

## ABSTRACT

Title of Thesis: MORTALITY AND MOVEMENT OF  
ADULT ATLANTIC MENHADEN DURING  
1966-1969 ESTIMATED FROM MARK-  
RECAPTURE MODELS

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Atlantic Menhaden *Brevoortia tyrannus* is an economically and ecologically important forage fish. I built a multi-state mark-recapture model to estimate movement, fishing mortality, and natural mortality rates during 1966-1969. Movement from mid-Atlantic regions to North and South Carolina in the winter was lower than previously described, and natural mortality was approximately three times greater than previously estimated. Fishing mortality was highest in North and South Carolina. We evaluated the model's performance by generating mark-recapture data sets from known values of mortality and movement then fitting the mark-recapture model to those data. The model estimated movement rates  $> 0.05$  to within 33% of the true value even under different scenarios of spatiotemporally distributed releases and fishing effort. Distributing the fishing effort more evenly across regions substantially improved the estimates of movement and fishing mortality, and increasing the number of marked fish released had a small positive effect on accuracy of estimates.

MORTALITY AND MOVEMENT OF ADULT ATLANTIC MENHADEN  
DURING 1966-1969

by

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# Chapter 1: Estimation of Movement and Mortality using Mark-recapture from 1966-1969 Incorporating Bayesian Techniques

## Abstract

Atlantic Menhaden *Brevoortia tyrannus* is an economically and ecologically important forage fish that is targeted by large-scale commercial reduction and bait fisheries. In the late 1960s, the National Marine Fisheries Services conducted a mark-recapture study in which they tagged over one million adult Atlantic Menhaden. Mark-recapture models at the time did not, however, 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. Results indicated that Atlantic Menhaden largely remained within the same coastal region from June to October. In the winter, an estimated 55% of the population north of the Chesapeake Bay moved southward to the Chesapeake Bay and North and South Carolina. However, the fraction of the population undertaking of these movements was substantially smaller than previously described. The estimated instantaneous natural mortality rate,  $1.17 \text{ yr}^{-1}$  (1.09 - 1.23 95% CI), was greater than previously reported. Instantaneous fishing mortality was spatially and temporally

variable and as high as  $1.74 \text{ yr}^{-1}$  in North and South Carolina during 1967.

Understanding the spatial dynamics of a stock can help with improving survey design and fishery management.

### Introduction

Forage fish are small schooling pelagic species that are the primary food source to many marine predators (Pikitch et al. 2012). Forage fish can exert major control on trophic dynamics because they occupy an intermediate position in the food web (Cury et al. 2000). They connect primary production to secondary and tertiary consumers, sometimes moving nutrients and energy to offshore areas (Cury et al. 2000; Deegan 2011). Forage fish are also commercially important, comprising 37% of global marine fish catch, valued at \$5.6 billion USD per year in 2006 (Pikitch et al. 2012). Many forage fish species are important sources of fish oil and fish meal, which are used in agriculture and aquaculture (Tacon and Metian 2009; Pikitch et al. 2014).

Management of forage fish is challenging because of their complex spatial and temporal dynamics as well as their short life spans and variable recruitment patterns (Sætre et al. 2002; Bergh and Butterworth 2010). Their populations often span state or national boundaries and can exhibit movement among regions (Sissener and Bjørndal 2005; Gutierrez et al. 2007). Differences in nutrient availability can influence their spatial distribution seasonally, annually, or decadal, which can affect predator populations (Suryan et al. 2002; Gende and Sigler 2006; Ruzicka et al. 2012). Increased understanding of the spatial dynamics of forage species is important

for promoting sustainable fisheries because the timing and location of fishing can be conducted in such a way to reduce potential effects of overharvest.

Mark-recapture (or capture-recapture) studies can be used to estimate movement and survival from observations of marked individuals (Cormack 1964; Schwarz 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 (Rubin 1976; Chao 1989; Calvert 2009).

Atlantic Menhaden *Brevoortia tyrannus* is an ecologically and economically important forage fish that inhabits U.S. Atlantic coastal waters from Maine to Florida (Figure 1.1; Ahrenholz et al. 1991). Atlantic Menhaden are an important prey species for sea birds, predatory fishes, and cetaceans (Buchheister *in press*). 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, approximately 23% of these landings go towards the bait fishery, which provides bait for commercially and recreationally species such as striped bass, 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-recapture study of Atlantic Menhaden during 1966-1969. 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). This general description of the Atlantic Menhaden seasonal movement patterns that emerged from these initial analyses supported and reinforced by earlier studies that examined age, size structure, and effort of the commercial purse seine fishery during 1952-1959 (June and Reintjes 1959; Roithmayer 1963; Nicholson 1971). Although the seasonal patterns of Atlantic Menhaden movement have been well described qualitatively, quantitative estimates of movement rates have not been made (Dryfoos et al. 1973; Nicholson 1978).

The Atlantic Menhaden seasonal movement patterns described in the 1970s are under scrutiny today because there is evidence 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).

Spatiotemporal differences in stock availability may have consequences for the size and age distribution of the catch. Management efforts have aimed to account for these differences. For example, a dome-shaped selectivity curve for the reduction fishery was implemented in a previous stock assessment over concerns of reduced susceptibility to the fishery for older individuals and was supported by fishery-independent data (SEDAR 2015). One possible justification for a dome-shaped selectivity curve is that individuals in the northernmost regions, which are older and larger, may be remaining outside the range of the reduction fishery centered on the Chesapeake Bay (SEDAR 2015). Our study aims to estimate Atlantic Menhaden movement rates using updated statistical techniques and available data.

Advances in mark-recapture approaches allow the simultaneous estimation of movement and mortality rates, which can be used to update and reassess Atlantic Menhaden movement and mortality rates. 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).

## Methods

We developed a Bayesian version of the Brownie dead recovery model parameterized with instantaneous mortality rates (Hoenig et al. 1998) that also included movement among four regions (Figure 1.1). The model estimated natural mortality, fishing mortality, and the probability of movement. The model was implemented AD Model Builder (Fournier et al. 2012) and was fitted to mark-recapture data from a large-scale tagging study of Atlantic Menhaden conducted during 1966-1969.

### Mark-recapture Data

The NMFS began capturing and tagging adult Atlantic Menhaden with individually numbered ferromagnetic tags in July 1966 off the coast of 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 (Figure 1.1). Atlantic Menhaden were obtained from commercial purse-seine and pound-net catches and as well 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 x 3.0 x 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 across 97 time and region combinations (Table A.1.5-A.1.8).

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 recapture 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 recapture data and data of reduction plant magnet efficiency trials (SEDAR 2015). However, approximately 20% of the release and recapture data remain lost. Therefore, we used the mark-recapture data summarized by region and month by Coston (1971), which are complete. 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-recapture 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.

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 (Figure 1.1; Coston 1971). Locations of where the tagged fish were recaptured 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 rates of 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 (Dryfoos et al. 1973).

Supplementary data of the total landings and effort of each reduction plant for each month during 1966-1969 were provided by the NMFS Southeast Fisheries Science Center and used to weight the relative importance of each plant to the region's tag detection probability and to calculate fishing mortality. 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 to the May to November period.

#### 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-recapture study.

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,  $\varepsilon_p$ . 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 recapture 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,  $\varepsilon_p$ , weighted by the proportion of landings 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 recoveries for that plant in the redigitized data,  $\varepsilon_p$ , was set to 0. This applied principally to 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. We also assume that the proportion of landings in each plant for each month/region combination are known without error.

### Mark-recapture Model

The mark-recapture model was an instantaneous rate version of the Brownie dead recovery model (Hoenig et al. 1998) modified to allow movement among four regions (Figure 1.1). 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,  $I_{T,R}$ ,

$$N_{T,R,t,r} = I_{T,R}(1 - G_R). \quad (3)$$

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,  $S_{t,r}$ ,

$$N_{T,R,t+1,r}^* = N_{T,R,t,r} S_{t,r}. \quad (4)$$

Our model included the assumption of no movement during the month of release by applying movement after monthly mortality. Individuals released in a given month were not recovered in other regions during that month, which indicated that movement did not occur until after the first month.

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

$$S_{t,r} = e^{-M-F_{t,r}}. \quad (5)$$

Natural mortality was 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,  $E_{t,r}$ ,

$$F_{t,r} = q_{m,r} E_{t,r}. \quad (6)$$

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

$$q_{m,r} = Q_r e^{\theta_{m,r}}. \quad (7)$$

This parameterization for catchability assumes that catchability for a month and region was constant over years. For the parameters to be uniquely identifiable,  $\theta_{m,r}$  in July was set to 0, and for month-region combinations without fishing effort,  $q_{m,r}$  was set to 0 (Table A.1.1). After accounting for survival, the vector of abundance of a cohort in each region,  $\mathbf{N}_{T,R,t+1}$ , was calculated as the product of the movement probability matrix,  $\boldsymbol{\phi}$ , and the vector of post survival abundance by region,  $\mathbf{N}_{T,R,t}^*$ ,

$$\mathbf{N}_{T,R,t+1} = \boldsymbol{\phi} \mathbf{N}_{T,R,t}^* \quad (8)$$

Each value in a movement matrix indicated the probability of an individual moving from the region indicated by that column to the region indicated by that row in 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, but  $\boldsymbol{\phi}$  was fixed as an identity matrix for the remaining months. We assumed that the estimated 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,

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

### Parameter Estimation

We estimated the parameters using a Bayesian approach. The negative posterior probability on the log-scale was the sum of the negative log of the prior probabilities and the negative log likelihood for the recapture data,

$$P = NegLL_c + p. \quad (10)$$

We assumed that the recaptures followed a negative binomial distribution, with an overdispersion value  $k = 2.5$ ,

$$NegLL_c = \sum_T \sum_R \sum_{t>T} \sum_r -\log_e \left( \frac{\Gamma(k + J_{T,R,t,r})}{\Gamma(k) \Gamma(J_{T,R,t,r})} \left( \frac{k}{k + C_{T,R,t,r}} \right)^k \left( \frac{C_{T,R,t,r}}{k + C_{T,R,t,r}} \right)^{J_{T,R,t,r}} \right). \quad (11)$$

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 difficult to estimate.

A uniform prior was placed on natural mortality, constraining the value between 0.006 and 148.4 per month,

$$M \sim U(0.006, 148.4) . \quad (12)$$

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. 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,  $\sigma_w$ . 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) (Table A.1.9-A.1.10). 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 were unique for each regional transition (Table A.1.12),

$$\varphi_{i,j} = \int \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx. \quad (13)$$

The winter priors were designed differently, because if diffusion was assumed across a six-month period, a majority of individuals would be expected to 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.

We assumed that the effective sample size,  $\nu$ , of the Dirichlet distribution was 10. The negative of the natural logarithm of the Dirichlet distribution (with additive constants removed) was

$$P_\varphi = \sum_m \sum_{r1} \sum_{r2} -\nu \varphi_{m,r1,r2} \log_e(\varphi_{m,r1,r2}). \quad (14)$$

For values of  $\nu$  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.

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

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

The variance of the prior for catchability,  $\sigma_q^2$ , 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 1000<sup>th</sup> 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.

### 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<sup>-1</sup>, 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 (Table A.1.9; Table A.1.11). Sensitivity was summarized as the effect on estimates of  $M$ , the average total catchability, and the average yearly instantaneous fishing mortality.

### Net Movement

To determine the net effect of monthly movement, we simulated releases of 1000 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.

### Results

#### Magnet Efficiency Trials

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 plant ranged from 59% to 92% (Table 1.2). Region 2 had the lowest average magnet efficiency, and region 3 had the highest average magnet efficiency.

## Model Fit

The model fit the observed recaptures relatively well across the four regions (Figure 1.2; Table A.1.1). 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.

## Movement

There were temporal patterns to the estimated movement probability, with 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 the region 2 in June (Figure 1.3; Table A.1.13). 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 1.3). 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.

## Mortality

The estimated instantaneous natural mortality rate across all regions and months was  $0.098 \text{ mo}^{-1}$  (0.091 - 0.102, 95% CI), which corresponds to an instantaneous natural mortality rate of  $1.17 \text{ yr}^{-1}$  (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 1968 for all regions except region 1 (Figure 1.4). Region 3 had the highest average fishing mortality ( $1.66 \text{ yr}^{-1}$ ), more than six times the second largest value,  $0.25 \text{ yr}^{-1}$ , in region 2; average fishing mortality was about  $0.18 \text{ yr}^{-1}$  in region 1 and  $0.10 \text{ yr}^{-1}$  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 (Figure 1.5). 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  $0.02 \text{ mo}^{-1}$ , 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  $0.17 \text{ mo}^{-1}$ . The maximum fishing mortality rate in region 3 was  $0.45 \text{ mo}^{-1}$  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  $1.47 \times 10^{-4}$  to 0.013 and averaging 0.0025 vessel week<sup>-1</sup>. Region 3 had the greatest average catchability, 0.006 vessel week<sup>-1</sup>, and the lowest average catchability,  $7.69 \times 10^{-4}$  vessel week<sup>-1</sup>, was estimated in region 2. During May-November catchability decreased in regions 1, 2, and 3, but stayed approximately the same throughout most the year in region 4 with an increase at the end of the year.

### Sensitivity Analyses

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%. 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  $w$ ,  $\sigma_q$ ,  $k$ , or  $M$ . Decreasing the effective sample size of the Dirichlet distribution to 5 reduced the fraction of 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 1.4), 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  $0.82 \text{ yr}^{-1}$ , had the second greatest effect on the other parameter estimates among the sensitivity analyses (Table 1.4), with average catchability increasing by about 37% and average fishing mortality increasing by about 32%.

Decreasing the standard deviation for the catchability prior,  $\sigma_q$ , 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  $\sigma_q$  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.

### Discussion

We used data from a large-scale mark-recapture 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 the northernmost two 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 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-recapture 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 1.3; 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). Fishing effort was also 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 of  $1.17 \text{ yr}^{-1}$ , which was about 2.3 times greater than previous estimates, ranging from  $0.50 \text{ yr}^{-1}$  to  $0.52 \text{ yr}^{-1}$  (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 ( $1.47 \text{ yr}^{-1}$ ), and subtracted off fishing mortality ( $0.95 \text{ yr}^{-1}$ ), to estimate natural mortality. Our natural mortality estimate should be more reliable because it is estimated from the mark-recapture data rather than the age structure of catch. Furthermore, testing of the mark-recapture model

revealed that estimated natural mortality was relatively unbiased (Chapter 2). Based on the previous estimates, the most recent stock assessment used an age-varying natural mortality rate, ranging from 0.52-1.23 yr<sup>-1</sup> which is scaled by weight to the tagging estimate 0.50 yr<sup>-1</sup> for age 4-6+ individuals (SEDAR 2015). 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.

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 recaptures. 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 time frame. 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. A portion of the population being present in these regions during the winter, when coastwise spawning is at its highest, could also explain their 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 recaptures. 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 recaptures seems reasonable. Older individuals may not be as susceptible to fishing mortality because there are fewer large individuals and therefore smaller schools. The reduction fishery selectively harvests larger schools, which may have 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 recover process. Two kinds of magnets were installed in the reduction plants: primary magnets located at the conveyer 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. Furthermore, the estimated monthly probability of

staying in the same region was usually higher than the mean of the prior distribution, the exception being movement from region 3 to 2 from May to June and June to July.

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 cause large changes 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 determine which tag type and tagging method minimize this value have aided in several other forage fish studies (Fridriksson and Aasen 1950; Hamre 1970; Dommasnes 1978). The passive tag recovery system used in this mark-recapture 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-recapture 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-recapture 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-recapture 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 (Chapter 2).

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 like those used in this study, with a single recapture/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).

The Atlantic Menhaden mark-recapture study is among the largest studies of its kind. A large-scale Skipjack Tuna *Katsuwonus pelamis* tagging study was conducted from 1977-1980 wherein about 94,000 individuals were tagged to estimate movement across the Pacific Ocean (Sibert et al. 1998). Upwards of 200,000 ducks and 150,000 geese and swans are banded in North America each year by the U.S. Geological Survey to estimate movement rates across the United States and Canada and to detect population units. In mark-recapture studies involving forage fish, which have large population sizes and ranges, the number of tagged individuals typically do not exceed 50,000 (Clark and Janssen 1945; Wheeler and Winters 1984; Armannson et al. 2007). In contrast, the mark-recapture experiment on adult Atlantic Menhaden tagged over 1 million individuals in the span of only 3.5 years, making it one of the largest mark-recapture studies ever conducted. Having a large number of tagged individuals allowed the estimation of relatively low movement rates. Smaller scale mark-recapture studies may have to define the geographic regions such that there is substantial ( $>0.1$ ) movement probability between time steps.

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  $1.17 \text{ yr}^{-1}$  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.

Tables and Figures

TABLE 1.1. 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 Figure 1.1
r	Region of cohort presence	See Figure 1.1
d <sub>r</sub>	Lateral distance between 25° 45' N and a region's northern boundary	See Figure 1.1

**Likelihood components**

NegLL <sub>c</sub>	Negative log likelihood for recaptures
p <sub>q</sub>	Log prior for catchability
p <sub>φ</sub>	Log prior for movement rates
P <sub>q</sub>	Log posterior for catchability
P <sub>φ</sub>	Log posterior for movement rates

**Data**

L	Landings	
E	Effort	
I <sub>T,R</sub>	Releases	See Table A.1.5-A.1.8
J <sub>T,R,t,r</sub>	Recoveries	

**Specified quantities**

ε	Magnet efficiency	See Table 1.2
G <sub>R</sub>	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 <sub>q</sub>	Variance for distribution of total catchability	1

**Calculated quantities**

N <sub>T,R,t,r</sub>	Abundance of a tagged cohort
S <sub>t,r</sub>	Survival

$F_{t,r}$	Fishing mortality
$q_{m,r}$	Catchability
$C_{T,R,t,r}$	Estimated Recoveries
$\sigma_m$	Variance of diffusion process for migration priors
$\phi_{i,j}$	Prior probability of movement

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TABLE 1.2. 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

TABLE 1.3. Proportion of individuals in each region without fishing or natural mortality from simulated releases of 1,000 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 1.4. 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

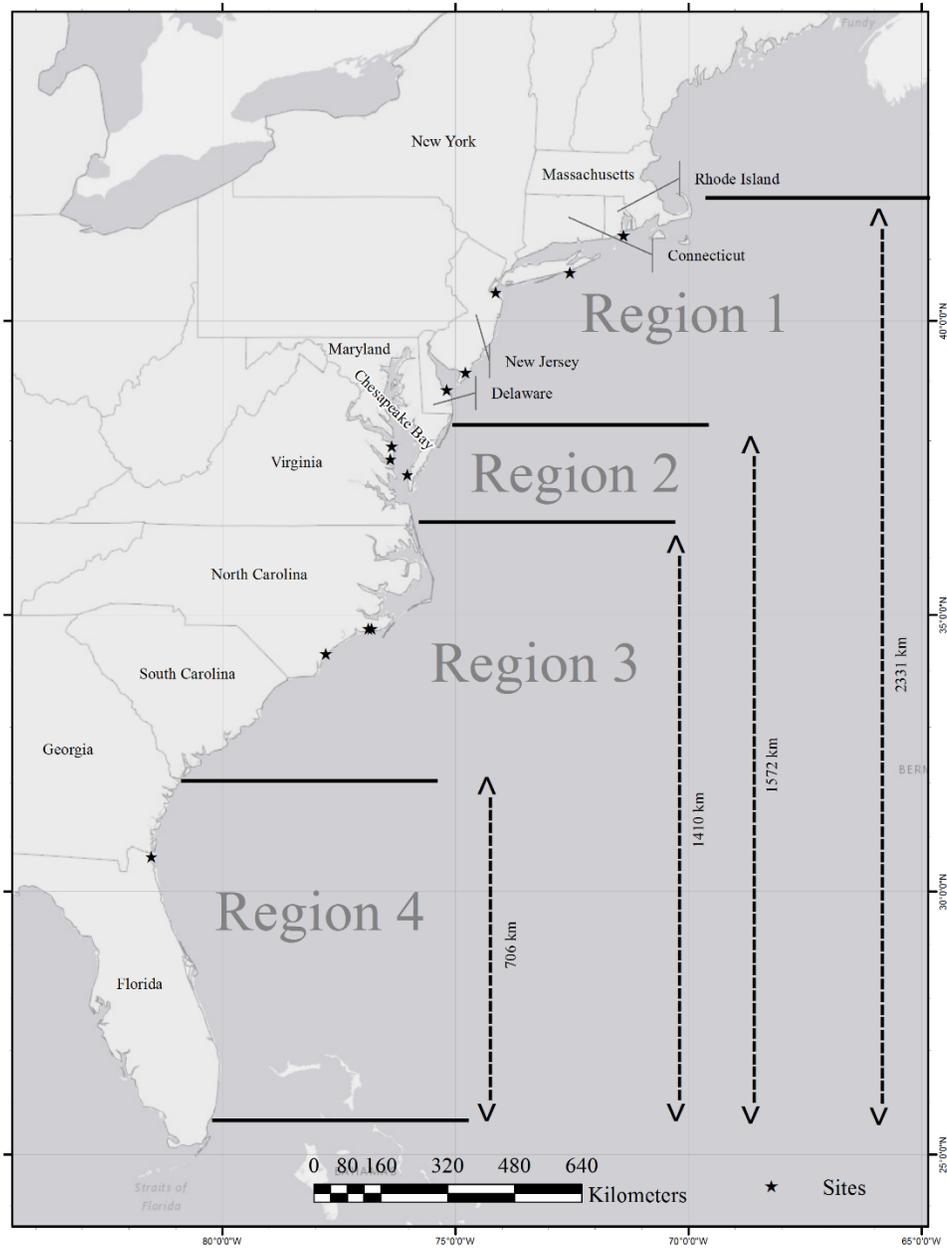


FIGURE 1.1. Locations of the four regions used in the model to estimate movement, adapted from Coston (1971). Stars indicate the locations of reduction plants, and some stars represent multiple plants.

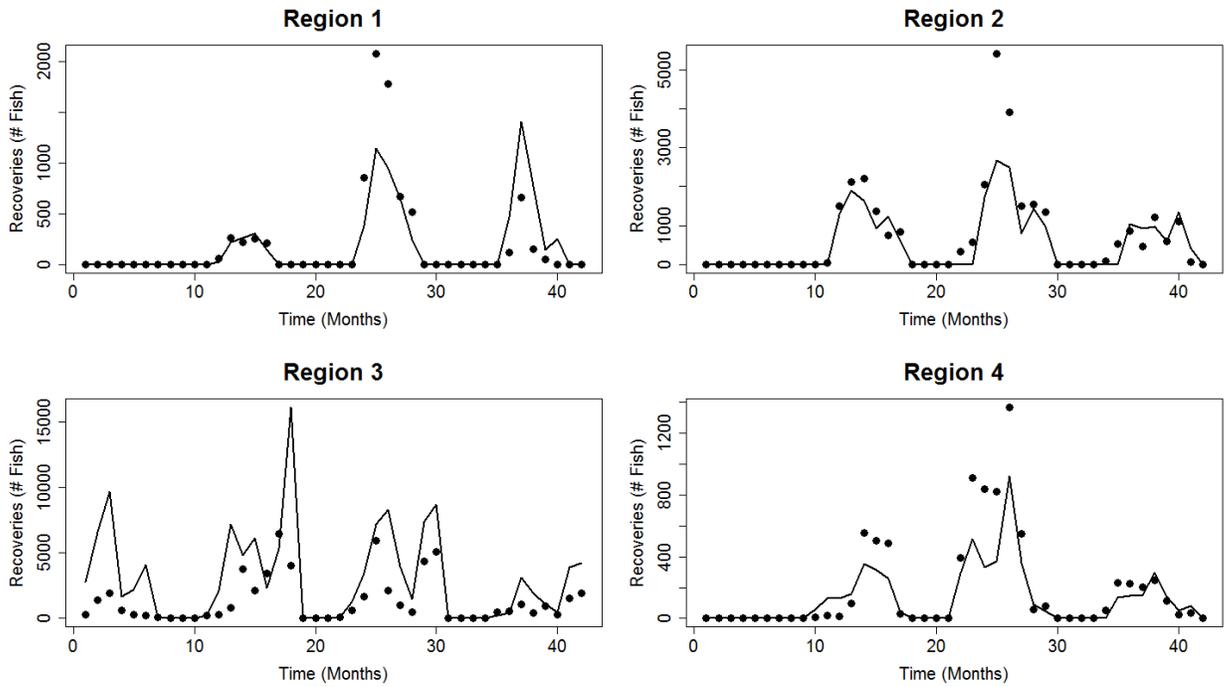


FIGURE 1.2. Predicted (line) and observed (circles) number of recovered tags for each month after June 1966 in by regions.

