THE ROLE OF CLIMATE CHANGE IN THE DECLINE OF NARRAGANSETT BAY WINTER FLOUNDER

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THE ROLE OF CLIMATE CHANGE IN THE DECLINE OF NARRAGANSETT BAY WINTER FLOUNDER

BY

JOSEPH A. LANGAN

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN OCEANOGRAPHY

UNIVERSITY OF RHODE ISLAND

2021
ABSTRACT

Winter flounder (*Pseudopleuronectes americanus*) has historically supported productive commercial and recreational fisheries throughout its range in the northwest Atlantic. As a small flatfish that inhabits estuaries, bays, and the coastal zone, this species is vulnerable to shifting environmental conditions in many of the habitats critical to its life cycle. At the southern edge of the species range, the Southern New England/Mid-Atlantic Bight winter flounder stock entered a steep decline during the 1980s following a period of overfishing. Despite repeated reductions in harvest during the proceeding decades, the population has yet to recover. A decreasing trend in recruitment has led to speculation that increased mortality during the early life cycle is preventing this stock from rebuilding. While it is well known that environmental stressors, predation, competition, and anthropogenic disturbances all can impact the survival of juvenile flounder, it remains unclear which of these factors are most important in regulating population productivity. To answer this question for the Narragansett Bay, Rhode Island winter flounder subpopulation, part of the Southern New England/Mid-Atlantic Bight stock, this dissertation aims to model the winter flounder life cycle and its patterns of habitat use to better understand the population dynamics and future recovery potential of this climate-challenged species.

The first chapter aimed to model the winter flounder early life cycle to uncover patterns of population regulation and identify trends in juvenile mortality. Using a structural equation model fit to abundance indices of 29 year classes progressing through seven life stages gathered from multiple scientific surveys in Rhode Island waters, it was determined that winter flounder year class strength does not appear to be
fully determined until cohorts join the spawning population. However, an increasing trend in mortality was identified during the first summer of life that was linked to rising summer temperatures, hypoxia, and predation. This result supports the hypothesis that juvenile mortality linked to environmental conditions may be inhibiting population productivity.

The second chapter used the structural equation model fit in Chapter 1 to project Narragansett Bay winter flounder abundance under potential future environmental and fishery conditions. The projection model was first calibrated using interstage mortality rates from previous research and environmental conditions observed during the 1970s immediately preceding rapid growth in this winter flounder subpopulation. Projections of future abundance were then made under “business as usual” and optimistic environmental conditions. In both cases, however, the results suggest winter flounder are unlikely to recover to historic high abundance levels. Even so, it was determined that population growth to a more moderate abundance level was possible under the right conditions.

The third chapter employed spatiotemporal conditional autoregressive models to study patterns of Narragansett Bay winter flounder habitat use throughout the life cycle during the population decline. Two phases of habitat use were identified: 1) a preference for shallow nursery habitats in the upper estuary during the first 15 months of life, and 2) a growing preference for deeper habitats in the lower estuary beginning in the first year, lasting through sexual maturity and the onset of participation in seasonal migrations. Although the studied spatial distributions were highly variable and did not exhibit detectable trends over time as the subpopulation declined, two important
patterns were identified. First, an increasing concentration of mature winter flounder in lower Narragansett Bay and coastal waters during spring was indicative of a potential shift in spawning migration timing that could impact the reproductive capacity of the population. Second, an apparent adherence to historic nursery habitats vulnerable to the effects of climate change and anthropogenic disturbance in the shallow upper Bay suggests that juvenile winter flounder will be increasingly exposed to unsuitable conditions for growth and survival in the future. Combined with the results of the first two chapters, this second pattern indicates that juvenile mortality may continue to increase and impact the capacity of this subpopulation to recover.

The research in this dissertation aims to provide scientists and fisheries managers with an enhanced understanding of the role of climate change in the decline of winter flounder near the southern edge of their range. The methods and insights developed here are meant to not only inform management of winter flounder, but contribute knowledge to the progression toward ecosystem-based management of climate-challenged fisheries in a rapidly warming ocean.
ACKNOWLEDGMENTS

What a journey this has been. I would first like to thank my major advisor, Jeremy Collie. Thank you for your belief in me, your unending patience, and for pushing me to become a better scientist and person. Your expertise and support throughout all aspects of my graduate education have helped me to learn and grow tremendously. I look forward to maintaining our research collaborations and friendship in the years to come.

I would also like to thank my other major advisor and committee member Gavino Puggioni. You have always challenged me to take one more step and learn one more lesson, believing in my abilities even when my own confidence faltered. I am and will forever be tremendously grateful for your and Jeremy’s help and support as I took on two degree programs. Working so closely with and learning from both of you over these past six years has been an honor.

I would next like to thank my remaining committee members, Austin Humphries and Rich Bell. You both were always generous with your time and expertise whenever I needed assistance with my research or a sounding board for ideas. The lessons I learned from both of you in research and in the classroom are invaluable to me and will help to shape my future career.

This dissertation was funded with support from Rhode Island Sea Grant, for which I am grateful. Further, this research could not have been completed without additional funding and support of my various projects from the University of Rhode Island, the Rhode Island Division of Marine Fisheries, the Bureau of Ocean Energy Management, NOAA Fisheries, the National Sea Grant College Program, and the New England
Fishery Management Council. Additionally, the work within this dissertation benefited significantly from the thoughtful input of the Rhode Island Marine Fisheries Institute.

I would next like to thank the GSO community and the staff of the Rhode Island Division Marine Fisheries. I believe that it takes a village to train a scientist, and I could not have had a better village to be a part of during graduate school. So many of you were so generous with your time, your expertise, and your support. I can only hope to pay some of that forward in the future. I would especially like to thank Candace Oviatt and Conor McManus. You both have been a mentor, collaborator, friend, sounding board, and role model to me and I am so appreciative to have had the opportunity to work with you. Similarly, I have been very fortunate to be a part of the welcoming, encouraging, and supportive Collie lab. The members, past and present, have always helped me and commiserated with me over the years and I am truly grateful. Anna Mercer, Rich Bell, Jason McNamee, Chris Orphanides, Conor McManus, Corinne Truesdale, Joe Zottoli, Adrien Tableau, Maggie Heinichen, Nina Santos, Rachel Marshall, Shaina Harkins, Annabelle Leahy, Adena Schonfeld, Connor Jones, Alyssa Gavlik, Ali Frey, Robert Krulee, and Tyler Richman- I have learned so much from all of you. I would also like to thank my many collaborators across my different research projects and endeavors. It has been a joy to work with all of you and I cherish having had the opportunity to conduct research alongside each of you. I hope that our collaborations will extend far into the future.

To my fellow graduate students and friends- thank you for your tireless support and for helping me to make such fond memories during graduate school. Having the opportunity to watch so many of you grow into amazing scientists and people has been
a privilege. To my family- your unending encouragement and support has kept me motivated and grounded on this journey. I will always be grateful for the role you played in my success.

Finally, I could not have achieved any of this without the love, support, patience, and understanding of my partner Lauren. From listening to me rant about statistical models to joining me on the fish trawl, you have been my biggest cheerleader and my rock through all of it. You have picked me up when I felt discouraged and knocked me back into my place when I got too high. You have always been understanding and supportive when I had late nights coding or woke you up early in the morning as I left for field work. During this last, challenging year under a global pandemic, you have taken on so much to help and encourage me as I finished my degrees. You are my hero and I cannot express how grateful I am for your support. I would not be half the scientist or a person I am today with you and I cannot wait to continue to grow with you in the next chapter of our lives.
PREFACE

This dissertation is formatted in accordance with the manuscript format guidelines established by the Graduate School of the University of Rhode Island. The first manuscript is formatted for, and in revision in, the journal *Canadian Journal of Fisheries and Aquatic Sciences*, with co-authors Jeremy Collie and Cóilín Minto. The second manuscript is formatted for submission to the journal *Fisheries Oceanography*, with co-authors Richard Bell and Jeremy Collie. The third manuscript is formatted for submission to the journal *Estuarine, Coastal and Shelf Science*, with co-authors Gavino Puggioni, Conor McManus, Richard Bell, and Jeremy Collie.
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INTRODUCTION

Climate change is causing the redistribution of marine species throughout the global oceans, both through shifts in spatial distributions and changes in latitudinal gradients of population productivity (Nye et al. 2009; Poloczanska et al. 2016; Pinsky et al. 2020). While significant research effort has been devoted to studying the poleward and offshore shifts of species colonizing new ecosystems, these redistributions pose challenges for the management of commercially important species in decline at the trailing edge of their range. Species at the warm edge of their range can be more susceptible to trophic interactions with invading warm-water species (Drinkwater 2005; Boudreau et al. 2015), leading to accelerated declines in productivity and creating the potential for rapid, unpredictable shifts in the biological community. As seasonal cycles in habitat suitability change, species may also reduce the length of time spent in habitats important for growth and reproduction (Langan et al. 2021). In cases where efforts to recover populations of climate-vulnerable species in decline come into conflict with economic opportunities presented by expanding fisheries for warm-water taxa, these dynamics create difficult tradeoffs for fisheries managers faced with regulating evolving species portfolios (Szuwalski and Hollowed 2016). To successfully navigate such tradeoffs, it is critically important to develop an in-depth understanding of how climate change is impacting the population dynamics of managed species and develop realistic assessments of future potential productivity.

These considerations are becoming particularly urgent on the Northeast United States Continental Shelf, a large marine ecosystem undergoing extreme rates of
warming (Pershing et al. 2015) linked both to climate change and shifts in ocean circulation (Chen et al. 2020; Gonçalves Neto et al. 2021). Many species in this ecosystem are both high in commercial value (National Marine Fisheries Service 2018) and vulnerable to climate change (Hare et al. 2016), creating a fast-evolving set of challenges in fisheries management. In addition to poleward and seasonal distribution shifts in response to changes in water temperature (Nye et al. 2009; Henderson et al. 2017), changes in productivity have been observed in many species (Xu et al. 2018; O’Leary et al. 2019; Tableau et al. 2019). As a result, the population levels of several historically productive stocks have declined to a depressed state (Northeast Fisheries Science Center 2017).

One such population is the Southern New England/Mid-Atlantic Bight stock of winter flounder (*Pseudopleuronectes americanus*). Winter flounder is a small, coastal and estuarine flatfish historically distributed between North Carolina and Labrador, Canada (Pereira et al. 1999). This species spawns between winter and spring in shallow bays, estuaries, and coastal areas (Pereira et al. 1999; Fairchild et al. 2013; Fairchild 2017; Siskey et al. 2020), displaying high fidelity to these spawning sites (Saila 1961). Eggs deposited on the seafloor hatch in 15-18 days and the pelagic larvae spend about 60 days in the water column prior to settlement in shallow nursery habitats (Pereira et al. 1999; Collette and Klein-MacPhee 2002). Juvenile winter flounder are thought to reside within their natal estuaries or spawning areas, making limited movements prior to reaching maturity (Pearcy 1962; Saucerman and Deegan 1991; Pereira et al. 1999; Taylor et al. 2016). Around age-2 winter flounder may begin to participate in seasonal migrations to inhabit cool offshore waters in summer before
returning to the coastal zone in winter, where spawning commences at age-2 or 3 (Pereira et al. 1999; Northeast Fisheries Science Center 2011). However, recent investigations suggest more complicated movement dynamics are present within populations, where some individuals may remain close to spawning areas throughout the year (Sagarese and Frisk 2011; Ziegler et al. 2019).

One of three management units in US waters, the Southern New England/Mid-Atlantic Bight stock of winter flounder has historically supported productive fisheries (Oviatt et al. 2003). However, the stock began to decline following a period of overfishing during the 1970s and 1980s and has since failed to rebound despite repeated reductions in harvest due in large part to decreased recruitment (Northeast Fisheries Science Center 2011, 2020), leading to speculation that increased mortality during the early life cycle is inhibiting recovery. Sources of mortality during the early life stages of winter flounder have been well-studied. Temperatures during the winter spawning season may influence the duration of spawning and the subsequent predation on eggs and larvae (Pereira et al. 1999; Taylor and Collie 2003; Taylor and Danila 2005). Following settlement and throughout the juvenile stages, significant predation may occur from fish (Manderson et al. 1999, 2006; Sagarese et al. 2011), seabirds (Pilon et al. 1983), and marine mammals (Boulva and McLaren 1979; Payne and Selzer 1989). In shallow nursery habitats, winter flounder are also vulnerable to the effects of high temperatures, hypoxia, and anthropogenic disturbances (Pereira et al. 1999; Meng et al. 2002; Taylor and Collie 2003; Gallagher et al. 2015). While all these stressors likely have some impact on survival during the early life cycle, it
remains unclear which are most important in regulating the productivity of individual subpopulations.

The spawning site fidelity and limited juvenile movements exhibited by this species make it possible to intensively study the cohorts of a single subpopulation on a tractable geographic scale. Therefore, this dissertation aims to investigate the role of climate in winter flounder productivity for the subpopulation in Narragansett Bay, Rhode Island by 1) modeling the early life history dynamics of winter flounder and identifying factors contributing to juvenile mortality, 2) projecting future winter flounder abundance to evaluate the recovery potential of this subpopulation under different environmental conditions, and 3) characterizing patterns of habitat use throughout the life cycle and determining if changes in the spatiotemporal distribution have coincided with, or potentially contributed to, the population decline. The first chapter combines datasets from multiple fisheries-independent surveys to construct a structural equation model of the winter flounder life cycle and investigate patterns of mortality. The second chapter uses the fitted structural equation model, in conjunction with temperature projections from global climate models and other environmental data, to project winter flounder abundance under possible future conditions. Finally, the third chapter uses the same winter flounder datasets in a spatial context to construct spatiotemporal conditional autoregressive models of habitat use patterns at different life stages to identify trends and investigate their potential causes.

REFERENCES


Detecting Population Regulation of Winter Flounder from Noisy Data

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Keywords: climate change, density dependence, key-factor analysis, measurement errors, recruitment, structural equation modeling, winter flounder

Publication status: in revision in Canadian Journal of Fisheries and Aquatic Sciences
ABSTRACT

Year-class size of marine fish is thought to be determined during the first year of life, with density-dependent mortality during the larval or juvenile stages. However, investigations of such dynamics are often limited by data availability. To test this paradigm for winter flounder (*Pseudopleuronectes americanus*) in Narragansett Bay, Rhode Island, the abundances of 29 year classes moving through seven life stages, from egg to age-2, were analyzed with a novel extension of key-factor analysis. Evidence of density dependence was identified between the egg and July young-of-the-year stages and high process-error variance was detected throughout the life cycle, indicating year-class size may not be fully determined until age-2. However, the first summer appeared to be a critical life stage for winter flounder, during which high temperatures, hypoxia, and predator abundance contributed to increased mortality rates behind a long-term population decline. Due to its general data requirements, the key-factor analysis method developed here may be applied to other marine populations to identify the impacts of external stressors at particular life stages and the degree to which they are compensated by density-dependent processes.
INTRODUCTION

Population fluctuations arise from the interplay of density dependence, environmental forcing, and demographic stochasticity (Bjornstad and Grenfell 2001). Population growth and mortality rates are affected by a suite of density-dependent and density-independent processes acting at different stages of the life cycle. Density-independent processes generally increase the inter-annual variance in cohort abundance (variance generating or controlling) whereas compensatory density-dependent processes reduce variance (variance damping or regulating) (van der Veer et al. 2000; Minto et al. 2008). The strength of density-dependent compensation determines a population’s resilience to perturbations, including those of human origin. It is therefore important to identify and partition density-dependent and density-independent processes. Estimating the strength of density dependence is especially important in managing pest populations and for conserving fish and wildlife species.

For populations with stage-specific abundance data measured over time, it is possible to estimate the corresponding stage-specific mortality rates. Key-factor analysis uses the variance structure of the mortality rates to identify the life stages contributing most to changes in population abundance and population stability (Manly 1990). Stage-specific mortality rates may also be regressed against abundance at the beginning of the stage to test for density dependence, where the stages with density-dependent mortality are often different from the key factors (Manly 1990). There have been several recent applications of key-factor analysis to a number of plant and animal species for which detailed stage-specific abundance data have been collected (e.g. Yukawa et al. 2016, 2018; Takeshita et al. 2018). However, several sampling and
statistical problems hinder the routine application of key-factor analysis, particularly in difficult-to-sample marine populations. The different life-history stages must often be collected with different types of samplers, which for highly dispersed marine populations can entail a prohibitive amount of sampling effort. Secondly, the data must be of sufficient duration to cover a range of population levels and environmental regimes (Hassell et al. 1989). A more serious statistical problem is that errors in estimating stage-specific abundance can bias the conclusions of a key-factor analysis (Podoler and Rogers 1975; Freckleton et al. 2006).

Measurement errors are pervasive in ecological studies, but their magnitude is often unknown. One approach is to use the sample variability to approximate the measurement-error variance at each life stage (Myers and Cadigan 1993). The basis of this approach is to formulate an expected variance-covariance matrix of the stage-specific abundances, as a function of density-dependent mortality, process noise, and measurement errors. This predicted matrix is compared with the observed variance-covariance matrix, with parameters estimated to minimize the difference. With data from 11 to 19 cohorts, Myers and Cadigan (1993) were able to obtain adequate fits of this model to data on two stages of juvenile marine fish, with relatively unbiased parameter estimates. This method was also used to demonstrate density-dependent mortality in juvenile Atlantic cod on the Norwegian coast (Fromentin et al. 2001). State-space models can be used to estimate stage-specific mortality rates, while accounting for measurement and process errors (e.g. Maunder and Deriso 2011; Stige et al. 2019; Zhang et al. 2020), but often require the estimation of additional parameters relative to a model of the variance-covariance matrix alone.
Demographic studies of marine fish species focus on recruitment of young fish to the mature or harvestable population (Myers 2001). According to the generally accepted paradigm, cohort size (year-class strength) is determined sometime during the first year of life. Mortality during the egg and early larval stages is thought to be mainly density-independent (variance generating) with density-dependent regulation occurring during larval settlement or in the juvenile stages (variance damping) (Houde 1987; van der Veer et al. 2000; Stige et al. 2019). However, stage-specific data to test this paradigm are rare, and several of the best examples are for anadromous fish because the freshwater life stages are more readily sampled than marine fish larvae (e.g. Elliott 1993). In the few examples of marine fishes, there is evidence of key factors (Bailey et al. 1996) and density-dependent mortality (Myers and Cadigan 1993; Bailey et al. 1996; DeLong et al. 2001; Fromentin et al. 2001; Stige et al. 2019) during the larval and juvenile stages. The general paradigm is therefore mostly supported, but the key factors in some species may extend to the juvenile life stage(s) as a result of year-class strength not being fully determined until later in life (Sissenwine 1984; Bogstad et al. 2016).

*Pseudopleuronectes americanus* (Walbaum), the winter flounder, is a good candidate for detecting population regulation. Winter flounder spawn in shallow bays, estuaries, and the coastal ocean (Pereira et al. 1999; Fairchild et al. 2013; Fairchild 2017; Siskey et al. 2020) and tagging studies have shown that adult flounder exhibit fidelity to spawning areas (Saila 1961). Demersal eggs are spawned during winter and spring, peaking between February and March, and hatch in 15-18 days (Pereira et al. 1999; Collette and Klein-MacPhee 2002). The larval stage lasts about 60 days, after
which the juveniles settle to shallow nursery areas. Juvenile winter flounder are thought to reside near to where they were spawned (Pearcy 1962; Taylor et al. 2016). Around age-2 the flounder may commence a seasonal migration, moving offshore to cooler water in the summer and onshore during the winter, where spawning commences at age-2 or 3 (Pereira et al. 1999). However, recent research suggests that resident contingents within winter flounder populations may remain close to their spawning habitats throughout the year (Sagarese and Frisk 2011; Ziegler et al. 2019). The discrete nature of winter flounder populations makes it possible to follow cohorts during their early life history (Pearcy 1962). Sources of mortality at the egg (Taylor and Danila 2005), larval (Keller and Klein-MacPhee 2000), and juvenile stages (Taylor and Collie 2003; Manderson et al. 2006) have been well studied and are known to vary with environmental conditions (DeLong et al. 2001; Bell et al. 2014). Given their dependence on estuarine and coastal habitats, winter flounder are also particularly sensitive to human impacts, such as power plants and discharge from waste-water treatment facilities.

