North American Journal of Fisheries Management 25:361–373, 2005

DOI: 10.1577/M04-033.1

[Article]

Movements and Mortality Rates of Striped Mullet in North Carolina

NATHAN M. BACHELER*

Center for Marine Sciences and Technology, Department of Zoology, North Carolina State University, 303 College Circle, Morehead City, North Carolina 28557, USA

RICHARD A. WONG[1]

North Carolina Division of Marine Fisheries, 3441 Arendell Street, Morehead City, North Carolina 28557, USA

JEFFREY A. BUCKEL

Center for Marine Sciences and Technology, Department of Zoology, North Carolina State University, 303 College Circle, Morehead City, North Carolina 28557, USA

Abstract.—Striped mullet *Mugil cephalus* is an economically important species to commercial and recreational fishermen, as well as an ecologically significant detritivore linking lower trophic levels with a wide variety of estuarine and marine fish and birds. Despite this importance, striped mullet migration patterns and mortality rates are poorly understood. Approximately 15,000 striped mullet were tagged in North Carolina between 1997 and 2001, and monthly movement information was collected on recovered individuals (n = 384) from commercial and recreational fishermen and state agency personnel. A tag return model was used to estimate an instantaneous total mortality rate, and this rate was partitioned into natural and fishing components by means of life history methods. Nearly all (98.2%) striped mullet were recovered in North Carolina, the remaining few being recovered in nearby states. Striped mullet moved southward of their tagging locations and had the highest daily movement rate between the months of August and November. Movements corresponded to the months when spawning migrations are thought to occur in North Carolina. A smaller but substantial proportion of fish were recovered north of their tagging locations in late fall. Instantaneous total mortality rates of 2.12 and 1.71 were estimated using the two most parsimonious models for individuals larger than 300 mm fork length, comparing well with preliminary estimates from an independent statistical catch-at-age model. Concomitant holding tank experiments suggested that tag retention and posttagging survival, two central assumptions of the tag return model, were extremely high for adult striped mullet. These results will be incorporated into the North Carolina striped mullet fishery management plan currently in development.

Striped mullet *Mugil cephalus* occur worldwide in subtropical and temperate coastal waters and have been noted as the most abundant inshore teleost in the world (Thomson 1963; Odum 1970). Striped mullet fisheries carry considerable economic importance, particularly in the South Atlantic Bight (SAB) of the USA. The striped mullet is the seventh most commercially harvested finfish species in the Atlantic and Gulf coasts of the USA, averaging 10 million kg (US$15 million, landings value) annually over the past 10 years (National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, Maryland; available: www.st.nmfs.gov). They are also an important recreational species in the SAB. In North Carolina, for instance, more striped mullet and white mullet *M. curema* (by number) are captured by recreational anglers than other popular species such as weakfish *Cynoscion regalis*, spotted seatrout *Cynoscion nebulosus*, red drum *Sciaenops ocellatus*, black sea bass *Centropristis striata*, dolphinfish *Coryphaena hippurus*, striped bass *Morone saxatilis*, and flounder *Paralichthys* spp. (National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, Maryland; available: www.st.nmfs.gov).

Striped mullet form an important ecological link in the energy flow between lower trophic levels

* Corresponding author: nate_bacheler@ncsu.edu

[1] Present address: Delaware Department of Natural Resources and Environmental Control, Division of Fish and Wildlife, Post Office Box 330, Little Creek, Delaware, 19961, USA.

Received February 26, 2004; accepted August 12, 2004
Published online March 7, 2005

and a wide variety of piscivorous birds and fish. Diet is composed primarily of microcrustacea, diatoms, and detritus in larval and juvenile stages (De Silva 1980; Cardona 2001) and detritus in adult stages (Odum 1970; Eggold and Motta 1992). Among the economically important fish species known to feed on striped mullet are red drum (Scharf and Schlicht 2000), spotted seatrout (Breuer 1957), and southern flounder *P. lethostigma* (Gunter 1945).

Despite the economic and ecological importance of striped mullet, there is a paucity of basic information concerning the species' movement patterns and mortality rates. Movements in the northern part of the fish's southeastern U.S. range have not been investigated, except from one early study. Higgins (1926) asserted that migrations were not extensive in North Carolina and made no comments specifically regarding spawning migrations. Distinct movements associated with spawning migrations have been described in Georgia (Pafford 1983) and Florida (Idyll and Sutton 1952; Broadhead and Mefford 1956; Funicelli et al. 1989). These studies noted that fall migrations of striped mullet resulted in high concentrations of fish in localized areas, which increased their susceptibility to fishermen.

Because the harvest of striped mullet in North Carolina primarily occurs during prespawn periods when fish are often highly concentrated, it is also imperative that mortality rates be estimated in order to understand the impact of fishing on this population. Instantaneous rates of total mortality (Z) of fish populations can be estimated using catch curve analyses, coded ages, or directly from length data (Hilborn and Walters 1992). Another common approach to estimate Z is tag return methodology (Hoenig et al. 1998a, 1998b; Pine et al. 2003).

Tag return models can be considered special extensions of capture–recapture models (Seber 1982) in which tagged fish are harvested and returned by the fishery and returns occur over a longer period of time, such as a fishing season (Pine et al. 2003). Instantaneous rates of natural (M) and fishing (F) mortality can be determined using tag return models if the tag reporting rate can be estimated with a reward tagging study, creel survey, port sampling, planted tags, or observers (Pollock et al. 1991, 2001, 2002; Hearn et al. 2003). In practice, the tag reporting rate is difficult to estimate reliably (Hightower et al. 2001).

Tag return models can estimate Z for a fish population without the need for an estimate of reporting rate. However, an independent estimate of either M or F is required to partition Z. Many researchers have developed ways to estimate M from life history information, such as maximum age or growth coefficient (Pauly 1980; Hoenig 1983; Jensen 1996). The instantaneous natural mortality rate can then be subtracted from Z to estimate F. An advantage of this method is that it usually requires minimal data. However, the precision of these estimates is unknown (Vetter 1988; Pascual and Iribarne 1993), and M is often required to be constant among ages, seasons, or years (Hightower et al. 2001).

Here, we quantify movement patterns of striped mullet in North Carolina and estimate Z using maximum likelihood techniques with a tag return model. We use life history methods to partition Z into F and M. Our elucidation of movement patterns and mortality rates of striped mullet in North Carolina is particularly timely because the North Carolina Division of Marine Fisheries (NCDMF) is in the process of developing a first-ever stock assessment and fishery management plan for the species in the state.

Methods

Tagging.—Striped mullet were tagged between December 1997 and April 2001 throughout coastal regions of North Carolina by the NCDMF (Figure 1a). Two sampling strategies were used to collect striped mullet for tagging in our study. First, striped mullet were collected concurrent with regular monitoring programs by all NCDMF offices using a wide variety of gears, including gill nets, trammel nets, electroshocking, seines, and cast nets. Second, a sampling crew out of the Morehead City office was involved in directed efforts to collect striped mullet throughout the state. Most of this directed effort was focused in the lower Neuse River, Beaufort Inlet, and surrounding areas due to their proximity to Morehead City, but efforts were also made to sample striped mullet in a wide variety of areas and habitats throughout North Carolina. Gill nets, trammel nets, electroshocking equipment, seines, and cast nets were also used to collect striped mullet in directed sampling. Efforts were made to collect a robust sample of striped mullet during every month of the study.

