



Estimation of movement and mortality of Atlantic menhaden during 1966–1969 using a Bayesian multi-state mark-recovery model

Emily M. Liljestrand^{a,*}, Michael J. Wilberg^a, Amy M. Schueller^b

^a Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, P.O. Box 38, Solomons, MD, 20688, USA

^b National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, 101 Pivers Island Road, Beaufort, NC, 28516, USA

ARTICLE INFO

Handled by A.E. Punt

Keywords:

Brownie dead recovery model
Forage Fish
Natural mortality
Fishing mortality
Brevoortia tyrannus

ABSTRACT

Atlantic Menhaden *Brevoortia tyrannus* is an economically and ecologically important forage fish targeted by large-scale commercial reduction and bait fisheries. In the late 1960s, the National Marine Fisheries Service conducted a mark-recovery study in which they tagged over one million adult Atlantic Menhaden. Mark-recapture models at the time did not allow for estimation of movement rates. Our objective was to reanalyze these data to simultaneously estimate natural mortality, fishing mortality, and movement probability during 1966–1969. We developed a Bayesian version of the Brownie model that incorporated fishing mortality, natural mortality, and movement among four regions of the northwest Atlantic continental shelf ecosystem at a monthly time step. The model also accounted for both tag loss and tag detection probability. During May–June, an estimated 91% of Atlantic Menhaden from North and South Carolina moved northwards. Atlantic Menhaden largely remained within the same coastal region from June to October. In the winter, an estimated 55% of the tagged sample north of the Chesapeake Bay moved southward to the Chesapeake Bay and North and South Carolina. However, the fraction of the tagged sample undertaking these movements was substantially smaller than previously described. The estimated instantaneous natural mortality rate, 1.17 yr^{-1} ($1.09\text{--}1.23 \text{ yr}^{-1}$, 95% CI), was greater than previously reported. Instantaneous fishing mortality was spatially and temporally variable and as high as 1.74 yr^{-1} in North and South Carolina during 1967. Understanding the historical seasonal spatial dynamics of this stock will improve contemporary survey design and management, as these dynamics may persist today.

1. Introduction

Mark-recapture (or capture-recapture) studies can be used to estimate movement and survival from observations of marked individuals (Arnason, 1972, 1973; Brownie et al., 1993). However, simultaneously estimating movement and mortality rates from traditional tagging studies remains challenging. Often, movement and mortality estimates are confounded because emigration from the system is indistinguishable from natural mortality using mark-recapture data (Hilborn, 1990; Schwarz and Arnason, 1990; Sibert et al., 1996). Obtaining precise estimates from traditional mark-recapture studies that employ conventional tags typically requires large sample sizes or supplementary information. Bayesian mark-recapture models have increasingly been employed to estimate movement and mortality parameters even when data are missing or incomplete (Dupuis, 1995; Calvert et al., 2009).

Atlantic Menhaden *Brevoortia tyrannus* is an ecologically and

economically important forage fish that inhabits U.S. Atlantic coastal waters from Maine to Florida (Fig. 1; Ahrenholz et al., 1991). Atlantic Menhaden are an important prey species for sea birds, predatory fishes, and cetaceans (Buchheister et al., 2017). Atlantic Menhaden support the largest fishery on the U.S. Atlantic coast by volume, with a total allowable catch of 200,000 metric tons for 2017 (NMFS, 2015). Currently, about 23% of these landings go towards the bait fishery, which provides bait for commercial and recreational species such as striped bass *Morone saxatilis*, crabs, and lobster (SEDAR, 2015). The remaining landings go towards the reduction fishery, where Atlantic Menhaden are processed to make fish oil and fish meal in large scale reduction fishery plants (SEDAR, 2015). Historically, the reduction fishery comprised a much larger ($\approx 95\%$) fraction of the total landings (SEDAR, 2015).

The National Marine Fisheries Service (NMFS) conducted a large-scale mark-recovery study of Atlantic Menhaden during 1966–1969.

* Corresponding author.

E-mail address: liljest3@msu.edu (E.M. Liljestrand).

<https://doi.org/10.1016/j.fishres.2018.10.015>

Received 16 March 2018; Received in revised form 11 October 2018; Accepted 15 October 2018

Available online 02 November 2018

0165-7836/ © 2018 Elsevier B.V. All rights reserved.

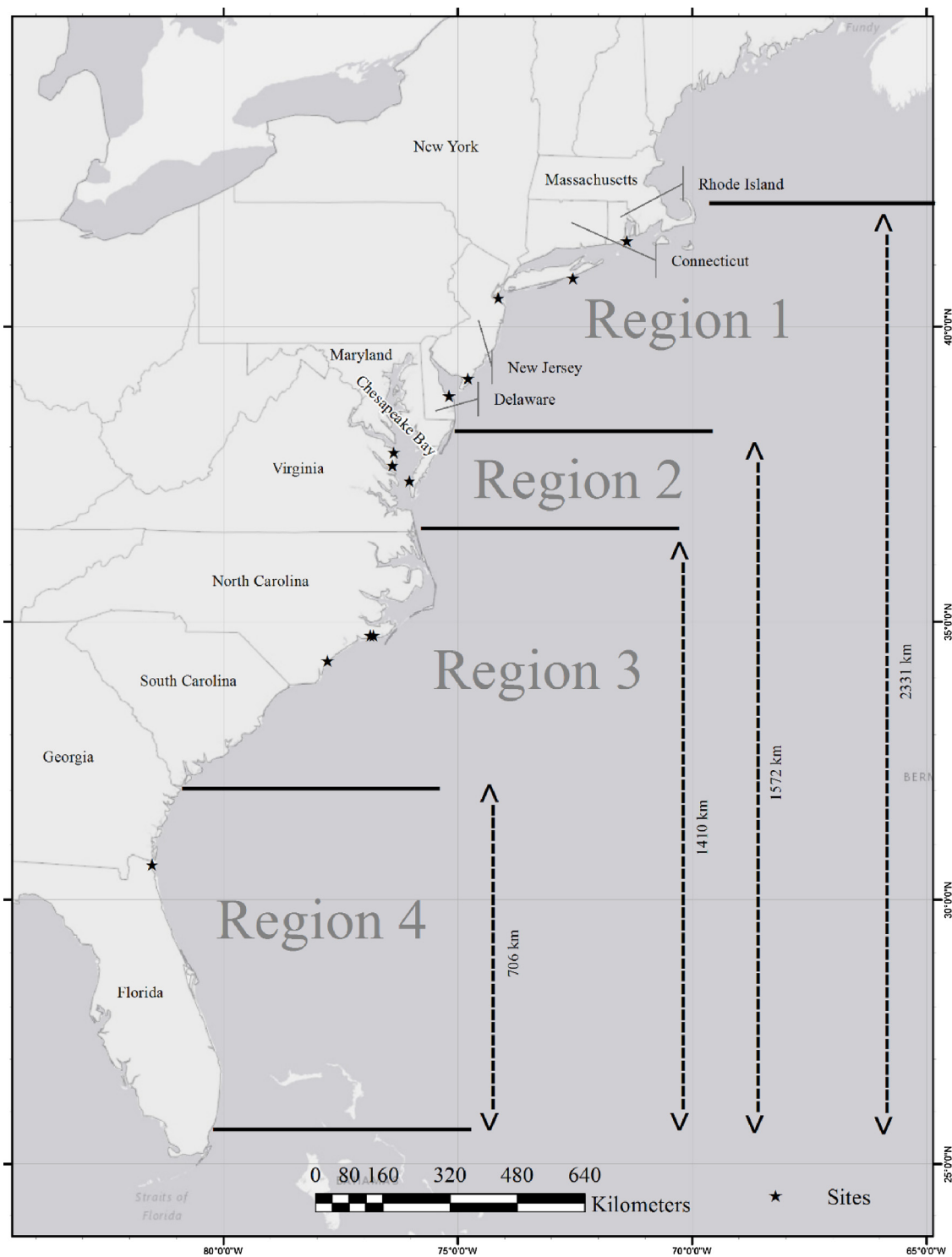


Fig. 1. Locations of the four regions used in the model to estimate movement, adapted from Coston (1971). Stars indicate the locations of reduction plants, and some stars represent multiple plants.

