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Original Article

Spatial and temporal dynamics of Atlantic menhaden (*Brevoortia tyrannus*) recruitment in the Northwest Atlantic Ocean

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Atlantic menhaden, *Brevoortia tyrannus*, is an abundant, schooling pelagic fish that is widely distributed in the coastal Northwest Atlantic. It supports the largest single-species fishery by volume on the east coast of the United States. However, relatively little is known about factors that control recruitment, and its stock–recruitment relationship is poorly defined. Atlantic menhaden is managed as a single unit stock, but fisheries and environmental variables likely act regionally on recruitments. To better understand spatial and temporal variability in recruitment, fishery-independent time-series (1959–2013) of young-of-year (YOY) abundance indices from the Mid-Atlantic to Southern New England (SNE) were analysed using dynamic factor analysis and generalized additive models. Recruitment time-series demonstrated low-frequency variability and the analyses identified two broad geographical groupings, the Chesapeake Bay (CB) and SNE. Each of these two regions exhibited changes in YOY abundance and different periods of relatively high YOY abundance that were inversely related to each other; CB indices were highest from ca. 1971 to 1991, whereas SNE indices were high from ca. 1995 to 2005. We tested for effects of climatic, environmental, biological, and fishing-related variables that have been documented or hypothesized to influence stock productivity. A broad-scale indicator of climate, the Atlantic Multidecadal Oscillation, was the best single predictor of coast-wide recruitment patterns, and had opposing effects on the CB and SNE regions. Underlying mechanisms of spatial and interannual variability in recruitment likely derive from interactions among climatology, larval transport, adult menhaden distribution, and habitat suitability. The identified regional patterns and climatic effects have implications for the stock assessment of Atlantic menhaden, particularly given the geographically constrained nature of the existing fishery and the climatic oscillations characteristic of the coastal ocean.

Keywords: Atlantic menhaden, Atlantic Multidecadal Oscillation, climate, dynamic factor analysis, recruitment, young of year.

Introduction

Understanding the complex processes that control recruitment of marine fishes remains a challenge in fisheries science and management. From the inception of this discipline, a goal has been to predict future juvenile recruitment from information on stock size, fishing pressure, and environmental conditions (Smith, 1994; Houde, 2009). Although the size of the adult spawning stock is linked to the production of juveniles, stock–recruitment relationships are often poorly defined, due in part to variability in system productivity, female condition, hydrography, and other environmental factors (Shepherd *et al.*, 1990; Myers, 2001; Rose *et al.*, 2001). Many fishes, particularly small pelagic fishes, can experience dramatic changes in recruitment and production over decadal scales, at times attributable to climate-related variability in ocean conditions, but the mechanisms for such changes are often not well understood (Ottersen *et al.*, 2001; Fréon *et al.*, 2005; Brunel and Boucher, 2007; Houde, 2009).

Atlantic menhaden (*Brevoortia tyrannus*, hereafter menhaden) is an abundant and important clupeid that has exhibited large variability in recruitment, for which the underlying drivers and spatial patterns of variability are not well understood. The menhaden population is widely distributed along the Atlantic coast of North America from Florida, United States to Nova Scotia, Canada, and is believed to be a single stock (SEDAR, 2015). Menhaden is an important forage species that is consumed by many piscivorous fishes,

marine mammals, and seabirds (Rogers and Van Den Avyle, 1989; Walter *et al.*, 2003; Viverette *et al.*, 2007). Menhaden also supports the largest fishery by volume on the US Atlantic coast with annual landings ranging from 167 to 735 thousand metric tons in the past 75 years. Menhaden is harvested by a reduction and a bait fishery that account for an average of 83 and 17%, respectively, of the total annual catch from 1950 to 2013 (SEDAR, 2015). The fisheries primarily harvest fish ages 1–3. The reduction fishery uses purse-seines and processes (or "reduces") the catch into fishmeal, fishoil, and fish solubles. In contrast, the bait fishery uses a variety of gears (small purse-seines, poundnets, gillnets, etc.) and sells menhaden as bait for other fisheries. Due to changes in regional menhaden availability, odour abatement issues, and economics, processing capacity in the reduction fishery decreased from 23 plants (from Florida to Maine) in 1955 to 1 plant in Virginia (SEDAR, 2015). Historically, the fishery was largely unregulated, but a harvest cap was established for Chesapeake Bay (CB) in 2005 and a coast-wide total allowable catch of 170 800 mt was set in 2012.

Given the commercial and ecological importance of menhaden, there is substantial interest in developing indices for use in forecasting future recruitments for fisheries management. One commonly reported index of recruitment measures the abundance of young-of-year (YOY) menhaden sampled in Maryland (MD) waters of the CB; this index has varied by more than two orders of magnitude and it shows periods of high and low recruitments (Figure 1). Large, low-frequency recruitment variability such as that depicted in Figure 1 challenges traditional management efforts, because it may indicate alternative ecosystem states, fuelling discussion of the relative importance of environmental and anthropogenic factors as controls over recruitment and fish production. Moreover, any distinct and consistent spatial variability in YOY recruitment along the coast could have implications for management, but to our knowledge there have been no empirical evaluations of such spatial patterns for menhaden.

Several interrelated drivers have been hypothesized or documented to influence recruitment of menhaden through effects on production, growth, and mortality. As a coastal, migratory species, menhaden spawns in coastal waters during fall and winter and its larvae are advected into estuarine nursery areas along the coast according to regional currents and flow regimes (Higham and
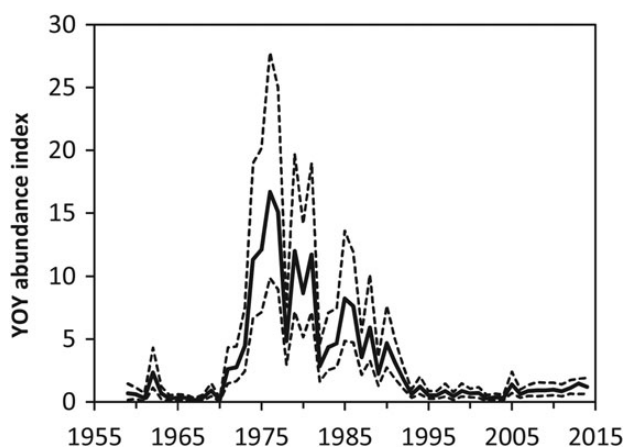
Nicholson, 1964; Reintjes and Pacheco, 1966; Quinlan *et al.*, 1999). It is therefore probable that climatic variables affect larval transport (e.g. Nelson *et al.*, 1977; Quinlan *et al.*, 1999) and larval ingress (Warlen *et al.*, 2002; Lozano and Houde, 2013). Environmental variables, including temperature, salinity, and river discharge, can alter habitat suitability and growth potential in ocean and estuary systems (Lewis, 1966; Govoni, 1997; Edwards, 2009; Humphrey *et al.*, 2014). Biological factors such as food availability, predation pressure, and stock size also influence menhaden recruitment (MDSG, 2009; Annis *et al.*, 2011). Finally, fishery removals, which have contracted to the waters near CB in recent decades, affect the production potential for the menhaden population (SEDAR, 2015).

