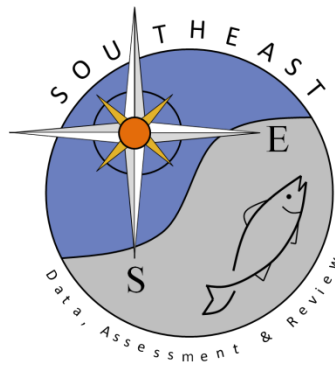


Understanding Atlantic Menhaden Population Demographics: Re-evaluation of the 1960's NMFS Tagging Data- Revised with February 2025 Supplemental Materials

Jerald S. Ault¹, Jiangang Luo¹ & Clarence E. Porch²

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Point Work Group by J. Ault

Understanding Atlantic Menhaden Population Demographics: Re-evaluation of the 1960's NMFS Tagging Data

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Executive Summary

This report details an extensive reanalysis of the NMFS July 1966-February 1971 Atlantic menhaden mark-recovery study data and model results to objectively evaluate previous conclusions regarding demographic rates. The NMFS study used ferro-magnetic tags released and recovered over 5 geographical regions extending from Maine to Florida, and was comprised of two principal multi-year data components: (1) mark-recovery; and, (2) plant magnet tag-recovery efficiency. Data assimilation involved two different documented mark-recovery data sets: (i) “Coston”, summarizations of tag releases and recoveries provided in the Coston (1971) technical report for the period July 1966 through December 1969; and (ii) “Schueller”, a very detailed data set containing a subset of all batch releases and individual recoveries from July 1966 through February 1971; and, detailed plant magnet efficiency trials from May 1966 through December 1971. The “Schueller” set is maintained by Amy Schueller of NMFS, Beaufort, NC. We focused on the July 1966 through December 1969 period to facilitate comparisons with the “Liljestrand” multi-state mark-mark-recovery model (Liljestrand et al. 2019). “Coston” mark-recapture data contained 1,066,357 tagged-releases and subsequent 102,992 individual recaptures. “Schueller” mark-recapture data had 805,251 tagged-releases and 112,014 recaptures for 1966-1971. For July 1966 through December 1969 there were 768,877 tagged-releases and 93,335 recaptures. Another 9,255 menhaden (about 10% more) from the 1966-1969 releases were recaptured in 1970. The plant magnet efficiency study had 95,986 tagged-releases and 69,338 recaptures. We estimated nominal fishing effort (f) by month by area by year for two principal effort data sets (i.e., “Liljestrand” and “Mroch-SEDAR”) by assuming that f was proportional to recaptures. We estimated demographic rates using four model classes: (1) survivorship ratios following “Dryfoos” (Dryfoos et al. 1973); (2) Chapman-Robson (1960) survivorship; (3) life span demographics; and, (4) “Liljestrand” Bayesian multi-state mark-recovery model. About 6.7% ($n = 53,754$) of the menhaden tagged-released between 1966-1969 were measured for fork length (FL); these fish ranged between 92 mm FL (3.62 in FL) to 761 mm FL (29.96 in FL). Almost 100 of the measured tagged-released Atlantic menhaden were > 500 mm FL, indicating that unexploited menhaden typically grow to relatively large sizes (> 20 inches FL). The data suggested truncation of the population size structure. The current (≥ 2020) maximum size is about 400 mm FL and 11 years of age. Our analyses were in agreement with the previous (i.e., < 2010) modeling efforts by investigators like “Dryfoos” and others. Using identical methods and data we were able to duplicate their results with both data sets. Using data identical to those found in “Liljestrand”, our analyses generally replicated their results (see Case 1). However, we found that their recapture data were inaccurate. It appeared that the “Coston” data used by “Liljestrand” underestimated recaptures by more than 8% to 13%, and further, “Coston” recaptures were less than “Schueller” (i.e., for 1966 releases: “Schueller” = 7,516 $>$ “Coston” = 5,887 recaptures). In addition, menhaden released in 1966 survived to at least early 1971. Using corrected “Coston” and the new “Schueller” data we obtained results that vary considerably from those of “Liljestrand.” For example, our estimated range of the natural mortality rate was $M \in [0.2723, 0.5454]$, a range consistent with the literature. We believe that most likely estimates of survivorship ranged from $S \in [0.1282, 0.1914]$, and natural mortality from $M \in [0.5153, 0.5454]$. The best estimate of $\hat{M} = 0.5454$ using the “Schueller” data with the “Liljestrand” model was about 54% lower than that used in SEDAR 69.

1.0 Introduction

The goal of this research was to improve understanding of Atlantic menhaden (*Brevoortia tyrannus*) demographics and population dynamics through re-analysis of data from the NMFS Atlantic menhaden tag-recapture study spread over 5 geographical regions extending along the Atlantic coast from Maine to Florida running from July 1966 to February 1971.

The data documenting this study were obtained from two principal sources: (1) “Coston’s” (Coston 1971) NMFS Technical Report on monthly tags and recaptures for the period extending from July 1966 to December 1969; (2) “Schueller’s” re-digitized “Field Release” tag-recapture data and “Plant Test” magnet efficiency trial data that documented release batches and individual recoveries for the period from July 1966 to February 1971 provided to us in unedited form by Amy Schueller of NMFS Southeast Fisheries Science Center, Beaufort, North Carolina.

All data from source (1) were provided as summaries contained in the NMFS Technical Report of Coston (1971), pointed out to us by Mike Wilberg, University of Maryland. Data from source (2) “Field Releases” were provided to us in 11 raw unedited Excel spreadsheets with descriptions of tag data layouts for the following records: (i) parent (tagged); (ii) first type children (tagged, measured and recovered); and, (iii) second type children (tagged and recovered). Data from source (2) “Plant Tests” were provided to us in 5 raw unedited Excel spreadsheets with descriptions by Smith (2013) of tag data layouts for the following records: (i) parent; and, (ii) children. We developed computer-intensive algorithms using the R-programming language that facilitated development of statistical-mathematical methods for data assimilation, parameter estimation and modeling for detailed analyses of these data (see Appendix 1). Some data and parameters were obtained from “Liljestrand’s (Liljestrand et al. 2019) paper and associated appendices.

After analysis and summary of these data, we then used the “Liljestrand” model to obtain and refine estimates of menhaden demographic (survival, migration and exploitation) central to stock assessment and ecosystem dynamics modeling, an area of effort that we have significantly contributed to ASMFC efforts in the past (Luo et al. 2005).

1.1 Brief History of the Atlantic Menhaden Fishery

The Atlantic menhaden fishery on the coastal eastern seaboard of the United States, stretching from Maine to Florida, has a very long history of exploitation. Atlantic menhaden are an integral part of America’s history, fished since the 1600s (17th century) when Native Americans taught the Pilgrims to fish to support farming. In the nascent years, menhaden schools were reported as sometimes stretching 40 miles long (Franklin 2007). Americans have actively pursued menhaden since at least the early 1700s. From the 1860s to today, the catch of menhaden has been America’s largest fishery; however, menhaden landings have only been documented since the late 1800s (**Fig. 1.1A**), a time when there were about 100 reduction plants operating along the eastern seaboard ranging from Maine to Florida (**Fig 1.1B**). During the 20th century there was a precipitous decline in menhaden reduction plants. By 1955, reduction plants had dwindled to about 25, but landings peaked at 738,499 mt in 1956. By the mid-1960s reduction plants had dropped to 20 and catches plummeted to an all-time low of 162,333 mt in 1969 (**Fig. 1.1C**, **Table 1.1**). Today only one reduction plant operates along the entire Atlantic coast, located in Reedville, VA, the historical center of the Atlantic menhaden stock distribution.

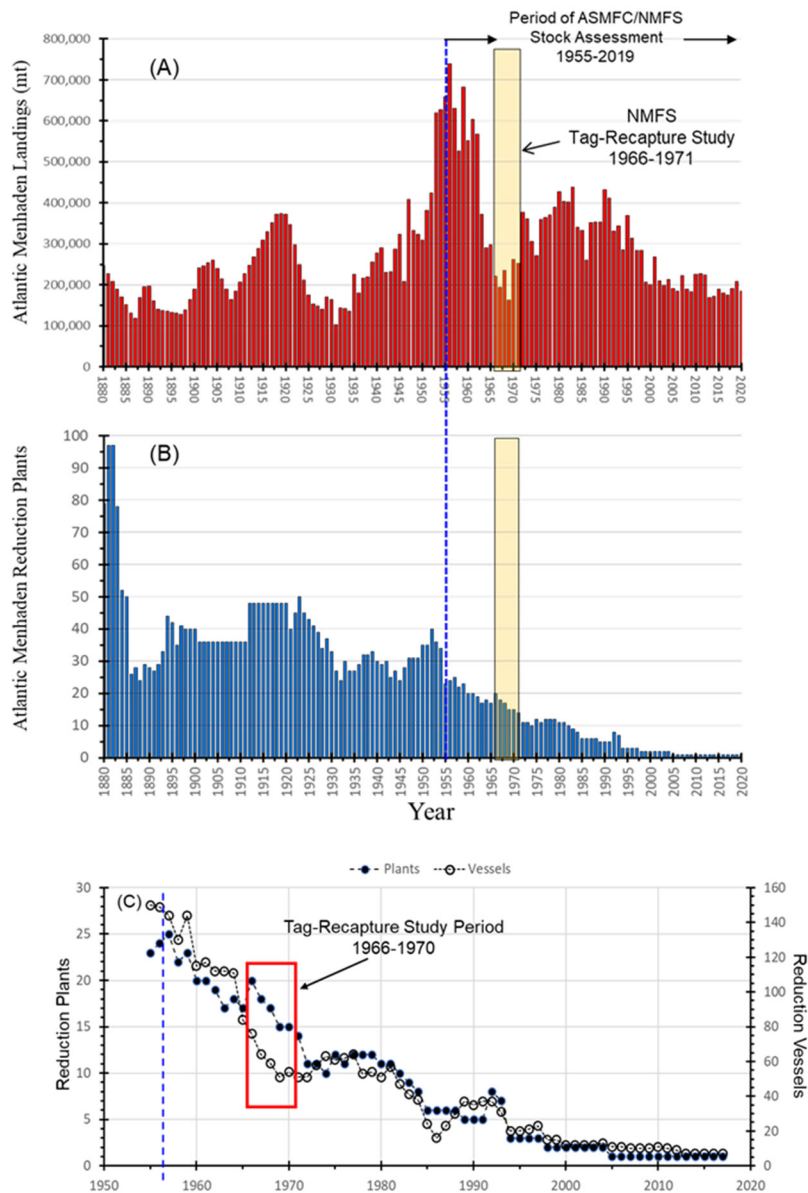


Figure 1.1 Time series of: (A) 1880 to 2020 Atlantic menhaden industrial landings (mt). Note that the data used in the latest stock assessment (SEDAR 69, 2019) was based on the 1955-2017 time period; (B) operating Atlantic menhaden reduction plants along the US eastern seaboard from 1880-2020; (C) operating vessels and reduction plants from 1955-2017 (redrawn from SEDAR 69 2019).

1.2 NMFS 1966-1971 Atlantic Menhaden Tagging Study

The Atlantic menhaden (*Brevoortia tyrannus*) tagging program conducted by NOAA Fisheries' Beaufort Laboratory, Southeast Fisheries Science Center, marked and released adult Atlantic menhaden on the fishing grounds from May 1966 to February 1971. The program has played an important role in improving understanding of menhaden population migratory patterns, stock structure, growth and demographics along the Atlantic coast (Dryfoos et al., 1973).

The tagging program employed a large numbered ferro-magnetic stainless steel tag measuring $14.0 \times 3.0 \times 0.5$ mm. This tag was inserted into the body cavity just above and behind the origin of the pelvic fin with a tagging "gun" for adult menhaden, and a smaller stainless steel tag ($7.0 \times 2.5 \times 0.4$ mm) for juvenile menhaden (Dryfoos et al., 1973). Each tag was unique and identifiable with a prefixed letter and five digits. The small tags, however, were identifiable in lots of 100 with either three digits, a letter and two digits, or two letters and one digit. Adult Atlantic menhaden used for tagging were obtained from commercial purse-seine catches (Dryfoos et al., 1973; Pristas and Willis, 1973; Levi, 1981). Length measurements and scale samples for age determinations were taken systematically from approximately 5% of the fish tagged.

For the study, the U.S. Atlantic coast from Maine to Florida was divided into five tagging areas based on activities of the commercial fishery (**Fig. 1.2**). Boundaries between areas were drawn through waters where little fishing occurred, and each area was generally limited to the range limits of menhaden vessels fishing within that area.

Area 1: Waters along the southern coast of Long Island east of a line due south of Moriches Inlet (lat $40^{\circ} 46'$ N and long $72^{\circ} 44'$ W), Long Island Sound, and waters northward.

Area 2: Waters north of a line due east of the Maryland-Virginia line (lat $38^{\circ} 02'$ N and long $75^{\circ} 15'$ W) to the southern boundary of area 1.

Area 3: Chesapeake Bay proper and coastal waters outside the Bay lying between False Cape, Va. (lat $36^{\circ} 35'$ N and long $75^{\circ} 53'$ W) and the southern boundary of area 2. Purse seine fishing is prohibited in Maryland waters of Chesapeake Bay.

Area 4: Waters north of a line running due east from the South Carolina-Georgia line at the mouth of the Savannah River (lat $32^{\circ} 02'$ N and long $80^{\circ} 53'$ W) to the Southern boundary of area 3.

Area 5: Waters south of the southern boundary of area 4.

Tagging within each area was conducted during most of the seasonal periods when menhaden were present. During the period from July 1966 to December 1969, more than 1.066 million adult fish captured by commercial purse seines were marked and released with small internal binary coded tags and then released back into five (5) areas along the Atlantic seaboard. A fraction of those released menhaden were subsequently unknowingly recaptured in the catches of commercial purse seines and delivered to 20 menhaden reduction processing plants along the east coast.

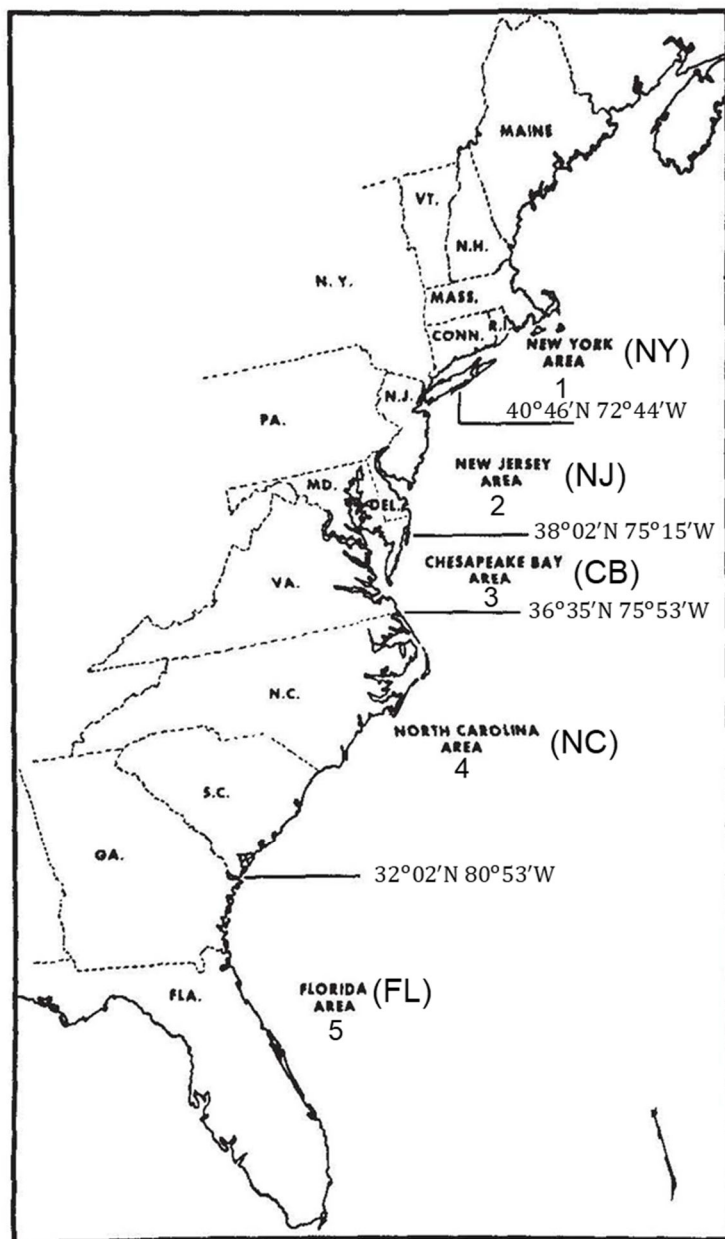


Figure 1.2.- Location of the five release-recapture areas used in the 1966-1971 NMFS Atlantic menhaden tag-recapture study.

1.2.1 Tag Recovery Process

In general, mark-recapture studies using external marks requiring visual detection were considered impractical for the Atlantic menhaden fishery. This is because landings by individual commercial menhaden purse seine vessels may range from 100,000 to 2,000,000 fish, which are loaded and unloaded by fish pumps. Moreover, at least 95% of the commercial menhaden landings on the Atlantic coast are for reduction into fish meal and oil. Estimates of the numbers of fish landed annually range into the billions (Mroch 2023).

After capture by purse seines, tagged menhaden delivered in the landings that entered reduction plants were recovered by powerful magnets installed at strategic points along the processing system. Some of the magnets had already been installed earlier by the companies to remove stray pieces of metal from the fish scrap in the course of normal operations. Additional magnets were provided by the NMFS to increase tag collection efficiency and installed by plant personnel. Three types of industrial magnets were used: plate, grate (or drawer) tubular, and rotating grate. Descriptions are found in Parker (1971). Magnets located adjacent the meal dryer and along the conveyor system to the scrap shed (primary magnets) normally recovered tags from fish within a few days of landing. Magnets located in the scrap storage shed and meal grinding area (secondary magnets) that recovered tags from landings made weeks or months earlier.

The recovery magnets were cleaned at intervals ranging from daily to several days, depending on the processing activities within the plant. Separation of tags from the material scraped from the magnets, a mixture of fish scrap and chunks of metal, required several steps. The collected mixture was spread over a flat surface and the metal concentrated and removed from the fish scrap with a magnetic sweeper. The concentrated metal was further sorted with sieves. The reduced mixture containing the tags and minute metal particles was then sorted by hand over a contrasting background (Parker, 1973). A rotating grate, and two kinds of plate magnets used to recover electronic detector-recovery ferromagnetic fish tags from the fish scrap system was successfully developed and used during the summer of 1967 (Parker, 1972). This system provided for the recovery of whole tagged fish. These recoveries were used to validate annulus formation on scales for Atlantic menhaden, examine tagging wounds for rates of healing, and determine the best site on the body of the menhaden for tag incision. However, this system was determined to be too costly and time consuming for routine tag recovery operations, so that it is very likely that all tags captured by the fleet were not recovered at the receiving reduction plants.

Table 1.1 Atlantic menhaden reduction plants operating during the 1966-1971 NMFS tag-recapture study. All these plants took part in the magnet efficiency investigations. Plants are listed by area, plant number, name, and location. Plant regional codes are: NY ≡ New York, NJ ≡ New Jersey, CB ≡ Chesapeake Bay, NC ≡ North Carolina, FL ≡ Florida. Actual plants operating was determined from the analysis of the Schueller (2022) “Field Release” and “Plant Test” magnet efficiency data.

Area	Code	Plant	Port	Name	City	State
		1	3	Atlantic Processing Company	Amagansett	NY
1	NY	23	2	Lipman Marine Products Co. (Gloucester Marine Protein)	Gloucester	MA
		25	11	Point Judith Byproducts Co.	Point Judith	RI
2	NJ	2	4	J. Howard Smith, Inc.	Port Monmouth	NJ
		4	8	New Jersey Menhaden Products Co.	Wildwood	NJ
		7	5	Standard Products Co.	Reedville	VA
		8	5	McNeal-Edwards (Standard Products Co.)	Reedville	VA
3	CB	9	5	Menhaden Co. (Standard Products Co.)	Reedville	VA
		10	5	Virginia Menhaden Products (Reedville Oil & Guano Co.)	Reedville	VA
		11	5	Standard Products Co.	White Stone	VA
		29	12	Cape Charles Processing Co.	Cape Charles	VA
		12	6	Fish Meal Co.	Beaufort	NC
		13	6	Beaufort Fisheries Inc.	Beaufort	NC
		14	6	Standard Products Co.	Beaufort	NC
4	NC	15	6	Standard Products Co.	Morehead City	NC
		16	6	North Carolina Menhaden Products	Morehead City	NC
		17	7	Standard Products Co.	Southport	NC
		28	6	Seashore Packing Co.	Beaufort	NC
5	FL	19	9	Quinn Menhaden Fisheries Inc.	Fernandina Beach	FL
		20	9	Nassau Oil & Fertilizer Inc.	Fernandina Beach	FL

2.0 Mark-Recapture Data Assimilation

2.1 Coston (1971) Technical Report

The NMFS Technical Report of Coston (1971) provided detailed monthly summaries from July 1966 through December 1969 of all tagged adult Atlantic menhaden released by area and all tags recovered by area along the Atlantic coast of the United States from New York to Florida. In the Coston (1971) report, no adjustments were made for tag recovery efficiency, which were shown to vary between plants by area and with time.

As previously stated, menhaden were tagged internally with numbered ferromagnetic metal tags that were recovered on magnets in reduction plants during the production of meal and oil. The metal tags were removed from fish scrap by magnets located in all active menhaden reduction plants along the Atlantic coast (see **Table 1.1**). Also, an electronic detector system which recovered whole fish before they entered the plant was used at two plants in North Carolina. The Coston (1971) report stated that only recoveries made on the detector or primary magnets were used. Primary magnets are the first magnets that fish scrap passes over after coming from the dryers. Magnets were routinely checked every day and tags recovered on the primary magnets were generally from fish that had been processed on that particular day, which gave a good indication of the date when tagged fish were caught.

The generalized arrangement of the tag release-recovery data found in Coston (1971) is shown in **Table 2.1.1**. The actual release-recovery data for 1966 is given in **Table 2.1.2**. In general, data analyses and model development took full advantage of the time-space correlation structure of the tag-recapture data to estimate population dynamic parameters.

2.1.1 Tag Mark & Release

Tag releases during the period from July 1966 through December 1969 reported in Coston (1971) are shown in **Table 2.1.3**. During this period a total of 1,066,357 tags were released. The percentage distribution of tag releases by areas was: Area 1, 1.21%; Area 2, 3.39%; Area 3, 28.91%; Area 4, 36.21%; and, Area 5, 30.27%. The seasonal organization of Dryfoos et al. (1973) is shown in the boxed areas of **Table 2.1.3**.

2.1.2 Tag Loss Due to Shedding & Mortality

Soon after tagging, some fish may have died as a result of handling or tagging, or may simply have shed their tag through the unhealed incision. As a consequence, errors may result in some population parameter estimates derived from the recovery data if the numbers released are not reduced with an accurate estimate additional mortality that results from tagging. The NMFS conducted a series of marking-survival experiments reported in Kroger and Dryfoos (1972), from which several applicable estimates of tagging loss (dead fish and shed tags) were obtained for juvenile and adult Atlantic menhaden. Estimates of loss (mortality) for adult fish tagged with the large tag were 24%. Estimates of losses of 37% (63% survivorship) were obtained for juveniles (mean FL = 83 mm) tagged with the small tag and 54% (46% survivorship) for those tagged with the large tags. Tag shedding/loss estimates by area made by Dryfoos et al. (1973) are given in **Table 2.1.4**. In addition, different vessels, taggers and seasons may have induced a differential rate of short-term tagging mortality. None of these factors were included in these tagging mortality estimates.

Table 2.1.2.- Monthly cohort releases and recoveries in 1966 from Coston (1971) organized along the lines of Table 2.1.1. Month of study is shown in brackets next to the month of year in first row of this Table.

Release Month	Seq	Release Area	Number Released	1	2	7	(1)	5	1	2	8	(2)	5	1	2	9	(3)	5	1	2	10	(4)	5	1	2	11	(5)	5	1	2	12	(6)	5
7	1	1	0																														
7	1	2	0																														
7	1	3	0																														
7	1	4	11,141				274					473					89					54					40					15	
7	1	5	0																														
8	2	1	0																														
8	2	2	0																														
8	2	3	0																														
8	2	4	34,322	0	0	0	0	0				957					401					97					52					42	
8	2	5	0																														
9	3	1	0																														
9	3	2	0																														
9	3	3	0																														
9	3	4	23,744														1454					145					107					41	
9	3	5	0																														
10	4	1	0																														
10	4	2	0																														
10	4	3	0																														
10	4	4	5,699																			335					76					38	
10	4	5	0																														
11	5	1	0																														
11	5	2	0																														
11	5	3	0																														
11	5	4	996																								40					18	
11	5	5	0																														
12	6	1	0																														
12	6	2	0																														
12	6	3	0																														
12	6	4	12,996																													88	
12	6	5	0																														
		Total	88,898	0	0	0	274	0	0	0	0	1430	0	0	0	0	1944	0	0	0	0	631	0	0	0	0	315	0	0	0	0	242	0

Table 2.1.3. Coston (1971) reported tagged & released Atlantic menhaden during the period from July 1966 through December 1969. Boxed-and-outlined data show the Spring-Summer and Fall designations by Dryfoos et al. (1973).

Coston (1971)		Area	1	2	3	4	5	Totals
Liljestrand (2019)		Region	1	2	3	4		
	release_month	Month						
1966	1	July	0	0	0	11,141	0	11,141
	2	August	0	0	0	34,322	0	34,322
	3	September	0	0	0	23,744	0	23,744
	4	October	0	0	0	5,699	0	5,699
	5	November	0	0	0	996	0	996
	6	December	0	0	0	12,996	0	12,996
1966		Totals	0	0	0	88,898	0	88,898
1967	7	January	0	0	0	7,729	0	7,729
	8	February	0	0	0	0	0	0
	9	March	0	0	0	644	0	644
	10	April	0	0	1,250	588	5,879	7,717
	11	May	0	0	14,510	8,614	15,395	38,519
	12	June	0	2,286	21,343	10,284	5,400	39,313
	13	July	176	1,399	19,872	25,276	9,078	55,801
	14	August	1,917	7,161	23,293	38,113	30,274	100,758
	15	September	0	2,245	8,113	10,378	16,705	37,441
	16	October	0	569	10,649	18,531	13,101	42,850
	17	November	0	0	1,098	22,680	0	23,778
	18	December	0	0	0	16,240	0	16,240
1967		Totals	2,093	13,660	100,128	159,077	95,832	370,790
1968	19	January	0	0	0	0	0	0
	20	February	0	0	0	37	0	37
	21	March	0	0	0	1,022	0	1,022
	22	April	0	0	14,915	4,420	22,520	41,855
	23	May	0	331	12,557	20,132	27,401	60,421
	24	June	0	5,810	36,052	30,065	16,789	88,716
	25	July	1,970	8,937	35,433	24,463	21,262	92,065
	26	August	400	3,622	9,639	17,086	22,016	52,763
	27	September	0	2,100	13,592	6,258	4,109	26,059
	28	October	0	989	10,408	0	4,198	15,595
	29	November	0	0	0	200	0	200
	30	December	0	0	0	5,437	524	5,961
1968		Totals	2,370	21,789	132,596	109,120	118,819	384,694
1969	31	January	0	0	0	1,300	0	1,300
	32	February	0	0	0	0	0	0
	33	March	0	0	0	0	0	0
	34	April	0	0	1,599	519	9,100	11,218
	35	May	1,000	700	9,484	1,641	14,698	27,523
	36	June	2,431	0	3,539	1,654	20,897	28,521
	37	July	3,960	0	23,525	11,077	14,070	52,632
	38	August	1,077	0	8,625	5,126	20,799	35,627
	39	September	0	0	13,264	4,070	19,100	36,434
	40	October	0	0	14,445	598	2,100	17,143
	41	November	0	0	1,100	3,091	7,386	11,577
	42	December	0	0	0	0	0	0
1969		Totals	8,468	700	75,581	29,076	108,150	221,975
6/2/2023 13:04		TOTAL	12,931	36,149 49,080	308,305	386,171	322,801	1,066,357

Table 2.1.4.- Tag shedding & loss by area G_A reported by Dryfoos et al. (1973). The term $1 - G_A$ represents survivorship of the monthly tagged & released batches (cohorts) reported in Coston (1971).

Area (A)	Location	G_A	$1 - G_A$
1	NY	0.10	0.90
2	NJ	0.10	0.90
3	CB	0.20	0.80
4	NC	0.25	0.75
5	FL	0.40	0.60

2.1.3 Tag Recoveries

The cumulative recoveries covering the period from July 1969 through December 1969 are given in **Table 2.1.5** for monthly groups of tagged & released batches (cohorts) by month by area for the 42 months of the data found in Coston (1971). A total of 102,992 tagged menhaden were recovered during this period. Of that total recovery of tagged menhaden, 1.77% were recovered in Area 1, 5.62% in Area 2, 36.58% in Area 3, 45.23% in Area 4, and 10.81% in Area 5.

The sequence of monthly recoveries for all menhaden tagged within a particular year are given in **Table 2.1.6**. The annual summaries of those data are given in **Table 2.1.7**. Of the total 102,992 tagged and released menhaden during the study period of July 1966 through December 1969, 4.7% were recaptured in 1966, 31.95% recaptured in 1967, 48.35% in 1968, and 15.01% in 1969.

2.2.4 Comparisons of Reported Data Sets

There were several discrepancies discovered in our analyses of the Coston (1971) data compared to those reported from various sources and used in publication(s). For example, **Table 2.1.8A** gives Appendix Table A.2 from Liljestrand et al. (2019) who reported 1,066,448 tagged menhaden, whereas the actual number was 1,066,357, a difference of +91 fish. **Table 2.1.8B** gives Appendix A.3 from Liljestrand et al. (2019) who reported 89,116 recaptured menhaden from July 1966 through December 1969, while our analyses in **Table 2.1.8C** indicated that 102,992 menhaden were recovered, an undercount of 13,876 fish or a 13.47% difference (**Table 2.1.8D**). Additional data provided by Mike Wilberg showed a total of 94,968 menhaden recovered which was about 7.79% below what was reported in Coston (1971).

Table 2.1.5.- Cumulative recoveries of tagged Atlantic menhaden organized by the particular area and month they were released as reported in Coston (1971) for the period July 1966 through December 1969.

