

Striped Bass (*Morone saxatilis*) Literature Review on Environmental Influences on Stock Dynamics

Introduction

Striped bass (*Morone saxatilis*) is an anadromous species native to the northeastern and central Atlantic coast of the United States and has a complex life cycle involving spawning in coastal rivers and estuaries, followed by long-range migrations to feeding and overwintering grounds. The striped bass fishery holds commercial, recreational, and ecological importance (Hartman and Margraf 2003). In Maine, striped bass fishing is a popular recreational activity, with the recreational harvest of striped bass routinely surpassing that of the commercial harvest. Historically, striped bass used to spawn in numerous rivers along coastal New England, but now rely on Chesapeake Bay and the Hudson River for the majority of spawning (Little 1995). Approximately 90% of the striped bass population spawn in the Chesapeake Bay region (Little 1995). The striped bass fishery supports numerous shore-side businesses for Maine's economy, such as boat sales and rentals, bait and tackle shops, and fishing guide businesses. Striped bass landings are dependent upon the migration timing and persistence in Maine waters, which have experienced changes associated with ocean warming (Peer and Miller 2014; Secor et al. 2020). Changes in the timing and persistence of ecologically and economically important migratory species such as striped bass can lead to implications to both the management of this species, as well as the economic value of the fishery to the state. Information on the state of the ecosystem is needed to improve our ability to make informed decisions in the face of climate change and to support a holistic, ecosystem-based fishery management approach in Maine's coastal waters.

Environmental Effects on Recruitment

Recruitment success of striped bass is affected by the circulation patterns in and around nursery grounds (North et al. 2005). Changes in circulation patterns and retention within nursery grounds may be influenced by means of wind events (North et al. 2005) or freshwater and tidal flows (Dunning et al. 2009; MacInnis 2012), where eggs and larvae are subject to redistribution post-spawning. Wind events and water flow also influence the circulation patterns of zooplankton, a food source for larvae striped bass. Thus, recruitment may also be indirectly affected by the availability of, and changes in temporal and spatial abundance of prey (Shieler and Houde 2014; Martino and Houde 2010). In Chesapeake Bay, years of high striped bass recruitment were associated with high abundance of zooplankton ($>250,000/\text{m}^3$), whereas poor recruitment years were associated with zooplankton abundance as low as $2000/\text{m}^3$ (Martino and Houde 2010).

Similar to water current and flow patterns influencing the circulation and movement of striped bass eggs and larvae, river flow pulses on the spawning ground may also affect recruitment timing (Conroy et al. 2015) and success (North et al. 2005). Jahn (2010) observed that after high (twice the average) magnitude pulses in seasonal river flow, striped bass egg abundance was generally higher. Conversely, low spring river discharge is often associated with poor recruitment of striped bass (Gross et al. 2022), and low rainfall during the spawning season is

associated with high recruitment success, as rainfall events have the ability to alter conditions such as temperature, water levels, water velocity, and salinity within a river (MacInnis 2012).

There is some evidence that toxic chemicals and contaminants in the environment may have negative effects on larval striped bass in the Chesapeake Bay stock (Goodyear 1985). Lethal effects from environmental contaminants decrease spawning potential by reducing the number of recruits. However, fishing mortality was still thought to have a greater negative effect on recruitment than environmental contaminants (Goodyear 1985).

Striped bass depend on thermal cues when initiating spawning timing. The speculated thermal cue range has varied amongst previous studies, but generally suggest optimal spawning temperatures around 12-19 °C (Setzler-Hamilton et al. 1980; Bain and Bain 1982; Secor et al. 2020), rather than a specific time of year. Rutherford and Houde (1995) suggested spawning timing occurs after a 2-3 °C increase in water temperatures within a several-day period, rather than a specific temperature range window. Regardless, warming water temperatures are typically associated with faster gonadal development (Kjesbu et al. 2010) and early spawning. In instances of a rapid temperature drop, spawning has been observed to stop (Combs 1979; Williams et al. 1984). In addition to temperature, day length is also believed to affect the gonadal maturation cycle of striped bass, where female striped bass exposed to long days (15 hours) demonstrated faster gonadal development (Clark et al. 2005). With the Striped bass recreational fishery having a fixed annual opening date (Peer and Miller 2014), temperature effects on Striped bass recruitment can be two-fold: 1) under warmer conditions, striped bass initiate migrations and spawning efforts earlier in the season and more egg-bearing females may have the opportunity to spawn prior to the fishery opening, or 2) under colder temperature conditions, spawning timing is delayed and more-egg bearing females are subject to the fishery before they are able to spawn (Peer and Miller 2014). Thus, warming waters may not only have a positive effect on striped bass recruitment, but may also affect distribution with potential increases in suitable thermal habitat (Kliesner et al. 2017).

