUE Anomaly	Sex Ratio	Average Length
Discharge	1							
Cum Ocean Anomaly	0.09	1						
Cum NAO	0.06	**0.54**	1					
Cum AMO	0.01	-0.18	**-0.33**	1				
Cum ENSO	0.05	-0.14	-0.15	**0.23**	1			
CPUE Anomaly	-0.17	-0.14	**-0.5**	**0.37**	-0.02	1		
Sex Ratio	-0.04	0.08	0.17	**-0.47**	**-0.26**	**-0.29**	1	
Average Length	0.1	**0.25**	**0.24**	**-0.35**	0.05	**-0.31**	**0.24**	1

	Discharge	River Anomaly	Velocity PDT	Wind PDT	CPUE Anomaly	Sex Ratio	Average Length
Discharge	1						
River Anomaly	-0.09	1					
Velocity PDT	**0.38**	0.01	1				
Wind PDT	**-0.23**	0.01	-0.15	1			
CPUE Anomaly	**-0.23**	0.03	-0.16	0.12	1		
Sex Ratio	0.03	0.01	0.08	-0.01	**-0.29**	1	
Average Length	**0.27**	-0.03	0.03	-0.09	**-0.31**	**0.24**	1

Table 2.4. Yearly averaged regression parameter estimates of the effect of environmental variables on Striped Bass migration and spawning timing. Days are the units of phenological variability used in this table. 95% confidence intervals are in parentheses. Bold estimates are parameters with significant p-values at the 0.05 level.

Variable	Spawning			
	Beginning	Midpoint	Peak	End
River Temperature (°C)	-2.0 (-4.2, 0.2)	**-3.1(-5.8, -0.4)**	**-3.3(-6.2, -0.3)**	**-3.8(-6.1, -1.6)**
Ocean Temperature (°C)	0.3 (-1.1, 1.7)	0.7(-1.1, 2.4)	0.7(-1.2, 2.7)	0.8(-0.8, 2.4)
Wind PDT (unitless)	0.06(-0.1, 0.3)	0.09(-0.1, 0.3)	0.09(-0.13, 0.31)	0.05(-0.1, 0.2)
Flow PDT (unitless)	0.03(-0.03, 0.09)	0.06(-0.01, 0.1)	0.07(-0.007, 0.15)	0.05(-0.02, 0.1)
Discharge (cfs)	**0.0005 (0.0001, 0.0009)**	**0.0007 (0.0002, 0.0013)**	**0.0007 (0.0002, 0.0013)**	**0.0006 (0.0001, 0.0011)**
Lagged CPUE Anomalies (fish/trip)	**-0.76 (-1.4, -0.16)**	-0.7(-1.5, 0.1)	-0.7(-1.6, 0.2)	-0.7(-1.4, 0.08)
NAO (anomaly units)	3.7(-0.5, 7.9)	4.6(-0.8, 9.9)	4.1(-1.8, 10.0)	4.7(-0.2, 9.5)
ENSO (anomaly units)	0.1(-2.4, 2.7)	1.0(-2.2, 4.2)	0.9(-2.6, 4.4)	2.0(-0.9, 4.8)
AMO (anomaly units)	-8.0 (-21.6, 5.7)	-3.9(-21.7, 13.8)	-2.8(-22.2, 16.5)	2(-14.4, 18.4)

Variable	Migration		
	Beginning	Midpoint	End
River Temperature (°C)	-4.36 (-10.8, 2)	**-4.4 (-8.6, -0.2)**	**-4.4 (-7.7, -0.6)**
Ocean Temperature (°C)	-1.48 (-4.7, 1.8)	-0.56 (-2.8, 1.7)	-0.56 (-2.6, 1.1)
Wind PDT (unitless)	**-0.32 (-0.5, -0.1)**	-0.11 (-0.3, 0.03)	-0.11 (-0.3, -0.03)
Flow PDT (unitless)	-0.09 (-0.2, 0.04)	0.00003 (-0.1, 0.1)	0.00003 (-0.1, 0.1)
Discharge (cfs)	0.1(-0.0005, 0.002)	**0.001 (0.0004, 0.002)**	**0.001 (0.0004, 0.002)**

Lagged CPUE Anomalies (fish/trip)	**-2.23 (-4, -0.5)**	**-1.39 (-2.6, -0.2)**	**-1.39 (-2.4, -0.4)**
NAO (anomaly units)	-8.47 (-23.1, 6.2)	-1.41 (-11.6, 8.8)	-1.41 (-8.8, 8.6)
ENSO (anomaly units)	3.05 (-2.8, 8.9)	3.71 (-0.2, 7.6)	3.71 (-1.42, 5.39)
AMO (anomaly units)	-9.25 (-39.2, 20.7)	7.28 (-13.2, 27.7)	7.28 (-21.1, 13.8)

Table 2.5. Regression equations for changes in river and ocean temperatures over time.

Equation	R^2	Slope p-value	df
River Temperature ~ 0.015 (Year) - 17.815 ; Slope CI: 0.004 - 0.026, Intercept CI: -39.767 - 4.138	0.001	0.0069	8,295
Ocean Temperature ~ 0.037 (Year) - 59.678 ; Slope CI: 0.026 - 0.047, Intercept CI: -80.250 - -39.105	0.006	<0.0001	8,423

Table 2.6. Average absolute error (days) of predicted values from retrospective forecast GAMs and the percentage of prediction distributions where the tails of the distribution contain the observed phenology DOY.

| Survey Type	Metric	Initialization Month	Percentage	Average Error (Days)	Standard Deviation (Days)
Egg	Beginning	Jan	57.7	4.4	4.0
Egg	Beginning	Feb	46.2	4.2	3.2
Egg	Beginning	March	53.8	3.9	2.6
Egg	Beginning	April	50.0	4.6	3.7
Egg	Midpoint	Jan	50.0	6.0	4.7
Egg	Midpoint	Feb	42.3	6.4	4.3
Egg	Midpoint	March	46.2	4.7	3.8
Egg	Midpoint	April	42.3	5.5	4.2
Egg	Peak	Jan	34.6	7.5	4.6
Egg	Peak	Feb	34.6	7.1	5.1
Egg	Peak	March	38.5	5.6	4.3
Egg	Peak	April	42.3	4.8	3.7
Egg	End	Jan	50.0	5.4	4.0
Egg	End	Feb	38.5	4.8	4.0
Egg	End	March	53.8	4.7	3.7
Egg	End	April	50.0	4.3	3.9
Creel	End	Jan	45.8	7.2	5.4
Creel	End	Feb	62.5	7.1	5.6
Creel	End	March	66.7	7.0	6.1
Creel	End	April	41.7	7.0	4.9
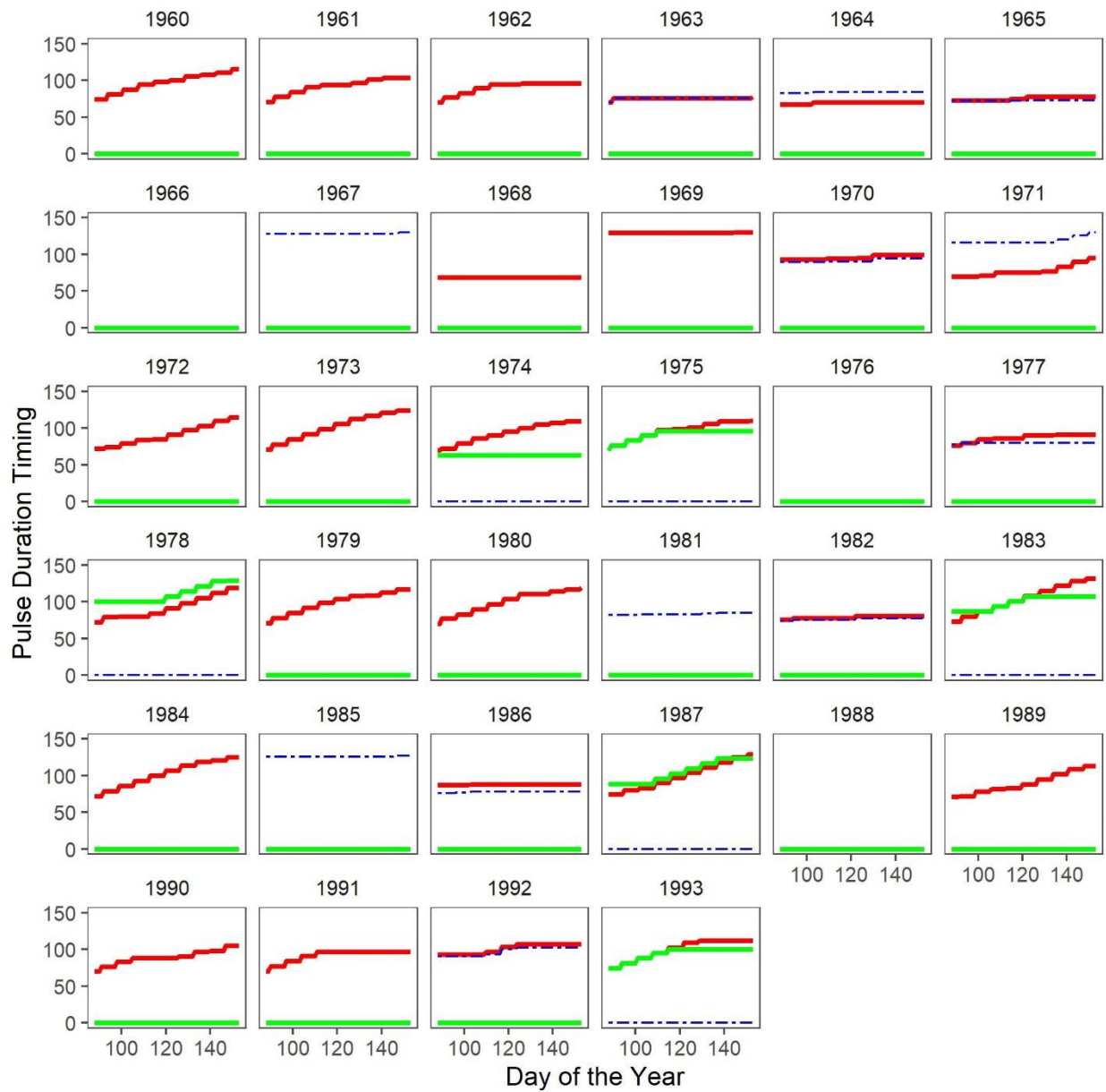
Figure 2.1. River discharge pulse duration timing values split up by year using three different calculation methods where the criteria for a pulse event is changed. Blue lines are a discharge-based method from Peer and Miller (2014); the red lines use a velocity pulse threshold of 2 m s⁻¹ and the green lines use a 3 m s⁻¹ threshold. This metric is cumulative over the course of the season.

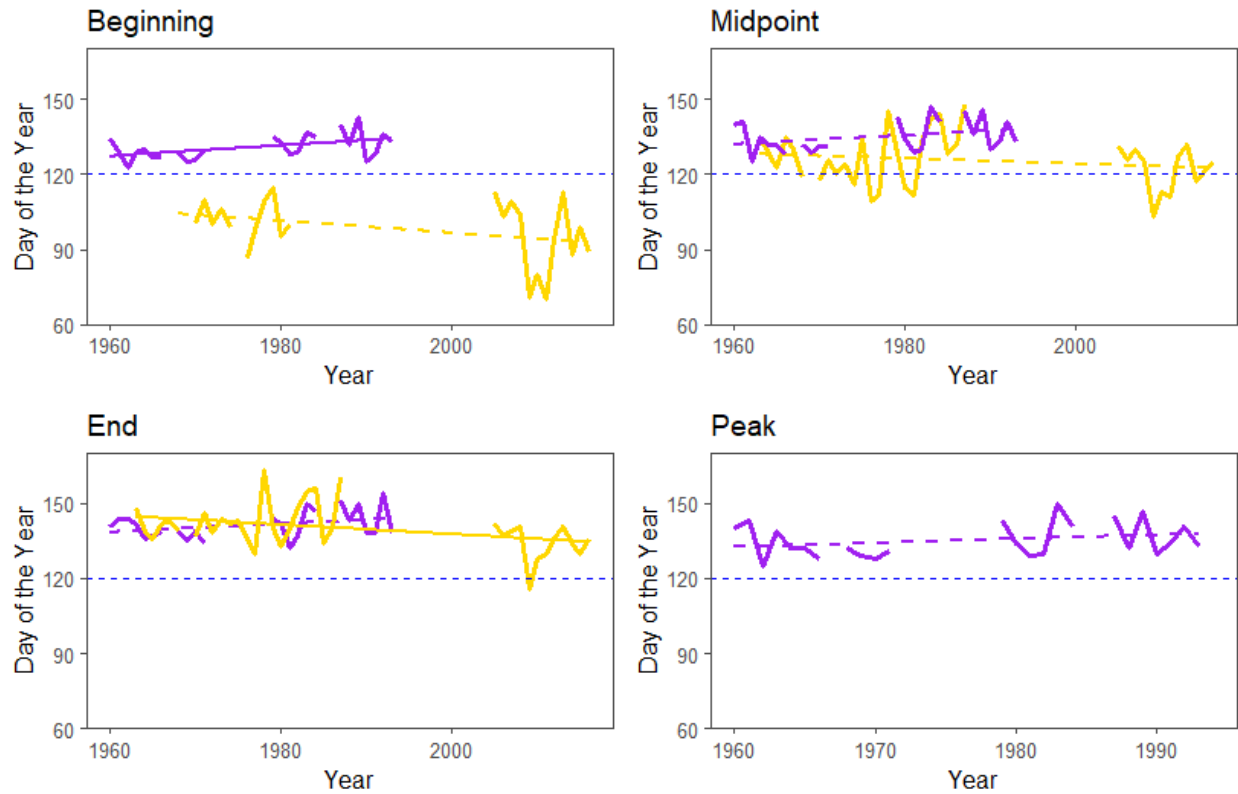*Figure 2.2. Phenological metrics from the egg and creel surveys. Solid regression lines indicate significant regression models at the 0.05 significance level, whereas dashed lines are non-significant. Yellow lines are migration phenology based on creel data and purple lines are spawning phenology based on egg survey data. The blue dotted line at DOY 120 is when the RRMA fishery typically closes for harvest.*

A: One year of data removed at a time to create different iterations of the dataset with different years missing in each iteration. All Iterations are also missing the predicted year of data

Iteration 1	Iteration 2	...
Year	Year	Year
~~1960~~	1960	1960
1961	~~1961~~	1961
1962	1962	~~1962~~
1963	1963	1963
~~1964~~	~~1964~~	~~1964~~
1965	1965	1965

