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Externally driven changes in the abundance of summer and winter flounder

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Marine organisms that utilize nearshore environments for major components of their life histories are subject to both local-scale forcing such as water quality and estuarine degradation as well as large-scale forcing such as fishing and decadal-scale climate variability. Large-scale forcing has the potential to synchronize the dynamics of subpopulations, while local-level forcing can produce asynchronous subpopulation trends. Summer flounder (*Paralichthys dentatus*) and winter flounder (*Pseudopleuronectes americanus*) are important commercial and recreational flatfish along the east coast of North America which spend their first year of life in coastal habitats. We found that the two exhibited significant within-species coherence in commercial landings and fisheries-independent surveys across the northeast shelf of the United States, suggesting large-scale external drivers. In laboratory studies, temperature has been found to be an important factor regulating survival during the egg, larva and settlement phases of both species. We reconstructed a 40-year time-series of coastal water temperature for the major spawning and nursery areas to examine changes in the thermally available habitat. Estimates of winter flounder abundance were negatively correlated with the winter water temperature, but not with fishing mortality. Summer flounder abundance, by contrast, was negatively correlated with fishing mortality, but exhibited no link with temperature. In addition, time-varying stock–recruitment relationships indicated that stock productivity declined for winter flounder over time, while summer flounder productivity has varied without a trend. While both species declined in the 1980s and early 1990s due to heavy fishing pressure, the reduction in fishing over the last two decades has led to rebuilding of the summer flounder stock and an expansion of its age structure. Declining productivity due to warming estuarine conditions has kept the winter flounder stock at low levels despite low fishing pressure. The two stocks illustrate the importance of controlling fishing mortality in the management of natural marine resources while also accounting for changes in productivity due to climate variability and change.

Keywords: environmental drivers, groundfish, Kalman Filter, recruitment, southern New England, state–space models, summer flounder, temperature, time-varying parameters, winter flounder.

Introduction

The abundance and distribution of marine organisms can be heavily impacted by fishing and the environment (Anderson and Piatt, 1999; Quinn and Deriso, 1999; Mann and Lazier, 2004; Worm *et al.*, 2009). While the effects of fishing are directly incorporated into assessments and management, the effects of environmental change can be harder to quantify and are therefore rarely accounted for in management regulations. A number of studies have shown that large-scale variations in climate have had major effects on the fish stocks along the east coast of the USA (Murawski, 1993; Mountain, 2002; Oviatt, 2004; Sullivan *et al.*, 2005; Hare and Able, 2007; Nye *et al.*, 2009). Mortality due to the environment and other factors is typically greatest for developing larval and juveniles, and thus the first year of life is often considered the most important period for determining the abundance of a year class (Houde, 1987). A growing body of work has shown that temperature during critical periods of development can have a strong impact on the survival of fish in their first year of life (Keller and Klein-MacPhee, 2000; Taylor and Collie, 2003; Sullivan *et al.*, 2005; Hare and Able, 2007; Manderson, 2008). Atlantic croaker larvae (*Micropogonias undulatus*) overwinter in estuaries where temperatures can reach their lower thermal limit. Colder winters result in higher larval mortality, while warmer winters result in higher survival, greater recruitment and an increase in total croaker biomass (Lankford and Targett, 2001; Hare and Able, 2007). Water temperature affects survival because it is directly related to the physiological limits of fish, and also influences predation risk and food availability.

Summer and winter flounder are two commercially and recreationally important flatfish that spend their first year of life in coastal habitats where changes in seasonal temperatures can have substantial effects (Collette and Klein-MacPhee, 2002). Summer flounder (*Paralichthys dentatus*) spawn in the fall as they migrate into deeper water, and their larvae overwinter in nearshore environments. Summer flounder recruitment has been linked to the North Atlantic Oscillation (Brodziak and O'Brien, 2005), however recruitment is not correlated with larval abundance in the late fall/early winter (Able *et al*., 2011). Since summer flounder larvae and post-settlement juveniles exhibit high mortality below about 2–4°C (Malloy and Targett, 1991, 1994; Szedlmayer *et al*., 1992), it has been suggested that warmer winters result in higher overwintering survival, particularly in the northern part of its range, because of the increase in the number of estuaries with thermally suitable habitat. Warmer conditions would result in higher recruitment and an increase in stock biomass (Able *et al*., 2011).

Winter flounder (*Psuedopleuronectes americanus*) is a cold-water species in which the coastal stocks migrate into estuaries and spawn in the late winter/early spring. It has been hypothesized that low temperatures offer the developing eggs and larvae a thermal refuge from predation because very few predators reside in estuaries during the winter (Jeffries and Johnson, 1974; Collette and Klein-MacPhee, 2002; Taylor and Collie, 2003). Over the past few decades, the southern stock of winter flounder (SNE/MAB) has declined, while winter temperatures have increased (Jeffries and Terceiro, 1985; Nixon *et al*., 2004; Nye *et al*., 2009; NEFSC, 2011). Mesocosm and lab studies have shown that egg survival decreases while predation on both eggs and larvae increases with increasing water temperature (Keller and Klein-MacPhee, 2000; Taylor and Collie, 2003). Warmer winter temperatures and earlier warming in the spring may allow predators to enter estuaries earlier, eliminating the thermal refuge (Taylor, 2005). Since the early 1990s, winter flounder recruitment in different estuaries in southern New England and the mid Atlantic Bight (SNE/MAB) has shown increasing coherence, suggesting that a large-scale factor such as the environment is driving recruitment, and not estuarine-specific factors such as shoreline loss or pollution (Manderson, 2008).

Given the potentially positive effects of rising temperatures on summer flounder and negative effects on winter flounder, their future abundances and long-term viability could have important ecological and economic consequences for the US northeast shelf. Our goal was to examine whether an environmental driver could provide a mechanism for regulating the stocks of the two species. To identify the effects of a potential driver, we developed a set of criteria with which to evaluate summer and winter flounder.

(i) A clear mechanistic link needed to be identified between the external driver and its effects on the organism. Based on the lower thermal limit hypothesis for summer flounder larvae and the thermal refuge from predation hypothesis for winter flounder, we identified estuarine winter temperature as our environmental external driver. Fishing pressure is also a major factor for many marine species and was tested as a potential external driver as well.

(ii) The subpopulations of an organism should be synchronized at the scale of the external driver. If a large-scale driver such as decadal-scale climate variability or fishing was an important factor it would result in synchronized dynamics over broad spatial scales. Abundance estimates in different areas throughout an organisms range would exhibit similar trends. Alternatively, if smaller-scale factors such as water quality or coastal habitat degradation within estuaries were the main drivers, there would be no expectation of synchrony across estuaries.

(iii) Abundance estimates should exhibit some type of relationship with the external driver.

(iv) Predictive models that incorporate the external driver should improve estimates of abundance. Based on the hypotheses for the mechanistic links, we developed two sets of stock–recruitment relationships for the flounder species. We tested a general hypothesis that changes in the environment would in turn affect the vital rates of a marine organism and that changes in vital rates would alter stock productivity over time. The more general hypothesis was tested with a time-varying state–space model to examine if summer and winter flounder had exhibited changes in productivity over time. Following the productivity analysis, we incorporated the estuarine temperature into the stock–recruitment relationships to determine if an environmental factor was an important driver affecting recruitment.