NMFS researchers injected 1,066,357 adult Atlantic Menhaden with individually numbered ferromagnetic tags, which were then passively recovered on magnets installed in reduction fishery plants (Ahrenholz et al., 1991). From these data, researchers determined qualitative migration patterns and estimated the natural mortality rates of adult Atlantic Menhaden (Dryfoos et al., 1973; Nicholson, 1978; Reish et al., 1985). They concluded that the stock consisted of a single population that congregates in late autumn in waters along the North Carolina coast and subsequently moves northward in the spring and summer

with older, larger individuals traveling farther north (Nicholson, 1978). The general description of the Atlantic Menhaden seasonal movement patterns that emerged from these initial analyses supported earlier studies that examined age, size structure, and effort of the commercial purse seine fishery (June and Reintjes, 1959; Roithmayr, 1963; Nicholson, 1971). Although the seasonal patterns of Atlantic Menhaden movement have been well described qualitatively, quantitative estimates of movement rates have not been determined (Dryfoos et al., 1973; Nicholson, 1978).

Advances in mark-recovery approaches allow the simultaneous estimation of movement and mortality rates, thus the tagging study can be used to estimate Atlantic Menhaden movement and mortality rates. Atlantic Menhaden seasonal movement patterns are of interest today because evidence exists that the southward movement in the autumn and winter from the mid-Atlantic region may not be as substantial as previously believed. Larval Atlantic Menhaden abundance was high in the mid-Atlantic during winter months indicating the presence of adults (Simpson et al., 2016, 2017). Our objectives were to estimate movement, natural, and fishing mortality rates for Atlantic Menhaden during 1966–1969. We developed a Bayesian model that estimated natural mortality, region- and time- specific fishing mortality, and monthly movement. The model explicitly accounted for tag shedding/tagging mortality and tag reporting because supplementary studies were conducted to estimate values for these processes (Kroger and Dryfoos, 1972).

2. Methods

We developed a Bayesian version of the Brownie dead recovery model parameterized with instantaneous mortality rates (Brownie et al., 1993; Hoening et al., 1998) that also included movement among four regions (Fig. 1). The model estimated natural mortality, fishing mortality, and the probability of movement. The model was implemented using AD Model Builder (Fournier et al., 2012) and was fitted to mark-recovery data from a large-scale tagging study of Atlantic Menhaden conducted during 1966–1969.

2.1. Mark-recovery data

The NMFS began capturing and tagging adult Atlantic Menhaden with individually numbered ferromagnetic tags in July 1966 in North Carolina (region 3; Dryfoos et al., 1973). The program was expanded during 1967–1969 to include the full range of the Atlantic Menhaden fishery, from Massachusetts to northern Florida (Fig. 1). Atlantic Menhaden were obtained from commercial purse-seine and pound-net catches and by NMFS researchers through purse-seines, pound-nets, and haul seines (Ahrenholz et al., 1991). Ferro-magnetic stainless steel tags with rounded corners (14.0 × 3.0 × 0.5 mm) were injected using hand-held tagging guns (Carlson and Reintjes, 1972; Kroger and Dryfoos, 1972). A total of 1,066,378 individuals were released (Tables A.5–A.8).

Tags were recovered on magnets installed in the seven reduction plants in operation in region 3 in 1966 and 17 of the 18 reduction plants in operation on the Atlantic coast during 1967–1969. The data were maintained on computers at NMFS's Southeast Fisheries Science Center in Miami (SEDAR, 2015). The number of tagged fish released in each month and region and the month and region of recovery were also summarized in Coston (1971). During a data transfer in the 1990s, the raw electronic data were lost. A printed copy of the data were recently redigitized to create electronic copies of both the recovery data and data from reduction plant magnet efficiency trials (SEDAR, 2015). The release and recovery data were stored separately, but the numbers on the ferromagnetic tags allowed us to match recovered individuals to a specific time and location of release. However, approximately 20% of the release and recovery data remain lost due to damaged or missing data from certain regions and years. Therefore, we used the mark-recovery data summarized by region and month by Coston (1971), which are complete, albeit less specific (because the data at the tag number level were not included in the summary). Thus, we designed the model as if the tags represented a batch mark. Because we were limited to the temporal and spatial scale described in Coston (1971), the mark-recovery model was similarly constrained to a minimum time step of one month and a maximum of five geographic regions. The efficiency of magnets to collect the tags was estimated using the redigitized data from the plant magnet efficiency trials.

We used a slightly modified version of the regions from Coston

(1971). Region 1 included waters north of the Maryland-Delaware line (lat 38°02' N). Region 2 included Chesapeake Bay and the coastal waters between lat 36°35' N and the southern boundary of region 1. Region 3 included North and South Carolina between lat 32°02' N and the southern boundary of region 2, and region 4 included Georgia and Florida, the waters south of region 3 (Fig. 1; Coston, 1971). Locations of where the tagged fish were recovered were not recorded. Rather, the data indicate the region of the processing plant where the metallic tag was recovered. However, this is thought to be a reliable proxy of the region of capture because the regional boundaries were chosen in such a way that they largely separated fishing grounds from reduction plants in different regions (Coston, 1971; SEDAR, 2015).

Region-specific tag shedding and tagging mortality rates were estimated by the original researchers using laboratory experiments of tag shedding and the observed average size of individuals in each region (Kroger and Dryfoos, 1972; Dryfoos et al., 1973). The region-specific proportion of individuals experiencing tag shedding and tagging mortality (combined) was 0.1 in region 1, 0.2 in region 2, 0.25 in region 3, and 0.4 in region 4, which were originally reported in Dryfoos et al. (1973), but sample sizes and uncertainty were not reported.

Supplementary data on the total landings and effort of each reduction plant for each month during 1966–1969 were provided by the NMFS Southeast Fisheries Science Center. Fishing effort for each reduction plant was reported in vessel weeks, the number of vessels that were in operation for at least one day during a week. During December–March, most reduction plants outside region 3 suspended operations. No releases were conducted during November–May. This limited our ability to estimate monthly movement rates for the May to November period.

2.2. Magnet efficiency trials

Experiments were conducted to test the efficiency of magnets for collecting tags by introducing batches of tagged Atlantic Menhaden (usually 100 fish) directly into each reduction plant. These trials were conducted approximately once a week when the plant was in operation, and the total number of trials in each plant varied from 18 to 152, averaging 56 over the course of the 3.5 years of the mark-recovery study. Raw data of the trial outcomes were available, but the values of magnet efficiency used in previous models were not. Therefore, we estimated magnet efficiency by plant, and from those estimates, calculated magnet efficiency by month and region in a way that matched the spatial and temporal scale of the current model. A full description of the types of magnets their distribution in reduction plants is available in Ahrenholz et al. (1991).

The magnet efficiency for each plant was estimated from the efficiency trial data across all four years. For each trial, a , and plant, p , the likelihood of recovering x individuals from a batch of n releases was modeled using a binomial distribution and the estimated magnet efficiency for that plant, ε_p . We estimated magnet efficiency for each plant by minimizing the negative log likelihood, $NegLL_p$,

$$NegLL_p = \sum_a -\log_e \left(\frac{n_a!}{x_a!(n_a - x_a)!} \varepsilon_p^{x_a} (1 - \varepsilon_p)^{(n_a - x_a)} \right) \quad (1)$$

Because the recovery data were summarized by region and the amount of harvest by each plant varied over time, we calculated magnet efficiency for region, r , and at time, t , by averaging the efficiency of each plant, ε_p , weighted by the proportion of landings (individuals), L , from that plant,

$$\varepsilon_{t,r} = \sum_p \frac{\varepsilon_p L_{t,p}}{\sum_p L_{t,p}} \quad (2)$$

If a reduction plant had recorded landings at a given time, but there were no magnets installed, indicated by an absence of data for that plant in the redigitized data, ε_p , was set to 0. This applied to all

Table 1
Symbols used in estimation model with description and values.

