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Original Article

Spawning locations and larval dispersal of Atlantic Menhaden during 1977–2013

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Atlantic Menhaden *Brevoortia tyrannus* exhibit particularly complex recruitment dynamics as a coastal-spawning species with seasonal migrations along the North American Coast from Nova Scotia, Canada, to Florida, United States. Despite a coast-wide reduction in juvenile production from the 1970s to the 1990s, Atlantic Menhaden continues to support one of the oldest and largest commercial fisheries on the US east coast. We used a stochastic partial differential equation model to estimate spawning location and larval dispersal on the Atlantic Coast over two time periods, with data from the Northeast Fisheries Science Center ichthyoplankton surveys conducted in 1977–1987 and 2000–2013. Within the study area, Atlantic Menhaden spawning appears to occur primarily near shore over a large spatial range, from southern New England to North Carolina over the majority of the year, but at greatest levels during November and December. Larger, older larvae were found over a similar spatial and temporal range, dispersing farther from shore. Between the two periods, we observed an increase in secondary, spring-time spawning events. We observed no major, directional spatial shift in spawning or dispersal. However, estimated spawning activity increased near Delaware Bay. Both small and large larvae were most abundant in the Southern portion of the study area during both periods. Yet, total spatial coverage of all larvae varied greatly among years until the mid-2000s, when the Atlantic Menhaden population was believed to have recovered reduction in juvenile production from the 1970s to the 1990s. In most recent years, we observed consistent and large areas of spawning and larval dispersal.

Keywords: *Brevoortia tyrannus*, early life, larvae, recruitment, spatial analysis.

Introduction

Recruitment dynamics in marine fisheries are often very complex, due to a dynamic interplay between physical and biological factors (Fogarty *et al.*, 1991). In open marine populations, local production of offspring may have little direct impact in setting local population size (Caley *et al.*, 1996) because of a combination of complex life history and variation in physical environments. Therefore, knowledge of detailed spatial and temporal variation in early recruitment allows scientists to separate localized from population-scale fluctuations in abundance and examine such changes in relation to physical and biological factors.

Atlantic Menhaden *Brevoortia tyrannus* is an abundant forage fish species on the Atlantic Coast of North America. Not only are they an important prey species, transferring energy up the food web (Ahrenholz 1991, Annis *et al.*, 2011), but they are economically valuable and support one of the oldest industrialized fisheries in the United States (Vaughan and Smith 1988, Friedland *et al.*, 1989). Atlantic Menhaden are migratory, coastal spawners, ranging from Nova Scotia, Canada, to Florida, United States (Reintjes 1969). Eggs are released and hatch in the coastal ocean before larvae are transported to nursery habitats (i.e. estuaries) where they metamorphose into juveniles (Ahrenholz 1991). Although the stock is currently not overfished and overfishing is not occurring, managers and scientists remain concerned about low recruitment relative to historical levels (SEDAR 2015).

While the stock appears to have recovered from historical overexploitation in the 50s and 80s, there have not been substantial changes in coast-wide juvenile abundance since the 1990s (SEDAR 2015). However, recruitment patterns are not consistent across space. While recruitment in nursery habitats in southern New England are highly correlated with each other, as are patterns in nursery habitats near the Chesapeake Bay, the two regions show inverse patterns (Buchheister *et al.,* 2016). Historical estimates suggest that the Chesapeake Bay contributed as much as 69% of total recruits to the spawning stock (Ahrenholz *et al.,* 1989, ASMFC 2004). Although still proportionally the most important nursery area, more recent research conducted in during 2009–2011 has suggested a lower but variable contribution from the Chesapeake Bay, between 25 and 59% (Anstead *et al.,* 2016).

Examining the early life stages of Atlantic Menhaden, beginning with spawning may provide insight into sources of variation in Menhaden recruitment. Menhaden spawning has not been directly observed in nature. Thus, knowledge of spawning behaviour has been inferred from planktonic sampling of Menhaden eggs and larvae (e.g. Checkley *et al.,* 1999, Hare *et al.,* 1999) and ova classification of adult females (e.g. Lewis *et al.,* 1987). It is generally accepted that the bulk of spawning occurs in the coastal ocean, peaking during the winter off of Cape Hatteras, North Carolina (Ahrenholz *et al.,* 1987). However, some spawning is believed to take place throughout the species' range during most of the year (Nelson *et al.,* 1977). Massmann *et al.,* (1962) suggested that spawning likely occurs up to 64 km offshore based on the observation that, larger larvae occurred at greater abundance at stations closer to shore, while eggs and smaller larvae were absent from coastal waters. Following this work, cross-shelf transport dynamics were thought of as the dominant process bringing larvae to nursery areas (e.g. Epifanio and Garvine 2001). Then, in the late 1990s, a multi-disciplinary effort known as the South Atlantic Bight Recruitment Experiment (SABRE) provided evidence from hydrodynamic modeling that along-shelf flow is the dominant process in delivering larvae, and that shallow (20–60m), inshore regions are the primary spawning sites (e.g. Hare *et al.,* 1999, Checkley *et al.,* 1999, Rice *et al.,* 1999). Checkley *et al.,* (1999) documented some egg patches over 40 km from shore, but found near shore spawning was of higher importance based on hydrological conditions and model results.

Although general trends in spawning have been relatively well understood, more recent research has suggested more spatial variation in larval Atlantic Menhaden dynamics than previously thought. Walsh *et al.,* (2015) found no significant changes in spatial distribution of larval Atlantic Menhaden when 1977–1988 was compared to 1999–2008. However, Buchheister *et al.,* (2016) found increasing relative juvenile abundance in southern New England estuaries, which may suggest a northward shift in spawning or suitable habitat for young Menhaden. Alternatively, there may be different trends in early life mortality over space.

Long-term changes in the timing of the occurrence of Atlantic Menhaden larvae have been observed on the East Coast of the United States. Walsh *et al.,* (2015) detected significant changes in the temporal distribution of Atlantic Menhaden larvae between 1977–1988 and 1999–2008 with more larvae occurring later in the season. In New Jersey, there has also been an observed shift in the timing of ingress, from a fall peak to June and July, since the late 1990s (Able and Fahay 2010).

The primary goal of this study was to assess changes in the pattern and timing of Atlantic Menhaden larval distribution. By examining the spatial distribution of different sizes of larvae, we were able to infer Atlantic Menhaden spawning locations and larval dispersal patterns. We used a spatial model of the smallest larvae to characterize the location and timing of spawning. Given higher abundances of all size classes of Atlantic Menhaden larvae nearshore (Simpson *et al.,* 2016), we expected to see the probability of spawning to be greatest nearshore. Additionally, we expected spawning potential to increase southward, peaking offshore of North Carolina, in the winter (Lewis *et al.,* 1987, Stegmann *et al.,* 1999). We also characterized the distribution of larger larvae to determine patterns of dispersal. Given the net southward flow of water near the coast in the Mid Atlantic Bight (Checkley *et al.,* 1999), we expected the concentration of older larvae to increase southward, dispersing away from likely spawning locations.

Methods

Larval data

Larval data were obtained from two National Oceanic and Atmospheric Administration sampling programs conducted on the U.S. Atlantic Coast: the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program and the Ecosystem Monitoring (EcoMon) program. MARMAP was conducted during 1977–1987, and EcoMon, which began in 1992, is an ongoing program, although only ichthyoplankton samples from 1999 to 2013 were processed and available for this analysis. Both were multi-species programs that sampled the same spatial area from Nova Scotia, Canada, to Cape Hatteras, North Carolina, United States. MARMAP used both a fixed station design covering the sample area of each survey approximately evenly and a random-stratified design based on the Northeast Fisheries Science Centre (NEFSC) bottom trawl survey design (Sibunka and Silverman, 1984). EcoMon uses a random-stratified design also based on the NEFSC bottom trawl survey, and strata are based on the bottom trawl survey strata with delineation being primarily by depth and latitude. The narrow inshore stratum and the offshore shelf-break stratum of the bottom trawl survey were combined in the EcoMon plankton sampling design, thus there are 47 plankton strata compared to 108 bottom trawl survey strata (Walsh *et al.,* 2015).

