

ABSTRACT

Title of Dissertation: THE ROLE OF CONNECTIVITY AND SPATIAL STRUCTURE ON THE POPULATION DYNAMICS OF MARINE FISHES

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Migrations regulate population structure, which can play an important role in conferring stability at aggregate scales via asynchronous responses of population sub-components to perturbation; however, little is known about the importance of spatial structure in population persistence in fishes. My dissertation aims to explore the role of spatial structure on the population dynamics of marine fishes. Two species that exhibit different types of population structure were considered: (i) Atlantic mackerel (*Scomber scombrus*) in the Northwest Atlantic, comprised of two components that have distinct spawning regions off Canada (northern contingent) and the US (southern contingent); and (ii) striped bass (*Morone saxatilis*) in the Hudson River (HR), which exhibit early-life partial migration whereby a portion of juveniles remain in their natal freshwater habitats, while others migrate into higher salinity habitats. In Chapter 2, I used otolith stable isotopes ($\delta^{18}\text{O}/\delta^{13}\text{C}$) to understand contingent mixing of the Northwest Atlantic mackerel over two decades (2000–2019). Prevalent contingent mixing

occurred within the US waters, indicating that the northern contingent may provide subsidies to the US mackerel fishery. In Chapter 3, I combined machine learning with otolith $\delta^{18}\text{O}$ isoscapes to predict the geographic origin of the Northwest Atlantic mackerel spanning four decades (1975–2019). Contingent mixing occurred over four decades, including the 1970s when intensive foreign fisheries took place in US waters. Nursery hotspots were detected within spawning regions, but shifted over time. In Chapter 4, for HR juvenile striped bass, I explored the influence of early-life conditions and environmental drivers on partial migration. Otolith chemistry uncovered four dominant early migration modes. Partial migration was associated with larval growth, albeit facultatively controlled by environmental conditions. In Chapter 5, I evaluated how HR striped bass early-stage partial migration influenced recruitment patterns to the adult population over a 3-decade span. As an outcome of partial migration, adults recruited from a variety of nurseries, which exhibited asynchronous dynamics in response to climate variables. Through a comparative analysis of two species that exhibit different types of population structure, I demonstrated how spatial structure can play key roles in the population dynamics of marine fishes, with implications for management and conservation.

THE ROLE OF CONNECTIVITY AND SPATIAL STRUCTURE ON THE
POPULATION DYNAMICS OF MARINE FISHES

by

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Chapter 5

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Figure 5.3 Proportional nursery contributions for striped bass adult samples estimated from otolith chemistry for year-classes 1987–1991, 2005, 2007, and 2009–2015. Each bar represents an individual recruit. The mean brackish nursery index (outside parenthesis) and the western Long Island Sound (WLIS) nursery index (inside parenthesis) for each year-class is shown in the bottom right corner of each panel.

Figure 5.4 GAMLSS partial effects of (a) freshwater flow on the mean of the brackish nursery index, and (b) the winter severity within the Hudson River (HR) on the mean western Long Island Sound (WLIS) nursery index. Shaded areas depict standard errors and the rug along the x-axis indicates the distribution of observations.

Figure 5.5 Comparison of the baseline striped bass young-of-the-year (YOY) freshwater and brackish habitat proportion (YOY) and recruited adult nursery contributions (Adult) for year-classes 2005, 2007, and 2009–2015. Numbers at the bottom of each bar plot indicate the sample size of adults for each year-class. The level (low, moderate, high) of freshwater flow and YOY recruitment (see Figure S5.7) compared to the long-term mean are also shown at the top of each bar plot for each year-class.

Figure 5.6 Fitted von Bertalanffy growth curves for (a) female and (b) male striped bass adult size-at-age data. Points are colored by the brackish nursery index ranging from 0 to 1. Relationship between growth curve-extracted residuals and the brackish nursery index for (c) females and (d) males. The dashed horizontal line indicates zero.

Figure 5.7 Fitted logistic regression model assessing the relationship between striped bass adult sex and the brackish nursery index. The solid line and shaded area indicate the predicted value and 95% confidence intervals from the model. Adult sex data had binary values of 0 (male) or 1 (female) on the y-axis, but a small random variation was added to each point to prevent overplotting. The dashed horizontal line indicates 0.5 female probability.

Figure 5.8 Schematic diagram illustrating adult nursery contributions, carry-over effects, and young-of-the-year (YOY) habitat frequencies for Hudson River striped bass in years of low/moderate versus high freshwater flow. The thickness of the black arrows indicates the relative contributions from freshwater and brackish nurseries to the recruitment of adults. Nursery experiences carried over to influence adult sex: freshwater residents or late brackish migrants were more likely to develop into males, whereas early brackish migrants developed into either males or females. In low/moderate flow years, YOY brackish habitat predominated, and both freshwater and brackish habitat contributed roughly proportionately to adult production. In high-flow years, while the frequency of YOY freshwater and brackish habitats were roughly equal, brackish habitats disproportionately contributed more to adult production. Symbols courtesy of the University of Maryland Center for Environmental Science Integration and Application Network.

Chapter 1: Introduction

1.1 Overview

A long-standing question in ecology is whether biodiversity gives rise to ecosystem stability (MacArthur, 1955; McCann, 2000; Ives and Carpenter, 2007). Species-rich ecosystems, in general, are temporally stable because individual species with similar ecosystem functions exhibit weakly correlated or independent dynamics that confer stability at aggregate scales (Tilman, 1996; Doak et al., 1998). Such variance-dampening of ecosystems through asynchronous responses of species or functional groups to perturbation is termed the “portfolio effect” — a concept stemming from financial investment theory, where financial portfolio diversification often results in stable returns compared to simple portfolios (Figge, 2004; Schindler et al., 2015). Recently, there is increased recognition that population diversity within individual species may play an important role in population stability through differential responses of population sub-components to ecosystem conditions. This stabilizing effect has been observed across a wide range of taxa including plants (Abbott et al., 2017; Waddle et al., 2019), insects (Hui et al., 2017), birds (Ringsby et al., 2002), and fishes (Hilborn et al., 2003; Secor et al., 2009; Kerr et al., 2010; Schindler et al., 2010).

The focus of fisheries ecology and science throughout the 20th century have been in understanding the causes of fluctuation in population abundance through time (Hjort, 1914; Cushing, 1990; Houde, 2008). The emphasis on the temporal dynamics of populations has frequently led to simplified views on the spatial aspects of

populations, which has been evident in fisheries stock assessment and management. Assessments rely on the unit stock concept — a traditional simplification of a group of fish within the same geographic area assumed to have homogenous internal dynamics (growth, mortality, reproduction) and limited exchange with other stocks (Cadrin and Secor, 2009). Ignoring seasonal distributions specific to a population sub-component (i.e., spatial structure) in assessment models can bias stock status indicators (Kerr et al., 2014; Goethel and Berger, 2017; Van Beveren et al., 2019) and lead to overexploiting of local spawning components (Ricker, 1958; Cadrin and Secor, 2009; Kerr et al., 2017). Thus, there has been a call that fishery stock assessment models and management units reflect greater realism in spatial structure assumptions (Secor, 1999; Smedbol and Stephenson, 2001; Wilberg et al., 2008; Cadrin, 2020).

Unique population sub-components within individual species can arise from multi-generational return of adults to a fixed spawning site (i.e., philopatry) that may allow larvae to encounter favorable oceanographic conditions to enhance survival (Sinclair, 1988). The exchange of individuals between local populations and habitats is termed connectivity (Cramer et al., 2023), maintained through processes such as (i) larval dispersal, (ii) straying (juvenile/adult movement away from natal populations), and (iii) entrainment (juvenile/adult drawn into one population to another during periods of spatial overlap) (Figure 1.1a). Spatial structure within populations is frequently attributed to individual behaviors that arise from interactions between conditional responses early in life and environmental drivers, in which the most traditional view is the coexistence of residents and migrants within a population (i.e.,

partial migration; Jonsson and Jonsson, 1993; Chapman et al., 2012; Secor, 2015; Figure 1.1b). Here, I examine two fish species that exhibit population structure and connectivity at different spatial scales.

1.2 Otolith Microstructure and Chemical Analysis

Otolith microstructure and chemical analysis have been widely used as a tool to uncover spatial structure and population connectivity of marine fishes (Elsdon et al., 2008; Kerr and Campana, 2014; Tanner et al., 2016; Avigliano, 2022; Reis-Santos et al., 2023). Otoliths, the biogenic calcium carbonate tissue forming part of the inner ear of teleost fishes, have long been used for fish ageing given that seasonal growth differences appear as annual increments in otoliths. The discovery of daily growth increments within otolith microstructure by (Pannella, 1971) was one of the greatest breakthroughs in advancing the field of fisheries science and ecology (Secor, 2010). Since then, otolith microstructure has been used to accurately estimate age, growth, and survival during the early life stages of fishes (Campana and Neilson, 1985; Secor and Houde, 1995; Campana and Thorrold, 2001), as well as to identify the presence of spatially and temporally segregated cohorts through hatch date estimation (e.g., Limburg, 2002; Callihan et al., 2008; Arai et al., 2020).

Because otoliths are metabolically inert and permanently record growth and ambient environment conditions, otolith microstructure combined with chemical analysis enables the reconstruction of lifetime movement paths of fishes (Campana, 1999; Elsdon et al., 2008; Walther and Limburg, 2012; Walther, 2019). In particular, elements such as strontium (Sr) and barium (Ba) have been widely applied to reconstruct diadromous fish movements across salinity gradients (e.g., Tsukamoto et

al., 1998; Miller, 2011; Conroy et al., 2015; Itakura et al., 2020; Nelson et al., 2021).

This is because these elements (i) generally exhibit distinct values between freshwater and marine end-members, and (ii) are incorporated proportionally into the otolith from ambient waters without major environmental and/or physiological effects (Secor and Rooker, 2000; Kraus and Secor, 2004b; Hüsey et al., 2020).

Otolith stable isotopes, such as oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$), have also been used as a reliable tool for addressing questions of potential origin and movement of marine fishes (e.g., Rooker et al., 2008; Clarke et al., 2010; Trueman et al., 2012; Wells et al., 2015; Artetxe-Arrate et al., 2021). A less frequent, but rigorous approach seeks to reconstruct movement patterns by matching the stable isotopic composition of the animal tissue to the predicted isotopic composition over a spatial gradient (i.e., "isoscapes"; West et al., 2010; Bowen, 2010). This approach has been frequently used to track movements of birds, bats, and insects in the terrestrial environment (e.g., Flockhart et al., 2017; Vander Zanden et al., 2018; Bowen and West 2019; Campbell et al., 2020), although application to marine organisms has been limited given that the isotopic variation in marine ecosystems varies dynamically over multiple spatiotemporal scales (Elsdon et al., 2008; but see MacKenzie et al., 2014; Vander Zanden et al., 2015; Trueman et al., 2017; Torniaainen et al., 2017; Matsubayashi et al., 2020; Martino et al., 2022).

1.3 Dissertation Goals and Model Species

Using otolith chemistry, long-term datasets, and machine learning approaches, I aim to understand the role of connectivity and spatial structure on the population dynamics of marine fishes. To achieve this goal, two species that exhibit different

types of population structure and connectivity will be considered in my dissertation: the Atlantic mackerel (*Scomber scombrus*) in the Northwest Atlantic, and striped bass (*Morone saxatilis*) in the Hudson River. Population structures of these two species are underlain by different types of partial migration. Population sub-components of Atlantic mackerel originate from different natal regions but coningle during non-breeding seasons (i.e., natal divergence), whereas Hudson River striped bass share the same spawning ground but utilize different nursery habitats (nonnatal divergence; Secor, 2015). Furthermore, these two species are very different in terms of their life history traits (opportunistic vs. periodic; Winemiller and Rose, 1992), migration patterns (marine shelf vs. anadromous), and trophic position (forage fish vs. apex predator), but as marine species may exhibit spatial structuring that confers population stability to prevent unexpected stock collapse (Petitgas et al., 2010). A comparative analysis of these contrasting species could show that spatial structure is general to marine fishes, playing an important role in population persistence. Further, understanding the mechanisms that underpin the stability of populations is relevant under the recent period of climate change and non-stationarity in marine ecosystems.

1.3.1 Atlantic Mackerel in the Northwest Atlantic

Complex spatial structure has been reported for the Northwestern population of the Atlantic mackerel (Sette, 1950; Moores et al., 1975; Moura et al., 2020; Redding et al., 2020; Bourret et al., 2023), a migratory pelagic schooling species consumed around the globe, and a dominant forage fish species in the North Atlantic (Overholtz et al., 2000; Tyrrell et al., 2008). The population of the Northwest Atlantic mackerel has been traditionally broken into northern and southern “contingents” or

sub-groups with different spawning sites, nursery areas, and migration behaviors (Sette, 1950; Secor, 1999). The southern contingent spawns off southern New England in April and May (Sette, 1943; Berrien, 1978), and the northern contingent migrates to spawn in the southern Gulf of St. Lawrence in June and July (Sette, 1943; Mbaye et al., 2020; Brosset et al., 2020; Van Beveren et al., 2022; Figure 1.2a). In late fall, the northern contingent migrates into the US shelf waters and mixes with the southern contingent throughout late-fall and early-spring, where they are both exploited by the US winter fishery (Sette, 1950; Van Beveren et al., 2019; Redding et al., 2020; Figure 1.2b). As the biomass of the northern contingent is roughly an order of magnitude larger than that of the southern contingent (NEFSC, 2018; Richardson et al., 2020; DFO, 2021), the degree of contingent mixing likely influences US fisheries landings. However, contingent mixing levels and spatial structure of the Northwest Atlantic mackerel are highly uncertain and dynamic, and have only recently been quantified using otolith tracer approaches (Moura et al., 2020; Redding et al., 2020).

1.3.2 Striped Bass in the Hudson River

Striped bass is widely distributed throughout Atlantic US and Canada, ranging from the Gulf of Mexico to the St. Lawrence River, and supports one of the most important commercial and recreational fisheries in the US Atlantic waters (NEFSC, 2019). The Hudson River, Chesapeake Bay, and Delaware River have been identified as key spawning regions contributing to the overall Atlantic striped bass population (NEFSC, 2019). Striped bass are an anadromous species, in which adults spend most of their lifetime in coastal waters showing diverse oceanic migrations (Secor and

Piccoli, 1996; Zlokovitz et al., 2003; Gahagan et al., 2015), but migrate into fresh tidal regions to spawn in the spring (Secor et al., 2020; Pan et al., 2023). Semi-buoyant eggs and pelagic larvae are generally retained above the salt front, but subsequently disperse throughout the estuary following metamorphosis into the juvenile stage (Boreman and Klauda, 1988; Dovel, 1992). Striped bass juveniles exhibit partial migration in the Albemarle Sound (Mohan et al., 2015), Chesapeake Bay (Conroy et al., 2015), and St. Lawrence Estuary (Morissette et al., 2016; Vanalderweireldt et al., 2019), whereby a portion of juveniles remain in their natal freshwater or oligohaline habitats, while others migrate downstream into higher salinity habitats. The Hudson River striped bass population could also exhibit such facultative migration behavior, associated with conditional responses during the early life stage that subsequently carry over to influence adult life history characteristics (Kraus and Secor, 2004a; Gallagher et al., 2018). Further, while juveniles frequently occur in the coastal western Long Island Sound (WLIS) region outside the principal nursery region in the Hudson River (HR), the importance of the WLIS region to the Hudson River adult population remains unknown (Dunning et al. 2009; Figure 1.3).

1.4 Dissertation Structure and Key Findings

*Chapter 2: “Multi-decadal trends in contingent mixing of Atlantic mackerel (*Scomber scombrus*) in the Northwest Atlantic from otolith stable isotopes.”*

In Chapter 2, I used archived otoliths and stable isotope analysis ($\delta^{18}\text{O}/\delta^{13}\text{C}$) to compare contingent composition characteristics of the Northwest Atlantic mackerel from recent periods (2013–2019) with samples from the early 2000s (Redding et al.,

2020) to evaluate decadal trends in contingent mixing. I further examined the relationship between contingent mixing and US fisheries landings to test whether US fisheries received important seasonal subsidies from the dominant northern contingent. Classification of age ≥ 2 adults demonstrated that northern contingent mixing was prevalent within the US continental shelf waters during the past two decades (2000–2019), despite substantial depletion in spawning stock biomass of the dominant northern contingent. A significant positive relationship occurred between northern contingent mixing and US fisheries landings, implying that northern contingent mixing is important in subsidizing the US winter mackerel fishery. This chapter has been published in *Scientific Reports* (Arai et al., 2021).

Chapter 3: “Integrating machine learning with otolith isoscapes: reconstructing connectivity of a marine fish over four decades.”

In Chapter 3, I developed a new framework that combines a machine-learning ensemble classifier with continuous otolith $\delta^{18}\text{O}$ isoscapes to assess contingent mixing and predict the geographic origin of the Northwest Atlantic mackerel over four decades (1975–2019). The ensemble classifier indicated prevalent, yet highly varied contingent mixing levels within the US waters over four decades, including the 1970s when intensive foreign fleet fisheries occurred within US waters. The integrated approach revealed geographic nursery hotspots in known spawning regions and detected geographic shifts over time. This integrated framework can be applied to other marine species to understand migration at a high spatial resolution to guide future conservation and management efforts. This chapter has been published in *PLoS ONE* (Arai et al., 2023).

Chapter 4: “Early growth and environmental conditions control partial migration of an estuarine-dependent fish.”

In Chapter 4, I used otolith microstructure and chemistry to examine the influence of early life conditions and environmental drivers on the early-stage partial migration of Hudson River juvenile striped bass in two consecutive years (2019 and 2020) with contrasting hydrologic conditions. Time series clustering analysis on otolith Sr and Ba transects uncovered four dominant early migration modes in both years: (i) freshwater residents, (ii) oligohaline migrants, (iii) small mesohaline migrants, and (iv) large mesohaline migrants. Juvenile partial migration appeared to be a conditional strategy linked to a growth-mediated threshold, with the propensity to migrate early related to slower larval growth. Freshwater residency and delayed migration were associated with faster larval growth. In a dry year (2020), the timing of dispersal to mesohaline habitats coincided with high freshwater flow and tidal currents, but not in the second wet year (2019). The slow-growing oligohaline migrants exhibited compensatory growth following dispersal to productive brackish habitats in both years. Recruitment to the coastal western Long Island Sound (WLIS) habitat occurred both during the larval and juvenile phases.

Chapter 5: “Spatial structuring via partial migration promotes population persistence in an estuarine-dependent fish under changing climate.”

In Chapter 5, I used otolith chemistry and retrospective analysis to test adult nursery contributions and carryover effects associated with early-life partial migration in the Hudson River striped bass over a 3-decade span. Early-life partial migration resulted in varied nursery use of freshwater, brackish water, and coastal habitats, from

which juveniles recruited to the adult population. Contributions from brackish nurseries increased with freshwater flow, while the western Long Island Sound nursery produced more adults during severe winter years. In most years, patterns in recruited adult nursery use reflected the relative abundance of young-of-the-year (YOY) between freshwater and brackish habitats; nevertheless, brackish habitats disproportionately produced more adults during high-flow years when overall YOY recruitment was poor. First-year nursery experiences were associated with adult sex, but not growth: while the majority of adult females recruited from brackish nurseries, males recruited from both freshwater and brackish nurseries. Differential population outcomes of nursery utilization could thus be influenced by climate variables and environmental sex determination.

Appendix Chapter: “Sub-annual cohort representation among young-of-the-year recruits of the western stock of Atlantic bluefin tuna.”

In the Appendix Chapter, I used hatch date analysis based on otolith microstructure to identify the presence of spatially and temporally segregated cohorts of the western stock of Atlantic bluefin tuna (*Thunnus thynnus*). I tested whether age-0 recruits occurring in the US Mid-Atlantic Bight originated from the Northwest Atlantic Slope Sea — a newfound spawning region outside the principal spawning region in the Gulf of Mexico. Hatch dates exhibited a unimodal distribution and corresponded to spawning and production period for the Gulf of Mexico, showing no evidence of recruits from the newfound Slope Sea spawning region. This chapter has been published in *Fisheries Research* (Arai et al., 2020) and included in my dissertation as an Appendix Chapter.

1.5 Broader Applications and Implications to Management

Through a comparative analysis of two species that exhibit different types of population structure and connectivity, I demonstrated how spatial structure can play key roles in the population dynamics of marine fishes, with implications for management and conservation.

In Chapters 2 and 3, I found prevalent contingent mixing of the Northwest Atlantic mackerel within the US waters over four decades (Arai et al., 2021, 2023). Despite evidence of transboundary contingent mixing, the two nations separately manage jurisdictional fisheries, with Canada assessing the northern contingent as a single stock, and the US treating the two contingents as components of a single transboundary stock (NEFSC, 2018; DFO, 2021). Information on contingent composition could aid in the development of spatially explicit stock assessment models that provide advice designed to preserve the productivity and stability of this depleted two-component population (Cadrin and Secor, 2009; Goethel et al., 2011; Cadrin, 2020).

In Chapter 3, I established a new framework that translates the biogenic stable isotope information into a probabilistic prediction of geographical origin in the marine environment (Arai et al., 2023). This combined approach could be used to study fine-scale migration and connectivity in any marine species, especially those that form carbonate biominerals such as otoliths. Because otoliths are often retained and stored in abundance for the purpose of fisheries stock assessment, they can be used to infer population-level migration and connectivity of fishery resources, allowing management units to better reflect the spatial structure of biological

populations (Tanner et al., 2016; Kerr et al., 2017; Cadrin, 2020; Avigliano, 2022). Archived hard parts may be useful in reconstructing fine-scale migration patterns over decadal periods, which would help understand the importance of spatial structure in species persistence in the face of climate change (Siskey et al., 2016; von Leesen et al., 2020; Cordoleani et al., 2021).

In Chapter 4, I revealed how Hudson River (HR) striped bass early-life partial migration emerged as a conditional strategy linked to larval growth and environmental conditions. This growth-mediated partial migration resulted in a complex spatial structure with consequences on how populations respond to climate regimes (Chapter 5). As environmental conditions change rapidly due to climate change (Najjar et al., 2009; Seekell and Pace, 2011), understanding and preserving key drivers that promote diverse life history traits, as well as maintaining a mosaic of habitats across the HR landscape will be critical to ensure the persistence of the striped bass population. Whether early-life partial migration and nursery experiences may affect lifetime adult migration patterns is poorly known and warrants further research, particularly because adults exhibit size-dependent migration modalities that may have implications for population dynamics (Secor and Piccoli, 1996; Wingate and Secor, 2007; Gahagan et al., 2015). Future population modeling work (e.g., Kerr et al., 2010) could further elucidate how early-life partial migration and diverse nursery use could contribute to population stability, resilience, and productivity in HR striped bass and other species that depend on complex spatial structure in a changing climate.

Figures

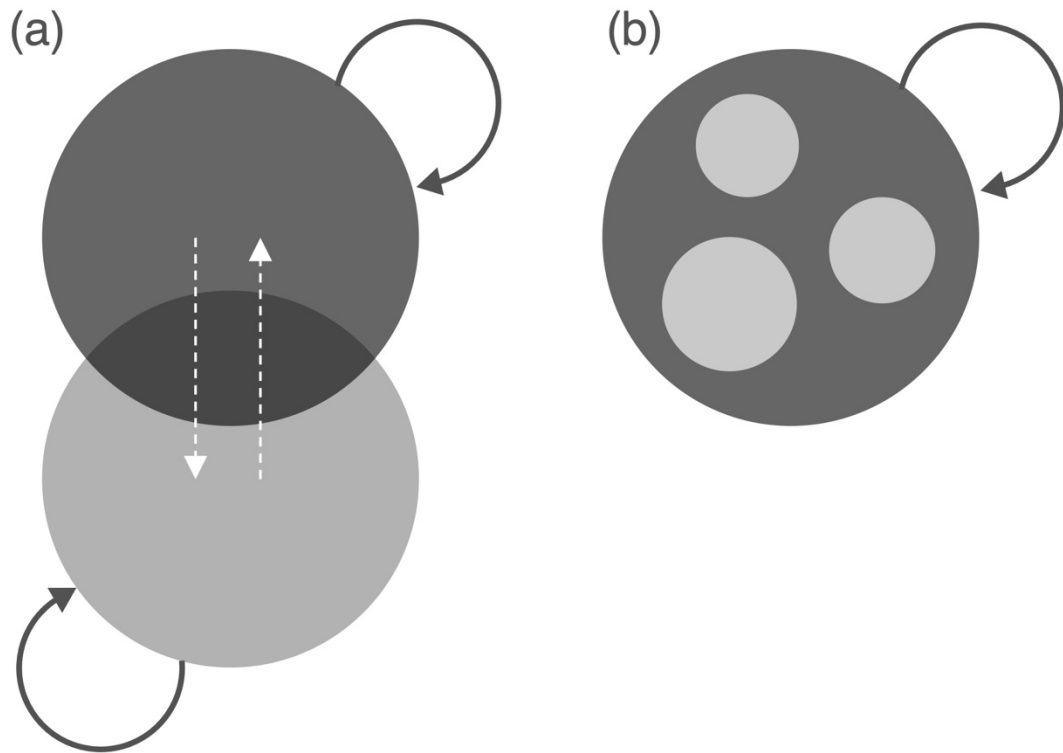


Figure 1.1 (a) Schematic diagram of (a) spatially overlapping populations with individual exchange occurring through connectivity, and (b) a single population with spatial structure. Circles represent population components, dotted arrows indicate connectivity, and curved arrows illustrate recruitment through a common stock-recruitment function.

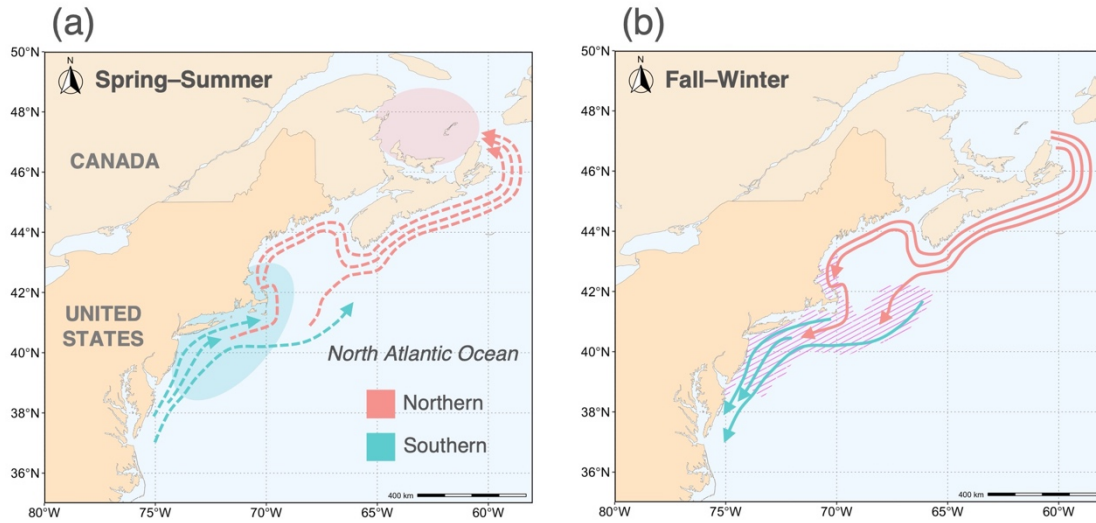


Figure 1.2 Distributions and migration patterns of the Northwest Atlantic mackerel northern and southern contingents during (a) spring-summer and (b) fall-winter seasons. Dotted arrows represent spring migrations and solid arrows depict fall migrations. Shaded ellipses in the Gulf of St. Lawrence and the US continental shelf depict principal spawning sites for the northern and southern contingents. Hatched areas in the US continental shelf illustrate contingent mixing regions during winter.

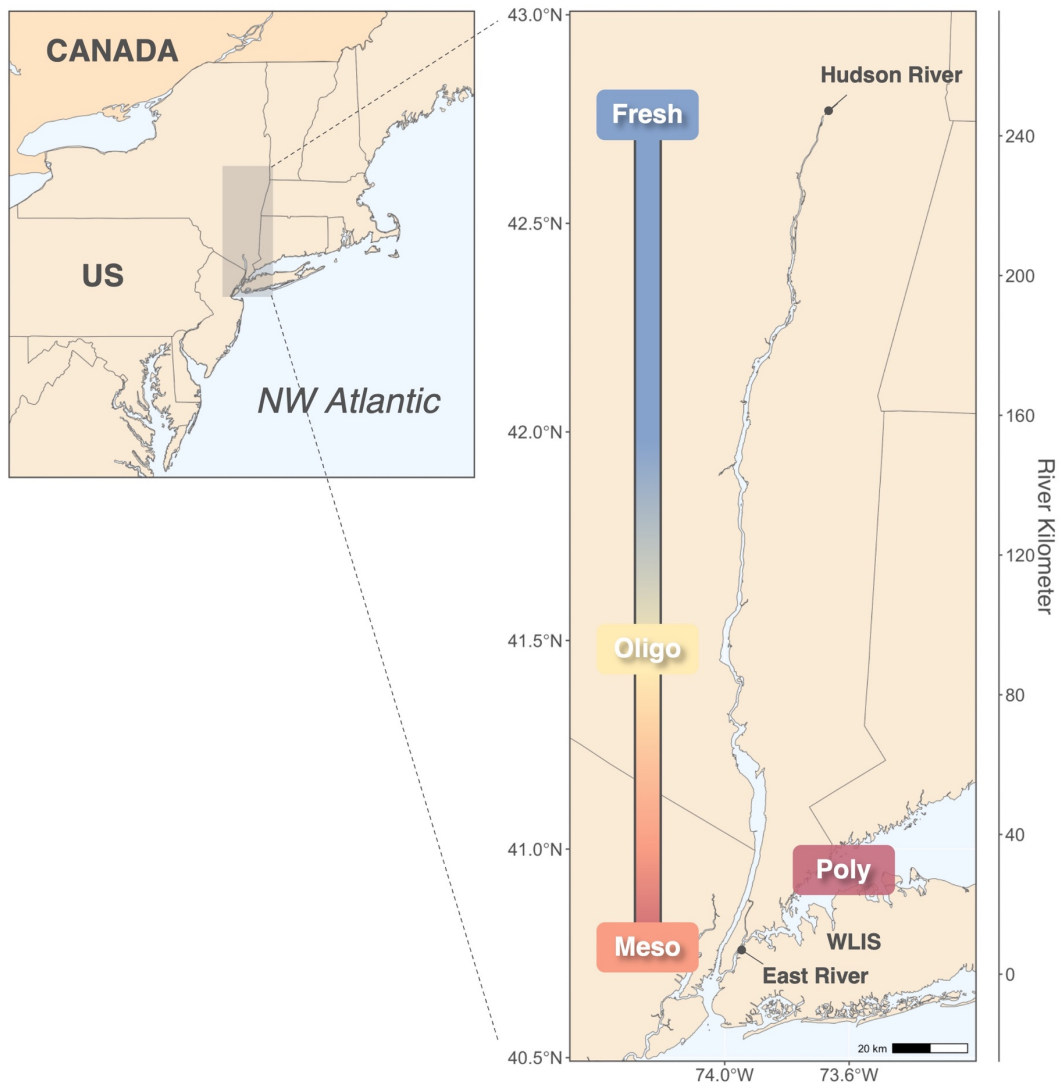


Figure 1.3 Map of the Northwest Atlantic Ocean, Hudson River, and western Long Island Sound (WLIS). The y-axis depicts the latitude and river kilometers from the mouth of the Hudson River. The color bar illustrates the salinity zones: Fresh = Freshwater, Oligo = Oligohaline, Meso = Mesohaline, Poly = Polyhaline.

Chapter 2: Multi-decadal trends in contingent mixing of Atlantic mackerel (*Scomber scombrus*) in the Northwest Atlantic from otolith stable isotopes

Arai, K., Castonguay, M., and Secor, D. H. (2021). Multi-decadal trends in contingent mixing of Atlantic mackerel (*Scomber scombrus*) in the Northwest Atlantic from otolith stable isotopes. *Sci. Rep.* 11, 6667. doi: 10.1038/s41598-021-86116-2.

2.1 Abstract

The Atlantic mackerel (*Scomber scombrus*) in the Northwest Atlantic is comprised of northern and southern components that have distinct spawning sites off Canada (northern contingent) and the US (southern contingent), and seasonally overlap in US fished regions. Thus, assessment and management of this population can be sensitive to levels of mixing between contingents, which remain unknown. Multi-decadal trends in contingent mixing levels within the US fisheries region were assessed, and the contingent composition across seasons, locations, ages, and size classes were characterized using archived otoliths and developing a classification baseline based on juvenile otolith carbon and oxygen stable isotopes ($\delta^{13}\text{C}/\delta^{18}\text{O}$ values). Classification of age ≥ 2 adults demonstrated that northern contingent mixing was prevalent within the US continental shelf waters during the past two decades (2000–2019), providing an important seasonal subsidy to the US winter fishery despite substantial depletion in spawning stock biomass of the dominant northern contingent. While the majority of older fish were of the northern contingent during the early 2000s, the southern contingent contribution increased with age/size class during the recent period (2013–2019). Spatial mixing was most prevalent during

February and March when the northern contingent occurred as far south as the Delmarva Peninsula, but were mostly absent from US waters in May. A positive relationship (albeit not significant; $r = 0.60$, $p = 0.07$) occurred between northern contingent mixing and US fisheries landings, which could imply that higher contingent mixing levels might be associated with greater landings for the US winter mackerel fishery. The yield of the Northwest Atlantic mackerel depends upon the status of the northern contingent, with the southern contingent possibly more prone to depletion. Spatially explicit stock assessment models are recommended to conserve both productivity and stability in this two-component population.

2.2 Introduction

Complex spatial structure is a common attribute in fish populations (Tsukamoto et al., 1998; Fromentin and Powers, 2005; Kerr and Secor, 2009; Cadrin et al., 2010) that confers stability and resilience through asynchronous responses of population sub-components to the same environmental conditions (i.e., portfolio effect; Doak et al., 1998; Tilman et al., 1998; Secor et al., 2009). Yet fisheries stock assessment and management commonly rely on the unit stock concept — a traditional simplification of a group of fish within the same geographic area assumed to have homogenous internal dynamics (growth, mortality, reproduction) and limited exchange with other stocks (Cadrin and Secor, 2009). Stock mixing occurs when stock separation is incomplete and distributions overlap across defined geographic boundaries over an extended period of time (Secor, 2014). Applying the unit stock concept to a mixed-stock fishery can potentially lead to over exploitation of the subordinate spawning component as it receives a greater proportion of fishery removal relative to the more

productive spawning component (Ricker, 1958; Cadrin and Secor, 2009; Kerr et al., 2017). Additionally, ignoring spatial structure and stock mixing in assessment models can bias stock status indicators, resulting in flawed scientific advice (Kerr et al., 2014; Goethel and Berger, 2017; Van Beveren et al., 2019). Fishery stock assessment models and management units should therefore reflect the spatial structure of biological populations (Cadrin, 2020).

Complex spatial structure has been reported for the Northwestern population of the Atlantic mackerel (*Scomber scombrus*) (Sette, 1950; Moores et al., 1975; Redding et al., 2020), a migratory pelagic schooling species consumed around the globe, and a dominant forage fish species in the North Atlantic (Overholtz et al., 2000; Tyrrell et al., 2008). Two distinct stocks are recognized: one in the Northeast Atlantic off the coast of northern Europe, and another in the Northwest Atlantic centered off the US and Canada (Jansen and Gislason, 2013). The Northeastern population has experienced an increase in abundance and geographical expansion of its distribution from the mid-2000s, currently supporting one of the largest fisheries in the world (Nøttestad et al., 2016; Olafsdottir et al., 2019; FAO, 2020). The Northwest Atlantic mackerel fisheries have fluctuated greatly over time, showing relatively high landings during the early 2000s, although the stock is currently in a depleted phase with spawning stock biomass and landings at historically low-levels (NEFSC, 2018; DFO, 2019).

Defining the unit stock is crucial to fisheries management for the Northwest Atlantic mackerel, but a challenge given its highly dynamic migrations and broad spawning areas that transverse the border between the US and Canada, which

separately manage jurisdictional fisheries. The population of the Northwest Atlantic mackerel has been traditionally broken into northern and southern “contingents” or sub-groups with different spawning sites, nursery areas, and migration behaviors (Sette, 1950; Secor, 1999). The northern contingent centered in Canadian waters spawns primarily in the southern Gulf of St. Lawrence in June and July (Sette, 1943) (Figure 2.1), and the southern contingent spawns off southern New England in April and May (Sette, 1943; Berrien, 1978), although the spawning distribution and suitable habitat of the southern contingent has shifted northeastward over the past few decades (Overholtz et al., 2011; McManus et al., 2018; Richardson et al., 2020). The northern contingent migrates into the US shelf waters in late-fall and mixes with the southern contingent throughout late-fall and spring, where they are both exploited by the US winter fishery (Sette, 1950; Moores et al., 1975; Van Beveren et al., 2019; Redding et al., 2020) (Figure 2.1). In late-spring, the northern contingent migrates back to spawn in the Gulf of St. Lawrence, and the two contingents are separated throughout the summer seasons (Sette, 1950; Moores et al., 1975). As the biomass of the northern contingent is roughly an order of magnitude larger than that of the southern contingent (NEFSC, 2018; Richardson et al., 2020), the degree of contingent mixing likely influences US fisheries landings. However, contingent mixing levels and spatial structure of the Northwest Atlantic mackerel is highly uncertain and dynamic, and has only recently been quantified using otolith tracer approaches (Moura et al., 2020; Redding et al., 2020).

Otolith oxygen and carbon stable isotopes ($\delta^{18}\text{O}/\delta^{13}\text{C}$ values) have been widely used as a tool for addressing questions of population structure and migration of

marine fishes (Rooper et al., 2008; Clarke et al., 2010; Wells et al., 2015; Moreira et al., 2018). Because the Northwest Atlantic mackerel are exposed to Northwest Atlantic shelf waters of differing temperature and water chemistry during their juvenile period (Trueman et al., 2012; McMahon et al., 2013), this likely results in regional differences in the stable isotope composition in the otolith of the two contingents. Applying otolith oxygen stable isotope composition ($\delta^{18}\text{O}$ values), Redding et al., (2020) discriminated between the two contingents by applying a year-class specific baseline approach, where a specific baseline was developed for each year-class to account for inter-annual variations in the stable isotope composition; then, unknown adult samples were aged and assigned to a year-class and matched with a corresponding year-class baseline. For the period of 2000–2003, the majority of age >2 adults sampled from US shelf waters (in March) were classified as the northern contingent members, confirming the premise of seasonal mixing between the two contingents (Redding et al., 2020). Moura et al., (2020) demonstrated a clear separation between the two contingents using a combination of bulk otolith chemistry and morphometrics, although sampling was both spatially and temporally restricted and from a single age-class.

In this study, contingent composition characteristics of the Northwest Atlantic mackerel from the recent periods (2013–2019) were compared with samples from the early 2000s (Redding et al., 2020) to evaluate changes in contingent composition over multi-decadal timescales, and to assess how changes in spawning stock biomass and age structure influence contingent composition characteristics. Contingent mixing levels are likely to change over time due to contingent-specific production and

migration patterns (Secor, 2014). Further, the relationship between contingent mixing and US fisheries landings was examined to test whether US fisheries receive important seasonal subsidies from the dominant northern contingent. It was hypothesized that higher contingent mixing levels are associated with strong year-classes of the more dominant northern contingent, which will result in greater US fisheries landings, particularly during the winter period when contingent mixing is most prevalent (Sette, 1950). The classification baseline of Redding et al., (2020) was updated by including otolith $\delta^{13}\text{C}$ values as a second predictor, which reflects the carbon isotopic composition of dissolved inorganic carbon (DIC) and the diet source (Kalish, 1991; Solomon et al., 2006; Tohse and Mugiya, 2008), with the metabolic rate controlling the proportion of dietary carbon in the otolith in a temperature-dependent manner (Chung et al., 2019). Further, instead of developing a specific baseline for each year-class (Redding et al., 2020), a common classification baseline was developed by aggregating across year-class baselines (Rooker and Secor, 2019), and accounting for the inter-annual variations in the baseline stable isotope composition through a mixed effects modelling approach. The main goal of this study was to evaluate long-term trends in contingent mixing of the Northwest Atlantic mackerel within the principal US fisheries region, and to characterize contingent composition across seasons, locations, ages and size classes.

2.3 Methods

2.3.1 Sample Collection

A total of 217 otolith samples were selected from the Northwestern population of the Atlantic mackerel caught in the US winter fishery from October to November and January to March during 2013–2019 in the Mid-Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GB), and Gulf of Maine (GOM; Figure 2.1, Table S2.1). Fish collected in areas with high mackerel landings were selected for analysis. A total of 67 samples from the Northeast Fisheries Science Center (NEFSC) fishery-independent bottom trawl survey from March to May during 2013–2014, 2017, and 2019 were selected to augment age-1 juvenile baseline and age ≥ 2 adult samples for which US winter fishery samples were insufficient in sample size (Figure 2.1). It is important to note that the sampling region of the NEFSC bottom trawl survey substantially overlaps with the US commercial mackerel fishery. A total of 99 otolith samples were selected from fish collected in the summer Canadian fishery from July to October during 2013–2016, and 2018 in the Gulf of St. Lawrence (Figure 2.1). Samples were archived at the NEFSC Fisheries Biology Program in Woods Hole, Massachusetts, United States, and Fisheries and Oceans Canada (DFO), Maurice Lamontagne Institute, Mont-Joli, Québec, Canada. All samples had been aged by expert NEFSC and DFO scientists using whole otoliths mounted in clear resin viewed under reflected light. Ageing was generally conducted without prior information (e.g., fish length, weight) except for the date of capture. US commercial and survey samples collected in 2013–2019 achieved high ageing precision with the coefficient of variation (CV) ranging 0.0–1.5% and percent agreement ranging 95.7–

100%. Month and location of capture, and length data were also available for almost all otolith samples. No live animals were used in this study and no specific permissions were needed for sampling activities as all otolith samples of Atlantic mackerel (not endangered nor protected) analyzed in this study represented archived material collected from commercial fisheries and government surveys.

2.3.2 Otolith Preparation and Stable Isotope Analysis

Otolith oxygen and carbon stable isotope composition of age-1 juvenile samples were used to develop the baseline to classify age ≥ 2 unknown adult samples collected within the US shelf waters. Collection sites of age-1 juvenile samples were assumed to represent their natal habitats and exchange of individuals between the two contingents before the adult stage was presumed to be limited. This assumption is supported by evidence from size distribution analysis and extensive tagging programs that suggest localized migration patterns of age-0 juvenile mackerel (Sette, 1950; Uriarte et al., 2001). Additionally, passive drift during the early life stage is predominately driven by wind forcing and occurs only for the short period before active swimming initiates at c. 20 days post hatch (Sette, 1943; Mendiola et al., 2007). As age-1 juveniles of the northern contingent are rarely encountered by Canadian commercial fisheries, age-2 samples collected in the summer Canadian fishery in the Gulf of St. Lawrence were used to complement the 2016 year-class baseline for which age-1 samples of the northern contingent were insufficient in sample size. The use of age-2 fish as a baseline for the northern contingent is supported by evidence that immigration of the southern contingent into Canadian waters is not prevalent (Sette, 1950; Moores et al., 1975). The otolith material within

the first annulus representing the early life stage and residence within the natal nursery habitats was isolated and converted to a powder using a New Wave Research MicroMill (Fremont, California, USA), following the method of Redding et al., (2020). An automated series of 30 μm depth passes (10–13 passes) were made within the first annulus with a 500- μm carbide dental drill bit (Brasseler USA, Savannah, Georgia, USA) to extract the otolith material. The mass of powdered otolith material used for analysis ranged from 0.04–0.1 mg to achieve the best data quality.

$\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of the otolith material were measured using an automated carbonate preparation device (KIEL-III; Thermo Fisher Scientific, Inc., Bremen, Germany) interfaced with a dual-inlet isotope ratio mass spectrometer (Finnigan MAT 252; Thermo Fisher Scientific, Inc., Bremen, Germany) at the University of Arizona's Environmental Isotope Laboratory. Powdered otolith material was reacted with dehydrated phosphoric acid at 70 °C under vacuum, and liberated CO_2 was analyzed for stable isotope composition. All isotope values were reported in delta notation with respect to Vienna-Pee Dee Belemnite (V-PDB). Analytical precision of the mass spectrometer was calibrated based on repeated measurements of NBS-19 and NBS-18, and determined to be $\pm 0.10\text{‰}$ for $\delta^{18}\text{O}$ and $\pm 0.08\text{‰}$ for $\delta^{13}\text{C}$ (1 sigma).

