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An integrated tagging and catch-curve model reveals high and seasonally-varying natural mortality for a fish population at low stock biomass

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ABSTRACT

Rebuilding of exploited fish stocks at low biomass requires accurate mortality estimates. Weakfish (*Cynoscion regalis*) abundance is at historical lows caused by an increasing instantaneous total mortality (*Z*) in recent years, but uncertainty exists regarding the relative importance of instantaneous fishing mortality (*F*) and natural mortality (*M*) to *Z*. Data from a tag-return study and catch-curve of weakfish in North Carolina were analyzed jointly using a Bayesian statistical framework to estimate seasonal and annual mortality (i.e., *F*, *M*, and *Z*). We accounted for key auxiliary parameters in the tag-return portion of the model (i.e., tag-reporting rate and tag loss) through field studies and an experimental design, including use of high-reward tags and double tagging. Estimates of *Z* from the joint model were similar in magnitude to the weakfish stock assessment. From mid-2014 to 2017, we estimated a constant annual instantaneous mortality rate of 0.05 yr^{-1} (95 % credible interval [CrI]: 0.04, 0.07) for *F* and 2.33 yr^{-1} (CrI: 2.10, 2.6) for *M*. In the most recent stock assessment, estimates of *M* had an upper bound of 1.0; thus, our findings suggest that these estimates of *M* are biased low and *F* biased high. Our seasonal analyses showed that a large portion of mortality occurred from fall to spring, coinciding with weakfish migration and overwintering periods on the continental shelf. Through an integrated modeling approach, our study provides insights into the magnitude, timing, and sources of weakfish mortality, and enhances understanding of weakfish population dynamics to guide management strategies.

1. Introduction

Effective rebuilding of exploited fish stocks with a low biomass requires accurate estimates of fishing and natural mortality. The fishing mortality rate (*F*) allows management to meet stock rebuilding goals through comparisons with target and threshold levels based on biological reference points (Hilborn and Walters, 1992). The natural mortality rate (*M*) affects estimates of stock size and productivity, which ultimately determine harvest rates (Clark, 1999). In a typical stock assessment, catch-at-age data provide direct information about *F* (Walters and Martell, 2004), but *M* is more difficult to estimate reliably because natural deaths are rarely observed in aquatic systems (Quinn and Deriso, 1999). Natural mortality is often estimated externally based on life-history parameters and environmental variables (e.g., Pauly, 1980; Hoenig, 1983; Lorenzen, 1996; Griffiths and Harrod, 2007; reviewed by Kenchington, 2014), and used as a fixed input parameter in fishery stock assessments (Vetter, 1988). However, these estimates of *M* do not account for time- or location-specific factors and have an unknown certainty (Vetter, 1988; Pascual and Iribarne, 1993). Stock assessment models and consequently derived reference points are particularly sensitive to input values of *M* (Clark, 1999; Williams, 2002).

Tag-return experiments can directly estimate *F* and indirectly *M*, thereby generating near real-time estimates of *F* to track fishery harvest trends, validating catch-at-age analysis, and determining if target harvest rates are being maintained (Walters and Martell, 2004). These models partition the instantaneous total mortality rate (*Z*) into estimates of *F* and *M* (Hoenig et al., 1998a). However, precise mortality estimates depend on key auxiliary parameters: tag-reporting rate (λ), tag loss (Ω), and survival from the tagging procedure (ϕ; Pollock, 1991; Pollock et al., 2001; Miranda et al., 2002; Brenden et al., 2010). Multi-year tagging studies of rigorous design can estimate the auxiliary parameters, leading to reliable estimates of mortality (e.g., den Heyer et al., 2013; Kerns et al., 2015) and providing insight into the timing and causes of mortality because estimates can be made at less than one-

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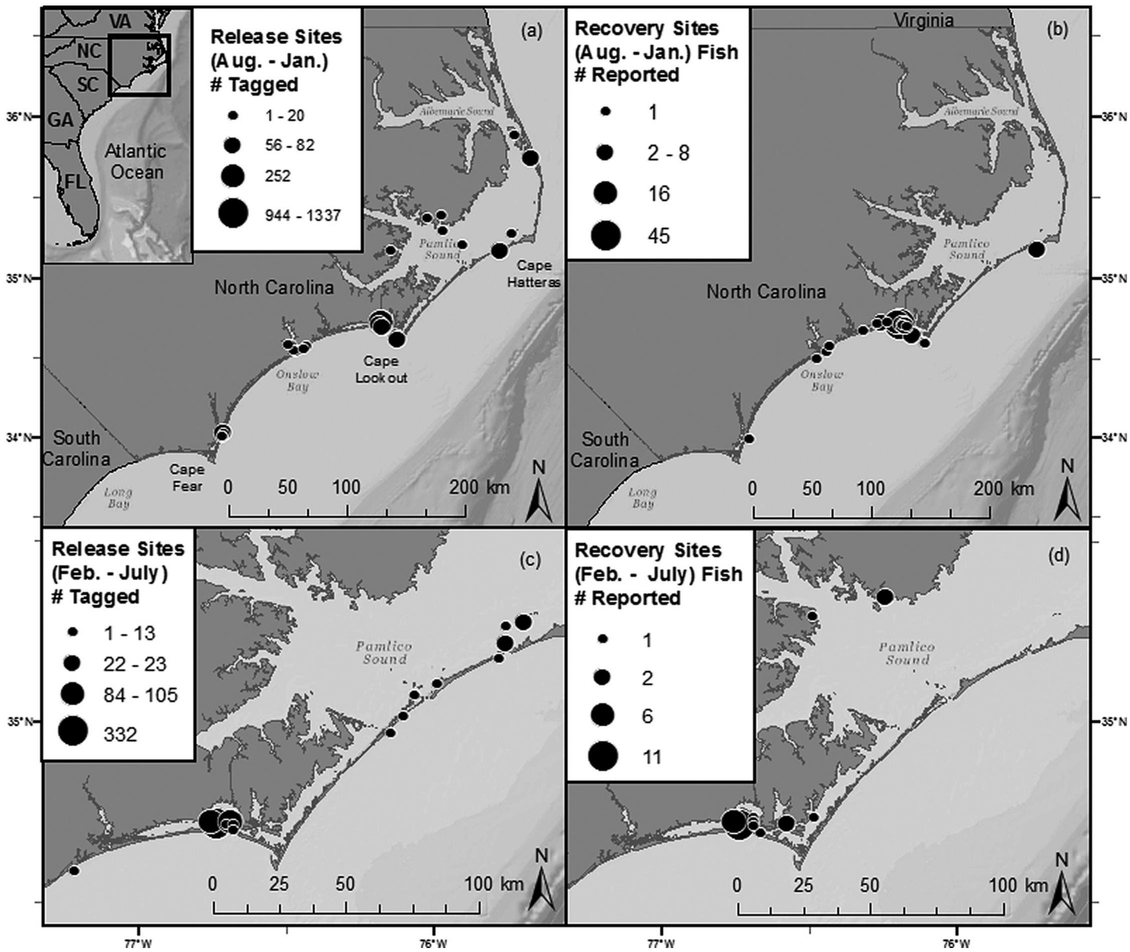

Fig. 1. Maps showing the locations where weakfish were tagged and released in North Carolina during the months a) August to January (n = 3,063 tagged) and c) February to July (n = 609) from November 2013 to May 2017. Reported recoveries during September 2014 to October 2017 from weakfish tagged during b) August to January (n = 112 recoveries) and d) February to July (n = 28).

year intervals (e.g., monthly or seasonally; Harris and Hightower, 2017; Ellis et al., 2018; Sackett et al., 2018).

The ability of tag-return experiments to provide robust estimates of mortality depends on adequate returns from the fishery. In recovering fisheries where tight regulation has kept the *F*s low, the estimates of *M* can be imprecise (Pollock et al., 2004). This limitation can be overcome by using multiple data sources in a combined analysis (e.g., Burnham, 1993; Powell et al., 2000; Pollock et al., 2004; Schaub et al., 2007; Dudgeon et al., 2015). Pollock et al. (2004) found that a combined telemetry and tag-return analysis provides substantially better precision for estimates of *F* and *M* than either individual method. The strength of the telemetry method was estimating *M*, whereas the tag return was better at estimating *F* (Pollock et al., 2004). A hallmark of many stock assessments is the estimation of *Z* from a catch-curve that tracks the sequential decline observed in fish cohorts. A combined tag-return and catch-curve model can simultaneously estimate *F*, *M*, and *Z* to increase parameter precision in low exploitation fisheries.