Sampling was conducted on a roughly bimonthly basis (for more information on sampling procedures and processing see Simpson *et al.,* 2016). Double oblique tows were a minimum of 5 min in duration, and fished from the surface to within 5 m of the seabed or to a maximum depth of 200 m at a tow speed of $\sim$1.5 knots. The volume filtered of all collections was measured with mechanical flowmeters mounted across the mouth of each net. Samples were fixed in a 5% formalin solution at sea and larvae were transferred to ethanol during processing. Samples were processed at the Morski Instytut Rybacki in Szczecin, Poland, or the Northeast Fisheries Science Centre to determine the number of Atlantic Menhaden larvae collected. For each sample net, a maximum of 50 individuals were measured to the nearest 0.1 mm;

if more than 50 individuals were present, a random subsample of 50 was taken to characterize the length composition. Larval abundance for each sample was standardized to an areal abundance (number of larvae per $10 \cdot m^{-2}$).

Although the sampling protocol was generally consistent between MARMAP and EcoMon, the sampling mesh was changed from a 505 to a 333 μm plankton net. The smaller mesh size has been found to return greater abundances for fish <9 mm (Johnson and Morse 1994). To avoid potential bias caused by the gear change, the presence and absence model was run separately for MARMAP and EcoMon periods. In the present study, we also separated Menhaden larvae into two different size groups: ≤6 and >6 mm with the small size group indicating spawning location and large size group indicating dispersal processes.

We restricted our analyses to tows conducted within the 25 strata in the Southern New England and the Mid Atlantic Bight regions because very few Atlantic Menhaden larvae were observed outside these regions (Figure 1). We used inner strata referring to the strata adjacent to shore, outer strata referring to the strata near the shelf edge, and middle strata referring strata between inner and outer strata. We paired months (Sep–Oct, Nov–Dec, Jan–Feb, Mar–Apr, May–Jun, and Jul–Aug) to reflect the bi-monthly sampling design. Tows conducted in July and August were excluded because no Menhaden larvae were observed during July and only 15 were observed during August over the entire study period during both sampling programs (catches during the other months ranged from 1468 to 304 931 individuals). September was treated as the beginning of the larval year such that larvae that hatched during September–December would be added to those from January through May of the following year to capture seasonal spawning dynamics.

Larval size distribution

We examined the size distributions of all larvae at each of the 25 strata sampled in southern New England and the Mid Atlantic Bight (Figure 1a). Given the limited observations, tows were treated as replicates within each of the sampled strata. We weighted each Atlantic Menhaden size observation by abundance-at-length for that given size and tow in order to best represent the actual numbers of larvae present of a certain size.

Estimating spawning locations

To examine spawning location and timing, only the smallest individuals were of concern. As a consequence, the length cut-off for the smallest individuals was 6 mm. Based on growth of ingressing larvae in the Chesapeake Bay during the 2000s (Lozano *et al.*, 2012), 6 mm approximately corresponds to 1 week post hatch. During the MARMAP period, 2 years (1979 and 1980) and 2 bi-monthly categories (Jan–Feb and Mar–Apr) (# tows = 2540) were removed due to zero positive observations of small Atlantic Menhaden larvae. Although this reduced the sample size by almost half, this was necessary for the model because annual and seasonal fixed effects diverged with no positive data. All larger individuals were excluded from this part of the analysis.

After excluding large individuals (>6 mm), the abundance information was converted to presence/absence because the abundance data were skewed with a large number of zero catches. This simplification is appropriate for this analysis because our question addresses where and when larvae are occurring in order to infer likely locations of spawning and general patterns of dispersal.

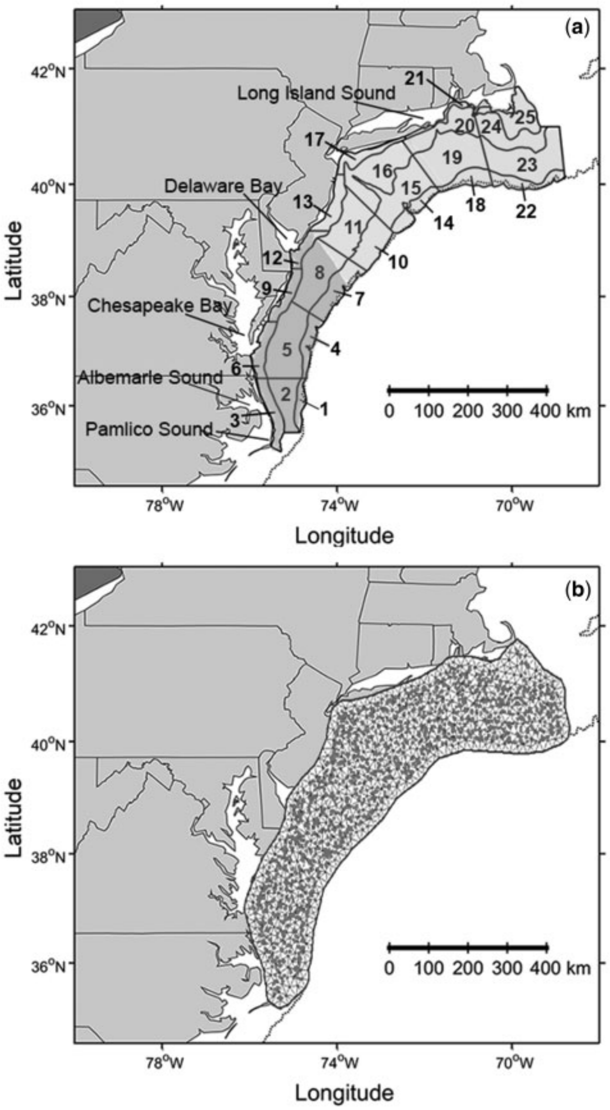

Figure 1. (a) Plankton strata included in spatial analysis. Shaded grey colour correspond with northern (strata 18–25), middle (strata 10–17), and southern (strata 1–8) of sampled area and to Figures 2 and 7. (b) The triangular mesh constructed in INLA used for the SPDE models on MARMAP (1977–1987) and EcoMon (2000–2012) for the characterization of Atlantic Menhaden spawning activity. Red points designate locations of tows conducted during both periods.

Classical kriging is a common tool for mapping and identifying spatial patterns. However, classical kriging relies on Gaussian and stationarity assumptions (Webster and Oliver 2007), which are un-realistic for presence/absence data. Kriging also faces computation challenges incorporating trends due to the $O(n^3)$ matrix inversion algorithm. Alternatively, Bayesian hierarchical modelling is a flexible framework for incorporating spatio-temporal trends through structured random effects (Cressie and Wikle 2015). However, Bayesian hierarchical modelling still requires the computationally intensive Markov chain Monte Carlo algorithm. A new statistical approach (Rue *et al.*, 2009, Martins *et al.,* 2013) addresses the computational challenges in Bayesian modelling by approximating the marginal posterior using the Integrated Nested Laplace Approximation (INLA). The INLA approach facilitates efficient Bayesian inference through O($n\log n$) sparse matrix algorithms. We used a stochastic partial differential equation (SPDE, Lindgren *et al.,* 2011) model in the R-INLA package to fit a realistic model to a large presence/absence data set with efficiency and reliability (Krainski *et al.,* 2015).

