Investigation of Atlantic Menhaden Mortality Rates- IN REVIEW

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SEDAR 102 WP-10: Ault and Luo (2025, in review) Update of Ault et al. (2023)

This working paper is an update of the original Ault et al. (2023) working paper (SEDAR 102 WP-02) based on their work with the Menhaden M Work Group. It was provided to ASMFC on July 24, 2025 and was not reviewed by the Menhaden SAS or ERP WG prior to submission to the SEDAR process.

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Abstract:	Atlantic menhaden mortality rates were reevaluated. The SEDAR 69 (2019) benchmark stock assessment used Liljestrand et al.'s (2019a) natural mortality rate estimate of M = 1.17 yr-1, which was 2.3 times greater than the SEDAR 40 (2015) assessment. Their rate was derived from multistate mark-recovery model analysis of the 1966-1971 Atlantic menhaden mark-recovery study which released over one million tagged adults recaptured in four areas extending from Massachusetts to Florida. Our evaluation revealed the Liljestrand paper had at least five significant errors: (1) overstated tag releases; (2) under reported tag recoveries by 13%; (3) overstated tag recovery efficiency by using "all" magnets instead of "primary" magnets (4) under reported annual fishing effort by an annual average of -47.8%; and (5) modeled time-area magnet efficiencies as constants. After corrections, analyses using direct modeling on two versions of the mark-recovery data produced a revised natural mortality estimate of M = 0.52 yr-1, less than half of that used in SEDAR 69, and consistent with both the pre-2019 literature and life history theory. Given the pivotal role of natural mortality in stock assessments, adoption of this revised M for the Atlantic menhaden stock will significantly influence status evaluations, recommended harvest rates, and the coastwide quota determinations.

UNIVERSITY OF MIAMI
ROSENSTIEL SCHOOL of
MARINE, ATMOSPHERIC
& EARTH SCIENCE

July 10, 2025

TO: Jason Cope, Associate Editor, Fisheries Research
Andre E. Punt, Ph.D., Editor-in-Chief, Fisheries Research

FR: Jerald S. Ault, Ph.D.

RE: Second Revision of Regular Paper FISH-13999.R1

Please find our revision of the manuscript FISH-13999.R2 entitled, *Investigation of Atlantic menhaden mortality rates*, being considered for publication in *Fisheries Research* as a Regular Paper.

We have revised the manuscript and the Supplemental Materials in response to the recommended/suggested comments of Reviewer #2. Reviewer #3 and the Associate Editor had very minor comments that were also addressed.

This revision includes the following materials:

(1) Responses to Reviewers.
(2) Revised manuscript.
(3) Supplemental materials.

We look forward to hearing from you. Thank you for your consideration.

Sincerely,

Jerald S. Ault, Ph.D.
Professor Emeritus
Department of Environmental Science and Policy
University of Miami

Investigation of Atlantic menhaden mortality rates

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Keywords: Mark-recapture, *Brevoortia tyrannus*, forage fish, survivorship, total mortality, natural mortality, fishing mortality

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ABSTRACT

Atlantic menhaden mortality rates were reevaluated. The SEDAR 69 (2019) benchmark stock assessment used Liljestrand et al.'s (2019a) natural mortality rate estimate of M = 1.17 yr^{-1}, which was 2.3 times greater than the SEDAR 40 (2015) assessment. Their rate was derived from multistate mark-recovery model analysis of the 1966-1971 Atlantic menhaden mark-recovery study which released over one million tagged adults recaptured in four areas extending from Massachusetts to Florida. Our evaluation revealed the Liljestrand paper had at least five significant errors: (1) overstated tag releases; (2) under reported tag recoveries by 13%; (3) overstated tag recovery efficiency by using "all" magnets instead of "primary" magnets (4) under reported annual fishing effort by an annual average of -47.8%; and (5) modeled time-area magnet efficiencies as constants. After corrections, analyses using direct modeling on two versions of the mark-recovery data produced a revised natural mortality estimate of M = 0.52 yr^{-1}, less than half of that used in SEDAR 69, and consistent with both the pre-2019 literature and life history theory. Given the pivotal role of natural mortality in stock assessments, adoption of this revised M for the Atlantic menhaden stock will significantly influence status evaluations, recommended harvest rates, and the coastwide quota determinations.

1. Introduction

Atlantic menhaden (*Brevoortia tyrannus*) have played a pivotal role in American history. As early as the 1500s, Native Americans taught colonists to use menhaden as fertilizer to enhance agricultural productivity (Franklin, 2007). Historically abundant from the Gulf of Maine to central Florida, menhaden schools were reported to stretch up to 40 miles in length (Goode and Atwater, 1880; Hildebrand, 1948; Reintjes, 1969), As a primary forage species for a variety of fishes, marine mammals, and seabirds, menhaden are vital to the sustainability of the Atlantic coastal ocean ecosystem (Anstead et al., 2021). Prior to the discovery of petroleum in 1859, whale oil was the primary source of fuel, lubrication and illumination. By the mid-19th century, declining whale populations off New England spurred the search for alternative oil sources. The emerging menhaden fishery filled this void, providing a low-cost substitute for lamp oil (Reintjes, 1969; Nicholson, 1971; Ahrenholz et al., 1987). Menhaden landings began to be systematically documented in 1870, as the fishery expanded to become the largest in the United States (**Fig. 1A**). By the 1880s, nearly 100 operational reduction factories were concentrated in New England and Long Island, New York. However, by 1895, the fishery north of Cape Cod had collapsed, prompting a geographic shift to the mid- and south Atlantic coast (Nicholson, 1971).

A post-World War II resurgence in the menhaden fishery was fueled by technological advancements such as large commercial purse seiners, spotter aircraft, nylon nets, and aluminum-hulled boats. These innovations led to record landings between 1952 and 1962, peaking at 738,499 metric tons in 1956 (Reintjes, 1969; Nicholson, 1971; Ahrenholz et al., 1987; Fogarty et al., 1999; Vaughan et al, 2002). However, by the mid-1960s, landings and reduction factories dropped sharply—to 162,333 mt and 20 plants—prompting serious concerns about the fisheries' sustainability (Ahrenholz et al., 1987) (**Fig. 1B**; Supplemental Table 1). In response, the National Marine Fisheries Service (NMFS) launched a large-scale mark-recapture study from 1966 to 1971 along the US Atlantic coast, from Massachusetts to northern Florida (Coston, 1971; Dryfoos et al., 1973; Nicholson, 1978; Reish et al., 1985; Ahrenholz, 1987; Ahrenholz et al., 1991).

Mark-recapture experiments are widely accepted as robust tools for estimating stock structure, migratory patterns, survivorship, mortality rates and population size (Schaaf and Huntsman, 1972; Ricker, 1975; Beverton & Holt, 1957; Brownie et al., 1985, 1993; Vetter, 1988; Ahrenholz et al., 1991; Hoenig et al., 1998; Fonteneau and Pallares, 2005; Maunder et al., 2023). These estimates serve as key inputs to stock assessment models, which are foundational to fishery management. Accurate mortality rates are essential for credible assessments and sustainable management strategies (Quinn & Deriso, 1999; Punt et al., 2021; Cope & Hamel, 2022; Punt, 2023; Maunder et al., 2023; Artetxe-Arrate et al., 2024).

The SEDAR 69 (2019) Atlantic menhaden benchmark stock assessment adopted a natural mortality estimate of M = 1.17 yr^{-1} from Liljestrand et al (2019a), a 2.3-fold increase over the M = 0.50 yr^{-1} used in SEDAR 40 (2015) assessment and 14 standard deviations above the mean of more than dozen prior peer-reviewed estimates (Schaaf and Huntsman, 1972; Dryfoos et al., 1973; Reish et al., 1985; Ahrenholz et al., 1987; Vaughan and Smith, 1988; Vaughan, 1990; Ahrenholz, 1991; Cadrin and Vaughan, 1997; Vaughn et al. 2002; SEDAR 3, 2003; Luo et al., 2005; SEDAR 20, 2010; SEDAR 40, 2015). The Liljestrand et al. (2019a) estimate was also unusually high compared to recent U.S. and international stock assessments (**Fig. 2**). Based on this input, SEDAR 69 (2019) concluded that the menhaden spawning stock was over 80% of the unfished population size. However, it is well established that overestimation of M leads to underestimation of fishing mortality rates (F) (Clark, 1999; Punt et al., 2021), which can result in overly optimistic conclusions about stock health and sustainability (Zabel et al., 2003; Ault et al., 2014; Punt et al., 2021; Punt, 2023).

In 2023, we submitted findings from a preliminary review of the Liljestrand et al. (2019a) paper and its underlying data to the Atlantic State Marine Fisheries Commission (ASMFC), highlighting several errors in the study. In response, the ASMFC's Stock Assessment Subcommittee (SAS) formed a dedicated natural mortality (M) working group (hereafter: SAS M WG) to review our findings and reassess the data and methods used. The apparent overestimation of M in Liljestrand et al. (2019) likely stems from at least five sources of error: (1) overstated tag releases; (2) underreported tag recoveries by 13%; (3) overstated tag recovery efficiency by using "all" magnets instead of "primary" magnets; (4) underreported fishing effort by an annual average of -47.8% (SAS M WG, pers. comm.); and (5) modeled time-area magnet efficiencies as constants.

Given these issues and the critical role of M in stock assessment outcomes, a reanalysis was clearly warranted. The objective of this study was to re-examine the data, model and conclusions of Liljestrand et al. (2019), using the NMFS 1966-1971 Atlantic menhaden tag-recapture data, with the goal of improving natural mortality estimates and refining our understanding of Atlantic menhaden population dynamics.

2. Methods and materials

Two classes of analytical methods were used to estimate natural mortality for Atlantic menhaden: (1) *indirect methods,* which rely on empirical correlations between natural mortality (M) and species longevity, grounded in life history theory and evolutionary biology (Alagaraja, 1984; Hoenig, 1983, 2017; Ehrhardt and Ault, 1992; Kenchington, 2014; Hamel, 2015; Then et al., 2015; Hamel and Cope, 2022; Hamel et al., 2023; Duriel and Froese, 2022; Cope and Hamel, 2022; Maunder et al., 2023), and (2) *direct methods,* based on multi-year, multi-area mark-recapture models that use tag-recovery data to estimate mortality directly (Beverton and Holt, 1957; Chapman and Robson, 1960; Robson and Chapman, 1961; Paulik, 1962; Dryfoos et al, 1973; Brownie et al., 1985, 1993; Vetter, 1988; Lebreton et al., 1992; Hoenig et al., 1998; Quinn and Deriso, 1999; Liljestrand et al., 2019a; Punt et al., 2021; Cope and Hamel, 2022; Maunder et al., 2023).

2.*1 Indirect: life history & longevity*

Lifespan is a fundamental determinant of a species' natural mortality rate and can be used to establish biologically realistic bounds on its magnitude. Indirect methods for estimating natural mortality (M) rely on empirical relationships with maximum observed age and are grounded in the general law of exponential population decay, expressed as: $N_a = N_0 \exp^{-Za}$, where N_a is the number of individuals alive at age a, N_0 is the initial population number, and Z is the total mortality rate, defined as $Z = (M + F)$, with M representing natural mortality (i.e., accounting for predation, starvation, disease, senescence, and environmental stressors) and F is fishing mortality. Assuming mortality is constant over age, sex and time, survival to age a in the presence of both fishing and natural mortality is: $S_a = N_a/N_0 = \exp^{-Za}$ (Ricker, 1975; Vetter, 1998; Vaughan et al., 2002; Maunder et al., 2023). In the absence of fishing $(F = 0)$, survivorship depends solely on natural mortality: $S = \exp^{-M(a)}$. The unexploited age structure of a population is constrained by survivorship to the "true", though unobserved, maximum age a_λ, where few individuals remain alive: $\left(S_\lambda = \exp^{-M(a_\lambda - a_0)} \approx 0.0\right)$, with age at birth defined as $a_0 = 0$.

Beverton and Holt (1957) introduced the concept of "juvenescence"—a phenomenon where exploitation reduces the probability of individuals surviving to a_λ, leading to a younger observed age distribution. As a result, the "observed" maximum age $a_{\max}$ is often lower than the true maximum age ($a_{\lambda} \geq a_{\max}$). Numerous studies have shown that $a_{\max}$ is one of the most informative empirical indicators for estimating M: species with longer lifespans tend to experience lower natural mortality rates (Then et al., 2015; Dureuil and Froese, 2021; Hamel and Cope, 2022; Maunder et al., 2023).

Given $a_{\max}$, the expected proportion of cohort surviving to that age is: $p_{\max} = S_{\max} = \exp^{-Ma_{\max}}$. Rearranging the equation gives an estimator for the natural mortality rate (M): $\widehat{M} = -\ln(p_{\max})/a_{\max}$ (Alagaraja, 1984; Maunder et al., 2023). This theory-based approach is especially useful in data-poor contexts (e.g., Brodziak et al., 2011). We reviewed empirical life history methods from U.S. and international stock assessment literature to apply these models (Supplemental Table S.2). A common heuristic assumes that 5% of a cohort survives to $a_{\max}$, or $p_{\max} = S(a_{\max}) = 0.05$, leading to: $\widehat{M} = -\ln(p_{\max})/a_{\max} - \ln(0.05) = 2.9957 \approx 3.0$ yields $\widehat{M} = 3/a_{\max}$ (e.g., Rugolo et al., 1998). However, this assumption is somewhat arbitrary, and the choice of $p_{\max}$ can vary depending on ecological or stock-specific factors. Several researchers have developed refined predictive relationships (Hoenig, 1983; Then et al., 2015; Dureuil and Froese, 2021; Hamel and Cope, 2022). For example, Hoenig (1983) and Then et al. (2015) provided empirical regressions of M on longevity. Dureuil and Froese (2021) suggested that across taxa, $p_{\max} \approx 0.015$. Hamel and Cope (2022) noted that the Then et al. (2015) models did not account for heteroscedasticity and proposed an improved estimator $\widehat{M} = 5.4/a_{\max}$ (Maunder et al., 2023), which corresponds to $p_{\max} = 0.0045$ (Hoyle et al. 2023).

2.2 Direct: mark-recapture

Atlantic menhaden is a euryhaline clupeid found primarily within 15 miles of the U.S. Atlantic coast and in larger bays and sounds, ranging from West Palm Beach, Florida, to Nova Scotia, Canada. To study their population dynamics, the NMFS conducted a large-scale mark-recapture study from July 1966 to February 1971 dividing the Atlantic coast into five regions based on commercial fishing activity (Coston, 1971; Dryfoos et al, 1973; Ahrenholz et al., 1987, 1991): (1) North Atlantic (north of Long Island, New York); (2) Middle Atlantic (New Jersey, Delaware); (3) Chesapeake Bay (Virginia, Maryland); (4) South Atlantic (North Carolina, South Carolina); and (5) Georgia-Florida (**Fig. 3**). Liljestrand et al. (2019a) later consolidated these into four areas by combining the North and Middle Atlantic regions. At the time of the mark-recapture study, 20 reduction processing plants were in operation (Supplemental Table S.1).

Tagging and recovery efforts were carried out seasonally using commercial purse seines operating near reduction plants when menhaden were present (Nicholson, 1978). Individual fish were tagged onboard in batches of approximately 100 using small (1.4 × 0.3 × 0.05 mm) ferro-magnetic stainless-steel tags. The tags were inserted into the body cavity through a small incision just above and behind the pelvic fin using a spring-loaded tagging device (Carlson and Reintjes, 1972; Dryfoos et al., 1973; Pristas and Willis, 1973). Each tag was uniquely coded with prefixed letters and a two-digit identifier (00-99). Approximately 5% of tagged fish were randomly sampled for biological measurements, including fork length (mm FL) and scale samples collected for age determination (Coston, 1971).

Tagged fish were immediately released back into the water at the same site of capture. Some tagged fish likely experienced mortality due to handling stress or tag shedding (Kroger et al., 1974). If unaccounted for, these losses could bias parameter estimates by inflating the assumed numbers of released individuals. To address this issue, Kroger and Dryfoos (1972) and Dryfoos et al. (1973) conducted mark-survival experiments to estimate area-specific tagging loss and post-tagging mortality. These estimates were used to adjust release numbers accordingly.

2.2.1 Dataframes

Two dataframes documenting the NMFS mark-recapture study were used in this analysis: (1) Coston's (1971) technical report (hereafter called "Coston data"); and (2) the NMFS (2022) digital files (hereafter called "NMFS data"). The Coston data summarized the number of menhaden tagged and released by month and area, along with subsequent recoveries by plant-based "primary" magnets, organized by monthly cohorts and recovery location. However, this dataset lacked detailed information collected on individual tag histories, such as tagging vessel ID, recovery plant, or secondary magnet detection (**Table 1**).

The NMFS digital database was originally stored at the NOAA Southeast Fisheries Science Center (SEFSC) in Miami, FL. During a computer system upgrade and data transfer in the early 1990s, the original digital data files were lost (SEDAR 40, 2015). Recognizing the importance of these data for stock assessments, the Atlantic States Marine Fisheries Commission (ASMFC) reconstructed the database from surviving 40 year old paper records. This effort recovered approximately 76% of the original records, more than 70.7% of which were from regions 3 and 4. The reconstructed dataset consists of two dataframes: (1) field-released (fr) tags and associated recoveries; and (2) plant test (pt) trials for evaluating magnet efficiency. Each dataframe contains daily entries from July 1966 to February 1971 and includes unique tag serial numbers, allowing precise identification of individual fish. Unlike the Coston data, the NMFS (2022) dataset includes recoveries from both primary and secondary magnets (i.e., all recovery stations).

Data organization and analyses were performed using R (The R Foundation for Statistical Computing 2021; Wickham and Grolemund, 2020). The Field release (fr) data were originally stored in 10 Excel files and were restructured into three sub-dataframes for the years 1966-1969 (**Table 1A**):

(1) fr_releases – batches of released tags.
(2) fr_lengths – length measurements for approximately 5% of tagged individuals.
(3) fr_recoveries – individual tags recovered at all plants by all magnets.

The Plant Test (pt) data, from five Excel files, were reorganized into two sub-dataframes (**Table 1B**):

(1) pt_releases – batches of series-labeled individual tags "seeded" into vessel landings at specific plants.
(2) pt_recoveries – individual tags recovered at plants by both primary and secondary magnets.

To ensure comparability with the analyses by Liljestrand et al. (2019a), we aggregated the NMFS data following the same structure as the Coston data--by month and area over the 42-month study period.

2.2.2 Plant magnet tag recovery efficiency

The mark-recapture study assumed complete mixing of tagged and untagged fish in the ocean and, consequently, a 100% reporting rate for tags recovered by commercial purse seine vessels. After landing, catches were delivered to processing plants (Supplemental Table S.1), where implanted ferromagnetic tags were recovered using high-strength magnets installed throughout each plant's processing system. These magnets were originally designed by plant operators to remove all potentially harmful metal debris from the fish meal (Kroger and Dryfoos, 1972; also see Fig. 8 of Ahrenholz et al, 1991).

For proper use of the Coston data, a principal issue was how to establish a quantitative definition of "Primary" magnets. This was resolved by cross-referencing the 1966 NMFS tag release data with Coston's records. This revealed complete overlap in equivalent numbers (i.e., 88,898) of menhaden released (c.f., **Table 4**), confirming that recovery stations 1 and 2 corresponded to "Primary" magnets (Supplemental Table S.3). This designation aligned precisely with the recoveries reported in Coston (1971). The NMFS data included recoveries from "All" (i.e., all recovery stations) magnets at each plant (Supplemental Table S.4), encompassing all primary and secondary units.

"Primary" magnets were installed near the meal dryer along the conveyor system that transported cooked and dried fish scrap to storage areas. These magnets typically recovered tags within two days of the fish entering a plant (Parker, 1973; Nicholson, 1978). "Secondary" magnets, defined as recovery stations beyond stations 2, were located further downstream in the processing--typically near grinders where fish scrap was processed into meal. Because fish scrap could remain in storage prior to grinding, secondary magnets could recover tags days to weeks after initial processing (Nicholson, 1978). The data recorded only the plant where the tag was recovered, not the original location where the tagged fish was caught. Recovery magnets were cleaned at varying intervals, from daily to several days, depending on plant processing activity. Tag separation involved a multistep procedure: (1) material scraped from magnets (a mixture of fish scrap and metal debris) was spread on a flat surface; (2) a magnetic sweeper was used to concentrate metal fragments; (3) the collected metal was sorted through sieves; and (4) the remaining mixture was manually searched over a contrasting background to isolate tags (Parker, 1973).

Despite these efforts, not all implanted tags were recovered. To assess magnet recovery efficiency, experimental batch trials were conducted at 19 of the 20 menhaden reduction plants in operation between 1966 and 1971 (no trials were conducted at plant #8). Each trial involved seeding approximately 100 known tagged menhaden into commercial landings and monitoring recovery. In total, 964 batch trials were conducted.

For each batch trial *b* at plant *p*, the number of recovered tags *m* from *r* releases was modeled using a binomial distribution, with magnet efficiency (ε_p) estimated as the probability of recovery at each plant (see Eq. 1 of Liljestrand et al., 2019a). Magnet efficiencies (i.e., fraction of recovered tags per batch) were calculated for two different magnet configurations: (1) "Primary" magnets only, to align with Coston data structure; and (2) "All" magnets, to match the NMFS data structure. Annual magnet efficiency was calculated for each plant across all six years, including zero-recovery batches (Supplemental Tables S.3A & S.4A). Area-level efficiencies were then derived by averaging plant-specific efficiencies from 1966 to 1971 across all batch trials within each of the four geographical areas (Supplemental Tables S.3B & S.4B).

2.3 Nominal fishing effort

To support modeling, we developed a time- and space-resolved structure of nominal fishing effort, stratified by year, month (m), and area (a), denoted as $f_{m,a}$, covering the period from July 1966 through December 1969. Due to confidentiality restrictions imposed by the fishing industry, we did not have access to detailed commercial fishing effort and landings data by month, plant, and area. However, we were able to obtain coastwide monthly estimates of Atlantic menhaden fishing effort and landings for 1966-1970, provided by Ray Mroch (NOAA SEFSC, Beaufort, NC, pers. comm.). Fishing effort was reported in vessel weeks (vw), and landings were reported in both metric tons (mt) and industry-standard numbers (1,000 standard fish, ksf). These data revealed that Liljestrand et al. (2019a) underreported fishing effort (vw) by an average of -47.8% annually (SAS M WG, pers. comm.). To construct the required model input matrix of fishing effort data, the following steps were taken:

(1) Coastwide annual fishing effort data (vw) were disaggregated by area (a) using the annual effort proportions reported in Liljestrand et al.'s (2019a, Table A.4) for 1966-1969.

(2) Assuming that observed recaptures were proportional to fishing effort, we distributed annual effort across months using monthly recapture probabilities to generate fishing effort by month by area $f(\mathrm{m,a})$.