Here, we investigated recruitment dynamics of menhaden by analysing and modelling 13, fishery-independent time-series of recruitment on the Atlantic coast of the United States. We sought to quantify spatial and temporal variability in menhaden recruitment dynamics over a broad spatial domain. Our two objectives were to (i) determine the extent of coherence among multiple recruitment time-series both through time (1959–2013) and across space (Virginia to Rhode Island, United States; Figure 2) and (ii) determine the relationships between observed menhaden recruitment and
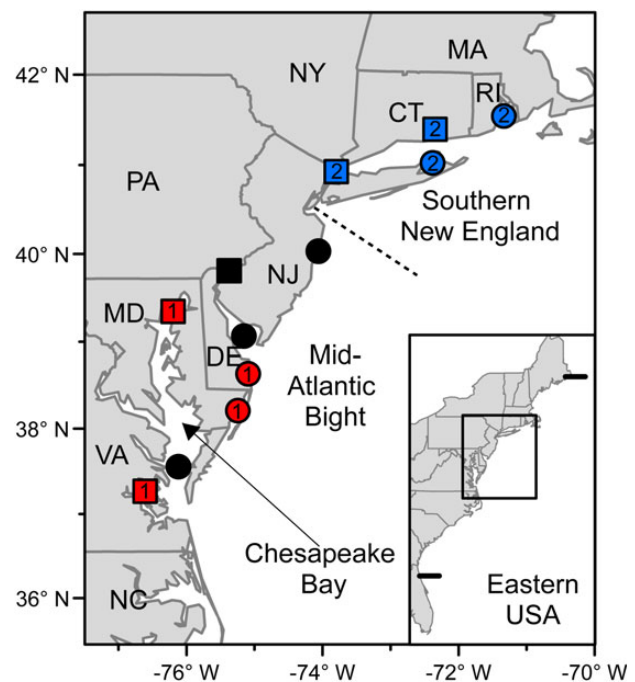
Figure 2. Approximate locations of fishery-independent seine (squares) and trawl (circles) surveys used to generate indices of Atlantic menhaden recruitment along the east coast of the United States. Descriptions of survey locations are available in Table 1. Survey symbols are numbered and colour-coded based on the results of correlation and dynamic factor analyses, indicating surveys with similar recruitment trends through time (1 and red – Chesapeake Bay pattern; 2 and blue – Southern New England pattern; no number and black – other). Dashed line represents the distinction between Southern New England and the Mid-Atlantic Bight. States are labelled with conventional abbreviations (NC – North Carolina, VA – Virginia, MD – Maryland, DE – Delaware, PA – Pennsylvania, NJ – New Jersey, NY – New York, CT – Connecticut, RI – Rhode Island, MA – Massachusetts). Thick lines in the inset delineate the approximate population range of Atlantic menhaden along the eastern United States. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Figure 1. Annual YOY abundance index (solid line) for Atlantic menhaden from MD, United States with 95% confidence interval (dashed lines). The index is the geometric mean catch-per-haul from a beach-seine survey operated by the state resource management agency (http://dnr2 .maryland.gov/fisheries/Pages/striped-bass/juvenile-index.aspx).

Table 1. Summary of fishery-independent surveys used to derive recruitment indices of Atlantic menhaden.

Survey name	Code	Region	n	Years	Months	Location
Rhode Island Trawl Survey	RI.t	N	24	1990–2013	January–December	Narragansett Bay, RI
Connecticut River Seine Survey	CT.s	N	27	1987–2013	July–October	Lower Connecticut River
Connecticut Long Island Sound Trawl Survey*	CT.t	N	17	1996–2013	April–June; September–October	Long Island Sound
New York Peconic Bay Trawl Survey	NY.t	N	19	1991–2013	May–October	Peconic Bay, NY
New York Seine Survey	NY.s	N	26	1987–2013	May–October	Western Long Island Sound
New Jersey Ocean Trawl Survey	NJ.t	N	26	1988–2013	January, April, June, August, October	Cape May to Sandy Hook, NJ; out to 90 feet depth
New Jersey Seine Survey	NJ.s	S	29	1985–2013	June–November	Delaware River (River miles 54–126)
Delaware Bay 16-Foot Trawl Survey	DE.t	S	31	1980–2013	April–October	Delaware Bay
Delaware Inland Bays Trawl Survey	DE.t2	S	28	1986–2013	April–October	Coastal inland bays of Delaware
Maryland Coastal Bays Trawl Survey	MD.t	S	25	1989–2013	April–October	Maryland coastal bays
Maryland Striped Bass Seine Survey	MD.s	S	55	1959–2013	July–September	Upper CB and major MD tributaries
Virginia Juvenile Fish and Blue Crab Trawl Survey	VA.t	S	26	1988–2013	January–December	Lower CB and major VA tributaries
Virginia Striped Bass Seine Survey	VA.s	S	36	1968–2013	July–September	James, York, Rappahannock Rivers

Surveys are organized approximately by latitude. Codes represent the US state abbreviation (see Figure 2) followed by a gear abbreviation (s, seine; t, trawl). Region classifications (N, North; S, South) were used for generalized additive modelling. The start and end years of each time-series are listed along with the sample size (*n*) of years with estimable recruitment indices. Sampling months and locations are noted. The asterisk denotes a survey not used in DFA due to its shorter time-series.

potential climatic, environmental, biotic, and fishing-related drivers. This research contributes to the knowledge of broad-scale processes that affect variability in production of menhaden, a model species for other widely distributed coastal-spawning fishes. Specifically, we identify spatial patterns in juvenile abundance, regionally distinct periods of higher recruitment, and covariates associated with the recruitment trends.

Methods
Recruitment indices

Indices of YOY menhaden abundance from fishery-independent surveys conducted by state agencies along the US east coast were obtained from a recent stock assessment (SEDAR, 2015; Figure 2 and Table 1). Complete details of survey methods and index calculation are presented elsewhere (SEDAR, 2015). Briefly, surveys sampled multiple river, estuarine, or coastal sites using standardized protocols (Table 1). Beach-seine and bottom trawl surveys were conducted mostly from late spring to early fall, such that fish produced during the peak spawning period from fall to winter would be available to the gear. Although seines and trawls are not ideal for sampling pelagic schooling species like menhaden, concerns of gear differences affecting trends in relative abundance are minimized by two observations: (i) similar interannual patterns of relative menhaden abundance in MD waters were observed using synoptic, paired sampling by trawls and seines over 4 years (Carlos Lozano, University of Maryland Center for Environmental Science, pers. comm.) and (ii) seine and trawl survey indices in the present study were found to be correlated within regions (see the Results section). For surveys that capture multiple age-classes of fish, data were censored for YOY individuals based on region- and month-specific length thresholds that account for spatial and temporal differences in YOY size (SEDAR, 2015). Annual indices of juvenile abundance were calculated from raw, station-level survey data using generalized linear models that standardized the raw data to account for spatial and seasonal changes in catchability (SEDAR, 2015).

For our analyses, we focused on 13 recruitment time-series (geographic range from VA to RI, United States; Figure 2), each with a minimum of 15 years of data (Table 1). Each time-series was assumed to be an independent measure of relative juvenile menhaden abundance. To meet normality and homogeneity of variance assumptions of statistical methods, all indices were ln-transformed and then z-transformed to have a mean of 0 and standard deviation (SD) of 1. In a preliminary examination of recruitment relationships, Pearson correlation coefficients were calculated among all recruitment time-series, and surveys were then clustered based on the complete linkage method using correlation as the distance metric. Analyses were conducted within the R statistical software, version 3.1.1 (www.r-project.org), using the "cluster" package (Maechler *et al.*, 2014).

Covariates

We chose 16 climatic, environmental, biological, and fishing-based metrics for our analyses based on *a priori* consideration of their effects on recruitment of menhaden (Table 2). Covariate time-series were obtained from reliable data sources and have been used for many other scientific studies. All covariate time-series were z-transformed to have a mean of 0 and SD of 1.

Four climatic and oceanographic indices were selected for the analyses (Table 2), because they represent atmospheric and oceanographic forcing at large spatio-temporal scales and have been linked

Table 2. Covariates evaluated in statistical models of annual Atlantic menhaden recruitment along the northeast coast of the United States.