The first step of building this model was constructing a triangular grid (i.e. mesh; Figure 1b) over the entire area where samples were collected during the two programs. Next, the monitoring data were projected onto the mesh. Sparse basis functions were evaluated over the adjacent grid points and used to approximate the spatial effect. Default options of the built-in R-INLA commands were used to carry out the projections (Krainski *et al.,* 2015).

Once the data were paired with the locations from the projector matrix, we were able fit the following model,

$$larv = \mu + M + Y + f(S) \tag{3.1}$$

where *larv* was 0 or 1 based on absence or presence of small larvae in a tow, μ was the intercept, *M* was the bimonthly category (Sep–Oct, Nov–Dec, Jan–Feb, Mar–Apr, and May–Jun) within which the tow took place, *Y* was the year (MARMAP 1977–1987, EcoMon 1999–2013), and *f(S)* was the spatial index, which we assumed had a conditional normal prior distribution. The averaged year effects for each group over two different periods were calculated, e.g. the averaged year effect for small larvae during MARMAP vs. the averaged year effect during EcoMon. The difference in the year effect reflected the change of sampling mesh size from 505 to 333 μm and potential changes in larval distribution between two periods. The year effect allows a comparison in spawning location and area between two different periods.

Spatial prediction of occurrence probability was conducted by running the model (3.1) separately over the periods covered by the MARMAP and EcoMon programs. Thus, the overall means and spatio-temporal random effects were not constrained to be similar between programs. This enables evaluation of long-term changes in spatial pattern, and adjustment of the change in sampling mesh size from 505 to 333 μm. Within each period, the final model was run to interpolate the occurrence probability over a regular grid with cell size ~15 × 12 km. The seasonal and annual random effects were fixed at their approximated marginal distribution for each bi-month category and year. The predicted probability was then mapped by further interpolating the fitted values on the grid onto a finer resolution grid (500 × 500 m) using multi-level B-Splines (Finley and Banerjee 2014) and cropped within 0.20 decimal degree of an observed data point.

We assessed model fit by comparing the predicted values to the actual observations using receiver operating characteristic (ROC) curves, because standard residual analyses are not informative for binary data. The annual effects (*Y* in 3.1) were fixed at the mean value for each bi-monthly category to identify long-term hot spots of spawning activity. For a particular probability threshold, we compared the model presence with actual presence to calculate sensitivity and specificity for that threshold. The false positive and true positive rates were joined for multiple thresholds to construct the ROC curves. We used area under the ROC curves to quantify the overall accuracy of model prediction. From the ROC curves, we also selected the optimal threshold for each bi-monthly category that maximized the sensitivity and specificity of the decision. This quantified annual and seasonal changes in likely spawning locations, and allowed us to convert continuous probabilities to presence/absence predictions, in order to look at the total predicted occupied area.

Examining larval dispersal

Finally, we analysed the presence/absence data for larvae >6 mm over our two study periods using the same models as were used for the smaller larvae. Assuming mortality was spatially uniform, the spatial pattern of larvae older than 1 week represents where they were transported post-spawning.

Results

General summary

The 25 strata covering the Mid Atlantic Bight (MAB) and Southern New England (SE) regions were heavily sampled in the MARMAP and EcoMon ichthyoplankton programs. From 1977 to 1987, 5159 tows were conducted during MARMAP, and from 2000 to 2013, 3805 tows were conducted during EcoMon. The mean number of tows was 206 and 152 per stratum during MARMAP and EcoMon, respectively (Table 1). Even with greater sampling in the earlier program, total abundance from all strata was 6.5 times higher in EcoMon than MARMAP, with 2 times higher total abundance in individuals >6 mm and 26.5 times higher in individuals 6 mm and smaller. The differences reflected both potential changes in larval abundance between the two periods and the change of sampling mesh size.

Similarly, when considering the number of tows with positive Atlantic Menhaden catches, EcoMon had 2.3 times greater positive tows than MARMAP, with 2 times greater positive catch for individuals >6 mm and 5 times greater catch for individuals 6 mm and smaller. Overall, 9% of tows conducted during MARMAP had positive Menhaden catch compared to 12.4% of tows conducted during EcoMon. Excluding the northern most strata, inner strata demonstrated higher positive catch and total abundance when compared to their outer and middle strata counterparts even after correcting for differences in sampling among strata. Inner strata were sampled an average of 101.8 times compared to strata further from the shore including both middle and outer strata, which were sampled 215.7 times on average.

Size distributions

Atlantic Menhaden larvae were observed at greatest abundances in nearshore strata. For this reason, in order to examine how larvae of different sizes were distributed in space, we focused on inner strata and middle strata, excluding the northern most strata due to low abundance. The average overall abundance by strata was 1090 ind/m^2, while total abundance was 50 and 0 ind/m^2 for strata 24 and 25 during MARMAP, respectively, and 35 and 20 ind/m^2 in strata 24 and 25 during EcoMon, respectively. Therefore, strata 24 and 25 were excluded from the length analysis.

Small larvae (<6 mm) were observed both nearshore and adjacent to shore during both sampling programs. However, the majority of the small larvae were detected in the southern portion, near the Chesapeake Bay during MARMAP. During EcoMon, we observed a comparable relative proportion of small larvae in the south, but also observed a substantial increase in small larvae in the central portion of the study area along the New Jersey and

Table 1. Summary of abundance and number of positive catch of larval Atlantic Menhaden by plankton stratum for two size classes (small: 0–6mm, large: > 6mm).

					Small				**Large**			
			Tows		**Abundance**		**# Positive**		**Abundance**		**# Positive**	
Strata	**Lat**	**Lon**	**M**	**E**	**M**	**E**	**M**	**E**	**M**	**E**	**M**	**E**
1	36.05	−74.83	75	64	0	8.32	0	2	20.69	65.05	3	8
2	36.10	−75.15	126	131	30.52	681.4	2	14	967.71	469.53	9	31
3	**35.86**	**−75.46**	**145**	**97**	**48.17**	**68.02**	**3**	**9**	**651.44**	**703.49**	**24**	**25**
4	37.21	−74.64	127	90	0	6.16	0	1	6.91	35.88	1	5
5	37.12	−75.15	408	323	392.08	2340.89	8	30	1809.09	6585.4	17	37
6	**37.00**	**−75.70**	**164**	**114**	**2.62**	**4015.93**	**1**	**19**	**187.33**	**1217.94**	**19**	**31**
7	38.04	−74.01	213	152	0	0	0	0	11.7	45.39	2	6
8	38.38	−74.48	387	263	13.05	8115.88	1	35	68.14	2289.94	6	45
9	**38.01**	**−75.11**	**113**	**59**	**158.26**	**292.61**	**4**	**8**	**433.71**	**404.45**	**8**	**16**
10	38.89	−73.15	136	176	0	0	0	0	0	15.54	0	3
11	39.24	−73.73	266	242	19.17	4776.19	3	18	75.47	1603.76	9	32
12	**38.81**	**−74.78**	**98**	**52**	**3.59**	**451.3**	**1**	**12**	**46.85**	**131.23**	**4**	**15**
13	**39.60**	**−74.09**	**219**	**106**	**57.25**	**2272.36**	**5**	**13**	**349.9**	**2051.87**	**18**	**35**
14	39.56	−72.16	154	78	0	0	0	0	0	0	0	0
15	39.78	−72.61	295	250	0	88.12	0	7	11.62	153.76	2	9
16	40.22	−73.12	400	268	169.28	734.77	8	27	471.3	1988.44	26	30
17	**40.49**	**−73.41**	**179**	**61**	**10.75**	**988.45**	**3**	**12**	**265.97**	**580.85**	**15**	**21**
18	40.08	−70.87	131	77	0	0	0	0	0	0	0	0
19	40.44	−71.39	334	296	6.55	18.41	1	2	5.02	43.52	1	2
20	41.00	−71.48	307	210	16.74	302.9	3	17	321.16	159.46	13	15
21	**41.07**	**−71.74**	**62**	**42**	**8.39**	**238.45**	**2**	**11**	**173.22**	**577.12**	**5**	**8**
22	40.07	−69.59	91	77	0	6.2	0	1	0	4.6	0	1
23	40.48	−69.62	437	315	5.33	0	1	0	5.1	16.16	1	3
24	40.88	−70.10	237	198	16.99	5.1	2	1	34.53	33.42	5	6
25	**41.17**	**−69.93**	**55**	**64**	**0**	**0**	**0**	**0**	**0**	**22.8**	**0**	**1**

Total tows conducted and mean latitude and longitude sampled within each strata are also shown. Columns with the "M" header show information from MARMAP (1977–1997), and columns with the "E" header show information from EcoMon (2000–2012). Strata closest to shore are in bold.