Variable	Description	Value
m	Month	1–12 from January–December
T	Time of cohort release	1–42, 1: July 1966, 42: December 1969
t	Time of cohort presence	1–42, 1: July 1966, 42: December 1969
R	Region of cohort release	See Fig. 1
r	Region of cohort presence	See Fig. 1
d _r	Lateral distance between 25° 45' N and a region's northern boundary	See Fig. 1
Likelihood components		
NegLL _c	Negative log likelihood for recoveries	
P _q	Log prior for catchability	
P _φ	Log prior for movement rates	
P _q	Log posterior for catchability	
P _φ	Log posterior for movement rates	
Data		
L	Landings	
E	Effort	
I _{T,R}	Releases	See Table A.1.5–A.1.8
J _{T,R,t,r}	Recoveries	
Specified quantities		
ε	Magnet efficiency	See Table 2
G _R	Tag Shedding/Mortality	1: 0.1, 2: 0.2, 3: 0.25, 4: 0.4
k	Overdispersion value	2.5
v	Effective sample size of dirchelet distribution	10
w	Average swimming speed	3 lengths/sec
l	Average length of tagged menhaden	19.38 cm
σ _q	Variance for distribution of total catchability	1
Calculated quantities		
N _{T,R,t,r}	Abundance of a tagged cohort	
S _{t,r}	Survival	
F _{t,r}	Fishing mortality	
q _{m,r}	Catchability	
C _{T,R,t,r}	Estimated Recoveries	
σ _m	Variance of diffusion process for migration priors	
φ _{i,j}	Prior probability of movement	

reduction plants in regions 1, 2, and 4 in 1966, and one plant in which no magnets were installed for the four years of the study. The results of these magnet efficiency trials were assumed to be known at their estimated values, rather than including process error, to simplify the model. We also assumed that the proportion of landings in each plant for each month/region combination are known without error.

2.3. Mark-recovery model

The mark-recovery model was an instantaneous rate version of the Brownie dead recovery model (Hoenig et al., 1998) modified to allow movement among four regions (Fig. 1). Variables used in the model and their descriptions are available in Table 1. The model tracked tagged cohorts of individuals released from a single region and month. We assumed that all individuals in a cohort experienced the same dynamics regardless of age or release location within the region. The number of individuals from a cohort released in region, *R*, at time, *T*, that were alive in region, *r*, at time, *t*, *N_{T,R,t,r}*, was calculated using time- and region-specific movement and survival rates. The initial magnitude of the cohort was calculated by applying the region-specific tagging mortality rate, *G_R*, to the releases, *I_{T,R}*,

$$N_{T,R,T,R} = I_{T,R}(1 - G_R) \tag{3}$$

We assumed that region-specific tagging mortality was known and that tagged individuals were well mixed and independent. Survival and

movement were modeled as sequential processes with movement occurring after survival in each time step. Abundance of the cohort after survival but before movement, *N_{T,R,t+1,r}*^{*}, was calculated from region- and time- specific survival rates, *S_{t,r}*,

$$N_{T,R,t+1,r}^* = N_{T,R,t,r} S_{t,r} \tag{4}$$

Our model included the assumption of no movement during the month of release by applying movement after monthly mortality. No individuals were recovered outside of their release area during the month of release.

Survival rates were estimated from the time- and region-specific instantaneous fishing, *F_{t,r}*, and natural, *M*, mortality rates,

$$S_{t,r} = e^{-M-F_{t,r}} \tag{5}$$

Natural mortality was assumed to be constant over regions and time, and the fishing mortality rate for a given region and time was calculated as the product of month- and region- specific catchability, *q_{m,r}*, and fishing effort, *E_{t,r}*,

$$F_{t,r} = q_{m,r} E_{t,r} \tag{6}$$

Catchability was calculated as the product of a region-specific effect, *Q_r*, and a month-by-region effect,

$$q_{m,r} = Q_r e^{\theta_{m,r}} \tag{7}$$

This parameterization for catchability assumes that catchability for a month and region was constant over years. For the parameters to be uniquely identifiable, *θ_{m,r}* in July was set to 0, and for month-region combinations without fishing effort, *q_{m,r}*, was set to 0 (Table A.1). After accounting for survival, the vector of abundance of a cohort in each region, *N_{T,R,t+1}*, was calculated as the product of the movement probability matrix, *φ̂*, and the vector of post survival abundance by region, *N_{T,R,t}*^{*},

$$N_{T,R,t+1} = \hat{\phi} N_{T,R,t}^* \tag{8}$$

Each element of a movement matrix indicated the probability of an individual moving from the region indicated by that column to the region indicated by that row during that time step. Movement parameters were estimated for each month during May – October. Monthly movement parameters could not be estimated during October – May because reduction plant operations were suspended in regions 1, 2, and 4 during the winter and early spring, and in all regions during February – March. Movement rates were only estimated for one month during October–May, and *φ̂* was fixed as an identity matrix for the remaining months. We assumed that the monthly movement rates from October–November reflect all net movement between October and May.

The estimated recoveries for each cohort were the product of time- and region- specific abundance, *N_{T,R,t,r}*, the proportion of mortality due to fishing, and the fraction of the population that died (i.e., the Baranov catch equation; Quinn and Deriso, 1999), and the time- and region-specific magnet efficiency rate,

$$C_{T,R,t,r} = N_{T,R,t,r} \frac{F_{t,r}}{Z_{t,r}} (1 - e^{-M-F_{t,r}}) \epsilon_{t,r} \tag{9}$$

We assumed that there was no additional natural mortality between release and recovery in the first month (*t = T*, *r = R*) after release (for calculation of *N_{T,R,t,r}*). Individuals were tagged adjacent to or onboard commercial purse seining vessels (Pristas and Willis, 1973). Consequently, tagged fish were immediately released in the same localized areas as the commercial fishery. However, the model includes simultaneous fishing and natural mortality such that the number of expected recaptures is affected by natural mortality in the first month after release.

2.4. Parameter estimation

We estimated the parameters using a Bayesian approach. The objective function was the sum of the negative log of the prior probabilities and the negative log likelihood for the recovery data,

$$P = \text{NegLL}_c + p_\varphi + p_q \tag{10}$$

We assumed that the estimated recoveries followed a negative binomial distribution, with an overdispersion value $k = 2.5$, where J denotes the observed recoveries,

$$\begin{aligned} \text{NegLL}_c &= \sum_T \sum_R \sum_{t>T} \sum_r \\ &-\log_e \left(\frac{\Gamma(k + J_{T,R,t,r})}{\Gamma(k)\Gamma(J_{T,R,t,r})} \left(\frac{k}{k + C_{T,R,t,r}} \right)^k \left(\frac{C_{T,R,t,r}}{k + C_{T,R,t,r}} \right)^{J_{T,R,t,r}} \right) \end{aligned} \tag{11}$$

We assumed a negative binomial distribution, rather than a multinomial or Poisson distribution, to better address data overdispersion, which is frequently a feature of tagging data, especially when effort is patchy and the species schools (Michielsens et al., 2006). The overdispersion arises, in part, because the number of fish in each month and region from a tagged cohort is unknown. We assumed that tag recoveries were independent. We used this distribution because the number of tagged individuals in each region and time was unknown. We specified the value for k because testing using simulated data indicated that it was not estimable. While it is possible that k may have been estimable with a strong, informative prior, we chose to evaluate the effects of our assumptions through sensitivity analyses instead.

A uniform prior was placed on natural mortality, which constrained the value between 0.006 and 148.4 per month, (-5 and 5 on the log scale),

$$M \sim U(0.006, 148.4) \tag{12}$$

The data were too sparse at certain times and regions to estimate movement probabilities without imposing a prior. We included weakly informative priors on the movement probabilities by assuming that they followed a Dirichlet distribution with means generated from a one-dimensional diffusion model. A weakly informative prior that mimicked diffusion dynamics was more appropriate than an uninformative, flat prior which unrealistically assumes movement to an adjacent region is equivalent to movement to a non-adjacent region in the same time. We assumed that the effective sample size, ν , of the Dirichlet distribution was 10. The negative of the natural logarithm of the Dirichlet distribution (with additive constants removed) was

$$p_\varphi = \sum_m \sum_{r1} \sum_{r2} -\nu \varphi_{m,r1,r2} \log_e(\widehat{\varphi}_{m,r1,r2}) \tag{13}$$

For values of ν below about 5, it was difficult to estimate the parameters, and for values above 10, the prior began to have a noticeable effect on the movement parameter estimates. We used an effective sample size of 10 because it achieved a reasonable balance between the data and the prior informing the estimates.