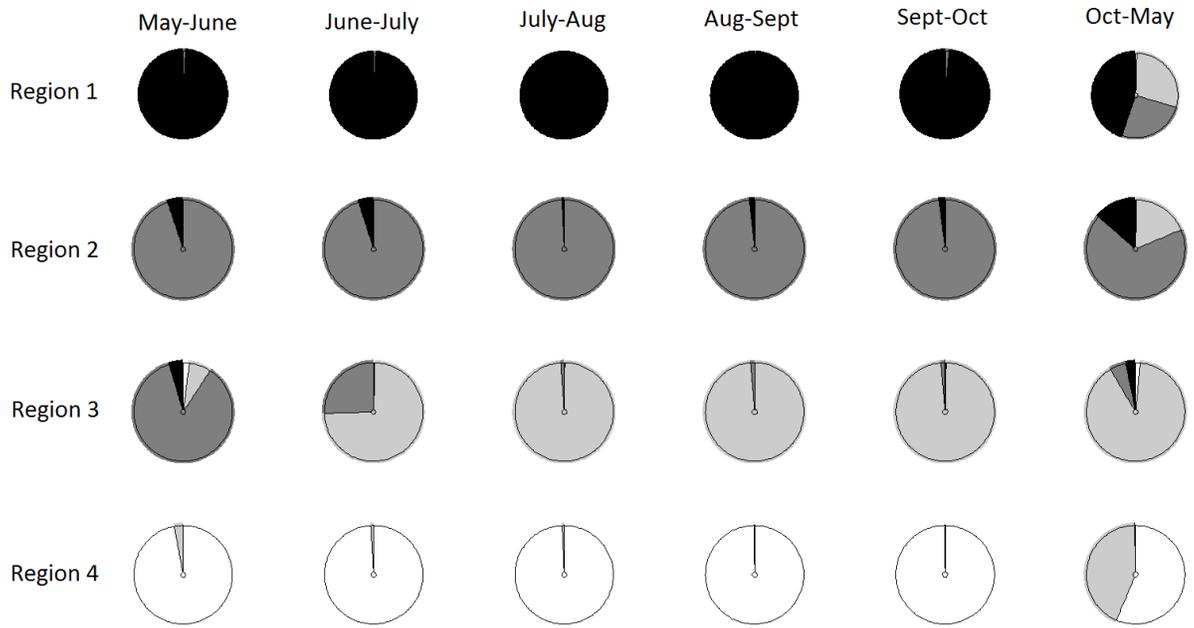


FIGURE 1.3. Estimated movement rates for each month May through October and between October and May. Each pie chart shows the fraction of the population in a region that was estimated to move to each of the other regions. Colors indicate regions: Region 1- black, Region 2- dark gray, Region 3- light gray, and Region 4- white.

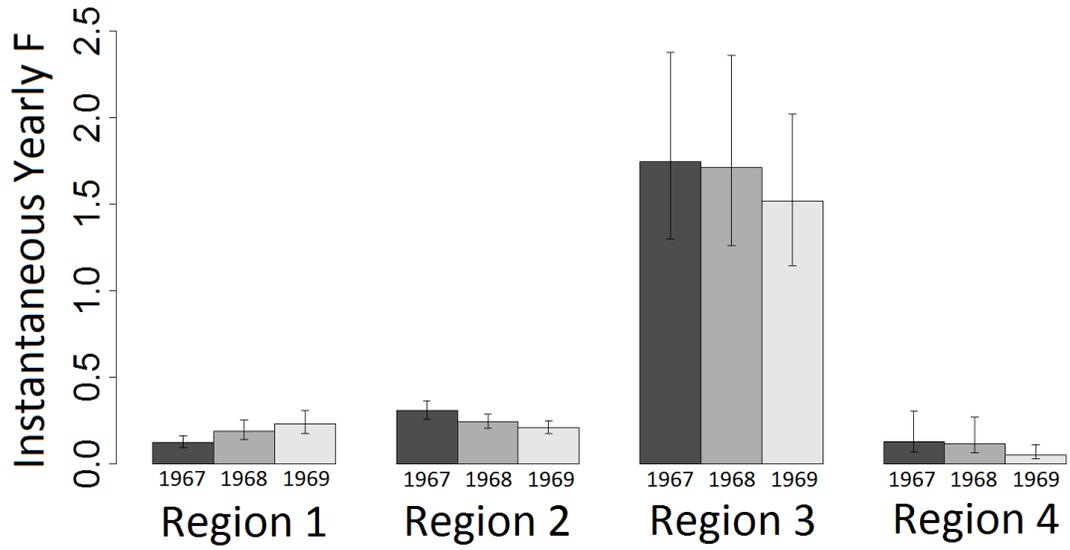


FIGURE 1.4. Estimated instantaneous fishing mortality rates ( $F \text{ yr}^{-1}$ ) for Atlantic Menhaden by year and region. Error bars indicate 95% credibility intervals.

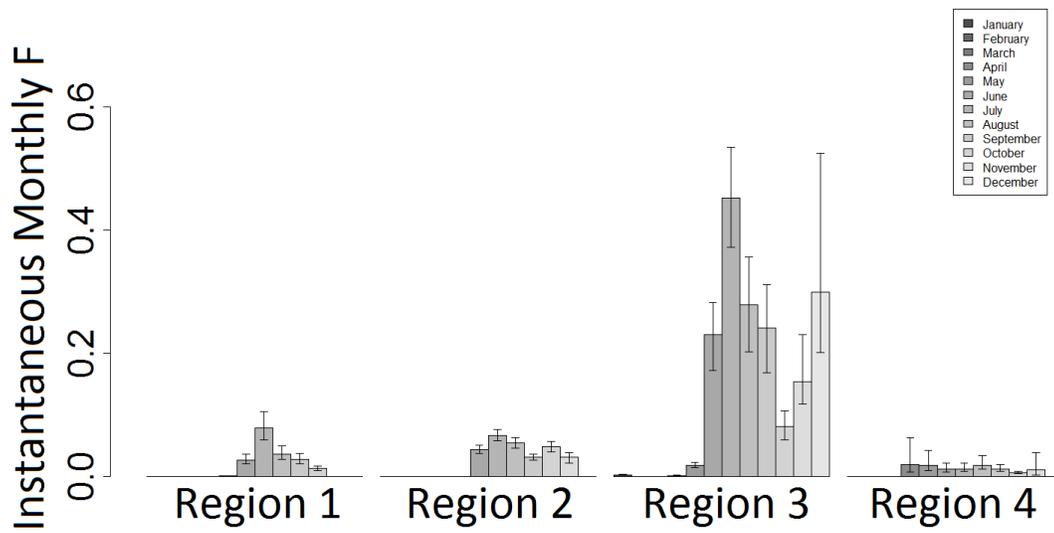


FIGURE 1.5. Estimated average instantaneous fishing mortality rates ( $F \text{ mo}^{-1}$ ) for Atlantic Menhaden by month and region. Error bars indicate 95% credibility intervals.

## Chapter 2: Multi-state Dead Recovery Mark-recapture Model Performance with Spatially Uniform Releases and Fishing Effort

### Abstract

Multi-state mark-recapture models are used to estimate movement and mortality rates of terrestrial and aquatic animals. These models have become especially popular in the last 20 years since technology and statistical techniques have improved to accommodate the extensive data requirements. However, performance of multi-state mark-recapture models to estimate movement rates has received little evaluation with few studies exploring the effects of alternative release and recapture designs on model bias and precision. Our objectives were to evaluate the effects of the spatio-temporal pattern of releases, pattern of recovery efforts, and number of releases on the performance of a multi-state mark-recapture model. We generated mark-recapture data from a spatial model and fitted them with a multi-state dead recovery model that included prior distributions on movement rates, natural mortality, and catchability. We generated data using a spatially variable schedule of releases and effort, and a release size of about 1 million individuals to mimic a mark-recapture study conducted for Atlantic Menhaden in the late 1960s. We also ran alternative scenarios of sample size and spatially uniform releases and effort, either by themselves or in combination to determine their effects on accuracy of the estimates. For movement rates  $> 0.05$  per time step, the median relative error was less than 33%. Movement rate and catchability were more accurately and precisely estimated in scenarios that included spatially uniform fishing effort, while spatially uniform releases had little to no effect on bias or precision of estimated movement rates. Increased sample size improved

accuracy of all parameter estimates except for the smallest movement rates. Future mark-recapture experiments that use a multi-state dead recovery model may benefit from distributing recapture effort uniformly over time and space.

### Introduction

Multi-state mark-recapture models explicitly account for marking and recaptures across multiple sites, i.e., states, which allows estimation of movement and mortality rates (Arnason 1973; Schwarz et al. 1993). In addition to movement and mortality, multi-state mark-recapture models can estimate reproductive state, or age- and weight- specific parameters (Nichols et al. 1994; Nichols and Kendall 1995; Sippel et al. 2015). Multi-state mark-recapture models have become more popular with the development of software like program MARK and increased computational power (Lebreton and Cefe 2002). Multi-state dead recovery models, which have only one tagging and one possible recovery event for each individual, are one type of mark-recapture model still in popular use (Hestbeck et al. 1991; Brownie et al. 1993; Schwarz et al. 1993). Unlike multiple resighting models, which use detection as a proxy for survival, dead recovery models use detection to directly estimate mortality (Lindberg 2012). Because dead recovery studies have at most two records of an individual's location (i.e. release and recapture), these models require large sample sizes to be able to detect low frequency movement events (Lindberg and Rexstad 2002).

Identifiability among mortality, movement, and detection probability is particularly difficult in multi-state models when movement and mortality are time dependent

(Kendall and Nichols 2002; Schaub et al. 2004). Increasingly, this shortcoming has been addressed by incorporating prior probability distributions on parameters (Newman 2000; Gimenez et al. 2007; Calvert et al. 2009). Including prior distributions has been useful when the data are limited or of poor quality, which is frequently the case when recaptures are often obtained opportunistically (Martell and Walters 2002; Michielsens et al. 2011).

Simulation studies have been used to evaluate the accuracy and performance of complex multi-state models that include Bayesian statistical components (Faubet et al. 2007; Vermard et al. 2010). Data are generated using known values (e.g. mortality, catchability, and biomass), which are used to fit models that estimate these same values. The estimates are compared against the known values to determine model accuracy (Chao 1987; Lee et al. 2011; Wetzel and Punt 2011). For multi-state mark-recapture models, simulation studies have helped determine the optimal schedule of releases and recapture effort that reduce bias of movement rate parameter estimates (Ovaskainen et al. 2008). Spreading fishing effort across a broader spatial range can lead to more accurately estimated movement rates (Albanese et al. 2003; Yamamura et al. 2003). However, it is not yet understood how the combination of distribution of releases, recovery effort, and sample size affect the performance of a mark-recapture model that simultaneously estimates mortality and movement.

Our goal was to evaluate the accuracy and precision of a multi-state dead recovery mark-recapture model that simultaneously estimates mortality and movement. Our specific objectives were to determine whether model performance improved with 1) increased sample size, 2) spatiotemporally homogenous sampling effort, and 3)

spatiotemporally homogenous releases. The mark-recapture model also used supplementary data of tag shedding/tagging mortality, detection probability, and fishing effort to estimate monthly movement rates among four regions, month- and region- specific catchability, and monthly natural mortality. We generated data under similar conditions as the 1966-1969 Atlantic Menhaden mark recapture study and several alternative release and recovery scenarios.

### Methods

Mark-recapture data were generated with known values of movement, natural mortality, and catchability and under different scenarios of release size, spatio-temporal patterns of fishing effort, and spatio-temporal patterns of releases. The mark-recapture model was then fitted to the data to estimate movement, natural mortality, and catchability. Accuracy was assessed by comparing the estimated values to those used to generate the data. The process was repeated 500 times for each scenario. The data generating and mark-recapture models were run in AD Model Builder (Fournier et al. 2012), and analysis of the results were conducted in R (R Core Team 2015).

#### Data Generating Model

The data generating model generated mark-recapture data over a 42-month period and across four regions to replicate the structure of the July 1966-December 1969 data from Chapter 1. The initial size of the cohort upon release, when  $t=T$  and  $r=R$ , was calculated as the product of the number released,  $I_{T,R}$ , which varied between

scenarios, the region-specific tagging mortality rate,  $G_R$ , 0.1 in region 1, 0.2 in region 2, 0.25 in region 3, and 0.4 in region 4, from (Dryfoos et al. 1973),

$$N_{T,R,T,R} = I_{T,R}(1 - G_R). \quad (1)$$

We calculated the size of a tagged cohort,  $N_{T,R,t,r}$ , present at time,  $t$ , and region,  $r$ , that were released at time,  $T$ , in region,  $R$ , by sequentially applying mortality and movement rates to the number of individuals that survived until that time. The number of individuals before applying movement,  $N_{T,R,t,r}^*$ , was calculated from the instantaneous monthly fishing and natural mortality. Natural mortality,  $M$ , was fixed at  $0.10 \text{ mo}^{-1}$ , approximately the value estimated in Chapter 1. Fishing mortality was the product of month- and region-specific catchability,  $q_{m,r}$ , and effort,  $E_{t,r}$ , which depended on the scenario,

$$N_{T,R,t,r}^* = N_{T,R,t,r} e^{-M - q_{m,r} E_{t,r}}. \quad (2)$$

The number of individuals after movement occurred,  $\mathbf{N}_{T,R,t+1}$ , was calculated as the product of the movement rate matrix,  $\boldsymbol{\phi}_t$ , (Table A.1.13), and the vector of individuals in each region,  $\mathbf{N}_{T,R,t}^*$ ,

$$\mathbf{N}_{T,R,t+1} = \boldsymbol{\phi}_t \mathbf{N}_{T,R,t}^*. \quad (3)$$

No movement occurred between November to May, i.e.,  $\phi_t$ , was an identity matrix.

The number of recaptures from each release event was generated using a binomial distribution with the number of individuals present in a region and the probability of observation,  $p_{t,r}$ ,

$$C_{T,R,t,r} \sim \text{Binom}(N_{T,R,t,r}, p_{t,r}). \quad (4)$$

The probability of observation was calculated as the product of the probability of being captured (based on the Baranov catch equation) and time- and region-specific detection efficiency,  $\varepsilon_{t,r}$ ,

$$p_{t,r} = \frac{q_{m,r} E_{t,r}}{M + q_{t,r} E_{t,r}} (1 - e^{-M - q_{m,r} E_{t,r}}) \varepsilon_{t,r}. \quad (5)$$

#### Estimation Model

Parameters were estimated by fitting a mark-recapture model to the generated data sets. The mark-recapture estimation model was a multi-state version of the Brownie dead recovery model that included prior probabilities on movement rates, instantaneous natural mortality, and catchability parameters (Hoenig et al. 1998; Chapter 1). The estimation model had 42 monthly time steps and tracked the abundance over time and across four regions based on the movement rate and natural and fishing mortality using the same equations as the data generating model. The estimated recaptures were fit to observed data using maximum likelihood, assuming a

negative binomial distribution. A Dirichlet distribution was used as a prior on the movement rates, a uniform distribution was placed on the log scale natural mortality rate, and catchability was conditioned such that deviations from the mean on the log scale were normally distributed. Tag shedding and mortality, detection probability, and the overdispersion value of the negative binomial distribution were assumed to be known without error.

#### Model performance

Error was calculated as the difference between the estimated parameter value and the true value and relative error was calculated as the error divided by the true value,

$$relative = \frac{estimate - true}{true}. \quad (6)$$

The root mean squared error, *RMSE*, was calculated for each estimate,

$$RMSE = \sqrt{\frac{\sum_{i=1}^{500} (estimate_i - true)^2}{500}}. \quad (7)$$

The *RMSE* was calculated over all movement estimates (every model estimated 96 movement rates),

$$RMSE_{\varphi} = \sqrt{\frac{\sum_{i=1}^{500} \sum_{p=1}^{96} (estimate_{i,p} - true_p)^2}{500 * 96}}. \quad (8)$$

The *RMSE* was calculated for all catchability estimates where  $P=48$  for uniform effort scenarios and  $P=33$  for variable effort scenarios,

$$RMSE_q = \sqrt{\frac{\sum_{i=1}^{500} \sum_{p=1}^P (estimate_{i,p} - true_p)^2}{500 * P}}. \quad (9)$$

#### Data Generating Scenarios

Five hundred mark-recapture data sets were generated for each of the 12 scenarios, which altered the release size, spatial and temporal distribution of effort, or the spatial and temporal distribution of releases (Table 2.1). In the base model (“Base”), the release size, effort structure, and release structure were set to the same conditions as in the Atlantic Menhaden mark-recapture model (Table 1.1; Table A.1.5-Table A.1.8). A total of 1,066,357 individuals were released across 42 months, to match the Atlantic Menhaden mark-recapture study from Chapter 1. The fishing effort was the actual values of Atlantic Menhaden reduction fishery during July 1966-December 1969, and for confidentiality reasons cannot be reproduced in its entirety. A summary by year is available in Table A.1.4. Effort was greatest in region 2, about half as much as region 2 in regions 1 and 3, and about 10% as much as region 2 in region 4. Effort

was low or zero for all regions between November-April. Effort totaled 4,290 vessel weeks across regions and time steps. Catchability,  $q_{m,r}$ , was set to the values estimated in Chapter 1, ranging from  $1.47 \times 10^{-4}$  to 0.013 and averaging 0.0025 vessel<sup>-1</sup> week<sup>-1</sup>. The average catchability in region 2 was about 10% of the other three regions. Catchability was highest between July-September.

The effect of release size was evaluated by scaling the number of releases by 0.5 (500K) or 2.0 (2mil), relative to the base scenario. The total number releases also depended on the release structure, and slightly fewer individuals were released when the release structure was homogenous (see below).

The effect of spatio-temporally uniform fishing effort (Effort) was tested by setting the effort,  $E_{t,r}$  to 50 vessel weeks for every time step and region, totaling 8,400 vessel weeks across regions and time steps. The catchability,  $q_{m,r}$ , was set to  $2.5 \times 10^{-3}$  for every month and region. Detection efficiency,  $\varepsilon_{t,r}$ , was set to 0.67 in region 1, 0.47 in region 2, 0.82 in region 3, and 0.61 in region 4 for every time step.

The effect of spatio-temporally variable releases (Releases) was tested by setting the number of releases,  $I_{t,r}$  to 5000 individuals in every time step and region, or 840,000 individuals total in the base release size scenario.

To assess the model's ability to accurately estimate natural mortality during the 1966-1969 Atlantic Menhaden tagging study, additional data-generation scenarios were also done by setting the monthly natural mortality to  $0.15 \text{ mo}^{-1}$  or  $0.05 \text{ mo}^{-1}$  under the base release size, effort structure, and release structure.

## Results

Performance of the mark-recapture model differed under alternative data generating scenarios. The multistate mark-recapture model produced accurate estimates of most of the parameters, although some parameters had consistent bias. We characterized bias as the median difference between the estimated and true value and precision as the standard deviation the estimates. Scenarios that had uniformly distributed effort performed best compared to the base scenario. Increasing the release size led to improvements in accuracy, decreasing bias and improving precision, but spatiotemporally uniform releases had little to no effect on performance.

Movement rates were accurately estimated across scenarios, but were more accurate in scenarios with spatiotemporally uniform effort and increased releases. The average median relative error for monthly movement rates in the base scenario was 18%, in the uniform effort and release scenario was -5%, and in the 2Mil scenario was -.02%. These average median relative error values were largely influenced by a few large median relative errors of small movement rates (e.g., the relative difference between 0.0001 and 0.0002 is 100%). The largest median relative error values (> 100% or < -100%) occurred for the smallest movement rates (< 0.001). Movement rates with true values >0.05 were estimated fairly accurately with a median relative errors less than 33%, and movement rates with true values >0.1 had median relative errors less than 9%. In all the scenarios with the same number of releases as the base scenario, several parameters with true values <math>10^{-3}</math>, such as those between non-adjacent regions, had median relative errors larger than 200%. However, the difference in accuracy between the base scenario and the uniform effort and increased release scenarios was

most noticeable for larger movement rates (Figure 2.2). Including uniform effort increased precision for some larger movement rates as well as decreasing bias. Increasing the number of released individuals increased the precision and decreased bias of movement rate estimates with one exception (Figure 2.3; Figure A.2.14-A.2.18); the estimated movement rates between regions 1 and 4 became more negatively biased with increased releases. Doubling the release size increased the median relative error of estimated movement between regions 4 and 1 by 1-13%. However, the median relative error was less than 100%, despite the small values of these movement rates ( $10^{-7}$  -  $10^{-6}$ ) (Figure A.2.8-A.2.12). The median error was within  $\pm 0.02$  for all monthly movement rates between May and October for all variable effort and release scenarios (Figure A.2.1-A.2.4). The scenario that included both uniform effort and releases decreased the median error of estimated movement rates relative to the base scenario by an average of 0.0009. The scenario with uniform effort alone reduced the bias of the movement rate estimates to about the same degree as the scenario that included both uniform effort and releases, but did not improve precision by as much as the uniform effort and release scenario. The scenario with uniform releases alone did not notably improve the accuracy of movement rates compared to the base scenario. Estimated movement rates under scenarios with uniform releases were less precise than under scenarios with variable releases.

In the base scenario, the half-year movement rates had a 21% greater average median relative error compared to the monthly movement rates. Scenarios that included uniform effort and releases and scenarios with increased release size increased the accuracy of half-year movement rates relative to the base; the estimates were more

precise and had less bias (Figure 2.4-2.5). The average median relative error for half-year movement rates in the base scenario was 36%, in the uniform effort scenario was -2%, in the uniform release scenario was 38%, in the uniform effort and release scenario was -9%, and in the 2Mil scenario was 25%. The larger half-year movement rates had higher error, but lower relative error (Figure A.2.13; Figure A.2.19).

Estimated movement to region 1 was positively biased and movement to region 3 was negatively biased for all scenarios (Figure 2.4-2.5). The half-year movement rates were less precise and more biased compared to monthly movement rates.

Scenarios with uniform effort had lower RMSEs for movement and catchability parameters than scenarios with a uniform distribution of releases or the base scenario (Figure 2.1). Adding uniform effort to a scenario decreased RMSE of movement parameters by 45-57%. For all scenarios, adding uniform effort decreased RMSE of catchability parameters by 65-69%. Both uniform effort and releases together decreased the RMSEs of movement parameters by 55-59% and the RMSEs of catchability parameters by 64-68% compared to the base. For all parameters and scenarios, doubling the release size decreased the RMSEs by 10-25%.

Natural mortality was estimated accurately and precisely with very little bias in all scenarios (Figure 2.6). The median relative error of the estimated natural mortality rate across all scenarios, including those where natural mortality was increased to  $0.15 \text{ mo}^{-1}$  or decreased to  $0.05 \text{ mo}^{-1}$ , was approximately 1-3%. Under the base scenario the median error of the monthly natural mortality was approximately  $0.007 \text{ mo}^{-1}$ , under the low M scenario it was  $0.0008 \text{ mo}^{-1}$ , and under the high M scenario it was  $0.003 \text{ mo}^{-1}$ . The estimates became less biased with increased sample size.

Scenarios that included uniform effort and releases, by themselves or in combination, did not improve estimates of natural mortality. Precision improved in scenarios that included uniform effort.

The patterns of error in the estimated fishing mortality rate were similar across scenarios (Figure 2.4). Estimates were negatively biased in regions 1 and 3 and positively biased in region 2. The smallest median error was in region 4 for all scenarios. Fishing mortality rates (per year) were estimated to within  $0.15 \text{ yr}^{-1}$  of the true value. The true value of fishing mortality varied from  $0.09 \text{ yr}^{-1}$  to  $1.55 \text{ yr}^{-1}$  across regions under variable effort scenarios and was  $1.08 \text{ yr}^{-1}$  in scenarios with uniform effort. For regions with average annual fishing mortality  $<0.30 \text{ yr}^{-1}$ , the median error did not exceed  $0.05 \text{ yr}^{-1}$ . The scenario with uniform effort most strongly changed the error in region 3 where the median error increased by  $0.03 \text{ yr}^{-1}$ . Adding uniform effort to the base scenario decreased the precision in regions 1, 2, and 4 while increasing the precision in region 3. Doubling the release size decreased the median bias and improved precision of yearly fishing mortality in all regions and years (Figure A.2.20).

### Discussion

Our multi-state mark-recapture model estimated movement and mortality rates precisely and accurately. As expected, accuracy increased when fishing effort was uniformly distributed over space and time (Ovaskainen et al. 2008). Additionally, a larger number of releases generally resulted in more accurate estimates. For the monthly movement rates, the largest values,  $>0.1$ , had the largest range of error

values, though the median relative error was less than 2%. Uniform releases alone did not improve estimates of movement probabilities or fishing mortality rates, likely because sufficient sampling is required in all regions and times to detect movements. Additionally, spatially and temporally uniform releases decreased the number of releases in most months from region 3, which was an area of high sampling under the base scenario. The estimated natural mortality rate was nearly unbiased in all scenarios with the bias and RMSE decreasing with sample size. The model estimated natural mortality well regardless of the true value. In simulated stock assessment models, natural mortality estimates were slightly positively biased for the majority of species studied (Lee et al. 2011). Mortality rates can also become positively biased if there is emigration out of the system (Pine et al. 2011).