(3) Because no tagging occurred in areas 1, 2, and 4 in 1966, and no recaptures were reported, monthly effort distribution for those areas in 1966 were estimated using the average monthly distribution from 1967 to 1969, weighted by the area-specific annual fishing effort.

2.4 Multistate mark-recovery model

To facilitate direct estimation of mortality rates, we employed the multistate mark-recovery (MMR) model of Liljestrand et al. (2019a), coded in AD Model Builder (ADMB) software (Fournier et al., 2012), that used a Bayesian parameter estimation approach applied to the Brownie dead recovery model (Brownie at al., 1993; Hoenig et al., 1998). Survival and mortality rates derived from tagging data using the Brownie model have been extensively studied (e.g., Seber, 1982; Brownie et al., 1985; Lebreton et al., 1992). The MMR model assumed that all tagged-and-released cohorts released in each month (m) and area (a) were independent and well-mixed, with known area-specific tagging shedding/mortality rates $\left(G_{A_i}\right)$. Additionally, all individuals within a given area were assumed to experience the same dynamics, regardless of age or size. The initial cohort size in area A_i was calculated by applying the tagging mortality rate G_{A_i} to releases (see Eq. 3 of Liljestrand et al., 2019a). The number of individuals in a cohort released in area A_i at time *t* who were still alive in an area A_j at time $t + \Delta t$ was used to estimate the time- and area-specific survivorship rates. The MMR model tracked released cohorts with variable instantaneous mortality rates and movement probabilities between areas. Specific model parameter values are described in **Table 2**. At each time step Δt ($\Delta t = 1$ month), survival and movement were modeled sequentially, with movement occurring after survival was computed. The number of tagged fish ($N_{T,A,t,a}$) in each month and area, from an initial tagged cohort ($N_{T,A,T.A}$) after release, was determined as a function of tagging mortality, migration, and both natural and fishing mortality. Mortality equations were combined as follows:

$$Z_{t,a} = M + F_{t,a} = M + Q_a e^{\theta_{m,a}} f_{t,a} \quad (1)$$

where $Z_{t,a}$ and $F_{t,a}$ represent total and fishing mortality rates, respectively, at each monthly time step $(t = 1, \cdots, 42)$, area $(a = 1, \cdots, 4)$, and calendar month $(m = 1, \cdots, 12)$. Natural mortality rate M was treated as a single constant parameter value over all months and areas. Fishing mortality rate (F) was simultaneously estimated as a product of three components: (1) Q_a, the area-specific catchability effect; (2) $\exp^{\theta_{m,a}}$, an exponential month-by-area catchability effect; and (3) $f_{t,a}$, the time-by-area nominal fishing effort. The time by area nominal fishing effort $[f_{t,a}]$ matrix was used to compute estimated recoveries for each monthly released cohort. This calculation incorporated four steps: (i) the product of time- and area-specific abundance $N_{T,A,t,a}$; (ii) the proportion of total mortality attributed to fishing; (iii) the fraction of the population that died from natural causes; and (iv) the time- and area-specific magnet efficiency rate $\varepsilon_{t,a}$ (see Eq. 9 of Liljestrand et al., 2019a). In the first month between release and recovery $(t = \mathrm{T}, \mathrm{a} = \mathrm{A})$, it was assumed that there was no natural mortality for calculation of $N_{T,A,t,a}$. The time-area specific magnet efficiency $\varepsilon_{t,a}$ to recover the ferromagnetic tags at each reduction plant *p* for each trial *a* was estimated as shown in Supplemental Tables S.2-S.6. Natural (M) and fishing (F) mortalities were estimated as monthly values. The constant annual M rate was obtained by multiplying the monthly rate by 12. Annual fishing mortality for each year was a more complicated calculation because the $F_{t,a}$ values were different for each time step (t) and area (a). For each year (y) and area, annual fishing mortality $F_{y,a}$ was calculated in Liljestrand et al.

(2019a) as the sum of the monthly $F_{t,a}$ values within the year for each area. However, we corrected the computation of annual F_y for all areas, assuming tags are proportional to the population, as the annual average of the $F_{y,a}$ for each area weighted by the number of tags still out in the water in that area.

2.5 Model analyses & magnet efficiencies

The Multistate Mark-Recovery (MMR) model was adapted and applied to achieve several objectives: (1) recreating the analyses of Liljestrand et al. (2019a); (2) evaluation and comparison of the Coston and NMFS dataframes; (3) use of multiple methods to determine magnet efficiencies and assess the statistical efficacy of resultant natural mortality estimates. Experimental design of these analyses is presented in **Table 3**. Initially, our approach followed the methodology of Liljestrand et al. (2019a) with fixed values of $k = 2.5$, $v = 10$, constant area-specific vector of Q_a values; and $\theta_{m,a}$ estimated for each month and area. The MMR model was further utilized to examine the two types of magnet efficiency estimates: (1) an area "constant" approach in which the mean area magnet efficiencies were the same over all months in which recaptures occurred; and (2) an as "parameters" approach in which the MMR model estimated magnet efficiencies as parameters (**Table 3**). These two methodological approaches allowed us to assess how different representations of magnet efficiency influenced the estimation of mortality rates and the model's statistical performance.

2.5.1 Constant average plant-area magnet efficiencies $(\varepsilon_{t,a})$

The "constant" method computed area averages of plant magnet efficiencies from 1966-1971 as fixed values in the $\varepsilon_{t,a}$ matrix consistent with the approach used by Liljestrand et al. (2019a). These area-specific constant values were applied at time steps corresponding to observed tag recoveries in each area. Liljestrand et al. (2019a) also used the area-specific landings as a weighting factor for the average $(\bar{\varepsilon}_a)$; however, we were denied landings data by industry. Analysis of the plant-level batch trial data revealed substantial temporal and spatial variability in magnet efficiencies, indicating that area-averaged values were poor descriptors of the underlying statistical distributions. Observed magnet efficiency coefficients $(\varepsilon_{m,a})$, from plant trials ranged from 0.00 (very low detection) to 1.00 (near-perfect detection), with a mean of 0.5566 and standard deviation of 0.2722, yielding a 95% confidence interval of [0.02, 1.00]. To evaluate this constant-efficiency scenario, model assessments were conducted using both the Coston and

NMFS dataframes. After achieving positive definite Hessians, a Markov Chain Monte Carlo (MCMC) simulation with 4,000,000 iterations was used to estimate the posterior mean and standard error of the natural mortality (M) parameter. The same MCMC simulation was performed for all datasets and approaches. The impact of catch-weighted magnet efficiencies by month and area was found to be minimal compared to the actual variation observed in the batch trials (Supplemental Fig. S.1; SAS M WG, pers. comm.).

2.5.2 Magnet efficiencies $(\varepsilon_{t,a})$ *estimated as model parameters*

Empirical analysis of the plant-level magnet efficiency data showed that the $\varepsilon_{t,a}$ deviated significantly from normality, and instead followed random, nonparametric distributions (**Figs. 4-5**). Thus, area-averaged values were poor representatives of actual efficiencies, particularly across time and space. To address this issue, we implemented a modeling approach in which magnet efficiencies were treated as estimable parameters, denoted $\hat{\varepsilon}_{t,a}$, similar to Liljestrand et al.'s (2019a) treatment of the catchability parameter $\Theta_{t,a}$. The MMR model was modified to estimate each $\hat{\varepsilon}_{t,a}$ individually, based on the number of non-zero recapture cells in the time-area matrix. The total number of estimated magnet efficiency parameters was equal to the number of non-zero time-area recapture cells. For example, the Coston dataframe contained 100 such non-zero elements, requiring 100 additional parameters for estimation. These parameter values were estimated on the log scale as $\ln(\hat{\varepsilon}_{1,n})$, consistent with the estimation of $\ln(\Theta_{t,a})$ in the model. Log-transformed parameter bounds were imposed to constrain estimates within biologically plausible ranges: (i) Coston data (primary magnets) within log bounds of [-3.5 to -0.05], corresponding to efficiencies of $[0.03, 0.95]$; and (ii) NMFS data (all magnets) within log bounds of [-2.0 to -0.05], corresponding to efficiencies of $[0.135, 0.95]$. Adding these 100 new parameters to the original 106-parameter MMR model brought the total parameter count to 206. The data matrix used in the model was defined as:

$$\text{months tagged} \times \text{Areas} \times \text{months recaptured} \times \text{Areas} = 42 \times 4 \times 42 \times 4 = 28{,}224 \qquad (6)$$

This yielded 28,224 data points and, after parameter estimation, 28,018 degrees of freedom (i.e., $28{,}224 - 206$). This definition of "degrees of freedom" was not used for statistical inference *per se* (e.g., as in GAMs or likelihood ratio tests), where effective degrees of freedom and autocorrelation adjustments would be necessary. Instead, we simply make a basic comparison of the number of estimated parameters to the total number of observations to ensure that model robustness remained unaffected with additional parameters.

To evaluate and compare model performance, we used the Akaike Information Criterion (AIC):

$$\mathrm{AIC} = -2\ln(\mathrm{L}) + 2\mathrm{K} \qquad (5)$$

where K represents the number of estimated parameters in the model, and L is the maximum value of the likelihood function. AIC provides a measure of predictive accuracy and allows objective model selection. Lower AIC values indicate better-fitting models, balancing model complexity with goodness of fit.

2.5.3 Magnet efficiency sensitivity

To help evaluate the influence of magnet efficiency (ME) assumptions on model outcomes, we developed a "stepwise" method that was designed as a heuristic tool to explore the sensitivity of natural mortality estimates to increasing model complexity, the spatial-temporal resolution of MEs, and to assess the internal consistency of recapture predictions under varying assumptions of magnet efficiency—specifically, how different assumptions affected the model's ability to replicate observed recoveries. This was done simply to inform model comparisons and interpretation, not as a formal hypothesis-testing framework. In contrast to the "parameters" method where MEs are estimated as model parameters, the "stepwise" method served as a diagnostic tool, systematically estimating MEs in stages to assess how sensitive model performance was to changes in magnet efficiency. The "stepwise" method began with the use of area-constant magnet efficiencies, then progressively incorporated adjusted efficiency values estimated directly from the model. This approach is analogous to scenario testing and was not intended for *post hoc* parameter tuning or model calibration. To keep the main text concise, we included a description of the "stepwise" method in the Supplemental Materials (Table S.7), including parameter configurations and results. This method showed that both AIC and prediction error decreased sharply when moving from constant ME (Step 0) to estimated ME (Step 1), indicating that fixed average values for magnet efficiency were suboptimal.

3.0 Results

Results were produced from indirect and direct approaches. Survivorship at maximum age information from the stock assessment literature was used in the indirect approach, and both the Coston and NMFS dataframes were used in the direct approach.

3.1 Indirect estimation of natural mortality

A review of national-international stock assessments of natural mortality rates (M) as a function of observed maximum age ($a_{\max}$) across a broad spectrum of exploited species indicated that the majority ($> 92\%$) of these natural mortality rates fell within lifespan survivorship probabilities bounded by $S_{\max}(0.05)$ and $S_{\max}(0.0045)$ (**Fig. 2**; Supplemental Table S.2). Notably, the SEDAR 40 (2015) natural mortality rate of $\widehat{M} = 0.50$ fell within these bounds, but the $\widehat{M} = 1.17$ used in SEDAR 69 (2019) was significantly greater than the $S_{\max}(0.0045)$ probability. In fact, the SEDAR 69 estimate was +14 standard deviations higher than the mean of more than a dozen previously published peer-reviewed papers. Schueller et al. (2014), based on a half-million aged observations, showed that even under exploitation that Atlantic menhaden longevity likely is $a_{\max} \geq 10$ year. Assuming $a_{\max} = 10$ represents a reasonable minimum bound, employing empirical life history principles suggests $M \in [0.30, 0.54]$ as the most reasonable range for the natural mortality rate of Atlantic menhaden.

3.2 Direct: mark-recovery & magnet efficiency

We were unable to replicate the analyses of Liljestrand et al. (2019a) to verify their conclusions using the Coston data due to several reporting errors in their study. Some of these errors were relatively minor, such as an overreporting of total tagged releases in their Appendix Table A.2, which listed 1,066,448 releases — 91 more than the actual 1,066,357 reported releases. However, other errors were substantially more significant. For example, their Table A.3 listed 89,116 total recaptures, some 13,876 fish less (~ -13.5%) than the 102,992 recaptures reported in Coston. Additionally, plant magnet tag recovery efficiency was overstated by Liljestrand et al. (2019a) because they used "All" recovery magnets in their analyses, whereas Coston specifically stated that recoveries were from only "Primary" magnets.

In terms of the actual Coston data, between July 1966 and December 1969 1,066,357 tagged releases were spread over four areas; 65.1% of these releases occurred in Areas 2 (Chesapeake Bay) and 3 (North & South Carolina) (**Table 4A**). From the Coston releases there were 102,992 recaptures, of which approximately 82.5% of these were also made in Areas 2 and 3 (**Table 5A**). With respect to the NMFS dataframe summarized monthly by year and area between July 1966 through December 1969 similar to the organization of Coston, a total of 767,954 releases were recorded; about 63.1% of these occurred in Areas 2 and 3 (**Table 4B**). Approximately 7% $(n = 53{,}746)$ of the NMFS releases were measured for fork length (FL), and some fish exceeded 600 mm FL (23.6 in FL). Comparison of the Coston and NMFS data showed similar time-space release and recovery patterns, which to some extent was expected since the NMFS data was a subset of the Coston data. A total of 93,335 (12.2%) of the NMFS releases were recovered, with 82.6% of these recaptures occurring in Areas 2 and 3 (**Table 5B**), which closely matched the 82.5% for the same areas in Coston (**Table 5A**). On the other hand, the total recoveries-to-release ratios for the two dataframes differed by about 3%. The Coston ratio was $102{,}992/1{,}066{,}357 = 0.0966$; while the NMFS ratio was of $93{,}335/768{,}877 = 0.1214$. This difference resulted from the fact that NMFS data included recoveries from "All" magnets (all recovery stations), whereas Coston accounted for recoveries only by "Primary" magnets. The number of magnet efficiency batch trials per plant varied between 2 and 151, averaging about 50 per plant (Supplemental Tables S.3-S.4). Analysis of the distributions of magnet efficiencies, measured as the fraction of tags recovered per batch, showed that for "Primary" magnets the area-specific mean magnet efficiency estimates were $[\text{Area 1}, \text{Area 2}, \text{Area 3}, \text{Area 4}] = [0.5790, 0.4211, 0.6075, 0.5063]$, and for "all" magnet efficiency by area were $[0.7451, 0.6618, 0.8190, 0.6758]$. Visual inspection of the magnet efficiency trial data revealed non-normal distributions and parametric area-means did not accurately represent the central tendency, either when considering individual plants by areas or by all plants combined within areas (**Figs. 4 & 5**).

3.*3* *Nominal fishing effort*

More than 100 vessels participated in the NMFS mark-recovery study during 1966 to 1969, which likely did not constitute a complete census of all operating commercial menhaden fishing vessels. Working recently with the SAS M WG, we discovered that the 1966-1969 nominal fishing effort was under-reported by Liljestrand et al. (2019a) by an annual average of -47.8%, with a maximum error of -102% in 1967. In contrast, our total fishing effort reconstruction showed relatively good agreement (**Table 6**). Estimated nominal fishing effort by year, month, area is given in Supplemental Table S.6.

3.4 Direct estimation of population mortality rates

Model fits to data from initial runs for the Coston & NMFS data and two magnet efficiency methods (i.e., "constant" and "parameters") are compared graphically in **Fig. 6**. Left column panels show Coston data analyses, while right column panels show NMFS data analyses. The "constant" method is shown in **Figs. 6A & 6C**, and the "parameters" method in **Figs. 6B & 6D**.

Both "constant" and " parameters" methods achieved positive definite Hessians. MCMC analyses showed the variability of the M parameter estimates (**Fig. 7**).

Standard statistical criteria using both data sources were applied to facilitate selection of the best MMR model estimates of mortality rates using three key metrics: (1) the Akaike Information Criterion (AIC), (2) the differences (Δ) between observed and model-predicted recaptures, and (3) visual inspection of the fit between observed versus model-predicted recaptures. For both datasets, $\mathrm{AIC}_{\mathrm{constant}} \gg \mathrm{AIC}_{\mathrm{parameters}}$ (**Table 7**). For the Coston data, the "constant" method over-estimated tag recoveries by +89.9%, whereas the "parameters" approach was significantly more accurate with slight over-estimation of recoveries at +9.8% above the observed with an AIC reduction of 9.3%. For the NMFS data, the 'constant" method over-estimated tag recoveries by +42.8%, whereas the "parameters" method was only +13.6% greater than observed, with an AIC reduction of 13.5%. Visualization inspection of initial run fits further supported the "parameters" approach (**Fig. 6**). MCMC estimates (**Fig. 7**) using the "parameters" method were slightly lower than initial run estimates with mean M values of 0.50, as compared to 0.55 for the initial runs using Coston data. The mean M values were 0.54 compared to 0.57 for the initial runs using NMFS data (**Table 7**). For the Coston data, $\widehat{M} = 0.50$ $(\mathrm{sd} = 0.0696)$ (**Fig. 7B**); and for the NMFS data, $\widehat{M} = 0.54$ $(\mathrm{sd} = 0.0398)$ (**Fig. 7D**). The "constant" method obtained $\widehat{M} = 0.90$ $(\mathrm{sd} = 0.0331)$ for both Coston and NMFS data (**Fig. 7A, C**). Other Stepwise cases are given in the Supplemental Materials (Table S.8 & Fig. S.2). Summary results from MMR model runs for $S, Z, M,$ and F are provided in **Table 7**. The resulting frequency distributions of primary ME parameters using the Coston dataset are shown in **Fig. 8**. Of the 100 ME parameters, eight were estimated at the bounds (i.e., 7 at the lower bound of 0.03 and 1 at the upper bound of 0.95), while the remaining parameters fell well within the allowable range.

Annual instantaneous fishing mortality rates varied substantially across areas (**Fig. 9**), ranging from 0.33 in Area 2 in 1969 to 3.51 in Area 3 in 1968. Annual average instantaneous fishing mortality rates calculated as the simple average of the area-specific rates did not account for the differing proportions of the population between areas (**Fig. 9A**). The weighted-average annual fishing mortality rate, using population abundance estimates derived from the model to weight each area's contribution are shown in **Fig. 9B**. The annual average fishing mortality rate (F), calculated as the sum of these weighted values for each year, and the overall average F (reported in **Table 7**) were computed as the mean across all years. The "constant" method yielded lower F values—ranging from 0.79 (Coston) to 1.06 (NMFS)—compared to the "parameters" method, which produced higher F estimates of 1.35 (NMFS) and 1.46 (Coston). The estimated $\mathrm{M/F}$ ratios for the "constant" method ranged from 0.85 (Coston) to 1.13 (NMFS). These ratios were identical at 0.37 under the "parameters" method. Overall, these $\mathrm{M/F}$ ratios indicated that fishing mortality (F) accounted for a much larger portion of total mortality (Z) than previously reported by Liljestrand et al. (2019a).

4.0 Discussion

Natural mortality significantly influences assessment model dynamics and plays a vital role in determining stock productivity and status relative to sustainability reference points (Punt et al., 2021; Cope and Hamel, 2022; Hoyle et al., 2023; Hamel et al., 2023; Maunder et al., 2023; Artetxe-Arrate et al., 2024). More than a dozen published estimates of the Atlantic menhaden natural mortality rate prior to 2019 ranged from M = 0.37 to 0.53 with a mean of 0.46. In the absence of fishing this rate corresponds to an annual mortality rate (A) of 36.9%. Fogarty et al. (1989) considered $M = 0.45\ \mathrm{yr}^{-1}$ to be high relative to other pelagic marine prey species, such as Atlantic herring $(\mathrm{i.e.}, \mathrm{A} = 0.18, M \approx 0.20)$. Since Atlantic menhaden are the largest and longest-lived species of the genus *Brevoortia* (Ahrenholz, 1991), Fogarty et al. (1989) suggested that a low value of M would be logical. Misspecification of M can result in significant bias in the perception of stock status. Overestimation of M leads to underestimation of fishing mortality and overly optimistic estimates of spawning stock size, which impacts recommended harvest rates and quotas (Mertz and Myers, 1997; Clark, 1999; Kraak et al., 2008; Punt et al., 2021; Ault et al. 2022). SEDAR 69's (2019) use of Liljestrand et al.'s (2019a) $\widehat{M} = 1.17$ required that recruitment (R_0, addition of the youngest age class to the stock each year) and stock biomass had to be 29 and 3.2 times larger, respectively, than in SEDAR 40 (2015) to achieve equivalent yields.

Our reevaluation of stock mortality rates resulted in a revised natural mortality estimate of M = 0.52, less than half of Liljestrand et al.'s (2019) estimate. After correcting errors, the primary driver of the difference in M was not the confidential fishing effort data, but rather methodological differences in methodological application of the tag recovery efficiencies. These findings should facilitate evaluation of management objectives against risk tolerance (Ault et al., 2019, 2022; Maunder et al., 2023; Cope, 2024).

4.1 Indirect: life history & longevity

The utility of age data for estimation of natural mortality is widely recognized. Since maximum age ($a_{\max}$) is a direct empirical observation—not a model assumption—it provides an independent line of evidence about lifespan and mortality rates, especially when considered alongside tagging data to produce the most scientifically robust estimates of natural mortality. While some ages may be misclassified, and aging uncertainty should be accounted for, this does not invalidate the broader distribution of observed ages in the data, particularly such as the large number of aged Atlantic menhaden. Ageing error increases for the oldest fish, making it more likely that the estimated ages for the oldest fish would be biased low due to difficulty in discerning individual bands in slow-growing fish at old age (Hamel and Cope, 2023). Beverton (1992) noted that the accuracy of $a_{\max}$ was less dependent on sample size than might be thought.

More than 50 years and a half-million aged individuals have shown that Atlantic menhaden were repeatedly observed to live to at least 10 yrs old (Schueller et al. 2014; SEDAR 69, 2019). These data provide an informative upper bound on natural mortality, so that dismissing the aging data entirely risks excluding a valuable source of information. From a life history-longevity perspective, Liljestrand et al.'s (2019a) $\widehat{M} = 1.17$ is untenable since at that natural mortality rate a fish would have no chance (i.e., 0.000008 probability) of surviving to reach the observed maximum age ($a_{\max}$). Conversely, assuming $S_{\max} = 0.015$ following Dureuil and Froese (2012), then $a_{\max} \cong 3.6$ years which again implies that in an unexploited population very few fish would survive beyond age 4. This does not align with the data. The majority of M-values used in national-international fish stock assessments identified in our review of stock assessments, including those for pelagic forage fishes, fell between indirect methods probability bounds, specifically $\mathrm{S}_{\max}(0.05)$ and $\mathrm{S}_{\max}(0.0045)$ (**Fig. 2**). Using these survivorship boundaries, we found that the range $\mathrm{M} \in [0.30, 0.54]$ encompassed every Atlantic menhaden natural mortality rate estimate prior to that of Liljestrand et al. (2019a).