Methods

Temperature

Independent, long-term water temperature datasets were developed for five estuaries on the northeast shelf: Woods Hole, Massachusetts (Nixon *et al*., 2004); Narragansett Bay, Rhode Island (Collie *et al*., 2008); Long Island Sound (Milford Laboratory, NOAA); Delaware Bay (Susan Ford, Haskin Shellfish Research Laboratory); and Chesapeake Bay [Gary Anderson (VIMS, 2003)]. A combination of surface temperature datasets in each estuary roughly covered the period from 1959–2012, but did contain some erroneous datapoints and missing records. Erroneous datapoints were defined as individual points that were outside of three Median Absolute Deviations (MADs) from the median. A MAD is roughly equivalent to the standard deviation, but is a more robust measure of variability that is based on the median (Verzani, 2005). Errors were identified and removed. The MAD was based on the median over all years available. In a number of estuaries, the historical temperature datasets were combined with buoy data from the NOAA Tide Prediction Center or the National Estuarine Research Reserve System (NERRS). Predicted water temperature based on observed air temperature data (Bates and Conklin, 2005; Hare and Able, 2007) was used to fill in gaps in certain estuaries to get a complete record through 2012. (See the Supplementary data for details on the different temperature time-series.) Four temperature metrics were developed for the analysis.

(i) The mean winter temperature in each estuary was calculated as the mean temperature over all weeks from January–March. The mean winter temperature in each year was averaged across the five estuaries to produce a single mean winter temperature.

(ii) The date of the end of winter metric was calculated based on a more flexible definition of winter. The calendar was restructured to focus on the coldest months, so that a year started in July and ended the following June. Winter year 1999 went from July 1999 to June 2000. The winter was defined as the longest span of time over which the mean temperature was 3°C. This accounted for warming and cooling periods, varied from year to year, and had start and end dates which typically captured the initial temperature decline going into the winter and the temperature increase as the winter was ending. The end of winter metric was the week of the year defining the end of the period when the mean temperature was 3°C. In some years, the temperature in certain estuaries never went below 3°C and there was no winter. The mean end of winter was determined for each estuary and subtracted from the time-series to provide an end of winter deviance from the mean. The deviance each year was averaged across the five estuaries to give a single metric.

(iii) The mean thermally available habitat area ($\overline{\text{area}}$) was the mean area over all five estuaries each year that was considered suitable for eggs, larvae and settlement. The total length of the winter was not considered as important as the timing of the end of the winter and the amount of time the winter projected into spring. The end date was subtracted from a fixed point in time (15 December) to provide the number of days in each estuary (*est*), each year (*yr*) ($\text{days}_{est,yr} = \text{wtr end}_{est,yr} - 15$ Dec). The mean thermally available habitat area ($\overline{\text{area}}$) was:

$$\overline{\text{area}}_{yr} = \frac{\sum_{est=1}^{5} \text{days}_{est,yr} \cdot \text{area}_{est}}{\sum_{est=1}^{5} \text{days}_{est,yr}}. \tag{1}$$

(iv) The summed available habitat (sum area) was the summed number of days times the area of each estuary.

$$\text{sum area}_{yr} = \sum_{est=1}^{5} \text{days}_{est,yr} \cdot \text{area}_{est}. \tag{2}$$

The temperature metrics were regressed against the abundance time-series and used in the environmentally driven stock–recruitment relationship. Based on the working hypotheses, if winter temperature was important, winter flounder abundance would be expected to be positively correlated with longer, colder temperatures, and summer flounder abundance would be positively correlated with shorter, warmer temperatures. The mean thermally available habitat area and the summed available habitat would be positively correlated with winter flounder abundance and negatively correlated with summer flounder abundance.

Estuaries digital elevation models

The total area at depth of each estuary was compiled from digital elevation models (DEMs) available from NOAA's National Ocean Service (http://estuarinebathymetry.noaa.gov/finddata.html, last accessed October 2012). The total area <5 m deep in each estuary was summed as a measure of the total potential spawning and nursery habitat. The Chesapeake Bay was the only estuary with significant freshwater habitat contained within the DEMs that would not be suitable for summer and winter flounder. We estimated 1000 km^2 of freshwater habitat (NOAA, 1985; Anonymous, 1999) and subtracted this from the total area of Chesapeake Bay <5 m as a conservative measure of potential habitat.

Fishery-independent survey data

Long term, fishery-independent survey data for the entire stock of summer flounder and the SNE/MAB stock of winter flounder were available from the Northeast Fisheries Science Center (NEFSC) stock assessments (NEFSC, 2011; Terceiro, 2012), the Massachusetts Division of Marine Fisheries (MADMF), the Graduate School of Oceanography, University of Rhode Island (GSO) (Collie *et al.*, 2008), the Millstone Power Plant/Dominion, CT (Dominion Resources Services, 2007), the Connecticut Department of Environmental Protection (CTDEP) and the Virginia Institute of Marine Science juvenile trawl survey (VIMS). The NEFSC indices were the fall stratified mean number per tow (all size classes) for summer flounder and spring stratified mean number per tow (all size classes) for winter flounder. Massachusetts Division of Marine Fisheries indices, stratified mean number per tow, were the fall survey for summer flounder and the spring survey for winter flounder (data from NEFSC stock assessments). The GSO indices were the mean of the monthly mean abundance of total catch (all size classes). The winter flounder indices from the Millstone Power Plant/Dominion were the annual delta-mean standardized catch per tow of individuals ≥15 cm. The CTDEP indices (geometric mean per tow) of summer flounder were from the fall survey. The VIMS data were from the juvenile trawl survey (Tuckey and Fabrizio, 2013). VIMS standardized summer flounder data (geometric mean catch per trawl) were available from the 2012 stock assessment (Terceiro, 2012). The VIMS winter flounder data were the geometric mean calculated for all individuals ≤15 cm caught in June and July by stratum and weighted by stratum size. They are not fully standardized for changes in the survey design and prior to 1988 are more of a presence/absence indicator than relative index of abundance (T. Tuckey, pers. comm.).

Commercial landings

Landings data without fishing effort are not a good indicator of abundance, however the US domestic fleet was relatively small prior to the implementation of the Exclusive Economic Zone (EEZ), and effort could be assumed to be relatively constant or increasing slightly. Domestic fishing effort and fleet capacity increased substantially in the 1980s and then decreased in the mid-1990s as regulatory controls were put in place (Murawski *et al.*, 2002). The commercial data prior to the 1980s, therefore, provide some indication of the abundance of the two stocks that goes back further than the fishery-independent surveys.

Summer and winter flounder commercial landings data for the Atlantic region of the USA were available by state from the NOAA commercial landings website (http://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index, last accessed March 2013).

Data analysis

Synchrony among the different datasets for each species fishery-independent survey and commercial landings was examined with Kendall's coefficient of concordance Kendall's Wt. Kendall's Wt measures the coherence of datasets on a scale from 0–1. One indicates perfect alignment, while zero indicates no coherence.

A simple linear model was developed to examine the relationship between external drivers and abundance. Fishing mortality (F_t) was regressed against the spawning stock biomass (SSB_t) for each species ($SSB_t = \beta_0 + F_t \cdot \beta_1$), and recruits per spawning stock biomass (R_t/SSB_{t-1}) were regressed against the four winter temperature metrics ($T_{i,t-1}, i = 1-4$) $\left(\frac{R_t}{SSB_{t-1}} = \beta_0 + T_{i,t-1} \cdot \beta_1\right)$. The different abundance indices were based on the life stage in which the driver would potentially affect the stocks.

A strong negative relationship between F_t and SSB_t indicates that fishing is one of the major drivers of abundance. A weak or non-significant relationship, however, suggests that while fishing may be important, other factors have greater control over abundance. Factors such as additional mortality due to predation, the physical environment, or changes to growth, fecundity, or other vital rates due to the environment, alter the productivity of the stock and exert a strong influence on fish abundance. Estimates of F_t and SSB_t were taken from the summer and winter flounder stock assessments (SNE/MAB) (NEFSC, 2011; Terceiro, 2012).

Time-varying recruitment function

To examine potential changes in the productivity of the summer and winter flounder stocks, we fit a Ricker spawner–recruit model with a time-varying productivity parameter to the output of the NEFSC stock assessments (Peterman *et al.*, 2000, 2003; Collie *et al.*, 2012). In the standard Ricker model, the number of recruits (R) is a function of the number of spawners (S) times their productivity (a) dampened by a density-dependent or compensation term (b) (Quinn and Deriso, 1999). The Ricker model was fit within a state–space framework with maximum likelihood using a Kalman filter. The productivity parameter (a) was allowed to vary as a function of a random walk. Within the Kalman filtering and smoothing process, a parameter only varied in time if the data warranted it.