Movement rates were most accurately estimated when uniform releases were combined with uniform recapture effort, although the release structure had less of an effect than effort. A previous study also found that making recapture effort more spatially and temporally uniform can improve the accuracy of movement estimates (Ovaskainen et al. 2008). Conventional tags can underestimate movement distances when effort is not well distributed spatially, compared to electronic tags, likely because conventional tags rely directly on the fishery, rather than electronic monitors for detections (Bolle et al. 2005). Similarly, the lower movement rates (i.e. the further distances) may also be poorly estimated without enough fishing on the extremes of a stock's range. High intensity trapping in close proximity to the release area can negatively bias movement rate estimates by removing those individuals who might otherwise have undergone movement, essentially decreasing the sample size

(Yamamura et al. 2003). Our results show that there may be a similar effect in this model. The highest monthly fishing mortality rate ( $0.45 \text{ mo}^{-1}$ ) was in July in region 3, and in the base scenario the average median relative error of movement rates from region 3 from July-October (26%) was higher than from May-July (5%).

The model was unable to accurately estimate very low movement probabilities. When the true movement probability was  $<10^{-3}$ , median relative errors often exceeded 300-400% (Figure A.2.8-A.2.13). A much larger number of releases than used in our study is likely necessary to accurately estimate these low movement probabilities. For example, the true movement rate between regions 1 and 4 did not exceed  $10^{-5}$ , which would require at least 100,000 marked individuals in each region to expect at least one to move to the other region. Furthermore, low fishing effort in these regions would exacerbate the problem because individuals that did move would be unlikely to be captured. Making the effort more uniform increased effort in under-fished regions, and, consequently, increased the accuracy of estimates of low movement rates in the range of  $10^{-5}$  to  $10^{-3}$  (like movement from region 3 to 1 or region 4 to 2). Movement in the opposite direction, from region 1 to 3 or region 4 to 2, respectively, did not see quite the same improvement with uniform effort, likely because regions 2 and 3 already had high fishing effort.

Very low movement rates among subpopulations, which are critical for understanding speciation, biodiversity, and conservation, are often detected using genetic data rather than mark-recapture information (Hey and Nielsen 2004). One of the original objectives of the 1966-1969 Atlantic Menhaden mark-recapture study was to determine if there were two populations separated by Cape Hatteras (Dryfoos et al.

1973). Fish tagged north of Cape Hatteras were recaptured with high frequency in the south and vice versa, which confirmed that a single coast-wide population does exist, a finding that has since been supported by genetic studies (Anderson 2007; Lynch et al. 2010). However, under the base release size of about 1 million individuals, movement rates  $<10^{-3}$  were estimated with more than 200% median relative error, which increased to more than 600% in the uniform effort scenario. Therefore, models similar to the one we tested are incapable of reliably detecting “one individual every other generation” that keeps relatively isolated populations genetically coherent (Wright 1930).

Although making the releases and fishing effort more spatially and temporally uniform increased the accuracy and precision of the movement rate estimates in our study, it is often impractical to implement such a schedule in a real study. The Atlantic Menhaden fishery did not continue after October in the New England, New York, or New Jersey regions because the conditions became unfavorable for fishing and the fish more difficult to locate (Bigelow and Schroeder 1953; June 1961). Although increasing effort to 50 vessel weeks during the winter in the northernmost regions would help to accurately estimate Atlantic Menhaden movement and natural mortality, the recoveries are dependent on the reduction fishery and therefore constrained by their patterns of operation. Getting the broad spatial range of recaptures necessary to improve the movements of this mark-recapture model would likely necessitate strong participation from the fishery including fishing at times when they otherwise would not.

The number of tagged individuals should be scaled according to the goals of the study, the fishing mortality rates, and the detection probabilities. We simulated a very large number of releases to replicate the Atlantic Menhaden mark-recapture study from the 1960s. Accuracy generally increased with increased number of releases, and the scenarios with 2 million released individuals produced the most accurate and precise estimates of movement, natural mortality, and fishing mortality rates. The accuracy was still reasonably high when 1 million individuals were released, but decreased substantially for some movement rates when the releases were decreased to 500,000. Increasing the releases to 2 million individuals marginally improved movement estimates except for the lowest movement rates between regions 1 and 4. Large-scale studies are possible, but require a lot of planning and working with partners to implement. The U.S. Geological Survey has an ongoing bird banding study that has tagged nearly 40 million individuals across half a century, but most short term mark-recapture studies do not come close to a sample size of 420,000, the lowest release size across all our scenarios. Thus, studies that rely on dead recovery approaches to estimate movement appear to require large sample sizes. Dead recovery studies with sample sizes smaller than we simulated will likely not be able to estimate movement rates accurately, unless the geographic regions are defined such that there is a substantial ( $>0.1$ ) probability of moving between those regions for each time step. Movement rates  $>0.1$  were accurately estimated and largely unaffected by reductions in release size.

Other scenarios may be necessary to understand the dynamics and effectiveness of this estimation model. We may also assess the model performance by comparing the

Bayesian posterior distributions of parameter estimates against the values used to generate mark-recapture data. Dead recovery models can be used to accurately estimate movement and mortality if there is sufficient sampling and supplementary information on tag shedding and tag reporting or detection, which is frequently confounded with natural mortality (Hilborn 1990). Additionally, an effective mark-recapture study that estimates movement rates should have releases, recaptures, and quantitative fishing effort data in all regions and times and for the full range of the species or else movement to regions of low sampling may be misestimated (Hilborn 1990; Schwarz et al. 1993). Bias caused by low sampling may be present in our movement and mortality estimates from Chapter 1, although we accounted for the lack of fishing in all regions during the late fall and winter by estimating all movement between October and May as a single event. Uniform effort in all regions and months could increase accuracy of half-yearly movement rates. Because our estimation model has supplementary tag shedding and detection efficiency data necessary for an effective multi-state dead recovery mark recapture model and because we demonstrated that movement and mortality parameters are well estimated under the 1966-1969 mark recapture design, we can be confident of our findings.

*Tables and Figures*

TABLE 2.1. Data generating scenario with descriptions of release size, and release and effort structure. Variable effort structure was spatiotemporally heterogeneous according to the 1966-1969 Atlantic Menhaden fishery, and uniform effort was set to 50 vessel weeks in every time and region. Variable release structure was spatiotemporally heterogeneous according to the 1966-1969 Atlantic Menhaden mark-recapture study, and uniform release structure had 5,000 releases in every time and region.

Model	Release Size	Effort Structure	Release Structure
500K	533,179	Variable	Variable
500K + Effort	533,179	Uniform	Variable
500K + Release	420,000	Variable	Uniform
500K + Effort + Release	420,000	Uniform	Uniform
Base	1,066,357	Variable	Variable
Effort	1,066,357	Uniform	Variable
Release	840,000	Variable	Uniform
Effort + Release	840,000	Uniform	Uniform
2mil	2,132,714	Variable	Variable
2mil + Effort	2,132,714	Uniform	Variable
2mil + Release	1,680,000	Variable	Uniform
2mil + Effort + Release	1,680,000	Uniform	Uniform

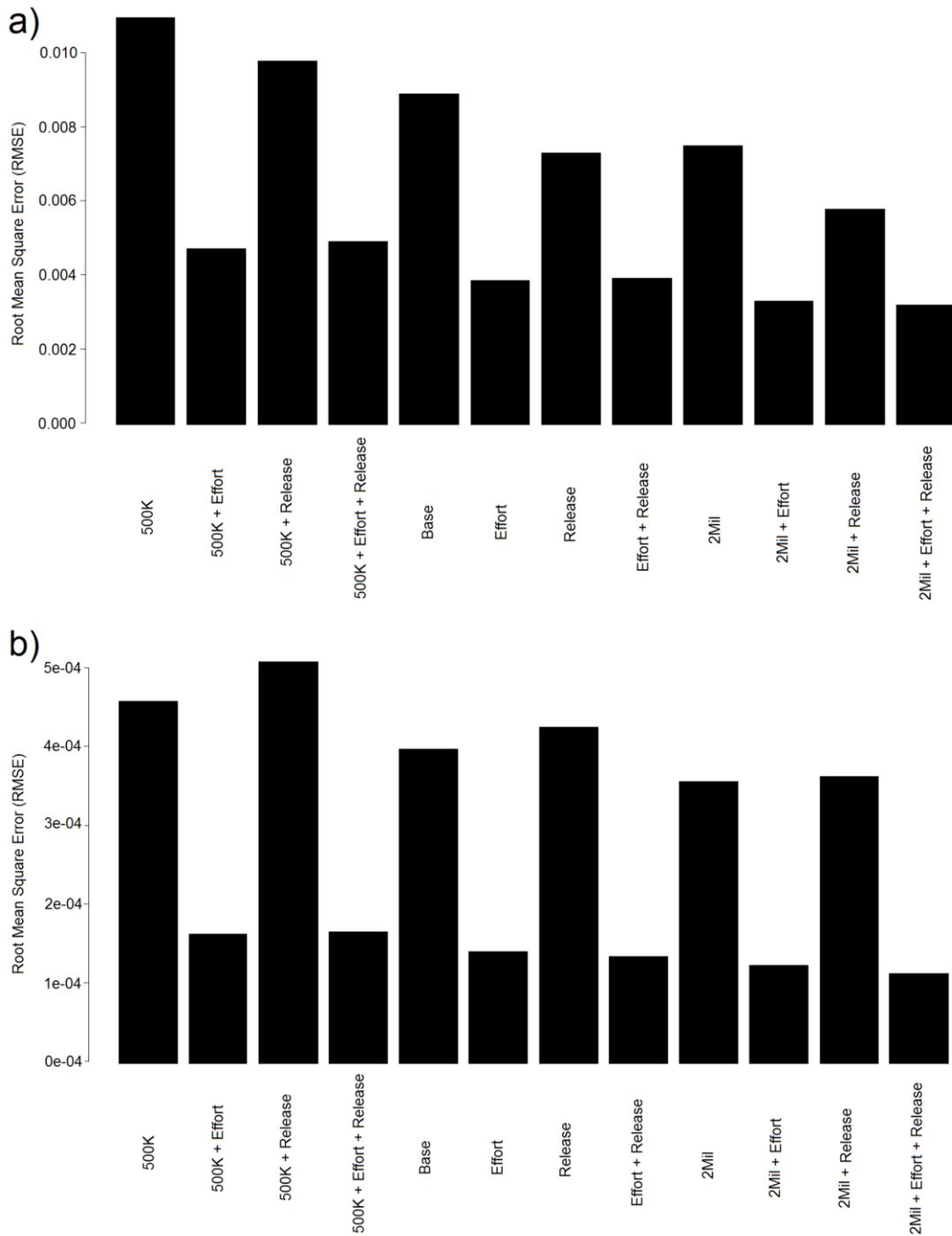


FIGURE 2.1. Total root mean squared error (RMSE) of estimated parameters of a) movement and b) catchability by scenario. A lower RMSE value indicates more accurate estimates.

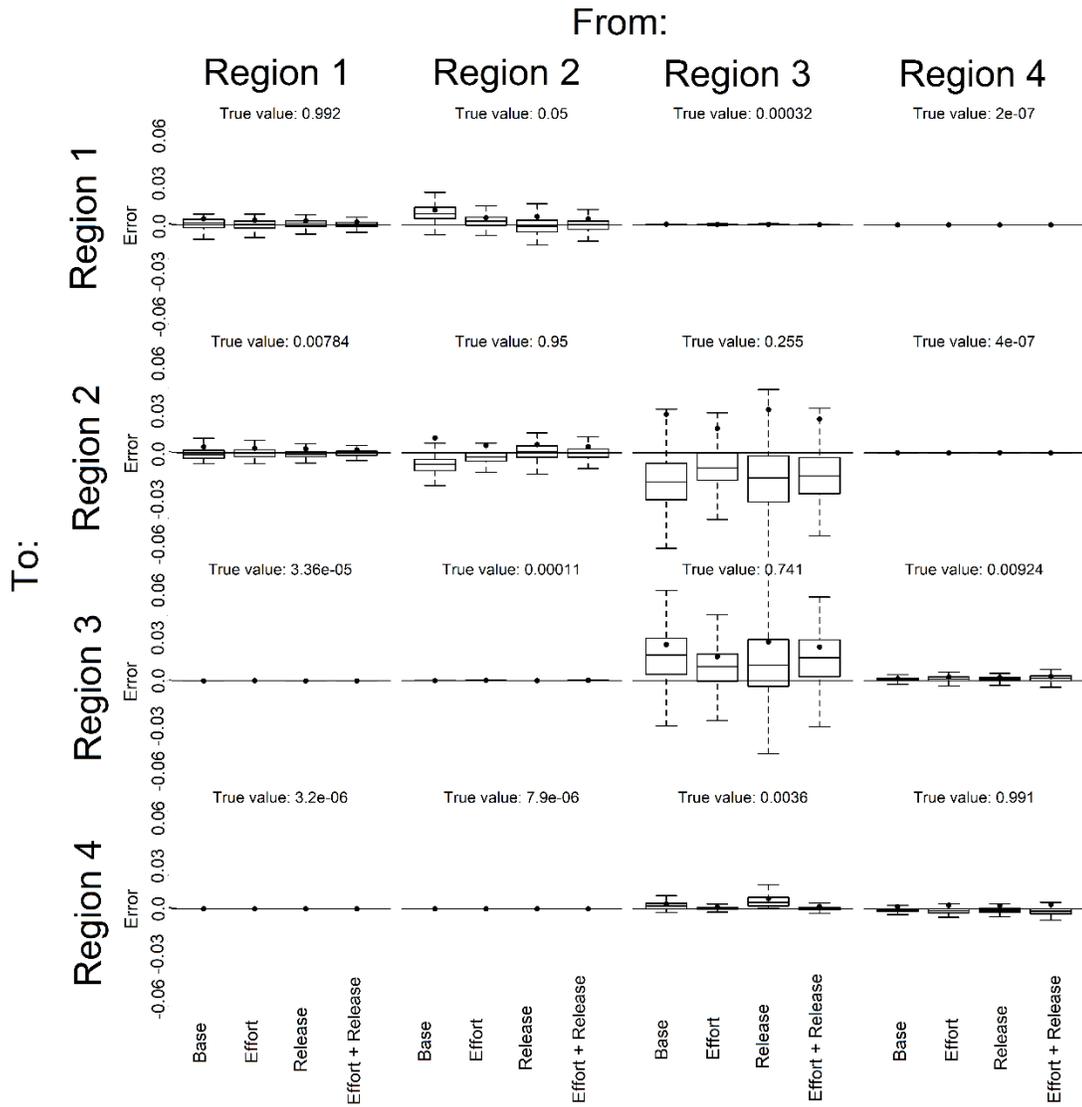


FIGURE 2.2. Box plots of errors (estimate-true value) of monthly movement rates from June to July for four scenarios of effort and release structure. See Table 2.1 for scenario definitions. The boxes represent the 25% and 75% quantiles, and the line in the center line indicates the median value. Whiskers indicate the 95% interval of error values and the points indicate the root mean squared error.

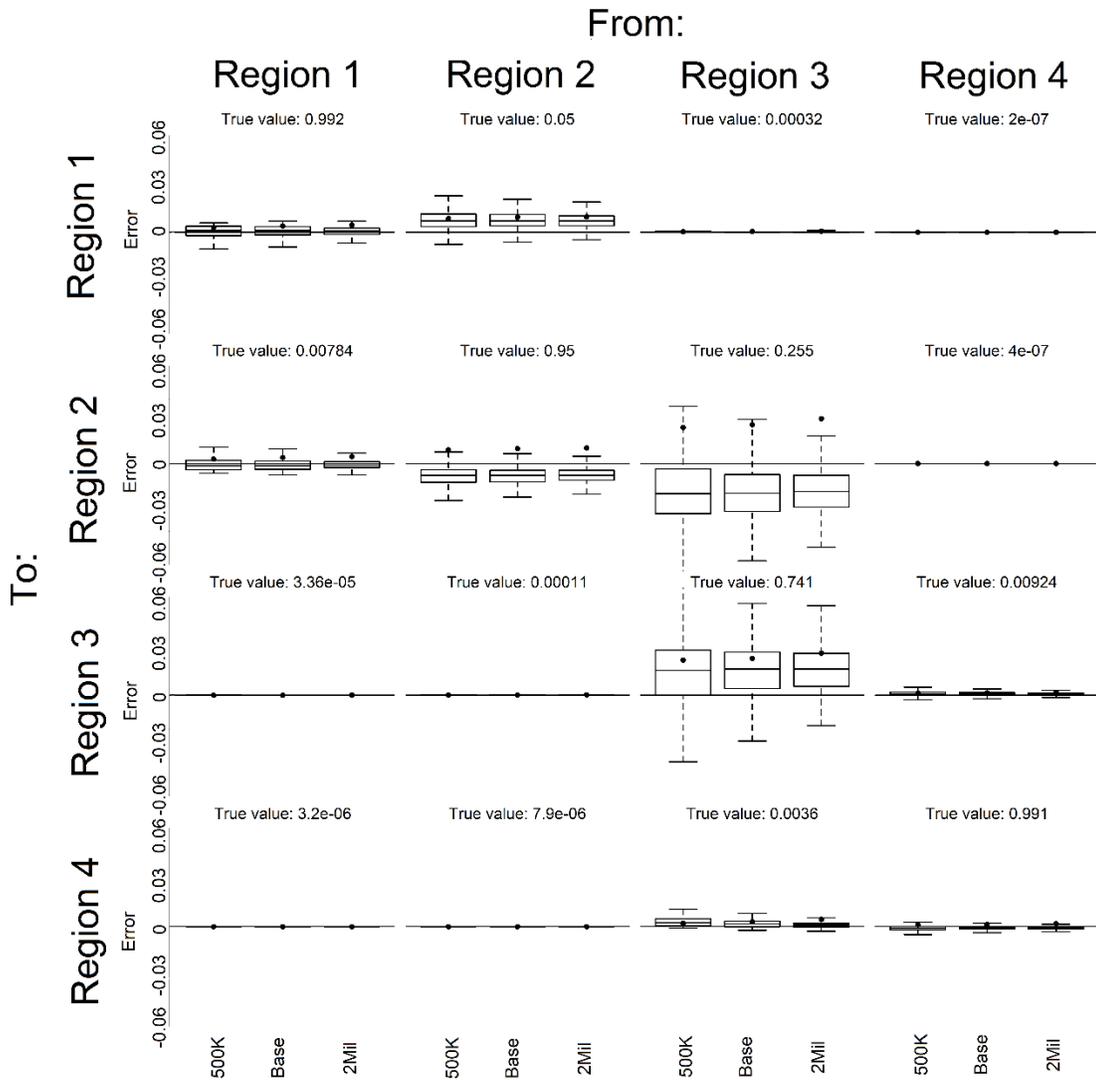


FIGURE 2.3. Box plots of errors (estimate-true value) of monthly movement parameters from June to July for three scenarios of release size. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure 2.2.

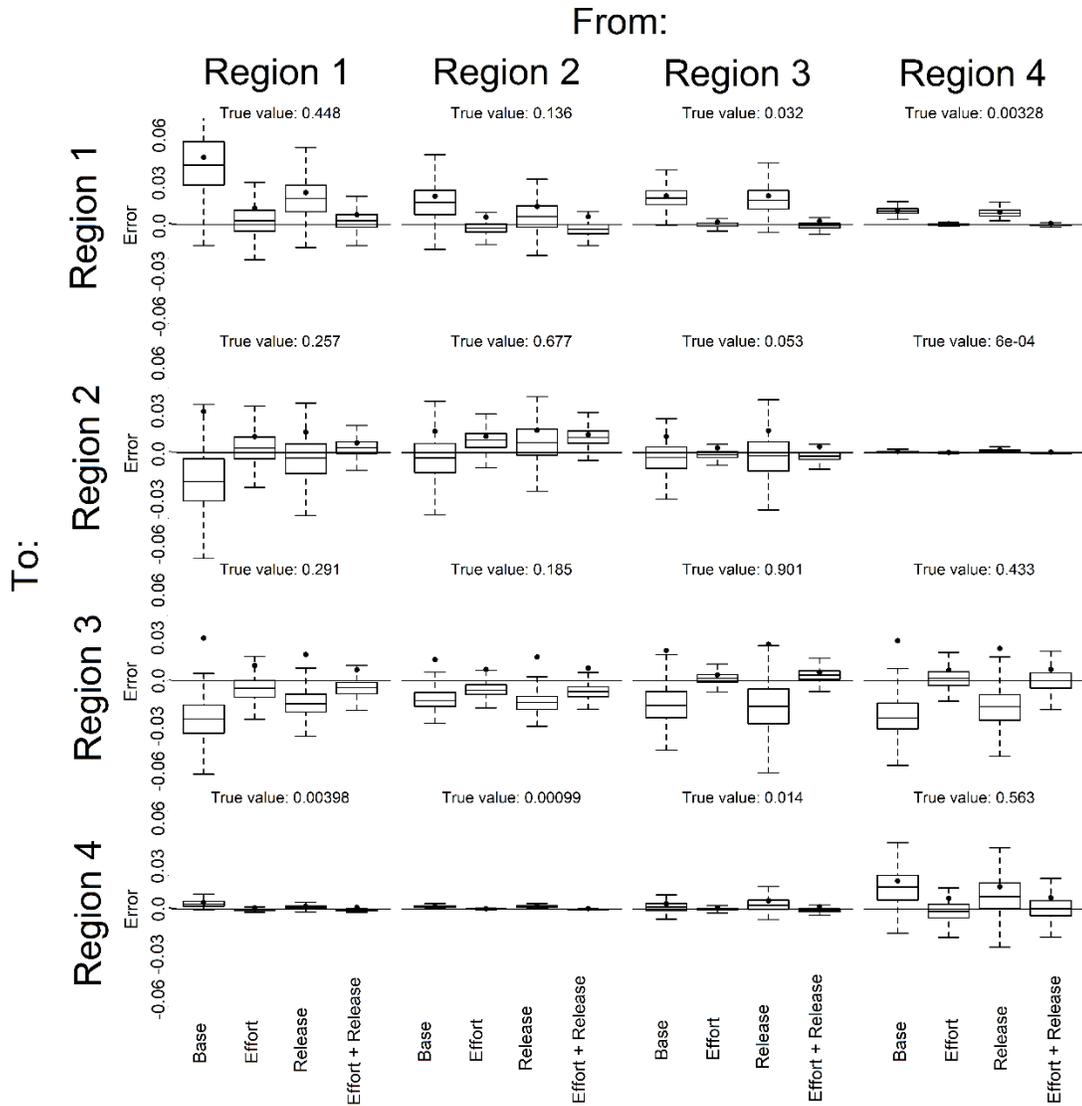


FIGURE 2.4. Box plots of errors (estimate-true value) of half year movement parameters from October to May for four scenarios of effort and release structure. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure 2.2.