8/3/2023 10:58	Month			Area			
RELEASE YEAR		1	2	3	4	5	Total
1966	7				1,080		
	8				1,747		
	9				2,031		
	10				645		
	11				118		
	12				266		
	1966	0	0	0	5,887	0	5,887
		1	2	3	4	5	
	1				1,101		
	2						
	3				101		
	4			236	114	47	
	5			2,611	797	289	
	6		445	4,478	1,055	230	
1967	7	33	142	3,793	2,269	476	
	8	272	873	3,907	6,862	682	
	9		166	1,213	2,366	654	
	10		90	1,632	5,168	483	
	11			192	3,997		
	12				1,566		
	1967	305	1,716	18,062	25,396	2,861	48,340
		1	2	3	4	5	
	1						
	2				2		
	3				44		
	4			1,962	254	1,793	
	5			1,950	1,382	2,239	
	6		1,405	5,490	2,596	1,060	
1968	7	265	1,667	4,394	5,899	1,061	
	8	37	506	947	1,617	700	
	9		352	1,016	581	82	
	10		133	953		190	
	11				6		
	12				436		
	1968	302	4,063	16,712	12,817	7,125	41,019
		1	2	3	4	5	
	1				52		
	2						
	3						
	4			112	24	230	
	5	49	6	300	177	445	
	6	453		197	65	170	
1969	7	554		1,225	926	35	
	8	158		250	537	190	
	9			285	414	65	
	10			523	71	6	
	11			12	213	2	
	12						
	1969	1,214	6	2,904	2,479	1,143	7,746
Total		1,821	5,785	37,678	46,579	11,129	102,992
Fraction of Total		0.0177	0.0562	0.3658	0.4523	0.1081	1.0000

Table 2.1.6.- Recoveries by month and area for all monthly cohorts released within in a year during 1966-1969 per Coston (1971).

		1	2	1966	3	4	5		1	2	1967	3	4	5		1	2	1968	3	4	5		1	2	1969	3	4	5		Total	Total
Releases	Month																														
	1								0	0	0	45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45		
	2								0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2		
	3								0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
	4								0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	1	0	0	5			
	5								0	0	3	22	3	0	0	1	1	0	0	0	0	2	0	0	0	0	0	32			
	6								0	0	138	32	1	0	22	23	0	0	3	0	0	0	0	0	0	0	0	219			
1966	7	0	0	0	274	0	0	7	80	11	2	7	25	36	1	0	5	7	1	0	0	0	0	0	0	0	0	456			
	8	0	0	0	1,430	0	0	23	67	25	5	7	13	18	0	1	4	0	1	0	0	0	0	0	0	0	1,594				
	9	0	0	0	1,944	0	0	39	34	9	5	1	7	4	1	0	0	0	0	0	0	0	0	0	0	0	2,044				
	10	0	0	0	631	0	0	18	15	1	4	5	4	15	0	0	0	0	2	1	0	0	0	0	0	0	696				
	11	0	0	0	315	0	0	0	19	43	8	0	0	12	38	0	0	0	0	0	7	0	0	0	0	0	442				
	12	0	0	0	242	0	0	0	0	57	0	0	0	0	43	0	0	0	0	0	9	0	0	0	0	0	351	5,887			
1967	1							0	0	0	26	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	28				
	2							0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
	3							0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1				
	4							0	0	0	0	8	0	0	174	121	80	0	0	26	0	1	0	0	0	410					
	5							0	0	36	217	14	0	1	163	267	68	0	0	114	13	0	0	0	0	893					
	6							0	60	1,370	234	10	0	528	1,185	262	34	37	58	150	18	0	0	0	0	0	3,946				
	7							0	253	2,033	813	97	94	871	2,213	254	13	83	272	43	25	1	0	0	0	0	7,065				
	8							0	353	2,150	3,741	548	154	801	1,151	132	51	46	72	124	0	0	0	0	0	0	9,323				
	9							0	213	1,341	2,116	500	31	364	401	61	10	4	19	30	4	0	0	0	0	0	5,094				
	10							0	195	729	3,417	486	74	154	525	99	5	0	0	181	1	0	0	0	0	0	5,866				
	11							0	0	820	6,396	30	0	0	472	1,688	122	0	0	14	196	0	0	0	0	0	9,738				
	12							0	0	0	3,985	0	0	0	0	1,717	0	0	0	0	274	0	0	0	0	0	5,976	48,340			
1968	1														0	0	0	0	0	0	0	0	0	0	0	37	0	37			
	2														0	0	0	0	0	0	0	0	0	0	1	0	1				
	3														0	0	0	0	0	0	0	0	0	0	2	0	2				
	4														0	0	149	3	313	0	0	48	1	40	554						
	5														0	0	412	378	845	0	0	328	428	12	2,403						
	6														0	306	850	1,428	806	38	50	595	442	5	4,520						
	7														15	1,193	3,168	5,706	807	105	288	175	564	8	12,029						
	8														131	1,117	2,733	1,988	1,316	33	76	420	115	4	7,933						
	9														25	297	1,085	949	537	1	28	101	55	4	3,082						
	10														36	353	961	416	53	0	3	542	23	1	2,388						
	11														0	0	823	2,548	78	0	0	18	552	0	4,019						
	12														0	0	0	3,339	0	0	0	0	712	0	4,051	41,019					
1969	1																			0	0	0	16	0	0	16					
	2																			0	0	0	0	0	0	0	0				
	3																			0	0	0	0	0	0	0	0				
	4																			0	0	0	0	13	0	13					
	5																			0	0	83	28	217	328						
	6																			20	11	108	61	218	418						
	7																			477	147	235	469	194	1,522						
	8																			317	10	674	284	242	1,527						
	9																			17	2	464	855	109	1,447						
	10																			0	0	384	276	25	685						
	11																			0	0	27	757	38	822						
	12																			0	0	0	968	0	968	7,746					
		0	0	0	4,836	0	0	1,161	8,835	21,191	1,721	580	6,056	16,578	21,441	5,139	1,190	1,043	4,891	7,198	1,132					102,992	102,992				

Table 2.1.7.- Tagged Atlantic menhaden recoveries reported by Coston (1971) by year and area as for the period July 1966 through December 1969: (A) annual release cohort cumulative number of recaptures; and, (B) number of recovered tags by year and region.

(A)

8/3/2023 10:52		1966					1967					1968					1969					TOTAL
Colston (1971)		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	
Liljestrand (2019)			1	2	3	4		1	2	3	4		1	2	3	4		1	2	3	4	
RELEASES																						
1966		0	0	0	4,836	0	0	87	356	246	28	20	71	113	84	1	12	7	7	19	0	5,887
1967							0	1,074	8,479	20,945	1,693	353	2,719	6,284	4,602	383	170	421	682	533	2	48,340
1968												207	3,266	10,181	16,755	4,755	177	445	2,227	2,932	74	41,019
1969																	831	170	1,975	3,714	1,056	7,746
Total		0	0	0	4,836	0	0	1,161	8,835	21,191	1,721	580	6,056	16,578	21,441	5,139	1,190	1,043	4,891	7,198	1,132	102,992
Fraction of Total				0.0470					0.3195					0.4835					0.1501			1.0000

(B)

		Region					
Year	1	2	3	4	5	Total	
	1	2	3	4	5		
1966	0	0	0	4,836	0	4,836	
1967	0	1,161	8,835	21,191	1,721	32,908	
1968	580	6,056	16,578	21,441	5,139	49,794	
1969	1,190	1,043	4,891	7,198	1,132	15,454	
Total	1,770	8,260	30,304	54,666	7,992	102,992	
		10,030					
Year	1	2	3	4	5	Total	
	1	2	3	4	5		
1966	0	0	0	4,836	0	4,836	

1967	0	1,161	8,835	21,191	1,721	32,908
1968	580	6,056	16,578	21,441	5,139	49,794
1969	1,190	1,043	4,891	7,198	1,132	15,454
Total	1,770	8,260	30,304	54,666	7,992	102,992
		10,030				

Table 2.1.8.- Differences in Atlantic menhaden tag-recapture study statistics reported in Liljestrand et al.'s (2019), as compared to summarization of the Coston (1971) Technical Report.

(A) Release data by year and area reported in Appendix Table A.2 of Liljestrand et al. (2019).

Year	Area					Total
	1	2	3	4	5	
1966	0	0	0	88,989 ¹	0	88,989
1967	2,093	13,660	100,128	159,077	95,832	370,790
1968	2,370	21,789	132,596	109,120	118,819	384,694
1969	8,468	700	75,581	29,076	108,150	221,975
Total	12,931	36,149	308,305	386,262	322,801	1,066,448

¹ = 88,898 (+91 difference)

(B) Recapture data by year and area reported in Appendix Table A.3 of Liljestrand et al. (2019).

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

(C) Recapture data from Coston (1971) analysis conducted for this report.

Year	Area					Total
	1	2	3	4	5	
	1	2	3	4	5	
1966	0	0	0	4,836	0	4,836
1967	0	1,161	8,835	21,191	1,721	32,908
1968	580	6,056	16,578	21,441	5,139	49,794
1969	1,190	1,043	4,891	7,198	1,132	15,454
Total	1,770	8,260	30,304	54,666	7,992	102,992
	10,030					

(D) Comparative differences between reported recapture by area summary statistics.

Source	Area				sum	Δ %
	1 & 2	3	4	5		
Coston (1971)	10,030	30,304	54,666	7,992	102,992	0.00%
Wilberg (2022)	7,894	29,047	50,244	7,783	94,968	-7.79%
Liljestrand (2019)	8,906	24,427	50,610	5,173	89,116	-13.47%

2.2 Schueller (2022) “Field Release” Data

The Field Release data provided by Amy Schueller (2022) of NMFS, hereafter referred to as the “Schueller” field release data, consisted of 10 separate Excel files that contained various information outlined in the Word documents written by J.W. Smith (2013) who detailed the contents of these files by defining variables in what he described as “parent” and two types of “children” records. We assimilated these 10 Excel data files using specialized R-code we developed for this Technical Report (**Appendix 1**). An example summary of the data assimilation and creation of the specific R-based data frames is given in **Table 2.2.1**, which have been combined to create an “annual” file by study year. **Table 2.2.2** provides details of the contents of the individual Excel files and principal variables assimilated into the R data frames for the 10 Field Release (fr) data files. These include data frames for the tag releases (fr_releases), tag recoveries (fr_recoveries), and length observations for a subset of the total tagged fish (fr_lengths). These contents constituted the corner points of the mark-recapture data analyses that followed. These files were organized for years 1966-1970, that defined the time range for releases, lengths if they were collected, number of release batches (of variable size), and total number of releases. For recapture data that spanned the years 1966-1971, the files were organized in terms of time range of the observations, and ultimately total recaptures by years (**Table 2.2.2**).

2.2.1 Marked Releases

A summary of the menhaden tagged and released by month by area by year is given in **Table 2.2.3** for the period July 1966 through September 1970. Note that for the period extending from July 1966 through September 1970, a total of 805,251 menhaden were tagged and released. However, for the immediate focal period of this study, July 1966 through December 1969, at total of 760,877 menhaden were tagged and released (**Table 2.2.4**).

2.2.2 Size Distribution of Marked Releases

An approximate 5% subset of menhaden tagged and released annually had their total length (TL) measured and recorded. The size frequency distribution of tagged menhaden that were measured for size for the years 1967 ($n = 11,584$), 1968 ($n = 13,928$) and 1969 ($n = 28,242$) are shown in **Fig. 2.2.1**. No units for these size measurements were given in the metadata provided documentation of J.W. Smith (2013), but we assumed that it was fork length (TL). Note that in **Fig. 2.2.1** that a number of menhaden > 625 mm FL (24.6 in FL) are apparent in these annual distributions.

Table 2.2.1.- Summary of data assimilation of *Field Release* files and creation of data frames for tagging study year 1969 by R-program fr69_combo.r. The two merged Excel files were FieldRelease 8 and 9 which in total contained the tag-release (fr_releases), recovery (fr_recovery), and length composition data for 1969.

```
> str(fr_releases)
```

```
tibble [2,204 x 10] (S3: tbl_df/tbl/data.frame)
 $ release_fulldate: Date[1:2204], format: "1969-04-28" "1969-04-28" "1969-04-28" "1969-04-28" ...
 $ release_area   : num [1:2204] 3 3 3 3 3 3 3 3 3 3 ...
 $ series        : chr [1:2204] "F360" "F361" "F362" "F363" ...
 $ tag_subgroup   : num [1:2204] 0 0 0 0 0 0 0 0 0 0 ...
 $ release_week   : num [1:2204] 175 175 175 175 175 175 175 175 175 175 ...
 $ location       : num [1:2204] 377632 377632 377632 377632 377632 377632 ...
 $ vessel         : num [1:2204] 0 0 0 0 0 0 0 0 0 0 ...
 $ number_tagged  : num [1:2204] 100 100 100 100 100 100 100 100 100 100 ...
 $ len            : logi [1:2204] NA NA NA NA NA NA NA ...
 $ age            : logi [1:2204] NA NA NA NA NA NA NA ...
```

```
> dim(fr_releases)
```

```
[1] 2204 10
```

```
> summary(fr_releases$release_fulldate)
```

```
   Min.   1st Qu.   Median     Mean   3rd Qu.    Max.
"1969-01-02" "1969-06-12" "1969-07-23" "1969-07-26" "1969-09-08" "1969-11-25"
```

```
> str(fr_recovery)
```

```
tibble [19,228 x 11] (S3: tbl_df/tbl/data.frame)
 $ recovery_fulldate: Date[1:19228], format: "1970-07-22" "1969-12-22" "1969-05-06" "1969-08-25" ...
 $ series          : chr [1:19228] "F360" "F360" "F360" "F360" ...
 $ tag_subgroup     : num [1:19228] 0 0 0 0 0 0 0 0 0 0 ...
 $ id              : num [1:19228] 5 6 12 34 41 43 50 61 63 66 ...
 $ len             : logi [1:19228] NA NA NA NA NA NA NA ...
 $ age             : logi [1:19228] NA NA NA NA NA NA NA ...
 $ recovery_area    : num [1:19228] 3 4 3 3 3 3 3 4 3 3 ...
 $ recovery_week    : num [1:19228] 239 209 176 192 197 181 232 209 177 181 ...
 $ recovery_plant    : num [1:19228] 10 16 10 7 10 10 7 16 10 10 ...
 $ recovery_station : num [1:19228] 1 2 1 1 2 2 6 2 2 1 ...
 $ magnet           : num [1:19228] 2 6 6 3 3 1 3 6 7 1 ...
```

```
> dim(fr_recovery)
```

```
[1] 19228 11
```

```
> summary(fr_recovery$recovery_fulldate)
```

```
   Min.   1st Qu.   Median     Mean   3rd Qu.    Max.
"1969-01-07" "1969-08-27" "1969-12-01" "1970-01-21" "1970-06-24" "1971-02-01"
```


Table 2.2.2.- Contents of the 10 individual *Field Release* Excel spreadsheet files comprised of five years of release-recovery data for Atlantic menhaden in the “Schueller” (2022) data.

Field		6/20/2023 11:28		RELEASES						RECOVERIES			
Release		Start	End	Lengths	L(year)	Batches	Total	Total	Year	Start	End	Total	Year
10	1970	5/25/1970	8/28/1970	9	9	368	368	36,374	36,374	1/12/1970	2/1/1971	9,448	9,448
9	1969	4/23/1969	11/12/1969	12,490		1,409		140,492		4/24/1969	2/1/1971	10,376	
8		1/2/1969	11/25/1969	15,752	28,242	794	2,203	78,191	218,683	1/7/1969	2/1/1971	8,852	19,228
7		5/15/1968	10/22/1968	5,748		588		58,308		5/21/1968	2/1/1971	12,513	
6	1968	4/4/1968	9/9/1968	5,097	13,928	838	2,233	82,133	220,789	4/10/1968	2/1/1971	14,467	34,540
5		4/9/1968	7/30/1968	3,083		807		80,348		4/10/1968	12/23/1970	7,560	
4		4/5/1967	9/25/1967	6,165		1,274		127,038		4/10/1967	12/23/1970	11,810	
3	1967	7/10/1967	10/2/1967	2,793	11,559	587	2,417	58,176	240,507	7/12/1967	1/8/1971	13,743	41,263
2		4/25/1967	8/14/1967	2,601		556		55,293		5/29/1967	1/7/1971	15,710	
1	1966	7/14/1966	12/27/1966	0	0	893	893	88,898	88,898	7/21/1966	1/7/1971	7,532	7,532
		06/20/23			53,738		8,114		805,251				112,011

Table 2.2.3.- Schueller (2022) releases by year, area & month from July 1966 through December 1970. The outlined section correspond to the spring-summer and fall seasons of Dryfoos et al. (1973).

	Dryfoos (1973)	Area	1	2	3	4	5	Totals		
8/23/2023 17:57										
	Release Month	Month								
1966	1	July				11,141		11,141		
	2	August				34,322		34,322		
	3	September				23,744		23,744		
	4	October				5,699		5,699		
	5	November				996		996		
	6	December				12,996		12,996		
1966		Totals	0	0	0	88,898	0	88,898		
1967	7	January						0		
	8	February						0		
	9	March						0		
	10	April			1,250		5,879	7,129		
	11	May			14,510	7,771	15,395	37,676		
	12	June			21,433	10,376	5,400	37,209		
	13	July			19,842	25,276	9,078	54,196		
	14	August			23,293	29,118	28,574	80,985		
	15	September			8,113	9,899	4,800	22,812		
	16	October			100	400		500		
	17	November						0		
	18	December						0		
	1967		Totals	0	0	88,541	82,840	69,126	240,507	
	1968	19	January						0	
		20	February						0	
		21	March						0	
		22	April			14,915		22,520	37,435	
		23	May			12,557		27,401	39,958	
24		June			36,052		16,789	52,841		
25		July			35,433		21,362	56,795		
26		August			9,639		11,429	21,068		
27		September			12,593			12,593		
28		October			99			99		
29		November						0		
30		December						0		
1968			Totals	0	0	121,288	0	99,501	220,789	
1969		31	January						1,300	
	32	February						2		
	33	March						0		
	34	April			1,599	519	8,900	11,018		
	35	May	1,000	700	8,984	1,641	14,598	26,923		
	36	June	2,231		3,345	1,554	20,497	27,627		
	37	July	3,960		23,525	10,777	13,970	52,232		
	38	August	1,077		8,625	5,126	20,499	35,327		
	39	September			13,164	3,970	18,800	35,934		
	40	October			14,145	598	2,100	16,843		
	41	November						1,100	2,991	7,386
	42	December								0
	1969		Totals	8,268	700	74,487	28,478	106,750	218,683	
	1970	43	January						0	
44		February						0		
45		March						0		
46		April						0		
47		May			21,189			21,189		
48		June			14,600	200		14,800		
49		July						0		
50		August						385	385	
51		September						0		
52		October						0		
53		November						0		
54		December						0		
1969			Totals	0	0	35,789	585	0	36,374	
8/23/2023 17:57			Area	1	2	3	4	5	Totals	
		TOTAL	8,268	700	320,105	200,801	275,377		805,251	

Table 2.2.4.- Schueller (2022) “Field Releases” data shown for all areas of release combined by month and year from July 1966 to December 1969.

Monthly tagged-releases between July 1966 and December 1969.

	YEAR	1966	1967	1968	1969	TOTALS
Month						
1					1,300	1,300
2					2	2
3						0
4			7,129	37,435	11,018	55,582
5			37,676	39,958	26,923	104,557
6			37,209	52,841	27,627	117,677
7		11,141	54,196	56,795	52,232	174,364
8		34,322	80,985	21,068	35,327	171,702
9		23,744	22,812	12,593	35,934	95,083
10		5,699	500	99	16,843	23,141
11		996			11,477	12,473
12		12,996				12,996
6/20/23		88,898	240,507	220,789	218,683	768,877

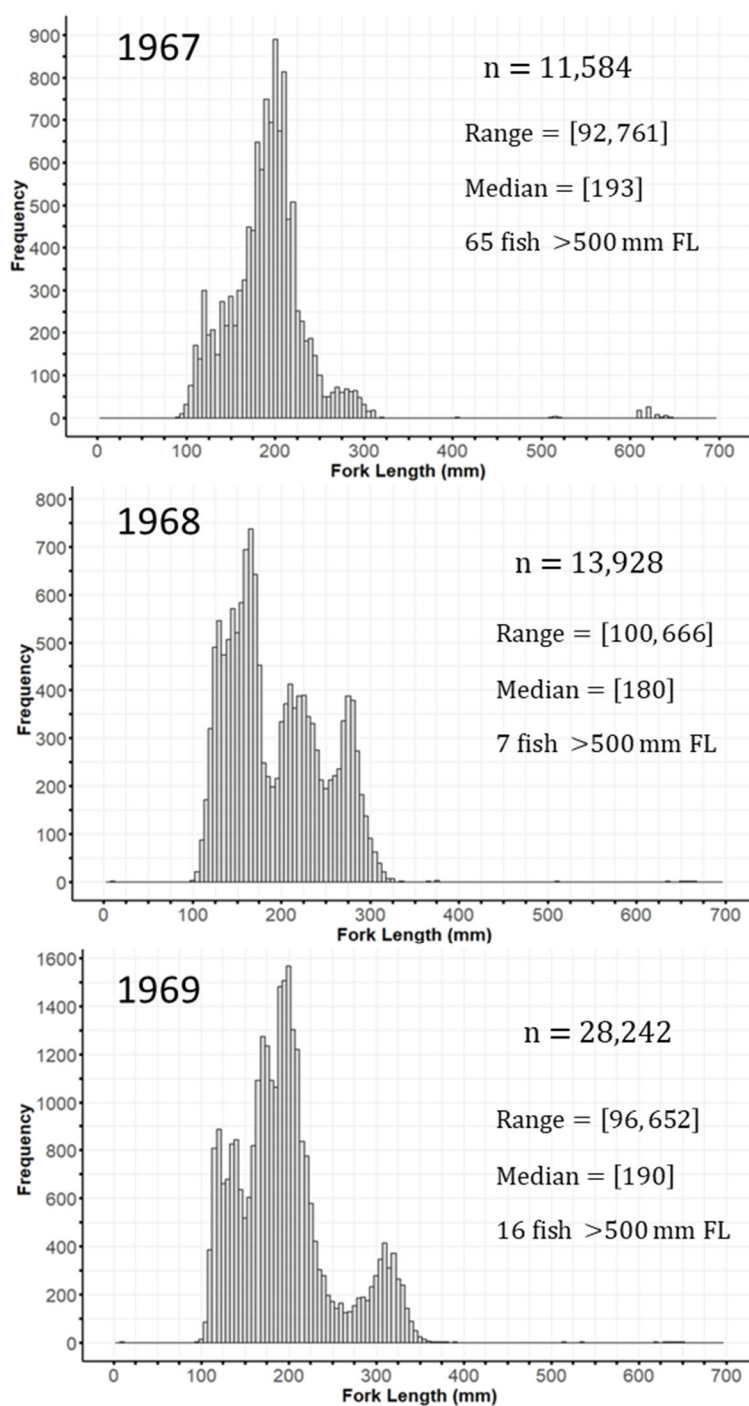


Figure 2.2.1.- Size-frequency distributions of tagged & released menhaden from 1967-1969 for a total of 53,754 measured fish. Note the very large sizes apparent in the right side of the 1967 length frequency (top panel), where the maximum size fish was 761 mm FL. A menhaden of 500 mm FL is 19.7 inches FL, and 650 mm FL is 25.6 inches FL. Presumably these large fish are around the theoretical L_{∞} .

2.2.3 Tag Recoveries

For the truncated period of recovery, a total of 93,335 menhaden were recovered from those menhaden tagged between July 1966 through December 1969 (**Table 2.2.5**). The total recaptures of 93,335 had 1.85% recovered in Area 1, 0.01% in Area 2, 56.90% in Area 3, 26.19% in Area 4, and 15.04% in Area 5. The total recaptures by year for 1966 were 8.05%, 1967 for 43.90%, 1968 for 35.98%, and 1969 for 12.07%.

Annual summaries of releases by month and area and cumulative recaptures from 1966-1970 are given in **Table 2.2.6A-E**. That data truncated through 1969 was 93,335 fish (**Table 2.2.6F**). However, if the tags from the group released between July 1966 through December 1969 are followed out to the end of the program in February 1971, then another 7,972 fish were recaptured between January 1970 and February 1971, making a total of 102,590 of these tags were recovered, or an additional 10.2% recoveries (**Table 2.2.6F**). If you were to add in the 1970 releases and recaptures (**Table 2.2.6E**), then 112,038 menhaden were recaptured (**Table 2.2.6F**), or a 20.04% increase over the 1966-1969 total.

The distribution of tag recoveries per released batch for 1966-1969 is shown in **Fig. 2.2.2**. the median percentage ranged from 6.1-17.0%, but was as high as 75% for the 1966-1968 tagging period. Notably, a little more than 7.11% of the tags batches released had zero recoveries (**Table 2.2.7**), which varied among years. It would make good sense to remove these individual batch observations from the releases as they contained zero information, and there was no reasonable idea as to why no individual tagged menhaden from these zero batches were ever recovered.

A summary of releases and recoveries for the 1966-1969 period is given in **Table 2.2.8**, both for the 1966-1969 recovery period, and recoveries made > 1969. The distribution of those recoveries by reduction plant by area by year is given in **Table 2.2.9**. Reduction plants in Area 3 dominated the recoveries, with the most recoveries occurring in 1967.

2.2.4 Comparison of the Coston (1971) & Schueller (2022) Releases & Recoveries

A comparison of the tags released and recovered between data sets and investigators is shown in **Table 2.2.10** and **Table 2.2.11**. The uncorrected recovery to release ratios varied among data sets: (1) $102,992/1,066,357 = 0.0966$ for the Coston (1971) data set; while it was, (2) $93,335/768,877 = 0.1214$ for the Schueller (2022) data set, a 2.48% increase for (2) (**Table 2.2.10A, Table 2.2.11**). In addition, the Schueller (2022) set had an identical number of 1966 releases in comparison to the Coston (1971) data, but it contained 27.67% more observations for that year (**Table 2.2.10B**).

Table 2.2.5.- Total cumulative recoveries by cohort batch release month and area running from July 1966 through December 1969 from the Schueller (2022) data.

Seq	9/2/2023 20:01	Area					Total	Fraction
		1	2	3	4	5		
1	July	0	0	0	1,258	0	1,258	
2	August	0	0	0	2,168	0	2,168	
3	September	0	0	0	2,601	0	2,601	
4	October	0	0	0	878	0	878	
5	November	0	0	0	183	0	183	
6	December	0	0	0	428	0	428	
	1966	0	0	0	7,516	0	7,516	0.0805
7	January	0	0	0	0	0	0	
8	February	0	0	0	0	0	0	
9	March	0	0	0	0	0	0	
10	April	0	0	333	0	98	431	
11	May	0	0	3,778	937	610	5,325	
12	June	0	0	6,382	1,381	476	8,239	
13	July	0	0	5,507	2,714	935	9,156	
14	August	0	0	5,693	5,859	1,112	12,664	
15	September	0	0	1,874	2,850	259	4,983	
16	October	0	0	41	126	0	167	
17	November	0	0	0	0	0	0	
18	December	0	0	0	0	0	0	
	1967	0	0	23,608	13,867	3,490	40,965	0.4389
19	January	0	0	0	0	0	0	
20	February	0	0	0	0	0	0	
21	March	0	0	0	0	0	0	
22	April	0	0	3,231	0	2,309	5,540	
23	May	0	0	3,193	0	2,850	6,043	
24	June	0	0	8,697	0	1,311	10,008	
25	July	0	0	6,841	0	1,402	8,243	
26	August	0	0	1,485	0	675	2,160	
27	September	0	0	1,570	0	0	1,570	
28	October	0	0	31	0	0	31	
29	November	0	0	0	0	0	0	
30	December	0	0	0	0	0	0	
	1968	0	0	25,048	0	8,547	33,595	0.3599
31	January	0	0	0	92	0	92	
32	February	0	0	0	0	0	0	
33	March	0	0	0	0	0	0	
34	April	0	0	147	35	331	513	
35	May	180	11	478	233	831	1,733	
36	June	612	0	325	117	358	1,412	
37	July	758	0	1,841	1,133	102	3,834	
38	August	179	0	422	609	274	1,484	
39	September	0	0	466	458	90	1,014	
40	October	0	0	756	77	9	842	
41	November	0	0	21	310	4	335	
42	December	0	0	0	0	0	0	
	1969	1,729	11	4,456	3,064	1,999	11,259	0.1206
	Total	1,729	11	53,112	24,447	14,036	93,335	1.0000
	Fraction of Total	0.0185	0.0001	0.5690	0.2619	0.1504	1.0000	

Table 2.2.6.- Summary of batches (events), zero events (no recaptures), releases and recaptures (recoveries) by month and area for the four release years: (A) 1966; (B) 1967; (C) 1968; (D) 1969; and, € 1970. In addition, the last column shows the number of recaptures made outside the time frame (> 1969) of this comparison.

(A) 1966

year_rel	month_rel	release_area	events	zero events	releases	recoveries	adj recovs	u	1966-1969	> 1969
1966	7	4	113	3	11,141	1,262	1,259	0.1130	1,258	1
1966	8	4	345	50	34,322	2,220	2,170	0.0632	2,168	2
1966	9	4	238	3	23,744	2,608	2,605	0.1097	2,601	4
1966	10	4	57	0	5,699	883	883	0.1549	878	5
1966	11	4	10	0	996	183	183	0.1837	183	0
1966	12	4	130	57	12,996	489	432	0.0332	428	4
06/20/23			893	113	88,898	7,645	7,532		7,516	16
Positives			780	0.8735						

(B) 1967

year_rel	month_rel	release_area	events	zero events	releases	recoveries	adj recovs	u	1966-1969	> 1969
1967	4	3	13	0	1,250	336	336	0.2688	333	3
1967	4	5	59	23	5,879	121	98	0.0167	98	0
1967	5	3	146	0	14,510	3,812	3,812	0.2627	3,778	34
1967	5	4	78	3	7,771	942	939	0.1208	937	2
1967	5	5	154	77	15,395	690	613	0.0398	610	3
1967	6	3	216	0	21,433	6,424	6,424	0.2997	6,382	42
1967	6	4	105	10	10,376	1,393	1,383	0.1333	1,381	2
1967	6	5	54	4	5,400	481	477	0.0883	476	1
1967	7	3	199	0	19,842	5,570	5,570	0.2807	5,507	63
1967	7	4	253	5	25,276	2,727	2,722	0.1077	2,714	8
1967	7	5	92	7	9,078	947	940	0.1035	935	5
1967	8	3	236	0	23,293	5,760	5,760	0.2473	5,693	67
1967	8	4	292	0	29,118	5,876	5,876	0.2018	5,859	17
1967	8	5	285	94	28,574	1,210	1,116	0.0391	1,112	4
1967	9	3	82	0	8,113	1,902	1,902	0.2344	1,874	28
1967	9	4	99	0	9,899	2,867	2,867	0.2896	2,850	17
1967	9	5	48	10	4,800	271	261	0.0544	259	2
1967	10	3	1	0	100	41	41	0.4100	41	0
1967	10	4	4	0	400	126	126	0.3150	126	0
06/20/23			2,416	233	240,507	41,496	41,263		40,965	298
Positives			2,183	0.9036						

Table 2.2.6 (cont.)