State–space modelling is a means to account for measurement error within real data. Real world observations are comprised of the true state of the variable being recorded and measurement error. The observation equation, the Ricker model in this analysis, accounts for the measurement error in the data by explicitly modelling the variance. This allows the true state of the variable to be modelled in the process equation, the random walk.

$$ln\left(\frac{R_t}{S_{t-1}}\right) = a_t - bS_{t-1} + v_t \tag{3}$$

$$a_t = a_{t-1} + w_t^a \tag{4}$$

$$v_t \sim N(0, V) \tag{5}$$

$$w_t^a \sim N(0, W_a) \tag{6}$$

The observation error (v_t) and random walk parameter (w_t) are normally distributed with mean 0. The parameter (a_t) is a random walk where the random component w_t captures the annual change in production potential. The model estimates three parameters, the density-dependent term (b) the variance of v_t (V), and the variance of the random walk (W_a) for the time-varying value (a). The time-varying parameter captures potential changes in the production potential of the stock. The changes could be due to changes in the external environment such as habitat availability or to changes in the biology of the fish themselves (changes in fecundity, spawner success etc.). The random walk captures the empirical changes in the parameters directly from the data.

Three models of increasing complexity were fit to each dataset for comparison. The first model was a simple linear regression with the estimate of observation error (V) calculated as:

$$\sigma^2 = \frac{1}{n-2}\sum_i^n residuals^2. \tag{7}$$

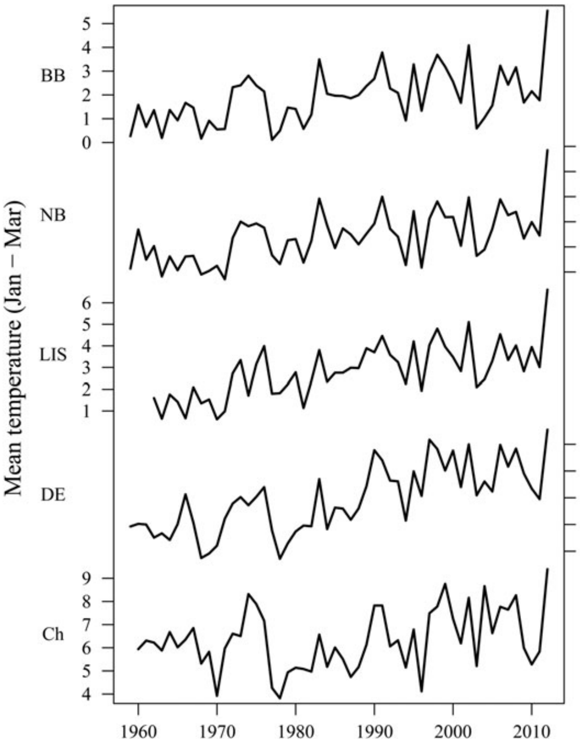

Figure 1. The mean water temperature over the period Jan–Mar. (BB = Buzzards Bay–Woods Hole, NB = Narragansett Bay, LIS = Long Island Sound, DE = Delaware Bay, Ch = Chesapeake Bay).

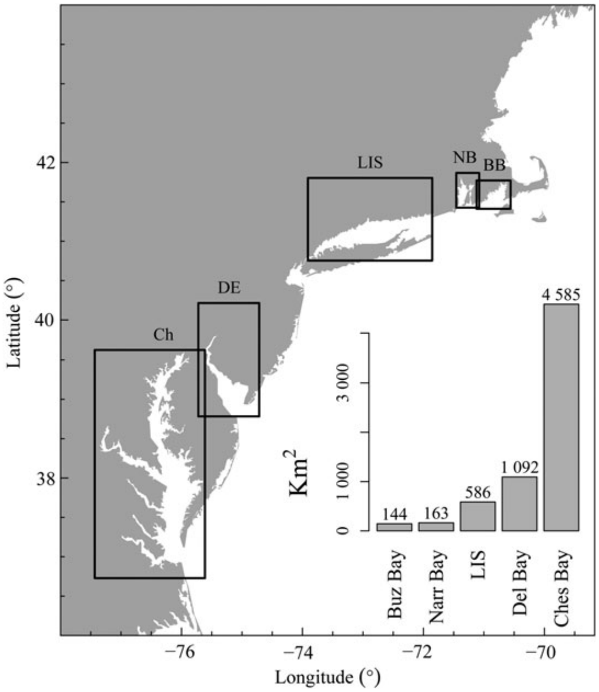

Figure 2. The location of the five estuaries along the east coast of the USA. The area of each estuary <5 m depth was calculated from the digital elevation models. The estuaries range from Chesapeake Bay (Ches Bay) in the south to Buzzards Bay (Buzz Bay) in the northeast, with Delaware Bay (Del Bay), Long Island Sound (LIS) and Narragansett Bay (Narr Bay) in between.

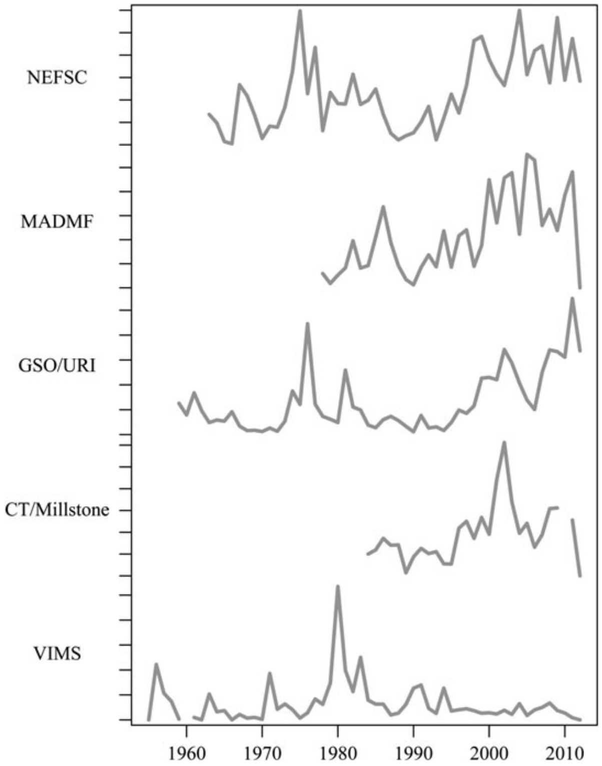

Figure 3. Long-term fisheries-independent data for summer flounder in the northeast USA. The *y*-axes for the separate surveys are on different scales. (NEFSC = Northeast Fisheries Science Center ground fish survey, MADMF = Massachusetts Division of Marine Fisheries, GSO/URI = the Graduate School of Oceanography, University of Rhode Island, Millstone/CT = the Millstone Environmental Laboratory (Dominion), CT = the Connecticut Department of Environmental Protection, VIMS = the Virginia Institute of Marine Science juvenile trawl survey.)