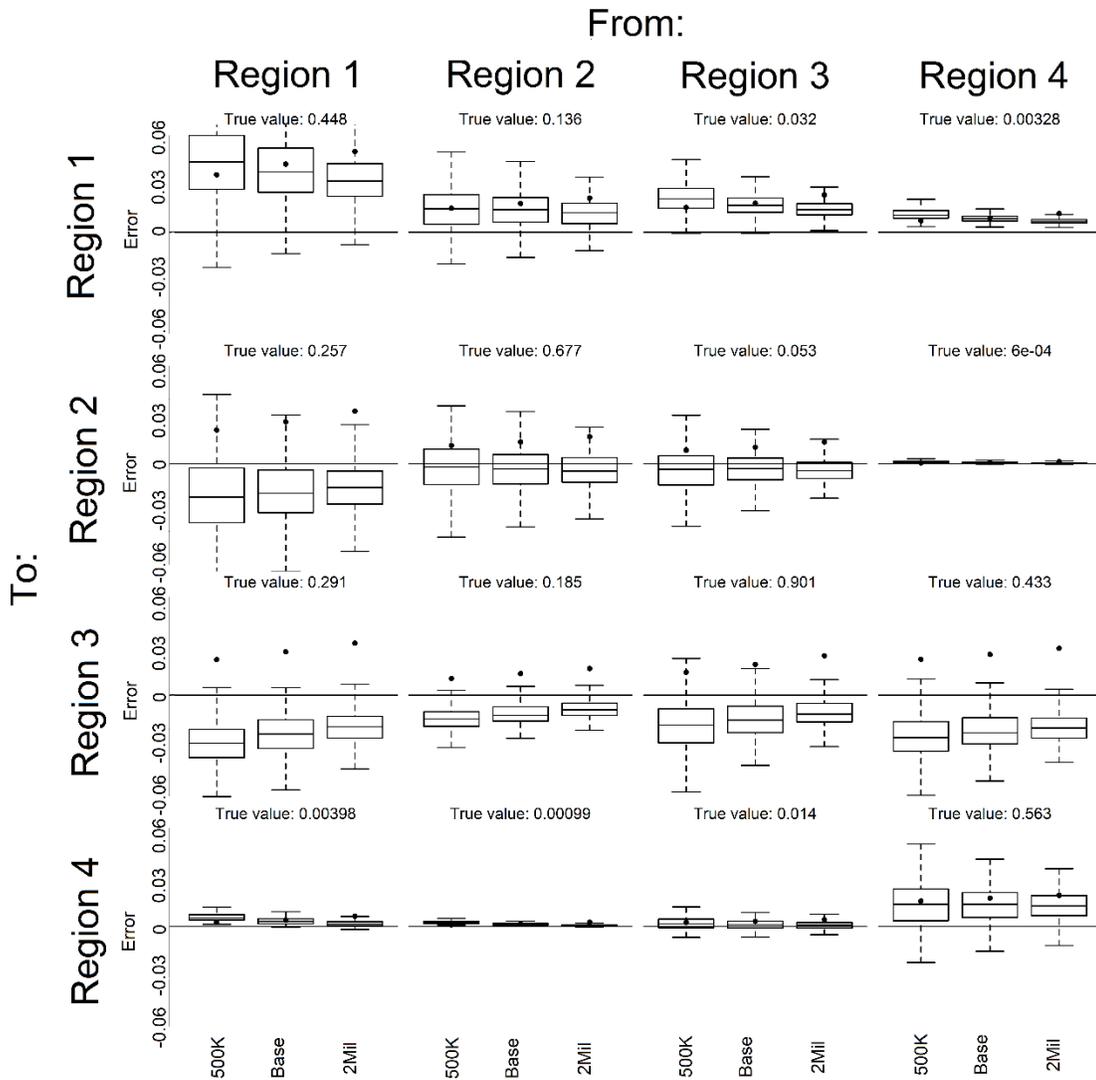


FIGURE 2.5. Box plots of errors (estimate-true value) of half year movement parameters from October to May for three scenarios of release size. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure 2.2.

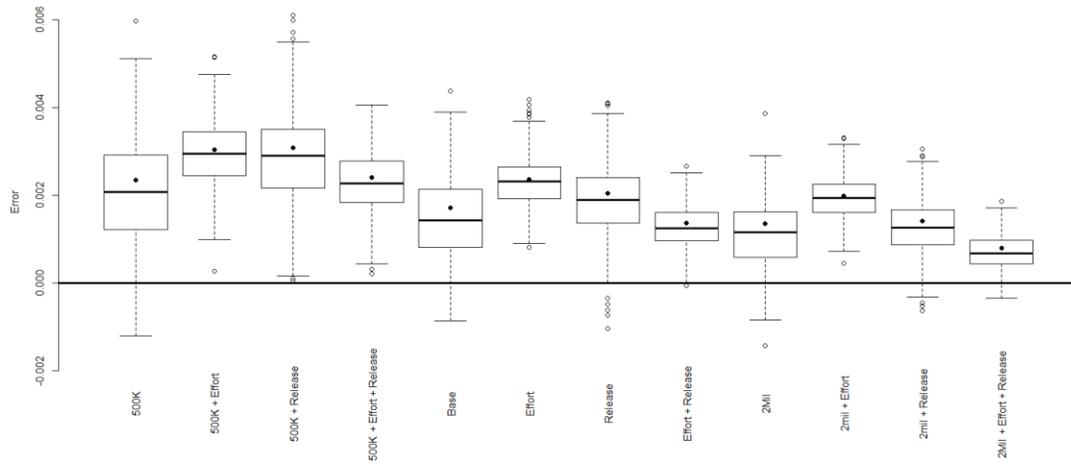


FIGURE 2.6. Box plots of errors (estimate-true value) of monthly natural mortality parameters for 12 scenarios of release size, and effort and release structure. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure 2.2.

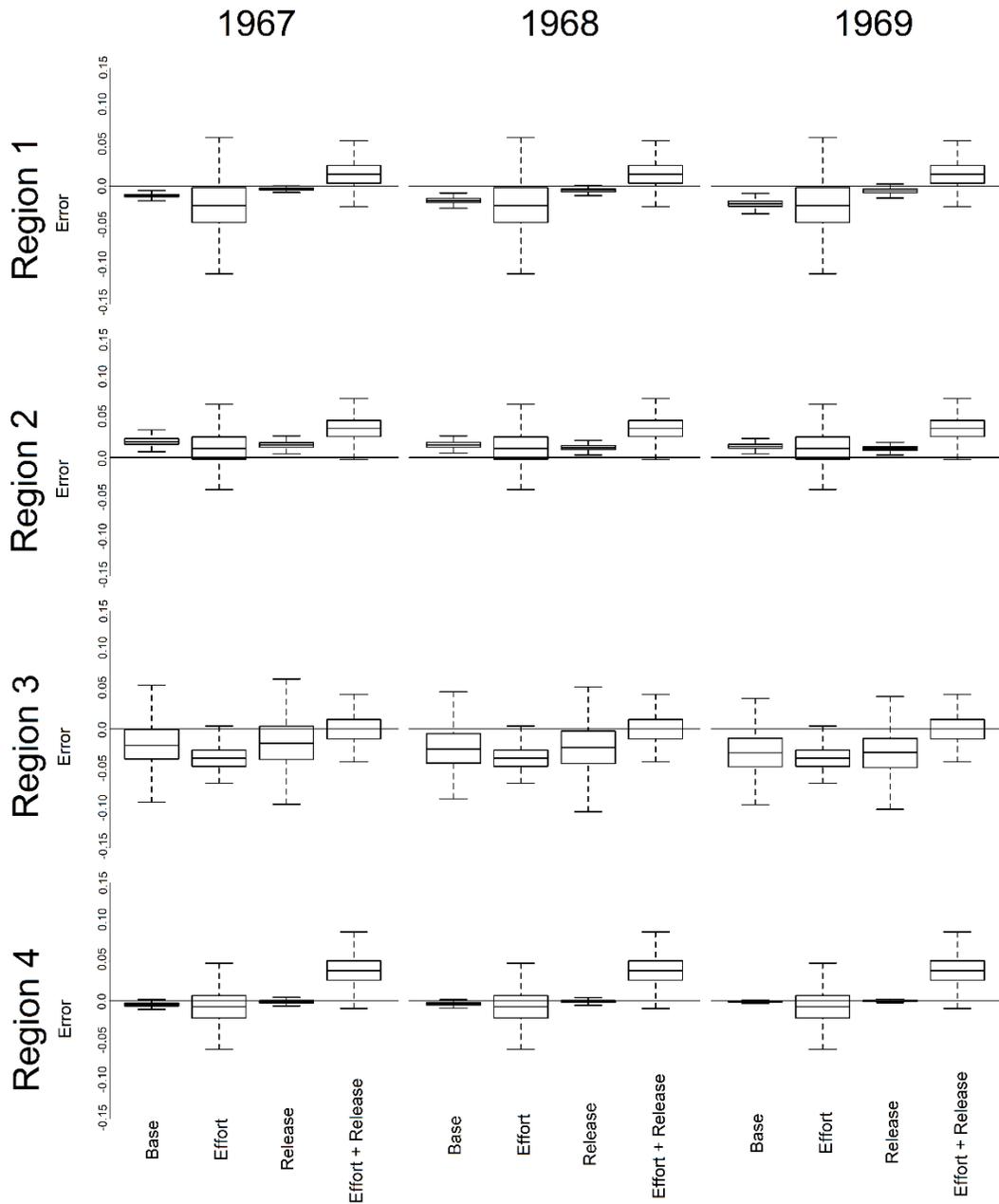


FIGURE 2.7. Box plots of errors (estimate-true value) of yearly fishing mortality by region and year for four scenarios of effort and release structure. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure 2.2.

## Appendix 1

TABLE A.1.1. Table showing how the month- and region-specific catchability parameters were estimated. Cells containing dashes indicate where no value was estimated because fishing effort was zero for all years of the study.

Month	Region 1	Region 2	Region 3	Region 4
Jan	--	--	$\exp(\theta_{14})$	--
Feb	--	--	--	--
Mar	--	--	--	--
Apr	--	--	$\exp(\theta_{15})$	$\exp(\theta_{23})$
May	$\exp(\theta_1)$	$\exp(\theta_7)$	$\exp(\theta_{16})$	$\exp(\theta_{24})$
Jun	$\exp(\theta_2)$	$\exp(\theta_8)$	$\exp(\theta_{17})$	$\exp(\theta_{25})$
Jul	1	1	1	1
Aug	$\exp(\theta_3)$	$\exp(\theta_9)$	$\exp(\theta_{18})$	$\exp(\theta_{26})$
Sep	$\exp(\theta_4)$	$\exp(\theta_{10})$	$\exp(\theta_{19})$	$\exp(\theta_{27})$
Oct	$\exp(\theta_5)$	$\exp(\theta_{11})$	$\exp(\theta_{20})$	$\exp(\theta_{28})$
Nov	$\exp(\theta_6)$	$\exp(\theta_{12})$	$\exp(\theta_{21})$	$\exp(\theta_{29})$
Dec	--	$\exp(\theta_{13})$	$\exp(\theta_{22})$	--

TABLE A.1.2. Number of tagged Atlantic Menhaden released by year and region.

Year	Region				Total
	1	2	3	4	
1966	0	0	88,989	0	88,989
1967	15,753	100,128	159,077	95,832	370,790
1968	24,159	132,596	109,120	118,819	384,694
1969	9,168	75,581	29,076	108,150	221,975
Total	49,080	308,305	386,262	322,801	1,066,448

TABLE A.1.3. Number of recovered tags by year and region.

Year	Region				Total
	1	2	3	4	
1966	0	0	4,836	0	4,836
1967	1,101	7,295	20,614	1,678	30,688
1968	5,789	13,696	19,013	2,871	41,369
1969	2,016	3,436	6,147	624	12,223
Total	8,906	24,427	50,610	5,173	89,116

TABLE A.1.4. Fishing effort (in vessel weeks) by year and region. Note that the 1966 values only include effort during July-December.

Year	Region				Total
	1	2	3	4	
1966	92	687	318	75	1,172
1967	88	429	209	24	750
1968	115	499	324	57	995
1969	135	428	236	29	828
Total	430	2,043	1,087	185	3,745

TABLE A.1.5. Number of tagged Atlantic Menhaden released in 1966 by month and region.

Month	Region				Total
	1	2	3	4	
July	0	0	11,141	0	11,141
August	0	0	34,322	0	34,322
September	0	0	23,744	0	23,744
October	0	0	5,699	0	5,699
November	0	0	996	0	996
December	0	0	12,996	0	12,996
Total	0	0	88,898	0	88,898

TABLE A.1.6. Number of tagged Atlantic Menhaden released in 1967 by month and region.

Month	Region				Total
	1	2	3	4	
January	0	0	7,729	0	7,729
February	0	0	0	0	0
March	0	0	664	0	664
April	0	1,250	588	5,879	7,717
May	0	14,510	8,614	15,395	38,519
June	2,286	21,343	10,284	5,400	39,313
July	1,575	19,873	25,276	9,078	55,802
August	9,078	23,293	38,113	30,274	100,758
September	2,245	8,113	10,378	16,705	37,441
October	569	10,649	18,531	13,101	42,850
November	0	1,098	22,680	0	23,778
December	0	0	16,240	0	16,240
Total	15,753	100,129	159,097	95,832	370,811

TABLE A.1.7. Number of tagged Atlantic Menhaden released in 1968 by month and region.

Month	Region				Total
	1	2	3	4	
January	0	0	0	0	0
February	0	0	37	0	37
March	0	0	1,022	0	1,022
April	0	14,915	4,420	22,520	41,855
May	331	12,557	20,132	27,401	60,421
June	5,810	36,052	30,065	16,789	88,716
July	10,907	35,433	24,463	21,262	92,065
August	4,022	9,639	17,086	22,016	52,763
September	2,100	13,592	6,258	4,109	26,059
October	989	10,408	0	4,198	15,595
November	0	0	200	0	200
December	0	0	5,437	524	5,961
Total	24,159	132,596	109,120	118,819	384,694

TABLE A.1.8. Number of tagged Atlantic Menhaden released in 1969 by month and region.

Month	Region				Total
	1	2	3	4	
January	0	0	1,300	0	1,300
February	0	0	0	0	0
March	0	0	0	0	0
April	0	1,599	519	9,100	11,218
May	1,700	9,484	1,641	14,698	27,523
June	2,431	3,539	1,654	20,897	28,521
July	3,960	23,525	11,077	14,070	52,632
August	1,077	8,625	5,126	20,799	35,627
September	0	13,264	4,070	19,100	36,434
October	0	14,445	598	2,100	17,143
November	0	1,100	3,091	7386	11,577
December	0	0	0	0	0
Total	9,168	75,581	29,076	108,150	221,975

Table A.1.9. Age and length distributions from the subset of individuals measured.

Age	Count	Length(cm)	Count
0	101	0.0-4.9	33
1	7,850	5.0-9.9	3
2	3,544	10.0-14.9	32
3	386	15.0-19.9	11,780
4+	8	20.0-24.9	21,557
		25.0-29.9	13,654
		30.0-34.9	4,821
		35.0+	2,679
Sum	11,889	Sum	54,559

Table A.1.10. The number of individuals measured for length information by month/year and region.

Month/Year	Region 1	Region 2	Region 3	Region 4
Jul-66	0	0	0	0
Aug-66	0	0	0	0
Sep-66	0	0	0	0
Oct-66	0	0	0	0
Nov-66	0	0	0	0
Dec-66	0	0	788	0
Jan-67	0	0	0	0
Feb-67	0	0	0	0
Mar-67	0	0	0	0
Apr-67	0	66	0	295
May-67	0	701	369	748
Jun-67	0	965	508	260
Jul-67	0	968	1,274	409
Aug-67	0	1,079	1,485	1,295
Sep-67	0	405	496	210
Oct-67	0	5	21	0
Nov-67	0	0	0	0
Dec-67	0	0	0	0
Jan-68	0	0	0	0
Feb-68	0	0	0	0
Mar-68	0	0	0	0
Apr-68	0	324	0	1,218
May-68	0	452	0	781
Jun-68	0	3,227	0	758
Jul-68	0	3,441	0	667
Aug-68	0	937	0	486
Sep-68	0	1,538	0	0
Oct-68	0	99	0	0
Nov-68	0	0	0	0
Dec-68	0	0	0	0
Jan-69	0	0	40	0
Feb-69	0	0	0	0
Mar-69	0	0	0	0
Apr-69	0	134	363	357
May-69	417	1,428	527	819
Jun-69	620	1,504	502	1,011

Jul-69	985	2,419	3,207	813
Aug-69	271	1,950	1,281	1,664
Sep-69	0	1,163	1,011	1,205
Oct-69	0	864	146	57
Nov-69	0	21	2,770	702
Dec-69	0	0	0	0

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Table A.1.11. The number of individuals measured for age information by month/year and region.

Month/Year	Region 1	Region 2	Region 3	Region 4
Jul-66	0	0	0	0
Aug-66	0	0	0	0
Sep-66	0	0	0	0
Oct-66	0	0	0	0
Nov-66	0	0	0	0
Dec-66	0	0	2	0
Jan-67	0	0	0	0
Feb-67	0	0	0	0
Mar-67	0	0	0	0
Apr-67	0	54	0	260
May-67	0	620	338	627
Jun-67	0	839	441	229
Jul-67	0	876	1,073	348
Aug-67	0	1,003	1,235	1,175
Sep-67	0	377	427	165
Oct-67	0	5	19	0
Nov-67	0	0	0	0
Dec-67	0	0	0	0
Jan-68	0	0	0	0
Feb-68	0	0	0	0
Mar-68	0	0	0	0
Apr-68	0	0	0	1
May-68	0	0	0	0
Jun-68	0	0	0	0
Jul-68	0	1	0	2
Aug-68	0	0	0	1
Sep-68	0	1	0	0
Oct-68	0	0	0	0
Nov-68	0	0	0	0
Dec-68	0	0	0	0
Jan-69	0	0	0	0
Feb-69	0	0	0	0
Mar-69	0	0	0	0
Apr-69	0	0	0	149
May-69	0	0	0	204
Jun-69	0	0	18	442

Jul-69	0	1	131	382
Aug-69	0	0	117	227
Sep-69	0	0	71	0
Oct-69	0	2	19	0
Nov-69	0	0	7	0
Dec-69	0	0	0	0

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TABLE A.1.12. Prior monthly movement probability, based on diffusion from the center point of the initial region.  $\varphi_{i,j}$  is the movement probability from region j to region i during one month, and is dependent on  $d_r$  the distance between the northern border of region  $r$  and 26°02'N, and the variance  $\sigma_w$ .

Prior	Value
$\varphi_{1,1}$	$\int_{-\frac{d_1-d_2}{2}}^{\infty} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$
$\varphi_{1,2}$	$\int_{-\frac{d_1-d_2}{2}-(d_2-d_3)}^{\frac{d_1-d_2}{2}} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$
$\varphi_{1,3}$	$\int_{-\frac{d_1-d_2}{2}-(d_2-d_4)}^{\frac{d_1-d_2}{2}-(d_2-d_3)} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$
$\varphi_{1,4}$	$\int_{-\infty}^{\frac{d_1-d_2}{2}-(d_2-d_4)} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$
$\varphi_{2,1}$	$\int_{\frac{d_2-d_3}{2}}^{\infty} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$
$\varphi_{2,2}$	$\int_{\frac{d_2-d_3}{2}}^{\frac{d_2-d_3}{2}} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$
$\varphi_{2,3}$	$\int_{-\frac{d_2-d_3}{2}-(d_3-d_4)}^{\frac{d_2-d_3}{2}} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$
$\varphi_{2,4}$	$\int_{-\infty}^{\frac{d_2-d_3}{2}-(d_3-d_4)} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$
$\varphi_{3,1}$	$\int_{\frac{d_3-d_4}{2}+(d_2-d_3)}^{\infty} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$
$\varphi_{3,2}$	$\int_{\frac{d_3-d_4}{2}}^{\frac{d_3-d_4}{2}+(d_2-d_3)} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$

$$\varphi_{3,3} = \frac{\frac{d_3-d_4}{2}}{\frac{d_3-d_4}{2}} \int_{\frac{d_3-d_4}{2}}^{\frac{d_3-d_4}{2}} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$$

$$\varphi_{3,4} = \int_{-\infty}^{\frac{d_3-d_4}{2}} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$$

$$\varphi_{4,1} = \int_{\frac{d_4+(d_2-d_4)}{2}}^{\infty} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$$

$$\varphi_{4,2} = \int_{\frac{d_4+(d_3-d_4)}{2}}^{\frac{d_4+(d_2-d_4)}{2}} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$$

$$\varphi_{4,3} = \int_{\frac{d_4}{2}}^{\frac{d_4+(d_2-d_4)}{2}} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$$

$$\varphi_{4,4} = \int_{-\infty}^{\frac{d_4}{2}} \frac{1}{\sqrt{2\sigma_w^2\pi}} e^{-\frac{x^2}{2\sigma_w^2}} dx$$

TABLE A.1.13. Movement probability parameter estimates

**MEAN**

May - June

From →

To ↓	Region 1	Region 2	Region 3	Region 4
Region 1	0.992008	0.051343	0.045995	1.83E-07
Region 2	0.007904	0.94844	0.86162	4.09E-07
Region 3	8.55E-05	0.000208	0.072494	0.029472
Region 4	2.42E-06	9.12E-06	0.019891	0.970527

June - July

From →

To ↓	Region 1	Region 2	Region 3	Region 4
Region 1	0.99212	0.050015	0.000322	2.44E-07
Region 2	0.007843	0.949863	0.254607	4.36E-07
Region 3	3.36E-05	0.000114	0.741467	0.009243
Region 4	3.18E-06	7.91E-06	0.003605	0.990757

July - August

From →

To ↓	Region 1	Region 2	Region 3	Region 4
Region 1	0.998716	0.007429	0.000214	5.97E-08
Region 2	0.001256	0.992455	0.010877	7.44E-07
Region 3	2.46E-05	0.000109	0.987133	0.007088
Region 4	3.63E-06	6.94E-06	0.001775	0.992911

August - September

From →

To ↓	Region 1	Region 2	Region 3	Region 4
Region 1	0.997118	0.017408	0.000271	1.46E-07
Region 2	0.002845	0.98241	0.01324	2.84E-07
Region 3	3.40E-05	0.000173	0.984928	0.002227
Region 4	2.98E-06	8.83E-06	0.001561	0.997772

September - October

From →

To ↓	Region 1	Region 2	Region 3	Region 4
Region 1	0.986011	0.020733	0.000577	5.59E-07
Region 2	0.01389	0.978727	0.013898	2.78E-07
Region 3	9.75E-05	0.000524	0.982755	0.000611
Region 4	1.43E-06	1.57E-05	0.002769	0.999388

October - May

From →

To ↓	Region 1	Region 2	Region 3	Region 4
Region 1	0.448107	0.136474	0.032295	0.003284
Region 2	0.257143	0.677331	0.052718	0.0006
Region 3	0.290774	0.185207	0.900644	0.432632
Region 4	0.003976	0.000988	0.014343	0.563484

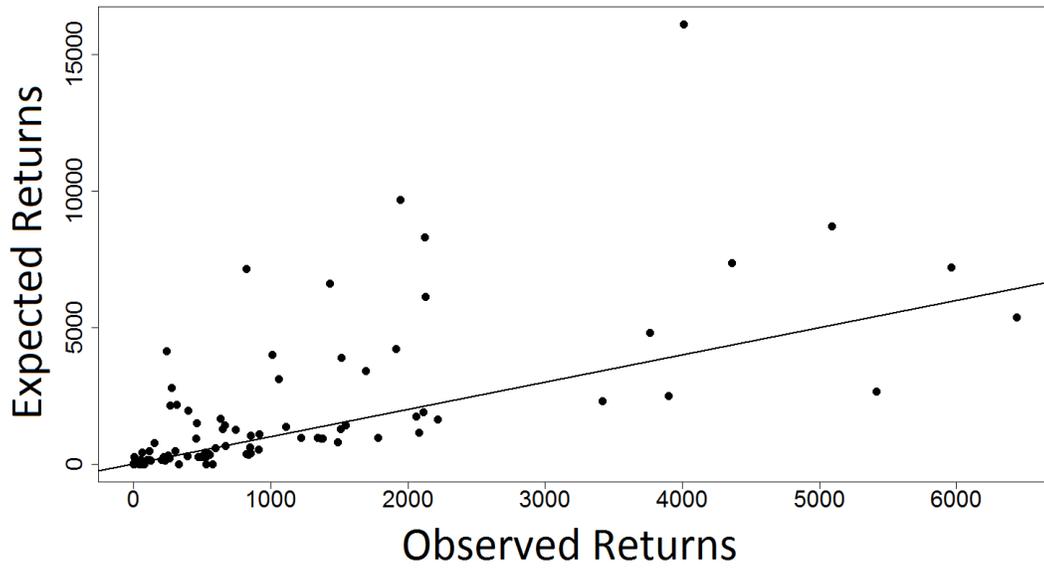


FIGURE A.1.1. Observed returns versus model predictions.