The true unfished lifespan a_λ of Atlantic menhaden is basically unknown since the stock has been exploited since the 1500s (Franklin, 2007). However, a_λ is likely greater than the maximum age observed in today's fishery (i.e., about four years and mid-300 mm FL). Notably, in the 1960s large menhaden ≥ 550 mm FL were observed (NMFS, 2022) which is consistent with maximum sizes reported by Goode (1879), Hildebrand (1963), Cooper (1965), and Smith and O'Bier (1996). Ahrenholz (1987) stated numerous dominant year classes with broad age structure and presence of large menhaden observed in the mid-1960s were due to strong recruitment events in the 1950s. However, due to intensive exploitation, by the late 1960s Atlantic menhaden stock size contracted, recruitment declined and age/size structure was truncated with few dominant year classes.

4.2 Direct: mark-recapture

The Atlantic menhaden mark-recapture study has contributed to scientific understanding of stock structure, migratory patterns, survivorship, fishing and natural mortality rates (Dryfoos et al., 1973; Nicholson, 1978; Reish et al., 1985; Ahrenholz, 1991), and informed assessments (SAR 99-01, 1999; SEDAR 3, 2003; SEDAR 20, 2010; MSVPA-X, 2010; SEDAR 40, 2015; SEDAR 69, 2019). While estimation of M is challenging and remains a major source of uncertainty in stock assessments (Vetter 1988; Hampton, 2000; Then et al., 2015; Punt et al., 2021; Hamel and Cope, 2022), data from well-designed mark-recapture studies is thought to provide the most promising direct method to estimate M (Maunder et al., 2023).

4.2.1 Dataframes

Coston and NMFS data were used in the MMR model to: (1) attempt verification of the Liljestrand et al. (2019a) findings for the 1966-1969 period; and (2) compare results for this time period between dataframes.

4.2.2 Tag recovery efficiency at plants

Brownie models assume reporting rates are a function of complete mixing, i.e., tagged animals completely intermingle with the overall population after release, reflecting the probability that a tag is reported once recaptured. As a result, recaptured animals are mixed into catches in their tagged/untagged proportions and then delivered to the respective plants. Thus, under such models reporting rates are ~100%. Equating reporting rates with magnet efficiencies is not consistent with how detection processes worked in the mark-recapture study. Detection rates of tags at plants were a distinctly separate process from population dynamics (mixing). Although it was suggested during the SAS M WG process that adjustment of magnet efficiencies to fit recapture data equates to altering population dynamics equations, this notion conflates detection probability with population mixing, two separate model components.

Magnet efficiencies represent the probability of tag detection after tagged fish recaptured in the ocean were landed at a particular plant and processed. Incomplete mixing would affect the spatial distribution of tagged fish—not the magnet detection efficiency at plants. Plant batch-trial data revealed that magnet efficiency distributions deviated significantly from symmetric (normal), and instead resembled random nonparametric distributions (**Figs. 4-5**), indicating that all levels of magnet recovery efficiency were equally probable. Consequently, area-averaged magnet efficiencies led to inefficient use of the data and produced unreliable estimates of natural mortality. Magnet efficiency parameter distributions estimated across the four areas (**Fig. 8)** demonstrate that model-derived estimates better reflect the underlying data structures without imposing predefined probability functions. While this pattern does not exactly match the plant test data *per se*, nor was it expected to, it effectively captures the full range of observed magnet efficiencies which further underscores the limitations of using simple averages to represent these complex data.

4.3 Nominal fishing effort

Our method for generating nominal fishing effort by month and area effectively characterized effort during the period of the 1966-1969 mark-recapture study. The SAS M WG, which had direct access to the confidential fishing effort data, reported that our estimated effort was 99% accurate.

4.4 Model analyses & magnet efficiencies

A key decision was how to best represent magnet efficiencies in the estimation process. The modeling approach we employed to estimate magnet efficiencies (MEs) using observed tag recaptures and a negative log-likelihood framework directly linked the observed data with parameter estimation, minimizing reliance on external assumptions. Although the Brownie model assumes complete mixing to describe movements and mortality, plant-based magnet efficiency trials revealed considerable variation in tag detection across time, space, and facilities (**Figs. 4 & 5**). Rather than relying on simple parametric averages of non-parametric distributions, we incorporated all the empirical data to ensure a comprehensive estimation framework for natural mortality. Integrating both recapture data and the variability of trial-based magnet efficiency distributions was critical for achieving reliable model fits and scientifically robust mortality estimates.

4.4.1 Time constant average plant-area MEs

The empirical data showed highly variable non-parametric distributions of magnet efficiencies across plants, areas, and time, rather than a clustering around a central mean. Consequently, assuming constant mean efficiency for each area over time, as assumed by

Liljestrand et al. (2019a), was both statistically and biologically flawed. Correcting their errors using the "constant" method resulted in a 23.1% reduction in estimated M (i.e., 1.17 versus 0.90). Adjusting the area-average efficiencies by simple catch-weighting resulted in a minor difference of M = 0.94 (+0.04), and variation in the efficiencies remained far below that observed in batch trials (**Figs 4 & 5**). However, this simplification misrepresented the underlying uncertainty in magnet efficiencies and biased recapture predictions—over-estimating them by about 90% (**Table 7**).

4.4.2 MEs estimated as model parameters

Estimating magnet efficiencies (MEs) as model parameters provided a robust and data-driven alternative. The random, non-parametric distributions of plant magnet efficiencies made it especially difficult to derive informative mean values, and treating these efficiencies as fixed inputs would have misrepresented the true variability and structure of the plant-specific data. Our model was based on the Bayesian multi-state mark-recovery framework described in Liljestrand et al. (2019a), with updates to incorporate corrected input data. The primary modification was the estimation of magnet efficiencies as parameters, using the mean values from plant test data as prior estimates. This approach avoided strong distributional assumptions and better reflected the empirical heterogeneity observed in the plant trials. The ME parameters were optimized to align model-predicted recaptures with observed values, with estimation evaluated using an AIC framework. We acknowledge, however, that a fully Bayesian formulation could potentially integrate all available information and improve estimation, particularly for plants with sparse data.

Some simulation studies have argued that movement and mortality can be estimated under fixed "constant" magnet efficiency assumptions, but our results indicated that doing so with incorrect efficiency values leads to poor fits and biased estimates. Based on our discussions and correspondence with the authors of Liljestrand et al. (2019a), their primary objective was to estimate the movements of Atlantic menhaden between areas and seasons—that is, to derive a migration matrix. We used the prior distributions of movement parameter estimates from Liljestrand et al. (2019a) as initial conditions for all our model simulations, along with corrected releases, recaptures, and nominal fishing effort data. The model then re-estimated these movement parameters using the magnet efficiency method, fully incorporating the corrected data. Notably, the re-estimated movement parameters revealed seasonal and spatial movement patterns that were broadly consistent with those reported in the original study. In addition, parameter estimates, such as magnet efficiencies, consistently falling at their upper or lower bounds may indicate overparameterization or lack of sufficient information to support reliable estimation of all parameters. In our model for the Coston data, 8 out of 100 magnet efficiency parameters were estimated at the bounds (i.e., 7 at 0.03 lower bound, and 1 at 0.95 upper bound). Most estimated parameters fell well within the allowable range.

Finally, estimating magnet efficiencies as "parameters" allowed the model to reconcile both the recovery data and tag detection variability, yielding more accurate and defensible results, and aligned observed and predicted tag recaptures without relying on subjective assumptions. The "parameters" approach substantially improved model fits and reduced natural mortality rate (M) estimates. This approach was data-informed rather than parameter-driven, with the primary objective of aligning predicted recaptures with observed data. For both datasets, models that estimated magnet efficiencies as "parameters" produced recapture predictions much closer to the observed values, validating the approach.

4.5 Summary

Results from all analyses are summarized in **Table 7,** which presents survival (S), total mortality (Z), natural mortality (M), and fishing mortality (F) estimates for both Conston and NMFS dataframes. For the Coston data, which used only recoveries by "Primary" magnets, we found S $\in [0.14, 0.15]$, Z $\in [1.90, 1.96]$, M $\in [0.50, 0.90]$ and F $\in [1.06, 1.35]$. For the NMFS data, which included all magnet recoveries with a larger recovery fraction, S $\in [0.13, 0.19]$, Z $\in [1.69, 2.02]$, M $\in [0.54, 0.90]$ and F $\in [0.80, 1.46]$. The most probable survivorship estimates were S $\in [0.13, 0.15]$, with M $\in [0.50, 0.54]$, aligning well with prior literature (**Fig. 2**). Results were consistent between the Coston and NMFS datasets (**Table 7**). From the "parameters" approach, the average MCMC-based natural mortality estimates were M = 0.50 (Coston) and M = 0.54 (NMFS), with an average of M = 0.52, which was close to the life-history $p_{\text{max}} = 0.0045$ estimate of M = 0.54. We therefore recommend a natural mortality rate of $M \leq 0.52$ for use in Atlantic menhaden stock assessments. Given the ecological importance of Atlantic menhaden as a foundational prey species for a range of predators--including iconic sportfish, seabirds, and marine mammals—managing the stock to achieve and maintain maximum abundance should be a central goal of ecosystem-based fisheries management (Chagaris et al., 2020; Anstead et al., 2021).

Credit authorship contribution statement JSA developed the concept of the paper; **JSA** and **JL** created the initial draft and structure; both authors contributed to writing and editing.

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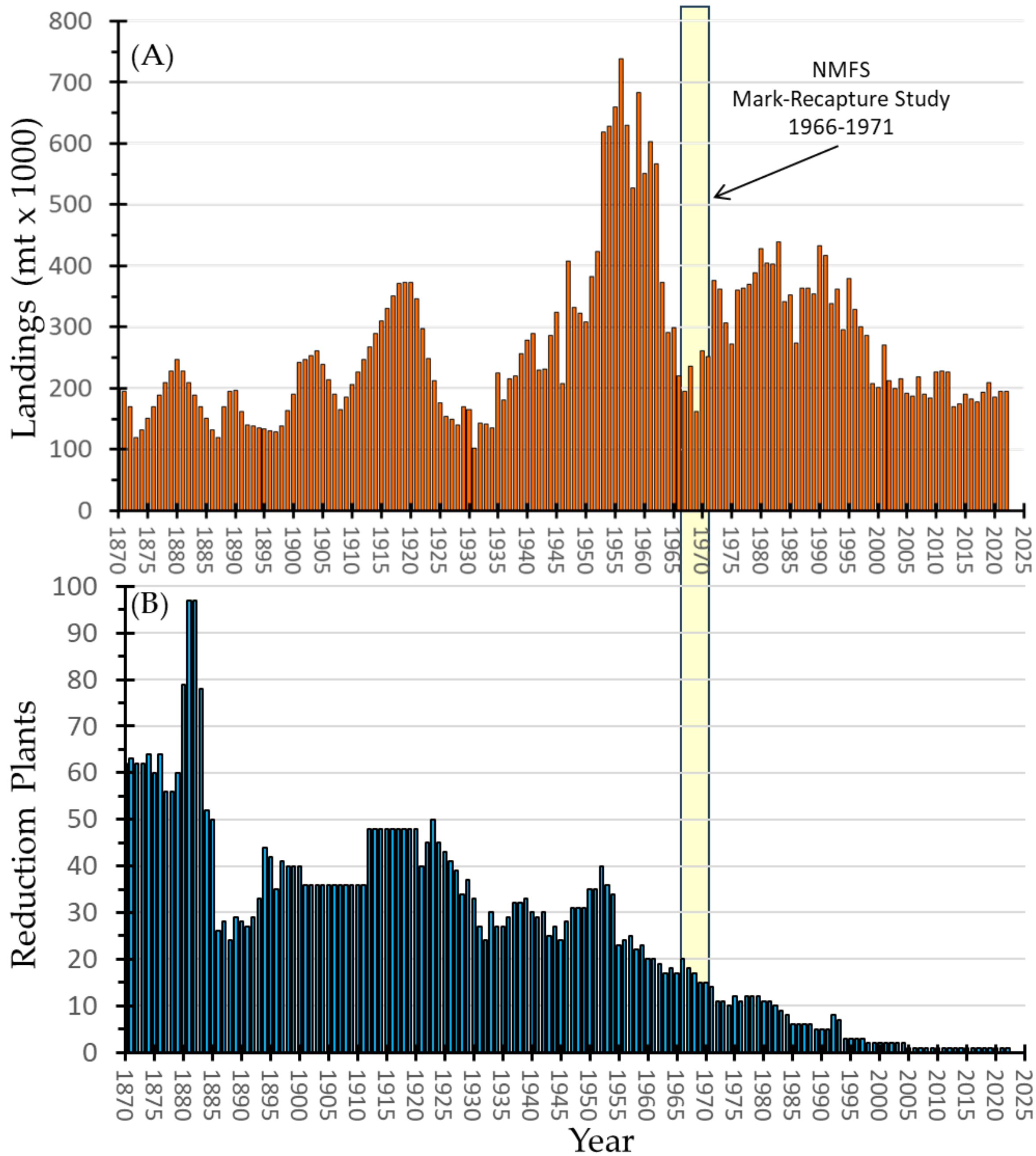

Figure 1.- 1870-2022 time series for the Atlantic menhaden fishery along the eastern United States seaboard: (A) landings (mt x 1000) which peaked at 738,499 mt in 1956. Cumulative landings were 41,262,505 mt (or 90,968,143,949 lbs); and (B) operational menhaden reduction plants which peaked at 98 in 1882. Vertical yellow bar highlights the 1966-1971 NMFS mark-recapture study period.

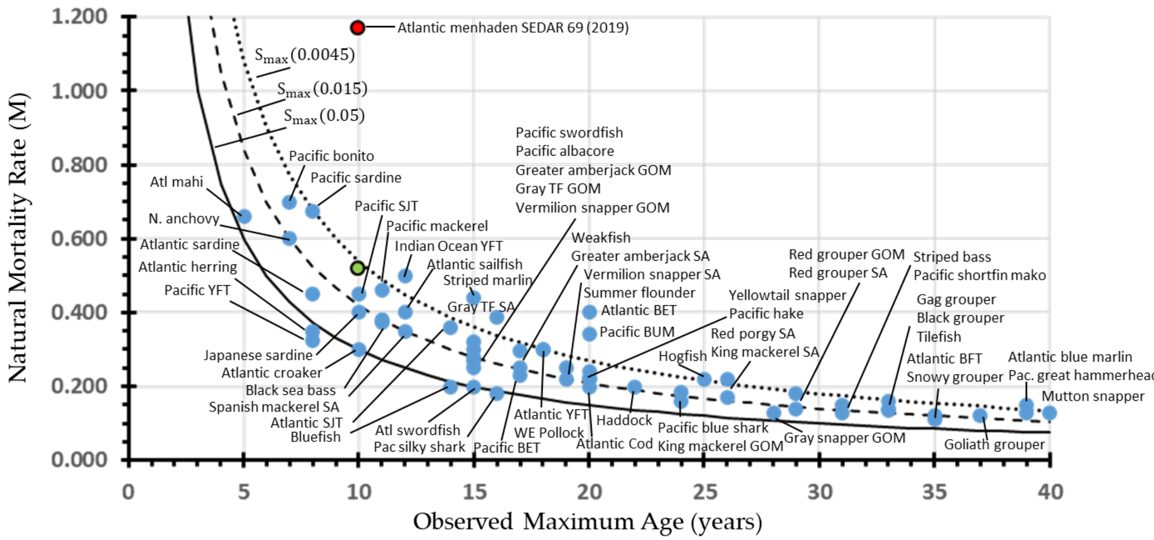

Figure 2.- Natural mortality (M) rate as a function of maximum age $M = f(a_{\max})$ for individual species (blue filled circles) used in >60 recent national (USA) and international fishery management council and commission stock assessments (see Table S.2). Lower solid hyperbolic line is $S_{\max}(0.05)$ probability of $M = f(a_{\max})$ of Alagaraja, 1984; dashed line is $S_{\max}(0.015)$ probability of Dureuil and Froese, 2021; and, dotted line is the $S_{\max}(0.0045)$ probability of Hamel and Cope, 2022. Note the significantly increased value of M (red filled circles) in the SEDAR 69 (2019) Atlantic menhaden stock assessment. Green circle is the best Atlantic menhaden natural mortality rate estimated in this paper.

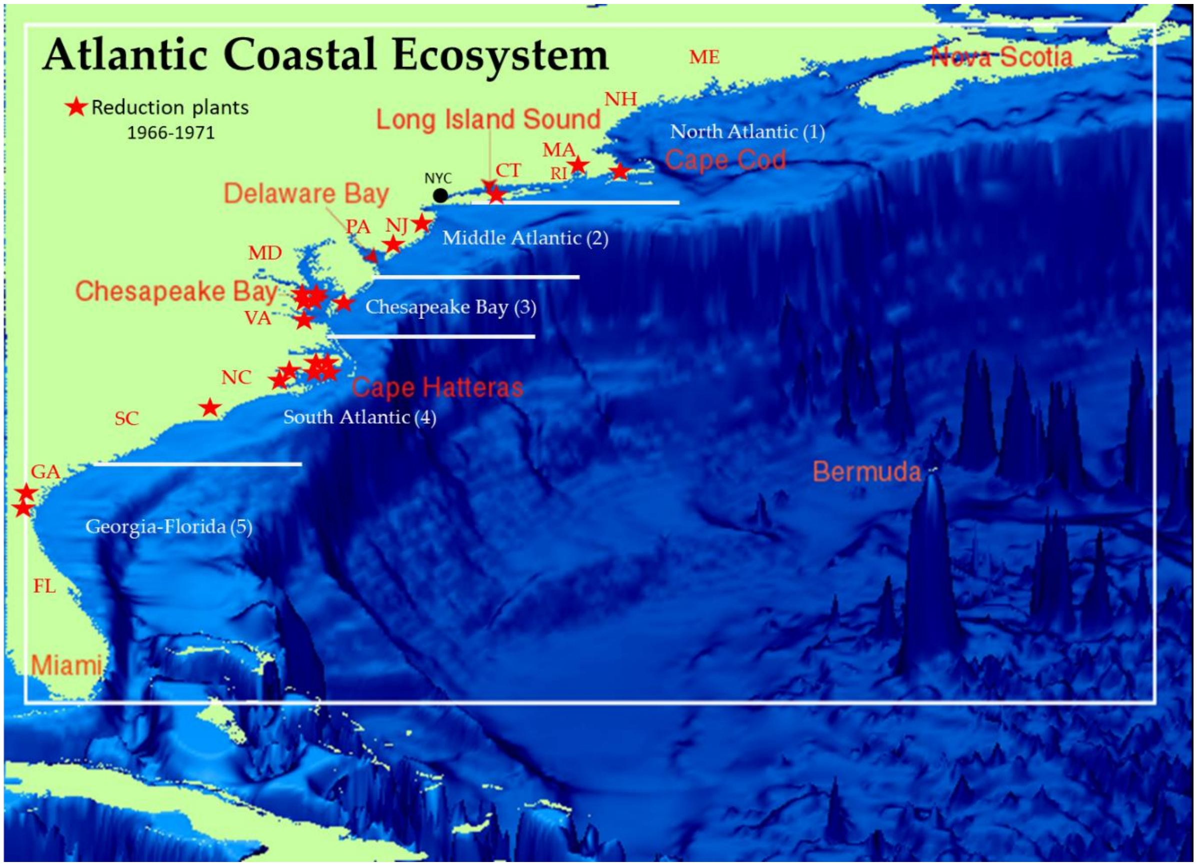

Figure 3.- Map of the Atlantic coastal ecosystem showing the five regions of the NMFS 1966-1971 Atlantic menhaden mark-recapture study. Red stars show the locations of the reduction plants in operation during 1966-1971 (see Supplemental Table S.1).

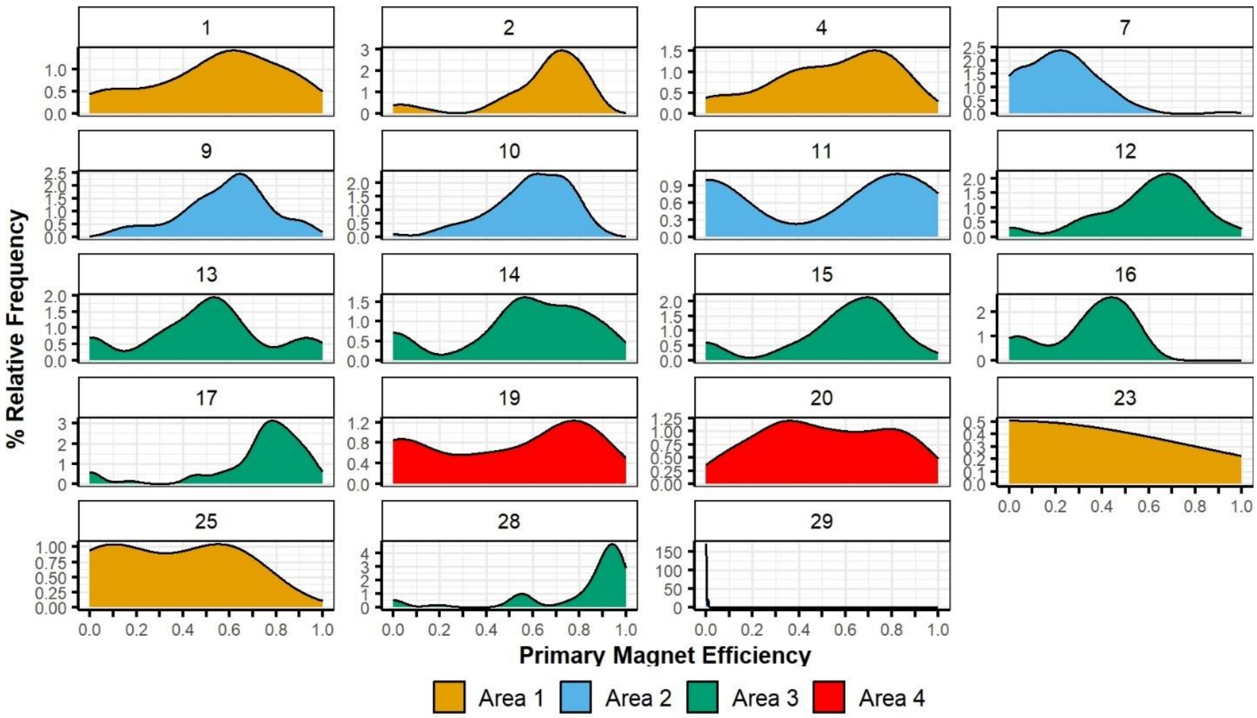

Figure 4.- Distributions of "Primary" magnet efficiencies for all individual batch trials conducted during 1966-1971 at 19 reduction plants within four geographical areas (see Supplemental Table S.1).