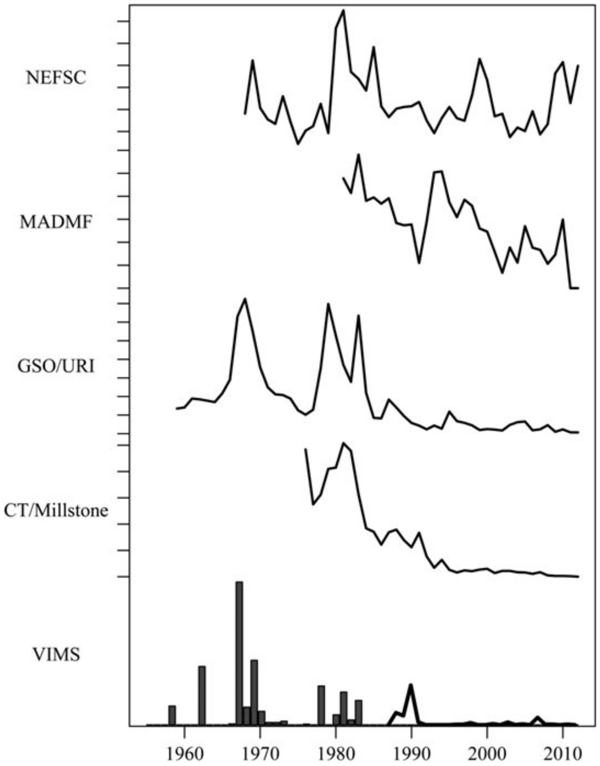

Figure 4. Long-term fisheries-independent data for winter flounder in the northeast USA. The *y*-axes for the separate surveys are on different scales. Prior to 1988 the VIMS survey was not fully standardized and is represented with bars. The continuous time-series begins in 1988 with the line. (NEFSC = Northeast Fisheries Science Center ground fish survey, MADMF = Massachusetts Division of Marine Fisheries, GSO/URI = the Graduate School of Oceanography (University of Rhode Island), Millstone/CT = the Millstone Environmental Laboratory, Dominion, CT = the Connecticut Department of Environmental Protection, VIMS = the Virginia Institute of Marine Science juvenile trawl survey.)

The remaining models were all fit by maximum likelihood within a state–space framework. The time-invariant model estimated only the variance of the observation error (V). The variance of the random walk component was held to zero ($W_a = 0$) and should result in an almost identical fit to the initial linear model. The time-varying intercept model estimated the variance of the observation error (V) and the variance of the intercept random walk component (W_a). These models were fit with the package dlm (Dynamic Linear Modelling) in the software package R (Petris *et al.*, 2009).

Environmentally driven stock–recruitment model

Environmentally driven Ricker and Beverton-and-Holt recruitment models were developed to integrate the environment directly into the spawner–recruit relationship (Quinn and Deriso, 1999; Levi *et al.*, 2003). The model parameters have the same values as above (productivity ($ln(\alpha) = a$) and compensation (b)), along with an additional environmental parameter (c). The models were fit with maximum likelihood in the software R, assuming a Gamma-distributed error structure, $R \sim \text{Gamma}(shape, \frac{mean}{shape})$. The Gamma distribution was parametrized with shape (s) and the mean where scale = mean/shape. The four estuarine temperature metrics were used as the environmental time-series—Ricker:

$$R_t = \alpha e^{c\cdot environ_{t-1}} \cdot S_{t-1} e^{-bS_{t-1}}; \tag{8}$$

Beverton and Holt:

$$R_t = \frac{\alpha S_{t-1} e^{c\cdot environ_{t-1}}}{1 + bS_{t-1}}. \tag{9}$$

Models were compared based on the AIC.

Results

Temperature

The combination of the observed water and air temperature datasets provided an independent, long-term temperature record for each estuary. The water and air temperature data were highly correlated, resulting in good estimates of predicted water temperature for missing records.

The mean winter temperature for each estuary was strongly coherent (Wt = 0.821, p-value < 0.0001) (Figure 1). Winter temperatures were generally colder in the later half of the 1960s, particularly the late 1960s and then rose through the 1970s. The winters were colder in the late 1970s and early 1980s and then increased through 2012. There have been occasional cold winters since the 1980s, but in general winter temperatures have been warming over the past three decades.

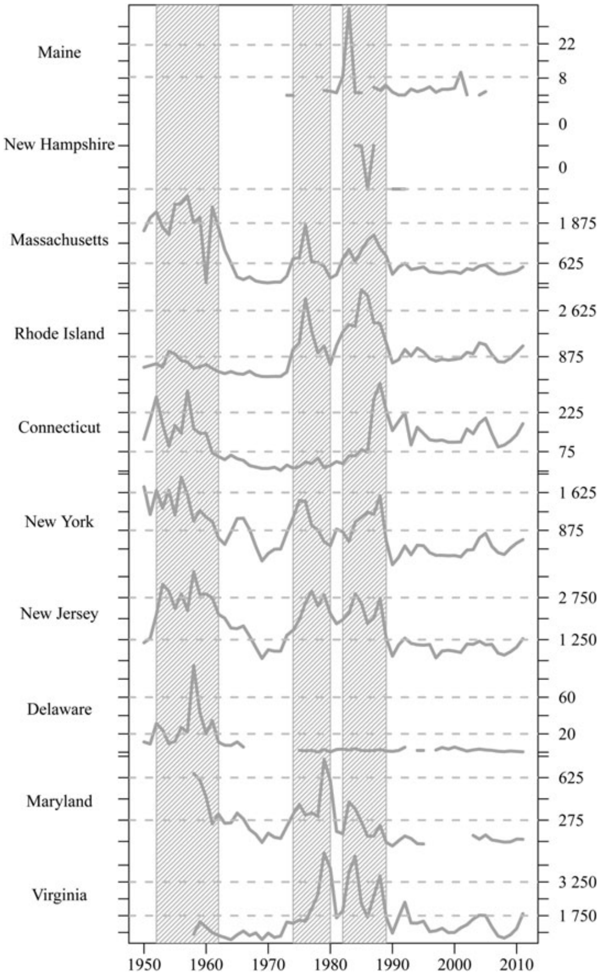

Figure 5. The commercial landings data by state in metric tons for summer flounder in the northeast USA. The *y*-axes of the different states are on different scales. Shaded regions show coherent peaks among states. The dashed lines are 20% and 80% of maximum catch in each state over the time-series.

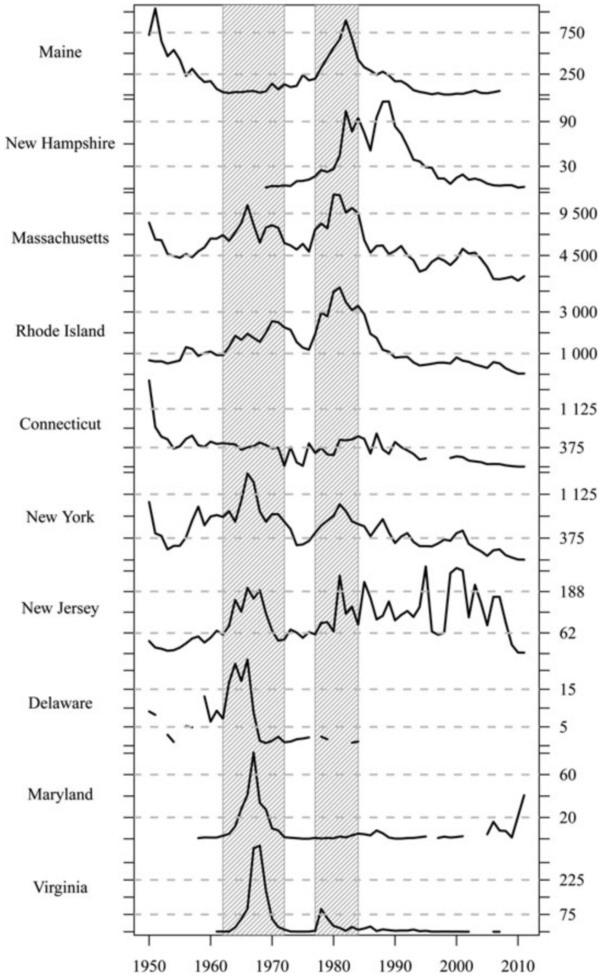

Figure 6. The commercial landings data by state in metric tons for winter flounder in the northeast USA. The *y*-axes of the different states are on different scales. Shaded regions show coherent peaks among states. The dashed lines are 20% and 80% of maximum catch in each state over the time-series.