B: Each Iteration uses GAM to predict phenology of 1964

C: Predictions become violin distribution

Egg Beginning January
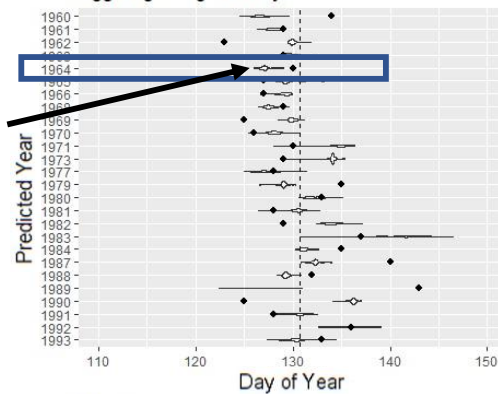
Points are observed phenology of predicted year

Figure 2.3. Conceptual diagram explaining development of the retrospective GAM forecasts. Distributions of predicted phenology are created for one year at a time based on multiple iterations of the same GAM model with each iteration missing one year of that is different from the other iterations.
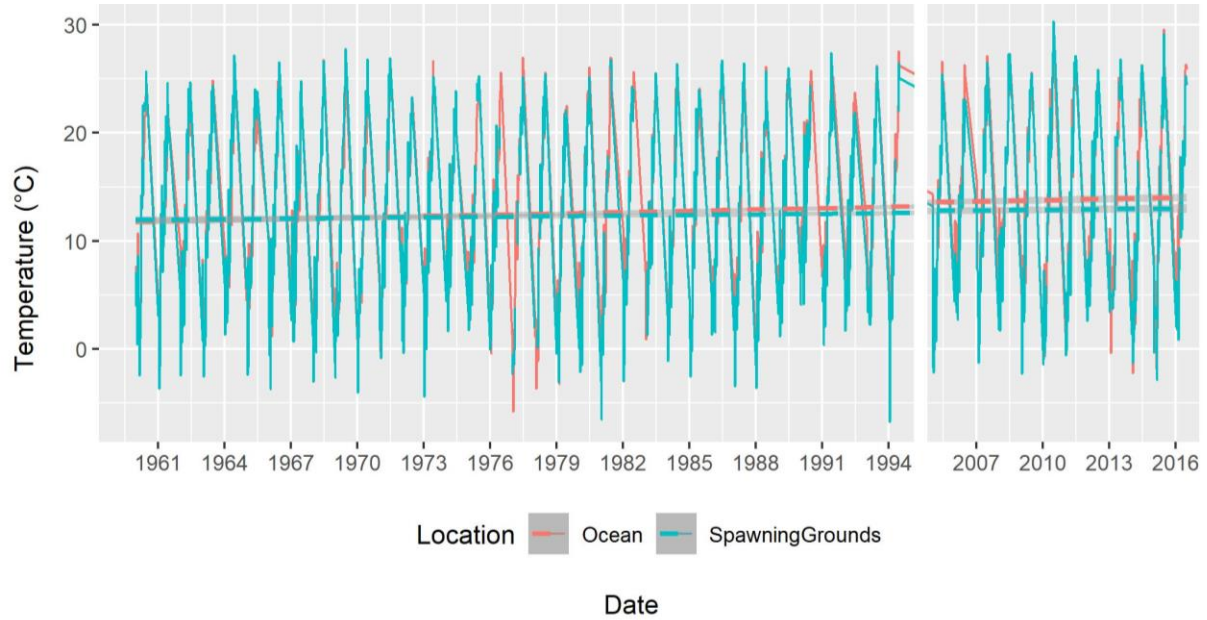
Figure 2.4. Weekly averaged winter and spring (January 1 – June 30) temperatures from the bias corrected river air temperatures at Roanoke Rapids and ocean temperatures from Oceana Naval Air Station, Virginia Beach. Dashed lines are both significant regression models of temperature over time at the 0.05 significance level (Table 2.5). The gap between 1994 and 2005 is due to insufficient biological data during that period was available for modeling.
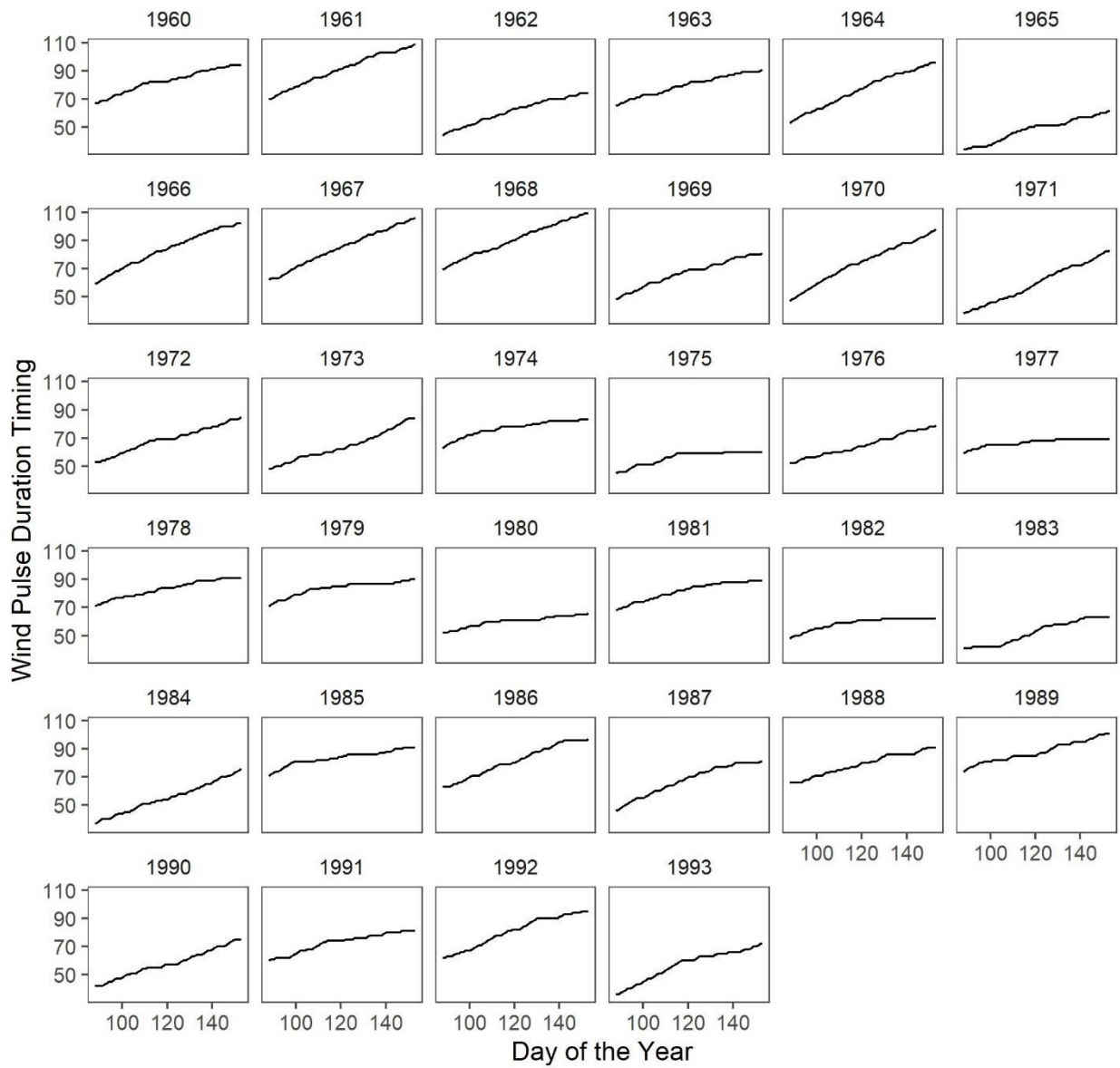
Figure 2.5. Wind Pulse Duration Timing (PDT) split up by year over the historical period. This metric is cumulative over the course of the season.
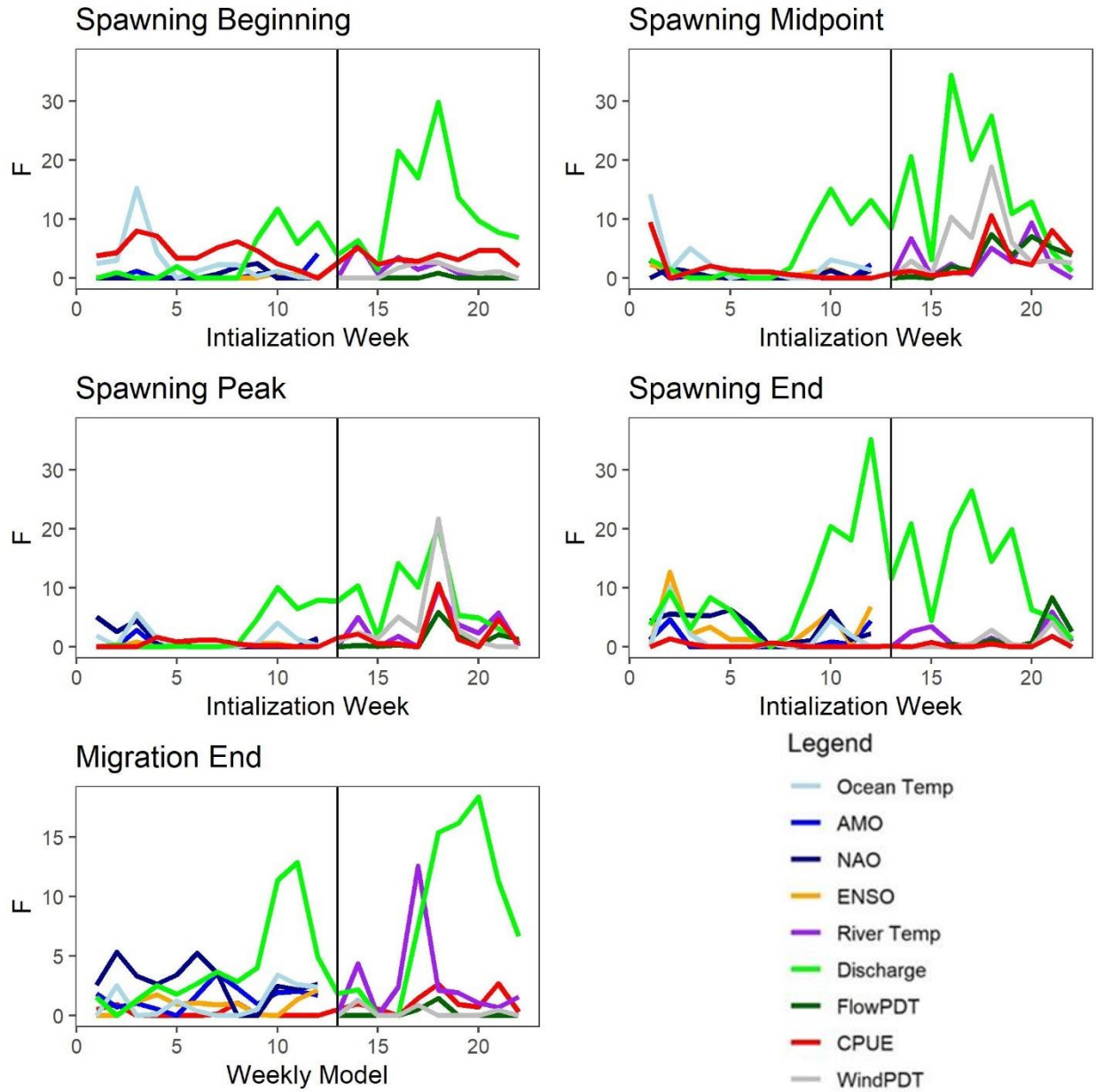
Figure 2.6. F statistics from weekly GAMs. Vertical line at week 13 initialization represents the shift from ocean variable-based models to river variable-based models. Initialization week 0 begins on Jan 1st.
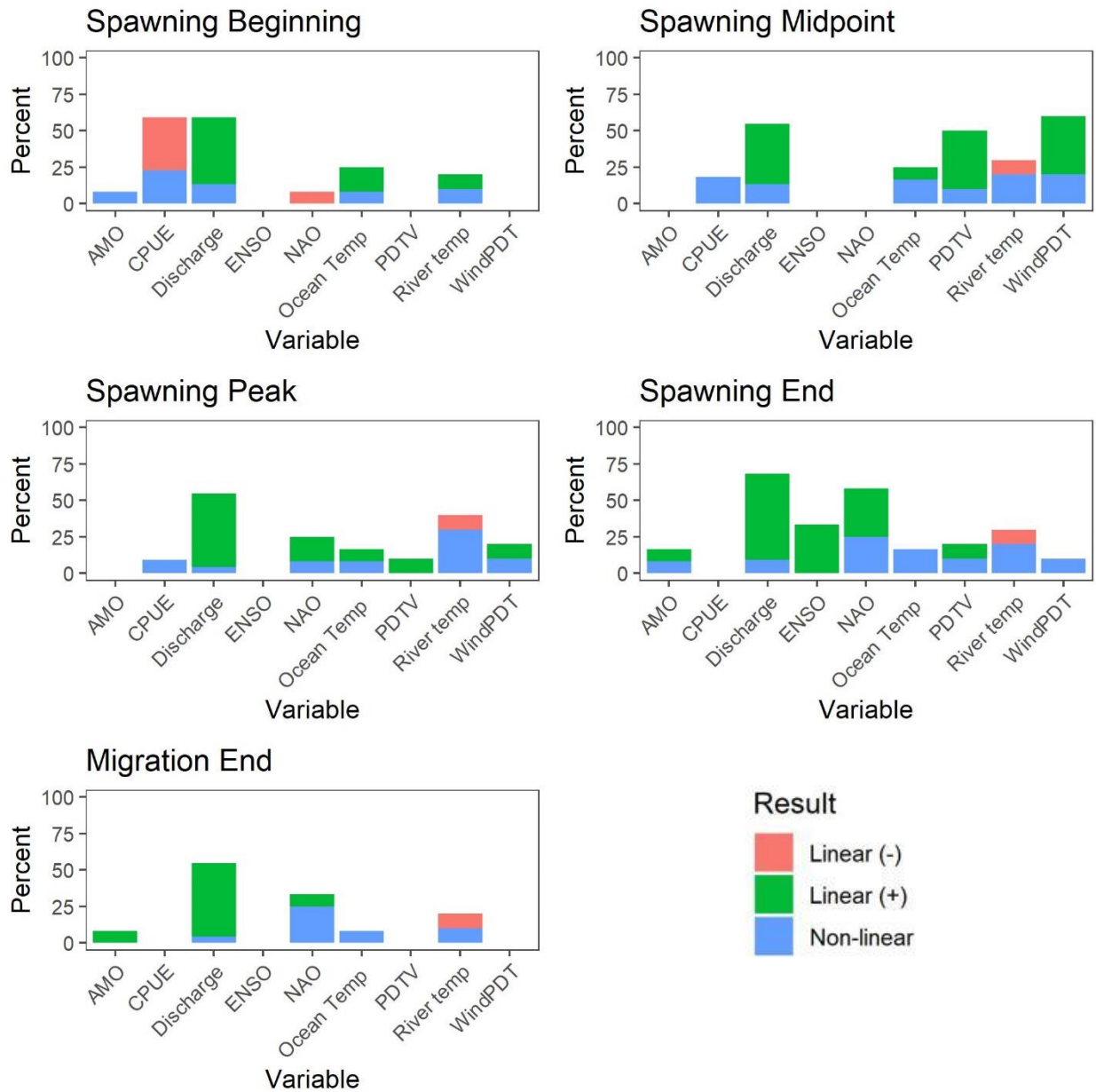
Figure 2.7. Summary of GAM output plots characterized by response curve shape and direction. The percentages shown in this graph reveal how frequent a given variable was or was not significant. Plots where the confidence intervals for the modeled relationship included zero across the full range of an environmental variable were cosidered as having an insignificant impact. An example demonstrating how GAM response curve shape was characterized is included in Appendix Figure 1.