Upon capture, fish were implanted with a single, 80-mm plastic dart tag (Hallprint Pty, Ltd., Adelaide, Australia) in their dorsal musculature approximately 15 mm ventral to the second dorsal spine. The barb of the tag was locked behind the pterygiophore. Each tag was labeled with a unique number, NCDMF address, and reward information.

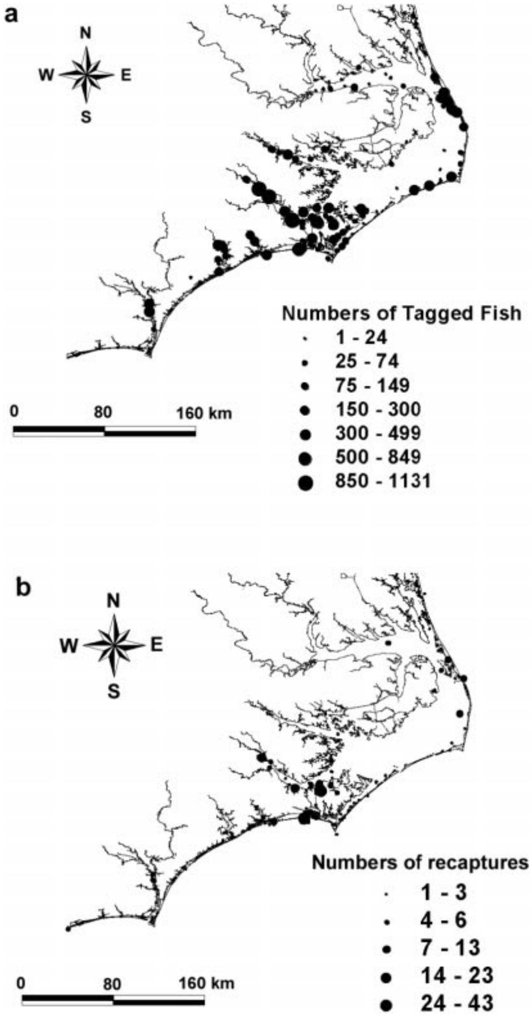

FIGURE 1.—Maps showing the locations where striped mullet were **(a)** tagged and **(b)** recovered in North Carolina. Not shown are seven recoveries in other states outside of North Carolina.

Fork length (FL, mm) of fish and location were recorded at the site of capture. Reward posters were given to bait and tackle shops and to fish distributors throughout eastern North Carolina. Five dollars or a tagging program baseball cap was offered for each returned tag and associated information. Requested information from fishermen included tag number, date and location of capture, gear used, FL, and total length (TL). During subsequent tagging periods by NCDMF, previously tagged striped mullet were recovered using gill nets, trammel nets, and electroshocking equipment. When this occurred, striped mullet were measured (mm FL) and released.

Movement patterns.—Directionality and distance traveled by tagged striped mullet were summarized by month. Only striped mullet recovered within 30 d of marking were used for movement analyses. A time period of 30 d was chosen as a tradeoff between reduced sample sizes using shorter time intervals and biased directional interpretations using longer intervals. For each fish, the midpoint of its time at large was used to determine its month of recovery. Striped mullet were only considered to have moved southward or northward if they moved further than 5 km from their initial marking location to account for measurement error in locations and mapping. Otherwise, fish were classified as stationary.

Mortality and recovery rate estimates.—A single-age tag recovery model was used to estimate mortality of striped mullet based on the recoveries of tagged fish by commercial and recreational fishermen (Brownie et al. 1985). This method uses maximum likelihood techniques (a well-developed theory for the efficient estimation of parameters) to estimate mortality from tag returns (Robson and Youngs 1971; Brownie et al. 1985; Pollock et al. 1990; Lebreton et al. 1992). Tag return methodology does not require reporting rate to be known and allows mortality and recovery rates to vary. This tag recovery model estimates two parameters: an annual survival rate S (i.e., the probability that an individual, alive when the given cohort is tagged, will survive during the time interval of study) and an annual recovery rate f (i.e., the probability that a tagged individual will be harvested and its tag reported within the time interval of study; Brownie et al. 1985). All analyses were performed using Program MARK with default functions (White and Burnham 1999).

Following the notation and structure of Williams et al. (2002), a recovery matrix of the data structure for a single-age tag recovery can be described by

$$\begin{pmatrix} R_1 & m_{11} & m_{12} \\ R_2 & & m_{22} \end{pmatrix}, \tag{1}$$

where R_i equals the number of animals tagged in period i and m_{ij} equals the number of animals tagged in period i and recovered in period j.

In this example, animals are tagged and released in each of 2 years, and recoveries in each period are made after tagging. This can be represented in terms of the parameters of the S_t, f_t (time-dependent S and f) model as

$$\begin{pmatrix} R_1 & R_1 f_1 & R_1 S_1 f_2 \\ R_2 & & R_2 f_2 \end{pmatrix}, \tag{2}$$

where S_i equals the survival from period i, j to period $i + 1$, $j + 1$, and f_i equals the recovery rate of animals in period i. The maximum likelihood estimator of the recovery rate f in period 2 is

$$f_2 = \frac{m_{22}}{R_2}, \tag{3}$$

so that the estimated number of animals released that survive until the beginning of period 2 (M_{12}) is

$$\hat{M}_{12} = \frac{m_{12}}{\hat{f}_2}. \tag{4}$$

Survival from period 1 to period 2 can then be estimated by

$$\hat{S}_1 = \frac{\hat{M}_{12}}{R_1}. \tag{5}$$

The maximum likelihood estimator for survival rate is biased (Williams et al. 2002); however, an unbiased estimator for S_i is given by

$$\hat{S}_i = \left(\frac{m_{i.}}{R_i}\right)\cdot\left(1 - \frac{m_{.i}}{T_i}\right)\cdot\left(\frac{R_{i+1} + 1}{m_{i+1} + 1}\right), \tag{6}$$

where T_i equals the total of all recoveries across all tagging years (up to and including i, $i = 1, \ldots, k - 1$); $m_{i.}$ equals the number of fish tagged in period i and subsequently recovered in all following periods; and $m_{.i}$ equals the number of animals tagged in all periods and subsequently recovered in period i (Brownie et al. 1985; Williams et al. 2002).