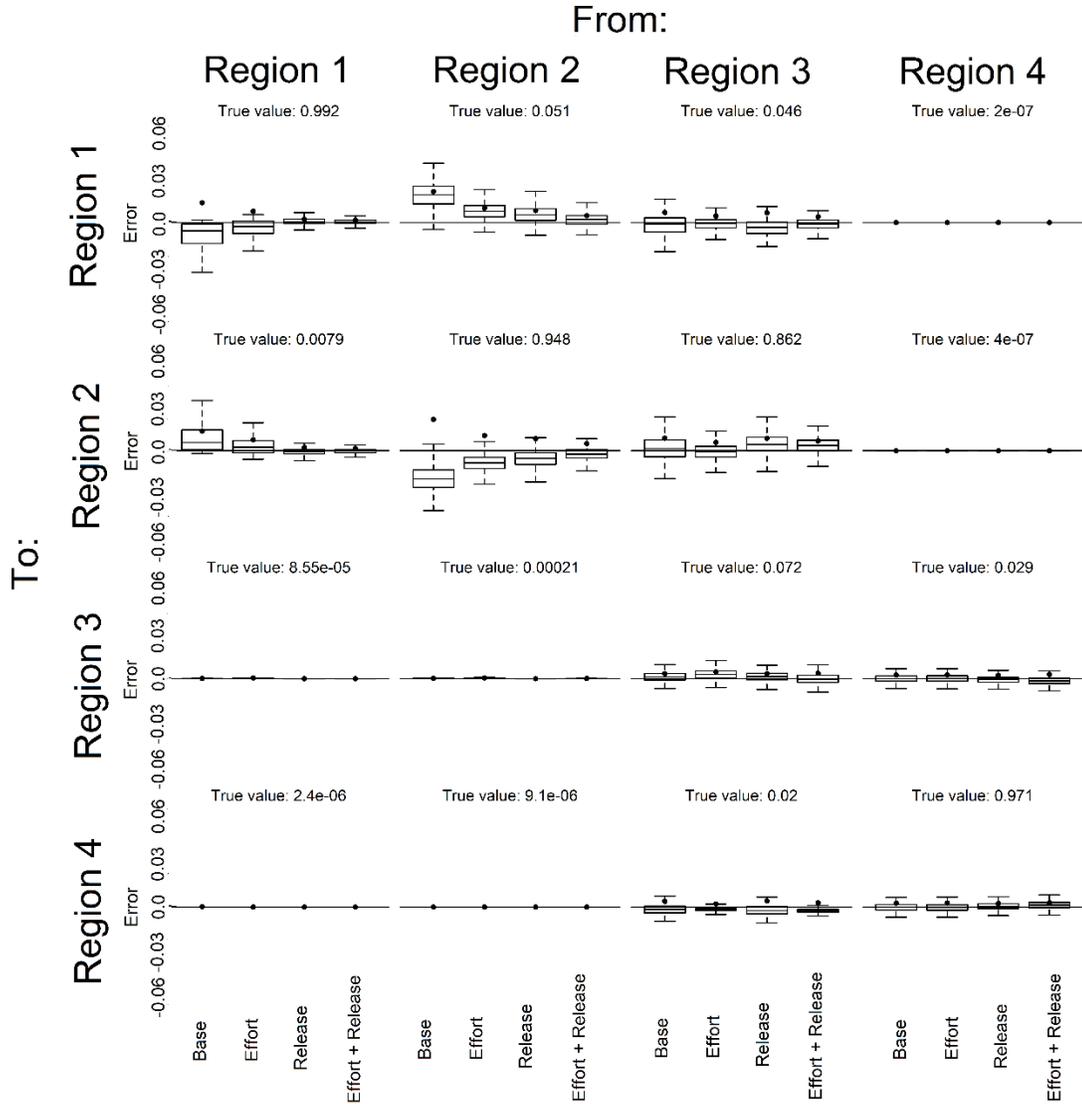


FIGURE A.2.1. Box plots of errors (estimate-true value) of monthly movement parameters from May to June for four scenarios of effort and release structure. See Table 2.1 for scenario definitions. The boxes represent the 25% and 75% quantiles, and the line in the center line indicates the median value. Whiskers indicate the 95% interval of error values and the points indicate the root mean squared error.

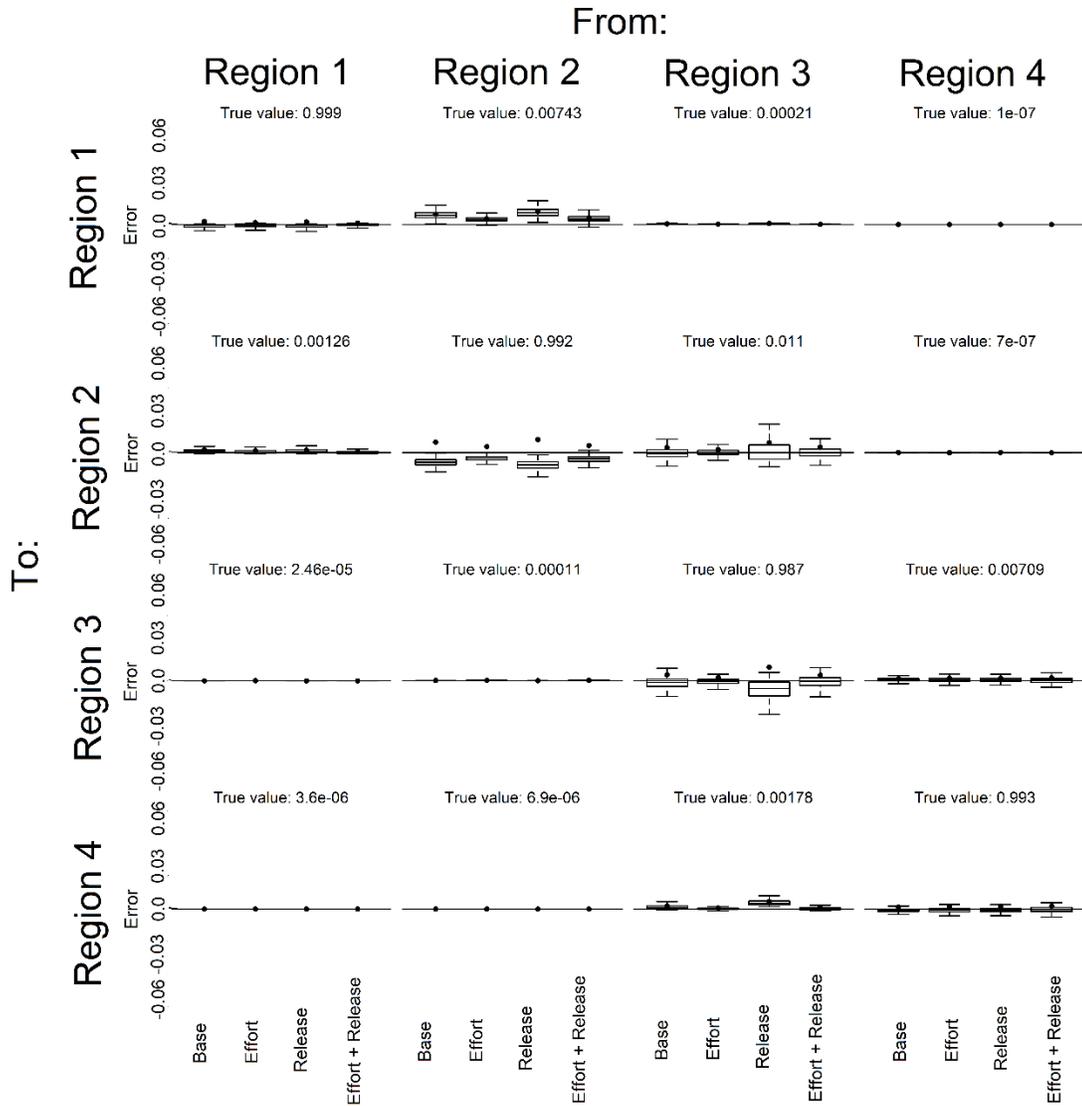


FIGURE A.2.2. Box plots of errors (estimate-true value) of monthly movement parameters from July to August for four scenarios of effort and release structure. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

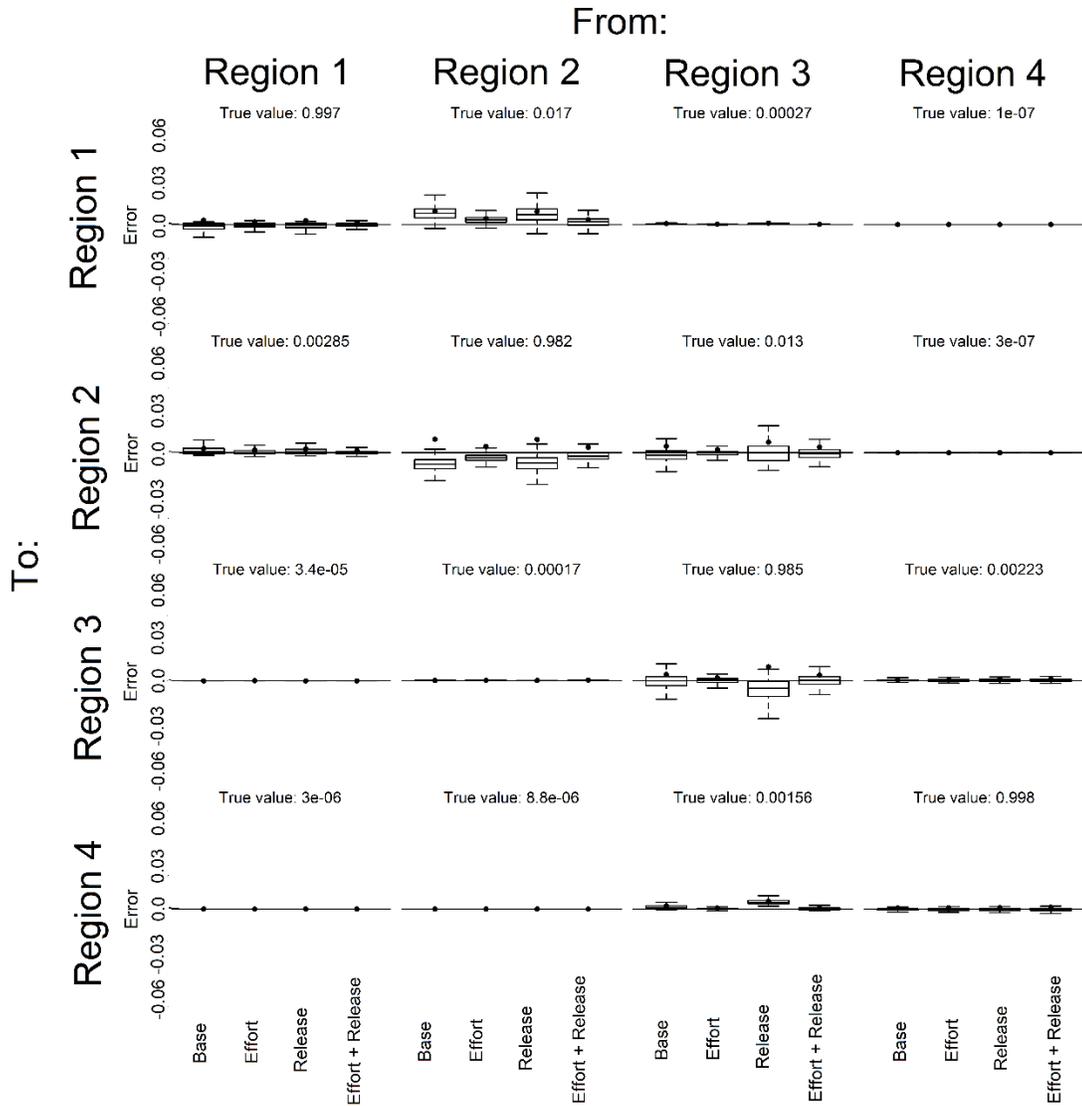


FIGURE A.2.3. Box plots of errors (estimate-true value) of monthly movement parameters from August to September for four scenarios of effort and release structure. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

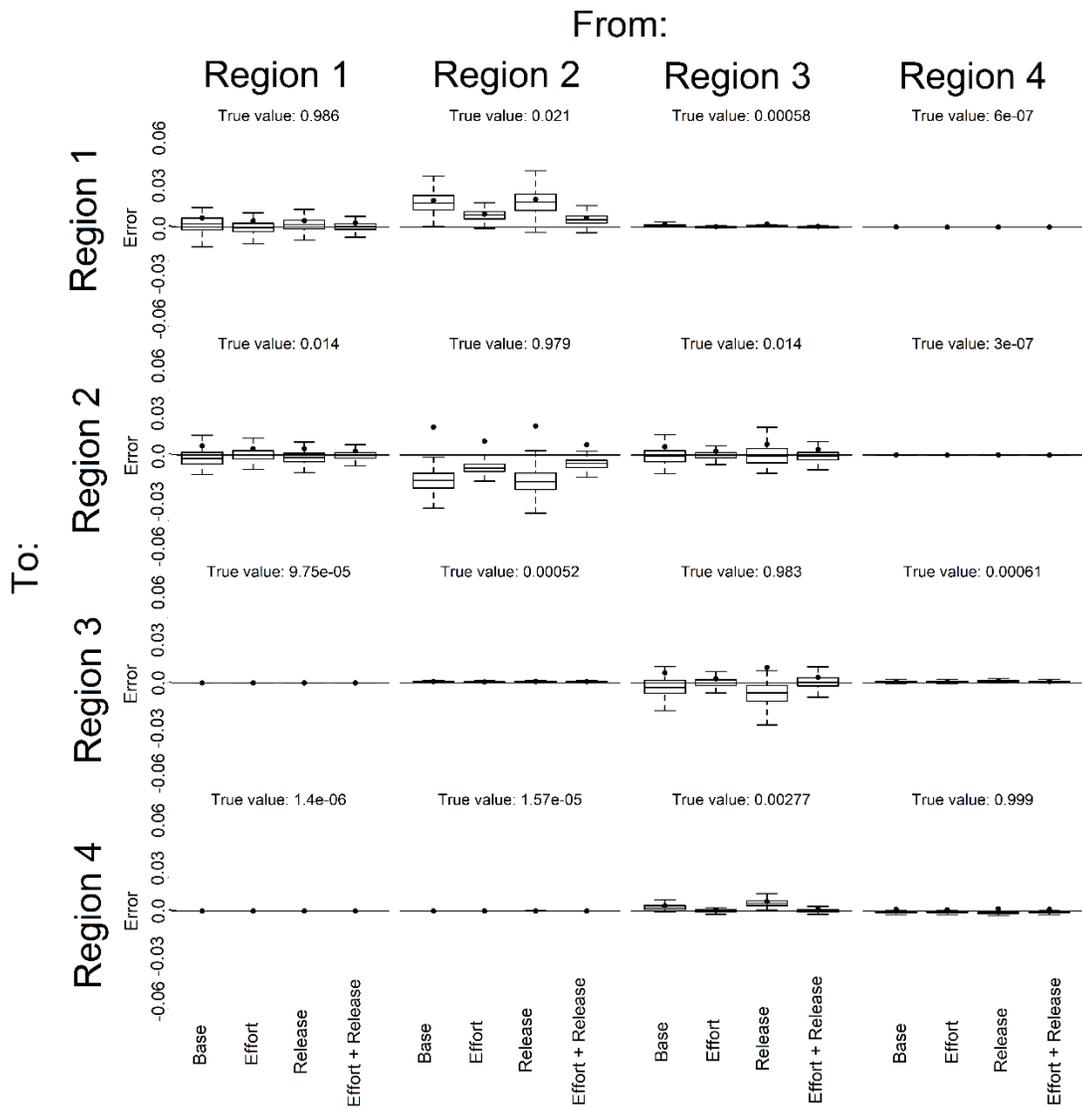


FIGURE A.2.4. Box plots of errors (estimate-true value) of monthly movement parameters from September to October for four scenarios of effort and release structure. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

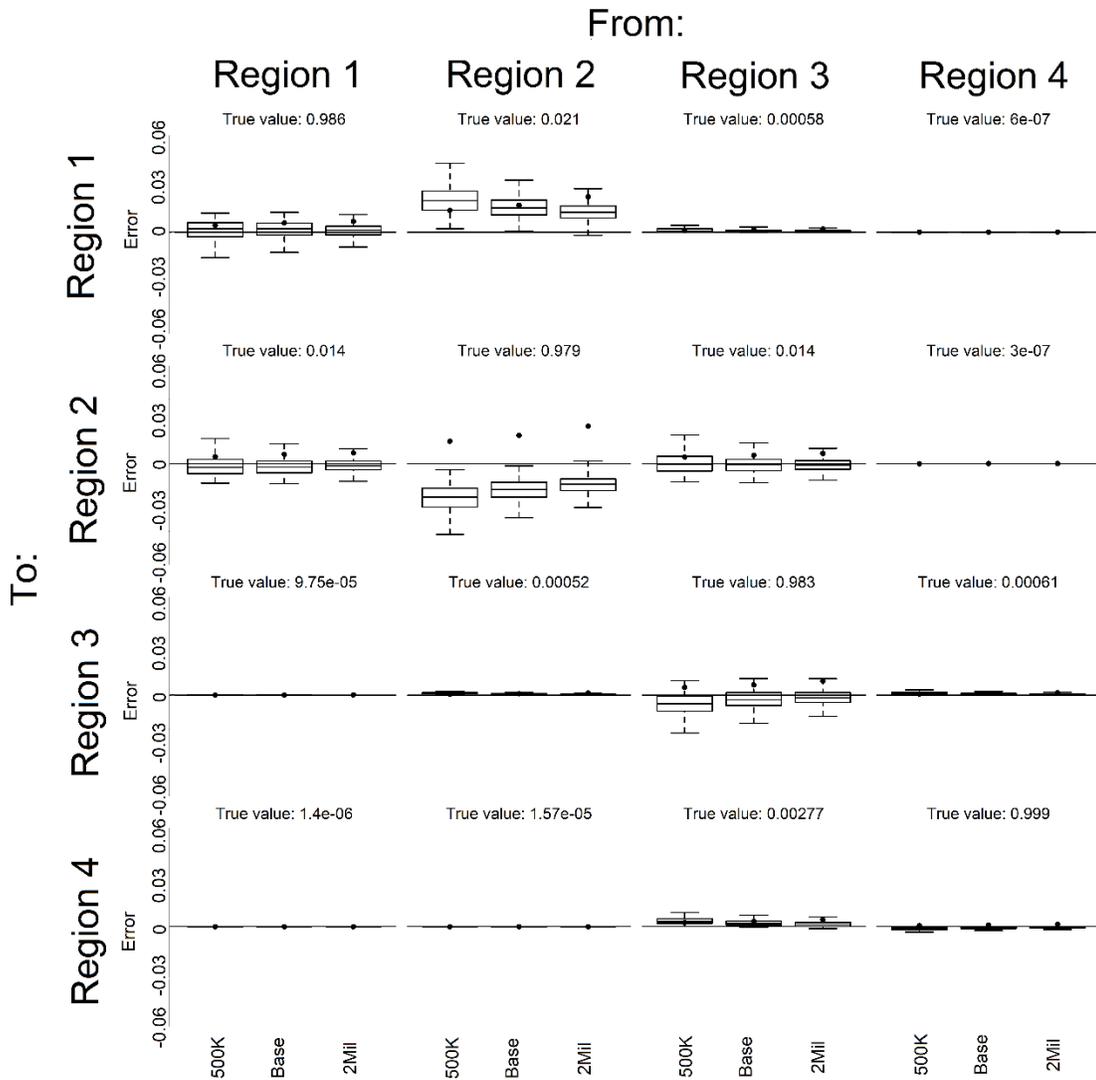


FIGURE A.2.5. Box plots of errors (estimate-true value) of monthly movement parameters from May to June for three scenarios of release size. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

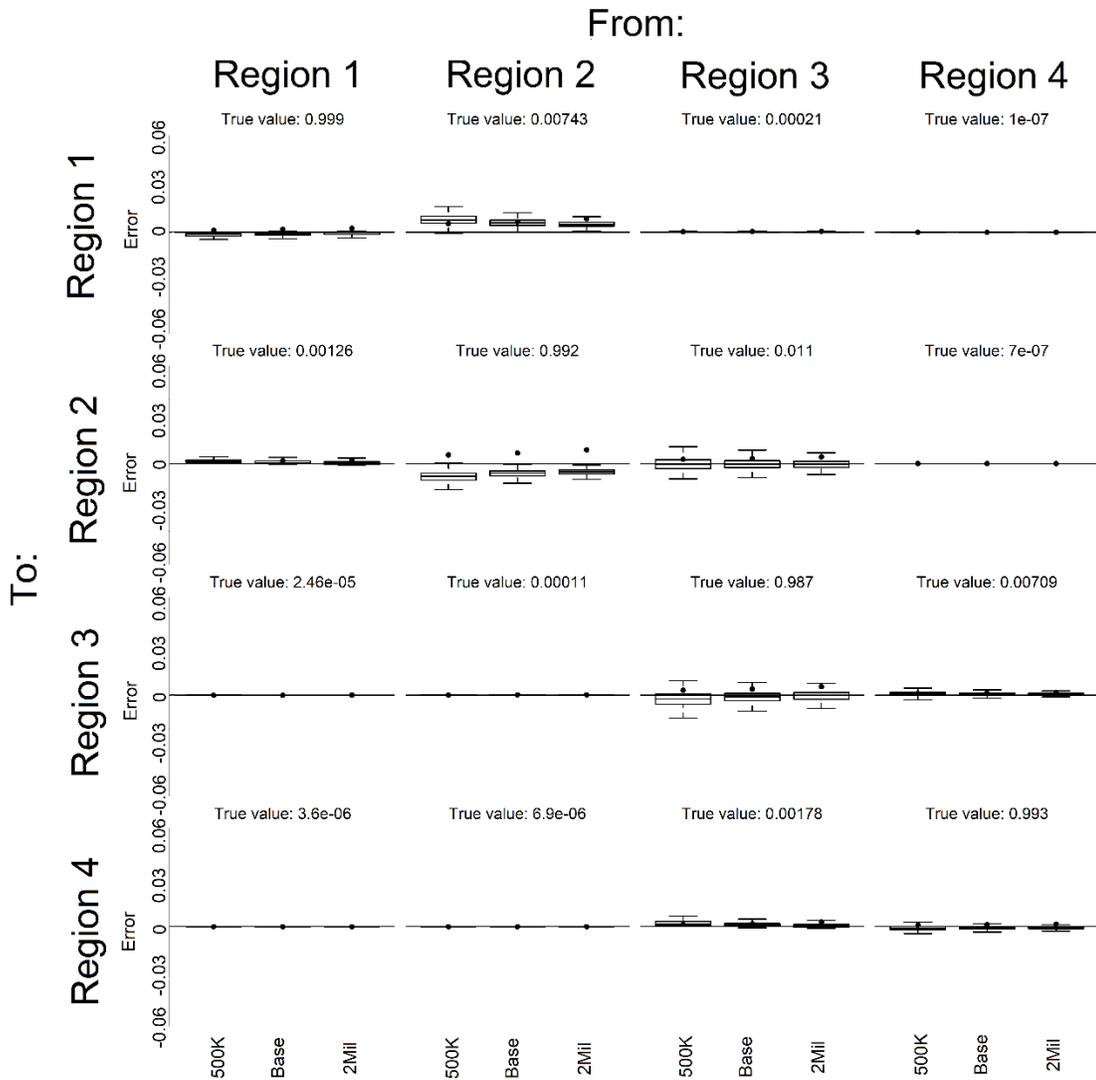


FIGURE A.2.5. Box plots of errors (estimate-true value) of monthly movement parameters from July to August for three scenarios of release size. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

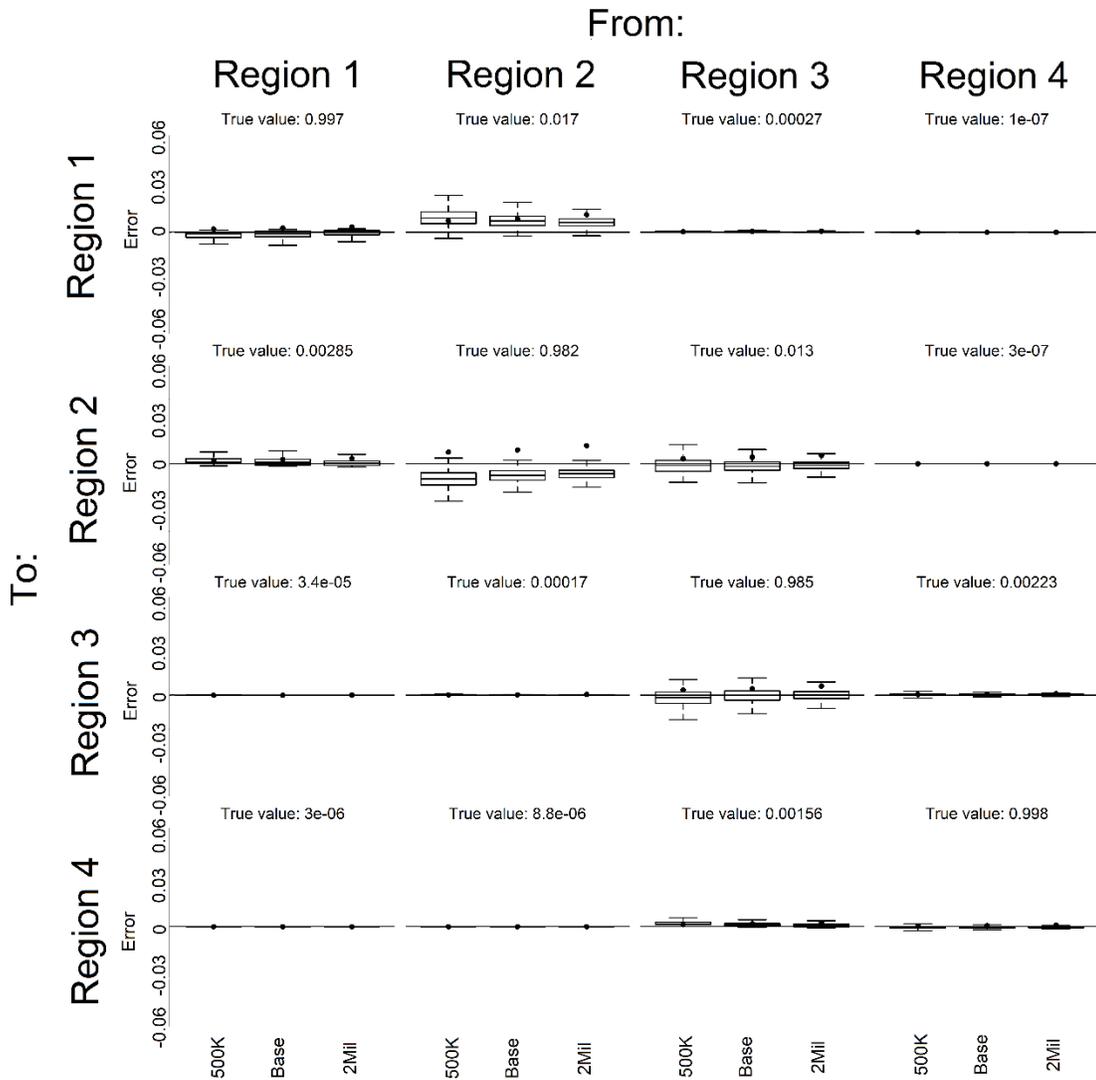


FIGURE A.2.6. Box plots of errors (estimate-true value) of monthly movement parameters from August to September for three scenarios of release size. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