Environmental Effects in Distribution

Juvenile striped bass <20cm have been observed leaving natal estuaries for non-natal estuaries and residing in those non-natal estuaries for several years after (Able et al. 2012). This suggests the importance of non-natal habitat, and the potential for recolonization in non-natal estuaries. In the Saint John River during winter months, striped bass demonstrated an observed preference for “sheltered” habitat, either within cove areas or below stratified water layers (Andrews et al. 2020). Striped bass may also hold a preference for habitat with warmer (2-7 °C), oxygenated (>60% DO), and low salinity (<4.6 ppt) conditions (Able et al. 2012; Andrews et al. 2019; Andrews et al. 2020).

Overwintering striped bass have also been observed aggregating in warm waste-water discharge from power plants rather than migrating south, leaving them susceptible to large mortality events from rapidly changing water temperatures if plant processes are disrupted (Williams and Waldman 2010; Buhariwalla et al. 2016)

Although some studies suggest warming conditions may benefit striped bass via increases in suitable thermal habitat (Kliesner et al. 2017), extreme warming conditions may negatively affect available striped bass habitat as extreme thermal conditions are associated with hypoxia. Two studies found that when sea surface temperatures exceeded 25-28 °C, striped bass habitat quality and quantity was reduced by means of a temperature-oxygen squeeze effect (Costantini et al. 2008), and striped bass avoided hypoxic areas (Kraus et al. 2015). The growth of striped bass has not been previously constrained by temperature-oxygen squeeze (Costantini et al. 2008), however this may change if regional climate warming continues.

Environmental Effects on Growth

Striped bass are known to either remain residents in natal estuaries, or migrate to new habitats (Able et al. 2012; Vanalderweireldt et al. 2019). The location of residency, and its corresponding environmental conditions juvenile striped bass choose may affect growth rates and mortality. In the upstream habitat of the St. Lawrence Estuary, one study observed high levels of intraspecific competition, predation pressure, and resource limitation, these conditions not only likely contributed to the faster growth rates observed, but also likely contributed to dispersal of fish downstream (Vanalderweireldt et al. 2019). Vanalderweireldt et al. (2019) also found resident fish to have higher growth rates on average than their migratory counterparts, possibly due to the significant energy cost and predation increase associated with migration.

Salinity has shown some effect on Chesapeake Bay striped bass somatic growth (Secor et al. 2000), and little to no effect on other regional populations (Secor et al. 2000; Kenter et al. 2018). However, latitude may hold a greater effect on growth rates as some studies have found an inverse relationship between population latitude and somatic growth rates, where juvenile striped bass from northern latitudes exhibited greater growth rates than juveniles from more southern populations (Conover et al. 1997; Secor et al. 2000). The strong positive correlation with latitude of origin may be a result of northern populations having increased growth rates to compensate for the shorter duration of the “growing season” (Conover et al. 1997). Another study found juvenile striped bass demonstrated *slower* growth rates in South Carolina and Nova Scotia areas than migratory Atlantic and Gulf coast striped bass (Kenter et al. 2018). Kenter et al. (2018) claim these discrepancies may be the result of differences in water temperatures chosen for these lab studies, where smaller juveniles have demonstrated optimal growth at higher temperatures (24-28 °C), than their larger juvenile or sub-adult counterparts (20 °C; Duston et al. 2004; Cook et al. 2006).

Feeding success has been linked to high growth rates of fish larvae (Pepin et al. 2014). Between 1980-2000, recreational fishers noted a decrease in the weight of striped bass (Peros 1999, as cited in Nelson et al. 2006), raising the possibility that the striped bass population experienced reduced prey availability during that time (Nelson et al. 2006).