Digital elevation maps

The five estuaries with long-term temperature data captured the majority of the range of summer founder and the SNE/MAB winter flounder stock (Figure 2). Chesapeake Bay was the largest estuary and had the greatest amount of shallow-water spawning and nursery habitat (<5 m deep).

Fishery-independent surveys

The fishery-independent surveys exhibited significant coherence for summer flounder ($\text{Wt} = 0.458$, p-value < 0.0001) and winter flounder ($\text{Wt} = 0.378$, p-value < 0.0001). Summer flounder showed strong coherence in the later part of the time-series (mid-1990s to the present) except for the VIMS survey (Figure 3). Two of the longer surveys also had a peak in abundance in the mid-1970s. The different surveys indicated that winter flounder exhibited peaks in abundance in the late 1960s and the late 1970s to early 1980s (Figure 4). The NEFSC and the MADMF surveys indicated additional peaks in the 1990s that were not present in surveys further south.

Commercial landings

There was significant coherence across the state landing data for both summer flounder ($\text{Wt} = 0.35$, p-value < 0.0001) and winter flounder ($\text{Wt} = 0.33$, p-value < 0.0001). The 1950s through the early 1960s was a period of higher summer flounder landings followed by a period of elevated winter flounder landings from the mid-1960s through 1970 (Figures 5 and 6). Summer flounder landings increased again in the 1970s with another peak in the mid-1980s when fishing effort was high. Landings in the Gulf of Maine, Maine and NH, typically considered outside of the range of summer flounder, had small landings as well. Winter flounder landings exhibited another peak in the early 1980s in the northern part of their range when fishing effort was high, but landings were low or absent through much of the Mid-Atlantic Bight. Winter flounder were caught and landed in Virginia, however, during the two colder periods.

Data analysis

The relationship between estimated *SSB* and *F* for summer and winter flounder exhibited contrasting patterns (Figure 7). The

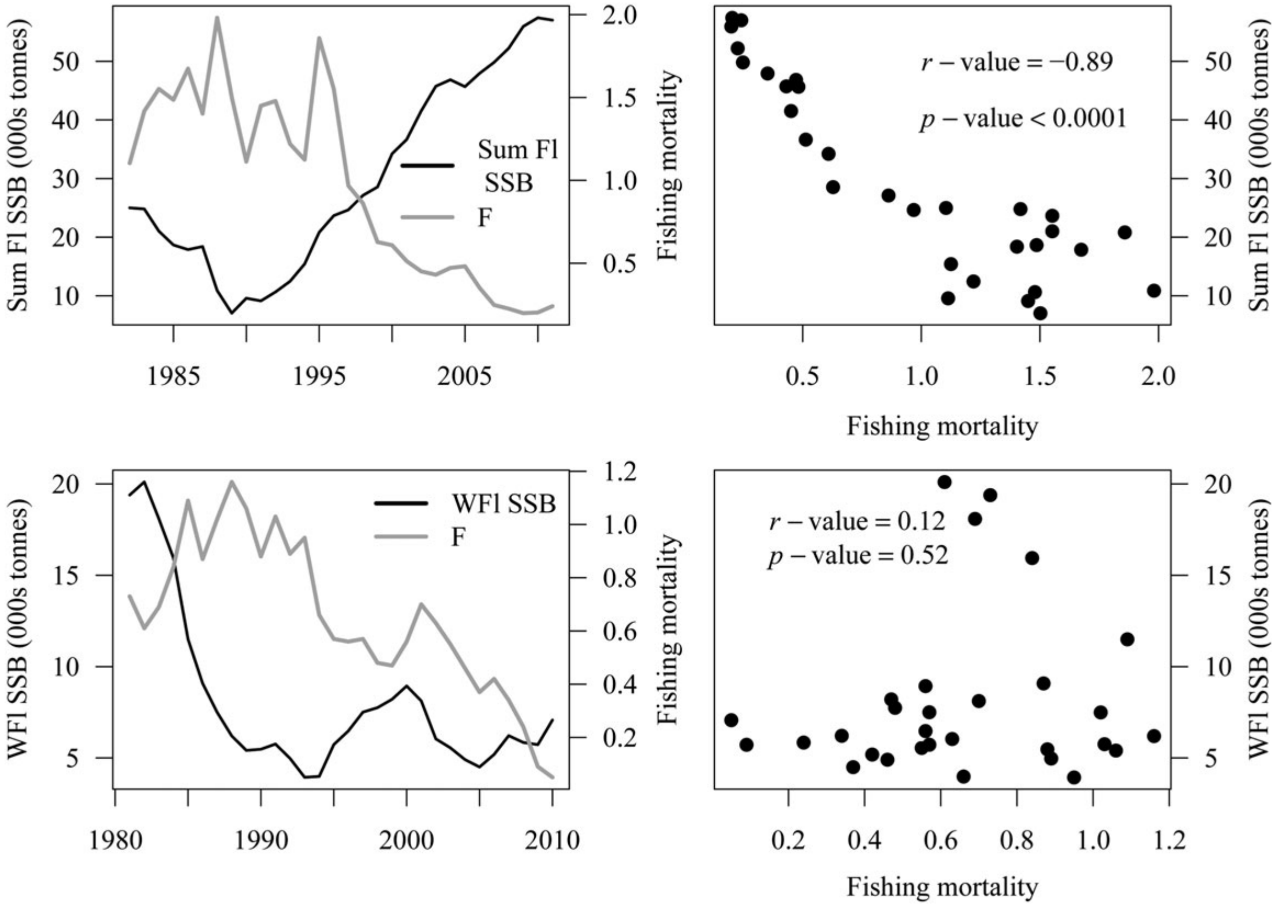

Figure 7. The estimated spawning stock biomass (*SSB*) and fishing mortality (*F*) for summer and winter flounder. The two were negatively correlated for summer flounder ($r = -0.89$, p-value < 0.0001), but were not significant correlated for winter flounder (p-value $= 0.52$).

fishing mortality for both stocks was high in the 1980s and early 1990s, but declined considerably over the last 15 years. The drop in fishing mortality showed a significant relationship with an increase in summer flounder abundance ($r = -0.89$, p-value < 0.0001), but was not significant related to winter flounder abundance (p-value $= 0.52$). Both *SSB* and *F* are derived values from an assessment model, however some type of model is required to calculate estimates of *SSB* and *F*. The summer and winter flounder assessment models provide the most scrutinized and vetted models available (NEFSC, 2011; Terceiro, 2012). The correlations suggest that the major driver of summer flounder over the last 30 years is mortality due to fishing. Similarly, winter flounder may have been heavily affected by fishing in the early 1980s; however over the last 20 years, other factors likely superseded fishing pressure as the major control on abundance.

Based on the working hypotheses of how the environment could affect the early life stages of both stocks, the temperature metrics were regressed against the recruits divided by spawners (Table 1 and Figure 8). None of the environmental metrics were significantly correlated with summer flounder recruits over spawners. There was no evidence of a relationship between the estuary winter temperature and subsequent recruitment (Table 1).

Three of the four metrics for winter flounder were significantly correlated with recruits over spawners, and the mean winter temperature had the strongest relationship (Table 1). The correlations lend support to the hypothesis that warmer winters and earlier warming in the spring reduce the thermal refuge from predation, leading to lower recruitment.

Table 1. Pearson's product-moment correlation between each environmental factor and recruits divided by spawners for the two species.

Species	Factor	*r*	*p*-value
SUMFL	Wtr Mean	0.004	0.98
SUMFL	Wtr Mean End	−0.004	0.98
SUMFL	Mean End Area	−0.153	0.43
SUMFL	Sum End Area	−0.134	0.49
WFL	Wtr Mean	−0.54	0.002
WFL	Wtr Mean End	0.46	0.012
WFL	Mean End Area	0.34	0.074
WFL	Sum End Area	0.41	0.029

Wtr Mean = mean winter temperature, Jan–Mar temperature averaged across estuaries; Wtr Mean End = the number of days between the end of winter and the mean end of winter averaged across estuaries, Mean End Area = the mean thermal habitat area available each year, Sum End Area = the summed thermal habitat area available each year.