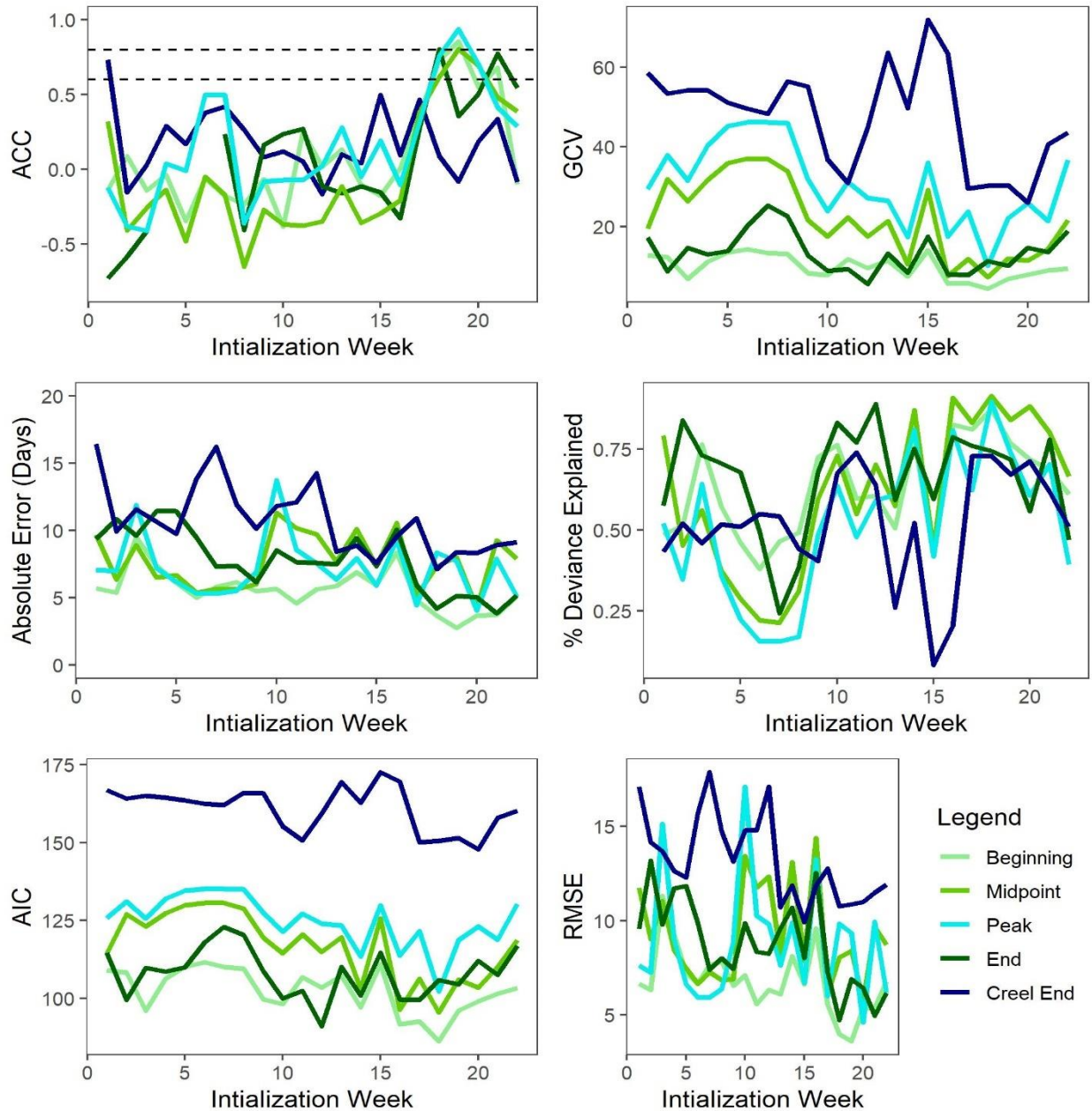
Figure 2.8. Performance metrics for all weekly based GAMs.   AIC, RMSE and absolute error are plotted to track changes over initialization weeks and not changes between the phenology metrics. In the upper left plot, the lowest dashed line shows an ACC score of 0.6, which is when a forecast is considered useful. The upper dashed line shows an ACC score of 0.8, which is when forecast skill is considered highly accurate
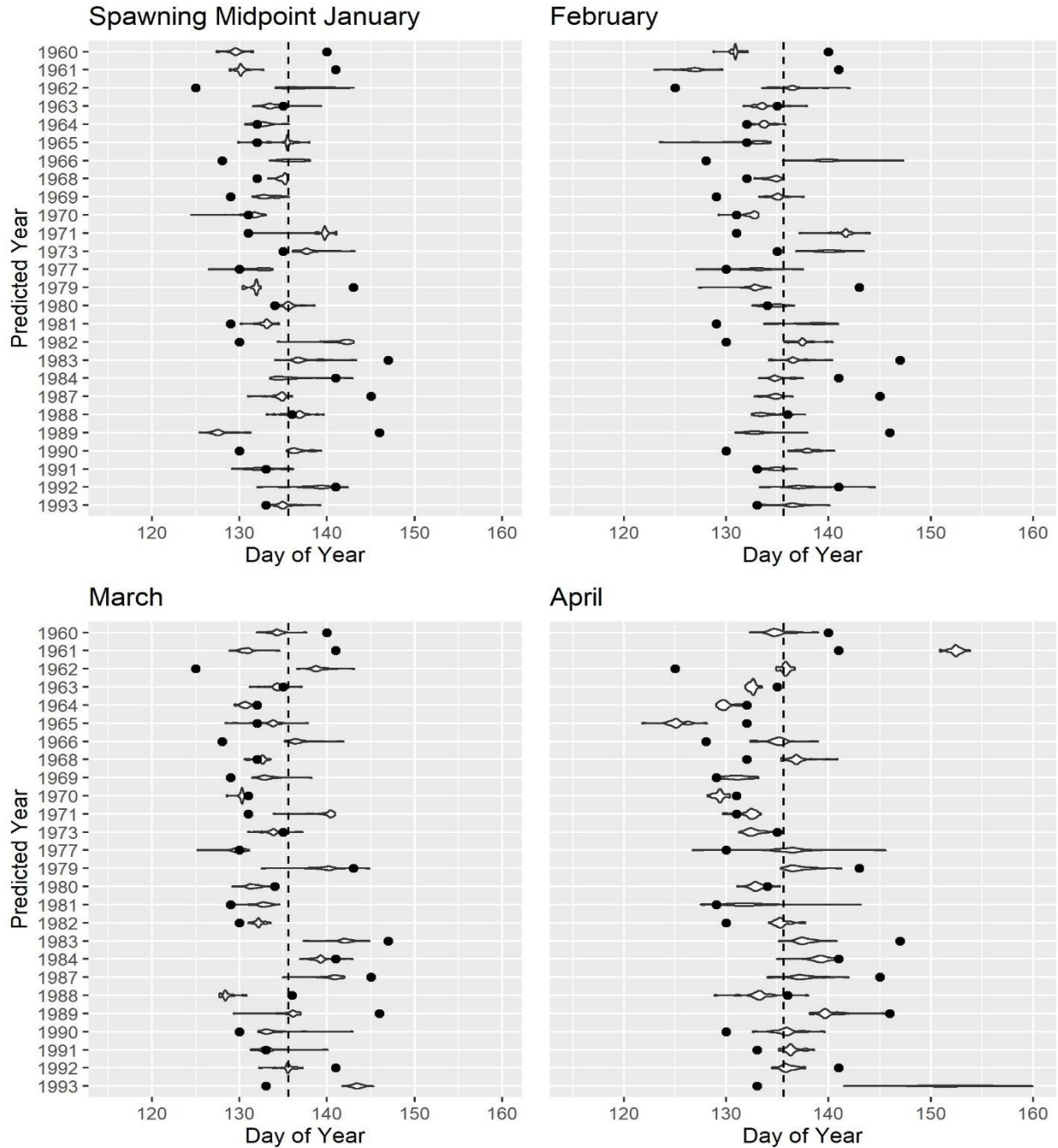
Figure 2.9. Distribution of predicted egg midpoint phenology using a retrospective forecast. Graphs of predictions for other metrics are available in Appendix Figures 6-9. Dashed line is the average egg midpoint day of the year, black dots showed observed phenology, and violin plots show the distribution of model predictions, with thicker areas indicating more frequently predicted values.
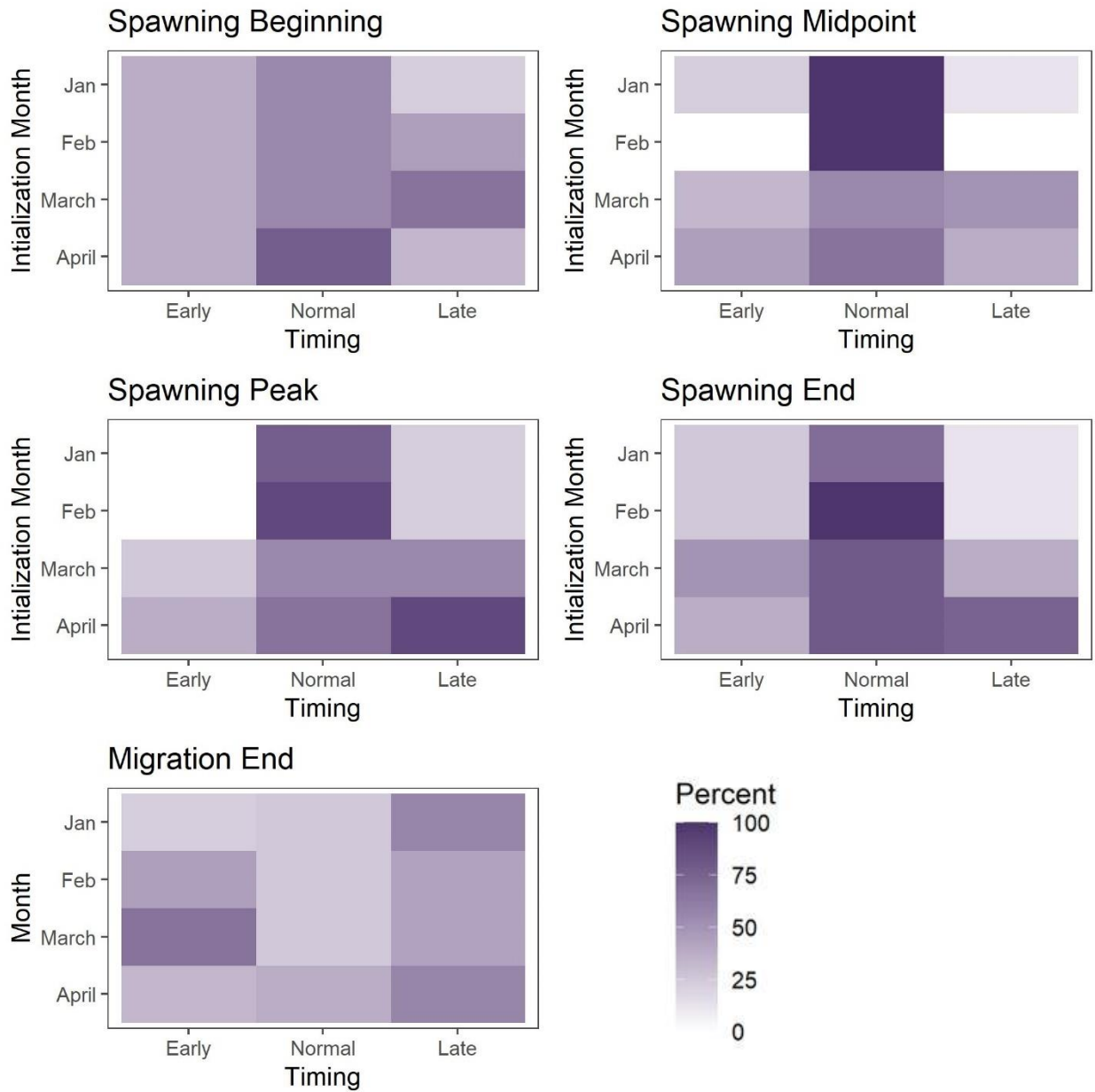
Figure 2.10. This graph estimates prediction skill using the average predicted spawning metric dates from the egg and creel survey based on retrospective forecast GAMs. The timing bins are defined by evenly dividing the historical spawning metric dates into three categories: early, normal, and late. The percentage represents the number of predicted years that fell within the correct range of the binned observations.
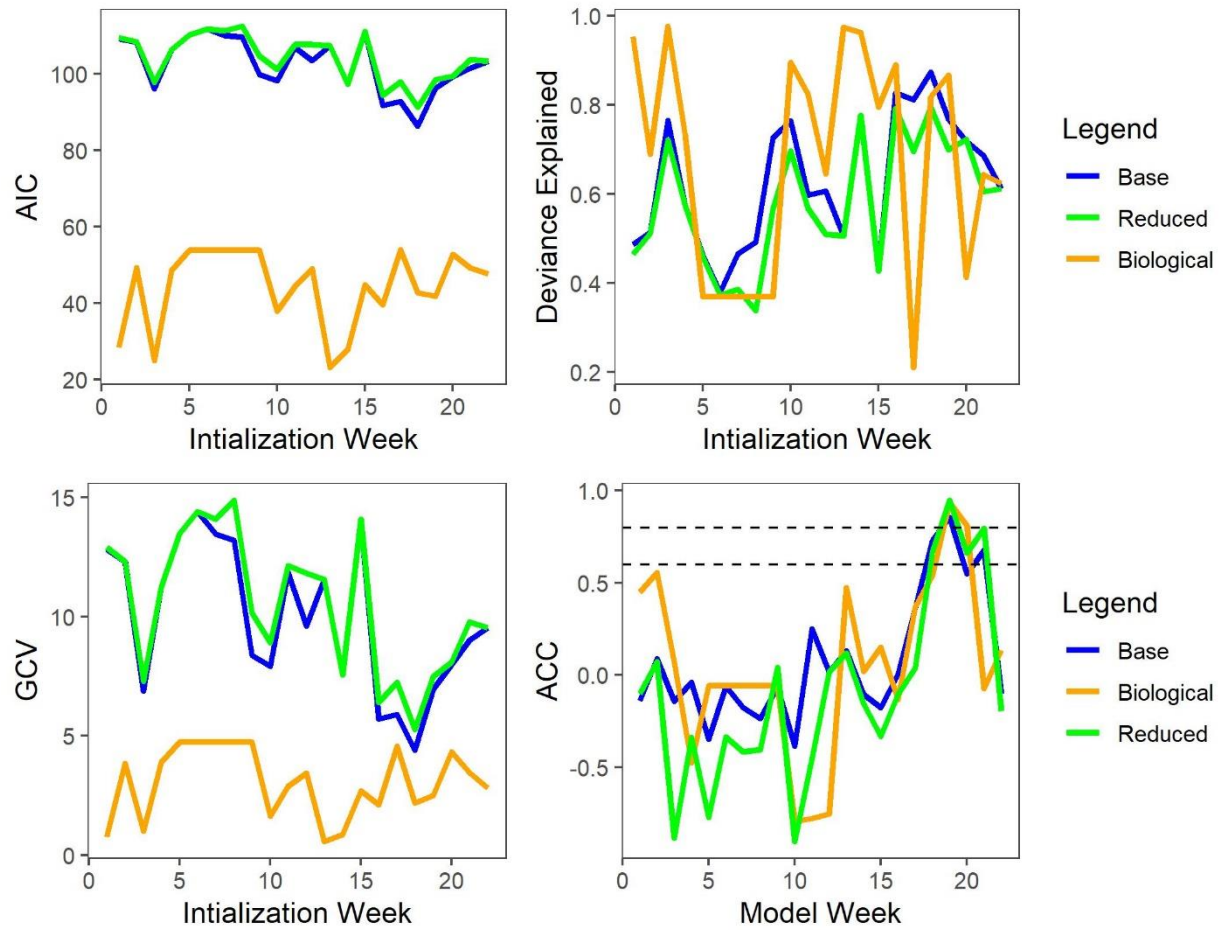
Figure 2.11. Performance metrics for biological model comparisons. The lowest dashed line in the lower, righthand subplot shows an ACC score of 0.6, which is when a forecast is considered useful. The upper dashed line shows an ACC score of 0.8, which is when forecast skill is considered highly accurate.