(C) 1968

year_rel	month_rel	release_area	events	zero events	releases	recoveries	adj recovs	u	1966-1969	> 1969
1968	4	3	154	0	14,915	3,298	3,298	0.2211	3,231	67
1968	4	5	226	4	22,520	2,337	2,333	0.1036	2,309	24
1968	5	3	131	0	12,557	3,277	3,277	0.2610	3,193	84
1968	5	5	275	8	27,401	2,901	2,893	0.1056	2,850	43
1968	6	3	363	0	36,052	8,989	8,989	0.2493	8,697	292
1968	6	5	169	20	16,789	1,357	1,337	0.0796	1,311	26
1968	7	3	359	2	35,433	7,038	7,036	0.1986	6,841	195
1968	7	5	214	7	21,362	1,451	1,444	0.0676	1,402	42
1968	8	3	98	0	9,639	1,540	1,540	0.1598	1,485	55
1968	8	5	116	4	11,429	700	696	0.0609	675	21
1968	9	3	127	1	12,593	1,690	1,689	0.1341	1,570	119
1968	10	3	1	0	99	32	32	0.3232	31	1
09/02/23			2,233	46	220,789	34,610	34,564		33,595	969
Positives			2,187	0.9794						

(D) 1969

year_rel	month_rel	release_area	events	zero events	releases	recoveries	adj recovs	u	1966-1969	> 1969
1969	1	4	13	0	1,300	123	123	0.0946	92	31
1969	2	4	1	1	2	0	-1	-0.5000	0	0
1969	4	3	16	0	1,599	188	188	0.1176	147	41
1969	4	4	7	0	519	90	90	0.1734	35	55
1969	4	5	89	8	8,900	412	404	0.0454	331	73
1969	5	1	10	0	1,000	192	192	0.1920	180	12
1969	5	2	7	0	700	12	12	0.0171	11	1
1969	5	3	89	3	8,984	641	638	0.0710	478	160
1969	5	4	18	0	1,641	263	263	0.1603	233	30
1969	5	5	146	5	14,598	1,116	1,111	0.0761	831	280
1969	6	1	23	0	2,231	635	635	0.2846	612	23
1969	6	3	34	0	3,345	398	398	0.1190	325	73
1969	6	4	16	0	1,554	179	179	0.1152	117	62
1969	6	5	205	55	20,497	591	536	0.0262	358	178
1969	7	1	40	0	3,960	802	802	0.2025	758	44
1969	7	3	239	8	23,525	2,695	2,687	0.1142	1,841	846
1969	7	4	108	2	10,777	1,373	1,371	0.1272	1,133	238
1969	7	5	140	65	13,970	229	164	0.0117	102	62
1969	8	1	11	0	1,077	191	191	0.1773	179	12
1969	8	3	87	2	8,625	633	631	0.0732	422	209
1969	8	4	52	0	5,126	789	789	0.1539	609	180
1969	8	5	205	72	20,499	523	451	0.0220	274	177
1969	9	3	133	3	13,164	970	967	0.0735	466	501
1969	9	4	40	0	3,970	591	591	0.1489	458	133
1969	9	5	188	4	18,800	1,503	1,499	0.0797	90	1,409
1969	10	3	143	0	14,145	2,026	2,026	0.1432	756	1,270
1969	10	4	6	0	598	105	105	0.1756	77	28
1969	10	5	21	1	2,100	182	181	0.0862	9	172
1969	11	3	11	0	1,100	150	150	0.1364	21	129
1969	11	4	30	0	2,991	696	696	0.2327	310	386
1969	11	5	75	0	7,386	1,161	1,161	0.1572	4	1,157
06/20/23			2,203	229	218,683	19,459	19,230		11,259	7,972
Positives			1,974	0.8961						

Table 2.2.6 (cont.)

(E) 1970

year_rel	month_rel	release_area	events	zero events	releases	recoveries	adj recovs	u	1966-1969	> 1969
1970	5	3	212	0	21,189	5,006	5,006	0.2363	0	5,006
1970	6	3	146	0	14,600	4,308	4,308	0.2951	0	4,308
1970	6	4	2	0	200	29	29	0.1450	0	29
1970	8	4	8	0	385	105	105	0.2727	0	105
06/20/23			368	0	36,374	9,448	9,448		0	9,448
Positives			368	1.0000						

(F) Summary 1966-1970 Tag-Release & Recovery

	Recapture Period		Total
	1966-1969	> 1969	
Release Year			
1966	7,516	16	7,532
1967	40,965	298	41,263
1968	33,595	969	34,564
1969	11,259	7,972	19,231
Total 1966-1969	93,335	9,255	102,590
1970	0	9,448	9,448
Total 1966-1970	93,335	18,703	112,038

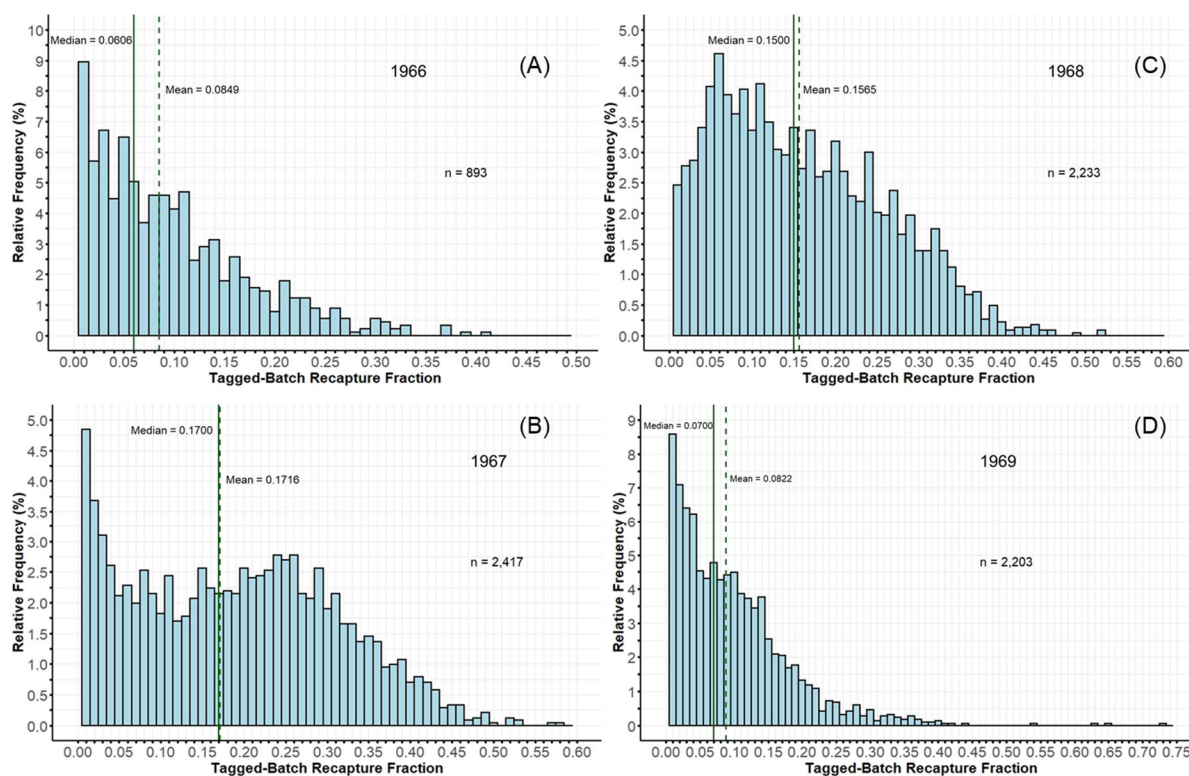


Figure 2.2.2.- Distributions of proportion of tagged fish recovered from of individual tagged batches (~100 fish each) for the total number of yearly released batches (n): (A) 1966; (B) 1967; (C) 1968; and, (D) 1969 for 8,119 batch releases of individual Atlantic menhaden.

Table 2.2.7.- Summary of batches released, batches with zero batches (no returns), and the number of menhaden tagged and released from July 1966 through December 1969. About 7.11% of the total batches released had zero returns.

	Tagged	Batches	Zero Batches	Fraction
1966	88,898	893	113	0.1265
1967	240,507	2,416	233	0.0964
1968	220,789	2,233	46	0.0206
1969	218,683	2,203	229	0.1039
Total	768,877	7,745	621	0.0802

Table 2.2.8.- Summary of Schueller (2022) Atlantic menhaden tagged-releases and recoveries by year. Data are organized into two periods: (1) July 1966 through December 31, 1969; and, (2) > 1969, i.e., January 1, 1970 through February 1971.

	Releases	Recoveries	Recoveries	Total	
	1966-69	1966-69	>1969	Recoveries	u
1966	88,898	7,516	16	7,532	0.0847
1967	240,507	40,965	298	41,263	0.1716
1968	220,789	33,595	969	34,564	0.1564
1969	218,683	11,259	7,972	19,231	0.0879
	768,877	93,335	9,255	102,590	0.1334
		0.1214		0.1334	

Table 2.2.9.- Tagged menhaden recoveries by reduction plant by area by year from the Schueller (2022) redigitized Plant Magnet study data from July 1966 through February 1971. Tags recovered between July 1, 1966 to December 31, 1969, are calculated by removing tags recaptured after 1969 for the 1966-1969 cohorts (9,255 fish), and ignoring the 1970 cohort of tagged menhaden (9,448 fish).

Area	Plant	COHORT					Plant	Area	Area
		1966	1967	1968	1969	1970			
	9/2/23	n	n	n	n	n	Totals	Totals	fractions
1	1	47	424	131	1,219		1,821		
	23						0	1,821	0.0163
	25						0		
2	2	174	2,176	527	755	52	3,684		
	4	44	766	228	3		1,041	4,725	0.0422
3	7	150	4,762	6,087	2,215	1,246	14,460		
	8	16	134				150		
	9	60	1,240				1,300	55,607	0.4963
	10	412	9,101	10,826	5,084	5,536	30,959		
	11	113	2,795	1,691	904	2,351	7,854		
	29	7	297	565	15		884		
	12	110	1,082	1,032	347	11	2,582		
	13	2,966	5,703	1,832	1,947	33	12,481		
	14	244	1,201	1,234	559	23	3,261		
4	15	251	1,005	871	310	16	2,453	39,282	0.3506
	16	205	1,494	1,914	932	87	4,632		
	17	41	528	1,678	1,200		3,447		
	28	2,640	5,866	160	1,667	93	10,426		
5	19	28	1,929	4,128			6,085		
	20	24	760	1,660	2,074		4,518	10,603	0.0946
Total		7,532	41,263	34,564	19,231	9,448		112,038	1.0000
fraction		0.0672	0.3683	0.3085	0.1716	0.0843		1.0000	
> 1969		16	298	969	7,972			9,255	
		7,516	40,965	33,595	11,259			93,335	

Table 2.2.10.- Menhaden Releases & Recaptures: 1966-1969. (A) Comparison of the reported release and recapture data from the various sources. (B) Comparison of the recaptures from the 1966 releases.

Source	Releases	Recaptures	Δ	μ
Coston (1971) – Wilberg	1,066,357	94,968	-7.79%	0.0891
Coston (1971) – Liljestrand	1,066,448	89,116	-13.47%	0.0836
	Table A.2	Table A.3		
Coston (1971) – Ault	1,066,357	102,992	0.00%	0.0966
Schueller (2022) – Ault	768,877	93,335	1966-69	0.1214
	805,251	112,038	1966-70	0.1391
Schueller – Ault-revised	706,875	93,335	1966-69	0.1320
corrected for zero batches				

(A)

(B) For the 1966 release cohort (July-December 1966) a total of 88,898 tagged-menhaden were released. The Coston (1971) paper indicates that only 5,887 of these fish were recaptured through December 1969. On the other hand, reanalysis of the Schueller (2022) data indicated that 7,516 tagged menhaden were recovered in the period running between July 1966 through December 1969. Another 16 fish from the 1966 cohort were recaptured between January 1, 1970 and February 28, 1971. In summary, these total recaptures constitutes a 27.67% increase over those reported in Coston (1971).

1966	Coston (1971)	Schueller (2022)	Increase in Recoveries
88,898	5,887	7,516	27.67%
		(through December 1969)	

Table 2.2.11.- Comparison of Coston and Schueller data sets compositions of releases and recaptures by area for the 1966-1969 period.

			Area			
Coston	1	2	3	4	5	Total
Releases	12,931	36,149	308,305	386,171	322,801	1,066,357
Recaptures	1,821	5,785	37,678	46,579	11,129	102,992
Fraction	0.1408	0.1602	0.1222	0.1206	0.0345	0.0966
Schueller	1	2	3	4	5	Total
Releases	8,268	700	320,105	201,801	275,377	768,377
Recaptures	1,729	11	53,112	24,447	14,036	93,335
Fraction	0.2091	0.0157	0.1659	0.1211	0.0510	0.1214

2.3 Plant Magnet Efficiency

A fundamental understanding of the mark-recapture study conducted for Atlantic menhaden was that not all of the tags that entered a plant in the landings of a purse seiner are recovered by the series of magnets. Mark-recovery data in general require one or more types of quantitative adjustments to satisfy assumptions necessary for some analytical procedures, especially those that estimate population mortality rates or abundance. The internal ferromagnetic mark-recapture data shared many analytical problems with external, visually detected, and voluntarily reported data, and have some more or less unique characteristics as well, and these biases and errors that can occur in parameter estimation when assumptions are not met are reviewed in Ricker (1975).

The “Plant Test” data provided by Amy Schueller (2022) of NMFS consisted of 5 separate Excel files that contained various information outlined in two Word documents written by J.W. Smith (2013) that detailed the contents of these files by defining variables in what he described as “parent” and “children” records. We assimilated these 5 Excel data files using specialized R-code we developed for this Technical Report (**Appendix 1**). An example summary of the data assimilation and creation of the specific R-based data frames is given in **Table 2.3.1**. Each of the five files were analyzed individually to ascertain their contents (**Table 2.3.2**). From these analyses data were combined into a single file and **Table 2.3.3** provides some details of the contents of the individual Excel files assimilated into the R data frames. These included data frames for the tag releases (`fr_releases`) and tag recoveries (`fr_recoveries`).

Experimental trials to test the efficiency of magnets at specific plants in areas were conducted by introducing known batches of tagged Atlantic menhaden (~90-100 fish) directly into the catches received at various reduction plants. These trials were conducted weekly at individual operational plants distributed along the Atlantic coast in the five areas. The number of tagged individuals by year by area released into the landings that were delivered at reduction plants is given in **Table 2.3.4**. This accounted for 95,986 tagged menhaden seeded into catches received by the plants. The number of trials (batches released) at each plant varied between 2 and 151, averaging about 50 trials per plant over the 6 years of the release-recovery plant magnet study.

Magnet efficiency for each plant was estimated from the trial data across four years. For each trial a , and plant p , the likelihood of recovering m marked individuals from a batch of r tagged releases was modeled. We used a binomial GLM to estimate the magnet efficiency ε_p for each plant. Magnet efficiency for each plant was estimated by minimizing the negative log likelihood

$$-LL_p = \sum_a -\log_e \left(\frac{r_a!}{m_a!(r_a-m_a)!} \right) \varepsilon_p^{m_a} (1 - \varepsilon_p)^{(r_a-m_a)} \quad (2.3.1)$$

These methods allowed us to estimate magnet efficiency by plant by area by year for 5 years (1967-1971) of “Plant Test” magnetic tag recovery data for 19 reduction plants distributed across the 5 regions. (**Table 2.3.5**). These efficiency coefficients by area were used to correct the recapture data (**Table 2.3.6**).

Table 2.3.1.- Contents of the component files of the combined “Plant Test” Excel spreadsheets.

```
> set("c:/jsa/trcp/mcp/2022/science/m/sedar/magnet/pt"5/")

> str(base$release_data)
tibble [141 x 6] (S3: tbl_df/tbl/data.frame)
 $ release_fulldate: Date[1:141], forma": "1971-04"2"" "1971-05"1"" "1971-05"1"" "1971-09"27" ...
 $ release_area   : num [1:141] 4 4 4 4 4 4 4 4 4 4 ...
 $ series        : chr [1:14] "C"7"" "C"7"" "C"7"" "C"75" ...
 $ release_week   : num [1:141] 279 281 282 283 284 285 286 287 288 289 ...
 $ vessel        : num [1:141] 171 171 171 171 171 171 171 171 171 171 ...
 $ number_tagged  : num [1:141] 100 100 100 100 100 100 100 100 100 100 ...

> dim(base$release_data)
[1] 141 6

> summary(base$release_data$release_fulldate)
   Min.   1st Qu.   Median     Mean   3rd Qu.     Max
"1971-03"0"" "1971-06"1"" "1971-08"0"" "1971-08"0"" "1971-09"1"" "1971-12"31"

> str(base$recovery_data)
tibble [9,881 x 8] (S3: tbl_df/tbl/data.frame)
 $ recovery_fulldate: Date[1:9881], forma": "1971-05"1"" "1971-05"0"" "1971-05"1"" "1971-05"18" ...
 $ series          : chr [1:988] "C"7"" "C"7"" "C"7"" "C"71" ...
 $ id              : num [1:9881] 0 2 4 5 7 9 11 12 13 14 ...
 $ recovery_area   : num [1:9881] 4 4 4 4 4 4 4 4 4 4 ...
 $ recovery_week   : num [1:9881] 282 280 281 282 281 280 282 280 280 280 ...
 $ recovery_plant   : num [1:9881] 17 17 17 17 17 17 17 17 17 17 ...
 $ recovery_station : num [1:9881] 5 2 5 5 5 2 5 2 2 2 ...
 $ magnet          : num [1:9881] 5 5 2 5 2 5 5 5 5 5 ...

> dim(base$recovery_data)
[1] 9881 8

> summary(base$recovery_data$recovery_fulldate)
   Min.   1st Qu.   Median     Mean   3rd Qu.     Max
"1971-01"0"" "1971-06"2"" "1971-08"0"" "1971-08"0"" "1971-09"1"" "1972-11"07"
```


Table 2.3.2.- Five Excel files containing “Plant Test” data summarizing the plant magnet efficiency trials conducted between May 1966 and December 1971.

Plant Test	Start	End	Batches	Releases	Recoveries
11	5/13/1966	11/6/1970	245	24,490	16,361
12	6/8/1967	5/7/1970	178	17,594	14,569
13	4/11/1968	12/15/1970	236	23,530	16,696
14	5/21/1968	11/19/1970	164	16,367	11,839
15	3/3/1971	12/31/1971	141	14,005	9,873
		TOTAL	964	95,986	69,338

Table 2.3.3.- Contributions of tags by year found in the 5 “Plant Test” Excel spreadsheets.

			Plant Test				
	11	12	13	14	15		Total
1966	5,994						5,994
1967	8,196	14,451					22,647
1968	3,900	1,494	8,898	6,992			21,284
1969	6,100	1,549	7,532	5,575			20,756
1970	300	100	7,100	3,800			11,300
1971					14,005		14,005
	24,490	17,594	23,530	16,367	14,005		95,986

Table 2.3.4.- Number of tagged individuals by year by area released into catches that were delivered at reduction plants to determine magnet capture efficiency for the five “Plant Test” Excel files.

		RELEASE AREA					Total	
		1	2	3	4	5		
Plant Test File								
1966	11				4,698	1,296	5,994	
	12						0	
	13						0	5,994
	14						0	
	15						0	
	1966	0	0	0	4,698	1,296		
1967	11		2,500	1,100	998	3,598	8,196	
	12			11,176	3,275		14,451	
	13						0	22,647
	14						0	
	15						0	
	1967	0	2,500	12,276	4,273	3,598		
1968	11	1,100	500	2,300			3,900	
	12				1,494		1,494	
	13	400	2,399		999	5,100	8,898	21,284
	14			6,295	697		6,992	
	15						0	
	1968	1,500	2,899	8,595	3,190	5,100		
1969	11		1,300	4,800			6,100	
	12			100	1,449		1,549	
	13		1,800		900	4,832	7,532	20,756
	14	1,400			4,175		5,575	
	15						0	
	1969	1,400	3,100	4,900	6,524	4,832		
1970	11		200	100			300	
	12				100		100	
	13			1,300	4,000	1800	7,100	11,300
	14			3,600	200		3,800	
	15						0	
	1970	0	200	5,000	4,300	1,800		
1971	11						0	
	12						0	
	13						0	14,005
	14						0	
	15	600	699	5,295	5,611	1,800	14,005	
	1971	600	699	5,295	5,611	1,800		
		1	2	3	4	5		
6/21/2023	Grand Total	3,500	9,398	36,066	28,596	18,426	95,986	95,986
	fraction	0.0365	0.0979	0.3757	0.2979	0.1920	1.0000	

Table 2.3.5.- Plant magnet test efficiencies by area by plant by year. Some 95,986 tagged menhaden were used in controlled releases (in 964 batch releases) mixed into vessel catches to determine the tag recapture efficiency by area by plant by year.

Area	Plant	1966		1967		1968		1969		1970		1971		Weighted		
		n	mean	n	mean	n	mean	n	mean	n	mean	n	mean	Average		Plants
			6/7/2023 14:04													
	1					15	0.6687	14	0.7714					0.7183		
1	23											2	0.0250	0.0250		
	25											4	0.3300	0.3300		
															0.52	5
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	0.5874		
	9			21	0.7826									0.7826		
3	10			35	0.8656	37	0.8152	25	0.7236	25	0.6584	29	0.6356	0.7513	0.61	5
	11			30	0.8006	3	0.8400			19	0.4579			0.6776		
	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	0.6578		
	13	11	0.8927	17	0.9652	9	0.9233	12	0.8958	10	0.7610	16	0.7168	0.8582		
	14	5	0.5740	6	0.8733	1	0.8300	7	0.7936	8	0.7650	4	0.6500	0.7489		
4	15	5	0.7400	5	0.8160	2	0.7384	4	0.8325					0.7867	0.78	7
	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	0.9219		
5	19	3	0.7667	21	0.6679	28	0.7782							0.7330		
	20	10	0.6788	15	0.6313	23	0.5235	49	0.6133	18	0.6900	18	0.8806	0.6513	0.69	2
	Batches	60		228		213		209		113		141		964		

Table 2.3.6.- Average efficiency of magnets in reduction plants and the number of plants in each area. Efficiency was calculated from efficiency trials (see Tables 2.3.4 and 2.3.5), where a known number of tagged Atlantic menhaden were introduced directly into vessel catches received at the various reduction plants. The average efficiency was the weight means among plants and sample sizes in each area.

Area (A)	Magnet efficiency ε_A	Plants
1-2	0.52	5
3	0.61	5
4	0.78	7
5	0.69	2

2.4 Nominal Fishing Effort

Industry denied our information request(s) for access to basic commercial Atlantic menhaden reduction fishery catch and effort data by plant by area by month for the July 1966 through December 1969 period of the NMFS tagging study. As a consequence, we had to become particularly creative in employing a statistical fix to generate the nominal fishing effort data necessary for our demographic modeling efforts.

2.4.1 Participating Reduction Fishery Vessels

In our analyses of the “Field Release” and “Plant Test” data sets we were able to identify plants and areas where catches were landed. Our analyses of these data revealed that there were > 100 vessels that participated in the NMFS tagging program during 1966-1971, distributed across the five areas over the 5+ years of the study (**Table 2.4.1**). This was not a complete census or listing of vessels participating in the fishery *per se*, since it does not include the full list of actual fishery participants. It does, however, contain those vessels who participated in the two study components in the particular areas that tags were released and recovered.

2.4.2 Conversion of 1966-1969 Annual Coast-wide Fishing Effort to Month by Area

Ray Mroch of NOAA Fisheries Beaufort, NC, provided summarized landings and effort data for the Atlantic menhaden reduction fishery 1966-1969. Landings were expressed in the industry-standard 1,000 standard fish (ksf), or metric tons (mt). Vessel effort was in trips (**Table 2.4.2**). We compared the catch and vessel effort data that we obtained from Mroch (2023) to several other sources, including those reported in the SEDAR 69 (2019) benchmark stock assessment (**Table 2.4.3**). Notably, the Liljestrand et al. (2019) nominal fishing effort data were reported in units of vessel weeks (vw), while the Mroch (2023) data were reported in units of vessel trips, which required a conversion to vw. To do so, we found that the catch data of SEDAR 69 (2019) and Mroch (2023) agreed exactly to the decimal point, so we assumed that there was a direct translation between the fishing effort of Mroch (2023) in units of trips with those of SEDAR 69 (2019) in terms of vessel weeks (vw). Essentially, the scale factor required to convert vessel trips to vessel weeks was approximately 3.1.

We also required total coast-wide nominal fishing effort to be distributed by area by year for the 1966-1969 period. To do so, we used the nominal effort by area by year reported in

Liljestrand et al. (2019) in **Table 2.4.4A**, and converted that to portions of effort by area by year (**Table 2.4.4B**). With these ratios were converted the Mroch (2023) coast-wide nominal fishing effort by year to by year by area (**Table 2.4.4C**).

Finally, we made the assumption that vessel effort was proportional to the recapture of menhaden tags by month by area by year. Thus, were converted the “Field Release” recapture data from **Table 2.3.3** to within year recapture probabilities by month by area (**Table 2.4.5**). The effort transformation assumed proportionality between nominal fishing effort and recaptures. For estimation purposes, we also required supplementary data on total effort and catch by month by area by year. We made an evaluation of monthly fishing effort and landings data for 5 regions for the 1966-1969 period. Since tagging occurred in only a portion of 1966 (i.e., July-January), and all releases and recaptures were constrained to Area 4, we used only a fraction of the total vessel effort in 1966. To estimate that fraction, we used the effort data (vw) in Liljestrand et al. (2019) (**Table 2.4.4A**) and evaluated the fraction of total annual coast-wide effort that occurred in the specific areas (**Table 2.4.4B**). However, the tag-recapture effort only occurred in the months July-January or 81.34% of the total annual effort (3,765/4,629) reported by Mroch. Thus, total effort in trips in Area 4 during 1966 was 1,021.57 trips. Nominal effort conversions proceeded along these lines for the Mroch (2023), SEDAR 69 (2019, viz Ault) and Liljestrand et al. (2019) data (**Table 2.4.6**). A comparison of the monthly total observed and predicted nominal fishing effort for the Mroch (2023) data is shown in **Fig. 2.4.1**, which are in relatively good agreement.

(A) “Field Release” vessels.

				Year			
	Loc	1966	1967	1968	1969	1970	Total
Area							
1	NY				3		3
2	NJ						
3	CB		32	29	11	1	73
4	NC	9	7		9	2	27
5	FL		5	8	6		19
Total		9	44	37	29	2	122

(B) “Plant Test” vessels

[illegible]

Table 2.4.2.- Atlantic menhaden commercial landings (ksf \equiv thousands of standard fish, mt \equiv metric tons) and nominal fishing effort (trips) by month along the entire US Atlantic coast from Maine to Florida (Mroch 2023).

Year	Month	Landings (ksf)	Landings (mt)	Trips
1966	4	3,389	1,030	24
1966	5	15,139	4,601	145
1966	6	65,809	19,999	695
1966	7	78,383	23,821	774
1966	8	95,790	29,111	884
1966	9	75,067	22,813	725
1966	10	79,820	24,257	570
1966	11	208,172	63,263	572
1966	12	98,974	30,078	220
1966	13	5,636	1,713	20
		726,179	220,686	4,629
1967	4	7,918	2,406	38
1967	5	22,245	6,760	159
1967	6	92,430	28,089	751
1967	7	84,609	25,713	621
1967	8	94,033	28,577	723
1967	9	48,334	14,689	468
1967	10	60,872	18,499	505
1967	11	140,295	42,636	492
1967	12	88,925	27,024	257
	13	0	0	0
		639,661	194,393	4,014
1968	4	9,302	2,827	57
1968	5	36,800	11,184	186
1968	6	95,891	29,141	562
1968	7	148,442	45,112	678
1968	8	99,988	30,386	641
1968	9	66,967	20,351	537
1968	10	106,347	32,319	470
1968	11	123,166	37,430	401
1968	12	87,649	26,637	223
1968	13	1,569	477	5
		776,121	235,863	3,760
1969	4	1,686	512	11
1969	5	28,088	8,536	131
1969	6	64,608	19,634	461
1969	7	81,692	24,826	550
1969	8	62,246	18,917	447
1969	9	43,344	13,172	379
1969	10	100,936	30,674	409
1969	11	100,368	30,502	323
1969	12	48,657	14,787	119
1969	13	2,540	772	7
		534,165	162,333	2,837

Table 2.4.3.- Comparison of coast-wide nominal fishing effort by the Atlantic menhaden commercial reduction fleet during 1966-1970 from various sources in different units.

	(A)	(B)	(C)	(D)	
Source	Liljestrand	Dryfoos	Mroch	SEDAR 69	Scale
	(2019)	(1973)	(2023)	(2019)	Factor
units	vw	vw	trips	vw	(C)/(D)
Year					
1966	1,172		4,629	1,368	3.3398
1967	750	757	4,014	1,316	3.0502
1968	995	601	3,760	1,209	3.1100
1969	828	519	2,837	995	2.8513
1970		501		906	

Table 2.4.4.- Total nominal fishing effort (in vessel weeks, vw) by year and region for the 1966-1969 portion of the menhaden release-recapture study (from Liljestrand et al. 2019, Appendix A.4).

(A) Nominal fishing effort by region (source: Liljestrand et al. 2019)

Year	Area				Total
	1 & 2	3	4	5	
	NY/NJ	CB	NC	FL	
1966	92	687	318	75	1,172
1967	88	429	209	24	750
1968	115	499	324	57	995
1969	135	428	236	29	828

(B) Conversion of Liljestrand et al. (2019) annual effort in (A) to fractions by region by year.

Year	Area				Total
	1 & 2	3	4	5	
1966	0.0785	0.5862	0.2713	0.0640	1.0000
1967	0.1173	0.5720	0.2787	0.0320	1.0000
1968	0.1156	0.5015	0.3256	0.0573	1.0000
1969	0.1630	0.5169	0.2850	0.0350	1.0000

(C) Conversion of SEDAR 69 (2019) annual nominal fishing effort f effort (in vessel week) for the reduction fleet along the entire Atlantic coast to effort by regions using the Liljestrand et al. (2019) annual effort fractions from (B). Total nominal fishing effort for 1966 was calculated from Table 2.4.2 as the fraction of annual nominal effort from Mroch (2023) relative to the July-December study period, i.e., $= 3,765/4,629 \times \text{annual } f = 0.8134 \times 1,386$.

Area	1 & 2	3	4	5	
Region	1	2	3	4	Total
1966	88.49	660.80	305.87	72.14	1,127.30
1967	154.41	752.75	366.73	42.11	1,316.00
1968	139.73	606.32	393.68	69.26	1209.00
1969	162.23	514.32	283.60	34.85	995.00

Table 2.4.5.- Elements of the conversion of annual coast-wide fishing effort to coast-wide effort by year by month by area: (A) Total recaptures by year by month by area from July 1966 through December 1969 from Table 2.3.3; and, (B) Recapture probabilities by year by month by area for July 1966 through December 1969.