The best model to fit the data were selected from four models with varying time-dependent S and f assumptions using Akaike's information criterion (AIC; Akaike 1973). The model with the lowest AIC value was considered to provide the best trade-off between the number of parameters and likelihood of the models. The four models compared were as follows: (1) the full model, where S and f vary by time interval (S_t, f_t), (2) constant S and time-dependent f model ($S.$, f_t), (3) time-dependent S and constant f model (S_t, $f.$), and (4) constant S and constant f model ($S.$, $f.$). In our study, S was converted to Z using the equation

$$Z = -\log_e(S).$$

Model assumptions.—The key assumptions underlying tag recovery models are as follows: (1) the sample is representative of the population under investigation, (2) there is no tag loss, (3) the month of tag recovery is correctly tabulated, (4) survival rates are not affected by tagging, (5) the fates of individuals are independent, (6) all individuals have the same survival and recovery rates, and (7) tagging occurs at the midpoint of each time period (Brownie et al. 1985).

Natural and fishing mortality estimates.—Life history data from female striped mullet in North Carolina were used to calculate M because a majority of striped mullet longer than 300 mm FL are females (R. A. Wong, unpublished). Five estimators of constant lifetime natural mortality were used: (1) a prediction of M from asymptotic length or weight, the von Bertalanffy growth coefficient (K), and mean annual water temperature (Pauly 1980); (2) relating Z to maximum age—since the relationship was constructed from unexploited or lightly exploited stocks, Z approximates M (Hoenig 1983); (3) relating M to age at maturity (Jensen 1996); (4) another method relating M to K (Jensen 1996); and (5) using length at maturity and asymptotic length to predict M (Jensen 1996). The geometric mean of the five Ms was then calculated and subtracted from Z to compute F.

Tag retention and posttagging survival.—We captured 58 striped mullet on 9 December 2002 using cast nets in Back Creek, North Carolina. Fish were tagged using procedures and materials as described above. They were then released into two flow-through cylindrical holding tanks to investigate tag retention and posttagging survival (hereafter referred to as experiment 1). The tanks were 2.0 m in diameter and 1.0 m deep, with a volume of 3.1 m^3. Twenty-nine striped mullet were released into each tank and monitored every 1–3 d. On 3 January 2003, surviving fish ($n = 20$) were given a formalin dip (i.e., 250 mg of 100% formalin/L of water for 1 h) in response to dermal infections. Fifteen fish were moved into a large raceway tank (2.0 m wide, 5.0 m long, and 0.5 m deep, for a volume of 5.0 m^3). The remaining five fish were held in one aforementioned cylindrical tank. Fish were monitored every 1–3 d for the next 4.5 months.

Due to low initial survival of fish in the first holding tank experiment, a second holding tank experiment was initiated (hereafter referred to as experiment 2). On 21 February 2003, we collected 75 striped mullet via electrofishing in Hancock Creek, North Carolina. We tagged 36 of these fish and left 39 fish as untagged control fish. After 1-h transport, fish were released into a large, cylindrical recirculating tank (6.0 m diameter, 1.0 m deep, with a volume of 28.3 m^3.) Fish were monitored every 1–3 d for a duration of 3 months.

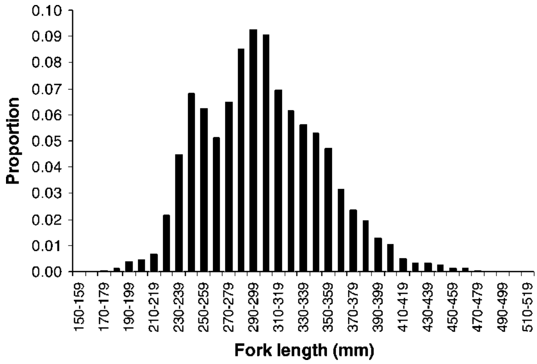

FIGURE 2.—Length frequency distribution of tagged striped mullet (n = 14,937) in North Carolina. Only fish greater than 300 mm (fork length) at tagging were used in the mortality rate analyses.

Water temperature was recorded in tanks as a possible explanation for any mortalities.

Results

Tagging

A total of 14,987 mullet were tagged, and reliable length information was available for 14,937 of these (mean FL = 301.5 mm; SE = 0.39; range = 155–578 mm; Figure 2). In all 10,305 (68.8%) were captured using gill and trammel nets; 3,516 (23.5%) by electroshocking; 899 (6.0%) by seines; and 267 (1.8%) by cast nets. Striped mullet were tagged throughout most coastal regions of North Carolina (Figure 1a), but the largest proportion of fish were tagged within the central coastal region, including the Neuse River, Core Sound, and Beaufort Inlet. More fish were tagged in 1999 (5,425) and 2000 (7,299) than in other years, and greater numbers of fish were tagged in the spring (4,341) and summer (4,361) than in the fall (3,762) and winter (2,523) over all years (Table 1).

Tag Recoveries

Overall, 384 tags (2.6%) were recovered between 21 February 1998 and 6 November 2002.

TABLE 1.—Numbers of striped mullet tagged by year and season in North Carolina. Winter includes the months of December, January, and February; spring includes March, April, and May; summer includes June, July, and August; and fall includes September, October, and November. Year-round sampling did not occur in 1997 and 2001.

Year of release	Winter	Spring	Summer	Fall	Total
1997	1	0	0	0	1
1998	343	223	630	1,044	2,240
1999	1,006	855	1,352	2,212	5,425
2000	1,171	3,243	2,379	506	7,299
2001	2	20	0	0	22
Total	2,523	4,341	4,361	3,762	14,987

The NCDMF-recovered fish had a mean FL of 334.1 mm (SE = 4.7; range = 267–470), and the mean length of NCDMF-recovered fish at tagging (mean = 326.9; SE = 4.30; range = 198–434) was significantly larger than the mean length for all tagged fish (mean = 301.5; SE = 0.39; range = 155–576 mm; analysis of variance [ANOVA]: F = 24.16, df = 1, $P < 0.0001$). An average growth rate of 0.071 mm/d was calculated for fish recovered by NCDMF. Most fish were recovered in 2000, but recoveries occurred every year from 1998 to 2001. Commercial fishermen accounted for the largest proportion of tag recoveries (n = 256, or 66.7% of all recoveries), while NCDMF and recreational fishermen accounted for 87 (22.7%) and 41 (10.7%) recoveries, respectively. A majority of recovered fish was caught with gill or trammel nets (64.8%), but seines, electrofishing, hook and line, cast nets, and gigging were also used to recover tagged fish (Table 2). Fish collected with seines for tagging purposes had a significantly higher recovery rate (6.1%) than those collected using other gear types (χ^2 = 50.01; df = 3; P = 0.001). Large tagged fish (>300 mm FL) were recovered more often than small tagged fish (χ^2 = 130.87, df = 6, $P < 0.0001$; Figure 3). Fish were recovered between 0 and 837 d at large (mean = 107.5 d, SE = 7.0; Figure 4) throughout

TABLE 2.—Numbers of striped mullet tagged and recovered by collection gear type in North Carolina.