Weakfish (*Cynoscion regalis*) are an important recreational, commercial, and ecological species that primarily inhabit estuarine and coastal waters between North Carolina and Massachusetts. The spawning stock biomass has declined since 1982 to historic lows in the late 2000s, with the cause of the decline attributed to increased *Z* (ASMFC, 2006). Despite rigorous regulatory measures, stocks have failed to rebuild, and the most parsimonious explanation for the increase in *Z* was an increase in *M* (first noted in the 2006 weakfish stock assessment and expounded on in the 2009 assessment [ASMFC, 2006; NEFSC, 2009]). Subsequent stock assessment efforts to improve estimates of *M* culminated in a Bayesian statistical catch-at-age model that internally estimated a time-varying *M* (Jiao et al., 2012; ASMFC, 2016). The model included 14 fisheries-independent and 1 fisheries-dependent indices of abundance, as well as commercial and recreational harvest and discards. The prior distribution for the 1982 *M* estimate was based on a meta-analysis of published estimates from similar species and fisheries (uniform prior 0.1 to 0.4 yr^{-1}), and subsequent *M* estimates were allowed to vary through the time-series (1982–2017) using a random-walk approach (ASMFC, 2016). Post-1982 *M* estimates had an upper bound of 1 yr^{-1} (Yan Jiao, Virginia Tech, personal communication). *M* was estimated to increase through the time-series and approached the upper bound from 2007 to 2015 at > 0.9 yr^{-1} (ASMFC, 2019).

An upper bound on *M* may result in overestimation of *F*. That is, if *Z* increases as a result of *M* increasing above the upper bound then the extra mortality will be assigned to *F*. In this scenario, the *Z* is assumed accurate, but the partitioning of *F* and *M* becomes biased. The assumptions on the bounds and priors of *M* are not weakfish specific (i.e., meta-analysis derived) as assessments on other species (e.g., ASMFC, 2015; Monk and He, 2019; SEDAR 58, 2020) have used this approach and for most species an upper bound of $M = 1.0$ yr^{-1} would be sufficient. However, *Z* estimates for weakfish from the stock assessment update are very high and have remained high during a period of decreased harvest; currently, the estimates of *F* from the stock assessment update make up ~50 % of *Z* during the last three years of the time-series (2015–2017; ASMFC, 2019). Estimates of *F* and *M* from the weakfish stock assessment have never been compared to external estimates of F and M from a tagging study.

We used data from two semi-concurrent yet independent studies: (1) a multi-year, high-reward external tagging initiative by North Carolina State University (NCSU) and (2) a fishery-independent gill net survey conducted by the North Carolina Division of Marine Fisheries (NCDMF) in Pamlico Sound. Tagging data informed monthly F and M estimates, whereas a catch-curve based on catches of aged fish from the survey estimated seasonal and annual estimates of Z. Mortality estimates are presented for each model alone and jointly. A simulation provides insight into the strengths and weaknesses of tag-return studies for fisheries with low exploitation rates. Our study presents a new modeling framework for robustly estimating mortality from a joint catch-curve and tag-return model. For weakfish, the study contributes important information on the magnitude, timing, and sources of mortality that can guide management strategies.

2. Material and methods

2.1. NCSU tag-return study

From November 2013 to May 2017, weakfish were continually tagged and released in North Carolina, with the highest concentration in the vicinity of Cape Lookout (Fig. 1a and c). Researchers captured and released the majority of weakfish in this study (67 %), while the remainder were captured and released by 11 compensated guides and recreational anglers using standard hook-and-line methods. All taggers were trained to ensure consistency in handling and tagging methodology. We also recruited the assistance of compensated guides in Delaware Bay during 2015, but tagging was discontinued in 2016 due to the low release ($n < 10$) and lack of returns.

We restricted tagging to mouth-hooked individuals greater than 305 mm total length (TL) that had no physical signs of trauma (e.g., bleeding or visible tissue damage). Three types of internal anchor tags were used in the project to test tag retention: polyethylene tubing over a stainless-steel wire core (steel), monofilament covered with vinyl tubing (mono), and vinyl tubing (vinyl; Model FM-95W, FM-89SL, and FM-84; respectively: Floy Tag, Inc., Seattle, WA). Each tag was red in color, with a tube length of 63.5 mm, and a laminated oval anchor disk measuring 4.8 × 15.9 mm. All tags were high-reward, with black text message “CUT TAG $100 REWARD”, a unique tag number preceded by “NC”, and a toll-free phone number preceded by “NCSU” printed length-wise on the tube. Each anchor tag was inserted ventrally through a small incision immediately posterior of the pelvic fin. Approximately one-third of weakfish were single-tagged with anchor placement on the left-lateral side, whereas the remaining two-thirds were double-tagged, bilaterally, to estimate tag loss. Initially, all taggers double-tagged every third fish, but after estimating a high chronic tag-loss (~40 %) during 2014, we modified our protocol to increase the likelihood of returns by having only NCSU researchers double-tag every fish. Treatments consisted of single steel, mono, and vinyl, and double-tagged steel x steel, steel x mono, and steel x vinyl in which steel tag was always placed on the left-lateral side. In a second approach to estimate tag loss, PIT tags (23 mm half duplex) were evenly implanted across all anchor tag treatments in 24 % of total fish. The PIT tag was inserted into the coelomic cavity through the left-lateral incision prior to anchor tag insertion. For the year 2015, an additional treatment of PIT tag-only fish ($n = 109$) was released to estimate survival from tagging procedure (ϕ; i.e., compare return rates of conventionally tagged fish with PIT tag-only fish). Because this treatment had different detection probabilities when compared to conventionally tagged fish and only a single return, we excluded PIT tag-only releases and returns from all modeling and future results. Collaborators only performed single and double tagging using steel tags. The order of treatments was randomized (i.e., number of tags per fish and treatment type), and the tag number, date, fish TL (mm), and location associated with each individual release were recorded.

Information on recaptured weakfish in this study was provided by fishery participants and researchers. Reporting of tagged fish was promoted by advertising across several media outlets throughout the study. Recapture data ascertained during a follow-up phone interview included the tag number(s), date and location of recapture, fish TL, general condition and number of tags, fishery sector (commercial or recreational), picture of fish when available, and fate of the fish and tag (i.e., kept, released with tag intact, or released with tag cut off). Fishermen were required to mail the tag(s) to researchers to collect the reward. Weakfish captured by non-public personnel (NCDMF fisheries biologists, collaborative taggers, and NCSU researchers) and fishery-dependent samplers (creel clerks and fish house samplers) were scanned for PIT tags.

2.1.1. Tag-return assumptions

1 The tagged sample mix completely with the untagged population such that tagged fish are assumed to be representative of the entire population. Although we continually released weakfish over the study time-period, this assumption may have been violated over the spatial scale of North Carolina, as over 90 % of fish were released in the vicinity of Cape Lookout.
2 All tagged individuals considered in the model have the same survival and recovery probabilities. Equal survival was ensured, as all fish were tagged within a narrow size range. Recovery probabilities were assumed equal, as 99.7 % of tagged fish were > 305 mm TL, the legal harvest size within the commercial and recreational sectors.
3 Tagged fish have independent fates. This assumption may be violated because weakfish aggregate around structures during spring and fall (i.e., bridges, rock jetties, deeper holes), allowing for individual anglers ($n = 14$) to recapture multiple tagged fish, albeit never on the same day. Violations of this assumption make the precision lower than it appears, but violations do not lead to bias (Pollock et al., 2004).
4 The month of tag recovery is correctly tabulated. We assumed anglers correctly reported the date of tag recovery.
5 Survival rates (ϕ) were not affected by tagging (i.e., 100 % post-release survival), based on sound handling practices, and capture depth of < 15 m to reduce barotrauma. Ellis et al. (2018) used the same conventional tags and handling methods and did not observe any initial or chronic tag-induced mortality in a laboratory study of the congener spotted seatrout (*Cynoscion nebulosus*). Furthermore, we tested the model's sensitivity to violations of this assumption under the scenarios of 50 % and 75 % post-release survival. Finally, we assumed individual tagger effects on survival were negligible as 67 % of fish were released by researchers and a further 23 % were released by an experienced collaborative tagger.
6 The tag-reporting rate was 100 % ($\lambda = 1.0$), as all tags were high-reward at $100 and double-tagged fish retaining both were worth $200. We tested the model's sensitivity to violations of this assumption under the scenarios of 50 % and 75 % tag-reporting.
7 Tag loss can be estimated from the Barrowman and Myers (1996) exponential decay model. Monthly tag retention was estimated as a function of at-liberty days for double-tagged fish that were returned with either one or two tags. The model estimates tag retention from ρ, the probability of tag retention immediately after tagging and Ω, the chronic instantaneous rate of tag loss. For a recapture of individuals subsequently released with tags intact (i.e., a multi-recapture fish), only the first recapture was included in the model regardless of the method of capture (i.e., fishery or scientific sampling). The model assumes that double-tagged fish represent a random subset of all tagged weakfish, in which each of the two tags was lost or retained independently, regardless of

placement laterality, and tag loss did not differ by laterality. The latter assumption may have been violated, as 12 out of 13 returns with only one tag were lost on the right-lateral side, a percentage greater than expected as compared to random chance (i.e., 50 %). In addition, we assumed that fish behavior, *M*, and ϕ were unbiased by whether a fish was tagged with one versus two tags (Wetherall, 1982; Hearn et al., 1991). Lastly, we assumed that retention by tag types was similar based on returns by tag type (see Results).