Chapter 3. Determination of the optimal sampling frequency for investigating phenological change for anadromous fish spawning

3.1 Introduction:

The seasonality of many marine species is changing due to climate change (Ji et al. 2010; Mackas et al. 2012; Asch et al. 2015). Shifting phenology is often an early indication of climate change impacting species and ecosystems (Mackas et al. 2012; Asch et al. 2015, Kharouba et al. 2018). However, it is difficult for ecologists to document these changes since it is more costly to conduct high-frequency surveys in marine and aquatic environments that require ship time compared to equivalent terrestrial sampling (McClatchie et al. 2014; Staudinger et al. 2019). As many marine species surveyed are mobile, they may have varying levels of site fidelity making it difficult to decouple phenology changes from distribution changes and migration patterns (Staudinger et al. 2019).

Richardson and Poloczanska (2008) highlight that terrestrial ecosystems have had far more research assessing the impacts of climate change compared to marine ecosystems even though marine species appear to be far more vulnerable to changing conditions by some measures. Marine species are expanding at their leading range edge an order of magnitude faster than expansions in terrestrial species (Poloczanka et al. 2013). Many marine taxa, such as phytoplankton, and more generally summer and spring spawning taxa, have shifted toward earlier phenology at faster rates than in terrestrial environments (Poloczanka et al. 2013). Terrestrial ecosystems are often more easily sampled, have better funded resources, and have better representation of scientists in international efforts, such as the IPCC, than the marine environment (Richard & Poloczanska 2008; Genner et al. 2010). Many marine surveys tend to be

nearshore surveys, mostly in the northern hemisphere, that sample a limited range of taxa (Ji et al. 2010; Mackas et al. 2012; Poloczanka et al. 2013).

Monitoring phenology change can be difficult when there are large temporal gaps between observations and available data are patchy (Mackas et al. 2012; Staudinger et al. 2019). Frequent sampling in marine environments of zooplankton and ichthyoplankton often is on the scale of weekly to monthly, with at least biweekly sampling being enough to capture interannual variability (Ji et al. 2010; Genner et al. 2010; Mackas et al. 2012). Surveys at this temporal scale have high temporal resolution but are often limited in spatial scope (Genner et al. 2010; Mackas et al. 2012). River-based sampling of anadromous species is often more frequent on a daily to weekly scale (Anderson & Beer 2009; Peer & Miller 2014; Lombardo et al. 2019). Many marine surveys cover broader spatial areas with reduced temporal resolution at the monthly to seasonal scale (Mackas et al. 2012; McClatchie et al. 2014). Timing of peak abundance is often of prime interest in survey design; however, this metric can be sensitive to data patchiness and most accurate when using spatial averages of multiple samples (Mackas et al. 2012). Differences in phenology can exist within a species range with greater shifts in phenology observed in leading range edges vs. trailing edges, making adequate spatial coverage an important methodology factor to separate differences within a population (Poloczanka et al. 2013). Surveys with approximately monthly sampling may be able to solely report monthly to seasonal scale information on phenology, but not fine-scale (weekly) variations and changes (Mackas et al. 2012; McClatchie et al. 2014). Much of the effectiveness at different frequencies is, however, based on data from mid-to-high latitudes. Warmer water taxa grow faster and likely need more frequent sampling to achieve similar levels of precision (Mackas et al. 2012; Poloczanka et al. 2013). As sampling frequency increases, it allows for more complex analysis techniques to be

used, which can provide more precise information and additional metrics. This can be especially important for surveys with irregular spacing between samples or for species that exhibit more than one distinct peak in abundance, such as Chinook Salmon in the Columbia River, USA, which have three distinct migrations upriver by three distinct stocks (Anderson & Beer 2009; Mackas et al. 2012).

Monitoring ecological change could be made more efficient by investigating the trade-offs between reduced sampling frequency and changes in the accuracy of phenological data. Zooplankton commonly have interannual variability in phenological metrics of one to two months and peak abundance duration of one to two months (Ji et al. 2010; Mackas et al. 2012; Staudinger et al. 2019). While early work on fish phenology assumed that most species had very little interannual variation in reproductive phenology (Cushing 1974), more recent research demonstrates that many fish species exhibit a similar amount of phenological interannual variability and similar long-term trends in phenology to those of zooplankton (Asch 2019). For example, Gulf of Alaska walleye pollock show similar spawning season length and variability (Rogers et al. 2018).

To determine the optimal sampling frequency for documenting changes in fish phenology, historical Striped Bass (*Morone saxatilis*) egg survey data were used to assess the effectiveness of reduced egg survey sampling. This egg survey is ideal to study this issue since this time series surveyed Striped Bass eggs multiple times a day surpassing the sampling frequency of many other river-based surveys and far more than most marine surveys. North Carolina is home to the Albemarle Sound/Roanoke River (A/R) stock of Striped Bass, which is the southernmost spawning population of anadromous Striped Bass on the east coast of the US. The A/R stock is a specific management unit to describe the Striped Bass population that spawns

primarily in Weldon, NC in the lower Roanoke River below the Roanoke River Dam (Callihan et al. 2014, 2015). Spawning onset is associated with temperatures rising above 18º C in the Roanoke River (Hassler et al. 1981; Rulifson 1993). Egg survey data used in this study show that spawning seasons typically last ten days but can range from four to twenty-one days in length (See Chapter 2). The start of the spawning season begins as early as May 2nd and the spawning season has ended as late as May 31st, with an average beginning date of May 7th ($\pm$ 5.3 S.D. days). The goal of this analysis is to show how different reduced sampling schedules of Striped Bass eggs may affect the ability to detect phenology metrics. In turn, this can reveal how different survey designs may affect our ability to assess phenological changes in fish species that may not have been sampled as intensively as the A/R Striped Bass population.

3.2 Methods:

A historical survey spanning from 1960-1993 collected Striped Bass eggs along the Roanoke River in North Carolina with sub-daily temporal resolution (Hassler et al. 1981; Rulifson et al. 1993). This survey created a rich long-term dataset that was able to effectively capture the timing of the Striped Bass spawning in that period. Striped Bass eggs hatch within 48 hours of fertilization making them effective indicators of spawning activity (Hassler et al. 1981). Prior to initial work on this project, these surveys had not been converted to spreadsheet format and some have never been digitized. The initial phase of data processing included digitizing all relevant data sources from the historical surveys using Able2Extract conversion software (investintech.com/prod_a2e.htm#convert).

The survey collected Striped Bass eggs from late April through mid-June below the Striped Bass spawning ground in Halifax, NC. During the period of 1960-1987 when the surveys conducted by William Hassler from North Carolina State University, scientists generally did not

begin their full sampling effort until after April 29, with only the occasional once a day sample taken before late April to assess the presence of any Striped Bass eggs. As a result, some years started sampling too late to produce an accurate spawning beginning metric. Years in which the start of spawning (as defined below) occurred in the first week of sampling were excluded from analyses since the survey may not have sampled the true beginning of the spawning run. There should be multiple days with zero catch early in an annual dataset to indicate that spawning had not yet begun (Staudinger et al. 2019). In these years when the survey began late relative to spawning, a substantial portion of the eggs were observed before the occurrence of days with zero catches. Years removed from my analysis due to this issue were 1967, 1972, 1974, 1975, 1979, 1985, and 1986.

The egg surveys used a 10-inch diameter, 6:1 mouth-to-tail ratio bongo net with a 500-µm mesh. The nets used solid sample cups and a low-speed flow meter to calculate water filtered. Through 1987, eggs were sampled with 5-minute surface tows every three hours (Hassler et al. 1981; Rulifson 1993). In the years 1988-1993, the egg survey was conducted by Dr. Roger Rulifson from East Carolina University with a key difference being the sampling always started on April 15th and ended on June 15th (Rulifson et al. 1993). Between 1988-1993 sampling intervals changed from every three hours to every four hours (Rulifson et al. 1993). Relative to other fish species, Striped Bass eggs are large, with an average diameter of 3.4 mm (Hassler et al. 1981). American Shad (*Alosa sapidissima*) eggs are the only other similar sized egg occurring in the Roanoke River, but they lack a distinctive oil globule that Striped Bass have (Hassler et al. 1981).

Standardized daily estimated egg abundance was used to account for the constantly changing cross-sectional area of the river. Counts of eggs per volume of water sampled were

multiplied by cross sectional area at the sampling site to standardize egg counts. Using standardized data from these egg production surveys, this analysis used three indicators of Striped Bass spawning phenology: start of season (15th cumulative percentile of egg concentration each year), season midpoint (50th percentile), and season end (85th percentile). These cumulative percentiles are well-established indicators of interannual phenological variability and have been used to study phenology of marine organisms across many ecosystems (Greve et al. 2005; Chiba et al. 2012; Mackas et al. 2012). Research on Striped Bass in Chesapeake Bay established that these metrics are useful for assessing interannual phenological variability in this species (Peer & Miller 2014). Many years of the egg surveys exhibit a distinct and large burst of egg abundance with sometimes a few small peaks in egg abundance following later (Rulifson 1993). Consequently, a peak spawning metric was included that represents the highest daily standardized abundance of eggs estimated in a single day to assess interannual variation in this important feature of the Striped Bass spawning run.

To test how sampling frequency may affect estimation of these phenological metrics, reduced sampling schedules were generated (Figure 3.1). Multiple sampling schedules were created based on the number of days per week that sampling would occur. Sampling frequency schedules between one day a week to five days per week were considered. Given the condensed nature of the Striped Bass spawning season, sampling frequencies less than once a week were not considered. Reduced sampling schedules assumed approximately even spacing between sampling days. All combinations of possible evenly spaced sampling schedules were extracted (Figure 3.1, panel A). The phenology metrics were then recalculated individually for all possible iterations (Figure 3.1, panel B). All the phenology metrics for each iteration were then averaged to create a mean for each year and each sampling schedule frequency (Figure 3.1, panel C). To

assess the accuracy of sampling at different frequencies, anomalies of phenology metric were calculated by subtracting the observed phenological metrics (i.e., those from the full sampling schedule of seven days a week) from the mean values from the reduced sampling schedules.

3.3 Results:

Across metrics, the four and five days per week sampling schedules had smaller anomalies than the less frequent sampling schedules (Figures 3.2, 3.3). Increasing sampling effort reduces error in phenology metrics with the five days per week schedule having the lowest average absolute anomaly (0.85 days) and the one day per week schedule (2.09 days) having the highest (Table 3.1). The midpoint (±1.5 days S. D.) and end (±1.4 days S. D.) metrics have lower standard deviations across years and sampling schedules than the beginning (±2.6 days S. D.) and peak (±2.4 days S. D.) metrics and showed smaller anomalies from observed phenology within each sampling schedule (Table 3.1; Figure 3.3). The peak metric anomalies were greater and more variable than the other phenology metrics indicating that sampling for a single, short-lived spawning peak may be more difficult to detect accurately than broader patterns that reflect cumulative measurements throughout the whole spawning period (Table 3.1; Figure 3.3). The beginning metric had the top five largest anomalies across all metrics and schedules (Figure 3.2). Most of these particularly large anomalies occurred in 1983. The 1983 spawning season length was slightly longer than average and didn't exhibit comparatively large peaks in single day egg abundance.

3.4 Discussion:

Monitoring phenology at lower temporal resolutions can still lead to highly accurate results (Figure 3.3). Striped Bass spawning occurs in a discrete area of the Roanoke River with an average spawning season length of ten days. The small sampling errors and standard deviations are particularly encouraging given that Striped Bass spawning events on the Roanoke River are short and condensed. Even greatly reduced sampling schedules of two days a week showed very similar modes of variability of egg abundance compared to the full sampling effort. All sampling schedules had similar patterns in interannual variability with the overall size of the anomalies being the primary difference between schedules. This is notable as interannual variability in Striped Bass of the A/R stock can be as much as six weeks (Callihan et al. 2014). Anomalies from the reduced sampling schedule were never biased toward occurring early or late timing, since two standard deviations of the mean always contained zero (Table 3.1). Researchers looking to assess spawning phenology of marine species, especially anadromous species with similar ecology to Striped Bass, might accurately assess spawning timing with a sampling frequency on a less than daily scale. Hassler et al. (1981) concluded that egg abundances did not significantly vary with time of day. This trend may not persist with the phenology of all species and may need to be assessed when developing a survey designed to monitor spawning or migration phenology. Other marine plankton surveys sampling species with a much longer season length should also consider the role of sampling frequency in analysis; however, the levels of precision described here is for a species whose spawning season length is 1-2 weeks rather than 1-2 months seen in other species (Mackas et al. 2012). Researchers weighing sampling design decisions for taxa with a short spawning season, can use this analysis to consider tradeoffs between sampling frequency and accuracy of phenological data. A similar analysis should be conducted with an available data from a marine plankton survey that has a

high sampling frequency (~1-2 weeks) to assess if these results hold true for other taxa that are

typically sampled on a monthly-to-seasonal basis.