Covariate	Justification	Months	Regions	Data source
Climatic and oceanographic				
Atlantic Multidecadal Oscillation (AMO)	Indicator of climate conditions; linked to recruitment variability of NW Atlantic fishes	—	—	NOAA
North Atlantic Oscillation (NAO) Index	Indicator of climate conditions; linked to changes in fish communities and stocks	DJFM	—	NCAR
Ekman Transport Index (EKTR)	Indicator of westward (EKTRx) and southern (EKTRy) oceanic transport of eggs and larvae to estuaries	DJF	(37.5°N, 285.5°E)	NOAA
GSI	Indicator of oceanographic conditions that can influence egg and larval transport	—	—	J. Nye and Y.-O. Kwon, pers. comm.
Environmental				
Temperature (TEMP)	Affects fish physiology, behaviour, and various basic system properties	—	CB, SNE	CB—UMCES Pier data; SNE—NCDC
Minimum winter temperature (TEMP$_{min}$)	Measure of winter severity with potential effects on survival	NDJFM	CB, SNE	CB—UMCES Pier data; SNE—NCDC
Salinity (SAL)	Affects fish physiology, behaviour, available habitat, and various basic system properties	—	CB	UMCES Pier data
River discharge (RIV)	Alters availability of high-salinity habitat, affects nutrient loading, production, hypoxia, and foodweb structure	MAM	CB (Susq. Riv.), SNE (CT Riv.)	USGS
Precipitation (PCP)	Alters availability of high-salinity habitat, affects nutrient loading, production, hypoxia, and foodweb structure	—	CB, SNE	NCDC
Palmer drought index (PALM)	Long-term indicator of drought conditions; reflects river discharge and precipitation	—	CB, SNE	NCDC
MTL	Local manifestation of climate forcing and sea-level rise	—	—	NOAA
Biological				
Chlorophyll-*a* in estuary (CHL)	Proxy for primary production; influences food availability; related to eutrophication intensity	—	CB (oligo- and poly-haline)	L. Harding, pers. comm.
Predator biomass indices (PRED_Ms, PRED_Ps)	Indicator of predation pressure from striped bass (Ms) and bluefish (Ps)	—	—	NMFS (2012), Nelson (2013)
Number of eggs produced (NUM_eggs)	Estimate of coast-wide population fecundity and production	—	—	SEDAR (2015)
Fishing				
Coast-wide menhaden landings (LAND)	Direct biomass removal and indicator of fishing mortality	—	—	SEDAR (2015)
Reduction landings-per-unit-effort (LPUE)	Crude index of Atlantic menhaden abundance	—	—	SEDAR (2015)

Variables were grouped into four general categories (italics). Covariates were representative of all months and regions (—) or specific to certain months (using the first letter abbreviation) and regions (CB, Chesapeake Bay; SNE, Southern New England).

to various biological processes including the distribution and recruitment of fishes (Collie *et al.*, 2008; Ottersen *et al.*, 2010; Nye *et al.*, 2011). The Atlantic Multidecadal Oscillation (AMO) represents the sea surface temperature anomaly from 0 to 60°N in the Atlantic that has been linearly detrended to account for anthropogenic climate change (Nye *et al.*, 2014). AMO data were obtained from the Earth System Research Laboratory (ESRL, 2015). The North Atlantic Oscillation (NAO) Index is derived from a principal component-based analysis of sea-level pressure in the North Atlantic and it tracks the difference between the Icelandic low pressure and Azores high pressure systems (Hurrell *et al.*, 2003). NAO data were obtained from the National Center for Atmospheric Research (NCAR, 2014). The Gulf Stream Index (GSI) represents the latitudinal position of the Gulf Stream as defined by subsurface temperature at 200 m depth (Joyce *et al.*, 2000). GSI data were provided by Young-Oh Kwon (Woods Hole Oceanographic Institute, pers. comm.). Finally, Ekman transport indices along east-west (EKTRx) and north-south (EKTRy) axes were obtained for the continental shelf (37.5°N, 285.5°E) based on 6-hourly, synoptic measurements of geostrophic windstress (Schwing *et al.*, 1996) downloaded from NOAA Coastwatch (NOAA-CW, 2014). EKTRx and EKTRy were calculated as the mean value for December–February, a period of relatively high menhaden larval ingress to Mid-Atlantic Bight (MAB) estuaries (Lozano *et al.*, 2012).

Environmental covariates included variables generally associated with water quality and precipitation (Table 2). Preliminary analyses indicated that many variables were spatially autocorrelated from North Carolina to Maine. Where possible, information was obtained for the CB and Southern New England (SNE) because these regions represented spatial environmental differences along the coast and they also corresponded to regional recruitment patterns. For temporally autocorrelated variables, preliminary analyses and biological justifications (e.g. migration and life history characteristics) were used to select an appropriate period (e.g. yearly vs. seasonal mean) for the analyses (Table 2). CB water temperature and salinity data were obtained from long-term pier sampling at the Chesapeake Biological Laboratory in the mouth of the Patuxent River at Solomons, MD (CBL, 2015). For SNE, air temperatures obtained from the National Climate Data Center (NCDC, 2014) served as a proxy for water temperatures (e.g. Hare and Able 2007). The lowest monthly mean of air temperatures (typically in February) was used as a measure of annual winter severity. The annual mean daily river discharge for spring months (March, April, and May) was obtained from the US Geological Survey for the Susquehanna and Connecticut Rivers, representing CB and SNE, respectively (USGS, 2014). Mean annual precipitation by state from the NCDC database (NCDC, 2014) was averaged across states to derive regional precipitation for CB (VA and MD) and SNE (CT, RI, and MA). The NCDC database also provided Palmer Drought Severity Index (PALM) values that were aggregated by year and region, similar to the precipitation data. PALM is a comprehensive, long-term drought indicator that accounts for water supply and demand on land. Annual average mean tide level (MTL; the average of mean high water and mean low water) was obtained from a NOAA data station at Sewells Point, VA (NOAA-TC, 2014); based on preliminary analyses, annual MTL was representative of all seasons and coastal states.

Biological covariates represented measures of ecosystem productivity, prey availability, and predation pressure on YOY menhaden (Table 2). Indices of predation pressure at a coarse scale were derived from stock assessment estimates of spawning-stock biomass (SSB) of two dominant menhaden predators, the striped bass (*Morone saxatilis*) and the bluefish (*Pomatomus saltatrix*; NMFS, 2012; Nelson, 2013). These coast-wide biomass estimates were used because localized estimates of striped bass and bluefish biomass were not available for most of the systems sampled for menhaden during the periods examined. Coast-wide biomasses were hypothesized to be an informative metric of regional changes in predation pressure given the large changes observed in these two stocks from the 1980s (i.e. striped bass increased 10–16 fold, and bluefish decreased to nearly 20% of its initial biomass). Data for other major predators (e.g. birds and marine mammals) were not available in sufficiently long time-series for inclusion in the analysis. Mean annual surface chlorophyll-*a* served as a proxy for net annual integrated primary production (Harding *et al.*, 2002), and was obtained for CB from Harding *et al.* (2013).

Spawning-stock and fishing covariates represented the coast-wide status of the menhaden population and the fishing pressure on it. The logged number of eggs produced annually by the adult menhaden population (as estimated in the stock assessment) was used as a metric of SSB and stock productivity (SEDAR, 2015). Coast-wide menhaden landings (LAND) by all menhaden fisheries and landings-per-unit-effort (LPUE) in the directed purse-seine fishery were used to represent the broad-scale fishing pressure on the menhaden stock. Data on LAND and fishing effort (number of vessel-weeks fished) were obtained from the most recent stock assessment (SEDAR, 2015). Effort was not included as a separate covariate, because it was strongly correlated with LAND (Pearson $R =$ 0.79) and LPUE (Pearson $R = -0.77$). LAND was also significantly correlated with fishing mortality from the assessment (Pearson $R =$ 0.62, $p < 0.05$).