The one-dimensional diffusion model described the probability of an individual moving a distance north or south as a normal distribution. The distribution of distance traveled from the center of a region in one month had mean zero and standard deviation, σ_w . The standard deviation was calculated from an average swimming speed per day and number of days in a month (i.e. the distance traveled under directed swimming). We used a mean length, l , 19.38 cm, estimated from the tagged fish that also had length information (about 5% of the fish tagged). We used an average directed swimming speed of 3.0 body lengths per second, which was slightly greater than the 2.5 lengths/second maximum measured by Durbin and Durbin (1975) during feeding, because we assumed feeding would be slower than swimming during non-feeding times. The mean prior probability of moving from

region j to region i , $\varphi_{i,j}$ was calculated by integrating the probability density over the distance between the center of starting region and the ending region's northern and southern boundaries. The limits of integration, a and b were unique for each regional transition (Table A.9),

$$\varphi_{i,j} = \int_a^b \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx \tag{14}$$

The winter priors were designed differently, because if diffusion was assumed across a six-month period, a majority of individuals would be expected to be outside of the natural range of Atlantic Menhaden. For the half-year movement matrix that describes the October to May period, the prior values were calculated assuming individuals move to each region in proportion to the north-south distance within a region, and was independent of the starting location.

Catchability was conditioned such that deviations from the mean on the log scale were normally distributed,

$$p_q = \sum_m \sum_r \frac{(\log_e(q_{m,r}) - \log_e(\bar{q}))^2}{2\sigma_q^2} \tag{15}$$

The variance of the prior for catchability, σ_q^2 , was set to 1.0, to allow for substantial variation in catchability among regions and months. The joint posterior distribution of the parameters was characterized using Markov chain Monte Carlo (MCMC) with a Metropolis-Hastings algorithm in ADMB. We ran three parallel MCMC chains for 4,000,000 iterations, thinning the chains by saving every 1000th iteration. The first half of each chain was discarded as a burn in (Gelman et al., 2004). Posterior distributions from the MCMC were characterized in R and convergence was assessed using Geweke and Gelman-Rubin convergence diagnostics (Geweke, 1991; Gelman and Rubin, 1992). Equal-tailed credibility intervals (CI) were defined by the 2.5 and 97.5 percentiles of the posterior distributions.

2.5. Sensitivity analysis

We conducted sensitivity analyses to evaluate the effect of the priors and assumed constants on the model estimates. We evaluated the model's sensitivity to the prior distributions on catchability and the movement parameters by doubling or halving the standard deviation around catchability or the effective sample size of the Dirichlet distribution. Model sensitivity to the movement priors was evaluated by increasing or decreasing the assumed average swimming speed by 0.5 body lengths per second, and increasing or decreasing the overdispersion parameter to 1.0 or 4.0. Sensitivity was also tested by fixing instantaneous yearly natural mortality at 0.82 yr⁻¹, the average natural mortality at age from the most recent stock assessment (SEDAR, 2015), weighted by age composition of the tagged individuals; about 1% of tagged individuals were sampled for age. Sensitivity was summarized as the change in estimates of M , the average total catchability, and the average yearly instantaneous fishing mortality from the base model.

2.6. Net movement

To determine the net effect of monthly movement, we simulated releases of individuals from each region in May and determined the location of those individuals after one year of movement using the estimated movement parameters. The simulation was run without fishing or natural mortality to isolate the effect of movement. The results were summarized as the number of individuals in each region during May.

3. Results

During July 1966 - December 1969, 17 of the 18 operating Atlantic Menhaden processing plants were evaluated for the efficiency of their magnets to collect tags. With the exception of one processing plant, with an estimated 23% efficiency, the efficiency of magnets in each

Table 2

Average efficiency of magnets in reduction plants and the number of plants in each region. Efficiency was calculated from efficiency trials, where a known number of tagged Atlantic Menhaden were introduced directly into the reduction plant. The average efficiency was the average among plants weighted by the landings for each plant within a region.

Region	Magnet Efficiency	Number of Plants
1	0.52	4
2	0.61	7
3	0.78	7
4	0.70	2

plant ranged from 59% to 92% (Table 2). Region 1 had the lowest average magnet efficiency, and region 3 had the highest average magnet efficiency.

The model fit the observed recoveries relatively well across the four regions (Fig. 2; Fig. A.1). Increased returns in the summer and fall were present in both the expected and observed values. The model underestimated returns in 1967 and 1968 in regions 1, 2, and 4, but overestimated returns in region 3. Region 3 had the poorest fit overall, but the fit improved after the first year.

The estimated movement probabilities indicated net northward movement in the spring and net southward movement in the late fall and winter. More than 95% of individuals were expected to stay in the same region from month to month during June–October, with a single exception; approximately 25% of individuals were estimated to move from region 3 to region 2 in June (Fig. 3; Table A.10). During May–June the estimated movement rate from region 3 to region 2 was about 86%. During the winter, most individuals in regions 3 and 4 remained in the same region, but 55% and 33% of individuals left regions 1 and 2, respectively. The majority of the departures from regions 1 and 2 were to region 3. During the winter, the second highest estimated movement probability from region 4, 0.43, was also to region 3.

Individuals released in region 1 exhibited a net southward movement, while individuals released in regions 3 and 4 exhibited net northward movement (Table 3). In simulations of releases in each of the four regions, 44–62% of the individuals released in regions 1, 2, and 4

were in their respective starting region one year later. Approximately half the individuals released in region 3 were in region 2 one year later.

The estimated instantaneous natural mortality rate across all regions and months was 0.098 mo^{-1} (0.091 - 0.102, 95% CI), which corresponds to an instantaneous natural mortality rate of 1.17 yr^{-1} (1.09–1.23, 95% CI). The estimated instantaneous fishing mortality rate was relatively stable over years in each region. Fishing mortality was greatest in 1967 for all regions except region 1 (Fig. 4). Region 3 had the highest average fishing mortality rate (1.66 yr^{-1}), more than six times the second largest value, 0.25 yr^{-1} , in region 2. Average fishing mortality was about 0.18 yr^{-1} in region 1 and 0.10 yr^{-1} in region 4.

The month with the highest average fishing mortality rate was July for regions 1, 2, and 3, and April for region 4 (Fig. 5). In regions 1 and 2, fishing mortality rates peaked at $0.07\text{--}0.08 \text{ mo}^{-1}$. Fishing mortality in region 4 peaked at 0.02 mo^{-1} , but also exhibited similar values throughout the summer and fall. Maximum monthly fishing mortality rates in regions 1, 2, and 4, were much lower than the average monthly fishing mortality rate in region 3, which was 0.17 mo^{-1} . The maximum fishing mortality rate in region 3 was 0.45 mo^{-1} in July, but fishing mortality remained high into the early winter.

Catchability had different yearly and monthly patterns than fishing mortality because effort was not spatially or temporally uniform. Catchability varied considerably among months and regions, ranging from 1.47×10^{-4} to 0.013 and averaging $0.0025 \text{ vessel week}^{-1}$. Region 3 had the greatest average catchability, $0.006 \text{ vessel week}^{-1}$, and the lowest average catchability, $7.69 \times 10^{-4} \text{ vessel week}^{-1}$, was estimated in region 2. During May–November catchability decreased in regions 1, 2, and 3, but stayed approximately the same throughout most of the year in region 4 with an increase at the end of the year.