The objective of this study is to identify the life stages that regulate the abundance of winter flounder in Narragansett Bay, a highly productive, large estuary located in southern New England, USA. Winter flounder are distributed throughout the Bay, with highest densities in the northern reaches including the Providence River and Mt. Hope Bay, a small embayment in the northeast corner of Narragansett Bay (Fig. 1-1). Formerly one of the most abundant demersal fish species in the Bay, winter flounder has declined to very low levels (Collie et al. 2008; Gibson 2013). Although stringent measures have been taken to reduce fishing mortality, the population has not
recovered as expected and has led to speculation at the regional level that additional mortality during the early life cycle is to blame (Northeast Fisheries Science Center 2011). To investigate the causes of this decline, we extend the methodology of Myers and Cadigan (1993) and Fromentin et al. (2001) to include additional life stages. The analysis partitions the total variance in stage-specific abundance into components due to density dependence, random environmental fluctuations, and measurement error. The results are interpreted to identify the life-stages that contribute most to population regulation and the stages that contribute most to variability in mortality during the two-year juvenile period. Furthermore, we test whether the stage-specific mortality rates can be explained with a set of environmental variables including abiotic factors (e.g. temperature), anthropogenic impacts, and predator abundance.

MATERIAL AND METHODS

Data Sources

The life-stage data for winter flounder come from several standardized research surveys, whose sampling procedures are summarized in Table 1-S1. From 1979 to 2016, the mean abundance and measurement error of the larval stage was recorded from weekly sampling conducted by Normandeau Associates, Incorporated (NAI, Bedford, NH) in Mt. Hope Bay (Fig. 1-1). The Rhode Island Department of Environmental Management (RIDEM), Division of Marine Fisheries (DMF), has since 1988 conducted a beach-seine survey, which samples the age-0 (or young-of-the-year, YOY) stage at 15 fixed stations throughout Narragansett Bay, in June, July, August, September and October each year. Because not all individuals in a cohort are settled to the bottom in June (DeLong et al. 2001) we used the July and October samples to
represent the start and end of the first summer. Based upon the length-at-age information reported by Gibson (2013) and Taylor et al. (2016), captured individuals of at least 11 cm in total length were assumed to be from the prior year class and removed.

Randomized, depth-stratified otter trawl surveys have been performed in the spring and autumn since 1979 by the DMF and all winter flounder caught have been measured to the nearest centimeter. Relative abundance indices for age-1 in the autumn and age-1 and age-2 in the spring were extracted from the length-frequency data with a Gaussian mixture model. Specifically, the length-frequency data for spring and autumn of each year were log-transformed and a three-component mixture model, representing ages 0-2+ in autumn and 1-3+ in spring, was fit for the aggregated 1979-2018 data for each season using the “mixtools” package (Benaglia et al. 2009) in R (R Core Team 2020). Here, it was assumed that the component variances were approximately equal on the log scale, corresponding to a lognormal distribution of length-at-age, as commonly assumed in growth models (Minto et al. 2018) and in agreement with observations of approximately lognormally distributed length frequencies in juvenile winter flounder in Narragansett Bay (Taylor et al. 2016). Due to the low number of flounder captured after 2000, model estimation of the mean sizes-at-age and mixing proportions could not be performed for individual years. Instead, model fits of individual years only estimated the mixing proportions while assuming the mean sizes-at-age were equal to the means estimated by a mixture model fit to the full time series, thus accounting for differences in relative abundance among age classes in a given year. Each individual fish captured by the DMF seasonal
surveys was then assigned proportionally among the age classes in that season based upon the probabilities of belonging to each group by the year-specific mixture model fits. The time series mean estimated total lengths-at-age are summarized in Table 1-S2.

A yearly index of egg abundance was estimated from the spring survey length-frequency data using published length-weight relationships and estimates of egg production by weight (Buckley et al. 1991), percent mature at length (O’Brien et al. 1993), and proportion female at length from the University of Rhode Island, Graduate School of Oceanography (URI-GSO) weekly trawl survey as in DeLong (2003). The mean log abundances for each stage were then standardized to the same density scale (number/100m² seafloor area). To test for changes in total mortality over time in the life stage transitions, relative interstage instantaneous mortality rates (Eq. 1) were calculated as the difference between the log abundances of adjacent stages and evaluated with linear regression.

The seine survey was used to measure abundance of age-0 winter flounder in the autumn because this stage was infrequently observed in the autumn DMF seasonal trawl survey. Abundances for winter flounder over age-1 in autumn and age-2 in spring were also excluded from further modeling due to the difficulty of assigning older individuals, which are more similar in size, to age classes. To corroborate the results found using the DMF trawl data, the same calculations were performed for the age-1+ and egg stages with data from the URI-GSO trawl survey. Because this survey is performed each week, the mean abundances of the spring and autumn life stages were assessed between April and July and between August and December,
respectively. The mean sizes at age estimated from the DMF data were used for the mixture models fit to individual years in the URI-GSO data. These alternative indices of abundance were then included in subsequent analyses to measure agreement with the result obtained using the DMF data.

**Structural Equation Models**

Mortality, $z_{s,y}$, is expressed as an instantaneous rate

$$N_{s+1,y} = N_{s,y} e^{-z_{s,y}}$$  

where $N_{s,y}$ is the abundance of stage $s$ in cohort $y$. Mortality rates between successive stages were estimated as the difference in the natural logarithm of observed abundances. Following the approach of Manly (1990) total mortality ($z_{s,y}$) was apportioned into mean, random and density-dependent components,

$$N_{s+1,y} = N_{s,y} e^{-\mu_s - (1-\lambda_s) \ln(N_{s,y}) + \epsilon_{s,y}}$$

where $\mu_s$ is the mean of the density-independent component of the mortality rate, $\lambda_s$ expresses density dependence, and the process error $\epsilon_{s,y}$, is the random component of mortality for cohort $y$, stage $s$ (Myers and Cadigan 1993; Fromentin et al. 2001).

Process errors are assumed to be independent, normally distributed random deviates with mean zero and variance $\psi_s$. The magnitude of $\lambda$ determines the nature of density dependence: $\lambda = 1$, $0 < \lambda < 1$ is compensatory density dependence, and $\lambda > 1$ is depensation. Taking the natural logarithm of both sides yields a linear equation

$$\ln(N_{s+1,y}) = -\mu_s + \lambda_s \ln(N_{s,y}) + \epsilon_{s,y}$$

The survey estimates of relative abundance, $\widehat{N}_{s,y}$, taken as the mean of the observed survey catches for stage $s$, cohort $y$, are related to true abundance in a state-
space framework with a model that accounts for measurement error and a scaling
factor that adjusts the relative abundance measures to absolute abundance. If we define
\( \hat{l}_{s,y} = \ln(\bar{N}_{s,y}) \), \( c_s \) to be the catchability of stage \( s \) relative to cohort abundance, and
\( \delta_{s,y} \) to be measurement error of stage \( s \) in cohort \( y \), then
\[
(4) \quad \hat{l}_{s,y} = \ln(\bar{N}_{s,y}) = c_s + \ln(N_{s,y}) + \delta_{s,y}
\]
It is assumed that the measurement errors are independent and normally
distributed with mean zero and variance \( \theta_s \) and that the \( \ln(N_{Eggs,y}) \) are independent
and normally distributed with variance \( \phi \). Abundance indices, estimated as the mean
of survey catches, are commonly assumed to have lognormally distributed error (e.g.
Fromentin et al. 2001); thus the \( \delta_{s,y} \) are normally distributed. The normality
assumptions allow for the use of structural equation modeling (Raykov and
Marcoulides 2000), which fits the model predicted \( \text{cov}(l_s, l_t) \) to the observed
\( \text{cov}(\hat{l}_s, \hat{l}_t) \); the model output includes estimates of the \( \lambda_s \), \( \phi \), and \( \psi_s \) and their standard
errors. Because the structural equation model is fit to the covariance structure of the
data, \( \mu_s \) (equation 3) and \( c_s \) (equation 4) were not estimated. Multivariate normality of
the abundance-at-stage data was verified with Mardia’s test using the “MVN” package
(Korkmaz et al. 2014) in R.

Measurement error variance for the log-abundance of the egg, YOY, age-1, and
age-2 stages was estimated from the sampling variability of the surveys using the delta
method as in (DeLong 2003), where \( n_{s,y} \) is the number of year classes in the data:
\[
(5) \quad \theta_{s,y} = \frac{1}{\bar{N}_{s,y}^2} \frac{\text{var}(N_{s,y})}{n_{s,y}}
\]
The mean of these estimated measurement error variances was then used in the structural equation model. The measurement error variance for the larval stage was taken from the confidence bounds around the abundances reported by NAI. To check the sensitivity of the model result to not fully accounting for estimation variability in the measurement error of the egg stage, a model variant was fit and compared in which the measurement error of the egg stage was doubled.

PROC CALIS (SAS 9.3) was used to fit the structural equation models. In two occurrences in which the mean catch for a cohort in a year was zero, the input value was set to one-half the lowest non-zero catch. Two diagnostics were used to measure model goodness of fit. The chi-squared, $\chi^2$, value indicates whether the observed covariance matrix of abundance indices does not deviate significantly from the one predicted by the model. The root mean square error of approximation (RMSEA) is an alternative index of the degree to which the model does not fit the data. A good fit was determined to be one in which the $\chi^2$ p-value was greater than 0.05 and the 90% RMSEA confidence interval included zero (Raykov and Marcoulides 2000).

Parameter values of the fitted model were used to identify the key factor(s) and to test for density-dependent mortality (DeLong 2003). The required quantities, $var(z_s)$, $var(z_{tot})$ and $cov(z_s, z_{tot})$, were calculated across years from the definition of $z_s$ (Eq. 1) and the variance-covariance matrix predicted by the unconstrained structural equation model of the $l_s$, where $z_{tot}$ is the total instantaneous mortality from Eggs to Spring age-2:

$$var(z_s) = var(l_s) + var(l_{s+1}) - 2cov(l_s, l_{s+1})$$

(6) $$var(z_{tot}) = var(l_{Eggs}) + var(l_{Spring\ age-2}) - 2cov(l_{Eggs}, l_{Spring\ age-2})$$
\[
cov(z_s, z_{tot}) = cov(l_s, l_{Eggs}) - cov(l_s, l_{Spring \ age-2}) - cov(l_{s+1}, l_{Eggs}) + cov(l_{s+1}, l_{Spring \ age-2})
\]

These variances and covariances were used to estimate the regression coefficient of the mortality rate for life-stage \( s \) and total mortality, \( \beta_s \), and the correlation between the mortality rate for life-stage \( s \) and total mortality, \( \rho_s \), as in Podoler and Rogers (1975):

\[
\beta_s = \frac{\text{cov}(z_s, z_{tot})}{\text{var}(z_{tot})} \quad \text{and} \quad \rho_s = \frac{\text{cov}(z_s, z_{tot})}{\text{sd}(z_s) \times \text{sd}(z_{tot})}
\]

(7)

These two tests for the key factor often yield the same ecological conclusions since they are mathematically similar. The value and standard error of the parameter \( \lambda_s \) was used to determine the significance (\( \lambda_s \neq 1 \)) of density-dependent mortality rates, with \( \lambda_s \) significantly different from 1 indicating density dependence. If the 95\% confidence interval for \( \lambda_s \) included one, mortality was considered density-independent and the parameter was fixed at one to increase parsimony (Run 1a). The Bayesian information criterion (BIC) was used to explore the effect of fixing parameters. The implemented SAS programs (Code 1-S1) are provided as supplementary materials.

**Environmental Factors**

We examined the correlation between these estimated mortality rates and several environmental factors that are potential stressors to winter flounder and for which time-series measurements are available (Table 1-1). The abiotic factors included water temperature, precipitation, discharge from waste-water treatment facilities, dissolved oxygen, salinity and Brayton Point power plant heat load and flow. Precipitation was included as a possible proxy for salinity or stratification, with the notion that
precipitation decreases salinity and increases stratification. Based upon laboratory experiments (Capuzzo et al. 1977) and suggestions from the fishing community, it is possible that high chlorine, or other components of effluent, discharge from wastewater treatment may induce high winter flounder mortality events.

The available biotic factors included fishing mortality and abundance of winter flounder predators. Although juvenile winter flounder are not targeted by commercial fishermen, it is likely that by-catch is related to fishing effort or mortality. Striped bass (*Morone saxitalis*), bluefish (*Pomatomus saltatrix*), summer flounder (*Paralichthys dentatus*), striped sea robin (*Prionotus evolans*) (Manderson et al. 1999; Sagarese et al. 2011), harbor seals (*Phoca vitulina*) (Boulva and McLaren 1979; Payne and Selzer 1989) and double-crested cormorants (*Phalacrocorax auritus*) (Pilon et al. 1983) are considered predators of winter flounder. For some of these environmental variables, several different measures were considered (Table 1-1).

Additional model runs (Runs 2a-c) were conducted to determine those environmental variables that best predict (correlate with) winter flounder mortality rates. The effects of environmental variables were tested by incorporating them into the structural equation models. This direct approach avoids potential problems of post-hoc analyses. Environmental covariates were selected based on a priori hypotheses of which life stages they were likely to affect and the anticipated direction of the effect. For example, winter flounder mortality would not be expected to be negatively correlated with discharge from wastewater treatment plants. Inclusion of a significant covariate is expected to reduce the unexplained process error for that stage. Variables were included via forward selection if their coefficient was significantly different from
zero and in its a priori hypothesized effect direction. The values of $\lambda_s$ were reassessed after the inclusion of the selected environmental variables to determine if they indicated density dependence or could be fixed at one. To test for consistency across data sets, the selected model based upon the DMF trawl data (Run 2a) was refit using the URI-GSO data (Run 2c) for comparison.

RESULTS

Patterns in Life Stage Abundance

Declining trends in abundance are apparent for all life stages in Narragansett Bay (linear regressions, $p < 0.05$; Fig. 1-2). However, the rate of decline was less severe for the Larvae and July YOY stages than for the stages beginning with October YOY; the decline was steepest for the Spring age-2 stage, suggesting additional sources of mortality may be present. Stronger and weaker year classes are visible in the data, especially from the YOY through age-2 stages, which confirms that the different surveys are sampling the same cohorts of winter flounder. For example, the 1992 and 2004 cohorts were of relatively high abundance and the 1991 and 2010 cohorts were of relatively low abundance at most of the life stages (Fig. 1-2). Supporting this pattern, an increase in correlation strength among adjacent life stages was detected during the first summer (Fig. 1-3). This period therefore clarified the apparent strength of year classes in the data as they entered the second year of life (Spring age-1 to Spring age-2, Fig. 1-3). Trends in total interstage mortality rates were observed for two transitions in the DMF data (linear regression, $p < 0.05$): mortality increased over time between July YOY and October YOY and between Autumn age-1 and Spring age-2. In the URI-GSO data, however, total interstage mortality appeared to decrease
over time between Autumn age-1 and Spring age-1 and increase between October YOY and Spring age-1 2 (linear regression, p < 0.05). Due to the disagreement in mortality trends among the older life stages between the two trawl survey datasets, clear evidence of increasing mortality was only present during the first summer (Fig. 1-4).

**Structural Equation Models**

The measurement-error variance in the observed abundance indices was lowest for the Larvae and of a similar magnitude for the remaining stages based on seine- and trawl-survey data (Table 1-2). The baseline model revealed significant density-dependent mortality during the Eggs – Larvae and marginal density-dependent mortality during the Larvae – July YOY stage transitions (Table 1-3). There was no evidence of density dependence in the subsequent life stages until Autumn age-1; where the estimated λ indicated depensation between this stage and Spring age-2. Process-error variances were large throughout the life cycle, with the maximum value occurring during the Autumn age-1 – Spring age-2 transition. The regression (βs) and correlation (ρs) coefficients were highest for the first (Eggs – Larvae) and last (Autumn age-1 – Spring age-2) life stage transitions and lacked a clear pattern in the intermediate stages. These results identify the boundary life stage transitions as key factors. Run 1b addressed concerns that measurement error in the egg stage (θ_{Eggs}) was underestimated due to unaccounted estimation error. Doubling this parameter slightly increased λ_{Eggs} and slightly decreased \( \psi_{Eggs-Larvae} \) without significantly changing the model fit (Table 1-4).
Environmental Factors

Four environmental factors (Fig. 1-5) were found to have relationships with the mortality rates in two early life stage transitions (Table 1-4, Run 2a). The April-June catch-per-tow of striped searobin in the URI-GSO trawl survey was associated with increased mortality in the Larvae – July YOY transition. The remainder of the environmental factors acted during the first summer; there was no evidence to suggest that collinearity among them may be impacting interpretation. Mortality between the July YOY and October YOY stages was positively related to the summer (July - September) mean sea surface temperature recorded by the URI-GSO trawl survey and the number of double-crested cormorant nesting pairs counted by RIDEM and negatively related to the minimum late spring – summer monthly mean dissolved oxygen recorded by NAI in central Mt. Hope Bay. No environmental factors were identified as having a significant relationship with mortality in any of the older life stages.

The structural equation model fit described in Run 2a indicated that the inclusion of environmental covariates significantly reduced the July YOY – October YOY process error but did not impact the suggested depensation between the Autumn age-1 and Spring age-2 life stages. Setting \( \lambda_{\text{Autumn age-1}} \) to one (i.e. assuming no density dependence) resulted in a good model fit based upon the RMSEA and \( \chi^2 \) statistics, but caused a slight increase in the BIC and a higher process error for the Autumn age-1 – Spring age-2 transition (Run 2b). When the model described by Run 2a was fit using the URI-GSO trawl data for the life stages beginning at age-1 (Run 2c), similar results were achieved, despite high uncertainty during the first winter that appeared to prevent
a good model fit, and indicate the identified dynamics are generally robust to decisions regarding which indices of abundance to use. There were two noteworthy deviations between Runs 2a and 2c. First is in the estimates of $\lambda_{\text{Autumn age-1}}$, where the fitted value of 0.48 obtained when using the URI-GSO data suggests compensation during this life stage transition. Depensatory density dependence is unlikely in marine fish populations (Perälä and Kuparinen, 2017) and, given the divergent estimates of $\lambda_{\text{Autumn age-1}}$ and opposing trends in estimated mortality between datasets, as well as the large process errors estimated for this life stage transition, there is insufficient evidence in these data to conclude density-dependent dynamics exist between Autumn age-1 and Spring age-2 winter flounder in Narragansett Bay. Second was in the statistical significance of summer surface temperature between the July YOY and October YOY stages, where a significant negative coefficient was estimated in Run 2a and an insignificant coefficient was estimated in Run 2c. Given that a linear regression representing this life stage transition found a significant ($p < 0.05$) coefficient that was insignificantly different from the estimate in Run 2a, we conclude that summer temperature likely plays a significant role in mortality and the estimate in Run 2c may have been impacted by the high uncertainty in adjacent life stages. In summary, Runs 2b and 2c generally provide alternate and consistent structural equation models for winter flounder with environmental covariates.

**DISCUSSION**

In this study we extended the methodology developed by Myers and Cadigan (1993) and applied by (Fromentin et al. 2001) from two to multiple life-stages to identify the key life-history stages in one of the most intensively studied marine
species in the world. This partitioning of mortality into its density-dependent, deterministic and stochastic components could not be achieved with conventional techniques. The discrete-time, biological model is appropriate because it makes few assumptions about the dynamics of winter flounder beyond the mathematical form of the density-dependent relationship, the normality of the measurement and process errors and the stationarity of the parameters across the years studied. Model diagnostics (p-values, distribution of residuals, and RMSEA estimates) indicated good fits of realistic models to the observed data. We have found three results that are consistent with all the data and are robust to a reasonable range of assumptions. Firstly, density-dependent mortality appears to be most important between hatching and the end of the settlement period. We believe that evidence of density dependence so early may be due to an unusual aspect of winter flounder life-history: the eggs are demersal. With demersal eggs, there could be density-dependent effects related to predation (Keller and Klein-MacPhee 2000), for example by the sand shrimp, *Crangon septemspinosa* (Taylor and Danila 2005) that may extend into the larval stage (Taylor 2004). As suggested by Rose et al. (1996), we found evidence of density dependence during the settlement period, which may be associated with predation or competition for suitable habitat (Stige et al. 2019).

Secondly, the moderate rates of process-error variation throughout the life cycle suggests year class size is not fully determined before winter flounder join the spawning stock. This result is supported by the identification of key factors at the Eggs – Larvae and Autumn age-1 – Spring age-2 life stage transition. While it is possible that ageing error stemming from the use of a mixture model to assign flounder to life
stages contributed to the high uncertainty in later life stages, the similarity between the estimated total lengths-at-age (Table 1-S2) and recent stock assessments (Northeast Fisheries Science Center 2011) suggests it is unlikely to play a dominant role in the measured variability. Non-stationarity in the catchability and availability of the different life stages or shifts in spawning or movement phenology, if present, could also have contributed to the process errors and particularly in the more mobile life stages sampled by trawl surveys. While it is not possible to determine if such changes have caused the measurement errors to be underestimated from the available data, sensitivity runs of the structural equation models in which the measurement errors were increased resulted in nearly identical results.