Table 3.3. Summary of absolute value of anomalies from the reduced sampling schedules compared to the observed phenology

Metric	Sampling Schedule	Average Anomalies (days)	Standard Deviation (days)
Beginning	1 Day/Week	2.3	3.0
Beginning	2 Days/Week	1.9	3.0
Beginning	3 Days/Week	1.4	2.6
Beginning	4 Days/Week	1.2	2.3
Beginning	5 Days/Week	1.0	2.2
Midpoint	1 Day/Week	1.7	1.9
Midpoint	2 Days/Week	1.5	1.7
Midpoint	3 Days/Week	1.2	1.6
Midpoint	4 Days/Week	0.9	1.2
Midpoint	5 Days/Week	0.6	0.8
Peak	1 Day/Week	2.5	2.9
Peak	2 Days/Week	2.5	2.8
Peak	3 Days/Week	2.1	2.5
Peak	4 Days/Week	1.7	2.0
Peak	5 Days/Week	1.3	1.6
End	1 Day/Week	1.8	2.2
End	2 Days/Week	1.2	1.7
End	3 Days/Week	0.8	1.1
End	4 Days/Week	0.6	0.8
End	5 Days/Week	0.4	0.5

Figure 3.1. Methodology used to create reduced sampling schedules from which estimated phenology metrics would be calculated. This process was repeated for sampling frequencies or 1-5 days/week. From left to right, the green boxes will be referred to as panels A, B, and C.
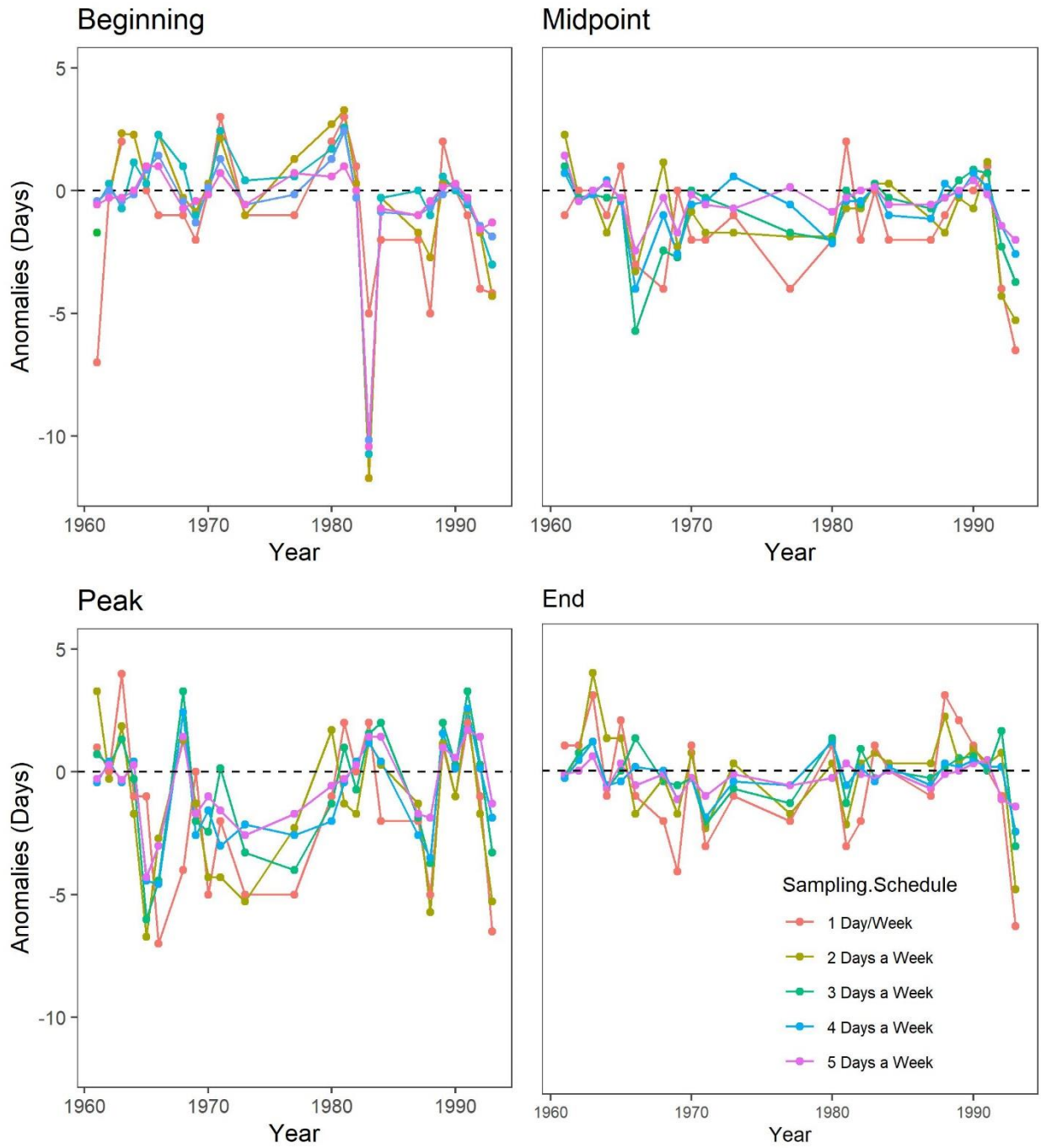
Figure 3.2. The difference in the day of the year of observed phenology metrics and metrics calculated from several reduced sampling schedules.
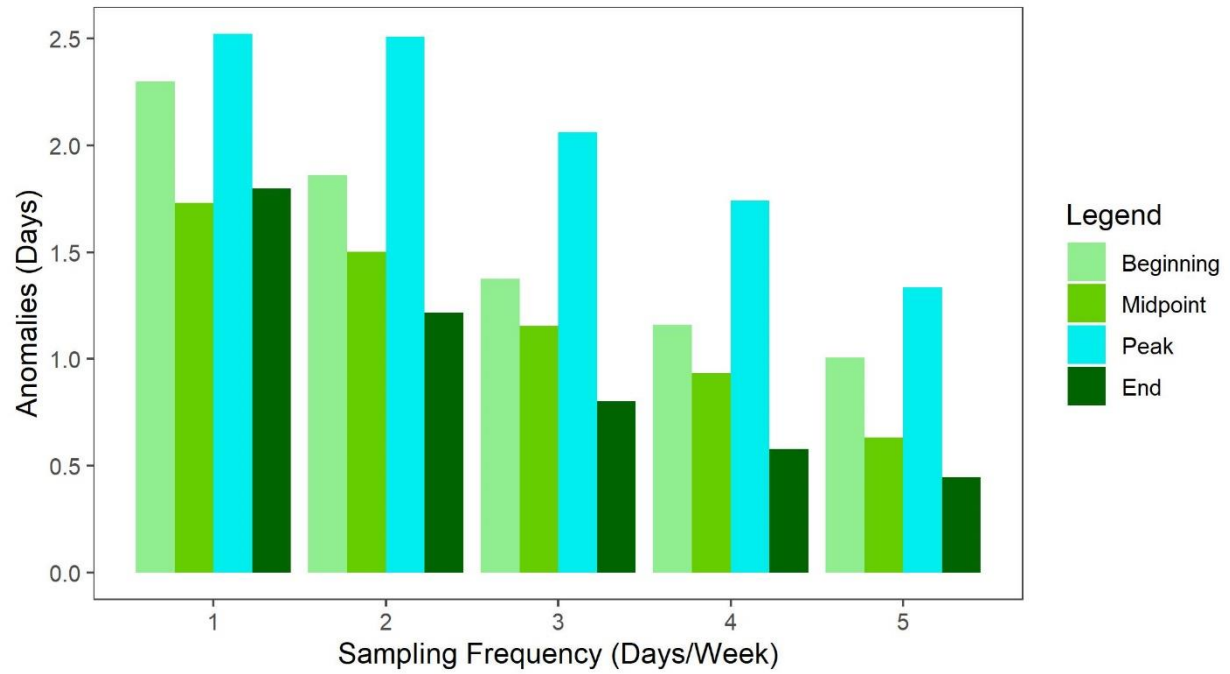
Figure 3.3. Average of absolute value of anomalies across phenology metrics and sampling frequencies.

Chapter 4. Management Applications and Future Directions

4.1 Conclusions and Management Implications:

Historical creel and egg surveys measure different aspects of Striped Bass phenology among the A/R stock. The spawning phenology metrics showed greater predictive skill and model fit than the migration phenology end metric. This indicates that models based on data from fisheries-independent surveys are more adept at forecasting A/R stock spawning phenology. A formal egg survey on the Roanoke River has not taken place since 1993. A renewal of this egg survey could be an important step towards identifying changes in A/R stock spawning phenology and forecasting future phenology. This is especially important as changes in the management of the Kerr Dam release protocol may be impacting spawning and migration phenology given the important role that discharge plays in cuing migrating and spawning phenology. Results from the sampling frequency analysis indicate that egg surveys with greatly reduced effort could still accurately capture many aspects of spawning phenology.

The end of migratory phenology indicates a trend toward earlier average phenology with a significant regression relationship (Figure 2.4). This shift could make current management measures that open and close the fishing season in need of adjustment to be more in line with the changes in observed phenology. Additional efforts to forecast Striped Bass phenology more accurately could help aid stock recovery from its status as overfished and experiencing overfishing through protecting the spawning stock biomass. With estimated river and ocean temperatures rising, climate change could continue to push the migration phenology earlier (Poloczanka et al. 2013). In its current form the weekly forecast cannot produce skillful predictions with weekly or monthly lead times. However, a nowcast, or forecast with a very short lead time (1-2 weeks) may be possible given the high ACC scores for all spawning metrics

starting in late April (Figure 2.10). Some of the first forecasts of living marine resources were nowcasts and can be effective management tools in the right fishery (Payne et al. 2017).

For ecological forecasts to be effectively utilized, the lead times at which key management or business decisions need to line up with lead times of a skillful forecast (Hobday et al. 2016). This forecast is highly useful for a variety of stakeholders who could be further involved in a formalized survey to establish the lead times involved in decision making. Decisions of interest in the fishery could be when managers need to close the RRMA portion of the fishery, when commercial fishermen deploy their boats, or when recreational fishermen plan fishing trips. The ASMA commercial fishery is currently a bycatch fishery meaning Striped Bass has to be less than 50% of landings by weight. Improved forecasts could help commercial ASMA fisherman by making them more aware of Striped Bass movements so they can prevent overfishing. A survey or a series of interviews with key informants could give a concrete picture of how this project is perceived by stakeholders and help secure future funds to develop an operation nowcast. A social science survey to understand decision lead times would target stakeholders, such as managers in the fishery, commercial fishermen, recreational anglers, water resource managers, and for-hire captains. The survey would be aimed at gaging general interest in using an ecological forecast for the Striped Bass migration. Short interviews of a few key individuals could also be useful in gathering information on stakeholder responses to the project. There may be points when knowing about the upcoming migration season is either too far in advance or too close to the migration to be actionable. Involving various stakeholders could not only help aid in developing an operational forecast, but also increase the communities use of its efforts (Hobday et al. 2016).

4.2 Future Modeling Directions:

Due to differences in the travel distance needed to return to their spawning grounds, migratory phenology is likely to differ among different size classes of A/R Striped Bass, with some indication that larger females arrive later at the spawning grounds in the A/R stock (Callihan et al. 2015). These differences could have a strong effect on migration time given the lack of unbiased length data (Table 2.1) and the limited number of large females at the time of the Hassler and Rulifson surveys, it cannot be included in a wholistic modeling approach. Ideally, data for improved forecast development would include the proportion of fish in these size classes: < 600 mm TL, 600-900 mm TL, and >900 mm TL. These size classes coincide with those identified in Callihan et al. (2015). Percentages of individuals in each size class could be an important predictor of spawning phenology in future models that better consider their overwintering ground differences. Future GAM modeling approaches could also be adapted by using a threshold GAM that changes based on the percentages of fish over a specific length threshold. For example, most fish under 600 mm TL will not enter ocean water and will likely not be affected by any ocean conditions that may affect larger individuals. Better sources of A/R stock characteristics should be sought out given their likely importance in improving predictive skill.

A/R Striped Bass is a very well-studied stock with a variety of different surveys currently conducted that may be used to assess phenology or aid in future research. Some of these datasets could be potentially leveraged in the future to expand on the research presented herein. There two primary surveys that collect information on juvenile Striped Bass in the Albemarle Sound. A weekly beach seine is conducted weekly from June to mid-July and a biweekly trawl survey has been implemented since 1955 with sampling occurring from July to October (Lee et al. 2020).

North Carolina implements a creel survey in the ASMA during the harvest period for Striped Bass with a similar sampling design to the RRMA creel survey (Lee et al. 2020). A gill net survey from 1990 to present has been sampling in the fall and winter (November to February) and the spring (March through May) where effort is concentrated in the western ASMA to target Striped Bass (Lee et al. 2020). Sampling occurs seven days a week with sampling locations selected randomly (Lee et al. 2020). A weekly electroshocking survey started in 1990 in the upper Roanoke River near the Striped Bass spawning grounds during the spring and continues through the present (Lee et al. 2020). These additional biological datasets may provide additional information on multiple A/R stock characteristics, including phenology, which could be used in future research. However, these surveys were not used in the current analysis as they either lack proximity to the spawning grounds, do not sample the appropriate life stage, lack high sampling frequency, or have reduced years of available data.

Current forecast results indicate that river and ocean temperatures were not important for forecasting A/R Striped Bass phenology. Specific temperature thresholds that relate to physiological tolerances or spawning preferences may be more important to Striped Bass than the temperature anomalies that were used for this study. To assess the impact of using temperature thresholds in the forecast, two different types of thresholds were calculated. The day of the year (DOY) when ocean temperatures exceed 9º C was used to assess when Striped Bass begin entering the Roanoke River (Callihan et al. 2014). The DOY when river temperatures reach 18º C was recorded to assess when Striped Bass would initiate spawning (Hassler et al. 1981; Rulifson 1993). The DOY when a temperature threshold crossed and remained over that threshold was recorded rather than the first time that threshold was crossed. An approach similar to the biological model comparison was used to assess the impacts of using temperature

thresholds on forecast predictive skill. A fully parameterized base model from the weekly

forecasts was compared to a similar version of the weekly forecast with a variable of the DOY

when the temperature thresholds were crossed each year. The ocean model (Equation 2 in

Chapter 2) used the 9º C threshold DOY and the river model (Equation 3 in Chapter 2) used the

18º C threshold DOY. Versions of the reduced and biological models from the biological model

comparison were generated using the temperature thresholds rather than anomalies. The fully

parameterized threshold model had two weeks of 'good' forecasts (e.g., ACC > 0.60) in mid-

March (Appendix Figure 10). The reduced threshold model also produced two 'good' forecasts

in January and February. The biological model using temperature thresholds showed little

difference from the base model using anomalies. These results indicate that using the timing of

yearly temperature thresholds results in greater overall model predictive skill than using weekly

temperature anomalies. These results will continue to be investigated by applying threshold

models to other phenology metrics in future research.