The model exhibited low to moderate changes in response to the sensitivity analyses. Changing the prior probabilities for the movement rate parameters by adjusting the average swimming speed changed the mortality or average catchability parameter estimates by less than 10% (Table 4). Both increasing or decreasing the average swimming speed increased estimated natural mortality and decreased estimated average catchability and fishing mortality. Estimated monthly movement rates were insensitive to changes to w , σ_q , k , or M . Decreasing the effective sample size of the Dirichlet distribution to 5 reduced the fraction of

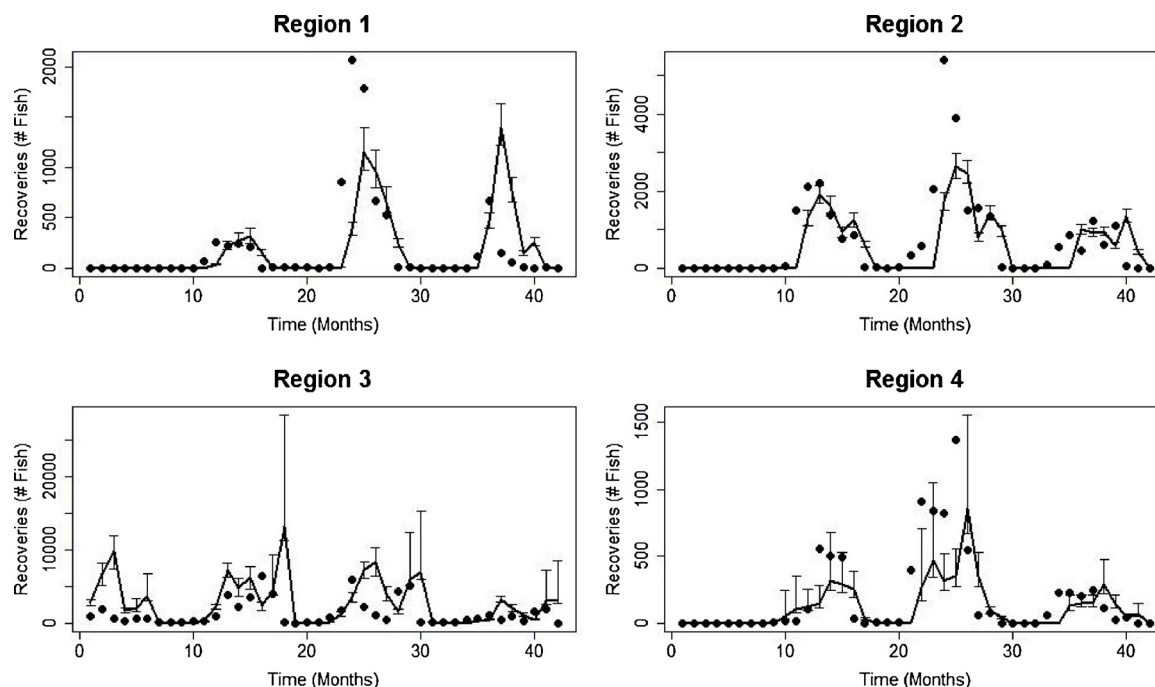


Fig. 2. Predicted (line) and observed (circles) number of recovered tags for each month after June 1966 in by regions. The predicted values are the median of the posterior probability distribution and the error bars indicate 95% credibility intervals.

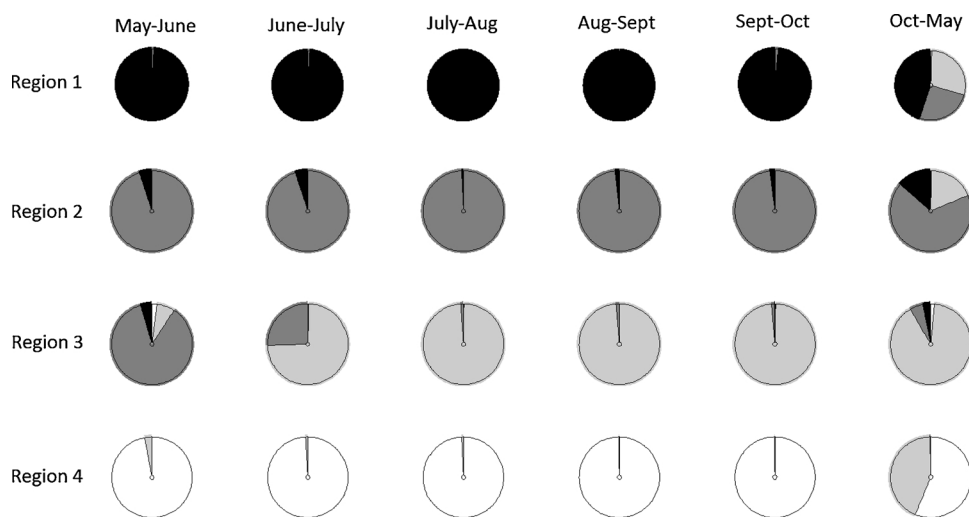


Fig. 3. Estimated movement rates for each month May through October and between October and May. Each pie chart shows the fraction of the population in a region that was estimated to move to each of the other regions. Colors indicate regions: Region 1- black, Region 2- dark gray, Region 3- light gray, and Region 4- white.

Table 3

Proportion of individuals in each region without fishing or natural mortality from simulated releases of 1000 individuals in each region beginning in May and ending in May the following year, following the pattern of movement estimated in the model.

	Release Region				
	1	2	3	4	
Region After 1 Year	1	0.438	0.179	0.167	0.006
	2	0.271	0.619	0.579	0.008
	3	0.288	0.2	0.241	0.449
	4	0.004	0.001	0.013	0.537

Table 4

Sensitivity analysis results. Columns indicate the estimated parameter values, or average value, and the percent difference from the baseline value. *M* is natural mortality, Average *Q* is catchability averaged across all estimated values, and Average *F* is yearly fishing mortality averaged across all years and regions. Rows indicate sensitivity scenarios.

	M	% Diff	Average Q	% Diff	Average F	% Diff
Base	0.098		0.002		0.548	
$v = 5$	0.099	1.37	0.004	60.63	0.862	57.35
$v = 20$	0.095	-2.63	0.002	-4.98	0.542	-1.13
$w = 2.5$	0.099	1.55	0.002	-5.68	0.533	-2.7
$w = 3.5$	0.099	1.68	0.002	-4.63	0.531	-3.03
$\sigma_q = 0.5$	0.096	-1.64	0.002	-9.91	0.520	-4.99
$\sigma_q = 2.0$	0.099	1.08	0.003	12.48	0.543	-0.81
$k = 1.0$	0.095	-2.21	0.002	-17.11	0.509	-7.07
$k = 4.0$	0.095	-3.02	0.003	27.32	0.624	13.99
Fixed M	0.068	-30.28	0.003	37.06	0.724	32.1

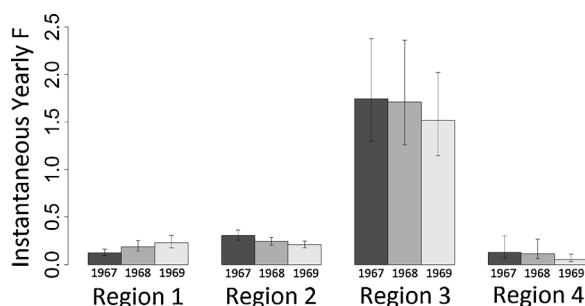


Fig. 4. Estimated instantaneous fishing mortality rates ($F \text{ yr}^{-1}$) for Atlantic Menhaden by year and region. Error bars indicate 95% credibility intervals.

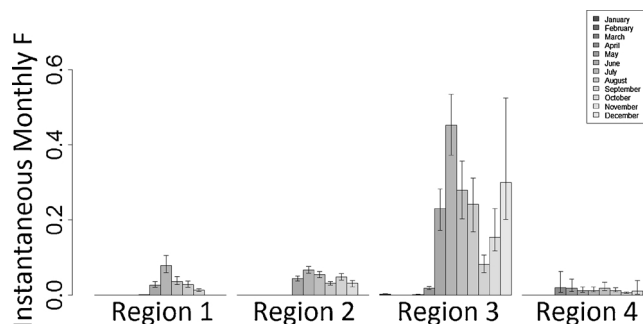


Fig. 5. Estimated average instantaneous fishing mortality rates ($F \text{ mo}^{-1}$) for Atlantic Menhaden by month and region. Error bars indicate 95% credibility intervals.

individuals remaining in region 1 during the winter by 0.29 and increased the fraction of individuals remaining in region 4 by 0.18. The general patterns of movement were consistent across sensitivity tests.