		Number recovered							
Capture gear	Number tagged	Gill or trammel nets	Electro-shocker	Seines	Hook and line	Cast nets	Gig	Total	Percent recovered
Gill or trammel nets	10,305	190	8	14	10	3	0	229	2.2
Electroshocker	3,516	20	41	26	7	1	0	95	2.7
Seines	899	31	0	19	0	2	3	55	6.1
Cast nets	267	4	0	0	1	0	0	5	1.9
Total	14,987	249	49	59	18	6	3	384	2.6

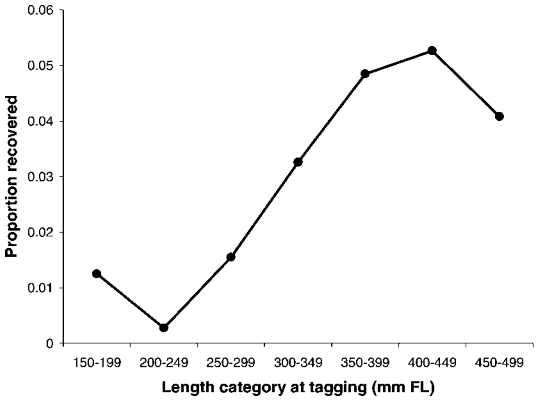

FIGURE 3.—Proportion of tagged striped mullet recovered by the North Carolina Division of Marine Fisheries within various length categories.

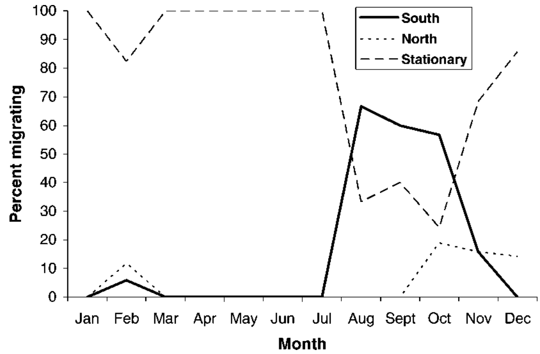

FIGURE 5.—Percentage of striped mullet moving southward or northward or remaining stationary between tagging and recovery by month in North Carolina. Only striped mullet recovered within 30 d of tagging were used. Fish were considered to have moved southward or northward only if they moved more than 5 km from their initial tagging location in either direction; otherwise, they were classified as stationary. Sample sizes for each month were: January (0), February (17), March (21), April (2), May (0), June (3), July (6), August (3), September (5), October (37), November (19), and December (14).

many locations of coastal North Carolina (Figure 1b).

Movement Patterns

Based on all 384 recoveries, striped mullet were recovered between 0 and 860 km from their original tagging location (mean = 28.2 km; SE = 4.1). Nearly all fish (n = 377, or 98.2%) were recovered in North Carolina waters, with the remaining seven fish caught in Virginia (1), South Carolina (3), or Florida (3). The total distance moved by striped mullet between tagging and recovery was not related to fork length of fish at tagging ($P = 0.87$; $R^2 = 0.0001$), but was significantly related to the number of days at liberty ($P < 0.0001$), although days at liberty explained very little of the variation in distance moved ($R^2 = 0.13$).

A seasonal striped mullet movement pattern was apparent for fish recovered within 30 d of tagging. The largest proportion of individuals recovered southward of their tagging location occurred in late summer and early fall, mainly in August (67%), September (60%), and October (57%; Figure 5). Alternatively, a smaller but substantial proportion of northward-moving fish was observed in October (19%), November (16%), and December (14%).

The mean distance moved by individual striped mullet was also seasonal (Figure 6). Since there was a significant difference in the mean days at large for striped mullet among months (ANOVA: $F = 2.13$, df = 10, $P = 0.028$), we used mean

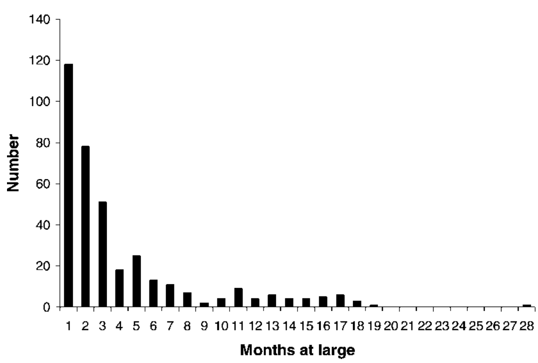

FIGURE 4.—Months at large for striped mullet between tagging and recovery in North Carolina.

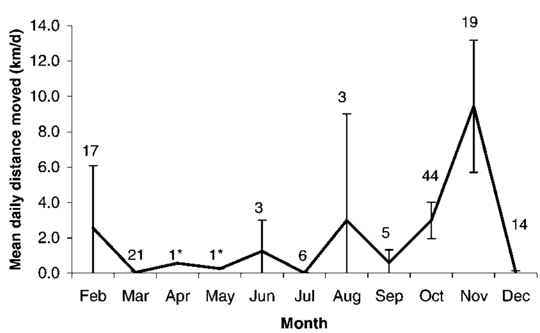

FIGURE 6.—Mean daily distance moved for striped mullet recovered within 30 d of tagging in North Carolina. The numbers within the figure are the monthly sample sizes, and the error bars indicate 95% confidence intervals. Asterisks denote sample sizes of 1, for which confidence intervals could not be shown. January was not included because its sample size was 0.

TABLE 3.—Recovery matrix for all harvested striped mullet used for mortality rate analyses in North Carolina. Only fish harvested by commercial and recreational fishermen and greater than 300 mm fork length at tagging were used.

Date	Number released	Apr–Jun 1998	Jul–Sep 1998	Oct–Dec 1998	Jan–Mar 1999	Apr–Jun 1999	Jul–Sep 1999	Oct–Dec 1999	Jan–Mar 2000	Apr–Jun 2000	Jul–Sep 2000	Oct–Dec 2000	Total
Apr–Jun 1998	224	3	0	1	0	0	0	0	0	0	0	0	4
Jul–Sep 1998	630		3	3	0	0	0	0	1	0	0	0	7
Oct–Dec 1998	1,046			42	3	1	3	1	0	0	0	0	50
Jan–Mar 1999	1,016				5	3	2	4	0	0	0	0	14
Apr–Jun 1999	856					0	1	1	0	0	0	0	2
Jul–Sep 1999	1,358						3	11	1	2	0	0	17
Oct–Dec 1999	2,195							12	27	4	0	5	49
Jan–Mar 2000	1,191								4	3	1	2	10
Apr–Jun 2000	3,259									6	5	26	37
Jul–Sep 2000	2,343										3	50	53
Oct–Dec 2000	506											12	12
		3	3	46	8	4	9	29	33	15	9	95	254

daily distance moved by fish to compare movement among months. The largest mean daily distance moved by striped mullet occurred during the fall months of October (3.0 km/d) and November (9.4 km/d), and was low in all other months except February (2.6 km/d) and August (3.0 km/d).

Mortality Estimates

Because the proportion of recovered fish was heterogeneous across size categories of tagged mullet (see Figure 3), only individuals tagged 300 mm FL or larger were used in the mortality analyses. Thus, mortality estimates are only applicable to this size category of striped mullet. The recovery matrix was based upon 254 recoveries from commercially and recreationally caught striped mullet (Table 3). The most parsimonious model selected was the $S_., f_t$ model (i.e., constant survival and time-dependent recovery rate; Table 4). This model yielded a Z equal to 2.12 (95% CI: 1.71–2.81). The 3-month recovery rate (f) of striped mullet varied from a low of 0.004 in the January–March 1999 period to a high of 0.065 in the October–December 1998 period (Figure 7).