(A)

Year	Month	AREA					Total
		1	2	3	4	5	
1966	7	0	0	0	277	0	277
	8	0	0	0	1,554	0	1,554
	9	0	0	0	2,230	0	2,230
	10	0	0	0	825	0	825
	11	0	0	0	489	0	489
	12	0	0	0	484	0	484
	TOTAL	0	0	0	5,859	0	5,859
1967	1	0	0	0	86	0	86
	2	0	0	0	14	0	14
	3	0	0	0	60	0	60
	4	0	0	0	10	18	28
	5	0	0	37	245	79	361
	6	0	0	1,623	282	104	2,009
	7	0	11	2,450	908	429	3,798
	8	0	72	2,771	3,954	908	7,705
	9	0	109	2,036	1,667	548	4,360
	10	0	111	923	2,183	436	3,653
	11	0	18	878	1,879	64	2,839
	12	0	0	13	1,783	0	1,796
	TOTAL	0	321	10,731	13,071	2,586	26,709
1968	1	0	0	5	148	0	153
	2	0	0	20	44	0	64
	3	0	5	0	22	0	27
	4	0	0	621	116	384	1,121
	5	0	2	706	214	1,109	2,031
	6	0	466	3,032	325	962	4,785
	7	58	737	6,323	364	951	8,433
	8	116	620	5,028	287	1,461	7,512
	9	23	336	2,785	349	613	4,106
	10	42	159	2,073	103	114	2,491
	11	0	0	1,640	3,225	173	5,038
	12	0	15	114	4,465	8	4,602
		239	2,340	22,347	9,662	5,775	40,363
1969	1	0	0	142	214	0	356
	2	0	9	218	97	0	324
	3	0	0	227	28	0	255
	4	0	0	332	8	60	400
	5	26	0	539	378	304	1,247
	6	95	94	1,213	399	314	2,115
	7	592	549	530	1,064	257	2,992
	8	368	153	1,400	418	740	3,079
	9	23	64	952	962	178	2,179
	10	0	229	1,398	337	101	2,065
	11	0	241	547	1,562	48	2,398
	12	485	14	2	2,420	52	2,973
		1,589	1,353	7,500	7,887	2,054	20,383

Table 2.4.5.- (continued)

(B)

Year	Month			AREA			
		1	2	3	4	5	Total
1966	7	0.0000	0.0000	0.0000	0.0473	0.0000	0.0473
	8	0.0000	0.0000	0.0000	0.2652	0.0000	0.2652
	9	0.0000	0.0000	0.0000	0.3806	0.0000	0.3806
	10	0.0000	0.0000	0.0000	0.1408	0.0000	0.1408
	11	0.0000	0.0000	0.0000	0.0835	0.0000	0.0835
	12	0.0000	0.0000	0.0000	0.0826	0.0000	0.0826
	TOTAL	0.0000	0.0000	0.0000	1.0000	0.0000	1.0000
1967	1	0.0000	0.0000	0.0000	0.0032	0.0000	0.0032
	2	0.0000	0.0000	0.0000	0.0005	0.0000	0.0005
	3	0.0000	0.0000	0.0000	0.0022	0.0000	0.0022
	4	0.0000	0.0000	0.0000	0.0004	0.0007	0.0010
	5	0.0000	0.0000	0.0014	0.0092	0.0030	0.0135
	6	0.0000	0.0000	0.0608	0.0106	0.0039	0.0752
	7	0.0000	0.0004	0.0917	0.0340	0.0161	0.1422
	8	0.0000	0.0027	0.1037	0.1480	0.0340	0.2885
	9	0.0000	0.0041	0.0762	0.0624	0.0205	0.1632
	10	0.0000	0.0042	0.0346	0.0817	0.0163	0.1368
	11	0.0000	0.0007	0.0329	0.0704	0.0024	0.1063
	12	0.0000	0.0000	0.0005	0.0668	0.0000	0.0672
	TOTAL	0.0000	0.0120	0.4018	0.4894	0.0968	1.0000
1968	1	0.0000	0.0000	0.0001	0.0037	0.0000	0.0038
	2	0.0000	0.0000	0.0005	0.0011	0.0000	0.0016
	3	0.0000	0.0001	0.0000	0.0005	0.0000	0.0007
	4	0.0000	0.0000	0.0154	0.0029	0.0095	0.0278
	5	0.0000	0.0000	0.0175	0.0053	0.0275	0.0503
	6	0.0000	0.0115	0.0751	0.0081	0.0238	0.1185
	7	0.0014	0.0183	0.1567	0.0090	0.0236	0.2089
	8	0.0029	0.0154	0.1246	0.0071	0.0362	0.1861
	9	0.0006	0.0083	0.0690	0.0086	0.0152	0.1017
	10	0.0010	0.0039	0.0514	0.0026	0.0028	0.0617
	11	0.0000	0.0000	0.0406	0.0799	0.0043	0.1248
	12	0.0000	0.0004	0.0028	0.1106	0.0002	0.1140
	TOTAL	0.0059	0.0580	0.5537	0.2394	0.1431	1.0000
1969	1	0.0000	0.0000	0.0070	0.0105	0.0000	0.0175
	2	0.0000	0.0004	0.0107	0.0048	0.0000	0.0159
	3	0.0000	0.0000	0.0111	0.0014	0.0000	0.0125
	4	0.0000	0.0000	0.0163	0.0004	0.0029	0.0196
	5	0.0013	0.0000	0.0264	0.0185	0.0149	0.0612
	6	0.0047	0.0046	0.0595	0.0196	0.0154	0.1038
	7	0.0290	0.0269	0.0260	0.0522	0.0126	0.1468
	8	0.0181	0.0075	0.0687	0.0205	0.0363	0.1511
	9	0.0011	0.0031	0.0467	0.0472	0.0087	0.1069
	10	0.0000	0.0112	0.0686	0.0165	0.0050	0.1013
	11	0.0000	0.0118	0.0268	0.0766	0.0024	0.1176
	12	0.0238	0.0007	0.0001	0.1187	0.0026	0.1459
	TOTAL	0.0780	0.0664	0.3680	0.3869	0.1008	1.0000

(C) ALP conversion matrix from the Schueller recapture fractions of Table 2.4.5(B) collapsed from five Areas to the four Regions of Liljestrand et al. (2019). Unsampled Areas in 1966 (i.e., Areas 1&2, 3, and 5) were averaged monthly by regions over the 1967-1969 period to create 1966 monthly regional fractional values.

		REGION			
ALP		1	2	3	4
1966	7	0.2772	0.2439	0.0907	0.2177
	8	0.2552	0.2918	0.1380	0.4529
	9	0.1807	0.1922	0.1056	0.1813
	10	0.1752	0.1689	0.0793	0.0968
	11	0.0482	0.1005	0.2499	0.0379
	12	0.0636	0.0027	0.3366	0.0134
	TOTAL	1.0000	1.0000	1.0000	1.0000
1967	1	0.0000	0.0000	0.0066	0.0000
	2	0.0000	0.0000	0.0011	0.0000
	3	0.0000	0.0000	0.0046	0.0000
	4	0.0000	0.0000	0.0008	0.0070
	5	0.0000	0.0034	0.0187	0.0305
	6	0.0000	0.1512	0.0216	0.0402
	7	0.0343	0.2283	0.0695	0.1659
	8	0.2243	0.2582	0.3025	0.3511
	9	0.3396	0.1897	0.1275	0.2119
	10	0.3458	0.0860	0.1670	0.1686
	11	0.0561	0.0818	0.1438	0.0247
	12	0.0000	0.0012	0.1364	0.0000
	TOTAL	1.0000	1.0000	1.0000	1.0000
1968	1	0.0000	0.0002	0.0153	0.0000
	2	0.0000	0.0009	0.0046	0.0000
	3	0.0019	0.0000	0.0023	0.0000
	4	0.0000	0.0278	0.0120	0.0665
	5	0.0008	0.0316	0.0221	0.1920
	6	0.1807	0.1357	0.0336	0.1666
	7	0.3083	0.2829	0.0377	0.1647
	8	0.2854	0.2250	0.0297	0.2530
	9	0.1392	0.1246	0.0361	0.1061
	10	0.0779	0.0928	0.0107	0.0197
	11	0.0000	0.0734	0.3338	0.0300
	12	0.0058	0.0051	0.4621	0.0014
	TOTAL	1.0000	1.0000	1.0000	1.0000
1969	1	0.0000	0.0189	0.0271	0.0000
	2	0.0031	0.0291	0.0123	0.0000
	3	0.0000	0.0303	0.0036	0.0000
	4	0.0000	0.0443	0.0010	0.0292
	5	0.0088	0.0719	0.0479	0.1480
	6	0.0642	0.1617	0.0506	0.1529
	7	0.3878	0.0707	0.1349	0.1251
	8	0.1771	0.1867	0.0530	0.3603
	9	0.0296	0.1269	0.1220	0.0867
	10	0.0778	0.1864	0.0427	0.0492
	11	0.0819	0.0729	0.1980	0.0234
	12	0.1696	0.0003	0.3068	0.0253
	TOTAL	1.0000	1.0000	1.0000	1.0000

Table 2.4.6.- ALP matrices for nominal fishing (f) effort conversion of Atlantic coast-wide annual to monthly effort by year by region by month according to the monthly recapture probabilities shown in Table 2.4.5(C): (A) ALP(Liljestrand) – annual nominal effort (vw); and (B) ALP(SEDAR 69) – Atlantic coastwide trips from Mroch (2023) converted to monthly SEDAR 69 nominal f in vessel weeks (vw).

(A) ALP (Liljestrand)

Year	Month		REGION			
		1	2	3	4	Total
1966	7	20.74	136.31	23.46	13.28	
	8	19.09	163.03	35.69	27.62	
	9	13.52	107.40	27.30	11.06	
	10	13.11	94.37	20.52	5.91	
	11	3.61	56.13	64.63	2.31	
	12	4.76	1.53	87.05	0.82	
	TOTAL	74.83	558.77	258.65	61.00	953.25
1967	1	0.00	0.00	1.38	0.00	
	2	0.00	0.00	0.22	0.00	
	3	0.00	0.00	0.96	0.00	
	4	0.00	0.00	0.16	0.17	
	5	0.00	1.48	3.92	0.73	
	6	0.00	64.88	4.51	0.97	
	7	3.02	97.95	14.52	3.98	
	8	19.74	110.78	63.22	8.43	
	9	29.88	81.39	26.65	5.09	
	10	30.43	36.90	34.91	4.05	
	11	4.93	35.10	30.04	0.59	
	12	0.00	0.52	28.51	0.00	
	TOTAL	88.00	429.00	209.00	24.00	750.00
1968	1	0.00	0.11	4.96	0.00	
	2	0.00	0.45	1.48	0.00	
	3	0.22	0.00	0.74	0.00	
	4	0.00	13.87	3.89	3.79	
	5	0.09	15.76	7.18	10.95	
	6	20.78	67.60	10.90	9.50	
	7	35.45	141.19	12.21	9.39	
	8	32.82	112.27	9.62	14.42	
	9	16.01	62.19	11.70	6.05	
	10	8.96	46.29	3.45	1.13	
	11	0.00	36.62	108.15	1.71	
	12	0.67	2.55	149.73	0.08	
	TOTAL	115.00	499.00	324.00	57.00	995.00
1969	1	0.00	8.10	6.40	0.00	
	2	0.41	12.44	2.90	0.00	
	3	0.00	12.95	0.84	0.00	
	4	0.00	18.95	0.24	0.85	
	5	1.19	30.76	11.31	4.29	
	6	8.67	69.22	11.94	4.43	
	7	52.36	30.25	31.84	3.63	
	8	23.91	79.89	12.51	10.45	
	9	3.99	54.33	28.79	2.51	
	10	10.51	79.78	10.08	1.43	
	11	11.06	31.22	46.74	0.68	
	12	22.90	0.11	72.41	0.73	
	TOTAL	135.00	428.00	236.00	29.00	828.00

(B) ALP (SEDAR 69)

Year	Month	1	REGION 2	3	4	Total
1966	7	24.53	161.20	27.74	15.70	
	8	22.58	192.80	42.21	32.67	
	9	15.99	127.01	32.29	13.08	
	10	15.50	111.60	24.26	6.99	
	11	4.27	66.38	76.43	2.74	
	12	5.63	1.80	102.95	0.97	
	TOTAL	88.49	660.80	305.87	72.14	1,127.30
1967	1	0.00	0.00	2.41	0.00	
	2	0.00	0.00	0.39	0.00	
	3	0.00	0.00	1.68	0.00	
	4	0.00	0.00	0.28	0.29	
	5	0.00	2.60	6.87	1.29	
	6	0.00	113.85	7.91	1.69	
	7	5.29	171.86	25.48	6.99	
	8	34.63	194.38	110.94	14.79	
	9	52.43	142.82	46.77	8.92	
	10	53.39	64.75	61.25	7.10	
	11	8.66	61.59	52.72	1.04	
	12	0.00	0.91	50.02	0.00	
	TOTAL	154.41	752.75	366.73	42.11	1,316.00
1968	1	0.00	0.14	6.03	0.00	
	2	0.00	0.54	1.79	0.00	
	3	0.27	0.00	0.90	0.00	
	4	0.00	16.85	4.73	4.61	
	5	0.11	19.16	8.72	13.30	
	6	25.25	82.26	13.24	11.54	
	7	43.07	172.56	14.83	11.41	
	8	39.88	136.42	11.69	17.52	
	9	19.45	75.56	14.22	7.35	
	10	10.89	56.24	4.20	1.37	
	11	0.00	44.50	131.40	2.07	
	12	0.81	3.09	181.93	0.10	
	TOTAL	139.73	606.32	393.68	69.26	1,209.00
1969	1	0.00	9.74	5.37	0.00	
	2	0.50	14.95	8.24	0.00	
	3	0.00	15.57	8.58	0.00	
	4	0.00	22.77	12.55	1.02	
	5	1.43	36.96	20.38	5.16	
	6	10.42	83.18	45.87	5.33	
	7	62.92	36.35	20.04	4.36	
	8	28.73	96.01	52.94	12.56	
	9	4.80	65.28	36.00	3.02	
	10	12.63	95.87	52.86	1.71	
	11	13.29	37.51	20.68	0.81	
	12	27.53	0.14	0.08	0.88	
	TOTAL	162.23	514.32	283.60	34.85	995.00

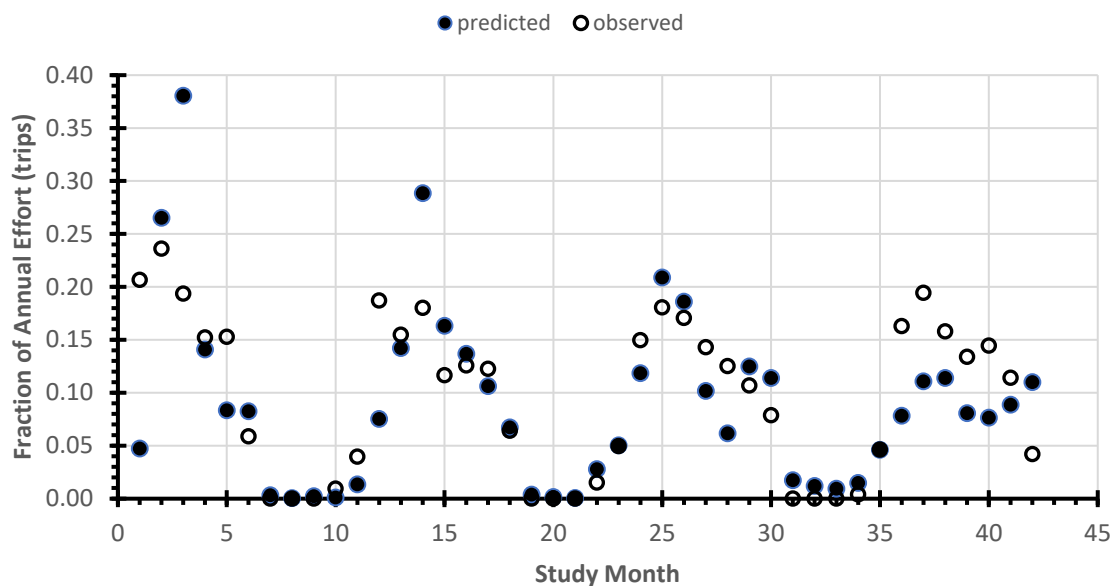


Figure 2.4.1.- Comparison of the observed fractions of annual nominal vessel effort from Mroch's (2023) observed trip fractions (open circles) relative to the predicted vessel week (vw) fractions (black closed circles) from conversions via the recapture probabilities of Table 2.4.5B.

3.0 Modeling Menhaden Demographic Rates

In this section we compared findings from several published methods for evaluation of Atlantic menhaden survivorship using the NMFS tagging data of Coston (1971) and Schueller (2022).

3.1 Ratio-based survivorship estimation

We calculated estimates of annual survival rate(s) for Atlantic menhaden tagged-releases by seasons ($S \equiv$ spring – summer; $F \equiv$ fall) by determining the ratios of recoveries in successive years following Dryfoos et al. (1973). We did so by considering the fundamental population dynamics abundance equation for survivorship between some time period (presumably a year) $0 \rightarrow t$.

$$N_t = N_0 e^{-Zt} \quad (3.1.1)$$

where N_0 is the initial cohort size, N_t is the number of those alive at time t , and Z is the total mortality rate. It follows that the cohort survivorship through the time period Δt is

$$S_t = \frac{N_t}{N_0} = e^{-Z\Delta t} \quad (3.1.2)$$

where Δt is one year. Thus, the standard compounded projection of N_t is for y years is

$$N_t = N_0 S_t^y \quad (3.1.3)$$

Total mortality rate, separated into components of fishing (F) and natural mortality (M), can be calculated in the same manner as Eq. 3.1.1 using the standard exponential decay model of population dynamics,

$$N_t = N_0 e^{-(M+F)t} \quad (3.1.4)$$

Tag recoveries can provide estimates of survival and exploitation rates that are independent of those obtained from catch and effort (Widrig 1954). Between July 1966 to December 1969, about 202,943 tagged Atlantic menhaden were recovered in Areas 1-5 from a total of 1,066,357 releases (Table 3.1.1A). Estimates of annual survival rates were calculated for releases for each of two seasons (Summer is March-October; Fall is November-February) by determining the ratio of recoveries in successive years (Table 3.1.1C). The survivorship rates for seasonal tagged cohorts varied considerably, presumably because of fluctuations in availability of menhaden to the reduction fleet (Table 3.1.1C).

Table 3.1.1.- Elements of computation of Dryfoos et al.'s (1973) Atlantic menhaden survival analyses for multiple-release tagging experiments using the July 1966-December 1969 Coston (1971) data. Seasons: S is Spring-Summer (March-October); F is Fall (November-February). All S and F releases in 1966 were in Area 4, and second row in (A) is from Table 3.1.2 computations. Recoveries by area were corrected for magnet efficiency: (A) Seasonal releases and recaptures; (B) Annual recaptures from seasonal releases of (A); and, (C) Estimated survivorship by year and season computed from the data of (A). These results replicate those found in Table 14 of Dryfoos et al. (1973).

(A)

		S 66	F 66	S 67	F 67	S 68	F 68	S 69	F 69	Total
Releases		74,906	21,721	324,141	38,920	378,533	7,461	217,584	3,091	1,066,357
1966	S	5,316								
	F	984	424							
1967	S	890	1,578	35,891						
	F	184	172	13,109	5,188					
1968	S	388	790	22,606	3,310	59,552				
	F	139	212	6,403	1,094	12,558	480			
1969	S	43	89	2,208	440	8,627	324	13,353		
	F	21	32	716	129	2,327	74	2,890	402	
Total		7,965	3,297	80,933	10,161	83,064	878	16,243	402	202,943

(B)

	S 66	F 66	S 67	F 67	S 68	F 68	S 69	F 69	
1966	6,300	424	0	0	0	0	0	0	
1967	1,074	1,750	49,000	5,188	0	0	0	0	
1968	527	1,002	29,009	4,404	72,110	480	0	0	
1969	64	121	2,924	569	10,954	398	16,243	402	
	7,965	3,297	80,933	10,161	83,064	878	16,243	402	202,943

(C)

		Fall	Summer	Fall	Summer	Fall
		67/66	68/67	68/67	69/68	69/68
1966	S	0.1870	0.4360	0.7554	0.1108	0.1511
	F		0.5006	1.2326	0.1127	0.1509
1967	S			0.4884	0.0977	0.1118
	F				0.1329	0.1179
1968	S					0.1853
	F					
Average		0.1870	0.4683	0.8255	0.1135	0.1434

Table 3.1.2.- Seasonal blocking of Atlantic menhaden releases from the Coston (1971) data following the methods of Dryfoos et al. (1973). This particular blocking strategy replicates that found in their Tables 1-8. *Seq* column values are months of the July 1966-December 1969 tagging study since inception; S-S is Spring-Summer (March-October); F is Fall (November-February).

					AREA					Seasonal Releases					
Year			1	2	3	4	5	Totals		1	2	3	4	5	
			NY	NJ	CB	NC	FL			NY	NJ	CB	NC	FL	
	Seq	Month													Combined
1966	1	July	0	0	0	11,141	0	11,141	1966						
	2	August	0	0	0	34,322	0	34,322	S-S				74,906		74,906
	3	September	0	0	0	23,744	0	23,744							
	4	October	0	0	0	5,699	0	5,699							
	5	November	0	0	0	996	0	996							
	6	December	0	0	0	12,996	0	12,996	F				21,721		21,721
1966		Totals	0	0	0	88,898	0	88,898							
1967	7	January	0	0	0	7,729	0	7,729	1967						
	8	February	0	0	0	0	0	0							
	9	March	0	0	0	644	0	644							
	10	April	0	0	1,250	588	5,879	7,717							
	11	May	0	0	14,510	8,614	15,395	38,519							
	12	June	0	2,286	21,343	10,284	5,400	39,313							
	13	July	176	1,399	19,872	25,276	9,078	55,801							
	14	August	1,917	7,161	23,293	38,113	30,274	100,758	S-S	2,093	13,660	100,128	112,428	95,832	324,141
	15	September	0	2,245	8,113	10,378	16,705	37,441							
	16	October	0	569	10,649	18,531	13,101	42,850							
	17	November	0	0	1,098	22,680	0	23,778							
	18	December	0	0	0	16,240	0	16,240	F	0	0	0	38,920	0	38,920
1967		Totals	2,093	13,660	100,128	159,077	95,832	370,790							
1968	19	January	0	0	0	0	0	0	1968						
	20	February	0	0	0	37	0	37							

	21	March	0	0	0	1,022	0	1,022							
	22	April	0	0	14,915	4,420	22,520	41,855							
	23	May	0	331	12,557	20,132	27,401	60,421							
	24	June	0	5,810	36,052	30,065	16,789	88,716							
	25	July	1,970	8,937	35,433	24,463	21,262	92,065							
	26	August	400	3,622	9,639	17,086	22,016	52,763	S-S	2,370	21,789	132,596	103,483	118,295	378,533
	27	September	0	2,100	13,592	6,258	4,109	26,059							
	28	October	0	989	10,408	0	4,198	15,595							
	29	November	0	0	0	200	0	200							
	30	December	0	0	0	5,437	524	5,961	F	0	0	0	6,937	524	7,461
1968			2,370	21,789	132,596	109,120	118,819	384,694							
1969	31	January	0	0	0	1,300	0	1,300							
	32	February	0	0	0	0	0	0							
	33	March	0	0	0	0	0	0							
	34	April	0	0	1,599	519	9,100	11,218							
	35	May	1,000	700	9,484	1,641	14,698	27,523							
	36	June	2,431	0	3,539	1,654	20,897	28,521							
	37	July	3,960	0	23,525	11,077	14,070	52,632							
	38	August	1,077	0	8,625	5,126	20,799	35,627	S-S	8,468	700	75,581	24,685	108,150	217,584
	39	September	0	0	13,264	4,070	19,100	36,434							
	40	October	0	0	14,445	598	2,100	17,143							
	41	November	0	0	1,100	3,091	7,386	11,577							
	42	December	0	0	0	0	0	0	F	0	0	0	3,091	0	3,091
1969		Totals	8,468	700	75,581	29,076	108,150	221,975							
		TOTAL	12,931	36,149	308,305	386,171	322,801	1,066,357	TOTAL	12,931	36,149	308,305	386,171	322,801	1,066,357

Table 3.1.3.- Conversion of the 1966 Fall release and recapture data from Schueller (2022) “Field Releases” into the seasonal format used Dryfoos et al. (1973). Seasonally converted data were used to compare survival rates estimated by use of the catch curve analysis methods of Chapman-Robson (1960) and Robson-Chapman (1961). Release numbers following Table 3.1.2 are corrected for tag loss/shedding. Left-side column recapture values by area are uncorrected, while the right-side columns have been corrected by magnet efficiency (G_A) by area A . Right-most Total column is the data used in the following Chapman-Robson (1961) survival model analysis of Section 3.2.

[illegible]

3.2 Chapman-Robson (1960) catch curve analysis outlined in Paulik (1962)

In general, there is increasing importance attached to accurate estimates of mortality rates in the study of the dynamics of populations. Chapman and Robson (1960) established the theory of catch-curve analysis for the situation in which both year-class strength and annual survival rates are constant. Robson and Chapman (1961; Table 3, p. 187) generated a Table to produce an efficient estimate of survival rate from a segment of a catch curve. They noted that the age distribution of a random sample, to the “catch curve” from a stationary fish population, provides information on the annual survival rate of the population. Chapman & Robson’s (1960) catch curve method produces unbiased estimates of annual survival rate if the assumptions of constant year-class strength (here we are following a single cohort) and survival rate hold true, and all fish beyond some minimum size (age) are equally vulnerable to the sampling gear (Robson & Chapman 1961). Annual survival rates were also obtained using Robson-Chapman (1961) catch curve analysis following the modifications by Paulik (1962).

Table 3.2.1.- Parameters of the Chapman-Robson (1960) survival estimator outlined in Paulik (1961).

Symbol	Definition	Units
R	Number of tags released (adjusted for loss)	
n	Total number recaptured (i.e., sample size)	
$K + 1$	Number of recapture periods of equal length	yr
N_i	Number recaptured in period i	
T	Total	
S	Rate of survival	
μ	Rate of exploitation (fraction of population removed)	
F	Fishing mortality rate	
X	Non-fishery generated losses of tagged fish	
M	Natural mortality rate	

Consider a single release of R tagged fish for which the number of recaptures during each $K + 1$ recapture periods of equal length is known. It is assumed that S , the survival rate, is constant for all recapture periods. In addition, fishing intensity and vulnerability are assumed to remain constant during the entire recapture period.

$$T = N_1 + 2N_2 + 3N_3 = \sum_{i=0}^3 (i \times N_i) \quad (3.2.1)$$

$$S = \frac{T}{n+T-1} \quad (3.2.2)$$

$$\text{var}(S) = \frac{T}{n+T-1} \left(\frac{T}{n+T-1} - \frac{T-1}{n+T-2} \right) \quad (3.2.3)$$

$$SE = \sqrt{\text{var}(S)} \quad (3.2.4)$$

$$S = e^{-(F+X)} \quad (3.2.5)$$

$$\mu = F[1 - e^{-(F+X)(k+1)} / F + X] \quad (3.2.6)$$

$$\hat{F} = -\mu \frac{\ln(S)}{1-S^{k+1}} \quad (3.2.7)$$

$$\mu = E = \frac{F}{F+M} (1 - e^{-F-M}) \quad (3.2.8)$$

Chapman-Robson rates computed for the entire recovery period were the most consistent (**Tables 3.2.2 & 3.2.3**).

Using the Chapman-Robson methods on the Coston (1971) data we can state that with 95 percent confidence, if survival rates are constant, the true Atlantic menhaden annual survival rate (S) falls somewhere between 21.87 and 23.52 percent, with the best point estimate being $S = 0.2270$.

Using the Chapman-Robson methods with the Schueller (2022) data, we can state that with 95 percent confidence, if survival rates are constant, the true Atlantic menhaden annual survival rate (S) falls somewhere between 20.44 and 21.96 percent, with the best point estimate being $S = 0.2120$.

These two survivorship estimates cover the same probability space and thus are not significantly different. Thus, results of these catch curve analyses indicated that Atlantic menhaden natural mortality (\hat{M}) estimates ranged from [0.5153, 0.5339].

Table 3.2.2.- Computation of the Robson-Chapman (1961) catch-curve survival model for Summer 1966 using Dryfoos et al.'s (1973) methodology recapture data corrected for magnet efficiency from Table 3.1.1B. Releases were corrected (R_c) for tag loss/shedding. Last two lines of this Table give the estimates shown in Dryfoos et al. (1973).

Coston (1971)		$R_c =$	56,180		
Years post	Coded		No.		
release	Age	N_i	Recaptured		T
0	0	N_0	6,300		
1	1	N_1	1,074		1074
2	2	N_2	527		1054
3	3	N_3	64	μ	192
		$n =$	7,965	0.1418	2,320
			S(Paulik)	S(C-R)	SE(S)
$X_k =$	0.2913		0.2330	0.2270	0.004122
	S	Z	E = μ	F	M
Ault et al. (2023)	0.2330	1.4566	0.50	0.9496	0.5070
Atlantic menhaden	S	Z	E	F	M
Dryfoos (1973)	0.23	1.4697	0.50	0.9543	0.5153

Table 3.2.3.- Computation of the Robson-Chapman (1961) catch-curve survival model for Summer 1966 seasonal release-recapture using Schueller (2022) data from the right-most column of Table 3.1.3. Releases were corrected (R_c) for tag loss/shedding, and recaptures corrected for magnet efficiencies.

Schueller (2022)		$R_c =$	56,180		
Years post	Coded		No.		
release	Age	N_i	Recaptured		T
0	0	N_0	7,326		
1	1	N_1	1,224		1224
2	2	N_2	511		1022
3	3	N_3	64	μ	192
		$n =$	9,125	0.1624	2,438
			S(Paulik)	S(C-R)	SE(S)
$X_k =$	0.2672		0.2234	0.2120	0.003794
	S	Z	E	F	M
Ault et al. (2023)	0.2234	1.4989	0.50	0.9650	0.5339

3.3 Survivorship & Total Mortality

Natural mortality (M) is a highly influential demographic parameter on quantities that are important for providing management advice in fisheries stock assessment (Punt et al. 2021, Maunder et al. 2023), particularly in the context of how it directly affects estimates of stock productivity and sustainability reference points decision making. Stock assessments generally include sensitivity analyses to the (assumed) value for M . Sensitivity analysis requires some notion of relative plausibility of the different levels of M . Management of some species is very sensitive to the value of M because the management rules are based on both fishing mortality rates and stock status determinations.

While M is a demographic parameter central to fishery stock assessment, it is invariably very difficult to estimate (typically due to lack of informative and unbiased data, such as tagging data or age-composition in the absence of fishing). Natural mortality M is also usually assumed to be constant over time, age, and sex. Nonetheless, a general accepted notion in stock assessments is that it is advisable to use a variety of approaches to estimate M (e.g., Quinn and Deriso, 1999; Cope and Hamel, 2022). The sensitivity of stock assessments to uncertainty in M remains an important area for quantitative exploration.

The concept of natural mortality can be thought of mathematically in the context of a component of survivorship. M is generally defined as the instantaneous rate of natural mortality and represented on an annual basis, such that the concept of M can be considered in the context of population survivorship over a year in the absence of fishing (Maunder et al. 2023). In general, M represents all mortality not attributed to the fishery (e.g., predation, starvation, disease, senescence), but it could include some forms of human-induced mortality not due to fishing. In these cases, it's probably useful to separate M into components. Additionally, M is a fundamental part of modelling structured (e.g., age, length, or stage) population dynamics.