2.1.2. Tag-return only model

We estimated *F* and *M* from the recoveries of single- and double-tagged weakfish following the tag-return model of Ellis et al. (2018; see paper for equations), which is based on the instantaneous rates formulation of the Brownie tag-return model (Brownie et al., 1985; Hoenig et al., 1998a, 1998b; Polacheck et al., 2006). The model accounted for both harvest and catch-and-release (hereafter referred to as discard) mortality by following the approach of Jiang et al. (2007), where tags at-risk were modeled as opposed to tagged fish. This approach required that additional recaptures of individuals released with tags intact, beyond the first recapture, be ignored (Bacheler et al., 2008). This effect on sample size was minimal, as only three tagged weakfish were caught and reported more than once. The model did not include fish caught by scientific sampling, as the fates after recapture (mortality verses releases) may not be representative of the fishery. Our model differed from Ellis et al. (2018) by omitting internal estimation of the auxiliary parameters of ϕ (assumed to be 1.0 based on aforementioned assumptions) and Ω. We externally estimated the initial tag-retention ρ and chronic tag loss Ω as this allowed for the use of extra information from a daily time-step (instead of monthly time-step of tag-return model) as most fish were returned within 100 days and the incorporation of returns from scientific sampling (not included in tag-return model). A monthly time-step was chosen for the tag-return model to examine seasonal variability in mortality.

Tag-returns were organized into nine tables (3 × 3): fishery type (recreational, commercial, discards) x tag type (single-tag released fish, double-tag released fish returned with 1 tag, and double-tag released fish returned with 2 tags). Recreational and commercial tables consisted of harvested fish from each sector. Discards (n = 48) mostly consisted of fish captured recreationally, with only 4 commercial discard returns, therefore a single table represented catch-and-release from both fishing sectors. Recoveries were assumed to follow a multinomial distribution (Polacheck et al., 2006; Ellis et al., 2018).

The model estimated instantaneous fishing mortality for commercial (F_c) and recreational fisheries (F_r), discards (F'), and *M*, all of which represent loss rates for tags. A 10 % discard mortality was assumed in the latest benchmark stock assessment (ASMFC, 2016), and F' was multiplied by 0.1 to provide an estimate of the rate of mortality for discarded fish instead of the rate of discarding (Jiang et al., 2007). The total fishing mortality (F_{fish}) was equal to $F_c + F_r +$ adjusted F', and total mortality (*Z*) equaled $F_{fish} + M$ for a specific time-period.

We implemented all models using the Bayesian statistical software package JAGS (Plummer, 2003) called from R (R Core Team, 2019). In the tag-loss model, uninformative prior distributions were used for ρ [uniform (0,1); estimated on probability scale] and Ω [uniform (0,2); estimated as instantaneous rate]. The latter was uninformative as the estimated daily rate was very close to 0. For the mortality model, an uninformative prior distribution [uniform (−10,2)] was used for the natural logarithm of F_r, F_c, F', and *M*. The prior has worked well in previous studies (e.g., Ellis et al., 2018) when some rates are close to 0 (e.g., when mortality is very low in some months). The model was run for 43 periods from June 2014 to December 2017, which corresponded to the first release and one month after the last return. We released 50 fish in November 2013, but had no returns and did not release any additional fish until June 2014; therefore with a paucity of releases and returns we did not include the months of November 2013 to May 2014 in the model. Preliminary modeling with time-varying parameters indicated little variation in *F* parameters among periods, but strong seasonality in *M*. Three candidate models were compared using deviance information criterion (DIC; Spiegelhalter et al., 2002) and its effective number of parameters (pD; Plummer, 2002). Our best model had constant *F* parameters, and estimated a shared seasonal *M*. The seasons were winter, spring, summer, and fall which consisted of the months January to March, April to June, July to September, and October to December, respectively. Additional details on the alternative models and the selection process can be found in Krause (2019). Parameter posterior distributions from all models were estimated using three Markov chains of at least 50,000 samples, with the first 10,000 samples excluded to remove bias associated with initial parameter values, and thinning was not conducted following the recommendations of Link and Eaton (2012). Chain convergence was determined by visually inspecting time-series plots of parameter values, and through calculation of the Brooks-Gelman-Rubin statistic (Brooks and Gelman, 1998). All parameter estimates are presented as posterior medians with a 95 % credible interval (CrI).

2.1.3. Tag-return simulation

A tag-return simulation evaluated the precision and bias of mortality estimates under varying sample size scenarios. Fish were released annually across 3 years and the fourth year was returns only. The number of annual released fish was constant across five sample size scenarios: 500, 1,000, 1,200, 1,500, or 2,000. The 1,200 fish released annually most closely approximated our study design. A tag-return matrix was generated from a known set of parameters that were similar to our tag-return study estimates. The simulated *F* was estimated annually across 4 years and was 0.1 yr^{-1} for all years. The remaining simulation parameters were constant (average) rates for all four years ($M = 2.1\ yr^{-1}$, $\lambda = 1$, and $\Omega = 0.27$). Within each scenario, mortality estimates and associated credible intervals were averaged from 1000 simulation repetitions.

2.2. NCDMF fishery-independent gill net survey

We used a Pamlico Sound fishery-independent gill net survey (IGNS) data collected by the NCDMF from February 2002 through December 2017 to estimate a seasonal *Z* in our catch-curve only model. Although IGNS data were available from multiple estuaries in the state, Pamlico Sound was selected because of the length of the time-series and high catches of weakfish. The seasons were winter, spring, summer, and fall, consisting of the same month increments as the tag-return only model. Through a stratified random sampling design based on region and water depth (i.e., shallow < 1.83 m and deep > 1.83), eight strata in Pamlico Sound were sampled from mid-February to mid-December each year. Strata were sampled only once in February and December months, and twice monthly in all other months. Specific detail on the sampling protocol and experiment gill net mesh sizes can be found in Ellis et al. (2018). Collected weakfish were enumerated and measured in TL, with a subsample retained for age analysis. The IGNS data were also incorporated as a fisheries-independent time-series into the 2016 weakfish stock assessment and subsequent 2019 update (ASMFC, 2016; 2019).

2.2.1. Catch-curve only model

We employed the catch-curve model described by Ellis et al. (2018; see paper for equations) to estimate *Z* by cohort across seasons from catch-at-age data from the IGNS by cohort. Many weakfish captured in the IGNS were not aged; therefore, we used North Carolina weakfish aging data grouped by season within a year to convert IGNS-catch data in TL to an estimated age (Fig. A.1). These aging data were compiled by the NCDMF from multiple fishery-dependent and fishery-independent surveys across 15 years (February 2002 to December 2017; n = 7,952). Estimated survey catch by age was then summed across all length frequencies for each seasonal period and standardized across all seasonal periods. Standardization was achieved by calculating age-dependent catch-per-unit-effort (CPUE), the number of weakfish per age group captured per hour of gill net set in each seasonal period, and scaling CPUE upwards by 50,000 h.

The model estimated an initial (relative) abundance of cohort i (N_i) and assumed the decline in numbers over time represented Z. By including all ages in our model (age-1 to age-8), we assumed that weakfish within this age range share a common Z. Although the IGNS included late age-0 s, we excluded age-0 s for consistency with the tagging data. The model accounted for age- and season-specific vulnerability of weakfish to the IGNS. The model estimated γ_a (the survey selectivity for age a) and α_p (the multiplier for seasonal p availability of weakfish to the survey). The γ_a was defined as asymptotic with a single increasing logistic function to estimate age-based selectivity of weakfish, where β_1 and β_2 are the intercept and slope parameters, respectively (Quinn and Deriso, 1999; Ellis et al., 2018). Weakfish emigrate from estuaries during their overwintering migration to the continental shelf. As such, we accounted for the seasonal availability of weakfish to the IGNS, which was assumed constant across ages and years.