Delaware coasts (Figure 2). Large larvae, although more abundant overall during the later EcoMon period, were relatively less abundant in the southern portion of the study area and comparable in abundance to the early MARMAP period. In particular, mean abundance of individuals >20 mm decreased across strata near the Chesapeake Bay and south (Figure 2, 114 ind/m^2 during MARMAP vs. 73 ind/m^2 during EcoMon in strata 2, 3, 5, 6, and 9). During both periods, larval abundance was highest in the southern third of the study area and lowest in the northern third (Table 1 and Figure 2). The greatest difference in size distributions (Figure 3) and overall magnitude (Table 1) between inner strata and middle strata was observed in the southern part of the study area for both periods (Figure 3). The difference in size distribution reflected potential changes in size structure between the two periods and the change of sampling mesh size.

INLA models

We ran four models to characterize the spatial distribution of large and small larvae over the two periods. The models used between 2619 and 5159 observations. Sampling was performed more consistently across months during the EcoMon program than during MARMAP, which sampled considerably more during warmer months (Table 2). During both periods, the proportion of positive detections for large larvae was greater than small. For both large and small larvae, there was a greater proportion of positive tows in the later sampling program (Table 2).

The year effect in the INLA model reflected the impacts of changes in sampling mesh size and potential long-term changes. The averaged year effect for small larvae was -0.47 ± 1.27 during MARMAP and -0.30 ± 1.31 during EcoMon. The averaged year effect for large larvae was -0.36 ± 0.93 during MARMAP and -0.20 ± 0.71 during EcoMon.

The seasonal effect reflected the abundance in a given month relative to the overall mean abundance, i.e. the log Odds ratio of positive catch during each season over the baseline in the current model structure. Across all models, Nov–Dec had the greatest mean positive effect (Figure 4). For small larvae, during both time periods, Sep–Oct was second most positive, followed by May–Jun. During the MARMAP program, Jan–Feb had the second greatest mean positive effect followed by both Sep–Oct and Mar–Apr (Figure 4). During the EcoMon program, Sep–Oct and Jan–Feb were tied for the second greatest mean positive effect, followed by Mar–Apr (Figure 4).

The overall average predicted probability of encountering larvae was low for small larvae (<6 mm) and large larvae (>6 mm) in both MARMAP and EcoMon periods due to large seasonal and interannual variation (Figure 5). The predicted probability of encountering a larvae and potential occupied area was higher for both small and large individuals during EcoMon than during MARMAP. To illustrate spatial patterns, we selected the year in each period in which the probability of encountering larvae was greatest (Figure 6). Similar spatial patterns were observed in years

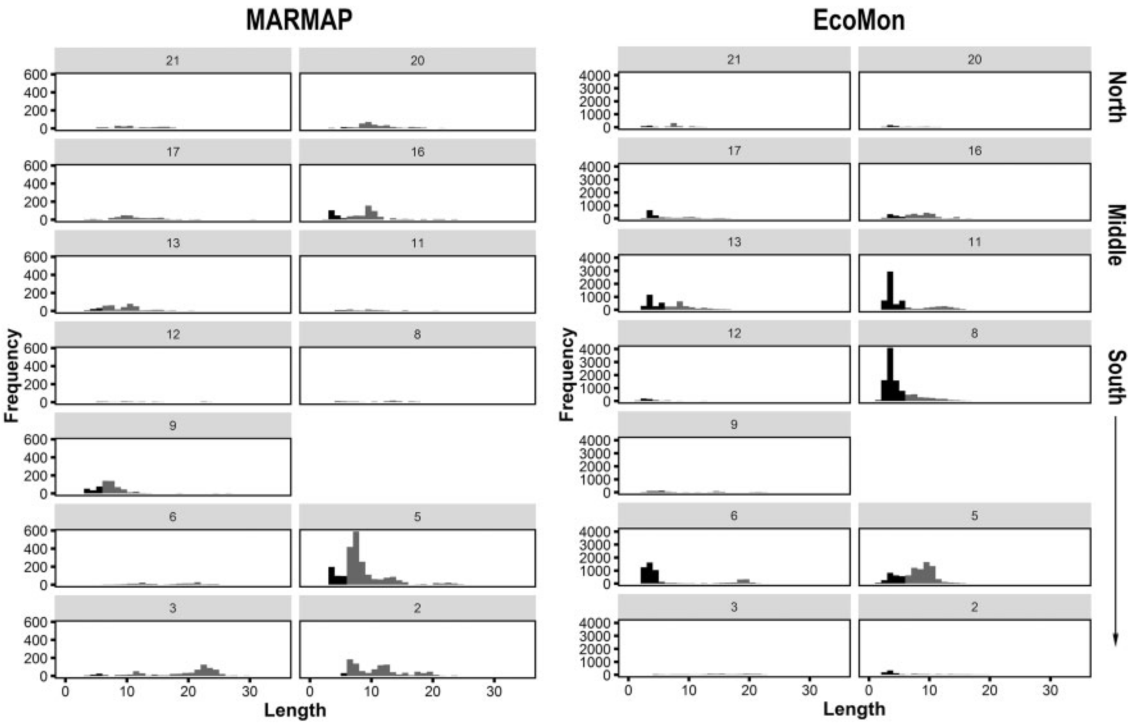

Figure 2. Frequency distributions of all larval Atlantic Menhaden sizes (measured length, weighted by total abundance per tow) at each stratum from the MARMAP and EcoMon icthyoplankton programs. Black bars show larvae 0–6 mm, and grey show larvae >6 mm. Grey bars on right side of the figure denote the sampling region (north, middle, or south; Figure 1a).

when Menhaden larvae had relatively high abundance. Our model predicted consistently higher probabilities of encountering small larvae throughout the sampling range during the EcoMon program (Figures 5 and 6). In both map predictions, there is a clear pattern of increasing probabilities of encountering larvae towards shore. During MARMAP, there were hotspots in predicted probabilities near Long Island Sound, New York Bight, between the Chesapeake and Delaware Bays, as well as south of the Chesapeake Bay, with highest predictions near New York Bight. During EcoMon, hotspots were predicted in similar regions all near the mouths of major estuaries along the coast, but at consistently higher probabilities, with the greatest probabilities being predicted along the Southern New England Coast and near the mouth of Delaware Bay.

The predicted probabilities for small and large larvae in two different periods showed the same patterns across months and years, but at different intensities dependent on the mean effect of bimonthly category and year, respectively. In order to best view spatial patterns, representative plots were shown for the times of greatest projected probabilities of detections. During both programs, there were higher predicted probabilities of observing larvae above 6 mm (Figure 5c and d). Again, the greatest probabilities were predicted near-shore, but in a more continuous distribution along the coast. Highest abundance of large larvae during MARMAP was concentrated in the southernmost portion of the range, south of Chesapeake Bay. During EcoMon, there was consistently high abundance of large larvae from Long Island, New York, through the southernmost area.

