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## ARTICLE

## Estimates of Red Drum Mortality via Acoustic Telemetry

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### Abstract

Subadult (age < 3) Red Drum *Sciaenops ocellatus* support a valuable recreational fishery, and mortality estimates for young Red Drum are needed for proper management. To obtain these estimates, age-1 and age-2 Red Drum were implanted with acoustic transmitters and external Floy tags in two coastal Alabama rivers (Fowl and Dog rivers). Fates of tagged fish were inferred from stationary receiver detections and active relocations over 1 year. These fates were used in a Bayesian multistate model to estimate instantaneous monthly and annual mortality and emigration rates for each river and overall from both rivers. Instantaneous monthly fishing mortality ( $F$ ) ranged from 0.001 to 0.112 (annual  $F = 0.414$ ) in Dog River, from 0.001 to 0.126 in Fowl River (annual  $F = 0.309$ ), and was 0.001–0.054 (annual  $F = 0.337$ ) overall. Instantaneous monthly natural mortality ( $M$ ) ranged from 0.001 to 0.002 (annual  $M = 0.069$ ) in Dog River, from 0.001 to 0.036 (annual  $M = 0.178$ ) in Fowl River, and from 0.001 to 0.017 (annual  $M = 0.090$ ) overall. The overall annual estimate of instantaneous total mortality ( $Z$ ) was 0.435. The median escapement percentage was estimated at 36.3% (95% posterior credible interval = 19.5–56.0%) using  $M$  and  $Z$  from the overall model. Unfortunately, the error on this estimate was large and inconclusive as to whether the 30% escapement goal for juvenile Red Drum to the adult population from Dog and Fowl rivers is being met. Monthly residency estimates were typically greater than 0.90, and overall annual residency was estimated at 0.716. Fishing mortality estimates from the current study are higher than recent catch curve estimates that did not include young Red Drum. These results demonstrate that young Red Drum need to be accounted for when generating mortality estimates and provide needed data for the Red Drum recreational fishery.

Mortality of fishes is an essential piece of information for proper fisheries management, stock assessment, and the continued persistence of valuable fish stocks in response to variable fishing and environmental pressures (Hilborn and Walters 1992; Harris and Hightower 2016; Hightower and Harris 2017). Fish mortality rates can be obtained using a variety of techniques, such as catch curve analysis (Ricker 1975; Hilborn and Walters 1992), longevity estimators (Hoenig 1983; Hewitt and Hoenig 2005; Then et al. 2015), and/or mark–recapture models (Pine et al. 2003, 2013). Total mortality ( $Z$ ) must be divided into natural mortality ( $M$ ) and fishing mortality ( $F$ ) for

exploited species, and using telemetry studies as extensions of traditional mark–recapture designs is one way to obtain these mortality components (Hightower et al. 2001; Hightower and Harris 2017). This method can provide benefits over traditional tagging studies because (1) fish do not have to be physically recaptured and (2) multiple fish fates, including  $M$  and  $F$ , may be inferred from detection data (Hightower et al. 2001; Hightower and Harris 2017). Furthermore, mortality estimation across multiple spatial and temporal scales may be possible, elucidating seasonal, regional, and environmental drivers of mortality (Bacheler et al. 2009a; Ellis et al. 2017).

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The Red Drum *Sciaenops ocellatus* is an estuarine-dependent, euryhaline fish that supports valuable recreational fisheries along the Atlantic and Gulf of Mexico (GOM) coasts. Harvest of all Red Drum in GOM federal waters has been closed since 1988 given steep population declines prior to the closure, and a 30% escapement goal from state waters was implemented to rebuild the adult spawning stock (Gulf of Mexico Fishery Management Council 1988; Powers and Burns 2010; Powers et al. 2012). Escapement is defined as the number of Red Drum from the inshore fishery that escape to the adult spawning stock divided by the number that would have contributed to the spawning stock given no inshore fishery (Gulf of Mexico Fishery Management Council 1988). To meet this goal, each GOM state has implemented a harvest slot size and daily bag limits (ADCNR 2018; FWC 2018; LDWF 2018; MDMR 2018; TPWD 2018). In Alabama, the slot is from 406.4 to 660.4 mm (16–26 in); anglers can keep three Red Drum per person per day, and one of those may be over the slot range (ADCNR 2018).

Unfortunately, the biology and life history of Red Drum make it difficult to empirically calculate and define escapement. Adult Red Drum spawn near estuary passes during the fall, and larvae are carried into estuaries, where they settle (Overstreet 1983; Lowerre-Barbieri et al. 2018). Juvenile and subadult Red Drum remain in estuaries and reach the lower end of the harvestable slot limit between ages 1 and 2 (Porch 2000). After maturation (ages 2–6), these fish presumably move out of the estuary and offshore into federal waters (Overstreet 1983; Wilson and Nieland 1994; Winner et al. 2014), where it is assumed that they contribute to the adult spawning stock and have escaped the fishery, given the harvest moratorium. However, many adult Red Drum utilize estuarine and near-shore waters and estuarine spawning aggregations have been found (Lowerre-Barbieri et al. 2008; Reyier et al. 2011; Powers et al. 2012). These adult fish that remain nearshore and within estuaries are still vulnerable to harvest in many GOM states, including Alabama, where anglers can harvest Red Drum above the slot limit (ADCNR 2018). Although mature adult fish can still be harvested and maturation timing differs, escapement must still be calculated. Therefore, escapement has been functionally defined and calculated as the number of fish that survive to age 4 divided by the number that would have survived to age 4 in the absence of a fishery (AMRD 2008; Powers and Burns 2010). This is because the majority of fish at age 4 (72%) are mature (Wilson and Nieland 1994) and are assumed to be offshore (Overstreet 1983).

Although federal waters have been closed to harvest since 1988, recreational landings have continued to increase within state waters (Porch 2000; SEDAR 2016). Recent Red Drum mortality estimates from the northern GOM do not account for this recreational mortality

because catch curve estimates have only included age-3 and older fish (Hightower et al. 2016), and by age 3 all fish are likely outside of the slot range (Porch 2000). Therefore, the need for mortality and escapement estimates for the subadult inshore fishery exists and was identified during the recent data-limited stock assessment for GOM Red Drum (SEDAR 2016). Given this need, the main objective of the present study was to provide estimates of  $F$  and  $M$  for the inshore Red Drum population from two coastal Alabama rivers. Instantaneous rates of  $F$ ,  $M$ , and  $Z$  were obtained on monthly and annual time scales with acoustic telemetry, and the annual rates were used to calculate overall escapement from both rivers.

## METHODS

**Study sites.**— Mobile Bay is a large-river drowned estuary in Alabama, receiving the second-largest river discharge into the GOM (Dzwonkowski et al. 2011). The estuary on average is 3 m deep, 50 km long, and 14–34 km wide (Schroeder et al. 1990; Schroeder and Wiseman 1999; Dzwonkowski et al. 2011). In addition to the main riverine inputs into Mobile Bay, smaller river drainages empty into the estuary along both the eastern and western shorelines. Dog and Fowl rivers are tidally influenced rivers located along the western shore of Mobile Bay (Figure 1). Dog River, located in northern Mobile Bay, is 12.94 km long in the main channel and has two large tidal creeks that enter the river on the west side. Fowl River is located further south and has historically been split into two sections: East Fowl and West Fowl. East Fowl is connected to Mobile Bay by a narrow river mouth, and West Fowl is connected to Mississippi Sound via a large river mouth. These two sections of river are connected by a narrow (0.2-km-wide), man-made channel, allowing water and fish movement between these river sections. Fowl River is 12.23 km long from the mouth of West Fowl to the connection with East Fowl, and East Fowl is 11.53 km long from freshwater sources to the river mouth.

**Fish collection and tagging.**— Red Drum were collected via hook and line in Dog and Fowl rivers during August, September, and October 2016 and were fitted internally with acoustic transmitters. Upon collection, Red Drum were transferred to an aerated recirculating live well to allow for recovery from hooking and fight stress and to monitor for immediate hooking mortality. After a minimum of 5 min in the live well, a Red Drum was removed and placed in a plastic container with ambient water and tricaine methanesulfonate (MS-222) to anesthetize the fish. After anesthetization, the Red Drum was measured, weighed, and placed upside-down in a tagging cradle, with ambient water flowing across the gills. All Red Drum were fitted with a Vemco V-13 acoustic transmitter programmed on high power, with a ping interval randomly