Decreasing the effective sample size of the Dirichlet distribution by half had the greatest effect on the parameter estimates (Table 4), with average catchability increasing by 61% and average fishing mortality increasing by 57%. This was caused mostly by a large increase in fishing mortality in region 1. In contrast, increasing the effective sample size had little effect (< 5% change) on the average catchability or fishing mortality. Fixing the natural mortality at 0.82 yr^{-1} , had the second largest effect on the other parameter estimates among the sensitivity analyses (Table 4), with average catchability increasing by about 37% and average fishing mortality increasing by about 32%.

Decreasing the standard deviation for the catchability prior, σ_q , resulted in average catchability decreasing by 10%, and increasing the standard deviation resulted in average catchability increasing by 12%. The average fishing mortality rate decreased by 5% when σ_q was decreased to 0.5. Similarly, decreasing the overdispersion parameter also decreased the average catchability by 17%, and increasing the overdispersion value increased the catchability by about 27%. Estimated fishing mortality did not change more than 4% when the overdispersion parameter was adjusted.

4. Discussion

We used data from a large-scale mark-recovery study to simultaneously estimate Atlantic Menhaden movement and mortality rates during 1966–1969. We found that during May to June 86% of

individuals from region 3 moved northward into region 2, and then a month later 25% of individuals from region 3 also moved to region 2. During June to October, individuals mainly stayed within the same regions. In the winter, the majority of individuals (71–81%) from the regions north of North Carolina (regions 1 and 2) remained in these two northernmost regions; 45% of individuals from region 1 and 68% of individuals from region 2 stayed in their respective regions during the winter.

Our estimated movement patterns were similar to those identified in previous research, but differed in the magnitude of movement during the winter in the northernmost regions. From October to May we found that about 55% of individuals from region 1 moved southwards into regions 2 and 3. In contrast, Roithmayr (1963) and Nicholson (1971) concluded that the “majority” of the Atlantic Menhaden population overwinters south of North Carolina (region 3) based on purse-seine fishery effort and age and length distributions. Dryfoos et al. (1973) qualitatively examined movement using the same mark-recovery data set used in this study using yearly time steps. They describe that during the North Carolina fall fishery, individuals from progressively more northern areas are caught, but they did not have the temporal resolution to estimate movement rates from summer to fall (Dryfoos et al., 1973). Dryfoos et al. (1973) estimated movement on a yearly time scale from summer 1967 to summer 1968 and from summer 1968 to summer 1969. They estimated movement as the proportion of tags recovered in one region that originated from each region or as the proportion released in one region that were recovered in each region. They found that more than 99% of individuals released in regions 1 and 2 were recovered in those regions one year later, which is higher retention than we estimated in our simulations (Table 3; Dryfoos et al., 1973). Our estimated movement patterns in the spring and summer were similar to those described by Dryfoos et al. (1973).

The differences between our findings and those of previous research are likely due to different approaches used to analyze the data. Previous research took the lack of Atlantic Menhaden schools sightings by commercial fishermen in northern coastal surface waters as an indication of southward movement, though absence may be caused by vertical or offshore migration (June and Reintjes, 1959). Reported absences of Atlantic Menhaden may also be due to low fishing effort. Fishing effort was used as a proxy for regional presence-absence in studies of Atlantic Menhaden movement and mortality (Roithmayr, 1963). However, effort is not only determined by fish abundance, and can be influenced by poor weather, economic factors, and movement of fish vertically or offshore (Mangel, 1982). Our finding that Atlantic Menhaden appear to overwinter in the northern part of their range agrees with recent studies of larval distribution. Simpson et al. (2016) found high Atlantic Menhaden larval abundance in near-shore waters during the winter in our regions 1 and 2. This pattern was relatively consistent over the period of their study, 1977–2013, suggesting a substantial number of adults in those areas during winter. Furthermore, consistency of the pattern of larval abundance during 1977–2013 may indicate that the movement patterns we estimated from the late 1960s are still relevant today.

Our model estimated natural mortality to be 1.17 yr^{-1} , which was about 2.3 times greater than previous estimates, ranging from 0.50 yr^{-1} to 0.52 yr^{-1} (Dryfoos et al., 1973; Reish et al., 1985). Dryfoos et al. (1973) used catch curve analysis of the 1966–1968 commercial catch to estimate total mortality (1.47 yr^{-1}), and subtracted off fishing mortality (0.95 yr^{-1}), to estimate natural mortality. Our natural mortality estimate should be more reliable because it is estimated from the mark-recovery data rather than the age structure of catch. Furthermore, testing of the mark-recovery model revealed that estimated natural mortality was relatively unbiased (Liljestrand et al., 2018). Based on the previous estimates, the most recent stock assessment used an age-varying natural mortality rate, ranging from 0.52 to 1.23 yr^{-1} , which is scaled by weight to the tagging estimate 0.50 yr^{-1} for age 4–6+ individuals (SEDAR, 2015). Given the structure of the model, a time-

varying natural mortality rate was not estimable, though realistically, conditions such as predator abundance and temperature likely lead to variation in natural mortality. Consequently, the variance in natural mortality in this model represents uncertainty about mean natural mortality, and spatial and temporal variation in natural mortality may be reflected in the estimated fishing mortality rates.

Underestimating natural mortality can result in an overestimate of fishing mortality (Clark, 1999). If fishing mortality is overestimated, excessive limitations may be put in place, which may not achieve management objectives. The high average yearly fishing mortality, 1.66 yr^{-1} , in region 3 is reasonable because this is a large and centralized region that can support a high abundance of Atlantic Menhaden. Additionally, we found that many individuals move into region 3 from October to May, which could support high landings during the substantial North Carolina fall fishery.

A primary limitation of our analysis was that we could not estimate monthly movement during winter and spring because there was little fishing effort, and thus few or no recoveries. We treated October to May as one period for movement, which meant that the movement rate estimates represented the net effect of movement over this period. Having such a long time step may mask the movement that occurred at a shorter time scale. For example, seasonal movement may have occurred as late as November and December, and northward movement may have begun as early as April (Nicholson, 1971). Because our model only accounts for net movement between those months, it cannot discern if individuals from northern regions are moving southward then returning to their initial region within that period. However, the high levels of larval abundance in northern regions during the winter indicate that Atlantic Menhaden are likely overwintering in the northern portion of their range (Simpson et al., 2016). If a majority of the population moved southward then northward from October to May, we would not expect abundant larvae in the northern regions during winter. Using otolith microchemistry Anstead et al. (2017) estimated that approximately 30% of age-2 and -3 Atlantic Menhaden used northeastern estuaries as nursery habitat. They attributed the relatively large fraction of individuals from this region to larger fecund females being present in these regions during the summer and fall. However, juvenile aging work in Chesapeake Bay indicated that most young-of-the-year resulted from spawning during late winter (Atkinson and Secor, 2017). Thus, winter spawning in northern regions could also explain Anstead et al.'s findings.

Our model did not allow for age-specific movement or fishing mortality rates because age data were not present in the Coston (1971) summaries of releases and recoveries. Larger, older individuals are thought to travel farther north during summer (Nicholson, 1978). By not including age structure, our model estimates an average movement rate for the ages that were tagged; the average age at tagging was 1.35 years. Our model also assumes that all ages and regions experience the same natural mortality rate.

Adult Atlantic Menhaden of the same age and length tend to school together (Smith, 1991), which may violate model assumptions of independence and no age effect for movement. Tagged individuals from a batch of 100 tags could remain together in a school, so the probability of catching one may increase the probability of catching others from the same release. However, the data showed that individuals from the same batch of tags were usually recovered over several weeks and by several plants. Therefore, the assumption of independence among recoveries seems reasonable. Older individuals are hypothesized to not be as susceptible to fishing mortality because there are fewer large individuals and therefore smaller schools (SEDAR, 2015). If the reduction fishery selectively harvests larger schools, then the fishery may be harvesting younger, smaller individuals because Atlantic Menhaden school by age, and younger individuals should be more abundant than older ones (Smith, 1991). If fishing mortality rates decreased for older ages, our estimate of the natural mortality rate may be biased high, and the movement rate estimates may disproportionately reflect the

dynamics of smaller, younger individuals.