The ROC analysis determined the probability cut-off for fish presence by calculating the area under the curve. Additionally, it assessed model performance by comparing the predicted binary classification against the actual presence and absence observations. In the present study, ROC analysis showed mostly good model performance, where the model predictions were accurate more than 80% of the time, in both larval size groups, during both ichthyoplankton programs, according to the area under the ROC curve (AUC; Figure 7). Year-bimonthly combinations with more positive observations yielded smoother ROC curves. Cut-off values of the probability of larval presence in a tow determined from the ROC analysis ranged from 0.004 to 0.294 for all year-bimonthly projections for all four models. Year-bimonthly projections with greater numbers of positive observations yielded higher, thus stricter, cut-off values.

Comparing the proportion of occupied area where we predicted small and large larvae, we observed a shift in the dominant size class among the three regions (Figures 8 and 9). In the northern region, on average, we predicted small larvae to be present in 17.5% of the region during MARMAP and 9.3% of the region during EcoMon (Figure 8), compared to large larvae predicted in 9.0 and 6.1%, respectively (Figure 9). In either case, small larvae were predicted to occupy between 1.5 and 1.9 times more space than large. In the middle region, we predicted small larvae to be present in 26.5% of the region during MARMAP and 33.4% during EcoMon, compared to large larvae predicted in 27.3 and 40.8%, respectively. Thus, in both surveys large larvae were modelled to be present in a greater area than small, but only slightly greater during MARMAP and 1.2 times greater during EcoMon. Finally, in the southernmost region, we predicted small larvae to occupy 38.6 and 56.1% of the total area, during MARMAP and EcoMon, respectively, compared to large larvae in 44.2 and 73.5%. In this region, large larvae occupied 1.1 times more area during MARMAP and 1.3 times more area during EcoMon.

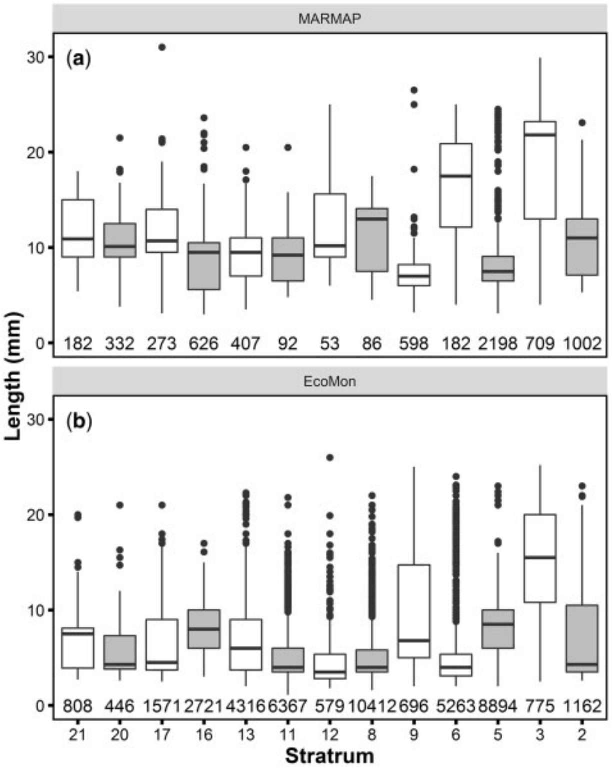

Figure 3. Box-and-whisker plot of abundance-at-length adjusted size observations of larval Atlantic Menhaden collected in 13 Atlantic Coast strata (Figure 1a) during (a) MARMAP (1977–1987) and (b) EcoMon ichthyoplankton sampling programs. Sample sizes are shown beneath the corresponding stratum. Box shading indicates nearshore (white) and offshore (gray) strata.

Comparing between the two periods, for both large and small larvae, we predicted Atlantic Menhaden to be present over a greater area overall during EcoMon (Figures 8 and 9). However, in the northern one-third portion of our study area this was not the case. In this region, we predicted the total area of likely larval Atlantic Menhaden occurrence to decrease between the earlier and later time periods.

The area with predicted probabilities higher than the threshold values determined in the ROC curve increased from north to south for small larvae during both EcoMon and MARMAP programs. In both programs, interannual variation appeared to be greater than seasonal variation. During the MARMAP program (Figures 8 and 9), Sep–Oct and Nov–Dec both resulted in similar and the highest amount of area where larvae would be predicted to be present. May–Jun exhibited a similar pattern across years, but with a lower proportion of area predicted to have positive detections. Similarly, during the later program, there was a slightly different pattern in bimonthly periods with Nov–Dec having the greatest proportion area coverage followed by Jan–Feb, Mar–Apr, Sep–Oct, and May–Jun.

During the EcoMon program, predictions were more similar seasonally than during the MARMAP program. There were several good years for small Atlantic Menhaden larvae during the MARMAP survey: 1977, 1982, 1983, and 1985–1987. However, during EcoMon, predictions were consistently high from 2006 onwards despite considerable variation among years from 2000 to 2005.

Similar to the models of the smallest larvae, models applied to the larger larvae showed greater predicted area of occurrence further south. During both programs the predictions of proportional area were greatest during fall/winter (Sep–Oct, Nov–Dec, Jan–Feb) compared to spring and summer (Mar–Apr and May–Jun). During MARMAP, Jan–Feb showed higher predictions than Sep–Oct. However, this trend was reversed during EcoMon. In 1977, predictions were moderate, in the southern region, just over 50% of the area was predicted to have large Atlantic Menhaden larvae present during the highest month. The next several years showed lower predictions, but with an increasing trend through the 1980s (Figures 8 and 9). On average, there was higher predicted areas of positive abundance during the EcoMon program. In the southern portion of the study area, during Nov–Dec, the model predicted from 43 to 99% of the area to likely contain larger larvae.

Discussion

Within the study area, Atlantic Menhaden spawning is likely occurring over an extremely large temporal and spatial range and is not primarily concentrated off the coast of North Carolina, as some previous research has suggested (Lewis *et al.,* 1987). Other studies have proposed that spawning occurs over a greater range to the offshore edge of the shelf (Nelson *et al.,* 1977), as our work supports. More recently, there has been a shift in thinking that spawning was predominantly offshore, to predominately nearshore as our study indicates (Checkley *et al.,* 1999, Hare *et al.,* 1999, Rice *et al.,* 1999, Stegmann *et al.,* 1999, Werner *et al.,* 1999). Hare *et al.,* (1999) and Rice *et al.,* (1999) also found that spawning in the Mid Atlantic Bight between the Chesapeake Bay and the Delaware had the largest contribution to larval ingress into North Carolina inlets. Our work shows this region to be an important spawning ground during both icthyoplankton programs. Additionally, we found support of spawning hotspots even further north, near Long Island, New York. Although larvae were more commonly found during the early winter, there was some evidence of spawning throughout most of the year, excluding July and August.

The clearest gradient observed on the maps of our predictions was inshore-offshore rather than north-south. Both small and large larvae had considerably higher probabilities of detection closer to shore. However, large larvae were predicted over a smoother gradient along the coast, and likely occurred further offshore than small larvae. This gives some evidence that spawning is most likely occurring near shore, with larvae transported both along and across the shelf. The most likely direction of transport is north to south (Quinlan *et al.,* 1999). This theory may be supported by our observation of more large larvae, relative to small, in the southern portion of our study (Figure 2). However, we expect faster growth and lower mortality rates in southern regions due to warmer temperatures (Ferraro 1980). This, too, would contribute to the observed pattern.