The third item that we have identified is a stage transition during which total mortality has increased over time. Specifically, the July YOY – October YOY mortality rate increased by an average of approximately 0.06 per year, with a noteworthy increase after 2000 (Fig. 1-4), and appeared to be explained by several environmental factors. Though this life stage transition was not identified as a key factor due in part to high process variability throughout the life cycle, this mortality trend has likely played an important role in the population decline. There was also some evidence of increasing mortality during the Autumn age-1 – Spring age-2 transition, but high uncertainty and disagreement between the DMF and URI-GSO datasets prevented confidence in this conclusion. Winter flounder are thought to begin extensive seasonal movements at this age (Pereira et al. 1999), so it is also possible that what appears as mortality in the model may in fact be changing availability patterns. Other demersal fish species in Narragansett Bay, for example, have been
observed to have significantly shifted the timing of seasonal migrations in response to warming temperatures (Langan et al. 2021). If such a shift was occurring in winter flounder and resulting in declining availability of older life stages, it could mimic a decline in survival.

The results of this work were similar to the findings of an earlier analysis of Narragansett Bay winter flounder conducted by DeLong (2003). Both studies found evidence of compensatory density dependence early in the life cycle and an increasing trend in mortality, or decreasing trend in availability, between the Autumn age-1 and Spring age-2 life stages. Similarly, the Eggs – Larvae and Autumn age-1 – Spring age-2 life stages were mutually identified as potential key factors. DeLong (2003) also identified summer temperatures and cormorant predation as factors contributing to increased mortality during the early life stages. However, this past work came to different conclusions regarding the other environmental factors, including precipitation, discharge from wastewater treatment plants, predation by summer flounder, and fishing mortality, that play a role in mortality. The direct testing of covariates within the structural equation models and use of significantly longer time series in this work may explain the differences in the stressors identified as contributing to the population decline.

Our results generally agree with the paradigm of population regulation in marine fish species as elucidated by other studies of early life history. As with walleye pollock (Bailey et al. 1996), potential key factors were identified at a transition during the first year of life (between Eggs and Larvae) and between the late juvenile stages. Combined with the results of the structural equation model, this implies that year-class
strength is not fully determined until the end of the juvenile stage, which for winter flounder is age two. Density dependence during the egg-to-larval stage transition is atypical of most marine fish, and flatfish in general (Myers and Cadigan 1993), for which density dependence is usually strong in the post-larval juvenile stage when the fish settle to the bottom as was also found here. Although not reported in other fish species, there is evidence of density-dependent mortality during the egg-to-larval stage in both the Narragansett Bay and Niantic River winter flounder populations (Dominion Resources Services Inc. 2004). While the larval data were collected in Mt. Hope Bay, they appear to be representative of the entire Bay in that they follow the general trend of the YOY summer data (Fig. 1-3). It is also possible that the apparent density dependence between the egg and larval stage stems from the estimation of egg abundance from observations of the spawning stock. If, for example, a change in availability of spawning winter flounder was responsible for the apparent increasing trend in mortality observed in the Autumn age-1 – Spring age-2 transition, the egg abundance would be underestimated. In this case, more larvae would be observed than would be expected from the estimated egg abundance and thus there would appear to be compensation during this life stage transition. Because the demersal eggs of winter flounder are very difficult to sample, it is not possible to fully investigate the accuracy of the egg abundance estimates made here and thus the model results at this stage should be viewed with some caution. Nevertheless, our results identify the Eggs – Larvae and Autumn age-1 – Spring age-2 transitions as the key factors for this population.
Predation is an important source of juvenile mortality (van der Veer et al. 2000). Several potential predators of winter flounder—striped bass, summer flounder, striped searobin, seals, and cormorants—have increased in abundance in Narragansett Bay. Our finding of a significant relationship between striped searobin abundance and winter flounder mortality during settlement is consistent with several studies from New Jersey and Narragansett Bay, which indicated this species consistently consumes winter flounder at this life stage (Manderson et al. 2006; Heinichen, M., Unpubl. data). Double-crested cormorants are also known to prey upon winter flounder during the first two years of life (Pilon et al. 1983). Historically, Rhode Island was a migratory stopover for cormorants, but since 1981 a breeding population has been established (French Mccay and Rowe 2004). Based on these results, it appears high predation has likely contributed to the decline, and could retard the recovery, of the winter flounder population.

Both water temperature and dissolved oxygen were correlated with mortality of winter flounder during the first summer, consistent with the known environmental vulnerability of this relatively immobile life stage that relies upon shallow nursery habitats (Saucerman and Deegan 1991; Pereira et al. 1999; Taylor et al. 2016). Previous work shows that YOY winter flounder avoid temperatures above 25°C and oxygen levels below 4.0 mg/L (Taylor et al. 2016). Data from the DMF seine survey, which began recording dissolved oxygen in 1995, indicate both thresholds are increasingly often breached during the summer months in the shallow waters of upper Narragansett Bay. Furthermore, it can be expected that summer water temperatures and the frequency and severity of hypoxic events will increase in the future due to
climate change (Paerl 2006; Oviatt et al. 2017). It is difficult to project future changes in these hypoxic events, however, because dissolved oxygen in Mt. Hope Bay did not display a significant correlation with summer temperature in this study, possibly due to changes in Narragansett Bay water quality in recent decades (Oviatt et al. 2017). These physical factors may also have synergistic effects with other causes of mortality. For example, it has been shown that high temperatures and low oxygen levels can slow growth of juvenile winter flounder (Pereira et al. 1999; Taylor and Collie 2003; Gallagher et al. 2015). As rising temperatures result in the increased abundance and residence of warm-water fish predators (Collie et al. 2008; Langan et al. 2021), slower growth may leave juvenile winter flounder more vulnerable to predation by a wider range of species for a greater duration. Finally, there was no evidence that fishing activities significantly contributed to juvenile mortality in this winter flounder population. Given that life stages prior to recruitment to the fishery were the focus of this study, it is possible that the discard mortality rates of juvenile flounder are not strongly correlated with the estimated fishing mortality rate estimated for older ages that was available for testing within the model framework.

CONCLUSIONS

In the past, key-factor analyses have been difficult to perform on marine populations because different life-stages are located in different hydrographic and geographic areas and are sampled by different surveys with different gear types; it was difficult (or impossible) to accurately scale these survey indices of abundances to one another to calculate mortality rates. The method used here, which combines classic key-factor analysis techniques with structural equation modeling to yield greater
insights into population dynamics, is based on the covariance structure among stage-specific abundances and does not require absolute mortality rates. The generality of the data requirements should make this method applicable to other fish and wildlife populations. The main requirement is that measurement-error variances can be estimated from the sampling variability or that multiple survey indices are available (Myers and Cadigan 1993) for each life-history stage. Further developments of this measurement-error methodology will include alternate formulations of density dependence (Bjornstad and Grenfell 2001) and state-space models that allow the stage-specific mortality rates to be estimated (Zhang et al. 2020).

ACKNOWLEDGEMENTS

We thank Chris Powell and Tim Lynch at the RIDEM and Mike Scherer at Normandeau Associates, Inc. for the providing us with survey data and details of the sampling methodology. Allison K. Delong conducted an earlier analysis of these data based on year classes up to 1999, with assistance from Richard Bell, Choudary Hanumara, and Mark Gibson. Ransom A. Myers conceived the study and contributed to an earlier draft of the manuscript. This project was made possible through funding from the RI Department of Environmental Management, Project No. P0200696 and RI Sea Grant project number 2016-R/F-1618-31-2-RES. This paper is a contribution of the RI Marine Fisheries Institute.

REFERENCES


### TABLES

**Table 1-1.** List of potential winter flounder stressors and the hypothesized affected life stage and direction of effect.

<table>
<thead>
<tr>
<th>Stressor</th>
<th>Description of Measure</th>
<th>Stages Impacted, Effect Direction</th>
<th>Years Available</th>
<th>Data Source(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>Monthly/Seasonal minimum, mean, maximum</td>
<td>All, both</td>
<td>1979-2017</td>
<td>URI-GSO trawl survey</td>
</tr>
<tr>
<td>Precipitation</td>
<td>Number of days registering totals &gt;1”, 1.5”, 2”</td>
<td>All, both</td>
<td>1979-2017</td>
<td>NOAA National Centers for Environmental Information¹</td>
</tr>
<tr>
<td>Dissolved oxygen</td>
<td>Minimum spring – summer monthly mean</td>
<td>All, both</td>
<td>1985-2017</td>
<td>NAI trawl survey</td>
</tr>
<tr>
<td>Salinity</td>
<td>Monthly/Seasonal minimum, mean</td>
<td>All, both</td>
<td>1982-2017</td>
<td>DMF seine survey</td>
</tr>
<tr>
<td>Brayton Point Power Station</td>
<td>Mean monthly water flow, sum total heat load</td>
<td>All, negative</td>
<td>1980-2017</td>
<td>NAI</td>
</tr>
<tr>
<td>Seal predation</td>
<td>Number of strandings per year</td>
<td>YOY, negative</td>
<td>1980-2017</td>
<td>Mystic Aquarium</td>
</tr>
<tr>
<td>Cormorant predation</td>
<td>Number of nests recorded, sum of daily abundance</td>
<td>YOY to Autumn Age-1, negative</td>
<td>1980-2017</td>
<td>Chris Raithel (RIDEM)</td>
</tr>
<tr>
<td>Finfish predator abundance</td>
<td>Monthly number per tow</td>
<td>YOY to Autumn Age-1, negative</td>
<td>1979-2017</td>
<td>URI-GSO trawl survey, DMF trawl survey; MRIP²</td>
</tr>
<tr>
<td>Chemical discharge</td>
<td>Seasonal mean biochemical oxygen demand, total suspended solids, total residual chlorine, fecal coliform bacteria concentration</td>
<td>All, negative</td>
<td>1989-2017</td>
<td>Angelo Liberti (RIDEM)</td>
</tr>
</tbody>
</table>

¹Theodore Francis Green Memorial State Airport Station (https://www.ncdc.noaa.gov/cdo-web/datasets/GSOM/stations/GHCND:USW00014765/detail)

²Rhode Island catch data, Marine Recreational Information Program (MRIP) (https://www.fisheries.noaa.gov/topic/recreational-fishing-data)
Table 1-2. Mean and variance of stage-specific abundance data for Narragansett Bay winter flounder. $\hat{I}_s$ is the logarithm of observed abundance; $\bar{n}$ is the mean number of samples per year, and $\theta_s$ is the estimated mean measurement error variance. The mean number of annual samples of the larval stage is approximate based upon the documented sampling protocol. YOY refers to young-of-the-year life stages.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Mean $\hat{I}_s$</th>
<th>var($\hat{I}_s$)</th>
<th>$\bar{n}$</th>
<th>$\theta_s$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eggs</td>
<td>8.62</td>
<td>1.28</td>
<td>25.8</td>
<td>0.14</td>
</tr>
<tr>
<td>Larvae</td>
<td>4.67</td>
<td>0.59</td>
<td>17.9</td>
<td>0.02</td>
</tr>
<tr>
<td>July YOY</td>
<td>0.65</td>
<td>0.95</td>
<td>15.1</td>
<td>0.23</td>
</tr>
<tr>
<td>October YOY</td>
<td>-1.27</td>
<td>1.64</td>
<td>15.7</td>
<td>0.22</td>
</tr>
<tr>
<td>Spring age-1</td>
<td>-4.08</td>
<td>1.49</td>
<td>25.8</td>
<td>0.18</td>
</tr>
<tr>
<td>Autumn age-1</td>
<td>-4.12</td>
<td>1.52</td>
<td>26.0</td>
<td>0.15</td>
</tr>
<tr>
<td>Spring age-2</td>
<td>-5.38</td>
<td>3.90</td>
<td>25.8</td>
<td>0.22</td>
</tr>
</tbody>
</table>
Table 1-3. Parameter estimates from the fully parameterized base-line model for Narragansett Bay winter flounder: $\lambda$ is the density-dependent term, $\beta$ is the regression coefficient, $\rho$ is the correlation coefficient, and $\phi$ is the variance in egg abundance. Measurement-error variances ($\theta$) were input from Table 2. YOY refers to young-of-the-year life stages. Values of $\lambda$ in italics were fixed because the initial estimates were not significantly different than 1. The calculations of $\beta$ and $\rho$ were performed using an unconstrained model in which all $\lambda$ values were estimated. The estimated variance of abundance during the Eggs stage, $\phi$, was 1.14.

<table>
<thead>
<tr>
<th>Stage</th>
<th>$\lambda$</th>
<th>$se(\lambda)$</th>
<th>$\psi$</th>
<th>$var(z_i)$</th>
<th>$cov(z_i,z_{tot})$</th>
<th>$\beta$</th>
<th>$\rho$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eggs – Larvae</td>
<td>0.33</td>
<td>0.13</td>
<td>0.45</td>
<td>1.12</td>
<td>1.03</td>
<td>0.22</td>
<td>0.45</td>
</tr>
<tr>
<td>Larvae – July YOY</td>
<td>0.58</td>
<td>0.21</td>
<td>0.51</td>
<td>0.86</td>
<td>0.56</td>
<td>0.12</td>
<td>0.28</td>
</tr>
<tr>
<td>July YOY – October YOY</td>
<td>1.00</td>
<td>-</td>
<td>0.53</td>
<td>1.05</td>
<td>0.63</td>
<td>0.13</td>
<td>0.29</td>
</tr>
<tr>
<td>October YOY – Spring age-1</td>
<td>1.00</td>
<td>-</td>
<td>0.31</td>
<td>0.82</td>
<td>0.21</td>
<td>0.05</td>
<td>0.11</td>
</tr>
<tr>
<td>Spring age-1-Autumn age-1</td>
<td>1.00</td>
<td>-</td>
<td>0.44</td>
<td>0.80</td>
<td>0.43</td>
<td>0.09</td>
<td>0.22</td>
</tr>
<tr>
<td>Autumn age-1-Spring age-2</td>
<td>1.41</td>
<td>0.16</td>
<td>0.81</td>
<td>1.46</td>
<td>1.85</td>
<td>0.39</td>
<td>0.71</td>
</tr>
<tr>
<td>Eggs – Spring age-2</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>4.71</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 1-4. Summary of additional structural equation models fit to Narragansett Bay winter flounder, where the model defined in Table 3 is included as Run 1a. Run 1b is the same as 1a except that the egg measurement error was doubled. Run 2b is the same as Run 2a except that $\lambda_{Autumn\ age-1}$ was fixed at 1. Italicized values were fixed at 1; blank cells indicate parameters that were not included in the model. The Bayesian Information Criterion can be compared among runs with the same number. The subscripts of the regression coefficients ($\gamma$) refer to the following covariates: Searobin catch: April-June catch-per-tow of striped searobin, Summer ST: summer (July-September) surface temperature in Narragansett Bay, Dissolved oxygen: minimum summer monthly mean dissolved oxygen recorded in Mt. Hope Bay.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Run 1a</th>
<th>Run 1b</th>
<th>Run 2a</th>
<th>Run 2b</th>
<th>Run 2c</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\lambda_{Eggs}$</td>
<td>0.33</td>
<td>0.38</td>
<td>0.35</td>
<td>0.35</td>
<td>0.34</td>
</tr>
<tr>
<td>$\lambda_{Larvae}$</td>
<td>0.58</td>
<td>0.58</td>
<td>0.30</td>
<td>0.30</td>
<td>0.33</td>
</tr>
<tr>
<td>$\lambda_{July\ YOY}$</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>$\lambda_{October\ YOY}$</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>$\lambda_{Spring\ age-1}$</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>$\lambda_{Autumn\ age-1}$</td>
<td>1.41</td>
<td>1.41</td>
<td>1.41</td>
<td>1.00</td>
<td>0.48</td>
</tr>
<tr>
<td>$\gamma_{Eggs-Larvae}$</td>
<td>0.45</td>
<td>0.43</td>
<td>0.43</td>
<td>0.43</td>
<td>0.45</td>
</tr>
<tr>
<td>$\gamma_{Larvae-July\ YOY}$</td>
<td>0.51</td>
<td>0.51</td>
<td>0.30</td>
<td>0.30</td>
<td>0.40</td>
</tr>
<tr>
<td>$\gamma_{July\ YOY-October\ YOY}$</td>
<td>0.53</td>
<td>0.53</td>
<td>0.04</td>
<td>0.04</td>
<td>0.13</td>
</tr>
<tr>
<td>$\gamma_{October\ YOY-Spring\ age-1}$</td>
<td>0.31</td>
<td>0.31</td>
<td>0.31</td>
<td>0.31</td>
<td>1.48</td>
</tr>
<tr>
<td>$\gamma_{Spring\ age-1-Autumn\ age-1}$</td>
<td>0.44</td>
<td>0.44</td>
<td>0.40</td>
<td>0.45</td>
<td>0.33</td>
</tr>
<tr>
<td>$\gamma_{Autumn\ age-1-Spring\ age-2}$</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>1.14</td>
<td>0.99</td>
</tr>
<tr>
<td>$\gamma_{Searobin\ catch}$</td>
<td>-0.17</td>
<td>-0.17</td>
<td>-0.17</td>
<td>-0.17</td>
<td></td>
</tr>
<tr>
<td>$\gamma_{Summer\ ST}$</td>
<td>-0.59</td>
<td>-0.59</td>
<td>0.14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\gamma_{Dissolved\ oxygen}$</td>
<td>0.34</td>
<td>0.34</td>
<td>0.43</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\gamma_{Cormorants}$</td>
<td>-0.85</td>
<td>-0.86</td>
<td>-1.07</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIC</td>
<td>66.17</td>
<td>66.17</td>
<td>143.13</td>
<td>144.19</td>
<td>188.52</td>
</tr>
<tr>
<td>RMSE LB</td>
<td>0.07</td>
<td>0.07</td>
<td>0.00</td>
<td>0.00</td>
<td>0.18</td>
</tr>
<tr>
<td>$\chi^2$ p-value</td>
<td>0.02</td>
<td>0.02</td>
<td>0.11</td>
<td>0.06</td>
<td>0.00</td>
</tr>
</tbody>
</table>
Figure 1-1. Map of Narragansett Bay, Rhode Island, USA.
Figure 1-2. Relative abundance indices of Narragansett Bay winter flounder by life-stage and year class with 95% confidence intervals (gray) constructed from the estimated measurement error variances. The horizontal lines were placed at mean abundance and offset by 3 to minimize the overlap between series. The rate of decline (B) of log life stage abundance over time is given above each mean abundance line. The vertical dotted lines identify the 1991, 1992, 2004, and 2010 year classes discussed in the text.
Figure 1-3. Correlation structure among life stages of winter flounder in Narragansett Bay (1988–2016 year classes). Scatterplots of stage comparisons are shown in the upper triangle, where the red lines are loess smoothers with a span of 0.67. Pearson correlation coefficients are given in the lower triangle, where the font size is proportional to correlation strength.
Figure 1-4. Trends in observed instantaneous mortality rate for the July young-of-the-year (YOY) – October YOY life stage transition in the DMF trawl survey, the October YOY – Spring age-1 transition in the URI-GSO data, and the Autumn age-1 – Spring age-2 life stage transition in both the DMF and URI-GSO trawl surveys. Each time series was standardized to have a mean of zero to improve interpretability in light of catchability differences among life stages and surveys. The trend in each time series is denoted by a loess smoother (black) with a span 0.67.
Figure 1-5. Time series plots (1988-2016) of the three covariates identified as having a significant impact on mortality of winter flounder in Narragansett Bay.
SUPPLEMENTS

Table 1-S1. Summary of the methods employed in each of the research surveys from which data was accessed. RI DMF: Rhode Island Division of Marine Fisheries. URI-GSO: University of Rhode Island Graduate School of Oceanography.

<table>
<thead>
<tr>
<th>Survey</th>
<th>Targeted Life Stage(s)</th>
<th>Tow Characteristics</th>
<th>Net Dimensions</th>
<th>Mesh Size</th>
<th>Sampling Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normandeau Associates, Inc.</td>
<td>Larvae</td>
<td>Bottom-to-surface tow of a bongo net</td>
<td>60 cm opening</td>
<td>333 or 555 ( \mu )m</td>
<td>Weekly (every ( \leq 7 ) days) sampling of at least 5 stations from March-May</td>
</tr>
<tr>
<td>RI DMF seine survey</td>
<td>Young-of-the-Year</td>
<td>Beach seine net deployed by boat and retrieved from shore</td>
<td>61 x 3.1 m</td>
<td>0.64 cm</td>
<td>Monthly sampling of 15 stations</td>
</tr>
<tr>
<td>RI DMF trawl survey</td>
<td>Age-1+</td>
<td>Bottom trawl at 1.29 m/s for 20 minutes</td>
<td>6.7 m effective opening</td>
<td>0.6 cm mesh liner in codend</td>
<td>Seasonal sampling of 13 fixed stations and a varying number of depth-stratified random stations</td>
</tr>
<tr>
<td>URI-GSO trawl survey</td>
<td>Age-1+</td>
<td>Bottom trawl at 1.03 m/s for 30 minutes</td>
<td>6.5 m effective opening</td>
<td>5.1 cm in codend</td>
<td>Weekly at two stations</td>
</tr>
</tbody>
</table>
Table 1-S2. The time series mean total lengths estimated by the Gaussian mixture models for each age class. Note that only the Spring age-1 to Spring age-2 stages were included in structural equation modeling.