3.3.1 Survivorship Expectations Based on Life History Demographics

Many M values used in stock assessments remain based on life history demographic (LHD) theory, maximum age, and some regression approaches. The ratio and catch curve analyses shown in Sections 3.1 and 3.2, while dependent on many assumptions that are likely to be violated, should be considered and compared to LHD methods, especially when multiple years of catch-at-age data are available from the start of fishing or from unfished populations. Dureuil and Froese (2021) stated that mean adult M can be approximated from the general law of decay if the average maximum age reached by an individual in a cohort is known. Conceptually, estimators based on maximum age should be preferred because maximum age, or longevity, relates more directly to, or arises from, M (or more accurately total mortality). General theory of LHD estimates for natural mortality are derived from the usual population model of Baranov (1913). The total mortality rate Z consists of two additive rate components, fishing mortality Z and natural mortality M . But we are considering lifetime survivorship to a maximum age a_λ in an unexploited (virgin) population. Now, let a_λ be the maximum observed age, so

$$N_\lambda = N_0 e^{-M(a_\lambda - a_0)} \quad (3.3.1)$$

Where N_0 is cohort abundance at birth, a_0 is age at birth, and a_λ is maximum observed age. Thus, survivorship to maximum age in an unexploited population is

$$S_\lambda = \frac{N_{a_\lambda}}{N_{a_0}} = e^{-M(a_\lambda - a_0)} \quad (3.3.2)$$

Where total mortality Z is the sum of the rates of natural M and fishing F mortality. If we assume that fishing mortality is zero ($F = 0$), then the decay model of Eq. 3.2 can be rearranged so that the proportion p living to at least a given maximum age a_λ following Alagaraja (1982), and $a_0 = 0$, then

$$p_\lambda = \frac{N_\lambda}{N_0} = e^{-(M+0)(a_\lambda - 0)} = S_\lambda \quad (3.3.3)$$

Eq. 3.3.3 can then be used to determine the probability of observing fish in an unexploited population surviving to a given maximum, given aged fish in a sample from the population (while ignoring ageing error).

3.3.2 Atlantic menhaden estimates based upon maximum age

Atlantic menhaden estimates of natural mortality rate can be evaluated considering life history demographic principles. For example, $S_\lambda = e^{-Ma_\lambda}$ in an unexploited population defines lifetime survivorship to evolutionary and genetically predisposed maximum age a_λ . Intuitively, a_λ (and S_λ) should represent an age at which senescence leads to high M and therefore relatively few older individuals. The maximum observed age in an exploited population is a_{\max} . For fish populations under exploitation, increased exploitation leads to decreased survivorship and a truncation of the population size/age structure, and as a consequence for stocks exploited for some time a_λ is largely unknown. But the oldest/largest observed (a_{\max}) animals provide some insight into a_λ . It is assumed for a population under exploitation that $a_\lambda > a_{\max}$. The question is the proportion of the exploited population S_{\max} that survives to a_{\max} . Notably, in the Schueller (2022) menhaden tagging data, fish as large as 650 mm TL (22.32 inches) were recorded.

The proportion of a population surviving to the observed maximum age generally varies from $S_\lambda(0.05)$ (e.g., see Alagaraja 1982) to about $S_\lambda(0.01)$ (e.g., see Hoenig 1984). A popular heuristic (rule of thumb) employed in international stock assessment circles is $M = 3/a_{\max}$ which derives from rearrangement of Eq. 3.3.3, where Alagaraja's $S_{\max} = 0.05$ is the assumed probability that 5% of the initial cohort of fish born at $a_0 = 0$ will survive to a maximum age of a_{\max} or older, assuming constant M with age. Since the maximum observed age of Atlantic menhaden is $a_{\max} = 11$ years (Fig. 3.1, Schueller et al. 2014), some provisional estimates of \hat{M} can be estimated:

$$S_{\max} = 0.05: \quad \hat{M} = -\frac{\ln(S_{\max}=5\%)}{t_{\max}} \quad \hat{M} = -\frac{\ln(0.05)}{11} = 0.2723 \quad (3.3.4)$$

$$S_{\max} = 0.01: \quad \hat{M} = -\frac{\ln(S_{\max}=1\%)}{t_{\max}} \quad \hat{M} = -\frac{\ln(0.01)}{11} = 0.4187 \quad (3.3.5)$$

Note that this equation $\hat{M} = \log_e(p_\lambda)/a_{\max}$ is derived from the first principle exponential law of decay, with two variables representing biological traits, i.e., the average maximum age a_{\max} and the typical proportion p_λ surviving to a_{\max} . The eldest individual found, aged, and recorded might serve as the proxy for a_{\max} in a wild population. Using these life history demographic principles, one could assume that a reasonable estimate of M for Atlantic menhaden would range between [0.27, 0.42]. Recently, Dureuil and Froese (2022) suggested that universally across the animal Kingdom the proportion of individuals surviving to the observed maximum age in a cohort is surprisingly similar across a wide range of species at 1.5% (i.e., $S_{\max}(0.015)$)

$$S_{\max} = 0.015: \quad \hat{M} = -\frac{\ln(S_{\max}=1.5\%)}{t_{\max}} \quad \hat{M} = -\frac{\ln(0.015)}{11} = 0.3818 \quad (3.3.6)$$

Maunder et al. (2023) in their recent review of natural mortality rates suggested using less than one-half of one percent survivorship $S_{\max}(0.0045)$

$$S_{\max} = 0.0045: \quad \hat{M} = -\frac{\ln(S_{\max}=0.45\%)}{t_{\max}} \quad \hat{M} = -\frac{\ln(0.0045)}{11} = 0.4912 \quad (3.3.7)$$

Up through about 2010, the mean of the range of M estimates was routinely used in Atlantic menhaden stock assessments (**Table 3.1.1**). As noted in SEDAR 03 (2003), an $M = 0.45 \text{ yr}^{-1}$ was equivalent to an annual reduction in population numbers of 36.24% (i.e., $S = e^{-0.45} = 0.6376 \Rightarrow A = 1 - S = 1 - 0.6376 = 0.3624$) in the absence of fishing. At that time, the $M = 0.45 \text{ yr}^{-1}$ rate estimate was considered quite high compared to other pelagic marine species. Fogarty (1989) had shown that Atlantic herring, for example, was characterized by an 18% annual natural mortality rate ($S = 0.82 = e^{-0.198450939}$). Undoubtedly for Atlantic menhaden, the unexploited $a_\lambda > 11$ years, so it would appear that a relatively small M would be a preferable choice.

Thus, what is really unknown is the true a_λ , the maximum age that occurred when the Atlantic menhaden stock was unexploited. For Atlantic menhaden, knowledge of the true value of a_λ is at the very best tenuous because the stock has been fished since at least the mid-1700s (Franklin 2007). There are reports of menhaden having reached sizes of >650 mm TL and 2.71 kg.

Ahrenholz (1987) chronicled historical status trends for the Atlantic menhaden stock (Smith & O'Bier 1996). The 1950s were reported to have numerous dominant year classes and broad age structure, but by the 1960s the stock contracted, recruitment declined as there were few dominant year classes, and the age structure became truncated. This is reflected in the small spattering of very large menhaden ≥ 600 mm TL (524.48 mm FL) in **Fig. 2.2.1** tag-recapture data. Conversion of life history demographics for length were facilitated by Smith et al. (2008), but substantially outside their regression range

$$TL = -1.65 + 1.15FL$$

$$FL = 2.48 + 0.87TL$$

And for weight

$$W = 0.000004057TL^{3.205}$$

$$W = 0.000005112FL^{3.241}$$

In general, to date most national-international stock assessments have adopted M -values for a broad range of species, including pelagic forage fishes, that fall between the $S_{\max}(0.05)$ and $S_{\max}(0.01)$ probability bounds, i.e., $S_{\max} = e^{-Ma_{\max}}$, where $S_{\max} \equiv$ is survivorship to maximum observed age a_{\max} . Recent stock assessments have used much larger M estimates than would be expected via life history demographics or population dynamics theory. In fact, since about 2010 a curious pattern of menhaden natural mortality estimates has emerged over the past decades (**Table 3.3.1 & Fig. 3.2**).

SEDAR 69 (2019) used $\hat{M} = 1.18$, thus $S_{\lambda} = 0.000002306$

$$S_{\max} = 0.0045: \quad \hat{M} = -\frac{\ln(S_{\max}=0.45\%)}{t_{\max}} \quad \hat{M} = -\frac{\ln(0.0045)}{11} = 0.4912 \quad (3.3.8)$$

If $S_{\lambda} = 0.01$, then $a_{\lambda} = 3.90$ years. Given the observations of Fig. 3.3, this is untenable given the observation of **Fig. 3.1**, where $a_{\lambda} > 11$ years.

That particular idea was supported by a comprehensive analysis of the global literature on natural mortality rates used in stock assessments by US regional and international fishery management councils and commissions. Given these fundamental concepts, what we would describe as a curious pattern of natural mortality rates for Atlantic menhaden has emerged in stock assessments over the past two decades (**Fig. 3.2**).

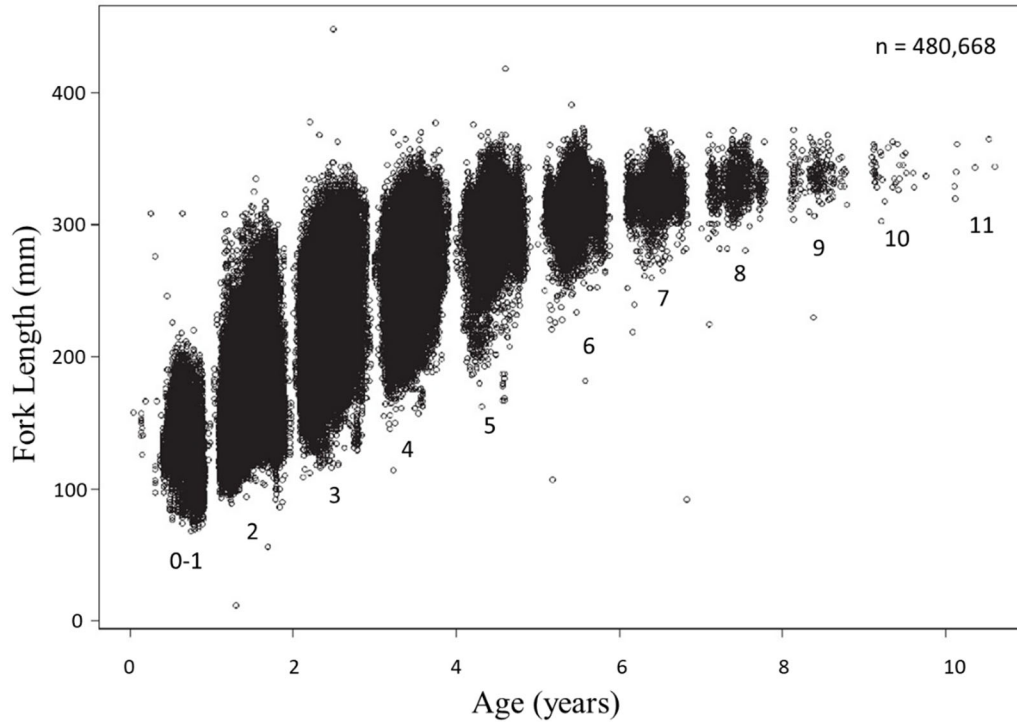


Figure 3.1.- Atlantic menhaden fork length (FL) dependent on age (years) in sampled reduction fishery landings from 1955-2011 (Source: Fig. 9 from Schuller et al. 2014). Note the maximum observed age a_{\max} is at least 11 years. It is likely that menhaden lived much longer years ago when the stock was lightly exploited or unexploited.

Table 3.3.1.- Range of Atlantic menhaden natural mortality rate estimates from a review of the population dynamics and scientific stock assessment literature.

Source	\hat{M} Estimates	Age range
Prior to 2010		
Schaaf & Huntsman (1972)	0.37	
Dryfoos et al. (1973)	0.52	
Reish et al. (1985)	0.43	
Ahrenholz et al. (1987)	0.45	
Cadrin & Vaughan (1997)	0.45	
SEDAR 3 (1999)	0.45	
Fogarty et al. (1989)	0.20	
Dureuil & Froese (2021)	0.49	
≥ 2010		
SEDAR 20 (2010)	0.76	averaged over ages 0-10
SEDAR 40 (2014)	0.73	averaged over ages 0-10
Liljestrand et al. (2019)	1.17	
SEDAR 69 (2019)	1.18	averaged over ages 0-4

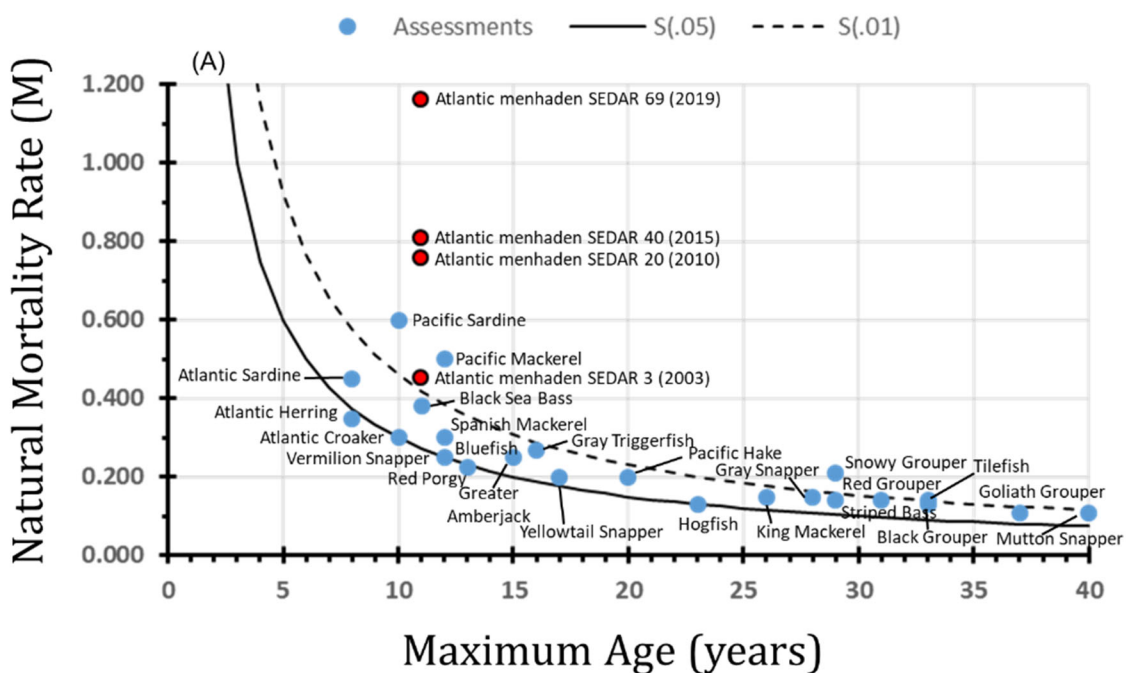


Figure 3.2.- Distribution from a global literature review of natural mortality rates used in a range of national and international fish stock assessments species. Note that Atlantic menhaden M estimates departed from the $[S_{\lambda}(0.05), S_{\lambda}(0.01)]$ probability bounds in about 2010.

3.4 Mark-Recovery Model of Liljestrand et al. (2019)

Mark-recapture data can be the basis for reliable ways to estimate M (Vetter, 1988; Fonteneau and Pallares, 2005). This is based on belief that careful repeated tagging/marking experiments probably hold the most promise for determining M with any reasonable degree of accuracy (Maunder et al. 2023). The basis for estimating survival rates in most tagging methods is the ‘Brownie model’ which has been well studied, and the properties of the commonly used estimators are well understood (e.g., Seber, 1982; Brownie et al., 1985; Lebreton et al., 1992). The general notion is that given an estimate of the reporting rate, this method allows the estimation of natural and fishing mortality. Some recent tagging-based methods (e.g. Hoenig et al., 1998a; 1998b, Myers and Hoenig, 1997, Jiang et al., 2007a; b) may allow relaxation of some of the violated assumptions required for historical methods for analyzing tagging data. Hoenig et al. (1998a) extended the basic approach so that fishing effort can be used as an index of fishing mortality, and Hoenig et al. (1998b) illustrated how to allow for non-mixing of tagged animals. Analyses of tagging data are considered to be the most promising direct method to estimate M for stocks for which a well-designed study has been conducted; nonetheless, it is difficult and expensive to design and implement a traditional tagging study that addresses all the issues that can bias the results. Even in data-rich cases there is considerable debate whether M estimates are reliable (Cadigan, 2016; Rose and Walters, 2019; Regular et al., 2022), as \hat{M} and its variability are still very poorly known for even the most studied fish stocks subjected to continuous exploitation for decades.

3.4.1 Mark-Recovery Model Structure

The mark-recovery model of Liljestrand et al. (2019) employed here was an instantaneous rate version of the Brownie et al. (1993) dead recovery model of Hoenig et al. (1998) that allowed movement among areas (**Fig. 1.2**).

Variables in the model and their descriptions are given in **Table 3.2.1**. The model tracked tagged monthly cohorts of individuals released from a single stratum (area) in a given month. It was assumed that all individuals in a cohort experienced the same dynamics regardless of size or age or release location within a stratum.

The number of individuals in a cohort released in area A_i at time t that were alive in an area A_j at time $t + \Delta t$, i.e. , was calculated using time and area specific survival rates. The initial magnitude of a released cohort was calculated by applying the area-specific tagging mortality and shedding rate, G_{A_i} , to the releases, N_{0T,A_i} ,

$$N_{T,A_i} = N_{0T,A_i} (I - G_{A_i}) \quad (3.4.1)$$

Area-specific tagging mortality and shedding was assumed to be known following Dryfoos et al. (1973) and that tagged individuals were well mixed in the area and independent. Survival and movement were modeled as sequential processes with movement occurring after survival in each time step, here considered to be one month. Cohort abundance after survival but before movement was calculated from area- and time-specific survival rates. A complete model description is given in Liljestrand et al. (2019).

3.4.2 Demographic Parameter Estimation

The data components critical to this analysis have been assimilated, as shown in earlier sections of this report.

The Liljestrand et al. (2019) model used a Bayesian parameter estimation approach. The model's objective function was the sum of the negative log of the prior probabilities and the negative log-likelihood for the recovery data

$$P = NegLL_c + p_\phi + p_q \quad (3.4.2)$$

In the model it is assumed that the estimated recoveries followed a negative binomial distribution, with a variable over-dispersion value (k), where r denotes the observed recoveries:

$$\min(NegLL_c) = \sum_T \sum_A \sum_t \sum_a -\log_e \left(\frac{\Gamma(k+r_{T,A,t,a})}{\Gamma(k)\Gamma(r_{T,A,t,a})} \left(\frac{k}{k+C_{T,A,t,a}} \right)^k \left(\frac{C_{T,A,t,a}}{k+C_{T,A,t,a}} \right)^{r_{T,A,t,a}} \right) \quad (3.4.3)$$

Here a negative binomial distribution is assumed to better address over-dispersion, which is typical for tag-recapture data, especially when fishing effort is spatially patchy and involves a schooling species (i.e., typical of Atlantic menhaden). In fact, the number of tagged fish ($N_{T,A,t,a}$) in each month and area from a tagged cohort ($N_{T,A,T,A}$) after release is unknown due to the effects of tagging mortality, migration, natural mortality, and fishing mortality. Thus, it is an obvious complicating factor that requires making some thoughtful assumptions to estimate this number. Briefly, some model details associated with the objective function are:

$N_{T,A,t,a}$ is defined as the number of tagged individuals from a cohort (batch of tags) released in area A at time T that were alive in area a at time t . The initial size (magnitude) of the cohort is calculated by applying the area-specific tagging mortality rate G_A to the releases $R_{T,A}$ so that $N_{T,A,T,A} = R_{T,A}(1 - G_A)$.

Tagged individuals are assumed to be well-mixed. Survival is modeled as a sequential process in each time step. Abundance of the cohort $N_{T,A,t,a}^*$ is calculated from region and time-specific survival rates $S_{t,a}$ as $N_{T,A,t,a}^* = N_{T,A,t,a} S_{t,a}$. Survival rates were estimated from time- and area-specific instantaneous fishing $F_{t,a}$ and natural M mortality rates as $S_{t,a} = e^{-(M+F_{t,a})}$. Natural mortality rate is assumed to be constant over regions and time, and the fishing mortality rate for a given region and time will be calculated as the product of month- and region-specific catchability $q_{m,r}$ and nominal fishing effort $f_{t,a}$, such that, $F_{t,a} = q_{m,a} f_{t,a}$. This parameterization assumes that catchability for month and region was constant over years.

Note: Despite not receiving these data directly, we were able to generate a work-around by synthetically generating the matrix $f_{t,a}$ by month by region, representing the commercial reduction fishing fleet, from the tag-recapture data and information on the total monthly nominal fishing effort. Finally, the estimated recoveries for each cohort is the product of the time- and

region-specific abundance $N_{T,A,t,a}$, the proportion of total mortality due to fishing, the fraction of the population that died, and the time- and region-specific magnet efficiency rate $\varepsilon_{t,a}$, such that,

$$C_{T,A,t,a} = N_{T,A,t,a} \frac{F_{t,a}}{Z_{t,a}} (1 - e^{-M} e^{-a}) / \varepsilon_{t,a} \quad (3.4.4)$$

It was assumed that there was no additional natural mortality between release and recovery in the first month ($t = T, a = A$) after release (for calculation of $N_{T,A,t,a}$). Individuals were tagged onboard commercial vessels. Consequently, tagged fish were immediately released in the same local areas as the commercial fishery. However, the model include simultaneous fishing and natural mortality such that the number of expected recaptures is affected by natural mortality in the first month after release.

The magnet efficiency ε_p for each plant p for each trial a was estimated by minimizing the negative log-likelihood

$$\min(NegLL_p) = \sum_a -\log_e \left(\frac{n_a!}{x_a!(n_a - x_a)!} \varepsilon_p^{x_a} (1 - \varepsilon_p)^{(n_a - x_a)} \right) \quad (3.4.5)$$

The annual survival rate is

$$S_j = \exp(-M_j - F_j) \quad (3.4.6)$$

When fishing effort and fishing mortality are constant over the year then u_t reduces to

$$\mu_t = \mu_t(F, M) = \frac{F_t}{F_t + M} \left(1 - \exp(-F_j - M) \right) = E \quad (3.4.7)$$

$$Y_N = F\bar{N} = N_0 \frac{F}{F+M} (1 - e^{-(F+M)}) = N_0 E \quad (3.4.8)$$

$$E = \mu \quad (3.4.9)$$

Table 3.4.1.- Parameter symbols, definitions and units used in the Liljestrand et al. (2019) parameter estimation model. Time domain of observed data is $t = 1, \dots, 42$ months covering the period from July 1966 to December 1969.

Parameter	Definition	Units
m	Month	month
T	Time of cohort release	month
τ	Time of cohort recovery	month
$A = 1, \dots, 5$	Area (region) of cohort release	
$a = r$	Area (region) of cohort recovery	
$t = m$	Time step of estimation	month
	Likelihood models	
NegLL_c	Negative log-likelihood for recoveries	
NegLL_p	Negative log-likelihood for magnet efficiency	
	Data	
f_a	Nominal fishing effort in area a	
$R_{T,A}$	Observed releases	
$r_{T,A,\tau,a}$	Observed recoveries	
	Defined Quantities	
G_A	Tag shedding & mortality by area A	
$1 - G_A$	Tag survivorship by area A	
k	Over-dispersion (negative binomial)	
ν	Dirichlet distribution sample size	
$\varepsilon_{t,a}$	Plant magnet efficiency by time t and region a	
Θ_t	Theta in study month t	
σ_q	Standard deviation of q catchability	
$\varphi_{m,r}$	Migration matrix	
\bar{L}_t	Average length of tagged menhaden	mm FL
w	Swimming speed	body lengths sec^{-1}
	Predicted 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	
$\hat{C}_{T,A,t,a}$	Estimated tag recoveries	
M	Natural mortality rate	
Z	Total mortality rate	
E	Exploitation rate	

3.4.3 Base Input & Sensitivity Parameters

We conducted base model runs and a number of sensitivity analysis runs with the principal Liljestrand et al. (2019) model data and parameters, i.e., releases, recaptures, fishing effort, k , ν , and G_A (Table 3.4.2).

Table 3.4.2.- Organizational structures of Atlantic menhaden tag-recaptures for model and data inputs to the base and sensitivity runs: (A) range of model parameters for the base and sensitivity runs; (B) sources for release-recapture data and nominal fishing effort for 1966-1969 period.

(A)

Parameters	Base	Sensitivity
k	2.5	1.0, 1.5, 2.5, 4.0
ν	10	1, 5, 10, 15, 20
$1 - G_A$	[0.9, 0.8, 0.75, 0.6]	[0.9, 0.8, 0.75, 0.6]
G_A	[0.1, 0.2, 0.25, 0.4]	[0.1, 0.2, 0.25, 0.4]
ε_A	[0.52, 0.61, 0.78, 0.69]	[0.52, 0.61, 0.78, 0.69]

(B)

Data Source	Parameters	Analysts		
		ALP	Wilberg	Liljestrand
Coston (1971)	Releases	1,066,357	1,066,357	1,066,448
	Recaptures	102,992	94,968	89,116
Schueller (2022)	Releases	768,877	--	--
	Recaptures	93,335	--	--
	Fishing Effort	alp(SEDAR 69)	alp(Liljestrand)	--

Table 3.4.2 (continued): (C) Initial annual regional catchability input parameters: $Q_r = \exp(\log(q_r))$; while, parameters $\theta_{m,r}$ are month and region-specific catchability multipliers that affect nominal fishing effort during the time-region sequence. Total month and region catchability $q_{m,r}$ is defined as $q_{m,r} = Q_r \times e^{\theta_{m,r}}$.

(C)

Region	Parameter	Mean	sd		Q_r	$e^{\theta_{m,r}}$
1	$\log(q_1)$	-6.1231	0.1444		0.002192	
2	$\log(q_2)$	-7.4326	0.0732		0.000591	
3	$\log(q_3)$	-4.3529	0.0912		0.012869	
4	$\log(q_4)$	-7.1710	0.2730		0.000769	
Month, Region						
5, 1	θ_1	-2.8721	0.6045			0.05658
6, 1	θ_2	-0.1032	0.1282			0.90195
8, 1	θ_3	-0.5559	0.1037			0.57357
9, 1	θ_4	-0.6686	0.1174			0.51245
10, 1	θ_5	-1.2162	0.1250			0.29635
11, 1	θ_6	-2.8547	0.5954			0.05758
5, 2	θ_7	0.6267	1.0182			1.87146
6, 2	θ_8	-0.3598	0.0858			0.69784
8, 2	θ_9	-0.2333	0.0800			0.79194
9, 2	θ_{10}	-0.8638	0.0888			0.42157
10, 2	θ_{11}	-0.3451	0.0906			0.70817
11, 2	θ_{12}	-0.6478	0.1378			0.52319
12, 2	θ_{13}	0.6072	1.0298			1.83532
3, 1	θ_{14}	-3.9025	0.2027			0.02019
3, 4	θ_{15}	-2.6491	0.2005			0.07071
3, 5	θ_{16}	-2.3013	0.1460			0.10013
3, 6	θ_{17}	-0.6075	0.1450			0.54474
3, 8	θ_{18}	-0.0018	0.1485			0.99820
3, 9	θ_{19}	-0.1382	0.1617			0.87091
3, 10	θ_{20}	-0.8134	0.1530			0.44333
3, 11	θ_{21}	-1.6215	0.2372			0.19761
3, 12	θ_{22}	-1.8739	0.3391			0.15352
4, 4	θ_{23}	1.0525	0.4790			2.86480
4, 4	θ_{24}	0.2822	0.3002			1.32607
6, 4	θ_{25}	0.2239	0.1812			1.25093
8, 4	θ_{26}	0.2673	0.1747			1.30646
9, 4	θ_{27}	0.1136	0.1778			1.12034
10, 4	θ_{28}	-0.3425	0.2132			0.71000
11, 4	θ_{29}	0.7142	0.8447			2.04253

Table 3.4.2 (continued): (D) Initial catchability $q_{m,r} = Q_r \times e^{\theta_{m,r}}$ by month and region.

		Region		
Month	1	2	3	4
1	0.00000	0.00000	0.00026	0.00000
2	0.00000	0.00000	0.00000	0.00000
3	0.00000	0.00000	0.00000	0.00000
4	0.00000	0.00000	0.00091	0.00220
5	0.00012	0.00111	0.00129	0.00102
6	0.00198	0.00041	0.00701	0.00096
7	0.00219	0.00059	0.01287	0.00077
8	0.00126	0.00047	0.01285	0.00100
9	0.00112	0.00025	0.01121	0.00086
10	0.00065	0.00042	0.00571	0.00055
11	0.00013	0.00031	0.00254	0.00157
12	0.00000	0.00109	0.00198	0.00000

Table 3.4.2 (continued): (E) Initial reduction plant magnet efficiency $\varepsilon_{m,r}$ by month and region (a_r).

Time	Month	Region			
		1	2	3	4
1	7	0.430	0.800	0.930	0.770
2	8	0.430	0.800	0.930	0.770
3	9	0.430	0.800	0.930	0.770
4	10	0.430	0.800	0.930	0.770
5	11	0.430	0.800	0.930	0.770
6	12	0.430	0.800	0.930	0.770
7	1	0.430	0.800	0.930	0.725
8	2	0.430	0.800	0.928	0.680
9	3	0.430	0.800	0.925	0.635
10	4	0.430	0.800	0.935	0.590
11	5	0.430	0.800	0.945	0.720
12	6	0.430	0.800	0.220	0.691
13	7	0.430	0.800	0.640	0.661
14	8	0.430	0.800	0.589	0.632
15	9	0.430	0.800	0.537	0.603
16	10	0.430	0.800	0.486	0.574
17	11	0.430	0.800	0.434	0.544
18	12	0.430	0.800	0.383	0.515
19	1	0.430	0.800	0.331	0.435
20	2	0.430	0.857	0.280	0.355
21	3	0.450	0.817	0.510	0.710
22	4	0.447	0.332	0.740	0.671
23	5	0.445	0.410	0.970	0.633
24	6	0.489	0.200	0.644	0.594
25	7	0.533	0.234	0.180	0.555
26	8	0.577	0.268	0.382	0.516
27	9	0.621	0.303	0.585	0.478
28	10	0.664	0.337	0.788	0.439
29	11	0.708	0.371	0.990	0.400
30	12	0.752	0.405	0.658	0.310
31	1	0.796	0.513	0.327	0.685
32	2	0.840	0.385	0.323	0.670
33	3	0.820	0.493	0.860	0.725
34	4	0.455	0.407	0.868	0.520
35	5	0.462	0.610	0.875	0.520
36	6	0.468	0.260	0.883	0.520
37	7	0.475	0.301	0.891	0.517
38	8	0.482	0.341	0.898	0.514
39	9	0.488	0.382	0.906	0.511
40	10	0.495	0.423	0.914	0.509
41	11	0.502	0.464	0.921	0.506
42	12	0.508	0.504	0.929	0.503

Table 3.4.2 (continued): (F) Monthly migration transition probabilities $\varphi_{m,r}$ between regions for May through October. The $\varphi_{m,r}$ were fixed as an identity matrix for the remaining months of November through April.