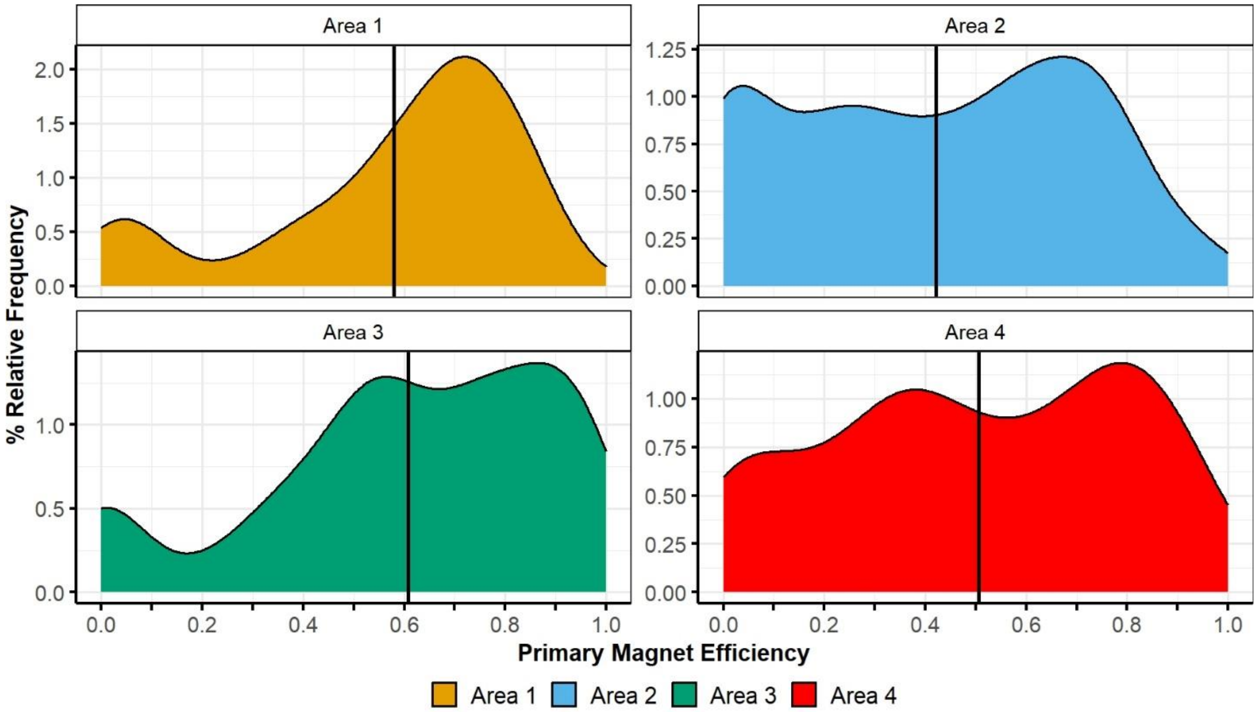

Figure 5.- Distributions of batch trial magnet efficiencies (ME) for "Primary" magnets at plants within four geographical areas (see Supplemental Table S.1) during 1966-1971. Vertical black line in each panel is the area-specific 1966-1971 parametric mean magnet tag recovery efficiency.

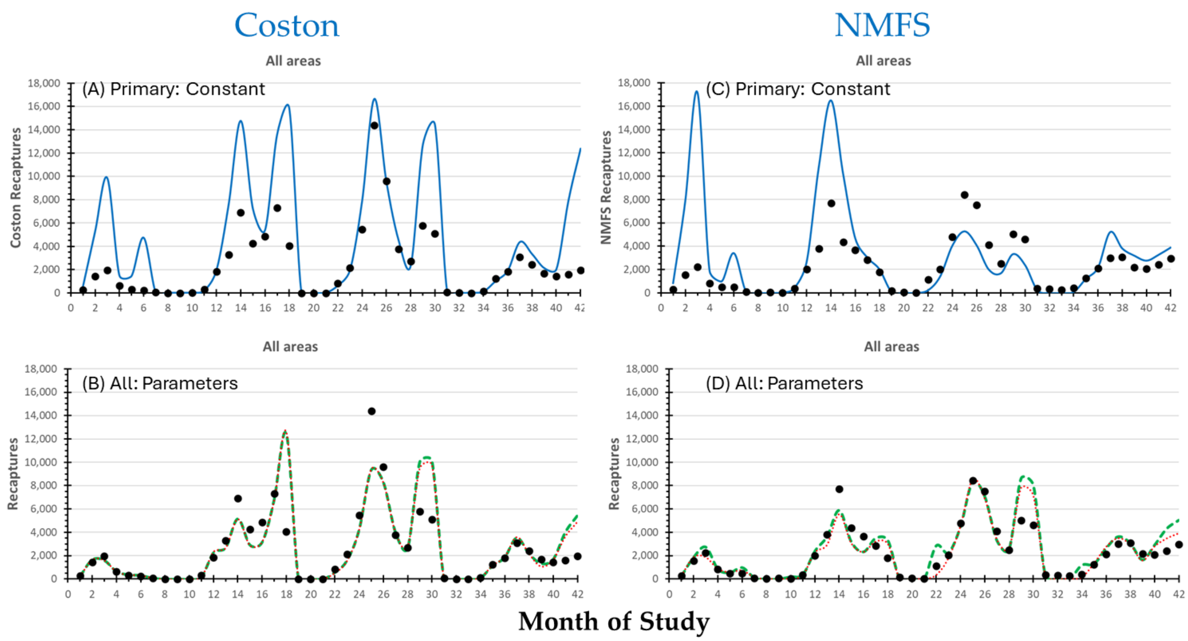

Figure 6.- Summary visualizations of single-run results comparing observed (black dots) and predicted (dotted lines) for the two data sources and all areas combined: (left column-**Coston**): (A) constant "primary" magnet efficiency (ME) coefficients; (B) "parameters" estimated analysis with ME coefficients constrained between $[0.03, 0.95]$; and (right column-**NMFS**): (C) constant "all" ME coefficients; and (D) "parameters" estimated analysis with ME coefficients constrained between $[0.135, 0.95]$.

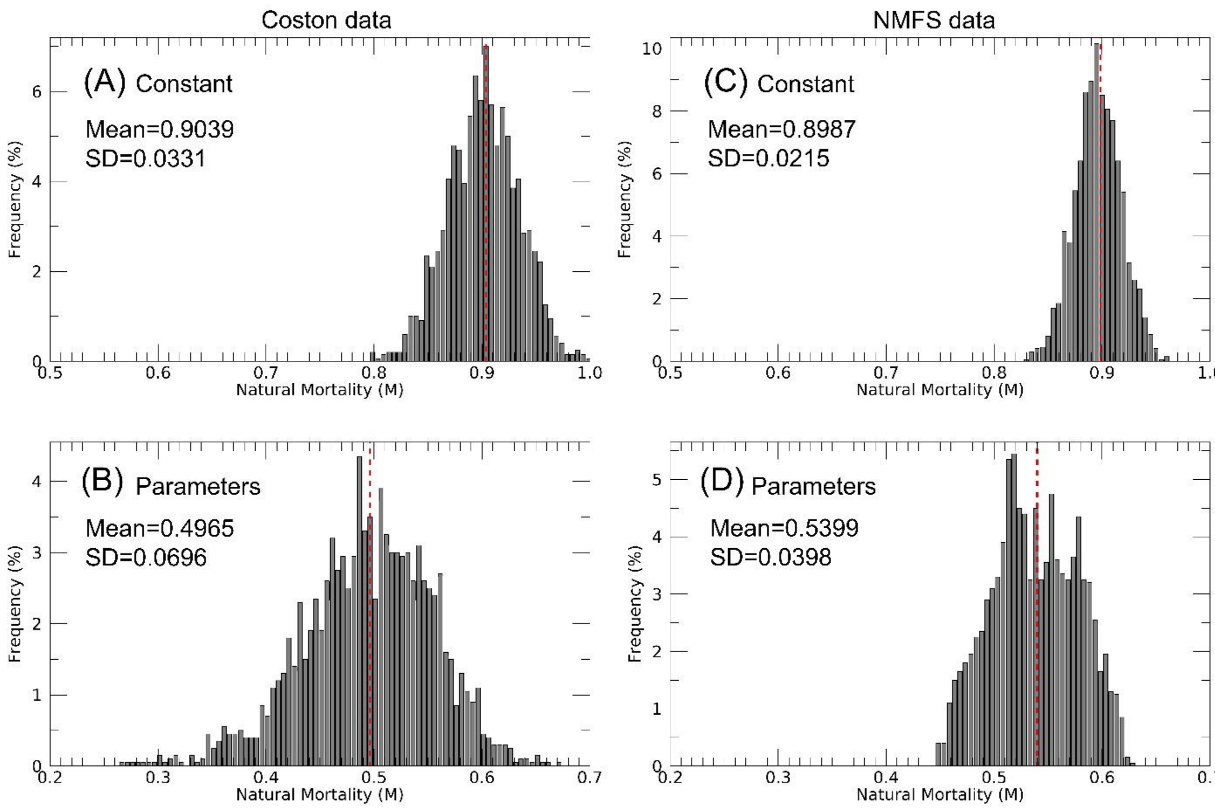

Figure 7.- Summary of natural mortality rate distributions using Monte Carlo Markov Chain (MCMC) trials that directly correspond to the initial run results of **Fig 6**: (left column-**Coston**): (A) "constant" with **Primary** magnet's efficiencies (MEs); (B) ME "parameters" estimated; and (right column-**NMFS**): (C) "constant" with **ALL** magnet's MEs; (D) ME "parameters" estimated.

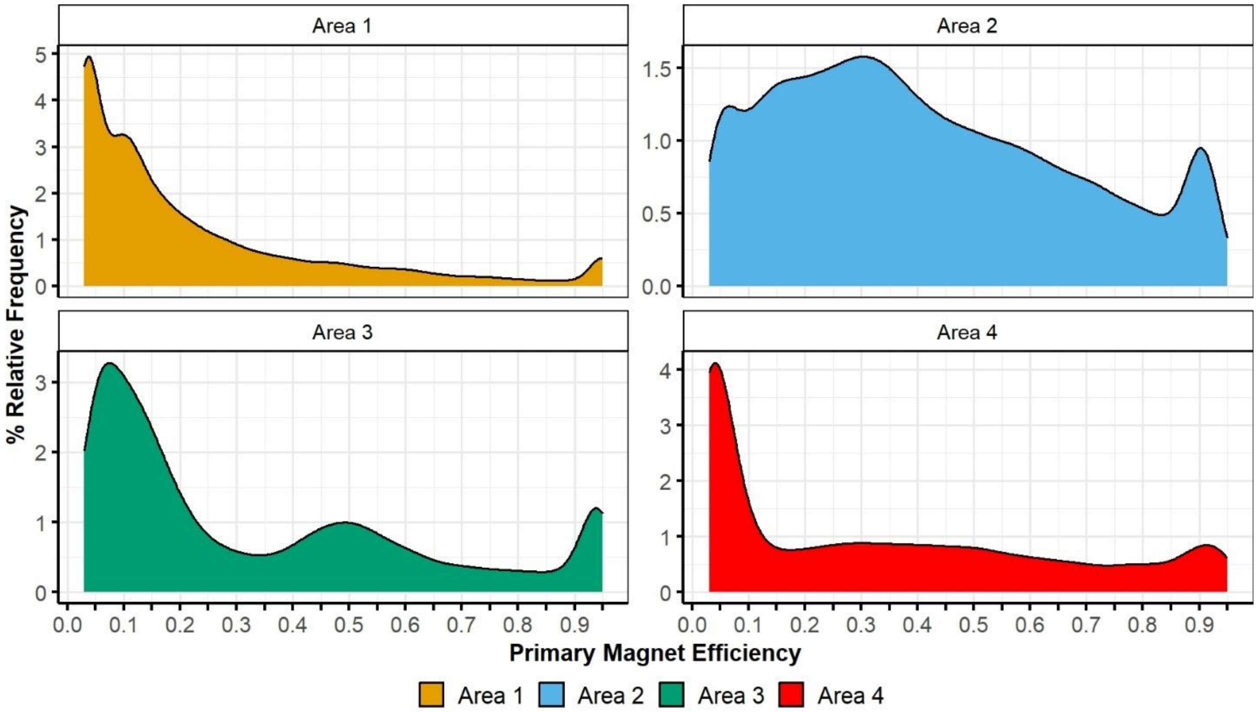

Figure 8.- MCMC modeled primary magnet efficiency distributions constrained between 0.03-0.95 derived from second half of 4,000,000 trials of "parameters" estimation method using Coston data saved every 1000 steps.

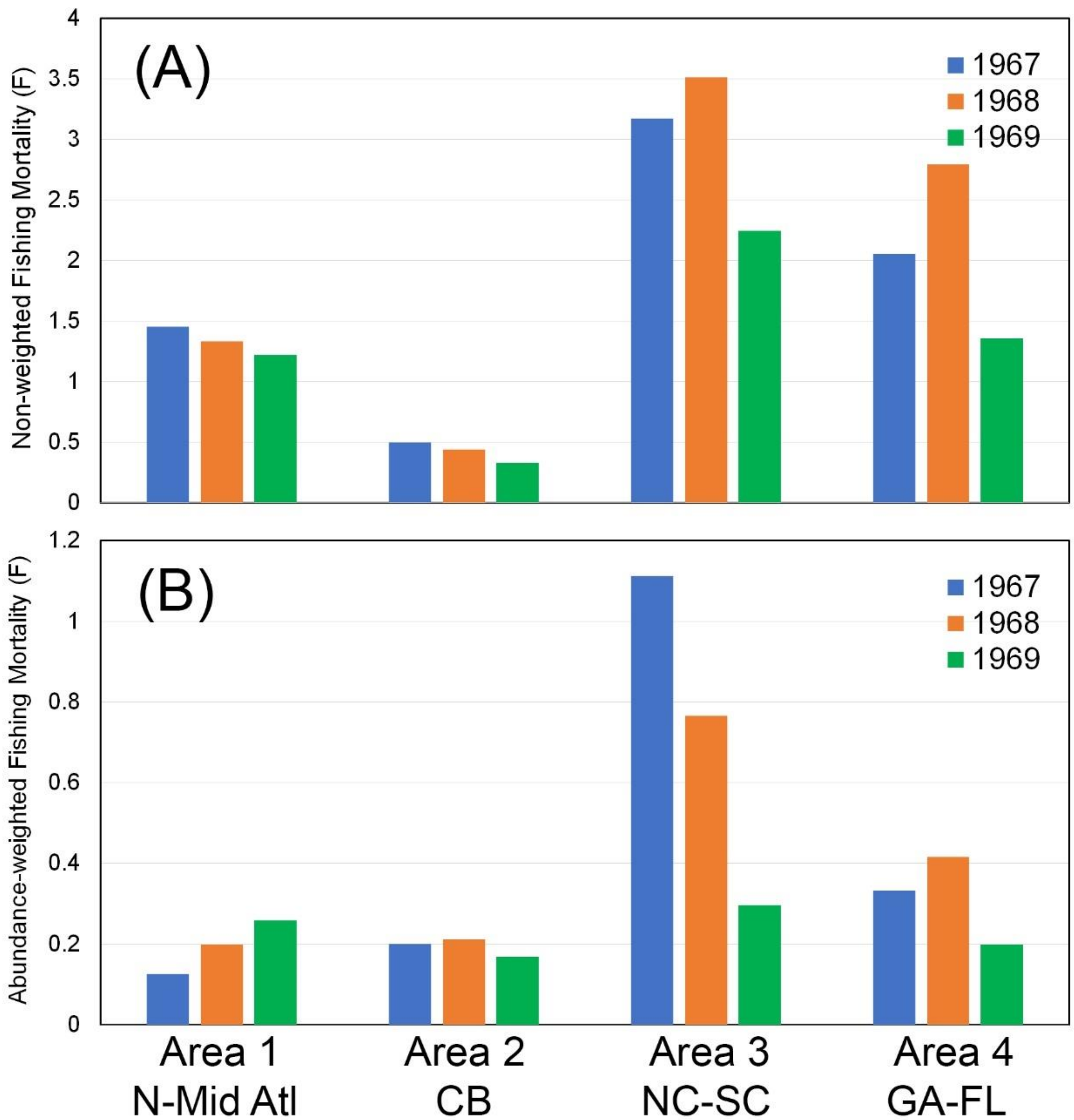

Figure 9.- MMR model estimated annual instantaneous fishing mortality rates (F yr^{-1}) by area by year for Atlantic menhaden using the Coston data and the "parameters" method of estimating magnet efficiencies: (A) non-weighted area annual F; and (B) abundance-weighted area annual F. Total domain annual F is the sum of the F in the four areas (c.f., **Table 7**).

Table 1.- Key primary and foreign variables in the NMFS relational data tables available as Excel spreadsheets converted into two dataframes: (A) field release (fr); and (B) plant tests (pt).

(A) **Field Releases & Recaptures (fr)**

RELEASES	
Variables	**Description**
Area	Study areas: (1) NY; (2) NJ; (3) CB (MD-VA); (4) NC-SC; (5) FL-GA
Date	day-month-year
series	Alphanumeric sequence distinguishing tag batch (~100 tags). Each tag contained marking with 6 digits (2 alphabetical, 4 numeric) for identification.
id	Unique tag identification number, last two of six digits range between 00-99
tagger	Unique individual tagger number
location	Location where fish were caught and released (10' x 10' lat-lon cells)
vessel	Unique purse seine identification number
numbers caught	Amount of fish (thousands of standard fish, = 0.3333 kg)
LENGTHS	
Area	Study areas: (1) NY; (2) NJ; (3) CB (MD-VA); (4) NC-SC; (5) FL-GA
Date	day-month-year
series	Alphanumeric sequence distinguishing tag batch (~100 tags). Each tag contained marking with 6 digits (2 alphabetical, 4 numeric) for identification.
id	Unique tag identification number, last two of six digits range between 00-99
length	Fork length in mm of tagged fish that were measured before release
RECOVERIES	
Area	Study Areas: (1) NY; (2) NJ; (3) CB (MD-VA); (4) NC-SC; (5) FL-GA
Date	day-month-year
series	Alphanumeric sequence distinguishing tag batch (~100 tags). Each tag contained marking with 6 digits (2 alphabetical, 4 numeric) for identification.
id	Unique tag identification number, last two of six digits range between 00-99
plant	Reduction plant where tag was recovered
magnet station	Magnet station within reduction plant where tag was recovered

(B) **Plant Tests (pt)**

RELEASES	
Variables	**Description**
Area	Study areas: (1) NY; (2) NJ; (3) CB (MD-VA); (4) NC-SC; (5) FL-GA
Date	day-month-year
series	Alphanumeric sequence distinguishing tag batch (~100 tags). Each tag contained marking with 6 digits (2 alphabetical, 4 numeric) for identification.
id	Unique tag identification number, last two of six digits range between 00-99
tagger	Unique individual tagger number
location	Location where fish were caught and released (10' x 10' lat-lon cells)
vessel	Unique purse seine identification number
numbers caught	Amount of fish (thousands of standard fish, = 0.3333 kg)
RECOVERIES	
Area	Study areas: (1) NY; (2) NJ; (3) CB (MD-VA); (4) NC-SC; (5) FL-GA
Date	Day-Month-Year
series	Alphanumeric sequence distinguishing tags batch (~100). Each tag contained marking with 6 digits (2 alphabetical, 4 numeric) for identification.
id	Unique tag identification number, last two of six digits range between 00-99
plant	Reduction plant where tag was recovered
magnet station	Magnet station within reduction plant where tag was recovered

Table 2.- Parameters, definitions, values and sources of information for Liljestrand et al.'s (2019a) multistate mark-recovery (MMR) model used in the Atlantic menhaden data analyses.

Parameter	Definition	Values		Source
	Mark-Recapture Data			
T	Time of release			
A	Area of release			
t	Time of recapture			
a	Area of recapture			
$R_{T,A}$	Observed releases (totals)	1,066,448	Tables A.2, A.5-A.8	Liljestrand (2019a,b)
		1,066,357	Table 4A, this paper	Coston (1971)
		767,954	Table 4B, this paper	NMFS (2022)
$r_{T,A,\tau,a}$	Observed recoveries (totals)	89,116	Table A.3	Liljestrand (2019a) - Coston
		102,992	Table 5A, this paper	Coston (1971)
		93,335	Tables 5B, this paper	NMFS (2022)
$f_{t,a}$	Fishing effort at time t and area a		Table 7, this paper	NMFS (2023)
	Defined Quantities			
G_A	Tag shedding/mortality by areas A (regions 1-4)		[0.10, 0.20, 0.25, 0.40]	Dryfoos et al. (1973)
$1 - G_A$	Tag survivorship by area A (regions 1-4)		[0.90, 0.80, 0.75, 0.60]	Dryfoos et al. (1973)
k	Over-dispersion (negative binomial)		1.0	This paper, sensitivity range
ν	Dirichlet distribution sample size		10.0	This paper, sensitivity range
$\varepsilon_{t,a}$	Plant magnet efficiency in time t and area a		[0.52, 0.61, 0.78, 0.69]	Table 8, this paper
$\Theta_{m,a}$	Catchability $\exp(\theta_{m,a})$ in month m and area a		Table A.1	Liljestrand et al. (2019a)
σ_q^2	Variance of q catchability		Table 1	Liljestrand et al. (2019a)
$\varphi_{m,a}$	Movement probabilities in month m and area a		Tables A.1; A.9 & A.10	Liljestrand et al. (2019ab)
	Estimated Quantities			
$N_{T,A,t,a}$	Abundance of a tagged cohort			
$S_{t,a}$	Survivorship to time t in region a			
$F_{t,a}$	Fishing mortality rate at time t in region a			
$q_{m,a}$	Catchability coefficient in month m in region a			
Q_a	Area-specific catchability			
$\hat{C}_{T,A,t,a}$	Estimated tag recoveries			
M	Natural mortality rate			
Z	Total mortality rate			
E	Exploitation rate			

Table 3.- Experimental design two Atlantic menhaden release-recapture dataframes using life history and MMR model analyses, at each monthly time step $(t = 1, \cdots, 42)$, region $(a = 1, \cdots, 4)$, and calendar month $(m = 1, \cdots, 12)$. Parameters are: $[f_{t,a}]$ ≡ matrix of time-step by area fishing effort; $[Q_a]$ ≡ area-specific effect on catchability; $[\theta_{m,a}]$ ≡ month by region exponential variability of catchability; and $[\varepsilon_{t,a}]$ ≡ time-step by region magnet tag recovery efficiency. The matrix of movement probability parameters by calendar month by region $[\varphi_{m,a}]$ was an input.