Some earlier work has suggested a significant peak in spawning off the coast of Cape Hatteras, North Carolina, in the winter (Higham and Nicholson 1964, Kendall and Reintjes 1975), while Judy and Lewis (1983) observed large amount of Menhaden eggs and larvae in the South Atlantic Bight. Within the study area, we found a broad trend of increasing small larvae southward; however, we did not see evidence of such a dramatic peak. Although, we have very little data south of Cape Hatteras, North Carolina, because that was the southern extent of sampling. This means the overall spawning patterns in this southern-most region are still

Table 2. Sample sizes (n), number of tows with positive detection (positive), percent positive by month (%), and in total for each of the four INLA models run for large and small Atlantic Menhaden larvae during MARMAP (1977–1987) and EcoMon (2000–2013) sampling programs.

		Sep–Oct	Nov–Dec	Jan–Feb	Mar–Apr	May–Jun	Total
Small MARMAP	*n*	797	601	NA	NA	1221	2619
	positive	13	33	NA	NA	2	48
	%	1.6	5.5	NA	NA	0.2	1.8
Small EcoMon	*n*	770	786	685	778	786	3805
	positive	68	130	3	5	33	239
	%	8.8	16.5	0.4	0.6	4.2	6.3
Large MARMAP	*n*	976	648	480	1563	1492	5159
	positive	19	101	36	28	4	188
	%	1.9	15.6	7.5	1.8	0.3	3.6
Large EcoMon	*n*	770	786	685	778	786	3805
	positive	73	202	57	34	19	385
	%	9.5	25.7	8.3	4.4	2.4	10.1

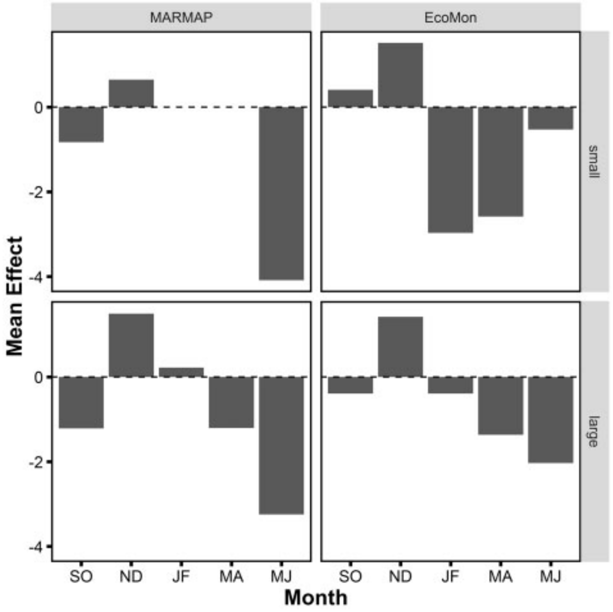

Figure 4. Mean effect by bimonthly category (SO: Sep–Oct, ND: Nov–Dec, JF: Jan–Feb, MA: Mar–Apr, MJ: May–Jun) from the four INLA models applied to larval Atlantic Menhaden presence/absence data obtained from MARMAP (1977–1987) and EcoMon (2000–2013) sampling programs. We displayed the mean effect of bimonthly category on the probability of observing larvae in a given tow as deviations from the mean. Any positive mean effect showed greater than average probability of detecting larvae, while any negative mean effect showed less than average probability of detecting larvae. (a) larvae 0–6 mm, MARMAP; (b) larvae 0–6 mm, EcoMon; (c) larvae >6 mm, MARMAP; and (d) larvae >6 mm, EcoMon.

unknown. During the MARMAP program, the coastal waters south of New York were predicted to have the greatest probability of larval occurrence. During EcoMon, the greatest probability of detection was near Delaware Bay and Long Island, New York. However, we did find the southern-third of our spatial range, from just north of Delaware Bay to Cape Hatteras, North Carolina, to have the greatest total area of which spawning was likely to occur. And, the majority of detections took place during November and December. Thus, the species' southward winter migration is likely an important time for spawning (Ahrenholz 1991).

Occupied area of small larvae was quite variable among years prior to 2006. However, from 2006 to 2013, the total area predicted to have small larvae stayed fairly constant. We believe this is due to the recovery of the adult population, particularly the recovery of a full age-structure. From 2006 onwards, fishing mortality remained constant and low while the adult biomass was estimated to be higher than it has been in the past several decades (SEDAR 2015). Our work supports the findings of the most recent assessment that the population is not being overfished in such a way that recruitment is being limited by adult abundance.

Since the mid-2000s, when the Atlantic Menhaden population is believed to have recovered, the occupied area of both large and small larvae has been consistent. This suggests that a healthy adult biomass is the most important factor in ensuring high larval supply (Warlen 1994). Occupied area of large larvae, shows less variation among years than that of small larvae. Even years in which no small larvae were observed (1979, 1980), nearly 25% of the southern region was predicted to have large larvae present. The difference between large and small larvae could indicate that the sampling frequency may not be adequate for small larvae because larvae were sampled bimonthly in both MARMAP and EcoMon whereas 6 mm larvae are approximately 1 week post hatch (Lozano *et al.*, 2012). In years where spatial coverage of small larvae was greatest, the spatial coverage of large larvae was predicted to be similar. Larger larvae are expected to disperse away from spawning locations as they develop to decrease competition as well as mortality by adults (Shanks 1995). Larvae ingressing into Chesapeake Bay in a study conducted from 2009 to 2011 found ages ranging 9–96 d with an average of 44–50 d post-hatch (Lozano *et al.*, 2012). One of the more surprising findings of our analysis was that we observed a decrease in average abundance of larvae >20 mm in the strata south of the Delaware Bay despite an overall increase in larval abundance and occupied area of large larvae. These largest larvae are the ones most similar to the observed mean size at ingress (Lozano et al 2012). Ingress at larger sizes is favourable because advection into coastal estuaries before larvae have developed swimming abilities would make them highly susceptible to predation in the more productive nursery areas (Shanks 1995). Our observation may indicate changes in pre-ingress survival from large (>6 mm) individuals to very large individuals (>20 mm) and perhaps changes in size at ingress, which could in turn affect post-ingress survival. These changes may explain continued low juvenile survey catch inside