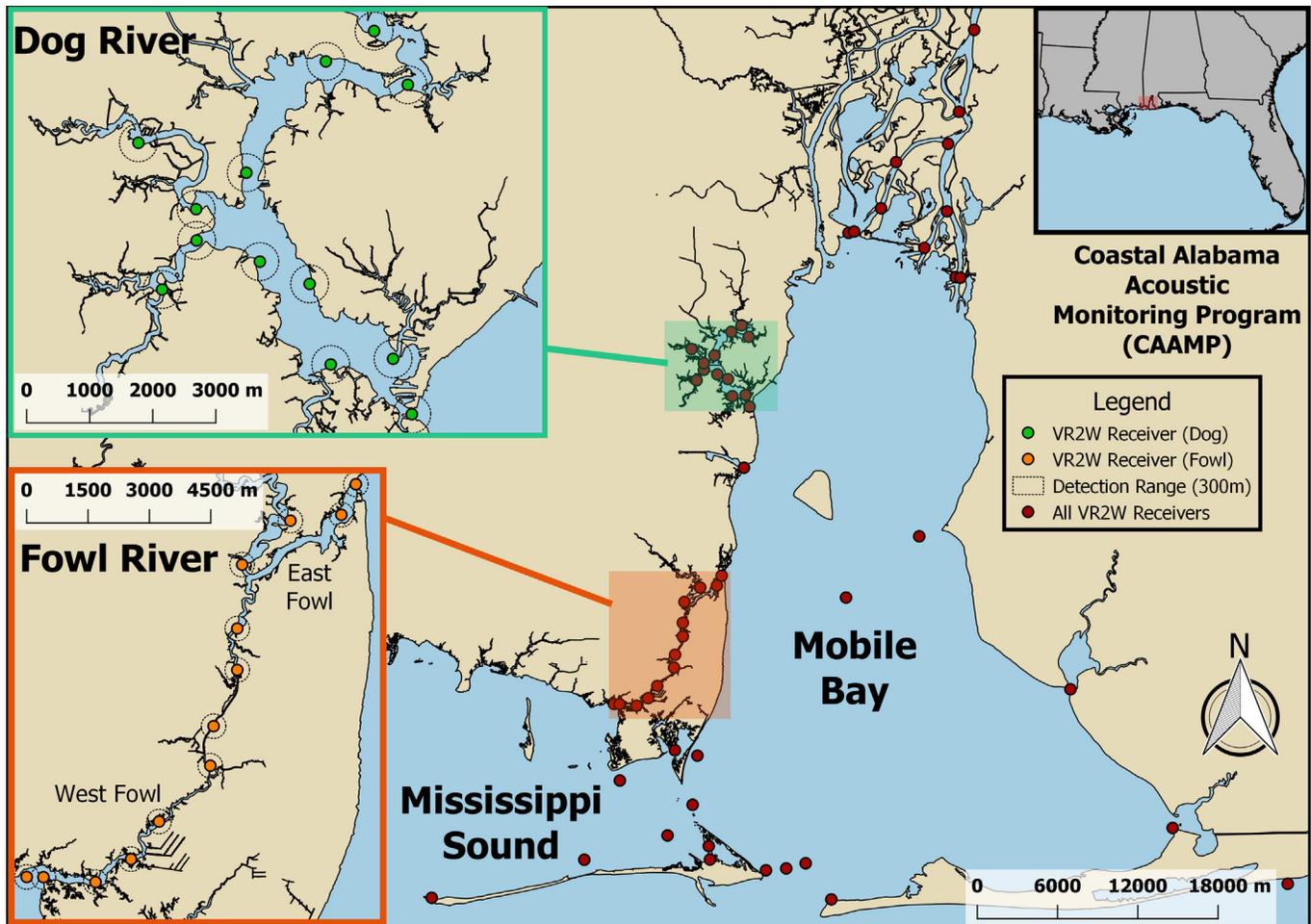


FIGURE 1. Locations of Vemco VR2W acoustic receivers in Dog River and Fowl River, Alabama, and within the larger Coastal Alabama Acoustic Monitoring Program.

ranging from 30 to 90 s, resulting in an estimated 362 d of battery life. The transmitter was implanted in the body cavity of the Red Drum with a small incision at least 2 cm anterior to and 1 cm dorsal of the anus. The incision was made parallel to the body and closed with two to three interrupted monofilament sutures after tag insertion. An internal anchor Floy tag (FT-1-94) was placed on the opposite side of the body cavity mirroring the incision site location and included an externally visible tag with reporting information and the word “reward.” A low-value reward was used for this project, and anglers would receive either a t-shirt or hat after reporting a recaptured fish. After tagging, all Red Drum were returned to the live well and allowed to recover until swimming behavior returned to normal; fish were then released back into the study system near where collection occurred.

*Telemetry methods, fate assignment, and mortality analysis.*—Tagged Red Drum were monitored with a combination of passive acoustic detections and active

relocations. Vemco VR2W receivers were deployed within each river (Dog River:  $n = 13$ ; Fowl River:  $n = 13$ ; Figure 1). The mouths of both rivers were completely covered by the minimal detection range (300 m) of at least one receiver to detect Red Drum emigration from their respective receiver array. Detection range was tested using suspended transmitters and caged, telemetered Red Drum. Briefly, transmitters and fish were moved at fixed 100-m intervals (from 0 to 1,000 m) away from a stationary receiver in each river and were held for 5 min. At 300 m, 100% of detections occurred, consistent with other studies (Ellis et al. 2017); in calm conditions, transmitters were even detected as far as 700 m away. False detections were identified with the False Detection Analysis tool in Vemco VUE software (Vemco 2019), and detections that were deemed questionable—given a greater number of long detection intervals (12 h) than short ones (30 min)—were investigated to determine their validity. All questionable detections ( $n = 88$ ) were retained in analyses given that the

time and receiver locations between detections were feasible. These tight river arrays were placed within the broad Coastal Alabama Acoustic Monitoring Program array (Figure 1), thereby allowing for confirmation of some Red Drum emigration during the study.

Active relocation of Red Drum occurred on a monthly interval and involved use of the Vemco VR100 and VH-165 omnidirectional hydrophone. This hydrophone was mounted to either a small skiff or a stand-up paddleboard, and all accessible water was checked for telemetered Red Drum. The boat or paddleboard moved through the rivers and adjacent tidal creeks at a constant speed of around 3 km/h until a tag was intercepted, and then all movement was ceased to obtain at least two detections of a tag before movement re-commenced. The VR100 recorded the date, time, and GPS coordinates of the receiver for each detection. If multiple transmitters were detected in an area, as evident through many signals colliding on the VR100, movement did not resume until all unique present transmitter IDs received two detections.

Monthly observed fates of telemetered Red Drum were inferred from both passive detections and active relocations following previously developed methods (Hightower et al. 2001; Bacheler et al. 2009a; Ellis et al. 2017). Red Drum assigned as alive (fate = 1) were fish that had moved between active relocations, had been detected on more than one receiver in a given month, or had a detection history on a single receiver indicative of movement (time between detections was greater than the maximum ping interval of 90 s; Harris and Hightower 2011). Red Drum that died of natural causes (i.e., natural mortalities; fate = 2) were identified as stationary tags that remained within the river system: either constant detections on a single receiver or active relocations of an individual in the same location for 4 months, with no movement data from the stationary array. Red Drum that emigrated from the array within a given month (fate = 3) were identified based on having their last detection on receivers at river mouths and no subsequent detections within the river receiver arrays. Red Drum with transmitters not detected either on the stationary array or during the monthly VR100 search were classified as unobserved (fate = 4). All fate assignments were placed in the month immediately after a deterministic fate occurred. For example, if the last time a tag was detected in an array was October 15, the tag was clearly moving before then, and the tag did not pass the receivers at the mouth of the river, then that fish received a fate of 1 for October given that it was alive in October and it received a fate of 4 for November and all remaining months until tag expiration. A censorship interval of 7 d posttagging was used to account for tagging effects (Friedl et al. 2013; Ellis et al. 2017); if an emigration or mortality occurred within this time period, then these Red Drum were censored from all analyses. Total length at fate was

calculated by taking the difference in predicted length from northern GOM growth curves (Porch 2000) between age-1 (328.27 mm) and age-2 (561.21 mm) Red Drum or between age-2 and age-3 (715.34 mm) Red Drum and dividing that by 365 (<561 mm: 0.64 mm/d; ≥561 mm: 0.42 mm/d). Depending on TL at tagging, the appropriate value was multiplied by days detected and added to TL to obtain the predicted TL at fate. Predicted weight (WT, kg) at fate was calculated with the length–weight equation ( $WT = 10^{-8} \times TL^{2.9972}$ ) from Hightower et al. (2016).

A Bayesian multistate model adapted from Ellis et al. (2017) and Hightower and Harris (2017) was used to generate monthly instantaneous estimates of  $F$ ,  $M$ ,  $Z$ , emigration rate ( $E$ ), detection probability ( $p$ ), and discrete residency within rivers ( $R = e^{-E}$ ). The flexibility of this framework also allowed for annual instantaneous estimates of  $F$ ,  $M$ ,  $Z$ , and  $E$  and the resulting discrete estimates of annual mortality ( $A$ ), survivability ( $S$ ), and residency ( $R$ ) from September 2016 to August 2017. This interval was chosen for annual estimates given the low numbers of fish present in the study ( $n = 18$ ) during August 2016. Briefly, this model utilized two probability matrices: one for the true fate transitions, and one for generating the probability that the observed fates were correct. Instantaneous mortality estimates were generated based on the probability of the fate at time  $t + 1$  given fate at time  $t$ , where  $t = \text{month}$  in this model. The estimate of  $M$  was generated based on the probability that an alive Red Drum transitioned from fate 1 to fate 2, the estimate of  $E$  was generated based on the probability that an alive Red Drum transitioned from fate 1 to fate 3, and the estimate of  $F$  was generated based on the probability that an alive Red Drum transitioned from fate 1 to fate 4 (Appendix). Although the monthly fates of unobserved Red Drum were unknown, when fish were unobserved for multiple months the probability of harvest increased. This model was run on each river, and overall estimates were obtained by combining rivers. Models were implemented with JAGS (Plummer 2003), running through R version 3.5.1 (R Core Team 2018), and were initiated with uninformative priors (natural logarithms of  $E$ ,  $F$ , and  $M$  [uniform{−10, 1}];  $p$  [uniform{0, 1}]). Three Markov chains with 60,000 iterations (1,000 iterations used for burn-in) were used to estimate the posterior probability distributions for each parameter. Convergence was assessed both through visual inspection of the trace plots and with the Brooks–Gelman–Rubin statistic.