Time-varying recruitment function

The three different Ricker stock–recruitment models were fit to the data from the summer and winter flounder stock assessments (NEFSC, 2011; Terceiro, 2012), and all the models converged.

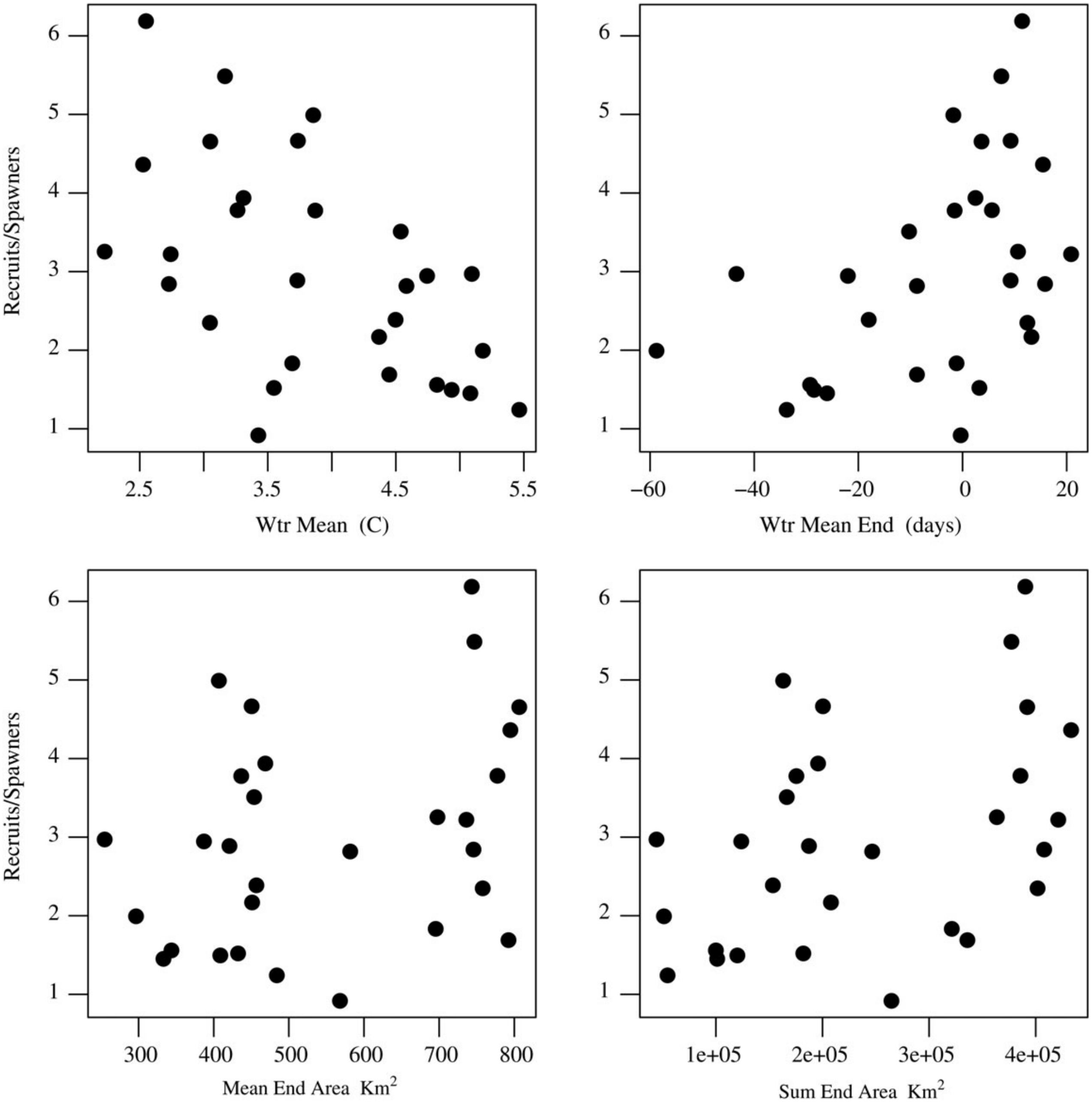

Figure 8. The four temperature environmental drivers and winter flounder recruits divided by spawners. (Wtr Mean = mean winter temperature Jan–Mar temperature averaged across estuaries, Wtr Mean End = the number of days between the end of winter and the mean end of winter averaged across estuaries, Mean End Area = the mean thermal habitat area available each year, Sum End Area = the summed thermal habitat area available each year.)

With the data available for summer flounder, the time-varying model did not fit better than the constant model, and the model selection process indicated that the standard Ricker model was the best model (Table 2 and Figure 9). Though recruitment varied, the data provided no evidence that the production potential of the summer flounder stock had changed over time.

The Ricker model with a time-varying production parameter (a) was the best model for winter flounder (Table 3). The time-varying recruitment model indicated that the productivity of the winter flounder stock, the number of recruits per spawner, had generally declined over the time-series, suggesting that an environmental driver may improve the fit over the standard Ricker stock–recruitment relationship (Figure 9).

Environmentally driven stock–recruitment function

The environmentally driven stock–recruitment models all converged without priors or constraining the parameters. The environmental terms did not improve the fit of the summer flounder stock–recruitment relationship over the standard model, but did improve the fit for winter flounder (Tables 4 and 5, Figure 10). For winter flounder, both the Ricker and Beverton-and-Holt models performed similarly and output similar results. Based on the AIC, the model with the mean winter temperature term was selected as the best model. The maximum potential productivity and compensation of the stock increased with the environmental models compared with the standard model, leading to higher productivity during favourable environmental conditions and lower productivity during unfavourable environmental conditions. Over the time-series of recruitment (1981–2010), productivity ($\alpha e^{c\cdot environ_{t-1}}$) was high in the 1980s, the mid 1990s and the early 2000s: the periods when winters were colder. Productivity was lowest in the early 1990s, late 1990s and the mid-to-late 2000s (Figure 11).

Discussion

The northeast shelf of the USA has experienced decadal-scale environmental variability over the last 50 years. The colder 1960s were followed by warmer 1970s and then cooler early 1980s. Since the end of the 1980s, the water temperature has increased, with the 2000s having some of the warmest years on record. Summer and winter flounder are marine poikilotherms whose vital rates (metabolism, growth, fecundity, mortality etc.) are responsive to the external environment. The degree to which the physical environment regulates abundance, however, varies over time, depending on the conditions and other factors such as shoreline effects, pollution and fishing.

Table 2. Variance and parameter estimates from the three different Ricker models for summer flounder.

Model	V	W_a	exp(a)	b	AICc
lm	0.112	–	4 616.9	0.000 037	–
Constant MLE	0.112	–	4 616.9	0.000 037	1.34
Varying MLE	0.111	0.001	4 600.2	0.000 037	3.64

The W_a parameter is the variance of the random walk component and the exponential of a, exp(a) is the mean of the productivity parameter in the Ricker Model. The three models were the linear version of the Ricker model fit by linear regression (lm); the state–space model fit by maximum likelihood with a constant productivity parameter (Constant); and the state–space model fit by maximum likelihood with a time-varying productivity parameter (Varying).

The landings and fishery-independent surveys showed significant synchrony across the full range of the two stocks, indicating that a large-scale driver was influencing abundance despite potential small-scale variation between estuaries. In the early part of the time-series, there is some evidence from both landings and survey data that summer and winter flounder were alternating in a pattern which relates to mean winter estuarine temperature. Summer flounder abundance was higher in the warm 1950s and 1970s, while winter flounder abundance was high in the cooler 1960s and late 1970s to early 1980s. The rapid increase in fishing effort in the 1980s and early 1990s, however, appeared to supersede the environmental factors and drive both stocks to low abundance (NEFSC, 2011; Terceiro, 2012). Since fishing pressure declined, the two species have exhibited contrasting patterns with respect to environmental correlates, stock productivity and abundance.