We estimated Z seasonally, and calculated annual estimates of Z within the model. Uninformative prior distributions were used for the natural log of N_i [uniform (−15,15)] and Z [uniform (−10,2)], α [uniform (0,1)], β_1 [uniform −20,1)], and β_2 [uniform (1,12)]. Preliminary modeling suggested the seasonal availability of weakfish to the IGNS was highest from April to June; therefore, the prior distribution of α_2 was fixed at 1.0 such that all other α_p were estimated relative to α_2. Model validation included assessing model fit visually between the observed CPUE for each cohort within a season and that predicted by the model. Parameter posterior distributions were estimated using three Markov chains of 50,000 samples with the first 10,000 samples excluded. The convergence of Markov chains was assessed as previously described and all parameter estimates are presented as posterior medians with a 95 % CrI.

2.3. Joint model

The tag-return and catch-curve only models were integrated to robustly estimate mortality. The tag-return model alone estimated extremely high annual Z (> 99 % on a discrete scale) across multiple years that did not match the empirical evidence of older age fish in the population (Fig. A.1). The catch-curve provided additional information to increase the accuracy and precision of Z during years of study overlap (summer 2014 to fall 2017), and solely informed Z estimates prior to the tagging study (winter 2002 to spring 2014). The catch-curve component of the model excluded age-0s for consistency with the tagging data. Fish were assumed to experience similar Zs between both datasets because our tagging study encompassed Pamlico Sound (Fig. 1). In the joint model, the catch-curve model was the same as described earlier, but the tagging model differed in how F and M were estimated. For the jointly estimated Zs, an uninformative Dirichlet distribution partitioned Z among four sources (commercial [F_c] and recreational fisheries [F_r], discards [F'], and natural mortality [M]). The catch-curve estimated Z's on a seasonal time-step, hence they were divided by 3 for use in the monthly time-step of the tagging model.

Preliminary models explored how best to estimate the proportion of each of mortality source. In a model that assumed the proportion of each mortality source as constant across the time frame of the study, monthly F rates changed because of fluctuations in Z, and as such was not used. We selected a model that estimated the proportion of F and M seasonally (i.e., winter, spring, summer, and fall), but constant across years. Our tag-return only model supported the seasonality in M, and we modeled F similarly to allow insight into the timing of exploitation. We also estimated the probability that weakfish in our study had an average annual M less than 1, 1.5, and 2 yr^{-1}, which spanned from mid-2014 to 2017 (using the *step* function in JAGS). Although the IGNS was used in the assessment, we felt justified in comparing our estimates from the joint models to the assessment given that the IGNS data was only 1 of 14 fisheries-independent time-series used in the 2016 weakfish stock assessment (ASMFC, 2016). Parameter posterior distributions were estimated using three Markov chains of 1,400,000 samples with the first 700,000 samples excluded. The convergence of Markov chains was assessed as previously described and all parameter estimates are presented as posterior medians with a 95 % CrI. The joint model R code is provided.

3. Results

3.1. NCSU tag-return study

A total of 3672 weakfish were tagged in North Carolina from November 2013 through May 2017 (Fig. 1a,c), consisting of 1772 releases with a single high-reward tag (48 %) and 1900 releases with double high-reward tags (52 %). Released weakfish ranged in TL from 262 to 612 mm, with an overall mean of 353 (± 0.6 SE) mm. A total of 140 fish was returned over four years, with the last on October 13, 2017. Of the returned fish, 3 were recaptured multiple times (i.e., fishermen cut off only one of two tags upon initial capture, or the fish was released with all tags intact after being caught through scientific sampling).

Tagged weakfish were recovered throughout North Carolina estuarine and coastal waters (Fig. 1b and d). Most recoveries were near the site of release (Fig. 1a and c), with subtle differences based on the release month for the remaining recoveries. For fish released in spring/early summer (February to July), recoveries occurred in areas north and east of release (i.e., Pamlico Sound; Fig. 1d), whereas fish released in fall/early winter (August to January) were recovered in areas south and west of release (i.e., Onslow Bay; Fig. 1b).

Of the 3179 steel, 502 mono, and 505 vinyl tags used, 117 steel (3.7 %), 26 mono (5.2 %), and 24 vinyl (4.8 %) were recovered. Fifty-five single-tagged and 82 double-tagged fish were recovered, with respective return rates of 1.5 % and 2.2 %. Out of the double-tagged returns, 13 fish shed a tag (1 mono and 12 steel), 12 from the right side and 1 from the left (Fig. 2a). An increased mortality for double-tagged fish was not evident when considering the return rates for only left or right-lateral inserted tags from a double-tagged fish (left = 4.2 %, 81 returns/1900 releases; right = 3.7 %, 70 returns/1900 releases) as compared to left inserted tags from single-tagged fish (3.1 %; 55 returns/1,772 releases).

Days-at-liberty averaged 49.6 (+ 4.2 SE) with a range of 1–682, with the maximum value based on a second recapture. The percentage of all returns coming from fish at-liberty for at least 100 days was 8% and was higher for fish released in spring as compared to those in the fall (Fig. 2b). A total of 578 weakfish were released from March to June across study years, 28 were returned (4.8 % return rate), of which 25 % were recovered after 100 days-at-liberty. In contrast, a total of 3014 weakfish were released from August to December, 112 were returned (3.7 % return rate), of which only 3.6 % were recovered after 100 days-at-liberty. Only 4 returns occurred after a weakfish was released in spring or fall and recovered post-winter in subsequent years.

The recreational fishing sector reported 89 external tags in total, comprised of 31 single-tagged and 58 double-tagged specimens, of which 45 (51 %) were reported as discards. The commercial fishing sector reported 26 tags in total, comprised of 14 single-tagged and 12 double-tagged specimens, of which 4 (15 %) were reported as discards. Almost all commercial returns were captured in a gill net (n = 23), of which 17 occurred on the ocean side of coastal barrier islands (Fig. 1b). Two were captured via hook-and-line, and the remaining one in an estuarine shrimp trawler. Most of the commercial returns (n = 18) were in 2014, with minimal returns in subsequent years (n = 1, 3, and 4; respectively). During scientific sampling, a total of 25 fish were recaptured, of which 14 were released (1 subsequently recaptured by a