Dynamic factor analysis

Recruitment indices were modelled using dynamic factor analysis (DFA), which is a multivariate, dimension-reduction technique appropriate for analysing a set of short (15+ years), non-stationary time-series (Zuur *et al.*, 2003a). DFA has been used successfully in several fisheries investigations (e.g. Zuur *et al.*, 2003b; Colton *et al.*, 2014). The set of time-series is modelled as a function of four components: (i) a weighted, linear combination of independent common trends, (ii) a constant level parameter, (iii) any explanatory covariates, and (iv) a noise or residual error component (Zuur *et al.*, 2003a,b). In matrix notation, the model is defined as:

$$\boldsymbol{y}_t = \boldsymbol{Z}\boldsymbol{\alpha}_t + \boldsymbol{c} + \boldsymbol{D}\boldsymbol{x}_t + \boldsymbol{e}_t, \tag{1}$$

where $\boldsymbol{y}_t$ is a vector ($n \times 1$) containing the values of the n recruitment time-series at time t, $\boldsymbol{Z}$ is a matrix ($n \times m$) of the time-series weightings or factor loadings for each of the m common trend, $\boldsymbol{\alpha}_t$ is a vector ($1 \times m$) with the values of the m common trends at time t, $\boldsymbol{c}$ is a vector ($n \times 1$) of constants to shift the linear combination of common trends up or down and is equivalent to the intercept in a regression model, $\boldsymbol{D}$ is a matrix ($n \times \ell$) containing regression coefficients for the explanatory covariates, $\boldsymbol{x}_t$ is a vector ($1 \times \ell$) containing the ℓ explanatory covariates at time t, and $\boldsymbol{e}_t$ is a vector ($n \times 1$) of residual error assumed to be normally distributed with a diagonal error covariance matrix. Whereas response variables ($\boldsymbol{y}_t$) may have missing data (which are substituted by the overall mean), explanatory covariates ($\boldsymbol{x}_t$) can have no missing data points. The common trends, $\boldsymbol{\alpha}_t$, represent latent variables that describe shared information in the set of time-series that cannot be explained by the measured explanatory covariates. Comparing the canonical correlations of each time-series

with the common trends is useful to infer the degree of relationships among common trends and each response variable and also which group of response variables are related to the same common trend (Zuur *et al.*, 2003b). The regression coefficients (***D***) indicate the relative influence of each explanatory covariate on each response variable.

DFA models were fitted to recruitment data using different explanatory variables. We also explored models in which the covariates were lagged 1 year to evaluate any delayed covariate effects on menhaden recruitment (e.g. AMO in 1990 affects recruitment in 1991). DFA models were restricted to have a single covariate to avoid overparameterization. Four forms of models, with the following characteristics, were fitted: (i) one common trend and no explanatory variables, (ii) two common trends and no explanatory variables, (iii) one common trend with one explanatory variable, and (iv) two common trends with one explanatory variable. Explanatory variables were selected from the list of covariates, provided they had a sufficiently long time-series because DFA models cannot handle missing covariate data. DFA models were fitted with the Brodgar software package (Highland Statistics Ltd, Newburgh, United Kingdom), and support for competing models was assessed using Akaike's information criterion (AIC). AIC differences (ΔAIC), defined as the AIC value of each model minus the minimum AIC value of all models, describe the relative level of empirical support for declaring a given model as the best model. Generally, models with ΔAIC < 2 have substantial support for being the best model of those evaluated, whereas models with ΔAIC within 4–7 have less support, and models with ΔAIC > 10 have little support (Burnham and Anderson, 2002).

Models were fitted using data from 1959 to 2013, representing the length of the longest recruitment time-series. Some covariates were excluded because the length of the covariate time-series had to match the length of available recruitment time-series. To avoid excluding some covariates from analysis because of missing data in 2013, any such missing values were assigned the previous 5-year mean. Additional runs were conducted using data from 1987 to 2013 to allow for inclusion of additional covariates that had shorter time-series (e.g. predator biomass and chlorophyll-*a*) and to reduce the influence on the analysis of a period of high recruitment in MD and VA that occurred before the initiation of most other surveys. Results for the two periods were similar; therefore, we focus on results for the longer period. Trawl survey data from Connecticut (CT.t) were excluded from the DFA models due to a shorter time-series that resulted in model convergence issues.

Generalized additive models

In addition to the DFA, we fitted univariate, generalized additive models (GAMs) to the recruitment time-series data. This was done to examine the effects of multiple covariates simultaneously, to visualize the form of covariate effects, and to explore any non-linearities in the relationships. GAMs allow covariate effects to be modelled non-parametrically with smooth, spline functions. The model was defined as:

$$Y_t = \alpha + \sum f_j(X_{tj}) + \varepsilon_t, \qquad (2)$$

where Y_t is the recruitment in year t, α is the intercept, the f_j are non-parametric smoothing functions for each covariate X_{tj}, and ε_t is the residual error assumed to be independent and normally distributed. Thin-plate regression splines were used as the basis for all smooths, and splines were restricted to have fewer than five estimated degrees

of freedom to avoid over-parameterization (Wood, 2006). All GAMs were fitted using the "mgcv" package (version 1.8-3) in *R*.

Two types of GAM analyses were conducted using the list of explanatory variables from Table 2. First, we modelled each of the 13 time-series individually to identify the best explanatory variables for each survey without the added variability from other surveys. Second, we fit a GAM that included data from all surveys together in a single model (termed the "global" model). For the global model, we added region as a parametric explanatory variable to account for any broad differences in recruitment levels or trends across space. Regions were broadly defined as being either north (N) or south (S) of Cape May, NJ (Table 1). For the global model, we evaluated the possible interaction between region and some covariates (AMO, NAO, GSI, and MTL) based on preliminary explorations of the data and hypothesized regional differences in climatic effects. For the individual and global GAMs, recruitment indices from each survey were associated with region-specific environmental variables based on where the survey was conducted (e.g. CB water temperatures were used for surveys in the southern region, and SNE water temperatures were used for surveys in the northern region). All possible combinations of covariates from Table 2 were fitted (with the addition of the region–covariate interactions identified above for the global model), but models were restricted to have no more than four covariates in a single model. For all sets of GAMs, the best model was determined with an information-theoretic approach using AIC-corrected for small samples sizes (Burnham and Anderson, 2002).

Results

Pearson correlations and cluster analysis of recruitment time-series indicated spatial relationships in index values (Figure 3). Recruitment time-
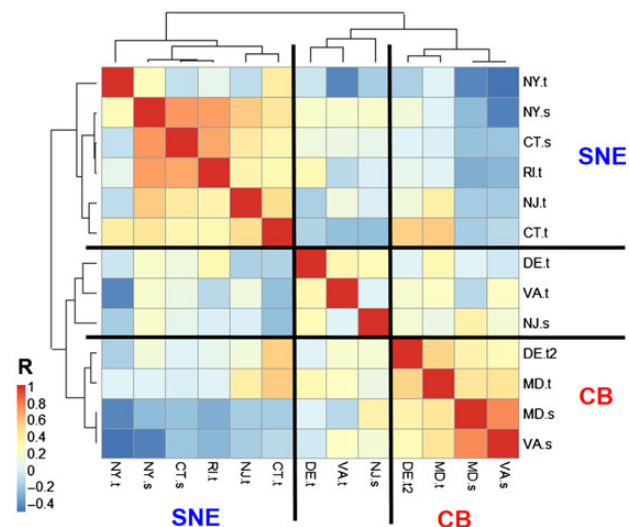
Figure 3. Correlation matrix for juvenile Atlantic menhaden recruitment indices from different surveys. Fishery-independent survey indices are identified by the US state abbreviation (see Figure 2 for abbreviations) followed by a gear label (s, seine; t, trawl). Strength of Pearson correlations (*R*) are denoted by colour (see legend). Relationships among recruitment indices are depicted with dendrograms from a cluster analysis. The three strongest cluster groupings are indicated by bold vertical and horizontal lines and labelled by broad region (SNE, Southern New England; CB, Chesapeake Bay and neighbouring waters).