<table>
<thead>
<tr>
<th>Life Stage</th>
<th>Mean Total Length (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn age-0</td>
<td>8.5</td>
</tr>
<tr>
<td>Spring age-1</td>
<td>12.2</td>
</tr>
<tr>
<td>Autumn age-1</td>
<td>17.4</td>
</tr>
<tr>
<td>Spring age-2</td>
<td>19.1</td>
</tr>
<tr>
<td>Autumn age-2+</td>
<td>26.7</td>
</tr>
<tr>
<td>Spring age-3+</td>
<td>28.9</td>
</tr>
</tbody>
</table>
**Code 1-S1.** SAS Code used to fit the structural equation models.

```sas
data winterflounder;
    inFILE "c:\---\Data.csv" delimiter="," firstobs=2 dsd MISSOVER;
    input Year Eggs Larvae JulYOY OctYOY Sp1 Fl1 Sp2 summer DOC SRClar Cormorants;
    proc print;
    run;

    proc corr;
    proc corr cov;
    run;

    proc corr data=winterflounder nocorr nomiss cov noprint outp=cov(type=cov);
    title 'winter flounder';
    *;
    title3 "Run 1A";
    proc calis cov data=cov method=ml res se short;
    lineqs
        Eggs = f0 + e1,
        Larvae = f1 + e2,
        JulYOY = f2 + e3,
        OctYOY = f3 + e4,
```
Sp1 = f4 + e5,
Fl1 = f5 + e6,
Sp2 = f6 + e7,
f1 = l1 f0 + d1,
f2 = l2 f1 + d2,
f3 = f2 + d3,
f4 = f3 + d4,
f5 = f4 + d5,
f6 = l6 f5 + d6;

std

e1 = 0.14,
e2 = 0.02,
e3 = 0.23,
e4 = 0.22,
e5 = 0.18,
e6 = 0.15,
e7 = 0.22,
f0 = phi,
d1 = psi1,
d2 = psi2,
d3 = psi3,
d4 = psi4,
d5 = psi5,
d6 = psi6;
bounds
psi1>1E-8,
psi2>1E-8,
psi3>1E-8,
psi4>1E-8,
psi5>1E-8,
psi6>1E-8;
run;

title3 "Run 1B";
proc calis cov data=cov method=ml res se short ;
lineqs
   Eggs = f0 + e1,
   Larvae = f1 + e2,
   JulYOY = f2 + e3,
   OctYOY = f3 + e4,
   Sp1 = f4 + e5,
   Fl1 = f5 + e6,
   Sp2 = f6 + e7,
   f1 = l1 f0 + d1 ,
   f2 = l2 f1 + d2,
   f3 = f2 + d3,
\[ f_4 = f_3 + d_4, \]
\[ f_5 = f_4 + d_5, \]
\[ f_6 = l_6 f_5 + d_6; \]

\textit{std}
\[ e_1 = 0.28, \]
\[ e_2 = 0.02, \]
\[ e_3 = 0.23, \]
\[ e_4 = 0.22, \]
\[ e_5 = 0.18, \]
\[ e_6 = 0.15, \]
\[ e_7 = 0.22, \]
\[ f_0 = \phi, \]
\[ d_1 = \psi_1, \]
\[ d_2 = \psi_2, \]
\[ d_3 = \psi_3, \]
\[ d_4 = \psi_4, \]
\[ d_5 = \psi_5, \]
\[ d_6 = \psi_6; \]

\textit{bounds}
\[ \psi_1 \geq 1E-8, \]
\[ \psi_2 \geq 1E-8, \]
\[ \psi_3 \geq 1E-8, \]
\[ \psi_4 \geq 1E-8, \]
psi5 >1E-8,
psi6 >1E-8;
run;

title3 "Run 2A";
proc calis cov data=cov method=ml res se short ;
lineqs
  Eggs = f0 + e1,
  Larvae = f1 + e2,
  JulYOY = f2 + e3,
  OctYOY = f3 + e4,
  Sp1 = f4 + e5,
  Fl1 = f5 + e6,
  Sp2 = f6 + e7,
  f1 = l1 f0 + d1 ,
  f2 = l2 f1 + d2+B1 SRClar,
  f3 = f2 + d3 + B2 summer +B3 DOC +B4 Cormorants,
  f4 = f3 + d4,
  f5 = f4 + d5,
  f6 = l6 f5 + d6;
std
  e1 =0.14,
  e2 = 0.02,
\[ e_3 = 0.23, \]
\[ e_4 = 0.22, \]
\[ e_5 = 0.18, \]
\[ e_6 = 0.15, \]
\[ e_7 = 0.22, \]
\[ f_0 = \phi, \]
\[ d_1 = \psi_1, \]
\[ d_2 = \psi_2, \]
\[ d_3 = \psi_3, \]
\[ d_4 = \psi_4, \]
\[ d_5 = \psi_5, \]
\[ d_6 = \psi_6; \]

bounds
\[ \psi_1 > 1E-8, \]
\[ \psi_2 > 1E-8, \]
\[ \psi_3 > 1E-8, \]
\[ \psi_4 > 1E-8, \]
\[ \psi_5 > 1E-8, \]
\[ \psi_6 > 1E-8; \]

run;

title3 "Run 2B";

proc calis cov data=cov method=ml res se short ;
lineqs

Eggs = f0 + e1,
Larvae = f1 + e2,
JulYOY = f2 + e3,
OctYOY = f3 + e4,
Sp1 = f4 + e5,
Fl1 = f5 + e6,
Sp2 = f6 + e7,
f1 = l1 f0 + d1 ,
f2 = l2 f1 + d2 + B1 SRClar,
f3 = f2 + d3 + B2 summer + B3 DOC + B4 Cormorants,
f4 = f3 + d4,
f5 = f4 + d5,
f6 = f5 + d6;

std

e1 = 0.14,
e2 = 0.02,
e3 = 0.23,
e4 = 0.22,
e5 = 0.18,
e6 = 0.15,
e7 = 0.22,
f0 = phi,
d1 = psi1,
\[d2 = psi2,\]
\[d3 = psi3,\]
\[d4 = psi4,\]
\[d5 = psi5,\]
\[d6 = psi6;\]

bounds
\[psi1>1E-8,\]
\[psi2>1E-8,\]
\[psi3>1E-8,\]
\[psi4>1E-8,\]
\[psi5>1E-8,\]
\[psi6>1E-8;\]

run;

*********************************************************************
GSO Data*

data winterfloundergso;

   inFILE "c:\---\GSOData.csv" delimiter="", firstobs=2 dsd MISSOVER;

   input Year Eggs Larvae JulYOY OctYOY Sp1 Fl1 Sp2 summer DOC SRClar Cormorants;

proc corr;
proc corr cov;
run;

proc corr data=winterfloundergso nocorr nomiss cov noprint outp=cov(type=cov);
title 'winter flounder gso';

title3 "Run 2C";
proc calis cov data=cov method=ml res se short ;
lineqs

    Eggs = f0 + e1,
    Larvae = f1 + e2,
    JulYOY = f2 + e3,
    OctYOY = f3 + e4,
    Sp1 = f4 + e5,
    Fl1 = f5 + e6,
    Sp2 = f6 + e7,
    f1 = l1 f0 + d1 ,
    f2 = l2 f1 + d2+B1 SRClar,
    f3 = f2 + d3 + B2 summer +B3 DOC +B4 Cormorants,
    f4 = f3 + d4,
    f5 = f4 + d5,
    f6 = l6 f5 + d6;

std
e1 = 0.12,
e2 = 0.02,
e3 = 0.23,
e4 = 0.22,
e5 = 0.36,
e6 = 0.09,
e7 = 0.08,
f0 = phi,
d1 = psi1,
d2 = psi2,
d3 = psi3,
d4 = psi4,
d5 = psi5,
d6 = psi6;
bounds
psi1 > 1E-8,
psi2 > 1E-8,
psi3 > 1E-8,
psi4 > 1E-8,
psi5 > 1E-8,
psi6 > 1E-8;
run;
Taking stock: is recovery of a depleted population challenged by climate change possible?

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Keywords: climate change, depleted population, recovery, future temperature, winter flounder, fisheries management, life-cycle model

Publication status: in preparation for submission to Fisheries Oceanography
ABSTRACT

As the impacts of climate change become more severe throughout the global oceans, fisheries managers will be increasingly challenged to rebuild stocks exhibiting declining productivity. In such cases, detailed knowledge of species life history will be necessary to both restrict harvest and manage other environmental conditions, where possible, that impact survivorship. A current example of these challenges, the Southern New England/Mid-Atlantic Bight winter flounder stock remains in a persistently depleted state due to a combination of past harvest and the effects of climate change mediated through increased predation. To explore the recovery capacity of a subpopulation of this stock, a life-cycle model was fit to 29 year classes of stage-specific winter flounder data from surveys conducted in Narragansett Bay, Rhode Island and used to project future subpopulation abundance. Supporting a prevailing hypothesis, the results indicated that environmental factors influencing juvenile mortality were largely responsible for inhibiting recovery. Furthermore, recovery of the subpopulation to past levels of abundance was determined to be unlikely even under optimistic future conditions resulting from aggressive management interventions. Taken together, the findings of this work pose important questions regarding the realism of assessing climate-challenged populations against biological reference points set under past environmental regimes and the degree to which harvest restrictions to promote recovery of such stocks should be allowed to limit warm-water fisheries thriving in a warming ocean.
INTRODUCTION

Many studies have documented the poleward movement of marine species distributions due to rising temperatures, driven both by shifts in movement patterns and alterations in latitudinal gradients of productivity (Nye et al., 2009; Pinsky et al., 2020). While much focus has been placed on the poleward edge of such range expansions, the redistribution of commercially important species presents challenges for fisheries managers as abundance declines at the trailing edge. Though past research suggests the warm edges of species’ ranges may not track climate velocities as well as cold edges (Fredston-Hermann et al., 2020), several studies have documented a heightened sensitivity to competition and predation in these areas (Boudreau et al., 2015; Drinkwater, 2005) that can accelerate decreases in productivity and lead to rapid shifts in the biological community. Particularly in cases where potential regulations to recover populations of declining cold-water species would limit growing fisheries for warm-water taxa, managers are faced with difficult decisions in regulating evolving species portfolios (Szuwalski & Hollowed, 2016). Due to the expectation that the impact of continued climate change on marine ecosystems will make such tradeoffs more common, it is critical to develop methods to evaluate the recovery potential of climate-challenged species and regulatory frameworks to accommodate non-stationarity in stock productivity.

An example of a species in decline at the equatorward edge of its range, the winter flounder (*Pseudopleuronectes americanus*) is a coastal flatfish that has historically supported productive fisheries in the northwest Atlantic (Northeast Fisheries Science Center, 2011; Oviatt et al., 2003). The Southern New England/Mid-
Atlantic Bight stock, one of three managed stock units in US waters, has exhibited a decades-long decline in abundance despite repeated reductions in harvest (Northeast Fisheries Science Center, 2011, 2017, 2020). Previous research indicates that increased mortality during the early life cycle may be responsible for the lack of recovery (Keller & Klein-MacPhee, 2000). Winter flounder in this region spawn during winter in estuarine or coastal waters (Siskey et al., 2020), where winter temperatures may influence the duration of spawning and intensity of predation of eggs and larvae (Pereira et al., 1999; Taylor & Collie, 2003; Taylor & Danila, 2005). Even after juveniles settle to the seafloor, significant predation may occur (Manderson et al., 1999, 2006; Pilon et al., 1983; Sagarese et al., 2011). During and following this settlement period, high temperatures and low dissolved oxygen can also limit growth and, due to links between warming and increased predator abundance (Collie et al., 2008; Langan et al., 2021; Taylor et al., 2016), survival (Gallagher et al., 2015; Pereira et al., 1999; Taylor & Collie, 2003). As a result, projections of future abundance based on forecasted atmospheric temperatures have been used to suggest that rebuilding the Southern New England/Mid-Atlantic Bight stock may be challenging (Bell et al., 2018). However, these investigations conducted at the regional level have involved vague connections between population dynamics and climate that may not provide the specificity needed for the development of targeted management actions in specific ecosystems.

To rectify this gap, Langan et al. (in rev.) fit a life-cycle model to the winter flounder subpopulation in Narragansett Bay, Rhode Island, part of the Southern New England/Mid-Atlantic Bight stock, to characterize the life stages at which there was a
mortality bottleneck and identify potential causes of decreased survival. The results revealed that the summer water temperature, summer dissolved oxygen concentration, and predation by a warm-water fish (striped searobin, *Prionotus evolans*) and protected water bird (double-crested cormorant, *Phalacrocorax auratus*) played a large role in mortality during the first year of life, while there was significant unexplained variability in the dynamics of older life stages. Given evidence of linkages between climate change and the decline of winter flounder in Narragansett Bay, this work raised questions regarding potential management strategies and the future viability of the subpopulation.

Due to the exceptional availability of time series of abundance across life stages and an emerging mechanistic understanding of how climate change is impacting productivity, the Narragansett Bay winter flounder subpopulation is an ideal case study to evaluate management options for a species in decline at the equatorward edge of its range. Therefore, the goal of this work is to expand on Langan et al. (in rev.) through use of fitted structural equation models for Narragansett Bay winter flounder to project future abundance under a variety of ecosystem conditions. Through modifying the fishing mortality rates applied to the spawning stock and altering the values of the environmental covariates identified as contributing to juvenile mortality, the role of these factors in the future productivity of this subpopulation are assessed to both inform management of the local fishery and provide insight into emerging challenges in regulating fish stocks in a warming ocean.
METHODS

This work used the winter flounder life cycle dataset described in Langan et al. (in rev.) and followed similar modeling methods. Briefly, abundance data (1988-2016) for six life stages (Larvae, July young-of-the-year [YOY], October YOY, Spring age-1, Autumn age-1, and Spring age-2) were gathered from ichthyoplankton sampling conducted by Normandeau Associates, Incorporated (NAI, Bedford, NH) and a trawl survey conducted by the Rhode Island Division of Marine Fisheries (RIDMF). Annual abundance estimates of Eggs were made using the length-frequency data from the RIDMF trawl survey as in Langan et al. (in rev.). The relative abundance indices were first scaled for expected average interstage mortality rates to account for differences in catchability (Table 2-1), using literature values chosen such that the population was able to recover under suitable conditions to ensure the models employed here were not overly pessimistic. The data were then fit with a structural equation model described by the following two equations:

\[ \ln(N_{s+1,y}) = -\mu_s + \lambda_s \cdot \ln(N_{s,y}) + \epsilon_{s,y} \quad (1) \]
\[ \hat{l}_{s,y} = \ln(N_{s,y}) = c_s + \ln(N_{s,y}) + \delta_{s,y} \quad (2) \]

where \( N_{s,y} \) is the abundance of stage \( s \) in cohort \( y \), \( \mu_s \) is the mean of the density-independent component of the mortality rate, \( \lambda_s \) expresses density dependence, and the process error \( \epsilon_{s,y} \), is the random component of mortality for cohort \( y \), stage \( s \) (Fromentin et al., 2001; Myers & Cadigan, 1993), \( \hat{l}_{s,y} \) is the measured log abundance of stage \( s \) in cohort \( y \), \( c_s \) is an intercept term describing the abundance and catchability of stage \( s \) relative to stage \( s+1 \), and \( \delta_{s,y} \) is the measurement error of stage \( s \) in cohort \( y \).
Process and measurement errors are assumed to be independent, normally distributed random deviates with mean zero and variances $\psi_s$ and $\theta_s$, respectively. Similarly, the time series of egg abundance, $\ln(N_{Eg gs,y})$, is assumed to be independent and normally distributed with variance $\phi$. Estimates of measurement error variance for each life stage were taken from Langan et al. (in rev.). In two cases in which the mean catch for a cohort in any year was zero, the input value was set to one-half the lowest non-zero catch. PROC CALIS (SAS 9.3) was used to fit the structural equation and all subsequent analyses were performed in R (R Core Team, 2020). While Langan et al. (in rev.) fit the variance-covariance structure of the data, the mean structure was fit here in order to generate interpretable abundance projections. For the purposes of projection of future subpopulation abundance, the modeled Narragansett Bay winter flounder life cycle was extended through age-13 to match recent stock assessments in the region (Northeast Fisheries Science Center, 2011, 2020).

External environmental covariates were included in all models for several early life stages. Based on evidence of predation impacting survival during the settlement period (Manderson et al. 1999, Langan et al. in rev.), the April – June mean catch-per-tow of striped searobin (*Prionotus evolans*) in the University of Rhode Island Graduate School of Oceanography (URI-GSO) trawl survey (Collie, J., unpubl. data) was used as a covariate during the Larvae-July YOY stage transition. During the July YOY – October YOY transition, meanwhile, the summer (July-September) mean surface temperature recorded by the URI-GSO trawl survey, the minimum monthly mean hypoxia recorded by NAI in central Mt. Hope Bay (Figure 2-1), and the number of double-crested cormorant (*Phalacrocorax auratus*) nesting pairs observed in
proximity to Narragansett Bay by the Rhode Island Department of Environmental Management were included. Together, these factors were used to study the effects of past and potential future environmental conditions on winter flounder productivity.

Three model variants were used in the analysis based on the results of Langan et al. (in rev.) (Table 2-2). Variant A allowed for the presence of density-dependence during the Larvae – July YOY transition, while Variant B additionally included density-dependence during the Eggs-Larvae transition. Whereas Variants A and B assumed that transitions between age classes of winter flounder age-3 or older were associated with the same process-error variance as the Autumn age-1 – Spring age-2 transition, Variant C fixed the process-error variance for these older age classes at 0 to isolate the effect of dynamics in the early life cycle and determine if assumptions made about the spawning population were altering the projections.

To assess the potential recovery of Narragansett Bay winter flounder between 2017 and 2050 under a variety of scenarios, the future values of fishing mortality and the environmental covariates were modified for each of the three model variants (Table 2-3). Prior to testing potential future conditions, a check was needed to determine both if the fitted structural equation model variants predicted subpopulation growth under suitable conditions with the assumed interstage mortality rates and if varying the identified mortality factors was sufficient to allow recovery. Specifically, the model, scaled relative abundances, and interstage mortality rates were considered properly calibrated if at least one model variant projected that the population would most likely recover when initialized with conditions suitable for growth and if historically observed winter flounder abundances between the late 1970s and late
1980s were within the range of the projections by 2050. Therefore, the “Past Growth” scenario comprised the current fishing mortality rate (Northeast Fisheries Science Center, 2020) and mean covariate values from the last time period outside the time interval used in model fitting during which this winter flounder subpopulation significantly increased in abundance (1975-1978, Figure 2-2). Specifically, striped searobin abundance and summer surface temperature values were taken from the URI-GSO trawl survey. Summer dissolved oxygen concentration was obtained from data provided by NAI, as in Langan et al. (in rev.). Based on the reported absence of cormorants in Narragansett Bay prior to the 1980s (French Mccay & Rowe, 2004), the number of nesting pairs was set to 0. For this and all other scenarios, the natural mortality rate was set to 0.3 for age-2+ flounder as in recent stock assessments for the Southern New England/Mid-Atlantic Bight Stock (Northeast Fisheries Science Center, 2011, 2020).

In order to test the hypothesis that the persistent depleted state of this subpopulation is due primarily to factors other than harvest, fishing mortality was set to zero and recent conditions (2013-2016 mean, Figure 2-2) were used to parameterize the covariates in the “No Fishing” scenario. The data to parameterize this scenario came from the same sources. For the remaining scenarios, fishing mortality and covariate values were assumed to change linearly from these 2013-2016 conditions to the chosen values over a 10-year period before stabilizing. The “Business As Usual” scenario consisted of matching conditions to the No Fishing scenario except for fishing mortality, which was obtained from the 2013-2016 mean value of a recent stock assessment (Northeast Fisheries Science Center, 2020), and summer sea surface
temperature. Narragansett Bay summer sea surface temperature was projected through 2050 by identifying the grid cell(s) containing the estuary in six “business as usual” (scenario SSP5–8.5) climate models from the Coupled Model Intercomparison Project Phase 6 (CMIP6) (Eyring et al., 2016; O’Neill et al., 2016) (Table 2-4, Table 2-S1). These downscaled summer air temperature projections were then linearly related to and aligned with past summer surface temperatures (1995-2014 mean) in the estuary using the delta method as in Bell et al. (2018) (Figure 2-3).