The model included assumptions about detection efficiency that may have oversimplified the tag recovery process. Two kinds of magnets were installed in the reduction plants: primary magnets located at the conveyor system collected about 85% of the tags within the first two days of processing, and secondary magnets in other locations of the plants, which often did not accumulate tags until months after the individual entered the plant and were not checked as regularly (Dryfoos et al., 1973). The Coston (1971) data did not identify whether a tag was recovered on a primary or secondary magnet. Therefore, some recoveries may have been misattributed to later months. One reduction plant in region 2 never had magnets installed. The model accounted for this lack of magnets in the landings-weighted average magnet efficiency by assuming magnet efficiency of zero for this plant.

Because our estimates indicated less movement than previous studies, it is possible that our estimates simply reflected the priors that assumed a substantial probability of staying in the same region. The monthly movement rate estimates did not seem to be overly-influenced by the priors. In the sensitivity analyses, changing the prior Dirichlet distribution did not substantially change the monthly movement rate estimates. Doubling or halving the effective sample size, which respectively increases or decreases the influence of the prior, did not change any monthly movement rate estimates by more than 0.09 mo^{-1} . Furthermore, the estimated monthly probability of staying in the same region was usually higher than the mean of the prior distribution.

Improving understanding of Atlantic Menhaden movement patterns may assist current management efforts. Movement can have important implications for assessment accuracy and fishery management reference points (Goethel et al., 2011; Laretta and Goethel, 2017). Changing fishery management practices with consideration for spatio-temporal distribution has been shown to increase biomass and catch in simulation models (Fahrig, 1991; Walters et al., 1993; Pelletier and Magal, 1996). Including spatial considerations in stock assessment models can also lead to large changes in the estimated fishing mortality rates (Langseth and Schueller, 2017). Introducing spatial dynamics into Atlantic Menhaden assessment and management may be important given changes in the reduction fishery industry since the 1970s. As of 2005, there is only one remaining menhaden reduction fishery on the east coast, located in Chesapeake Bay (SEDAR, 2015). Therefore, the reduction fishery principally operates between North Carolina and New Jersey (primarily our region 2) and does not extend throughout the Atlantic Menhaden's full range. If the population is not as well-mixed as previously believed, this may have consequences for the perceived abundance based on the catch. Additionally, the bait fishery, which extends throughout the full geographic range of this species, has begun to constitute a larger fraction of the total Atlantic Menhaden landings in recent years (SEDAR, 2015; Smith and O'Bier, 2011).

Our model required supplementary information on tagging mortality, detection efficiency, fishing effort, and landings. Experiments to quantify tag mortality and loss and to determine which tag type and tagging method minimized tagging mortality have aided several other forage fish studies (Fridriksson and Aasen, 1950; Hamre, 1970; Dommasnes, 1978). The passive tag recovery system used in this mark-recovery study facilitated experiments to estimate detection efficiency, which is necessary to distinguish between natural and fishing mortality (Pollock et al., 2001). There was insufficient information in the mark-recovery study alone to estimate natural and fishing mortality, but it was possible to distinguish these mortality rates by including fishing effort data.

Ideally, a mark-recovery study on a forage fish species such as Atlantic Menhaden would include sampling over all periods and regions. If the entire geographic range is not considered in the sampling design, then emigration becomes indistinguishable from natural mortality (Schwarz et al., 1993). Because over 1 million adult Atlantic Menhaden were tagged in this mark-recovery study, relatively low movement rates were estimable (e.g., 5% transition from region 3 to

region 1 from May to June). However, a more uniform distribution of fishing effort would likely have improved our ability to estimate movement rates (Liljestrand et al., 2018).

Tags that allow continuous tracking have become popular for studying movement. However, small species, such as most forage fishes, require small tags. Because we are limited in our ability to use continuous tracker tags on forage fishes, it is important to continue developing and improving dead recovery tagging models. Conventional tagging methods such as those used in this study, with a single recovery/detection event were used to monitor forage fish in the 1970s (IMARPE, 1972; Leary and Murphy, 1975) and are still used today (Isley and Tomasso, 1998; Ely et al., 2008).

We found that there may be less southward movement of Atlantic Menhaden during the winter than previously described and that natural mortality may be greater than previously estimated. Having a sizable population of Atlantic Menhaden in the north may influence sampling design and the distribution of fishing in the future. Winter surveys may need to direct additional effort north of the Chesapeake Bay to sufficiently sample and characterize the stock. Fisheries for Atlantic Menhaden may be feasible in new regions in the north. We recommend that the 1.17 yr^{-1} estimated natural mortality rate be used in future stock assessments. Additionally, we recommend that future surveys be designed to sample the Atlantic Menhaden stock over its full range.

Declarations of interest

None

Acknowledgments

We thank the original researchers for conducting this mark-recovery study and the Atlantic States Marine Fisheries Commission for funding the effort to redigitize the data. Ray Mroch provided harvest and effort data, Joseph Smith assisted with the proposal for our study, and Tom Miller who offered suggestions to improve this research and provided helpful comments on a previous draft of this manuscript. We also thank the two anonymous reviewers who provided comments and suggestions to improve this manuscript. This research was supported by Maryland Sea Grant, through the graduate research fellowship program [grant number NA14OAR4170090].

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.fishres.2018.10.015>.

References

- Ahrenholz, D.W., Dudley, D.L., Levi, E.J., 1991. Overview of mark-recovery studies on adult and juvenile Atlantic menhaden, *Brevoortia tyrannus* and Gulf menhaden, *B. patronus*. *Mar. Fish. Rev.* 53, 20–27.
- Anstead, K.A., Schaffler, J.J., Jones, C.M., 2017. Contribution of nursery areas to the adult population of Atlantic menhaden. *Trans. Am. Fish. Soc.* 146 (36), 46.
- Arnason, A.N., 1972. Parameter estimation for mark-recapture experiments on two populations subject to migration and death. *Res. Popul. Ecol.* 13, 97–113.
- Arnason, A.N., 1973. The estimation of population size, migration rates, and survival in a stratified population. *Res. Popul. Ecol.* 15, 1–8.
- Atkinson, A.N., Secor, D.H., 2017. Influence of winter conditions on the age, hatch dates, and growth of juvenile Atlantic menhaden in the Choptank River, Maryland. *Trans. Am. Fish. Soc.* 146, 1126–1136.
- Brownie, C., Hines, J.E., Nichols, J.D., Pollock, K.H., Hestbeck, J.B., 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49, 1173–1197.
- Buchheiser, A., Miller, T.J., Houde, E.D., 2017. Evaluating ecosystem-based reference points for Atlantic menhaden. *Mar. Coast. Fish.* 1, 457–478.
- Calvert, A.M., Bonner, S.J., Jonsen, I.D., Flemming, J.M., Walde, S.J., Taylor, P.D., 2009. A hierarchical Bayesian approach to multi-state mark-recapture: simulations and applications. *J. Appl. Ecol.* 46, 610–620.
- Carlson, F.T., Reintjes, J.W., 1972. Suitability of internal tags for Atlantic menhaden. *Fish. Bull.* 70, 514–517.
- Clark, W., 1999. Effects of an erroneous natural mortality rate on simple age-structured