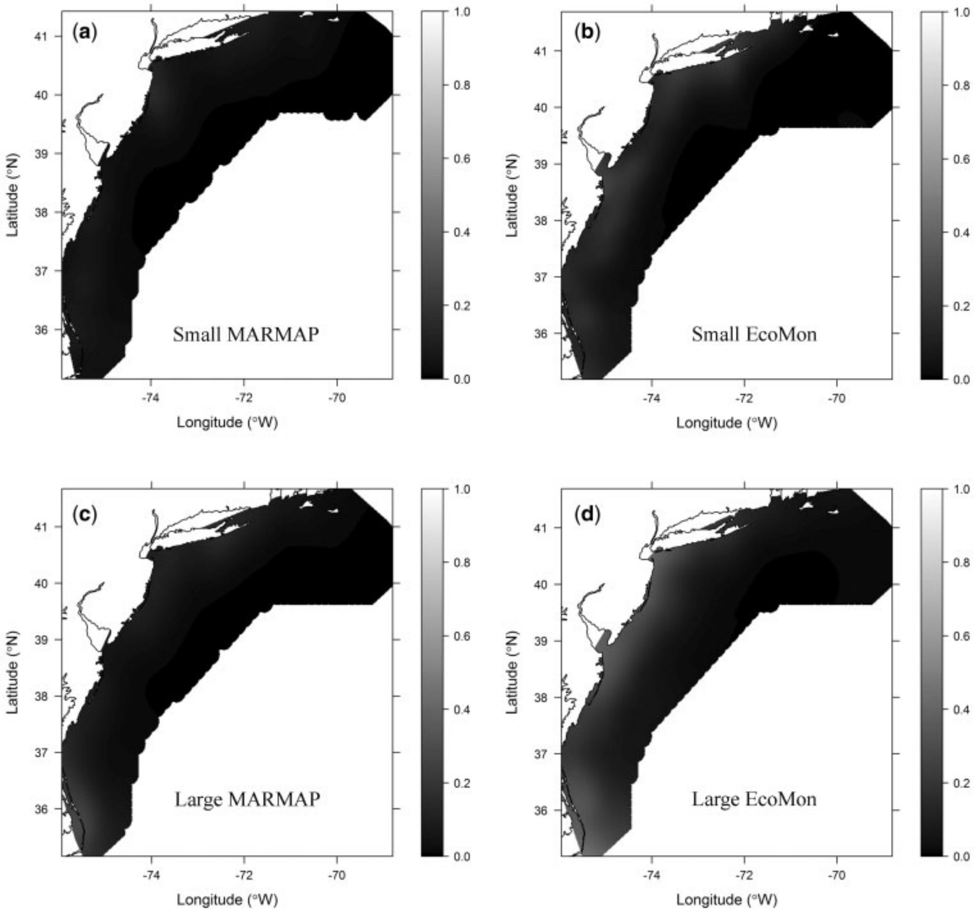

Figure 5. Averaged probability of the occurrence of Atlantic Menhaden larvae during November and December from four INLA models applied to data collected from MARMAP (1977–1987) and EcoMon (2000–2013) sampling programs. (a) larvae 0–6 mm, (b) larvae 0–6 mm, (c) larvae >6 mm, and (d) larvae >6 mm.

Chesapeake Bay (SEDAR 2015), despite increasing trends in abundance of larvae (Simpson *et al.,* 2016) and recovered adult biomass (SEDAR 2015). Quinlan and Crowder (1999) theorized from a matrix model that Atlantic Menhaden population growth rate was significantly related to the growth and mortality rates of the late larval stage that ingresses to estuaries.

Our study is limited by the spatial extent of the sampling programs. In years where we observed zero small Atlantic Menhaden larvae, we know that there were still many present. Shallow near-shore water is likely to be important spawning ground given the general pattern of increased probability of encountering small and large larvae near shore. However, areas closest to shore were not sampled in either program due to vessel limitations. Although traditionally thought of as coastal spawners (Ahrenholz 1991), eggs have been found in northern estuaries (Keller *et al.,* 1999) suggesting some spawning may also be occurring within such estuaries. Additionally, the programs we studied only extended as far south as Cape Hatteras. Historically, the Chesapeake Bay has been thought to be the most important nursery habitat for juvenile Atlantic Menhaden (Ahrenholz *et al.,* 1989, ASMFC 2004, Anstead *et al.,* 2016). Given the north to south near-shore current, we would expect the bulk of larval supply to be coming from the north, but larval Menhaden were more abundant in the south. More spatial and temporal coverage in the south would be beneficial to this analysis, as adult Menhaden have been commonly found as far south as northern Florida (SEDAR 2015).

Examining both small and large larvae over the three distinct regions (north, middle, and south), we were able to compare how large and small larvae occupied space. Our observation of a shift from small larvae occupying relatively more space in the north to large larvae occupying relatively more space in the south could be explained by the environment or survival differences. Hydrodynamically, larvae have a net southwards movement pattern in the Mid-Atlantic Bight (Quinlan *et al.,* 1999). Given a net southward movement of larvae, we would not expect to see great numbers of larvae in the northern portion of our study area, as there would be limited larval supply coming from further north due to the limited spawning north of Cape Cod, Massachusetts (Able and Fahay 2010). The middle and southern regions could receive larvae from the north in addition to individuals spawned nearby. This effect would be cumulative moving south, particularly for large larvae. Additionally, there may be differences in survival. A higher level of mortality in the northern region would also contribute to observing small larvae occupying more space.

Due to low numbers of observations, we were unable to examine month-to-month or year-to-year changes in space. The model results we have shown represent an average spatial distribution

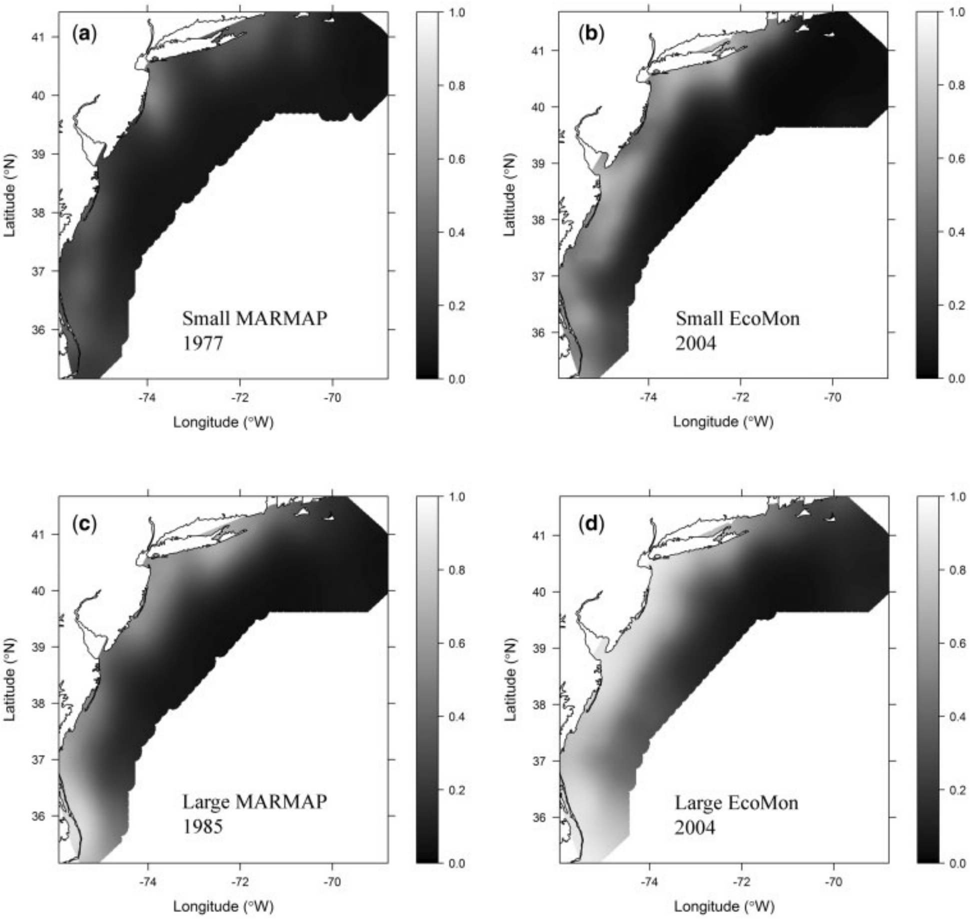

Figure 6. Representative probability of the occurrence of Atlantic Menhaden larvae during November and December from four INLA models applied to data collected from MARMAP (1977–1987) and EcoMon (2000–2013) sampling programs. (a) larvae 0–6 mm (1977), (b) larvae 0–6 mm (2004), (c) larvae >6 mm (1985), and (d) larvae >6 mm (2004).