	1	2	3	4	
1	0.9995	0.0028	0.0149	0.0000	May
2	0.0005	0.9972	0.6875	0.0000	
3	0.0000	0.0000	0.2774	0.0353	
4	0.0000	0.0000	0.0202	0.9647	
	1	2	3	4	
1	0.9997	0.0122	0.0019	0.0000	June
2	0.0003	0.9878	0.2478	0.0000	
3	0.0000	0.0000	0.7497	0.0354	
4	0.0000	0.0000	0.0006	0.9646	
	1	2	3	4	
1	0.9998	0.0007	0.0001	0.0000	July
2	0.0002	0.9993	0.0171	0.0000	
3	0.0000	0.0000	0.9825	0.0204	
4	0.0000	0.0000	0.0002	0.9796	
	1	2	3	4	
1	0.9997	0.0017	0.0002	0.0000	August
2	0.0003	0.9983	0.0340	0.0000	
3	0.0000	0.0000	0.9655	0.0019	
4	0.0000	0.0000	0.0003	0.9981	
	1	2	3	4	
1	0.9996	0.0152	0.0002	0.0000	September
2	0.0004	0.9848	0.0367	0.0000	
3	0.0000	0.0000	0.9628	0.0003	
4	0.0000	0.0000	0.0002	0.9997	
	1	2	3	4	
1	0.5400	0.2261	0.0124	0.0055	October
2	0.0000	0.6573	0.0809	0.0356	
3	0.4600	0.1166	0.8957	0.0319	
4	0.0000	0.0000	0.0110	0.9270	
	1	2	3	4	
1	0.4481	0.1365	0.0323	0.0033	November - April
2	0.2571	0.6773	0.0527	0.0006	
3	0.2908	0.1852	0.9006	0.4326	
4	0.0040	0.0010	0.0143	0.5635	

Table 3.4.3.- Organization of the sensitivity analyses for the four primary Cases involving release-recapture data sources and model parameter estimation.

Case	Coston (1971)		Schueller (2022)		Q_r	$\theta_{m,r}$	$\varepsilon_{m,r}$	Effort	k	v
	Releases	Recaptures	Releases	Recaptures						
0.1	1,066,357	94,968	--	--	fixed	fixed	fixed	alp(<i>Lilj</i>)	range	range
0.2	1,066,357	94,968	--	--	fixed	fixed	adjusted	alp(<i>Lilj</i>)	" "	" "
1.1	1,066,357	94,968	--	--	estimated	estimated	fixed	alp(<i>Lilj</i>)	" "	" "
1.2	1,066,357	94,968	--	--	estimated	estimated	adjusted	alp(<i>Lilj</i>)	" "	" "
2.1	1,066,357	102,992	--	--	estimated	estimated	fixed	alp(<i>SEDAR</i>)	" "	" "
2.2	1,066,357	102,992	--	--	estimated	estimated	adjusted	alp(<i>SEDAR</i>)	" "	" "
3.1	--	--	768,875	93,335	estimated	estimated	fixed	alp(<i>SEDAR</i>)	" "	" "
3.2	--	--	768,875	93,335	estimated	estimated	adjusted	alp(<i>SEDAR</i>)	" "	" "

3.4.4 Parameter Estimation & Sensitivity Analyses

The model results presented below pivoted on the $k = 2.5$ and $v = 10$ scenarios which were the centroid of the results presented in the Liljestrand et al. (2019) study. However, we also ran a complete range of sensitivities to parameter ranges of $k \in [1.0, 1.5, 2.5, 4.0]$ and $v \in [1, 5, 10, 15, 20]$ for each of the eight Cases presented (**Tables 3.4.4 - 3.4.11**). In these cases we found, in general, that as k increased, so did the $\text{neg}(\text{LL})$. In addition, as v increased, so did the $\text{neg}(\text{LL})$. Thus, our case comparisons are focused at the level of $k = 2.5$ and $v = 10$. The organization of data sources and parameter estimation techniques used in the sensitivity analyses for the various cases is given in **Table 3.4.3**. Overall, the model fits to the observed recapture data for each of the scenario cases were generally good (**Fig. 3.4.1**).

Case 0

For comparison purposes with the Liljestrand et al. (2019) study, Case 0.1 was a base run using the Coston (1971) release-recapture data and fixed model parameters of “Liljestrand”, roughly equivalent to those reported in Liljestrand et al. (2019). The distinction was in two areas: (1) we used recaptures time-space matrix provided by Mike Wilberg, University of Maryland, which were used in the “Liljestrand” study, although these recapture data were 7.8% less than what we found in our own assessment of the recapture data in Coston’s (1971) technical report; and, (2) nominal fishing effort was estimated using our method mentioned previously, but scaled to the year by area Liljestrand’s nominal fishing effort (i.e., $\text{alp}(\text{Lilj})$). Case 0.2 adjusted the plant magnet efficiencies $\varepsilon_{m,r}$ to improve the model fit, because the variation of plant magnet efficiencies were large. For Case 0, $\hat{S} \in [0.1494, 0.1649]$ and $\hat{M} \in [1.0185, 1.0212]$. Not surprisingly, even given the considerable statistical efforts necessary on our part to obtain time series of nominal fishing effort, we were able to generally reproduce “Liljestrand’s” results (**Tables 3.4.4-3.4.5**). Case 0.2’s model fits by region to observed recapture data are shown in **Fig. 3.4.2**.

Case 1

Case 1.1 used the same data as in Case 0. For Case 1.1, the parameters Q_r and $\theta_{m,r}$ were estimated, and $\varepsilon_{m,r}$ were fixed. For Case 1.2, the parameters Q_r and $\theta_{m,r}$ were estimated, and $\varepsilon_{m,r}$ were adjusted. These results are given in **Tables 3.4.6-3.4.7**. For the primary Case 1 runs, $\hat{S} \in [0.0967, 0.1408]$ and $\hat{M} \in [0.9582, 1.14422]$. Notably, Case 1.1’s estimate of natural mortality was very close to that of “Liljestrand” and had a lower $\text{neg}(\text{LL})$ than Case 0.1. The estimated fishing mortality rate ($\hat{F} = 1.1917$) associated Case 1.1 was greater than that reported in either Liljestrand et al. (2019) or SEDAR 69 (2019). The Case 1.2 \hat{M} is a 18.5% reduction from that reported in Liljestrand et al. (2019).

Case 2

Case 2 runs also used the release data from Coston (1971); however, it instead used the actual “Coston” recapture data, which was more than 8% greater than that reported by “Liljestrand”. For Case 2.1, the parameters Q_r and $\theta_{m,r}$ were estimated, and $\varepsilon_{m,r}$ were fixed. For Case 2.2, the parameters Q_r and $\theta_{m,r}$ were estimated, and $\varepsilon_{m,r}$ were adjusted. These results are given in **Tables 3.4.8-3.4.9**. For the primary Case 2 runs, $\hat{S} \in [0.1282, 0.1613]$ and $\hat{M} \in [0.8165, 0.9665]$. The Case 2.2 \hat{M} was a 30.6% reduction from that reported in Liljestrand et al. (2019).

Case 3

Case 3 runs used the extremely detailed “Schueller” (2022) tag and recapture data. For Case 1, the parameters Q_r and $\theta_{m,r}$ were estimated, and $\varepsilon_{m,r}$ were fixed. For Case 3.2, the parameters Q_r and $\theta_{m,r}$ were estimated, and $\varepsilon_{m,r}$ were adjusted. These results are given in **Tables 3.4.10-3.4.11**. For the primary Case 3 runs, $\hat{S} \in [0.1426, 0.1914]$ and $\hat{M} \in [0.5428, 0.5454]$. The Case 3.2 \hat{M} was a 53.6% reduction from that reported in Liljestrand et al. (2019). Case 3.2’s model fit to observed recapture data is shown in **Fig. 3.4.3**. The analyses in Case 3 were directly comparable to those in Case 2, as the Case 3 data represented a subset of the full release-recapture data set (**Fig. 3.4.4**).

By and large, in these sensitivity runs we found substantially higher survivorship, and consequently, much lower M estimates. The average survivorship between Cases 1, 2 and 3 was $\bar{S}_{\text{Case 1}} = 0.1188 < \bar{S}_{\text{Case 2}} = 0.1448 < \bar{S}_{\text{Case 3}} = 0.1670$. The resultant combined estimates of $F + M = Z$ were different between Cases 1 and 3 data-parameter sets. For Case 1, the ratio of $M/F = 0.9559$, while for Case 3 it was $M/F = 0.4923$. This has two apparent implications: (1) the Case 1 \hat{M} was larger relative to F , indicating that natural mortality is a bigger component of total mortality Z (about 49%), producing a lower survivorship; and, (2) Case 3 had a much lower representation of \hat{M} relative to F in total mortality Z (about 33%), and thus, overall survivorship S was greater. The resultant M/F ratio indicated that fishing mortality was a greater proportion of total mortality than that reported in Liljestrand et al. (2019).

Liljestrand et al. (2019) concluded their best model estimate of natural mortality was $\hat{M} = 1.176 \text{ yr}^{-1}$, about 2.3 times greater than any of the previous published estimates that ranged from 0.5 to 0.52 yr^{-1} (e.g., Dryfoos et al. 1973, Reish et al. 1985 but also see **Table 3.3.1**). Our Chapman-Robson (1960) survival estimates completely aligned with Dryfoos et al. (1973) and Reish et al. (1985). Liljestrand et al. (2019) further stated that their “natural mortality estimate should be more reliable because it is estimated from the mark-recovery data rather than age structure of the catch”. That statement was incorrect, as Dryfoos et al. (1973) explicitly used the mark-recapture data of Coston (1971) to estimate survivorship and natural mortality. As stated by Liljestrand et al. (2019), “underestimating M can result in an overestimate of fishing mortality”. Conversely, overestimating M can result in an underestimate of fishing mortality. This would give a false view of stock size and spawning stock size, and an overoptimistic view of stock size relative to sustainability standards (e.g., Ault et al. 2022).

In summary, we believe that the best estimates of survivorship likely ranged from $S \in [0.1512, 0.1914]$, and the best estimates of natural mortality ranged from $M \in [0.5153, 0.5454]$.

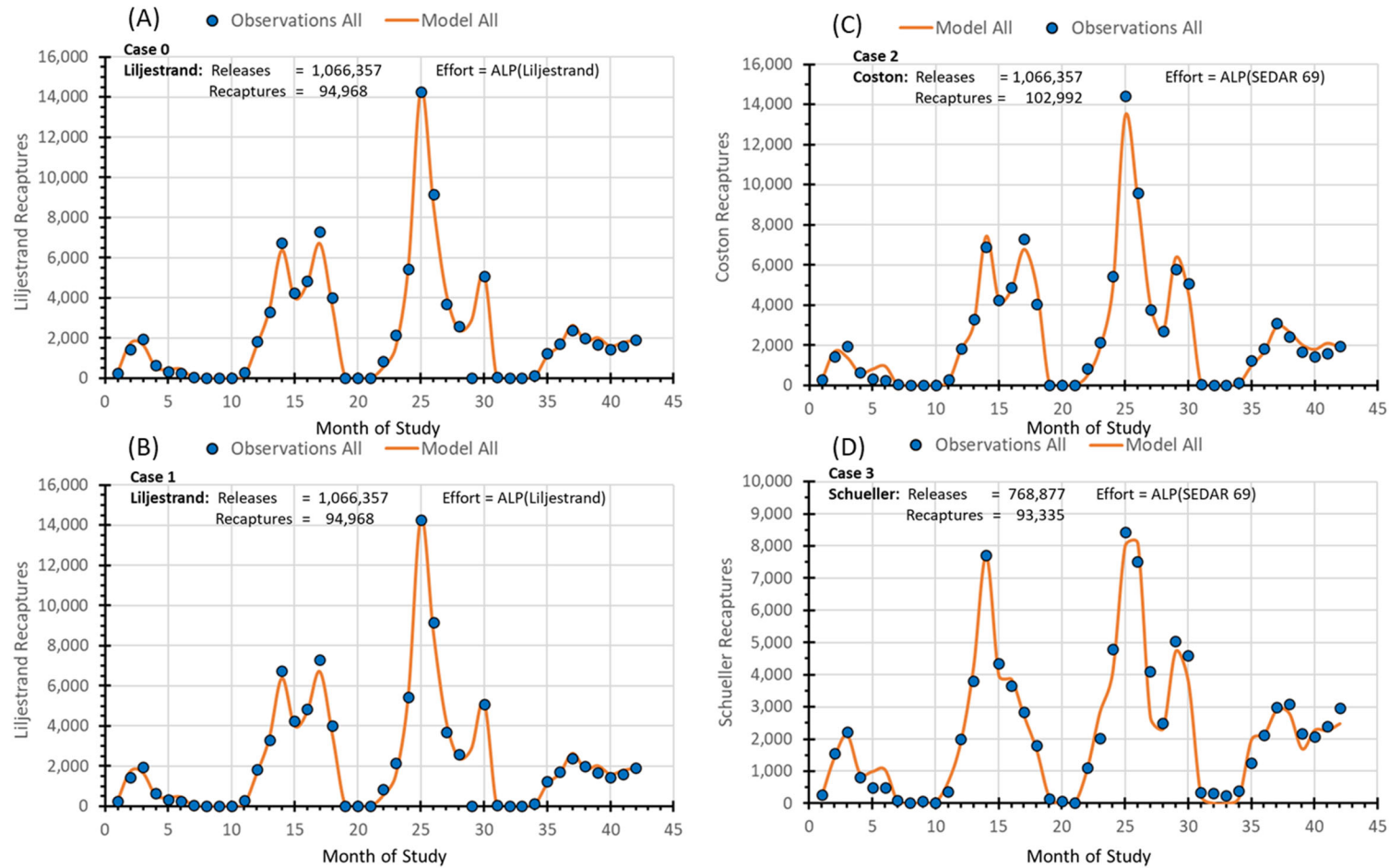


Figure 3.4.1.- Summary of model fits to observed data for the 4 principal sensitivity analysis cases: (A) Case 0.2; (B) Case 1.2; (C) Case 2.2; and, (D) Case 3.2.

Table 3.4.4.- Case 0.1: Coston releases = 1,066,357; Wilberg recaptures = 94,968; ALP(Liljestrand) effort. Parameters Q_r , $\theta_{m,r}$ and $\epsilon_{m,r}$ were fixed.

(A) $k = 2.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
1.0155	0.7882	1.8037	0.1647	0.3838	2.5	1	0.90	0.80	0.75	0.60	10,905.10
1.0177	0.7860	1.8037	0.1647	0.3838	2.5	5	0.90	0.80	0.75	0.60	10,990.10
1.0212	0.7812	1.8024	0.1649	0.3840	2.5	10	0.90	0.80	0.75	0.60	11,085.40
1.0250	0.7742	1.7991	0.1654	0.3844	2.5	15	0.90	0.80	0.75	0.60	11,172.30
1.0286	0.7660	1.7946	0.1662	0.3850	2.5	20	0.90	0.80	0.75	0.60	11,252.90

(B) $k = 1.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
1.0368	0.7933	1.8300	0.1604	0.3802	1.5	1	0.90	0.80	0.75	0.60	9,838.65
1.0399	0.7899	1.8297	0.1605	0.3802	1.5	5	0.90	0.80	0.75	0.60	9,921.85
1.0449	0.7813	1.8262	0.1610	0.3807	1.5	10	0.90	0.80	0.75	0.60	10,012.80
1.0498	0.7703	1.8201	0.1620	0.3815	1.5	15	0.90	0.80	0.75	0.60	10,094.20
1.0541	0.7597	1.8138	0.1630	0.3824	1.5	20	0.90	0.80	0.75	0.60	10,169.60

(C) $k = 1.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
1.0523	0.7965	1.8488	0.1578	0.3777	1.0	1	0.90	0.80	0.75	0.60	9,302.04
1.0566	0.7911	1.8477	0.1576	0.3778	1.0	5	0.90	0.80	0.75	0.60	9,383.23
1.0634	0.7779	1.8413	0.1586	0.3787	1.0	10	0.90	0.80	0.75	0.60	9,469.85
1.0694	0.7641	1.8335	0.1599	0.3797	1.0	15	0.90	0.80	0.75	0.60	9,546.97
1.0916	0.7603	1.8519	0.1569	0.3773	1.0	20	0.90	0.80	0.75	0.60	9,612.61

(D) $k = 4.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.9845	0.7767	1.7612	0.1718	0.3897	4.0	1	0.90	0.80	0.75	0.60	12,338.20
0.9875	0.7756	1.7631	0.1715	0.3894	4.0	5	0.90	0.80	0.75	0.60	12,424.90
0.9910	0.7729	1.7639	0.1714	0.3893	4.0	10	0.90	0.80	0.75	0.60	12,523.60
0.9944	0.7686	1.7630	0.1715	0.3894	4.0	15	0.90	0.80	0.75	0.60	12,615.10
0.9978	0.7631	1.7610	0.1710	0.3897	4.0	20	0.90	0.80	0.75	0.60	12,700.70

Table 3.4.5.- Case 0.2: Coston releases = 1,066,357; Wilberg recaptures = 94,968; ALP(Liljestrand) effort. Parameters Q_r and $\theta_{m,r}$ were fixed, and $\epsilon_{m,r}$ were adjusted.

(A) $k = 2.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
1.0146	0.8884	1.9030	0.1491	0.3724	2.5	1	0.90	0.80	0.75	0.60	9,665.04
1.0164	0.8864	1.9028	0.1492	0.3724	2.5	5	0.90	0.80	0.75	0.60	9,754.92
1.0185	0.8829	1.9015	0.1494	0.3726	2.5	10	0.90	0.80	0.75	0.60	9,858.10
1.0204	0.8780	1.8984	0.1498	0.3730	2.5	15	0.90	0.80	0.75	0.60	9,953.05
1.0222	0.8721	1.8942	0.1504	0.3736	2.5	20	0.90	0.80	0.75	0.60	10,041.00

(B) $k = 1.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
1.0175	0.8896	1.9071	0.1485	0.3719	1.5	1	0.90	0.80	0.75	0.60	9,019.29
1.0203	0.8867	1.9070	0.1485	0.3719	1.5	5	0.90	0.80	0.75	0.60	9,108.19
1.0238	0.8804	1.9042	0.1489	0.3723	1.5	10	0.90	0.80	0.75	0.60	9,208.02
1.0264	0.8713	1.8977	0.1499	0.3731	1.5	15	0.90	0.80	0.75	0.60	9,297.17
1.0289	0.8618	1.8907	0.1510	0.3740	1.5	20	0.90	0.80	0.75	0.60	9,378.29

(C) $k = 1.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
1.0213	0.8902	1.9115	0.1479	0.3713	1.0	1	0.90	0.80	0.75	0.60	8,717.26
1.0251	0.8859	1.9110	0.1479	0.3714	1.0	5	0.90	0.80	0.75	0.60	8,804.84
1.0297	0.8752	1.9049	0.1488	0.3722	1.0	10	0.90	0.80	0.75	0.60	8,900.25
1.0327	0.8619	1.8947	0.1504	0.3735	1.0	15	0.90	0.80	0.75	0.60	8,983.14
1.0362	0.8495	1.8857	0.1517	0.3747	1.0	20	0.90	0.80	0.75	0.60	9,058.11

(D) $k = 4.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
1.0135	0.8867	1.9002	0.1495	0.3728	4.0	1	0.90	0.80	0.75	0.60	10,550.00
1.0146	0.8853	1.8999	0.1496	0.3728	4.0	5	0.90	0.80	0.75	0.60	10,640.30
1.0158	0.8833	1.8990	0.1497	0.3729	4.0	10	0.90	0.80	0.75	0.60	10,745.20
1.0170	0.8807	1.8976	0.1499	0.3731	4.0	15	0.90	0.80	0.75	0.60	10,843.40
1.0183	0.8772	1.8955	0.1502	0.3734	4.0	20	0.90	0.80	0.75	0.60	10,936.00

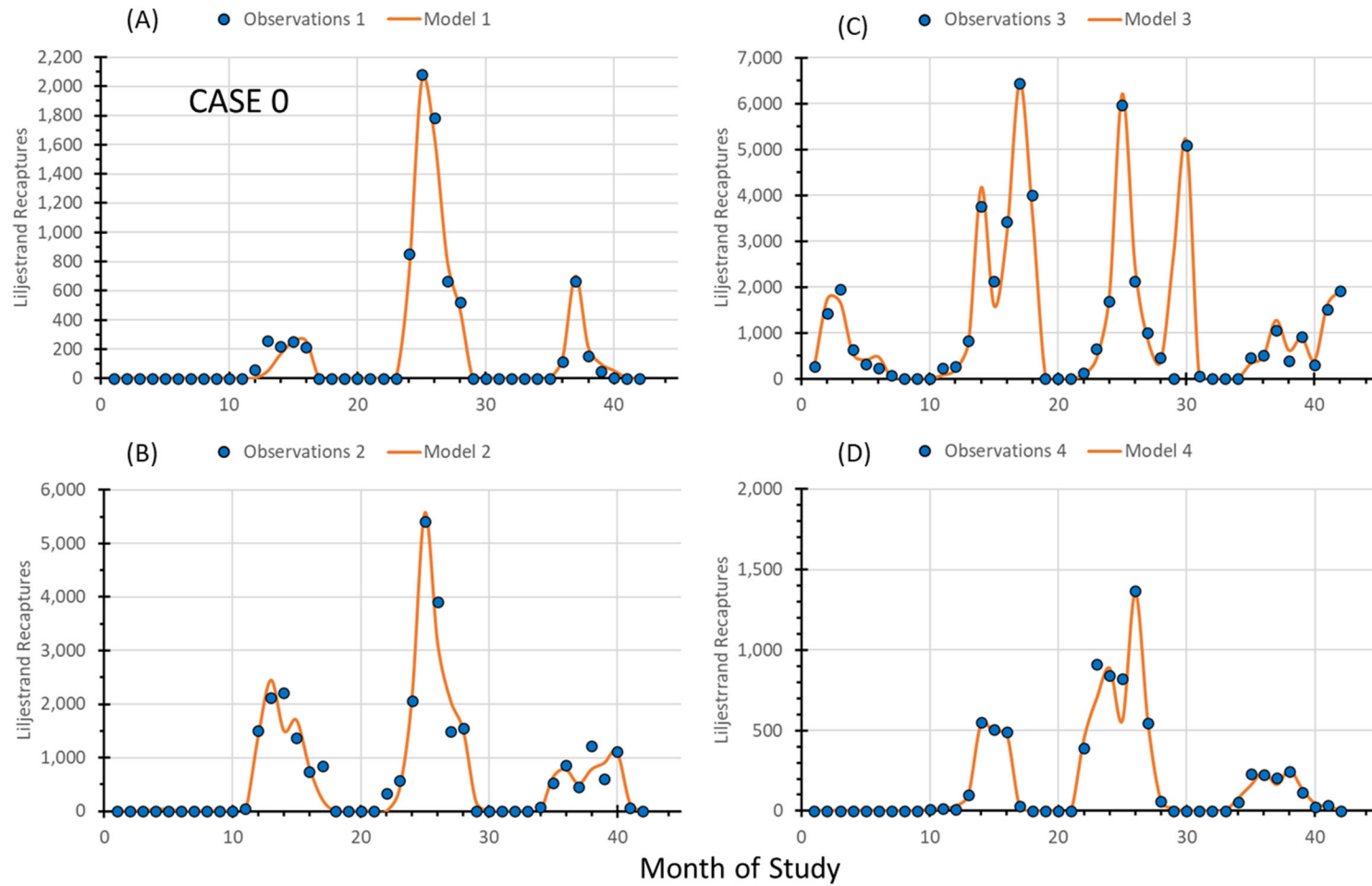


Figure 3.4.2.- Case 0.2 observed and modeled recaptures by month and region during the July 1966 to December 1969 study period: (A) region 1 (New York-New Jersey); (B) region 2 (Chesapeake Bay); (C) region 3 (North Carolina-South Carolina); and (D) region 4 (Florida-Georgia).

Table 3.4.6.- Case 1.1: Coston releases = 1,066,357; Wilberg recaptures = 94,968; ALP(Liljestrand) effort. Parameters Q_r and $\theta_{m,r}$ were estimated, and $\varepsilon_{m,r}$ were fixed.

(A) $k = 2.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
1.1547	1.1851	2.3398	0.0963	0.4769	2.5	1	0.90	0.80	0.75	0.60	9,964.93
1.1501	1.1868	2.3369	0.0966	0.4791	2.5	5	0.90	0.80	0.75	0.60	10,056.60
1.1442	1.1917	2.3360	0.0967	0.4830	2.5	10	0.90	0.80	0.75	0.60	10,160.90
1.1388	1.1966	2.3354	0.0968	0.4878	2.5	15	0.90	0.80	0.75	0.60	10,256.60
1.1345	1.2001	2.3346	0.0969	0.4919	2.5	20	0.90	0.80	0.75	0.60	10,345.10

(B) $k = 1.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
1.1519	1.1704	2.3223	0.0980	0.4752	1.5	1	0.90	0.80	0.75	0.60	9,156.44
1.1453	1.1726	2.3179	0.0985	0.4785	1.5	5	0.90	0.80	0.75	0.60	9,246.90
1.1371	1.1788	2.3159	0.0987	0.4844	1.5	10	0.90	0.80	0.75	0.60	9,347.34
1.1308	1.1837	2.3144	0.0988	0.4910	1.5	15	0.90	0.80	0.75	0.60	9,437.08
1.1278	1.1836	2.3113	0.0991	0.4966	1.5	20	0.90	0.80	0.75	0.60	9,518.84

(C) $k = 1.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
1.1515	1.1579	2.3094	0.0993	0.4727	1.0	1	0.90	0.80	0.75	0.60	8,780.49
1.1426	1.1608	2.3034	0.0999	0.4775	1.0	5	0.90	0.80	0.75	0.60	8,869.48
1.1324	1.1683	2.3007	0.1002	0.4861	1.0	10	0.90	0.80	0.75	0.60	8,965.56
1.1277	1.1694	2.2971	0.1006	0.4941	1.0	15	0.90	0.80	0.75	0.60	9,049.52
1.1276	1.1624	2.2900	0.1013	0.4992	1.0	20	0.90	0.80	0.75	0.60	9,125.92

(D) $k = 4.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
1.1601	1.1957	2.3558	0.0948	0.4766	4.0	1	0.90	0.80	0.75	0.60	11,107.30
1.1568	1.1973	2.3541	0.0950	0.4783	4.0	5	0.90	0.80	0.75	0.60	11,199.70
1.1525	1.2016	2.3541	0.0950	0.4811	4.0	10	0.90	0.80	0.75	0.60	11,306.20
1.1483	1.2058	2.3541	0.0950	0.4841	4.0	15	0.90	0.80	0.75	0.60	11,405.70
1.1446	1.2095	2.3540	0.0950	0.4872	4.0	20	0.90	0.80	0.75	0.60	11,499.20

Table 3.4.7.- Case 1.2: Coston releases = 1,066,357; Wilberg recaptures = 94,968; ALP(Liljestrand) effort. Parameters Q_r and $\theta_{m,r}$ were estimated, and $\varepsilon_{m,r}$ were adjusted.

(A) $k = 2.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.9780	0.9649	1.9430	0.1433	0.4081	2.5	1	0.90	0.80	0.75	0.60	9,801.85
0.9636	0.9944	1.9580	0.1411	0.4182	2.5	5	0.90	0.80	0.75	0.60	9,861.29
0.9582	1.0024	1.9606	0.1408	0.4223	2.5	10	0.90	0.80	0.75	0.60	9,983.17
0.9499	1.0131	1.9630	0.1404	0.4280	2.5	15	0.90	0.80	0.75	0.60	10,095.40
0.9433	1.0250	1.9683	0.1397	0.4341	2.5	20	0.90	0.80	0.75	0.60	10,199.00

(B) $k = 1.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.9681	0.9696	1.9376	0.1440	0.4114	1.5	1	0.90	0.80	0.75	0.60	9,069.31
0.9640	0.9769	1.9409	0.1436	0.4149	1.5	5	0.90	0.80	0.75	0.60	9,173.75
0.9553	0.9876	1.9428	0.1433	0.4211	1.5	10	0.90	0.80	0.75	0.60	9,291.77
0.9447	1.0045	1.9492	0.1424	0.4301	1.5	15	0.90	0.80	0.75	0.60	9,396.51
0.9387	1.0175	1.9563	0.1414	0.4385	1.5	20	0.90	0.80	0.75	0.60	9,490.77

(C) $k = 1.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.9715	0.9537	1.9252	0.1459	0.4077	1.0	1	0.90	0.80	0.75	0.60	8,746.25
0.9789	1.0153	1.9942	0.1361	0.4362	1.0	5	0.90	0.80	0.75	0.60	8,861.32
0.9520	0.9803	1.9323	0.1448	0.4222	1.0	10	0.90	0.80	0.75	0.60	8,962.07
0.9569	1.0409	1.9978	0.1356	0.4469	1.0	15	0.90	0.80	0.75	0.60	9,078.94
0.9384	1.0094	1.9477	0.1426	0.4435	1.0	20	0.90	0.80	0.75	0.60	9,144.56

(D) $k = 4.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
1.0012	0.9511	1.9524	0.1419	0.4270	4.0	1	0.90	0.80	0.75	0.60	10,726.10
0.9990	0.9585	1.9575	0.1412	0.4295	4.0	5	0.90	0.80	0.75	0.60	10,834.90
0.9963	0.9675	1.9638	0.1403	0.4326	4.0	10	0.90	0.80	0.75	0.60	10,962.30
0.9937	0.9768	1.9705	0.1394	0.4359	4.0	15	0.90	0.80	0.75	0.60	11,082.50
0.9913	0.9864	1.9777	0.1384	0.4391	4.0	20	0.90	0.80	0.75	0.60	11,196.30

Table 3.4.8.- Case 2.1: Coston releases = 1,066,357; Coston (ALP) recaptures = 102,992. ALP (SEDAR 69) effort. Parameters Q_r and $\theta_{m,r}$ were estimated, and $\varepsilon_{m,r}$ were fixed.

(A) $k = 2.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.9736	1.0856	2.0593	0.1275	0.4797	2.5	1	0.90	0.80	0.75	0.60	10,561.10
0.9704	1.0860	2.0564	0.1279	0.4817	2.5	5	0.90	0.80	0.75	0.60	10,651.30
0.9665	1.0875	2.0540	0.1282	0.4851	2.5	10	0.90	0.80	0.75	0.60	10,754.50
0.9630	1.0883	2.0513	0.1286	0.4887	2.5	15	0.90	0.80	0.75	0.60	10,849.60
0.9601	1.0879	2.0480	0.1290	0.4924	2.5	20	0.90	0.80	0.75	0.60	10,938.50

(B) $k = 1.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.9644	1.0900	2.0544	0.1282	0.4826	1.5	1	0.90	0.80	0.75	0.60	9,792.42
0.9608	1.0903	2.0511	0.1286	0.4854	1.5	5	0.90	0.80	0.75	0.60	9,881.40
0.9562	1.0916	2.0478	0.1290	0.4904	1.5	10	0.90	0.80	0.75	0.60	9,980.85
0.9527	1.0911	2.0438	0.1295	0.4958	1.5	15	0.90	0.80	0.75	0.60	10,070.80
0.9507	1.0876	2.0383	0.1302	0.5006	1.5	20	0.90	0.80	0.75	0.60	10,153.60

(C) $k = 1.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.9494	1.0962	2.0455	0.1293	0.4874	1.0	1	0.90	0.80	0.75	0.60	9,439.45
0.9497	1.0947	2.0444	0.1295	0.4899	1.0	5	0.90	0.80	0.75	0.60	9,527.60
0.9471	1.0958	2.0429	0.1297	0.4964	1.0	10	0.90	0.80	0.75	0.60	9,623.33
0.9459	1.0920	2.0379	0.1303	0.5028	1.0	15	0.90	0.80	0.75	0.60	9,708.31
0.9464	1.0833	2.2097	0.1314	0.5076	1.0	20	0.90	0.80	0.75	0.60	9,786.10

(D) $k = 4.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.9790	1.0815	2.0605	0.1274	0.4773	4.0	1	0.90	0.80	0.75	0.60	11,649.60
0.9766	1.0822	2.0588	0.1276	0.4789	4.0	5	0.90	0.80	0.75	0.60	11,740.50
0.9737	1.0839	2.0576	0.1278	0.4813	4.0	10	0.90	0.80	0.75	0.60	11,845.80
0.9709	1.0852	2.0561	0.1279	0.4839	4.0	15	0.90	0.80	0.75	0.60	11,944.60
0.9685	1.0859	2.0544	0.1282	0.4865	4.0	20	0.90	0.80	0.75	0.60	12,037.80

Table 3.4.9.- Case 2.2: Coston releases = 1,066,357; Coston (ALP) recaptures = 102,992. ALP (SEDAR 69) effort. Parameters Q_r and $\theta_{m,r}$ were estimated, and $\varepsilon_{m,r}$ were adjusted.