Finally, the “Best Case” scenario represented an optimistic, but plausible, set of future conditions. In this projection, searobin abundance was decreased by 50%, which could occur if they became a species targeted by fishing effort or changing trophic interactions limited abundance in this ecosystem. Projected summer sea surface temperatures from the CMIP6 models were made using scenario SSP1–2.6, which represents a much more optimistic trajectory for future warming (O’Neill et al., 2016) (Table 2-4, Figure 2-3, Table 2-S1). Summer dissolved oxygen concentrations were increased by approximately 25% as if water quality improvements successfully reduced incidences of hypoxia to the upper range of conditions observed in recent decades. Cormorant abundance was reduced by 70% to match the approximate reduction in adult cormorant feeding days achieved by aggressive management measures enacted on Oneida Lake, New York (Coleman et al., 2016). Finally, fishing mortality was reduced by 50% to mimic a case in which harvest of winter flounder was prohibited and bycatch mortality in fishing activities targeting other species was successfully reduced. In addition to the four scenarios, additional projections were conducted in which single covariates or fishing mortality were altered from the recent
conditions of the Business As Usual scenario to those of the Best Case scenario to assess the impact of varying each individually.

To initialize the subpopulation projections, the spring abundance for ages 1-13 in 2016 was estimated using the past abundances of age-1 and age-2 flounder and the total mortality rates-at-age assumed in the Southern New England/Mid-Atlantic Bight winter flounder stock assessments (Northeast Fisheries Science Center, 2011, 2017, 2020). Each year class (2017-2050) was then simulated 25,000 times with each of the fitted structural equation model variants. Specifically, egg abundance was estimated using the egg production-at-weight relationship reported by (Buckley et al., 1991) with published weight-at-age (2006-2010) relationships and the percent mature-at-age values reported in recent stock assessments (Northeast Fisheries Science Center, 2011). The eggs were then projected between life stages according to the fitted structural equations to simulate spring abundance up to the year 2050, sampling the estimated process error distribution during each life stage transition. Because large estimated process-error variances were sufficient to produce negative mortality rates in the older life stages if unconstrained, the process-errors were sampled from truncated normal distributions using the R package “truncnorm” (Mersmann et al., 2018). Specifically, symmetric truncation was applied to the process error distributions such that it was impossible to generate a negative mortality rate. It is important to note that this truncation only had a significant effect on the sampled process errors as mortality rates decreased with age, beginning as flounder entered the second year of life (age-1). Therefore, this approach only had a large impact on the variability in inter-stage mortality rates after the effects of density dependence and the
studied environmental covariates had been assessed during the critical early life stages.

Due to the focus on early life cycle dynamics in this work, it was assumed that, after Spring age-2, density-dependent mortality did not occur in subsequent life stages and total mortality followed recent estimates from stock assessments (Northeast Fisheries Science Center, 2011, 2017, 2020). During each simulation in which summer surface temperature was allowed to change, one of the six included CMIP6 climate model projections was randomly selected in each iteration and used to generate future temperature values. The forecasted 2050 abundance distribution for each scenario was then compared to a recovery threshold equal to the mean estimated spring Narragansett Bay winter flounder abundance between 1984 and 1986, since 1985 was the most recent year in which the Southern New England/Mid-Atlantic Bight stock was above the “overfished” limit (Northeast Fisheries Science Center, 2020). Because it is unclear what represents a healthy abundance level within Narragansett Bay, this threshold was used under the assumption that the estuary abundance followed an approximately linear relationship with that of the regional stock unit. Past spring abundance levels were estimated using the expected average mortality between ages (Table 2-1), to correct for differences in availability or catchability. Thus, this recovery threshold should be viewed as a rough approximation.

RESULTS

The fitted parameters of Variants A and B were similar to the results of Langan et al. (in rev.) (Table 2-2). While that work fit structural equation models to the covariance structure of the data, fitting the mean structure here only added intercept
terms to each life stage transition without significantly impacting any of the other parameters. Variant C was the same as Variant A, except the process error for ages 3+ was assumed to be 0 instead of 1.14, and produced similar results.

The results of the Past Growth scenario indicate that only Variants A and C project that the Narragansett Bay winter flounder subpopulation would most likely recover by 2050 under past conditions that supported rapid subpopulation growth (Table 2-3, Figures 2-2 and 2-4), while Variant B was less optimistic. The abundance levels forecasted by Variant A were similar to or higher than those observed following the rapid subpopulation growth of the late 1970s and thus indicated that the model and assumed mortality rates were well-calibrated. The observed abundance levels of the late 1970s and early 1980s fell within the 2050 90% projection interval (Figure 2-4). Due in large part to the significant uncertainty, indicated by large process errors, in the model fits, the confidence bounds on the forecasted abundances were wide near the end of the forecast window in all three variants (Figure 2-4).

Narragansett Bay winter flounder recovery by 2050 was very unlikely for all three model variants when recently observed conditions were projected into the future and fishing mortality was set to zero (No Fishing scenario) or future warming due to climate change was included (Business As Usual scenario, Table 2-3, Figure 2-4). Similarly, the highest probability of recovery under the Best Case scenario was less than 16% in Variants A and C. In the Business as Usual and Best Case scenarios, notably, the forecasted abundance of Narragansett Bay winter flounder exhibited a slight declining trend (Business as Usual) or a variable plateau (Best Case) beginning in the late 2030s to early 2040s as mean summer surface temperatures approached 22
℃ (Figures 2-3 and 2-4). This suggests that climate change, both under the “business as usual” (SSP5–8.5) and more optimistic (SSP1–2.6) temperature trends considered here, will within the next 25 years overwhelm any increased winter flounder productivity resulting from relief from fishing or the other studied environmental factors.

Altering fishing mortality and the studied environmental factors one-by-one between the Business As Usual conditions and the Best Case conditions suggested that a decrease in cormorant or searobin abundance would have the largest positive impact on winter flounder abundance (Table 2-5). While decreased cormorant abundance had the single largest effect, it is important to consider that the Best Case conditions specified a lesser decline in striped searobin and that the regression coefficient on cormorant abundance was both highly uncertain and marginally significant using a two-sided test (p = 0.04). Changes in fishing mortality, dissolved oxygen levels, and summer temperature projections, meanwhile, produced similar results. Notably, the summer temperature projections used in the Business As Usual and Best Case scenarios exhibited a small average difference between 2040 and 2050 (0.45 ℃, Figure 2-3), with considerable overlap in the range of projections from individual climate models. Because both appeared to reach temperatures sufficient to halt or reverse growth in this winter flounder subpopulation prior to the end of the simulation window, a greater divergence in temperature projections would likely be needed to determine its importance relative to the other tested environmental factors.

**DISCUSSION**
The results of this work suggest that it is unlikely the Narragansett Bay winter flounder subpopulation will recover to past levels of abundance. Due to a combination of, and linkage between, changing physical habitat conditions and increased predation, juvenile mortality is limiting the reproductive capacity of the subpopulation. While fishing mortality is a contributing factor, it does not appear to play a primary role in the persistence of low abundance levels in agreement with established hypotheses (Northeast Fisheries Science Center, 2011). Management measures may be able to relieve some of the stressors impacting winter flounder productivity, but the results are likely to be temporary as water temperatures continue to warm.

The projections of the Past Growth scenario suggest that the fitted structural equation model variants forecast subpopulation growth when suitable conditions like those observed during the mid-1970s are held constant. However, the model variants differed in the projected subpopulation abundance. The projection from Variants A and C equilibrated at an abundance slightly higher than what was observed in the RIDMF trawl survey during the 1980s and similar to abundance levels observed further in the past (Gibson, 2013). Subpopulation growth in Variant B, on the other hand, was limited by the offsetting effect of compensation in adjacent life stage transitions. The similarity of the projections from Variants A and C suggest that the assumptions made about process variability in the spawning stock did not significantly affect the results. The agreement with both past abundance levels and patterns of early life cycle population dynamics identified in other species (Stige et al., 2019) indicates that Variant A is likely the most realistic model parameterization tested. However, the rapid pace of subpopulation growth observed historically compared to the relatively
slow rise of the median projected abundance in Variant A, where conditions suitable for subpopulation growth were held constant, indicates that additional external drivers or changes in life history characteristics not included in this analysis likely play an important role in winter flounder productivity. For example, lesser impacts from other environmental factors like predation by crangon shrimp (*Crangon septemspinosa*) (Taylor & Collie, 2003) may have aided in supporting the rapid growth of the 1970s. It is also possible that the relationship of winter flounder to the studied covariates or the assumed interstage mortality rates of other life stages have changed over time. Yet, the agreement between the projections of Variant A and past abundances, as well as the inclusion of rapid growth rates to higher abundances within the projected abundance distribution, indicates that the studied environmental factors and fishing mortality are at least major factors regulating productivity whose variation within historically observed values may be sufficient to allow this winter flounder subpopulation to recover.

The projections of the No Fishing and Business As Usual scenarios indicate that under present conditions absent harvest or present conditions with projected warming of summer water temperatures due to climate change, high rates of juvenile mortality make recovery of Narragansett Bay winter flounder very unlikely. This is largely in agreement with past work indicating that predation (Manderson et al., 1999, 2006; Sagarese et al., 2011; Taylor & Collie, 2003), low dissolved oxygen (Pereira et al., 1999) and warming temperatures (Gallagher et al., 2015; Pereira et al., 1999; Taylor & Collie, 2003) can limit winter flounder productivity. The low probability of recovery observed in the No Fishing scenario supported the hypothesis that the current depleted
state of this subpopulation is not primarily the result of harvest pressure. Similarly, Bell et al. (2018) found that projections of the Southern New England/Mid-Atlantic Bight stock using a temperature-dependent stock-recruitment relationship indicated that population was unlikely to recover and that any increasing trend in abundance would reverse during the 2030s. Despite differences in the spatial scale and methods used in that analysis, the strong agreement with the results of this work corroborates the conclusion that climate change will increasingly present a barrier to the recovery of winter flounder in Southern New England in the coming decades.

Under the most optimistic future conditions deemed plausible in this analysis, the Best Case Scenario, recovery of the Narragansett Bay winter flounder subpopulation still appeared inhibited by juvenile mortality. It is possible that other conditions related to winter flounder productivity not studied in this work may become more suitable in the future, but comparison with the Past Growth scenario indicates that changes in predator abundance and summer temperature and dissolved oxygen both play a major role in regulating the subpopulation and are unlikely to improve to a state that allows significant recovery in the future. While recovery to 1985 levels was not achieved, it is important to note that the population was likely to grow to levels similar to those observed during the early 1990s and stay near that abundance in the medium term. However, achieving these Best Case conditions would involve a massive investment by multiple management agencies. For example, the reduction of cormorant predation on fishes of Oneida Lake, NY involved destruction of nests and daily harassment of birds during portions of the year (Coleman et al., 2016). Similarly, further boosting water quality to reduce hypoxia would require additional investment and regulation.
across many stakeholders (Oviatt et al., 2017). In order to reduce striped searobin abundance, a fishery and supporting market would likely need to be created to facilitate their removal from the ecosystem.

Making matters more complicated, the drivers of winter flounder productivity considered in this work were assumed to act in isolation due to the lack of significant correlation among the time series used in model fitting. However, it is known that these factors covary and may produce synergistic effects in the future. It has been shown that YOY winter flounder avoid low dissolved oxygen concentrations and high water temperatures (Taylor et al., 2016). Yet, continued warming is expected to contribute to increased severity and duration of hypoxic events (Oviatt et al., 2017; Paerl, 2006). Exposure to such conditions has been linked to decreased growth rates (Gallagher et al., 2015; Pereira et al., 1999; Taylor & Collie, 2003) that result in a greater duration of time spent at small sizes vulnerable to predation by striped searobins (Manderson et al., 1999, 2006) or cormorants (Pilon et al., 1983). Further, striped searobin abundance (Collie et al., 2008) and seasonal residence time (Langan et al., 2021) are increasing in Narragansett Bay due to warming temperatures, resulting in greater densities of searobins present when winter flounder are at appropriate sizes for consumption. Additionally, the development of a searobin fishery may have unintended effects: their demersal behavior and habitat preferences suggest that additional fishing effort directed at this species will likely increase bycatch, and thus mortality, of winter flounder (Manderson et al., 1999). As a result, the projections produced in this work based upon independent covariate effects may in fact be too optimistic and bolster the conclusion that the recovery of winter flounder in
Narragansett Bay to high levels of abundance is unlikely even with significant management investment.

In agreement with (Boudreau et al., 2015), predation appeared to have a strong impact on the early life cycle mortality of this subpopulation near the southern (warm) edge of the species’ range. Reduction in cormorant and searobin abundance produced the largest increases in the projected abundance of Narragansett Bay winter flounder. Notably, this is due in part to the projected decline in winter flounder productivity with minimal additional warming. The Business As Usual and Best Case scenarios suggest that any increasing trend in abundance was reversed as summer temperatures approached 22 °C, a threshold that was exceeded three times between 2010 and 2016 (Figure 2-3). Thus, it is not surprising that the difference in the projected abundance of winter flounder was small between projections made using these two CMIP6 scenarios given that recent temperature conditions are already at or near a critical level.

The Narragansett Bay winter flounder subpopulation provides a case study of a climate loser in an evolving ecosystem. As fisheries managers are faced with such challenges more frequently in the future, management frameworks to handle these situations will become essential. Due to a suite of ecological, anthropogenic, and environmental factors, most of them climate-linked, this subpopulation is unlikely to recover to the past abundance levels used as biological reference points even with significant management investment. From an empirical economic perspective, one seeking to maximize the present value of this subpopulation would advocate to harvest any captured winter flounder (Clark, 1973). However, such action may not account for the sociocultural value of a historical fishery in the region (Oviatt et al., 2003). At the
same time, recovering the subpopulation to an abundance level that could support a productive fishery may require restrictive measures on fishing effort targeting other species. If so, winter flounder may become a choke species and significantly impact revenue and increase uncertainty for affected fishers (Holland, 2010). Because the present laws governing US fisheries require efforts to recover depleted stocks (National Oceanic and Atmospheric Administration, 2006), these challenges argue for a middle ground. Stocks exhibiting non-stationarity in population processes due to climate change must be regulated with non-stationary management targets (Szuwalski & Hollowed, 2016). Biomass thresholds used to assess the health of fished populations should reflect their present productivity in a warming ocean. In the case of winter flounder, such a dynamic threshold could be lowered to an abundance target similar to the abundance of the mid-1990s as opposed to the current target level that mirrors 1980s abundance. In cases of mixed stock fisheries containing climate winners and losers, cost-benefit analyses will become important tools in determining the measures managers use to promote growth of depleted stocks toward their climate-adjusted baselines (Szuwalski & Hollowed, 2016). By building such adaptability into management systems, regional fisheries will be able to remain productive and take advantage of revenue opportunities as their species portfolios continue to evolve in a changing climate.

ACKNOWLEDGEMENTS

We thank the RI Division of Marine Fisheries, RI Division of Fish and Wildlife, and Normandeau Associates, Inc. for contributing data to this work. We also acknowledge the World Climate Research Programme, which, through its Working
Group on Coupled Modelling, coordinated and promoted CMIP6. We thank the climate modeling groups for producing and making available their model output, the Earth System Grid Federation (ESGF) for archiving the data and providing access, and the multiple funding agencies who support CMIP6 and ESGF. Hirotsugu Uchida provided comments and suggestions that improved this work. This project was made possible through funding from the RI Department of Environmental Management, Project No. P0200696 and RI Sea Grant project number 2016-R/F-1618-31-2-RES. This paper is a contribution of the RI Marine Fisheries Institute.

REFERENCES


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TABLES

**Table 2-1.** Published interstage survival rates used to adjust for differences in catchability among the modeled Narragansett Bay winter flounder life stages. YOY: Young-of-the-Year.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Literature Survival Rate</th>
<th>Reference</th>
<th>Value used</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eggs</td>
<td>0.002</td>
<td>Rose et al. 1996</td>
<td>0.005</td>
</tr>
<tr>
<td>Larvae</td>
<td>0.02-0.17</td>
<td>Rose et al. 1996</td>
<td>0.08</td>
</tr>
<tr>
<td>July YOY – October YOY</td>
<td>0.17</td>
<td>DeLong et al. 2001</td>
<td>0.17</td>
</tr>
<tr>
<td>October YOY – Spring age-1</td>
<td>0.59</td>
<td>Rose et al. 1996</td>
<td>0.59</td>
</tr>
<tr>
<td>Spring age-1 – Spring age-2</td>
<td>0.41</td>
<td>Pearcy 1962</td>
<td></td>
</tr>
<tr>
<td>Spring age-1 – Autumn age-1</td>
<td>Used ½ year value of above as $\sqrt{0.41}$</td>
<td>0.64</td>
<td></td>
</tr>
<tr>
<td>Autumn age-1 – Spring age-2</td>
<td>Used ½ year value of above as $\sqrt{0.41}$</td>
<td>0.64</td>
<td></td>
</tr>
</tbody>
</table>
Table 2-2. Estimated parameter values for each of the life stage transitions in the three tested structural equation model variants (superscripted letters). Only one value is given when the parameter estimate is the same in all variants. The intercept (c) and measurement error variance (θ) apply exclusively to the younger stage in each transition. The density dependence (λ) and process error variance (ψ) terms listed for the Spring age-2 – Spawners transition also apply for all subsequent transitions within the Spawners group. Only significant regression coefficients (γ) and their respective covariates are listed. YOY: Young-of-the-Year. ST: Surface temperature.

<table>
<thead>
<tr>
<th>Life Stage Transition</th>
<th>c</th>
<th>θ</th>
<th>λ</th>
<th>ψ</th>
<th>γ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eggs – Larvae</td>
<td>5.64</td>
<td>0.14</td>
<td></td>
<td>1.00&lt;sup&gt;A&lt;/sup&gt;</td>
<td>0.72&lt;sup&gt;A&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.35&lt;sup&gt;B&lt;/sup&gt;</td>
<td>0.43&lt;sup&gt;B&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.00&lt;sup&gt;C&lt;/sup&gt;</td>
<td>0.72&lt;sup&gt;C&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Larvae – July YOY</td>
<td>0.34</td>
<td>0.02</td>
<td></td>
<td>0.29&lt;sup&gt;A&lt;/sup&gt;</td>
<td>-0.17, Searobin catch</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.30&lt;sup&gt;B&lt;/sup&gt;</td>
<td>0.29&lt;sup&gt;C&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>July YOY – October YOY</td>
<td>-1.81</td>
<td>0.23</td>
<td>1.00</td>
<td>0.04</td>
<td>-0.59, Summer ST</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.34, Dissolved Oxygen</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-0.86, Cormorants</td>
</tr>
<tr>
<td>October YOY – Spring age-1</td>
<td>8.71&lt;sup&gt;A&lt;/sup&gt;</td>
<td>8.72&lt;sup&gt;B&lt;/sup&gt;</td>
<td>8.71&lt;sup&gt;C&lt;/sup&gt;</td>
<td>0.22</td>
<td>1.00</td>
</tr>
<tr>
<td>Spring age-1 – Autumn Age-1</td>
<td>8.18&lt;sup&gt;A&lt;/sup&gt;</td>
<td>8.19&lt;sup&gt;B&lt;/sup&gt;</td>
<td>8.18&lt;sup&gt;C&lt;/sup&gt;</td>
<td>0.18</td>
<td>1.00</td>
</tr>
<tr>
<td>Autumn age-1 – Spring age-2</td>
<td>7.73&lt;sup&gt;A&lt;/sup&gt;</td>
<td>7.75&lt;sup&gt;B&lt;/sup&gt;</td>
<td>7.73&lt;sup&gt;C&lt;/sup&gt;</td>
<td>0.15</td>
<td>1.00</td>
</tr>
<tr>
<td>Spring age-2 – Spawners</td>
<td>7.29&lt;sup&gt;A&lt;/sup&gt;</td>
<td>7.30&lt;sup&gt;B&lt;/sup&gt;</td>
<td>7.29&lt;sup&gt;C&lt;/sup&gt;</td>
<td>0.22</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.14&lt;sup&gt;B&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
Table 2-3. Mortality and environmental covariate values used for the four projection scenarios (top) and the results of the projections of winter flounder population abundance for model Variants A-C. The 95% projection interval (PI) of projected abundance levels (number/100m²) and the probability of the abundance being above the 1985 threshold level (0.47/100 m²) in 2050 are provided.