An overall escapement percentage of Red Drum to the adult spawning stock biomass was estimated from both rivers using the following equation within the Bayesian multistate model (Appendix):

$$\text{Escapement} = e^{-Z \times 3} / e^{-M \times 3},$$

where  $Z$  and  $M$  are the annual instantaneous total and natural mortality rates, respectively. This equation assumes

that instantaneous mortality operates to the same extent on all ages of fish and that fish from age 1 to age 4 are vulnerable to recreational harvest. The model also assumes that fish at age 4 are mature and contributing to the adult spawning stock biomass. A multiplier of 3 years was used for this calculation given that fish are assumed to recruit to the inshore recreational fishery at around age 1. Although some age-0 fish could be harvested given the minimum slot size (406.4 mm) in Alabama, most age-0 fish are below this size (Hightower et al. 2016).

Telemetry-based multistate models involve the assumptions of traditional mark–recapture models and further telemetry assumptions outlined by Hightower et al. (2001) and Hightower and Harris (2017). The first assumption is that all telemetered Red Drum in specified states have equal mortality rates and detection probabilities; this was assumed to be true. Second, transmitter failure and expulsion are assumed to be negligible; this assumption has been confirmed elsewhere (Bacheler et al. 2009a; Moulton et al. 2016), and multiple tags lasted beyond the expiration date in this study, providing support for proper transmitter operation. The third assumption is that tagging mortality is acute and happens within the first 7 d of tagging (i.e., a function of the 7-d censorship period). Fourth, telemetered Red Drum are assumed to behave independently with respect to detection and mortality probabilities (this was assumed to be true). The fifth assumption is that telemetered Red Drum are representative of the unmarked population and thoroughly mix with them; this was confirmed through reporting of angler harvest of tagged and untagged fish together. Sixth, emigrated Red Drum are assumed to be correctly identified. The seventh assumption is that detections are classified without error. Although telemetry-based multistate models have these assumptions, many were accounted for and those that were not are highlighted in the Discussion.

## RESULTS

Seventy-nine Red Drum were tagged during the study, and 69 were included in analyses after the censorship period. Thirty-six fish ranging in size from 291 to 637 mm TL were implanted with acoustic transmitters in Dog River, and 31 tags were viable for use in mortality and movement analyses (Tables 1, 2). Two Red Drum emigrated within 1 week of tagging, and three fish were likely surgery mortalities given that no movement occurred from the tagging site for the smallest two individuals (291 and 310 mm TL) and movement ceased within 1 week of tagging for the other fish. Forty-three Red Drum ranging in size from 333 to 667 mm TL were tagged in Fowl River, and 38 fish were viable for mortality and movement analyses (Tables 1, 2). One Red Drum was censored because of likely surgery mortality, given no movement from the tagging site;

three fish were only detected on the day of tagging; and one fish emigrated 6 d after tagging.

Red Drum were frequently encountered on both stationary and mobile receivers, resulting in reliable detection histories (Dog River: 1,431,151 detections; Fowl River: 1,053,445 detections), and harvest of 16 Red Drum (Dog River: 9 fish; Fowl River: 7 fish) was inferred from both rivers (Tables 1, 2, A.1, A.2). Forty-four percent of inferred harvests in Dog River were confirmed on our tagging hotline, and 14% of inferred harvests in Fowl River were confirmed. One tag was found stationary in an illegal gill net in Fowl River as well. Median instantaneous monthly rates of  $F$  ranged from 0.001 to 0.112 in Dog River, ranged from 0.001 to 0.126 in Fowl River, and were 0.001–0.054 overall (Figure 2). Annual median estimates of instantaneous  $F$  (September 2016–August 2017) were 0.414 (95% posterior credible interval [CrI] = 0.205–0.742) in Fowl River, 0.309 (95% CrI = 0.131–0.616) in Dog River, and 0.337 (95% CrI = 0.194–0.545) overall (both rivers). Two Red Drum that were confirmed harvests would have been misclassified as emigrations without angler reporting on our hotline, given that their last detections were on receivers at river mouths; thus, there is the potential that other unconfirmed emigrated fish (Dog River: 1 fish; Fowl River: 5 fish) were harvested. Therefore, models were re-run with fates changed from emigration to harvest for these individuals, resulting in elevated  $F$ -estimates (Table 3).

Three natural mortalities were observed in Fowl River, and none was observed in Dog River; all three natural mortalities in Fowl River were stationary tags that were found via active VR100 relocations (Tables 2, A.2). Although no natural mortalities were observed in Dog River,  $M$  was retained in the model to account for potential error. The estimated monthly instantaneous median  $M$  ranged from 0.001 to 0.002 in Dog River, from 0.001 to 0.036 in Fowl River, and from 0.001 to 0.017 overall (Figure 2). Annual median estimates of instantaneous  $M$  in Dog River were 0.069 (95% CrI = 0.015–0.233), 0.178 (95% CrI = 0.060–0.415) in Fowl River, and 0.090 (95% CrI = 0.031–0.204) overall. Although unlikely, four Red Drum that were inferred harvests may have been small enough (<500 mm) to be removed by avian predators (Tables 1, 2), and models were re-run with these fish as natural mortalities, resulting in elevated estimates of  $M$  (Table 3).

The instantaneous monthly mortality estimates were used to calculate annual total instantaneous mortality rates, discrete annual survival and mortality, and the overall escapement percentage from both rivers. Annual instantaneous  $Z$ -estimates were similar among Dog River (0.498; 95% CrI = 0.265–0.848), Fowl River (0.502; 95% CrI = 0.264–0.869), and overall (0.435; 95% CrI = 0.269–0.663). Therefore, discrete annual  $S$ -estimates for Dog River (0.608; 95% CrI = 0.428–0.767), Fowl River (0.605;

TABLE 1. Duration for which each Red Drum was detected (days detected) within Dog River, Alabama, and outside of the river (in parentheses); Red Drum TL (mm) at tagging; and the predicted TL (TL [fate]) and weight (WT [fate]; kg) when fate assignment occurred. The final assigned fate of each Red Drum (emigration [*E*], fishing mortality [*F*], or alive [*A*]) is indicated, and confirmed fates are denoted as *CE*, *CF*, and *CA*, respectively. Tag reporting of harvested fish confirmed *F* if the harvest occurred during the study period and confirmed *A* if the harvest occurred after the study. Emigrations were also confirmed through tag reporting of harvested fish outside of Dog River or tag detections on receivers outside of the river during the study period.

Tag ID	Days detected	TL	TL (fate)	WT (fate)	Final fate
43522	135.71	494	581	1.93	<i>E</i>
43530	277.83	441	618	2.32	<i>F</i>
43553	360.36	511	741	3.99	<i>CA</i> , harvested Sep 7, 2017, Dog River
43577	335.87	486	700	3.37	<i>A</i>
43606	312.28 (326.93)	460	659	2.81	<i>CE</i> , harvested Jun 7, 2018, Dog River
43607	366.26	480	714	3.57	<i>CA</i> , harvested May 23, 2019, Dog River
43610	347.8	489	711	3.53	<i>CA</i> , harvested Sep 9, 2017, outside river
43611	371.69	488	725	3.74	<i>A</i>
43612	42.75	504	531	1.47	<i>F</i>
43613	261.38	342	509	1.3	<i>F</i>
43614	255.52	346	509	1.3	<i>CF</i> , harvested Jun 3, 2017, Dog River
43615	343.48 (371.63)	510	729	3.8	<i>CE</i>
43616	370.1	386	622	2.36	<i>A</i>
43617	39.8	637	654	2.75	<i>CF</i> , harvested Nov 8, 2016, Dog River
43618	204.33 (208.38)	456	586	1.98	<i>CE</i>
43619	150.31	504	600	2.12	<i>CF</i> , harvested Feb 18, 2017, Dog River
43621	191.69	354	477	1.07	<i>F</i>
43622	365.96	358	592	2.04	<i>A</i>
43623	366.69	478	712	3.54	<i>A</i>
43624	168.7 (204.90)	351	459	0.95	<i>CE</i>
43625	366.39	348	582	1.94	<i>A</i>
43626	206.81	357	489	1.15	<i>F</i>
43627	366.79	347	581	1.93	<i>CA</i> , caught and released Jul 30, 2017
43628	366.66	386	620	2.34	<i>A</i>
43629	356.85	400	628	2.43	<i>A</i>
43630	366.91	351	585	1.97	<i>A</i>
43631	366.13	345	579	1.91	<i>A</i>
43632	366.54	357	591	2.03	<i>A</i>
43633	368.72	330	565	1.77	<i>A</i>
43664	251.82 (261.98)	369	530	1.46	<i>CE</i> , harvested Jul 7, 2017, outside river
43665	207.15	342	474	1.05	<i>CF</i> , harvested May 8, 2017, Dog River

95% CrI = 0.419–0.768), and overall (0.647; 95% CrI = 0.515–0.764) were similar as well. These *S*-estimates resulted in discrete *A*-estimates of 0.392 (95% CrI = 0.233–0.572) for Dog River, 0.395 (95% CrI = 0.232–0.581) for Fowl River, and 0.353 (95% CrI = 0.236–0.485) overall. Using the overall instantaneous rates of *Z* and *M*, the median escapement percentage to age 4 was estimated at 36.3% (95% CrI = 19.5–56.0%) and remained near 30% in the other fate models (Table 3). The Raftery–Lewis diagnostic was greater than 19,175 for all variables, indicating that sampling iterations were sufficient. All parameters converged, no patterns were observed in trace plots, and the Brooks–Gelman–Rubin statistic was no higher than 1.003 for all parameters.