(A) $k = 2.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.8200	0.9890	1.8091	0.1638	0.4387	2.5	1	0.90	0.80	0.75	0.60	10,287.90
0.8183	0.9976	1.8159	0.1627	0.4425	2.5	5	0.90	0.80	0.75	0.60	10,381.60
0.8165	1.0083	1.8248	0.1613	0.4470	2.5	10	0.90	0.80	0.75	0.60	10,489.60
0.8389	1.0301	1.8690	0.1543	0.4461	2.5	15	0.90	0.80	0.75	0.60	10,674.50
0.8363	1.0404	1.8766	0.1531	0.4523	2.5	20	0.90	0.80	0.75	0.60	10,665.70

(B) $k = 1.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.8513	0.9897	1.8410	0.1587	0.4285	1.5	1	0.90	0.80	0.75	0.60	9,633.65
0.8237	0.9957	1.8193	0.1621	0.4428	1.5	5	0.90	0.80	0.75	0.60	9,731.22
0.8434	1.0196	1.8630	0.1552	0.4432	1.5	10	0.90	0.80	0.75	0.60	9,826.72
0.8395	1.0341	1.8736	0.1536	0.4522	1.5	15	0.90	0.80	0.75	0.60	9,918.69
0.8366	1.0449	1.8815	0.1524	0.4608	1.5	20	0.90	0.80	0.75	0.60	10,002.50

(C) $k = 1.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.8561	0.9837	1.8398	0.1589	0.4271	1.0	1	0.90	0.80	0.75	0.60	9,341.85
0.8513	1.0009	1.8523	0.1589	0.4355	1.0	5	0.90	0.80	0.75	0.60	9,431.36
0.8456	1.0228	1.8684	0.1544	0.4475	1.0	10	0.90	0.80	0.75	0.60	9,529.27
0.8415	1.0378	1.8793	0.1527	0.4590	1.0	15	0.90	0.80	0.75	0.60	9,614.86
0.8386	1.0506	1.8892	0.1512	0.4702	1.0	20	0.90	0.80	0.75	0.60	9,691.71

(D) $k = 4.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.8172	0.9942	1.8113	0.1634	0.4393	4.0	1	0.90	0.80	0.75	0.60	11,192.20
0.8161	1.0005	1.8166	0.1626	0.4419	4.0	5	0.90	0.80	0.75	0.60	11,286.60
0.8149	1.0083	1.8231	0.1615	0.4452	4.0	10	0.90	0.80	0.75	0.60	11,396.80
0.8140	1.0161	1.8300	0.1604	0.4486	4.0	15	0.90	0.80	0.75	0.60	11,500.20
0.8378	1.0360	1.8738	0.1535	0.4471	4.0	20	0.90	0.80	0.75	0.60	11,574.40

Table 3.4.10.- Case 3.1: Schueller releases = 768,877 & recaptures = 93,335; ALP(SEDAR 69) effort. Parameters Q_r and $\theta_{m,r}$ were estimated, and $\varepsilon_{m,r}$ were fixed.

(A) $k = 2.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.5557	1.3697	1.9254	0.1458	0.5800	2.5	1	0.90	0.80	0.75	0.60	7,732.66
0.5526	1.3809	1.9336	0.1446	0.5850	2.5	5	0.90	0.80	0.75	0.60	7,818.48
0.5428	1.4050	1.9478	0.1426	0.5964	2.5	10	0.90	0.80	0.75	0.60	7,908.73
0.5415	1.4156	1.9571	0.1413	0.6040	2.5	15	0.90	0.80	0.75	0.60	7,988.84
0.5407	1.4196	1.9603	0.1408	0.6101	2.5	20	0.90	0.80	0.75	0.60	8,063.99

(B) $k = 1.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.5622	1.3714	1.9336	0.1446	0.5832	1.5	1	0.90	0.80	0.75	0.60	7,270.13
0.5579	1.3941	1.9520	0.1420	0.5922	1.5	5	0.90	0.80	0.75	0.60	7,352.58
0.5480	1.4110	1.9591	0.1410	0.6043	1.5	10	0.90	0.80	0.75	0.60	7,435.30
0.5467	1.4145	1.9612	0.1407	0.6123	1.5	15	0.90	0.80	0.75	0.60	7,510.57
0.5462	1.4116	1.9578	0.1412	0.6187	1.5	20	0.90	0.80	0.75	0.60	7,580.77

(C) $k = 1.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.5682	1.3864	1.9547	0.1416	0.5884	1.0	1	0.90	0.80	0.75	0.60	7,085.62
0.5547	1.4037	1.9585	0.1411	0.5989	1.0	5	0.90	0.80	0.75	0.60	7,163.74
0.5522	1.4112	1.9634	0.1404	0.6099	1.0	10	0.90	0.80	0.75	0.60	7,242.88
0.5512	1.4076	1.9589	0.1410	0.6184	1.0	15	0.90	0.80	0.75	0.60	7,314.41
0.5512	1.3968	1.9480	0.1426	0.6246	1.0	20	0.90	0.80	0.75	0.60	7,380.75

(D) $k = 4.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.5358	1.3858	1.9216	0.1464	0.5825	4.0	1	0.90	0.80	0.75	0.60	8,500.91
0.5399	1.3864	1.9263	0.1457	0.5835	4.0	5	0.90	0.80	0.75	0.60	8,526.82
0.5423	1.3866	1.9289	0.1453	0.5854	4.0	10	0.90	0.80	0.75	0.60	8,618.52
0.5365	1.4029	1.9394	0.1438	0.5940	4.0	15	0.90	0.80	0.75	0.60	8,703.24
0.5352	1.4159	1.9511	0.1421	0.6011	4.0	20	0.90	0.80	0.75	0.60	8,783.43

Table 3.4.11.- Case 3.2: Schueller releases = 768,877 & recaptures = 93,335; ALP(SEDAR 69) effort. Parameters Q_r and $\theta_{m,r}$ were estimated, and $\varepsilon_{m,r}$ were adjusted.

(A) $k = 2.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.5500	1.1038	1.6538	0.1913	0.7131	2.5	1	0.90	0.80	0.75	0.60	7,653.71
0.5491	1.1028	1.6529	0.1917	0.7154	2.5	5	0.90	0.80	0.75	0.60	7,742.12
0.5454	1.1079	1.6533	0.1914	0.7207	2.5	10	0.90	0.80	0.75	0.60	7,842.15
0.5422	1.1129	1.6551	0.1911	0.7270	2.5	15	0.90	0.80	0.75	0.60	7,933.46
0.5403	1.1165	1.6568	0.1907	0.7333	2.5	20	0.90	0.80	0.75	0.60	8,018.44

(B) $k = 1.5$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.5551	1.1017	1.6568	0.1908	0.7048	1.5	1	0.90	0.80	0.75	0.60	7,258.77
0.5534	1.0991	1.6525	0.1916	0.7082	1.5	5	0.90	0.80	0.75	0.60	7,345.29
0.5484	1.1058	1.6542	0.1912	0.7164	1.5	10	0.90	0.80	0.75	0.60	7,440.82
0.5453	1.1108	1.6561	0.1909	0.7250	1.5	15	0.90	0.80	0.75	0.60	7,526.66
0.5447	1.1125	1.6572	0.1907	0.7327	1.5	20	0.90	0.80	0.75	0.60	7,605.99

(C) $k = 1.0$

M	F	Z	S	E	k	v	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.5618	1.0929	1.6547	0.1912	0.6982	1.0	1	0.90	0.80	0.75	0.60	7,097.95
0.5543	1.1070	1.6613	0.1899	0.7050	1.0	5	0.90	0.80	0.75	0.60	7,182.57
0.5504	1.1066	1.6570	0.1907	0.7154	1.0	10	0.90	0.80	0.75	0.60	7,272.85
0.5487	1.1093	1.6581	0.1905	0.7257	1.0	15	0.90	0.80	0.75	0.60	7,353.81
0.5504	1.1069	1.6573	0.1907	0.7341	1.0	20	0.90	0.80	0.75	0.60	7,428.28

(D) $k = 4.0$

M	F	Z	S	E	k	V	$1 - G_1$	$1 - G_2$	$1 - G_3$	$1 - G_4$	negLL
0.5564	1.3074	1.8639	0.1551	0.6037	4.0	1	0.90	0.80	0.75	0.60	8,428.08
0.5456	1.1093	1.6549	0.1911	0.7226	4.0	5	0.90	0.80	0.75	0.60	8,310.34
0.5429	1.1131	1.6560	0.1909	0.7263	4.0	10	0.90	0.80	0.75	0.60	8,413.65
0.5402	1.1172	1.6574	0.1906	0.7308	4.0	15	0.90	0.80	0.75	0.60	8,509.18
0.5668	1.2499	1.8167	0.1626	0.6530	4.0	20	0.90	0.80	0.75	0.60	8,728.95

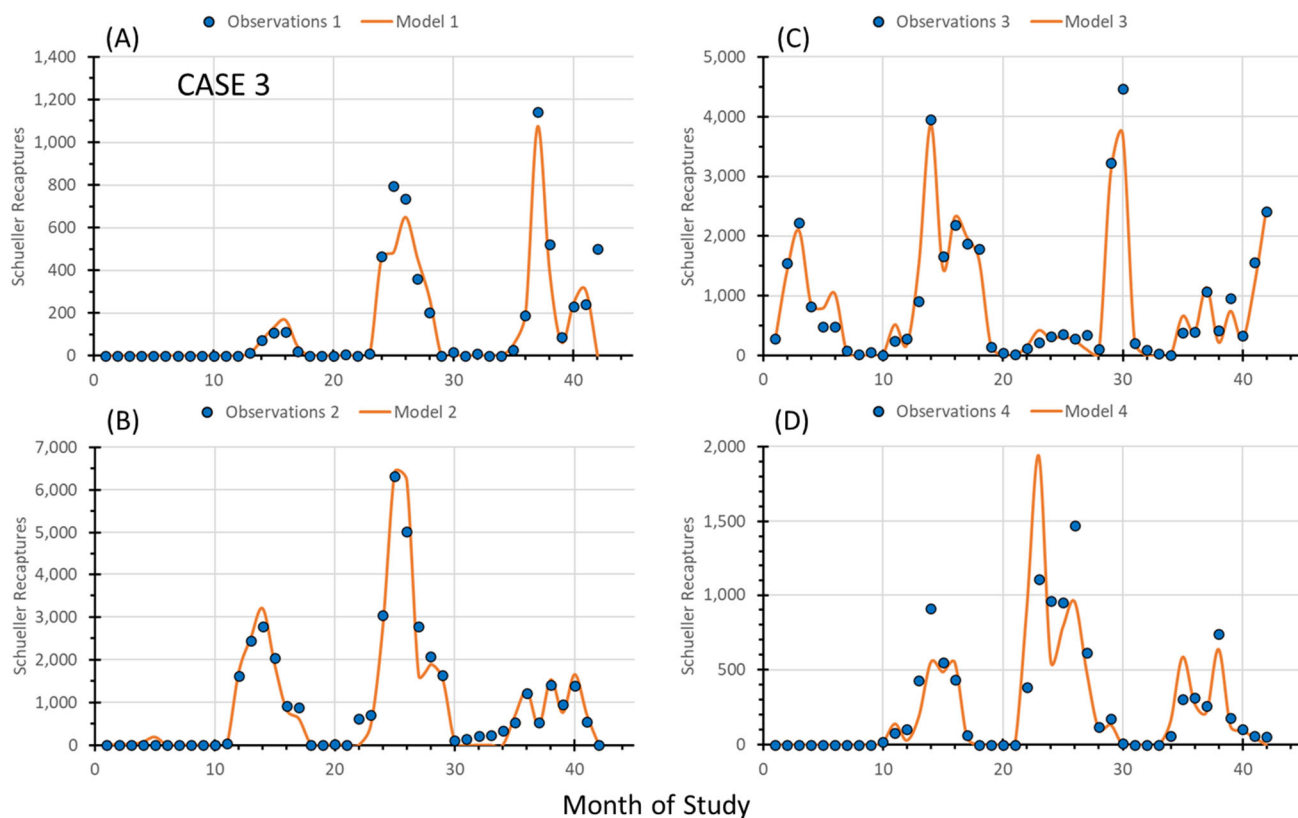


Figure 3.4.3.- Case 3.2 observed and modeled recaptures by month and region during the July 1966 to December 1969 study period: (A) region 1 (New York-New Jersey); (B) region 2 (Chesapeake Bay); (C) region 3 (North Carolina-south Carolina); and (D) region 4 (Florida-Georgia).

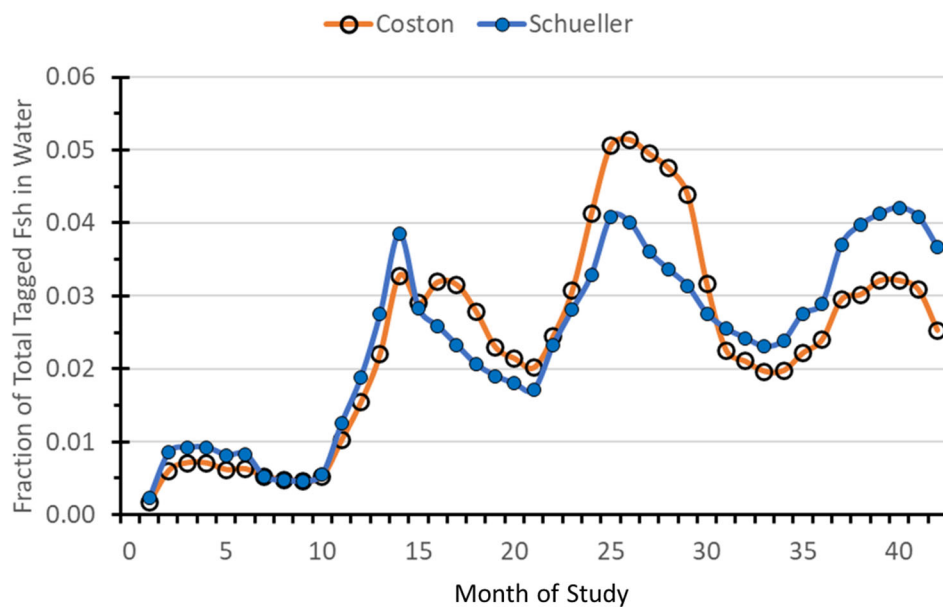


Figure 3.4.4.- Comparison of the modeled fraction of the sum of total tagged menhaden in the water relative to month of study for the Coston (1971) data from Case 2 and the Schueller (2022) data from Case 3. Notice the high correlation between estimated tags in the water between modeled data sets.

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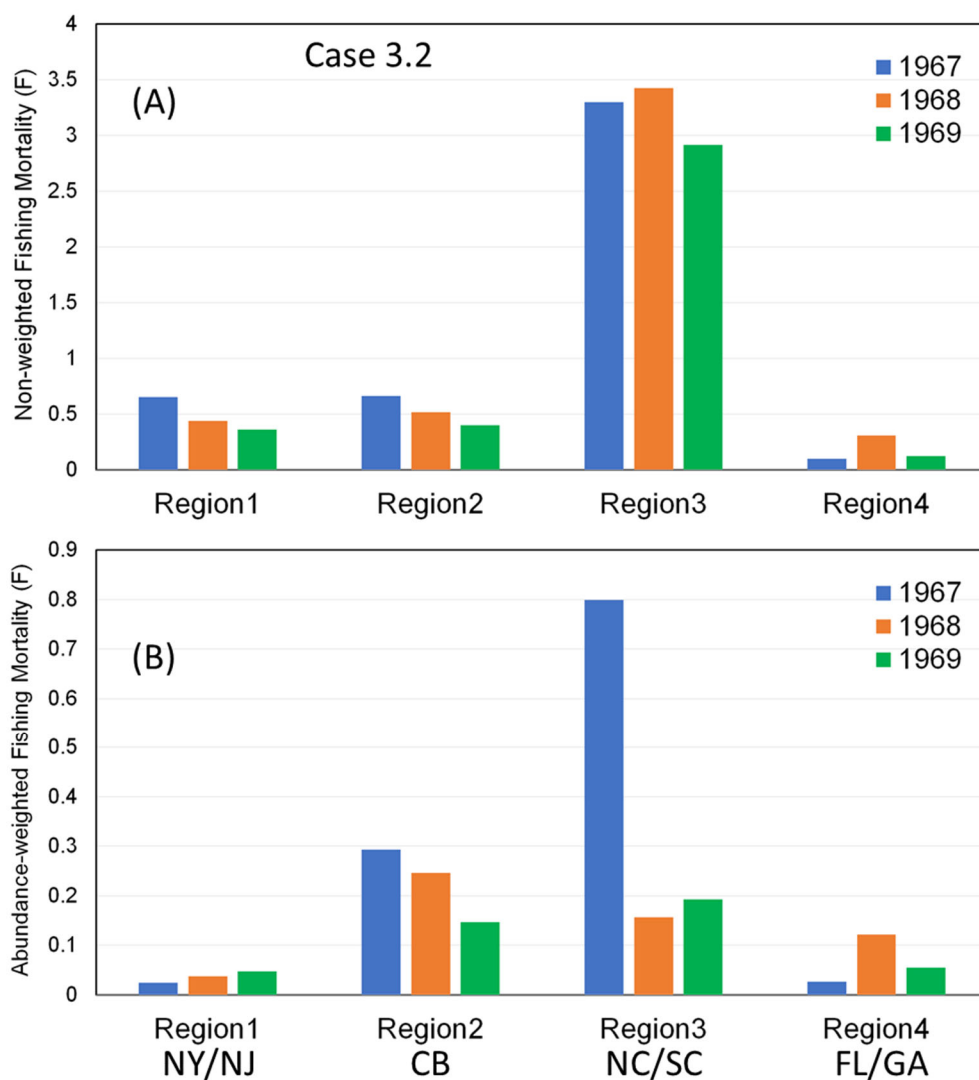


Figure 3.4.5.- Distribution of fishing mortality by region by year from Case 3.2. With the exception of region 3 in 1967, fishing mortality was generally comparable in regions over years.

3.5 Results & Interpretation

The NMFS Atlantic menhaden tagging program conducted from 1966-1971 and its resultant data have made major contributions to scientific knowledge of the species' biology, migration, demographics and population dynamics. In the 20th century, returns from the adult tagging program provided documentation for generating hypotheses of Atlantic menhaden stock structure and migratory patterns (Ahrenholz 1991). In addition, over the year estimates of natural mortality (\hat{M}) from these same mark-recapture data were published by a number of investigators (**Table 3.3.1**). Since about the mid-1980s, these data and results have provided necessary demographic parameters to support stock assessment analyses (Reish et al. 1985, Nelson and Ahrenholz 1986, Ahrenholz et al. 1987, SEDAR 3, SEDAR 20, SEDAR 40, SEDAR 69).

This current study provided a re-evaluation of these NMFS tagging data to evaluate previous conclusion and improve understanding Atlantic menhaden population demographics, and to build confidence in the data that supports the population demographics estimates incorporated into Atlantic menhaden stock assessments. To do so, a range of data sources and modeling methods were employed. A summary of the demographic modeling results from the current study are shown in **Table 3.5.1**.

There was general agreement in our analyses with the natural mortality rate estimates obtained in earlier studies (**Table 3.3.1**). The modeling results obtained in the sensitivity analyses of Cases 2 and 3 (**Tables 3.4.8-3.4.11**) strongly suggested the need to revise (lower) the estimate of natural mortality to about $\hat{M} = 0.55$. The range of feasible estimates of natural mortality and survivorship were consistent among the various methods we applied.

There are obvious consequences for Atlantic menhaden stock assessment. Lowering of the M estimate and apparent increases in the relative magnitude of F will likely have the following impacts: (1) increased survivorship with decreased \hat{M} ; and, (2) shift in the composition of spawning stock biomass (SSB) to older (mature) ages. The $\hat{M} = 1.176$ reported by Liljestrand et al. (2019), the highest estimate to date, and used in the recent stock assessment (SEDAR 69 2019) required that stock biomass be about 3.2 times greater to achieve equivalent yields as compared to the $\hat{M} = 0.55$ obtained in this study. Additionally, the higher M rate also requires that recruitment (R_0 , addition of the youngest age class to the stock each year) be 29.3 times greater. At the higher rate of natural mortality, fishing has little apparent impact. On the other hand, fishing will likely have substantially greater stock impact with the lowered \hat{M} .

To get an even more balanced estimate of menhaden demographic rates, a logical complimentary extension of these current analyses would be to include recapture data from the "Schueller" 1966-1969 release batches that were subsequently recaptured in the 1970-1971 time frame, outside the 1966-1969 period of this analysis. This temporal extension would add another 9,255 recaptures to inflate the 1966-1969 recaptures to 102,566 (**Table 2.2.6F**), an increase of about 9.92% recaptures. This, of course, would require a 12-month addition to the "Liljestrand" model for analysis. It is likely that \hat{M} may be further decreased.

Table 3.5.1.- Summary of demographic modeling results for Atlantic menhaden.

[illegible]

4.0 References

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This report addresses the ASMFC’s SAS M workgroup’s request, dated February 12, 2025, for a detailed description of our Stepwise method used to estimate magnet efficiencies (MEs). This report also compares this method to the “Constant” and “MEs as parameters” approaches. The results from these analyses were then incorporated into a comprehensive evaluation of the two Atlantic menhaden mark-recapture databases to derive the best estimate of the natural mortality rate (M) for the species. We concluded that $M = 0.52$ is the best estimate of the annual natural mortality rate for Atlantic menhaden.

I. Constant Average Plant and Area Magnet Efficiencies (ϵ_{ta})

Appropriate use of the Coston (1971) data required establishment of a quantitative definition of what constituted “primary” magnets. Because NMFS data for 1966 completely overlapped with the releases given in Coston, we were able to determine that recovery stations 1 and 2 should be defined as “primary magnets (p12)” in the “Plant Test” database, aligning perfectly with the reported recaptures in the Coston (1971) technical report. Determination of plant and area magnet efficiencies during 1966-1971 was accomplished through analysis of 964 batch trials conducted at 19 processing plants in 4 geographical areas (**Table S1**; note: no batch trials were conducted at plant #8), as was done by the ASMFC SAS M workgroup. Each batch trial consisted of release of approximately 100 known tagged menhaden into vessel catches received at the respective plants. The fraction of the known tags recovered was assessed for each batch according to two different magnet configurations relative to the database being analyzed: (1) Coston data required only “primary magnets (p12 -- recovery stations 1 and 2)”; while, (2) NMFS data used “all magnets” (all recovery stations). Comparisons of magnet efficiencies by plants and areas for the two databases are shown in **Fig. I.1**.

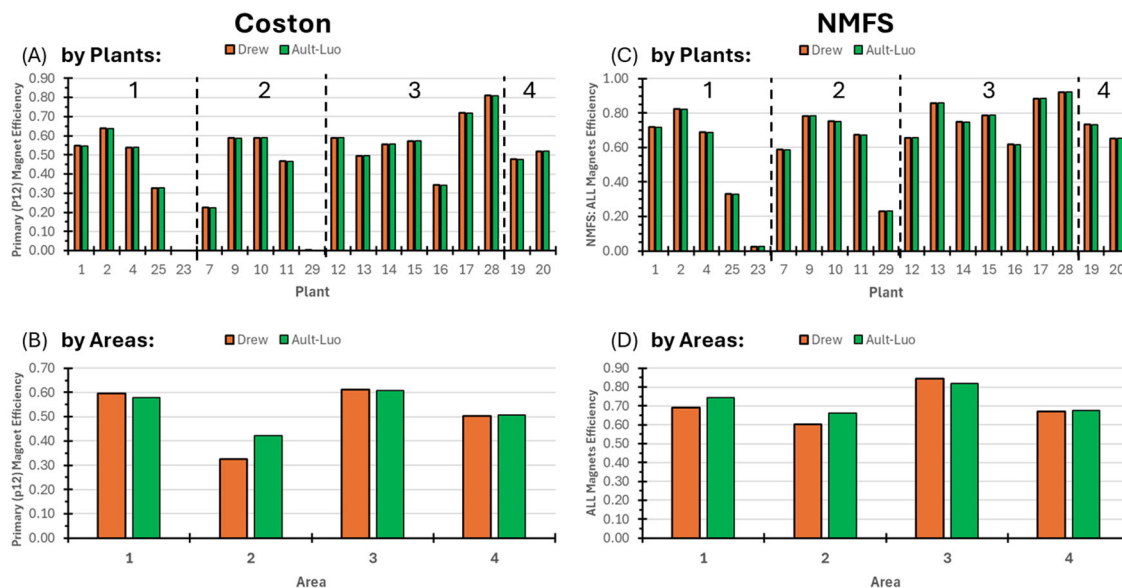


Figure I.1.- Average tag recovery magnet efficiencies over 1966-1971 at 19 reduction plants and four geographic areas for the two principal data sources: (A-B) “primary” magnets for Coston; and (C-D) “all” magnets for NMFS.

For the two data sources, average ME estimates were equivalent by plants (**Figs. I.1 A & C**); and, area averages were only marginally different due to the catch weighting of coefficients by ASMFC. However, inspection of the statistical distributions of magnet efficiencies for all plants and areas combined shows these data are not normally distributed and are not well represented by the arithmetic mean as the central value of these data; nor are they either by individual plants or areas (**Figs. I.2-I.4**).

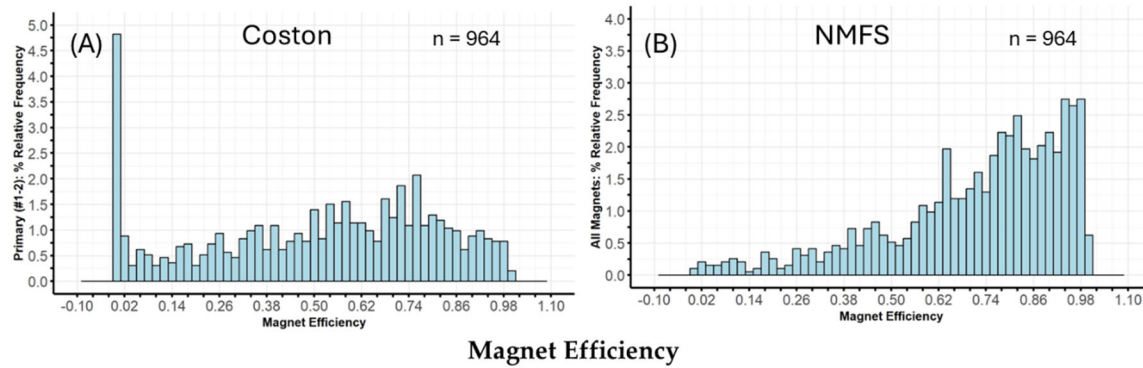


Figure I.2.- Distributions of combined magnet efficiencies for all plants and areas from 964 batch trials: (A) “primary” magnets (recovery stations 1 and 2) relevant to the Coston data; and (B) “all” magnets (all plant recovery stations) relevant to the NMFS data.

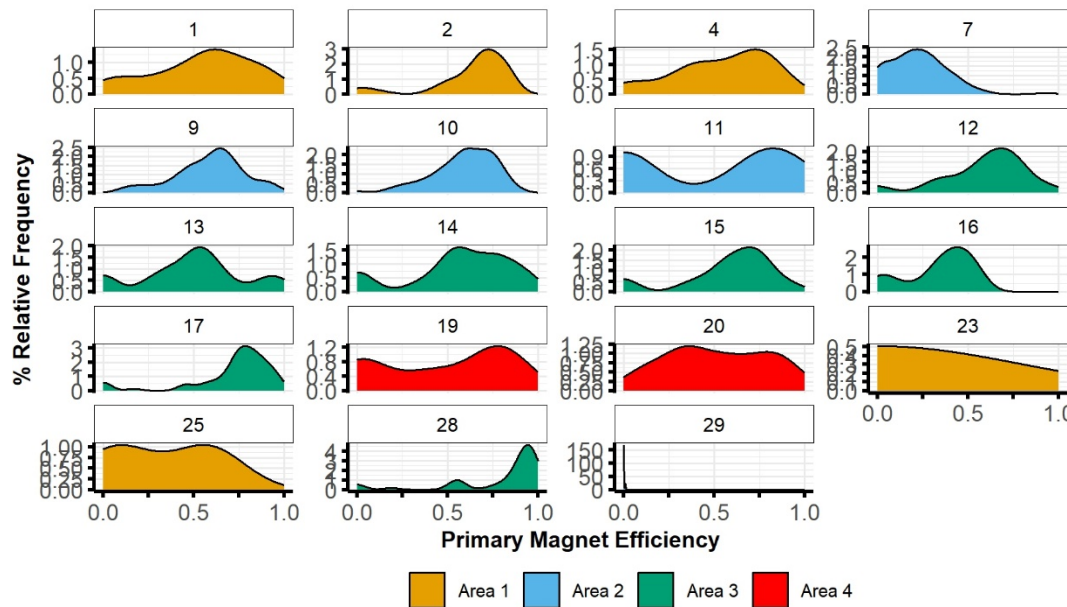


Figure I.3.- Plant-specific distributions of individual batch trial magnet efficiencies for “primary” (p12) magnets at 19 Atlantic menhaden reduction plants contained within four geographical areas (see **Table S1**) during 1966-1971.