series from SNE surveys (NY.t, NY.s, CT.s, RI.t, NJ.t, and CT.t) clustered together and were more strongly correlated with each other, as were

**Table 3.** Highest ranking DFA models of Atlantic menhaden recruitment using data spanning two different periods.

Period	Model rank	Covariate	*m*	ΔAIC
1959–2013	**1**	**AMO (lag 1)**	**2**	**0.0**
	2	**LAND (lag 1)**	**2**	**2.1**
	3	TEMP_SNE (lag 1)	2	8.1
	4	PCP_SNE	2	10.3
	5	LAND	2	11.0
1987–2013	**1**	**LAND (lag 1)**	**2**	**0.0**
	2	**AMO (lag 1)**	**2**	**1.6**
	3	PCP_SNE	2	5.3
	4	PRED_Ms	2	5.7
	5	PALM_SNE	2	6.2

Models with different covariates and different numbers of common trends (*m*) were ranked based on AIC differences (ΔAIC). Covariates include the Atlantic Multidecadal Oscillation (AMO), coast-wide menhaden landings (LAND), water temperature (TEMP), precipitation (PCP), predator biomass of striped bass *M. saxatilis* (PRED_Ms), and the Palmer drought index (PALM). Some models had covariates that were specific to the SNE region (_SNE) and some had covariates lagged by 1 year. Bolded models have substantial support for being the best model.

survey indices from the CB region (DE.t2, MD.t, MD.s, and VA.s). These two survey clusters (SNE and CB) were typically negatively correlated with each other. Three surveys (DE.t, VA.t, and NJ.s) formed a third cluster grouping with weaker correlations among surveys. The SNE and CB clusters each included correlated indices from both trawl and seine surveys minimizing concerns of strong gear differences and suggesting that both gears were representative of trends in relative menhaden abundance. There was a high degree of autocorrelation in some of the recruitment time-series; MD.s, VA.s, and CT.s indices had significant 1-year lag autocorrelations of 0.67, 0.60, and 0.49, respectively, and they were each significantly autocorrelated for up to 6, 5, and 1 years, respectively.

The top 25 DFA models (based on AIC), for both periods (1959–2013 and 1987–2013), included two common trends. ΔAIC values identified two models for each of the two periods as being most supported by the data (Table 3 and Supplementary Figure S1). For the 1959–2013 models, the best model included lagged AMO as a covariate (ΔAIC = 0), but a model with lagged LAND also had substantial support (ΔAIC = 2.1). The same two covariates (lagged AMO and lagged LAND) were also included in the two best 1987–2013 models, although their rank order was reversed (Table 3).
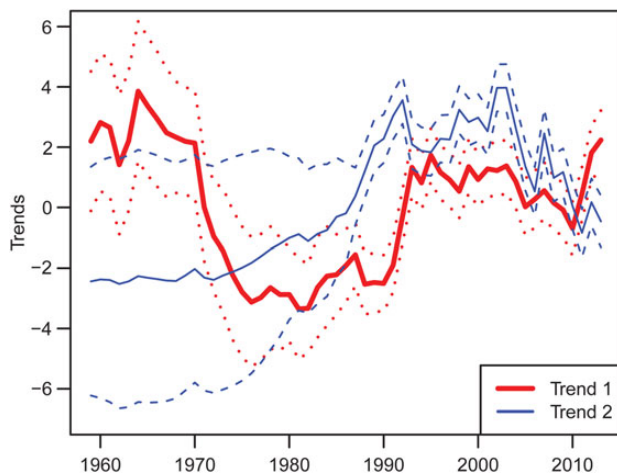
The best-fit DFA model for 1959–2013, with lagged AMO as a covariate, captured observed trends in recruitment for many
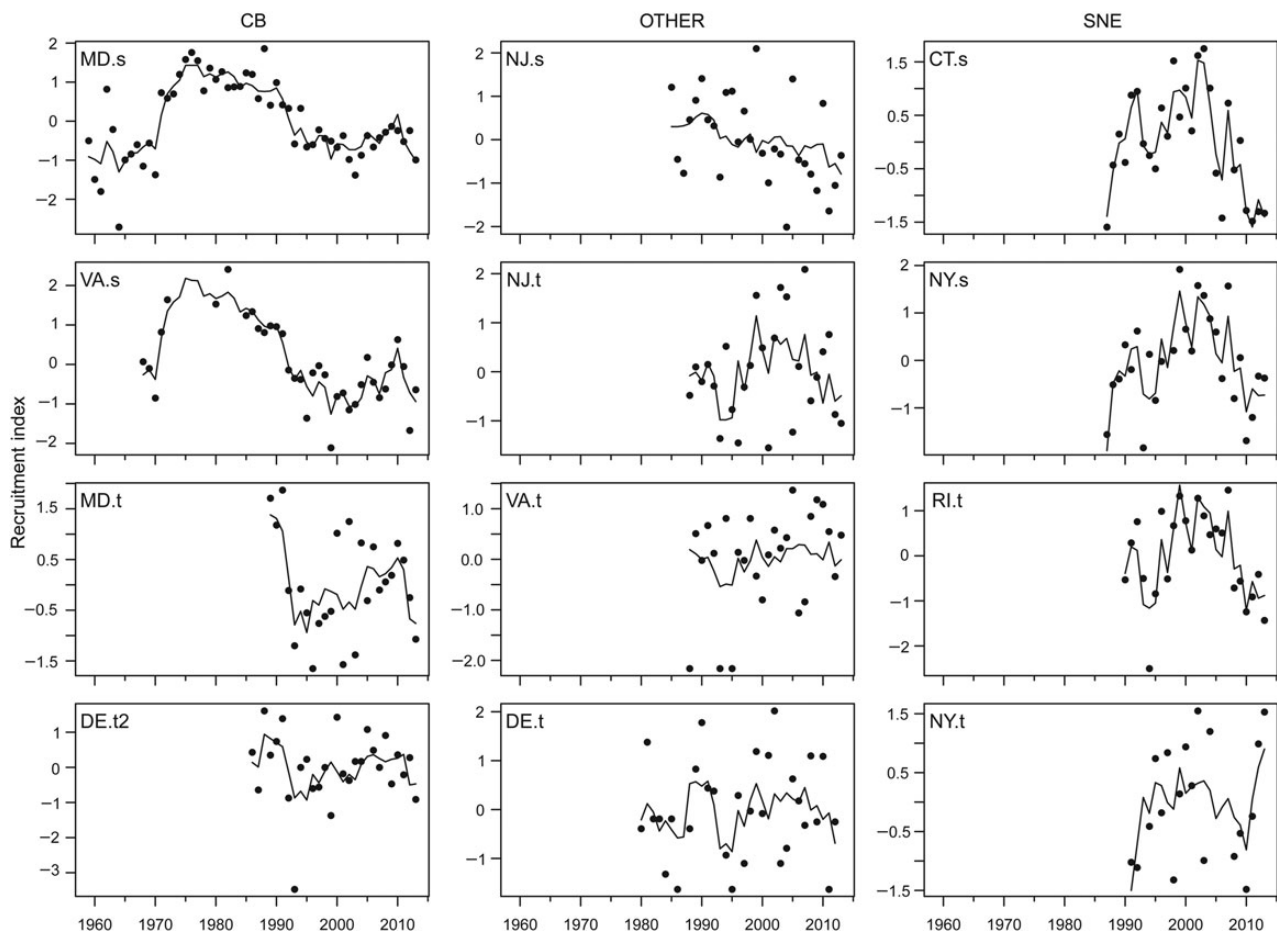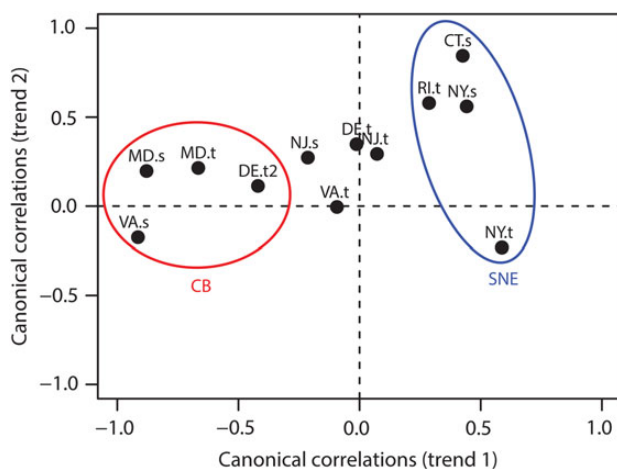
Figure 4. DFA model fits for Atlantic menhaden recruitment indices from 1959 to 2013, based on the best model with two common trends and a lagged AMO covariate. Fitted values (lines) and observed values (points) are plotted for each of the 12 recruitment time-series. Indices were standardized to have a mean of 0 and SD of 1, and indices are identified by the US state abbreviation (see Figure 2) followed by a gear label (s, seine; t, trawl). Time-series are grouped by columns based on similarity of canonical correlations of data with the modelled common trends as identified in Figure 6 (CB, Chesapeake Bay; SNE, Southern New England; OTHER, other surveys).