Dataframe & Approach	Releases	Recoveries	$[f_{t,a}]$	$[Q_a]$	$[\theta_{m,a}]$	$[\varepsilon_{t,a}]$
Coston						
constant	1,066,357	102,992	Ault-Luo	estimated	estimated	constant
parameters	1,066,357	102,992	Ault-Luo	estimated	estimated	parameters
NMFS						
constant	767,954	93,335	Ault-Luo	estimated	estimated	constant
parameters	767,954	93,335	Ault-Luo	estimated	estimated	parameters

Table 4.- Tagged releases of Atlantic menhaden between July 1966 through December 1969: (A) Coston data releases by year and area; and (B) NMFS data releases by year and area. Areas were: (1) North & Middle Atlantic (N-Mid Atl); (2) Chesapeake Bay (CB); (3) North & South Carolina (NC-SC); and (4) Georgia-Florida (GA-FL). The sum of Area 2 & 3 percentage released are given in the last lines of Tables (4A) and (4B).

(A) Coston

Area	1	2	3	4	Total
	N-Mid Atl	CB	NC-SC	GA-FL	
1966	0	0	88,898	0	88,898
	0.0000	0.0000	1.0000	0.0000	1.00
1967	15,753	100,128	159,077	95,832	379,790
	0.0425	0.2700	0.4290	0.2585	1.00
1968	24,159	132,596	109,120	118,819	384,694
	0.0628	0.3447	0.2837	0.3089	1.00
1969	9,168	75,581	29,076	108,150	221,975
	0.0413	0.3405	0.1310	0.4872	1.00
Total	49,080	308,305	386,171	322,801	1,066,357
	0.0460	0.2891	0.3621	0.3027	1.00
		Areas 2 & 3	65.1%		

(B) NMFS

Area	1	2	3	4	Total
	N-Mid Atl	CB	NC-SC	GA-FL	
1966	0	0	88,898	0	88,898
	0.0000	0.0000	1.0000	0.0000	1.00
1967	0	88,551	82,748	69,128	240,425
	0.0000	0.3683	0.3442	0.2875	1.00
1968	0	120,807	0	99,221	220,028
	0.0000	0.5491	0.0000	0.4509	1.00
1969	8,968	74,587	28,578	106,470	218,603
	0.0410	0.3412	0.1307	0.4870	1.00
Total	8,968	283,945	200,224	274,817	767,954
	0.0117	0.3697	0.2607	0.3579	1.00
		Areas 2 & 3	63.1%		

Table 5.- Recovered Atlantic menhaden (marked with internal ferro-magnetic tags) by release year and area from July 1966 through December 1969: (A) Coston recoveries by "primary" plant magnets of releases given in Table 4A; and (B) NMFS recoveries by "all" plant magnets of releases given in Table 4B. Twenty (20) reduction plants were involved in tag recoveries distributed across four areas (see **Fig. 3** and **Table S.1**): (1) North & Middle Atlantic (5 plants); (2) Chesapeake Bay (6 plants); (3) North & South Carolina (7 plants); and (4) Georgia-Florida (2 plants). The percentage recovered for the sum of Areas 2 & 3 are given in the last lines of Tables (5A) and (5B).

(A) Coston

Area	1	2	3	4	Total
	N-Mid Atl	CB	NC-SC	GA-FL	
1966	0	0	4,836	0	4,836
	0.0000	0.0000	1.0000	0.0000	1.00
1967	1,101	8,835	21,191	1,721	32,908
	0.0353	0.2685	0.6439	0.0523	1.00
1968	6,636	16,579	21,440	5,139	49,794
	0.1333	0.3330	0.4306	0.1032	1.00
1969	2,233	4,891	7,198	1,132	15,454
	0.1445	0.3165	0.4658	0.0732	1.00
Total	10,030	30,305	54,666	7,992	102,992
	0.0974	0.2942	0.5308	00776	1.00
		Areas 2 & 3	82.5%		

(B) NMFS

Area	1	2	3	4	Total
	N-Mid Atl	CB	NC-SC	GA-FL	
1966	0	0	5,859	0	5,859
	0.0000	0.0000	1.0000	0.0000	1.00
1967	321	10,730	13,071	2,586	26,708
	0.0120	0.4018	0.4894	0.0968	1.00
1968	2,584	22,342	9,664	5,783	40,373
	0.0640	0.5534	0.2394	0.1432	1.00
1969	2,942	7.503	7,888	2,062	20,396
	0.1443	0.3679	0.3868	0.1011	1.00
Total	5,847	40,575	36,482	10,431	93,335
	0.0628	0.4347	0.3909	0.1118	1.00
		Areas 2 & 3	82.6%		

Table 6.- Estimated nominal fishing effort $\left[f_{m,a}\right]$ in vessel weeks (vw) by year by area from July 1966 through December 1969. The percentage of total domain effort relative to Areas 2 & 3 combined is given in the last line. The four areas are: (1) North & Middle Atlantic (N-Mid Atl); (2) Chesapeake Bay (CB); (3) North & South Carolina (NC-SC); and (4) Georgia-Florida (GA-FL).

Area	**1**	**2**	**3**	**4**	**Total**
	N-Mid Atl	**CB**	**NC-SC**	**GA-FL**	
1966	**108**	**803**	**381**	**93**	**1,386**
	0.0782	0.5794	0.2751	0.0673	**1.00**
1967	**220**	**1,030**	**522**	**57**	**1,829**
	0.1201	0.5633	0.2853	0.0313	**1.00**
1968	**169**	**824**	**566**	**100**	**1,656**
	0.1020	0.4967	0.3411	0.0602	**1.00**
1969	**186**	**588**	**465**	**45**	**1,285**
	0.1451	0.4576	0.3622	0.0351	**1.00**
Total	**684**	**3,245**	**1,934**	**295**	**6,158**
	0.1110	0.5270	0.3141	0.0479	**1.00**
		Areas 2 & 3	**84.1%**		

Table 7.- Summary of results from two analytical methods applied to the Coston and NMFS dataframes. Symbols are: K ≡ number of estimated model parameters; neg(LL) ≡ model's negative log-likelihood; Δ ≡ difference between predicted and observed recaptures; $\%\Delta$ ≡ percent difference between predicted and observed recaptures; AIC ≡ Akaike Information Criterion; $\widehat{\text{M}}$ ≡ estimated annual natural mortality rate; $\widehat{\widehat{\text{M}}}_{\text{MCMC}}$ ≡ MCMC mean estimated annual natural mortality rate; S ≡ survival rate; Z ≡ total mortality; F ≡ abundance-weighted average annual fishing mortality; and $\text{M}_{\text{MCMC}}/\text{F}$ ≡ ratio of M to F.

Dataframe & Method											
	K	$\mathbf{neg(LL)}$	Δ	$\%\Delta$	**AIC**	$\widehat{\mathbf{M}}$	$\widehat{\mathbf{M}}_{\mathbf{MCMC}}$	**S**	**Z**	**F**	$\widehat{\mathbf{M}}_{\mathbf{MCMC}}/\mathbf{F}$
Life history theory [estimate range]						[0.2996, 0.5404]		[0.05, 0.0045]			
COSTON											
Constant	106	10,579	92,613	89.9%	21,370	0.8963	0.9039	0.1414	1.9561	1.0598	0.8529
Parameters: constrained	206	9,484	10,125	9.8%	19,380	0.5488	0.4965	0.1497	1.8994	1.3505	0.3676
NMFS											
Constant	106	8,044	39,944	42.8%	16,300	0.8909	0.8987	0.1854	1.6855	0.7946	1.1310
Parameters: constrained	206	6,839	12,669	13.6%	14,090	0.5689	0.5399	0.1321	2.0243	1.4554	0.3710

Supplemental Materials: FISH-13999.R2

Ault, J.S., Luo, J. 2025. Investigation of Atlantic menhaden mortality rates. Fisheries Research

Table S.1- Atlantic menhaden reduction processing plants spread across four geographical areas along the U.S. eastern Atlantic coast involved in the 1966-1971 plant-area magnet efficiency trials (= batches) as part of the NMFS mark-recapture study. Source: SEDAR 69 (2019; Table 12) and NMFS (2022) dataframe.

Area	Region	Area Name	Plant	Trials	Plant Name	City	State
			1	29	Atlantic Processing Company	Amagansett	New York
	1		23	4	Lipman Marine Products Co. (Gloucester Marine Protein)	Gloucester	Maine
			25	2	Point Judith Byproducts Co.	Point Judith	Rhode Island
1		**North & Mid Atlantic**					
	2		2	69	J. Howard Smith, Inc.	Port Monmouth	New Jersey
			4	25	New Jersey Menhaden Products Co.	Wildwood	New Jersey
			7	120	Standard Products Co.	Reedville	Virginia
			8	0	McNeal-Edwards (Standard Products Co.)	Reedville	Virginia
2	**3**	**Chesapeake Bay**	9	21	Menhaden Co. (Standard Products Co.)	Reedville	Virginia
			10	151	Virginia Menhaden Products (Reedville Oil & Guano Co.)	Reedville	Virginia
			11	52	Standard Products Co.	White Stone	Virginia
			29	18	Cape Charles Processing Co.	Cape Charles	Virginia
			12	31	Fish Meal Co.	Beaufort	North Carolina
			13	75	Beaufort Fisheries Inc.	Beaufort	North Carolina
			14	31	Standard Products Co.	Beaufort	North Carolina
3	**4**	**North & South Carolina**	15	16	Standard Products Co.	Morehead City	North Carolina
			16	22	North Carolina Menhaden Products	Morehead City	North Carolina
			17	64	Standard Products Co.	Southport	North Carolina
			28	49	Seashore Packing Co.	Beaufort	North Carolina
4	**5**	**Georgia-Florida**	19	52	Quinn Menhaden Fisheries Inc.	Fernandina Beach	Florida
			20	133	Nassau Oil & Fertilizer Inc.	Fernandina Beach	Florida
	Total		**20**	**964**			

Table S.2A- Sources of life history demographic data from stock assessments used for construction of Figure 2 in manuscript.

- Southeast Data Assessment and Review (SEDAR): SEDAR Assessments (https://sedarweb.org/assessments\sedar-assessments/)
- International Scientific Commission for Tuna & Tuna-like Species in the North Pacific Ocean (ISC): Stock Assessment Reports (https://isc.fra.go.jp/reports/stock_assessments.html)
- Inter American Tropical Tuna Commission (IATTC): Fishery Status Reports (https:/iattc.org/en-US/publication/commission/Stock Assessment-Report)
- International Commission for Conservation of Atlantic Tunas (ICCAT): Stock Assessments & Executive Summaries (https:/www.iccat.int/en/assess.html)
- NOAA Northeast Fisheries Science Center Stock Assessment Workshops (SAW): Stock Assessment Documents (https://www.fisheries.noaa.gov/resource/peer-reviewed-research/stock-assessment-documents-northeast-fisheries-science-center)
- Pacific Fishery Management Council (PFMC): (https://www.pcouncil.org/stock-assessments-and-fishery-evaluation-safe-documents/)
- International Council for Exploration of the Seas (ICES): (https://www.ices.dk/data/assessment-tools/Pages/stock-assessment/)
- Indian Ocean Tuna Commission (IOTC): (www.commissionoceanindien.org/en/iotc/)
- Atlantic States Marine Fisheries Commission (www.asmfc.org)

Table S.2B- Natural mortality (M) rate as a function of maximum age ($M = f(a_{\max})$) for individual species used in recent stock assessments by national (USA) and international fishery management council and commission. $a_{\max}$ is stock maximum observed age.

	Species	Scientific name	M	$a_{\max}$	Year	Stock Assessment Source
1	Atlantic bigeye tuna (BET)	*Thunnus obesus*	0.402	20	2021	International Commission for Conservation of Atlantic Tunas 2021
2	Atlantic blue marlin (BUM)	*Makaira nigricans*	0.148	39	2024	International Commission for Conservation of Atlantic Tunas 2024
3	Atlantic bluefin tuna (BFT; E. Atlantic)	*Thunnus thynnus*	0.110	35	2019	Block et al. (2019). Scientific Reports 4818; ICCAT 2022
4	Atlantic cod (Gulf of Maine)	*Gadus morhua*	0.200	20	2013	NOAA Northeast Fisheries Science Center 55th SAW
5	Atlantic croaker	*Micropogonias undulatus*	0.300	10	2010	NOAA Southeast Data & Assessment Review 3/20
6	Atlantic herring	*Clupea harengus*	0.350	8	2022	NOAA Northeast Fisheries Science Center SAW Update
7	Atlantic mahi (dolphinfish)	*Coryphaena hippurus*	0.660	5	2024	Prager. 2000. NMFS SEFSC/SAFMC/ICCAT
8	Atlantic menhaden	*Brevoortia tyrannus*	0.520	10	2010	Ault & Luo. 2025. Fisheries Research (in review)
9	Atlantic menhaden	*Brevoortia tyrannus*	1.170	10	2019	NOAA Southeast Data & Assessment Review 69
10	Atlantic sailfish	*Istiophorus albicans*	0.400	12	2023	International Commission for Conservation of Atlantic Tunas 2023
11	Atlantic sardine	*Sardina pilchardus*	0.450	8	2024	International Council for Exploration of the Seas 2024
12	Atlantic skipjack tuna (SJT; E. Atlantic)	*Katsuwonus pelamis*	0.360	14	2024	International Commission for Conservation of Atlantic Tunas 2024
13	Atlantic swordfish (North Atlantic)	*Xiphias gladius*	0.200	15	2022	International Commission for Conservation of Atlantic Tunas 2022
14	Atlantic yellowfin tuna (YFT)	*Thunnus albacares*	0.300	18	2024	International Commission for Conservation of Atlantic Tunas 2024
15	Black grouper	*Mycteroperca bonaci*	0.140	33	2017	NOAA Southeast Data & Assessment Review 19/48
16	Black sea bass (South Atlantic)	*Centropristis striata*	0.375	11	2023	NOAA Southeast Data & Assessment Review 2/25/56/76
17	Bluefish	*Pomatomus saltatrix*	0.200	14	2015	Buckel. Fish. Bull. 97(4) - NOAA
18	Gag grouper	*Mycteroperca microlepis*	0.159	33	2021	NOAA Southeast Data & Assessment Review 10/33/71
19	Goliath grouper	*Epinephelus itajara*	0.120	37	2016	NOAA Southeast Data & Assessment Review 6/23/47
20	Gray snapper (Gulf of Mexico)	*Lutjanus griseus*	0.130	28	2022	NOAA Southeast Data & Assessment Review 51/75
21	Gray triggerfish (Gulf of Mexico)	*Balistes capriscus*	0.270	15	2015	NOAA Southeast Data & Assessment Review 9/32/43
22	Gray triggerfish (South Atlantic)	*Balistes capriscus*	0.386	16	2022	NOAA Southeast Data & Assessment Review 32/41/82
23	Greater amberjack (Gulf of Mexico)	*Seriola dumerili*	0.280	15	2020	NOAA Southeast Data & Assessment Review 9/70 & Website
24	Greater amberjack (South Atlantic)	*Seriola dumerili*	0.250	17	2025	NOAA Southeast Data & Assessment Review 15/70 Website
25	Haddock (Georges Bank)	*Melanogrammus aeglefinus*	0.200	22	2024	NOAA Fisheries, Northeast Fisheries Science Center, 2024 Mgmt Track Assessment
26	Hogfish	*Lachnolaimus maximus*	0.220	25	2013	NOAA Southeast Data & Assessment Review 6/37
27	Indian Ocean yellowfin tuna	*Thunnus albacares*	0.462	11	2024	Indian Ocean Tuna Commission; Collect. Vol. Sci. Pap. ICCAT, 76(6): 725-739

28	Japanese sardine	*Japanese sardinella*	0.400	10	2024	N. Pacific Fish. Comm. NPFC-2025-COM09-1P06
29	King mackerel (Gulf of Mexico)	*Scomberomorus cavalla*	0.160	24	2014	NOAA Southeast Data & Assessment Review 5/16/38
30	King mackerel (South Atlantic)	*Scomberomorus cavalla*	0.170	26	2014	NOAA Southeast Data & Assessment Review 5/16/38
31	Mutton snapper	*Lutjanus analis*	0.129	40	2024	NOAA Southeast Data & Assessment Review 15a/79
32	Northern anchovy	*Engraulis mordax*	0.600	7	2022	Pacific Fishery Management Council; Ault & Olson. Trans. Amer. Fish. Soc. 125(3)
33	Pacific albacore	*Thunnus alalunga*	0.300	15	2023	International Sci. Comm. Tuna & Tuna-like Species N. Pacific ISC/23/Annex/08
34	Pacific bigeye tuna	*Thunnus obesus*	0.230	17	2022	Inter American Tropical Tuna Commission (IATTC) SAP SAC-13-05: No. 24-2024
35	Pacific blue marlin	*Makaira mazara*	0.342	20	2021	International Sci. Comm. Tuna & Tuna-like Species N. Pacific ISC/21/Annex/10
36	Pacific blue shark	*Prionace glanca*	0.186	24	2022	International Sci. Comm. Tuna & Tuna-like Species N. Pacific ISC/22/Annex/12
37	Pacific bluefin tuna	*Thunnus orientalis*	0.240	20	2024	International Sci. Comm. Tuna & Tuna-like Species N. Pacific ISC/24/Annex/13
38	Pacific bonito	*Sarda chiliensis*	0.700	7	2025	Runde et al. 2025. N. Amer. J Fish. Mgmt; California Department of Fish & Wildlife
39	Pacific great hammerhead shark	*Sphyrna mokarran*	0.130	39	2022	Inter American Tropical Tuna Commission (IATTC) SAP No. 24-2024
40	Pacific hake	*Merluccius productus*	0.220	20	2024	Joint Technical Committee Pacific Hake/Whiting Agreement USA & Canada
41	Pacific mackerel	*Scomber japonicus*	0.500	12	2023	Pacific Fishery Management Council FMC NOAA-TM-NMFS-SWFSC-688
42	Pacific sardine	*Sardinops sagax*	0.675	8	2025	Pacific Fishery Management Council NOAA-TM-NMFS-SWFSC-719
43	Pacific shortfin mako	*Isurus oxyrinchus*	0.128	31	2023	International Scientific Commission for Tuna & Tuna-like Species N. Pacific ISC/23/Annex/16
44	Pacific silky shark	*Carcharhinus falciformis*	0.180	16	2022	Interamerican Tropical Tuna Commission (IATTC) SAP No. 24-2024
45	Pacific skipjack tuna	*Katsuwonus pelamis*	0.450	10	2022	Interamerican Tropical Tuna Commission (IATTC) SAP SAC-13-07: No. 24-2024
46	Pacific striped marlin (E. Pacific Ocean)	*Kajikia audax*	0.440	15	2023	International Sci. Comm. Tuna & Tuna-like Species N. Pacific ISC/23/Annex/14
47	Pacific swordfish	*Xiphias gladius*	0.320	15	2023	International Sci. Comm. Tuna & Tuna-like Species N. Pacific ISC/23/Annex/11
48	Pacific yellowfin tuna	*Thunnus albacares*	0.325	8	2022	Inter American Tropical Tuna Commission (IATTC) SAP SAC-11-07: No. 24-2024
49	Red grouper (Gulf of Mexico)	*Epinephelus morio*	0.180	29	2025	NOAA Southeast Data & Assessment Review 12/42/61/88
50	Red grouper (South Atlantic)	*Epinephelus morio*	0.140	29	2019	NOAA Southeast Data & Assessment Review 19/41/53/61
51	Red porgy (South Atlantic)	*Pagrus pagrus*	0.220	26	2020	NOAA Southeast Data & Assessment Review 1/60
52	Red snapper (Gulf of Mexico)	*Lutjanus campechanus*	0.090	57	2024	NOAA Southeast Data & Assessment Review 7/31/52/74
53	Snowy grouper	*Hyporthodus niveatus*	0.120	35	2014	NOAA Southeast Data & Assessment Review 4/36
54	Spanish mackerel (Gulf of Mexico)	*Scomberomorus maculatus*	0.380	11	2023	NOAA Southeast Data & Assessment Review 28/81
55	Spanish mackerel (S. Atlantic)	*Scomberomorus maculatus*	0.350	12	2022	NOAA Southeast Data & Assessment Review 17/28/78
56	Striped bass	*Morone saxatilis*	0.150	31	2019	NEFSC 66th SAW/Hightower et al. (2001)
57	Summer flounder	*Paralichthys dentatus*	0.250	19	2019	NOAA Northeast Fisheries Science Center 66th SAW Ref. Doc 19-01

58	Tilefish (golden – S. Atlantic)	*Lopholatilus chamaeleonticeps*	0.135	33	2024	NOAA Southeast Data & Assessment Review 4/22/89
59	Vermilion snapper (Gulf of Mexico)	*Rhombopoplites aurorubens*	0.250	15	2020	Southeast Data & Assessment Review 9/45/67
60	Vermilion snapper (South Atlantic)	*Rhombopoplites aurorubens*	0.220	19	2018	Southeast Data & Assessment Review 2/17/55
61	Walleye pollock (Gulf of Alaska)	*Gadus chalcogrammus*	0.300	18	2023	North Pacific Fishery Management Council, NOAA Alaska Fisheries Science Center
62	Weakfish	*Cynoscion regalis*	0.295	17	2016	NOAA Northeast Fisheries Science Center 40th SAW
63	Yellowtail snapper	*Ocyurus chrysurus*	0.223	20	2025	NOAA Southeast Data & Assessment Review 3/27/64/96

Table S.3A- Average annual magnet recovery efficiencies for NMFS data at each reduction plant during 1966-1971 using only **Primary** magnets (i.e., recovery stations 1 and 2). n is the number of released batches consisting of ~100 tags. $\bar{\varepsilon}$ is the yearly average plant magnet efficiency. $\bar{\bar{\varepsilon}}$ is the 1966-1971 average plant magnet recovery efficiency. A total of 95,986 tags were seeded into vessel landings at plants, and 49,349 of these were recovered (0.5141) by primary magnets.

Region	**Plant**	**1966**		**1967**		**1968**		**1969**		**1970**		**1971**			**Batches**
		n	$\bar{\varepsilon}$	n	$\bar{\varepsilon}$	n	$\bar{\varepsilon}$	n	$\bar{\varepsilon}$	n	$\bar{\varepsilon}$	n	$\bar{\varepsilon}$	$\bar{\bar{\varepsilon}}$	
	1					15	0.4340	14	0.6686					**0.5472**	
1	**23**											2	0.0000	**0.0000**	
	25											4	0.3275	**0.3275**	
															129
2	**2**			18	0.6861	24	0.7061	18	0.4433	2	0.7250	7	0.7582	**0.6382**	
	4			7	0.5800	5	0.7300	13	0.4438					**0.5392**	
	7			33	0.3217	34	0.1645	23	0.1452	6	0.0033	24	0.3083	**0.2247**	
	9			21	0.5865									**0.5865**	
3	**10**			35	0.6347	37	0.6513	25	0.6268	25	0.4948	29	0.5029	**0.5890**	362
	11			30	0.7314	3	0.8300			19	0.0011			**0.4702**	
	29			5	0.0020	12	0.0008	1	0.0000					**0.0011**	
	12	8	0.4875	7	0.7916	1	0.6300	5	0.5600	7	0.5471	3	0.5400	**0.5910**	
	13	11	0.4155	17	0.4863	9	0.7733	12	0.5458	10	0.4060	16	0.4143	**0.4938**	
	14	5	0.0060	6	0.6850	1	0.5400	7	0.6327	8	0.7325	4	0.5700	**0.5564**	
4	**15**	5	0.4320	5	0.7400	2	0.6482	4	0.4975					**0.5717**	288
	16	5	0.1780	5	0.3800	1	0.0700	7	0.4829	3	0.3267	1	0.3200	**0.3427**	
	17	5	0.8635	3	0.2067	7	0.5122	18	0.7983	13	0.7292	18	0.7572	**0.7188**	
	28	8	0.6088			11	0.9250	13	0.8680	2	0.9150	15	0.7673	**0.8096**	
5	**19**	3	0.0000	21	0.2965	28	0.6614							**0.4759**	185
	20	10	0.5643	15	0.4987	23	0.4496	49	0.3920	18	0.6672	18	0.7867	**0.5176**	
	Total	60		228		213		209		113		141			**964**

Table S.3B- Average magnet recovery efficiencies for NMFS (2022) data using only **Primary** magnets (recovery stations 1 and 2) by area by reduction plant for the 1966-1971 period. Trials is the number of released batches of ~100 tags. Fraction is the average magnet efficiency for that plant. A total of 78 trial batches had zero recoveries. Area mean magnet efficiency is the right-most column.