2.3.3 Data Analysis

Classification baselines were developed separately for the older (1998–2000) and recent (2011–2016) year-classes due to a large shift in $\delta^{18}\text{O}$ values (see results). Analyses for year-classes 1998–2000 and 2011 relied on data from Redding et al.,

(2020) but used a different classification procedure. Two-way multivariate analysis of variance (MANOVA) was used to test joint differences in the stable isotope composition ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values) of juvenile baseline samples across contingents (northern and southern), year-classes (2011–2016), and interaction. A separate two-way MANOVA was conducted to test joint differences in the otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of US-collected juvenile samples across sub-regions (Gulf of Maine, Georges Bank, and Southern New England; Figure 2.1), year-classes (2011–2016), and interaction. Significance of two-way MANOVAs was based on Pillai's trace statistic. A binomial generalized linear mixed model (GLMM; *glmer* in the *lme4* package; Bates et al., 2015) was fitted to the age-1 juvenile baseline data with a binomial distribution and logit link function. $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values were used as fixed effects to estimate the probability of fish belonging to either contingent (northern or southern), and year-class was fitted as a random intercept in the model (i.e., the intercept is permitted to vary by year-class) to account for the interannual variation in the baseline stable isotope composition (Harrison et al., 2018). We also attempted to allow all predictors to have separate slopes for each year-class (i.e., random slopes), although increased model complexity resulted in (near) singular fits and almost no improvement in classification accuracy (<1.5%). The parsimonious random intercept model was therefore accepted as the best model for contingent classification. Random oversampling (with replacement) was employed prior to model fitting to balance sample sizes for year-classes 2000 and 2011 baselines, in which the southern contingent made up >60% of the baseline. For these year-classes, northern contingent data were randomly oversampled from the dataset within the specific year-class.

Model diagnostics through residual inspections were performed with the *DHARMA* package (Hartig, 2020). Classification accuracy of the baseline model was assessed through 10-fold cross-validation. In classifying baseline samples to each contingent, threshold classification probability levels of >0.5 and >0.7 were employed. Individuals that fell below the threshold probability level of >0.7 were unassigned to either contingent. This baseline was then used to predict contingent membership (northern or southern) of age ≥ 2 unknown adult samples collected within the US shelf waters. For adult classification, a threshold classification probability level of >0.7 was employed for probability of assignment to each contingent to account for the lack of strong separation between the two contingents in the baseline stable isotope composition (Kerr et al., 2020). Adult samples that fell below this threshold probability were unassigned to either contingent and were excluded from further analyses. Based on results of adult classification, contingent composition of Atlantic mackerel collected within US waters was characterized by year-class, age, size, and month and region of capture. For assessing contingent composition across regions, samples collected within each area during 2013–2019 were categorized into four broader regions: MAB, SNE, GB, and GOM (Figure 2.1). Differences in frequencies of contingents across year-classes, age, size, and month of capture were assessed using Fisher’s exact tests with p -values estimated through 2000 Monte Carlo simulations. The influence of contingent mixing on US commercial fisheries landings was examined by fitting a linear regression of log-transformed US commercial fisheries landings against estimated proportion of the northern contingent by year of capture through ordinary least squares minimization and assessed using Pearson’s

correlation coefficient (r). Landings from November to April were used to represent months with high landings (Figure 2.2) and when contingent mixing is expected to be most prevalent (Sette, 1950; Moores et al., 1975). As peak landings have shifted to occur earlier in the season during the past two decades (Figure 2.2), we selected the top three monthly landings during November to April to represent this historical winter fishery. We further assessed the relationship between contingent mixing levels and combined landings from July to October to test whether contingent mixing levels have no influence on landings during months when the northern contingent are expected to be absent from US waters. Statistical analyses were performed with R version 4.0.2 (R Core Team, 2020) with a significance alpha of 0.05.

2.4 Results

2.4.1 Baseline Otolith Stable Isotope Composition

Among recent year-class samples, significant differences of baseline otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values were detected between contingents (Two-way MANOVA, $p_{\text{contingent}} < 0.001$; Figure 2.3), and across year-classes ($p_{\text{year-class}} < 0.001$), but the interaction between contingent and year-class was not significant ($p_{\text{contingent:year-class}} = 0.14$). No significant sub-regional differences of baseline otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values were detected for US-collected juvenile samples (Two-way MANOVA, $p_{\text{sub-region}} = 0.64$, $p_{\text{year-class}} < 0.001$, $p_{\text{sub-region:year-class}} = 0.53$). Baseline otolith $\delta^{18}\text{O}$ values showed a pronounced shift during the past two decades: the northern contingent exhibited higher values than the southern contingent for the older samples (1998–2000 year-classes), but showed lower values for the recent samples (2011–2016 year-classes).

The two contingents exhibited similar $\delta^{13}\text{C}$ values for the older samples, although the northern contingent exhibited higher values for some year-classes during the recent period (i.e., year-classes 2013 and 2015).

2.4.2 Classification Accuracy of the Common Classification Baseline

Cross-validated mean classification accuracy of the mixed effects model was 79.7% for the recent (2011–2016), and 97.9% for the older (1998–2000) year-class baselines with a threshold probability level of >0.7 (Table 2.1). For both baselines, including $\delta^{13}\text{C}$ values as a second predictor and accounting for year-class effects as a random intercept in the model improved classification accuracy by 5.5% (recent) and 4.6% (older), and reduced the proportion of unassigned fish by 25.1% (recent) and 12.0% (older; Table 2.1). For the older year-class baseline, classification accuracy of the common baseline approach (97.9%) was higher than that of the year-class specific approach which used a Random Forest procedure that relied only on $\delta^{18}\text{O}$ for classification (range: 74.5–92.3%; Redding et al., 2020).

2.4.3 Contingent Mixing on the US Continental Shelf and Contingent Composition Characteristics

A threshold classification probability level of >0.7 resulted in an exclusion of 12 and 123 (10.9% and 46.1% of total samples) age ≥ 2 adult samples from the older and recent year-classes. Additionally, a probability level of >0.5 was tested (resulting in no excluded individuals), which resulted in no to small changes ($<10\%$) in contingent membership across most categories of interest (Table S2.2). While moderate changes ($>15\%$) in contingent memberships occurred in few categories with small sample

size, contingent composition characteristics were generally consistent between two threshold probability levels. Classification of age ≥ 2 adults based on otolith carbon and oxygen stable isotopes indicated that mixing between the northern and southern contingents was prevalent during the past two decades in US shelf waters (Figure 2.4). Contingent membership frequencies of assigned samples (probability >0.7) were significantly different across recent year-classes (Fisher's exact test, $p < 0.001$). Among assigned samples, the northern contingent was dominant for the 2015 year-class (75% northern), but the southern contingent dominated year-classes 2011 (87% southern), and 2016 (83% southern).

Contingent composition estimated by age-class for recent year-classes indicated that among individuals that met the probability threshold level of >0.7 , age-2 fish were composed largely of the northern contingent, but ages 3 and 4 were more likely to be of the southern contingent (Fisher's exact test, $p < 0.001$; Figure 2.5a). This pattern is in stark contrast to that of the year-classes drawn for the earlier period where age-2 fish were dominated by the southern contingent, and the majority of ages 3 and 4 were of the northern contingent (Fisher's exact test, $p < 0.001$; Figure 2.5a). Contingent frequencies were significantly different across size for the recent year-classes (Fisher's exact test, $p < 0.001$), in which the proportion of the southern contingent increased with fish length (Figure 2.5b).

Estimated contingent composition by region at capture for recent year-classes indicated that during the period of January to May, the northern contingent co-occurred with the southern contingent off the Delmarva Peninsula (Delaware, USA) in the south, to the Gulf of Maine in the north (Figure 2.6). Significant differences in

contingent frequencies among assigned samples (probability >0.7), were found across months at all regions (Fisher's exact test, $p_{MAB} < 0.05$; $p_{GB} < 0.05$; $p_{GOM} < 0.01$), except for the SNE (Fisher's exact test, $p_{SNE} = 0.07$). In January, samples from SNE ($n_{\text{south}} = 4$, $n_{\text{north}} = 0$) were dominated by the southern contingent, with all samples from the GOM ($n_{\text{south}} = 0$, $n_{\text{north}} = 4$) represented by the northern contingent. The majority of samples in February in the MAB ($n_{\text{south}} = 18$, $n_{\text{north}} = 20$), SNE ($n_{\text{south}} = 3$, $n_{\text{north}} = 8$), and GB ($n_{\text{south}} = 2$, $n_{\text{north}} = 10$) were of the northern contingent, with a greater proportion of the northern contingent occurring in the SNE than in the previous month. The northern contingent further dominated samples from the MAB ($n_{\text{south}} = 11$, $n_{\text{north}} = 20$) and SNE ($n_{\text{south}} = 1$, $n_{\text{north}} = 2$) in March. The southern contingent dominated sample composition in the MAB ($n_{\text{south}} = 6$, $n_{\text{north}} = 0$) during April, although samples caught in SNE ($n_{\text{south}} = 1$, $n_{\text{north}} = 2$), GB ($n_{\text{south}} = 1$, $n_{\text{north}} = 1$) and GOM ($n_{\text{south}} = 5$, $n_{\text{north}} = 5$) were composed of nearly equal proportions of both contingents. In May, nearly all samples collected in GB ($n_{\text{south}} = 5$, $n_{\text{north}} = 1$) and GOM ($n_{\text{south}} = 8$, $n_{\text{north}} = 0$) were exclusively from the southern contingent.

A positive, although not statistically significant relationship (Pearson's $r = 0.60$, $p = 0.07$, $n = 10$), was observed between the estimated proportion of northern contingent in the US shelf waters (age ≥ 2) and landings during peak winter months, with larger residuals occurring for high stock mixing levels (Figure 2.7a). No relationship was apparent (Pearson's $r = 0.10$, $p = 0.78$, $n = 10$) between northern contingent contribution and landings from July to October (Figure 2.7b).

2.5 Discussion

Evaluation of contingent mixing of Northwest Atlantic mackerel revealed decadal changes in the relative availability of the northern contingent to US fisheries. Despite substantial decrease in spawning stock biomass of the dominant northern contingent (DFO, 2019) (Figure S2.1a), contingent mixing persisted during the past two decades (2000–2019), providing an important seasonal subsidy to the US commercial fishery, particularly during the winter months when peak landings occur. Still, the relative contribution of the northern contingent has diminished in some year-classes during the most recent decade.

Spatial and temporal trends in contingent composition among samples collected in 2013–2019 corresponded well with traditional views on seasonal migration patterns and population structure of the Northwest Atlantic mackerel (Sette, 1950; Moores et al., 1975; NEFSC, 2018; Smith et al., 2020). Some degree of spatial segregation occurred between the two contingents in January, consistent with the onset of the southerly (fall) migration and overwintering by the northern contingent in US shelf waters (Figure 2.6). Spatial mixing was strongest during February and March when the northern contingent occurred as far south as the Delmarva Peninsula, which matches results from tag-recapture studies (Moores et al., 1975). These months correspond well with periods when peak landings occur in the US fishery (Figure 2.2), most likely because the northern contingent are subjected to exploitation in those regions. The near absence of the northern contingent from the MAB in April, and from the GB and GOM in May aligns with the departure of the northern contingent from the US continental shelf waters to make their northerly (spring) migration

towards the spawning sites in the Gulf of St. Lawrence. Interestingly, during part of the spawning season, April, the northern contingent co-occurred with the southern contingent, which could provide support for straying between the two contingents should the northern contingent be spawning within US waters (Lambrey de Souza et al., 2006).

Otolith stable isotope composition analysis presented here and by Redding et al., (2020) indicate prevalent contingent mixing within the US continental shelf during the past two decades (2000–2019). Contingent mixing levels of the Northwest Atlantic mackerel within the US continental shelf could be influenced by changes in migration behaviors and/or relative abundance differences between the two contingents (Secor, 2014). Distribution shifts and range expansion by Atlantic mackerel has been associated with changes in oceanographic conditions (Overholtz et al., 2011; Radlinski et al., 2013) and stock size (Nøttestad et al., 2016; Olafsdottir et al., 2019). Yet the apparent winter distribution of the northern contingent was consistent with historical distributions (Moores et al., 1975) (Figure 2.6), and contingent mixing persisted during the past two decades despite substantial depletion in spawning stock biomass (SSB) of the dominant northern contingent (DFO, 2019) (Figure S2.1a). Still, the apparent disappearance of older/larger members of northern contingents during the recent decade (2013–2019; Figure 2.5) likely reflects depleted stock status and severe age truncation experienced by the northern contingent (DFO, 2019).

Contingent mixing levels were highly variable among year-classes: the northern contingent dominated sample composition of the 2015 year-class, but the

majority of samples for year-classes 2011, and 2016 were of the southern contingent (Figure 2.4). This variation could be partially explained by the recruitment strength of the northern contingent, in which high mixing levels in the 2015 year-class samples was attributed to the moderately strong 2015 year-class, and low mixing levels of the 2016 year-class reflecting historically low recruitment levels (DFO, 2019) (Figure S2.1b). The strongest year-class in the past two decades occurred in 1999 (Castonguay et al., 2008), although recruitment strength was not reflected in the contingent composition for that year-class (Figure 2.4: 46.7% northern). This inconsistency could be due to relatively strong egg and larval productions of the southern contingent during the early 2000s (McManus, 2017; Richardson et al., 2020). While contingent mixing levels are likely strongly influenced by relative recruitment strengths of both contingents, recruitment estimates for the southern contingent remains highly uncertain given that the US assesses both contingents as a unit stock, whereas Canada assesses the northern contingent in isolation. Still, recruitment strength of the northern contingent should have a larger effect on the observed stock mixing dynamics as the northern contingent is more productive than the southern contingent (NEFSC, 2018). It is also important to note that contingent mixing levels within each year-class could be influenced by the unbalanced sample size of age-classes for some year-classes (e.g., 2000, 2016), given the observed ontogenetic trends in contingent mixing levels (Figure 2.5a).

The hypothesis of whether contingent mixing levels are associated with US landings during the winter period was tested. A positive correlation (albeit not significant) occurred between the northern contingent contribution and landings

during peak winter months when contingent mixing is expected to be most prevalent (Figure 2.7a). Further, in line with our expectations, contingent mixing levels had negligible influence on landings during periods when northern contingents should be absent from the US waters (July–October). While small sample size precludes strong inferences, these results could imply that higher contingent mixing levels might be associated with greater landings for the US winter mackerel fishery, such as was observed for the strong 2015 northern contingent year-class (year of capture: 2017 and 2018). It is also worth highlighting that the US winter fishery has shifted from a multi-month fishery through January to April (2000–2010), to one which depends on a single-month pulse during November to February (2011–2019; Figure 2.2). This transition towards a single-month pulse fishery during the recent decade (2011–2019) could be indicative of the diminished stock status of the northern contingent, and could be one reason for the lack of a strong relationship between northern contingent contribution and US winter landings. Additionally, fluctuations in mackerel landings also reflect factors that are independent of mackerel availability including regulations related to the incidental catches of river herring/shad (*Alosa* spp.), market demands, fuel costs, and fleet and processing capacity.

Otolith stable isotope composition ($\delta^{18}\text{O}/\delta^{13}\text{C}$ values) baselines for the recent year-class samples (2011–2016) exhibited significant differences between the two contingents (Figure 2.3), which follows previous studies that have successfully discriminated between the two contingents through otolith tracer approaches (Moura et al., 2020; Redding et al., 2020). Significant temporal variability occurred in the baseline stable isotope composition, which could be due to regional shifts in

temperature and water chemistry. Notably, baseline otolith $\delta^{18}\text{O}$ values exhibited a pronounced shift during the past two decades (2000–2019; Figure 2.3). Interdecadal shifts in the baseline otolith stable isotope composition has been reported for Atlantic bluefin tuna, attributed to the decrease in $\delta^{13}\text{C}$ values of atmospheric CO_2 and increase in seawater $\delta^{18}\text{O}$ values in the Atlantic Ocean over the past several decades (Schloesser et al., 2009, 2010). Because otolith aragonite forms close to isotopic equilibrium with the oxygen isotope composition of ambient water (Kalish, 1991; Thorrold et al., 1997; Campana, 1999), the decadal shift in otolith $\delta^{18}\text{O}$ values could be associated with changes in large-scale oceanographic drivers including the Atlantic meridional overturning circulation (AMOC; Caesar et al., 2018), which alters seawater composition within the US continental shelf (Saba et al., 2016). Accelerated warming trends within the US continental shelf waters from the late 2000s (Pershing et al., 2015; Brickman et al., 2018) could also influence natal otolith $\delta^{18}\text{O}$ values through temperature-dependent fractionation (Kalish, 1991; Thorrold et al., 1997). Failing to incorporate such temporal variability in the baseline stable isotope composition could confound the performance of stock classification.

Temporal variability in otolith chemistry often requires (i) matching of unknown adults to a corresponding year-class baseline (Thorrold et al., 2001; Gillanders, 2005; Redding et al., 2020); or (ii) aggregating across multiple year-classes to fully represent temporal variation within the baseline (Rooker and Secor, 2019). We adopted a hybrid approach through application of a mixed effects model, in which the intercept was permitted to vary by year-class (Harrison et al., 2018). Classification accuracy was further improved by incorporating $\delta^{13}\text{C}$ values as a

second predictor, which could be indicative of regional differences in the carbon stable isotope composition of the food source and/or dissolved inorganic carbon (DIC) in seawater (Kalish, 1991; Solomon et al., 2006; Tohse and Mugiya, 2008), as well as differences in contingent-specific metabolic rates during their juvenile growth period (Høie et al., 2004; Chung et al., 2019; Martino et al., 2020).

Results on stock composition can vary based on the classification threshold probability of choice. A threshold probability level of >0.7 was employed for individual assignment to account for the incomplete separation between the baseline stable isotope composition of the two contingents, although caution must be exercised when estimating stock composition through individual assignment as it ignores uncertainty associated with each individual assignment. Future studies should consider employing mixture analysis which estimates stock composition jointly on all individuals rather than summing independent assignments (Manel et al., 2005). It is also important to note that biases could arise from incomplete spatiotemporal sampling, although the majority of samples in this study were collected in areas with high mackerel landings and during months when contingent mixing was expected to be most prevalent (Sette, 1950; Moores et al., 1975). Analyzing samples from both the spring and fall NEFSC bottom trawl survey should be valuable next steps to fully uncover the seasonal migration patterns of the Northwest Atlantic mackerel, and to understand any potential sampling bias. Further, given that contingent mixing is highly dynamic and is likely to change over longer time scales (Siskey et al., 2016), future efforts should focus on analyzing samples during periods of exceptionally high landings (i.e., 1970s) when southern contingent contribution to the overall population

was expected to be high (Richardson et al., 2020). Additionally, while contingent mixing is more likely to occur within the US fishery (Sette, 1950), it is important to assess the contribution of the southern contingent to the Canadian fishery and whether this can change over time.

Harvesting a mixed-stock comprised of multiple population sub-components of unique demographics under a unit stock concept can potentially lead to overexploiting the less productive component as it receives a greater proportion of fishery removal than the productive component (Ricker, 1958; Cadrin and Secor, 2009; Kerr et al., 2017). It is important to guard against loss of such minority components as they can contribute to population stability and resilience through the “portfolio effect” (Secor et al., 2009; Kerr et al., 2010). Information on contingent composition could further help develop spatially explicit stock assessment models for the Northwest Atlantic mackerel population to provide advice designed to conserve both contingents (Cadrin and Secor, 2009; Goethel et al., 2011; Van Beveren et al., 2019). Observed contingent mixing among the Northwest Atlantic mackerel during the past two decades (2000–2019) provides support for incorporating spatial structure in stock assessment and management which could potentially conserve both productivity and stability of this depleted two-component population.

2.6 Acknowledgements

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Tables

Table 2.1 Cross-validated mean classification accuracy and proportion of unassigned fish of the classification model that relied only on $\delta^{18}\text{O}$ values and the mixed effects model which included $\delta^{13}\text{C}$ values as a second predictor and accounted for year-class effects as a random intercept. Classification accuracy is shown for threshold classification probability level of >0.7 (outside parenthesis) and >0.5 (inside parenthesis). Classification accuracy of the year-class specific approach which used a Random Forest procedure that relied only on $\delta^{18}\text{O}$ values is also shown (Redding et al., 2020).

Model	Older (1998–2000 year-class)		Recent (2011–2016 year-class)	
	%classification accuracy	%unassigned	%classification accuracy	%unassigned
Contingent $\sim \delta^{18}\text{O}$	93.3 (88.0)	16.2	74.2 (62.9)	72.3
Contingent $\sim \delta^{18}\text{O} + \delta^{13}\text{C} + (1 \text{Year-class})$	97.9 (96.9)	4.2	79.7 (69.8)	47.2
Random Forest (Redding et al., 2020)	Range: 74.5–92.3%	—	—	—

Figures

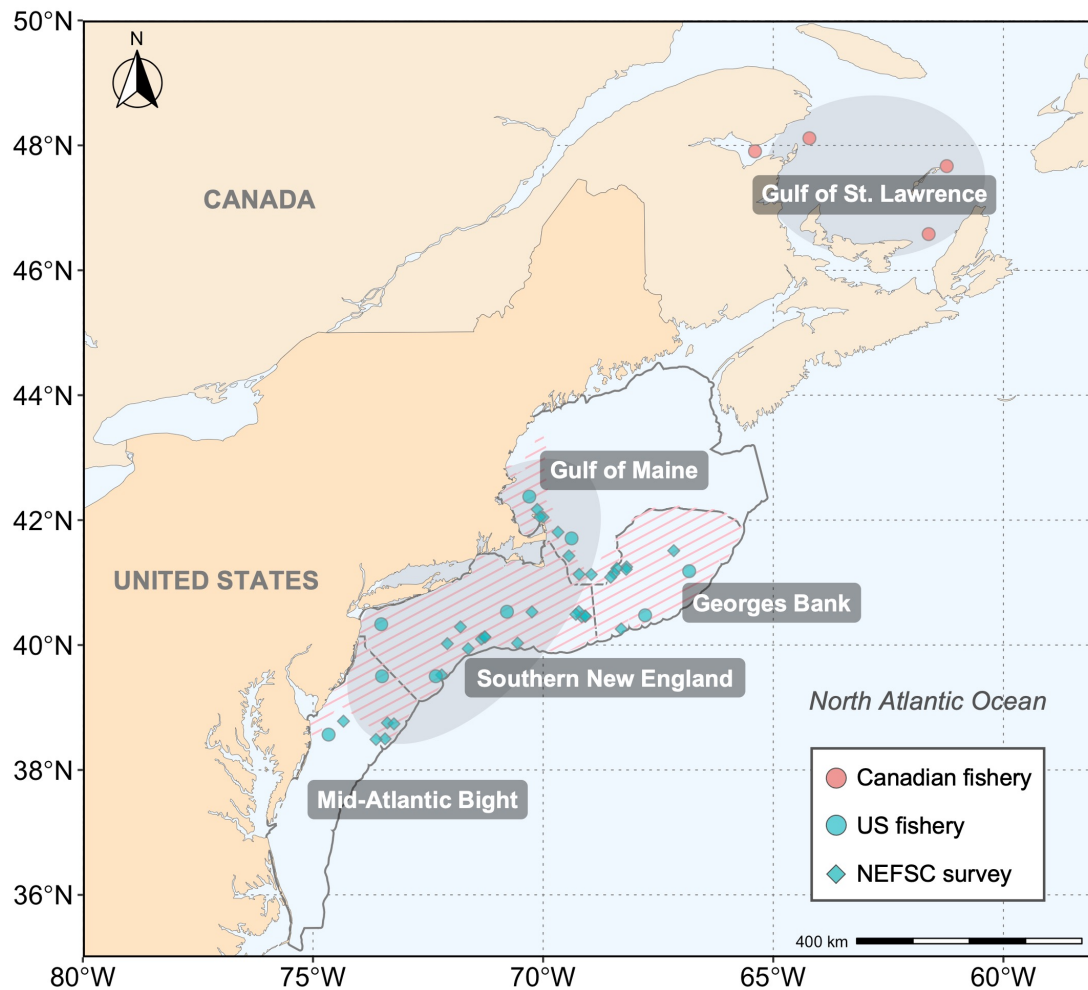


Figure 2.1 Map of the western North Atlantic Ocean illustrating sampling areas and spawning sites of the Northwest Atlantic mackerel. Sample locations are shown for the US winter fishery, the Canadian summer fishery, and the Northeast Fisheries Science Center (NEFSC) fishery-independent bottom trawl survey. Shaded ellipses in the Gulf of St. Lawrence and US continental shelf depict principal spawning sites for the northern and southern contingents. Hatched areas in the US continental shelf illustrate principal contingent mixing regions during winter. The map was created in R using the ggplot2 package version 3.3.2 URL: <https://ggplot2.tidyverse.org> (Wickham, 2016).

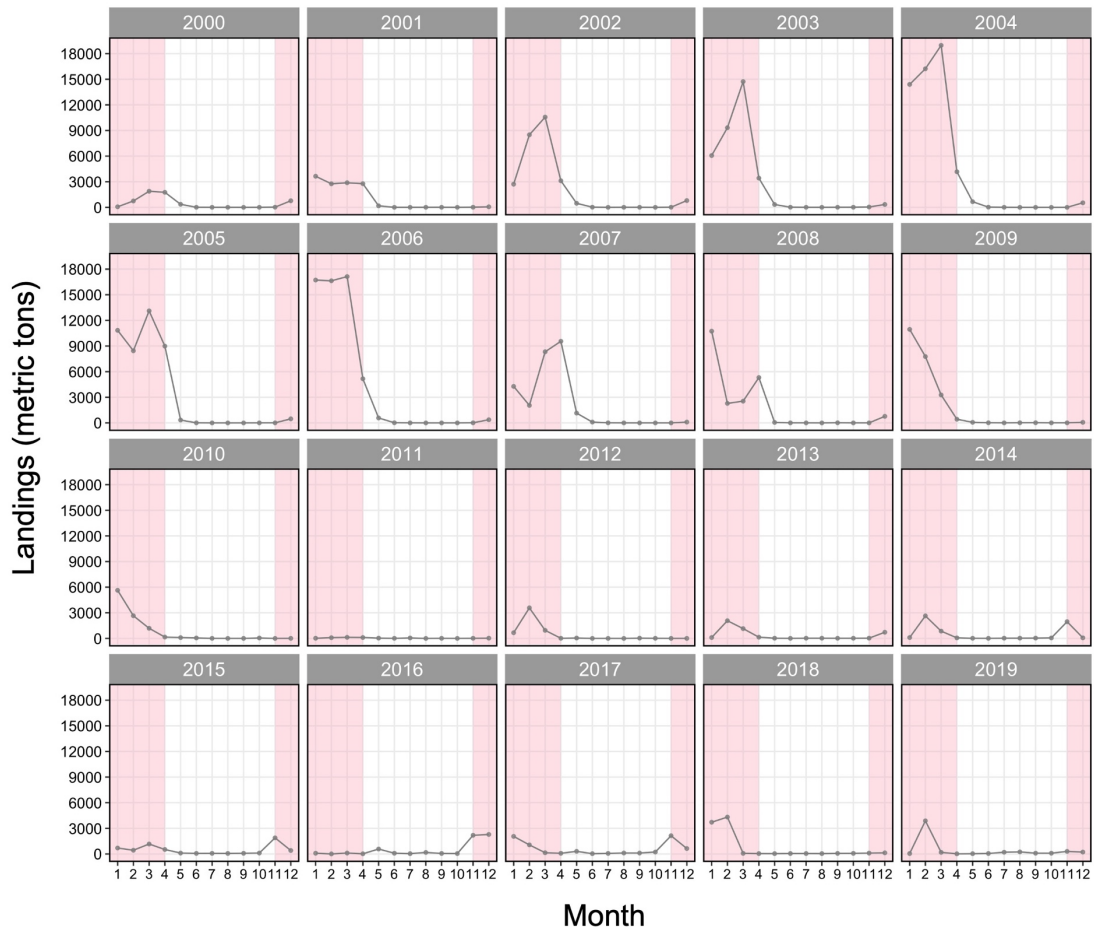


Figure 2.2 Monthly time series of US commercial mackerel landings from 2000 to 2019. Shaded backgrounds represent months with typically high landings (November–April). Data obtained from National Marine Fisheries Service, Northeast Fisheries Science Center (NMFS-NEFSC).

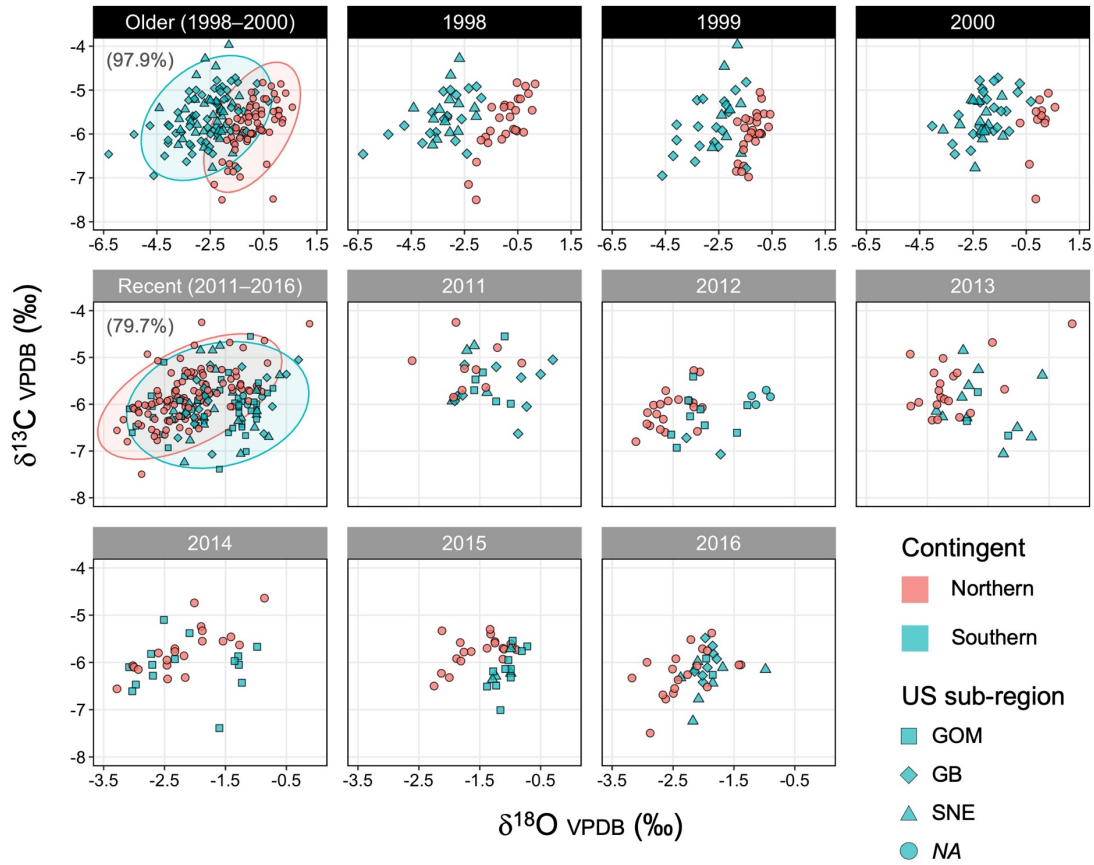


Figure 2.3 Otolith oxygen and carbon stable isotopes ($\delta^{18}\text{O}/\delta^{13}\text{C}$ values) for Northwest Atlantic mackerel juvenile baseline samples collected in Canadian and US waters for older (black headers: 1998–2000) and recent (gray headers: 2011–2016) year-classes. The left plots in the first and second rows provide values for all year-classes combined with 95% confidence ellipses and cross-validated classification accuracy with threshold probability level of >0.7 shown. Different symbols within US juvenile samples represent samples collected at different regions within US waters with *NA* indicating samples with no information on location of capture. All isotope values were reported in delta notation with respect to Vienna-Pee Dee Belemnite (V-PDB). Age-2 samples collected in the summer Canadian fishery in the Gulf of St. Lawrence were included in baselines for year-classes 1998, 1999, 2011, and 2016 to complement age-1 northern contingents that were insufficient in samples size. Note that the scales of the x-axis differ between older and recent samples. Data for year-classes 1998–2000 and 2011 are from Redding et al., (2020).

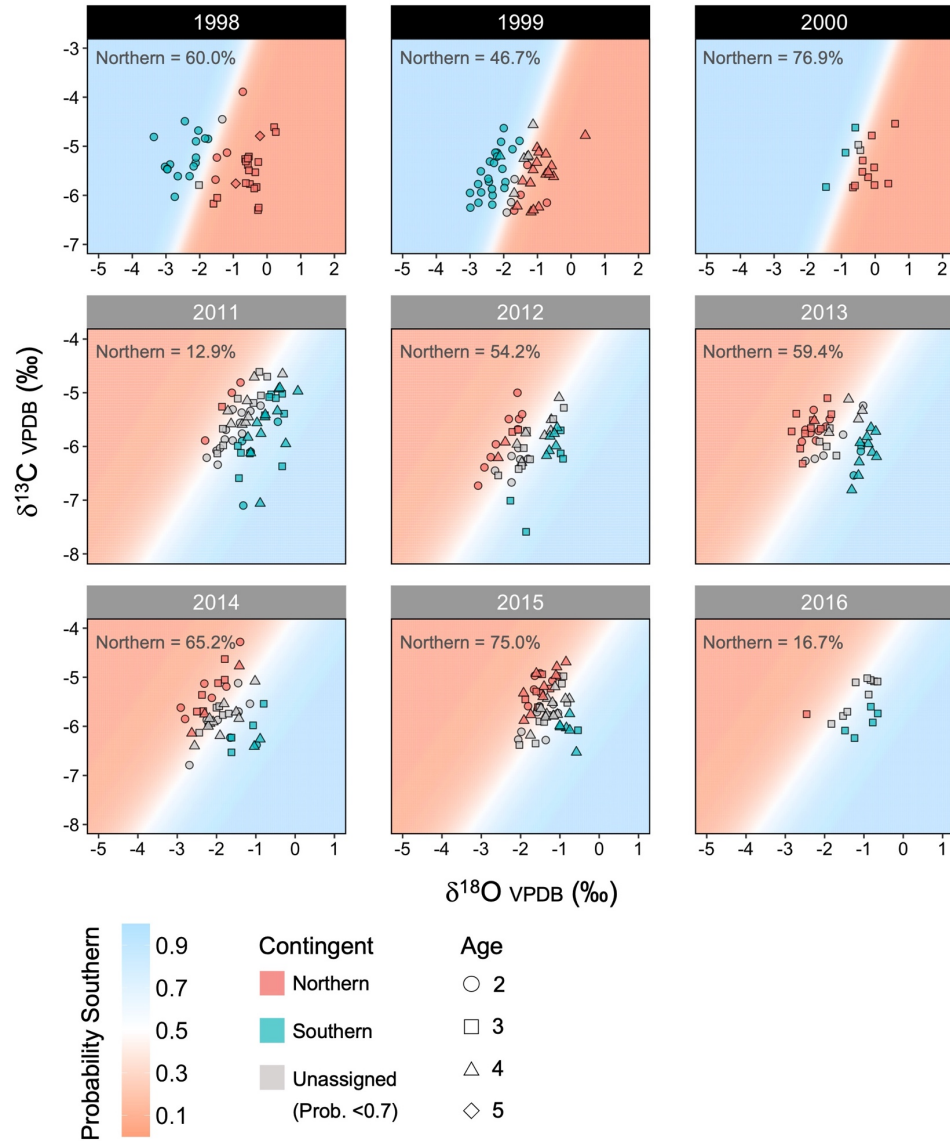


Figure 2.4 Otolith oxygen and carbon stable isotopes ($\delta^{18}\text{O}/\delta^{13}\text{C}$ values) for age ≥ 2 unknown adult Northwest Atlantic mackerel samples collected in the US shelf waters for 9 year-classes (1998–2000 and 2011–2016) classified based on the binomial generalized linear mixed model. Background colors indicate the probability of each individual assigned to either contingent (0.7 threshold). Different symbols represent different age-classes within each year-class. The proportion of the northern contingent of assigned fish (probability > 0.7) for each year-class is shown in the top left corner of each panel. All isotope values were reported in delta notation with respect to Vienna-Pee Dee Belemnite (V-PDB). Note that classification baselines were developed separately for the older and recent year-classes and the scales of the x- and y-axes differ between those panels.

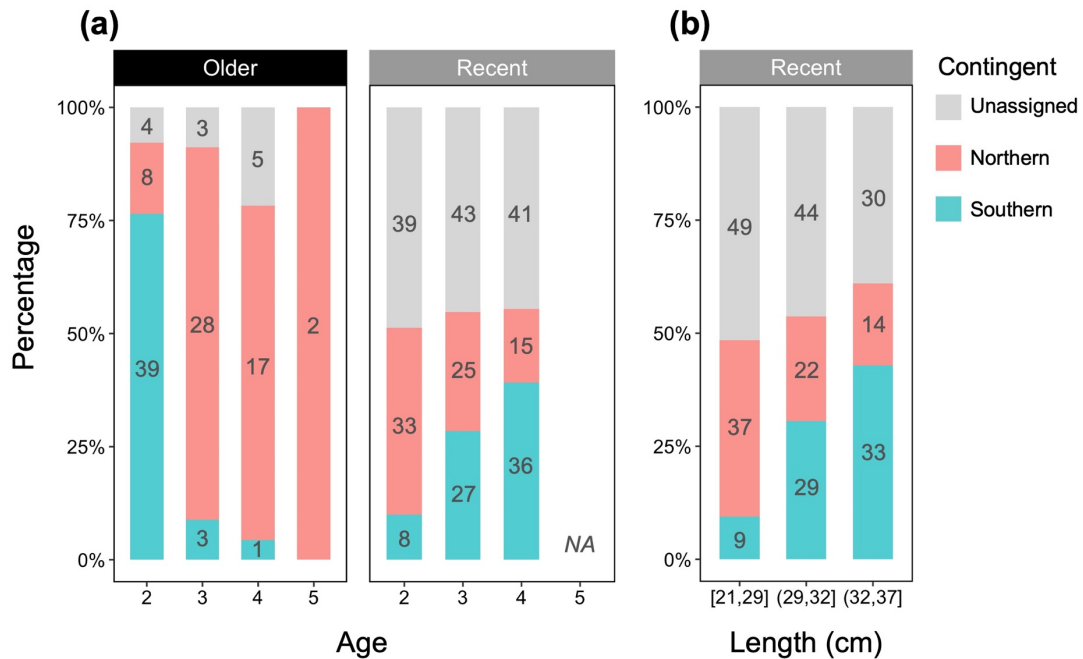


Figure 2.5 Contingent composition of Northwest Atlantic mackerel age ≥ 2 adult samples across (a) age class for older (1998–2000) and recent (2011–2016) year-classes, and (b) size class (cm) for the recent year-class samples. Numbers in each bar plot indicate the sample size of northern and southern contingents, and unassigned fish (probability < 0.7) for each age and size class.

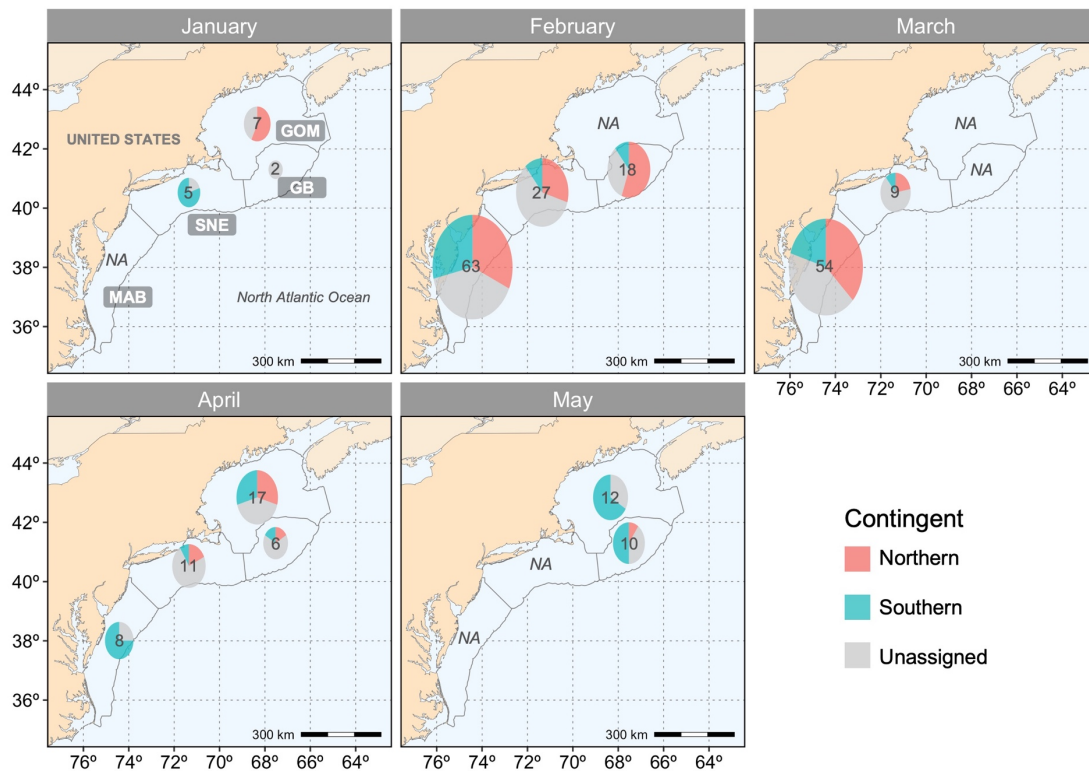


Figure 2.6 Contingent composition of Northwest Atlantic mackerel age ≥ 2 adult samples by region at capture through January and May collected in 2013–2019. The four regions (MAB, SNE, GB, GOM) are shown in outlined boxes. Each pie chart indicates the number of samples collected within each region, and is proportional to the sample size. The map was created in R using the ggplot2 package version 3.3.2 URL: <https://ggplot2.tidyverse.org> (Wickham, 2016).

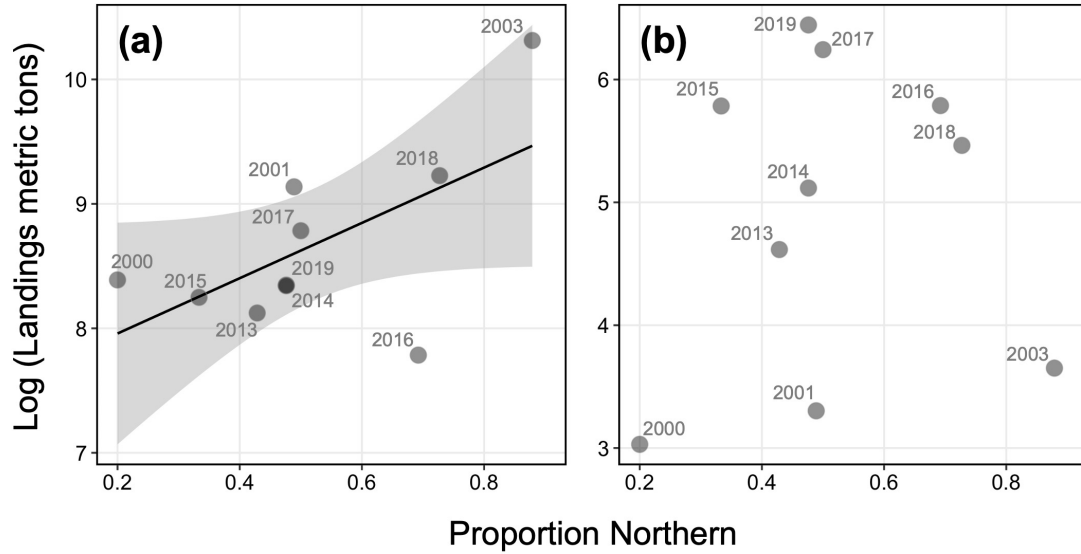


Figure 2.7 Relationship between the estimated annual proportion of northern contingents of assigned fish (probability >0.7) occurring within the US shelf waters and (a) combined top three monthly US commercial landings during November to April and (b) combined landings from July to October. Data points are labeled by year of capture. The black line indicates the linear regression line fitted to the data and the shaded area indicates 95% confidence intervals. Note that the scale of the y-axis differs among panels.

Supplementary Material

Table S2.1 Northwest Atlantic mackerel otolith sample size by year-class, sampling period, collection site, and age-class. Data for year-classes 1998–2000 and 2011 are from Redding et al., (2020).