- stock assessment. *Can. J. Fish. Aquat. Sci.* 56, 1721–1731.
- Coston, L.C., 1971. Summary of Tags Released and Recovered for the Atlantic Menhaden, 1966-69. U.S. Dep. Commer. Nat. Mar. Fish. Serv. Data Rep. 66, 117pp.
- Dommasnes, A., 1978. Survival of tagged Barents Sea capelin (*Mallotus villosus* Müller) and estimates of the 1973, 1974 and 1975 spawning stocks from tag returns. *Fisk. Skr. HavUnders.* 16, 339–358.
- Dryfoos, R.L., Cheek, R.P., Kroger, R.L., 1973. Preliminary analysis of Atlantic menhaden, *Brevoortia tyrannus*, migrations, population structure, survival and exploitation rates, and availability as indicated from tag returns. *Fish. Bull.* 71, 719–734.
- Dupuis, J.A., 1995. Bayesian estimation of movement and survival probabilities from capture-recapture data. *Biometrika* 82, 761–772.
- Durbin, A.G., Durbin, E.G., 1975. Grazing rates of the Atlantic menhaden *Brevoortia tyrannus* as a function of particle size and concentration. *Mar. Biol.* 33, 265–277.
- Ely, P.C., Young, S.P., Isely, J.J., 2008. Population size and relative abundance of adult Alabama shad reaching Jim Woodruff Lock and Dam, Apalachicola River, Florida. *N. Am. J. Fish. Manage.* 28, 827–831.
- Fahrig, L., 1991. Simulations Relevant to the 1/3 Harvesting Rule for Northern Cod. CAFSAC. Research Document 91/34, Halifax. .
- Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A., Sibert, J., 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim. Methods Softw.* 27, 233–249.
- Fridriksson, A., Aasen, O., 1950. The Norwegian-Icelandic herring tagging experiments. *Fisk. Skr. HavUnders.* 9, 1–43.
- Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. *Stat. Sci.* 7, 457–472.
- Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. *Bayesian Data Analysis*. Chapman and Hall, New York.
- Geweke, J., 1991. Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. In: In: Bernardo, J.M., Berger, J.O., Dawid, A.P., Smith, A.F.M. (Eds.), *Bayesian Statistics*, vol. 4 Clarendon Press, Oxford, U.K.
- Goethel, D.R., Quinn, T.J., Cadrin, S.X., 2011. Incorporating spatial structure in stock assessment: movement modeling in marine fish population dynamics. *Rev. Fish Biol. Fish.* 19, 119–139.
- Hamre, J., 1970. Internal Tagging Experiments of Mackerel in the Skagerak and the North-eastern North Sea. ICES CM. 1970/H:25. .
- Hilborn, R., 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. *Can. J. Fish. Aquat. Sci.* 47, 635–643.
- Hoenig, J.M., Barrowman, N.J., Hearn, W.S., Pollock, K.H., 1998. Multiyear tagging studies incorporating fishing effort data. *Can. J. Fish. Aquat. Sci.* 55, 1466–1476.
- IMARPE (Instituto del mar del peru “Institute of the Peruvian Sea”), 1972. Report on the second session of the panel of experts on the population dynamics of Peruvian anchovy. *Bol. Inst. Mar Perú-Callao* 2, 373–458.
- Isley, J.J., Tomasso, J.R., 1998. Estimating fish abundance in a large reservoir by mark-recapture. *N. Am. J. Fish. Manage.* 18, 269–273.
- June, F.C., Reintjes, J.W., 1959. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1952-55: with a brief review of the commercial fishery. *U.S. Fish Wildl. Serv. Pec. Sci. Rept. Fish.* 317.
- Kroger, R.L., Dryfoos, R.L., 1972. Tagging and tag-recovery experiments with Atlantic menhaden, *Brevoortia tyrannus*. NOAA Tech. Rep. U.S. Dept. Commer. NMFS SSRF-664, 11pp.
- Langseth, B.J., Schueller, A.M., 2017. Calculation of population level fishing mortality for single- versus multi-area models: Application to models with spatial structure. *Can. J. Fish. Aquat. Sci.* 74, 1821–1831.
- Lauretta, M.V., Goethel, D.R., 2017. The robustness of Brownie tag return models to complex spatiotemporal dynamics evaluated through simulation analysis. *Can. J. Fish. Aquat. Sci.* 74, 1845–1861.
- Leary, D.F., Murphy, G.I., 1975. A successful method for tagging the small, fragile engraulid *Stolephorus purpureus*. *Trans. Am. Fish. Soc.* 104, 53–55.
- Liljestrand, E.M., Wilberg, M.J., Schueller, A.M., 2018. Multi-state dead recovery mark-recapture model performance for estimating movement and mortality rates. *Fish. Res.* In press.
- Michielsens, C.G.J., McAllister, M.K., Kuikka, S., Pakarinen, T., Karlsson, L., Romakkaniemi, A., Pera, I., Mantyniemi, S., 2006. A Bayesian state-space mark-recapture model to estimate exploitation rates in mixed-stock fisheries. *Can. J. Fish. Aquat. Sci.* 63, 321–334.
- Mangel, M., 1982. Search effort and catch rates in fisheries. *Eur. J. Oper. Res.* 11, 361–366.
- Nicholson, W.R., 1971. Coastal movements of Atlantic menhaden as inferred from changes in age and length distributions. *Trans. Am. Fish. Soc.* 100, 708–716.
- Nicholson, W.R., 1978. Movements and population structure of Atlantic menhaden indicated by tag returns. *Estuaries* 1, 141–150.
- NMFS (National Marine Fisheries Service), 2015. *Fisheries of the United States*. U.S. Department of Commerce, pp. 2014 NOAA-NMFS Curr. Fish. Stat. No.2014.
- Pelletier, D., Magal, P., 1996. Dynamics of a migratory population under different fishing effort allocation schemes in time and space. *Can. J. Fish. Aquat. Sci.* 53, 1186–1199.
- Pollock, K.H., Hoenig, J.M., Hearn, W.S., Calingaert, B., 2001. Tag reporting rate estimation: 1. An evaluation of the high-reward tagging method. *N. Am. J. Fish. Manage.* 21, 521–532.
- Pristas, P.J., Willis, T.D., 1973. Menhaden tagging and recovery: part 1- Field methods for tagging menhaden, genus *Brevoortia*. *Mar. Fish. Rev.* 35, 31–35.
- Quinn, T.J., Deriso, R.B., 1999. *Quantitative Fish Dynamics*. Oxford University Press, New York.
- Reish, R.L., Deriso, R.B., Ruppert, D., Carroll, R.J., 1985. An investigation of the population dynamics of Atlantic menhaden (*Brevoortia tyrannus*). *Can. J. Fish. Aquat. Sci.* 42, 147–158.
- Roithmayr, C.M., 1963. Distribution of fishing by purse seine vessels for Atlantic menhaden, 1955-59. *U.S. Fish Wildl. Serv. Pec. Sci. Rept. Fish.* 22 No. 434.
- SEDAR (Southeast Data, Assessment, and Review), 2015. SEDAR 40 – Atlantic Menhaden Stock Assessment Report. SEDAR, North Charleston, SC, pp. 643.
- Schwarz, C.J., Arnason, A.N., 1990. Use of tag-recovery information in migration and movement studies. *Am. Fish. Soc. Symp.* 7, 588–603.
- Schwarz, C.J., Schweigert, J.F., Arnason, A.N., 1993. Estimating migration rates using tag-recovery data. *Biometrics* 49, 177–193.
- Sibert, J.R., Hampton, J., Fournier, D., 1996. Skipjack movement and fisheries interaction in the western Pacific. *FAO Fish. Tech. Pap.* 365, 402–424.
- Simpson, C.A., Wilberg, M.J., Bi, H., Schueller, A.M., Nessler, G.M., Walsh, H.J., 2016. Trends in relative abundance and early life survival of Atlantic menhaden during 1977–2013 from long-term ichthyoplankton programs. *Trans. Am. Fish. Soc.* 145, 1139–1151.
- Simpson, C.A., Bi, H., Liang, D., Wilberg, M.J., Schueller, A.M., Nessler, G.M., Walsh, H.J., 2017. Spawning locations and larval dispersal of Atlantic menhaden during 1977–2013. *ICES J. Mar. Sci.* 74, 1574–1586.
- Smith, J.W., 1991. The Atlantic and Gulf menhaden purse seine fisheries: origins, harvesting technologies, biostatistical monitoring, recent trends in fisheries statistics, and forecasting. *Mar. Fish. Rev.* 53, 28–41.
- Smith, J.W., O’Bier, B., 2011. The bait purse-seine fishery for Atlantic menhaden, *Brevoortia tyrannus*, in the Virginia portion of Chesapeake Bay. *Mar. Fish. Rev.* 73, 1–12.
- Walters, C.J., Hall, N., Brown, R., Chubb, C., 1993. Spatial model for the population dynamics and exploitation of the Western Australian rock lobster, *Panulirus cygnus*. *Can. J. Fish. Aquat. Sci.* 50, 1650–1662.