survey time-series (Figure 4). Model fits were particularly good for the MD.s, VA.s, CT.s, NY.s, and RI.t surveys. However, model fits were poorer for some surveys, with predicted recruitment unable to replicate the high degree of variability evident in the observations (e.g. NJ.s, VA.t, and DE.t). Seven of the 12 recruitment series for menhaden (MD.s, VA.s, MD.t, NJ.t, CT.s, NY.s, and RI.t) demonstrated evidence of low-frequency variation (Figure 4). The low-frequency variation was most evident in the two surveys with the longest time-series from CB (e.g. MD.s and VA.s) for which autocorrelations were significant. These two surveys indicated high recruitment from 1971 to 1991 with abrupt changes in the early 1970s, early 1990s, and arguably ca. 2010 (Figure 4 and Supplementary Figure S2). Although only the MD.s and VA.s surveys extended back to
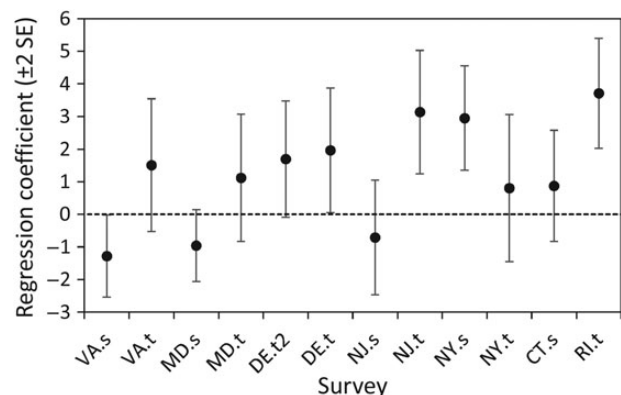
the 1960s and 1970s, the decline in the early 1990s was detected to varying extents by the other surveys classified into the CB region (MD.t and DE.t2). The northern group of surveys in the SNE region tended to have higher recruitment from the mid-1990s to the mid-2000s (particularly CT.s, NY.s, and RI.t), with those periods also being defined by relatively abrupt changes that are largely coincident with periods of change in the CB surveys (Figure 4 and Supplementary Figure S2).

The best DFA model for the 1959–2013 period included two common trends, with each trend representing differing temporal patterns in recruitment (Figure 5). Canonical correlations between recruitment time-series and these two common trends highlighted the spatial structure of recruitment trends (Figure 6); the southernmost surveys in the CB region (VA.s, MD.s, MD.t, and DE.t2) were strongly negatively correlated with common trend 1, whereas northern surveys from SNE (CT.s, RI.t, NY.s, and NY.t) were positively correlated with trend 1 or negatively correlated with trend 2 (Figures 2 and 6).

Regression coefficients of the best-fit DFA model quantified the linear relationship between lagged AMO and each recruitment time-series within the model (Figure 7). Several recruitment indices were significantly, positively associated with lagged AMO (RI.t, NY.s, NJ.t, and DE.t), with the strongest associations occurring in the SNE region. The two longest time-series (VA.s and MD.s from CB) were negatively associated with lagged AMO.

GAM results generally reinforced the DFA identification of AMO and LAND as significant predictors of recruitment in the time-series, but for simplicity, we only present GAM results for MD.s, because it had the longest time-series and most data. The best model for MD.s included AMO and LAND in addition to GSI and MTL as the best covariates for recruitment (Figure 8). This MD.s model explained 60.8% of the deviance in the dataset. MD recruitment was linearly related to AMO, with greater recruitment occurring when the AMO was in a negative state. The effects of the other covariates were non-linear. Low GSI values were associated with lower recruitment. Effects of MTL were weak but sinusoidal. LAND and recruitment were positively associated, although three high values of landings distorted the relationship at that extreme.

The global GAMs, which included all survey data in a single model, had relatively poor fits with weak covariate effects. The best global GAM only explained 27.7% of the deviance in the full