Emigration was assigned to 17 Red Drum during the study (Dog River: 6 fish; Fowl River: 11 fish), and 9 were detected on receivers within the broader Coastal Alabama Acoustic Monitoring Program array (Tables 1, 2, A.1, A.2). Two of the fish that emigrated from Dog River and were detected elsewhere were also harvested, and one harvest occurred back in Dog River 1 year after emigration. Two emigrating fish from Fowl River that were not detected on the broad array were also harvested elsewhere, confirming true emigration from the study system (Tables 1, 2). Posterior median instantaneous monthly *E* ranged from 0.001 to 0.087 for Dog River, from 0.001 to 0.270 for Fowl River, and from 0.001 to 0.168 overall (Figure 2). The August 2016 emigration

TABLE 2. Duration for which each Red Drum was detected (days detected) within Fowl River, Alabama, and outside of the river (in parentheses); Red Drum TL (mm) at tagging; and the predicted TL (TL [fate]) and weight (WT [fate]; kg) when fate assignment occurred. The final assigned fate of each Red Drum (emigration [*E*], fishing mortality [*F*], natural mortality [*M*], or alive [*A*]) is indicated, and confirmed fates of *E*, *F*, and *A* are denoted as *CE*, *CF*, and *CA*, respectively. Tag reporting of harvested fish confirmed *F* if the harvest occurred during the study period and confirmed *A* if the harvest occurred after the study. Emigrations were also confirmed through tag reporting of harvested fish outside of Fowl River or tag detections on receivers outside of the river during the study period.

Tag ID	Days detected	TL	TL (fate)	WT (fate)	Final fate
35078	360.88 (366.46)	521	751	4.16	<i>A</i>
35084	336.16	391	605	2.18	<i>CA</i> , harvested Oct 23, 2017, outside river
35137	299.86	375	566	1.78	<i>F</i>
43524	134.35	622	679	3.07	<i>F</i>
43525	118.76	629	679	3.07	<i>E</i>
43565	139.86 (343.59)	495	584	1.96	<i>CE</i>
43583	39.55	467	493	1.18	<i>M</i>
43588	371.91	508	745	4.06	<i>A</i>
43589	12.71 (65.62)	632	637	2.54	<i>CE</i>
43590	38.02	625	641	2.59	<i>CE</i> , harvested Sep 30, 2016, outside river
43591	9.53	470	476	1.06	<i>E</i>
43605	350.84	506	730	3.82	<i>A</i>
43620	338.96 (371.31)	543	759	4.29	<i>CE</i>
43636	197.95	647	731	3.83	<i>CE</i> , harvested Dec 8, 2016, outside river
43638	226.79	339	484	1.11	<i>M</i>
43639	366.88	540	774	4.55	<i>CA</i> , harvested May 13, 2018, outside river
43640	68.74	647	676	3.03	<i>E</i>
43641	268.95 (278.02)	541	713	3.56	<i>CE</i>
43643	221.19	344	485	1.12	<i>E</i>
43644	357.36	667	818	5.37	<i>A</i>
43645	105.23	371	438	0.83	<i>CF</i> , detected in gill net Apr 14, 2017
43646	371.96	359	596	2.08	<i>CA</i> , caught and released Aug 28, 2017
43647	350.26	359	582	1.94	<i>CA</i> , harvested Sep 12, 2017
43648	310.58	358	556	1.69	<i>F</i> , caught and released Mar 26, 2017
43649	366.80	342	576	1.88	<i>CA</i> , harvested Apr 7, 2019, outside river
43650	92.99	339	398	0.62	<i>F</i>
43651	72.62	354	401	0.63	<i>F</i>
43652	366.92	341	575	1.87	<i>CA</i> , harvested Mar 7, 2018, outside river
43653	184.82	358	476	1.06	<i>E</i>
43654	345.93	333	554	1.67	<i>CA</i> , harvested Sep 3, 2017, Fowl River
43655	366.99	360	594	2.06	<i>CA</i> , harvested Sep 30, 2017, Fowl River
43656	371.15	343	580	1.92	<i>A</i>
43657	55.78	633	657	2.78	<i>CF</i> , harvested Nov 18, 2016, Fowl River
43658	53.23	516	550	1.63	<i>M</i>
43659	350.80 (352.90)	646	794	4.91	<i>A</i>
43661	346.37	533	754	4.21	<i>A</i>
43662	366.71	526	760	4.31	<i>A</i>
43663	366.98	523	757	4.26	<i>A</i>

peak in Fowl River (Figure 2) was due to the emigration of newly tagged Red Drum coupled with low sample size, but given that these emigrations occurred more than 1 week after tagging they were still included. Instantaneous annual median *E*-estimates were 0.320 (95% CrI = 0.137–0.640) for Dog River, 0.388 for Fowl River (95%

CrI = 0.180–0.729), and 0.334 (95% CrI = 0.187–0.551) overall. Median discrete monthly *R*-estimates ranged from 0.917 to 0.999 in Dog River, from 0.764 to 0.999 in Fowl River, and from 0.845 to 0.999 overall. Therefore, discrete annual median *R*-estimates were 0.726 (95% CrI = 0.528–0.872) for Dog River, 0.678 (95% CrI

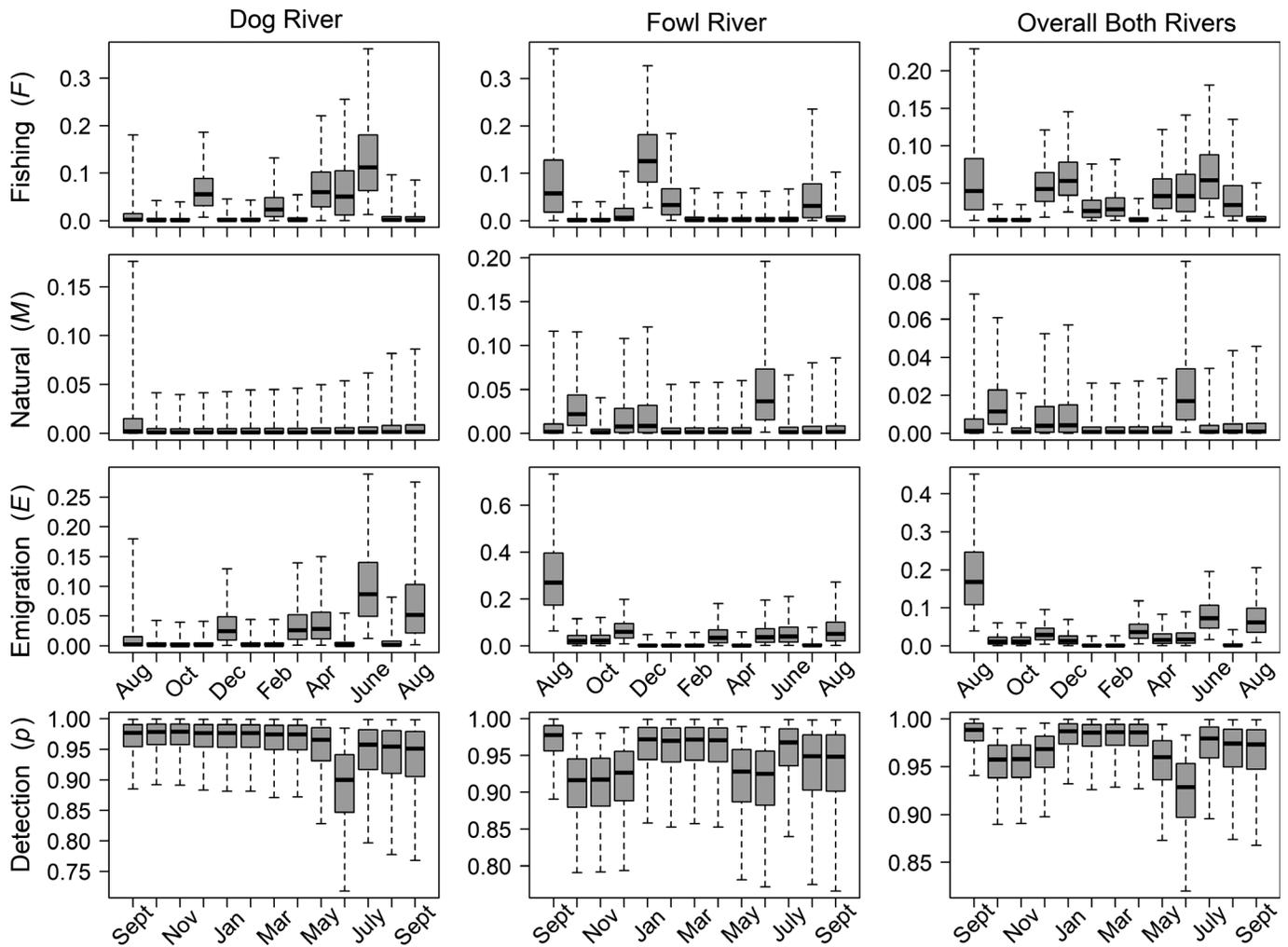


FIGURE 2. Monthly instantaneous rates of fishing mortality ( $F$ ), natural mortality ( $M$ ), emigration from rivers ( $E$ ), and detection probability ( $p$ ) for Dog River, Fowl River, and overall (both rivers). In each box plot, the bar within the box corresponds to the posterior median estimate, the ends of the box represent the 25% and 75% quartile estimates, and the whiskers represent the 95% posterior credible interval (2.5% and 97.5% quartiles).