Warmer winters are potentially favourable for summer flounder, such that the available thermal habitat does not constrain stock size. The stock was highly correlated with fishing mortality and exhibited

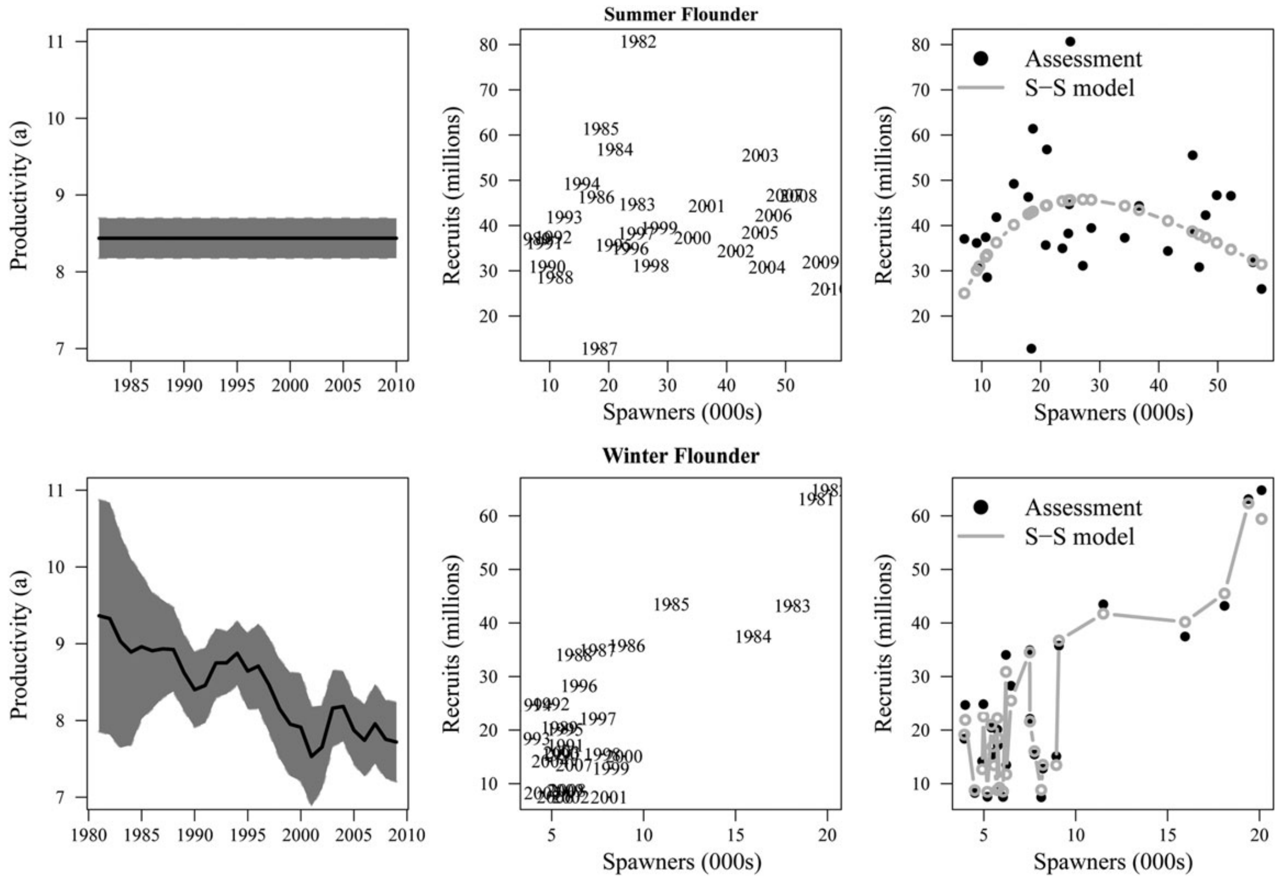

Figure 9. Results of the best fit, time-varying, state–space Ricker model for summer flounder and winter flounder. Left column: the estimate of the productivity parameter (a or ln α) over time. Centre column: the spawner and recruit data. Right column: the best fit stock–recruit relationship.

constant spawner productivity over the time-series. With productivity unchanged, the decline in fishing mortality since the mid-1990s resulted in an expansion of the age structure and an increase in the stock. Fishing pressure is the main regulator of abundance, and therefore controlling fishing mortality leads to effective management. Once the stock is in equilibrium with the fishing mortality rate there is the potential for an environmental signal to manifest itself, however there is currently no evidence from this study that it is a major factor altering the abundance of the summer flounder stock.

The declining productivity for winter flounder, however, suggests that the rebuilding targets for the SNE/MAB winter flounder stock are not feasible and that biomass reference points may be set too high. Winter flounder abundance did not exhibit a relationship with fishing mortality and has shown little if any rebuilding with a decline in mortality. During colder periods, the winter flounder stock increased, supporting commercial fisheries down into Chesapeake Bay. The large amount of habitat in the Chesapeake that may have become available when winters were cooler could have been an important component of the increase. As the temperatures have warmed, the stock has decreased and retreated north (Nye *et al.*, 2009). Warmer winters potentially decreased the thermal predation refuge, altering the productivity of the stock (Jeffries and Johnson, 1974; Taylor, 2005). Recruitment declined with warmer winters, despite lower fishing pressure resulting in a continued low level of the SNE/MAB winter flounder stock. The current reference points were set under steady-state conditions, effectively assuming the mean stock productivity (NEFSC, 2011). The declining stock productivity, which is currently lower than the mean level, suggests that even in the absence of fishing the stock would be unable to achieve the steady-state reference points.

Table 3. Variance and parameter estimates from the three different Ricker models for winter flounder.

Model	V	W_a	exp(a)	b	AICc
lm	0.244	–	2 743.5	0.000 002	–
Constant MLE	0.244	–	2 743.5	0.000 002	19.88
Varying MLE	0.024	0.071	5 249.8	0.000 066	−3.78

The W_a parameter is the variance of the random walk component and the exponential of a, exp(a), is the mean of the productivity parameter in the Ricker Model. The three models were the linear version of the Ricker model fit by linear regression (lm); the state–space model fit by maximum likelihood with a constant productivity parameter (Constant); and the state–space model fit by maximum likelihood with a time-varying productivity parameter (Varying).

The time-varying state–space model provides a mechanism to identify potential climate effects on natural marine resources (Collie *et al.*, 2012). By testing a more general hypothesis—that changes in the physical conditions impact vital rates, which alter productivity—we found that winter flounder were affected by the environment, whereas over the available time-series, summer flounder were not. Our four criteria for identifying external drivers, then, provided the framework for determining the major factors affecting abundance.

Estuarine temperature was the major external driver for winter flounder because it defined the habitat area available for the early life stages, i.e. the carrying capacity of the estuaries. In this context, habitat is not the simple sum of the area of each estuary, but a moving envelope, which varies at multiple scales in both space and time. The habitat consists of the number of estuaries that are within the appropriate environmental conditions for the appropriate amount of time. During certain years, such as the 1960s, estuaries from Buzzards Bay to the Chesapeake were cold enough, and the winters were long enough that the thermally available habitat was large and able to support large winter flounder year classes. In more recent years, warmer winters and/or shorter spans of time below threshold temperatures have decreased the available thermal habitat, resulting in smaller year classes.

Recruitment estimates from a number of estuaries are quite low compared with historic numbers (Dominion Resources Services, 2007; NEFSC, 2011), but recruitment may be close to the carrying capacity given the warmer conditions. Despite reduced levels of *SSB*, the number of active predators could be constraining the total number of winter flounder that can survive in each estuary. While predation during warmer years is the specific mechanistic link, it is the changes in environmental conditions that regulates the carrying capacity and drives winter flounder recruitment. The inclusion of the estuarine winter temperature into the environmentally driven stock–recruitment model incorporates the changes in thermal habitat into the recruitment process. The result is a time-varying estimate of productivity that tracks with temperature and closely follows the estimate of productivity from the time-varying state–space model.