TABLE 4.—Model comparison output from Program MARK (White and Burnham 1999) based on tag recoveries from striped mullet greater than 300 mm (fork length) in North Carolina. The model with the lowest Akaike information criterion (AIC) value was considered the most parsimonious and therefore most appropriate. Parameters in the models are either time dependent (indicated by the subscript t) or have a constant survival (S) or recovery rate (f) (indicated by the subscripted period).

Model	AIC value	Model likelihood	Number of parameters
$S_., f_t$	2,449.9	0.97	12
S_t, f_t	2,456.8	0.03	21
$S_t, f_.$	2,555.1	0.00	11
$S_., f_.$	2,590.9	0.00	2

Visual inspection of the time-dependent recovery rates in Figure 7 revealed asymmetric confidence intervals in time periods 1, 5, 6, and 7. Asymmetric confidence intervals indicate poor model fit in these periods. In order to evaluate the extent to which poor model fit may influence our mortality estimates, we compared mortality estimates of the $S_., f_t$ model to those of the least complex model ($S_., f_.$). Mortality estimates under each model were nearly identical (Z = 2.12 for the $S_.$, f_t model; Z = 1.95 for the $S_., f_.$ model).

With the exception of the October–December 1999 period when Hurricane Floyd precluded much of the commercial mullet fishing in coastal North Carolina (Wong, unpublished), the recovery rate was generally higher in the fall periods, suggesting a fall pulse fishery. Thus, we also estimated Z by using a model with 1-year time inter-

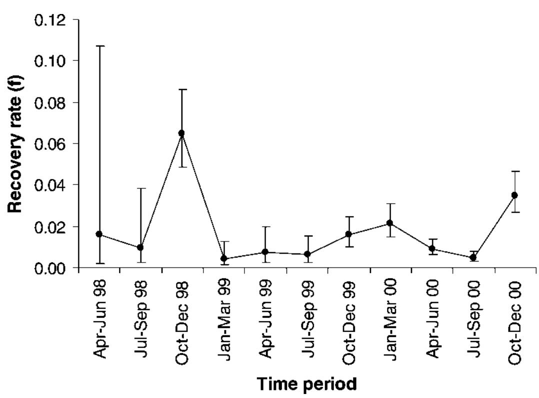

FIGURE 7.—Recovery rates of striped mullet in North Carolina, 1998–2000. Error bars indicate 95% confidence intervals.

TABLE 5.—Methods used to estimate instantaneous natural mortality rates (M) for female striped mullet greater than 300 mm (fork length) in North Carolina. Because Hoenig (1983) based his estimator on unexploited or lightly exploited populations, total mortality (Z) in his equation approximates the natural mortality rate. Independent variables are as follows: L_{inf}, maximum length (50.4 cm); K, growth coefficient (0.40); T, mean temperature (18.0°C); $t_{\max}$, maximum age (11 years); x_m, age at maturity (3). Source of life history data: R. A. Wong, North Carolina Division of Marine Fisheries, unpublished.

Method	Relationship	M
Pauly (1980)	$\log(M) = -0.0066 - 0.279 \log(L_{\mathrm{inf}}) + 0.6543 \log(K) + 0.4634 \log(T)$	0.85
Hoenig (1983)	$\log_e(Z) = 1.709 - 1.084 \log_e(t_{\max})$	0.41
Jensen (1996)	$M = 1.65/x_m$	0.55
Jensen (1996)	$M = 1.5K$	0.60
Jensen (1996)[a]	$M = 1.6K$	0.64

[a] Equation was obtained using data for K and M from Pauly (1980) for 175 different species.

vals because tagging and recovery periods occurred on a yearly basis. For these analyses, we used fish tagged during the summer months (June–August) and recovered in the late fall and winter (November–January). The most parsimonious model was the *S., f.* model, yielding a Z equal to 1.71 (95% CI: 1.24–2.66) and f equal to 0.018.

Natural and Fishing Mortality Estimates

Estimates of M for female striped mullet (>300 mm FL) based on the five life history methods ranged from 0.41 to 0.85 (Table 5). Subtracting the geometric mean of these values (0.59) from the range of Z yielded estimates of F ranging from 0.65 to 2.22 (Table 6).

Tag Retention and Posttagging Survival

All striped mullet (mean FL = 263.9 mm; SE = 4.2; range = 226–461 mm) from experiment 1 retained their tags, although only eight fish survived the entire 5-month period. All fish recovered dead in the tanks also retained their tag. Survival was very low during the first month of experiment 1, but water temperature did not appear to correlate with striped mullet mortalities. All tagged fish surviving the duration of experiment 2 retained their tag. Survival was much higher throughout the entire 3-month study for experiment 2, with only five mortalities (4 tagged, 1 control) occurring exclusively when fish jumped out of the tank after the tank overflowed accidentally. Untagged control (mean FL = 308.9 mm; SE = 4.6; range = 266–408 mm) and tagged fish (mean FL = 304.4 mm; SE = 5.0; range = 266–384 mm) in experiment 2 were larger than fish in experiment 1.

Discussion

Movement Patterns

Striped mullet were found to migrate over relatively large distances during short time periods and then to remain relatively site specific during other periods. Movement patterns were also tightly linked with time of year. Most movement southward was detected in the late summer and fall, while most northward movement was noticeable in the fall, lagging behind the southward migration by roughly 2 months. This is the first quantification of the direction and distance moved by striped mullet on a monthly basis. Most previous studies on striped mullet movement made only broad generalizations in movement direction, timing, or distance moved (e.g., Idyll and Sutton 1952; Kesteven 1953; Thomson 1955; Broadhead and Mefford 1956; Funicelli et al. 1989). For instance, Idyll and Sutton (1952) found that 89.8% of striped mullet moved less than 32 km between tagging and recovery in Florida, but the authors did not relate movement patterns to season. Broadhead and Mefford (1956) found that the distance moved by

TABLE 6.—Striped mullet annual survival (S) and instantaneous rates of total (Z), natural (M), and fishing mortality (F). Annual survival was calculated from a tag recovery model using either a 3-month or 1-year time interval. The instantaneous rates of total mortality were calculated from S. The 95% confidence intervals for S and Z are given in parentheses. The ranges of the instantaneous rates of natural mortality (M) from five life history methods (Table 5) are also shown (geometric mean in parentheses). Estimates of F were calculated by subtracting the geometric mean of the five M estimates from the range of Z-values.

Estimator	S	Z	M	F
3-month interval	0.12 (0.06–0.18)	2.12 (1.71–2.81)	0.41–0.85 (0.59)	1.12–2.22
1-year interval	0.18 (0.07–0.29)	1.71 (1.24–2.66)	0.41–0.85 (0.59)	0.65–2.07

striped mullet was not related to days at large or size at marking, but was instead related to season. However, no quantification of these patterns was provided.