Year-class	Years collected	Collection site	Age				
			1	2	3	4	5
1998 (N = 102)	1999–2001, 2003	Canada	15	13			
		Gulf of Maine					
		Georges Bank	18	10	7		
		Southern New England	14	11	7		2
		Mid-Atlantic Bight			5		
		NA					
1999 (N = 107)	2000, 2001, 2003	Canada	12	15			
		Gulf of Maine					
		Georges Bank	19	14		4	
		Southern New England	8	16		16	
		Mid-Atlantic Bight				3	
		NA					
2000 (N = 66)	2001, 2003	Canada	12				
		Gulf of Maine					
		Georges Bank	24		2		
		Southern New England	15		7		
		Mid-Atlantic Bight			6		
		NA					
2011 (N = 89)	2012–2015	Canada		9			
		Gulf of Maine	6	7		16	
		Georges Bank	10	4	10		
		Southern New England	4		2	4	
		Mid-Atlantic Bight		9	8		
		NA					
2012 (N = 80)	2013–2016	Canada	20				
		Gulf of Maine	9			7	

2013 (N = 79)	2014–2017	Georges Bank	2	15	3
		Southern New England			2
		Mid-Atlantic Bight		15	3
		NA	4		
		Canada	20		
		Gulf of Maine	3		
		Georges Bank			
		Southern New England	11		
		Mid-Atlantic Bight		15	15
		NA			
2014 (N = 80)	2015–2018	Canada	20		
		Gulf of Maine	15		
		Georges Bank			
		Southern New England			12
		Mid-Atlantic Bight		15	15
		NA			
		Canada	20		
		Gulf of Maine	11	7	5
		Georges Bank			2
		Southern New England	4		15
2015 (N = 92)	2015–2019	Mid-Atlantic Bight		8	3
		NA			4
		Canada	20		
		Gulf of Maine	11	7	5
		Georges Bank			2
		Southern New England	4		15
		Mid-Atlantic Bight		8	3
		NA			4
		Canada	20		
		Gulf of Maine	11	7	5
2016 (N = 52)	2017–2019	Georges Bank			2
		Southern New England	4		15
		Mid-Atlantic Bight		8	3
		NA			4
		Canada	20		
		Gulf of Maine	11	7	5
		Georges Bank			2
		Southern New England	4		15
		Mid-Atlantic Bight		8	3
		NA			4
2016 (N = 52)	2017–2019	Canada	20		
		Gulf of Maine	11	7	5
		Georges Bank			2
		Southern New England	4		15
		Mid-Atlantic Bight		8	3
		NA			4
		Canada	20		
		Gulf of Maine	11	7	5
		Georges Bank			2
		Southern New England	4		15
		Mid-Atlantic Bight		8	3
		NA			4
2016 (N = 52)	2017–2019	Canada	20		
		Gulf of Maine	11	7	5
		Georges Bank			2
		Southern New England	4		15
		Mid-Atlantic Bight		8	3
		NA			4
		Canada	20		
		Gulf of Maine	11	7	5
		Georges Bank			2
		Southern New England	4		15
		Mid-Atlantic Bight		8	3
		NA			4
2016 (N = 52)	2017–2019	Canada	20		
		Gulf of Maine	11	7	5
		Georges Bank			2
		Southern New England	4		15
		Mid-Atlantic Bight		8	3
		NA			4
		Canada	20		
		Gulf of Maine	11	7	5
		Georges Bank			2
		Southern New England	4		15
		Mid-Atlantic Bight		8	3
		NA			4

Table S2.2 Summary contingent composition of Northwest Atlantic mackerel age ≥ 2 adult samples by year-class, age-class, size-class, and region of capture through January to May estimated using a binomial generalized linear mixed model with threshold classification probability level of 0.7 and 0.5. Note that contingent composition for threshold probability level of 0.7 show proportion of samples that met the 0.7 threshold. Values in parentheses for the sample size (n) indicate the percentage of samples below the 0.7 threshold (unassigned). Data for year-classes 1998–2000 and 2011 are from Redding et al., (2020).

Category		Contingent	n	Composition Prob. >0.7 (%)	n	Composition Prob. >0.5 (%)
Year-class	1998	Northern	40 (4.8)	60.0	42	59.5
		Southern		40.0		40.5
	1999	Northern	45 (15.1)	46.7	53	50.9
		Southern		53.3		49.1
	2000	Northern	13 (13.3)	76.9	15	80.0
		Southern		23.1		20.0
	2011	Northern	31(48.3)	12.9	60	25.0
		Southern		87.1		75.0
	2012	Northern	24 (46.7)	54.2	45	46.7
		Southern		45.8		53.3
	2013	Northern	32 (28.9)	59.4	45	60.0
		Southern		40.6		40.0
	2014	Northern	23 (48.9)	65.2	45	66.7
		Southern		34.8		33.3
	2015	Northern	28 (50.9)	75.0	57	71.9
		Southern		25.0		28.1
	2016	Northern	6 (60.0)	16.7	15	13.3
		Southern		83.3		86.7
Age-class (Older)	2	Northern	47 (7.8)	17.0	51	21.6
		Southern		83.0		78.4
	3	Northern	31 (8.8)	90.3	34	88.2
		Southern		9.7		11.8
	4	Northern	18 (21.7)	94.4	23	91.3
		Southern		5.6		8.7
	5	Northern	2 (0.0)	100.0	2	100.0
		Southern		0.0		0.0
Age-class (Recent)	2	Northern	41 (48.8)	80.5	80	67.5
		Southern		19.5		32.5
	3	Northern	52 (45.3)	48.1	95	48.4

Size-class (cm)	4	Southern		51.9		51.6	
		Northern	51 (44.6)	29.4	92	39.1	
		Southern		70.6		60.9	
	<29	Northern	63 (33.7)	71.4	95	67.4	
		Southern		28.6		32.6	
	29–32	Northern	34 (64.2)	41.2	95	46.3	
		Southern		58.8		53.7	
	>32	Northern	47 (39.0)	29.8	77	36.4	
		Southern		70.2		63.6	
	January	MAB	Northern	—	—	—	—
Southern				—		—	
SNE		Northern	4 (20.0)	0.0	5	20.0	
		Southern		100.0		80.0	
GB		Northern	0 (100.0)	—	2	0.0	
		Southern		—		100.0	
GOM		Northern	4 (42.9)	100.0	7	85.7	
		Southern		0.0		14.3	
February		MAB	Northern	38 (39.7)	52.6	63	60.3
			Southern		47.4		39.7
	SNE	Northern	11 (59.3)	72.7	27	70.4	
		Southern		27.3		29.6	
	GB	Northern	12 (33.3)	83.3	18	72.2	
		Southern		16.7		27.8	
	GOM	Northern	—	—	—	—	
		Southern		—		—	
	March	MAB	Northern	31 (42.6)	64.5	54	53.7
			Southern		35.5		46.3
SNE		Northern	3 (66.7)	66.7	9	77.8	
		Southern		33.3		22.2	
GB		Northern	—	—	—	—	
		Southern		—		—	
GOM		Northern	—	—	—	—	
		Southern		—		—	
April		MAB	Northern	6 (25.0)	0.0	8	0.0
			Southern		100.0		100.0
	SNE	Northern	3 (72.7)	66.7	11	45.5	
		Southern		33.3		54.5	
	GB	Northern	2 (66.7)	50.0	6	33.3	
		Southern		50.0		66.7	
	GOM	Northern	10 (41.2)	50.0	17	52.9	

May	MAB	Southern		50.0		47.1
		Northern	—	—	—	—
	SNE	Southern		—		—
		Northern	—	—	—	—
	GB	Southern		—		—
		Northern	6 (40.0)	16.7	10	30.0
	GOM	Southern		83.3		70.0
		Northern	8 (33.3)	0.0	12	16.7
		Southern		100.0		83.3

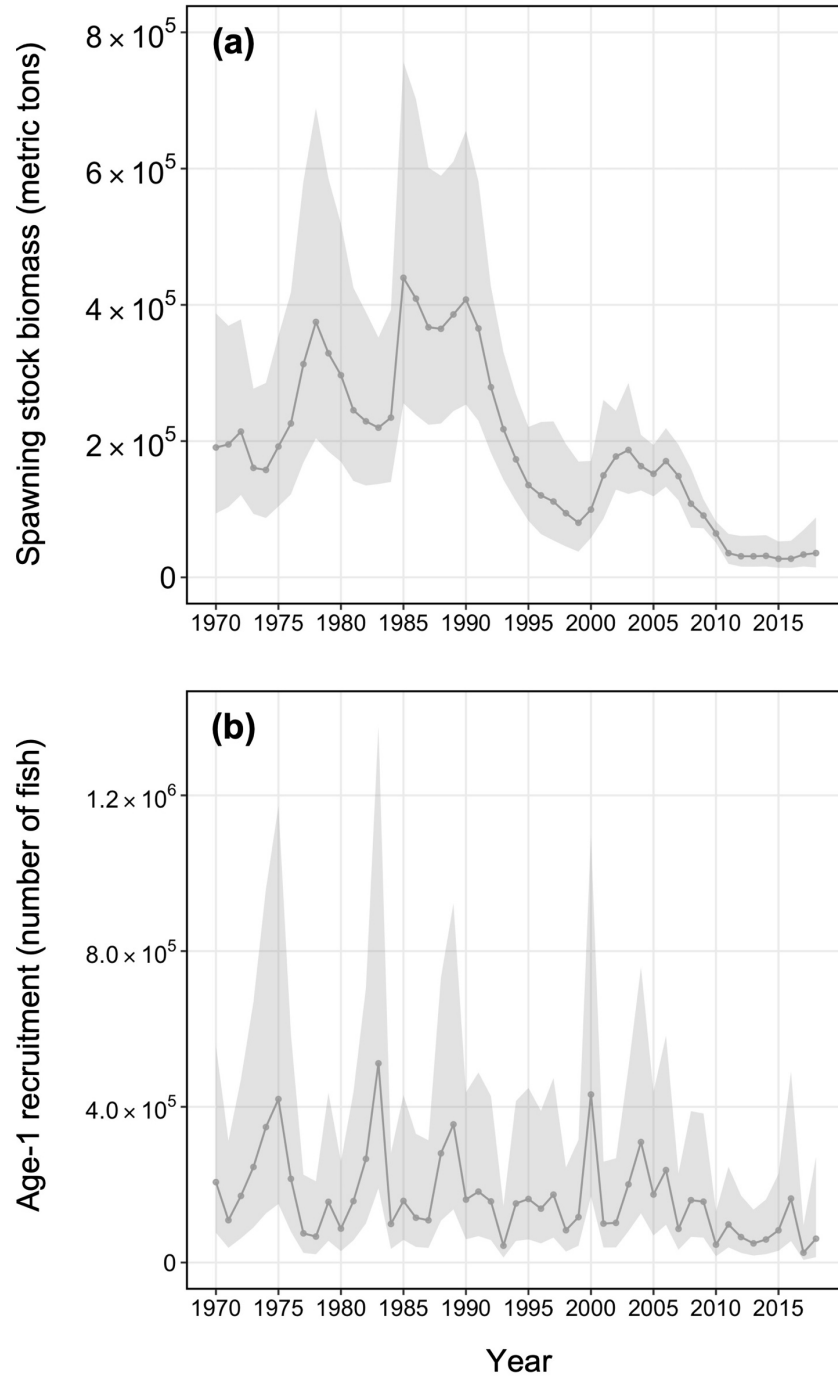


Figure S2.1 Time series (1970–2018) of Northwest Atlantic mackerel northern contingent (a) spawning stock biomass and (b) age-1 recruitment estimated by the censored-catch statistical catch-at-age model (DFO, 2019). Shaded regions indicate 95% confidence intervals. Data obtained from Fisheries and Oceans Canada (DFO).

Chapter 3: Integrating machine learning with otolith isoscapes: reconstructing connectivity of a marine fish over four decades

Arai, K., Castonguay, M., Lyubchich, V., and Secor, D. H. (2023). Integrating machine learning with otolith isoscapes: reconstructing connectivity of a marine fish over four decades. *PLoS ONE* 18, e0285702. doi: 10.1371/journal.pone.0285702.

3.1 Abstract

Stable isotopes are an important tool to uncover animal migration. Geographic natal assignments often require categorizing the spatial domain through a nominal approach, which can introduce bias given the continuous nature of these tracers. Stable isotopes predicted over a spatial gradient (i.e., isoscapes) allow a probabilistic and continuous assignment of origin across space, although applications to marine organisms remain limited. We present a new framework that integrates nominal and continuous assignment approaches by (1) developing a machine-learning multi-model ensemble classifier using Bayesian model averaging (nominal); and (2) integrating nominal predictions with continuous isoscapes to estimate the probability of origin across the spatial domain (continuous). We applied this integrated framework to predict the geographic origin of the Northwest Atlantic mackerel (*Scomber scombrus*), a migratory pelagic fish comprised of northern and southern components that have distinct spawning sites off Canada (northern contingent) and the US (southern contingent), and seasonally overlap in the US fished regions. The nominal approach based on otolith carbon and oxygen stable isotopes ($\delta^{13}\text{C}/\delta^{18}\text{O}$) yielded high contingent classification accuracy (84.9%). Contingent assignment of unknown-

origin samples revealed prevalent, yet highly varied contingent mixing levels (12.5–83.7%) within the US waters over four decades (1975–2019). Nominal predictions were integrated into mackerel-specific otolith oxygen isoscapes developed independently for Canadian and US waters. The combined approach identified geographic nursery hotspots in known spawning sites, but also detected geographic shifts over multi-decadal time scales. This framework can be applied to other marine species to understand migration and connectivity at a high spatial resolution, relevant to management of unit stocks in fisheries and other conservation assessments.

3.2 Introduction

Migration is ubiquitous across a wide range of taxonomic groups and is among the most spectacular phenomena in nature (Dingle, 2014). Migrations regulate population structure and species persistence (Secor, 2015), alter community structure, and facilitate energy flow (Bauer and Hoyer, 2014). Yet, increased anthropogenic activities pose serious threats to highly migratory organisms (Berger, 2004; Wilcove and Wikelski, 2008; Robinson et al., 2009; Tamario et al., 2019). A better understanding of migration and habitat use of highly migratory species could therefore provide valuable insights for conservation and management, particularly in the face of climate change.

Natural markers (e.g., trace elements, stable isotopes) recorded in biogenic tissues have been employed as a powerful tool to uncover migration and its ecological functions (Hobson, 1999; Elsdon et al., 2008; Trueman et al., 2012; Flockhart et al., 2017; Voigt and Lehnert, 2019). Here, the most common approach to reconstructing migration paths of organisms is by matching the tracer of the organism's tissue to a

finite number of potential areas of origin that have been identified *a priori* (i.e., the nominal assignment approach; Wunder, 2012). This method requires that a baseline is established for all known source habitats, and classification methods are applied to assign individuals of unknown origin to their potential source (i.e., the geographic origin is categorical). The categorization of the spatial domain into discrete geographic areas can potentially introduce bias given the continuous nature of tracers, particularly with trace elements and stable isotopes that are distributed throughout the system as a gradient. Natal assignment of the nominal approach can also depend on the classification method of choice (Jones et al., 2017). For instance, while technological advances in machine learning-based approaches have shown promise in improving natal assignment performances (Mercier et al., 2011; Maguffee et al., 2019; Smoliński et al., 2020), common statistical methods such as discriminant function analysis (DFA) remain prevalent in the literature (but see, e.g., Zhang et al., 2016; Wright et al., 2018; Artetxe-Arrate et al., 2019)

Recent advances in stable isotope research have allowed probabilistic estimates of natal origin across continuous spatial domains (i.e., the geographic origin is continuous; Wunder, 2012). This less frequent, but rigorous approach seeks to reconstruct migration and connectivity by matching the isotopic signature of the animal tissue to the predicted isotopic composition over a spatial gradient, known as “isoscapes” (Bowen, 2010; West et al., 2010). In contrast to the nominal assignment approach, “continuous” assignment does not require predefined geographic locations and explicitly incorporates multiple sources of variance-generating processes. Further, isoscapes allow for an in-depth understanding of the biogeochemical

processes that give rise to the spatial isotopic gradient, which is frequently ignored in nominal approaches. The continuous assignment approach has been successfully applied to track migration paths of birds, bats, and insects in the terrestrial environment (Bowen and West, 2019). In comparison, application to marine organisms has been limited to a handful of studies because the isotopic gradient in marine ecosystems varies dynamically over multiple spatiotemporal scales (Vander Zanden et al., 2015; Torniaainen et al., 2017; Trueman et al., 2017; Matsubayashi et al., 2020; Martino et al., 2022).

Oxygen and carbon stable isotopes ($\delta^{18}\text{O}/\delta^{13}\text{C}$ values) in otoliths (or ear stones) have been widely employed as a natural marker to study migration and connectivity of marine fishes (e.g., Rooker et al., 2008; Clarke et al., 2010; Trueman et al., 2012; Wells et al., 2015; Artetxe-Arrate et al., 2021). Otolith aragonite forms near isotopic equilibrium with the oxygen isotopic composition of ambient water, which generally varies globally as a function of salinity (LeGrande and Schmidt, 2006). The otolith–water oxygen isotopic fractionation has also been shown to be temperature-dependent, with minor differences across species (Kalish, 1991; Thorrold et al., 1997; Høie et al., 2004; Sakamoto et al., 2017; Willmes et al., 2019). Otolith $\delta^{13}\text{C}$ reflects the carbon isotopic composition of dissolved inorganic carbon (DIC) and the diet source (Kalish, 1991; Solomon et al., 2006; Tohse and Mugiya, 2008), with the proportion of dietary carbon in the otolith controlled by the metabolic rate in a temperature-dependent way (Chung et al., 2019). As a result of these features, otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ exhibit a predictable spatial gradient, making them suitable for the continuous (isoscape) approach in marine environments.

Here, we present a combined approach that integrates predictions from a nominal assignment approach (machine learning classification) with a continuous assignment approach (isoscape) to uncover the connectivity and spatial structure of a migratory species in the Northwest Atlantic Ocean over multi-decadal time scales. We first developed a multi-model ensemble classifier as a nominal assignment approach using the Bayesian model averaging (BMA) framework, where outcomes of multiple machine learning classifiers were aggregated with weights corresponding to their latest prediction performance (Hoeting et al., 1999; Raftery et al., 2005; Soliman et al., 2019). Then, categorical predictions from the nominal approach were integrated into a species-specific isoscape to estimate the probability of origin across the entire spatial domain using a Bayesian assignment framework (continuous assignment approach). This two-part process emulates the widely applied delta (or hurdle) model approach, wherein the probability of zero observations and non-zero values within the same dataset are modeled separately using two independent models (Maunder and Punt, 2004; Fletcher et al., 2005). We demonstrate that the integration of powerful machine learning algorithms with continuous isoscapes allows for an accurate estimation of connectivity and spatial structure of a migratory marine species at a fine spatial-temporal resolution. We further discuss the broader application of our new analytical framework to identify stock structure and habitat use of migratory species in marine ecosystems, and the implications for fisheries stock assessment and management.

3.3 Methods

3.3.1 Study Species

The Northwestern population of the Atlantic mackerel (*Scomber scombrus*) is a migratory and pelagic schooling species that support important fisheries in the Northwest Atlantic Ocean. Landings within the US waters have fluctuated greatly, with an intensive foreign fleet fishery occurring in the 1970s reaching historically high landings (> 400,000 metric tons); however, the population is currently in a depleted phase experiencing a marked decrease in landings and spawning stock biomass (< 20,000 metric tons; NEFSC, 2018; DFO, 2021). The Northwest Atlantic mackerel population consists of two sub-components: the northern and southern “contingents” that exhibit distinct spawning and nursery regions, as well as seasonal migration patterns that transverse the border between the US and Canada (Sette, 1950; Secor, 1999). The two nations separately manage jurisdictional fisheries with Canada assessing the northern contingent as a single stock, and the US treating the two contingents as components of a single transboundary stock (NEFSC, 2018; DFO, 2021). While the estimated median age-at-maturity is about 2 years for both contingents, the spawning stock biomass of the northern contingent is roughly an order of magnitude larger than that of the southern contingent (Studholme et al., 1999; NEFSC, 2018; Richardson et al., 2020; DFO, 2021). The dominant northern contingent spawns primarily in the southern Gulf of St. Lawrence in June and July (Sette, 1943; Brosset et al., 2020; Mbaye et al., 2020; Van Beveren et al., 2022). The subordinate southern contingent spawns off southern New England and the Gulf of Maine in April and May (Sette, 1943; Berrien, 1978), although the spawning

distribution and nursery habitats of the southern contingent have shifted northeastward over the past four decades (Overholtz et al., 2011; McManus et al., 2018; Richardson et al., 2020) (Figure 3.1). The distribution of the two contingents is mostly separate during the summer spawning season, yet contingent mixing is prevalent throughout late fall, winter, and spring when the northern contingent migrates south and mixes with the southern contingent in US shelf waters where both contingents are subjected to exploitation (Sette, 1950; Moores et al., 1975) (Figure 3.1). Strong latitudinal gradients of SST and water chemistry across Northwest Atlantic shelf waters have recently allowed otolith chemical and stable isotope tracers to accurately discriminate between the two contingents, which confirmed past views on the role of contingent mixing on Atlantic mackerel population dynamics (Moura et al., 2020; Redding et al., 2020; Arai et al., 2021). Mapping the spatial structure of the Northwest Atlantic mackerel at fine spatiotemporal scales will offer insight into the assessment and management of this valuable yet depleted two-component population.

3.3.2 Otolith Collection and Stable Isotope Analysis

We used a previously published (Redding et al., 2020; Arai et al., 2021) and unpublished dataset consisting of otolith stable oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotope values of Northwest Atlantic mackerel. Otoliths were collected in the US winter fishery, the Northeast Fisheries Science Center (NEFSC) fishery-independent spring bottom trawl survey, and the summer Canadian fishery from 1999–2001, 2003, and 2012–2015 ($n = 364$; Redding et al., 2020) and 2013–2019 ($n = 463$; Arai et al., 2021) (Table S3.1; Figure 3.1). In addition to the published dataset, we analyzed samples collected in the NEFSC fishery-independent spring bottom trawl survey and

the summer Canadian fishery from 1974–1976 and 1978 ($n = 135$; unpublished; Table S3.1; Figure 3.1).

Detailed methods for otolith processing and stable isotope analysis are available in Redding et al., (2020) and Arai et al., (2021). Briefly, we developed a contingent classification baseline using known-origin age-1 juveniles to assign contingent membership to age ≥ 2 unknown-origin adult samples collected within US waters. We assumed that the collection sites of age-1 juvenile samples represented their natal habitats and that the exchange of individuals between the two contingents before reaching adulthood was limited. These assumptions are supported by evidence from size distribution analysis and extensive tagging programs that suggest localized migration patterns of juvenile mackerel (Sette, 1950; Uriarte et al., 2001). We used a New Wave Research MicroMill (Fremont, California, USA) to isolate the otolith material within the first annulus representing the early life stage and residence within the natal nursery. Otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of additional samples included in this study were measured using an automated carbonate preparation device (KIEL-III; Thermo Fisher Scientific, Inc., Bremen, Germany) interfaced with a dual-inlet isotope ratio mass spectrometer (IRMS; Finnigan MAT 252; Thermo Fisher Scientific, Inc., Bremen, Germany) at the University of Arizona’s Environmental Isotope Laboratory. All isotope values were reported in delta notation with respect to Vienna-Pee Dee Belemnite (VPDB). No live animals were used in this study and no specific permissions were needed for sampling activities as all otolith samples of Atlantic mackerel (not endangered nor protected) analyzed in this study represented archived material collected from commercial fisheries and government surveys.

3.3.3 Contingent Classification Methods

The classification baseline was developed using the age-1 juvenile dataset from a total of 11 year-classes (1973, 1974; 1998–2000; 2011–2016; step A in Figure 3.2). For some year-classes in which the northern contingent baseline was insufficient in sample size, age-2 northern contingent samples were included to augment the baseline. The inclusion of age-2 fish in the northern contingent baseline is supported by evidence that immigration of the southern contingent into Canadian waters is uncommon (Sette, 1950; Moores et al., 1975). Random oversampling (with replacement) was conducted for all year-classes to balance the sample size within each year-class (total baseline sample size: $n = 674$). A two-way multivariate analysis of variance (MANOVA) was conducted to test joint differences in otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values between contingents, year-classes, and interaction. Assumptions of MANOVA were verified based on scatterplots of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ on each grouping variable (i.e., contingent and year-class) prior to analysis, and statistical significance was assessed based on Pillai's trace statistic which has been shown to be robust to any violations of assumptions (Scheiner, 2001; Finch, 2005). A post-hoc multivariate pairwise comparison with Bonferroni adjustment was performed to test significant differences in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ between contingents nested within each year-class using the “*mvpaircomp*” function in the “*biotools*” package (da Silva, 2021).

We assessed a total of 10 classifiers for contingent membership assignment: four basic statistical methods (Logistic Regression [LR], Mixed-Effect Logistic Regression [MELR], Linear Discriminant Analysis [LDA], and Quadratic Discriminant Analysis [QDA]), and six machine learning methods (Artificial Neural

Networks [ANN], Decision Trees [DT], k -Nearest Neighbors [k NN], Naïve Bayes [NB], Random Forest [RF], and Support Vector Machines [SVM]). For all classifiers, otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ were included as predictors to estimate the probability of contingent membership (northern or southern) for each individual. Both predictors were standardized to z scores to facilitate model fitting. “Year-class” was included as an additional variable to account for inter-annual variations in otolith stable isotope values (Arai et al., 2021). For the MELR classifier, we allowed all predictors to have separate slopes for each year-class (i.e., random slopes). Hyperparameter tuning of machine learning classifiers was conducted through the grid search method on 10 cross-validated folds to find the optimal hyperparameters (Table S3.2). Further, an intercept-only “null” model was included to benchmark the classification performance of all classifiers. Model fitting was performed using the *tidymodels* (Kuhn and Wickham, 2020) and *lme4* (Bates et al., 2015) R packages.

3.3.4 Multi-model Ensemble using Bayesian Model Averaging

A weighted multi-model ensemble classifier was developed using Bayesian model averaging (BMA). BMA was applied to aggregate predictions from K top-performing classifiers ($k = 1, \dots, K$) based on weights associated with the most recent classification performance (Soliman et al., 2019). Weights for each model were proportional to the cross-validated classification accuracy (i.e., the number of correctly classified samples out of all samples) and were normalized so that the weights summed up to 1. Weights were defined as:

$$w(k) = \frac{\text{Accuracy}(k)}{\sum_{k=1}^K \text{Accuracy}(k)} \quad (\text{Eq. 3.1})$$

where $\text{Accuracy}(k)$ corresponds to the k th classifier. Let the predicted values from each classifier be $\text{Pred}(k)$ for $k = 1, \dots, K$. The BMA prediction (i.e., probability of contingent membership) with Accuracy as weights was given by:

$$\text{Pred}_{\text{BMA}} = \sum_{k=1}^K w(k) \text{Pred}(k). \quad (\text{Eq. 3.2})$$

The performance of all classifiers, including the BMA classifier, was assessed through 10-fold cross-validation using three evaluation metrics: classification accuracy, Area Under the Receiver Operating Characteristic Curve (AUC), and Logarithmic-Loss. Higher classification accuracy and AUC, and lower Logarithmic-Loss imply better classification performance. The classifier with the highest overall performance was selected to assign contingent membership (northern or southern) to age ≥ 2 unknown adults collected within US waters (step B in Figure 3.2). We employed a > 0.7 classification probability threshold to assign contingent membership, and those below the threshold were unassigned and excluded from geographic natal assignment analysis (Arai et al., 2021).

3.3.5 *Otolith Oxygen Isoscape*

Otolith oxygen isoscapes were generated to make geographic natal assignments of binary-classified adults (step C in Figure 3.2). Contingent-specific isoscapes were generated to account for temporal differences in spawning dates and

the first growing season: a northern isoscape spanning Newfoundland (NL), Gulf of St. Lawrence (GSL), and Scotian Shelf (SS) was applied to assign individuals classified as the northern contingents, and the southern isoscape spanning the Gulf of Maine (GOM), Georges Bank (GB), Southern New England (SNE), and Mid-Atlantic Bight (MAB) was applied to those assigned the southern contingents. The $\delta^{18}\text{O}$ values of otoliths ($\delta^{18}\text{O}_{\text{oto}}$) can be described by a simple linear fractionation equation with the $\delta^{18}\text{O}$ ($\delta^{18}\text{O}_{\text{seawater}}$) and temperature (T) of ambient seawater, with species-specific constant γ and β parameters:

$$\delta^{18}\text{O}_{\text{oto}} - \delta^{18}\text{O}_{\text{seawater}} = \gamma T + \beta. \quad (\text{Eq. 3.3})$$

We generated a spatiotemporally resolved mackerel-specific otolith oxygen isoscape by coupling temperature and $\delta^{18}\text{O}_{\text{seawater}}$ estimates of seawater with an empirically driven congeneric chub mackerel (*Scomber japonicus*) fractionation equation (Nakamura et al., 2020). Isoscapes were generated at a seasonal resolution by averaging over months that represented the period with the highest growth during the first year of life. We averaged temperature and $\delta^{18}\text{O}_{\text{seawater}}$ for three consecutive months from the peak spawning date for each contingent (southern: May–July; northern: June–August; Sette, 1943; Berrien, 1978; Brosset et al., 2020; Mbaye et al., 2020; Van Beveren et al., 2022), given that rapid growth occurs up to 90-days post-hatch (D’Amours et al., 1990; Simard et al., 1992). To account for inter-annual variations in temperature and $\delta^{18}\text{O}_{\text{seawater}}$ experienced among individuals of different year-classes, we generated seasonal otolith $\delta^{18}\text{O}$ isoscapes for each year that

corresponds to all the year classes in which empirical measurements of $\delta^{18}\text{O}_{\text{oto}}$ values were available (i.e., 1973, 1974; 1998–2000; 2011–2016).

Otolith $\delta^{18}\text{O}$ isoscapes were generated using temperature and salinity data at 5 m depth from the EN4 of the Met Office Hadley Centre “EN” series (version EN 4.2.2; Good et al., 2013), which comprises global temperature and salinity data from 1900 to the present at a monthly/ 1° spatial grid resolution with 42 depth levels (downloaded February 3, 2022). Data at 5 m depth were used to closely reflect the conditions experienced during the early life stage of Atlantic mackerel during the summer growing season (Studholme et al., 1999). A North Atlantic Ocean mixing line from LeGrande and Schmidt, (2006) was used to estimate $\delta^{18}\text{O}_{\text{seawater}}$ values across the Northwest Atlantic Ocean (assuming linear mixing lines), except for the Gulf of St. Lawrence region where a large freshwater influx from the St. Lawrence River results in distinct salinity– $\delta^{18}\text{O}_{\text{seawater}}$ relationships from the rest of the Northwest Atlantic Ocean (Khaliwala et al., 1999). The following salinity– $\delta^{18}\text{O}_{\text{seawater}}$ mixing lines were used:

$$\delta^{18}\text{O}_{\text{seawater (VSMOW)}} = 0.55 \times S - 18.98 \text{ (North Atlantic)} \quad (\text{Eq. 3.4})$$

$$\delta^{18}\text{O}_{\text{seawater (VSMOW)}} = 0.27 \times S - 10.3 \text{ (Gulf of St. Lawrence)} \quad (\text{Eq. 3.5})$$

where $\delta^{18}\text{O}_{\text{seawater}}$ is the $\delta^{18}\text{O}$ [‰ Vienna Standard Mean Ocean Water (VSMOW) scale] of seawater and S is the salinity. Otolith $\delta^{18}\text{O}$ values for each point on the $1^\circ \times 1^\circ$ grid were then estimated using a fractionation equation of chub mackerel (*Scomber japonicus*) (Nakamura et al., 2020):

$$\delta^{18}\text{O}_{\text{oto}} (\text{VPDB}) = -0.25T + 4.46 + \delta^{18}\text{O}_{\text{seawater}} (\text{VSMOW}) \quad (\text{Eq. 3.6})$$

where $\delta^{18}\text{O}_{\text{oto}}$ is the otolith $\delta^{18}\text{O}$ [‰ Vienna-Pee Dee Belemnite (VPDB) scale] and T is the temperature (°C). This resulted in a total of 11 years of mackerel-specific otolith $\delta^{18}\text{O}$ isoscapes estimated across known habitats for each contingent representing the highest growth period of Atlantic mackerel (1° grid resolution).

3.3.6 Geographic Natal Nursery Assignment

We calculated individual probability-of-origin density surfaces for each binary-classified adult sample (northern or southern) using otolith $\delta^{18}\text{O}$ isoscapes (step D in Figure 3.2). Geographic natal assignments were made using isoscapes specific to their estimated natal region: a northern isoscape for northern contingent samples, and a southern isoscape for southern contingent samples. Probability-of-origin density surfaces were calculated following the approach by Wunder, (2010), assuming otolith $\delta^{18}\text{O}$ values to be normally distributed at each grid point and calculating the probability of obtaining the measured isotopic information of the adult sample from normal distributions with an expected mean parameter derived from the isoscapes. The variance model defining the probability distribution of the otolith $\delta^{18}\text{O}$ value at any given location included (i) analytical error and (ii) within-population variance, which was jointly modeled assuming normality and independence using the following equation (Wunder, 2010; Brennan and Schindler, 2017; Vander Zanden et al., 2018):

$$\sigma_{combined} = \sqrt{\sigma_{analytical}^2 + \sigma_{within-pop}^2} \quad (\text{Eq. 3.7})$$

where the $\sigma_{analytical}^2$ was defined as the repeated measurements of NBS-19 standards from the IRMS (0.1‰), and $\sigma_{within-pop}^2$ reflected the variance of otolith $\delta^{18}\text{O}$ values among age-0 individuals captured at the same known-origin location (0.29‰, S. G. Redding; unpublished data). We then applied Bayes' rule to invert the conditional probability of the measured otolith $\delta^{18}\text{O}$ values, given the sampling location:

$$P(A_i|B) = \frac{P(B|A_i)P(A_i)}{\sum_i P(B|A_i)P(A_i)} \quad (\text{Eq. 3.8})$$

where $P(A_i|B)$ is the posterior probability distribution of a fish originating in geographic location i , given the measured otolith $\delta^{18}\text{O}$ value. $P(B|A_i)$ is the likelihood probability distribution of obtaining the observed otolith $\delta^{18}\text{O}$ value at geographic location i , and $P(A_i)$ is the prior probability distribution of a fish originating in geographic location i . The denominator integrates into a constant, and thus the probability density function becomes proportional to the numerator. A uniform prior probability equal to 1 was used for this analysis, such that all locations within the isoscape were equally likely. However, natal origin assignments were constrained within the continental shelf region where most mackerel spawning takes

place (Sette, 1943; Studholme et al., 1999). The above equation reduces to the following likelihood term:

$$P(A_i|B) \propto L(y|\mu_i, \sigma_{combined}^2) = \frac{1}{\sqrt{2\pi\sigma_{combined}^2}} e^{\frac{-(y-\mu_i)^2}{2\sigma_{combined}^2}} \quad (\text{Eq. 3.9})$$

where i is the geographic location within the Northwest Atlantic, y is the measured otolith $\delta^{18}\text{O}$ value of the binary-classified adult sample, μ_i is the predicted otolith $\delta^{18}\text{O}$ value at location i from the isoscape, and $\sigma_{combined}^2$ is the combined variance defined above. After posterior probabilities were calculated across the region, the value at each cell was divided by the sum of all probabilities so that all cells would sum to 1. Then, the value at each cell was divided by the maximum posterior probability to enable comparisons across individuals.

To assess multi-decadal trends in population-level geographic nursery hotspots, individual probability-of-origin density surfaces were summarized through the binary transformation approach by designating each grid cell as a “likely (1)” or “unlikely (0)” location of origin using a defined threshold (step E in Figure 3.2; Vander Zanden et al., 2015, 2018). Grid cells with posterior probabilities in the upper 25% of all grid cells were assigned “likely” and the remaining 75% as “unlikely” (see 3.3.7 *Accuracy and Precision of the Otolith Oxygen Isoscape* section for details). Individual binary assignment surfaces were summed for each year-class, which produced summary maps with grid cells representing the total number of fish assigned to that location using the defined threshold (step F in Figure 3.2). Summary

maps for each year-class were then divided by the total number of fish for a given year-class so that values ranged from 0 to 1. For visualization purposes, all maps were interpolated using bilinear interpolation.

3.3.7 Accuracy and Precision of the Otolith Oxygen Isoscape

Age-0 juveniles collected in the NEFSC fishery-independent bottom trawl survey from September to October 1996, 2001, and 2003 in the MAB, SNE, GB, and GOM provided a unique opportunity to validate the performance of the southern otolith $\delta^{18}\text{O}$ isoscape (step G in Figure 3.2; Table S3.3; Figure S3.1; $n = 59$; S. G. Redding, unpublished data). We assumed collection sites of age-0 juveniles to closely represent their natal nurseries given the highly localized migration patterns of age-0 juveniles (Sette, 1950; Uriarte et al., 2001). Isoscapes for 1996, 2001, and 2003 were generated and geographic natal assignments were made for each age-0 juvenile following the steps defined above. Individual probability-of-origin surfaces were transformed into binary surfaces by designating each grid cell as likely (1) or unlikely (0) through a 75th percentile threshold (see previous section; Vander Zanden et al., 2015, 2018). Individual fish were deemed correctly assigned when grid cells within their collected subregion (e.g., MAB, SNE) included likely grid cells. Accuracy was defined as the proportion of correctly assigned samples to their known collected subregion, and precision (i.e., threshold) was the proportion of grid cells that were assigned as likely among all grid cells. There is often a trade-off between accuracy and precision: defining a stringent threshold (high precision) reduces the number of likely grid cells and thus leads to lower accuracy, and vice-versa (Vander Zanden et al., 2015, 2018; Brennan and Schindler, 2017). As such, the threshold was determined

by assessing the accuracy of the isoscape across a range of precision thresholds (5 to 95%), and the threshold that provided the best accuracy-precision balance was selected.

3.4 Results

3.4.1 Baseline Otolith Stable Isotope Composition

Significant differences of baseline otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ were detected between contingents (Two-way MANOVA, $p_{\text{contingent}} < 0.001$; Figure 3.3), and across year-classes ($p_{\text{year-class}} < 0.001$), with a significant interaction effect between contingent and year-class ($p_{\text{contingent:year-class}} < 0.001$). Multivariate pairwise comparison between contingents nested within each year-class detected significant differences in all year-classes except for 1974 and 2016 (Figure 3.3). Baseline otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of year-classes 1973 and 1974 showed less distinction between contingents compared to those from year-classes 1998–2000 (Redding et al., 2020), but exhibited similar patterns to those from the recent year-classes (2011–2016; Arai et al., 2021) in which the northern contingent generally exhibited lower $\delta^{18}\text{O}$ and higher $\delta^{13}\text{C}$ values compared to the southern contingent.

3.4.2 Classification Performance

The performance of individual classifiers was grouped into three broad categories based on cross-validated mean classification accuracy: low (accuracy < 0.6: LDA, LR, and NB), moderate (accuracy < 0.76: QDA and DT), and high (accuracy > 0.76: MELR, SVM, ANN, RF, and $k\text{NN}$) performance (Figure 3.4). Note, however, that classification performance was generally consistent across all three

metrics. Thus, predictions from high-performing classifiers ($K = 5$) were aggregated into the multi-model ensemble classifier using BMA. Overall, the BMA classifier outperformed all other individual methods, showing one of the highest classification accuracies (mean: 84.9%), and achieving the highest AUC (mean: 0.93) and lowest logarithmic-loss (mean: 0.38) values.

Using the > 0.7 threshold probability level, the cross-validated mean classification accuracy of the BMA classifier was 66.7, 97.8, and 94.3% for year-classes 1973–1974, 1998–2000, and 2011–2016, respectively (Figure 3.3; Table 3.1). The classification performance of the BMA classifier for year-classes 1998–2000 was comparable to previous approaches using Random Forest (74.5–92.3%; Redding et al., 2020) and mixed-effect logistic regression (97.9%; Arai et al., 2021), although the new approach increased classification accuracy by 14.6 percentage points (p.p.) and reduced the percentage of unassigned baseline samples by 12.8 p.p. for samples from year-classes 2011–2016. Thus, the BMA classifier was further employed to assign contingent membership to age ≥ 2 unknown adult samples.

3.4.3 Adult Classification and Contingent Mixing on the US Continental Shelf

Contingent composition estimates from the BMA classifier for year-classes 1998–2000 and 2011–2016 generally agreed with previous estimates from Redding et al., (2020) and Arai et al., (2021), with only minor changes ($< 10\%$) in contingent composition. BMA classification of age ≥ 2 adults indicated a strong dominance of the northern contingent for the 1973 and 1974 year-class (Figure 3.5). Northern contingent mixing within US shelf waters was prevalent in most year-classes, except for year-classes 2011, 2012, and 2016, yet mixing levels varied greatly over the past

four decades. The flexible non-linear classification boundary of the BMA classifier, stemming from the fusion of five independent classifiers, allowed the ensemble classifier to successfully handle the strong temporal variability in the baseline $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values (Figure 3.5). A threshold classification probability of > 0.7 resulted in a total of 146 unassigned adult samples (33.8% of total samples). The percentage of unassigned adult samples of year-classes 1998–2000 using the BMA classifier was similar (12.7%) compared to a previous method (10.9%) using a mixed-effect modeling approach (Table 3.1; Arai et al., 2021). However, for year-classes 2011–2016, the percentage of unassigned adult samples was reduced (39.7%) compared to the previous approach (46.1%).

3.4.4 Otolith Oxygen Isoscape

The predicted mackerel-specific otolith oxygen isoscape exhibited a strong latitudinal trend across the Northwest Atlantic Ocean (Figure 3.6). Within the US shelf waters, low $\delta^{18}\text{O}_{\text{oto}}$ values occurred in the MAB and SNE, with a northeastward increase toward the GOM and GB. Within Canadian waters, low $\delta^{18}\text{O}_{\text{oto}}$ values were predicted within the SS and southern GSL regions, whereas higher values were observed in the southern and northern NL regions. While the broad spatial pattern in $\delta^{18}\text{O}_{\text{oto}}$ values across the Northwest Atlantic Ocean persisted over four decades, strong temporal variation was observed at regional scales, particularly in the southern GSL, the western GOM, SNE, and MAB regions.

3.4.5 Geographic Natal Assignment

The accuracy of the isoscape was assessed using age-0 juvenile samples collected in 1996, 2001, and 2003 in US waters (data shown in Figure S3.1). For all year-classes, the accuracy was above 60% for a range of thresholds, although accuracy decreased as the threshold became more restrictive toward 1 (Figure S3.2). The 75th percentile threshold provided a balanced accuracy-precision trade-off that maintained a high percentage of correct assignment (i.e., accuracy) while also constraining the area of geographic assignment (i.e., precision). Thus, the 75th percentile threshold was further employed for binary transformation (i.e., grid cells with posterior probabilities in the upper 25% of the total grid cells were assigned as likely locations). The majority of age-0 juveniles – 70% (1996), 87.5% (2001), and 82.6% (2003) – were correctly assigned to their collected subregions with the selected threshold.

Geographic natal nursery assignments were compiled for binary-classified adult samples using the mackerel-specific otolith oxygen isoscape, which resulted in a total of 111 and 175 individual probability-of-origin surfaces for the southern and northern contingents, respectively (Figure 3.7). Individual probability-of-origin surfaces were binary-transformed and subsequently summed for each year-class to identify hotspots in nursery habitat use and geographical shifts across multi-decadal scales (Figure 3.8). Nursery hotspots centered around the southern GSL and SS in most but not all year-classes for the northern contingent (Figure 3.8a). In year-classes 1998–2000, nurseries were predicted outside the GSL, concentrating around the northeastern and southwestern shelves of NL. For those assigned the southern

contingent, natal nurseries generally concentrated in the MAB and SNE across all year-classes, although nursery hotspots expanded northeastward to the western GOM after 2000 (Figure 3.8b).

3.5 Discussion

By integrating modern machine learning algorithms with continuous otolith $\delta^{18}\text{O}$ isoscapes, we accurately predicted the geographic origin of a migratory marine species at fine spatiotemporal scales across the Northwest Atlantic Ocean over multiple decades. This new analytical framework should be applicable to a range of migratory species in the marine environment to inform future conservation and management actions.

3.5.1 Integrating Machine Learning with Isoscapes

Natal assignment of the nominal approach can vary according to the classification method of choice, and often involves selecting a single “best” model, which ignores model uncertainty. The BMA-based multi-model ensemble classifier outperformed all individual classifiers (Figure 3.4) and substantially improved classification performance compared to previous approaches on the same dataset (Redding et al., 2020; Arai et al., 2021) (Table 3.1). The BMA approach not only retains all model uncertainty but is also robust to model misspecification as the portfolio of models bet-hedges against misclassification (Hoeting et al., 1999; Hinne et al., 2020). Further, machine learning classifiers outperformed conventional statistical approaches (e.g., LDA, LR; Figure 3.4), successfully handled non-linear patterns in the dataset, and were particularly robust to strong temporal variations,

which is common in natural tracer-type datasets (Gillanders, 2005; Elsdon et al., 2008; Schloesser et al., 2009).

The integration of BMA-based predictions with spatiotemporally resolved isoscapes allowed accurate geographic natal assignment of a migratory marine species at a fine spatial resolution (Figure 3.7). Previous studies have applied the nominal and continuous approaches independently to address the question of interest (Brennan et al., 2015; Vander Zanden et al., 2015; Brennan and Schindler, 2017). However, instead of applying the two approaches independently, this study leveraged the nominal approach to inform the continuous approach. The nominal approach required predefined geographic locations but was highly accurate and enabled the inclusion of an informative otolith $\delta^{13}\text{C}$ predictor that could be challenging to model across space. The nominal approach further constrained geographic origin predictions of the continuous approach that modeled the otolith tracer as a continuum and explicitly propagated multiple variance-generating processes. The resulting combined framework provided fine-scale geographic origin estimates on predefined locations, which would be particularly informative for management and conservation applications that often require defined boundaries. Compiling individual probability surface maps into summary heatmaps further enabled the detection of population-level geographic nursery habitat shifts over multi-decadal time scales (Figure 3.8) — a key finding that would have been otherwise overlooked by relying upon the nominal approach alone.

3.5.2 Spatial Structure of Northwest Atlantic Mackerel Over Four Decades

Contingent assignment using otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values presented here, and assignments by Redding et al., (2020) and Arai et al., (2021) revealed prevalent contingent mixing within US waters over four decades (1975–2019), supporting traditional views on the spatial structure of the Northwest Atlantic mackerel (Sette, 1950) (Figure 3.5). It is important to exercise caution when interpreting contingent mixing levels, as some year-classes (e.g., 1974, 2016) exhibited weak stable isotopic distinction (Figure 3.3). Nonetheless, the aggregated year-class baseline compensates for temporal variation and enables year-classes with less distinct isotopic signatures to draw information from those that are more distinct, bringing them closer to the global mean. Furthermore, a conservative 0.7 classification threshold was applied to reduce misclassification of unknown adult samples.