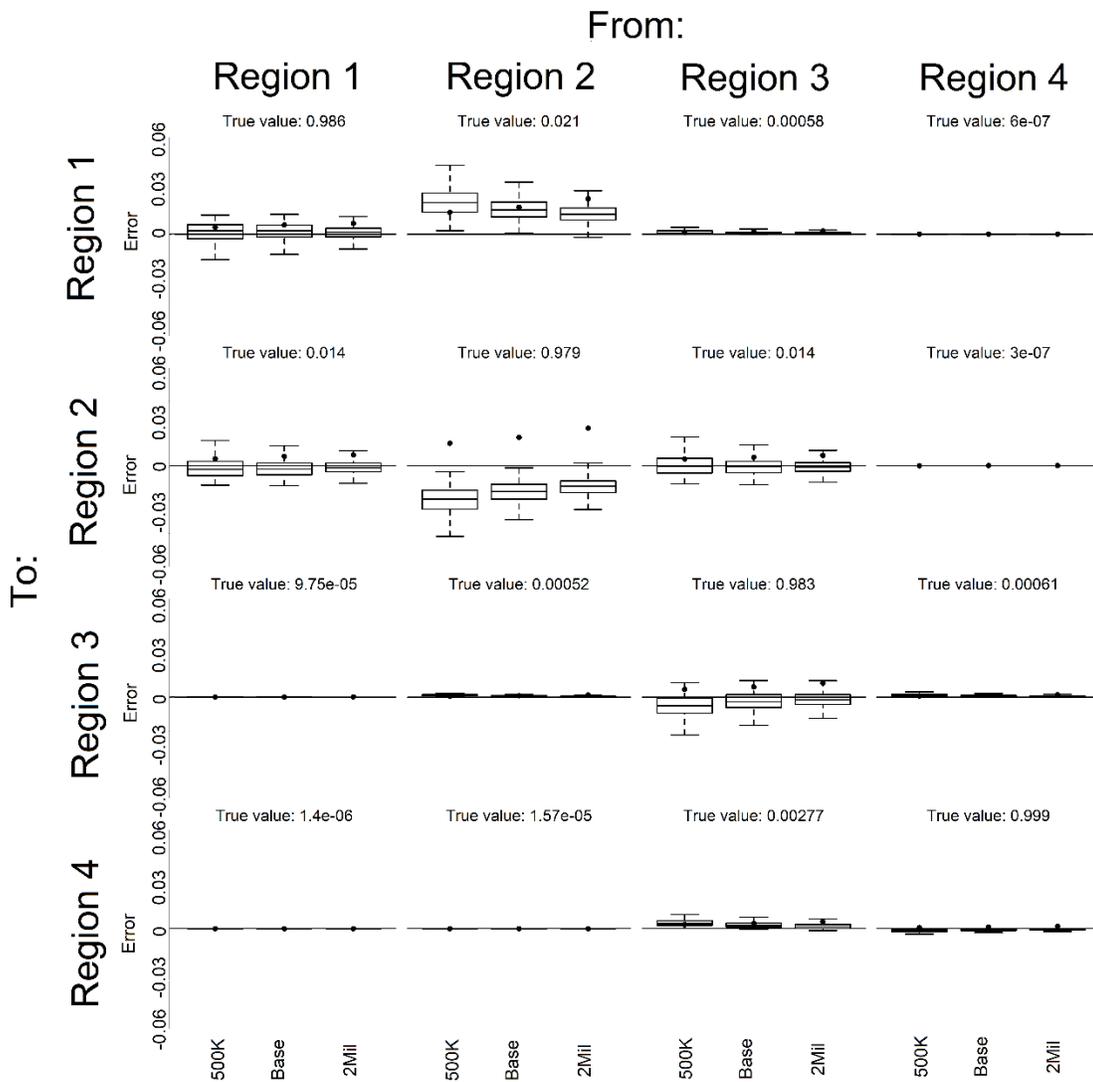


FIGURE A.2.7. Box plots of errors (estimate-true value) of monthly movement parameters from September to October for three scenarios of release size. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

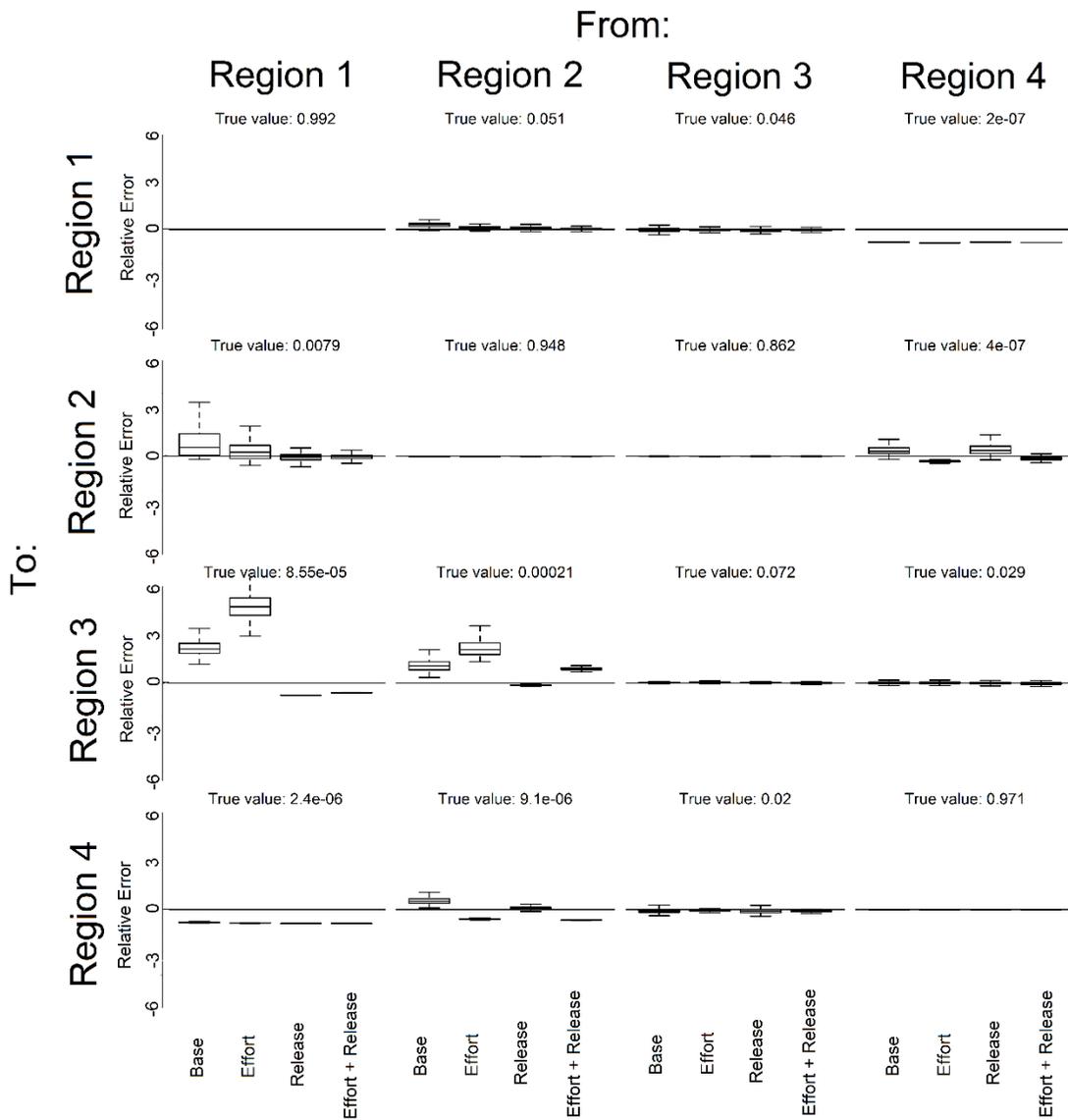


FIGURE A.2.8. Box plots of relative errors (estimate-true value)/true value of monthly movement parameters from May to June for four scenarios of effort and release structure. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

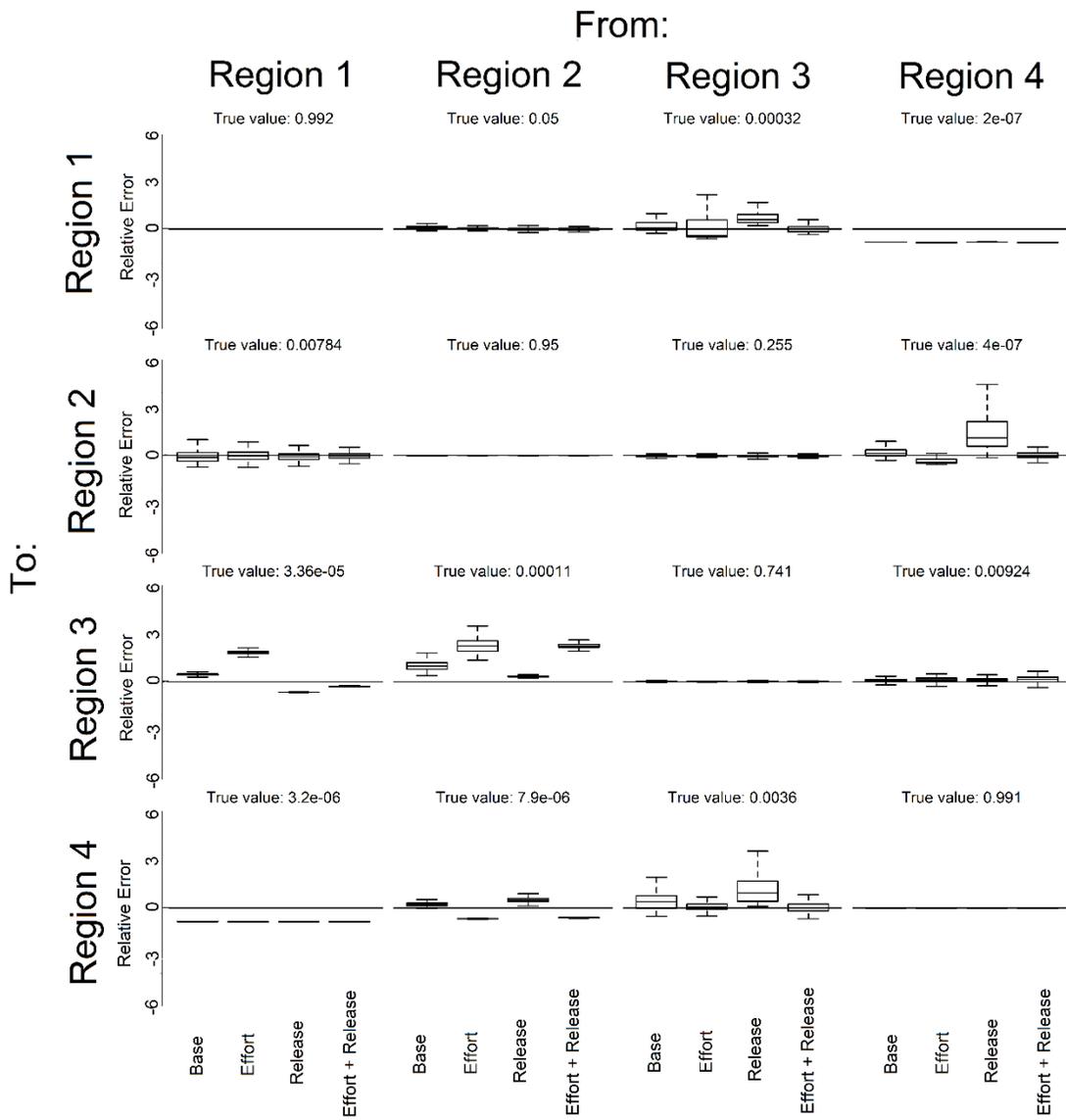


FIGURE A.2.9. Box plots of relative errors (estimate-true value)/true value of monthly movement parameters from June to July for four scenarios of effort and release structure. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

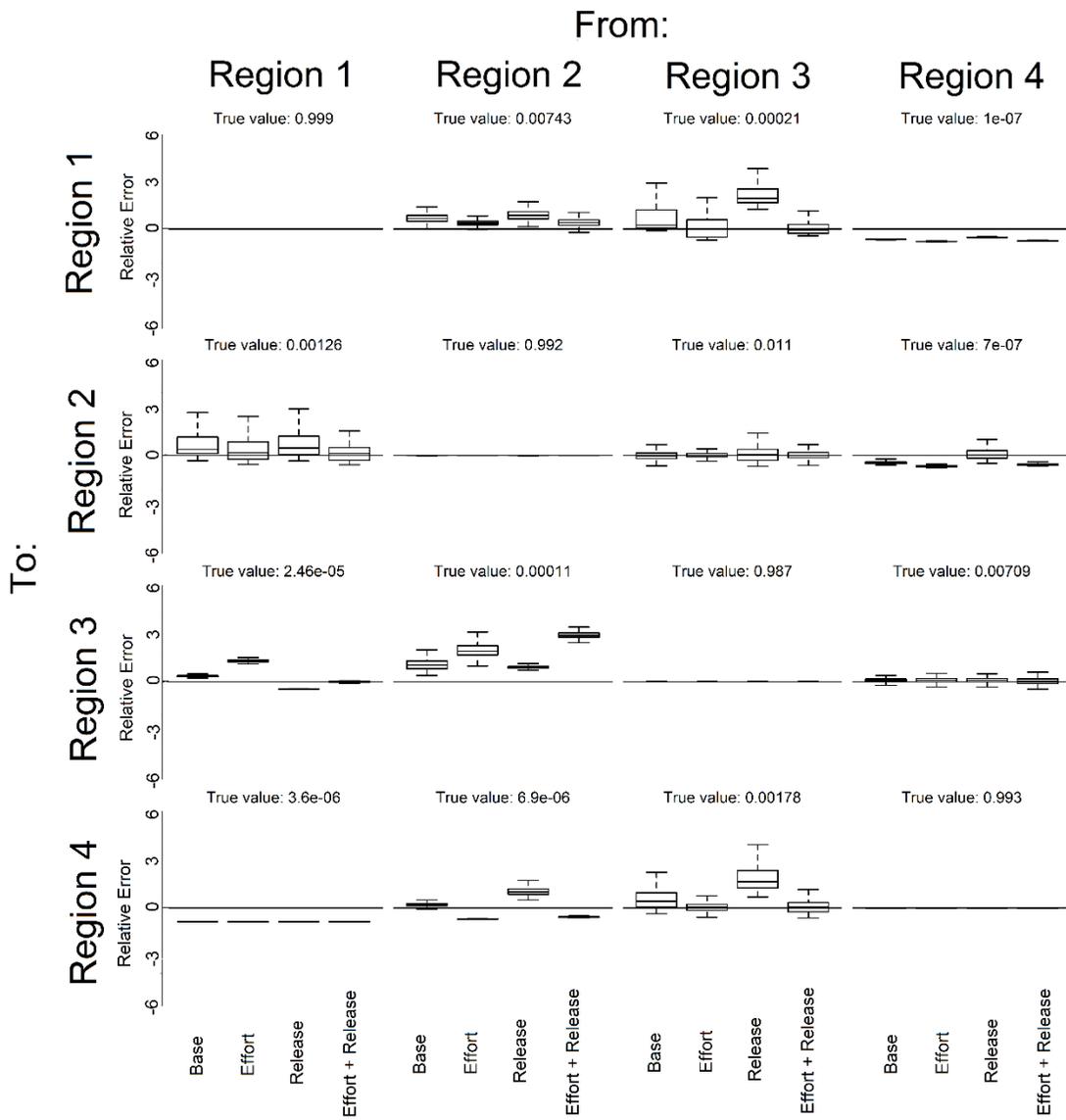


FIGURE A.2.10. Box plots of relative errors (estimate-true value)/true value of monthly movement parameters from July to August for four scenarios of effort and release structure. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

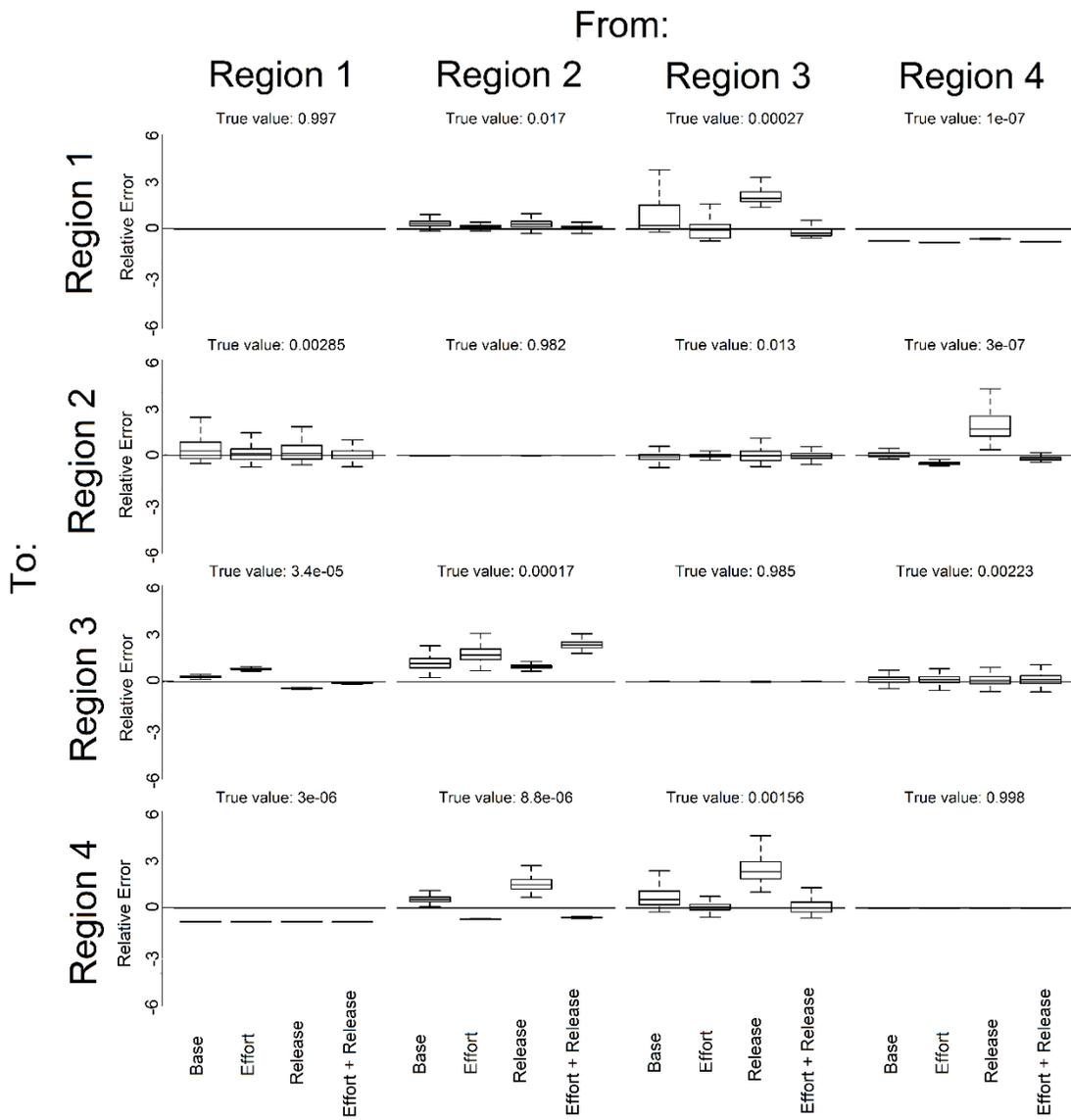


FIGURE A.2.11. Box plots of relative errors (estimate-true value)/true value of monthly movement parameters from August to September for four scenarios of effort and release structure. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

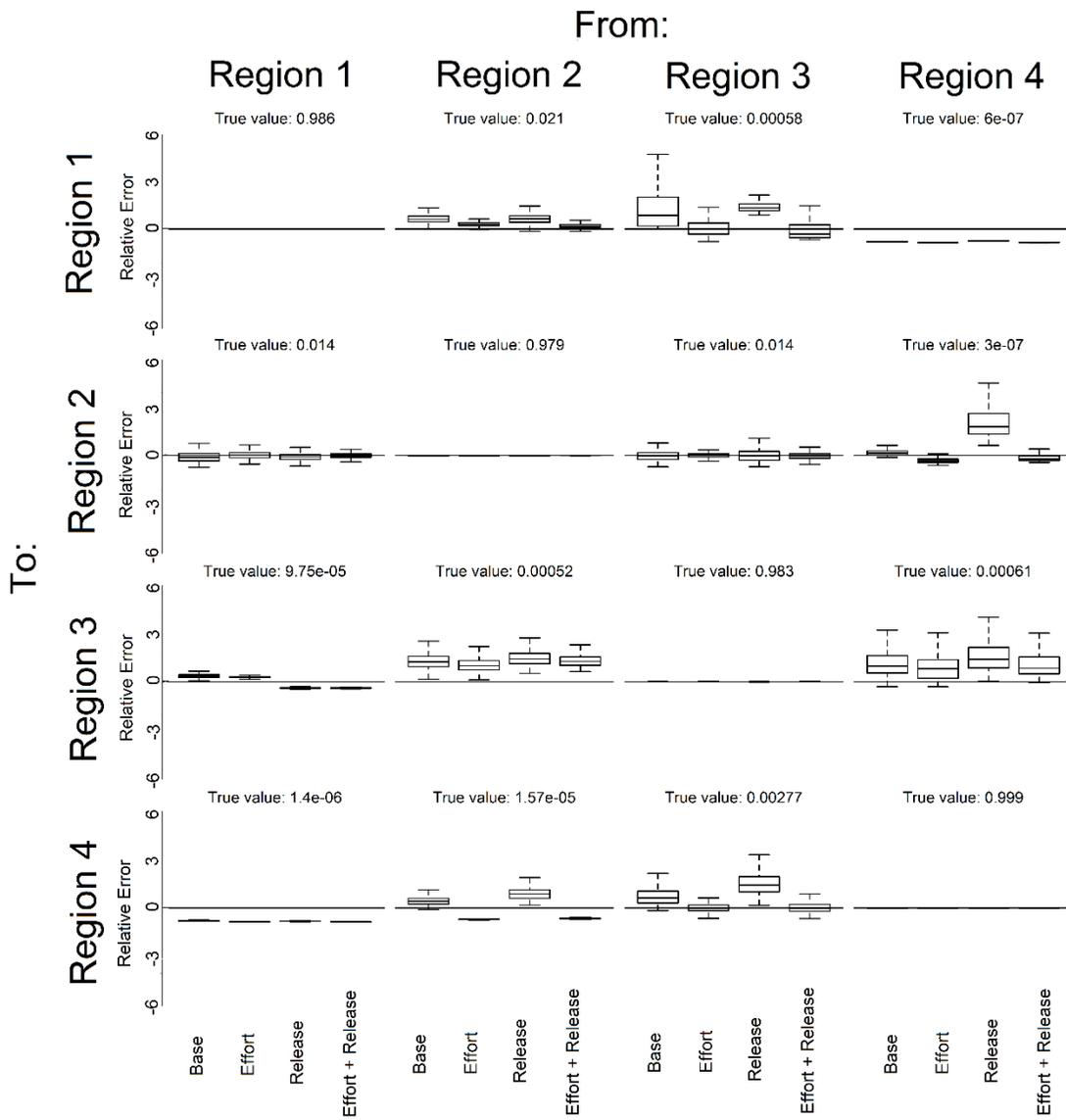


FIGURE A.2.12. Box plots of relative errors (estimate-true value)/true value of monthly movement parameters from September to October for four scenarios of effort and release structure. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