Perhaps the most comparable data on striped mullet migration patterns comes from Funicelli et al. (1989), who found striped mullet movement linked with season in Everglades National Park, Florida. Although no discernable pattern of movement was apparent in fish during the prespawning season (July through November), 50 of 80 fish recovered between December and February had moved north or northwest of their original marking location, and 5 of 24 fish recovered in the postspawning season had moved southeast from their marking locations. Our results were similar but differed in two important aspects. First, migration occurred approximately 2 months earlier in our study than in southern Florida. This pattern may be entirely explained by differences in water temperature since photoperiod varies minimally between the two areas (~10° latitude), but this hypothesis remains untested. Secondly, the direction of migrations in Florida was opposite to those found in the present study. Migration direction is likely related to the prevailing currents in each region. Striped mullet migration in the SAB occurs southward against the northward-flowing Gulf Stream currents. On the west coast of Florida, however, striped mullet migration occurs northward against the prevailing southward-flowing Loop Current off the western continental shelf (Lugo-Fernández et al. 2001). However, the extent to which the temporally and spatially dynamic continental shelf waters on the western Florida shelf (Yang et al. 1999; He and Weisberg 2003) influence adult migrations and larval drift is unknown.

Southward migration of striped mullet may be associated with spawning. Reproductive development of striped mullet in North Carolina occurs from September to December (Bichy 2004), so it is likely that striped mullet are making southward migrations for spawning purposes and then returning to inshore habitats after reproduction. No tagged striped mullet were captured over continental shelf waters during this study. However, previous studies that collected larval striped mullet in the SAB have found the smallest larvae (e.g., <6 mm TL) nearest the edge of the continental shelf, so this area was assumed to be the primary spawning location for striped mullet (Anderson 1958; Powles 1981; Collins and Stender 1989). The only reliable documentation of striped mullet spawning in the USA came from Arnold (1958), who verified striped mullet spawning 65–80 km offshore in the Gulf of Mexico by watching the spawning behavior of adult striped mullet and collecting fertilized eggs and various sizes of larvae. It is therefore likely that striped mullet are not only migrating southward in North Carolina for reproductive purposes but offshore as well. The lack of striped mullet tag returns from offshore locations during this study is most likely due to a lack of exploitation in these areas.

The few recoveries from nearby states (1.8%) suggest that striped mullet are year-round residents in North Carolina, but caution must be exercised when drawing this conclusion because fishing effort is not constant along the entire SAB coast. For instance, South Carolina, Virginia, and Georgia have limited commercial and recreational fisheries for striped mullet, so many fewer fish are harvested in these states compared with North Carolina (National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, Maryland; available: www.st.nmfs.gov). Unequal exploitation rates across states and unavailability to nearshore gears could potentially bias conclusions regarding statewide residency. In a South Carolina tagging study, where in-state harvest is lower compared with that of nearby states (especially North Carolina and Florida), a much higher percentage of out-of-state tag recoveries (9%) occurred (McDonough 2001). Hence, although it appears that adult striped mullet are state residents in North Carolina, adult movement patterns remain uncertain. Telemetry or otolith microchemistry techniques may help to elucidate movement patterns of adults in the SAB.

Mortality and Recovery Rate Estimates

Estimates of M and F for adult female striped mullet in this study were moderately higher than estimates elsewhere in the USA where they are a commonly sought-after commercial species. In Gulf of Mexico states, for instance, estimates of Z from catch curve and mark–recapture techniques have been partitioned using Pauly's (1980) life history estimator to estimate an M equal to 0.30–0.44 and an F equal to 0.50–1.0 for female striped mullet (Mahmoudi 1993; Lazauski 1995). Our mortality estimates, in fact, correspond more closely to estimates from Asian waters ($Z = 1.69$) where striped mullet commercial fishing operations caused age composition shifts towards younger ages and declining catches (Hwang et al. 1990).

These results are also consistent with independent estimates of Z from preliminary analyses of striped mullet in North Carolina. Wong and Hightower (unpublished) used a statistical catch-at-age model based on growth, age, and landings data to estimate Z-values ranging from 1.32 to 1.99 for age-3 and older female striped mullet between 1997 and 2000. Close agreement of mortality estimates from these two independent methods is encouraging.

Mortality estimates produced from a tag return model depend heavily on its assumptions. Therefore, a detailed discussion of each assumption follows. First, is the sample representative of the population under investigation? There is no reason to suggest tagged fish were not representative of all striped mullet in North Carolina because fish were tagged and recovered in many coastal locations in the state. Multiple gears used to collect and recover striped mullet may have helped reduce bias associated with any particular gear type due to the selectivity that can occur due to gear morphology or specific habitats sampled. Second, is tag loss occurring? Our results indicate that dart tag loss in striped mullet is zero when held in holding tanks for periods up to 5 months. However, algal growth on tags (see Tag Retention and Posttagging Survival below) is a form of tag loss, but the extent to which algal growth covered tags in the wild is not known. Third, is the period of tag recovery correctly tabulated? We believe that commercial and recreational fisherman correctly documented the date of recovery of tagged fish since this information was explicitly requested on each tag. Moreover, incorrect tabulation of the date of tag recovery would influence our results very little unless they were extremely inaccurate because recovered fish could still be recorded in the correct 3-month or 1-year time interval. Fourth, is survival affected by tagging? Our results suggest that the survival of tagged striped mullet may be size dependent. Smaller fish may be more negatively affected than larger ones, which justifies the use of only large (>300 mm FL) individuals in the mortality rate analyses. However, we could not conclusively rule out other factors that may have influenced the survival of small striped mullet in experiment 1, such as water temperature, disease, capture gear, or density of fish in tanks. Fifth, are the fates of all tagged striped mullet independent? If tagged striped mullet travel together in groups, then independence may be violated and the consequence is an underestimation of sampling variances (Brownie et al. 1985). Striped mullet are a schooling fish, but the extent to which independence was violated was not known. Sixth, do all individuals have the same mortality and recovery rates? It was assumed that all fish have equal mortality and recovery rates after sexual maturation, which for striped mullet in North Carolina occurs at approximately 300 mm FL (Bichy 2004). Only fish greater than 300 mm FL at tagging were used in the mortality estimation analyses. Seventh, did the tagging occur at the midpoint of the time period? Although tagging and recoveries occurred continuously throughout the current study, it is necessary to assume that the tagging occurred at the midpoint of the study. As such, estimates were generated using models (3 months or 1 year) specifying the smallest time period possible without producing a matrix of recovered individuals that was overly sparse of recoveries. We chose to use a 3-month period for tagging and recovery. Matrices with time periods smaller than 3 months were very sparse and produced imprecise estimates, while estimates using time periods longer than 3 months were biased due to continuous tagging over long time periods.

Natural Mortality Estimates

Estimates of M for female striped mullet were moderately variable using five life history estimators, ranging from 0.41 to 0.85/year. Natural mortalities are notoriously difficult to quantify because natural deaths are often unseen, so little evidence exists about their timing or magnitude. A common approach to estimating M is using life history methods (Pauly 1980; Hoenig 1983; Jensen 1996). Approaches based on life histories of fish are advantageous because they require minimal data, but they often produce imprecise estimates of M for any given group of fish and they generally cannot account for variability in M across sizes, ages, or years (Vetter 1988). In order to account for some of the variability in M, we used the mean of five life history estimators here in hopes of approximating the true M for striped mullet in the state.