<table>
<thead>
<tr>
<th>Covariate/Mortality</th>
<th>Past Growth</th>
<th>No Fishing</th>
<th>Business as Usual</th>
<th>Best Case</th>
</tr>
</thead>
<tbody>
<tr>
<td>Striped searobin abundance (number/tow)</td>
<td>0.55</td>
<td>5.78</td>
<td>5.78</td>
<td>2.89</td>
</tr>
<tr>
<td>Summer surface temperature (°C)</td>
<td>20.40</td>
<td>21.55</td>
<td>CMIP 6 Projection SSP5–8.5</td>
<td>CMIP 6 Projection SSP1–2.6</td>
</tr>
<tr>
<td>Dissolved oxygen concentration (ppm)</td>
<td>3.65</td>
<td>4.05</td>
<td>4.05</td>
<td>5.00</td>
</tr>
<tr>
<td>Cormorant Nesting Pairs</td>
<td>0</td>
<td>1870</td>
<td>1870</td>
<td>561</td>
</tr>
<tr>
<td>Fishing Mortality</td>
<td>0.18</td>
<td>0.00</td>
<td>0.18</td>
<td>0.09</td>
</tr>
<tr>
<td>Natural Mortality</td>
<td>0.30</td>
<td>0.30</td>
<td>0.30</td>
<td>0.30</td>
</tr>
<tr>
<td>Variant A 95% PI [Recovery %]</td>
<td>(0.66, 3.05)</td>
<td>(0.01, 0.06)</td>
<td>(0.00, 0.03)</td>
<td>(0.11, 0.72)</td>
</tr>
<tr>
<td>Variant B 95% PI [Recovery %]</td>
<td>(0.17, 72)</td>
<td>(0.01, 0.03)</td>
<td>(0.00, 0.02)</td>
<td>(0.04, 0.22)</td>
</tr>
<tr>
<td>Variant C 95% PI [Recovery %]</td>
<td>(0.63, 2.84)</td>
<td>(0.01, 0.06)</td>
<td>(0.00, 0.03)</td>
<td>(0.11, 0.68)</td>
</tr>
</tbody>
</table>
### Table 2-4.
The selected Coupled Model Intercomparison Project Phase 6 (CMIP6) global climate models and experiments used to project Narragansett Bay summer surface temperatures from 2017–2050.

<table>
<thead>
<tr>
<th>Institution(s)</th>
<th>Model</th>
<th>Experiment</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canadian Centre for Climate Modelling and Analysis</td>
<td>Canadian Earth System Model version 5 (CAN)</td>
<td>Historical</td>
<td>Swart et al. (2019b)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SSP1–2.6</td>
<td>Swart et al. (2019c)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SSP5–8.5</td>
<td>Swart et al. (2019a)</td>
</tr>
<tr>
<td>State Key Laboratory of Numerical Modeling for Atmospheric Sciences and Geophysical Fluid Dynamics, Institute of Atmospheric Physics, Chinese Academy of Sciences</td>
<td>Flexible Global Ocean–Atmosphere–Land System Model: Grid-Point Version 3 (FGOALS)</td>
<td>Historical</td>
<td>Li (2019a)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SSP1–2.6</td>
<td>Li (2019b)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SSP5–8.5</td>
<td>Li (2019c)</td>
</tr>
<tr>
<td>Meteorological Research Institute</td>
<td>Earth System Model version 2.0 (MRI)</td>
<td>Historical</td>
<td>Yukimoto et al. (2019a)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SSP1–2.6</td>
<td>Yukimoto et al. (2019b)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SSP5–8.5</td>
<td>Yukimoto et al. (2019c)</td>
</tr>
<tr>
<td>Beijing Climate Center, China Meteorological Administration</td>
<td>medium-resolution Climate System Model version 2 (BCC)</td>
<td>Historical</td>
<td>Wu et al. (2018)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SSP1–2.6</td>
<td>Xin et al. (2019a)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SSP5–8.5</td>
<td>Xin et al. (2019b)</td>
</tr>
<tr>
<td>Geophysical Fluid Dynamics Laboratory, National Oceanic and Atmospheric Administration</td>
<td>Earth System Model Version 4 (GFDL)</td>
<td>Historical</td>
<td>Krasting et al. (2018)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SSP1–2.6</td>
<td>John et al. (2018a)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SSP5–8.5</td>
<td>John et al. (2018b)</td>
</tr>
<tr>
<td>Center for Climate System Research; University of Tokyo; Japan Agency for Marine-Earth Science and Technology; National Institute for Environmental Studies</td>
<td>Model for Interdisciplinary Research on Climate version 6 (MIROC)</td>
<td>Historical</td>
<td>Tatebe &amp; Watanabe (2018)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SSP1–2.6</td>
<td>Shiogama et al. (2019a)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SSP5–8.5</td>
<td>Shiogama et al. (2019b)</td>
</tr>
</tbody>
</table>
Table 2-5. The 95% projection interval (PI) of the projected abundance (number/100m²) of the Narragansett Bay winter flounder population in 2050 if fishing mortality or the individual environmental covariates (columns) are changed from the Business As Usual scenario to the Best Case scenario value one at a time. The baseline 95% PIs from the Business as Usual scenario in 2050 are given in the left-hand column.

<table>
<thead>
<tr>
<th>Model Variant</th>
<th>Business As Usual</th>
<th>Fishing Mortality</th>
<th>Striped Searobin</th>
<th>Summer Temperature</th>
<th>Dissolved Oxygen</th>
<th>Cormorants</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>(0.00, 0.03)</td>
<td>(0.01, 0.04)</td>
<td>(0.01, 0.06)</td>
<td>(0.01, 0.04)</td>
<td>(0.01, 0.05)</td>
<td>(0.02, 0.15)</td>
</tr>
<tr>
<td>B</td>
<td>(0.00, 0.02)</td>
<td>(0.00, 0.02)</td>
<td>(0.01, 0.03)</td>
<td>(0.00, 0.02)</td>
<td>(0.00, 0.03)</td>
<td>(0.01, 0.06)</td>
</tr>
<tr>
<td>C</td>
<td>(0.00, 0.03)</td>
<td>(0.00, 0.03)</td>
<td>(0.01, 0.06)</td>
<td>(0.01, 0.04)</td>
<td>(0.01, 0.05)</td>
<td>(0.02, 0.14)</td>
</tr>
</tbody>
</table>
FIGURES

Figure 2-1. Map of Narragansett Bay, Rhode Island.
Figure 2-2. Annual winter flounder catch-per-trawl time series from the University of Rhode Island Graduate School of Oceanography (URI-GSO) and Rhode Island Division of Marine Fisheries (RIDMF) trawl surveys. The time periods used to represent recovery (Past Growth scenario) and recent (No Fishing [NF] and Business As Usual [BAU] scenarios) conditions are highlighted in green and red, respectively. The time period of data used to train the structural equation models is shaded in gray.
Figure 2-3. Observed (1970–2016) and projected (2017–2050) summer surface temperature for Narragansett Bay, Rhode Island from six global climate models (Table 2-4) under the SSP1–2.6 and SSP5–8.5 scenarios of the Coupled Model Intercomparison Project Phase 6.
Figure 2-4. Top: Estimated (1979-2016, black) and projected (2017-2050, blue) spring abundance of winter flounder in Narragansett Bay, Rhode Island for the four projection scenarios (rows) under model Variant A. The estimated 1985 spring abundance threshold level is designated by a horizontal dashed line. Bottom: Violin plot of the projected 2050 log abundance of Narragansett Bay winter flounder for the four projection scenarios and model Variants A-C. The estimated 1985 spring abundance threshold level is designated by a horizontal dashed line.
### Table 2-S1

The files used to generate the summer surface temperature projections for Narragansett Bay, Rhode Island using the six CMIP6 global climate models described in Table 2-4.

<table>
<thead>
<tr>
<th>CMIP6 Model</th>
<th>Model file(s)</th>
</tr>
</thead>
</table>
| Canadian Earth System Model version 5 (CAN) | tas_Amon_CanESM5_historical_r1i1p1f1_gn_185001-201412.nc  
tas_Amon_CanESM5_ssp126_r1i1p1f1_gn_201501-210012.nc  
tas_Amon_CanESM5_ssp585_r1i1p1f1_gn_201501-210012.nc |
| Flexible Global Ocean–Atmosphere–Land System Model: Grid-Point Version 3 (FGOALS) | tas_Amon_FGOALS-g3_historical_r1i1p1f1_gn_199001-199912.nc  
tas_Amon_FGOALS-g3_historical_r1i1p1f1_gn_200001-200912.nc  
tas_Amon_FGOALS-g3_historical_r1i1p1f1_gn_201001-201612.nc  
tas_Amon_FGOALS-g3_ssp126_r1i1p1f1_gn_201501-201912.nc  
tas_Amon_FGOALS-g3_ssp126_r1i1p1f1_gn_202001-202912.nc  
tas_Amon_FGOALS-g3_ssp126_r1i1p1f1_gn_203001-203912.nc  
tas_Amon_FGOALS-g3_ssp126_r1i1p1f1_gn_204001-204912.nc  
tas_Amon_FGOALS-g3_ssp126_r1i1p1f1_gn_205001-205912.nc  
tas_Amon_FGOALS-g3_ssp585_r1i1p1f1_gn_201501-201912.nc  
tas_Amon_FGOALS-g3_ssp585_r1i1p1f1_gn_202001-202912.nc  
tas_Amon_FGOALS-g3_ssp585_r1i1p1f1_gn_203001-203912.nc  
tas_Amon_FGOALS-g3_ssp585_r1i1p1f1_gn_204001-204912.nc  
tas_Amon_FGOALS-g3_ssp585_r1i1p1f1_gn_205001-205912.nc |
| Earth System Model version 2.0 (MRI) | tas_Amon_MRI-ESM2-0_historical_r1i1p1f1_gn_185001-201412.nc  
tas_Amon_MRI-ESM2-0_ssp126_r1i1p1f1_gn_201501-210012.nc  
tas_Amon_MRI-ESM2-0_ssp585_r1i1p1f1_gn_201501-210012.nc |
| medium-resolution Climate System Model version 2 (BCC) | tas_Amon_BCC-CSM2-MR_historical_r1i1p1f1_gn_185001-201412.nc  
tas_Amon_BCC-CSM2-MR_ssp126_r1i1p1f1_gn_201501-210012.nc  
tas_Amon_BCC-CSM2-MR_ssp585_r1i1p1f1_gn_201501-210012.nc |
| Earth System Model version 4 (GFDL) | tas_Amon_GFDL-ESM4_historical_r1i1p1f1_gr1_195001-201412.nc  
tas_Amon_GFDL-ESM4_ssp126_r1i1p1f1_gr1_201501-210012.nc  
tas_Amon_GFDL-ESM4_ssp585_r1i1p1f1_gr1_201501-210012.nc |
| Model for Interdisciplinary Research on Climate version 6 (MIROC) | tas_Amon_MIROC6_historical_r1i1p1f1_gn_195001-201412.nc  
tas_Amon_MIROC6_ssp126_r1i1p1f1_gn_201501-210012.nc  
tas_Amon_MIROC6_ssp585_r1i1p1f1_gn_201501-210012.nc |
Ontogenetic patterns of spatiotemporal habitat use in Narragansett Bay winter flounder

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Publication status: in preparation for submission to Estuarine, Coastal and Shelf Science
ABSTRACT

Stock-level management of marine species innately treats populations as homogenous, experiencing a single synchronous set of environmental conditions and anthropogenic disturbances across habitats. However, variations in habitat suitability and stressors at smaller spatial scales can in aggregate have large effects on population productivity. Such considerations are particularly relevant for southern New England winter flounder (*Pseudopleuronectes americanus*), a climate-challenged flatfish that has exhibited persistently low abundance due to the presumed impacts of climatic and anthropogenic stressors on juvenile mortality. To better understand how such factors may influence spatial population dynamics, this work uses spatiotemporal models to characterize patterns of winter flounder habitat use in Rhode Island waters throughout its life cycle. The results suggest that winter flounder exhibit two primary phases of habitat use: 1) an adherence to shallow nursery areas highly vulnerable to climate change during the first 15 months of life, and 2) a move to deeper estuarine and coastal habitats as flounder approach and achieve sexual maturity. Given that past research has concluded that the first year of life may be a mortality bottleneck for this subpopulation, targeted management interventions to mitigate stressors in shallow nursery areas may improve productivity. In generating such insights, this work serves as an example of an analytical approach to help develop a nuanced, spatially explicit view of the distribution and population dynamics of depleted marine species being impacted by anthropogenic activities and environmental change.
INTRODUCTION

Patterns of abundance and productivity in managed marine populations are most often considered at the stock level, where it is implicitly assumed that survival and growth are homogenous across space. Particularly for vulnerable early life stages, however, environmental factors, predation, and variations in habitat suitability acting at smaller spatial scales have been shown to significantly affect the population dynamics of species such as Atlantic cod (*Gadus morhua*) (Ciannelli et al., 2007; Rogers et al., 2017), Atlantic halibut (*Hippoglossus hippoglossus*) (Boudreau et al., 2017), windowpane flounder (*Scophthalmus aquosus*) (Neuman and Able, 2009), and Pacific rockfish (*Sebastes spp.*) (Markel et al., 2017). In such cases, it is important to develop a more nuanced view of patterns of subpopulation productivity at the local level to successfully manage a stock at the regional level. In the Gulf of Maine American lobster (*Homarus americanus*) fishery, for example, warming temperatures have been shown to boost productivity at the population level while having differential effects across the discrete areal units used in management of the fishery (Tanaka et al., 2019). These considerations are especially important for stocks in decline, where targeted management interventions may be more successful than a generalized approach.

An example of such a population, the Southern New England/Mid-Atlantic Bight stock of winter flounder (*Pseudopleuronectes americanus*) has undergone a severe decline in recent decades despite repeated restrictions to harvest (Northeast Fisheries Science Center, 2020, 2011). Due to the known vulnerability of winter flounder to warming due to climate change (Bell et al., 2018; Hare et al., 2016) and the decrease
in recruitment to this stock (Northeast Fisheries Science Center, 2020), this decline is often attributed to heightened mortality during the early life cycle. However, as a result of its fidelity (Buckley et al., 2008; Collette and Klein-MacPhee, 2002) to estuarine and coastal spawning sites (Fairchild, 2017; Pereira et al., 1999; Siskey et al., 2020), the Southern New England/Mid-Atlantic Bight stock comprises a mosaic of geographic subpopulations. These subpopulations employ resident and migratory movement strategies (Sagarese and Frisk, 2011; Ziegler et al., 2019), such that factions of the population may experience different habitat conditions or exposure to fishing activities. Therefore, juvenile and adult winter flounder in different coastal ecosystems throughout the region can be expected to experience unique habitat conditions and stressors that impact fitness and survival (Howell et al., 2016). Without understanding such patterns at the local level, broad regional management approaches may be unsuccessful in addressing the factors limiting winter flounder productivity.

Near the geographic center of southern New England, Rhode Island waters have historically supported a highly abundant winter flounder subpopulation (Collie et al., 2008; Gibson, 2013) and productive fishery (Oviatt et al., 2003). However, similar to regional trends, this subpopulation entered a precipitous decline during the 1980s that has been attributed to increased mortality during the early life stages (Collie et al. 2008; Langan et al. in rev.). Specifically, Langan et al. (in rev.) found that climate factors, including temperature, hypoxia, and predation during the first summer of life were at least in part responsible for limiting winter flounder productivity. While this view of the subpopulation in aggregate is informative, it does not consider the complex gradients in habitat and anthropogenic impacts throughout Rhode Island.
waters and the Narragansett Bay estuary (Oviatt et al., 2017) or the large spatial variability in juvenile winter flounder abundance (Taylor et al. 2016; McManus et al. in rev.). Understanding how spatial patterns of winter flounder habitat use across life stages have changed during the population decline is imperative for implementing effective interventions that improve subpopulation productivity.

The goal of this work is to develop a deeper understanding of spatial habitat use patterns of Rhode Island winter flounder throughout the life cycle and investigate if they have changed over time. To do this, we collate data for two fisheries-independent surveys to characterize abundance in seven life stages. We construct spatiotemporal models for each life stage individually to 1) characterize patterns of habitat use, 2) evaluate coherence in spatial patterns among life stages, and 3) test the effects of temperature and other environmental covariates in altering winter flounder distribution, and 4) identify any changes in habitat use that coincided with, or potentially contributed to, the decline of this population. In doing so, we provide the most comprehensive view to date of ontogenetic changes in winter flounder habitat use within a single subpopulation and provide insights for the management of coastal species vulnerable to anthropogenic disturbance and environmental change.

**METHODS**

Life-stage-specific data for winter flounder were obtained from two standardized research surveys conducted by the Rhode Island Department of Environmental Management, Division of Marine Fisheries (RIDMF). First, a beach-seine survey has been performed since 1988 to sample the age-0 (or young-of-the-year, YOY) stage flounder at 15 fixed stations throughout Narragansett Bay in June, July, August,
September and October of each year (Figure 3-1) using a 61 x 3.1 m net with 0.64 cm mesh. Environmental information, including temperature and salinity, are recorded for each sample. Because not all individuals in a cohort are settled to the bottom in June (DeLong et al., 2001), we used the July and October samples to represent the start and end of the first summer of life. Based upon the length-at-age information reported by Gibson (2013) and Taylor et al. (2016), captured individuals of at least 11 cm in total length were assumed to represent the prior year class and were removed.

Second, since 1979, RIDMF has performed randomized, depth-stratified otter trawl surveys in the spring (mid-April – mid-May) and autumn (mid-September – early October) using a net with a 6.7 m effective opening and a 0.6 cm mesh liner in the codend towed at 1.29 m/s for 20 minutes. In these seasonal surveys, sampling at 13 fixed stations in Narragansett Bay is supplemented by net tows at a varying number of additional fixed and randomly selected stations throughout all of Rhode Island state waters (Figure 3-1). Auxiliary information, such as temperature and depth, is recorded for each tow and all captured winter flounder are measured to the nearest centimeter.

To extract life-stage information in the absence of an ageing program, relative abundance indices for age-0-2+ in the autumn and age-1-3+ in the spring were estimated from the length-frequency data with a gaussian mixture model following the methods of Langan et al. (in rev.). Specifically, the length-frequency data for spring and autumn of each year were log-transformed and season-specific three-component mixture models, representing the three age classes for each season, were fit for the 1979-2018 data using the “mixtools” package (Benaglia et al., 2009) in R (R Core Team, 2020). It was assumed that the component variances were approximately equal.
on the log scale, corresponding to a lognormal length-at-age distribution, as commonly assumed in growth models (Minto et al., 2018). Due to small numbers of flounder captured after 2000, model estimation of the mean sizes-at-age and mixing proportions could not be performed for individual years. Instead, model fits of individual years only estimated the mixing proportions while assuming the mean sizes-at-age were equal to the means estimated by Langan et al. (in rev.), thus accounting for differences in relative abundance among age classes in a given year. Each individual fish captured by the RIDMF seasonal surveys was then assigned to its most likely age class in that season, based upon the probabilities of belonging to each group estimated by the individual mixture models fit to each year. Because the autumn age-0 (YOY) stage is more effectively sampled by the seine survey, the abundance index for this group estimated from the trawl survey was excluded from the analysis. Furthermore, only abundance data from 1988 forward was considered in further modeling to match the temporal coverage of the seine survey and because trawl location information was sparsely recorded in earlier years.

The Narragansett Bay estuary and surrounding coastal waters were then segmented into 10 spatial areas, based upon the distribution of seine and trawl survey data (Figure 3-1), which were similar to past research (Keller et al. 1999, McManus et al. in rev.). Specifically, each polygon was drawn such that it contained at least 1 of the 15 stations sampled by the seine survey and one of the 13 fixed stations sampled by the seasonal trawl surveys each season. Waters outside of Narragansett Bay are not sampled by the seine survey and thus this area was excluded from analyses of the YOY life stages. Within the Bay, spatial areas were drawn to represent three
embayments/river mouths at the head of the estuary (Greenwich Bay, Providence River, and Mt. Hope Bay) and north-south divisions of the three longitudinal passages (West Passage, East Passage, and Sakonnet River). Each sampling event in the seine or trawl survey, including the fixed and random stations, was then assigned to the area in which it occurred. For each year, the total number of winter flounder in each age class captured in all sampling events in an area was calculated.

The spatial abundance pattern observed over time for each age class was fit with a spatiotemporal conditional autoregressive (STCAR) model using the R package CARBayesST (Lee et al., 2018). Here, the total number of winter flounder captured in all net tows in $K$ spatial areas during $T$ years was modeled with a Poisson distribution with mean $\mu_{k,t}$ as in the model proposed by Rushworth et al. (2014) and relative to an expected value as in Puggioni et al. (2020). Specifically, the expected values were calculated in five-year bins as the mean catch-per-tow across all areas within a time bin multiplied by the number of tows conducted in each area. Because the available time series spanned 31 years, the first temporal bin (1988-1993) contained six years. The mean abundance was then related to potential covariates as follows:

$$Y_{k,t} \mid \mu_{k,t} \sim Po(\mu_{k,t})$$

$$\mu_{k,t} = E_{k,t}M_{k,t}$$

$$\log(M_{k,t}) = X'_{k,t}\beta + \psi_{k,t}$$

where $Y_{k,t}$ is the observed count in area $k$ and year $t$, $E_{k,t}$ is the expected number of captured winter flounder, $M_{k,t}$ is the relative risk, referred to herein as the relative abundance, calculated as the ratio of the observed catch-per-tow in an area to the
average catch-per-tow observed across all areas in the corresponding time bin, \( X'_{k,t} \beta \) is the linear predictor, and \( \psi_{k,t} \) is a spatiotemporal random effect. The random effects were assumed to follow a multivariate normal distribution, where for the vector \( \psi_t = (\psi_{1,t}, ..., \psi_{K,t}) \):

\[
\psi_t | \psi_{t-1} \sim N(\rho_T \psi_{t-1}, \tau^2 Q(W, \rho_s)^{-1}), \text{ for } t = 2, ..., T
\]

\[
\psi_1 \sim N(0, \tau^2 Q(W, \rho_s)^{-1})
\]

Here, the mean random effect evolves through time as a multivariate first-order autoregressive process with temporal correlation \( \rho_T \). Spatial autocorrelation is introduced by the variance term \( \tau^2 Q(W, \rho_s)^{-1} \). The variance parameter \( \tau^2 \) is multiplied by the precision matrix \( Q(W, \rho_s)^{-1} \) proposed by (Leroux et al., 2000):

\[
Q(W, \rho_s) = \rho_s [\text{diag}(W1) - W] + (1 - \rho_s)I
\]

where \( W \) is the adjacency matrix of the defined spatial areas, \( \rho_s \) is the spatial autocorrelation, \( 1 \) is a \( K \times 1 \) matrix of 1s, and \( I \) is a \( K \times K \) identity matrix.