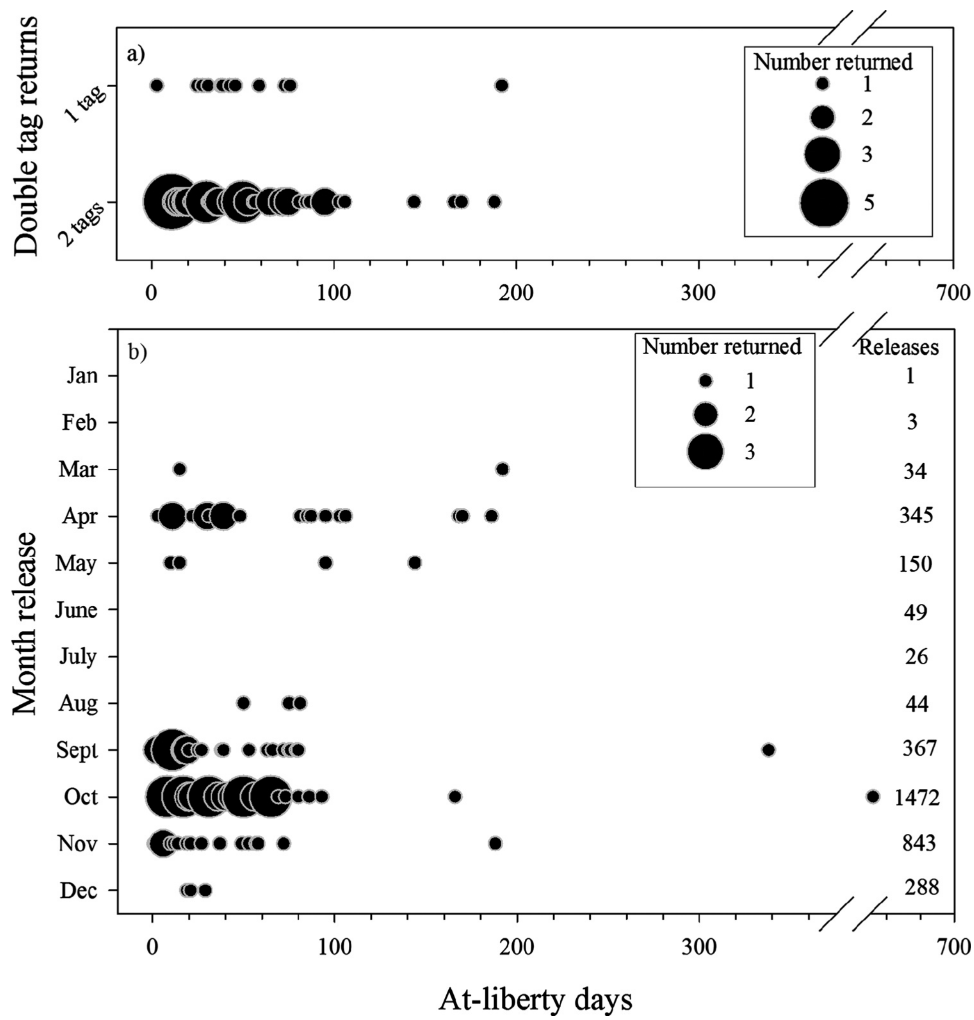

Fig. 2. a) Double tag returns (n = 82) by at-liberty days for fish that lost a tag (1 tag, n = 12) or were returned without tag loss (2 tags, n = 70). b) Tags returns by at-liberty days according to the release month (n = 140). The number of releases for a particular month are shown. All fish releases occurred from June 2014 to May 2017 in the state of North Carolina, and returns occurred from September 2014 to October 2017.

recreational angler), and the remaining 11 sacrificed for research purposes.

The auxiliary parameters Ω and ρ were estimated from the returns of 82 fish that were originally double-tagged. These returns included 15 from scientific sampling and 67 from fisheries, accounting for only the first recapture of fish (out of repeated captures). The days-at-liberty were similar between fish that retained both tags (1–188 days) compared to the 13 fish that lost a tag (3–192; Fig. 2a). The exponential decay model for tag retention converged on posterior median estimate of 0.95 (CrI: 0.88, 0.99) for ρ and 0.02 (CrI: < 0.01, 0.07) for the monthly Ω used in the tag-return model. On an annual scale, the probability of retaining a tag was 0.72 (CrI: 0.43, 0.91), and if the fish was double-tagged as a majority of fish were, the probability of retaining at least one tag increased to 0.92 (0.67, 0.99).

3.1.1. Tag-return only model

The tag-return only model estimated a low F_{fish} that was constant by assumption (Fig. 3a). Temporal variation was apparent in M during winter months (Fig. 3b). The winter monthly M was the highest at 1.56 month^{-1} (CrI: 1.16, 2.08), as compared to spring at 0.08 month^{-1} (CrI: < 0.01, 0.42), summer at 0.19 month^{-1} (CrI: < 0.01, 0.52), and fall at < 0.01 month^{-1} (CrI: < 0.01, 0.16). The estimates of M were imprecise compared to F_{fish} (Fig. 3a and b). From June 2014 to December 2017, the annual F was low across fishing sectors and minimal compared to M (Fig. 4). F' was 0.05 yr^{-1} (CrI: 0.04, 0.07), F_c was 0.02 yr^{-1} (CrI: 0.01, 0.03), and F_r was 0.04 yr^{-1} (CrI: < 0.01, 0.06). When comparing F and M, F_{fish} was 0.07 yr^{-1} (CrI: 0.06, 0.10), whereas M was 5.71 yr^{-1} (CrI: 4.40, 7.40). Given the relatively low F values, the seasonal Z followed the same trend as M (Fig. 5), with winter being the highest, as compared to spring, summer, and fall.

In additional sensitivity runs with lower assumed tag-reporting or post-release survival, annual F_{fish} increased but made a negligible change in M and Z. For example, F_{fish} for the post-release survival scenarios of 75 % and 50 % were 0.10 yr^{-1} (CrI: 0.07, 0.13) and 0.15 yr^{-1} (CrI: 0.11, 0.19). Estimates of M were static between 75 % and 50 % scenarios (5.67 yr^{-1} [CrI: 4.36, 7.36]; 5.59 yr^{-1} [CrI: 4.28, 7.28]; respectively), as well as for Z (5.76 yr^{-1} [CrI: 4.45, 7.47]; 5.74 yr^{-1} [CrI: 4.41, 7.44]; respectively). The 75 % and 50 % scenarios for testing violations of the 100 % tag-reporting assumption also had minimal effect on estimates of F_{fish}, M, and Z, and were not reported.

3.1.2. Tag-return simulation

Estimates of F were robust to low samples sizes and exploitation rate. In all sample size scenarios, F in years 1–3 ($F1$ to $F3$) were unbiased and precise (Fig. 6). The F in year 4 ($F4$) were imprecise because no additional tagged fish were released in that year and almost no tagged fish were available to be caught from previous year releases (Fig. 6). In low exploitation rate scenario, M was imprecise, although precision did increase with sample size (Fig. 6). Based on the 1200 fish released annually scenario, our study can robustly estimate F, but not M

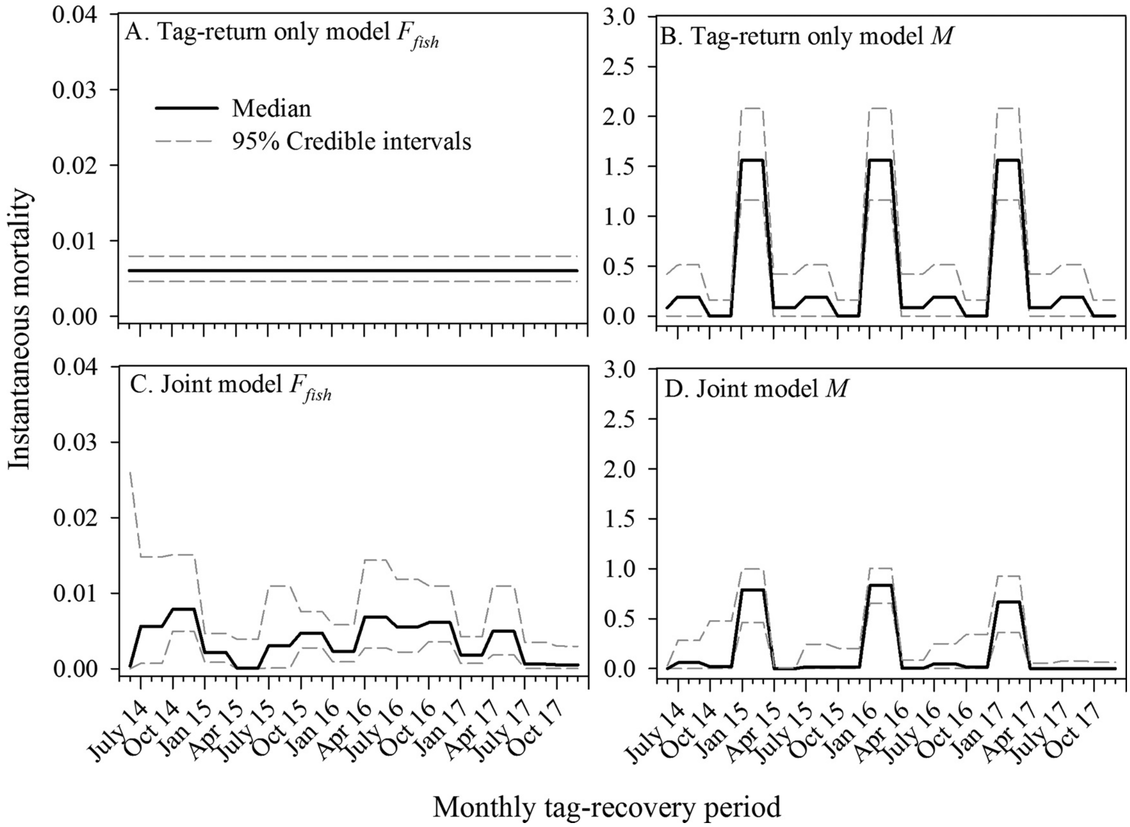

Fig. 3. A comparison of F_{fish} and M between the tag-return only model and joint model across 43 monthly tag-recovery periods (June 2014 to November 2017) from weakfish tagged in North Carolina waters. The F_{fish} was the combined commercial and recreational harvest and an assumed 10 % discard mortality rate for both sectors.