Tag Retention and Posttagging Survival

Dart tag retention rates were high for striped mullet held in holding tanks in this study. Striped mullet retained all dorsally inserted dart tags in both laboratory experiments for either 5 or 3 months ($n = 8$ and $n = 32$, respectively). In contrast, however, Ludwig et al. (1990) found that of 45 striped mullet tagged with internally anchored spaghetti tags, only 40 (89%) retained their tags when held in tanks for 10 d. Tag retention rates in striped mullet appear to vary considerably depending on the style of tag being used.

The holding tank experiments indicated size-based differences in tag placement and may have resulted in a size-based, tag-induced mortality. Fish in experiment 1 were substantially smaller than those tagged in experiment 2. After dissecting multiple dead fish from experiment 1, it became clear that the dart tags did not lock with the pterygiophores properly; instead, the dart was inserted across the entire back of the small fish, locking with the muscle on the opposite side of the back from which the dart was inserted. That dart tags were too large may have been a source of mortality for small striped mullet used in experiment 1. This phenomenon was not observed in experiment 2, where fish were generally larger. In this experiment, dart tags were locked with the pterygiophores, no fish suffered tagging or handling mortalities, and all fish appeared to behave normally. This further justifies that only large (e.g., >300 mm FL) striped mullet be used for mortality rate estimation in this study.

In both holding tank experiments, algal growth on the dart tags completely obscured its bright yellow color, making the tags difficult to notice. An algae-obscured tag would effectively be tag loss. Because algal growth on the tags would be time dependent (i.e., more algae accumulating the longer the fish was at large), the tag loss assumption would be violated and would positively bias mortality rate estimates. The extent to which algae-covered tags occurs in the wild is not known. As opposed to most recreationally caught fish which are handled individually, striped mullet are often collected in large groups at the same time (e.g., large beach seining events), so it would not be surprising if fishermen did not notice and return tags. After being handled by commercial fishermen, though, fish houses usually process individual striped mullet, but the extent to which fish processors would return tags is not known. Therefore, if algae-covered tags were overlooked by fishermen, our mortality estimates may have been overestimated.

Management Implications

Mahmoudi et al. (2001) estimated that an F equal to 0.45 would be necessary to achieve a spawning potential ratio (SPR) of 35% for striped mullet in Florida. Our range of F-values for striped mullet in North Carolina (0.65–2.22) is moderately to approximately five times higher than Mahmoudi et al.'s (2001) reference point. Although a higher F-value in North Carolina is suggestive of an unsustainable fishery, the life history characteristics of striped mullet between the two areas have not been evaluated, so direct comparisons are not possible. Estimates of fishing mortality and reference points for striped mullet in North Carolina are currently being estimated using a statistical catch-at-age model (Wong and Hightower, unpublished). This information, along with our independent estimate of mortality rates, will help in assigning stock status (e.g., overfished or viable) for striped mullet in North Carolina.

Information on adult striped mullet movements is extremely important in defining stock boundaries for management purposes in North Carolina. Our tagging results suggest that adults tend to be moderately residential in North Carolina. However, larval drift patterns are poorly understood. The ingress of larval striped mullet into waters in the Mid-Atlantic Bight suggests that adults in North Carolina and southward are seeding states to the north (Wang and Kernehan 1979). In terms of management of striped mullet in North Carolina, this phenomenon raises two important questions. One, to what extent are striped mullet in states south of North Carolina seeding the North Carolina stock? And two, how important are North Carolina resident adult striped mullet to the recruitment of juvenile striped mullet in North Carolina? Future research directed at answering these questions would assist in understanding the population dynamics of striped mullet in North Carolina and other SAB states.

Acknowledgments

These analyses were completed while N.M.B. was a Marine Sciences Fellow supported by North Carolina Sea Grant and NCDMF. Funding for these analyses was provided by National Oceanic and Atmospheric Administration (NOAA) awards NA16FG1220 and NA16RG2251. We sincerely thank NCDMF for extensive work in tagging and recapturing fish, especially Marc Hamric and James Francesconi. We also thank the NOAA laboratory in Beaufort, North Carolina, and in particular James Morris, for providing space, guidance, and assistance with the holding tank experiments. Ken Pollock provided valuable guidance with the tag return model. We thank Louis Daniel, John Carmichael, and three anonymous reviewers for providing insightful comments on this manuscript.

References

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petran and F. Csaaki, editors. Second International Symposium on Information Theory. Akadeemiai Kiadi, Budapest, Hungary.

Anderson, W. W. 1958. Larval development, growth, and spawning of striped mullet (*Mugil cephalus*) along the south Atlantic coast of the United States. U.S. Fish and Wildlife Service Fishery Bulletin 58: 501–519.

Arnold, E. L., Jr. 1958. Offshore spawning of the striped mullet, *Mugil cephalus*, in the Gulf of Mexico. Copeia 1958:130–132.

Bichy, J. B. 2004. A life history assessment on the reproduction and growth of striped mullet, *Mugil cephalus*, in North Carolina. Master's thesis. North Carolina State University, Raleigh.

Breuer, J. P. 1957. Ecological survey of Baffin and Alazan bays, Texas. Publications of the Institute of Marine Science University of Texas 4:134–155.

Broadhead, G. C., and H. P. Mefford. 1956. The migration and exploitation of the black mullet *Mugil cephalus* in Florida, as determined from tagging during 1949–1953. Florida State Board of Conservation, Technical Series 18, Coral Gables, Florida.

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data: a handbook, 2nd edition. U.S. Fish and Wildlife Service, Resource Publication 156, Washington, D.C.

Cardona, L. 2001. Noncompetitive coexistence between Mediterranean grey mullet: evidence from seasonal changes in food availability, niche breadth, and trophic overlap. Journal of Fish Biology 59:729–744.

Collins, M. R., and B. W. Stender. 1989. Larval striped mullet (*Mugil cephalus*) and white mullet (*Mugil curema*) off the southeastern United States. Bulletin of Marine Science 45:580–589.

De Silva, S. S. 1980. Biology of juvenile grey mullet: a short review. Aquaculture 19:21–36.

Eggold, B. T., and P. T. Motta. 1992. Ontogenetic dietary shifts and morphological correlates in striped mullet, *Mugil cephalus*. Environmental Biology of Fishes 34:139–158.

Funicelli, N. A., D. A. Meineke, H. E. Bryant, M. R. Dewey, G. M. Ludwig, and L. S. Mengel. 1989. Movements of striped mullet, *Mugil cephalus*, tagged in Everglades National Park, Florida. Bulletin of Marine Science 44:171–178.

Gunter, G. 1945. Studies on marine fishes of Texas. Publications of the Institute of Marine Science University of Texas 1:1–190.