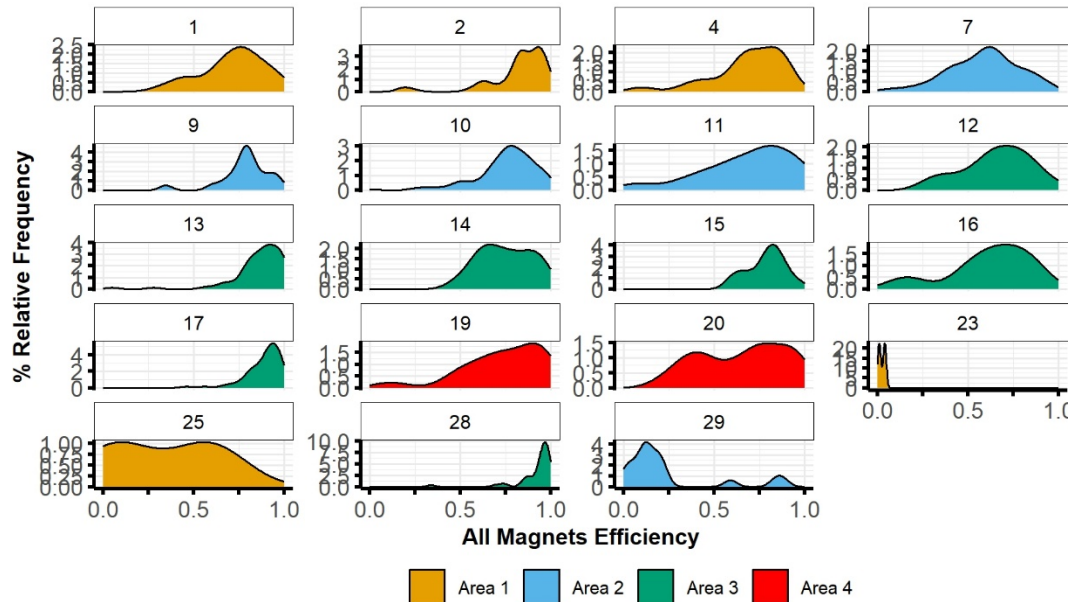


Figure I.4.- Plant-specific distributions of individual batch trials of magnet efficiencies for “ALL” magnets at 19 Atlantic menhaden reduction processing plants contained within four geographical areas (see **Table S1**) during 1966-1971.

Figs. I.2-I.4 each clearly show that the combined and individual magnet efficiency data were apparently distributed as uniform random variables ranging between 0 and 1, i.e., $U(0,1)$. A "uniform distribution" means all possible outcomes in the range have an equal probability of occurring.

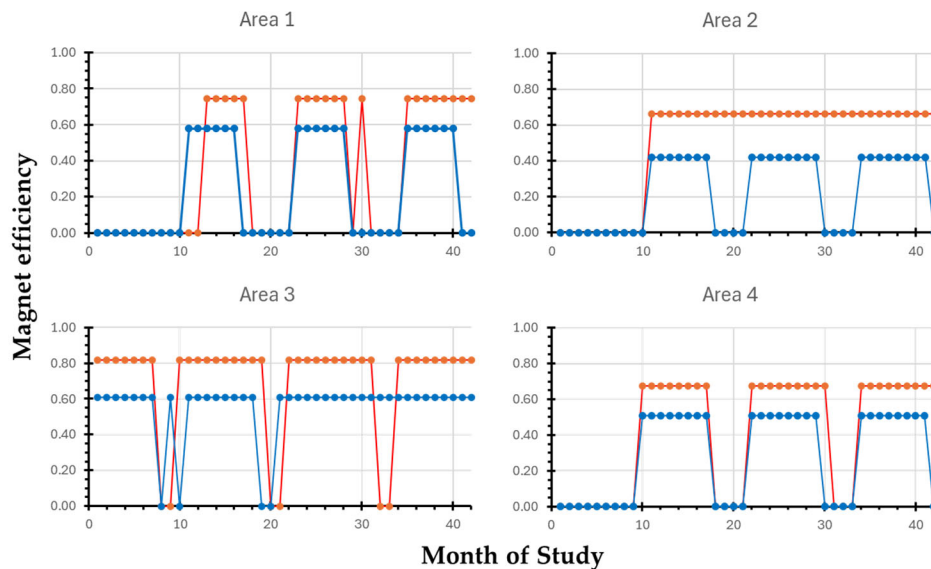


Figure I.5.- Temporal distribution of area averaged estimates of magnet efficiency within 4 geographical Areas over the 42 month (July 1966-December 1969) study. MEs are applied during months when recaptures were observed. Coston (p12) averages (blue closed dots) are from **Fig. I.1B**; while NMFS (all recovery stations) averages (red closed dots) are from **Fig. I.1D**.

In the null “Constant” modeling approach, Area averages were used by the SAS as monthly inputs by area for the estimated magnet efficiency matrix if recoveries were observed in that Area. However, given the uniform distributions of magnet efficiencies by plants, areas and all plants and areas combined, the Area mean is a poor descriptor of the underlying data.

As such, single run mean assessments were run. If the model converged, then and MCMC run of 4,000,000 trials was conducted to establish the mean and standard error of the estimated natural mortality parameter.

II. Stepwise Analysis of Magnet Efficiencies ($\varepsilon_{t,a}$)

Recoveries (theoretical catch of tagged cohorts of menhaden) for each month t and area a of tagged cohorts ($C_{T,A,t,a}$) is the product of the unknown time and area-specific tagged fish abundance, $N_{T,A,t,a}$, the proportion of mortality due to fishing $F_{t,a}$ and natural M causes, and the time and area specific plant magnet efficiency rate $\varepsilon_{t,a}$.

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

The Stepwise procedure is conducted as follows:

Step 0: Input the matrix of “Constant” average “primary” magnet efficiencies $[\hat{\varepsilon}_{0,t,a}]$ determined in the Section I analyses for each area a ($a = 1, \dots, 4$) and month t ($t = 1, \dots, 42$). Input these values and conduct a single run, letting the model estimate recaptures $C_0(t, a)$ according to Eq. (1).

Simple rearrangement of Eq. (1) produces a mean area-time estimate of magnet efficiency $\hat{\varepsilon}_{t,a}$.

$$\hat{\varepsilon}_{1,t,a} = \frac{\text{Observed } C_{t,a}}{N_{t,a} \frac{F_{t,a}}{(F_{t,a}+M)} (1 - e^{-(F_{t,a}+M)})} = \frac{\text{Observed } C_{t,a}}{\hat{C}_0(t,a)} \quad (2)$$

where,

$$\hat{C}_0(t, a) = N_{t,a} \frac{F_{t,a}}{(F_{t,a}+M)} (1 - e^{-(F_{t,a}+M)}) \quad (3)$$

The denominator of Eq. (2) is calculated internally in the model through sequencing tagged cohorts released over time in the 4 areas, resulting in an updated estimate of magnet efficiency.

Step 1: Use the theoretical numbers of tagged fish (Eq. 1) from Step 0, or “actual unknown” recaptures $(\hat{C}_0(t, a))$, without application of $\hat{\varepsilon}_{1,t,a}$, to re-estimate magnet efficiencies as: $\hat{\varepsilon}_{1,t,a} = \text{Observed } C_{t,a} / \hat{C}_0(t, a)$. Use these adjusted $\hat{\varepsilon}_{1,t,a}$ values as magnet efficiency parameters.

Additionally, minimum and maximum limits on the area-specific estimates of magnet efficiencies ($\hat{\epsilon}_{t,a}$) were set to range between 0.10 – 0.98 for “primary” magnet when using the Coston data. This constraint was reduced to 0.20 – 0.98 for “all” (all recovery stations) when using NMFS data. Upon model convergence, the new matrix of magnet efficiencies $[\hat{\epsilon}_{S_{t,a}}]$ was used in the Stepwise analysis process.

Step 2: Use Step 1’s theoretical catch of tagged fish $(\hat{C}_1(t, a))$ to re-estimate magnet efficiencies $[\hat{\epsilon}_{1_{t,a}}]$ and use as Step 2 model inputs.

The Akaike Information Criterion (AIC) was the estimator of prediction error and thereby relative quality of the statistical models for the given sets of data. Given a collection of models for a given set of data, AIC estimates the quality of each model, relative to each of the other models. Thus, AIC provides an objective means for model selection.

$$AIC = -2\ln(L) + 2K \quad (4)$$

Where, $K \equiv$ number of estimated parameters in the model; and, $L \equiv$ maximum value of the likelihood function for the model. A lower AIC indicates a better fit and thus better model.

Step 3+: Continue stepwise procedure outlined above until an objective stopping criterion is met.

Step	\hat{M}	neg(LL)	\hat{R}	R	Δ	AIC
0	0.8963	10,579	195,603	102,992	92,611	21,370
1	0.7289	9,795	143,697	102,992	40,705	19,802
2	0.6891	9,777	100,340	102,992	-2,652	19,766
3	0.5956	9,744	97,346	102,992	-5,646	19,700
4	0.5149	9,751	96,422	102,992	-6,570	19,714
5	0.4406	9,763	96,044	102,992	-6,948	19,738
6	0.3790	9,773	95,753	102,992	-7,239	19,758
7	0.3243	9,784	95,569	102,992	-7,423	19,780

Table II.1.- Stepwise analysis of the Coston data. Symbols are: $\hat{M} \equiv$ estimated annual natural mortality rate; neg(LL) \equiv model’s negative log-likelihood; $\hat{R} \equiv$ total estimated recaptures by the model; ; R \equiv observed total recaptures; $\Delta \equiv$ difference between predicted and observed recaptures; AIC \equiv Akaike Information Criterion.

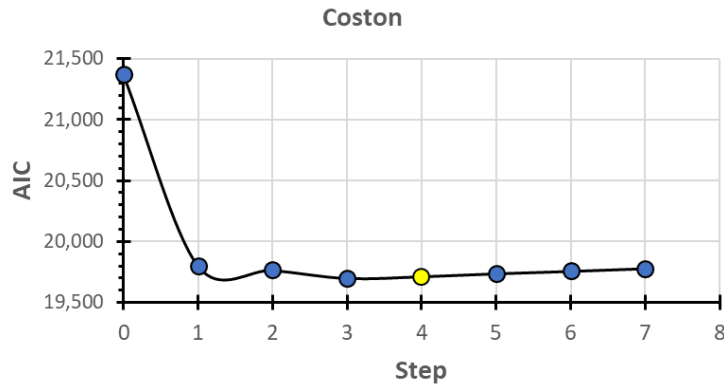


Figure II.1.- AIC reduction using the Stepwise iterative procedure for the Coston data. Minimum AIC was identified as Step 4.

Stepwise analysis for the NMFS data showed a minimum AIC in Step 7 (**Table II.2 & Fig. II.2**).

Step	\hat{M}	neg(LL)	\hat{R}	R	Δ	AIC
0	0.8909	8,044	133,279	93,335	39,944	16,300
1	0.8174	7,532	94,784	93,335	1,449	15,276
2	0.7737	7,500	88,188	93,335	-5,147	15,212
3	0.6938	7,505	95,008	93,335	1,673	15,222
4	0.6564	7,515	95,649	93,335	2,314	15,242
5	0.6294	7,519	95,962	93,336	2,626	15,250
6	0.5609	7,405	113,129	93,337	19,792	15,022
7	0.5279	7,372	107,830	93,338	14,492	14,956
8	0.4863	7,373	108,519	93,339	15,180	14,958
9	0.4498	7,377	108,746	93,340	15,406	14,966

Table II.2.- Stepwise analysis of the NMFS data. Symbols are: \hat{M} \equiv estimated annual natural mortality rate; neg(LL) \equiv model's negative log-likelihood; \hat{R} \equiv total estimated recaptures by the model; R \equiv observed total recaptures; Δ \equiv difference between predicted and observed recaptures; AIC \equiv Akaike Information Criterion.

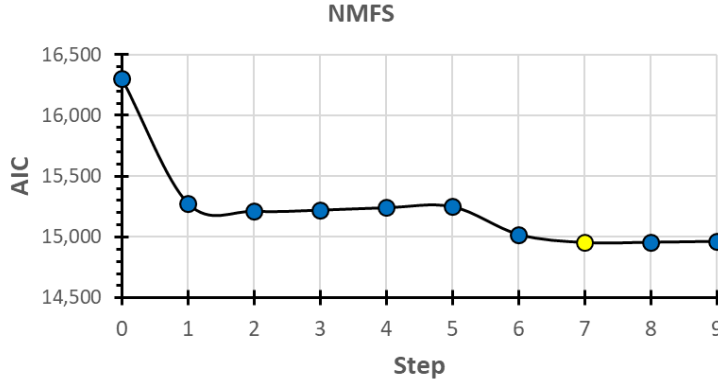


Figure II.2.- AIC reduction using the Stepwise iterative procedure for the NMFS data. Minimum AIC was identified as Step 7.

III. Magnet Efficiencies ($\epsilon_{t,a}$) as Model Parameters

The probability distribution of estimated plant time-area magnet efficiencies closely resembled a uniform random distribution $U(0, 1)$ (**Fig. III.1**), and was not well represented by the average across all plants and areas over years. Thus, another reasonable method was to estimate magnet efficiencies $\hat{\epsilon}_{t,a}$ by area and time $\hat{\epsilon}_{t,a}$ by treating them as model parameters, done in the same way that the theta parameters (catchability $\Theta_{t,a}$) are already estimated in the model. To this end, we modified the model code to allow magnet efficiencies $\hat{\epsilon}_{t,a}$ to be estimated as model parameters. The number (n) of non-zero recapture elements by area and time was used to determine the number of $\hat{\epsilon}_{1-n}$ parameters, which map to the $[\hat{\epsilon}_{0,t,a}]$ matrix. We employed a way similar to how the theta parameters were estimated as the natural log of theta, $\ln(\Theta)$, in the model, the log of magnet efficiencies, $\ln(\hat{\epsilon}_{1-n})$, that were estimated in the model. We also constrained the log-parameter boundary to range from -3.5 to -0.05 for the Coston data, and from -2.0 to -0.05 for the NMFS data. The number of non-zero recaptures elements in Coston data is 100; thus, when estimating magnet efficiencies we have additional 106 parameters that needed to be estimated by the model, that is, a total of 206 parameters for the model. The model input data of releases and recaptures creates a matrix of:

$$\text{Months tagged} \times \text{Areas} \times \text{Months recaptured} \times \text{Areas} = 42 \times 4 \times 42 \times 4 = 28,224 \text{ d. f.}$$

For a total of 28,224 data points. Thus, the degrees of freedom are not significantly affected by the increase of 106 parameters to estimate time-area magnet efficiencies

$$28,224 - 106 = 28,118 \text{ d. f.}$$

IV. Summary

Results of these analyses are summarized graphically for the three model types and two data sources as comparative single model fits of observed data for the “Constant” (Figs. IV.1A-C), “Stepwise” (Figs. IV.1B-E) and “Parameters estimated” (Figs. IV.1C-F) methods for the Coston (left panels) and NMFS (right panels) data. The observed model fits to data are superior for both Stepwise and Parameter methods as compared to the Constant method.

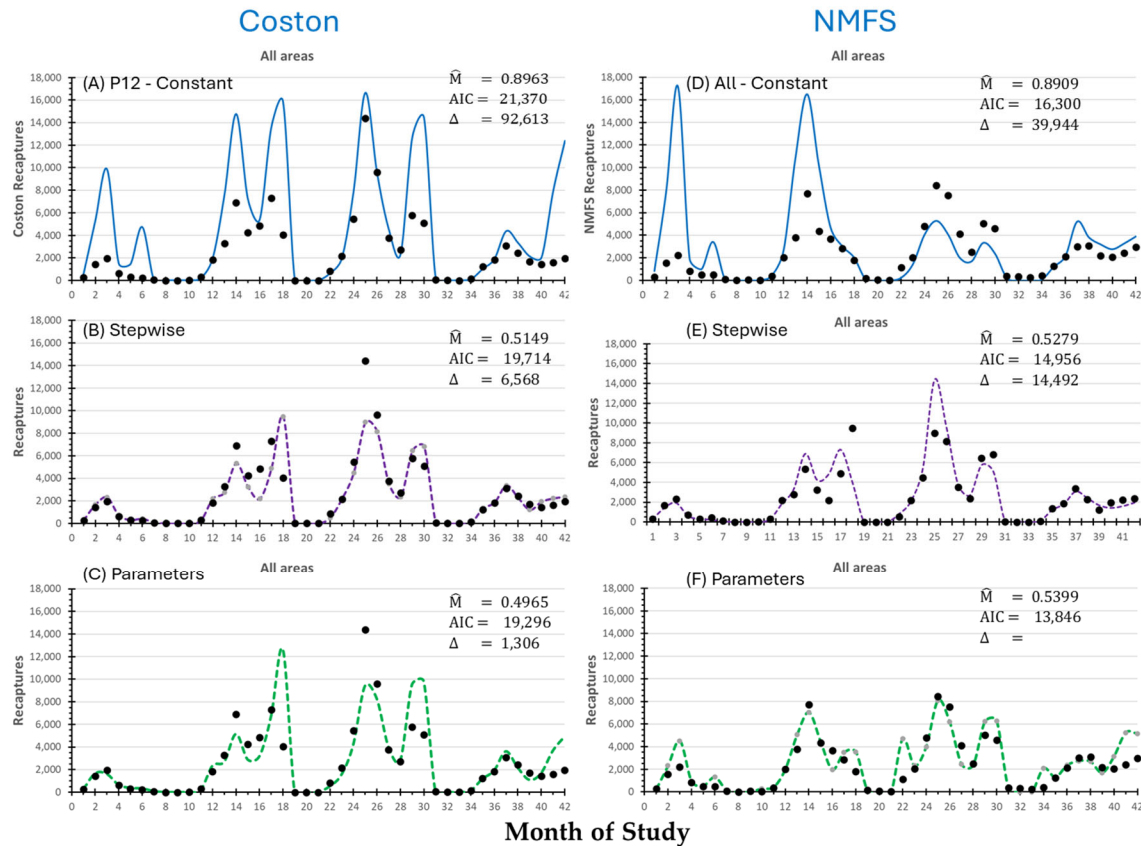


Figure IV.1.- Summary visualizations of single run results for the two data sources: **Coston:** (A) primary magnets with constant ME coefficients; (B) stepwise analysis (Step #4); (C) ME parameters estimated by model. **NMFS:** (D) all magnets with constant ME coefficients; (E) stepwise analysis (Step #7); (F) ME parameters estimated by model.

Given that all three models converged, MCMC analyses, each consisting of 4,000,000 trials, were completed (Fig. IV.2). While the unconstrained case for the ME parameter estimation was exploratory, it did produce an estimate of natural mortality lower than what we expected, and further, what we would probably consider to be unrealistic. In contrast, placing realistic constraints on the ME estimates marginally increased the AIC (Coston about +0.43%; NMFS about +1.8%), but significantly increased the value of M (Coston about +68.2%; NMFS about +83.6%) (Tables IV.1 & IV.2).

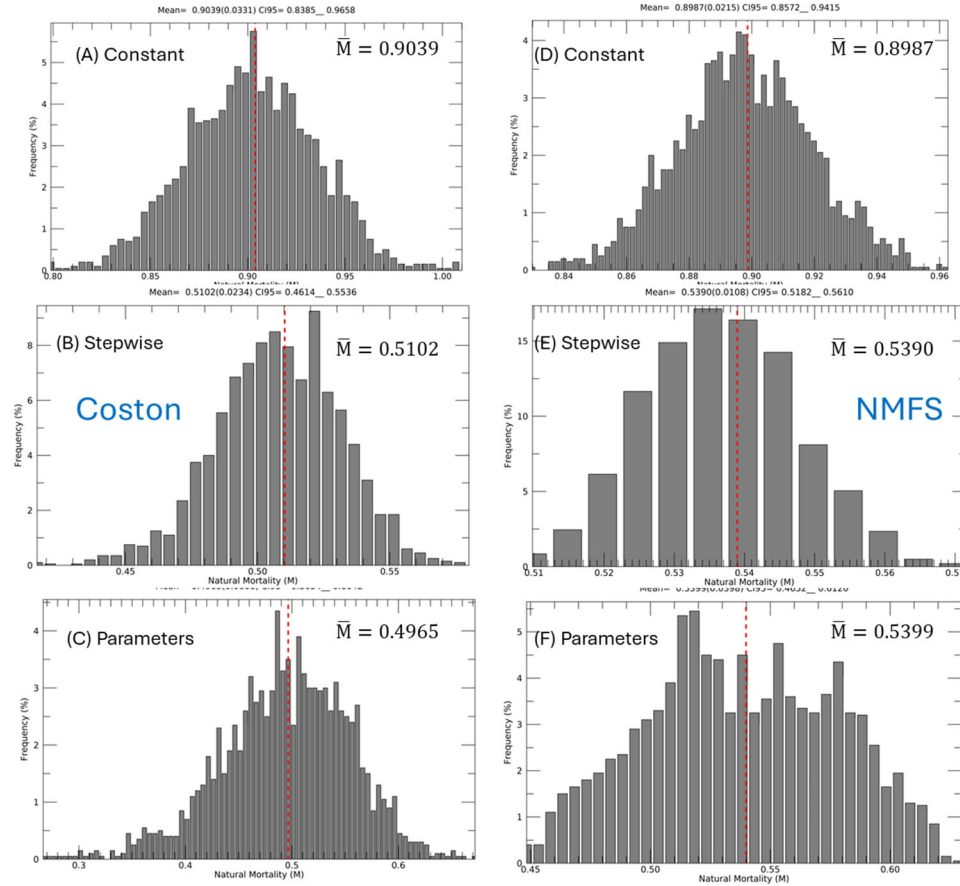


Figure IV.2.- Summary of MCMC trial results corresponding directly to the single-run results of **Fig IV.1**. **Coston**: (A) primary magnets with Constant MEs; (B) Stepwise analysis (Step #4); (C) ME Parameters estimated. **NMFS**: (D) ALL magnets with Constant MEs; (E) Stepwise analysis (Step #7); (F) ME Parameters estimated.

Method	K	neg(LL)	Δ	AIC	\hat{M}	\hat{M}_{MCMC}
Constant:	106	10,579	92,611	21,370	0.8992	0.9039
Step 4:	106	9,751	-6,570	19,714	0.5149	0.5102
As parameters:						
Unconstrained	206	9,442	8,296	19,296	0.3406	0.2939
Constrained	206	9,484	10,123	19,380	0.5488	0.4965

Table IV.1.- Summary of results from three analytical methods applied to the Coston data. Symbols are: K \equiv number of estimated model parameters; neg(LL) \equiv model's negative log-likelihood; Δ \equiv difference between predicted and observed recaptures; AIC \equiv Akaike Information Criterion; \hat{M} \equiv estimated annual natural mortality rate; \hat{M}_{MCMC} \equiv MCMC mean estimated annual natural mortality rate.

Method	K	neg(LL)	Δ	AIC	\hat{M}	\hat{M}_{MCMC}
Constant:	106	8,044	39,944	16,300	0.8909	0.8987
Step 7:	106	7,372	14,492	14,956	0.5279	0.5390
As parameters:						
Unconstrained	206	6,717	1,306	13,846	0.2935	0.2940
Constrained	206	6,839	12,669	14,090	0.5689	0.5399

Table IV.2.- Summary of results from three analytical methods applied to the NMFS data. Symbols are: $K \equiv$ number of estimated model parameters; $neg(LL) \equiv$ is the model's negative log-likelihood; $\Delta \equiv$ difference between predicted and observed recaptures; $AIC \equiv$ Akaike Information Criterion. $\hat{M} \equiv$ estimated annual natural mortality rate; $\hat{M}_{MCMC} \equiv$ MCMC mean estimated annual natural mortality rate.

Using the all the data, the three central and most important metrics for assessing the efficacy of the model analyses are: (1) the AIC; (2) differences (Δ) between observed and predicted recaptures; and (3) visual inspection of the plot of the observed versus model-predicted recaptures. In general, for both data sets: $AIC_{constant} \gg AIC_{stepwise} > AIC_{parameters}$, which suggests that MEs estimated as parameters should be the best model choice. For the Coston data, the reduction in AIC ranged between -7.7% to -9.3% for the stepwise versus parameters, respectively. For the NMFS data, the reduction in AIC ranged between -8.2% to -13.6% for the “stepwise” versus “ $\varepsilon_{t,a}$ as estimated parameters” approaches, respectively. It is obvious that both stepwise and ME parameter estimation methods are better fits to the data than constant MEs (Fig. IV.1).

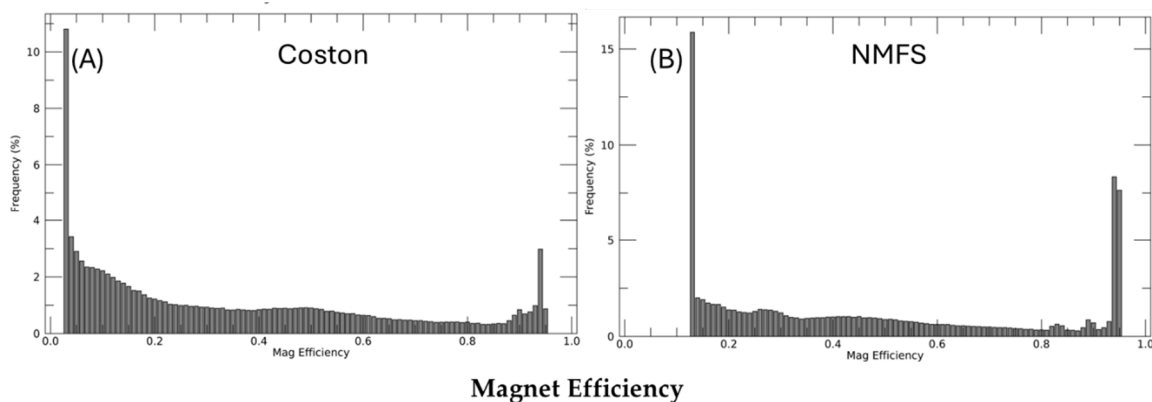


Figure IV.2.- Modeled magnet efficiency parameter estimates for: (A) Coston; and (B) NMFS data sources. Note the similarity to the observed empirical plant test magnet efficiency data shown in Fig. I.2.

V. Conclusions

As discussed by the SAS M workgroup, our analyses estimated a natural mortality rate (M) of approximately 0.54 or lower using multiple methods and two data sources. In contrast, Schueller et al. estimated an M of about 0.92 based solely on the averaged plant-area magnet efficiencies. As it turns out, the largest driver of this difference was not the confidential effort data withheld by industry, nor was it the underlying magnet efficiency data *per se*. It was simply methodological differences associated with how the tag recovery-magnet efficiency data were applied.

In our opinion, it is inappropriate to use arithmetic averages of plant- and area-specific magnet efficiencies. The Plant Test trial data show that magnet efficiencies are uniformly distributed, meaning any level of magnet recovery efficiency is equally possible (**Figs. I.2-I.4**). Consequently, averaging magnet efficiencies by area results in a poor and inefficient use of the Plant Tests data. Therefore, we employed two alternative methods: a “Stepwise” approach which was initiated with arithmetic mean efficiencies, and then in an iterative stepwise process used observed and theoretical recoveries to improve the $[\hat{\epsilon}_{S_{t,a}}]$; and a “Parameter Estimation” approach which directly estimated the MEs as model parameters. Both of these alternative methods substantially improved model fits, and also substantially lowered the natural mortality rate (M) estimates.

The preferred method(s) should be one(s) that utilize the entire data set. For both datasets, model(s) that estimated magnet efficiency parameters as a distribution produced recapture estimates closest to those observed. Similar results were obtained between the Stepwise and Parameter Estimation methods, and between the two data sources (**Tables IV.1 & IV.2**). Given the uniform random distribution of magnet efficiencies, the use of the simple weighted arithmetic averages of magnet efficiency by areas will naturally produce the highest estimates of natural mortality, and also the most unreliable.

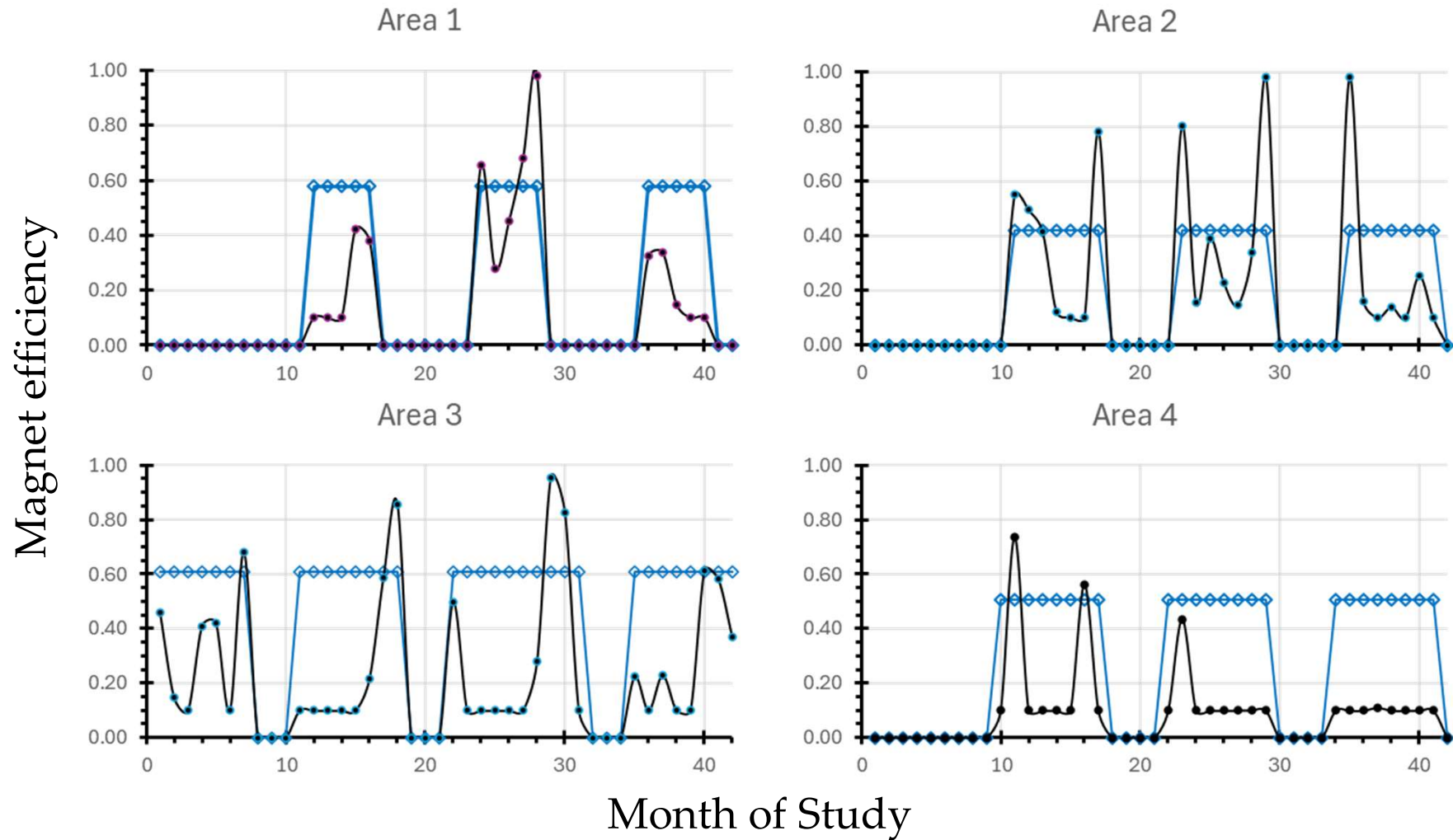
In summary, our analyses that used appropriate statistical metrics strongly indicate that the most likely annual natural mortality rate estimate for Atlantic menhaden ranges between 0.50 to 0.54. These estimates represent a 43.3% and 40.0% reduction compared to the constant ME estimates derived from simple averaging of either the Coston and NMFS data, respectively. Therefore, we concluded that $\hat{M} = 0.52$ is the best estimate of annual natural mortality rate for Atlantic menhaden.

Supplemental

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

Table S1.- Regional reduction processing plants distributed across four areas along the Atlantic coast that were involved in the 1966-1971 plant-area magnet efficiency trials as part of the Atlantic menhaden mark-recapture study conducted by the National Marine Fisheries Service.

Coston Stepwise #4



Stepwise (black dots) & Constant (blue diamonds)