Temporal variation in mixing levels could reflect changes in the recruitment strength and migration patterns by the dominant northern contingent (Secor, 2014; Arai et al., 2021). Namely, high mixing levels for year-classes 1973, 1974, and 2015 reflected strong northern contingent cohorts, and low mixing in the 2016 year-class corresponded to historically low recruitment levels (Smith et al., 2020). Of particular interest was the presence of the northern contingent during the 1970s — periods when an intensive foreign fleet fishery occurred within US waters. While small sample sizes and high unassignment rates preclude strong inferences for this period, these results could imply that the northern contingent could have provided an important seasonal subsidy to support the large historical fishery.

Nursery hotspots were detected by compiling individual binary surface maps (Figure 3.8). Northern contingent nursery hotspots generally occurred in the known and monitored spawning site in the southern GSL region (Sette, 1943; Mbaye et al., 2020; Van Beveren et al., 2022) (Figure 3.8a). Interestingly, in 1998–2000, hotspots were identified in the northeastern and southwestern shelves of NL, where spawning activity is small and sporadic (Grégoire et al., 2013). This apparent “spill-over” could be a result of a density-dependent range expansion associated with the exceptionally strong 1999 year-class (MacCall, 1990; Castonguay et al., 2008). However, there is little evidence of increased egg production and spawning stock biomass in the southern GSL in the 2000s following the arrival of the exceptional 1999 year-class (Brosset et al., 2020). This, combined with our findings suggests that the 1999 year-class may have utilized nurseries outside the GSL, perhaps off southern NL. Density-dependent range expansion has been well-documented for the Northeastern population of the Atlantic mackerel (Nøttestad et al., 2016; Olafsdottir et al., 2019), and is further supported by the increase in landings in NL during years of strong recruitment (DFO, 2021). For the southern contingent, the expansion of nursery hotspots into the western GOM over the recent decade corresponds remarkably well to reported northeastward shifts in adult, egg, and larval habitat distributions, primarily driven by changes in temperature (Overholtz et al., 2011; Radlinski et al., 2013; McManus et al., 2018; Richardson et al., 2020) (Figure 3.8b). As these distribution shifts and complex spatial structure pose challenges for fisheries management, it is vital to further incorporate predictions from habitat suitability models (McManus et al., 2018; Mbaye et al., 2020) and egg survey data (Richardson

et al., 2020; DFO, 2021) into our continuous framework to provide fine spatial information on this depleted population. Furthermore, nursery hotspot predictions from year-classes with small sample sizes (e.g., 1973, 2000, 2016) are prone to bias and may not be indicative of the contingent-level nursery habitat and should be considered with caution.

3.5.3 Spatial Patterns in Mackerel Otolith Oxygen Isoscapes

Predicted mackerel $\delta^{18}\text{O}_{\text{oto}}$ values were distributed across the Northwest Atlantic as a gradient, highlighting the suitability of the continuous approach to stable isotope applications (Figure 3.6). The latitudinal $\delta^{18}\text{O}_{\text{oto}}$ gradient was consistent with the differences in natal $\delta^{18}\text{O}_{\text{oto}}$ values between juvenile northern and southern contingent baselines (Figure 3.3). The spatial pattern of $\delta^{18}\text{O}_{\text{oto}}$ is largely governed by physical processes including the Gulf Stream, Labrador Current, and the St. Lawrence River, which drive changes in the $\delta^{18}\text{O}$ of seawater ($\delta^{18}\text{O}_{\text{seawater}}$) and temperature across the Northwest Atlantic (Richaud et al., 2016; Saba et al., 2016). In the southern GSL, ^{18}O -depleted freshwater from the St. Lawrence River combined with warm temperatures leads to a localized pool of low $\delta^{18}\text{O}_{\text{oto}}$ (Koutitonsky and Bugden, 1991; Khatiwala et al., 1999). The latitudinal $\delta^{18}\text{O}_{\text{oto}}$ gradient within the US shelf waters is likely governed by the temperature gradient attributed to the Gulf Stream rather than $\delta^{18}\text{O}_{\text{seawater}}$, resulting in a northeastward increase in $\delta^{18}\text{O}_{\text{oto}}$ toward the GOM and GB. This spatial pattern corresponds well with sub-regional differences in measured $\delta^{18}\text{O}_{\text{oto}}$ values of age-0 juveniles collected across the US shelf waters (Figure S3.1b).

Strong inter-decadal variation in both measured juvenile $\delta^{18}\text{O}_{\text{oto}}$ (Figure 3.3) and isoscapes (Figure 3.6) could be related to changes in large-scale oceanographic features, such as the Atlantic meridional overturning circulation (AMOC; Caesar et al., 2018). The weakening of AMOC during recent decades has been associated with the northward shift of the Gulf stream position combined with the poleward retreat of the Labrador Current, leading to warmer US shelf waters and consequently lower $\delta^{18}\text{O}_{\text{oto}}$, particularly in the western Gulf of Maine region (Pershing et al., 2015; Saba et al., 2016; Gonçalves Neto et al., 2021). There was no clear inter-decadal pattern in the measured juvenile baseline for otolith $\delta^{13}\text{C}$ values (Figure 3.3); however, the decline in atmospheric $\delta^{13}\text{C}$ values has been linked to a significant declining trend in baseline otolith $\delta^{13}\text{C}$ in Atlantic bluefin tuna (i.e., Suess effect) (Schloesser et al., 2009). These strong temporal patterns in otolith stable isotopes further highlight the importance of accounting for such variation in the baseline for accurate natal assignment.

3.5.4 Broader Applications and Implications to Management

The combined approach proposed here requires a reference baseline and a species-specific otolith $\delta^{18}\text{O}$ isoscape generated from temperature and salinity data through a species-specific fractionation equation. In particular, $\delta^{18}\text{O}$ of ambient seawater ($\delta^{18}\text{O}_{\text{seawater}}$) was determined from salinity data which could be problematic for species that inhabit regions that are heavily influenced by multiple sources of freshwater inputs, in which the salinity– $\delta^{18}\text{O}_{\text{seawater}}$ relationship may be highly dynamic (Fairbanks, 1982). In this case, direct $\delta^{18}\text{O}_{\text{seawater}}$ measurements should be

preferred for otolith $\delta^{18}\text{O}$ isoscape development, although the spatiotemporal resolution could be reduced (Schmidt et al., 1999). Furthermore, because otolith $\delta^{13}\text{C}$ is influenced by an unknown combination of ambient DIC, food source, and metabolic rates (Kalish, 1991; Solomon et al., 2006; Tohse and Mugiya, 2008), we were unable to establish a spatiotemporally accurate otolith $\delta^{13}\text{C}$ isoscape. Instead, we employed otolith $\delta^{13}\text{C}$ data as a predictor in the nominal approach, which was then used to inform the continuous approach. As global-scale estimations of these values have become more readily available (McMahon et al., 2013; Schmittner et al., 2013; Becker et al., 2016; Magozzi et al., 2017; St John Glew et al., 2021), a multi-isotope isoscape model could be developed and applied to provide a more accurate geographic origin estimate in marine species (Vander Zanden et al., 2015; Tornaiainen et al., 2017).

Overall, we provide a promising framework that translates the biogenic stable isotope information into a probabilistic prediction of geographic origin in a marine environment. The application of the continuous assignment approach to marine species has been limited given the lack of spatial information on geochemical tracers in marine ecosystems (but see, e.g., Martino et al., 2022). The increased accessibility of modern machine learning algorithms (Kuhn and Wickham, 2020), combined with biomineral $\delta^{18}\text{O}$ isoscapes predicted from readily available data (i.e., temperature and salinity), makes this approach widely applicable to any marine species, but particularly those that form carbonate biominerals (e.g., otoliths). As these hard parts are commonly retained and stored in abundance for fisheries stock assessment purposes, they can be used to infer population-level migration and connectivity of

important fishery resources (Tanner et al., 2016; Avigliano, 2022). Archived hard parts could be particularly useful in reconstructing fine-scale migration patterns across decadal time scales to understand the effects of climate change (Siskey et al., 2016; von Leesen et al., 2020). Understanding migration and connectivity at fine spatial-temporal scales will not only allow fisheries management units to better reflect the spatial structure of biological populations (Secor, 1999; Smedbol and Stephenson, 2001; Wilberg et al., 2008; Kerr et al., 2017; Cadrin, 2020), but also expand our knowledge on the role of migration in population structuring and species persistence in the face of climate change.

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Tables

Table 3.1 Summary of classification accuracy, and percentage of unassigned baseline and adult samples using the Bayesian model averaging (BMA) classifier. Cross-validated classification accuracy is shown for probability thresholds 0.7 (outside parenthesis) and 0.5 (inside parenthesis). Classification accuracy and percentage of unassigned baseline and adult fish are also shown for the mixed-effect logistic regression classifier that included otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ as predictors and accounted for year-class effects as a random intercept (Arai et al., 2021), and the Random Forest classifier that relied only on $\delta^{18}\text{O}$ values (Redding et al., 2020).

	1973–1974 year-class			1998–2000 year-class			2011–2016 year-class		
Model									
	%accuracy	%unassigned (baseline)	%unassigned (adult)	%accuracy	%unassigned (baseline)	%unassigned (adult)	%accuracy	%unassigned (baseline)	%unassigned (adult)
Bayesian model averaging (This study)	66.7 (71.2)	66.2	47.3	97.8 (97.4)	8.2	12.7	94.3 (81.4)	34.4	39.7
Mixed-effect logistic regression (Arai et al., 2021)	–	–	–	97.9 (96.9)	4.2	10.9	79.7 (69.8)	47.2	46.1
Random Forest (Redding et al., 2020)	–	–	–	74.5–92.3	–	–	–	–	–

Figures

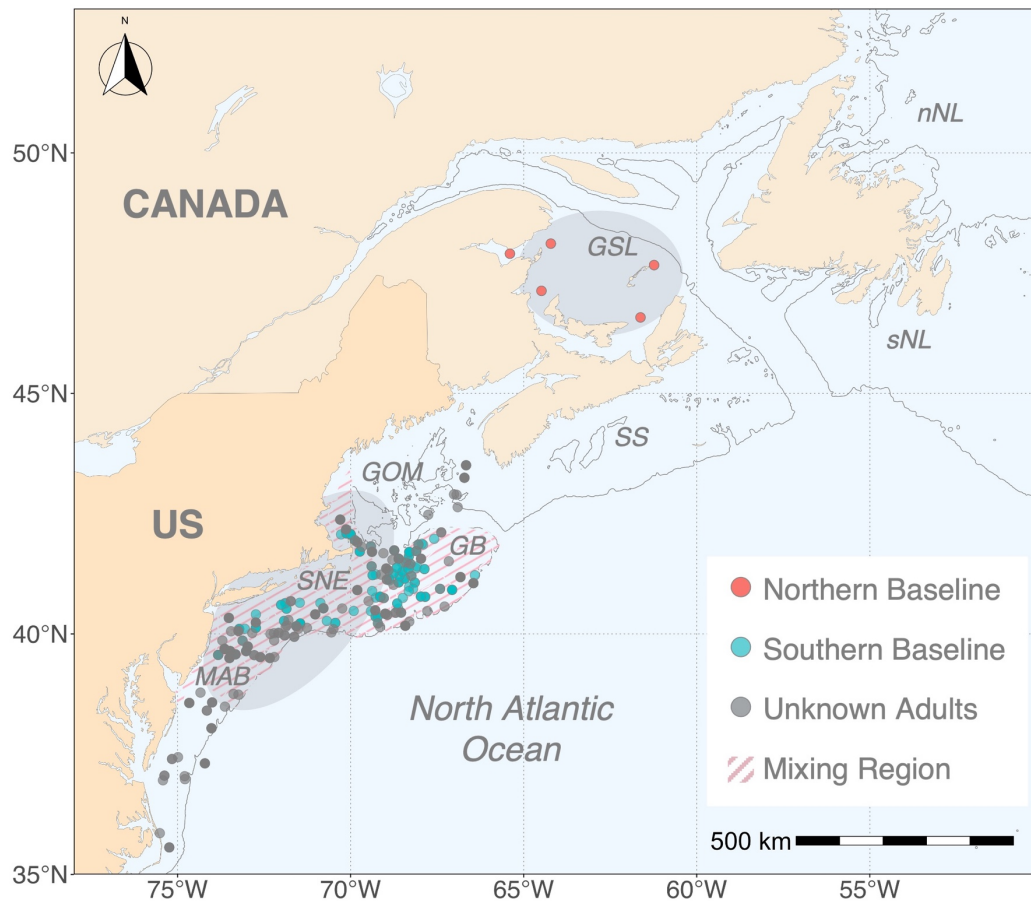


Figure 3.1 Map of the western North Atlantic Ocean depicting collection sites of the Northwest Atlantic mackerel. Shaded ellipses in the southern Gulf of St. Lawrence and US shelf waters indicate principal spawning sites for the northern and southern contingents, respectively. The solid dark line refers to the 200 m isobath. nNL = northern Newfoundland, sNL = southern Newfoundland, GSL = Gulf of St. Lawrence, SS = Scotian Shelf, GOM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, MAB = Mid-Atlantic Bight. The map was created using the *rworldmap* package (South, 2011) in R.

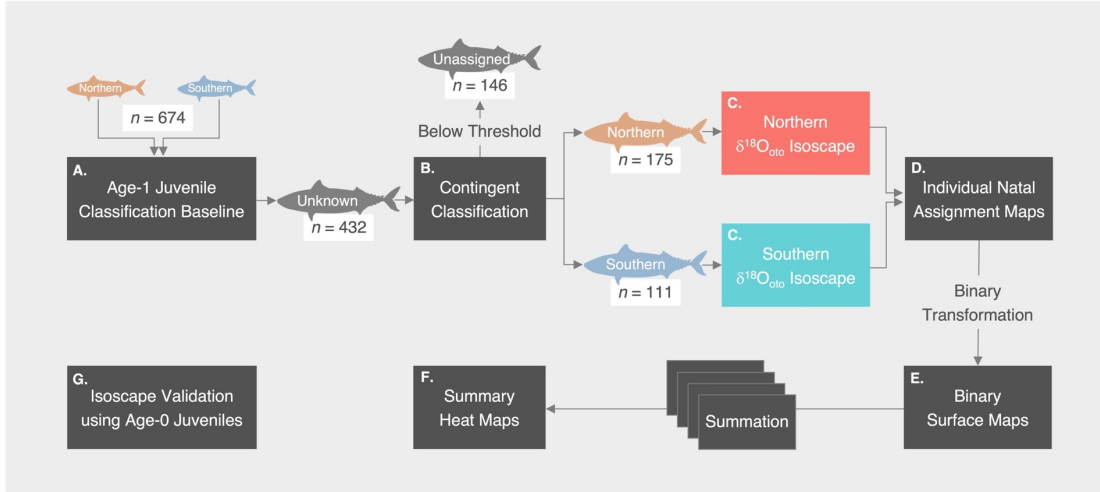


Figure 3.2 Schematic of the steps followed to assign contingent membership and to produce geographic natal assignment maps for the Northwest Atlantic mackerel using Bayesian model averaging (BMA) classification and otolith oxygen ($\delta^{18}\text{O}$) isoscapes. (A) Contingent classification baseline development using known-origin age-1 juvenile samples. (B) Binary contingent classification (northern or southern) of age ≥ 2 unknown adult samples using Bayesian model averaging (BMA) classifier based on otolith stable oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotope values. Individuals below the classification probability threshold were excluded from further analyses. (C) Binary-classified adults integrated into spatiotemporally resolved contingent-specific otolith $\delta^{18}\text{O}$ isoscapes generated by coupling sub-surface temperature and salinity (seawater $\delta^{18}\text{O}$) data with the chub mackerel fractionation equation. (D) Computing individual probability-of-origin surfaces of binary-classified adults using a Bayesian assignment framework. (E) Binary transformation of individual probability-of-origin surfaces to produce binary surface maps comprising grid cells with a “likely” or “unlikely” location of origin using a defined threshold. (F) Summation of individual binary surface maps for each year-class to produce summary heat maps representing the total number of fish assigned to that location using a defined threshold. (G) Performance validation of the otolith oxygen isoscape using age-0 juvenile samples.

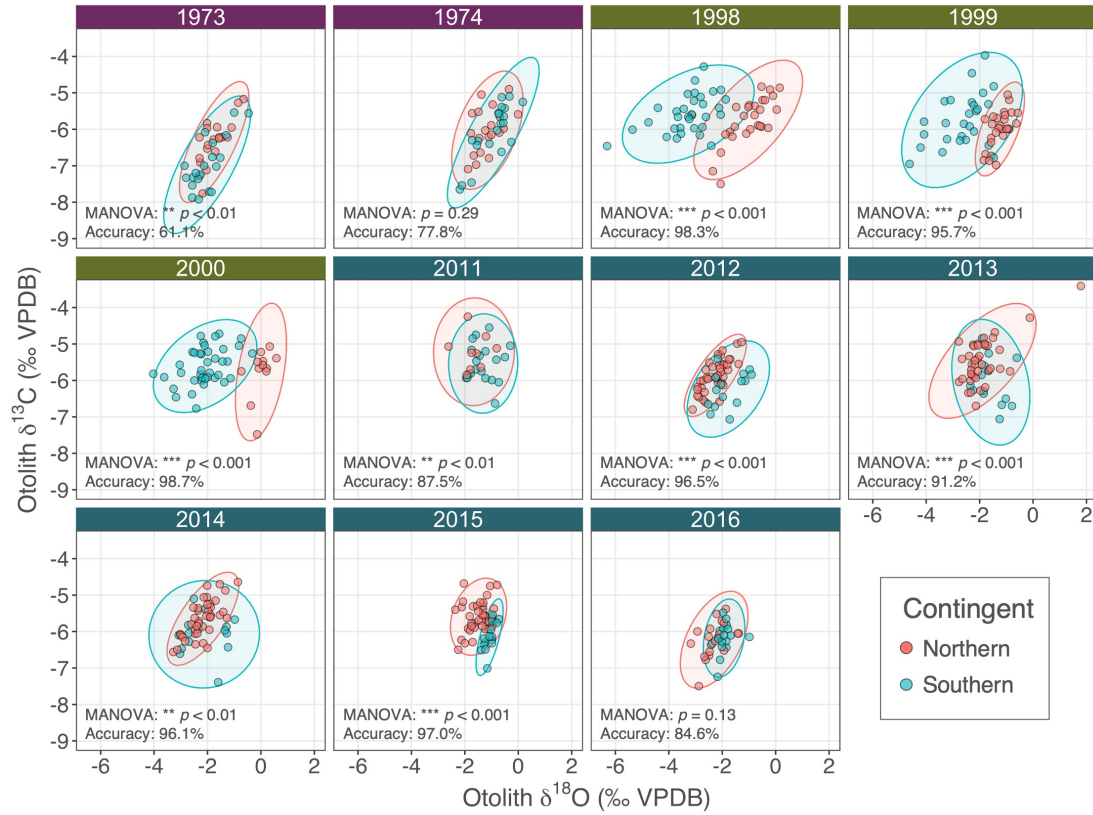


Figure 3.3 Northwest Atlantic mackerel baseline otolith oxygen and carbon stable isotope values ($\delta^{18}\text{O}/\delta^{13}\text{C}$). Northern and southern contingent baselines are shown for year-classes 1973, 1974 (purple headers), 1998–2000 (green headers), and 2011–2016 (blue headers). 95% confidence ellipses are provided for each contingent. Results from two-way multivariate analysis of variance (MANOVA) pairwise comparison and cross-validated mean classification accuracy with a threshold probability level of 0.7 are shown for each year-class. Data for year-classes 1998–2000 and 2011–2016 are from Redding et al., (2020) and Arai et al., (2021).

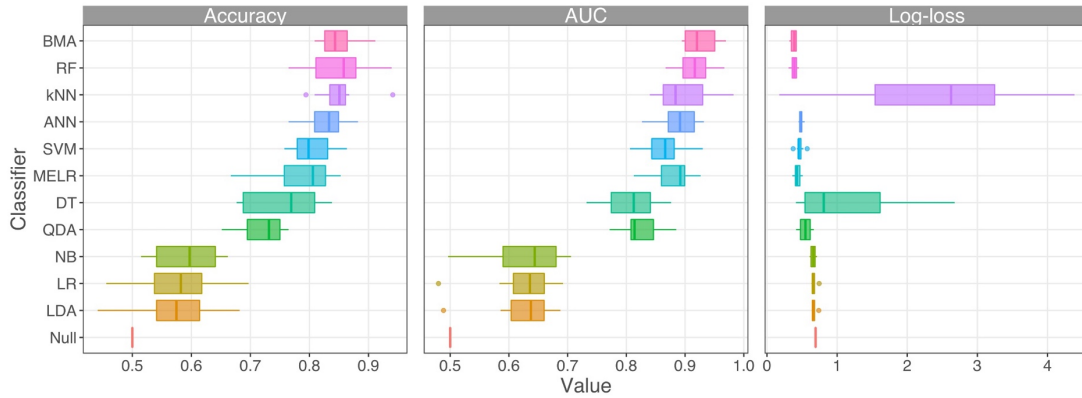


Figure 3.4 Classification performance metrics for 12 different classifiers from 10-fold cross-validation. Performance metrics include classification accuracy (Accuracy, left), Area under the Receiver Operating Characteristic Curve (AUC, middle), and Logarithmic-Loss (Log-loss, right). BMA = Bayesian model averaging classifier, RF = Random Forest, k NN = k -nearest neighbors, ANN = Artificial Neural Networks, SVM = Support Vector Machines, MELR = Mixed-Effect Logistic Regression, DT = Decision Trees, QDA = Quadratic Discriminant Analysis, NB = Naïve Bayes, LR = Logistic Regression, LDA = Linear Discriminant Analysis, Null = Intercept-only “null” classifier. Note that the scales of the x-axis differ across metrics.

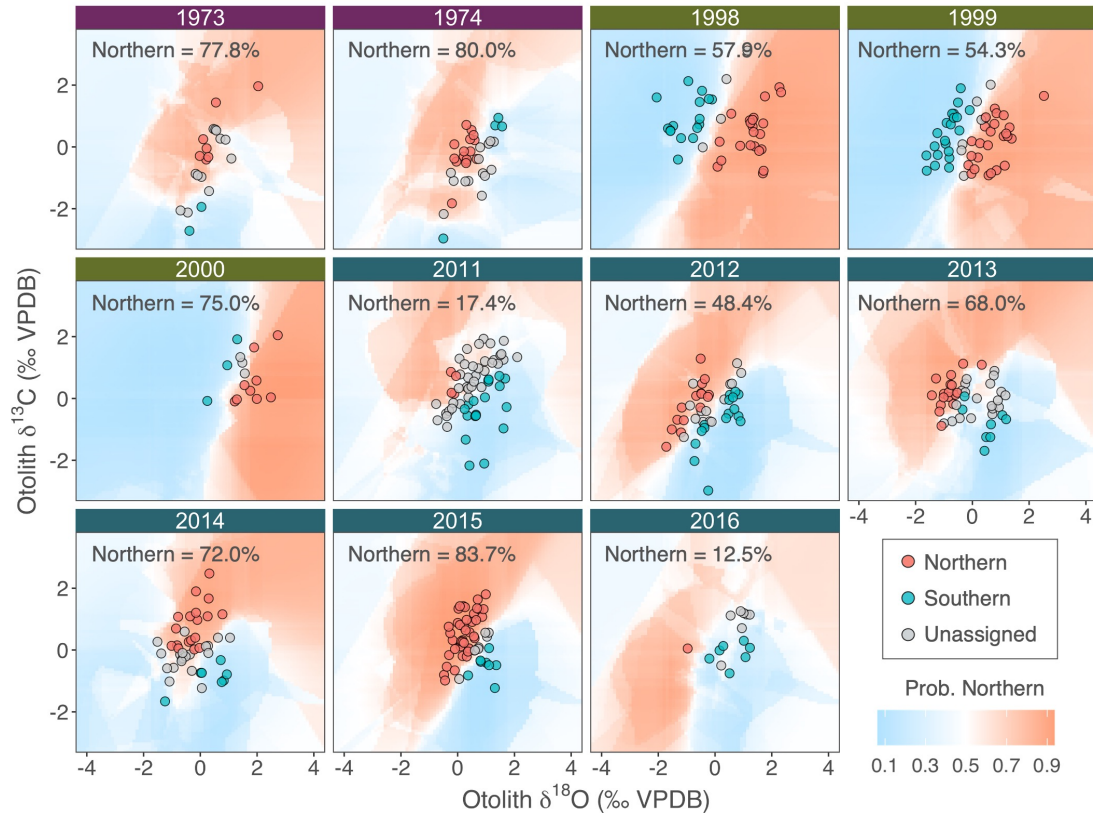


Figure 3.5 Northwest Atlantic mackerel otolith oxygen and carbon stable isotope values ($\delta^{18}\text{O}/\delta^{13}\text{C}$) for age ≥ 2 unknown adults collected in US waters. Contingent membership assignment results using the Bayesian model averaging (BMA) classifier are shown for year-classes 1973, 1974 (purple headers), 1998–2000 (green headers), and 2011–2016 (blue headers). Background colors depict the probability of contingent membership (northern or southern). Individuals below the 0.7 classification probability threshold were unassigned. The percentage of the northern contingent of assigned fish (probability > 0.7) for each year-class is shown in the top left corner of each panel. Isotope values are shown as z scores with mean 0 and SD 1.

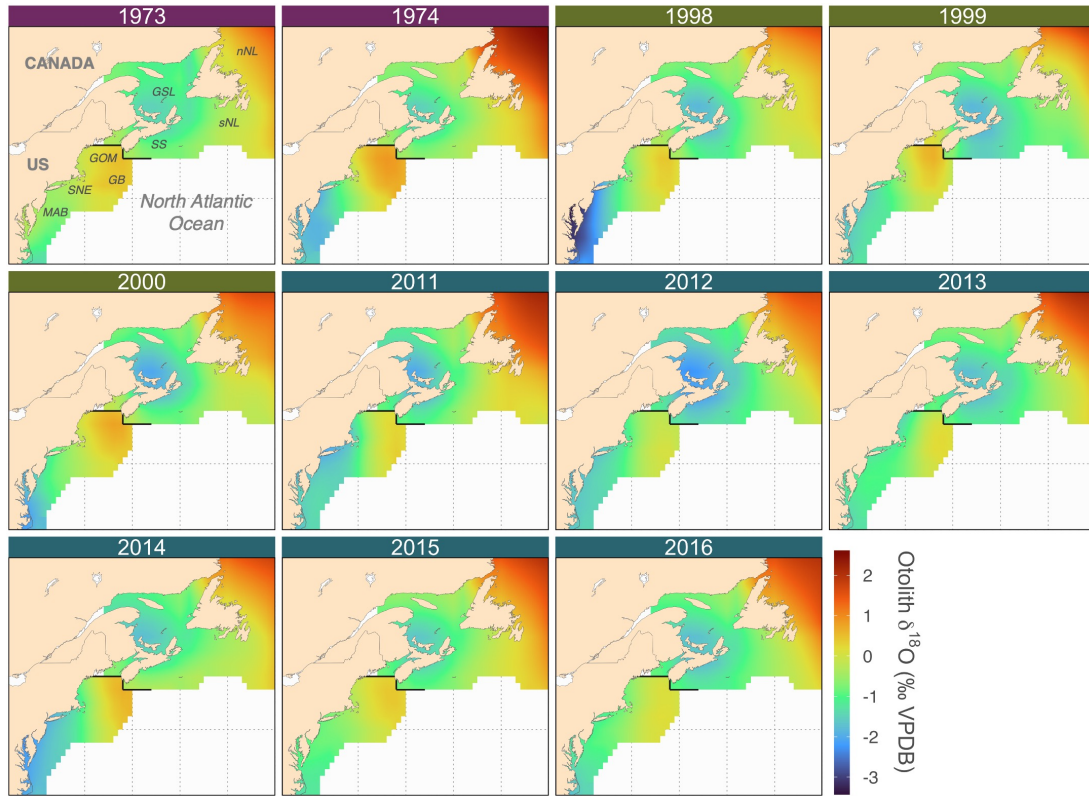


Figure 3.6 Mackerel-specific otolith oxygen isoscapes for 11 years. Isoscapes are depicted for year-classes 1973, 1974 (purple headers), 1998–2000 (green headers), and 2011–2016 (blue headers). Note that the northern and southern isoscapes were generated separately by averaging over months of highest growth during the first year of life of Atlantic mackerel (southern: May–July; northern: June–August) and delineated with the solid black line. nNL = northern Newfoundland, sNL = southern Newfoundland, GSL = Gulf of St. Lawrence, SS = Scotian Shelf, GOM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, MAB = Mid-Atlantic Bight. The map was created using the *rworldmap* package (South, 2011) in R.

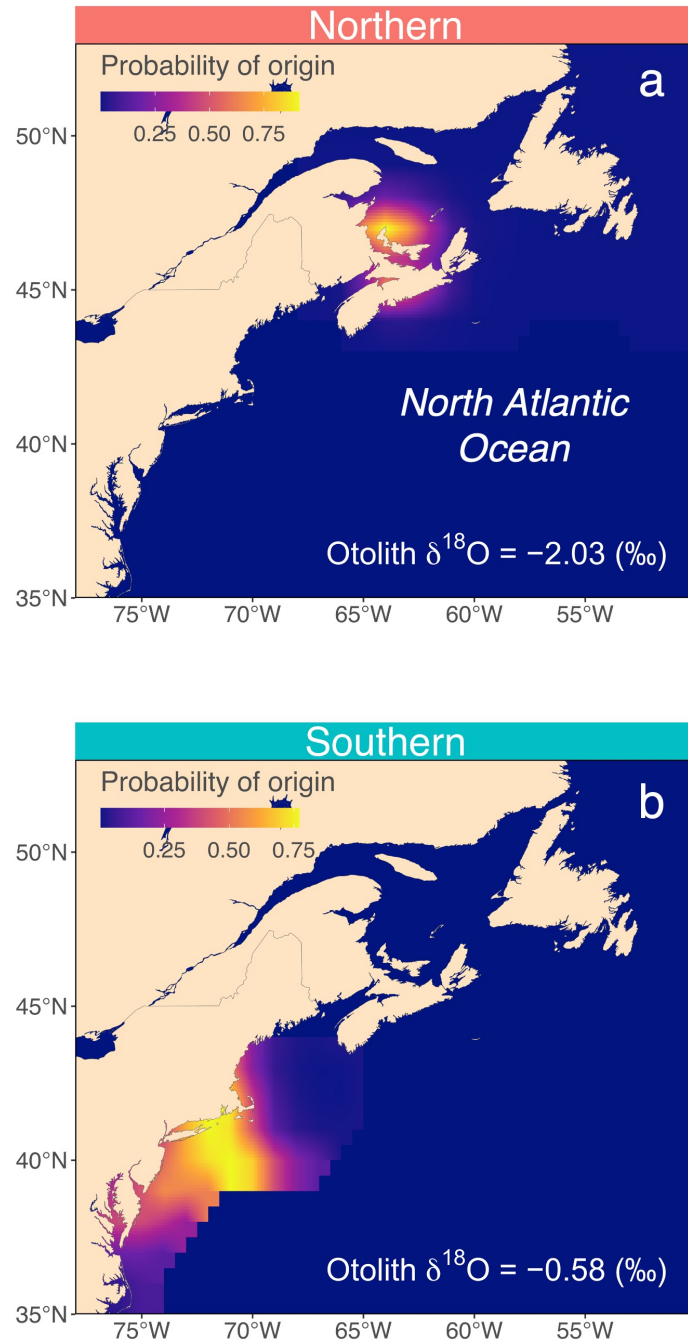


Figure 3.7 Example individual probability-of-origin surfaces of Northwest Atlantic mackerel. Plots include fish assigned the northern ($\delta^{18}\text{O}_{\text{oto}} = -2.03\text{‰}$) and southern ($\delta^{18}\text{O}_{\text{oto}} = -0.58\text{‰}$) contingents from the 2015 year-class. The map was created using the *rworldmap* package (South, 2011) in R.

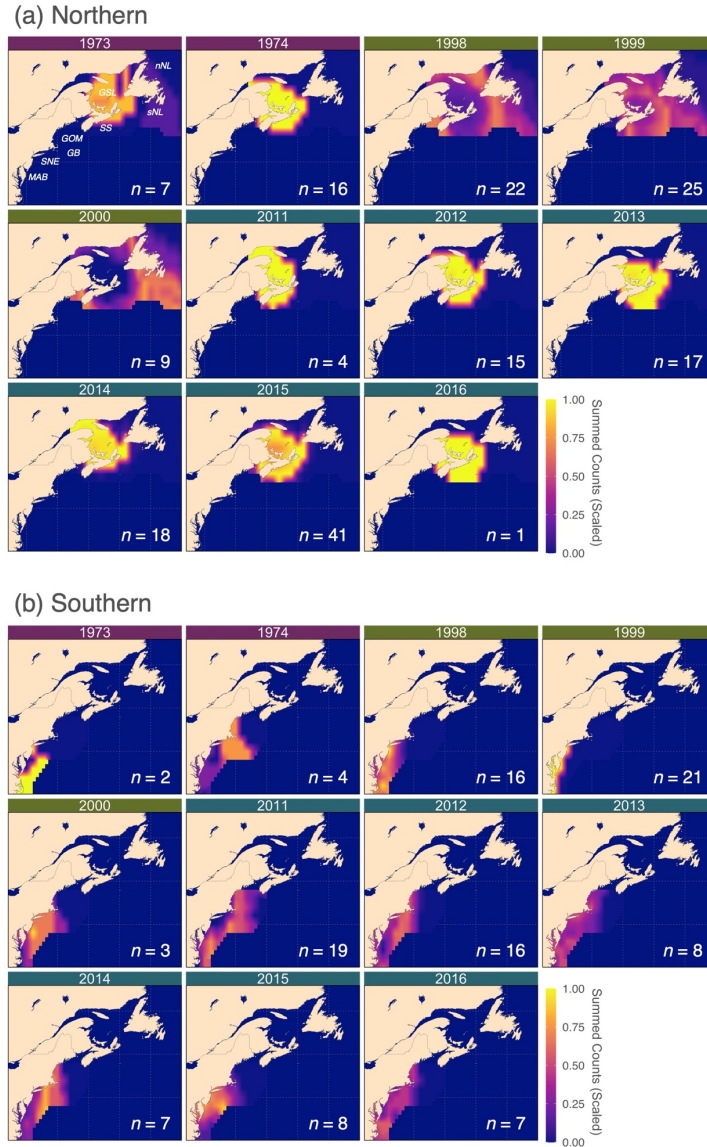


Figure 3.8 Summary heat maps in nursery habitat use for northern (a) and southern (b) contingents. Heat maps are depicted for year-classes 1973, 1974 (purple headers), 1998–2000 (green headers), and 2011–2016 (blue headers). Heat maps were computed by summing individual binary assignment surfaces for each year-class and scaled by the sample size such that all values range from 0 to 1. A 75th percentile threshold was employed for binary surface transformation prior to summation. The sample size included for each heat map for each year-class is also shown. nNL = northern Newfoundland, sNL = southern Newfoundland, GSL = Gulf of St. Lawrence, SS = Scotian Shelf, GOM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, MAB = Mid-Atlantic Bight. The map was created using the *rworldmap* package (South, 2011) in R.

Supplementary Material

Table S3.1 Northwest Atlantic mackerel otolith sample size by year-class, sampling period, collection site, and data type. Data for year-classes 1998–2000 and 2011 are from Redding et al., (2020), and data for year-classes 2012–2016 are from Arai et al., (2021).

Year-class	Years collected	Collection site	Sample size		
			Northern baseline	Southern baseline	Unknown adult
1973 (N = 61)	1974, 1975	Canada	20		
		Gulf of Maine			
		Georges Bank		20	6
		Southern New England			15
		Mid-Atlantic Bight			
		US (subregion unknown)			
1974 (N = 74)	1975, 1976, 1978	Canada	20		
		Gulf of Maine			
		Georges Bank			20
		Southern New England		20	
		Mid-Atlantic Bight			14
		US (subregion unknown)			
1998 (N = 102)	1999–2001, 2003	Canada	28		
		Gulf of Maine			
		Georges Bank		18	17
		Southern New England		14	20
		Mid-Atlantic Bight			5
		US (subregion unknown)			
1999 (N = 107)	2000, 2001, 2003	Canada	27		
		Gulf of Maine			

		Georges Bank	19	18
		Southern New England	8	32
		Mid-Atlantic Bight		3
		US (subregion unknown)		
2000 (N = 66)	2001, 2003	Canada	12	
		Gulf of Maine		
		Georges Bank	24	2
		Southern New England	15	7
		Mid-Atlantic Bight		6
		US (subregion unknown)		
2011 (N = 89)	2012–2015	Canada	9	
		Gulf of Maine	6	23
		Georges Bank	10	14
		Southern New England	4	6
		Mid-Atlantic Bight		17
		US (subregion unknown)		
2012 (N = 100)	2013–2016	Canada	40	
		Gulf of Maine	9	7
		Georges Bank	2	18
		Southern New England		2
		Mid-Atlantic Bight		18
		US (subregion unknown)	4	
2013 (N = 99)	2014–2017	Canada	40	
		Gulf of Maine	3	
		Georges Bank		
		Southern New England	11	
		Mid-Atlantic Bight		45
		US (subregion unknown)		

2014 (N =					
100)	2015–2018	Canada	40		
		Gulf of Maine		15	
		Georges Bank			
		Southern New England			12
		Mid-Atlantic Bight			33
		US (subregion unknown)			
2015 (N =					
112)	2015–2019	Canada	40		
		Gulf of Maine		11	12
		Georges Bank			2
		Southern New England		4	28
		Mid-Atlantic Bight			11
		US (subregion unknown)			4
2016 (N = 52)	2017–2019	Canada	19		
		Gulf of Maine		2	1
		Georges Bank		8	2
		Southern New England		8	4
		Mid-Atlantic Bight			1
		US (subregion unknown)			7

Table S3.2 Hyperparameters selected for six machine learning classifiers using the grid search method on 10 cross-validation folds.

Classifier	Hyperparameters	
Artificial Neural Networks (ANN)	Number of Hidden Units: 10	Amount of Regularization: 0.00001
Decision Trees (DT)	Cost-Complexity: 0.00001	Tree Depth: 13
<i>k</i> -Nearest Neighbors (<i>k</i> NN)	Number of Neighbors: 3	–
Naïve Bayes (NB)	Kernel Smoothness: 0.8	Laplace Correction: 1.3
Random Forest (RF)	Number of Trees: 3000	Minimal Node Size: 3
Support Vector Machines (SVM)	Cost: 3	–

Table S3.3 Age-0 juvenile Northwest Atlantic mackerel otolith sample size by year-class, sampling period, and collection site.

Year-class	Years collected	Collection site	Sample size
1996 (N = 20)	1996	Gulf of Maine	2
		Georges Bank	8
		Southern New England	10
		Mid-Atlantic Bight	
2001 (N = 16)	2001	Gulf of Maine	3
		Georges Bank	1
		Southern New England	6
		Mid-Atlantic Bight	6
2003 (N = 23)	2003	Gulf of Maine	3
		Georges Bank	3
		Southern New England	13
		Mid-Atlantic Bight	4

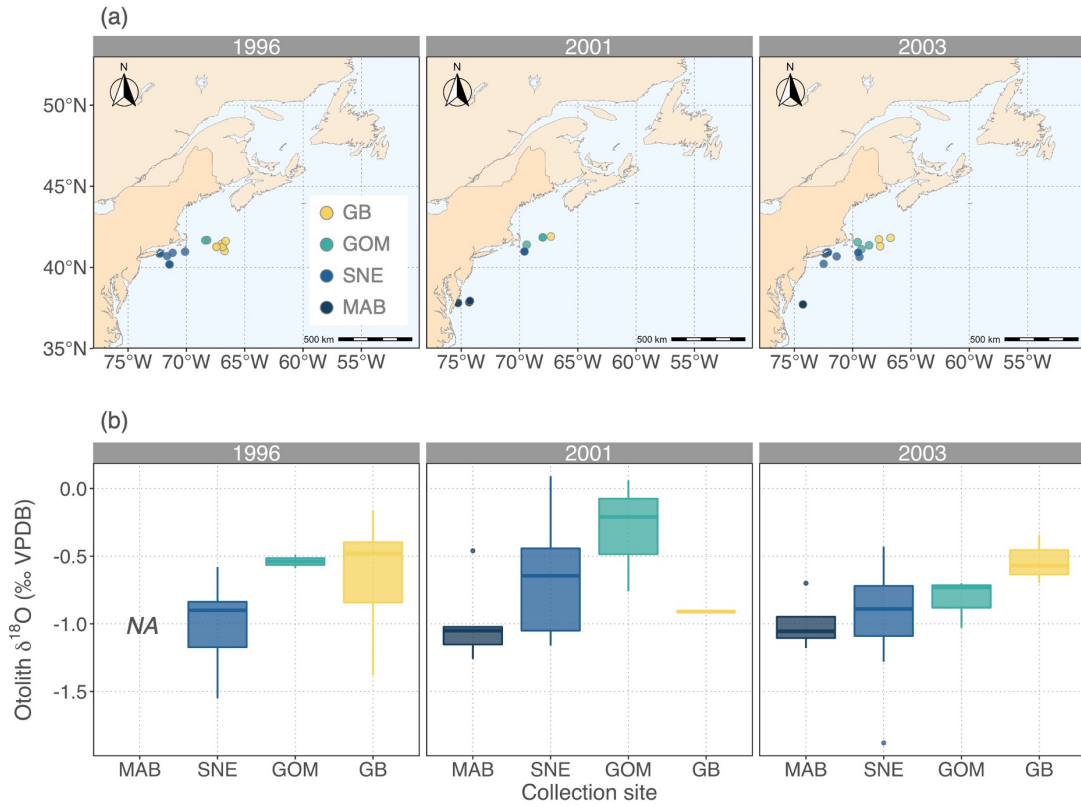


Figure S3.1 Collection sites (a) and measured otolith oxygen stable isotope values (b) of age-0 juvenile Northwest Atlantic mackerel collected in 1996, 1999, and 2003. GB = Georges Bank, GOM = Gulf of Maine, SNE = Southern New England, MAB = Mid-Atlantic Bight. The map was created using the *rworldmap* package (South, 2011) in R.

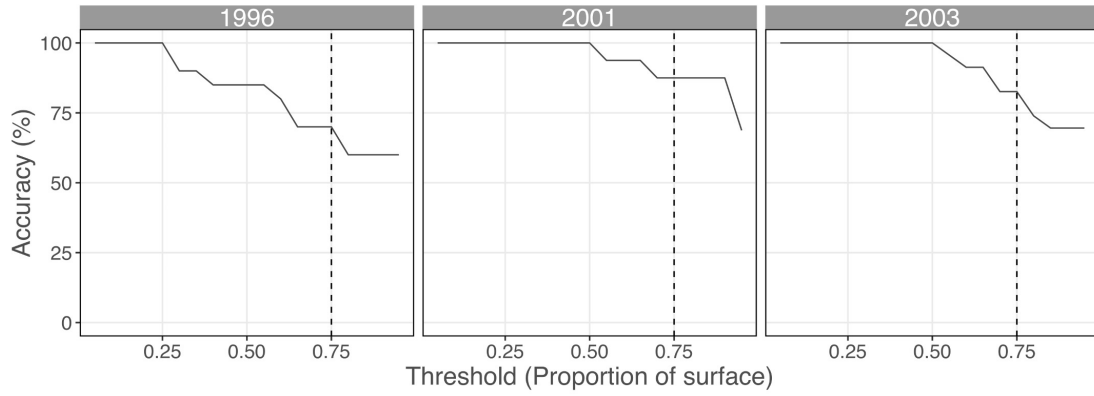


Figure S3.2 Geographic natal origin assignment accuracy computed from known-origin age-0 juvenile Northwest Atlantic mackerel collected in US shelf waters in 1996, 2001, and 2003 ($n = 59$). Accuracy was computed over a range of thresholds (i.e., precision) from 0.05 to 0.95. The 75th percentile threshold (dotted vertical line) provided a balanced accuracy-precision trade-off and was selected for binary transformation, where grid cells with posterior probabilities in the upper 25% of all grid cells were assigned “likely” and the remaining 75% as “unlikely” location of origin.

Chapter 4: Early growth and environmental conditions control partial migration of an estuarine-dependent fish

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4.1 Abstract

Partial migration is a widespread phenomenon in animals, whereby multiple groups follow different migration behaviors (i.e., contingents) within a single population. Fishes exhibit particularly high diversity in their early dispersal behaviors; however, whether these represent conditional partial migration behaviors remain unclear. I combined otolith microstructure and chemistry to assess the influence of early life conditions and environmental drivers on juvenile-stage partial migration of the anadromous striped bass (*Morone saxatilis*) in the Hudson River in two consecutive years with contrasting hydrologic conditions. Time-series clustering analysis on otolith Sr and Ba profiles revealed four dominant early migration contingents in both years: (i) freshwater residents, (ii) oligohaline migrants, (iii) small mesohaline migrants, and (iv) large mesohaline migrants. In both years, juvenile partial migration appeared to be a conditional strategy linked to a growth-mediated threshold. The propensity to migrate early was related to slower larval growth, whereas freshwater residency and delayed migration were associated with faster larval growth. Differences in hatch dates may have indirectly affected contingent membership by exposing larvae to varying environmental conditions. In a dry year, dispersal timing to mesohaline habitats coincided with high freshwater flow and tidal

currents, but not so in the second higher flow year. Following dispersal, the slow-growing oligohaline migrants exhibited compensatory growth in both years.