= 0.482–0.835) for Fowl River, and 0.716 (95% CrI = 0.577–0.829) overall.

Red Drum that were not assigned as mortalities or emigrations survived the duration of the study or were harvested during the last month of the study (Tables 1, 2). During September 2017, one fish from Dog River and three fish from Fowl River were reported harvests, but given that they were alive at the start of September 2017 they received a fate of “alive” for that month. Another fish that was classified as alive through July 2017 and censored for the remainder of the study (given tag expiration) was also harvested from Dog River in September 2017. Furthermore, four of the remaining alive Red Drum and another fish that had an expired tag have been harvested since study completion, demonstrating that alive fish fates were assigned correctly.

## DISCUSSION

Instantaneous rates of  $F$  and  $M$  were estimated across monthly and annual time scales, and an escapement percentage was generated for inshore Alabama Red Drum. Mortality estimation also occurred across most of the size or age range that is vulnerable to harvest in the inshore recreational fishery. Although at the time of tagging, many Red Drum were smaller than the legal harvestable size, when fishing mortalities were inferred all individuals would have grown to the legal slot size—except for two individuals that were slightly below (8 and 5 mm) this size (Porch 2000; Powers et al. 2012). Furthermore, many Red Drum remained in the river where they were tagged, suggesting that some Red Drum may be resident to specific areas, which would result in possible regional separation and region-specific mortality

TABLE 3. Results of varying Red Drum fate assignments. Models were run for Dog River, Fowl River, and overall (both rivers) with original fate assignments (Org) and when questionable emigrated fish were assigned a fate of fishing mortality (+*F*) given that their last detections were on receivers at river mouths. Additional models were run assigning a fate of natural mortality (+*M*) to small fish (<500 mm) that were inferred harvests, given the possibility of avian predation; both of these varying fate assignments were run together (+*FM*) in another set of models. The number of Red Drum assigned fates of emigration (*E*), fishing mortality (*F*), and natural mortality (*M*) as well as annual estimates of instantaneous *F*, *M*, and 95% posterior credible intervals (95% CrIs) for each model are presented. Overall escapement percentages (Ecp) with 95% CrIs are also included.

Model	Fate			<i>F</i> annual estimate (95% CrI)	<i>M</i> annual estimate (95% CrI)	Ecp (95% CrI)
	<i>E</i>	<i>F</i>	<i>M</i>			
<b>Dog River</b>						
Org	6	9	0	0.414 (0.205–0.742)	0.069 (0.015–0.233)	
+ <i>F</i>	5	10	0	0.445 (0.226–0.782)	0.069 (0.015–0.232)	
+ <i>M</i>	6	7	2	0.339 (0.155–0.645)	0.144 (0.045–0.354)	
+ <i>FM</i>	5	8	2	0.369 (0.175–0.681)	0.144 (0.045–0.352)	
<b>Fowl River</b>						
Org	12	7	3	0.309 (0.131–0.616)	0.178 (0.060–0.415)	
+ <i>F</i>	7	12	3	0.463 (0.233–0.820)	0.177 (0.060–0.415)	
+ <i>M</i>	12	5	5	0.228 (0.080–0.509)	0.258 (0.106–0.526)	
+ <i>FM</i>	7	10	5	0.384 (0.179–0.717)	0.259 (0.108–0.526)	
<b>Overall</b>						
Org	18	16	3	0.337 (0.194–0.545)	0.090 (0.031–0.204)	36.3 (19.5–56.0)
+ <i>F</i>	12	22	3	0.435 (0.269–0.660)	0.090 (0.031–0.203)	27.1 (13.8–44.6)
+ <i>M</i>	18	12	7	0.259 (0.135–0.447)	0.168 (0.078–0.313)	35.1 (20.0–56.9)
+ <i>FM</i>	12	18	7	0.354 (0.206–0.562)	0.168 (0.079–0.313)	34.5 (13.5–46.6)

rates. Our estimates of *F*, *M*, and escapement percentage from the inshore recreational fishery provide important data that are needed for proper Red Drum management, as identified during the 2016 GOM data-limited stock assessment (SEDAR 2016).

### Violations of Model Assumptions and Fate Assignments

Although all median estimates of *p* were above 0.90 and most tags that remained in rivers were encountered each month, there is the potential to misclassify fish fates based on detection data. Red Drum were inferred to be alive when detection data indicated tag movement within rivers. However, tags that are not within a fish or tags that are present within fish carcasses could move as a result of water flow, as has been shown in other studies (Muhametsafina et al. 2014; Hightower and Harris 2017). These tidal rivers do not experience high flow rates from rainfall or tidal influences, and two fish tags that were inferred surgery mortalities were detected constantly on a single receiver for the duration of the study. Therefore, movement of carcasses and tags outside of Red Drum likely did not bias the alive fate classification. Tag movement within the stomach of an aquatic predator is another potential source of bias in the alive fate classification (Romine et al. 2014; Gibson et al. 2015; Daniels et al. 2018). If an aquatic predator consumed a tagged Red Drum and remained in the river, then the Red Drum would be assumed alive initially after predation; however,

tag movement would have likely ceased within 1 month given tag expulsion from the predator (Friedl et al. 2013; Schultz et al. 2015). In this situation, the mortality would have been shifted forward, violating the assumption of fates being identified correctly in the month that they occur, but natural mortalities would have been correctly identified within 1 month of occurrence, thereby avoiding bias to overall estimates.

When a tag was found stationary within a river after the 7-d censorship period, it was assumed that the Red Drum died of natural causes and this fate was likely identified correctly. Tag shedding after the censorship period could have caused misclassification of this fate: the tag would have been stationary, but the Red Drum could have been alive. Previous studies have shown that tag shedding is minimal in this species (Bacheler et al. 2009a; Moulton et al. 2016), and Red Drum that were harvested by anglers and returned to the lab all retained their transmitters. Therefore, tag shedding was not a concern in this study and likely did not bias estimates of *M*.

Emigration was determined when Red Drum received their last detection on receivers at river mouths, and this fate classification may have been biased. In two instances, Red Drum that were harvested would have been considered emigrations if their tags had not been reported by anglers. There is no way to disentangle this confounding fate assignment with the current study design, so models were re-run, treating any unconfirmed emigrations ( $n = 6$ )

as fishing mortalities. This change lowered the monthly median estimates of  $E$  and elevated the estimates of  $F$  for August, March, and May in Fowl River and for January in Dog River. To avoid this confounding effect on fate assignments, future studies could employ a large receiver curtain outside of the exit of the study system to obtain 100% detection coverage of emigrated fish outside of the system. Predation was likely not a confounding effect on emigration fate assignments, as all emigrating Red Drum were larger (Tables 1, 2) than the typical fish size taken by common bottlenose dolphins *Tursiops truncatus* (Barros and Wells 1998; Gannon and Waples 2004; Bowen 2011) and the occurrence of Red Drum in the common bottlenose dolphin diet is minimal (Gannon and Waples 2004; Berens McCabe et al. 2010; Dunshea et al. 2013). Furthermore, the majority of Bull Sharks *Carcharhinus leucas* that are encountered in Alabama inshore waters are juveniles (Betha et al. 2015) and likely are too small to have consumed the emigrating Red Drum in this study. Bull Shark detections around Dog and Fowl rivers have also been shown to be low (Drymon et al. 2014). Finally, five of the seven fish that were confirmed emigrations without harvest elsewhere (Table 1, 2) were detected for 28 d or longer on the broad receiver array; this interval is likely too long for a predator to retain an ingested tag (Friedl et al. 2013; Schultz et al. 2015).

Fishing mortality was inferred when detections of moving tags ceased within the estimated tag life and these Red Drum did not receive their final detections on receivers at river mouths. This detection pattern is indicative of tag removal from the study system, and the majority of tag removals likely occurred through human predation (harvest). Removal of tagged fish by piscivorous avian predators would also result in the same detection pattern, and ospreys *Pandion haliaetus* and bald eagles *Haliaeetus leucocephalus* are present along these rivers. However, all Red Drum except four were likely too large (>500 mm) to have been removed through osprey (Carss and Godfrey 1996) or bald eagle (Markham and Watts 2008) predation when  $F$  was inferred (Tables 1, 2). Furthermore, Red Drum are not typically found in the diets of ospreys (Glass and Watts 2009) or bald eagles (Markham and Watts 2008; Hanson and Baldwin 2017). However, these studies were conducted in Chesapeake Bay and Florida Bay and may not be representative of coastal Alabama. Although unlikely, the four small fish that were inferred harvests were reclassified as natural mortalities and models were re-run, which resulted in increased  $M$  and decreased  $F$  during December in Fowl River and during April in Dog River. The American alligator *Alligator mississippiensis* is another piscivorous predator that could remove tags from the water through predation. However, alligators typically feed on small fishes in estuaries, and whenever sciaenids have occurred in alligator diets they were treated

as unidentified and accounted for 0.8% of diet items (Nifong et al. 2015; Nifong 2016). If these sciaenids were Red Drum similar to the size of tagged individuals in our study, then they should have been identifiable. Although likely not prevalent in our study, removal of fish and tags from the water through predation by birds or other terrestrial piscivores could be investigated in future studies by using combined acoustic and radio tags (Cooke et al. 2013). Finally, early expiration of tags would also be inferred as fishing mortalities based on detection criteria; however, 24 tags were detected beyond their predicted tag life (Tables 1, 2). Therefore, early tag expiration was not a concern and the loss of tags in rivers likely represented removal via angler harvest.