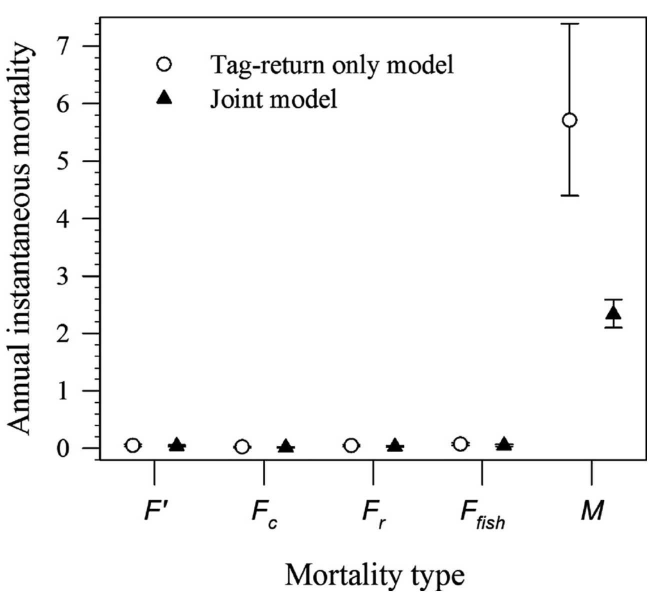

Fig. 4. Comparison between our tag-return only model and joint model for the annual instantaneous rates of discards (i.e., death of tags but fish released alive; F'), sector specific fishing mortality from recreational harvest (F_r), commercial harvest (F_c), and overall fishing mortality (total harvest plus an assumed 10 % mortality for discards; F_{fish}), and natural mortality (M). Estimates are the average mortality from mid-2014 to 2017 derived from the recoveries of weakfish tagged in North Carolina waters. Median estimates of the posterior distribution with associated 95 % credible intervals are shown.

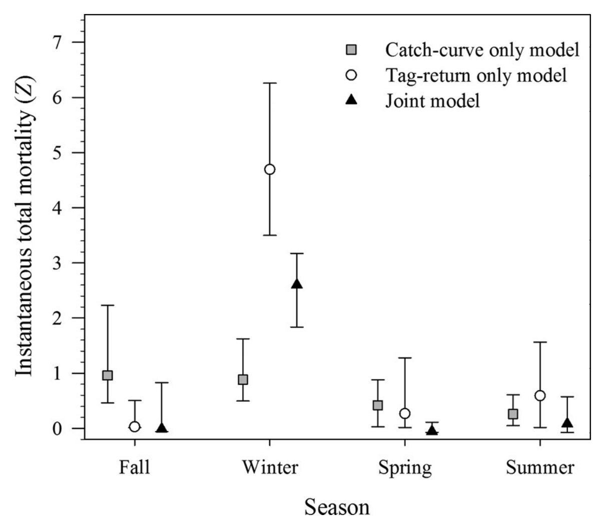

Fig. 5. Average seasonal estimates of instantaneous total mortality (Z) from the catch-curve only, tag-return only, and joint models from summer 2014 to fall 2017. Seasonal periods are 3 months and consist of January to March, April to June, July to September, and October to December. Median estimates of the posterior distribution are shown with associated 95 % credible intervals.

when using tag-return information only.

3.2. NCDMF fishery-independent gill net survey

A total of 3805 weakfish were captured in the IGNS from February 2002 to December 2017, with TL ranging from 137 to 721 mm (mean + SE: 320.2 + 1.0), and converted into fractional catches-at-age for

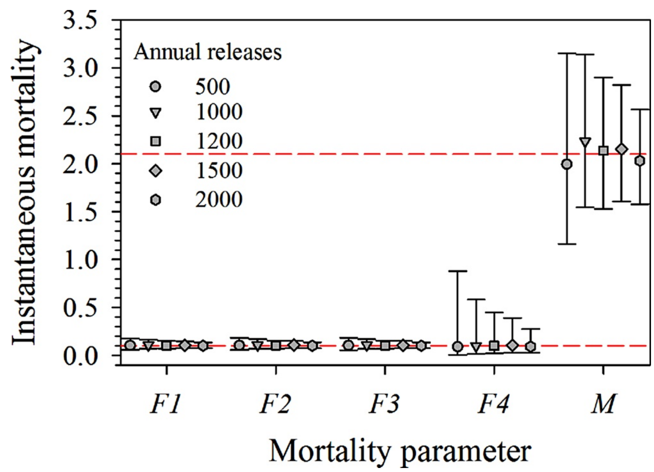

Fig. 6. Simulation of F and M across varying sample sizes. The 1200 annual releases most closely matched the releases in our weakfish tagging study. The F was estimated annually and M constant across all years. The true F was 0.1 for all years and M was 2.1 and are indicated by red dashed lines (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

ages that ranged from 0 to 8 (Fig. A.1). The majority (65 %) of weakfish collected in the IGNS were age-2 (33 %) and age-3 (32 %). During the time-series, weakfish estimated to be ages 5–8 were present in catches from 2002 to 2007, but were nearly nonexistent from 2008 to 2017 (Fig. A.1).

3.2.1. Catch-curve only model

A visual assessment of model fit found agreement between the observed CPUE for each cohort within a season and that predicted by the model (Fig. A.2). Seasonal availability of weakfish to the IGNS, or α, was the highest during spring ($\alpha_3 = 1.0$), lowest during winter at 0.10 (CrI: 0.08, 0.13), and moderate during summer at 0.69 (CrI: 0.54, 0.88) and fall at 0.70 (CrI: 0.52, 0.87). Intercept (β_1) and slope (β_2) parameters of the age-selectivity logistic function (γ_a) were estimated to be -10.33 (CrI: -10.86, -9.80) and 3.15 (CrI: 3.02, 3.28), respectively, which corresponds to a precipitous increase from low selectivity at age-1 to full selectivity at approximately age-3.

Seasonal estimates of Z were consistently highest during fall, winter, and spring and never summer during the catch-curve time-series (Fig. 7). We averaged the seasonal Z to match the timing of the tag-return study (summer 2014 to fall 2017), and found that fall and winter were comparable, but higher than spring and summer (Fig. 5). The highest seasonal Z estimate occurred either in the fall or winter for both the catch-curve and tag-return data (Fig. 5). The annual estimates of Z from catch-curve data increased through the time-series ranging from 0.96 yr^{-1} (2015; CrI: 0.38, 1.76) to 4.71 yr^{-1} (2007; CrI: 3.90, 5.20), which is equivalent to the discrete rate of annual population loss of 62–99 % (annual estimates can be summed from Fig. 7 seasonal Zs).

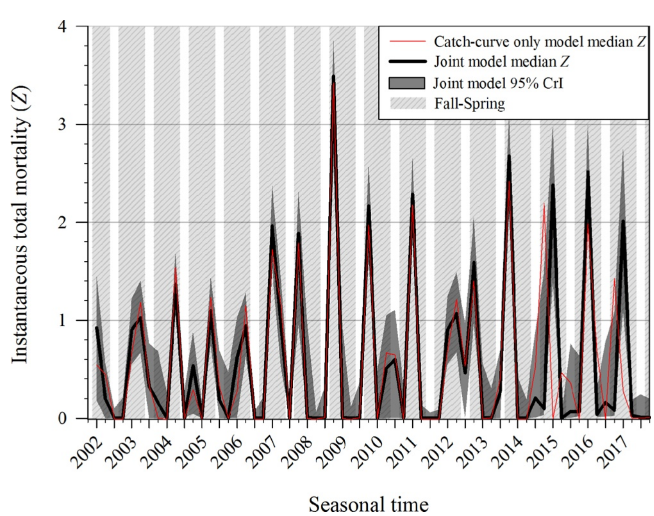

Fig. 7. Seasonal estimates of instantaneous total mortality (Z) from a catch-curve only model during 2002-2017 and a joint model that incorporates the catch-curve model and a tag-return model from mid-2014 to 2017. See Fig. 5 caption for breakdown of season by month. Median estimates of the posterior distribution with associated 95 % credible intervals are shown.