Figure 5. The two common trends of the best dynamic factor model (with lagged AMO as a covariate) for Atlantic menhaden recruitment indices from 1959 to 2013. Common trend 1 (thick, red, solid line), common trend 2 (thin, blue, solid line), and their respective 95% confidence intervals (dotted and dashed lines) are shown, and the values are unitless. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Figure 6. Biplot of canonical correlations between observed Atlantic menhaden recruitment time-series and common trends from the best DFA model for 1959–2013. Ellipses identify time-series that have similar trends through time, classified as the CB and SNE regions. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Figure 7. Regression coefficients (± 2 SE) for the effect of lagged AMO on Atlantic menhaden recruitment time-series, based on the best-fit DFA model for 1959–2013. Recruitment time-series from surveys are organized approximately by increasing latitude on the *x*-axis and are identified by codes as defined in Table 1.
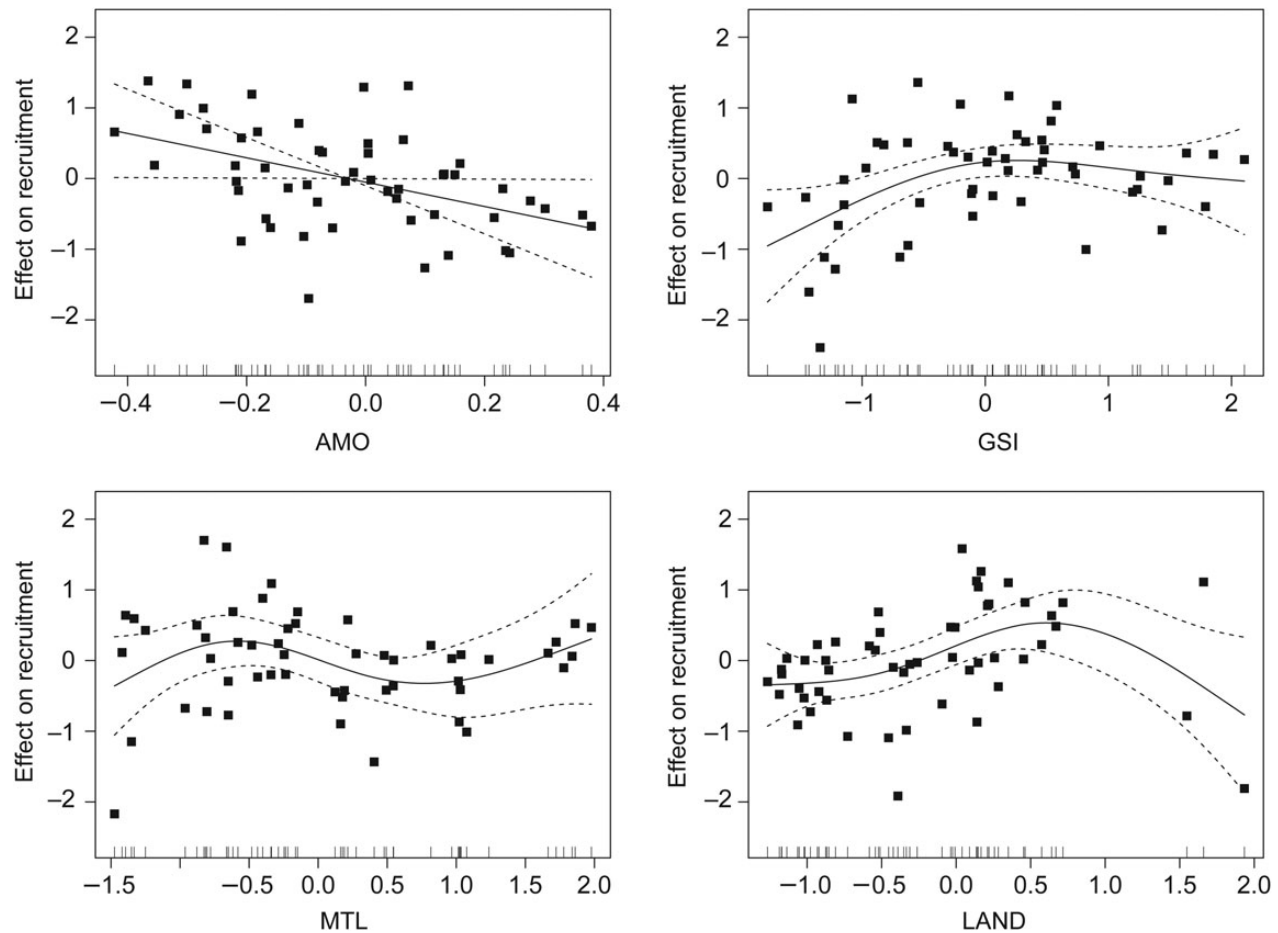
Figure 8. Partial effects of covariates on Atlantic menhaden recruitment, as estimated from the best-fit generalized additive model of MD seine survey data. Covariates include the Atlantic Multidecadal Oscillation (AMO), Gulf Stream Index (GSI), mean tidal level (MTL), and coast-wide menhaden landings (LAND). Solid lines are the mean partial effects for each covariate, dashed lines represent the approximate 95% confidence intervals, and points are the partial residuals. Sampling intensity for each covariate is indicated by tick marks on the *x*-axis.

dataset, whereas GAMs based on individual surveys explained between 45 and 90% of the deviance. This highlights the variability in recruitment–covariate relationships across surveys and the weak predictive power of covariates across the coast. The best global model included separate AMO and MTL smoothers for the northern (NJ–RI) and southern (VA–NJ) surveys and smoothers for LPUE and minimum winter temperature (TEMP$_{min}$), but relationships were not strong (Supplementary Figure S3). However, an interesting pattern of note was a weak, positive relationship between recruitment and AMO for the northern surveys, whereas for southern surveys recruitment tended to be higher at the lowest AMO values (Supplementary Figure S3).

Discussion

Our analyses indicated that juvenile Atlantic menhaden exhibited low-frequency variations in abundance over long decadal periods from 1959 to 2013, with distinct spatial patterns along two broad geographic regions of the Northeast United States. Specifically, recruitment trends were largely coherent within each of the CB and SNE regions, but patterns between regions were out of phase and negatively correlated with each other. Each region experienced relatively abrupt changes in YOY menhaden abundances. Over the entire coast, the AMO was one of the best predictors of menhaden

recruitment trends, suggesting that broad-scale climate forcing is an important controller of recruitment dynamics, although the specific mechanisms remain as yet unidentified. The use of multivariate, statistical models for time-series allowed for the examination of large-scale patterns and environmental drivers of recruitment trends by synthesizing many fisheries-independent surveys, and this approach has applicability to other broadly distributed and monitored species of management interest.

Temporal patterns

Our DFA indicated a surprising coherence among surveys. Many surveys were characterized by abrupt shifts in YOY menhaden abundances particularly during the early 1970s, early 1990s, and around 2010. Large-scale shifts in abundance and recruitment have been noted for other taxa in the Northwest Atlantic in similar periods, indicative of structural changes in the broader ecosystem. For example, Beaugrand *et al.* (2008) demonstrated abrupt shifts in phytoplankton, zooplankton, and cod (*Gadus morhua*) recruitment in the North Atlantic ecosystem in the late 1980s. Groundfish populations (e.g. Atlantic cod, haddock *Melanogrammus aeglefinus*, and American plaice *Hippoglossoides platessoides*) experienced dramatic and often abrupt changes in abundances in the late 1980s and early 1990s that have been attributed both to overfishing (Myers *et al.*,

1996; Shelton *et al.*, 2006) and to environmental changes (Halliday and Pinhorn, 2009; Rothschild and Jiao, 2012). Frisk *et al.* (2008) documented similar abrupt shifts in elasmobranch populations during similar periods, and inferred environmentally mediated changes in spatial distribution as the driving factor. Estuarine systems, such as CB and Narragansett Bay, have also experienced shifts in fish assemblages during the early 1990s (Collie *et al.*, 2008; Wood and Austin, 2009), with menhaden being one of the affected species in CB.

The shifts we have documented in menhaden recruitment and many of the notable shifts documented above appear correlated with broad-scale climate indices that exhibit low-frequency variation, like the AMO, which was the best explanatory variable in this study. The AMO is strongly autocorrelated and has a period of ∼60 years. In the last 50 years, the AMO exhibited a minimum in the mid-1970s, transitioned into a positive phase in the 1990s, and reached a maximum in the 2000s (Alexander *et al.*, 2014; Nye *et al.*, 2014). Effects of the AMO on physical and oceanographic processes vary spatially, but the effects can be profound (Enfield *et al.*, 2001; Alexander *et al.*, 2014; Pershing *et al.*, 2015). The AMO has been correlated with various biological responses in aquatic systems, including shifts in dominant zooplankton taxa (Kane, 2011), changes in natural mortality of fish species (Jiao *et al.*, 2012), large-scale shifts in fish distributions (Nye *et al.*, 2009), changes in community structure (Collie *et al.*, 2008; Wood and Austin, 2009), and depressed production in important demersal fisheries (Pershing *et al.*, 2015). In our study, it must be emphasized that although the low values of the AMO in the 1970s and 1980s generally correspond to the period of increased menhaden recruitment in the CB region, our DFA model indicates a stronger increase in recruitment in 1971 and a stronger decrease in recruitment in 1992, beyond what is predicted from AMO alone. Also, DFA models with greater AMO lags (up to 8 years) did not yield a better model fit to the data, as has been documented for other species (Gröger *et al.*, 2010).

Our analyses strongly support a role for broad-scale climate forcing in influencing recruitment levels in menhaden, but the underlying mechanistic linkages remain obscure and may in fact be a combination of multiple, interacting processes (Ottersen *et al.*, 2010). Inclusion of many covariates in our analyses was intended to identify some dominant mechanisms regulating recruitment. Although effects of specific covariates (e.g. GSI, Ekman transport, precipitation, and predator biomass) were significant in GAMs of some individual surveys, the overall effect of these more mechanistically informative variables was relatively weak on the coast-wide scale. Instead, the menhaden recruitment signals could result from a larger, AMO-driven suite of biotic and abiotic ecosystem responses, as described for other marine fishes by Ottersen *et al.* (2010). Three AMO-related hypotheses for potential mechanisms include (i) changes in oceanographic processes and larval transport caused by AMO-associated changes in wind and water circulation patterns, (ii) temperature-mediated changes in distribution, timing, and location of spawning that influence larval transport to estuaries, and (iii) effects of temperature and other climate-related factors on habitat quality or system production that have cascading influences on survival of larval or juvenile menhaden in either oceanic or estuarine habitats. Continued research on how climatic indicators like AMO affect physical and biological processes in the Northwest Atlantic (e.g. Ottersen *et al.*, 2010; Alexander *et al.*, 2014; Nye *et al.*, 2014) will aid in evaluating the support for these three potential mechanisms in controlling menhaden recruitment.