Recruitment to important coastal nurseries outside the Hudson River occurred during both larval and juvenile phases. Early dispersal modes could carry over to influence adult life histories, which may have important implications for population persistence in a highly stochastic estuarine environment, relevant to fisheries management and conservation for this important species.

4.2 Introduction

Partial migration is a common attribute observed for a range of animals, in which a single population contains multiple groups that follow different migration trajectories (i.e., contingents) (Lundberg, 1988; Chapman et al., 2011; Berg et al., 2019; Menz et al., 2019). The most traditional view of such a phenomenon is the coexistence within populations of individuals that remain in a single habitat (i.e., residents) and those that migrate between multiple habitats (i.e., migrants). Partial migration can alter the food web and community structure (Peller et al., 2023), and regulate population structure and species persistence (Kerr et al., 2010), all of which can have important ecological, evolutionary, and conservation consequences (Schindler et al., 2010; Secor, 2015). Yet, little is known about the potential drivers that regulate partial migration and the consequences of this behavior, especially for fishes.

Partial migration in fishes has long been recognized among salmonid species (Jonsson and Jonsson, 1993; Dodson et al., 2013), but has been shown to be prevalent among fishes in general (Kerr et al., 2009; Chapman et al., 2012; Secor, 2015).

Discrete migration modes have been shown to arise from a conditional response early in life in which intrinsic factors such as early development interact with extrinsic factors like environmental conditions and resource availability (Lundberg, 1988; Secor, 2015). Such conditional strategy operates through a threshold model where the decision to migrate or to remain resident is dependent upon threshold responses related to early life conditions such as body size and growth (Pulido, 2011; Dodson et al., 2013). Accelerated early growth has been associated with residency in Arctic charr (*Salvelinus alpinus*), Atlantic salmon (*Salmo salar*), and brown trout (*Salmo trutta*) (Nordeng, 1983; Aubin-Horth and Dodson, 2004; Olsson et al., 2006), but in other populations, the opposite has been shown, with higher growth favoring a migratory strategy (Metcalf et al., 1989; Forseth et al., 1999; Rikardsen and Elliott, 2000). Conditional responses could be multi-modal, as in the case of Atlantic salmon, where (i) the fastest-growing juveniles mature early and remain resident (i.e., residents), (ii) the intermediate-growing juveniles migrate early after brief residency (i.e., early migrants), and (iii) the slowest-growing juveniles migrate later in life after remaining resident for a longer period (i.e., late migrants) (Secor, 2015). Outside of salmonids, the estuarine-dependent white perch (*Morone americana*) also forms resident and migratory contingents linked to early growth, with the faster-growing individuals adopting a resident life cycle in freshwater habitats (Kraus and Secor, 2004; Kerr and Secor, 2010; Gallagher et al., 2018). However, the slower-growing migratory contingent exhibited compensatory growth, wherein juveniles accelerated their post-dispersal growth by taking advantage of the more productive brackish water environment (Kerr and Secor, 2009; Gallagher et al., 2018).

Partial migration can be considered a series of ecological carryover effects, in which conditions experienced during one life stage affect the behavior of subsequent life stages (Pechenik, 2006; O'Connor et al., 2014). Hatch dates and early-life environmental conditions (e.g., temperature, food availability) can directly influence early growth, which in turn determines whether an individual adopts a particular migratory strategy (Kraus and Secor, 2004; Kerr and Secor, 2010; Gallagher et al., 2018). As such, inter-annual fluctuations in weather conditions would cause annual variations in juvenile contingent membership and nursery habitat use that carry over to influence adult life history, which ultimately contribute to population-level stability and resilience (Kraus and Secor, 2004; Kerr et al., 2010).

The potential causes and consequences of partial migration during the early life stage were investigated for the Hudson River (HR) population of striped bass (*Morone saxatilis*), an estuarine-dependent fish that supports important commercial and recreational fisheries in the US Atlantic waters (NEFSC, 2019). Striped bass are an anadromous species, in which most adults spend the majority of their lifetime in coastal waters showing diverse oceanic migrations (Zlokovitz et al., 2003; Secor and Piccoli, 2007; Gahagan et al., 2015), but migrate into fresh tidal regions to spawn in the spring (Secor and Houde, 1995; Secor et al., 2020; Pan et al., 2023). Semi-buoyant eggs and pelagic larvae are redistributed by freshwater flow and tidal currents, but are generally retained above the salt front (Boreman and Klauda, 1988; Dovel, 1992; Secor et al., 2020). Following metamorphosis (ca. 15 mm TL; Mansueti, 1958), juveniles occur throughout a wide range of salinity in the HR (Dovel, 1992).

Striped bass juveniles exhibit partial migration in the Albemarle Sound (Mohan et al., 2015), Chesapeake Bay (Conroy et al., 2015), and St. Lawrence Estuary (Morissette et al., 2016; Vanalderweireldt et al., 2019), whereby a portion of juveniles remain in their natal freshwater or oligohaline habitats, while others migrate downstream into higher salinity habitats. Slower early growth was associated with a propensity to migrate, and the timing of dispersal was related to a high-flow event in the Chesapeake Bay population (Conroy et al., 2015). I hypothesized that HR striped bass might similarly exhibit juvenile migrations that were both conditional — influenced by larval growth — and facultative — influenced by flow. In addition to the principal nursery region within the HR, juveniles frequently occur outside the HR, in the nearby western Long Island Sound (WLIS) region (Figure 4.1), which may provide important contributions to the HR adult population (Dovel, 1992; Dunning et al., 2009). Dunning et al., (2009) showed that the combination of freshwater and tidal flow can transport larvae from the HR to WLIS via the highly channelized East River, although dispersal dynamics to this “extra” coastal nursery remain highly uncertain.

Here, I used otolith microstructure and microchemistry to understand how early life conditions and environmental drivers are related to the partial migration of juvenile HR striped bass in two consecutive years (2019 and 2020) with contrasting hydrologic conditions and age-0 juvenile recruitment levels (Figure S4.1). Fine-scale lifetime movement patterns were reconstructed by leveraging otolith microstructure and chemical analyses with time series clustering and machine learning algorithms. Because otoliths are metabolically inert and permanently record daily growth and ambient environment condition, elements such as Sr and Ba have been used

extensively to understand diadromous fish migrations across salinity gradients at high-resolution (Elsdon et al., 2008; Walther and Limburg, 2012; Walther, 2019). I hypothesized that (i) HR striped bass juveniles would exhibit distinct early migration modes (i.e., migration contingents); (ii) that differences in larval growth would lead to distinct migration contingents; (iii) that migration contingents would be indirectly influenced by hatch dates and early life environmental conditions through the effect of these variables on larval growth; (iv) that dispersal timing would be associated with environmental drivers; and (v) that migrants would compensate for their slower growth by enhancing post-dispersal juvenile growth in productive brackish habitats (Figure 4.2).

4.3 Methods

4.3.1 Sample Collection

Age-0 striped bass juveniles were collected by the New York State Department of Environmental Conservation annual young-of-year survey with a 30.5 m × 1.2 m and 61.0 m × 1.2 m beach seine from July to November 2019 ($n = 193$), and from June to November 2020 ($n = 448$). Collections took place in freshwater (salinity < 0.4 ppt), oligohaline (0.4–3 ppt), and mesohaline (3–18 ppt) habitats in the Hudson River, and in polyhaline (salinity > 18 ppt) habitats outside the Hudson River estuary in the western Long Island Sound (Figure 4.1). Total length (TL) was measured to the nearest 1 mm and the sagittal otolith was extracted from all samples. Otoliths for microstructure and microchemistry were subsampled from months after June assuming that juveniles would have completed their initial dispersal and settled in their nurseries

by this time (Dovel, 1992; Conroy et al., 2015), and included subsamples from July to October 2019 ($n = 69$) and from July to August 2020 ($n = 62$). To the extent possible, subsamples were evenly selected across freshwater, oligohaline, mesohaline, and polyhaline regions; within regions, individuals were drawn randomly to obtain a representative size distribution (Table S4.1).

4.3.2 Otolith Microstructure

Hatch dates and early growth were estimated through otolith microstructure analysis (step A in Figure 4.2). Following Secor et al., (1991), otoliths were embedded and sectioned transversely. Otolith sections were subsequently polished using 320, 600, and 1200 grit materials until the primordium was visible. Then, sections were buffed on a wet microcloth with 0.3 μm alumina powder to remove pits and abrasions. Because the daily deposition of microstructural increments in sagittal otoliths has been validated for juvenile striped bass (Secor and Dean, 1989), increments were enumerated from the primordium to the otolith edge to determine daily age. A second read on a subset of samples ($n = 30$) detected no ageing bias and high ageing precision (see *Supplementary material*). The following equation from Houde and Morin, (1990) was used to adjust the initial age estimate (a_{initial}) for the effects of temperature on the formation of the first daily increment in striped bass otoliths ($a_{\text{corrected}}$):

$$a_{\text{corrected}} = a_{\text{initial}} + (11.56 - 0.45 \times T), \quad (\text{Eq. 4.1})$$

where T is the mean daily temperature (°C) at the preliminary hatch date calculated using $a_{initial}$. Age adjustments were small and ranged from 0 to 4 days. Temperature data were obtained from the United States Geological Survey (USGS) monitoring station below Poughkeepsie (site: 01372058) in 2019, and near Poughkeepsie (site: 01372043; Figure 4.1) in 2020, because single-site data were not available for both years.

The otolith radius (OR, μm) along the ventral transverse axis from the primordium to a given daily increment was measured using Infinity Analyze and Capture (Teledyne Lumenera software). The biological intercept method was then used to back-calculate the TL (mm) of an individual at any given age by the following equation (Campana, 1990):

$$TL_a = TL_c + \frac{(OR_a - OR_c) \times (TL_c - TL_i)}{(OR_c - OR_i)}, \quad (\text{Eq. 4.2})$$

where subscripts i , a , and c correspond to initial, at-age, and at-capture values, respectively, of OR and TL. Values of 23.9 μm and 6.1 mm were used as inputs for OR_i and TL_i , respectively (Conroy et al., 2015). Back-calculated size-at-age was used to estimate specific growth rates (SGR, % day⁻¹) during the larval (ages 0 to 30 days) and early juvenile stages (ages 30 to 50 days) (Mansueti, 1958) using the following equation:

$$SGR = \frac{\log(TL_t) - \log(TL_i)}{t} \times 100, \quad (\text{Eq. 4.3})$$

where TL_t and TL_i are final and initial total lengths, respectively, and t is the age between those two lengths. I used a theoretical size-at-hatch (i.e., age 0) of 3.81 mm for larval growth estimates (Conroy et al., 2015).

4.3.3 Otolith Microchemistry

Early dispersal history for each age-0 juvenile was reconstructed using otolith microchemistry (step B in Figure 4.2). Elemental concentrations in otoliths were measured using an Elemental Scientific NWR193 excimer laser ablation (LA) system (193 nm, 4 ns pulse width) coupled to an Agilent 7500ce inductively coupled plasma mass spectrometer (ICP-MS) at the University of Texas at Austin. All otoliths and standards processed on the LA-ICP-MS were loaded into a large format cell with fast washout times (< 1 s). Following pre-ablation (50 μm diameter spot, 50 $\mu\text{m s}^{-1}$ scan rate, 3.9 J/cm² fluence) to remove shallow surface contaminants of the otolith section, a laser transect scan was performed from the primordium (start of life) along the longest growth axis to the otolith edge (end of life) with a 25 μm diameter spot, 5 $\mu\text{m s}^{-1}$ scan rate, 2.77 ± 0.06 J/cm² fluence, 20 Hz repetition rate, and carrier gas flows of 0.8 L min⁻¹ for argon and helium. All elements (²⁴Mg, ⁴⁴Ca, ⁵⁵Mn, ⁸⁸Sr, ¹³⁸Ba) were measured on the LA-ICP-MS system with 10 ms integration times. Measured intensities were converted to elemental concentrations (ppm) using Iolite software (Paton et al., 2011), using ⁴³Ca as the internal standard and a Ca index concentration value of 38.3 wt% for otolith unknowns. USGS MACS-3 (synthetic aragonite) was used as the primary calibration standard and NIST 612 and ECRM-752-NP were used as external reference standards. The grand average of secondary standard recovery

fractions for all elements was typically within 5% of reference values (<http://georem.mpch-mainz.gwdg.de>).

4.3.4 Statistical Analysis

Elemental concentration profiles from the otolith core to the edge were smoothed by consecutive moving median and average filters using a 7-point boxcar width (5 μm equivalent distance) to remove high-frequency outliers. Multivariate time-series clustering using dynamic time warping (DTW) was employed to identify distinct early migration modes of age-0 juveniles based on the shapes of otolith elemental profiles (Aghabozorgi et al., 2015; Hegg and Kennedy, 2021) (step C in Figure 4.2). DTW is a machine learning algorithm that clusters time series that are similar in shape, but are offset in time (Aghabozorgi et al., 2015). The algorithm reports the cost of “warping” the temporal dimension to match two time series by iteratively matching each point in the two time series in a one-to-multiple approach. In this way, otolith elemental profiles that are similar in shape but vary temporally are clustered together as a unique migration contingent. Clustering was performed jointly on Sr and Ba profiles with the R package “*dtwclust*” (Sardá-Espinosa, 2019) using agglomerative hierarchical clustering with Ward’s distance. A Sakoe-Chiba window of 1.5% was used to restrict the warping path between two time series. All elemental concentration time series were standardized to *z* scores before analysis. The dendrogram was cut (i.e., the number of clusters) at the location that produced interpretable distinct migration contingents with a high Silhouette index (Rousseeuw, 1987), while also maintaining a minimum ($n > 10$) within-cluster sample size for subsequent analysis.

Partial migration is likely shaped by multiple factors, such as early life experiences, rather than just the conditional response to larval growth (step D in Figure 4.2). Thus, in addition to larval growth, I explored the environmental conditions and food availability experienced by age-0 juveniles during their first 30 days of life. The mean temperature, river flow, and chlorophyll-a concentration experienced by each individual during their first 30 days of life were calculated for all individuals. Here, chlorophyll-a concentrations were used as a surrogate for estuarine production and trophic resources as zooplankton prey (data unavailable) are expected to be positively associated with primary production (Pace et al., 1998). Data on daily temperature, river flow, and chlorophyll-a concentration were acquired from the USGS Poughkeepsie monitoring station (site: 01372058 [2019], 01372043 [2020]), USGS Green Island monitoring station (site: 01358000), and the National Estuarine Research Reserve System (NERRS) at Tivoli North Bay, respectively (Figure 4.1). To examine the effect of larval growth, hatch dates, and early life experiences on migration contingents, a multinomial logistic regression analysis was conducted using the R package “*nnet*” (Venables and Ripley, 2002). The migration contingent was modeled as a categorical response variable, and larval growth, hatch dates, and experienced environmental conditions (i.e., mean temperature, river flow, and chlorophyll-a) were included as continuous predictor variables. Given the strong collinearity ($r > 0.6$ or < -0.6) among hatch dates and experienced environmental conditions, I initially conducted a principal component analysis on these correlated variables and included the first principal component (PC1, > 90% variance explained) as a continuous predictor in the model (Figure S4.2). The relationship between the

log-odds of belonging to any migration contingent j relative to a reference category (1) and continuous predictors was modeled as follows:

$$\log\left(\frac{p_j}{p_1}\right) = \beta_{0j} + \beta_{1j}(\text{Larval Growth}) + \beta_{2j}(\text{PC1}), \quad (\text{Eq. 4.4})$$

where *Larval Growth* and *PC1* (i.e., first principal component) are continuous predictors. Separate models were fitted to 2019 and 2020 data, and the best model was selected by comparing Akaike’s Information Criterion corrected for small sample sizes (AICc). Predicted probabilities of migration contingents associated with each predictor were visualized using the R packages “*emmeans*” (Lenth et al., 2018) and “*ggeffects*” (Lüdtke, 2018). Univariate comparisons of hatch dates and early life experiences across migration contingents and years are shown in the *Supplementary material*.

The hypothesis related to dispersal timing (step E in Figure 4.2) was assessed using time-series changepoint analysis with the pruned exact linear time (PELT) algorithm in the R package “*changepoint*” (Killick and Eckley, 2014), which detected major concentration shifts within the individual otolith Sr transect. The PELT algorithm detected multiple shifts in mean and variance in Sr concentration for each fish, resulting in multiple stable otolith signature segments for a given transect. For each stable segment, I calculated the mean concentration of four elements (i.e., Mg, Mn, Sr, Ba); then, each segment was assigned to one of four habitats using a random forest (RF) algorithm in the R package “*ranger*” (Wright and Ziegler, 2017): freshwater (salinity < 0.4 ppt), oligohaline (0.4–3.0 ppt), mesohaline (3.0–18.0 ppt),

and polyhaline (> 18.0 ppt). Mean elemental concentrations of the recently formed otolith edge, corresponding to the last 20 μm of the laser transect, were used as the reference baseline for habitat assignment, assuming that it reflects the habitat from which the sample was collected (Figure S4.3a). Hyperparameter tuning of the RF classifier was conducted through a grid search method on 10 cross-validation folds to find the optimal hyperparameters (*mtry* = 2, *minimal node size* = 1, *number of trees* = 1000). The accuracy of the RF classifier was further assessed through 10-fold cross-validation. For each fish, detected changepoints and assigned habitats were visually inspected, and erroneous changepoints and assignments associated with unstable means were manually removed. The changepoint detected near the core region was also removed given that the elemental signature near the core may be maternally derived (Kalish, 1990; Volk et al., 2000; Hegg et al., 2019). I defined the size and age at dispersal to brackish habitats as the first point at which an individual transitioned from freshwater to brackish water habitats (i.e., oligohaline, mesohaline, or polyhaline). I further evaluated the size and age of WLIS entrance for fish that were collected in polyhaline habitats in WLIS. Given the distinct otolith Ba signature in WLIS habitats (Figure S4.3b), a similar changepoint analysis with the PELT algorithm was performed on otolith Ba transects, using only the transects past the point of initial dispersal to brackish water habitats. Mean stable segments were further assigned to a specific habitat using RF to detect WLIS entry. I defined WLIS entry as the point at which the fish entered polyhaline habitats and demonstrated subsequent usage of polyhaline habitats after entry. To assess the effect of the initial dispersal size to brackish habitats on the number of days spent in brackish water

before entering WLIS, a generalized linear model with a negative binomial distribution and a log-link function was used in the R package “*MASS*” (Venables and Ripley, 2002).

The effect of environmental conditions on dispersal timing was assessed using nonlinear regression models (step F in Figure 4.2). Because the shift in Sr concentration for oligohaline migrants was less apparent (see Results) and could potentially bias estimates of dispersal date, this analysis was limited to fish that dispersed to mesohaline and polyhaline habitats (2019: $n = 30$, 2020: $n = 26$). The number of fish dispersed on a given day was estimated from the dispersal date of each fish, then smoothed using a 5-day centered moving average window to account for potential ageing error. The smoothed daily number of fish dispersed was then compared to the daily mean temperature, river flow, and tidal amplitude data acquired from the USGS Poughkeepsie monitoring station (site: 01372058 [2019], 01372043 [2020]), USGS Green Island monitoring station (site: 01358000), and the NOAA Tide and Currents Peekskill monitoring station (site: 8518949), respectively. I employed a generalized additive mixed model (GAMM) in the R package “mgcv” (Wood, 2017) to assess the influence of environmental conditions on dispersal timing. The smoothed number of fish dispersed on a given day t , Y_t , was specified using a gamma distribution as the response variable, modeled as a combination of additive smooth terms through a log link function defined as:

$$Y_t \sim \text{Gamma}(\mu_t) \quad (\text{Eq. 4.5})$$

$$\log(\mu_t) = \beta_0 + s(\text{Temperature}_t) + s(\text{Flow}_t) + s(\text{Tide}_t) + \text{Year} + \varepsilon_t$$

$$\varepsilon_t \sim AR(1),$$

where $s(Temperature_t)$, $s(Flow_t)$, and $s(Tide_t)$ indicate smooth functions for daily mean temperature, river flow, and tidal amplitude fitted using thin plate regression splines. *Year* indicates a non-smooth term for year 2019 and 2020. Temporal residual autocorrelation was modeled using the 1st-order autoregressive structure (AR1). The best model was selected by comparing AICc. After the assumptions of homoskedasticity, uncorrelatedness, and normality of residuals were verified, the significance of the model coefficients was assessed. To facilitate model fitting, one fish that dispersed in late August 2020 was regarded as an outlier and removed from the analysis.

The compensatory growth hypothesis was tested using two-way analysis of variance (ANOVA) to detect differences in larval and juvenile growth rates of age-0 juveniles across migration contingents, years (2019 and 2020), and their interaction (step G in Figure 4.2). A post-hoc Tukey test was employed for multiple comparisons of these variables across contingents within each year using the “*emmeans*” R package (Lenth et al., 2018).

4.4 Results

4.4.1 Migration Contingents

Time-series clustering of otolith Sr and Ba transects with dynamic time warping detected three and four distinct clusters, or migration contingents, in 2019 and 2020, respectively (Figure 4.3). However, the first cluster in 2019 exhibited two

separate migration contingents given the large differences in Sr and Ba concentrations, leading to a total of four dominant migration contingents for both 2019 and 2020. The first group that consistently showed low Sr concentration, indicative of lifetime freshwater habitat use, was assigned “freshwater residents”. The second group, referred to as “oligohaline migrants”, comprised fish that showed an abrupt shift in Sr concentration that leveled off at around 1500 ppm, indicating dispersal to oligohaline habitats (mean dispersal size: 42.5 mm [2019]; 14.3 mm [2020]). The third group, assigned “large mesohaline migrants”, initially showed low Sr concentrations, but displayed a marked increase later in life and consistently high Sr concentration around 2500 ppm, indicating dispersal and subsequent mesohaline habitat use (mean dispersal size: 51.2 mm [2019]; 46.0 mm [2020]). The fourth and final group, assigned “small mesohaline migrants”, displayed Sr concentrations that increased rapidly early in life and were persistently high, reflecting dispersal to mesohaline habitats at a small size (mean dispersal size: 21.3 mm [2019]; 20.5 mm [2020]). A small number of samples ($n = 18$ of 131 total) displayed consistently low Sr concentrations despite being collected in brackish water habitats. These fish were considered recent migrants where the otolith chemical signature did not yet reflect the ambient condition of the brackish water collection site. Thus, to prevent erroneous contingent assignment, these samples were excluded from cluster analysis and were manually assigned a contingent membership based on their collection site and total length.

4.4.2 The Effect of Larval Growth and Early Life History Characteristics on Migration Contingents

Multinomial logistic regression analysis indicated that covarying larval environmental conditions were associated with contingent membership in 2020 but not in 2019, where only larval growth explained contingent membership (Table 4.1). In 2019, fish that showed the slowest larval growth rates were more likely to become oligohaline migrants, although the relationship with larval growth was not apparent with other migration contingents (Figure 4.4). For 2020 samples, larval growth, and a principal component defined by larval environmental characteristics (strong loadings of hatch dates and experienced temperature inversely covarying with flow and chlorophyll-a; see Figure S4.2) were retained as important variables (Table 4.1). Predicted contingent membership probabilities indicated that oligohaline migrants arose from individuals with the slowest larval growth and later hatch dates associated with high temperature, low flow, and low chlorophyll-a concentration (Figure 4.4). In contrast, individuals that exhibited the highest larval growth and early hatch dates during a period of low temperature, high flow, and high chlorophyll-a concentration migrated to mesohaline habitats at a large size (Figure 4.4). Freshwater residents and small mesohaline migrants arose from individuals exhibiting intermediate larval growth and hatch dates.

4.4.3 Dispersal Timing and Environmental Drivers

The changepoint analysis combined with random forest habitat assignment (classification accuracy: 96.7%) detected the dispersal size and age (date) to brackish water habitats. Dispersal events in 2019 were spaced out in time from late-June to

late-August 2019, with no more than 27% of total fish emigrating from freshwater in any given week (Figure 4.5). While there were a few major peaks in both flow and tidal amplitude, there was no clear relationship between these environmental drivers and the timing of dispersal. In 2020, the majority of fish (> 70%) emigrated from freshwater habitats within a two-week window from June 29 to July 13, 2020, coinciding with a period of high flow and high tidal amplitude. The final GAMM of the effect of environmental conditions on dispersal timing included daily tidal amplitude, although the coefficient estimate of the smooth term was not statistically significant (effective degrees of freedom = 1, F -value = 0.54, p = 0.47; Table S4.2).

4.4.4 Western Long Island Sound Entry

The size at ingress to WLIS was broad, taking place both during the late-larval (TL < 20 mm) and juvenile (TL > 30 mm) phases (Figure 4.6a). The estimated coefficient of the GLM showed a significant negative relationship between the initial dispersal size to brackish habitats and the number of days spent in brackish water before entering WLIS (coefficient $\pm$ SE = -0.03 ± 0.01 , p < 0.01; Figure 4.6b).

4.4.5 Compensatory Growth

Significant differences in larval growth rates were detected between contingents (two-way ANOVA, p < 0.001) and years (p < 0.001), but not their interaction (p = 0.15; Figure 4.7a). In both years, oligohaline migrants exhibited significantly slower growth rates compared to residents (Tukey test, p < 0.05) and large mesohaline migrants (p < 0.05). Larval growth rates were on average higher in 2019 compared to 2020 (p < 0.001). For juvenile growth rates, no significant

contingent (two-way ANOVA, $p = 0.3$), year ($p = 0.36$), or interaction effects ($p = 0.15$) were detected (Figure 4.7b), supporting the hypothesis of compensatory growth during the juvenile period.

4.5 Discussion

Juvenile partial migration of Hudson River striped bass was associated with larval growth rates in a manner consistent with hypothesized conditional strategy, albeit facultatively controlled by environmental drivers. I uncovered four dominant early migration modes for two successive years with contrasting hydrologic conditions and juvenile densities (Figure S4.1). In both years, migration contingents were similarly associated with larval growth: oligohaline migrants arose from individuals with the slowest larval growth, whereas those with the fastest larval growth migrated to mesohaline habitats at a larger size after a prolonged period of freshwater residency. Intermediate larval growth rates were associated with lifetime freshwater residency in a dry 2020 season, but not in a wet 2019 season. Differences in the timing of hatch in the dry year may have indirectly affected contingent membership by exposing larvae to various environmental conditions. Dispersal timing coincided with a period of relatively high freshwater and tidal flow in the dry 2020 season, although no clear relationship was found between dispersal timing and environmental variables for the wet 2019 season. In both years, the slow-growing oligohaline migrants exhibited compensatory growth following dispersal to brackish environments.

4.5.1 Early Migration Contingents in Juvenile Striped Bass

High-resolution otolith microchemistry data coupled with dynamic time warping cluster analysis uncovered cryptic early migration modes in juvenile striped bass in the Hudson River (Figure 4.3). These modes were discrete with underlying trajectories informing inferences on dispersal sizes and fates. Similar migration modes have been observed for striped bass populations in the Chesapeake Bay (Conroy et al., 2015), St. Lawrence Estuary (Morissette et al., 2016; Vanalderweireldt et al., 2019), and Albemarle Sound (Mohan et al., 2015), with some juveniles remaining in their natal freshwater or oligohaline habitats while others migrate downstream into higher salinity habitats. This suggests that partial migration during the early life stages could be prevalent among striped bass populations along the Atlantic coast, which may have developed as a plastic response to nonstationary environments (Kerr et al., 2010).

The dispersal size of small and large mesohaline migrants was comparable in both years (Figure 4.3). However, the dispersal size of oligohaline migrants was substantially larger in 2019 than in 2020, which could be an artifact of our approach that relied on otolith chemistry to infer movement across salinity gradients. Given the higher flow in 2019, the salinity gradient in the estuary may have been too small to detect any spatial differences between upstream and downstream habitats and biased the dispersal size high (later in the season). High flow in 2019 could also explain the lower otolith Sr concentration of oligohaline migrants compared to 2020 (Figure 4.3). Still, identified migration contingents were consistent between years despite contrasting hydrological conditions and age-0 juvenile recruitment levels.

How striped bass recruit to WLIS nurseries via the East River has been a long-standing question (Dovel, 1992; Dunning et al., 2009). The otolith multi-elemental approach revealed that WLIS entry occurred during both the late-larval (TL < 15 mm) and juvenile (TL > 30 mm) phases, confirming previous views on WLIS recruitment dynamics (Dunning et al., 2009; Figure 4.6a). However, I cannot rule out the possibility that variation in recruitment size to the WLIS nursery could be explained by juveniles entering the WLIS from other systems, namely the nearby Connecticut River, where adult striped bass are also present (Davis et al., 2012). Nonetheless, no direct evidence of striped bass spawning in the Connecticut River has been found (Waldman et al., 1988; Gephard and McMenemy, 2004), and the majority of WLIS-recruited fish are thought to have originated in the HR. For individuals that recruited to the WLIS, the initial dispersal size to brackish habitats appeared to influence the amount of time spent in the lower HR before entering WLIS, with smaller dispersers spending more time in the lower HR, and vice-versa for larger dispersers (Figure 4.6b). A plausible explanation for this relationship could be that the greater swimming ability of larger fish facilitated a shorter transit time through the East River, where the net tides flow against transit, back towards the lower HR Estuary (Blumberg and Pritchard, 1997; Blumberg et al., 1999). Smaller fish, on the other hand, may need to adjust their vertical position in the water column to utilize the eastward residual flow in the upper water column and passively transition through this high-velocity strait, delaying WLIS entry.

4.5.2 Partial Migration as a Conditional Strategy

Early migration contingents of HR striped bass were associated with early growth rates (Figure 4.4), corroborating past studies across varied taxa (Jonsson and Jonsson, 1993; Chapman et al., 2012; Dodson et al., 2013; Secor, 2015) and supporting a growth-mediated movement threshold for juvenile striped bass. The propensity to migrate early or to migrate to proximate oligohaline habitats was related to slower larval growth, whereas freshwater residency or delayed migration to distant mesohaline habitats was associated with faster larval growth (Figure 4.4). Fast-growers thus forgo migration, whereas slow-growers undertake a riskier strategy to search for suitable habitats to enhance future fitness outcomes. A similar relationship between early growth and migration propensity has been observed in several freshwater and coastal species including the congeneric white perch (Kraus and Secor, 2004; Kerr and Secor, 2010) and striped bass from the Chesapeake Bay (Conroy et al., 2015) and St. Lawrence Estuary populations (Vanalderweireldt et al., 2019).

Protracted spawning of striped bass exposes larval cohorts to various environmental and foraging conditions, leading to extreme variation in larval growth rates (Houde, 1997; Secor, 2000). Early growth and hatch dates were closely related in 2020, with the fast-growing large mesohaline migrants hatching significantly earlier than the slow-growing oligohaline migrants (Figure 4.4). Despite being exposed to a significantly lower temperature and higher flow, the fast-growing early-hatched cohort experienced higher chlorophyll-a concentrations compared to their later-hatched slow-growing peers, which if associated with secondary production,

may have resulted in their accelerated larval growth rates (Figures 4.4 and S4.4). Intraspecific competition may have also played an important role where early-hatched cohorts pre-occupied favorable habitats for early growth, forcing later-hatched cohorts to utilize suboptimal habitats (MacCall, 1990; Mohan et al., 2015). Significant larval growth differences occurred in 2019 despite the substantial overlap in hatch date distributions (Figures 4.4 and S4.4). This suggests influences of early growth beyond temporal match-mismatch dynamics and could be related to variations in the spawning location of adult striped bass (Secor et al., 2020).

Environmental drivers did not appear to have a major effect on dispersal timing in 2019, and GAMM models detected no significant effects of environmental drivers on dispersal (Figure 4.5). Nonetheless, a major dispersal event coincided with a period of relatively high freshwater and tidal flow, consistent with a larval dispersal event described for striped bass in the Chesapeake Bay (Conroy et al., 2015; Figure 4.5). One plausible explanation for this relationship could be that the growth-mediated movement threshold interacts with environmental drivers, wherein high flow and tidal currents serve as a trigger that initiates the dispersal behavior of individuals below a specific growth threshold (Nathan et al., 2008; Conroy et al., 2015). Alternatively, the apparent relationship between dispersal and flow events could be due to the simple advection of dispersive larvae.

4.5.3 Consequences of Migration

I predicted accelerated growth to occur in more productive brackish habitats as an immediate consequence of migration. As determined by larval growth comparison, oligohaline migrants were significantly slower in growth compared to

their peers prior to dispersal (Figure 4.7a). The slow-growing oligohaline migrants, however, demonstrated comparable juvenile growth to their counterparts in both years following dispersal to brackish habitats, supporting the concept of compensatory growth (Metcalf and Monaghan, 2001; Figure 4.7b). Such compensatory responses have been reported in a range of fishes, including congeneric white perch in the Chesapeake Bay (Kerr and Secor, 2009) and Hudson River (Gallagher et al., 2018). Within the HR, oligohaline and mesohaline habitats are generally more productive than freshwater habitats, which may provide greater foraging opportunities for dispersers (Sirois and Fredrick, 1978; Howarth et al., 2006). Thus, greater biomass of zooplankton coupled with increased consumption rates may have resulted in compensatory growth. However, it is important to note that our approach looks at only the survivors, and the potential cost associated with migration remains unknown. The benefit of accelerated growth following migration to brackish habitats is traded off against the cost of increased predation mortality due to the higher abundance of piscivorous predators (e.g., bluefish [*Pomatomus saltatrix*]) with increased salinity and depth (Juanes et al., 1993; Buckel et al., 1999). The energetic cost of migration itself and osmoregulatory responses to higher salinity may also be an indirect source of mortality (Chapman et al., 2012).

Partial migration early in life could have important consequences on the HR adult striped bass population dynamics. Early life migration contingent behaviors and vital rates can carry over to influence adult growth and life histories, which exhibit demographic differences that could contribute to population persistence (Kraus and Secor, 2004; Kerr et al., 2010; Gallagher et al., 2018). Further, early migration modes

detected in this study were linked to various nursery habitat use patterns, which could exhibit asynchronous dynamics in response to environmental conditions that could confer stability at aggregate scales (i.e., portfolio effect; Schindler et al., 2010; Secor, 2015; Stier et al., 2020). Such spatial “bet-hedging” strategy, stemming from diverse early migration modes, could serve as a buffer to highly varied estuarine environments. For conservation and management applications, future efforts should focus on assessing how these different nurseries produce individuals that recruit to the adult population.

Importantly, long-term increases in freshwater flow and temperature in the HR due to climate change may modify striped bass partial migration responses and population dynamics (Najjar et al., 2009; Seekell and Pace, 2011; Figure S4.1). Earlier spawning of adult striped bass is predicted with increased temperature (Pan et al., 2023), which may influence temporal match-mismatch of prey and larvae, and affect juvenile partial migration dynamics. Predicted higher flow may increase the proportion of the migratory contingent by interacting with the growth-mediated behavioral threshold and/or by facilitating downstream advection of dispersive larvae. Furthermore, because flow is strongly and inversely related to primary productivity in the HR (Howarth et al., 2000; Gallagher and Secor, 2018), projected higher flow could result in slower larval growth, favoring the migratory contingent. Given the unique and complementary roles that diverse early migration traits play in the population dynamics (Kraus and Secor, 2004; Kerr et al., 2010), a potential decline in the freshwater resident contingent could jeopardize the long-term persistence of the HR striped bass population. Thus, understanding and preserving key drivers that

promote diverse life history traits could provide valuable insights for sustainable fisheries and conservation strategies for this important species in the face of climate change.

4.6 Acknowledgements

I thank Michelle Sluis for the assistance and training with the LA-ICP-MS analysis. This research was funded by the Hudson River Foundation under grant number 004/19A. KA was financially supported by a fellowship from Japan Student Services Organization.

Tables

Table 4.1 Akaike's information criterion (corrected for small sample size; AICc) rankings of the multinomial logistic regression model to assess the probability of migration contingent membership in relation to early life characteristics.

Year	Rank	Model	df	AICc	Δ AICc
2019	1	Larval growth	6	191.33	0.00
	2	Larval growth + PC1	9	195.40	4.07
	3	Intercept	3	195.94	4.61
	4	PC1	6	199.89	8.57
2020	1	Larval growth + PC1	9	136.65	0.00
	2	PC1	6	154.46	17.81
	3	Larval growth	6	163.42	26.77
	4	Intercept	3	176.25	39.60

Note: The first principal component (PC1) includes hatch dates and experienced environmental conditions during the first 30 days of life (i.e., mean temperature, flow, and chlorophyll-a). Δ AICc shows the differences in Akaike's information criterion (corrected for small sample size) between the best model (rank 1) and a given model. df = degrees of freedom.

Figures

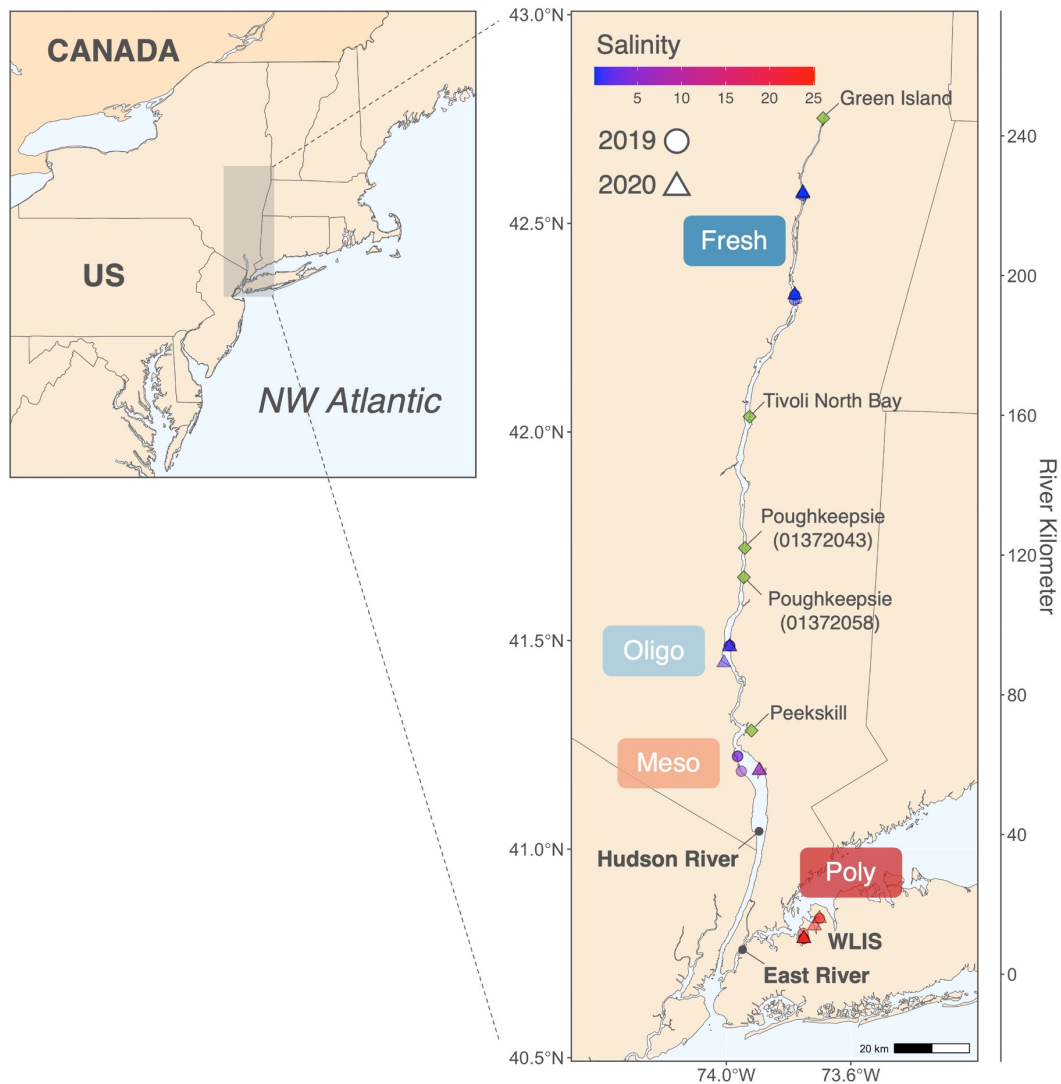


Figure 4.1 Map of the Northwest Atlantic Ocean, Hudson River, and western Long Island Sound (WLIS), with age-0 juvenile striped bass collection sites in 2019 and 2020. Collection sites are colored by the salinity at collection. Green diamonds display stations where environmental variables were obtained. The y-axis depicts the latitude and river kilometers from the mouth of the Hudson River. Fresh = Freshwater, Oligo = Oligohaline, Meso = Mesohaline, Poly = Polyhaline.

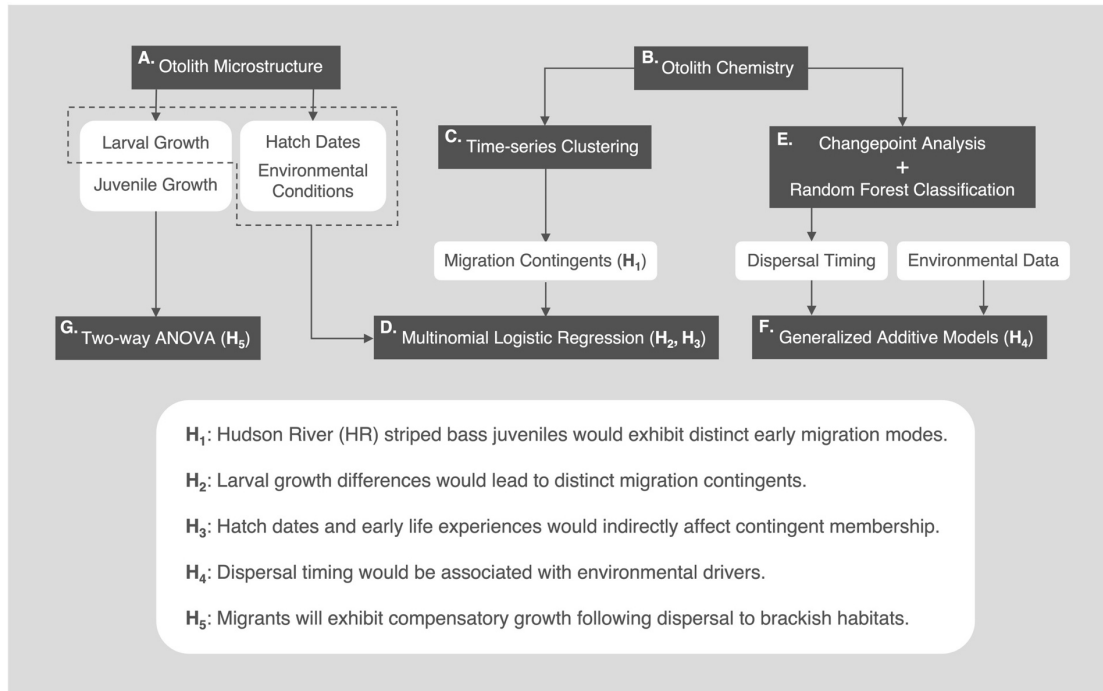


Figure 4.2 Flow chart showing steps for otolith microstructure, chemistry, statistical analyses, and testing of related hypotheses (H_1 – H_5) for Hudson River (HR) juvenile striped bass. (A) Otolith microstructure analysis to estimate larval and juvenile growth, hatch dates, and experienced environmental conditions (temperature, flow, and chlorophyll-a) during the first 30 days of life for each individual. (B) Otolith microchemistry to reconstruct early dispersal history for juvenile striped bass. (C) Time-series clustering on otolith chemistry to identify distinct early migration modes of juveniles. (D) Multinomial logistic regression to assess the effect of larval growth, hatch dates, and early life history experiences on migration contingents. (E) Time-series changepoint analysis with random forest classification to detect the size and age at dispersal to brackish habitats. (F) Generalized additive models to assess the influence of environmental conditions on dispersal timing. (G) Two-way analysis of variance (ANOVA) to detect differences in larval and juvenile growth to test the compensatory growth hypothesis following dispersal.