3.3. Joint model

The partitioning of Z into F and M was informed by the tag-return study, whereas the catch-curve exclusively informed Z. The proportion of Z attributable to M in winter was 0.99, 0.27 in spring, 0.87 in summer, and 0.61 in fall. Joint model estimates of F and M were precise and showed variation in the timing of mortality (Fig. 3c and d). The joint model and tag-return only model estimates of M peaked during winter months (Fig. 3b and d). The joint model F was similar in magnitude to the tag-return only model (Fig. 3a and c), and showed seasonal variation (usually highest in fall months; Fig. 3c). When comparing the annual joint model F with the tag-return only model from June 2014 to December 2017, the annual F was similarly low across fishing sectors (Fig. 4); F' was 0.03 yr^{-1} (CrI: 0.02, 0.04), F_c was 0.02 yr^{-1} (CrI: 0.01, 0.03), F_r was 0.03 yr^{-1} (CrI: 0.02, 0.04), and F_{fish} was 0.05 yr^{-1} (CrI: 0.04, 0.07). The joint model M at 2.33 yr^{-1} (CrI: 2.10, 2.59) was considerably less than the tag-return only model M at 5.71 yr^{-1} (CrI: 4.40, 7.40), but was still substantially higher than F (Fig. 4). The annual joint model Z was 2.41 yr^{-1} (CrI: 2.16, 2.66). Seasonal joint model Z estimates were more precise than the tag-return only model, and followed mortality seasonal trends of the tag-return only model (Fig. 5). Total mortality peaked in the winter (2.30 $season^{-1}$; CrI: 1.65, 2.80) and was lowest during the spring (0.03 $season^{-1}$; CrI: 0.01, 0.17), summer (0.15 $season^{-1}$; CrI: 0.01, 0.56), and fall (0.06 $season^{-1}$; CrI: 0.02, 0.78). The summed seasonal Z estimates from the joint model were the same as the catch-curve only model at 2.53 yr^{-1} as compared to the tag-return only model at 5.05 yr^{-1}.

The annual estimates of Z from our joint model were similar in trend and magnitude to the annual estimates of Z from the stock assessment update (Fig. 8; ASMFC, 2019) although there are years with large

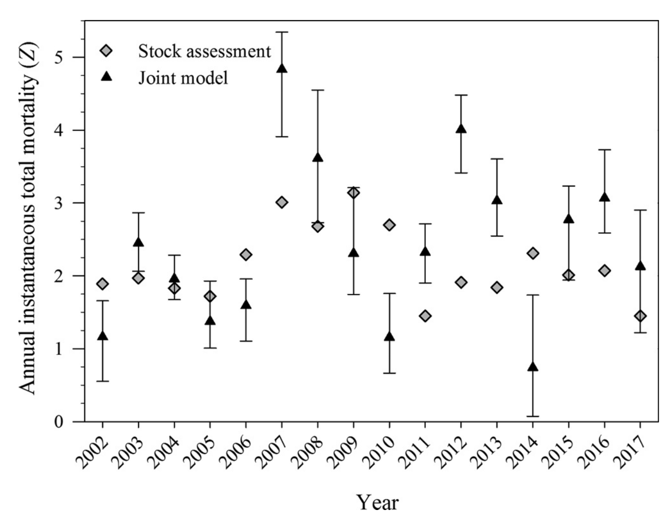

Fig. 8. Annual instantaneous mortality rates (Z) from 2002-2017 from the 2019 weakfish stock assessment update report (ASMFC, 2019) as compared to a joint tagging and fishery-independent gill net survey data (this study). The right y-axis converts annual Z to a discrete total mortality. Median estimates of the posterior distribution with associated 95 % credible intervals are shown for the joint model.

differences. The main difference between our joint model and the stock assessment exists in the percentage of Z that is F and M. Our joint model estimated that 97 % of Z was M for any given year from 2015–2017, and the remaining 3 % F. In contrast, the stock assessment M comprised between 42 %–57 % of Z, and F ranged between 43 % and 58 % (ASMFC, 2019). According to our model, the probability that M was less than 1 yr^{-1} and 1.5 yr^{-1} was 0 and 0.002 when less than 2 yr^{-1}. For only years when tagging comprised a full year, the joint model 2015 M was 2.75 yr^{-1} (CrI: 2.19, 3.17) and F_{fish} was 0.04 yr^{-1} (CrI: 0.02, 0.06), 2016 M was 2.95 yr^{-1} (CrI: 2.51, 3.5) and F_{fish} was 0.06 yr^{-1} (CrI: 0.04, 0.10), and 2017 M was 2.15 yr^{-1} (CrI: 1.42, 2.89) and F_{fish} was 0.03 yr^{-1} (CrI: 0.02, 0.05).

4. Discussion

Weakfish stock biomass is low and management actions have not led to rebuilding (ASMFC, 2016); therefore elucidating the sources of high mortality are important to guiding management. We used a tag-return study and fisheries-independent gill net catch-curve to estimate mortality at a seasonal scale, allowing for insight into the timing and possible causes of mortality. After accounting for key auxiliary parameters (i.e., tag-reporting rate and tag loss), our integrated tag-return and catch-curve model conclusively shows that M is the driving force in weakfish population dynamics, consistent with previous stock assessment conclusions (ASMFC, 2006; 2016; NEFSC, 2009). Furthermore, our work strongly suggests that the current weakfish stock assessment has been underestimating M in recent years and the timing of M occurs during weakfish migration and overwintering periods.

Weakfish stock assessment estimates of F may be overestimated if M is underestimated. The stock assessment estimated an increasing M from 1982 to 2017 (ASMFC, 2016, 2019), but the uncertainty remains in how much of Z is attributable to M. The upper bound assumption was based on the best available data in the form of life-history derived M estimates at the time of the stock assessment model development (Yan Jiao, Virginia Tech, personal communication). In addition, to our knowledge an annual M greater than 1 yr^{-1} for multiple years is an uncommon occurrence for non-forage species such as weakfish (e.g., Gislason et al., 2010). Our joint model estimates of M were > 1 yr^{-1} from 2015–2017 which contradicts the stock assessment M assumption. In addition, stock assessment estimates of M from 2007 to 2017 approached the upper bound of 1 yr^{-1} suggesting that an uninformative or higher bound may have led to higher estimates of M (Fig. 49 in ASMFC, 2019). For stock assessments that internally estimate M, the estimates of F and M are inherently confounded and their accuracy relies on the validity of the assumptions surrounding M (Lee et al., 2011; Johnson et al., 2015).

The current management plan appears to be effective in reducing harvest. For our study, the annual percentage of Z due to F was miniscule at 3% (2015–2017), and encompassed mortality from both the commercial and recreational fisheries in North Carolina. At a coast-wide scale, landings and discards have been consistently low at < 1,000 metric tonnes (t) since 2008 as compared to the high of ~18,000 t in 1986 (ASMFC, 2019). Currently, commercial harvest is limited to a 45-kg daily bycatch trip-limit and recreational creel limit to one fish with TL over 305 mm (ASMFC, 2016). With the implementation of stricter minimum size and bag limits, the number of discards tend to increase (Harper et al., 2000). Despite the relatively high number of discards (49 out of 115 tag returns), we assumed that only 10 % of the released fish died (ASMFC, 2016); therefore, discard mortality (F' * 0.10) had minimal impact on the final estimates of overall F. The estimates of F would be negatively biased should actual mortality of discarded fish be greater than 10 %, either due to catch-and release-mortality or inaccurate reporting (i.e., reported as discard when fish was in fact harvested). However, even 100 % mortality of discards would not affect the overall determination that M, relative to F, accounted for the majority of annual Z.

Annual joint model estimates of M were consistently high. Extensive periods of high M may be the cause for dramatic population fluctuations in the weakfish stock since the late eighteenth century (Cushing, 1982; Jiao et al., 2012; ASMFC, 2016). Longer periods of high M (i.e., multi-year) is in direct contrast to the episodic M (i.e., single year) experienced by spotted seatrout, a congener of weakfish. Spotted seatrout in North Carolina and Virginia experience elevated M based on winterkill events (Ellis et al., 2017, 2018). However, both spotted seatrout and weakfish can endure high M, as they exhibit r-selected traits such as rapid growth, early maturation, a protracted spawning period and prolificacy (Merriner, 1976; Shepherd and Grimes, 1984; Lowerre-Barbieri et al., 1995; Bortone, 2003; Nye et al., 2008).

Weakfish estimates of M and Z indicated seasonal variability. The tag-return only model estimates of M and Z were highest during winter, whereas based on the last 3.5 years of time-series, the catch-curve only model estimates were highest in the fall. Across 17 years of seasonal Z estimates from the catch-curve only model, the highest peaks were always during fall, winter, and spring, aligning with the weakfish overwintering period where weakfish emigrate from natal estuaries to warmer continental shelf waters in the fall, and return to spawn the following spring. The timing of weakfish estuarine emigration and immigration are year-dependent (Krause et al., 2020), possibly leading to the interannual seasonal variation in high Z across the time-series of the catch-curve only model. Regardless of the exact timing of mortality, a large percentage of weakfish are not surviving the overwintering period. For the tag-return only model, the high winter Z essentially eliminates all tags at-risk during this season. The timing of tag-returns matches the model output, as only 4 out 140 weakfish returned after winter. Although mortality was not estimated (nor any key auxiliary parameters), the Virginia Gamefish Tagging Program found similar results in the timing of returning fish (Lucy et al., 2000; Lucy and Bain, 2001). A total of 8980 t-bar tagged, low-reward weakfish were released from 1996 to 1999, of which only 1 out of 65 returns was returned after going through a winter. In a coast-wide telemetry study of weakfish released in summer and fall, only 2 out of 149 fish with long-lived transmitters (> 300 days) were detected alive in the subsequent year after overwintering (Krause et al., 2020). The most likely explanation for the high estimates of M or Z during the overwintering period is predation (Krause, 2019). Weakfish overwinter with their main predators on the continental shelf and total predator consumption was similar in magnitude to the sum of the stock assessment biomass attributable to M (Krause, 2019).