To investigate the factors that influence the seasonal distribution of winter flounder throughout the life cycle, spatial and environmental covariates were tested in each STCAR model. Specifically, the mean temperature of all tows conducted in each area in the survey relevant to a particular life stage was considered for each year. Additionally, the mean and extreme temperatures (summer: maximum, winter: minimum) of the time interval since the observation of the prior life stage were considered. For the life stages after the first year, these temperature values were obtained from a monthly trawl survey conducted by RIDMF since 1990 at the same 13 fixed stations sampled in the seasonal surveys. Because salinity was consistently
measured for the entire seine survey time series, it was evaluated for influence on the abundance patterns of YOY flounder. Similar to temperature, the mean and minimum salinity during the first summer were also tested in the YOY models. Based upon evidence of the impacts of predation on YOY winter flounder by striped searobin (*Prionotus evolans*) and summer flounder (*Paralichthys dentatus*) (Manderson et al., 1999, 2006), the mean catch-per-tow observed in the RIDMF monthly trawl survey for the preceding months (July YOY: April–July, October YOY: August–October) in each area was included in these models. Due to the semi-randomized sampling design of the seasonal RIDMF trawl survey, the mean depth of all tows conducted in each area was considered in models of the age-1+ life stages. To test for a latitudinal pattern among super-areas within Rhode Island waters, four aggregate regions (Figure 3-1) were created and evaluated as a categorical variable. Finally, the fitted log relative abundance from the model fit of the prior life stage was tested to assess coherence in spatial abundance patterns among adjacent life stages.

Because STCAR models require that covariates have no missing values, such cases were imputed. Infrequent missing values were replaced with the mean of the values up to the five previous and following years in that area. For years near to the beginning or the end of the time series, the mean consisted of as many years as were available in this decadal interval. Covariates were included in the model fits via forward selection if the 95% posterior credible interval on their coefficients did not include zero. Each STCAR model was run for 15,000,000 iterations, where 5,000,000 were discarded as the burn-in period and a thinning interval of 10,000 was applied in order to yield 1,000 posterior samples of each parameter. To summarize the fitted
abundance patterns and investigate if the concentration of winter flounder abundance in Rhode Island waters had changed over time, the spatial Gini coefficient (Rey and Smith, 2013) was calculated by year using the posterior samples across areas for each life stage with the R package “lctools” (Kalogirou, 2020).

RESULTS

Sampling effort by the RIDMF seine survey was stable over time in both July and October (Figure 3-2). There were five cases in which no samples were recorded within an area in July and zero in October. However, individual stations were sampled multiple times within a month in some years for both July and October, resulting in larger sample sizes. The RIDMF seasonal trawl survey effort was similarly stable through time in both spring and autumn (Figure 3-2), with the most notable deviation stemming from a single tow being conducted in coastal waters (Area 10, Figure 3-1) in spring 1993 compared to time series mean of 16.0. This survey exhibited much larger differences among areas in the number of tows conducted over time due primarily to differences in the distribution of random stations. To determine the efficacy of the spatiotemporal conditional autoregressive (STCAR) models in removing spatiotemporal autocorrelation, the residuals were compared to the observed data and the residuals of generalized linear models (GLMs). Specifically, the observed and fitted winter flounder catch-per-tow values for each life stage were used in analysis. Missing values in the raw data, resulting from cases when no survey tows were performed in an area in a given year, were imputed using the mean catch-per-tow value observed in that area within its 5-year time bin. These time bins were composed of the same year intervals as were used to create the offsets for the STCAR models. In order to assess if the inclusion of the
selected covariates alone was sufficient to remove spatiotemporal autocorrelation from the catch data, GLMs with quasi-poisson distributed errors were fit using the same formulae as in the life stage-specific STCAR models.

The observed data and residuals from the STCAR models and GLMs were then tested for spatial and temporal autocorrelation in R (R Core Team, 2020). Temporal autocorrelation was evaluated using the autocorrelation function (ACF) of the data series in each of the fitted areas individually and pooled across areas to a maximum lag of ten years (Figure 3-A1). Spatial autocorrelation was assessed using permutation tests on the Geary’s C and Moran’s I statistics with the “spdep” package (Bivand and Wong, 2018). Permutation tests of each statistic using 1,000 simulations were performed on the three data sets for each year and the corresponding p-value, describing the probability that the null hypothesis of no autocorrelation was true, was recorded (Figure 3-A1). The results of these tests and the ACFs were then qualitatively compared among the observed data, the GLM residuals, and the STCAR residuals.

Particularly in the older winter flounder life stages, significant temporal and spatial autocorrelation was present in the observed catch-per-tow data. These patterns were not resolved by the GLM fits, which did not remove the spatial autocorrelation and, in several cases, increased the temporal autocorrelation. The STCAR fits, however, were generally successful in removing both sources of autocorrelation. The STCAR residuals suggest that different areas of Rhode Island waters displayed different degrees of temporal autocorrelation. This may simply be a function of spatial differences in sampling variability, stemming from either different levels of sampling effort among areas or unknown factors generating greater variation in winter flounder
abundance in some locations over time. Due to these differences in temporal
correlation strength in the abundance data, the STCAR residuals were negatively
autocorrelated for certain areas in some of the life stages when the average correlation
strength was removed by the model fit. However, these patterns did not appear to be
severe. Spatial autocorrelation, on the other hand, was very effectively modeled in the
STCAR fits. Across all life stages, the p-values for both test statistics were increased
relative to tests on the observed data. Particularly for older life stages that exhibited
higher levels of spatial correlation, this resulted in a large reduction in the number of
years in which the Geary’s C or Moran’s I statistics suggested that spatial
autocorrelation was present compared to the observed data and GLM residuals. Based
on this evidence, we conclude that the STCAR model structure was necessary to
model the spatial winter flounder abundance data analyzed in this work and performed
sufficiently in removing spatiotemporal autocorrelation. 1). As a result of its large
size and the sampling distribution of the RIDMF trawl surveys, by far the most tows
have been conducted in Area 10 during the available time series. There were nine
cases in which no trawl tows were performed in a given year and area in spring and
seven such cases in autumn.

As noted in previous work (Collie et al. 2008, Langan et al. in rev.), the
Narragansett Bay winter flounder population significantly declined throughout the
study period (Figure 3-3). This decline was recorded in both the seine and trawl
surveys conducted by RIDMF, with similar patterns present throughout the life cycle.
Average winter flounder catch-per-tow in the seine survey appeared to increase with
latitude; the highest abundances occurred in the Providence River (Figure 3-3). In
contrast, the catch-per-tow values recorded for age–1+ flounder by the trawl survey were spatially heterogenous. The size ranges assigned to each life stage by the mixture models are reported in Table 3-1.

**First Year of Life**

The STCAR model fits of the July and October YOY life stages suggested that there is weak spatial coherence in winter flounder abundance patterns among areas of Narragansett Bay during their first summer (Table 3-2). However, there was evidence of a large-scale spatial pattern that was relatively stable throughout the time series. Bay region was a significant covariate for the July life stage, where abundance decreased from north to south (all posterior probabilities of pairwise coefficient comparisons > 0.97, Figure 3-4). The estimated spatial abundance pattern of spawning winter flounder (Spring age-3+) did not correspond to the observations of the July YOY stage.

The fitted log relative abundance of each area in July predicted the observed abundance pattern in October. However, Bay region was not selected in the October model, even when the July relative abundance was omitted, suggesting that the north-south abundance pattern identified in July was less pronounced or absent at the end of the first summer (Figure 3-S1a). In contrast, the spatial correlation of abundance patterns among areas appeared to strengthen between July and October (probability = 0.940). None of the tested environmental covariates were significant predictors in either of the YOY stage models (Table 3-2) and there was no evidence that the concentration of YOY winter flounder across habitats in Rhode Island waters had changed over time.
Second Year of Life

Spatial synchrony in abundance patterns among areas of Narragansett Bay appeared to increase from the July YOY to Autumn age-1 stages (probabilities between 0.94-0.99, Table 3-2), with the possible exception of the October YOY – Spring age-1 transition (probability = 0.717). Both Spring age-1 and Autumn age-1 winter flounder were observed in higher abundances when samples were taken from deeper locations, suggesting a preference for deeper habitats develops during the second year of life (Figures 3-S1b-c). This pattern was particularly pronounced in autumn, when, for example, the estimated annual relative abundance values in the deep Upper East Passage (Area 5; Figure 3-1) were greater than those estimated for the July (probability = 0.876) and October (probability = 0.911) YOY stages. The October YOY relative abundance was a significant predictor of the abundance patterns observed in Spring age-1 flounder, but this Spring age-1 pattern was not a significant predictor for the Autumn age-1 stage. The largest differences in estimated relative abundances between the Spring and Autumn age-1 stages were observed in the Sakonnet River (Figure 3-1), where the probability of observing lower relative abundances in autumn was 0.817 in Area 6 and 0.761 in Area 9, and in Mt Hope Bay (Area 3), where the probability of observing higher abundances in autumn was 0.763. As in the YOY life stages, temperature was not a significant predictor of the observed abundance and there was not a clear time trend in patterns of habitat use or concentration of abundance.
Spawning Population

As winter flounder joined the spawning population, spatial correlation in abundance across Rhode Island waters remained high during the spring (ages 2 and 3+; Table 3-2). Notably, the estimated temporal correlation was higher in autumn than in spring life stages beginning in the first year of life (probabilities in pairwise comparisons > 0.98). Coherence in spatial abundance patterns among sequential life stages continued into the spawning population, when the Autumn age-1 relative abundance was a significant predictor in the Spring age-2 model and the Spring age-2 relative abundance was a significant predictor in the Autumn age-2+ model. While these life stages appeared to occupy similar habitats, the lack of significance of the Autumn age-2+ relative abundance in the Spring age-3+ model suggests seasonal differences among the oldest, migratory life stages. Relatedly, there were regional differences in abundance patterns for the adult Spring life stages (Figures 3-5, 3-S1d).

The Coastal Waters region, which encapsulates Rhode Island waters outside of Narragansett Bay, exhibited higher abundances than all other regions for both Spring age-2 (probabilities > 0.99) and Spring age-3+ (probabilities > 0.99) flounder (Table 3-2). Furthermore, there was also strong evidence that the Lower Narragansett Bay region exhibited higher abundances than the Mid- and Upper Bay for the Spring age-2 (probabilities > 0.93) and Spring age-3+ (probabilities > 0.95) groups. Taken together, these results suggest late juvenile and adult winter flounder are most abundant in deeper, more southerly habitats in spring. The spatial Gini coefficient also suggested that Spring age-3+ flounder had become more concentrated in these habitats over time, where the estimated coefficient was considerably higher in the last five years of
the time series compared to the first five years (probability = 0.978, Figure 3-6). No such pattern in the concentration of abundance was detected for the Spring age-2 or Autumn age-2+ groups. Matching the results for earlier life stages, the tested temperature covariates were not significant predictors of spatial abundance patterns for any of the adult life stages.

**DISCUSSION**

The results of this work suggest that there are two phases of spatial habitat use in the life cycle of winter flounder in Rhode Island waters that have stayed consistent over time. During the first phase, from settlement through the end of the first winter, winter flounder are generally present throughout Narragansett Bay with particularly high abundances in the shallow Upper Bay region immediately following larval settlement and in deeper habitats as they approach age-1. This distribution pattern changes significantly during the second summer, the transition to the second phase, when the preference for deeper habitats increases and greater abundances are observed in the Mid- and Lower-Bay and Coastal Waters regions as flounder mature and begin to join the spawning adult population (Pereira et al., 1999). Lack of correspondence to temperature or other environmental conditions suggests that these patterns are best explained by ontogenetic evolution in habitat preferences and movement in agreement with past studies of winter flounder movement patterns (McCracken, 1963; Pearcy, 1962; Saucerman and Deegan, 1991). However, an increased concentration of abundance of Spring age-3+ flounder over time in deeper, more southerly habitats suggests a potential shift in movement patterns or timing has occurred within the spawning population.
The results of the fitted mixture models used to assign winter flounder to age classes appeared to agree with past research. The mean total length and length range assigned to each age class were similar to the age-length relationships estimated for the Southern New England/Mid-Atlantic Bight stock (Northeast Fisheries Science Center, 2011). There is certainly some degree of ageing error in these assignments that cannot be estimated without corresponding age information for the Narragansett Bay subpopulation. However, this agreement with the stock assessment suggests that the error is likely small, and the results can be viewed as applying to winter flounder length intervals that approximate age classes. Although there was considerable variability in observed abundance estimates across areas and years, the STCAR model fits identified significant temporal and spatial correlation in the winter flounder catch data. This variability was particularly severe for life stages and areas for which there were few samples recorded per year, either due to the sampling design of the seine survey (YOY stages) or the distribution of random stations in the seasonal trawl surveys. It is also possible that variability in sampling dates, while they were generally stable through time, impacted observations of the abundance of mobile older life stages. Nevertheless, the identified spatiotemporal autocorrelation patterns were able to be successfully captured in the STCAR models (Appendix I).

The fitted abundance pattern for the July YOY stage suggests the Upper Bay serves as an important winter flounder nursery, corroborating the results of previous research (Meng et al. 2002, Taylor et al. 2016, McManus et al. in rev.). The highest catch rates were generally observed in the Providence River and in Greenwich Bay (Figure 3-1), indicating that these areas serve as spawning habitat. Nursery habitats
exhibiting high abundances of winter flounder are often good depositional habitats used by spawning adults to enhance larval retention (Pereira et al. 1999, McManus et al. in rev.). While the abundance of Spring age-3+ winter flounder was not a significant predictor in the July YOY STCAR model, this may be because the spring RIDMF trawl survey is conducted during the outmigration period following spawning (Pereira et al., 1999).

Although there was a clear north-south gradient in catch rates during the July YOY stage, the pattern was no longer detectable by the end of the first summer. July abundance in each region was predictive of October observations, but the latitudinal pattern was not evident even in the absence of this covariate. While YOY winter flounder exhibit extremely limited movements (McCracken, 1963; Saucerman and Deegan, 1991), Taylor et al. (2016) noted that catch rates of this age class rapidly declined in seine surveys during the autumn as water temperatures cooled. This raises the possibility that a similar dynamic could be at play in this analysis if the shallow waters of the Upper Bay cooled faster than the Mid- and Lower-Bay. However, no significant difference was detected in recorded water temperatures among Bay regions in the October seine survey (ANCOVA with year included as a continuous covariate, p=0.40), suggesting an alternative mechanism to differential cooling rates.

Several studies have noted that high temperatures and low oxygen may reduce growth (Gallagher et al., 2015; Pereira et al., 1999; Taylor and Collie, 2003) and survival (Pereira et al. 1999, Langan et al. in rev.) during the first summer. The Upper Bay exhibited the highest maximum summer temperatures recorded in the seine survey (ANCOVA with Tukey’s Honest Significant Differences, p < 0.01) and past
work has shown that this region has also historically experienced the highest rates of human disturbance and hypoxia (Meng et al., 2002; Oviatt et al., 2017). Thus, it may be that the July north-south gradient in YOY abundance is eliminated by a north-south gradient in mortality during the proceeding months, but further data collection would be necessary to confirm this hypothesis. If this is the case, then the maintenance of Upper Bay nursery habitats over time may be contributing to the population decline. A significant portion of each year class of winter flounder is being exposed to increasingly unsuitable conditions in areas that have been highly productive in the past. Rather than population productivity being limited by shrinking habitat area, it is possible that a stubborn maintenance of historic habitat extent (Meng et al., 2002) is contributing to the rise in juvenile mortality identified by Langan et al. (in rev.).

The observed distribution of catch rates of Spring age-1 winter flounder were broadly similar to those of the October YOY stage, suggesting a lack of extensive movements during the first year of life. However, Spring age-1 fish were most abundant in deeper habitats in agreement with past results indicating winter flounder move to deeper waters as temperatures cool (Taylor et al., 2016) and become more photonegative during the first winter (McCracken, 1963; Pearcy, 1962; Pereira et al., 1999). The lack of relationship between Spring age-1 and Autumn age-1 abundance patterns suggests that winter flounder may begin to move among more distant habitats during the second summer. The largest differences between these stages were in Mt. Hope Bay and the two areas representing the Sakonnet River (Figure 3-1). Area 6 exhibited warmer maximum summer temperatures recorded by the RIDMF monthly trawl survey than the other Mid-Bay areas (ANCOVA including year as a covariate
and with Tukey’s Honest Significant Differences, p < 0.05), while the sampled Area 9 stations were the shallowest of the Lower Bay areas (ANOVA with Tukey’s Honest Significant Differences, p < 0.01). A growing preference for deeper, cooler habitats (Pereira et al., 1999) may have driven this movement, but further data collection would be necessary to draw a confident conclusion and explain the increased relative abundance in Mt. Hope Bay. Even so, the results suggest that the Sakonnet River serves primarily as a spawning and nursery habitat, in agreement with past tagging studies (Powell, 1991; Saila, 1962), and not a preferred habitat for older juveniles (Figures 3-4, 3-5, 3-S1a-e). The steady increase in estimated spatial correlation among sampling areas throughout the 15 months of life may be the result of this noted growth in mobility of juvenile flounder. However, it is difficult to rule out that the more abundant, YOY stages did not simply exhibit higher sampling variability. Because most areas were only sampled once or twice per month by the seine survey, the lower sample sizes relative to those of the trawl survey in many areas could have caused high sampling variance to mask spatial correlation.

The pattern of higher abundances in deeper habitats found for the Autumn age-1 stage appears similar to the observations for the Spring age-2 and Autumn age-2+ stages. However, the fitted Autumn age-2+ relative abundance was not a significant predictor of that in the Spring age-3+ stage. This suggests that older juveniles use deep habitats throughout the Bay that are inhabited by mature flounder in the autumn. Both the Spring age-2 and age-3+ stages displayed a north-south increase in relative abundance that was not evident in the Autumn age-1 and age-2+ stages. Because some Spring age-2 flounder may be sexually mature (Northeast Fisheries Science Center,
2011; Pereira et al., 1999), it is possible their similarity to the Spring age-3+ stage represents some participation in spawning and/or the following outmigration.

Past work has shown that both resident and migratory movement strategies are present in mature winter flounder in southern New England (Sagarese and Frisk, 2011; Ziegler et al., 2019). Such mixed movement patterns within the Narragansett Bay subpopulation could complicate observations of these abundance patterns. Furthermore, adult winter flounder have been shown to form dynamic assemblages in offshore habitats following spawning that contain fish from a variety of spawning sites (Phelan, 1992). The higher abundances observed in spring in the Coastal Waters region (Area 10) may therefore reflect abundances of flounder that use alternate spawning sites such as the coastal lagoons along the south shore of Rhode Island (Taylor et al., 2016). While further research is therefore necessary to fully interpret these patterns, the difference between the spring and autumn distributions of mature winter flounder suggests that different phases of the inshore-offshore movements of the migratory population component are being sampled. If so, it may help to explain the seasonal differences in spatial and temporal correlation strength among these groups.

No relationships were detected between winter flounder abundance patterns and temperature at any life stage. Similarly, salinity and predator abundance were not found to be significant covariates for the YOY life stages. While such environmental factors almost certainly have some effect on distribution, these signals may have been small relative to the magnitude of the recorded sampling variability. On the other hand, the coherence in spatial patterns throughout the first 15 months (July YOY–
Spring age-1) of life suggests that the small-scale movements made by these life stages (McCracken, 1963; Pereira et al., 1999; Saucerman and Deegan, 1991) in response to environmental factors would likely be smaller than extent of the spatial areas used in this study.