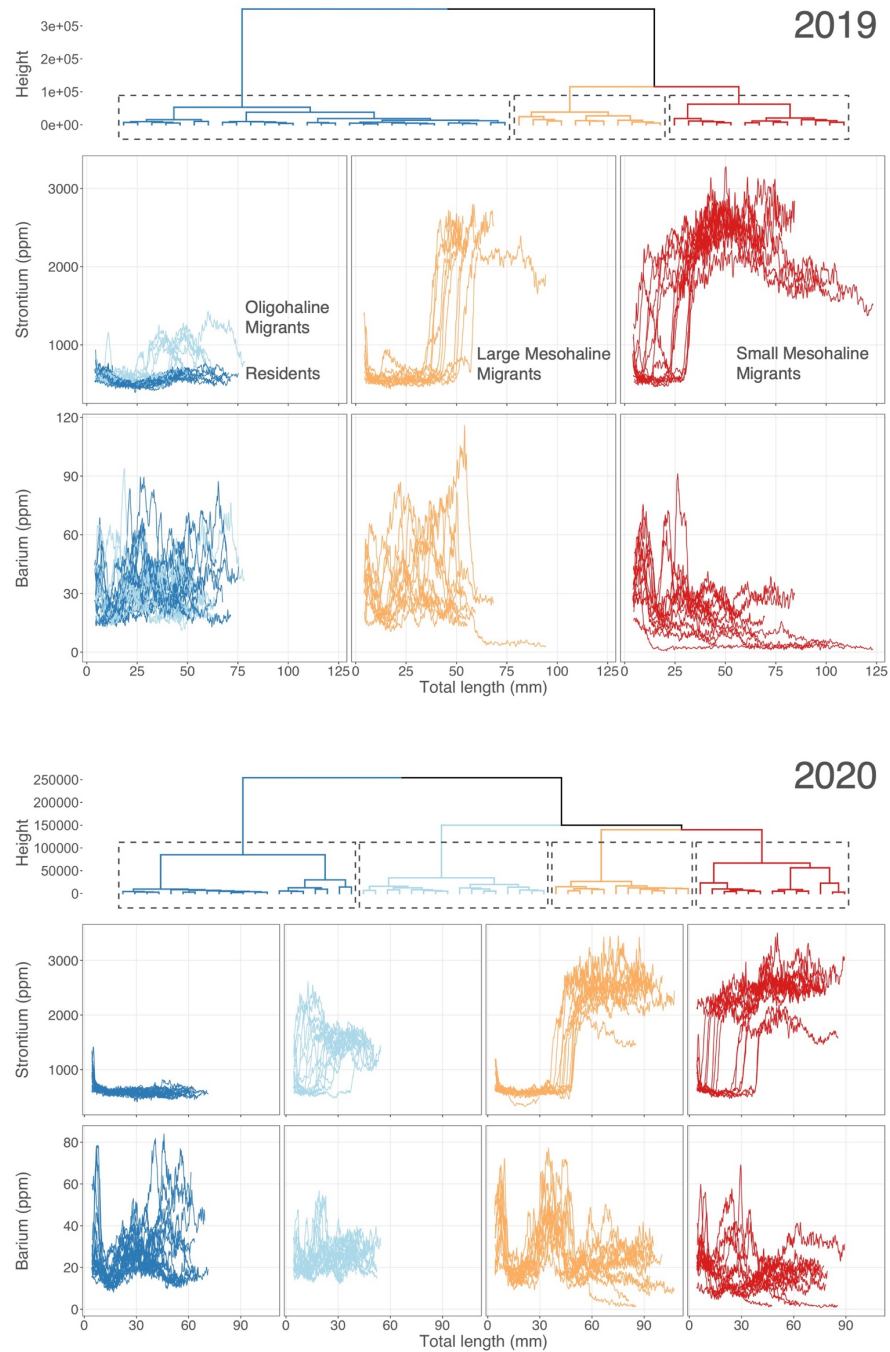


Figure 4.3 Hierarchical dynamic time warping clustering results using otolith Sr and Ba transects of Hudson River juvenile striped bass for 2019 (top) and 2020 (bottom). Different colors and dashed rectangles on the dendrogram illustrate distinct clusters (i.e., migration contingents): residents (dark blue), oligohaline migrants (light blue), large mesohaline migrants (yellow), and small mesohaline migrants (red).

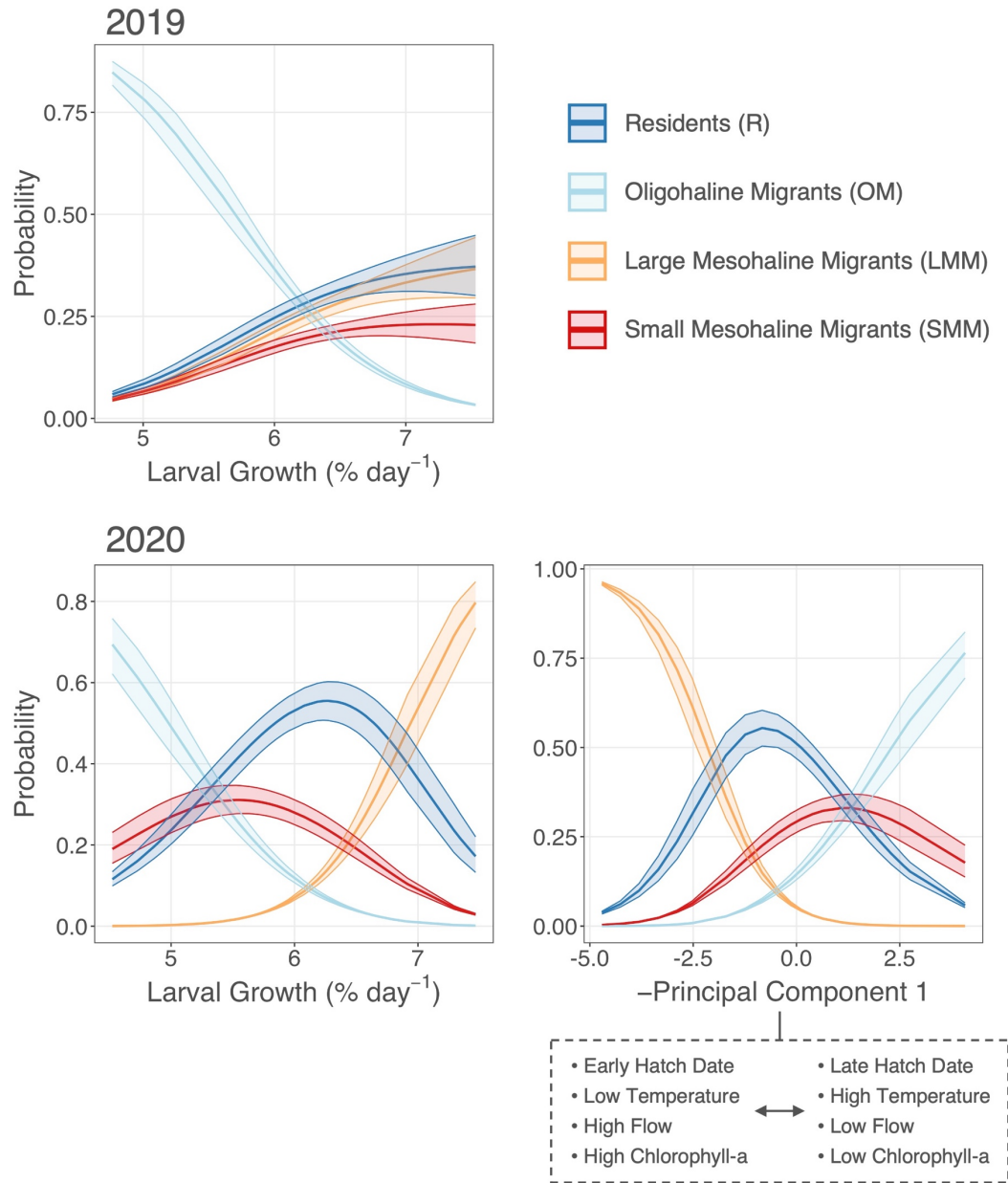


Figure 4.4 Predicted contingent membership probabilities as a function of specific larval growth and early life characteristics (principal component 1) of juvenile striped bass in 2019 (top) and 2020 (bottom) from multinomial logistic regression analysis. The first principal component included hatch dates and environmental conditions experienced (temperature, flow, and chlorophyll-a) by individuals during the first 30 days of life. Shadings indicate 95% confidence intervals. Note that the direction of the x-axis for the first principal component score was reversed to facilitate interpretation: higher principal component scores reflect individuals with later hatch dates exposed to high temperature, low flow, and low chlorophyll-a concentration. Because larval growth was the only predictor retained as an important variable

explaining contingent membership in 2019 (see Table 4.1), the relationship between contingent membership probability and principal component 1 is not displayed for 2019.

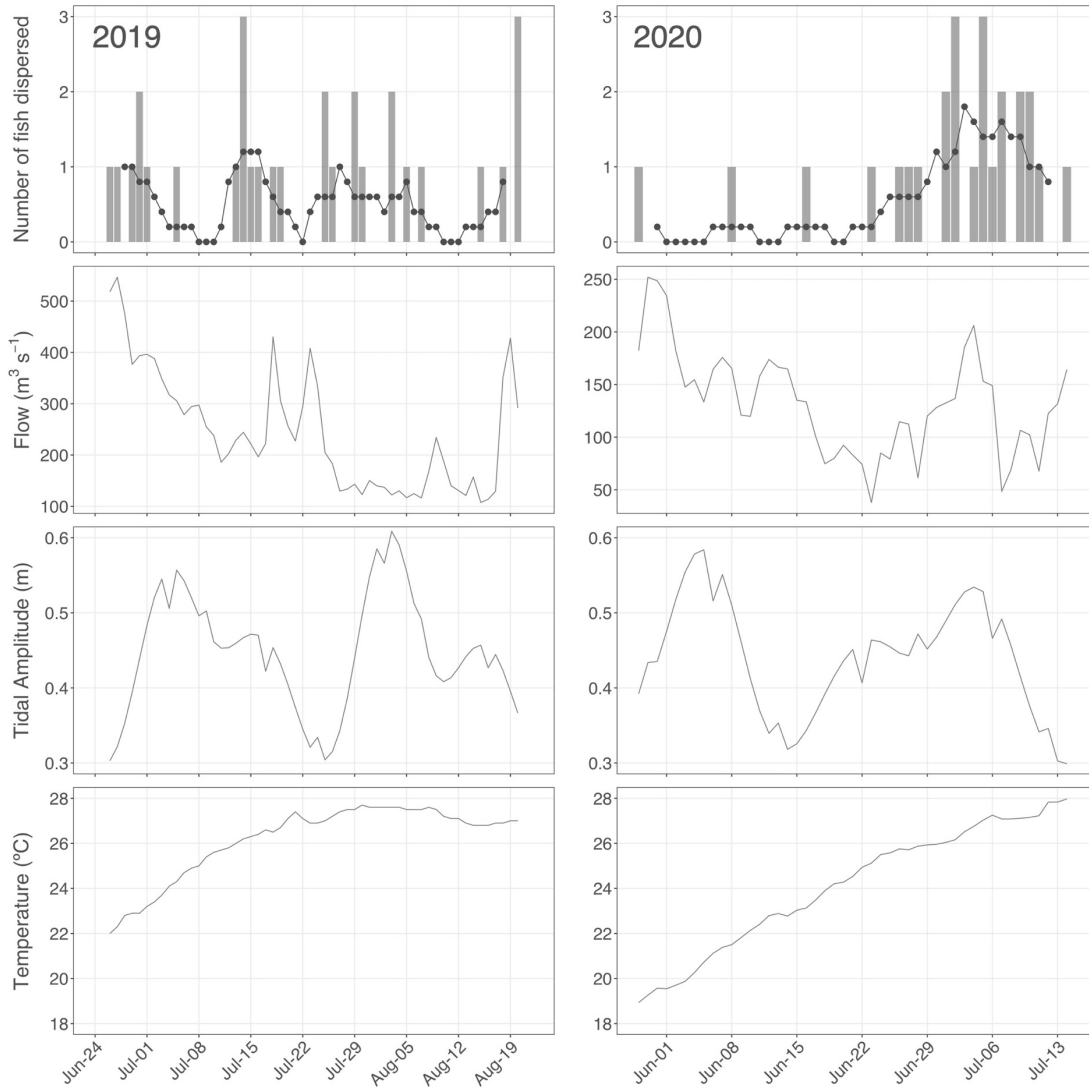


Figure 4.5 The daily number of striped bass dispersed to mesohaline habitats displayed with daily mean flow, tidal amplitude, and temperature for 2019 (left) and 2020 (right). Solid circles and lines illustrate the smoothed 5-day centered moving average of the daily number of fish dispersed to mesohaline habitats. Note that the scales of the x-axis and y-axis for daily mean flow differ between years.

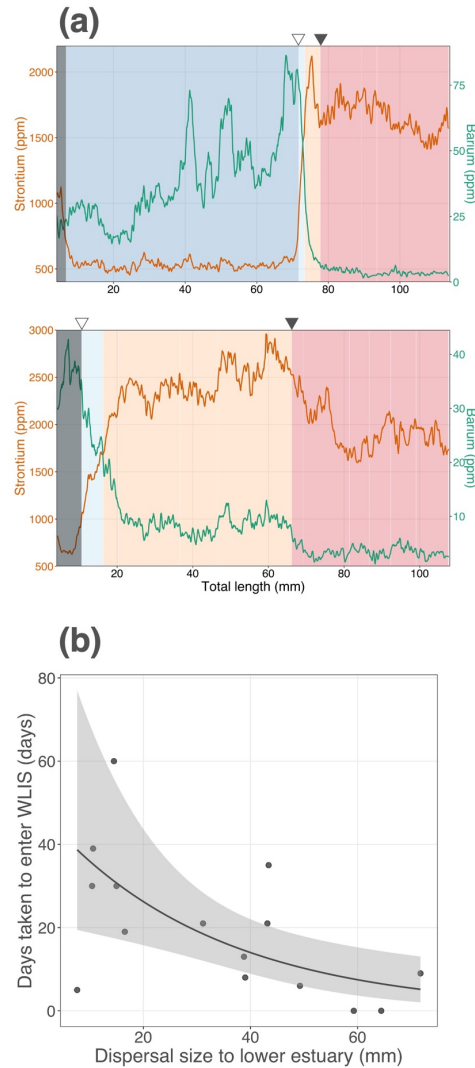


Figure 4.6 (a) Example otolith Sr (orange) and Ba (green) transects and predicted habitats of two juvenile striped bass that dispersed to brackish habitats during the juvenile (top) and larval (bottom) phases. Background colors illustrate predicted nurseries from changepoint analysis and random forest classification. Open and solid triangles between the two nurseries indicate the dispersal size to brackish habitats and polyhaline habitats (WLIS), respectively. Note that otolith chemistry in the shaded region near the early life stage may be maternally derived and was not considered as a changepoint. (b) The relationship between the dispersal size to brackish habitats and the total number of days spent in the lower Hudson River (HR) Estuary before entering western Long Island Sound (WLIS) for striped bass collected in WLIS in 2019 and 2020. The solid line and shaded area indicate the predicted value and 95% confidence intervals from the generalized linear model with a negative binomial distribution.

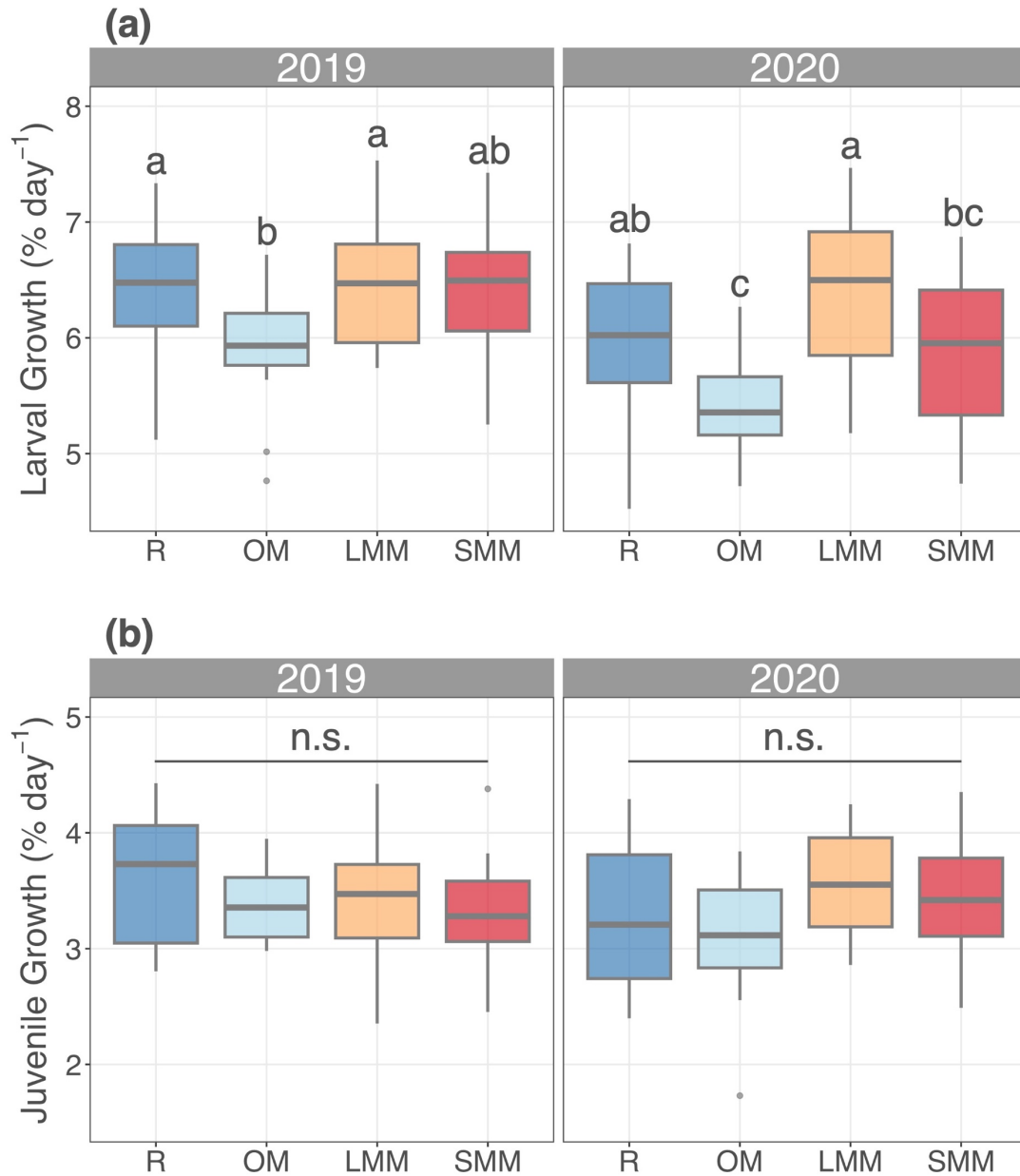


Figure 4.7 Box and whisker plots of specific (a) larval and (b) juvenile growth rates of resident (R; dark blue), oligohaline migrant (OM; light blue), large mesohaline migrant (LMM; yellow), small mesohaline migrant (SMM; red) striped bass in 2019 and 2020. Different letters above each box show significant growth differences based on post-hoc Tukey tests ($p < 0.05$). N.S. = no significant differences detected.

Supplementary Material

Univariate Comparison of Hatch Dates and Early-life Experiences

Two-way analysis of variance (ANOVA) was used to test differences in hatch dates and early-life experiences (i.e., mean temperature, river flow, and chlorophyll-a) of age-0 juveniles across migration contingents, years (2019 and 2020), and their interaction. A post-hoc Tukey test was employed for multiple comparisons of these variables across contingents within each year. When Levene's test detected unequal variances across the years, the model was fitted using generalized least squares using the “*varIdent*” function in the “*nlme*” R package (Pinheiro et al., 2022), which allowed for different variances per treatment (i.e., heteroscedastic). A post-hoc Tukey test was further employed for multiple comparisons of these variables across contingents within each year using the “*emmeans*” R package (Lenth et al., 2018).

For hatch dates, significant effects of contingent (Two-way ANOVA, $p < 0.01$), year ($p < 0.001$), and their interaction ($p < 0.001$) were detected. In 2020, post-hoc contrasts indicated that oligohaline migrants hatched significantly later compared to residents (Tukey test, $p < 0.05$) and large mesohaline migrants ($p < 0.001$), whereas large mesohaline migrants hatched significantly earlier compared to their peers ($p < 0.01$; Figure S4.4a). No significant differences in hatch dates were detected across contingents in 2019, although hatch dates on average occurred later in 2019 compared to 2020. Mean temperature exposure during the first 30 days of life was significantly affected by contingent (Two-way ANOVA, $p < 0.05$) with a significant interaction effect between year and contingent ($p < 0.001$). As a result of differences in hatch dates in 2020, oligohaline migrants experienced significantly higher

temperatures compared to residents (Tukey test, $p < 0.05$) and large mesohaline migrants ($p < 0.001$), whereas large mesohaline migrants were exposed to significantly cooler temperatures compared to their peers ($p < 0.01$; Figure S4.4b). No significant differences in experienced temperature were detected across contingents for 2019 given similar hatch dates. Mean river flow experienced during the first 30 days of life was significantly influenced by contingent (Two-way ANOVA, $p < 0.001$), year ($p < 0.001$), and their interaction ($p < 0.05$). Post-hoc contrasts showed that large mesohaline migrants experienced significantly higher flow compared to their counterparts in 2020 given earlier hatch dates (Tukey test, $p < 0.001$; Figure S4.4c). No significant differences in mean flow were detected across contingents in 2019, although river flow during this period was significantly higher in 2019 compared to 2020. Food availability measured by chlorophyll-a concentration during the first 30 days of life was significantly affected by years (Two-way ANOVA, $p < 0.001$) and interaction between contingent and years ($p < 0.001$). In 2020, large mesohaline migrants were exposed to significantly higher mean chlorophyll-a concentrations given early hatch dates (Tukey test, $p < 0.001$; Figure S4.4d). No differences in mean chlorophyll-a exposure were detected across contingents in 2019, although chlorophyll-a concentrations were significantly higher during this period in 2019 than in 2020.

Ageing Bias and Precision

To evaluate ageing bias and precision, a subsample ($n = 30$) of juvenile striped bass otoliths was read twice by the same reader. Prior to the exercise, the reader had

received training and had previous experience reading daily increments in striped bass otolith structure. Systematic bias in matched pairs of ages between the two reads was assessed using paired t -test and the test of symmetry (Hoenig et al., 1995), and was visually assessed through age-bias plots (Campana et al., 1995). Precision between matched pairs was quantified as the mean coefficient of variation (CV) following the method by (Chang, 1982).

The average age difference was 1.6 days and was within 4 days for all matched pairs analyzed. Daily increment counts from the two reads closely followed the identity line (i.e., replicate estimated ages are equal) of the age-bias plot (Figure S4.5). No systematic bias was detected between the two reads (paired t -test, $p = 0.08$; test of symmetry, $p = 0.29$). Ageing precision between the two reads measured in the form of mean CV was 1.5%, indicating very high precision compared to literature values (Campana, 2001).

References for Supplementary Material

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Table S4.1 Sample size and total length (mean $\pm$ SD) of juvenile striped bass used for otolith microstructure and microchemistry analysis collected in each Hudson River sampling location for 2019 and 2020.

Region	2019		2020	
	Total length (mm)	N	Total length (mm)	N
Freshwater	56.7 $\pm$ 10.2	19	57.9 $\pm$ 8.1	20
Oligohaline	52.4 $\pm$ 10.6	20	46.4 $\pm$ 6.5	16
Mesohaline	60.0 $\pm$ 11.6	21	83.4 $\pm$ 14.6	20
Polyhaline	90.3 $\pm$ 26.8	9	71.7 $\pm$ 15.5	6

Table S4.2 Akaike's information criterion (corrected for small sample size; AICc) rankings of the generalized additive mixed model (GAMM) to assess the influence of environmental conditions on the timing of dispersal of juvenile striped bass.

Rank	Model	df	AICc	Δ AICc
1	Tidal amplitude + Year	6	36.1	0.00
2	Temperature + Year	6	36.8	0.64
3	Tidal Amplitude + Temperature + Year	8	39.3	3.19
4	Tidal amplitude + Flow + Year	8	45.9	9.76
5	Flow + Year	6	46.5	10.39
6	Flow + Temperature + Year	8	47.2	11.07
7	Tidal Amplitude + Temperature +Flow + Year	10	50.0	13.92

Note: Δ AICc shows the differences in Akaike's information criterion (corrected for small sample size) between the best model (rank 1) and a given model. df = degrees of freedom.

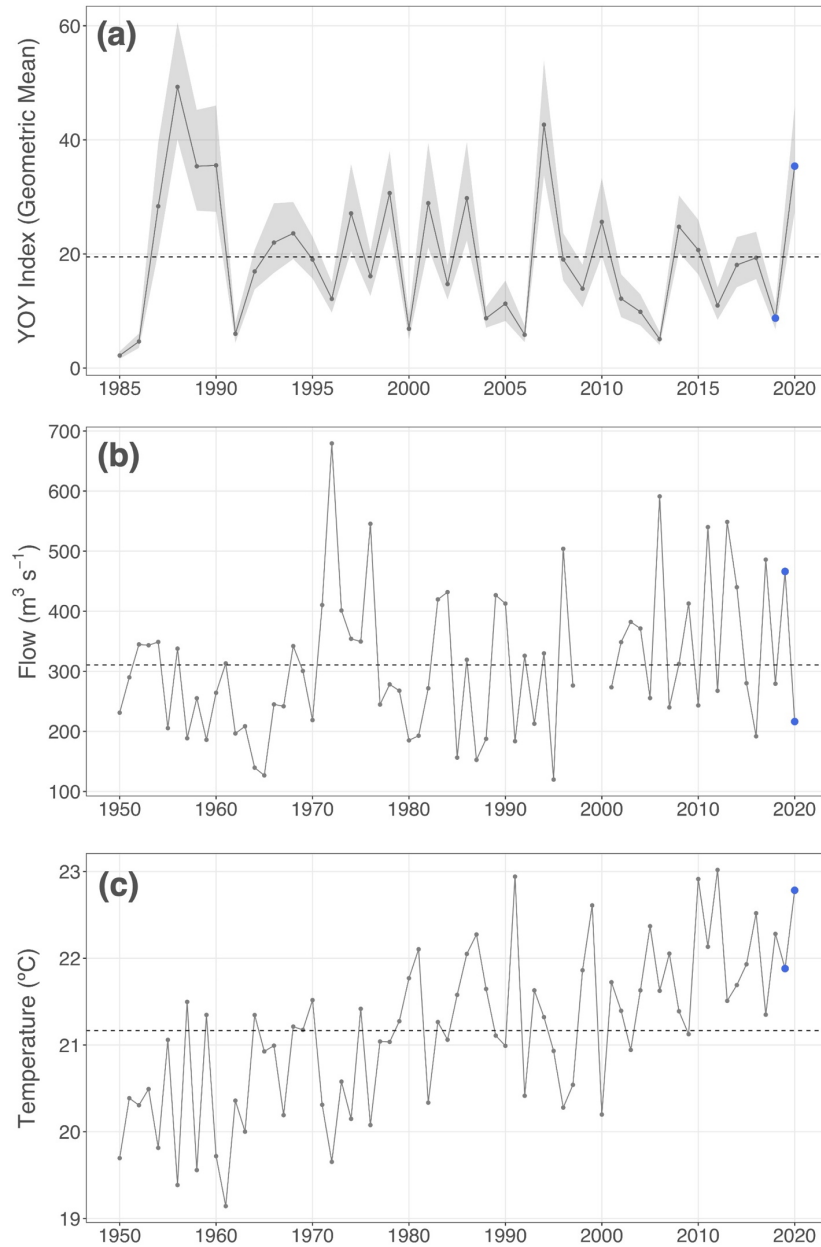


Figure S4.1 (a) Annual YOY striped bass abundance index (1985–2020) estimated from the New York Department of Environmental Conservation (NYDEC) Hudson River beach seine survey, with shadings indicating 95% confidence intervals. (b) Annual mean (May–August) freshwater flow in the Hudson River (1950–2020), acquired from the USGS Green Island monitoring station (site: 01358000). (c) Annual mean (May–August) temperature in the Hudson River acquired from the Poughkeepsie Water Treatment Facilities (1950–1991) and USGS monitoring stations (site: 01372058 [1992–2019], 01372043 [2020]) near Poughkeepsie. Blue points for each time series indicate the years of this study (i.e., 2019 and 2020).

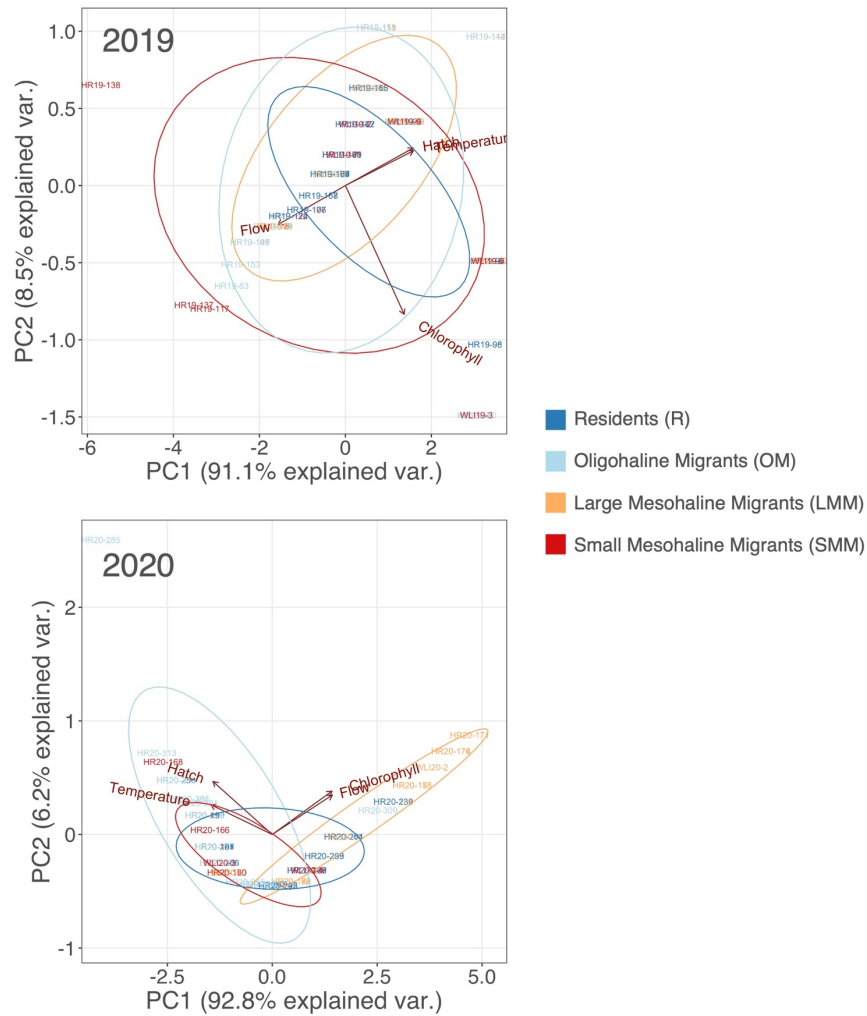


Figure S4.2 Principal component analysis (PCA) plot depicting the relationship between the hatch date and environmental conditions experienced (mean temperature, flow, and chlorophyll-a) during the first 30 days of life for individual juvenile striped bass in 2019 (top) and 2020 (bottom). Each point is labeled by a unique fish ID and different colors indicate assigned migration contingents. Ellipses denote 95% confidence for each migration contingent. Arrows indicate the direction and strength of each variable on the overall distribution. The first two principal components are shown with the variance levels explained on the axes.

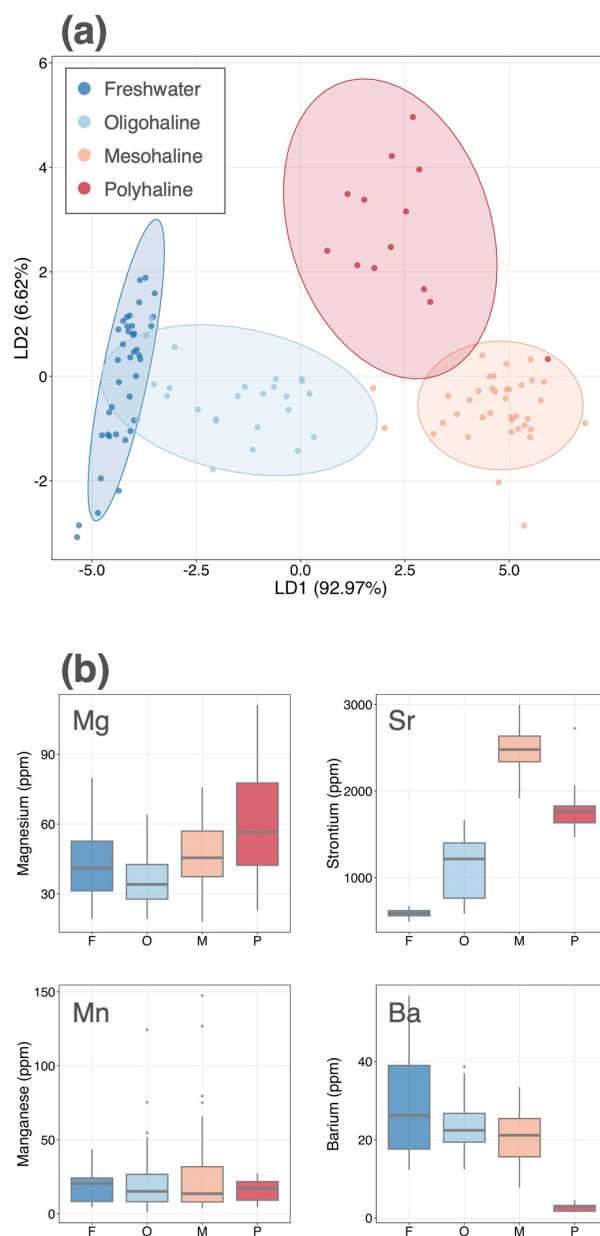


Figure S4.3 (a) Linear discriminant analysis (LDA) score plot showing the mean edge otolith magnesium (Mg), manganese (Mn), strontium (Sr), and barium (Ba) for each juvenile striped bass collected in freshwater (salinity < 0.4 ppt), oligohaline (0.4–3.0 ppt), mesohaline (3.0–18.0 ppt), and polyhaline (> 18.0 ppt) habitats used as the reference baseline for Random Forest habitat assignment. Ellipses show 95% confidence for each habitat. (b) Box whisker plots of mean otolith elemental concentrations (Mn, Mg, Sr, Ba) of the otolith edge for juvenile striped bass collected in different salinity zones in the Hudson River in 2019 and 2020. F = Freshwater, O = Oligohaline, M = Mesohaline, P = Polyhaline.

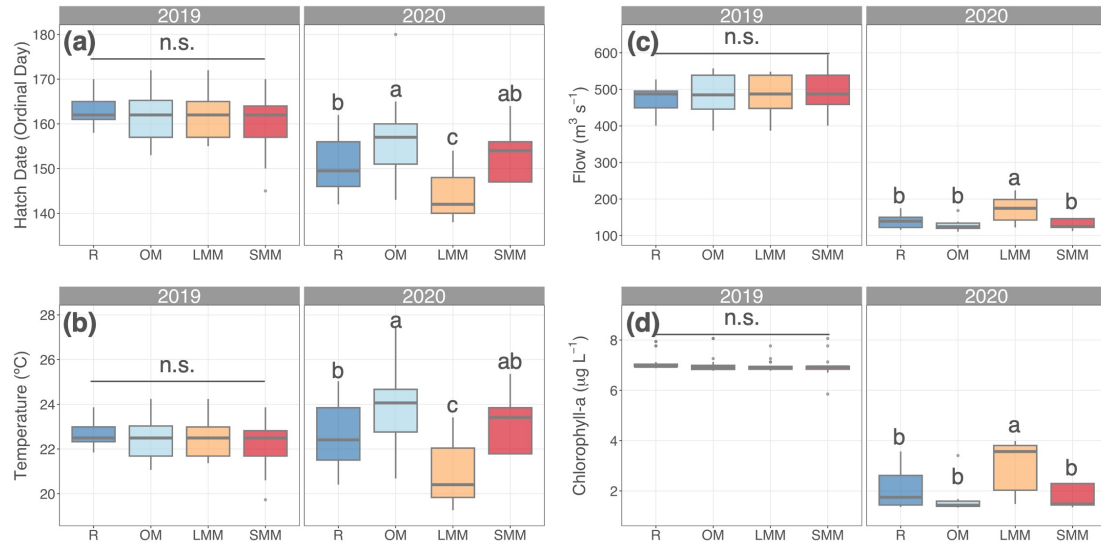


Figure S4.4 Box whisker plots of (a) Hatch dates, and mean (b) temperature, (c) flow, and (d) chlorophyll-a calculated for the first 30 days of life for resident (R; dark blue), oligohaline migrant (OM; light blue), large mesohaline migrant (LMM; yellow), small mesohaline migrant (SMM; red) striped bass in 2019 and 2020. Different letters above each box show significant growth differences based on post-hoc Tukey tests ($p < 0.05$). N.S. = no significance detected.

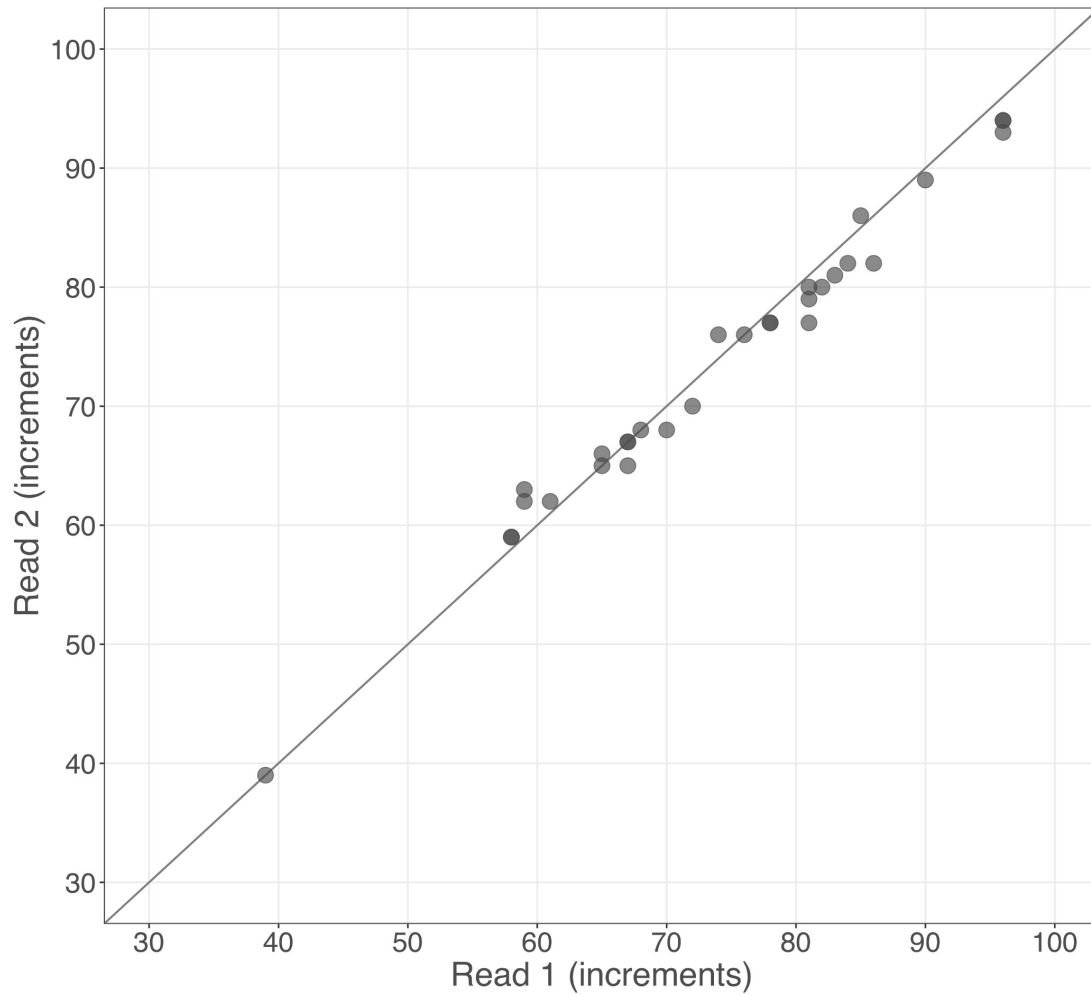


Figure S4.5 Age-bias plot illustrating matched pairs of otolith daily increments between two reads. The solid diagonal line indicates the identity line and divergence from the line indicates the degree of systematic differences in matched pairs of increment counts between two reads.

Chapter 5: Spatial structuring via partial migration promotes population persistence in an estuarine-dependent fish under changing climate

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5.1 Abstract

Complex spatial structure within populations confers population stability and resilience through asynchronous responses of population sub-components to perturbation (i.e., portfolio effect). In fish populations, spatial structure frequently develops via early-life partial migration, leading to diversified nursery habitat use. However, whether adult recruitment from different nurseries exhibits asynchronous dynamics in response to climatic variables, and whether nursery experiences carry over to influence adult demographics remains poorly known. I used otolith chemistry and retrospective analysis to test adult nursery contributions and carryover effects associated with early-life partial migration in the estuarine-dependent anadromous striped bass (*Morone saxatilis*) in the Hudson River over a 3-decade span. Otolith chemistry revealed that early-life partial migration led to varied nursery utilization of freshwater, brackish, and coastal habitats, which recruited to the adult population. Recruitment from the brackish nursery was positively related to freshwater flow; however, both freshwater and brackish habitats contributed proportionately to adult recruitment under moderate-flow conditions. Adult recruitment from the coastal western Long Island Sound habitat increased during severe winter years. First-year

nursery experiences carried over to influence adult sex, but not growth: while the majority of females utilized brackish nurseries during their first year of growth, adult males recruited from both freshwater and brackish nurseries. Restoring and maintaining a mosaic of habitats across the landscape will be critical to supporting early-life partial migration and long-term population persistence for striped bass and other species that depend on complex spatial structuring.

5.2 Introduction

Complex spatial structure within populations is a common attribute across a range of taxa, including insects, birds, and fishes (Ringsby et al., 2002; Hilborn et al., 2003; Menz et al., 2019). There is growing recognition that complex spatial structure may play an important role in conferring stability and resilience at aggregate scales through asynchronous responses of population sub-components to perturbation (i.e., portfolio effect; Secor et al., 2009; Schindler et al., 2010). Understanding the role of complex spatial structure in long-term population persistence has important conservation and management implications in the face of growing anthropogenic pressures such as overexploitation, habitat degradation, and climate change (Stier et al., 2020; Cordoleani et al., 2021).

In fish populations, complex spatial structure is frequently attributed to partial migration, in which a single population contains multiple groups that follow distinct migration pathways (i.e., contingents; Jonsson and Jonsson 1993; Kerr et al., 2009; Chapman et al., 2012; Secor 2015). The most traditional view of such a phenomenon is the coexistence within populations of individuals that remain in a single habitat (i.e., residents) and those that migrate between multiple habitats (i.e., migrants).

Diverse migration modes have been shown to arise from an early-life conditional response in which intrinsic factors such as early growth interact with extrinsic factors like environmental conditions and resource availability (Lundberg, 1988; Dodson et al., 2013). Through diverse migration trajectories and consequently differing habitat use, contingents display asynchronous dynamics to environmental conditions that can shape overall population dynamics (Kerr et al., 2010; Schroeder et al., 2016; Nelson et al., 2021). For example, in the estuarine-dependent white perch (*Morone americana*) population in the Chesapeake Bay, the brackish migratory contingent influenced population resilience and productivity, while the freshwater resident contingent sustained a small but critical reproductive segment, conferring population stability (Kraus and Secor, 2004; Kerr et al., 2010). This led the authors to conclude that conserving habitat mosaics that sustain contingent behaviors stabilized population dynamics. This strategy contradicts the nursery-role concept, which advocates for the preservation of only those habitats that promote the highest juvenile survival and growth (i.e., high nursery “value”) and recruitment to the adult population (Beck et al., 2001).

Complex spatial structure and partial migration can arise from a series of ecological carryover effects, in which conditions experienced during one life stage affect the behavior of subsequent life stages (Pechenik, 2006; O’Connor et al., 2014; Moore and Martin, 2019). Hatch dates and environmental conditions (e.g., temperature, food availability) can directly influence early-life growth and physiological condition, which in turn determines whether an individual adopts a particular migration behavior (Thorpe et al., 1998; Kerr and Secor, 2010; Dodson et

al., 2013; Conroy et al., 2015). As such, fluctuations in weather conditions during spawning and the larval period can cause annual variations in juvenile contingent membership and nursery habitat use (Kraus and Secor, 2004). Subsequently, differences in experienced environmental conditions and food webs among different nurseries can carry over to influence adult demographics such as growth, reproduction, and sex (Kraus and Secor, 2004; Lee et al., 2012; Gillanders et al., 2015). For instance, fish can often compensate for their poor development during their early life stage by accelerating growth under later favorable conditions (Metcalf and Monaghan, 2001); however, fish that exhibited compensatory growth are more likely to have long-term detrimental effects on growth and breeding performance later in the adult stage (Morgan and Metcalfe, 2001; Lee et al., 2012). For the white perch population in the HR and Chesapeake Bay, adults that recruited from brackish nurseries attained a larger size-at-age and matured earlier compared to those that did not disperse as juveniles (i.e., freshwater residents; Kraus and Secor, 2004; Gallagher et al., 2018). Early-life density-dependent processes and growth are linked to later sex differentiation in catadromous temperate eels (*Anguilla* spp.), where higher early growth is typically associated with male production, which further carries over to the propensity to remain in estuaries or migrate upstream into freshwater habitats (Geffroy and Bardonnnet, 2016).