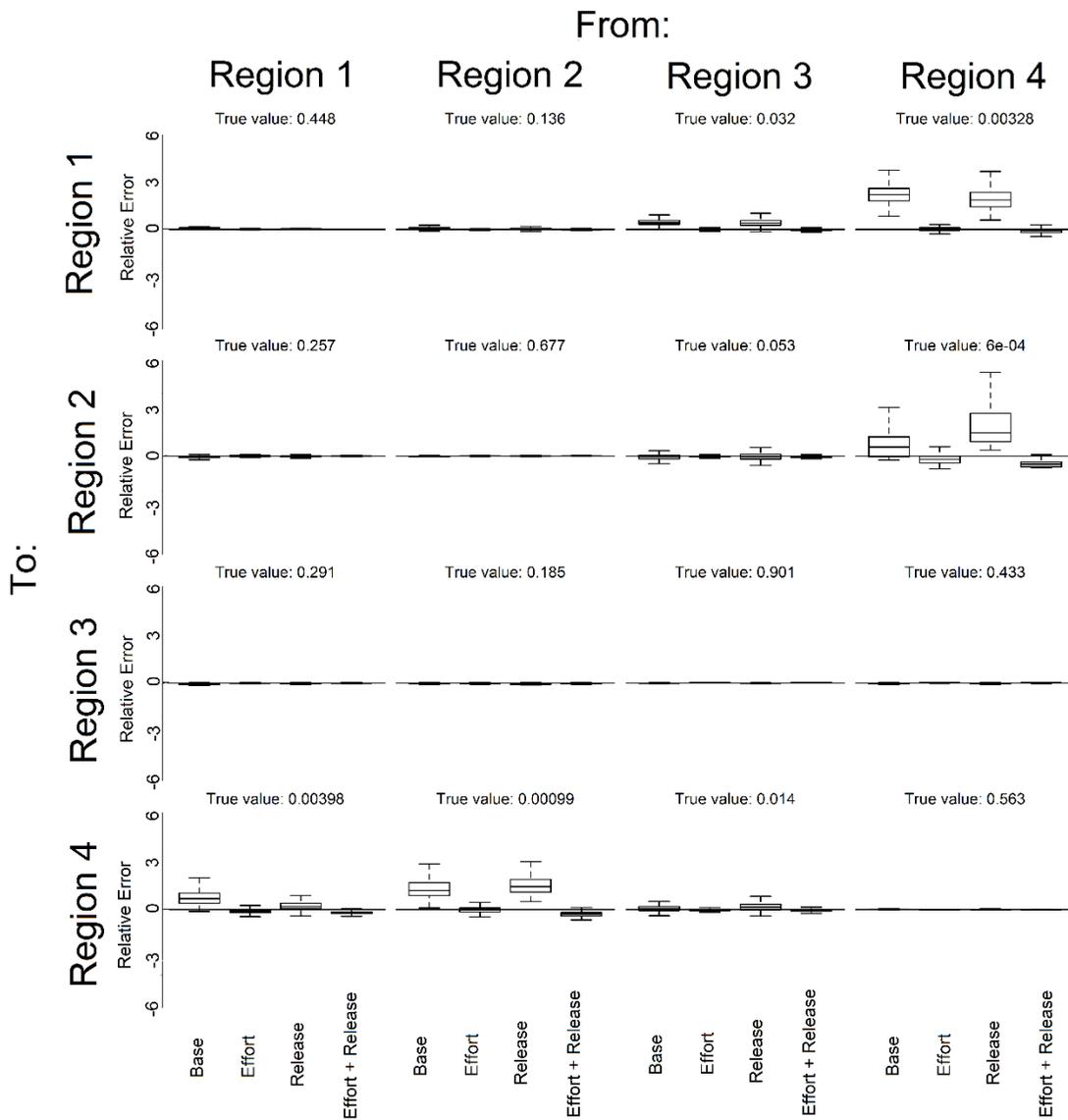


FIGURE A.2.13. Box plots of relative errors (estimate-true value)/true value of half-year movement parameters from October to May for four scenarios of effort and release structure. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

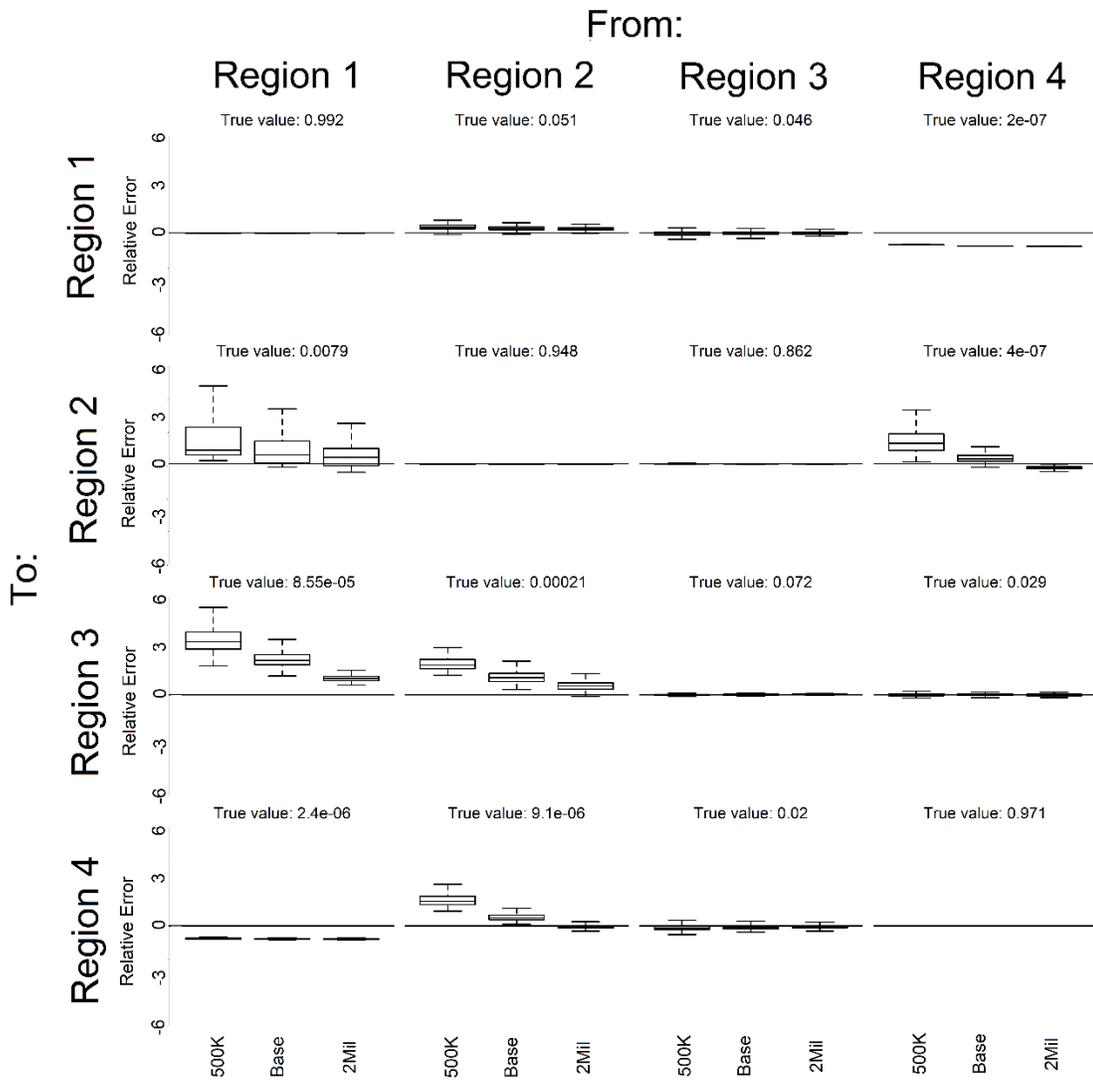


FIGURE A.2.14. Box plots of relative errors (estimate-true value)/true value of half-year movement parameters from May to June for three scenarios of release size. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

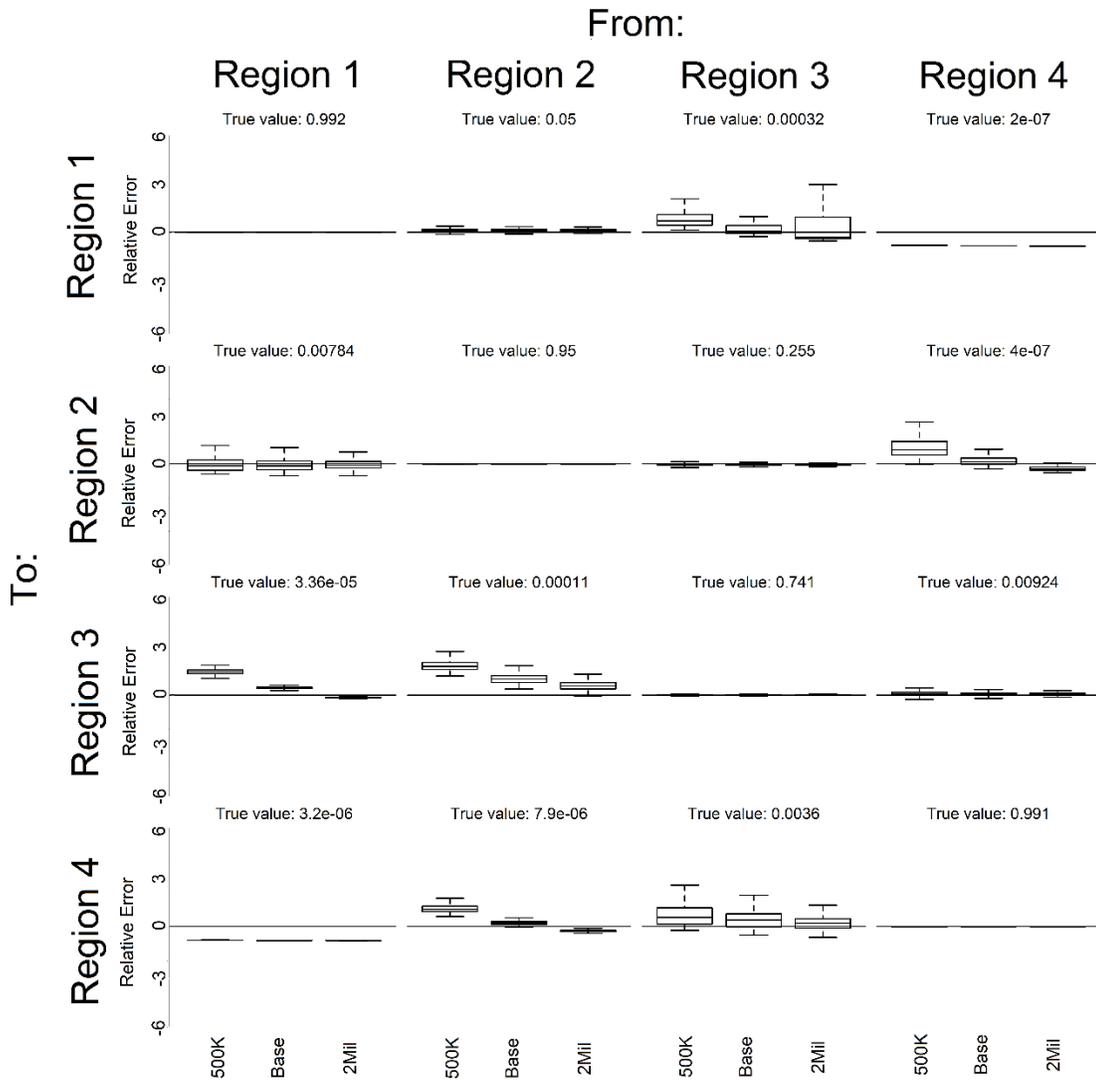


FIGURE A.2.15. Box plots of relative errors (estimate-true value)/true value of half-year movement parameters from June to July for three scenarios of release size. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

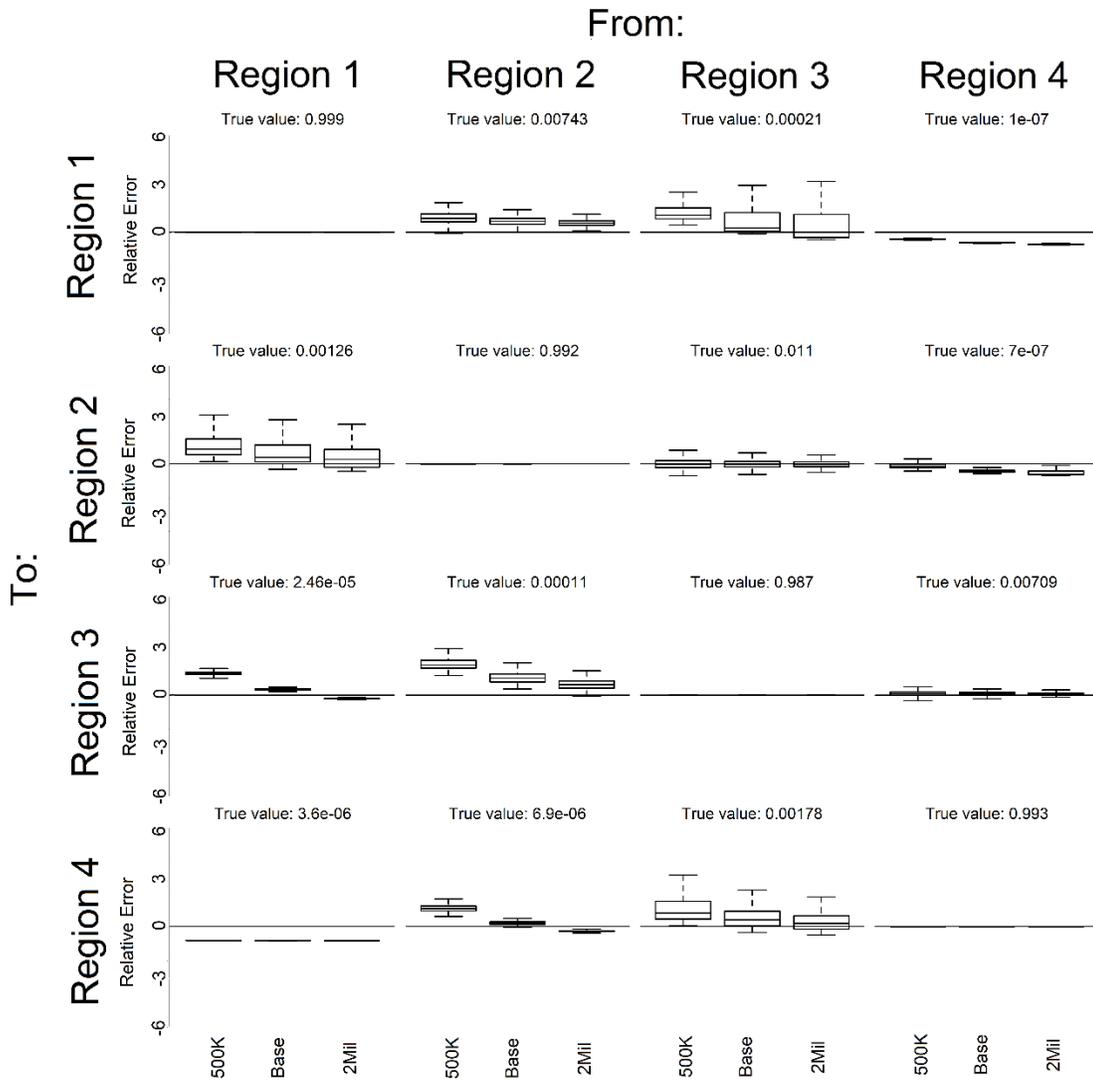


FIGURE A.2.16. Box plots of relative errors (estimate-true value)/true value of half-year movement parameters from July to August for three scenarios of release size. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

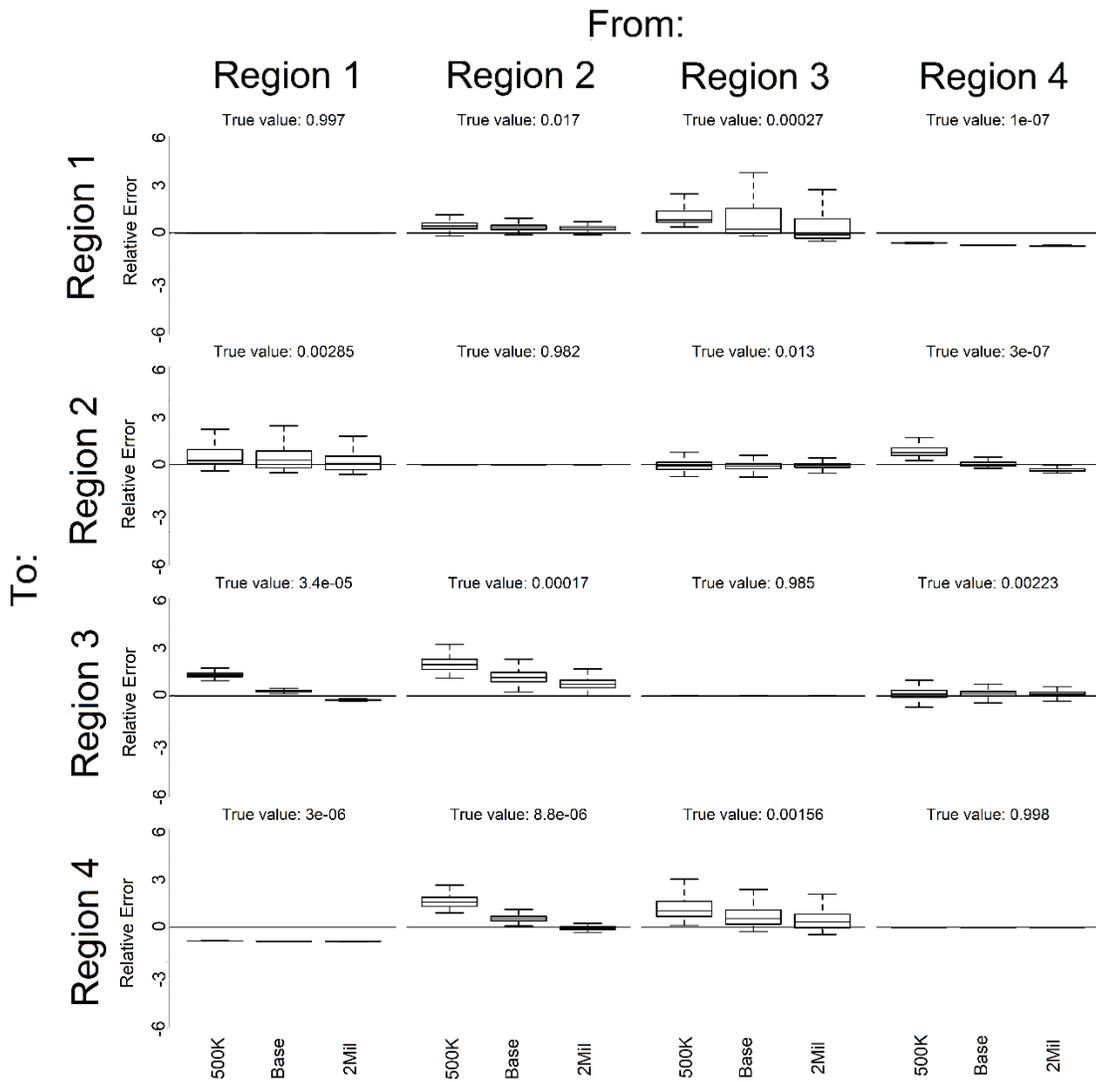


FIGURE A.2.17. Box plots of relative errors (estimate-true value)/true value of half-year movement parameters from August to September for three scenarios of release size. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

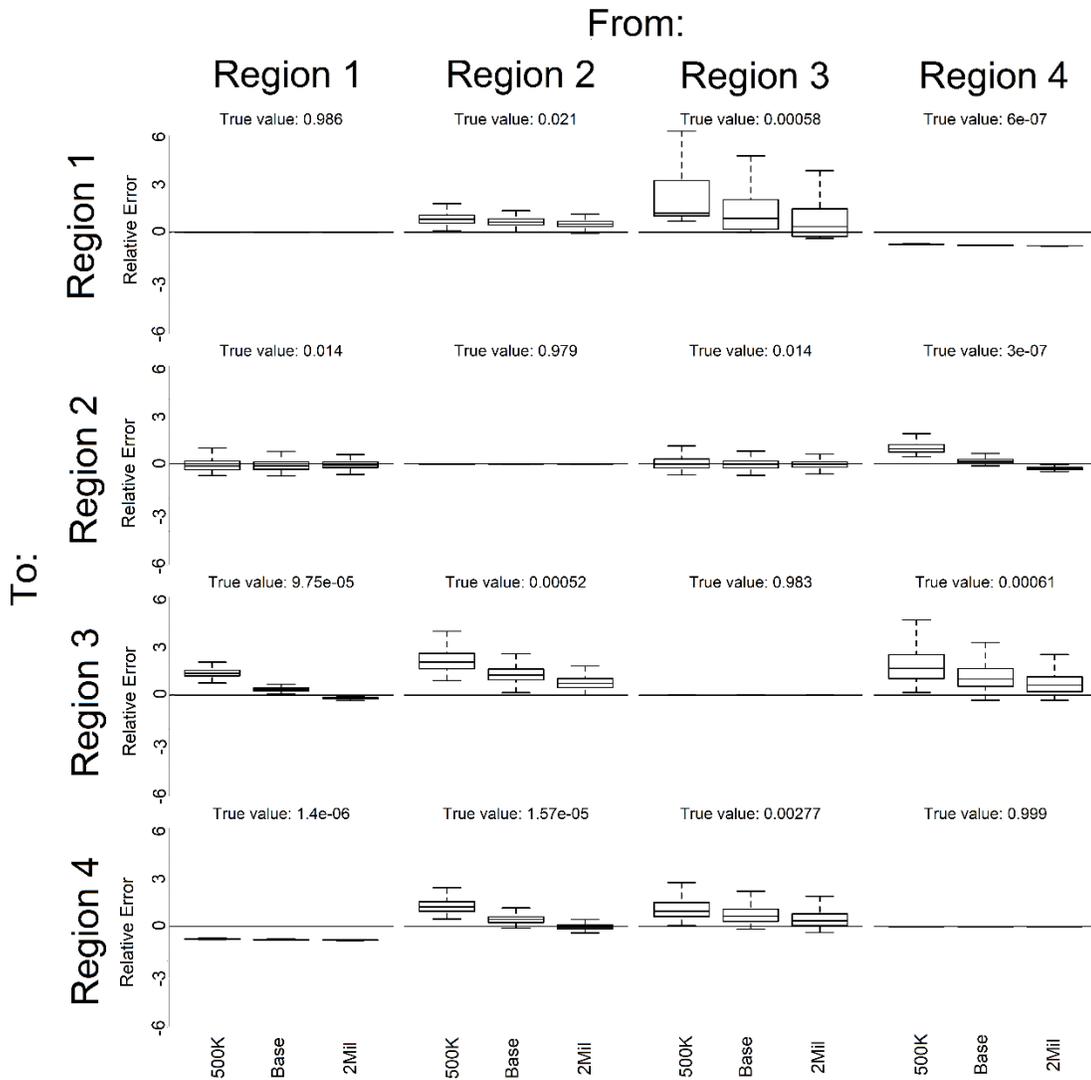


FIGURE A.2.18. Box plots of relative errors (estimate-true value)/true value of half-year movement parameters from September to October for three scenarios of release size. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