Environmental Effects on Natural Mortality

Environmental factors appear to impact early life- and developmental stages of striped bass disproportionately more than their mature counterparts and survival success of early life stages may impact future population sizes more than spawning stock size or reproduction potential (Cooper and Polgar 1981). Survival of early life stages may be influenced by salinity levels. Cook et al. (2010) observed striped bass eggs and larvae can tolerate a wide range of salinities (2-20 ppt), but demonstrate a reduced survival rate (47%) at 30 ppt (Cook et al. 2010). In addition to salinity, age 0 striped bass may also be subject to size-dependent winter mortality, where larger (>10 cm) individuals are more likely to survive through the winter, likely due to increased tolerance to unfavorable temperature or other environmental conditions (Hurst and Conover 1998). However, other studies have found no evidence for relationships between thermal tolerance and body size in juveniles (Penny and Pavey 2021). Age 1 abundance of striped bass has demonstrated correlations with winter severity, defined as the number of degree-days below 4°C (Hurst and Conover 1998), which suggests mortality rates are linked to low temperatures.

While thermal tolerances may differ between age or body size of individuals, tolerances may also differ by location as northern populations have demonstrated a higher thermal tolerance threshold than southern populations (Cook et al. 2006; Penny and Pavey 2021). Northern striped bass populations are known to be more migratory than southern populations (Raney and Wolcott 1955; Dudley et al. 1977; Bulak et al. 1997; Secor et al. 2000; Conroy et al. 2015), and thus may be exposed to a broader range of environmental conditions than less migratory populations (Penny and Pavey 2021).

Hypoxic conditions may also affect striped bass natural mortality. Crustaceans and fish make up a high proportion of striped bass diets (Nelson et al. 2003; Nelson et al. 2006; Manooch et al. 2008; Overton et al. 2009), and food availability may increase as a result of increased predator-prey encounters in areas of oxygenated waters (Costantini et al. 2008). However, if small prey fish have a higher tolerance for low oxygen conditions, areas of low DO may be a refuge and reduce predator-prey encounters (Robb and Abrahams 2003; Costantini et al. 2008). Asynchronies in food and other resources are more likely to occur as a result of spatial and temporal shifts in predator-prey dependent species, which may negatively affect various population dynamics and ecosystem functions (Doney et al., 2012; Durant et al. 2013; Staudinger et al. 2013).