I evaluated whether early-life partial migration and diversity in nursery habitat use influences recruitment patterns to the adult population. I also evaluated the influence of climate variables including flow, winter severity, and thermal regimes on contingent recruitment patterns. The striped bass (*Morone saxatilis*) population in the

Hudson River (HR), an estuarine-dependent fish that supports important commercial and recreational fisheries in US Atlantic waters (NEFSC, 2019), served as a model species for this study. Striped bass are an anadromous fish that spend most of their lifetime in coastal waters but migrate into natal fresh tidal regions to spawn in the spring (Secor and Piccoli, 1996; Zlokovitz et al., 2003; Gahagan et al., 2015). Spawned eggs and hatched larvae are displaced by freshwater flow and tidal currents, but are generally retained above the salt front (Boreman and Klauda, 1988; Dovel, 1992; Secor et al., 2020). Following metamorphosis (ca. 15 mm TL; Mansueti, 1958), juveniles occur throughout a wide range of salinity in the HR (Dovel, 1992). Striped bass juveniles in the HR and in other populations exhibit partial migration, whereby a portion of juveniles remain in their natal freshwater or oligohaline habitats, while others migrate downstream to utilize higher salinity habitats (Mohan et al., 2015; Conroy et al., 2015; Morissette et al., 2016; Vanalderweireldt et al., 2019; see also Chapter 4). In the HR, slower larval growth was associated with a propensity to migrate early in life, and the timing of dispersal was related to periods of high freshwater flow (Chapter 4). However, by potentially increasing consumption rates in more productive brackish habitats, the slow-growing migrants enhanced post-dispersal juvenile growth (Chapter 4), which may carry over into adulthood (Kraus and Secor, 2004; Gallagher et al., 2018). In addition to the principal nursery region within the HR, juveniles frequently occur outside of the HR, in the nearby western Long Island Sound (WLIS) region (Figure 5.1). Dunning et al., (2009) suggested that the combination of freshwater flow, tidal currents, and density-dependent processes transport larvae from the HR to the WLIS via the heavily channelized East River,

although the contribution of this “extra” coastal nursery to the HR adult population is unknown.

Here, I used otolith microchemistry and retrospective analysis to test nursery contributions and carryover effects associated with partial migration in the HR striped bass population over a 29-yr span of year-classes (1987–2015). Fine-scale nursery habitat use was reconstructed by leveraging otolith chemistry with time series analysis and machine learning algorithms. Striped bass longevity (> 15 years) allowed me to reconstruct adult nursery contributions across several decades. Each year-class represents different environmental conditions and early-stage recruitment levels that were assessed for their influence on nursery contributions. Specifically, I hypothesized that (i) striped bass early-stage partial migration would lead to differing nursery habitat use; (ii) that adult recruitment from different nurseries would respond asynchronously to climate variables, with contributions from brackish and WLIS habitats increasing during years of high flow, high early-life stage abundances, and severe winters; and (iii) that early life nursery experiences would carry over to influence subsequent adult growth and sex characteristics.

5.3 Methods

5.3.1 Sample Collection

A total of 379 archived otoliths were selected from the adult striped bass samples collected in 1995, 2016, 2017, and 2019 in the Hudson River during peak spawning periods from April to June (Figure 5.1; Table S5.1). Samples came from four different sources: (i) commercial river herring (*Alosa* spp.) monitoring (anchored

gill net), (ii) contaminant monitoring program (drift gill net, haul seine, electrofishing), (iii) adult striped bass spawning stock survey (haul seine, electrofishing, herring haul seine), and (iv) juvenile Atlantic sturgeon abundance sampling (anchored gill net). Information on total length (TL mm), sex, and the location of capture was available for all samples. The size and age distributions were similar between sampling years and should not have influenced how year-classes (i.e., the year the fish was born) were represented (Figure S5.1).

5.3.2 Otolith Processing and Age Determination

For all samples, age and year-class of each fish were determined through otolith analysis. Following Secor et al., (1991), sagittal otoliths were embedded and sectioned transversely. Otolith sections were subsequently polished using 320, 600, and 1200 grit materials until the core was clearly visible. Then, sections were buffed on a wet microcloth with 0.3 um alumina powder to remove pits and abrasions. Because striped bass otolith annuli have been validated to form at a yearly rate (Secor et al., 1995), annuli were enumerated from the otolith core to the edge to determine the age. An additional count on a subset of samples ($n = 177$) by a second reader detected no ageing bias (test of symmetry, $p = 0.20$; Figure S5.2; Hoenig et al., 1995), and high precision (CV = 2.0%; Chang, 1982). Each fish was assigned a year-class by subtracting the age from the collection year.

5.3.3 Otolith Microchemistry

Otolith microchemistry was used to reconstruct nursery habitats utilized by adults during their first year of growth. A total of 190 samples were selected for

otolith microchemistry to represent as many year-classes as possible, while also maintaining a minimum sample size ($n \geq 5$) within each year-class and a balanced sample size across year-classes (Figure S5.3a). I also attempted to balance the sex ratio within year-classes whenever possible (Figure S5.3b). Elemental concentrations in otoliths were measured using an Elemental Scientific NWR193 excimer laser ablation (LA) system (193 nm, 4 ns pulse width) coupled to an Agilent 7500ce inductively coupled plasma mass spectrometer (ICP-MS) at the University of Texas at Austin. All otoliths and standards processed on the LA-ICP-MS were loaded into a large format cell with fast washout times (< 1 s). Following pre-ablation (50 or 60 μm diameter spot, 50 or 75 $\mu\text{m s}^{-1}$ scan rate, 3.2–3.9 J/cm^2 fluence) to remove shallow surface contaminants of the otolith section, a laser transect scan was performed from the core (start of life) along the longest growth axis to the first annulus (end of the first growing season; the ventral growth axis) with a 25 μm diameter spot, 5 $\mu\text{m s}^{-1}$ scan rate, 2.79 ± 0.04 J/cm^2 fluence, 20 Hz repetition rate, and carrier gas flows of 0.78–0.82 L min^{-1} for argon and 0.80 L min^{-1} for helium. All elements (^{24}Mg , ^{44}Ca , ^{55}Mn , ^{88}Sr , ^{138}Ba) were measured on the LA-ICP-MS system with 10 ms integration times. Measured intensities were converted to elemental concentrations (ppm) using Iolite software (Paton et al., 2011), using ^{43}Ca as the internal standard and a Ca index concentration value of 38.3 wt% for otolith unknowns. USGS MACS-3 (synthetic aragonite) was used as the primary calibration standard and NIST 612 and ECRM-752-NP were used as external reference standards. The grand average of secondary standard recovery fractions for all elements was typically within 5% of reference values (<http://georem.mpch-mainz.gwdg.de>). Elemental concentration profiles were

smoothed by consecutive moving median and average filters using a 7-point boxcar width (5 μm equivalent distance) to remove high-frequency outliers.

5.3.4 Statistical Analysis

Adult nursery use was reconstructed using a combination of time series changepoint analysis and machine learning classification on measured otolith transects, following the method in Chapter 4 (section 4.3.4). First, time series changepoint analysis with the “pruned exact linear time” (PELT) algorithm in the R package “*changepoint*” (Killick and Eckley, 2014) was used to detect major concentration shifts within the individual otolith Sr transect. The PELT algorithm detected multiple shifts in mean and variance in Sr concentration for each fish, resulting in multiple stable otolith profile segments for a given transect (Figure 5.2). For each stable segment, I calculated the mean concentration of four elements (i.e., Mg, Mn, Sr, Ba); then, each segment was assigned to one of four habitats using a random forest (RF) algorithm in the R package “*ranger*” (Wright and Ziegler, 2017): freshwater (salinity < 0.4 ppt), oligohaline (0.4–3.0 ppt), mesohaline (3.0–18.0 ppt), and polyhaline (> 18.0 ppt). Elemental concentrations of the otolith edge of young-of-the-year (YOY) HR striped bass samples ($n = 114$) collected in 2019 and 2020 served as a reference baseline for habitat assignment (Chapter 4; Figure S5.4a). Mean elemental concentrations of the recently formed otolith edge, corresponding to the last 20 μm of the laser transect, were assumed to reflect the broad salinity zones (0.13–25.1 ppt) from which YOY samples were collected. The otolith Ba transect was then used to understand polyhaline WLIS habitat use, given the distinct otolith Ba concentration in polyhaline WLIS habitats (Figure S5.4b). Using only the otolith Ba

transect past the point of first entry to brackish habitats (i.e., oligohaline, mesohaline, or polyhaline) determined above, a similar changepoint analysis with the PELT algorithm was performed on otolith Ba transects, resulting in multiple mean stable segments. Mean stable segments were further assigned to a specific habitat using random forest classification to detect the transition from mesohaline to polyhaline habitats (Figure 5.2cd). This analysis provided the experienced nursery salinity zones of each adult sample during its first growing season. I then calculated a brackish nursery index by converting experienced salinity to the proportion of time spent in brackish habitats (i.e., oligohaline, mesohaline, and polyhaline) during the first year of growth, which ranged from 0 to 1. Thus, 0 represented fish that remained in freshwater habitats throughout their first growing season, whereas 1 represented fish that dispersed early in life and exclusively utilized brackish habitats for their entire first growing season. I also calculated a WLIS nursery index in which the time spent in polyhaline WLIS habitats was converted to a proportion ranging from 0 to 1, with 0 representing fish that never utilized WLIS habitats, and 1 indicating fish that spent their first growing season exclusively in polyhaline WLIS habitats. The brackish and WLIS nursery index for each individual was averaged across samples within each year-class to obtain a mean brackish and WLIS nursery index for each year-class.

The effect of environmental conditions and density-dependence on nursery use was assessed using a Generalized Additive Model for Location, Scale, and Shape (GAMLSS) in the R package “*gamlss*” (Rigby and Stasinopoulos, 2005). Each year-class (total of 14 year-classes) of adult samples reflects a particular set of environmental conditions and early-life stage abundances that can be tested for their

influence on nursery utilization during their juvenile life stage. Two separate GAMLSS models were fitted to assess the influence of water temperature, freshwater flow, winter severity, and post-yolk-sac larval (PYSL) abundance (i.e., predictors) on brackish and WLIS nursery indices (i.e., response; Table 5.1). Daily temperature data prior to 1992 was acquired from the Poughkeepsie Water Treatment Facilities (PWTF), while data after 1992 were obtained from the United States Geological Survey (USGS) monitoring station below Poughkeepsie (site: 01372058; Figure 5.1) because single-site data were not available for the period examined. To correct for slight bias between the two data sources, a linear regression by Seekell and Pace (2011) was used to adjust the PWTF data. Missing data were filled in using linear interpolation in the R package “*zoo*” (Zeileis and Grothendieck, 2005). Daily freshwater flow data was obtained from the USGS Green Island monitoring station (site: 01358000) located at the head of the HR Estuary. Temperature and flow were calculated as the annual mean from April to July, which corresponds to periods of striped bass spawning and early-life development in the HR (Boreman and Klauda, 1988; Secor et al., 2020; Pan et al., 2023). Winter severity was calculated as the sum of degree-days below 4°C using the following equation by Hurst and Conover (1998):

$$\text{Winter severity} = \sum(4.0 - t_i), \quad (\text{Eq. 5.1})$$

where t_i is the daily temperature for each day below 4°C for the entire year. The annual abundance index for PYSL was obtained from the “Year Class Reports” for the Hudson River Biological Monitoring Program (HRBMP), an extensive survey

conducted since 1974 (ASA Analysis & Communication, 2019). I used PYSL abundance as a measure for density-dependence although other early-life stage abundances (i.e., egg, yolk-sac larvae, and YOY) were also available. This is because the PYSL stage is when striped bass settle in littoral habitats and when density-dependent effects are expected to be most intense (Gallagher and Secor, 2018). This assumption was further supported by life-cycle analysis, which modeled the transitions between early life history stages, and found evidence of density-dependent mortality only during the transition from PYSL to YOY; all other transitions were linear (Figure S5.5).

The GAMLSS allows modeling of the location (μ , or the mean) of the underlying distribution while simultaneously modeling the scale (σ , variance), and shape parameters (ν , skewness; τ , kurtosis), which all can depend on non-linear semi-parametric predictors (Stasinopoulos and Rigby, 2007). The brackish or WLIS nursery index (continuous values in the range $[0, 1]$), $Y_{t,j}$, for year-class t and fish j was specified using a four-parameter beta-inflated distribution as the response variable, modeled as a combination of additive smooth terms through a logit link function defined as:

$$Y_{t,j} \sim \text{BetaInf}(\mu_{t,j}, \sigma_{t,j}, \nu_{t,j}, \tau_{t,j}) \quad (\text{Eq. 5.2})$$

$$\begin{aligned} \text{logit}(\mu_{t,j}) = & a_0 + a_1 s(\text{Temperature}) + a_2 s(\text{Flow}) + a_3 s(\text{Winter}) \\ & + a_4 s(\text{PYSL}) \end{aligned}$$

$$\text{logit}(\sigma_{t,j}) = b_0$$

$$\ln(\nu_{t,j}) = c_0$$

$$\ln(\tau_{t,j}) = d_0,$$

where $s(Temperature)$, $s(Flow)$, $s(Winter)$, and $s(PYSL)$ indicate that penalized splines were used as smooth functions for temperature, flow, winter severity, and PYSL abundance. An intercept was only specified for the scale (σ) and shape (ν , τ) parameters. The final model was selected by comparing Akaike's information criterion corrected for small sample sizes (AICc), and statistical significance of the estimated model coefficients was assessed using individual t -tests, with significance level $\alpha = 0.05$. Randomized quantile residuals of the fitted models were assessed using the standard diagnostic plots for homoskedasticity, uncorrelatedness, and normality.

To test whether different YOY habitats may contribute disproportionately to adult recruitment, I estimated the relative YOY abundance between freshwater and brackish habitats in the HR — the “brackish habitat proportion” — and compared it with the adult brackish nursery index derived from retrospective otolith chemistry analysis. The brackish habitat proportion was estimated using YOY standing stocks from the Beach Seine Survey provided in the HRBMP “Year Class Reports” estimated in 13 river sections spanning from Albany to Manhattan at a bi-weekly resolution from June to October (ASA Analysis & Communication, 2019). Salinity data from HRBMP was used to designate each river section as freshwater or brackish water based on a salinity threshold of 0.4 ppt. The brackish habitat proportion was calculated by the following equation:

$$\text{Brackish habitat proportion} = \frac{n_{\text{brackish}}}{n_{\text{freshwater}} + n_{\text{brackish}}}, \quad (\text{Eq. 5.3})$$

where n_{brackish} and $n_{\text{freshwater}}$ are the summed YOY standing stock across river sections designated as brackish and freshwater habitats, respectively from June to October. The brackish habitat proportion served as a baseline for the expected contributions of freshwater and brackish habitats to the adult population, which was then compared to the realized adult brackish nursery index to evaluate the ecological importance of putative habitats. Baseline brackish habitat proportions were estimated for every year that corresponds to the adult year-classes, except for the years 1987–1991, where HRMBP data was not available.

To assess whether nursery conditions experienced during the first growing season carried over to influence adult growth, von Bertalanffy growth curves were fitted to size-at-age data using the following equation:

$$L_t = L_\infty (1 - e^{-K(t-t_0)}), \quad (\text{Eq. 5.4})$$

where L_t is the expected mean length at age t , L_∞ is the asymptotic mean length, K is the growth coefficient which determines how rapidly L_∞ is approached, and t_0 is a nuisance parameter that represents the theoretical age at which the mean length is zero. Growth models were fitted separately for males and females, and parameters were estimated using the *FSA* package (Ogle et al., 2022) in R. Confidence intervals for the parameters were obtained through bootstrap methods. To assess whether nursery experiences influenced adult size-at-age, residuals (i.e., the difference

between observed and fitted TL) were extracted from growth models, and the relationship with the brackish nursery index was examined by fitting a linear regression and assessed using Pearson's correlation coefficient (r). To further explore the influence of experienced nurseries on adult sex, a logistic regression model with a binomial distribution and a logit link function was used. The response variable was sex determined upon collection, and the brackish nursery index served as a predictor.

5.4 Results

5.4.1 Nursery Habitat Use of Adults

Changepoint analysis combined with random forest habitat assignment (classification accuracy 96.7%) revealed fine-scale nursery habitat use patterns during the first growing season of adult samples (Figure 5.2). Four general patterns of nursery use occurred (see also Chapter 4). Some fish displayed consistently low Sr concentration, indicative of freshwater habitat use during their entire first year of growth (Figure 5.2a). Others initially showed low Sr concentration that then increased later in life, leveling off around 2000–2500 ppm, indicating dispersal and subsequent use of brackish habitats (Figure 5.2b). Of those that entered brackish habitats, some YOY fish showed a marked decline in Ba concentration, representing entry into polyhaline WLIS habitats (Figure 5.2c). Some individuals showed consistently high Sr concentration, consistent with exclusive brackish habitat use during their first year of growth (Figure 5.2d).

Brackish nursery contributions for recruited adults were greater than freshwater nurseries, with an overall mean brackish nursery index of 0.78 (Figure

5.3). However, nursery contributions varied by year-class: higher contributions from brackish nurseries occurred in 2011, 2014, and 2015, with mean brackish nursery indices of 0.93, 0.90, and 0.95, respectively; whereas brackish nursery contributions were lower in 2007, 2009, and 2012, with mean brackish nursery indices of 0.62, 0.60, 0.48, respectively. The overall mean WLIS nursery index was 0.15, but this also differed by year-class: higher contributions from WLIS nurseries occurred for 1988 and 2014, with mean WLIS nursery indices of 0.29 and 0.27, respectively; while contributions from WLIS nurseries were lower in 2005, 2009, and 2012, with mean WLIS nursery indices of 0.04, 0.03, and 0.04, respectively (Figure 5.3).

5.4.2 The Effect of Environmental Conditions and Density-dependence of Nursery Contribution

The best GAMLSS model for the brackish nursery index included only freshwater flow (t -value = 2.67, $p < 0.01$; Table 5.2). Partial effect plots revealed a strong positive effect of flow on brackish nursery contributions until roughly $350 \text{ m}^3 \text{ s}^{-1}$, but then plateaued as flow increased (Figure 5.4a). In the final model for WLIS nursery index, winter severity was identified as the single best predictor (t -value = 2.29, $p < 0.05$; Table 5.2). The partial effect plot indicated that contributions from WLIS nurseries increased linearly with HR winter severity (Figure 5.4b).

5.4.3 Comparison of YOY Habitat and Realized Adult Nursery Habitat Use

The estimated brackish habitat proportion within the HR showed that YOY brackish habitats were more prevalent than freshwater habitats, with an overall mean brackish habitat proportion of 0.65 (Figure 5.5). However, there were large

differences among years: brackish habitats dominated in the years 2005, 2007, 2009, and 2015, with mean annual brackish habitat proportions of 0.87, 0.72, 0.74, and 0.76 respectively; whereas brackish habitats were less prevalent in the years 2011, 2012, and 2013, with mean annual brackish water proportions of 0.53, 0.50, and 0.41. The estimated brackish habitat proportion also exhibited a general seasonal trend, with freshwater habitats dominating in early summer, and the proportion of brackish habitats increasing in the late summer and fall (Figure S5.6).

A comparison of baseline brackish habitat proportions with the brackish nursery index of recruited adults showed that brackish habitats were disproportionately more represented in adult samples than in the baseline YOY habitats in year-classes that coincided with high-flow conditions, namely 2011, 2013, and 2014 (Figure 5.5). Baseline YOY brackish habitats were slightly underrepresented or roughly proportionate to the adult brackish nursery index in other year-classes with low to moderate flow conditions.

5.4.4 Carryover Effects on Adult Growth and Sex

Parameter estimates for von Bertalanffy growth curves indicated that females attained a larger maximum size ($L_{\infty} = 1265.1$ mm), but grew slower ($K = 0.11$) compared to males ($L_{\infty} = 760.6$ mm, $K = 0.33$; Figure 5.6ab), although 95% bootstrap confidence intervals for each parameter overlapped (Table S5.2). Growth model-extracted residuals were not significantly associated with the brackish nursery index for either females (Pearson's $r = -0.11$, $p = 0.37$) or males (Pearson's $r = 0.02$, $p = 0.86$; Figure 5.6cd).

The estimated coefficient of the logistic regression model demonstrated a significant positive relationship between the brackish nursery index and female probability (coefficient $\pm$ SE = 2.22 ± 0.65 , $p < 0.001$; Figure 5.7), indicating that juveniles that spent a greater period in brackish habitats during their first growing season had a higher probability of developing into females as adults.

5.5 Discussion

Here, by combining otolith chemistry with retrospective analysis, I revealed how early-life partial migration resulted in complex spatial structures with consequences on how populations respond to climate variables. Early-life partial migration led to varied nursery utilization of freshwater, brackish water, and coastal habitats. Contributions from brackish nurseries increased with freshwater flow, while the WLIS nursery produced more adults during severe winter years. While patterns in the recruited adult nursery use reflected baseline YOY habitats in most years, brackish habitats disproportionately produced more adults during high-flow years when overall YOY recruitment was poor (Figure S5.7). First-year nursery experiences were associated with adult sex, but not growth: while the majority of adult females recruited from brackish nurseries, males recruited from both freshwater and brackish nurseries. Differential population outcomes of nursery use thus depend on climate variables and environmental sex determination.

5.5.1 Nursery Contribution to the Adult Population

As a result of early-life partial migration, adult striped bass recruited from a variety of nurseries, including freshwater and brackish nurseries within the HR, as

well as the coastal nursery in the WLIS (Figure 5.3). Adult representation from the brackish nursery was higher than that of the freshwater nursery in most year-classes (Figure 5.5), with the brackish nursery contribution increasing in high-flow years (Figure 5.4a). However, because the baseline YOY brackish habitat proportion decreased in high-flow years (e.g., 2011, 2013, 2014; Figure 5.5), the positive relationship between flow and brackish nursery contribution was not likely due to the increased representation of the juvenile migratory contingent under high-flow conditions (Conroy et al., 2015; Chapter 4). Rather, the disproportionately higher brackish habitat recruitment in high-flow years suggests that these habitats promote better juvenile growth and survival under high-flow conditions compared to freshwater habitats. In the HR, freshwater flow is strongly and negatively associated with primary productivity (Howarth et al., 2000; Gallagher and Secor, 2018). However, the negative impact of flow on recruitment may be less severe in brackish environments, which are generally more productive and could provide greater foraging opportunities for dispersers (Sirois and Fredrick, 1978; Howarth et al., 2006). Furthermore, increased flow may reduce the abundance of piscivorous predators (e.g., bluefish [*Pomatomus saltatrix*]) that favor higher salinity habitats (Juanes et al., 1993; Buckel et al., 1999), resulting in lower predation mortality in brackish habitats under high-flow conditions. Thus, while overall YOY recruitment in the HR is generally low during high-flow years (Strayer et al., 2008; Figure S5.7be), as was the case in year-classes 2011 and 2013 (Figure 5.5), brackish habitats could function as a refuge for juveniles, preventing complete recruitment failure under unfavorable conditions (Figure 5.8). Conversely, relative adult recruitment from

freshwater nurseries increased under low-flow conditions, particularly in the 2012 year-class, which was attributed to the increased YOY freshwater habitat (Figure 5.5). Under moderate flow conditions (e.g., 2005, 2007, 2015), when overall YOY recruitment was high, the realized adult nursery contributions broadly reflected baseline YOY abundances (Figure 5.5), with both habitats proportionately contributing to adult recruitment.

While the small adult sample size precludes strong inference, these results could imply that adult recruitment dynamics from different nurseries may respond asynchronously to climate variables, ultimately contributing to the long-term persistence of HR striped bass. Specifically, brackish habitats may confer population stability by producing small, but critical recruitment under unfavorable conditions (i.e., high flow), whereas both freshwater and brackish habitats may together contribute to population productivity and resilience by producing high adult recruitment when favorable conditions are met. However, nursery contributions for each year-class were retrospectively estimated using adult samples drawn from different size and age distributions, with some year-classes exhibiting a skewed sex-ratio (Figure S5.3b). For example, because adult males were more likely to recruit from freshwater nurseries (Figure 5.7), freshwater contribution may have been biased greater in year-classes that had higher male representation (e.g., 1990, 1991, 2012; Figure S5.3b).

The possibility that the coastal WLIS habitat contributes to the HR striped bass adult population has long been debated, but I have demonstrated that this coastal habitat may function as an “extra” HR nursery, particularly in years with severe

winters (Figures 5.3 and 5.4b). While freshwater flow and density-dependent processes have been linked to larval and juvenile recruitment from the HR to WLIS habitats via the East River transit (Dunning et al., 2009), winter severity was the only predictor included in all candidate GAMLSS models for WLIS adult contribution (Table 5.2). Recruitment of HR striped bass has been associated with winter mortality through the effects of diminished osmoregulatory capacity at low temperatures, with higher salinity reducing osmoregulatory costs and leading to higher YOY survival compared to freshwater conditions (Hurst and Conover, 1998, 2002). Winter temperatures and salinity are often higher in coastal WLIS habitats than in HR habitats (Blumberg et al., 1999; Figure S5.8), which could enhance juvenile survival during severe winters and increase adult production from WLIS habitats. Curtailing connectivity between the HR and WLIS habitats could lead to a potential loss of this “extra” HR nursery, which could consequently result in a population less resilient to severe winters.

5.5.2 Carryover Effects on Adult Demographics

Adult males and females displayed large differences in early-life migration patterns and nursery experiences (Figure 5.7). Males utilized a wide range of nurseries, from those that remained in freshwater habitats to those that dispersed early and exclusively used brackish habitats during their first year of growth. Alternatively, with the exception of one resident fish, all females dispersed and utilized brackish habitats for some portion of their first growing season (Figure 5.7). While the mechanisms underlying striped bass sex determination remain poorly known, sex determination and differentiation in teleost fishes can be a result of a combination of

genetic and environmental factors (Devlin and Nagahama, 2002; Sandra and Norma, 2010). Sex-specific disparities in early-life migration patterns and nursery experiences could be related to differences in early growth rates — an intrinsic factor associated with early partial migration in striped bass (Conroy et al., 2015; Chapter 4), and an important attribute related to sex differentiation in other fish species (Díaz et al., 2013; Geffroy and Bardonnnet, 2016). In the European sea bass (*Dicentrarchus labrax*, Moronidae), a related taxa with environmentally determined sex, females are more likely to develop from fish that grow faster in their early life stages, whereas both males and females emerge from slower-growing individuals (Saillant et al., 2003; Papadaki et al., 2005; Díaz et al., 2013). In catadromous temperate eels (*Anguilla* spp.), slower early growth is typically associated with the development of females, which are more likely to undertake upstream migration compared to males (Geffroy and Bardonnnet, 2016). For HR juvenile striped bass, the propensity to migrate early to brackish habitats was related to slower larval growth, whereas freshwater residency and delayed migration were associated with faster larval growth (Chapter 4). Hormonal treatment studies in striped bass have suggested that the larval to early-juvenile stages of striped bass may represent a sexually labile period (Schutz and Harrell, 1999). Thus, early sex determination preconditions growth and dispersal trajectories, or conversely larval growth and dispersal controls sex expression. I favor the latter argument that striped bass with slower larval growth that migrate early to brackish habitats can develop into either males or females, whereas those with faster larval growth that remain in freshwater or migrate later to brackish habitats are more likely to develop into males.

Based on previous research on congeneric white perch (*Morone americana*), I expected adults that recruited from brackish habitats to grow faster and attain larger sizes than those that recruited from freshwater habitats, possibly due to increased productivity and higher consumption rates in brackish habitats (Kraus and Secor, 2004; Kerr and Secor, 2009; Gallagher et al., 2018) or subsequent migration to ocean environments (Gahagan et al., 2015). However, I found no evidence of juvenile nursery experiences carrying over to influence subsequent adult growth in HR striped bass (Figure 5.6cd). This neutral effect of nursery experiences on adult growth could be related to the negative effects of early compensatory growth on later adult growth and reproduction (Morgan and Metcalfe, 2001; Lee et al., 2012). In a complementary study on HR juvenile striped bass (Chapter 4), I detected compensatory growth in slow-growing fish following dispersal to brackish habitats (Chapter 4). Such compensation may have hampered subsequent adult growth by offsetting the favorable conditions for growth in brackish habitats. Alternatively, this neutral influence of nursery experiences on adult growth may have occurred as a result of fish experiencing similar growth habitats after their first year of growth.

5.5.3 Broader Applications and Implications for Management

Adult recruitment from different nurseries exhibited asynchronous dynamics in response to climate variables, which may have implications for the long-term persistence of the HR striped bass population. Estimated nursery contributions could inform a population model and simulation framework that could further elucidate how early-life partial migration and diverse nursery use could contribute to population stability, resilience, and productivity in HR striped bass under different

climate scenarios (Kerr et al., 2010; Anderson et al., 2015). Future studies should also explore how early-life partial migration and nursery experiences affect lifetime adult migration patterns. Adults exhibit size-dependent migration modalities, with smaller fish remaining resident within the HR and larger fish more likely to undertake coastal migrations, all of which may have consequences for population dynamics (Secor and Piccoli, 1996; Wingate and Secor, 2007; Gahagan et al., 2015).

Long-term increases in freshwater flow and temperature in the HR due to climate change may alter striped bass early-life partial migration, nursery use, and ultimately the population dynamics (Najjar et al., 2009; Seekell and Pace, 2011). High-flow conditions are generally linked to poor YOY recruitment in the HR; however, brackish habitats may facilitate higher juvenile growth and survival under such conditions, producing a small but resilient segment of the population. While recruitment is the outcome of numerous physical and biological processes operating at various spatiotemporal scales during the pre-recruit life stages, brackish habitats in the HR may become of greater importance under future climate scenarios. Increased contributions from brackish habitats could potentially reduce male production, which is uniquely dependent on freshwater recruits. A decline in smaller males could affect population stability and resilience, given that adult striped bass exhibit size-dependent oceanic migration patterns that spatially hedge against regional disparities in exploitation, pollution, and food web conditions (Secor and Piccoli, 1996; Wingate and Secor, 2007; Gahagan et al., 2015). As environmental conditions change rapidly due to climate change, restoring and maintaining a mosaic of habitats across the HR nurseries and “extra” coastal nurseries will be critical to supporting early life history

diversity and long-term population persistence for striped bass and other species that depend on complex spatial structuring.

5.6 Acknowledgements

This research was funded by the Hudson River Foundation under grant number 004/19A. I thank the Hudson River Biological Monitoring Program (HRBMP) and Applied Science Associates (ASA) for allowing me to obtain striped bass standing stock data from Year Class Reports. I wish to thank Samara Nehemiah for assistance with otolith ageing. KA was financially supported by a fellowship from Japan Student Services Organization.

Tables

Table 5.1 Response and predictor variables used in the Generalized Additive Model for Location, Scale, and Shape (GAMLSS) to assess the effect of environmental conditions and density-dependence on adult brackish and western Long Island Sound (WLIS) nursery indices.

Variable	Type	Units	Source
Brackish nursery index	Numerical response (range: 0–1)	Unitless	Otolith chemistry
WLIS nursery index	Numerical response (range: 0–1)	Unitless	Otolith chemistry
Water temperature	Numerical predictor	(°C)	PWTF, USGS below Poughkeepsie
Freshwater flow	Numerical predictor	(m ³ s ⁻¹)	USGS Green Island
Winter severity	Numerical predictor	(°C)	PWTF, USGS below Poughkeepsie
PYSL abundance	Numerical predictor	Unitless	HRBMP Year Class Reports

Note: PYSL = post-yolk-sac larval abundance, PWTF = Poughkeepsie Water Treatment Facility, USGS = United States Geological Survey, HRBMP = Hudson River Biological Monitoring Program.

Table 5.2 Akaike’s information criterion (corrected for small sample size; AICc) rankings of Generalized Additive Model for Location, Scale, and Shape (GAMLSS) models to assess the influence of environmental conditions and density dependence on brackish and western Long Island Sound (WLIS) nursery contributions.

Response	Rank	Models	df	AICc	Δ AICc
Brackish nursery	1	Flow	8	259.3	0.0
	2	Flow + Winter Severity	12	259.6	0.3
	3	Flow + Temperature	9	260.1	0.8
	4	Flow + Temperature + Winter Severity	12	260.8	1.5
	5	Flow + Temperature + Winter Severity + PYSL	14	261.3	2.0
WLIS nursery	1	Winter Severity	5	243.4	0.0
	2	Winter Severity + Temperature	6	243.7	0.3
	3	Winter Severity + Flow + PYSL	7	243.8	0.4
	4	Winter Severity + Flow	6	243.9	0.5
	5	Winter Severity + Temperature + PYSL	7	244.5	1.1

Note: Δ AICc shows the differences in Akaike’s information criterion (corrected for small sample size) between the best model (rank 1) and a given model. PYSL = post-yolk-sac larval abundance, df = degrees of freedom.

Figures

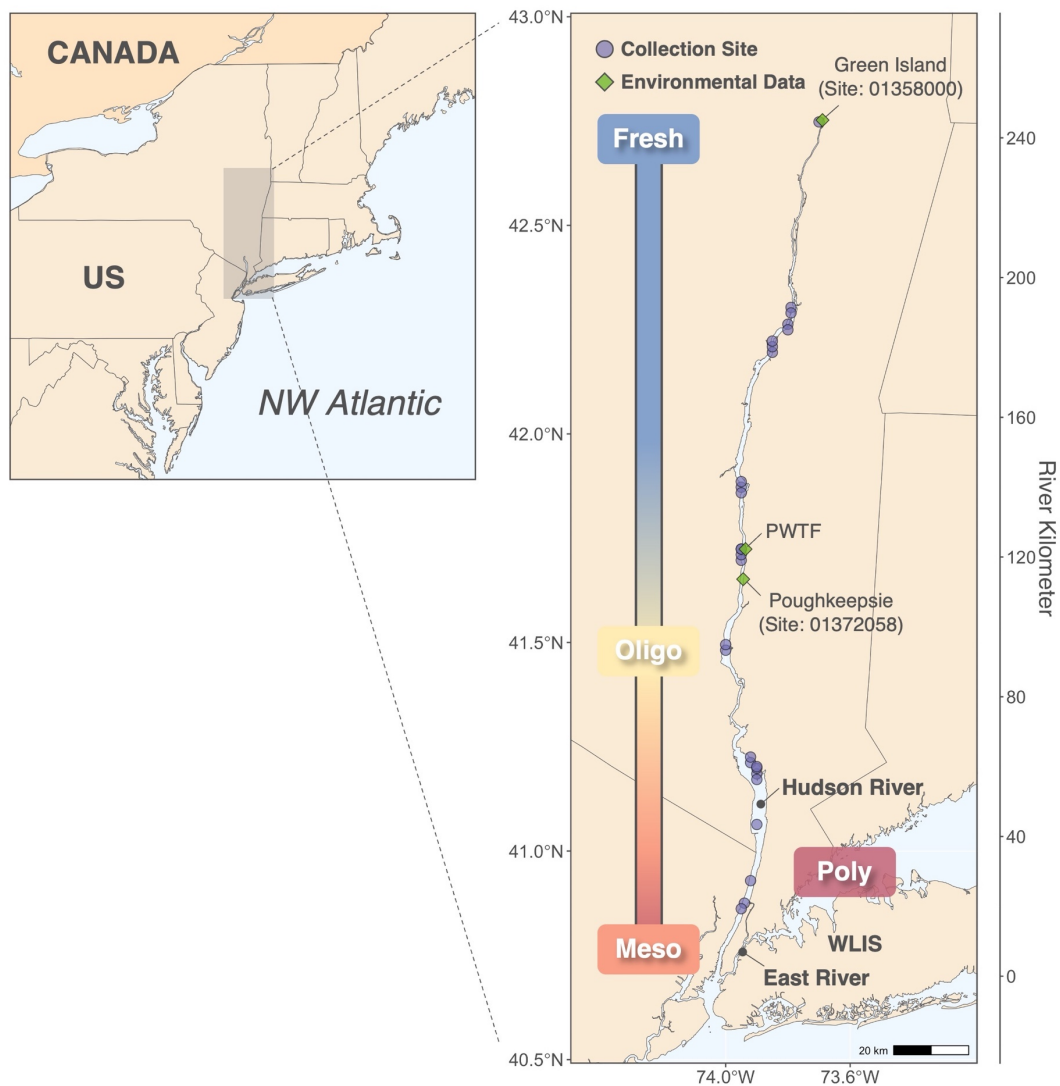


Figure 5.1 Map of the Northwest Atlantic Ocean, Hudson River, and western Long Island Sound (WLIS), with adult striped bass collection sites in 1995, 2016, 2017, and 2019. Green diamonds display stations where environmental variables were obtained. The y-axis depicts the latitude and river kilometers from the mouth of the Hudson River. The color bar illustrates the salinity zones: Fresh = Freshwater, Oligo = Oligohaline, Meso = Mesohaline, Poly = Polyhaline. PWTf = Poughkeepsie Water Treatment Facility.

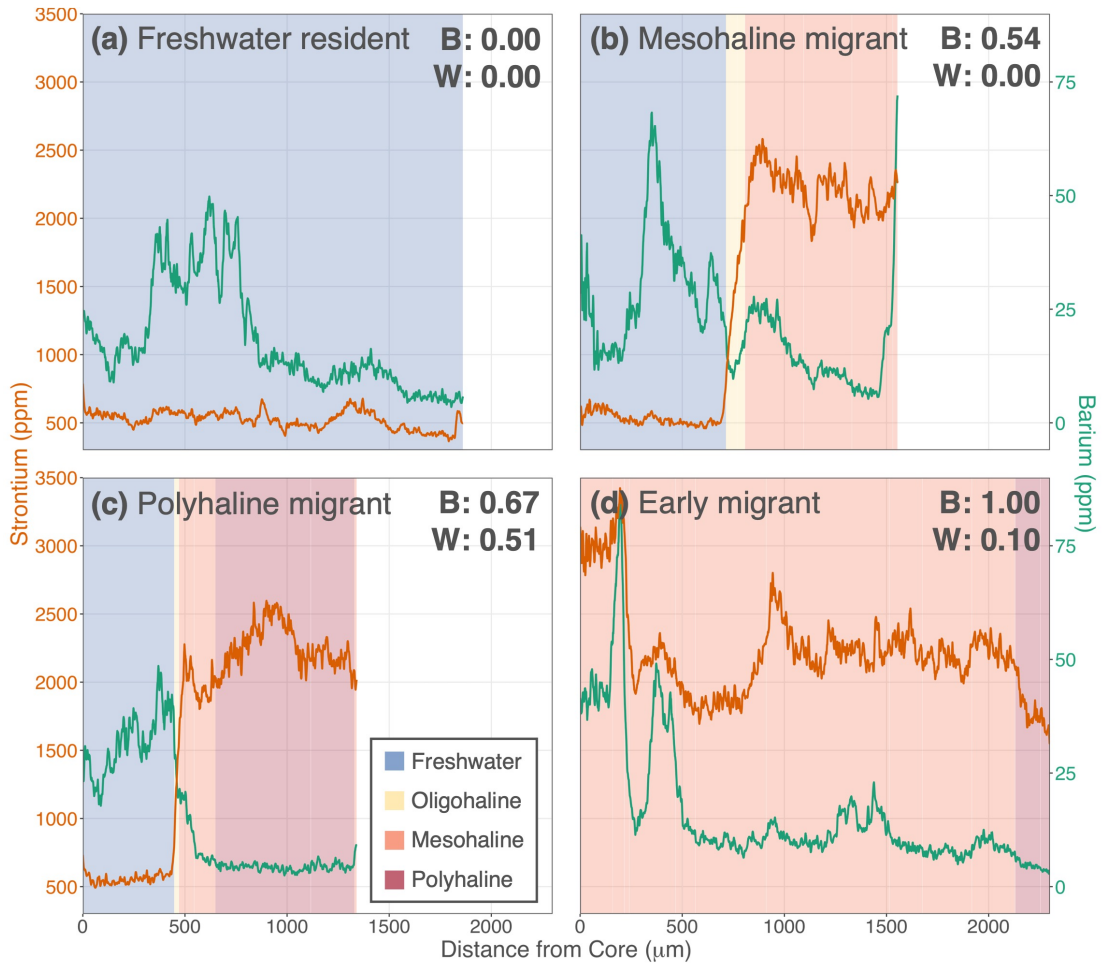


Figure 5.2 Example striped bass adult otolith Sr (orange) and Ba (green) transects and predicted habitats of striped bass adults displaying (a) freshwater resident, (b) mesohaline migrant, (c) polyhaline migrant, and (d) early migrant behaviors during the first growing season. Background-colored rectangles indicate stable segments identified using changepoint analysis, with colors representing predicted habitats for each stable segment using random forest classification. The brackish (B) and western Long Island Sound (W) nursery indices which range from 0 to 1, are shown in the top right corner of each panel.

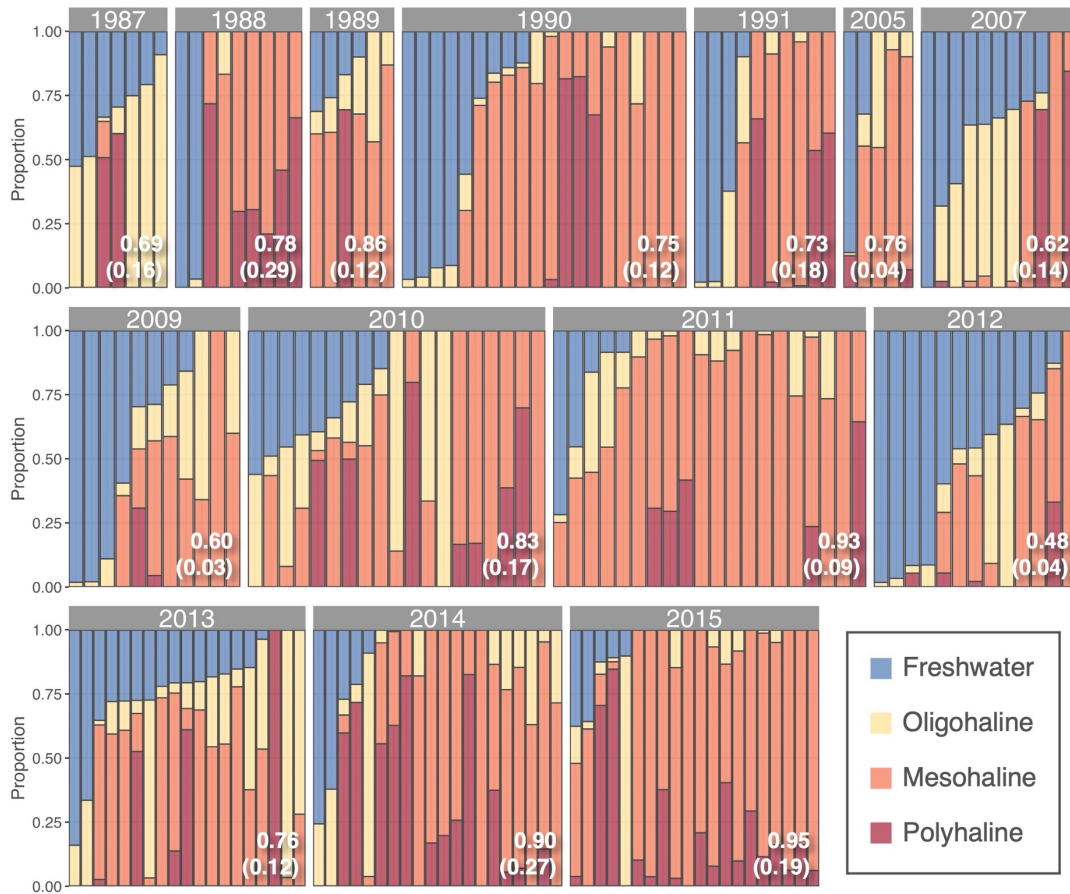


Figure 5.3 Proportional nursery contributions for striped bass adult samples estimated from otolith chemistry for year-classes 1987–1991, 2005, 2007, and 2009–2015. Each bar represents an individual recruit. The mean brackish nursery index (outside parenthesis) and the western Long Island Sound (WLIS) nursery index (inside parenthesis) for each year-class is shown in the bottom right corner of each panel.

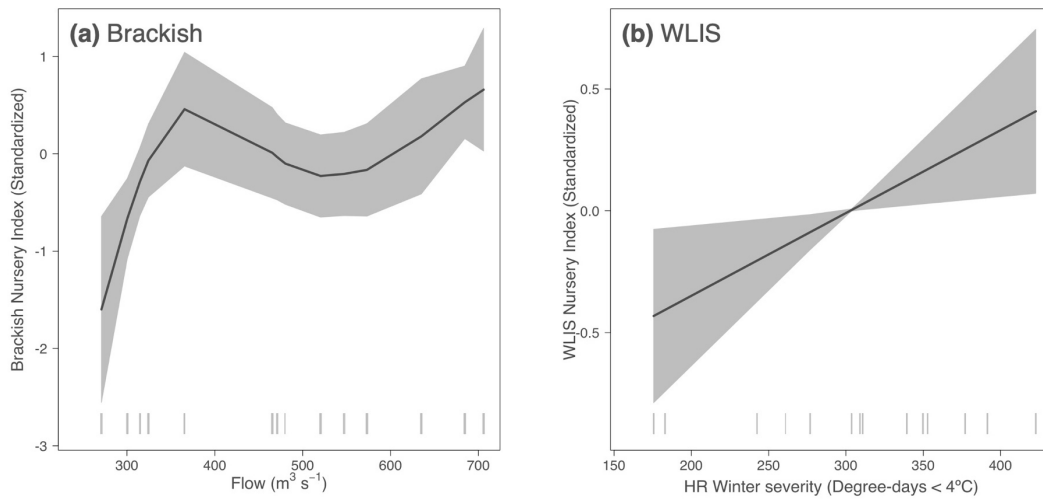


Figure 5.4 GAMLSS partial effects of (a) freshwater flow on the mean of the brackish nursery index, and (b) the winter severity within the Hudson River (HR) on the mean western Long Island Sound (WLIS) nursery index. Shaded areas depict standard errors and the rug along the x-axis indicates the distribution of observations.