Area	Region	Plant	Area Name	Trials	negLL	average	stdev	recovered	released	fraction	min	max	zeros	Area mean
	1	1		29	0.55	0.55	0.2770	1,587	2,900	0.5472	0.01	0.95	0	
	1	25		4	0.33	0.33	0.2919	131	400	0.3275	0.06	0.59	0	**0.5790**
1	1	23	**North & Mid Atlantic**	2	0	0	0	0	200	0.0000	0.00	0.00	2	
	2	2		69	0.64	0.64	0.2131	4,402	6,898	0.6382	0.00	0.88	2	
	2	4		25	0.54	0.54	0.2562	1,348	2,500	0.5392	0.03	0.86	0	
				129				**7,468**	**12,898**	**0.5790**	**0.00**	**0.95**	**4**	
	3	7		120	0.22	0.22	0.1594	2,691	11,981	0.2246	0.00	0.93	10	
	3	9		21	0.59	0.59	0.1926	1,227	2,092	0.5865	0.14	0.91	0	
2	3	10	**Chesapeake Bay**	151	0.59	0.59	0.1743	8,885	15,085	0.5890	0.00	0.91	2	**0.4211**
	3	11		52	0.47	0.47	0.4127	2,378	5,108	0.4655	0.00	1.00	17	
	3	29		18	0.01	0	0.0032	2	1,800	0.0011	0.00	0.01	16	
				362				**15,183**	**36,066**	**0.4210**	**0.00**	**1.00**	**45**	
	4	12		31	0.59	0.59	0.2292	1,825	3,091	0.5904	0.00	0.95	2	
	4	13		75	0.49	0.5	0.2752	3,658	7,393	0.4948	0.00	1.00	7	
	4	14		31	0.56	0.56	0.2913	1,723	3,097	0.5563	0.00	0.94	3	
3	4	15	**North & South Carolina**	16	0.57	0.57	0.2639	914	1,599	0.5716	0.00	0.93	2	**0.6075**
	4	16		22	0.34	0.34	0.1794	754	2,200	0.3427	0.00	0.55	1	
	4	17		64	0.72	0.72	0.2345	4,597	6,395	0.7188	0.00	0.98	2	
	4	28		49	0.81	0.8	0.2653	3,898	4,821	0.8085	0.00	1.00	3	
				288				**17,369**	**28,596**	**0.6074**	**0.00**	**1.00**	**20**	
4	5	19	**Georgia-Florida**	52	0.48	0.48	0.3428	2,474	5,198	0.4760	0.00	0.93	7	**0.5063**
	5	20		133	0.52	0.52	0.2754	6,855	13,228	0.5182	0.00	0.99	2	
				185				**9,329**	**18,426**	**0.5063**	**0.00**	**0.99**	**9**	
	Total			**964**				**49,349**	**95,986**	**0.5141**			**78**	

Table S.4A- Average annual magnet recovery efficiencies for NMFS data at each reduction plant during 1966-1971 using **ALL** magnets (i.e., all recovery stations). n is the number of released batches consisting of ~100 tags. $\bar{\varepsilon}$ is the yearly average plant magnet efficiency. $\bar{\bar{\varepsilon}}$ is the 1966-1971 average plant magnet recovery efficiency. A total of 95,986 tags were seeded into vessel landings at plants, and 69,338 of these were recovered (0.7224) by ALL magnets.

Region	Plant	1966		1967		1968		1969		1970		1971			Batches
		n	$\bar{\varepsilon}$	n	$\bar{\varepsilon}$	n	$\bar{\varepsilon}$	n	$\bar{\varepsilon}$	n	$\bar{\varepsilon}$	n	$\bar{\varepsilon}$	$\bar{\bar{\varepsilon}}$	
	1					15	0.6687	14	0.7714					**0.7183**	
1	**23**											2	0.0250	**0.0250**	
	25											4	0.3300	**0.3300**	
															129
2	**2**			18	0.8506	24	0.8744	18	0.6889	2	0.8300	7	0.9084	**0.8220**	
	4			7	0.6414	5	0.7880	13	0.6746					**0.6880**	
	7			33	0.7059	34	0.5343	23	0.5765	6	0.5200	24	0.5271	**0.5877**	
	9			21	0.7826									**0.7830**	
3	**10**			35	0.8656	37	0.8152	25	0.7236	25	0.6584	29	0.6356	**0.7513**	362
	11			30	0.8006	3	0.8400			19	0.4579			**0.6756**	
	29			5	0.4040	12	0.1758	1	0.0200					**0.2306**	
	12	8	0.6425	7	0.8304	1	0.6300	5	0.6100	7	0.5643	3	0.6033	**0.6576**	
	13	11	0.8927	17	0.9652	9	0.9233	12	0.8958	10	0.7610	16	0.7168	**0.8569**	
	14	5	0.5740	6	0.8733	1	0.8300	7	0.7936	8	0.7650	4	0.6500	**0.7488**	
4	**15**	5	0.7400	5	0.8160	2	0.7384	4	0.8325					**0.7867**	288
	16	5	0.3120	5	0.7420	1	0.6900	7	0.7886	3	0.5433	1	0.4700	**0.6173**	
	17	5	0.9278	3	0.5600	7	0.8463	18	0.9450	13	0.9023	18	0.8656	**0.8838**	
	28	8	0.9638			11	0.9763	13	0.9202	2	0.9200	15	0.8613	**0.9223**	
5	**19**	3	0.7667	21	0.6679	28	0.7782							**0.7329**	185
	20	10	0.6788	15	0.6313	23	0.5235	49	0.6133	18	0.6900	18	0.8806	**0.6532**	
	Total	60		228		213		209		113		141			**964**

Table S.4B- Average magnet recovery efficiencies for NMFS (2022) data using only **ALL** magnets (all recovery stations) by area by reduction plant for the 1966-1971 period. Trials is the number of released batches of ~100 tags. Fraction is the average magnet efficiency for that plant. A total of 78 trial batches had zero recoveries. Area mean magnet efficiency is the right-most column.

Area	Region	Plant	Area Name	trials	negLL	average	stdev	recovered	released	fraction	min	max	zeros	Area mean
	1	1		29	0.72	0.7183	0.1717	2,083	2,900	0.7183	0.32	0.99	0	
	1	25		4	0.33	0.3300	0.2950	132	400	0.3300	0.06	0.60	0	
1	1	23	**North & Mid Atlantic**	2	0.025	0.0250	0.0212	5	200	0.0250	0.01	0.04	0	**0.7451**
	2	2		69	0.82	0.8220	0.1700	5,670	6,898	0.8220	0.18	0.99	0	
	2	4		25	0.69	0.6880	0.1959	1,720	2,500	0.6880	0.10	0.89	0	
								9,610	**12,898**	**0.7451**			**0**	
	3	7		120	0.59	0.5875	0.1926	7,039	11,981	0.5875	0.03	0.95	0	
	3	9		21	0.78	0.7830	0.1372	1,638	2,092	0.7830	0.35	0.98	0	
2	3	10	**Chesapeake Bay**	151	0.75	0.7513	0.1672	11,333	15,085	0.7513	0.02	0.99	0	**0.6618**
	3	11		52	0.67	0.6735	0.2508	3,440	5,108	0.6735	0.03	1.00	0	
	3	29		18	0.23	0.2306	0.2614	415	1,800	0.2306	0.01	0.88	0	
								23,865	**36,066**	**0.6617**			**0**	
	4	12		31	0.66	0.6571	0.1855	2,031	3,091	0.6571	0.28	0.97	0	
	4	13		75	0.86	0.8584	0.1524	6,346	7,393	0.8584	0.05	1.00	0	
3	4	14		31	0.75	0.7488	0.1443	2,319	3,097	0.7488	0.47	0.98	0	
	4	15	**North & South Carolina**	16	0.79	0.7867	0.1049	1,258	1,599	0.7867	0.59	0.97	0	**0.8190**
	4	16		22	0.62	0.6173	0.2258	1,358	2,200	0.6173	0.10	0.92	0	
	4	17		64	0.88	0.8838	0.1015	5,652	6,395	0.8838	0.46	0.99	0	
	4	28		49	0.92	0.9222	0.1085	4,446	4,821	0.9222	0.34	1.00	0	
								23,410	**28,596**	**0.8186**			**0**	
4	5	19	**Georgia-Florida**	52	0.73	0.7330	0.2227	3,810	5,198	0.7330	0.08	0.98	0	**0.6758**
	5	20		133	0.65	0.6534	0.2367	8,643	13,228	0.6534	0.16	1.00	0	
								12,453	**18,426**	**0.6758**			**0**	
		Total		**964**				**69,338**	**95,986**	**0.7224**			**0**	

Table S.5- Estimated nominal fishing effort $[f_{m,a}]$ in vessel weeks (vw) by month by area for July 1966 through December 1969.

Year	Month	Sequence		Area			
			1	2	3	4	Annual $f_{\sum a}$
1966	**7**	1	4.46	49.53	7.25	4.27	
	8	2	32.60	229.10	68.34	37.55	
	9	3	46.90	344.70	97.67	38.24	
	10	4	16.14	125.43	43.45	10.12	
	11	5	8.31	51.27	53.91	2.17	
	12	6	0.00	2.94	110.69	0.86	
	TOTAL		**108.41**	**802.97**	**381.31**	**93.21**	**1,385.90**
1967	**1**	7	0.00	0.00	5.89	0.00	
	2	8	0.00	0.00	0.96	0.00	
	3	9	0.00	0.00	4.11	0.00	
	4	10	0.00	0.00	0.83	1.09	
	5	11	0.86	14.28	6.22	3.36	
	6	12	14.91	106.27	11.41	4.98	
	7	13	29.54	188.96	34.01	7.57	
	8	14	77.07	312.35	114.46	23.74	
	9	15	43.05	182.59	63.54	9.39	
	10	16	33.11	148.32	63.15	5.57	
	11	17	21.07	74.99	96.88	1.47	
	12	18	0.00	2.59	120.39	0.00	
	TOTAL		**219.61**	**1,030.35**	**521.85**	**57.17**	**1828.98**
1968	**1**	19	0.00	0.00	6.28	0.00	
	2	20	0.00	0.00	2.63	0.00	
	3	21	0.00	0.00	1.11	0.00	
	4	22	0.00	35.39	3.55	7.1	
	5	23	2.65	39.21	22.75	18.83	
	6	24	22.17	140.77	20.15	13.46	
	7	25	40.62	231.37	55.49	18.92	
	8	26	44.53	160.63	78.46	24.95	
	9	27	24.38	91.97	42.66	9.66	
	10	28	13.54	54.01	30.64	4.13	
	11	29	21.23	67.24	115.79	2.69	
	12	30	0.00	3.01	186.03	0.00	
	TOTAL		**169.12**	**823.60**	**565.54**	**99.74**	**1,658.00**
1969	**1**	31	0.00	0.00	22.44	0.00	
	2	32	0.00	0.00	20.43	0.00	
	3	33	0.00	0.00	16.08	0.00	
	4	34	0.00	20.94	1.78	2.49	
	5	35	3.88	42.04	20.70	11.99	
	6	36	20.63	95.65	11.64	5.42	
	7	37	30.37	126.38	25.74	6.13	
	8	38	39.04	102.91	42.68	9.48	
	9	39	27.39	75.53	29.75	4.71	
	10	40	23.89	69.60	33.53	3.16	
	11	41	22.39	51.81	75.74	1.24	
	12	42	18.83	3.15	164.94	0.52	
	TOTAL		**186.42**	**588.01**	**465.45**	**45.14**	**1,285.02**

Table S.6- Summary of NMFS (2022) Atlantic menhaden: (A) tagged-releases and recoveries by year from 1966-1969; and, (B) batches released and batches with zero recoveries. About 8.02% of 1966-1969 total batch releases had zero returns.

(A) Tagged-releases and recoveries with "ALL" plant magnets:

Year	Total Releases	Recoveries 1966-69	Recoveries/Releases
1966	88,898	7,516	0.0845
1967	240,425	40,965	0.1704
1968	220,028	33,595	0.1527
1969	218,603	11,259	0.0515
Total	**767,954**	**93,335**	**0.1215**

(B) NMFS tagged-batches released & those with no recoveries:

Year	Batches Released	Batches Zero Recovered	Zeros Recovered/Releases
1966	893	113	0.1265
1967	2,417	233	0.0964
1968	2,233	46	0.0206
1969	2,203	229	0.1039
Total	**7,745**	**621**	**0.0802**

Table S.7- Description of the Stepwise sensitivity method to calibrate plant area-time magnet efficiencies.

Stepwise sensitivity analysis of plant area-time magnet efficiency $(\varepsilon_{t,a})$:

Recoveries representing the theoretical catch of tagged menhaden cohorts for each month t and area $(C_{T,A,t,a})$ are modeled as the product of three components:

1. The latent tagged fish abundance by the time and area $(N_{T,A,t,a})$;
2. The proportion of mortality due to the combined effects of fishing $(F_{t,a})$, and natural mortality (M); and
3. The plant-specific magnet efficiency rate for each time and area $(\varepsilon_{t,a})$.

This relationship is expressed as:

$$C_{T,A,t,a} = \left[N_{T,A,t,a} \frac{F_{t,a}}{(F_{t,a}+M)}\left(1 - e^{-(F_{t,a}+M)}\right)\right] \varepsilon_{t,a} \quad \text{(S.7.1)}$$

To explore the sensitivity of recapture predictions to magnet efficiency assumptions, we implemented a stepwise diagnostic procedure that incrementally refined estimates of $(\varepsilon_{t,a})$ through repeated model runs:

Step 0 – Initialization:

We began with a matrix of "constant" average magnet efficiencies $(\hat{\varepsilon}_{0_{t,a}})$ by area and month, derived from either "primary" or "all" recovery station data (see Section 2.5.1). These values were input to the model to generate predicted recaptures $(C_0(t,a))$ using Equation S.7.1. Rearranging S.1 yields a formula for updated estimates of magnet efficiency:

$$\hat{\varepsilon}_{1_{t,a}} = \frac{\text{Observed } C_{t,a}}{N_{t,a}\frac{F_{t,a}}{(F_{t,a}+M)}\left(1-e^{-(F_{t,a}+M)}\right)} = \frac{\text{Observed } C_{t,a}}{\hat{C}_0(t,a)} \quad \text{(S.7.2)}$$

where:

$$\hat{C}_0(t,a) = N_{t,a} \frac{F_{t,a}}{(F_{t,a}+M)}\left(1 - e^{-(F_{t,a}+M)}\right) \quad \text{(S.7.3)}$$

The $\hat{C}_0(t,a)$ is computed each time when the model run is completed, thus can be used to update the magnet efficiency estimate in next step.

Step 1 – First Update:

Using the predicted recaptures $\hat{C}_0(t,a)$ from Step 0, we calculated new magnet efficiency estimates $\hat{\varepsilon}_{1_{t,a}}$ using Equation S.7.2. These updated values were incorporated into the input file for the next model run. To ensure biological plausibility and model stability, bounds were applied to the area-specific estimates of magnet efficiencies $(\hat{\varepsilon}_{t,a})$: primary magnets (Coston data) 0.03-0.95, and all stations (NMFS data) 0.135-0.95.

After each model run, the updated $\hat{\varepsilon}_{t,a}$ matrix was used for the next iteration.

Step 2 and Beyond - Iterative Refinement:

The process was repeated by recalculating magnet efficiencies based on updated predicted recaptures from the previous step. Each iteration refined the alignment between observed and modeled recaptures. The number of iterations was determined by model convergence and improvement in fit metrics.

Model Evaluation:

To evaluate model performance at each step, we used two statistical metrics:

1. Akaike Information Criterion (AIC) to assess relative model fit:

$$\mathrm{AIC} = -2\ln(\mathrm{L}) + 2\mathrm{K} \quad \text{(S.7.4)}$$

where L is the likelihood and K is the number of estimated parameters. Lower AIC values indicate better model performance.

2. Prediction Error (Δ**)** is the difference between observed and modeled recaptures.

Results

The results of the stepwise analysis are presented in **Table S.8** and **Figure S.2**. For both the Coston and NMFS datasets, AIC consistently decreased across iterations, indicating improved model fit. Specifically:

- For the **Coston data**, AIC reached a minimum at **Step 3**.
- For the **NMFS data**, the minimum AIC was observed at **Step 7**.

Most notably, the AIC (**Fig S.2)** and Prediction Error (Δ**)** (**Table S.8**) declined sharply from **Step 0** (constant efficiency assumptions) to **Step 1** (estimated magnet efficiencies), suggesting that using fixed average values for magnet efficiency (as derived from plant tests) was suboptimal.

Table S.8- Stepwise sensitivity analyses of the two mark-recovery dataframes: (A) Coston; and, (B) NMFS. Symbols are: $\widehat{M}$ ≡ estimated annual natural mortality rate: neg(LL) ≡ MMR model negative log-likelihood; $\widehat{R}$ ≡ total estimated recaptures by the MMR model; R ≡ total observed recaptures; Δ ≡ difference between predicted and observed recaptures; AIC ≡ Akaike Information Criterion; and, avg $\bar{\varepsilon}$ ≡ average magnet efficiency.

(A) Coston

Step	$\widehat{M}$	neg(LL)	$\widehat{R}$	R	Δ	AIC	$\bar{\varepsilon}$
0	0.8963	10,579	195,603	102,992	92,611	21,370	0.389
1	0.7289	9,795	143,697	102,992	40,705	19,802	0.340
2	0.6891	9,777	100,340	102,992	-2,652	19,766	0.307
3	0.5956	9,744	97,346	102,992	-5,646	19,700	0.293
4	0.5149	9,751	96,422	102,992	-6,570	19,714	0.284
5	0.4406	9,763	96,044	102,992	-6,948	19,738	0.278
6	0.379	9,773	95,753	102,992	-7,239	19,758	0.273
7	0.3243	9,784	95,569	102,992	-7,423	19,780	0.269

(B) NMFS

Step	$\widehat{M}$	neg(LL)	$\widehat{R}$	R	Δ	AIC	$\bar{\varepsilon}$
0	0.8909	8,044	133,279	93,335	39,944	16,300	0.583
1	0.8174	7,532	94,784	93,335	1,449	15,276	0.538
2	0.7737	7,500	88,188	93,335	-5,147	15,212	0.518
3	0.6938	7,505	95,008	93,335	1,673	15,222	0.504
4	0.6564	7,515	95,649	93,335	2,314	15,242	0.495
5	0.6294	7,519	95,962	93,335	2,627	15,250	0.488
6	0.5609	7,405	113,129	93,335	19,794	15,022	0.479
7	0.5279	7,372	107,830	93,335	14,495	14,956	0.463
8	0.4863	7,373	108,519	93,335	15,184	14,958	0.451
9	0.4498	7,377	108,746	93,335	15,411	14,966	0.443

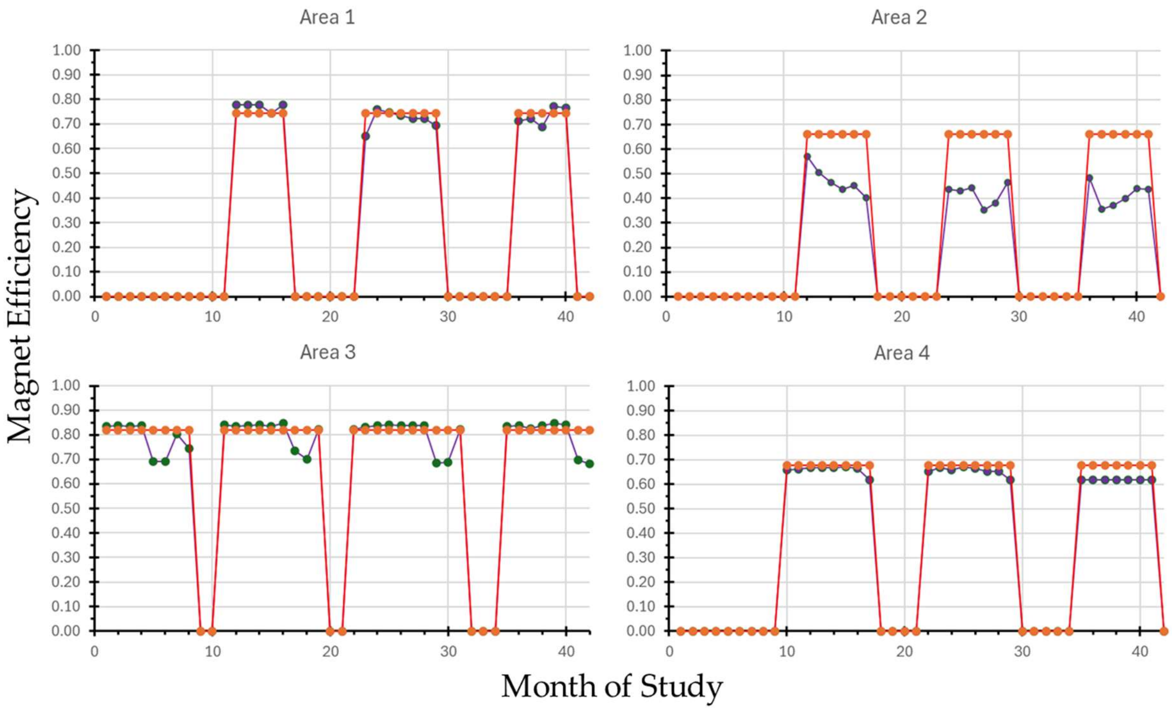

Figure S.1.- Comparative monthly distributions of constant average magnet efficiency for "ALL" magnets by areas from Liljestrand et al. (2019a, black solid dots) and this paper (orange solid dots) using the area mean estimates from Table S.4B.