### Mortality, Seasonality, and Residency

Instantaneous estimates of  $F$  were greater than recent estimates from Alabama using catch curve and longevity methods for both fishery-independent and fishery-dependent samples (Hightower et al. 2016). Hightower et al. (2016) calculated annual instantaneous  $F$  of 0.14–0.18 for fishery-independent samples and 0.00–0.01 for fishery-dependent samples. The fishery-independent samples from Hightower et al. (2016) were collected from 2006 to 2015 in both inshore (within Mobile Bay and Mississippi Sound) and offshore Alabama waters using a bottom longline survey, purse seine collections, and gill nets. However, no samples were collected within tidal rivers or small bays. The fishery-dependent samples in that study were collected at a reoccurring fishing tournament from 2009 to 2014 and could have been taken from Louisiana to Florida, although the majority of Red Drum were likely caught in Alabama given that the tournament was located there. The low  $F$  for fishery-dependent samples in the Hightower et al. (2016) study is below the 95% CrI for all  $F$ -estimates in the current study; however, sampling locations, gear type, and timing differed between studies and their catch curve model did not include any Red Drum younger than age 3. At the time of tagging, Red Drum in our study were likely ages 1 and 2 (Porch 2000; Powers et al. 2012), indicating that  $F$  on young Red Drum may be higher than that on larger adults and has been unaccounted for in previous mortality estimates. Furthermore, if misclassification of emigrated Red Drum did occur, the instantaneous  $F$ -values for subadult Red Drum from our study would be even greater than those reported by Hightower et al. (2016).

Overall instantaneous rates of  $M$  were similar to those obtained from longevity estimators and previous telemetry work but were lower than previous age-specific estimates for young Red Drum. The overall annual estimate of instantaneous  $M$  was between the longevity estimates of 0.07 (Hoenig 1983) and 0.11 (Hewitt and Hoenig 2005), obtained with a maximum age of 40 in the Hightower et al. (2016) study. However, comparisons of these estimates

may be unfair given that longevity estimators apply to adult fish. The telemetry  $M$ -estimates are also lower than those previously calculated for age-1 (0.26) and age-2 (0.19) fish (Porch 2000). Furthermore, during many months instantaneous  $M$  was similar to the rates from the telemetry and combined models in Bacher et al. (2009a), and in both studies annual instantaneous  $M$  was less than 0.1. These low  $M$ -estimates provide further evidence that natural mortality is lower than previously predicted for subadult Red Drum. If the four Red Drum that may have been removed through avian predation are assigned as natural mortalities, the overall median annual estimate is increased to 0.168, but this is still lower than previous  $M$ -estimates for young Red Drum. Unfortunately, funding restrictions limited the number of Red Drum that could be tagged, and error on the estimates of  $F$  and  $M$  in Dog and Fowl rivers was large. This error could be reduced in future studies by increasing the number of tagged individuals, coupling with a traditional tagging study, and including high-reward external tags for 100% reporting of  $F$  (Pollock et al. 2001; Pine et al. 2003; Sackett and Catalano 2017). Although the telemetry estimates are based on a small portion of the population, these results highlight the need for mortality estimates that account for subadult Red Drum given that  $F$  may be higher and  $M$  may be lower than previously predicted.

Unfortunately, the large error around the median escapement percentage (36.3%; 95% CrI = 19.5–56.0%) for Red Drum was inconclusive as to whether the 30% escapement goal for GOM states (Gulf of Mexico Fishery Management Council 1988) is being met. Varying fate assignments also resulted in escapement percentages around 30%, with the lowest estimate of 27.1% when all questionable emigrated fish were assigned as fishing mortalities. However, all error still ranged from below to above 30%. This escapement percentage is only representative of Red Drum from Fowl and Dog rivers and could underestimate the escapement of fish older than age 3 given that all individuals in this study were likely younger than age 3 at tagging. Age-specific mortality and escapement could not be calculated given that mortality rates were generated across all sizes of Red Drum tagged in the study, and sample sizes were too low for this type of analysis. As mentioned above, greater numbers of tagged individuals in this study would have decreased the error associated with all mortality rates and the resulting escapement percentage. Future telemetry studies should strive to generate age-specific mortality rates to provide more precise mortality and escapement estimates; however, the cost of transmitters and the encounter rate of older fish may be prohibitive. Escapement percentage calculations could be further improved in the future by multiplying age-specific escapement estimates by the percentage of each age-class that is mature and taking

the sum of these estimates. This is shown in the following equation:

$$\text{Escapement} = \sum[(e^{-Z_i}/e^{-M_i}) \times \text{Mat}_i],$$

where  $Z$  and  $M$  are the total and natural mortality rates for each age-class  $i$  and  $\text{Mat}$  is the percentage of each age-class that is mature. This would overcome the incorrect assumption that all age-4 fish are mature in current functional escapement calculations and does not ignore fish that mature and contribute to the spawning stock before age 4. Extending this calculation beyond age 4 could also account for harvest mortality that occurs on fish above the slot limit, which remain vulnerable to the recreational fishery within state waters.

Seasonal peaks of  $F$  were evident in both rivers and could be investigated given the monthly time interval for instantaneous mortality estimation. Fishing mortality peaked during the fall in Fowl River and during the spring in Dog River, with the highest monthly instantaneous  $F$  recorded in December (0.126) and June (0.105), respectively. Furthermore, five Red Drum were reported as harvested during September 2017 at the study's end, although these could not be included in the model. The fall and spring are peak times in which anglers target these rivers (personal communications with multiple local anglers), and the highest catch from Alabama Marine Recreational Information Program data also occurred during September–October in both 2016 and 2017 (National Marine Fisheries Service, Fisheries Statistics Division, personal communication). When both rivers were combined into an overall model, elevated  $F$  still occurred in the fall and spring. A fall peak in  $F$  was also found for Red Drum in North Carolina (Bacher et al. 2009a) by using similar telemetry methods coupled with a traditional mark–recapture study. Annual instantaneous recreational  $F$ -estimates obtained with the Bacher et al. (2009a) combined model (0.11–0.22) were lower than what was found using the telemetry estimates here. However, if the commercial estimate is added to the recreational estimate, the total annual instantaneous  $F$  is 0.18 for 2007 and 0.35 for 2006 (Bacher et al. 2009a). The 2006 estimate is similar to the overall telemetry estimate here. It is possible that some of the  $F$  observed in these rivers was a result of harvest by non-sportfishing anglers (e.g., subsistence anglers; recreational catch by commercial fisherman), given that one Red Drum was observed in an illegal gill net. However, no commercial Red Drum fishery exists in Alabama. These seasonal peaks in  $F$  are an indicator of angler behavior and fishing effort in coastal Alabama and are likely present elsewhere.

Many Red Drum remained in the rivers where they were tagged throughout the year, but around 30% of Red Drum did emigrate. Telemetered Red Drum in Texas

(Dance and Rooker 2015), North Carolina (Bacheler et al. 2009b; Kenworthy et al. 2018), and South Carolina (Dresser and Kneib 2007) have been shown to exhibit high residency. However, within-river residency was not always the case; when Red Drum emigrated, large (60-km), bay-scale movements were detected. These large movement distances have also been observed elsewhere (Bacheler et al. 2009b; Moulton et al. 2016) and indicate that many Red Drum in our study did not remain near rivers once emigration occurred. Emigration peaked during June and August 2017 in Dog River and was highest during August 2016 in Fowl River but was also elevated in November 2016 and August 2017. It is possible that these emigration peaks in the summer and fall coincided with fish maturation and movement out of rivers to join spawning aggregations, given that peak spawning occurs in the fall (Overstreet 1983; Lowerre-Barbieri et al. 2018). This residency of subadult Red Drum indicates that some of the population may remain where they settle during the juvenile phase, potentially resulting in regional isolation of Red Drum groups and region-specific mortality. Separate subadult groups of Red Drum within estuaries have been suggested elsewhere (Kenworthy et al. 2018) and could be a mechanism to reduce adverse density-dependent effects on growth (Bacheler et al. 2012). This potential for separate groups coupled with differences in river-specific  $F$ -values found in this study, albeit nonsignificant, demonstrates that different areas of estuaries may have different fishing pressure. Region-specific differences in  $F$  would result in different mortality rates among estuarine locations and waterbodies, and investigation should continue in future studies.

## Conclusions

The instantaneous mortality estimates obtained in this study provide valuable information about the inshore population of Red Drum that may be difficult to obtain using other methods. The telemetry-based mortality estimates also provide data on seasonal peaks of  $F$  and some insight into angler habits in coastal Alabama. The median escape percentage of 36% is near the 30% escapement goal; unfortunately, the error around this estimate was large and inconclusive as to whether this goal is being met. The residency of many individuals and the river-specific  $F$ -values also provide some evidence for region-specific groups of subadult Red Drum within the estuary that may experience different mortality rates among locations. This potential for specific groups of Red Drum within estuarine waters should be investigated further through more tagging efforts and may be elucidated with other techniques, such as otolith chemistry. Determining whether area-specific groups occur, how they respond to fluctuating abiotic parameters, and whether they experience different mortality rates is essential for proper management and conservation of this

species and other estuarine fishes in the presence of shifting fishing pressure, environmental conditions, and climate change. The need for mortality estimates that include subadult fish if they are vulnerable to harvest has also been demonstrated and should be accounted for in future work estimating the vital rates of fishes.