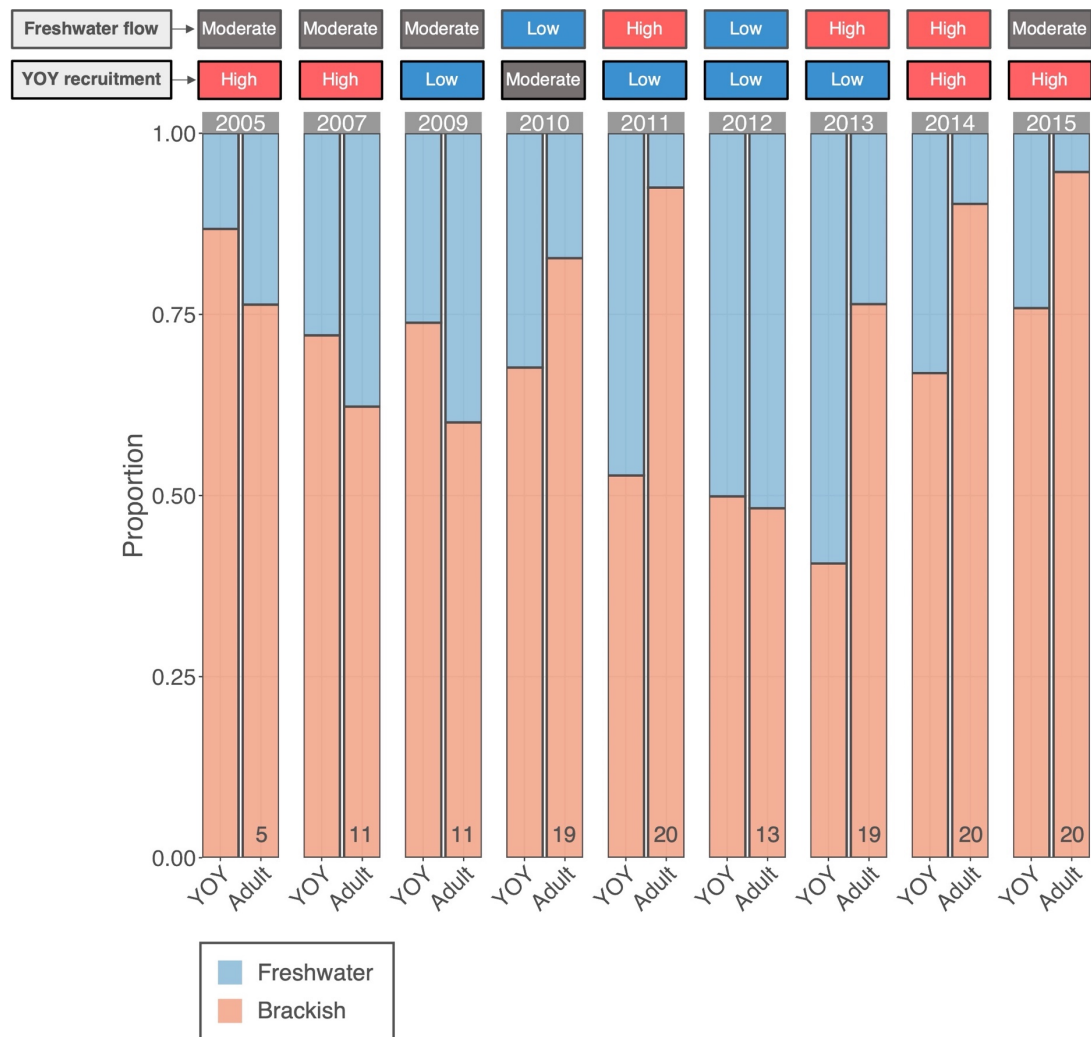


Figure 5.5 Comparison of the baseline striped bass young-of-the-year (YOY) freshwater and brackish habitat proportion (YOY) and recruited adult nursery contributions (Adult) for year-classes 2005, 2007, and 2009–2015. Numbers at the bottom of each bar plot indicate the sample size of adults for each year-class. The level (low, moderate, high) of freshwater flow and YOY recruitment (see Figure S5.7) compared to the long-term mean are also shown at the top of each bar plot for each year-class.

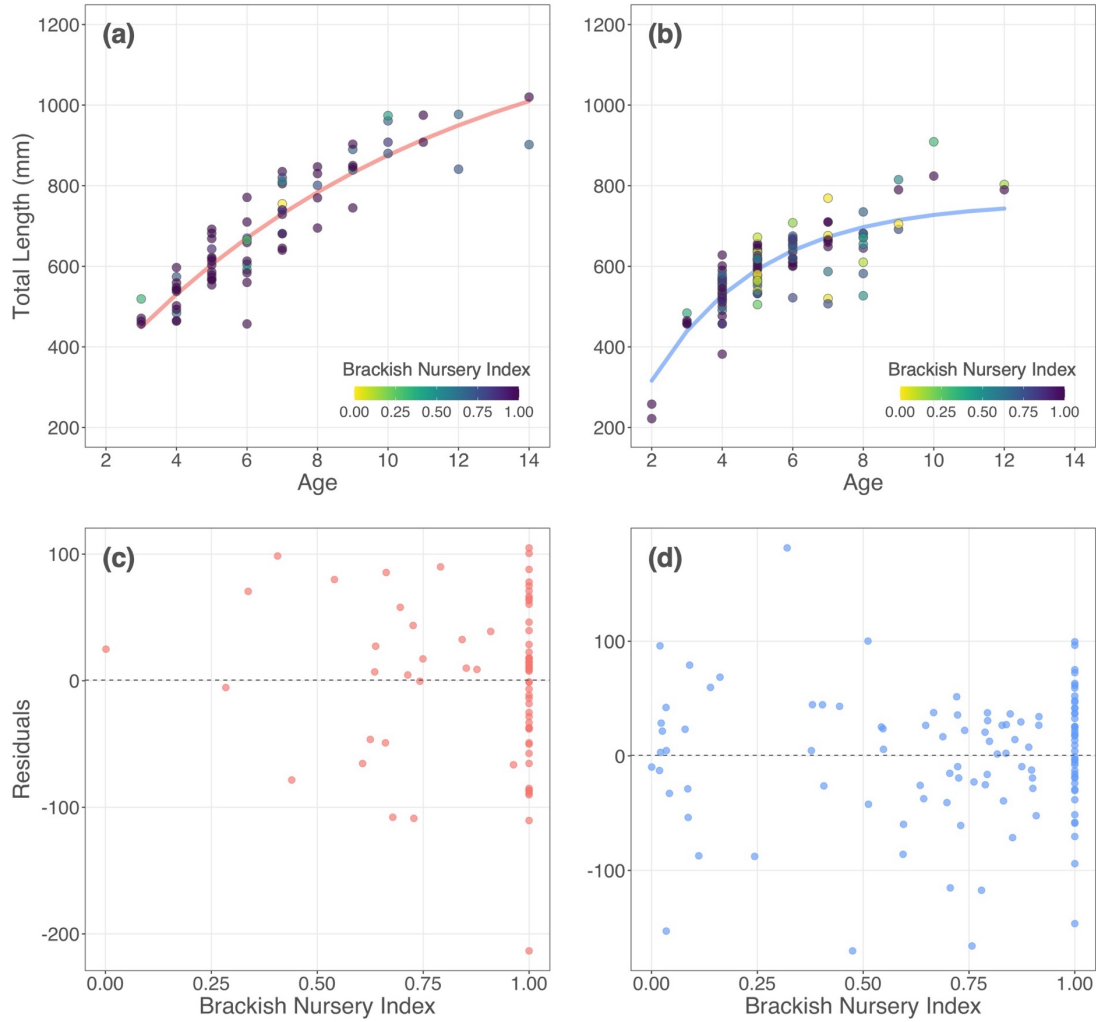


Figure 5.6 Fitted von Bertalanffy growth curves for (a) female and (b) male striped bass adult size-at-age data. Points are colored by the brackish nursery index ranging from 0 to 1. Relationship between growth curve-extracted residuals and the brackish nursery index for (c) females and (d) males. The dashed horizontal line indicates zero.

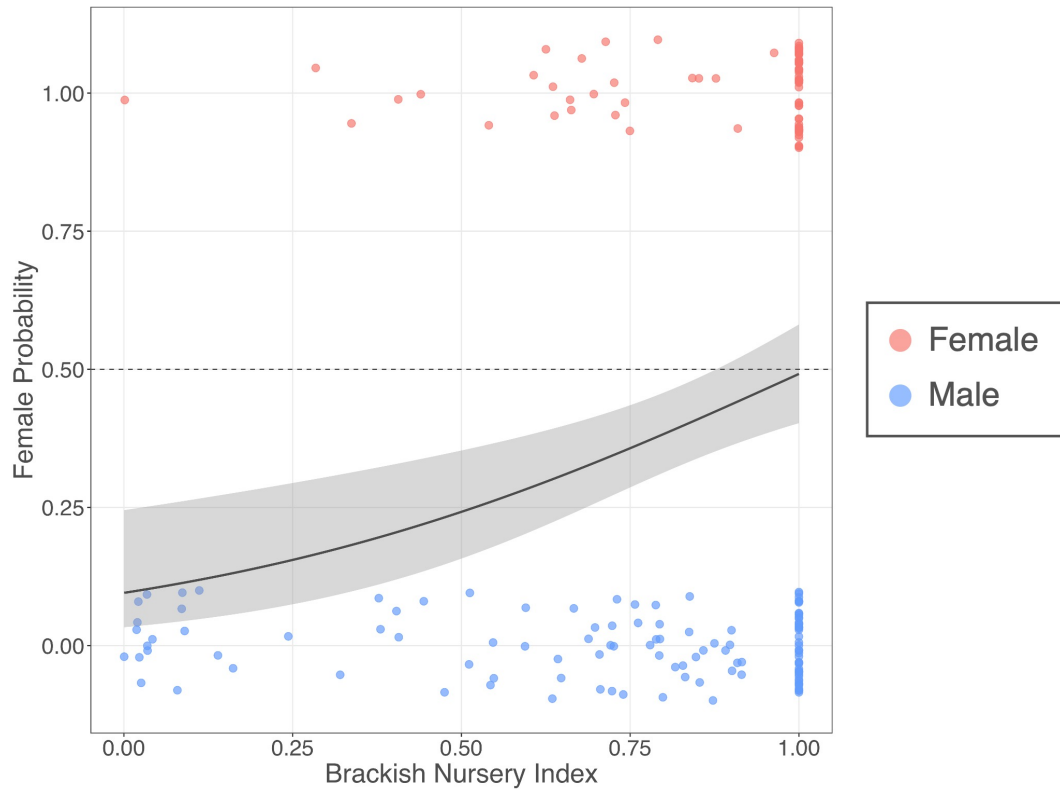


Figure 5.7 Fitted logistic regression model assessing the relationship between striped bass adult sex and the brackish nursery index. The solid line and shaded area indicate the predicted value and 95% confidence intervals from the model. Adult sex data had binary values of 0 (male) or 1 (female) on the y-axis, but a small random variation was added to each point to prevent overplotting. The dashed horizontal line indicates 0.5 female probability.

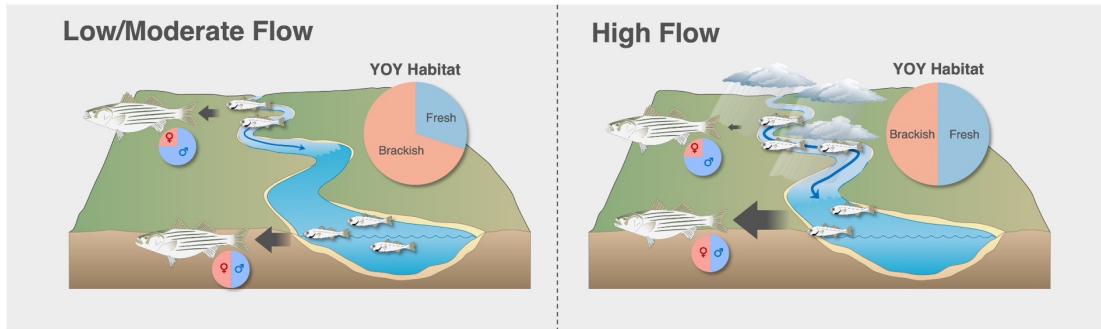


Figure 5.8 Schematic diagram illustrating adult nursery contributions, carry-over effects, and young-of-the-year (YOY) habitat proportions for Hudson River striped bass in years of low/moderate versus high freshwater flow. The thickness of the black arrows indicates the relative contributions from freshwater and brackish nurseries to the recruitment of adults. Nursery experiences carried over to influence adult sex: freshwater residents or late brackish migrants were more likely to develop into males, whereas early brackish migrants developed into either males or females. In low/moderate flow years, YOY brackish habitat predominated, and both freshwater and brackish habitat contributed roughly proportionately to adult production. In high-flow years, while the proportion of YOY freshwater and brackish habitats were roughly equal, brackish habitats disproportionately contributed more to adult production. Symbols courtesy of the University of Maryland Center for Environmental Science Integration and Application Network.

Supplementary Material

Table S5.1 Mean total length, standard deviation, and sample size of adult striped bass categorized by collection year, sex, and sampling source.

Year	Sex	Program	Mean TL (mm)	SD	n
1995	Female	Contaminant	740.7	125.6	18
	Male	Contaminant	616.4	73.6	58
2016	Female	Commercial	587.3	35.3	9
		Contaminant	642.3	95.2	19
		Sturgeon	576.7	9.8	3
		Spawning	827.6	134.7	5
	Male	Commercial	624.0		1
		Contaminant	609.1	53.5	17
		Sturgeon	620.7	7.0	3
		Spawning	600.1	164.7	18
2017	Female	Contaminant	687.1	67.2	15
		Sturgeon	488.3	50.5	7
		Spawning	842.9	115.4	7
	Male	Contaminant	660.0	83.8	46
		Sturgeon	497.6	72.0	11
		Spawning	608.4	110.8	12
2019	Female	Contaminant	655.6	135.5	39
		Sturgeon	509.8	40.9	11
		Spawning	812.6	114.0	20
	Male	Contaminant	627.3	102.8	31
		Sturgeon	518.0	14.8	3
		Spawning	551.8	154.8	26

Note: Contaminant = contaminant monitoring program, Commercial = commercial river herring (*Alosa* spp.) monitoring, Sturgeon = juvenile Atlantic sturgeon abundance sampling, Spawning = adult striped bass spawning stock survey.

Table S5.2 Parameter estimates and 95% bootstrap confidence intervals for von Bertalanffy growth models fitted for female and male adult striped bass.

Sex	Sample size	Parameter	Estimate	95% LCI	95% UCI
Female	74	L_{∞}	1265.061	1017.634	1929.572
		K	0.106	0.049	0.187
		t_0	-1.140	-2.787	0.219
Male	116	L_{∞}	760.585	679.669	1109.762
		K	0.325	0.080	0.551
		t_0	0.346	-4.352	1.142

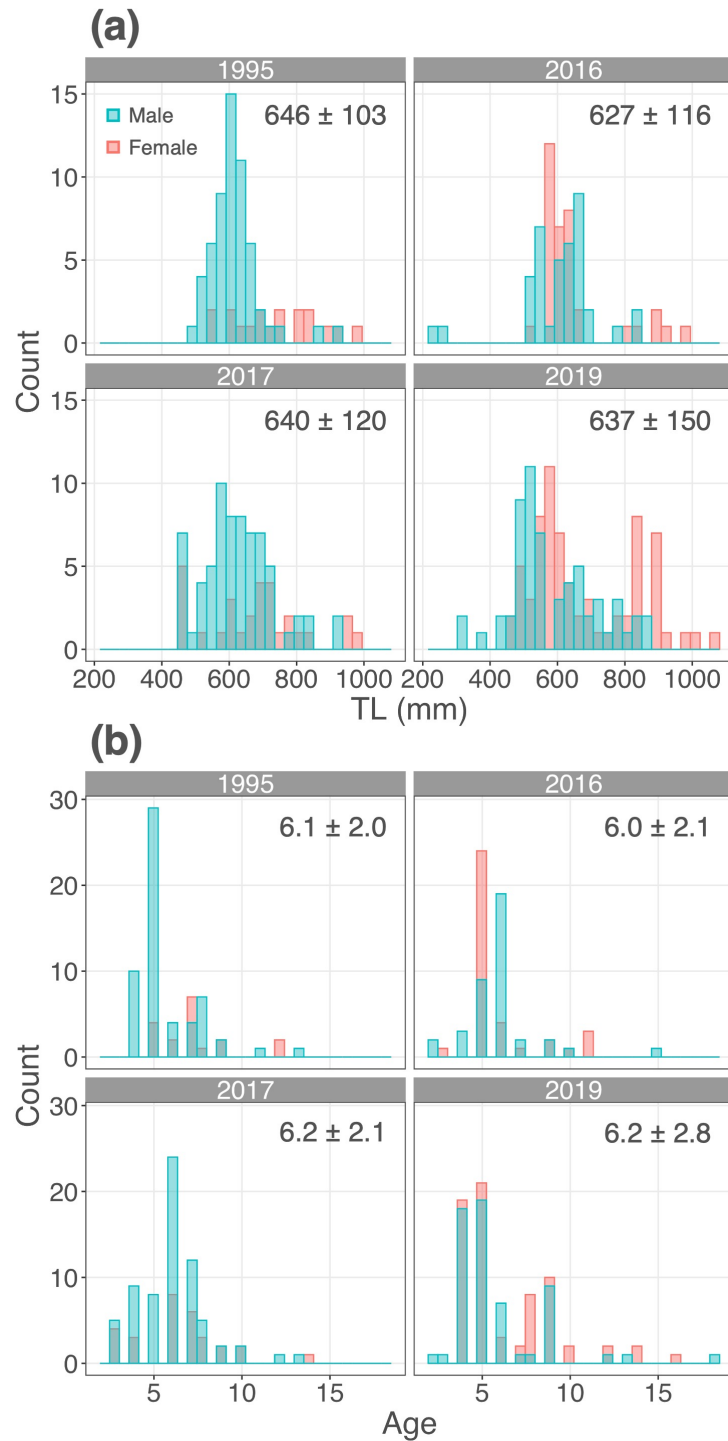


Figure S5.1 Striped bass adult total length (a) and age (b) distributions collected in the years 1995, 2016, 2017, and 2019 in the Hudson River. Associated mean $\pm$ standard deviations are shown in the top right corner of each panel. Bars are colored by sex.

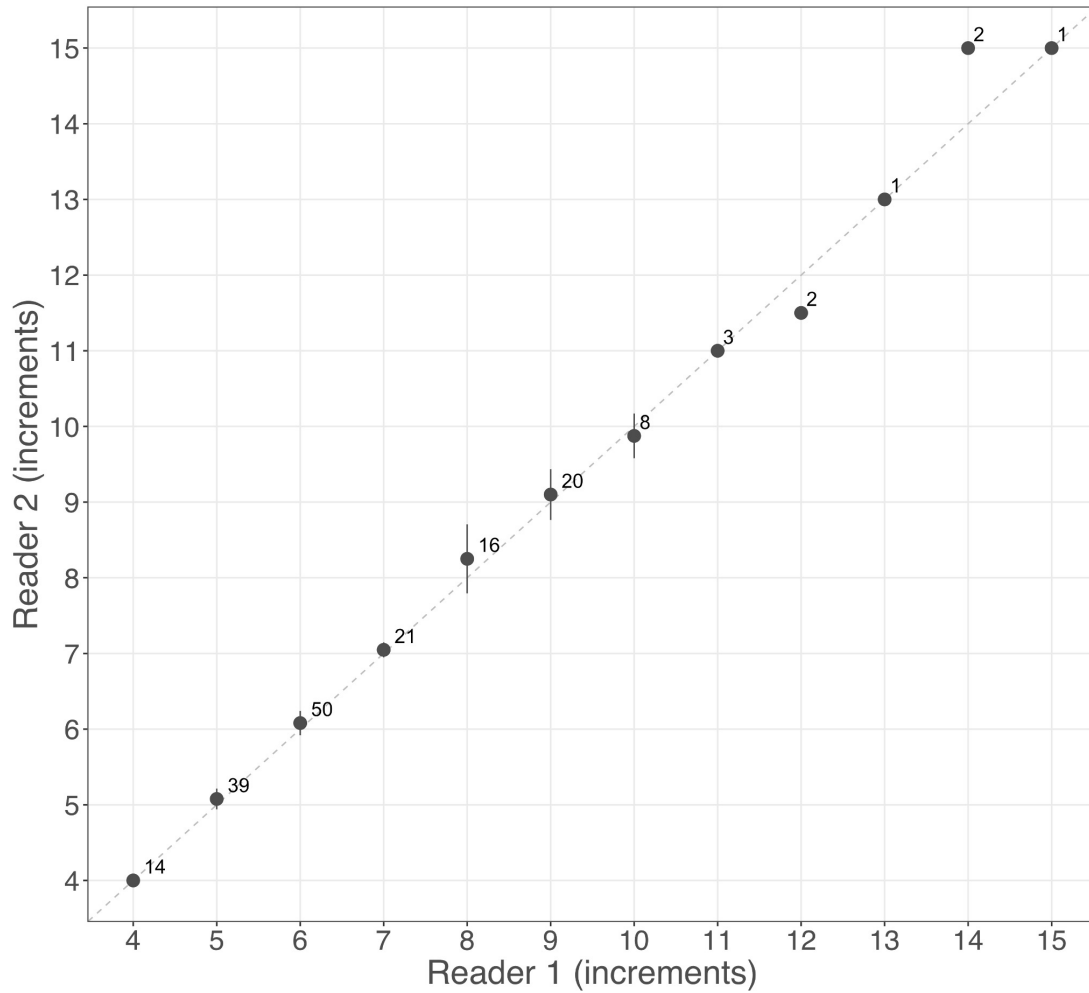


Figure S5.2 Age-bias plot illustrating matched pairs of striped bass adult otolith annuli between two reads with the mean and 95% confidence intervals and sample sizes for individual age classes. The dashed diagonal line indicates the identity line and divergence from the line indicates the degree of systematic differences in matched pairs of increment counts between two readers.

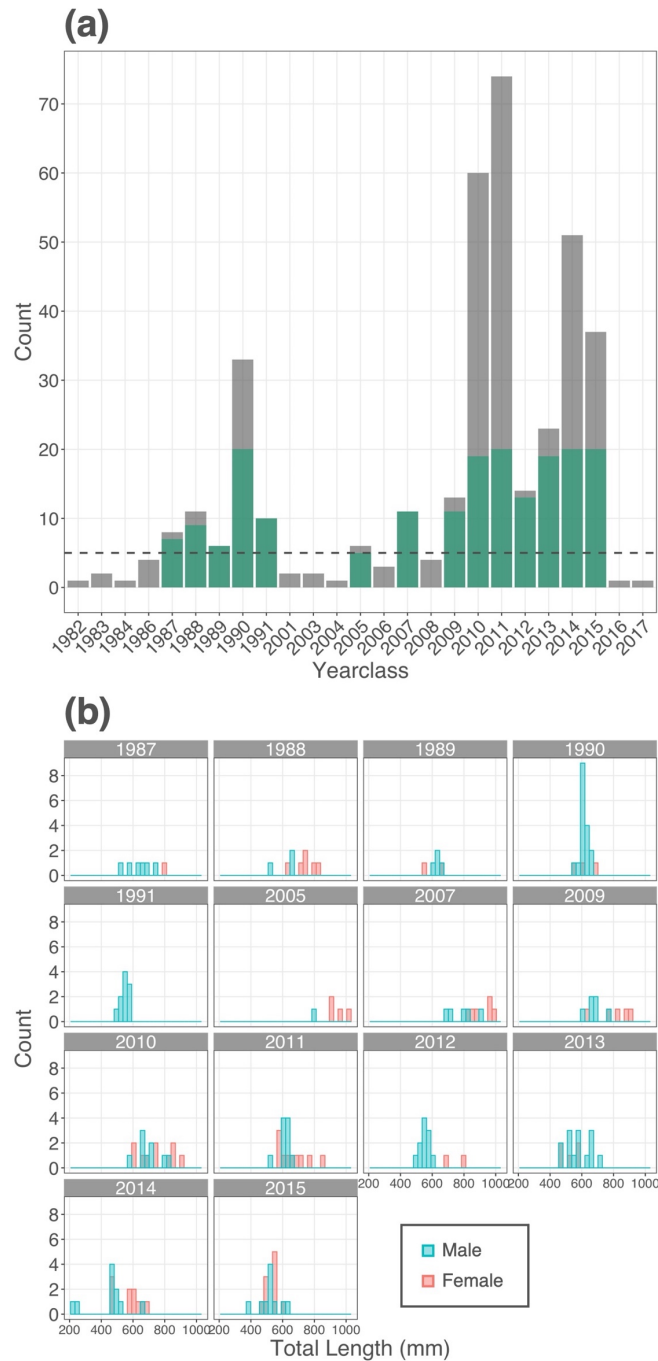


Figure S5.3 (a) Striped bass adult sample size distribution across year-classes (i.e., the year the fish was born). Green bars depict samples selected for otolith microchemistry ($n = 190$). The dashed horizontal line indicates the minimum sample size ($n \geq 5$) within each year-class selected for analysis (total of 14 year-classes). (b) Striped bass adult total length distribution by year-class selected for otolith microchemistry. Bars are colored by sex.

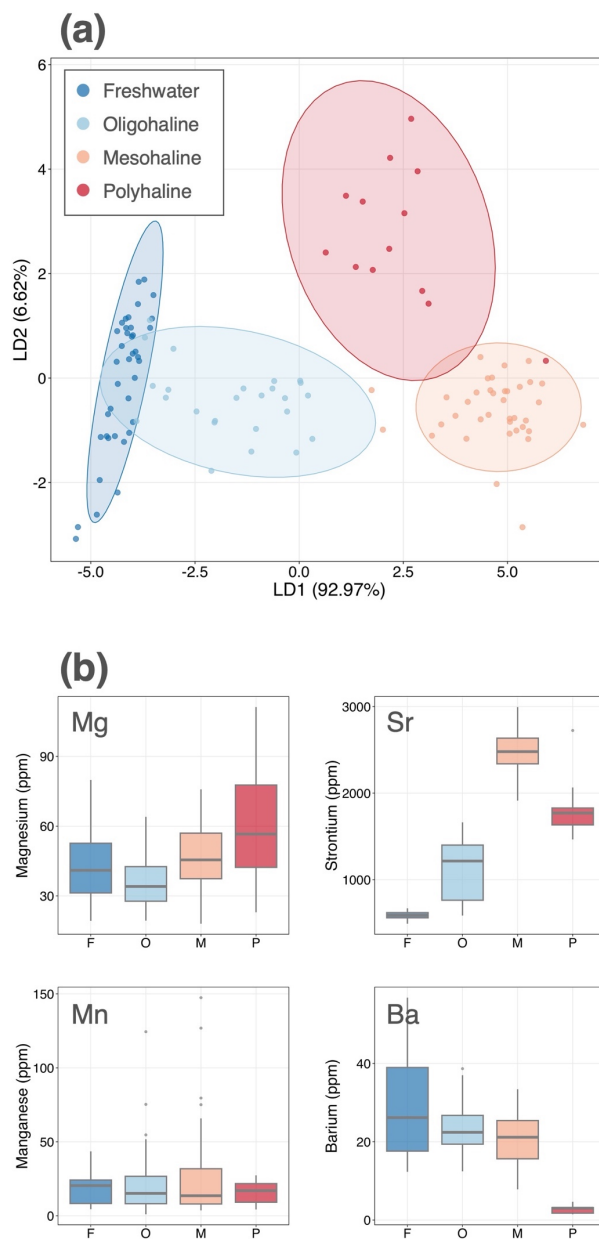


Figure S5.4 (a) Linear discriminant analysis (LDA) score plot showing the mean edge otolith magnesium (Mg), manganese (Mn), strontium (Sr), and barium (Ba) for each juvenile striped bass collected in freshwater (salinity < 0.4 ppt), oligohaline (0.4–3.0 ppt), mesohaline (3.0–18.0 ppt), and polyhaline (> 18.0 ppt) habitats used as the reference baseline for random forest habitat assignment from Chapter 4. Ellipses show 95% confidence for each habitat. (b) Box whisker plots of mean otolith elemental concentrations (Mn, Mg, Sr, Ba) of the otolith edge for juvenile striped bass collected in different salinity zones in the Hudson River in 2019 and 2020. F = Freshwater, O = Oligohaline, M = Mesohaline, P = Polyhaline.

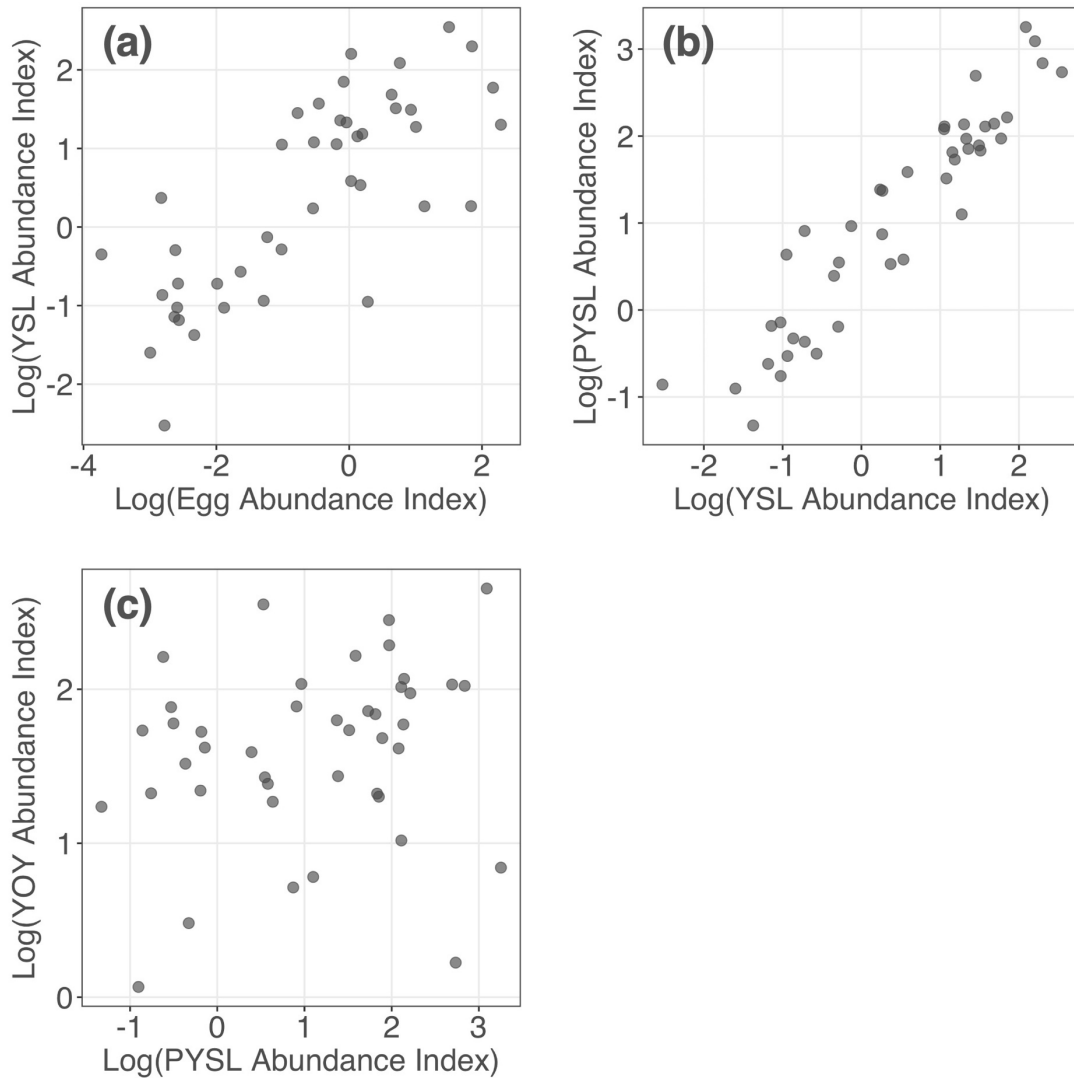


Figure S5.5 Relationships between striped bass early-life stage abundances for (a) egg–yolk-sac larvae (YSL), (b) YSL–post-yolk-sac larvae (PYSL), and (c) PYSL–young-of-the-year (YOY). Data was obtained from the “Year Class Reports” for the Hudson River Biological Monitoring Program (ASA Analysis & Communication, 2019). Note that scales of all axes are log-transformed and differ among panels.

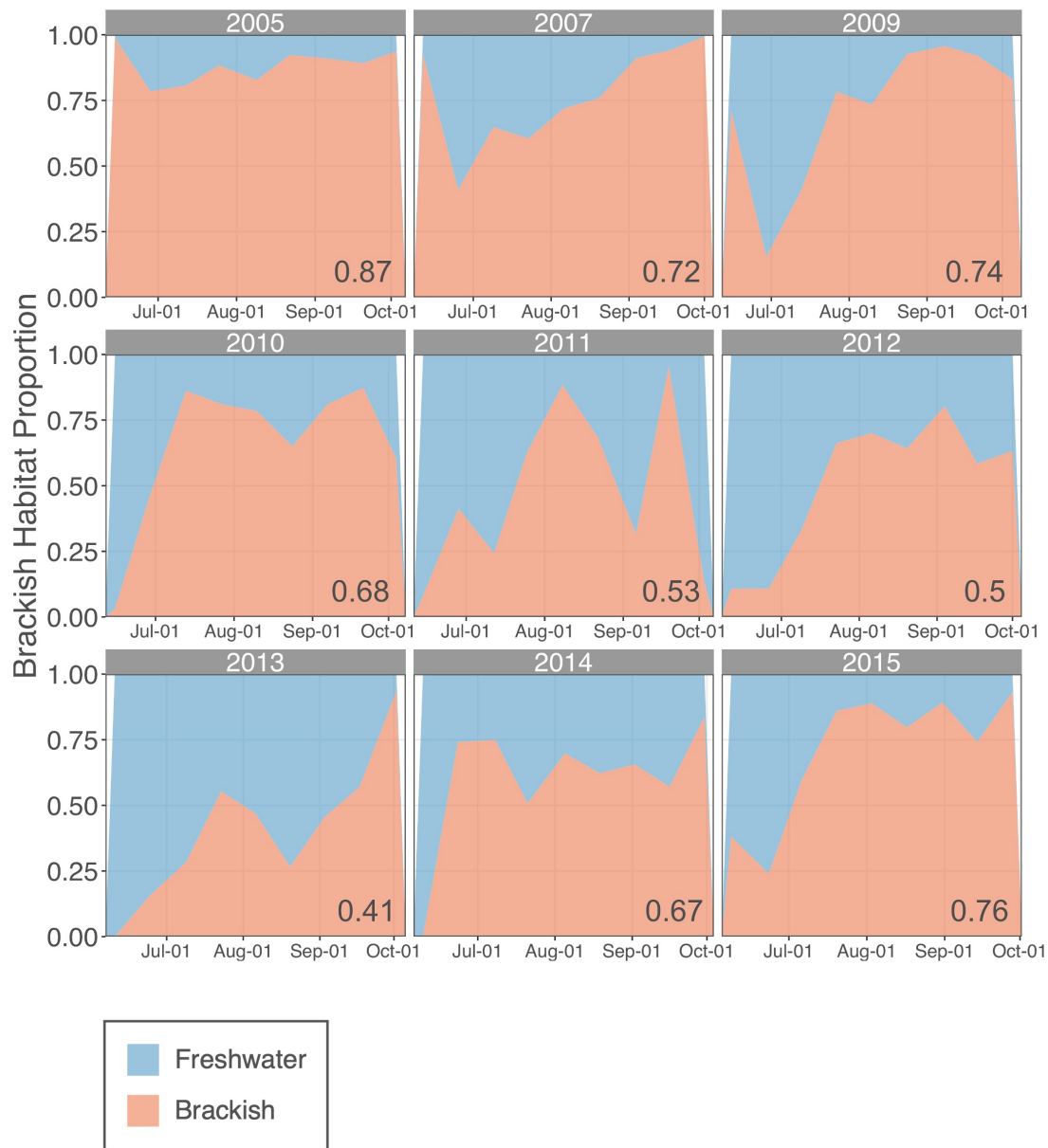


Figure S5.6 Temporal trends in baseline young-of-the-year (YOY) freshwater and brackish habitat proportions for year-classes 2005, 2007, and 2009–2015. The overall brackish habitat proportion for each year-class is shown in the bottom right corner of each panel.

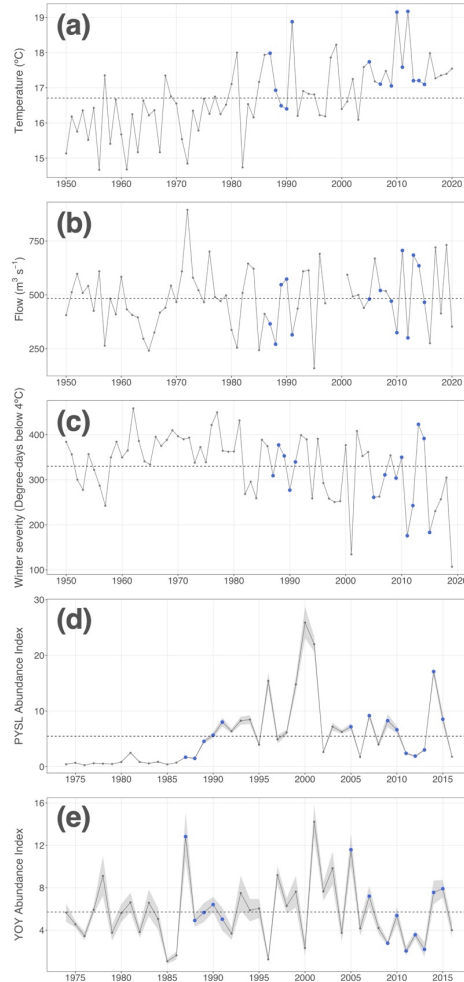


Figure S5.7 (a) Annual mean (April–July) temperature in the Hudson River acquired from the Poughkeepsie Water Treatment Facilities (1950–1991) and USGS monitoring station (site: 01372058 [1992–2020]) below Poughkeepsie. (b) Annual mean (April–July) freshwater flow in the Hudson River (1950–2020), acquired from the USGS Green Island monitoring station (site: 01358000). (c) Winter severity calculated as the sum of degree-days below 4°C (1950–2019). (d) Annual striped bass post-yolk-sac larval abundance index and standard errors (1974–2016) obtained from the “Year Class Reports” for the Hudson River Biological Monitoring Program (HRBMP) (ASA Analysis & Communication, 2019). (e) Annual striped bass young-of-the-year (YOY) abundance index and standard errors (1974–2016) obtained from the “Year Class Reports” for the Hudson River Biological Monitoring Program (HRBMP) (ASA Analysis & Communication, 2019). The horizontal dashed lines for each time series indicate the long-term mean for each variable. Blue points for each time series indicate the year-classes represented by adult samples (i.e., 1987–1991, 2005, 2007, 2009–2015).

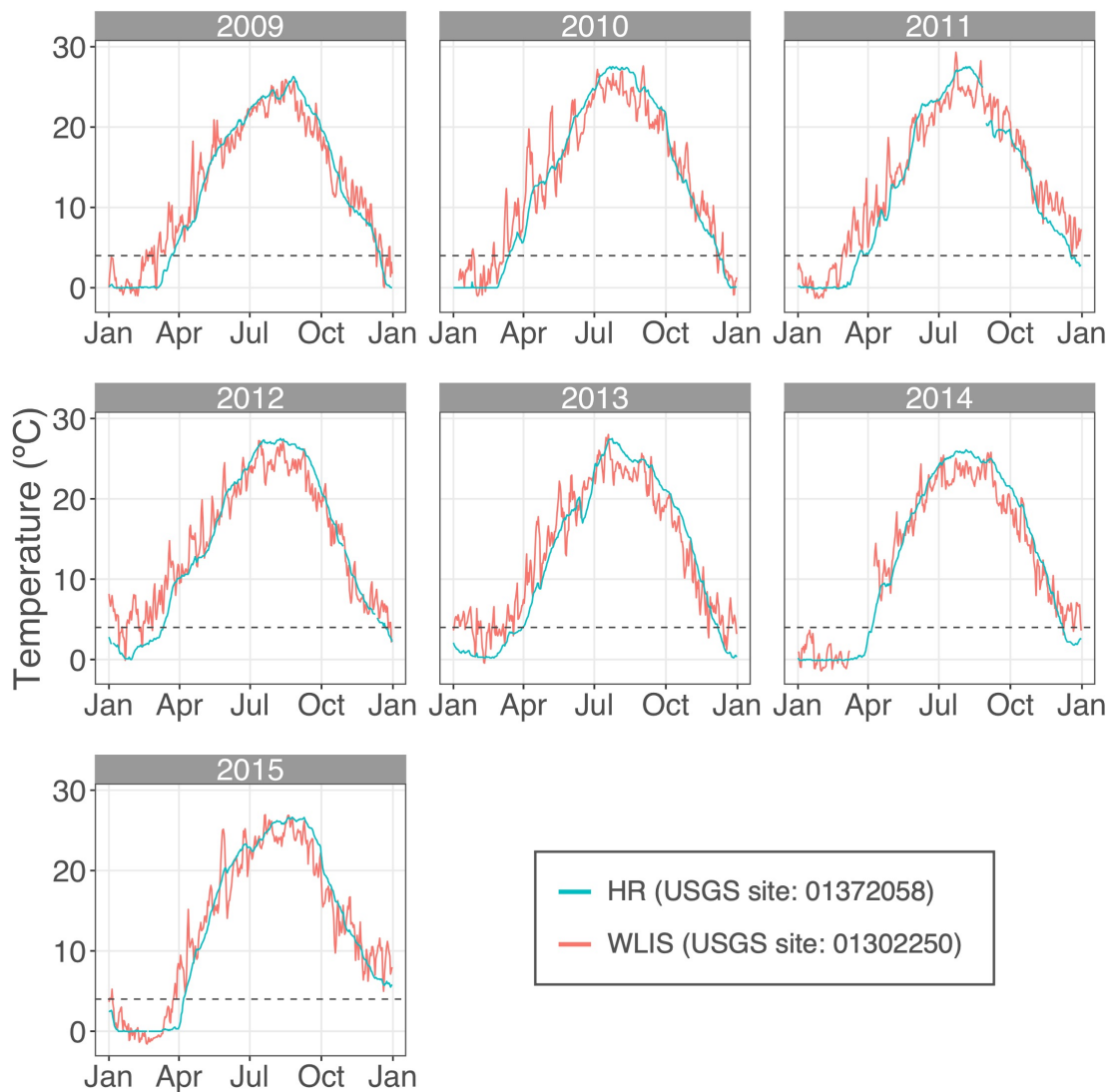


Figure S5.8 Daily temperature for the years 2009–2015 in the Hudson River (HR) acquired from the USGS below Poughkeepsie monitoring station (site: 01372058), and the western Long Island Sound (WLIS) acquired from the USGS East Creek at Sands Point NY monitoring station (site: 01302250). The horizontal dashed line indicates the 4°C threshold used to calculate the winter severity index.

Appendix Chapter: Sub-annual cohort representation among young-of-the-year recruits of the western stock of the Atlantic bluefin tuna

Arai, K., Graves, J. E., and Secor, D. H. (2020). Sub-annual cohort representation among young-of-the-year recruits of the western stock of Atlantic bluefin tuna. *Fish. Res.* 225, 105476. doi: 10.1016/j.fishres.2019.105476.

A.1 Abstract

The western stock of Atlantic bluefin tuna receives recruits principally from spawning habitats in the Gulf of Mexico although the recent discovery of bluefin tuna larvae in the western North Atlantic Slope Sea calls into question whether there is another key source of recruits to the western stock. We tested whether age-0 juveniles occurring in the US Mid-Atlantic Bight during the late summer might originate from Slope Sea spawning by estimating the hatch date distribution based on otolith microstructural analysis given larval production occurs approximately two months later in the Slope Sea (late June to early August) than in the Gulf of Mexico (early April to mid-June). Following a review of the literature on ageing methodology for Thunnini species, we attempted trials on both sectioned and whole un-sectioned otoliths, and adopted the latter based on higher precision levels. Estimated ages ranged from 122 to 175 (days post hatch) for fish ranging 23.2 to 36.3 cm fork length. Hatch dates ranged 20 March to 12 May 2010, exhibiting a unimodal distribution. Hatch dates mainly occurred in early-April 2010, which corresponded to the spawning and larval production period for the Gulf of Mexico. Estimated growth rate

(size-at-age) was 1.1 mm d^{-1} . Thus, we failed to observe evidence for recruitment from the newfound Slope Sea spawning region, albeit our sample represents only a single year and region. More conclusive inferences on recruitment from the Slope Sea spawning will depend on a greater sample of age-0 juveniles sampled across years or molecular approaches that can identify recruits in older juveniles and adults.

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Chapter 1

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Chapter 4

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