In addition to oceanic and riverine temperature, estuarine temperatures in Albemarle

Sound during the pre-spawning staging period may influence migration and spawning

phenology. To the best of my knowledge, there is not a sustained time series of in situ estuarine

temperature covering the full period of egg production surveys. It is possible that river and ocean

temperatures are sufficient to model the impact of temperature on the A/R stock migration, and

estuarine temperatures may not aid predictive skill. To assess this possibility, Albemarle Sound

water temperature data from the ASWQMP from 2009-2016 at the Scuppernong River mouth

site was compared to river and ocean temperature for the same period (Appendix Figure 11).

Albemarle Sound water temperatures at the mouth of the Scuppernong River were very similar to

river and ocean temperatures used in the current modeling so would likely not add predictive skill or better model fit to forecasts.

The current modeling approach is limited by availability of data for the historical period that extends between 1960-1993 (Table 2.1). The recent rise in available ecological forecasts for living marine resources is largely brought on by recent availability of skillful nowcasts and forecasts of ocean temperature and ocean color (Hobday et al. 2019). Certain technologies and datasets that are now more standard in the development of ecological forecasts, such as satellite-based ocean data, were not available to cover the historical period (Payne et al. 2017; Fennel et al. 2019). Starting in 2007, there are multiple daily USGS water temperature loggers along the Roanoke River that could be more effective sources of river water temperature. With satellite data and greater availability of ocean water temperatures, a composite of ocean water temperatures that stretch across the entire overwintering grounds up to the Mid-Atlantic Bight or a single actual water temperature buoy could be a better source of overwintering ground ocean temperatures. Future modeling approaches could make use of newer and potentially more accurate data sources if a fisheries-independent survey for assessing Striped Bass phenology is resumed.

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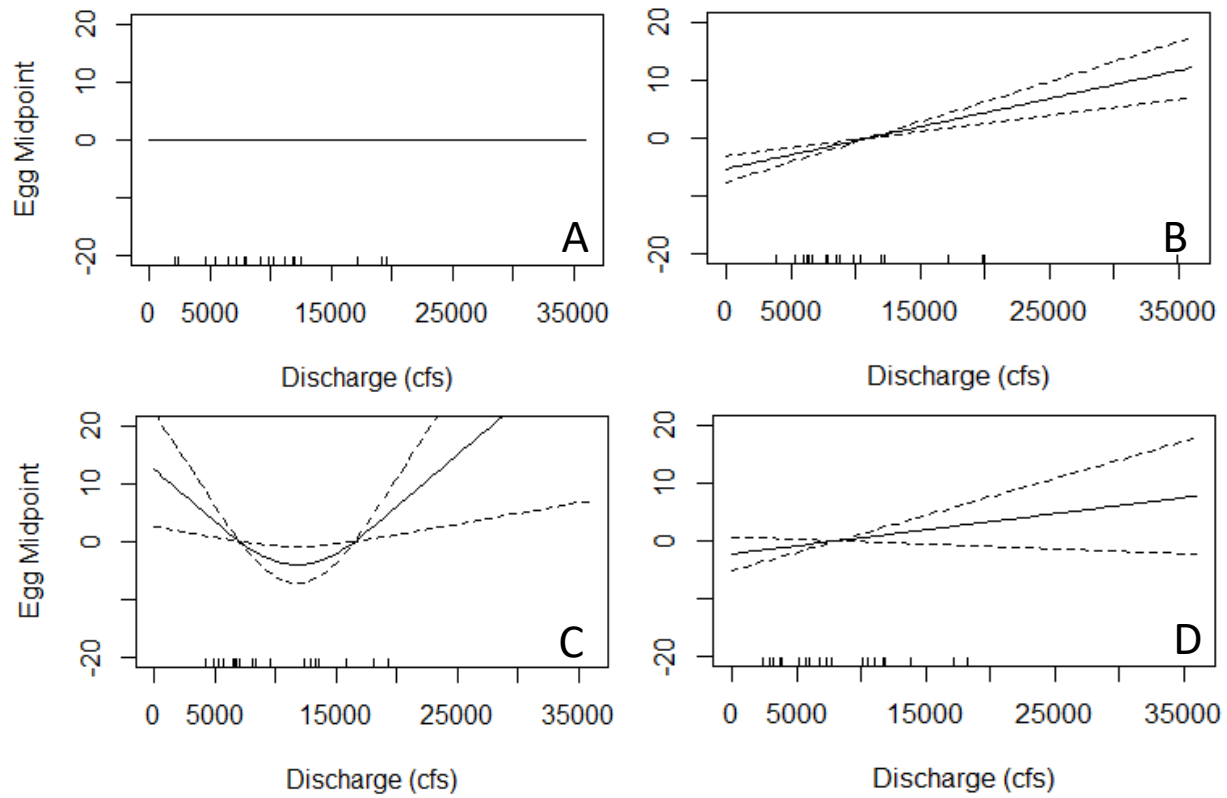
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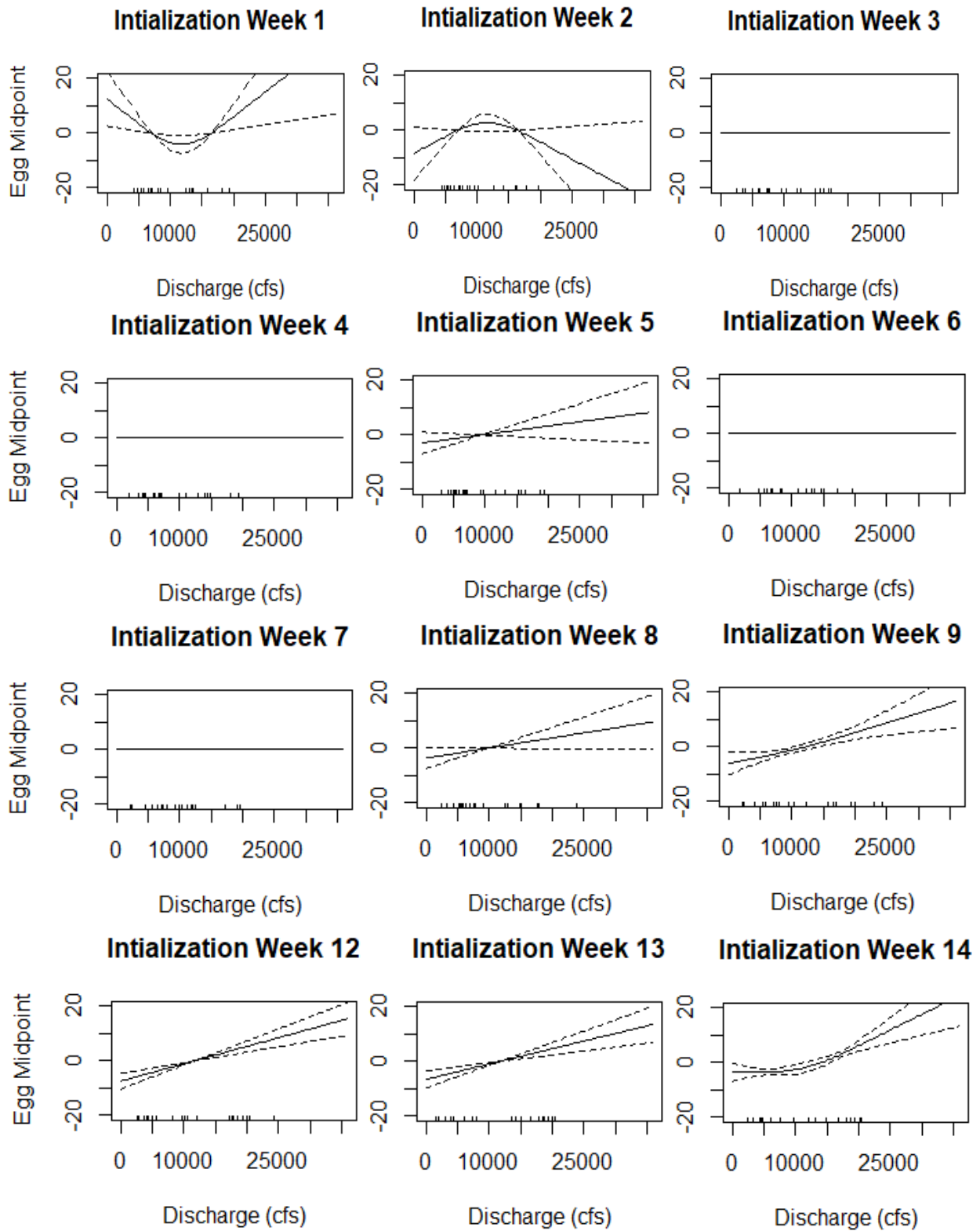
Appendix:

Appendix Table 1. DAIC scores under 10 of weekly full GAMs. Model week refers to the data from the week of the year which created the model (i.e., forecast initialization week). All models contain the full suite of variables in the primary weekly modeling approach. Models are compared across weeks and not within weeks.
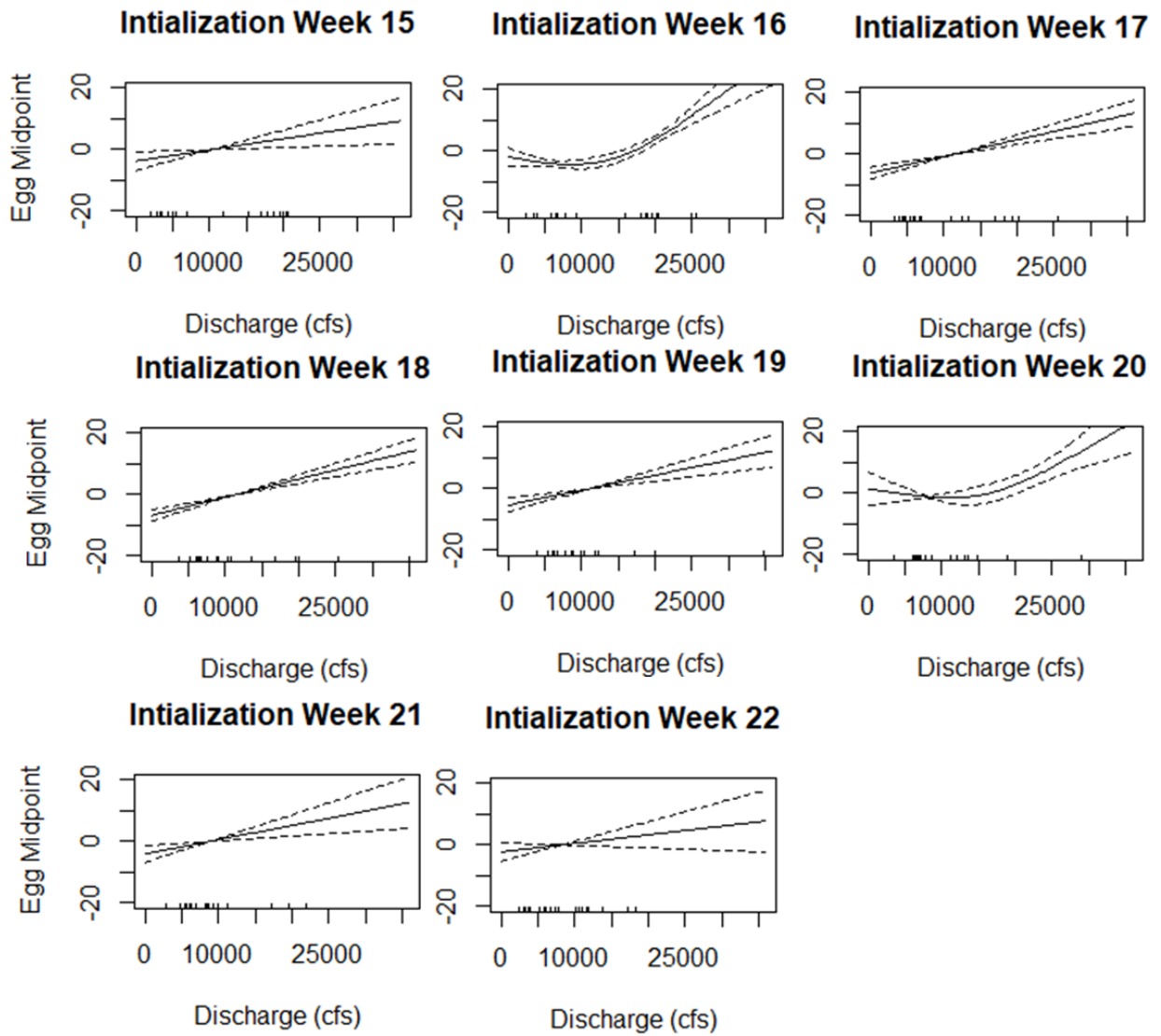
Beginning		Midpoint		Peak		End		Migration End	
Weekly Model	ΔAIC	Weekly Model	ΔAIC	Weekly Model	ΔAIC	Weekly Model	ΔAIC	Weekly Model	ΔAIC
18	0	18	0	18	0	12	0	20	0
16	5.5	16	0.9	19	2.3	2	8.5	17	2.2
17	6.4	14	7.5			17	8.5	18	2.7
3	9.8	20	7.9			16	8.6	11	2.9
						10	8.9	19	3.6
						14	9.8	10	7.3

Appendix Figure 1. Examples of GAM output plots that were classified into the following categories: A shows no response curve due to use of the double penalty approach for eliminating insignificant variables from a model, B is positive, linear, C is non-linear, and D is non-significant as its confidence intervals contain zero across the entire range, (Marra & Wood 2011). In each subplot, the solid line indicates estimates from the GAM, while the dotted lines indicate 95% confidence intervals

Appendix Figure 2. Discharge GAM output plots for the egg midpoint metric.