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### Appendix: R and JAGS Code for Multistate Models and Monthly Detection Tables

The following is supplemental R and JAGS code for implementing the multistate Bayesian model that was used to obtain Red Drum mortality estimates (adapted from Ellis et al. [2017] and Hightower and Harris [2017]).

```
# Load required packages
library(coda)
library(R2OpenBUGS)
library(rjags)
library(plyr)

# clear the workspace
rm(list = ls(all = T))

source("post_summ_function.R") ##function written by Ben Staton for ease of dealing with ##mcmc obj.

#read observation data into r
data=as.matrix(read.csv("FR_final_ob.csv",header=F)) ##place detection matrix csv here

##model code for JAGS####
mod = function() {
  # Parameters
```

```

# Z: Instantaneous total mortality rate between t and t + 1
# F: Instantaneous fishing mortality rate between t and
t + 1
# M: Instantaneous natural mortality rate between t and
t + 1
# E: Instantaneous emigration rate between t and t + 1
# p: Probability of being detected in the receiver array
# States
# 1 Alive
# 2 Natural Death
# 3 Emigrated
# 4 Harvest
# Observations
# 1 Detected alive
# 2 Detected natural mortality
# 3 Detected emigrating
# 4 Not Detected
# Priors, constraints, and calculated values
for (t in 1:(Periods-1)) {
  lnF[t] ~ dunif(-10,1) # uninformative prior
  lnM[t] ~ dunif(-10,1) # uninformative prior
  lnE[t] ~ dunif(-10,1) # uninformative prior
  F[t] <- exp(lnF[t])
  M[t] <- exp(lnM[t])
  E[t] <- exp(lnE[t])
  R[t] <- exp(-E[t])
  Z[t] <- F[t]+M[t]+E[t]
  S[t] <- exp(-Z[t])
  Z_mort[t] <- F[t]+M[t] # total instantaneous mortality rate for fish
  S_mort[t] <- exp(-Z_mort[t]) # discrete survival rate for fish
  A_mort[t] <- 1-(exp(-Z_mort[t])) # discrete mortality rate for fish
}
p[1] <- 1 # Model conditioned on first capture, estimate separate p for remaining periods
for (t in 2:(Periods)) {
  p[t] ~ dunif(0, 1)
}
# Define state-transition and observation matrices
for (i in 1:nFish) {
  # Define probabilities of state (t + 1) given state (t). First index is state at time t, next is
  #state at t + 1
  for (t in first[i]:(last[i]-1)) {
    ps[1,i,t,1] <- S[t]
    ps[1,i,t,2] <- M[t]*(1-S[t])/Z[t]
    ps[1,i,t,3] <- E[t]*(1-S[t])/Z[t]
    ps[1,i,t,4] <- F[t]*(1-S[t])/Z[t] #place predictive quant here to look at covariate effect on F
    ps[2,i,t,1] <- 0
    ps[2,i,t,2] <- 1
    ps[2,i,t,3] <- 0
    ps[2,i,t,4] <- 0
    ps[3,i,t,1] <- 0
    ps[3,i,t,2] <- 0
    ps[3,i,t,3] <- 1
    ps[3,i,t,4] <- 0
    ps[4,i,t,1] <- 0

```

```

    ps[4,i,t,2] <- 0
    ps[4,i,t,3] <- 0
    ps[4,i,t,4] <- 1
  } #t
for (t in first[i]:(last[i])){
  # Define probabilities of observed (t) given state (t). First index is state, last index is
  #observed
  po[1,i,t,1] <- p[t] # State=alive, detected alive
  po[1,i,t,2] <- 0 # State=alive, natural death
  po[1,i,t,3] <- 0 # State=alive, emigrated
  po[1,i,t,4] <- 1-p[t] # State=alive, not detected
  po[2,i,t,1] <- 0 # State=natural mortality, detected alive
  po[2,i,t,2] <- p[t] # State=natural mortality, detected natural mortality
  po[2,i,t,3] <- 0 # State=natural mortality, detected emigration
  po[2,i,t,4] <- 1-p[t] # State=natural mortality, not detected
  po[3,i,t,1] <- 0 # State=emigrated, detected alive
  po[3,i,t,2] <- 0 # State=emigrated, detected natural mortality
  po[3,i,t,3] <- 1 # State=emigrated, detected emigration
  po[3,i,t,4] <- 0 # State=emigrated, not detected
  po[4,i,t,1] <- 0 # State=harvested, detected alive
  po[4,i,t,2] <- 0 # State=harvested, detected natural mortality
  po[4,i,t,3] <- 0 # State=harvested, detected emigration
  po[4,i,t,4] <- 1 # State=harvested, not detected
} #t
} #i

# Likelihood
for (i in 1:nFish){
for (t in 1:(first[i]-1)) {Alive[i,t]<-0}
  z[i,first[i]] <- 1 # Individuals have known status (alive) at first occasion in study
  Alive[i, first[i]] <- 1
  for (t in (first[i]+1):last[i]){
    z[i,t] ~ dcat(ps[z[i,t-1], i, t-1,]) # State process: draw state (t) given state (t-1)
    Alive[i,t] <- step(-z[i,t]+2) # Should be 1 for z = 1, 0 for z = 2 or 3
  } #t
  for (t in (last[i]+1):Periods){Alive[i,t]<- 0}
  for (t in first[i]:last[i]){
    y[i,t] ~ dcat(po[z[i,t], i, t,]) # Observation process: draw observed (t) given state (t)
  } #t
} #i
for (t in 1:Periods){FishAtRisk[t] <- sum(Alive[,t])}

#Derived values
F_y <- sum(F[2:13]) #inst. Annual F Sep 2016 - Aug 2017
M_y <- sum(M[2:13]) #inst. Annual M Sep 2016 - Aug 2017
E_y <- sum(E[2:13]) #inst. Annual E Sep 2016 - Aug 2017
Z_y <- F_y + M_y #inst. Annual Z Sep 2016 - Aug 2017
S_y <- exp(-Z_y) #Discrete Annual Survival
Amort_y <- 1 - (exp(-Z_y)) #Discrete Annual Mortality
R_y <- exp(-E_y) #Discrete Annual Residency within rivers
Aemm_y <- 1 - (exp(-E_y)) ##Discrete fish loss to emigration
Ecp_4 <- exp(-Z_y*3)/exp(-M_y*3)##escapement estimator used for combined model only
##defined as #Drum@age 4/#Drum@ age 4 with no F
}

```

```

# write model to a text file
model.file = "model.txt"
write.model(mod, model.file)
#####get data for model to run#####

y=data
nFish=dim(data) [1]
Periods=dim(data) [2]
first <- numeric()
for (i in 1:dim(y) [1]) {
first [i] <-min(which(y[i,]!=0))}
last <- numeric()
for (i in 1:dim(y) [1]) {
last [i] <-max(which(y[i,]!=0))}
f <- first
l <- last

jags.data <- list (y=y,nFish=nFish,first=first,last=last,Periods=Periods)

###generate initial values for z and run model#

y.init <- function(y, f) {
  #State 1 = Obs1 (alive) State 2 = Obs 2 (natural death)
  #State 3 = Obs3 (emigration) Start w/known states from
  ##obs capture history
  ##replace 4 (unobserved) with possible states
  y.iv <- y
  for (i in 1:dim(y.iv) [1]) {y.iv[i,1:f[i]] <- NA}
  y.iv[y.iv==4] <- -1
  y.iv[y==0] <- NA

  for(i in 1:nrow(y.iv)) {
    if(max(y.iv[i,],na.rm=TRUE) < 2) {
      y.iv[i, (f[i]+1):l[i]] <-1}# Not detected dead so initialize as alive (after release period)
      # until tag expiration l[i]

    if(max(y.iv[i,],na.rm=TRUE) ==2) {
      m <- min(which(y.iv[i,]==2))
      y.iv[i, (f[i]+1):m] <- 1 # Initialize as alive up to period prior to detected natural death
      y.iv[i, m:l[i]] <- 2 # Initialize as dead after det. natural death until tag expiration l[i]
    }

    if(max(y.iv[i,],na.rm=TRUE) = =3) {
      e <- min(which(y.iv[i,]==3))
      y.iv[i, (f[i]+1):e] <- 1 # Initialize as alive up to period prior to emigration
      y.iv[i, e:l[i]] <- 3 # Initialize as emigrated after emigration only places 3 at emigration
      # Given that after emigration fish are censored
    }
  }
}
return(y.iv)
}

jags.inits <- function() {list (lnF=runif (Periods-1, -10, 1),
lnM=runif (Periods-1, -10, 1), lnE=runif (Periods-1, -10, 1),
z=y.init (y, f))}