In addition to the AMO index, coast-wide menhaden landings were also associated with the temporal trends in YOY menhaden abundance. However, interpretation of the positive relationship between landings and recruitment is complicated by major spatial changes in historical fishing effort due to the closure of processing plants along the coast in the latter half of the 20th century (SEDAR, 2015). The significance of the 1-year lagged landings in the DFA may suggest that menhaden catches were indicative of SSB that contributed to greater YOY production the following year. We found no evidence of a negative LAND−recruit relationship that might indicate strong, direct, and immediate effects of fishing. It bears noting that as a covariate, the number of eggs produced by menhaden (as a measure of SSB) had no substantial effects on recruitment trends throughout the coast. The lack of a strong SSB-recruitment signal is consistent with the recent menhaden stock assessment, in which recruitment is not modelled using a stock−recruit function (SEDAR, 2015) because of the noise and variability associated with other factors not explicitly accounted for in the modelling.

Spatial patterns

The distinct and inverse spatial patterns in recruitment relationships constitute a central finding revealed by our analyses. One hypothesis that could explain the spatial recruitment dynamics would invoke spatial changes in larval supply to the estuaries. Menhaden migrate northward along the eastern US coast in spring and early summer, with larger, older individuals migrating farther north towards the Gulf of Maine (Dryfoos *et al.*, 1973). Subsequently, menhaden migrate southward in autumn and winter. Menhaden spawn broadly over a protracted period throughout the coast during the southward migration, although traditionally, peak spawning is believed to occur off North Carolina from December to February (Higham and Nicholson, 1964; Reintjes and Pacheco, 1966; SEDAR, 2015). Recent evidence highlights the importance of fall spawning in the MAB and SNE (Quinlan *et al.*, 1999; Warlen *et al.*, 2002; Light and Able, 2003). Importantly, hydro-dynamic modelling indicates that larvae that ingress into MAB and SNE estuaries are likely spawned to the north and advected southward along the coast due to wind-driven coastal flow regimes (Quinlan *et al.*, 1999). Given that larger, older individuals migrate farther north, recruitment to SNE estuaries may be more strongly influenced by the older fish that have the potential to spawn in more northerly waters (Quinlan *et al.*, 1999). Changes in the spatial distribution and northern extent of menhaden and larval supply may also be influenced by climate change and the AMO, as indicated by the poleward shift of many fish stocks of the coastal Northwest Atlantic in the recent warming decades (Nye *et al.*, 2009). Thus, changes in menhaden age structure and distribution through time could alter the northern extent of the menhaden population and the relative supply of larvae to those estuaries, decoupling the recruitment patterns along the coast. Evaluating this hypothesis is challenging due to a lack of long-term fishery-dependent and fishery-independent data that can provide catch-at-age information along the coast, but future research should focus on addressing the potential linkages among population age structure, spatial distribution of the stock, and the spatial recruitment patterns we detected.

An alternative hypothesis to explain the spatial recruitment patterns invokes temporal variability in spawning that influences patterns of physical transport and survival along the coast, perhaps resulting from broad-scale climate forcing. There is evidence of

distinct shifts in timing of larval menhaden ingress—shifts that differ spatially along the coast. Specifically, ingress into a New Jersey estuary has shifted substantially from peaking in fall and winter to peaking in June–July beginning in 1998 (Able and Fahay, 2010), whereas ingress into CB remains dominant during winter (Ribeiro *et al.*, 2015). In coastal waters, occurrence of menhaden larvae has shifted later towards spring (from the 1980s to the 2000s) which has been attributed to climate change, but spatial changes in larval occurrence were not detected on the Northeast US continental shelf (Walsh *et al.*, 2015). Timing and location of menhaden spawning could affect survival and larval transport due to the flow regimes, coastal currents, and water temperatures experienced, as well as the match–mismatch with food supplies (e.g. Stegmann *et al.*, 1999; Houde, 2009). Thus, spatial differences in the timing of peak egg production may be a viable mechanism underlying the broad spatial trends in recruitment documented in our analyses, particularly through its effect on larval transport, growth, and survival.

Finally, the spatial recruitment patterns could relate to regional patterns in factors regulating juvenile growth and mortality within the nursery areas after larval ingress. Within the CB, studies have linked abundance and growth of age 0 menhaden to primary production, phytoplankton biomass, predation, and other environmental variables (Uphoff, 2003; MDSG, 2009; Annis *et al.*, 2011; Humphrey *et al.*, 2014). The significance of these relationships do not always hold across broader spatial or temporal scales (Love *et al.*, 2006; this study), which is a common challenge in examining recruitment. However, these are still potential mechanisms that could help explain the regional patterns we observed, particularly if controlled by broader-scale, bottom-up mechanisms within the CB and SNE regions, as the significance of the AMO in our DFA model might suggest. Interestingly, there was evidence of a region-specific effect of the AMO on menhaden recruitment, based on the DFA coefficients and the global GAM. Unfortunately, the SNE time-series do not extend sufficiently back in time when the AMO was strongly negative to allow for a greater contrast in the SNE region and a complete evaluation of this interaction. However, a region–AMO interaction could indicate different underlying mechanisms of influence in the CB and SNE regions, or it could be related to the regionally variable effects that AMO can have on environmental conditions and processes (Enfield *et al.*, 2001; Alexander *et al.*, 2014).

An important caveat to this study is that the analyses do not address the relative magnitude or importance of recruitment across the regions. Previous estimates based on data from the 1970s suggested that CB contributed ∼69% of recruits to the coast-wide stock, with lower contributions from SNE of <15% (Ahrenholz *et al.*, 1989; ASMFC, 2004). However, recent estimates for 2008–2011, based on otolith microchemistry, suggest lower CB contributions of 17–59% (depending on the year and cohort) and higher SNE contributions of 18–49% (Anstead, 2014). Important nurseries are also present in the southeast United States (i.e. Florida to North Carolina) and can contribute substantially to coast-wide menhaden production (Anstead, 2014), but our study was unable to assess recruitment patterns in this region due to insufficient data. The regional and temporal recruitment patterns we present could be indicative of shifts in the contribution of regional nursery areas to coast-wide production, but the biological significance and the magnitude of the effects on population dynamics and fisheries management remain to be fully evaluated.

Management implications

Our study has two primary implications to support the management and sustainability of fisheries for menhaden and similar species. First, our results suggest that coast-wide assessment and management of species like menhaden may be obscuring important processes occurring at regional scales. Understanding and accounting for recruitment dynamics at appropriate spatial scales may lead to more effective management. The most recent menhaden stock assessment added regional dynamics in fishing as well as regional fishery-independent indices of adult abundance (SEDAR, 2015), and our results suggest that a similar regional approach would be merited in the development of juvenile abundance indices with a regional break around Cape May, NJ. The second important implication pertains to the non-stationarity of recruitment time-series, particularly in the CB region. AMO-associated changes in recruitment success along the coast suggest that management reference points developed from the full time-series may be inappropriate if ecosystem state and nursery quality fluctuate between favourable and unfavourable conditions. Our work on the spatial and temporal dynamics of menhaden recruitment and its drivers can thus help improve fisheries management, but more generally it also contributes to a broader understanding of the recruitment variability of widely distributed fish populations in coastal and estuarine waters.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

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