Intialization Week 15 — Egg Midpoint vs Discharge (cfs)

Intialization Week 16 — Egg Midpoint vs Discharge (cfs)

Intialization Week 17 — Egg Midpoint vs Discharge (cfs)

Intialization Week 18 — Egg Midpoint vs Discharge (cfs)

Intialization Week 19 — Egg Midpoint vs Discharge (cfs)

Intialization Week 20 — Egg Midpoint vs Discharge (cfs)

Intialization Week 21 — Egg Midpoint vs Discharge (cfs)

Intialization Week 22 — Egg Midpoint vs Discharge (cfs)

Appendix Figure 2 continued. Discharge GAM output plots for the egg midpoint metric.
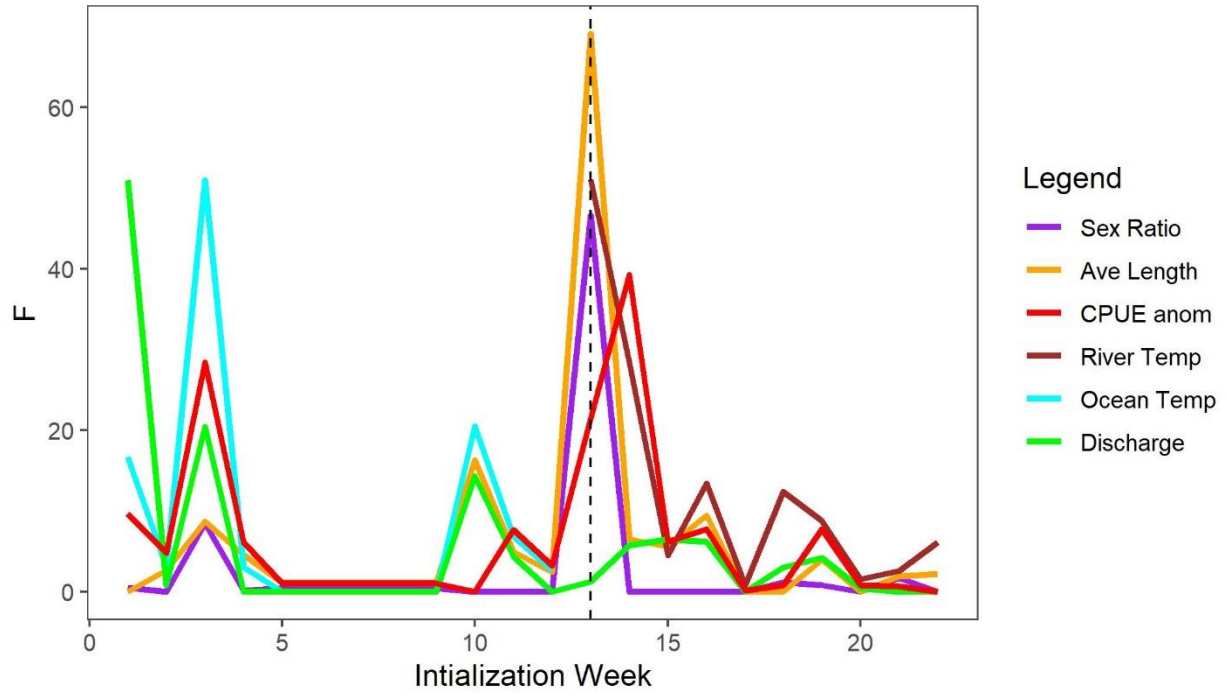
Appendix Figure 3. F scores from biological models. The black line at initialization week 13 is when the models switch from being based on ocean variables to being based on river variables
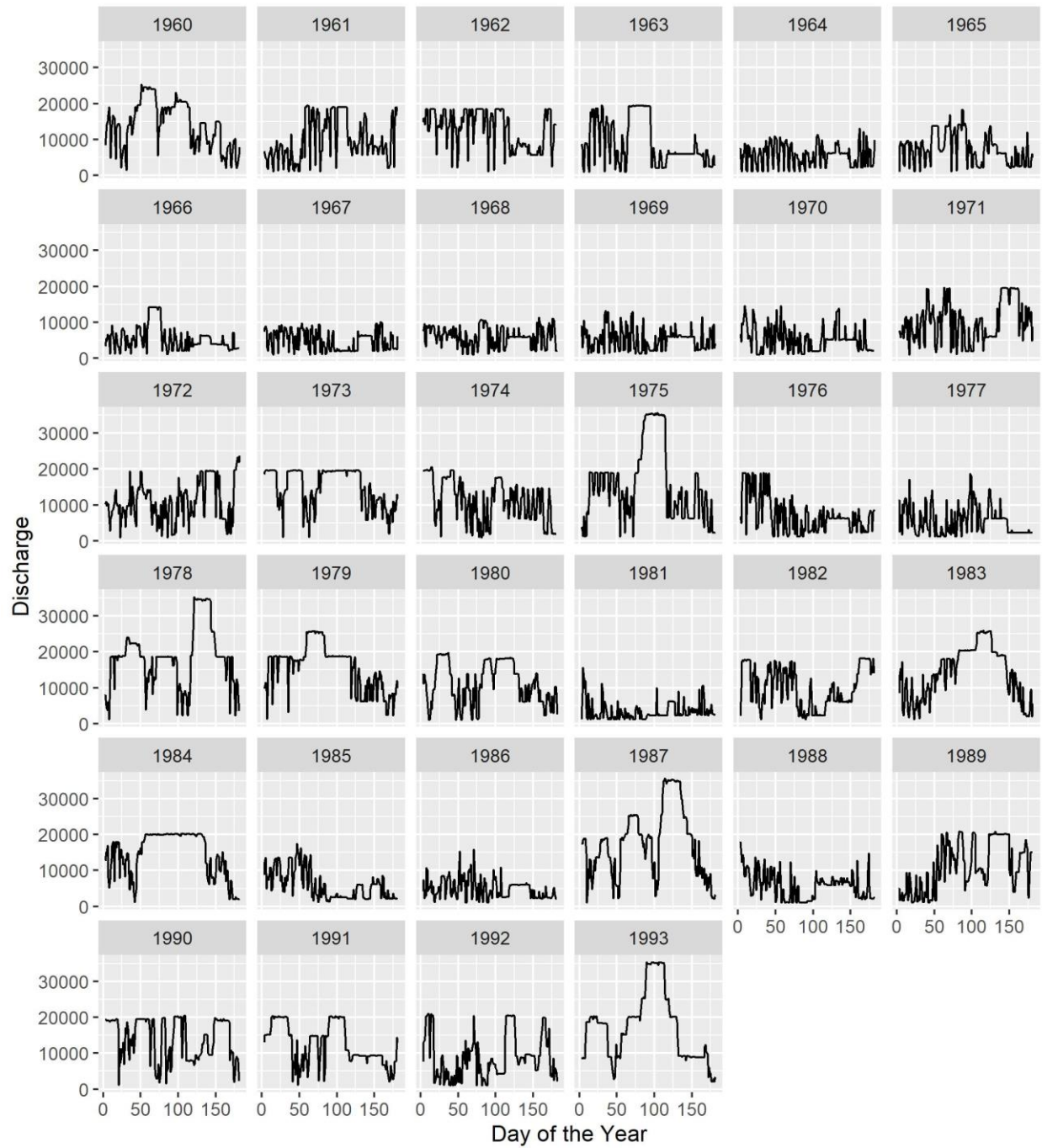
*Appendix Figure 4. Discharge (cfs) at Roanoke Rapids broken down by year*
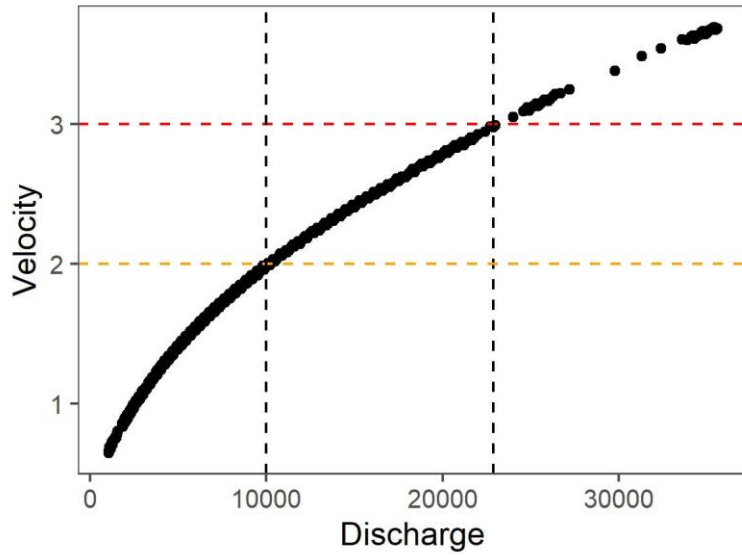
Appendix Figure 5. Comparison between discharge (cfs) and calculated velocity (ms^{-1}) of the Roanoke River and Roanoke Rapids. The intersection at 2 m s^{-1} (yellow dashed line) represents a moderate velocity barrier to Striped Bass migration, with the 3 m $^{s-1}$ intersection (red dashed line) marking a severe velocity barrier to Striped Bass.
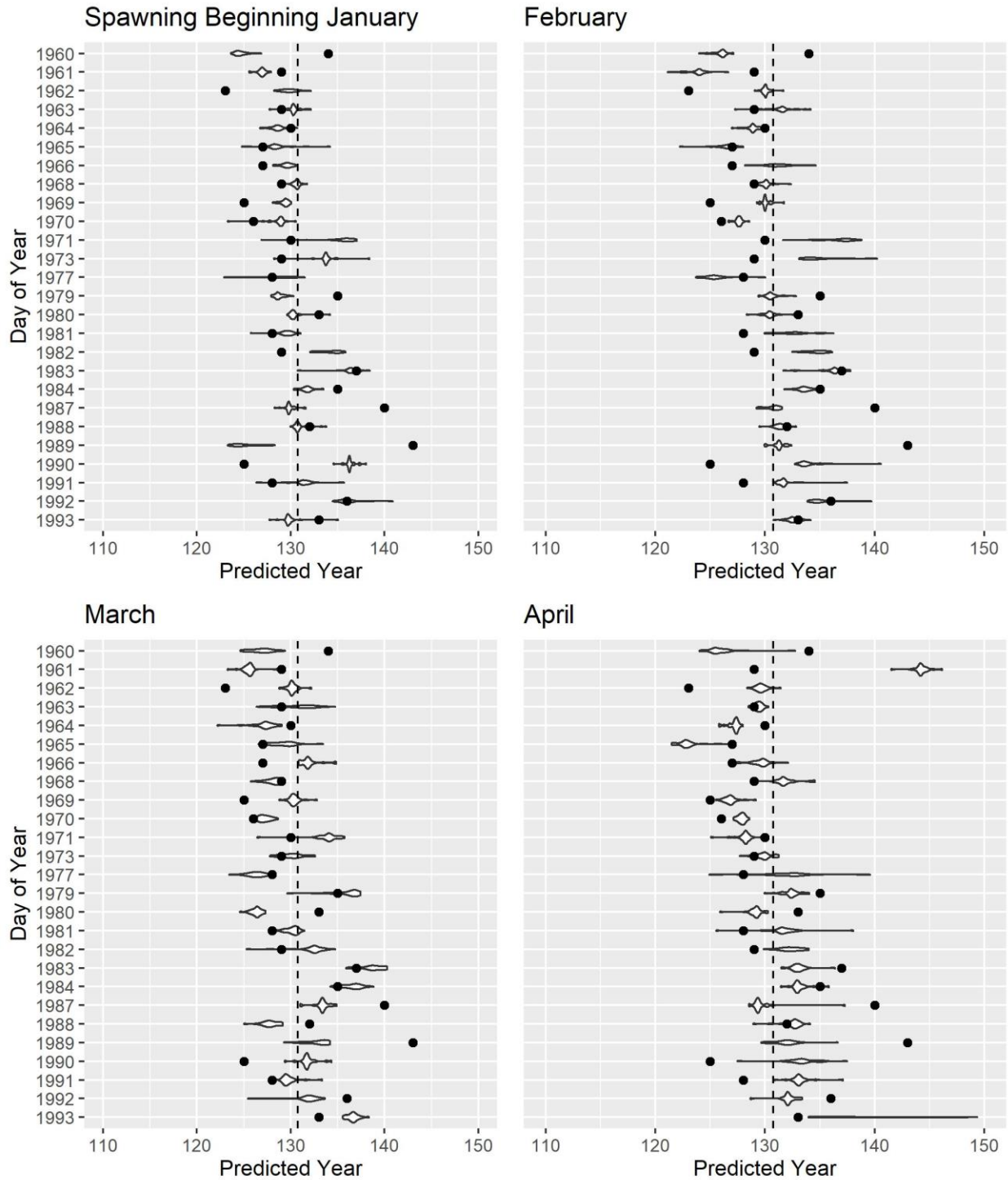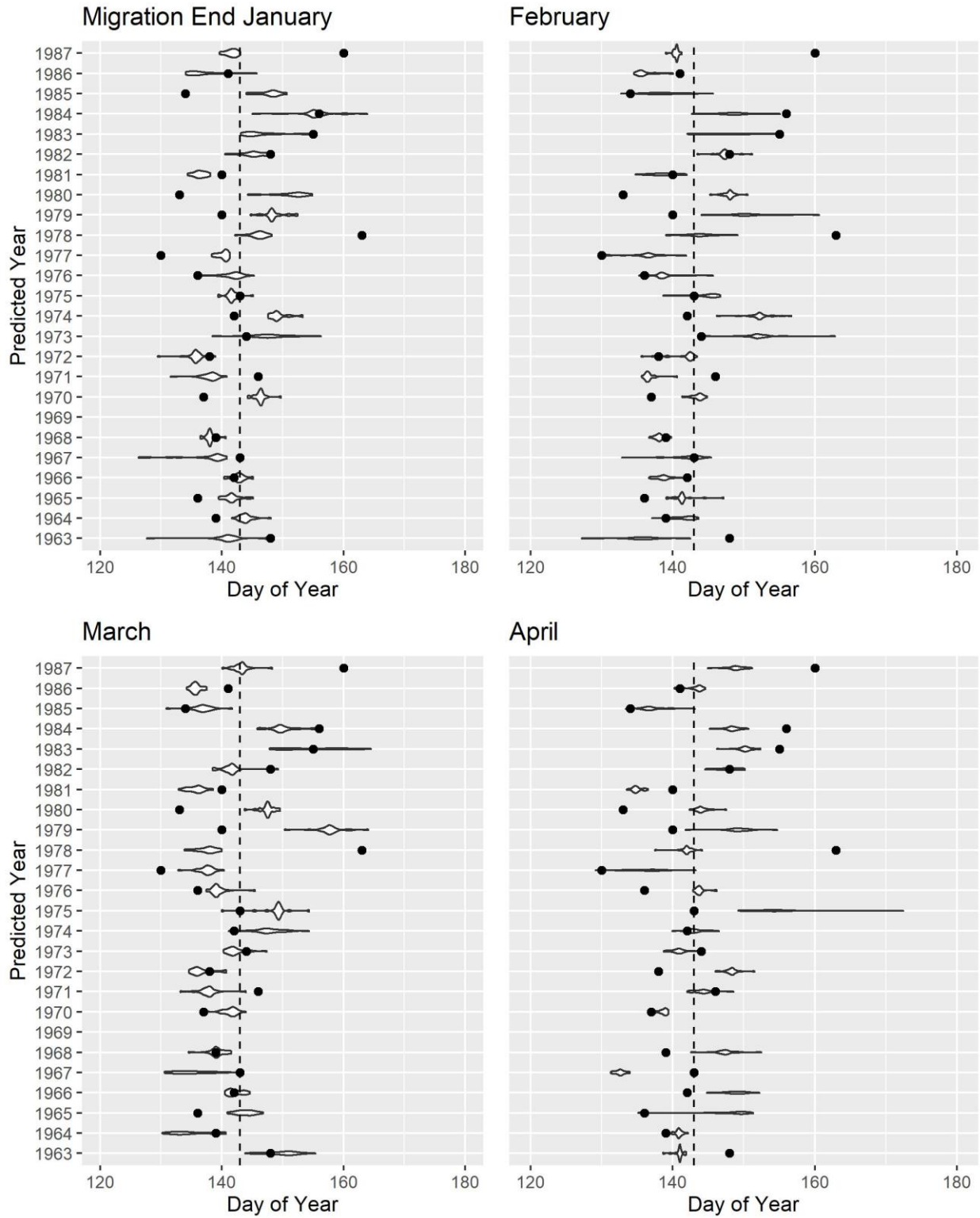
Appendix Figure 6. Distribution of predictions from the retrospective forecast for the spawning beginning metric. Dashed line is the average observed egg beginning day of the year.
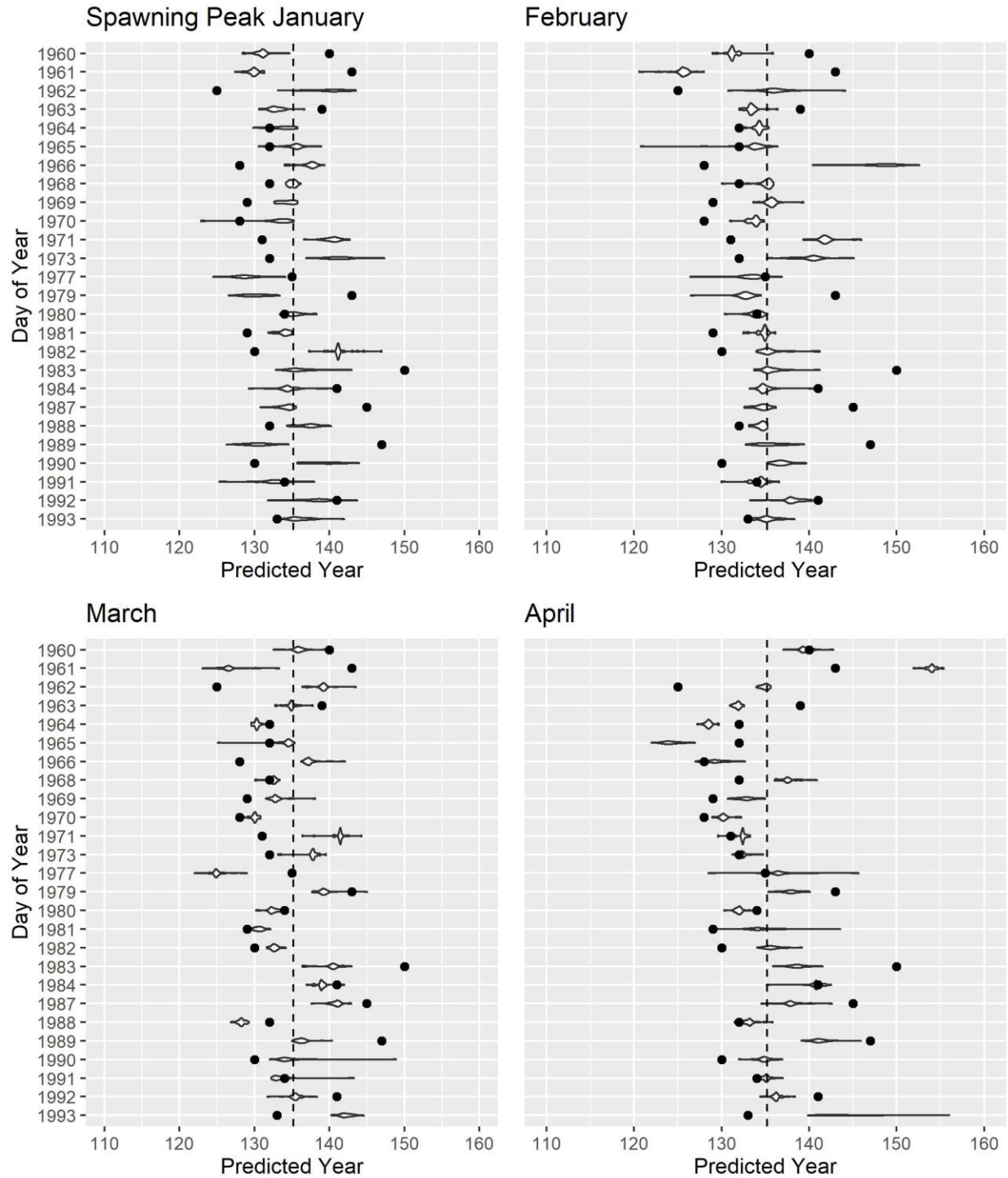
Appendix Figure 7. Distribution of predictions from the retrospective forecast for the spawning peak metric. Dashed line is the average observed egg peak day of the year
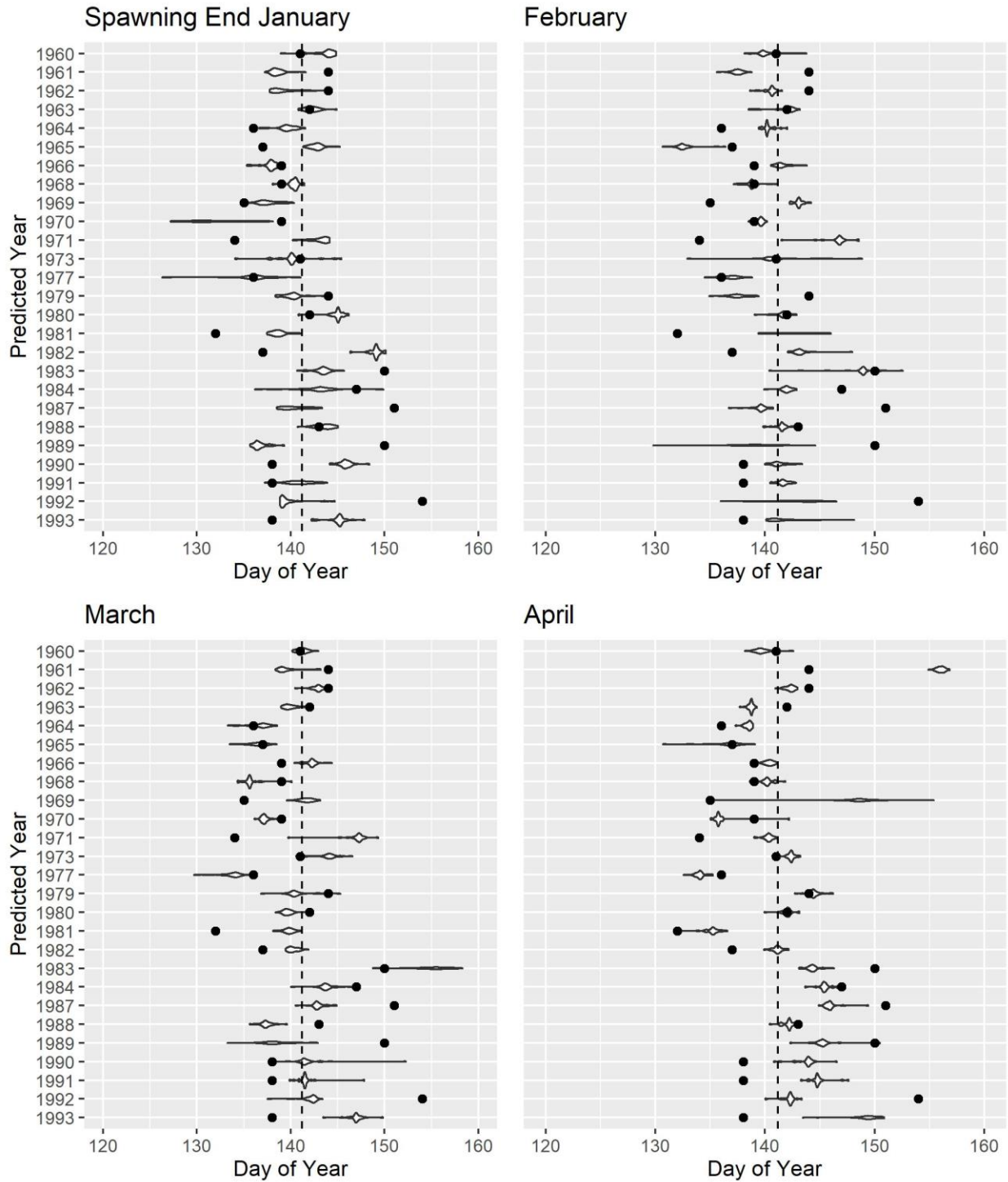
Appendix Figure 8. Distribution of predictions from the retrospective forecast for the spawning end metric. Dashed line is the average observed spawning end day of the year