Our tag-return model estimates of F were robust based on our simulation. However estimates of Z and M appeared to be biased high in our tag-return only model, given the presence of older fish in the population (Fig. A.1). Tag-return only mortality estimates were robust to gross violations of the 100 % post-release survival and tag-reporting, and we accounted for tag-loss. We found that our estimates of M were imprecise compared to F, a symptom of low tag-return numbers caused by management restricting F to < 0.1 (Pollock et al., 2004). A concurrent weakfish telemetry study similarly estimated annual Z on discrete scale to be > 99 % (Krause et al., 2020). Simulations for telemetry models that estimate F and M, show M (and consequently Z) is biased high at low sample sizes (n < 25 telemetered fish; Hightower and Harris, 2017). The high loss rates observed with the weakfish stock (~90 % annual mortality) would lead to low sample sizes of telemetered fish and may have led to mortality rates that were biased high in the Krause et al. (2020) study; this same phenomenon may be a potential explanation for the apparent bias in the tag-return study. Additional simulations demonstrated that the tag-return model M and consequently Z were hypersensitive to the number of tag-returns recovered after an overwintering period, especially when approaching 0 returns with low numbers of at-risk tagged fish (Krause, unpublished data). We did not include second recapture events to remove any biases of catch and release mortality, causing the exclusion of a fish that was recaptured after two overwintering periods (at-liberty = 682 days).

Another possible explanation as noted by Seitz et al. (2019) for biased mortality estimates is that predators may select for or be more successful at capturing tagged weakfish over non-tagged weakfish; this would lead to *M* and *Z* estimates to be biased high. Regardless of the bias, the conclusion that weakfish mortality is high still holds as evidenced by the high annual total mortality estimated in the joint model.

The catch-curve only model estimated annual *Z*s comparable to the latest weakfish stock assessment update report (ASMFC, 2019). As IGNS is conducted every year, new data can be incorporated into the catch-curve model with relative ease, allowing for seasonal estimates of *Z* within 12 months of data collection. Hence, management can promptly respond to changes in *Z* using information from the catch-curve only model as compared to waiting multiple years until the next stock assessment update.

Integrating multiple independent datasets promotes accurate and precise estimates of mortality. The tag-return study allowed for a partition of *Z* into *F* and *M*, whereas the catch-curve model solely estimated *Z*. In a tagging study, the ability to robustly estimate *M* is impaired when *Z* is high as noted earlier. Increased sample size may allow for greater detection of tags that survived an overwintering period (Liljestrand et al., 2019), but may be cost-prohibitive for weakfish because of a high *Z*. Jointly estimating *Z* using the catch-curve and tagging models overcame the aforementioned limitation. The *F* estimates were similar between the tag-return only and joint models, and our simulation showed that *F* was reliably estimated. The tag-return and catch-curve only models had high temporal resolution (i.e., month or seasons) in mortality estimates that both exhibited mortality peaks during the fall and winter, and was manifested in the joint model estimates.

Future weakfish stock assessments need to incorporate additional information to accurately estimate *M*. The bounds for the 2015–2017 estimates of *M* in the stock assessment could be informed by our joint model estimates. It is true that the spatial scales differ between the stock assessment and our study which is North Carolina centric (catch-curve only = Pamlico Sound, tag-return only = North Carolina [heavily weighted toward the vicinity of Cape Lookout]), but our study results may be representative of the entire stock. North Carolina landings comprised 32 % of total recreational landings and 40 % of total commercial landings (averaged from 2002 to 2014; ASMFC, 2016). The peaks in *M* also occur when much of the stock overwinters purportedly off the coast of North Carolina (Nesbit, 1954). In addition, with predation hypothesized as the main cause of *M* (ASMFC, 2006; Krause, 2019), fisheries management can incorporate this information into the stock assessment to increase precision of *M*, such as partitioning *M* into M_1 and M_2, where M_1 is residual natural mortality and M_2 is predation natural mortality (e.g., Overholtz et al., 2008), or creating a predation pressure index (Richards and Jacobson, 2016; Cao et al., 2017). Explicit incorporation of predation mortality may allow for more realistic recovery times (e.g., Harvey et al., 2008).

The accuracy of our tag-return mortality estimates and ultimately our joint model relied on fulfilling model assumptions (see Methods), especially for the key auxiliary parameters ϕ, Ω, ρ, and λ. We assumed acute and chronic tagging mortality (ϕ) to be zero because of our strict landing, handling, and release requirements; over 91 % of tagged fish released by researchers and an experienced collaborative tagger; and a low field-estimated catch-and-release mortality of 10 % (Malchoff and Heins, 1997; Swihart et al., 2000; Gearhart, 2002; ASMFC, 2016). Our field-based tag loss approach estimated a low immediate tag shedding (ρ) at 5%, but chronic loss (Ω) on a discrete scale was substantial at 24 % annually. We based our tag type and procedure on Ellis et al. (2018), who estimated similar tag shedding rates on a congener species (ρ = 3%; Ω, = 27 % [discrete scale]). The apparent difference in tag loss laterality (i.e., right or left lateral side of fish) could not be adequately modeled based on the low number of returns, but any potential bias would not affect the finding that *F* is low relative to *M*. Historically, tagging weakfish with t-bar tags has yielded relatively low return rates at < 1% (Music and Pafford, 1984; Lucy and Bain, 2001; Clark, 2008). Our study, in combination with Ellis et al. (2018) and Music and Pafford (1984), suggest return rates can be increased with the use of internal anchor tags. Additionally, double-tagging and high-reward tags appeared to have increased the percentage of tags returned compared to previous studies (Lucy and Bain, 2001; Clark, 2008). Furthermore, high-reward tags allowed us to simplify our model (i.e., fewer tag-return matrices) with the assumption of 100 % reporting (Sackett and Catalano, 2017). It is possible that the use of high-reward tags may have biased *F* high as fishermen may have been influenced to target weakfish. It is often argued that high-reward tagging programs are too expensive to conduct (Miranda et al., 2002; Meyer and Schill, 2014). However, for weakfish and others with low exploitation rates, tag-return studies would not be possible without the high-reward component (Pollock et al., 2001; Meyer and Schill, 2014; Sackett et al., 2018). For long-term sustainability of valuable exploited stocks, management needs to weigh the importance of robust estimates of *M* against the monetary cost of a high-reward study.

5. Conclusions

Mortality estimates are paramount to understanding population dynamics, especially for weakfish, whose stock has not rebuilt despite harvest restrictions (ASMFC, 2019). Our weakfish tag-return study clarified the relative importance of *F* and *M* to *Z*, elucidating that *M* consistently and substantially exceeded *F*. In addition, the weakfish specific estimate of *M* from our joint model, indicates the stock assessment may have underestimated *M* and overestimated *F* in recent years. For stocks such as weakfish that are not recovering after harvest restrictions, stock assessment scientists need to scrutinize the assumptions surrounding *M* and recommend research and funding for studies estimating species specific *M* (e.g., tagging studies). The stock assessments of weakfish in recent periods have continually refined estimates of *M* based on best available data (ASMFC, 2006; 2016; NEFSC, 2009), and we hope that our findings will be useful to future weakfish stock assessments. With natural mortality currently driving weakfish population dynamics, further harvest restrictions would most likely be ineffective in stock rebuilding. Peaks in mortality were highest fall to spring, providing additional evidence that the cause of the high *M* is predation during the weakfish migration and overwintering periods (Krause, 2019). Estimating mortality through a joint model that incorporates comprehensive tag-return study and IGNS catch-curve complements traditional stock assessment approaches by providing independent and reliable information on the sources and levels of mortality for a stock with low biomass.

CRediT authorship contribution statement

Jacob R. Krause: Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **Joseph E. Hightower:** Conceptualization, Methodology, Software, Writing - review & editing. **Stephen J. Poland:** Resources, Data curation, Writing - review & editing. **Jeffrey A. Buckel:** Conceptualization, Writing - review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fishres.2020.105725.

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