He, R., and R. H. Weisberg. 2003. West Florida shelf circulation and temperature budget for the 1998 fall transition. Continental Shelf Research 23:777–800.

Hearn, W. S., J. M. Hoenig, K. H. Pollock, and D. A. Hepworth. 2003. Tag-reporting rate estimation, III. Use of planted tags in one component of a multicomponent fishery. North American Journal of Fisheries Management 23:66–77.

Higgins, W. 1926. Investigations conducted during 1926. Progress in Biological Inquires 1926:519–560.

Hightower, J. E., J. R. Jackson, and K. H. Pollock. 2001. Use of telemetry methods to estimate natural and fishing mortality of striped bass in Lake Gaston, North Carolina. Transactions of the American Fisheries Society 130:557–567.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York.

Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. Fisheries Bulletin 82:898–903.

Hoenig, J. M., N. J. Barrowman, W. S. Hearn, and K. H. Pollock. 1998a. Multiyear tagging studies incorporating fishing effort data. Canadian Journal of Fisheries and Aquatic Sciences 55:1466–1476.

Hoenig, J. M., N. J. Barrowman, K. H. Pollock, E. N. Brooks, W. S. Hearn, and T. Polacheck. 1998b. Models for tagging data that allow for incomplete mixing of newly tagged animals. Canadian Journal of Fisheries and Aquatic Sciences 55:1477–1483.

Hwang, S., C. Kuo, and S. Tanaka. 1990. Stock assessment of grey mullet *Mugil cephalus* in Taiwan by cohort analysis. Nippon Suisan Gakkaishi 56: 1955–1963.

Idyll, C. P., and J. W. Sutton. 1952. Results of the first year's tagging of mullet *Mugil cephalus* L., on the west coast of Florida. Transactions of the American Fisheries Society 81:69–77.

Jensen, A. L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Canadian Journal of Fisheries and Aquatic Sciences 53:820–822.

Kesteven, G. L. 1953. Further results of tagging sea mullet, *Mugil cephalus* Linnaeus, on the eastern Australian coast. Australian Journal of Marine and Freshwater Research 157:251–306.

Lazauski, H. G. 1995. Unpublished stock assessment for striped mullet in Alabama. Alabama Department of Conservation and Natural Resources, Marine Resources Division, Gulf Shores.

Lebreton, J., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Ludwig, G. M., J. E. Skjeveland, and N. A. Funicelli. 1990. Survival of Florida bay fish tagged with internally anchored spaghetti tags. Florida Scientist 53:38–42.

Lugo-Fernández, A., M. V. Morin, C. C. Ebesmeyer, and C. F. Marshall. 2001. Gulf of Mexico historic (1955–1987) surface drifter data analysis. Journal of Coastal Research 17:1–16.

Mahmoudi, B., L. Foushee, M. McGlothlin, G. Geoghegan, and A. Weinkauf. 2001. Biology and stock assessment of striped mullet, *Mugil cephalus*, from the east coast of Florida. Florida Fish and Wildlife Conservation Commission, Florida Marine Research Institute, St. Petersburg, Florida.

Mahmoudi, B. 1993. Update on black mullet stock assessment. Final report submitted to the Florida Marine Fisheries Commission, Tallahassee.

McDonough, C. J. 2001. Cooperative research on the biology and stock assessment of fishes along the southeast coast of the U.S., part IV. Striped mullet. South Carolina Department of Natural Resources, Marine Fisheries Initiative Final Report, Charleston.

Odum, W. E. 1970. Utilization of the direct grazing and plant detritus food chains by the striped mullet *Mugil cephalus*. Pages 222–240 *in* J. J. Steele, editor. Marine food chains. Oliver and Boyd, Ltd., Edinburgh, UK.

Pafford, J. M. 1983. Life history aspects of the striped mullet, *Mugil cephalus*, in Georgia's St. Simons estuarine system. Master's thesis. Georgia Southern College, Statesboro.

Pascual, M. A., and O. O. Iribarne. 1993. How good are empirical predictions of natural mortality? Fisheries Research 16:17–24.

Pauly, D. 1980. On the interrelationship between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. Journal du Conseil International pour l'Exploration de la Mer 39:175–192.

Pine, W. E., K. H. Pollock, J. E. Hightower, T. J. Kwak, and J. A. Rice. 2003. A review of tagging methods for estimating fish population size and components of mortality. Fisheries 28(10):10–23.

Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert. 2002. Tag reporting rate estimation, 2. Use of high reward tagging and observers in multicomponent fisheries. North American Journal of Fisheries Management 22:727–736.

Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert. 2001. Tag reporting rate estimation, 1. An evaluation of the high reward tagging method. North American Journal of Fisheries Management 21:521–532.

Pollock, K. H., J. M. Hoenig, and C. M. Jones. 1991. Estimation of fishing and natural mortality when a tagging study is combined with a creel survey or port sampling. Pages 423–434 *in* D. Guthrie, J. M. Hoenig, M. Holliday, C. M. Jones, M. J. Mills, S. A. Moberly, K. H. Pollock, and D. R. Talhelm, editors. Creel and angler surveys in fisheries management. American Fisheries Society, Symposium 12, Bethesda, Maryland.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture−recapture experiments. Wildlife Monographs 107.

Powles, H. 1981. Distribution and movements of neustonic young of estuarine-dependent (*Mugil* spp., *Pomatomus saltatrix*) and estuarine-independent (*Coryphaena* spp.) fishes off the southeastern United States. Rapports et Procès-Verbaux des Réunions, Conseil International pour l'Exploration de la Mer 178:207–209.

Robson, D. S., and W. D. Youngs. 1971. Statistical analysis of reported tag−recaptures in the harvest from an exploited population. Cornell University, Biometrics Unit, BU-369-M, Ithaca.

Scharf, F. S., and K. K. Schlicht. 2000. Feeding habits of red drum (*Sciaenops ocellatus*) in Galveston Bay, Texas: seasonal diet variation and predator−prey size relationships. Estuaries 23:128–139.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, 2nd edition. Charles Griffin, London.

Thomson, J. M. 1955. The movements and migrations of mullet (*Mugil cephalus* L.). Australian Journal of Marine and Freshwater Research 6:328–347.

Thomson, J. M. 1963. Synopsis of the biological data on the grey mullet *Mugil cephalus* Linnaeus 1758. CSIRO (Australia Commonwealth Scientific and Industrial Research Organization Division of Fisheries and Oceanography Fisheries Synopsis 1:1− 8: 14.

Vetter, E. F. 1988. Estimation of natural mortality in fish stocks: a review. Fishery Bulletin 86:25–43.

Wang, J. C., and R. J. Kernehan. 1979. Fishes of the Delaware estuaries: a guide to the early life histories. EA Communications, Towson, Maryland.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival rate estimation from both live and dead encounters. Bird Study 46(Supplement):S120–S139.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego.

Yang, H., R. H. Weisberg, P. P. Niiler, W. Sturges, and W. Johnson. 1999. Lagrangian circulation and forbidden zone on the West Florida Shelf. Continental Shelf Research 19:1221–1245.