Appendix Figure 9. Distribution of predictions from the retrospective forecast for the spawning migration end metric. Dashed line is the average observed migration end day of the year
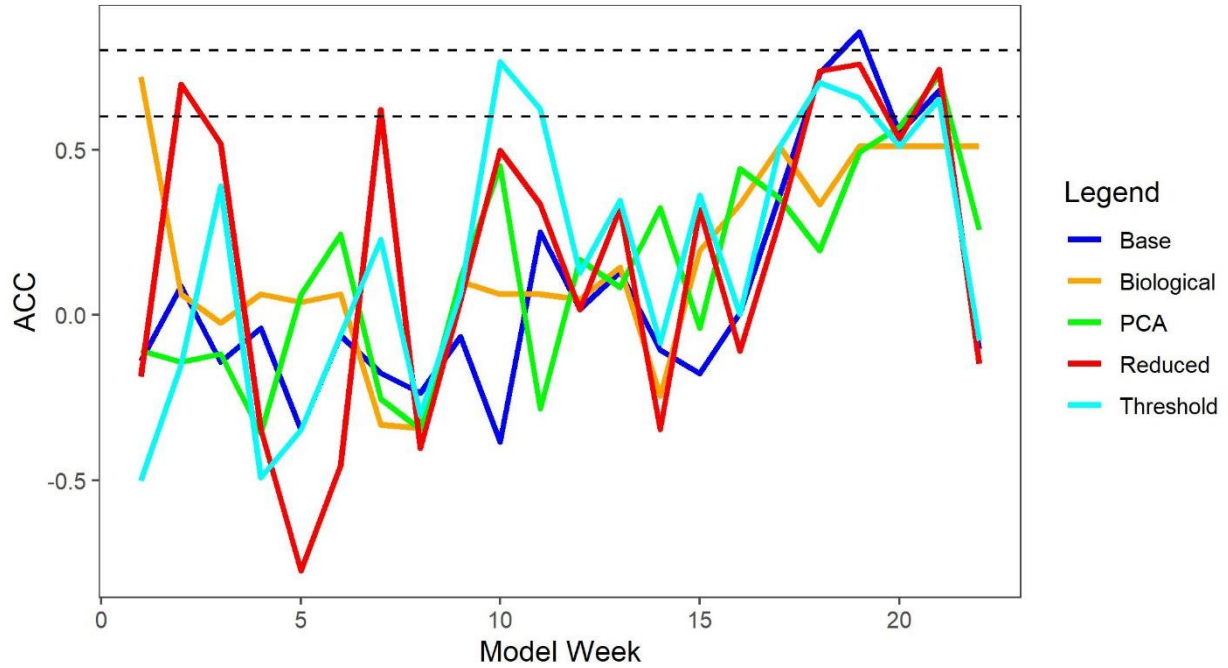
Appendix Figure 10. Anomaly correlation coefficient scores for the weekly temperature threshold-based forecast of spawning beginning. The lowest dashed line shows an ACC score of 0.6, which is when a forecast is considered useful. The upper dashed line shows an ACC score of 0.8, which is when forecast skill is considered highly accurate.
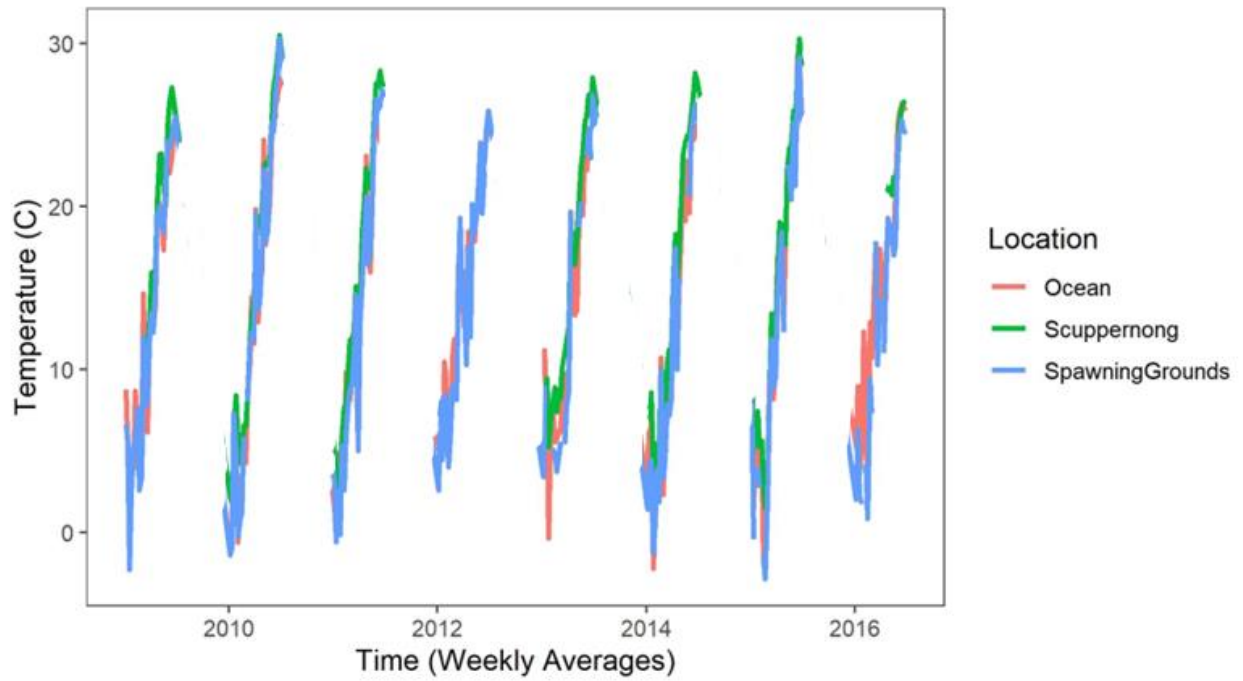
Appendix Figure 11. Weekly averages of temperatures, from Jan 1-June 30 for three primary regions used by Striped Bass. Scuppernong is water temperatures from the mouth of the Scuppernong River that flows into the Albemarle Sound