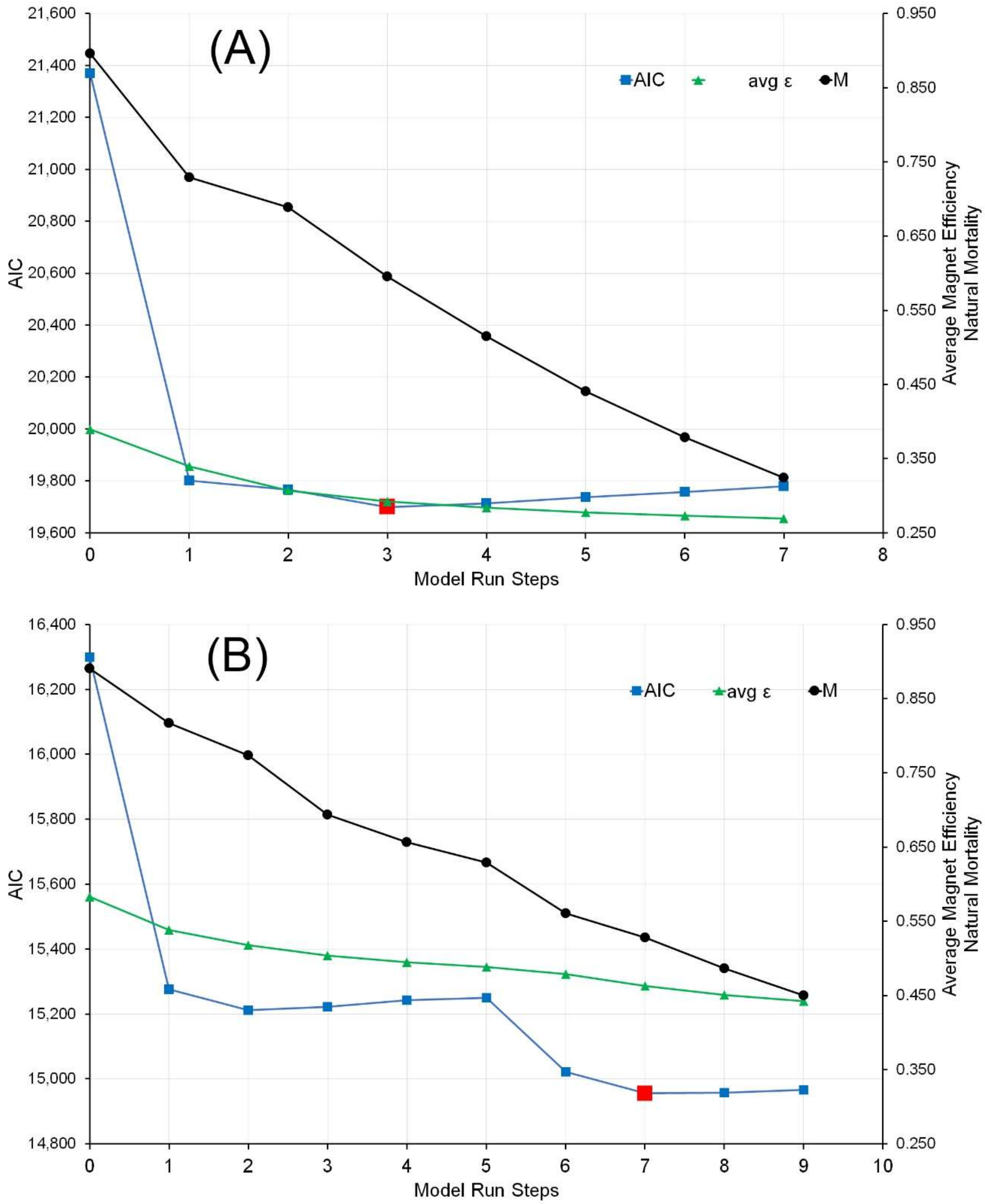

Figure S.2.- Stepwise sensitivity analyses showing the AIC (blue squares), average magnet efficiency (green triangles), and natural mortality rate (black dots) as function of model run step for the two mark-recovery dataframes: (A) Coston; and (B) NMFS. The large red square in each panel indicates the minimum AIC value.

Ref.: Ms. No. **FISH13999.R2**: Investigation of Atlantic menhaden mortality rates.
Fisheries Research

Dear Editor,

We have resubmitted our revision of the manuscript (FISH13999.R1), updated primarily in response to the comments by Reviewer #2. In addition, we have also addressed the relatively minor comments raised by Reviewer #3 and the Associate Editor. Below you find the reviewer's comments in italics, followed by our responses:

1. Are the objectives and the rationale of the study clearly stated? Please provide suggestions to the author(s) on how to improve the clarity of the objectives and rationale of the study.

Reviewer #2: *The objectives of the study are much more clearly defined compared to the previous version of this paper.*

Response: Thank you!

Reviewer #2: *The paper lists a bunch of minor issues with the Liljestrand et al 2019 paper (these may be incorrectly reported values in the tables that are correct in the model), but does not mention the inconsistency between the assumptions of the magnet efficiency being all tags compared to the data which only includes recaptures by primary magnets.*

Response: We respectfully disagree with the characterization of these as "minor issues." However, we do gratefully acknowledge and appreciate Reviewer #2's perspective. Several of the reviewer's comments were valuable, and addressing all of them has strengthened both the paper and our confidence in the analysis.

Our review identified multiple discrepancies in the Liljestrand et al. (2019) paper and Tables, including a critical inconsistency and misapplication of the magnet efficiency data. Specifically, the authors applied recovery efficiencies from all magnets to the **Coston** dataset, despite **Coston** clearly stated that recoveries were made only by **Primary** magnets (i.e., recovery stations 1 and 2), which excluded tags recovered by secondary magnets and other methods (e.g., hand sorting or visual detection). This mistake resulted in an **overestimation of tag recovery efficiency** and, consequently, natural mortality.

These findings were original to our analyses and were later independently confirmed by the ASMFC Stock Assessment Subcommittee M Working Group, with whom we have worked closely and shared data, methods, and algorithms throughout the review process. There were additional inconsistencies in tag release and recovery data reported in the Liljestrand et al. Tables that further limited the verifiability of their modeling results. The Working Group also confirmed the significant errors in the treatment of magnet efficiency and in fishing effort reported by Liljestrand et al.

These are **not minor errors**--they introduce substantial bias that inflates natural mortality estimates, directly impacting the accuracy and reliability of Atlantic menhaden stock assessments.

Reviewer #3: Yes

Response: Thank you!

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2. If applicable, is the application/theory/method/study reported in sufficient detail to allow for its replicability and/or reproducibility? Please provide suggestions to the author(s) on how to improve the replicability/reproducibility of their study.

Reviewer #2: Mark as appropriate with an X: Yes [] No [X] N/A []

1. *There is no description of the meta-analysis that they talk about in the results and discussion. How were these studies collected? How were the specific assessments in the figure decided to be included or not (is it a census of all assessments done by these bodies)? Are these M estimates derived from an indirect life history relationships? Only assessments that have independent or directly estimated values of natural mortality not estimated from indirect life history relationships should be included in the meta-analysis!*

Response: A detailed description of the stock assessment data selection process has been added to the manuscript and Supplemental Materials, which includes an extensive Table describing the sources of the data.

2. *The methods of the stepwise model are not clear. In the methods it sounds as if only a single iteration of the procedure is performed. Additionally, there is no criteria for when to stop the procedure or determination if the model has 'converged'. Such iterative methods are generally not regarded as best practices (see Thorson 2019 "Perspective: Let's simplify stock assessment by replacing tuning algorithms with statistics" https://doi.org/10.1016/j.fishres.2018.02.005). The magnet efficiencies are essentially data that are put into the model at fixed values. The stepwise methodology could be performed to change the predicted recaptures to better match the magnet efficiencies and such approach would not be deemed appropriate. Therefore, the stepwise model should be removed from the manuscript because the methodology does not appear to be statistically valid.*

Response: We appreciate the reviewer's comments regarding the clarity and statistical validity of the Stepwise model. We have revised the Methods section of our manuscript to more clearly explain the Stepwise method's purpose and implementation.

But to clarify, in contrast to the parameter-based approach, where magnet efficiencies (ME) are estimated directly as model parameters, the Stepwise method serves as a diagnostic tool, systematically estimating ME in stages to assess how sensitive model performance is to changes in magnet efficiency. To keep the main text concise, we included the Stepwise method in the supplemental materials. This approach was designed solely to explore the sensitivity of natural mortality estimates to increasing model complexity and the spatial-temporal resolution of ME, not as a formal hypotheses-testing framework. In our analysis, the Stepwise method functioned as a heuristic tool to inform model comparisons and interpretation. We agree that Stepwise procedures and tuning algorithms should not replace statistically robust estimation, as emphasized in Thorson (2019). The results showed that both AIC and prediction error decreased sharply when moving from constant ME (Step 0) to estimated ME (Step 1), indicating that using fixed average values for magnet efficiency was suboptimal.

Further, to address the reviewer's concern and to avoid any confusion, we have:

1. Revised the manuscript to remove references to the Stepwise method as a standalone inference tool.
2. Moved the Stepwise method and analyses to the Supplementary Materials, where it is presented explicitly as a sensitivity or diagnostic exercise.
3. Clarified in both the text and Figure captions that no parameter estimation or optimization was performed and that these outputs should be strictly interpreted qualitatively.

3. *The stepwise production of the stratified year, month and area fishing effort is improved but there is still some portions that are unclear, specifically, step 1, 3, and 4.*

Response: This has been revised for greater clarity.

a. *In step 1 states that effort was 'expanded by year and month to area' however the data are only in year. This wording is confusing and should indicate the yearly effort data were expanded to year and area data (do not include month).*

Response: We appreciate the reviewer's observation regarding the description of the effort expansion procedure in Step 1. The wording has been clarified to report that effort data were available at an monthly resolution, but only at a coastwide level. Our intention was to indicate that these yearly values were disaggregated spatially across areas. There was no monthly component in the effort expansion at this step. Our revised wording in the manuscript reads: "Annual fishing effort data (vw) were disaggregated by area to produce effort estimates by year and area…"

b. *Step 3 of the effort creation step is not clear. Does this mean that all fishing effort in 1966 was allocated to area 3?*

Response: Step 3 should actually be just one step. The first part stated why we needed to do this.

c. *Step 4 is not clear in the methodology, the weighted average of what quantity is used? what is providing the weighting of the averaging? It seemed as though the data were already separated into year, month, and area by step 2 so it's not apparent what is occurring in steps 3 and 4.*

Response: Thank you for your careful review. We agree that the original wording did not adequately describe the operation performed or its connection to the preceding steps. In response, we have revised the manuscript to improve clarity and have combined Steps 3 and 4 into a single, streamlined Step 3. The revised text now reads: "(3) Due to the lack of tagging effort in areas 1, 2, and 4 in 1966, no recaptures were reported in these areas for that year. Therefore, we estimated monthly fishing effort for areas 1, 2, and 4 in 1966 based on the average monthly distribution of fishing effort from 1967 to 1969, weighted by the area-specific annual fishing effort."

4. *Numerous time through out the manuscript the authors reference equations from Liljestrand et al 2019. It seems like it would be more appropriate to present those equations in the manuscript than require the reader to look up the equation in another publication.*

Response: It was not clear which way was better because including the equations here would also require that we included descriptions of the equations. This would greatly increase the length of the manuscript which is a concern to this reviewer. Considering that readers of this paper will likely be very familiar with Liljestrand et al paper, we have instead opted to quote their equations.

5. *The authors use the delta symbol multiple times in the analysis to represent different quantities (e.g., difference in predicted and observed tags and difference in AIC values). Symbols should only be used once to represent a single variable so as not to confuse the reader.*

Response: Symbols have been modified to ensure consistency in the presentation.

6. *Table 2 does not have an entry for Q_a to indicate whether this parameter is estimated or fixed.*

Response: The Q_a parameters are time-constant, and area-specific parameters are estimated by the model.

7. *The methods could be clarified that each model estimates the parameters using penalized maximum likelihood approach and then the MCMC analysis is conducted. Currently, that methodology only appears to apply to the constant model.*

Response: No, we disagree. MCMC analysis was conducted for each model to evaluate uncertainty and posterior distributions of the parameters. We have revised the Methods section to explicitly state that this is a two-step process: (1) penalized maximum likelihood estimation followed by; (2) MCMC—applied consistently across all model configurations, not just the "constant" method.

Reviewer #3: Mark as appropriate with an X: Yes [X] No [] N/A []

Response: Thank you!

Reviewer #2: *The paper references earlier work and available code that can be used to reproduce the results, and can be evaluated again if desired.*

Response: Code has been added to the Supplemental materials.

3. If applicable, are statistical analyses, controls, sampling mechanism, and statistical reporting (e.g., P-values, CIs, effect sizes) appropriate and well described? Please clearly indicate if the manuscript requires additional peer review by a statistician. Kindly provide suggestions to the author(s) on how to improve the statistical analyses, controls, sampling mechanism, or statistical reporting..

Reviewer #2: Mark as appropriate with an X: Yes [] No [X] N/A []

1. *The authors goes to great lengths to list the "significant errors" in the Liljestrand et al analysis. However, the authors proceed to use the estimated movement parameters from this 'flawed' analysis. The estimates of movement and fishing mortality (and thus total mortality) are strongly correlated in multi-area tag recovery models. Therefore, the analysis should not use any estimates from the previous analysis given the incorrect application of the assumptions with regard to the magnet efficiencies. This will change the fishing mortality, movement and likely the natural mortality estimates. All model scenarios must estimate the movement parameters for this study to be publishable!*

Response: Based on our discussions and correspondence with the authors of Liljestrand et al. (2019a), one of their primary objectives was to estimate the movement of Atlantic menhaden between areas and seasons—that is, to derive a migration matrix. We used the prior distributions of movement parameter estimates from Liljestrand et al. (2019a) as initial conditions for all our model simulations. The model then re-estimated these movement parameters using the magnet efficiency method, incorporating corrected release, recapture, and fishing effort data. Notably, the re-estimated movement parameters revealed seasonal and spatial movement patterns that were broadly consistent with those reported in the original study.

2. *As stated above the stepwise method is not a statistically valid methodology. This must be removed from the manuscript.*

Response: See description of actions regarding the Stepwise methodology above. The Stepwise estimation section has now been removed from the manuscript and added to the Supplemental Materials as a sensitivity test on magnet efficiencies.

3. *The authors should state if a positive definite Hessian is obtained from each of the models and if there are parameters that are estimated on the upper or lower bounds of the parameter*.

Response: Thank you for this comment. Yes, all models used to estimate magnet efficiencies achieved a **positive definite Hessian**, indicating successful convergence and reliable estimation of standard errors.

We also examined the posterior distributions for the Coston data to assess boundary behavior. Of the 100 magnet efficiency parameters:

- **7 were estimated at the lower bound** of **0.03.**
- **1 was estimated at the upper bound** of **0.95.**

The remaining parameters were estimated well within the specified bounds. This outcome is consistent with the use of boundary constraints and suggests that the majority of parameter estimates are not unduly influenced by those limits. We have clarified this point in our revised manuscript.

4. *The model that estimates the magnet efficiency should include an informative prior distribution based on the plant release tag so that ALL data are being used in the analysis as the authors incorrectly state is being done. The magnet efficiency should be parameterized as logit transformed values, so subjective upper and lower bounds do not need to be chosen for the log normal deviates.*

Response: The random non-parametric distributions of plant magnet efficiencies made it difficult to derive meaningful and informative mean values. Our model was initialized using the overall framework described in Liljestrand et al. (2019a), which is a Bayesian multi-state mark-recovery model. Beyond updating the model with corrected input data, our primary modification was to estimate magnet efficiencies as model parameters, using the mean values from plant test data as prior estimates rather than treating them as fixed input. Using fixed input values could misrepresent the true variability and structure of plant-specific magnet efficiency data.

Regarding the parameterization of magnet efficiency, we appreciate the reviewer's suggestion to use a logit transformation, which appropriately constrains efficiency values to the (0, 1) interval and avoids the need for arbitrarily selected upper and lower bounds. In the current model, we applied a log transformation—consistent with the treatment of migration parameters in Liljestrand et al. (2019)—primarily for computational tractability. However, we acknowledge that this approach can impose implicit bounds that may appear subjective. Additionally, since the model operates on a monthly time step, the estimated parameters should reflect the average monthly efficiency, rather than the outcome of individual trials.

5. *The calculation of the degrees of freedom for the tagging data is incorrect. The models use the ratio of the tag recaptures divided by the release events for determining the survival rates and other model parameters. Therefore, the degrees of freedom is likely the count of recapture events with unique recapture area, and time and release event area and time. Degrees of freedom are generally, not calculated for tagging data because the number of recaptures cannot be assumed to be independent of one another due to the time series nature of the data and finite number of tags released. Therefore, these calculation should be removed from the manuscript. Instead the authors should report on whether the models are able to estimate all parameters away from the upper and lower bounds and whether the model gives a positive definite Hessian. If the model gives a non-positive definite Hessian error warning then the model is overparameterized.*

Response: We thank the reviewer for highlighting the issue of degrees of freedom in the context of tag-recapture modeling. We agree that our initial treatment of degrees of freedom was overly simplistic and not well suited to the structure of tagging data. As the reviewer correctly notes, the number of unique recapture events defined by release and recapture area and time does not imply statistical independence, due to factors such as temporal autocorrelation, shared release conditions, and the finite number of tagged individuals. These properties of tag-recapture data limit the applicability of standard degrees of freedom calculations, which are typically not used for inference in such datasets. In our case, each recapture entry represents the number of fish recaptured at a specific location and time, conditional on the original release event, summarized at a monthly resolution. While multiple recaptures may occur within a given month, we acknowledge that these are not independent observations. That said, we are not using degrees of freedom for statistical inference (e.g., as in GAMs or likelihood ratio tests), where Effective Degrees of Freedom (EDF) and autocorrelation adjustments would be necessary. Rather, we applied a basic comparison of the number of estimated parameters to the total number of observations using the simple formula:

Degrees of Freedom = Number of Observations − Number of Parameters

Our sole intention was to demonstrate that the model was not overparameterized. In our case, the number of parameters is less than 1% of the number of observations. We have revised the manuscript text accordingly to clarify this limited and descriptive use of the term "degrees of freedom".

Reviewer #3: Mark as appropriate with an X: Yes [X] No [] N/A []

Response: Thank you!

4. Could the manuscript benefit from additional tables or figures, or from improving or removing (some of the) existing ones? Please provide specific suggestions for improvements, removals, or additions of figures or tables.

Reviewer #2: *There is an error in Table 7B where the number of tag recaptures increases with additional rows after the 5th iteration*

Response: Yes, that was a minor error that occurred when entering the numbers. We thank you for pointing this out. The error has been corrected and Table 7B has been removed from the Manuscript and moved to the Supplemental Materials as Table S.8 as indicated above.

Tables 8 and 9 are duplicative in reporting many of the same values. These should be consolidated in some manner

Response: These two Tables have been consolidated into a single Table (now **Table 7**) following the recommendation of the Reviewer.

Figure 2 should be removed since there is no description of the meta-analysis procedure and includes numerous values that are derived from indirect models

Response: Thank you for the comment, but we disagree. We respectfully acknowledge that the previous manuscript version lacked details regarding the meta-analysis underlying Figure 2. In the Supplemental Materials associated with our revision, we have included a highly detailed Table S.2 that lists the **specific** national (USA) and international fishery management council and commission stock assessments published reports for each data point to improve transparency and traceability.

Reviewer #3: *The tables and figures are adequate*

Response: Thank you!

5. If applicable, are the interpretation of results and study conclusions supported by the data? Please provide suggestions (if needed) to the author(s) on how to improve, tone down, or expand the study interpretations/conclusions.

Reviewer #2: Mark as appropriate with an X: Yes [] No [X] N/A []

The conclusions are based on flawed methodology that used fixed movement estimates from the paper that they are criticizing for having numerous things incorrect. Additionally, the methods used for the stepwise are not statistically valid and the estimation of the magnet efficiencies does not make use of all data, namely the factory release tags that should be included in that model as prior distributions on each estimated parameter. Therefore, the conclusions made from this study are not sound.

Response: Thank you for this relatively constructive critique. We appreciate the opportunity to address the concerns raised.

First, while we initially used movement estimates from Liljestrand et al. (2019) as prior distributions, all movement parameters were re-estimated in our final model runs using corrected release and recapture data, revised effort data, and an updated treatment of magnet efficiency. These re-estimated movement parameters were not significantly different from those reported in the original study, but they were derived independently within a consistent and corrected framework.

Second, regarding the Stepwise model selection procedure, we acknowledge that this approach can have limitations. Our intention was to explore the sensitivity of natural mortality estimates to increasing model complexity and spatial-temporal resolution of magnet efficiency. The Stepwise process was used as a heuristic tool to guide model comparisons and interpretation, not as a formal hypothesis testing framework. That material has now been moved to Supplemental Materials (Tables S.7 & S.8).

Finally, we recognize the concern about not incorporating the plant trial release tag data as informative priors in the estimation of magnet efficiencies. While our current approach uses maximum likelihood estimation without explicit priors, we agree that a Bayesian formulation—including plant-specific prior distributions informed by release data—may better integrate all available information and improve estimation, particularly for plants with sparse data. However, given the random non-parametric nature of the magnet efficiency data we observed, we believe that imposing any parametric distribution in the prior could misrepresent the true characteristics of the data.

While some limitations may remain, we have addressed the major methodological concerns through re-estimation of key parameters and correction(s) of input data.

Reviewer #3: Mark as appropriate with an X: Yes [X] No [] N/A []

Response: Thank you!

6. Have the authors clearly emphasized the strengths of their study/theory/methods/argument? Please provide suggestions to the author(s) on how to better emphasize the strengths of their study.

Reviewer #2: *Yes. The authors very strongly attempt to argue for the use of the stepwise and parameter models. However, these models are statistically invalid and should not be used or need to include appropriate priors as discussed above.*

Response: We respectfully disagree. No rationale was provided by the reviewer to support the statement "statistically invalid". In fact, we used the same parameter estimation methodology as Liljestrand et al. (2019a), and further, these issues have been addressed in many of our previous comments.

Reviewer #3: *Yes*

Response: Thank you!

7. Have the authors clearly stated the limitations of their study/theory/methods/argument? Please list the limitations that the author(s) need to add or emphasize.