Changes in stock productivity can have important considerations for the management of fished species. Reference points and rebuilding targets are typically set assuming a constant environment

Table 4. Output of the the standard and environmental spawner–recruit models for summer flounder (Ricker: $R_t = \alpha e^{c\cdot environ_{t-1}} \cdot S_{t-1} e^{-bS_{t-1}}$; Beverton and Holt: $R_t = \frac{\alpha S_{t-1} e^{c\cdot environ_{-1}}}{1+bS_{t-1}}$).

Factor	Model	α	b	s	c	AIC
Standard	Ricker	4 949	0.000 04	11.22	–	1 033
	Bev–Holt	30 903	0.000 71	10.96	–	1 033
Wtr Mean	Ricker	4 771	0.000 04	11.25	0.011 223 50	1 034
	Bev–Holt	28 953	0.000 59	10.79	−0.027 774 99	1 035
Wtr Mean End	Ricker	4 974	0.000 04	11.36	0.000 695 02	1 035
	Bev–Holt	30 250	0.000 70	10.90	−0.000 017 32	1 035
Mean End Area	Ricker	5 882	0.000 04	12.00	−0.000 274 81	1 032
	Bev–Holt	34 836	0.000 69	11.65	−0.000 234 29	1 034
Sum End Area	Ricker	5 607	0.000 04	12.03	−0.000 000 45	1 033
	Bev–Holt	32 540	0.000 67	11.54	−0.000 000 38	1 034

The s is the shape parameter from the Gamma-distributed error structure. Wtr Mean = mean winter temperature, Jan–Mar temperature averaged across estuaries, Wtr Mean End = the number of days between the end of winter and the mean end of winter averaged across estuaries, Mean End Area = the mean thermal habitat area available each year, Sum End Area = the summed thermal habitat area available each year.

Table 5. Output of the the standard and environmental spawner–recruit models for winter flounder (Ricker $R_t = \alpha e^{c \cdot environ_{t-1}} \cdot S_{t-1} e^{-bS_{t-1}}$, Beverton and Holt $R_t = \frac{\alpha S_{t-1} e^{c \cdot environ_{t-1}}}{1+bS_{t-1}}$).

Factor	Model	α	b	s	c	AIC
Standard	Ricker	3 243	0.000 01	4.88	–	1 018
	Bev–Holt	3 311	0.000 01	4.88	–	1 018
Wtr Mean	Ricker	12 352	0.000 03	7.44	−0.321 039	1 007
	Bev–Holt	13 157	0.000 04	7.44	−0.319 457	1 007
Wtr Mean End	Ricker	3 600	0.000 02	6.31	0.011 976	1 011
	Bev–Holt	3 678	0.000 02	6.37	0.011 841	1 011
Mean End Area	Ricker	2 376	0.000 02	5.53	0.000 584	1 016
	Bev–Holt	2 490	0.000 03	5.51	0.000 602	1 015
Sum End Area	Ricker	2 504	0.000 02	5.93	0.000 001	1 013
	Bev–Holt	2 667	0.000 04	6.07	0.000 001	1 013

The *s* is the shape parameter from the Gamma-distributed error structure. Wtr Mean = mean winter temperature, Jan–Mar temperature averaged across estuaries, Wtr Mean End = the number of days between the end of winter and the mean end of winter averaged across estuaries, Mean End Area = the mean thermal habitat area available each year, Sum End Area = the summed thermal habitat area available each year.

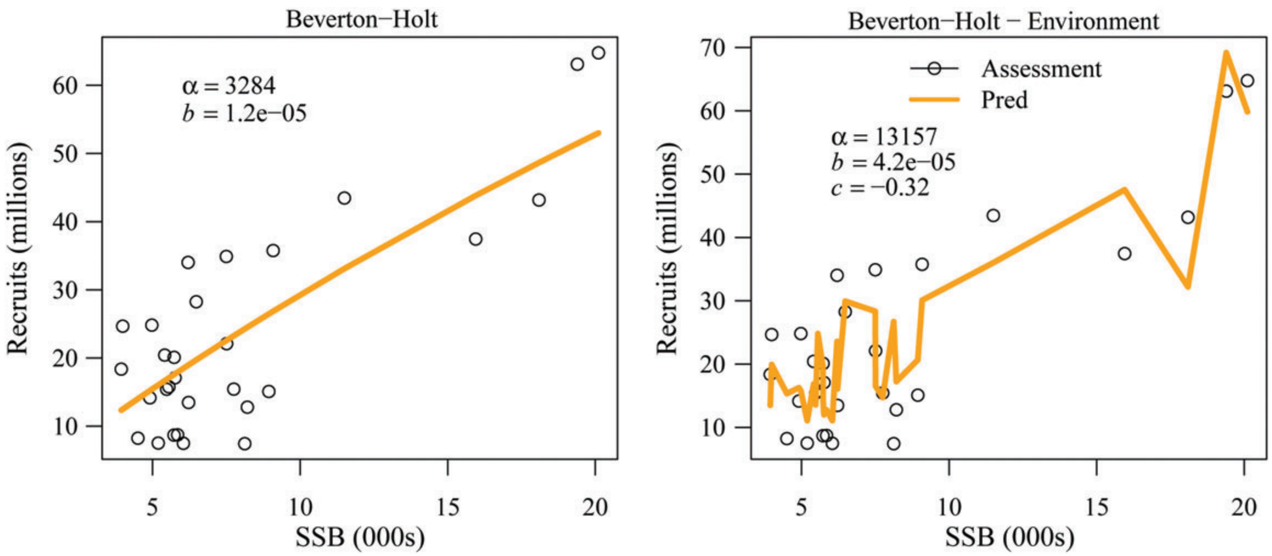

Figure 10. Beverton–Holt stock–recruitment model output for the standard and environmentally driven model. The environmental parameter was the mean winter temperature over all estuaries.

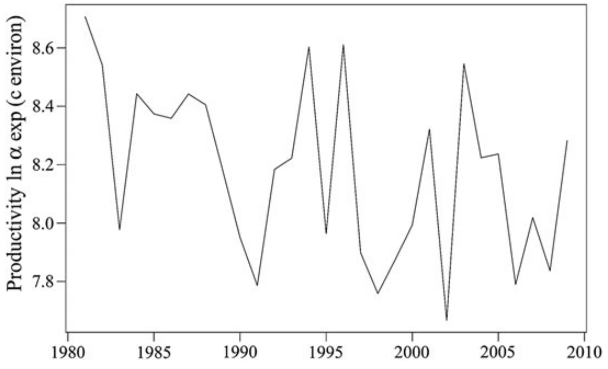

Figure 11. Changes in the natural log of productivity for winter flounder based on the environmentally driven stock–recruitment relationship (productivity = $\alpha e^{c \cdot environment_{t-1}}$).

and consider only the effect of fishing mortality on the status of stocks (Hilborn and Walters, 1992; Quinn and Deriso, 1999). As the environment alters vital rates, leading to changes in stock productivity, reference points developed under steady state conditions are no longer applicable, and rebuilding targets could be unattainable. Alternatively, steady-state reference points for stocks in favourable environmental conditions could be too low, leading to lost yield.

The combined effects of fishing and the environment are major factors regulating the abundance and distribution of natural marine resources (Hare *et al.*, 2010; Engelhard *et al.*, 2011; Richardson *et al.*, 2011; Bell *et al.*, 2012). To be effective, policy decisions must account for both factors. Fisheries management cannot control the environmental conditions, but can develop reference points that account for fishing and vary with the environmental conditions. Time-varying reference points may not increase yield, but should provide more realistic and achievable targets for stock abundance and landings.

Supplementary data

Supplementary data are available at *ICES Journal of Marine Science* online.

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