Table 1: Summary Highlights by Stock Dynamic

Stock Dynamic	Related Information	Source
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Recruitment	<ol style="list-style-type: none"> 1. Eggs and larvae are transported by freshwater flow, tidal currents, or wind events. <ol style="list-style-type: none"> a. Using early juvenile life stage abundance data can lead to overestimation of recruitment. 2. Zooplankton Abundance associated with high recruitment. 3. River flow/discharge associated with recruitment timing and success. 4. Environmental contaminants decrease the number of recruits, thus also decreasing spawning potential of the population. 5. Temperature Impacts spawning timing and gonadal development. <ol style="list-style-type: none"> a. Spawning temperature cue around 12-19 C. b. Increased temperatures and longer day-length associated with faster gonadal development. 	<ol style="list-style-type: none"> 1. North et al. 2005; Dunning et al. 2009; MacInnis 2012 2. Shielder and Houde 2014; Martino and Houde 2010 3. Conroy et al. 2015; North et al. 2005; Gross et al. 2022) 4. Goodyear 1985 5. Setzler-Hamilton et al. 1980; Bain and Bain 1982; Clark et al. 2005; Kjesbu et al. 2010; Peer and Miller 2014; Secor et al. 2020
Distribution	<ol style="list-style-type: none"> 1. Suggested preference for warmer (2-7C), oxygenated (>60% DO), and low salinity (<4.6 ppt) conditions. 2. Some striped bass observed overwintings in warm wastewater areas of power plants. 3. Suggested increases in suitable thermal habitat with increasing temperatures. 4. Observed avoiding hypoxic areas. 	<ol style="list-style-type: none"> 1. Able et al 2012; Andrews et al. 2019; Andrews et al. 2020. 2. Williams and Waldman 2010; Buhariwalla et al. 2016 3. Kliesner et al. 2017 4. Kraus et al. 2015
Natural Mortality	<ol style="list-style-type: none"> 1. Early life stages show wide tolerance to salinity (2-20 ppt), but show reduced survival at 30 ppt. 2. Some evidence of size-dependent mortality with winter severity (number of degree-days below 4°C) 3. Northern populations have demonstrated a higher thermal tolerance threshold than southern populations. 4. Hypoxia may have contributed to striped bass recovery in some locations by forcing prey fish into upper, more oxygenated waters, increasing prey density and encounter rate for striped bass. 5. Environmental contaminants increase natural mortality, thus decreasing the number of recruits and decreasing spawning potential of the population. 6. Spatial and temporal shifts in predator and prey species can lead to mismatches in food and other resources. 	<ol style="list-style-type: none"> 1. Cook et al. 2010 2. Hurst and Conover 1998 3. Cook et al. 2006; Penny and Pavey 2021 4. Costantini et al. 2018 5. Goodyear 1985. 6. Doney et al., 2012; Durant et al. 2013; Staudinger et al. 2013
Growth	<ol style="list-style-type: none"> 1. High levels of intraspecific competition, predation pressure, and resource limitation contribute to faster growth rates and likely dispersal of fish downstream. <ol style="list-style-type: none"> a. Resident fish have higher growth rates on average than their migratory counterparts. 2. Salinity may have some effect on somatic growth. 	<ol style="list-style-type: none"> 1. Vanalderweireldt et al. 2019 2. Secor et al. 2000 3. Conover et al. 1997; Secor et al. 2000 4. Duston et al. 2004;

	3. Inverse negative relationship found between population latitude and somatic growth rates. 4. Size-dependent optimal growth rates <ul style="list-style-type: none"> a. Juvelies show optimal growth rates at higher temps (24-28 C) than larger juvenile or sub-adult counterparts (20 C). 5. Declines in weight 1980-2000, which suggests striped bass may have experienced food limitations .	Cook et al. 2006 5. Peros 1999 as cited in Nelson et al. 2006
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Table 2: Candidate drivers of Striped Bass population dynamics, hypothetical impact and potential time series (and data source) that may index this impact.

Potential Driver	Hypothetical Impact	Time series	Data Source
Freshwater flow/ discharge, Wind events	Larval transport, recruitment timing & success (recruitment)	USGS for freshwater discharge (ft3/s) NERACOOS for wind	USGS Monthly discharge data by river https://waterdata.usgs.gov/nwis/monthly (rivers) ecodata::hudson_river_flow Northeastern Regional Association of Coastal Ocean Observing Systems (NERACOOS)? http://www.neracoos.org/ (for Ocean)
Zooplankton abundance	recruitment	Seasonal zooplankton abundance anomalies	NOAA Ecosystem Monitoring (EcoMon) - See Ryan Morse as potential contact point ecodata::zoo_abundance_anomalies
Environmental contaminants	Recruitment, natural mortality	PCBs?	?
Temperature	Time-varying growth or natural mortality, recruitment, distribution	Sea surface temperature anomaly River Temperature	NASA Optimum Interpolation Sea Surface temp. (OISST) ecodata::seasonal_oisst_anom USGS water data portal daily/monthly/annually (rivers)

Salinity	Distribution, natural mortality, growth	River salinity Ocean salinity	USGS water data portal daily/monthly/annually (rivers) Survey salinity? Global Ocean Physics Reanalysis?
Dissolved oxygen	Distribution, natural mortality	River DO (mg/L) Ocean DO	USGS water data portal daily/monthly/annually (rivers) ?
Population Latitude	Somatic growth	Survey data with lat/lon recorded?	?
Prey availability	Distribution, natural mortality, growth	Prey abundance (alewives, flounder, sea herring, menhaden, mummichogs, sand lance, silver hake, tomcod, smelt, silversides, eels, lobsters, crabs, soft clams, small mussels, sea worms, and squid)	<ul style="list-style-type: none"> • DisMAP has latitude/depth data for many of these species, but not abundance • Survey data for abundance? • Ecodata has forage fish abundance

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