The preference for deeper habitats documented in the 1-year old life stages and the greater movements during the second summer would align with a preference for habitats that experience less extreme temperatures (Pereira et al., 1999). However, none of the temperature covariates could explain these patterns. Langan et al. (2021) found that a variety of fish in Narragansett Bay adjusted their spatial distributions on weekly time scales to intra-estuarine gradients in temperature conditions. If juvenile winter flounder are responding to temperature or other physical conditions on similar time scales, it is possible that the seasonal nature of the data used in this analysis was insufficient to detect these movements or that winter flounder are selecting habitats relative to the suitability gradients available in their immediate surroundings within one of the studied spatial areas. For example, 1-year old winter flounder may move to deeper, cooler habitats within the same spatial area to avoid high temperatures during the summer, as suggested by the literature (Pereira et al., 1999), regardless of the exact magnitude of those temperatures. In this case, one would expect to see the preference for deep habitats, as detected in this study, as opposed to a significant relationship with recorded temperatures.

Similarly, the lack of a relationship between temperature and the spatial abundance patterns of winter flounder age-2 or older may be due to the RIDMF seasonal trawl survey being conducted during the migratory periods (Pereira et al.,
Ziegler et al., 1999; Ziegler et al., 2019) and sampling flounder executing multiple movement strategies (Sagarese and Frisk, 2011; Ziegler et al., 2019). Langan et al. (2021) also found that many species in Narragansett Bay have significantly altered their migration timing in response to temperature. However, that analysis required decades of weekly trawl measurements to characterize such changes, while the RIDMF trawl survey is conducted during short time intervals in spring and autumn. Even so, the increasing trend in concentration of abundance of Spring age-3+ flounder in the Lower-Bay and Coastal Waters regions suggests that the timing of these inshore-offshore movements may be changing. While winter flounder was not included in the analysis by Langan et al. (2021), the increased concentration of abundance in more southerly habitats would be consistent with earlier egress from the estuary following spawning. This signal may also be the result of differential patterns of habitat use or within habitat movements by some or all components of the population. A tagging study of winter flounder in the Long Island Sound determined that movement is catalyzed by a complex mixture of stimuli beyond temperature (Ziegler et al., 2019). This suggests that the roles of factors like photoperiod or lunar cycle may stabilize and complicate the migration timing of winter flounder compared to other migratory species. The absence of the concentration signal in the Autumn age-2+ and Spring age-2 groups suggests it is most likely connected to the spring outmigration after spawning, but additional data would need to be collected to confirm this hypothesis.

CONCLUSIONS

The results of this work present important information for the management of winter flounder both in Narragansett Bay and throughout their range. The many
connections between habitat factors and growth (Gallagher et al., 2015; Pereira et al., 1999; Taylor et al., 2016; Taylor and Collie, 2003), productivity (Howell et al., 2016), and survival (Pereira et al. 1999, Langan et al. in rev., McManus et al. in rev.) in this species mandate that consideration is given to the spatial pattern of stressors present across the areas used by winter flounder populations. Several studies have suggested that the recovery of winter flounder populations in southern New England is primarily being limited by juvenile mortality (Bell et al. 2014, 2018, Langan et al. in rev.). The results of this work indicated that winter flounder remain in or near shallow nursery habitats for approximately the first 15 months of life. In Narragansett Bay, the Upper Bay primary nursery areas are heavily impacted by human disturbances (Meng et al., 2002; Oviatt et al., 2017). Reducing these anthropogenic impacts may reduce hypoxia (Oviatt et al., 2017) or other stressors and, accompanied by other habitat restoration efforts, boost juvenile survival. However, other contributors to mortality during the first year of life are beyond the control of management. As climate change continues, warming temperatures, and the resulting increase in hypoxia (Oviatt et al., 2017; Paerl, 2006) and temperature-linked predation (Manderson et al. 1999, Taylor & Danila 2005, Langan et al. in rev.) may overwhelm efforts to reduce human impacts on the winter flounder life cycle.

While the benefits of management intervention may therefore be temporary, understanding the habitats critical to the survival of these early life stages can inform protective measures. Similarly, the preference for deeper habitats by juvenile winter flounder may make them more vulnerable to bycatch in fishing activities targeting other species. Spatiotemporal closures protecting such habitats could assist in
maintaining population productivity. Finally, an understanding of the seasonal movement patterns of adult winter flounder can build understanding of their vulnerability to being caught by fishermen and help to improve the efficacy of harvest rules. In this manner, this work serves as an example of the type of detailed analyses that will be required to develop spatially explicit, ecosystem-based management approaches for winter flounder and other depleted species being heavily impacted by anthropogenic activities. Through understanding the habitats that support survival and growth throughout the life cycle, fisheries managers can be successful in developing targeted management tools that confront tradeoffs in ecosystem services and help to preserve vulnerable species challenged by climate change in an evolving ocean.

ACKNOWLEDGEMENTS

We thank the Rhode Island Division of Marine Fisheries for contributing data to this work. This project was made possible through funding from the Rhode Island Department of Environmental Management, Project No. P0200696 and Rhode Island Sea Grant project number 2016-R/F-1618-31-2-RES. This analysis is a contribution of the Rhode Island Marine Fisheries Institute.

REFERENCES


https://doi.org/10.3354/meps12120


Oceanogr. Collect. 18, 39–64.


TABLES

Table 3-1. The time series average mean and range of total lengths (cm) used to assign winter flounder to each life stage based upon the fitted gaussian mixture model.

<table>
<thead>
<tr>
<th>Life Stage</th>
<th>Mean Total Length</th>
<th>Total Length Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring age-1</td>
<td>12.2</td>
<td>&lt; 16</td>
</tr>
<tr>
<td>Autumn age-1</td>
<td>17.4</td>
<td>12 – 24</td>
</tr>
<tr>
<td>Spring age-2</td>
<td>19.1</td>
<td>16 – 24</td>
</tr>
<tr>
<td>Autumn age-2+</td>
<td>26.7</td>
<td>&gt; 24</td>
</tr>
<tr>
<td>Spring age-3+</td>
<td>28.9</td>
<td>&gt; 24</td>
</tr>
</tbody>
</table>
The selected spatiotemporal conditional autoregressive (STCAR) model fits for each of the seven winter flounder life stage. The years included in each model fit, resulting from the time lags associated with the inclusion of prior life stages as covariates, are given in parentheses under each life stage. When the fitted log relative abundance of the prior life stage is included as a covariate, it is indicated by the life stage name. The posterior median and 95% credible interval, calculated on the real scale, is provided for each parameter. The continuous covariates are reported in terms of relative risk for an increase of one standard deviation of the covariate. The standard deviations of the continuous covariates are as follows: July YOY: 62.89, October YOY: 22.29, Autumn age-1: 20.55, Spring age-2: 27.25, Sampling Depth (spring): 6.49, Sampling Depth (autumn): 5.77. The larger spatial regions were abbreviated as follows: UB- Upper-Bay, MB: Mid-Bay, LB: Lower Bay, CW- Coastal Waters.

<table>
<thead>
<tr>
<th>Life Stage</th>
<th>$\rho_T$</th>
<th>$\rho_S$</th>
<th>Covariates</th>
<th>Coefficients (CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>July YOY (1988-2018)</td>
<td>0.47</td>
<td>0.13</td>
<td>MB Region</td>
<td>0.28 (0.07, 1.02)</td>
</tr>
<tr>
<td></td>
<td>(0.32, 0.65)</td>
<td>(0.01, 0.33)</td>
<td>LB Region</td>
<td>0.05 (0.01, 0.21)</td>
</tr>
<tr>
<td>October YOY (1988-2018)</td>
<td>0.33</td>
<td>0.38</td>
<td>July YOY</td>
<td>91.96 (68.81, 118.08)</td>
</tr>
<tr>
<td></td>
<td>(0.10, 0.56)</td>
<td>(0.13, 0.63)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring age-1 (1989-2018)</td>
<td>0.26</td>
<td>0.49</td>
<td>October YOY Depth</td>
<td>28.05 (23.67, 33.59)</td>
</tr>
<tr>
<td></td>
<td>(0.06, 0.44)</td>
<td>(0.27, 0.70)</td>
<td></td>
<td>7.17 (6.82, 7.46)</td>
</tr>
<tr>
<td>Autumn age-1 (1988-2018)</td>
<td>0.76</td>
<td>0.75</td>
<td>Depth</td>
<td>6.25 (5.88, 6.57)</td>
</tr>
<tr>
<td></td>
<td>(0.64, 0.86)</td>
<td>(0.55, 0.87)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring age-2 (1989-2018)</td>
<td>0.35</td>
<td>0.73</td>
<td>Autumn age-1 MB Region</td>
<td>31.28 (23.40, 41.38)</td>
</tr>
<tr>
<td></td>
<td>(0.11, 0.62)</td>
<td>(0.48, 0.88)</td>
<td>LB Region</td>
<td>0.92 (0.39, 1.93)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>CW Region</td>
<td>2.44 (0.66, 7.24)</td>
</tr>
<tr>
<td>Autumn age-2+ (1989-2018)</td>
<td>0.74</td>
<td>0.39</td>
<td>Spring age-2 MB Region</td>
<td>35.70 (30.73, 42.32)</td>
</tr>
<tr>
<td></td>
<td>(0.57, 0.87)</td>
<td>(0.09, 0.70)</td>
<td>LB Region</td>
<td>7.92 (1.70, 30.88)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>CW Region</td>
<td></td>
</tr>
<tr>
<td>Spring age-3+ (1990-2018)</td>
<td>0.49</td>
<td>0.74</td>
<td>MB Region</td>
<td>1.27 (0.65, 2.56)</td>
</tr>
<tr>
<td></td>
<td>(0.33, 0.68)</td>
<td>(0.55, 0.85)</td>
<td>LB Region</td>
<td>2.41 (0.79, 6.05)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>CW Region</td>
<td>12.18 (2.94, 43.38)</td>
</tr>
</tbody>
</table>
Figure 3-1. Map of Narragansett Bay and coastal Rhode Island waters including the areas (numbers) and regions (colors) used in modeling. The locations of the RIDMF seine survey (blue) and fixed seasonal trawl survey (red) stations are indicated by points. Random stations sampled by the RIDMF seasonal trawl survey between 1988 and 2018 are indicated by red crosses.
Figure 3-2. The number of tows performed in the RIDMF seine survey (left) and seasonal trawl survey (right) between 1988 and 2018 (top) and by spatial area (bottom). The months (seine survey, blues) and seasons (trawl survey, reds) of sampling are indicated by different color shades.
Figure 3-3. The mean catch-per-tow (CPT) of winter flounder captured in Rhode Island waters between 1988 and 2018 (top) and by spatial area (bottom) for both the RIDMF seine survey and seasonal trawl survey.
Figure 3-4. The fitted relative abundance of the July Young-of-the-Year (YOY) stage by spatial area averaged over the time bins used in generating the offsets for the STCAR model.
Figure 3-5. The fitted relative abundance of the Spring age-3+ stage by spatial area averaged over the time bins used in generating the offsets for the STCAR model.
Figure 3-6. The median (line) and 95% credible interval (shading) of the spatial Gini coefficient calculated using the fitted annual abundance patterns of Spring age-3+ winter flounder.
SUPPLEMENTS

**Figure 3-S1.** The fitted relative abundance of the remaining winter flounder life stages by spatial area averaged over the time bins used in generating the offsets for the STCAR model.

**a. October Young-of-the-Year (YOY)**
b. Spring age-1
c. Autumn age-1
d. Spring age-2
e. Autumn age-2+
Appendix I

Evaluation of the removal of spatiotemporal autocorrelation by the STCAR model fits

To determine the efficacy of the spatiotemporal conditional autoregressive (STCAR) models in removing spatiotemporal autocorrelation, the residuals were compared to the observed data and the residuals of generalized linear models (GLMs). Specifically, the observed and fitted winter flounder catch-per-tow values for each life stage were used in analysis. Missing values in the raw data, resulting from cases when no survey tows were performed in an area in a given year, were imputed using the mean catch-per-tow value observed in that area within its 5-year time bin. These time bins were composed of the same year intervals as were used to create the offsets for the STCAR models. In order to assess if the inclusion of the selected covariates alone was sufficient to remove spatiotemporal autocorrelation from the catch data, GLMs with quasi-poisson distributed errors were fit using the same formulae as in the life stage-specific STCAR models.

The observed data and residuals from the STCAR models and GLMs were then tested for spatial and temporal autocorrelation in R (R Core Team, 2020). Temporal autocorrelation was evaluated using the autocorrelation function (ACF) of the data series in each of the fitted areas individually and pooled across areas to a maximum lag of ten years (Figure 3-A1). Spatial autocorrelation was assessed using permutation tests on the Geary’s C and Moran’s I statistics with the “spdep” package (Bivand and Wong, 2018). Permutation tests of each statistic using 1,000 simulations were performed on the three data sets for each year and the corresponding p-value,
describing the probability that the null hypothesis of no autocorrelation was true, was recorded (Figure 3-A1). The results of these tests and the ACFs were then qualitatively compared among the observed data, the GLM residuals, and the STCAR residuals.

Particularly in the older winter flounder life stages, significant temporal and spatial autocorrelation was present in the observed catch-per-tow data. These patterns were not resolved by the GLM fits, which did not remove the spatial autocorrelation and, in several cases, increased the temporal autocorrelation. The STCAR fits, however, were generally successful in removing both sources of autocorrelation. The STCAR residuals suggest that different areas of Rhode Island waters displayed different degrees of temporal autocorrelation. This may simply be a function of spatial differences in sampling variability, stemming from either different levels of sampling effort among areas or unknown factors generating greater variation in winter flounder abundance in some locations over time. Due to these differences in temporal correlation strength in the abundance data, the STCAR residuals were negatively autocorrelated for certain areas in some of the life stages when the average correlation strength was removed by the model fit. However, these patterns did not appear to be severe. Spatial autocorrelation, on the other hand, was very effectively modeled in the STCAR fits. Across all life stages, the p-values for both test statistics were increased relative to tests on the observed data. Particularly for older life stages that exhibited higher levels of spatial correlation, this resulted in a large reduction in the number of years in which the Geary’s C or Moran’s I statistics suggested that spatial autocorrelation was present compared to the observed data and GLM residuals. Based
on this evidence, we conclude that the STCAR model structure was necessary to
model the spatial winter flounder abundance data analyzed in this work and performed
sufficiently in removing spatiotemporal autocorrelation.

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https://doi.org/10.1007/s11749-018-0599-x

**Figure 3-A1.** The calculated autocorrelation functions (top) and the annual p-values of the permutation tests (bottom) used to investigate spatial autocorrelation for the observed data (left), GLM residuals (center), and STCAR residuals (right) for the seven studied winter flounder life stages (a-g). Autocorrelation values outside the gray shaded region (top panels) are statistically significant (p < 0.05). The red dashed line in the bottom panels marks the p=0.05 level.

**a.** July Young-of-the-Year (YOY).
b. October Young-of-the-Year (YOY)
c. Spring age-1.
d. Autumn age-1.
e. Spring age-2.
f. Autumn age-2+
g. Spring age-3+
CONCLUSIONS

The results of this dissertation both corroborate previous research and provide new considerations regarding the impacts of climate change on winter flounder productivity and its implications for fisheries management. Clear evidence of increased juvenile mortality, particularly after 2000, was identified during the first summer of life in agreement with the decline in recruitment observed in recent stock assessments (Northeast Fisheries Science Center 2011, 2020). This mortality was attributed, at least in part, to the direct and indirect effects of climate change in the form of physical factors and predation. As temperatures continue to warm, it can be expected that hypoxia will increase in Narragansett Bay if water quality does not significantly change (Paerl 2006; Oviatt et al. 2017). Recent work has also shown that the abundance and coastal residency of striped searobin, an important predator identified in Manuscript 1, is likely to continue to rise with temperature (Collie et al. 2008; Langan et al. 2021). Supporting the results found here, all three of these factors have been identified by previous research as having a significant effect on juvenile survival in winter flounder (Pereira et al. 1999; Manderson et al. 1999; Gallagher et al. 2015).

It is very likely that there are additional factors that play a significant role in juvenile winter flounder mortality that could not be identified here, potentially due to imperfect or unavailable data. For example, sand shrimp (*Crangon septemspinosa*) has been identified as a predator of winter flounder eggs and larvae in Narragansett Bay (Taylor and Collie 2003; Taylor and Danila 2005). However, their role could not be tested in this work due to a lack of an abundance index of shrimp in the estuary. The
mosaic of geographic subpopulations that make up the Southern New England/Mid-
Atlantic Bight stock also presents the possibility of different stressors being most
important in the different groups. It is possible that the additional finfish predators of
winter flounder identified by Sagarese et al. (2011), for example, contribute to the
mortality of winter flounder in the Long Island Sound more so than in Rhode Island
waters. Thus, the factors identified here should be viewed as an important, but not
exhaustive, list of stressors impacting winter flounder productivity. Additional
research should be undertaken to investigate additional factors impacting winter
flounder survival throughout their range.

The model projections produced in Manuscript 2 indicate that the identified
environmental factors are likely sufficient to inhibit the recovery of the Narragansett
Bay winter flounder subpopulation to past high levels of abundance. Notably, these
projections, which are not meant to replace a standard stock assessment model,
required assumptions about mean juvenile mortality rates and were based on structural
equation models that could not explain a significant amount of variance within the
winter flounder life cycle. If there are yet unidentified factors significantly
contributing to the mortality patterns of Narragansett Bay winter flounder, it is
possible that their inclusion would alter the projected future abundance of this
subpopulation. However, the current depleted state and the expected increase in
severity of summer temperatures, hypoxia, and searobin predation indicate that such
an unexplained factor would need to produce a very large positive effect to overcome
increasing juvenile mortality and allow the population to fully rebuild. This conclusion
is corroborated by the spatiotemporal modeling in Manuscript 3, which suggested that
the timing of spring egress following spawning may have shifted earlier and that winter flounder are maintaining nursery habitats in areas of Narragansett Bay that experience high temperatures and low oxygen concentrations (Oviatt et al. 2017). Taken together, these patterns indicate that the spawning duration may be shrinking, with unknown impacts on egg production, and that young-of-the-year flounder will be increasingly exposed to unsuitable summer conditions in the future. Based on this stability in nursery habitat, it is unlikely that the relationships between juvenile mortality and temperature and hypoxia estimated in the structural equation models will be mitigated by a future shift in spatial distribution within coastal waters.

Although the results of this work do not suggest Narragansett Bay winter flounder are likely to return to the abundance levels observed in the early 1980s, it is notable that the abundance projections in Manuscript 2 suggested substantial population growth was plausible under the right conditions. Rising summer temperatures cannot be controlled at the level of regional fisheries management, but great success in improving water quality, thereby reducing hypoxia, has already been achieved in Narragansett Bay (Oviatt et al. 2017). Further improvements in water quality, perhaps coupled with the removal of searobins if they were made a viable fisheries target species, would likely have a measurable positive effect on winter flounder. While not included in the models in this work, other habitat improvements targeting the nursery areas would likely also improve the productivity of the subpopulation. The spatiotemporal models in Manuscript 3 suggested that winter flounder stay in or near shallow nursery habitats in the upper Bay for their first 15 months of life. Protection and enhancement of these habitats would therefore benefit year classes until they
achieved greater mobility and could participate in greater active habitat selection and
avoid unsuitable conditions (McCracken 1963; Pereira et al. 1999). Although it may
not be possible to return this winter flounder subpopulation to the high abundances of
the past, improvement from the current state is likely possible.

As a population near the warm edge of the species range (Pereira et al. 1999), the
results of this work demonstrate that Narragansett Bay winter flounder productivity is
in large part a function of climate. Viewed from this perspective, it is unsurprising that
Manuscript 2 suggested that the best way to achieve population recovery is to turn
back time. This finding likely generally holds for the Southern New England/Mid-
Atlantic Bight Stock as a whole, though variation among subpopulations is possible.
Winter flounder are not the only species in the Northeast United States Continental
Shelf ecosystem experiencing declining productivity due to climate change (Pershing
et al. 2015; Xu et al. 2018; Tableau et al. 2019), resulting in challenges in stock
assessment and management. When species exhibit non-stationarity in productivity
and other population processes, they should be regulated with non-stationary
management targets (Szuwalski and Hollowed 2016). The current laws governing the
management of marine fisheries in the United States mandate that attempts are made
to recover depleted stocks (National Oceanic and Atmospheric Administration 2006).
However, attempting to recover climate-challenged stocks to a level last achieved
under very different environmental conditions would likely significantly impact other
healthy fisheries and may ultimately be unsuccessful anyway. Instead, developing
dynamic management targets that reflect climate conditions may allow for successful
management of climate-challenged stocks while preventing them from becoming
choke species in other successful fisheries (Holland 2010). One way to achieve this would be the greater inclusion of environmental information in stock assessment, in that biological reference points could be calculated to reflect current productivity trends. This has already been investigated for winter flounder (Bell et al. 2018), but thus far such an approach has not been used in management of the fishery (Northeast Fisheries Science Center 2020). The results of this work therefore emphasize the need to continue these research efforts to include climate and other habitat suitability factors in assessment models and work toward ecosystem-based fisheries management.

We hope that this work provides scientists and fisheries managers, present and future, with additional information and insights to use in the management of winter flounder and all other climate-challenged species facing a warming ocean.

REFERENCES


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