```

```

##parameters to monitor during model run
params <- c('F','M','Z','S','p','E','R','FishAtRisk','A_mort','Z_mort','F_y','M_y','
Z_y','S_y','Amort_y','Ecp_4','E_y','Aemm_y','R_y')

##model condition
ni = 60000 ##number iterations
nt = 1 ##number thin
nb = 1000 ##number burn-in
nc = 3 ##number MCMC chains

##run model in JAGS
starttime = Sys.time()
jmod = jags.model(file = 'model.txt', data = jags.data, inits = jags.inits, n.chains = nc, n.adapt = 1000)
update(jmod, n.iter = nb, by = 1, progress.bar = 'text')
post = coda.samples(jmod, params, n.iter = ni, thin = nt)
Sys.time() - starttime

#####inference#####
bgr <- gelman.diag(post, multivariate = F) ##BFG stat
bgr <- as.data.frame(bgr[1])
colnames(bgr) <- c('Point.est.','Upper.C.I.')
##write gelman stat to have for later
write.csv(bgr, 'BGR.csv')

Raft_diag <- effectiveSize(post) ##should be around 3000, Raftery-Lewis diagnostic
Raft_diag <- as.data.frame(Raft_diag)
##write effective size diag to have for later
write.csv(Raft_diag, 'Raft.csv')

results <- summary(post)
##write quantile estimates to csv to use later without re-running model
write.csv(results$quantiles, 'results.csv')
}

##subset post object and generate trace plots for visual convergence investigation
#using awesome function written by Ben Staton
post.summ(post, 'F[, do.plot=TRUE)
post.summ(post, 'M[, do.plot=TRUE)
post.summ(post, 'E[, do.plot=TRUE)
post.summ(post, 'Z[, do.plot=TRUE)
post.summ(post, 'p[, do.plot=TRUE)
post.summ(post, 'R[, do.plot=TRUE)
post.summ(post, 'F_y', do.plot=TRUE)
post.summ(post, 'M_y', do.plot=TRUE)
post.summ(post, 'Z_y', do.plot=TRUE)
post.summ(post, 'S_y', do.plot=TRUE)
post.summ(post, 'Amort_y', do.plot=TRUE)
post.summ(post, 'E_y', do.plot=TRUE)
post.summ(post, 'Aemm_y', do.plot=TRUE)
post.summ(post, 'R_y', do.plot=TRUE)
post.summ(post, 'Ecp_4', do.plot=TRUE)

```

TABLE A.1. Number of receivers on which each Red Drum was detected during a given month within Dog River, Alabama. During months in which fish were detected on a single receiver, the maximum time interval (h) between consecutive detections is listed in parentheses; "SD" indicates that only a single detection was recorded. The months for which emigration (E), natural mortality (M), or fishing mortality (F) was inferred are indicated with the appropriate letter. Some Red Drum were only detected on the Vemco VR100 (VR), a single fish was unobserved (0 detections) for 1 month, and another fish was assigned an alive fate based on the month of angler tag return (AR). Cells are blank for the months before fish were tagged and after the end of predicted tag life.

Tag ID	Aug 2016	Sep 2016	Oct 2016	Nov 2016	Dec 2016	Jan 2017	Feb 2017	Mar 2017	Apr 2017	May 2017	Jun 2017	Jul 2017	Aug 2017	Sep 2017
43522	5	3	3	6	1 (7.75)	E	E	E	E	E	E	E		
43530	4	2	2	3	4	3	2	2	2	2	F	F		
43553	4	4	2	2	2	2	2	2	2	2	2	2		
43577	2	1 (312)	1 (470)	2	4	2	1 (1.63)	1 (1.09)	VR	1 (114)	2	1 (20)		
43606	2	2	2	4	5	4	2	2	2	2	3	E		
43607	4	2	1 (SD)	2	3	4	2	2	2	2	2	4		
43610	2	2	1 (8.78)	1 (9.25)	2	5	2	2	2	2	3	3	3	3
43611	2	2	2	2	2	4	7	2	2	2	2	3	2	5
43612	2	2	2	2	F	F	F	F	F	F	F	F	F	F
43613	3	2	2	2	2	2	2	2	1 (194)	2	2	F	F	F
43614	3	5	5	3	9	7	6	5	4	5	4	F	F	F
43615	5	3	3	4	4	4	3	3	4	4	4	5	5	E
43616	6	2	2	2	4	4	2	2	2	2	2	2	2	7
43617	2	5	5	AR	F	F	F	F	F	F	F	F	F	F
43618	2	2	2	4	5	6	2	2	4	E	E	E	E	E
43619	2	2	2	3	4	3	2	F	F	F	F	F	F	F
43621	2	2	7	2	4	4	4	4	2	F	F	F	F	F
43622	2	2	2	2	4	4	2	2	2	2	2	2	2	3
43623	2	2	2	3	4	2	2	2	2	2	2	3	3	5
43624	3	8	8	2	4	9	4	6	E	E	E	E	E	E
43625	5	2	2	2	3	3	3	3	3	1 (9.13)	3	1 (86)	2	1 (13)
43626	2	9	2	2	3	3	2	2	2	F	F	F	F	F
43627	2	2	2	2	4	2	2	2	2	2	2	2	2	2
43628	2	2	2	2	4	2	2	2	2	2	2	4	2	2
43629	7	4	4	1 (44)	1 (71)	1 (62)	1 (56)	1 (279)	1 (145)	1 (158)	1 (45)	1 (51)	1 (71)	1 (64)
43630	2	2	2	2	4	2	3	2	2	3	2	2	2	3
43631	2	2	2	1 (162)	2	2	1 (59)	1 (122)	2	1 (SD)	VR	2	2	2
43632	2	2	2	2	4	3	4	2	3	4	2	2	2	2
43633	4	1 (112)	2	2	2	2	2	2	2	1 (2.02)	0	1 (508)	2	2
43664		3	3	2	3	4	2	4	3	4	5	E	E	E
43695		4	4	2	4	4	2	2	2	2	F	F	F	F

TABLE A.2. Number of receivers on which each Red Drum was detected during a given month within Fowl River, Alabama. During months in which fish were detected on a single receiver, the maximum time interval (h) between consecutive detections is listed in parentheses; "SD" indicates that only a single detection was recorded. The months for which emigration (E), natural mortality (M), or fishing mortality (F) was inferred are indicated with the appropriate letter. Some Red Drum were only detected on the Vemco VR100 (VR); in a couple of instances, fish were unobserved (0 detections) for a single month at a time. Cells are blank for the months before fish were tagged and after the end of predicted tag life.

Tag ID	Aug 2016	Sep 2016	Oct 2016	Nov 2016	Dec 2016	Jan 2017	Feb 2017	Mar 2017	Apr 2017	May 2017	Jun 2017	Jul 2017	Aug 2017	Sep 2017
35078	9	3												
35084	2	3	4	5	6	4								
35137	2	F	F				F	F	F	F	F	F		
43524	2	1 (0.09)	2	2	2	F	E	F	E	E	E	E	E	
43525	3	3	2	2	E	E	E	E	E	E	E	E	E	
43565	5	E	E	E	E	E	E	E	E	E	E	E	E	
43583	2	1 (152)	M	M	M	M	M	M	M	M	M	M	M	
43588	2	2	2	3	2	6	1 (23)	1 (27)	1 (41)	2	2	2	2	
43589	3	E	E	E	E	E	E	E	E	E	E	E	E	
43590	2	3	E	E	E	E	E	E	E	E	E	E	E	
43591	2	E	E	E	E	E	E	E	E	E	E	E	E	
43605	2	1 (195)	2	6	4	3	3	4	2	2	2	2	2	
43620	2	2	2	9	3	11	3	10	13	10	4	6	4	E
43636	10	E	1 (0.03)	E	E	E	E	E	E	E	E	E	E	E
43638	3	3	8	6	2	6	2	2	2	1 (0.61)	M	M	M	
43639	1	1 (61)	1 (434)	1 (83)	7	8	1 (46)	1 (206)	2	1 (295)	2	3	2	2
43640	2	2	3	3	E	E	E	E	E	E	E	E	E	E
43641	2	2	2	10	8	8	1 (4)	4	4	1 (11)	4	4	4	E
43643	1	1 (88)	1 (578)	1 (203)	7	4	1 (137)	1 (207)	4	4	4	4	4	E
43644	2	2	0	2	9	3	2	1 (43)	1 (5.64)	3	0	3	1 (21.7)	1 (170)
43645	2	2	2	1 (0.08)	10	3	F	F	F	F	F	F	F	F
43646	1	1 (23)	3	8	9	8	1 (12)	1 (16)	1 (25)	1 (23)	1 (70)	5	2	11
43647	2	2	1 (66)	0	7	7	1 (138)	1 (240)	1 (237)	1 (19)	1 (0.05)	1 (525)	2	1 (45)
43648	3	1 (89)	1 (89)	1 (83)	3	11	1 (18)	2	2	4	8	4	F	F
43649	2	2	2	1 (32)	2	2	2	1 (20)	2	1 (26)	1 (52)	1 (59)	2	1 (63)
43650	1	1 (37)	1 (101)	2	9	2	F	F	F	F	F	F	F	F
43651	5	1 (SD)	1 (SD)	10	9	F	F	F	F	F	F	F	F	F
43652	1	1 (17)	1 (132)	1 (109)	8	9	3	2	1 (21)	1 (42)	1 (43)	1 (128)	1 (108)	1 (86)
43653	1	1 (22)	2	1 (66)	1 (93)	2	2	4	E	E	E	E	E	E
43654	2	2	9	0	6	9	4	VR	2	1 (53)	3	3	1 (23)	3
43655	1	1 (43)	1 (28)	2	4	4	3	3	3	2	4	3	2	3
43656	2	2	1 (229)	2	3	8	1 (96)	1 (143)	1 (146)	1 (141)	3	1 (17)	1 (20)	2
43657	3	3	10	9	F	F	F	F	F	F	F	F	F	F
43658	3	3	2	6	0	M	M	M	M	M	M	M	M	M
43659	1	1 (2.2)	3	7	6	4	0	1 (0.08)	3	3	5	3	3	10
43661	2	2	0	6	6	6	2	1 (1.22)	VR	0	3	5	3	5
43662	3	3	2	4	7	9	0	1 (22)	1 (161)	3	5	10	3	3
43663	3	3	1 (115)	1 (56)	7	10	1 (22)	1 (24)	1 (39)	3	5	3	4	5