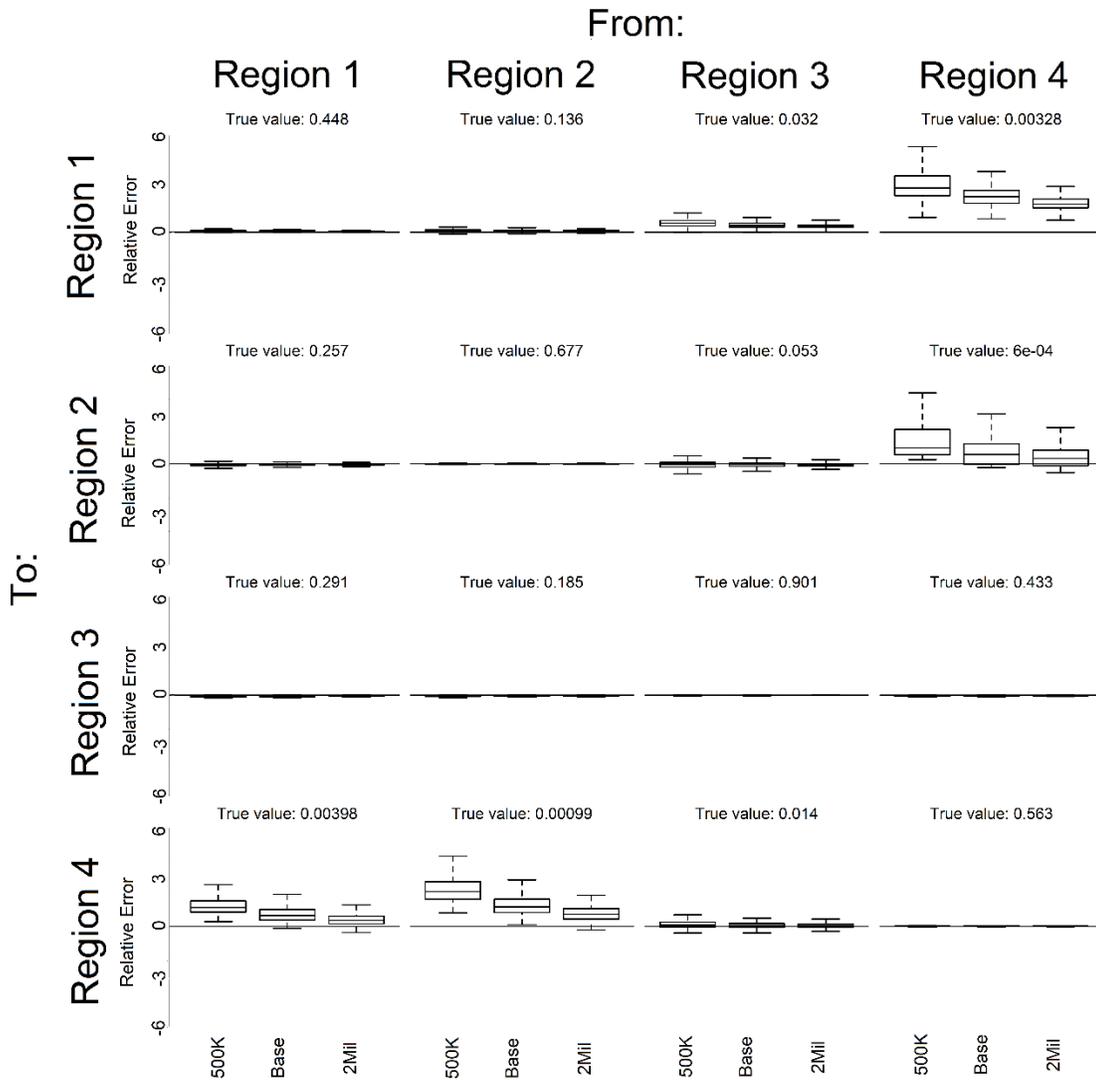


FIGURE A.2.19. Box plots of relative errors (estimate-true value)/true value of half-year movement parameters from October to May for three scenarios of release size. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

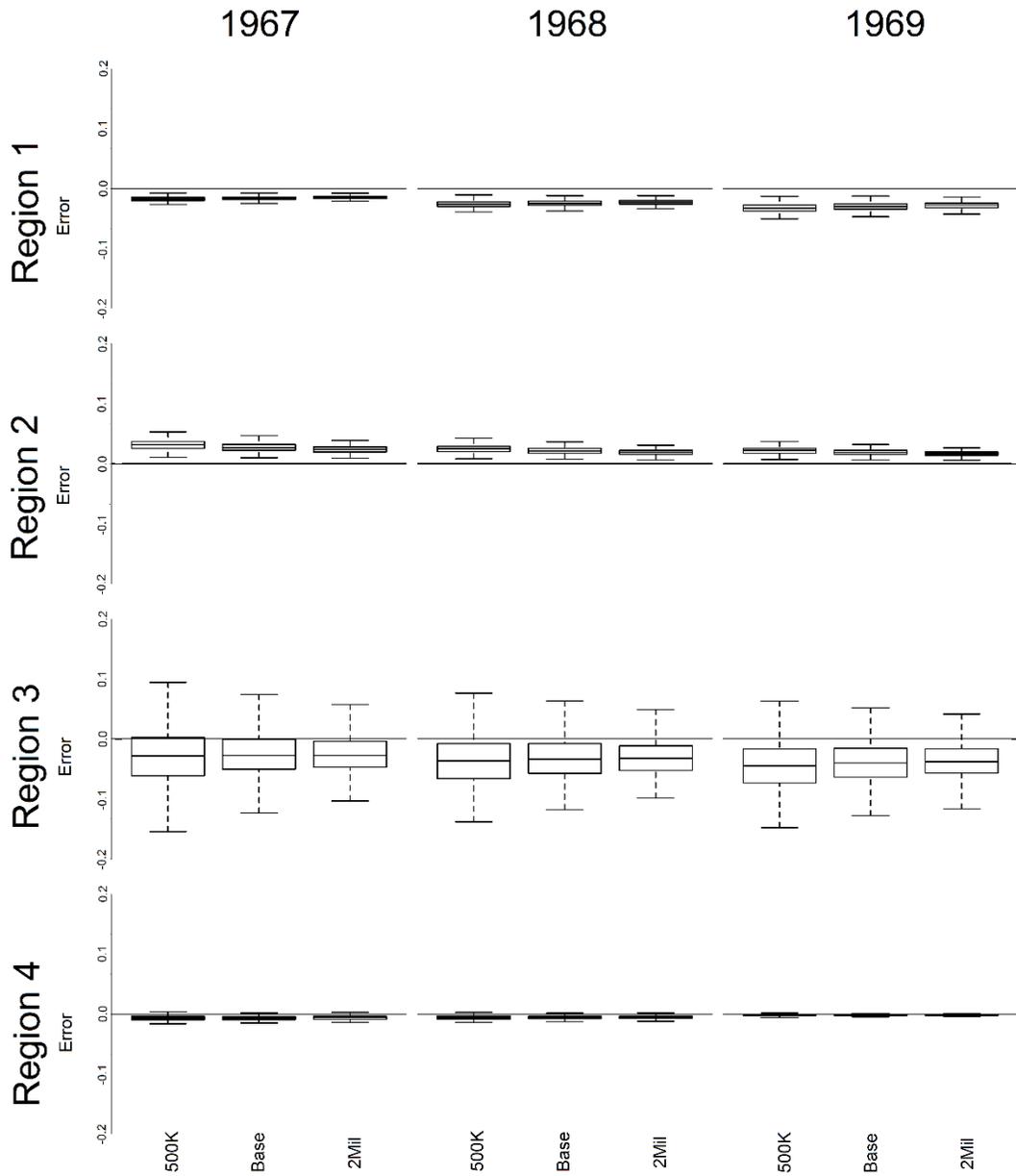


FIGURE A.2.20. Box plots of errors (estimate-true value) of yearly fishing mortality by region and year for three scenarios of release size. See Table 2.1 for scenario definitions. Box plot definitions are the same as Figure A.2.1.

## Bibliography

- Ahrenholz, D.W., D. L. Dudley, and E.J. Levi. 1991. Overview of mark-recovery studies on adult and juvenile Atlantic Menhaden, *Brevoortia tyrannus* and Gulf Menhaden, *B. patronus*. *Marine Fisheries Review* 53:20-27.
- Albanese, B., P.L. Angermeier, and C. Gowan. 2003. Designing mark-recapture studies to reduce effects of distance weighting on movement distance distributions of stream fishes. *Transactions of the American Fisheries Society* 132:925-939.
- Anderson, J.D. 2007. Systematics of the North American menhadens: molecular evolutionary reconstructions in the genus *Brevoortia* (Clupeiformes: Clupeidae). *Fishery Bulletin* 205:368-378.
- Armansson, H., S.T. Jonsson, J.D. Neilson, and G. Marteinsdottir. 2007. Distribution and migration of saithe (*Pollachius vierns*) around Iceland inferred from mark-recapture studies. *ICES Journal of Marine Science* 64:1006-1016.
- Arnason, A.N. 1973. The estimation of population size, migration rates and survival in a stratified population. *Researches on Population Ecology* 15:1-8.
- Bigelow, H.B. and W.C. Schroeder. 1953. *Fishes of the Gulf of Maine* 53:113-118.
- Bolle, L.J., E. Hunter, A.D. Rijnsdorp, M.A. Pastoors, J.D. Metcalfe and J.D. Reynolds. 2005. Do tagging experiments tell the truth? Using electronic tags to evaluate conventional tagging data. *ICES Journal of Marine Science* 62:236-246.
- Brownie, C., J.E. Hines, J.D. Nichols, K.H. Pollock and J.B. Hestbeck. 1993. Analysis of multiple capture-recapture data using band-recovery methods. *Biometrics* 49:1173-1187.
- Buchheister, A., T. J. Miller and E. D. Houde (in press). Evaluating ecosystem-based reference points for Atlantic menhaden (*Brevoortia tyrannus*). *Coastal and Marine Fisheries*.
- Calvert, A.M., S.J. Bonner, I.D. Jonsen, J.M. Flemming, S.J. Walde, and P.D. Taylor. 2009. A hierarchical Bayesian approach to multi-state mark-recapture: simulations and applications. *Journal of Applied Ecology* 46:610-620.
- Carlson, F.T., and J.W. Reintjes. 1972. Suitability of internal tags for Atlantic Menhaden. *Fishery Bulletin of the National Oceanic and Atmospheric Administration* 70:514-517.
- Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43:783-791.
- Chao, A. 1989. Estimating population size for sparse data in capture-recapture experiments. *Biometrics* 45:427-438.
- Clark, F.N. and J.Janssen. 1945. Results of tagging experiments in California waters on the sardine (*Sardinops caerulea*). *Fisheries Bulletin* 61:1-93.
- Clark, W. 1999. Effects of an erroneous natural mortality rate on a simple age-structured stock assessment. *Canadian Journal of Fisheries and Aquatic Science* 56:1721-1731.
- Cormack, R.M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429-438.

- Coston, L.C. 1971. Summary of tags released and recovered for the Atlantic Menhaden, 1966-69. US Department of Commerce, NOAA, NMFS.
- Cury, P., A. Bakun, R.J.M. Crawford, A. Jarre, R.A. Quiñones, L.J. Shannon and H.M. Verheye. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science* 57:603-618.
- Deegan, L.A. 2011. Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. *Canadian Journal of Fisheries and Aquatic Sciences* 50:74-79.
- Dryfoos, R.L., R.P. Cheek, and R.L. Kroger. 1973. Preliminary analysis of Atlantic Menhaden, *Brevoortia tyrannus*, migrations, population structure, survival and exploitation rates, and availability as indicated from tag returns. *Fishery Bulletin of the National Oceanic and Atmospheric Administration* 71:719-734.
- 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. *Fiskeridirektoratets skrifter, Serie Havundersøkelser* 16:339-358.
- Durbin, A.G. and E.G. Durbin. 1975. Grazing rates of the Atlantic Menhaden *Brevoortia tyrannus* as a function of particle size and concentration. *Marine Biology* 33:265-277.
- Ely, P.C., S.P. Young, and J.J. Isely. 2008. Population size and relative abundance of adult Alabama Shad reaching Jim Woodruff Lock and Dam, Apalachicola River, Florida. *North American Journal of Fisheries Management* 28:827-831.
- Fahrig, L. 1991. Simulations relevant to the 1/3 harvesting rule for northern cod. *Canadian Atlantic Fisheries Scientific Advisory Committee, Research Document* 91/34. Halifax.
- Faubet, P., R.S. Waples, and O.E. Gaggiotti. 2007. Evaluating the performance of a multilocus Bayesian method for the estimation of migration rates. *Molecular ecology* 16:1149-1166.
- Fournier, D.A., H.J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M.N. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software* 27:233-249.
- Fridriksson, A. and O. Aasen. 1950. The Norwegian-Icelandic Herring tagging experiments. *Fiskeridirektoratets skrifter, Serie Havundersøkelser* 9:1-43.
- Gelman, A. and D.B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical science* 7:457-472.
- Gelman, A., J.B. Carlin, H.S. Stern, and D.B. Rubin. 2004. *Bayesian data analysis*. Chapman and Hall, New York.
- Gende, S.M. and M.F. Sigler. 2006. Persistence of forage fish ‘hot spots’ and its association with foraging Steller sea lions (*Eumetopias jubatus*) in southeast Alaska. *Deep Sea Research Part II: Topical Studies in Oceanography*. 53:432-441.
- Geweke, J. 1991. Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. *Federal Reserve Bank of Minneapolis Research Department Staff Report* 148.

- Gimenez, O., V. Rossi, R. Choquet, C. Dehais, B. Doris, H. Varella, J. Villa, and R. Pradel. 2007. State-space modelling of data on marked individuals. *Ecological Modelling* 206:431-438.
- Goethel, D.R., T.J. Quinn II, and S.X. Cadrin. 2011. Incorporating spatial structure in stock assessment: movement modeling in marine fish population dynamics. *Reviews in Fisheries Science* 19:119-139.
- Gottlieb, S.J. 1998. Nutrient removal by age-0 Atlantic menhaden (*Brevoortia tyrannus*) in Chesapeake Bay and implications for seasonal management of the fishery. *Ecological Modelling* 112:111-130.
- Gutierrez, M., G. Swartzman, A. Bertrand, and S. Bertrand. 2007. Anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) spatial dynamics and aggregation patterns in the Humboldt Current ecosystem, Peru, from 1983–2003. *Fisheries Oceanography* 16:155-168.
- Hamre, J. 1970. Internal tagging experiments of mackerel in the Skagerak and the north-eastern North Sea. ICES CM. 1970/H:25
- Hey, J. and R. Nielsen. 2004. Multilocus methods for estimating population sizes, migration rates, and divergence time with applications to the divergence of *Drosophila pseudoobscura* and *D.persimilis*. *Genetics* 167:747-760.
- Hilborn, R. 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. *Canadian Journal of Fisheries and Aquatic Sciences* 47:635-643.
- Hoenig, J.M., N.J. Barrowman, W.S. Hearn, and K.H. Pollock. 1998. Multiyear tagging studies incorporating fishing effort data. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1466-1476.
- IMARPE (Instituto del mar del peru “Institute of the Peruvian Sea”). 1972. Information about the second session of the panel of experts on the population dynamics of Peruvian Anchovy Bulletin of the Institute of the Peruvian Sea 2:373-458.
- Isley, J.J. and J. R. Tomasso. 1998. Estimating fish abundance in a large reservoir by mark-recapture. *North American Journal of Fisheries Management* 18:269-273.
- June, F.C. and J.W. Reintjes. 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 and Wildlife Service Special Scientific Report- Fisheries No. 317.
- June, F.C. 1961. The menhaden fishery of the United States. US Bureau of Commercial Fisheries, Fish Leaflet 521.
- Kendall, W.L. and J.D. Nichols. 2002. Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. *Ecology* 83:3276-3284.
- Kroger, R.L., and R.L. Dryfoos. 1972. Tagging and tag-recovery experiments with Atlantic Menhaden, *Brevoortia tyrannus*. U.S. Department of Commerce NOAA Technical Report NMFS SSRF-664.
- Langseth, B.J. and A.M. Schueller. 2017. Calculation of population level fishing mortality for single- versus multi-area models: Application to models with

- spatial structure. *Canadian Journal of Fisheries and Aquatic Sciences* doi: 10.1139
- Lauretta, M.V., D.R. Goethel. 2017. The robustness of Brownie tag return models to complex spatiotemporal dynamics evaluated through simulation analysis. *Canadian Journal of Fisheries and Aquatic Sciences* doi: 10.1139
- Leary, D.F. and G.I. Murphy. 1975. A successful method for tagging the small, fragile engraulid *Stolephorus purpureus*. *Transactions of the American Fisheries Society* 104:53-55.
- Lebreton, J.D. and R. P. Cefe. 2002. Multistate recapture models: modelling incomplete individual histories. *Journal of Applied Statistics* 29:353-369.
- Lee, H., M.N. Maunder, K.R. Piner and R.D. Methot. 2011. Estimating natural mortality within a fisheries stock assessment model: An evaluation using simulation analysis based on twelve stock assessments. *Fisheries Research* 109:89-94.
- Lindberg, M.S. and E.A. Rexstad. 2002. Capture-recapture sampling designs. *Encyclopedia of environmetrics*, John Wiley and Sons Ltd, pp 251-262.
- Lindberg, M.S. 2012. A review of designs for capture-mark-recapture studies in discrete time. *Journal of Ornithology* 152:S355-S370.
- Lynch, A. J., J. R. McDowell, J. E. Graves. 2010. A molecular genetic investigation of the population structure of Atlantic menhaden (*Brevoortia tyrannus*). *Fishery Bulletin* 108:87-97.
- Mangel, M. 1982. Search effort and catch rates in fisheries. *European Journal of Operational Research* 11:361-366.
- Martell, S.J.D., and Walters, C.J. 2002. Implementing harvest rate objectives by directly monitoring exploitation rates and estimating changes in catchability. *Bulletin of Marine Science* 70:695–713.
- Michielsens, C.G.J., M.K. McAllister, S. Kuikka, T. Pakarinen, L. Karlsson, A. Romakkaniemi, I. Pera, and S. Mantyniemi. 2011. A Bayesian state-space mark-recapture model to estimate exploitation rates in mixed-stock fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* 63:321-334.
- National Marine Fisheries Service. 2015. Fisheries of the United States, 2014. U.S. Department of Commerce, NOAA Current Fishery Statistics No.2014.
- Newman, K.B. 2000. Hierarchic modeling of salmon harvest and migration. *Journal of Agricultural, Biological, and Environmental Statistics* 5:430-455.
- Nichols, J.D., J.E. Hines, K.H. Pollock, R.L. Hinz, and W.A. Link. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture-recapture data. *Ecology* 75:2052-2065.
- Nichols, J.D. and W.L. Kendall. 1995. The use of multi-state capture-recapture models to address questions in evolutionary ecology. *Journal of Applied Statistics* 22:835-846.
- Nicholson, W.R. 1971. Coastal movements of Atlantic Menhaden as inferred from changes in age and length distributions. *Transactions of the American Fisheries Society* 100:708-716.
- Nicholson, W.R. 1978. Movements and population structure of Atlantic Menhaden indicated by tag returns. *Estuaries and Coasts* 1:141-150.

- Ovaskainen, O. H. Rekola, E. Meyke, and E. Arjas. 2008. Bayesian methods for analyzing movements in heterogeneous landscapes from mark-recapture data. *Ecology*. 89:542-554.
- Pelletier, D., and P. Magal. 1996. Dynamics of a migratory population under different fishing effort allocation schemes in time and space. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1186-1199.
- Pikitch, E., P.D. Boersma, I.L. Boyd, D.O. Conover, P. Cury, T. Essington, S.S. Heppell, E.D. Houde, M. Mangel, D. Pauly, and É. Plagányi. 2012. Little fish, big impact: managing a crucial link in ocean food webs. Lenfest Ocean Program, Washington, DC.
- Pikitch, E.K., K.J. Rountos, T.E. Essington, C. Santora, D. Pauly, R. Watson, U.R. Sumaila, P.D. Boersma, I.L. Boyd, D.O. Conover, and P. Cury. 2014. The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries*, 15:43-64.
- Pine, W.E., K.H. Pollock, J.E. Hightower, T.J. Kwake and J.A. Rice. 2011. A review of tagging methods for estimating fish population size and components of mortality. *Fisheries*. 28:12-23.
- Pollock, K.H., J.M. Hoenig, W.S. Hearn, and B. Calingaert. 2001. Tag reporting rate estimation: 1. An evaluation of the high-reward tagging method. *North American Journal of Fisheries Management* 21:521-532.
- Quinn, T.J. and R.B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.
- R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reish, R.L. R.B. Deriso, D. Ruppert, and R.J. Carroll. 1985. An investigation of the population dynamics of Atlantic Menhaden (*Brevoortia tyrannus*). *Canadian Journal of Fisheries and Aquatic Sciences* 42:147-158.
- Roithmayr, C.M. 1963. Distribution of fishing by purse seine vessels for Atlantic Menhaden, 1955-59. U.S. Fish and Wildlife Service Special Scientific Report-Fisheries No. 434.
- Rubin, D.B. 1976. Inference and missing data. *Biometrika* 63:581-592.
- Ruzicka, J.J., R.D. Broudeur, R.L. Emmett, J.H. Steele, J.E. Zamon, C.A. Morgan, A.C. Thomas, and T.C. Wainwright. 2012. Interannual variability in the Northern California Current food web structure: Changes in energy flow pathways and the role of forage fish, euphausiids, and jellyfish. *Progress in Oceanography* 102:19-41.
- Schwarz, C.J. and A.N. Arnason. 1990. Use of tag-recovery information in migration and movement studies. *American Fisheries Society Symposium* 7:588-603.
- Schwarz, C. J., J. F. Schweigert, and A. N. Arnason. 1993. Estimating migration rates using tag-recovery data. *Biometrics* 49:177-193.
- Simpson, C.A, M. J. Wilberg, H. Bi, A. M. Schueller, G. M. Nessler, and H. J. Walsh. 2016. Trends in Relative Abundance and Early Life Survival of Atlantic Menhaden during 1977-2013 from Long-Term Ichthyoplankton Programs. *Transactions of the American Fisheries Society* 145:1139-1151.

- Simpson, C.A., H. Bi, D. Liang, M.J. Wilberg, A.M. Schueller, G.M. Nesslange and H.J. Walsh. 2017. Spawning locations and larval dispersal of Atlantic Menhaden during 1977-2013. *ICES Journal of Marine Science* doi: 10.1093
- Smith, J.W. 1991. The Atlantic and Gulf Menhaden purse seine fisheries: origins, harvesting technologies, biostatistical monitoring, recent trends in fisheries statistics, and forecasting. *Marine Fisheries Review* 53:28-41.
- Smith, J.W. and B. O'Bier. 2011. The bait purse-seine fishery for Atlantic Menhaden, *Brevoortia tyrannus*, in the Virginia portion of Chesapeake Bay. *Marine Fisheries Review* 73:1-12.
- Sibert, J., J. Hampton and D. Fournier. 1996. Skipjack movement and fisheries interaction in the western Pacific. *FAO Fisheries Technical Paper* 401-418.
- Sibert, J.R., J. Hampton, D.A. Fournier, and P.J. Bills. 1998. An advection-diffusion-reaction model for the estimation of fish movement parameters from tagging data, with application to skipjack tuna (*Katsuwonus pelamis*). *Canadian Journal of Fisheries and Aquatic Sciences* 56:925-938.
- Sippel, T., J. P. Eveson, B. Galuardi, C. Lam, S. Hoyle, M. Maunder, P. Kleiber, F. Carvalho, V. Tsontos, S.L.H. Teo, and A. Aires-da-Silva. 2015. Using movement data from electronic tags in fisheries stock assessment: A review of models, technology, and experimental design. *Fisheries Research* 163: 152-160.
- Sissener, E.H. and T. Bjørndal. 2005. Climate change and the migratory pattern for Norwegian spring-spawning herring—implications for management. *Marine Policy* 29:299-309.
- SEDAR (Southeast Data, Assessment, and Review). 2015. SEDAR 40 – Atlantic Menhaden Stock Assessment Report. North Charleston, SC.
- Suryan, R.M., D.B. Irons, M. Kaufman, J. Benson, P.G.R. Jodice, D.D. Roby and E.D. Brown. 2002. Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the black-legged kittiwake *Rissa tridactyla*. *Marine Ecology Progress Series* 236:273-287.
- Tacon, A.G. and M. Metian. 2009. Fishing for aquaculture: non-food use of small pelagic forage fish—a global perspective. *Reviews in Fisheries Science*, 17:305-317.
- Vermard, Y., E. Rivot, S. Mahevas, P. Marchal, and D. Gascuel. 2010. Identifying fishing trip behavior and estimating fishing effort from VMS data using Bayesian Hidden Markov Models. *Ecological Modeling* 221:1757-1769.
- Walters, C.J., N. Hall, R. Brown, and C. Chubb. 1993. Spatial model for the population dynamics and exploitation of the Western Australian Rock Lobster, *Panulirus Cygnus*. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1650-1662.
- Wetzel, C.R. and A.E. Punt. 2011. Performance of a fisheries catch-at-age model (Stock Synthesis) in data-limited situations. *Marine and Freshwater Research* 62:927-936.
- Wheeler, J.P. and G.H. Winters. 1984. Homing of Atlantic Herring (*Clupea harengus harengus*) in Newfoundland waters as indicated by tagging data. *Canadian Journal of Fisheries and Aquatic Sciences* 41:108-117.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16: 97-159.