Reviewer #2: *The authors have done a much better job discussing the limitations of the study compared to the previous version. However, their interpretation of the linkage between reporting rates and complete mixing of tags is incorrect. All Brownie models make the necessary assumption that tags are fully mixed with the population. Therefore, reporting rates and magnet efficiencies are not related to the amount of mix as the author is suggesting in the discussion. I believe the authors are taking issue with the weighting of the plant based magnet efficiencies by the landings at each plant as was done by Liljestrand. If tags are fully mixed (which is an implicit assumption in ALL Brownie models) then the correct way to predict the number of expected returns is to weight the efficiency of each plant by the landings of that plant.*

Response: You are correct that complete mixing of tagged and untagged fish is a fundamental assumption of all Brownie models. Our intent was not to challenge this assumption, but rather to highlight that **heterogeneity in recovery effort** (i.e., plant-specific magnet efficiencies) may interact with **uneven mixing in practice**, especially when tagging and recovery efforts are not uniformly distributed across space and time. Because the distribution of magnet efficiencies is clearly non-parametric, the parametric mean simply does not adequately represent the observed variation. We agree that **if the magnet efficiencies were normally distributed**, weighting plant-specific efficiencies by their respective landings would likely be an appropriate approach.

Take for example 2 plants with magnet efficiencies of 0.1 and 0.9. If the plant with an efficiency of 0.1 lands 80% of the landings you would expect much fewer tag recaptures than if a simple average of the two magnet efficiencies was used. To account for this in the model a magnet efficiency of 0.26 would be more appropriate than an average value of 0.5 Thus the methodology presented by Liljestrand et al for calculating the landings weighted magnet efficiencies is correct and results in a time varying reporting rate that the constant methodology presented in this paper does not adequately address.

Response: No, we disagree. We are not questioning the **weighting approach** itself. The issue lies in how the values of **0.1 and 0.9** were derived. These values are intended to represent the **mean magnet efficiency** for each region; however, the underlying distributions are **highly variable and non-parametric**, with substantial spread across the range. As a result, the values of 0.1 and 0.9 are **not representative summaries** of the data. Due to this non-parametric distribution, the mean magnet efficiency estimates are **biased even before applying the weighting**, which affects the interpretation of the regional averages.

Reviewer #3: *While the degree of uncertainty could be emphasized more in the final summary, the reporting of multiple approaches, natural mortality estimates, and uncertainties from these approaches does address the uncertainty.*

Response: Thank you! We have added emphasis to the degree of uncertainty in the final summary as noted by this reviewer.

8. Does the manuscript structure, flow or writing need improving (e.g., the addition of subheadings, shortening of text, reorganization of sections, or moving details from one section to another)? Please provide suggestions to the author(s) on how to improve the manuscript structure and flow.

Reviewer #2:
1. *The section 2.1 Indirect: life history and longevity appeared to be an extension of the introduction. It was completely lacking in methodology describing how values were selected for the meta-analysis. This section should be moved to the introduction and expansion the actual methodology of the 'meta-analysis' is required.*

Response: We have extensively revised this materials describing how natural mortality and maximum age values were chosen for the construction of **Figure 2**. The Supplemental Materials now contain a highly detailed **Table S.2** that lists the **specific references and sources** for each data point to improve transparency and traceability.

2. *The "13 previously published peer-reviewed papers" should be presented and cited in the introduction*

Response: These publications have been cited and detailed.

3. *The last paragraph of the results appears to be mostly things that should be put into the discussion.*

Response: Paragraph edited and moved to the Discussion as suggested.

4. *Line 508-512 reiterates information that was previously presented in the introduction. Unless there is something new that is being suggested this repetition should be removed.*

Response: Redundant information removed.

Reviewer #3: It flows well.

Response: Thank you!

9. Could the manuscript benefit from language editing?

Reviewer #2: No

Response: Thank you!

Reviewer #3: No

Response: Thank you!

Editor Comments. *The manuscript is improved, especially in readability, but Reviewer #2 still notes major inconsistencies and deficiencies with the analyses that they request further treatment. Please address all of these issues specifically so the reviewer can easily track responses to their concerns. I look forward to the next version of the paper and progress toward publication.*

Response: Thank you! We believe that we have completely and adequately addressed all (especially Reviewer #2's) comments.

Reviewer #2: *General comment. some reported value use 2 significant figures while others use 4. They* *should all be consistent.*

Response: Done.

Line 22: *Overstated is a single word. Needs to be overstated the number of tag releases.*

Response: Corrected.

Line 23: *Magnet efficiency statement should indicate that an incorrect assumption was made regarding magnet efficiencies and don't focus on the percentage difference*

Response: Wording change made.

Line 24: *The modeling approach of the magnet efficiencies is not subjective. I don't know where this comes from and it is not substantiate in the document.*

Response: Revision to sentence was made.

Line 39-41: *This background information could be removed as it is not completely relevant or shorted to help reduce the length of this already long paper*

Response: We feel that background information is relevant for reader's not familiar with the history of the fishery.

Figure 2. *Once again this does not explain the methods used to select these species. Is this all species for which there are assessments in these regions? Do these assessments use empirical relationships or are the estimated by the assessment? If all of these assessments use some sort of empirical relationship then they should not be included in the meta-analysis and only M values estimated internal to the assessment model or other direct estimates should be presented, otherwise the argument is circular.*

Response: An expanded explanation of the origin of these data has been added to the manuscript.

Line 76-78: *These statements needs to be more fully explained and proof shown of these accusations.*

Response: A full explanation of these statements is provided. These were determined by comparing data, and the fishing effort discrepancies are from the ASMFC SAS M Working Group's findings.

Line 110: *Change surviving to survive*

Response: Change made.

Line 124: *Change Hoyle et al 2023 to Hamel and Cope 2022*

Response: Change made.

Line 148 to 153: *This is a run on sentence and it is very difficult to interpret*

Response: Sentence has been rewritten for clarity.

Line 183: *Remove first 'by'*

Response: Done.

Line 204: *"These data..." Which data are you referring to?? The previous sentences are about magnet efficiency. Therefore, it's completely obscured what data is being referred to. The previously mentioned data are the NMFS data but the fields in table 1 show a magnet station entry so I'm completely lost on what this is referring to.*

Response: Text modified to address comment, antecedent identified in the revised sentence.

Line 221: *Present the equation here*

Response: For the reasons we stated earlier in this response, we opted to allow the reader to reference the Liljestrand et al. (2019a) paper. To include the equations here will also require that we include the descriptions of the equations, thus greatly increasing the length of the paper.

Line 224-225: *(should be Table S2A and S3A. Additionally, the caption for S2A and S3A should include the proportion of tags that are caught by only primary magnets for all plants combined instead of total tags recovered.*

Response: Corrections made.

Line 225: *An area average...*

Response: Done.

Line 225-226: *This wording makes it sound like a simple average across all the plants by area is being performed. However, the values reported don't correspond to such an average and the table suggests that a weighted average is used. The weighted average methods used should be described. Additionally, the difference between this methodology and that of Liljestrand et al should be included in the discussion*

Response: The difference between our methodology and Liljestrand et al is included in the Discussion. We did not use a weighted average as the catch data were not directly available to us. However, the effect of catch-weighting was minimal (c.f., ASMFC SAS M Working Group report).

Line 226: *(1.) This should be table S2B & S3B. (2.) It is not clear what all of the columns in that table represent. A clear description of each column in these tables is required including a label for the bold values on the far right which requires some sort of column label and a description in the caption.*

Response: Column definitions in Supplementary Materials Tables (now) S.3B and S.4B were edited and clarified.

Line 234: *Where does this value come from? If you are going to accuse another author of making a mistake the least you can do is to show where these differences occur. It's probably sufficient to include it in the supplementary materials since the effort in Liljestrand was also only presented in the supplementary materials. Is this just a miscalculation when summing the monthly values that are actually used in the model code and are merely reported incorrectly in the supplementary materials or is it an actual problem with the data in the model?*

Response: Actually this was Line 235. This comes from the ASMFC SAS M Working Group's findings based on information provided by NMFS Southeast Fisheries Science Center. The effort in vessel weeks (vw) was also incorrect in SEDAR 69 and Liljestrand et al. The errors in fishing effort were an issue for the Liljestrand et al. analyses.

Line 238: *Table S4*

Response: The reference to this Table found in the Supplementary materials of Liljestrand et al. (2019a) was clarified.

Line 258: *Present equation in this manuscript*

Response: See rationale for exclusion above.

Line 287: *What abundance is being used? Is this tag abundance or population abundance? If it is the* *former then I wouldn't call this an abundance. If it is population abundance you should state where the estimate is coming from.*

Response: We corrected the description of the computation of annual fishing mortality F_y for all areas, assuming that tags were proportional to the population, as the annual average of the $F_{y,a}$ for each area weighted by the number of tags still out in the water in that area.

Line 301: *As parameters approach should use the plant release tags as informative priors to use all of the data available to inform these difficult to estimate model parameters.*

Response: We acknowledge the reviewer's concern about not incorporating the plant batch trial tag-release data as informative priors in the estimation of magnet efficiencies. However, our approach used maximum likelihood estimation without explicit priors. It is possible that a Bayesian formulation—including plant-specific prior distributions informed by release data—may better integrate all available information, particularly for plants with sparse data. However, given the random, non-parametric nature of the observed magnet efficiency data, we strongly believe that imposing any parametric distribution in the prior would misrepresent the true statistical characteristics of the data.

Line 305-307: *Run-on sentence that I was not able to interpret*

Response: This sentence has been rewritten for clarity.

Line 314: *'single-run constant mean assessment' I'm not sure what this is referring to. Do you mean that the penalized maximum likelihood was maximized and proved point estimates of model parameters?*

Response: Revised text to "initial run" for clarity.

Line 313-316: *These should be moved to somewhere else to explain that these procedures were conducted for all models because it sounded like this was only done for this model.*

Response: This section has been edited for clarity.

Line 316-318: *I would agree except for region 2 where the efficiency is well above that estimated by Liljestrand and there is substantial variation over time. This region has 1/3 of the releases and over 1/4 of the recaptures. Thus these differences could make a big impact on the estimates of F and M. Also the constant method proposed here is constant across time which is not the same as Liljestrand, it's a simplifying assumption. Another scenario should be computed which uses landings weighted magnet efficiencies and compared to the constant regional value used.*

Response: Thank you for this insightful observation. We agree Area **2** is where magnet efficiency estimates are notably higher than those reported by Liljestrand et al. and where substantial temporal variation exists. These differences could significantly influence estimates of fishing mortality (F) and natural mortality (M). Given that Area 2 accounts for roughly one-third of all tag releases and over one-quarter of recaptures, capturing this variability accurately is indeed critical.

Regarding the **constant method**, we acknowledge that it represents a simplifying assumption by treating magnet efficiency as constant over time, unlike Liljestrand's time-varying approach using catch-weighting. We agree that this simplification may mask important temporal dynamics in magnet efficiency. However, given that we were denied access to the time- and area-specific landings data, we were unable to use landings-weighted magnet efficiencies. These were done by the ASMFC SAS M Working Group and when compared the effects were minor, with less than +0.04 difference between their M estimate using this approach.

Line 331: *Eq.(1) to Eq.(2)*

Response: Corrected and these materials were moved to Supplemental Materials as Table S.7.

Line 365: *The notation of the number of parameters to be estimated doesn't make sense because if n >1 then you have a negative parameter index which is generally not allowed.*

Response: Notation was modified to address the reviewer's concerns.

Line 367-369: *(1.) Generally these parameters are estimated as logit transformed parameters so that they can be estimated to be any value between 0 and 1 given the bounds of the parameter and do not require choosing subjective upper and lower bounds for the log distribution (2.) The range of parameters here do not match with those presented in the caption of Figure 6. "Such fundamental errors made it virtually impossible for us to verify their conclusions."*

Response: Thank you:
(1) We agree that using **logit-transformed parameters** is a standard approach for estimating values constrained between 0 and 1, as it avoids the need to impose subjective upper and lower bounds inherent in log-normal or other bounded parameterizations. In our modeling, we used a log transformation consistent with the approach taken in Liljestrand et al. (2019a) to facilitate comparability with their work. However, we recognize that this can introduce implicit bounds that may appear arbitrary.

(2) Regarding the range of parameters **and the caption of Figure 6**, we do appreciate your close attention to this detail. There was a mismatch between the parameter ranges and the values

presented in the caption. We have shifted the discussion of the Stepwise method to the Supplemental Materials (Table S.7), and further, removed the Stepwise panels from Figure 6.

Line 372-378: *Remove this discussion on degrees of freedom as this is not correctly calculated and typically only applies to linear models.*

Response: The discussion on "degrees of freedom" was addressed earlier and clarified.

Line 387-389: *This sentence is poorly worded and I cannot interpret what is intended.*

Response: This sentence was reworded for clarity.

Line 394: *The reasonable range of values does not have any description of the methodology used to come to this conclusion. The reader should be able to come to the conclusion by presenting results not dictating how they should be interpreted.*

Response: These are the survivorship probability bounds when $p_{\max} = 0.05$ and $p_{\max} = 0.0045$.

Line 402: *Overstated*

Response: Corrected.

Line 404: *Why is such an abrasive and combative language used in the results section? The results section is to describe the result of the current study, whereas the discuss is where you can contrast the results with other studies. However, I would recommend against using such strong and demeaning language.*

Response: This was certainly not our intent and we have revised this sentence accordingly.

Line 408: *82.5%.*

Response: Corrected.

Why is this sentence in this paragraph. Why is it in the manuscript at all?

Response: It points out the strong correlation between the fractions of releases and recapture in in Areas 2 & 3 found in the Coston and NMFS data (Tables 4 & 5).

Line 424-427: *What is more important is can you exactly replicate the 4,836 of recaptures in Coston* *with the definition used in the NMFS dataset? If not exactly how close?*

Response: Yes, we were able to exactly replicate the recaptures found in Coston using our definition of "Primary" magnet only tag recoveries. We openly passed this important information on to the ASMFC SAS M Working Group.

Table 6: *Would be a good place to compare the Liljestrand values presented and what is used in this study.*

Response: While we appreciate the suggestion, such a table is not needed because the ASMFC SAS M Working Group also confirmed the Table errors and other significant errors in the magnet efficiency and fishing effort data used by Liljestrand et al. Further, it would only add unnecessary complexity to the presentation.

Figure 6: *The caption needs to explain what delta means otherwise people will think that it is the delta AIC which is what is usually reported and presented as delta.*

Response: Caption revised.

For the model that estimates the magnet efficiencies as parameters, does it achieve a positive definite hessian? How many of these parameters are estimated at the upper or lower bound.

Response: Yes, the model estimating magnet efficiencies as parameters achieves a **positive definite Hessian**, which indicates that the optimization has successfully converged to a local minimum and that standard errors can be reliably estimated.

Regarding boundary behavior, out of 100 estimated magnet efficiency parameters:

- **7 parameters** were estimated at the **lower bound** of **0.03**.
- **1 parameter** was estimated at the **upper bound** of **0.95**.

The remaining parameters were well within the specified bounds. This distribution of parameter estimates is expected given the imposed boundary limits; further, it indicates that most of the efficiency estimates are not artificially constrained.

Table 7: *Has numerous issues. (1.) R in the NMFS table had R that increases for 5 and higher. (2.) Such tables generally include a column for number of parameters estimated. (3.) However, the stepwise methodology is statistically flawed and should be removed from the manuscript, thus so should this table.*

Response: The Stepwise sensitivity analysis Table (now Supplemental Table S.8) was revised as suggested, and then moved to the Supplemental materials. We have addressed the Stepwise sensitivity procedure above and also moved those materials to the Supplemental section (Table S.7).

Line 473-477: *This seems like statement that should be in an Atlantic menhaden stock assessment report and not in the scientific literature. The work in the published literature should speak for itself and not need to advocate for an approach to be used in a stock assessment.*

Response: Revised for clarity.

Line 508-512: *This is a repetition of what was presented in the introduction, it does not need to be repeated here*

Response: Sentence was revised.

Line 518: *Remove "data documented"*

Response: Sentence clarified by removing word "data".

Line 539: *An informative upper bound*

Response: Edit done.

Line 539-540: *", more so than in many other species assessments," This statement does not appear to be based on anything other than an opinion. I suggest removing this portion of the sentence*

Response: Sentence modified.

Line 542: *8e-6 probability: This assumes that an average M of 1.17 is used across all ages. In the stock assessment they use a Lorenzen natural mortality at age curve which is likely to have a higher probability of surviving to age 10 (though still likely small) this what should be reported.*

Response: We disagree, the Lorenzen S at $a_{\max}$ should be equal to $S = e^{-1.17\times 10}$ at 10 years of age.

Line 558-560: *The statement is not consistent with recent stock assessments of Atlantic menhaden. These conclusions are based on dated references and this sentence does not have any reference. Therefore, these statements are unlikely to be representative of current conditions and should be removed.*

Response: We respectfully disagree. These statements appear prominently in the literature. The most recent Atlantic menhaden stock assessment used the dubious natural mortality value as described in this paper, which was recently acknowledged as incorrect by the ASMFC Stock Assessment Subcommittee (SAS) M Working Group.

Line 577-586: *This paragraph should be removed because the logic is flawed. All Brownie models assume that the tags are fully mixed with the population. This assumption has nothing to do with reporting rates. Reporting rates are a measure of the proportion of tags that are recaptured that are returned and reported to the tagging agency (this is similar in idea to the magnet efficiency in that both are proportions that reduce the expected number of reported tags in the model).*

Response: We respectfully disagree. This issue has been addressed previously in this response.

Line 589-593: *While I do not disagree that there is a large amount of variability in the magnet efficiencies, the methodology used in this analysis is not consistent with what was done in Liljestrand et al.2019. Why were the time varying reporting rates not used in this analysis? The negative binomial models could be used to estimate the area specific by month magnet efficiencies. However, this will weight plants that have higher sample sizes or plant releases, which may not be reflective of the plants with higher landings and thus a higher probability of recapturing tags.*

Response: Thank you. You are correct that the methodology used in our analysis differs from that of Liljestrand et al. (2019), and we appreciate the opportunity to clarify our rationale.

While Liljestrand et al. applied time-varying reporting rates, our analysis focused on estimating magnet efficiencies directly using observed tag recoveries and corrected data inputs, rather than modeling reporting rates as a separate latent process. Our intent was to isolate and evaluate the effects of revised magnet efficiency estimates under different spatial and temporal structures, using maximum likelihood and MCMC frameworks, rather than reproducing the full structure of the previous model.

Regarding your suggestion to use negative binomial models to estimate area- and month-specific magnet efficiencies, we agree that this may be a statistically valid approach, especially for over dispersed count data. However, as you pointed out, this method implicitly weights plants with more tag batch releases or tag recoveries, which may not align with the probability of tag recapture driven by plant-specific landings. This creates a potential mismatch between data availability and biological relevance, especially if high-release areas do not correspond to high-catch locations.

Line 594-595: *How is completely removing the magnet efficiencies from the model for the stepwise and parameter models an efficient use of the data since is not being used at all? This argument is nonsensical.*

Response: We used the magnet efficiency trials data and we know that magnet efficiencies are distributed as a nonparametric distribution and can not be represented by a parametric mean. In addition, the variance observed in the magnet efficiency test data preserved in our parameters estimation approach.

Figure 8: *This figure looks like there are a large proportion of the estimates at the upper and lower bounds of the specified ranges. This suggests that these parameters are not well estimated by the model and means that they should be fixed using the data available or these data should be used as an informative prior on these parameters in the Bayesian model.*

Response: The distributions by area in this Figure captures the variation seen in the observed data, but are not intended to look exactly like the data since they are a random nonparametric realization. In addition, these estimates are well within the bounds of the observed data.

Line 617-618: *" ..the preferred estimation method should be on that utilizes the entire dataset." This statement creates so many conflicts with the conclusions the author is trying to push. 1. The models should then include the dataset for factory releases, 2. The NMFS data set for the full time series should be used. 3. the models should rely only on the data available and not fixed parameters from a previous incorrect analysis of the data.*

Response: Thank you for this comment. We agree that the statement about using the "entire dataset" needed to be more precise and consistent with the methodology we employed. We have modified that language to reflect that it was essential to use both the observed recapture data and the appropriate statistical distributions of the magnet efficiencies to obtain the best model fit(s) to the observed recaptures, thereby producing the most scientifically defensible estimates of natural mortality.

Line 627-628: *I'm concerned about the validity of the parameter estimates from the model that has the magnet efficiencies estimated at the bounds of the parameters. This generally indicates that the model is overparameterized beyond what information is available in the tag recaptures.*

Response: Thank you for raising this important concern. You are correct that when parameter estimates—such as magnet efficiencies—consistently fall at their upper or lower bounds, it can indicate **overparameterization** or a lack of sufficient information in the data to support reliable estimation of all parameters.

In our model, we observed that **8 out of 100 magnet efficiency parameters** were estimated at the bounds (7 at the lower bound of 0.03 and 1 at the upper bound of 0.95) for the Coston data. While the majority of parameters fell well within the allowable range, we recognize that boundary estimates may signal areas where **tag recovery data are sparse or inconsistent**, limiting the model's ability to resolve plant- or time-specific efficiency.

This issue highlights the trade-off between model complexity and data support. In areas with limited recapture data, estimating too many parameters can lead to identifiability problems and reduce confidence in those estimates.

Line 631-633: *The methodology of average efficiency weighted by catches should be a scenario that is presented in this manuscript!*

Response: We don't have this data; however, the ASMFC SAS M Working Group used these to produce an M estimate that was only +0.04 different from what we estimated without catch-weighting of the magnet efficiencies.

Line 647-648: *If you are conducting a Bayesian analysis then you must assume some prior distribution. If you don't explicitly assign a distribution but put ranges on the possible parameter values then you are implicitly assuming a uniform distribution for these parameters. This is an incorrect statement and does NOT make use of all available data, which should be used to create the informative prior for these logit transformed parameters.*

Response: We did not alter the overall model framework used by Liljestrand et al. (2019). Aside from updating the model with corrected input data, our main modification was to **estimate magnet efficiencies as parameters**, rather than treating them as fixed input values calculated from the **mean of a non-parametric distribution**—an approach that can misrepresent the true variability and structure of the plant-specific magnet efficiency data.

Line 664: *Do you mean estimated as random effects?*

Response: Sentence revised for clarity.

Line 678-679: *Where does the one sided inequality come from? What basis is this decision made on?*

Response: Because all of the direct and indirect natural estimates obtained were $\leq \mathrm{M} = 0.54$.

Line 681-682: *The largest stock size will be obtained when fishing mortality is zero. This is a possible option but does not match the management of all other species where we try to maximize yield while allowing for a sufficient stock size to continue this into the future. This sentence should be removed or reworded.*

Response: As noted, not everyone agrees that yield(s), especially of critical forage fish like menhaden, must be maximized. The sustainability of associated (charismatic and economically/ecologically valuable) predators must be considered as a basis for ecosystem-based management, instead of simply catching as much fish as possible.

Reviewer #3: *The authors have responded adequately to this reviewer's suggestions, and in addition, the paper is a much easier read in this revised form.*

Response: Thank you!

I found two typos to be fixed:

Equation 2, line 325: *There should be a minus sign in the exponent.*

Response: Corrected. Thank you!

Line 678: *0.54 rather than 054*

Response: Corrected. Thank you!

In accordance with Fisheries Research policy and my ethical obligation as a researcher, I am reporting that I have no financial and/or business interests in any company or entity that may be affected by the research reported in the enclosed paper.