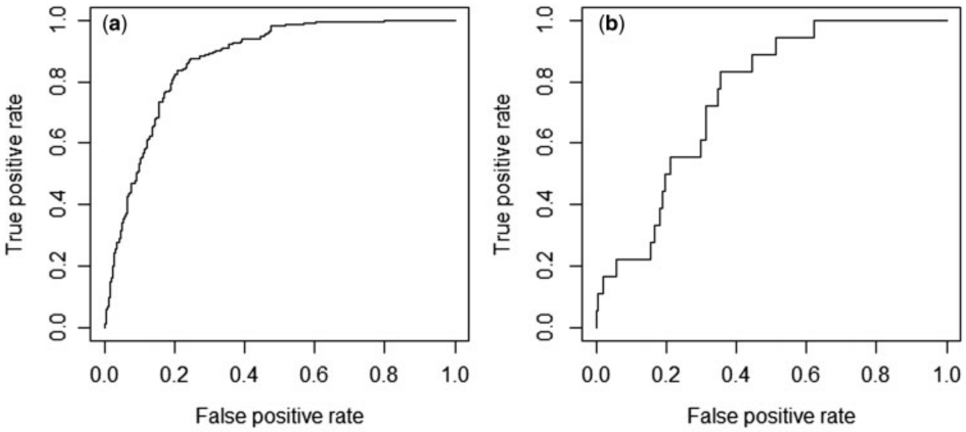

Figure 7. Example ROC curves created to determine cutoff values for presence/absence of small and large Atlantic Menhaden larvae during MARMAP (1977–1987) and EcoMon (2000–2013) ichthyoplankton surveys for 5 bimonthly periods. (a) Small (0–6 mm) larvae during Sep–Oct from MARMAP (b) large (>6 mm) larvae during Nov–Dec from EcoMon.

during each of the two time periods among months and years. Given more information, it would be informative to examine how spatial distribution changes over shorter time periods. Atlantic Menhaden are known to exhibit high levels of variability among years, particularly in terms of recruitment (e.g. Vaughan and Merriner 1991, Keller *et al.*, 1999, Warlen *et al.*, 2002).

Even still, our research supports previous work showing no major directional change in spatial distribution of larvae between

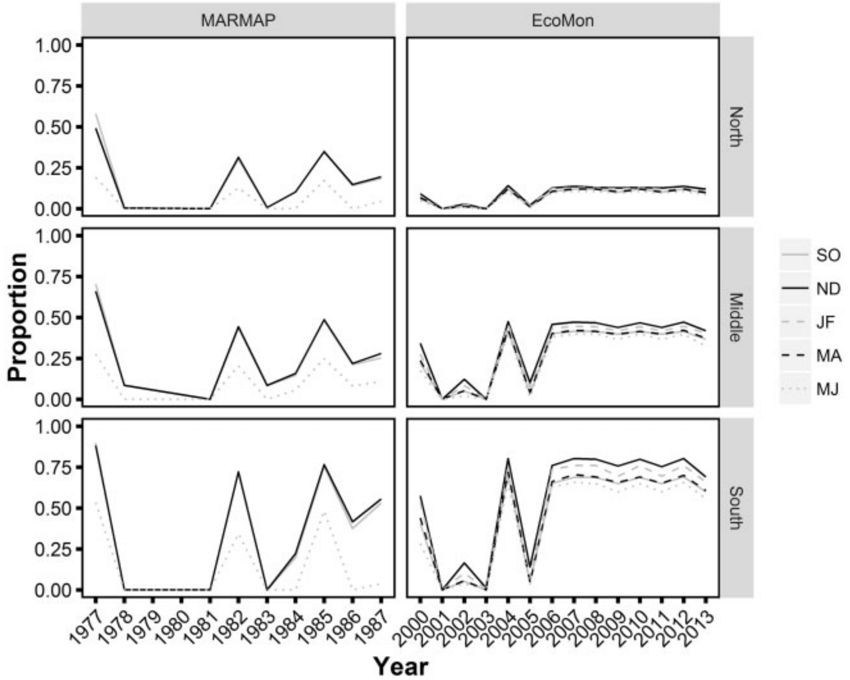

Figure 8. Proportion of region (North to South) predicted to have small larvae (0–6 mm) during both MARMAP (1977–1987) and EcoMon (2000–2013) sampling programs based on results of four SPDE models (SO: Sep-Oct, ND: Nov-Dec, JF: Jan-Feb, MA: Mar-Apr, MJ: May–Jun). North: eastern Long Island, NY, to Cape Cod, MA; Middle: western Long Island, NY, to north of Delaware Bay; South: Delaware Bay to North Carolina.

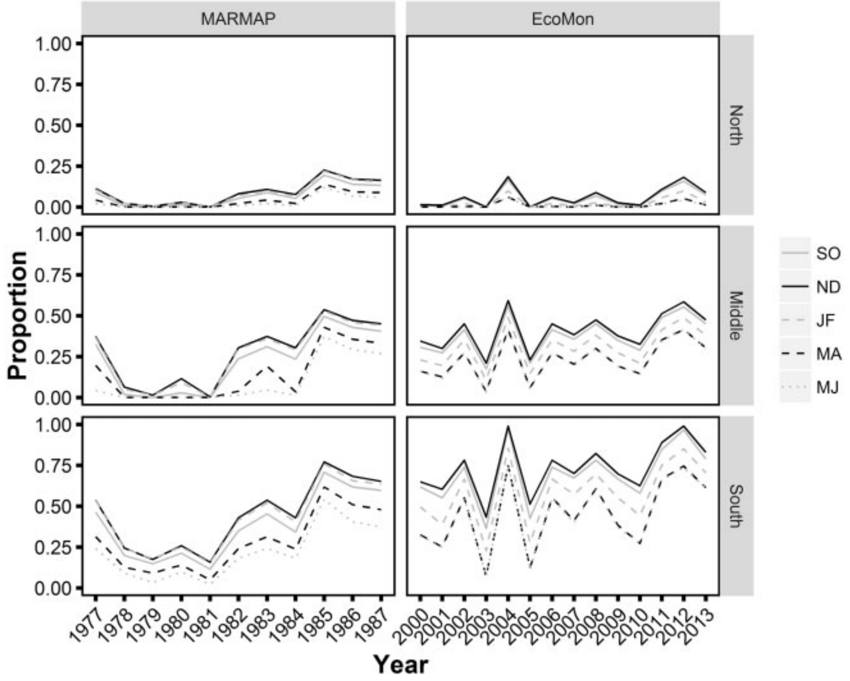

Figure 9. Proportion of region (North to South) predicted to have large larvae (>6 mm; dashed line) during both MARMAP (1977–1987) and EcoMon (2000–2013) sampling programs based on results of four SPDE models (SO: Sep–Oct, ND: Nov–Dec, JF: Jan–Feb, MA: Mar–Apr, MJ: May–Jun). North: eastern Long Island, NY, to Cape Cod, MA; Middle: western Long Island, NY, to north of Delaware Bay; South: Delaware Bay to North Carolina.

the two time periods (Walsh *et al.*, 2015). This was true for both small and large larvae, indicating no major spatial shift in spawning or dispersal. Our finding is particularly interesting in relation to recent observations in juvenile spatial distribution. Buchheister *et al.*, (2016) found evidence that juvenile abundance has increased in New England and is negatively correlated with estuaries to the south over a similar time period. From this, we would suggest greater investigation into early life survival, particularly between coastal, larval hatch and estuarine, pre-juvenile stages.

Walsh *et al.*, (2015) found a temporal shift in the presence of larvae among years using the same data, but with different analytical techniques. Although, during both periods, early winter is when the majority of larvae were observed, we found evidence for an increase in spring spawning during the more recent period. Similarly, we observed more large larvae during the spring in the more recent program. This may partially explain the observed shift in peak larval ingress to New Jersey estuaries from fall to early summer after 1990 (Able and Fahay 2010).

Recent research in the Chesapeake Bay has indicated that although the bulk of larvae are ingressing in the winter, surviving juveniles were more often hatched in the spring (Lozano *et al.*, 2012). One proposed mechanism for this observation is that individuals hatched in spring, encounter more favourable growing conditions as larvae, a fitness that continues into their juvenile life stage (Atkinson and Secor 2016). Houde *et al.*, (2016) concluded that, similar to other small pelagics, abundance of Atlantic Menhaden is dependent on strong year classes and recruitment is regulated by bottom-up processes. Therefore, in order to have a complete understanding of recruitment, we must have a better understanding of factors affecting early life survival.

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